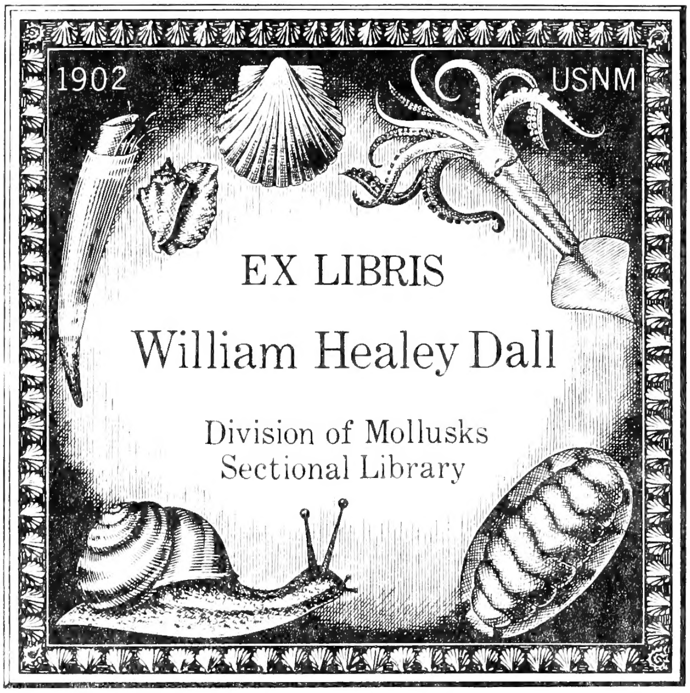
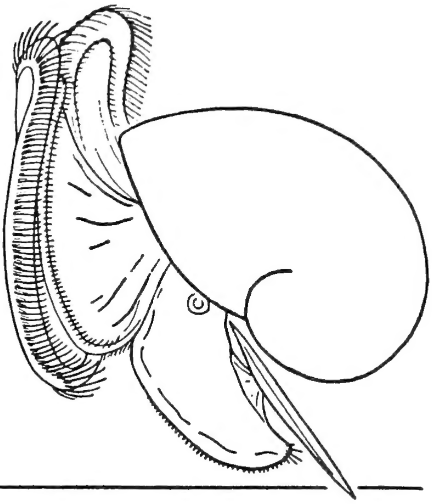


THE VELIGER



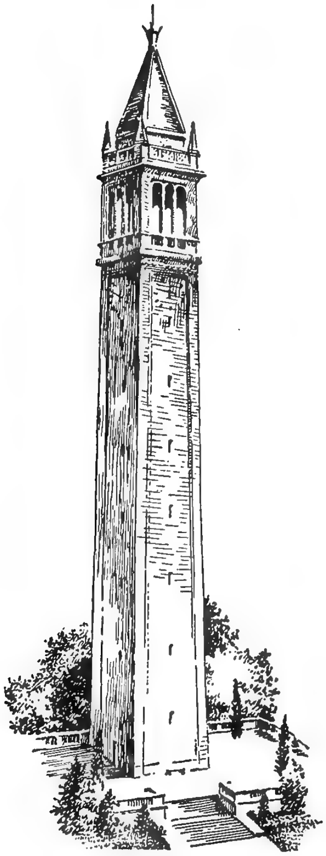
A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

Volume 15

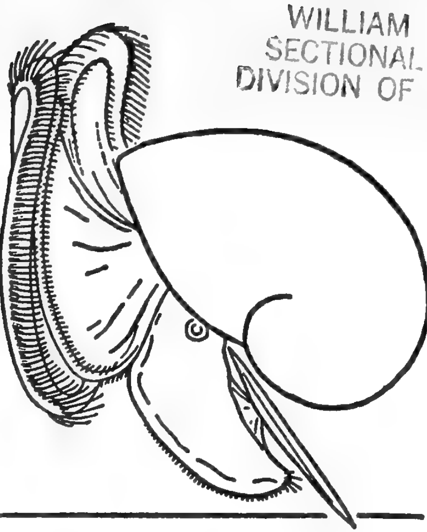
July 1, 1972 to April 1, 1973

TABLE OF CONTENTS

AUTHOR INDEX



THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

Volume 15 | July 1, 1972 | Number 1

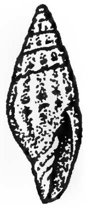
Contents

[Continued on Inside Front Cover]

Distributed free to Members of the California Malacozoological Society, Inc.
Subscriptions (by Volume only) payable in advance to Calif. Malacozool. Soc., Inc.
Volume 15: $18.- Domestic; $19.50 in the Americas; $20.- in all other Foreign Countries
Single copies this issue $10.-. Postage extra.
Send subscription orders to Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957. *Address all other correspondence to* Dr. R. Stohler, *Editor,* Department of Zoology, University of California, Berkeley, California 94720

Second Class Postage Paid at Berkeley, California

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

Observations on *Hexabranchus* from the Australian Great Barrier Reef

(Gastropoda : Opisthobranchia)

BY

T. E. THOMPSON

Zoology Department, University of Bristol, United Kingdom

(2 Text figures)

INTRODUCTION

The swimming display of *Hexabranchus* is one of the most splendid sights a malacologist may hope for. Despite the interest this has aroused there are great gaps in our knowledge of the genus. The normal diet is unknown, for instance, and the taxonomic situation is very confused, with dozens of proposed species. In order to help towards the solution of these problems, the present paper contains a description of the external features and anatomy of Australian specimens, together with notes on the gut contents and the swimming behaviour. These have been compared with observations on *Hexabranchus* by Morton (1964: Australia), Gohar & Soliman (1963: Red Sea), Vicente (1963: Madagascar) and Edmunds (1968: Tanzania). A suggested synonymy concludes the paper.

Miss J. A. Langhorne prepared the drawings for publication.

SOURCE of MATERIAL

Alive: One specimen, length 21 cm, creeping over coral sand near the reef crest at Heron Island, Capricorn Group, Australian Great Barrier Reef, June 1968. The specimen weighed 334 gr, and the pH of the skin was neutral.

Preserved: Several specimens in the collections of the Queensland Museum and of Miss Isobel Bennett of the University of Sydney.

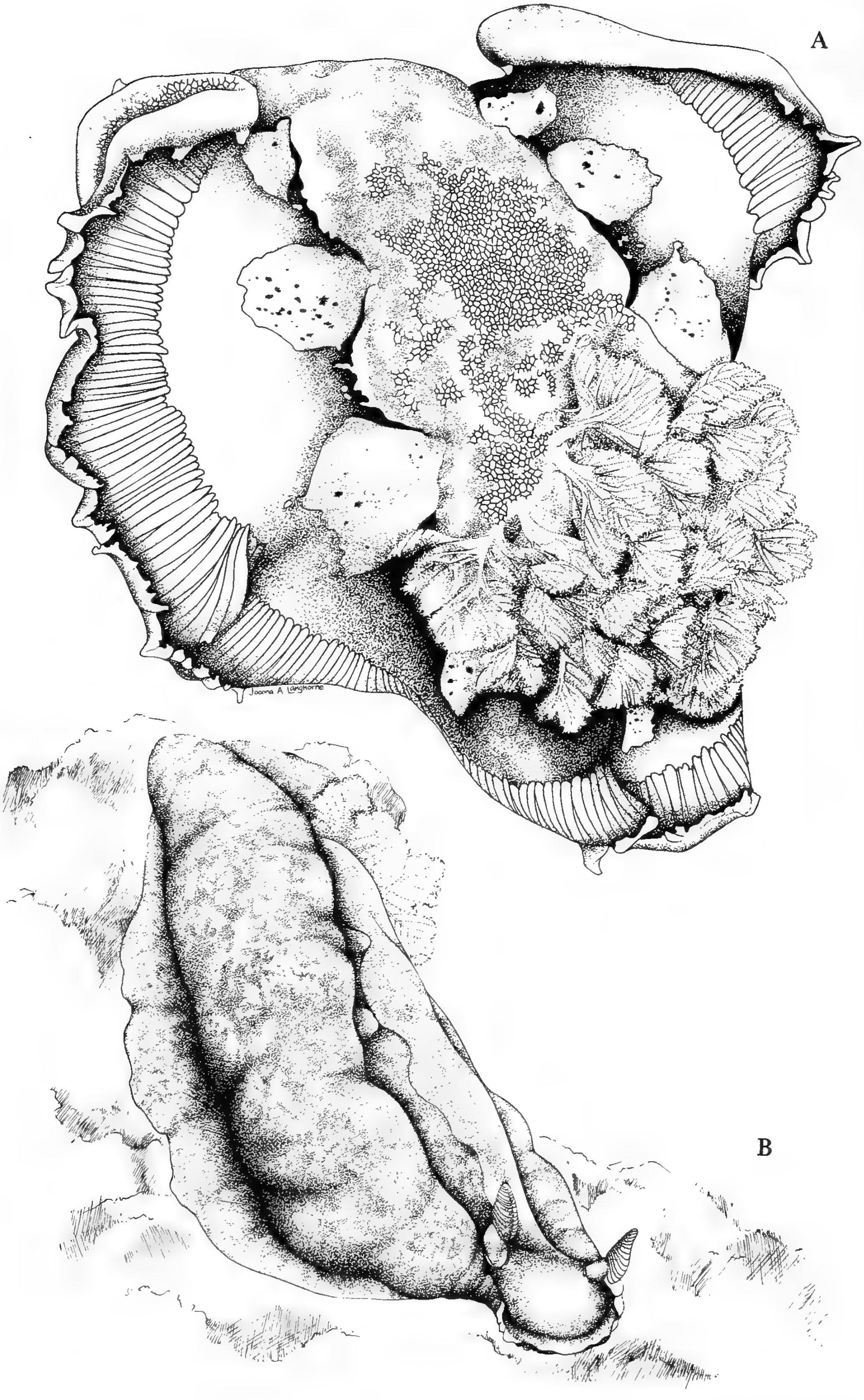
Other Material: Kodachromes from life of Great Barrier Reef individuals, kindly given by Mr. D. Henderson and by Dr. L. Harris.

DESCRIPTION

A. External Features (Figures 1 and 2)

The basic colour of the body was rich dark red, with irregular pale mottling. The rhinophoral tentacles were red-brown; the rims of the rudimentary pallial sheaths were bright red, with pale radiating markings. The pedal sole was paler in colour than the rest of the body. The oral tentacles took the form of a pair of flattened lobes (Figure 2C), with frilled edges. The gills, 7 in number, were ample and tripinnate, each being retractile into a separate pallial pit (*i. e.* phanerobranchiate). The gills twitched continuously. Within the ring of gills lay the conspicuous white anal papilla and the nephroproct (Figure 2**B**).

The colour pattern described above is that which can be seen in the creeping animal. If alarmed, however, the mantle edges are spread out and the animal takes on a vivid aspect, in marked contrast to the well camouflaged resting stage. The unrolling of the mantle margins exhibits the white edges and brilliant purple sub-marginal zones, observable in both dorsal and ventral views. In the dorsal view can be seen an additional feature, where brilliant red radial streaks penetrate the purple zones. There are also approximately bilaterally symmetrical slightly embossed patches of pink surrounding bright red spots; these are partially concealed when the animal is creeping (Figure 2**A**).


A
Joanna A Langhorne
B

B. Swimming Behaviour

In swimming, the enrolled mantle skirt is spread out, dilated, and strong locomotor waves are propagated rearwards from the anterior pallial margin. The waves are synchronous on the two sides of the body, and each wave takes about 4 seconds to travel its course. Two waves are usually in progress along the sides of the body at any moment. At the same time, the body undergoes great dorso-ventral flexions, a full cycle of activity occupying about 4 seconds. Swimming may continue for many minutes, and it is probable that this is more than a simple escape reaction. Certainly, a brilliant display of colour accompanies the unrolling of the mantle edge, and it may be that swimming here is the behavioural component of an aposematic or warning display. While swimming, the lateral edges of the foot are brought together in order to conceal the sole and the rhinophores are held back against the dorsal mantle.

C. Anatomy

The central nervous system was orange-pink in colour and pustulose like that of a pleurobranchomorph. The blood-gland (of uncertain function) was large and dark red, overlying the pallial nerves behind the nerve ring. A conspicuous pear-shaped gastric caecum was present. The penis was extremely large, 3 cm or more in preservative. The penial sheath was helically coiled around the narrow vas deferens. The penis was unarmed.

The jaws were dark brown, lying one on each side of the oral canal. They exhibited antero-posterior wrinkles and were composed of minute rods of chitin. The radular formula was 48 × 91 · 0 · 91. This is somewhat different from Red Sea specimens (40 × 60 · 0 · 60 to 60 × 78 · 0 · 78, according to Gohar & Soliman, 1963). The hooked simple teeth lacked subsidiary denticulations of any kind.

D. Diet

The hindgut was filled with fragments of greenish material which contained minute calcareous spicules. Dr. P. Kott kindly identified these remains as the ascidian *Didemnum moseleyi* Herdman. This is the first record of such a diet for *Hexabranchus*. Other authors have identified the gut contents as sponges (Young, 1969), or as foraminiferans, worm-tubes, and gastropod and echinoderm shells (Eales, 1938).

(← on facing page)

Figure 1

Hexabranchus sanguineus

A Swimming vigorously

B The same, creeping over coral debris, Heron Island, Great Barrier Reef

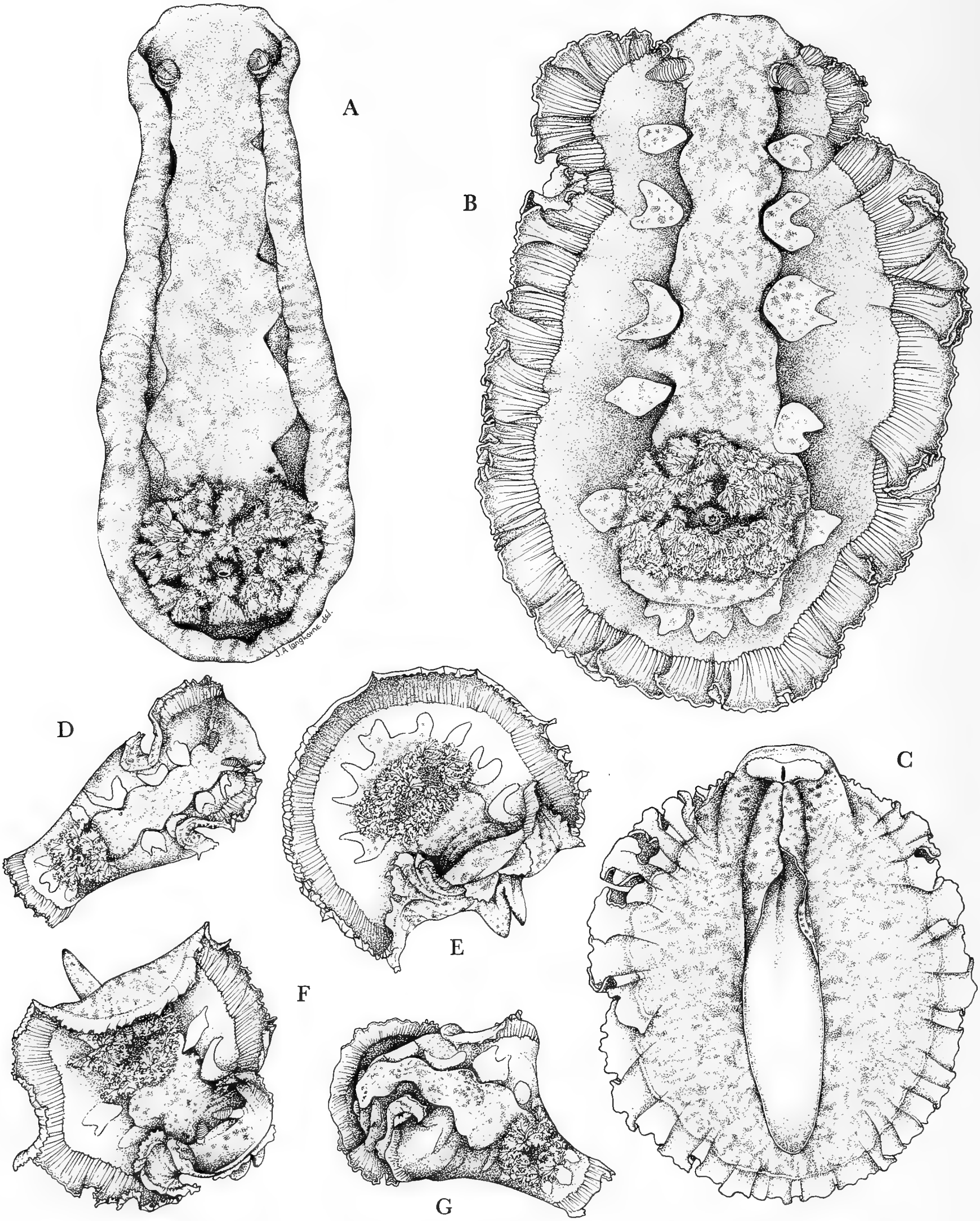
DISCUSSION

Many species of *Hexabranchus* have been proposed, but as long ago as 1909, Eliot stated that "It may be doubted whether the species of *Hexabranchus* are for the most part more than colour varieties". In the following year, this distinguished authority again made it clear that he doubted the validity of nearly all the claimed specific divisions (Eliot, 1910). Since that time, Ostergaard (1955) and Marcus & Marcus (1962) have added new proposed species of *Hexabranchus* but without seriously attempting to distinguish their specimens from previous described species. Indeed, apart from a minor difference in radular morphology, the only important feature distinguishing *H. morsomus* Marcus & Marcus, 1962, from older described forms is the fact that it came from the Virgin Islands in the Atlantic Ocean, whereas other records had been exclusively from the Indo-Pacific. Only in Gohar & Soliman's (1963) paper is there an attempt to describe and illustrate the variations which may occur in the colour patterns within a particular sea-area. Their results support Eliot's view that there may be only one valid species of *Hexabranchus*. Edmunds (1968) claimed to have detected differences in the swimming behaviour of Tanzanian specimens compared with published accounts of Australian material (Morton, 1964), but his illustrations do not support this contention. His plate 1 (1) shows two waves on the mantle margin on each side, despite his assertion in the text of his paper that only one is present in Tanzanian material. There are thus no substantial differences either in behaviour or colouration in *Hexabranchus* recorded from localities all over the Indo-Pacific Basin. The published records probably all refer to a single species. The name *Doris sanguinea* Rüppell & Leuckart, 1828, appears to have priority.

CONCLUSION

List of Principal Synonyms of *Hexabranchus sanguineus* (Rüppell & Leuckart)

Doris sanguinea Rüppell & Leuckart, 1828 (Red Sea)
Hexabranchus proetextus Ehrenberg, 1831 (Red Sea)
Doris flammulatus Quoy & Gaimard, 1832 ("Île des Amis")


A
B
D
C
E
F
G
J.A Langkome del.

Doris marginatus Quoy & Gaimard, 1832 (China, Madagascar, Red Sea, Ryukyu Islands, Japan, Caroline Islands, Marshall Islands, Australia [Great Barrier Reef to Abrolhos Islands], New Caledonia, Hawaii, Tonga, British Solomon Islands, Fiji, Ceylon)
Doris cardinalis Gould, 1852 (Hawaii)
Doris sandwichensis Eydoux & Souleyet, 1852 (Hawaii)
Hexabranchus pulchellus Pease, 1860 (Hawaii)
Hexabranchus pellucidulus Abraham, 1876 (unknown locality)
Hexabranchus suezensis Abraham, 1876 (Red Sea)
Hexabranchus aneiteumensis Abraham, 1877 (New Hebrides)
Hexabranchus mauritianus Abraham, 1877 (Mauritius)
Hexabranchus orbicularis Abraham, 1877 (Mauritius)
Hexabranchus aneitus Bergh, 1878 (Philippines)
Albania formosa Collingwood, 1881 (Formosa)
Hexabranchus imperialis Kent, 1897 (Abrolhos Islands)
Hexabranchus lacer Bergh, 1900 (not Cuvier, 1804) (unknown locality)
Hexabranchus plicatus Hägg, 1901 (unknown locality)
Hexabranchus digitatus Eliot, 1906 (Maldive Islands)
Hexabranchus tinkeri Ostergaard, 1955 (Hawaii)
Hexabranchus aureomarginatus Ostergaard, 1955 (Hawaii)

(← on facing page)

Figure 2

Hexabranchus sanguineus

A Creeping posture
B Spread out on a table, dorsal view
C The same, ventral view
D - G Various views of the vigorous swimming movements

Literature Cited

Eales, Nellie B.
1938. A systematic and anatomic account of the Opisthobranchia. Sci. Rep. John Murray Exped. **5:** 77 - 122

Edmunds, Malcolm
1968. On the swimming and defensive response of *Hexabranchus marginatus* (Mollusca, Nudibranchia). Journ. Linn. Soc. (Zool.) **47:** 425 - 429

Eliot, Charles N. E.
1909. Notes on a collection of nudibranchs from Ceylon. Spolia Zeylanica **6:** 78 - 95
1910. Nudibranchs collected by Mr. Stanley Gardiner from the Indian Ocean in H. M. S. *Sealark*. Trans. Linn. Soc. London (Zool.) **13:** 411 - 438

Gohar, H. A. F. & G. N. Soliman
1963. The biology and development of *Hexabranchus sanguineus* (Rüpp. and Leuck.) (Gastropoda, Nudibranchiata). Publ. Mar. Biol. Sta. Al-Ghardaqa **12:** 219 - 247

Marcus, Ernst & Eveline du Bois Reymond Marcus
1962. Opisthobranchs from Florida and the Virgin Islands. Bull. Mar. Sci. Gulf & Carib. **12** (3): 450 - 488; 28 text figs.

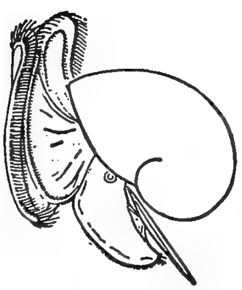
Morton, John Edward
1964. Locomotion. *In* Physiol. Mollusca **1:** 383 - 423

Ostergaard, Jens Mathias
1955. Some opisthobranchiate Mollusca from Hawaii. Pacif. Sci. **9:** 110 - 136

Rüppell, E. & F. S. Leuckart
1828. Neue wirbellose Thiere des Rothen Meeres. Prt. 5 *in* Atlas zu der Reise im nördlichen Afrika von E. Rüppell. Frankfurt a. M.

Vicente, N.
1963. Une des plus belles espèces de nudibranches: *Hexabranchus marginatus* Q. et G. Rec. Sta. marit. Endoume **43:** 99 - 106

Young, David K.
1970. The functional morphology of the feeding apparatus of some Indo-West-Pacific dorid nudibranchs. Malacologia **9:** 421 - 446 (20 July 1970)



New Records of Pleistocene Marine Mollusca from Pacific Beach, San Diego, California

BY

M. J. BISHOP AND S. J. BISHOP

Sidney Sussex College, Cambridge, CB2 3HU, England

PREVIOUS COLLECTIONS of Pleistocene marine Mollusca from Pacific Beach, San Diego County, California, have been described by ARNOLD (1903), GRANT & GALE (1931), STEPHENS (1929), and VALENTINE (1961). Here we present a list of a further 15 species, together with a description of our collecting site, and an interpretation of the ecological conditions at the time of deposition.

The site is at the cliff top, 10 m north of the City of San Diego Pump Station at the foot of Loring Street. The Pleistocene marine bed is horizontal. It rests unconformably on Pliocene sands, and is covered by 2.40 m of soil and alluvium. The marine bed is 0.50 m in thickness and contains boulders which are 0.20 - 0.25 m in the largest diameter. These are set in a fine sand which is solidly packed with whole and broken shells and smaller pebbles. In places the sand is cemented with calcium carbonate. The bed is exposed for a distance of 3 m, being obscured on either side by talus.

The collection contains a total of 78 species of molluscs, the following being new to Pacific Beach. The nomenclature follows that used by MCLEAN (1969).

GASTROPODA:

Acmaea mitra Rathke, 1833; *Collisella asmi* (Middendorff, 1847); *C. conus* (Test, 1945); *C. limatula* (Carpenter, 1864); *Calliostoma gemmulatum* Carpenter, 1864; *Tegula brunnea* (Philippi, 1848); *Opalia funiculata* Carpenter, 1857; *Crepidula aculeata* (Gmelin, 1791); *C. perforans* (Valenciennes, 1846); *Ocenebra minor* (Dall, 1919); *Maxwellia gemma* (Sowerby, 1879).

PELECYPODA:

Septifer bifurcatus (Conrad, 1837); *Pseudochama exogyra* (Conrad, 1837); *Gari californica* (Conrad, 1849); *Penitella penita* (Conrad, 1837).

The total list of species from Pacific Beach contains molluscs of several present day habitats. Many of the shells are worn, and only those which appear to have been freshly dead can be taken as indicators of the ecological conditions at the time of deposition. Six species of bivalves were collected as paired closed valves: *Protothaca staminea* (Conrad, 1837); *Tresus nuttallii* (Conrad, 1837); *Cumingia californica* (Conrad, 1837); *Donax gouldii* Dall, 1921; *Cryptomya californica* (Conrad, 1837); and *Penitella penita*. *Protothaca* in particular is very common in the deposit, and it is likely that the paired valves are in the life position.

The habitat and tidal range of these species, as described by MCLEAN (1969), considered in conjunction with the nature of the bed and with the total species list seems to indicate a low intertidal or shallow sublittoral habitat on a partially sheltered outer coast.

The material is deposited in the San Diego Museum of Natural History.

Literature Cited

ARNOLD, RALPH
1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Calif. Acad. Sci. Mem. 3: 420 pp.; 37 plts. (27 June 1903)

GRANT, ULYSSES SIMPSON, IV & HOYT RODNEY GALE
1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. San Diego Soc. Nat. Hist. Mem. 1: 1 - 1036; 15 text figs.; plts. 1 - 32 (3 November 1931)

MCLEAN, JAMES HAMILTON
1969. Marine shells of southern California. Los Angeles County Mus. Nat. Hist. Sci. Ser. 24, Zool. no. 11: 104 pp.; 54 text figs.

STEPHENS, FRANK
1929. Notes on marine Pleistocene deposits of San Diego County, Calif. San Diego Soc. Nat. Hist. Trans. 5 (16): 245 - 256

VALENTINE, JAMES WILLIAM
1961. Paleoecologic molluscan geography of the Californian Pleistocene. Univ. Calif. Publ. Geol. Sci. 34 (7): 309 - 442; 16 text figs. (17 May)

Some Notes on the Genus *Teramachia*

(Volutidae : Calliotectinae)

BY

HARALD A. REHDER

National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560

(1 Plate)

THE RECEIPT OF TWO SPECIMENS of the genus *Teramachia* from the South China Sea has led to the following paper, to which I have added some comments on recently published statements dealing directly with this genus.

For the opportunity of examining the specimens of *Teramachia* I am indebted to Dr. and Mrs. Richard K. Williams of Courtland Farm, Hanover, Virginia, and to Dr. Tadashige Habe of the National Science Museum, Tokyo, Japan. To these individuals my thanks for allowing me to study and photograph these interesting mollusks.

Teramachia Kuroda, 1931

The discovery of the presence of two oblique folds on the columella of *Teramachia johnsoni* Bartsch and of its new subspecies described in this paper, and their alleged absence in the type species, *T. tibiaeformis* Kuroda, led me to file away a section of an early whorl of a specimen of *tibiaeformis*. This operation revealed the presence of two low, obliquely ascending folds on the columella, which become obscure in the adult stage, although a low mound can be seen on the columellar lip in the region where the upper fold should occur.

The diagnosis, therefore, usually given for the genus *Teramachia* must be emended to state that two obliquely ascendant folds are present but one or both may become obscure in the adult stage.

WEAVER & DUPONT (1970, p. 176) state that the radular characters of the genus are unknown. KURODA (1962, p. 132, fig. 12) gives a figure of the radula of *Teramachia tibiaeformis*, which agrees closely with that of *Calliotectum* given by WEAVER & DUPONT (1970, p. 176, fig. 40).

"Teramachia" barthelowi (Bartsch, 1942)

Prodallia barthelowi BARTSCH, 1942, p. 12, pl. 2, fig. 2.
Teramachia barthelowi (Bartsch), WEAVER & DUPONT, 1970, p. 177, pl. 75, figs. C, D.

Although Bartsch said in his original description that this species, collected off Cagayan Island, northern Sulu Sea, Philippines, has two folds on the columella, Weaver & duPont state that the columella is without plaits. An examination of the unique holotype shows that there are in fact two folds that are fairly stout and only slightly oblique, not as strongly ascending as in the other species of *Teramachia*. This fact, and the character of the whorls which are flattened, not convex, the slender shape of the shell, its small size, set it apart from the other members of the genus.

It very closely resembles the fossil species that MacNeil described from Okinawa as *Benthovoluta okinavensis* MACNEIL (1961, p. 96, pl. 9, figs. 2–3), which has two columellar folds, rather flattened whorls, and is of the same size as *B. barthelowi*.

Benthovoluta Kuroda & Habe, 1950 is described as having three folds on the columella. An examination of two specimens of the type species, *B. hilgendorfii* (von Martens, 1897) in the collections of the National Museum of Natural History showed that, at least in the adult stage, this character is a variable one, as one specimen showed only one fold with the suggestion of another, whereas the other, slightly larger shell showed three strong folds and a suggestion of a fourth basal one, all placed on a rather strong callus. This variability leads me to believe that the increase to three or more folds may be a gerontic character, and on opening up one of the earlier whorls of one of our specimens I found only two ascending folds, just as in *B.*

barthelowi Bartsch and *B. okinavensis* MacNeil.

I believe, therefore, that *"Teramachia" barthelowi* (Bartsch) should be placed in *Benthovoluta* Kuroda & Habe. Additional species are the fossil *B. plicifera* (Yokoyama, 1920) and *B. gracilior* Rehder, 1967 (see MacNeil, 1961, p. 96, and Rehder, 1967, p. 183).

Benthovoluta belongs in the Turbinellidae (Kuroda, 1965, pp. 50–52 and Rehder, *op. cit.*, pp. 183–184), and not in the Volutidae where MacNeil placed it (MacNeil, *loc. cit.*).

In a paper on new species dredged by the R/V *John Elliott Pillsbury* in the Caribbean, F. M. Bayer describes a new species as *Teramachia chaunax* (Bayer, 1971, p. 198, fig. 55). He assigns this species, together with *Fasciolaria (Mesorhytis) meekiana* Dall, 1889 and *Mesorhytis costata* Dall, 1890 to *Teramachia* on the basis of a comparison with *T. barthelowi* Bartsch, placing the genus *Teramachia* in the Turbinellidae on the basis of the characters of the radula and operculum of his new species and of *T. meekiana* (Dall). He adds that we must await future research before we can know whether small species such as *T. barthelowi* are congeneric with larger forms such as *T. tibiaeformis* and *T. mirabilis* (Clench & Aguayo).

The Caribbean species that Bayer placed in *Teramachia* with *T. barthelowi* differ, however, in possessing three, not two, ascending folds on the columella and, in this respect resemble the genus *Mesorhytis* Meek, 1876, from the Upper Cretaceous, where Dall originally placed his species mentioned above. The opportunity of studying the radula and soft parts of *Mesorhytis costata* Dall, which resembles the type species of *Mesorhytis, M. gracilenta* Meek, in its convex whorls, and which at present is known only from the unique holotype dredged off St. Kitts in the Caribbean, would assist materially in understanding the proper allocation of this group of small Caribbean species.

Teramachia johnsoni johnsoni (Bartsch, 1942)

(Figures *3, 7*)

Prodallia johnsoni Bartsch, 1942, p. 12, pl. 2, fig. 3.
Teramachia johnsoni (Bartsch), Weaver & duPont, 1970, p. 178, pl. 75, figs. G, H.

This was described from a single, immature specimen 102.3 mm long (the original description cites the length as 104 mm). The type locality is 3½ miles NW of Cagayan Island in the northern Sulu Sea, in 340 fathoms (USBF Sta. D 5424).

Recently a fully adult specimen of this species, also collected during the Philippine *Albatross* Expedition, was found in the alcoholic collection of the Division of Mollusks of the National Museum of Natural History, where it had remained undiscovered for over 55 years. It had apparently been dredged up alive but unfortunately the alcohol had deteriorated, the soft parts had rotted long ago, and the specimen is brown-stained. This specimen (USNM 696513), measuring 140.7 mm in length (see table of measurements below), was collected at USBF Sta. D 5535, 5 miles E of Dumaguete, southern Negros Island, in 310 fathoms; this is 150 miles to the east of the type locality. Because the descriptions of this species are based on an immature shell, I have deemed it advisable to give a description of the adult specimen.

Description: Shell large, 140 mm in length, narrowly and elongately fusiform. Protoconch missing, remaining postnuclear whorls 10½, gently convex, very narrowly channeled, ornamented with strong, slightly arcuate axial ribs which become increasingly sigmoidal and opisthocline; the interspaces, at first broader than the ribs, become increasingly narrower; the ribs continue onto the penultimate whorl but then become obsolete. Last whorl-and-a-half smooth, marked by irregular growth lines and microscopic wavy striae, which increase in strength towards the base. Aperture elongate, outer edge strongly arcuate, parietal wall straight, merging with the slightly sinuous columellar lip; the latter bears two fairly strong, ascending folds; parietal and columellar walls covered with a thin glaze whose abapertural edge is strongly curved; anteriorly the aperture is acuminate, ending in a fairly broad, shallow canal; at the juncture of the outer lip and parietal wall is a small v-shaped sinus marking the end of the channeled suture.

Remarks: The discovery of an adult specimen of *Teramachia johnsoni* allows us to correct previous descriptions of the axial sculpture of this species, showing that it basically agrees with that of the other species of *Teramachia*.

Measurements: See under following new subspecies.

Teramachia johnsoni ***williamsorum*** Rehder, subspec. nov.

(Figures *1, 2, 4*)

Diagnosis: Shell large, broader than *T. johnsoni* Bartsch, whorls of spire broader and slightly more convex, the axial sculpture becoming obsolete before the penultimate whorl rather than continuing on the penultimate whorl.

Distribution: 28 to 150 fathoms off Tung-Chiang (also spelled Tung Kang and Tong Kang), Taiwan.

Description: Shell rather large, 121 to 133.6 mm (4¾ to 5½ inches) in length, elongate fusiform, body whorl and penultimate whorl purplish gray, earlier whorls yellowish white or white. Protoconch missing, remaining whorls of holotype 9¾, early postnuclear whorls corroded, later ones somewhat convex but gently concave below the narrowly canaliculate suture, showing strong axial ribs slightly arcuate, increasingly opisthocline and sigmoidal, in early whorls as broad as interspaces, but later become broader than the intercostal spaces and slightly thickened below the channeled suture; obscure spiral striae are faintly visible, especially suprasuturally; ribs are 33–35 in number on last completely ribbed whorl; ribs become obsolete on last quarter of antepenultimate whorl; the last two whorls smooth, marked only by irregular growth lines and microscopic wavy striae which increase somewhat in strength towards the base; the body whorl is anteriorly rather acutely attenuate. Aperture elongate, with parietal lip forming a slight angle with the long, rather straight columellar lip which bears a low ascending fold near its juncture with the parietal wall, and another less obvious one just below. Outer lip arcuate, gently sinuous both posteriorly, where there is a small v-shaped sinus at the end of the sutural channel, and anteriorly where it joins at a 45° angle with the tip of the columellar lip, forming the angled anterior end of the broad siphonal canal. A thin glaze with a well marked arcuate abapertural border covers the area of the parietal and columellar lip, the upper part of the latter pale in color. The interior of the outer lip is of a grayish purple with a brownish margin just inside the whitish edge of the lip. Operculum horny, elongate ovate, with terminal nucleus, and rugose growth lines that at outer edge are increasingly curved towards the posterior end.

Specimens examined: Holotype (USNM 707229): in 150 fathoms 30 miles south of Tung-Chiang, Taiwan. Paratype (Nat. Science Museum Tokyo 40647): in 27 to 38 fathoms off Tung-Chiang, Taiwan.

Measurements (in mm)

Teramachia	*length*	*width*	*aperture length*	*width/ length*
T. johnsoni Bartsch (USNM696513)	140.7	36.9	64.5	0.262
*T. j. **williamsorum*** Rehder (USNM-707229)	133.6	41.6	67.0	0.311
*T. j. **williamsorum*** Rehder (Nat. Sci. Mus. Tokyo 40647)	120.9	38.9	58.4	0.322

Remarks: The most obvious differential characters of this geographic subspecies have already been mentioned in the diagnosis given above. In addition the sutural channel, although still narrow, appears to be more pronounced than in the typical form. Whether the purplish gray color of the subspecies is a constant character is not known since the paratype in the National Science Museum in Tokyo was dead when collected, and of the known specimens of *Teramachia johnsoni* the holotype was dead when dredged, and the paratype was left in alcohol for over fifty years. The locality of the subspecies *T. j. **williamsorum*** lies about 900 miles north of the area of *T. johnsoni johnsoni.*

This subspecies is named for Dr. and Mrs. Richard Kennon Williams, who first brought my attention to this form, and who generously donated the holotype to the National Museum of Natural History.

Teramachia shinzatoensis MacNeil, 1961

(Figures *5, 6*)

Teramachia shinzatoensis MacNeil, 1961, p. 96, pl. 9, fig. 1

I am figuring this fossil species here because the author compares it to *Teramachia johnsoni* Bartsch, and indeed a comparison of the figure of this species with the upper half of the figures of *T. j. **williamsorum*** Rehder, shows a close similarity to that subspecies. *Teramachia shinzatoensis,* which was found in the Shinzato formations of Okinawa, Ryukyus, Japan, assigned to the Miocene or Pliocene but more probably Pliocene, is smaller (69.8 mm in length), relatively broader, the axial ribs slightly more numerous and continuing on into the last half of the penultimate whorl, and the subsutural sinus of the outer lip is shallower. It is known only from the unique holotype (USNM 562840). This species also shows the two ascending folds on the columellar lip.

Literature Cited

Bartsch, Paul

1942. Some deep-sea Philippine volutids. The Nautilus **56** (1): 9 - 13; plt. 2 (23 July 1942)

Bayer, Frederick Merkle

1971. New and unusual mollusks collected by R/V *John Elliott Pillsbury* and R/V *Gerda* in the tropical western Atlantic. Bull. Mar. Sci. **21** (1): 111 - 236; figs. 1 - 72 (March 1971)

Cernohorsky, Walter Oliver

1970. Systematics of the families Mitridae and Volutomitridae (Mollusca : Gastropoda). Bull. Auckland Inst. & Mus. No. **8**: i - iv; 1 - 190; plts. 1 - 18; text figs. 1 - 222 (1 October 1970)

Dall, William Healey

1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U. S. Coast Survey steamer "Blake," ... XXIV. Report on the Mollusca. — Part II. Gastropoda and Scaphopoda. Bull. Mus. Comp. Zool. **18**: 1 - 492; plts. 1 - 40 (January-June 1889)

1890. Scientific results of exploration by the U. S. Fish Commission steamer *Albatross.* No. VII.— Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887-'88. Proc. U. S. Nat. Mus. **12** (773): 219 - 362; plts. 5 - 14 (7 March 1890)

Kuroda, Tokubei

1952. (Some important radulae of Japanese gastropods). Illustr. Cat. Japan. Shells **1** (18): 132, figs. 1 - 12 (20 June 1952)

MacNeil, Frederick Stearns
1961. Tertiary and Quaternary gastropods of Okinawa. U. S. Geol. Survey Prof. Paper 339 (1960): i - iv + 1 - 148; plts. 1 - 19 (distr. 17 March 1961)
Rehder, Harald Alfred
1967. A new genus and two new species in the families Volutidae and Turbinellidae (Mollusca : Gastropoda) from the Western Pacific. Pacif. Science 21 (2): 182 - 187; figs. 1 - 11
Weaver, Clifton Stokes & John Eleuthère duPont
1970. Living volutes: a monograph of the Recent Volutidae of the world. Delaware Mus. Nat. Hist. Mon. Ser. No. 1: xv + 375 pp.; 79 col. plts.; 44 figs.; 13 maps
Wenz, Wilhelm
1943. Gastropoda Prosobranchia. Handb. Paläozool., Bd. 6, Teil 1, Lief. 7: 961 - 1200; figs. 2788 - 3416

Plate Explanation

Figure *1*: *Teramachia johnsoni* ***williamsorum*** Rehder, subspec. nov. Holotype, USNM No. 707229 133.6 mm

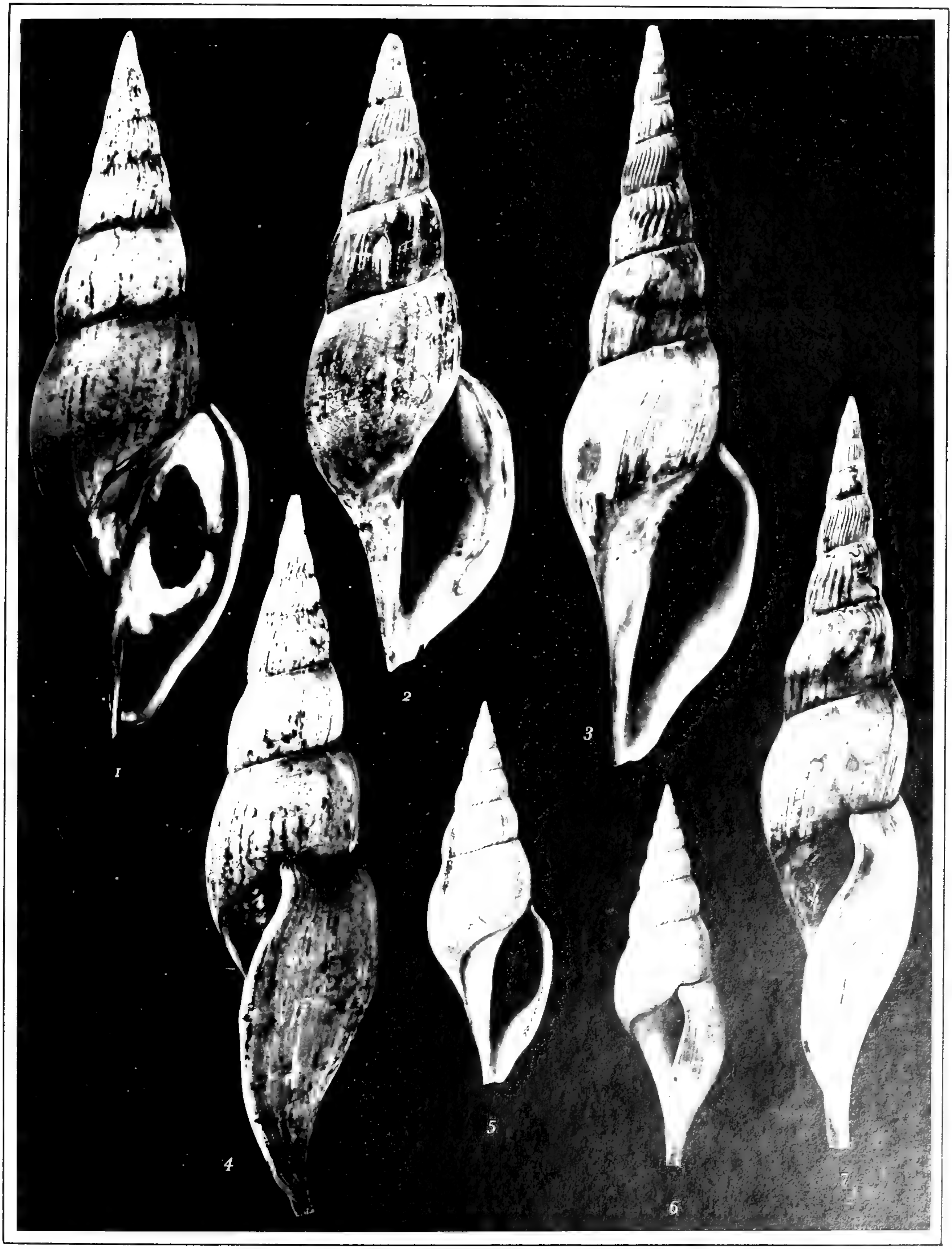
Figure *2*: *Teramachia johnsoni* ***williamsorum*** Rehder, subspec. nov. Paratype, Nat. Sci. Museum, Tokyo No. 40647 120.9 mm

Figure *3*: *Teramachia johnsoni johnsoni* (Bartsch). USNM No. 696513 140.7 mm

Figure *4*: *Teramachia johnsoni* ***williamsorum*** Rehder, subspec. nov. Holotype, USNM No. 707229 133.6 mm

Figures *5*, *6*: *Teramachia shinzatoensis* MacNeil. Holotype, USNM No. 562840 69.8 mm

Figure *7*: *Teramachia johnsoni johnsoni* (Bartsch). USNM No. 696513 140.7 mm


1
2
3
4
5
6
7

Further Comments on Deepwater Volutidae from off Southeast Africa, with Descriptions of Two New Species of *Volutocorbis*

BY

HARALD A. REHDER

National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560

(1 Plate)

THE SPECIMENS OF THE FAMILY Volutidae collected off the coasts of South Africa and Mozambique on Cruises 7 and 8 of the *Anton Bruun* during the International Indian Ocean Expeditions have been turned over to me for study. As several new species have turned up in this material, as well as some interesting extensions of distribution I have considered it worthwhile to publish a paper supplementary to my two previous papers in "The Veliger" (Rehder, 1969 and 1970).

Fusivoluta von Martens, 1902

Fusivoluta von Martens, 1902, p. 237; REHDER, 1969, p. 205; WEAVER & DUPONT, 1970, p. 181.

Fusivoluta barnardi Rehder, 1969

Fusivoluta barnardi Rehder, 1969, p. 207, pl. 40, fig. 9, pl. 43, figs 40-43; WEAVER & DUPONT, 1970, p. 182, pl. 77, figs. A, B.

When I described this species I had specimens before me from off southern Zululand and northern Natal only, and so I was led to comment that the related *Fusivoluta clarkei* Rehder occupied a more northerly range than did *F. barnardi*. Now, however, I find in the collection before me three typical specimens of *F. barnardi* dredged in 875 to 890 fathoms 48 miles due east of Cabo das Correntes, south of Inhambane. This is over 400 miles north of the previously known range of *F. barnardi*, and the distribution of this species now overlaps that of *F. clarkei*.

These specimens are from considerably greater depth than that from which the earlier known specimens were dredged, and are also notably smaller. Whether this size difference is correlated with the greater depth is a matter for speculation.

Specimens Examined: (USNM 717640 and 717650): about 48 miles ESE of Cabo Inhambane, Mozambique (Lat. 24°05'S; Long. 36°13'E); IIOE, *Anton Bruun* Cruise 7, Sta. 369F, Aug. 17, 1964; 890-875 fms. (Agassiz Trawl).

	Measurements (in mm.)		
length	56.7	50.1	45.8
width	23.6	(lip broken)	18.2
aperture length[1]	30.7	25.4	22.7

---

[1] Measured to end of anterior canal

Fusivoluta clarkei Rehder, 1969

Fusivoluta clarkei Rehder, 1969, p. 206, pl. 40, fig. 8, pl. 43, figs. 37-39; WEAVER AND DUPONT, 1970, p. 183, pl. 77, figs. C, D.

Twelve specimens were dredged by the *Anton Bruun* on Cruise 8 at three stations (396B, 397C, and 398B). The first two stations are off Delagoa Bay in 246 to 358 fms. in the general area where the type series was collected. The eight specimens collected here are quite typical though averaging somewhat smaller than those on which the original description was based; the adults range in length from 62.5 mm to 76.4 mm.

The four specimens from Station 398B were dredged in 404 fathoms southeast of Ponta São Sebastião and about 23 miles off the coast; this is about 300 miles north of the type locality. These shells differ from those found farther south by the ribs on the second and third post nuclear whorls becoming more numerous and more slender, and by the axial ribbing disappearing on the penultimate and antepenultimate whorls. In addition, the spiral sculpture is slightly sharper. Even though this northern population shows these differences in sculpture I hesitate to describe it as a distinct geographical race until more material is forthcoming from the intervening area.

Volutocorbis Dall, 1890

Volutocorbis Dall, 1890, p. 75; Rehder, 1969, p. 200; Weaver & duPont, 1970, p. 9.

Volutocorbis gilchristi (Sowerby, 1902)

Figures *1, 2* and *6*

Volutilithes gilchristi Sowerby, 1902, p. 99, pl. 2, fig. 5.
Volutocorbis gilchristi (Sowerby) Rehder, 1969, p. 204, pl. 40, fig. 1, pl. 42, figs. 23, 24; Weaver & duPont, 1970, p. 12, pl. 3, figs. J, K.

Three specimens, two adults and one immature, of this relatively rare species were dredged about 30 miles off Durban, Natal in 240 fathoms; IIOE: *Anton Bruun* Cruise 7, Sta. 390 C. Both adult specimens are fresh and in perfect condition, and I am figuring both shell and nucleus (Figures *1, 6*) of the largest one.

	Measurements (in mm.)	
length	29.5	23.2
width	13.8	11.3

Volutocorbis boswellae Rehder, 1969

Volutocorbis boswellae Rehder, 1969, p. 202, pl. 40, fig. 5, pl. 44, figs. 16–19; Weaver & duPont, 1970, p. 10, pl. 3, figs. E–G.

I must call attention to an error in Weaver and duPont's outstanding book on the living Volutidae. On plate 3, figure E, which is identified in the explanation as an example of *Volutocorbis abyssicola* Adams and Reeve, actually represents *V. boswellae* Rehder. This is the same specimen from the Helen Boswell collection that is figured in my 1969 paper (plate 41, figs. 16 and 17).

The designation by Weaver and duPont of this shell as an example of *Volutocorbis boswellae* may account for the statement under *V. disparilis* Rehder, 1969 in their book (Weaver & duPont, 1970, p. 11) that the latter species may "prove to be a form of *V. abyssicola.*" Actually *disparilis* is much closer to *V. boswellae*.

*Volutocorbis **mozambicana*** Rehder spec. nov.

(Figures *3–5, 7–9*)

Diagnosis: Shell small, adult shells from 14.1 to 19.9 mm (½ to ¾ inches) in length, upper part of whorls subplanulate at suture, whorls with strong ribs that are crossed by conspicuous grooves, deepest in upper part of whorls where the ribs are thereby made nodulose. Outer lip thin, not reflected, columella with numerous fine folds.

Distribution: from off Lourenço Marques to south of Inhambane, southern Mozambique in 480 to 880 fathoms.

Description: Shell small, adult shells 14.1 to 19.9 mm (½ to ¾ inches) in length, elongate ovate to subfusiform, straw yellow to grayish-yellow in color. Apical whorls eroded on all specimens. Post nuclear whorls strongly shouldered, flattened at strongly impressed suture and weakly convex below shoulder; sculptured by strong, angular ribs (17 on penultimate whorl) which are cut on spire whorls by a strong spiral groove below the shoulder and two successively weaker ones below; this results in two series of strong, subconical, somewhat axially elongate nodes. Body whorl with same sculpture on upper part, lower part with weak spiral grooves that make axial ribs weakly nodulose, the axial ribs gradually disappearing towards base. Aperture elongate ovate, with anterior end forming a broad sinus; outer lip angulate at posterior end, only slightly thickened; inner lip with six to eight folds, the lowest one the strongest; a thin gray-white callus is present on the parietal wall and columella.

Plate Explanation

Figures *1, 2*: *Volutocorbis gilchristi* Sowerby. USNM No. 717971. 30 miles E of Durban, Natal, South Africa × 2

Figure *3*: *Volutocorbis **mozambicana*** Rehder, spec. nov. Holotype, USNM No. 717909. 95 miles SE of Inhaca Id., Mozambique × 2

Figures *4, 5*: *Volutocorbis **mozambicana*** Rehder, spec. nov. Paratypes, USNM No. 717647. 50 miles off Cabo das Correntes, Mozambique × 2

Figure *6*: *Volutocorbis gilchristi* Sowerby. Protoconch and early postnuclear whorls. USNM No. 717971 × 2

Figure *7*: *Volutocorbis **mozambicana*** Rehder, spec. nov. Holotype, USNM No. 717909 × 2

Figures *8, 9*: *Volutocorbis **mozambicana*** Rehder, spec. nov. Paratypes, USNM No. 717647 × 2

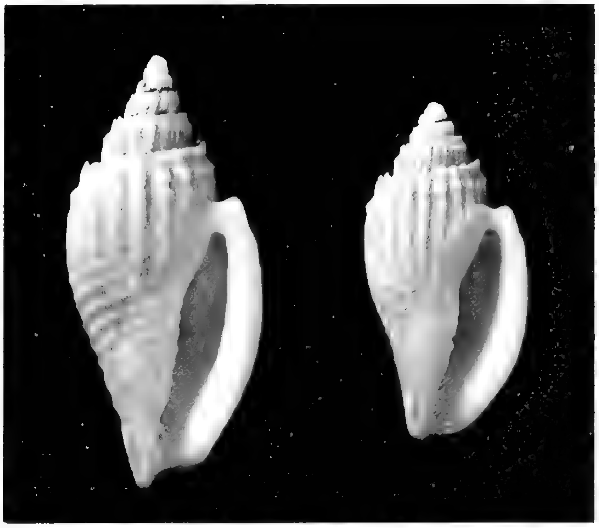


Figure *1* Figure *2*


Figure *3* Figure *4* Figure *5*

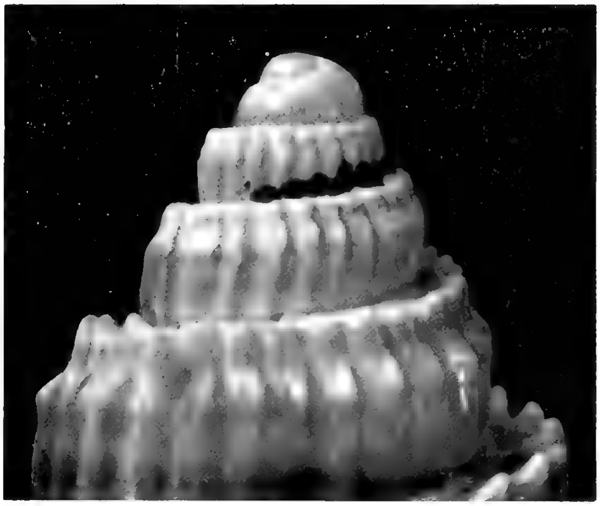


Figure *6*


Figure *7* Figure *8* Figure *9*

Figures *1*, *2*: *Volutocorbis gilchristi* Sowerby. USNM No. 717971. 30 miles E of Durban, Natal, South Africa × 2

Figure *3*: *Volutocorbis* ***mozambicana*** Rehder, spec. nov. Holotype, USNM No. 717909. 95 miles SE of Inhaca Id., Mozambique × 2

Figures *4*, *5*: *Volutocorbis* ***mozambicana*** Rehder, spec. nov. Paratypes, USNM No. 717647. 50 miles off Cabo das Correntes, Mozambique × 2

Figure *6*: *Volutocorbis gilchristi* Sowerby. Protoconch and early postnuclear whorls. USNM No. 717971 × 2

Figure *7*: *Volutocorbis* ***mozambicana*** Rehder, spec. nov. Holotype, USNM No. 717909 × 2

Figures *8*, *9*: *Volutocorbis* ***mozambicana*** Rehder, spec. nov. Paratypes, USNM No. 717647 × 2

Holotype: about 95 mi SE of Inhaca Id., Mozambique in 490 fms.; IIOE *Anton Bruun* Cruise 7, Sta. 373H (USNM 717909).

Paratypes: One specimen from type locality (USNM 702610); 3 specimens from 30 miles SSE of Cabo das Correntes, Mozambique in 480 fms. IIOE *Anton Bruun* Cruise 7, Sta. 370D (USNM 717665); fifteen specimens from 50 miles E of Cabo das Correntes, Mozambique in 880 fms. IIOE *Anton Bruun* Cruise 7, Sta. 369J (USNM 717647).

Measurements (in mm)	height	diameter
Holotype (Sta. 373 H)	19.9	9.2
Paratype (Sta. 373 H)	15.6	7.4
Paratype (Sta. 370 D)	16.9	8.0
Paratype (Sta. 370 D)	16.5	7.9
Paratype (Sta. 369 F)	16.7	8.0
Paratype (Sta. 369 F)	16.0	7.6
Paratype (Sta. 369 F)	15.6	7.6
Paratype (Sta. 369 F)	15.4	7.5
Paratype (Sta. 369 F)	14.1	7.6

Remarks: This small species is closest to *Volutocorbis disparilis* Rehder but a paratype of the latter almost twice the size of the holotype of *V.* ***mozambicana*** has the same number of whorls. The whorls are narrower, more straight-sided below the suture, less convex than in *V. disparilis,* the subsutural shelf is broader and more obvious, and the axial ribs are fewer in number and more strongly nodose in *V.* ***mozambicana***.

Volutocorbis sp.

In the material sent me by Mrs. Helen Boswell is a specimen from the Kenneth Fuller collection that I am unable to assign unequivocally to any of the known species of *Volutocorbis.* Unfortunately it is not only a single specimen but is rather worn with the apical whorls missing. I am therefore unwilling to describe it as a new species.

This specimen is apparently adult, 20.4 mm. in length, ovate with a heavy varicose outer lip. Its main distinctive character is that the whorls are not subcanaliculate with a narrow shelf below the impressed suture, but the whorls are adpressed at the suture. Substantiation of this difference as a consistent distinguishing character must await the discovery of further material.

Festilyria Pilsbry and Olsson, 1954

Festilyria Pilsbry and Olsson, 1954, p. 294; Weaver & duPont, 1970, p. 54.

Festilyria queketti (E. A. Smith, 1901)

Voluta (Lyria) queketti E. A. Smith, 1901, p. 234, fig.
Lyria (Lyria) queketti (E. A. Smith) Weaver & duPont, 1970, p. 24, pl. 6, figs. C, D; figs. 4d–e.

One specimen was dredged in 37 to 38 fathoms about 45 miles NE of Durban, Natal (*Anton Bruun* Cruise No. 8, Sta. 394B). This species has usually been placed in the genus *Lyria* largely on the basis of the presence of an operculum (Barnard 1959, p. 22) and the nature of the radula. However the fact that the numerous folds on the parietal wall typical of the genus *Lyria* are absent in the species *queketti* has led me to place it in *Festilyria,* one of the two groups in the Fulgorariinae whose species possess an operculum; the other group is the subgenus *Saotomea* Habe, 1943 of the genus *Fulgoraria.*

In sculpture it is closest to *Festilyria africana* (Reeve), since it has the spiral striae that are found in that species. In addition the five to six columellar plaits of *F. queketti* are very similar to those of *F. africana,* with the upper two or three plaits usually obscure. *F. africana,*however, has a dome-shaped and paucispiral nucleus with the whorls of the teleoconch adpressed at the suture, while *F. queketti* has a mammillate protoconch, and the sutures are impressed in the postnuclear shell with a narrow subsutural shelf present. *F. duponti* Weaver has a similar pupiform, deeply sutured protoconch. Apparently the species of the genus vary considerably in the characters of their nuclear whorls, and it may be that there are several lineages involved in this group.

The radula of *Festilyria queketti* is very close to that of other species of *Festilyria* (Weaver & duPont, 1970, p. 55), and the operculum illustrated by Barnard (1959, p. 21, fig. 5) is not too dissimilar from that figured for *F. duponti* by Weaver & duPont (1970, p. 55, fig. 11e–f).

Literature Cited

Barnard, Keppel Harcourt
1959. Contributions to the knowledge of South African marine Mollusca, Part II: Gastropoda: Prosobranchiata: Rhachiglossa. Ann. South African Mus. 45 (1): 1 - 237; 52 figs. (June 1959)

Dall, William Healey

1890. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Tertiary mollusks of Florida. Part I. Pulmonate, opisthobranchiate and orthodont gastropods. Trans. Wagner Free Inst. Sci. **3**: 1 - 200; plts. 1 - 12 (August 1890)

Martens, Eduard [Carl] von

1902. Einige neue Arten von Meer-Conchylien aus den Sammlungen der deutschen Tiefsee-Expedition. Sitzungsber. Ges. Naturf. Freunde, Berlin, **1902**: 237 - 244

Pilsbry, Henry Augustus & Axel Adolph Olsson

1954. Systems of the Volutidae. Bull. American Paleont. **35** (152): 271 - 306; plts. 25 - 28 (7 September 1954)

Rehder, Harald Alfred

1969. *Volutocorbis* and *Fusivoluta*, two genera of deepwater Volutidae from South Africa. The Veliger **11** (3): 200 - 209; plts. 40 - 43 (1 January 1969)

1970. Supplementary comments on deep water Volutidae from the South China Sea and South Africa. The Veliger **12** (4): 415 - 416; plt. 61 (1 April 1970)

Smith, Edgar Albert

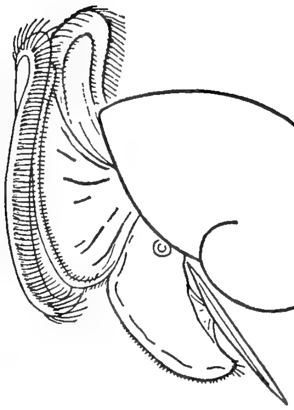
1901. A list of the known forms of Volutidae from South Africa, with descriptions of two new species of *Voluta* from Natal. Proc. Malacol. Soc. London 4 (6): 231 - 235; fig. (October 1901)

Sowerby, George Brettingham (3rd of name)

1902. Mollusca of South Africa. Cape of Good Hope Dept. Agricult. Marine Invest. in South Africa (**1902**): 93 - 100; plt. II

Weaver, Clifton Stokes & John Eleuthère duPont

1970. Living volutes: a monograph of the Recent Volutidae of the world. Delaware Mus. Nat. Hist. Mon. Ser. No. **1**: xv+375 pp.; 79 col. plts.; 44 figs.; 13 maps



Notes on Abyssal Gastropods of the Eastern Pacific, with Descriptions of Three New Species

BY

FRANK J. ROKOP

Scripps Institution of Oceanography, University of California, San Diego
La Jolla, California 92037

(2 Plates)

INTRODUCTION

THE DEEP-SEA GASTROPOD FAUNA is presently very poorly known. CLARKE (1962a, 1962b) listed 491 species and subspecies of prosobranch gastropods recorded from depths greater than 1000 fathoms in the world oceans. More recently, LUS (1969) cited only 93 abyssal prosobranch species from the entire Pacific. In contrast, shelf prosobranchs are much better known with an estimated 1200 species occurring at depths less than 100 fathoms from Point Barrow, Alaska to Panama alone. Considering the paucity of abyssal lowerings and the recent unexpected find of a very high species diversity in the deep-sea environment (HESSLER & SANDERS, 1967; SANDERS & HESSLER, 1969) it is expected that a significantly large number of deep-sea gastropod species are yet to be discovered. This paper is a brief report on several new and little known species of abyssal gastropods collected by Scripps Institution of Oceanography research vessels during the past few years.

Abbreviations for institutions mentioned in the text are as follows: LACM – Los Angeles County Museum of Natural History; SIO – Scripps Institution of Oceanography, University of California, San Diego; USNM – United States National Museum (more properly known as the National Museum of Natural History), Washington, D. C.

SEGUENZIIDAE

Seguenzia Jeffreys, 1896

Seguenzia ***megaloconcha*** Rokop, spec. nov.

(Figure *1*)

Description: Shell small, white, turbiniform, with a nacreous surface. Protoconch minute, smooth, and globular; teleoconch of 5½ whorls. Spiral sculpture of the spire consists of 2 principal carinae, the more prominent of these situated approximately midway between the sutures and the other located adapical to the medial carina, near the suture. Sutures confluent with a peripheral carina which is visible only on the body whorl. Basal disc with an additional 17 narrow carinae. Numerous fine spiral threads occur between the carinae, increasing in number abapically. Axial sculpture of numerous equal and equally spaced sinuous threads, numbering more than 100 on the body whorl. Abapical to the peripheral carina on the base these threads are markedly opisthocryst; adapically and adaxially toward the medial carina these threads are opisthocline and prosocryst; adapical to the medial carina toward the suture they are opisthocryst and prosocline. Umbilicus very deep and narrow, approximately ⅛ the diameter of the body whorl. Aperture subquadrate and irregular. Columellar pillar arcuate, slightly reflected outward.

Holotype: USNM 701260, shell height 9.2 mm, last whorl 6.2 mm, aperture 4.4 mm, maximum diameter 8.3 mm.

Paratype: LACM 1550 (poor condition), shell height 9.0 mm, last whorl 6.7 mm, aperture 4.8 mm.

Type Locality: SIO67-115. SW of Farallon Islands and W of Pioneer Seamount, off northern California; 37°22′ N, 123°54′ W to 37°16′ N, 123°53′ W; 1964 - 2077 fathoms; June 14-15, 1967; R/V *T. Washington.*

Remarks: This species most closely resembles *Seguenzia giovia* Dall, 1919 (DALL, 1919: 343; OLDROYD, 1927: 245; plt. 33, figs. 1 - 3). *Seguenzia giovia* differs markedly in having only one carina on the spire, fewer basal carinae, and obscure sutures.

Muricidae

Trophonopsis Bucquoy, Dautzenberg & Dollfuss, 1882

Trophonopsis ***hubbsi*** Rokop, spec. nov.
(Figures *2, 3*)

Description: Shell moderately small, white, rather light and delicate, about 4 whorls (protoconch defective). Axial sculpture of closely spaced, imbricate lamellae, approximately 40 in number on the last whorl. Spire moderately high, upper surface of whorls tabulate. Body whorl with 4 strong spiral ribs, the penultimate and earlier whorls with only the 3 uppermost ribs, the lowermost spiral rib below the suture. None of the ribs extend to the anterior canal which possesses only the finely imbricate lamellae. The junction of the varicose lamellae and spiral ribs is marked by fluting of the varices into open "spine-like" processes. Anterior canal long and slender, slightly recurved distally. Aperture pyriform, as long as the anterior canal. Outer lip with 4 grooves, fimbriate at the margins corresponding to the junction of the spiral ribs and the varicose lamellae. Inner lip smooth with a very slight callus on the columella.

Holotype: USNM 701258, shell height 19.2 mm, last whorl 15.8 mm, aperture and canal 12.9 mm, maximum diameter 8.8 mm.

Parataypes: USNM 701259, shell height 12.7 mm, last whorl 9.6 mm, aperture and canal 7.4 mm, maximum diameter 7.5 mm. LACM 1549, shell height 17.3 mm, last whorl 14.4 mm, aperture and canal 11.0 mm, maximum diameter 8.7 mm.

Type Locality: SIO70-22. On abyssal plain off Patton Escarpment, approximately 225 miles W of Cabo Colnett, Baja California, Mexico; 31°19.7′N, 119°39.2′W to 31°08.2′N, 119°35.5′W; 1968 - 2010 fathoms; December 18, 1969; R/V *Melville.*

Remarks: This species very closely resembles *Trophonopsis crystallinus* Kuroda (Kuroda, 1953: 188; figs. 3 - 4) from 97 fathoms off Miyako, east coast of Honshu, Japan. *Trophonopsis crystallinus,* however, differs in having only 2 spiral ribs on the spire and a greater number of axial lamellae (about 50). Also the interspaces between spiral ribs are noticeably greater in *T. crystallinus.*

This species is dedicated to the renowned ichthyologist Dr. Carl L. Hubbs, Professor Emeritus, Scripps Institution of Oceanography, University of California. For many years his collecting programs have obtained many new and otherwise noteworthy fishes and invertebrates. Consequently his activities have substantially increased our knowledge of Eastern Pacific mollusks.

Volutidae

Sigaluta Rehder, 1967

Sigaluta ***cukri*** Rokop, spec. nov.
(Figures *4, 5*)

Description: Shell moderately large, rather light, thin, and extremely fragile; very narrowly ovate in shape with 4 whorls. Spire obtuse with flattened whorls; protoconch bulbous, smooth. Outer lip thin and gently arcuate. Columella without thickenings or callus; columellar plicae 2 in number, very weakly elevated and strongly ascending. Completely devoid of sculpture and color markings. Overall color a very light tan with a slightly lustrous surface.

Holotype: USNM 701261, shell height 65 mm, last whorl 57 mm, aperture 49 mm, maximum diameter 24.5 mm.

Type Locality: SIO66-547. The abyssal plain WSW of Cortes Bank, approximately 225 miles W of Ensenada, Baja California, Mexico; 32°05′N, 120°29′W to 32°03′N, 120°30′W; 2064 - 2072 fathoms; December 11, 1966; R/V *Horizon.*

Remarks: The genus *Sigaluta* was erected to receive 2 specimens of an unusual species of volute collected in 208 fathoms in the South China Sea off Hong Kong which

Plate Explanation

Figure *1*: *Seguenzia* ***megaloconcha*** Rokop, spec. nov. Holotype, USNM 701260. SW of the Farallon Islands and W of Pioneer Seamount, off northern California. 1964 - 2077 fathoms. Height 9.2 mm, diameter 8.3 mm × 6.8

Figures *2* and *3*: *Trophonopsis* ***hubbsi*** Rokop, spec. nov. Holotype, USNM 701258. Off Patton Escarpment, approximately 225 miles W of Cabo Colnett, Baja California, Mexico. 1968 - 2010 fathoms. Height 19.2 mm, diameter 8.8 mm × 5.4

Figures *4* and *5*: *Sigaluta* ***cukri*** Rokop, spec. nov. Holotype, USNM 701261. WSW of Cortes Bank, approximately 225 miles W of Ensenada, Baja California, Mexico. 2064 - 2072 fathoms. Height 65 mm, diameter 24.5 mm × 1.3

Figures *6* and *7*: *Tractolira sparta* Dall, 1896. The abyssal plain WSW of Cortes Bank, approximately 225 miles W of Ensenada, Baja California, Mexico. 2064 - 2072 fathoms. Height 64 mm, diameter 20 mm × 1.3

Figure *1*

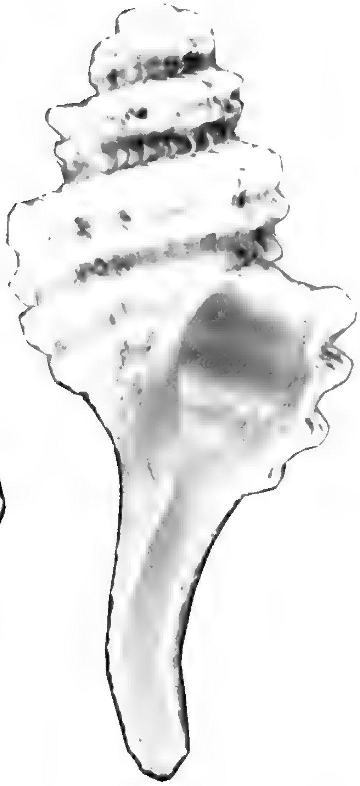


Figure *2*

Figure *3*

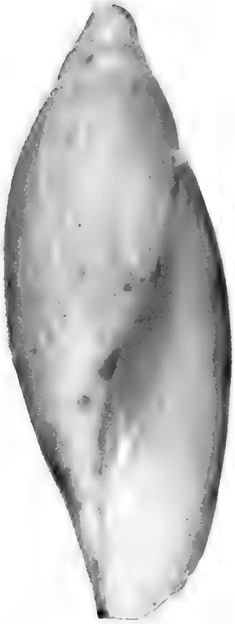


Figure *4*

Figure *5*

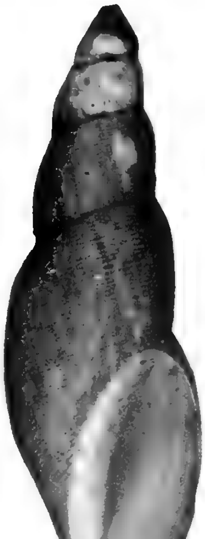


Figure *6*

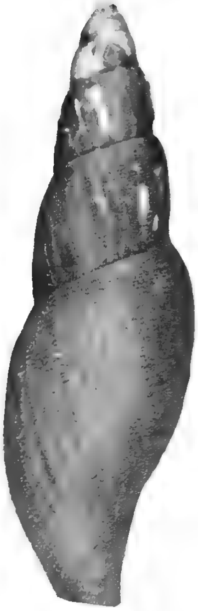


Figure *7*

Rehder (1967) described as *Sigaluta pratasensis.* Subsequently Rehder (1970) reported another, much larger specimen of *S. pratasensis* originally obtained by a fisherman in Kaohsiung, Taiwan. Consequently the genus has hitherto been represented only from the South China Sea in moderate depths. The present new species, an abyssal Eastern Pacific representative, can be readily distinguished from *S. pratasensis* by its very thin, fragile shell, much narrower shape, and weak columellar plicae.

It gives me great pleasure to name this species in the memory of a very close friend and colleague, Thomas Cukr. As a museum scientist, his endeavors in the SIO Invertebrate Collection were outstanding. He died tragically at the age of 28 in a SCUBA accident in July, 1969.

Tractolira Dall, 1896

Tractolira sparta Dall, 1896

(Figures *6, 7*)

1896. *Tractolira sparta* Dall, Proc. U. S. Nat. Mus. **18:** 13

1907. *Tractolira sparta* Dall. Dall, Smithson. Misc. Coll. **48:** 366

1908. *Tractolira sparta* Dall. Dall, Bull. Mus. Comp. Zool. **43:** 299; plt. 2, fig. 7

1943. *Tractolira sparta* Dall. Wenz, Gastropoda, Teil 1, Lfg. **6:** 1350; fig. 3824

1961. *Tractolira sparta* Dall. Wolff, Galathea Reprt. **5:** 150

1964. *Tractolira sparta* Dall. Parker, Vidensk. Medd. fra Dansk naturh. Foren. **126:** 86

1971. *Tractolira sparta* Dall. Keen, Sea shells of tropical West America: 620; fig. 1356

This is the only Recent species in the genus; one other species is known from the ?Oligocene of South America (Wenz, 1943).

Previous Records: Known only from 5 abyssal stations in tropical northern latitudes of the Eastern Pacific:

1) *Albatross* stations 3360, 3374, 3414, and 3415 in 1672 to 2232 fathoms in the region off Acapulco, Mexico to the Gulf of Panama (Dall, 1908).

2) *Galathea* station 716 at 1950 fathoms in the same Acapulco-Panama area (Wolff, 1961).

3) One SIO station approximately 100 miles W of the Islas Marías, near the mouth of the Gulf of California in 1635 to 1640 fathoms (Parker, 1964).

SIO Collection: SIO66-547. The abyssal plain WSW of Cortes Bank, approximately 225 miles W of Ensenada, Baja California, Mexico. 32°05′N, 120°29′W to 32°03′N, 120°30′W; 2064 - 2072 fathoms; December 11, 1966; R/V *Horizon*; 2 specimens.

Distribution: Off Ensenada, Baja California, Mexico to Panama; 1600 - 2200 fathoms.

Fusinidae

Fusinus Rafinesque, 1815

Fusinus rufocaudatus (Dall, 1896)

(Figures *8, 9*)

1896. *Fusus? rufocaudatus* Dall, Proc. U. S. Nat. Mus. **18:** 12

1908. *Fusinus (Exilia?) rufocaudatus* (Dall). Dall, Bull. Mus. Comp. Zool. **43:** 302; plt. 3, fig. 3

1964. *Fusinus rufocaudatus* (Dall). Parker, Vidensk. Medd. fra Dansk naturh. Foren. **126:** 86; plt. 9, fig. 4; plt. 10, fig. 4

1971. *Fusinus rufocaudatus* (Dall). Keen, Sea shells of tropical West America: 619; fig. 1350

Previous Records: Five abyssal stations in tropical northern latitudes of the Eastern Pacific:

1) *Albatross* stations 3360, 3374, 3392, and 3415 in 1270 to 1879 fathoms in the Acapulco-Panama region (Dall, 1908).

2) One SIO station approximately 100 miles W of the Islas Marías, near the mouth of the Gulf of California in 1635 to 1640 fathoms (Parker, 1964).

SIO Collection: SIO70-22. On abyssal plain off the Patton Escarpment, approximately 225 miles W of Cabo Colnett, Baja California, Mexico; 31°19.7′N, 119°39.2′W to 31°08.2′N, 119°35.5′W; 1968 - 2010 fathoms; December 18, 1969; R/V *Melville*; 1 specimen.

Distribution: Off Cabo Colnett, Baja California, Mexico to Panama; 1300 - 2000 fathoms.

Buccinidae

Morrisonella Bartsch, 1945

Morrisonella pacifica (Dall, 1908)

(Figures *10, 11*)

1908. *Leucosyrinx? pacifica* Dall, Bull. Mus. Comp. Zool. **43:** 270; plt. 12, fig. 3

1921. *Irenosyrinx pacifica* (Dall). Dall, U. S. Nat. Mus. Bull. **112:** 69

1927. *Irenosyrinx pacifica* (Dall). Oldroyd, The marine shells of the west coast of North America **2** (1): 67

1945. *Morrisonella pacifica* (Dall). Bartsch, Nautilus **59:** 23; plt. 3, figs. 11 - 14

This species was placed within the Turridae until Bartsch (1945) examined the external morphology and radula of the holotype and found it to be a unique member of the Buccinidae, erecting the genus *Morrisonella* to receive it.

Previous Records: Known only from the type (USNM 122590) from *Albatross* station 2859 off Sitka, Alaska in 1569 fathoms.

SIO Collection: SIO67-115. SW of the Farallon Islands and W of Pioneer Seamount, off northern California; 37°22′N, 123°54′W to 37°16′N, 123°53′W; 1964 - 2077 fathoms; June 14-15, 1967; R/V *T. Washington*; 11 specimens.

Distribution: Sitka, Alaska to the Farallon Islands off northern California; 1600 - 2100 fathoms.

Aulacofusus Dall, 1918

Aulacofusus dimidiatus Dall, 1919

(Figures *12*, *13*)

1919. *Aulacofusus (Limatofusus) dimidiatus* Dall, Proc. U. S. Nat. Mus. **56**: 319

1921. *Colus (Aulacofusus) dimidiatus* (Dall). Dall, U. S. Nat. Mus. Bull. **112**: 95

1925. *Colus (Aulacofusus) dimidiatus* (Dall). Dall, Proc. U. S. Nat. Mus. **66**:; plt. 2, fig. 3

1927. *Colus (Aulacofusus) dimidiatus* (Dall). Oldroyd, The marine shells of the west coast of North America **2** (1): 220; plt. 8, fig. 3

Previous Records: Known only from the type locality of *Albatross* station 3346 off Tillamook Bay, Oregon in 786 fathoms.

SIO Collections: Two abyssal stations off northern California:

1) SIO66-52. Off Eureka, California; 40°30.5′N, 125°45.2′W; 1640 - 1650 fathoms; May 22, 1966, 1 specimen.

2) SIO67-115. SW of the Farallon Islands and W of Pioneer Seamount; 37°22′N, 123°54′W to 37°16′N, 123°53′W, 1964 - 2077 fathoms; June 14-15, 1967, R/V *T. Washington*; 32 specimens.

Remarks: The general appearance of the holotype resembles that of an immature form. Examination of the soft parts of several of the newly acquired *Aulacofusus dimidiatus* reveals, however, that this appearance is characteristic of the species. An "immature" outer lip is found in all individuals, even when sexually mature.

Distribution: Off Tillamook Bay, Oregon to northern California; 790 - 2100 fathoms.

Turridae

Steiraxis Dall, 1896

Steiraxis aulaca (Dall, 1896)

(Figures *14*, *15*)

1896. *Pleurotoma (Steiraxis) aulaca* Dall, Proc. U. S. Nat. Mus. **18**: 14

1908. *Steiraxis aulaca* (Dall). Dall, Bull. Mus. Comp. Zool. **43**: 273; plt. 2, fig. 5

1943. *Steiraxis (Steiraxis) aulaca* (Dall). Wenz, Gastropoda, Teil 1, Lfg. 6: 1401; fig. 3958

1964. *Steiraxis aulaca* (Dall). Parker, Vidensk. Medd. fra Dansk naturh. Foren. **126**: 87; plt. 9, fig. 7; plt. 10, fig. 3

1971. *Steiraxis aulaca* (Dall). Keen, Sea shells of tropical West America: 713; fig. 1665

Previous Records: Known from 3 abyssal stations in the Acapulco-Panama region:

1) *Albatross* station 3415 off Acapulco, Mexico in 1879 fathoms (holotype) and station 3381 E of Malpello Island, Gulf of Panama in 1772 fathoms (Dall, 1908).

2)One SIO station off the Gulf of Tehuantepec in 1930 to 1945 fathoms (Parker, 1964).

SIO Collection: SIO67-115. SW of the Farallon Islands and W of Pioneer Seamount, off northern California, 37°22′N, 123°54′W to 37°16′N, 123°53′W; 1964 - 2077 fathoms; June 14-15, 1967; R/V *T. Washington*; 7 specimens.

Plate Explanation

Figures *8* and *9*: *Fusinus rufocaudatus* (Dall, 1896). On abyssal plain off Patton Escarpment, approximately 225 miles W of Cabo Colnett, Baja California, Mexico. 1968 - 2010 fathoms. Height 28.7 mm, diameter 9.6 mm × 3.5

Figures *10* and *11*: *Morrisonella pacifica* (Dall, 1908). SW of the Farallon Islands and W of Pioneer Seamount, off northern California, 1964 - 2077 fathoms. Height 31.1 mm, diameter 11.4 mm × 3.5

Figures *12* and *13*: *Aulacofusus dimidiatus* Dall, 1919. SW of the Farallon Islands and W of Pioneer Seamount, off northern California, 1964 - 2077 fathoms. Height 22.6 mm, diameter 11.5 mm. ×3.5

Figures *14* and *15*: *Steiraxis aulaca* (Dall, 1896). SW of the Farallon Islands and W of Pioneer Seamount, off northern California. 1964 - 2077 fathoms. Height 21.7 mm, diameter 9.8 mm × 3.5


Figure *8*


Figure *9*


Figure *10*

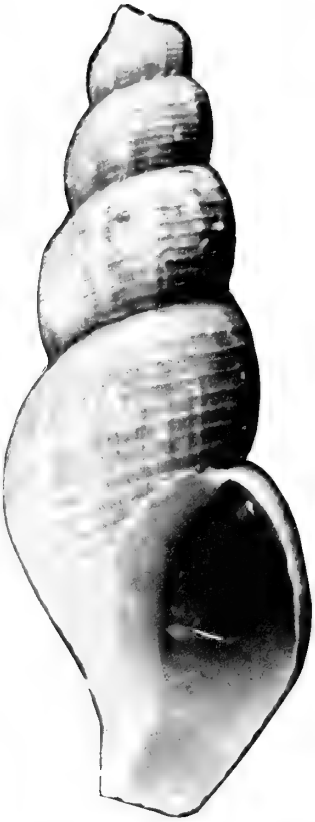


Figure *11*


Figure *12*


Figure *13*

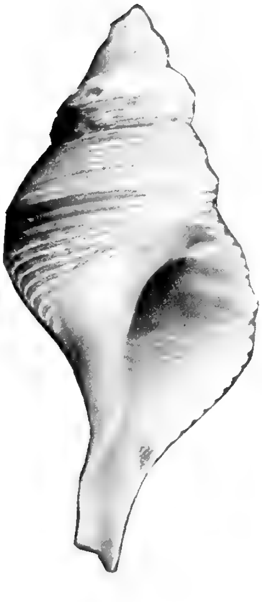


Figure *14*

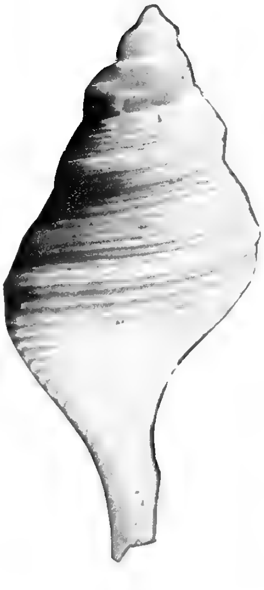


Figure *15*

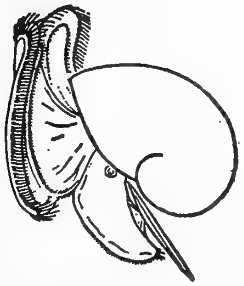
Distribution: Off northern California to Panama, 1800 to 2100 fathoms.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. James H. McLean of the Los Angeles County Museum of Natural History for making available his photographs of Dall's types for comparison and study. I am indebted to Dr. William A. Newman, Assistant Curator of Invertebrates at Scripps Institution of Oceanography, for the opportunity to study the mollusk collection. I would like to thank Charles Farwell, Curator of the Scripps Aquarium-Museum, for his assistance in preparing the photographs. My foremost indebtedness is due to the many individuals involved in the collection of the specimens discussed in this paper.

Literature Cited

BARTSCH, PAUL
1945. *Morrisonella,* a new genus of East Pacific deep sea mollusks. The Nautilus **59** (1): 23; plt. 3, figs. 11 - 14 (July 1945)
CLARKE, ARTHUR H., Jr.
1962a. Annotated list and bibliography of the abyssal marine molluscs of the world. Nat. Mus. Canad. Bull. **181:** 1 - 114; 2 maps; 1 table
1962b. On the composition, zoogeography, origin and age of the deep-sea mollusk fauna. Deep-Sea Res. **9:** 291 - 306; 4 tables; 2 charts
DALL, WILLIAM HEALEY
1896. Diagnoses of new species of mollusks from the west coast of America. Proc. U. S. Nat. Mus. **18** (1034): 7 - 20 (23 April 1896)
1907. A review of the American Volutidae. Smithson. Misc. Coll. **48** (1663): 341 - 373 (4 February 1907)
1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer *"Albatross,"* during 1891, Lieut.-Commander Z. L. Tanner, U. S. N., commanding. XXXVII. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer *"Albatross,"* from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N., commanding. XIV. The Mollusca and Brachiopoda. Bull. Mus. Comp. Zool. **43** (6): 205 - 487; plts. 1 - 22 (22 October 1908)
DALL, WILLIAM HEALEY
1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. Proc. U. S. Nat. Mus. **56** (2295): 293 - 371 (30 August 1919)
1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. U. S. Nat. Mus. Bull. **112:** 1 - 217; plts. 1 - 22 (24 February 1921)
1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. Proc. U. S. Nat. Mus. **66** (2554): 1 - 41; plts. 1 - 36 (22 September 1925)
HESSLER, ROBERT R. & HOWARD L. SANDERS
1967. Faunal diversity in the deep-sea. Deep-Sea Res. **14:** 65 - 78; 3 text figs.; 6 tables (February 1967)
KEEN, A. MYRA
1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)
KURODA, TOKUBEI
1953. On the Japanese species of *"Trophon."* Venus, the Japanese Journ. Malacol. **17** (4): 186 - 202; 1 plt. (November 1953)
LUS, V. YA.
1969. Gastropoda, Prosobranchia. *In:* V. G. KORT, ed.: The Pacific Ocean, vol. 7, Biology of the Pacific Ocean. prt. 2; The deep sea bottom fauna. Pleuston, pp. 37 - 42 Moscow ("Nauka" Publ. House) (in Russian)
OLDROYD, IDA SHEPARD
1927. The marine shells of the west coast of North America. **2** (1): 297 pp.; 22 plts. Stanford Univ. Press, Stanford, Calif.
PARKER, ROBERT H.
1964. Zoogeography and ecology of some macro-invertebrates, particularly mollusks, in the Gulf of California and continental slope off Mexico. Viddensk. Medd. fra Dansk naturh. Foren **126:** 1 - 178; 15 plts.; 29 text figs.; 7 tables (17 February 1964)
REHDER, HARALD ALFRED
1967. A new genus and two new species in the families Volutidae and Turbinellidae (Mollusca: Gastropoda) from the Western Pacific. Pacif. Sci. **21** (2): 182 - 187; 12 figs. (April 1967)
1970. Supplementary comments on deep water Volutidae from the South China Sea and South Africa. The Veliger **12** (4): 415 - 416; plt. 61 (1 April 1970)
SANDERS, HOWARD L. & ROBERT R. HESSLER
1969. Ecology of the deep-sea benthos. Science **163:** 1419 - 1424; 3 text figs.; 3 tables (28 March 1969)
WENZ, WILHELM
1943. Gastropoda. *In:* O. H. SCHINDEWOLF, ed., Handb. Paläozool. vol. **6**, prt. 1, fasc. 6: 1201 - 1506; figs. 3417 - 4211. Gebr. Borntraeger, Berlin (October 1943)
WOLFF, TORBEN
1961. Animal life from a single abyssal trawling. Galathea Reprt. **5:** 129 - 164; plts. 7 - 10 (28 December 1961)



The Genus *Chelidonura* from the Marianas Islands

(Opisthobranchia : Cephalaspidea)

BY

C. H. CARLSON AND P. J. HOFF

University of Guam

THE MARIANAS ISLANDS, a part of Micronesia, are located in the Western Pacific south of Japan and north of New Guinea. Guam, the southernmost of the Marianas, is 13°28′ north of the equator and Farallon de Pajaros, the northernmost of the Marianas, lies at 20°32′ N.

From March 1969 through July 1971 very regular collections of opisthobranchs have been made at Guam both by snorkeling and by SCUBA diving. One brief collecting trip was made to Pagan in April, 1971, and another to Anatahan (16°22′ N), Sarigan (16°42′ N), Guguan (17°19′ N) and Pagan (18°07′ N) during the latter part of June, 1971. During this time 3 species of the genus *Chelidonura* have been observed:

> *Chelidonura hirundinina* (Quoy & Gaimard, 1832)
> *Chelidonura fulvipunctata* (Baba, 1938)
> *Chelidonura inornata* (Baba, 1949).

Of the 3 species, more specimens have been found of *Chelidonura inornata* which has been seen at Guam during all months except September, October and November. *Chelidonura inornata* is numerous at Guam during the latter part of May, when the animals are frequently observed breeding. Specimens of *C. inornata* were also found at Sarigan and Pagan. Several were breeding at Sarigan during the latter part of June. *Chelidonura inornata* is most frequently encountered at depths of 20 to 30 feet (6 m to 9 m), but has also been found as deep as 65 feet (19.5 m) and on the reef top in less than 2 feet (60 cm) of water.

Chelidonura hirundinina has been found at Guam in January, February, June and July between 3 and 30 feet (90 cm and 9 m); at Sarigan in June at 20 feet (6 m); and at Pagan in April and June from 5 to 25 feet (1.5 m to 7.5 m).

Only 2 specimens of *Chelidonura fulvipunctata* have been collected at Guam, both from about 3 feet (90 cm) of water in a small boat channel which goes through the reef. One specimen was found at Pagan in June at 25 feet (7.5 m).

No *Chelidonura* were observed at Anatahan or Guguan.

Chelidonura inornata and *C. hirundinina* have previously been reported from Micronesia by MARCUS & MARCUS, 1965; *C. inornata* was found at Ifaluk, Caroline Islands and *C. hirundinina* was found in Bikini Atoll, Marshall Islands.

Literature Cited

BABA, KIKUTARÔ
1938. Opisthobranchia of Kii, Middle Japan. Journ. Dept. Agric. Kyushu Imp. Univ. 6 (1): 1 - 19; 14 text figures
1949. Opisthobranchia of Sagami Bay, collected by his Majesty the Emperor of Japan. Iwanami Shoten, Tokyo, 104 pp.; 50 plts.; 7 text figs.
MARCUS, ERNST & EVELINE DU BOIS REYMOND MARCUS
1965. Some opisthobranchia from Micronesia. Malacologia 3 (2): 263 - 286; 41 text figs. (9 December 1965)
QUOY, JEAN RENÉ CONSTANT & JOSEPH PAUL GAIMARD
1832-1834. Voyage de la corvette *l'Astrolabe* exécuté par ordre du Roi, pendant les années 1826-1829, sous le commandement de H. J. Dumont d'Urville; Mollusques. Zoologie. Paris. 2 (1): 1 - 350; Atlas (1833): plt. 66 (bis), figs. 20 - 22

Dentaliid Taxa Referred to the Siphonodentaliidae

(Mollusca : Scaphopoda)

with a Description of a New Species

BY

JOHN N. KRAEUTER

University of Georgia Marine Institute, Sapelo Island, Georgia 31327

(3 Text figures)

INTRODUCTION

WHILE EXAMINING RADULAE of the Western North Atlantic Dentaliidae for a comprehensive systematic revision, it became apparent that the subgenus *Compressidens* Pilsbry & Sharp (1897) belonged within the Siphonodentaliidae. This familial arrangement was first suggested by WATSON (1879) and most recently by EMERSON (1962), but the subgenus had been retained in the Dentaliidae pending knowledge of the radular characters of the group.

The type of *Compressidens* has been firmly established as *Dentalium pressum* Pilsbry & Sharp (1897: 123). This species was originally described as *D. compressum* WATSON (1879), but the name was preoccupied by *D. compressum* d'Orbigny (1850) and Watson's taxon was renamed by PILSBRY & SHARP (1897).

In the original description WATSON (1879) stated: "It is very possible that this [*Dentalium compressum*] may be a *Siphodentalium*, . . . " but by the time he had completed the *Challenger* Report, WATSON (1885) states: "In my Prelim. Report (loc. cit) I said that it was very possible that this might be a *Siphodentalium* . . . Mr. Dall (loc. cit) seems to have been able from his material to settle this point, for he speaks positively on the matter and says, 'it is not a *Siphonodentalium*.'" DALL (1881: 38) had stated: "this turns out not to be a *Siphonodentalium*, after all", but he gave no evidence for his decision.

When Pilsbry & Sharp renamed *Dentalium compressum* Watson (1879), they selected a new type, Academy of Natural Sciences at Philadelphia Cat. No. 72365, but Watson's type must be accepted as the holotype, thus relegating Pilsbry & Sharp's typological specimen to the status of a hypotype.

EMERSON (1962) suggested that *Compressidens* be placed within *Pulsellum*, and his suggestion is accepted pending radular studies of the Siphonodentaliidae. The following revised classification of *Pulsellum* is suggested, and the supraspecific diagnoses are modified after EMERSON (1962).

METHODS

The study is based on materials from the American Museum of Natural History (AMNH), United States National Museum (USNM), Academy of Natural Sciences at Philadelphia (ANSP), National Marine Fisheries, Woods Hole, Massachusetts (NMFS), and the Museum of Comparative Zoology (MCZ). I attempted to examine all materials in these collections. Radular and shell drawings were made with a camera lucida. All radular and shell measurements are in millimeters (mm) and centimeters (cm), respectively, and the following abbreviations are used: L – length; W – apertural width; A – arc; and T – apical width.

SYSTEMATIC ACCOUNT

Pulsellum Stoliczka, 1868

Pulsellum Stoliczka, 1868, Mem. Geol. Surv. India, Palaeontologica Indica 2 (5): 441. – COSSMANN, 1888, Ann. Soc. Roy. Malacol. Belg. 23: 15. – EMERSON, 1962, Journ. Paleontol. 36 (3): 475.

Siphonentalis G. O. Sars, 1878, Mollusca regionis Arcticae Norvegiae: Universitetsprogram for 1878: 104; Christiania.

---

[1] Based, in part, on a Ph. D. dissertation submitted to the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Contribution from University of Georgia Marine Institute, Sapelo Island, Georgia 31327.

Siphonodentalis, Clessin, 1896, Systemat. Conchyl. Cabinet, Nürnberg 6 (5): 30.

Type Species: By subsequent designation, COSSMANN (1888), *Pulsellum lofotense* (M. Sars, 1865).

Diagnosis: Shell size – small to medium, moderately to strongly curved; sculpture – lacking or rarely longitudinally ribbed; largest diameter at or immediately posteriad to oral aperture. Aperture circular or dorsoventrally compressed. Apex simple.

Remarks: This siphonodentaliid genus has been amended to include the forms transferred from the Dentaliidae.

(Compressidens) Pilsbry & Sharp

Compressidens Pilsbry & Sharp, 1897, *in* TRYON, Man. Conch. 17: 123. – EMERSON, 1962, Journ. Paleont. 36 (3): 474.

Type Species: By original designation, *Dentalium pressum* Pilsbry & Sharp, 1897.

Diagnosis: Shell size – small, moderately curved; sculpture – smooth, or rarely longitudinally ribbed, or with weak transverse growth lines. Aperture dorsoventrally compressed producing an elliptical section. Apex simple. Radula – median tooth higher than wide. Median teeth do not extend to anterior end of ribbon.

Remarks: This subgenus is redefined to include all dorsoventrally compressed forms originally assigned to *Pulsellum s. l.* Further radular and soft part studies may prove this in error, and perhaps *Compressidens* will be raised to generic status.

(Pulsellum) s. s.

Diagnosis: Shell moderately to strongly curved, slightly tapering, largest diameter at the oral aperture, typically circular in section; ... surface smooth, without sculpture other than growth lines; apex simple, without lobes or slits; foot of animal with a pedal disk as in *Siphonodentalium,* but pedal disk convex, not concave, and provided with a central filament.

Remarks: The diagnosis is quoted from EMERSON (1962), but has been amended by eliminating reference to dorsoventral compression.

Pulsellum (Compressidens) pressum (Pilsbry & Sharp)
(Figures 1a to 1f)

Dentalium compressum Watson, 1879, Journ. Linn. Soc. London 14: 516 (*non D. compressum* d'Orbigny, 1850). – DALL, 1881, Bull, Mus. Comp. Zool. 9: 38. – WATSON, 1885, *Challenger* Rept. 42: 9; plt. 1, fig. 9. – DALL, 1889, Bull. Mus. Comp. Zool. 18: 426. – DALL, 1889, Bull. U. S. Nat. Mus. 37: 76 and reprint 1903.

Dentalium (Compressidens) pressum Pilsbry & Sharp, 1897, *in* TRYON, Man. Conch. 17: 124; plt. 7, fig. 11; plt. 22, figs. 50 - 52. – HENDERSON, 1920, Bull. U. S. Nat. Mus. 111: 83; plt. 14, figs. 3, 6, 8. – EMERSON, 1952, Smithson. Misc. Coll. 117 (6): 7.

Original Description: SHELL. – Compressed between its concave and convex curves to the extent of 0.016 in.; bent, as in young shells, a little more towards the apex, and the curve greater on the convex slope, slightly carinated on each side. SCULPTURE. – Faint, but very regular, longitudinal striae, about 0.01 in. apart, apparently in the texture of the shell, which thus seems to be built up of minute, square-faced rods laid side by side. Crossing these at right angles are sharp, irregular scratches in the line of growth, nearly circular, but bent a little forwards on the concave curve. L. 0.45. B. at mouth 0.05 (least), 0.06 (greatest), apex 0.019.

It is very possible that this may be a *Siphodentalium,* as M. Gwyn Jeffreys suggested; but in the absence of the animal and the rubbed condition of both ends of the shell it is impossible to say. It resembles *S. tetragonum* Brocchi more than any other, but the want of the angles, the different character of the longitudinal striae, and above all, the compression, separate it completely. There is only the one dead discoloured and somewhat rubbed specimen.

Type Depository: British Museum, Cat. No. 1877.2.9.35.

Type Locality: North of Culebra Island, West Indies, 18°38'30" N; 65°05'30" W, 714 m.

Geographic Range: Northern limit: *Gosnold* Sta. 1854, North Blake Plateau, 617 m.[2] Southern limit: *Chain* 50 Sta. 169 off Recife, Brasil, 08°03.0' to 08°02.0' S; 34°23' to 34°25' W, 587 m, MCZ, no Cat. No.[2]

Description of *Dentalium (Compressidens) pressum* Pilsbry & Sharp, 1897

Shell small, slightly and evenly curved, thin, considerably tapering, the tube strongly compressed between its convex and concave sides, almost subangular on the lateral sides. White, somewhat shining. Sculpture: faint, low, regular, longitudinal riblets with very shallow intervals, crossed at right angles by close, "sharp, irregular scratches in the line of growth," bent forward on the concave side of the

---

[2] New record

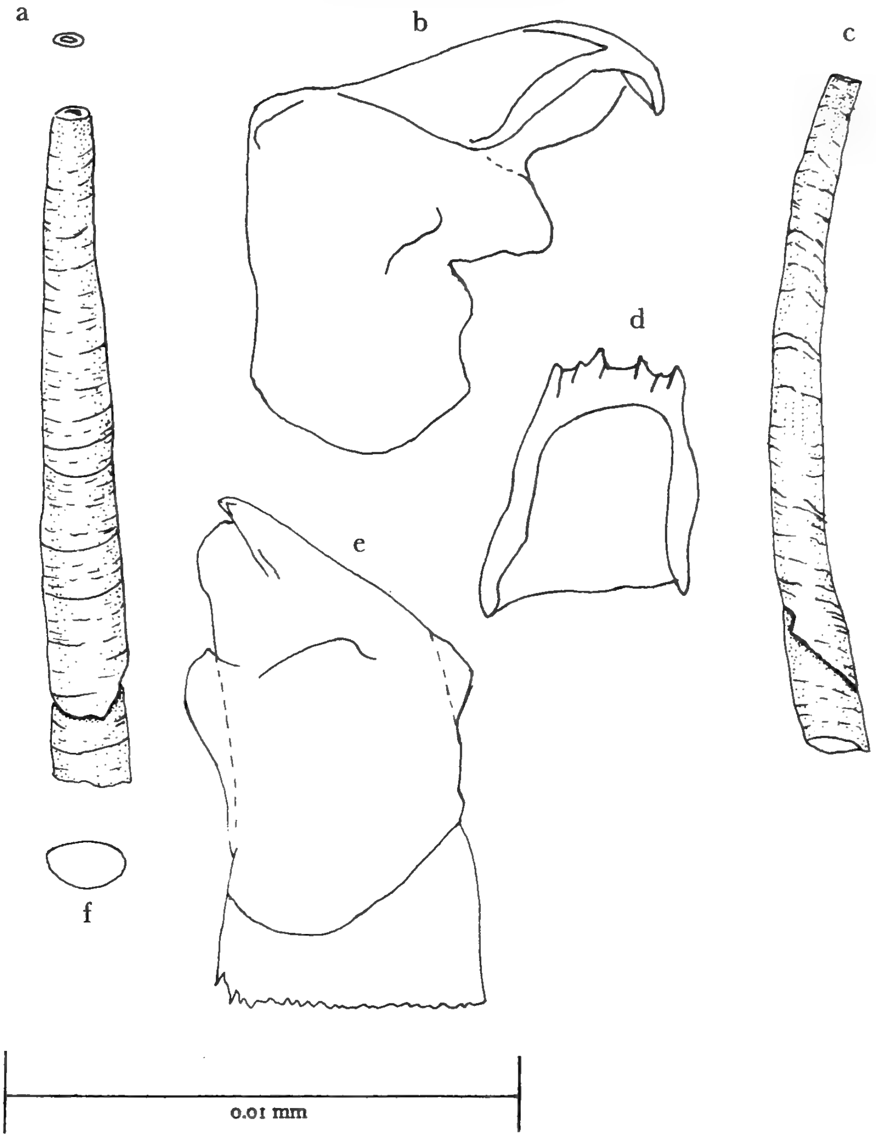


Figure 1

Shell and Radula of *Pulsellum pressum* (Pilsbry & Sharp, 1897)
a – apex and shell; b, e – lateral teeth; c – shell, side view;
d – median tooth; f – aperture; scale 0.01 mm (teeth only)
Shell: AMNH Cat. No. 146285; length 1.77 mm; width (narrow) 0.18 mm; aperture 0.10 mm

tube, which is also faintly wrinkled in the same direction toward the larger end. Aperture decidedly oblique, oval, the arc along the concave side generally less curved than the rest of the peristome. Apical orifice oval, without slit or notch.

Length 12, greatest diam. of aperture 2, least 1.75 mill., diam. at apex 0.75 mill. (S. & P. type).

Length 0.45, greatest diam. at aperture 0.06, least 0.05 inch., diam. at apex 0.019 inch = 11.25, 1.5, 1.25, 0.475 mill. (Watson's type).

Type Depository: British Museum, Cat. No. 1887.2.9.35.

Type Locality: Herein selected North of Culebra Island, West Indies, 18°38′30″ N; 65°05′30″ W; 714 m.

Remarks: I have not seen the type, but Mrs. K. M. Way at the British Museum (Natural History) has located the type lot. The type locality is set by Watson's selection of the type. Pilsbry & Sharp (1897) did not designate a type locality for *Dentalium pressum* and, to avoid confusion, it is herein selected (see above).

Radula: Median tooth is higher than wide while the lateral teeth are shortened and the cusps more prominent than the typical *Dentalium* types. Even without the altered laterals, the median radular tooth relegates this species to the Siphonodentaliidae. This taxon is the type of *Compressidens,* and as such, the subgenus must be moved also. Emerson (1962) suggested such a possibility, and he also suggested the subgenus be placed in *Pulsellum s. l.* All radular specimens were dried materials and until soft parts can be examined, Emerson's (*op. cit.*) suggestion is accepted. The outstanding feature of *Compressidens,* dorso-ventral compression, separates it as a subgenus of *Pulsellum.*

Size: The largest individual is U. S. N. M. Cat. No. 314578 and measures L 20.0, W (lesser) 2.1, A 1.0, T 0.6. The shallowest recorded specimen is U. S. N. M. Cat. No. 108161 in 172 m and the deepest is *Gosnold* Sta. 1829 in 1431 m.

Materials Examined: All materials listed by Henderson (1920), except U. S. N. M. Cat. No. 323776, were examined. All other materials in the museums were examined and the following are supplemental materials from the faunal area.

MATERIALS EXAMINED

			Location		
Catalog Numbers	Institution	Depth	North Latitude	West Longitude	Number of Individuals
1854	NMFS	617 m	33°51.0′	75°59.4′	1
1853	NMFS	853 m	33°44.7′	75°57.3′	5
1835	NMFS	766 m	33°04.3′	76°27.1′	1
1834	NMFS	881 m	32°56.2′	76°23.1′	2
1828	NMFS	881 m	32°37.0′	76°41.8′	5
1829	NMFS	1431 m	32°31.9′	76°31.8′	7
1752	NMFS	499 m	31°28.7′	79°29.0′	2
1726	NMFS	494 m	29°32.8′	80°00.0′	4
1725	NMFS	460 m	29°20.4′	80°01.3′	5
1723	NMFS	494 m	29°10.4′	79°55.3′	22
1638	NMFS	406 m	28°40.5′	79°50.4′	6
1635	NMFS	348 m	28°30.8′	79°52.0′	1
1632	NMFS	479 m	28°06.6′	79°43.2′	6
1628	NMFS	529 m	27°49.8′	79°41.4′	1
1561	NMFS	261 m	25°39.7′	80°02.7′	4
146285	AMNH	348 m	off Fowey Light, Florida		1
no Cat. No.	USNM	348 m	*Eolis* Sta. 377 off Fowey Light, Florida		2
no Cat. No.	USNM	256 m	*Eolis* Sta. 379 off Fowey Light, Florida		1
1595	NMFS	500 m	24°54.8′	80°03.5′	2
72365	ANSP	787 m	33½ mi S Rebecca Shoals, Rush		1
148327	AMNH	620 m	24°08′	82°15′	1
186630	MCZ	1051 m	23°21′	80°23′	1
no Cat. No.	MCZ	1074 m	08°03.0′ - 08°02.0′ S	34°23′ - 34°25′ W	1

Pulsellum (Compressidens) ophiodon Dall, 1881

(Figures 2a to 2g)

Dentalium ophiodon Dall, 1881, Bull. Mus. Comp. Zool. **9:** 38. – Dall, 1889, Bull. Mus. Comp. Zool. **18:** 427; plt. 26, fig. 9. – Dall, 1889, Bull. U. S. Nat. Mus. **37:** 76; plt. 26, fig. 9, and reprint 1903.

Dentalium (Compressidens) ophiodon, Pilsbry & Sharp, 1897, *in* Tryon, Man. Conch. **17:** 126; plt. 7, fig. 13; pl. 22, figs. 61, 62. – Henderson, 1920, Bull. U. S. Nat. Mus. **111:** 84; plt. 14, fig. 2. – Emerson, 1952, Smithson. Misc. Coll. **117** (6) : 7. – Turner, 1955, Deep Sea Res. **3** (Suppl.): 319, paratype in MCZ.

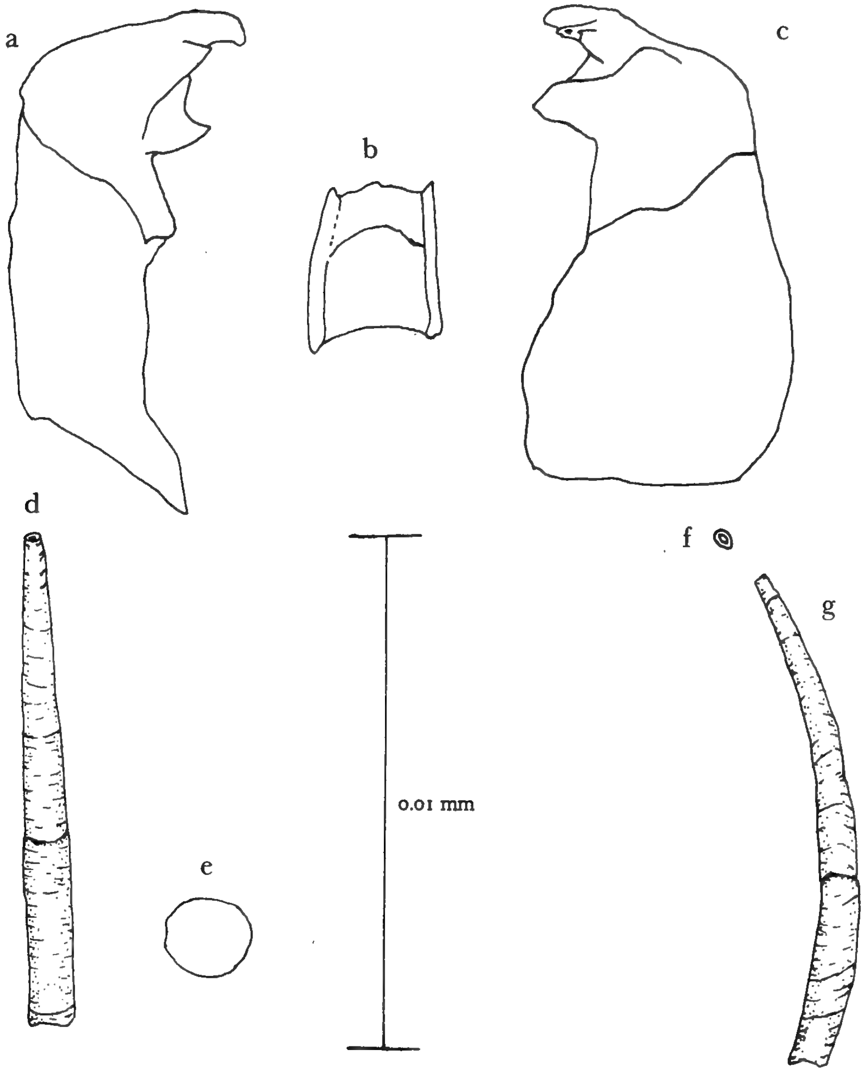


Figure 2

Shell and Radula of *Pulsellum ophiodon* (Dall, 1881)
a, c – lateral teeth; b – median tooth; d – shell; e – aperture;
f – apex; g – shell, side view; scale 0.01 mm (teeth only)
Shell: AMNH Cat. No. 148328; length 1.28 mm; width (narrow)
0.12 mm; aperture 0.13 mm

Original Description: About the same length as the last species [*Dentalium compressum*], more slender, more acute, more translucent, more curved, and without the evanescent indications of longitudinal striation; the compression results in less tendency to angulation, and there is an evident tendency, in adult specimens, for the diameter at the mouth to be somewhat less than at a short distance behind it, – a very marked distinction as between the two. The shell is quite translucent, and very thin; there is very little variation between the specimens. Lon. 12.5. Anal diam. 0.27. Major oral diam. 1.3. Minor do. 1.1 mm.

Station 19, 310 fms.; Station 20, 220 fms.; Station 21, 287 fms.

The flattening is most prominent a little way behind the mouth in the adult, and is best seen in an adolescent specimen.

Type Depository: Lectotype, U. S. N. M. Cat. No. 95344.

Type Locality: Herein selected, *Blake* Sta. 20 off Bahia Honda, Cuba, 402 m.

Geographic Range: Northern limit: Off Fernandina, Florida, 30°58′30″ N; 79°38′30″ W; 531 m; U. S. N. M. Cat. No. 314834. Southern limit: Off Lazaretto, Barbados, 238 - 256 m; U. S. N. M. Cat. No. 314835. I have not seen this specimen.

Remarks: Dall (1881) relied on comparing this species with *Pulsellum (Compressidens) pressum* for his description and thus relegated *P. (C.) ophiodon* to the Dentaliidae, but median radular tooth morphology makes this untenable. Henderson (1920) selected U. S. N. M. Cat. No. 95344 as the type and Turner (1955) followed this designation. The type locality is herein selected as indicated above.

There is no reason to separate this species from *Compressidens* at present, but it could as easily be placed in *Cadulus (Gadila)* with *Cadulus acus* Dall and *C. dominguensis* d'Orbigny. The latter species is suggestive of, but may belong to a shallower province than, *Pulsellum ophiodon*.

Radula: The median tooth is higher than wide, and it and the lateral teeth are nearly identical with those of *Pulsellum pressum*. The largest individual is L 15.5, W (lesser) 1.5 (Pilsbry & Sharp, 1897). I have not seen this specimen.

This is an outer continental shelf/upper continental slope species. The shallowest recorded specimens are from 128 to 165 m off Fowey Light, U. S. N. M. Cat. No. 314583, and the deepest are from 439 to 549 m (Emerson, 1952). Specimens from shallow waters assigned to this species are probably *Cadulus acus*.

Materials Examined: I have seen all materials listed by Henderson (1920) except U. S. N. M. Cat. No. 314835. The following are additional records from the Western North Atlantic.

MATERIALS EXAMINED

Catalog Numbers	Institution	Depth	Location		Number of Individuals
			North Latitude	West Longitude	
1728	NMFS	533 m	29°49.3′	79°57.8′	1
129436-A	AMNH		Biscayne Bay, Florida, June 1947 (sp.?)		3
148328	AMNH	128- 165 m	*Eolis* Sta. 373 off Fowey Light, Florida		1
312615	ANSP	183 m	Alligator Reef Light, Lower Florida Keys, J. Moore, 1965		40+
306338	ANSP	366- 421 m	S. W. Egmont Key, D. Steger, May 1962		60+
no Cat. No.	MCZ	218 m	80 mi S. W. Cape San Blas, Florida		1
134108	AMNH	1097-1280 m	off Fresh Creek, Andros, Bahamas		1
72366	ANSP	366 m	Campeche-Yucatan (Rush)		1
7727	MCZ	567 m	*Blake* Sta. 19 off Bahia Honda, Cuba		1
7728	MCZ	402 m	*Blake* Sta. 20 off Bahia Honda, Cuba		1
7729	MCZ	525 m	*Blake* Sta. 21 off Bahia Honda, Cuba		1
191272	MCZ	457 m	23°11′	81°55′	1

Pulsellum (Compressidens) ***wellsiana*** Kraeuter, spec. nov.

(Figures 3a to 3f)

DIAGNOSIS – Shell: Thick except at apex and aperture; delicate appearance; aperture strongly dorsoventrally compressed; ovate in cross section except for smallest tip; no keels; arc slight, greatest in posterior quarter; diameter increases rapidly, then tapers to anterior; convex side expands more rapidly than concave. Greatest diameter behind aperture. **Apex:** with slight indications of notches on convex and concave sides of young; older shells laterally excavated. **Color:** white or grayish white; translucent to semitransparent or mottled; rib surface sometimes glassy. **Sculpture:** consists of 11 primary ribs intercalated by one rib in each interspace, intercalations completed within one-third of shell length from apex; intercalated ribs expand and equal primary ribs; second intercalation of one rib in each intercostal space by three-fourths shell length from apex; secondary intercalating ribs never equal primary ribs or primary intercalating ribs. Primary ribs initially narrower than intercostal spaces; interspaces concave, gradually merging into ribs. After secondary intercalation primary ribs and primary intercalating ribs nearly equal intercostae; all ribs reach aperture. Transverse sculpture confined to fine growth lines, clearest immediately posterior to aperture.

Radula: With 17 tooth rows; median tooth higher than wide; slightly bidentate from corners, medially serrated (?); lateral teeth short, three major denticles; somewhat similar to others in subgenus.

Measurements of Holotype: L 6.2, W (narrow) 0.7, W (wide) 0.9, A 0.3, T 0.2. Largest individual: L 6.6, W (narrow) 0.7, W (wide) 0.9, A 0.4, T 0.2.

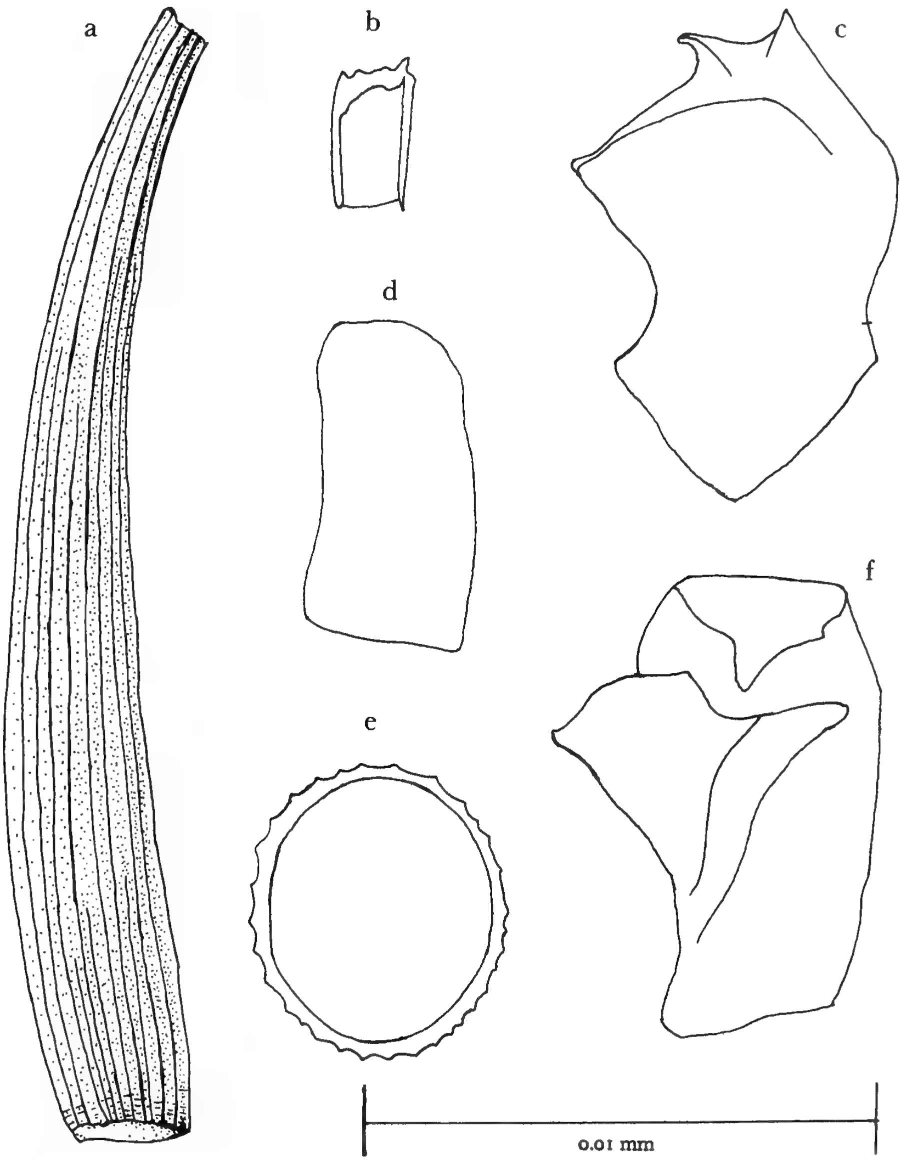


Figure 3

Shell and Radula of *Pulsellum wellsiana* Kraeuter, spec. nov.
a – shell; b – median tooth; c, f – lateral teeth; d – marginal tooth; e – aperture; scale 0.01 mm (teeth only)
Shell: Holotype: length 6.2 mm; width 0.7 mm; aperture 0.3 mm

Type Depository: Holotype ANSP Cat. No. 320993. Paratypes ANSP Cat. No. 300672, 5 individuals; only known specimens.

Type Locality: Sta. 14 James Tyler, 31 to 38 m, outer slope of beach, 1 mile W Georgetown, Grand Cayman Island, October 1964.

Remarks: This is the first siphonodentaliid, other than *Entalina,* known to possess definite ribs. ***Pulsellum wellsiana*** is included in *Compressidens* primarily because of the dorsoventral compression of the shell. It is similar to *P. ophiodon* in general shape, but is much smaller and has definite ribs. It differs from other *Pulsellum* and resembles *Cadulus* by having the greatest diameter behind the aperture. Until a revision of the Siphonodentaliidae is attempted, it seems best to modify *Pulsellum* and keep the compressed forms together.

The species is named in honor of Dr. and Mrs. Harry W. Wells.

ACKNOWLEDGMENTS

Dr. R. Turner (MCZ) and Dr. H. Sanders (WHOI) have kindly given permission to publish the southern records from the MCZ collections. All materials listed as NMFS were lent to the author by Dr. R. Wigley, NMFS, Woods Hole, Massachusetts, and his generosity is greatly appreciated. Acknowledgment must also be given to Dr. K. Boss, Dr. W. K. Emerson, Dr. R. Robertson and Dr. J. Rosewater of MCZ, AMNH, ANSP, and USNM, respectively, for their assistance, hospitality, and use of their institution's collections. Dr. Erik Rasmussen (University Zoological Museum, Copenhagen, Denmark) and Dr. W. K. Emerson have been of considerable help by critically examining the manuscript. The author, however, is responsible for any errors of commission or omission.

Literature Cited

Dall, William Healey
1881. Preliminary report on the Mollusca. *In*: Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877-79, by the United States Coast Survey steamer *"Blake"* ... Bull. Mus. Comp. Zool. 9 (2): 33 - 144 (July to December 1881)

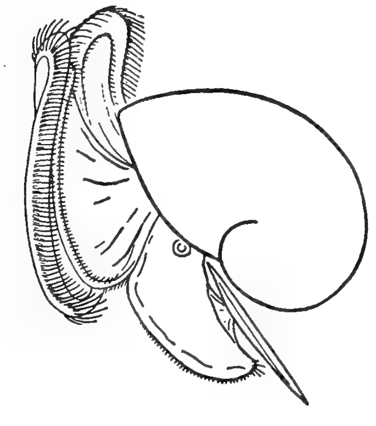
Emerson, William Keith
1962. A classification of the scaphopod mollusks. Journ. Paleont. **36** (3): 461 - 482

Henderson, J. B.
1920. A monograph of the East American scaphopod mollusks. U. S. Nat. Mus. Bull. **111**: i - vi + 1 - 177; plts. 1 - 20

Orbigny, Alcide Dessalines d'
1850. Prodrome de paléontologie stratigraphique, i No. 135, p. 233

Pilsbry, Henry Augustus & B. Sharp
1897 - 1898. Scaphopoda. *In*: G. W. Tryon, Jr., Manual of Conchology, ser. 1, **17**: xxxii, 144 [1897], 145 - 280 [1898]; plts. 1 - 39

Watson, R. B.
1879. Mollusca of the *Challenger* Expedition. Prts. 1 and 2, Preliminary report on Solenoconchia. Journ. Linn. Soc. Zool. London **14**: 506 - 529
1886. Report on the Scaphopoda collected by H. M. S. *Challenger* during the years 1873-1876. *Challenger* Reports (Zool.) **42**: i - v + 1 - 24; plts. 1 - 3



The Use of the Foot and the Captacula in the Feeding of *Dentalium*

(Mollusca : Scaphopoda)

BY

LOUIS F. GAINEY, Jr.

Department of Biological Science, Florida State University, Tallahassee, Florida 32306

(5 Text figures)

INTRODUCTION

SCAPHOPODS, COMMONLY KNOWN as Tusk Shells, are, as a class, the only exclusively infaunal marine mollusks; they are worldwide in distribution and have an elongate conical shell that is open at both ends. There have been three different feeding mechanisms described for the genus *Dentalium*. YONGE (1937) stated that detritus brought through the smaller shell opening into the mantle cavity with the respiratory current provides a source of food in addition to that obtained by the captacula. MORTON (1959) postulated that the captacula collect Foraminifera on their pad-like tips by a combination of suction and mucus. The captacula then retract into the mantle cavity where the food is transferred to the proboscis. DINAMANI (1963) described another mode of feeding in which small particles of detritus are carried up the length of the captacula by cilia. In none of these descriptions were the organisms observed feeding in their natural position, that is, buried in the substratum. Therefore, the purpose of this study was to observe the feeding of *Dentalium* while the animal was more normally oriented and to resolve the discrepancies reported by previous investigators.

MATERIALS AND METHODS

Living specimens of *Dentalium (Antalis) pseudohexagonum* Ihering (HENDERSON, 1920: 46) and *D. (Graptacme) eboreum* Conrad, 1846 (HENDERSON, *op. cit.*: 66) were dredged in the channel of the Edward Ball Marine Laboratory at Turkey Point, Franklin County, Florida. Specimens were kept in small glass containers with flat sides and filled with sand from the channel. The chambers were placed in a 2-gallon capacity aerated aquarium. Observations were made with a Wild dissecting microscope mounted horizontally. Observations of feeding behavior were made with the animal buried in the sand next to the wall of the container, although manipulation of food within the mantle cavity was observed in a living specimen which had been removed from its shell.

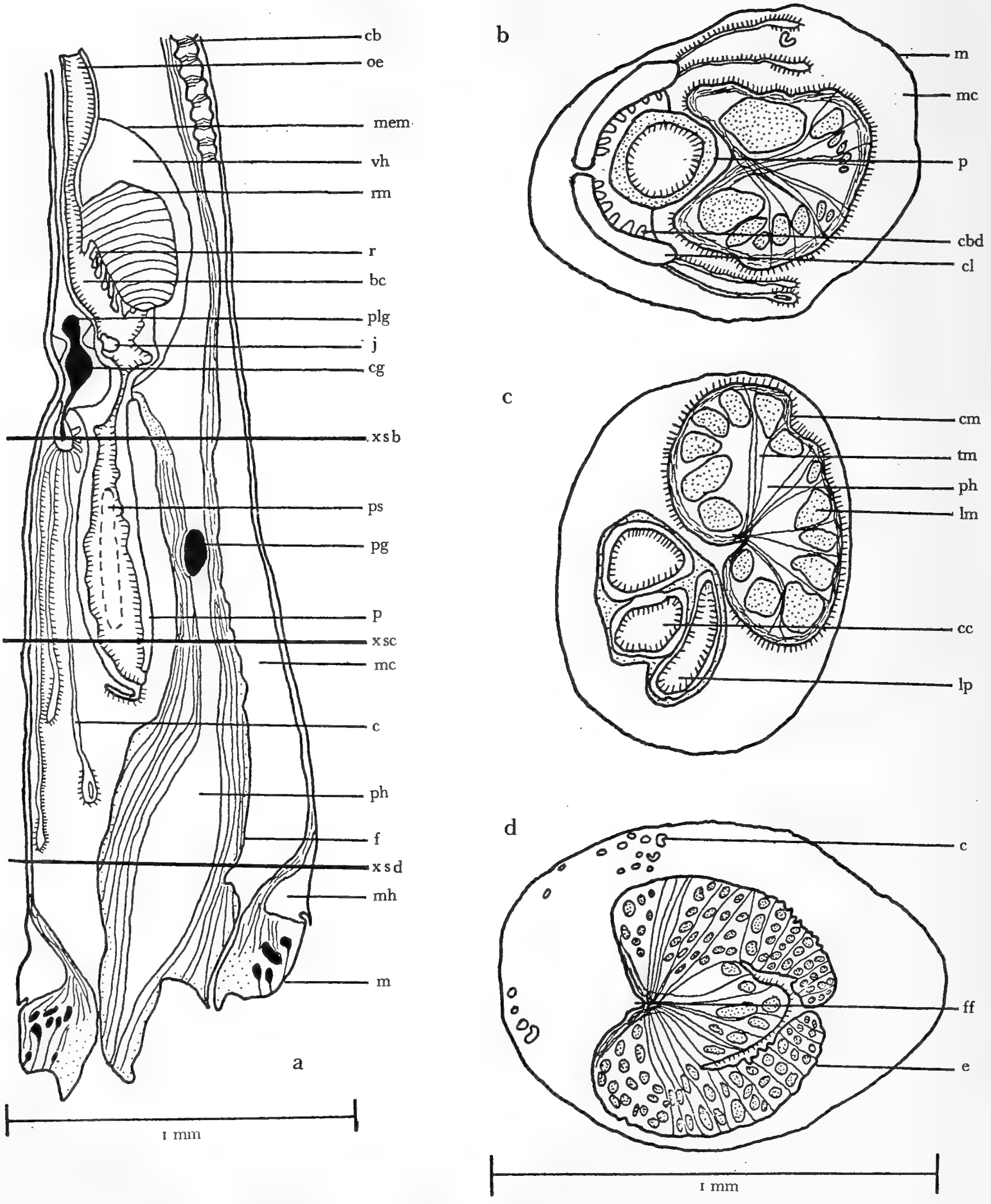
Several specimens of *Dentalium eboreum* were sectioned, and stained in Mallory's triple stain to observe general anatomy and histology. A few sections were stained with Periodic Acid Schiffs (PAS) and Alcian Blue as a test for mucus.

OBSERVATIONS

Anatomy: The foot of *Dentalium eboreum* resembles that of other members of the genus (Figure 1). There are 2 epipodial lobes (e) near the tip of the foot which assist the animal in burrowing; dorsally there is a furrow (ff) which runs from the region of the epipodia to the base of the proboscis. This furrow and the epipodia lack cilia; the rest of the foot is covered with cilia that sweep particles into the foot furrow.

The proboscis (p) extends forward from the posterior end of the mantle cavity and is dorsal to the foot. The mouth (m), located at the tip of the proboscis, is surrounded by 5 lips (l) which resemble the leaves of a tree (Figure 2). The cilia on the margins of the lips pass particles towards the groove, where cilia beat towards the mouth. Lateral to the central cavity of the proboscis (cc) is a pair of pouches (Figure 1, c). These pouches (lp) are lined by a ciliated epithelium which, according to LACAZE-DUTHIERS (1856), is secretory.

The captacula (c) arise from 2 bands of tissue (cl), in the shape of a horseshoe, above the proboscis (Figure 1, b). The tip of each captaculum is expanded and bears a trough, termed the alveolus (Figure 3, a). The entire tip


cb
oe
mem
vh
rm
r
bc
plg
j
cg
xsb
ps
pg
p
xsc
mc
c
ph
f
xsd
mh
m
a
1 mm
b
m
mc
p
cbd
cl
c
cm
tm
ph
lm
cc
lp
d
c
ff
e
1 mm

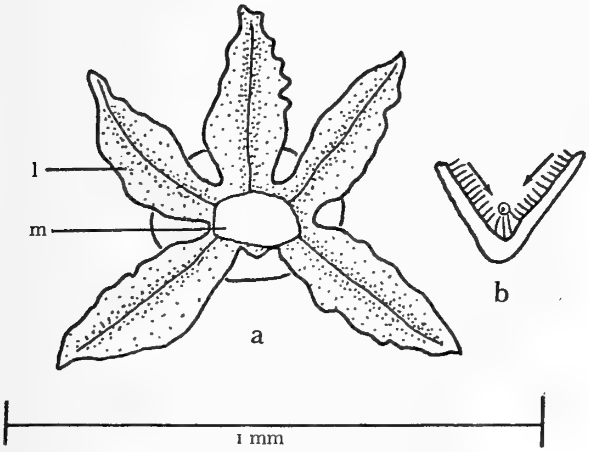


Figure 2

a: anterior view of the proboscis showing relationship of mouth (m) to the lips (l) **b:** cross section of a lip showing direction of ciliary tracts

(t) and the alveolus (a) are covered with long cilia. The filament (fil) also bears cilia which form a tract (ct) leading from the base of the alveolus. Each captaculum has a ganglion (g) in its tip which is connected to the body of the animal by a nerve passing through the center of the filament. The tip also contains a number of large mucous cells (sc) that surround the ganglion; these cells bear ducts (sd) opening into the alveolus. Staining with PAS indicated that the secretory cells produce a mucin of neutral pH containing a large number of vicinyl hydroxyl groups. Several longitudinal muscle fibers (lm) pass through the filament to the base of the tip where they branch into small bundles. The entire captaculum is permeated by connective tissue which may function to re-extend the longitudinal muscles (MORTON, 1959).

(← on facing page)

Figure 1

a: sagittal section of *Dentalium eboreum*; **b, c, d:** cross sections at levels indicated on "**a**"

bc – buccal cavity c – captaculum cb – ciliated bands
cbd – captaculum bud cc – central cavity of proboscis
cg – cerebral ganglion cl – band of tissue giving rise to captacula
cm – circular muscle e – epipodium f – foot
ff – foot furrow j – jaw lm – longitudinal muscle
lp – lateral pouch of proboscis m – mantle mc – mantle cavity
mem – membrane separating pedal and visceral hemocoels
mh – mantle hemocoel p – proboscis pg – pedal ganglion
ps – slit between lateral pouch and central cavity
ph – pedal hemocoel plg – pleural ganglion r – radula
rm – radula musculature tm – transverse muscles
vh – visceral hemocoel

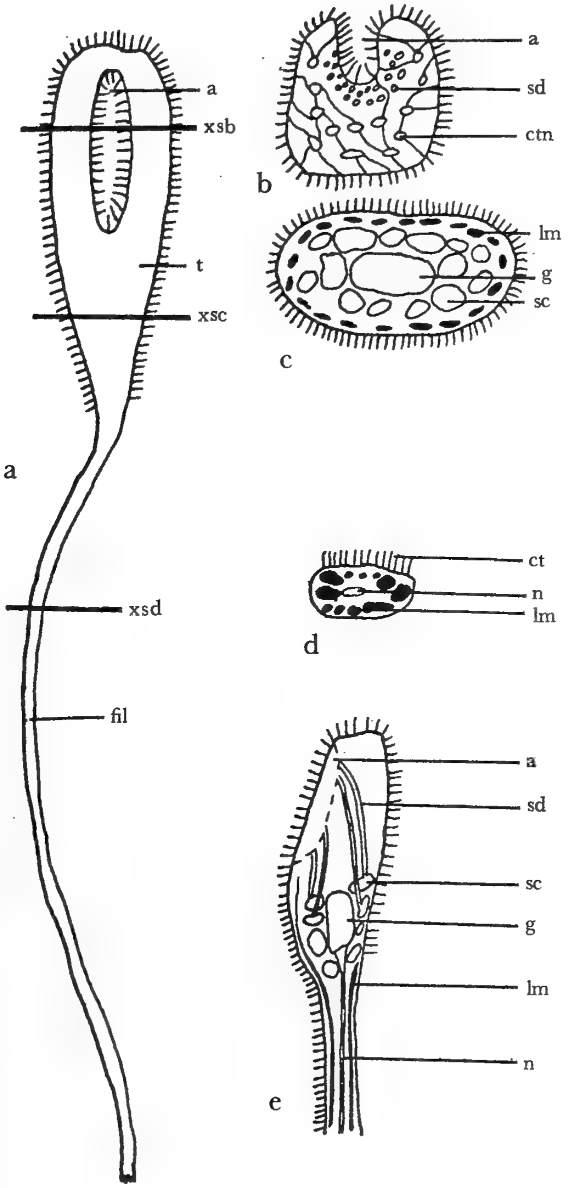


Figure 3

a: distal portion of a captaculum **b, c, d:** cross sections of a captaculum at levels indicated on "**a**"

a – alveolus ct – ciliated tract ctn – connective tissue nucleus
fil – filament g – ganglion lm – longitudinal muscle
n – nerve sc – secretory cell sd – secretory duct t – tip

Feeding: When buried in sand, both *Dentalium eboreum* and *D. pseudohexagonum* lie with the dorsal surface up. The apex of *D. eboreum* lies beneath the surface of the sand, an observation which has not been reported before, while that of *D. pseudohexagonum* lies above the surface. However, the distance which *D. eboreum* lies below the surface and *D. pseudohexagonum* above the surface is variable. A small cavity in the sand, about the size of the expanded foot, was present at the anterior end of both species (Figure 4).

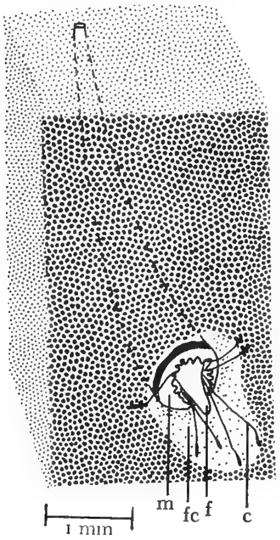


Figure 4

Diagrammatic representation of *Dentalium pseudohexagonum* in the substratum

c – captaculum f – foot fc – feeding cavity m – mantle

The foot has several functions with respect to feeding. Its primary one is burrowing downwards, which enables the animal to penetrate the substrate and obtain food (Trueman, 1967). Movement in an upward direction was also observed and has not been previously described (Figure 5). The cycle begins with the slow extension of the foot out of the mantle cavity. The second step consists of the expansion of the tip and epipodial lobes of the foot. The third step occurs as the circular muscles of the foot contract, resulting in pedal extension, the animal moving backwards (up) in the sand. This is possible since the tip of the foot and the epipodia are expanded to form a firm anchor in the substratum. The last step occurs as the tip of the foot and the epipodia are collapsed. This shifts the anchorage from the foot to the shell. This cycle was usually repeated several times; the animal would then burrow back down into the substratum, but at a different angle than before. This whole sequence moved the animal to a new feeding area.

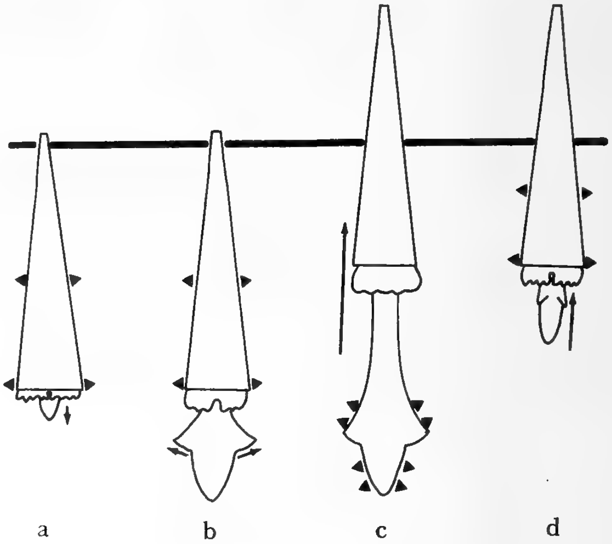


Figure 5

Diagram illustrating the steps in reverse burrowing

a: slow extension of the foot out of the mantle cavity **b:** pedal expansion to form a penetration anchor **c:** movement of shell in a posterior direction **d:** pedal retraction with the shell acting as terminal anchor. Black triangles indicate points of anchorage in substratum. Arrows indicate direction of movement.

A second function of the foot is the preparation of a feeding cavity. After the animal has burrowed, the foot makes probing movements similar to those that take place during burrowing. The probes which construct the feeding cavity, however, are perpendicular to the major axis of the body and are made in a circle around the body. These probes pack the sand; the end result is a cavity similar to that pictured in Figure 4. The rhythmical probes of the foot pass detritus back along its surface. Most of these particles fall off; however, some of them are passed to the foot furrow where they are ingested by the proboscis.

When the animal is in a feeding position, the foot makes slow rhythmical movements in and out of the mantle cavity. These movements consist of a slow extension and dilation of the foot followed by a faster withdrawal. The movements are generally slow and serve to expel water in a posterior direction through the smaller opening of the shell. Occasionally, these movements are more intense and particles of sand and detritus are sucked into the mantle cavity from the feeding cavity, where they are gathered by the captacula and the cilia on the foot. This process is similar to that observed by Dinamani (1963), although his observations were not made on a buried animal. The dorsal foot furrow functions as a collecting site for food; particles brought into the mantle cavity by the captacula were observed to fall frequently onto the foot where they were swept up by the lips of the proboscis and passed to the mouth.

The captacula have two basic modes of gathering food. When *Dentalium* was observed feeding, numerous captacula were extended from the space between the mantle and the foot. Most of these captacula probed the walls of the feeding cavity with their tips, while the filaments were stretched taut between the tips and the mantle cavity. The tips moved over the walls of the cavity with the alveoli pressed against the substratum. The alveoli opened and closed, which resulted in small particles of detritus being swept into the alveoli by cilia and passed back along the filament to the mantle cavity. Observations on a dissected living specimen suggest that once inside the mantle cavity the particles fell onto the foot or were wiped off by the lips of the proboscis or other captacula. In the latter case, the shorter captacula, which remain in the mantle cavity, pick particles off the extended captacula. Masses of detritus were observed being passed towards the mouth from one captaculum to another. These masses may have been formed by the accumulation of small particles by the shorter captacula. Periodically, one of the extended captacula was observed withdrawing with its tip wrapped around a large particle. This mechanism was proposed by Morton (1959), although he never observed its occurrence.

During burrowing, the cycle was periodically interrupted, and several captacula extended into the substratum; the animal would then prepare a feeding cavity, or burrow to a greater depth where the process was repeated. Intermittently during feeding, several captacula extended in groups into the sand above the feeding cavity. These captacula withdrew rapidly, dislodging detritus and sand from the roof of the feeding cavity. This sequence placed the particulate material in the bottom of the feeding cavity where other captacula could probe it for food.

DISCUSSION

Dentalium eboreum lies buried with the apex of the shell beneath the substratum, while *D. pseudohexagonum* is buried with the apex exposed. The situation in *D. eboreum* may conceal the animal from epibenthic predators. *Dentalium eboreum* might filter-feed from the respiratory current as proposed by Yonge (1937) for *D. entalis*; if *D. eboreum* does feed by this method, then the position of the apex beneath the substratum could be an adaptation to bring particulate matter from the surrounding sand into the respiratory current. No evidence was found, however, to suggest that either *D. pseudohexagonum* or *D. eboreum* feeds by means of the respiratory current.

Previous descriptions of burrowing accounted only for the downward movement of the animal into the substratum. With the discovery of reverse burrowing the life style of *Dentalium* comes into sharper focus. Not only can the animal burrow down into the substratum, but it can periodically move in reverse to a shallower depth, then burrow back into the substratum at a different angle or direction than before. The dynamics of moving in reverse are scarcely different from those described for forward burrowing by Trueman (1967). The foot, in forward burrowing, forms a terminal anchor which acts as a fixed point when the shell and body are retracted into the substratum; the shell forms a penetration anchor which acts as a fixed point during extension of the foot. In reverse burrowing, the foot forms a penetration anchor, while the shell forms a terminal anchor.

Dinamani (1964) suggested that the feeding cavity serves primarily as a space for food to filter in from the surface. I propose that its major function is to provide an exposed surface for the captacula to browse upon. In order for the ciliary mechanism of captacular feeding to be functional, the captacula have to remain straight. When extended into the sand the captacula are curved and twisted and are non-functional as ciliary feeding organs. Acquisition of larger particles by the tips of the captacula was not observed among those captacula which were extended into the sand. Presumably there is too much resistance encountered from sand grains for a captaculum to retract with a large particle on its tip. The predominance of feeding by means of ciliary tracts over the capture of large particles by the alveoli is most likely a function of the concentrations of the various types of food, smaller particles being dominant in the sand used in the observation tanks.

In addition to their role as feeding organs the captacula also have a sensory function. This was deduced from the presence of a ganglion in the tip of each captaculum and the captacular probing movements described in conjunction with burrowing. These probes could test the suitability of the substrate for feeding. If food is present, the animal will stop burrowing and prepare a feeding cavity; if food is lacking, the animal will burrow to a greater depth.

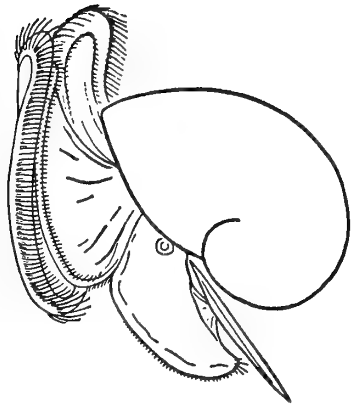
The presence of two different feeding organs, the foot and the captacula, raises the question as to which is the primitive feeding organ. The major function of the foot is burrowing. The role of the foot in feeding may have evolved concurrently with the evolution of the feeding cavity. Although the captacula originally may have been sensory tentacles, they are probably the primitive feeding organs in the Scaphopoda. The capture of large particles by the captacula is perhaps the more primitive captacular feeding mechanism as suggested by the presence of the well developed radula for handling such particles. Ciliary feeding on small particles may have evolved as an adaptation to living in sand containing a high percentage of detritus. In conclusion, observations of *Dentalium eboreum* and *D. pseudohexagonum* clearly show that they feed by a combination of captacular mechanisms rather than a single one as implied by the works of Morton (1959) and Dinamani (1963).

ACKNOWLEDGMENT

I would like to thank Dr. Charles R. Stasek for his help and suggestions in preparing the manuscript and figures.

Literature Cited

Dinamani, P.
1963. Feeding in *Dentalium conspicuum*. Proc. Malacol. Soc. London **36:** 1 - 5
1964. Burrowing behavior of *Dentalium*. Biol. Bull. **126:** 28 - 32
Henderson, John B.
1920. A monograph of the East American scaphopod mollusks. U. S. Nat. Mus. Bull. **111:** 1 - 177
Lacaze-Duthiers, Felix Joseph Henri de
1856. Histoire de l'organisation et du developpement du Dentale. Ann. Sci. Nat. Zool. 6 (4): 225 - 281
Morton, John Edward
1959. The habits and feeding organs of *Dentalium entalis*. Journ. Mar. Biol. Assoc. U. K. **38:** 225 - 238
Trueman, E. R.
1967. The burrowing process of *Dentalium* (Scaphopoda). Journ. Zool. **154:** 19 - 27
Yonge, Charles Maurice
1937. Circulation of water in the mantle cavity of *Dentalium entalis*. Proc. Malacol. Soc. London **22:** 333 - 336



A Systematic Note on *Ocenebra poulsoni* Carpenter, 1865

BY

GEORGE E. RADWIN

San Diego Natural History Museum, San Diego, California 92112

(6 Text figures)

Few West American muricid species have defied satisfactory generic placement as stubbornly as *Ocinebra poulsoni* Carpenter, 1865 (Figure 1). This taxon has been alternately associated with *Ocenebra* and *Tritonalia* because of the nomenclatural confusion surrounding these two names. It is, however, a matter of record that the most frequent name combination for it has been *Ocenebra poulsoni.*

In the course of work on the radulae of muricid species and genera, and on an illustrated guide to that family,

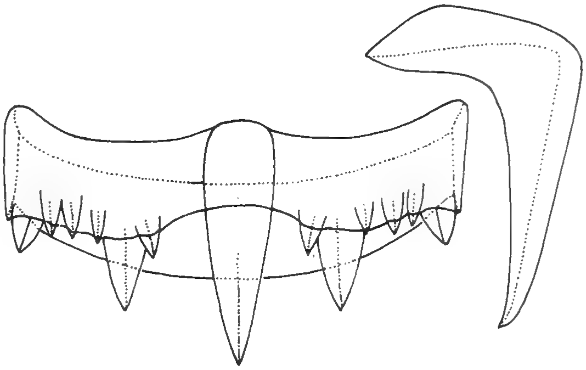


Figure 2

Two-thirds of a radular row of *"O." poulsoni* Cpr., 1865

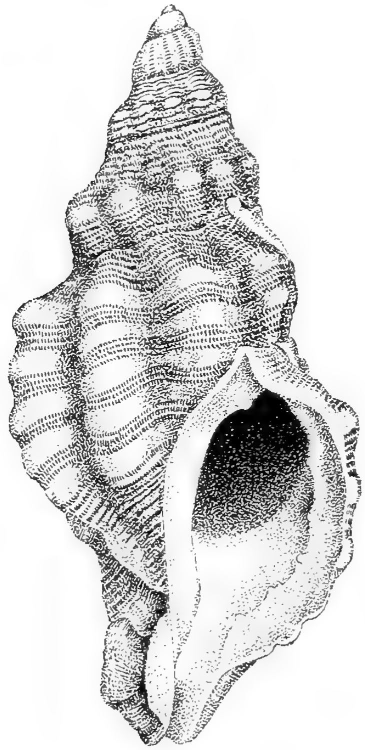


Figure 1

Shell of *Ocenebra poulsoni* Carpenter, 1865 (SDSNH 42372)

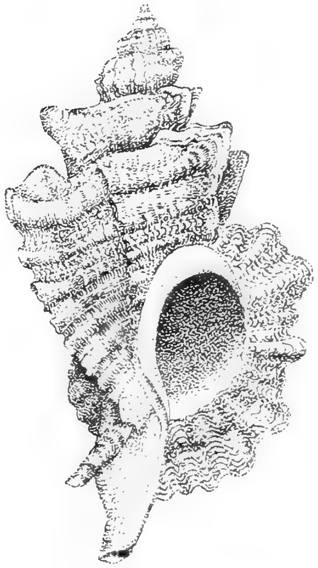


Figure 3

Shell of *Ocenebra erinaceus* (Linnaeus, 1758) (Coll. D'Attilio) an attempt was made to assign this species to an appropriate genus. The radula is unquestionably ocenebrine (Figure 2), but the shell appears to differ substantially from typical *Ocenebra.*

The type species of *Ocenebra* (*O. erinaceus* (Linnaeus, 1758)) (Figure 3) typically has a moderately large (40 to 45 mm), broadly trivaricate shell with a sealed siphonal canal and a strongly scabrous shell surface. In contrast to this, *O. poulsoni* has a somewhat larger (50 to 60 mm), relatively slender, fusiform shell with an open siphonal canal, varices that are erratic in number and placement, and very fine sculpture consisting primarily of numerous, finely incised grooves and fine axial lamellae. This imparts a microscopically scabrous texture to the shell surface.

The obvious distinctness of *Ocenebra poulsoni* from all other West American ocenebrine species had led to its comparison with other muricids encountered in the preparation of an impending worldwide guide to the family. The only species with a shell of suitable size, form and other features is *Ergalatax contracta* (Reeve, 1846) (Figure 4). An examination of the radula (Figure 5), however, has indicated no close relationship between the two species.

This suggested the necessity of a new generic taxon for this species until I became aware of two papers that bear on the subject. These are by Dall (1898) and Lowe (1931).

In the first of these papers Dall described a new species, *Fusus roperi* (Figure 6) and, although commenting on its resemblance to *Ocenebra* and *Muricidea,* concluded by erecting for it a new "section," *Roperia.* Dall's comparisons with *Fusus colus, Sipho* and *Chrysodomus,* although causing him to separate the species in question from members of these genera, are indicative of his assumption of

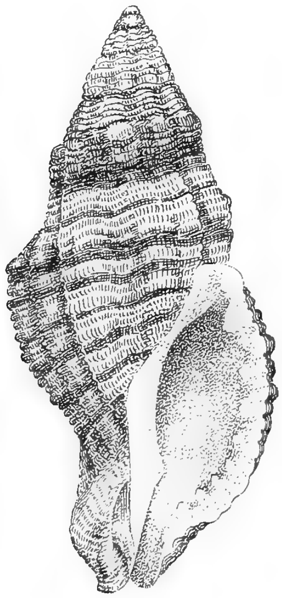


Figure 4

Shell of *Ergalatax contracta* (Reeve, 1846) (Coll. D'Attilio)

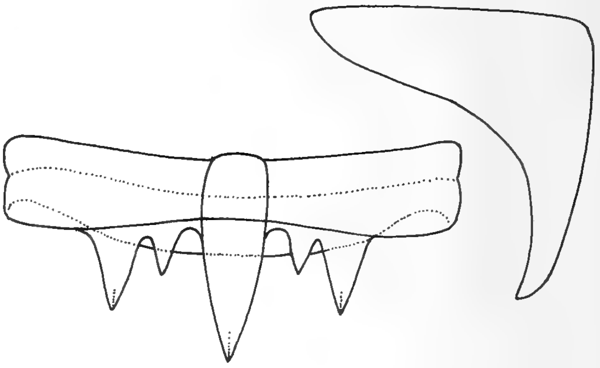


Figure 5

Two-thirds of a radular row of *Ergalatax contracta* (Reeve, 1846)

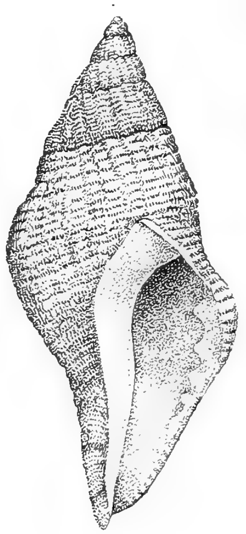


Figure 6

Shell of juvenile specimen of *"O." poulsoni* Cpr., 1865 (SDSNH 50738) [1]

---

[1] Figure 6 represents a juvenile specimen of the approximate size and age of Dall's holotype of *Roperia roperi.* I have seen this holotype and the figured specimen (SDSNH 50738) differs from it only in possessing teeth on the inner surface of the outer lip and in its locality.

a buccinid placement for the genus. Somewhat mysteriously, Dall's holotype remained the unique specimen of *Roperia roperi* for 33 years, in spite of its well-collected type locality (San Pedro, California).

In the second paper (LOWE, 1931) Dall's species was conclusively shown to be synonymous with *Tritonalia poulsoni* (Carpenter, 1865), Dall's confusion apparently resulting from his misinterpretation of a juvenile as an adult. This successfully solved the problem of the identity of *Roperia roperi,* but did nothing to ascertain the appropriate generic placement of "*Ocenebra*" *poulsoni.*

At the present time "*Ocenebra*" *poulsoni* cannot be assigned to any of the generally accepted West American muricid genera. In spite of this, there appears to be no need to erect an entirely new generic taxon for the species. The systematic placement of "*O.*" *poulsoni* can be expressed as follows:

Roperia Dall, 1898. Type species: *Roperia roperi* Dall, 1898 (=*Ocinebra poulsoni* Carpenter, 1865), by original designation.

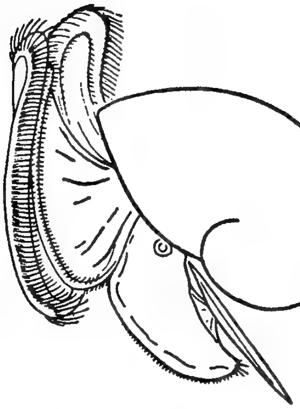
Thus the correct combination of names for this species is *Roperia poulsoni* (Carpenter, 1865).

ACKNOWLEDGMENTS

Many thanks are due Mr. Anthony D'Attilio for his illustrations and Alicia Cuarenta and Grace M. Boyne for typing drafts of the manuscript.

Literature Cited

DALL, WILLIAM HEALEY
1898. On a new species of *Fusus* from California. The Nautilus 12 (1): 4-5 (1 May 1898)
LOWE, HERBERT NELSON
1931. What is *Roperia roperi* Dall? With notes on Turridae and Columbellidae. The Nautilus 45 (2): 51-52



Aerial and Aquatic Respiratory Responses to Temperature Variations in *Acmaea digitalis* and *Acmaea fenestrata*

BY

SHARON ROSE DORAN

Department of General Science, Oregon State University, Corvallis, Oregon 97331

AND

DONALD S. McKENZIE

Department of Biology, Lewis and Clark College, Portland, Oregon 97219

(2 Text figures)

INTRODUCTION

Acmaea digitalis Eschscholtz, 1833 and *Acmaea fenestrata* (Reeve, 1855), two limpets commonly found on the Pacific coast, are most abundant at intertidal levels vertically separated by approximately 4 feet. Exposure periods vary widely, suggesting different respiratory responses for each species.

A number of recent workers have attempted to correlate intertidal location and distribution with aerial and aquatic respiratory activity: SANDEEN, STEPHENS & BROWN (1954), SANDISON (1966), MICALLEF & BANNISTER (1967), SANDISON (1967), BALDWIN (1968) and KINGSTON (1968). Several have worked specifically with the ecology of *Acmaea*: TEST (1945), SHOTWELL (1950), FRANK (1965), JESSEE (1968), MILLARD (1968), and MILLER (1968).

Acmaea fenestrata is generally submerged during both high tides and one low tide in the Pacific coast mixed tidal cycle, while higher level *A. digitalis* are exposed during both low tides. The purpose of this study was to compare aerial and aquatic rate of respiration of the two species, within a normal summer field temperature range, 8.5° C to 31° C (KENNY, 1968).

METHODS AND MATERIALS

Animals were collected weekly from rocks south of Yaquina Head, Oregon (44° N longitude and 124° W latitude). Collections were made during a two-hour period, one hour preceding and one hour following the lower low tide of the day during May and June 1970. *Acmaea digitalis* were taken from the +4 to the +6 foot level and *A. fenestrata* from the −1 to the +2 foot level. They were immediately transferred to containers of filtered, uv-treated sea water and maintained at 12° C in a darkened incubator for at least 22 hours. Forty-two animals (3 per vessel) were placed in 14 (15 ml GME - 130) reaction vessels in a Gilson Differential Respirometer (Model GRP 14) (GILSON, 1963). The respirometer measured oxygen consumption and allowed for carbon dioxide absorption by means of 0.2 ml 10% KOH in vessel side arms closed off by a standard taper 7/15 venting plug.

Temperature equilibrations for 4 temperatures (10°, 15°, 20°, and 25° C consecutively) were conducted for 2 hours prior to taking respirometer measurements and readings (in microliters – μl) were made at $\frac{1}{2}$-hour intervals following equilibration. Respiratory rates were based on the total oxygen consumption over the 2-hour period.

The Oregon State University Control Data Corporation (Model 3300) Computer was used for all statistical analyses.

One-half of the specimens were tested for all 4 temperatures, during a 17-hour period (0700 to 2400) while the remaining specimens were tested in 2 8-hour periods. The two lowest temperatures were used on the first day and the two highest temperatures the next to facilitate detection of possible temperature stress.

Ten animals of each species were exposed to aerial and aquatic conditions. Aerial conditions were simulated by first shaking the organisms to remove excess water and then placing them on dry powder paper in dry vessels. Filtered, uv-treated sea water covered the animals when aquatic oxygen consumption was determined. Experimental trials were repeated 3 times with 30 individuals of each species used at each temperature and in each of the 2 experimental conditions. The reaction vessels were agitated at 90 oscillations per minute during each trial.

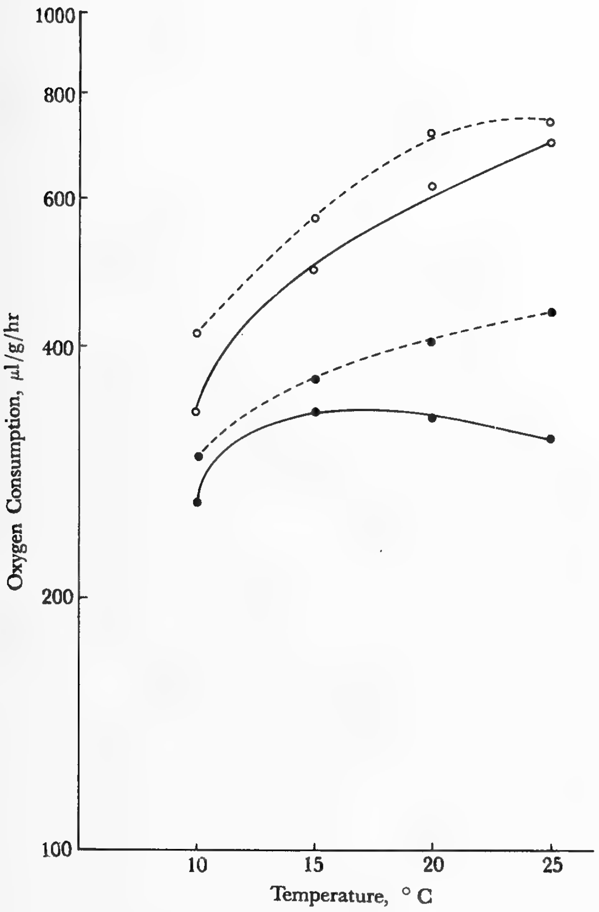


Figure 1

Oxygen consumption of *Acmaea digitalis* at temperatures between 10° C and 25° C. Average rates of oxygen uptake in air (○) and in water (●). Eight-hour trials are represented by broken lines and 17-hour trials by solid lines.

After a trial, animals were removed from their shell and weighed (wet weight) on an H16 Mettler balance. They were then dried at 60° C for 24 hours and reweighed (dry weight).

RESULTS

Mean respiratory rates of the two species are shown separately in Figures 1 and 2. Four 30-minute intervals, taken consecutively during a 2-hour recording period were used to determine the mean respiratory rate. Table 1 includes the means and standard deviations.

The aerial respiration rate for *Acmaea digitalis* was consistently higher than the aquatic respiratory rate. Aerial consumption increased with rising temperatures. The rate of increase was most rapid between 10° C and 15° C and leveled off slightly from 20° C to 25° C. Aquatic consumption rates rose similarly during the 8-hour trials but at reduced levels, while during the 17-hour trials rates leveled off or decreased slightly between 15° C and 20° C.

There were no significant rate differences between aquatic and aerial respiration in *Acmaea fenestrata.* Oxygen consumption, for this species, was highest at 15° C and slowly decreased with increasing temperatures.

DISCUSSION

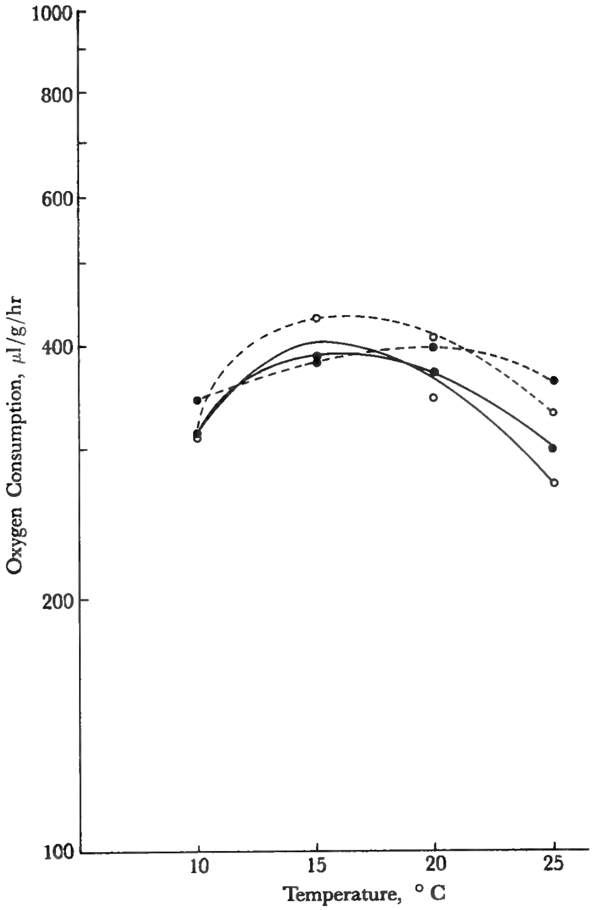
Data were statistically analyzed by an F-test based on values from an n-factorial analysis of variance computer program where n = 4. The 4 factors used in the analysis were: 1) the 10 replications; 2) the 2 experimental conditions – aerial and aquatic; 3) the 2 species; and 4) the 4 temperatures. Table 2 shows the F-test values used to determine statistical significance. The analysis showed significant differences in aerial and aquatic respiratory rates for *Acmaea digitalis* and no significant differences in *A. fenestrata.*

The respiratory rate of *Acmaea digitalis* during aerial conditions was significantly higher than under aquatic conditions, and respiratory peaks for each condition occurred at different temperatures (Figures 1 and 2). Aquatic rates leveled off or declined between 15° C and 20° C during the 8-hour trial. Higher temperatures may induce heat coma in this species. The occurrence of heat coma (Sandison, 1967) may explain the difference between the aerial and aquatic respiratory responses, or the difference may simply reflect an ability of the organism

Table 2

An Analysis of Variance of the Effect of Temperature and Aerial and Aquatic Conditions on *Acmaea digitalis* and *Acmaea fenestrata*

Source of Variation	Test Value	Significance Values	Degrees of Freedom	Probability
8 hour trial				
CS	63.23	3.91	1, 144	0.05
ST	10.84	2.67	3, 144	0.05
CT	3.00	2.67	3, 144	0.05
CST	2.63	2.67	3, 144	0.05
17 hour trial				
CS	84.93	3.91	1, 144	0.05
ST	17.86	2.67	3, 144	0.05
CT	6.03	2.67	3, 144	0.05
CST	10.43	2.67	3, 144	0.05
C – Condition		S – Species	T – Temperature	



(← adjacent column)

Figure 2

Oxygen consumption of *Acmaea fenestrata* at temperatures between 10° C and 25° C. Average rates of oxygen uptake in air (○) and in water (●). Eight-hour trials are represented by broken lines and 17-hour trials by solid lines.

Table 1

Mean Respiratory Rates for *Acmaea digitalis* and *Acmaea fenestrata* based on the μl of Oxygen consumed per gram (dry weight) per hour (μl/g/hr). The Means and Standard Deviations are included for each Temperature.

8 hour trial	Condition	Species	10° C	15° C	20° C	25° C
	aerial	*Acmaea digitalis*	413.45 ± 49.98	561.35 ± 64.36	718.96 ± 112.09	730.86 ± 96.82
	aerial	*Acmaea fenestrata*	307.84 ± 85.38	430.66 ± 90.49	404.41 ± 92.81	331.44 ± 103.35
	aquatic	*Acmaea digitalis*	293.08 ± 79.23	361.85 ± 113.14	404.29 ± 121.86	437.24 ± 102.42
	aquatic	*Acmaea fenestrata*	341.88 ± 65.92	378.39 ± 77.09	396.14 ± 108.60	361.36 ± 86.05
17 hour trial						
	aerial	*Acmaea digitalis*	332.94 ± 30.01	494.64 ± 39.92	621.38 ± 49.92	695.56 ± 63.77
	aerial	*Acmaea fenestrata*	308.93 ± 60.06	431.76 ± 64.04	350.37 ± 106.27	273.26 ± 104.63
	aquatic	*Acmaea digitalis*	262.21 ± 80.12	333.68 ± 121.16	326.44 ± 106.66	309.20 ± 98.36
	aquatic	*Acmaea fenestrata*	313.71 ± 69.80	388.56 ± 85.48	374.83 ± 75.25	301.11 ± 42.37

to respire more actively during aerial conditions. The principal difference between trials of different time duration was shown in the aquatic response (Figure 1). This difference could be influenced by a combination of temperature effect and duration of exposure (Orr, 1955). *Acmaea digitalis* may be exposed each day to desiccation and abrupt temperature changes (Frank, 1965). This fact was the rationale for short acclimation periods.

Hardin (1968) indicated 32° C as lethal for *Acmaea digitalis*, a value greater than our findings. However, its apparent heat coma temperature was consistent with our data (Hardin, *op. cit.*).

Evans (1948) observed normal metabolic activity in *Patella* sp. up to 30° C. Sandison (1967) found littoral marine gastropods tolerant of 6.5° C to 22.5° C; however, between 22° C and 25° C, respiratory rates increased or became very irregular (Newell & Northcroft, 1967). *Monodonta turbinata* (Micallef & Bannister, 1967), *Patella aspera* and *P. vulgata* (Davies, 1966) show irregular respiratory rates between 25° C and 33° C.

In contrast, *Acmaea digitalis* and *A. scabra* have greater oxygen consumption during aquatic conditions (Baldwin, 1968). One factor that may explain the divergent results between Baldwin's report and our findings is the difference in experimental conditions. To simulate aerial conditions, Baldwin exposed his organisms to greater desiccation. Field observations indicate that the area under the limpets' shells always retains sea water against the rock substrate. Thus, it seems that Baldwin's procedure which eliminates this type of protection would surpass the normal desiccation caused by exposed rock.

Desiccation from exposure is an important factor for limpet survival in the mid-littoral zone (Stephenson & Stephenson, 1949). Because they are situated above the lower high tide line, many individuals are exposed twice as long per day as if they were below this level (Shotwell, 1950). High surf activity and a small amount of shade most accurately characterize their microhabitat. The thick shell with a high apex, narrow ventral aperture, and relatively large water storage capacity, enables *Acmaea digitalis* to withstand drying. Behavioral adaptations such as increased nighttime activity on submerged or dampened rocks, further facilitate existence in their harsh environment.

Acmaea fenestrata, in contrast to *A. digitalis*, occupies a zone subject to shorter exposure periods and lower temperatures. Its thin, smooth shell has an almost circular ventral aperture. It follows the receding tide, and wedges its knife-like shell into the sand around and under smooth rocks where it remains moist until the return of the tide. *Acmaea fenestrata* is unique among limpets in this behavioral adaptation (Test, 1945).

The data from *Acmaea fenestrata* concur with a statement by Prosser (1950) that the thermal properties of water protect and, at the same time, fix the temperature limits of aquatic animals.

SUMMARY

Mean respiratory rates of *Acmaea digitalis* were similar to those of *A. fenestrata* at 10° C and 15° C. Significant differences occurred at 20° C and 25° C. These higher temperatures appeared to exceed the tolerance of *A. fenestrata*.

Aerial and aquatic respiratory rates did not differ significantly for *Acmaea fenestrata*. Our results indicate that 15° C is the highest tolerable temperature which is within the average summer water temperature range of 8.5° C to 16° C (Kenny, 1968).

ACKNOWLEDGMENTS

We thank Dr. Michael C. Mix for reading the manuscript and Dr. Roger Peterson and Gerald Caton for statistical information in analysing data. Also, we wish to thank Janice Sivula and Martin Ikkanda for their aid in collecting animals.

Various aspects of the research have been aided by a grant from the General Research Fund by the Graduate Council of Oregon State University.

Literature Cited

Baldwin, Simeon
1968. Manometric measurements of respiratory activity in *Acmaea digitalis* and *Acmaea scabra*. The Veliger **11** (Supplement): 79-82; 3 text figs.; 2 tables (15 July 1968)

Davies, Peter Spencer
1966. Physiological ecology of *Patella*. I. The effect of body size and temperature on metabolic rate. Journ. Marine Biol. Assoc. U. K. **46**: 647 - 658

Evans, Ronald G.
1948. The lethal temperature of some common British littoral gastropods. Journ. Animal Ecology **17**: 165 - 173

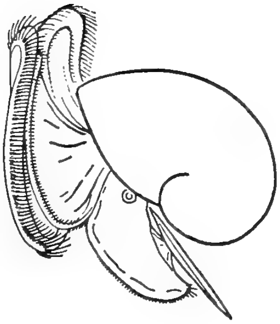
Frank, Peter Wolfgang
1965. The biodemography of an intertidal snail population. Ecology **46** (6): 831 - 844; 8 figs.; 6 tables

Gilson, W. E.
1963. Differential respirometer of simplified and improved design. Science **141**: 531 - 532

Hardin, Dane D.
1968. A comparative study of lethal temperatures in the limpets *Acmaea scabra* and *Acmaea digitalis*. The Veliger **11** (Supplement): 83 - 87; 4 text figs. (15 July 1968)

Jessee, William Floyd
1968. Studies of the homing behavior in the limpet *Acmaea scabra* (Gould, 1846). The Veliger **11** (Supplement): 52 - 54; 4 tables (15 July 1968)

Kenny, Ron
1969. Growth characteristics of *Acmaea persona* Eschscholtz. The Veliger **11** (4): 336 - 339; 4 text figs. (1 April 1969)
Kingston, Roger S.
1968. Anatomical and oxygen electrode studies of respiratory surfaces and respiration in *Acmaea*. The Veliger **11** (Supplement): 73 - 78; plt. 7; 6 text figs. (15 July 1968)
Micallef, H. & W. H. Bannister
1967. Aerial and aquatic O_2 consumption in *Monodonta turbinata* (Mollusca : Gastropoda). Journ. Zool. London **151**: 479 - 482
Millard, Carol Spencer
1968. The clustering behavior of *Acmaea digitalis*. The Veliger **11** (Supplement): 45 - 51; 4 text figs.; 1 table (15 July 1968)
Miller, Alan Charles
1968. Orientation and movement of the limpet *Acmaea digitalis* on vertical rock surfaces. The Veliger **11** (Supplement): 30 - 44; 18 text figs.; 4 tables (15 July 1968)
Newell, R. C. & H. R. Northcroft
1967. A reinterpretation of the effect of temperature on the metabolism of certain marine invertebrates. Journ. Zool. London **151**: 277 - 298
Orr, Paul R.
1955. Heat death. I. Time-temperature relationships in marine animals. Physiol. Zool. **27**: 290 - 294
Prosser, Clifford Ladd
1955. Physiological variations in animals. Biol. Rev. Cambridge Philosoph. Soc. **30** (3): 229 - 263
Sandeen, M. I., G. C. Stephens & F. A. Brown, Jr.
1954. Persistent daily and tidal rhythms of oxygen consumption in two species of marine snails. Physiol. Zool. **27**: 350 - 356
Sandison, E. E.
1966. The oxygen consumption of some intertidal gastropods in relation to zonation. Journ. Zool. London **149**: 163 - 173
1967. Respiratory response to temperature and temperature tolerance of some intertidal gastropods. Journ. Exper. Mar. Biol. and Ecol. **2**: 271 - 281
Shotwell, Jesse Arnold
1950. The vertical zonation of *Acmaea*, the limpet. Ecology **31** (4): 647 - 649; 3 figs.
Stephenson, T. A. & Anne Stephenson
1949. The universal features of zonation between tide-marks on rocky coasts. Journ. Ecol. **37**: 289 - 305
Test, Avery Ransome
1945. Ecology of California *Acmaea*. Ecology **26** (4): 395 - 405



Geographic Distribution of *Pinna rugosa* Sowerby, 1835

(Mollusca : Bivalvia)

and its Occurrence on Clipperton Island

BY

B. SALVAT AND F. SALVAT

École Pratique des Hautes Études, 55 Rue de Buffon, Paris, France

WE HAVE RECEIVED from Mme. Bourrouilh (Laboratoire de Géologie historique, Université de Paris) some mollusks taken in the lagoon of Clipperton in 1968 by the Bougainville expedition organised by the Centre de Recherches du Service de Santé des Armées (C. R. S. S. A).

The malacological fauna of Clipperton has been reviewed in a previous paper (SALVAT & EHRHARDT, 1970), with a discussion of its composition and biogeographic affinities.

Among the material recently received were three fragments of a representative of the family Pinnidae, which we were able to identify as *Pinna rugosa* Sowerby, 1835 because one fragment showed the characteristic muscle scar divided by a ridge inside, and the large undulation outside. Research on this species in our collection added further geographic information.

The presence of a *Pinna* on Clipperton was indicated by HERTLEIN & ALLISON (1966: 138), who had incomplete specimens. The mollusks known from the island (outer reefs and lagoon) number now 90 species (70 gastropods, 20 pelecypods). *Pinna rugosa,* as all other bivalvia collected in the lagoon of Clipperton, is only present as dead specimens.

The type locality of *Pinna rugosa* is Isla Rey, Panama (SOWERBY, 1835: 84). The species is known from Baja California to Panama; published records show it in the northwestern three-fourths of the Panamic province, where it has been cited by several authors, for example: MABILLE (1895: 73); LAMY (1909: 226); HERTLEIN & STRONG (1943: 165; 1955a: 176); DURHAM (1950: 57); EMERSON & PUFFER (1957: 18); KEEN (1958: 61; 1971: 75); OLSSON (1961: 143); DUSHANE *et al.* (1962: 42; 1967: 417; and 1968: 238). The record by SMITH (1890: 305), cited with doubt, of *P. rugosa* at Saint Helena Island in the eastern Atlantic probably refers to *P. rudis* Linnaeus, 1758. In their revision of the Pinnidae of the Atlantic, TURNER & ROSEWATER (1958: 285 - 326) do not report this species at this locality.

Among unidentified material in the Laboratory of Malacology at the Museum National d'Histoire Naturelle de Paris, we have recognized some specimens of *Pinna rugosa* collected in Baja California by Du Petit-Thouars in 1839 and by Leguillou in 1841, although labelled as "Californie." In some collections of mollusks from Ecuador, made by Mr. Hoffstetter, we have found one right valve of *Pinna rugosa,* with a locality notation that indicates the occurrence of the species at both Manta and Salinas. This extends the range southward from Panama to latitude 2° S. It therefore actually ranges through most of the Panamic marine province. HOFFSTETTER (1954: 23 to 24) recorded the presence of the genus *Pinna,* which we infer to be this species, in his list of subfossil material from the salt beds of Salinas.

The offshore islands of west central America carry a predominantly Panamic molluscan fauna (EMERSON, 1967; SALVAT, 1967). This is the case with Guadalupe, the Tres Marias, and the Revillagigedo Islands (STRONG & HANNA, 1930), but no species of Pinnidae has been recorded on them. So also for the Galapagos Islands (HERTLEIN & STRONG, 1955b) and Cocos Island (HERTLEIN, 1963). Thus, Clipperton is the only island of this group with representatives of the family Pinnidae or with *Pinna rugosa.* The molluscan fauna of Clipperton has an Indo-Pacific cast, for of the 90 species, nearly 50% of the 70 gastropods are Indo-Pacific, and of the 20 bivalve species 4 occur in the central Pacific, one both in the Pacific and on Panamic coasts, and 15 are exclusively Panamic in distribution.

Literature Cited

Durham, John Wyatt

1950. The 1940 E. W. Scripps cruise to the Gulf of California. Part II. Megascopic Paleontology and marine stratigraphy. Mem. Geol. Soc. Amer. 43 (2): 1 - 216

DuShane, Helen

1962. A checklist of mollusks for Puertocitos, Baja California, Mexico. The Veliger 5 (1): 39 - 50; 1 map (1 July 1962)

DuShane, Helen & Roy Poorman

1967. A checklist of mollusks for Guaymas, Sonora, Mexico. The Veliger **9** (4): 413 - 440; 1 map (1 April 1967)

DuShane, Helen & Gale G. Sphon

1968. A checklist of intertidal mollusks for Bahía Willard and the southwestern portion of Bahía San Luis Gonzaga, State of Baja California, Mexico. The Veliger **10** (3): 223 - 246; plt. 35; 1 map (1 January 1968)

Emerson, William Keith

1967. Indo-Pacific faunal elements in the tropical eastern Pacific, with special reference to the mollusks. Venus **25** (3 - 4): 85 - 93; fig.

Emerson, William Keith & Elton L. Puffer

1957. Recent mollusks of the 1940 "E. W. Scripps" cruise to the Gulf of California. Amer. Mus. Novit. **1825:** 1 - 57; 2 figs.

Hertlein, Leo George

1963. Contribution to the biogeography of Cocos Island, including a bibliography. Proc. Calif. Acad. Sci. (4) **32** (8): 219 - 289; 4 figs.

Hertlein, Leo George & Edwin C. Allison

1966. Additions to the molluscan fauna of Clipperton Island. The Veliger **9** (2): 138 - 140 (1 October 1966)

Hertlein, Leo George & Archibald McClure Strong

1943. Eastern Pacific expeditions of the New York Zoological Society XXXII. Mollusks from the west coast of Mexico and Central America. Part II. Zoologica **28** (19): 149 - 168; plt. 1

1955a. Marine mollusks collected during the "Askoy" expedition to Panama, Colombia, and Ecuador in 1941. Bull. Amer. Mus. Nat. Hist. **107** (2): 159 - 318; plts. 1 - 3 (28 November 1955)

1955b. Marine mollusks collected at the Galapagos Islands during the voyage of the *Velero III*, 1931-32. pp. 111 - 145 *in* : D. Halmos (ed): Essays in the natural sciences in honor of Captain Allan Hancock. Univ. South. Calif. Press, Los Angeles, Calif.: 1 - 345

Hoffstetter, Robert

1954. Moluscos subfosiles de los estanques de sol de Salinas (Pen de Santa Elena, Ecuador). Comparacion con la fauna actuel de Ecuador. Bol. Infor. Cient. Nac. Quito **62:** 20 - 47; 2 figs. and **63:** 137 - 170; 9 figs.

Keen, A. Myra

1958. Sea shells of tropical West America: marine mollusks from Lower California to Colombia. i - xi + 624 pp.; 10 col. plts.; 1700 text figs. Stanford Univ. Press, Stanford, Calif. (5 Dec. 1958)

1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

Lamy Édouard

1909. Pelecypodes recueillies par M. L. Diguet dans le Golfe de Californie (1894-1905). Journ. de Conchyl. **57:** 207 - 254

Mabille, Jules François

1895. Mollusques de la Basse Californie recueillis par M. Diguet. Bull. Soc. Philomathique Paris **7** (2): 54 - 76

Olsson, Axel Adolf

1961. Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panama-Pacific faunal province (Panama to Peru). Panamic-Pacific Pelecypoda. Paleont. Res. Inst. Ithaca, N. Y., 574 pp.; 86 plts. (10 March 1961)

Salvat, B.

1967. Importance de la faune malacologique dans les atolls polynésiens. Cahiers du Pacifique **11:** 7 - 49; figs. 1 - 7; photo. 1 - 12

Salvat, B. & J. P. Ehrhardt

1970. Mollusques de l'île de Clipperton. Bull. Mus. Nat. Hist. Nat. (2) **42** (1): 223 - 231

Sowerby, George Brettingham

1835. Characters and observations on new genera and species of Mollusca and Conchifera collected by Mr. Cuming. Proc. Malacol. Soc. London: 84 - 86

Smith, Edgar Albert

1890. Report on the marine molluscan fauna of the Island of St. Helena. Proc. Zool. Soc. London for **1890:** 247 - 317; plts. 21 - 24 (August 1890)

Strong, Archibald McClure & G Dallas Hanna

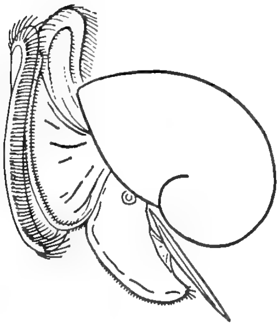
1930a. Marine Mollusca of Guadalupe Island, Mexico. Proc. Calif. Acad. Sci. (4) **19** (1): 1 - 6 (4 June 1930)

1930b. Marine Mollusca of the Revillagigedo Islands. Mexico. Proc. Calif. Acad. Sci. (4) **19** (2): 7 - 12 (4 June 1930)

1930c. Marine Mollusca of the Tres Marias Islands, Mexico. Proc. Calif. Acad. Sci. (4) **19** (3): 13 - 22 (4 June 1930)

Turner, Ruth Dixon & Joseph Rosewater

1958. The family Pinnidae in the Western Atlantic. Johnsonia **3** (28): 285 - 326; plts. 149 - 171



Evidence for a Pheromone in the Marine Periwinkle, *Littorina littorea* Linnaeus

BY

INGRID DINTER AND PETER J. MANOS[1]

University of Massachusetts, Boston, Biology Department, 100 Arlington Street, Boston, Massachusetts 02167
and
Harvard University, The Biological Laboratories, 16 Divinity Avenue, Cambridge, Massachusetts 02138

(1 Text figure)

INTRODUCTION

A PHEROMONE IS A SUBSTANCE released by an animal which, if sensed by a second animal of the same species, causes a change in the probability pattern of the receiving animal's behavior. For an excellent review of chemical communication in animals the reader is referred to an article by WILSON, 1970.

MATERIALS AND METHODS

Specimens of *Littorina littorea* Linnaeus, 1758, were collected at the rocky shore of Nahant, Massachusetts. Fresh sea water was also collected. Experiments were performed within 3 days of the collection day.

Our first attempts to set up a situation in which a specimen of *Littorina littorea* could "choose" to move toward another member of its species were failures due to the fact that the snail usually would not move at all. Then we took advantage of the fact that periwinkles are negatively geotropic in the dark (KANDA, 1916). We placed the snails on plates of glass to which they adhered, set the glass at a vertical angle in an aquarium and covered the aquarium with a foil-covered, light-proof cardboard box. Under these conditions most snails moved upward.

Five-gallon capacity aquaria were used for the experiments. Two glass test tubes (192×36 mm) were attached to a glass plate with waterproof electrical tape (Figure 1). A plastic platform taped 30 mm below the test tube openings served as a holder for the experimental animals. The glass plate was inserted into the aquarium and set at an angle of approximately 34° from the vertical.

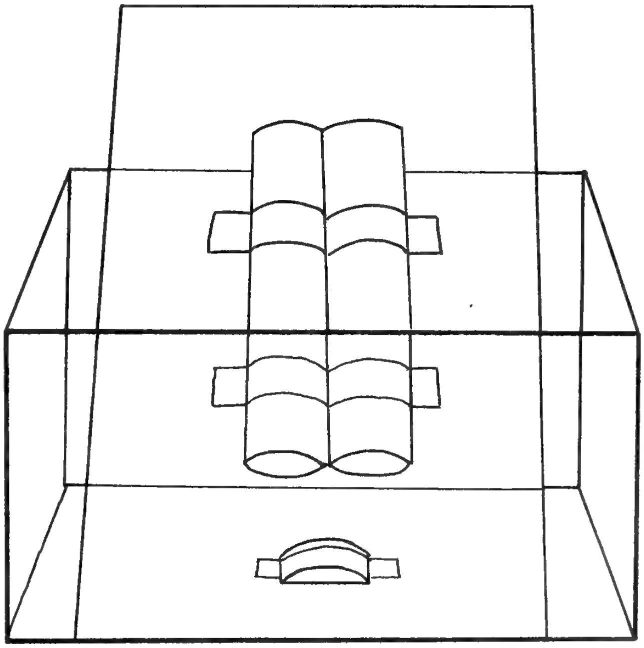


Figure 1

Apparatus for the demonstration of a pheromone in *Littorina littorea*
Attracting snail is placed at top of right tube, test snail is placed on starting platform

---

[1] We wish to acknowledge the financial support of a United States Public Health Service Training Grant, 2 T01-GM 00036 (13)

The tubes and aquarium were filled with seawater. Usually an experiment was run with a series of 10 test snails. A snail was placed on the platform and allowed to move up the plate or into the left or right tube. Fifty-six percent of all snails run entered a test tube. All the data presented in this report are for snails which entered one tube or the other. At the beginning of the series the water temperature was 7° C, at the end 14 ± 2° C. All experiments were performed in darkness.

EXPERIMENTS AND RESULTS

Experiment 1 was intended to show if *Littorina littorea* demonstrated any preferred direction of movement with no guiding stimulus present. The tubes were filled with fresh seawater, a periwinkle placed on the platform by hand, and the aquarium covered. After 10 minutes the box was removed and the position of the snail recorded. The snail was then marked, measured, and its sex identified (Linke, 1933; Fretter & Graham, 1962). A new snail was placed on the platform and the experiment repeated. Whenever a snail entered a tube, the glass plate and tubes were replaced with fresh ones in order to eliminate any possibility of build-up of substances within the tubes.

The results showed that *Littorina littorea* has a strong tendency to move to the left side (Table 1). Of the females 84% (39 out of 46) and of the males 75% (24 out of 32) entered the left tube.

Since periwinkles naturally tended to move to the left, we set up Experiment 2 in which an "attracting" snail was placed into the right tube and allowed to adhere. Both tubes were filled with seawater and rubber stoppers prevented convection currents from mixing the water in the tubes with that in the rest of the aquarium. The rationale was to allow any substance emitted by the "attracting" snail to become concentrated within the right tube. After one hour the stoppers were removed and the experiment conducted as before. Each time a snail entered a tube it was carefully removed by prying it loose with a spatula. If it went into the left tube, the water was blown out with rubber tubing and the test tube then refilled.

The results of this experiment showed that when a snail was present in the right tube other snails exhibited a strong tendency to enter that tube (Table 1). Of the females 62% (31 out of 50) and of the males 66% (26 out of 39) entered the right tube. To demonstrate the statistical significance of the difference between experiments 1 and 2 we assumed that there was no expected difference (the null hypothesis) and calculated the chi-square value on this assumption (Table 1). The probability that these results occurred by chance alone is less than 0.005.

Experiment 3 was designed to eliminate the possibility that the test snail was being attracted into the right tube by other than chemical stimuli. A specimen of *Littorina littorea* was inserted into the right tube and left for 5 hours. Both tubes were stoppered. The snail was then removed from the tube to insure that only the pheromone, if present, would be attracting other snails. This experiment was then performed like Experiment 2.

The results again showed that snails preferentially entered the right tube (Table 1). Comparing these results with those of Experiment 1, using the null hypothesis, shows that this distribution of data would occur by chance with a probability of less than 0.005.

Table 1

Preferential Entry of Left or Right Tube

	Number of snails entering	
	left tube	right tube
Experiment 1	63	15
Experiment 2	32	57
Experiment 3	3	11

for Experiments 1 and 2, $X^2 = 32.2$, $p < 0.005$
for Experiments 1 and 3, $X^2 = 17.8$, $p < 0.005$

DISCUSSION

Even a cursory glance at Table 1 gives the impression that snails are attracted into the right tube in Experiments 2 and 3. When these results are compared, using the null hypothesis, with the results of Experiment 1, the statistical significance of the results is even clearer. In both cases these results could be expected to occur by chance only 5 times in 1000 trials.

The simplest hypothesis which explains these results is that *Littorina littorea* emits a substance (or substances) which attracts other snails.

A total of 321 specimens of *Littorina littorea* were tested. It was demonstrated that periwinkles have a strong tendency to move up to the left in the dark. It is of interest to compare this observation with that made by Hayes (1929) on *L. littorea* moving on a horizontal surface: "It may be said that the individuals appeared to be totally indifferent as to which way they turned ... The fact that the shells are dextral appears to have no effect in determining such activities." Either an unequal distribution of weight or the snails' inherent dextrality might explain why, in Experiment 1, 4 times as many snail moved to the left as to the right.

We found no significant difference in the ability of males or females placed in the right tube to attract either males or females. We did note, however, a tendency for a higher percentage of snails to enter the right tube (in either Experiment 2 or 3) as the season changed from early March to early May. It is of interest that spawning takes place in March, April, and May, in this species (LINKE, 1933; FRETTER & GRAHAM, 1952; WILLIAMS, 1964; 1970). After this period the reproductive organs of males and females are reduced to a minimum size and develop again the following spring.

Snails ranging from 7.8 mm to 13 mm in height of shell never entered a right tube, seldom a left tube, instead usually moved to the right or the left of the glass plate. It has been shown that only rarely do specimens below 11 to 12 mm in shell height attain sexual maturity (WILLIAMS, 1970). Snails ranging from 13 to 26 mm in shell height entered the right tube in Experiment 2 and Experiment 3. These facts along with the observation that a higher percentage of animals moved into the right tubes as the mating season progressed indicate that a sex pheromone may be involved.

Literature Cited

FRETTER, VERA & ALASTAIR GRAHAM
1962. British prosobranch molluscs, their functional anatomy and ecology. London, Ray Soc. xvi+755 pp.; 316 figs.

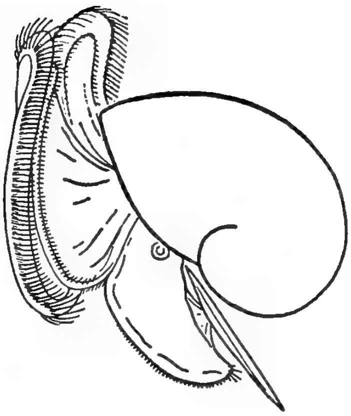
HAYES, F. R.
1929. Contributions to the study of marine gastropods III. Development, growth and behavior of *Littorina littorea* L. Contr. Canad. Biol. Fish. N. S. 4: 413 - 430

KANDA, SAKYO
1916. Studies on the geotropism of the marine snail, *Littorina littorea* L. Biol. Bull. 30: 57 - 84

LINKE, OTTO
1933. Morphologie und Physiologie des Genitalapparates der Nordseelittorinen. Komm. Wissensch. Unters. deutsch. Meere 19: 1 - 60 (December 1933)

WILLIAMS, E. E.
1964. Growth and distribution of *Littorina littorea* L. on a rocky shore in Wales. Journ. Animal Ecol. 33: 413 - 432
1970. Seasonal variations in the biochemical composition of the edible winkle *Littorina littorea* L. Comp. Biochem. Physiol. 33 (3): 655 to 661 (4 April 1970)

WILSON, EDWARD O.
1970. Chemical communication within animal species. *In*: ERNEST SONDHEIMER & JOHN B. SIMEONE (eds.): Chemical ecology. Acad. Press, London



The Mucus Holdfast of *Littorina irrorata* and its Relationship to Relative Humidity and Salinity

BY

FRASIER O. BINGHAM

Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149[1]

(7 Text figures)

INTRODUCTION

THE SALT MARSH PERIWINKLE, *Littorina irrorata* (Say, 1822), is common in salt marshes along the eastern coast of the United States from New York State to central Florida, and along the northern coast of the Gulf of Mexico. The species shows a disinclination to remain submerged and is usually found attached, by dried mucus, to marsh grasses above the water level, or foraging on marsh floors exposed at low tide.

Many other members of the family Littorinidae have, as well, been noted to employ a small amount of dried mucus (or holdfast) for attachment of the shell to substrates during periods of air exposure.

During a recent study of the species' behavior (BINGHAM, in press), the process of holdfast formation, and the relationship of holdfast formation to relative humidity and salinity were observed.

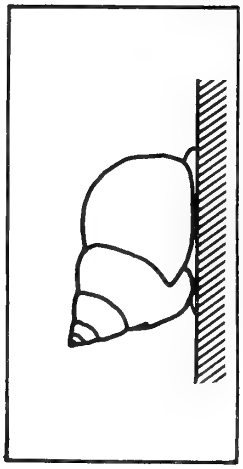


Figure 1

Normal spire-down position of *Littorina irrorata*

HOLDFAST FORMATION

The animal assumes a spire-down position (Figure 1) before secretion of the holdfast is begun and then, with the anterior end of the pedal sole, performs a single slow sweep of the uppermost interior portion of the shell lip. This action is depicted in various stages in Figure 2, and was completed in an average time of 9½ minutes by 20 specimens. Re-orientation into the spire-down position, when the vertical substrate was inverted, was seen so long as the pedal lick had not begun. After the pedal lick had started, inversion of the substrate did not visibly affect holdfast formation, and an unstable position, as seen in Figure 3, resulted.

The holdfast consists of 2 semicircular films of mucus attached to the substrate and joined along a line of shell attachment (Figure 4). This line is shown in Figure 5 to lie slightly within the shell lip.

EFFECTS OF RELATIVE HUMIDITY

In studying the effects of various relative humidities on the latency of holdfast formation, 50 adult specimens were kept submerged in ambient sea water of 33‰ salinity for 1 hour, dried with a paper towel, and 10 each placed in 5 jars of one gallon capacity containing stable relative humidities of 0%, 25%, 50%, 75%, and 100%. These hu-

---

[1] Contribution No. 1479 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science, 10 Rickenbacker Causeway, Miami, Florida 33149

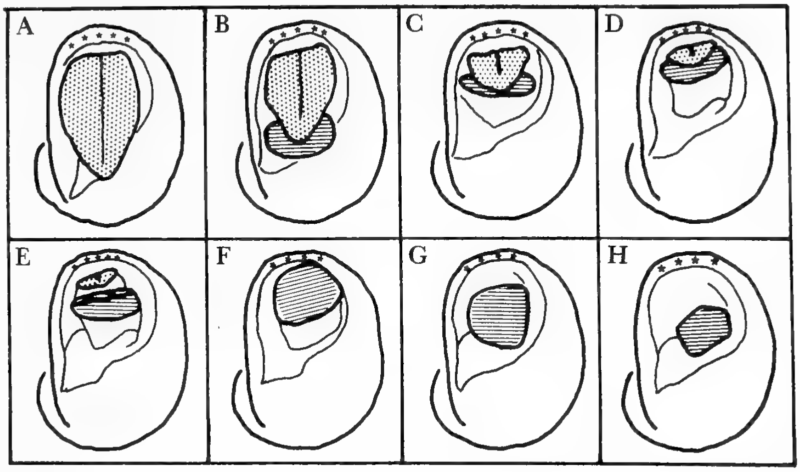


Figure 2

Stages in pedal sweep during holdfast formation

░ foot ▤ operculum

**** region in which holdfast is formed

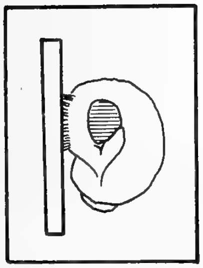


Figure 3

Unstable attached position as viewed from above

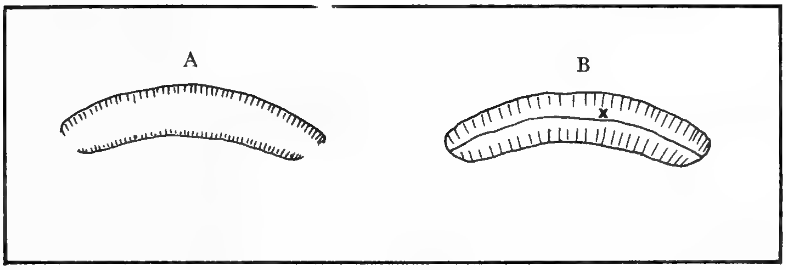


Figure 4

Holdfast of *Littorina irrorata*

A as seen through a glass substrate

B as seen with animal removed X line of shell attachment

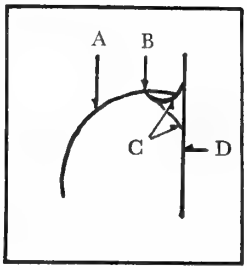


Figure 5

Holdfast of *Littorina irrorata,* cross section

A shell B point of shell attachment C holdfast

D substrate

midities were created by placing in each jar a bowl containing sulphuric acid solutions of known concentrations and a known constant temperature (25° C), according to the method described by Salomon (1951).

The length of time before each specimen was seen to complete a holdfast was noted and the average time in each group calculated. All of the specimens in relative humidities of 75% and below formed holdfasts, with each group forming them in a shorter average time than the group kept at the next higher level of relative humidity (Figure 6). None of the specimens kept in the 100% relative humidity atmosphere formed a holdfast during 3 days of observation.

EFFECTS OF SALINITY

In the determination of salinity effects on holdfast formation, 140 specimens which had been kept submerged in ambient sea water of 33‰ salinity for one hour, were placed, 10 each, in 14 different salinities ranging from that of tap water to 75‰. The solutions were aerated and

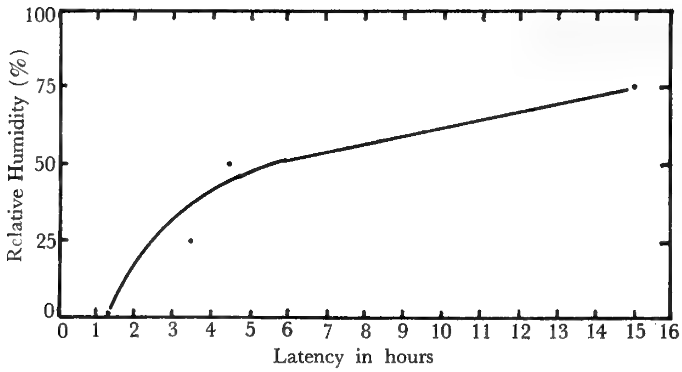


Figure 6

Latency of holdfast formation as related to relative humidity

maintained at a temperature of 25 ± 1° C. Plastic screen cages were used to keep the snails submerged. Low salinity solutions were prepared with sea water and distilled water. Solutions of higher than normal sea water salinity were prepared by evaporation of sea water. Salinity determinations were made with a Goldberg refractometer.

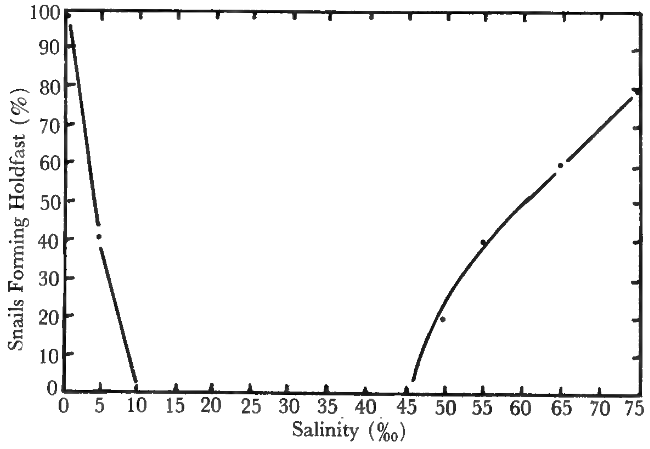


Figure 7

Occurrence of holdfast formation as related to salinity

In Figure 7, which illustrates the relationship of holdfast formation and salinity, it may be noted that at only one salinity – that of tap water – did all of the snails form a holdfast; therefore, the percentage of snails forming holdfasts is presented rather than the latency of holdfast formation.

No holdfasts were formed (during 3 days of observation) by the specimens maintained in the 10 to 45‰ salinity range. Above 45‰ salinity, the percentage of specimens forming holdfasts increased as salinity increased. Below 10‰ salinity the percentage of specimens forming holdfasts increased as salinity decreased.

DISCUSSION

The holdfast is seen as a valuable adaptation to the supralittoral environment in that it affords a means of maintaining position without continued exertion and leaves the snail free to withdraw into its shell to escape environmental stress conditions, such as low relative humidity or low and high salinities when such salinities cannot be avoided through upward movement.

In this study, the holdfast was formed only during unfavorable conditions and was secreted under water as well as in the air. Upon appropriate stimulation, the holdfast was disposed of through feeding movements of the proboscis and radula.

Literature Cited

Bingham, Frasier O.

In Press. The influence of environmental stimuli on the direction of movement of the supralittoral gastropod *Littorina irrorata*. Bull. Mar. Sci.

Salomon, M. E.

1951. Control of humidity with potassium hydroxide, sulphuric acid, or other solutions. Bull. Entomol. Res. 42: 543 - 554

Morum dennisoni Reeve (Gastropoda : Cassidae) and *Strombus costatus* Gmelin (Gastropoda : Strombidae) Collected Off the North Carolina Coast

BY

EDWARD J. PETUCH

Department of Zoology, University of Wisconsin – Milwaukee, Milwaukee, Wisconsin 53201

(1 Plate)

FOUR ADULT SPECIMENS of *Strombus costatus* (Gmelin, 1791) and a juvenile specimen of the rare *Morum dennisoni* (Reeve, 1842) were collected off the North Carolina coast during the month of August, 1971. These exciting finds extend the ranges of these two Caribbean species well into the Carolinian Province. Previously, the northern limit to the range of *S. costatus* was fixed as southeast Florida (ABBOTT, 1954; 1961; MORRIS, 1951; WARMKE & ABBOTT, 1961). From there it extends into the southern Gulf of Mexico and the Caribbean area where it is a common species. *Morum dennisoni* has been previously reported as far north as Great Inagua Island and Stranger's Cay in the Bahamas, off Tarpon Springs and Pensacola, Florida, and SSE of Freeport, Texas (DANCE & EMERSON, 1967). Its center of distribution appears to be the Southern Caribbean (WARMKE & ABBOTT, *op. cit.*). To find it in a dredge off North Carolina was quite a surprise.

The 4 specimens of *Strombus costatus* were collected at two dredging stations by the Duke University Marine Laboratory research vessel *Eastward* on cruise number E-20-71. These stations were *Eastward* station no. 17663, with coordinates 33°31.8′ N, 77°22.4′ W, and *Eastward* station no. 17666, with coordinates 33°30.7′ N, 77°24.4′ W. The former took place at 11:50 pm on August 3, the latter at 1:30 am on August 4. Both stations were approximately 5.7 miles north of Frying Pan Light, off Cape Fear, North Carolina. The samples were dredged at a depth of 25 m, and the bottom temperature was 21-22° C. Judging from the dredge contents, the substrate appeared to be composed of marl heavily encrusted with living *Arca zebra* Swainson, 1845, the red alga *Eucheuma* sp., and occasional heads of the tropical reef corals *Solenastrea hyades* (Dana, 1848) and *Siderastrea siderea* (Ellis & Solander, 1848). Two live specimens were taken at station 17663, while one live and one dead specimen were taken at station 17666. The first specimen collected at station 17663 was the largest, measuring 154 mm in length and 99 mm in width. It was an old adult, as the outer lip was heavy and thick with a silvery glaze. The other specimen, a mature adult, measured 125 mm in length and 77 mm in width. Of the specimens collected at station 17666, the largest one was a mature living adult, with a well-developed lip, and measured 128 mm in length and 78 mm in width. The smaller one, measuring 110 mm in length and 68 mm in width, was a dead specimen occupied by a hermit crab. This was a mature specimen with a well-developed but thin lip. The individuals collected conformed to the general description of Florida and Caribbean specimens and showed no apparent deviations from the typical *Strombus costatus* (Figure *1*).

The *Morum dennisoni* collected measured 40 mm in length and 24 mm in width (Figure *2*). It was taken at *Eastward* station 17663 along with the 2 live *Strombus costatus* and a live *Cypraea cervus* Linnaeus, 1771. Although it was a juvenile specimen, collected dead and occupied by a hermit crab, there can be no doubt as to its identity. It conforms to the descriptions and illustrations in the literature (DANCE, 1966; DANCE & EMERSON, 1967), and shows no distinct differences from other recorded specimens.

Altogether, these 5 individuals represent a very interesting and important find. The North Carolina specimens of *Strombus costatus* and *Morum dennisoni* extend the range of these species northward by an appreciable distance. At present, their extreme northern limit appears to be the Cape Fear area. However, future dredgings might extend the range further northward to off Cape Lookout and the Onslow Bay area. Here there are outcroppings of tropical reef corals offshore (MACINTYRE & PILKEY, 1969) where many tropical molluscan species such as *Cypraea cervus, C. spurca acicularis* Gmelin, 1791 (D. WOLFE & N. WOLFE, 1970); *Cassis madagascariensis spinella* Clench, 1944 (ABBOTT, 1954; PORTER, 1965; D. WOLFE & N. WOLFE, 1970), *Conus juliae* Clench, 1942, and *Lyropecten nodosus* (Linnaeus, 1758) (ABBOTT, 1954, 1961; WARMKE & ABBOTT, 1961) are regularly taken.

ACKNOWLEDGMENTS

I would like to thank the following persons: Dr. Richard B. Searles, Professor of Botany, Duke University, for allowing me to take part in the R/V *Eastward* cruise; for critical reading of the manuscript and helpful suggestions I am indebted to Ronald Mollick, Christopher Newport College, College of William and Mary, and Kimberly Matthews, Duke University. I also acknowledge the support of the Oceanographic Program of Duke University Marine Laboratory for use of the R/V *Eastward* on cruise E-20-71. The Oceanographic Program is supported by the National Science Foundation Grant no. GA-27725.

Literature Cited

ABBOTT, ROBERT TUCKER
1954. American seashells. Princeton, New Jersey. D. van Nostrand Co., Inc.; xiv+541 pp.; 40 plts.; 100 text figs.
1961. How to know the American marine shells. New York. Signet Key paperback; 222 pp.; 12 plts. in color; 402 text figs.
DANCE, STANLEY PETER
1966. Shell collecting; an illustrated history. Univ. Calif. Press, Berkeley and Los Angeles: 344 pp.; 35 plts.; 31 text figs.
DANCE, STANLEY PETER & WILLIAM KEITH EMERSON
1967. Notes on *Morum dennisoni* (Reeve) and related species (Gastropoda : Tonnacea). The Veliger **10** (2): 91-98; plt. 12 (1 October 1967)
MACINTYRE, IAN G. & ORRIN H. PILKEY
1969. Tropical reef corals: tolerance of low temperatures on the North Carolina Continental Shelf. Science **166** (3903): 374-375; 3 text figs. (17 October 1969)
MORRIS, PERCY A.
1951. A field guide to the shells of our Atlantic and Gulf coasts. Houghton Mifflin Co. Inc., Boston, Mass. iii+236 pp.; 45 plts.
PORTER, HUGH J.
1965. *Cassis madagascariensis spinella* off the North Carolina coast. The Nautilus **78** (2): 106
WARMKE, GERMAINE L. & ROBERT TUCKER ABBOTT
1961. Caribbean seashells; a guide to the marine mollusks of Puerto Rico and other West Indian islands, Bermuda and the lower Florida Keys. Livingston Publ. Co., Narberth, Pa. x+345 pp.; 44 plts.; 34 text figs.
WOLFE, DOUGLAS A. & NANCY WOLFE
1970. Molluscs of North Carolina. Beaufort, North Carolina; a check list published by Center for estuarine and Menhaden research. U. S. Bur. Comm. Fisheries, with regional marine sci. proj. 69 pp.; 1 fig.

Plate Explanation

Figures *1* and *2*: *Strombus costatus* (Gmelin 1791)
Figures *3* and *4*: *Morum dennisoni* (Reeve, 1842)

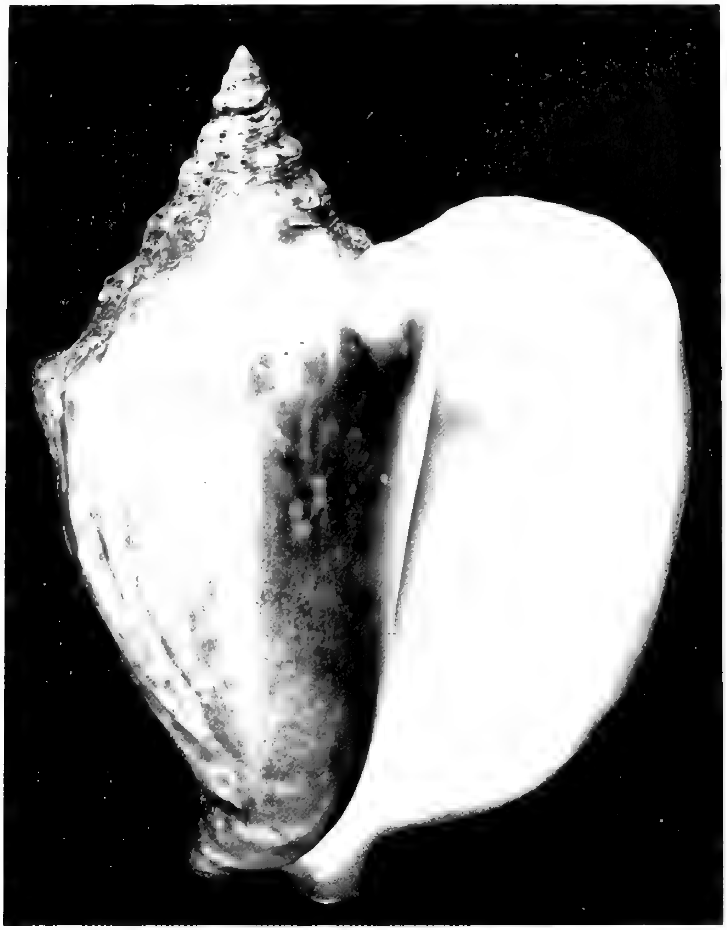


Figure *1*

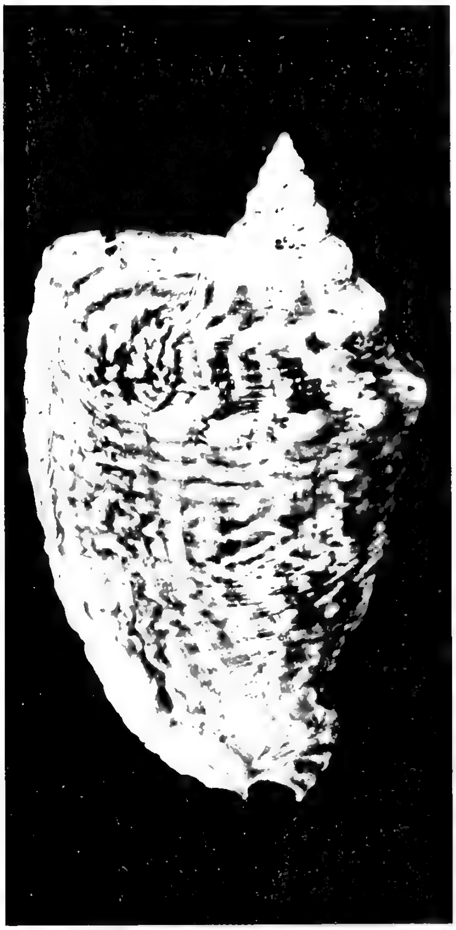


Figure *2*

Figure *3*

Figure *4*

Range Extensions of *Conualevia alba* Collier & Farmer, 1964

BY

ANTONIO J. FERREIRA

Beta Research Oceanographic Laboratories, Inc., 2060 Clarmar Way, San Jose, California 95128

Conualevia alba Collier & Farmer, 1964, was first described from the rocky mud flats of Newport Bay (lat. 33°36′N, long. 117°54′W) where it was found to occur rather abundantly during the months of November and December. Lance (1966) reported finding this cryptobranch at Point Loma, San Diego County (lat. 32°40′N, long. 117°14′W) and under stones at Bahía Tortuga, Baja California, Mexico (lat. 27°41′N, long. 114°53′W) along the outer coast of Lower California. A range extension north from Newport Bay was recorded by Sphon & Lance (1968) with the observation of *C. alba* at Tajiguas (lat. 34°20′N, long. 120°08′W) and Coal Oil Point, Santa Barbara County, California, in 15 to 30 feet [4.5 to 9 m] of water.

The collections reported here extend the known range of *Conualevia alba* substantially both to the north and to the south, and to depths not hitherto indicated. The first specimen of *C. alba* was found under a fairly large stone in the intertidal zone on the northern side of Bahía de Banderas, Nayarit, Mexico (lat. 20°40′N, long. 105°17′W) on March 21, 1971 while we were collecting at Manzanilla. In all of its external features, this specimen conformed well to the original description. However, the animal was 10-gilled-bipinnate (not 8-gilled-tripinnate, as indicated in the original description); also it was considerably larger than previously reported specimens, measuring 30 mm in length and 24 mm in width while at rest on a rock, whereas Collier & Farmer's largest speciman was said to have been 24×14 mm while actively crawling. The notum of the Nayarit specimen was uniformly papillose (Collier & Farmer noted that the notum of these animals is quite variable, in some entirely smooth, papillose in others) with papillae about 0.1 - 0.2 mm in diameter. Around the margin of the notum there were several white glands in a row, more abundant on the right side. This specimen has been deposited with the California Academy of Sciences, Department of Invertebrate Zoology (CASIZ) collection, together with 35 mm color slides (CASIZ nos. 2573 - 2577, incl.).

The northerly find occurred on August 19, 1971, at Cypress Point (lat. 36°35′N, long. 121°59′W), Pacific Grove, Monterey County, California. While SCUBA-diving with Gene Daily and Robert Western, Sr., from the R/V *Kiwi*, as part of the research activities of the Beta Research Oceanographic Laboratories, we came across a small white dorid that later was identified as *Conualevia alba*. The animal was found in 50 feet [15 m] of water on a rocky substratum covered mostly with coralline algae. The time was about noon, on a very calm but overcast day. The specimen measured 12×7 mm while crawling actively. However, when disturbed, the animal was observed to stop and contract, becoming virtually circular with dimensions of 9×9 mm. The notum was papillose, with papillae closely set, uniform in appearance and size (0.1 - 0.2 mm). The body was quite translucent, and under appropriate tangential light it seemed as if light-catching white lines (spicules?) tended to converge towards the papillae, making for a star-like effect. The rhinophores were smooth, rounded at the tip, yellowish in color, and when fully extended about 1 mm in length and 0.3 mm in average width. Along the right border of the notum there were about 6 white dots (glands) in a row. In all respects, then, the specimen corresponded to the original description of *Conualevia alba*, with only one notable exception: the gill branches, 8 in number, were unipinnate instead of tripinnate.

On August 22, 1971 a second specimen was found, in Monterey Bay. While SCUBA-diving from the Janss Foundation's R/V *Searcher*, a specimen was found in 55 feet [16.5 m] of water on Chase Reef, slightly east of Aumentos Rock (lat. 36°38′N, long. 121°55′W) in Monterey Bay. The animal was motionless, clinging to the underside of a rock. It was virtually identical with the one found at Cypress Point. In the laboratory it measured 13 mm in length, 7 mm in width, and 3.5 mm in height. It had numerous glands along the margin of the notum, on both sides, showing as conspicuous opaque white dots measuring as much as 0.3 mm in diameter. The gills were 9-branched, unipinnate.

Both specimens were kept alive in the laboratory for 4 days prior to being preserved. During this, time they were seen crawling about very slowly, their speed never exceeding 1 cm per minute. They were also observed floating upside down, suspended from the water surface for long periods.

Both specimens have been deposited in the California Academy of Sciences, Department of Invertebrate Zoology collections, together with 35 mm color slides (CASIZ nos. 2578 - 2582, incl.).

Marcus & Marcus (1967) indicated that the genus *Conualevia* seemed to be restricted to the coast of California south of Point Conception. The observations here reported extend the range of *Conualevia alba* some 1000 miles [1600 km] to the south and 350 miles [560 km] to the north of the previously reported range (Lance, 1966; Sphon & Lance, 1968; Keen, 1971) to waters much colder and depths much greater than heretofore known.

The specimens here reported did not quite completely conform to Collier & Farmer's description as to the number of branches and division of the gills. Whether these variations in the branching and pinnation of the gills are of taxonomic significance remains to be seen.

ACKNOWLEDGMENTS

The help and assistance provided by Hans Bertsch and Allyn G. Smith in the pursuit of this and other work is appreciated and hereby acknowledged.

Literature Cited

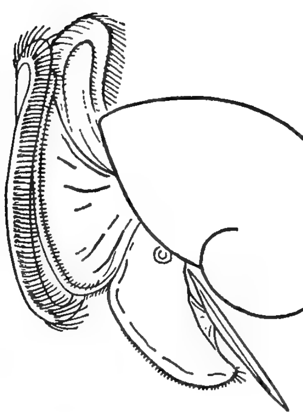
Collier, Clinton L. & Wesley Merrill Farmer
1964. Additions to the nudibranch fauna of the east Pacific and the Gulf of California. Trans. San Diego Soc. Nat. Hist. **13** (19): 377 - 396; plts. 1 - 6; 3 text figs. (30 December 1964)

Keen, A. Myra
1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

Lance, James Robert
1966. New distributional records of some northeastern Pacific opisthobranchiata with descriptions of two new species. The Veliger **9** (1): 69 - 81; 12 text figs. (1 July 1966)

Marcus, Eveline du Bois Reymond & Ernst Marcus
1967. American opisthobranch mollusks. Studies in tropical oceanography (Univ. Miami Inst. Marine Sci., Miami, Florida), no. 6: viii + 256 pp.; figs. 1 - 155 + 1 - 95 (December 1967)

Sphon, Gale G. & James Robert Lance
1968. An annotated list of nudibranchs and their allies from Santa Barbara County, California. Proc. Calif. Acad. Sci. (4) **36** (3): 73 - 84; 1 text fig. (25 September 1968)



Stenoplax circumsenta Berry, 1956, in the Gulf of California

BY

ANTONIO J. FERREIRA

Beta Research Oceanographic Laboratories, Inc., 2060 Clarmar Way, San Jose, California 95128

(1 Plate)

THE SAND FLATS west of Isla Concha, Scammon's Lagoon (lat. 27°50′N; long. 114°20′W), Baja California, were considered as type locality for *Stenoplax circumsenta* Berry, 1956. The holotype bears the number 13 602 in the Berry collection, and paratypes have the number 13 627 in the same collection.

The Puritan-American Expedition of 1959 collected two more specimens from the east side of Isla Concha (Station P-5, at a depth of 4 feet [1.2 m]) which, preserved in alcohol, now bear the number 10 056 in the A. G. Smith collection at the California Academy of Sciences in San Francisco.

To date, the species has never been illustrated. KEEN (1958, 1971) makes no mention of this species in either edition of "Sea Shells of Tropical West America."

On October 25, 1970, at Bahía de San Gabriel (lat. 24°26′N, long. 110°21′W), Isla Espíritu Santo, in the Gulf of California, I came across, on the underside of a rock in some 3 feet [90 cm] of water, a specimen of *Stenoplax* decidedly different from the rather common *S. limaciformis* (Sowerby, 1832). The specimen was brought to the attention of Mr. Allyn G. Smith, Associate Curator, Department of Invertebrate Zoology, California Academy of Sciences, who identified it as *Stenoplax circumsenta* Berry, 1956. This particular specimen measured in the dried state 25×9×4 mm. The shell valves were a mottled dark gray; the girdle was characterized by the presence, in addition to minute scales, of numerous translucent spinelets of triangular outline, sharply pointed, which give the girdle a rather rough appearance.

On July 11, 1971, two more specimens of *Stenoplax circumsenta* were found, again under stones in two feet [60 cm] of water at Pichilinque (lat. 24°15′N, long. 110°17′W) some 17 km east of La Paz, Baja California. Once dried, their sizes were 26×11 mm and 27×10 mm, respectively.

At this point it became tempting to speculate that *Stenoplax circumsenta* was to be found only at shallow depths and in calm and very protected waters – the common features of the localities: Scammon's Lagoon, Bahía de San Gabriel, Pichilinque, where the species had so far been found.

The validity of this theory was put to a test on a subsequent collecting trip to La Paz and the Gulf of California. On September 1, 1971, an attempt was made to collect the species again in the Bahía San Gabriel (Isla Espíritu Santo), and in Pichilinque and adjacent coves. But an effort equivalent to 8 man-hours of search under rocks (mostly snorkeling) did not turn up any specimen of *Stenoplax circumsenta* among more than 200 chitons sighted.

However, a few days later, while on a fish collecting expedition with the Steinhart Divers for the California Academy of Sciences aboard the R/V *Marisla II* a specimen of *Stenoplax circumsenta* was found unexpectedly. Alone, under a turnable stone in 50 feet [15 m] of water, the specimen measured, when dried, 19×9 mm. The locality was the reef that stretches out from the southwest corner of Isla Partida (lat. 24°32′N, long. 110°24′W), some 20 nautical miles N of La Paz, Baja California. The waters over the reef, although calm and serene at the time of collecting, in no way evoked the image of being "protected" in the way it could be said of Scammon's Lagoon, Bahía San Gabriel, or Pichilinque; and the depth at which the specimen was located was certainly much greater than for the specimens previously collected.

The colors of the specimens reported here are varied: two specimens are creamy, speckled with brown and gray; one is mostly a rusty brown with minute whitish specks; another is a dark gray variously suffused with white. Inside, the valves are intensely pink and blue in 3 specimens; in the other specimen the inner surfaces of the valves are white with blue triangular areas in valves ii, iv, and v.

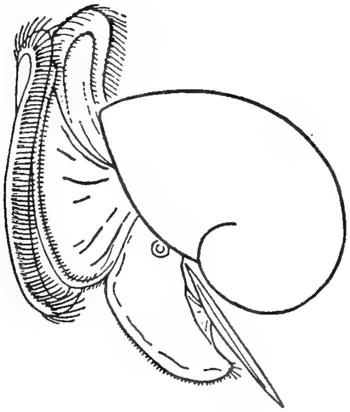
The first specimen of *Stenoplax circumsenta* collected in the Gulf of California, at Bahía de San Gabriel, Isla Espíritu Santo, November 1970, was deposited with the California Academy of Sciences and is now part of the collection in the Department of Geology (loc. no. 45 418).

ACKNOWLEDGMENT

I wish to express my gratitude to Allyn G. Smith for his invaluable help in the preparation of this report, and for the kind teaching with which he has so enriched my interest in invertebrates.

Literature Cited

Berry, Samuel Stillman
1956. Diagnoses of new eastern Pacific chitons. Leafl. Malacol. 1 (13): 71 - 74 (19 July 1956)
Keen, A. Myra
1958. Sea shells of tropical West America: marine mollusks from Lower California to Colombia. i - xi + 624 pp.; 10 col. plts.; 1700 text figs. Stanford Univ. Press, Stanford, Calif. (5 Dec. 1958)
1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)



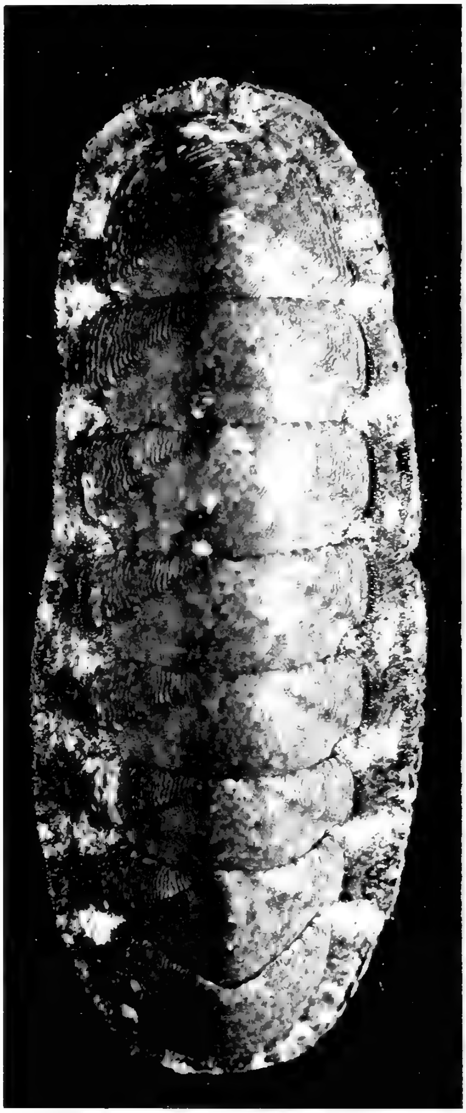


Figure 1

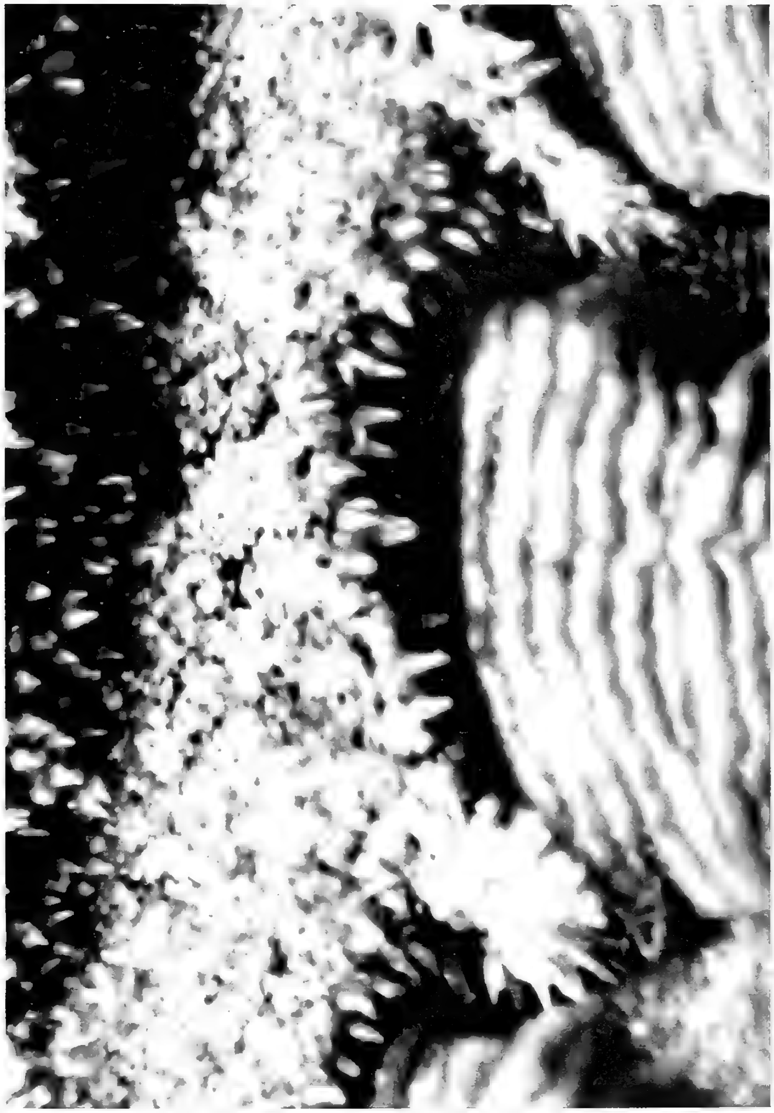


Figure 2

Figure *1*: *Stenoplax circumsenta* Berry, 1956. Pichilinque, Baja California, A. J. Ferreira, coll., July 1971. Length 27 mm
Figure *2*: Enlarged view of a portion of the girdle, showing the characteristic triangular spinelets

photographs by A. J. FERREIRA

Observation of the Glochidium, Metamorphosis, and Juvenile of *Anodonta californiensis* Lea, 1857

BY

PETER N. D'ELISCU

Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721

(1 Plate; 1 Text figure)

Anodonta californiensis Lea, 1857, is a bivalve inhabitant of freshwater ponds with muddy bottom substrates and lotic conditions. The specimens used in this study of its larval and juvenile biology were collected from Santa Ana Creek, a tributary of the Pajaro River, near Hollister, California. The observations were carried out at San Jose State College.

The glochidia larvae of *Anodonta californiensis* possess teeth at each shell lip and a moderately long attachment thread. A single adductor muscle is also present. The 0.2 mm larvae proved surprisingly hardy. Glochidia maintained in unaerated, ice-bath cooled water at 15 to 16° C survived up to 36 hours. Infestation possibilities are surely enhanced by this long free-state viability of an eventual obligate parasite.

When these larvae become attached to gill arches and filaments, fins, or barbules of a host fish, a chemical action is initiated. The usual response of the host to the parasite is tissue proliferation at the attachment site. Rapid growth of tissue at the site covers the parasite and a cyst is formed around it.

Several mosquito fish, *Gambusia affinis* (Baird & Girard, 1839), were employed as artificial hosts in this study. Lefevre & Curtis (1908) found the Anodontinae not very host-specific. They found North American species of the bivalve subfamily able to utilize as hosts any number of common fresh-water fish, including various bass, trout, many perch-like fishes, and some catfish. Artificial infestation of the mosquito fish was accomplished by maintaining them for several hours in vigorously aerated water suspending many glochidia removed from a live, gravid female clam. Permanent attachment areas on this host included the gills, opercular edge, and all fins. Encystment, measured from the time of attachment to cyst completion, required 3 to 4½ hours at 20° C.

The length of the parasitic period following excystment is variable, depending upon temperature. *Anodonta californiensis* remained encysted on *Gambusia affinis* for 26 to 27 days at an average temperature of 20° C. The excystment period for the juveniles ranged over two days, corresponding to the findings of Lefevre & Curtis, 1908. They showed that spring infections from winter-breeding Unionids, including *Anodonta,* often result in narrow-span excystment periods.

Excystment marks the completion of a metamorphosis. The morphologically infective glochidium is transformed into an early juvenile clam, possessing some adult characteristics and organs. The structures evident at this stage include the paired, trilobed livers or "digestive glands;" two prominent adductor muscles; a mantle with a ciliated edge; a bilobed, ciliated foot possessing an adhesive structure (byssal gland); and one pair of gills. The siphons and immature gonads noted by various observers were not evident in the juvenile *Anodonta californiensis.* The glochidial shell teeth and attachment thread are lost during metamorphosis. The byssal gland is lost early in adult life. Howard (1914: 46) mentions that the outer gills in *Anodonta* are not acquired until the second year of growth. This latter set of gills is important in the Anodontinae as female marsupia, holding many developing glochidia during reproduction. The long marginal shell hinge of the glochidium becomes more apical and concentrated in the early juvenile (Figure 1 and Figure 2).

Behavior and growth of the juvenile stage was noted upon excystment. The foot of the young clam was long and ciliated. The foot could be extended more than twice the length of the clam shell. When the foot was extended, the antero-apical cilia began to beat. The ciliary activity ceased when the foot attached to the substrate. Rapid contraction of the foot after attachment caused the body

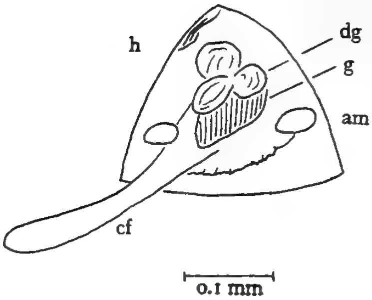


Figure 1

Early excysted juvenile – longitudinal view with left valve removed
h – hinge; cf – ciliated foot; dg – digestive gland;
g – gill; am – adductor muscle

mass to be pulled forward. The valves were maintained open at an angle of about 45° during movement, but could be closed quickly when the animal was disturbed or overturned; the small clam righted itself with the aid of the cylindrical, adhesive foot.

Juvenile growth studies revealed a very rapid rate. An average daily increase of 0.15 mm (long axis) amounted to an 840% increase in size over a 14 day period. This growth rate correlates with the results of Howard (1922: 69-70), investigating the growth rates of another Unionid, *Lampsilis luteola* Lamarck, 1819. The overall growth rates of the juveniles of both *Anodonta californiensis* and *L. luteola* were about 50 times that of the larger adults.

Following the discovery that the larval stages of many fresh-water clams are parasitic on fish, many attempts were made to raise adults in captivity. These efforts were directed toward providing a food source, shell material for the once active "pearl button" industry, and information concerning the effects of glochidia on the fresh-water fisheries. No particular difficulty was experienced in carrying certain species through the parasitic stage, but few investigators were able to maintain the clams through the juvenile stage to reproductive or harvestable adulthood. Artificial propagation experiments, in which fish were mechanically infested with glochidia and released, appeared ineffective. Survival of the juveniles depended solely on the chance that the host fish would be over the proper habitat conditions at the time of excystment. Studies by Isely (1911) and D'Eliscu (1970 MS) showed that few or no juveniles live in the observed adult habitat.

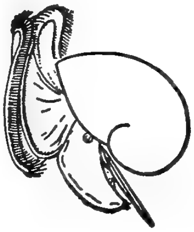
Juveniles were difficult to collect for many species, including *Anodonta californiensis*. The juveniles of some species possess byssal glands and inhabit loose gravel, while the adults live in deep mud or sand (Howard, 1914: 8). The morphology, physiology and difficulty of collection of the juvenile stage seem to indicate occupation of an entirely different habitat from that of the adult. This separation of different age groups may be similar to marine bivalve forms with motile larvae that do not compete directly with adults for food. Direct implantation of excysted Unionid juveniles into their specific habitat requirements would greatly facilitate increased production in terms of individual survival rates.

Literature Cited

Howard, Arthur Day
1914. Experiments in the propagation of freshwater mussels of the Quadrula group. U. S. Bureau Fish. Doc. 801: 1 - 52
1922. Experiments in the culture of freshwater mussels. Bull. U. S. Bur. Fish. 38 (916): 63 - 90

Isely, Fred B.
1911. Preliminary note on the ecology of the early juvenile life in the Unionidae. Biol. Bull. 20: 77 - 80

Lefevre, George & Winterton C. Curtis
1908. Experiments in the artificial propagation of freshwater mussels. Bull. U. S. Bur. Fish. 28: 617 - 626



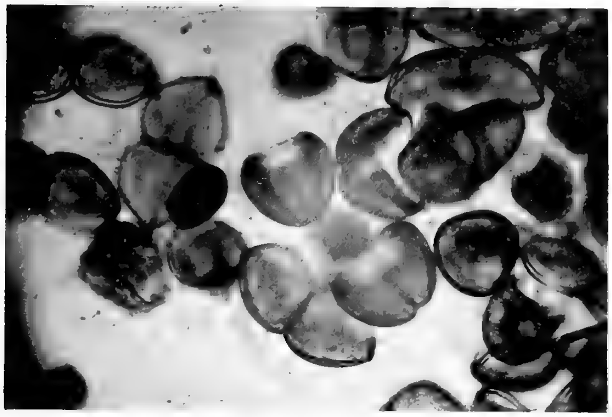


Figure 2

Several glochidia of *Anodonta californiensis* showing valves, single adductor muscle, and dark shell teeth

Opisthobranch Mollusks Dredged in San Francisco Bay During the Period 1966 to 1971

BY

JOHN J. HOLLEMAN

Biological Science Department, Merritt College, Oakland, California 94619

(1 Text figure)

INTRODUCTION

PREVIOUSLY UNREPORTED NUDIBRANCHS from San Francisco Bay have been dredged from 1966 to 1971. Extensive accounts of the opisthobranch mollusks of the central California coast have been given by MARCUS (1961); STEINBERG (1963) and MACFARLAND (1966), while the occurrence of nudibranchs in San Francisco Bay has been reported by GOSLINER & WILLIAMS (1970) and BEHRENS (1971). APLIN (1967) reports that nudibranchs were dredged and collected intertidally during his study, but not identified.

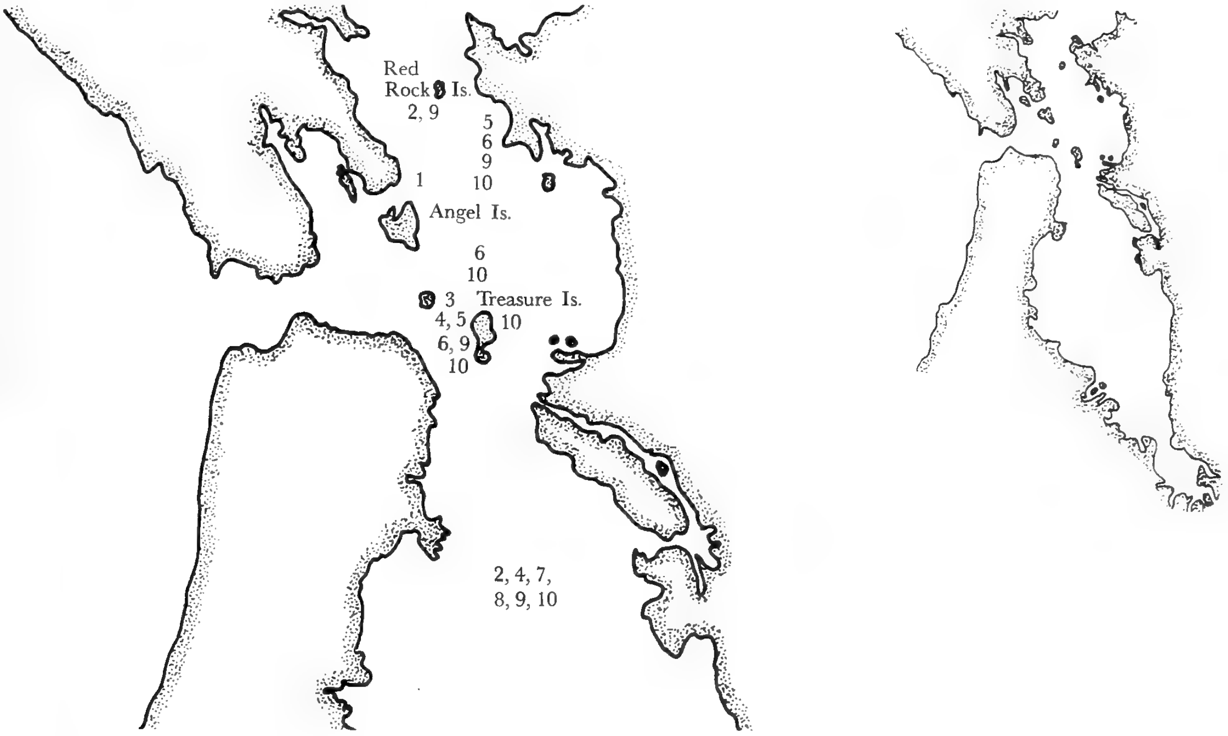


Figure 1

San Francisco Bay from Red Rock Island on the north to South Bay. Insert shows San Francisco Bay.

1. *Acanthodoris nanaimoensis*; 2. *Aeolidia papillosa*; 5. *Armina californica*; 6. *Dendronotus frondosus*;
3. *Anisodoris nobilis*; 4. *Archidoris montereyensis*; 7. *Diaulula sandiegensis*; 8. *Dirona picta*;
9. *Hermissenda crassicornis*; 10. *Tritonia exsulans*

Biological samples were taken in San Francisco Bay using an Otter trawl and a bag dredge periodically from May 1966 to August 1971. Nudibranchs were encountered frequently during the summer months and rarely in winter months.

DISTRIBUTION AND OCCURRENCE

Acanthodoris nanaimoensis O'Donoghue, 1921
July 1971
North of Angel Island
Aeolidia papillosa (Linnaeus, 1761)
July, August 1969
South of Red Rock Island; south San Francisco Bay
Anisodoris nobilis (MacFarland, 1905)
May 1968
West of Treasure Island
Archidoris montereyensis (Cooper, 1862)
July 1966; August 1971
West of Treasure Island; south San Francisco Bay
Armina californica (Cooper, 1862)
July, August 1971
West of Treasure Island; South Hampton Shoal
Dendronotus frondosus (Ascanius, 1774)
June, July 1966; July 1968; July 1971
West and north of Treasure Island; South Hampton Shoal
Diaulula sandiegensis (Cooper, 1862)
July 1966; August 1969
South San Francisco Bay
Dirona picta MacFarland in Cockerell & Eliot, 1905
December 1969
South San Francisco Bay
Hermissenda crassicornis (Eschscholtz, 1831)
July 1966; May 1968; July 1969; July 1971
South San Francisco Bay; west of Treasure Island; South Hampton Shoal; south of Red Rock Island
Tritonia exsulans Bergh, 1894
May, June, July 1966; May, July 1968; January 1969; January 1970; July 1971
East, west, and north of Treasure Island; South San Francisco Bay; South Hampton Shoal

The most frequently encountered and most numerous nudibranch was *Tritonia exsulans* which occurred in the northern and southern regions of San Francisco Bay and throughout the sampling period.

During the summer months *Dendronotus frondosus* and *Hermissenda crassicornis* were dredged and maintained in the laboratory where numerous egg masses were laid.

Occurring infrequently in summer months were *Archidoris montereyensis* and *Diaulula sandiegensis.*

Aeolidia papillosa, Anisodoris nobilis and *Armina californica* rarely occurred, but when collected, numerous individuals of each species were obtained.

Acanthodoris nanaimoensis and *Dirona picta* were represented by single individuals only.

Literature Cited

Aplin, J. A.
1967. Biological survey of San Francisco Bay 1963-1966. Calif. Dept. Fish & Game, Mar. Resources Oper. no. 67-4: 1 - 131
Behrens, David W.
1971. The occurrence of *Ancula pacifica* MacFarland in San Francisco Bay. The Veliger **13** (3): 297 - 298 (1 January 1971)
Gosliner, Terrence M. & Gary C. Williams
1970. The opisthobranch mollusks of Marin County, California. The Veliger **13** (2): 175 - 180; 1 map (1 October 1970)
MacFarland, Frank Mace
1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. **6**: xvi+546 pp.; 72 plt. (8 April 1966)
Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger **3** (Supplmt. I): 1 - 85; plts. 1 - 10 (1 February 1961)
Steinberg, Joan Emily
1963. Notes on the opisthobranchs of the west coast of North America. — IV. A distributional list of opisthobranchs from Point Conception to Vancouver Island. The Veliger **6** (2): 68 - 73 (1 October 1963)

NOTES & NEWS

Unusual Egg-Deposit by a Cuttlefish

BY

S. v. BOLETZKY

Laboratoire Arago, 66 Banyuls-sur-Mer, France

(1 Text figure)

In an aquarium, a dead cuttlefish was observed with a few eggs attached to its pendent tentacles (Figure 1). They had been laid by a female living in the same tank.

The common cuttlefish, *Sepia officinalis* Linnaeus, 1758, usually attaches its eggs, singly, to marine plants, branches of gorgonians, twigs or similar objects (Bott, 1938). In general, eggs are laid in great numbers, on the same spot, regardless of whether or not other supports are available (Grimpe, 1928). The eggs are attached to a support by two processes of the egg-case; these are fastened, by using the tips of the lateral arms, around the support so as to form a ring. In captivity, cuttlefish drop their eggs to the bottom if a suitable support is not available (Grimpe, *op. cit.*).

As Grimpe reported, it is rare that eggs are laid on non-sedentary animals such as crabs, brittle-stars or even sea-horses.

The observation of eggs laid on the pendent tentacles of a dead (or moribund) cuttlefish might illustrate how stimulating these vertical structures, having an ideal diameter for fastening eggs, are for a female *Sepia* ready to spawn. However, under similar circumstances this mode of egg-deposit had never before been observed by the author.

In view of the fact that only a few eggs were attached to both tentacles of the dead animal, it may be assumed that the female cuttlefish had started spawning at early dawn when, in the opaque concrete tank, the pendent tentacles became barely visible. With increasing light, the visual association of the egg-support with the fellow-cuttle floating at the surface (moribund and dead cuttlefish have strong positive buoyancy) may have inhibited further egg-fastening; presumably, the numerous eggs lying on the bottom of the tank were then released.

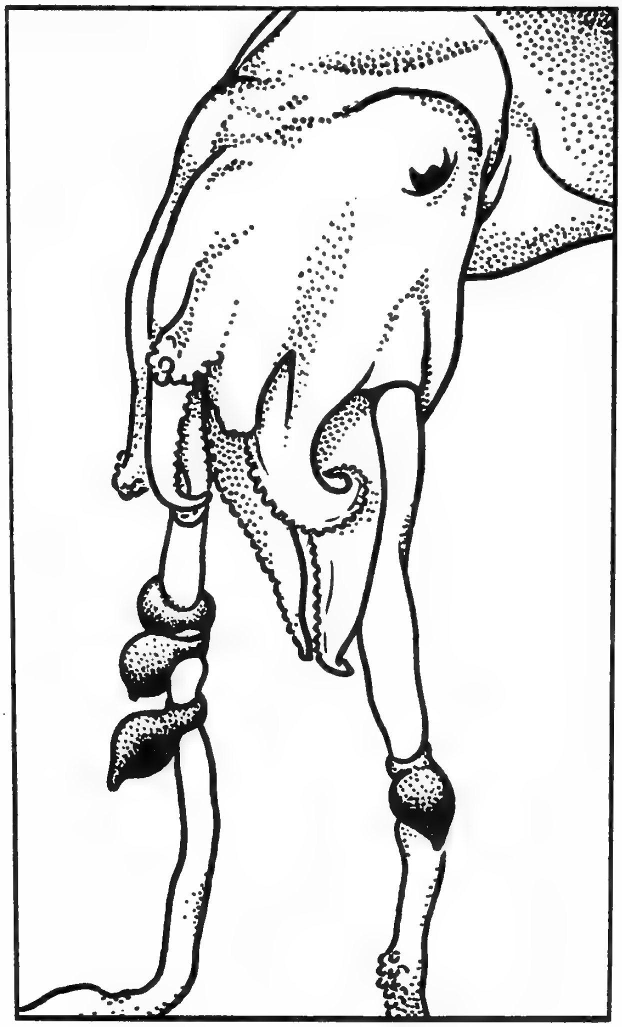


Figure 1

Dead specimen of *Sepia officinalis*, with eggs attached to its tentacles

Literature Cited

Bott, Richard
1938. Kopula und Eiablage von *Sepia officinalis* L. Zeitschr. Morphol. Oekol. d. Tiere **34** (1): 150 - 160

Grimpe, Georg
1928. Pflege, Behandlung und Zucht der Cephalopoden für zoologische und physiologische Zwecke. Abderhalden Handb. biol. Arbeitsmeth. IX, **5**: 331 - 402

The San Diego Shell Club Does It Again!

For the fourth year in a row, the San Diego Shell Club has made a generous contribution to the Veliger. This latest donation has been added to the Veliger Endowment Fund, where it will help us to achieve our eventual goal: to keep membership dues to the lowest possible level without reducing either size or quality of our journal. Thus, all future members of our society will benefit from this repetition of the Club's generosity.

The California Malacozoological Society, Inc.
announces

Backnumbers of

THE VELIGER

and other publications

Volumes 1 through 8: out of print

Volume 9: $22.-
Volume 10: $24.-
Volume 11: $24.-
Volume 12: $28.-
Volume 13: $24.-
Volume 14: $28.-

Supplement to Volume 3: $6.-* plus $-.75 handling charge
[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;

Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

[The two parts are available separately at $3.- each plus a handling charge of $-.75 or as indicated above. If purchased separately, each part is subject to the California State sales tax if mailed to California addresses.]

Supplement to Volume 7: $2.-* plus $-.60 handling charge
[Glossary of A Thousand-and-One Terms used in Conchology, compiled by Winifred H. Arnold]

Supplement to Volume 11: $5.-* plus $-.75 handling charge.
[The Biology of *Acmaea* by Prof. D. P. Abbott *et al.*, ed.]

Supplement to Vol. 14: $5.-* plus $-.75 handling charge
[The Northwest American Tellinidae by Dr. E. V. Coan]

Items marked with * are subject to sales tax in the State of California; residents of that State please add the appropriate amount to their remittances.
Prices subject to change without notice.

Send orders with remittance to:
Mrs. Jean M. Cate, *Manager,* Post Office Drawer R, Sanibel, Florida 33957. Please make checks payable to C. M. S., Inc.

Shipments of material ordered are generally made within two weeks after receipt of remittance.

Subscription to Volume 15: $18.- domestic, $19.50 in Canada, Mexico, Central and South America; $20.- in all other foreign countries.

{We are pleased to announce that we have completed arrangements with Kraus Reprint Co. to reprint those of our publications that are out of print. Inquiries regarding the availability and price(s) of desired items should be addressed to:

Kraus Reprint Co.
16 East 46th Street,
New York, N. Y. 10017

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first working day of the month following receipt of the remittance. The same policy applies to new members.

Affiliate Membership for the fiscal year July 1, 1972 to June 30, 1972 has been set at $8.-. Postage for members in Canada, Mexico, Central and South America $1.50, for members in any other foreign country $2.- additional.

Effective January 1, 1967 there will be an initiation fee of $2.- for persons joining the Society.

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.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $2.50 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Supplements

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

Requests to be placed on this special mailing list should be sent to the Manager, Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957.

General Notices

REGARDING POSTAL SERVICE

While increases in postal charges were anticipated, the actual amount involved could not be ascertained until 4 days before the effective date. Thus, we have been unable to adjust our membership dues and subscription rates to cover these increases. Effective immediately, we must also raise our handling charges for backissues and other materials. Further, we will not acknowledge the receipt of manuscripts, unless an addressed envelope with the necessary postage is enclosed.

We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address). We are not able to replace lost copies free of charge but must charge single copy rates. There will, of course, be only the usual charge of $1.00 for re-forwarding a copy *IF* it has been returned by the post office to us. We also must urge our members and subscribers to place written complaints with the U. S. Post Office Department in case of loss, as every copy of our journal carries our guarantee for return postage. Thus, destruction of a copy of our journal by postal employees constitutes gross negligence and the person concerned deserves an official reprimand, at least.

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. Post Office 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.

Moving?

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

change of address – $1.-
change of address and re-mailing of a returned issue – $2.-.

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.

CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Endowment Fund

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

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

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

INFORMATION DESK

What's the Difference?

Authorship of a Taxon

BY

EUGENE V. COAN

Department of Geology, California Academy of Sciences
Golden Gate Park, San Francisco, California 94118

THERE HAS BEEN no little confusion about the interpretation and citation of the authorship of taxa. According to Article 51(a) of the International Code of Zoological Nomenclature (STOLL, *et al.*, 1964), "The name of the author does not form part of a taxon and its citation is optional." However, authors' names are almost always cited in zoological publications for clarity, for bibliographic purposes, to prevent confusion among homonyms, and for historic reasons.

The Code establishes a clear basis for decisions about the authorship of taxa, or put another way, the responsibility for taxa:

> "Article 50. Author of a name. — The author (authors) of a scientific name is (are) the person (persons) who first publish(es) it ... in a way that satisfies the criteria of availability ..., unless it is clear from the contents of the publication that only

one (or some) of the joint authors, or some other person (or persons), is alone responsible both for the name and the conditions that make it available."

The key phrases in this part of Article 50 are: "the criteria of availability" and "the conditions that make it available." If a species or other taxon is validated in a work, the author of that taxon is the author of the entire work or of some subunit of the work containing the taxon and the features that validate the name. This person is not necessarily the person who first recognized the taxon to be new and who first thought up the name.

Sometimes we may choose to add to our citation of the "official" authorship of a taxon additional bibliographic information, either about the larger work of which a subunit is a part or about who thought up the new name. In either case, the main criterion for doing so is clarity.

For instance, information about the person who invented the name is often included to clear up past or potential confusion about a taxon's authorship. This is generally done only in major revisions or systematic reviews. For example:

Macoma inflata Dawson, 1872, *ex* Stimpson MS

This species was described by an author, Dawson, in his own work, but the species was first recognized and its name invented by another person. The courtesy reference "*ex* Stimpson MS" is optional, but I would include it because it clarifies an often confused authorship.

Information about the author of a larger, encompassing work is especially useful and is often added if some subunit of a larger work is not a formal and easily or generally cited part in a Bibliography or Literature Cited section. For example:

Macoma orientalis Scarlato, *in* Golikov & Scarlato, 1967

This is a species described by only one author in a work by two authors. The description of this species is not a formal and easily cited section of the entire article, so the more complicated combination is necessary to key a reader to a Literature Cited section.

Another example:

Choristes Carpenter, *in* Dawson, 1872

The description of this new genus was the only part of the article by Carpenter.

On the other hand, workers rarely do the following:

Tellina rotundata Sowerby, *in* Reeve, 1867

Sowerby's monograph on *Tellina* is in Reeve's "Conchologia Iconica," the parts of which are generally cited alone. "Sowerby, 1867," would be sufficient. Details about the location of Sowerby's monograph in Reeve's set, like details about an article in a journal, can be reserved for the Literature Cited section.

A further example:

Tellina proxima Sowerby, *in* Gray, 1839, *ex* Brown MS

Here the section by Sowerby includes more than just the description of this one species, but the section is small and not generally cited by itself; therefore a full citation is given. The "*ex* Brown MS," on the other hand, is not essential and would be given only in a major revision.

More difficult problems of interpretation arise in the case of works published anonymously. If the true author of a work is known or later becomes known but was not indicated in the original, the author's name is cited in square brackets following Recommendation 51A of the Code. An example:

Conus araneosus [Lightfoot, 1786], *ex* Solander MS

Not only was the "Portland Catalogue" an anonymous publication by Lightfoot, but it was largely based on previous work by Solander. The citation "*ex* Solander MS" is not essential. When a species is transferred from an original genus to another, the square brackets should be placed inside the resulting parentheses, although some workers prefer to drop them to avoid clutter.

The principle of responsibility also applies in the case of posthumous publication. If a work is published substantially as the deceased left it, even after a considerable passage of time, then the deceased remains the author of the taxa therein. Two examples:

Tegula eiseni Jordan, 1936

Eubranchus occidentalis MacFarland, 1966

If, on the other hand, a work is much edited, rewritten, and otherwise changed, the author is the person responsible for the actual publication. For example:

Distorsio Röding, 1798, *ex* Bolten MS

This book was partly the work of Bolten, including the creation of the new names, but it was so substantially rewritten by Röding that he is now considered to be the author.

Literature Cited

STOLL, NORMAN RUDOLPH *et al.*, (editors)
1964. International code of zoological nomenclature adopted by the XV International Congress of Zoology, ed. 2. London (Intern. Trust for Zool. Nomencl.) i - xx + 1 - 176; 5 appendices & glossary

BOOKS, PERIODICALS, PAMPHLETS

Tertiary Molluscan Fauna from the Yakataga District and Adjacent Areas

by Saburo Kanno. Paleontological Society of Japan, Special Paper No. 16, pp. 1 - 154; 18 plts. Paleontological Society of Japan, % Department of Geology, Kyushu University, Fukuoka (Hakata), 812, Japan. $15.00. December 25, 1971.

This is the first thoroughly illustrated modern treatment of Tertiary molluscan fauna from the Gulf of Alaska. Emphasis is on Miocene molluscan assemblages from the Poul Creek and Yakataga Formations. Included among the 104 molluscan taxa are several new species and many western Pacific species previously unknown from Alaska. The bulk of the report consists of a thorough taxonomic treatment of these mollusks including detailed analysis of species of the extinct nautiloid *Aturia* and the deep water bivalve *Calyptogena*.

Of particular interest are the author's biogeographic and paleoclimatic inferences. Early Miocene assemblages from the Poul Creek Formation are of warm water aspect and have strong affinities with faunas from lower latitudes in the eastern North Pacific. Middle Miocene assemblages from the overlying Yakataga Formation, however, are of cold water aspect and are characterized by species from Miocene faunas of Hokkaido and Kamchatka of the western North Pacific.

This will be an extremely useful reference for anyone interested in the origin and migration of shallow water Tertiary faunas of the North Pacific. It is superbly illustrated and is written in English.

W. O. Addicott

Molluscan Digest

the International Publication for Malacological Research. Steven J. Long and Jack Brookshire, eds.

Sample copies are available at US$0.75 each from Steven J. Long, 110 Cuyama Avenue, Pismo Beach, California 93449.

Number 3 of the second volume has just reached our desk. It is gratifying to see the steady development into an ever more useful publication of this monthly magazine. In view of the ever increasing - in spite of price freezes and Phases - one is astonished at the modest price of the publication ($4.50 for private individuals in the United States, Canada and Mexico and $5.50 in other countries).

In addition to the "Current Citations," a list the editors endeavor to make as complete and as up-to-date as possible, there are usually about 2 pages of "Personal Notes" with information on current research or "Current Events" with information on recent and future meetings of interest to malacologists.

RS

Malacological Review

vol. 3, continued. Pages 103 to 192; illustrated.

Five research papers and several brief communications are contained in this, the concluding number of the third volume of the periodical. Its delivery was delayed partly by difficulties in obtaining the necessary permission and by the prolonged dock strike on the Pacific Coast of the U. S. A.

vol. 4, no. 2: pp. 121 to 290; illustrated.

In addition to several research papers and brief communications, this issue provides information on the publication dates of the earlier issues of 'Malacological Review.' It also contains a number of book reviews as well as the reproductions of the tables of contents of various malacological publications. This latter feature, as far as we are aware, was an innovation by this publication and is of great help to all serious workers who may not have ready access to a first-rate private or public library subscribing to the many journals. In view of the very great service this review provides, the subscription rate of $5.00 for private subscribers in North America and $5.50 for non-North American private subscribers is unbelievably modest. Institutional subscriptions are $8.00 if placed directly and $9.00 if placed through subscription agents. This differential is made to compensate for the extra handling required. In our own experience we would conclude that this is really an inadequate difference. Subscriptions can be entered at Post Office Box 801, Whitmore Lake, Michigan 48189.

RS

Australian Shells

Illustrating and Describing 600 Species of
Marine Gastropods from Australian waters

by B. R. Wilson & Keith Gillett. 168 pp. of which about half are full-page color plates. Charles E. Tuttle Company, Rutland, Vermont. $21.50. Published in 1972.

We could express our impression of this book in a single word: Magnificent! However, there is more to it than just the exquisite photography and the extraordinarily fine color reproductions. There is also the text which is of equally high quality, both in 'literary style', if such a term may be applied to a work of this sort, and its truly scholarly approach.

In the introduction, Dr. Wilson gives some information on classification and names of Australian shells as well as a good outline of the biology of gastropods in general (anatomy, reproduction, etc.). The main body of the book is, of course, devoted to the illustration and description of the 600 species. Especially spectacular are the photographs of many living animals, showing that the body of a snail may be as spectacularly colored and patterned as the shell. This aspect may come as a welcome surprise to many shell collectors who never had the opportunity to 'get their feet wet' and who have been limited in their efforts to purchase and exchange of the empty shells.

It may be worth mentioning that the number of pages is no real indication of the size of the book: the pages are approximately 22 by 28.5 cm (8.5 by 11 inches).

If our readers gained the impression that we like the book – they are quite correct.

RS

Opisthobranchia (Mollusca) from the Mediterranean Waters of Israel

by A. Barash & Z. Danin. Israel Journal of Zoology, vol. 20, pp. 151 - 200; 2 maps; 3 plates. 1971.

This work, dealing with a portion of the Mediterranean Sea heretofore little explored, is based on collections made during the past 20 years or so. The authors stress the fact that the Pyramidellidae are not included in this report. There are 70 species of opisthobranchs, of which 43 are reported from this area for the first time. In an extensive table the authors present information also on the distribution of the species outside of Israel. In the text part, under the entry of each species, are given collecting localities with benthic and substrate data, as well as localities reported in the literature with bibliographic references.

This paper is of importance to the student of opisthobranch distribution and of Zoogeography in general.

RS

A Catalogue of Living and Fossil Cowries

Taxonomy and Bibliography of Triviacea and Cypraeacea
(Gastropoda Prosobranchia)

by Maria Schilder & Franz Alfred Schilder.
Mémoires, Institut Royal des Sciences Naturelles de Belgique, 2nd series, part 85: 246 pages; with a preface by Maxime Glibert. Published in 1971.

The number of pages is scarcely an indication of the great wealth of information presented in this work. It is based on about 80 years of combined study by the two authors. In their efforts to organize the immense amount of detailed information, the authors have, over the years, developed an ingenious system of symbols and special abbreviations. The most recent innovation, perhaps, is their method of identifying literature citations which, in their system, will always remain the same, no matter where published in connection with what other papers cited. Instead of using the letters a, b, etc. for distinguishing different papers by the same author published in the same year, they use a capital letter taken from an initial of an important word in the title of the paper. Some of the other symbolism employed by the authors can be learned easily enough by the constant user of the works by the Schilders. In these days of the ever mounting costs of publication, the possible slight inconvenience of having to familiarize oneself with this system is amply justified.

The present work was completed only after the death of Dr. Franz Schilder. However, Dr. Maria Schilder was more than just qualified to see the work through its final stages.

The entire work can be described essentially as three lists: a systematic list of all sufficiently characterized taxa, arranged according to the authors' view at the time of the preparation of the manuscript; an alphabetical list of all 3720 names proposed for cowries with exact references and a bibliography of 3650 titles of books and papers concerning cowries. It is impossible, without going into lengthy details, to give an adequate idea of the wealth of information packed into these relatively few pages. It is a case of 'seeing is believing.'

RS

Studies in Tropical American Mollusks

Edited by Frederick M. Bayer & Gilbert L. Voss. Coral Gables, Florida 33124: University of Miami Press, 236 pages, illustrated. Cloth, $12.50. 1 November 1971.

This book contains four papers: Cephalopods collected in the Gulf of Panama by Gilbert L. Voss (included are descriptions of 3 new species of *Octopus* and a new genus, *Euaxoctopus* with the new species *E. panamensis*; in addition to the discussion of previously known species collected in the Gulf of Panama, of which 11 species are new records for the area); Mollusks from the Gulf of Panama by Axel A. Olsson (2 new species of Bivalvia and 13 new species, 1 new genus and 1 new subgenus of gastropods are described); The Conidae of the Pillsbury Expedition by James Nybakken (11 species were obtained; of these *Conus poormani* Berry, 1968 is here illustrated for the first time); and New and unusual Mollusks collected, by Frederick M. Bayer (55 species of gastropods are reported, of which 15 are new; 1 new genus and 2 new subgenera are also established; 4 species of bivalves, of which 2 are new, including 1 in a new genus, are discussed).

The illustrations are of high quality throughout and the collection of these four papers constitutes an important contribution to malacology.

RS

Le Monde Vivant des Atolls

Polynésie française Tuamotu-Gambier

published by *Société des Océanistes*, Musée de l'Homme, Paris XVI^e, **28:** v+148 pp.; 1 map; 43 plates, some color.

This beautifully illustrated book contains various chapters contributed by different specialists. Of special interest to our readers is Chapter 5 on the molluscan fauna, pages 37 to 56 with plates 12 to 17.

According to the preface, this book contains a collection of articles presented in a way to transmit to the reader a coherent picture of an atoll and its flora and fauna. No claim is made that it contains important new discoveries. It is, however, a charmingly compiled and very well written collection of essays in a easily understandable vein.

We regret that we cannot inform our readers what the book costs; however, this information may be obtained, no doubt, from the Société des Océanistes in Paris.

RS

Kelp Habitat Improvement Project

Annual Report, 1 July, 1970 – 30 June, 1971. Wheeler J. North, Principal Investigator. W. M. Keck Laboratory of Environmental Health Engineering, California Institute of Technology, Pasadena, California. ix+150 pp.; illustrated; published in 1972.

This is the 8th of these annual reports. Evidence presented indicates that the investigators seem to be well on the way to the finding of a solution of the problem of re-establishing the once plentiful kelp beds off the coast of Southern California.

RS

of Sea and Shore

Vol. 3, No. 1: 50 pages, illustrated; color pictures of shells on front and back covers. Published by 'of Sea and Shore' Publications, Post Office Box 33, Port Gamble, Washington 98364.

With this issue the separately published book by Glenn and Laura Burghardt, entitled 'West Coast Chitons' is being reprinted, one portion at a time. The color plates from that work are inserted separately and loose, so that at the conclusion of volume 3 of 'of Sea and Shore' the subscribers will have the complete book.

Various articles, all well illustrated, complete this issue.

RS

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.

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 other 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, may be published in the column "NOTES and NEWS"; in this column will also appear notices of meetings of regional, national and international malacological organizations, such as A. M. U., U. M. E., W. S. M., etc., as well as news items which are deemed of interest to our Members and subscribers in general. Articles on "METHODS and 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, and 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.

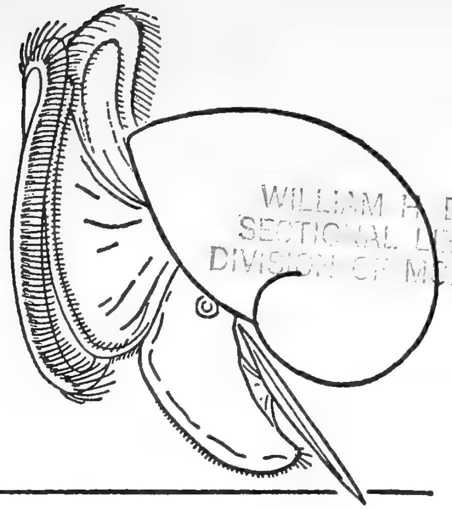
Manuscripts should be typed in final form on a high grade white paper, not exceeding 8½" by 11", at least double spaced and accompanied by a clear carbon or photo copy. A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon 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.

EDITORIAL BOARD

EDITOR-IN-CHIEF

ASSOCIATE EDITOR

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

Volume 15 October 1, 1972 Number 2

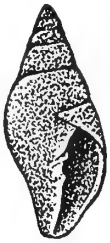
Contents

[Continued on Inside Front Cover]

Distributed free to Members of the California Malacozoological Society, Inc.
Subscriptions (by Volume only) payable in advance to Calif. Malacozool. Soc., Inc.
Volume 15: $18.- Domestic; $19.50 in the Americas; $20.- in all other Foreign Countries
Single copies this issue $10.-. Postage extra.
Send subscription orders to Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957. *Address all other correspondence to* Dr. R. Stohler, *Editor,* Department of Zoology, University of California, Berkeley, California 94720

Second Class Postage Paid at Berkeley, California

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

Observations on Removal of Spines by Muricid Gastropods During Shell Growth

BY

MELBOURNE R. CARRIKER

Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

(3 Plates)

INTRODUCTION

WHILE INVESTIGATING the comparative functional morphology of the boring mechanism of muricacean and naticacean gastropods (CARRIKER, 1961), we had an opportunity to observe the behavior of many of the snails closely. Two species of Muricidae, *Murex brevifrons* Lamarck, 1822 and *Murex fulvescens* Sowerby, 1834, whose shells are ornamented with conspicuous varices and spines which run the breadth of the whorls, particularly drew our attention because of the possible role of the accessory boring organ (CARRIKER, 1969; CARRIKER & VAN ZANDT, 1972) in removal of the spines during shell growth.

As pointed out by FRETTER & GRAHAM (1962) and by ROBERTSON (1965), in the process of spiral growth of the helicocone, the snail has to remove the older spines which come to lie along the inner lip of the aperture in order to make room for the new shell of the enlarging body whorl. If the spines were not removed, they would block the aperture and interfere with the movements of the snail in and out of its shell. In the case of *Murex brevifrons,* blockage would be almost complete; in that of *M. fulvescens,* only partial.

How snails remove these spines has not been reported. Since the molluscan mantle has the capacity to secrete shell as well as to remove what it has deposited (FRETTER & GRAHAM, 1962; SMITH, 1969; SOLIMAN, 1969), Fretter and Graham postulated that the spines and varices may be resorbed by the mantle. ROBERTSON (1965) hypothesized that the spines may be broken or rasped off, or may be removed chemically, possibly by the same means that boring snails use to excavate holes in the shell of prey.

In *Murex brevifrons* and *M. fulvescens* a strong thick varix is formed at the edge of the outer lip of the body whorl at regular intervals. Each varix represents a resting period in the growth of the shell. The intervarices of the shell represent active periods of shell deposition. Little is known about how long it takes snails to lay down the spines or the shell between the varices. ABBOTT (1954) suggested less than two days for growth from one varix to the next in Muricidae.

This paper reports the results of observations in the laboratory on the deposition of shell and the removal of spines during growth of the body whorl from one varix to the next in *Murex brevifrons* and *M. fulvescens.*

ACKNOWLEDGMENTS

John W. Blake and Langley Wood assisted in the investigation. Dr. Juan A. Rivero had *Murex brevifrons* sent from Puerto Rico, and Paul Shave later collected snails of the same species in the same area. Dr. Virginia Peters collaborated in the use of the scanning electron microscope. The research in 1959 was supported in part by a grant from the U. S. Fish and Wildlife Service; that in 1968 and thereafter by Public Health Service Research Grant DE 01870 from the National Institute of Dental Research. This assistance is gratefully acknowledged. Systematics-Ecology Program Contribution No. 268.

MATERIALS AND METHODS

The specimens of *Murex brevifrons* were collected in the vicinity of Mayaguez, Puerto Rico, packed moist, and shipped by airmail. The snails survived the flights in good condition, fed actively, grew new shell, and deposited egg capsules in our running seawater trays. We collected specimens of *M. fulvescens* on a rock jetty off Shackleford Banks, North Carolina. These individuals likewise acclimatized readily to laboratory conditions. Both species were fed oysters, *Crassostrea virginica* (Gmelin, 1791).

Principal observations were made at the Institute of Fisheries Research, University of North Carolina, Morehead City, during the period August 1 to September 11, 1959. Salinity of the seawater ranged from 31 to 35‰ and the temperature from 24 to 29° C. Both species came from high salinity, partially sheltered habitats. Supplementary observations were made on individuals of *Murex brevifrons* at the Marine Biological Laboratory in 1968. Salinity of the seawater in running seawater trays was approximately 32‰ and the temperature ranged from 20 to 21° C. In both laboratories snails were illuminated by daylight coming through the laboratory windows, and during the early part of the evening by standard overhead artificial light.

For the observations in 1959, five *Murex brevifrons,* ranging in shell height from 64 to 95 mm, were placed in an aquarium 30 × 30 × 60 cm in size; and six *M. fulvescens,* ranging in shell height from 95 to 100 mm were set in a similar tank. A stream of seawater about 7 mm in diameter ran into and overflowed from each aquarium. The tanks had wooden ends and glass on two sides, and were placed with one glass side against the wall so that the back was partially shaded. Position and feeding activity of the snails were watched through the front glass and top of the aquaria. To examine the amount of deposition of new shell and progress in removal of spines, we lifted snails off the bottom without taking them out of the water. To photograph them, we removed them from the water for brief periods. Frequency of examinations varied from daily to weekly, depending upon the rate of shell deposition and proximity of the mantle edge to the base of the spines. We marked *M. brevifrons* by tying fine red plastic twine of various lengths to one of the large dorsal spines. Individual *M. fulvescens* were identified by shell form.

Microscopic examination of shell spines was done with a JEOLCO scanning electron microscope, JSM-U3, in Woods Hole, Massachusetts. Spines which were partly eroded at the base in living *Murex brevifrons* were broken off, rinsed in distilled water, dried quickly, coated with gold in a vacuum evaporator, and studied at magnifications ranging from 45 to 5 000 ×.

OBSERVATIONS

During the varix periods (Figure *1*) when no shell growth was taking place, snails crawled actively about the aquaria, bored oysters, and fed voraciously through their boreholes. At the onset of the intervarix period and deposition of new shell, they crawled to the shaded parts of the aquaria and remained there with little or no movement, the foot firmly appressed to the substratum. They remained relatively stationary until the end of the intervarix period. During this period they were difficult to dislodge from the bottom. When placed at the lighted side of the aquaria, snails returned to the more shaded spots. Dislodgment from the bottom caused them to retract within the shell, generally drawing the operculum into the aperture. In the hope of watching the normal activity of the mantle edge at the base of the spines under water, we had placed squares of clean glass plate on the bottom of the aquaria; glass on which a snail might settle could then be upended to bring the aperture into view without disturbing the snail. Unfortunately, the snails avoided the glass plates.

We were able to follow closely the cleaning of the parietal area, removal of spines, and deposition of new shell by several *Murex brevifrons.* Observations on one individual (Table 1) were confirmed by those on others. During

Explanation of Figures *1* to *6*

Figure *1*: Apertural view of *Murex brevifrons* in the varix stage. To the snail's right (bottom of photograph) is the most recently formed varix and row of spines along the edge of the outer lip, and to the left (top) is an older varix and row of spines which will be removed as the body whorl grows 1.5 ×

Figure *2*: Apertural view of *Murex brevifrons* in an early phase of the intervarix stage. A thin layer of new shell is being deposited on the outer lip, and the base of the spines and shell surface on the inner lip are being eroded 2 ×

Figure *3*: Apertural view of *Murex brevifrons* at the end of the intervarix stage. The old row of spines has been completely removed. The thin new intervarix shell of the body whorl has been formed, and the lacy, convoluted, outturned flanges of the lip mark the location of the new varix and new row of spines 2 ×

Figure *4*: Apertural view of *Murex fulvescens* in an early phase of the intervarix stage (comparable to that in Figure *2*). Thin new shell is being added to the outer lip, and the base of the spines and parietal shell surface are being eroded 1.2 ×

Figure *5*: Close view of a spine of *Murex fulvescens* on inner lip of aperture whose base has been almost completely eroded. The parietal surface in front of and between the spines has also been eroded. Mid intervarix stage 4 ×

Figure *6*: Apertural view of *Murex fulvescens* at the beginning of the varix stage, photograph taken 10 days after that in Figure *4*. The row of new spines on the outer lip is almost completely formed, the inner lip has been coated with a glaze of new shell, and a zone of new shell, 11 mm in width, has been added to the outer lip 1.5 ×

Figure *1*

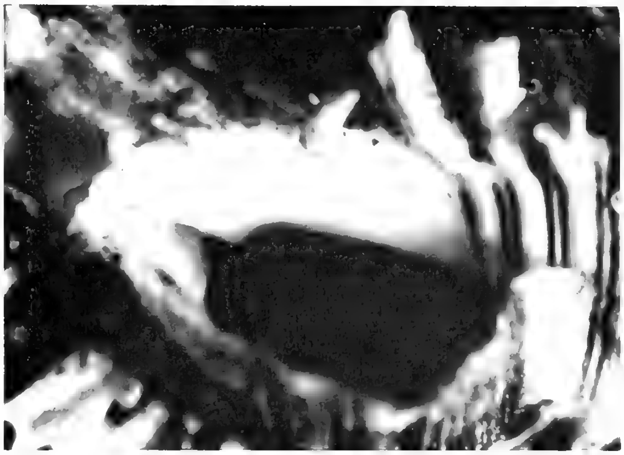


Figure *2*

Figure *3*

Figure *4*

Figure *5*

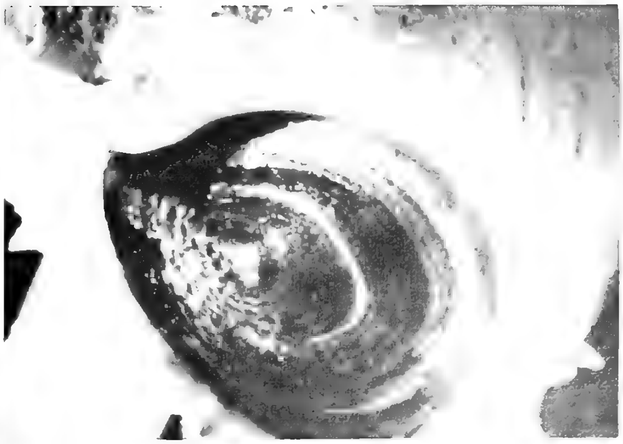


Figure *6*

Table 1

Rate of deposition of shell on body whorl and removal of spines by *Murex brevifrons* during one intervarix period, August 7 to September 11

Days	Shell Height	Snail Activity	Width of New Shell Added to Outer Lip	Fate of Spines on Inner Lip
0	64 mm	End of feeding period	None	Spines intact (Figure *1*)
12		Inactive	Trace	Inner lip eroded to base of spines
18		Inactive	4 mm	Base of spines being eroded (Figure *2*)
31	69 mm	Inactive	26 mm	Spines removed and stumps covered with new parietal shell
35	74 mm	End of inactive period	30 mm, including new varix and flaring base of new spines	Position of removed spines now almost on the level with new varix at posterior base of aperture (Figure *3*)

the intervarix period which lasted about 35 days, this snail grew from 64 to 74 mm in shell height, and added a maximum width of 30 mm of new intervarix shell to the outer lip, most of the new varix, and the accompanying row of spines.

As accurately as we could determine, it took this snail about 8 to 10 days to remove a single row of spines. Incompletely removed spines showed conspicuous evidence of erosion at the base just above the level of attachment to the parietal area of the aperture and on the side facing the mantle edge (Figure *2*). The area of erosion was restricted to the parietal area and to the base of the spines. Spines were removed close to the surface of the inner lip so that after the new coat of shell had been deposited over the newly cleaned parietal area, there was no trace of them (Figure *3*). The freshly deposited intervarix shell on the outer lip was extremely thin (Figure *2*). During the following varix period this was thickened by deposition of more shell interiorly by the mantle, resulting in the characteristically thick valve of the species.

The manner and time for removal of spines by *Murex fulvescens* was approximately similar to that by *M. brevifrons* (Figures *4* to *6*). The snail in Figure *4*, for example, had deposited a rim of thin new shell 12 mm wide on the outer lip, and dissolution of the parietal area and the base of the spines had begun. Ten days later (Figure *6*) the spines had been completely removed and the parietal wall had been coated with a smooth layer of shell which completely hid the site of the original row of spines.

The advancing edge of erosion of the surface of the shell in the inner lip was more or less uniform up to the spines. As the base of the spines was attacked, areas of shell removal extended between the spines and slightly beyond (Figures *2, 4*). After the spines had been removed, the border of erosion again straightened.

Study by scanning electron microscopy of the partially eroded base of the spines of *Murex brevifrons* clearly revealed a delicately etched shell surface, and exposed a strikingly variegated pattern of complexly oriented shell prisms (Figures *7* to *10*; *11* to *14*). Figures *7* and *8* are low magnifications of the area of solution of the shell at the base of two spines. The topography of the eroded areas was divisible into an upper portion with conspicuous vertical striae, and a lower portion in which the striae were much less prominent and ran horizontally. Two prominent keels on each side of each spine separated the front from the sides.

No radular rasp marks were visible on the eroded surfaces of the spines. When rasping hard surfaces, muricid snails employ mainly the tricuspate rachidian teeth (Carriker & Van Zandt, 1972). The width of rachidian teeth in *Murex brevifrons* ranged from 200 to 300μ, and the distance between the points of adjacent cusps varied from 65 to 75μ. Thus had rasp marks been present, the interval between the individual cusp traces would have ranged between 65 and 75μ. At a magnification of 45 × (Figures *7, 8*) the traces would have been about 3 mm apart; at a magnification of 100 × (Figure *9*), about 7 mm apart.

At low magnifications (Figures *7, 8*) the striae, but for their branching, did resemble rasp marks; at higher magnifications (Figure *10*; Figures *11* to *13*), however, the striae resolved into differentially dissolved strata of shell prisms. The ridges of the vertical striae (Figures *10*; *11, 12*) were comprised of slender prisms whose long axes came close to paralleling the general plane of dissolution, whereas the narrow depressions represented similar prisms whose ends abutted more nearly at right angles to the plane of dissolution. In the horizontal striae the difference in elevation between the layers of prisms was slight, and the long axes of the prisms in the ridges and the valleys, though appearing at approximately right angles to each other, formed nearly similar angles with the plane of dissolution (Figures *13, 14*).

DISCUSSION AND CONCLUSIONS

These observations demonstrated that removal by *Murex brevifrons* and *M. fulvescens* of spines obstructing the aperture during growth of the shell is done by chemical dissolution at the mantle edge. After the base is eroded through, the spines fall away. This conclusion is based on the pattern of the advancing edge of dissolution over the parietal area to, and past, the spines, the ultrastructural appearance of the eroded surface, and the absence of rasp marks on the eroded area. The remarkable capacity of the gastropod mantle to function both in shell dissolution and deposition is mentioned briefly by Fretter & Graham (1962). What portion of the complex mantle border secretes the dissolving substance, and what portion deposits shell, or whether the same tissue functions alternately in shell formation and shell dissolution, are not known. If the latter were the case, it would be interesting to speculate on the nature of the snail's integrating mechanism which brings this about, and what triggers the change from dissolution to deposition. Related aspects of the problem of shell deposition were treated by Bevelander & Nakahara (1970), Digby (1968), Saleuddin (1970), and Wilbur (1964).

Because of the active role of the radula in boring holes in shell of prey (Carriker & Smith, 1969; Carriker & Van Zandt, 1972), we anticipated when the study was begun that the radula might be involved in removal of the spines. There is no apparent anatomical barrier to such a possibility as the proboscis of these snails is long enough to permit rasping around the inner lip of the aperture. Although we found no evidence of rasp marks on the eroded portion of the spines, even with the scanning electron microscope, the possibility may exist that we examined the snails at a time when only chemical activity was taking place. Since, however, the mantle edge dissolves the surface of the parietal area as well as the base of the spines, it is more likely, as our observations suggest, that the operation of cleaning the shell surface and removing obstructions as the body whorl enlarges is done entirely by the mantle. Furthermore, the hardness of the shell of these snails would suggest, as is the case with *Urosalpinx cinerea* (Carriker & Van Zandt, 1972), that radular cusps, if used, would have only minor impact on the surface of the spines anyway.

Examination with the scanning electron microscope of the dissolved surface of the spines revealed an unexpectedly complex organization of strata of shell prisms. Interdigitation of the strata in the spines undoubtedly contributes to the strength of these structures. MacClintock (1967) described the light microscopical structure of the shell of patelloid and bellerophontoid gastropods in detail, and illustrated crossed layers similar to those in the spines of *Murex brevifrons.*

Prisms whose long axes tended to parallel the surface of dissolution comprised the ridges of the striae, and those ending most nearly at right angles to the surface of dissolution formed the depressions. This pattern suggests that the sides of the prisms were slightly less soluble to the secretion of the mantle than the ends of the prisms. Differential dissolution may have resulted from the orientation of the molecules in the prisms, or from more protection afforded the sides of the prisms than the ends by the organic matrix. The matter needs experimental verification.

Whether the prominent keels on the base of the partially dissolved spines resulted from the way the mantle edge

Explanation of Figures 7 to *10*

Figure *7*: Scanning electron micrograph of the base of a spine in the mid intervarix stage of *Murex brevifrons* showing the three faces of the eroded region 45 ×

Figure *8*: Scanning electron micrograph of a second spine in the mid intervarix stage of the same *Murex brevifrons* showing the right, middle, and part of the left faces of erosion and the fracture surface where the spine was attached to the body whorl 45 ×

Figure *9*: The juncture on the middle face of the planes of erosion illustrated in Figure *8*. Vertical striae are at the top portion and the horizontal striae are at the bottom portion of the micrograph 100 ×

Figure *10*: Vertical striae shown in Figure *9*. Scanning electron micrograph 500 ×

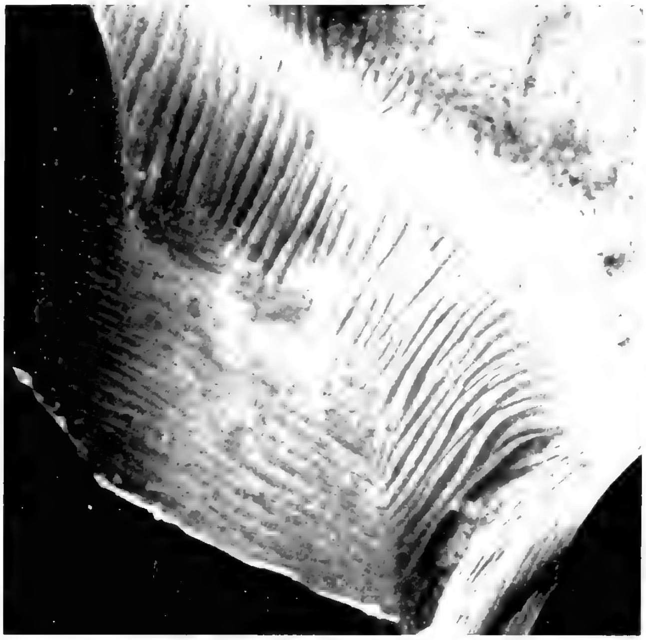


Figure 7

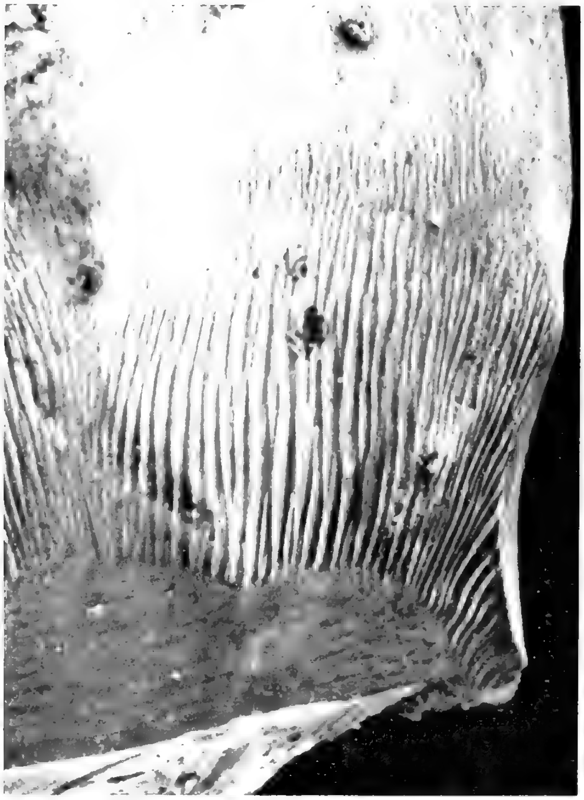


Figure 8

Figure 9

Figure 10

surrounded the spines, possibly creasing at the line of the keels, or from the presence in the keels of less soluble shell, is not known.

Because of the major role of the accessory boring organ of muricid gastropods in boring the shell of prey (Carriker & Van Zandt, 1972), we wondered if this organ might also aid in the removal of shell spines. All Muricidae which have been studied to date are shell borers, and all possess an accessory boring organ (Carriker, 1961; Carriker & Yochelson, 1968). Contrary to Wells' (1958) report, this also includes *Murex fulvescens* which bores holes primarily between the edges of the valves of its prey (Carriker & Yochelson, *op. cit.*). The "halo" which Wells observed at the inner site of entry was dissolution of shell by the accessory boring organ. From a purely functional point of view, it is difficult anatomically to visualize a muricid snail moving the extended accessory boring organ over the full length of the inner lip of the shell while cleaning the parietal area and removing the spines. Furthermore, it is questionable whether the delicate microvillar surface of the organ could withstand the abrasion, or whether the organ could produce enough secretion to accomplish the task. The mantle, on the other hand, effecting continuous close contact over the area to be dissolved, would function smoothly and economically. Not all muricid borers (*Thais lapillus,* for example), possess spines, and then there are gastropods which possess conspicuous spines (for example, some forms of *Melongena corona corona*) but are not borers (Clench & Turner, 1956). The latter are likewise faced with the problem of spine removal during shell growth. It does not seem likely, therefore, that the accessory boring organ is employed in spine removal.

The practice of secreting a thin layer of shell onto the outer lip of the body whorl during the intervarix phase which is later reinforced on the inside during the varix phase, has also been reported for other muricid snails. Mackenzie (1961), for example, observed that in *Eupleura caudata* the intervarix stage lasted about 3 weeks, and the varix stage, about 4 weeks. This is a smaller snail than the two species of *Murex* reported in this paper, and may account for the shorter intervarix period. Abbott's (1954) suggestion of 2 days for growth from one varix to the next in Muricidae seems too brief, but he may have referred to a species of much smaller size.

Spiny gastropods are widely distributed and in tropic and semi-tropic waters, occur in abundance. Whether all species use the mechanism for removal of spines employed by *Murex brevifrons* and *M. fulvescens,* has yet to be determined. It is likely that they do. A good subject for study with extremely long spines is the beautiful *M. cabritii* from the Gulf of Mexico and the West Indies (Robertson, 1965). Some muricids lacking spines, like *Urosalpinx cinerea,* add new shell to the body whorl gradually (Blake, 1966). It would be instructive to determine if individuals of *U. cinerea* could remove artificial calcareous spines imposed experimentally on the inner lip in advance of the mantle edge, and what effect artificial removal of the spines of *M. brevifrons* would have on growth of the body whorl.

Not all gastropods solve the problem of obstructing shell ornamentation in the path of the growing body whorl by its removal. In the genus *Epitonium,* for example, prominent costae are simply covered over by new shell, resulting in a more widely coiled univalve than in Muricidae (Clench & Turner, 1951). Muricids with long spines have no recourse than to remove the offenders if the shell is to grow and the animal is to survive; snails with short spines could cover them as do individuals of *Epitonium.* What determines which of the two courses is followed, is not known.

SUMMARY

The prosobranch gastropods, *Murex brevifrons* and *M. fulvescens,* were maintained in captivity for observations on the removal of spines and the deposition of shell during growth of the body whorl from one varix to the next. Spine removal is necessary to eliminate blockage of the aperture and to permit easy movement of the snail in and out of its shell. Snails fed voraciously on oysters during the varix stage after boring holes in them, and then crawled to a quiet shady spot in aquaria to clean the parietal area and remove old spines on it, and to add new shell and spines to the outer lip. The parietal area was cleaned and the spines were removed at the base by the mantle by chemical dissolution. The mantle likewise secreted the new intervarix shell and spines. Scanning electron microscopy revealed a complex organization of strata of shell prisms in the dissolved surface of the spines. No radular marks were evident. The accessory boring organ was probably not employed in removal of spines.

Literature Cited

Abbott, Robert Tucker
1954. American seashells. Princeton, New Jersey. D. van Nostrand Co., Inc.; xiv+541 pp.; 40 plts.; 100 text figs.

Bevelander, Gerrit & Hiroshi Nakahara
1970. An electron microscope study of the formation and structure of the periostracum of a gastropod, *Littorina littorea.* Calc. Tiss. Res. **5:** 1 - 12; 11 figs.

Blake, John Wilson

1966. Inherent differences between populations of the oyster drilling gastropod, *Urosalpinx cinerea*, reared under laboratory conditions. Second Internat. Oceanogr. Congr., Abstr. of Papers, Moscow, 30 May-9 June, 1966. No. 45 - SIIc., 1p.

Carriker, Melbourne Romaine

1961. Comparative functional morphology of boring mechanisms in gastropods. Amer. Zool. **1** (2): 263 - 266; 1 fig.

1969. Excavation of boreholes by the gastropod *Urosalpinx*: an analysis by light and scanning electron microscopy. Amer. Zool. **9** (3): 917 - 933; 31 text figs.; 2 tables (August 1969)

Carriker, Melbourne Romaine & Edmund Hobart Smith

1969. Comparative calcibiocavitology: summary and conclusions. Amer. Zool. **9** (3): 1011 - 1020; 1 table (August 1969)

Carriker, Melbourne Romaine & Dirk Van Zandt

1972. Predatory behavior of a shell-boring muricid gastropod. Chapt. 5 *in* Behavior of marine animals: Current perspectives in research, vol. 1, Invertebrates. H. E. Winn & B. L. Olla (eds.), Plenum Press, New York, N. Y., pp. 157 - 244; 37 figs.; 7 tables

Carriker, Melbourne Romaine & Ellis Leon Yochelson

1968. Recent gastropod boreholes and Ordovician cylindrical borings. Contr. Paleont., Geol. Surv. Prof. Paper **593-B:** B1 - B26; 5 plts.

Clench, William John & Ruth Dixon Turner

1951. The genus *Epitonium* in the Western Atlantic (Part I). Johnsonia **2** (30): 249 - 288; plts. 108 - 130 (28 September 1951)

1956. The family Melongenidae in the Western Atlantic. Johnsonia **3** (35): 161 - 188; plts. 94 - 109

Digby, Peter S.

1968. The mechanism of calcification in the molluscan shell. Symp. Zool. Soc. London, no. **22:** 93 - 107; 6 figs. *In*: Studies in the structure, physiology and ecology of molluscs, Vera Fretter & J. F. Peake (eds.), Acad. Press, London

Fretter, Vera & Alastair Graham

1962. British prosobranch molluscs, their functional anatomy and ecology. London, Ray Soc. xvi+755 pp.; 316 figs.

MacClintock, Copeland

1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Peabody Mus. Nat. Hist., Yale Univ. Bull. **22:** i - ix+1 - 140; 128 text figs.; 32 plts.

Mackenzie, Clyde Leonard, Jr.

1961. Growth and reproduction of the oyster drill *Eupleura caudata* in the York River, Virginia. Ecology **42** (2): 317 - 338; 12 figs.; 15 tables (April 1961)

Robertson, Robert

1965. A spiny murex. Frontiers **29** (4): 101 - 103; 4 figs.

Saleuddin, A. S. M.

1970. Electron microscopic study of the mantle of normal and regenerating *Helix*. Canad. Journ. Zool. **48** (3): 409 - 416; 33 figs.

Smith, Edmund Hobart

1969. Functional morphology of *Penitella conradi* relative to shell-penetration. Amer. Zool. **9** (3): 869 - 880; 7 figs.

Soliman, Gamil N.

1969. Ecological aspects of some coral-boring gastropods and bivalves of the northwestern Red Sea. Amer. Zool. **9** (3): 887 - 894; 5 figs.

Wells, Harry Wilson

1958. Feeding habits of *Murex fulvescens*. Ecology **39** (3): 556 - 558

Wilbur, Karl Milton

1964. Shell formation and regeneration. *In* K. M. Wilbur & C. M. Yonge (eds.) Physiology of Mollusca. Acad. Press, New York, N. Y. **1:** 243 - 282; 14 figs.; 3 tables

Explanation of Figures *11* to *14*

Figure *11*: Juncture of vertical and horizontal striae shown in Figure 9. Scanning electron micrograph 500 ×

Figure *12*: Higher magnification of the juncture of vertical and horizontal striae shown in Figure *11*. Scanning electron micrograph 1000 ×

Figure *13*: Horizontal striae shown in Figure 9. Scanning electron micrograph 500 ×

Figure *14*: Higher magnification of a portion of the layers of prisms shown in Figure *13*. Scanning electron micrograph 2000 ×

Figure *11*

Figure *12*

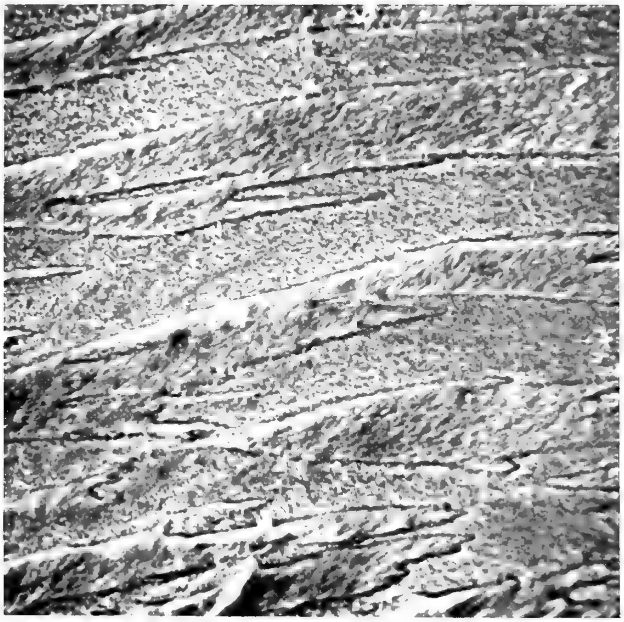


Figure *13*

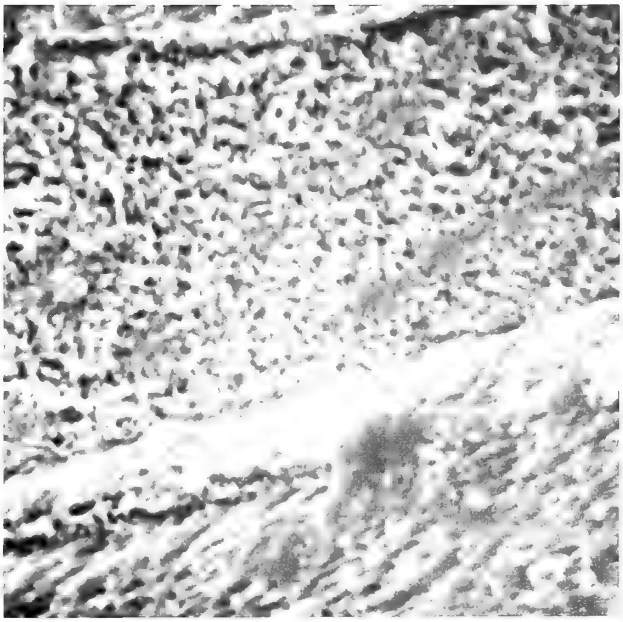


Figure *14*

The Ecology and Behavior of *Nautilus pompilius* in the Philippines

BY

NORINE HAVEN

Department of Biological Sciences, Simon Fraser University, Burnaby 2, British Columbia, Canada

(2 Plates; 2 Text figures)

INTRODUCTION

Observations were made on various aspects of the ecology and behavior of *Nautilus pompilius* Linnaeus, 1758, during the course of a study of reproduction of the animal where it occurs in the Philippines. There have been few previous studies of living *N. pompilius,* studies on living animals in the field having been done on only two previous occasions. Willey (1902) worked in the New Hebrides for 3 years, and Dean (1901) did a much shorter study in the Philippines. Observations on aquarium specimens of a different species (*N. macromphalus*) have been made by Bidder (1962) and Catala (1964). Moseley (1879) described the activities of a single specimen of *N. pompilius* in a bucket, while Bidder (1962) observed one specimen of *N. pompilius* "immediately after it was brought to the surface", but did not further differentiate its activities from those described for *N. macromphalus.*

The present observations were made on animals trapped and kept in holding cages in the ocean, as well as on animals held in an aquarium. Studies were made in the water with the aid of SCUBA gear. Field studies were done from June until mid-October, 1971.

MATERIALS and METHODS

Specimens were caught in traps set in Tañon Strait, which lies between the islands of Negros and Cebu (Figure 1), and were kept for months at a time in holding cages at 60 m. Some animals were also kept for as long as 2 weeks in holding cages set at 10 m and at 25 m, where observations were made by SCUBA diving. Observations of free swimming animals were also made by SCUBA diving. Animals kept in aquaria with a continuous flow of seawater remained healthy and reactive so long as the water was cooled to 23° C, but field conditions precluded cooling for more than 48 hours. All animals were fed at least every other day.

GEOGRAPHICAL DISTRIBUTION

Two coastal areas of the island of Negros were surveyed in an attempt to ascertain the distribution of *Nautilus pompilius* in the area. Along one, on the northern coast of Negros Occidental between Escalante and Cadiz (Figure 1), *N. pompilius* is seldom, if ever, encountered alive. Empty beach washed shells are occasionally found but the animal is never trapped alive. Stories were persistent among the fishermen of frightened animals deserting their shells. These same fishermen brought in the pelagic octopus, *Tremoctopus violaceus* della Chiaje, 1830, caught near Bantayan Island, saying this was the animal which lived in *Nautilus* shells. It is interesting to note that the fishermen call this octopus by the local name for *Nautilus* ("lagang"), instead of by the name they usually use for an octopus ("cogeta"). From extensive questioning, and our own field search, it appears that if *N. pompilius* occurs in these waters at all, it is certainly rare.

The southern coast of Negros was also surveyed from Bais City on the east, to Bayawan on the west coast (Figure 1). Here *Nautilus pompilius* is encountered as an incidental catch in the local fish traps. These bamboo fish traps are not baited, and are left in place at a depth of 60 to 120 m for a period of 1 to 3 weeks. Estimates given by the fishermen of the frequency of *N. pompilius* catches in the fish traps show that it may be more abundant on the southwest coast of Negros around Bayawan, where an average of 20 per year are caught, than in the southeast portion of the coast from Dumaguete to Siaton (Figure 1), where an average of 7 specimens were encountered per year per trap. Animals purchased in this region were

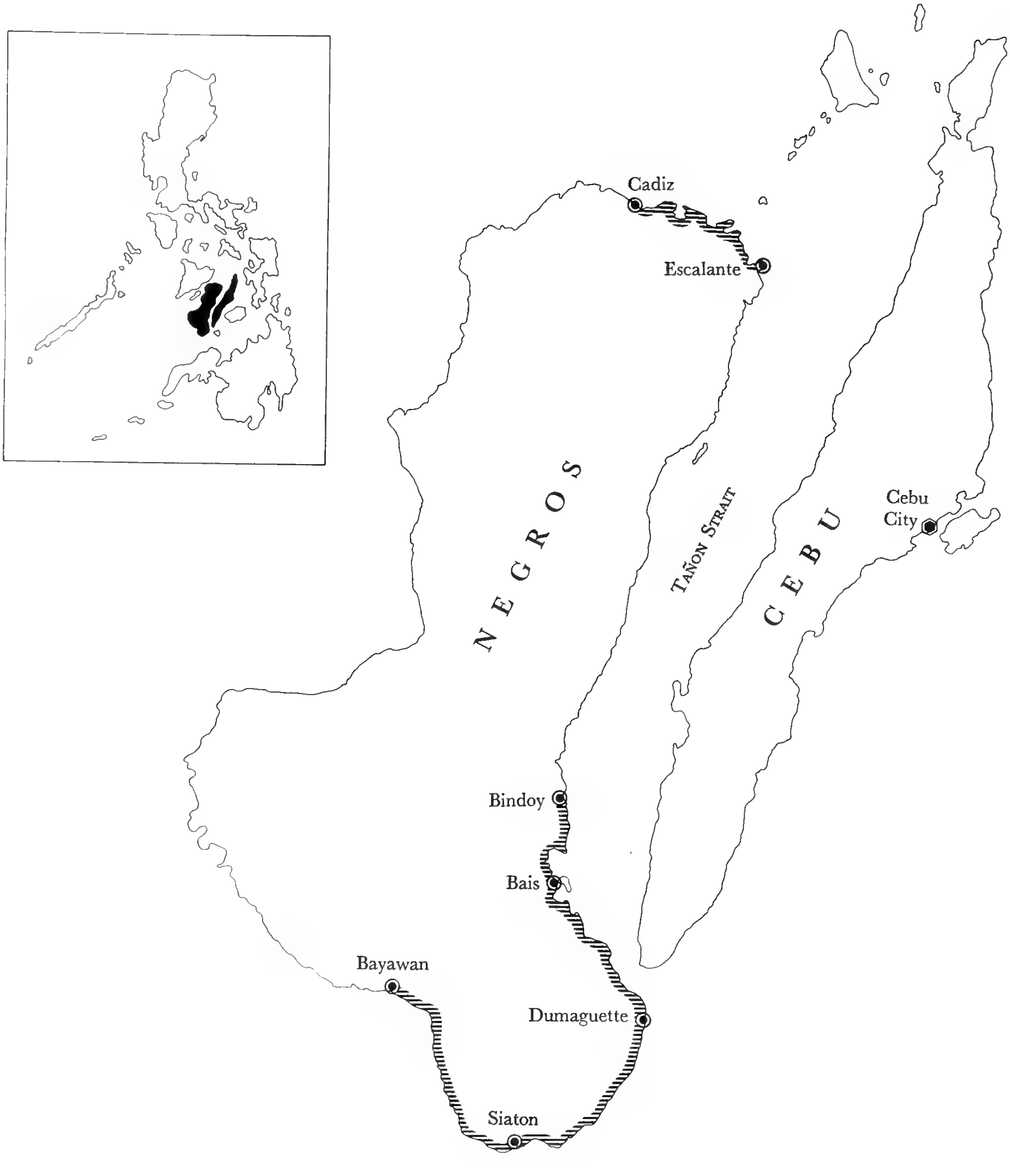


Figure 1

Negros Island, the Philippines, where work on *Nautilus pompilius* was undertaken. Shaded areas of coast represent survey areas. Inset shows Negros and Cebu (black) in relation to rest of Philippine Islands positively identified as *N. pompilius*. There were no stories here of *N. pompilius* abandoning its shell.

Four fishermen who trap exclusively for *Nautilus pompilius* were eventually located. Philippine fisheries biologists, university scientists and shell collectors had indicated no knowledge of living *N. pompilius* being taken anywhere in the islands, and the finding of these fishermen marked the discovery of a good supply of *N. pompilius* for the first time in 70 years. Dean (1901) had worked with fishermen near Bais, where *N. pompilius* is no longer known as a commercial animal. Talavera & Faustino, writing in 1931, state that at that time there was no longer any commercial fishing of *N. pompilius* in the Philippines.

At present, 4 fishermen from Negros Oriental set traps near Tinaogan Reef, north of Bindoy (Figure 1) (9°48′ N, 123°10′E). Bobos – traditional bamboo fish traps similar to those described by Dean (1901) – are baited with fresh chicken, fish or pork and set on the bottom, from 60 to 240 m deep. The traps are pulled each morning, and although catches may range from 0 to 19 *Nautilus pompilius* per trap, the average daily haul is 5 specimens per trap. The meat of the animal is sold in the local market, and shells are shipped to Cebu City where they are wholesaled by shell dealers. However, the overwhelming majority of *N. pompilius* shells shipped from the Philippines each year have been found during the typhoon season washed up on shore in regions such as the island of Bohol. Bohol lies southeast from the island of Cebu.

ECOLOGICAL DISTRIBUTION

The bobos used by the nautilus fishermen are set near coral reef areas where the bottom drops from 40 m to approximately 240 m within a mile from shore. The Tañon Strait deepens to 400 - 600 m a short distance beyond. It is likely that *Nautilus pompilius* could be found in the deeper regions, but the physical effort of hauling up traps from these depths precludes any trapping there. Fishermen in the area report the bottom environment on the north side of Tinaogan Reef to be rocks and coral heads to about 90 m, and mud to limits of their trapping there (approximately 150 m). The bottoms of traps brought up sometimes drip a grey mud.

In experimental trapping at various depths, no *Nautilus pompilius* were ever captured shallower than 58 m. Experiences with the animals in holding cages, aquaria, and experimental release observed with SCUBA gear, as well as in their transport from the field, strongly suggested that temperature limits vertical distribution.

Table 1 summarizes trapping data for a 6-week period between August 8, 1971 and September 15, 1971. Most traps are set between 80 and 180 m where catches are

Table 1

Records of *Nautilus pompilius* caught in traps
near Bindoy, Negros Oriental
from August 8 to September 15, 1971

Depth (meters)	Number of *Nautilus* per haul average	range	Number of hauls
58 - 70	1	0 - 3	3
71 - 90	4	0 - 10	17
91 - 110	6	0 - 19	20
111 - 130	5	0 - 12	48
131 - 150	3	1 - 9	12
151 - 170	7	0 - 15	13
171 - 190	5	0 - 10	13
191 - 210	4	0 - 7	2
211 - 230	6	4 - 8	4
231 - 250	5	0 - 9	7
260	2		1

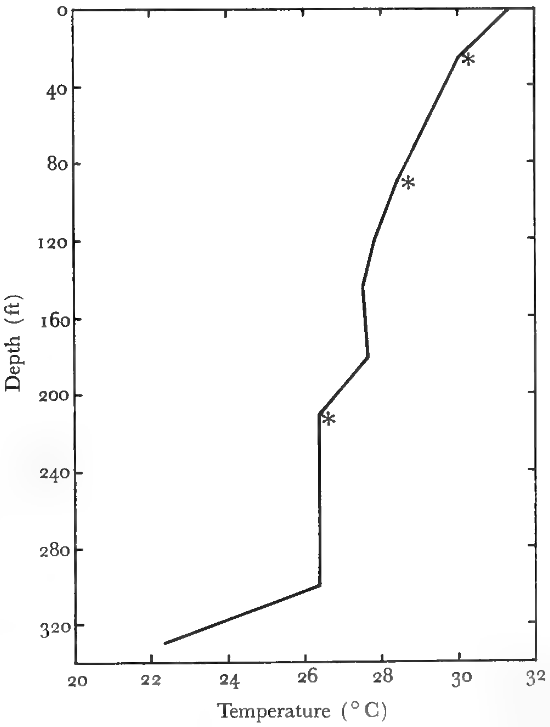


Figure 2

Morning temperatures at holding cage sites (*) and trapping areas, Tañon Strait, September 2 and 3, 1971 consistently good, and the depths convenient for working. Figure 2 shows temperatures taken at various depths during a 2-day period in early September 1971. The data indicate that *Nautilus pompilius* lives at depths where water temperature may be as much as 9° C lower than in the more shallow waters adjoining.

ANOMALOUS DISTRIBUTION OF SEXES

In the 6-week period between early August and mid-September, 1971, 534 specimens were caught in baited traps, and less than 5% of these were females. Eight chance catches (*i. e.,* from an ordinary fish trap or hook and line) were brought in from the southern coast of Negros during July and August. Five of these, or over 60%, were females. Baited traps were set 3 times in one of these locations just south of Dumaguete that had yielded most of the females, in an attempt to determine whether the composition of the population differed there, but no *Nautilus pompilius* at all were caught on these occasions.

Willey (1902) experienced a similar, though less drastic, reduction of females in the animals he trapped in New Britain. Approximately one-third of the *Nautilus pompilius* he trapped there over a period of 9 months were females.

Trapping data covering an entire year are being obtained in the present study. These data will show if the low percentage of females caught is a seasonal phenomenon.

COMMENSALS

Commensal copepods, identified as *Anchicaligus nautili* (Willey, 1896), were numerous on the interior aspect of the ala infundibulae, that is, the mantle flaps that lie at the rear of the hood area dorsolaterally and which regulate water intake. *Anchicaligus nautili* were also commonly found in the posterior dorsal portion of the funnel.

Although the vast majority of *Nautilus pompilius* shells are free of settled animals, 2 living specimens were found with attached barnacles. One had a balanoid type barnacle on the rear of its shell. Another had a stalked barnacle attached about midline ventrally. These shells were accidentally discarded, so further identification of the barnacles was not possible.

The kidneys of freshly killed animals were examined at 500 × magnification under a dissecting microscope, and no evidence of mesozoan infestation was found.

DIURNAL ACTIVITY

Experimental trapping near Bindoy, Negros Oriental, confirmed the observation that activity is diurnal (Willey, 1902). Baited traps placed out during daylight hours (7 AM to 5 PM) at depths from 110 to 180m, caught no *Nautilus pompilius,* while those similarly placed for 24 hours produced average yields.

Nautilus pompilius kept in holding cages in the ocean at 10 and 25m and observed with SCUBA gear, were occasionally seen eating dead fish placed in the cage during the day. However, most feeding activity was during the night.

In the aquarium, *Nautilus pompilius* usually rested quietly during the day, attached by the distal portion of one or more tentacles to the wall of the aquarium (Figure *3*). In the holding cages, where chicken wire provided little support, animals often attached their tentacles to one another's shell. Where portions of the holding cages were lined with burlap, the animals frequently hid in the folds during the day.

It is highly likely that the normal daytime activity of *Nautilus pompilius* is to remain attached to coral rubble or crevices in its natural habitat. Not only did animals usually remain attached during the day when in captivity, but field experiments lent further support to this hypothesis. A healthy *N. pompilius* was released above a sloping coral reef, and swam slowly down at an angle until it came to rest on the reef, where it fastened itself to a coral head and rested quietly, much as it had been observed to do in the aquarium. This behavior was elicited each time it was removed by a diver and released again

Explanation of Figures *3* to *6*

Figure *3*: *Nautilus pompilius* in daytime resting pose, one tentacle fastened to wall of aquarium

Figure *4*: *Nautilus pompilius* beak compared to contour of break in shell of young male *Nautilus pompilius*

Figure *5*: Comparison of normal shell of female *Nautilus pompilius,* left, with a similar shell whose contour has been severely altered by bites

Figure *6*: *Nautilus pompilius* in aquarium with shortened tentacles

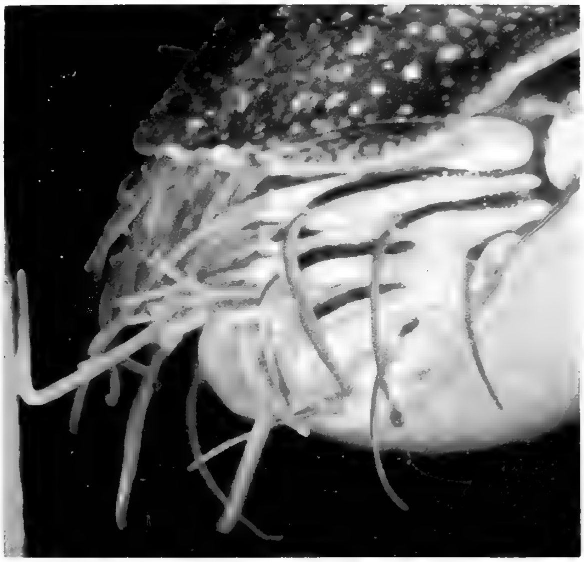


Figure *3*

Figure *4*

Figure *5*

Figure *6*

Figure *3*: *Nautilus pompilius* in daytime resting pose, one tentacle fastened to wall of aquarium
Figure *4*: *Nautilus pompilius* beak compared to contour of break in shell of young male *Nautilus pompilius*
Figure *5*: Comparison of normal shell of female *Nautilus pompilius*, left, with a similar shell whose contour has been severely altered by bites
Figure *6*: *Nautilus pompilius* in aquarium with shortened tentacles

at progressively deeper depths. At 20m the released *N. pompilius* landed about 2 feet from a cave that was approximately 4 feet long and 2 feet deep, formed by coral overhang on the slope. Upon landing, *N. pompilius* turned, swam forward, and fastened itself to the coral rubble back in the darkened recess, with the rear of its shell facing outward. Here it remained until removed by the diver, and pieces of coral rubble had to be forcibly removed from its tentacles. It should be particularly noted that *N. pompilius* was never observed to swim forward at any other time except when feeding (see subsequent section). Such purposive behavior suggests that *N. pompilius* preferred a sheltered spot during the daytime.

SPEED of SWIMMING

Animals released in the ocean were never found to swim quickly, although here, as elsewhere (see Bidder, 1962), the local people claimed the animals could swim very fast. A diver could keep up with a *Nautilus pompilius* by swimming with a slow breast stroke. Animals may give fairly strong jerks in an attempt to wrench themselves free from a restraining grip, and these sudden movements may give rise to the erroneous belief that the animal is a speedy swimmer.

Attempts were made to frighten free-swimming animals by swimming directly at them, or by touching the hood or an eye. When so annoyed, *Nautilus pompilius* made no attempt to escape or clamp shut, but merely turned the rear of the shell to the source of irritation. Similar behavior was elicited when pictures were taken of animals in the aquarium, even though flash bulbs were not used. I would view with caution statements belittling the intelligence of this animal.

FIGHTING

Irregular breaks are common along the anterior margins of shells of both male and female *Nautilus pompilius*. When a young male kept in a holding cage with several other adult males received a bite in its hood and a clean V-shaped break in its shell, the break was found to conform closely in contour to the upper beak of *N. pompilius* (Figure *4*). Comparison of breaks along the edge of other adult *N. pompilius* shows that fighting within the species – for whatever reason – is fairly common. Both males and females are bitten and some so severely as to alter the contour of the shell (Figure *5*).

TENTACLE POSITIONS

The tentacles of *Nautilus pompilius* are structurally divided into two parts, with a thick sheath at the base, into which a slender cirrus can be withdrawn. The cirri are highly distensible and the tentacles can be held in a variety of positions that seem to lend themselves to categorization, although the function of these positions is not always clear.

(a) **Shortened Tentacles** (Figure *6*): The cirri are well retracted into the fleshy base. This position was common when the animals were in an apparently stressful situation, such as being in warm water or water containing abundant plankton.

(b) **Trailing Tentacles** (Figures *7, 8*): All of the tentacles are fairly well retracted with the exception of one or two of the lowermost outer pairs. These trail during ocean swimming, as in Figure *7*, or may extend forward or down on more stationary specimens respiring in the aquarium (Figure *8*).

(c) **Moderately Extended Tentacles** (Figure *9*): These may be combined with trailing tentacles, as in Figure *9*, or are seen when the animal is attached and resting (Figure *3*), usually when specimens are in aquarium water with a temperature close to that of their normal environment.

(d) **"Cat's Whiskers" Pose** (Figure *10*): Three to 4 pairs of tentacles radiate outward as in Figure *10*. In the aquarium, *Nautilus pompilius* would pump itself to the surface and drift downward with tentacles splayed out in this position. The increased ability to become aware of objects close by seems obvious, thus the name of "cat's whiskers" for this position.

(e) **Extended Feeding Tentacles** (Figure *11*): The tentacles are extended to apparently the maximum length during feeding (Figure *11*). The tentacles are arrayed in Bidder's "cone of search" during the search for food and their use during feeding appears to correspond to that of *Nautilus macromphalus* (Bidder, 1962). A more detailed description of feeding can be found in the next section.

FEEDING

When dead fish or chicken is given to *Nautilus pompilius* in captivity, small pieces approximately 5 mm square are neatly bitten off by the beak. Large amounts may be stored in the esophagus, to await processing by the gizzard. The esophagus is thin-walled, but highly distensible. Specimens removed from baited traps usually had 20 to 30 ml of bait in the esophagus, but one specimen had stored 100 ml of bait. Little information was obtained on the natural food of *N. pompilius,* but pieces of decapod crustacean carapaces were occasionally found in the gizzard, and appeared to come from crabs with a carapace 1 cm in width.

Specimens kept in holding cages were fed both live and killed crabs and fish. There was no clear evidence that the crabs or fish were ever taken alive. The fish, however, had to be large enough so as not to escape through the chicken wire mesh of the cage and were 9 - 13 cm long. Observations with SCUBA gear showed that dead fish and crabs placed in the cages were sometimes eaten during the day, but the greatest feeding activity occurred in the night.

Aquarium specimens would search for food during the night. The cirri of the tentacles were stretched out approximately 9 cm and *Nautilus pompilius* would cruise forward with the tentacles extended downward (Bidder's "cone of search", 1962) with the tips touching the bottom. These tentacles moved quite rapidly, exploring the bottom and trailing a short distance behind. When food was offered for the first time and dropped in the aquarium 2 feet away, it was located within one minute. The forward swimming did not cease until the tentacles touched the food, which meant that for a moment, the main body of the animal would continue ahead, leaving the tentacles trailing behind, wrapped around the food. Thus, in the aquarium, although the stimulus that initiated the food search was chemosensory in nature, food was definitely located by touch.

It is of particular interest that *Nautilus pompilius* swam forward when searching for food, since this was the only time the animals were ever observed to swim forward, with one exception, when one moved to a hiding place (see "Diurnal Activity"). It makes sense adaptively that with sensory tentacles in the front *N. pompilius* moves forward and makes use of these tentacles as an exploratory apparatus when searching for food, rather than always swimming backwards.

The searching-touch phenomenon of feeding in the aquarium, coupled with the relatively slow swimming movements strongly suggests that *Nautilus pompilius* is a bottom feeder. It is possible that in addition to feeding on small crustaceans, *N. pompilius* is a scavenger. Lack of predation on live food in the holding cages plus the highly distensible esophagus would suggest this as a possible way of life. The method of trapping with dead bait is also evidence for this argument, which needs to be further tested in the field.

ACKNOWLEDGMENTS

I am indebted to Robin Coulon for much of the field work and many original observations, and to Wilson Vailoces for his part in collecting data and animals. I am grateful to the Biology Department of Silliman University, Dumaguete City, for research space and particularly to Mr. Daniel Sycip who offered invaluable field research facilities and help. I thank Dr. Gilbert L. Voss, School of Marine and Atmospheric Sciences, Miami, Florida, for identification of the octopus, and Dr. Paul Illg of the Zoology Department, University of Washington, Seattle, Washington, for identifying the commensal copepod. This project was supported in part by a grant from the Penrose Fund of the American Philosophical Society.

Literature Cited

Bidder, Anna M.
1962. Use of tentacles, swimming and buoyancy control in the pearly *Nautilus.* Nature **196:** 451 - 454
Catala, Rene L. A.
1964. Carnival under the sea. Ed. R. Sicard, Paris: 141 pp.; 48 figs.; 27 plts.
Dean, Bashford
1901. Notes on living *Nautilus.* Amer. Natural. 35 (418): 819-837
Moseley, Henry Nottidge
1879. Notes by a naturalist on the "*Challenger.*" Macmillan & Co., London: xvi+620 pp.; col. frontisp.; illust.; col. plts.; fold. map
Talavera, Florencis & L. A. Faustino
1931. Industrial shells of the Philippines. Philipp. Journ. Sci. 45 (3): 344 - 347
Willey, Arthur
1898-1902. Contribution to the natural history of the pearly *Nautilus* in Zoological results based on material from New Britain, New Guinea, Loyalty Islands, and elsewhere collected during the years 1895, 1896 and 1897. Pt. **6:** 691 - 827

Explanation of Figures *7* to *11*

Figure *7*: *Nautilus pompilius* descending after release in ocean, with lowermost pair of tentacles trailing

Figure *8*: *Nautilus pompilius* in aquarium with lower pair of tentacles trailing

Figure *9*: Moderately extended tentacles on *Nautilus pompilius* in aquarium

Figure *10*: *Nautilus pompilius* in aquarium displaying "cat's whiskers" arrangement of tentacles. Specimens pump to surface and drift down in this attitude

Figure *11*: *Nautilus pompilius* with tentacles extended in feeding position. Piece of fish is being grasped by tentacles next to beak


Figure 7


Figure 8


Figure 9


Figure 10

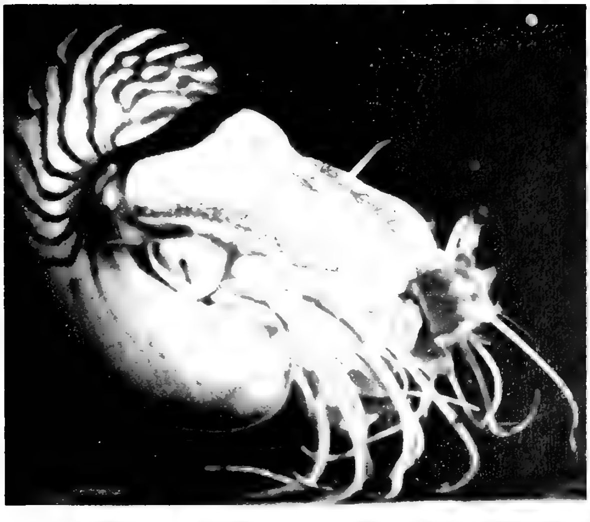


Figure 11

Microarmature and Barriers in the Aperture of Land Snails

BY

ALAN SOLEM

Department of Zoology, Field Museum of Natural History
Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605

(5 Plates)

Development of various folds, ridges, calluses, tubercles, constrictions or lamellar plates that effectively narrow the shell aperture is a common phenomenon in non-operculated land snails. With the obvious exception of slugs or taxa with partly (Succineidae, Vitrinidae) to drastically (some Helicarionidae, Testacellidae) reduced shells and visceral humps, most families show at least a few species with apertural narrowing caused by such constrictions. There is no agreed nomenclature for these structures, which have most frequently been cited as "teeth". Since this has obvious gustatory connotations, a better term for general usage would be to refer to these as "barriers". This generic term can be modified to indicate the form of the structure by use of the more traditional terms as modifiers.

The general assumption has been that these barriers are effective in reducing predation by arthropods (see Cooke, 1895: 63). Along with the production of distasteful mucus by slugs, an offensive odor (as in *Oxychilus,* see Lloyd, 1970), issuing an irritating froth or liquid (as in *Liguus,* see Eisner & Wilson, 1970), and self amputation of the posterior tail (as in *Prophysaon,* see Pilsbry, 1948: 680), such barriers are a basic defense mechanism of pulmonate snails. They are partial substitutes for the operculum of prosobranchs, which forms a nearly impregnable defense against small predators.

The number, position, shape and size of these barriers frequently has been used as identification or diagnostic features for both genera and species, particularly in such groups as the Clausiliidae, Tornatellinidae, Urocoptidae, Endodontidae (*s.l.*) and Pupillidae (*s.l.*) where the shell is rather uniform in appearance. Virtually no attention has been paid to their structure and formation. The development of "prickly nodes" on apertural lamellae in *Strobilops* (Pilsbry, 1948: 862, fig. 466), calcareous hooks that point towards the outside of the aperture on the lamellae in *Thaumatodon multilamellata* (Garrett, 1872) (see Pilsbry, 1893–1895: plt. 4, fig. 38), plus numerous observations on the internal ridges in various Urocoptidae are among the few exceptions.

Scanning Electron Microscope (hereafter SEM) examination of barriers and apertural surfaces in several land snail families has shown that a high percentage of species have microarmature, not just on the barrier edges, but over much of the lip surface, particularly the columellar and parietal regions of the aperture. This report is concerned with the basic pattern of such microarmature, its probable function, and how more sophisticated microarmature could have evolved from the generalized condition. As necessary background information, a brief survey of barrier types is presented. A second report (Solem, in press) will discuss structural differences in the armature found on the barriers in species of Charopidae and Endodontidae.

ACKNOWLEDGMENTS

The photographs illustrating this paper were taken on both Cambridge and Jeolco SEM's over the past two years. For assistance in SEM operation and photography, I am indebted to Mr. Akira Kabaya and Dr. John Russ of Jeolco (USA), Inc.; Miss L. Marchant of Franklin Institute Research Laboratories, Philadelphia; and to Dr. Harvey Lyon, Mr. John Lenke, and Mr. George Najarian of the American Dental Association Research Institute, Chicago. Mr. Fred Huysmans, Photographer at Field Museum of Natural History prepared the published prints, and Mrs. Dorothy Karall mounted the figures. Part of this work was sponsored by National Science Foundation grant GB-6779. Their support is gratefully acknowledged.

Patterns of Apertural Narrowing

There is no single strategy for barrier formation, but rather a great variety of experiments. Most involve deposition of calcareous ridges, inward lip edge growth, or a combination of both. Large and complex barriers can be present in early and mid-juvenile stages, then become greatly reduced to absent in the adults. The Tornatellinidae (see Cooke & Kondo, 1960: 113, figs. 50, a, d, e), Cerionidae (see Pilsbry, 1946: 161, fig. 76), and zonitoid taxa such as *Ventridens* (see Pilsbry, 1946: 438, fig. 235) exemplify this approach. These barriers are formed early, added to anteriorly and resorbed posteriorly during juvenile growth, and then mostly resorbed before or when the animal reaches terminal size. In other groups, such as the Urocoptidae, Strobilopsidae, Charopidae and Endodontidae, the barriers may be formed early, growth follows the same pattern as in the first type, but then the barriers are retained at essentially full size during the adult stage.

Perhaps most common is for the juvenile shell to totally lack any barriers or constrictions of the aperture, with the adult animal secreting complex barriers upon reaching maximum size. Such families as the Pupillidae (*s.l.*), Streptaxidae, Odontostominae and Polygyridae (especially *Polygyra, Stenotrema* and *Triodopsis*) have a majority of species with well developed barriers. Frequently only a few genera in a family will show this development. Bulimulid genera such as *Auris, Eudolichotus* and *Otostomus,* camaenid genera such as *Labyrinthus, Traumatophora, Moellendorffia* and most of the West Indian derivatives from *Pleurodonte,* bradybaenid taxa such as *Metodontia, Semibuliminus, Pseudaspasita* and *Odontotrema,* and various European helicid taxa have greatly developed apertural barriers although most taxa in these families have not or only slightly constricted apertures. Even in the helicarionid taxa, genera such as *Brazieria* and *Sesara* depart from the normal open aperture by developing high, transverse lamellae. Occasionally as in some pupillids, juveniles will have one form of barriers and adults a totally different set.

A few taxa build barriers at regular intervals. In *Helicodiscus* (see Pilsbry, 1948: 626, fig. 339, b) there are tubercles at about quarter-whorl intervals. Apparently these are not resorbed, or only resorbed after several new barriers have been erected. Members of the Corillidae have carried this approach to its logical conclusion. Highly complex barriers are "... formed on the completion of each half of a whorl, after which the previous set is absorbed by the animal. I have observed several specimens which contained two sets of barriers at a distance of half a whorl; in some cases the older set had almost vanished..." (Gude, 1914: 55).

Finally, the clausilium and barriers found in members of Clausiliidae and the most unusual apertural closing attributed to *Thyrophorella* from Sao Thomé, a hinged flap (see Girard, 1896), are additional strategies for apertural narrowing.

All of these barriers should be viewed as representing structures partly compensatory for the absence of the prosobranch operculum. That is, they hinder possible predators from reaching the animal after it retreats behind the barriers. This was perhaps suggested first by Guilding (1829: 168) in an oft quoted sentence—"I know not whether the use of the teeth and laminae of the *Pupadae* (=Pupillidae, *s. l.*) has been explained; they may answer the purpose of an operculum to keep out enemies, while they afford no obstacle to the motions of the soft and yielding body of the animal." Subsequently Godwin-Austen (1874: 611) reported finding small insects stuck between the barriers in two specimens of the corillid genus *Plectopylis.* While not frequently observed, anybody who has sorted field collections of small land snails that have large and complex apertural barriers can attest to the reality of this phenomenon.

At times the barriers come so close to filling the aperture of the shell that it is difficult to conceive how the buccal

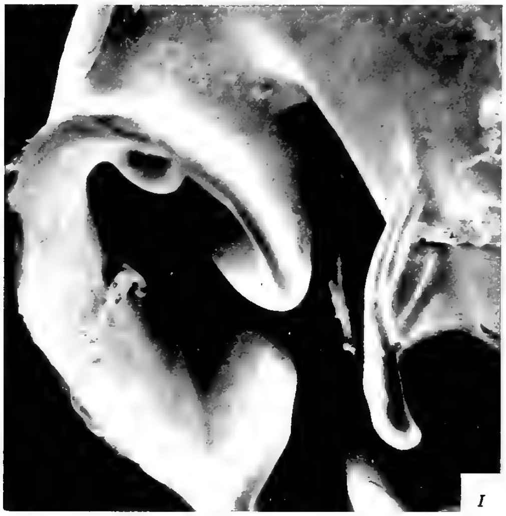
Explanation of Figures *1* to *6*

Tornatellina plicosa Odhner, 1922

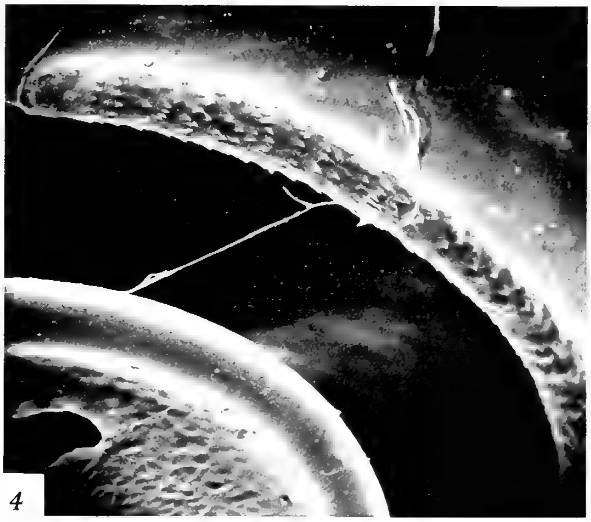
Figures *1* to *3*: Southwest slope at 500 - 530 m elevation, Portazuelo, Masatierra, Juan Fernandez Islands. Field Museum of Natural History number 167976. Figure *1*: partial view of shell aperture at 76× showing columellar (upper center), parietal (lower right center), and lower palatal (bottom center) lamellae. Figure *2*: lower side of outer edge of columellar lamella at 880× showing concentration of microdenticles on sides of lamellae. Figure *3*: part of a cluster of denticles from same area at 4230×.

Tekoulina pricei Solem, 1972

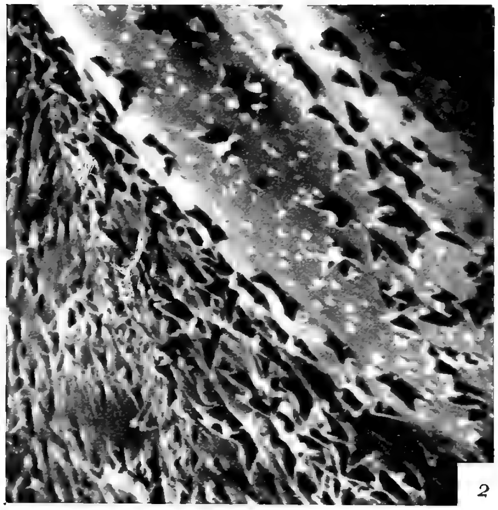
Figures *4* to *6*: Station R-11, summit of Mt. Te Kou, Takuvaine Valley, 1930 feet elevation, Rarotonga, Cook Islands. Field Museum of Natural History number 153414. Figure *4*: Palatal (upper with serrations) and columellar (lower and smooth) lamellae near posterior end of palatal (upper left) at 139×. Figure *5*: Surface of palatal lamella at 826× showing positioning of denticles on upper surface. Figure *6*: Details of denticle shape and relation to surface of lamella at 4646×.



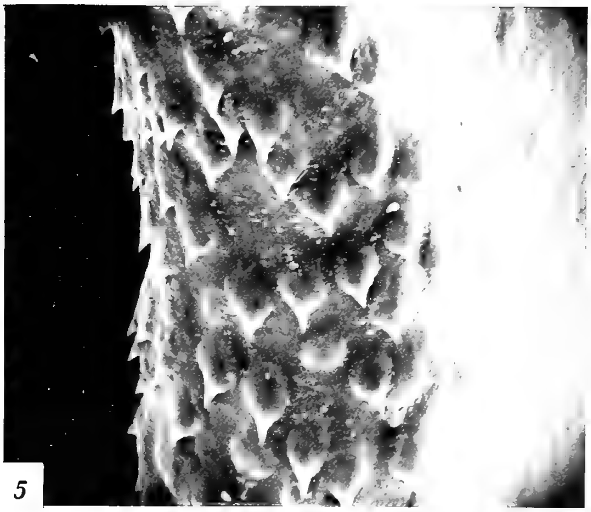
1



4

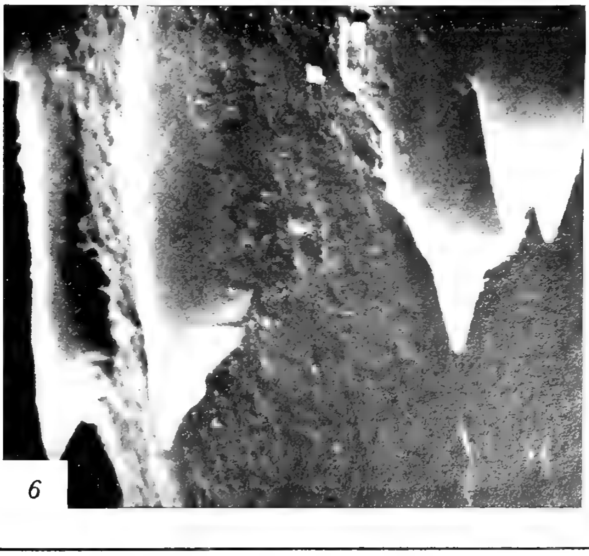


2



5

3



6

mass and muscular foot can be successfully withdrawn and protruded. In the polygyrid genus *Stenotrema* (Figure *23*), for example, the aperture is effectively narrowed to a thin slit by lip extensions and a parietal lamella. In such Florida species as *Polygyra uvulifera* (Shuttleworth, 1852) and *P. auriculata* Say, 1818 (see Pilsbry, 1940: 595, fig. 384) the degree and complexity of constriction is even greater. In many of the minute Tornatellinidae (for example, Cooke & Kondo, 1960: 107, fig. 47, a–c), Pupillidae (for example, see Pilsbry, 1948: 897), and endodontoid taxa (Solem, in press, figs. 1–6) high lamellar barriers come close to overlapping in the middle of the aperture. Such structures are not limited to minute or medium sized land snails. *Labyrinthus otis* (Lightfoot, 1786) is a South American camaenid ranging from 39–54 mm in diameter. A combination of a raised parietal lamella and a huge palatal tubercle that shows on the outside of the shell as a deep indentation combine to grossly restrict the shell opening (see Solem, 1966: 110, fig. 30, *b*). The internal barriers of the 10–25 mm *Plectophylis* are equally effective (see Gude, 1914: 87, fig. 35).

There is no simple relationship between relative size of the barriers and the size of the organism. In the Polygyridae, small sized genera such as *Polygyra* and *Stenotrema* (see Archer, 1948) do have large barriers, while the larger *Triodopsis* and *Mesodon* have reduced or vestigial denticles. However, the small *Praticolella* whose distribution overlaps that of *Polygyra* and *Stenotrema*, totally lacks such barriers. In the Pupillidae (*s. l.*) the minute *Vertigo* and relatively large *Pupilla* lack barriers or have very small ones, while the extremely complex barriers occur in the medium sized *Gastrocopta*. In contrast, the larger species of *Labyrinthus* have proportionately larger barriers than do the small species (Solem, unpublished data). What is needed before relative barrier size can be interpreted functionally is hard data on the predators of particular species. Unfortunately, this is mostly unavailable.

Arthropod Predators and Barrier Effectiveness

While it is a text book statement that snails are preyed upon by carabid beetles, larval fire flies, silphid beetles, and various sciomyzid flies, we know nothing concerning the identity of predators on micro-species. Essentially all published records are about larger insects feeding on European or North American helicoid and zonitoid taxa. Predaceous mites, the smaller staphylinid beetles, plus a huge variety of less familiar groups belonging to the litter fauna are potential suspects. Until these receive more study, analogies will have to be drawn from data on the larger snail-eating insects.

Carabid beetles, both adult and larval stages, are active predators on medium to large sized land snails. Indeed, one tribe, the Cychrini, is almost exclusively malacophagous. Data concerning both adult and larval feeding patterns in *Carabus* have been given in a recent review (Sturani, 1960). The larva or adult enters the snail's aperture (Sturani, 1960: 94, fig. 6), gradually consuming the occupant. In some cases, pieces of the shell are broken off to facilitate feeding (Sturani, 1960: 123, fig. 14; p. 136; p. 140, fig. 23). Similar patterns are shown by the snail-eating Silphidae. Both narrowing and elongation of the head and thoracic region are associated with this habit. In an elegant paper, Boettger (1921) demonstrated coevolution between predator and prey, with increasing size of palatal aperture barriers in the North African helicid snail *Otala* (*Deserticola*) *tigri* (Gervais, 1857) countered by decreased width of head and thorax in the carabid beetle *Carabus morbillosus* Fabricius, 1792.

Considerable information about larval feeding on snails in the lampyrid beetles *Lampyris* and *Phausis* is given by Schwalb (1961: 456–470), including experimental tests concerning prey location and method of attack.

The significant feature in both the carabid and lampyrid method of feeding is that efficient utilization of the food source requires the predator entering or breaking the shell at some point. If a crawling snail is caught and the head and extended foot bitten or pulled off, considerable volume of the snail still remains inside the shell. For a small predator that cannot crush the shell, only entry into the aperture permits utilizing this part of the prey. If the snail is retracted into the shell, then it is available to the predator only by entering the aperture. Hence the evolution of barriers behind which the snail can retreat would be an effective means of defense. Even if the snail lost a tentacle to an initial grab by a predator, a quick retreat behind the barriers would be effective, if the opening that remained was too small for the predator to gain entry and the predator could not crack the shell.

The utility of such barriers to a particular land snail would depend upon the local predators. Most predators have a size range of objects that are recognized as possible "prey", while things that are smaller or larger than this size are "non-prey". It is also well established that for many predators, the food sources will differ according to the season of the year. Hence the patterns of apertural barriers in land snails that vary from present in adult but absent in juveniles to the exact opposite situation would reflect selective pressure under particular circumstances.

Ornamentation on Apertural Surfaces

With the above background information on the occurrence, age correlation, and function of barriers in larger species of land snails, it becomes possible to discuss the ornamentation found on the surface of these barriers in smaller species. While in some taxa the barriers have shown an absolutely smooth surface even at 2 000× magnification, in most of the small species there have been marked protuberances. These are particularly well developed in the Endodontidae and Charopidae (Solem, in press). The data reported on here represent only a tiny sampling of the world fauna. It is too early to say that this is an almost universal phenomenon, but the discovery of these structures in more than 85% of the species examined to date suggests that it is very widespread.

Tornatellina plicosa Odhner, 1921 (Figures *1–3*) is a very small species, found on ferns or under leaves, from Masatierra, Juan Fernandez Islands. The maximum recorded adult size is 5.1 mm in height. The photographed individual is a 2.47 mm high subadult. Optical measurement of the distance from the outer edge of the basal lip to the upper margin of the parietal lamella (left part of Figure *1*) is 0.69 mm. When the surfaces of the major barriers, both top and sides, are examined at 880× (Figure *2*) and 4 230× (Figure *3*), they are seen to be covered with scattered to densely clustered calcareous hooks and tubercles. The hooks do not form a clear pattern, but lie at a variety of angles from the vertical and point in almost any direction. *Tekoulina pricei* Solem, 1972 (Figures *4–6*) from Rarotonga, Cook Islands also is a tornatellinid. It reaches 9.1 mm in height and is a much more elongated species than the *Tornatellina*. Apertural armature is much less complex, with only single parietal, columellar and palatal apertural barriers. The columella (Figure *4*, lower left) is smooth, but the palatal lamella (Figure *4*, upper right) and parietal (not shown) have the top and upper side covered with raised denticles that point towards the outside of the aperture. Inspection at higher magnifications shows that these denticles have their anterior fifth free of the surface (Figure *6* at 4 646×) and their outer margin slopes back to the surface at about a 30° angle (left side of Figure *5* at 826×). From a broad base, each denticle narrows to an elongated, spear-like tip. Please also note that the surface of the columellar wall (Figure *4*, extreme lower left) has vague irregularities.

Barriers in the Tornatellinidae are present when the young hatch, grow anteriorly as the shell grows, and are absorbed posteriorly. The resorption margin on the palatal lamella in *Tekoulina* can be seen at the upper left of Figure *4*. Both in structure, orientation and distribution, there are major differences between these two tornatellinids, indicating that variation within family units can be extensive.

Explanation of Figures *7* to *12*

Vertigo milium (Gould, 1840)

Figures *7* to *10*: Menard County, Illinois. Field Museum of Natural History number 18776: Figure *7*: Aperture and body whorl at 74×. Figure *8*: Lateral view of parietal lamella edge at 2 450×. Figure *9*: View from lower side of parietal lamella at 1 879×. Figure *10*: Vertical view of denticles on parietal lamella at 5 980×.

Virpazaria adrianae Gittenberger, 1969

Figures *11*, *12*: "Velika jama," near Soko Mt., near Dupilo, west of Virpazar, Montenegro, Jugoslavia. Rijksmuseum van Natuurlijke Historie, Leiden. Figure *11*: Aperture of shell at 79×. Figure *12*: Edge of palatal barrier at 935×.

Explanation of Figures *13* to *18*

Strobilops labyrinthica (Say, 1817)

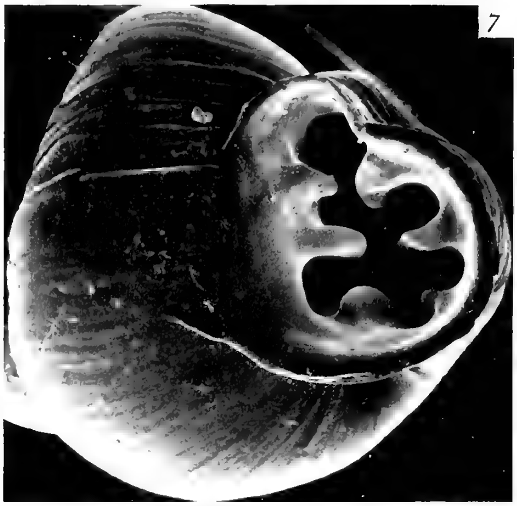
Figures *13* to *15*: Below Esterville, West Fork, Desmoines River, Emmet County, Iowa. Field Museum of Natural History number 154121. Figure *13*: Parietal lamellae at 195×. Figure *14*: Lateral view of small denticles at 2 090×. Figure *15*: Detail of a single denticle at 6 250× showing relationship of denticle and parietal lamellar surface.

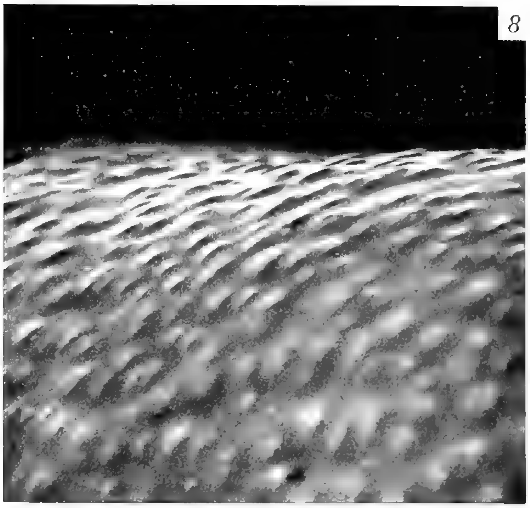
Phrixgnathus erigone (Gray, 1850)

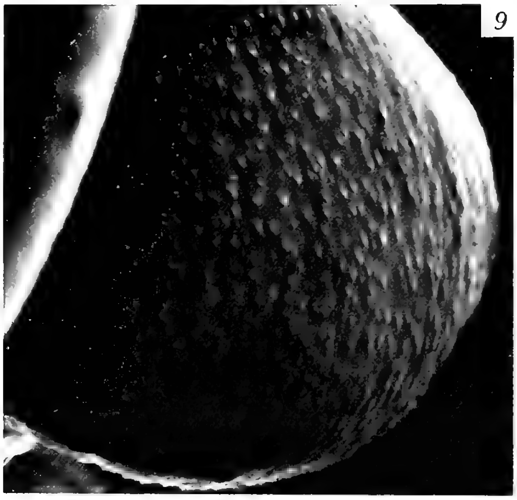
Figure *16*: Waitakere Range, north of Auckland, North Island, New Zealand. Field Museum of Natural History number 135477. Denticles on columellar wall at 2 485×.

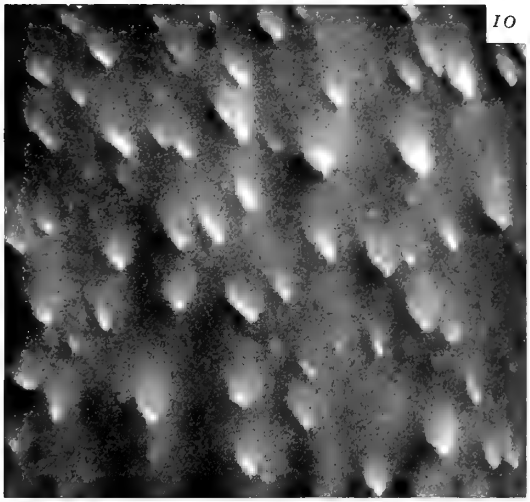
Dentherona bairnsdalensis (Gabriel, 1930)

Figures *17*, *18*: Jemmy's Point, Lakes Entrance, Victoria, Australia. National Museum of Victoria, Melbourne. Figure *17*: Aperture of shell with outer lip partly broken off at 73×. Figure *18*: Low angle view towards posterior of parietal lamellar surface at 2 435×.

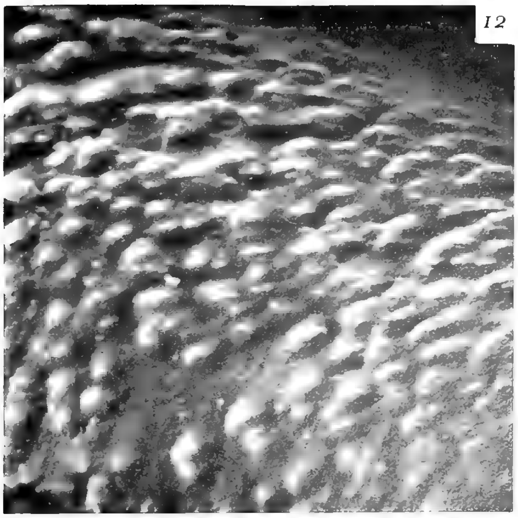

7

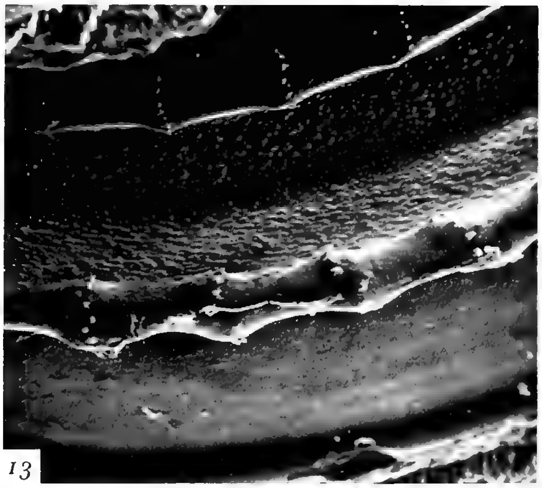

8


9

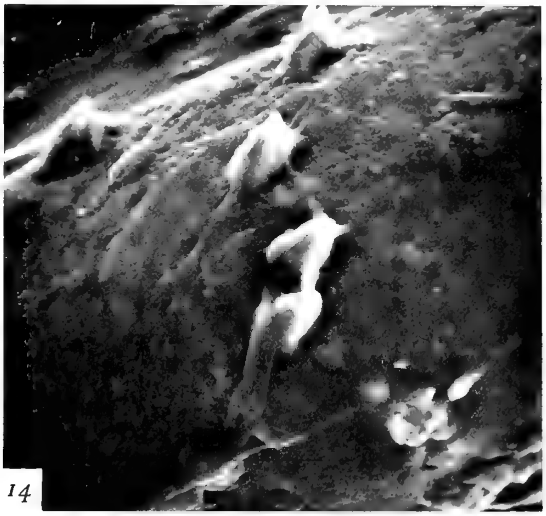

10


11

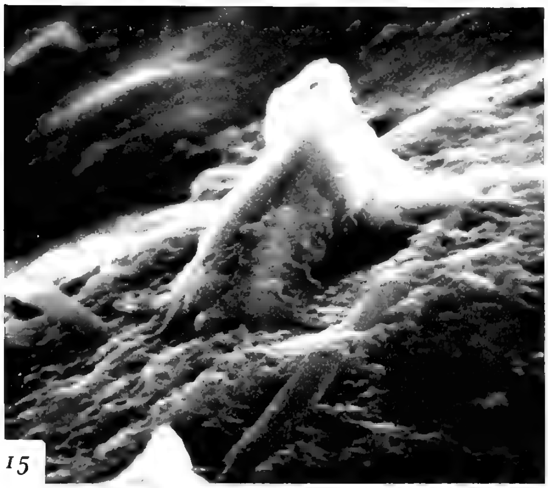

12



13

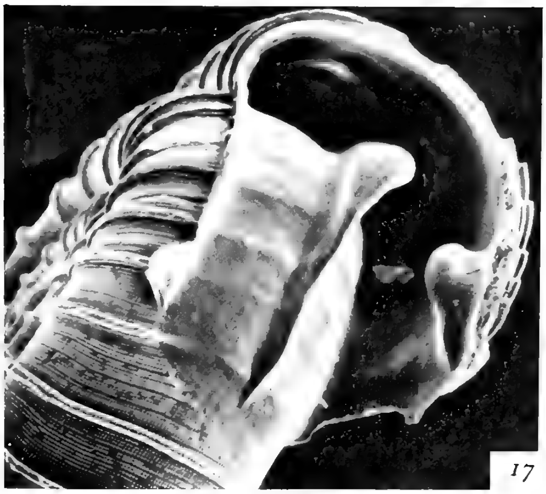


14

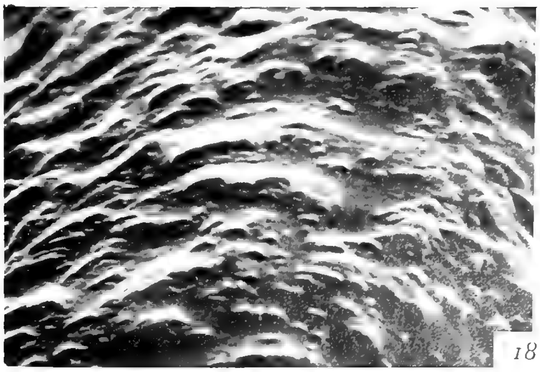


15

16



17



18

Vertigo milium (Gould, 1840) is a common North American pupillid. The aperture (Figure 7 at 74×) has several high and prominent lamellae. In this group the lamellae only form at adulthood, while the young lack these denticles. On most apertural surfaces there are extremely small, roughly triangular denticles. On the parietal lamella edge (Figure *9* at 1 879×) they point partly towards the narrow central opening of the aperture and partly towards the outside of the aperture. When viewed almost horizontally from an anterior position looking diagonally backward (Figure *8* at 2 450×), they are seen to weakly denticulate the surface. A more vertical view (Figure *10* at 5 980×) shows that they have a triangular point coming from a nearly square base. Despite their minute size, these are equivalent to the clear hooks and scales of the tornatellinids.

Virpazaria adrianae Gittenberger (1969: 298, fig. 4) has a large transversely situated parietal lamella combined with an inwardly elevated palatal and basal lip to effectively narrow the aperture. The specimen shown in Figure *11* has been tilted so that the edges of both the parietal (lower right) and palatal (upper right) barriers are visible. Tops and sides of these barriers are covered with dense pustulations (Figure *12* at 935×). These lack the sharp definition of the structures found in the previously discussed species. They are comparable to the irregularities seen on the columellar wall of *Tekoulina* (extreme lower left of Figure *4*).

Another orthurethran, *Strobilops labyrinthica* (Say, 1817) (Figures *13–15*), has lamellae that show the same basic growth pattern as in *Tekoulina,* that is, anterior growth and posterior resorption. Instead of a continuous cluster of scale-like denticles, there are single rows of denticles at regular intervals. A low magnification picture (Figure *13* at 195×) provides orientation for the view of a single row of denticles (Figure *14* at 2 090×) and of a single denticle (Figure *15* at 6 250×) found on the parietal lamellae. The individual denticles are sharply elevated with only slight anterior inclination, restricted to the upper edge of the lamella, and formed of the same type crystals as the lamellar surface. The bands of denticles only start about one-quarter whorl behind the apertural lip and extend to the posterior edge of the lamella. These photographs were made of the upper parietal (large lower lamella in Figure *13*) and the small interparietal (upper lamella in Figure *13*) at a point about one-third of a whorl behind the apertural lip. Please note the irregular "pebbling" of the parietal wall surface lying between the lamellae in Figure *13*.

Such structures are not limited to orthurethrans. The huge dagger-like denticles that line the edges of the main parietal lamella in the New Zealand charopid, *Ptychodon microundulata* (Suter, 1890), have been figured previously (Solem, 1970: plt. 60). Illustrations of more typical endodontid and charopid taxa will be presented elsewhere (Solem, in press). Here I show only two aulacopod examples. *Phrixgnathus erigone* (Gray, 1850) (Figure *16*) is a New Zealand punctid without barriers, although other species in the genus (as presently defined) have well developed ones. Particularly on the columellar wall, but to a lesser extent on the other surfaces of the aperture, there are small raised denticles that point towards the outside of the aperture (Figure *16 at* 2 485×). These are irregular in form. They look like slanted flecks of mica crystals in rock and do not show a regularly defined shape. Similarly, the Australian charopid, *Dentherona bairnsdalensis* (Gabriel, 1930) (Figures *17, 18*), has the surface of the barriers and the callus covered with fine irregularities that denticulate the surface (Figure *18* at 2 435×).

The same type of microarmature covers the apertural surfaces in the Malayan streptaxid *Oophana diaphanopepla* van Benthem Jutting (1954: 105, fig. 13). Apertural narrowing is effected by three structures—a high sinuated parietal lamella, inward deflection of the outer palatal lip, and inward extension of the basal lip. SEM examination of the surfaces shows sharply defined elevated plates. In vertical view at 800× (Figure *19*) and 4 345× (Figure *20*) their shape and spacing is seen to approximate that of *Phrixgnathus* (Figure *16*) and *Vertigo* (Figures *9, 10*) although quite different in size. Viewed laterally from a low angle at 1 585× (Figure *21*) and 6 345× (Figure *22*), the sharp anterior edge (left side of photographs) and gradual posterior slope of the denticles is obvious.

At times the size of such platelets becomes very large. In *Stenotrema barbatum* (Clapp, 1904), a common polygyrid land snail of eastern North America (see Archer, 1948), they can be detected with optical equipment at relatively low magnification. Even at 27.5× (Figure *23*) their presence over all apertural surfaces is obvious. Viewed at 3 100× (Figure *24*) they are seen to be a series of overlapping "shingles" that point towards the outside of the apertural opening. While not yet viewed under the SEM, 100× optical examination of various clausiliid, bulimulid, camaenid, helicid and enid taxa shows that equivalent structures are present on the lip and barrier surfaces in many species of these families.

DISCUSSION

What at first would seem to be a confusing mass of different structures can be classified into two types. First, it is evident that the presence of partly elevated platelets, generally very small in size, is almost the normal situation.

These occur on lip edges, calluses and barrier surfaces. They have been observed in species, such as *Phrixgnathus erigone,* that lack any apertural barriers. Where high, lamellar barriers that extend posteriorly for a fair distance are present, as in the Tornatellinidae, Strobilopsidae, Endodontidae and some Charopidae, these can be partly or completely replaced by hook-like denticles, the second type of structure. In all cases the sharp edge or point of the microstructure faces towards the apertural opening.

While the probable function of the hook-like structures is easy to hypothesize, their origin and the utility of the platelets is not immediately obvious. Barriers function to hinder or deny access by predators to the retreated animal. Addition of barbules that point towards the exterior and are located on top of the barriers as in *Tekoulina* (Figures *4–6*), *Ptychodon* (Solem, 1970: plt. 60), and the Endodontidae (Solem, in press) reinforces and complements this protection. A small arthropod attempting to crawl between the lamellae could get setal hairs, antennal parts, or tarsal fringes caught under the free edge of the denticles. These could be freed most easily by backing out. Forward motion would most likely result in further entanglements, while retreat would bring liberation at the price of continued hunger.

The platelets do not have an incised anterior that could entangle these arthropod parts (see Figures *16, 21, 22, 24*). Their anterior margin is vertical. They do, however, have this vertical margin on the outside facing edge of the platelet. I suggest that they function as an aid to the snail in extending its body from the shell. Contractions of the free muscle system and shift of the body fluids into the pallial cavity enable the foot and head to be withdrawn into the shell, but the problem of regaining the outside is more difficult. Increased turgor will cause swelling and relaxing the free retractor muscles will help extrude the foot and head, but, in particular, the parietal and columellar margin of the visceral hump would have difficulty in moving forward after a deep retraction. Just as sand or cinders on an icy sidewalk improve traction for a human walking, so the provision of a rough surface on the columellar and parietal walls could aid the snail to pull its body forward. If a snail is prodded to retreat deep within its shell, then left alone, the edges of the mantle region are moved forward to near the lip edge before the head and foot are unfolded. The anterior vertical edges of these platelets would provide micro gripping surfaces for the mantle collar.

Current techniques of SEM specimen preparation are not adequate to allow effective study of the cellular surfaces on the mantle collar. When preparation technique catches up with the viewing capabilities of the SEM, then a study to test the validity of this hypothesis becomes possible. That these platelets are not restricted to land snails has been demonstrated by Robertson (1971: plt. 9, figs. 32–34). The larval shell of *Pedicularia decussata* Gould, 1855 has these platelets on the columellar and basal lip edge. Hence it may well be that these platelets are a basic structure of snail shells that was not detected previously because of the limits inherent to optical viewing.

SEM study of species without apertural barriers and comparisons of barrier and non-barrier species in the same genus must be undertaken. Since the aperture of *Stenotrema* is far more constricted proportionately than is the aperture of *Oophana,* for example, the large size of the platelets in the former could result from selection for rougher surface. If increasing platelet size is selected for when the aperture is narrowed, then this can be viewed as a pre-adaptation for development of hooks or points to entangle micro-arthropods. Once the anterior plate edge is elevated, then any mutation that incises the anterior margin would tend to discourage crawlers. The deeper the incising, the greater the discouragement, hence the selective pressure leading to the change from a plate-like ridge to a pointed hook. Once the hooked points are present, the functional use of the platelets would be less important, and a degeneration to the irregularities seen in *Tekoulina* (Figure *4*) and *Strobilops* (Figure *13*) becomes probable.

Thus the complex denticles in the Tornatellinidae and endodontoid taxa can be derived quite simply from the micro-platelets that are found in many taxa, first by selection pressure for better gripping by the snail's mantle during extension of the body from a retracted position, then by selection for indenting the elevated anterior edge as a means to discourage predators.

Explanation of Figures *19* to *22*

Oophana (Haploptychius) diaphanopepla van Benthem Jutting, 1954

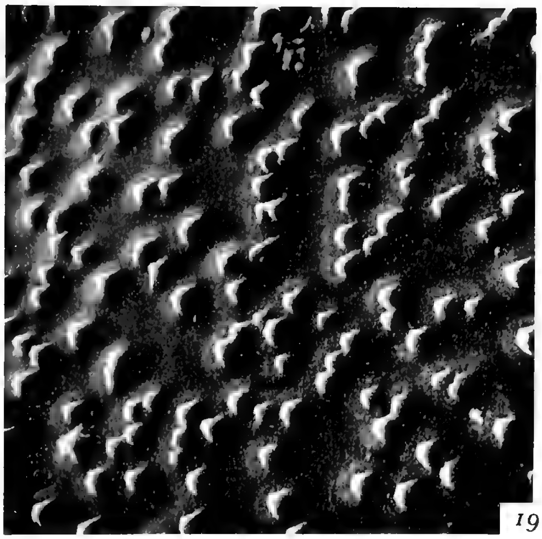
Figures *19* to *22*: South face of Bukit Serdam, near Raub, Pahang, Malaya. Field Museum of Natural History number 147666.

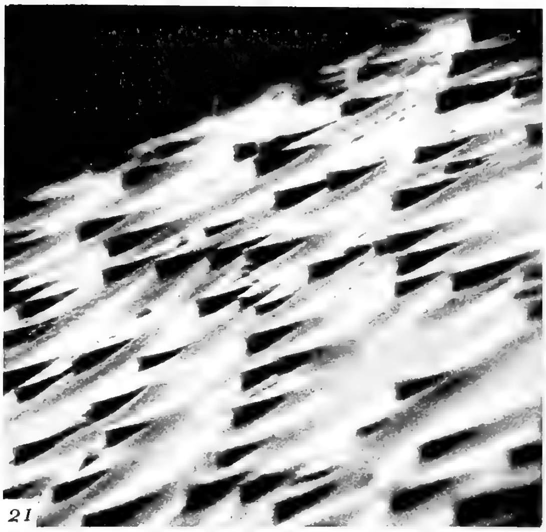
Figure *19*: Vertical view of microdenticles on palatal lip of shell at 800×. Figure *20*: Details of microdenticles on palatal lip at 4345×. Figure *21*: Lateral view of microdenticles at 1585×. Figure *22*: Detail of microdenticles on palatal lip at 6345×.

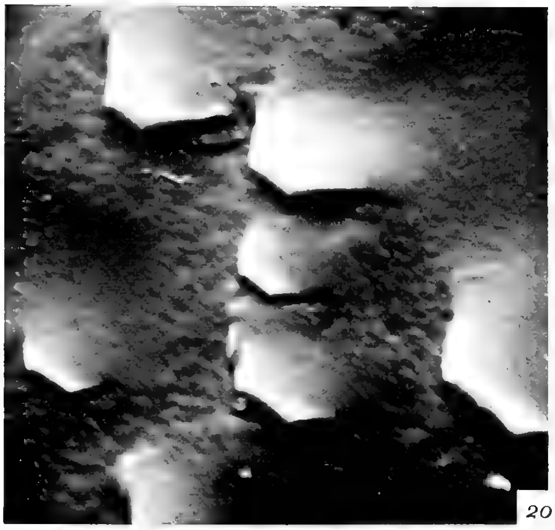
Explanation of Figures *23* and *24*

Stenotrema barbatum (Clapp, 1904)

Figures *23, 24*: Medora, Jackson County, Indiana. Field Museum of Natural History number 61296. Figure *23*: View of shell aperture at 27.5×. Figure *24*: Lateral view of platelets on parietal barrier at 3100×.

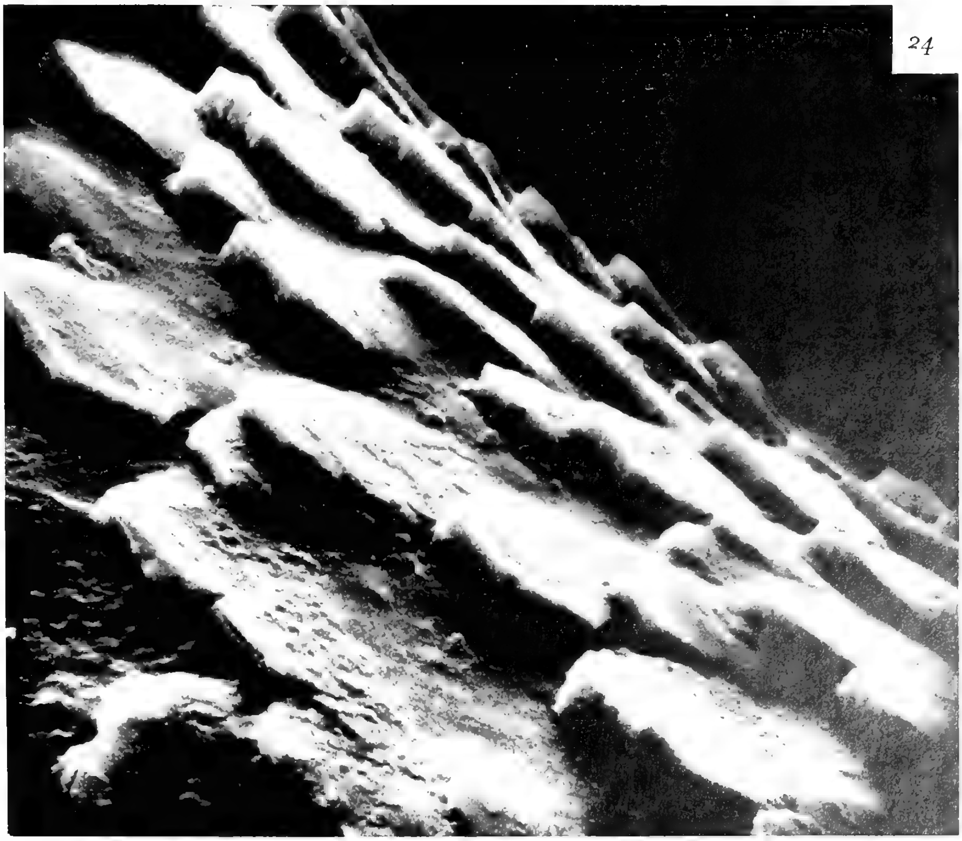

19


21


20


22


23


24

SUMMARY

Many land snails are shown to have a dense microarmature of platelets on the inner surfaces of the shell aperture. These are visible at low magnifications when the shell aperture has been greatly constricted by barrier formation, but mostly at 900–3 000× magnification in more typical species. It is hypothesized that this microarmature aids the snail when it extends the body after being retracted into the shell. The microplatelets would become larger when the aperture became more constricted, since the snail would have more difficulty in squeezing its foot and buccal mass through the narrowed opening.

The various patterns of barrier formation in land snails are reviewed and the presence of hook-like denticles, generally on the barrier edges, that point towards the outside of the aperture is documented. These can be evolved from the common platelets by progressively deeper incision of their anterior margin and narrowing from a broad anterior margin to a point. The function of these hooks is to hinder the attempts of small arthropod predators to enter the snail shell by providing crevices (the under edges of the hooks) in which setae, antennae or tarsal fringes can become entangled.

Literature Cited

Archer, Allan F.
1948. Land snails of the genus *Stenotrema* in the Alabama Region. Geol. Surv. Alabama, Mus. Pap. **28:** 85 pp.; 10 plts.

Boettger, Caesar R.
1921. *Carabus morbillosus* Fabr. und *Otala tigri* Gerv., eine Studie gegenseitiger Anpassung. Abhdl. Senckenberg. Naturforsch. Gesell. **37** (4): 319 - 326; plts. 30, 31

Cooke, Alfred Hands
1895. Molluscs. Cambridge Nat. Hist. **3:** xii+1 - 459; 311 text figs.; 4 maps

Cooke, C. Montague & Yoshio Kondo
1960. Revision of the Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). Bernice P. Bishop Mus., Bull **221:** 303 pp.; 123 text figs. (30 December 1960)

Eisner, T. & E. O. Wilson
1970. Defensive liquid discharge in Florida tree snails (*Liguus fasciatus*). The Nautilus **84** (1): 14 - 15; 1 text fig. (16 July 1970)

Girard, Albert Alexandre
1896. Sur le "*Thyrophorella thomensis*", Greef, Gastéropode terrestre muni d'un faux opercule à charnière. Jorn. Sci. Math., Phys. e Natur., Acad. Real Sci. Lisboa (2) **4** (13): 28 - 32; 1 plt.

Gittenberger, E.
1969. Beiträge zur Kenntnis der Pupillacea I. Die Spelaeodiscinae. Zool. Meded. **43** (22): 287 - 306; plt. 1; 8 text figs. (16 July 1969)

Godwin-Austen, H. H.
1874. Description of five new species of Helicidae of the subgenus *Plectopylis*, with remarks on all the other known forms. Proc. Zool. Soc. London **1874:** 608 - 613; plt. LXXIII (17 November 1874)

Gude, Gerard K.
1914. Mollusca. — II (Trochomorphidae-Janellidae). The fauna of British India. pp. xii+520; 164 text figs.

Guilding, Lansdown
1829. Observations on the zoology of the Caribaean islands. Zool. Journ. **4** (14): 164 - 175

Lloyd, D. C.
1970. The function of the odour of the garlic snail *Oxychilus alliarius* (Pulmonata: Zonitidae). Malacologia **10** (2): 441 - 449; 1 text fig.; 2 tables

Pilsbry, Henry Augustus
1893 - 1895. Manual of conchology. Second series: Pulmonata. **9:** xlviii+366 pp.; 71 plts. (16 November 1893 to 2 February 1895)
1940. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Philadelphia, Monogr. 3, **1** (2): vii, 575 - 994; text figs. 378 to 580 (1 August 1940)
1946. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Philadelphia, Monogr. 3, **2** (1): vi, 1 - 520; text figs. 1 - 281 (6 December 1946)
1948. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Philadelphia, Monogr. 3; **2** (2): xlvii, 521 - 1113; text figs. 282 - 585 (19 March 1948)

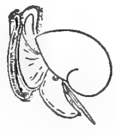
Robertson, Robert
1971. Scanning electron microscopy of planktonic larval marine gastropod shells. The Veliger **14** (1): 1 - 12; plts. 1 - 9 (1 July 1971)

Schwalb, Hans Helmut
1961. Beiträge zur Biologie der einheimischen Lampyriden *Lampyris noctiluca* Geoffr. and *Phausis splendidula* Lec. und experimentelle Analyse ihres Beutefang- und Sexualverhaltens. Zool. Jahrb., Syst. **88** (4): 399 - 550; 100 text figs.

Solem, Alan
1966. The neotropical land snail genera *Labyrinthus* and *Isomeria* (Pulmonata, Camaenidae). Fieldiana: Zool. **50:** 226 pp.; 61 text figs.; 16 tables (31 May 1966)
1970. Malacological applications of scanning electron microscopy I. Introduction and shell surface features. The Veliger **12** (4): 394 to 400; plts. 58 - 60; 1 table (1 April 1970)
1973. Apertural barriers in Pacific island land snails of the families Endodontidae and Charopidae. In press, The Veliger

Sturani, Mario
1962. Osservazioni e ricerche biologiche sul genere *Carabus* Linnaeus (*sensu lato*). Mem. della Soc. Entomol. Ital. **41:** 85 - 202; 59 text figs.; plt. 9

van Benthem Jutting, W. S. S.
1954. The Malayan Streptaxidae of the genera *Discartemon* and *Oophana*. Bull. Raffles Mus. Singapore **25:** 71 - 106; 13 text figs. (December 1954)



Thecacera picta spec. nov. from Suruga Bay, Japan

(Nudibranchia : Doridoidea : Polyceridae)

BY

KIKUTARÔ BABA

Shigigaoka 35, Minami-11-jyo, Sango-cho, Ikoma-gun, Nara-ken, Japan

(1 Text figure)

THE GENUS *Thecacera* Fleming, 1828 was established on the type *Doris pennigera* from Devon, England. But the original description of this species by MONTAGU (1815) was poor. Also, it is unfortunate that ALDER & HANCOCK's (1855) figures of *T. pennigera* were based on an animal "in a sickly state," and so deformation presumably occurred by contraction at certain parts of the body of that animal. According to one of the color photographs taken in 1956 by Dr. A. Inaba of the Mukaishima Marine Biological Station on the Inland Sea of Seto, Japan from a very active specimen of *T. pennigera* and shown to me, the rhinophorial and branchial appendages are found to terminate altogether in an acutely pointed tip, not forming a blunt end as appeared in Alder & Hancock's figures.

The main species of *Thecacera* of the world are:

1. *Thecacera pennigera* (Montagu, 1815)
   Distribution: England; France; the Mediterranean; Brazil; Australia; Japan
2. *Thecacera darwini* Pruvot-Fol, 1950
   Distribution: Chile
3. *Thecacera maculata* Eliot, 1905
   = *T. lamellata* Barnard, 1933
   Distribution: Karachi, India; South Africa
4. *Thecacera inhacae* Macnae, 1958
   Distribution: Inhaca, South Africa

The present new species is evidently distinct from the forms listed above by having (1) a different coloration of the body, and (2) a crescent-shaped ridge at the outer base of each rhinophorial appendage.

Thecacera ***picta*** Baba, spec. nov.

(Japanese name: Tsunozaya-umiushi)

(Figure 1)

Type: Collected by Mr. K. Suzuki, Curator in the Marine Science Museum of Tokai University and his assistants, SCUBA-divers of the Museum, from Uchiura-coast (35° 02′N; 138°53′E) near Osezaki, NE of Suruga Bay, Japan, in 35 m, on 17 November, 1971.

Description: The living animal, when fully extended, attains a length of 10 mm. The external form of the body is essentially as in Dr. Inaba's *Thecacera pennigera* (see above). The rhinophore is long, cylindrical, and perfoliated above. The rhinophorial appendage or sheath is incomplete (*cf.* ABRAHAM, 1877: 231); it takes the form of a triangular valve more or less narrowed and tapering to the tip. The anterior margin of the valve at its base is folded back to the stalk of the rhinophore. In this new species there is a crescent-shaped ridge situated at the outer base of each rhinophorial appendage. The gill is formed of 7 bipinnate plumes, set around the anus. The branchial appendage or post-branchial process is elongated conical and pointed to the tip. The foot-corners are horn-like. The genital orifices are located immediately below and behind the right rhinophorial sheath.

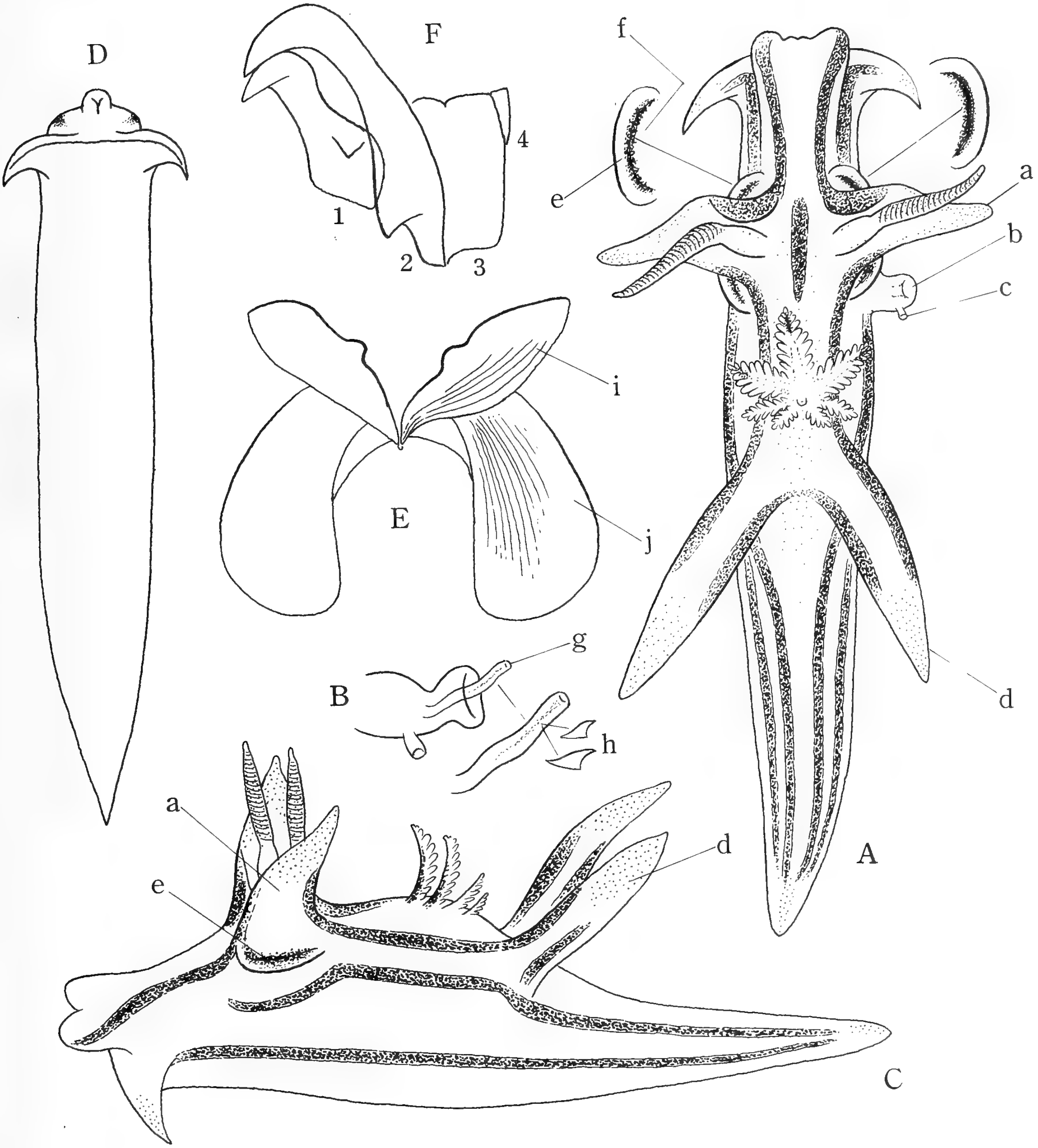
In the preserved state, the rhinophorial and branchial appendages of the animal become markedly shortened,

(on facing page →)

Figure 1

Thecacera ***picta*** Baba, spec. nov.

A, C, and D: Living animal in dorsal, lateral, and ventral views; length 10 mm
B: Copulatory organ in extruded state
E: Paired jaws from outside (× 40)
F: Right half-row of radula (× 100)
a – rhinophorial sheath b – male orifice c – female orifice
d – post-branchial process e – crescent-shaped ridge
f – hollowed space g – penis h – hooks
i – jaw proper j – wing
1 to 2 – inner laterals 3 to 4 – outer laterals


D
F
1
2
3
4
E
i
j
B
g
h
f
e
a
b
c
d
A
a
e
d
C

and rounded as well, at their extremity. The rhinophores are completely retracted within sheaths.

The ground color of the body above is translucent yellowish white. In this new species a conspicuous band of chocolate brown appears: (1) on the mid-dorsal line in front of the gill; (2) along the lateral margin of the head and back, including the lower half of the rhinophorial and branchial appendages; (3) on the crescent-shaped ridge at the outer base of the rhinophorial sheath; (4) on each side of the length of the body, and (5) on the foot-brim. The tip of the rhinophorial and branchial appendages, foot-corners and tail are vividly tinted orange yellow. The rhinophore is orange yellow on the perfoliated portion, and yellowish white on the stalk. The gill is yellowish white, the largest plumes of it being provided with orange yellow pigmentation on the tip and a longitudinal chocolate brown vein on the rachis on the outside. The sole is uniformly yellowish white.

The shape of the jaws and radula is typical of the genus. Each jaw is accompanied by a wing. The radula formula is 10 × 2·2·0·2·2. The inner laterals are hamate (the first is smaller than the second), and the outer ones simply scale-like. In *Thecacera darwini* a wing is absent from the jaws; also, this species is unusual in having a median tooth of the radula (MARCUS, 1959: 58). The penis is armed with chitinous hooks as usually found in the genus.

ACKNOWLEDGMENTS

I wish to thank Mr. Katsumi Suzuki and his assistants for supplying the type collection for my taxonomic study. Acknowledgment also is made to Dr. Akihiko Inaba for a photograph referred to for comparison.

Literature Cited

ABE, TAKEO
1964. Opisthobranchia of Toyama Bay and adjacent waters. Tokyo. Hokuryu-Kan: ix+99 pp.; 36 plts.

ABRAHAM, PHINEAS S.
1877. Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. Proc. Zool. Soc. London **1877**: 196 - 269; plts. 27 - 30 (August 1877)

ALDER, JOSHUA & ALBANY HANCOCK
1844-1855. A monograph of the British nudibranchiate Mollusca, with figures of all the species. London, Ray Soc. prts. 1 - 7: 438 pp.; 84 plts.

ALLAN, JOYCE K.
1957. Some Opisthobranchia (class Gastropoda) new to Australia or otherwise of interest. Journ. malacol. Soc. Australia **1** (1): 3 - 7; figs. 1 - 3

BABA, KIKUTARÔ
1960. The genera *Polycera, Palio, Greilada* and *Thecacera* from Japan (Nudibranchia - Polyceridae). Publ. Seto Mar. Biol. Lab **8** (1): 75 - 78; plt. 6

BARNARD, KEPPEL HARCOURT
1933. Description of a new species of *Thecacera*. Journ. Conchol. London **19** (9): 294 - 295; fig. 1

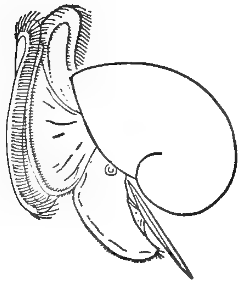
ELIOT, CHARLES N. E.
1905. Nudibranchs from the Indo-Pacific: I. Notes on a collection dredged near Karachi and Maskat. Journ. Conchol. London **11** (8): 237 - 256; plt. 5; 1 text fig.

MACNAE, WILLIAM
1958. The families Polyceridae and Goniodoridae (Mollusca, Nudibranchiata) in southern Africa. Trans. Roy. Soc. South Africa **35** (4): 341 - 372; plts. 17, 18; text figs. 1 - 23

MARCUS, ERNST
1959. Lamellariacea and Opisthobranchia. *In*: Reports of the Lund University Chile Expedition 1948-49, No. 36. Lunds Univ. Årsskr. N. F. (2) 55 (9): 1 - 133; figs. 1 - 196 (20 March 1959)

MONTAGU, GEORGE
1815. Descriptions of several new or rare animals, principally marine, discovered on the south coast of Devonshire. Trans. Linn. Soc. London **11** (1): 1 - 26; plts. 1 - 5

PRUVOT-FOL, ALICE
1950. Le genre *Thecacera* Fleming 1828 et une espèce nouvelle, *Thecacera darwini*. Journ. Conchyl. Paris **90** (1): 48 - 52; figs. 1 - 4



A New Species of Monoplacophoran from the Abyssal North Pacific

BY

FRANK J. ROKOP

Scripps Institution of Oceanography, University of California, San Diego – La Jolla, California 92037

(2 Plates; 5 Text figures)

INTRODUCTION

SEVERAL RECENT SPECIES of Monoplacophora belonging to the subgenera *Neopilina* and *Vema* have been reported since the initial discovery of *N. (N.) galatheae* Lemche, 1957, by the Galathea Expedition in 1952. A total of approximately 60 specimens, representing 5 species, have been collected from 19 stations in the Eastern Tropical Pacific (FILATOVA & ZENKEVICH, 1969). Only 3 specimens have been recorded from other regions: the Gulf of Aden in the Indian Ocean (TEBBLE, 1967); the South Atlantic off the tip of South America (ROSEWATER, 1970); and the Central Pacific southwest of Hawaii (FILATOVA *et al.*, 1968). All have been recorded in depths ranging from 1650 to 6350m.

With the exception of the Central Pacific monoplacophoran, all have been collected in relatively close proximity to continents. SOKOLOVA (1969) described these oceanic regions near the continental land masses where primary production is high as "eutrophic", in contrast to the sterile central "oligotrophic" areas. The Central Pacific specimen was collected by the R/V *Vityaz* from 2000m on the slope of a guyot in the Marcus-Necker Submarine Mountains. Since the associated macrofauna was relatively diverse and abundant, FILATOVA *et al.* (1968) concluded that the feeding conditions on the raised guyot were more favorable than on the more characteristic, deeper oligotrophic regions that surround it. They further postulated that the distribution of monoplacophorans was restricted to eutrophic areas or to environments within otherwise oligotrophic regions with favorable feeding conditions.

However, on Leg 7 of the Scripps Institution of Oceanography Expedition *Seventow* in the North Pacific a species of monoplacophoran was obtained from a depth of more than 6000m underlying the sterile, central water mass. The collection site is located in the center of the oligotrophic region where the estimated biomass of the bottom fauna (0.01 to 0.05 g/m^2) is extremely low (FILATOVA, 1969). Thus, contrary to previous information, monoplacophorans are able to survive in nutrient-poor, oligotrophic environments.

This Central North Pacific species of monoplacophoran is distinct from other known species and is described in this report as a new species of the genus *Neopilina*. In addition, a series of scanning electron micrographs illustrating the details of the elaborate shell sculpture of the new species is included.

SYSTEMATICS

MONOPLACOPHORA
Wenz in Knight, 1952

TRYBLIDIOIDEA Lemche, 1957

TRYBLIDIACEA Pilsbry in Zittel, 1899

TRIBLIDIIDAE Pilsbry in Zittel, 1899

Neopilina Lemche, 1957

Neopilina (Neopilina) ***oligotropha*** Rokop, spec. nov.

(Figures 1 to 5 and *6* to *9*)

Description of Holotype: Shell small, thin, patelliform and semitransparent. Shell sculpture of concentric and radial elevated threads. Radial threads increasing in number abapically from approximately 40 near the apex to 135 - 140 peripherally. Concentric threads 12 in number anterior to the apex and 32 in number along the midline from apex to posterior margin. The intersection of radial and concentric threads producing raised nodes and delimiting quadrate depressions (150 - 200/mm^2). Aperture

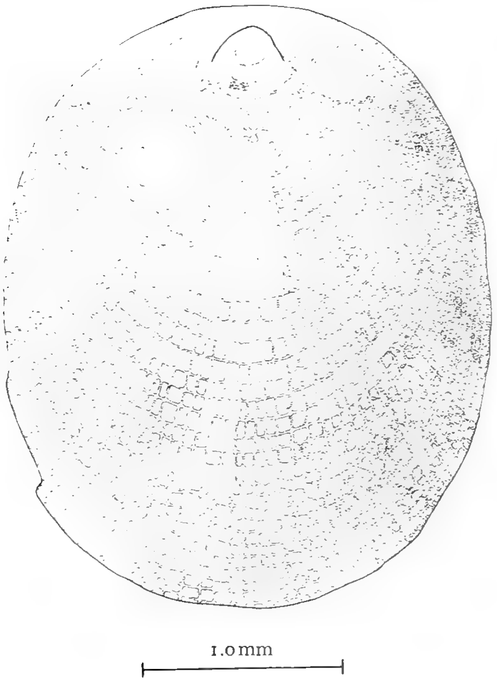


Figure 1

Dorsal view of the shell of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov. Holotype, USNM no. 723796

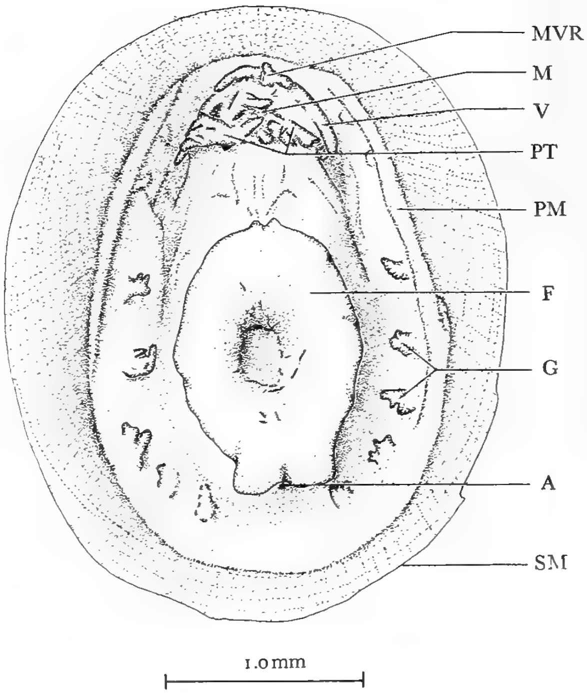


Figure 2

Ventral view of the holotype of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov.

MVR – median velar ridge M – mouth V – velum
PT – postoral tentacles PM – pallial margin F – foot
G – gills A – anus SM – shell margin

ovate, slightly longer than wide. Apex prominent, discoidal, positioned slightly posterior of anterior margin. Periostracum pale yellowish and transparent, noticeable only along the margin where it projects beyond the shell.

The external morphology of the animal is exposed in ventral view. The prominent subcircular foot is surrounded laterally by the marked depression of the pallial area. Along each side is a row of 5 small, lobate gills. The oral region is bound anterolaterally by the velum and posteriorly by numerous postoral tentacles. The gut, with 4 distinct coils, terminates posteriorly at the anus, located at the base of the foot.

Dimensions: Shell length 3.0 mm, width 2.5 mm, maximum height (depth) 0.9 mm, apex height 0.7 mm, apex to anterior margin 0.1 mm.

Comparisons: On the basis of gill number, the present new species has been placed in *Neopilina s. s.* rather than

Explanation of Figures 6 and 7

Scanning electron micrographs of the shell surface features of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov.

Figure 6: Oblique view of the entire shell fragment showing the overall pattern of the radial and concentric sculpture. × 40
Figure 7: Portion of the fractured edge of the shell fragment illustrating the relief of the sculpture and the granular, porous nature of the shell structure. × 510
sm – shell margin c – concentric thread r – radial thread
fe – fractured edge

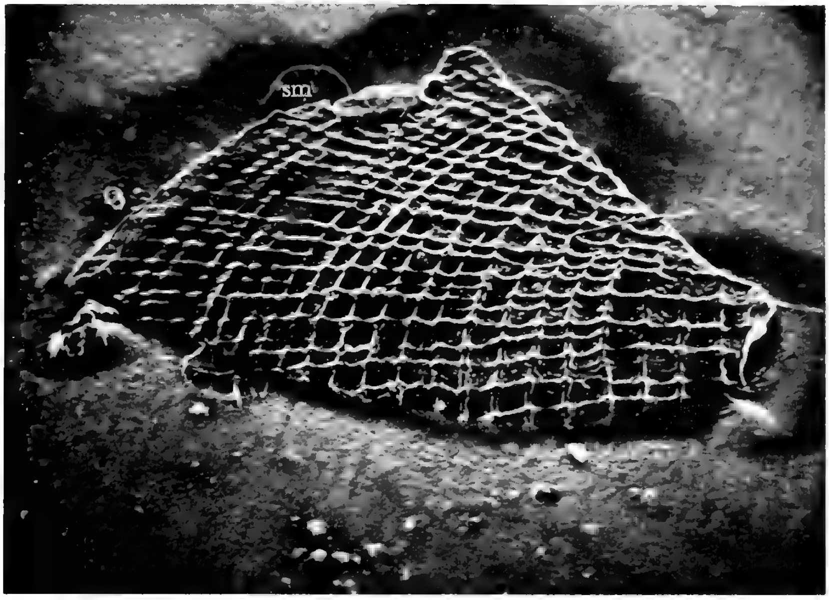


Figure 6

Figure 7

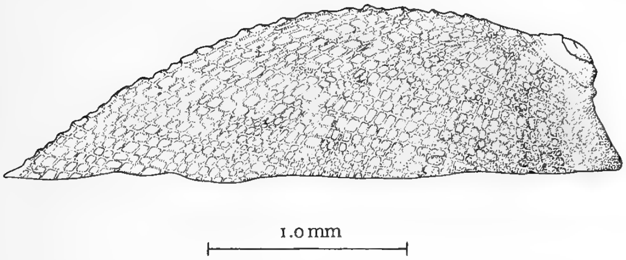


Figure 3

Lateral view of the holotype of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov.

the subgenus *Vema.* Members of *Vema,* of which *N. (V.) ewingi* Clarke & Menzies, 1959, is the type, possess 6 pairs of gills in contrast to the 5 pairs present in the subgenus *Neopilina.*

Of the other members of the subgenus *Neopilina,* the present new species most closely resembles *N. (N.) veleronis* Menzies & Layton, 1962. Both *N. (N.) veleronis* and *N. (N.)* ***oligotropha*** are small (1 - 3mm), distinctly ovate in outline, and have small lobate gills. However, the postoral tentacles are simple, unbranched projections in *N. (N.) veleronis* and the shell apex characteristically extends beyond the anterior margin; *N. (N.)* ***oligotropha*** differs in having multiple postoral tentacles and a shell apex which does not extend anteriorly over the margin of the aperture.

Collection: Scripps Institution of Oceanography Expedition *Seventow,* Leg 7, Station H-30. Central North Pacific, approximately 680 miles N of Hawaii (30°05'N, 156°11'48"W), 6065 - 6079m, 8 July 1970, R/V *Thomas Washington.* Gear: Epibenthic Sled (Hessler & Sanders, 1967) equipped with a 0.5mm mesh trawl bag. One specimen (holotype) and 1 shell fragment.

Holotype Deposition: National Museum of Natural History (U. S. N. M.), Smithsonian Institution, Washington, D. C. USNM No. 723796.

Key to the Species of the Subgenus *Neopilina*

1. Specimens large (10 - 36mm); shell almost circular in outline; gills branching, with 5 - 8 lamellae 2
– Specimens small (1 - 3mm); shell longer than wide, ovate in outline; gills with 1 - 4 small lobes 4
2. Postoral tentacles well developed and numerous; gills with 6 - 8 lamellae 3
– Postoral tentacles reduced; gills with 5 lamellae .... *Neopilina (N.) bruuni* Menzies, 1968
3. Shell apex almost immediately over the anterior margin .... *N. (N.) galatheae* Lemche, 1957
– Shell apex set back from the anterior margin .... *N. (N.) adenensis* Tebble, 1967
4. Postoral tentacles simple, unbranched; shell apex projecting beyond the shell margin .... *N. (N.) veleronis* Menzies & Layton, 1962
– Postoral tentacles multiple; shell apex not extending beyond the shell margin .... *N. (N.)* ***oligotropha*** Rokop, spec. nov.

REMARKS

Size: Members of the benthic fauna of oligotrophic areas of the deep-sea are characteristically very small in size. All the gastropods and pelecypods from the same epibenthic sled lowering (Station H-30) were under 6mm in maximum dimensions and the majority were smaller than 3mm. Hence, *Neopilina (Neopilina)* ***oligotropha*** is not unusually small but rather of moderate size for this particular environment. Furthermore, the size range of the 14 specimens of *N. (N.) veleronis* collected by the R/V *Velero IV* off Baja California was 1.1 to 2.6mm and those close to 2mm in length had mature ova (Menzies & Layton, 1962). Thus, there is no compelling reason to suspect that the type of *N. (N.)* ***oligotropha*** is an immature growth stage of a larger form.

Protoconch: The apex of *Neopilina (Neopilina)* ***oligotropha*** is smooth and discoidal, displaying no distinct coiled protoconch. A small dark area, however, is present a short distance behind the apex center (Figure 4). This mark possibly indicates one of the places of contact of a lost protoconch as in *N. (N.) galatheae* (Lemche & Wingstrand, 1959: plt. 10, fig. 35).

Figure 4

Apical portion of the shell of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov.

Shell Sculpture and Structure: The concentric threads on the shell of *Neopilina (Neopilina)* ***oligotropha*** are not all continuous. The posterior-most threads do not continue completely around the shell anteriorly; instead, they disappear abruptly along the lateral margin. In addition, several short threads are interspersed between longer ones, particularly along the midline. Thus, these concentric laminations cannot be considered as growth increments, but only as structural and sculptural aspects of the shell design.

In addition to the intact holotype of *Neopilina (Neopilina)* ***oligotropha,*** a fragment approximately 2 mm long was obtained in the same epibenthic sled sample. This fragment had fresh mantle tissue adherent to its undersurface indicating that another complete specimen was damaged during collection. Judging from the shell sculpture and curvature of the margin, the fragment originated from the left postero-lateral portion of a specimen nearly equal in size to the holotype (Figure 5).

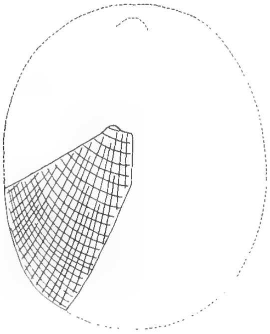


Figure 5

Diagrammatic representation of the relative position of the shell fragment of *Neopilina (Neopilina)* ***oligotropha*** Rokop, spec. nov.

This fragment was utilized for detailed shell sculpture studies employing a scanning electron microscope (Cambridge S4 Stereoscan). The advantages of the scanning electron microscope over conventional optical methods of examination of shell surface features are numerous (Solem, 1970). Particularly with regard to depth-of-field at high magnifications, the scanning electron microscope is far superior.

The entire shell fragment is shown in Figure *6*. Of particular interest are the radial threads which are seen to increase numerically abapically maintaining nearly equal quadrate depressions upon intersection with the concentric threads. The radial threads usually originate and terminate in contact with the concentric sculpture, thereby retaining the integrity of the quadrate depressions. At the intersection of the radial and concentric threads, raised nodes are produced which are nearly twice as high as either thread alone (Figure *7*). These nodes are not distinct, independent features of the shell design, but merely the result of the overlap of the radial threads over the concentric sculpture (Figures *8, 9*). Also, the radial threads are seen to be slightly wider than the concentric threads, both of which are separated by interspaces one to three times as wide.

The shell structure of *Neopilina (Neopilina) galatheae* and three species of fossil monoplacophorans has been described (Schmidt, 1959; Erben *et al.*, 1968). *Neopilina (N.)* ***oligotropha*** seems to differ in having a much more irregular type of shell construction. As shown in the fractured edge view of Figure *7*, the shell wall appears spongy and porous, consisting of minute, variable sized calcareous granules having irregular contacts with their neighbors. This appearance may, however, be due to partial dissolution and recrystallization of the shell fragment during preservation and storage of the sample.

Ecology: At this time very little can be stated conclusively about the ecological aspects of *Neopilina (Neopilina)* ***oligotropha.*** Such information can only be inferred from the contents of the trawl, bottom type, and the morphology of the animal. Direct observations of the living animal under natural conditions are of course not available.

The habitat of *Neopilina (N.)* ***oligotropha*** is that of a red clay, manganese nodule bottom. Most of the nodules in this region are buried (Menard, 1964), the exposed nodules covering only a small percentage of the sea floor. The importance of these manganese nodules as a possible substrate for this species is uncertain. *Neopilina (N.) galatheae* has been collected from muddy clays which contained no hard objects suitable as substrates (Lemche & Wingstrand, 1959). Similarly, *N. (Vema) ewingi* is considered a soft-bottom animal (Menzies *et al.*, 1959). On the other hand, the *Vityaz* monoplacophoran was firmly

Explanation of Figures *8* and *9*

Figure *8*: Surface view of the shell sculpture showing the arrangement of the radial and concentric threads. × 200

Figure *9*: Surface view of the shell sculpture illustrating the details of radial and concentric thread intersection. × 525

r – radial thread c – concentric thread

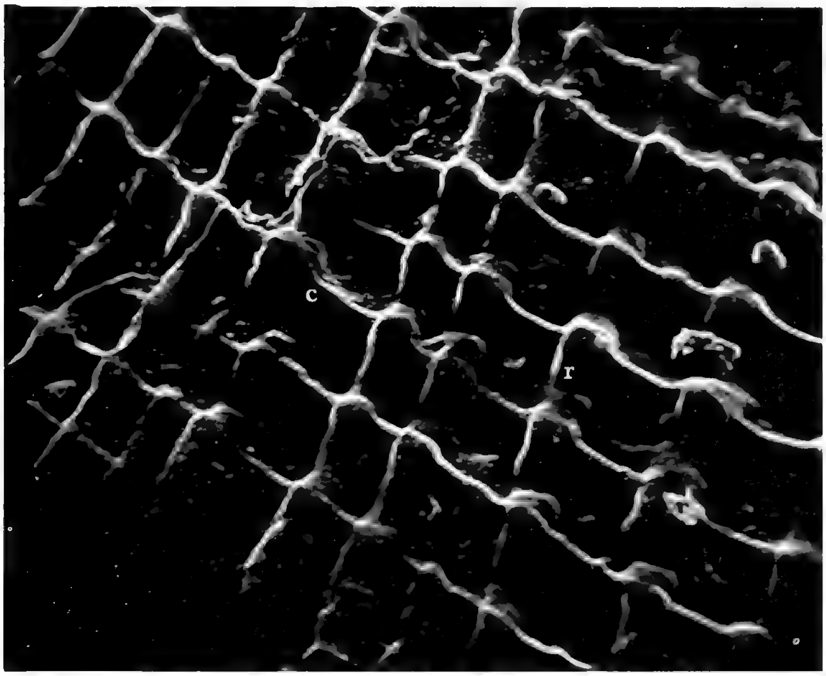


Figure 8

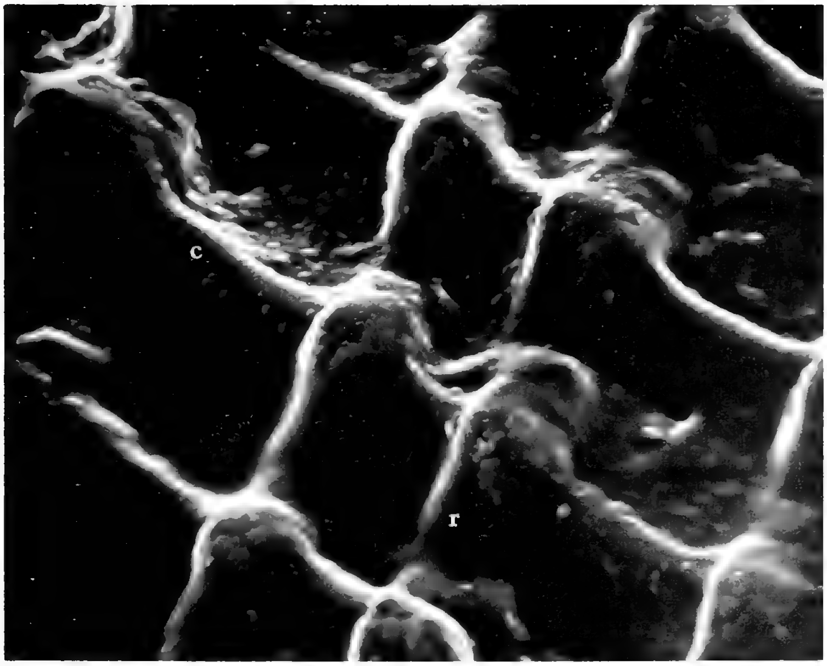


Figure 9

attached to the surface or a basalt block that was covered with a ferromanganese crust (FILATOVA *et al.,* 1968). Although *N. (N.)* ***oligotropha*** was not attached to any hard substrates in the trawl sample, the specimen may have been dislodged during collection.

The coiled intestine of the holotype of *Neopilina (Neopilina)* ***oligotropha*** is clearly visible through its thin shell. The intestine appears to be filled with dark-colored sediment, indicating a deposit-feeding mode of life. Deposit feeding seems to be characteristic of the monoplacophorans. Sediment-filled guts were also found in *N. (N.) galatheae* (LEMCHE & WINGSTRAND, 1959; WOLFF, 1961), *N. (V.) ewingi* (MENZIES *et al.,* 1959), and in the *Vityaz* specimen (FILATOVA *et al.,* 1968).

ACKNOWLEDGMENTS

This study is part of a continuing program at Scripps Institution of Oceanography involved in the investigation of the structure of open-ocean, deep-sea benthic communities supported by the National Science Foundation Grants GB 14488 and GA 31344X.

I wish to express my gratitude to Ronald T. La Borde, Staff Research Associate at Scripps Institution of Oceanography, for taking the scanning electron micrographs and to Bryan R. Burnett, also at Scripps Institution, for his assistance in preparing the text illustrations. I thank Dr. Joseph Rosewater, Curator of Mollusks at the Smithsonian Institution, for loaning the South Atlantic monoplacophoran specimen for comparison and study. I particularly wish to acknowledge Dr. Robert R. Hessler, Associate Professor of Biological Oceanography at Scripps Institution of Oceanography, for the opportunity to report the present new species and for his critical reading of the manuscript.

Literature Cited

CLARKE, ARTHUR H., Jr. & ROBERT J. MENZIES
1959. *Neopilina (Vema) ewingi,* a second living species of the Paleozoic Class Monoplacophora. Science **129:** 1026 - 1027; 1 text fig.; 1 table (17 April 1959)

ERBEN, H. K., G. FLAJS & A. SIEHL
1968. Über die Schalenstruktur von Monoplacophoren. Akad. Wiss. Lit. Abhandl. Math.-Naturwiss. Kl., Mainz **1968** (1): 1 - 24; plts. 1 - 17

FILATOVA, Z. A.
1969. Quantitative distribution of the deep-sea benthic fauna. *In* V. G. KORT (ed.), The Pacific Ocean, vol. VII, Biology of the Pacific Ocean, prt. 2, The deep sea bottom fauna. Pleuston, pp. 202 - 216 [in Russian]. Moscow ("Nauka" Publ. House)

FILATOVA, Z. A., M. N. SOKOLOVA & R. YA. LEVENSTEIN
1968. Molluscs of the Cambro-Devonian Class Monoplacophora found in the Northern Pacific. Nature **220:** 1114 - 1115; 3 text figs. (14 December 1968)

FILATOVA, Z. A. & L. A. ZENKEVICH
1969. Present distribution of ancient primitive Monoplacophora in the Pacific Ocean and the fossilized Pogonophora in deposits of Cambrian seas. [in Russian] Okeanologia **9:** 162 - 171; 1 plt.; 2 text figs.; 1 table

HESSLER, ROBERT R. & HOWARD L. SANDERS
1967. Faunal diversity in the deep-sea. Deep-Sea Res. **14:** 65 - 78; 3 text figs.; 6 tables (February 1967)

LEMCHE, HENNING
1957. A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora. Nature **23:** 413 - 416; 4 text figs. (23 Feb. '57)

LEMCHE, HENNING & KARL G. WINGSTRAND
1959. The anatomy of *Neopilina galatheae* Lemche, 1957 (Mollusca, Tryblidiacea). Galathea Reprt. **3:** 9 - 71; 56 plts.; 1 text fig.; 1 table

MENARD, H. W.
1964. Marine Geology of the Pacific. McGraw-Hill, San Francisco, Calif. pp. 1 - 271; 121 text figs.; 10 tables

MENZIES, ROBERT J.
1968. New species of *Neopilina* of the Cambro-Devonian Class Monoplacophora from the Milne-Edwards deep of the Peru-Chile Trench, R/V *Anton Bruun.* Mar. Biol. Assoc. India, Proc. Sympos. Mollusca, held at Cochin from January 12 to 16, 1968, Mandapam Camp, India. Symp. Ser. **3:** 1 - 9; 4 plts.

MENZIES, ROBERT J. & WILLIAM LAYTON, Jr.
1962. A new species of monoplacophoran mollusc *Neopilina (Neopilina) veleronis* from the slope of the Cedros Trench, Mexico. Ann. Mag. Nat. Hist. **5:** (55): 401 - 406; plts. 7 - 10

MENZIES, ROBERT J., MAURICE EWING, J. LAMAR WORZEL & ARTHUR H. CLARKE, Jr.
1959. Ecology of the Recent Monoplacophora. Oikos **10** (2): 168 to 182; 10 figs.; 2 tables

ROSEWATER, JOSEPH
1970. Monoplacophora in the South Atlantic Ocean. Science **167:** 1485 - 1486; 1 text fig. (13 March 1970)

SCHMIDT, W. J.
1959. Bemerkungen zur Schalenstruktur von *Neopilina galatheae.* Galathea Reprt. **3:** 73 - 77; 2 plts.

SOLEM, ALAN
1970. Malacological application of Scanning Electron Microscopy I. Introduction and shell surface features. The Veliger **12** (4): 394 to 400; plts. 58 - 60 (1 April 1970)

SOKOLOVA, M. N.
1969. Distribution of deep-sea benthic invertebrates in relation to their methods and conditions of feeding. *In* V. G. KORT (ed.), The Pacific Ocean, vol. VII, Biology of the Pacific Ocean, prt. 2, The deep sea bottom fauna. Pleuston, pp. 182 - 201 [in Russian] Moscow ("Nauka" Publ. House)

TEBBLE, NORMAN
1967. A *Neopilina* from the Gulf of Aden. Nature **215:** 663 - 664; 3 text figs. (5 August 1967)

WOLFF, TORBEN
1961. Animal life from a single abyssal trawling. Galathea Reprt. **5:** 129 - 164; plts. 7 - 10 (28 December 1961)

A New Species of *Conus* from Taiwan

BY

EDWARD JAMES PETUCH

Department of Zoology, University of Wisconsin - Milwaukee, Milwaukee, Wisconsin 53201

AND

GEORGE MENDENHALL

416 Bayview Avenue, Millbrae, California 94030

(1 Plate)

A LARGE SPECIMEN of a new species of *Conus* was trawled from deep water off the Taiwan coast during December, 1970. It was quite distinct from any other species found in that area. Because of the possession of several unique morphological characteristics, the following taxon is being proposed.

GASTROPODA — PROSOBRANCHIA

NEOGASTROPODA

CONIDAE Linnaeus, 1758

Conus fletcheri Petuch & Mendenhall, spec. nov.

Description: Shell glossy, elongate and sharply tapered towards the anterior end; body whorl incised with 25 deep spiral sulci which become wider apart toward the shoulder and closer together at the anterior tip; between each 2 of the major sulci there are less depressed spiral grooves which become coarser and more numerous near the columella; shoulder smooth, rounded and faintly coronated; spire relatively sharp and elevated, comprising 11 whorls and encircled with 3 spiral threads; spire angle approximately 40°; first 6 spire whorls showing faint coronations; protoconch broken off on the holotype; aperture narrow and more or less equal in width throughout its length. Ground color white with 2 broken bands of brown flammules. The band near the shoulder covers half the body whorl while the other is only half as large. Scattered small brown flammules are also found on the spire.

Holotype: Length 105 mm; width 44.5 mm

Occurrence: The type was trawled from a depth of approximately 300 feet (90 m), southwest of the Penghu Island Group, Taiwan, Republic of China.

Type Depository: California Academy of Sciences, Geology catalog no. 48862.

Remarks: At first glance, this species appears to be related to the *Conus profundorum* Kuroda, 1957 complex mainly in shape. However, it can easily be separated out of this group by its lacking a well-stepped spire and by possession of heavy incised spiral grooves. The latter characteristic would suggest a relationship to the subgenus *Asprella* Schaufuss, 1869, but its general shape, large size and high polish point to a relationship with the subgenus *Chelyconus* Mörch, 1852.

The holotype was collected dead, and unfortunately none of the soft parts could be studied. The lip was also badly broken and the shell was stained in places from being buried in mud. Still, the remaining morphological characteristics are so distinct that this species cannot be readily confused with any other member of the genus.

This species is named in honor of Dr. Louis R. Fletcher, M. D., now Research Associate in the Geology Department, California Academy of Sciences, San Francisco.

Figure *1*

Figure *2*

Biology of *Okenia ascidicola* spec. nov.[1]

(Gastropoda : Nudibranchia)

BY

M. PATRICIA MORSE

Marine Science Institute, Northeastern University, Nahant, Massachusetts 01908[1]

(5 Text figures)

In the early summer of 1968, two nudibranchs were collected at East Point, Nahant, Massachusetts. They were placed in an aquarium at the Marine Science Institute where feeding behavior, mating, depositing of eggs and subsequent development were observed. It was determined that the specimens represented a new species of the genus *Okenia* Menke, 1830. The name ***Okenia ascidicola*** spec. nov. is based on their habit of feeding on solitary ascidians followed by taking up temporary residence in the empty ascidian test.

This work was supported by the Northeastern Office of Research Administration Grant No. 8024. I wish to express my appreciation to Dr. N. W. Riser, Mrs. Eveline Marcus, Dr. William Clench and Dr. Tucker Abbott for their help in the preparation of this paper.

Okenia ***ascidicola*** Morse, spec. nov.

Species Diagnosis: Length 12mm, width 5mm; branchial plumes 11, anterior one bifid, thus displaying 12 free tips; mantle forms pallial ridge with 14 tentacular appendages, anterior 4 elongate and equal, 8 smaller on lateral edges and a single bifid posterior pair; single small mid-dorsal appendage just anterior to branchial plumes; ground color of red-brown with dark and light yellow blotches; radula, 24 rows, formula 1 · 1 · 0 · 1 · 1, inner lateral tooth 0.16mm with 14 - 16 prominent denticles on the cusp, outer marginal 0.09mm and smooth; incomplete labial armature of 3 paired units containing stout and slender elements. Penial spines small, scale-like with broad bases.

Type Locality: Nahant, Massachusetts

Type Date: June 1968

Type: Holotype, USNM 577681
Paratype – Radular preparation, labial armature and dissected specimen in author's collection

Description: Both of the living nudibranchs measured 12.0mm in length and 5.0mm in width. The mantle is drawn out into a veil which surrounds the notum and has 14 tentacular extensions (Figure 1). There are 4 elongate anterior appendages of equal length, 8 smaller tentacular extensions on the dorso-lateral ridges and a longer postero-lateral pair of bifid tentacular extensions, one on either side of the branchial plume. A single small appendage is found just anterior to the branchial plume in the mid-line of the body. In the holotype this appendage is pyramidal in shape as in the living specimens but in the preserved paratype it is now a blunt papilla. In both cases the single appendage is smaller than any other extensions of the mantle.

In the holotype the partially retractile branchiae number 11. The anterior branchia is bifid and on first glance gives the impression of 12 branchiae. The posterior pair is more slender and slightly shorter than the others. The branchiae are simply bipinnate with alternating lamina from the central stem. Their tips are pointed and they form a complete circle around the anus. The branchiae number 10 in the paratype with bifid anterior and posterior ones resulting in 12 free tips. They are more uneven in size in the circle than in the holotype. It is difficult to tell how much of this latter variation is due to fixation.

The rhinophores are laminated on the posterior side for about $\frac{3}{4}$ of their length. The laminae are rounded, slightly concave and number about 25. In an undisturbed crawling nudibranch, the rhinophores are held upright with a slight posterior bend at the half-way point. They are stout, being twice as thick and slightly longer than the tentacular extensions of the anterior mantle veil (Figure 1). When the

---

[1] Contribution No. 16, Marine Science Institute, Northeastern University

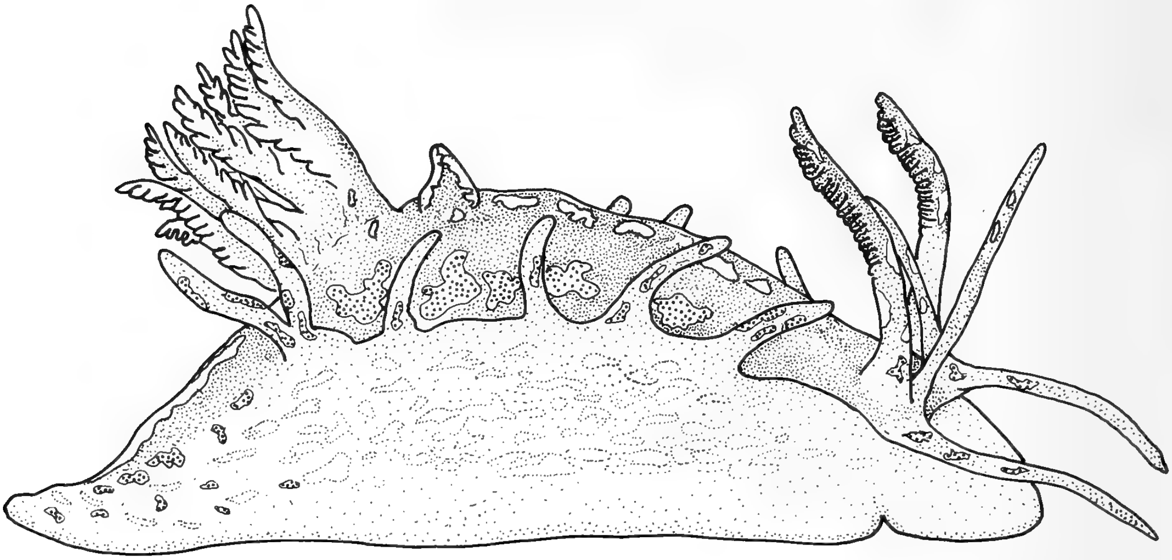


Figure 1

Okenia ascidicola Morse, spec. nov.
(drawn from the living type specimen)

nudibranchs are disturbed, they go through a characteristic reaction. The branchiae are partially retracted, the rhinophores lie back flat against the mantle, the lateral mantle extensions fold toward the mid-dorsal line (the most posterior ones folding over the branchiae), and the anterior 4 tentacles curl dorsally inward.

From a ventral aspect, the foot is transparent with parallel sides, rounded anterior angles, and an obtusely pointed posterior end. The upper portion of the posterior end of the foot fuses with the mantle behind the branchiae and forms a slight ridge posteriorly to the tip. In sections, the foot is seen to be ciliated with a greater concentration of cilia at the anterior end. Epidermal and subepidermal gland cells are particularly abundant at the anterior end of the foot. The head is rounded, giving a bilobed appearance in the living animal and the reduced oral tentacles form a thick fleshy veil surrounding the antero-posterior slit which is the entrance to the mouth. A groove separates the foot from the oral veil; the latter two structures lie in a similar plane in the crawling nudibranch.

The overall coloration of the living animal (Figure 1) is red-brown with 2 distinct hues of yellow forming epidermal blotches on the tentacular extensions and dorsal surface of the nudibranch. The lemon-yellow coloration forms a line on the mid-dorsal mantle from the rhinophores to the branchiae and from just posterior to the branchiae on the ridge of the tip of the "foot". There are additional smaller blotches on the sides between the pallial ridge and the foot. A darker yellow, canary yellow color, is found in large blotches on either side of the mid-dorsal region. Smaller blotches occur dorsad on either side of the posterior portion of the "foot", and on the tips of the tentacular extensions of the notum. The red-brown color is mostly confined to the upper portions of the animal and slowly grades to a translucent white toward the foot. The lighter lateral aspects of the animal are further enhanced by the smaller blotches of lemon-yellow.

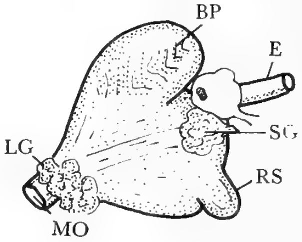


Figure 2

Dissection of the anterior portion of the digestive system of *Okenia ascidicola* Morse, spec. nov.
BP – buccal pump E – Esophagus LG – labial glands
MO – mouth opening RS – radular sac

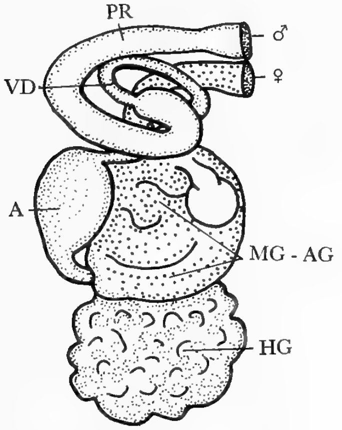


Figure 3

Dissection of the reproductive complex of *Okenia* ***ascidicola*** Morse, spec. nov.
A – ampulla HG – hermaphroditic gland
MG - AG – mucus gland - albumen gland complex
PR – prostatic region of the vas deferens VD – vas deferens
♀ – female genital opening ♂ – male genital opening

The internal morphology of *Okenia* ***ascidicola*** is similar to that described for other members of the genus (Marcus, 1957; Marcus & Marcus, 1967). The radula from the paratype has 24 rows of teeth of the generic radular formula 1 · 1 · 0 · 1 · 1. The inner (lateral) tooth measures 0.16 mm (Figure **4C**) and bears 14 - 16 prominent denticles on the cusp. The outer (marginal) tooth measures 0.09 mm (Figure **4B**) and lacks denticles. The cusp of the marginal tooth is strongly recurved.

The labial armature of *Okenia* ***ascidicola*** (Figure 5) is composed of 3 paired elements which do not form a complete ring around the mouth. The largest element is triangular in overall shape and consists of numerous stout teeth. The tips are bidentate medial of the paired elements and become monodentate toward the lateral apices of the triangles. The elements are closely packed together and are pigmented with a brown-yellow coloration. The second paired elements are composed of elongate denticles which are narrow at their attachment and broader toward the apex. There is a tendency for the most distal denticles to be curved and to have an uneven margin. The denticles are all directed at right angles to those of the triangular elements. This second pair of elements is closely associated with the previous paired elements and is located parallel to the longer side of the triangle of the large pair. The third pair of elements consists of 2 patches of very irregular denticles which are haphazardly arranged in a pattern radiating from a center point. They are few in number and represent the lightest in coloration of the paired elements.

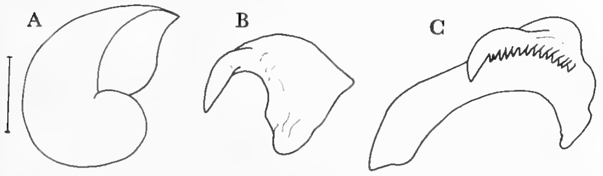


Figure 4

Okenia ***ascidicola*** Morse, spec. nov.
A – veliger shell B – outer (marginal) tooth of radula
C – inner (lateral) tooth of radula Scale = 0.05 mm

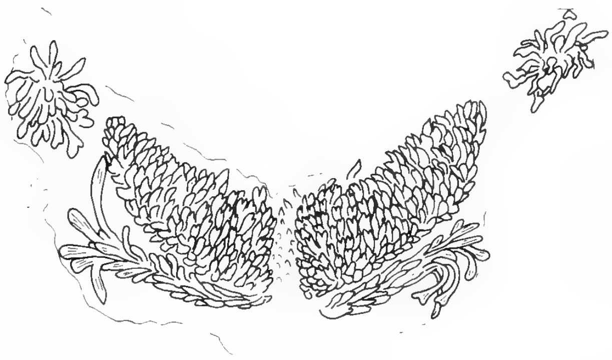


Figure 5

Labial armature of *Okenia* ***ascidicola*** Morse, spec. nov.

The oral tube, surrounded by the fleshy oral veil, leads into the muscular buccal mass. Glandular areas (Figure 2, **LG**) surround the oral tube. The dorsal portion of the buccal mass is expanded into a muscular buccal pump (Figure 2, **BP**) which is similar to that of *Acanthodoris pilosa* (Abildgaard, 1776) (*vide* Morse, 1968). The labial armature as described previously, appears to be capable of protraction to the area of feeding through the oral tube. Paired follicular salivary glands enter on the postero-lateral sides of the buccal mass and the esophagus exits from the posterior surface and enters the stomach. The digestive gland surrounds the ventral stomach and the intestine terminates at the anus in the center of the branchial plume. The hermaphroditic gland is located on the dorsal surface of the digestive gland (Figure 3). The male system consists of the vas deferens enlarging into the ampulla and quickly narrows to connect up with a prostatic portion of the duct and eventually opens on the anterior right side of the nudibranch. Abundant scale-like spines occur on the penis.

BIONOMICS

Okenia ***ascidicola*** is so named because of the feeding behavior and subsequent activity of the animal. The first animal was found associated with a clump of *Molgula manhattensis* and the second mature specimen was located inside of an empty ascidian tunic.

Preference experiments were set up utilizing *Ciona intestinalis,* and *Molgula manhattensis.* The nudibranchs would only feed on the latter. The animal approaches the base of the tunicate and rasps a circular hole in the tunic. It then proceeds to plow head first toward the interior, sucking in the soft contents and disappearing within the tunic until only the circle of branchiae is visible. This procedure requires about 4 hours. The nudibranchs are barely visible in this position. After several days, the tunic collapses, the nudibranch withdraws and moves away. When observing the collapsed tunic under higher magnification, the entrance hole was clearly visible and was surrounded by mucus.

REPRODUCTIVE BEHAVIOR

Two nudibranchs were placed in an aquarium on June 18. The animals were observed copulating on several occasions. This occurred on the bottom of the aquarium with a random approach of one animal to the other and with no adhesion to the bottom. On June 21, one nudibranch was found on its side (left) with the egg string being extruded from the enlarged female opening. Two other long strings measuring 6 cm were found in the tank. The egg strings were only slightly coiled. The veliger shell (Figure 4A) measured 1 mm in width. The free swimming veligers died very soon after hatching.

DISCUSSION

Two species belonging to the genus *Okenia* have been reported from New England waters. In 1875, VERRILL described *Idalia modesta* and in 1882 listed its distribution from Block Island Sound, New York and Vineyard Sound, Massachusetts in 17 to 40 fathoms of water. In 1879, he reported specimens of *I. pulchella* Alder & Hancock, 1854 which were collected by Mr. Emerton at Salem, Massachusetts. Verrill noted that the drawings and the specimen given to him by Emerton agreed with the description of SARS (1878), especially in regard to external characteristics and dentition, but not so well with those of ALDER & HANCOCK (1854, 1845-55). In 1882, VERRILL listed those two species in the genus *Idaliella* based on the lack of mid-dorsal appendages in accordance with BERGH's 1881 monograph on the genus *Idalia.*

The short, incomplete description of *Idalia modesta* by VERRILL (1875) makes it difficult to compare it with *Okenia* ***ascidicola.*** In the latter, the presence of a dorsal appendage, the differences in coloration, and the length of the tentacular extensions of the mantle (compared to conical papillae in Verrill's description) are distinctive.

The primary distinguishing characteristic of *Okenia* ***ascidicola*** from *Idaliella pulchella* is the labial armature. The variety of elements in *O.* ***ascidicola*** is not described for *I. pulchella.* In addition, the elements figured for *I. pulchella* by ALDER & HANCOCK (1845-55) are not similar to those found in *O.* ***ascidicola.*** The descriptions of *I. pulchella* are of animals of a similar size to the two specimens of *O.* ***ascidicola*** and thus the lack of any mid-dorsal appendages in the former is not due to an age difference. Although MARCUS & MARCUS (1967) noted the difficulty in seeing the poorly developed mid-dorsal appendages in *O. sapelona,* the appendages none the less are obviously present in *O.* ***ascidicola*** in both the living animals and in the type specimen after fixation in formalin and storage in 70% ethyl alcohol.

Four other species of *Okenia* have been described from the western Atlantic waters. MARCUS (1957) and MARCUS & MARCUS (1967) reported *O. evelinae* Marcus, 1957, *O. impexa* Marcus, 1957, and *O. sapelona* Marcus & Marcus, 1967 as being present along Miami, North Carolina and Georgia coasts respectively. Recently, VOGEL & SCHULTZ (1970) reported an additional species *Okenia (Cargoa) cupella* (Vogel & Schultz, 1970), nov. comb. from Chesapeake Bay, Maryland.

Okenia ***ascidicola*** is similar to *O. impexa* in that both have a single papilla on the back but differs in the rhinophores, dentition and labial armature. *Okenia* ***ascidicola*** is separated from *O. evelinae* and *O. sapelona* by the single papilla, differences in the number of lateral appendages, shapes of the radular teeth and labial armature. *Okenia cupella,* which in text seems very similar to *O. impexa,* differs from *O.* ***ascidicola*** by the rhinophores and dentition. It is unfortunate that no indication of labial armature is given for *O. cupella.*

Bergh (1881) characterized the genus *Idalia* as possessing mid-dorsal appendages, and having a complete ring forming the labial armature and the genus *Idaliella* by the absence of mid-dorsal appendages and an incomplete labial armature of hamate lateral plates. (*Idalia* is not available since it is preoccupied.)

Thiele (1931) listed *Okenia* with the two subgenera *Okenia (Idaliella)* and *Okenia (Okenia).* As pointed out by **Lemche** (1971), the generic name *Cargoa* established by **Vogel & Schultz** (1970) is a junior objective synonym of the genus *Okenia* and the latter name should be retained. **Marcus** (1957) discussed the genus *Okenia* in some detail and listed the valid species, indicating the subgenus to which each belonged. New additions were listed in 1967 by **Marcus & Marcus**. ***Okenia ascidicola*** has a dorsal cirrus on the back and an incomplete labial armature which invalidate the subgeneric designations. Thus, in conclusion, the genus *Okenia* is a valid genus within which species are found with and without mid-dorsal appendages between the rhinophores and branchiae and with and without a complete labial armature.

Literature Cited

Alder, Joshua
1854. IX. Notice of some new species of British Nudibranchiata. Ann. Mag. Nat. Hist. **14:** 102 - 105

Alder, Joshua & Albany Hancock
1845-1855. A monograph of the British nudibranchiate Mollusca, with figures of all species. London, Ray Soc.,prts. 1 - 7; 438 pp.; 84 plts.

Bergh, Ludwig Sophus Rudolf
1881. Über die Gattung *Idalia* Leuckart. Arch. Naturgesch. **47** (1): 140 - 181; plts. 6 - 8

Lemche, Henning
1971. *Okenia* Menke, 1830, and *Idaliella* Bergh, 1881 (Mollusca, Opisthobranchia): Proposed addition to the official list. Z. N. (S.) 1931. Bull. Zool. Nomencl. **27** (5/6): 265 - 266

Marcus, Ernst
1957. On Opisthobranchia from Brasil II. Journ. Linn. Soc. London **43** (292): 390 - 486; figs. 1 - 246

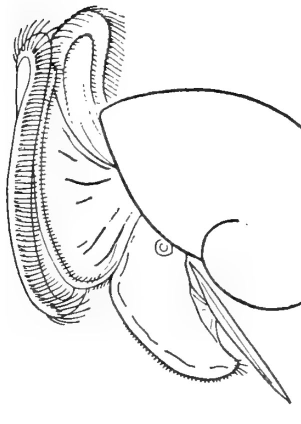
Marcus, Eveline du Bois Reymond & Ernst Marcus
1967. Some opisthobranchs from Sapelo Island, Georgia, U. S. A. Malacologia **6**(1-2): 199 - 222; figs. 1 - 19 (31 December 1967)

Morse, M. Patricia
1968. Functional morphology of the digestive system of the nudibranch mollusc *Acanthodoris pilosa.* Biol. Bull. **134** (2): 305 - 319

Sars, G. O.
1878. Bidrag til Kundskaben om Norges Arktiske fauna: I Mollusca Regionis Arcticae Norvegiae pp. I - XIII + 1 - 466; 34 + XVIII plts. Christiania

Verrill, Addison Emery
1875. Results of recent dredging expeditions off the coast of New England. Amer. Journ. Sci. **10:** 36 - 43
1879. Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part 1 - Annelida, Gephyraea, Nemertina, Nematoda, Polyzoa, Tunicata, Mollusca, Anthozoa, Echinodermata, Porifera. Proc. U. S. Nat. Mus. **2:** 165 - 206
1882. Catalogue of marine Mollusca added to the fauna of New England during the past ten years. Trans. Conn. Acad. Arts Sci. **5** (2): 447 - 587

Vogel, Rosalie M. & Leonard P. Schultz
1970. *Cargoa cupella,* new genus and new species of nudibranch from Chesapeake Bay, and the generic status of *Okenia* Menke, *Idalia* Leuckart, and *Idalla* Ørsted. The Veliger **12** (4): 388 - 393; 5 text figs. (1 April 1970)



Note on Secondary Homonymy

BY

EMILY H. VOKES

Department of Geology, Tulane University, New Orleans, Louisiana 70118

The nomenclatural problem of secondary homonymy is one that is a trial to all workers, one that causes innumerable shifting back and forth of names and one that clearly is not always understood. This is made apparent in a recent paper by Cernohorsky (1971: 188), who states that he does not consider *Murex aculeatus* Lamarck, 1822, a secondary homonym of *Aranea aculeata* Perry, 1811, nor of *Muricites aculeatus* Schlotheim, 1820.

According to the International Code of Zoological Nomenclature, Article 57: "The Law of Homonymy applies to species-group names originally published in (primary homonyms), or later brought together in (secondary homonyms) the same genus or collective group, except as noted in Article 59c." The latter states that: "A name rejected after 1960 as a secondary homonym is to be restored as the valid name whenever a zoologist believes that the two species-group taxa in question are not congeneric, unless it is invalid for other reasons."

Secondary homonyms are created by bringing together two species formerly not in the same nominal genus. Such is the case presented by the genus *Aranea* Perry, 1810. Perry chose to employ the name "*Murex*" for species of the Fasciolariidae, and to create a new name, *Aranea,* for those spinous species today included in *Murex s. s.* This was a perfectly legal restriction of the multigeneric *Murex* of Linnaeus, which did include the Fasciolariidae as well as the Muricidae. However, as a result, the species named in the genus *Aranea* Perry are all valid, incontestable members of *Murex,* as recognized today. Even though they were named in a nominally different genus, they have been "secondarily brought together" in *Murex,* and I do not think there is any zoologist who will say that most are not congeneric with the type species of *Murex.* There are a few species that might be transferred to a genus *Bolinus,* in which case *Aranea conspicua* (= *Murex cornutus,* subgenus *Bolinus*) would no longer preoccupy *Murex conspicuus* Braun, 1863. But *Aranea aculeata* and *Aranea pallida* are both congeneric with *Murex,* and as such preoccupy *Murex aculeatus* Lamarck, 1822, and *Murex pallidus* Broderip, 1833, regardless of the fact that the junior species are a *Chicoreus* and a Trophon, respectively.

Once a species is named in a genus, the subsequent generic placement is irrelevant. *Murex aculeatus* Lamarck can never escape its *Murex* birthright, a "*Murex*" it will always be. The only exception to this is in the case of two species named in different biologic genera, which have homonymous names (Code, Art. 57-c). An example would be two species with the same name described in *Centronotus* Schneider, 1801 (a fish), and *Centronotus* Swainson, 1833 (a *Hexaplex*).

According to the Code (Art. 52) "homonymy is the identity in spelling of available names," and "the difference of a single letter is sufficient to prevent homonymy" (Art. 56-a and 57-d). However, there are several exceptions to this noted in the Code. At the species-group level there are 12 exceptions cited (Art. 58) whereby differences in spelling do not prevent homonymy, nor do differences in termination due to gender have any effect (Art. 57-b-i). At the generic level there is a single exception, as noted in Art. 56-b, and this applies solely to names originally proposed for fossils. Article 20 states: "If an existing genus-group name has been modified by substituting *-ites, -ytes,* or *-ithes* for the original termination, the modified name if applied only to fossils is not available, except for the purposes of the Law of Homonymy" (*i. e.,* it would preoccupy a subsequently proposed **genus** of the same name). Names including *Muricites* Schlotheim, along with others of its kind, such as *Pectinites* and *Tellinites,* were used to denote fossil representatives of the Recent genera *Murex, Pecten,* and *Tellina,* respectively. Thus, *Muricites* and *Murex, Pectinites* and *Pecten, Tellinites* and *Tellina,* are considered to be **identical** names, and the species named in either member of the pair are affected by the Law of Homonymy (Art. 57). Whether they are primary homonyms, by act of legislation, or secondary homonyms by default, is a somewhat nebulous matter; perhaps it would be best to consider the *-ites* termination an unjustified emendation of the generic name, which does not affect species-group homonymy (Art. 57-b). In any case, the rules of homonymy apply and *Muricites aculeatus* Schlotheim, 1820, preoccupies *Murex aculeatus* Lamarck, 1822; *Muricites cognatus* Schlotheim, 1820, preoccupies *Murex cognatus* Bellardi, 1872; and *Muricites funiculatus* Schlotheim, 1820, preoccupies *Murex funiculatus* Reeve, 1845.

Literature Cited

Cernohorsky, Walter Oliver
1971. Contribution to the taxonomy of the Muricidae (Gastropoda: Prosobranchia). The Veliger 14 (2): 187 - 191; 1 plt. (1 Oct. '71)

Two Additions to the Opisthobranch Fauna of the Southern Gulf of California

BY

HANS BERTSCH[1]

(1 Plate; 3 Text figures)

During the summer of 1969 I used the facilities of the Las Cruces Biological Station to study the opisthobranch fauna in the La Paz area of Baja California del Sur, Mexico. From this research in the southwestern Gulf of California, one new species has already been named (Bertsch, 1970b). In the paper, I describe a new species of Cephalaspidean and discuss the occurrence of a member of the nudibranch genus *Limenandra* in the Panamic province.

CEPHALASPIDEA

Aglajidae

Aglaja ***regiscorona*** Bertsch, spec. nov.

(Figures 1, *2* to *5*)

Type Material: Holotype: mounted shell, California Academy of Sciences, Invertebrate Zoology Type Collection, no 556. Paratypes: Three specimens, CASIZ Type Collection, nos. 553, 554, 555. Three specimens, Los Angeles County Museum of Natural History, no. 1617. Two color transparencies of the living animal have also been deposited with the holotype material, CASIZ color slide series, nos. 2723 and 2724.

Type Locality: Bahía Las Cruces, Baja California del Sur, Mexico (24°13′N; 110°05′W); the type specimens were found crawling on the alga *Spyridia filamentosa,* intertidally, July 19 to 22, 1969; collector, Hans Bertsch.

Description: Length in life: 3 to 5 mm; width 1.25 to 1.75 mm; body color cream white, dorsum center darker dirty white (verging on light greenish-brown); edges of posterior lobes transparent white; cephalic hood frontal margin, and edges and sides of parapodia with numerous small black flecks; posterior lobes with some black spots; dorsum and cephalic shield covered with numerous papillae, some tipped with black (see Figure 1).

Head shield triangular, projecting posteriorly and upwards to a small, three-pointed crown. Parapodia small, held tight against sides of body, not extending over the

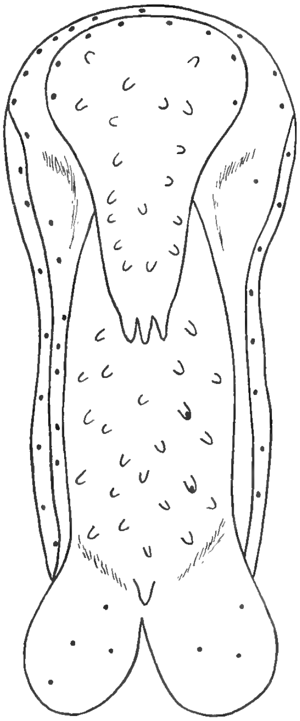


Figure 1

Dorsal view of *Aglaja regiscorona* Bertsch, spec. nov. Drawing of living animal by author

---

[1] Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118. Permanent address: Franciscan School of Theology, 1712 Euclid Avenue, Berkeley, California 94709

dorsal surface. Two lobes project from rear, neither with a flagellum.

Shell (Figure *2)* calcified, 0.55 mm long; nuclear whorl 0.18 mm wide. Nucleus of shell with one complete whorl; small flange projects laterally at right angle to plane of whorl (Figures *3* and *4*). Small ridges, separated by a slight notch, circles the lateral edge of the whorl (Figure *4*). Wing bends sharply vertically to plane of nuclear whorl, and folds again nearly parallel to the plane of the whorl. Distal end rectangular (Figure *5*).

Discussion: Numerous factors distinguish *Aglaja* ***regiscorona*** from the other American species of *Aglaja.* The specific name (from the Latin: King's crown) was chosen in reference to its highly distinctive cephalic shield which resembles a royal crown. None of the other *Aglaja* species in the eastern Pacific, nor in the western Atlantic, have this unique configuration to their head shields. The coloration of *Aglaja* ***regiscorona*** resembles that of *A. nana* Steinberg and Jones, 1960. However, *A. nana* lacks the dorsal papillae, the three-point cephalic shield, and has less prominent posterior lobes. The body colors of *A. purpurea* (Bergh, 1893), *A. diomedea* (Bergh, 1893), *A. adellae* (Dall, 1894), *A. pusa* Marcus and Marcus, 1967, *A. felis* Marcus and Marcus, 1970, and *A. hummelincki* Marcus and Marcus, 1970, are all dark, in contrast to the light coloration of *A.* ***regiscorona.***

The left posterior lobe of *Aglaja ocelligera* (Bergh, 1893) has a flagellum, while *A.* ***regiscorona*** does not. *Aglaja gemmata* (Mörch, 1863) and *A. punctilucens* (Bergh, 1893) can be distinguished from *A.* ***regiscorona*** by their longitudinal dark striping.

The shell of *Aglaja* ***regiscorona*** has a distinct whorl, curved apical border (rather than a flattened edge), and a broad, flat, not in-curled wing. This serves to distinguish it from the other species in the genus.

NUDIBRANCHIA

AEOLIDIIDAE

Limenandra nodosa Haefelfinger and Stamm, 1958

(Figures 6, 7)

Occurrence, Morphology and Zoogeographical Comments: The original description of *Limenandra nodosa* Haefelfinger and Stamm, 1958, was based on approximately 50 specimens from the French Riviera. HAEFELFINGER & STAMM (1958) established a new genus (*Limenandra*) for the species, and included a second species: *Baeolidia fusiformis* Baba, 1949. Until recently, *L. nodosa* had been known only from the Mediterranean and *L.*

Table 1

Comparison of morphology of *Limenandra fusiformis* from Japan (column I), *L. nodosa* from the Mediterranean (column II), and *L. nodosa* from the Gulf of California (column III)

	I *Limenandra fusiformis*	II *Limenandra nodosa*	III *Limenandra nodosa* (Gulf)
Radula	11 × 0·1·0 60 denticles	8 - 10 × 0·1·0 30 - 50 denticles	9 × 0·1·0 30 denticles
Cerata	rounded 12 - 15 rows 10 - 11 cerata in largest rows smooth	flattened 12 - 14 rows 1 - 9 cerata per row papillated	flattened 12 rows 1 - 8 cerata per row central cerata papillated on rows 4, 6, 8, 10, 11
Color	ashy brown yellowish spots	dull olive green white-yellow-red-white circlets small white spots over entire body	pale green yellow and pink circlets green-brown speckled over entire body
Jaws	smooth masticatory edge	long masticatory border very finely striated, but without denticulation	long, smooth masticatory border
Length	10 - 20 mm	15 - 25 mm	12 mm
Rhinophores	studded on posterior margin with papilliform granules	papillae over entire surface	papillae start about ½ way up length of rhinophores; very few on front, concentrated on posterior portion

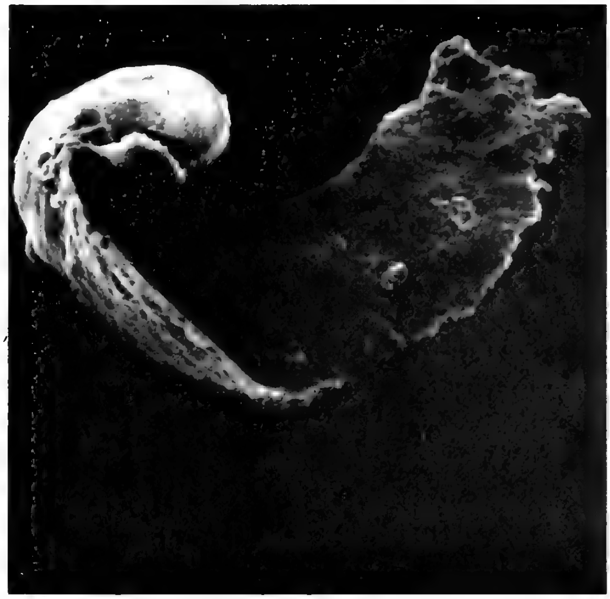


Figure 2

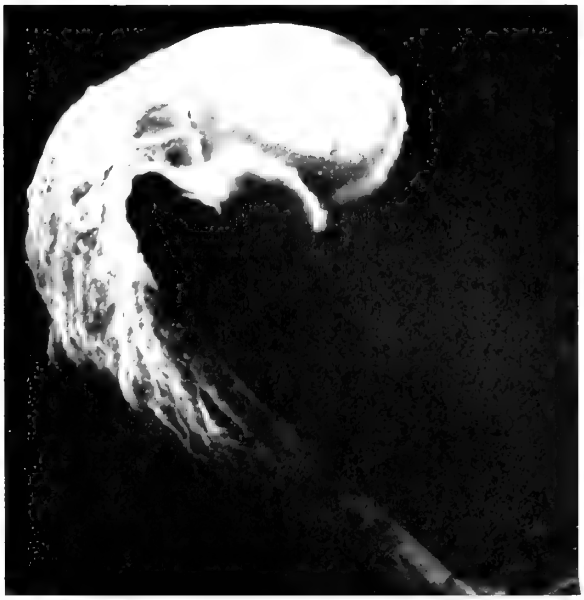


Figure 3

Figure 4

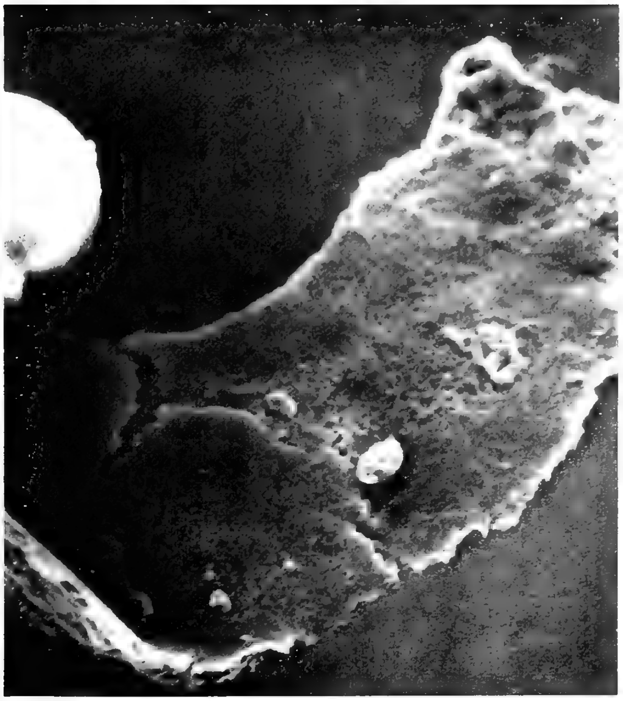


Figure 5

fusiformis only from Japan. MARCUS & MARCUS (1970) reported a specimen of *L. nodosa* from Bonaire Island, Lesser Antilles, in the Caribbean, about 50 miles off the northern coast of Venezuela.

On July 11, 1969, I found one 12 mm long specimen of *Limenandra nodosa* at Bahía Las Cruces, Baja California del Sur, Mexico. It was under a rock, in about four feet of water. This is the first specimen of *Limenandra* from the Pacific coast of America (BERTSCH, 1971).

Table 1 compares the morphology of the two known species of *Limenandra* with the specimen from the Gulf of California. A definite overlapping of characteristics is evident, which further complicates the taxonomy of this genus. The radula, jaws, external coloration, and size are similar among the Mediterranean *L. nodosa, L. fusiformis,* and my specimen from the Gulf of California. The radula and jaws of *L. nodosa* from the Gulf of California are illustrated in Figures 6 and 7. The cerata of the Gulf animal are flattened and papillate (as in the Mediterranean *L. nodosa*), in contrast to the rounded, smooth cerata described for *L. fusiformis.* The yellow-pink color circlets of the Gulf specimen appear intermediate between the white-yellow-red-white circlets of *L. nodosa,* and the yellowish spots on the back of *L. fusiformis.* However, the shape of the rhinophores of the Gulf animal more closely resemble that of *L. fusiformis.*

Only the further collection and comparison of a great number of these animals, with concomitant attempts at interbreeding, can determine whether these variations are all characteristic of one, two, or three species.

It is of interest that recent papers (e.g., MARCUS, 1961; COLLIER & FARMER, 1964; MARCUS & MARCUS, 1967, 1970; BERTSCH, 1970a; and SPHON, 1971) have reported an increasing number of circum-tropical or circum-subtropical opisthobranch species from the Gulf of California, indicating certain faunistic relationships for opisthobranchs on the species level between the Panamic province and other tropical or subtropical regions.

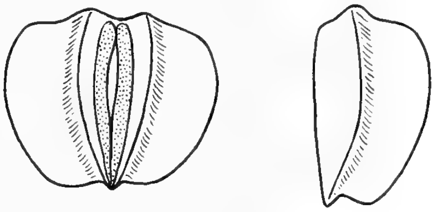


Figure 6

Limenandra nodosa Haefelfinger & Stamm, 1958: jaws of the specimen from the Gulf of California; height 0.5 mm

Natural History: The specimen of *Limenandra nodosa* collected from Bahía Las Cruces had the cream white egg sacs of a small copepod between the 7th and 8th rows of cerata.

The nudibranch was kept alive in an aquarium for a few days to study its locomotion patterns. As do many nudibranchs, it would periodically float upside down at the water surface. The crawling behavior was by the extension-contraction method, with simultaneous forward and backward pumping of the cerata. All the cerata were jerked uniformly backward, pivoting at the base where the cerata are attached to the body. Then they were jerked upward, and the animal's body was extended forward longitudinally. The backward stroke was repeated, the animal contracted; then the forward jerk, extension, and animal's progression. The forward movement of the animal was in a regular rhythm with the ceratal pumping. It is not known whether the ceratal movement assisted or caused the animal's forward progression, or was just a side effect of the extension-contraction locomotory method.

This specimen from the Gulf of California has been deposited as a hypotype in the California Academy of Sciences, Department of Invertebrate Zoology Type series, number 557.

ACKNOWLEDGMENTS

Many persons assisted me in the research and writing of this article. Mr. Hugh Bertsch supplied the financial aid necessary to make the trip to the Gulf of California. The

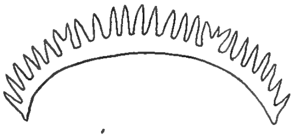


Figure 7

Limenandra nodosa: radular row of animal from the Gulf of California

Explanation of Figures *2* to *5*

Aglaja regiscorona Bertsch, spec. nov.

Figure *2*: Scanning electron micrograph of entire shell

Figure *3*: SEM close-up of nuclear end of shell, showing the bending of the wing vertically to the plane of the nucleus

Figure *4*: Nuclear whorl of shell, SEM close-up, showing lateral flange and small, encircling ridge

Figure *5*: Distal end of wing of shell, SEM enlargement

staff and research workers at the Las Cruces Biological Station (particularly Dr. Rita Schafer and Rev. Alberic A. Smith) were quite friendly and helpful to me, even interrupting their own research to assist me. Gale G. Sphon, Allyn G. Smith, and James T. Carlton read the manuscript, offering criticism and encouragement; Richard A. Roller performed the dissections of the material and did the original drawings of the jaws and radula of *Limenandra nodosa.* Dr. Thomas Hayes, Donner Laboratory of the Lawrence Radiation Laboratory, University of California, Berkeley, made the scanning electron micrographs of the *Aglaja* ***regiscorona*** shell. To all these, friends and colleagues, I offer my sincerest thanks.

Financial aid to publish this paper was provided by the Janss Foundation.

Literature Cited

Baba, Kikutarô
1949. Opisthobranchia of Sagami Bay, collected by his Majesty the Emperor of Japan. Iwanami Shoten, Tokyo, 104 pp.; 50 plts.; 7 text figs.

Bergh, Ludwig Sophus Rudolf
1893. Die Gruppe der Doridiiden. Mittheil. zool. Stat. Neapel **11** (1-2): 107-135; plt. 8 (25 September 1893)

Bertsch, Hans
1970a. *Dolabrifera dolabrifera* (Rang, 1828): Range extension to the Eastern Pacific. The Veliger **13** (1): 110-111; 1 text fig. (1 July 1970)
1970b. Opisthobranchs from Isla San Francisco, Gulf of California, with the description of a new species. Santa Barbara Mus. Nat. Hist. Contrib. Sci. **2:** 16 pp.; 13 text figs. (1 December 1970)
1971. Natural history and occurrence of opisthobranchs of Las Cruces, Baja California, Mexico, and vicinity. The Echo **3:** 16 (7 March 1971)

Collier, Clinton L. & Wesley Merrill Farmer
1964. Additions to the nudibranch fauna of the east Pacific and the Gulf of California. Trans. San Diego Soc. Nat. Hist. **13** (19): 377-396; plts. 1-6; 3 text figs. (30 December 1964)

Dall, William Healey
1894. Description of a new species of *Doridium* from Puget Sound. The Nautilus **8** (7): 73-74 (1 November 1894)

Haefelfinger, Hans-Rudolf & Roger A. Stamm
1958. *Limenandra nodosa* gen. et spec. nov. (Nudibranch, Aeolidiidae propr.), un opisthobranche nouveau de la méditerranée. Vie et Milieu **9** (4): 418-423; 1 text fig.

Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger **3** (Supplmt. I): 1-85; plts. 1-10 (1 February 1961)

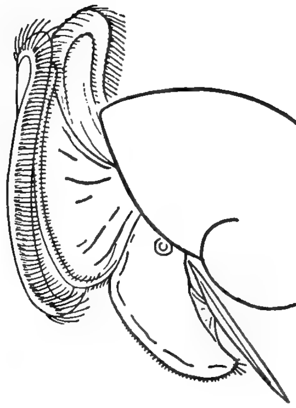
Marcus, Ernst & Eveline du Bois Reymond Marcus
1970. Opisthobranchs from Curaçao and faunistically related regions. Stud. Faun. Cur. Caribb. Isl. **33** (122): 1-129; 160 text figs.

Marcus, Eveline du Bois Reymond & Ernst Marcus
1967. American opisthobranch mollusks. Studies in tropical oceanography (Univ. Miami Inst. Marine Sci., Miami, Florida), no. 6: viii + 256 pp.; figs. 1-155 + 1-95 (December 1967)

Mörch, Otto Andreas Lowson
1863. Contributions à la faune malacologique des Antilles danoises. Journ. Conchyl. 3e ser., **3** (11): 21-43 (1 January 1863)

Sphon, Gale G.
1971. New opisthobranch records for the eastern Pacific. The Veliger **13** (4): 368-369 (1 April 1971)

Steinberg, Joan Emily & Meredith L. Jones
1960. A new opisthobranch of the genus *Aglaja* in San Francisco Bay. The Veliger **2** (4): 73-75; plt. 16 (1 April 1960)



Review of the Bathyal Gastropod Genus *Phanerolepida* (Homalopomatinae) and Description of a New Species from the Oregon Oligocene

BY

CAROLE S. HICKMAN

Department of Biology, Swarthmore College, Swarthmore, Pennsylvania 19081

(1 Plate; 1 Text figure)

INTRODUCTION

Two specimens of a new species of *Phanerolepida* Dall, 1907, from separate localities in the middle member of the lower Oligocene Keasey Formation in Oregon, constitute the first record of this deep-water genus outside of Japan and Okinawa. The new species also represents the earliest record of the genus, extending its stratigraphic range back into the Paleogene. It is the purpose of this report to describe the new species, to review the known occurrences of the genus, and to present some hypotheses regarding the evolution, ecological biogeography, and disjunct distribution of the genus.

It is remarkable that a poorly known genus from the Late Tertiary and Recent Japanese deep-water fauna should appear in an early Oligocene deep-water fauna on this side of the Pacific, widely separated in both time and space. *Phanerolepida transenna* (Watson, 1879), the sole living species, is restricted geographically to the area between 33° and 35° N latitude and bathymetrically to muddy substrates in the bathyal (archibenthal) zone, where it is most common between 600 and 800m (Okutani, 1968). Latitudinal and bathymetric restrictions on the species are further qualified by a unique vertical temperature structure at these latitudes along the Pacific coast of Honshu resulting from the meeting and mixing of the warm surface waters of an offshoot of the Kuroshio current and a submerged offshoot of the cold Oyashio current of Subarctic origin. Thus the temperature between 600 and 800m in the vicinity of Sagami Bay, where *P. transenna* occurs, is about 6° to 8° C, compared with temperatures in the overlying Kuroshio water averaging 15° C and temperatures in the underlying Western Pacific Bottom Water of 2° to 4° C (Okutani, *op. cit.*). Uda (1937) designates this system between 600 and 800m as the Intermediate Water, and Okutani (1967, 1968) discusses the characteristics and origin of the bathyal fauna, noting a high proportion of endemic molluscan species with the same restrictions imposed by geography, bathymetry, and water system as *P. transenna*. It is against Okutani's detailed background information on the Recent bathyal fauna of Japan that the significance of the Oregon *Phanerolepida* material can be evaluated.

The TYPE SPECIES in JAPAN

Phanerolepida is characterized by a sturdy turbinate shell of considerably larger size than the small to minute shells of *Homalopoma* Carpenter, 1864. It is further distinguished by a thin, concavo-convex operculum on which the spirals are not externally visible, in contrast to the thick paucispiral external whorl characterizing the operculum of *Homalopoma*. The callus is extensively developed, and in the type species it is divided into a thick portion proximal to the aperture and a thin distal portion through which the underlying ornamentation of the body whorl is visible. The most diagnostic feature of *Phanerolepida* is the net-like, finely-incised rhombohedral pattern of surface sculpture which appears to be unique among the Gastropoda. Both Watson (1879) and Dall (1907) described this surface pattern as having the appearance of shagreen. It is unusual in that the oblique rows of rhombs are not collabral, but inclined in the opposite direction from the aperture and growth lines. The pattern becomes increasingly fine on successive whorls and is sometimes irregularly developed or interrupted by areas of smooth shell deposit.

If *Phanerolepida* were a Recent monotypic genus, one might place less importance on the uniqueness of the net-like surface texture of the shell. However, the pattern now appears to be characteristic not of a single species, but of a lineage that has existed for at least 40 million years. At the same time, the potential for producing a similar but not identical surface pattern apparently exists within the closely related genus *Homalopoma,* as evidenced by its expression in another endemic Japanese species, *Homalopoma granulifera* Nomura & Hatai, 1940. The species occurs in shallow water (less than 100m) along the Japanese coast north of 35° N latitude. Its small size (less than 10mm high), features of the operculum, and the predominance of spiral sculpture are typical of *Homalopoma.* However, a more faintly developed axial sculpture gives the shell a granular appearance. Under magnification the granules exhibit more or less square outlines and either vertical or irregular arrangement (Figure *16*), in contrast to the oblique rows in *Phanerolepida.*

Watson based his original description of *Phanerolepida transenna* on a single live specimen dredged by the *Challenger* from a depth of over 1000m in the Sea of Enshu-Nada (Station 235). He placed his species in the genus *Turbo* Linnaeus, 1758. The original description (Watson, 1879), which was not illustrated, was repeated by Watson (1885-1886) in the *Challenger* Reports, and the holotype was figured.

A second specimen, obtained from deep water in Tokyo Bay by the *Albatross* in 1906 prompted Dall (1907: 168) to propose *Phanerolepida* as a subgenus of *Leptothyra* Pease, 1869. The name is introduced in a discussion at the end of Dall's description of *Basilissa babelica* because the specimen occurred in the same haul with the new species. There are no records indicating that *P. transenna* was collected during the 50 years that followed. Habe (1964: 20) states that the species is "rarely collected from 200 to 500 meters in Sagami Bay."

Okutani (1964) presents the most complete record of *Phanerolepida transenna* in a report based on collections by the R. V. *Soyo-Maru* between 1955 and 1963. He records 10 empty shells and 16 living specimens of *P. transenna* from stations between 550 and 800m in Sagami Bay. Dr. Okutani has graciously provided 7 of these specimens, from 700m in Sagami Bay, for comparison with the new species from the Oregon Oligocene. Two of these specimens have been donated to the U. S. National Museum and are figured in this report (Figures *1, 2, 5, 6, 9,* and *10*).

FOSSIL OCCURRENCES

There are 3 accounts of *Phanerolepida* as a fossil from localities in the Western Pacific. All 3 occurrences are in strata near or above the Miocene-Pliocene boundary, in contrast to the new Oregon species, which comes from strata near the Eocene-Oligocene boundary. Kuroda (1931) described *P. expansilabrum* from the Pliocene of the Nagano prefecture (36°19′N, 138°07′E). Hatai & Nisiyama (1952: 230) consider the age of the strata to be Miocene. I have not seen the holotype, but the spire appears to be higher than in the type species and demarcated by a slightly impressed suture. Kuroda's figure is not good enough to show details of surface pattern. Otuka (1968) documents the occurrence of *P. transenna* from the Pliocene Tomiya sandstone of the Chiba prefecture (35°12′N, 139°51′E). Okutani (1968) discusses the paleoecology of the Tomiya fossil assemblage and cites evidence that it formed under a similar set of environmental restrictions as those found in the vicinity of Sagami Bay. The Recent and fossil occurrences of *Phanerolepida* in Japan are summarized in Figure 17.

One western Pacific occurrence of *Phanerolepida* has been recorded outside of Japan proper. MacNeil (1960:

Plate Explanation

Phanerolepida transenna Watson

Figures *1, 5,* and *9*: USNM 707162. Hypotype. Apertural, top, and side views. Recent, Japan. × 1.5

Figures *2, 6,* and *10*: USNM 707163. Hypotype. Apertural, top, and side views. Recent, Japan. × 1.5

Figure *14*: USNM 707163. Hypotype. a – Detail of surface texture from penultimate whorl. b – Detail of surface texture from body whorl. × 10

Phanerolepida rehderi MacNeil

Figures *3, 7,* and *11*: USNM 562794. Holotype. Apertural, top, and side views. Miocene or Pliocene, Okinawa. × 1.5

Figure *13*: USNM 562795. Topotype. Top view. Miocene or Pliocene, Okinawa. × 1.5

Phanerolepida ***oregonensis*** Hickman, spec. nov.

Figures *4, 8,* and *12*: USNM 646902. Holotype. Apertural, top, and side views. Oligocene, Oregon. × 1.5

Figure *15*: USNM 646902. Holotype. Detail of surface texture from body whorl. × 10

Homalopoma granulifera Nomura & Hatai

Figure *16*: ANSP 242880. Hypotype. Detail of surface texture from body whorl. Recent, Japan. × 10

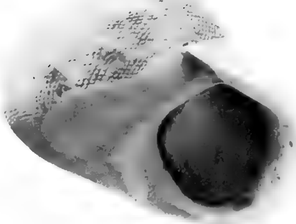


Figure *1*

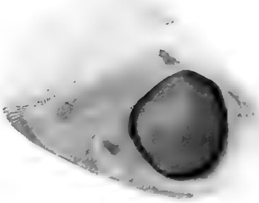


Figure *2*

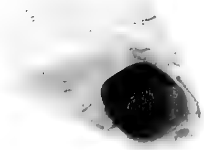


Figure *3*


Figure *4*

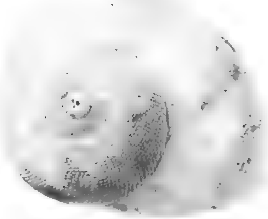


Figure *5*

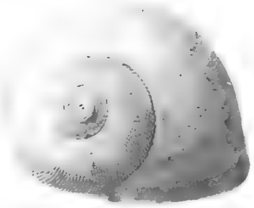


Figure *6*


Figure *7*

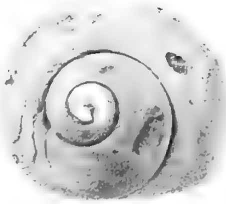


Figure *8*

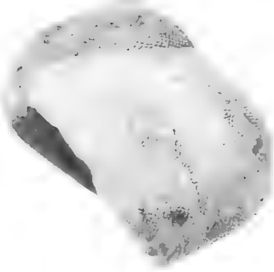


Figure *9*

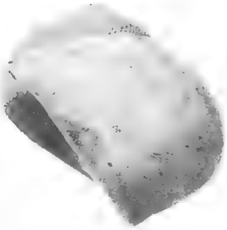


Figure *10*

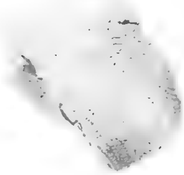


Figure *11*


Figure *12*


Figure *13*

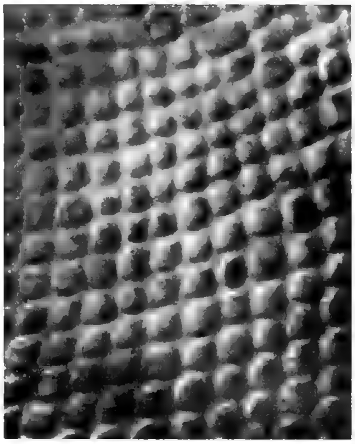


Figure *14* a

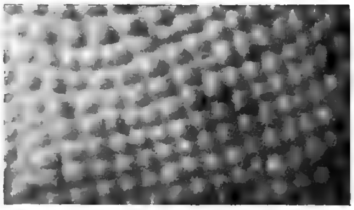


Figure *14* b

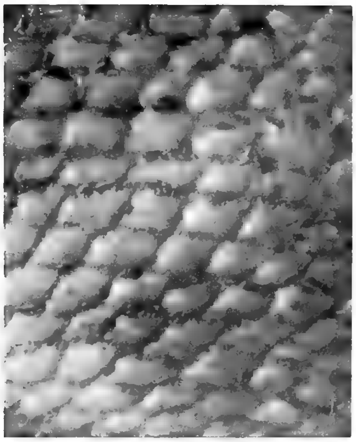


Figure *15*

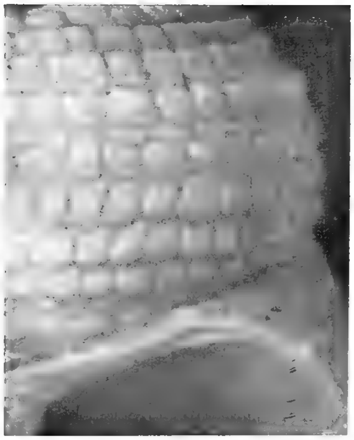


Figure *16*

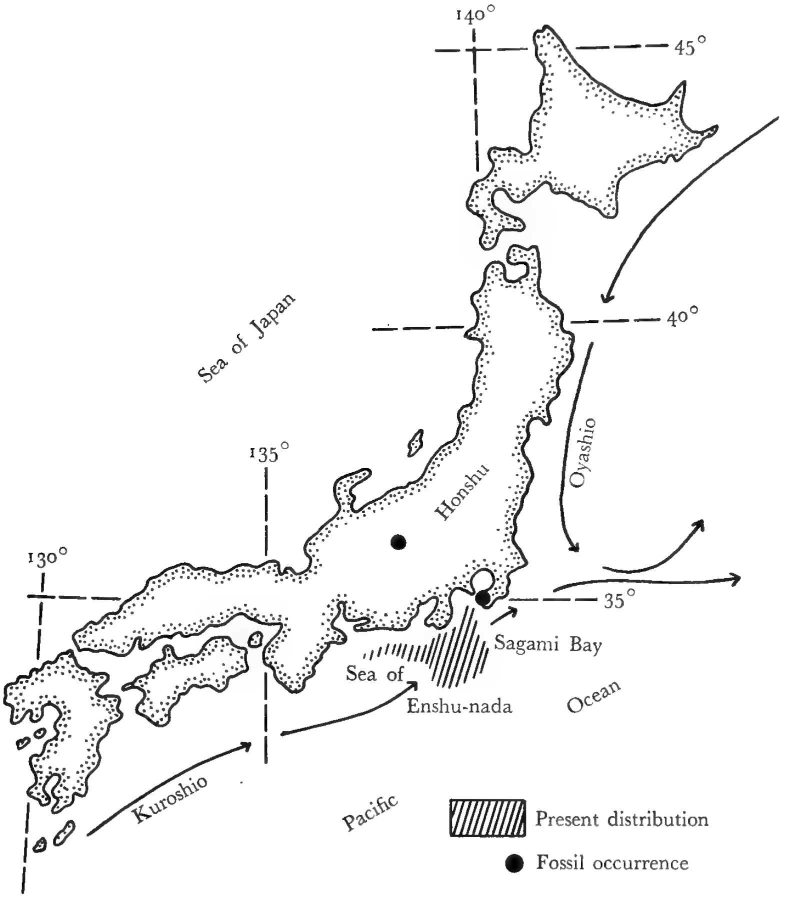


Figure 17

Recent and fossil occurrences of *Phanerolepida* in Japan

30) described *P. rehderi* from beds near the Miocene-Pliocene boundary on Okinawa, at the southern end of the Ryukyu Islands south of Japan. The species is represented by 5 specimens from 2 localities in the Shinzato tuff member of the Shimajiri Formation between 26°05′ and 26°20′N latitude on Okinawa. MacNeil's species has sculpture which is intermediate in coarseness between *P. transenna* and the new species from the Keasey Formation. The shell has a distinctive outline resulting from an abrupt steepening of the apical whorls. Interruption of the reticulate sculpture pattern seems to be more common in *P. rehderi* than in the Recent *P. transenna*. Sharply demarcated areas of unornamented shell are present on the holotype, and on the topotype most of the body whorl lacks reticulate sculpture (Figures *3, 7, 11, 13*).

The Shinzato tuff fauna is a deep-water assemblage which resembles the Keasey fauna in the presence of *Bathybembix* and a diverse component of turrid gastropods. MacNeil (1960: 17) examined depth ranges of living relatives of species in the Shinzato tuff and reported that most occur between 560 and 720m.

SYSTEMATIC PALEONTOLOGY

Turbinidae

Homalopomatinae

Phanerolepida Dall, 1907

Type, by monotypy, *Turbo transenna* Watson, 1879. Living, Japan.

Phanerolepida oregonensis Hickman, spec. nov.

(Figures *4, 8, 12*)

Description: Shell large for subfamily, robust, heavy, with 3 whorls on type specimen; apex abraded; aperture circular and nacreous within, prosocline at an angle of about 60° from the axis of coiling; inner lip covered by a broad crescent-shaped callus; suture slightly canaliculate; surface cross-hatched by impressed irregularly spaced spiral and oblique axial lines which divide the surface into small rhombs and give the shell a scaly or net-like appearance. The oblique rows of rhombs are not collabral but inclined in the opposite direction from the aperture and lines of growth. The surface pattern may be interrupted by small areas of shell with faint spiral sculpture, and on early whorls there is faint spiral sculpture superimposed on the rhombohedral sculpture.

Dimensions of Holotype: height 19 mm; maximum diameter 23.2 mm.

Hypotype: height 10.5 mm; maximum diameter 15 mm.

Remarks: *Phanerolepida oregonensis* differs from both *P. transenna* and *P. rehderi* in having a much more strongly prosocline aperture, a more compressed form, and coarser surface sculpture.

Phylogenetic Implications: In the known species of *Phanerolepida,* the rhombohedral surface sculpture has become progressively finer since the beginning of the Oligocene. The hypothesis that coarse sculpture is primitive in the genus is supported by the preservation of coarse sculpture on the early whorls of all species, since it is in accord with the principle that mutations which affect early ontogeny are less often viable than alterations in later stages of development (Figures *1* to *15*).

Origin of *Phanerolepida* from a *Homalopoma*-like ancestor is suggested by the faintly spiral ridges on the early whorls of the Miocene or Pliocene species (Figures *7, 13*) and the superposition of faint spiral sculpture on the rhombohedral sculpture of early whorls in the Oligocene species (Figure *12*). Faint spiral sculpture occurs on the early whorls of some specimens of the Recent species, but it is not discernible on most. There are areas on both the Paleogene and Neogene species where the characteristic reticulate texture is replaced by an apparent relapse of smooth shell deposit marked by faint spiral ridges. One such area occurs on the body whorl of the holotype of *P. oregonensis* (Figure *4*). The term "relapse" seems particularly appropriate with respect to the topotype of *P. rehderi,* on which the reticulate sculpture moves from coarse to fine and back to coarse again before it finally disappears on the body whorl (Figure *13*).

Holotype: U. S. National Museum 646902. Hypotype: USNM 646903.

Occurrences: The holotype was collected by the author in the blue-gray massively bedded siltstone exposed in the abandoned Smithwick-Haydite Quarry on the Spokane, Portland, and Seattle Railroad; NW¼ Sec. 8, T3N, R4W; Vernonia Quadrangle (USGS locality 25031). The type locality falls in the upper part of what has informally been designated as the middle member of the Keasey Formation (Warren & Norbisrath, 1946). Lower Oligocene.

A smaller, poorly-preserved specimen was discovered in a collection made by Harold Vokes in conjunction with the geologic mapping of northwestern Oregon (Warren *et al.,* 1945). The specimen comes from USGS locality 15267, the second large cut from the south end of the high trestle crossing Oregon Highway 47, 1.4 miles due west of Hoffman Hill Lookout, Vernonia Quadrangle. This locality is separated from the type locality by about 5 km. USGS loc. 15267 appears to be slightly lower in the middle member of the formation, although the precise vertical separation cannot be determined because the two localities are on opposite sides of a heavily forested valley and attitudes are too variable in the region for accurate extrapolation.

DISCUSSION

The discovery of *Phanerolepida* in the early Oligocene of western North America raises some interesting questions of historical biogeography and lends new perspective to the question of the pronounced endemism in the Japanese bathyal fauna.

Discussions of endemism in living species have focussed on the distinctions between relict (paleoendemic) and newly evolved (neoendemic) taxa (Stebbins & Major, 1965: 3). *Phanerolepida* is now a relict or paleoendemic genus. It is not clear, however, whether the sole Oligocene occurrence represents a neoendemic phase, nor is it possible to determine whether the genus made its first appearance in the Eastern or Western Pacific.

There are two major possible patterns of distribution for the genus during the Tertiary. It might have been a geographically widespread and broadly adapted member of the bathyal fauna that has declined to a small, highly specialized relict population; or it may have evolved as a specialist and migrated as a small narrowly adapted population as its peculiar environment shifted through time and space. Although there is no fossil evidence to support the first hypothesis, fossil deep-water molluscan assemblages are so rare and poorly known that we have no basis for rejecting the possibility that the genus was more abundant earlier in its evolutionary history. Most documented cases of endemism in taxa with long geologic histories show that the living species are relicts of broader patterns of distribution (see STEBBINS & MAJOR, 1965).

The alternative hypothesis that the genus might have evolved in the Eastern Pacific and migrated to its present location in the Western Pacific invites closer examination of the conditions under which *Phanerolepida* currently lives. Although the bathyal zone is usually a stable region, the bathyal zone between 600 and 800 meters in Sagami Bay has many of the same characteristics as the unstable transition zone in the surface waters between the Kuroshio and Oyashio fronts. OKUTANI (1968: 79) suggests that the supply of water from the Oyashio Undercurrent may not be constant and that populations of warm- and cold-water species may undergo some of the same alternate fluctuations of establishment and extinction as those that have been observed in the transition zone in surface waters to the north. In addition to the unique mixture of northern and southern faunal elements, the Intermediate Water fauna is characterized by 85% endemic species (OKUTANI, 1967: 140). It is likely that this endemism not only reflects adaptations to unique stratification of water masses of very different properties, but also adaptations to fluctuations in the bathyal environment.

There is no firm basis for postulating similar instability in the bathyal zone in which the Keasey Formation was deposited. It may be worth noting, however, that the late Eocene-early Oligocene was a time of climatic transition from widespread tropical conditions to the differentiation of cold water masses at northern latitudes. Current patterns off northwestern Oregon might have involved a similar interplay of warm and cold water masses.

Another unusual feature which links all the occurrences of *Phanerolepida* is the presence of a deep water environment very near shore. The similarity of inferred depositional environments of the Keasey Formation and the Shinzato tuff member of the Shimajiri Formation illustrate this parallelism particularly well. Both were deposited in tectonically mobile belts on the western slopes of deep trenches where the bathyal zone was developed very close to shore. Both contain a high proportion of tuffaceous material with occasional ash beds and indications of active volcanism on the adjacent landmasses (MACNEIL, 1960; WARREN & NORBISRATH, 1946).

There are additional links between the living Japanese bathyal fauna and the fauna of the Keasey Formation. *Bathybembix aeola* (Watson, 1878) and *Acanthotrophon echinus* (Dall, 1918), both elements of the restricted Intermediate Water fauna occurring from the lower shelf to 800m between 33° and 35°N latitude, have morphological analogs in the Keasey Formation. The author intends to explore this parallelism further in a forthcoming systematic treatment of the Keasey gastropod fauna.

Previous recognition that the Keasey Formation was deposited in deep water rests on a variety of general and specific observations. MOORE & VOKES (1953) point out a number of general features indicating deep water: the lack of bedding, the diversity of turrid genera and species, the absence of typical shallow water genera, and the depth ranges of some analogous species, particularly bivalves from Recent faunas on the Pacific Coast. ZULLO *et al.* (1964), examining a specific faunal assemblage within the Keasey Formation, were able to postulate, on the basis of the abundance of an echinoid and coral species with modern counterparts, that the depth of the specific habitat represented was approximately 365 m.

The close affinities of the Keasey gastropod fauna with the modern bathyal fauna off Central Japan provide important new insight into the nature of the Keasey paleoenvironment and the evolution and historical biogeography of a number of molluscan lineages.

ACKNOWLEDGMENTS

I am grateful to Takashi Okutani of the Tokai Regional Fisheries Research Laboratory in Tokyo for the loan of material and for permission to retain reference specimens, which have been deposited in the U. S. National Museum. Robert Robertson of the Academy of Natural Sciences of Philadelphia provided helpful suggestions and assistance in the photography of shell textures. I thank Druid Wilson for arranging the loan of type specimens from the U. S. National Museum. A. Myra Keen, Warren O. Addicott, and James C. Hickman kindly read and criticized the manuscript.

Literature Cited

DALL, WILLIAM HEALEY
1907. Descriptions of new species of shells, chiefly Buccinidae, from the dredgings of the U. S. S. *"Albatross"* during 1906, in the northwestern Pacific, Bering, Okhotsk, and Japanese Seas. Smithson. Misc. Coll. 50 (1727): 139 - 173 (9 July 1907)

HABE, TADASHIGE
1964. Shells of the western Pacific in color, vol. II. Osaka, Japan, Hoikusha, pp. 1 - 233; plts. 1 - 66; 1 map; 2 pp. text figs.

Hatai, Kotora & Syozo Nisiyama
1952. Check list of Japanese Tertiary marine Mollusca. Tohoku Imp. Univ. Sci. Reprts., 2nd. ser. (Geology), spec. vol. **3:** 464 pp.

Kuroda, Tokubei
1931. Fossil Mollusca. *In*: F. Homma: Shinano Chubu Chishitsu-Shi [Geology of central Shinano]; part **4:** 1 - 90; plts. 1 - 13

MacNeil, Francis Stearns
1960. Tertiary and Quaternary Gastropoda of Okinawa. U. S. Geol. Survey Prof. Paper **339:** 148 pp.; 31 plts.; 17 text figs.

Moore, Raymond Cecil & Harold Ernest Vokes
1953. Lower Tertiary crinoids from northwestern Oregon. U. S. Geol. Survey Prof. Paper **233-E:** 113 - 148; 13 figs.; plts. 14 - 24

Okutani, Takashi
1964. Report on the archibenthal and abyssal gastropod Mollusca collected mainly from Sagami Bay and adjacent waters by the R. V. *Soyo-Maru* during the years 1955-1963. Journ. Fac. Sci., Univ. Tokyo, Sect. II, **15** (3): 371 - 447; plts. 1 - 7
1967. Characteristics and origin of archibenthal molluscan fauna on the Pacific coast of Honshu, Japan. Venus, Japan. Journ. Malacol. **25** (3, 4): 136 - 146; 6 text figs.
1968. Systematics, ecological distribution, and paleoecological implication of archibenthal and abyssal Mollusca from Sagami Bay and adjacent areas. Journ. Fac. Sci., Univ. Tokyo, Sec. II, **17** (1): 1 - 91; 1 plt.; 43 text figs.

Otuka, Yanosuke
1949. Fossil Mollusca and rocks of the Kiyosumi Group exposed at Minatomachi, Chiba Prefecture and its environs. Japan. Journ. Geol. Geogr. **21:** 295 - 315; plt. 13; text figs. 1 - 3

Stebbins, George Ledyard & Jack Major
1965. Endemism and speciation in the California flora. Ecol. Monogr. **35:** 1 - 35

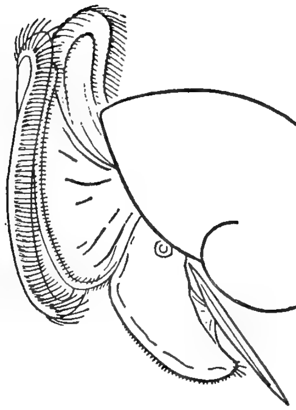
Uda, Michitaka
1937. Results of hydrographical investigation in Sagami Bay in connection with "buri" (*Seriola quinqueradiata* T. & S.) fishing. Journ. Imp. Fish. Exp. Sta. **8:** 1 - 50

Warren, W. C., Hans Norbisrath & R. M. Grivetti
1945. Geology of northwestern Oregon west of Willamette River and north of latitude 45°15′. U. S. Geol. Surv. Oil and Gas Investig. Prelim. map 42; geol. map and text

Warren, W. C. & Hans Norbisrath
1946. Stratigraphy of upper Nehalem River Basin, northwestern Oregon. Amer. Assoc. Petr. Geol. Bull. **30:** 213 - 237; 2 text figs; 1 table

Watson, Robert Boog
1879. Mollusca of H. M. S. '*Challenger*' Expedition. IV. Trochidae continued, *viz.* the genera *Basilissa* and *Trochus*, and the Turbinidae, *viz.* the genus *Turbo*. Journ. Linn. Soc. London **14:** 692 - 716
1885-1886. Report on the Scaphopoda and Gastropoda collected by H. M. S. *Challenger* during the years 1873-1876. Reprt. Scient. Res. Voyage H. M. S. *Challenger*, Zoology **15:** 1 - 722; plts. 1 - 50

Zullo, Victor, R. F. Karr, John Wyatt Durham & Edwin C. Allison
1964. The echinoid genus *Salenia* in the eastern Pacific. Palaeont. **7** (2): 331 - 349; plt. 56; text figs. 1 - 6



A Report on Cephalopods Collected by Stanford Oceanographic Expedition 20 to the Eastern Tropical Pacific Ocean September to November, 1968

BY

W. GORDON FIELDS AND VERONICA A. GAULEY

Department of Biology, University of Victoria, Victoria, British Columbia, Canada

(1 Text figure)

INTRODUCTION

THE CEPHALOPODS collected by the Stanford Oceanographic Expedition 20 are described and their location of capture noted in order to increase recorded knowledge of cephalopod fauna of the eastern tropical Pacific Ocean. The expedition, aboard the RV "*Te Vega*", left Guayaquil, Ecuador on 17 September, 1968 and arrived in San Diego, California on 29 November, 1968. The cruise track and stations where cephalopods were collected are shown in Figure 1.

Reports on the cephalopod fauna of the eastern tropical Pacific are few. HOYLE (1904), ROBSON (1948), CLARKE (1966), McGOWAN & OKUTANI (1968), OKUTANI & McGOWAN (1969), ROPER (1969) and YOUNG (1971) have described various cephalopod species from this general area.

METHODS

The collection consists of 17 specimens held by the University of Victoria (UV) in the "*Te Vega*" collection (TVG). The 6 different species identified have been described in detail by previous authors; therefore, these descriptions will not be repeated here except for an outline of the distinguishing features. Five of the specimens are unidentifiable to species due to loss of parts, digested state and larval stage. Specimens were collected by Tucker trawl, bongo net and hand line. Three specimens of *Symplectoteuthis* were found among material regurgitated by a Colombian booby, *Sula leucogaster etesiaca* Thayer & Bangs, 1905.

The measurements and morphometric indices given in the systematic section and in Tables 1 and 2 are defined by Voss (1956). The eight morphological characteristics measured include: total length (TL); dorsal mantle length (ML); mantle width (MW); head width (HW); head length (HL); fin length (FL); fin width (FW); and arm length (AI - IV). Seven indices were calculated from these measurements: head width index (HWI); mantle width index (MWI); fin length index (FLI); fin width index (FWI); mantle arm index (MAI); arm length index (ALI); and head length index (HLI). In addition, length of the fin as measured along the plane of attachment (FL′) (BERRY, 1912) and the index for this measurement (FLI′) were used.

SYSTEMATIC SECTION

OCTOPODIDAE

Octopus sp.

Specimens: Two larvae, UV-TVG 4 and 5, ML 7.0 and 4.0mm; station F-52, 4°53′N, 84°07′W, 2330 hrs., 20 October 1968; Tucker trawl, 100m to surface.

Because of the small size of the specimens and lack of literature on larval octopods of this region, definite identification was not attempted. Both specimens are complete

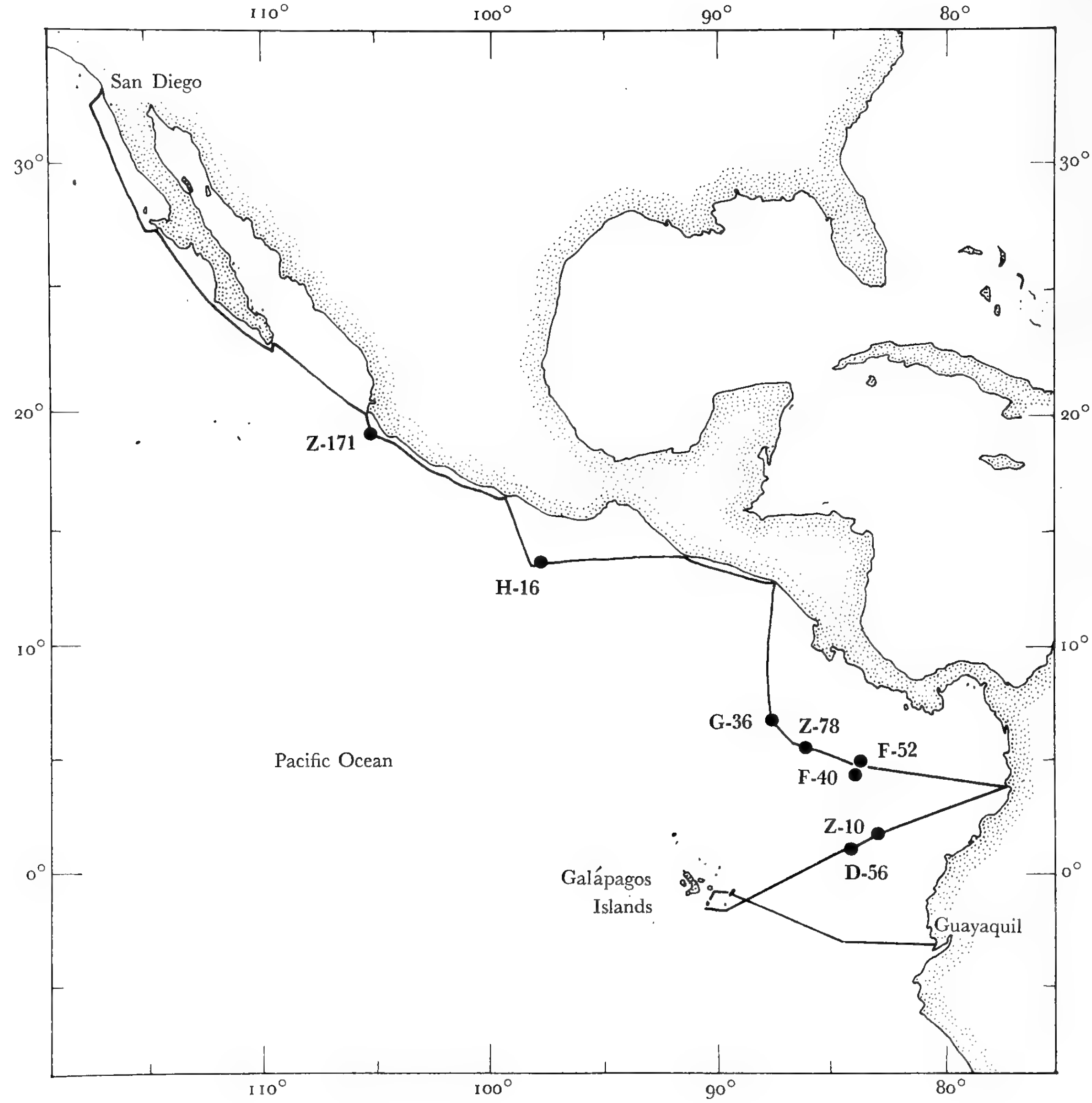


Figure 1

Cruise track and stations where cephalopods were collected on Stanford Oceanographic Expedition 20

Table 1

Measurements

Species	Collection No.	Measurements in millimeters											
		TL	ML	MW	HL	HW	FL	FL'	FW	AI	AII	AIII	AIV
Octopus sp.	4	16	7	4.5	/	4.5	/	/	/	5.5	5.5	6	5.5
Octopus sp.	5	7	4	3	/	3	/	/	/	2.5	3	3	2.5
Japetella sp.	14	32	18	17*	/	13	/	/	/	8.5	10	12	9
Abraliopsis affinis	6	55	26	12	9	8*	20	17	33	16	16.5	17	18
Abraliopsis affinis	7	26	13	5	4	4	8.5	7	16	8	10	10	10
Abraliopsis affinis	15	73	30	10	12	11	22	19	31	30	31	27	32
Abraliopsis affinis	16	–	29	13*	–	–	20	18	32	–	–	–	–
Bathyteuthis abyssicola	13	35*	–	–	7	9	–	–	–	8	8	9	9
Bathyteuthis bacidifera	1	22	12	6	5	7	3	2	4	3.5	4	4	4.5
Bathyteuthis bacidifera	2	35	16	10	8	13	6.5	4	11	7	10	10	11
Symplectoteuthis oualaniensis	8	24	15	5	4	4	4	3	7	4	5	5	3
Symplectoteuthis oualaniensis	10	90*	61	13	9	11	20*	17*	–	19*	22*	25*	20*
Symplectoteuthis oualaniensis	11	–	55*	16	11	13	–	–	–	14*	19*	14*	14*
?*Symplectoteuthis* sp.	12	64*	–	–	–	–	–	–	–	–	–	–	–
?*Symplectoteuthis* sp.	9	–	8	–	–	–	2	2	4	–	–	–	–
Dosidicus gigas	17	598	325	90*	65	55	63	49	204	195	202	200	187
Helicocranchia pfefferi	3	23	16	–	2	6	2	1	3	4	6	8	3

/ = measurement not applicable
* = measurement approximate
– = measurement not taken

Table 2

Morphometrics

Species	Collection No.	HWI	HLI	MWI	FLI	FLI'	FWI	MAI	ALI
Octopus sp.	4	64.3	/	64.2	/	/	/	116.7	37.5
Octopus sp.	5	75.0	/	75.0	/	/	/	133.3	42.9
Japetella sp.	14	72.2	/	–	/	/	/	150.0	37.5
Abraliopsis affinis	6	30.7*	34.6	46.2	76.9	65.4	127.0	69.2	32.7
Abraliopsis affinis	7	30.8	30.8	38.5	65.4	53.8	123.1	76.9	38.5
Abraliopsis affinis	15	36.7	40.0	33.3	73.3	63.3	103.3	106.7	43.8
Abraliopsis affinis	16	–	–	44.8*	69.0	62.1	110.3	–	–
Bathyteuthis abyssicola	13	–	–	–	–	–	–	–	25.7
Bathyteuthis bacidifera	1	58.3	41.7	50.0	25.0	16.7	33.3	37.5	20.5
Bathyteuthis bacidifera	2	81.3	50.0	62.5	40.6	25.0	68.8	68.8	31.4
Symplectoteuthis oualaniensis	8	26.7	26.7	33.3	26.7	20.0	46.7	33.3	20.8
Symplectoteuthis oualaniensis	10	18.0	14.8	21.3	32.8*	27.9*	–	41.0*	27.8*
Symplectoteuthis oualaniensis	11	23.6*	20.0*	29.1*	–	–	–	34.5*	–
?*Symplectoteuthis* sp.	12	–	–	–	–	–	–	–	–
?*Symplectoteuthis* sp.	9	–	–	–	25.0	25.0	50.0	–	–
Dosidicus gigas	17	16.9	20.0	27.7*	19.4	15.1	62.8	62.2	33.8
Helicocranchia pfefferi	3	37.5	12.5	–	12.5	6.3	18.8	50.0	34.8

/ = index not applicable
* = index approximate
– = index not calculated

and in good condition. They have 6 large reddish-brown chromatophores on the dorsal side of the head, a double row of very small chromatophores on the aboral side of each arm, and many small chromatophores of a faint reddish-brown on the dorsal posterior mantle and ventral mantle. Hoyle (1904) has described 10 species of Octopus from the eastern tropical Pacific.

Bolitaenidae

Japetella sp.

Specimens: One female, UV-TVG 14, ML 18mm; station H-16, 13°25′N, 98°14′W, 2000 hrs., 8 November 1968; bongo net, 1500m.

Japetella is a soft-bodied octopod with a wide mantle opening, uniserial suckers, and large eyes directed laterad. This specimen is a small, immature female and is in fair condition with a "wrinkled" mantle and damaged web. It has large, prominent gills which are 10mm long and have 11 lamellae in the outer demibranch. The funnel extends to the anterior edge of the eyes. It is broad and thin-walled. The funnel organ is not discernible. The longest arm is 37% of the total length of the animal. Due to the condition and immaturity of this specimen identification to species was not made. Hoyle (1904) has described two species of *Japetella* from this area.

Enoploteuthidae

Abraliopsis affinis (Pfeffer, 1912)

Specimens: One female, UV-TVG 6, ML 26mm; one male, UV-TVG 7, ML 13mm; station F-52, 4°53′N, 84°07′W, 2330 hrs., 20 October 1968; Tucker trawl, 100 m to surface.

One male, UV-TVG 15, ML 30mm; station Z-171, 19°04′N, 104°40′W, 2100 hrs., 18 November 1968; Tucker trawl, 300m to surface.

One male, UV-TVG 16, ML 29mm; mantle only, no data.

This species is noted for the arrangement of the photophores on the ventral side of the short, semi-fusiform mantle. They are situated in longitudinal rows with a wide, median bare area terminating in a bare, circular patch on the distal third of the mantle. There are 2 large and 3 small photophores on the eye ball. The club has 3 large and 4 small hooks in a double row and a semilunar membrane on the outer side. In the male, the right ventral arm is hectocotylized with 3 offset semilunar crests; the left ventral arm has a large swimming web 3 times the width of the arm.

The mature female, UV-TVG 6, has both tentacles and the right eye missing. Ripe eggs fill the posterior mantle cavity. Approximately 16 discharged spermatophores are embedded in the internal side of the dorsal mantle just to the right and behind the nuchal cartilage.

The male, UV-TVG 7, is a juvenile with reproductive organs in a developmental stage. The ventral mantle photophores are in the typical longitudinal arrangement but are not as numerous as in the adult.

UV-TVG 15 is a mature male in fair condition with the left tentacle and the tips of the first right and third left arm missing. The semilunar crests of the hectocotylus have been destroyed but the swimming web of the left ventral arm is well developed and in good condition. There are many mature spermatophores 6.5mm long in the penis and spermatophoric sac.

Although the fourth specimen, a mature male, UV-TVG 16, is missing the head, arms and data, it is included here because the mantle and internal organs are in very good condition and have the same morphology as UV-TVG 15. Spermatophores are present in the penis and the spermatophoric sac. Although they are much less numerous than in UV-TVG 15, they have the same length of 6.5mm.

McGowan & Okutani (1968) have compared *Abraliopsis affinis* with 3 other North Pacific species and have indicated its distribution in the eastern tropical Pacific. Hoyle (1904), Pfeffer (1912) and Clarke (1966) also note its distribution in this area.

Bathyteuthidae

Bathyteuthis abyssicola Hoyle, 1885

Specimens: One ?, UV-TVG 13, ML –; station G-36, 7°29′N, 87°58′W, 2055 hrs., 27 October 1968; Tucker trawl, 2500m to surface.

Bathyteuthis is noted for its deep red colour, separate terminal fins and 6 oval light organs, one each at the base of the first 3 dorsal pairs of arms. *Bathyteuthis abyssicola* is distinguished from *B. bacidifera* Roper, 1968, by its thick, fleshy, protective arm membranes unsupported by trabeculae, smaller gills and smaller tentacular clubs with fewer suckers; it differs from *B. berryi* Roper, 1968 by having smaller gills and fewer suckers on shorter, blunt arms (Roper, 1968: 171; table 1). The morphology and distribution of these species are discussed in detail in Roper (1969). This specimen of *B. abyssicola* is in poor condition. The mantle is everted and most of the internal organs are missing. Hoyle (1904), Robson (1948), Clarke (1966), and Roper (1969) note the presence of this species in the eastern tropical Pacific.

Bathyteuthis bacidifera Roper, 1968

Specimens: One juvenile, UV-TVG 1, ML 12mm; station D-56, 1°19′N, 84°07′W, 1415 hrs., 6 October 1968; Tucker trawl, 2500m to surface.

One female, UV-TVG 2, ML 16mm; station F-40, 4°29′N, 84°10′W, 2245 hrs., 19 October 1968; Tucker trawl, 200 - 350m to surface.

Bathyteuthis bacidifera possesses all those features previously mentioned for *Bathyteuthis.* Its most distinctive characteristic is the long free trabeculae which replace the protective membranes on the proximal half of the arms. Roper (1968, 1969) has made detailed descriptions of this species and notes its distribution as being bathypelagic in the " ... Eastern Pacific Equatorial Water Mass and possibly in the Indian Ocean Equatorial Water Mass (based on Chun's [1910] single specimen)." (Roper, 1969: 49).

The juvenile is missing the right tentacular club but it is in better condition than the female which is missing both tentacles and the right second arm. Both specimens possess the typical long, free trabeculae on the arms.

Ommastrephidae

Symplectoteuthis oualaniensis (Lesson, 1830)

Specimens: One juvenile, UV-TVG 8, ML 15mm; station F-52, 4°53′N, 84°07′W, 2330 hrs., 20 October 1968; Tucker trawl, 100m to surface.

One male, UV-TVG 10, ML 61mm; one?, UV-TVG 11, ML 55mm approx., station Z-78, 5°34′N, 86°58′W, 1930 hrs., 22 October 1968; from stomach of Colombian booby, *Sula leucogaster etesiaca* Thayer & Bangs, 1905.

The distinctive feature of juveniles and adults of this species is the fusion of the mantle with the funnel at the junction of the two perpendicular grooves of the funnel cartilage. Clarke (1965, 1966) describes a form of this species which has a large light organ on the dorsal mantle surface. This was not observed in any of the "*Te Vega*" specimens of *Symplectoteuthis.*

Symplectoteuthis oualaniensis has been reported from the eastern tropical Pacific by Hoyle (1904), Voss (1963), and Clarke (1966). It has also been recorded from the western Pacific Ocean and the Indian Ocean (Sasaki, 1929; Voss, 1963; Clarke, 1966).

The juvenile specimen, UV-TVG 8, is in good condition. Specimens UV-TVG 10 and 11 have been partially destroyed by digestion with the arms being the most affected. The dorsal and ventral sides of the stomach and caecum of specimen UV-TVG 10 are parasitized by approximately 140 immature specimens of the family Didymozoidae.

?Symplectoteuthis sp.

Specimens: One mantle with part of funnel, UV-TVG 9, ML 8mm; station F-52, 4°53′N, 84°07′W, 2330 hrs., 20 October 1968; Tucker trawl, 100m to surface.

One mantle, UV-TVG 12, ML 64mm; station Z-78, 5°34′N, 86°58′W, 1930 hrs., 22 October 1968; from stomach of a Colombian booby, *Sula leucogaster etesiaca.*

Specimen UV-TVG 9 was tentatively identified as *Symplectoteuthis* sp. on the basis of the structure of the funnel cartilage and its fusion to the mantle. The taxonomic position of UV-TVG 12 is even less certain as only the mantle remains. However, since it has the same form, colour and approximately the same size as specimens UV-TVG 10 and 11 and was collected from the same source at the same time, it has been placed under *?Symplectoteuthis* sp.

Dosidicus gigas (d'Orbigny, 1835)

Specimens: One male, UV-TVG 17, ML 325mm; station Z-10, 2°51′N, 83°16′W, 2030 hrs., 19 September 1968; hand line.

Dosidicus gigas is characterized by its robust arms which become very attenuate at the extremities where they bear numerous, very small suckers. Adults attain a very large size, between 4 and 12 feet [1.20m and 3.60m] (Phillips, 1961; Clarke, 1966). The "*Te Vega* " specimen is a small male in good condition. This species has been frequently recorded from the eastern tropical Pacific; a few of these authors are: d'Orbigny (*in* de Férussac & d'Orbigny, 1835), Steenstrup (1880), Berry (1912), Pfeffer (1912), Phillips (1933, 1961), and Clarke (1966). It has also been recorded from Australia and the Solomon Islands (Brazier, 1892 *in* Clarke, 1966).

Cranchiidae

Helicocranchia pfefferi Massy, 1907

Specimens: One juvenile, UV-TVG 3, ML 16mm; station F-40, 4°29′N, 84°10′W, 2245 hrs., 19 October 1968; Tucker trawl, 200 - 350m to surface.

This species is noted for its pedunculate fins, the regular arrangement of chromatophores in rows on the sides of the mantle, the extremely large funnel wich extends two thirds the length of the ventral arms and the large, stalked, conical eyes which bear a luminous organ. The arm formula is 3 > 2 > 1 > 4 or 3 > 2 > 4 > 1. *Helicocranchia pfefferi* has been reported from the Pacific only by Okutani & McGowan (1969). These specimens and the "*Te Vega*" specimen have a small swelling on the dorsal surface of the head. There is a semilunar chromatophore against the swelling and a pair of circular chromatophores on both sides between the cephalic pillar and eye stalks. The "*Te Vega*" specimen is in good condition except that the tentacles and eyes have been damaged and some of the arm suckers are missing.

ACKNOWLEDGMENTS

We would like to thank Dr. Jack Littlepage of the University of Victoria for providing us with the cephalopod specimens from Stanford Oceanographic Expedition 20 operating under NSF Grants GB 6870 and GB 6871. The authors are grateful to Dr. L. Margolis of the Fisheries Research Board of Canada, Nanaimo, for identifying parasites and to Dr. William G. Pearcy of Oregon State University for the loan of *Japetella heathi* (Berry, 1911) specimens. We would also like to thank Mr. Steve Brocco of the University of Washington for his suggestions concerning the paper. Study of these specimens at the University of Victoria was supported by National Research Council of Canada Grant A 1968 and by a grant from the University of Victoria Faculty Research Fund.

Literature Cited

Berry, Samuel Stillman
1912. A review of the cephalopods of western North America. Bull. U. S. Bur. Fish. 1 (XXX), Doc. 761: 267 - 336; plts. 32 - 56; 18 text figs. (24 July 1912)

Clarke, Malcolm R.
1965. Large light organs on the dorsal surfaces of the squids *Ommastrephes pteropus, Symplectoteuthis oualaniensis* and *Dosidicus gigas*. Proc. Malacol. Soc. London **36**: 319 - 321
1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. **4**: 91 - 300; 59 figs.

Férussac, André de & Alcide d'Orbigny
1835-1848. Histoire naturelle générale et particulière des cephalopodes acetabulifères vivants et fossiles. pp. 1 - 361; 144 plts.

Hoyle, William Evans
1904. Reports on the scientific results of the expedition to the eastern tropical Pacific . . . *Albatross*. V. Reports on the Cephalopoda. Bull. Mus. Comp. Zool. Harvard **43** (1): 1 - 71; 10 plts.

McGowan, John Arthur & Takashi Okutani
1968. A new species of enoploteuthid squid, *Abraliopsis* (*Watasenia*) *felis*, from the California current. The Veliger **11** (1): 72 - 79; plts. 9, 10; 1 map (1 July 1968)

Okutani, Takashi & John Arthur McGowan
1969. Systematics, distribution, and abundance of the epiplanktonic squid (Cephalopoda, Decapoda) larvae of the California current April, 1954 - March, 1957. Bull. Scripps Inst. Oceanogr. **14**: 1 - 90; 36 figs.

Pfeffer, Georg J.
1912. Die Cephalopoden der Plankton-Expedition. Zugleich eine monographische Übersicht der oegopsiden Cephalopoden. Ergeb. Plankt.-Exped. Humboldt Stift. **2**: i - xxi + 1 - 815; Atlas 48 plts.

Phillips, Julius B.
1933. Description of a giant squid taken at Monterey with notes on other squid off the California coast. Calif. Fish & Game **19** (2): 128 - 136
1961. Two unusual cephalopods taken near Monterey. Calif. Fish & Game **47** (4): 416 - 417

Robson, Guy Coburn
1948. The Cephalopoda Decapoda of the Arcturus Oceanographic Expedition, 1925. Zoologica **33** (3): 115 - 132

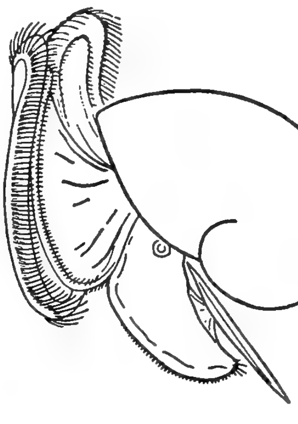
Roper, Clyde F. E.
1968. Preliminary descriptions of two new species of the bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). Proc. Biol. Soc. Wash. **81**: 161 - 172; 7 plts.
1969. Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). Bull. U. S. Nat. Mus. **291**: 1 - 210; 74 figs.

Sasaki, Madoka
1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. Journ. Coll. Agr. Hokkaido Imp. Univ. **20**: 1 - 357; 158 figs.; 30 plts.

Steenstrup, Japetus
1880. *In*: "The cephalopod papers of Japetus Steenstrup", transl. by A. Volsøe, J. Knudsen & W. Rees (1962). Dan. Sci. Press, Copenhagen; pp. 1 - 330; illust.

Voss, Gilbert L.
1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf and Carib. **6** (2): 85 - 178; 18 figs.
1963. Cephalopods of the Philippine Islands. Bull. U. S. Nat. Mus. **234**: 1 - 180; 4 plts.; 36 text figs.

Young, Richard E.
1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contrib. Zool. [in press]



Selective Predation and Prey Location in the Sea Slug *Navanax inermis*

BY

GREG M. BLAIR AND ROGER R. SEAPY

Department of Population and Environmental Biology, University of California, Irvine, Irvine, California 92664

(2 Text figures; 1 Map)

INTRODUCTION

THE SEA SLUG *Navanax inermis* (Cooper, 1862) occurs on low littoral and shallow sublittoral bottoms and is known to be a voracious predator on opisthobranch mollusks (RICKETTS & CALVIN, 1968). The prey preferences of *N. inermis* from a sandy bottom bay and an exposed rocky coastline were studied by PAINE (1965) at San Diego, California. In both environments the most abundant species of opisthobranchs (*Bulla gouldiana* Pilsbry, 1893 in the bay and 3 species of nudibranchs on the rocky coastline) represented the dominant components of *N. inermis*' diet. However, prosobranchs were conspicuously absent from its diet, and PAINE (1963) observed that *N. inermis* would not ingest the prosobranchs *Conus californicus* Hinds, 1844, *Nassarius tegula* (Reeve, 1853), or *Olivella biplicata* (Sowerby, 1825).

On the mud-sand bottom surrounding Balboa Island at Newport Beach, California, *Navanax inermis* is a common and conspicuous macroinvertebrate. In this environment, available gastropod prey include the opisthobranchs *Haminoea virescens* (Sowerby, 1833) and *Phyllaplysia taylori* Dall, 1900, and the prosobranch *Nassarius tegula*. If *N. inermis* selects opisthobranch prey in proportion to their abundance in the environment, *N. inermis* occurring at Balboa Island should preferentially feed on *H. virescens* and *P. taylori*.

Chemoreception is known to exist (KOHN, 1961) in a variety of gastropods. Distance chemoreception has been demonstrated in several nudibranchs (STEHOUWER, 1952; BRAAMS & GEELEN, 1953) and in the neogastropod *Conus* (KOHN, 1959). However, *Navanax inermis* actively tracks and captures its prey by contact chemoreception. Unlike the nudibranch *Dirona albolineata* MacFarland, 1912, which appears to locate prey by direct chemoreceptive contact (ROBILLIARD, 1971), *N. inermis* locates its prey by first recognizing the presence of an acceptable prey mucus trail, and then following that mucus trail to its producer. MARCUS (1961) showed that *N. inermis* has two chemoreceptive areas located on either side of its head and that it characteristically follows the mucus trails of its prey by placing one or both of these areas directly on the mucus trail. It then simply follows the trail, overtakes, and then ingests the prey. This predatory behavior pattern permits the experimental manipulation of predator and prey. For example, PAINE (1963) guided *Bulla gouldiana* (a known prey type of *N. inermis*) in a figure nine pattern, but stopped the animal just before completing the circular portion of the number. When following the trail from the base of the figure nine pattern, *N. inermis* would pass *B. gouldiana* by only 2 cm, but would not deviate from the trail. Instead it followed the figure nine to where the *B. gouldiana* stopped. In the present study, variations on this experimental approach were executed by manipulating various prey types along the prescribed mucus pathways or along pathways comprised of the mucus trails of different prey types. *Navanax inermis* was then placed in the vicinity of each trail and its movements observed and recorded.

MATERIALS AND METHODS

During April to June of 1971 *Navanax inermis* was observed and collected on the eastern shore of Balboa Island, Newport Beach, California (Figure 1) either above or near the low water mark. Specimens were observed on mud bottoms in the proximity of *Zostera marina* Linnaeus, 1753, or occasionally within the eelgrass itself. Individuals used in the food preference study were collected as they were encountered in the field and retained in 1-gallon capacity buckets for an average of 48 hours and allowed to

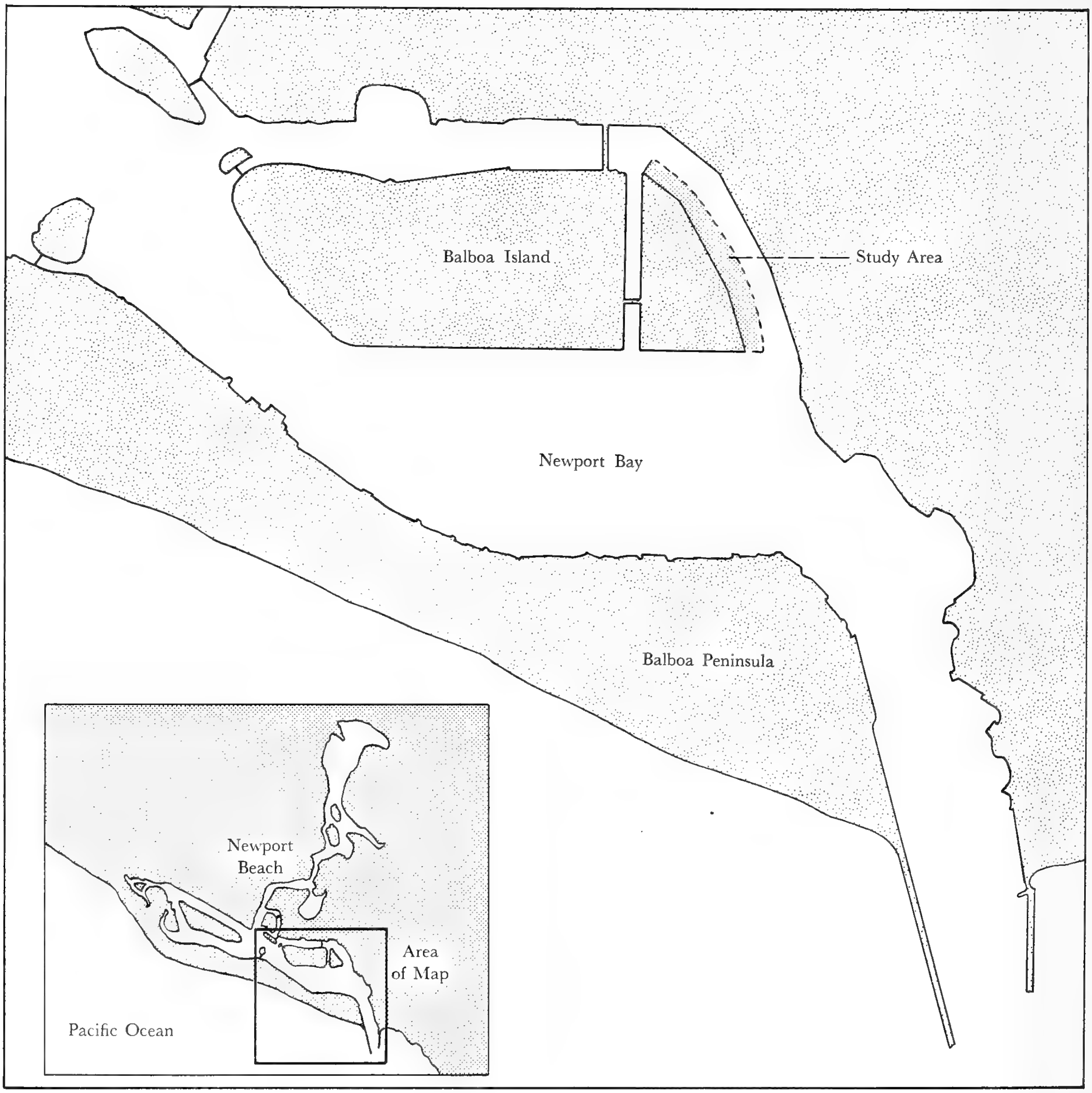


Figure 1

Location of study area on Balboa Island, Newport Beach, California at 33°36′20″ N latitude, 117°53′10″ W longitude

defecate any hard parts. This period of time was quite adequate since in the study by Paine (1965) only 20 to 30 hours were normally required for *N. inermis* to clear its gut. The buckets were kept in a shaded outdoor closet at temperatures that ranged from 18.0 to 20.7° C. The sea water in each bucket was replenished daily.

Two areas of beach were selected to estimate the local abundance of the possible prey types of *Navanax inermis*

Table 1

Gut Content Analyses of *Navanax inermis*

Weight of *N. inermis* (g)	Time of day	Prey defecated	Prey length (mm)
10.5	Afternoon	None	
10.8	Afternoon	None	
11.5	Afternoon	*Haminoea virescens*	5
11.8	Afternoon	*Teinostoma supravallatum*	2
12.0	Morning	*Haminoea virescens*	7, 8
12.3	Morning	None	
19.7	Afternoon	None	
25.3	Afternoon	None	
26.5	Morning	None	
29.3	Afternoon	None	
32.3	Afternoon	None	
33.2	Afternoon	None	
39.8	Afternoon	None	
82.3	Afternoon	*Haminoea virescens*	13, 14, 16
		Crucibulum spinosum	9[1]
		Hermissenda crassicornis	4[2]
90.7	Afternoon	*Hermissenda crassicornis*	3[2]
		unidentified crustacean	8
119.1	Afternoon	*Haminoea virescens*	11, 12, 13, 14 14, 14, 15, 16, 17
125.0	Afternoon	None	
130.2	Afternoon	*Haminoea virescens*	12, 12, 13
		Crucibulum spinosum	9

---

[1] defecated in the living state

[2] length of radula

and their distribution relative to each other. One area contained dense beds of eelgrass (7 m wide) and the other contained relatively sparse patches of eelgrass (12 m wide). The length of each area extended from the high tide level down to a depth at which visibility in the water was minimal – usually about 2 m. Sampling was carried out during one high tide, one intermediate tide, and 3 low tides.

In the study on location of prey, a wading pool 1 m in diameter was placed on the beach at the edge of the tide beneath the shadow of a pier. Sufficient sand was placed inside the pool to cover the bottom and the pool was filled to capacity with sea water. Temperature of the pool water was never more than 3°C warmer than the nearshore surface water temperature that ranged from 19 to 20°C. Various prey types were placed on the sand and guided by means of forceps to fit each distinct experimental design. The nudibranch *Hermissenda crassicornis* (Eschscholtz, 1831) and the tectibranch *Bulla gouldiana* were used in the majority of experiments because they were the most motile and easily guided species of prey. A specimen of *Navanax inermis* was next placed on the sand (taking care to place the animal well away from the trail so that it would encounter the trail "by chance" during its movements within the pool) and its movements observed and recorded. For each experimental arrangement, an average of 7 replications were recorded.

RESULTS

Very few *Navanax inermis* were collected within eelgrass beds. The great majority were found on undisturbed sandy-mud bottoms. The hard parts defecated by *N. inermis* (Table 1) revealed a predominance of *Haminoea virescens* in the diet. *Haminoea virescens* represented 75%

of the total number of prey passed through the guts of those specimens studied; *Hermissenda crassicornis* represented 8%; and *Teinostoma supravallatum* (Carpenter, 1864), *Crucibulum spinosum* (Sowerby, 1824), *N. inermis* and an unidentified crustacean comprised 17%. Particularly noteworthy is the record of no prey hard parts from *N. inermis* between the sizes of 12 and 82g. The length of ingested *H. virescens* ranged from 5 to 17mm. Prey *H. virescens* of less than 8mm were selectively eaten by 11 to 12g *N. inermis,* while *H. virescens* of greater than 11 mm length were eaten only by *N. inermis* of greater than 82g weight.

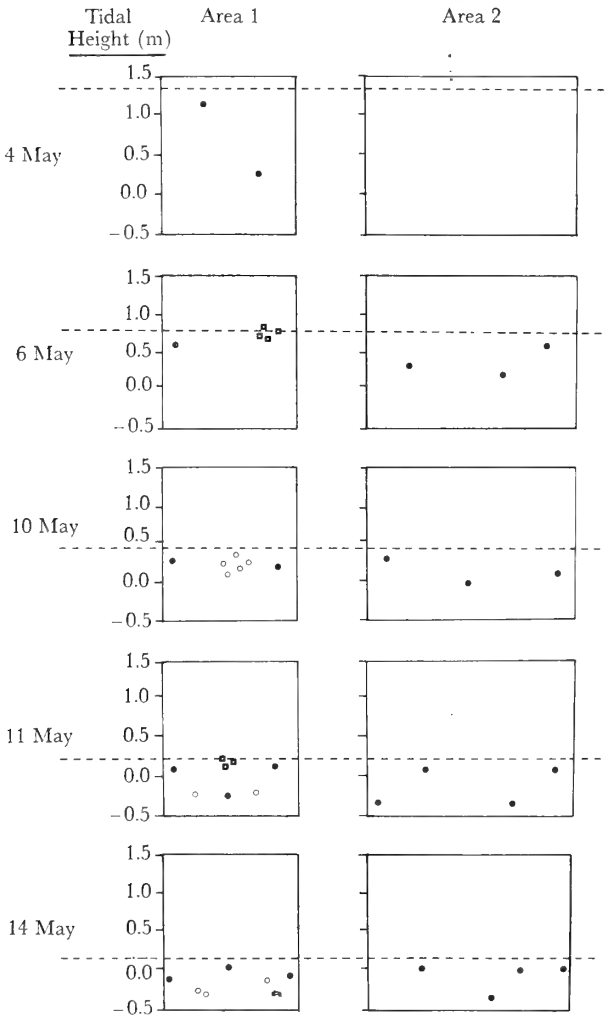


Figure 2

Occurrence of gastropods in sampling areas 1 and 2 at Balboa Island, Newport Bay. For each date the tidal height at the time of observation is indicated by the horizontal dashed line. Observed gastropods in the two areas include *Nassarius tegula* (□), *Phyllaplysia taylori* (○) and *Haminoea virescens* (●)

When all the data on the occurrence of prey in the 2 sampling areas (Figure 2) were added together, *Haminoea virescens* comprised 62%, *Phyllaplysia taylori* 20%, and *Nassarius tegula* 18% of the gastropods collected. The summation of data from Figure 2 was justified on the basis that *Navanax inermis* occurred randomly on sandy-mud bottoms throughout the study area and that the numbers of available *N. inermis* limited to any specific area were too few for the adequate analysis of gut contents.

Because sample sizes were small it was not possible to quantitatively assess population densities or describe the types of dispersion exhibited by each prey species. However, it appeared (Figure 2) that *Nassarius tegula* was strongly aggregated; *Phyllaplysia taylori* was weakly aggregated; and *Haminoea virescens* was uniformly dispersed. Both *N. tegula* and *P. taylori* were conspicuously absent from the 12m area of sparse eelgrass.

During the present study a "searching" posture (with the body fully extended and the head occasionally making small sweeps) was observed consistently for each *Navanax inermis,* whether it had previously contacted a trail or not. When *N. inermis* detected the presence of a trail, the sweeping motion became much reduced, and the animal then followed the trail. The angle at which *N. inermis* made first contact with the mucus trail varied, and did not appear to affect its ability to initiate movement upon the trail. After *N. inermis* made initial contact with the prey, it moved its head from one side of the prey shell or body to the other side and then ingested it directly. Following ingestion of the prey, the *N. inermis* immediately resumed its "searching" posture.

The results of the specific experiments conducted on prey location are summarized in Table 2. *Hermissenda crassicornis* was used (Experiment 1) to describe a circular pathway. *Navanax inermis* made contact with the circular trail and followed it to the site of initial contact, whereupon it veered away. An alpha-shaped trail (Experiment 2) was made with *H. crassicornis*; *N. inermis* entered the trail at its origin and followed the trail to its end. The remaining experiments involved use of straight trails. In the first of these experiments (Experiments 3 and 4), the trail of a known prey type was interrupted and replaced by the trail of a different known prey type. In both experiments *N. inermis* did not veer away at the intersection of the 2 trails. If one known prey type was replaced at the end of its mucus trail by a different known prey type (Experiments 5 and 6), *N. inermis* followed the path and ingested the prey directly. However, when

Table 2

Response of *Navanax inermis* to Gastropod Mucus Trails

Experiment Number	Experimental Design	Results	Number of Replicates
1	A circular mucus trail (30 to 40 cm diameter) made by *Hermissenda crassicornis*	*Navanax inermis* entered, followed the trail and exited at the point at which it first made contact with the trail	6
2	A mucus trail in an alpha (α) configuration (circular part 35 to 45 cm diameter) made by *Hermissenda crassicornis*	*Navanax inermis* entered one arm of the alpha configuration, and followed the trail through to the end, with no hesitancy or deviation at the intersection of the loop	6
3	A straight trail (50 to 60 cm), one-half consisting of mucus from *Bulla gouldiana,* and the other half from *Haminoea virescens*	*Navanax inermis* followed the entire trail without hesitancy at the point where the *Haminoea virescens* trail began	6
4	A straight trail (55 to 65 cm), one-half consisting of mucus from *Bulla gouldiana,* and the other half from *Hermissenda crassicornis*	*Navanax inermis* followed the entire trail without hesitancy at the point where the *Hermissenda crassicornis* trail began	7
5	A straight trail of *Bulla gouldiana* (25 to 40 cm) with *Haminoea virescens* placed at the end of the trail immediately before contact by *Navanax inermis*	*Navanax inermis* followed the trail and, upon completing the trail, immediately ingested the substituted *Haminoea virescens*	7
6	A straight trail of *Hermissenda crassicornis* (35 to 40 cm) with *Haminoea virescens* placed at the end of the trail immediately before contact by *Navanax inermis*	*Navanax inermis* followed the trail and, upon completing the trail, immediately ingested the substituted *Haminoea virescens*	6
7	A straight trail (50 to 60 cm), one-half consisting of mucus from *Hermissenda crassicornis,* and the other half from *Nassarius tegula*	*Navanax inermis* followed the *Hermissenda crassicornis trail* and veered away immediately after contacting the trail of *Nassarius tegula*	7
8	A straight trail of *Hermissenda crassicornis* (30 to 40 cm) with *Nassarius tegula* substituted immediately before contact by *Navanax inermis*	*Navanax inermis* followed the *Hermissenda crassicornis* trail and did not ingest the *Nassarius tegula* at the end of the trail	7
9	A straight trail of *Bulla gouldiana* (30 to 40 cm) with *Nassarius tegula* substituted immediately before contact by *Navanax inermis*	*Navanax inermis* followed the *Bulla gouldiana* trail and did not ingest *Nassarius tegula* at the end of the trail	7

the latter half of this mucus path was replaced with the mucus from the neogastropod *Nassarius tegula* (Experiment 7), *Navanax inermis* lost the trail at the point where it contacted the mucus of *Nassarius tegula.* Furthermore, *Navanax inermis* could not be induced into eating *Nassarius tegula* (Experiments 8 and 9) by placing *Nassarius tegula* at the end of a trail of a known prey type.

DISCUSSION

Haminoea virescens represented 62% of the total gastropod species present in the environment and 74% of the diet of *Navanax inermis.* Although *Phyllaplysia taylori* and *Nassarius tegula* were relatively abundant in the field (20% and 18%, respectively, of the gastropods present), both of these species were absent from the diet of *N. inermis.* The absence of *Nassarius tegula* from the diet is predictive in light of the present experimental evidence on rejection by *N. inermis.* Additionally, the distinctive behavioral characteristics of *P. taylori* and *Nassarius tegula* would reduce the probability of their encounter in the field by *N. inermis. Phyllaplysia taylori* normally occurs (MacGinitie & MacGinitie, 1968) in beds of eelgrass. In the present study only small *N. inermis* were infrequently encountered in eelgrass. Species of *Nassarius* remain burrowed in bay bottoms until stimulated by distant chemoreceptive detection of decaying flesh when they will rise to the surface and aggregate around the dead animal (Kohn, 1961). In the present study, *Nassarius tegula* was periodically observed in small groups of 4 or 5 individuals, either moving across the bay bottom or feeding on decaying fish. Thus, the aggregated distribution of *Nassarius tegula* decreases the probability of encounter in the field by *N. inermis,* whose movements during prey location appear to be random. In contrast to the aggregated distribution of *P. taylori* and *Nassarius tegula, H. virescens* appeared to be uniformly spaced (Figure 2) along the bottom. This spacing greatly enhances the probability of *N. inermis* meeting the mucus trail of an individual *H. virescens.* Thus, in addition to its abundance in the field, an important factor in favoring predation on *H. virescens* could be its optimal accessibility.

In the experiments on prey location, *Navanax inermis* responded positively to a combination of mucus trails from different known prey types. It did not follow the mucus trails of *Olivella biplicata, Conus californicus* (Paine, 1963), or *Nassarius tegula* (as demonstrated in the present study). Indeed, *Navanax inermis* could not be induced to accept *Nassarius tegula* even if the mucus trail of it was preceded by that of an acceptable prey type or when *Nassarius tegula* was placed halfway within the mucus sheath at the end of a mucus trail made by *Haminoea virescens.* When *Nassarius tegula* was replaced by *H. virescens,* the latter was quickly ingested. Thus, not only was *Nassarius tegula* observed to be inaccessible to *Navanax inermis* in the field, it was not an acceptable prey. Whether this reaction represented chemoreceptive rejection or was simply a lack of response by *Navanax* toward the presence of *Nassarius tegula* is an area for future experimentation.

Navanax inermis did not exhibit any hesitancy in movement when following trails comprised of 2 different known prey types. Apparently, *N. inermis* will follow the mucus trail of opisthobranch prey without regard to the particular species involved in the interaction. If encountering overlapping trails from 2 known prey types in the field, this characteristic would confer the adaptive advantage on *N. inermis* of continuing to follow one mucus path rather than hesitating and possibly losing track of both trails.

The ability to utilize contact chemoreception in prey location makes *Navanax inermis* a highly efficient predator. The evolution of this chemoreceptive mechanism has resulted in the reduction of energy required for prey capture. The ability to differentiate acceptable opisthobranch prey from unacceptable prosobranch prey further reduces energy losses during prey location.

CONCLUSIONS

The carnivorous sea slug *Navanax inermis* exhibits distinctive prey selectivity and a unique mechanism for prey location. The diet of *N. inermis* occurring on sandy-mud bottoms is different from that previously reported from a sand-bottom bay and exposed rocky coastline. On sandy-mud bottoms *Haminoea virescens* is the most accessible prey type occurring in the environment as well as the most abundant prey type in the diet of *N. inermis.* Two potential species of prey (*Nassarius tegula* and *Phyllaplysia taylori*) were abundant in the field but were not accessible to *N. inermis* and were absent from its diet.

Navanax inermis utilizes contact chemoreception to locate and follow the mucus trails of its opisthobranch prey. In the field, mucus trails were made over sand by carefully guiding various gastropod prey through predetermined pathways. In every case when a prey type was used that was known to be a preferred prey species, *N. inermis* would follow the mucus trail, overtake, and ingest the prey. By replacing one prey type with another halfway through the trail, various combinations of mucus trails were obtained. *Navanax inermis* continued to follow a trail comprised of 2 different known prey types, but would not follow the last half of a trail if it was made by a gastropod other than a known prey type. The utilization of contact chemoreception in the location of acceptable prey is an important mechanism of energy conservation.

Literature Cited

Braams, W. G. & Hannie F. M. Geelen
1953. The preference of some nudibranchs for certain coelenterates. Arch. néerl. Zool. **10** (3): 241 - 262

Kohn, Alan Jacobs
1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. **29:** 47 - 90
1961. Chemoreception in gastropod molluscs. Amer. Zool. **1:** 291 to 308

MacGinitie, George Eber & Nettie MacGinitie
1949. Natural history of marine animals. McGraw-Hill Book Co., New York, N. Y. xii+473 pp.; 286 text figs.

Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger **3** (Supplmt. I): 1 - 85; plts. 1 - 10 (1 February 1961)

Paine, Robert Treat
1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). The Veliger **6** (1): 1 - 9; 1 plt.; 1 text fig. (1 July 1963)
1965. Natural history, limiting factors, and energetics of the opisthobranch *Navanax inermis.* Ecology **46** (5): 603 - 619; 9 text figs.

Ricketts, Edward F. & Jack Calvin
1968. Between Pacific tides. Stanford Univ. Press, Stanford, Calif. v - xiii + 3 - 502; 46 plts.

Robilliard, Gordon A.
1971. Predation by the nudibranch *Dirona albolineata* on three species of prosobranchs. Pacif. Sci. **25** (3): 429 - 435

Stehouwer, H.
1952. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.) Arch. néerl. Zool. **10:** 161 - 170

Notes on Two Endemic South African *Cypraea*

BY

R. N. KILBURN AND D. W. AIKEN

Natal Museum, Pietermaritzburg, and P. O. Box 13035, Knights, South Africa

(1 Text figure)

THE INFREQUENCY with which endemic South African *Cypraea* (subgenera *Cypraeovula, Luponia* and *Bernaya*) are collected alive has resulted in our knowledge of their dentition and anatomy being sadly deficient. The radulae of *C. fultoni* Sowerby, 1903 and *C. capensis* Gray, 1828 are here described, together with notes on relationships and distribution, and observations on the anatomy of the second species.

Cypraea (Bernaya) fultoni Sowerby, 1903

(Text figure 1 A)

A portion of the radula of this species was found by the second author amongst the completely decomposed contents of a shell taken from the stomach of a fish caught in Natal, and kindly made available by Mrs. E. Visagé of Johannesburg.

The radula pattern is that of the group R1 of KAY (1960: 280), although far from typical. The rachidian, which is higher than wide, has a dumbbell-shaped internal bract, but neither a subtending bract nor basal denticles; the base is flat, with rounded corners. The laterals are similarly higher than wide, and are interesting in that they possess a pair of denticles on either side of the mesocone, instead of the normal single denticle; further examples are required to show whether this feature is usual for the species.

The only similar type of dentition that can be traced occurs in the Western Australian *Cypraea rosselli* (Cotton, 1948) (*cf.* WILSON & MCCOMB, 1967: plt. 334 E), which is presumably consubgeneric. Unfortunately nothing is known of mantle texture or the structure of the female genitalia in *C. fultoni.*

Distribution: While most specimens of *Cypraea fultoni* in collections are merely labelled "off Natal," the locality "off Durban" is not infrequently seen. It should be realised, however, that this port merely serves as the base of operations for most commercial fishing vessels in Natal, and hence as the point of sale for these and other readily marketable shells. The only reliable data available to the authors indicate the chief habitat of *C. fultoni* to be in the region of Aliwal Shoal, just south of Umkomaas (ca. 30°15'S). The map given by BURGESS (1970: 57) is highly misleading.

Cypraea (Cypraeovula) capensis Gray, 1828

(Text figure 1 B)

Recently two living examples of this species were collected by Mrs. P. W. Faulkner at Gonubie, near East London (28°01'E), and kindly forwarded in a preserved state to the first author, together with relevant field notes. Although the bodies could only be extracted piecemeal, the more important taxonomic characters were traceable. *Cypraea capensis* is the type species of the subgenus *Cypraeovula* Gray, 1824.

Both specimens were sexually mature females with bright orange ovaries containing ripe ova. A simple thin-walled bursa copulatrix and an apparently glandular receptaculum seminis were present. The mantle (in preservative) was thin, smooth and narrow, the siphonal margin apparently smooth. In life (pers. comm. Mrs. Faulkner) the mantle was not observed to be ever expanded over the shell; in colour it was brownish, with dark dots and faint white lines; the foot and tentacles were bright orange-yellow.

The radula of this species was figured by SCHILDER (1932: fig. 12), the present material agreeing in all features save for details of the shape of the cusps; the dentition type is that of Kay's category R1.

Unfortunately the radula cannot be interpreted taxonomically in view of the lack of information on the dentition of related species. Not unexpectedly there is a certain resemblance to BARNARD's figure (1963: 5c) of

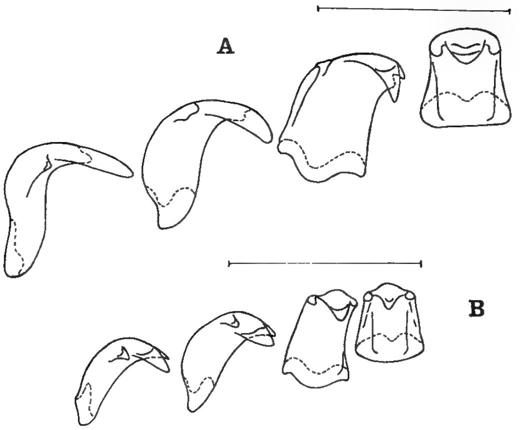


Figure 1

Radulae of
(A) *Cypraea fultoni* Sowerby and (B) *Cypraea capensis* Gray

Line represents 0.5 mm

the radula of the species recorded by him as a globose form of *Cypraea fuscorubra* Shaw, 1909 (although internal bracts were not indicated by him). Whatever the true identity of his material, it does seem to represent the subgenus *Luponia* Gray, 1832, which must be regarded as a synonym of *Cypraeovula, Cypraea (Cypraeovula) amphithales* Melvill, 1888 being completely intermediate in shell characters between the two groups.

Cypraea capensis clearly does not fit into either of KAY's anatomical categories (*op. cit.*: 285), combining an R1-type dentition with female genitalia of the *tigris*-type. It is interesting to note that WILSON & McCOMB (1967: 466) found a similar combination to occur in the subgenus *Zoila* Jousseaume, 1884. While *Cypraeovula* was referred, as a full genus, to the subfamily Cypraeovulinae by SCHILDER (1936: 84), *Zoila* was allocated first to the Cypraeinae, then (SCHILDER, 1965: 176) to the Cypraeorbinae.

For future statistical purposes we give the following quantitative data derived from the shells of the two female *Cypraea capensis* recorded above.

Specimen A:
Dimensions 29.7 × 17.6 mm; columellar teeth 41, labral[1] teeth 25
Specimen B:
Dimensions 29.3 × 18.3 mm; columellar teeth 44, labral teeth 26

These specimens were collected from under rocks in low tide pools and must be regarded as strays from the infratidal region.

The distribution data given by BURGESS (1970: 322) are almost completely erroneous. *Cypraea capensis* reaches its western limit at Jeffreys Bay (24°55′E), where even beach-worn shells are very rare. It is moderately common in the Port Alfred (26°54′E), to Kei River mouth (28°23′E) area, but becomes scarcer in Transkei waters, and appears to attain its eastern limit at Port St. Johns (29°32′E).

Literature Cited

BARNARD, KEPPEL HARCOURT
1963. Contributions to the knowledge of South African marine Mollusca. Part III. Gastropoda. Prosobranchiata. Taenioglossa. Ann. So. African Mus. **47** (1): 1 - 199; 37 text figs.
BURGESS, C. M.
1970. The living cowries. A. S. Barnes & Co., Cranbury, N. J. pp. 1 - 389; plts. 1 - 44
COX, LESLIE REGINALD
1960. General characteristics of Gastropoda. *In* R. C. MOORE (ed.) Treatise on invertebrate palaeontology, prt. I, **1**: 84 - 169; figs. 51 - 88E
KAY, ELIZABETH ALISON
1960. Generic revision of the Cypraeinae. Proc. Malacol. Soc. London **33** (6): 278 - 287; 8 text figs.; 1 table
ONIONS, C. T. (ed.)
1967. The shorter Oxford English dictionary. Third Edition; Clarendon Press, Oxford
SCHILDER, FRANZ ALFRED
1932. Beiträge zur Kenntnis der Cypraeacea. No. 16. Die Radula einiger bisher nur als Schalen bekannter Arten. Zool. Anz. **100** (7-8): 166 - 170
1936. Anatomical characters of the Cypraeacea which confirm the conchological classification. Proc. Malacol. Soc. London **22** (2): 75 - 112; 2 plts.
1965. The geographical distribution of cowries. The Veliger **7** (3): 171 - 183; figs. 1 - 3 (1 January 1965)
WILSON, BARRY R. & JENNIFER A. McCOMB
1968. The genus *Cypraea* (subgenus *Zoila* Jousseaume). Indo-Pacific Mollusca **1** (8): 457 - 484

---

[1] The adjective "labial," conventionally used to indicate the outer lip in cypraeid literature, is derived from the noun *labium*, which in reality refers to the inner lip (*cf.* COX, 1960: 131; ONIONS, 1967: 1095), *i. e.* in the present context "labial" would be synonymous with "columellar"!

Comments on the Authorship of Some Subfamilial Names in the Turridae

(Mollusca : Gastropoda)

BY

WALTER OLIVER CERNOHORSKY

Auckland Institute and Museum, Private Bag, Auckland, C. 1, New Zealand

THE MOST RECENT SUBFAMILIAL arrangement of the toxoglossan family Turridae is the one proposed by POWELL (1966). His arrangement has been extended and modified by McLEAN (1971). Both workers, however, overlooked chronological priorities for family-group names, and the existence of prior names and authorships requires changes.

CASEY'S (1904) proposal of new taxa of the rank of tribe must be given due consideration in a subfamilial classification since the categories of families and tribes are co-ordinate under the rules of article 36 of the Code of ICZN.

Cochlespirinae Powell, 1942

The subfamilial taxon Turriculinae Powell, 1942, cannot be maintained in turrid nomenclature for the group containing the genera *Turricula* Schumacher, 1817, and *Cochlespira* Conrad, 1865. Although not in use in Mitridae because of primary homonymy of the type genus, Turriculidae Carpenter, 1861, and Turriculinae A. Adams, 1864, based on the mitrid genus *Turricula* Fabricius, 1823, nevertheless preoccupy Turriculinae Powell, 1942. The subfamilial taxon Pseudotominae Bellardi, 1875 (and of Hoernes & Auinger, 1891, and Casey, 1904) cannot be utilized as a substitute because of primary homonymy of the type genus *Pseudotoma* Bellardi, 1875 (*non* Gray, 1825).

Turrinae Swainson, 1840

McLEAN (*op. cit.*) correctly credited the authorship of the taxon to Swainson and not to Powell. Synonyms are Pleurotominae Swainson, 1840, Taraninae Casey, 1904 (*ex* Taranini) and Lophiotominae Morrison, 1966.

Clavinae Casey, 1904

In the two recent arrangements of the family, the subfamilial taxon Clavinae has been credited to Powell, 1942, but CASEY, 1904 (*ex* Clavini) must be acknowledged as the author. Synonyms are Brachytominae Thiele, 1929, with its type genus *Brachytoma* Swainson, 1840, virtually a *nomen inquirendum,* Drilliinae Morrison, 1966 and Crassispirinae Morrison, 1966. The latter subfamily has been separated from the Clavinae by McLEAN (*op. cit.*).

Conorbiinae Pilgrim *in* Vredenburg, 1925

Usually cited as of Powell, 1942, the family-group name already appears as Conorbidae in VREDENBURG'S (1925) paper on the post-Eocene molluscs of India on page viii. In the preface to this work, G. E. Pilgrim is credited with the groupings of families in the table of contents after the untimely death of E. Vredenburg. Cryptoconinae Wenz, 1938, used by NORDSIECK (1968), is a synonym of Conorbiinae.

Daphnellinae Casey, 1904

The authorship of Daphnellinae has been credited to Hedley, 1922, by POWELL (*op. cit.*) and McLEAN (*op. cit.*), but the taxon has been established previously by Casey, 1904 (*ex* Daphnellini). The prior Raphitominae Bellardi, 1875, must be considered in case that *Raphitoma* Bellardi, 1848, is assigned to the same group as *Daphnella* Hinds, 1844. Curiously enough, Raphitominae has been proposed as a new subfamily by NORDSIECK (*op. cit.*), despite a prior usage by previous authors (*e. g.* Hoernes & Auinger, 1891; Powell, 1966). Pleurotomellinae Nordsieck, 1968, is a synonym of Daphnellinae Casey, 1904.

Clavatulinae H. & A. Adams, 1853

The erection of the subfamilial name Clavatulinae dates from 1853 and not from 1858 as generally quoted. Pusionellinae H. & A. Adams, 1853, and Clionellidae Stimpson, 1865, are synonyms.

Mitromorphinae Casey, 1904

Three subfamily names are available for the group of turrids centering around the *Mitromorpha-Mitrolumna* complex of species. Diptychomitrinae Bellardi, 1888, based on the type genus *Diptychomitra* Bellardi, 1888, a synonym of *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883, is the oldest available name, despite the synonymy of the type genus. The next available name is Mitromorphinae Casey, 1904 (*ex* Mitromorphini), published 19 May 1904, which has chronological priority over Mitrolumnidae Sacco, 1904, dating from August of that year. The group under discussion has been previously referred to as the "group of mitromorphid genera" and assigned to the Borsoniinae by Powell (1966), or as the "mitromorphine group of Turridae" (Cernohorsky, 1970). McLean (*op. cit.*) acknowledged the group as a distinct subfamily, but accepted the later Mitrolumninae Sacco, 1904.

The recent emendation of article 23(b) of the Code of ICZN by the International Commission on Zoological Nomenclature (1970) poses a minor taxonomic problem as far as the usage of at least 2 of the names is concerned. Synonymy of the type genus *Diptychomitra* does not invalidate the family-group name Diptychomitrinae, notwithstanding the fact that *Diptychomitra* Bellardi has not been used as a genus-group. Not one of the three subfamily names qualifies as having been in "general use" in the last 50 years, and a petition to the Commission for the acceptance of Mitromorphinae Casey, 1904, in precedence over Diptychomitrinae Bellardi, 1888, may be necessary for the stability of nomenclature.

Clathurellinae H. & A. Adams, 1858

McLean (1971) proposed the new subfamily name Clathurellinae, in which case he has been anticipated by H. & A. Adams, 1858, who proposed the taxon as a substitute name for Defranciinae H. & A. Adams, 1853. The latter subfamily is an invalid family-group name based on the homonymous type genus *Defrancia* Millet, 1826 (*non* Bronn, 1825). Powell (*op. cit.*) retained *Clathurella* Carpenter, 1857, and associated genera in the Mangeliinae.

Mangeliinae Fischer, 1883

Authors cite the subfamily name Mangeliinae as from Fischer, 1887, but the taxon was established by Fischer in fasc. 6 (p. 587) of his "Manuel de Conchyliologie," which dates from 20 December 1883. Mangeliinae has also been used by Tryon in 1884. Belinae Hoernes & Auinger, 1891 (credited to Bellardi) and Cytharinae Thiele, 1929, are synonyms. *Cythara* Schumacher, 1817, the type genus of Cytharinae, remains a dubious taxon.

Literature Cited

ADAMS, HENRY & ARTHUR ADAMS
1858. The genera of Recent Mollusca; arranged according to their organization. J. van Voorst, London, 2: 654 (November 1858)

BELLARDI, LUIGI
1888. I molluschi dei terreni terziarii del Piemonte e della Liguria. Mem. Real. Accad. Sci. Torino 39: 152 (20 September 1888)

CASEY, THOMAS L.
1904. Notes on the Pleurotomidae with descriptions of some new genera and species. Trans. Acad. Sci. St. Louis 14 (5): 123 - 170 (19 May 1904)

CERNOHORSKY, WALTER OLIVER
1970. Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). Bull. Auckl. Inst. & Mus. No. 8: 1 - 190; plts. 1 - 18; 222 text figs. (1 October 1970)

FISCHER, PAUL
1883. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles. F. Savy, Paris, fasc. 6: 513 - 608 (20 December 1883)

HOERNES, RUDOLF & M. AUINGER
1891. Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der österreichisch-ungarischen Monarchie. Abhandl. k. k. geol. Reichsanst. 12 (7): 283 - 330; plts. 37 - 42

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE
1970. Declaration 43. Repeal of article 23(b). Bull. zool. Nomenclature 27 (3/4): 135 - 163 (December 1970)

MCLEAN, JAMES HAMILTON
1971. A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the Eastern Pacific. The Veliger 14 (1): 114 - 130; 4 plts. (1 July 1971)

MORRISON, JOSEPH PAUL ELDRED
1966. On the families of Turridae. Ann. Reprts. Amer. Malac. Union for 1965: 1 - 2

NORDSIECK, FRITZ
1968. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia) vom Eismeer bis Kapverden und Mittelmeer. Gustav Fischer Verlag, Stuttgart, pp. i - xiii + 1 - 273; plts. 1 - 31

POWELL, ARTHUR WILLIAM BADEN
1942. The New Zealand Recent and fossil Mollusca of the family Turridae with general notes on turrid nomenclature and systematics. Bull. Auckl. Inst. & Mus. No. 2: 1 - 188; plts. 1 - 14 (15 July 1942)
1966. The molluscan families Speightiidae and Turridae. An evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. Bull. Auckl. Inst. & Mus. No. 5: 1 - 184; plts. 1 - 23; text figs. (1 November 1966)

SACCO, FREDERICO
1904. I molluschi dei terreni terziarii del Piemonte e della Liguria. Carlo Clausen, Torino, prt. 30: 1 - 203 + i - xxxvi; plts. 1 - 31 (August 1904)

TRYON, GEORGE WASHINGTON, JR.
1884. Manual of conchology; structural and systematic. Pleurotomidae. Philadelphia, 6: 151 - 413; plts. 14 - 34

VREDENBURG, E.
1925. Descriptions of Mollusca from the post-Eocene Tertiary formation of North-Western India: Cephalopoda, Opisthobranchiata, Siphonostomata. Mem. Geol. Surv. India 50 (1): i - xii + 1 - 350; Index pp. i - xvi; plts. 1 - 13 (13 July 1925)

The Rôle of Wave Impact and Desiccation on the Distribution of *Littorina sitkana* Philippi, 1845

BY

SYLVIA BEHRENS

Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada[1]

(1 Text figure)

INTRODUCTION

Two species of periwinkles, *Littorina scutulata* Gould, 1849, and *L. sitkana* Philippi, 1845, coexist on most beaches near the city of Vancouver, in the Gulf Islands and on the west coast of Vancouver Island, British Columbia. *Littorina sitkana,* unlike *L. scutulata,* is absent from dry beaches and from wave exposed sites lacking shelter, but thrives in wave-sheltered and damp habitats such as mud flats, tide pools and crevices (Behrens, 1971).

Littorina scutulata has a planktonic dispersal stage, whereas *L. sitkana* develops directly from benthic egg masses (Behrens, *op. cit.*). Thus, the maintenance of *L. scutulata* populations in any one place is dependent upon constant planktonic recruitment whereas the persistence of *L. sitkana* populations is dependent upon the survival of all developmental stages in the life cycle. Results from this study indicate that the physical factors such as desiccation acting on juveniles and wave impact affecting adults can select against *L. sitkana* and exclude this species from some beaches.

THE RÔLE OF WAVE IMPACT ON THE DISTRIBUTION OF *Littorina sitkana*

Extremely small *Littorina scutulata* are found on wave-swept and crevice-less beaches such as Chesterman's Island on the west coast of Vancouver Island. To investigate the action of intense surf as a possible factor acting selectively against *L. sitkana* as well as against large animals of both species, series of laboratory and field tests were performed.

METHODS

An equal number of animals of both species, or of a single species, but of two size classes, were painted with cellulose-base paint. When species comparisons were made, *Littorina scutulata* and *L. sitkana* were matched for size. The animals were then dipped in sea water and allowed to attach to the rock or barnacle substratum of the beach and were then subjected to wave action of the incoming tide. After a trial period ranging from 6 hours to 2 days, the test site and adjacent areas were carefully searched. All missing animals were assumed to have been dislodged by waves. Laboratory experiments using concrete slabs as substrata and a running sea water jet to simulate wave force were performed to check field results.

RESULTS AND DISCUSSION

Both field and laboratory data indicate that *Littorina scutulata* are less likely to be dislodged by waves than are *L. sitkana* (Table 1). *Littorina sitkana,* with its round shape and many grooves, may offer more resistance to wave action than the more streamlined *L. scutulata.*

Large *Littorina sitkana* were more easily dislodged by wave impact than smaller ones (Table 1). Large *L. scutulata* appeared as resistant to wave force as smaller ones (Table 1). Thus, young (or small) *L. sitkana* could presumably live on exposed beaches; however, wave action would select against them as they attained reproductive size (ca. 5 mm).

---

[1] Present address: Department of Biology, University of Oregon, Eugene, Oregon 97403

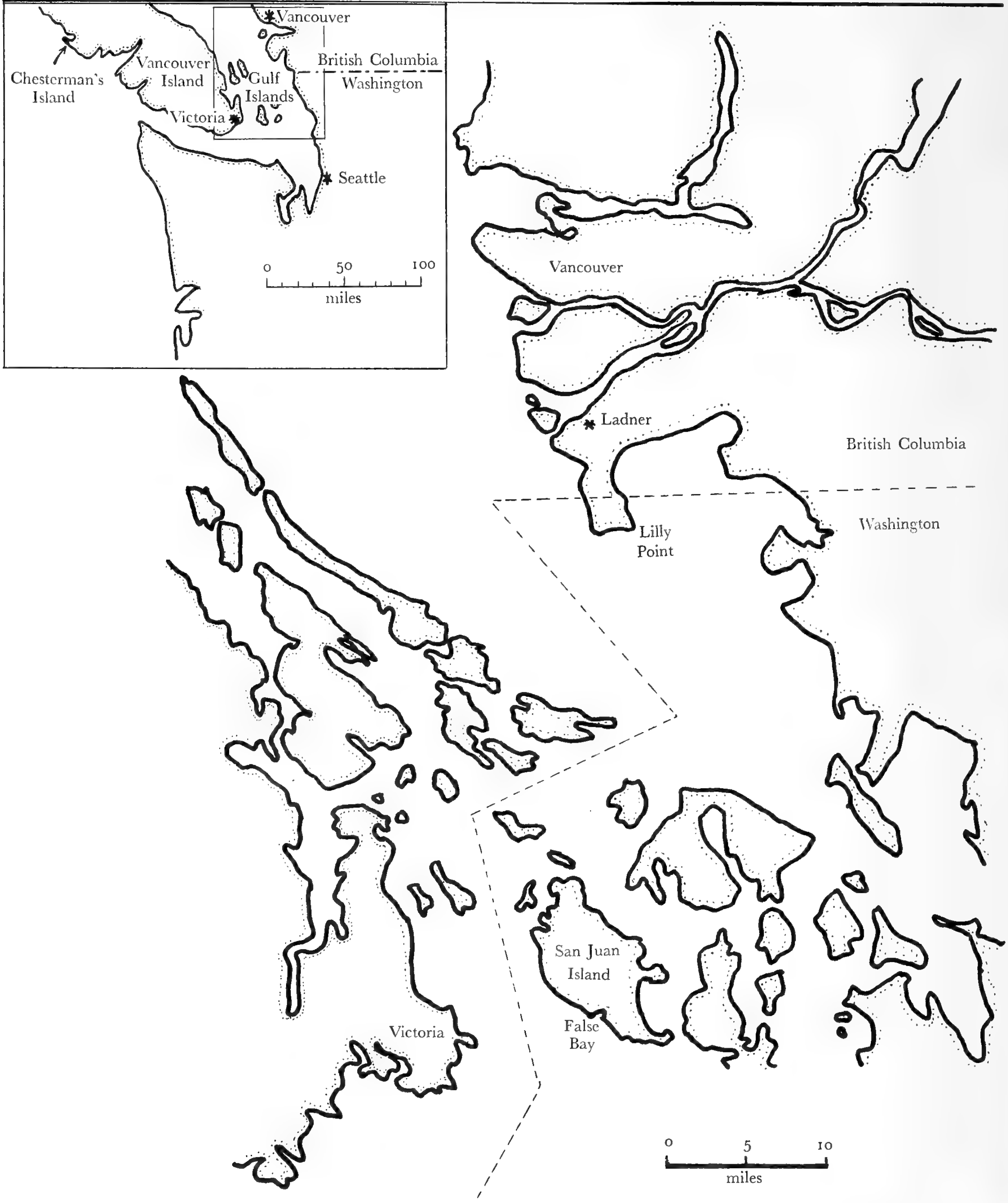


Figure 1

Map of Puget Sound and Vicinity showing locations of study areas

Table 1

Ability of *Littorina sitkana* and *Littorina scutulata* to resist wave exposure in the field and in the laboratory

Source of data	Proportions of animals remaining on substrate after test interval		Difference between comparisons Chi squared	
	L. sitkana	*L. scutulata*		
Field pooled data from 8 runs	254/487	366/487	55.657	***
Laboratory pooled data from 3 runs	3/54	19/54	12.842 (Y)	***
	small *L. scutulata*	large *L. scutulata*		
Field	35/50	34/50	N. S.	
	small *L. sitkana*	large *L. sitkana*		
Field	34/50	19/50	9.0325	**
Laboratory pooled data from 6 runs	37/121	15/126	12.947	***

(Y) – Yates correction for small cell frequencies was used numbers of * indicate level of significance when the null hypothesis of no difference between values has been rejected. * = α 0.05; ** = α 0.01; *** = α 0.001; n. s. indicates no significant difference

DESICCATION OF JUVENILE STAGES AS A POSSIBLE FACTOR RESTRICTING THE DISTRIBUTION OF *Littorina sitkana*

Survival of juvenile *Littorina sitkana* in a location inhabited naturally by *L. scutulata* only was investigated at Lilly Point (Figure 1). The rocky foreshore in this area is characterised by barnacle-covered cobble and rocks, not larger than 15 cm in diameter, resting on a sandy bottom. The low intertidal area is mostly sand interspersed with 4 barnacle covered concrete blocks (50 × 50 × 50 cm). I worked on the site of an abandoned fish cannery where an artificial substratum, consisting of compressed tin can scraps and cobble, is completely covered with barnacles and extends from the mid to the high intertidal region. Numerous barnacle-covered pilings (the remains of the cannery's pier) run in rows from the mid to high intertidal area. Absence of shade, as well as good drainage, tend to make the Lilly Point site a dry beach at low tides in sunny weather. Animals cannot find shelter under the cobble and rocks, for these are embedded in coarse sand.

To determine the critical factor in the life history which could prevent *Littorina sitkana* from living at Lilly Point, adults, egg masses and newly hatched snails were transplanted to the area.

MATERIALS AND METHODS

To determine whether adult *Littorina sitkana* could live at Lilly Point, 500 young *L. sitkana* (not more than 5 mm in length) were released on the "compressed tin can rock" and on one piling stump in May of 1969.

Eight "cages" were prepared by pulling a square of fine plankton netting over the concave half of little neck clam shells. Four of the cages contained 10 newly hatched snails each and 4 cages contained 5 older snails (1 mm or longer). One of each type of cage was set up in the following locations: on pilings at the 13 foot tidal level, in artificial tide pools (32 ounce orange juice jars) at the 13 foot tidal level, on pilings at the 9 foot level, and in artificial tide pools at the 9 foot tidal level. The "tide pools" and cages were attached to the piling stumps using rubber bands cut from an inner tube. The number of surviving animals, salinity, and temperature of the tide pools and air were recorded the next day (Table 2).

Egg masses collected from False Bay, San Juan Island (Figure 1) were divided into two parts. Each half was

Table 2

Survival of two size classes of juvenile *Littorina sitkana* caged at the 9 foot and 13 foot tidal levels at Lilly Point from May 17 to May 18, 1969

Position of cages	Salinity of pools	Temperature	Recovery of *Littorina sitkana*
medium tidal level (9 ft) pool	30‰	27° C water	7 small (newly hatched) snails all with their foot moving. Cage with larger (1.0 mm or longer) snails was lost
medium tidal level (9 ft) dry		20° C air	9 small snails, all alive, 5 large snails, all but one opened operculum when moistened
high tidal level (13 ft) pool	25‰	27° C water	8 small snails, all alive; 5 large snails, all alive
high tidal level (13 ft) dry		20° C air	9 small snails, all dead; 4 large snails, 3 alive, 1 with broken shell

placed into a plastic petri dish lid and fine plankton netting was wrapped around the dishes. These "cages" were attached to the pilings at the high tide levels and to concrete blocks at the low tide levels, so that half of each egg mass was represented at each tidal level. The number of hours of exposure to direct mid-day sunshine at the 5 and 12 foot tide level was estimated from weather data (for Ladner, British Columbia, compiled by Mrs. M. A. Behrens) and a tide table. The condition of the egg masses and the number of hatched snails were recorded subsequently (Table 3).

Table 3

Hatching success of *Littorina sitkana* egg masses at Lilly Point

Five egg masses of *Littorina sitkana* were divided in two. One half of each egg mass was attached to pilings at the high tide level and the other half to concrete blocks at the low tide level at Lilly Point

Initial color of egg mass	Tidal height of cage	Number of hatched *Littorina sitkana* September 1	September 7
pink	5 ft	not sampled	50 alive *
	11 ft	red egg mass	0 alive
light pink	5 ft	not sampled	7 alive *
	13 ft	yellow and dry	0 alive
dark pink	6 ft	25 hatched	32 alive
	13 ft	red and dry	0 alive
light pink	6 ft	red egg mass	47 alive
	13 ft	2 hatched	0 alive
light pink	9 ft	lost	
	13 ft	covered with sediment	covered with silt

* indicates puncture in cage

RESULTS

After one year, 6 of the 500 *Littorina sitkana* were recovered on the tin can rock. All the animals had grown to roughly 10 mm in length. The rest of the animals had either died or dispersed from the investigated area. One yellow egg mass located on the wave- and sun-sheltered side of a piling stump was found in May 1970. The egg mass, however, dried up before the embryos could hatch.

All the young *Littorina sitkana* caged for 26 hours at the mid-tidal level survived and those retained inside the high tide pools survived (Table 2). However, all the small snails (less than 1.0 mm) caged to the high piling stump were dead. The cages and pool at the high tide level (13 foot) were calculated to be exposed to approximately 11 hours of direct sunshine, those at the mid-tide level (9 foot) for about 6 hours during the duration of the experiment. It would seem that desiccation and not the high temperatures *per se* killed the small snails at the high tide level, since the temperature in the high pool was 7° C higher than the air temperature at the time of measurement (Table 2).

From weather and tide data during the period August 23 to September 1, the 5 foot tide level was estimated to be exposed to a total of 6 hours of direct mid-day sun and the 12 foot level to at least 30 hours. A total of 161 young *Littorina sitkana* hatched at the 5 foot level as opposed to only 2 at the 11 foot level. All the egg masses at the high level had dried out by September 7 (Table 3). This correlation suggests that desiccation was responsible for egg mass mortality at the high tide level but not at the lower.

CONCLUSIONS

The fact that the transplanted *Littorina sitkana* survived at Lilly Point for a year, grew and even reproduced, indicates that no major selective factor was operating during this period of time to prevent adult *L. sitkana* from living at Lilly Point.

Desiccation, acting on egg masses and newly hatched individuals may be a critical factor preventing *Littorina sitkana* from living at Lilly Point and other dry beaches. It is conceivable that a permanent population of *L. sitkana* could be established at Lilly Point if tide pools or damp crevices were added. Egg masses hatched at low tide levels, but the abrasive action of shifting sand and silt, especially during storms, seems to prevent any grazers from living there permanently.

ACKNOWLEDGMENTS

This study forms part of a Master's thesis done at the University of British Columbia. I would like to thank my advisor Dr. Robin Harger, and Dr. John Stimpson for their encouragement and criticism.

This research was financed by the National Research Council of Canada Grant No. 67660 to Dr. J. R. E. Harger.

Literature Cited

Behrens, Sylvia
1971. The distribution and abundance of the intertidal prosobranchs *Littorina scutulata* and *Littorina sitkana*. MSc. thesis. Zool. Dept., Univ. British Columbia

Seasonal Migration and Population Regulation in the Limpet *Acmaea (Collisella) digitalis*

BY

PAUL A. BREEN

Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada [1]

(7 Text figures)

INTRODUCTION

THE LIMPET SPECIES *Acmaea digitalis* Rathke, 1833 occupies a broad band within the intertidal zone, from near mid-tide almost to high tide level in the study area described below. Within this band are many different types of microhabitat, and superimposed are seasonal changes in physical and biotic conditions in the intertidal zone. The stresses placed on a species living in such a mosaic result in many adaptations that can be studied relatively easily.

FRANK (1965), in an extensive study of a population of *Acmaea digitalis* in Oregon, found that behavioural adaptations are responsible for determining the vertical range and the size distribution at a given place within the range. He found that small limpets settle at the lower end of the shore and migrate upward in successive years, so that larger individuals tend to be found on the higher parts of the range. This has also been observed in a species of *Patella* in Britain (LEWIS, 1954). FRANK also found that local density of limpets appeared to be regulated by dispersing behaviour.

The object of this study, carried out in British Columbia in 1969 and 1970, was to examine further the relation between behaviour and population regulation. Two behaviour patterns were studied: homing and seasonal migration. Homing behaviour has been discussed in a previous paper (BREEN, 1971); this paper deals with seasonal migration.

Many of the experiments and results described below confirm experiments carried out by FRANK (1965). This paper is perhaps justified, however, in consideration of Frank's statement "what does a limited though extensive set of observations and measurements, gathered over a relatively short time span and in a small portion of the species' range, signify regarding the performance of this and similar sorts of animals over their total area of distribution? These limitations ... clearly imply that independent confirmation of significant conclusions is particularly important."

ECOLOGY OF *Acmaea digitalis*

PHYSICAL FACTORS

This study was carried out on a rocky shore near Port Renfrew, British Columbia, known locally as Botanical Beach in reference to the Seaside Station maintained there by the University of Minnesota from 1900 to 1910. Botanical Beach consists of a broad sandstone shelf, intruded by hard metamorphic rock, which is up to 100 m wide at low tide. The shelf has been eroded into a complex array of pools, benches, and prominences. (HALL, 1906, gives a more complete geological description.)

Although the beach borders the Strait of Juan de Fuca, it is directly exposed to Pacific storms and wave action coming from the west and northwest, and is an exposed shore. Tides are mixed semi-diurnal, with a range of from 6.1 to 12.6 feet (1.8 to 3.8 m).

Tides, sea conditions and weather combine to produce a drastic contrast in shore conditions between winter and summer. In summer, lower low tide occurs between dawn and noon during most of the lunar cycle, and lower high tide in the afternoon. Summer weather usually includes long periods of hot, dry weather, so the shore is exposed to drying conditions during most of the day. The sea remains relatively calm. In winter, lower low tide occurs between dusk and midnight, while higher high tide occurs during the day, so the shore is covered during most of the daylight hours. Winter weather is cool and wet, with almost constant rainfall and fogs. Sea conditions are much

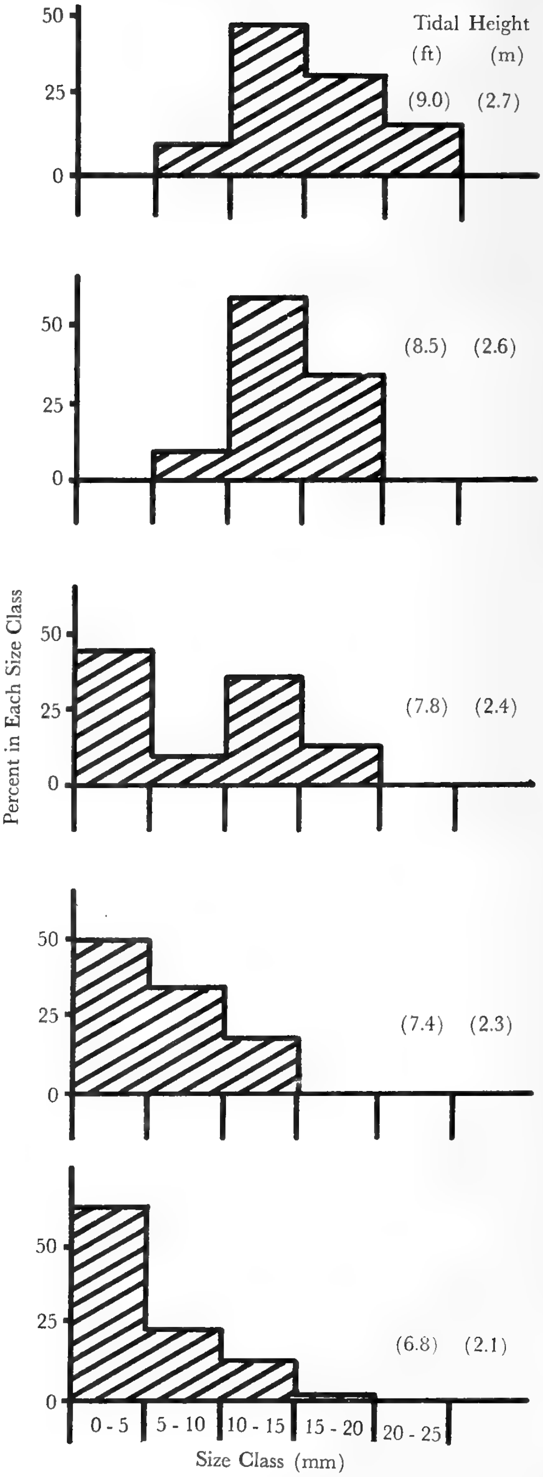
---

[1] Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada.

Figure 2

Size frequency distribution of limpets at different tidal heights along a transect. Tidal height of each sample is given in parentheses

(adjacent column →)



rougher than in summer, and so the rocks are washed far above the actual tide height. The result of these factors is that the shore is never dry between mid-October and late spring, while during the summer it is generally dry during most of the day.

Freezing conditions, such as those observed by **Frank** (1965) in Oregon, were not present during the winter encompassed by this study. The effects of very cold weather and ice on limpet populations could therefore not be evaluated.

Distribution of *Acmaea digitalis*

The distribution of *Acmaea digitalis* was determined quantitatively in May, 1969, by means of a transect on a gently sloping part of the shore which was partly protected from direct wave action. A line was laid down the shore and marked at 1 m intervals. Limpets were counted and removed from within 10 cm of the line, and were later measured. Tidal heights of points along this transect were

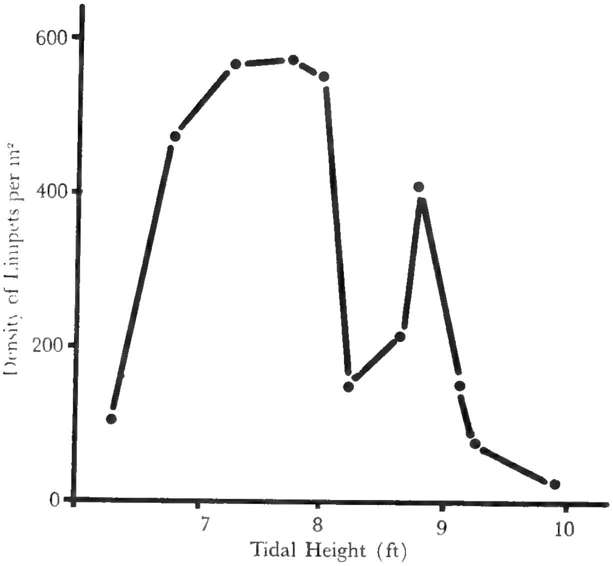


Figure 1

Density of *Acmaea digitalis* vs. tidal height along a transect determined later, in conjunction with a mapping survey, by means of a surveyor's level.

Acmaea digitalis were found at this site from 6.0 to 10.0 tidal feet (1.8 to 3.1 m). Density of limpets along the transect is shown in Figure 1. Density reaches a peak at 7.2 feet (2.2 m) and then declines with increasing tidal height, except that around 8.5 feet (2.6 m) was found an abundance of small, shallow pools in which *A. digitalis* does not occur. Figure 2 shows the distribution of size frequencies at different heights. The modal size class increases with increasing tidal height. These observations agree with those of Frank (1965), and support his suggestion that limpets settle at the lower end of the vertical range and migrate upward in successive years. Very small limpets (2 - 5 mm) began to appear in April and May, 1970, from 6.0 to 8.0 feet along the transect. It should be noted that in a steeper area more directly exposed to surf, the species occurred between 9.0 and 14.0 feet (2.7 to 4.3 m). Tidal height is thus only a relative measurement, subject to modification by local factors.

Although this was essentially a one-species study, the distributions of other species of limpets were noted casually on the transect site. *Acmaea pelta* Rathke, 1833 and *A. paradigitalis* Fritchman, 1960, occurred partially within the same vertical range as *A. digitalis,* but appeared to be mostly in pools and on very flat surfaces, whereas *A. digitalis* was found on sloping surfaces and almost never in pools. Very few limpets of other species were ever seen in *A. digitalis* aggregations. Haven (1971) found a division of habitat between *A. digitalis* and *A. scabra* (Gould, 1846) in California. *Acmaea scutum* Rathke, 1833, occurred only below 7.5 feet (2.3 m), and a slight overlap with the lower population of *A. digitalis* occurred.

Distribution and Abundance of Food

In summer, few macrophytes occurred within the range of *Acmaea digitalis,* except for a few tufts of *Gelidium* sp. and *Fucus* sp., which the limpets did not appear to graze. A thin film of microscopic plants covered the substrate; when grazers were excluded the film thickened and proved to be composed of colonial diatoms.

In October, 1969, the thin film became a dense mat, composed of strands up to 3 mm long, covering most of the middle and upper intertidal zone. Castenholz (1961) observed a similar thickening of the mat in Oregon, and attributed it to a decrease in littorine density. At Port Renfrew the dense mat appeared in October even in areas where littorines had never occurred; so its appearance was not caused by a decrease in littorine abundance. An alternate explanation might be the change in physical conditions which occurred in October.

The diatom mat quickly disappeared in areas adjacent to dense aggregations of limpets and declined slowly in the other areas of the shore. After 4 months it had reached summer levels again, except in one place where there were no grazers at all; here it remained until March. Grazing, thus, is a likely cause of the mat's decline.

Individual *Porphyra* sp. settled on the upper intertidal zone in November, but quickly disappeared below 12.0 feet (3.7 m). Grazing by limpets and littorines might have been responsible for this disappearance. This alga remained above 12 feet until late spring.

From these observations it was inferred that the main diet of *Acmaea digitalis* consists of diatoms, and that food is most abundant during the period from October through March.

OCCURRENCE
of SEASONAL MIGRATIONS

Two samples of individually marked limpets were used to determine whether or not seasonal migration occurs in the population at Port Renfrew. Both samples were

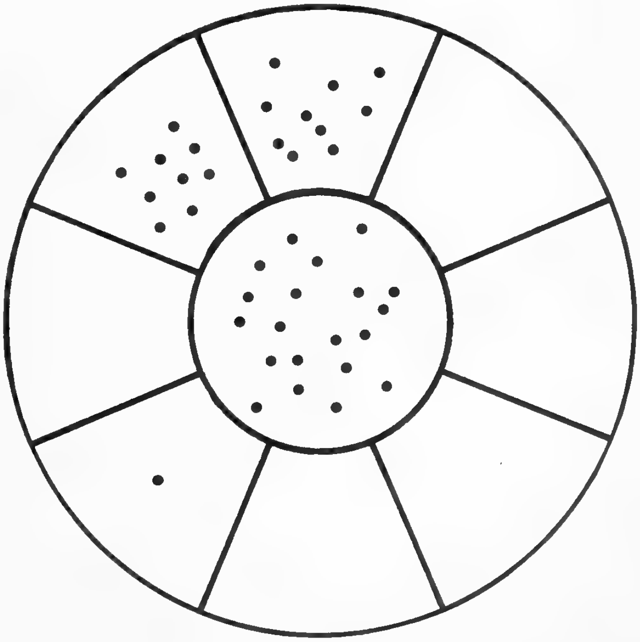


Figure 3

Directions of limpet migration during the period September 1, 1969 to February 16, 1970. Each dot represents one limpet; those in the centre circle represent non-migrants, those in the upper sector upward migrants, and so on marked in early summer, 1969 (see **Breen**, 1971, for discussion of marking technique). The positions of limpets were recorded in September, 1969, and February, 1970, with reference either to a fixed point on the rock (first sample) or to a grid (second sample). From these data the net fall and winter movement of each limpet could be determined. A limpet that remained within 1 m of its September position was considered not to have migrated.

Figures 3 and 4 show the directions in which migration occurred during this period. Although many limpets did not show net movement, an upward tendency was clearly demonstrated by migrants.

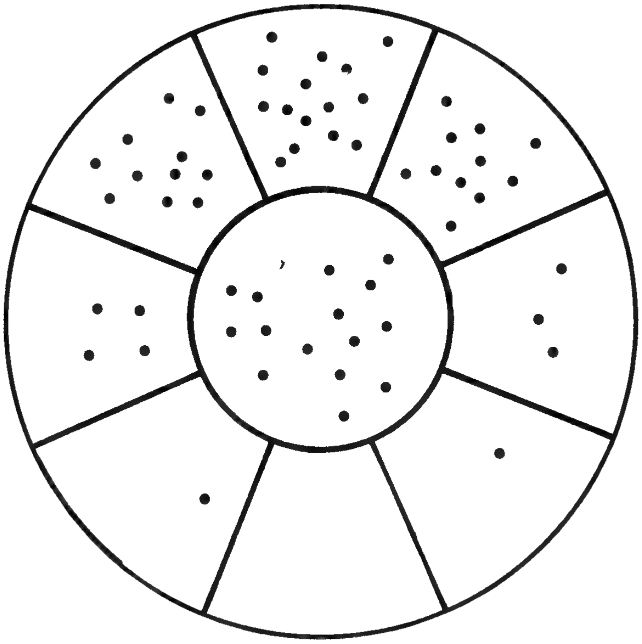


Figure 4

Directions of limpet migration during the same period as Figure 3 in a second sample

The positions of limpets in the first sample were again determined in June, 1970, and net movements between February and June were calculated. Although fewer limpets migrated during this period, a slight downward net movement was shown (Figure 5). It was concluded from this that seasonal migration does occur at Port Renfrew, with an upward migration in fall and winter and a lesser, downward migration in spring.

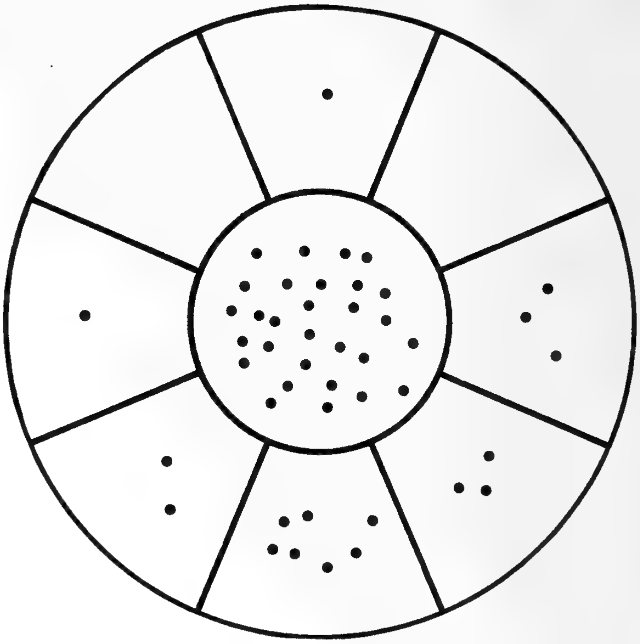


Figure 5

Directions of limpet migration during the period February 16 to June 5, 1970

RELATION of UPWARD MIGRATION with DENSITY

In June, 1969, an experiment was designed to test whether density affects the proportion of limpets which migrate from an area. A concretion was found on the shore which was 1.5 m across, 0.5 high, roughly circular and surrounded by a flat sandstone shelf. At the base of this, which was slightly concave, many limpets sheltered during low tide, and a few more were found on the top of the concretion. Two wedge-shaped areas were formed by placing 3 fences, of plastic mesh sealed to the rock with cement, from the top of the concretion out 1 m onto the sandstone shelf. Limpets within these two areas were then marked individually. The fences prevented lateral movements but allowed migration downward to the sandstone shelf and upward to the open top of the rock.

One area was designated a control group. Density of limpets in the other area was increased at intervals during the summer by the addition of unmarked limpets removed from elsewhere, until in August it was 3 times the original density. The position of each marked limpet was recorded at monthly intervals; and shell lengths were recorded on July 5 and November 22, 1969.

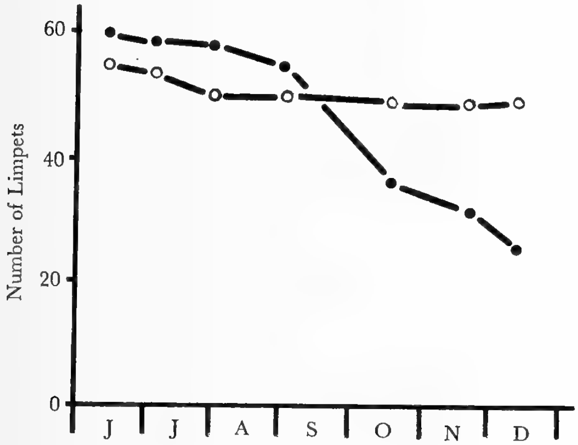


Figure 6

Number of limpets remaining in an experimentally crowded area (A) and in a control area (B) from June to December, 1969. (see text for explanation)

Figure 6 shows the number of limpets which remained in each area from June through December, 1969. Despite the large increase in density in the experimental area, most marked animals in each group remained until October. At that time the experimental group declined sharply, while the control remained relatively constant.

The change in the experimental group could have been caused by emigration, mortality, or both. A search was made for emigrant limpets in December, 1969, within a radius of 5 m from the concretion. One marked limpet from the control and 5 from the experimental group were found. It is known from other observations that limpets are capable of moving more than 5 m in a month, so these may not have been the only emigrants.

Mortality may have been partly responsible for the decline of limpets in the crowded group, since more than 30 limpets disappeared and only 5 could be found. It could be concluded, however, that emigration from the crowded group was greater than that from the control group, and that emigration did not occur until fall.

Growth rates of limpets in the two groups were compared by means of regressions of attained length on initial length (Table 1). Limpets in the control group grew significantly faster than the crowded limpets during the period July 5 to November 22.

Table 1

A comparison of the growth rates of experimentally crowded limpets with those of a control group. The regression lines compared are those of attained length on initial length (Ford-Walford plot)

	Group	
	crowded	control
Regression equation	$Y = 0.28 + 0.85X$	$Y = 0.42 + 0.80X$
Sample size	31	42
F from comparing slopes	0.40 n. s.	
F from comparing adjacent means ($x = 1.74$)	7.45 [3]	

---

[3] significant at $\alpha = 0.01$

SUMMER MORTALITY

In May, 1969, when this study was begun, there were many attachment scars of limpets found in the high intertidal zone. This indicated that individuals recently present had either died or migrated away. The radical change in physical conditions on the upper intertidal area, between winter and summer, coupled with the observation that limpets migrate into the upper intertidal area from lower areas during winter, suggests that mortality should

Table 2

Tidal heights and original number of limpets in 6 areas used to determine survival rate from May 1 to July 26, 1970 (Figure 7). Limpets in the lowest area were counted in 2 groups: those assumed to be newly-settled (2 - 5 mm), and older ones. These are given as groups 6a and 6b, respectively

Group	Tidal Height (feet)	(m)	Number of Limpets May 1
1	14.7	4.5	35
2	14.6	4.4	279
3	12.0	3.7	410
4	10.9	3.3	327
5	10.4	3.2	252
6a	9.4	2.9	287
6b	9.4	2.9	163

be high during summer as a result of warm dry conditions there.

This was tested by measuring survival in groups of limpets at different heights on the shore. Six permanent counting areas were marked on the rock in May, 1970, and all limpets in each area were counted periodically throughout the summer. As a check on migration from counting areas, some limpets in each of the upper 4 squares were marked with quick-drying paint, and searches were made for these outside the counting areas when counts were made. Emigration from counting areas was found to be negligible.

The tidal heights of each area (determined with a surveyor's level), original number of limpets in each and the percent survival are shown in Table 2 and Figure 7. The lowermost area contained both newly-settled limpets and older ones; these were counted separately and survival rates are presented for each. Survival was high in the lower 3 areas (either immigration to the areas occurred, or the initial counts were too low), but decreased with increasing tidal height. An exception to this pattern was seen in survival of newly-settled limpets in the lowermost area, which was the lowest of any group.

It was not possible to assign any one cause to the mortality observed in this group of observations. Direct effects of desiccation were tested in the following way: Limpets normally cling to the substrate sufficiently well that they are not dislodged by a tap on the side of the shell. Limpets weakened or dead, however, can be tapped loose from the rock. In July, 1969, after a period of dry weather and calm seas, limpets in the upper intertidal area were tested by using this 'tapping' method. Of several hundred tested, 75 were dislodged. These were placed immediately into cold seawater and examined half an hour later. Only 3 failed to revive in seawater. In 1970 the weather was cooler, and when the same test was carried out in July only very few limpets were dislodged. All revived when placed in seawater.

This crude test suggests that death resulting directly from desiccation is rare. Partly empty shells were sometimes found in small groups on the shore at low tide, which suggested that predation was responsible. Possible predators observed included mink, mice, crows, gulls, and shore birds. During prolonged observations of crows and shore birds no limpet was ever seen being eaten. Mink and mice, however, could not be observed closely enough to determine what was being eaten.

Predation might account for high mortality in the upper intertidal area if limpets are made more vulnerable to predation as a result of desiccation. FRANK (1965) observed a mouse removing limpets which were weakened by dry, hot weather, and suggests that mice probably cannot

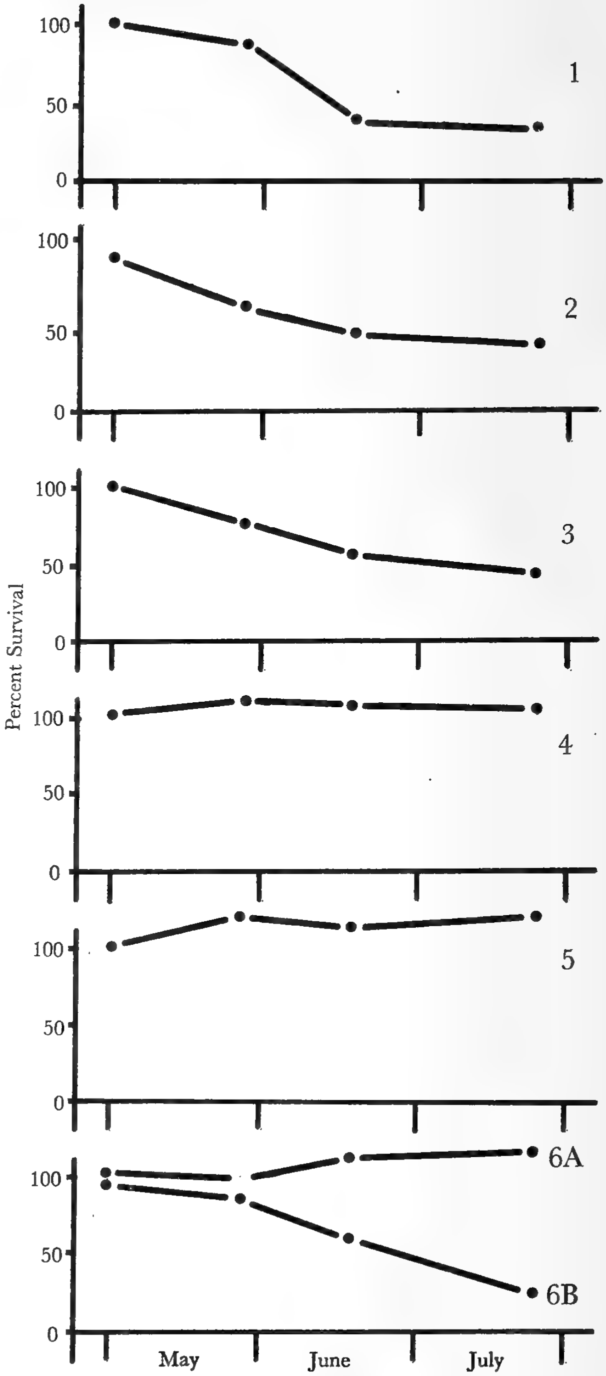


Figure 7

Survival of limpets from May 1 to July 26, 1970 in counting areas at different tidal heights. Tidal heights and the number of limpets originally present in each area are given in Table 2 remove a healthy limpet. Thus high mortality in summer might be considered an indirect effect of desiccation.

RELATION OF UPWARD MIGRATION WITH GROWTH

Growth of limpets that had migrated from an area in fall and winter was compared with growth in the limpets which remained in the area. Length data were obtained from the two groups of marked limpets used to determine whether upward migration occurred at Port Renfrew and discussed above. Limpets in each group were measured in July, 1969, and again in February, 1970, so within each group the growth of limpets migrating in fall could be compared with growth in those that did not migrate (Table 3). (Within each group the initial lengths of migrants and non-migrants were compared and found to be statistically equal, thus a t-test was used to compare the growth increments.) In both groups the migrant limpets grew more than the non-migrants during fall and winter.

Table 3

A comparison between the mean growth increments of migratory and non-migratory limpets in 2 samples of marked individuals, from July 1, 1969, to February 16, 1970

	Group 1	
	migratory	non-migratory
mean increment (cm)	0.064	0.119
variance of increment	0.0037	0.0022
F ratio of variances	1.65 n. s.	
value of 't'	2.71[4]	
	Group 2	
	migratory	non-migratory
mean increment (cm)	0.089	0.025
variance of increment	0.0056	0.0047
F ratio of variances	1.21 n. s.	
value of 't'	4.96[4]	

---

[4] significant at $\alpha = 0.05$

Better growth of migrants can be explained in two ways. First, density is lower at higher shore levels, and since migrants in fall and winter tend to move upward they possibly encounter less intraspecific competition for food. Second, the size distribution changes with increasing tidal height; larger size classes becoming more predominant. Castenholz (1961) found that large *Acmaea digitalis* are slightly less efficient at removing algae than smaller individuals. Stimson (1970) found that the territorial species *Lottia gigantea* (Gray, 1834) does not graze down to bare rock, but leaves a thin film of algae. Smaller species, such as *A. digitalis,* outside *Lottia* territories graze down to bare rock, and Stimson suggests that *Lottia* would be outcompeted if it did not defend its territory. An alternate explanation for greater growth in fall migrants at Port Renfrew might be that small *A. digitalis* graze more efficiently than larger individuals; and thus the different size composition found at higher shore levels is responsible for better growth there.

An experiment was designed in February, 1970, to determine the better of these explanations. Three adjoined plots, each 65 cm square, were constructed with plastic mesh fences. The natural biomass of limpets within each plot was determined by removing all limpets and measuring their shell length. Shell length was then converted to body dry weight by means of a regression developed from 107 limpets for this purpose. This regression was

$$\log_e \text{dry weight (g)} = -6.638 + 2.05 \text{ length (cm)}$$

The natural average biomass was found to be 6.87 g per plot.

Limpets 2.0 to 2.5 cm were collected from elsewhere, marked individually and measured. These were then added to the empty plots to form 3 treatments: (1) a control, consisting of enough marked limpets to equal the natural plot biomass, (2) a high density treatment, with double the natural plot biomass, and (3) a mixed high density

Table 4

Comparisons among mean growth increment of 3 groups of limpets (see text for explanation). The control mean is compared with the high density mean, and the high density mean with the mixed high density mean

Treatment	Control	High Density	Mixed High Density
number	25	30	26
mean growth increment (cm)	0.0048	−0.0417	−0.0677
variance of increment	0.00443	0.00208	0.00259
F ratio of variances		2.13 n. s.	1.24 n. s.
value of 't'		3.06[5]	1.99 n. s.

---

[5] significant at $\alpha = 0.01$ (one-tailed), d. f. = 53

treatment, consisting of a biomass of marked limpets equal to the natural biomass, plus an equal weight of smaller (1.25 to 1.75 cm) limpets. These biomasses were calculated using the regression above.

Treatments were maintained in each plot from February 19 to July 24, 1970, when all marked limpets were removed and again measured. Growth in both high density plots was significantly lower than in the control (Table 4), but there was only a slight, non-significant difference between the 2 high-density treatments. This indicates that growth is inhibited by high densities, as already shown above, but that the size composition of competing *Acmaea digitalis* makes little difference in growth.

DISCUSSION

Of the two behaviours examined in this study, seasonal migration appears to be the more important with respect to regulation of local densities. Although the component parts of this regulating mechanism have been examined in the preceding sections, it has not been studied as a whole, so its operation as described below must be treated as an hypothesis.

Fall migration appears to be density-dependent in that the proportion of limpets which migrate from an area depends on the density in the area. This might partially regulate density at all levels of the shore in the following way: If heavy settlement were to occur at the lower part of the range of *Acmaea digitalis,* migration of older limpets from that area in fall would reduce density there. The older limpets that migrated would, in turn, produce an increased density in the area to which they migrated, and migration of the limpets originally there would be expected. Thus the heavy settlement of young might produce a wave of fall migration up the shore. Lesser settlement of young could be expected to have a lesser effect. Density at a given level of the shore might not be controlled within rigid limits in this way, but at least partial regulation could occur.

Conditions which produce high mortality are not present on the upper shore levels during fall, so these areas can be invaded by fall migrants. Migration is dependent on density, so the number of limpets which move to the highest levels depends on the density at lower levels. Mortality during the next summer among migrants on high parts of the shore can therefore be thought of as density-dependent in the population as a whole, even though it is independent of density in the area in which it occurs. For instance, if density on the shore is fairly low, few limpets will migrate onto the higher levels, and the proportion of deaths due to summer mortality will be low. If density is high, however, a higher proportion will migrate to the higher levels, and the proportion of deaths in the next summer will be greater.

The fact that high mortality occurs in summer at high shore levels, while lesser mortality occurs at lower levels, suggests at first that upward migration in fall is being selected against. Such selection might be outweighed, however, by the fact that fall migrants show better growth than non-migrants, probably because of reduced intra-specific competition for food. If fecundity is also increased for the same reason, a selective advantage of upward migration can be postulated. It might be possible for a limpet that migrates onto the high intertidal area to leave more offspring, as a result of increased fecundity, than a limpet that does not migrate, even if the migrant dies during the next summer and the non-migrant survives. Newly-settled *Acmaea digitalis* observed in April and May indicate that breeding occurs in late winter or early spring, after the time at which food is most abundant. This is between the times of upward migration and summer mortality, so the selective advantage just postulated seems possible.

Frank (1965) found high winter mortality at the lower part of the shore and high summer mortality at the higher part. He suggests that seasonal movements, upward in fall and downward in spring, are an adaptive response to such mortality patterns. Migration may have evolved in response to other factors as well. It was noted earlier that settlement of *Acmaea digitalis* from the plankton occurred only below the 8 foot tidal level at Port Renfrew. A probable explanation for this is that small limpets cannot withstand desiccation as well as larger ones (Davies, 1969). A critical tide level (Doty, 1946) might occur for newly-setted limpets, which ceases to be critical after they have grown larger and can withstand longer exposure to drying.

Thus upward migration might be an adaptation allowing limpets, as they grow, to exploit habitats which were previously unsuitable. It would be advantageous for a limpet to migrate upward whenever possible because of the lower density at higher levels, and hence the better opportunities for growth there.

Downward migration obviously cannot be explained in these terms, and Frank's (1965) suggestion may be correct. It is important to note, however, that downward migration does not completely solve the problem of summer mortality, because net movements after migration are upward. This would suggest that, if both types of migration are advantageous in some respect, upward migration is more advantageous. If one considers only those factors dealt with here, this seems reasonable because migration upward confers the advantage of better opportunities for growth at virtually all shore levels. Migration downward is advantageous only at the upper levels of the shore where summer mortality is a serious factor.

Results from the crowding experiment show that limpets tend to be conservative in movement during summer, and migrate from crowded areas only when conditions change in the fall. Dangers from desiccation are presumably serious enough in summer that, even in very crowded conditions, limpets prefer to remain in familiar territory where shelter is assured rather than seek out less crowded areas. For this reason, seasonal migration is probably more important in population regulation than homing behaviour.

Homing is possibly an adaptation to reduce the risk of desiccation, such as aggregation behaviour is (Millard, 1968). Haven (1971) suggests that this is the case in *Acmaea scabra* in California. This could be tested by measuring the degree of homing in *A. digitalis* at different levels and at different times. The expectation would be that homing increases at higher shore levels and is greatest during the warm, dry months, even in those limpets that do not migrate seasonally.

A great deal of emphasis has been placed above on desiccation as an important factor of the environment of *Acmaea digitalis*. This approach provided the basis for a possibly acceptable conceptual model of how populations adapt to variation in space and time. It must be emphasized, however, that other factors might be equally or more important in producing adaptations within this species.

ACKNOWLEDGMENTS

This study formed part of a Master's degree programme at the University of British Columbia. My supervisor, Robin Harger, was helpful throughout the project, particularly when the time came to write it up. Dr. John Stimson gave freely of his time and advice, and was indirectly responsible for my having chosen limpets to work on. Dr. N. J. Wilimovsky very graciously allowed me to work at the Marine Biological Station at Port Renfrew, and Steve Heizer permitted me to work within his own area there. Steve, Khoo Hong Woo and John Himmelman added greatly to the sheer joy of working at Botanical Beach. These people, Sylvia Behrens and Ora Johannsson helped with some aspects of fieldwork described in this study.

This study was supported by a grant from the National Research Council of Canada to Dr. Robin Harger.

Literature Cited

Breen, Paul A.
1971. Homing behavior and population regulation in the limpet *Acmaea (Collisella) digitalis*. The Veliger 14 (2): 177 - 183; 10 tables (1 October 1971)

Castenholz, Richard William
1961. The effect of grazing on marine littoral diatom populations. Ecology 42: 783 - 794; 6 figs.; 3 tables

Davies, Peter Spencer
1969. Physiological ecology of *Patella*. III. Desiccation effects. Journ. Marine Biol. Assoc. U. K. 49: 291 - 304; 5 figs.; 3 tables

Doty, Maxwell Stanford
1946. Critical tide factors that are correlated with vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27: 315 - 328

Frank, Peter Wolfgang
1965. The biodemography of an intertidal snail population. Ecology 46: (6): 831 - 844; 8 figs.; 6 tables

Fritchman, Harry Kier, II
1960. *Acmaea paradigitalis* sp. nov. (Acmaeidae, Gastropoda). The Veliger 2 (3): 53 - 57; plts. 9 - 12 (1 January 1960)

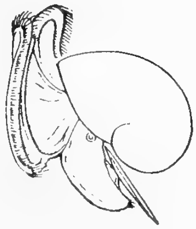
Hall, C. W.
1906. Some geological features of the Minnesota Seaside Station. Postelsia (1906): 305 - 347

Haven, Stoner Blackman
1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in Central California. The Veliger 13 (3): 231 - 248; 10 text figs. (1 January 1971)

Lewis, J. R.
1954. Observations on a high-level population of limpets. Journ. Animal Ecol. 23: 85 - 100

Millard, Carol Spencer
1968. The clustering behavior of *Acmaea digitalis*. The Veliger 11 (Suppl.): 45 - 51; 4 text figs.; 1 table (15 July 1968)

Stimson, John Secombe
1970. Territorial behavior of the owl limpet, *Lottia gigantea*. Ecology 51 (1): 113 - 118



Observations on Growth, Feeding, Reproduction, and Development in the Opisthobranch, *Fiona pinnata* (Eschscholtz)

BY

JOHN J. HOLLEMAN

Department of Biological Sciences, Merritt College, Oakland, California 94619

(5 Text figures)

INTRODUCTION

OBSERVATIONS ON GROWTH in nudibranchs have been reported by THOMPSON (1964), while THOMPSON (1967) discussed development in *Cadlina laevis* (Linnaeus, 1767) and development in opisthobranchs in general. POTTS (1970) discussed growth, feeding and reproduction of *Onchidoris fusca* (Müller, 1776).

In the summer of 1967, washed on to the shore at the Bodega Marine Laboratory and the beach at Salmon Creek, Sonoma County, California, following several storms were pieces of driftwood on which were observed the nudibranch *Fiona pinnata* (Eschscholtz, 1831) and the barnacle *Lepas anatifera* (Linnaeus, 1758). Observations have provided information on the growth, predation, reproductive activity and larval development of *Fiona pinnata*.

METHODS AND MATERIALS

The nudibranchs were removed from the driftwood and placed individually in finger bowls where they were maintained for 24 days. Water was changed daily; at that time food was added. Length and weight determinations were made on alternate days. The length measurements were made using an ocular micrometer, and wet weight determinations were obtained by using a Mettler semi-micro-analytical balance. The finger bowls were placed in a tray of running sea water to maintain a constant temperature.

On the 17th day of observations, pairs of the separately maintained nudibranchs were placed in finger bowls for a period of 8 to 10 hours, after which time the pairs were separated and returned to their individual bowls.

OBSERVATIONS

Growth: The 12 smallest individuals of *Fiona pinnata* collected from the driftwood were selected and used in the observations on growth. During these observations the stalked barnacle, *Lepas anatifera,* was supplied as food in excess as determined by the presence of live barnacles at the end of each 24-hour period. The average length of the nudibranchs was 3.37 mm when initially placed in the finger bowls and 29.97 mm at the conclusion of the observations (Figure 1). This represents approximately a 900% increase in length in a 24-day period or an average increase of 1.11 mm per day. The greatest increase in length by an individual was from 2.79 to 33.32 mm for an average increase of 1.27 mm per day.

The average wet weight gain for the observation period was from 1.3 mg to 448.8 mg. This represents an average increase of 18.64 mg per day during the period of observation (Figure 2).

Feeding: Ten *Lepas anatifera* were added each day to the finger bowls that contained individual *Fiona pinnata. Fiona* attacks *Lepas* by first positioning itself at the posterior junction of the peduncle with the base of the body proper; then, with the jaws holding the soft tissue just below the plates, the radula rasps away the tissue. Those barnacles actively feeding at the time of a nudibranch attack continued feeding during the initial phases of the attack. Several barnacles were able to dislodge the nudi-

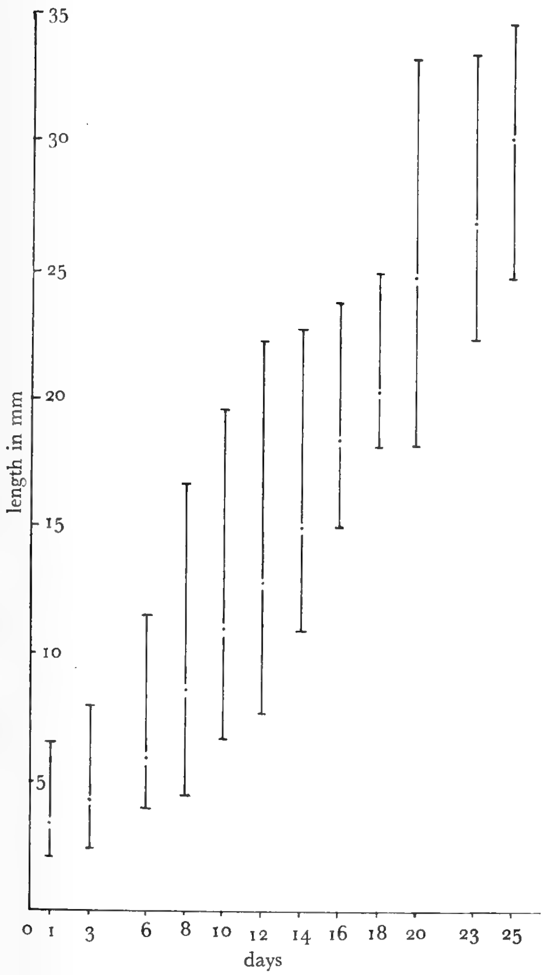


Figure 1

Increase in length in mm. The average length (dot) and the size range are indicated

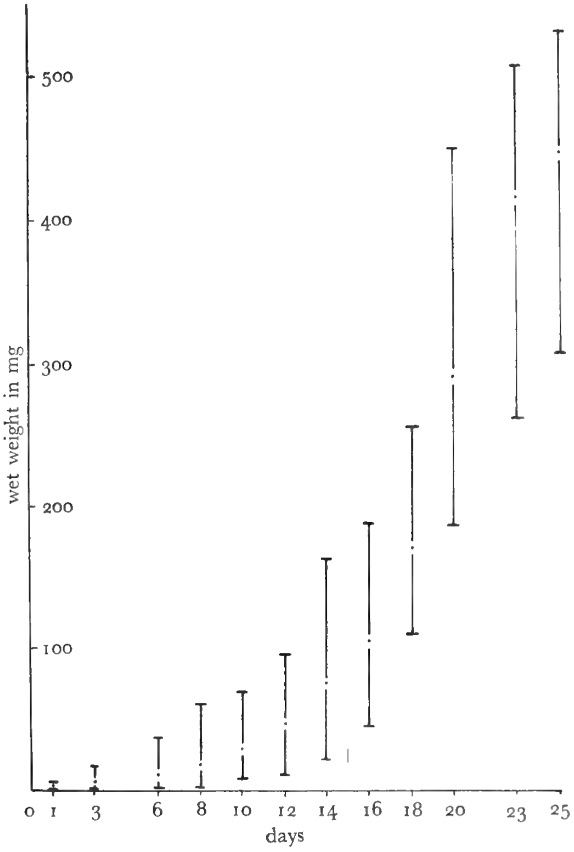


Figure 2

Increase in wet weight in mg. The average weight (dot) and the range of weights are indicated

branch by shaking back and forth and sideways. If the nudibranch was small, the action of the barnacles was successful and the nudibranch either moved away in search of another barnacle or returned to the attack. After a successful attack at the base of the body, the barnacles appear to be stunned or relaxed as the plates gape and no cirral activity was observed. The nudibranch moves to the front of the barnacle, enters in-between the open scutal and tergal plates and begins to feed. During feeding the action of the radula could be observed as well as the movement of the food in the cerata. The nudibranchs fed only on living barnacles and ignored all dead individuals that were placed in the finger bowls.

When *Fiona pinnata,* which had been starved for 2 days, was offered other sources of food, it became active, moving to the food. The hydroid *Obelia longissima* (Pallas, 1776) was offered to a nudibranch and it immediately moved onto the colony, but did not feed. The nudibranch appeared to be stung by nematocysts and moved off the hydroid in a very jerky fashion. Cardiac activity was observed to cease; however, after a 2-hour period, the nudibranch had returned to normal activity. Two other sources of food were offered: the stalked barnacle *Polycipes polymerus* (Sowerby, 1833) and the acorn barnacle, *Balanus glandula* (Darwin, 1854). In normal circumstances, *F. pinnata* was unable to attack either of these barnacles successfully. However, if either barnacle had a damaged

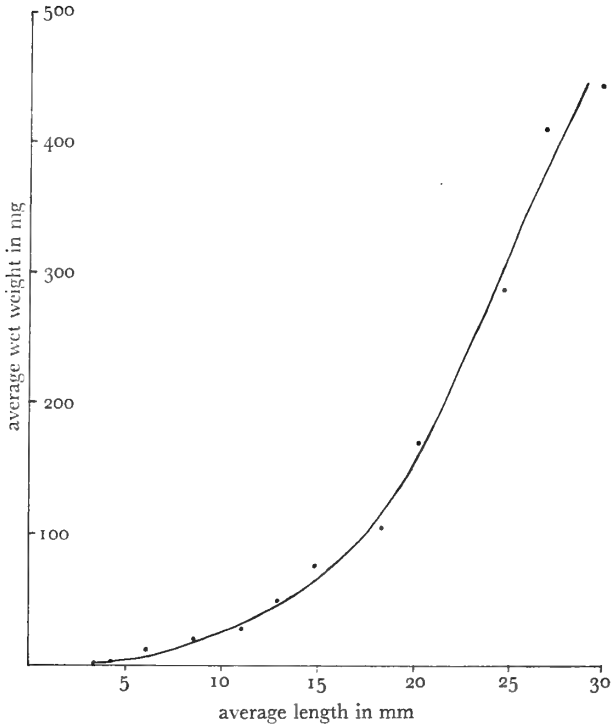


Figure 3

Relationship of the average length to the average wet weight

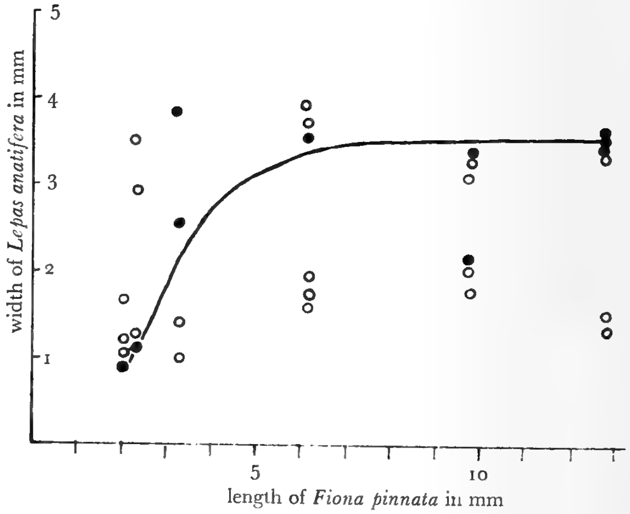


Figure 4

Relationship of the length of *Fiona pinnata* to the size of *Lepas anatifera* eaten. ● represents *Lepas anatifera* eaten, ○ represents individuals alive at the conclusion of 24 hours

scutum, tergum, or basis, or, in the case of the stalked barnacles, a damaged peduncle, *F. pinnata* would commence feeding at the injured site.

Observations were made on the relationship of the size of *Fiona pinnata* and the size of the food successfully eaten (Figure 4). The smaller nudibranchs, 2 to 3.3 mm, when offered a range of barnacle sizes would attack the smaller barnacles, ignoring the larger ones. Several feeding attacks were made on the larger barnacles, but the barnacles were able to successfully shake off the nudibranch. When individual nudibranchs 5 mm or larger were offered a range of barnacle sizes, the larger barnacles were selected.

Reproduction: On the 17th day of observations, 2 individual *Fiona pinnata* were placed in the same finger bowl. Immediately the rhinophores became elevated and active. The cerata, which had been lying flat, were erected. Moving about each other, the nudibranchs positioned themselves head to head and then advanced so that their right sides were in contact. Reciprocal copulation occurred immediately. This pair copulated for 5 minutes, then separated and moved apart for a period of 10 minutes, and then copulated a second time for another 5 minute period. Copulation lasted 10 to 15 minutes in 5 other pairs observed and after separation no further copulations were observed. The pairs were separated after an 8 to 10 hour period and returned to their individuals bowls.

Two individuals produced egg masses 12½ hours after copulation. Within 2 days, 10 of the 12 nudibranchs had laid egg masses, with 9 having laid 2 or more masses. The white egg masses laid in a spiral have a length of 5.2 mm and a height of 3.1 mm. The average size of an egg was 495 μ.

Five days after the first egg mass was laid, free swimming veligers were observed (Figure 5). The veligers swam actively for 7 days, but then began to die. Twelve days after the first egg mass was laid, the first adults died. All the adults had died by the 14th day following the initial laying of egg masses.

DISCUSSION

described. The adaptive advantage of the growth rate The previous observations on growth (Thompson, 1964; Potts, 1970) in nudibranchs were made on intertidal

Figure 5

Veliger, three days after hatching

and subtidal benthic species which have growth periods measured in months. *Fiona pinnata,* a pelagic species, has a much faster growth rate than any of those previously described. The adaptive advantage of the growth rate may be related to the transitory nature of the substrate on which these nudibranchs live; that is, drifting material may be deposited on a beach at any time. This is in contrast to intertidal or subtidal species where once the veliger has settled on a fixed substrate, growth may proceed at a slower rate since there is less likelihood of the destruction of the substrate.

MacFarland (1966) reports that *Fiona pinnata* is found in most instances upon driftwood and seaweed "subsisting upon hydroids, *Velella* and *Janthina.*" He also reported that specimens from Monterey, California, were collected from a drifting kelp stipe covered with *Lepas hilli* (Leach, 1818). Marcus (1961) reports finding *F. pinnata* on a board with lepadids at Dillon Beach, California. To the list of food sources is added the goose barnacle, *Lepas anatifera.* The fused plates of the acorn barnacles, *Balanus glandula,* and the tough skin of the peduncle of the leaf barnacle, *Polycipes polymerus,* prevent *F. pinnata* from feeding successfully.

The observations made do not provide any indication of the length of the veliger stage or what mechanism initiates settlement. The rapid development to the veliger stages places *Fiona pinnata* with those nudibranchs that are of the planktotrophic type that Thompson (1967) describes as having not only a short embryonic period but also small ova. However, the large size of the ova (495μ) of *F. pinnata* makes it markedly different from the planktotrophic type where ova size ranges from 40 to 170μ in diameter. The egg masses are of the type designated as type A by Hurst (1967) wherein eggs occur throughout the ribbon. The hatching of the veliger in 5 days compares favorably with other planktotrophic larvae where embryonic periods are reported to vary from 2 to 28 days and with opisthobranchs that have egg masses of type A. Rapid embryonic development to a free swimming veliger is probably advantageous in a pelagic animal where the possibility exists that the substrate for the attached egg masses could be stranded on a shore.

CONCLUSION

1. Growth in *Fiona pinnata* is rapid with an average increase in length of 1.11 mm and in wet weight of 18.64 mg per day.
2. *Fiona pinnata* preys on *Lepas anatifera,* selecting a prey size that can be attacked successfully.
3. Embryonic development to a free swimming veliger is rapid, taking only 5 days.

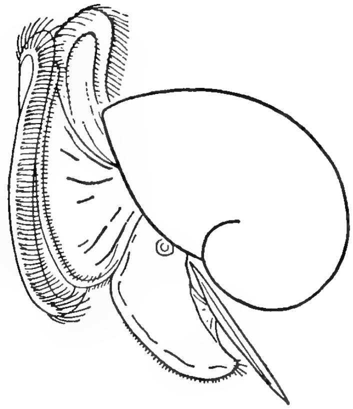
ACKNOWLEDGMENT

I wish to thank Dr. Cadet Hand, Director of the Bodega Marine Laboratory, for providing space and facilities at the laboratory where these observations were made.

Literature Cited

Hurst, Anne
1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. The Veliger 9 (3): 255 - 288; plts. 26 - 38; 31 text figs. (1 January 1967)

MacFarland, Frank Mace
1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. **6**: xvi+546 pp.; 72 plt. (8 April 1966)
Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger **3** (Supplmt. I): 1 - 85; plts. 1 - 10 (1 February 1961)
Potts, G. W.
1970. The ecology of *Onchidoris fusca* (Nudibranchia). Journ. Marine Biol. Assoc. U. K. **50**: 269 - 292
Thompson, Thomas Everett
1964. Grazing and the life cycles of British nudibranchs. ***In***: D. J. Crisp (ed.) Grazing in terrestrial and marine environments, pp. 275 - 295. Blackwell, Oxford, England
1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. Journ. Marine Biol. Assoc. U. K. **47**: 1 - 22



A Preliminary List of Known Opisthobranchs from the Galápagos Islands Collected by the Ameripagos Expedition

BY

GALE G. SPHON[1] AND DAVID K. MULLINER[2]

(1 Map)

INTRODUCTION

In March 1971, seven professional and amateur malacologists, calling themselves the Ameripagos Expedition, visited the Galápagos Islands, Ecuador. With the permission of the Charles Darwin Research Station, numerous species of mollusks were collected. Approximately 25 opisthobranch species were obtained from 38 stations. These stations ranged from intertidal to 38m in depth. Eleven of the opisthobranch species are included in this report.

The opisthobranch fauna (other than shelled cephalaspideans) of the Galápagos has been neglected by previous workers. Pilsbry & Vanatta (1902: 556) report *Doris peruviana* Orbigny, 1837 and Eales (1966: 364) cites *Aplysia juliana* Quoy & Gaimard, 1834. Keen (1971: 812) also reports *Tylodina fungina* Gabb, 1865. These are the only 3 species we have been able to find recorded in the literature. Only *Tylodina* was collected by the expedition.

The names of the islands used in this paper are the mixture of the Spanish and English names in common usage among the inhabitants of the archipelago.

Unless otherwise noted, at least one voucher specimen of each species discussed in this paper is deposited at the Los Angeles County Museum of Natural History. The specimens from Nayarit, Mexico, that are mentioned, have been deposited there also either as preserved specimens or radula slides.

STATION OBSERVATIONS

With the exception of the collections made at the Charles Darwin Research Station at Academy Bay, Santa Cruz Island, and Sullivan and Bartolomé Bays on Bartolomé Island, only a few hours were spent collecting at the other stations. This limited the amount and variety of opisthobranchs that could be taken.

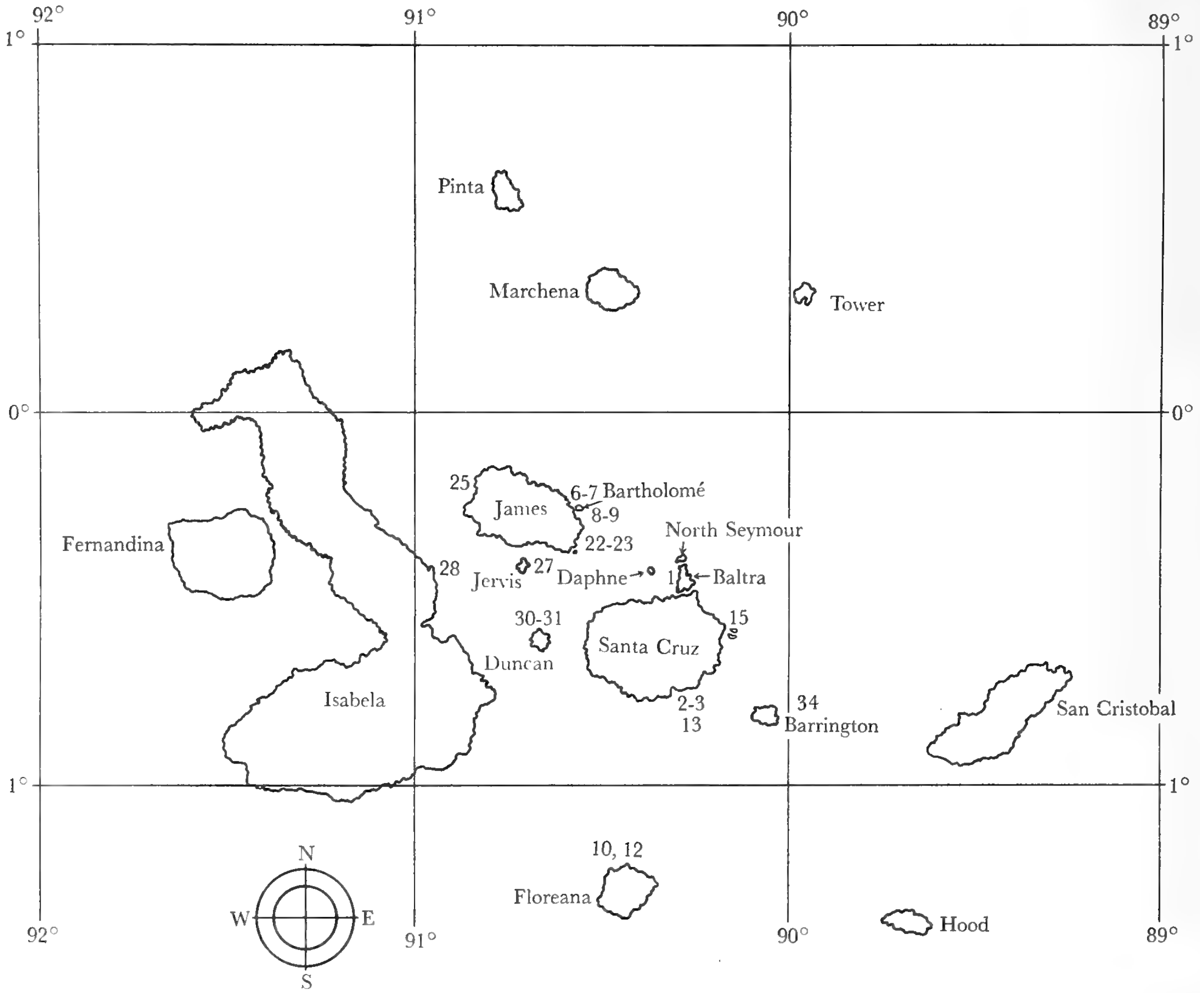
Most intertidal collections were made from lava rocks well cemented to the substrate. At the southwest corner of Baltra Island (station 18) there were few mollusks even though the area appears as though it should abound with them. A lava ledge extends out some distance, and it was one of the few areas where there were many small tide pools and turnable rocks. However, there was a yellowish clay-like sediment present that may have been an inhibiting factor for the intertidal mollusks. Only at this station did we find this peculiar sediment. In contrast, another site we observed close-up on Baltra was the boat docking area (station 1). Even though we made no attempt to collect opisthobranchs from station 1, the shoreline was made up of the characteristic Galápagos lava and did not have the peculiar yellowish clay-like sediment.

Flamingo Cove, near Post Office Bay on Floreana Island (station 10) has several large shallow pools with many small and medium sized rocks and was the only place where we found the green alga, *Caulerpa racemosa* Forskal & J. Agardh var. *occidentalis* C. Agardh & Børgesen. *Caulerpa* is well known for being host to a variety of sacoglossans. Although this is the only station where we actually encountered the alga, we were told by several people who live on the islands that it is not uncommon in the archipelago.

---

[1] Curatorial Assistant, Invertebrate Zoology, Los Angeles County Museum of Natural History, Los Angeles, California 90007

[2] Research Associate, San Diego Natural History Museum, San Diego, California 92112



Ameripagos Expedition Collecting Stations for the Galápagos Islands, Ecuador

Station Number

1 Boat dock, Baltra Island; 0°25′30″ S, 90°15′17″ W; intertidal

2 Charles Darwin Research Station, Academy Bay, Santa Cruz Island; 0°45′05″ S, 90°15′38″ W; intertidal

3 Charles Darwin Research Station, Academy Bay, Santa Cruz Island; 0°45′05″ S, 90°15′38″ W; in 1 to 3 meters

6 Sullivan Bay, Bartolomé Island; 0°17′20″ S, 90°33′30″ W; intertidal

7 Sullivan Bay, Bartolomé Island; 0°17′20″ S, 90°33′30″ W; in 1 to 3 meters

8 Bartolomé Bay, Bartolomé Island; 0°17′ S, 90°33′30″ W; intertidal

9 Bartolomé Bay, Bartolomé Island; 0°17′ S, 90°33′30″ W; in 1 to 3 meters

10 Flamingo Cove, near Post Office Bay, Floreana Island; 1°14′ S, 90°27′30″ W; intertidal

12 Corona del Diablo, near Post Office Bay, Floreana Island; 1°14′ S, 90°27′30″ W; in 2 to 4 meters

13 Academy Bay, Santa Cruz Island; 0°25′ S, 90°15′38″ W; 15 to 30 meters

15 South side of North Plaza Island; 0°34′36″ S, 90°09′40″ W; intertidal

18 Southwest corner of Baltra Island; 0°29′20″ S, 90°17′40″ W; intertidal

22 Sombrero Chino Island; 0°22′20″ S, 90°17′40″ W; intertidal

23 Sombrero Chino Island; 0°22′20″ S, 90°34′30″ W; in 1 to $2\frac{1}{2}$ meters

27 Jervis Island; 0°25′ S, 90°42′ W; in 3 to 23 meters

28 Punta Alfaro, Isabela Island; 0°25′20″ S, 90°57′10″ W; intertidal

30 Duncan Island; 0°35′50″ S, 90°39′15″ W; intertidal

31 Duncan Island; 0°35′50″ S, 90°39′15″ W; in 1 to 3 meters

34 Barrington Island; 0°51′30″ S, 91°02′30″ W; intertidal

Punta Alfaro, Isabela Island (station 28), was like most of the other areas where intertidal collecting was done, except for having a rocky rubble bar that is uncovered at low tide. There were also a few dead coral heads that had lodged on the bar, indicating that coral was present in the area.

Duncan Island (station 30) was, considering the short time we had there, the most productive of all our stations for opisthobranchs. We collected at a small cove or inlet protected by a large mass of rock that was almost big enough to be called an islet. Within the cove, the shoreline is the typical lava boulder type found throughout the archipelago. However, the bottom of the cove is made up of sand with large areas of living coral that can be easily reached by wading knee-deep at low tide. The diversification of habitats probably accounted for the variety of dorids, aeolids, sacoglossans, and pleurobranchs we found there.

SPECIES OBSERVATIONS

Bulla punctulata A. Adams, in Sowerby, 1850

Keen (1971) reported this species from Magdalena Bay, Baja California, Mexico, to Peru. It is the only species of shelled cephalaspidean that was found by this expedition.

This species was not taken alive intertidally; however, beach specimens were collected at Flamingo Cove (station 10), the south side of North Plaza Island (station 15) and the southwest corner of Baltra Island (station 18). Living specimens were taken from 1 - 3m at the Darwin Research Station (station 3), from 2 - 4m at Flamingo Cove (station 12), from 1 - 2½m at Sombrero Chino Island (station 23), and at Duncan Island stations 31 (1 - 3m), and 34 (10 - 25m).

Dolabrifera dolabrifera (Rang, 1828)

This is a circumtropical and circumsubtropical species that has recently been reported from the eastern Pacific. Bertsch (1970) based his record on one specimen collected at Las Cruces Bay, Baja California, Mexico (20 miles east of La Paz). It has also been taken at Cholla Bay, Sonora, Mexico, by Wesley Farmer and from Mazatlan, Sinaloa, Mexico by Antonio Ferreira (personal communications). We extend the range from the Gulf of California to the Galápagos Islands.

We collected this species at 6 localities: intertidally at Sullivan Bay, Bartolomé Island (station 6); Flamingo Cove, Floreana Island (station 10); Duncan Island (station 30); Sombrero Chino Island (station 22); on the bar at Punta Alfaro, Isabela Island (station 28); and intertidally and to 2m at the Darwin Research Station, Santa Cruz Island (station 2).

Tylodina fungina Gabb, 1865

This is a moderately common species and the recorded northern limit is Cayucos, San Luis Obispo County, California (Sphon & Lance, 1968). From there its range extends to Todos Santos, Baja California, Mexico. DuShane (1966) reports it from Punta Colorado in the Guaymas area of Sonora, Mexico. McBeth & Bowlus (1969) report it from Espiritú Santo Island in the Gulf of California, and Keen (1971) reports it from Costa Rica as well as from the Galápagos Islands. We collected 2 specimens intertidally at Bartolomé Bay (station 8) and 2 additional specimens were collected from 2 - 4m at Corona del Diablo, Floreana Island (station 12). All 4 animals were living on a bright yellow sponge which is the typical habitat for the species in southern California.

Umbraculum ovale (Carpenter, 1856)

Keen (1971) reports this species as occurring from Cape San Lucas, Baja California, Mexico, to Panama. One specimen was taken in 1 - 3m of water in Sullivan Bay, Bartolomé Island (station 7). This record extends the range of the species south from Panama to the Galápagos Islands.

The single specimen collected by the expedition is in the private collection of Mrs. Jackey Grundman, Downey, California.

Berthelinia chloris (Dall, 1918)

Berthelinia chloris is one of the sacoglossans that live and feed exclusively on the green alga *Caulerpa racemosa*. It resembles its host plant in color and can generally only be seen in the field when the light strikes the shiny shell in the duller algae. Nineteen specimens were collected intertidally at Flamingo Cove, Floreana Island (station 10). This was the only station where we saw *Caulerpa*.

The specimens were all attached by a mucous thread fastened near the base of the plant. No specimens were found on the younger portions of the alga. This may be due to the fact that they were collected at low tide when the *Caulerpa* was either out of water or in warm shallow pools no more than 45cm deep. When the animals are disturbed, they are able to withdraw completely into the shell and close it tightly.

Keen (1971) reports this species from Punta Abreojos, on the Pacific side of Baja California, Mexico, to the southern end of the Gulf of California and, possibly, at

Guaymas, Sonora, Mexico. We are able to extend the range of the species to the Galápagos Islands.

Lobiger souverbiei Fischer, 1856

While it was known for some years that this species occurs in the eastern Pacific, it has only been reported from Santa Cruz, Nayarit, Mexico, living on *Caulerpa* (Sphon, 1971a). This is a circumtropical species that is also found in Hawaii and the Caribbean.

Four specimens of this species were found on *Caulerpa racemosa* var. *occidentalis* from the intertidal region of Flamingo Cove, Floreana Island (station 10). It is probable that both this species and *Berthelinia* would be found where *Caulerpa* occurs. Both seem to live and feed exclusively on this green alga.

Berthellina engeli Gardiner, 1936

As Bertsch (1970) pointed out when he rejected the subspecific taxon *Berthellina engeli ilisima* Marcus & Marcus, 1967, a decision on the validity of the species will have to await the examination of the holotype. Even though Keen (1971) elevated *B. e. ilisima* to specific rank as a valid taxon, we consider that there is not enough difference between the Caribbean and Panamic specimens for even subspecific differentiation. We agree with Bertsch's conclusion that these animals should be considered as one species – *Berthellina engeli* Gardiner, 1936. The distribution is not an unusual one for opisthobranchs, as there are many species that occur world-wide in tropical or subtropical seas.

The northernmost locality record is one specimen reported by Lee & Brophy (1969) from 7½m off Santa Cruz Island, Santa Barbara County, California. It has also been taken several times in the Palos Verdes Peninsula area of Los Angeles County, California by Donald Cadien (personal communication). Bertsch (1970) cites many localities throughout the Gulf of California, Mexico, that have been mentioned in the literature.

We collected this species at 4 stations in the Galápagos Islands, and it is probably the most common externally shell-less opisthobranch occurring in the archipelago. Many more specimens were noted than were collected. The stations from which we have intertidal collections are: the Darwin Research Station at Academy Bay (stations 2 and 3); Flamingo Cove (station 10); and Duncan Island (station 30). In addition, 2 specimens were taken in 30m at a reef in Academy Bay (station 13).

Most of the specimens seen were the brilliant orange color that gives this species the common name of "orange blob." The one exception to this coloration was a specimen collected intertidally at Duncan Island (station 30) that was a bright lemon yellow. The radula, jaw plates, and shell are the same as those of the orange *Berthellina engeli.*

Pleurobranchus (Pleurobranchus) areolatus (Mörch, 1863)

Marcus & Marcus (1967) report this species from Florida to the Canal zone, Panama, in the western Atlantic and from Punta Peñasco to Guaymas, Sonora, Mexico, in the eastern Pacific. Bertsch (1971) reports it from the Las Cruces Bay area in Baja California, Mexico. The senior author also took this species intertidally at Sayulita, Nayarit, Mexico, in January 1970, and Keen (1971) extends the range to western Panama. Our collection records enable us to extend the range to the Galápagos Islands. We took one specimen from the intertidal area in Sullivan Bay (station 6) and one specimen from the intertidal area at Flamingo Cove (station 10). Two additional specimens were collected from 10½m at Jervis Island (station 27).

Chromodoris baumanni Bertsch, 1970

In his original description of the species, Bertsch (1970) cites locality records in the La Paz region of Baja California, Mexico, and from 20m in the Guaymas area of Sonora, Mexico. In January of 1970, the senior author also collected this species from the Santa Cruz and Sayulita areas in Nayarit, Mexico, where it was fairly abundant intertidally.

This species was photographed by Mr. Allyn G. Smith of the California Academy of Sciences, San Francisco, California, on his visit to Academy Bay in 1964 (personal communication). We also collected one specimen intertidally at the Darwin Research Station (station 2).

Chromodoris sedna (Marcus & Marcus, 1967)

Even though this species has only recently been named, it has long been known to be one of the most common nudibranchs from the Gulf of California to Nayarit, Jalísco, and Colima, in Mexico. The single specimen collected by us was taken intertidally at the Darwin Research Station on Academy Bay (station 2).

Hypselodoris agassizi (Bergh, 1894)

This species was synonymized with *Hypselodoris californiensis* (Bergh, 1879) by Pruvot-Fol (1959) and only recently reinstated as a valid species (Sphon, 1971b).

Hypselodoris agassizi ranges south along the Sonora coast of the Gulf of California in Mexico to its type locality in Panama. One specimen was collected intertidally at the Darwin Research Station on Academy Bay (station 2), and extends the range southward to the Galápagos Islands. Possibly it may range south to Peru or even to northern Chile.

Table 1

Species Collected	Collecting Stations																	
	2	3	6	7	8	9	10	12	13	15	18	22	23	27	28	30	31	34
Bulla punctulata A. Adams, 1850		×					×	×		×	×		×				×	×
Dolabrifera dolabrifera (Rang, 1828)	×		×				×					×			×	×		
Tylodina fungina Gabb, 1865					×			×										
Umbraculum ovale (Carpenter, 1856)				×														
Berthelinia chloris (Dall, 1918)							×											
Lobiger souverbiei Fischer, 1856							×											
Berthellina engeli Gardner, 1936	×	×					×		×								×	
Pleurobranchus areolatus (Mörch, 1863)			×				×							×				
Chromodoris baumanni Bertsch, 1970	×																	
Chromodoris sedna (Marcus & Marcus, 1967)	×																	
Hypselodoris agassizi (Bergh, 1894)	×																	

ACKNOWLEDGMENTS

We wish to extend our thanks to Twila Bratcher, Jackey Grundman, William E. Old, Jr., and Carolyn Stover for their help in the field. We also wish to thank Hans Bertsch, William K. Emerson, Richard Roller, Allyn G. Smith, and Edward Wilson for having critically read the manuscript. Most particularly, we wish to thank Mrs. Eveline Marcus for critically reading the manuscript and for her encouragement.

Literature Cited

ADAMS, ARTHUR
1850. Monograph of the family Bullidae. *In*: G. B. Sowerby, Thesaurus conchyliorum. London **2**: 553 - 608; plts. 119 - 125

AGARDH, J. G.
1872. Till algernes systematik, nya bidrag Forsta afd. Lunds Univ. Arsskr. **9** (8): 1 - 71

BERGH, LUDWIG SOPHUS RUDOLF
1879. On the nudibranchiate gastropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Proc. Acad. Nat. Sci. Philadelphia, prt. **1**: 71 - 132; plts. 1 - 8 (13 May 1879)
1894. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer "*Albatross*," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding. XIII. Die Opisthobranchien. Bull. Mus. Comp. Zool. Harvard Univ. **25** (10): 125 to 233; plts. 1 - 12 (October 1894)

BERTSCH, HANS
1970a. *Dolabrifera dolabrifera* (Rang, 1838): Range extension to the eastern Pacific. The Veliger **13** (1): 110 - 111 (1 July 1970)
1970b. Opisthobranchs from Isla San Francisco, Gulf of California, with the description of a new species. Contrib. Sci., Santa Barbara Mus. Nat. Hist. **1** (2): 1 - 16 (1 December 1970)
1971. Natural history and occurrence of opisthobranchs at Las Cruces, Baja California, Mexico, and vicinity. The Echo **3**: 16 (7 March 1971)

BØRGESEN, F.
1907. An ecological and systematic account of the Caulerpas of the Danish West Indies. Kongl. Danske Vidensk. Selsk. Skrift., vii, Naturvid. og Math. Afd. **4** (5): 337 - 392

CARPENTER, PHILIP PEARSALL
1856. Description of new species of shells collected by Mr. T. Bridges in the Bay of Panama and its vicinity, in the collection of Hugh Cuming, Esq. Proc. Zool. Soc. London, prt. **24** (for 1856): 159 - 166 (11 November 1856)

COCKERELL, THEODORE DRU ALISON & CHARLES ELIOT
1905. Notes on a collection of California nudibranchs. Journ. Malacol. **12** (3): 31 - 53

COLLIER, CLINTON L. & WESLEY MERRILL FARMER
1964. Additions to the nudibranch fauna of the east Pacific and Gulf of California. Trans. San Diego Soc. Nat. Hist. **13** (19): 377 - 396; illust. (30 December 1964)

DALL, WILLIAM HEALEY
1918. Description of new species of shells chiefly from Magdalena Bay, Lower California. Proc. Biol. Soc. Wash. **31**: 5 - 8 (27 Feb.)

DUSHANE, HELEN
1966. Range extension for *Tylodina fungina* Gabb, 1865 (Gastropoda). The Veliger **9** (1): 86 (1 July 1966)

EALES, NELLIE B.
1960. Revision of the world species of *Aplysia* (Gastropoda, Opisthobranchia). Bull. Brit. Mus. (Nat. Hist.), Zool. **5** (10): 269 - 404 (January 1960)

FISCHER, M.
1856. Descriptions d'espèces nouvelles. Journ. Conchyl., ser. 2, **1** (5): 273 - 277

GABB, WILLIAM MORE
1865. Descriptions of new species of marine shells from the coast of California. Proc. Calif. Acad. Sci. **3**: 182 - 190

GARDINER, A. P.
1936. Engel's paper on "The English species of the family Pleurobranchidae." Journ. Conchol. **20** (7): 195 - 198

KEEN, A. MYRA
1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

LEE, RICHARD S. & PATRICK BROPHY
1969. Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. The Veliger **12** (2): 220 - 221 (1 October 1969)

MCBETH, JAMES WARREN & R. D. BOWLUS
1969. Range extension of *Tylodina fungina* in the Gulf of California. The Veliger **12** (2): 229 (1 October 1969)

MACFARLAND, FRANK MACE
1905. A preliminary account of the Dorididae of Monterey Bay, California. Proc. Biol. Soc. Wash. **18**: 35 - 54 (2 February 1905)

MARCUS, EVELINE DU BOIS REYMOND & ERNST MARCUS
1967. American opisthobranch mollusks. Stud. Trop. Oceanogr. Miami, **6**: viii + 256 pp.; figs. 1 - 155 + 1 - 95 (December 1967)

MÖRCH, OTTO ANDREAS LOWSON
1863. Contributions à la faune malacologique des Antilles danoises. Journ. Conchyl. (3) **3** (11): 21 - 43

Orbigny, Alcide Dessalines d'

1837. Voyage dans l'Amérique Méridionale. Mollusques. Paris, **5** (3): 188

Pilsbry, Henry Augustus & Edward Guirey Vanatta

1902. Papers from the Hopkins Stanford Galapagos Expedition, 1898-1899. XIII. Marine Mollusca. Proc. Wash. Acad. Sci. **4**: 549 - 560; plt. 35 (30 September 1902)

Pruvot-Fol, Alice

1951. Révision du genre *Glossodoris* Ehrenberg. Journ. Conchyl. **91**(3-4): 76 - 164 (1 July 1951)

Rang, Paul Kabel Sander Leonard

1828. Histoire naturelle des aplysiens. Paris, Impr. Firmin Didot, 7+83 pp.; 25 plts.

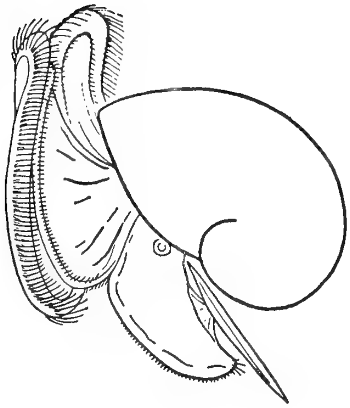
Sphon, Gale G.

1971a. New opisthobranch records for the eastern Pacific. The Veliger **13** (4): 368 - 369 (1 April 1971)

1971b. The reinstatement of *Hypselodoris agassizi* (Bergh, 1894) (Mollusca : Opisthobranchia). The Veliger **14** (2): 214 (1 Oct. '71)

Sphon, Gale G. & James Robert Lance

1968. An annotated list of nudibranchs and their allies from Santa Barbara County, California. Proc. Calif. Acad. Sci. (4) **36** (3): 73 - 84; 1 text fig. (25 September 1968)



Some Opisthobranchs (Mollusca:Gastropoda) from Oregon

BY

GALE G. SPHON

Los Angeles County Museum of Natural History, Los Angeles, California 90007

(1 Text figure)

INTRODUCTION

THE RUGGED ROCKY intertidal areas of coastal Oregon have been little explored for opisthobranchs, and literature pertaining to opisthobranchs from that geographical area is almost non-existent. Many of the collecting sites are in state parks, and collecting in them is either by permit from the Oregon State Fish Commission or is totally prohibited.

During the period from August 4 to 9, 1971, specimens of 19 species of opisthobranchs were collected intertidally at 5 localities in Oregon (Figure 1); these specimens are deposited in the Los Angeles County Museum of Natural History. All of the specimens collected, except those of *Coryphella fusca* O'Donoghue, 1921, were within the reported ranges of the respective species. Only *Acanthodoris nanaimoensis* O'Donoghue, 1921, has been reported from an Oregon locality (Coos Bay) (STEINBERG, 1963).

REVIEW OF THE LITERATURE

GOULD (1842: 311) stated: "Several nudibranchiate gastropods were observed in the Oregon region, but none of them were figured or described in sufficient detail to furnish specific characters." This is the first literature record that I am able to find of any opisthobranchs from Oregon. The first species cited was in 1857 when Carpenter recorded *Melibe leonina* (Gould, 1852). However, he gave no specific locality. O'DONOGHUE (1926: 236) stated that there was one locality from Oregon in his list of 101 species of opisthobranchs from the Pacific coast, but that locality is not to be found mentioned in his paper. MARCUS (1961) recorded 3 species: *Onchidella borealis* Dall, 1871, from Sunset Bay; *Aglaja diomedea* (Bergh, 1893), from Charleston; and *Armina columbiana* O'Donoghue, 1924 [=*A. californica* (Cooper, 1863a)] from Oregon. STEINBERG (1963) cited *Acanthodoris nanaimoensis* and BEEMAN (1963) recorded *Phyllaplysia taylori* Dall, 1900. Both species were from Coos Bay. OSIS & GIBSON (1970) figured *Hermissenda crassicornis* (Eschscholtz, 1831) and *Archidoris montereyensis* (Cooper, 1863a) but gave no specific locality for the specimens. The most recent record is by THOMPSON (1971) of two occurrences of *Tritonia exsulans* Bergh, 1894, from "off the Oregon coast" in depths of 1000 and 1200m.

COLLECTING LOCALITIES

1) Depoe Bay State Park, Lincoln County, Oregon

A small area of shelf rock, located directly across Highway 101 from the main shopping area, including several large tide pools, runnels, and surge channels.

2) Seal Rocks State Park, Lincoln County, Oregon

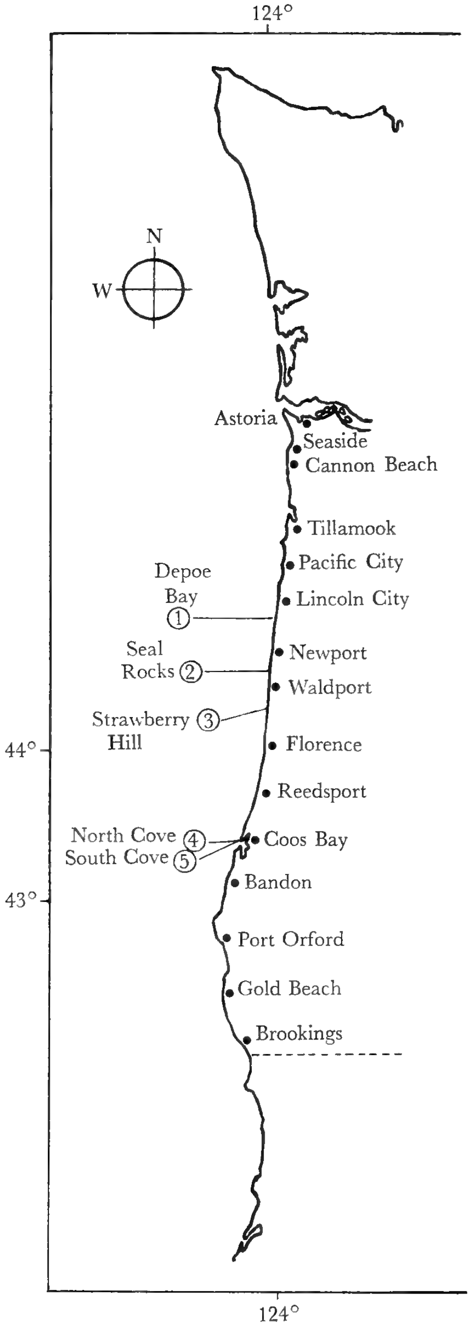
A large area with numerous undercut rock reefs and small islands; there are also many runnels and tide pools exposed at low tide. The majority of the specimens collected here were in tide pools, many of them clinging to the surface film of the water, others on the sides of the pools or on the algae in the pools.

3) Strawberry Hill, Neptune State Park, Lane County, Oregon

The area just south of Strawberry Hill consists of a gravel beach next to the bluffs, a series of rounded wave-washed boulders, and a large shelf area with large runnels and tide pools, uncovered at low tide.

4) North Cove, Cape Arago State Park, Coos County, Oregon

On a very low tide it is possible to make one's way out to Shell Island over the shelf rock. Much of the shelf is covered with boulders, tide pools and rock reefs which afford many varieties of habitats.



5) South Cove, Cape Arago State Park, Coos County, Oregon

The west side of this cove is generally made up of medium sized boulders and small tide pools. Most of the opisthobranchs from this locality were either in tide pools, on the sides of ledges or rocks, or gliding suspended from the surface film of the water.

Table 1

	Depoe Bay	Seal Rocks	Strawberry Hill	North Cove	South Cove
Acanthodoris hudsoni			1		
Acanthodoris nanaimoensis		4	14		
Antiopella barbarensis		15[1]	4[1]	7[1]	
Archidoris montereyensis	10[1]		8	1	
Catriona alpha					8
Coryphella fusca		1			
Coryphella trilineata					3
Dendronotus frondosus		2	6		
Diaulula sandiegensis	1	3	7	3	9
Dirona albolineata		10	17[1]	11[1]	
Eubranchus sp.			1		
Hermissenda crassicornis	3	1[1]	4[1]		4
Laila cockerelli					1
? *Pleurobranchus* sp.			1		
Rostanga pulchra	2	11	14	1	8
Trinchesia abronia				1	2
Trinchesia albocrusta		1			
Triopha carpenteri		7	20[1]	10[1]	6
Tritonia festiva				1	3

---

[1] many more specimens seen

LIST OF SPECIES

The species are arranged alphabetically, the names used being the currently accepted ones. The overall geographic distribution is given, as are a few remarks on the habitat. My major sources for the distributional data are: Gosliner & Williams, 1970; Hurst, 1967; Lance, 1961; Marcus, 1961; O'Donoghue, 1926; Roller, 1970; Roller & Long, 1969; Sphon & Lance, 1968; and Steinberg, 1963.

At the end of the list will be found names of additional species, culled from the literature, that have been reported as occurring in Oregon.

Acanthodoris hudsoni MacFarland, 1905

Vancouver Island, British Columbia, Canada, southward to Shell Beach, San Luis Obispo County, California.

Only one specimen was collected; it was found suspended from the surface film of a tide pool at Strawberry Hill.

Acanthodoris nanaimoensis O'Donoghue, 1921

Vancouver Island, British Columbia, Canada, southward to Shell Beach, San Luis Obispo County, California.

This species was found at Seal Rocks and Strawberry Hill. In every instance the specimens were on the sides of ledges or rocks in tide pools.

Antiopella barbarensis (Cooper, 1836b)

Vancouver Island, British Columbia, Canada, southward to San Quintín, Baja California, Mexico.

While this species was not found at Depoe Bay or South Cove, it remains the most common species (in number) collected or observed. The usual habitat was the surface film of the water in quiet tide pools. In one large pool at Strawberry Hill I counted over 125 specimens, both in the pool and clinging to the surface film of the water.

Archidoris montereyensis (Cooper, 1863)

Alaska southward to San Diego, San Diego County, California.

This species was not found at Seal Rocks or South Cove. Apparently it prefers the rough pounding of the open sea. At Depoe Bay it was found in deep surge channels in fair numbers and because of the inaccessibility of the habitat only a few could be collected; many more were observed.

At Strawberry Hill specimens were collected from under a seaweed-covered ledge that was exposed for only a short time at dead low tide.

At North Cove, 1 specimen was found under a seaweed-covered ledge at extreme low tide.

Catriona alpha (Baba & Hamatani, 1963)

San Juan Islands, Puget Sound, Washington, southward to San Diego, San Diego County, California; also found in Japan.

All specimens of this small aeolid were found under rocks in tide pools at South Cove. In a few instances egg masses were present at the time the specimens were collected.

Coryphella fusca O'Donoghue, 1921

Departure Bay, Vancouver Island, British Columbia, Canada, southward to Seal Rocks State Park, Lincoln County, Oregon (the former southern record was the San Juan Islands, Puget Sound, Washington).

One large specimen was found on an algal stipe in a tide pool at Seal Rocks.

Coryphella trilineata O'Donoghue, 1921

Vancouver Island, British Columbia, Canada, southward to Coronados Islands, Baja California, Mexico.

Only 3 specimens of this beautiful small aeolid were found; all were taken at South Cove under rocks in tide pools.

Dendronotus frondosus (Ascanius, 1774)

Cosmopolitan in the northern hemisphere.

This species was found at both Strawberry Hill and Seal Rocks. All specimens were crawling on the stipes of kelp in tide pools or large, quiet open areas.

Diaulula sandiegensis (Cooper, 1863a)

Alaska to Cabo San Lucas, Baja California, Mexico; also reported from Japan.

Diaulula sandiegensis was found at all 5 localities, but not in as great numbers as *Antiopella barbarensis* or *Hermissenda crassicornis*. Most of the specimens were located on the sides of ledges or rocks covered by the overhanging seaweed and were from 1 to 3 inches (25 to 75mm) in length. There was variation in both the basic color and oval markings. The color ranged from dark brown to almost white. The number of the "rings" varied from 4 to 18.

Dirona albolineata Cockerell & Eliot, 1905

Puget Sound, Washington, southward to San Diego, San Diego County, California; also reported from the U. S. S. R.

This is one of the most strikingly beautiful opisthobranchs collected. It was very abundant at 3 localities: Seal Rocks, Strawberry Hill, and North Cove. The size ranged from approximately 1 to 4 inches (25 to 100mm) in length. The habitat was either on the sides of tide pools or on the kelp in the pools. In a few cases, specimens had been stranded in exposed kelp as the tide receded.

Eubranchus sp.

One specimen was found in seaweed in a tide pool at Strawberry Hill.

Hermissenda crassicornis (Eschscholtz, 1831)

Sitka, Alaska, southward to Punta Eugenia, Baja California, Mexico.

While this species was not quite as abundant as *Antiopella barbarensis,* it was found at all 5 localities and in very much the same type of habitat.

Laila cockerelli MacFarland, 1905

Vancouver Island, British Columbia, Canada, southward to Cape San Lucas, Baja California, Mexico.

Only 1 specimen was found and it was taken at South Cove. The specimen was the typically colored "northern" form of the species with the row of white "buttons" down the center of the dorsum.

? *Pleurobranchus* sp.

One specimen was found on the side of a tide pool at Strawberry Hill.

Rostanga pulchra MacFarland, 1905

Vancouver Island, British Columbia, Canada, southward to Chile.

This species was found at all 5 localities. Most often it was in the open at the bottom of tide pools, but occasionally along the sides of rocks.

Trinchesia abronia (MacFarland, 1966)

Mukkaw Bay, Washington, southward to Pismo Beach, San Luis Obispo County, California.

Specimens were found at both North and South Coves at Cape Arago. Those at North Cove were on algal stipes, while those at South Cove were under rocks.

Trinchesia albocrusta (MacFarland, 1966)

Friday Harbor, Washington, southward to Pismo Beach, San Luis Obispo County, California.

One specimen was collected from seaweed at Seal Rocks.

Triopha carpenteri (Stearns, 1873)

Vancouver Island, British Columbia, Canada, southward to San Diego, San Diego County, California; also found in Japan.

The only locality where *Triopha carpenteri* was not found was Depoe Bay. It was moderately common to abundant at the other 4 sites. Ordinarily, *Triopha* was found in tide pools, either on the sides or bottom or crawling on the algae. Occasionally, as *Dirona,* it would be trapped in exposed seaweed when the tide receded. Specimens ranged from less than 1 inch (25 mm) to over 4 inches (100 mm) in length.

Tritonia festiva (Stearns, 1873)

Vancouver Island, British Columbia, Canada, southward to Los Coronados Islands, Baja California, Mexico.

Specimens were found on the undersides of rocks in tide pools at both North and South Cove.

ADDITIONAL SPECIES REPORTED FROM OREGON

Aglaja diomedea (Bergh, 1894)

Alaska southward to Morro Bay, San Luis Obispo County, California.

Armina californica (Cooper, 1863a)

Vancouver Island, British Columbia, Canada, southward to Panama.

Melibe leonina (Gould, 1852)

Alaska southward to Punta Hipolito, Baja California, Mexico.

Onchidella borealis Dall, 1871

Alaska southward to Duxbury Reef, Marin County, California.

Phyllaplysia taylori Dall, 1900

San Juan Islands, Puget Sound, Washington, southward to San Diego, San Diego County, California.

Tritonia exsulans Bergh, 1894

Alaska to Punta Santo Domingo, Baja California, Mexico; also reported from Japan; Manatee Bay, Florida; and Panama Bay on the Atlantic coast of Panama.

ACKNOWLEDGMENTS

I wish to express my thanks to the Fish Commission of Oregon for its help and the permit to collect in restricted areas (Permit no. 233-71). I also wish to thank Mr. Richard Roller for helping with the identifications of the aeolids and for critically reading the manuscript.

Literature Cited

ASCANIUS, PEDER
1774. Beskrivelse over en Norsk Sneppe Oget Søedyr (Molluscum *Amphitrite frondosa*). Det. Kong. Norsk. vidensk. selsk. skrift. **5:** 135 - 158 [not seen]

BABA, KIKUTARÔ & IWAO HAMATANI
1963. A cuthonid, *Cuthona alpha* n. sp. with a radula of *Catriona* type (Nudibranchia-Eolidoidea). Publ. Seto Mar. Biol. Lab. **11** (2): 339 - 343; plt. 11

BEEMAN, ROBERT DAVID
1963. Variation and synonymy of *Phyllaplysia* in the northeastern Pacific (Mollusca : Opisthobranchia). The Veliger **6** (1): 43 - 47; 5 text figs. (1 July 1963)

BERGH, LUDWIG SOPHUS RUDOLF
1894. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer "*Albatross*," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding. XIII. Die Opisthobranchien. Bull. Mus. Comp. Zool. Harvard Univ. **25** (10): 125 to 233; plts. 1 - 12 (October 1894)

CARPENTER, PHILIP PEARSALL
1864. Supplementary report on the present state of our knowledge with regard to the mollusca of the west coast of North America. Reprt. Brit. Assoc. Adv. Sci. for **1863:** 517 - 686 (August 1864)

COCKERELL, THOMAS DRU ALISON & CHARLES N. E. ELIOT
1905. Notes on a collection of California nudibranchs. Journ. Malacol. **12** (3): 31 - 53; plts. 7, 8

COOPER, JAMES GRAHAM
1862a. On some new genera and species of California Mollusca. Proc. Calif. Acad. Sci. (1) **1** (2): 202 - 207 (January 1863)
1862b. On new or rare Mollusca inhabiting the coast of California. Proc. Calif. Acad. Sci. (1) **3:** 56 - 60 (September 1863)

DALL, WILLIAM HEALEY
1871. Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. Amer. Journ. Conchol. **7** (2): 93 - 160; plts. 13 - 16 (2 November 1871)

ESCHSCHOLTZ, JOHANN FRIEDRICH
1831. Zoologischer Atlas enthaltend Abbildungen und Beschreibungen neuer Thierarten, während des Flottencapitains von Kotzebue zweiter Reise um die Welt, auf der russisch-kaiserlichen Kriegsschlupp *Predpriaetiĕ* in den Jahren 1823-1826. prt. **4:** 1 - 19; plts. 16 - 20 (Berlin, G. Reimer) [not seen]

Gosliner, Terrence M. & Gary C. Williams
1970. The opisthobranch mollusks of Marin County, California. The Veliger **13** (2): 175 - 180; 1 map (1 October 1970)

Gould, Augustus Addison
1852. United States exploring expedition during the years 1838, 1839. 1840, 1841, 1842 under the command of Charles Wilkes, U. S. N. **12:** Mollusca shells, pp. 1 - 510

Hurst, Anne
1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. The Veliger **9** (3): 255 - 288; plts. 26 - 38; 31 text figs. (1 January 1967)

Lance, James Robert
1961. A distributional list of southern California opisthobranchs. The Veliger **4** (2): 64 - 69 (1 October 1961)

MacDonald, Gary R.
1970. Range extensions for *Acanthodoris hudsoni* MacFarland, 1905, and *Onchidoris bilamellata* (Linnaeus, 1767). The Veliger **12** (3): 375 (1 January 1970)

MacFarland, Frank Mace
1905. A preliminary account of the Dorididae of Monterey Bay, California. Proc. Biol. Soc. Wash. **18:** 35 - 54
1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. **6:** xvi+546 pp.; 72 plt. (8 April 1966)

Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger **3** (Supplmt. I): 1 - 85; plts. 1 - 10 (1 February 1961)

O'Donoghue, Charles Henry
1921. Nudibranchiate Mollusca from the Vancouver Island region. Trans. Roy. Canad. Inst. **13** (1): 147 - 209; plts. 7 - 11 (21 Feb. '21)
1926. A list of the Nudibranchiate Mollusca recorded from the Pacific coast of North America with notes on their distribution. Trans. Roy. Canad. Inst. **15** (2): 199 - 247

Osis, Laimons & Gary Gibson
1970. A guide to Oregon's rocky intertidal areas. Educat. Bull. no. 5 (Fish Comm. Oreg.): 1 - 34 (July 1970)

Robilliard, Gordon A.
1971. Range extensions of some northeast Pacific nudibranchs (Mollusca : Gastropoda : Opisthobranchia) to Washington and British Columbia, with notes on their biology. The Veliger **14** (2): 162 - 165 (1 October 1971)

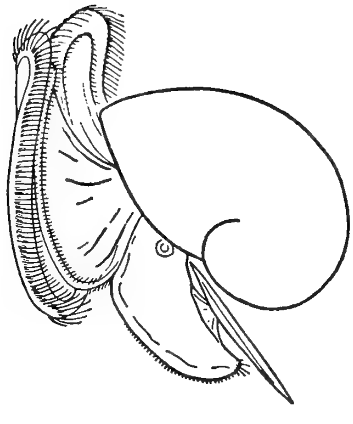
Roller, Richard A.
1970. A supplement to the annotated list of opisthobranchs from San Luis Obispo County, California. The Veliger **12** (4): 482 - 483 (1 April 1970)

Roller, Richard A. & Steven J. Long
1969. An annotated list of opisthobranchs from San Luis Obispo County, California. The Veliger **11** (4): 424 - 430; 1 map (1 April 1969)

Sphon, Gale G. & James Robert Lance
1968. An annotated list of nudibranchs and their allies from Santa Barbara County, California. Proc. Calif. Acad. Sci. **36** (3): 73 - 84; 1 text fig. (25 September 1968)

Steinberg, Joan Emily
1963. Notes on the opisthobranchs of the west coast of North America. — IV. A distributional list of opisthobranchs from Point Conception to Vancouver Island. The Veliger **6** (2): 68 - 73 (1 October 1963)

Thompson, Thomas Everett
1971. Tritoniidae from the North American Pacific coast (Mollusca: Opisthobranchia). The Veliger **13** (4): 333 - 338; 3 text figs. (1 April 1971)



NOTES & NEWS

First Recorded Occurrence of *Littorina tessellata* Philippi, 1847, from the Shores of North America

BY

FRASIER O. BINGHAM

Rosenstiel School of Marine and Atmospheric Science
University of Miami, Miami, Florida 33149 [1]

(1 Text figure)

On July 13, 1971, a single living specimen of *Littorina tessellata* Philippi, 1847, was collected by the writer from a concrete bulkhead located on the Biscayne Bay side of Key Biscayne, Florida (25°40′N, 80°10′W). The specimen, a female, has a shell length of 14½ mm.

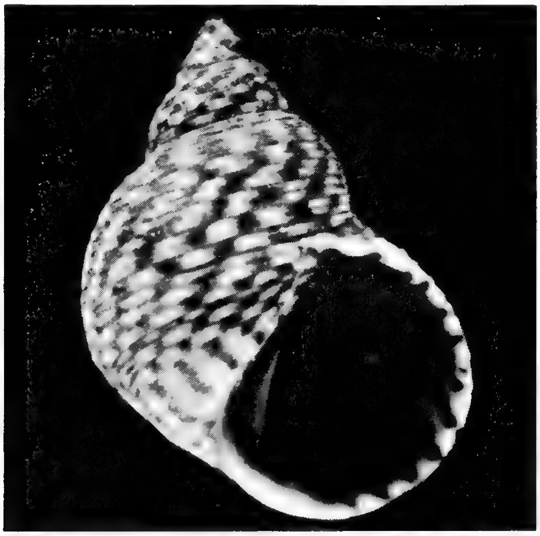


Figure 1

Littorina tessellata Philippi, 1847
14.5 mm

Bequaert (1943), who refers to the snail as *Littorina nebulosa tessellata,* lists its range at "Bahamas, Antilles and the Caribbean coast of South America." Warmke & Abbott (1961) also place the snail as a subspecies of *L. nebulosa* and note that it has been reported from Puerto Rico.

The museum of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, contains 2 lots of this species that may have been collected in the Florida Keys in the early 1920's. The data for these specimens, however, cannot be relied upon as the particular collection in which they appear had been badly neglected before being donated to the museum.

My thanks go to Dr. Joseph Rosewater of the United States National Museum who verified the identification of the species.

The specimen, shown in Figure 1, is now in the U. S. National Museum collection.

Literature Cited

Bequaert, Joseph Charles
1943. The genus *Littorina* in the western Atlantic. Johnsonia **7:** 1 - 28; plts. 1 - 7

Warmke, Germaine L. & Robert Tucker Abbott
1961. Caribbean seashells; a guide to the marine mollusks of Puerto Rico and other West Indian islands, Bermuda and the lower Florida Keys. Livingston Publ. Co., Narberth, Pa. x+345 pp.; 44 plts.; 34 text figs.

---

[1] Contribution No. 1504 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science, 10 Rickenbacker Causeway, Miami, Florida 33149

Supplement to Volume 7: $2.-* plus $-.60 handling charge

[Glossary of A Thousand-and-One Terms used in Conchology, compiled by WINIFRED H. ARNOLD]

Supplement to Volume 11: $5.-* plus $-.75 handling charge.

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Vol. 14: $5.-* plus $-.75 handling charge

[The Northwest American Tellinidae by Dr. E. V. Coan]

Items marked with * are subject to sales tax in the State of California; residents of that State please add the appropriate amount to their remittances.

Prices subject to change without notice.

Send orders with remittance to:

Mrs. Jean M. Cate, *Manager,* Post Office Drawer R, Sanibel, Florida 33957. Please make checks payable to C. M. S., Inc.

Shipments of material ordered are generally made within two weeks after receipt of remittance.

Subscription to Volume 15: $18.- domestic, $19.50 in Canada, Mexico, Central and South America; $20.- in all other foreign countries.

{We are pleased to announce that we have completed arrangements with Kraus Reprint Co. to reprint those of our publications that are out of print. Inquiries regarding the availability and price(s) of desired items should be addressed to:

Kraus Reprint Co.
16 East 46th Street,
New York, N. Y. 10017

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first working day of the month following receipt of the remittance. The same policy applies to new members.

Affiliate Membership for the fiscal year July 1, 1972 to June 30, 1973 has been set at $8.-. Postage for members in Canada, Mexico, Central and South America $1.50, for members in any other foreign country $2.- additional.

Effective January 1, 1967 there will be an initiation fee of $2.- for persons joining the Society.

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.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $2.50 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Supplements

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

Requests to be placed on this special mailing list should be sent to the Manager, Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address.

We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. Effective January 8, 1968 the following charges must be made:

change of address – $1.-
change of address and re-mailing of a returned issue – $2.-.

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.

General Notices

REGARDING POSTAL SERVICE

While increases in postal charges were anticipated, the actual amount involved could not be ascertained until 4 days before the effective date. Thus, we have been unable to adjust our membership dues and subscription rates to cover these increases. Effective immediately, we must also raise our handling charges for backissues and other materials. Further, we will not acknowledge the receipt of manuscripts, unless an addressed envelope with the necessary postage is enclosed.

We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address). We are not able to replace lost copies free of charge but must charge single copy rates. There will, of course, be only the usual charge of $1.00 for re-forwarding a copy *IF* it has been returned by the post office to us. We also must urge our members and subscribers to place written complaints with the U. S. Post Office Department in case of loss, as every copy of our journal carries our guarantee for return postage. Thus, destruction of a copy of our journal by postal employees constitutes gross negligence and the person concerned deserves an official reprimand, at least.

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

CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue

Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Endowment Fund

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

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

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

Western Society of Malacologists

THE SIXTH ANNUAL MEETING of the Western Society of Malacologists will be held at the Asilomar Conference Grounds in Pacific Grove, California July 11 to 14, 1973 and will feature contributed papers, symposia, displays and study workshops on molluscan subjects. Inquiries may be sent to the Secretary, Mrs. Edith Abbott, 1264 W. Cienega Avenue, San Dimas, CA 91773. Applications for membership in the Society should be sent to the Treasurer, Mr. Glenn Burghardt, 14453 Nassau Road, San Leandro, CA 94577. Dues are $2.50 for regular members and $1.00 for students.

Executive Board Members for the year are:
President: Mrs. Twila Bratcher; *First Vice-President*: Dr. James H. McLean; *Second Vice-President*: Dr. James Nybakken; *Secretary*: Mrs. Edith Abbott; *Treasurer*: Mr. Glenn Burghardt; *Members-at-Large*: Dr. George Radwin and Dr. George Davis; the three most recent *Past Presidents*: Dr. A. Myra Keen; Dr. Eugene V. Coan, and Mrs. Beatrice L. Burch.

BOOKS, PERIODICALS, PAMPHLETS

On some *Patinopecten* from North America

by KÔICHIRÔ MASUDA. Palaeontological Society of Japan Transactions, N. S. no. 83; pp. 166 - 178; plts. 19 - 21. September 20, 1971.

This useful report treats all species referred to the Miocene to Recent genus *Patinopecten*. The taxonomic focus, however, is on two zoogeographically significant Pliocene genera that have heretofore been incorrectly assigned to this eastern North Pacific genus. *Leopecten*, a new genus from the Gulf of California, provides early evidence of a land barrier between the Atlantic and Pacific Oceans. *Mizhuopecten* from coastal Washington is one of four western Pacific genera that migrated eastward during the Pliocene providing important ties across the North Pacific.

W. O. Addicott.

Seashells

by S. PETER DANCE. Hamlyn Publishing Group Limited, London. 159 pp.; 332 figs. in color; 40 pence. 1971.

This new paperback starts out like other introductory books on mollusks with the necessary survey of classes, habitats, and geographical distribution and the usual systematic review. Where it differs from others is by its frankly limiting the coverage to the mollusks with economic value, those that have been used by man in various ways or that have become objects much coveted by collectors.

Illustrations are by James Nicholls, original paintings of exceptional fidelity, almost photographic in texture. All are fresh and new, not copied from previous figures. The style of the book is easy, relaxed, and readable, with enough humor to maintain interest. The anectodes about the various species are carefully culled from the literature and have the ring of authenticity even though space is lacking for documentation. The author is in a position to provide trustworthy data, and he does; the work is scientific in format, even to complete adoption of the metric system (the reader must learn to cope not only with millimeters and centimeters for length but also with kilograms for weight). In a first reading of the book only a few minor points were noted that one suspects the author will correct in later editions, such as the inverted orientation of *Penicillus* (cited under the non-binomial name *Brechites*) and an unduly long range for the Californian *Serpulorbis squamigerus* (cited as "*Aletes*").

There are short chapters on collecting and buying, on books to read, and on shell clubs of the world. The latter list is admittedly incomplete but should prove useful to the neophyte. One wonders, however, what the basis was for selection of the 21 clubs mentioned, especially the 3 for the United States, for these cited would seem to be a very uneven sampling from the standpoint of size, activity, accessibility, and location.

This book can be recommended as one of the best of its kind on the current market, and it should appeal to a wide spectrum of readers.

VLL'

Malacological Review

P. O. Box 801, Whitmore Lake, Michigan 48189, U. S. A. vol. 5: 94 pp.; illust. 1972

In addition to 3 brief communications, this issue contains the abstracts and proceedings of the 'Mollusk Seminar, Ann Arbor, 1971.' A new addition to the list of departments is a section of obituaries. An announcement of a forthcoming supplement to the current volume, but not included in the subcription rate, should be of interest to serious students of malacology. The topic will be" The freshwater mollusks of Taiwan (Formosa).'

RS

Index to the Revista de la Sociedad Malacologica 'Carlos de la Torre'

Volumes 1-9, 1943-1954 (all volumes issued)

compiled by Morris K. Jacobson. Sterkiana **44**: pp. 1-44, December 1971. Copies available at US$1.00 from the compiler whose address is: 455 Beach 139th Street, Rockaway, N. Y. 11694.

While this work is not very exciting reading - such as a mystery story by one of the more skillful writers - it is, however, of far greater value. A few random samples convince us that the work is accurate and apparently exhaustingly complete. To the fortunate owners of the set of the 'Revista' or, for that matter, even a part of it, this will prove to be one dollar well spent.

RS

Proceedings of the First International Conference on Meiofauna

Neil C. Hulings, ed. Smithsonian Contributions to Zoology No. 76; Washington, D. C.; 1971. 205 pp.; illust. Available at $2.25 (paper cover) from Superintendent of Documents, U. S. Govmt. Printing Office, Washington, D. C. 20402

This work contains 27 papers of 30 presented at the first International Conference on Meiofauna, held in Tunis, Tunisia, July 1 to 11, 1969.

The various papers are arranged under 3 subheadings; 1. Systematics and ecology of meiofauna taxa; 2. Ecology of meiofauna; 3. Sampling for meiofauna.

Of special interest to malacologists is the paper by Bertil Swedmark: A review of Gastropoda, Brachiopoda, and Echinodermata in marine meiobenthos (pp. 41 to 45.

RS

British Prosobranchs

by Alastair Graham. Synopses of the British fauna (new series) no. 2. pp. 1 - 112; 119 text figures. Academic Press, London and New York. US$ 4.00. December 31, 1971.

The full title on the flyleaf reads: British prosobranch and other operculate gastropod molluscs, keys and notes for the identification of the species.

The material is well organized and the illustrations, line drawings, are of excellent quality. While, no doubt, this work will be of primary importance to our British and European readers, it will also be helpful to students of the groups treated, no matter where they may be working. In view of present-day book prices, the cost of this book seems modest.

RS

Australian Seashores in Colour

by Keith Gillett and John Yaldwin. C. E. Tuttle Company, Rutland, Vermont. 112 pp.; 64 color photographs, 49 black-and-white photographs. September 30, 1970. U. S. $5.00.

Aimed at the amateur, this book contains superb color photographs beautifully reproduced, of the more spectacular marine animals encountered along the Australian shores. It may be considered a companion volume to the next book.

RS

The Australian Great Barrier Reef in Colour

by Keith Gillett. C. E. Tuttle Company, Rutland, Vermont. 111 pp.; 50 color plates; 16 white-and black plates. August 9, 1971. No indication of price.

This book is also distinguished by its excellent color photographs. Ten of the color plates are devoted to some of the mollusks at home in the area of the Great Barrier Reef. We were especially pleased with the 5 plates portraying living animals. Other animal groups are also represented by pictures of living examples.

RS

Australian Crustaceans in Colour

by Anthony Healy and John Yaldwin. C. E. Tuttle Company, Rutland, Vermont. 112 pp.; 52 color plates. 1972. US$6.75.

Like the others in this series, this book appeals to the eye with its outstanding reproductions of excellent color photographs. Of interest to the malacologist will be the figures showing hermit crabs with the molluscan shell occupied and the commensal shrimp (not visible in the illustration) in the black-lip pearl oyster.

RS

{These three books are 18.5 cm (7$\frac{3}{8}$ inches) wide and 17.5 cm (6$\frac{7}{8}$ inches) high.}

The Sea Shells of Sagami Bay, collected by His Majesty the Emperor of Japan.

Described by Tokubei Kuroda, Tadashige Habe, and Katura Oyama. Edited by the Biological Laboratory, Imperial Household. Published by Maruzen Co., Tokyo. 1971. Pp. 1 - 741 in Japanese; 121 plates (105 in color); + pp. 1 - 489 in English; Index, pp. 1 - 51 in English and Japanese; 1 foldout map. 13 000 Yen ($58.-).

By any criterion, this is an impressive book – by the numbers of species that could be collected in a single Japanese bay; by the number and quality of the color plates; or by sheer size (it weighs a little over 8 pounds). The color illustrations are done at natural size; smaller forms that need greater magnification are included on the black and white plates.

New taxa are described by various combinations of the authors, and thus the citations may prove cumbersome; for example, in Muricidae, the genus *Reishia* Kuroda and Habe should also be cited as "in Kuroda, Habe, and Oyama." A new subfamily, Ergalataxinae, is proposed in Muricidae, to include some species hitherto classified in Trophoninae and Thaididae, subfamily Drupinae. Unfortunately, here as with a number of other of the new taxa, reasons for proposal and comparisons with the most closely related units are either omitted or are over-brief.

Synonymies are given for all of the 1121 species and subspecies, with a statement of type locality and exact localities of collection. Notes on general distribution and ecology of each one also are included. Of the taxa described as new there are 30 genera and subgenera and 104 species and subspecies. Because of the wide distribution of many of the species in the Indo-Pacific, the book will have usefulness far beyond the limits of southern Japan, and it is one that any collector could be proud to own.

MK

Latin and Greek for Biologists

by T. H. Savory. Pp. 1 - 34. Merrow Publishing Co., Ltd. Watford, England, 1971. US$ 4.00.

The author was spurred on to prepare this small (5$\frac{1}{2}$ by 8$\frac{1}{2}$ inches) booklet by the observation that the teaching of Latin and Greek has been more and more de-emphasized and finally completely abandoned in most schools. Consequently, modern biologists are ill equipped to understand the meanings of names of organisms nor are they able to savor the gentle – and, sometimes the not so gentle – humor of earlier authors. In the opinion of this reviewer, the lack of the so-called classical education accounts, no doubt, for the prevalence of patronymics used to name new taxa in relatively recent times.

This small booklet, within its limited scope, attempts to guide modern authors over some of the pitfalls caused by the lack of this knowledge. It could be wished that considerably more material had been presented without increasing the relatively high price, although the make-up of the booklet si worthy of a far more ambitious work.

RS

Molluscan Digest

The International Publication for Malacological Research volume 2, number 8, August 1, 1972; pp. 85 - 96. Obtainable on subscription (rates: inquire of either editor). Edited by Steven J. Long, 110 Cuyama Avenue, Pismo Beach, California 93449 and Jack Brookshire, 2962 Balboa Avenue, Oxnard, California 93030.

This publication, by being limited essentially to the citation of malacological articles and books, has an enviable record of keeping abreast of the current literature. The editors also seem to enjoy active cooperation from many sources, no doubt because the publication fills a very important need. Mr. Long will, upon request, send sample copies. The subscription rate, in view of the important service rendered, is modest.

RS

A Catalog of Dealers' Prices for Marine Shells

by Tom Rice. Third edition. 70 pp., 8½ by 11 inches. $3.-. Of Sea and Shore Publ. Port Gamble, Washington 98364. May 1, 1972.

As in the previous editions of this list, the prices quoted for shells seem more realistic than in some other similar publications. They can well be the basis for exchanges among collectors.

RS

Simpósio Brasileiro de Paleontologia

Anais da Academia Brasileira de Ciências, supplement to volume 40: 661 pp.; numerous illustrations. Rio de Janeiro GB, December 30, 1971.

The Brazilian Symposium on Paleontology was held in Rio de Janeiro September 20 to 25, 1971. This volume includes 47 of the papers presented; among them one by W. P. Woodring, entitled: Zoogeographic affinities of the Tertiary marine molluscan Faunas of Northeastern Brazil (pp. 119 - 124; 3 text figures). This seems the only paper that dealt with mollusks exclusively. Most papers are in Portuguese, 8 in English and 1 in French. As is to be expected, the topics run the gamut of about all branches of Paleontology and several papers are concerned with Foraminifera and several have a bearing on Gondwana.

Unfortunately we are unable to state how this valuable volume may be procured except by suggesting that those interested inquire of Dr. Herman Lent, President of the Editorial Commission, Caixa Postal 229 – ZC-00 – Rio de Janeiro, GB – Brazil.

RS

We are pleased to be able to include herewith the halftone plates which, due to circumstances beyond our control, had to be omitted from our July issue. The plates should be inserted to face the pages listed as follows:

Rehder, Figures *1* to *7*	10
Rehder, Figures *1* to *9*	12
Rokop, Figures *1* to *7*	16
Rokop, Figures *8* to *15*	18
Petuch	52
Ferreira	56
D'Eliscu	58

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.

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 other 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, may be published in the column "NOTES and NEWS"; in this column will also appear notices of meetings of regional, national and international malacological organizations, such as A. M. U., U. M. E., W. S. M., etc., as well as news items which are deemed of interest to our Members and subscribers in general. Articles on "METHODS and 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, and 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, not exceeding 8½" by 11", at least double spaced and accompanied by a clear carbon or photo 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.

EDITORIAL BOARD

Dr. Donald P. Abbott, *Professor of Biology*
Hopkins Marine Station of Stanford University

Dr. Jerry Donohue, *Professor of Chemistry*
University of Pennsylvania, Philadelphia, *and*
Research Associate in the Allan Hancock Foundation
University of Southern California, Los Angeles

Dr. J. Wyatt Durham, *Professor of Paleontology*
University of California, Berkeley, California

Dr. E. W. Fager, *Professor of Biology*
Scripps Institution of Oceanography, La Jolla
University of California at San Diego

Dr. Cadet Hand, *Professor of Zoology and*
Director, Bodega Marine Laboratory
University of California, Berkeley, California

Dr. Joel W. Hedgpeth, *Resident Director*
Marine Science Laboratory, Oregon State University
Newport, Oregon

Dr. A. Myra Keen, *Professor of Paleontology and*
Curator of Malacology, Emeritus
Stanford University, Stanford, California

Dr. Victor Loosanoff, *Professor of Marine Biology*
Pacific Marine Station of the University of the Pacific

Dr. John McGowan, *Associate Professor of*
Oceanography
Scripps Institution of Oceanography, La Jolla
University of California at San Diego

Dr. Frank A. Pitelka, *Professor of Zoology*
University of California, Berkeley, California

Dr. Robert Robertson, *Chairman and Pilsbry Chair*
of Malacology, Department of Malacology
Academy of Natural Sciences of Philadelphia

Dr. Peter U. Rodda,
Chairman and Curator, Department of Geology
California Academy of Sciences, San Francisco

Mr. Allyn G. Smith, *Research Associate*
Department of Geology
California Academy of Sciences, San Francisco

Dr. Ralph I. Smith, *Professor of Zoology*
University of California, Berkeley, California

Dr. Charles R. Stasek, *Associate Professor*
of Zoology
Florida State University, Tallahassee, Florida

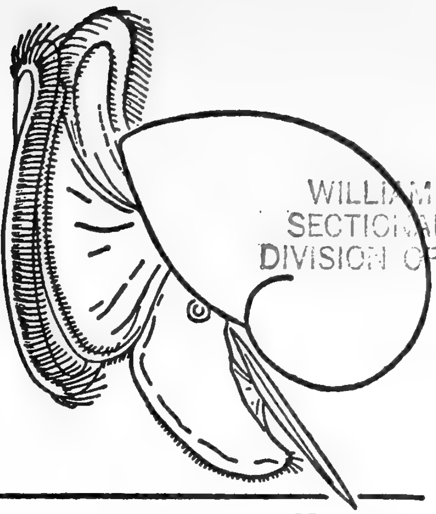
EDITOR-IN-CHIEF

Dr. Rudolf Stohler, *Research Zoologist,* Emeritus
University of California, Berkeley, California

ASSOCIATE EDITOR

Mrs. Jean M. Cate
Sanibel, Florida

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

VOLUME 15 January 1, 1973 NUMBER 3

CONTENTS

[Continued on Inside Front Cover]

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

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

Second Class Postage Paid at Berkeley, California

Contents — *Continued*

Distributed free to Members of the California Malacozoological Society, Inc.
Subscriptions (by Volume only) payable in advance to Calif. Malacozool. Soc., Inc.
Volume 15: $18.- Domestic; $19.50 in the Americas; $20.- in all other Foreign Countries
Single copies this issue $12.-. Postage additional.
Send subscription orders to Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957. *Address all other correspondence to* Dr. R. Stohler, *Editor,* Department of Zoology, University of California, Berkeley, California 94720

THE VELIGER

California Malacozoological Society, Inc.

% DEPARTMENT OF ZOOLOGY • UNIVERSITY OF CALIFORNIA • BERKELEY, CALIFORNIA

An Explanation

The regrettable increase in dues and subscription rates announced on page 259 of this issue is in part the result of an alarming and ever-increasing loss of individual copies of our journal in the mails. From a modest loss of one copy in our first year of publication, losses have now increased to an astonishing 6 percent of the total mailing. Since we endeavor to replace lost issues without additional cost to the individual recipient, the total labor and expense of producing "The Veliger" are increased, and in the last analysis this results in spreading the cost of the losses over the entire subscribership.

Although we lodge reports of losses and our complaints with the Berkeley Post Office, it is evident that the losses must be ascribed to distributing centers and local Post Offices at the points of destination, including a growing number of foreign countries.

Improvement of postal services can only be expected if all postal patrons who have suffered losses register their complaints with their own post offices at the same time they request from us the replacement of lost issues. We earnestly and urgently request that every member or subscriber who fails to receive his or her copy lodge a complaint with the local postmaster, with a carbon copy to
The Consumer Advocate
Office of the Postmaster General
Washington, D. C. 20260.
If losses or mishandlings are repeated, copies of such written complaints might also be sent to one's elected representatives in Congress.

Regrettably, we are unable to advise foreign members and subscribers how best to deal with their local postal authorities, but we believe that they too must find some way to appeal to their local Post Offices for more careful handling of posted material.

sig. / Cadet H. Hand,
President, C. M. S., Inc.

Convergence in Pulmonate Radulae

BY

ALAN SOLEM

Department of Zoology, Field Museum of Natural History
Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605

(4 Plates)

Optical observations of pulmonate radulae have revealed numerous similarities in cusp outlines, but the depth of field limitations inherent to optical study have limited the amount of data obtainable. Pilsbry (1893–1895: xiii–xiv) summarized the basic patterns of variation in cusp structure, focusing on departures from a primitive tricuspid pattern either to the broad, gouge-like cusps found in arboreal snails or a reduction to bicuspid or unicuspid structures. Despite numerous drawings of radular cusps published subsequently, our knowledge concerning the trends and patterns of radular evolution remains essentially at the level of Pilsbry's summary.

The scanning electron microscope is a tool that will revolutionize our knowledge of radular structure. Summaries of the initial uses of this instrument in malacology and a report on radular preparation and viewing techniques recently have been published (Solem, 1970, 1972). The latter paper reported the existence of an interlock system between the rows of teeth during feeding. Sympatric species of Australian Camaenidae were figured to show varying patterns of interlock.

This paper traces the evolution of very similar support mechanisms in the endodontoid family Charopidae, surveys stages in the evolution of algae-scraping cusps in the Enidae, and demonstrates the functionally identical, but structurally different, pattern of cusp structure in the Partulidae.

ACKNOWLEDGMENTS

Illustrations for this paper were made at the Electron Optics Laboratory of the American Dental Association during cooperative research on the feeding mechanisms of mollusks. I am indebted to Dr. Harvey Lyon, Mr. John Lenke, and Mr. George Najarian of the ADA for invaluable technical assistance in SEM operation, and to Miss Barbara Walden, Mrs. Nancy Kozlowski, and Mrs. Dorothy Karall for assistance with specimen and manuscript preparation. The quality of the SEM photographs in Solem (1970, 1972) and this paper owe much to the skill and dedication of Mr. Fred Huysmans, photographer at Field Museum of Natural History. Work on the Charopidae was done under sponsorship of National Science Foundation Grant GB-6779. Their support is gratefully acknowledged.

MATERIALS AND METHODS

Specimens from the alcohol collections at Field Museum of Natural History were prepared for SEM observation according to the techniques outlined in Solem (1972). After initial orientation and viewing of the radula at 100× to 500× magnification, detailed observations were made from a variety of angles at 1 000× to 6 000×. The illustrations published here are selected from more extensive sets of photographs and were chosen to demonstrate the particular points under discussion rather than to show the overall tooth patterns and intergroup changes in cusp structure.

SYSTEMS OF SUPPORT

Snails feed by a complex set of movements involving protrusion of the radula and its supporting cartilages, moving the cartilages in relation to the substrate, and pulling the rows of teeth forward, up and around the tip of the cartilages, and then back into the mouth. The teeth are arranged in horizontal rows with the cutting edges (cusps) pointing towards the posterior of the radula. Complex folds and rotational movements mean that at times the cusps point towards the anterior end of the animal, at the moment of rounding the odontophoral tip they point towards the top of the animal, and after rounding the tip they point towards the posterior. Tooth orientation in terms of the body axis shifts with the stage in the feeding stroke. As a result the use of "anterior-posterior" terminology is best limited to ends of the radula and should not refer to body axis orientation.

When teeth in one row are brought into contact with a food source and cut or slice into the object, resistance pressure on the cusp is transmitted to the anterior portion of the basal plate (since the cusp points backward). In genera such as *Papuina* (Solem, 1972: figs. 12–16) there is a long anterior extension of the basal plate. Resistance encountered by the cusp is buttressed by this extension pressing against the underlying odontophoral cartilage.

The Australian Camaenidae were shown (Solem, 1972: figs. 21–29) to have very different patterns of support, with the anterior end of the tooth encountering resistance being forced down into contact with the posterior portion of the basal plate belonging to the tooth in the next anterior row. The three rather closely related Australian genera showed quite different systems of interlocking for the lateral teeth, although the pattern of interlocking for the marginals was virtually identical. Many other families show similar adaptations.

Evolution of Interrow Support Systems in the Charopidae

The Charopidae are the largest endodontoid family, with an extensive and complex radiation in Australia, New Zealand, New Caledonia, Lord Howe Island, Melanesia, Micronesia and part of Polynesia. Some species are known from South Africa and South America. This is the group variously referred to or fragmented into the Flammulinidae, Phenacohelicidae, Charopidae, and Pseudocharopidae by most workers. Data concerning its differentiation from the Punctidae and Endodontidae is presented elsewhere (Solem, in preparation). Here it is sufficient to note that the basic radular pattern is for tricuspid central and lateral teeth, with the marginals variously altered.

The commonest form of the teeth is found in such diverse areas as St. Helena, South Africa, Australia, New Zealand, Tonga, and South America. A good example of this type is *Pseudocharopa pinicola* (Pfeiffer, 1854) from Lord Howe Island (Figures *1, 2*). The central tooth (middle row in Figure *1*) is tricuspid and slightly but distinctly smaller than the adjacent laterals. Ectoconal and endo-

Explanation of Figures *1* to *6*

Pseudocharopa pinicola (Pfeiffer, 1854)

Figures *1* - *2*: Station 2, Max Nichol's Memorial, north end, Lord Howe Island. Field Museum of Natural History number 127872.

Figure *1*: central and first lateral teeth from posterior end of radula × 2320

Figure *2*: early marginal teeth × 2330

Maoriconcha oconnori (Powell, 1941)

Figures *3* - *4*: Bock Peak, near Mt. Stevens, Wakamarama Range, Collingwood, West Nelson, South Island, New Zealand (*ca.* 172°27′ E, 40°48′ S). Auckland Institute and Museum.

Figure *3*: early lateral teeth × 1545

Figure *4*: mid-marginal teeth × 1570

Suteria ide (Gray, 1850)

Figure *5*: Waiwera-Pohoi Road, north of Auckland, North Island, New Zealand. Field Museum of Natural History number 135430. Two lateral teeth with right tooth pulled partly loose from the basal plate × 2935

Mystivagor mastersi (Brazier, 1876)

Figure *6*: Station 17, near Goathouse, northeast slope of Mt. Lidgbird at 1200 feet elevation, south end of Lord Howe Island. Field Museum of Natural History number 127963. Early to mid-lateral teeth showing flared anterior basal plate with teeth in both elevated and resting position × 1315

Explanation of Figures *7* to *12*

Draparnaudia michaudi (Montrouzier, 1859)

Figures *7* - *8*: Station NC-13, Heinghene, northeast coast of New Caledonia. Field Museum of Natural History number 159299.

Figure *7*: central and early lateral teeth × 1480

Figure *8*: mid-marginal teeth from right side of radula at posterior end × 1470

Amimopina macleayi (Brazier, 1876)

Figures *9* - *10*: Little Stuart River, Silver Plains, Cape York Peninsula, Queensland, Australia. Australian Museum, Sydney, number C63785

Figure *9*: central and lateral teeth viewed from a moderately high angle looking diagonally anteriorly × 745

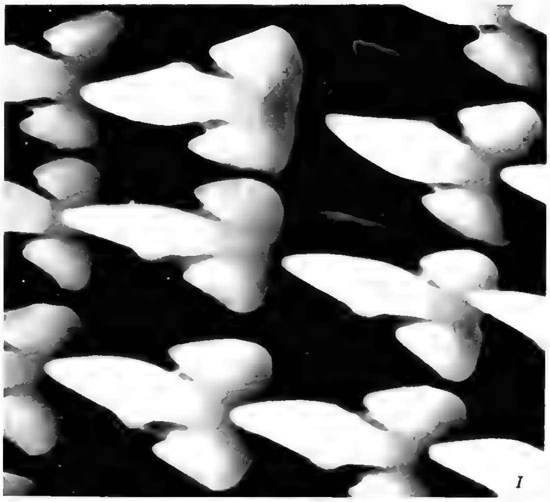
Figure *10*: mid-marginal teeth × 728

Rhachistia histrio (Pfeiffer, 1854)

Figures *11* - *12*: La Roche, Mare, Loyalty Islands, New Caledonia. Field Museum of Natural History number 109435.

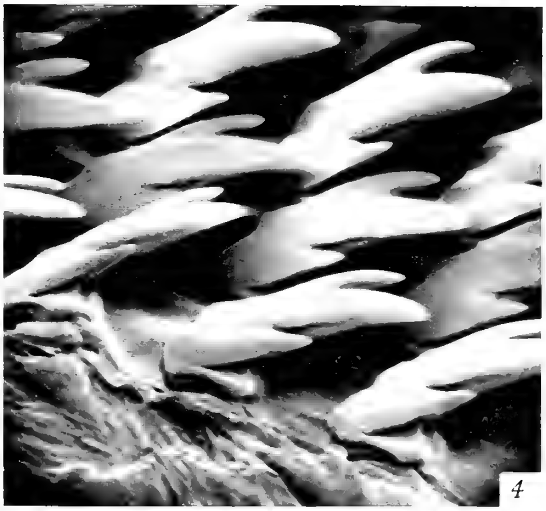
Figure *11*: central (lower left) and early lateral teeth viewed from almost directly above × 1575

Figure *12*: central and lateral teeth viewed from about a 55° angle looking diagonally forward × 835


1

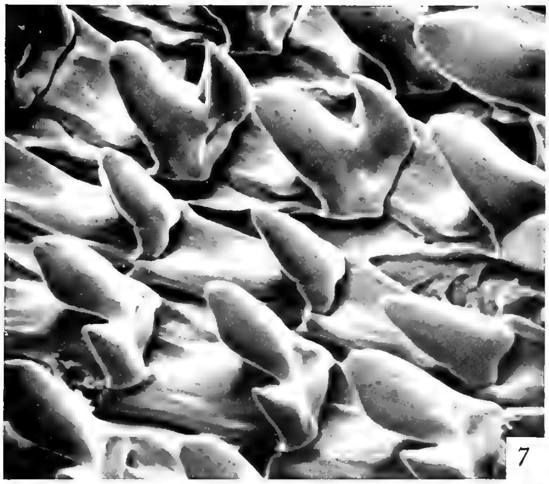

2

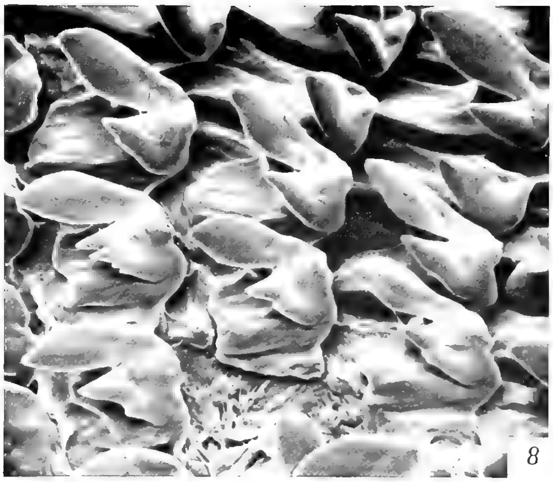

3


4


5

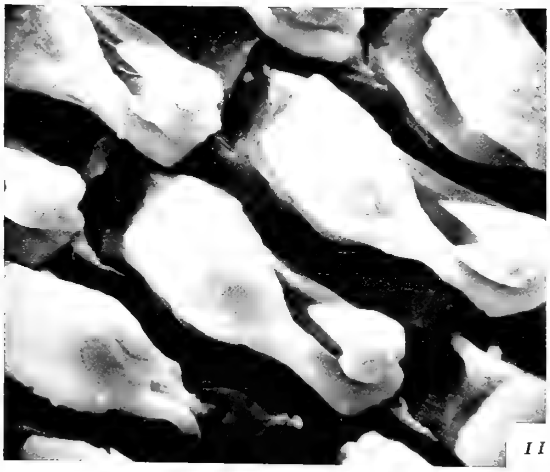

6

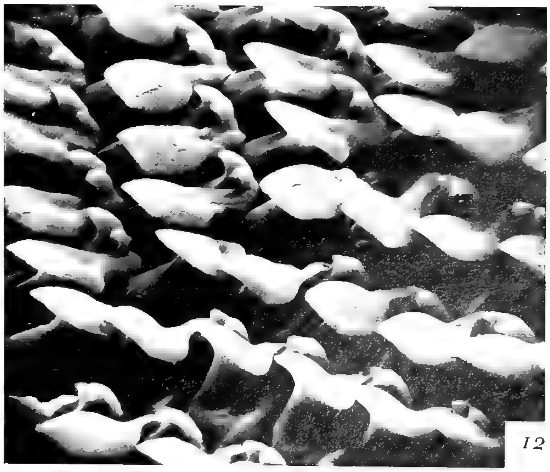

7


8


9


10


11


12

conal cusps of the laterals are equal in size and far smaller than the mesocone. Careful inspection shows that there is no clear overlap of the basal plates between rows going from middle to right of the photograph, and only slight overlap in going from right to left. Viewing the marginal teeth (Figure *2*) shows that the endocone (cusp on upper side in photograph) has become larger than the ectocone, the teeth sit on very small basal plates that are distinctly separated from each other, and the teeth lie at a sharp angle to the plane of the basal membrane. In this type of tooth there is no major interlock system between rows although probably under stress there could be slight overlap. Referring again to the central and lateral teeth (Figure *1*), note that the anterior margin of the tooth shows only a very slight indentation in the central and virtually no indentation in the laterals.

Maoriconcha oconnori (Powell, 1941), a New Zealand charopid with reduced shell, has slightly modified teeth (Figures *3, 4*). Compared with *Pseudocharopa,* the lateral teeth (Figure *3*) have the anterior margin of the tooth noticeably "notched". The supporting ridge under the mesocone of the tooth in the next anterior row (left in photograph) fits into the notch when the tooth is elevated and under stress. The teeth barely visible in the lower right portion of the photograph are elevated. It is clear that the anterior edge of the teeth is resting against the basal plate with the mesoconal ridge firmly wedged within the notch of the tooth in the immediately posterior (left) row. The marginal teeth, however, show very little difference in the basal plate structure or in the cusp form (Figure *4*). While the teeth are slightly more slender and distinctly more elongated than in the *Pseudocharopa,* the development of an interlock system for the central and lateral teeth required only alterations in the anterior part of the tooth.

Exactly the same modification is seen in *Suteria ide* (Gray, 1850) (Figure *5*). Utilizing a fold in the radula to extract information, the overlap of the teeth rows is evident. The anterior part of the radular basal plate is not attached, but angles upwards to extend above the posterior section of the basal plate in the next anterior row. The tooth on the lower side of this photograph has been torn loose from the basal membrane and is twisted upwards. The lower protruding ridge on the left margin is part of the attachment area. It obviously ends well short of the anterior margin of the cusp structure. Having this section free of the basal membrane and elevated permits its overlap, see the tooth in the upper portion of the photograph.

While this is the basic pattern in the Charopidae, with differences in the shape of the basal notch (compare Figures *3* and *5*) providing the main alterations, some species show a flared posterior ridge development exactly equivalent in function to that found in the Camaenidae. *Mystivagor mastersi* (Brazier, 1872) is a rare charopid found on Lord Howe Island. Mainly characterized by a succineiform shell (see Hedley, 1891: plt. 21, fig. 9), dissection shows that it is a modified charopid only generically differentiated from *Pseudocharopa* (Solem, unpublished). The radula (Figure *6*) retains the basic tricuspid teeth, but in the lateral teeth the anterior is flared outwards and upwards into a broad ridge that rests against the posterior basal plate section when the cutting edge is elevated. The relatively low magnification of this photograph permits seeing teeth in a number of stages between elevated and horizontal.

The Charopidae show a basic pattern of only slightly overlapping basal plates, as exemplified by *Pseudocharopa,* major overlap and interlocking during feeding stress, see *Maoriconcha* and *Suteria,* with some experiments into anterior ridge support as seen in *Mystivagor.* This is a far less dramatic pattern of change in radular support structure than was shown in just the three sympatric genera of Australian Camaenidae (Solem, 1972: figs. 21–29). The Charopidae are much smaller in size and presumably have a narrower range of both size and type of food materials than do the Camaenids. The Charopidae have not been investigated in terms of diet, but the extremely uniform cusp structure suggests that there may be comparatively little food resource use radiation.

The Pacific Island Endodontidae are equivalent to the Charopidae in habitat and patterns of radiation. Their pattern of cusp structure is markedly distinctive, but the basic support system is virtually identical. Lateral teeth from an undescribed genus related to *Thaumatodon* are shown in Figure *17*. This photograph is of a place where the radula was folded and creased, hence the teeth are in an abnormal position relative to each other. The cusps on the tooth in the center of the picture are pointing straight down and the underside of the anterior basal plate section is visible. This has not been torn free of the basal membrane, but is normally unattached. It angles upwards from the attached posterior basal plate section that is shown slanting towards the lower left corner of the picture next to the ectoconal cusp. If the tooth was rotated 135° upwards and to the left, this free section of the basal plate would come in contact with the basal plate of the tooth at upper left of the picture and its cusps would be in elevated, stressed position. The fact that the notching of the tooth is minimal does not alter the basic identity of the support pattern.

Algal Scraping Cusp Evolution in the Enidae

Development of broadened and gouge-like cusps in arboreal snails that feed on algae has occurred in many families. The pattern seen in *Papuina* was illustrated in

Solem (1972: figs. 12–16). Here the early lateral teeth were huge, almost vertically erected spade-like ridges with the later lateral teeth tending to develop minor side cusps. This is a logical evolutionary pattern in the Camaenidae where unicuspid central and early lateral teeth are very common, as for example in Australian desert camaenids used to show basal plate support systems (Solem, 1972: figs. 21–29).

The situation is quite different in the Enidae where bicuspid radular central and laterals are far more common than tricuspid teeth (see Hesse, 1933). Radulae from a New Caledonian endemic species, *Draparnaudia michaudi* (Montrouzier, 1859), an Australian endemic genus, *Amimopina,* and an African species introduced into New Caledonia and the New Hebrides, *Rhachistia histrio* (Pfeiffer, 1854), provide evidence of another pattern of evolving functional scraping cusps.

Specimens of *Draparnaudia* (Figures *7, 8*), although arboreal in habitat, have only weakly modified teeth. The mesocone of both central and lateral teeth (Figure *7*) is broadly rounded with only a slight blunting to the tip. While the central tooth retains only the slightest trace of side cusps, the laterals have a very prominent pointed ectocone. The angle of view in this picture is about 45° from the horizontal and looking slightly backwards from above the right side of the radula. Hence the ectocones on the functionally right side of the central tooth (lower part of photograph) appear to be aligned with the mesocone. However, when looking at the laterals from the left side of the radula (upper part of photograph), it is obvious that the ectocones are more sharply elevated and have their highest point of elevation well behind that of the ectocone on the same tooth. When functioning, the mesocone would come in contact with the food source first, the ectocone slightly later in the feeding motion. The ectocone is elevated almost to the same height as is the mesocone.

As in the Camaenidae and Charopidae, there is a sophisticated pattern of tooth interlock. The central tooth (middle row of Figure *7*) rests between two elevated ridges on the corner of the next anterior basal plate, while the laterals (upper and lower tooth rows) sit on a knob and ridge pattern. The knob would provide more vertical support, while the ridge would provide resistance to any lateral shift of the tooth upon encountering pressure. In contrast, the marginal teeth (Figure *8*) apparently have only an emergency overlap system with vague remnants of the basal plate ridge system (see tooth at upper left). The small, unicuspid teeth at the upper right are not central teeth, but part of a deformed row of lateral-marginal transition teeth. In the marginal teeth the ectocone shows a strong tendency to split into several cusps, is not elevated to the same extent as the mesocone, and is not situated in a clearly anterior position.

The Australian *Amimopina macleayi* (Brazier, 1876) (Figures *9, 10*) is more typical of arboreal taxa in cusp structure. In looking at the centrals and laterals (Figure *9*) the angle of viewing is slightly higher than in Figure 7, and the direction of view is reversed, that is, it is from the posterior end looking forward. Here the unicuspid central tooth has a spatulate, serrated edge, while the basal plate shows only a weak anterior extension that seems to barely overlap onto the edge of the next basal plate (lower right of photograph). Lateral teeth in the lower left section of the photograph show the cusp outlines quite clearly. The mesocone is greatly broadened and with blunt, serrated edge. Although the first lateral shows no trace of an endocone, progressive development of the same is seen going from the center to left corner of the photograph. The ectocone is seen as a basically unicuspid structure sitting well behind the mesocone with a tendency to split. When the view is shifted to the upper right section, the ectocone is seen to be a claw-like, almost vertical projection that is equal in height to the broad mesocone, but sitting almost at the anterior end of the basal plate. Marginal teeth (Figure *10*) have the endocone quite prominent in size, retain the broadened mesocone with traces of cusp edge

Explanation of Figures *13* to *17*

Samoana canalis (Mousson, 1865)

Figures *13, 15, 16*: Station 28, Vai'a'ata, near Vaiola, 900 feet elevation, Savaii, Western Samoa. Field Museum of Natural History number 152570.

Figure *13*: vertical view of central and lateral teeth from posterior end of radula × 1000

Figure *15*: low angle view of central and lateral teeth from posterior end of radula × 840

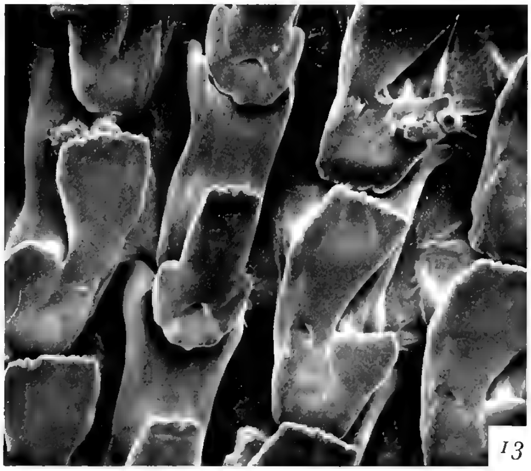
Figure *16*: view of lateral teeth from same area of radula from a steeper angle. The bits of porous material are contaminants of styrofoam dust from a storage box and not food particles or snail tissue × 770

Partula auraniana (Hartman, 1888)

Figure *14*: Mosina Bay, Vanua Lava, Banks Group, New Hebrides. Field Museum of Natural History number 109346. Angled view of single lateral tooth from right side of radula with a portion of the central tooth visible at upper left × 1865

New genus of Endodontidae

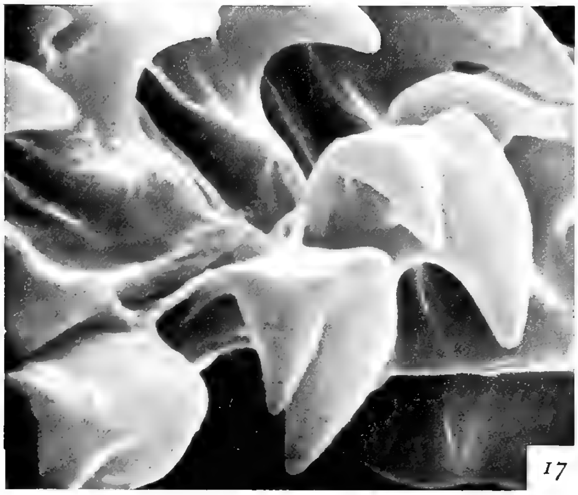
Figure *17*: Station F-7, west coast of Tuvutha, northeast Lau Archipelago, Fiji. Field Museum of Natural History number 168136. Lateral teeth bent by a sharp fold in the basal membrane showing free anterior portion of basal plate × 5130


13


14


15


16


17

serrations, while the ectocone is split into two cusps and lies markedly to the anterior of the mesocone. They differ from the laterals in that the ectoconal cusps are not posteriorly elevated, but lie in the plane of the slanted mesoconal protrusion.

The African *Rhachistia histrio* (Pfeiffer, 1854) (Figures *11, 12*) shows a slightly different pattern. Seen from above (Figure *11*) the mesocone has a very broad, blunt tip, while the ectocone is irregularly bicuspid. In the lower left portion of Figure *11* the anterior part of the central tooth can be seen. When viewed from above at a 55° angle looking diagonally forward (Figure *12*), the bicuspid ectocone is seen to extend vertically upwards in exactly the same fashion as the unicuspid ectocone of *Amimopina* (Figure *9*). Even rudimentary examination of Figures *9* and *11* shows that the details of mesoconal cusp broadening, pattern of anterior cusp elevation, and type of anterior basal plate termination are quite different. The functional aspects of the lateral teeth in the two radulae are identical. First a spatulate mesocone scrapes against the food source surface, then the elevated ectocone catches and pulls any loose pieces. The details of how this dual action mechanism is constructed in the two taxa are very different. Since the anatomical structures of *Rhachistia* and *Amimopina* are not similar, their evolution from different sections of the family is certain. The similarities in cusp position and structure are convergent. Both types were probably derived from a basic pattern similar to that found in *Draparnaudia* (Figures *7, 8*), which is standard in nearly all enids (see Hesse, 1933). As shown below, the functional pattern of a posterior scraping cusp followed by an equally elevated catching cusp also is found in the Partulidae (Figures *13–16, 18–21*).

Tooth Structure in the Partulidae

Following Kondo (1968), the three genera of the family Partulidae are *Eua, Samoana,* and *Partula.* He hypothesized that *Eua* was the most primitive, *Samoana* evolved from *Eua,* and *Partula* was derived from *Samoana.* The data presented here give no information concerning intergeneric relationships, but concentrate on the functioning similarities to the enid radulae and demonstrate that in addition to interlock systems between rows, there can be functional interlock systems between teeth in the same row.

When viewed from directly above (Figure *13*), the central tooth of *Samoana canalis* (Mousson, 1865) is seen to have remnant side cusps, while the anterior end of the basal plate rests firmly upon the posterior section of the basal plate in the next row. The lateral teeth have a spatulate mesoconal cusp with serrated edge, while the ectocone lies well anterior (towards bottom of the photograph) of the mesocone and also has a broadened, serrated cusp edge. The uppermost teeth in Figure *13* indicate the great extent of basal plate overlap in the laterals. When viewed from above at perhaps a 40° angle looking diagonally anteriorly (Figures *15* and *16*), the cusp relationships and pattern of basal interlock become clear. As in the enids, the ectoconal cusp is elevated to the same height as the mesocone (upper portions of Figures *15* and *16*) and consists of a single curved blade. This would be easily derived from the structures seen in *Draparnaudia* (Figure *7*) and is much less complicated than the ectoconal elevations seen in both *Amimopina* and *Rhachistia* (Figures *9* and *12*). Basal plate overlap is particularly obvious in Figure *16*. The anterior portion of each tooth normally lies directly above the posterior portion of the next anterior basal plate. It fits between two ridges on the basal plate and apparently (see upper left of Figure *16*) normally is only slightly raised above the recipient basal plate even when in a non-functioning position. This is even more clearly shown in *Eua globosa* (Pilsbry & Cooke, 1934) from Tonga (Figures *20, 21*). These photographs were taken at a lower angle and looking more directly anteriorly than in Figures *15* and *16*. As a result, the extent of basal plate overlap (Figure *20*) can be seen quite clearly, while a high magnification shot (Figure *21*) demonstrates the contact point between the basal plate and anterior termination. Figure *18* shows the overlap in the central tooth (upper complete row), with details of the central tooth overlapping seen in the upper left of Figure *20*. Comparisons between *Eua globosa* (Figure *18* and *20*) and *Samoana canalis* (Figures *15* and *16*) in regard to central tooth structure show changes in basal plate configuration and anterior tooth margin. Similarly, inspection of Figures *15* (*Samoana*) and *18* (*Eua*) shows that the lateral teeth of *Eua* have a much stronger basal ridge that is more transversely oriented (Figure *20*) than in *Samoana*. The anterior margin of the lateral teeth (Figures *16* and *18*) also show slight differences in shape. In *Partula auraniana* Hartman, 1888 from the New Hebrides (Figure *14*) the lateral teeth are essentially as in *Samoana* in regard to basal plate ridging, while the central tooth (partly shown in upper left of figure) has a more prominent ectoconal cusp than does the central tooth of either *Samoana* (Figure *13*) or *Eua* (Figures *18, 20*).

Marginal teeth of all three genera retain a spatulate mesocone, but have the ectocone reduced to a slender point (see upper left of Figure *19*). There is no basal plate overlap between rows of teeth, but instead the marginals have a support system whereby the blade of the tooth is supported by the basal plate of the next inner tooth in the same row (Figure *19).* This photograph is of marginal teeth from the left side of the radula and the view is from a very low angle looking towards the outer margin of the radula. The teeth are mid-marginals in position. At the bottom of the photograph, note how the right anterior margin of the tooth is curved upwards and how the cusp extends significantly towards the viewer in relation to its basal plate. Then observe how the same structure on the second tooth from the bottom in this photograph rests against an elevated ridge on the left margin of the first tooth's basal plate. The stress on the marginal teeth during feeding apparently involves lateral strain rather than the front axis stress on the lateral and central teeth. Hence the shift in support function from between row interlock in the central and laterals to between teeth of one row in the marginals.

Compared with the enids (Figures *7–12*), the partulids are identical in basic lateral tooth functioning, leading with a serrated mesocone and following with an equally elevated ectocone to catch loosened pieces. The pattern of interrow support and the details of tooth form are quite distinctive. Marginal teeth in the two families are very different from each other in form and structure, although the basic cusp patterns have many things in common. Both groups have taxa specialized for algal scraping and the functional aspects of the cusps are the same, yet the structure underlying this function differs radically. The similarity in cusp form was observed many years ago with optical equipment, but the differences in understructure could not be seen without use of the scanning electron microscope.

DISCUSSION

Examples from the Charopidae, Endodontidae, Enidae and Partulidae demonstrate some of the variety found in interrow supporting mechanisms in the pulmonate mollusks. This extends the observations on the Camaenidae that were reported previously (Solem, 1972). These interlock mechanisms differ widely within and between groups, but are functionally useful during the stress of actual feeding.

The observations made here have involved the use of excised radulae artificially mounted to simulate feeding position. While satisfactory to show the existence of the interlock mechanisms and to suggest hypotheses concerning their exact functioning, observations on radulae that are still in position on the odontophoral cartilages will be needed to interpret differences. Runham (1969) used freeze-drying techniques to observe partly dissected buccal masses with the odontophoral tip exposed and washed for observation. Critical point drying offers an equally useful technique for studying essentially *in situ* radular tips. Full understanding of the functional differences that led to the differentiation into lateral and marginal teeth will require *in situ* study, examination of the extracted radula, and feeding track observations. In all of these the scanning electron microscope will be an invaluable aid. Currently we are in the same stage in exploiting the use of this instrument that Robert Hooke and the Dutch microscopists were during the mid-1600's in their experiments using the optical microscope.

The cusp structure of arboreal snails in the Camaenidae (Solem, 1972: figs. 12–16), Enidae (Figures *7–12*), and Partulidae (Figures *13–16, 18–21*) is seen to involve broadly spatulate mesoconal cusps that in unworn condition have serrated tips. In the camaenid genus *Papuina* this is the sole mechanism, but in the Enidae and Partulidae the broad mesocone is followed (in a functional sense) by an equally elevated, pointed ectocone. In all three groups the details of understructure and patterns of stress supports are very different, indicating independent origins for these structures. The functional convergence in cusp patterns, however, strongly suggests that this scraping mesocone followed by a pointed or curved ectocone is an extremely efficient arrangement. Observations on radulae of sympatric arboreal species are planned to see whether these species show differences in cusp form that could be related to diet differences and hence indicate niche separation. Also studies of arboreal taxa in other families are being pushed to find out if the basic pattern of mesocone-ectocone sequence is followed in other taxa such as the Bulimulidae.

In two groups, the Charopidae and Enidae, species are illustrated that suggest stages in the evolution of row

Explanation of Figures *18* to *21*

Eua globosa (Pilsbry & Cooke, 1934)

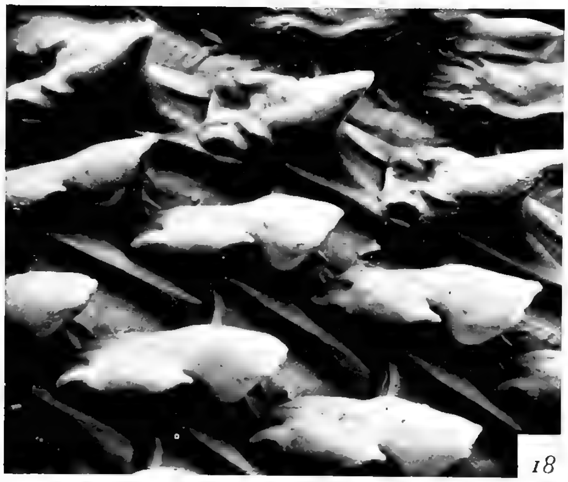
Figures *18 - 21*: Station T-19, above forestry camp at 600 feet elevation, Eua, Tonga. Field Museum of Natural History number 152388.

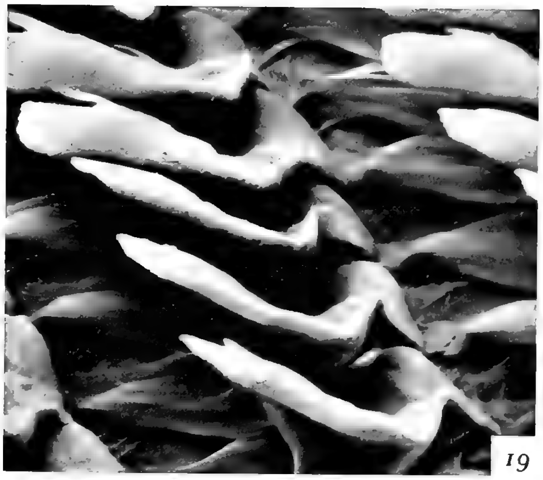
Figure *18*: central and early lateral teeth viewed at moderate angle from left side of radula × 1050

Figure *19*: marginal teeth on left side of radula viewed at very low angle looking towards edge of radula × 1570

Figure *20*: central and early lateral teeth viewed at low angle looking almost directly anteriorly × 1320

Figure *21*: contact point between anterior elevated cusp section with posterior part of next basal plate × 4335


18


19


20


21

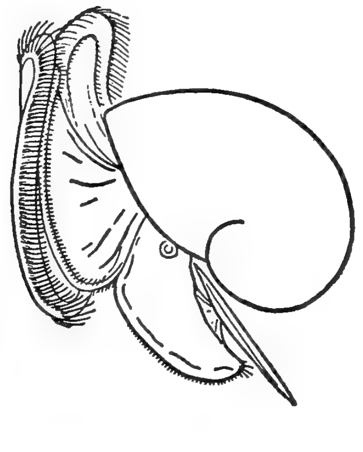
interlock (Charopidae) or algal scraping cusp structure (Enidae). These are not intended to represent linear evolutionary stages in any sense, but are simply chosen to demonstrate the basic structure and types of modifications needed to arrive at the advanced character state.

SUMMARY

Patterns of interlock between radular teeth in adjacent rows are present in many families of pulmonates. Possible basic patterns in structure and the types of progressive modifications are shown in the Enidae and Charopidae. Convergence in cusp form for the probable purpose of algal scraping is demonstrated in the Partulidae and Enidae, together with hypotheses concerning their functioning during feeding. These preliminary observations were possible only because of the scanning electron microscope. When combined with more advanced techniques in specimen preparation, far more data on the patterns of molluscan feeding can be obtained than was possible in the past.

Literature Cited

HEDLEY, CHARLES
1891. The land and fresh-water shells of Lord Howe Island. Rec. Austral. Mus. **1** (7): 134 - 144; plts. 21 - 22 (30 June 1891)
HESSE, PAUL
1933. Zur Anatomie und Systematik der Familie Enidae. Arch. Naturgesch., N. F. **2** (2): 145 - 224; 43 text figs.
KONDO, YOSHIO
1968. Partulidae: preview of anatomical revision. The Nautilus **81** (3): 73 - 77; 1 table (18 April 1968)
PILSBRY, HENRY AUGUSTUS
1893 - 1895. Manual of conchology. Second series: Pulmonata. **9:** xlviii + 366 pp.; 71 plts. (16 November 1893 to 2 February 1895)
RUNHAM, NORMAN
1969. The use of the Scanning Electron Microscope in the study of gastropod radula: The radulae of *Agriolimax reticulatus* and *Nucella lapillus*. Proc. 3rd Europ. Malac. Congr., Malacologia **9** (1): 179 to 185; 7 text figs.
SOLEM, ALAN
1970. Malacological applications of scanning electron microscopy. I. Introduction and shell surface features. The Veliger **12** (4): 394 to 400; plts. 58 - 60; 1 table (1 April 1970)
1972. Malacological applications of scanning electron microscopy. II. Radular structure and functioning. The Veliger **14** (4): 327 - 336; 6 plts.; 1 text fig. (1 April 1972)



External Description of a Living *Aranucus bifidus* (Odhner, 1936)

(Opisthobranchia : Dendronotacea)

BY

C. H. CARLSON AND P. J. HOFF

University of Guam

(2 Text figures)

THE DENDRONOTACEAN FAMILY Aranucidae was established by ODHNER (1936) to accommodate a single species collected in the Gilbert Islands by S. Bock in 1917. *Aranucus bifidus* does not appear to have been collected since the original specimen was reported and consequently there has been no description of the external parts of the living animal.

Aranucus bifidus is a commonly occurring species found throughout the year on both the windward and leeward reef flats of Guam. Specimens have also been found at Anatahan and Pagan Islands in the northern Marianas.

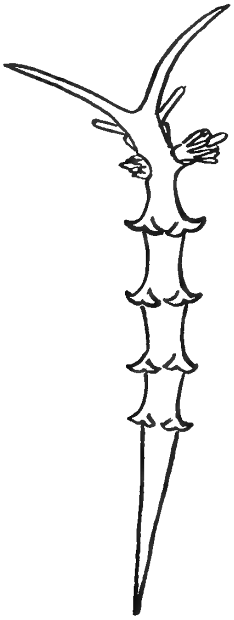


Figure 1
Aranucus bifidus (Odhner, 1936)
Dorsal View

Description of External Aspects: Length 7 to 12 mm. The body is long, higher than it is wide, with the back margins clearly marked off from the smooth sides (Figure 1). The dorsum is smooth from head back to tapering tail and normally has 4, rarely 5, pairs of smooth bifid projections along the margin. The first 3 pairs are of nearly equal size with the first pair being occasionally smaller and the fourth pair always smaller. One branch of each projection curves in toward the middorsum and on large animals overlaps the opposite projection; the other branch curves outward. On some animals there is a projection suggesting the beginning of a fifth pair and sometimes a single complete bifid projection.

The rhinophores are retractile into a high, wide sheath that has a fairly large pointed lobe projecting laterally and slightly anteriorly (Figure 2). The peduncle of the rhinophores is fairly heavy at the base, then narrows until it reaches the rhinophore club which is brush-like. The club is composed of a single long central papilla surrounded by 12 or 13 shorter, thin, digitiform papillae.

Figure 2
Aranucus bifidus (Odhner, 1936)
Rhinophore

The head has 2 pairs of tentacular processes, one pair long and tapering, directed forward; the other pair short, directed antero-laterally.

The foot, which projects very slightly past the body, is thin, widened and rounded anteriorly and is furrowed along its entire length. When not in contact with the substrate it is frequently folded at the midline.

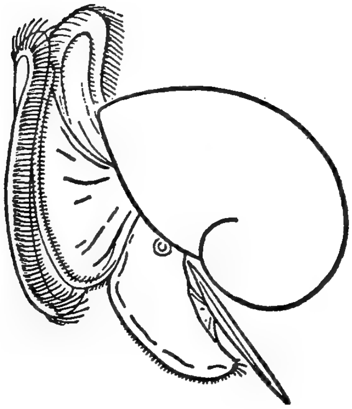
The genital pore is directly below the first set of marginal projections on the right and the anus is lateral between the first and second set. Eye spots are barely visible through the dorsum at the posterior base of the rhinophores.

Color: The color of the dorsum varies from a light pink to a dark magenta, darker at the base of the marginal projections. The sides are lighter with a very light streak just below the margin. There is an internal dark spot visible middorsally between the first pair of projections and the orange color of the ovaries shows through the dorsum beginning at the second set of marginal projections, sometimes extending back to the fourth set. The marginal projections are white, as is the tail.

The rhinophore sheath has a dark red-violet base, lighter on the outside. The projecting lobe is white. The peduncle of the rhinophore is transparent, the brush-like papillae are orange with the long central one having a white tip. The basal third of the longer tentacles is red-violet with the remainder white. The shorter tentacles are transparent on smaller animals, and pink and translucent white on larger animals. The foot is transparent with tiny specks of translucent white.

Literature Cited

Odhner, Nils Hjalmar
1936 Nudibranchia Dendronotacea. A revision of the system. Mélanges Paul Pelseneer. Mém. Mus. Roy. d'Hist. Nat. Belg., Ser. II, Fasc. 3: 1057 - 1128; 1 plt.; text figs. 1 - 47



Food-Preference of the Nudibranch *Aeolidia papillosa*, and the Effect of the Defenses of the Prey on Predation

BY

VIRGINIA L. WATERS

Pacific Marine Station, Dillon Beach, California 94929

(5 Text figures)

INTRODUCTION

It has long been known that at least European *Aeolidia papillosa* (Linnaeus, 1761) preys on anemones (Boutan, 1898; Eliot, 1910), and more recent observations have confirmed this (Miller, 1961; Swennen, 1961). However, there is little agreement as to which species are eaten or preferred (Table 1). It appears that *Aeolidia* may show a distinct preference within a particular locality, but that the species preferred may vary from place to place.

Of several factors which may cause the nudibranchs to feed on different species in different localities, I was particularly interested in the defense of the prey. There has been little work published on the effect of defenses on predation. Robson (1961) noticed that *Aeolidia* fed only on the base and column of *Stomphia coccinea*. The nudibranchs withdrew whenever they touched the tentacles. Not only were the tentacles effective in limiting predation, but the anemones swam away when *Aeolidia* contacted them, usually leaving the nudibranchs behind. Boutan (1898) briefly discussed the difficulties nematocysts caused *Aeolidia*. He noticed that the nudibranchs secreted large amounts of mucus upon contact with the anemones and that the nematocysts became entangled in this and so did not injure the nudibranchs. Russell (1942) stated that acontia of *Metridium marginatum* became caught in the large quantity of mucus secreted by the nudibranchs but that they were eaten along with the whole anemone. Wolter (1967) described the extrusion of acontia and contraction of *Metridium senile* as *Aeolidia* began to feed on the anemones, with no mention of the effect of such behavior on the nudibranchs. Rosin (1969) found that when *Anthopleura nigrescens* was attacked by the eolid *Herviella* spec. nov. the anemones regularly detached from the substrate within a few minutes. The nudibranchs would hold on to an anemone for a while, but eventually the animals would separate and the anemone would fall. The nudibranchs would then resume feeding on a new anemone.

The relationship between *Metridium senile* and *Aeolidia* is particularly interesting. Nearly all of the European workers and Russell (1942) in New England (Table 1) indicated that *Aeolidia* eats this species or even prefers it to others. No one has said that *Aeolidia* does not eat *Metridium*. However, observing animals from Puget Sound, Washington, I discovered that when I placed a nudibranch on such an anemone, the anemone immediately contracted and extruded acontia. The nudibranch for its part withdrew violently and became covered with thick mucus when touched to the anemone. When placed at the base of an *Epiactis prolifera,* it immediately began feeding. Yet, the acontia of European and New England *Metridium* did not seem to prevent the nudibranchs from attacking the anemones.

In addition to nematocysts, escape responses, and detachment, the occurrence of anemones in dense concentrations of individuals could minimize the effects of predation by reducing the chances that a given individual would be entirely consumed. The adaptive significance of the occurrence of the local *Anthopleura elegantissima* in dense groups could thus be related to predation by nudibranchs. The effectiveness of grouping would depend on the predatory methods of *Aeolidia,* however. In addition to grouping, the column of this anemone is covered with sand so that very little of the body surface is exposed. When the anemones are expanded, the tentacles and oral disk are the most accessible parts.

The primary objectives of this study were (1) to obtain preliminary information on the food of *Aeolidia papillosa*

---

[1] Present address: P. O. Box 103, Arcata, California 95521

Table 1

Species eaten or preferred by *Aeolidia* (from literature)[2]

Worker	Species preferred	Other species offered or mentioned
McMillan, 1942	not stated	*Tealia crassicornis*
Russell, 1942	not stated	*Metridium marginatum*
Stehouwer, 1952	*Metridium senile*	*Actinothoe anguicoma* *Diadumene cincta* *Tealia felina*
Braams & Geelen, 1953	*Actinia equina*	*Metridium senile* 6 species of hydroids, including *Tubularia indivisa*
Miller, 1961	*Actinia equina*	*Anemonia sulcata* *Sagartia troglodytes* *Tealia felina* *Tubularia indivisa*
Robson, 1961	*Stomphia coccinea*	*Metridium (senile?)* *Sagartia (troglodytes?)* *Tealia (felina?)*
Swennen, 1961	*Actinia equina*	*Metridium senile* *Tealia felina* *Actinothoe anguicoma* *Diadumene cincta* *Sagartia troglodytes*
Wolter, 1967	*Metridium senile*	*Actinia equina* *Sagartia troglodytes* *Tealia felina*

---

[2] The observations were made in different localities in Europe, except those of Russell, 1942, which were made on the Atlantic coast of the United States

in yet a different part of its range, and (2) to begin to answer the question "What governs local food preference?" by investigating the defensive responses of the prey. The effects of the following potential defenses on predation were studied: (**a**) nematocysts, particularly those of the acontia of *Metridium senile* and of *Diadumene luciae*, and (**b**) detachment or other escape responses. In addition, the effect of tentacles, sand on the column, dense groups, and the occurrence of detachment (if present) in *Anthopleura elegantissima* were studied. As a necessary adjunct to a study of defenses, the behavior of *Aeolidia* in detecting and locating prey and in feeding was observed.

MATERIALS AND METHODS

The study was conducted during the summer of 1969 at the Pacific Marine Station, Dillon Beach, California.

Individuals of all species of anemones found in the intertidal zone of various local beaches were collected to be used in the experiments and observations. They were:

Anthopleura artemisia (Pickering, 1848);
Anthopleura elegantissima (Brandt, 1835);
Anthopleura xanthogrammica (Brandt, 1835);
Corynactis californica Carlgren, 1936;
Diadumene luciae (Verrill, 1898) (called *Haliplanella luciae* by Hand, 1955);
Epiactis prolifera Verrill, 1869;
Metridium senile Linnaeus, 1767;
Tealia coriacea (Cuvier, 1798); and
Tealia crassicornis (Müller, 1776).

Anthopleura artemisia lives buried in sand and attached at the base to rocks in protected areas, such as between large boulders, in zones 3 and 4 of Ricketts & Calvin, 1968.

Anthopleura elegantissima occurs on rocks of the protected outer coast or in quiet waters of bays, in zone 3. The anemones occur in large dense masses of individuals which appear to originate from a single individual by longitudinal fission (Ford, 1964; Hand, 1955). Sand, gravel, and bits of shell adhere tightly to the exposed parts of the columns of these anemones.

Anthopleura xanthogrammica, the largest species of the 3, lives in more or less protected areas of the open coast as well as on the protected outer coast in the same localities as *A. elegantissima,* but below that species. The anemones are solitary or occur in small groups which are not as tightly packed as those of *A. elegantissima.*

Corynactis is a very small anemone occurring in protected areas on rocks in the protected outer coast, in zone 3 and below, in dense aggregations. The anemones have capitate tentacles with very large nematocysts.

Diadumene, an introduction from Japan (Ricketts & Calvin, 1968), occurs on oyster shells and rocks of bays and estuaries, in zone 2. Acontia are present.

Epiactis occurs in protected areas on rocks and algae in the protected outer coast, and on a variety of solid objects including plants in bays and estuaries, in zones 3 and 4.

Metridium is a large anemone occurring in rocks, wharf pilings, and floats in quiet water, in zone 4 and below. Acontia are present.

Tealia coriacea occurs in rocks in protected areas with shell, sand, and gravel attached to the column and often buried in sand and gravel. This species was difficult to obtain and was not used extensively in the study.

Tealia crassicornis, a large anemone, occurs on rocks of the open coast with *Anthopleura xanthogrammica,* in zone 4 and below.

When size or degree of aggregation of anemones is not mentioned, the anemones are not noteworthy in those respects.

Most of the nudibranchs studied were collected from rocks covered with *Anthopleura elegantissima* on the sandy beach below the marine station. A few were collected from rocks of the north jetty at the entrance to Bodega Bay, on which *A. elegantissima, A. xanthogrammica, Corynactis,* and *Epiactis* were the most abundant anemones. Some nudibranchs were also collected from rocks in Tomales Bay (Nick's Cove) which had *A. elegantissima* living on them. In all, about 20 nudibranchs were collected. Those from each locality were not studied separately, because I was unable to obtain enough individuals from the jetty or Nick's Cove.

EXPERIMENTS PERFORMED

The experiments to determine food preference were of 2 main types:

A. In the first, several nudibranchs were introduced into a plastic cage (30 × 19 × 12 cm) containing (with some exceptions) one individual of each species of anemone

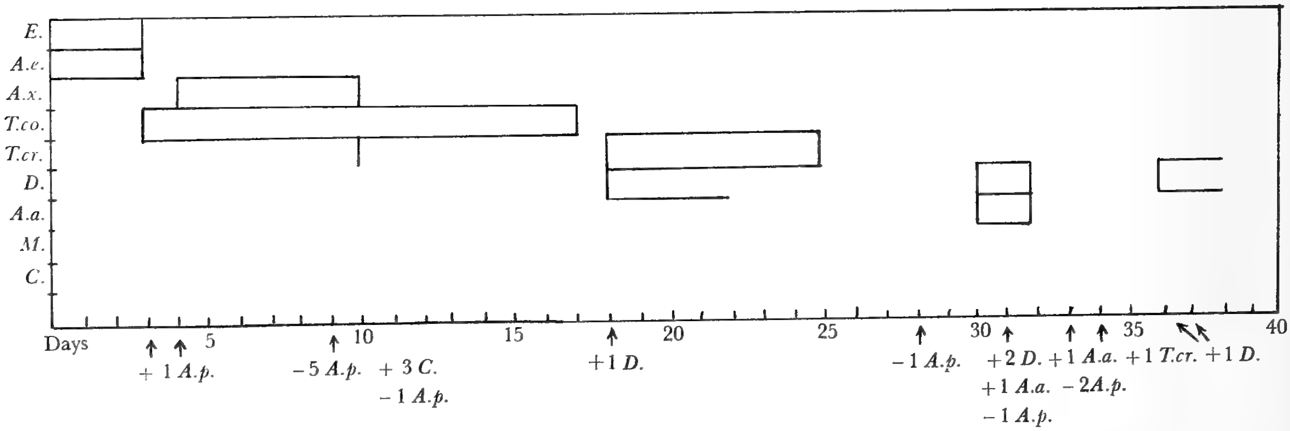


Figure 1

Experiment A, number 1: Number of days *Aeolidia* spent eating the different anemones and order in which they were eaten. Arrows show number of anemones (abbreviated as in Table 3) or nudibranchs (*Ap*) added (+) or removed (—) on that day. Open end of bars indicates anemones were not consumed entirely

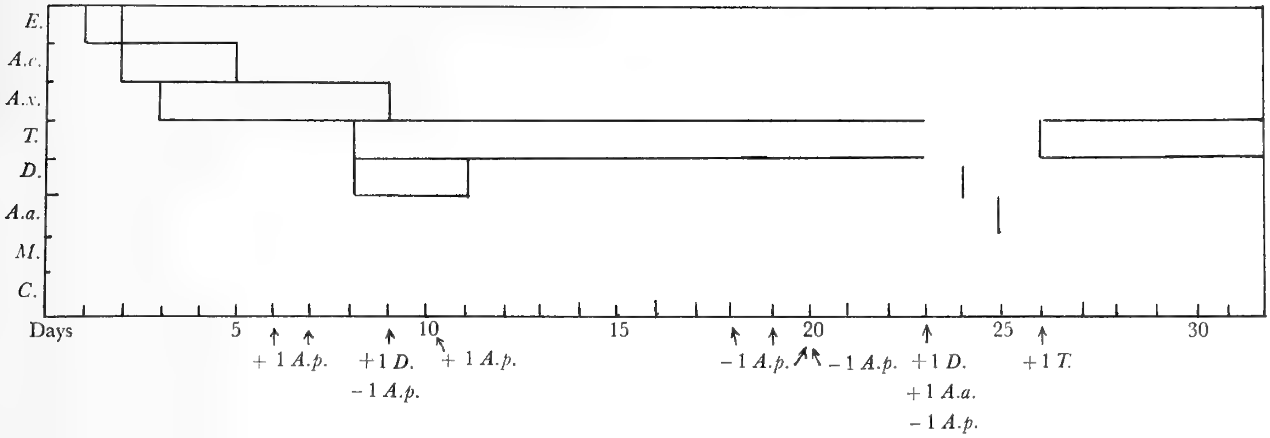


Figure 2

Experiment A, number 2: Number of days spent eating the different anemones and order in which they were eaten. Symbols as in Figure 1; * indicates nudibranch died

which had been allowed to attach. The cages were covered with cheese cloth to prevent escape of the nudibranchs. Two experiments of this type were run simultaneously for most of the research period (6 weeks). Since the cages also served as holding tanks for nudibranchs not being used in other experiments and as sources of nudibranchs for other experiments, the number in the cages shifted from time to time, as did the individuals involved. The duration of each experiment and the changes made in the numbers of nudibranchs present are shown in Figures 1 and 2. The criteria used to determine preference were: (1) which species were eaten; (2) the order in which the anemones were eaten; (3) the length of time taken to consume each anemone, and (4) the proportion of nudibranchs feeding during each observation relative to the proportion doing something else (being inactive or wandering). Observations were generally made twice a day.

B. The second type of food-preference experiment involved offering a group of 2 - 5 nudibranchs a choice between 2 species of anemones which had been put in uncovered glass dishes (11 cm in diameter) and allowed to attach. A few combinations were not used because of lack of time and nudibranchs, and because they were not crucial in determining preference. For the same reasons replications of some combinations were not made. Nevertheless, a given species of anemone was offered to groups of nudibranchs at least 6 times in combination with different species. Judgment of food-preference was based on the same criteria used for experiment A. Again, observations were made twice a day. The experiments were terminated when one or both anemones were completely eaten or when the nudibranchs persistently wandered or escaped rather than eating.

Three further types of experiments were performed to provide information on various aspects of the feeding behavior of *Aeolidia* and defenses of the anemones, and to provide supplementary information on food-preference.

C. To determine whether *Aeolidia* were attracted to food from a distance, a preferred species of anemone was placed upstream from the nudibranchs. In the first 2 experiments, nudibranchs were offered a choice between anemones and water alone to serve as a control for their response to currents. In the third experiment, the responses to 2 species offered at the same time were compared. In all cases water flowed gently into 2 plastic cages (30 × 19 × 12 cm) containing respectively either the anemones and water or the 2 species of anemones. A rubber tube ($\frac{1}{2}$ inch diameter) connected each of these cages with one at a slightly lower level containing the nudibranchs. The upper ones rested on the bottom halves of several plastic petri dishes 8 mm deep. The ends of the tubes extended to the bottom of all 3 cages. Water flowed out of the nudibranch cage through holes bored near the top. The anemones had been put in the bottom half of a petri dish and allowed to attach before being introduced to the cage. The experiments were run for 24 hours, after which the number of nudibranchs in the 3 cages was noted. Only 3 experiments were performed because of insufficient time, space, and nudibranchs.

D. To provide information on the defensive adaptations of anemones and their effect on the nudibranchs, as well as on searching and food-locating behavior of the nudibranchs, nudibranchs were introduced to bowls in which anemones had attached, and the behavior of predator and prey was observed.

E. The last type of experiment dealt with the feeding behavior and activity pattern of nudibranchs offered groups of *Anthopleura elegantissima* and the defenses of this species. Two experiments were performed. In the first, 2 nudibranchs were put into an uncovered enamel pan (17 × 29 × 5 cm) into which 20 anemones had been placed several weeks earlier and which had attached and spaced themselves out. The anemones were not tightly packed together as in nature but had spaces of several centimeters between most of them, nor did they have sand adhering to their columns. They had been collected from different localities at different times and thus were from different clones. Observations of the behavior of the nudibranchs and anemones were made usually twice a day for 10 days. For the second experiment about 20 anemones were collected from a single area on a rock below the marine station, put in an uncovered round glass dish (14 cm in diameter and 4 cm deep) with adhering sand and loose sand taken from the base of their rock, and allowed to attach. Three nudibranchs were then introduced. This experiment lasted 8 days and observations were made usually twice a day.

RESULTS

EXPERIMENT A, Number 1

At the beginning of the experiment 5 nudibranchs were put with the following anemones:

species	diameter of base (cm)
1 *Anthopleura elegantissima*	2.5
1 *Anthopleura xanthogrammica*	5.0
2 *Epiactis prolifera*	1.0 and 2.5
2 *Metridium senile*	both 3.5
1 *Tealia coriacea*	5.0
1 *Tealia crassicornis*	5.0

Later *Anthopleura artemisia, Corynactis californica, Diadumene luciae,* and another *Tealia crassicornis* were added. The number of individuals of each species added and the timing of the additions are indicated in Figure 1. The size of these anemones was not measured.

Figure 1 shows that the anemones were eaten in a definite order. The first ones eaten were *Epiactis* and *Anthopleura elegantissima.* The smaller *Epiactis* was completely eaten within two hours following introduction of the nudibranchs, while the larger one and *A. elegantissima* were started. The second ones eaten were *Tealia coriacea* and *A. xanthogrammica. Tealia* was attacked within 6 hours and *Anthopleura* within 24 hours after the first anemones were eaten. *Tealia crassicornis* was the last of the original anemones to be eaten. Although this anemone was first attacked on the day *A. xanthogrammica* was completely eaten, very little was eaten then. The nudibranchs did not really begin eating it until the second day after *T. coriacea* had been consumed.

Diadumene (introduced the day before) was attacked the same day as the second attack was made upon *Tealia crassicornis.* This same anemone was never completely eaten, although it was reduced to $\frac{3}{4}$ of the edge of the pedal disk by the 4th day. A period of 5 days elapsed following this day without the nudibranchs having eaten any parts of the remaining anemones: the original *Metridium* and the 3 *Corynactis* added on the 10th day of the experiment. However, the presence of extruded acontia and mucus in the water seen on 3 observations during this time indicated that *Metridium* had been attacked. At the end of this 5-day period, 2 more *Diadumene* and one *A. artemisia* were added. All 3 were soon attacked, and all but the pedal disk of one *Diadumene* were completely eaten within 2 days. The new *A. artemisia* and *T. crassicornis* added soon afterwards were not attacked during the remaining 8 days of the experiment. Likewise, *Corynactis* and *Metridium* were not attacked during this time.

DISCUSSION

Although the nudibranchs showed a distinct preference for certain species, their relative preference for others remained unclear. It appeared that *Epiactis* and *Anthopleura elegantissima* were preferred to others offered, but the preference (if any) between these 2 species was not clear. The fact that the smaller *Epiactis* was eaten before the other 2 (both the same size) indicated that size of prey may play a role in determining food-preference when other things are equal. Although *A. xanthogrammica* and *Tealia coriacea* were the same size and were attacked within a day of each other, *A. xanthogrammica* seemed to be preferred, judging by the comparatively short time taken to consume that anemone and by the smaller proportion of time spent wandering (Figures 1 and 3). The relative preference for *Diadumene* and *A. artemisia* was unclear. The first time the anemones were introduced one *Diadumene* was not completely eaten while *Anthopleura* was, whereas the second time they were added *Diadumene* was partially eaten while the other was not eaten at all. How the preference for *Diadumene* and *Anthopleura* fit into the order of preference for the original anemones could not be determined, since the original anemones were eaten by the time these last 2 were added. Likewise, the relative preference for *Diadumene* and *Tealia crassicornis* was unclear. The fact that both were attacked at the same time indicated equal preference, but the fact that *Diadumene* was not completely eaten indicated a stronger preference for *Tealia*. However, toward the end of the experiment the fact that the new *Tealia* was not eaten at all while 2 of the 3 *Diadumene* were at least partially eaten indicated a preference for *Diadumene*.

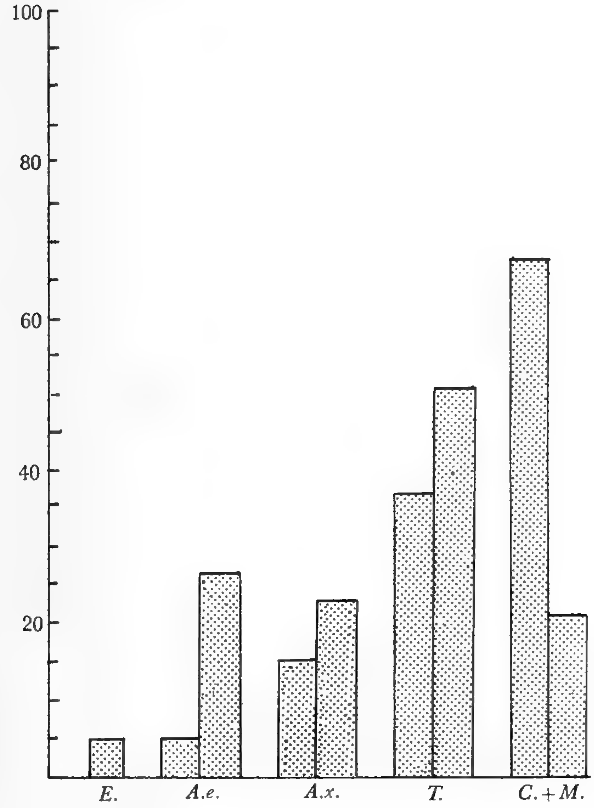


Figure 3

Experiment A, 1 and 2: Percent nudibranchs wandering during the observations made while they were eating each species. Names of anemones abbreviated as in Table 3. The data were obtained by counting the number of nudibranchs wandering during each observation, obtaining the total for the period in which each species was being eaten, and calculating the percent of the total nudibranch-observations. A few anemones were not included because of inconsistent results (*Anthopleura artemisia* and *Diadumene*) or because nudibranchs were not feeding on them during the observations, although they had been eating them previously (*Diadumene*, the smaller *Epiactis* of the first experiment, and the *Epiactis* of the second experiment). The data for *Corynactis* and *Metridium* in the first experiment were obtained only from the period of 5 days in which no other anemones were available. The data for these anemones in the second experiment were obtained during the period beginning after the original *Tealia* had been removed until the end of the experiment, although some anemones were available and were slightly eaten during this time. For both experiments, only the nudibranchs wandering during the time the first *Tealia crassicornis* was being eaten were included in the data for *Tealia*

In summary, the anemones can be arranged in the following order from most to least preferred: *Epiactis* and *Anthopleura elegantissima*; *A. xanthogrammica*; *Tealia coriacea*; *T. crassicornis*; *Corynactis* and *Metridium*. In addition, *Diadumene* and *A. artemisia* were preferred to *Corynactis* and *Metridium*.

EXPERIMENT A, Number 2

At the beginning of the experiment 5 nudibranchs were put with one each of the following species:

species	diameter of base (cm)
Anthopleura elegantissima	3.5
Anthopleura xanthogrammica	3.5
Corynactis californica	0.5
Epiactis prolifera	2.0
Metridium senile	3.5
Tealia crassicornis	7.0

Later *Anthopleura artemisia, Diadumene luciae,* and a new *Tealia crassicornis* were added. The number of individuals involved and the timing of the additions are indicated in Figure 2. The size of the new anemones was not measured.

Figure 2 shows that again the original anemones were eaten in a definite order. *Epiactis,* the first one eaten, was consumed between the 2nd and 3rd day, and *Anthopleura xanthogrammica* was attacked on the 4th day. *Tealia* was attacked on the 9th day, but was never completely eaten. It began to decompose on the 22nd day and was removed 2 days later.

The first *Diadumene* added was attacked on the day of its introduction. Neither the second *Diadumene* nor the

Anthopleura artemisia added later was eaten by the end of the experiment, although 2 days after their introduction a nudibranch was seen feeding on *Diadumene* and one day later one was feeding on *Anthopleura.* The new *Tealia* added still later was never consumed entirely, although it was first attacked on the day after its introduction and was grazed on throughout the rest of the experiment. Neither *Corynactis* nor *Metridium* was eaten, although acontia and mucus were seen in the water during several observations from the 10th day to the end of the experiment.

DISCUSSION

The apparent food-preference was similar to that of the first experiment. Again, *Epiactis* and *Anthopleura elegantissima* were the first anemones eaten. That *Epiactis* was eaten first may have been related to its smaller size. The preference for *A. elegantissima* over *A. xanthogrammica* was not as definite as in the first experiment. However, the facts that *A. elegantissima* was attacked first, was eaten in a shorter time (both were the same size), and less time was spent wandering (Figure 3) indicated a preference for that species. *Anthopleura xanthogrammica* was definitely preferred to *Tealia.* Again, the relative preference for *Tealia* and *Diadumene* was unclear. In the first instance it appeared that *Diadumene* was preferred, since it was eaten completely while *Tealia* was only grazed on slightly over a long time; while in the second instance it seemed as though *Tealia* were preferred, since the nudibranchs attacked *Tealia* before they had completely eaten the previously attacked *Diadumene.* There was only slight interest in *A. artemisia* and *Metridium* and none in *Corynactis.*

In summary, the order of preference seemed to be: *Epiactis* and *Anthopleura elegantissima; A. xanthogrammica; Tealia crassicornis; Corynactis* and *Metridium.* In addition, *Diadumene* was preferred to *A. artemisia, Corynactis* and *Metridium.*

These two experiments also revealed something of the predation methods of *Aeolidia.* (1) Generally, one or at most 2 anemones were attacked and fed upon simultaneously. (2) Once begun, the anemones were usually completely eaten (*Diadumene* being the primary exception, of which a portion of the pedal disk was often left). (3) The nudibranchs when not actually feeding on preferred anemones tended to remain inactive, usually near the anemone being eaten. However, when a less preferred species was being eaten or when an anemone was not being eaten at all more of the nudibranchs were wandering when observed (Figure 3). Thus, it seemed that in the latter cases nudibranchs spent more time wandering than when eating preferred anemones.

The great difference between the two experiments in the percent wandering when the data for *Corynactis* and *Metridium* were taken (Figure 3) was probably due to the much greater state of starvation of the second group of nudibranchs, 3 of which had already died of starvation (Figure 2). Evidence that death was due to starvation was the overall decrease in size of the nudibranchs since the beginning of the experiment, as well as a disproportionate decrease in size of the branches of the digestive gland within their cerata. No nudibranchs died during the first experiment. Those of the first experiment had completely eaten 2 large anemones after they had completed *Anthopleura xanthogrammica*: *Tealia coriacea* and *T. crassicornis.* In contrast, those of the second experiment had not even completed the one *T. crassicornis.* Further, the data for the second experiment were taken from a period beginning 2 days later from the onset of the study than for the first group. It is also noteworthy that the nudibranchs of the second experiment consistently spent more time wandering throughout the experiment (except the very end) than did those of the first one, thus spending more energy per unit time.

EXPERIMENT B

The combinations which were offered to *Aeolidia* and the number of times each was offered are indicated in Table 2. The number of experiments in which each species was eaten first, second, or at the same time as the other species, and the species offered with it for each category are shown in Table 3.

The anemones fell into 3 groups which could be ranked from most to least preferred. The first group included *Epiactis, Anthopleura elegantissima,* and *A. xanthogrammica.* These anemones were either eaten first or at the same time as the other species offered. They were eaten simultaneously, however, only with other members of this group (except for 2 experiments in which *Aeolidia* ate *A. elegantissima* and *Diadumene* together). The proportion of nudibranchs wandering when offered anemones of the first group in combination with any other species was less than the proportion wandering when offered only anemones of the other 2 groups (Figures 4 and 5). The 3 species could not be ranked within the group.

The second group included *Diadumene* and *Metridium.* In all cases in which *Diadumene* was eaten first, the anemones offered belonged to the least-preferred group. In 3 experiments it was not eaten at all. *Diadumene* was eaten in a much greater proportion of the experiments involving

Table 2

Combinations of anemones offered to *Aeolidia* in experiment type B. Letters denote each experiment of a particular combination which was performed

Combination	Base Diameter (cm)
Epiactis and *Anthopleura elegantissima*	a. 0.5 and 0.8, respectively
	b. no data
	c. both 2.0
Epiactis and *Anthopleura xanthogrammica*	a. 1.5 and 2.5
Epiactis and *Corynactis*	a. 1.5 and 0.8
Epiactis and *Metridium*	a. 1.0 and 1.5
Epiactis and *Tealia crassicornis*	a. 1.5 and 4.0
Anthopleura elegantissima and *A. xanthogrammica*	a. both 3.5
Anthopleura elegantissima and *A. artemisia*	a. both 1.5
	b. 2.0 and 3.0
Anthopleura elegantissima and *Corynactis*	a. 1.5 and 0.5
Anthopleura elegantissima and *Diadumene*	a. 1.5 and 0.5
	b. 1.5 and 0.5
Anthopleura elegantissima and *Metridium*	a. both 2.0
Anthopleura elegantissima and *Tealia*	a. 4.0 and 3.0
Anthopleura xanthogrammica and *Diadumene*	a. 4.0 and 1.0
Anthopleura xanthogrammica and *Metridium*	a. no data
Anthopleura xanthogrammica and *Tealia*	a. 3.5 and 3.0
Diadumene and *Anthopleura artemisia*	a. 0.5 and 1.5
	b. 0.5 and 1.5
Diadumene and *Corynactis*	a. both 0.5
	b. both 0.5
	c. both 0.5
Diadumene and *Metridium*	a. 1.0, no datum
	b. both 0.5
	c. 0.4 and 0.5
	d. 1.5 and 1.0
	e. 0.5 and 0.8
Diadumene and *Tealia*	a. 3.0 and 0.5
	b. 3.0 and 0.5
Metridium and *Anthopleura artemisia*	a. 0.8 and 1.5
Metridium and *Corynactis*	a. 0.8 and 0.5
Metridium and *Tealia*	a. 0.8 and 3.0
Corynactis and *Anthopleura artemisia*	a. 0.5 and 1.5
Corynactis and *Tealia*	a. 3.0 and 0.5

it than *Metridium* (80% vs. 45%). Nevertheless, it was surprising that *Metridium* was eaten in such a large proportion of the experiments. In 2 instances (when offerred with *Diadumene*) it was even the first one eaten. In the other cases, it was eaten only after the preferred one had been consumed. In every case in which *Metridium* was eaten, however, feeding occurred only after I had repeatedly replaced the nudibranchs, which kept escaping to the water table. It is also noteworthy that the anemones were small (1.5 - 2.0 cm). Evidence that the defenses of large *Metridium* may be more effective in preventing predation than those of smaller ones is presented in the section on behavior of *Metridium*. It is further interesting that (except for the cases with *Diadumene*) the nudibranchs ate *Metridium* only after eating other anemones. This fact indicated a greater tendency to attack *Metridium* after the nudibranchs had been feeding for a while than when they had not eaten at all.

The third group included *Anthopleura artemisia, Corynactis,* and *Tealia crassicornis.* These anemones were not

Table 3

Experiment B: Order in which anemones were eaten
Explanation in text

	first		with		together		with		second		with		not eaten		with	
sp.	n	%	sp.	n	n	%	sp.	n	n	%	sp.	n	n	%	sp.	n
E.	4	50	*A.e.*	1	4	50	*A.e.*	3	0	0	–	–	0	0	–	–
			M.	1			*A.x.*	1								
			C.	1												
			T.	1												
A.e.	6	50	*D.*	1	6	50	*E.*	3	0	0	–	–	0	0	–	–
			M.	1			*A.x.*	1								
			A.a.	2			*D.*	2								
			C.	1												
			T.	1												
A.x.	4	67	*D.*	1	2	33	*E.*	1	0	0	–	–	0	0	–	–
			M.	1			A.e.	1								
			T.	2												
D.	7	47	*A.a.*	2	2	13	*A.e.*	1	3	20	*A.x.*	1	3	20	*M.*	3
			C.	3							*M.*	2				
			T.	2												
M.	2	18	*D.*	2	0	0	–	–	3	27	*E.*	1	6	55	*D.*	3
											A.e.	1			*A.a.*	1
											A.x.	1			*C.*	1
															T.	1
A.a.	0	0	–	–	0	0	–	–	0	0	–	–	6	100	*A.e.*	2
															D.	2
															M.	1
															C.	1
C.	0	0	–	–	0	0	–	–	0	0	–	–	8	100	*E.*	1
															A.e.	1
															D.	3
															M.	1
															A.a.	1
															T.	1
T.	0	0	–	–	0	0	–	–	0	0	–	–	8	100	*E.*	1
															A.e.	1
															A.x.	2
															D.	2
															M.	1
															C.	1

E. – *Epiactis*; *A.e.* – *Anthopleura elegantissima*; *A.x.* – *Anthopleura xanthogrammica*; *D.* – *Diadumene*; *M.* – *Metridium*; *A.a.* – *Anthopleura artemisia*; *C.* – *Corynactis*; *T.* – *Tealia crassicornis*; n – number of experiments in each category; % – percent of the total number of experiments with given anemone

eaten at all during the course of the experiments (2 - 6 days). The preferred anemones, in contrast, were usually attacked within a few hours after introduction of the nudibranchs, and were completely eaten by the second or third day, the time taken related to the size of the anemones. When offered the least preferred anemones, the nudibranchs spent a high proportion of time wandering in the bowls or they escaped to the water table where they were frequently eating anemones stored there (Figures 4 and 5.) It is noteworthy that nudibranchs were never seen to be eating the species of the second or third groups on the water table, but only those of the first group.

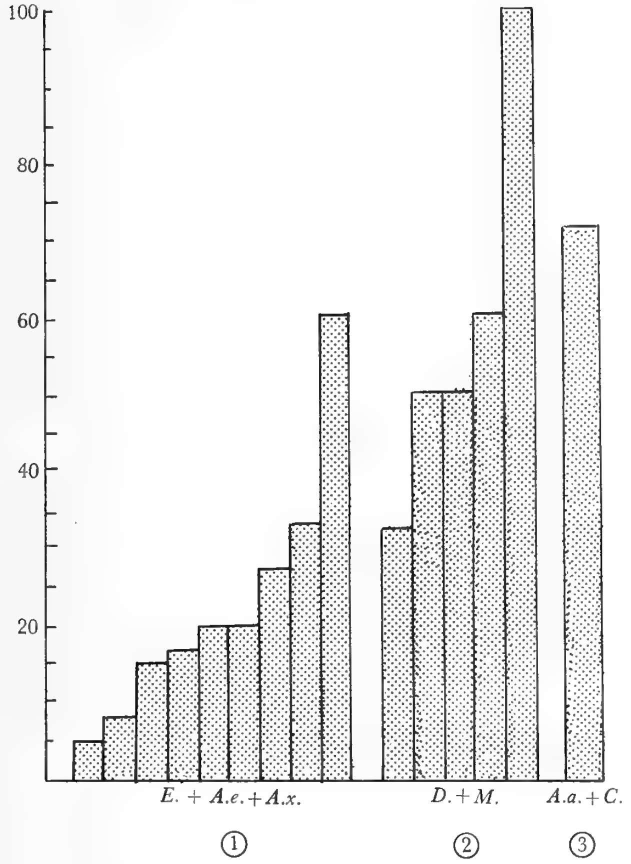


Figure 4

Experiment B: Percent wandering when offered a combination including: (1) the 3 most preferred anemones; (2) the 2 of intermediate preference, and (3) the 3 anemones of least preference. Each bar represents the percent of the total nudibranch-observations involving an anemone in each group in combination with one of the same or of a less preferred group. The observations including an anemone in combination with one of a more preferred group are omitted, since the more preferred species would govern the activity pattern

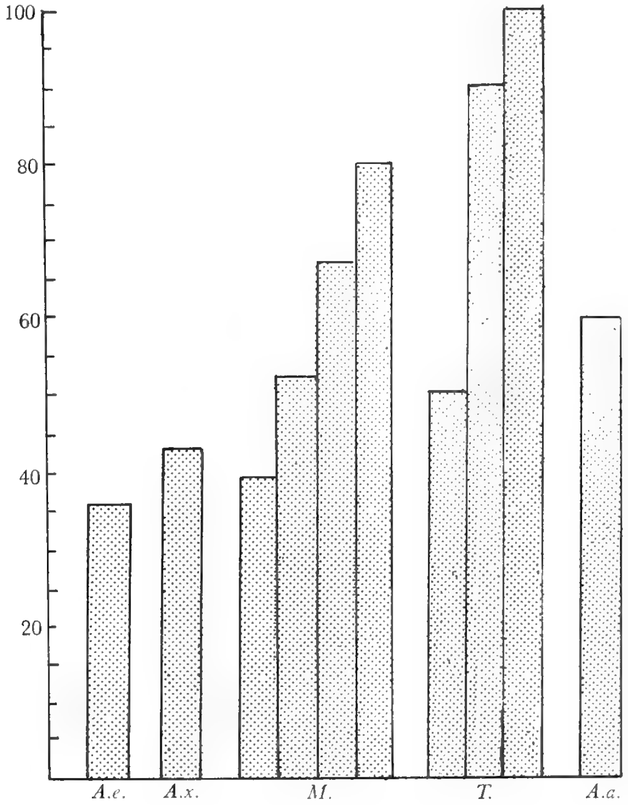


Figure 5

Experiment B: Percent wandering when each anemone was the only one available (after the preferred one had been eaten). Each bar represents the percent of the total nudibranch-observation for the periods in which each anemone was the only one available. Data are unavailable for *Epiactis* (eaten too rapidly), as well as for *Corynactis* and *Diadumene* (not offered alone)

DISCUSSION

The results of this series of experiments showed an order of preference similar to that shown by experiment type A. *Epiactis, Anthopleura elegantissima, A. xanthogrammica* were preferred to all others, and *Corynactis* was not eaten at all. The primary differences included (1) the lack of distinction in type B between the preference for *Epiactis* and *A. elegantissima* on the one hand, and *A. xanthogrammica* on the other; (2) the fact that some *Metridium* were eaten; and (3) the fact that *A. artemisia* and *Tealia* were not eaten at all.

This type of experiment provided further information on predation methods of groups of *Aeolidia.* (1) The nudibranchs fed on the preferred anemones during the same period of time, alternating between the 2 present, rather than eating one totally before attacking the other. (2) They completely consumed all anemones but *Diadumene.* (3) When offered a combination including a preferred species, the nudibranchs spent most of the time either eating or being inactive. They spent a relatively small amount of time wandering: 36% of the nudibranchs observed were eating, 38% were inactive, and only 26%

were wandering. With the less preferred species, however, only 10% were eating, 30% were inactive, and 60% were wandering.

EXPERIMENT C

In the first trial 5 nudibranchs were offered a choice between a group of *Epiactis* and water alone. Within the first 2 hours 2 nudibranchs had arrived in the anemone cage and a third was on its way in the tube. Within $8\frac{1}{2}$ hours all nudibranchs had gone across and were feeding on the anemones.

In the second trial 5 nudibranchs were offered a choice between a group of *Anthopleura elegantissima* and water alone. Two nudibranchs moved across within 9 hours, followed by 2 others within 24 hours from the start of the trial. All 4 nudibranchs were eating when observed. The 5th animal had escaped to the water table.

In the third trial 5 nudibranchs were given the choice between *Epiactis* and *Anthopleura elegantissima*. Within 24 hours one had gone across to each species. The other 3 were in the original cage wandering. Within 24 more hours they had escaped to the water table where they were eating an *A. elegantissima*. Why they did not go across to one of the 2 anemones is unclear. Perhaps they were equally attracted to both species and the resulting strong approach conflict resulted in indecision and ambiguous behavior.

In conclusion, these preliminary experiments showed that *Aeolidia* could use distance chemoreception to detect and locate its prey. That the nudibranchs were attracted to substances released by anemones was further indicated by an observation during a trial run using *Epiactis*. A nudibranch which was put at the end of the control tube (water only) showed no response other than to move away, while the same animal put at the end of the tube from the anemone cage immediately crawled in and arrived in that cage within 15 minutes.

BEHAVIORAL INTERACTIONS OF ANEMONES AND NUDIBRANCHS

1. Searching, Prey Locating, and Feeding Behavior of Nudibranchs

When a nudibranch which had been without food for 2 or more days was put in a bowl with a favored species of anemone (*Epiactis, Anthopleura elegantissima,* or *A. xanthogrammica*), the nudibranch often extended its body and moved the anterior $\frac{1}{3}$ - $\frac{2}{3}$ back and forth in the water with the oral tentacles and rhinophores extended. If the nudibranch did not contact an anemone, it reattached to the substrate and moved forward, perhaps repeating the head-raising behavior several times, and correcting its course to go more directly toward the anemone. Frequently the nudibranch did not raise the anterior part of the body off the substrate, but simply moved forward swinging the head and especially the extended oral tentacles from side to side and frequently touching the oral tentacles to the substrate. The rhinophores meanwhile were also moved around in the water in various directions. During searching the buccal mass was often protruded.

If while searching the nudibranch touched an anemone with the mouth or oral tentacles, it immediately retracted its head, pointed the anterior third of the cerata forward so that the anteriormost ones hid the head beneath them, and contracted the oral tentacles. This general contraction was followed by re-extension of its head and oral tentacles toward the stimulus. When contact occurred again, there was slight retraction, but the nudibranch continued forward, applied its mouth to the anemone, and began to feed. The nudibranchs generally began eating the part of the anemone first contacted (unless it were the tentacles), usually the base of the column. If the tentacles had been contacted (usually causing the nudibranch to retract more strongly than when the column or oral disk were touched), the nudibranchs often began eating the margin of the column just aboral to the tentacles. If while the nudibranch was moving along cerata happened to touch an anemone, the touched cerata contracted sharply, adjacent ones were pointed toward the touched ones, and the whole animal usually contracted. This initial response was followed by extension of the head toward the stimulus, contact (and slight contraction), and feeding.

When nudibranchs were feeding or otherwise inactive, their head, tail, rhinophores, and oral tentacles were retracted so that most of the body was hidden under the cerata. A feeding animal could be distinguished from a non-feeding one by the fact that the buccal mass of a feeding nudibranch was protruded and applied closely to the anemone. In this posture the nudibranchs strongly resembled anemones, especially *Anthopleura elegantissima*.

There was no striking difference in strength of response to contact with any of the anemones except *Corynactis* and *Metridium*, which elicited a stronger contraction. When these 2 anemones were touched the nudibranchs turned and moved away after their initial contraction. The clubbed tips of the tentacles of *Corynactis* adhered tightly to the part of the nudibranch touched, particularly to the cerata, and the nudibranch had to pull hard to free itself. The behavioral interactions of the nudibranch and *Met-*

ridium are described below. The essential difference in response to *Epiactis, Anthopleura elegantissima,* and *A. xanthogrammica* on one hand, and to *Corynactis, Diadumene, Metridium, Tealia,* and *A. artemisia* on the other, was that the nudibranchs usually turned toward and began eating the first 3 species of anemones, but turned and moved away from the latter 5 species. In addition, the nudibranchs usually did not exhibit clear-cut searching behavior when put with the latter anemones.

2. Behavior of Anemones

All anemones contracted sharply upon contact with the nudibranchs, the contraction being more rapid and stronger than when touched gently with a probe. Usually, *Epiactis, Anthopleura elegantissima, A. xanthogrammica,* and *Tealia* bent the column toward the nudibranchs with their tentacles still extended. With repeated or prolonged contact the anemones retracted their tentacles, closed the sphincter muscle around the margin of the oral disk, and contracted the column farther, becoming more or less round. When the nudibranchs began feeding on *Epiactis, A. elegantissima,* and *A. xanthogrammica,* the anemones usually contracted their muscles even more, but without decreasing much in size and losing much water; thus the column became hard and round. The column often tended to be thin-walled or inflated, especially on the side toward the nudibranch.

Epiactis invariably (8 observations) released its hold on the substrate within a few minutes after onset of feeding by a nudibranch. Detachment began in the area closest to the nudibranch and was initiated by contraction of the pedal disk margin, followed by lifting up of the margin and progressive detachment of the entire disk. *Anthopleura elegantissima* also often detached soon after feeding began (7 of 11 observations); *A. xanthogrammica* usually (5 observations) detached, at least partially, within a few minutes of being fed upon. None of the anemones detached when nudibranchs only touched them.

Anthopleura xanthogrammica tended to remain detached for an indefinite period of time after the nudibranchs had ceased feeding and released the anemones, while the other 2 species usually reattached. The reattachment subjectively had a greater tendency to occur in *A. elegantissima* than in *Epiactis.* The released anemones would lie on the substrate rounded up until they reattached.

The *Tealia* and *Metridium* which were eaten in the preference experiments were usually detached but not particularly inflated or turgid when the nudibranchs were eating them. The *Anthopleura artemisia* attacked during the preference experiments were detached and turgid though not particularly inflated while being eaten. *Diadumene* was the only species of anemone which did not detach while being eaten, although it became quite turgid. *Corynactis* never became inflated or detached.

None of the anemones showed a swimming escape response.

3. Behavioral Interactions of the Nudibranchs and *Metridium* and *Diadumene*

Metridium

Metridium showed no response to the presence of a nudibranch unless actual contact was made. Upon instantaneous contact with any part of the nudibranch an anemone immediately retracted its tentacles and contracted the column, although it usually did not extrude acontia. When small (less than 2 cm diameter) anemones were observed under a dissecting microscope, the acontia on the side touched could be seen to move upward and outward toward the nudibranch. Acontia were usually not extruded unless prolonged or repeated contact was made. When further contact was not made the anemone would soon re-extend itself and appear normal. When further contact was made, however, the anemone contracted again even more strongly, extruded acontia in the region of contact, and closed its sphincter over its tentacles and oral surface, remaining in that state for an indefinite period of time. Gentle contact of an expanded anemone with a probe caused only slight contraction, soon followed by re-extension.

The length of time of prolonged contact by a nudibranch necessary to cause extrusion varied somewhat. In a series of 8 observations, extrusion occurred after $\frac{1}{2}$ to 6 minutes with an average of 2.6, most occurring in 2 to 4 minutes. When the anemones were gently touched with a probe, in contrast, extrusion did not occur until after at least 8 minutes of repeated touching.

It is noteworthy that extrusion often continued after the nudibranch had left, and that the extruded acontia which remained attached to the anemone were eventually retracted.

When a nudibranch touched an acontium, it strongly contracted its whole body, especially the part touched, and turned sharply, moving away from the stimulus. All parts of the body were sensitive, including the foot. The nudibranch also secreted large amounts of viscous mucus. Usually the acontia became entangled in the mucus along with large numbers of discharged nematocysts. Whenever an acontium happened to contact the nudibranch itself, usually a ceras, it adhered tightly. When this happened, the nudibranch quickly and strongly contracted and bent the ceras to which the acontium was attached (sometimes autotomizing the ceras), erected the others and generally pointed them toward the stimulus, and tried to move away.

Although the nudibranchs used in the behavioral observations managed to free themselves, on 3 successive days in experiment A - 1 nudibranchs were found wrapped in thick mucus with acontia caught in the mucus and wrapped around some cerata. The first nudibranch was removed and placed on the water table where the next day it appeared normal except for contracted cerata in one area, and was feeding. It appeared to be completely recovered within 3 days. The other 2 nudibranchs were left in the cage where they recovered within one day.

Toward the end of experiment A - 2 a nudibranch was found nearly dead with the body wall of its back broken and with some of the viscera protruding through the hole. It is probable that it had been injured by acontia, although none were extruded at the time of observation, because the nudibranchs had been attacking *Metridium* during the past few days. Although it is possible that another nudibranch had attacked it, that possibility is unlikely because I saw no other evidence of possible cannibalism even after some nudibranchs had been without food for 3 weeks. Rather, it seems as though these 3 nudibranchs were weakened enough from starvation that their defenses were no longer effective.

Boutan (1898) noticed the same weakness in an *Aeolidia* spent from spawning which was not able to escape from an anemone onto which he had dropped it, but was taken in and digested. Healthy ones he had dropped onto an anemone were able to escape. I also found that anemones (*Anthopleura elegantissima* and *A. xanthogrammica*) would accept and digest dead or weakened nudibranchs. The feeding response was not just due to lack of a defensive response of the nudibranchs, but due to their own lack of defensive response as well.

That acontia were a very strong deterrent to predation was observed on many occasions. (1) Sometimes nudibranchs after their initial withdrawal upon contact with *Metridium* re-approached it with the buccal mass protruded and explored it with their oral tentacles and oral surface. This invariably elicited extrusion of acontia, and upon contact with them the nudibranchs contracted sharply and moved away. (2) On many occasions in choice experiments involving *Metridium*, threads of mucus were seen crisscrossing the bowl, with acontia, discharged nematocysts, and sometimes autotomized cerata caught in them, while *Metridium* remained intact.

Similarly, Yarnall (personal communication) frequently noticed in the field that *Aeolidia* in Monterey Bay, California, would cease feeding when acontia became entangled in their cerata. The nudibranchs in the laboratory which became entangled and could not free themselves died within 24 hours. He also found several moribund nudibranchs with acontia entangled in their cerata in the field. Nevertheless, he commonly found acontia in the stomachs of *Aeolidia*. Harris (1971) found that the defenses of *Metridium* usually prevented the nudibranchs from feeding on large anemones in New England. Some preliminary experiments I did showed that perhaps the local nudibranchs would also eat small ones but not larger ones. The effectiveness of the defenses of *Metridium* of different sizes merits further investigation.

Diadumene

The mutual responses of the nudibranchs and *Diadumene* were much less definite than those of the nudibranchs and *Metridium*. Again, contact was necessary to elicit a response. Upon contact, an anemone retracted its tentacles, partially contracted its column, and moved acontia upward in the region of the stimulus. Upon repeated or prolonged contact, the tentacles were retracted completely, the sphincter around the margin of the oral disk was contracted, hiding the tentacles, and the column was contracted strongly against the water inside. The acontia were moved farther upward or outward and were often extruded. Acontia were extruded once when a nudibranch crawled over an anemone, and once when one bit and began feeding on an anemone. The latter nudibranch continued eating, ignoring the acontia. Acontia generally caused the nudibranchs to withdraw slightly, but the nudibranchs did not respond significantly more strongly to acontia than to any other part of *Diadumene*. Their response to contact with any part of an anemone was like that to contact with a probe. Likewise, the anemone's response was not significantly different from that to such contact.

FEEDING BEHAVIOR AND ACTIVITY PATTERN OF NUDIBRANCHS OFFERED GROUPS OF *Anthopleura elegantissima*, AND DEFENSIVE RESPONSES OF THE ANEMONES

There were numerous difficulties in determining activity patterns. Individual nudibranchs and anemones were often difficult to recognize, and this was complicated by the fact that new nudibranchs would appear in the dishes and the ones being studied would disappear. The latter difficulty especially occurred during the second experiment, which took place in a submerged dish which was downstream from other anemones, including a partially eaten *Anthopleura xanthogrammica* to which the nudibranchs kept migrating. However, certain aspects of the activity pattern of the nudibranchs and of the behavior of the anemones became apparent.

1. The nudibranchs did not keep their hold on an anemone once they had attacked it initially, nor did they usually remain inactive nearby. Rather, they let go and wandered off when not feeding.
2. Periods of eating (lasting a few minutes to a few hours) alternated with periods of inactivity of longer duration (several hours to several days), and sometimes with periods of wandering as well.
3. In the absence of a definite current of water flowing over them (first experiment), the nudibranchs tended to eat individuals within a group only partially, rather than tending to consume one before moving to another. For example, at the end of the first experiment, after a nudibranch had been feeding within a group of 10 anemones for 4 days, there were pieces of 5 anemones (rims of pedal disks) and 4 slightly damaged anemones (epidermis missing in places) remaining. Only one anemone had disappeared. However, when a unidirectional current flowed over the nudibranchs (second experiment), it seemed as though they tended to attack and consume one anemone before attacking another. For example, the nudibranchs kept moving upstream to feed on the *Anthopleura xanthogrammica* mentioned above, rather than remaining with and feeding on the anemones in the group. Nevertheless, when not moving upstream the nudibranchs moved from anemone to anemone within the group without consuming any of them.
4. The anemones attacked during the second experiment (in which most of the anemones were in contact with each other) were those on the edge of small groups or which were solitary. The nudibranchs usually did not crawl over anemones to eat one in the midst of a group.
5. Relatively few anemones detached. Of 45 observed anemones 10 (22%) detached. About half of these reattached when left alone. The others remained detached, lying rounded up on the bottom, even though they had little damage and were not attacked again.
6. The attached anemones tended to move away from the nudibranch as they were being eaten and to continue moving after the nudibranch had stopped eating, so that within 24 hours an anemone had often moved 5 cm or more away from its location when first attacked (one anemone moved 5 cm in 4 hours). Some continued moving for several days (20 cm in 3 days, in one case).
7. The anemones in the second experiment dropped most of the sand adhering to them when collected when they were left undisturbed to attach before the nudibranchs were introduced, and they kept dropping the sand I repeatedly poured over them, making it impossible to determine the effect of sand on predation.

GENERAL DISCUSSION AND CONCLUSIONS

Food Preference

On the basis of experiments A and B, the anemones can be put into 3 groups which can be ranked from most to least preferred.

Group I includes *Epiactis prolifera, Anthopleura elegantissima* and *A. xanthogrammica.* These anemones were eaten whenever they were offered, were eaten first when nudibranchs were offered a choice between them and anemones of the other 2 groups, and were consumed rapidly with little wandering. The relative preference for the anemones within this group was less definite. Experiment A, however, provided some evidence that *Epiactis* and *A. elegantissima* may be preferred to *A. xanthogrammica* (see discussions following experiments). Field observations indicated a preference for *A. elegantissima.* Most of the nudibranchs were found on rocks with that species rather than with *Epiactis* or *A. xanthogrammica.*

Defenses seemed to play no role in determining which of the 3 anemones was preferred. Defenses involved nematocysts, inflation, detachment, and (indirectly) size (which appeared to be related to toughness). Only size seemed to govern the order and rapidity with which the anemones were eaten. *Aeolidia* ate the anemones in spite of the difficulties caused by nematocysts, or possible difficulties in maintaining a hold or in biting and rasping the anemones caused by inflation. Detachment caused no problem as long as the nudibranchs were eating, for they held the prey tightly. However, inflation coupled with detachment could be of value when the nudibranchs let go after feeding, by enabling the anemones to roll away. Detachment alone could be of value to large anemones, such as *Anthopleura xanthogrammica,* which could be torn from a nudibranch's grasp by a sudden surge of water or by its own weight. An additional defensive response of *A. elegantissima* was to move away as a nudibranch was eating it and to continue moving after the nudibranch had ceased feeding. This behavior would be safer than detaching, which is likely to result in an anemone falling onto an unsuitable substrate or being washed ashore.

Group II includes *Diadumene luciae* and *Tealia crassicornis,* both of which were sometimes eaten at least in part. They were not the first ones eaten, were often eaten only partially, and were eaten over a longer period of time, and more time was spent wandering than when anemones of group I were being eaten. In addition, nudibranchs were never seen near these species in the field.

Defenses did not seem to be important deterrents in the laboratory. Defenses included the nematocysts of both, the acontia and inflation of *Diadumene,* and the detachment and large size of *Tealia.* However, the bending in *Tealia* and those of group I of the column with still extended tentacles toward the nudibranch could be of advantage by causing the nudibranch to recoil. In recoiling it could contact another anemone which may be in a better position for attack. During several observations nudibranchs did not attack the first anemone they touched, but resumed searching after recoiling eventually to attack another anemone which they encountered.

Tealia was about the same size as the *Anthopleura xanthogrammica* used in the study, had equally effective defenses, and was made equally available in the laboratory, yet the nudibranchs distinctly preferred *Anthopleura.* Examination of the feces of nudibranchs which had been eating each species alone for several days indicated greater physiological adaptation to eating *Anthopleura* than *Tealia.* The feces of nudibranchs which had been eating the red anemone *Tealia* were pink. When examined microscopically, the feces proved to be full of discharged nematocysts, pink cells including some living clumps with beating flagella, and many ciliate protozoans. Those which had been eating *A. xanthogrammica* had white feces containing undischarged nematocysts, ciliates (the observed differences in the ciliate fauna were not investigated), and zooxanthellae. No intact living cells from the anemone itself were present. Amorphous white granular material probably represented undigested remains of the anemone. Although the nudibranchs seemed to be less efficient in processing *Tealia, Tealia* was able to support them well enough for them to lay eggs (which were pink instead of white as when eating *Anthopleura*), grow, and store food in the digestive gland (which was pink instead of green as when eating *Anthopleura*). The relative weights of the 2 anemones which must be eaten to provide the same rate of growth and egg production would be interesting to investigate.

The observations of *Tealia* suggest that learning may play a role in food preference. The only time a *T. crassicornis* was eaten completely, rapidly, and with little wandering was in experiment A - 1. This anemone was the original one in the cage and was attacked soon after *T. coriacea* had been consumed. The second *T. crassicornis,* added well after the first had been eaten, was not eaten at all. The *T. coriacea* was declining when attacked early in the experiment. The tendency of *Aeolidia* to attack wounded anemones is reported in the literature (e. g. Stehouwer, 1952). Thus, it is possible that the nudibranchs had a greater tendency to attack *T. coriacea* than they would have had if the anemone had been healthy. The fact that the original *T. crassicornis* was attacked soon after *T. coriacea* had been eaten while neither the new one nor those in other experiments were attacked, indicates that the nudibranchs may have become conditioned to eating this genus. The fact that the new *Tealia* added later was not attacked indicates that the conditioning must be frequently reinforced to persist. The possibility of conditioning is discussed further below.

Group III includes *Anthopleura artemisia, Corynactis californica,* and *Metridium senile.* These anemones were eaten very rarely, if at all. Further, the nudibranchs were not found with them in the field, although at least *Corynactis* and *Metridium* were very common and occurred in dense groups. *Anthopleura* and *Metridium* were preferred to *Corynactis,* the only anemone which was never eaten at all. The defenses of *Anthopleura* investigated were similar to those of the anemones of groups I and II, yet the anemones were very rarely eaten.

In contrast to all other species, the defenses of *Corynactis* and *Metridium* were an effective deterrent to predation. That is not to imply that without their defenses the nudibranchs would eat them readily. In fact, *Aeolidia* would not attack *Corynactis* even when the tentacles were retracted within the closed oral disk area. Nevertheless, the nudibranchs exhibited a very strong negative response to the clubbed tips of the tentacles of *Corynactis* and to the acontia of *Metridium.* Both of these were potentially dangerous, as behavioral observations showed. The primary defenses of nudibranchs against acontia were their abilities to secrete copious amounts of viscous mucus which prevented discharged nematocysts from touching their epidermis, and to pull away from acontia which managed to adhere despite the mucus. Weakened animals became entangled in acontia; escape was accompanied by loss of entangled cerata. Healthy animals also tended to lose cerata to which acontia had attached. Their defense against *Corynactis* was simply to contract strongly and pull away. It was interesting that the acontia of *Diadumene* did not elicit a strong avoidance response or the secretion of mucus.

Tealia, Diadumene, and *Metridium* are also mentioned in the literature as being eaten by *Aeolidia* (Table 1). Likewise, none of the workers indicated that *Tealia* was the preferred species. However, Swennen (1961) cited unpublished observations of *Diadumene* being preferred to *Metridium. Metridium* was indicated by two workers to be a preferred species and by 4 others as being eaten, including Swennen who raised young nudibranchs on it.

In addition to these published observations on *Metridium,* 4 people (L. Harris, V. Human, T. Gosliner, and J. Yarnall) have told me that they have found large numbers of *Aeolidia* among the abundant *Metridium* on submerged pilings (particularly in Monterey Bay, California), and have either seen the nudibranchs feeding on *Metridium* or have seen evidence that they feed on this species. Harris (personal communication) found the same relationship on the Atlantic coast of the United States as well as in Monterey. Only Harris and Yarnall noticed any particular adverse effect of acontia on the nudibranchs. However, they (like RUSSELL, 1964) noted that the nudibranchs would eat the acontia. The fact that few if any other anemones were present in the habitats observed suggests that perhaps in the absence of less dangerous prey the nudibranchs may learn to cope with the defenses of *Metridium* and come to eat the anemones in spite of the defenses. WOOD (1968) found that the prosobranch *Urosalpinx cinerea* (Say, 1822) had an increased tendency to feed on a species after eating it for a while, which he called "ingestive conditioning." Similar ingestive conditioning may occur in *Aeolidia* as suggested by the present observations on *Tealia* and those just described on *Metridium.* This possibility is supported by the observations of Yarnall (personal communication) that the nudibranchs which had been eating *Metridium* preferred *Metridium* even when given a choice between it and *Epiactis,* while those which had been eating *Epiactis* preferred that species to *Metridium.* However, Gosliner and Harris (personal communication) observed that the nudibranchs which had been eating *Metridium* preferred *Anthopleura elegantissima* when given a choice between it and *Metridium.* Ingestive conditioning was unlikely to have been governing the relative preference of the nudibranchs I studied for the 3 most preferred species, because they did not prefer *A. elegantissima* to *Epiactis* or *A. xanthogrammica,* although most had been feeding on that species before being collected. However, the lack of conditioning could explain why they would not eat *Metridium.* The various ramifications of ingestive conditioning would be interesting to investigate.

In conclusion, the facts that (1) when anemones were made equally available in the laboratory the nudibranchs exhibited definite preferences, (2) the defenses of the anemones other than *Corynactis* and *Metridium* were equally effective, and (3) ingestive conditioning was unlikely to be important in the nudibranchs studied, indicate that preference for particular anemones was not proximately determined by these 3 possible factors alone.

A fourth possible proximate factor is the relative nutritional value of the different anemones. Nutritional value would be related to the rapidity with which the anemones are eaten and digested and to the efficiency of processing by the nudibranchs, as well as to the original nutrient content. The efficiency with which nudibranchs can handle their prey and extract the nutrients would presumably be genetically based and be the result of evolutionary adaptations to eat and digest particular species. Thus relative nutritional value would involve an interaction between the nutrient makeup of the anemones and the processing efficiency of the nudibranchs. The potential nutrient value of the prey, however, would presumably be important as an ultimate factor in the evolution of food-preference and the concomitant feeding adaptations. These two aspects of nutritional value were not investigated as such, but the observations of the feces of nudibranchs which had been feeding on *Anthopleura xanthogrammica* or *Tealia* indicate that the nudibranchs may have different abilities to process the various species.

Relative palatability is a fifth possible proximate factor. Similar to nutritional value, this factor would be expected to involve an interaction between the original defensive adaptations (including the possession of distasteful or painful characteristics) of the prey and evolution of preference in the predator along with the co-occurring adaptations involved with handling the prey's defenses. Thus, palatability is more likely to be dependent on the evolution of food-preference than on some intrinsic property of the prey. To the extent that the relative degree to which a particular species was eaten is a measure of relative palatability, this possible factor was investigated.

Since some of the main possible proximate factors behind food-preference were either unimportant or depended in part on the adaptations of the predator, it seems that preference may be genetically determined in the local populations of *Aeolidia.* The evolution of preference may have been ultimately based on these factors, but they do not seem important any longer. Evidence is presented later that the evolution of preference for at least *Anthopleura elegantissima* and *A. xanthogrammica* may be related primarily to the tendency for these two species to occur in dense concentrations.

The hypothesis that preference is genetically determined is supported by the prediction (among others) made by EMLEN (1966) on the basis of a mathematical model that other things being equal, animals would be more selective when satiated and more indiscriminate when starved. His model concerned the caloric value and consumption times of different foods as a prediction of which ones would be eaten. Since *Aeolidia* was selective even when starving, it would seem as though something were operating to govern food-preference (other than degree of starvation relative to caloric value and consumption times of different foods), which is probably genetical predisposition for the reasons just presented.

Searching and Feeding Behavior

Experiment C, behavior observations, and the fact that escaped nudibranchs tended to congregate around and feed on the same anemone indicate that *Aeolidia* is attracted to its prey from a distance. In addition, contact of anemones especially with the oral tentacles was an important method of location and identification of prey. During searching the oral tentacles were greatly extended and swung from side to side as if feeling for something, and the behavior upon contact depended upon whether or not the touched anemone was a member of a preferred species.

Feeding on preferred anemones continued without interruption for a few minutes to several hours and usually ceased before the anemone was completely consumed. The principal exceptions involved small *Epiactis* and *Anthopleura elegantissima* which the nudibranchs ate rapidly with no observed cessation of feeding. Feeding rate seemed to depend on size of anemone (with size and state of starvation of nudibranchs equal), but when size of anemone was constant, the rate seemed to depend on the degree of toughness of the anemones. Although absolute feeding rate was not investigated, the subjective impression was that *Epiactis* was eaten the most rapidly for its size, followed by *A. elegantissima* and *A. xanthogrammica* in that order. Based on the translucence of the column and the thickness of the body wall, it seemed that *Epiactis* was the most delicate anemone, followed by *A. elegantissima* and *A. xanthogrammica*. The other anemones were not eaten regularly enough for an estimate to be made of the rapidity with which they were eaten.

Nudibranchs began feeding on any part of the anemones except the tentacles, although they rarely began with the oral disk. The principal damage to anemones which had been abandoned after the initial attack was to the epidermis and outermost layers of the underlying tissues. After a longer time and after several feeding periods the nudibranchs would often have eaten through the wall of the column to the gastrovascular cavity. Often the anemones were not abandoned until they had been reduced to doughnut-shaped pieces, apparently the rims of the pedal and oral disks. It is noteworthy that (judged subjectively) these parts were thicker and tougher than other parts of the column. When other preferred anemones were not available, the nudibranchs ate the entire anemone, including these rims, the tentacles, septal filaments, and even the acontia of *Metridium* and *Diadumene*.

When an abundance of a preferred species (*Anthopleura elegantissima* in experiment E) was available, the nudibranchs tended to begin a new anemone once they had ceased feeding and had let go of the first one. This tendency was caused partially by the behavior of the anemone: detachment and falling to the bottom or moving away on the pedal disk. It was also caused by the behavior of the nudibranchs, which let go after feeding. They sometimes began wandering upon cessation of feeding, but more frequently the nudibranchs remained quiescent for several hours and began wandering later. The later wandering seemed to be governed by hunger, and the anemone attacked seemed to be the first one contacted in its wandering in the absence of a definite current of water flowing over the animals. The first anemone contacted usually was not the original anemone, which had escaped from the immediate area.

In a definite current of water the nudibranchs seemed to be attracted to wounded anemones as Stehouwer (1952) found, since they congregated around single anemones upstream even when intact anemones were closer. In experiment E - 2 the scent of the wounded *Anthopleura xanthogrammica* exerted a stronger attraction than even the wounded *A. elegantissima* nearby on which the nudibranchs had been feeding. Yarnall (personal communication) saw good evidence that *Aeolidia* is attracted to damaged anemones (*Metridium*) in the field. In areas of dense concentrations of *Metridium* he found that the nudibranchs would be clustered around and feeding on a single anemone rather than being evenly scattered throughout the group of anemones and feeding alone. In the absence of a definite current, however, I found that the nudibranchs usually ate alone. The nudibranchs presumably ate alone because (1) they did not detect the anemones which nearby nudibranchs were eating, (2) the strength of the scent from anemones being eaten by nearby nudibranchs was not strong enough to attract them over the scent of or contact with nearer intact anemones, so that they consequently attacked the first anemone they found, or (3) the scent from nearby wounded anemones coming from different directions confused the nudibranchs, causing many changes in direction while wandering which might or might not result in the location of a wounded anemone. These possibilities may also explain why during experiments with a definite unidirectional current the nudibranchs tended to eat the anemones completely before attacking another, while they tended to wander from anemone to anemone in experiments without a definite current.

The facts that nudibranchs tended not to feed constantly until an anemone was completely consumed, that they let go when not feeding, that *Anthopleura elegantissima* escaped by either detaching or moving away on its pedal disk, that nudibranchs followed an inactive period by wandering and tended to attack the first anemone contacted (at least in still or turbulent water), and that nudibranchs tended to attack isolated anemones or those on the edge of groups, could have provided selective pressure in the evolution of grouping behavior in *A. elegantissima.* Grouping would minimize the chances that a given individual would be consumed.

Grouping would also benefit the nudibranchs, as it would provide an abundant source of food concentrated in definite localities enabling the nudibranchs to spend a minimal amount of time and energy searching for food. Further, *Anthopleura elegantissima* is not subject to large fluctuations in population size with the seasons. It is possible that *Aeolidia* is evolving specificity for *A. elegantissima,* since most nudibranchs in nature were with this species. Whether the local distribution of *Aeolidia* is governed by settlement preferences of the veligers or by searching of the postlarval stages would be interesting to discover.

Abundance, dense concentrations of individuals, and population stability are characteristics which would be necessary in a prey population for food specificity of a predator to evolve (MacArthur, 1961; Pianka & Pianka, 1970). One would expect specificity to evolve whenever possible, as it would enable the evolution of specific adaptations to handle the food efficiently. Further, it would be better for behavior to be controlled so that the nudibranchs would remain in an area of suitable food, rather than wandering here and there as they detect different species, as it would minimize the time and energy spent in the search for food.

Anthopleura elegantissima would be superior in at least some of the above attributes to the other anemones studied, with the possible exception of *A. xanthogrammica.* The latter species also occurs in great abundance and is a much larger anemone. Thus, one individual would provide food for a longer time, and the total biomass per unit area may be greater than for *A. elegantissima.* Possible disadvantages of specializing on *A. xanthogrammica* would include the more scattered distribution of individuals, the greater difficulty (with less digestive efficiency?) of eating a larger anemone with presumably tougher and thicker layers of connective tissue, and the greater potential effectiveness of detachment of a larger and heavier anemone.

SUMMARY

Food-preference, the effect of the defenses of the prey on predation, and feeding and prey-locating behavior of the anemone-eating nudibranch *Aeolidia papillosa* on the central California coast were investigated.

Based on the experiments and observations, the following generalizations can be made:

1. The 8 principal species of anemones occurring intertidally can be put into 3 groups depending on the degree of preference shown for them, with the order within the groups remaining unclear. From most to least preferred, the groups are:
   - I *Anthopleura elegantissima, A. xanthogrammica, Epiactis prolifera*;
   - II *Diadumene luciae, Tealia crassicornis*;
   - III *Anthopleura artemisia, Corynactis californica, Metridium senile.*

   The lack of preference for *Metridium* here differs from the distinct preference reported in the literature for European *M. senile.* The lack of preference seemed to be primarily due to the strong aversion of the nudibranchs to acontia. The extrusion of acontia was a definite defense response which invariably occurred when *Aeolidia* repeatedly and prolongedly contacted *Metridium.* The nudibranchs responded by secreting copious and viscous mucus, withdrawing sharply, and moving away.

2. Food preference seemed to be genetically determined, rather than being proximately due to:
   - a) defenses of the prey (except for the acontia of *Metridium* and nematocysts of the tentacles of *Corynactis*). The defenses observed were: nematocysts (present in all anemones); inflation of the column (present in *A. elegantissima, A. xanthogrammica, Epiactis, Diadumene, Metridium*); detachment from the substrate (*A. artemisia, A. elegantissima, A. xanthogrammica, Epiactis, Tealia, Metridium*); and acontia (*Diadumene, Metridium*);
   - b) accessibility of prey in nature;
   - c) learning (although evidence is presented which suggests that this may modify genetically determined preference);
   - d) relative nutritional value of different species of anemones;
   - e) relative palatability of the different species.

3. *Aeolidia* could detect and was attracted to the anemones of group I at a distance, and exhibited characteristic searching behavior. Prey location and identification were aided by contact of the anemone with the oral tentacles. Location by contact seemed to be the primary prey-detection mechanism in the absence of a definite current of water flowing over an anemone to the predator. In a definite current distance chemoreception seemed to be more important, and wounded

anemones exerted a stronger attraction than intact ones.

4. In regard to feeding activity pattern:
   a) Nudibranchs did not tend to feed continuously until an anemone was consumed;
   b) they released the anemone when not feeding;
   c) they tended to attack the first anemone of the preferred species contacted in the absence of a definite current of water;
   d) feeding was followed by an inactive period which in turn was followed by a period in which the nudibranchs wandered;
   e) only in the absence of other individuals of a preferred species did the nudibranchs consume an anemone completely.

5. The characteristics of the feeding behavior just described plus the fact that *A. elegantissima* either detached when being fed upon and fell to the bottom when released, or moved away on its pedal disk after being released, could make the occurrence of this species in dense masses of individuals an adaptation which would minimize the chance that a particular individual would be eaten.

6. Nearly all nudibranchs used in the study were found with *A. elegantissima*, rather than with the other species of anemones. This species would be predicted on theoretical grounds to be ideal prey for a food specialist (other things being equal). It is possible that specificity for *A. elegantissima* may be evolving in the local populations of *Aeolidia papillosa*.

ACKNOWLEDGMENTS

This study was conducted at Pacific Marine Station, Dillon Beach, California. I wish to express my sincere gratitude to Mr. David H. Montgomery, a visiting instructor, and to Dr. Edmund H. Smith, Director of Pacific Marine Station, for making my stay possible, and especially to Dr. Smith for his generous allocation of work space. I also wish to express my deep appreciation to Mr. Montgomery for all his enthusiasm and interest during the project, for his invaluable help in collecting the animals, and particularly for his careful reading of the manuscript. I wish to thank my husband, Dr. James F. Waters, for all his encouragement, advice, and patience during the preparation of the manuscript. Larry Harris, Vernon Human, Terrence Gosliner, and Jack Yarnall are in my debt for telling me of their observations of *Aeolidia* and *Metridium*, and making me realize that learning in *Aeolidia* may be more important than I had thought. My thanks also go to Jack Yarnall for his helpful comments on the manuscript. The students of the invertebrate zoology class, especially Miss Linda Welch, assisted me greatly in collecting the nudibranchs.

Literature Cited

Boutan, Louis
1898. Moeurs de l'*Eolis papillosa* Linné. Arch. Zool. exp. gén. ser. 3, no. 6, notes & rev. no. 10: XXXVII - XLII

Braams, W. G. & Hannie F. M. Geelen
1953. The preference of some nudibranchs for certain coelenterates. Arch. néerl. Zool. 10 (3): 241 - 264

Eliot, Charles N. E.
1910. A monograph of the British nudibranchiate Mollusca. Suppl. Ray Soc. London, part IV: 198 pp.

Emlen, J. M.
1966. The role of time and energy in food preference. Am. Nat. 100 (916): 611 - 617

Ford, C. E.
1964. Reproduction in the aggregating sea anemone, *Anthopleura elegantissima*. Pacif. Sci. 18 (2): 138 - 145

Hand, Cadet
1955. The sea anemones of central California, Part II: The endomyarian and mesomyarian anemones. Wasmann Journ. Biol. 13 (1): 37 - 99
1955. The sea anemones of central California, Part III: The acontiarian anemones. Wasmann Journ. Biol. 13 (2): 189 - 251

Harris, Larry
1971. Ecological observations on a New England nudibranch-anemone association. The Echo 4: 22

MacArthur, Robert H.
1961. Population effects of natural selection. Amer. Nat. 95 (882): 195 - 199

McMillan, N. F.
1942. Food of nudibranchs. Journ. Conch. London 21: 327

Miller, Michael Charles
1961. Distribution and food of the nudibranchiate mollusca of the South of the Isle of Man. Journ. Anim. Ecol. 30: 95 - 116

Pianka, E. R. & H. D. Pianka
1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. Copeia 1970 (1): 90 - 103

Ricketts, Edward F. & Jack Calvin
1968. Between Pacific tides. Stanford Univ. Press, Stanford, Calif. v - xiii + 3 - 502; 46 plts.

Robson, Elaine A.
1961. The swimming response and its pacemaker system in the anemone *Stomphia coccinea*. Journ. exp. Biol. 38: 685 - 694

Rosin, Ruth
1969. Escape response of the sea-anemone *Anthopleura nigrescens* (Verrill) to its predatory eolid nudibranch *Herviella* Baba, spec. nov. The Veliger 12 (1): 74 - 77 (1 July 1970)

Russell, Henry Drummond
1942. Observations on the feeding of *Aeolidia papillosa* L., with notes on the hatching of the veligers of *Cuthona amoena* A. & H. The Nautilus 55 (3): 80 - 82

Stehouwer, H.
1952. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.) Arch. néerl. Zool. 10: 161 - 170

Swennen, Charles
1961. Data on distribution, reproduction and ecology of the nudibranchiate Mollusca occurring in the Netherlands. Netherl. Journ. Sea Res. 1 (1 - 2): 191 - 240

Wolter, Helma
1967. Beiträge zur Biologie, Histologie und Sinnesphysiologie (insbesondere der Chemorezeption) einiger Nudibranchier (Mollusca, Opisthobranchia) der Nordsee. Zeitschr. Morph. Ökol. Tiere 60: 275 to 337

Wood, Langley
1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). Malacologia 6 (3): 267 - 318 (30 June 1968)

Embryonic Development of the Camaenid Snail, *Varohadra yeppoonensis*

BY

ALEX S. TOMPA AND JAMES N. CATHER

Department of Zoology, University of Michigan, Ann Arbor, Michigan 48104

(1 Plate)

JOURDAIN (1884) USED THE TERM podocyste to refer to the embryonic specialization of the foot of land snails which serves for respiration, excretion and albumenotrophy. SIMROTH (1912) noted that the podocyst is present in all stylommatophorans except in a species of the Succineidae, and in a camaenid, *Bulimus citrinus* Bruguière, 1792 (= *Amphidromis chloris* (Reeve, 1848). He bases his report on the single observation of SEMPER (1862) who briefly considered the development of *Amphidromis* in comparison to the more extensively studied *Ampullaria.*

In our previous work (CATHER & TOMPA, 1972) we have examined the physiological role of the podocyst especially with respect to albumenotrophy, and have confirmed the absence of the podocyst in a number of other succineid species. We have recently studied the development of the camaenid *Varohadra yeppoonensis* (Beddome, 1897) (see IREDALE, 1940) and have found it to be typically sigmurethran with respect to the structure and function of the podocyst. We suspect that Semper either worked with fixed material, and removed the podocyst by mistaking it for an extraembryonic membrane, or he lacked specimens which were at the stage of development required to confirm the presence of this embryonic organ.

Varohadra lays clutches of 70 - 100 eggs usually just beneath the surface of moist, loose soil or occasionally on the sides of the containers holding them. Eggs were removed after deposition, and kept at 22° C in a saturated atmosphere.

Each egg has an outer jelly-like protective layer surrounding a flexible shell made of loosely bound calcareous crystals. Within this shell is the transparent chorion surrounding the albumen and embryo. The oval shaped eggs are 2 - 3 mm long.

The ovum is approximately 200 μ in diameter and is moderately yolky for a land snail egg. The first 2 cleavages are equal, whereas later ones result in the formation of unequal micromeres and macromeres typical of spiral cleavage. In later stages of development, in order to preserve embryos with the podocyst fully expanded, we narcotized them in 0.35% NaCl saturated with propylene phenoxetol (Goldschmidt Chemical Division of Wilson Pharmaceutical and Chemical Corporation, New York, N. Y.).

The podocyst, similar to that of other sigmurethrans, is shown after 5 days of development (Figure *1*) when it is a very large, fan shaped organ extending from the posterior end of the foot. During the next days of development the podocyst expands and is brought forward dorsally to envelop the entire embryo (Figure *2*), while at the same time a portion of it lies in contact with the inside of the chorion. When the embryo is removed from the egg, the podocyst contracts and is pulled back from its position around the embryo, so that it trails behind the foot (Figure *3*). As the embryo grows, the podocyst is rapidly reduced in size, until just prior to hatching when it remains as a fringe-like membrane separated from the foot by a constriction (Figure *4*). By the time of hatching, after 12 - 16 days of development, no vestige of the podocyst remains.

Since we have found that the camaenid *Varahadra yeppoonensis* has a developmental pattern similar to other sigmurethrans, we must view the earlier, incomplete report of Semper, noting an absence of a podocyst, with skepticism. Thus we find that embryological evidence lends its weight to the concept that the Stylommatophora form a homogeneous group, excepting only the Heterurethra, as shown by the consistent development of the podocyst, which we view as an embryological adaptation for terrestrial life.

ACKNOWLEDGMENTS

We wish to thank Dr. J. B. Burch for the parental animals used in this study.

Literature Cited

CATHER, J. N. & ALEX S. TOMPA
1972. The podocyst in pulmonate evolution. Malacol. Rev. **5:** 1 - 3
IREDALE, TOM
1940. A basic list of the land mollusca of Australia. Part II. Austral. Zool. **9:** 1 - 39
JOURDAIN, S.
1884. Sur les organes segmentaires et le podocyste des embryons des Limaciens. C. R. Séances Soc. Biol. **98:** 308 - 310
SEMPER, C.
1862. Entwicklungsgeschichte der *Ampullaria polita* Deshayes nebst Mittheilungen über die Entwicklungsgeschichte einiger anderer Gastropoden aus den Tropen. Natuurk. Verhandl. Utrechtsch. Genootsch. Kunst. en Wetensch. **1:** 1 - 20; 4 plts.
SIMROTH, HEINRICH RUDOLF
1912. Pulmonata. *In*: Die Klassen und Ordnungen des Tier-Reichs. (H. G. Bronn, ed.). vol. III: Mollusca, Abt. II. Gastropoda, Buch 2.

Plate Explanation

Figure *1*: Embryo of *Varohadra* 5 days after spawning showing the podocyst (p) extending posteriorly from the foot (f). The shell (s) already covers the visceral hump × 32

Figure *2*: Embryo at 9 days of development viewed frontally to show the paired lobes of the podocyst (p) encompassing the body × 36

Figure *3*: The same embryo as in Figure *2* showing the podocyst retracted from the body of the embryo × 18

Figure *4*: Embryo at 11 days when the podocyst (p) is reduced to a degenerating vestige of the posterior end of the foot (f) × 26

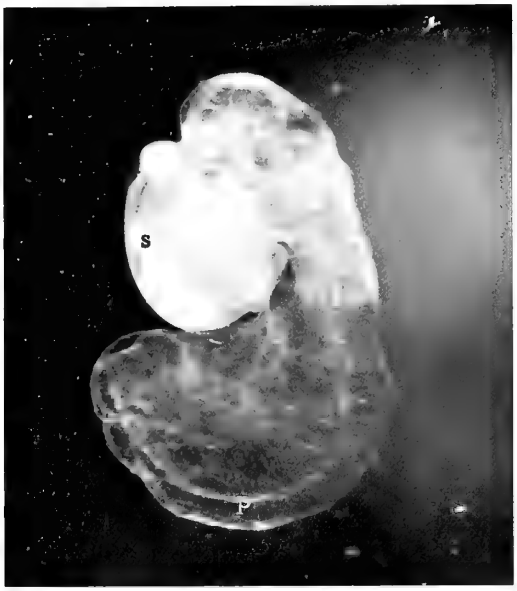


Figure *1*

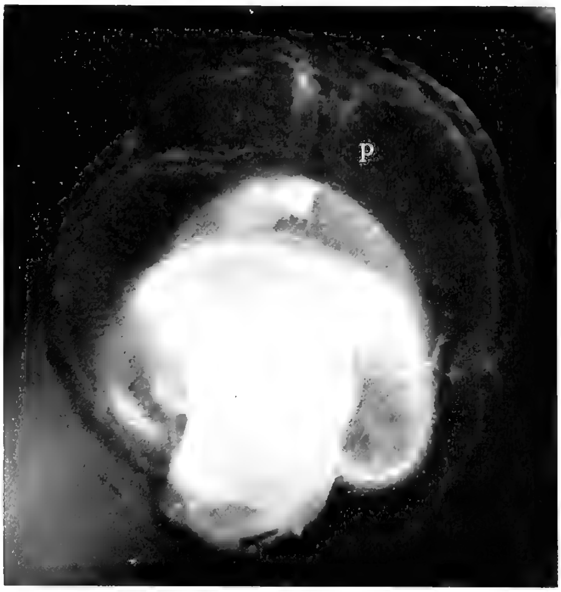


Figure *2*

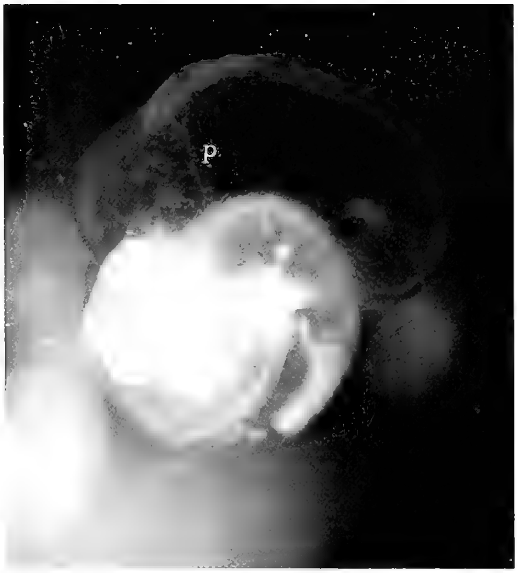


Figure *3*

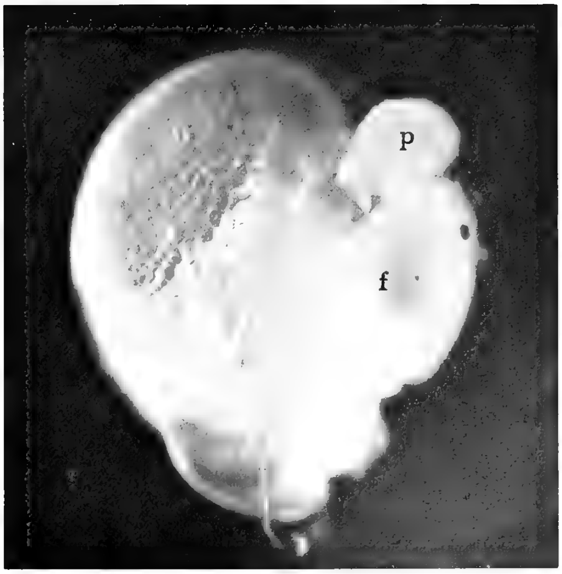


Figure *4*

Observations of the Feeding Habits of *Tochuina tetraquetra* (Pallas)

(Gastropoda : Tritoniidae)

BY

MARY K. WICKSTEN AND JOHN D. DEMARTINI

Department of Biology, Humboldt State College, Arcata, California 95521

BOTH THE LARGE nudibranch *Tochuina tetraquetra* (Pallas, 1788) and the alcyonacean *Gersemia rubiformis* (Pallas, 1788) are found subtidally to depths of at least 50 feet (15 m) in Trinidad Bay, Humboldt County, California (41°03′N, 124°08′W). In the field, *T. tetraquetra* was observed grazing solely on *G. rubiformis,* although other cnidarians were common in the area. Casual observations on specimens kept at the Marine Laboratory, Trinidad, California, suggested that the nudibranch would starve to death in the absence of *G. rubiformis.*

In an effort to determine whether the nudibranch was restricted to *Gersemia rubiformis* as a food source, we obtained 2 healthy specimens of *Tochuina tetraquetra* at a depth of 50 feet (15 m) on Prisoner's Rock, Trinidad Bay, California, during October, 1971. These animals were kept in a refrigerated aquarium at the Marine Laboratory, Trinidad.

The specimens were offered a variety of cnidarians as food, but only *Gersemia rubiformis* was accepted. *Tochuina tetraquetra* retracted violently upon contact with the tentacles of both *Corynactis californica* Carlgren, 1936, and *Anthopleura xanthogrammica* (Brandt, 1835). They ignored the coral *Paracyathus* sp.

Upon finding a colony of *Gersemia rubiformis, Tochuina tetraquetra* spread its oral veil over a portion of the colony. It then settled down for hours, slowly rasping a large groove into the colony. Colonies an average of 4 cm in diameter were eaten and totally digested within $1\frac{1}{2}$ days. When disturbed during feeding, the nudibranch might move for a while, but soon returned to its rasping. This feeding pattern is similar to that of *Tritonia hombergi,* as described by THOMPSON, 1958 (*in* HYMAN, 1967: 535).

Feces of *Tochuina tetraquetra* consisted almost entirely of spicules of *Gersemia rubiformis.* On occasion, the feces contained pieces of substrate to which the alcyonacean had been attached, indicating that the nudibranch had eaten the colony to the very base.

Following feeding, *Tochuina tetraquetra* often assumed a resting position. It contracted itself tightly into a hump. The rhinophores were retracted. It would stay motionless in this position for up to a day at a time. This posture seemed to have no relationship to the availability of food. Such a resting position has previously been reported for *Dendonotus iris* Cooper, 1863, by WOBBER (1970: 383), but that animal's posture is different from that of *T. tetraquetra.*

We have found a few colonies of *Gersemia rubiformis* at a depth of 50 feet (15 m) at Point Cabrillo, Mendocino County, Californa (39°21′N, 123°49′W). Although we did not find *Tochuina tetraquetra* there, it seems likely that the ranges of both animals follow the same patterns. *Tochuina tetraquetra* has been reported from northern Japan (THOMPSON, 1971: 335) to Santa Barbara (ROLLER & LONG, 1969: 429), while RICKETTS *et al.* (1969: 202) described *Gersemia rubiformis* as "boreal-arctic, reported as far south as Trinidad Head in Humboldt County, California." It seems likely that the scarcity of *T. tetraquetra* south of Trinidad Bay is directly related to the lack of abundant colonies of *G. rubiformis.*

Literature Cited

HYMAN, LIBBIE HENRIETTA
1967. The invertebrates, vol. 6: Mollusca I. McGraw-Hill, New York, N. Y. 792 pp.; 249 figs.

ROLLER, RICHARD A. & STEVEN J. LONG
1969. An annotated list of opisthobranchs from San Luis Obispo County, California. The Veliger **11** (4): 424 - 430; 1 map (1 April 1969)

THOMPSON, THOMAS EVERETT
1971. Tritoniidae from the North American Pacific coast (Mollusca: Opisthobranchia). The Veliger **13** (4): 333 - 338; 3 text figs. (1 April 1971)

WOBBER, DON R.
1970. A report on the feeding of *Dendronotus iris* on the anthozoan *Cerianthus* sp. from Monterey Bay, California. The Veliger **12** (4): 383 - 387; plts. 55 - 57 (1 April 1970)

Some Records on West American Cenozoic Gastropods of the Genus *Aforia*

BY

MAHDOKHT JAVIDPOUR

Isfahan University, Isfahan, Iran

(1 Plate; 2 Text figures)

INTRODUCTION

Six species of the turrid gastropod *Aforia* from the west coast of North America define a phylogenetic lineage which is potentially useful in age determination and correlation of the marine Cenozoic of this area. The purpose of this report is to describe and illustrate these species, one of which is new, and to define the morphologic characteristics upon which these species are differentiated.

Aforia appeared during the middle Oligocene on the Pacific margin. *Aforia campbelli* Durham, 1944 is the oldest known fossil record of the genus. The only other Tertiary records are from the Pliocene of Japan (Powell, 1966). The genus was especially abundant in and characteristic of moderately shallow water strata in middle Tertiary basins of coastal Oregon and Washington (Figure 16).

There are no known occurrences in the middle and the late Miocene, but the genus is represented in the Pliocene of the Gulf of Alaska by *Aforia circinata* (Dall) which ranges today from the Bering Sea to the northwest coast of Washington.

The genus has not previously been monographed, although Durham (1944) treated 3 middle Tertiary species from western Washington: *A. campbelli* Durham, *A. clallamensis* (Weaver), and *A. wardi* (Tegland). Powell (1966) reviewed the modern distribution of *Aforia* in the eastern Pacific, noting that its relatively shallow water occurrences near the equator are an excellent example of "biopolarity". Two of the 4 Oligocene and Miocene species from Washington referred to *Aforia* by Powell (1966: 44), *"A." borgenae* (Tegland) and *"A." marrowstonensis* (Durham), however, are here regarded as representing different turrid genera.

Species of *Aforia* are particularly useful in correlation of Oligocene and Miocene strata in western Oregon and Washington where a well-defined phylogenetic sequence is developed (Figure 17).

This lineage is defined upon a number of serial morphologic changes:

1) A secondary angulation, or carina, appears at the base of the body whorl in Oligocene and Miocene species, attains its strongest development on the late Oligocene and early Miocene species *Aforia clallamensis* and *A. tricarinata,* but is not developed on the Pliocene to Recent species *A. circinata.*

2) The primary angulation is located near the base of the whorls of the spire on the earliest species of *Aforia* but gradually moves toward a medial position in later species.

3) The subsutural slope is deeply concave in the oldest species but becomes gradually less so in newer species.

4) The position of the growth line sinus is located near the middle of the subsutural slope on the oldest species of *Aforia* but closer to the angulation on the latest species.

5) The angulation is sharp in the oldest species but becomes less so in successively younger species.

Aforia may be useful in determining paleobathymetry of Tertiary molluscan assemblages of the west coast of North America. Depth records of *A. circinata* from modern collections in the U. S. National Museum indicate a range of from 34 to 121 fathoms, with almost all of the records deeper than 50 fathoms. Accordingly, fossil occurrences of this genus may be representative of at least outer sublittoral (lower neritic) depths. The modern geographic range of this species from the Bering Sea to the Straits of Juan de Fuca, Washington, indicates association with cool temperate and cold water molluscan faunas.

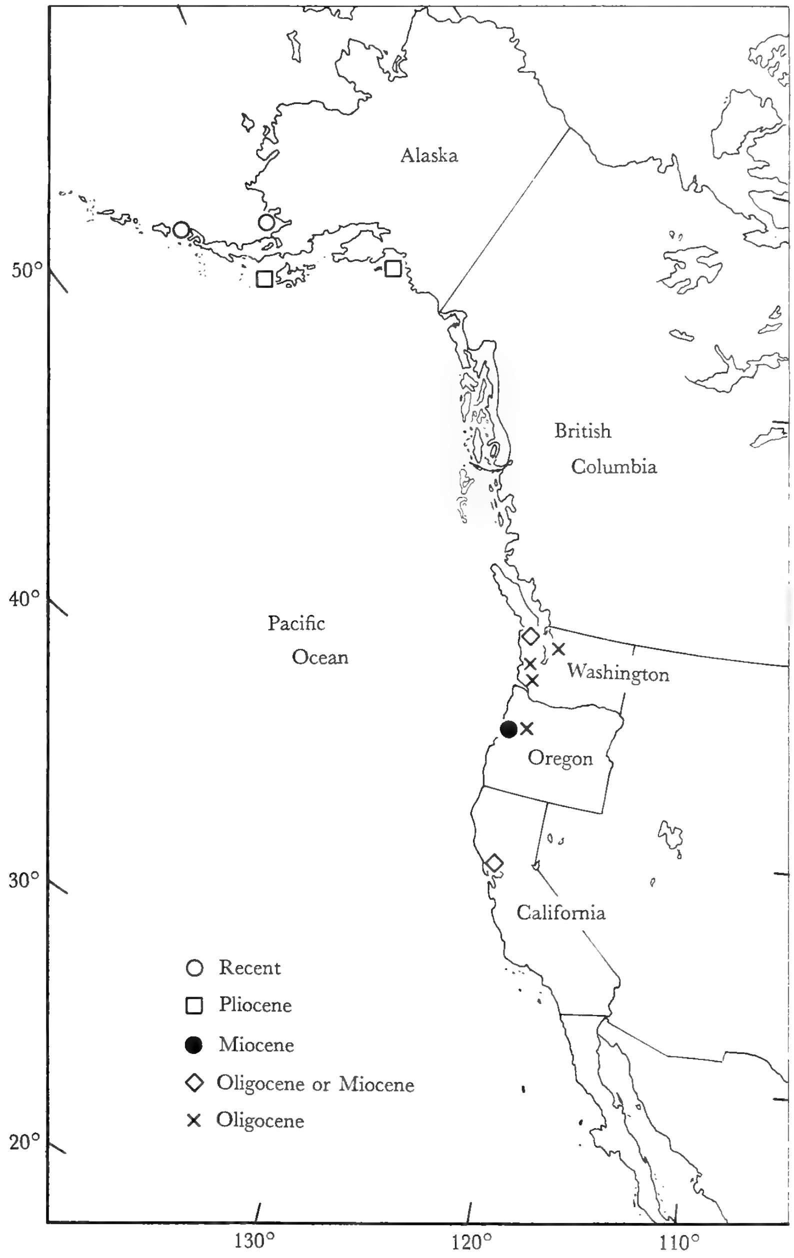


Figure 16

Index Map of Northwestern Pacific Ocean showing Occurrence of *Aforia*

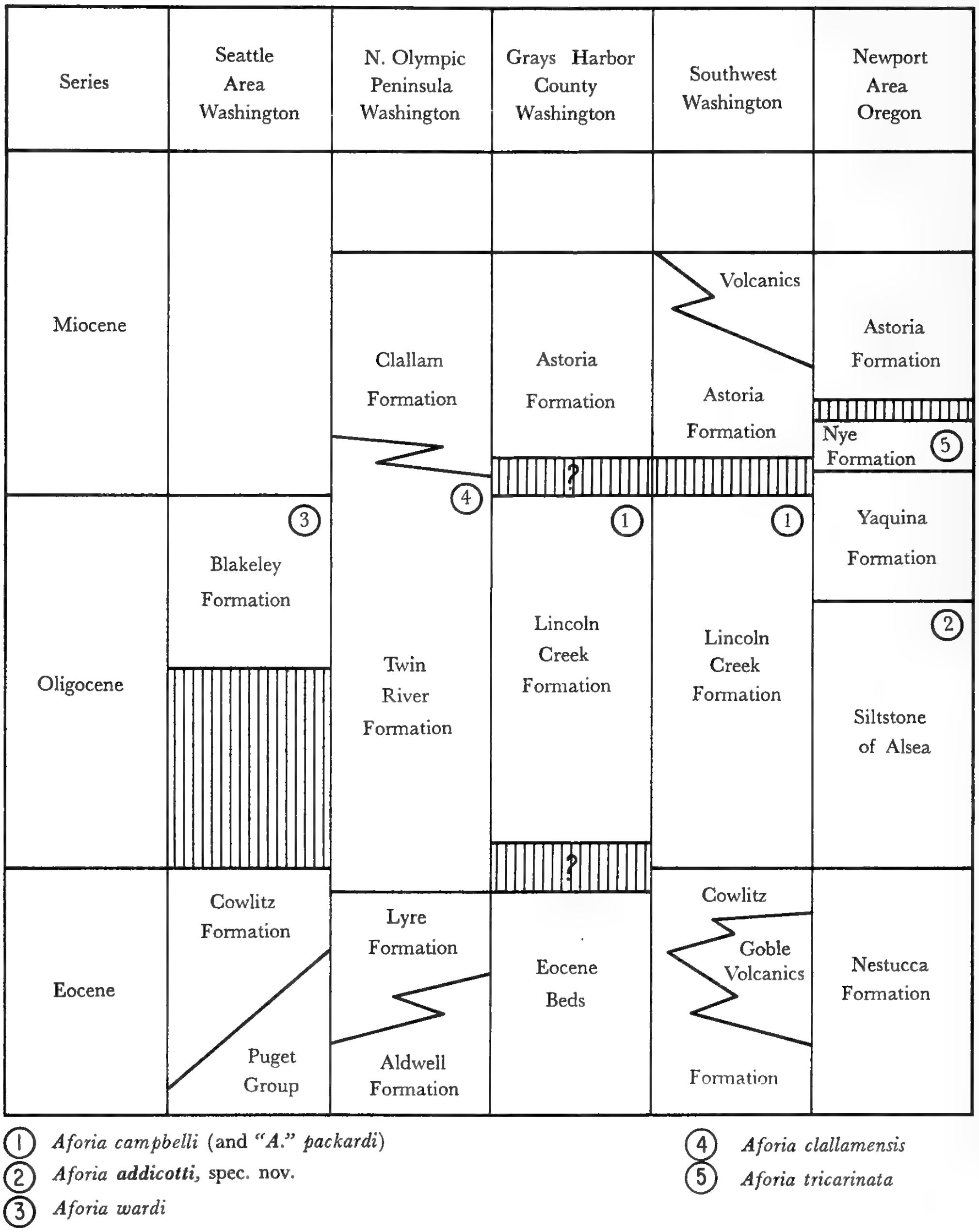


Figure 17

Correlation of some Western Washington and Oregon Marine Tertiary Formations (from Youngquist, 1961 and Snavely *et al*, 1969), showing occurrences of some species of *Aforia*

ACKNOWLEDGMENTS

The study was supervised by Dr. W. O. Addicott of the U. S. Geological Survey and Stanford University, who suggested the study and accorded me the excellent working facilities and placed at my disposal the species from Cenozoic collection to which he has dedicated so much of his effort. He also made arrangements for receiving species from different collections, and allowing me access to his personal library. His help and guidance concerning specific problems were invaluable. He patiently offered encouragement and corrected the entire manuscript. I wish to express my sincere thanks to Dr. Addicott, under whose direction and advice the paper was prepared. His continued support and enthusiasm are deeply appreciated.

Particular thanks go to the following persons for lending specimens: Dr. A. Myra Keen, Dr. J. T. Smith of the Stanford University; Dr. Leo G. Hertlein of the California Academy of Sciences; Dr. J. W. Durham, Mr. J. H. Peck of the Museum of Paleontology, University of California, Berkeley; and Mr. J. Armentrout of the Burke Memorial Museum, University of Washington.

Special thanks are due to Mr. Kenji Sakamoto of the U. S. Geological Survey for making the photographs used in this report. I am also indebted to Mr. John Miller of the U. S. Geological Survey for making rubber casts and for help during the course of this study.

The writer wishes to express her great appreciation to the Geology Department of Stanford University for extending an invitation to conduct post-doctoral studies during 1971 and for the use of all facilities.

SYSTEMATIC DESCRIPTIONS

Abbreviations for locality description and museum collections used in this section are:

CAS – California Academy of Sciences, San Francisco, California
SU – Stanford University, Stanford, California
SUPTC – Stanford University Paleontological Type Collection, Department of Geology, Stanford, California
UCMP – University of California Museum of Paleontology, University of California, Berkeley
USGS – U. S. Geological Survey, Washington, D. C. locality register
USGSM – U. S. Geological Survey, Menlo Park, California, cenozoic register
USNM – U. S. National Museum, Washington, D. C.
UW – University of Washington, Seattle, Washington

GASTROPODA

NEOGASTROPODA

Turridae

Aforia Dall, 1889

Type Species (OD) *Pleurotoma circinata* Dall, 1873. Pliocene to Recent.

Recent Range: Bering Sea southeastward to the Straits of Juan de Fuca, Washington.

Diagnosis: Shell large, high spired. Angulation distinct and located near the middle of the whorl. Lower part of whorl sculptured by numerous raised revolving lines, and more clearly, on the body whorl. A second prominent but less well developed angulation often occurs below the primary carina on the body whorl. Growth lines make a deep "V"-shaped sinus about the middle of the subsutural slope. Anterior canal slightly flexed and recurved.

Aforia campbelli Durham, 1944

(Figures *1, 6, 10*)

1942 *Aforia clallamensis wardi* (Tegland). Weaver, Univ. Wash. Publ. Geol. 5: 516 (in part); plt. 97, fig. 10
1944 *Aforia campbelli* Durham. Univ. Calif. Publ. Geol. Sci., Bull. **27** (5): 183; plt. 14, fig. 4

Holotype: UCMP no. 14961

Type Locality: UCMP loc. A-1636. Type "Porter" Bluffs along northeast side of highway beginning at a point 270 yards southeast of first exposure southeast of Porter station and extending 180 yards. Grays Harbor County, Washington, Lincoln Creek Formation; Middle Oligocene.

Description: Shell of moderate size, high spired. Whorls sharply angulated near base. Whorl profile above angulation deeply concave, ornamented by prominent growth lines. These lines constitute a deep, broadly "U"-shaped sinus located somewhat more than half the distance from the suture to the angulation. Lower part of angulation concave, ornamented by several revolving lines that are usually much finer and closer set than on the body whorl. A second strong spiral cord occurs below the angulation on the body whorl. Numerous fine revolving lines occur below the angulation, crossed by very fine longitudinal growth lines. Inner lip with well developed narrow callus. Anterior canal long and slightly inclined to the left.

Measurements of Holotype: height 71 mm; width 23 mm

Discussion: This species differs from *Aforia wardi* by a higher spire and the more concave area above the angulation. The angulation is less acute than on *A. wardi.*

Occurrence: UW locs. A-1603, A-395, A-3299, A-3282, 3314, Porter sec., Lincoln Creek Form. UCMP loc. A-1636 Lincoln Creek Form., Middle Oligocene, Grays Harbor County, Washington; locs. 9003, 9005, 9013, Lincoln Creek Form., Middle Oligocene, Grays Harbor County, Washington. USGS loc. 1895o, Lincoln Creek Form., Thurston County, Washington.

Aforia wardi (Tegland, 1933)

(Figures *11, 14*)

1933 *Leucosyrinx clallamensis wardi* Tegland. Univ. Calif. Geol. Sci., Bull. 23 (3): 124; plt. 10, figs. 5 - 8

1942 *Aforia clallamensis wardi.* WEAVER, Univ. Wash. Publ. Geol. 5: 516; plt. 97, fig. 6

1944 *Aforia wardi.* DURHAM, Univ. Calif. Publ. Geol., Bull. 27 (5): 184

Holotype: CAS no. 5471

Paratypes: UCMP nos. 32204, 32206; SUPTC no. 792

Type Locality: CAS loc. 227, "Bluffs along the east side of the N. P. G. N. and O. W. R. R. tracks at Georgetown", sec. 20, T. 24 N., R. 3 E., King County, Washington. Blakeley Formation, Late Oligocene.

Description: Shell medium sized, whorls strongly angulated. Sutures deeply impressed. Whorl profile between suture and shoulder gently concave, angulated area located near lower third of whorl. Area above angulation ornamented by a series of growth lines, which make a deep sinus at the middle of shoulder. Area below angulation exceedingly concave, ornamented by weak revolving lines. A secondary angulation appears on body whorl, forming a basal keel. There are numerous fine revolving lines on the body whorl. Canal not preserved.

Measurements of Holotype (canal incomplete)**:** height 40 mm; width 23 mm.

Discussion: This species is similar to *Aforia campbelli,* but can be distinguished by the lower spire and the less concave area above the angulation. The angulation is more acute than on *A. campbelli.*

Occurrence: UW locs. B-0356, B-0357, Middle fork Satsop River sec., Lincoln Creek Form.; UW loc. B-0273 Canyon River sec., Lincoln Creek Form. CAS loc. 227, Blakeley Form., Georgetown, Washington; UCMP locs. 681, 1804, A-8724, Blakeley Form., U. Oligocene, Kitsap County, Washington, loc. A-1806, Blakeley Form., U. Oligocene, Bainbridge Island, Kitsap County, Washington; Loc. F-17 (RAU, 1966), Lincoln Creek Form., Grays Harbor County, Washington. USGS loc. M-2589, Lincoln Creek Form., Wahkiakum County, Washington; loc. M-4043, Blakeley Form., Upper Oligocene, Kitsap County, Washington.

Plate Explanation

Figure *1*: *Aforia campbelli* Durham. U. C. M. P. 10786; loc. 9003. Height (incomplete) 21 mm, width 8 mm. Lincoln Creek Formation, Middle Oligocene. Grays Harbor County, Washington. × 1½

Figures *2, 7*: *Aforia clallamensis* (Weaver). U. S. N. M. 646831. U. S. G. S. loc. M-4038. Height (incomplete) 39 mm, width 16 mm. Upper part of Twin River Formation, Oligocene or Miocene. Clallam County, Washington.

Figure *3*: *Aforia circinata* (Dall). U. S. N. M. 646838. U. S. G. S. loc. M-4392. Height (incomplete) 28 mm, width 9 mm. Tugidak Formation, Pliocene. Tugidak Island, Alaska.

Figure *4*: *Pseudoperissolax merriami* Clark. Paratype. U. C. M. P. 11286. U. C. M. P. loc. 3055. Height 37 mm, width 22 mm. Kirker Tuff, Oligocene or Miocene. Contra Costa County, California.

Figure *5*: *"Aforia" packardi* (Weaver). Holotype. C. A. S. 473. C. A. S. loc. 256. Height 24 mm, width 11 mm. Lincoln Creek Formation, Oligocene. Lewis County, Washington.

Figure *6*: *Aforia campbelli* Durham. U. S. N. M. 64682. U. S. G. S. loc. 1895. Height 19 mm, width 6 mm. Lincoln Creek Formation, Middle Oligocene. Grays Harbor County, Washington. × 2

Figure *8*: *Aforia addicotti* Javidpour, spec. nov. U. S. N. M. 646834. U. S. G. S. loc. M-3191. Height (incomplete) 50 mm, width 25 mm. Siltstone of Alsea Formation, Upper Oligocene, Lincoln County, Oregon.

Figure *9*: *Aforia circinata* (Dall). S. U. P. T. C. 10057. Height 53 mm, width 26 mm. Recent. Kodiak Island, Alaska.

Figure *10*: *Aforia campbelli* Durham. Holotype. U. C. M. P. 14961. U. C. M. P. loc. 1636. Height 60 mm, width 18 mm. Lincoln Creek Formation, Middle Oligocene. Grays Harbor, Washington.

Figure *11*: *Aforia wardi* (Tegland). U. C. M. P. 10787. U. C. M. P. loc. 681. Height 39 mm, width 18 mm. Blakeley Formation, Upper Oligocene. Bainbridge Island, Kitsap County, Washington.

Figure *12*: *Aforia addicotti* Javidpour, spec. nov. Holotype. U. W. Burke Memorial Museum 60600 U. W. loc. B0058. Height (incomplete) 62 mm, width 30 mm. Siltstone of Alsea, Upper Oligocene. Lincoln County, Oregon.

Figure *13*: *Aforia clallamensis* (Weaver). U. S. N. M. 646832. U. S. G. S. loc. 4090. Height 56 mm, width 22 mm. Twin River Formation, Oligocene or Miocene. Clallam County, Washington.

Figure *14*: *Aforia wardi* (Tegland). Holotype. C. A. S. 5471. C. A. S. loc. 227. Height 40 mm, width 23 mm. Blakeley Formation, Upper Oligocene. Georgetown, Washington.

Figure *15*: *Aforia tricarinata* Addicott. U. S. N. M. 649126. U. S. G. S. loc. 15329. Height 68 mm, width 25 mm. Yaquina Formation, Lower Miocene. Lincoln County, Oregon.


1


2


3


4


5


6

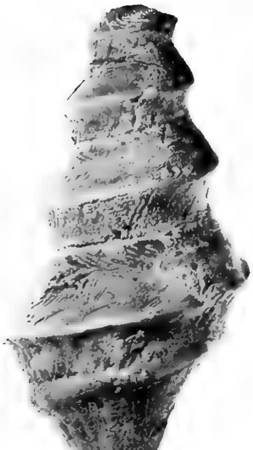

7


8


9


10


11


12


13


14


15

Aforia addicotti Javidpour, spec. nov.

(Figures *8, 12*)

Holotype: U. W. Burke Memorial Museum no. 60600

Type Locality: UW loc. B0058. Siltstone of Alsea, Upper Oligocene.

Description: Shell large and heavy. Sutures deeply impressed. Spire high. Periphery of spire and body whorl sharply angulated. Angulation occurs below middle of whorls of spire. Surface above angulation straight to slightly concave, ornamented by numerous growth lines that make deep sinus located just below the middle of the subsutural slope. Area below angulation concave, ornamented by about 12 revolving lines. A second strong spiral cord appears on the body whorl below the primary angulation. Body whorl ornamented by numerous revolving lines and much weaker longitudinal lines. Canal straight and very long. Inner lip smooth. Aperture calloused.

Measurement of Holotype: height, incomplete, 62 mm, width 30 mm

Discussion: In shape and appearance this species is similar to *Aforia wardi.* The angulation is near the middle of the whorl, relatively higher than on *A. wardi.* The area below the angulation is much less concave on the new species and the angulation is sharper on *A. wardi.*

Occurrence: U. W. Burke Memorial Mus. loc. B 0058. Siltstone of Alsea, Toledo Quarry, Yaquina Bay, Oregon. USGS locs. M-1979, M-3191, Siltstone of Alsea, Upper Oligocene.

Aforia clallamensis (Weaver, 1916)

(Figures *2, 4, 7, 13*)

1916 *Turris clallamensis* Weaver. Univ. Wash. Publ. Geol. **1:** 52; plt. 4, fig. 59

1918 *Pseudoperissolax merriami* Clark. Univ. Calif. Publ. Geol. Bull. **11** (2): 181; plt. 21, fig. 4 [not plt. 22, figs. 10, 15]

1933 *Leucosyrinx clallamensis.* TEGLAND, Univ. Calif. Publ. Geol. Bull. **23** (3): 123 - 124; plt. 10, figs. 3, 4

1942 *Aforia clallamensis.* WEAVER, Univ. Wash. Publ. Geol. **5:** 516; plt. 97, fig. 1

1944 *Aforia clallamensis.* DURHAM, Univ. Calif. Publ. Geol. Bull. **27** (5): 184

1963 *Aforia clallamensis.* MOORE, U. S. Geol. Survey Prof. Paper **419:** 47; plt. 10, figs. 16, 18

1966 *Aforia clallamensis.* ADDICOTT, Journ. Paleont. **40** (3): 641; plt. 76, figs. 10, 11

Holotype: CAS no. 555

Type Locality: UW loc. 258, sea cliff one-half mile west of Twin River, in sec. 22,T. 31 N. R. 10 W., Clallam County, Washington. Upper part of Twin River Formation, Late Oligocene or Early Miocene.

Description: Shell large, whorls of spire with distinct angulation located a little below the central portion of each whorl. Surface of whorls above angulation slightly concave, ornamented by numerous growth lines which make a deep sinus located somewhat above the middle of the subsutural slope. Faint longitudinal growth lines occur below the angulation and, more clearly, on the body whorl. A second prominent but less well developed angulation occurs below the primary carina on the body whorl and on the penultimate whorl. Aperture narrow and callused. Canal straight. Inner lip smooth.

Measurement of Holotype: height 66 mm, width 28 mm

Discussion: *Aforia clallamensis* (Weaver) is similar to *A. wardi* (Tegland) but differs by having a less sharp angulation and also less concave surface above the angulation. The profile of the body whorl is straight on *A. clallamensis* but concave on *A. wardi.*

Poorly preserved specimens that may represent *Aforia clallamensis* occur in a collection from UCMP loc. A-1806, together with at least one specimen that is clearly *A. wardi.* The lower angulation on the penultimate whorl of these specimens is extremely weak. They are doubtfully identified as *Aforia* cf. *A. clallamensis.*

Occurrence: UW loc. 258, Twin River Form., Clallam County, Washington, loc. 489, Twin River Form., Washington; loc. 271, Twin River Form., Washington. UCMP loc. A-3677, Twin River Form., Upper Oligocene, Clallam County, Washington, loc. A-6, Twin River Form., Oligocene, Clallam County, Washington, loc. 3055, Kirker Tuff, Contra Costa County, California. SU label no. 3024, Twin River Form., Oligocene, Clallam County, Washington. USGS loc. M-2120, Nye mudstone, Lincoln County, Oregon, loc. M-4038, Twin River Form., Clallam County, Washington, loc. 4090, Twin River Form., Oligocene or Miocene, Clallam County, Washington.

Aforia tricarinata Addicott, 1966

(Figure *15*)

1966 *Aforia clallamensis tricarinata* Addicott. Journ. Paleont. **40** (3): 641; plt. 76, figs. 9, 12, 13

Holotype: USNM no. 649125, a rubber cast
Type Locality: USGS Cenozoic loc. M-1990 in NE $\frac{1}{4}$ sec.

4, T. 11, S. R 11 W, Yaquina quadrangle, Lincoln County, Oregon. Nye Mudstone, Early Miocene.

Original Description: Large, fusiform, with seven whorls on incomplete type specimen. Whorls angulated near midpoint by coarse spiral cords, profile convex above and concave below. Upper half of later whorls with a centrally located broad spiral band: lower half with similar band located immediately above suture. Alternating spiral threads of secondary and tertiary strength occur on later whorls below medial carina. Suture collared, impressed. Body whorl and spire incomplete. Very fine growth lines indicate a sinus located near posterior quarter line on later whorls.

Measurements of Holotype: height (incomplete) 45 mm, width (incomplete) 20 mm

Discussion: *Aforia tricarinata* is closely related to *A. clallamensis* but differs in having a prominent spiral cord between the suture and the primary angulation on all but the earliest whorls.

Occurrence: USGS Cenozoic locs. 21806, M-1990, and M-3630, Nye Mudstone. USGS loc. 15329, upper part of Yaquina Form., and USGS locs. 2755 and 18907a, stratigraphic position doubtful, Lincoln County, Oregon.

Aforia circinata (Dall, 1873)

(Figures *3, 9*)

1873 *Pleurotoma circinata* Dall. Calif. Acad. Sci. Proc. **5:** 4; plt. 2, fig. 5
1902 *Pleurotoma circinata.* Dall, Proc. U. S. Nat. Mus. **24** (1264): 515; plt. 36, fig. 1
1921 *Aforia circinata.* Dall, U. S. Nat. Mus. Bull. **112:** 68; plt. 11, fig. 6
1927 *Aforia circinata.* Oldroyd, Stanford Univ. Publ. Geol. Sci. **2** (1): 63; plt. 4, fig. 1
1966 *Aforia circinata.* Powell, Bull. Auckland Mus. no. **5:** 43; plt. 5, fig. 12

Type Locality: Nateekin Bay, Captain's Bay, Unalaska. Recent.

Description: Shell thin, fusiform, with high spire and angulated whorls. Angulation located near the middle of the whorl. Growth lines make a deep "U"-shaped sinus on the lower half of the subsutural slope. Whorl profile above angulation slightly concave. Lower part of whorl sculptured by numerous raised revolving lines. Body whorl slightly shorter than spire, ornamented by numerous revolving lines which are crossed by alternately heavier and finer longitudinal lines. Aperture ovate, canal long and inclined to the left.

Discussion: This species differs from the Oligocene and Miocene species of *Aforia* in having a thin shell, a recurved anterior canal, and in lacking a secondary angulation on the body whorl. On some of the Recent specimens from Alaska, however, a poorly developed anterior angulation appears on the final quarter turn of the body whorl. The angulation is located almost on the central part of each whorl. Pliocene specimens from Alaska have a deep sinus that is located closer to the angulation than in modern specimens.

Occurrence: Recent: USNM locs. 225566, 225586, 211973, 222525, 222483, 222495, 209710, 130511, 222958, Pribiloff Islands, Bering Sea, 34 to 121 fathoms; locs. 211979, 211980, 206086, 209729, Unalaska, Aleutian Islands, 68 to 85 fathoms; loc. 222303, Numiak Island, Aleutian Islands, 85 fathoms; loc. 223933, off Unalaska, Aleutian Islands, 78 fathoms; loc. 211974, 223100, 211978, Unimak Island, Aleutian Islands, 60 to 81 fathoms; loc. 210158, Bering Sea, 62 fathoms; locs. 224079, 224246, 223879, 224218, 223174, 224429, 224633, off Pribiloff Islands, Bering Sea, 49 to 86 fathoms. Recent: SU loc. 51982, Bristol Bay, Alaska, 49 fathoms. Pliocene: USGS loc. M-2522, Yakataga Form., Middleton Island, Alaska; loc. M-4272, Gulf of Alaska; locs. M-4394, M-4392, M-4402, Tugidak Island, Alaska.

"Aforia" packardi (Weaver, 1916)

1916 *Turris packardi* Weaver. Univ. Wash. Geol. **1** (1): 55; plt. 5, fig. 64
1916 *Turris packardi.* Weaver, Wash. Geol. Surv. Bull. **13:** 313
1942 *Aforia packardi.* Weaver, Univ. Wash. Publ. Geol. **5:** 516; plt. 97, fig. 3
1944 *"Aforia" packardi.* Durham, Univ. Calif. Publ. Geol. Bull. **27** (5): 184

Holotype: CAS no. 473

Type Locality: UW loc. 256 in railway cuts on the O. W. R. R. and N. Co. One-fourth mile northwest of Galvin Station in sec. 27, T. 15 N., R. 3W., Lewis County, Washington, Lincoln Creek Formation, Oligocene.

Description: Shell small and pagodaform, whorls of spire strongly angulated near base. Two strong spiral cords located on the angulation of each whorl. Area above angulation somewhat concave, ornamented by 7 - 9 very faint revolving lines. Axial lines of growth prominent, forming a shallow sinus near base of whorls of the spire. Surface below angulation slightly concave, sculptured with about four faint revolving lines. Body whorl sculptured by about 22 prominent revolving lines below the angulation, and numerous faint longitudinal lines. Inner lip smooth, outer lip with sharp angulation. Canal deep, medium in length, inclined slightly to the left.

Measurements of Holotype: height 24 mm, width 11 mm

Discussion: This small species is distinguished by its pagodaform spire, and, especially, by having 2 spiral cords on the angulated area. But as Durham (1944: 184) mentioned, reference of this species to *Aforia* is questionable because the turrid notch is broad, not very deep, and its lower border crosses over the anglation.

Occurrence: UW loc. 256, Lincoln Creek Form., Lewis County, Washington; locs. A-575, A-52, Porter sec., Lincoln Creek Form. UCMP loc. T. 8, Lincoln Creek Form., Oligocene, Grays Harbor County, Washington. USGS Cenozoic loc. 18974, Lincoln Creek Form., Oligocene, Grays Harbor County, Washington; loc. M 1729, Lincoln Creek Form., Porter Bluffs, western Washington.

LOCALITY DESCRIPTIONS

C. A. S. California Academy of Sciences

loc. 227

Upper Oligocene, Blakeley Formation. "Bluffs along the east side of the N. P. G. N. and O. W. R. R. tracks at Georgetown."

S. U. Stanford University

3024

Oligocene or Miocene. Twin River Formation. Clallam County, Washington.

cat. no. 51982

Recent. Bristol Bay, Alaska, 49 fathoms, 55°20′ N, 164°00′ W.

U. C. M. P. University of California, Museum of Paleontology

loc. A-6

Oligocene or Miocene. Twin River Formation, Clallam County, Washington. Shale cliffs in first large embayment east of East Twin River.

loc T-8

Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. (*Turritella porterensis* and *Exilia lincolnensis* occur in the collection.)

loc. A-1636

Middle Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. Type "Porter" Bluffs along northeast side of highway beginning at a point 270 yards southeast of first exposure southeast of Porter station and extending 180 yards.

loc. A-3677

Oligocene or Miocene. Twin River Formation, Clallam County, Washington. In shale exposed in sea cliff. About in center of north line of the S. W. ¼ of sec. 23, T. 31 N, R. 10W.

loc. 681

Upper Oligocene. Blakeley Formation, Bainbridge Island, Kitsap County, Washington. Generalized locality for fossiliferous strata around Restoration Point.

loc. 1804

Upper Oligocene. Blakeley Formation, Kitsap County, Washington. Conglomerate on south side of Bremerton Inlet, Middle point. Sec. 15, T. 24 N., R. 2E.

loc. A-1806

Upper Oligocene. Blakeley Formation, Bainbridge Island. Kitsap County, Washington. From the sandstone at Restoration Point. Eastern boundary of section 12, T. 24 N., R. 2E.

loc. 3055

Oligocene or Miocene. In valley north of Sobrante Ridge, on west fork of Bear Creek ½ mile from source, on north bank in Tuff beds, elevation 800 feet, Contra Costa County, California. Long. 122°12′35″ W, lat. 37°55′58″ N.

loc. 9003

Middle Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. Clemons Logging R. R. 420 - 500 paces northwest of Saginaw Trail, Sec. 6, T. 16N., R. 6W.

loc. 9005

Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. Sec. 6, T. 16 N, R. 6W., M. loc. 5', Clemons Logging R. R. 1050 - 1100 paces northwest of Saginaw Trail in the NW ¼ of sec. 6.

loc. 9013

Middle Oligocene, Lincoln Creek Formation, Grays Harbor County, Washington. Clemons Logging R. R. 1200 - 1300 paces northwest of Saginaw Trail.

Rau (1966)

loc. F17

Upper Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. West fork of Satsop River, 1500 feet north, 400 feet west of S. E. cor. sec. 21, T. 21 N., R 7W.

U. S. G. S. United States Geological Survey, Washington, D. C., register

loc. 1895

Middle Oligocene. Lincoln Creek Formation, Grays Harbor quadrangle, Washington. Highway south of Porter 4750 feet east, 3510 feet north of S. W. cor. sec. 28, T. 17 N., R. 5 W. Malone quadrangle.

loc. 4090

Oligocene or Miocene. Twin River Formation, Clallam County, Washington. Lake Crescent, 15 quad. Sea Cliff exposure, west of mouth of West Twin River. Upper part of Twin River Formation.

loc. 15329

Middle Oligocene. Yaquina Formation, Lincoln County, Oregon. Fossils from concretions on shore of Yaquina Bay. N W. ¼, N. E. ¼ sec. 15, T. 11S, R 11W.

U. S. G. S. United States Geological Survey, Menlo Park, California, register

loc. 18974

Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. Grays Harbor quadrangle. Clemons Logging road 3750 feet east, 1750 feet north of S. W. corner sec. 25, T. 17N., R. 7W. Montesano quadrangle WN.

loc. M.-1729

Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington.

loc. M.-1979
Upper Oligocene. Lincoln County, Oregon. Waldport 15-min. quad. S. E. $\frac{1}{4}$ sec. 24, T. 13S, R. 12W. West of seawall, south side of Alsea Bay.
loc. M.-1990
Middle Oligocene. Yaquina quad. (15-min.), Lincoln County, Oregon. N. E. $\frac{1}{4}$, N. E. sec. 4, T. 11S, R. 11W. Jeffreys Creek.
loc. M.-2120
Oligocene or Miocene. Nye mudstone. Yaquina quad., Lincoln County, Oregon. 1900 feet north, 700 feet west of S. E. cor. sec. 24, T. 12S., R. 12 W.
loc. M.-2522
Pliocene. Yakataga Formation. Middleton Island, Alaska. Gulf of Alaska.
loc. M.-2589
Upper Oligocene. Lincoln Creek Formation, Wahikiakum County, Washington. Grays River quad. N. central sec. 1, T. 9N., R. 8W. North slope of Hill 498, south of South Fork of Crooked Creek. 2700 feet east and 1600 feet south of N. W. corner of the section.
loc. M.-3191
Upper Oligocene. Alsea Formation, Lincoln County, Oregon. Toledo 15-min. quad. 2550 feet west, 1550 feet south of N. E. cor. sec. 18, T. 11S., R. 10W. A. West side of West Yaquina Bay Road.
loc. M.-3630
Lower Miocene. Nye mudstone. Yaquina 15-min. quad., Lincoln Creek Formation, Oregon. Fill from access road to trailer park northeast of intersection of Big Creek and U. S. Route 101, 2200 feet south, 1550 feet west of N. E. cor. sec. 32, T. 10S., R. 11 W.
loc. M.-4038
Oligocene or Miocene. Twin River Formation, Clallam County, Washington. Lake Crescent 15-min. quad., sea cliff exposure above dirt road leading westward to quarry and loading dock, 2100 feet north, 1250 feet east of S. W. cor. sec. 23, T. 31N, R. 10W.
loc. M.-4043
Upper Oligocene. Blakeley Formation, Kitsap County, Washington, Duwamish Head $7\frac{1}{2}$-min. quad. Uppermost part of intertidal zone N. W. of Restoration Point. 600 feet west, 450 feet north of intersection of E. line sec. 12, T. 24N., R. 2E. and shore line.
loc. M.-4168
Upper Oligocene. Lincoln County, Oregon. Toledo quad. West side of city of Toledo at bend in Yaquina River. Center sec. 18, T. 11S., R 10W.
loc. M.-4272
Pliocene. Middleton Island, Alaska. Gulf of Alaska. Measured sec. at southwest end. 2845 to 2910 feet above base of measured portion.
loc. M.-4392
Pliocene. Trinity Islands, Alaska. Trinity Islands quad. Measured section on northwest coast of Tugidak Island, approximately 230 to 260 feet above base.
loc. M.-4394
Pliocene. Trinity Islands, Alaska. Trinity Islands quad. Measured section on northwest coast of Tugidak Island, approximately 580 to 610 feet above base.
loc. M.-4402
Pliocene, Trinity Islands, Alaska. Trinity Islands quadr. Measured section on northwest coast of Tugidak Island, approximately 1690 to 1720 feet above base.

U. W. University of Washington, Seattle, Washington
loc. A-52
Oligocene. Twin River Formation, Clallam County, Washington. East of West Twin River, T. 30N., R. 10W.
loc. A-395
Middle Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. Along east side Highway 12 in bluffs just south of Porter Creek. N. $\frac{1}{2}$ sec. 6, T. 16N., R. 6W.
loc. A-575
Middle Oligocene. Lincoln Creek Formation. Grays Harbor County, Washington. Along bluffs of Highway 12 just south of Porter. Secs. 27, 28, T. 17N, R. 5W.
loc. A-1603
Middle Oligocene. Lincoln Creek Formation. Grays Harbor County, Washington. From bluffs along Highway 12. 600 feet south of road along south side of Porter Creek, sec. 28, T. 17N., R. S. W.
loc. A-3282
Middle Oligocene. Lincoln Creek Formation. Grays Harbor County, Washington. Along bluffs of Highway 12 just south of Porter, secs. 27, 28, T. 17N., R. S. W.
loc. A-3299
Middle Oligocene. Lincoln Creek Formation. Grays Harbor County, Washington. Along bluffs of Highway 12 just south of Porter, secs. 27, 28, T. 17N., R. S. W.
loc. A-3314
Middle Oligocene. Lincoln Creek Formation. Grays Harbor County, Washington. Along bluffs of Highway 12 just south Porter, secs. 27, 28, T. 17N., R. S.W.
loc. B-0058
Upper Oligocene. Siltstone of Alsea, Toledo Quarry, Yaquina Bay, Oregon. Large quarry along Yaquina Bay road. 14 miles south of junction at Bay road with Highway 20 at Toledo. On west side of road. S. E. $\frac{1}{4}$, N. W. $\frac{1}{4}$ sec. 18, T. 11S., R. 11W.
loc. B-0273
Upper Oligocene. Lincoln Creek Formation, Grays Harbor County, Washington. South side of Canyon River at base of high cliff just west of Canyon River bridge. S. E. $\frac{1}{4}$, S. E. $\frac{1}{4}$ sec. 13, T. 21N., R. 6W.
loc. B-0356
Upper Oligocene. Lincoln Creek Formation, Mason County, Washington. South side of middle fork of Satsop River along base of high cliff running along E - W trace of river. S. W. $\frac{1}{4}$, N. W. $\frac{1}{4}$ sec. 20, T. 21N., R. 6W.
loc. B-0357
Upper Oligocene. Lincoln Creek Formation, Mason County, Washington. West side of meander bend of Middle Fork of Satsop River along base of high cliff. N. W. $\frac{1}{4}$, S. W. $\frac{1}{4}$ sec. 20, T. 21N., R. 6W.

loc. 256

Oligocene in railroad cut on O. W. R. R. and N. Co. One mile north of Galvin station in sec. 27, T. 15N., R. 3W.

loc. 258

Oligocene or Miocene. One half mile west of Twin post office, Clallam County, Washington. In sea cliff in sec. 27, T. 31N., R. 10W.

loc. 271

Oligocene or Miocene. Twin River Formation, Clallam County, Washington. Cliff, south shore of Straits of Juan de Fuca, about 1000 feet west of locality 258 which is ½ mile west of Twin post office, sec. 22, T. 31N., R. 9W.

loc. 489

Oligocene or Miocene. Twin River Formation, Clallam County, Washington.

Literature Cited

Addicott, Warren Oliver

1966. New Tertiary marine mollusks from Oregon and Washington. Journ. Paleont. **40** (3): 635 - 646; plts. 76 - 78

Bartsch, Paul

1945. Distribution list of the West Pacific species of the mollusk genus *Aforia*. Journ. Wash. Acad. Sci. **35** (12):

Burch, John Quincy

1942 - 1946. Distributional list of the West American marine mollusks from San Diego to the Polar Sea. Conch. Club So. Calif., minutes; 2 parts; pag. by issue; 3 plts.

Clark, Bruce Lawrence

1918. The San Lorenzo series of middle California. Univ. Calif. Publ. Geol. Sci. **11** (2): 45 - 234; plts. 3 - 24; 4 text figs. (16 July 1918)

Dall, William Healey

1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. U. S. Nat. Mus. Bull. **112**: 1 - 217; plts. 1 - 22 (24 February 1921)

Durham, John Wyatt

1944. Megafaunal zones of the Oligocene of northwestern Washington. Univ. Calif. Publ. Geol. Sci. **27** (5): 101 - 212; plts. 13 - 18; 7 text figs.; 1 map (14 November 1944)

Moore, Ellen James

1963. Miocene marine mollusks from the Astoria Formation in Oregon. U. S. Geol. Surv. Prof. Paper **419**: 1 - 109; plts. 1 - 33

Oldroyd, Ida Shepard

1927. The marine shells of the west coast of North America. **2** (1): 297 pp.; 22 plts. Stanford Univ. Press, Stanford, Calif.

Powell, Arthur William Baden

1966. The molluscan families Speightiidae and Turridae. An evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. Bull. Auckl. Inst. & Mus. No. 5: 1 - 184; plts. 1 - 23; text figs. (1 November 1966)

Rau, Weldon W.

1966. Stratigraphy and Foraminifera of the Satsap River area, Southern Olympic Peninsula, Washington. Wash. Div. Mines & Geol. Bull. **53**: 1 - 66 (24 June 1966)

Tegland, Nellie May

1933. The fauna of the type Blakeley upper Oligocene of Washington. Univ. Calif. Publ. Geol. Sci. **23** (3): 81 - 174; plts. 2 - 15; 2 maps (11 October 1933)

Tryon, George Washington, Jr.

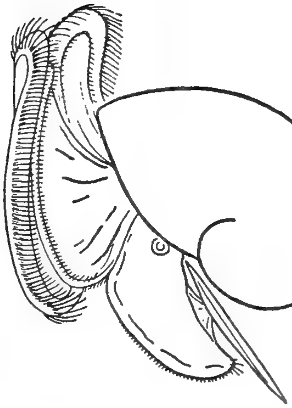
1884. Manual of Conchology. Philadelphia, ser. 1, **6**: 413 pp.; illust.

Weaver, Charles Edwin

1916. Tertiary faunal horizons of western Washington. Univ. Wash. Publ. Geol. **1** (1): 1 - 67; plts. 1 - 5

1916. The Tertiary formations of western Washington. Geol. Surv. Bull. **13**:

1942. Paleontology of the marine Tertiary formations of Oregon and Washington. Washington Univ. (Seattle) Publ. Geol. **5** (1-3): 789 pp.; 104 plts.



The Intertidal Behavior of the Bean Clam, *Donax gouldii* Dall, 1921

BY

THOMAS H. IRWIN

Department of Biology, Victor Valley College, Victorville, California 92392

(2 Plates; 3 Text figures)

INTRODUCTION

PELECYPOD MOLLUSKS of the family Donacidae, genus *Donax,* occur throughout the world mostly within the intertidal zone on sandy beaches in tropical and temperate climates. Most species of intertidal *Donax* inhabit only wave washed beaches and are found at various levels of the littoral where many are exposed at low tide and submerged at high tide. They occupy only the surface of the sand to a depth of about 5 cm and are easily observed in areas of great population density.

Studies of these organisms and their adaptations that allow them to successfully occupy this unstable habitat are far from complete. One of the many possible adaptations of *Donax* that deserves additional attention is a controversial behavioral phenomenon known as tidal migration. In exhibiting this behavior, the organism follows the rising tide up the beach and then retreats down the beach as the tide subsides. The possession of anatomical devices for extended movement need not be present as the animal could position itself to make use of the surge of the waves to change its position.

The following species of *Donax* have been reported to migrate or exhibit some form of tidal movement: *Donax semigranosis* Dunker, 1877 (MORI, 1938, 1950); *D. vittatus* La Costa (STOLL, 1937, 1938); *D. variabilis* Say, 1822 (PEARSE *et al.,* 1942; TURNER & BELDING, 1957; LOESCH, 1957; ALDRICH, 1959; TIFFANY, 1971); *D. fossor* Say, 1822 (= *D. variabilis* [ABBOTT, 1954; CHANLEY, 1969]) (JACOBSON, 1957); *D. denticulatum* Linnaeus, 1767 (WADE, 1964, 1967a); *D. gouldii* Dall, 1921 (JOHNSON, 1966a, 1966b); *D. striatus* Linnaeus, 1767 (WADE, 1967b); *D. aemulus* (PICHON, 1967); *D. elegans* (PICHON, 1967); *D. incarnatus* Gmelin, 1791 (ANSELL & TREVALLION, 1969); *D. spiculum* Reeve (ANSELL & TREVALLION, 1969).

In contrast, the following species of *Donax* have been observed not to exhibit migration or tidal movement: *Donax gouldii* (HEDGPETH, 1957; POHLO, 1967); *D. variabilis* (EDGREN, 1959); *D. faba* (PICHON, 1967); *D. vittatus* (ANSELL & TREVALLION, 1969).

It should be noted that several other beach-dwelling marine organisms have been observed to migrate. The sand crab, *Emerita analoga* Stimpson, 1857 (MACGINITIE, 1938; CUBIT, 1969) and the gastropods *Terebra salleana* Deshayes (KORNICKER, 1961) and *Bullia melanoides* Deshayes (ANSELL & TREVALLION, 1969) have been observed to migrate with the tides. JOHNSON (1966a) has suggested that the gastropod *Olivella biplicata* Sowerby, 1825 might also move landward during the rising tide.

The purpose of this study is to examine a population of *Donax* to find if tidal migration does occur and, if so, what factors are responsible or influential in this behavior pattern. An attempt will also be made to examine the potential advantages to the organism of such behavior.

MATERIALS AND METHODS

Observations were made on a population of *Donax gouldii* at Estero Beach (approximately 31°45′N, 116°38′W) near Ensenada, Baja California, Mexico. This particular location was selected because it usually maintains a high population density of these clams. Beaches in this area are also easily accessible by traveling by boat in the estero and crossing over a sand bar to the beach.

Observations on this population began in August, 1961 and continued through August, 1969. Detailed observations were made in August of each year, but shorter inspections of one week or less were conducted in other months of the year whenever possible.

Four stations were selected so that there were at least noticeable variations in the beach elevations between the stations. An attempt was made to use the same stations during the 8 year period of study. This was difficult, however, because the beach contours and sand dunes of the backshore changed considerably during the 8 year period of study. A concrete bench marker about 4 feet square was used as a base stake for one station, but upon returning 7 months later, it was found that this marker had been undercut by the surf and moved into the intertidal zone from high on the dunes behind the beach. The other stations were even more difficult to keep track of during this period, and it was possible only to estimate their location from year to year.

At each station a stake was placed above the high water line. From this stake a line graduated in meters was run down the intertidal zone at low tide to the low water line. The daily position of the population of *Donax gouldii* was noted by taking one-quarter square meter samples every 2 meters in the area occupied by the clams (Figure *1*). Sample areas to be collected were marked by using a wooden frame measuring $\frac{1}{2}$ meter on each side. This included an area of $\frac{1}{4}$ square meter. All the clams were removed from this area and placed in a wooden-framed sieve with $\frac{1}{8}$ inch hardware cloth bottom. This sieve was then used to separate the sand from the clams by washing the collection in the surf. Each sample of clams was then counted to obtain a quantitative estimate of the population and its position on the beach. If the sample contained only small numbers of clams each was counted individually. Samples containing large numbers were estimated by volume using a 350 ml can. When this method was used, 4 cans-full of clams were counted, and an average was taken to figure the number of clams per can. At monthly intervals the number of clams filling the can was recalculated to consider possible change in the population.

Observations were also made during high tides when the population was submerged. Quantitative sampling was difficult, but by using the transect line and a glass face plate the position of the population could be recorded.

The physical factors of the habitat which may have some influence on the migratory behavior of *Donax* were also recorded, including:

1. Air and water temperatures were taken during each observation with a laboratory grade thermometer. Readings corresponded to air and water temperatures found by Flores (1965) for this area.

2. Surf conditions were recorded throughout the time of observations. Unusual conditions during other periods were recorded by residents of Estero Beach Resort. The surf height was estimated using a meter stick.

3. Salinity data were taken from published data for the area (Flores, 1965).

4. Tidal conditions were taken from United States Coast and Geodetic Survey tide tables for 1961 through 1969. The 0.90 ratio was applied to the San Diego Data given to convert to readings for Todos Santos Bay. Time differences of -19 minutes for low tides and -17 minutes for high tides were used.

5. Sand was fractioned using standard 8 inch soil sieves from 40 mesh (0.42 mm) to 200 mesh (0.074 mm). Samples of 100 gr were shaken for 30 minutes by a mechanical shaker and the fractions were weighed to 0.01gr. The density of the sand was calculated using water displacement. The water-holding capacity of the sand was found by saturating dry sand with distilled water. As soon as water stopped dripping from the sand it was weighed, then oven-dried at 100° C for 4 hours and reweighed. The percentage of water to sand was then figured.

6. The beach contour was measured at the beginning and at the end of each observation period. The contour of the beach was measured at 2 m intervals by sighting through a transit located over the base stake upon a long graduated pole. All contours and distances were converted into feet so that they could be easily compared to the tidal data published by the United States Coast and Geodetic Survey. The contour measurements for each station were then drawn, and the daily position and population density of the clams at this station were plotted upon the contour drawing. With these data plotted, the vertical position of the clams with relation to the water or tidal level could easily be seen.

7. The presence of local currents was recorded by observing floating debris in the water.

Characteristics of this population of *Donax gouldii* that might influence migration were also studied. Clams from different levels of the beach were measured to determine if size segregation was present. Clams were also tested to determine their ability to withstand exposure by placing them on dry and damp sand under direct sunlight for various lengths of time. Tagging and transplanting experiments were also attempted.

DESCRIPTION OF THE WORK AREA AND *Donax* POPULATION

Estero Beach represents an isolated strip of sand situated between the rocky coast north of Ensenada and the cliffs at Punta Banda. An entrance to the estero (estuary) produces another barrier that separates the beach just south of Ensenada from the work area. The mountains surrounding the area and the islands in the entrance to Todos Santos Bay shelter the beach and work area from excessive winds and surf. Days are relatively calm with little overcast except during the late spring and early summer.

The conditions representing the work area were noted as follows:

1. For the year 1964, which was typical, air temperatures ranged from a low of 9.5° C on November 20 to a high of 23.0° C on October 20. Water temperatures within the surf were fairly constant, with winter temperatures averaging 16° C and summer temperatures averaging near 20° C.

2. Surf conditions were very stable. The surf along this protected beach seldom exceeds 3 feet in height. There were, characteristically, 4 or 5 rows of continuous breakers ranging in height from a few inches to 2 feet with a weak wash produced every 5 to 10 seconds. Storms or heavy winds produced little change in these conditions.

3. Salinity in the surf averaged 34.4‰ with a range between 33.9 and 35‰ (Flores, 1965)

4. Tidal conditions in the area are typical of the west coast of California. There are usually 2 high and 2 low tides each day. The mean tide level for Todos Santos Bay is 2.7 feet, with a mean tidal change of 3.6 feet. During the period when observations were made, tidal changes ranged from 0.3 feet on August 27, 1963, to 7.8 feet on August 25, 1965. The mean high and low tides are 4.7 and 0.9 feet respectively. This represents a 0.2 foot greater tidal change than the actual mean. The mean tide level was 2.8 feet, 0.1 foot higher than the actual mean for this area.

5. Sand within the intertidal zone was found to be extremely fine as compared to parts of the east coast (Pearse *et al.*, 1942) and to the optimum particle size favored by *Donax denticulatus* (Wade, 1964). Sand fractions showed that over 95% was between 0.177 mm and 0.074 mm. This is similar to the sand on the Texas coast (Hedgpeth, 1953). The density of the sand was 2.72, as compared to a density of 1.89 for the *Donax gouldii*. Water holding capacity was found to be 22.5%.

6. Variations in beach contour between the 4 stations are shown in Table 1. Local currents appeared to cause great changes in the beach profile from year to year (Table 2). The breakers rolled in at a slight oblique angle producing a weak local current toward the inlet of the estero. During tidal changes, a stronger current was produced by the exchange of water in the estero. This current was, perhaps, most responsible for the unstable conditions observed near the inlet of the estero.

Table 1

Comparison of Stations in August, 1962

Station Number	Beach profile ratio vertical to horizontal	Length of intertidal zone in meters	Average number of *Donax gouldii* per square meter in zone of high density
1	1 : 40	80	6400
2	1 : 28	54	7600
3	1 : 22	42	2600
4	1 : 28	54	3400

Table 2

Comparison of Variations in Station 3 from 1961 to 1967

Date	Beach profile ratio vertical to horizontal	Average number of *Donax gouldii* per square meter in zone of high density
August 24, 1961	1 : 15	120
August 10, 1962	1 : 22	2600
August 19, 1963	1 : 22	2800
March 23, 1964	1 : 23	60
August 23, 1965	1 : 29	5500
July 26, 1966	1 : 26	3800
March 24, 1967	1 : 27	2900

Plate Explanation

Figure *1*: Transect at Station One. The screen box is used to wash sand from clams. Samples are one quarter square meter

Figure *2*: Band of *Donax gouldii* exposed upon the intertidal zone. Frame shows one quarter square meter

Figure *3*: Close-up of *Donax gouldii* exposed on surface of sand

Figure *1*

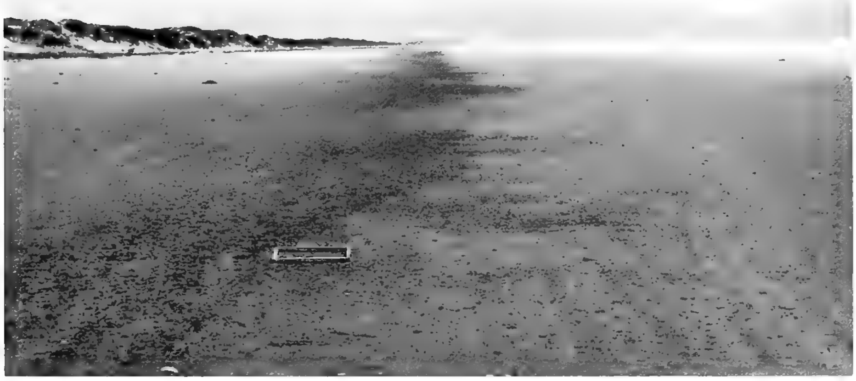


Figure *2*

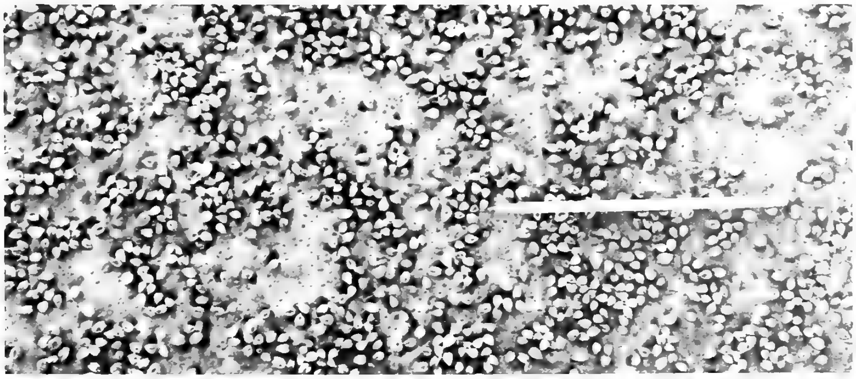


Figure *3*

The characteristics of the population of *Donax gouldii* at Estero Beach were found to be very similar to the population described by Coe (1953, 1955, 1956) at La Jolla, California. The number of clams varied considerably from year to year as well as from station to station (Tables 1 and 2). The clams showed no evidence of segregation by size nor was segregation noticed within the 8 to 31% of the clams carrying the hydroid commensal *Clytia bakeri* Torrey, 1904.

The population of *Donax* was found to occupy a relatively narrow band within the intertidal zone (Figure *2*) where practically all were exposed with each low tide and submerged with each high tide. When the tides receded, leaving the clams above the water line, the water in the sand usually drained around the valves of the clams near the surface. This made the sand more compact and left the upper layers of *Donax* exposed on the surface where they could easily be seen (Figure *3*), and where they were frequently used as a pavement by motorists (Figure *4*). If the upper surface of the sand contained a high water content, the clams could usually be found by locating the 2 small siphon holes of each on the surface (Figure *5*). When the tide rose and saturated the sand with water, the exposed clams quickly dug in or were washed for a short time by the surge. The clams that were covered with sand were usually washed to the surface by the surge. By using their enlarged foot, the clams could hold a position on the surface of the sand against even the largest breakers encountered.

MOVEMENTS OF THE POPULATION

Preliminary observations in the summer of 1961 and in early 1962 showed that *Donax gouldii* at this location did not follow a migratory pattern directly based upon rise and ebbing of the tide as reported for some of the other species. In fact, some day-to-day observations showed that the position of the population had changed little. Only when the daily positions of the clams were plotted over a period of days in relation to a fixed base stake was there any indication of movement up and down the beach. Figure 6 shows the positions occupied by the clams when transects were made at low tide in August, 1962. The clams at all stations showed similar movement with the exception that the distances of movement were greater when the beach contour was flatter, with a resultant longer intertidal zone. Movement was also found to be correspondingly shorter when the contour was steeper.

The results from transects taken since 1962 showed similar movement. Figure 7 illustrates the position of the clams in August, 1963. The main mass of the population was lost during a 5 day period as shown. This could have been the result of a lateral shift of the clams with the long-shore current. It was during this period that the postlarva of *Donax gouldii* were observed invading the beach in large numbers, transported by pelagic stages of red algae (probably *Hypnea* sp. and *Aglaothamnion* sp.) and other floating debris.

EXPERIMENTS

Tagging experiments were attempted several times without much success. One hundred *Donax gouldii* were marked by filing a groove in one valve and applying a quick-drying lacquer to the indentation. As soon as the lacquer dried, the clams were released in the area occupied by the population. None were recovered the next day.

Fifty clams were fixed with plastic bands so that they were unable to open their valves. These clams were washed to the extreme of the high tide and were recovered there when the tide subsided.

Thousands of *Donax gouldii* were transplanted to other levels on the beach and to other locations. Those tagged and moved to different levels on the beach could not be found after the tide changed. Presumably, these clams were either washed inshore to another location or rejoined the main population. When placed above the low water level, the clams remained on the surface of the sand until the rising tide reached their position. They were rolled by the surge until they dug in. Clams transported to other beaches nearby, both with and without surf, were not found after 2 days.

The ability of *Donax gouldii* to live without water was also tested. Groups of 100 clams were placed on wet and dry sand exposed to direct sunlight during different parts of the day. Their ability to stand exposure was tested at one-hour intervals by placing one of the groups that had been exposed into a large sand-filled container with several inches of fresh sea water covering the sand. Each group of clams was given 15 minutes for individuals to become active in the container. Individual clams that did not become active were classed as dead. As a control, one group, exposed for only 10 minutes, was placed in the container. Within 5 minutes, all of the individuals in the control group had actively dug into the sand. The experimental groups were placed on dry sand in the sun. The temperature on the surface of the sand averaged 31° C. After one hour 74% of the first group were still active when placed in the recovery container. The second group, after 2 hours of exposure on dry sand, had only 58% still active.

Clams exposed to the same conditions as above, but placed upon water saturated sand, survived over 10 hours with little loss of vigor. Although air temperatures ranged from 19° to 32° C, as long as the sand remained wet, the surface temperatures of the sand seldom exceeded 22° C. Temperatures were even lower in the sand on the underside of the clams.

Upon further investigation, it was found that at low tide, this population remained in an area where the sand contained between 19½ and 26% water. This is near or above the 22½% water holding capacity of the sand.

VERTICAL POSITION OF THE POPULATION IN RELATION TO THE TIDE LEVEL

The data from 124 transects taken over an 8-year period showed that the main mass of clams occupied a position at the extremes that ranged between the 0.9 foot tidal level and the 4.2 foot tidal level. The mean range was between the 2.05 foot and the 2.9 foot tide level (Figure 8). The mean level of occupation for this population of *Donax gouldii* was near the 2.4 foot tide level.

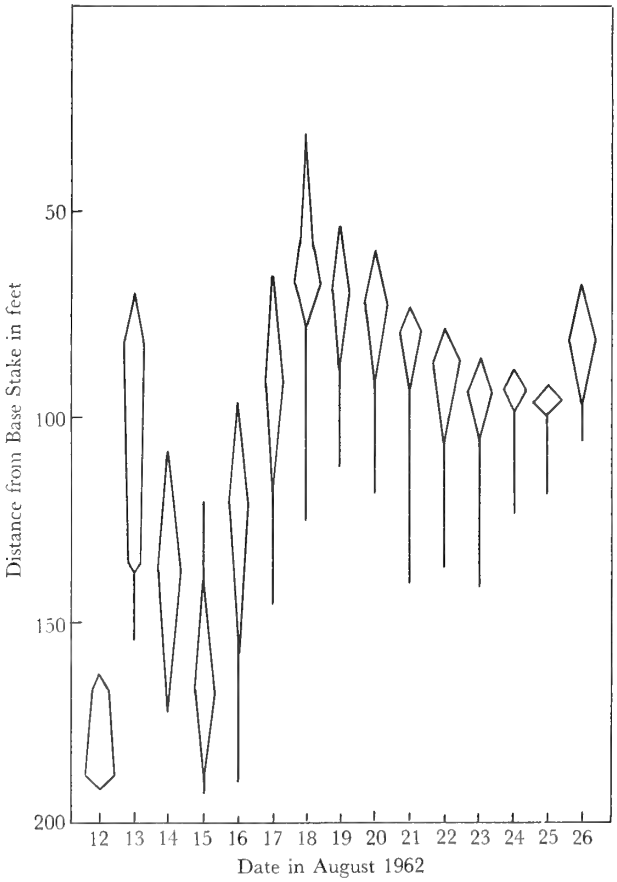


Figure 6

Position of *Donax gouldii* in relation to the beach from August 12 through August 26, 1962. Maximum density of the population is approximately 10 000 clams per square meter

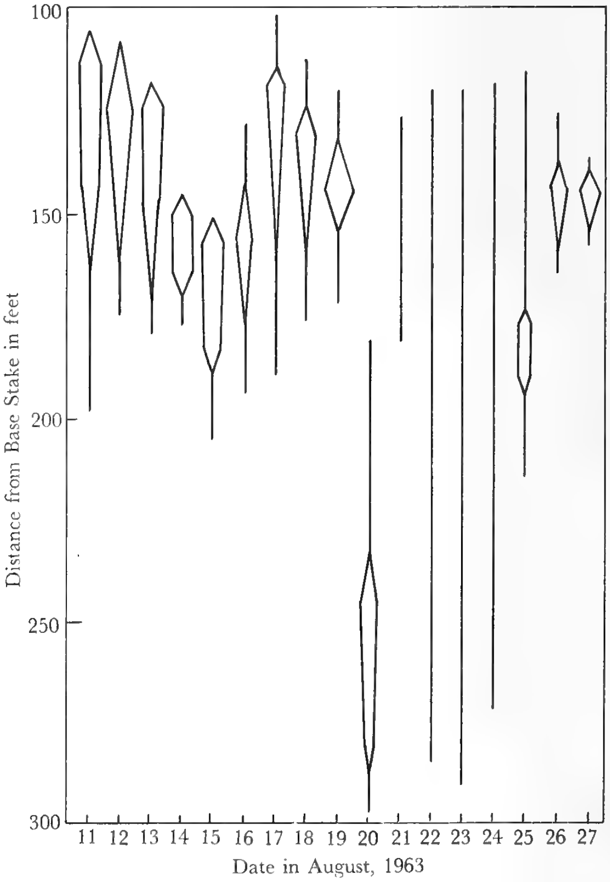


Figure 7

Position of *Donax gouldii* in relation to the beach from August 11 through August 27, 1963. Maximum density of the population is approximately 10 000 clams per square meter

Plate Explanation

Figure *4*: Exposed *Donax gouldii* used as a pavement by motorists. Note the compact nature of the sand

Figure *5*: Siphon holes of *Donax gouldii*

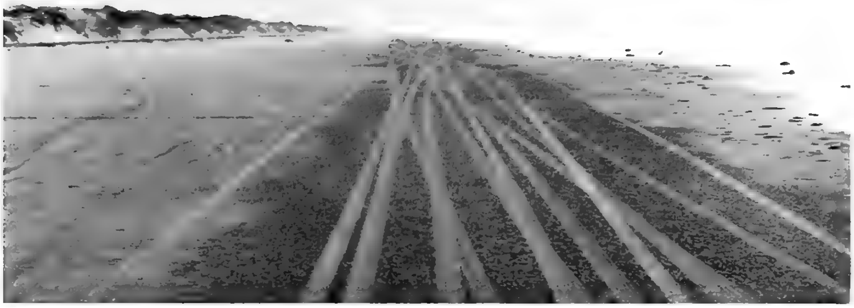


Figure *4*

Figure *5*

DISCUSSION

Donax gouldii at Estero Beach do exhibit movement up and down the intertidal zone (Figures 6 and 7). However, the movement demonstrated by these clams differs greatly from the tidal migration of other species as reported. This population did not continuously follow the rising and falling of each tide up and down the beach but seemed to move in an unpredictable manner. Many clams were seen rolling, momentarily, in the swash of each changing tide, but no great massive movements were observed as a result of individual breakers.

The movement of this population could not be directly correlated with any single factor or group of factors examined. There was, however, little movement of the population when the tidal change was less than 2 feet but movement was not necessarily greater during spring tides. Changes in surf conditions did not appear to have a great effect on the distance of movement, but higher than average surf did increase the speed of movement. Unusually high surf that could cause greater and more dramatic movements as described by Orton (1929) and Edgren (1959) did not occur here. The surf usually remained low and waves did not break on the beach but rolled in, producing little shock. It would be difficult to conclude that *Donax gouldii* here would not "pop" from the sand like other species observed under the influence of heavy surf. Regardless of the force of the breakers, the clams would have trouble pushing out of the fine, highly compact sand without the help of the surf wash.

The method by which the clams accomplished this movement was found to differ in several respects from that of other species as reported. The acoustical shock produced by the surf or by artificial means resulted in a digging response and not a general movement out of the sand. This response was also noted by Pohlo (1967). Digging occurred independent of tidal level, suggesting that an internal "clock-like" mechanism within the clam as proposed by Turner & Belding (1957) for *Donax variabilis* to trigger movement does not occur here.

A digging response also generally resulted when the clams were just placed on water-saturated sand or on dry sand that became water saturated. When clams were placed in a container of sand covered with water, the rate of digging by the clams was increased by tapping the container and simulating surf conditions.

The clams, as mentioned earlier, are found at low tide in, or exposed on, sand that is very wet; although it is not known exactly how the clams themselves might influence this water content. Concentrations of water, both higher and lower than the sand just above or below the zone of occupation, were recorded. The clams, therefore, may be able to remove or add small amounts of water to the sand when the population is highly concentrated, or they may retard the rate of evaporation by their shading effect when exposed.

When the data from all transects were plotted and graphed a nearly perfect unimodal curve with a mode, median, and mean near the 2.4 foot tide level was produced. The extremes of this curve are noted in Figure 8. From these data it appears that these clams do not move intentionally but attempt to maintain a position near the 2.4 foot tidal level as best they can. The movements or deviations from the mean could be the result of the instability of this environment; although the clams occupying this habitat must maintain a considerable degree of mobility to survive. Sand and beach profile conditions changed considerably during the observations. A mobile *Donax* population could continuously adjust its location as beach conditions changed. This constant adjustment

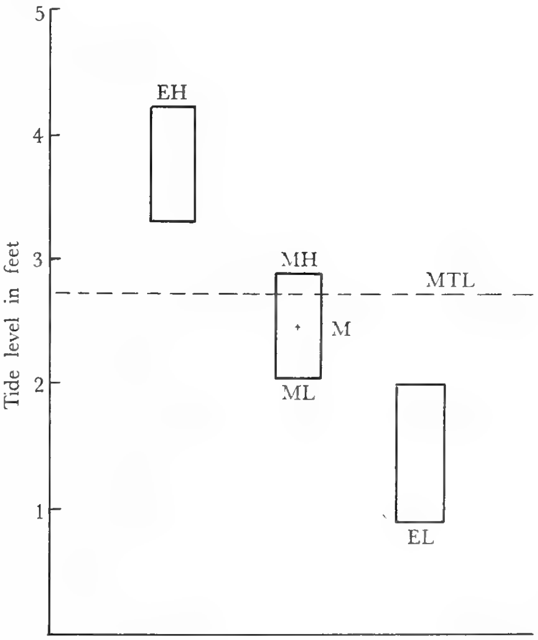


Figure 8

Vertical position of the population of *Donax gouldii* in relation to the tide level

EL – Extreme low location of the population (August 22, 1965)
EH – Extreme high location of the population (August 11, 1963)
MH – Mean high location of the population
M – Mean location of the population
ML – Mean low location of the population
MTL – Mean tide level

could prevent the burial of sessile clams as described by Johnson (1957).

It is yet too early to speculate if other species of *Donax* may exhibit a similar response in attempting to maintain a preferred position on beaches as this population of *D. gouldii* seems to do. There are many references in the literature, where a positioning is noted regardless if movement or migration has been observed, but there have been no quantitative, long term studies reported. It may be that *Donax* reacts much like *Emerita* (Cubit, 1969), but to a lesser degree. If this is the case the term "migration" with its implications is misleading.

ACKNOWLEDGMENTS

I am indebted to Manuel Flores V., former director at the Estacion de Biologia Marina, El Sauzal, Baja California, and his staff for their able assistance. My special thanks go to John E. Fitch, Donald J. Reish, Jack T. Tomlinson, Joseph H. Connell, Joseph S. Lidrich, and Joel W. Hedgpeth for their most useful suggestions.

Literature Cited

Abbott, Robert Tucker
1954. American seashells. Princeton, New Jersey. D. van Nostrand Co., Inc.; xiv+541 pp.; 40 plts.; 100 text figs.
Aldrich, J. W.
1959. Activities of coquina clams. Atlantic Nat. **4** (1): 41 - 43
Ansell, Alan David & Ann Trevallion
1969. Behavioral adaptations of intertidal mollusks from a tropical sandy beach. Journ. Exp. Mar. Biol. Ecol. **4** (1): 9 - 35
Chanley, Paul
1969. *Donax fossor*: a summer range extension of *D. variabilis*. The Nautilus **83** (1): 1 - 14
Coe, Wesley Roswell
1953a. Resurgent populations of marine littoral invertebrates and their dependence on ocean and tidal currents. Ecology **34** (1): 225 - 229
1953b. Resurgent populations of the bean clam, *Donax gouldi* Dall. Amer. Malacol. Union Ann. Reprt. **6**: 18 - 19
1955. Ecology of the bean clam, *Donax gouldi*, on the coast of Southern California. Ecology **36** (3): 512 - 514
1956. Fluctuations in populations of littoral marine invertebrates. Journ. Mar. Res **15** (3): 23 - 33
Cubit, John
1969. Behavior and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). Ecology **50** (1): 118 to 123
Edgren, Richard A.
1959. Coquinas: (*Donax variabilis*) on a Florida beach. Ecology **40** (3): 498 - 502
Flores, Manuel V.
1965. Temperatura ambiente, temperatura del aqua y salinidad de la zona eulitoral de El Sauzal, B. C. Contrib. Inst. Nat. Investig. Biolog.-Pesqueras, Mexico
Hedgpeth, Joel Walker
1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference ot the invertebrate fauna. Inst. Mar. Sci. **3**: 110 - 186
1957. Treatise on marine ecology and paleoecology. Vol. 1, Ecology. Geol. Soc. Amer. Mem. **67**: 599 - 601
Jacobson, Morris Karlmann
1955. Observations on *Donax fossor* at Rockaway Beach, New York. The Nautilus **68** (3): 73 - 77
Johnson, Phyllis T.
1966a. On *Donax* and other sandy-beach inhabitants. The Veliger **9** (1): 29 - 30 (1 July 1966)
1966b. Mass mortality in a bivalve mollusk. Limn. & Oceanogr. **11** (3): 429 - 431
Johnson, Ralph Gordon
1957. Experiments on the burial of shells. Journ. Geol. **65** (4): 527 - 535
Kornicker, Louis S.
1961. Observations on the behavior of the littoral gastropod *Terebra salleana*. Ecology **42** (1): 207
Loesch, Harold C.
1957. Studies of the ecology of two species of *Donax* on Mustang Island, Texas. Bull. Inst. Mar. Sci. **2** (2): 201 - 227
MacGinitie, George Eber
1938. Movements and mating habits of the sand crab, *Emerita analoga*. Amer. Midld. Natur. **19** (2): 471 - 481
Mori, Syuiti
1938. Characteristic tidal rhythmic migration of a mussel, *Donax semigranosis* Dunker, and the experimental analysis of its behavior at the flood tide. Dobutsugaka Zasshi **50** (1): 1 - 12 [in Japanese]
Orton, John H.
1929. Severe environmental mortality among *Abra* (= *Syndosmya*) *alba*, *Donax vittatus* and other organisms of the Lancashire Coast. Nature (London) **124** (3137): 911
Pearse, A. S., Harold J. Humm & G. W. Wharton
1942. Ecology of sand beaches at Beaufort, North Carolina. Ecol. Monogr. **12**: 135 - 190
Pichon, M.
1967. Contribution à l'étude des peuplements de la zone intertidale sur sables fins et sables vaseux non fixes dans la région de Tulear. Recl. Trav. Stat. Mar. Endoume, suppl. **7**: 57 - 100
Pohlo, Ross H.
1967. Aspects of the biology of *Donax gouldi* and a note on the evolution in Tellinacea (Bivalvia). The Veliger **9** (3): 330 - 337; 5 text figs. (1 January 1967)
Stoll, Eva
1937. Beobachtungen über die Fortbewegung bei einigen grabenden Muscheln. Rev. Suisse Zool. **44**: 383
1938. Sur la mode de locomotion de quelques mollusques marins. Trav. Stat. Biol. Roscoff **16**: 3 - 33
Tiffany, William J. III
1971. The tidal migration of *Donax variabilis* Say (Mollusca : Bivalvia). The Veliger **14** (1): 82 - 85 2 text figs. (1 July 1971)
Turner, Harry Jackson & David Belding
1957. The tidal migration of *Donax variabilis* Say. Limn. & Oceangr. **2** (2): 120 - 124
Wade, Barry A.
1964. Notes on the ecology of *Donax denticulatus* (Linné). Proc. Gulf & Caribb. Fish. Inst. 17th Ann. Session: 36 - 41
1967a. Studies on the biology of the West Indian beach clam, *Donax denticulatus* (Linné). 1. Ecology. Bull. Mar. Sci. Gulf & Caribb. **17** (1): 149 - 174
1967b. On the taxonomy, morphology, and ecology of the beach clam, *Donax striatus* Linné. Bull Mar. Sci. Gulf & Caribb. **17** (3): 723 to 740

Preliminary Note on Hermaphroditism and Embryonic Stages in *Diplodon variabilis*

BY

CELIA GLUZMAN DE PASCAR[1]

(2 Plates)

HERMAPHRODITISM is apparently an unusual phenomenon in mutelid mollusks. However, most of the observations of hermaphroditism were made by punction of the gonad. If the studies had been made by means of histological serial sections, the phenomenon would probably have been observed more frequently. The present paper deals with one case of hermaphroditism, where some other interesting features were found. The specimen was a *Diplodon variabilis* collected in Miguelin Rivulet, Punta Lara, Argentina during the summer. The shell of the animal measured 27 mm in length and 20 mm in height. The macroscopic study revealed a peculiar aspect of the gills, where numerous protuberances made us suspect the presence of parasites. The specimen was fixed *in toto* in Bouin's fixative and embedded in paraffin. Sections of 6μ were taken every 200μ and stained according to the Heidenhain-Azan trichrome method.

Microscope observations showed a marked male gonadal predominance, with only few female germinal elements.

The presence of numerous completely formed glochidia as well as a tumoral mass were evident in the internal gills.

Microscopic study of the male gonad revealed its normal topographic localization, over the foot of the animal. All stages of spermatogenesis were seen in the gonad.

The female elements of the gonad appeared in an abnormal position as they were formed dorsally with respect to the hepatopancreas and ventrally from the stomach (Figure *1*). Compared with a normal female specimen of the same season, the oocytes (Figure *2*) were not numerous and presented a reduced size; scant amount of vitellum was seen in the cytoplasm. In the same place, some oocytes undergoing segmentation were found surrounding a small group of male cells, included in the stroma of the ovary (Figure *3*). This finding represents an autofecundation phenomenon, which has not been reported previously.

Observations made on the left gill deserve special consideration since glochidia in complete organogenesis were found there. In studies made on this species, glochidia have been mentioned by CASTELLANOS (1965). These observations do not show any important morphological or histological features.

The glochidia appeared inserted in the water tubes of the gills and showed their normal components: the shell rudiment, the mantle, the foot, the gills, and the digestive system (Figure *4*). The section of the stomach shows the crystalline style. The typical epithelium, consisting of cells with long cilia, is evident in the intestinal wall.

The section of the hepatopancreas could also be seen (Figure *4*).

All these morphological features make the glochidium a perfect replica of the adult animal, except for the gonadal elements. We assume that in this species the development of the larval stage is direct, without an intermediate host.

The tumoral formation located in the gill (Figure *5*) may be a teratoma which leads to the assumption of a larval histolysis, perhaps due to an autodigestion of the normal tissues.

The tumoral mass is composed of several vesicles: a large dorsal one; two medial vesicles, one of them in the central cavity, and the other, small one situated laterally. Another vesicle appeared in the ventral zone (Figure *5*).

The dorsal formation presents a ciliated epithelium which covers a mass composed of glandular elements, connective tissue, and scarce muscle cells (Figure *6*).

Further studies may permit clarification of the fact that so many interesting features can appear together in the

---

[1] Present address: Laboratorio de Investigaciones Biológicas
Faculdad de Ciencias Médicas, Universidad de La Plata
Calle 60 y 120, La Plata – ARGENTINA

same specimen. The lack of references in this respect prevent us from making further conclusions.

ACKNOWLEDGMENTS

I would like to thank Prof. Dr. Herberto Prieto Díaz, Prof. Dr. César L. A. Gómez Dumm and Prof. Julián M. Echave-Llanos, and the members of the technical staff of our Laboratory.

Literature Cited

Castellanos, Zulma A. de
1965. Contribucion al estudio biológico de almejas nacaríferas del Río de La Plata. Rev. Mus. La Plata 8 (60): 99 - 147

Explanation of Figures *1* to *3*

Figure *1*: Internal gill (left side). Oocytes (arrow) × 50

Figure *2*: Normal oocytes × 120

Figure *3*: Female gonad showing several oocytes. Some of them (arrow) are undergoing segmentation. S – spermatozoa × 120

Explanation of Figures *4* to *6*

Figure *4*: Glochidium × 65
F – foot; M – mantle; G – gills; Sh – shell; I – intestine; St – crystalline style; H – hepatopancreas

Figure *5*: Tumoral formation located in the internal gill with its vesicles × 50

Figure *6*: Detail of the dorsal vesicle × 300

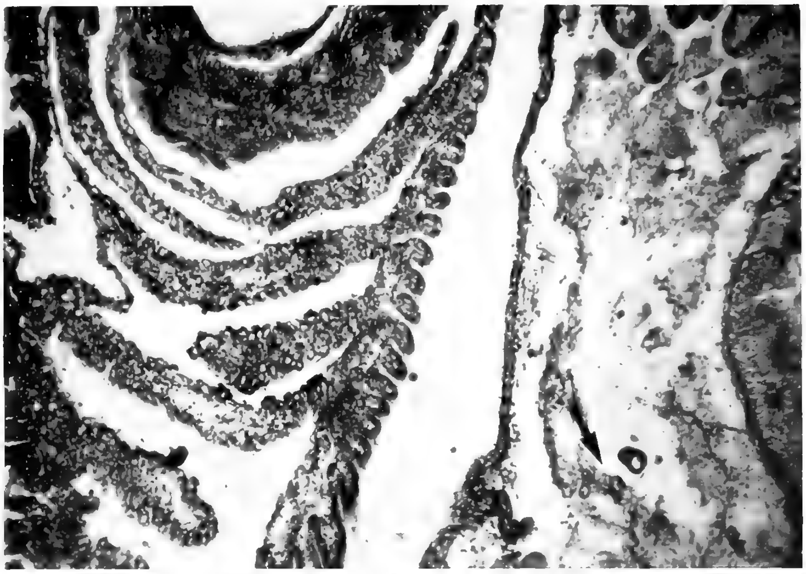


Figure *1*

Figure *2*

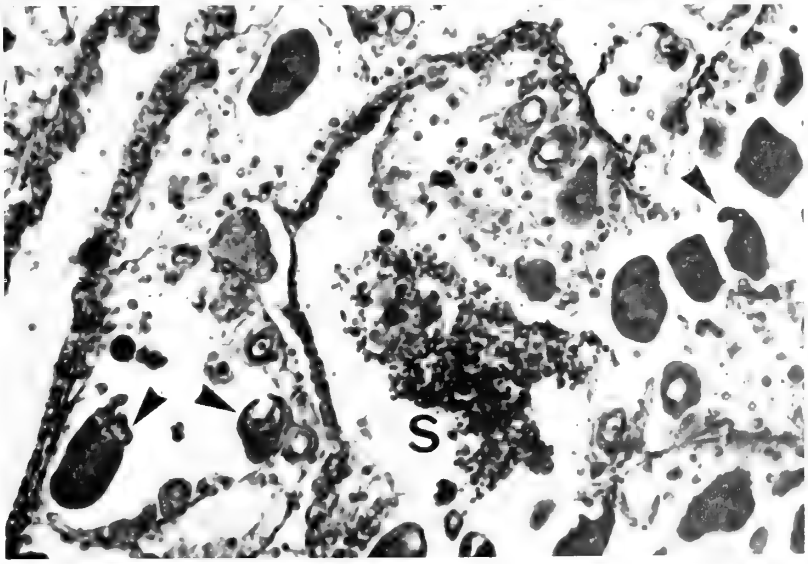


Figure *3*

Figure *4*

Figure *5*

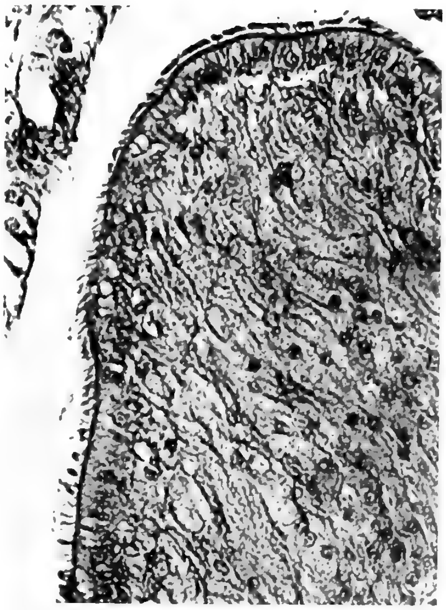


Figure *6*

Thermal and Salinity Effects on Ciliary Activity of Excised Gill Tissue from Bivalves of North and South Carolina

BY

ALAN H. SHOEMAKER

Belle W. Baruch Coastal Research Institute, University of South Carolina, Columbia, South Carolina 29208
and
Columbia Zoological Park, Columbia, South Carolina 29202

(4 Text figures)

INTRODUCTION

In the study of the distribution of marine animals, whether molluscan or of any other group, it was found that temperature and salinity have a pronounced effect on the animal (Gunter, 1957; Schlieper & Kowalsky, 1956a, 1956b). Similarly, substrate can have a marked effect on the distribution within the species' range (Bird, 1970).

In the past, most studies have emphasized the effect of temperature and salinity on the whole animal (Hoar & Robertson, 1959, on fish; Peiss & Field, 1950, on fish; Wells, 1961, on mollusks; McLeese, 1956, on lobsters). Whole organism studies, however, were not always reliable for mollusks because a whole animal response to tactile stimulation is used and a recovery period is necessary. Sublethal damage to bivalves would go unobserved and affect later tests if the same individuals were used again. Henderson (1929) subjected intact bivalves directly to water baths at constant temperatures and measured the temperatures needed to cause continued gaping of the valves after the mantle was touched with forceps. However, species which lock shut upon death would be useless here, as would measurement of autolysis or partial recovery of ciliary movement prior to death. Later, use of isolated gill tissue from bivalves was adopted to derive exact thermal and temporal determinations of ciliary responses (Schlieper, 1951, 1958; Vernberg *et al.*, 1963).

After collecting numerous mollusks in deep water on reefs off South Carolina, little information in the literature was found on physical tolerances of marine epibenthic bivalves. Since these reefs were just recently described (Menzies *et al.*, 1966), analysis of molluscan assemblages was still sketchy. While *Arca zebra* and *A. imbricata* have been recorded for many years in Carolina waters, popular references do little to clarify where these bivalves even occur, let alone thermal and salinity resistance (Abbott, 1954, 1963, 1968; Barrett & Patterson, 1957; Johnston, 1957). All that was said in such typical sources was that the bivalves were very common in shallow water. Since *A. imbricata* is found in from 15 - 25 m of water in Carolina waters and *A. zebra* down to 40 m, none of these sources is of much value in describing the distribution of these populations.

Recent studies by Stanley (1970) do little to shed light on the substrate preference or physiological tolerances of these bivalves. *Arca* populations studied by him were from south Florida and although both species were found in only 1 or 2 m of water, no habitat difference between the two species was discerned. Other studies of more southern populations (Houbrick, 1968) report the same shallow depth utilized by *Arca* populations in Florida. Other epibenthic bivalves, *Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837, have been noted living together in California waters (Harger, 1968a, 1968b, 1970). However, the ability of the byssus of these two species to withstand wave impact is the factor separating their niches. While the byssus of *A. imbricata* is proportionally larger than that of *A. zebra*, thermal tolerances would probably be more important in separating *A. zebra* and *A. imbricata* since wave effect is unimportant for northern populations in deep water.

NATURAL HISTORY

Arca zebra, A. imbricata, and *Chione cancellata* were chosen for this study because of the similarity in their modes of life. All three have the same geographical range and each is the dominant epibenthic bivalve in its habitat. Popular references (Abbott, 1954, 1968; Warmke & Abbott, 1963) describe *A. zebra* and *A. imbricata* as living attached to rocks in shallow water from North Carolina to the Lesser Antilles and Brazil. *Chione cancellata* is found in shallow water of the Southeast United States and West Indies. Reportedly, they are all common along their entire range. While this may be true in the West Indies and south Florida, northern researchers would find these comments on distribution somewhat misleading.

Arca zebra Swainson, 1883

Arca zebra, the largest of the three species, averages 3 inches (7½ cm) in length. It has a thick, strong shell twice as long as wide. Numerous brown zebra-like stripes cover the exterior, and growing over most of the outer shell is a shaggy green periostracum which partially disguises the tell-tale stripes. For further camouflage, *A. zebra* is covered with encrusting corals, sponges, bryozoans, tunicates, algae, and the herbivorous gastropods *Crepidula acuiformis* (Gmelin, 1791) and *Crucibulum striatum* Say, 1826. The inside of this bivalve is a dull purplish brown.

Arca zebra grows firmly attached to hard substrates. The foot produces a shiny, olive green byssal clump, short but strong, which protrudes through a byssal gape in the ventral edge of the shell. This gape is an opening along the middle of the valves and faces directly on the substrate selected for attachment. This surface to which it attaches may be rock, compressed shell, another shell of *Arca,* other bivalves, sponge, or soft coral. The animal is so firmly attached that only a concerted effort of much pulling and twisting will dislodge it; often the byssal clump is pulled completely out of the foot and remains on the substrate. Commonly, the sponge or bryozoan substrate later surrounds the animal, leaving only its dorsal hinge area exposed.

Arca zebra is reputed to be very common in shallow water. Warmke & Abbott (1963) describe it in Puerto Rico as living attached to rocks in only a few feet of water. Beaches of south Florida and the Florida Keys are littered with dead shells after storms, attesting to the shallow depths preferred in this part of their range. Observations in shallow water along the Carolina-Georgia coast, however, indicate it is completely absent and only extensive dredgings revealed the true habitat of northern populations. As a result of dredging from the R/V *Eastward,* this species was located on reefs which extend from Charleston, South Carolina to Onslow Bay and Lookout Shoals, North Carolina, offshore 15 to 50 miles (24 to 80 km). The reefs on which *A. zebra* live occur under the Gulf Stream in 25 to 40 m of water and can be visually located on the ship's depth recorder. Typically, they appear as large, rounded or jagged humps arising from the ocean floor. However, certain flat and bare reefs, undetectable on the depth recorder, may be adequate for attachment. Although *A. zebra* may occur in depths as shallow as 15 m, these populations are represented by only a few small, scattered individuals.

However, at any depth, bare rock alone is not sufficient for attachment. *Arca zebra* and *A. imbricata* occur only on those portions of reef which also support thick growths of coral and sponge. Apparently the Gulf Stream and its accompanying current and warm temperature may help keep an optimal level of food and sediment in the water column.

Arca imbricata Bruguière, 1789

Many of the comments concerning *Arca zebra* can also be applied to *A. imbricata.* Although having the same general shape, *A. imbricata* is slightly smaller, averaging 2 inches (5 cm) in length, thicker, fatter, with no stripes. As it reaches its maximum depth of 25 m, however, it is almost as large as the deeper occurring *A. zebra* and covered with the same green colored periostracum as found on *A. zebra.* The byssus is similar to that of *A. zebra* and attaches in the same manner.

Arca imbricata occurs on reefs and rocky surfaces, a habitat similar to that favored by *A. zebra.* Reefs with large populations were found in Onslow Bay and Lookout Shoals, North Carolina. Depth, however, seemed to be the obvious factor separating these two species. *Arca imbricata* was found in North Carolina in 15 to 17 m of water and extended to 25 m. The largest individuals of *A. imbricata* come from the deepest limit of their distribution where *A. zebra* begins to assume dominance. At the overlapping depth of approximately 25 m, *A. zebra* populations are composed of small individuals, but as soon as *A. imbricata* disappears, *A. zebra* assumes its normal size down to its maximum depth of 40 m, where only stunted individuals occur.

While *Arca imbricata* were collected in greatest numbers on North Carolina reefs in 15 - 25 m of water, this does not necessarily mean that they do not occur in shallower water. I have seen specimens collected from the beaches near Myrtle Beach, South Carolina, with valves still intact. This species, therefore, may be able to live in much shallower water if suitable surfaces for attachment occur. While inshore reefs are not commonly found off South Carolina, isolated rocky outcroppings or wrecks may provide suitable surfaces for these animals to establish themselves.

Chione cancellata Linnaeus, 1758

Chione cancellata is the shallowest occurring of the 3 species discussed, with the same geographical range as *Arca zebra* and *A. imbricata,* occurring from North Carolina to the West Indies. However, literature searches (Abbott, 1954, 1968) yield little information on substrate preference. In these and other sources, typical habitat is described as "common in shallow water" and "abundant in brackish water." This gives little preliminary aid in collecting large numbers of individuals for laboratory research. Substrate reference resulting from extensive dredging will be discussed later in "Results."

METHODS AND MATERIAL

General Care

These three species were chosen because of the similarity in their modes of life. All three are essentially nonmotile bivalves living on the surface of the bottom. *Arca zebra,* a deep water species, and *A. imbricata,* a medium depth species, were obtained in offshore waters of North and South Carolina by dragging a Cerame-Vivas rock dredge for half an hour across reefs of coral and rock, with the animals collected in a trailing chain mesh bag. The living animals were removed and kept aboard ship for several days in large aerated containers until the bivalves could be brought to the laboratory. Here they were scrubbed clean of all encrusting organisms to eliminate fouling and kept in a 100-gallon (360 l) capacity, temperature-controlled tank. Animals tested at ambient temperatures were used immediately, and other animals were temperature acclimated for at least 2 weeks. *Chione cancellata* was gathered with a homemade dredge of a design similar to that of the Cerame-Vivas dredge but proportionally smaller. The dredging time was only 5 or 10 minutes since the area to be sampled was much smaller. These animals were brought back to the laboratory the same day and placed directly in the holding tanks. *Chione cancellata* was seldom encrusted and required little cleaning. Those animals to be tested at ambient temperatures were also used within a week, while individuals to be acclimated were stored in a separate aquarium.

The salinity averaged 32‰ in both holding tanks, even though unfiltered sea water was periodically added to make up for evaporation. Although food matter and algae may have been present in the tanks and added water, these animals were essentially starved.

Half the animals captured were kept at the same temperature as the bottom from which they came. These individuals were tested after 2 days in the laboratory to allow for recovery from the shock of collection. When possible, animals were tested in 2 temperature baths simultaneously in groups of 4 or more.

Those animals dredged in the summer at 17 - 21° C were considered warm-acclimated. Therefore, the individuals to be cold-acclimated were exposed to water of 10° C. Animals coming from 9 - 10° C water were considered cold-acclimated and those to be warm-acclimated were subjected to 20° C for the 2-week acclimation period.

Preparation of Gill Tissue

The cilia on the bivalve's gills are rapidly beating hair-like structures at the end of the gill filament. These are easily seen under the high-power microscope and their rate of death and autolysis is easily predicted once the basic thermal tolerance has been determined. Most bivalve cilia of the same species stop beating at nearly the same temperature.

Previous studies (Henderson, 1932) have used the whole animal in thermal determinations, but here the exact time of death is in doubt. The researcher had to base his judgment on the time required before the two valves would open and not close again upon tactile stimulation. *Chione cancellata,* at death, does not always open but rather closes tightly, as do many other bivalves, rendering this approach useless.

To obtain the gill tissue, the bivalves were gently broken open with a hammer. With the body still intact, the gill

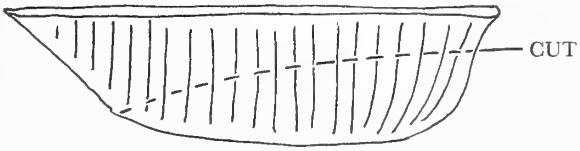


Figure 1

Diagrammatic view of gill tissue with the portion to be used indicated by dashed line (CUT) tissue was easily dissected from the other tissues and placed in a Petri dish of filtered sea water. Since the ventral half of the gill tissue contained the distal edge of the filament with cilia, and the entire gill filament was too long to fit on a microscope slide, the dorsal half of the filament was cut away and discarded (Figure 1). Then the tissue was easily cut into 3 mm sections, each containing many filaments with hundreds of cilia.

Cilia

The cilia used were terminal (Figure 2). *Arca zebra* and *A. imbricata* also have cilia on the sides of the gill filaments, but these have little thermal resistance. Only the middle section of the gill tissue was used because towards the end of the gill, the cilia and filament decrease in size and are too small to be observed accurately. *Chione cancellata* also has lateral cilia but only in small numbers. These cilia occur in clumps and are also more sensitive than terminal cilia.

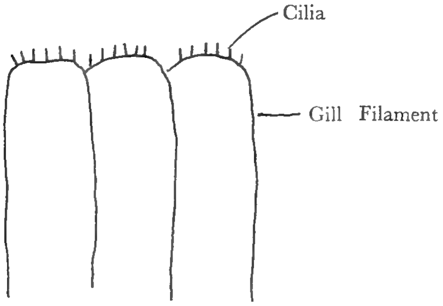


Figure 2

Terminal cilia on the end of gill filament sections

Whenever possible, separate gill pieces from one animal were subjected to several different water baths. Single individuals of *Arca zebra* and *A. imbricata* had enough gill sections available after dissection to allow 3 separate temperature or salinity tests being run simultaneously. *Chione cancellata*, on the other hand, was too small for more than one test per individual, and for longer periods of time, sections from 2 individuals of *C. cancellata* had to be placed in the same flask.

To test thermal resistance, the cilia were heated or cooled in a water bath. Stoppered flasks of filtered sea water were allowed at least 30 minutes to equilibrate with the water bath. Thermometers, accurate to 1/10 of one degree, were used to check both flask and water bath temperatures periodically to insure constant temperature. A large-bore pipette was used to transfer the gill sections from the Petri dish to the flask, care being taken to add as little water as possible to avoid unnecessary temperature change. Every 15 minutes one gill section was removed from each flask, placed on a microscope slide and covered with a coverslip. For thicker filaments, such as those of *Chione cancellata,* a depression slide was used, as the coverslip on a regular slide crushed the gill section. Under the high-power microscope (400×), the terminal cilia were easily visible and the rate of activity decrease was clearly discernible. The corresponding increase in autolysis was equally visible.

The activity chart (Table 1) was used to rate the decrease in movement of the cilia. Although some degree of subjectivity in the observation was evident, these levels of activity were easily separated.

Table 1

Activity Chart Used to Rate the Activity of Cilia from the Terminal End of Bivalve Gill Filaments

3 – Normal Activity
2 – Somewhat Reduced Activity
1 – Greatly Reduced Activity
0 – No Activity

Under the microscope, the terminal cilia appeared as a blur when beating at a normal rate of Activity 3. This beating was strong enough to create a current which could carry observed alga cells along its border. During decreases in activity, the cell began to lose cytoplasm from between its filaments. Activity 2 had only 75% of the cilia capable of movement, with each cilium readily visible. Autolysis then began, with cytoplasm exuding into the water medium. Activity 1 had only 10% of the cilia beating, quite slowly to barely a flicker. Cytoplasm and organelles covered the margins of the cells, with visibility of the cells becoming difficult at times. At rate 0, the cilia stopped beating entirely and the margin of the cell was barely discernible. Only upon introduction of the gill sections into the highest temperature water baths, where the gill sections lived less than 15 minutes, did the cell not rupture. Here, the cell appeared to go into a state of shock.

Thermal Resistance

The thermal resistance of gill tissue was determined as a function of time versus temperature. The gill sections awaiting testing in the Petri dishes were kept in sea water from the same container in which the animal lived to keep thermal and physiological changes to a minimum prior to being placed in the experimental flask. To hold the gill sections, stoppered Erlenmeyer flasks, filled with filtered sea water of 30‰ salinity, were suspended in a temperature-controlled water bath. These flasks were allowed at least 30 minutes to equilibrate after the bath had reached the desired temperature. To prevent mistakes in the time interval between observations, gill sections were placed in the flask only at intervals of 0, 15, 30, or 45 minutes past the hour. These sections were transferred as rapidly as possible to the flask to prevent temperature change.

The flask itself was filled to within one inch ($2\frac{1}{2}$ cm) of the top to keep temperature fluctuations to a minimum. Only one animal's gill section was included in each flask, except in the case of prolonged exposure for *Chione cancellata* where several individual's gill sections were kept together in one flask. At no time did the temperature drop more than 0.5° C, and seldom more than 0.1° C. After removal with a large-bore dropper, the gill sections were placed under a cover slip on a microscope slide, regular or depression (see above), and observed under the compound microscope, using the oil immersion objective.

In seeking the thermal tolerances, both upper and lower lethal limits were examined. Cilia were checked once every 15 minutes until Activity 0 was reached. This was continued for all species which could survive over 15 minutes at any given temperature. When the critical temperature was attained in less than 15 minutes, the cilia were checked every 5 minutes. When no activity was observed, regardless of time period, a second gill section was checked to exclude any individual tissue variation or dissection damage to the tissue.

At lower lethal limits, temperatures were checked every 15 minutes, as before, for up to 180 minutes. These levels were then decreased in 1° C intervals until –1° C was reached. Presumably, if the water temperature were lowered to freezing, –2° C, the gill sections would cease activity and die. Since this is an unnatural occurrence, natural conditions seldom going below 9° C, this low level was deemed unnecessary for this experiment.

Osmotic Resistance

Cellular osmotic resistance was measured by exposing gill tissue to various salinities. To cover the estuarine range, 15‰ and 25‰ were used for *Arca zebra* and *A. imbricata,* with 35‰ used as the control. For the more euryhaline *Chione cancellata,* the lower salinities acted as a control and 35‰ as the abnormal exposure. Ten or 12 sections were rinsed in distilled water and placed in a temperature-controlled refrigeration container. The temperatures tested were 10°, 25°, and 35° C for both natural (field) and acclimated individuals. The activity of the cilia was then observed at the following intervals: $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1, 2, 3, 4, 6, 12, 24, 48, and 72 hours. The salinities were measured with a refractometer since the salinity interval was fairly large and easily readable.

RESULTS

Osmotic Resistance

The osmotic resistance was determined by observing the ciliary activity at predetermined time intervals up to 72 hours. Each salinity measurement at each temperature was tested with 3 individuals of each species, both acclimated and ambient.

Gill cilia from all 3 species showed no difference in their ability to withstand abnormal salinity, whether raised, in the case of *Chione cancellata,* or lowered for *Arca zebra* and *A. imbricata.* Neither did thermal acclimation change the ciliary response to the unnatural salinity levels. Lower salinities were not deemed necessary, since these were far lower for *A. zebra* and *A. imbricata* than would ever occur in nature. While salinity on the reefs offshore does reach 29‰, nothing approaching 15‰ is probable. Similarly, while salinity has been noted at 10‰ in the area where *C. cancellata* was collected, these determinations were made from the surface and do not reflect epibenthic values which would probably be higher. Since *C. cancellata* does not occur littorally or in burrows, greatly reduced salinities do not occur.

Thermal Resistance

Data representing the length of time terminal cilia of both ambient and acclimated individuals of all 3 species can withstand upper maximum temperatures are presented in Table 2.

Both *Arca zebra* and *A. imbricata* showed no ability to acclimate, with values being equal for all temperatures. Since there was no possibility in this portion of their range for rapid daily or seasonal changes, the inability to acclimate was expected. At the lowest temperatures, sublethal damage only was done to the gill cilia, the activity rate being no lower than 2 when the experiment ended.

Table 2

Thermal Resistance Time at Elevated Temperatures (in minutes) of Isolated Gill Tissue of Bivalves

Temperature	Cold-Acclimated (10° C)		Warm-Acclimated (20° C)	
	Mean Time and Standard Error of the Mean	Range and Number of Determinations	Mean Time and Standard Error of the Mean	Range and Number of Determinations
		Arca zebra		
41	13.0±1.09	10 – 15 (5)	13.0±1.09	10 – 15 (5)
40	38.3±2.47	30 – 45 (9)	37.5±2.7	10 – 15 (5)
39	62.8±2.92	30 – 75(16)	64.5±2.5	45 – 75(14)
38	194.3±1.0	165 – 210 (7)	195.0±3.6	180 – 210(19)
37	over 180	– (5)	over 180	– (5)
		Arca imbricata		
43	15.0 –	– (4)	15.0 –	– (5)
42	57 ±1.71	30 – 60(20)	60.5±2.1	30 – 75(17)
41	102.5±2.53	90 – 105(11)	102.5±2.53	75 – 105(11)
40	over 240	– (5)	over 240	– (5)
		Chione cancellata		
42	under 5 –	5 (5)	under 5 –	5 (5)
41	15.0± 1.09	10 – 15 (5)	15.0 –	15 (15)
40	37.5± 2.47	30 – 45(10)	43.9± 2.34	15 – 60(14)
39	75.0± 2.92	45 – 105(15)	90.3± 4.55	45 – 120(19)
38	156.0±10.9	120 – 165 (5)	165.0± 1.0	105 – 210 (7)
37	over 210	– (5)	over 210	– (5)

The shallow water *Chione cancellata* did show some degree of acclimation. Since these are all estuarine individuals, slight acclimation was to be expected. At lower temperatures, 2 or more individuals were used in each flask. At 37° C the activity rate was still 3, even after 210 minutes. Occasionally, one individual's gill cilia would stop beating sooner than others', as reflected in the range. While outwardly healthy in appearance, these cilia would cease activity at temperatures lower than expected. Individuals of all species, regardless of acclimation, often would increase the level of activity just prior to death. From an activity of 1, they would suddenly increase to Activity 2 and then permanently cease ciliary movement. Figures 3 and 4 show the upper lethal limit of all 3 species in graphic form.

Low temperature experiments all showed normal activity for all species, regardless of acclimation. To prevent freezing at 0° and –1° C, methyl and isopropyl alcohol were added to the water bath. At all temperatures, from +5° down to –1° C, 5 individuals of each species were used. Even at these low temperatures, well below experienced field conditions for any of these 3 species, no reduction of ciliary activity was observed. All ciliary activity after 180 minutes was still at Activity 3.

Chione cancellata

Extensive inshore dredging revealed that this species is not very common, although general accounts in popular references state that it is a very abundant species. Benthic samples taken throughout the North Inlet Estuary, South Carolina, in an attempt to locate suitable populations of *Chione cancellata* for laboratory research, indicated that this species preferred a substrate very limited in geographical distribution. Most of the wider creeks draining into North Inlet have sandy bottoms or, in regions of very little current, mud bottoms. Both these substrates proved to be devoid of this bivalve species. Only deeply scoured areas, or regions with strong currents and hard shell bottoms, yielded large populations. Associated organisms, such as crabs, echinoderms, and subtidal oysters, were also much more abundant in these areas. In the area known as Clambank Creek, over 99% of the epibenthic bivalves were *C. cancellata. Chione cancellata* was not attached but simply lay on the bottom.

To compare this finding of limited substrate preference, similar dredgings were also made in Murrel's Inlet, South Carolina. Samples were taken from all the larger creeks leading into the inlet and throughout the inlet itself.

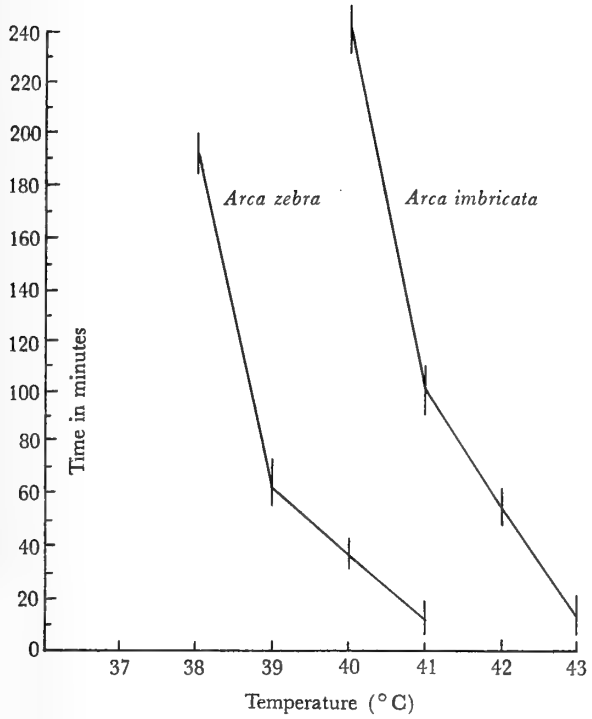


Figure 3

Upper lethal limits (in minutes) of gill cilia from warm- and cold-acclimated *Arca zebra* and *Arca imbricata*

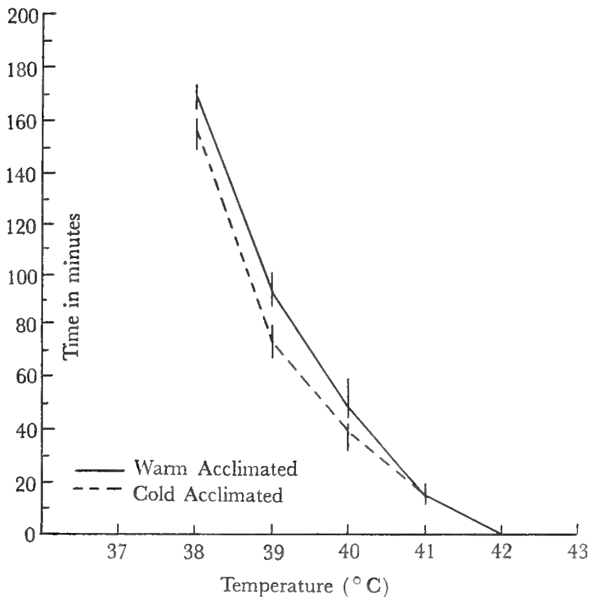


Figure 4

Upper lethal limits (in minutes) of gill cilia from warm- and cold-acclimated *Chione cancellata*

Only at locations with sufficient current to keep sediment deposition to a minimum was *Chione cancellata* found. This species was absent in inflowing creeks, all of which had mud bottoms, and throughout the inlet itself where the bottom was composed of sand. Only in that portion of the inlet where the main creeks join, the bottom being composed of oyster shell and hard mud, was *C. cancellata* common. Here it was found abundantly, as were many associated organisms.

CONCLUSIONS

In North and South Carolina, *Arca zebra* and *A. imbricata* were found only in offshore waters under the Gulf Stream where suitable reef sites occur. Both *A. zebra* and *A. imbricata* represent the most dominant epibenthic bivalve of their respective communities. *Arca zebra* does not live above 25 m, while *A. imbricata* can be found in water 15 to 25 m deep, but can probably live in shallower water if suitable substrates exist.

Arca imbricata, although smaller, has greater resistance to thermal stress than does *A. zebra.*

Chione cancellata has the same latitudinal range as *Arca zebra* and *A. imbricata* and is by far the most dominant epibenthic bivalve on its specialized substrate of hard shell, strong currents, and little sedimentation. Its estuarine distribution in the northern portion of the range does not overlap that of *A. zebra* or that of *A. imbricata.*

None of the cilia of these 3 species showed any response to altered salinities (15, 25, and 35‰) and after 72 hours the cilia moved at normal speed at temperatures of 10°, 25°, and 35° C.

Arca zebra and *Chione cancellata* are less heat tolerant than *A. imbricata,* ceasing ciliary activity 2° C lower than *A. imbricata.*

Literature Cited

Abbott, Robert Tucker

1954. American seashells. Princeton, New Jersey. D. van Nostrand Co., Inc.; xiv+541 pp.; 40 plts.; 100 text figs.

1963. Sea shells of the world. Golden Press, New York, 160 pp.

1968. Sea shells of North America. Golden Press, New York, 280 pp.

Barrett, Ralph & David Patterson

1967. Shells and shelling. Post Publ. Miami, Florida, 64 pp.

Bird, Samuel O.

1971. Shallow-marine and estuarine benthic molluscan communities from the area of Beaufort, North Carolina. Amer. Assoc. Betr. Geol. Bull. **54:** 1651 - 1676

Gunter, Gordon

1957. Temperature. *In*: Treatise on marine ecology and paleoecology. J. W. Hedgpeth (ed.); Geo. Soc. Amer. Mem. **67** (chapt. 8): 159 - 184

Harger, John Robin

1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. The Veliger **11** (1): 45 - 49; 3 text figs. (1 July 1968)

1970a. The effect of wave impact on some aspects of the biology of sea mussels. The Veliger **12** (4): 401 - 414; 9 text figs. (1 April 1970)

1970b. The effect of species composition on the survival of mixed populations of the sea mussels *Mytilus californianus* and *Mytilus edulis*. The Veliger **13** (2): 147 - 152; 5 text figs. (1 October 1970)

Hoar, William S. & G. Beth Robertson

1959. Temperature resistance of goldfish maintained under controlled photoperiods. Canad. Journ. Zool. **37:** 419 - 428

Houbrick, Joseph Richard

1968. A survey of the littoral mollusks of the Caribbean coast of Costa Rica. The Veliger **11** (1): 4 - 23; 1 text fig.; 1 map (1 July 1968)

Johnstone, Kathleen Y.

1957. Sea Treasure. Houghton-Mifflin Co., Boston, Mass. xii+242 pp.; 8 plts. (84 figs.)

McLeese, Donald W.

1956. Effects of temperature, salinity, and oxygen on the survival of the American lobster. Journ. Fish. Res. Brd. Can. **13:** 247 - 272

Menzie, Robert J., Orin H. Pilkey, Brenda W. Blackwelder, Deborah Dexter, Peter Hulins & Lawrence McCluskey

1966. A submerged reef off North Carolina. Internat. Rev. ges. Hydrobiol. **51** (3): 393 - 431

Peiss, C. N. & John Field

1950. The respiratory metabolism of excised tissue of warm- and cold-adapted fishes. Biol. Bull. **99:** 213 - 272

Schlieper, Carl V.

1951. Über die Temperatur-Stoffwechsel-Relation einiger eurythermer Wassertiere. Zool. Anz. suppl. **16:** 267 - 272

1958. New observations of the physiology of ciliated cells. XV Internat. Congr. Zool., Sect. VI, paper 5

Schlieper, Carl V. & Ruth Kowalsky

1956a. Quantitative Beobachtungen über Physiologisches Ionen Wirken im Brackwasser. Kieler Meeresforsch. **12:** 54 - 165

1956b. Über den Einfluss des Mediums auf die thermische und osmotische Resistenz des Kiemengewebes der Miesmuschel. Kieler Meeresforsch. **122:** 37 - 135

Stanley, Steven M.

1970. Relation of shell form to life habits of the Bivalvia. Geol. Soc. Amer. Mem. **25:** 296 pp.

Vernberg, Frank John, Carl V. Schlieper & David E. Schneider

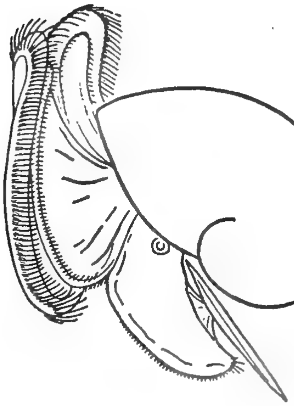
1963. The influence of temperature and salinity on ciliary activity of excised gill tissue of mollusks from North Carolina. Comp. Biochem. Physiol. **8:** 271 - 285

Warmke, Germaine L. & Robert Tucker Abbott

1961. Caribbean seashells; a guide to the marine mollusks of Puerto Rico and other West Indian islands, Bermuda and the lower Florida Keys. Livingston Publ. Co., Narberth, Pa. x+345 pp.; 44 plts.; 34 text figs.

Wells, Harry

1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. **31:** 239 - 266



A Field Study on the Clustering and Movement Behavior of the Limpet *Acmaea digitalis*

BY

JAMES W. WILLOUGHBY

Department of Natural Sciences, California State University, San Jose, California 95114

(1 Plate; 3 Text figures)

INTRODUCTION

Acmaea digitalis Eschscholtz, 1833, is one of the more commonly found limpets inhabiting the uppermost rock beaches. Stenotopically it occupies a restricted area in the intertidal zone, an ecological niche that excludes most other members of the genus *Acmaea*.

Its distribution extends from the Aleutian Islands to Lower California; however, it is reported to be in greatest abundance northward of Monterey Bay. Along the coast of central and northern California and probably elsewhere, *Acmaea scabra* and *A. digitalis* occupy the same habitats, often competing for shelter and possibly for food (Test, 1945). Although they are competitors, generally their rock preferences and dispersion are somewhat different. *Acmaea digitalis* frequently restricts itself to a narrow band along the upper vertical rock surfaces. Its cohabitant, more solitary in nature, prefers both the vertical and horizontal rocks with a slightly broader seaward range (Sutherland, 1970). However, at the lower limits of its vertical range, *A. digitalis* has been observed sharing horizontal slopes with *A. scabra,* especially where there is a high density of barnacles and algal growth (Haven, 1971).

Along the vertical rock surfaces, where the substrate permits, *Acmaea digitalis* will often be found resting in clusters with members of the same species. This clustering phenomenon, if occurring, has not been described in other west coast members of this genus.

It is generally recognized that limpet movement is initiated by the splash of the incoming tides. As the water level rises, their activity and range of movement increase. During an ebbing tide, the reverse pattern occurs, for as the water action subsides, the limpets regroup and appear to rest until the tidal cycle recurs. Their movements are apparently directed towards foraging and grazing on the microscopic algal film that grows on the rocks (Test, 1945). However, some movements can be attributed to seeking protection from direct exposure as they find shelter in cracks and crevices to avoid prolonged periods of direct sunlight.

In addition to this study, a few others have been undertaken to investigate the movement and clustering behavior of this particular species. Millard (1968) conducted a study at Pacific Grove, California, on the clustering behavior of *Acmaea digitalis* on granite rocks. Clusters of the animals were observed to shift their position from day to day, and they did not occupy exactly the same location or same amount of space from one day to the next. Although the clusters remained intact, there was a constant daily replacement occurring with new members taking the place of limpets leaving the cluster population. Millard's study indicated that limpet clustering was somewhat different from aggregations, for limpets regrouped each day in correlation with the tidal rhythms. The investigator offered land isopods for examples of aggregate behavior. After a period of activity, these animals rested in the dampest and shadiest locations available in close proximity with other members.

Miller (1968), also working at Pacific Grove, observed that during stationary periods at low tide, *Acmaea digitalis* orients itself downward and to the right more than any other position. He related his findings to evidence presented by Abbott's (1956) research on the water circulation in the owl limpet, *Lottia gigantea* (Gray, 1834). According to his study, factors resulting from physiological conditions might influence the limpets to assume this downward and to the right posture. However, the advantages of this position have not been clearly demonstrated with *A. digitalis.*

Miller also found that when these limpets are wetted by the incoming tides, they begin to move up on the rock surfaces as the water rises, and downward at periods of lower high tide. When the surf was rough, the entire population was observed to move upward to a higher level and down when the water action subsided. HAVEN (1971) also noted that the vertical movements of *Acmaea digitalis* along the central California coast were correlated with the seasonal changes. These limpets moved downward in the summer months and upward in the winter months.

Studies on homing of the species under investigation were done by MILLER (1968), GALBRAITH (1965), as well as VILLEE & GROODY (1940). FRANK (1964) conducted studies on this phenomenon along the Oregon coast and from his statistical data concluded that, although *Acmaea digitalis* does not exactly home, it does appear to have a home range. In a more recent study of this species, BREEN (1971) suggests that two distinct behavioral types of limpets may exist, those with homing tendencies and those showing non-homing tendencies.

This field study is directed towards 3 major objectives. First, it is to determine if *Acmaea digitalis* of a specific vertical rock microhabitat consistently return and rest with the same members of this microhabitat, or if their clustering behavior in terms of membership is a random occurrence. A microhabitat is defined as a natural protective site in the rocks (fissures, crevices, and depressions, etc.), where limpets cluster and rest together for shelter.

Secondly, it attempts to investigate whether these limpets assume a predominant orientation position during their resting periods. In relationship to orientation, it also attempts to determine whether any observable characteristics, such as contact with other members, might influence their grouping behavior.

Finally, within the scope of this study, it poses the question: are there any observable periodicities occurring in regard to the resting and movement patterns which are displayed by this particular species of *Acmaea?*

METHODS AND RESULTS

This project was initiated in the summer of 1970, and a year later a more comprehensive study was conducted in August, 1971. It was from the latter investigation that the majority of the data for this report was compiled. The observations described below were made at Davenport Landing, Santa Cruz County, California.

The work was carried out on the lower reaches of a vertical sandstone bench in an unprotected area along the open coast (Figure *1*). The specific habitat site consisted of a rock face parallel to the surf which received the full impact of the waves during periods of high tide. This particular rock surface measured 3.9 m × 2.4 m, and had 2 distinct topographical areas. The upper region was highly weathered and fractured, resulting in numerous small protective spaces where individuals or small groups of limpets could find protection. The lower portion of the cliff contained large smooth expanses with long angular fractures and folds which were adequate to hold larger clusters of limpets.

Below the area of study at the base of the cliff was a zone of abrasion which was surrounded by a composition of coarse sand and wave-washed rock debris. Limpets of this particular study were found restricted to the high tide range between approximately + 5.0 and + 8.0 feet (1.5 m and 2.4 m), but were exposed during tides below the + 4.0 feet (1.2 m) level.

Food reserves in the habitat area consisted of an unidentified microscopic algal film which was found covering a large portion of the rock face in close proximity to the cluster sites. Other macroscopic algal growths which were probably not used for food purposes were also observed in the study habitat. These included large patches of *Ulva* which covered the lower portion of the rock face with dispersed tufts of *Cladophora, Pelvetiopsis,* and *Ralfsia* randomly growing throughout the study site. No clusters or individuals of *Acmaea digitalis* were found resting in the macroscopic algal growth.

Three natural microhabitats were selected, all approximately 1.5 m above the sand base. Each contained clusters of limpets of various sizes and ages. Some immature *Acmaea digitalis* were present in the microhabitats, but those under 5 mm in length were not included as their size made it possible for them to reach areas difficult to observe.

Two of the microhabitats were fissures approximately 25 cm long, one vertical and one horizontal. The third was an irregular and angular depression formed by erosional processes on the cliff face. Thirty *Acmaea digitalis,* 10

Plate Explanation

Figure *1*: Photograph of wave-cut benches looking south from study site. Bases of the cliff provide a habitat for *Acmaea digitalis*
Figure *2*: Photograph of red microhabitat during study. Limpets in foreground and upper right hand corner are tethered to verify movement during the high tide periods

Figure *1*

Figure *2*

from each microhabitat, were marked *in situ* for the tracking part of the study. The identification procedure consisted of marking small colored tags (white, red, and yellow) with consecutive numbers, using India ink. These were attached to the shells with a quick-drying waterproof adhesive. On previous tests this adhesive, Aron Alpha no. 202, proved to be a non-toxic substance and also was found to be superior to the painted coding system used in the initial study.

In addition to the tagged limpets, 2 dummy clusters were positioned on the rock face with the above mentioned adhesive. A dummy cluster consisted of limpet shells filled with plaster of paris and mechanically adhered to the rocks to simulate a natural living cluster. Ten shells were boiled to remove all chemical traces, and another 10 were positioned on the rocks without any pre-conditioning. Both dummy clusters were placed in close proximity to the 3 selected microhabitats, but in unoccupied spaces. It is interesting to note that both of these pseudocluster sites were previously occupied by living clusters used in the previous summer's study.

After marking, and noting their original positions, the limpets were observed each day at low tide, for 10 consecutive days. Two additional periods were also used to observe movement and clustering behavior at high tide. The 10 tagged members of each microhabitat were traced to their resting positions each day with distance and direction in degrees measured. The position and orientation of each marked limpet was noted along with orientation of all other limpets in each of the 3 microhabitats.

On the third day of observation, a number of the marked limpets within the clusters appeared to be prolonging their resting period, and it was suspected that they were not moving during either of the 2 high tide periods. These limpets were then tethered to the rock so that on later observations a shift or change of position would be evident (Figure 2). Metal pegs were driven into the rocks approximately 2½ to 5 cm from each limpet suspected of remaining stationary. A 4-pound monofilament line was tied to the peg and weakly taped to the animal's shell. The tether had enough strength to withstand the force of the waves, but could easily be parted by the limpets on their shifting position or moving away from the cluster site.

In order to determine the stability of the 3 clusters in terms of continued membership, it was necessary to locate the resting site of each marked *Acmaea digitalis* on a daily basis. The observations revealed that 3 activities were occurring within each of the microhabitats. First, there was a periodic turnover of limpets with some moving out of the cluster while others would return to recluster during the period of low water. A residual number of limpets extended their resting period from one observation to the next (see Figure 3), and apparently did not respond to the stimuli of the incoming tide. The third factor observed was that some of the cluster members rotated or reoriented themselves in each of their respective sites. It is believed by this observer that by repositioning them-

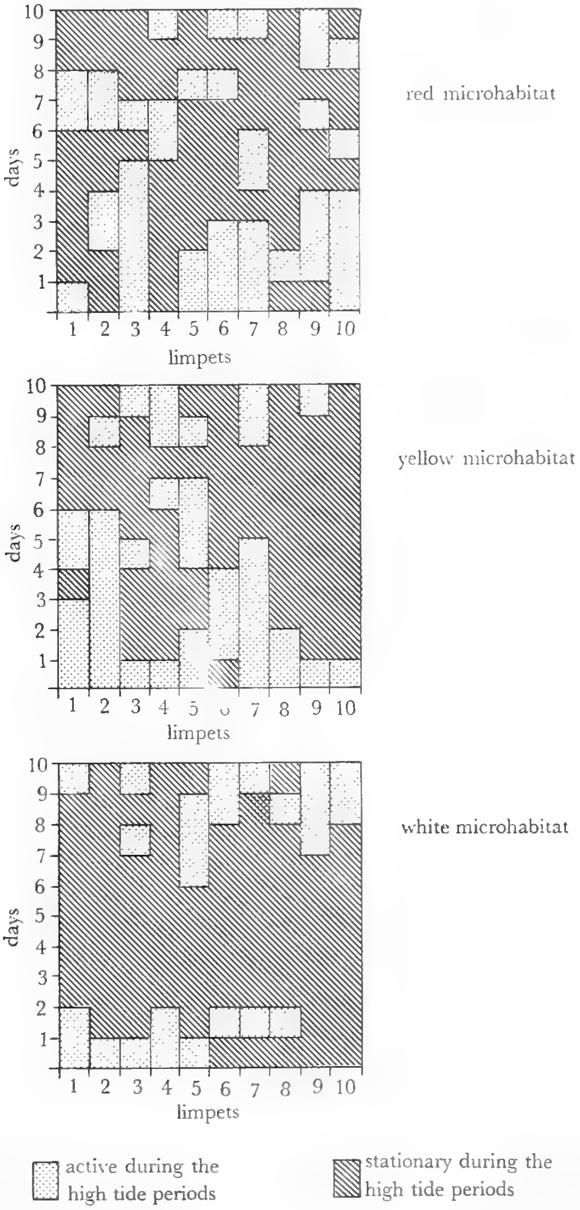


Figure 3

A 10-day observation of the movement and resting behavior of 30 marked individuals of *Acmaea digitalis* illustrated in consecutive days within 3 studied microhabitats selves, they would either benefit from improved locations, or they moved to make contact with other individuals or groups of limpets. The question of contact will be considered later.

Villee & Groody (1940) reported that *Acmaea digitalis* as a group demonstrated high rates of replacement. They interpreted this phenomenon as when one animal moved out, another moved in to take its place. Although a number of specific cases could be cited of this phenomenon, one prime example took place on the 9th and 10th days of the study. Two limpets, marked number 9 and number 10 from the white microhabitat had been resting in relatively the same cluster orientation and position for 8 consecutive days. Number 10 rested in a solitary position on the edge of the cluster 10 cm above number 9, which was in contact with 3 other *A. digitalis*. Each limpet was tethered to verify movement or rotational change. On August 13, number 9 moved up and into exactly the same position of number 10's resting site. Number 10 moved into the center of the cluster and made contact with one other limpet. The following day number 10 returned to exactly the same location and orientation as of August 13. Limpet number 9 returned approximately to the position held initially and made contact with 2 other members of the cluster. It appears that limpet number 10 had left its scar after an extended resting period, and upon returning had found its scar occupied by another member of the cluster.

The permanency of cluster membership was the next behavioral characteristic to be considered. Figure 4 focuses attention on the residual makeup of the clusters. Approximately 20% of the marked limpets from a specific microhabitat returned to their original cluster site where first observed. The figure correlates favorably with my findings of the initial study at the same location in August, 1970. During that investigation 47 limpets were marked, 15 of which were for the individual tracking. Of that number, 25% of the marked limpets returned to the original microhabitat.

The cluster membership remained remarkably stable during the course of the investigation. Even though there was a consistent turnover with new members, and regrouping of some old members on a daily basis, the number in each cluster remained essentially about the same.

Table 1 primarily reflects contact data, but also illustrates a stability in membership from one day to the next. This phenomenon is of interest, for I never found all the available space within each of the 3 sites fully occupied on any one resting period.

The second question of this study concerns the orientation taken by these gastropods as they seek shelter among the folds and crevices of the intertidal rocks. Table 2 accounts for the observations of 411 individual limpet orientations during an 11-day period. Only the clusters within designated microhabitats were used. As previously indicated, *Acmaea digitalis* prefer vertical rock surfaces, but will position themselves on the horizontal plane if so situated on the vertical surface. No one quadrant of the compass suggests a preferred position; however, in analyzing the data there was a slight tendency of the animals to orient with their anterior ends downward as opposed to the anterior ends pointing upward. Rock topography and point of contact with other limpets seemed to account for many of the positions taken. For example, Table 2

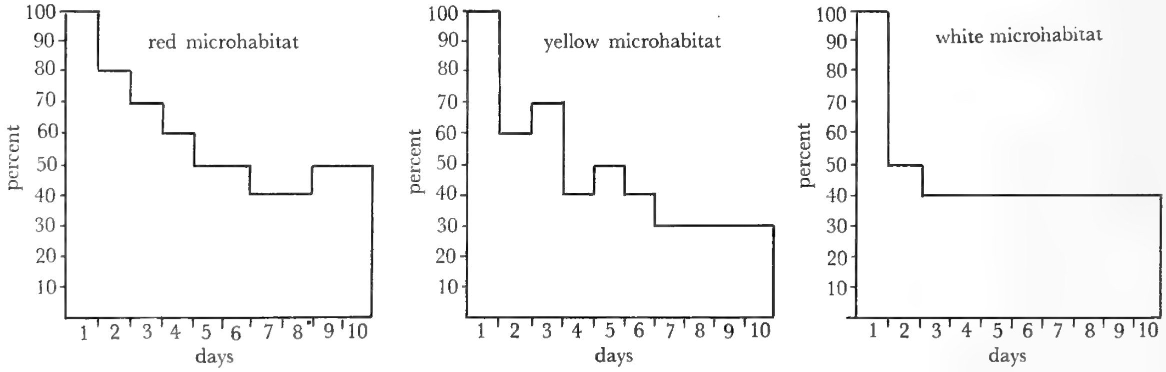


Figure 4

Observations of 30 marked limpets that returned to or remained in designated microhabitats, expressed in percent, August 4 to 14, 1971

Table 1

Frequency and percent of all resting *Acmaea digitalis* observed having contact with one or more limpets within the three studied microhabitats, and marked *Acmaea digitalis* observed in contact with other limpets outside the three studied microhabitats. Observations also include those *Acmaea digitalis* resting without contact both inside and outside of the studied microhabitats. N = 573

Date	number of limpets in contact within 3 studied microhabitats	number of limpets not in contact within 3 studied microhabitats	number of marked limpets in contact outside of 3 studied microhabitats	number of marked limpets not in contact outside of 3 studied microhabitats
August 4	30	4	–	–
August 5	34	5	–	–
August 6	38	2	12	1
August 7	34	6	11	5
August 8	37	4	11	5
August 9	32	7	13	4
August 10	34	6	14	4
August 11	30	9	13	4
August 12	36	3	12	4
August 13	34	7	10	4
August 14	27	11	10	6
Mean	33.3	5.8	11.7	4.1
Percent	85.1	14.9	74.2	25.8

reveals that in the white microhabitat a significant percentage of animals oriented with their anterior ends in the 270° - 360° quadrant. This may be attributed to the fact that the particular microhabitat had a wide, flat angle in its lower right hand quarter. Limpets which were foraging below the cluster found easy access in returning, as opposed to the steeper slope above and to the left hand margins of the cluster site. Their movements apparently ended within the group when contact was made with the shell of a resting limpet.

One observation during a receding high tide noted that one limpet while joining the cluster made contact with 2 *Acmaea digitalis* and one *A. scabra,* resting at the edge of the cluster. When these 3 resting limpets were stimulated by the movements of the incoming one, they rotated and shifted their positions slightly to allow it room to position itself.

An obvious phenomenon of this species is its contact behavior; however, as previously indicated, no prior studies have been found. All of the cluster constituents as well as the marked members outside the clusters were observed for contact. Table 1 reports 573 observations of contact with members of the same species. Approximately 85% of those limpets studied within the microhabitat were in contact with one or more other limpets, while approximately 74% were in contact with other limpets outside the 3 specified microhabitats. Again, it is believed that rock topography somewhat influences contact.

Table 2

Orientation frequencies (expressed in percent) of limpets found in quadrants within three studied microhabitats. Orientation position is determined by the degrees to which the limpet's anterior end is pointing

	Yellow Microhabitat					Red Microhabitat					White Microhabitat				
Date	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane [1]
August 4	0	3	4	4	2	1	0	1	2	6	5	1	2	3	–
August 5	3	3	1	0	1	1	3	3	1	6	0	0	6	2	–
August 6	0	4	2	0	3	1	3	6	2	5	4	0	1	4	–
August 7	0	4	4	0	4	2	2	5	1	6	2	2	4	4	–
August 8	2	3	2	3	3	3	4	3	0	7	3	1	4	4	–
August 9	0	3	3	1	3	2	5	3	1	4	3	1	4	4	–
August 10	2	3	0	0	4	0	3	5	3	6	2	4	4	2	–
August 11	0	4	1	1	3	2	3	8	0	5	3	2	3	5	–
August 12	1	3	1	1	4	0	5	4	1	6	0	1	4	7	–
August 13	1	3	0	0	4	2	5	5	1	7	1	2	3	6	–
August 14	1	2	2	0	5	0	4	5	0	6	0	5	3	4	–
Total	10	35	20	10	36	14	37	48	12	64	23	19	38	45	–
Percent	9	31.8	18.4	9	32.6	8	21.2	27.4	6.8	36.5	18.4	15.2	30.4	36	–

°s refer to a vertical plane

[1] no horizontal plane existed in this microhabitat

The latter mentioned percent occurred with marked members outside of the designated cluster sites. Many of these limpets rested in the upper highly fractured areas of the studied habitat providing solitary or at best few suitable resting sites for multiple contacts. Limpets within the cluster sites occurring along the smooth rock surface clearly demonstrated the highest contact phenomenon. In analyzing detailed field sketches of limpet orientation with reference to contact, no one specific part of an animal or its shell appeared to be predominantly in contact with the shells or bodies of other limpets. Mantle as well as shell contact apparently can be made in any orientation position.

In order to further explore this tactile phenomenon, dummy clusters were placed in previously occupied cluster sites. There were no instances where limpets made contact with either of the 2 pseudoclusters. Three limpets did rest within 7 cm of the dummy cluster, but at no time did they make contact.

The last aspect of behavior I considered was that of periodicity. It has been generally assumed that limpets forage daily when covered by the high tide and rest during the low tidal periods. Figure 5 shows the activity periods of *Acmaea digitalis* for a 10 day period. In all 3 clusters the limpets' total days of rest exceeded their total days of movement. The mean resting time for all members studied was 6.3 days, while the mean movement time was 3½ days. The maximum time at rest for any one individual was 9 days, and the longest time of activity during periods of high tide for one individual was 7 days.

Figure 3 demonstrates in consecutive days that in most instances the resting period extends beyond one day. There is also evidence that once the activity period is initiated, it continues uninterrupted during the high tides for an unpredictable length of time. Although there is a general cyclic pattern of rest and movement existing in the population, no one individual showed any synchronized behavior with its neighbors.

A hypothesis that there was no significant difference between the means of the 2 small samples was temporarily assumed. A "t test" of significance was applied to the data summarized in Figure 5 concerning members of the

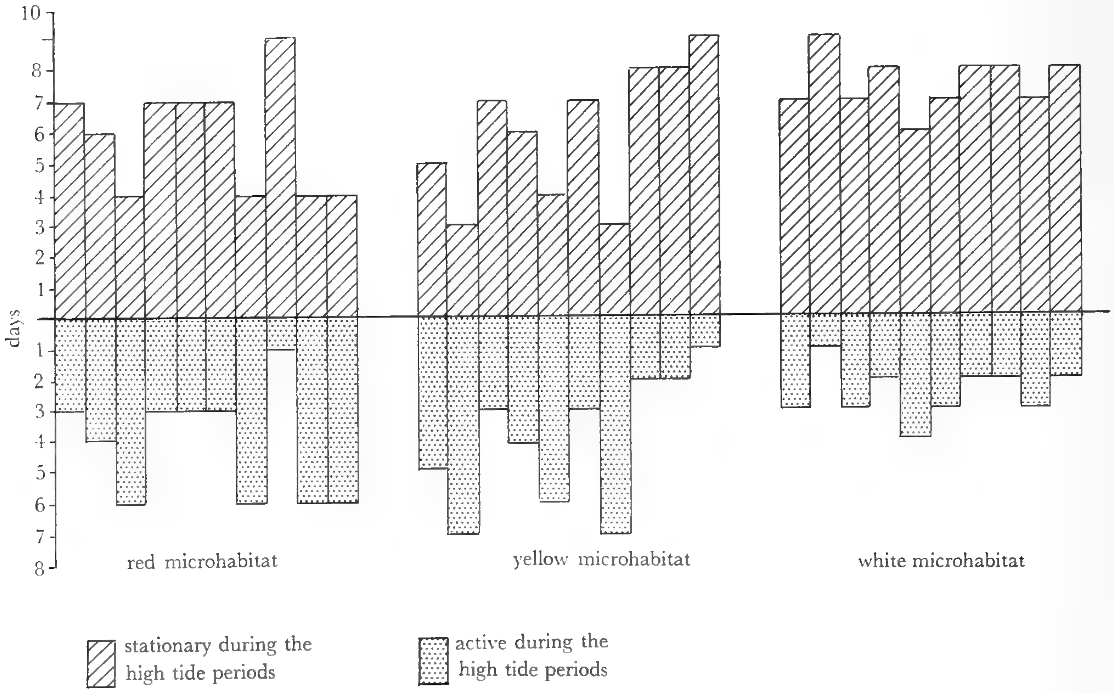


Figure 5

A 10-day study of the movement and resting behavior of 30 marked individuals of *Acmaea digitalis* within 3 studied microhabitats yellow and white clusters. A "t" value was determined to be 0.73. This value was above the 0.01 confidence level which allowed the observer to accept the hypothesis. It is therefore concluded that the difference is not statistically significant.

DISCUSSION

Data presented in this paper as well as other works on *Acmaea digitalis* document the fact that this species possesses some unique behavioral characteristics. Residing in the high intertidal zone, as the animals do, requires adaptations to prolonged dry periods and long hours of exposure. As a result, their clustering in the more protected or sheltered areas seems to be a well established and logical adaptive mechanism.

One of the questions raised here is whether this clustering behavior is a random occurrence or the result of an innate biological process. Neither this work nor others have clearly answered this question. However, some of the evidence shows that *Acmaea digitalis* does not haphazardly disperse in the upper part of the littoral zone.

It has been reported in at least 4 independent studies that *Acmaea digitalis* is not the consistent homer as is its cohabitant *A. scabra,* but does home approximately 25% of the time. This was substantiated by Miller (1968). In fact, Galbraith (1965) documents his homing evidence at 54%. It is evident that invariably a large portion of the membership does continually turn over, but there is a residual number that remains or returns, and it is this fact that establishes a stability factor in the cluster.

Not only is there some degree of stability in the group membership, but habitat areas are believed to contain rather permanent populations. Frank (1964), gathering his data on the home range of these limpets, concluded that *Acmaea digitalis* have the ability to somehow recognize the area which they inhabit. There was also some indication of home range in the present investigation. In accumulating the data it was noticed that out of 47 marked individuals used in the August, 1970 project, approximately 23% were only a few feet away from their original positions one year later. Probably a much higher percent would have been credited; however, the paint used in marking had been abraded during the intervening months.

From the observations made over the 2 summers' work, it is concluded that limpets do not randomly move great distances, but appear to stay within the confines of one specific localized habitat. Showing variations in their behavior, some demonstrate preference for one particular site, while others are apt to change clusters more readily.

There is also great variation in the orientation of this particular species. Data in this report show a slight tendency of the animals to orient themselves with their anterior ends downward. However, on the basis of these findings alone, it would be difficult to corroborate the information on the physiological conditions in *Lottia gigantea* influencing their downward and to the right position.

Test (1945) commented that limpets often orient themselves with the sloping part of their shells directed to break and lessen the force of the waves. A study of detailed drawings made during these field observations does not support this position either. From the data presented previously, it is believed that rock topography and the opportunity to make contact with other limpets of their own species are the important influences on orientation position.

This contact with others appears to be a very definite part of their resting behavior. In the light of their avoiding contact with inanimate objects, such as plaster in shells, it may be very possible that a chemical or tactile mechanism also influences their orientation and position within the cluster during the resting period. Even though contact appears to be a demonstrable part of their behavior, the full significance requires further investigation.

The factor of periodicity within a given time correlated with the daily tidal cycle; however, this study revealed no other circadial or longer rhythmic occurrences. There appears to be a strong tendency, which is not synchronized, towards longer resting intervals than activity periods. Only part of a cluster population responds to the tidal stimuli, while others remain at rest and seem oblivious to the tidal cycle. This fact might account for reducing the intra-species competition in grazing areas within a specific habitat.

The marked animals did not appear to be estivating, for all 30 individuals moved or shifted their position within the clusters during the 11 days of observation. Breen (1971) suggests that limpets are less active in their movements during the summer months when the danger of desiccation is greatest. An extended investigation on dormancy is necessary to ascertain if there are any seasonal periods of hibernation or estivation occurring within this species.

SUMMARY

1, While resting, *Acmaea digitalis* displays a clustering behavior which is characteristic of this species of limpets. There is evidence that this clustering phenomenon is not solely a random occurrence, but rather one that displays a certain degree of permanency and stability. Limpets

showed variations in their behavior with approximately 20% to 25% demonstrating preference for one cluster site, while others frequently changed their positions from one day to the next.

2, The limpets observed during their inactive periods at low tide showed a slightly higher tendency to point their anterior ends downward as compared to other orientation positions. It is believed that the topographical features of the rock forming the cluster site as well as the ability of these limpets to make contact with other members of their species are both highly significant in determining their resting position.

3, In addition to orientation, *Acmaea digitalis* also demonstrates a phenomenon of contact with other members during their inactive or resting periods. A recognition sense, either chemical or tactile, appears to influence this behavior.

4, Periodicity within this group is correlated with the tidal cycle. Limpets in general move when partly submerged by the high tide and remain inactive during low water. Although this is generally true for the entire population, many individuals differ. In the duration of this study, limpets rested for longer periods than they were active. Only part of the population responded to the stimulus of high tide while others rested days without showing any evidence of moving.

5, Although resting periods were of greater duration than activity periods, there was no synchronization of resting or movement behavior of the limpets in any one of 3 studied clusters.

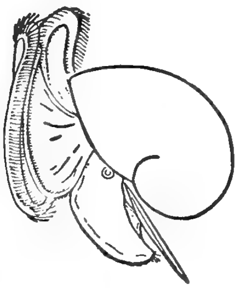
6, Some evidence was found that indicates limpet populations live from year to year in one specific habitat, and do not move randomly or continuously into new territories.

ACKNOWLEDGMENTS

The author wishes to thank Dr. Vida C. Kenk and Dr. John Ackermann for their technical advice and encouragement in undertaking this study. My sincerest appreciation is also given to the Natural Science staff of California State University, San Jose, especially Dr. Robert Hassur, for their assistance and suggestions in completing this project.

Literature Cited

Abbott, Donald Putnam
1956. Water circulation in the mantle cavity of the owl limpet *Lottia gigantea* Gray. The Nautilus **69** (3): 79 - 87; 1 fig.
Breen, Paul A.
1971. Homing behavior and population regulation in the limpet *Acmaea (Collisella) digitalis.* The Veliger **14** (2): 177 - 183; 10 tables (1 October 1971)
Frank, Peter Wolfgang
1964. On home range of limpets. Amer. Natural. **98** (899): 99 - 104
Galbraith, Robert T.
1965. Homing behavior in the limpets *Acmaea digitalis* and *Lottia gigantea.* Amer. Midld. Natural. **74** (1): 245 - 246
Haven, Stoner Blackman
1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in Central California. The Veliger **13** (3): 231 - 248; 10 text figs. (1 January 1971)
Millard, Carol Spencer
1968. The clustering behavior of *Acmaea digitalis.* The Veliger **11** (Supplement): 45 - 51; 4 text figs.; 1 table (15 July 1968)
Miller, Alan Charles
1968. Orientation and movement of the limpet *Acmaea digitalis* on vertical rock surfaces. The Veliger **11** (Supplement): 30 - 44; 18 text figs.; 4 tables (15 July 1968)
Sutherland, John Patrick
1970. Dynamics of high and low populations of the limpet *Acmaea scabra* Gould. Ecol. Monogr. **40** (2): 169 - 188
Test, Avery Ransome
1945. Ecology of California *Acmaea.* Ecology **26** (4): 395 - 405
Villee, Claude Alvin & Thomas Conrad Groody
1940. The behavior of limpets with reference to their homing instinct. Amer. Midld. Natural. **24** (1): 190 - 204; 25 figs.; 3 tables



Description of a New Species of the Genus *Latiaxis* Swainson, 1840 from the South Mozambique Channel, Indian Ocean

(Gastropoda : Coralliophilidae)

BY

MASAO AZUMA

1-42, Kamiyoshihara, Nishinomiya, Hyogo, Japan

(1 Text figure)

Recently, through the courtesy of Mrs. Helene Boswell of Valhalla, Transvaal, South Africa, I have had the opportunity to examine some specimens of the genus *Latiaxis* Swainson, 1840 which were trawled from the southern Mozambique Channel, Indian Ocean. A new species was amongst these specimens and is described as follows:

Latiaxis (Babelomurex) ***helenae*** Azuma, spec. nov.

Shell large for the genus *Latiaxis;* a fine crown shape at the lateral aspect of the shoulder keel for each whorl; solid, dirty white, with no gloss; spire very high; protoconch 2 whorls, very minute, dirty white; connected younger 5 whorls slightly expanded, with rather sharp shoulder keel and few spiral striations; penultimate whorl very large, abruptly expanded with strongly triangular shoulder keel; suture very deep; between suture to shoulder of each whorl no spiral striations; body whorl very large, with very strong shoulder keel with about 20 fin-shaped spines, about 25 spiral striae in all, and about 20 longitudinal ribs as nodules; aperture semicircular to ovate in form, outer lip glossy, thickened and strongly rising into the shoulder keel; siphonal canal widely, parallel, curved backward; operculum light brown, rather thin, semi-circular with a nucleus situated in the centre of the outer side; umbilicus very wide and large, and the front spread rather strong and widely curved backwards, and with about 20 weak keels on the fasciole; callus narrow, glossy, and curved inwardly.

Holotype: Length 65 mm; width 42 mm; 9 whorls. Azuma Coll. No. 15944

Paratype 1: Length 73 mm; width 43 mm; 9 whorls. Helene Boswell Coll.

Paratype 2: Length 65 mm; width 43 mm; 9 whorls. Helene Boswell Coll.

Type Locality: 50 miles E of Inhaea Island, South Mozambique Channel, trawled in approximately 270 fathoms depth.

Remarks: This is a very rare species with only a few known specimens as yet. The conchological features of this new species show that it is closely related to *Latiaxis (Babelomurex) kawamurai* Kira, 1959, but it differs as follows: shell surface has no scale-like spiral striations; last whorl very large; umbilicus wide and largely open.

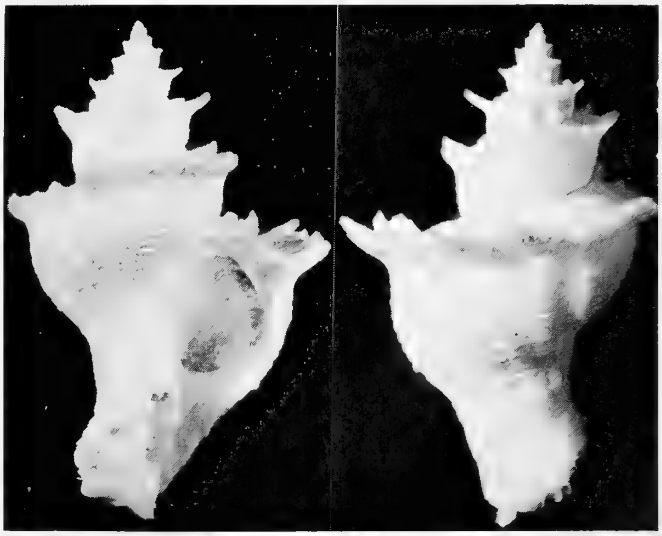


Figure 1

Latiaxis (Babelomurex) ***helenae*** Azuma, spec. nov. Dorsal and ventral aspects of the holotype

Additional Notes on Some Pacific Coast Mollusca - Geographical, Ecological, and Chronological

BY

ROBERT R. TALMADGE[1]

2850 Pine Street, Eureka, California 95501

For many years, most California malacologists, myself included, have assumed that the offshore benthic marine fauna of northern California was an extension of more northern faunas which were inhabiting suitable biomes in more southern latitudes. Such biomes would be characterized by a substratum normal to the species, plus a compatible isotherm in which the temperature requirements of the species would be met. During the past few years the local dragboat fishermen operating out of Humboldt Bay on the extreme northern California coast have brought in specimen material which appears to contradict this theory, as a number of species belong to what we have assumed to be southern faunas.

Based upon local fossiliferous deposits, it now appears that in many cases these northern and southern additions to our distributional records are not Recent, but in some cases the species can be traced in chronological order from Middle Pliocene to Recent.

I present these records in the hope that they will stimulate interest in the offshore benthic marine invertebrates, as not only the distribution, but the ecology and taxonomy of many are, to say the least, imperfectly known.

The project area is based upon the fishing regions of the local dragboat fleet, and extends from the submerged Noyo Canyon off Fort Bragg, Mendocino County, California north to off Mack Arch, Curry County, Oregon (lat. 39°30′N to 42°15′N). This region includes the major portion of the Pliocene Wildcat Group of Ogle, including the Centerville Sea Cliffs, and the Moonstone Beach Site as well as the Upper Pleistocene Crannell Site, which allows a comparison of the species found both as Recent material in dredgings and as fossil specimens.

AMPHINEURA

The nets of the dragboats skim over the seabed gathering in not only fish but also specimens of marine invertebrates, historical items, and geological specimens. Among these is a specialized rock type, a calciferous mudstone, pitted with holes and crevices, and extremely dense and heavy. I have never seen a similar rock on shore or even in one of our local fossil deposits. Most of this rock is obtained from between 200 and 400 fathoms (360 and 720 m) in depth; from this rock I have obtained 3 small chitons. These were found hidden amid the cavities, and represent one northern species and two that previously had been considered to belong to a southern fauna.

Ischnochiton abyssicola Smith & Cowan, 1966

Several small specimens of this benthic species have been found living on rock at depths which ranged from 240 to 400 fathoms (432 - 720 m). All of these were taken from off Trinidad, California (lat. 41°05′N). There was no noticeable difference in either the valves or the girdle between these specimens and a series of specimens from more northern waters in the collections of the California Academy of Sciences.

Ischnochiton golischi Berry, 1919

Four specimens were obtained by the *Flicker* in 1967, taken on a massive piece of pitted rock, dredged from 200 fathoms (360 m) near the submerged Eel Canyon (lat. 40°26′N). Berry's type locality is off Santa Monica, California in 100 fathoms (180 m), but Smith & Gordon (1948) reported the species from the deep intertidal levels down to 80 fathoms (144 m) at Monterey, California.

Ischnochiton cf. *I. stearnsii* Dall, 1902

A single specimen, matching in nearly all details *Ischnochiton stearnsii* Dall, 1902, was taken in 360 fathoms (648 m) off Trinidad, California (lat. 41°05′N) by the *Mineo Brothers*. The specimen was tentatively identified as this species; Mr. Allyn G. Smith concurred in this tentative identification. The slight variations from Dall's species may be due to age, geographical locality, or perhaps even to a different ecological situation. As far as I can

---

[1] Field Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118

determine, the variability of this little known chiton has never been worked out due to a lack of suitable material.

GASTROPODA

Epitonium indianorum (Carpenter, 1865)

Although the data on this species from within the project area do not add to the knowledge of the geographical distribution, the notes indicate an addition to the known benthic record, and some interesting information on the species in time within the same area. Specimens have reached me which have been taken from as deep as 150 fathoms (270 m) from numerous localities within the project area, usually from a sandy mud bottom. Fossil specimens from the Crannell Junction Site, Upper Pleistocene, match in all details the shells of the local intertidal specimens as well as the benthic material of this species. However, in the extreme Upper Pliocene at Moonstone Beach the species changes somewhat in the whorls and in the Middle to Lower Pliocene, Rio Dell Formations, the species is quite changed, but still closer to *Epitonium indianorum* than to any other species. At the present time the information is inconclusive as to whether the erection of a separate species or subspecies is warranted; only additional material will permit a decision whether the differences in physical characteristics are sufficient to justify a new taxon.

Crepipatella charabdis (Berry, 1940)

Berry's material was taken in the fossiliferous Palos Verdes Sands, but locally the species is found only as a Recent species. Specimens have been obtained from pits and crevices of rocks brought up from between 100 and 200 fathoms (180 to 360 m). Most specimens are small, under 10 mm in diameter, but a few are up to 20 mm in diameter. One shell, taken off the shell of a *Neptunea smirnia* (Dall, 1919) presents a problem, as it has the basic shape of *Crepipatella orbiculata* (Dall, 1919), rounded, inflated, and highly arched, but with the coarse ribbing of *C. charabdis*. Dr. James H. McLean (personal communication) considers this one specimen to be a pathological example of *C. orbiculata,* which locally is taken on the shells of the great white whelk, *Neptunea pribiloffensis humboldtiana* A. G. Smith, 1971.

Capulus californicus Dall, 1900

I have in my collection 3 specimens of this species, all taken as commensals on the large *Pecten (Patinopecten) caurinus* Gould, 1850. All were obtained in the vicinity of Trinidad, California (lat. 41°05′N), and in less than 100 fathoms (180 m), usually from a generalized sandy to sandy mud bottom, the normal habitat of this large scallop. *Capulus* have been known from this region to some malacologists prior to 1949, based upon specimens from both the Ferguson and the Talmadge collections, but this information had never been presented for publication. Although not common, the data indicate that the species is not too rare in these latitudes.

Megasurcula carpenteriana (Gabb, 1865)

Recent specimens of this species, taken off northern California, have been examined at the California Academy of Sciences; I have 2 in my collection from off Eureka, California, from a sandy bottom at a depth of 100 - 150 fathoms (180 - 270 m) (lat. 40°45′N). Mr. Roy Kohl, Technician for the Department of Geology, Humboldt State College, Arcata, California, has some specimens from the Lower Pleistocene, Crannell Junction Site, and WEAVER (1942, 1945) lists the species in the Pliocene Wildcat Formation of Oregon. I have not found the species in the Wildcat Formations of this area. It is quite possible, even probable, that in due time Recent specimens of this species will be found along either the Oregon or Washington coasts, or, perhaps both.

Trophonopsis dalli (Kobelt, 1878)

A soft mud seabed at a depth of about 200 fathoms (360 m) seems to be the obligatory habitat for this crenulated Trophon, which has been reported chiefly from northern waters. Most specimens have reached me from off the Centerville Sea Cliffs, near the submerged Eel Canyon (lat. 40°26′N) and from a depth of about 200 fathoms (360 m). There is a fossil Trophon in the Pliocene Centerville Sea Cliffs, which I cannot distinguish from the Recent specimens taken off this part of the coast. In 1964, Faustman used the name *Boreotrophon durhami* for the fossil species, and listed the range as in the Centerville Sea Cliffs and the Elk River Formations, at Cape Blanco, Oregon. Specimens of Recent *Trophonopsis dalli* were obtained from British Columbia waters for comparison with northern California material to see if there were any shell characteristics separating the more northern examples from the California material, and to double check the comparisons with the fossil material. I was unable to separate any of the material into other than a single species. With this information, I consider that *B. durhami* Faustman, 1964, is a synonym of *T. dalli* (Kobelt, 1878), and that the species has been present in northern California waters since Late Pliocene times up to the present.

ACKNOWLEDGMENTS

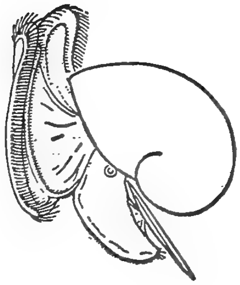
At this time I wish to express my appreciation to the crews of the dragboat fleet operating out of Humboldt Bay, whose assistance has made much of this project possible. The late Dr. Leo G. Hertlein, and Mr. Allyn G. Smith of the California Academy of Sciences in San Francisco gave me access to the collections under their care, as did Dr. A. Myra Keen of Stanford University, Stanford, California. Mr. Neil Russell of Victoria, British Columbia lent specimens of Trophons which had been collected in more northern waters. To each and all of these I express my thanks.

Literature Cited

Faustman, Walter F.
1964. Paleontology of the Wildcat group at Scotia and Centerville Beach, California. Univ. Calif. Publ. Geol. **41** (2): 97-160; plts. 1-3

Smith, Allyn Goodwin & MacKenzie Gordon, Jr.
1948. The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. Proc. Calif. Acad. Sci. (4) **24** (8): 147-245; plts. 3, 4; 4 text figs. (15 December 1948)

Weaver, Charles Edwin
1942. Paleontology of the marine Tertiary formations of Oregon and Washington. Univ. Washington Publ. Geol. Sci. **5** (1-3): vii-xiii + 789 pp.; plts. 1-104 [repr. Univ. Wash. 1958]
1945. Stratigraphy and paleontology of the Tertiary formations at Coos Bay, Oregon. Univ. Washington Publ. Geol. **6** (2): 31-62; maps



Polydora and Related Genera as Borers in Mollusk Shells and Other Calcareous Substrates

(Polychaeta : Spionidae)

BY

JAMES A. BLAKE

Pacific Marine Station, University of the Pacific, Dillon Beach, California 94929

AND

JOHN W. EVANS

Marine Sciences Research Laboratory, Memorial University of Newfoundland
St. John's, Newfoundland, Canada

(4 Text figures)

INTRODUCTION

THE BORING ACTIVITIES of worms in the shells of mollusks were first described by naturalists in the eighteenth century. As early as 1737, SWAMMERDAM noted that *Littorina* shells were eroded by small worms. In 1765, BASTER described a species of "Nereis" from shells of oysters and other mollusks. The genus of worm involved in these reports and others was named *Polydora* by Bosc in 1802. Bosc's species, named *Polydora cornuta,* became the type of the genus but was too poorly described to permit subsequent identification and today is indeterminable. *Leucodore* Johnston, 1838 is a synonymous name that was in common usage during much of the nineteenth century.

Three genera, *Polydora, Boccardia,* and *Pseudopolydora* are today recognized within the polydorid complex. Each genus contains species capable of boring and will be considered in the present paper.

Polydorids are polychaetous annelids of the family Spionidae. Genera of the polydorid complex are the only spionids capable of boring. The mechanism of this boring has been the subject of considerable speculation over the years. The boring activities of polydorids result in simple U-shaped burrows, complex branching burrows, shallow depressions, or mud-blisters. Mud-blisters are the result of the worm's boring activities, accumulation of silt and reaction of the bivalve to the worm.

Several species of *Polydora* are able to damage mollusk shells by their boring activities. Because of the economic implications of polydorid infestations in commercially important bivalves, several species of *Polydora* have received considerable study. Those species most often recorded from shells of bivalves are *Polydora ciliata* (Johnston, 1838), *P. hoplura* Claparède, 1870, and *P. websteri* Hartman, 1943. Other species from mollusks of no commercial importance have, on the other hand, received little attention. What records there are of such associations are widely scattered throughout a voluminous literature. Attempts to review this literature have generally dealt only with those species which penetrate commercially important bivalves. During the course of studies by the two of us on different aspects of *Polydora* biology, it became apparent that a published summary of this large literature would be useful.

It is the purpose of the present paper to summarize the known records of polydorids which penetrate calcareous substrates. Subsequent papers will deal with new investi-

---

[1] Contribution No. 31 from the Pacific Marine Station; Contribution No. 94 from the Marine Sciences Research Laboratory of the Memorial University of Newfoundland; and Contribution No. 288 from the Biology Department of the Memorial University of Newfoundland

gations currently in progress on burrow patterns, specificity of attack, infestation rates, larval development, and taxonomy of polydorids from various calcareous substrates.

MOLLUSCAN INFESTATIONS

Part A: Bivalvia

Several species of *Polydora* are known to damage the shells of bivalves. They are especially well known as pests of the oyster and scallop industry. For this reason the literature describing their associations is large and extends back more than a hundred years.

The harmful effects of *Polydora* on the host species vary with the intensity of infestation and the type of burrow formed. The burrow type, as reported by many authors, is constant under the specific conditions they describe. However, on a global basis, the form of the burrow appears to bear little relation to the species of *Polydora,* the species of the host, or even the geographical location.

Burrow Types

Three main types of *Polydora* burrows have been described on bivalve shells: 1) Surface fouling; 2) U-shaped burrows; 3) Mud-blisters.

Surface fouling occurs when *Polydora* settle on a surface but do not penetrate. The worms accumulate a thick layer of mud around themselves and over the surface of the substrate. The individual worms extend their burrows beyond this mat as 2 neat, round, mud-colored tubes. Through these tubes the head or pygidium emerge.

The European species, *Polydora ciliata,* is an important surface fouler both on subtidal harbor structures (Persoone, 1965) and on European oysters (Korringa, 1951). *Polydora ligni* Webster, 1879 causes surface fouling of some American east coast oyster beds (Mortensen & Galtsoff, 1944; Galtsoff, 1964).

U-shaped burrows penetrate the structure of the shell. These burrows have a distinctive form which makes them easily recognizable as the work of *Polydora.* This burrow has been illustrated and described by numerous workers,

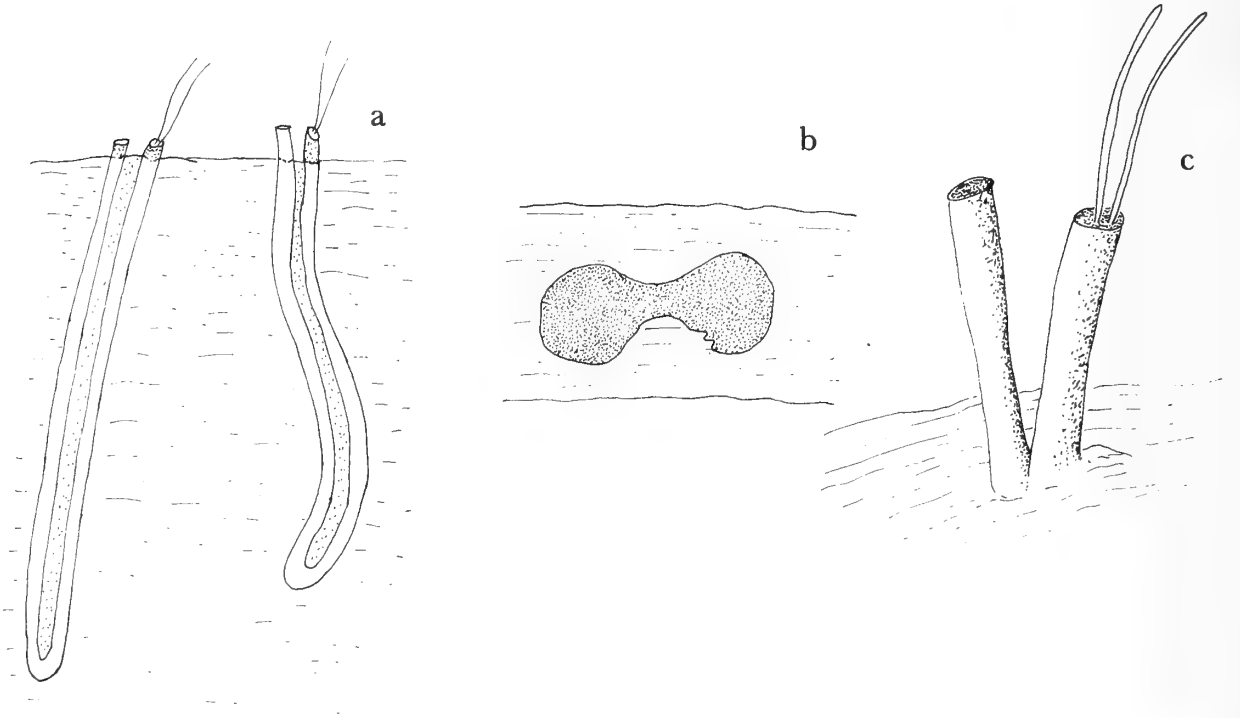


Figure 1

Basic structure of *Polydora burrow*
a: U-shaped burrow of *Polydora ciliata*
b: cross-section through burrow of *Polydora concharum* (after Evans, 1969)
c: external silty extensions of *Polydora* spp.

including Lamy & André, 1937; Davis, 1967; and Evans, 1969. It consists of an elongated U with the arms of the U being parallel and quite close together (Figure 1a). The worm lies rather loosely within the U. The space between arms is open but narrower, so that a cross section looks like a broad-centered figure 8 (Figure 1b). Most authors report that the burrow is a simple unbranched U, but Seilacher (1969) and Evans (*op. cit.*) describe burrows which branch repeatedly (Figure 3h). The ends of the burrow are extended by short mud-colored tubes which give the outside of the shell a hairy appearance.

Mud-blisters have been described by many authors, including Whitelegge (1890); Lunz (1941); and Korringa (1951). They are masses of mud accumulated on the inner surface of the shell by the recently settled *Polydora*. The host reacts first by secreting over the mud a roof of conchiolin and later a layer of nacreous material (Figure 2). The worms occupy the mud-filled chambers so formed and communicate with the exterior via pairs of tubes either at or close to the periphery of the shell. This is the most damaging effect of *Polydora* on bivalves.

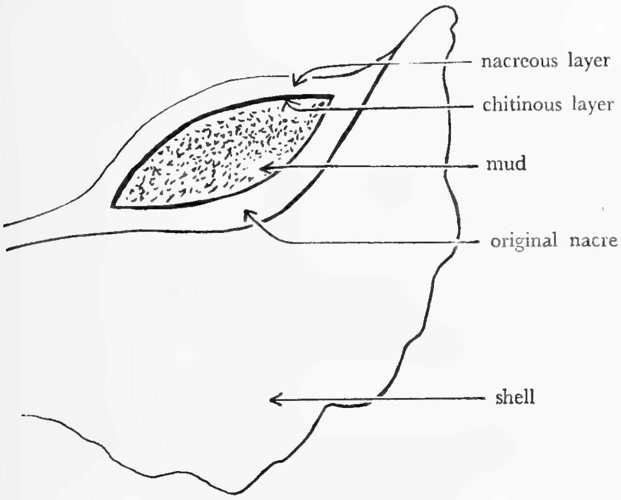


Figure 2

Diagrammatic section through shell of oyster and mud-blister (after Lunz, 1941)

Paleontological Occurrence

Both U-shaped burrows and mud-blisters are found in fossil shells.

The Treatise on Invertebrate Paleontology (Moore, 1962) described U-shaped boring tunnels, that look like *Polydora* burrows, called *Caulostrepsis* (Clarke, 1908) = *Polydorites* (Douville, 1908). These are found in shells of brachiopods, echinoids and mollusks from the Lower Devonian, Upper Triassic, and Tertiary.

Lunz (1941) reported mud-blisters in *Crassostrea virginica* (Gmelin, 1791) from Florida fossil beds, probably of the Pleistocene period.

Davis (1967) described the presence of the typical U-shaped "*Polydora*-type" burrows in the wedge clam, *Mesodesma arctatum* Conrad, 1830, from the Pleistocene in Maine.

Boekschoten (1967) reported the presence of *Polydora* burrows, both U-shaped and mud-blisters, in clam and oyster shells from the Tielrode Sands (Pliocene, Belgium). *Polydora* is found in *Cardium edule* Linnaeus, 1758 from the Wadden Sea (Boekschoten, 1966).

Cameron (1967; 1969) reported a Devonian fossil worm, *Vermiforafacta rollinsi* Cameron, 1967, which lived in a slightly curved, cylindrical burrow in the shell of a bivalve. He claimed that the worm resembled living members of the family Spionidae in form and habit. The circular cross section of this burrow, however, is quite unlike that of any known, living, shell-boring spionid.

Living *Polydora* and *Boccardia* that Form Associations with Bivalves

In European waters *Polydora ciliata* and *P. hoplura* are important pests of the oyster *Ostrea edulis* Linnaeus, 1758. There appears to be considerable disagreement in the literature concerning the tube-building behavior of these 2 species. Carazzi (1893) and Dollfus (1921) observed that *P. ciliata* formed mud-blisters in the oyster, the larva settling between the mantle and the edge of the shell. Dollfus also made the unlikely claim that *P. ciliata* occasionally bores cylindrical tunnels. Lamy & André (1937) and Korringa (1951) stated that *P. ciliata* forms U-shaped burrows. The latter author also observed that this species causes surface fouling.

Dollfus (1921) and Lamy & André (1937) claimed that *Polydora hoplura* forms U-shaped burrows in the oyster shell. The former author also claimed that this species forms mud-blisters by penetrating through the shell.

Korringa (1951) strongly presented the idea that *Polydora hoplura* and *P. ciliata* differ primarily on a behavioral basis in that *P. hoplura* only forms mud-blisters while *P. ciliata* only forms surface mats of U-shaped tunnels. He even extends this generalization to "biologically related" North American (*P. websteri*) and Australian (*P. ciliata*) mud-blister forming polydorids and suggests that these forms are actually more closely related to *P. hoplura*.

Table 1

Host, Geographical Location, and Burrow Type of *Polydora websteri*

Author and date	Host species	Burrow Type	Geographical Area
Kavanagh, 1940	*Crassostrea gigas*	mud-blister	Gulf of Mexico
Lunz, 1940, 1941	*Crassostrea virginica*	mud-blister	South Carolina
Needler, 1941	*Crassostrea virginica*	mud-blister	eastern Canada
Loosanoff & Engle, 1943 (includes Hartman's original description)	*Crassostrea virginica*	mud-blister	New England
Hartman, 1945	*Crassostrea virginica*	mud-blister	North Carolina
Frey, 1946	*Crassostrea virginica*	mud-blister	Potomac River
Medcof, 1946	*Crassostrea virginica*	mud-blister	eastern Canada
Hartman, 1951	"mollusc shells"	U-shaped tubes with mud blisters	Gulf of Mexico
Mackin & Cauthron, 1952	*Crassostrea virginica*	mud blister (?)	Gulf of Mexico
Owen, 1957	*Crassostrea virginica*	U-shaped tubes which may become mud blisters	
Hopkins, 1958	*Crassostrea virginica*	U-shaped tubes with mud blisters	Gulf of Mexico
Turner & Hanks, 1959	*Pecten irradians*	mud-blister	New England
Hartman, 1961	*Ostrea lurida* & *Patinopecten caurinus*	U-shaped burrows and mud blisters	California and Oregon coasts
Wells & Wells, 1962; Wells *et al.*, 1964	*Aequipecten gibbus*	mud-blister	North Carolina
Galtsoff, 1964	*Crassostrea virginica*	mud-blister	New England
Hartman, 1966	*Crassostrea virginica*	?	Hawaii
Davis, 1967	*Mesodesma deauratum*	U-shaped burrows	Gulf of St. Lawrence
Forbes, 1966	*Ostrea permollis*	mud-blister	Florida-Gulf of Mexico
Landers, 1967	*Mercenaria mercenaria*	mud-blister	New England
Blake, 1969a, b; 1971	*Placopecten magellanicus*	U-shaped burrow	Maine
Evans, 1969	*Placopecten magellanicus*	U-shaped burrow	Newfoundland
unpublished	*Mytilus edulis*	U-shaped burrow	Newfoundland
unpublished	*Modiolus modiolus*	U-shaped burrow	Newfoundland
unpublished	*Hinnites multirugosus*	U-shaped burrow	British Columbia

Whitelegge (1890) and Roughley (1922) described attacks of the mud worm *Polydora ciliata* on the Australian oyster *Ostrea cucullata.* In this area *P. ciliata* forms large and numerous mud-blisters which often lead to the death of the oyster.

In North American waters *Polydora websteri* is the most important pest species. This species is very similar to *P. ciliata* and prior to Hartman's (1943) description and renaming it was known by that name. Table 1 summarizes the host invaded, types of burrows formed and geographical location of *P. websteri* attacks. It will be noted that in all cases except *Mercenaria mercenaria* (Linnaeus, 1758) the bivalves attacked are surface dwelling or very shallow burrowing forms. The young *M. mercenaria* described by Landers (1967) were attacked because they were unable to burrow into soft substrate. In 1969, the second author collected large dead *M. mercenaria* on a beach near Redbank, New Jersey. These shells were bored by typical U-shaped *Polydora* burrows similar to those formed by *P. websteri* in *Placopecten magellanicus* (Gmelin, 1791) (Evans, 1969). These borings were probably made after the death of the clam when the shells were lying on the surface of the sand.

Polydora websteri infestations of *Crassostrea virginica, C. gigas* Thunberg, 1793, *Pecten irradians* Lamarck, 1819, *Aequipecten gibbus* Linnaeus, 1758, and young laboratory-reared *Mercenaria mercenaria* all cause the formation of mud-blisters. On the other hand, infestations of *Ostrea lurida* Carpenter, 1863 and *Patinopecten caurinus* (Gould, 1850) from the Pacific coast, of *Mesodesma deauratum* Turton, 1830 and *Placopecten magellanicus* from the Gulf of St. Lawrence and Newfoundland caused the formation of U-shaped burrows.

These observations would tend to contradict Korringa's concept of "biologically distinct" species in that *Polydora* *websteri* under different circumstances, does form 2 types of burrows.

Polydora ligni occurs on the Atlantic and Pacific coasts of North America. Usually it is free-living in mud (Galtsoff, 1964) or waterlogged wood (Hartman, 1945). However, it sometimes forms surface mats on oysters.

Nelson & Stauber (1940) reported that a worm tentatively identified as *Polydora ligni* occupied mud-blisters in the shells of oysters in Delaware Bay. There have never been any subsequent observations of *P. ligni* in mud-blisters so it is assumed that this was an erroneous identification; it was more likely *P. websteri*.

Polydora concharum Verrill, 1880, appears to have been very little discussed in the literature from a biological standpoint. Verrill (1880: 176) described it as "very common all along the coast from Cape Cod to Nova Scotia in 10 to 100 fathoms, in tortuous narrow galleries excavated in shells especially of *Cyprina islandica*." No figures of these burrows were included in his description.

Evans (1969) describes and illustrates the burrows of *Polydora concharum* in the shells of the sea scallop *Placopecten magellanicus* (Figure 3h). Blake (1969a; 1969b; 1971) described the adults and larvae of *P. concharum*. He noted that the species occurs commonly in shells of living *Placopecten magellanicus* and dead shells of *Mercenaria mercenaria* in Maine waters.

Verrill (1880) described a new species, *Polydora gracilis* as living gregariously in shells of *Placopecten magellanicus*. However, he did not describe the burrow type. Blake (1969a) considers that *P. gracilis* may be a synonym of *P. socialis* (Schmarda, 1861). The latter species was reported by Blake (1969a; 1969b; 1971) as being a common borer in shells of living *Placopecten magellanicus* and old dead *Mercenaria mercenaria* in the Damariscotta Estuary of Maine. In a larval study, Blake (1969b) noted that *P. socialis* larvae metamorphose on both shell and sediment. Juveniles bore into a shell, excavate a burrow and commence gathering silt from the water and construct a silty tube which projects from the burrow. The burrows themselves have a tough mucoid lining.

Boccardia hamata (Webster, 1879) (formerly placed within the genus *Polydora*) was reported from bivalve shells by Webster (1879a; 1879b) from New Jersey and Virginia. Hartman (1951) and Hopkins (1958) reported the species from oyster shells from the Gulf of Mexico. Rioja (1960) reported *B. hamata* from the Lagoon of Mandina (eastern Mexico) from bivalve shells. Blake (1966) redescribed the adults and reviewed the literature of the species while Dean & Blake (1966) described the larval development on the east and west coasts of North America.

Pillai (1965) described *Polydora cavitensis* from oysters in the Philippines, but did not discuss the ecology of that species.

Blake & Woodwick (1971, 1972) describe 3 new polydorids, *Boccardia berkeleyorum, Polydora convexa,* and *P. elegantissima* from California bivalve mollusks. *Boccardia berkeleyorum* and *P. convexa* inhabit shells of *Pododesmus macroschisma* (Deshayes, 1839). They note that *P. convexa* forms branched burrows similar to those of *P. concharum* as reported by Evans from *Placopecten* shells. *Polydora elegantissima* occurs in shells of *Tivela stultorum* (Mawe, 1823)

Methods of Attack by Mud-Blister Forming Polydorids

The information available concerning the route of invasion followed by the mud-blister forming polydorids is contradictory (Table 2). A number of authors claimed that the larva swims into the mantle cavity or burrows between the mantle and shell where it begins to accumulate mud. The presence of the burrows away from the periphery is explained by the subsequent growth of the bivalve shell. Others observed that the larva settles on the outside of the shell, penetrates to the mantle and there forms the mud blister. It seems possible that both routes of attack could, under different circumstances, be followed.

Part B: Gastropoda

Polydorids are common inhabitants of gastropod shells. In particular, shells occupied by hermit crabs seem to offer a suitable habitat. In contrast to the extensive studies of polydorid infestations in bivalves, there has been little investigation of the heavy infestation often seen in this habitat. Little information is available on infestation by polydorids in shells of abalone (*Haliotis* spp.). Day (1967) mentions that *Haliotis midae* from South Africa is heavily infested with *Polydora*. In California, Hansen (1970) found that 11% of *H. rufescens* Swainson, 1822 and 12% of *H. cracherodii* Leach, 1817 were infested with polydorids. He noted that the burrows began in the area of the protoconch and subsequently spread to other areas of the shell.

Twelve species of *Polydora* and 5 *Boccardia* have been recorded from gastropod shells (Table 3). These scattered accounts come mostly from Europe and the west coast of North America, while a few records come from New England, North Carolina, and South Africa.

Published information on the biology of gastropod shell inhabiting polydorids suggests two distinct methods by

Table 2

Summary of Route of Invasion of Mud-Blister Forming *Polydora*

Author and date	*Polydora* species	Host species	Route of attack
Whitelegge, 1890	*Polydora ciliata*	*Ostrea cucullata*	Larvae swim into open oyster; fix by head to shell margin
Carazzi, 1893	*Polydora ciliata*	*Ostrea edulis*	Between shell and mantle
Dollfus, 1921	*Polydora ciliata*	*Ostrea edulis*	Swims into open oyster; attaches by head to shell margin
	Polydora hoplura	*Ostrea edulis*	Penetrates shell
Kavanagh, 1940	*Polydora websteri*	*Crassostrea gigas*	Creeps within shell cavity causing oyster to form blister
Lunz, 1941	*Polydora websteri*	*Crassostrea virginica*	Swims into open oyster; secures a favorable position and gathers mud around itself
Needler, 1941	*Polydora websteri*	*Crassostrea virginica*	Enters oyster when small; lies between mantle and shell
Medcof, 1946	*Polydora websteri*	*Crassostrea virginica*	Establishes itself between pallium and shell near margin; accumulates mud in which it lives; oyster produces blister by roofing mud with limy shell
Korringa, 1951	*Polydora hoplura*	*Ostrea edulis*	Larvae penetrate between oyster mantle and shell
Hopkins, 1958	*Polydora websteri*	*Crassostrea virginica*	Larvae settle on surface of shells and excavate U-shaped burrows which may be expanded to mud blisters when the shell is penetrated
Galtsoff, 1964	*Polydora websteri*	*Crassostrea virginica*	Larvae settle on external surface of young oysters and form shoe-shaped burrows near extreme edge of shell
Wells *et al.*, 1964	*Polydora websteri*	*Aequipecten gibbus*	Larvae insert themselves between mantle edge and shell
Landers, 1967	*Polydora websteri*	*Mercenaria mercenaria*	Larvae settle on outside surfaces of laboratory-reared hard clams; not found in natural populations

Table 3

Records of *Polydora* and *Boccardia* from Gastropod Shells

Species	Host Shell	Hermit Crab Present	Locality	Reference
Polydora bioccipitalis	*Ocenebra poulsoni*	yes	California	Blake & Woodwick, 1972
	Olivella biplicata	yes	California	Blake & Woodwick, 1972
	Murex gemma	yes	California	Blake & Woodwick, 1972
	Polinices reclusianus	yes	California	Blake & Woodwick, 1972
Polydora capensis	?	no	South Africa	Day, 1955, 1963
Polydora ciliata	*Littorina littorea*	no	Norway	Söderström, 1920, 1923
	Littorina littorea	no	Norway	Dollfus, 1932
	Littorina littorea	no	Germany	Ankel, 1936
	Littorina littorea	no	Sweden (Gullmar Fjord)	Hannerz, 1956
	Littorina littorea	no	Germany	Hempel, 1957
	Littorina littorea	no	Sweden (Øresund)	Eliason, 1920
	Littorina littorea	no	Denmark (Øresund)	Thorson, 1946
	Littorina littorea	no	Sweden	Orrhage, 1969
	Littorina obtusata	no	Germany	Ankel, 1936
	Buccinum undatum	no	Germany	Hempel, 1957
	Crepidula fornicata	no	Germany	Hempel, 1957
	Gibbula cinereria	no	Germany	Ankel, 1936
	Nucella lapillus	no	Germany	Ankel, 1936
	Neptunea antiqua	no	Sweden (Øresund)	Eliason, 1920
	Patella vulgata	no	Sweden (Gullmar Fjord)	Hannerz, 1956

Table 3 [Continued]

Polydora commensalis	*Nassarius obsoletus*	yes	North Carolina	Andrews, 1891a, b
	Nassarius obsoletus	yes	Eastern Canada	Berkeley & Berkeley, 1956
	Thais lamellosa	yes	British Columbia	Berkeley & Berkeley, 1936
	Thais emarginata	yes	California	Woodwick, 1963b
	Lunatia heros	yes	Connecticut	Hatfield, 1965
	Polinices duplicata	yes	Connecticut	Hatfield, 1965
	Busycon canaliculatum	yes	Connecticut	Hatfield, 1965
	Buccinum undatum	yes	Connecticut	Hatfield, 1965
	Littorina littorea	yes	Connecticut	Hatfield, 1965
	Littorina littorea	yes	Maine	Blake, 1969a, b; 1971
	Olivella biplicata	yes	California	Woodwick, 1963a, b
	Ceratostoma nuttalli	yes	California	Woodwick, 1963b
Polydora convexa	*Tegula brunnea*	yes	California	Blake & Woodwick, 1972
	Olivella biplicata	yes	California	Blake & Woodwick, 1972
	Diodora aspera	no	California	Blake & Woodwick, 1972
Polydora elegantissima	*Olivella biplicata*	yes	California	Blake & Woodwick, 1972
Polydora hoplura	*Thais lapillus*	no	France	Fischer, 1930
Polydora punctata	?	yes	El Salvador	Hartmann-Schroeder, 1959
Polydora maculata	*Bullia laevissima*	yes	South Africa	Day, 1963
Polydora pygidialis (as *P. ciliata*)	*Tegula funebralis*	yes	California	Blake & Woodwick, 1972
	Thais lamellosa	yes	British Columbia	Berkeley & Berkeley, 1956
	Thais emarginata	yes	California	Woodwick, 1963b
	Tegula brunnea	yes	California	Woodwick, 1963b
	Tegula brunnea	yes	California	Blake, 1966
	Olivella biplicata	yes	California	Woodwick, 1963a, b
	Acanthina spirata	yes	California	Woodwick, 1963a
	Acanthina spirata	yes	California	Blake & Woodwick, 1972
Polydora websteri	*Littorina littorea*	yes	Maine	Blake, 1969a, b; 1971
Boccardia berkeleyorum	*Tegula brunnea*	yes	California	Blake & Woodwick, 1971
Boccardia columbiana	*Acanthina spirata*	yes	California	Woodwick, 1963a
	Tegula funebralis	yes	California	Woodwick, 1963a
	Tegula brunnea	yes	California	Woodwick, 1963b
	Thais emarginata	yes	California	Woodwick, 1963a
	Purpura foliata	yes	California	Woodwick, 1963a
	Olivella biplicata	yes	California	Woodwick, 1963a
	Diodora aspera	no	California	Woodwick, 1963a
	Jaton festivus	no	California	Woodwick, 1963a
Boccardia hamata	*Tegula brunnea*	yes	California	Blake, 1966
	Lunatia heros	yes	Connecticut	Dean & Blake, 1966
Boccardia proboscidea	*Tegula funebralis*	yes	California	Woodwick, 1963a
	Tegula brunnea	yes	California	Woodwick, 1963a
	Acanthina spirata	no	California	Woodwick, 1963a
	Jaton festivus	no	California	Woodwick, 1963a
	Olivella biplicata	yes	California	Woodwick, 1963a
Boccardia tricuspa	*Tegula brunnea*	yes	California	Woodwick, 1963a
	Ceratostoma nuttalli	yes	California	Woodwick, 1963a
	Olivella biplicata	yes	California	Woodwick, 1963a
	Thais emarginata	yes	California	Woodwick, 1963a

which they become established in the shells. The first and most common is where the worm first invades the outside of the shell and gradually erodes its substance. The one species which has been studied in this regard is *Polydora ciliata*. Hempel (1957) found that *P. ciliata* first attacked the sculptured areas of *Littorina littorea* Linnaeus, 1758 and *Buccinum undatum* Linnaeus, 1758. The larvae settled and perforated the seams from the outside with fine holes and in an advanced infestation eroded the entire apex. She did not find many of the burrows to penetrate the interior of the shell although Ankel (1936) had earlier found that the umbilicus of *Gibbula cinereria* Linnaeus, 1758 was almost always inhabited by *P. ciliata*.

Most species of *Polydora* and *Boccardia* listed in Table 3 probably become established in the manner described by Hempel. *Polydora commensalis* Andrews, 1891, however, invades gastropod shells in an entirely different manner. *Polydora commensalis* is known only from shells inhabited by hermit crabs. This commensal relationship is not specific with regard to host shell or crab (Hatfield, 1965; Blake, 1969a). Further, the species has been recorded from widely scattered geographical localities (Table 3). The external opening of a *P. commensalis* burrow occurs on the inner lip of the aperture of the shell as a conspicuous rounded hole (Andrews, 1891). This opening may or may not be visible from the outside of the shell (Blake, *op. cit.*). The burrow leads from the aperture in long passages around and within the columella (Andrews, *op. cit.*, Hatfield, *op. cit.*), to the apex of the shell. For most of its length the burrow is a shallow depression, roofed over with a thin calcareous mass. It is not known if the worm secretes or redeposits the roof.

Orrhage (1969) found that *Littorina littorea* having a shell shorter than 10 mm were not infested by *Polydora ciliata* and that the snails do not become sexually mature until they have reached those dimensions. He suggests that larvae of *P. ciliata* may be guided to *Littorina* by some substance which the snails secrete into the water. However, he has no data to support the latter contention.

CORAL INFESTATIONS

Four species of *Polydora* and 3 of *Pseudopolydora* have been reported to bore into coral. Okuda (1937) found *P. armata* Langerhans, 1880 living commensally with *Leptastrea purpurea* in Japan. Woodwick (1964) reported 5 species from the Marshall Islands which were taken from coral. The species were *P. armata*, *P. tridenticulata* Woodwick, 1964, *Ps. corallicola* Woodwick, 1964, *Ps. reishi* Woodwick, 1964, and *Ps. pigmentata* Woodwick, 1964. Light (1970a) described *Polydora alloporis* from central California. The species was found abundantly in burrows bored into the coenosteum of the hydrocoral *Allopora californica* Verrill, 1866. In a second paper, Light (1970b) described *P. wobberi* from a white gorgonian, *Lophogorgia* sp., from Baja California.

There have been no studies on the biology of coral infesting species. Hartman (1954) suggested that *Polydora* and other annelids may have a destructive effect on reef building processes of corals or coralline algae.

Table 4

Polydora and *Boccardia* from Coralline Algae

Species	Alga	Locality	Reference
Polydora ciliata	*Lithothamnion*	France	Mesnil, 1896
	Lithothamnion	Sweden	Hannerz, 1956
	–	California	Woodwick, 1963b
Polydora giardi	*Lithothamnion*	France	Mesnil, 1896
Polydora armata	*Lithothamnion*	France	Mesnil, 1896
	Lithothamnion	Japan	Okuda, 1937
	Prolithion oncodes	Marshall Islands	Woodwick, 1964
Polydora flava	*Lithothamnion*	France	Mesnil, 1896
	Lithothamnion	Sweden	Hannerz, 1956
Polydora caeca	*Lithothamnion*	France	Mesnil, 1896
	Lithothamnion	Ireland	Southern, 1914
Boccardia berkeleyorum	*Lithothamnion*	California	Blake & Woodwick, 1971
Boccardia columbiana	*Lithophyllum*	California	Woodwick, 1963a, b
Boccardia proboscidea	*Lithophyllum*	California	Woodwick, 1963a, b
Boccardia tricuspa	*Lithophyllum*	California	Woodwick, 1963a, b

INFESTATIONS of CORALLINE ALGAE

At least 5 species of *Polydora* and 3 of *Boccardia* have been recorded from coralline algae (Table 4). Mesnil (1896) records 5 species of *Polydora* as occurring in coralline algae in France, but gives no information as to their mode of infestation or ecology. Woodwick (1963a, 1963b) records *P. ciliata, B. tricuspa* (Hartman, 1939), *B. proboscidea* Hartman, 1940, and *B. columbiana* Berkeley, 1927 from *Lithophyllum* sp. The 2 former species produced clean burrows in the alga and were apparently true borers, while the 2 latter species, although able to erode the alga, were considered to be nestling forms.

DISCUSSION

Theories and Experimental Evidence Concerning Mechanisms of Shell Penetration by *Polydora*

The literature on this subject dates back well into the nineteenth century and includes ideas which have at times evoked considerable controversy among different investigators.

Lankester (1868) was the first person to treat the actual boring of a *Polydora, P. ciliata.* He did not believe that the heavy spines of the 5th setiger could in any way affect lime and concluded that the boring was accomplished by chemical means. He believed that an acid secretion was derived from segmental glands, later termed "poches glanduleuses" by Claparède (1870).

McIntosh (1868) strongly disagreed with Lankester because the worm could be found in burrows in substrates other than calcareous, namely shale and sandstone. He thus favored mechanical penetration over a purely chemical mechanism.

Whitelegge (1890) studied *Polydora ciliata* in Australian oysters. He advanced the idea that the worm did not bore at all but instead that the larvae entered the oyster from the inside, attached themselves to the inside of the shell and there surrounded themselves with mud. The irritated oyster then deposited a layer of lime over the animal. This type of structure is what we call a mud-blister. Actually, Haswell (1885) had earlier described similar blisters from Australian oysters, a work apparently overlooked by Whitelegge. McIntosh (1902) again disagreed with these findings, by pointing out that mud-blisters were not formed by the worms when they lived in other substrates and by the fact that very few British oysters have mud-blisters. In retrospect, it may well be that the apparent behavioral difference observed by these two authors for *P. ciliata* in Australia and Britain may be due to a taxonomic problem. Indeed, Korringa (1951: 97) has stated:

> "The most serious damage to the oyster industry in many parts of the world is imputed in the literature to *Polydora ciliata.* In practically every case presented *Polydora ciliata* could plead not guilty, and point to other members of the *Polydora* family as the culprits. I have not enough space here to clear up this confusion which is found in the literature on this point. It is enough to mention that *Polydora ciliata* most probably does not occur at all in America (Hartman, 1945), and Australia, from where its harmful effects have been reported.
>
> "Much of the havoc caused in many important oyster districts, and ascribed to *Polydora ciliata,* has in fact been caused by *Polydora hoplura* or by biologically closely related species like *Polydora websteri* Hartman. The latter species all show the same way of living differing from that of *Polydora ciliata.*"

Polydora hoplura and *P. websteri* are known to form mud-blisters in oysters while *P. ciliata* apparently does not. The first author has examined some of Haswell's material and has found that the specimens agree more closely with *P. websteri* than with *P. ciliata.*

Despite probable taxonomic problems, the controversy over mechanical versus chemical means of shell penetration continued into the early twentieth century.

Söderström (1920) first emphasized mechanical abrasion by the heavy spines of setiger 5 as he observed *Polydora ciliata* through thin burrows. He demonstrated that the U-shaped burrow resulted from an originally undivided hole in which an intermediate wall of detritus, etc., was built up. He considered that the boring was a joint effect between the secretion of an acid by the "poches glanduleuses," and mechanical abrasion of the modified bristles of setiger 5. In a later paper (Söderström, 1923) he changed his view by suggesting that the spines were merely a means of support or adhesion during ventilation or feeding and that the mechanism of boring was purely chemical.

In recent years the controversy of mechanical versus chemical boring has been revived.

Hannerz (1956) in an elegant larval study noted that *Polydora ciliata* larvae possessed a pair of opaque gray glands ventral to the heavy spines in setiger 5. Although different in structure from the "poches glanduleuses," which in adults occur in segments 7, 8, and 9, he considered them homologous. Hannerz felt that these glands in the 5th setiger of larvae secreted a substance which facilitates the initial boring by the worm. He was also very impressed with the musculature associated with the specialized 5th segment and disagreed with Söderström's contention that the so-called bore bristles were primarily for adhering the worm in one position. Hannerz was of the opinion that boring involved both a chemical and a mechanical action on the material. A substance secreted by the glands converts the lime into a more easily workable substance which is later eroded with the help of the bristles. Since the described glands were exclusively larval, he contended that boring in adults was accomplished entirely with the aid of bristles.

Hempel (1957) determined that *Polydora ligni, P. quadrilobata* Jacobi, 1883 and *P. ciliata* bore into hard clay with the setae of the 5th segment. The burrows in clay were similar to those made by *P. ciliata* in calcareous material. From this information and from the fact that she saw scratches in new bore holes she determined that *P. ciliata* bores by mechanical means only. She noted as Hannerz had that the musculature of the 5th setiger was especially well developed and that the setae showed distinct signs of wear. Specimens kept in sand did not show setal wear as did those taken and allowed to penetrate shells.

Dorsett (1961) favored the view that both chemical and mechanical methods were used by the worms to bore. Although no specific acid was identified, the use of a sequestering or chelating agent linked with the biochemistry of mucus was suggested. He also noted the heavy musculature of the 5th setiger and observed the behavior of recently metamorphosed worms on clay.

The majority of this literature has dealt with *Polydora ciliata*. Haigler (1969) and Evans (1969), however, have dealt with other species. Haigler (*op. cit.*) conducted experiments to determine the mechanism of boring in *Polydora websteri*. She made the remarkable discovery that when the heavy spines of setiger 5 were removed the worm could still bore. She further determined that larvae and post-larvae could bore if the setae and special glands were removed. If this seems to put to rest the idea that the spines of setiger 5 are responsible for boring, then the discovery of Evans (*op. cit.*) that *P. concharum* bores along most of its body is the final blow.

Evans (1969) found that *Polydora concharum* constructs long branching burrows quite unlike those of *P. ciliata* or *P. websteri*. He determined that all branches of this burrow system were being enlarged at the same time. It seems unrealistic to think that the worm could move its body from here to there so as to position the 5th segment to bore.

Based on the results of Haigler (1969) it would appear that the mechanical theory of boring has finally been put to rest. Although she has shown that the spines of setiger 5 are not needed by *Polydora websteri* to bore, it would be of considerable interest to learn what function they do perform. Indeed, the great degree of variation seen among species of *Polydora, Boccardia,* and *Pseudopolydora* of these setae suggests that each species has subtle differences in behavior which have manifested themselves over time in morphological diversity.

Perhaps it is as Söderström (1923) suggested, that the spines are merely used for anchoring the animal in position so that normal functions of respiration and feeding can take place. Why, then, have such species as *Boccardia columbiana, B. berkeleyorum* and *Pseudopolydora reishi,* all of which bore, evolved heavy spines which have the ends formed into brushes? These suggest some mechanism for maintenance of the general well-being of the tube, by cleaning.

Comparative Aspects of Burrow Structure among Species of *Polydora*

The U-shaped burrow, typical of *Polydora* shell infestations, assumes different shapes and forms among different species.

The simplest burrow is formed by *Polydora commensalis* which occupies hermit crab shells. The worm excavates a shallow depression and roofs it over with a thin calcareous layer (Figure 3c) (see earlier discussion and Blake, 1969a). The same type of burrow has been found for *P. bioccipitalis* by Blake & Woodwick (1971b). Both species form their burrows near the shell opening and on the columella.

The "typical" U-shaped burrow is formed by *Polydora ciliata* (Figure 3d). *Polydora websteri,* however, modifies the basic U pattern in several manners.

1) The U twists (Figure 3g) as in *Mercenaria mercenaria* infestations (Landers, 1967);
2) The U expands at the base and may be inflated, the shape assuming a "pear-shape" (Figure 3e);
3) The U may have a single branch at the bottom (Figure 3f) as in *Placopecten magellanicus* (Evans, 1969).

Polydora websteri also forms mud-blisters in oysters. Pear-shaped burrows have also been reported for *P. hoplura* by Korringa (1951).

The greatest deviation from the U pattern is the multiple branched burrow described by Evans (1969) for *Polydora concharum* in *Placopecten magellanicus* (see also earlier discussion). Here the burrows branch repeatedly (Figure 3h). Such burrow patterns are difficult to trace without X-Ray techniques (Figure 4). Similar burrows occur in other species, such as *P. convexa* (Blake & Woodwick, 1971b).

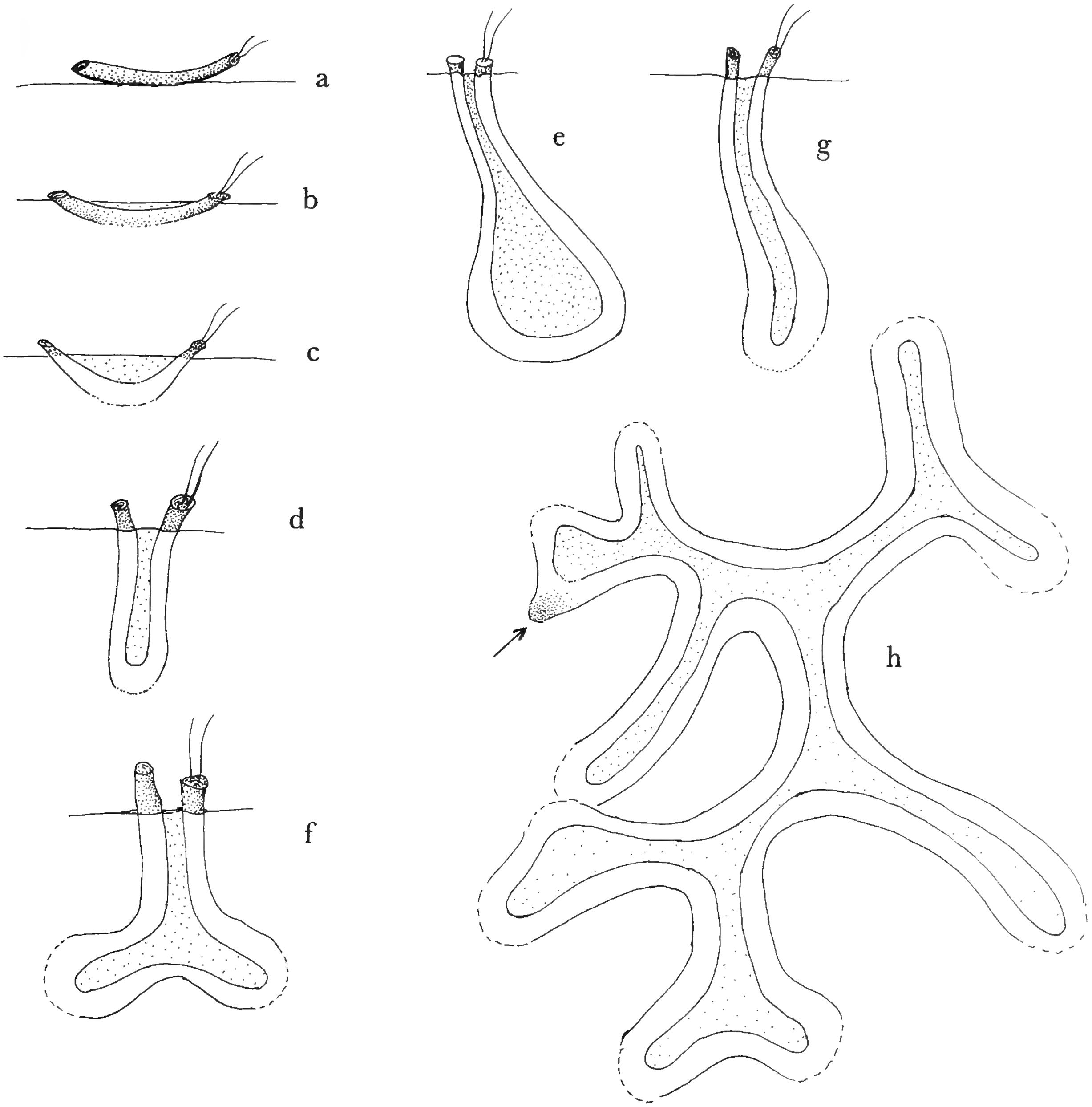


Figure 3

Diversity of burrow structure in *Polydora* species

a: tube of just settled larva; b: initial boring activity of worm, this is the stage reached by *Polydora commensalis;* c: continued boring; d: U-shaped burrow such as that formed by *Polydora ciliata*; e: pear-shaped burrow formed by *Polydora websteri*; f: single branched burrow formed by *Polydora websteri* in *Placopecten* shells; h: multiple branched burrow of *Polydora concharum* from shells of *Placopecten magellanicus* (after Evans, 1969)

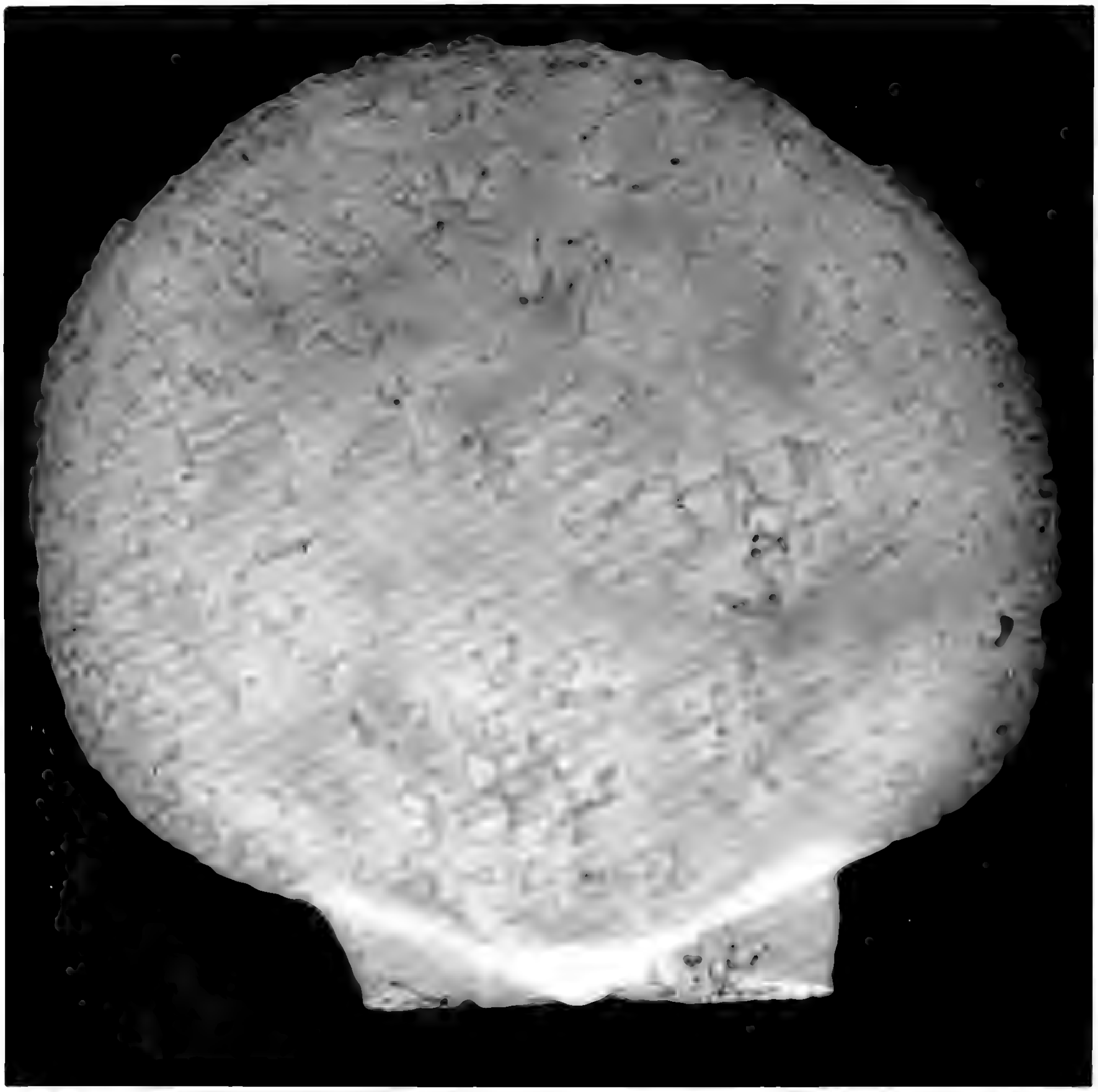


Figure 4

X-ray photograph of the upper valve of *Placopecten magellanicus.* Multiple branched burrows of *Polydora concharum* are clearly evident in the center of the shell, while the smaller burrows around the periphery are mostly those of *Polydora websteri*

Dependence of Polydorid Species on a Calcium Carbonate Substrate

A survey of the habitats of all known species of *Polydora, Pseudopolydora,* and *Boccardia* (Table 5) reveals that 26 species have been reported to occur only in calcareous substrates; 6 from both calcareous and non-calcareous substrates; 33 from various non-calcareous substrates; and 5 in which the exact habitat is not known.

The most often reported species, *Polydora ciliata* has been reported from both calcareous and non-calcareous substrates. The literature, however, is confused to say the

Table 5

Habitat Records of the Known Species of *Polydora, Boccardia* and *Pseudopolydora*

A. Species which occur exclusively in calcareous substrates	
Polydora alloporis	*P. maculata*
P. anophthalma	*P. pacifica*
P. armata	*P. pygidialis*
P. bioccipitalis	*P. tetrabranchia*
P. capensis	*P. websteri*
P. commensalis	*P. wobberi*
P. concharum	*Pseudopolydora corallicola*
P. convexa	*Ps. pigmentata*
P. elegantissima	*Ps. reishi*
P. giardi	*Boccardia berkeleyorum*
P. hoplura	*B. columbiana*
P. hornelli	*B. pseudonatrix*
P. langerhansi	*B. tricuspa*
B. Species reported from both calcareous and non-calcareous substrates	
Polydora socialis	*P. flava*
P. ciliata	*Boccardia hamata*
P. caeca	*B. proboscidea*
C. Species which occur exclusively in non-calcareous substrates	
Polydora abranchiata	*P. nuchalis*
P. aggregata	*P. paucibranchus*
P. anoculata	*P. quadrilobata*
P. cardalia	*P. rickettsi*
P. caulleryi	*P. spongicola*
P. cirrosa	*Pseudopolydora antennata*
P. citrona	*Ps. kempi*
P. colonia	*Ps. paucibranchiata*
P. fulva	*Ps. pulchra*
P. goreensis	*Boccardia basilaria*
P. laticephala	*B. chilensis*
P. ligni	*B. ligerica*
P. limicola	*B. natrix*
P. magna	*B. perata*
P. neocardalia	*B. polybranchiata*
P. normalis	*B. proboscidea*
	B. truncata
D. Species in which the exact habitat is not known	
Polydora hartmanae	*P. posthamata*
P. hermaphroditica	*P. saint-josephi*
P. heterochaeta	

least. It is probable that a majority of the records attributing *P. ciliata* to non-calcareous habitats actually refer to *P. limicola* Annenkova, 1937, or *P. ligni*. The literature also seems somewhat confusing with regard to *P. caeca* and *P. flava*. Both species have been reported from calcareous and non-calcareous habitats from widely scattered areas of the world. It seems possible that other species such as *P. concharum* may actually refer to some of these records. Considerable work remains to straighten out the taxonomic status of several of the "better known" species of *Polydora*.

NOTE ADDED IN PROOF

The paper by MOHAMMAD (1972) arrived too late to be incorporated in the text and tables of the present paper. This work includes the original description of *Polydora vulgaris* from the Pearl Oyster, *Pinctada margaritifera* (Linnaeus, 1758). Also included is information of the form of the burrow and rates of infestation. He indicates a total of 4.68% *Pinctada margaritifera* are infested with *Polydora vulgaris*. Infestation is higher in older oysters (14.77%), in those with pearls (19.43%) and highest in old pearl carriers (41.2%).

Literature Cited

ANDREWS, E. A.
1891a. Report on the Annelida Polychaeta of Beaufort, North Carolina. Proc. U. S. Nat. Mus. **14:** 277-302; plts. 12-18
1891b. A commensal annelid. Amer. Nat. **25:** 25-35; 2 plts.
ANKEL, WULFF EMMO
1936. Prosobranchia. *In:* G. GRIMPE & E. WAGLER, Die Tierwelt der Nord- und Ostsee, IX: 1-240 Akad. Verlagsgesellsch. Leipzig
BERKELEY, EDITH & CYRIL BERKELEY
1936. Notes on Polychaeta from the coast of western Canada I. Spionidae. Ann. Mag. Nat. Hist., Ser. 10, **18:** 468-477; 1 fig.
1956. On a collection of polychaetous annelids from northern Banks Island, from the South Beaufort Sea, and from northwest Alaska: together with some new records from the east coast of Canada. Journ. Fish. Res. Brd. Canada **13** (2): 233-246
BLAKE, JAMES ALAN
1966. On *Boccardia hamata* (Webster), new combination (Polychaeta, Spionidae). Bull. South. Calif. Acad. Sci. **65:** 176-184; 11 figs.
1969a. Systematics and ecology of shell-boring polychaetes from New England. Amer. Zool. **9:** 813-820; 9 figs.
1969b. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae). Ophelia **7:** 1-63; 40 figs.
1971. Revision of the genus *Polydora* from the east coast of North America (Polychaeta: Spionidae). Smthson. Contr. Zool. No. **75:** 1-32
BLAKE, JAMES ALAN & KEITH HARRIS WOODWICK
1971. A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. Bull. South. Calif. Acad. Sci. **70** (1): 31-42
1972. New species of *Polydora* (Polychaeta: Spionidae) from the coast of California. Bull. South. Calif. Acad. Sci. **70** (2): 72-79
BOEKSCHOTEN, G. J.
1966. Shell borings of sessile epibiontic organisms as palaeoecological guides (with examples from the Dutch coast). Palaeogeogr., Palaeoclimat., Palaeoecol. **2:** 333-379
1967. Palaeoecology of some Mollusca from the Tielrode Sands (Pliocene, Belgium). Palaeogeogr., Palaeoclimat., Palaeoecol. **3:** 311 to 362
CAMERON, BARRY
1967. Fossilization of an ancient (Devonian) soft-bodied worm. Science **155** (3767): 1246-1248
1969. Paleozoic shell-boring annelids and their trace fossils. Amer. Zool. **9:** 689-703
CARAZZI, DAVIDE
1893. Revisione del genero *Polydora* Bosc, e cenni su due specie che vivono sulle ostriche. Mitt. Zool. Stat. Neapel **11:** 4-45; plt. 2.

Claparède, Edouard

1870. Les annelides chetopodes du Golfe de Naples. Mém. Soc. Phys. Genève **20** (2): 365 - 542

Davis, John D.

1967. *Polydora* infestation of Arctic wedge clams: a pattern of selective attack. Proc. Nat. Shellfish. Assoc. **57:** 67 - 72

Day, John Hemsworth

1955. The Polychaeta of South Africa. Part 3: Sedentary species from Cape shores and estuaries. Journ. Linn. Soc. Zool. **42:** 407 - 452

1963. The polychaete fauna of South Africa. Part 7: Species from depths between 1,000 and 3,300 metres west of Cape Town. Ann. South Afr. Mus. **46** (14): 353 - 371

1967. A monograph on the Polychaeta of southern Africa. Part 2. Sedentaria. Brit. Mus. (Nat. Hist.) London, publ. **656:** 459 - 878; figs. 18 - 38

Dean, David & James Alan Blake

1966. Life-history of *Boccardia hamata* (Webster) on the east and west coasts of North America. Biol. Bull. **130** (3): 316 - 330

Dollfus, Robert-Philippe

1921. Résumé de nos principales connaissances pratiques sur les maladies et les ennemis de l'huître. Office Scient. Tech. Pêches Marit. (France). Notes et Mém. **7:** 46 pp.

Dorsett, D. A.

1961. The behaviour of *Polydora ciliata* (Johnst.). Tube building and burrowing. Journ. Mar. Biol. Assoc. U. K. **41:** 577 - 590

Eliason, Anders

1920. Polychaeta. Biologisch-faunistische Untersuchungen aus dem Oresund V. Lunds Univ. Arrskrift **16** (6): 1 - 103

Evans, John W.

1969. Borers in the shell of the sea scallop, *Placopecten magellanicus.* Amer. Zool. **9:** 775 - 782; 13 figs.

Fischer, Paul-Henri

1930. Association occasionelle du *Purpura lapillus* L. avec une annélide polychète (*Polydora hoplura* Claparède). Journ. de Conchyl. **74** (1): 35 - 38

Forbes, M.

1966. Life cycle of *Ostrea permollis* and its relationship to the host sponge, *Stelletta grubii.* Bull. Mar. Sci. **16:** 273 - 301

Frey, D. G.

1946. Oyster bars of the Potomac River. Spec. Sci. Reprt. no. 32, Dept. Inter. Fish & Wildlife Serv. pp. 80 - 93

Galtsoff, Paul Simon

1964. The American oyster *Crassostrea virginica* Gmelin. Fishery Bull. Fish & Wildlife Serv. **64:** 1 - 480; 400 figs.; 46 tables

Haigler, Sarah H.

1969. Boring mechanism of *Polydora websteri* inhabiting *Crassostrea virginica.* Amer. Zool. **9:** 821 - 828; 3 figs.

Hannerz, Lennert

1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil and Poecilochaetidae N. Fam. in the Gullmar Fjord (Sweden). Zool. Bidr. Uppsala **31:** 1 - 204; 57 figs.

Hansen, John C.

1970. Commensal activity as a function of age in two species of California abalones (Mollusca: Gastropoda). The Veliger **13** (1): 90 - 94; 2 plts.; 2 text figs. (1 July 1970)

Hartman, Olga

1943. Description of *Polydora websteri* Hartman. *In:* Loosanoff & Engle, *Polydora* in oysters suspended in the water. Biol. Bull. **85:** 69 - 78; 1 fig.

1945. The marine annelids of North Carolina. Duke Univ. Mar. Sta. Bull. **2:** 1 - 53; 10 plts.

1951. The littoral marine annelids of the Gulf of Mexico. Publ. Inst. Mar. Sci. **2** (1): 7 - 124; 27 plts.

1954. Marine annelids from the northern Marshall Islands. U. S. Geol. Surv. Prof. Paper **260-Q:** 619 - 644

1961. Polychaetous annelids from California. Allan Hancock Pac. Exped. **25:** 1 - 226; 34 plts.

1966. Polychaetous annelids of the Hawaiian Islands. Occ. Pap. Bernice P. Bishop Mus. **23** (11): 163 - 252; 2 figs.

Hartman-Schröder, Gesa

1959. Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. Beitr. Neotrop. Fauna **1** (2): 69 - 183

Haswell, William A.

1885. On a destructive parasite of the rock oyster. Proc. Linn. Soc. New So. Wales **10:** 272 - 275

Hatfield, Phyllis A.

1965. *Polydora commensalis* Andrews - Larval development and observations on adults. Biol. Bull. **128:** 356 - 368; 5 figs.

Hempel, Christine

1957. Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta, Sedentaria) der deutschen Küsten. Helgol. wiss. Meeresunters. **6:** 100 - 135; 16 figs.

Hopkins, Sewell H.

1958. The planktonic alrvae of *Polydora websteri* Hartman (Annelida, Polychaeta) and their settling on oysters. Bull. Mar. Sci. Gulf & Caribb. **8:** 268 - 277; 1 fig.

Kavanagh, L. D.

1940. Mud blisters in Japanese oysters imported to Louisiana. Louisiana Conserv. Rev., Autumn 1940: 31 - 34

Korringa, Pieter

1951. The shell of *Ostrea edulis* as a habitat: observations on the epifauna of oysters ilving in the Oosterchelde, Holland, with some notes on polychaete worms occurring there in other habitats. Arch. néerl. zool. **10** (1): 32 - 152; 13 figs.; 1 table; 1 map

Lamy, Édouard & Marc André

1937. Annélides perforants les coquilles des mollusques. Congr. Internat. Zool., 12 (Lisbon, 1935), Compt. Rend., vol. 2: 946 - 968

Landers, Warren S.

1967. Infestation of the hard clam *Mercenaria mercenaria* by the boring polychaete worm, *Polydora ciliata.* Proc. Nat. Shellfish. Assoc. **57:** 63 - 66

Lankester, E. Ray

1868. On lithodomous annelids. Ann. Mag. Nat. Hist., Ser. 4, **1:** 233 - 238; 1 plt.

Light, William J.

1970a. *Polydora alloporis,* new species, a commensal spionid (Annelida, Polychaeta) from a hydrocoral off Central California. Proc. Calif. Acad. Sci. 4th ser. **37** (14): 459 - 472

1970b. A new spionid (Annelida: Polychaeta) from the Gulf of California. Bull. South. Calif. Acad. Sci. **69** (2): 74 - 79

Loosanoff, Victor Lyon & James B. Engle

1943. *Polydora* in oysters suspended in the water. Biol. Bull. **85:** 69 - 78; 2 figs.

Lunz, Robert George

1940. The annelid worm, *Polydora,* as an oyster pest. Science **92** (2388): 310

1941. *Polydora,* a pest in South Carolina oysters. Journ. Elisha Mitchell Sci. Soc. **57:** 273 - 283

Mackin, J. G. & F. F. Cauthron

1952. Effect of heavy infestations of *Polydora websteri* on *Crassostrea virginica* (Gmelin) in Louisiana. Nat. Shellfish. Assoc. Conv. Addr. **1952:** 14 - 24

McIntosh, William Carmichael Arthur

1868. On the boring of certain annelids. Ann. Mag. Nat. Hist. ser. 4. **2:** 276 - 295; plts. 18 - 20

1902. Notes from the Gatty Marine Laboratory, St. Andrews. No. 22. 1 - 5. Ann. Mag. Nat. Hist. ser. 7, **9:** 291 - 308

Medcof, J. C.

1946. The mud-blister worm, *Polydora,* in Canadian oysters. Journ. Fish. Res. Bd. Canada **6:** 498 - 504

Mesnil, Felix

1896. Études de morphologie externe chez les annélides. Les spionidiens des côtes de la Manche. Bull. Sci. France et Belg. **29:** 110 - 287; plts. 7 - 15

Mohammad, Murad-B. M.

1972. Infestation of the pearl oyster *Pinctada margaritigera* (Linne) by a new species of *Polydora* in Kuwait, Arabian Gulf. Hydrobiol. **39** (4) 463 - 477; 9 figs.

Moore, Raymond Cecil

1962. Treatise on invertebrate paleontology. Part W. Miscellanea - trace fossils and problematica. Geol. Soc. Amer. & Univ. Kansas Press, 259 pp.

Mortensen, E. & Paul Simon Galtsoff

1944. Behavior and tube building of *Polydora ligni.* Biol. Bull. **87:** 164 - 165

Needler, A. W. H.

1941. Oyster farming in eastern Canada. Bull. Fish. Res. Brd. Canada **60:** 1 - 83

Nelson, T. C. & L. A. Stauber

1940. Observations of some common polychaetes on New Jersey oyster beds with special reference to *Polydora.* Anat. Rec. **78** (4), suppl.: 102 - 103

Okuda, Shiro

1937. Spioniform polychaetes from Japan. Journ. Fac. Sci. Hokkaido Univ., ser. 6, Zool. **5:** 217 - 254; 27 figs.

Orrhage, Lars

1969. On the shell growth of *Littorina littorea* (Linné) (Prosobranchiata, Gasteropoda) and the occurrence of *Polydora ciliata* (Johnston) (Polychaeta Sedentaria). Zool. Bidr. Uppsala **38:** 137 - 153

Owen, Malcolm H.

1957. Etiological studies on oyster mortality. II. *Polydora websteri* Hartmann (Polychaeta: Spionidae). Bull. Mar. Sci. Gulf & Caribb. **7:** 35 - 46

Persoone, G.
1965. The importance of fouling in the harbour of Ostend in 1964. Helgol. wiss. Meeresunters. **12:** 444 - 448

Pillai, T. Gottfried
1965. Annelida Polychaeta from the Philippines and Indonesia. Ceylon Journ. Sci., Biol. Sci. 5 (2): 110 - 177

Rioja, Enrique
1960. Estudios anelidologicos XXIV. Adiciones a la fauna de anelidos poliquetos de las costas orientales de Mexico. Anales Inst. Biol. Mexico **31:** 289 - 316; 39 figs.

Roughley, T. C.
1922. Oyster culture in the George's River, New South Wales. Technol. Mus. Sydney, Technic. Educ. Ser. no. **25,** 69 pp.

Seilacher, Adolph
1969. Paleoecology of boring barnacles. Amer. Zool. **9:** 705 - 719

Söderström, Adolph
1920. Studien über die Polychaetenfamilie Spionidae. Inaugur. Dissert. Univ. Uppsala: 286 pp., 1 plt.
1923. Über das Bohren der *Polydora ciliata.* Zool. Bidr. Uppsala **8:** 319 - 326

Southern, Rowland
1914. Clare Island Survey Part 47. Archiannelida and Polychaeta. Proc. Roy. Irish Acad. **31** (47): 1 - 160; 15 plts.

Thorson, Gunnar
1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). Medd. Komm. Havundersøg., Copenhagen, Ser. Plankton **4** (1): 1 - 523

Turner, Harry Jackson, Jr. & James E. Hanks
1959. Infestation of *Pecten irradians* by *Polydora.* The Nautilus **72** (4): 109 - 111

Verrill, Addison Emery
1880. Notice of some recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part II. Annelida, Gephyrea, Nemertina, Nematoda, Polyzoa, Tunicata, Echinodermata, Porifera. Proc. U. S. Nat. Mus. **2:** 165 - 205

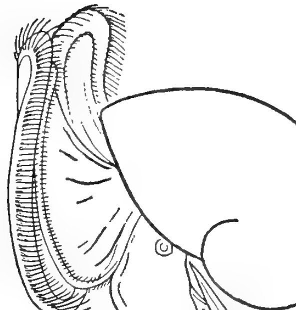
Webster, Harrison Edwin
1879a. Annelida Chaetopoda of the Virginian coast. Trans. Albany Inst. **9:** 202 - 209; 11 plts.
1879b. Annelida Chaetopoda of New Jersey. Ann. Reprt. New York State Mus. pp. 101 - 128

Wells, Harry W. & Mary Jane Wells
1962. The polychaete *Ceratronereis tridentata* as a pest of the scallop *Aequipecten gibbus.* Biol. Bull. **122** (1): 149 - 159

Wells, Harry W., Mary Jane Wells & Irving Emery Gray
1964. The Calico Scallop community in North Carolina. Bull. Mar. Sci. Gulf & Caribb. **14:** 561 - 593

Whitelegge, Thomas
1890. Report on the worm disease affecting the oysters on the coast of New South Wales. Rec. Austral. Mus. (Sydney) **1** (2): 41 - 54

Woodwick, Keith Harris
1963a. Comparison of *Boccardia columbiana* Berkeley and *Boccardia proboscidea* Hartman (Annelida, Polychaeta). Bull. South. Calif. Acad. Sci. **62** (3): 132 - 139
1963b. Taxonomic revision of two polydorid species (Annelida, Polychaeta, Spionidae). Proc. Biol. Soc. Wash. **76:** 209 - 216
1964. *Polydora* and related genera (Annelida, Polychaeta) from Eniwetok, Majuro, and Bikini Atolls, Marshall Islands. Pacif. Sci., vol. XVIII, no. 2: 146 - 159



Range Extensions of Several Littorinids

(Mollusca : Gastropoda)

in Florida

BY

FRASIER O. BINGHAM

Rosenstiel School of Marine and Atmospheric Science, University of Miami, 10 Rickenbacker Causeway
Miami, Florida 33149

INTRODUCTION

RANGES OF VARIOUS *Littorina* species endemic to the western Atlantic have been discussed by BEQUAERT (1943), HEDGPETH (1953), BORKOWSKI (1969), BINGHAM (1969), and SMALLEY (1970).

During my studies of the ecology of the Littorinidae of Florida, several species have been collected in areas from which they have not been reported previously.

The identifications of the species mentioned have been verified by Dr. Joseph Rosewater. The specimens are now included in the U. S. National Museum collection.

Littorina angulifera Lamarck, 1822

Five living specimens of *Littorina angulifera* were seen by the author on concrete bulkheads near Panama City, Florida (30°10′N; 85°40′W) on October 19, 1968. One of these specimens was collected and sent to the U. S. National Museum. Three specimens of the species were seen in the Panama City area on July 17, 1971. The largest specimen of *L. angulifera* had a shell length of 36 mm.

Panama City is approximately 240 miles (384 km) east of Grand Isle, Louisiana where *Littorina angulifera* was collected by SMALLEY (1970), and some 180 miles (288 km) northwest of Cedar Keys, Florida, where the species has been noted to occur (BEQUAERT, 1943).

Littorina lineolata D'ORBIGNY, 1840

Several hundred living specimens of *Littorina lineolata* were seen on a rock jetty at the mouth of St. Andrews Bay near Panama City, Florida (30°10′N; 85°40′W) on July 7, 1971. Several specimens were collected and sent to the U. S. National Museum. This species was seen only on the rock jetty and not on several concrete bulkheads in the Panama City area. The species was not seen on the rock jetty during frequent collecting trips to Panama City during the years 1968 to 1970.

BORKOWSKI (1969) found that *Littorina ziczac,* as known to BEQUAERT (1943) is actually a group of closely related species and *L. lineolata* is one of these.

Littorina meleagris Potiez & Michaud, 1838

In June, 1970, an extensive population of *Littorina meleagris* was noted by the author at Jupiter Blowing Rocks (28°58′ N; 80°05′ W), near Jupiter, Florida.

The population at Jupiter Blowing Rocks is found mainly on algae-covered boulders situated low in the intertidal zone. These boulders are exposed to air for only short periods and drying is minimal.

Whereas BEQUAERT (1943) notes that *Littorina meleagris* is found "in rather quiet water," the opposite is true of the population inhabiting Jupiter Blowing Rocks.

The population of *Littorina meleagris* at Jupiter Blowing Rocks has persisted from June, 1970 to the time of the writing of this report (January, 1972).

Littorina meleagris has previously been reported in Florida as far north as Boynton Beach, Palm Beach County (BEQUAERT, 1943), some 27 miles (43 km) south of Jupiter.

Littorina mespillum Mühlfeld, 1824

A single living specimen of *Littorina mespillum* was collected by the author at Jupiter Blowing Rocks (26°58′ N; 80°05′ W) near Jupiter, Florida on March 26, 1971. The specimen was taken from an exposed, algae-covered boul-

---

[1] Contribution No. 1560 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science, 10 Rickenbacker Causeway, Miami, Florida 33149

der situated low in the intertidal zone. Two additional specimens were collected from "splash pools" at the same location on April 24, 1971.

The range of this species in Florida was reported by Bequaert (1943) to be the southern Florida Keys. Thomas and Paul McGinty of Boynton Beach, Florida, collected the species from Yamato Rocks (26°26′ N; 80°04′ W) on July 16, 1961 (personal communication).

The Jupiter Blowing Rocks are some 31 miles (50 km) north of Yamato Rocks. The published range of the species is extended approximately 170 miles (272 km) northward along the Florida coast.

Littorina nebulosa Lamarck, 1822

A single living specimen of *Littorina nebulosa* was collected by the author from a wooden bulkhead on East Summerland Key, Florida Keys, Florida (24°40′ N; 81° 27′ W) on July 16, 1971. East Summerland Key and Panama City (Bingham, 1969) are the only localities where this species has been collected in Florida.

Littorina tessellata Philippi, 1847

Littorina tessellata was first noted in Florida only recently (Bingham, 1972).

A single living specimen of *Littorina tessellata* was collected by Miss Helen D. Albertson on July 16, 1971, from a wave-exposed wooden piling on lower Matecumbe Key, Florida Keys, Florida (24°52′ N; 80°42′ W). A third specimen of this species seen in Florida was collected by the writer from a wooden piling on the Biscayne Bay side of Key Biscayne, Florida (25°40′ N; 80°10′ W) on September 3, 1971.

In Florida, *Littorina tessellata* has thus far been reported only from the Florida Keys.

ACKNOWLEDGMENTS

I am indebted to Dr. Hilary B. Moore and Miss Helen D. Albertson for their aid during many collecting trips. Dr. Joseph Rosewater's verification or identification of many specimens is appreciated.

Literature Cited

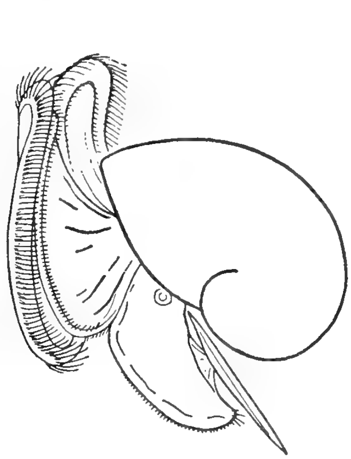
Bequaert, Joseph Charles
1943. The genus *Littorina* in the western Atlantic. Johnsonia **1** (7): 1 - 28; plts. 1 - 7

Bingham, Frasier O.
1969. *Littorina nebulosa* in Florida. The Nautilus **82** (4): 146 - 147
1972. First recorded occurrence of *Littorina tessellata* Philippi, 1847 from the shores of North America. The Veliger **15** (2): 158; 1 text fig. (1 October 1972)

Borkowski, Thomas V. & Marilynn R. Borkowski
1969. The *Littorina ziczac* species complex. The Veliger **11** (4): 408 - 414; plt. 66; 4 text figs. (1 April 1969)

Hedgpeth, Joel Walker
1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Texas. Univ. Inst. Mar. Sci. Publ. **3**: 107 - 224

Smalley, A. E.
1970. *Littorina* in Louisiana. The Nautilus **84** (1): 35 - 36



The Occurrence of *Polycera zosterae* O'Donoghue, 1924 in the Bodega Bay Region, California, with Notes on its Natural History

(Gastropoda : Nudibranchia)

BY

TERRENCE M. GOSLINER[1] AND GARY C. WILLIAMS[2]

University of California, Bodega Marine Laboratory, Bodega Bay, California 94923

(1 Map; 1 Text figure)

THE PHANEROBRANCH DORID *Polycera zosterae* O'Donoghue, 1924, is known in the literature only from the original description and from references to the taxon in the discussions of the genus *Polycera* from the Pacific coast of the Americas in MARCUS & MARCUS, 1967. The type locality is the Vancouver Island region, the habitat being the blades of the marine eelgrass, *Zostera marina* var. *latifolia* Morong, of the Zosteraceae. No other distributional or ecological data are recorded in either of the works cited above.

On June 25, 1971 7 examples of *Polycera zosterae* were observed under rocks of the jetty which extends from the southern entrance of Bodega Harbor, Sonoma County, California (lat. 38°18′N; long. 123°03′W). Individuals were found among assemblages of various species of sponges, bryozoans, hydroids, and tunicates. No relationship between the specimens of *P. zosterae* and a specific substrate was discernible at this time.

Three individuals of *Polycera zosterae* were found at Mason's Marina (lat. 38°20′N; long. 123°03′W), situated well within Bodega Harbor, on June 29, 1971. All animals were found on or in close proximity of *Bowerbankia gracilis* var. *aggregata* O'Donoghue, 1926, a ctenostomate bryozoan which abounds periodically during the year on the tires and floats in the marina.

On July 21, 1971, 2 examples of *Polycera zosterae* were found in the vicinity of Schuster's Rock (lat. 38°18′N; long. 123°00′W), an unprotected open coastal area directly south of Bodega Harbor. These animals were also

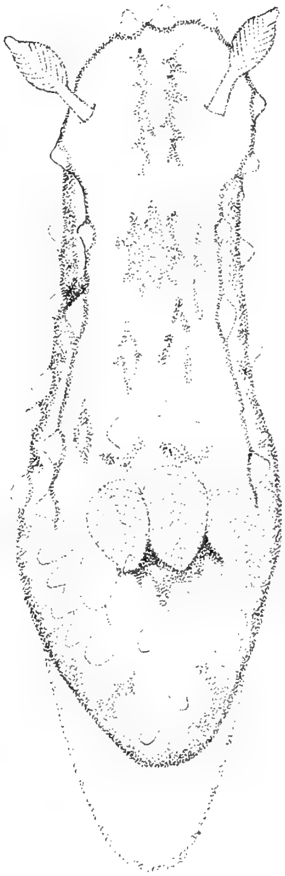


Figure 1

Polycera zosterae O'Donoghue, 1924 dorsal aspect of a 12 mm long specimen

---

[1] Permanent address: 859 Butterfield Road, San Anselmo, California 94960

[2] Permanent address: 267 Oak Manor Drive, Fairfax, California 94930

associated with *Bowerbankia gracilis.* Observations in the laboratory with the use of a dissecting microscope confirmed the assumption that *Bowerbankia* is a major food source of *P. zosterae.*

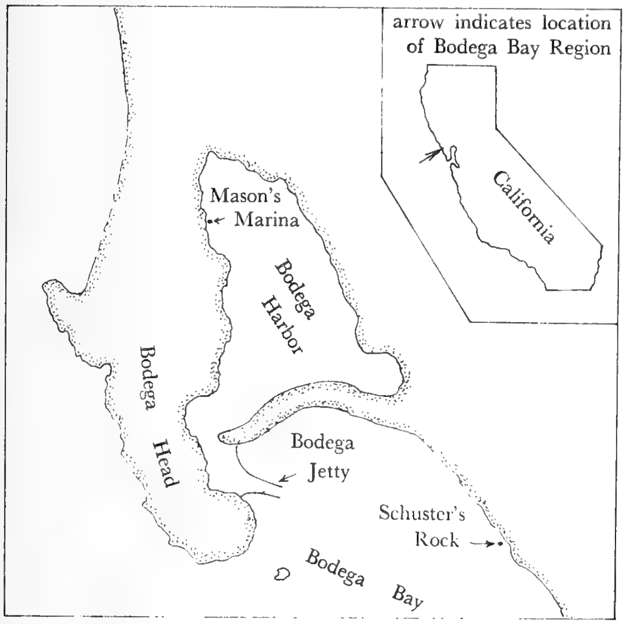


Figure 2

Map of the Bodega Bay Region, Sonoma County, California

Twenty-three additional examples of *Polycera zosterae* were seen throughout the month of July at the 3 locations previously mentioned. The animals from the jetty were always found on or near *Bowerbankia* in these additional observations.

Individuals ranged in size from 10 mm to 17 mm in length and usually were found in close proximity to their characteristic egg masses. The presence of egg masses directly adhering to the colonies of *Bowerbankia* was noticeable at both the jetty and the marina. The egg ribbons were typically polycerid in form, the numerous white open circlets being deposited among the zoöecia and stolons of the bryozoan colonies. The individual ribbon circlets rarely exceeded 10 mm in diameter.

The presence of *Polycera zosterae* in the Bodega Bay region constitutes a southern range extension of approximately 900 miles (1440 km).

It should be noted that additional observations were made at Mason's Marina in September, 1971 and January, 1972. No specimens of *Polycera zosterae* were seen at either of these times. Only sparse growths of *Bowerbankia* were observed. The presence of *P. zosterae* appears to be dependent upon the existence of substantial growths of *Bowerbankia,* although this is by no means conclusive. It is not known whether the fluctuations in the *Bowerbankia* population are dependent solely on seasonal conditions or whether succession within the marina is the determining factor. It should also be noted that *P. zosterae* apparently can tolerate a variety of habitat situations, including open rocky shores and protected rocky areas as well as the waters of calm bays.

Literature Cited

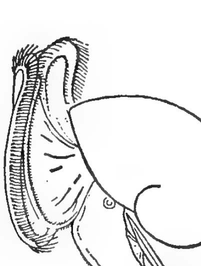
HOWELL, JOHN THOMAS
1970. Marin Flora. Univ. Calif. Press, Berkeley; 366 pp.

LIGHT, SOL FELTY, RALPH INGRAM SMITH, FRANK ALOYSIUS PITELKA, DONALD PUTNAM ABBOTT & FRANCES M. WEESNER
1964. Intertidal invertebrates of the central California coast. Univ. Calif. Press, Berkeley; xiv+446 pp.; 138 figs.

MARCUS, ERNST
1964. A new species of *Polycera.* The Nautilus 77 (4): 128 - 131

MARCUS, EVELINE DU BOIS REYMOND & ERNST MARCUS
1967. American opisthobranch mollusks. Studies in tropical oceanography (Univ. Miami Inst. Marine Sci., Miami, Florida), no. 6: viii+256 pp.; figs. 1 - 155 + 1 - 95 (December 1967)

O'DONOGHUE, CHARLES HENRY
1924. Notes on the nudibranchiate Mollusca from the Vancouver Island region. IV. Additional species and records. Trans. Roy. Canad. Inst. Mar. Sci. 15 (1): 1 - 33; plts. 1, 2 (December 1924)



METHODS & TECHNIQUES

Preserving Terrestrial Slugs by Freeze-Drying

BY

H. H. CROWELL

Department of Entomology, Oregon State University
Corvallis, Oregon 97331[1]

TERRESTRIAL SLUGS (families Limacidae, Arionidae, and others of the molluscan class Gastropoda) are usually preserved for study in alcohol or formalin solutions. Both of these preservatives deprive the specimens of much of their natural color, resulting in very unattractive displays. Furthermore, "wet" collections have the disadvantage of occupying more space and of requiring more maintenance than do "dry" collections. The process of freeze-drying was investigated, with the objective of developing a preservative securing more natural appearing specimens which could be stored and displayed easily as synoptic collections or teaching aids.

It soon became apparent that there were several independent steps to the process which were essential for producing acceptable specimens. These are as follows:

(1) the slug must be inactivated (or killed) in the natural extended position desired in the final product;
(2) frozen in the desired posture;
(3) freeze-dried (a process requiring a specialized piece of equipment);
(4) coated with a clear shiny material to bring out the color and markings of the specimen and to give it the appearance of a moist mucus coating; and finally
(5) mounted as a specimen for display or study.

It should be pointed out that freeze-dried slugs are probably not good material for serious taxonomic studies, since diagnostic characters in this group of organisms rely heavily on form and arrangement of various parts of the reproductive system and on the position of major muscle groups.

Drowning

Possibly the most important step in the freeze-dry process with slugs is the first – the immobilization of the specimen in a natural position for freezing. The time-honored method of killing slugs for preservation is by drowning in water. Because of the heavy secretion of mucus in the presence of irritating chemicals, most methods for killing and fixing small animals are not applicable to slugs. A drowned slug is usually well extended, but one must position the animal carefully before freezing to prevent dents, creases or other unnatural deformations.

A small slug can be drowned in a tightly capped container full of water at room temperature in about 12 hours. Almost 24 hours are required to drown a large specimen, such as a mature *Arion ater*. A "half-drowned" slug may appear dead, but will later contract into an undesirable position when placed in the freezer. An "over-drowned" slug decomposes rapidly.

The desired situation is to render the extended animal completely immobile so that it can be frozen in a natural posture within a reasonable length of time. Since the use of sugar, thymol, chloral hydrate, and other additives to the water used for drowning have been suggested by various workers for improving the appearance of slugs being readied for preservation, we studied the use of several drugs and other chemicals, hoping to reach the right state of immobility of the animals quicker and with more dependability than by simple drowning.

Use of Drugs, Salts, and other Chemicals

The test summarized here involved use of chemicals as additives to immersion water, and the results are given in Table 1. Some potential materials, such as Chloretone (HUBRICHT, 1951), were not tested in this rather cursory study. Propylene phenoxetal (ROSEWATER, 1963) used alone was not satisfactory, but the combination with Nembutol, described by RUNHAM (1965) as being rapidly effective against land slugs, was not tested.

Of the various treatments recorded in Table 1, none gave the results desired except ethyl alcohol. This treatment suggested itself because of the current popularity of using dishes of beer in home gardens for control of slugs (SMITH, 1970). Beer can substitute for the 5% alcohol dilution as a narcotizing agent.

An exposure time of 1½ hours in 4 - 6% ethyl alcohol is a minimum for large slugs to prevent them from moving after being put in the freezer. More studies are needed to determine how short an exposure would be necessary for

---

[1] Oregon Agricultural Experiment Station, Technical Paper No. 3275

immature forms or small species. Since over-night to 24 hour drowning is required with plain water, the use of alcohol greatly shortens the time needed to process a slug for freezing.

Freezing

Once the animal is completely immobilized, it should be positioned in a container (such as a Teflon-coated pie pan) which can later be placed in the lyophilizer. Any

Table 1

An annotated list of drugs and salts tested as narcotizing agents on slugs in immersion water solutions

Material and Concentrations of Immersion Solutions	Species tested [1]	Remarks
Benzocaine (0.01 - 0.1%)	*Deroceras* *Arion* *Limax* *Helix*	Ineffective at 0.01%; excessive sliming above 0.025%
Propylene Phenoxetol (3-phenoxypropanol) (0.5%)	*Arion* *Deroceras*	Excessive sliming and shrinkage even after prior exposure to benzocaine
Carbaryl (Sevin) (ca. 1% of 50% W. P.)	*Prophysaon*	Immersion for 24 hours; inferior to specimens drowned in water alone
Nembutol (sodium pentobarbitol) (0.25% - 4.0%)	*Helix* *Arion* *Deroceras* *Limax flavus* *Limax maximus*	Little sliming up to 2 hours in 4%, but animals still reactive to stimuli; quiet and positioned well, but contracted under refrigeration
Nembutol (2 - 4%) DMSO (dimethyl sulfoxide) (4 - 6%)	*Arion* *Helix* *Limax maximus* *Limax flavus*	Positioned poorly; tended to be stiff or excessively flaccid
Sucrose (1.0, 0.5, 0.1%)	*Arion* *Helix*	*Helix* swelled excessively; *Arion* slimed excessively
Salt Solutions:		
NaCl (0.9, 0.7, 0.5, 0.3, 0.1%)	*Arion* *Helix*	Excess sliming down to 0.3%; below this concentration no difference from water
$Ca_3(PO_4)$ [2]	*Arion* *Helix*	Good posture after 6 hours in 0.2 - 0.05%, but excess sliming with *Arion*
MgCl [2]	*Arion* *Helix*	Animals tend to swell excessively
KCl [2]	*Arion*	0.2% conc. gave better appearing specimens than water, but no reduction in time
$Na_3(PO_4)$ [2]	*Arion* *Helix*	Excessive sliming at 0.1%
Ethyl alcohol (4 - 8%)	*Arion* *Limax*	1½ hours in 4 - 6% very satisfactory: minimum sliming, no contraction in freezer; 3% not effective enough; 7% caused excessive sliming. Disadvantage: tentacles not well extended
Beer (ethyl alcohol content ±5%)	*Arion* *Limax*	Results similar to dilute ethyl alcohol. *Limax* tends to be more flaccid in beer

---

[1] Species tested were *Deroceras reticulatum, Arion ater, Helix aspersa, Prophysaon andersoni,* and *Limax flavus* unless otherwise stated

[2] Various concentrations tested in "effect – no effect" ranges

freezer which can keep ice cream hard is suitable for freezing slugs. If the specimen is to remain more than a day or two in the freezer, it should be covered to prevent dehydration or "freezer burn." Twenty-four hours in a freezer at −12° C or lower is sufficient to freeze a specimen solidly. An attempt to quick freeze a slug specimen not previously drowned or anesthetized, by dropping it into liquid nitrogen, produced a very unsatisfactory specimen. Even at the extremely low temperatures involved, the slug, a mature *Arion ater,* was able to contract its body and secrete a considerable amount of slime!

Lyophilizing

The equipment used successfully in these studies was the Virtis "UNITRAP", Model 10-103 (The Virtis Company, Inc., Gardiner, New York). The vacuum pump and motor do not come with this model and CENCO Hyvac 7 or equivalent is recommended by the Virtis Company for use with their "Unitrap" lyophilizer. Another accessory necessary for bulk freeze-drying of such things as slugs is a "heat rack." Instructions for the operation of the freeze-drier come with the equipment. Twenty-four to 48 hours are required to dry a pan of frozen slugs. The principal precaution to take for this step in the process is to arrange for transfer of the slug specimens from the freezer to the lyophilizer without thawing them to any degree. The specimens must be solidly frozen when they are placed into the readied lyophilizer.

Cleaning and Coating

Specimens taken directly from the lyophilizer have a faded and dusty appearance. This is partly due to the presence of freeze-dried mucus on the surface of their bodies. A camel's-hair brush can be used to remove most of the dry mucus. At this stage the specimen can be handled rather roughly.

To darken the specimen and bring out its natural pigments, we found that any clear coating material, such as shellac, lacquer or plastic preparation, was satisfactory. A high gloss material is best, since it leaves the animal shining as if it were moist with natural mucus. A fast drying liquid is essential, however, since the specimens must be handled and turned several times in order to get thorough coverage. Application of the liquid with a small brush proved to be rapid and effective. Use of an aerosol coating preparation (such as KRYLON Crystal Clear Spray Coating No. 1300A) is equally good, but more wasteful of material.

Mounting

Finally, the specimens can be mounted for display or study by pinning them as if they were insects. Large specimens require 2 pins to keep them from pivoting. We have found that freeze-dried slugs can be attacked and damaged by dermestid beetles just as are dried insects, but a supply of paradichlorobenzene in the box or case will protect them.

ACKNOWLEDGMENT

I wish to thank James F. Chalmers, former assistant in the Department of Entomology, who conducted most of the narcotization tests and operated the lyophilizer.

Literature Cited

Hubricht, Leslie
1951. The preservation of slugs. The Nautilus **64** (3): 90 - 91
Rosewater, Joseph
1963. An effective anesthetic for giant clams and other molluscs. Turtox News **41** (12): 300 - 302 (December 1963)
Runham, N. W., K. Isarandura & B. J. Smith
1965. Methods for narcotizing and anaesthetizing gastropods. Malacologia **2** (2): 231 - 238 (25 February 1965)
Smith, Floyd F. & A. L. Boswell
1970. New baits and attractants for slugs. Journ. Econ. Entomol. **63** (6): 1919 - 1922

A Device for Collecting Free-Swimming Bivalve Larvae from Laboratory Aquaria

BY

KEVIN J. ECKELBARGER

Marine Science Institute, Northeastern University
East Point, Nahant, Massachusetts 01908

(1 Text figure)

It is frequently difficult to collect planktotrophic larvae from large laboratory aquaria for use in experimental work. Removing free-swimming larvae from cultures by pipette is both tedious and inefficient. It would, therefore, be useful to have a device which automatically collects and stores larvae until needed. Such an apparatus was constructed while studying the effects of temperature and reduced salinity on the larvae of the wood-boring pelecypod, *Lyrodus pedicellatus* Quatrefages (1849) (Eckelbarger & Reish, 1973). Large numbers of larvae were periodically required for use in experiments, and hand collection became impossible. The larval collector (Figure 1) was constructed to alleviate this problem.

The collector consists of a 250 ml-capacity, wide-mouth glass jar sealed with a 2-holed rubber stopper. Plastic aquarium stems (which can be purchased at an aquarium shop) carry sea water into and out of the collector. The siphon tube (Figure 1) carries sea water and larvae, when present, into the collector. Sea water is pumped back into the gallon jar through the return line by compressed air. The return line both aerates the contents of the gallon jar and creates circulation for the movement of larvae towards the siphon tube. Larvae are prevented from leaving the collector by a "nytex" screen placed over the return line intake. The screen pore size was 125μ in this case but should be selected on the basis of larval size. The flow rate of sea water through the collector was approximately 200 ml/min.

Wood blocks containing adult *Lyrodus* were brought from the field and placed in 1-gallon-capacity wide-mouth glass jars containing filtered sea water at room temperature. The larval collector was attached to the side of the gallon jar and left operating from a few hours to overnight. Pediveligers released by the parents in response to temperature rise were collected in large numbers in a few hours. The collector was then opened and the larvae were removed when needed for use in experiments. If left operating overnight, the collector would effectively filter out virtually all of the larvae in the gallon culture jar.

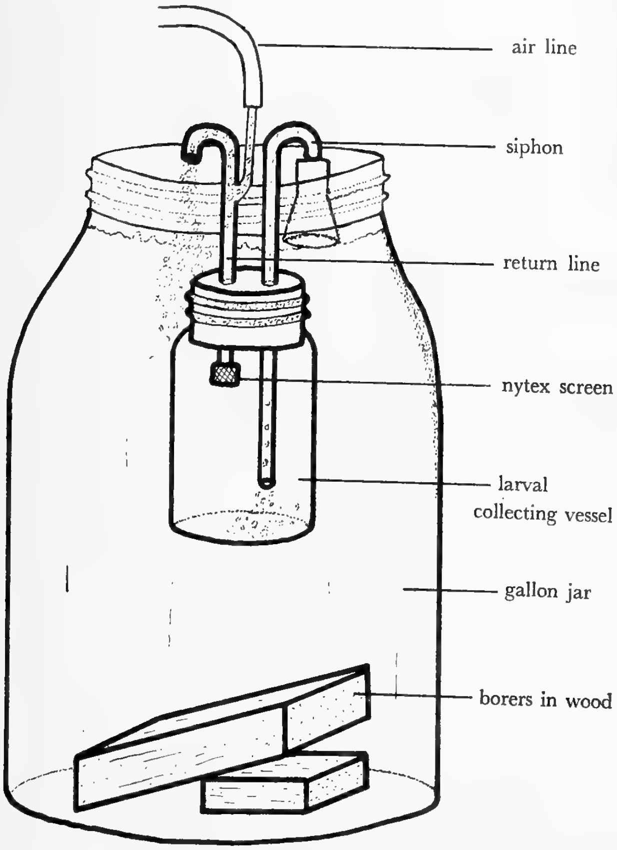


Figure 1
Larval Collecting Vessel

Although this collecting device was used only for gathering *Lyrodus* larvae, it could presumably be used for collecting free-swimming larvae from laboratory cultures containing a wide number of species. Minor adjustments could be made as to the pore size of the screen and the flow rate of the system according to the species involved.

Literature Cited

Eckelbarger, Kevin J. & Donald J. Reish
1973. The effects of temperature and reduced salinity on the settlement, growth and reproduction of the wood-boring pelecypod, *Lyrodus pedicellatus* Quatrefages. Bull. So. Calif. Acad. Sci. 71: in press

---

NOTES & NEWS

Spawning and Development of the Eggs, in the Laboratory, of *Illex coindetii*

(Mollusca : Cephalopoda)

BY

S. v. BOLETZKY, L. ROWE[1] AND L. AROLES
Laboratoire Arago, 66 Banyuls-sur-Mer, France

In mid-June 1972, an adult female squid, *Illex coindetii* (Verany, 1837), was recovered alive and undamaged, from a bottom trawl catch near Banyuls-sur-Mer (western Mediterranean). The animal was placed in a tank with running sea water at 15° C. It spawned in the early morning of the next day and soon died.

The completely transparent jelly of the egg mass covered the entire bottom of the tank (40 × 60 cm) and had

---

[1] Present address: Marine Sciences Research Laboratory of the Memorial University, St. John's, Newfoundland, Canada

a thickness of several centimeters (*cf.* Hamabe, 1963). The eggs enclosed in the jelly (50 000 to 100 000) were only a small fraction of the ovary content (18g) of the female (total weight 253g).

The newly hatched eggs measured 1 × 0.8mm. As in other decapods, the chorion strongly swells during embryonic development, attaining a diameter of about 2mm, which corresponds to the total length of the larva before hatching (mantle length 1.4mm). The general characteristics of the embryonic development observed by us match the figures given by Naef (1923: plts. 9 - 12) of an unidentified egg mass of a member of the Ommastrephidae.

Parts of the egg mass were removed and kept at 10° C and at room temperature (20° - 22° C), while the bulk of eggs remained at 15° C. All samples were kept in artificially aerated sea water.

At 10° C, the eggs did not develop and soon degenerated.

At 15° C, the eggs developed well. Unfortunately, the cooling system of the constant temperature room broke down after 3 days. The data obtained until then suggest that embryonic development will take - roughly estimated - about 10 to 14 days at 15° C.

At 20° - 22° C, embryonic development was much faster and took only 6 - 7 days to attain stage XX (according to Naef, 1923). Many larvae hatched prematurely, from about stage XVI onward, 4½ - 5 days after spawning. Presumably this would not occur under natural conditions.

The young animals that hatched "normally" were active swimmers showing the gentle jet propulsion typical of planktonic cephalopod larvae while maintaining an oblique position, head down.

In these larvae, the volume of the elongate internal yolk mass was not markedly smaller than at earlier stages of embryogenesis. It is likely that predation begins only several days after hatching when the fused tentacles are further developed.

To our knowledge, this is the first time that the eggs and embryos of an *Illex* species have been identified and studied alive. A detailed description of the embryonic development, allowing a comparison with observations on *Todarodes* (Hamabe, 1961), will be published later.

Literature Cited

Hamabe, Mototsugu

1961. Experimental studies on breeding habit and development of the squid, *Ommastrephes sloani pacificus* Steenstrup. III. Early embryonic development and morphological features of the larvae immediately after hatching. Zool. Mag. **70**: (12): 408 - 420

1963. Spawning experiments of the common squid, *Ommastrephes sloani pacificus* Steenstrup, in an indoor aquarium. Bull. Japan. Soc. Scient. Fish. **29** (10): 930 - 934

Naef, Adolf

1923. Die Cephalopoden. Fauna Flora Golfo Napl. 35th Monogr. vol. **1**: 1 - 148; 37 plts.; text figs. 1 - 62; vol. **2**: 149 - 863; text figs. 63 - 473

New Name for *Pyramidella (Triptychus) olssoni* Bartsch, 1926

BY

JAMES X. CORGAN

Austin Peay State University
Clarksville, Tennessee 37040

The first Pacific species referred to *Triptychus* Mörch, 1875, was *Pyramidella (Triptychus) olssoni* Bartsch (1926: 2; plt. 1, fig. 11). This species, from the Recent fauna of Santa Elena Bay, Ecuador, is correctly assigned to *Triptychus* and, in modern works, *Triptychus* is generally ranked as a genus (e. g.: Bartsch, 1955: 8). As the synonymy given below demonstrates, the name ***Pyramidella (Triptychus) olssoni*** Bartsch, 1926, is preoccupied. Since there is no known synonym, a replacement name seems necessary.

Triptychus ***pacificus*** Corgan, nom. nov.

Not *Pyramidella olssoni* Maury, 1917, p. 145; plt. 25, fig. 8
Pyramidella (Triptychus) olssoni Bartsch, 1926, p. 2; plt. 1, fig. 11

Derivation of Name: In allusion to its occurrence in the Pacific Ocean.

Literature Cited

Bartsch, Paul

1926. Additional new mollusks from Santa Elena Bay, Ecuador. Proc. U. S. Nat. Mus. 69 (20): 20 pp.; 3 plts. (16 December 1926)

1955. The pyramidellid mollusks of the Pliocene deposits of North St. Petersburg, Florida. Smithson. Misc. Coll. 125 (2): 102 pp.; 18 plts. (5 May 1955)

Maury, Carlotta Joaquina

1917. Santo Domingo type section and fossils. Part 1. Mollusca. Bull. Amer. Paleont. 5 (29): 251 pp.; 39 plts.

A. M. U.

The Annual Meeting of the American Malacological Union, Inc. will be held June 24 to 27, 1973, on the campus of the University of Delaware in Newark, Delaware. Co-hosts will be the Delaware Museum and the Wilmington Shell Club. A varied and interesting program is being planned. Details regarding attendance and participation may be obtained from the Membership and Publicity Chairman, Dr. John B. Burch, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104.

Stanford University
Cenozoic Mollusk Collection

The Stanford University conchological collection, which began in the early 1890's, was started as a supplement to the Tertiary fossil collection, for one can best understand the fossils by studying their Recent counterparts. The collection has since grown to be one of the two or three largest university-owned collections in the United States. During all these years the fossils and the Recent shells were kept in separate rooms. Now they are housed as a unit that is to be called the Stanford University Cenozoic mollusk collection. The exhibits of shells, which were the only part of the collection that the casual visitor saw, have been moved to a well-lighted and much more accessible room on the second floor of the Geology Building (Room 330). They can be seen by the public without interference or hazard to the main collection, which remains where it has always been, on the third floor (Room 341). The fossil collections -- in storage for the past several years -- have been moved to the area where the exhibits stood. Both parts (fossil and Recent) of this Cenozoic mollusk collection are open, by appointment, to qualified visitors.

Donations Received by the Veliger

The Veliger Endowment Fund has been the beneficiary of the generosity of the San Diego Shell Club and the Conchological Club of Southern California, as well as of an anonymous reader who sent the sum of $ 1000.- from Düsseldorf, W. Germany. As stated previously, these gifts, through the interest they earn for the Veliger Operating Fund, continue to assist us in our effort to keep the cost of our journal at the lowest possible level to our members and subscribers in spite of the ever increasing costs of production. We are most grateful for the encouragement implied by these generous donations.

Important Notices

It is with great regret that we must announce the following increases in Membership Dues and Subscription Rates. effective with volume 16:
Membership Dues are US$12.00; to this we must add US$1.50 for members living in Canada, Mexico, Brazil, and all Spanish speaking countries (postally known as PUAS-countries); for members in all other foreign countries, the postage charge will be US$2.00. The basic subscription rate is set at US$25.00; to this must be added the same postage charges as for members.

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$6.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$12.00 for all foreign addresses (including PUAS).

Because of the peculiar rate-fixing policies of the Postal Service (the so-called "temporary rates" which may be put in effect without advance notice, pending a final decision by the Rate Fixing Commission) we must reserve the right to ask our members and subscribers for additional payment for postage charges; however, because of the rather high cost such an extra collection would cause, we expect to absorb any but unbearable increases. That such increased charges may have to be reflected in future price schedules is evident.

It is general knowledge that in spite of the optimistic statements made in the propaganda disseminated by the U. S. Postal Service, the service continues to deteriorate. Regrettably, however, the United States of America is not alone in this respect. Evidence is accumulating in our offices to the effect that irregularities occur in other countries as well; to our surprise, Japan is one of these. Since we have designed a system which makes it impossible to omit mailing copies of our journal to any member or subscriber who is paid up, and because of the regulations pertaining to the second class mailing permits, we know that if a copy does not reach the addressee, the fault lies with the postal system of the country or area of destination. Our complaints to the local Post Office can bear no fruit in such cases. We must request our members and subscribers to inquire at their local post offices if their copies do not arrive. We cannot replace lost copies free of charge and, unless the journal were mailed by insured post, the Post Office will not indemnify the injured party. The losses we have sustained in the past years have been mounting steadily, and not in proportion to our increased circulation.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $2.50 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

THE CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.
announces

Backnumbers of

THE VELIGER

and other publications

Volumes 1 through 8: out of print

Volume 9: $22.- Volume 10: out of print
Volume 11: $24.- Volume 12: $28.-
Volume 13: $24.- Volume 14: $28.-

Supplement to Volume 3: $6.-* plus $-.75 handling charge
[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;

Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

[The two parts are available separately at $3.- each plus a handling charge of $-.75 or as indicated above. If purchased separately, each part is subject to the California State sales tax if mailed to California addresses.]

Supplement to Volume 7: $2.-* plus $-.60 handling charge

[Glossary of A Thousand-and-One Terms used in Conchology, compiled by WINIFRED H. ARNOLD]

Supplement to Volume 11: $5.-* plus $-.75 handling charge.

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Vol. 14: $5.-* plus $-.75 handling charge
[The Northwest American Tellinidae by Dr. E. V. Coan]

Items marked with * are subject to sales tax in the State of California; residents of that State please add the appropriate amount to their remittances.

Prices subject to change without notice.

Send orders with remittance to:

Mrs. Jean M. Cate, *Manager*, Post Office Drawer R, Sanibel, Florida 33957. Please make checks payable to C. M. S., Inc.

Shipments of material ordered are generally made within two weeks after receipt of remittance.

Subscription to Volume 15: $18.- domestic, $19.50 in Canada, Mexico, Central and South America; $20.- in all other foreign countries.

Subscription to Volume 16: $25.- domestic; $26.50 in Canada, Mexico, Central and South America, Spain and Spanish Morocco; $27.- in all other foreign countries.

{We are pleased to announce that we have completed arrangements with Kraus Reprint Co. to reprint those of our publications that are out of print. Inquiries regarding the availability and price(s) of desired items should be addressed to:

Kraus Reprint Co.
16 East 46th Street,
New York, N. Y. 10017

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first working day of the month following receipt of the remittance. The same policy applies to new members.

Affiliate Membership for the fiscal year July 1, 1972 to June 30, 1973 has been set at $8.-. Postage for members in Canada, Mexico, Central and South America $1.50, for members in any other foreign country $2.- additional.

Affiliate Membership for the fiscal year July 1, 1973 to June 30, 1974 has been set at $12.-. Postage for members in Canada, Mexico, Central and South America, Spain and Spanish Morocco $1.50; for members in any other foreign country $2.- additional.

Effective January 1, 1967 there will be an initiation fee of $ 2.- for persons joining the Society.

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.

Supplements

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

Requests to be placed on this special mailing list should be sent to the Manager, Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957.

General Notices

Moving?

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

change of address – $1.-

change of address and re-mailing of a returned issue – $2.-.

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.

REGARDING POSTAL SERVICE

We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address). We are not able to replace lost copies free of charge but must charge single copy rates. There will, of course, be only the usual charge of $1.00 for re-forwarding a copy *IF* it has been returned by the post office to us. We also must urge our members and subscribers to place written complaints with the U. S. Post Office Department in case of loss, as every copy of our journal carries our guarantee for return postage. Thus, destruction of a copy of our journal by postal employees constitutes gross negligence and the person concerned deserves an official reprimand, at least.

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

California Malacozoological Society, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

Endowment Fund

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

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

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

BOOKS, PERIODICALS, PAMPHLETS

The Geology and Paleontology of the Marine Pliocene of San Diego, California (Paleontology : Pelecypoda)

by LEO GEORGE HERTLEIN & U. S. GRANT, IV. San Diego Society of Natural History Memoir 2 (part 2B); pp. 135 - 411; text figs. 7 - 13; plates 27 - 57. $15.00 from the San Diego Natural History Museum. July 21, 1972.

This, the third part of a series on the San Diego Pliocene and the last of the late L. G. Hertlein's major publications on marine invertebrates, is the substantive taxonomic treatment of Pliocene pelecypods from the Pacific Coast. Nearly 150 specific and subspecific taxa are treated in this comprehensive and beautifully illustrated quarto size monograph. Fifteen taxa including a venerid genus, *Irusella,* and a glycymeridid subgenus, *Axinola,* are described as new.

Surprisingly, this is the first detailed treatment of the large molluscan fauna of the San Diego Formation, the largest previously listed fauna having been recorded by W. H. Dall about 100 years ago. Through the cooperation of George P. Kanakoff, who collected much of the material upon which this monograph is based, the number of pelecypod taxa initially listed by Dall has been increased some sevenfold.

The thoroughness of this monograph is indicated by the inclusion of diagnoses of families, genera, and subgenera. There are helpful keys to the genera, subgenera, and many of the species of the San Diego Formation. Each species or subspecies is carefully compared with similar or related fossil and living species from the North Pacific. Many comparisons are made with taxa from northwest Pacific faunas from Japan, Sakhalin, and Kamchatka. The geologic record of each genus is discussed together with the distribution and diversity of the known modern eastern Pacific species. The report is thoroughly documented; there are nearly 1 400 references and footnotes which, unfortunately, are in a separate section at the end of the text. Useful references to the anatomy, evolution, taxonomy, and zoogeography of genera are cited; many of these are from the European literature. Although there is neither a bibliography nor faunal checklist, there is a very useful index to generic and specific names.

A substantial part of the monograph – 43 pages and 9 plates – is devoted to a detailed treatment of the San Diego pectinids, this being the molluscan family on which the senior author was a widely recognized authority.

Inasmuch as the majority of the pelecypods from the San Diego Formation are still living, this comprehensive work will be of wide interest to Pacific Coast malacologists as well as to molluscan paleontologists.

W. O. Addicott

A Partial Bibliography of Oysters, with Annotations

by EDWIN A. JOYCE, Jr., Florida Department of Natural Resources Special Report No. 34; 845 pp.; June 1972.

This extensive bibliography includes more than 4 100 references, almost half of which are annotated. There is a useful subject index. Joyce's compilation supplements an earlier annotated bibliography on oysters and other commercial shellfish by J. L. Baughman (Texas A. & M.

Research Foundation, 1948) with coverage extending through mid-1969. Included are reports published prior to 1948 dealing with commercial bivalves that were not cited in Baughman's earlier bibliography.

Coverage is strongest for the United States and Canada with particular emphasis on the Atlantic coast. Many European and Japanese publications are included and there are a few Russian titles.

W. O. Addicott

Cirrate Octopods with Associated Deep-Sea Organisms: New Biological Data Based on Deep Benthic Photographs (Cephalopoda)

by Clyde F. E. Roper & Walter L. Brundage, Jr.
Smithsonian Contributions to Zoology, Number 121; 46 pp.; 53 figures in text; quarto. For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402; price 65 cents (paper cover).

This work is based on some of the advanced photographic techniques which have opened up new frontiers to research in the ocean deeps. A number of photographs from several deep-sea locations in the North Atlantic show that cirrate octopods live just above the bottom of the ocean in depths of 2500m and down to below 5000m. The animals exhibit typical cephalopodan locomotion; they also have a drifting and a hunting phase. In size these octopods range from 10 to 128cm in length.

Cirrate octopods are more abundant in the Virgin Islands Basin than in other areas investigated.

In addition to the astonishingly detailed photographs of the octopods, others show plant debris and animals, as well as traces of organisms that have been there; these pictures are interpreted to indicate that the abundance of pelagic and benthopelagic organisms is dependent on the presence of plant material of shallow-water provenance.

RS

The Systematics and Areal Distribution of Pelagic Cephalopods from the Seas off Southern California

by Richard Edward Young. Smithsonian Contributions to Zoology, Number 97. September 18, 1972. 159 pages, of which 38 are halftone plates; 15 figures in text; 25 tables; quarto. For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402; price $2.- (paper cover).

The abstract of this work indicates that 42 pelagic species of cephalopods are now known from off southern California. The fauna is part of the transitional and subarctic fauna off southern California, while off northern Lower California it includes primarily tropical species.

An abstract can never do a paper full justice. The work describes the study area and lists the material examined. It gives a key to the species described. After the systematic treatment of the species is given a checklist of cephalopods definitely known to occur in southern Californian and neighboring waters.

The new species described are:

Abraliopsis falco; pp. 13 - 17; figs. plt. 1A, B, 2A - G
Pyroteuthis addolux; pp. 22 - 25; figs. plt. 3B, 4I - Q, S
Octopoteuthis deletron; pp. 40 - 43; figs. plt. 10H - M, 11, 12A - D
Gonatus onyx; pp. 43 - 46; figs. plt. 13A, 14A, C - I, 17J
Gonatus onyx; pp. 49 - 51; figs. plt. 13A, 14A, C - I, 17J
Gonatus pyros; pp. 49 - 51; figs. plt. 13B, 14B, J - Q, 17G - I, K
Gonatus californiensis; pp. 51 - 56; figs. plt. 15B, 16B, J - P, 17D - F
Mastigoteuthis pyrodes; pp. 64 - 69; figs. plt. 25, 26I - Q
Chiroteuthis calyx; pp. 69 - 72; figs. plt. 20, 21A, B, 22 A - K, N - Q
Valbyteuthis oligobessa; pp. 72 - 74; figs. plt. 23A, B, 24 H - N, Q, R
Leachia dislocata; pp. 80 - 83; figs. plt. 30B, 31, 32

RS

Two New Species and a New Subgenus of Lucinidae with Notes on Certain Aspects of Lucinid Phylogeny (Mollusca : Bivalvia),

by Joseph C. Britton, Jr. Smithsonian Contributions to Zoology, Number 129. November 15, 1972. 19 pages, 6 figures in text; 3 tables; quarto. For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402; price 35 cents.

The new species described are *Lucina (Pleurolucina) hendersoni* and *Parvilucina (Bellucina) rehderi*. The new subgenus proposed is *Radiolucina* for *Parvilucina amiantus* (Dall, 1901), which is also the type species of the new taxon.

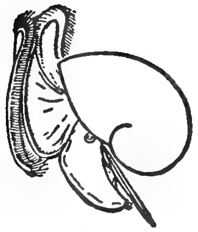
RS

Research Requirements for Development of Molluscan Farming in the United States

by Victor L. Loosanoff. University of Washington Publications in Fisheries, New Series, volume 5; pp. 165 - 179. 1972.

The article points out that shellfishery is still in a relatively primitive stage, mainly due to the lack of sufficiently intensive and extensive research into the food requirements, both qualitatively and quantitatively, of oysters and other commercially important bivalves. There is also insufficient knowledge regarding diseases of these mollusks. While the author seems to advocate the introduction of desirable exotic species, it must be assumed that such introductions would have to be exceedingly closely supervised in order to avoid upsetting the existing local ecological balances with a possible eradication of native desirable species; likewise, extreme care would no doubt have to be exercised in order to avoid the inadvertent introduction of parasitic or predacious species, such as have come to the shores of the United States with exotic oysters. Notwithstanding this one reservation by this reviewer, the paper is an excellent summary of the great number of fruitful research projects in the field of mariculture that await serious and continuous effort.

RS



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.

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 other 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, may be published in the column "NOTES and NEWS"; in this column will also appear notices of meetings of regional, national and international malacological organizations, such as A. M. U., U. M. E., W. S. M., etc., as well as news items which are deemed of interest to our Members and subscribers in general. Articles on "METHODS and 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, and 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.

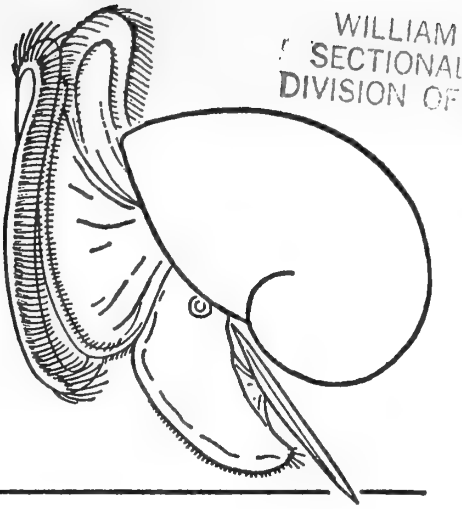
Manuscripts should be typed in final form on a high grade white paper, not exceeding 8½" by 11", at least double spaced and accompanied by a clear carbon or photo copy. A pamphlet with detailed suggestions for preparing manuscripts intended for publication in THE VELIGER is available to authors upon 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.

EDITORIAL BOARD

EDITOR-IN-CHIEF

ASSOCIATE EDITOR

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California

VOLUME 15 April 1, 1973 NUMBER 4

CONTENTS

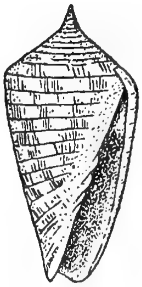
[Continued on Inside Front Cover]

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

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

Second Class Postage Paid at Berkeley, California

CONTENTS — *Continued*



Distributed free to Members of the California Malacozoological Society, Inc.
Subscriptions (by Volume only) payable in advance to Calif. Malacozool. Soc., Inc.
Volume 15: $18.- Domestic; $19.50 in the Americas; $20.- in all other Foreign Countries
Single copies this issue $12.-. Postage additional.
Send subscription orders to Mrs. JEAN M. CATE, Post Office Drawer R, Sanibel, Florida 33957. *Address all other correspondence to* Dr. R. STOHLER, *Editor,* Department of Zoology, University of California, Berkeley, California 94720

Settlement, Growth Rates and Depth Preference of the Shipworm *Bankia setacea* (Tryon) in Monterey Bay

BY

E. C. HADERLIE

AND

J. C. MELLOR

Department of Oceanography, Naval Postgraduate School, Monterey, California 93940

(3 Plates; 6 Text figures)

INTRODUCTION

For the past six years continuous studies have been in progress in Monterey Harbor and in the deeper water of Monterey Bay on fouling and boring organisms. The results of most of these investigations have been published (Miller, 1966; Mommsen, 1966; Haderlie 1968a, 1968b, 1969, 1970, 1971, 1972). Starting in June 1968 a series of separate studies was initiated whose aim was to make a detailed investigation of the settlement, growth rates and depth preferences of the shipworm *Bankia setacea* (Tryon, 1863). These studies continued until January 1972 and this paper presents not only the results of this latter 3½ year investigation but summarizes data on *Bankia setacea* from Monterey Bay collected earlier or already published.

The authors wish to acknowledge extensive help from various crew members of the Naval Postgraduate School's Hydrographic Research vessel for many hours of hard work at sea and the Department of Material Science and Chemistry of the Naval Postgraduate School for advice and use of radiographic and darkroom equipment. The Office of Naval Research (Foundation Program) and the Naval Oceanographic Office provided initial financial support for the project and the Naval Facilities Engineering Command has continued this support.

AREA OF STUDY

The principal focus of this study has been in the Monterey Harbor at a site under Municipal Wharf No. 2 (Figure 1). At this site wooden panels of a variety of sizes were continuously exposed to the marine environment for various times and at various depths for over five years from October 1966 to January 1972. In addition to douglas fir plywood panels and boards, blocks of Scotch pine and 4 × 4 inch fir timbers have also been exposed at various times during this period. The depth of water at this test site is approximately 23 feet at mean lower low water (MLLW) and the maximum spring tide range is about 9 feet. The Wharf is primarily supported by concrete piles spaced 8 to 10 feet apart, but has rows of creosoted douglas fir fender piles along each side. Some of these wooden piles have been in place for 25 years or more and many of them are severely bored by *Bankia setacea,* particularly near the mudline, and each year a few of these break off and must be replaced. All of the piles are covered with a luxurious fouling growth of acorn barnacles, anemones, mussels, ectoprocts, tunicates and polychaetes.

In addition to the harbor site, wooden panels designed to collect *Bankia* have been exposed in open water of Monterey Bay at depths of 50 feet off Del Monte Beach, at 100 feet depth off Del Monte Beach and off Fort Ord, and at 200 feet depth near "B" buoy off the Fort Ord Firing Range (Figure 1).

Sea surface bucket thermometer temperatures were taken daily in the harbor throughout the six year period of this study. These detailed temperature records are on file at the Naval Postgraduate School. Monthly temperatures are summarized from 1966 through 1971 in Figure 2. The monthly range of temperatures from minimum to maximum is represented by vertical bars. All daily sea surface temperatures for each month were averaged, plotted and connected by straight lines to represent average yearly temperature curves. The largest monthly temperature range of 11.3° to 16.8°C occurred in May 1967. The highest temperature (17.4°C) was recorded in September 1968, the lowest (9.5°C) in March 1971. The average temperatures indicate a general upward trend from January to September, with a sharp decline from September through December. Since the temperatures represented in Figure 2 are of the surface water in the harbor, they depict the highest temperatures and largest ranges in temperature to which harbor panels were exposed. Temperatures for January to June 1970 and July 1970 to January 1972 (see Figure 2) represent precise exposure temperatures for floating panels in the harbor. In the early phases of the project surface salinity in the harbor was determined weekly using a hydrometer. During the latter part of this study we relied on surface salinities for the southern part of Monterey Bay as determined by Hopkins Marine Station as part of the CalCOFI program (see Hopkins Marine Station, 1966–1971). Throughout this investigation surface salinities (when averaged monthly) ranged from 32.8% to 33.8%.

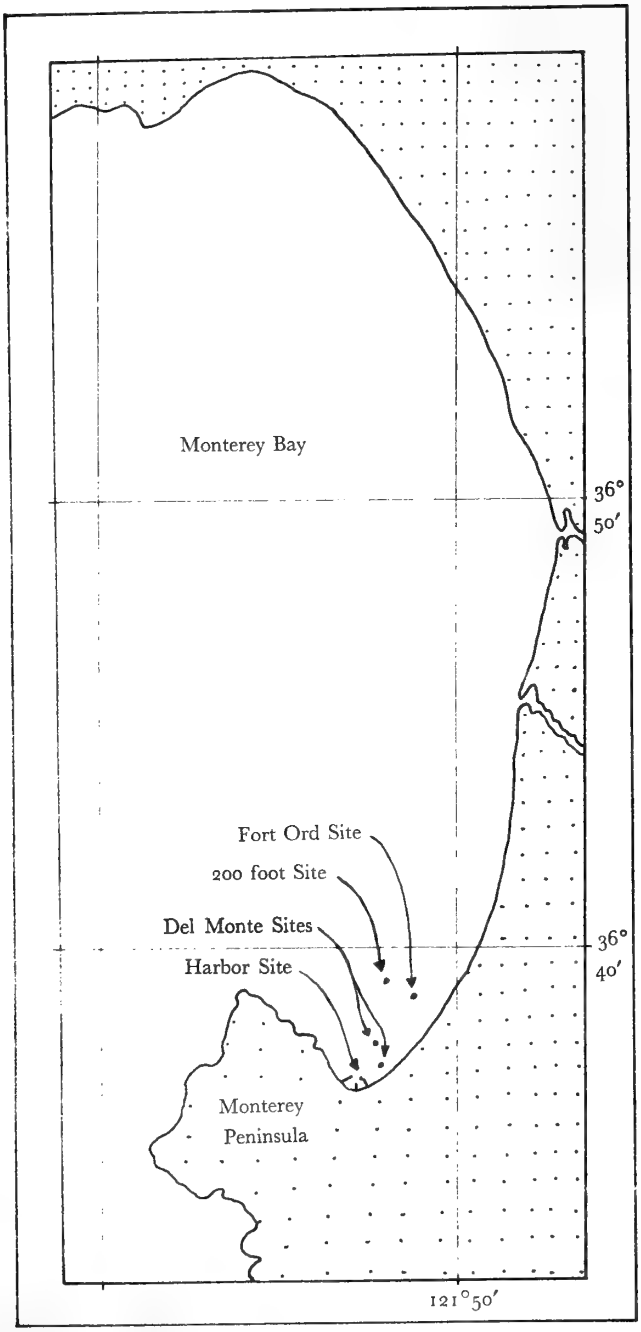


Figure 1

Map of Monterey Bay showing sites of experimental panels

MATERIALS AND METHODS

In the Monterey Harbor test site 8 × 10 × ¼ inch douglas fir plywood panels have been exposed continuously since October 1966. These panels were supported vertically in stainless steel racks; panels were spaced 3 inches apart. The racks were suspended from the wharf at various depths from the mid-intertidal to near the bottom at approximately 23 feet depth. Other racks were placed on floats at the water's surface. These panels were exposed for varying periods of time throughout the period of study (Haderlie, 1968a, 1969, 1970). The plywood panels were primarily employed in the harbor to collect fouling organisms. However, they also collected borers (both *Bankia setacea* and the gribble *Limnoria quadripunctata* Holthuis, 1949) and although ¼ inch panels proved unsuitable for determining growth rates and maximum size of *Bankia* they none-theless were useful in determining periods of settlement, for every two weeks at first and then monthly throughout the 5 year period panels were recovered and carefully analyzed with a binocular stereoscopic microscope (7× to 30× magnification). This made it possible to detect newly settled *Bankia* and to follow periods of settlement throughout the year at various depths. In the later stages of this project ¾ inch thick boards and 4 × 4 inch timbers of douglas fir were exposed simultaneously with the plywood panels and these surfaces collected far greater numbers of *Bankia* per settlement period. This indicated that ¼ inch plywood is not a suitable collector of shipworms and does not give a true indication of numbers of larvae present.

In the open water of Monterey Bay at depths of 50, 100 and 200 feet douglas fir boards 6 × 12 × ¾ inches were employed to collect borers. These are standardized panels being used by the Naval Oceanographic Office for long-

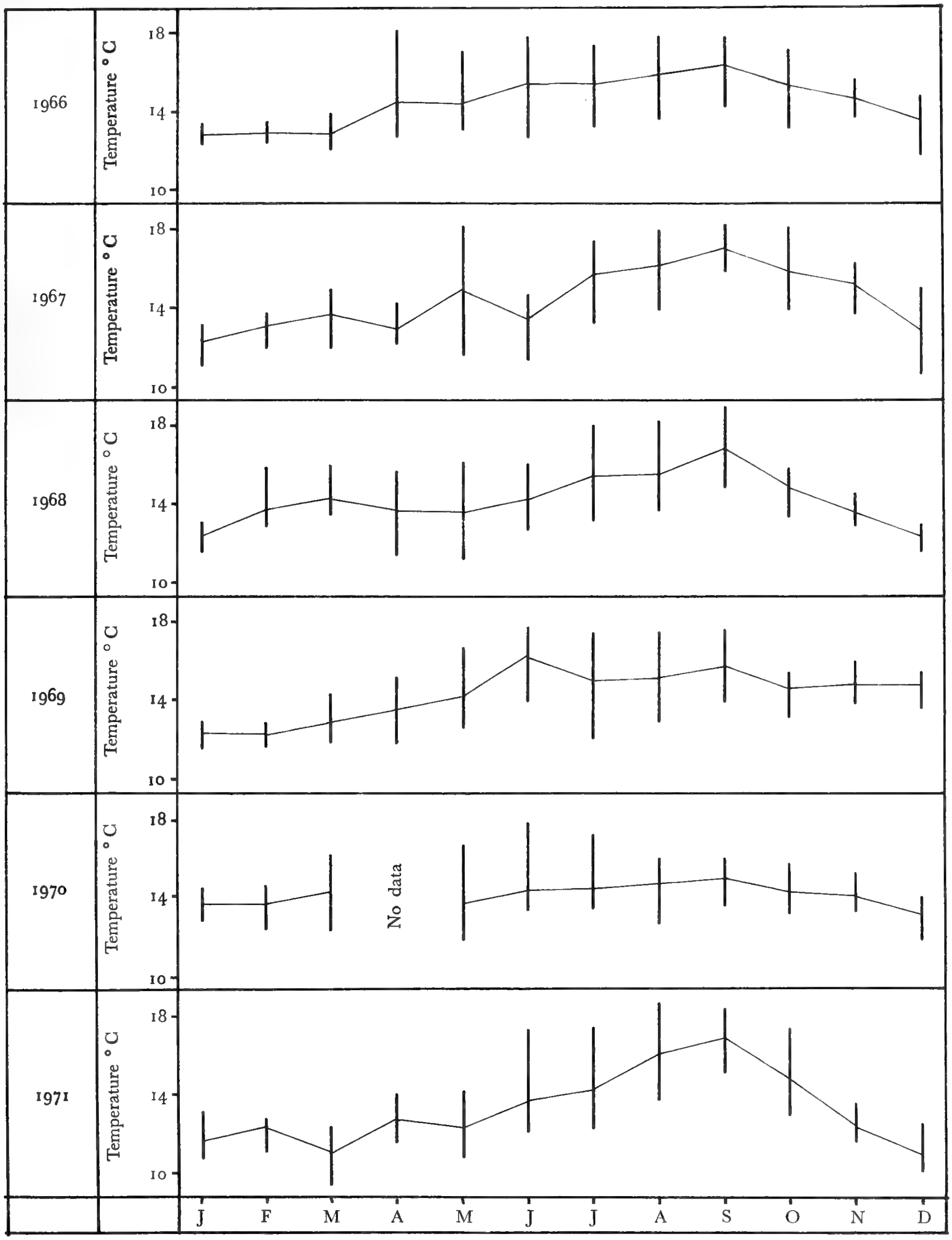


Figure 2

Summary of Surface Water Temperature in Monterey Harbor from 1966 through 1971
Vertical bars indicate monthly range of temperature; connecting lines indicate monthly average temperature

term studies of boring and fouling organisms in coastal waters of the world (DePalma, 1966). During the present studies these panels were arrayed on a taut line mooring system with an anchor on the bottom and floats on the surface. Each panel was attached at one end to the mooring line and was held vertically in the water near the bottom, yet was free to rotate and like flags could align itself with the prevailing currents (Haderlie, 1968b, 1971, 1972). Each month some panels were recovered and new ones exposed; others were allowed to remain in place for cumulatively longer periods of time up to one year. When returned to the laboratory these panels were analyzed with a microscope to detect newly settled borers. Panels harboring mature *Bankia* were either split open or x-rayed to determine number and size of the shipworms (see details of laboratory analyses below).

All of the studies so far described were primarily devoted to fouling organisms with only secondary attention given to borers. It was early realized that different techniques would have to be used in order to gather reliable data on growth rates and depth preferences.

Starting in June 1968 and continuing for 3½ years until January 1972 a series of boards, test blocks and timbers were exposed in the harbor area specifically for the purpose of collecting *Bankia setacea* and analyzing growth rates of shipworms at different depths and seasons. Settlement and growth of foulers was also monitored on most of these test surfaces but the fouling studies were incidental to the main effort devoted to the shipworms. As different test materials of varying sizes were used during the course of this study, it seems best to describe materials and methods used under 5 different headings, for there was this number of different techniques used. Several of these different series were overlapping in time or ran concurrently with one another as will be seen.

O. E. C. D. Project

From 1 June 1968 to 1 June 1969 we participated in a research program sponsored by the Committee for Research Co-operation on the Preservation of Wood in the Marine Environment. This Committee is part of the Organization for Economic Co-operation and Development (O.E.C.D.). The studies made in Monterey were part of a world-wide program whose objectives were to simultaneously study boring organisms, fouling and fungi that degrade wood in the marine environment. Similar test materials and techniques were used at a great number of coastal stations around the world. The only aspect of this year-long study to be reported here will be in connection with *Bankia setacea* settlement and boring into the test blocks.

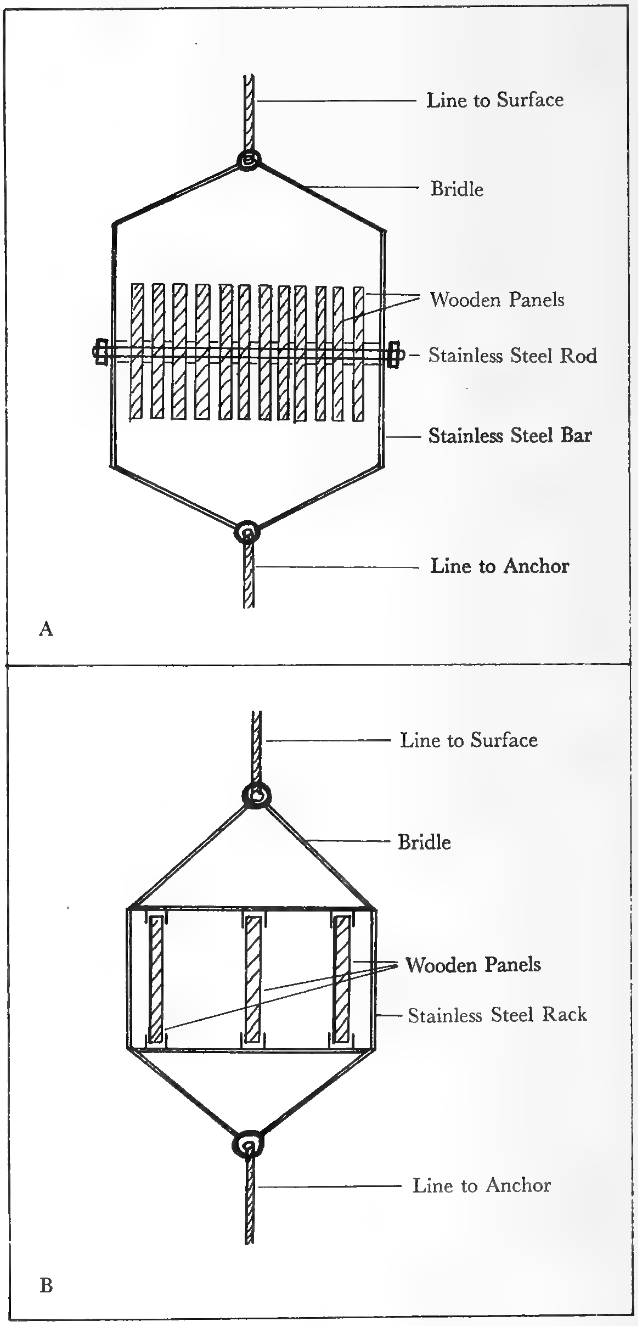


Figure 3

Sketch Illustrating Panel Arrays as Exposed in Monterey Harbor
A. Array used in *Bankia* Series I
B. Array used in *Bankia* Series II

The materials used in this part of the investigation were test blocks of flat sawn sapwood of Scotch pine (*Pinus sylvestris* Linnaeus). Two different-sized blocks were used: small blocks measuring 10 × 20 × 2 cm and large blocks measuring 10 × 10 × 50 cm. In each test block a hole was drilled at either end and lined with plastic tubing. A polypropylene line 18 inches long ran from the bottom hole to a small anchor weight that rested on the bottom in approximately 23 feet of water. From the upper hole in the test block a line ran up to the surface where it was secured to the wharf. Two of the small test blocks were installed on the first of each month throughout the year; one of these was recovered at the end of one month, the other remained exposed for two months before recovery. After removal from the water the small blocks were taken to the laboratory for analysis. After examining each block microscopically for foulers and borers the blocks were split to check for number and size of *Bankia setacea* present. Four large test blocks were exposed at the same position as the small ones, but remained in the water for longer periods of time. After being placed in the water on 1 June 1968 two of these large test blocks were removed after six months on 1 December 1968; the remaining two remained exposed for one year and were recovered on 1 June 1969. After recovery these large test blocks were analyzed by cutting three sections from each block at points corresponding to ¼, ½ and ¾ of the block length. The diameter and number of bore holes were recorded and, using a piece of graph paper to trace the outline of the remaining wood, an attempt was made to calculate the percentage of wood destroyed at each level. The results of these studies will be presented below.

Bankia Series I

In order to continue this specific investigation on *Bankia setacea* after the O.E.C.D. project was terminated a new series of panels consisting of 6 × 12 × ¾ inch flat sawn douglas fir (*Pseudotsuga douglasi* Carr) panels were exposed. This group of panels is referred to here as Bankia Series I and was followed, using slightly different techniques in the way the panels were arrayed, by Series II and Series III to be described below.

The Series I panels were arrayed as shown in Figure 3A. Twelve panels, each with a ½ inch hole drilled in the center, were strung on a stainless steel rod with a 1 inch plastic tubing spacer between each 2 panels. A stainless steel bar 18 inches long was secured by wing nuts to the ends of the rod and two bridles of ½ inch polypropylene line were secured at the ends of each bar. To the bottom bridle a 50 lb. concrete anchor was secured; with this anchor resting on the bottom in about 23 feet of water the center of each panel was about 2 feet above bottom. From the top bridle a line extended to the surface and was secured to the wharf. To make certain the entire bridle would remain taut and the panels kept above the bottom even after they became waterlogged and heavy with fouling growth a 5 × 9 inch plastic toggle float was placed on the recovery line just above the upper bridle. The panels were thus held vertically but were free to rotate end over end on the rod.

An array of 12 panels was initially exposed on 1 May 1969. On 1 June 1969 the array was lifted and one panel removed for analysis; a new so-called monthly panel was placed on the rod and the array submerged. On the first of each succeeding month two panels were removed; one was the monthly panel exposed for one month only, the other was a cumulative panel exposed for two months or more up to one year. In the laboratory each recovered panel was examined microscopically for newly settled *Bankia;* the panel was then split longitudinally by sawing with a band saw giving two panels approximately ¼ inch thick. The extent of *Bankia* damage and size of individual shipworms could then be determined.

Bankia Series II

Throughout the investigations so far described it was realized that a better technique for studying *Bankia* growth rates would be one where individual shipworms could be measured periodically without destroying or harming the animals or the panels in which they were living. We therefore deployed a new series of panels with the specific objective of following growth rates by radiographic means.

Attwood & Johnson (1924) were the first to publish an X-ray photograph of shipworm infested wood and many investigators since have used X-ray to estimate the intensity of wood infestation with marine borers. In studying the growth rates of *Teredo* Crisp, Jones & Watson (1953) used stereoscopic X-ray to follow growth rates and site of attack. Following each examination, the infested panels were returned to the water to permit continued development. Lane (1959) used a series of spaced X-ray examinations of *Teredo*-infested wood to determine size and average length of life of the shipworms. *Bankia* has been investigated using radiographic techniques of Ralph & Hurley (1952), Trussel, Greer & LeBrasseur (1956), Taylor (1956) and Quayle (1956, 1959).

In Monterey Harbor a group of panels referred to as Series II were exposed from 1 January 1970 to 1 July 1970 and another group called Series III were exposed from 1

July 1970 to 1 January 1972, with a few remaining exposed until 1 May 1972 when the project was terminated. Representatives of these panels were subjected to monthly X-ray examination and the analysis of these radiographs has given us considerable data on the growth rates and intensity of infestation of *Bankia* in the harbor.

Series II panels consisted of 5 × 13 × ¾ inch douglas fir boards which were placed in stainless steel racks that held the panels vertically with the edges parallel to the water surface. Three panels spaced 3 inches apart were arranged in the racks as shown in Figure 3B. A bridle on the bottom of the rack was connected to a line leading to an anchor weight that rested on the bottom. From an upper bridle a line extended to the surface and was secured to the wharf. A total of four racks each containing three panels was exposed at different depths. One rack, termed Shallow Rack, was positioned 1 foot below the lowest tide (3 feet below mean lower low water), a second Midwater Rack was positioned 10 feet below low tide (13 feet below MLLW) and a third called the Deep Rack was placed 20 feet below the lowest tide (23 feet below MLLW) and just above the bottom. A fourth rack was provided with a system of floats that kept the upper edges of the three panels at the water line. This Floating Rack was secured to the wharf by a series of pulleys and counterweights so that it continually floated at the surface regardless of tides or currents. The objectives in having racks at different depths was to determine depth preference of *Bankia* in the harbor and settlement time and growth rates at different depths.

All of these Series II panels remained in the water for six months except for the brief periods when some of them were removed for analysis. On the first of each month following initial exposure each of the four racks was recovered. From each rack Panel #2 and Panel #3 were removed. Panel #1 (control panel) remained in place in the rack and was immediately replaced in the water. The two remaining panels were taken to the laboratory. Panel #2 was treated exactly like Panel #3 except that only Panel #3 was X-rayed while Panel #2 was being examined for fouling organisms. The basic idea in having essentially two control panels was to see if removal from the water for short periods monthly had any influence on growth rates and especially to see if the radiation from the X-ray was harming (or stimulating) the living *Bankia*. When not being X-rayed all panels removed from the racks were kept in an aquarium with running sea water. Within an average of 2 hours the panels were returned to their racks in the harbor.

In the early phases of the study using X-ray analysis it was found that the external calcareous fouling growth often confused the resulting radiograph. To avoid this problem, panels used in the Series III study (to be discussed below) had the fouling growth removed from the panels by stripping off a plastic envelope that had been placed around the girth of the panel. In order to avoid injuring the siphons or pallets of living *Bankia* the fouling growth was not removed from the exposed ends of the panels. Panels to be X-rayed were labeled with distinctive designators composed of radio-opaque letters and numbers that provided a permanent legend on each radiograph. Each panel was then placed in a polyethylene bag and two such labeled panels were placed with the panel faces in contact with a sheet of Kodak NS-2T (no-screen medical) X-ray film measuring 11 × 14 inches. A Norelco Searchray, Type 1206, X-ray machine was used to expose the panels and film. Each set was exposed for 5 seconds with power of 30 Kv at 5 milliamperes. A plate of 1/16 inch aluminum was placed between the X-ray tube and panels to reduce short wave radiation. Examples of the resulting radiographs are shown in Figures *6–14* and *16–18*.

Bankia Series III

Toward the end of the six-month study on the Series II panels it was realized that it was very difficult to follow the growth of individual shipworms for some of the panels were so heavily infested and the tubes so intertwined that individual burrows could not be followed. The borers had initially entered the wood on all of the exposed surfaces and led to a confusing series of burrows. In addition many of the panels, especially the deeper ones, were so heavily infested and the shipworms so crowded that none of them could achieve maximum size due to space limitation (see Figure *16*). Calcareous fouling organisms encrusting the surface of the panels also added complexity to the interpretation of the radiographic pictures. A new series of panels was therefore deployed in an attempt to correct these deficiencies and to collect additional data.

Series III panels were first exposed on 1 July 1970 and all of them remained in the water for 18 months until 1 January 1972. Most of the panels were then removed, X-rayed, and sectioned but a few panels were left in place for an additional 4 months until 1 May 1972 to determine longevity and to gain additional data.

The panels in Series III were deployed in racks similar to the previous study (Series II described above) except that racks designed to hold four panels each instead of three were used. Three of the panels were treated as has been described above for the Series II group. The fourth panel was an additional control. At the time of lifting the racks each month this fourth panel was removed and merely allowed to remain in air in a protected area of the wharf until the panels removed to the laboratory were returned and then all panels were replaced in racks and replanted.

The position of the racks was exactly the same as in Series II except that one more rack was used. This additional rack of four panels was suspended from the Floating Rack and was positioned two feet below the water's surface. This rack moved up and down with the tide but remained submerged. To distinguish it and its panels from the Floating Rack it was designated Floating Submerged Rack. Three out of the four Series III panels were partially enclosed in a plastic envelope to prevent *Bankia* penetration except on the ends of the panels.

The panels were all exposed for 10 days until they became water-soaked. Then panels number 1, 2 and 3 were removed and wrapped snugly with wide Scotch #490 (Seran) tape. This tape covered all parts of the panel except the two ends. The tape did not stick to the wet wood but formed a tight impervious envelope for each panel. *Bankia* could enter the wood only from the exposed ends of the panels. Shipworms that may have entered other surfaces of the panel during the initial soaking period soon died due to being cut off from the water. The idea here was to limit the number of *Bankia* entering any one panel so that their growth could be more easily monitored and to provide each shipworm with enough space to achieve its full growth potential. The fouling growth which can easily confuse the interpretation of the radiographic pictures was removed prior to X-raying by removal of the plastic tape. Panel No. 4 in each rack was not covered with Seran but remained exposed on all surfaces. This panel from each rack was taken to the laboratory each month and examined for foulers but was not subjected to monthly X-ray. On 1 July 1971 after 12 months exposure it was finally removed permanently, X-rayed and sectioned for study. Routine monthly X-ray examination of Panel No. 3 in each rack continued for 18 months until 1 January 1972.

Experimental Piles

In addition to these panel studies in the harbor area a series of large timbers was also used. The earlier O.E.C.D. investigation had shown that blocks approximately 4 × 4 inches in cross section were excellent collectors of shipworms. To study the entire vertical range of *Bankia* attack in the harbor a series of experimental piles was used. These consisted of 4 × 4 inch planed clear douglas fir timbers 18 to 20 feet long. The two timbers were secured together with about a 3 foot overlap using stainless steel straps. This produced one long "pile" over 30 feet long. One end of the pile was placed in a pointed stainless steel cap filled with lead. The pile was then driven into the bottom so that the lower 6 inches of the pile was below midline. The pile stood vertically in the water and was long enough so that about the upper 10 feet extended above the waterline at 0 tide level. The experimental pile was secured at two points to strong cross timbers running between the regular supporting piles of the wharf. These experimental piles gave complete coverage of the water column from above the high tide level to below mudline level in water 23 feet deep at MLLW. Not only did these timbers allow investigation of *Bankia* penetration at all levels in the harbor but produced valuable data on the vertical distribution of fouling organisms throughout the same distance. These data on foulers will be published at a later date.

A total of four experimental piles were employed from 1 January 1970 to 1 January 1972. Each pile remained in the water for a 6-month period, either from January through June or from July through December of each year. At the end of each 6-month period a pile was removed and replaced by a new one. After removal the experimental pile was taken to the laboratory where it was carefully analyzed for foulers and was photographed section by section. After a period of drying the pile was cut into 6-inch sections from the area that was at the mudline to the area where the uppermost barnacles grew indicating high waterline. Each of these sections was then analyzed for number of *Bankia* bores, diameter of bore holes and percent destruction of the timber at that level.

PERIODS OF SETTLEMENT

In pioneering studies on shipworms of the Pacific coast Miller (1926) and Kofoid & Miller (1927) reported that *Bankia setacea* in San Francisco Bay has a breeding season and settlement beginning in February and ending in the early summer with a peak in April or May. Johnson & Miller (1935) found the principal season of settlement of *B. setacea* in the Friday Harbor area of Washington was during the months of October, November and December with little or no settlement in January and February. Settlement began again in March or April and continued sporadically during the summer until an acceleration to full peak was achieved in October. These authors concluded that a water temperature of from 7° to 12°C was the limit for breeding in Puget Sound. In southern California Coe (1941) found that breeding in *Bankia* occurred in the fall and spring with no spawning in summer or winter. In various places in British Columbia Neave (1943), Black & Elsey (1948), Brown (1955), Trussel, Greer & LeBrasseur (1956) and Quayle (1959) reported settlement of *Bankia setacea* at different times throughout the year. The main period seemed to be in the fall months but in many places breeding occurred throughout the year. Most of the above studies were of fairly short-term duration and Quayle (*op. cit.*) pointed out the need for continuous long-term observations.

Figure 4 presents data on the settlement of *Bankia setacea* in Monterey Bay for a period of five years from October 1966 to September 1971. Data are given for the four primary study sites at 20, 50, 100 and 200 feet depths. Essentially continuous observations were made in the

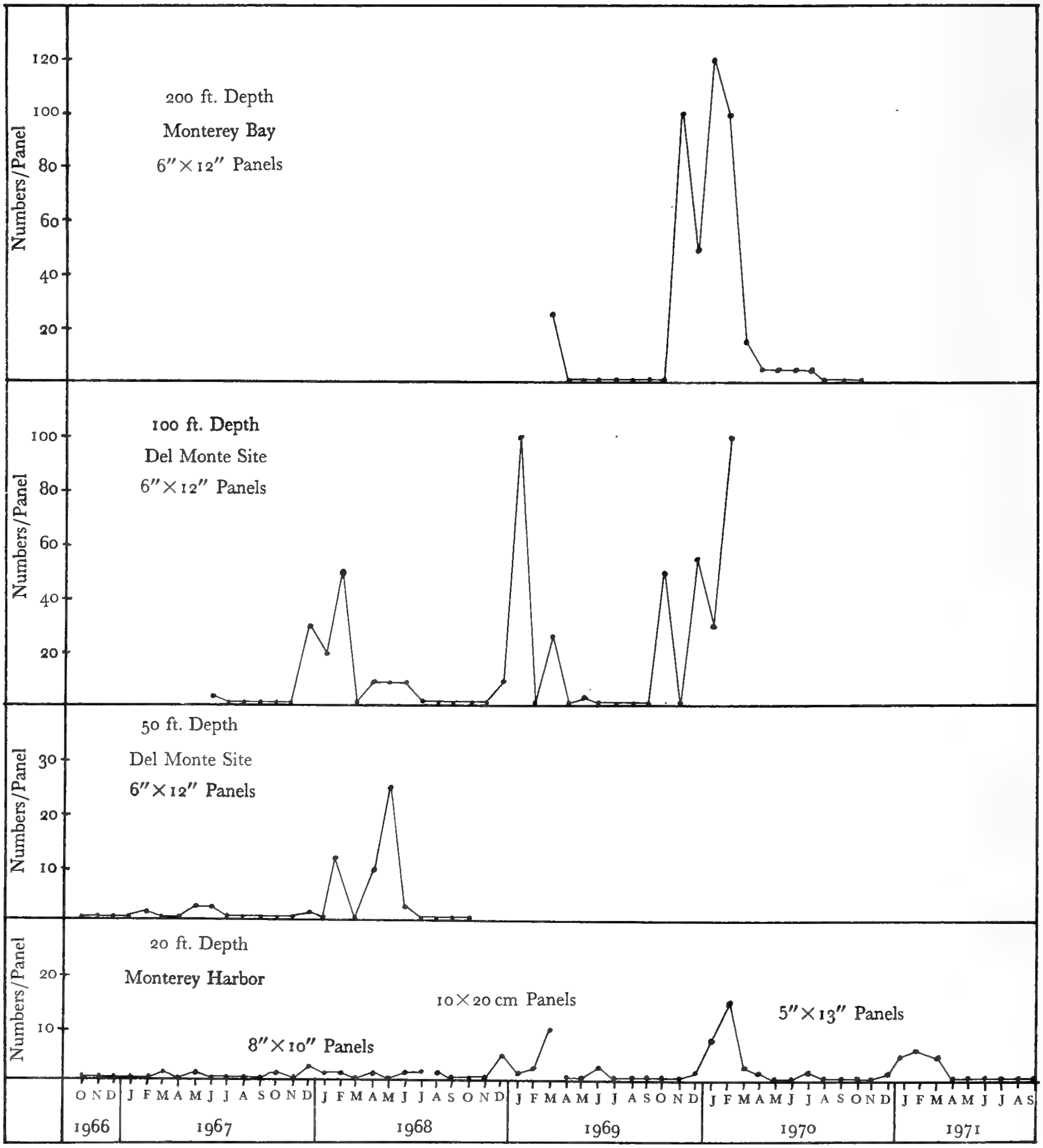


Figure 4

Numbers and Time of Settlement of *Bankia setacea* in Monterey Bay harbor area at depths of 20 feet for the entire five year period. In the deeper water the investigations were for shorter periods of from one and one half to nearly three years.

As has been mentioned above, standardized 6 × 12 × ¾ inch douglas fir panels were used continuously in the studies outside the harbor and were used (in slightly different dimensions) in the harbor during the last half of the project. Plywood and small Scotch pine test blocks were used during the initial half of the study in the harbor. The data in Figure 4 came only from panels that were in the water for a one month period, thus all of the shipworms counted settled during the month of exposure. In all cases, the flat surfaces of the panels were the only surfaces scanned microscopically to establish the counts, and many of our X-rays show that the majority of the shipworms entered the ends or the edges of the panels. The data given in Figure 4 therefore represent minimum counts per panel and are not an absolutely accurate representation either of settlement time or intensity. As all the panels were exposed for the same or overlapping periods, Figure 4 does make it possible to compare relative intensities of settlement and season at various depths in Monterey Bay.

As Figure 4 shows, the maximum number of shipworms settling on any one panel was directly correlated with water depth, the greatest intensity of settlement was at 200 feet depth, the least at 20 feet depth in the harbor. This finding is rather surprising for one would expect more larvae to be available for settlement in the harbor where there are many infested wooden piles and wooden hulled boats to serve as sources of shipworm larvae. The source of the larvae in deeper water is unknown, but benthic studies carried out in Monterey Bay for many years indicate that wood is not commonly found lying on the bottom and driftwood is not often seen. Other investigators (e.g., Coe, 1941; Quayle, 1953) have reported that the planktotrophic larvae of *Bankia setacea* have a long pelagic life and may have a swimming period of 4 weeks. The larvae penetrating panels in the deeper stations of this study may therefore have come from some distance away although the wooden structures in Monterey Harbor are the nearest source.

As indicated in Figure 4 the number of shipworms settling on any one monthly panel in the harbor, regardless of panel size or kind of wood, was quite low. The periods of maximum settlement in the harbor were March 1969 (45/sq. ft.), February 1970 (30/sq. ft.) and February 1971 (18/sq. ft.). In general, throughout the period, late summer and early fall were periods of minimal or no settlement in the harbor.

At depths of 50 feet in the open water of Monterey Bay (off Del Monte Beach approximately 1200 m from the harbor) shipworm settlement for a two year period was monitored (Haderlie, 1968b). Figure 4 presents the data from this study and shows that during late 1966 and throughout 1967 there were few *Bankia* settling but two peaks were recorded in 1968. In February there was a settlement of 24/sq. ft. and in May a settlement of 50/sq. ft.

Data from nearly three years of observations on shipworm settlement at 100 feet depth in Monterey Bay are also presented in Figure 4 (Haderlie, 1971). October through July appears to be the season of settlement at 100 feet depth. Peak settlement again occurred during the winter months: 90/sq. ft. in February 1968, 200/sq. ft. in January 1969 and 200/sq. ft. in February 1970. In late summer and early fall there was little or no settlement.

About 1½ year's data on *Bankia* settlement at 200 feet depth have been collected in Monterey Bay (Haderlie, 1972). The season of settlement appears to be the same as at shallow depths in the open water with maxima between November and March. A peak settlement of 240/sq. ft. of panel surface was recorded in January 1970. This is the most intense rate of settlement recorded so far in our studies in Monterey Bay. No settlement occurred between April and October 1969 but in the following year a few shipworms settled throughout the spring and summer up to August.

To summarize, data from various depths in Monterey Bay indicate that in general the settlement season of *Bankia setacea* is from late fall to early summer with a maximum settlement in most areas during the winter months and a minimum in late summer and early fall. The intensity of settlement increases with depth to 200 feet.

Other investigators studying *Bankia setacea* settlement in shallow water along the California coast have concluded that *Bankia* spawns and settles in the shallow water when water temperatures are at a minimum (Miller, 1926; Kofoid & Miller, 1927). This seems to be true also in the Monterey Harbor where minimum surface temperatures of about 11.5°C are recorded in the winter and spring months (Skogsberg, 1936; Haderlie, 1968a). Due to the influence of upwelling, however, in the open water of Monterey Bay at depths of from 10 to 100 m the minimum temperatures are found during May, June and July. At 50 m depth, for example, temperatures averaging 8.0°C are found in May and June, whereas the warmest temperatures of the year at this depth (approximately 11.0°C) are found during December and January (Skogsberg, 1936). Thus in the open water of Monterey Bay at depths

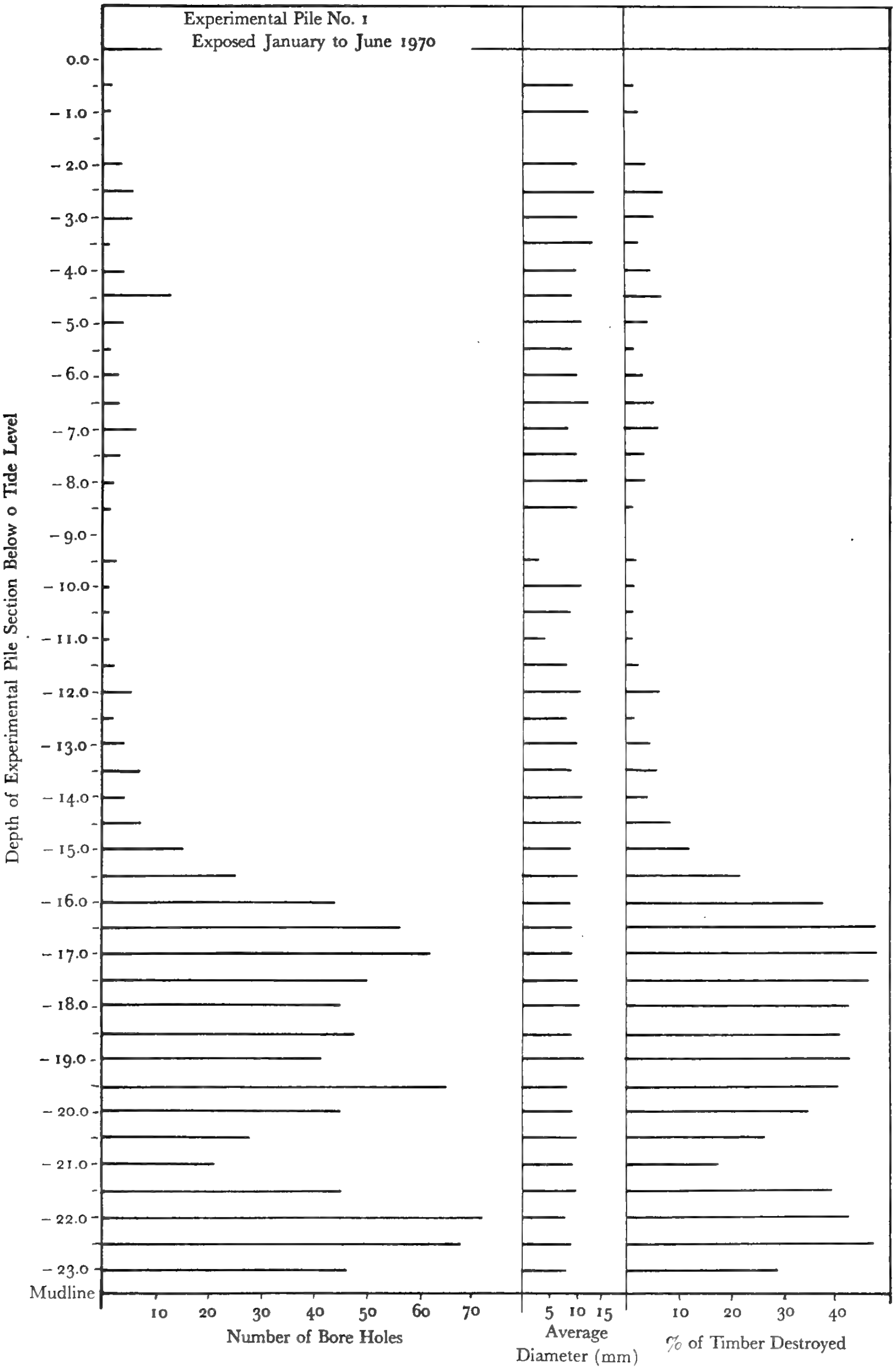


Figure 5

Number of *Bankia* Bore Holes, Average Diameter of Holes and Percent of Timber Destruction at Various Levels on Experimental Piles Exposed in Monterey Harbor

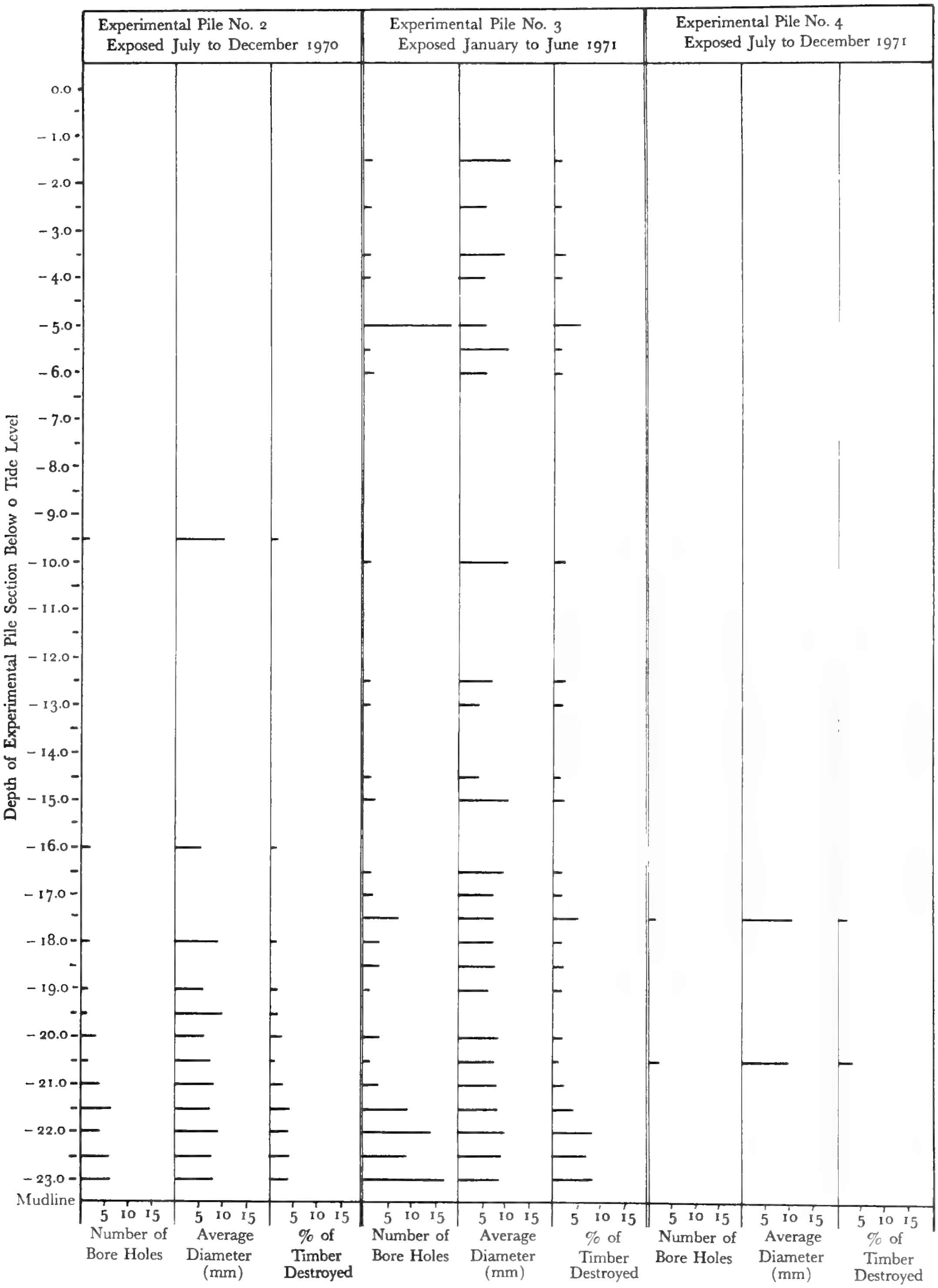


Figure 5 [continued]

Number of *Bankia* Bore Holes, Average Diameter of Holes and Percent of Timber Destruction at Various Levels on Experimental Piles Exposed in Monterey Harbor where these investigations were carried out *Bankia* settles following periods of maximum temperature in late fall and winter and may be inhibited following periods of minimum temperature in late summer and early fall.

DEPTH PREFERENCE

As has been discussed above, the intensity of *Bankia* settlement in Monterey Bay seems to increase with depth at least to 200 feet. And on panels exposed for long periods of time in the open water of the Bay it has been found that total destruction of untreated wooden panels occurs at all depths studied after about 7 months exposure provided initial exposure occurred during a period when *Bankia* was settling. In the harbor water, panels last for a longer period of time and may still be relatively intact after 12 months exposure.

It has been long known that *Bankia* tends to concentrate its attack near the mudline on pilings whereas a few feet above the mudline the wood may be relatively free of the borers (Kofoid & Miller, 1927). Panels suspended at various depths in Monterey Harbor are attacked throughout the water column, with greater settlement and destruction in the deeper positions. In none of our previous studies, however, did we have experimental wood exposed at all levels from below mudline to above the surface.

Starting on 1 January 1970 and continuing to 1 January 1972 four "experimental piles" were each exposed consecutively for six month periods. As explained above, the 4 × 4 inch douglas fir timbers were driven into the substrate and extended up vertically to above waterline. After a six month period these timbers were removed and sectioned at 6 inch intervals to determine number of bore holes, size of each, and the amount of timber destruction at each level. Data from the analysis of sections of these experimental piles are presented in Figure 5.

As discussed earlier, considerable variation occurs from year to year in the number of shipworm larvae settling on panels. The same was found to be true on the experimental piles as is obvious from the findings summarized in Figure 5. The first pile exposed (from January to June 1970) attracted the greatest number of *Bankia* and suffered the greatest amount of destruction. Some larvae settled on and bored into the wood at nearly all levels from the low intertidal to the mudline with the greatest attack on the pile within seven feet of the bottom. The maximum number of bore holes in the pile was found in a section cut one foot above mudline where 72 bore holes averaging about 8 mm in diameter were measured and these resulted in approximately 42% of the wood being destroyed at this level. Slightly fewer bore holes (68) were found 6 inches above mudline but because these averaged about 9 mm in diameter the total destruction of wood at this level was about 47%. The data from Pile #1 also indicates that the average size of the *Bankia* bores was remarkably uniform in diameter regardless of the level in the water column and regardless of the total number of shipworms infesting the wood. We cannot comment on the comparison of the length of the shipworms for in these pile studies we were not measuring length of burrows. In relatively thin panels it has been found that great numbers of *Bankia* in a single panel lead to crowding and limit the size of each bore hole. In this case of the experimental piles, however, the 4 × 4 inch cross sectional area was such that 70 or more shipworms forming burrows up to 10 mm in diameter could occur without excess crowding and stunting of growth.

Experimental Pile #3 (see Figure 5) was exposed during the same time interval in exactly the same spot but a year later (from January through June 1971). As can be seen, the pile was attacked from very low in the intertidal zone to the mudline, but not at all levels, and the number of shipworms settling was quite low compared to those settling in Pile #1 a year earlier. Panels exposed in the immediate vicinity of the experimental piles for the purpose of detecting settlement time showed that fewer *Bankia* settled in the first half of 1971 than in the comparable period in 1970. Again in this pile the major area of settlement was within 7 feet of the bottom. The maximum number of bores in this zone was at the mudline (total of 17). The curious anomaly seen in Figure 5, Experimental Pile #3, where a heavy settlement is indicated at –5.0 feet can be explained as follows: As described above, two 4 × 4 inch timbers were secured together in order to get a pile of sufficient length to extend from the bottom to above the water line. The lowest of

Explanation of Figures *6* to *11*

Consecutive monthly X-ray photographs (1 May 1971 to 1 January 1972) of a single *Bankia* specimen in a $5 \times 13 \times \frac{3}{4}$ inch douglas fir panel exposed floating just below the sea surface in Monterey Harbor

Figure *6*: *Bankia* specimen in burrow 48 mm long one month after initial detection

Figure *7*: Second month burrow; 116 mm in length

Figure *8*: Third month burrow; 211 mm in length

Figure *9*: Fourth month burrow; 279 mm in length

Figure *10*: Fifth month burrow; 363 mm in length

Figure *11*: Sixth month burrow; 437 mm in length

Figure *6*

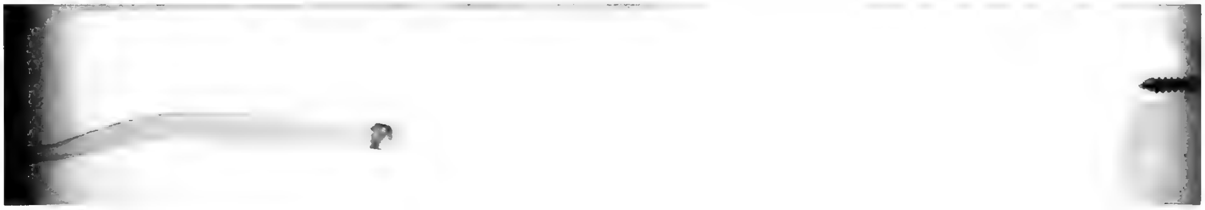


Figure *7*

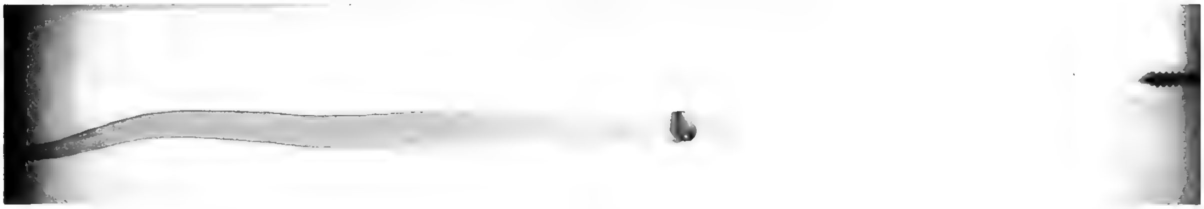


Figure *8*

Figure *9*

Figure *10*

Figure *11*

these two timbers extended up to just a few inches above the –5.0 ft. level. The exposed end grain of this timber apparently served as an attractive point of entrance for several shipworms which were detected when the timber was sectioned at the –5.0 ft. level just below this end.

Figure 5 also indicates that during the period July through December *Bankia* settlement was somewhat different from the first half of the year. In both Experimental Piles #2 and #4 exposed during the latter half of each year the number of shipworms settling was considerably smaller than earlier; they settled only in the lower half of the water column. During July 1970 there were *Bankia* larvae settling in the harbor, but no others settled until December (see Figure 4). Thus the shipworms detected in Experimental Pile #2 (that was removed for examination the last of December 1970) presumably settled in July and most of the burrows were of fairly uniform size. In 1971, however, there was no *Bankia* settlement detected in the harbor from April through September. Experimental Pile #4 carried only three *Bankia,* one at the –17.5 ft. level and two at the –20.5 ft. level. All of these were of average maximum diameter, so it is assumed that these settled in October to have grown to the size they attained by late December.

The above data show that considerable variation occurs from year to year. In the O.E.C.D. project described earlier and carried out in 1968 and 1969 a series of Scotch pine test blocks of approximately the same cross sectional area as the experimental douglas fir piles were suspended 2 feet above the bottom and it is interesting to compare the results of this investigation with the data presented in Figure 5. Table 1 presents the data from test blocks of the O.E.C.D. series that measured 10 × 10 × 50 cm in which *Bankia* penetrated. Only Test Blocks #1a and #1b of the O.E.C.D. series are comparable to the experimental piles, for they were in the water for a six month period. Test Blocks #2a and #2b were exposed for 12 months and therefore show not only considerably more shipworm bores but also a much higher percentage of wood destruction. In both June and July 1968 (during the initial period of O.E.C.D. test block exposure) *Bankia* larvae were settling in the harbor (see Figure 4). Table 1 shows that by the first of December 1968 these test blocks carried a total number of shipworms similar to what was found in sections of Experimental Pile #1 at comparable depths in June 1970.

GROWTH RATES

Due to the fact that the animals are hidden in the substrate there are many difficulties involved in studying the growth rates of boring organisms. Periodic sectioning of experimental panels infested with shipworms of known age has been the usual technique used, but this destroys the organisms and makes additional growth observations impossible. It has been long recognized that radiographic techniques should make it possible to follow the growth of individuals or populations of borers for long periods of time not only to determine rates of growth at different seasons but ultimate longevity of individual borers. Quayle (1956, 1959) was one of the first to use such techniques in the study of *Bankia setacea* and has reviewed the literature up to 1959.

The first growth studies in California on *Bankia* were conducted by Kofoid & Miller (1927). They determined growth rates in San Francisco Bay by measuring the size of bore holes in test blocks of known age and reported average rates of growth of from 23 mm per month for specimens 6 weeks old to 63 mm per month for an in-

Table 1

Bankia setacea bores, average diameter of bore holes and percent of Scotch pine blocks destroyed at different levels in 10 cm × 10 cm × 50 cm test blocks

Test block number	Period of exposure	Sectioned $\frac{1}{4}$ from lower end			Sectioned $\frac{1}{2}$ from lower end			Sectioned $\frac{3}{4}$ from lower end		
		No. of bores	Ave. diam. bore holes (mm)	% of wood destroyed	No. of bores	Ave. diam. bore holes (mm)	% of wood destroyed	No. of bores	Ave. diam. bore holes (mm)	% of wood destroyed
1a	1 June 1968 - 1 Dec. 1968	54	9.0	34	44	9.0	33	48	10.0	30
1b	1 June 1968 - 1 Dec. 1968	68	8.0	43	35	10.0	22	35	10.0	22
2a	1 June 1968 - 1 June 1969	100	10.0	79	83	10.0	65	88	8.0	44
2b	1 June 1968 - 1 June 1969	140	8.0	80	105	10.0	82	110	8.0	75

Table 2

Series II (1 January 1970 to 1 July 1970) terminal panel data

Panel Depth	Panel Number	Months of Growth	Total No. of *Bankia*	Maximum Length (mm)	Maximum Diameter (mm)	Average Growth for 3 Months (mm) / No. of Measurements	% Destruction	Average % Destruction at each Depth
Floating at Surface	1	3[1]	3	53	7	53/1	1	1
	2	3[1]	2	107	8	107/1	1	
	3	1	1	7	2	0	0	
3 ft. below MLLW (Shallow)	1	3[1]	40	360	9	138/25	21	19
	2	3[1]	45	290	11	114/34	22	
	3	3	47	247	9	118/34	14	
13 ft. below MLLW (Mid-Water)	1	3[1]	30	296	7	126/26	23	14
	2	3[1]	30	291	10	114/17	3	
	3	3	48	298	9	160/32	17	
23 ft. below MLLW (Deep)	1	3[1]	84	235	8	too crowded	26	28
	2	3[1]	145	312	10	too crowded	24	
	3	3	156	425	8	too crowded	34	

---

[1] assumed duration of growth

dividual 8 months old. At Friday Harbor, Washington, Johnson & Miller (1935) using similar techniques found the burrows of *Bankia* increased in length at an average rate of 10 mm per month.

Quayle (1956, 1959) carried out an experiment involving 8 fir panels of about the same size employed in our studies in Monterey Bay. These panels were suspended 3 feet below the surface in water at Ladysmith, British Columbia. Panels were removed at monthly intervals and X-rayed. With water temperature below 10°C growth rates were low (50 mm per month) but at temperatures above 10°C a rate of 100 mm per month was the average. The most rapidly growing individual shipworm attained a length of 610 mm in 5 months or a rate of growth of 122 mm per month. Quayle found that the rate of increase in the diameter of the burrow was similar to that of length, and the greatest diameter attained was 12 mm.

In our studies in Monterey Harbor *Bankia setacea* growth rates and destruction of the wood substrate will be discussed in terms of numbers of organisms within a given area of wood surface (settlement), growth in length and diameter for specific periods of time, and percentage destruction of wood through loss in panel weight. Radiographic techniques have added precision and insight to the growth measurements. Repetitive monthly X-rays of

Explanation of Figures *12* to *15*

Figure *12*: Seventh month burrow; 541 mm in length
Figure *13*: Eighth month burrow; 672 mm in length
Figure *14*: Ninth month burrow; 797 mm in length
Figure *15*: Standard photograph of split panel showing terminal burrow of shipworm shown in Figures 6 to 14

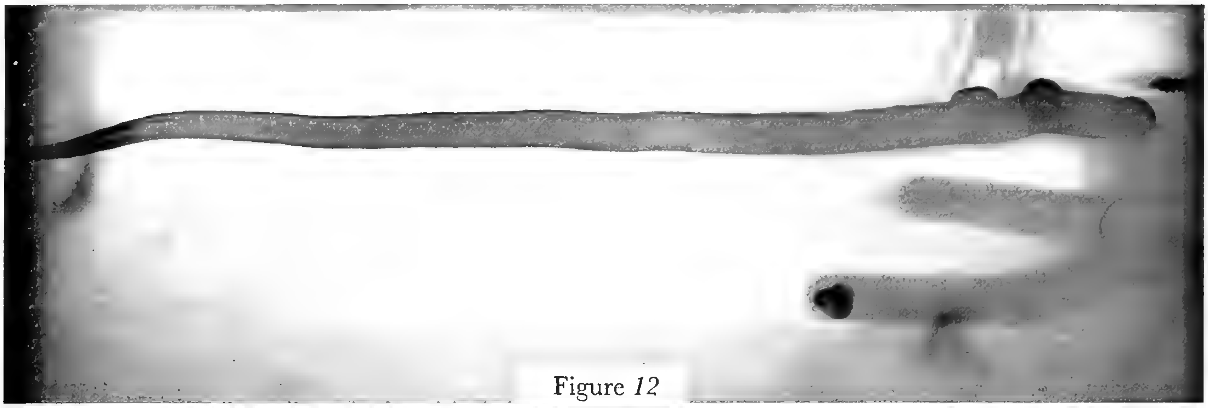


Figure *12*

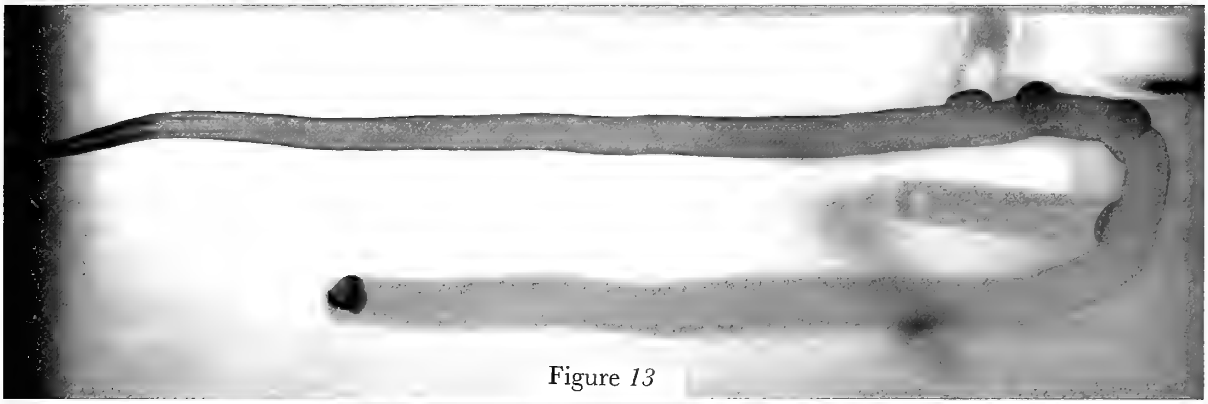


Figure *13*

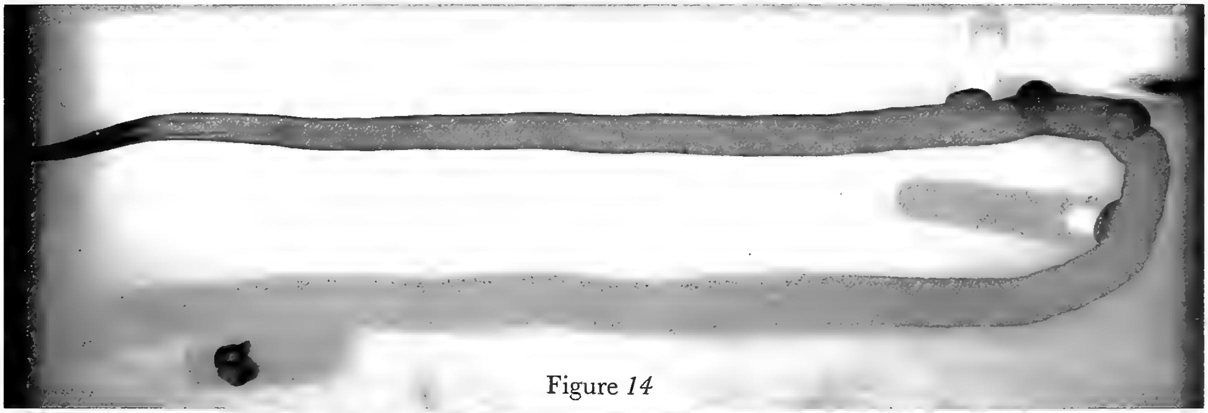


Figure *14*

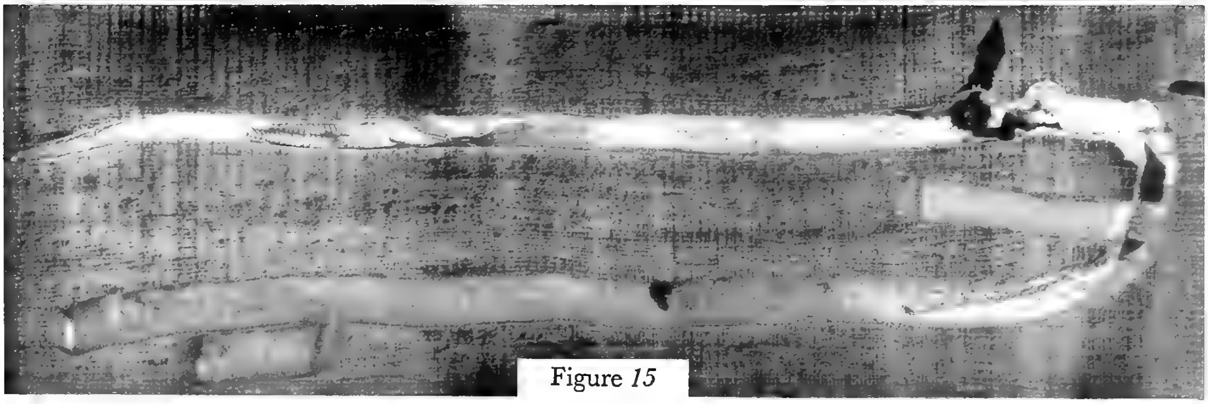


Figure *15*

the same panel made it possible to determine the date each shipworm specimen gained entrance to a panel and made possible observations of growth characteristics of each individual shipworm from month to month. From these specific shipworm growth measurements the magnitude of growth variabilities could be assessed and sometimes the reasons for growth variability could be recognized.

As has been explained earlier, Series II panels were exposed for a 6-month period from 1 January to 1 July 1970. Table 2 summarizes the data obtained from examining the X-ray photographs of this series. The panels were exposed to *Bankia* attack on all surfaces. Most of the settlement occurred between 1 March and 1 April 1970 and the period of observation of growth was for a period of three months from initial detection on 1 April until removal for final X-ray and examination on 1 July. The control panels in each rack (Panels #1 and #2; see Materials and Methods above) were X-rayed only at the end of the exposure period. The duration of growth of shipworms in these panels was assumed to be 3 months as they were probably infested at the same time as Panel #3 in the same rack which was the panel X-rayed monthly. On 1 April one of the deep panels (23 ft. below MLLW) contained 156 *Bankia* having an average length of 24 mm. No additional shipworms were found to have entered this panel in succeeding months, but the 156 specimens increased sufficiently in size that by 1 May the X-rays indicated that the borers were too crowded to make recognition of individuals possible for length measurements. The total surface area of each panel employed in Series II was approximately 1 square foot. Therefore, the total number of *Bankia* per panel was equivalent to settlement per square foot. In general, the number of borers per panel increased with depth in the harbor studies. The floating panels had only a few *Bankia,* while the shallow and mid-water panels had 30–40/sq. ft., and the deep panels contained 84–156/sq. ft.

Length measurements from Series II X-rays were made along the mid-line of the burrow from the point of entrance to the anterior end of the shell. The living shipworms often retracted their shells from the forward ends of the burrows, as may be seen in Figures *6–11*. Therefore, the length measurements recorded in Table 2 are either equal to or less than the actual length of the *Bankia* burrow. The burrow lengths could not be measured directly because of confusion caused by over-crowding (e.g., see Figure 16). The individual shipworm that achieved the greatest length (425 mm) in 3 months of growth was in a deep panel. Due to over-crowding it grew to only 8 mm diameter while a 290 mm *Bankia* in a less crowded panel (Shallow Panel #1) grew to 11 mm diameter. Average growth in the shallow and mid-water panels over the 3-month period ranged between 114 mm and 160 mm. The average monthly growth increment was 43 mm. Numbers and burrow lengths of *Bankia* in the floating panels were minimal partially due to the fact that the racks were occasionally hung up above the water. The mooring mechanism which kept the floating panels just below the water-air interface failed several times and allowed the panels to remain out of water following a period of high tide for up to 36 hours. A greater *Bankia* settlement and growth rate probably would have been recorded had the floating rack's mooring mechanism operated correctly.

The percentage destruction of the wooden panels was approximated by weighing each panel before exposure and comparing it with the weight of the panel after six months of exposure. Panels were air dried and all external fouling growth was removed prior to final weighing, but two factors contributed to minor inaccuracies. Calcium carbonate produced by the shipworms in the form of burrow lining, pallets, and shell added weight to the panel. Surface burrows caused by the gribble *Limnoria quadripunctata* on the ends of some panels decreased the weight. Gribble burrows appear in X-ray photographs as light streaks or as a cobwebbing near the panel ends (e.g., see Figure *18*). The increase in average percent destruction of the wood with increasing depth corresponds very closely to the increase in numbers of *Bankia* per panel. The largest average percent of panel destruction was 28% for the deep panels with almost no destruction occurring in the floating panels of this series.

Two of the three Series II panels at each depth served as controls during this study (see above, Materials and Methods, Series II). Average percentage of destruction for each Panel #1, #2 and #3 at all depths was 17.8%, 12.5% and 16.2% respectively. These values are very similar and indicate no influence on rates of *Bankia* growth relative to short periods of removal from the water and handling or small doses of radiation.

Series III panels were exposed for eighteen months from 1 July 1970 to 1 January 1972. This long term series was made possible by incorporating a modification of the techniques used in Series II. As explained earlier, in order to restrict *Bankia* settlement, Panels #1, #2 and #3 in each Series III rack were wrapped with Seran tape, leaving only the ends with 7 square inches of each panel exposed to the sea water (see Materials and Methods, Series III). In each rack Panel #1 was never removed from water except for brief periods when other panels were being removed and they each retained the original tape envelopes until the terminal X-rays on 1 January 1972. Panels #2, #3 and #4 were removed from the water each month for a similar period of time. Panel #2 in each rack was a control and although removed from the water it was not X-rayed until

Table 3

Monthly observed lengths (mm) of *Bankia setacea* burrows in Monterey Harbor

Panel Depth	*Bankia* Specimen Number	1970						1971												1972
		J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J
Floating at Surface	1	All panels initially exposed 1 July 1970	0	0	0	0	0	0	0	0	6	48	116	211	279	363	437	541	672	797
Floating 2 ft. below Surface	1		0	0	0	0	0	0	2	8	8	†								
	2		0	0	0	0	0	0	0	0	10	63	114	†						
3 ft. below MLLW (Shallow)	1		0	0	0	0	0	0	0	0	7	37	82	139	196	293	372	395	443	503
	2		0	0	0	0	0	0	0	0	6	50	121	228	300	405	448	493	544	563
	3		0	0	0	0	0	0	0	0	0	10	35	85	90	144	199	250	300	379
13 feet below MLLW (Mid-Water)	1	All panels initially exposed 1 July 1970	0	0	0	0	0	0	2	19	78	171	227	302	338	369	447	490	490	490
	2		0	0	0	0	0	0	0	3	21	96	158	251	337	395	476	523	552	573
	3		0	0	0	0	0	0	0	2	14	54	89	136	167	278	369	409	433	†
	4		0	0	0	0	0	0	0	1	12	52	105	143	159	205	294	357	424	503
	5		0	0	0	0	0	0	0	0	0	1	8	83	114	169	211	214	214	†
	6		0	0	0	0	0	0	0	0	0	0	7	42	93	218	331	406	420	420
	7		0	0	0	0	0	0	0	0	0	0	8	43	†					
23 feet below MLLW (Deep)	1		0	0	1	26	82	188	265	324	→	→	→	→619	647	647	†			
	2		0	0	0	1	29	106	165	228	313	384	456	558	606	655	704	754	802	834
	3		0	0	0	0	0	0	0	2	14	22	22	†						
	4		0	0	0	0	0	0	0	2	10	59	143	268	378	440	440	440	440	440
	5		0	0	0	0	0	0	0	0	6	53	127	240	285	→	→	→	→	→465
	6		0	0	0	0	0	0	0	0	0	9	27	77	125	244	309	344	344	†
	7		0	0	0	0	0	0	0	0	0	7	22	61	105	220	302	→	→	→405
	8		0	0	0	0	0	0	0	0	0	0	7	86	144	236	307	369	409	489
	9		0	0	0	0	0	0	0	0	0	0	2	31	87	193	244	→	→	→413
	10		0	0	0	0	0	0	0	0	0	0	0	0	0	7	70	152	→	→293
	11		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	32	92

---

[2] the dagger symbol (†) indicates shipworm was found dead on the first of the indicated month

Explanation of Figures *16* to *18*

Figure *16*: X-ray photograph of panel heavily infested with 145 specimens of *Bankia setacea* 3 months following initial detection of the shipworms. Entire panel exposed at a depth of 23 feet below MLLW in Monterey Harbor

Figure *17*: X-ray photograph of Control Panel No. 1 exposed at the location for the same period of time as the panel X-rayed monthly shown in Figure *14*. A second set of pallets is clearly visible.

Figure *18*: X-ray photograph of Control Panel No. 2 exposed at same location for the same period of time as the panel X-rayed monthly shown in Figure *14*

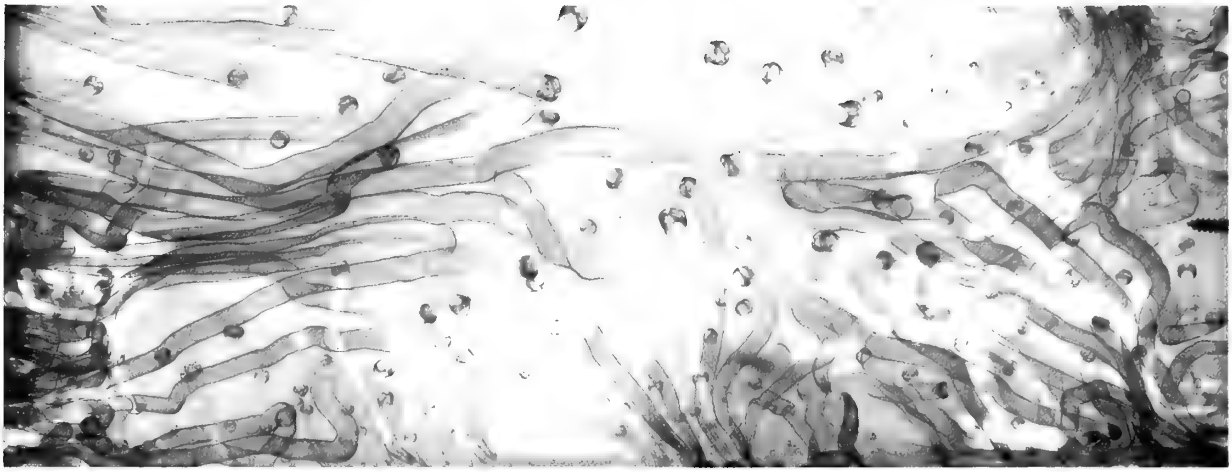


Figure *16*

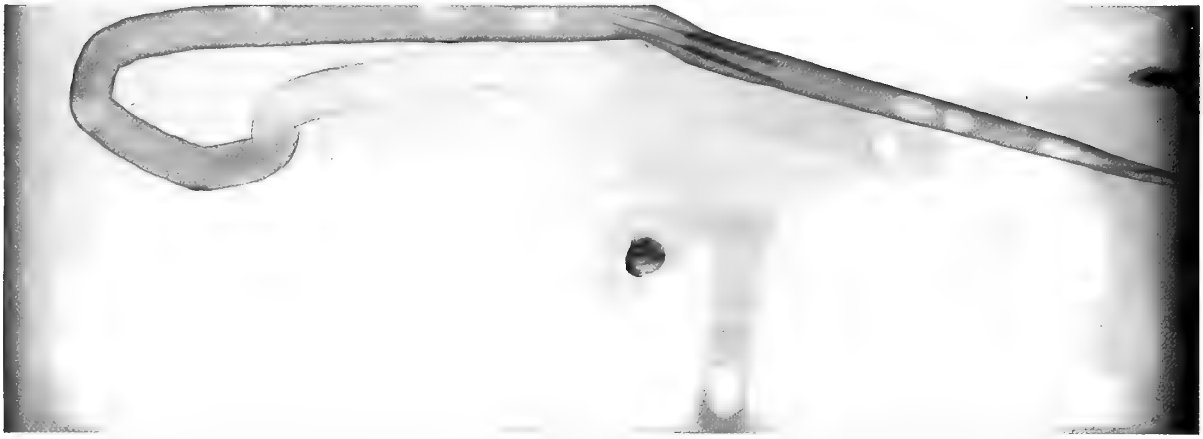


Figure *17*

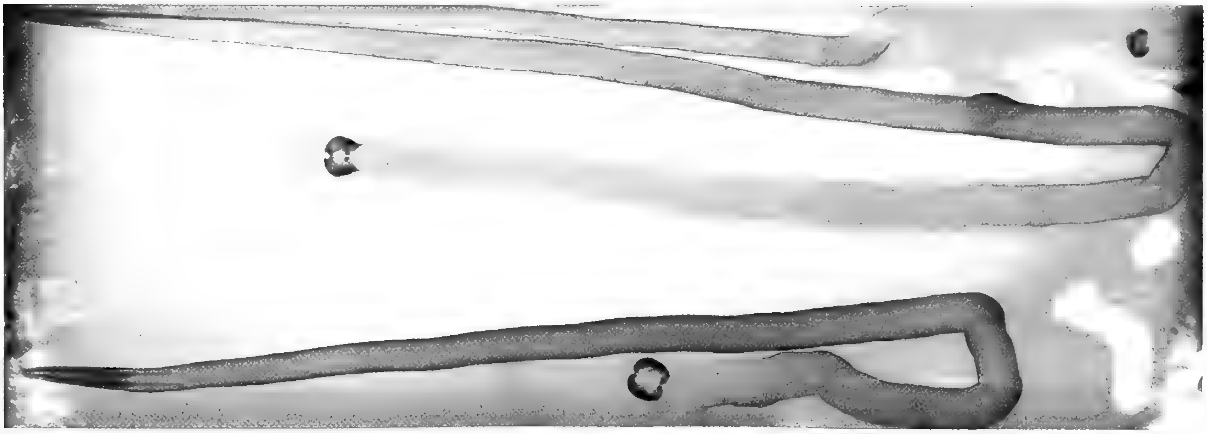


Figure *18*

the termination of the project. Panel #3 in each rack was removed monthly, stripped of the Seran tape, X-rayed, re-taped, and returned to the panel racks. Panel #4 in each rack was not covered with tape (all sides were exposed) and this panel was removed monthly and examined for fouling organisms and specifically for newly settled *Bankia*. On 1 July 1971 all of the #4 panels were removed permanently and X-rayed for the first time, but Panels #1, #2 and #3 were not terminated until 1 January 1972.

Table 3 summarizes length measurement data taken from monthly X-ray photographs of Panel #3 from each rack from each depth under the date of the X-ray, i.e., data listed under August were from X-rays taken on 1 August. Each length measurement represents the total length of the burrow on the first of the month listed in the table heading. Recently settled *Bankia* were recognized on the X-ray photographs when they were 1 mm long or longer. Upon initial detection, each *Bankia* specimen was assigned a specimen number which it retained through all subsequent observations. In this way the progress of each individual shipworm was observed from the date of initial detection to 1 January 1972. In all cases the duration of growth discussed herein disregards the period of growth prior to initial detection.

Length measurements from Series III monthly X-rays were made along the mid-line of the burrow from the point of entrance to the anterior end of the burrow. All exploratory burrows and pockets (*e.g.*, see Figure *10*) were included in the length measurement. After Series III panel exposure was terminated each panel was split longitudinally with a bandsaw for detailed observations of the burrows. The split panels were used to measure burrows and small side pockets that were poorly defined on the X-rays and to provide a terminal length measurement check (see Figure *15*).

The number of *Bankia* per panel increased with depth (Table 3). Settlement on deep panels was first detected on the October and November 1970 X-rays, and then again on photographs taken in March through June, September and November 1971. Settlement on mid-water, shallow and floating panels was observed only on X-rays taken on 1 February through 1 June 1971.

One *Bankia* measuring 6 mm in length was detected on the surface floating panel X-rayed on 1 April 1971. No other shipworms entered this panel during the study. The burrow length of this specimen increased to 797 mm by 1 January 1972 (see Table 3). The corresponding X-ray photographs of this shipworm and the infested panel beginning on 1 May 1971 are shown in Figures *6-14*. We have selected this particular set of photographs from the great number we have accumulated to illustrate the monthly growth of a single shipworm where no crowding is involved. Following this series of X-ray photographs is a standard photograph of the panel after it had been split to expose the burrow (Figure *15*). This panel was removed on 1 January 1972 and split and photographed for comparison with the final X-ray (Figure *14*). The burrows shown in the terminal X-ray and the split panel photograph are directly comparable in size and shape.

Bankia growth in all of the panels at the surface floating position was not significantly different as can be determined by comparing Figures *17* and *18* with Figure *14*. All three panels had the same approximate settling intensity and rate of growth. Panel #2 (Figure *18*) contained 3 shipworms, while Panels #1 and #3 each had one large shipworm (Figures *17* and *14*). The specimen in Panel #1 was one of two *Bankia* in the entire study that achieved a burrow length in excess of 900 mm.

The specimen shown in Figure *17* is of additional interest because of the appearance of two pairs of pallets in the X-ray. *Bankia* pallets consist of a number of interlocking calcareous cones and they are used to block the burrow entrance under adverse conditions. One well-developed pair of pallets can be seen 120 to 150 mm from the entrance, while a less developed pair remains at the burrow entrance. When the panel was split both pallet pairs were extracted. The tips of the well-developed pair had been broken off at some earlier date, and may have been too blunt to adequately seal the burrow entrance. In any event, *Bankia setacea* appear to have the capability to retract old pallets and regenerate and use a new pair.

Figure *16* is an X-ray photograph of a crowded panel with 98 shipworms boring into the wood. Borers growing under such crowded conditions have difficulty in achieving maximum growth potential. Panel destruction is relatively rapid and the longevity of individual shipworms is minimal. Measurements of individual *Bankia* burrows become increasingly difficult with increased crowding. Most burrow lengths are impossible to determine as can be seen in Figure *16*. It was for this reason that in our Series III panels we wrapped the boards with plastic to allow only a minimal number of shipworms to penetrate and to grow without undue crowding.

In general the burrow walls are more distinct near the entrance end in the X-ray photographs because a continuous calcareous burrow lining is deposited from 1 to 20 cm behind the anterior end of actively burrowing shipworms. If a borer's progress in one direction is hindered either by coming up against another burrow or the edge of the wood the animal can retract several centimeters and try again in another direction without being impaired by its own calcareous lining. When a new start is made in a

Table 4

Monthly increase in lengths of *Bankia setacea* burrows in Monterey Harbor

Panel Depth	*Bankia* Specimen Number	Initial Detection[3]	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Floating at Surface	1	4:71 – 6 mm	42	68	95	68	84	74	104	131	125					
Floating 2 feet below Surface	1	2:71 – 2 mm	6	0	†[4]											
	2	4:71 – 10 mm	53	51	†[4]											
3 feet below MLLW (Shallow)	1	4:71 – 7 mm	30	45	57	57	97	79	23	48	60					
	2	4:71 – 6 mm	44	71	107	72	105	43	45	51	19					
	3	5:71 – 10 mm	25	50	5	54	55	51	50	79						
13 feet below MLLW (Mid-Water)	1	2:71 – 2 mm	17	59	93	56	75	36	31	78	43	0	0			
	2	3:71 – 3 mm	18	75	62	93	86	58	81	47	29	21				
	3	3:71 – 2 mm	12	40	35	47	31	111	91	40	24	†[4]				
	4	3:71 – 1 mm	11	40	53	38	16	46	89	63	67	79				
	5	5:71 – 1 mm	7	75	61	25	42	3	0	†[4]						
	6	6:71 – 7 mm	35	51	125	113	75	14	0							
	7	6:71 – 8 mm	35	†[4]												
23 feet below MLLW (Deep)	1	10:70 – 1 mm	25	56	106	77	59	74	74	74	73	28	0	0	†[4]	
	2	11:70 – 1 mm	28	77	59	63	85	71	72	102	48	49	49	50	48	32
	3	3:71 – 2 mm	12	8	0	†[4]										
	4	3:71 – 2 mm	8	49	84	125	110	62	0	0	0	0				
	5	4:71 – 6 mm	47	74	113	45	36	36	36	36	36					
	6	5:71 – 9 mm	18	50	48	119	65	35	0	†[4]						
	7	5:71 – 7 mm	15	39	44	115	82	34	34	35						
	8	6:71 – 7 mm	79	58	92	71	62	40	80							
	9	6:71 – 2 mm	29	56	106	51	56	56	57							
	10	9:71 – 7 mm	63	82	70	71										
	11	11:71 – 1 mm	31	60												
	Average Increments	5 mm	29	56	74	72	68	51	62	65	52	44	49	50	48	32
	Number of Measurements	24	24	22	19	19	18	18	14	12	10	4	1	1	1	1

---

[3] date of initial detection followed by length of burrow

[4] dead

new direction, the blind abandoned burrow is often sealed off with a layer of calcareous lining. Borers that have completely stopped burrowing due to lack of space will line their entire burrow with calcium carbonate. These specimens no longer grow, but have been observed to continue living and adding to their calcareous lining for up to 5 months. To illustrate this point Table 3 shows specimen No. 4 in the deep panel with a static length of 440 mm for 5 months. The X-rays of this shipworm showed thicker and thicker burrow linings from September to January

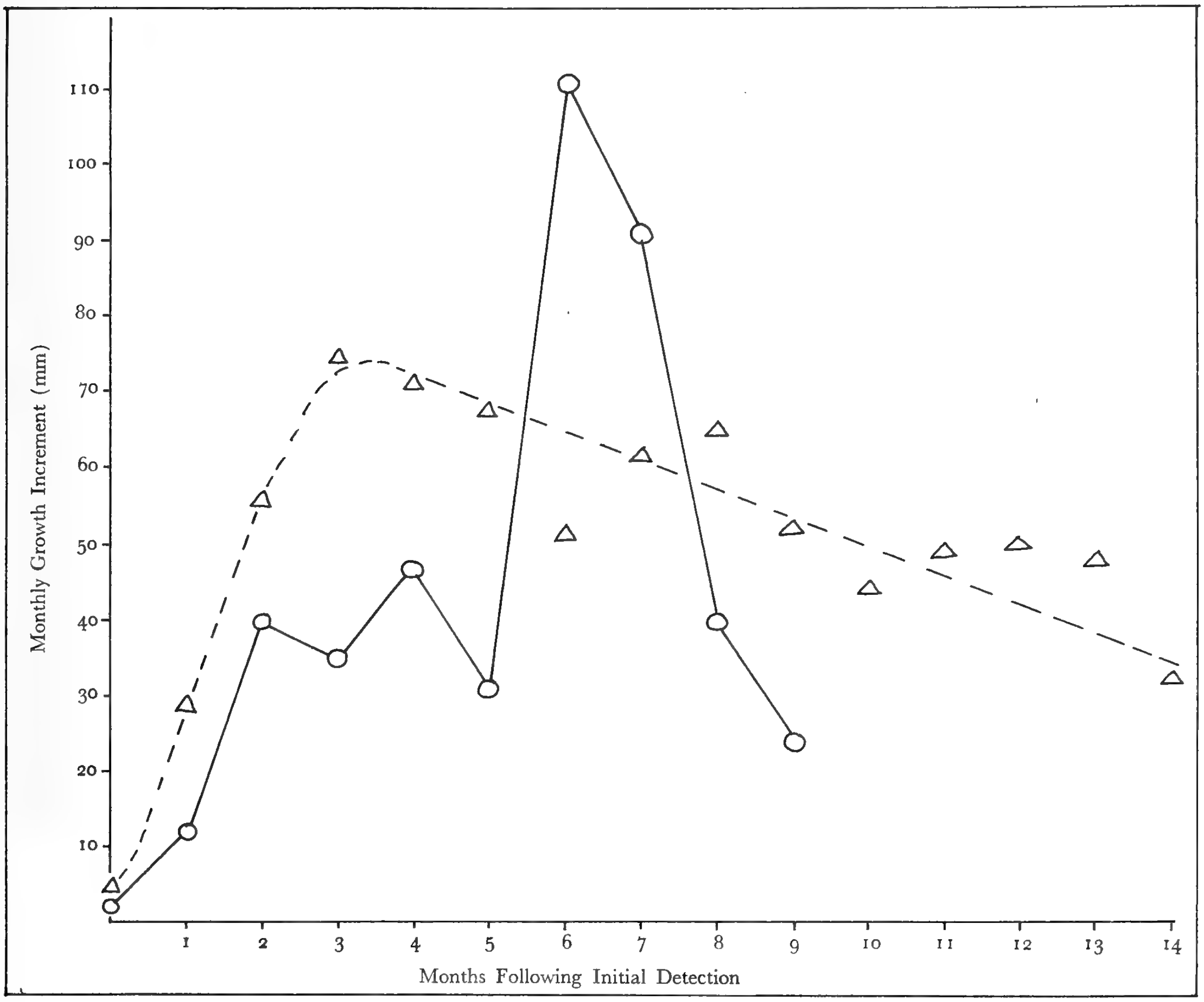


Figure 19

Monthly growth increments in *Bankia* burrow length in Series III panels

△ = Average for all panels
○ = Typical specimen (No. 3, Midwater Panel)

1972. The animal continued to entomb itself and was still alive on 1 January 1972.

Monthly burrowing rates were calculated from data presented in Table 3 and are tabulated in Table 4. If a particular specimen continued to live but did not burrow during a month a "0" was placed in the appropriate column. The average burrowing rates given at the bottom of Table 4 represent all the living specimens at all panel depths except those specimens with 0 burrow growth rate for any one month. Therefore, during the tenth month of burrowing only four values were averaged together. This gave an average burrow elongation of 44 mm in the tenth month. Only one borer had a growth duration exceeding ten months; this specimen burrowed for fourteen months until the panel exposure was terminated. This shipworm contributed the only measurement to the "average" for months eleven through fourteen. Peaks in burrowing activity were observed from the third through

Table 5

Series III (1 July 1970 to 1 January 1972) terminal panel data

Panel Depth	Panel Number	Total Number of *Bankia*	Months of Growth	Maximum Lengths (mm)	Maximum Diameters (mm)	Percent Destruction	Average % Destruction at each Depth
Floating at Surface	1	1	9[5]	923	14	19	21
	2	3	9[5]	740	14	25	
			9[5]	591	12		
			9[5]	369	10		
	3	1	9	797	14	20	
	4	4	3[5]	440	11	13	
Floating 2 feet below Surface	1	2	9[5]	815	12	24	19
			9[5]	743	13		
	2	6	9[5]	291	10	32	
			9[5]	222	13		
			9[5]	210	8		
	3	2	2	114	8	2	
	4	22	3[5]	408	11	18	
			3[5]	282	10		
			3[5]	247	11		
3 feet below MLLW (Shallow)	1	4	9[5]	732	14	22	24
			9[5]	503	13		
			9[5]	322	12		
	2	8	9[5]	575	12	30	
			9[5]	567	13		
			9[5]	350	9		
	3	3	9	563	12	20	
			9	503	12		
			8	379	11		
	4	30	3[5]	486	12	35	
			3[5]	329	10		
			3[5]	305	8		
13 feet below MLLW (Mid-Water)	1	3	9[5]	976	15	33	32
			9[5]	856	13		
			9[5]	583	11		
	2	3	9[5]	813	13	34	
			9[5]	693	11		
			9[5]	640	11		
	3	7	10	573	10	29	
			10	503	11		
			9	490	9		
	4	44	4[5] - 9	800	14	38	
			4[5]	440	11		
23 feet below MLLW (Deep)	1	21	7[5] - 14	635	13	48	38
			7[5] - 14	548	10		
			7[5] - 14	535	9		
	2	23	7[5] - 14	523	9	28	
			7[5] - 14	436	9		
			7[5] - 14	336	9		
	3	11	14	834	13	37	
			10	647	12		
			7	489	12		
	4	98	3[5] - 8	498	10	48	
			3[5] - 8	394	11		
			3[5] - 8	370	10		

---

[5] assumed duration of growth

Average % destruction = Average for panels nos. 1, 2, & 3 only the ninth months of growth. The largest one-month burrow elongation (131 mm) occurred during the eighth month of growth. The borer involved was specimen No. 1 in the surface floating panel. Most declines in burrowing rates were observed to be directly related to crowding and obstacle or panel edge avoidance.

The monthly burrowing rates for a typical *Bankia* in our studies are plotted in Figure 19. The average monthly rates are also plotted. As can be seen, the average monthly burrowing rate peaks between the third and fourth month of growth.

Table 5 summarizes the Series III terminal measurements after eighteen months of exposure for Panels #1, #2 and #3 and twelve months of exposure for Panel #4 at each depth. Up to three maximum burrow lengths and diameters were recorded for each panel relative to the months of growth required to achieve that size. Months of growth were known positively for borers in the #3 panels only; all borers in other panels have assumed months of growth approximated from dates of settlement at each depth as given in Table 3. A maximum burrow length of 976 mm with a diameter of 15 mm was recorded for a single borer in a mid-water panel.

The percentage destruction of panels was calculated by weight loss in the same manner used for Series II panels, and the same trend was noted; percentage destruction increased with depth. The deep panels showed up to 48% of the wood destroyed, yet these panels were still intact at the termination of the project.

SUMMARY

(1) General studies on boring and fouling organisms have been in progress in Monterey Harbor and the open water of Monterey Bay since 1966. From June 1968 to January 1972 studies specifically devoted to the biology of the shipworm *Bankia setacea* were carried out.

(2) Experimental wooden panels were exposed to the marine environment in the open water of the southern end of Monterey Bay at depths from 50 to 200 feet. Additional panels and experimental piles were exposed throughout the water column in Monterey Harbor.

(3) Initial settlement of *Bankia setacea* larvae was monitored for a period of 5 years. The settlement season was found to be from late fall to early summer with a maximum settlement in most areas during the winter months and a minimum in late summer and early fall. The intensity of settlement increased with depth with a maximum settlement of 240/ sq. ft. at 200 feet depth.

(4) In experimental piles exposed in the harbor, shipworm larvae settled and bored into the wood at nearly all levels from the low intertidal to the mudline some 23 feet below the surface with the greatest settlement and ultimate destruction of wood within 7 feet of the bottom. After 6 months a 4 × 4 inch timber could have up to 47% of the wood destroyed; after 12 months up to 82% destroyed.

(5) Radiographic techniques were used to follow growth of shipworms in infested panels. Control panels not subject to periodic X-ray were exposed in racks along with panels X-rayed monthly and terminal comparison of the radiated and control panels showed that the level of radiation used had no detectable influence on either the rate of growth or the ultimate size of radiated shipworms. Removal of panels from the water periodically for short periods of time for examination had no noticeable influence on growth of *Bankia* or the size attained.

(6) When all surfaces of an experimental panel were exposed to settling shipworm larvae the number that settled and bored into wood was often so great that crowding soon occurred and individual borers could not achieve maximum growth potential or size. The maximum size attained by an individual *Bankia* under crowded conditions was 425 mm long and 8 mm in diameter after 3 months growth. The monthly average growth of *Bankia* in length for panels crowded with borers was 43 mm. Under these crowded conditions as much as 34% of a panel could be destroyed in 3 months.

(7) When panels were wrapped with plastic that restricted the point of entrance of *Bankia* to the ends of the panels fewer shipworms gained entrance to the wood and were therefore less crowded and could achieve maximum growth. Under these conditions shipworm burrows have attained a length of 976 mm and a diameter of 15 mm in approximately 9 months and had an average monthly increment which peaked at 74 mm between the third and fourth months. After approximately 9 months of growth 3 individual shipworms destroyed 34% of one panel.

Literature Cited

ATTWOOD, W. D. & A. A. JOHNSON
1924. Marine structures: their deterioration and preservation. Nat. Res. Council, Washington, D. C.
BLACK, E. C. & C. R. ELSEY
1948. Incidence of wood borers in British Columbia waters. Bull. Fish. Res. Brd. Canada LXXX
BROWN, DOROTHY J.
1955. Eighth progress report on marine borer activity in test boards operated during 1945. Wm. Clapp Labor. Rept. no. 9440
COE, WESLEY ROSWELL
1941. Sexual phases in wood-boring molluscs. Biol. Bull 81: 168 - 176
CRISP, D. J., L. W. G. JONES & W. WATSON
1953. Use of stereoscopy for examining shipworm infestation *in vivo*. Nature 172: 408

DePalma, John R.
1966. A study of marine fouling and boring organisms at Admiralty Inlet, Washington. U. S. Naval Oceanogr. Office Inf. Man. Rept. 0-6-66: 1 - 23

Haderlie, Eugene Clinton
1968a. Marine fouling and boring organisms in Monterey Harbor. The Veliger **10** (4): 327 - 341; plt. 49; 3 text figs. (1 April 1968)
1968b. Marine boring and fouling organisms in open water of Monterey Bay, California. pp. 658 - 679 *In*: A. H. Walters & J. S. Elphick, eds., Biodeterioration of materials; microbiological and allied aspects. Elsevier Publ. Co., Barking, England
1969. Marine fouling and boring organisms in Monterey Harbor. - II. Second year of investigation. The Veliger **12** (2): 182 - 192; 2 text figs.; 2 tables (1 October 1969)
1970. Fouling organisms in the harbor at Monterey, California. pp. 581 - 594 *In*: Proceedings of the 2nd International Congress on Marine Corrosion and Fouling, Athens, Greece
1971. Marine fouling and boring organisms at 100 feet depth in open water of Monterey Bay. The Veliger **13** (3): 249 - 260; 2 text figs.; 2 tables (1 January 1971)
1972. Marine fouling and boring organisms at 200 feet depth in open water of Monterey Bay, California. pp. 432 - 442 *In*: A. H. Walters & E. H. Hueck-van der Plas, eds., Biodeterioration of materials, vol. 2. Applied Sci. Publ. Ltd., London

Hopkins Marine Station
1966-1971. CCOFI hydrographic data, collected on approximately weekly cruises on Monterey Bay, California. Ann. reprts. for years 1966 through 1971 (mimeogr.)

Johnson, Martin Wiggo & Robert Cunningham Miller
1935. The seasonal settlement of shipworms, barnacles and other wharf-pile organisms at Friday Harbor, Washington. Univ. Wash. Publ. Oceanogr. 2 (5): 1 - 18

Kofoid, Charles Atwood & Robert Cunningham Miller
1927. Biological section. pp. 188 - 343 *In*: Marine borers and their relation to marine construction on the Pacific Coast. Final reprt. San Francisco Bay Marine Piling Committee

Lane, C. E.
1959. Some aspects of the general biology of *Teredo*. pp. 137 - 156 *In*: Marine boring and fouling organisms. Wash. Univ. Press, Seattle, Wash.

Miller, Robert Cunningham
1926. Ecological relations of marine wood-boring organisms in San Francisco Bay. Ecology **7**: 247 - 254

Miller, Thomas Leroy
1966. Marine fouling organisms in Monterey Harbor, California. Unpubl. Master's Thes. Naval Postgrad. School, Monterey, California (October 1966)

Mommsen, Durward Belmont
1966. A study of marine fouling in Monterey Harbor. Unpubl. Master's Thes. Naval Postgrad. School, Monterey, Calif. (May 1966)

Neave, F.
1943. Seasonal settlement of shipworm larvae. Fish. Res. Brd. Canada Progr. Rprt. Pac. **54**: 12 - 14

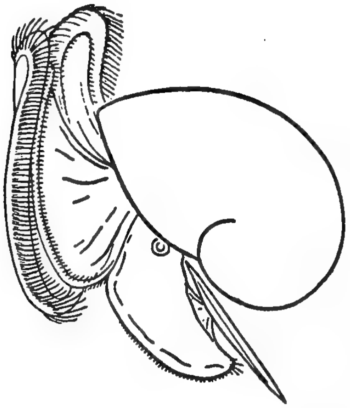
Quayle, Daniel Branch
1953. The larvae of *Bankia setacea* Tryon. Rprt. British Columb. Dept. Fisheries for **1951**: 88 - 91
1956. The British Columbia shipworm. Rprt. British Columb. Dept. Fisheries for **1955**: 92 - 104
1959. The growth rate of *Bankia setacea* Tryon. pp. 175 - 183 *In*: Marine boring and fouling organisms. Wash. Univ. Press, Seattle

Ralph, Patricia M. & D. E. Hurley
1952. The settling and growth of wharf-pile fauna in Port Nicholson, Wellington, New Zealand. Zool. Publ. Victoria Univ. Coll. **19**: 1 - 22

Skogsberg, Tage
1936. Hydrography of Monterey Bay, California. Thermal conditions, 1929-1933. Trans. Amer. Philos. Soc., N. S. **29**: 1 - 152

Taylor, F. H. C.
1956. The effectiveness of various preservatives on plywood in preventing attack by shipworms and gribbles. Pac. Biol. Sta. and Pac. Exp. Sta. Prog. Rprt. **107**: 13 - 18

Trussel, P. C., B. A. Greer & R. J. LeBrasseur
1956. Protection of saw logs against marine borers. II. Storage ground study. Pulp & Pap. Mag. Canada pp. 11 - 14



The Genera *Chromodoris* and *Felimida*

(Nudibranchia : Chromodorididae)

in Tropical West America: Distributional Data, Description of a New Species, and Scanning Electron Microscopic Studies of Radulae

BY

HANS BERTSCH,[1] ANTONIO J. FERREIRA,[2] WESLEY M. FARMER,[3]

AND

THOMAS L. HAYES[4]

(3 Text figures; 3 Plates)

INTRODUCTION

Tropical west America, or the Panamic province, consists of the eastern Pacific region between the warm- to cold-temperate Californian and Peruvian provinces. It extends along the American coastline from Bahía Magdalena, Baja California del Sur, Mexico, southward to Punta Aguja, Peru, with northward and westward extensions to include the Gulf of California and the Galápagos archipelago and other offshore islands (Keen, 1971).

The opisthobranch gastropod fauna in the Panamic province has been studied mainly from a small amount of material collected in the Gulf of California. Prior to 10 years ago, only 3 species of the extensive circumtropical nudibranch family Chromodorididae were known from the tropical eastern Pacific (Pruvot-Fol, 1951). Recent research in this region, however, has contributed 5 new species of *Chromodoris* and a new genus, *Felimida,* to the known representatives of this family.

Three species of Chromodorididae occur in the neighboring temperate Californian province. *Chromodoris macfarlandi* Cockerell, 1902, and *Hypselodoris porterae* (Cockerell, 1902) are recorded only from the Californian region; and *Hypselodoris californiensis* (Bergh, 1879) is recorded from both provinces. The occurrence of these species in the more northerly temperate waters is not an anomaly, but illustrates the faunistic relationships between these two provinces. Twenty-five % of the opisthobranch species occurring in the tropical west American province also occur in the temperate Californian province, and vice versa (Bertsch, 1973). Such overlapping of faunal elements is expected wherever zoogeographical provinces meet or are separated only by partial barriers (Darlington, 1957: 453). In the eastern Pacific, the Chromodorididae is a transitional family from the tropical region, contributing 3 species to the faunal complexity of the southern portion of the temperate Californian province.

This paper gathers together reported and new distributional data for the unicuspid Chromodorididae in tropical west America, discusses the taxonomy of the 2 "subspecies" of *Chromodoris banksi,* describes a new species of *Chromodoris* and its functional radular morphology based on scanning electron micrographs, and documents the deposition of the type material of *Felimida sphoni.*

---

[1] Bodega Marine Laboratory, University of California, Bodega Bay, California 94923, and Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118. Permanent address: Department of Zoology, University of California, Berkeley, California 94720

[2] Beta Research Oceanographic Laboratories, Inc., 2060 Clarmar Way, San Jose, California 95128

[3] 1327 East Donner Drive, Tempe, Arizona 85282

[4] Donner Laboratory, University of California, Berkeley, California 94720

Table 1 lists the location of each collecting site reported in this paper.

Table 1

Latitude and Longitude of Collecting Localities

Pacific Coast of Baja California

Isla Cedros	28°07′ N;	115°11′ W
Puerto Rompiente	27°43′ N;	115°00′ W
Bahía Magdalena	24°38′ N;	112°09′ W

East Coast of Baja California

Puertecitos	30°21′ N;	114°38′ W
Bahía San Luis Gonzaga	29°49′ N;	114°25′ W
Puerto Refugio, Isla Angel de la Guarda	29°33′ N;	113°35′ W
Bahía de Los Angeles	28°53′ N;	113°30′ W
Isla Coyote	26°44′ N;	111°54′ W
Bahía Concepcion	26°43′ N;	111°54′ W
Isla Santa Catalina	25°42′ N;	110°49′ W
Isla Santa Cruz	25°14′ N;	110°44′ W
Isla Las Animas	25°06′ N;	110°33′ W
Isla San Jose	25°03′ N;	110°35′ W
Isla San Francisco	24°50′ N;	110°35′ W
Los Islotes	24°36′ N;	110°24′ W
Isla Espíritu Santo	24°27′ N;	110°19′ W
Bahía Las Cruces	24°13′ N;	110°05′ W
La Paz	24°11′ N;	110°23′ W
SW Isla Cerralvo	24°09′ N;	109°49′ W

West Coast of Mainland Mexico

Puerto Peñasco, Sonora	31°18′ N;	113°35′ W
Puerto Lobos, Sonora	30°16′ N;	112°51′ W
Isla San Pedro Nolasco	27°59′ N;	111°24′ W
Bahía San Carlos, Sonora	27°56′ N;	111°04′ W
Guaymas, Sonora	27°55′ N;	110°54′ W
Isla Venado	23°14′ N;	106°27′ W
Mazatlan, Sinaloa	23°11′ N;	106°26′ W
Santa Cruz, Nayarit	21°30′ N;	105°16′ W
Sayulita, Nayarit	21°15′ N;	105°15′ W
Tenacatita, Jalisco	19°17′ N;	104°54′ W
Bahía Santiago, Colima	19°07′ N;	104°22′ W
Puerto Angel, Oaxaca	15°40′ N;	96°29′ W

Central and South America

Bahía Jobo, Costa Rica	11°02′ N;	85°45′ W
Isla Tortugas, Costa Rica (Isla Alcatraz and Isla Tolinga	9°50′ N;	84°53′ W
Bahía Ballena, Costa Rica	9°45′ N;	85°00′ W
Quepos, Costa Rica	9°24′ N;	84°10′ W
Deale Beach, Ft. Kobbe Beach, Panama	8°48′ N;	79°55′ W
Cocos Island	5°33′ N;	86°59′ W
Academy Bay, Isla Santa Cruz, Galápagos Islands	0°45′ S;	90°15′ W
Punta Aguja, Peru	5°50′ S;	81°03′ W

NUDIBRANCHIA

Doridoida

CHROMODORIDIDAE

Chromodoris banksi Farmer, 1963

Marcus & Marcus (1967) established the subspecies *Chromodoris banksi sonora* as distinct from *C. b. banksi* on the basis of the shape of the first inner lateral tooth. Lance (*in* Keen, 1971: 822) continued the separation, stating that *C. banksi sonora* should be raised to full specific status if the difference in radula proves consistent.

The innermost lateral tooth of *Chromodoris banksi sonora* possesses denticles (Marcus & Marcus, 1967: 175), and the description of *C. b. banksi* was illustrated by one innermost lateral tooth without any denticles. Farmer gave no written discussion of this pattern of denticulation to indicate whether his drawing showed a regular condition or merely a chance tooth that lacked denticles.

Examination of the holotype and paratype radula of *Chromodoris banksi banksi* (by Bertsch, with verification by Dustin Chivers and James T. Carlton of the California Academy of Sciences) revealed that the species named in 1963 by Farmer has denticles on the first lateral teeth. What Marcus & Marcus (1967) considered diagnostic

Explanation of Figures *1, 2*

Chromodoris marislae Bertsch, spec. nov.

Figure *1*: Five *Chromodoris marislae* in their natural habitat. alongside the egg mass of this species. Subtidal, near La Paz, Baja California del Sur, April 1972. Photograph by Edwin Janss

Figures *2*a and *2*b, paratype animal collected at Isla Las Animas; 80 mm total length

Figure *2*a: Antero-lateral view of entire animal; photograph by Antonio J. Ferreira

Figure *2*b: Close-up view of anterior dorsal portion of the animal; photograph by Hans Bertsch

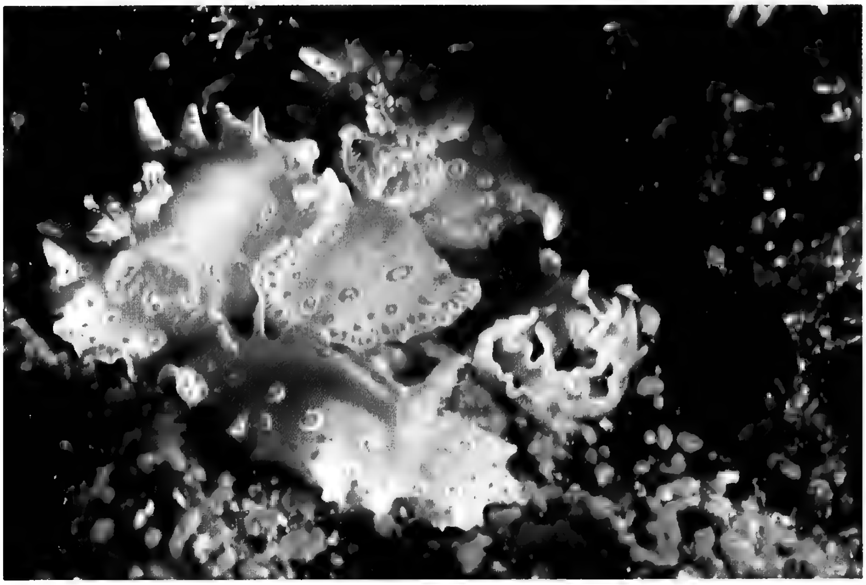


Figure *1*

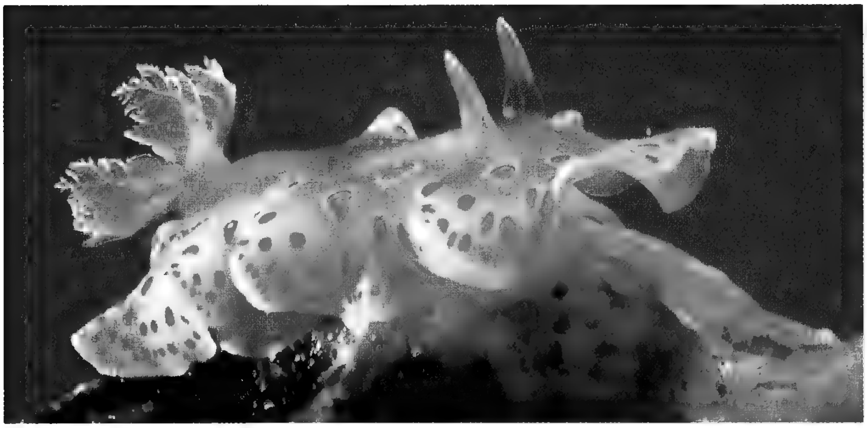


Figure *2* a

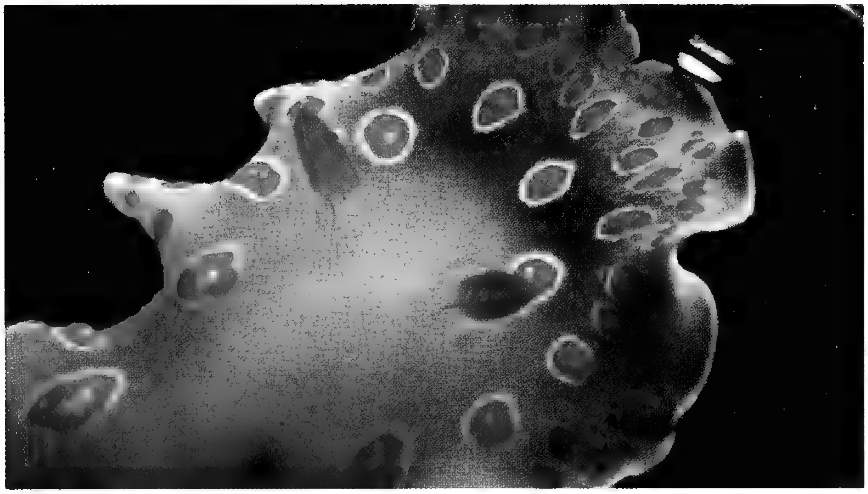


Figure *2* b

for their subspecies *C. banksi sonora* is not unique to their material, but is actually typical of the original *C. banksi* material. A separation between the 2 subspecies becomes impossible on the basis of denticulations on the first lateral teeth. Other similarities are mentioned by MARCUS & MARCUS (*op. cit.*: 175), that the slight color differences are simply variations on a basic pattern (a common occurrence among nudibranchs), and that the radular formula, and the shape of the rachidian pseudo-tooth approximate their material with that named by Farmer. According to modern taxonomic practice, subspecies are local populations that have become genetically distinct, but not so much as to prevent interbreeding (MAYR, 1969: 41 - 43). In view of the evident continuity, the overlapping range, and the probability of a high rate of gene flow of the species population in question, erection of subspecific taxa is not warranted. Separate subspecies do not exist within *Chromodoris banksi,* and *C. banksi sonora* Marcus & Marcus, 1967, should be considered a synonym of *C. banksi (banksi)* Farmer,1963. The radula of *C. banksi* should be described as having a unique pattern of denticulation among the unicuspid chromodorids from the Panamic province. The inner lateral teeth have denticles, and the outer ⅓ to ¼ of the half-row of teeth have no denticles.

The reported range of *Chromodoris banksi* is the northern half of the Gulf of California, from Puerto Peñasco (FARMER, 1967) to Bahía Concepcion (KEEN, 1971). It has also been found 3.8 km (2.3 miles) south of Puertecitos (type locality), at Bahía San Luis Gonzaga, Puerto Refugio (FARMER, 1963), Bahía San Carlos (Bertsch, Terrence Gosliner, and Gary Williams, December 1970, pers. observ.), and Isla San Pedro Nolasco (Ferreira, August 1972, pers. obser.). In September 1971, Ferreira collected one 30 mm long specimen from a depth of 10 m at Isla Las Animas in the southern Gulf of California, and in February 1972, he found 5 specimens while diving at Bahía Ballena and Islas Tortugas, Costa Rica. These new records establish *C. banksi* as occurring both intertidally and subtidally, and extend its range more than 3500 km (over 2200 miles) southeastward, toward the midpoint of the tropical west American province.

Chromodoris baumanni Bertsch, 1970

The range of *Chromodoris baumanni* is from Guaymas (BERTSCH, 1970) to Academy Bay in the Galápagos Islands (SPHON & MULLINER, 1972), with scattered intermediate occurrences in the Gulf of California at Isla San Francisco (type locality), SW Isla Cerralvo, Bahía Carisalito (4 km, 2½ miles, N of Las Cruces), and along the southern Pacific coast of Mexico at Santa Cruz and Sayulita (BERTSCH, 1970, and in press; SPHON & MULLINER, 1972). Ferreira has collected *C. baumanni* at other subtidal localities in the Gulf of California (20 m, Bahía San Carlos, December 1970; 10 m, Isla Espíritu Santo, November 1970), and he has also collected 4 specimens at Bahía Ballena, Costa Rica (February 1972), establishing an important intermediate record between the Mexican and Galapagan localities. What was a seemingly disjunct distribution for *C. baumanni* is now continuous, and should even be considered as representative of the typical pattern for opisthobranchs presently reported from the Gulf of California and the Galápagos Islands. This pattern of distribution (Gulf of California, southern Mexico, Central-South America, and the Galápagos Islands) is seen in the majority of the 14 opisthobranch species reported from the Galápagos (SPHON & MULLINER, 1972). Of these species, 13 occur in the Gulf of California (the one exception is the little-known *Doris peruviana*). Nine of these species have also been reported from the Central or South American coast (KEEN, 1971; SPHON, 1971; Ferreira, pers. obser.; and this paper): *Aplysia juliana* Quoy & Gaimard, 1832; *Bulla punctulata* A. Adams *in* Sowerby, 1850; *Dolabrifera dolabrifera* (Rang, 1828); *Tylodina fungina* Gabb, 1865; *Umbraculum ovale* (Carpenter, 1856); *Pleurobranchus areolatus* Mörch, 1863; *Chromodoris baumanni* Bertsch, 1970; *C. sedna* (Marcus & Marcus, 1967); and *Hypselodoris agassizii* (Bergh, 1894). Two other species occur along the open Pacific coast of southern Mexico (KEEN, 1971): *Lobiger souverbii* Fischer, 1857, and *Spurilla chromosoma* Cockerell & Eliot, 1905. Such faunal associations between the Gulf of California, Central America, and the off-shore Cocos and Galápagos Islands have been accounted for by both normal and southward-shifted water currents that allow a fairly continuous faunal exchange between these areas (HERTLEIN, 1963; ABBOTT, 1966).

Chromodoris marislae Bertsch, spec. nov.

Material examined: 1) **Holotype**. One specimen (40 mm long) collected subtidally at the north end of Santa Catalina Island (25°42′ N; 110°49′ W), Gulf of California, on June 25, 1964, by Dustin Chivers and Richard Adcock. This specimen has been deposited as the holotype in the collections of the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ no. 471. Three microscope slides of the radula and genitalia of this animal are in the CASIZ Type Slide Series, nos. 405, 406, and 407.

2) **Paratype:** One specimen (60 mm in length) collected from Los Islotes, subtidally in 30 m of water, crawling around in the open during the daytime, by Richard Adcock and Antonio J. Ferreira, July 16, 1971. The intact

whole animal has been deposited as a paratype at California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type Series, no. 472.

3) One specimen (80 mm long) collected subtidally, in 10 m of water, crawling on top of a rock, on the west side of Isla Las Animas, Gulf of California, on July 15, 1971, by Antonio J. Ferreira. The animal and its separately mounted radula have been deposited as a paratype specimen in the California Academy of Sciences, Department of Invertebrate Zoology, CASIZ Type Series, no. 473, and CASIZ Type Slide Series no. 411. The radula of this specimen is illustrated by the scanning electron micrographs (Figures *6* to *11*). Color photographs of this animal (Figures 2a and 2b) illustrate this paper.

4) Eleven specimens collected by Edwin Janss in the La Paz area, April 1972. The preserved material ranges from 24 to 42 mm in total length. Five of these specimens are deposited in the Los Angeles County Museum of Natural History, LACM no. 1618.

Description: The body color of the living animal (Figures *1* and *2*) is off-white, with 2 or 3 irregular rows of bright orange spots encircling the edge of the notum. The dots increase in size from the outer to the inner row, becoming both more irregular in shape and encircled or spotted by pure white markings. There is an additional row of large orange circlets beginning anterior to the rhinophores and continuing lengthwise along the animal's body just lateral to the mid-dorsal region. These ringlets vary in shape from circular to oval, and some may even be incompletely formed circles, open on one side. Each orange marking in this row is banded by a conspicuous pure white line, often with a few white specks on the orange coloration. This row contains the largest orange markings on the animal's body. The notum is covered by very low, closely placed tubercles. The distal portion of the rhinophores is a very light brown color, with a prominent median white longitudinal septum on both its anterior and posterior faces. Each rhinophore is perfoliated (18 - 28 leaves) and retractile into a low, smooth rim pocket.

The 7 or 8 bi- and tri-pinnate gills are light brown in color. Running along the center of each branching of the gills is a pure white ridge, slightly raised above the surrounding skin membrane.

The off-white colored foot has slight anterior corners and is bilabiate (Figure 3). A line of pure white completely encircles the edge of the foot. The free edge of the notum completely covers the foot.

The short oral tentacles are blunt and grooved laterally (Figure 3). The buccal armature on the jaw plates consists of numerous small rods and hooks (Figure 4).

The radular formula of the holotype is 59 × 59·1·59. The second paratype (illustrated by the scanning electron micrographs) has a radular formula of 62 × 40-53·1·40-53. The inconspicuous rachidian tooth is tipped with a slight, posteriorly directed hook (Figure 5). The lateral

Figure 3

Chromodoris marislae: antero-ventral view of holotype, showing the slight anterior foot corners and the oral tentacles; drawing by Wesley M. Farmer

Figure 4

Chromodoris marislae: jaw plate of holotype; drawing by Wesley M. Farmer

Explanation of Figures *6* to *8*

Chromodoris marislae Bertsch, spec. nov.

Stereoscopic scanning electron micrographs (by Thomas L. Hayes and Hans Bertsch) of the radula of paratype specimen collected at Isla Las Animas. Micrographs reproduced laterally to each other are stereo pairs; resolution into a three-dimensional image can be facilitated by a two-lensed stereoscopic viewer. The exceptionally bright areas in Figures *6, 9,* and *10* are charging artifacts of the scanning electron microscope, caused by reduced specimen collection or changes in collection efficiency because of distortion of the collection fields or both (Pawley, 1972). These charging artifacts are limited to changes in brightness, and have caused no distortion of the image shape, with the result that the informational content of the micrographs is still useful

Figure *6*: Rows of inner lateral teeth approximately ×50
Figure *7*: Inner lateral teeth; enlargement of bottom right center portion of Figure *6* approximately ×250
Figure *8*: Inner lateral tooth; enlargement of center area of Figure *7* approximately ×750

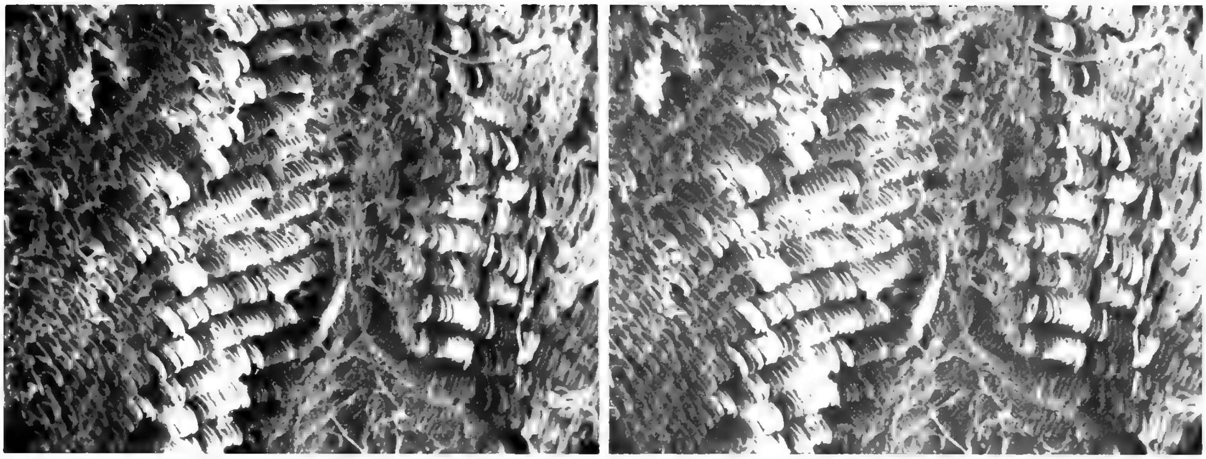


Figure *6*

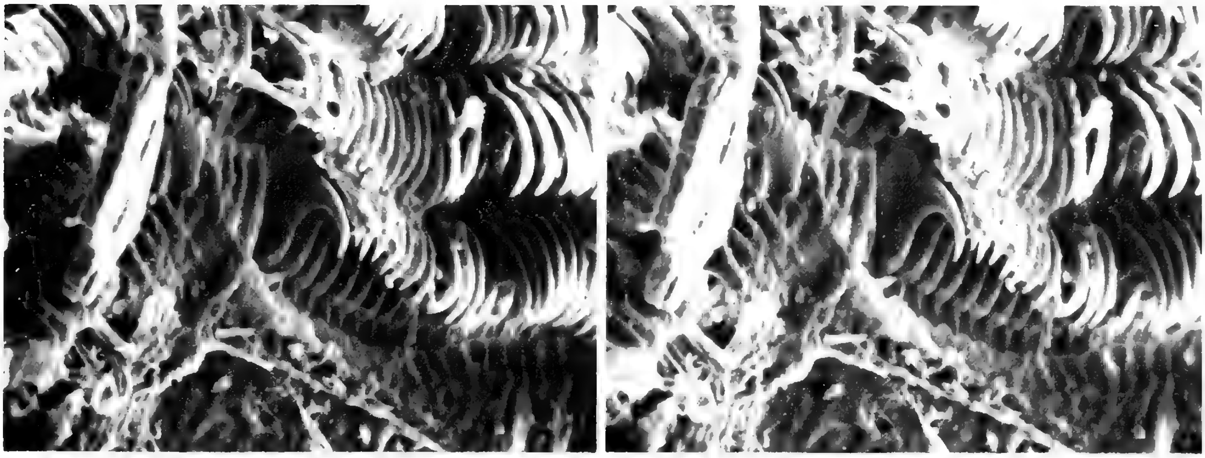


Figure *7*

Figure *8*

teeth (Figure 6) exhibit the characteristic *Chromodoris* unicuspidate shape. The inner laterals are completely smooth, with a thin hook slanting posteriorly above the basal portion of the tooth (Figure 7). The distal third of the hook bends sharply at almost a 90° angle downward from the main axis of the shaft. There is a ridge-like axial thickening on the anterior edge of these lateral teeth (Figure 8). The extensive set of hook-like inner teeth is flanked on the outer portion of the radula by thicker, more upright cusps (Figures 5, 6, and 9). The erect shaft of each cusp has a row of small denticles lengthwise along its posterior surface (Figure 10) and terminates distally in a large, posteriorly curving tip (Figure 11). The denticles randomly vary from 2 to 9.

Discussion: *Chromodoris marislae* is readily distinguishable from the other species of Chromodorididae within the Panamic province on the basis of its unique external coloration. None of the other species have the white-and -orange-circles pattern. The radula is distinctly different,

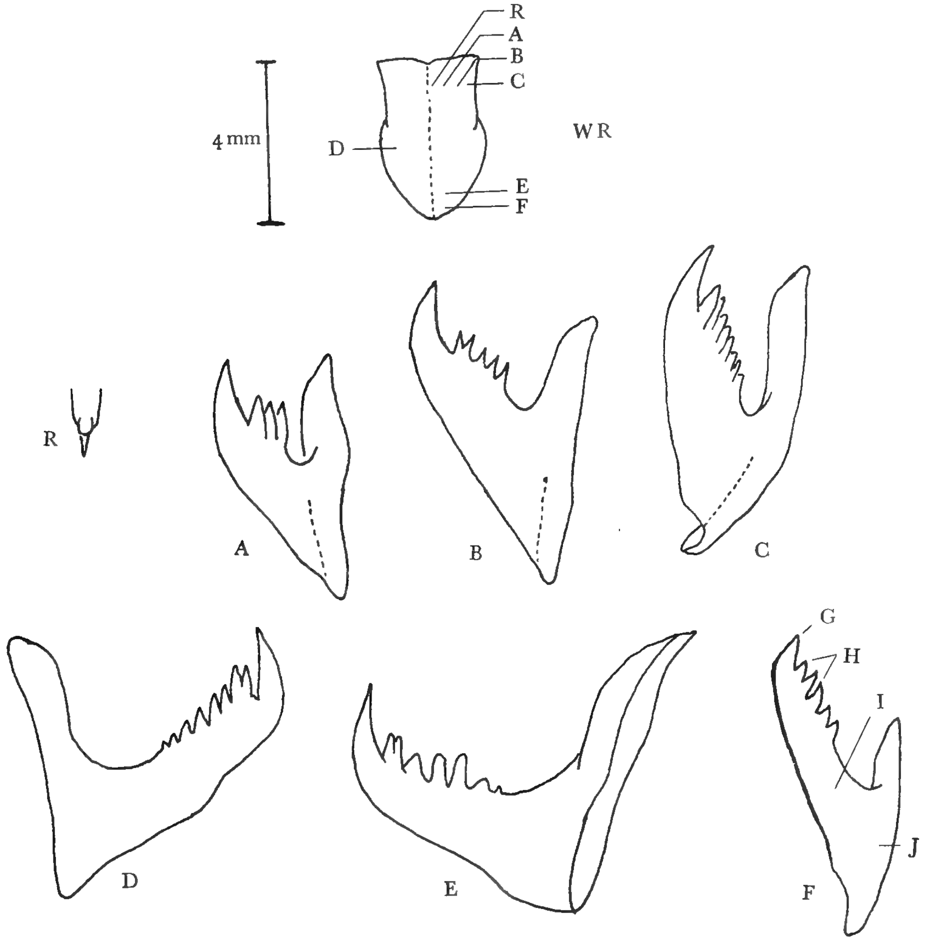


Figure 5

Chromodoris ***marislae:*** radula and representative teeth of the holotype (drawings by Wesley M. Farmer)
WR – entire radula, showing the positions of the individual teeth illustrated; R – rachidian tooth; A through F – outer lateral teeth; G – posteriorly curving tip of cusp; H – row of denticles along the length of the erect shaft; I – erect shaft of the cusp; J – basal portion of cusp

even considering the range of variation that often exists within *Chromodoris* species in number of rows of teeth and teeth per half row, and the number of denticles on each tooth. *Hypselodoris californiensis, H. agassizii,* and *H. aegialia* (Bergh, 1904) have bicuspidate lateral teeth; *Felimida sphoni, Chromodoris baumanni, C. norrisi, C. sedna,* and *C. tura* have denticulate inner and outer laterals; *C. banksi* has denticulate inner and smooth outer lateral teeth. *Chromodoris marislae* differs by having unicuspidate teeth, smooth inner laterals, and denticulate outer laterals. An additional comparison can be made with the scanning electron micrographs of radular teeth published in the original description of *C. baumanni.* The outer lateral cusps of *C. marislae* have shorter and sturdier shafts, and end in a more pronounced distal tip.

The specific name *marislae* is chosen to honor the R/V *Marisla* and its owners, Richard and Mary Lou Adcock, whose generous cooperation with numerous researchers has contributed much to our knowledge of the fauna of the Gulf of California.

Functional Radular Morphology: Several recent papers (Thompson & Hinton, 1968; Runham, 1969; Bertsch, 1970; Thomas, 1971; and Solem, 1972) have shown the advantages of scanning electron microscopy for understanding three-dimensional radular structures. The scanning electron micrographs of *Chromodoris marislae* provide additional information on the functioning of chromodorid radulae. Young (1970) summarizes the radular movements of rasping sponge-feeding dorids as a protrusion of the odontophore and radula to outside the buccal lips, followed by retraction in a forward and upward rasping stroke. Food intake depends on the effectiveness of this retraction stage. The radula passes over the tip of the odontophore, so that the teeth are erected and exposed to the feeding surface. The hooked tips of the radular teeth (aided by denticles when present) act to rasp away small pieces of food stuff and convey the particles to the esophagus (Young, *op. cit.*). This feeding method is similar to that of other gastropods, especially pulmonates and taenioglossan prosobranchs (Fretter & Graham, 1962: 179 ff.; Young, *op. cit.*: 432; Runham, 1969; Solem, 1972: 334).

The smooth inner laterals of *Chromodoris marislae* have a sharply bent hook that parallels the plane of the basal plate and then ends in a tip that curves downward. These teeth would be ineffective raspers if the radula were held completely flat during feeding. The denticulate outer laterals possess a thick, nearly upright shaft. This shaft protrudes upward even when the radula is flattened. The radular bending over the tip of the odontophore during its retraction exposes the down-curved points of the inner laterals so that they can gouge and claw out pieces of food. The denticulate edges of the outer laterals are simultaneously more effectively exposed to the food surface, and are pulled across it, rasping and tearing apart the food. The inner laterals can dig more deeply than the outer laterals, hooking chunks out of the food surface, while the outer laterals assist by rasping food from the surrounding tissue.

The necessary strength for this rasping action is provided to the radula not only by the buccal armature and musculature and the firmness of the supportive odontophore (Young, 1970: 430 - 434), but also by the positioning of teeth on the radula, and by the shape of each individual tooth.

The base of each tooth extends between pairs of teeth in the immediately adjacent anterior and posterior rows (Figures *7* and *10*). Although this interdigitation is not as distinct an interlocking system as that reported by Solem (1972: 334) for pulmonate radulae, the two systems can fulfill the same basic task of transferring pressure between teeth rows in order to raise the rasping rows of cusps to a more functional upright position.

The structure of each tooth has an inherent mechanical strength. The thin inner laterals are strengthened by the in-curving of the shaft, by the ridge-like thickening along the axis of the shaft, and by the triangular supporting tissue within the angle where the shaft joins the basal plate (Figure *8*). The upright outer laterals are strengthened by their sheer massiveness, with the shaft being quite broad along the antero-posterior axis (Figure *11*).

Chromodoris norrisi Farmer, 1963

Chromodoris norrisi has been found at numerous localities along the Pacific Coast of Baja California and throughout the Gulf of California: Isla Cedros, Puerto Rompiente, Isla Cerralvo (the type locality), Bahía de

Explanation of Figures *9* to *11*

Chromodoris marislae Bertsch, spec. nov.

Figure *9*: Rows of outer lateral teeth approximately ×75

Figure *10*: Outer lateral teeth; enlargement of center portion of Figure *9* approximately ×250

Figure *11*: Outer lateral teeth; enlargement of left-center area of Figure *10* approximately ×750

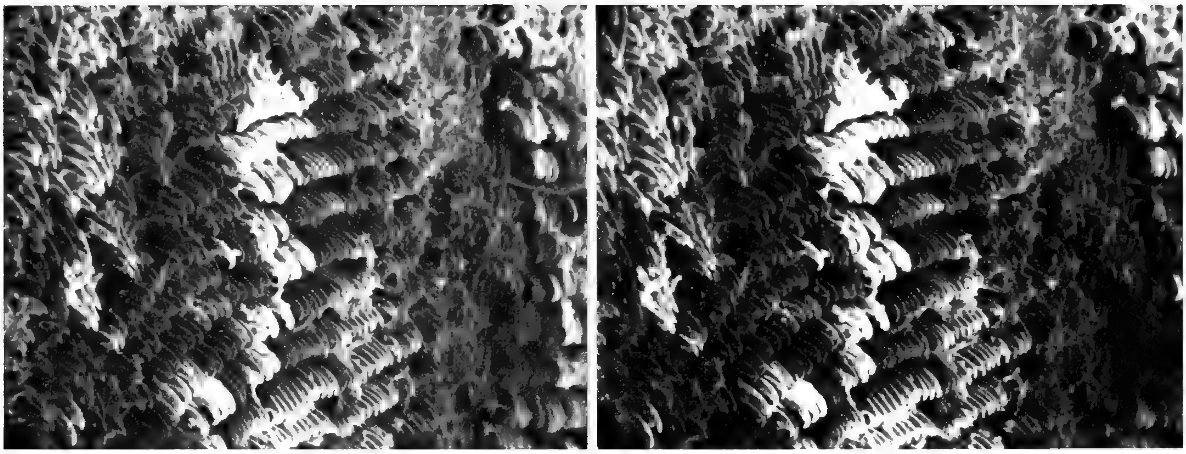


Figure *9*

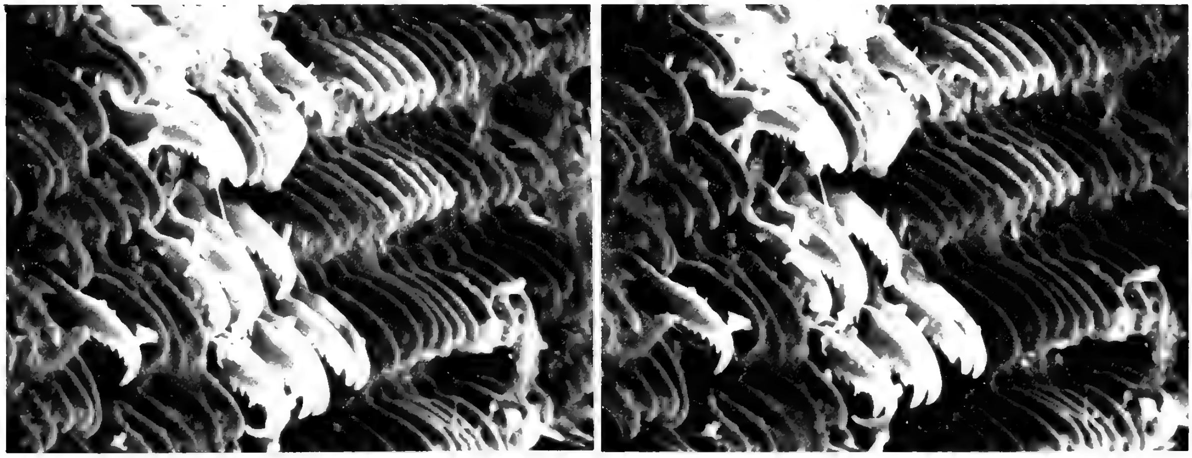


Figure *10*

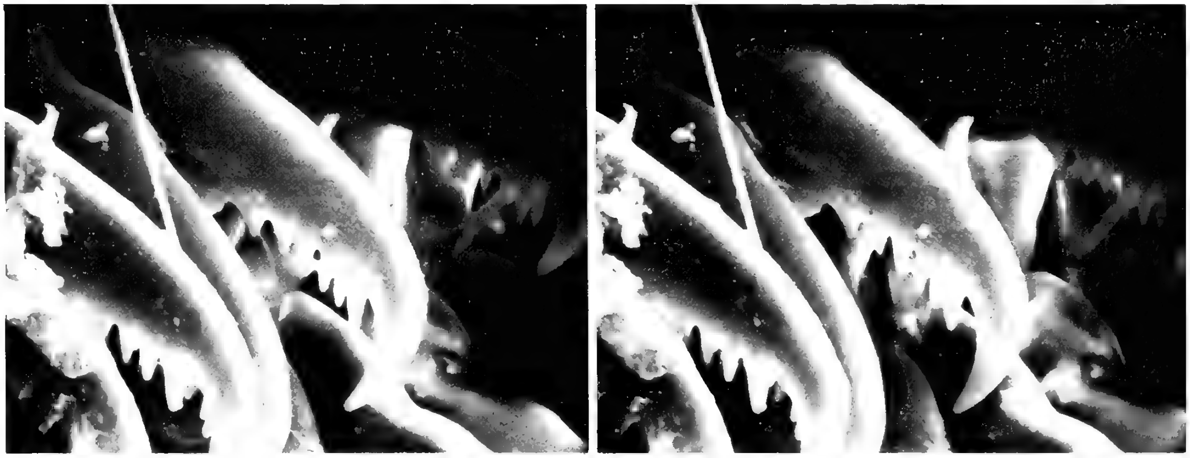


Figure *11*

Los Angeles, Bahía San Luis Gonzaga, Puerto Peñasco, Puerto Lobos, and Guaymas (Farmer, 1963, 1971; Marcus & Marcus, 1967). Ferreira has collected specimens of *C. norrisi* at Islas San José, Los Islotes, Las Animas (July 1971) and Coyote (June 1970). These intermediate records give *C. norrisi* a nearly continuous distribution along the Gulf coast of Baja California.

Specimens collected by Bertsch in July 1972 at Las Cruces, Baja California, showed a graded series of color variations, from animals with fewer and larger reddish-purple dots to animals with many small reddish-purple dots. All had distinct yellow dots on the white notum, with a median purplish band of variable intensity across the width of the notum.

Chromodoris sedna (Marcus & Marcus, 1967)

The common *Chromodoris sedna* ranges from Puerto Peñasco to Academy Bay in the Galápagos Islands (Sphon & Mulliner, 1972). It has been collected from Mexican waters at Las Cruces, Isla Cerralvo, Isla Santa Cruz, Isla Angel de la Guarda, Bahía San Luis Gonzaga, Guaymas, Mazatlán, Santa Cruz, and Tenacatita (Bertsch, 1970, 1971, and in press; the first cited paper established the synonymy of this species; Lance, 1968; Marcus & Marcus, 1967). Numerous specimens were collected in Costa Rica (by Ferreira, February 1972, at Bahía Jobo, Bahía Ballena, Islas Tortugas, and Quepos), establishing intermediate localities between its formerly disjunct occurrences in Mexico and the Galápagos Islands.

Chromodoris tura Marcus & Marcus, 1967

The known distribution of *Chromodoris tura* is based only on the holotype collected at Deale Beach (Fort Kobbe Beach) on the Pacific side of the Panama Canal Zone. In March 1971, Ferreira collected 4 specimens of *C. tura* intertidally at Sayulita, Nayarit, Mexico. These collections represent a northwestward range extension of approximately 3200 km (2000 miles), and a subtidal bathymetric extension.

Felimida sphoni Marcus, 1971

Marcus (1971) neither designated the type specimen of *Felimida sphoni* nor indicated the deposition of the type material. Marcus used 5 specimens in naming this genus and species, dissecting and retaining one, and returning the other 4 to Gale Sphon. Sphon deposited these syntypes in 3 museums: California Academy of Sciences, CA SIZ Type Series, no. 482; Santa Barbara Museum of Natural History, SBMNH no. 33185; and Los Angeles County Museum of Natural History, LACM no. 1616. It is premature to designate a lectotype specimen until the taxonomic status of this genus is revised.

In March, 1971, Ferreira obtained one specimen of *Felimida sphoni* SE of Isla Venado, near Mazatlán, Mexico, under a rock in 3 m of water. This is a northern range extension of 235 km (145 miles) from Santa Cruz, Nayarit, and a bathymetric extension into the subtidal region. In December, 1971, Ferreira found one specimen of *F. sphoni* at Puerto Angel, Oaxaca, Mexico, and in February, 1972, he found one specimen subtidally in 7 m of water at Islas Tortugas, Costa Rica. Both of these records are southern range extensions, the latter approximately 2500 km (1500 miles) south of its previously known southern distribution at Colima, Mexico.

ACKNOWLEDGMENTS

We thank Dustin Chivers and James T. Carlton of the California Academy of Sciences, Nelson Baker of the Santa Barbara Museum of Natural History, Dr. James H. McLean and Gale Sphon of the Los Angeles County Museum of Natural History, who helped us at various stages in the preparation of this paper. The collecting of specimens was aided by Richard and Mary Lou Adcock of the R/V *Marisla*, by Edwin Janss and the Janss Foundation who provided the R/V *Searcher* for the work done in Costa Rica, and Don Cadien, Pat LaFollette, and Prof. William A. Bussing of the University of Costa Rica.

We are also grateful to Prof. Michael T. Ghiselin of the University of California, Berkeley, who critically read the manuscript and helped throughout the writing of this paper.

Preparation of this manuscript was aided in part by National Science Foundation Grant NSF-GY-9815 to the Bodega Marine Laboratory, and the publication was sponsored by a grant (to Bertsch) from the Janss Foundation.

Literature Cited

Abbott, Donald Putnam
1966. Factors influencing the zoogeographic affinities of Galapagos inshore marine fauna. *In*: Robert I. Bowman (ed.), The Galapagos. Proc. Symp. Galap. Internat. Sci. Proj., Berkeley & Los Angeles, Univ. Calif. Press, pp. 108 - 122; 8 text figs.

Bergh, Ludwig Sophus Rudolf
1879. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Proc. Acad. Nat. Sci. Philadelphia, prt. 1; **31**: 127 - 188; plts 1 - 8 (10 May 1879)
1894. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer "*Albatross*," during 1891, Lieut. Commander Z. L. Tanner, U. S. N., commanding. XIII. Die Opisthobranchien. Bull. Mus. Comp. Zool. Harvard Univ. **25** (10): 125 to 233; plts. 1 - 12 (October 1894)

1904. Malacologische Untersuchungen: Nudibranchiata. *In*: C. Semper, Reisen im Archipel der Philippinen, Wissenschaftliche Resultate 9 (6):(1): 1-55; plts. 1-4 (2 February 1904)
9 (6):(2): 57-116; plts. 5-8 (7 March 1905)

Bertsch, Hans

1970. Opisthobranchs from Isla San Francisco, Gulf of California, with the description of a new species. Contrib. Sci., Santa Barbara Mus. Nat. Hist. **2**: 1-16; 13 text figs. (1 December 1970)

1971. Natural history and occurrence of opisthobranchs of Las Cruces, Baja California, Mexico, and vicinity. The Echo **3**: 16 (7 March 1971)

1973. Zoogeography of opisthobranchs from tropical West America. The Echo **5**: in press

in press Distribution and natural history of opisthobranch gastropods from Las Cruces, Baja California del Sur, Mexico. The Veliger **16**

Cockerell, Theodore Dru Alison

1902. Three new species of *Chromodoris*. The Nautilus **16** (2): 19-21 (June 1902)

Darlington, Philip J., Jr.

1957. Zoögeography: the geographical distribution of animals. xiii+675 pp.; illust. John Wiley & Sons, New York

Farmer, Wesley Merrill

1963. Two new opisthobranch mollusks from Baja California. Trans. San Diego Soc. Nat. Hist. **13** (6) 81-84; 1 plt.; 1 text fig. (27 September 1963)

1967. Notes on the Opisthobranchia of Baja California, Mexico, with range extensions. -- II. The Veliger **9** (3): 340-342; 1 text fig. (1 January 1967)

1971. Eveline Marcus, and Puerto de Lobos, Sonora, Mexico. The Echo **4**: 19 (27 December 1971)

Fretter, Vera & Alastair Graham

1962. British prosobranch molluscs, their functional anatomy and ecology. London, Ray Soc. xvi+755 pp.; 316 figs.

Hertlein, Leo George

1963. Contribution to the biogeography of Cocos Island, including a bibliography. Proc. Calif. Acad. Sci. (4) **32** (8): 219-289; 4 text figs. (20 May 1963)

Keen, A. Myra

1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i-xiv+1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

Lance, James Robert

1968. New Panamic nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California. Trans. San Diego Soc. Nat. Hist. **15** (2): 1-13; 2 plts.; 11 figs. (8 January 1968)

Marcus, Eveline du Bois Reymond

1971. On some euthyneuran gastropods from the Indian and Pacific Oceans. Proc. Malacol. Soc. London **39**: 355-369; 20 text figs.

Marcus, Eveline du Bois Reymond & Ernst Marcus

1967. American opisthobranch mollusks. Stud. Trop. Oceanogr. Miami, **6**: viii+256 pp.; figs. 1-155+1-95 (December 1967)

Mayr, Ernst

1969. Principles of systematic zoology. xi+428 pp.; illust. McGraw-Hill, New York

Pawley, James B.

1972. Charging artifacts in the scanning electron microscope. Scanning Electron Microscopy / **1972** (I): 153-160; 7 text figs.

Pruvot-Fol, Alice

1951. Révision du genre *Glossodoris* Ehrenberg. Journ. Conchyl. **91** (3-4): 76-164 (1 July and October 1951)

Runham, Norman W.

1970. The use of the Scanning Electron Microscope in the study of the gastropod radula: The radulae of *Agriolimax reticulatus* and *Nucella lapillus*. Proc. 3rd Europ. Malac. Congr., Malacologia **9** (1): 179 to 185; 7 text figs. (16 June 1970)

Solem, Alan

1972. Malacological applications of scanning electron microscopy. II. Radular structure and functioning. The Veliger **14** (4): 327-336; 6 plts.; 1 text fig. (1 April 1972)

Sphon, Gale G.

1971. The reinstatement of *Hypselodoris agassizi* [sic.] (Bergh, 1894) (Mollusca: Opisthobranchia). The Veliger **14** (2): 214 (1 Oct.)

Sphon, Gale G. & David K. Mulliner

1972. A preliminary list of known opisthobranchs from the Galápagos Islands collected by the Ameripagos Expedition. The Veliger **15** (2): 147-152; 1 map (1 October 1972)

Thomas, Ronald Frank

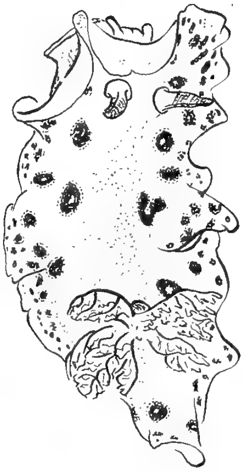
1971. A scanning electron microscope study of the marginal teeth of *Nerita peloronta* Linnaeus. The Nautilus **84** (4): 118-120 (April)

Thompson, Thomas Everett & H. E. Hinton

1968. Stereoscan electron microscope observations on opisthobranch radulae and shell-sculpture. Bijdr. tot de dierk. **38**: 51-52; 4 plts.

Young, David K.

1970. The functional morphology of the feeding apparatus of some Indo-West Pacific dorid nudibranchs. Malacologia **9** (2): 421-446; 2 tables; 17 text figs. (20 July 1970)



Embryonic and Larval Development in the New Zealand Rock Oyster, *Crassostrea glomerata* (Gould)

BY

P. DINAMANI

Fisheries Research Divison, Ministry of Agriculture and Fisheries, Wellington, New Zealand

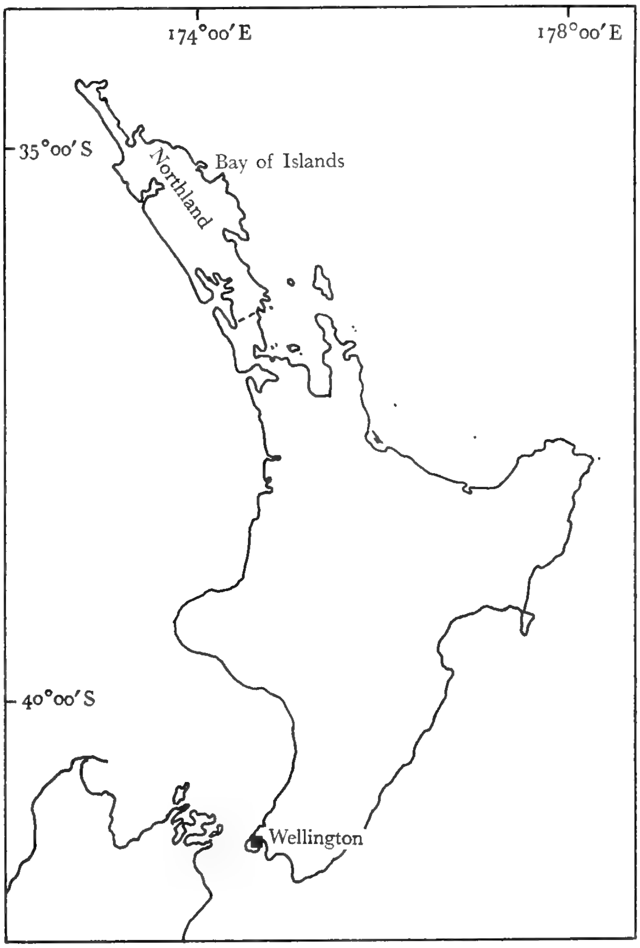
(3 Plates; 2 Text figures; 1 Map)

INTRODUCTION

THE BIOLOGY OF *Crassostrea glomerata* (Gould, 1850), the New Zealand rock oyster, is almost unknown, though the oyster has been cultivated in the northern parts of the country since 1964. Studies on the oyster, particularly on its reproduction and larval development, were begun in 1969, and some of the results of the study on development are described in this paper. The study adds to the data on the embryonic development of oviparous oysters, on which published information is sparse: the relevant studies are by BROOKS (1880) and GALTSOFF (1964) on *Crassostrea virginica* (Gmelin, 1791), by FUJITA (1929) on *C. gigas* (THUNBERG, 1793), by AMEMIYA (1926) and LE DANTEC (1968) on *C. angulata* (Lamarck, 1819), and by ROUGHLEY (1933) on *C. commercialis* (IREDALE & ROUGHLEY, 1933).

MATERIALS AND METHODS

Cleavage and development up to the early veliger stage was observed in a group of oysters which had spawned spontaneously in the laboratory and also in another group which was induced to spawn. Both groups of oysters had been collected at the same time from intertidal beds in the Bay of Islands (see Map) during the 1970 - 1971 breeding season and held for about 2 weeks in tanks in the laboratory in Wellington at 17° ± 1° C. Spawning occurred on 1 December 1970 in a group of oysters which had just been removed to a container of renewed sea water (temperature 18°C), and these embryos developed to the trochophore stage and then died. On 3 December 1970 a fresh group of oysters was placed in a pail of renewed sea water and the temperature of the water raised to 21° C. The oysters spawned within 90 minutes, and were afterwards removed from the pail. After about 2 hours, when cleavage had begun, the water, with the embryos, was



Map of North Island of New Zealand, showing locations of places mentioned in the text poured into shallow plastic trays or into 500-ml beakers through a fine nylon mesh (135 μm), which retained the debris. All stages of development up to the straight-hinged veliger were followed in this culture. Heavy mortalities on the third day nearly wiped out the whole stock of larvae, but some reared in sterile sea water survived until the ninth day after fertilization. Attempts to feed the larvae, begun on the third day, failed, since unialgal food such as *Isochrysis, Monochrysis,* and *Dicrateria* was not then readily available.

Plankton hauls for free-swimming larvae were made in the Bay of Islands from the second week of December 1970 onward, and sampling was repeated during the 1971-1972 season in many bays in Northland. Sampling lasted until the end of March in both years. All stages of larvae, from 85 to 320 μm in length, were recorded in the plankton during summer. The specific identification of planktonic larvae was confirmed by rearing late stages of larvae to settlement and also by examining recently settled pediveligers on spat collectors set in different parts of the bay.

Except for larvae of *Crassostrea commercialis,* for which data have been taken from ROUGHLEY (1933), dimensions of all other species of larvae have been verified by direct observation.

OBSERVATIONS

The times mentioned in the following description on early development refer to the time from fertilization.

The fertilized egg (Figure *1*), measuring about 40 μm, forms the first polar body within 30 min of the appearance of the fertilization membrane (Figure *2*), followed within 45 - 60 min by the second polar body. The division of the egg (Figures *3* to *6*) follows the usual pattern for molluscan eggs and results in the gastrula, 5 to 7 hrs after fertilization (Figure *7*).

The earliest free-swimming trochophores (Figure *8*) emerge within 12 to 18 hrs, and the trochophore stage persists for almost another 24 hrs. The larval shell develops after 36-42 hrs, and the first veligers, measuring 50-60 μm and 45-50 μm in height, appear. The characteristic feature of the early veliger of *Crassostrea glomerata* is its saddle-shaped dorsal margin with a shallow depression (Figure *9*). The larval shell is slightly asymmetrical with the anterior border more uniformly rounded than the posterior. D-stage veligers grew to a size of 70 × 68 μm by the fourth day, and though several larvae of this batch lived up to the ninth day, no further growth took place under laboratory conditions, primarily because of lack of suitable food.

Further development was followed in planktonic stages of the larvae collected in the field. The earliest planktonic stage larvae taken in samples were 80 to 90 μm long and were nearly the same height (Figure *10*).

The larval outline is nearly circular and well defined at this stage, with the valves nearly equal. The subsequent growth of the valves is unequal; at a larval length of about 110 μm the asymmetry is apparent and the umbones are nearly rounded. During further growth, the right umbo enlarges and begins to extend beyond the dorsal margin of the right valve. At the same time larval dimensions also change, and height begins to exceed length (Text figure 18): shell height begins to exceed the length from the time the larva is 120 μm long, and in later stages, from a length of 270 μm, this increase is very pronounced. When the larva is nearly 270 μm long and 290 μm tall (Figure *11*) a pigment spot develops and the larva soon enters the pediveliger stage. In the laboratory the pediveliger alternately swims by means of the velum or uses its foot to crawl along the bottom. The fully developed pediveliger (Figure *12*), usually 320 × 350 μm in size, spends more time crawling as it nears metamorphosis. From a length of 270 μm the umbones become more prominent as the larva approaches the pediveliger stage, with the right umbo rising prominently over the margin of the right valve (Figure *14*).

Attachment takes place when the larva is 320 to 330 μm long and 350 to 360 μm tall. The late-stage larva is usually a pale pinkish purple, which contrasts with the yellowish brown centre formed by the digestive diverticula. Fully developed larvae are darker, especially around the umbones. Nearly black larvae, 320 × 360 μm, are seen late in the breeding season.

Eyed larvae, 290 to 300 μm long, picked from plankton hauls and introduced into finger bowls in the laboratory,

Explanation of Figures *9* to *14*

Figure *9*: Straight-hinged veliger, 70×65 μm, fourth day

Figure *10*: A group of 6 larvae, showing stages of growth from a length of 90 μm to 180 μm; larvae are 90 × 90, 110 × 110, 150 × 155, and 180 × 190 μm

Figure *11*: Larva 270 × 290 μm; pigment spot formed

Figure *12*: Fully developed stage 320 × 360 μm just before settlement

Figure *13*: Lateral view of a pediveliger to show the prominent right umbo

Figure *14*: Apical region of spat, 3 days old, showing the prodissoconch

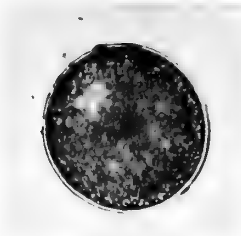


Figure *1*

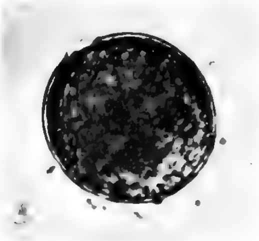


Figure *2*

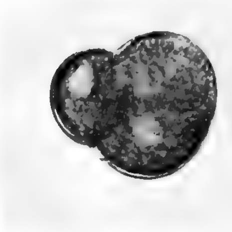


Figure *3*

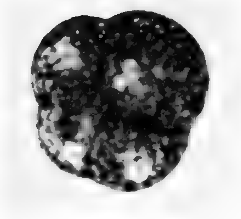


Figure *4*

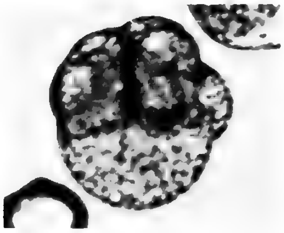


Figure *5*

Figure *6*

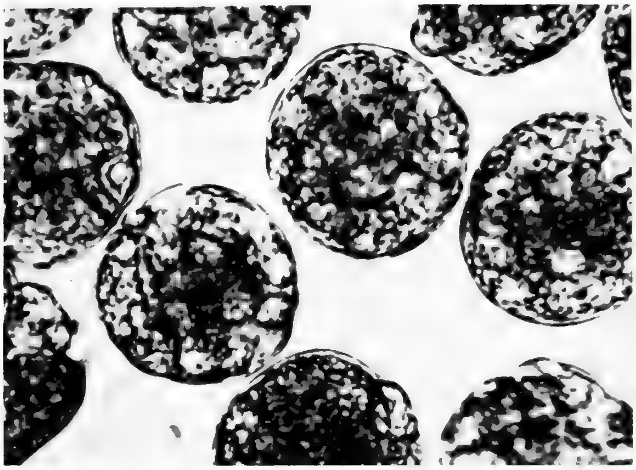


Figure *7*

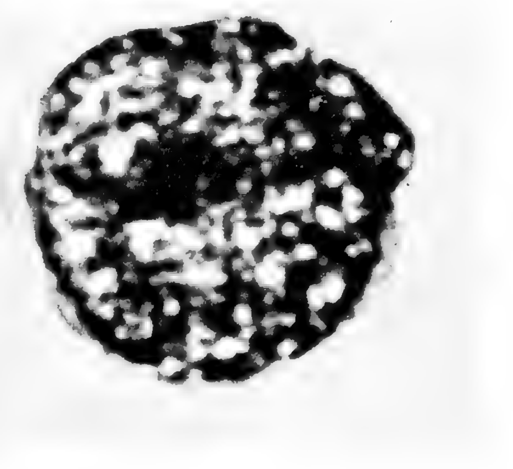


Figure *8*

Figure *1*: Fertilized egg, 40 μm
Figure *2*: Formation of first polar body
Figure *3*: First division, 2 blastomeres
Figure *4*: Second division, 4 blastomeres, D-sector largest
Figure *5*: Third division, 4 micromeres cut off apically
Figure *6*: Fourth division, ring of 8 micromeres
Figure *7*: Stages leading to gastrula
Figure *8*: Ciliated trochophore, 45 μm, 15 hr after fertilization

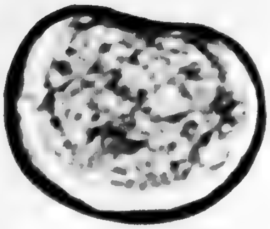


Figure *9*

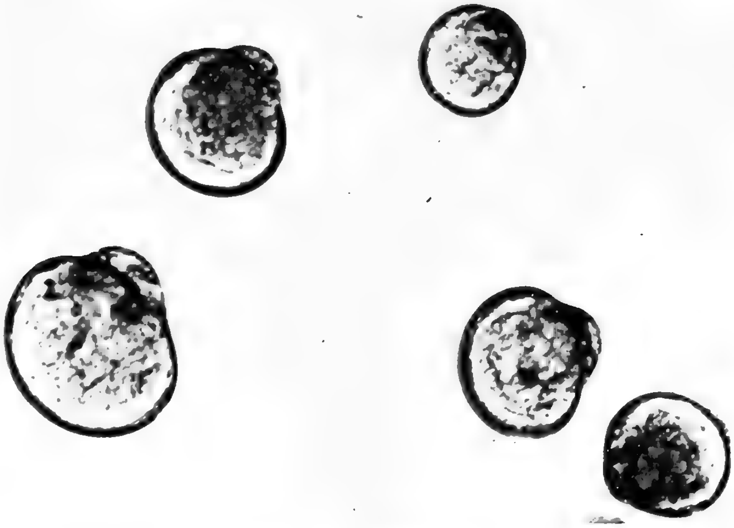


Figure *10*

Figure *11*

Figure *13*

Figure *12*

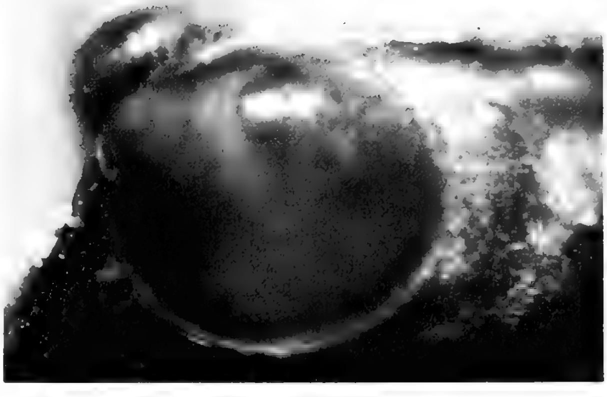


Figure *14*

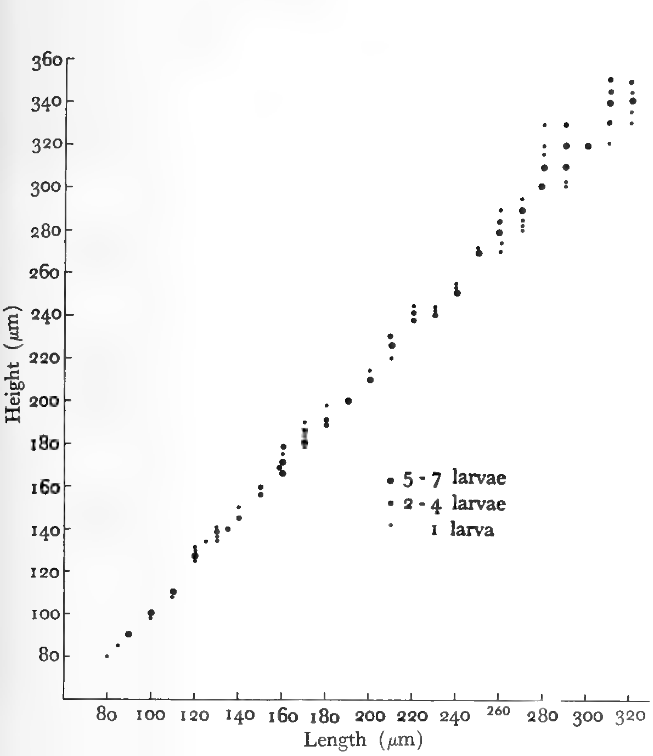


Figure 18

Length : height relationship of larvae of *Crassostrea glomerata* (n=215)

settled between the third and fifth day (mean temperature 21° C), and these spat were kept alive for several days. The spat are usually 350 to 370 μm long 1 day after settlement; the smallest spat observed on spat collectors that had been exposed for a week were also of this size. On the basis of times between the first appearance of recognizable planktonic larvae (assumed as 4 to 5 days old) and the first settlement, the length of larval life is estimated as 18 to 24 days (surface temperature 21-22° C).

The prodissoconch is very conspicuous in rock oyster spat (Figure *15*) and its shape and size make specific recognition of the spat possible. The spat is normally a brownish purple with a faint pale streak running radially across the right valve and is readily distinguished from spat of *Ostrea* sp., which frequently settle in the same areas (Dinamani, 1971).

Larval Shell

The prodissoconch develops in the free-swimming larva when it is 50 to 60 μm long, and shell length remains greater than shell height until the larva grows to a size of 75 μm, when the dimensions become equal. The broad provincular plate is discernible in larvae 140 to 150 μm long (Figure *15*) and consists of 2 anterior and 2 posterior teeth on either side of a central ridge. This remains symmetrical throughout larval development, with only slight changes in the size and shape of the plate and teeth (Figure *16*). There is no reduction of teeth (Figure *17*), such as has been noted by Pascual (1971) in *Crassostrea angulata* even in the fully developed larva. The larval ligament is anterior, immediately outside the provinculum.

DISCUSSION

Stages of development of the rock oyster, from cleavage to gastrulation, are essentially similar to those described for other *Crassostrea* species. The developmental sequence

Table 1

The Embryonic Development of *Crassostrea glomerata* Compared with that of Other Oviparous Oysters

Species: Source:	*C. angulata* Amemiya (1926)	*C. gigas* Fujita (1929) Amemiya (1931) [1]	*C. virginica* Galtsoff (1964) [3]	*C. commercialis* Roughley (1933)	*C. glomerata*
Temperature (° C):	20 - 23	25	23 - 25	25	17 - 18
Stages of development:					
Polar bodies	40 - 60 min	50 - 70 min	25 - 65 min	–	30 - 45 min
First cleavage	70 - 80 min	100 min	45 min	90 min	90 min
Second cleavage	80 - 90 min	180 min	50 - 120 min	120 min	120 min
Third cleavage	–	180 min	55 - 195 min	–	180 min
Morula	5 hr 30 min	4 - 6 hr	2 hr 15 min	2 hr 30 min	4 - 5 hr
Gastrula	8 hr	10 - 20 hr [2]	4 - 6 hr	5 hr	7 hr
Early trochophore	14 hr	24 - 30 hr [2]	8 - 9 hr	6 hr	12 - 18 hr
D-stage veliger	40 hr	48 hr	32 - 48 hr	34 hr	36 - 48 hr

[1] as tabled in Cahn (1950)
[2] Fujiya (1970)
[3] series B

and times of several species of oviparous oysters are compared in Table 1.

The length : height relationship of *Crassostrea glomerata* is broadly similar to those of other species up to the pediveliger stage, except *C. commercialis,* whose dimensions (Roughley, 1933) show larval length as greater than larval height at all stages up to 300 µm. Roughley records a remarkable change in dimensions at this stage, with height exceeding length; however, this needs verification.

There are 2 distinct phases of growth which occur at a length of about 120 µm and again at about 270 µm (Text figure 18). Le Dantec (1968) has pointed out a similar phenomenon in *Crassostrea angulata,* though not at the same larval sizes. Loosanoff, Davis & Chanley (1966) have recorded a change in dimensions occurring between 105 and 130 µm in both *C. virginica* and *C. gigas,* and have represented it in their graph as a curved line. Le Dantec (1968) has stated that the differential phases of growth may correspond with morphological and physiological changes in the larva. In *C. glomerata* these phases would correspond to (1) development of the umbonal larva, and (2) the onset of the pediveliger stage.

The late-stage pediveliger of both *Crassostrea commercialis* and *C. glomerata* is slightly taller (length 320 µm, height 350 µm) than that of *C. virginica* and of *C. gigas.* In *C. glomerata* and *C. commercialis* the larvae at metamorphosis measure 320 - 330 µm in length, but in *C. virginica* and *C. gigas* settle normally at a larval length of 300 to 315 µm. Except for larval dimensions referred to above, both *C. glomerata* and *C. commercialis* show identical features of larval development and shell form, and this is

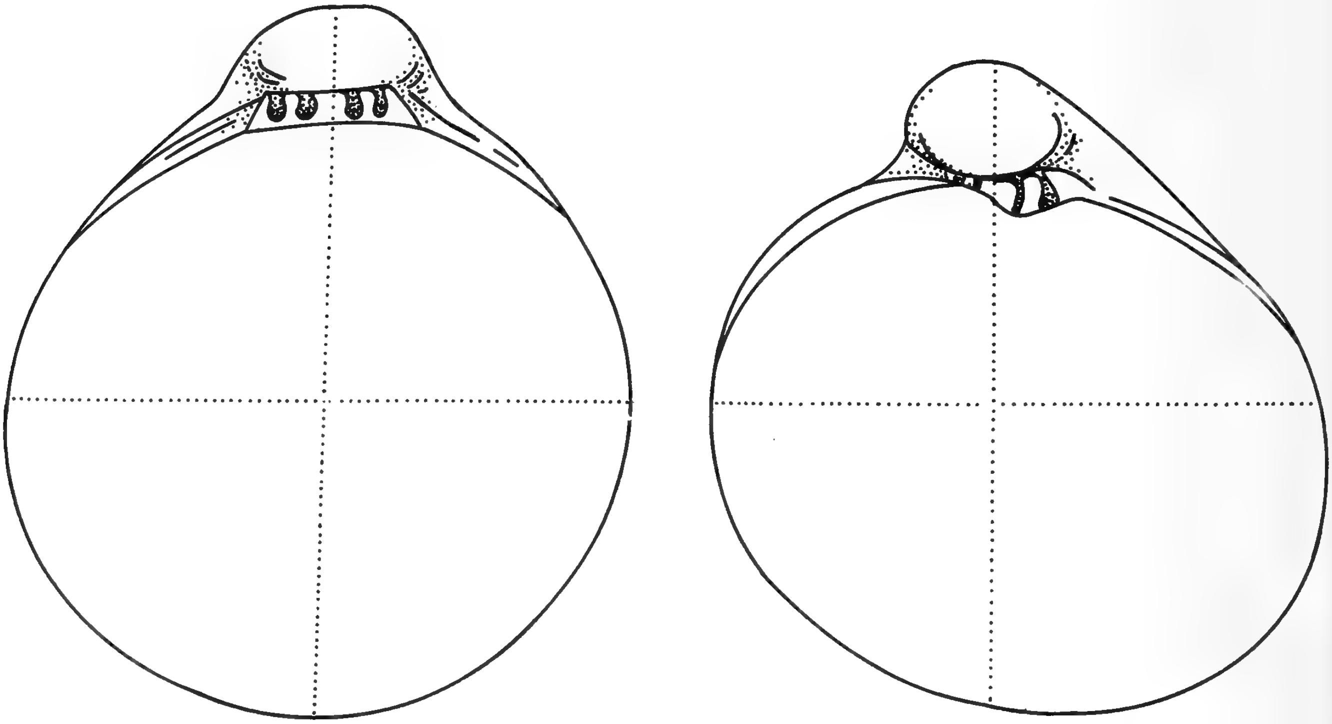


Figure 19

Diagrammatic representation of the left valves of two main prodissoconch types in *Crassostrea* to show differences in shell morphology

Right: *C. gigas, C. virginica,* and *C. angulata* Left: *C. glomerata* and *C. cucullata*

Explanation of Figures *15* to *17*

Figure *15*: Intact shell of a larva 140 µm long, showing the provinculum

Figure *16*: Left valve of a larva 180 µm long, showing the details of the provinculum

Figure *17*: Left valve of a late-stage larva, 300 µm long, showing details of teeth

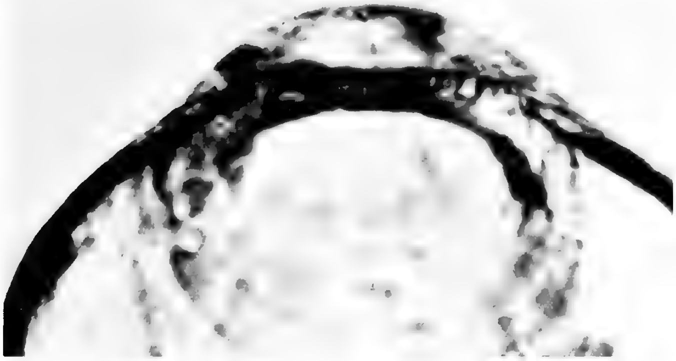


Figure *15*

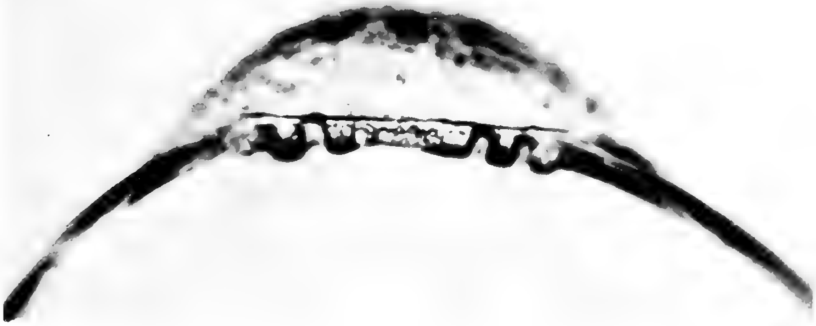


Figure *16*

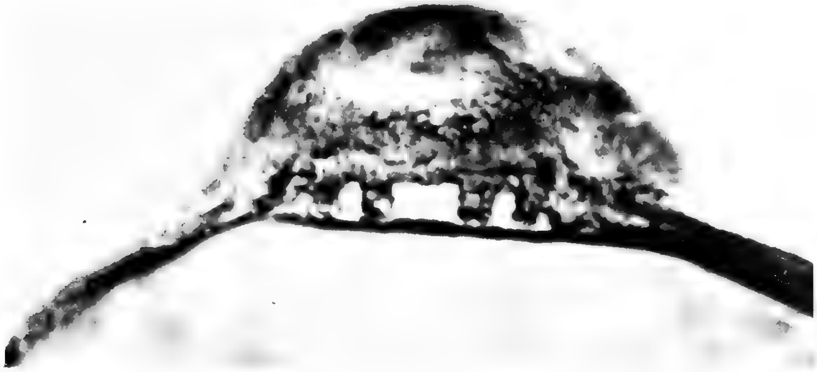


Figure *17*

also true of their adult shell and malacological characters. Thus it is necessary to consider whether they can be maintained as separate species.

The morphology of the larval shell of *Crassostrea glomerata* is distinctive and different from that of other species of *Crassostrea,* figured by Ranson (1967), including *C. cucullata,* which he regarded as synonymous with *C. glomerata.* Professor G. Ranson (pers. comm., 1971) confirms that the larval shell of *C. glomerata* is distinctive and different from that of *C. cucullata.* However, the fully developed prodissoconch of *C. glomerata* and *C. cucullata* share a common feature of possessing a broad provinculum and symmetrical shell and teeth, in contrast to *C. virginica, C. angulata,* and *C. gigas,* all of which have a modified provinculum and asymmetrical shell (Text figure 19). Preliminary results from a morphological study of the prodissoconchs of various species of *Crassostrea* point to the need for a more detailed study of the larval shell which will be useful in taxonomic studies (Ranson, 1943, 1960). This is being undertaken and will form the basis of a subsequent paper.

SUMMARY

Stages of development of the New Zealand rock oyster, *Crassostrea glomerata* (Gould), beginning with cleavage and leading through larval growth are described. The fully developed larva has a characteristic shape and form and has a planktonic life of 18 to 24 days. Features of larval shell morphology, such as the provinculum, are also distinctive and different from those of other main species of *Crassostrea.*

ACKNOWLEDGMENTS

Samples of larvae of various *Crassostrea* species were received from Dr P. R. Walne, Fisheries Experiment Station, Conway, Dr J. Le Dantec, Laboratoire d'Arcachon, and Dr W. S. Landers, Fisheries Biological Laboratory, Milford, to all of whom I am most grateful.

Literature Cited

Amemiya, Ikusaku
1926. Notes on experiments on the early developmental stages of the Portuguese, American and English native oysters, with special reference to the effect of varying salinity. Journ. mar. biol. Assoc. U. K. **14** (1): 161 - 175; 1 text fig.; 6 tables

Brooks, W. K.
1880. Development of the American oyster. Studies from the biol. labor., Johns Hopkins Univ., Baltimore, Md. **1** (4): 1 - 81

Cahn, Alvin Robert
1950. Oyster culture in Japan. Fishery Leafl. U. S. Fish Wildl. Serv. **383:** 80 pp.; 40 text figs.; 13 tables; 17 appended tables

Dinamani, P.
1971. Identification of oyster species competing with rock oysters for settlement space. Fish. Res. Div. Inf. Leafl. **1:** 9 pp.; 6 figs.

Fujita, Tsunenobu
1929. On the early development of the common Japanese oyster. Japan. Journ. Zool. **2** (3): 353 - 358; plt. 7

Fujiya, M.
1970. Oyster farming in Japan. Helgoländer wiss. Meeresunters. **20:** 464 - 479; 9 text figs.; 1 table

Galtsoff, Paul Simon
1964. The American oyster *Crassostrea virginica* Gmelin. Fishery Bull. U. S. Fish & Wildlife Serv. **64:** 1 - 480; 400 figs.; 46 tables

Le Dantec, Jean
1968. Ecologie et reproduction de l'huître Portugaise (*Crassostrea angulata* Lamarck) dans le bassin d'Arcachon et sur la rive gauche de la Gironde. Rev. Trav. Inst. Pêch. marit. **32** (3): 237 - 362; 56 text figs.; 18 tables.

Loosanoff, Victor Lyon, Harry Carl Davis & Paul E. Chanley
1966. Dimensions and shapes of larvae of some marine mollusks. Malacologia **4** (2): 351 - 435; 61 text figs. (31 August 1966)

Pascual, Emilio
1971. Morfología de la Charnela larvaria de *Crassostrea angulata* (Lmk.) en diferentes fases de su desarrollo. Investig. pesq. **35** (2): 549 - 563; 1 text fig.; 9 plts.

Ranson, Gilbert
1943. Les prodissoconques des Ostréidés actuels et fossiles. Classification et évolution des Ostréidés. Titres et Travaux Scientifiques de M. Gilbert Ranson, pp. 52 - 58; Masson et Cie., Paris
1960. Les prodissoconques (coquilles larvaires) des Ostréidés vivants. Bull. Inst. Océanogr. Monaco **1183:** 41 pp.; 136 figs.
1967. Les espèces d'huîtres vivant actuellement dans le monde, définies par leur coquilles larvaires ou prodissoconques. Étude des collections de quelques-uns des grands Musées d'Histoire Naturelle. Rev. Trav. Inst. Pêch. marit. **31** (2): 127 - 199; 25 figs.

Roughley, T. C.
1933. The life history of the Australian oyster (*Ostrea commercialis*). Proc. Linn. Soc. New So. Wales **58** (3/4): 279 - 333; plts. 10 - 27; 2 text figs.

Apertural Barriers in Pacific Island Land Snails of the Families Endodontidae and Charopidae

BY

ALAN SOLEM

Department of Zoology, Field Museum of Natural History
Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605

(7 Plates)

More than 140 years ago Guilding (1829: 168) speculated that the barriers found in the apertures of many land snails serve to lessen predation by arthropods. Comparatively little data has accumulated since then concerning barrier microstructure and patterns of growth. Solem (1972) briefly reviewed patterns of barrier formation, demonstrated that the barriers have weak to prominent microsculpture, and hypothesized that the pointed denticles found on the surface of many barriers evolved from a primitive, very widely distributed apertural microsculpture. This consists of platelets whose raised edges face the outer plane of the aperture, while their upper surface slopes gradually backwards to merge with the smooth surface of the inner lip and wall edges. When the aperture of the shell is greatly constricted by barriers, as in the polygyrid *Stenotrema* (Solem, 1972: figs. 23–24), the platelets are proportionately larger than in species that lack these barriers. The function of these platelets may be to aid the animal in extending its body after being retracted. The minute platelets would provide a roughened surface for the mantle edge to grip and hence help the snail obtain purchase for forward movement of the mantle collar from deeply recessed within the aperture to its typical position covering most of the parietal, columellar and palatal lips.

This report is concerned with patterns of denticle structure on apertural barriers in the Pacific Island land snail families Endodontidae and Charopidae. Prior to reviewing the anatomy of these groups, species with such barriers were placed in the genus *Endodonta* and species lacking such barriers in the genus *Charopa*. Barriers occur in both families and the traditional generic limits are totally incorrect. Data concerning the shell sculpture and anatomical differences between these groups will be given elsewhere (Solem, in press). The microarmature on the barriers is shown to characterize the two families just as strongly as do the anatomical or sculptural features.

Explanation of Figures *1* to *6*

Species studied (arrows indicating barriers shown on subsequent plates)

Figure *1*: Undescribed genus and species from Rapa, Austral Islands

Figure *2*: *Thaumatodon* spec. nov. from Eua Island, Tonga

Figure *3*: *Endodonta fricki* (Pfeiffer, 1858) from Waianae Mountains, Oahu, Hawaii

Figure *4*: "*Endodonta*" *callizonus* (Möllendorff, 1900) from Ponape, Caroline Islands

Figure *5*: Undescribed genus and species from Peleliu, Palau Islands

Figure *6*: "*Endodonta*" *graeffei* Mousson, 1869 from Upolu, Western Samoa

Scale lines equal 1 mm

Explanation of Figures *7* to *10*

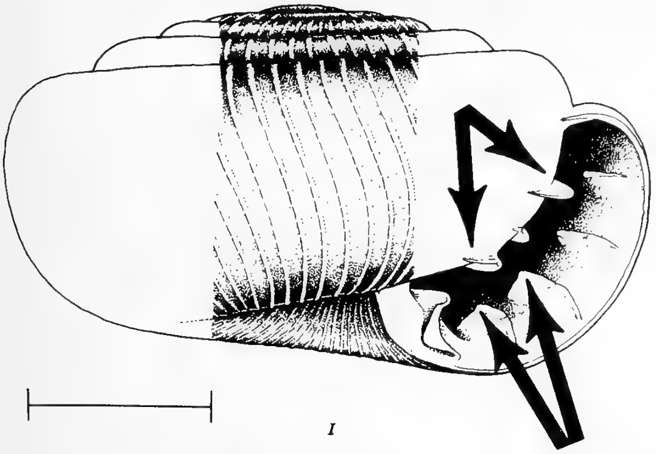
Apertural barriers in species from Rapa Island

Figure *7*: Anterior ends of 2nd and 3rd parietal barriers and portion of 1st parietal ×308

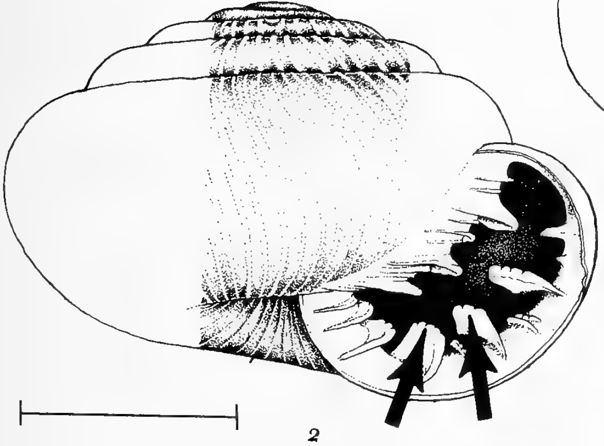
Figure *8*: Upper edge of 1st parietal barrier showing denticulated posterior portion ×937

Figure *9*: Detail of denticulated portion on 1st parietal barrier showing variation in denticle form ×3070

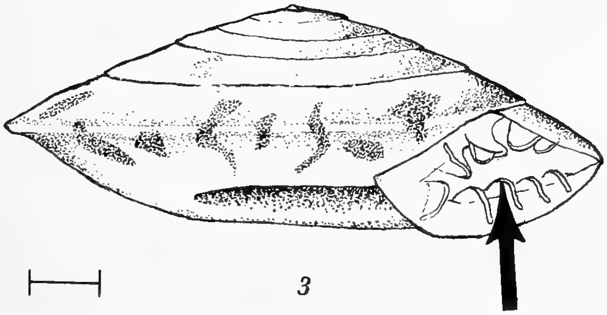
Figure *10*: Posterior margin of 1st and 2nd palatal lamellae showing limited portion of barrier on which denticles are present ×298



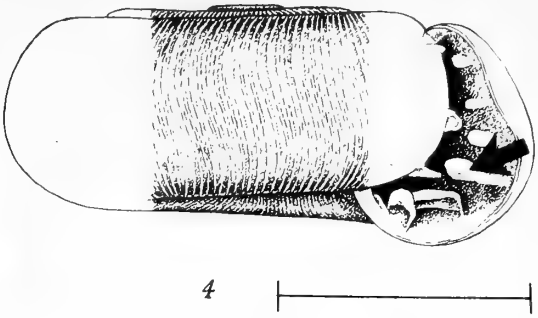
1



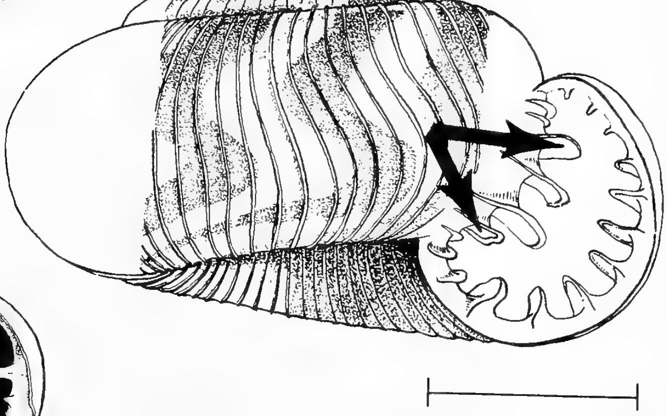
2

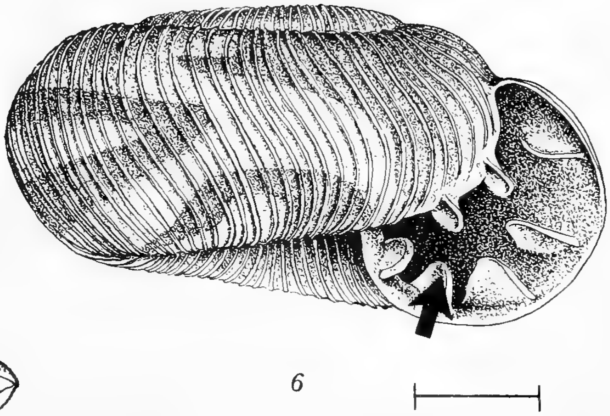


3



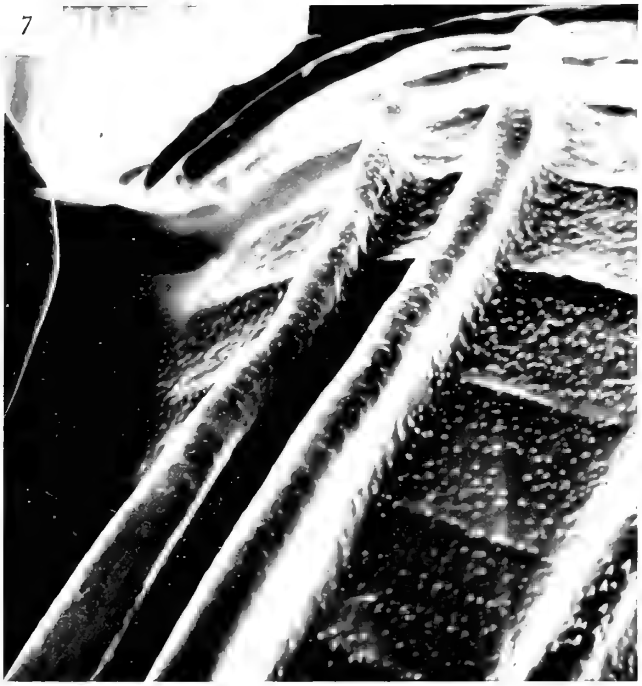
4





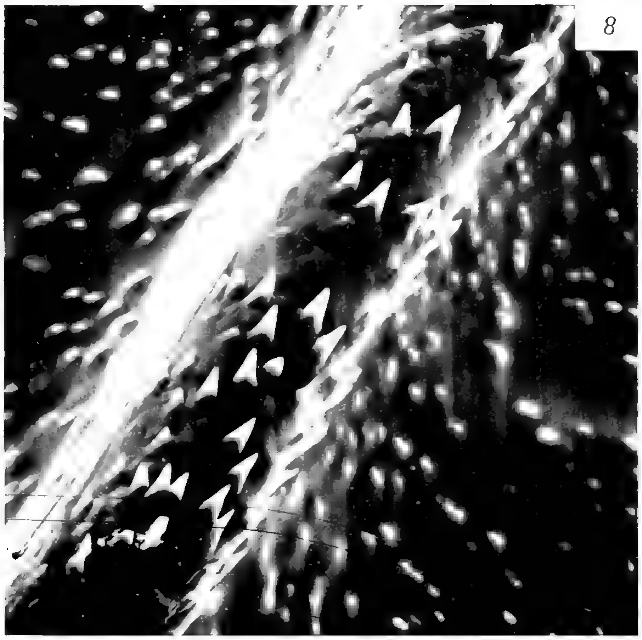
6

7

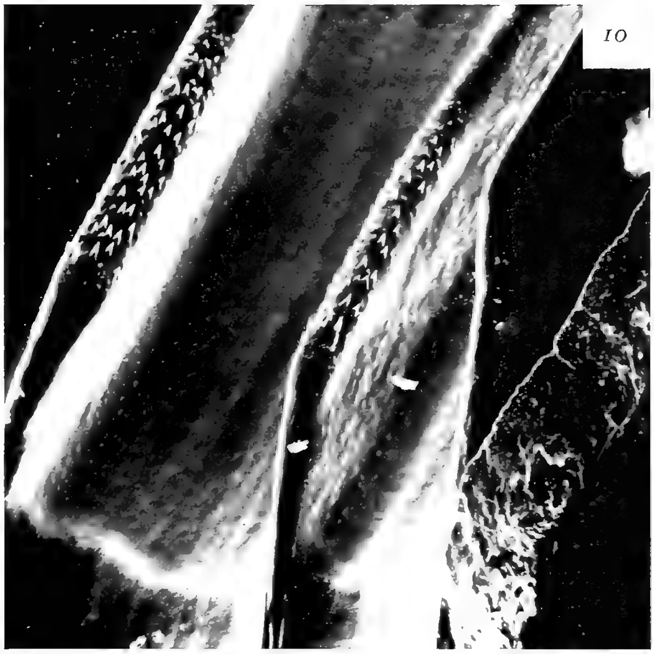


9

8



10



ACKNOWLEDGMENTS

Scanning electron microscope photographs illustrating this paper were taken with a Cambridge Mark I stereoscan at Alpha Research and Development Company in Blue Island, Illinois. I am deeply indebted to Mr. John Brown and his staff for their skilled operation of the microscope, to Fred Huysmans of Field Museum for his care in preparing prints, to Margaret Ann Moran, Jane Calvin and Sander Heilig for line drawings, and to both Field Museum and the National Science Foundation (GB-6779) for funding this research. The photographs were prepared some time ago, but publication has been withheld until exploratory work on apertural barriers in other families (Solem, 1972) could be completed and thus provide background data for understanding the significance of these microstructures.

PREVALENCE AND GROWTH OF BARRIERS

Species of both the Charopidae and Endodontidae have apertural barriers (Figures *1* to *6*), but the proportion of species with and without such barriers varies between the two families. Summarizing data from monographs of these groups (Solem, in press), the percentage of species level taxa with barriers is:

	Parietal barriers	Palatal barriers
Endodontidae	99.5% (of 185)	88.6%
Charopidae	32.6% (of 95)	28.4%

While the absence of apertural barriers would be highly suggestive that the unknown species belongs to the Charopidae, possession of such barriers gives no clue as to family unit. The only species of Endodontidae that completely lacks the barriers, *Nesodiscus fabrefactus* (Pease, 1864), has one race (*piceus*, Garrett, 1884) that retains traces of these barriers. Their absence is a secondary loss. Reduction in number and size of the barriers correlates, in general, with increasing shell size. In both families the barriers are present throughout the independent life of the snail. Hatchlings show a partial to complete set of barriers just inside the shell aperture. In some species the number of parietal or palatal barriers will increase from juvenile to adult. Barriers can extend posteriorly one-sixteenth to more than an entire whorl, depending on the species.

As the shell grows, the barriers are added to at the anterior margin and resorbed posteriorly. This is not a continuous process, since SEM examination of the resorption surface shows a layered pattern consistent with interrupted accretion (Solem, unpublished). Within a species population, the exact length of the barriers varies slightly from individual to individual, which also is consistent with a surge of posterior resorption alternating with a surge of anterior incremental growth. Through repeated alternations of growth and resorption the position of the barriers relative to the apertural lip remains virtually constant and the calcium investment in barrier formation remains stable. If an amount of calcium withdrawn from the posterior portion of the barriers is then deposited anteriorly, no or very little additional calcium must be extracted from the environment. If anterior deposition preceded posterior resorption, then an extra quantity of calcium would have to be first extracted, then deposited, resorbed posteriorly and stored in mantle tissue until the next growth surge. This would be far less efficient in terms of energy budget for the snail.

FORM AND NUMBER OF BARRIERS

At the optical level of study, size, position, number and shape of the barriers are very useful identification features. Often these details provide the easiest and quickest means of identifying sympatric species that are similar in shell size and shape. The differences between the species shown in Figures *1* to *6* are typical. This is not to be taken as indicating there is no intraspecific variation. Several endodontid species are known where the number of parietal barriers is either 3 or 4, with the ratios suggesting that simple Mendelian dominance controls the variation. One endodontid species from Rapa Island can have 0, 1, 2, 3, 4, or 5 palatal barriers, while a charopid from Guam has from 4 to 8 palatal barriers. These are extreme examples, with most species showing relatively trivial variation in barrier size and shape.

In general, most barriers are simple ridges. They are largest in size on the lower parietal and lower palatal walls. Some barriers may become sinuately twisted in adult specimens (see columellar barrier in Figure *1*), but most retain a ridgelike or semicircular profile. Quite frequently the parietal and palatal barriers will almost touch in the middle of the aperture. In some cases there even may be overlapping interdigitation of the barriers with the lower parietal, for example, extending to a point that it cuts the plane drawn between the upper edges of the two opposite palatal lamellae. The illustrated species have less highly developed barriers, but their pattern is essentially the same. Almost without exception, the upper parietal-palatal region of the aperture will have very small barriers with a clear open area leading to the shell interior. It is through this passage that the bulky foot and buccal mass must be withdrawn and extended. In the basal and middle regions of the aperture, the degree of narrowing by the barriers frequently is so great that there is insufficient room for either the foot or buccal mass to pass.

MICROARMATURE ON BARRIERS IN THE ENDODONTIDAE

Figures *1* to *3* illustrate the shells of three species belonging to different lineages in the family, while Figures *7* to *13* and *23* and *24* are scanning microscope photographs of the particular barrier edges indicated by the black arrows in Figures *1* to *3*. The undescribed species from Rapa Island (Figure *1*) is moderately specialized in terms of genitalia and belongs to the most diverse genus living on that island. Its barrier structure is typical of the more generalized Endodontidae. A low angled view of the parietal wall looking from inside the aperture (Figure 7) shows the anterior ends of the 2nd and 3rd parietals, plus a small section of the 1st parietal barrier (lower right margin of photograph). The pattern of a callus being deposited over the ribbed surface of the preceding whorl and the irregularly pustulose surface of the callus is quite clear. These pustulations are the primitive microarmature found on the parietal and columellar wall of many snails. Figure *10* shows the posterior margins of the 1st and 2nd palatal barriers. This demonstrates that the minute denticulations are restricted to the upper edge and posterior end of the barriers. Figures *8* and *9* show higher magnification details of the denticulated section on the 1st parietal barrier. On both parietal and palatal barriers the denticles are triangular and point towards the outside of the aperture. The exact form of the denticles can be observed on the sides of the barriers in Figures *8* and *9*. It must be emphasized that these denticles are additive elements to the barrier surface. That is, they are separate elements from the normal surface of the barrier. This is quite unlike the situation in *Ptychodon microundulata* (Suter, 1890) (Solem, 1970: plt. 60, figs. 13–15) where the denticles are surface layer crystals that are greatly enlarged and extended.

Thaumatodon (Figure *2*) is a genus from western Polynesia, with its center of diversity in the Lau Archipelago of Fiji. Other species are known from Ellice, Cook, Samoa and Tonga. Derivative genera are found in Lau and the Palau group. This complex of genera is distinguished anatomically by a major alteration in the terminal male genitalia, and conchologically by the development of small "beaded" sculpture on the surface of all major and some minor barriers. This is the most strongly differentiated group of genera in the family. High magnification observation of the barriers (Figures *11* to *13*) in *Thaumatodon hystricelloides* (Mousson, 1865) from Western Samoa shows that denticulations are restricted to the raised beads (Figure *11*). These denticles are the same triangular additive points seen in the more generalized taxa. In this species the tips of the points are subject to great variation. A tendency towards blunting is evident. The lower part of Figure *11* shows the posterior resorption edge of the palatal barriers. The layered nature of the callus is obvious, while the porous appearance at the angle between the resorption plane and the palatal surface is caused by the preliminary weak acid etching of the callus.

Endodonta fricki (Pfeiffer, 1858) (Figure *3*) from Oahu, Hawaii is the fourth largest species in the Endodontidae, averaging 9 mm in adult diameter. The barriers are massive and the form of the denticles (Figures *23, 24*) is slightly modified. Most denticles (Figure *23)* are broadly triangular, but in areas (Figure *24*) they have become flattened anteriorly and have a spade-like edge. The Hawaiian Endodontidae are anatomically conservative although showing rather large conchological variation. The form of these denticles is rather different from that seen in the other two illustrated genera. Whether this is correlated with the increased size of *Endodonta,* or represents a general pattern of divergence in the Hawaiian taxa is uncertain. The palatal barriers in *"Endodonta" nudus* Ancey, 1899 from Kaiwicki, Hilo, Hawaii (FMNH 90319) have the denticles on the upper edge of the barrier with spade-like anterior edge, although denticles on the lateral

Explanation of Figures *11* to *13*

Apertural barriers in *Thaumatodon hystricelloides* (Mousson, 1865) from Upolu, Western Samoa

Figure *11*: Posterior margin of 2nd (right) and 3rd (left) palatal barriers showing resorption face (bottom of photograph) and restriction of denticulations to the "beads" ×292

Figure *12*: Surface of one "bead" showing variation in shape and angulation of denticulations ×2880

Figure *13*: Individual denticles ×10400

Explanation of Figures *14* to *16*

Parietal barriers in undescribed snail from Peleliu, Palau Islands

Figure *14*: Parietal wall showing bifurcated 1st (left) and simple 2nd, 3rd, and 4th parietal barriers. ×140
Posterior margin at top of figure

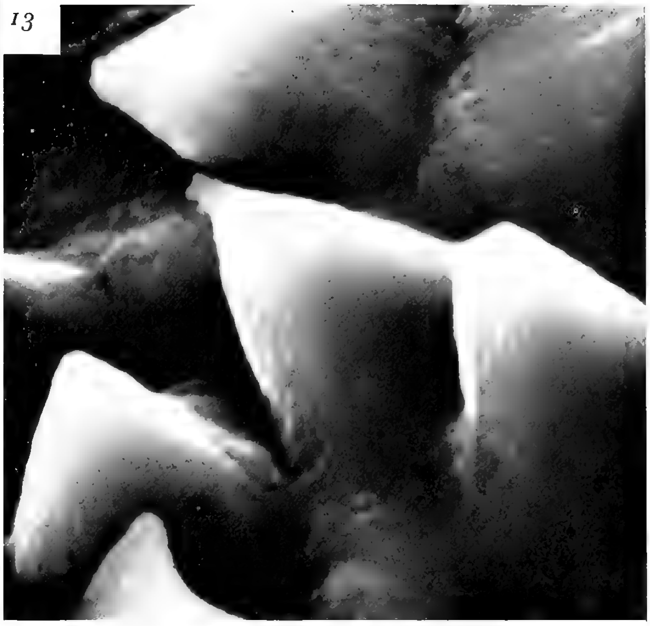
Figure *15*: Upper edge of 3rd parietal barrier ×1185

Figure *16*: Detail of transverse plates on upper edge of barriers ×3315

11

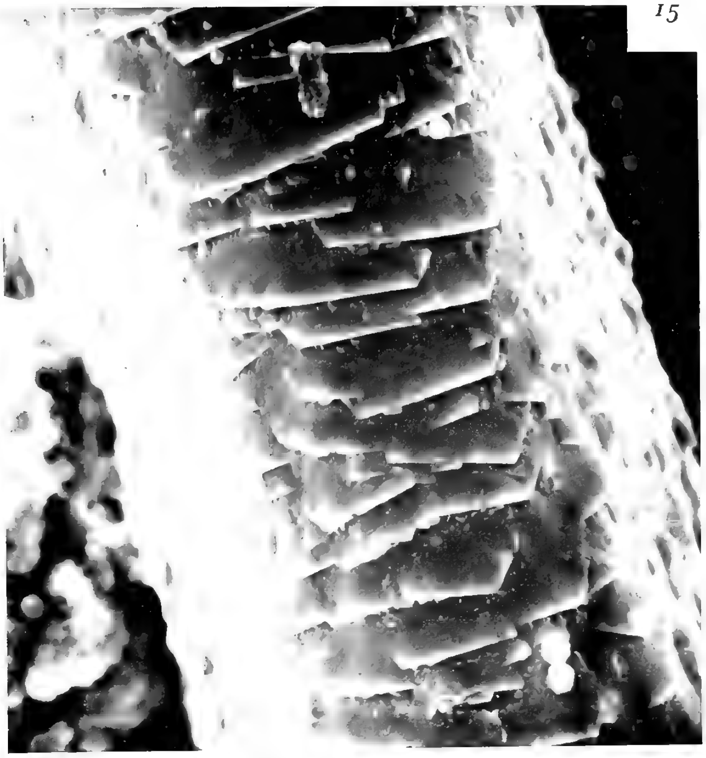
12

13

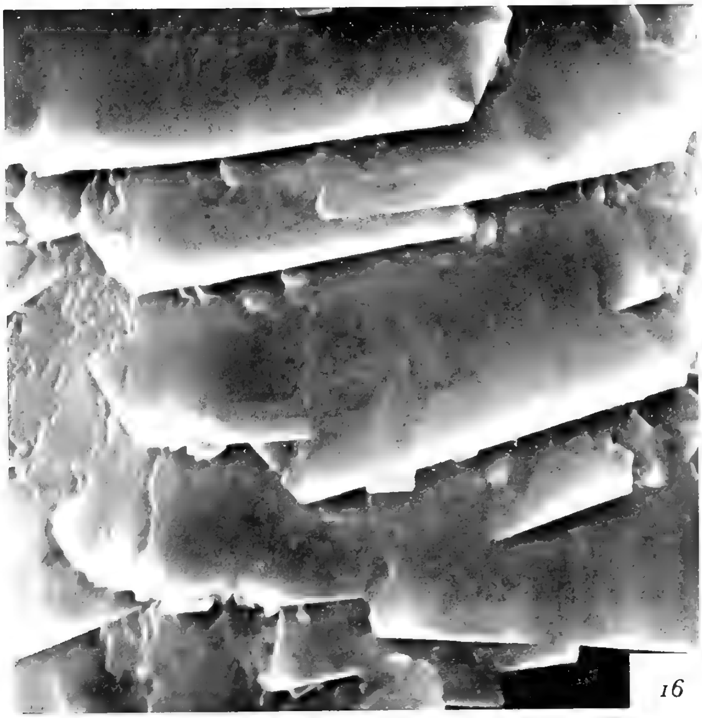


14

15



16



edges retain the triangular shape. In both of these species the denticles are added to the surface of the barrier.

Additional species from Fiji, Cook, Society, Austral, Marquesas, and Henderson Island have been examined with the SEM. They show a consistent pattern of triangular, additive denticles on the upper margin of the major barriers. There is considerable variation as to what percentage of the barrier length is covered by the denticles, whether the anterior portion of the barrier is tapering (Figure *7*) or sharply descending (Figure *3*), and whether the major barriers are simple or variously bifurcated. The triangular denticles are the one constant feature, being modified to a spade-like anterior edge only in Hawaiian taxa. This seems to be a secondary derivation, since the lateral edges of the barriers retain the triangular denticles common to other Endodontidae.

MICROARMATURE ON BARRIERS IN THE CHAROPIDAE

The Pacific Island Charopidae are far more diverse in terms of supraspecific phyletic units than are the Endodontidae. Four distinct lineages have colonized parts of the Pacific Islands. These show far greater differences in genitalia within each lineage than the total range of variation seen in members of the Endodontidae. Differences between the groups are dramatic. Probably each of these lineages will be accorded subfamily rank eventually. The Charopidae are the dominant land snail taxon of Tasmania, Eastern Australia, New Zealand, New Caledonia and Lord Howe Islands, apparently at least two of the Pacific Island lineages occur in New Zealand and Australia, and the anatomical patterns in these areas still are poorly understood. Thus formal subfamily recognition of these lineages is premature. In three of the groups, species with and other species without apertural barriers are found; in the fourth group only species with barriers are known. Table 1 surveys the size differences within each group in respect to the presence or absence of apertural barriers. For each species studied, measurements were made on all adult examples seen and mean dimensions calculated. The data used for this table thus consists of the mean adult shell diameter for each species. The listed mean is the average diameter for all species in the group. The range is the minimum and maximum mean shell diameter for included species.

Two conclusions are obvious. In each lineage the mean adult size of species with apertural barriers is considerably less than the mean adult size of species without such barriers. While the largest species with barriers may exceed the size of the smallest species without barriers, there is comparatively little size overlap between the groups. Secondly, there is no between-group concordance. Group III species with barriers are about the size of Group I species that lack barriers. Since the distribution patterns of the groups are to a considerable extent allopatric, the species have been subject to predation pressure from different arthropod faunas. Hence no necessary concordance between groups would be expected. There also are considerable differences between groups in respect to the proportion of species with and without barriers.

Table 1

Comparative Size of Charopidae
With and Without Apertural Barriers

	Barriers present		Barriers absent	
	Number of species	Shell diameter: Mean and range in mm	Number of species	Shell diameter: Mean and range in mm
Group I	12	1.90 (1.40-2.57)	54	3.21 (2.08-6.64)
Group II	10	2.27 (2.02-2.78)	3	3.74 (2.66-4.81)
Group III	6	3.37 (2.83-4.59)	4	4.88 (3.96-6.13)
Group IV	3	3.96 (3.32-5.23)		None

Members of three different groups are illustrated in Figures *4* to *6* and Figures *14* to *22*. No generic names have been published yet for any Pacific Island Charopidae, so the use in quotes of their original placement in the endodontid genus *Endodonta* has been continued as a nomenclatural necessity at this time. *"Endodonta" callizonus* Möllendorff, 1900 (Figures *4, 17* to *19*) is a Group II species from Ponape, Caroline Islands. It is a species whose apertural denticles may be somewhat distorted in shape as the result of secondary shell size reduction. Nevertheless, it shows quite clearly the nature of microarmature on the barrier upper edge. The other parietal and palatal barriers agree in basic microarmature, but because the anterior portion of the barrier is deflected rather sharply, the denticles show up quite clearly. Figure *17* shows the midsection of the 3rd and largest palatal barrier. The posterior resorption face is at the left of the photograph, while the far right section shows the flattened anterior area of the barrier. The central portion of this photograph is of the point where the barrier plunges sharply from its elevated posterior to the low and flat anterior extension. This is the section that would be encountered first by an arthropod attempting to crawl into the shell. This area would serve as the most effective barrier to the predator. The surface at 2 907× (Figure *18*) is seen to be sharply denticulated by blunt tipped crystals of varying size. These are anterior continuations of the crystalline layers that normally make up the posterior horizontal layers of the barrier. Figure *19* emphasizes the blunt nature of their anterior margins. This is a simple continuation of the growth surface, such as is revealed by fractures (see Wise, 1970).

Figures *5* and *14* to *16* are of an undescribed Group III species from Peleliu, Palau Islands. This is in the same undescribed genus as the well known *"Endodonta" heptaptychia* Quadras & Möllendorff, 1894 from Guam, Mariana Islands. The parietal wall (Figure *14*) shows the general microarmature present between the barriers and the varying form of the barriers themselves. The upper parietal barrier (left) is bifid and slender, with the 2nd and 3rd (left to right) progressively longer, thicker and higher. The reduced height and anterior (lower right) thickness of the 4th parietal probably results from its position relative to the 1st palatal barrier. The latter is so large that if the 4th parietal was of equal size they would meet and fuse together. Although the sides of the major barriers have only weak projections of the same type seen in many taxa (Solem, 1972: figs. 10, 12, 16) the upper edges (Figures *15, 16*) have "huge" transverse mica-like sheets, that, as always, have the sharp raised edge pointing towards the outside of the aperture. In the 3315× magnification of Figure *16* it can be seen that these are outgrowths from the surface layer of the barrier. In appearance they are quite similar to the barrier microarmature of *"Endodonta" callizonus* (Figures *17, 18*), but the great broadening of the tips and outgrowth from the upper surface layer in the Peleliu species is different than anterior extension of crystal layers in the Ponape shell.

Figure *6* and *20* to *22* are of *"Endodonta" graeffei* Mousson, 1869 from Upolu, Western Samoa, a species belonging to Group IV. This is from the same island as *Thaumatodon hystricelloides* (Figures *11* to *13*). At one time it apparently was sympatric with that endodontid species. Examination of the sharply descending anterior edge on the 1st palatal barrier (Figures *20, 21*) shows that the microarmature consists of plate-like projections in irregular rows across the front edge, with very little structure on the side of the barrier (left part of Figure *20*). When viewed from above (Figure *22*), the platelets are seen to be highly irregular in outline. Peculiarities of barrier growth and resorption will be discussed elsewhere, but serve to emphasize that the barriers in *"Endodonta" graeffei* are quite different from those in the other species.

Group I species with apertural barriers are rare species poorly represented in museum collections. At the time specimens of these were on loan for study, no SEM access was possible. The species are too rare to justify partial to complete destruction of a shell in order to check the barrier microarmature. I would predict that the barriers would show some variation of the spade-like or platelet armature.

Several Charopidae (*sensu lato*) from extralimital areas have been examined. The New Zealand *Ptychodon microundulata* (Suter, 1890) (Solem, 1970: figs. 12–15) has the topmost layer of the parietal barriers consisting of squarish crystals that angle upwards and point towards the aperture. Some of these are enlarged and extended forward to make two lines of hooks that border the barriers. A new species of *Helenoconcha* from St. Helena Island (Solem, in preparation) has the same type of upper layering to the barriers, but the prolongations are very small and triangular in shape. Under low magnification they appear identical to the structures seen in endodontids such as *Thaumatodon*. Whereas the latter are structures added to the surface layers, the denticles in *Helenoconcha* grow out of a specially oriented crystalline layer.

DISCUSSION

Questions of phylogenetic interpretation must lean heavily upon outgroup comparisons and use of the "law of parsimony." Complex structures, such as apertural barriers, normally are viewed as suggesting "common descent," since a hypothesis of one origin is more parsimonious than a hypothesis suggesting two or more origins. Originally, *"Endodonta"* and *"Charopa"* represented such a dichotomy in classifying Pacific Island species. The classical anatomists' views of homology and the classical pheneti-

Explanation of Figures *17* to *19*

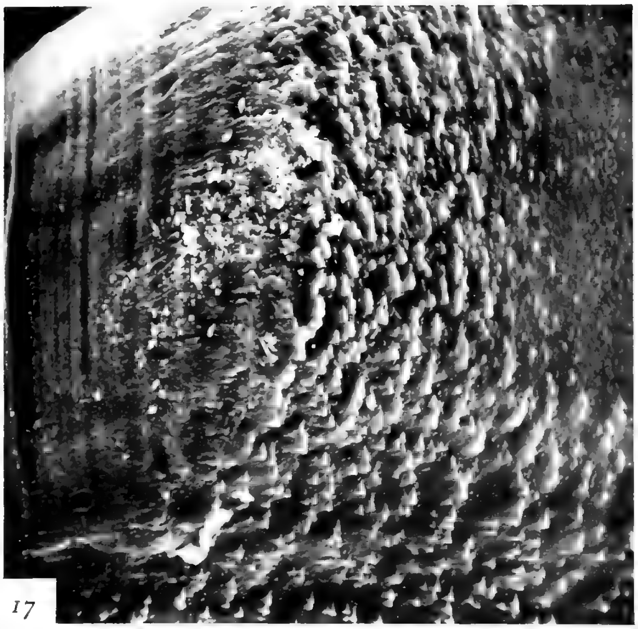
Palatal barrier in "*Endodonta*" *callizonus* (Möllendorff, 1900) from Ponape, Caroline Islands

Figure *17*: Sharply descending midsection and raised posterior end of 3rd palatal barrier ×958
Figure *18*: Protruding crystalline plates on anterior face of barrier ×2907
Figure *19*: Details of crystals ×9417

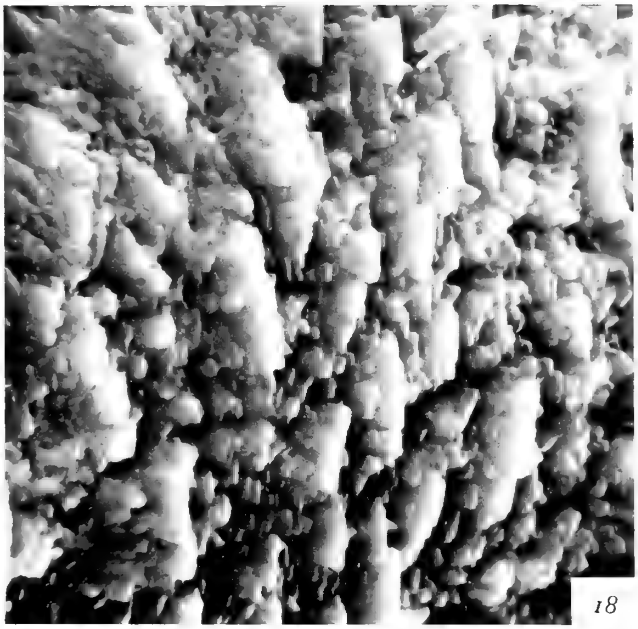
Explanation of Figures *20* to *22*

Palatal barrier in "*Endodonta*" *graeffei* Mousson, 1869 from Upolu, Western Samoa

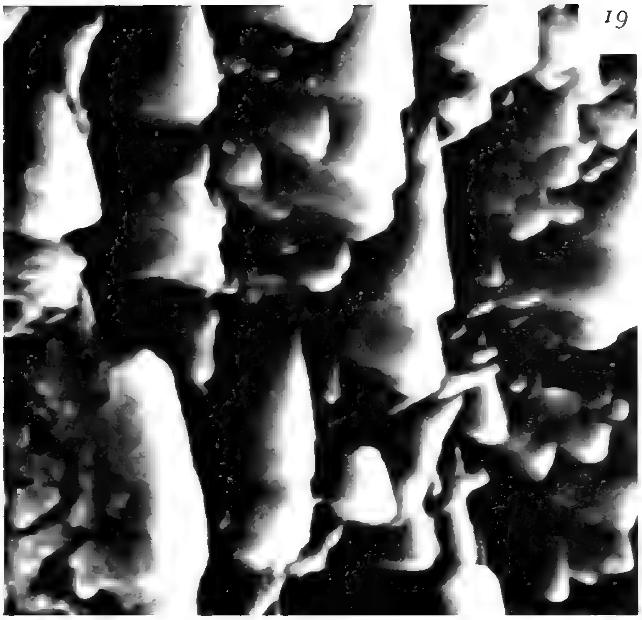
Figure *20*: Lateral front view of barrier ×390
Figure *21*: View of descending face on barrier ×1315
Figure *22*: Vertical view of platelet shape and spacing ×3835



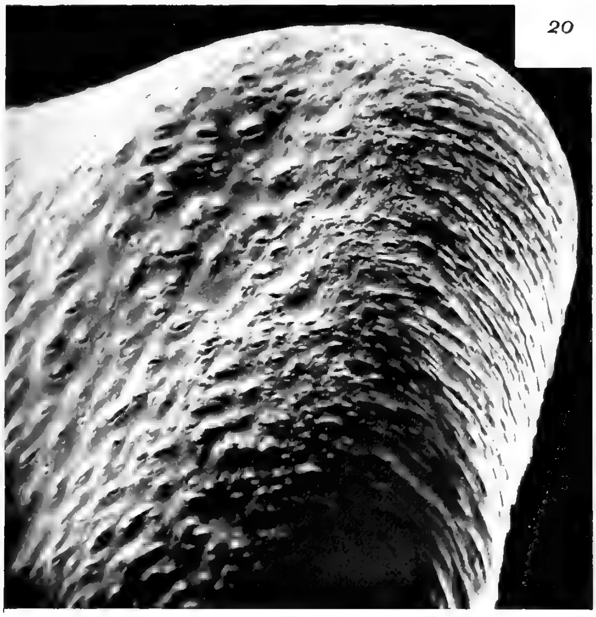
17



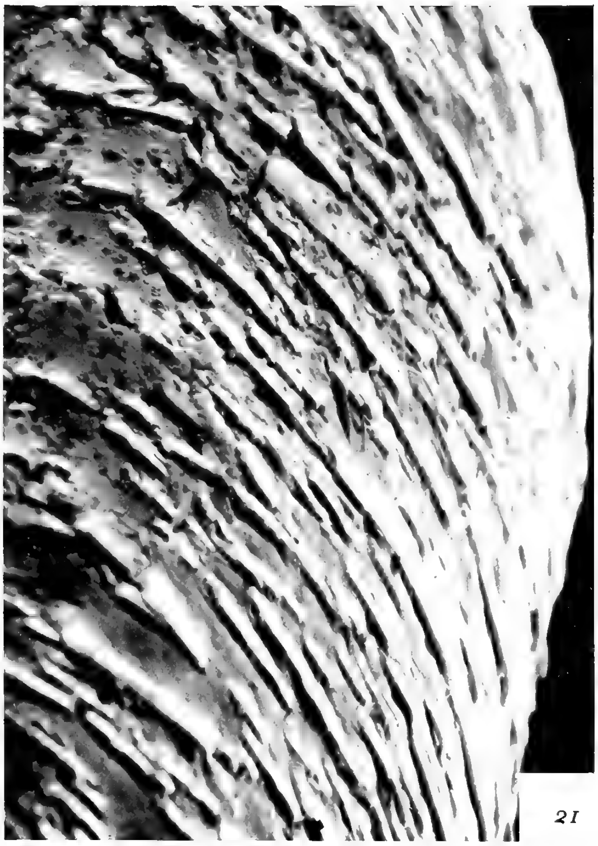
18



19



20



21

22

cists' views of "similarity" have much in common. If structures look the same and are in the same place, therefore they are the same and therefore the two organisms share common descent.

If more critical work shows that the structures are formed in a different way and merely perform the same function, then recognition that these are analogous or convergent becomes more parsimonious as a hypothesis. It is less difficult to propose separate and independent origins than to propose a single origin followed by secondary modifications whereby the same function was served in different ways from an originally common pattern.

Anatomical investigations demonstrated that two quite distinct families were present in the area. Members of both groups have species with apertural barriers. Were these barriers derived independently, or were they inherited from a common ancestor? SEM study was started in an attempt to answer these questions.

In relation to the microarmature on the apertural barriers, two kinds are present. One type consists of triangular points that are added to the upper surface of the barrier by an unknown process. This type is correlated with many anatomical features and, on the basis of a broad sampling of species, is predicted to occur throughout the Endodontidae. These are complex details of structure and function that are found on the upper edge of barriers that are highly variable in both length and form. Outgroup ancestors of the Endodontidae are either not yet recognized or are extinct and unreported from the fossil record. Hence questions concerning the origin of barriers in the Endodontidae cannot be answered by outgroup comparisons. It is unlikely that this complex microarmature would arise twice in exactly the same way. Therefore I conclude that the immediate ancestors to the Pacific Island Endodontidae had complex apertural barriers surmounted by additive triangular points. Reduction in size, length or number of the barriers would be a derived state in the context of this family unit.

The second type of barrier microarmature consists of triangular (*Helenoconcha*), blunt tipped (*"Endodonta" callizonus*), sheet-like (*"Endondonta" graeffei* and the undescribed species from Peleliu), or hook-like (*Ptychodon*) denticles. These may be expansions from a specially oriented layer of crystals (*Ptychodon* and *Helenoconcha*), simple horizontal extensions of surface layers that become denticles because of change in barrier profile (*"E." callizonus*), angled outgrowths from a typical surface layer (Peleliu species), or rows of plates on a sharply descending surface (*"E." graeffei*). The protective function of these microarmature denticles is the same as that of the triangular points in the Endodontidae. But their shape, method of formation, and position on the barrier is basically different. The Endodontidae have microarmature on the posterior upper edge of the barriers, rarely extending onto the anterior slope of the barrier. In the Charopidae, the denticles frequently (*"E." graeffei, "E." callizonus*) are on the anterior slope or over the entire raised edge (*Ptychodon,* Peleliu, *Helenoconcha*) of the barrier.

Hence I conclude that not only are barriers in the Charopidae derived independently from those found in the Endodontidae, but that the barriers in the Charopidae have evolved several different times. The charopid barriers show complex differences in form and method of formation. Therefore it is parsimonious to hypothesize that they have evolved independently. Data adequate to state whether the presence of barriers within a particular group of the Charopidae is primitive or derived are too voluminous to present here and discussion of this will be deferred until the main monograph is published. Here outgroup comparisons are both possible and helpful.

While the first level conclusion of these observations is that the Charopidae and Endodontidae differ in the microarmature on the barriers in the shell aperture, and thus provide a simple "identification" character, perhaps more significant is the attention this discussion can focus on the ways in which morphological and developmental evidence should be used in making phylogenetic analysis. Too often such statements are made in the sense of 19th century homology or early 1960 phenetic similarity. Structure, function and origin must be considered.

CONCLUSIONS

SEM examination of the apertural barriers in a number of Pacific Island Endodontidae and Charopidae showed that in the former family the microarmature consists of triangular denticles that are added to the upper edge layers of the barrier. In the Charopidae, barriers have a microarmature of usually spade-like or sheet-like crystals that generally grow out from a specially oriented upper crystalline layer. When triangular or pointed in shape, the different growth origin of denticles in the Charopidae is obvious at higher magnifications.

Because the complex denticles and barriers in the Endodontidae agree in fine detail of structure and evident growth pattern, it is concluded that the living Pacific Island Endodontidae are derived from a stock in which the barriers were fully developed. Secondary reduction or loss (*Nesodiscus fabrefactus*) of the barriers occurred after colonization of the Pacific area. In terms of the extant species, possession of these complex barriers with triangular additive microarmature is primitive, while reduced or lost barriers is a derived state.

In the Charopidae, barrier formation and microarmature show a variety of patterns. It is concluded that these barriers have evolved several different times in different stocks of the family. While the basic type of microarmature is very similar, how it is formed and upper surface growth patterns are distinct, thus indicating multiple origins.

SEM study of barriers can differentiate families, but may not enable prediction of group affinity within the Charopidae.

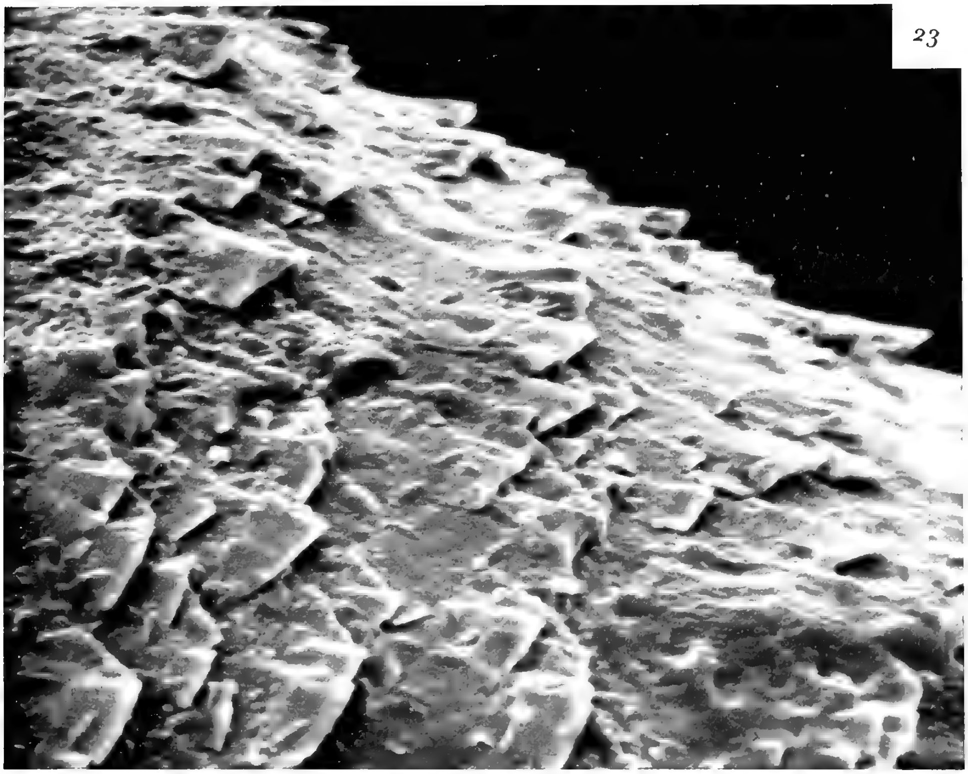
Literature Cited

GUILDING, LANSDOWN
1829. Observations on the zoology of the Caribbean Islands. The Zool. Journ. 4 (14): 164 - 175
SOLEM, ALAN
1970. Malacological application of Scanning Electron Microscopy I. Introduction and shell surface features. The Veliger 12 (4): 394 to 400; plts. 58 - 60 (1 April 1970)
1972. Microarmature and barriers in the apertures of land snails. The Veliger 15 (2): 81 - 87; 5 plts. (1 October 1972)
In press. Endodontoid land snails from Pacific Islands. Parts I and II. Fieldiana: Zoology
WISE, SHERWOOD W.
1970. Microarchitecture and mode of formation of nacre (Mother-of-Pearl) in pelecypods, gastropods and cephalopods. Eclog. Geolog. Helvet. 63 (3): 775 - 797; 4 figs.; 1 table; 10 plts. (December 1970)

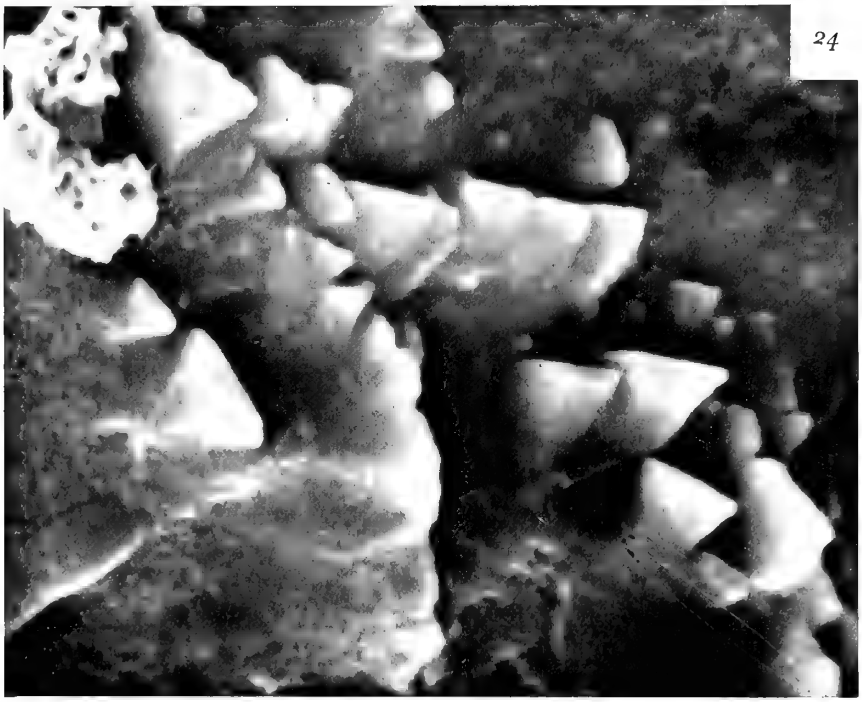
Explanation of Figures *23* and *24*

Surface of second palatal barrier in *Endodonta fricki* (Pfeiffer, 1858) from Waianae Mountains, Oahu, Hawaii

Figure *23*: Lateral view of upper edge ×2965 Figure *24*: Top view of same barrier ×14800



23



24

Systematics and Distribution of Western Atlantic *Ervilia*

(Pelecypoda : Mesodesmatidae)

with Notes on Living *Ervilia subcancellata*

BY

JOHN D. DAVIS

Northampton, Massachusetts 01060

(3 Plates; 2 Text figures)

INTRODUCTION

THE TYPE SPECIES of the bivalve mollusk *Ervilia* Turton is *Mya nitens* Montagu, 1808 by monotypy. The genus occurs in tropical and temperate waters, with fossil forms known from the Tertiary.

As part of this study I examined all *Ervilia* material in the Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts; U. S. National Musuem (USNM), Washington, D. C.; and the Academy of Natural Sciences of Philadelphia (ANSP). Diagnostic criteria were established for the genus and for western Atlantic species, and all unlabeled and erroneously identified material was re-identified according to these criteria. Type specimens of *E. concentrica, E. maculosa* and *E. rostratula* were studied.

During the summer of 1966 I collected living specimens of *Ervilia subcancellata* at the Bermuda Biological Station, which provided the first opportunity to study live material of this species.

SYSTEMATICS

Generic Features: The shell is small, usually inequilateral, and rather fragile, seldom exceeding 12 mm in length. The posterior of the shell is often extended, placing the umbo anterior to the midpoint. The umbo is not pronounced, and the valves are somewhat laterally compressed. The exterior is sculptured with equally prominent concentric ridges. The right valve has a prominent cardinal and chondrophore pit; the left valve has 2 small projections (not true cardinals) bracing the chondrophore. There are no lateral teeth, but the left valve has a groove on its dorsal margin which receives the corresponding marginal ridge of the right valve.

The posterior and anterior muscle scars are about equal. The pallial sinus is deep, extending almost beneath the umbo. Along the posterior ventral margin, the lower edge of the sinus and the pallial line combine to bend sharply outward before terminating near the ventral margin of the valve. This sudden outward sweep of the pallial sinus margin is an important diagnostic feature of the genus (DAVIS, 1967).

KEY TO WESTERN ATLANTIC SPECIES OF *Ervilia*

1 Posterior part of shell significantly rostrate (extended); radiating striae especially prominent on rostrate portion but often present over entire shell *E. subcancellata*

– Posterior part of shell not significantly rostrate; radiating striae restricted to posterior portion or absent 2

2 Concentric ridges especially prominent; radiating striae very much reduced or absent .... *E. concentrica*

– Concentric ridges reduced; radiating striae present but confined to posterior part of shell .... *E. nitens*

---

[1] Publication Number 566 of the Bermuda Biological Station for Research, St. George's West, Bermuda.

[2] This study was supported in part by a Grant-in-aid of Research from the Society of the Sigma Xi.

Ervilia nitens (Montagu, 1808)

(Figure *1*)

Mya nitens Montagu, 1808. Supplement to Testacea Britannica. p. 165 (Scottish Coast).

Ervilia nitens. Turton, 1822. Conchylia Dithyra Insularum Brittanicarum. p. 55; plt. 19, fig. 4 (on the Scottish Coast).

It is likely that the type material was adventitious, perhaps originally carried there in ballast. FORBES & HANLEY (1853) commented on the matter as follows:

"A West Indian shell [referring to *Ervilia nitens* as being spurious], introduced by Montagu as taken near Dunbar by Mr. Laskey. It is not unimportant to remark, as accounting in some measure for the very considerable number of exotic shells introduced from the neighbourhood of Dunbar by Mr. Laskey, that several vessels from foreign ports had, just before that gentleman's investigation, visited his subsequent dredging-ground, and their ballast was in all probability the fertile source of most of his additions to British Conchology, as it has in like manner added not a few spurious species to the Flora of the neighbouring district."

There are no later records of *Ervilia nitens* being taken in the waters of Great Britain, or indeed of the Eastern Atlantic. It is, therefore, strongly suggested that the Forbes and Hanley interpretation is correct. THIELE (1935) makes reference to "*E. nitens* (Laskey)," apparently referring to Mr. Laskey mentioned in the Forbes and Hanley discussion. Apparently, Mr. Laskey did the collecting, but Montagu did the diagnostic and descriptive work as well as authoring the resulting publication. As a result, Laskey has no taxonomic importance.

The genus is represented by a different species, *Ervilia castanea* Montagu, 1803 in the Eastern Atlantic. Its range extends from the south coast of England (Cornwall, Scilly Isles) to Brittany, Portugal, the Azores and Madeira. Possibly, erroneously identified specimens of *E. castanea* have led in the past to claims that *E. nitens* occurred on both sides of the Atlantic. There is no existing justification for this assumption, and unquestionably the distributional range of *E. nitens* is confined to the tropical and subtropical waters of the western Atlantic.

Diagnosis: Fairly large (frequently about 12 mm long), valves inequilateral and somewhat elongate but non-rostrate. Shells usually glossy white with occasional tints of pink concentrated in the umbo. Radiating striae often reduced and usually confined to the dorso-posterior part of the valve.

Distribution:[3] FLORIDA (U. S. A.): Boynton (ANSP, USNM); Miami (USNM); Fowey Light (USNM); Soldier Key (MCZ); Conch Key (USNM); Bahia Honda Key (ANSP). BAHAMA ISLANDS: Little Abaco Island (M

---

[3] Names in this and subsequent distributional lists indicate general localities, not specific collecting sites.

Explanation of Figures *1*, *2*

Figure *1*: *Ervilia nitens*. Paired valves selected from MCZ 21071, St. Thomas, Virgin Islands. Length 6.4 mm, height 4.6 mm; a, exterior, right valve; b, interior, right valve; c, exterior, left valve; d, interior, left valve.

Figure *2*: *Ervilia concentrica*. Lectotype of *Mesodesma concentrica* Holmes, selected by DAVIS (1967) from AMNH 11291 and subsequently catalogued AMNH 11291/1:1 and AMNH 11291/1:2. Length 6.6 mm, height 4.3 mm; a, exterior, right valve; b, interior, right valve; c, exterior, left valve; d, interior, left valve.

Explanation of Figure *3*

Figure *3*: Comparison of *Ervilia concentrica* and *E. maculosa*. Left column: paired valves, small specimen of *E. concentrica* selected from MCZ 262704, 34°20′30″ N, 75°57′30″ W. Length 4.0 mm, height 2.7 mm. Shell margin abraded. a, exterior, right valve; b, interior, right valve; c, exterior, left valve; d, interior, left valve. Right column: valves selected from syntypes of *E. maculosa*, USNM 92153, USFC Station 2610, 24 miles SE ½S of Cape Lookout, North Carolina. Valves are not paired but rather selected because of essentially identical dimensions. Length 3.1 mm, height 2.2 mm; e, exterior, right valve; f, interior, right valve; g, exterior, left valve; h, interior, left valve. Valves of right column photographed atop a millimeter scale which shows through the valves as a vertical dark bar in (e) and (f) and as a horizontal bar in (h). Apparent difference in shell proportions between left and right columns is caused by greater length of left column valves; they are 0.9 mm longer.

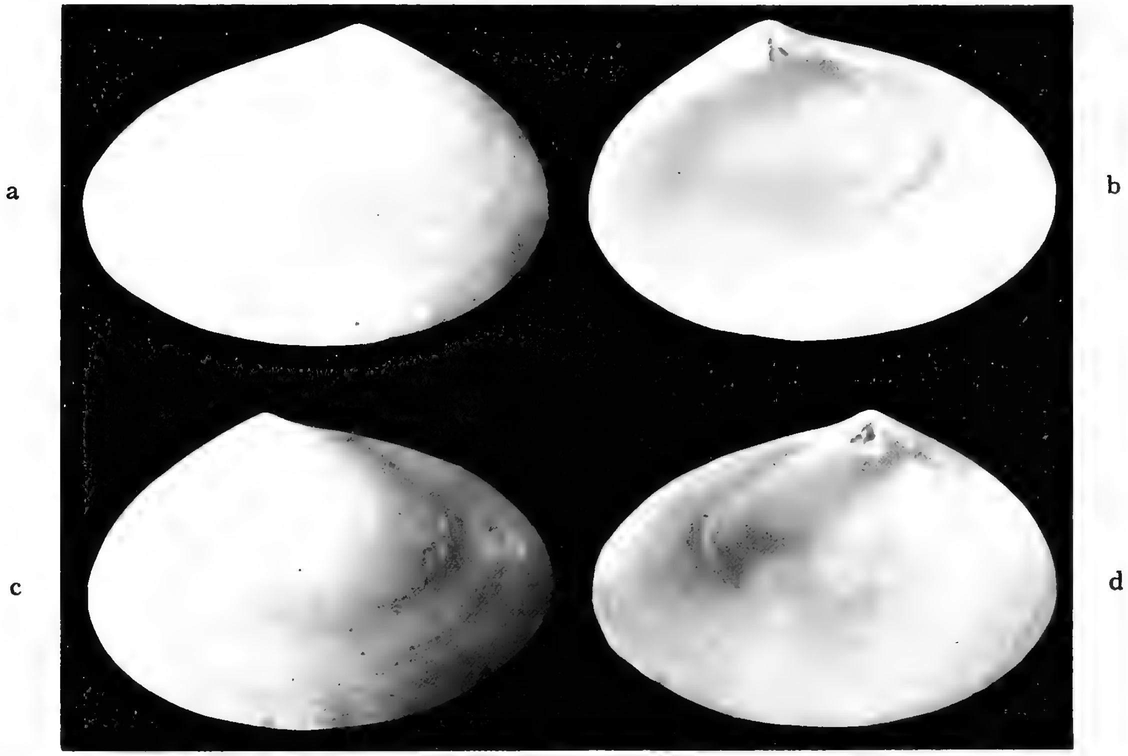


Figure *1*

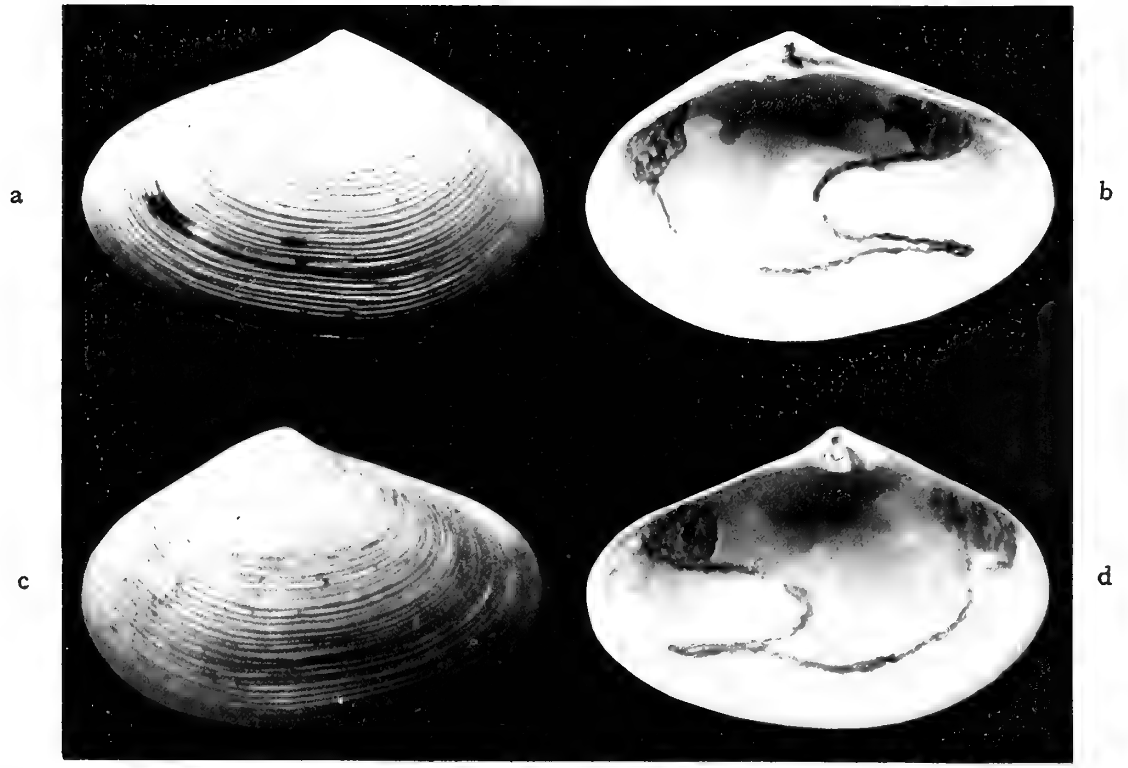


Figure 2

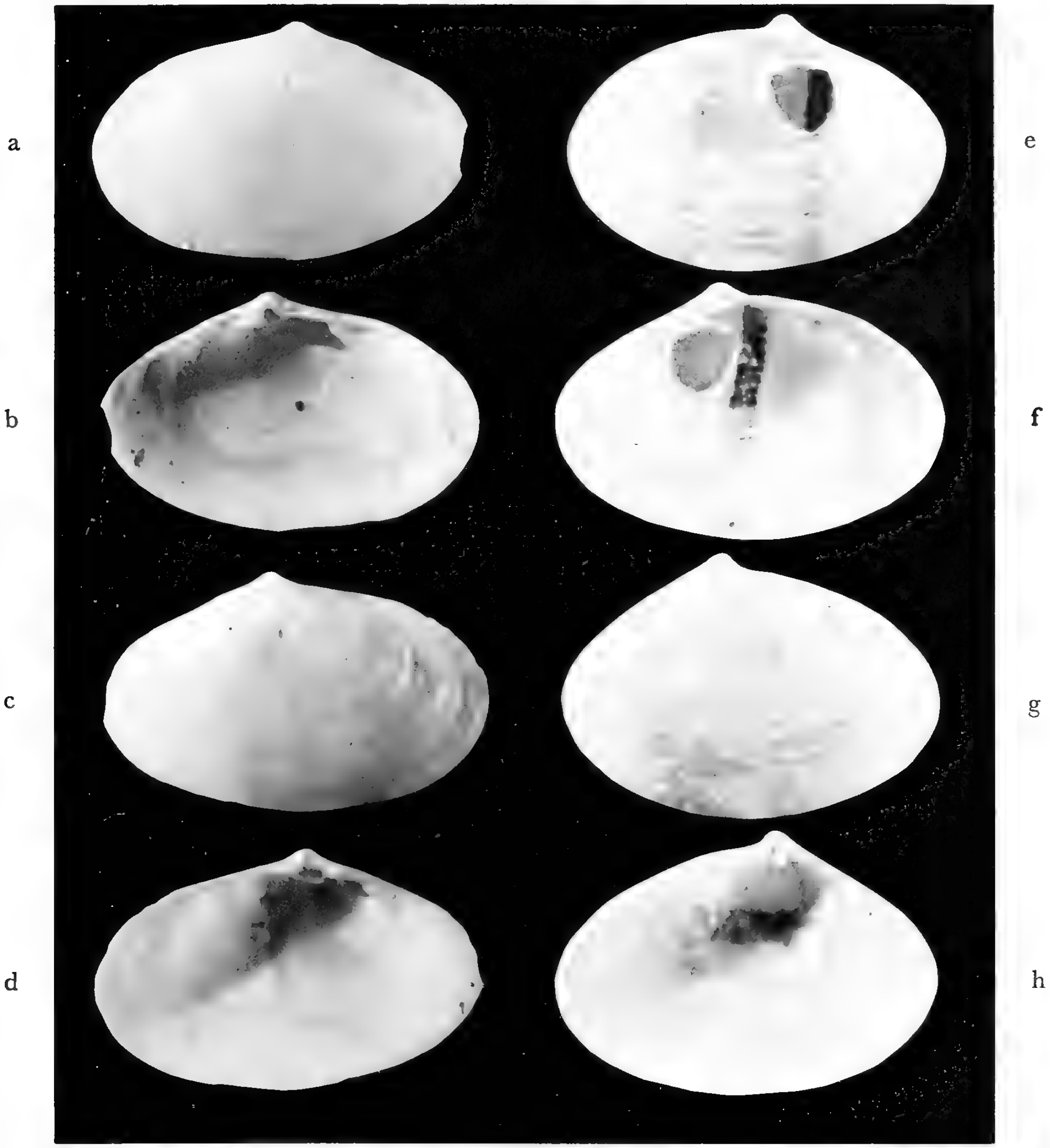


Figure *3*

CZ); Nassau, New Providence Island (MCZ). CUBA: Habana (MCZ); Santa Maria Key (MCZ). PUERTO RICO (ANSP). VIRGIN ISLANDS: St. Thomas (ASNP, MCZ, USNM). BARBUDA (MCZ, USNM). ANTIGUA (USNM). GUADELOUPE (MCZ, USNM). DOMINICA (USNM). CAYMAN BRAC (ANSP). GRAND CAYMAN ISLAND (ANSP). BRITISH HONDURAS: Pompion Cay (ANSP). BRASIL: Touros (ANSP) and Natal (ANSP), Rio Grande do Norte.

Ervilia concentrica (Holmes, 1860)

(Figures *2*a to *2*d)

Mesodesma concentrica Holmes, 1860. Post-Pleiocene Fossils of South Carolina. p. 44; plt. 6, fig. 10. (Simmons Bluff, Yonges Island, South Carolina, St. Pauls). Lectotype by DAVIS (1967), AMNH[4] 11291/1:1, AMNH 11291/1:2 (right and left valves respectively).

Ervilia concentrica. Gould, 1862a. Proc. Boston Soc. Nat. Hist. **8**: 281 [not figured]. (Coast of North Carolina). GOULD, 1862b, Otia Conchologia. p. 239 [not figured]. (Coast of North Carolina). Lectotype by JOHNSON (1964), Bull. **239**, U. S. Nat. Mus., p. 58; plt. 24, fig. 2. MCZ 169092. Paratypes: MCZ 169093, USNM 611263.

Ervilia maculosa Dall, 1896. Nautilus **10**: 26 [not figured]. (Off Cape Lookout, North Carolina, 22 fms., U. S. Fish Commission). Syntypes USNM 92153.

As indicated, there are several syntypes in the U. S. National Museum identified as *Ervilia maculosa*. This material is in no way distinctive or unique and, furthermore, meets all diagnostic criteria for inclusion in the species *E. concentrica*. Because of this similarity and because the *E. maculosa* came from the North Carolina coast (*E. concentrica* is the only species of the genus known from the area), I assume that the *E. maculosa* syntypes are small specimens of *E. concentrica* (see Figure *3* for comparison).

Diagnosis: Seldom more than 10 mm long. Valves are opaque, with concentric ridges of equal height. Radiating striae are absent, valves are moderately compressed and unequilateral. Posterior end is fairly rostrate. Shells are usually chalky white. See DAVIS (1967) for additional detailed discussion of this species.

Distribution: NORTH CAROLINA (U. S. A.): Off the coast (MCZ, USNM); Cape Lookout (MCZ, USNM); Cape Hatteras (USNM); Cape Fear (USNM); Pamlico Sound (MCZ). GEORGIA: Off the coast (USNM). FLORIDA: Frying Pan Shoals (ANSP, USNM); Miami (USNM); Fowey Light (USNM); Ajax Reef (USNM); Sand Key (USNM); Sugarloaf Key (MCZ); Big Pine Key (ANSP); Little Duck Key (ANSP); Bahia Honda Key (ANSP); Key West (USNM); Dry Tortugas (ANSP, USNM); Sanibel Island (MCZ); Boca Grande Key (USNM); Clearwater (ANSP); St. Joseph Bay (ANSP); St. Andrews Bay (ANSP, USNM); Destin (MCZ); Pensacola (USNM). BAHAMA ISLANDS: Great Inagua Island (MCZ). CUBA: Bahia Honda (USNM). GRAND CAYMAN ISLAND (ANSP).

Ervilia subcancellata Smith, 1885

(Figures *4*a to *4*d)

Ervilia subcancellata Smith, 1885. Report on the Lamellibranchiata collected by H. M. S. *Challenger* during the years 1873-76. Part 35, p. 80; plt. 6, figs. 2, 2a, 2b. The following syntypes are located in the British Museum (Natural History) under the following station and registration numbers: Sta. 33, No. 1887.2.9.2512 ($2\frac{1}{2}$ valves); Sta. 113A, No. 1887.2.9.2513a-15a (3 complete shells and 3 separate valves); Sta. 120, No. 1887.2.9.2511 (1 valve). Station 33 is off North Rock, Bermuda, 435 fathoms.

Ervilia rostratula Rehder, 1943. Proc. U. S. Nat. Mus. **93**: 189; plt. 19, figs. 1, 2. (Lake Worth, Florida). Holotype USNM 517059.

REHDER (1943) described *Ervilia rostratula* from material taken at Lake Worth, Florida. The holotype is 4.5 mm long, 3.3 mm high and 2.3 mm wide, but many specimens exceed 7 mm in length. Distinctive features are the pronounced rostration and a relatively greater height.

While spending 5 weeks at the Bermuda Biological Station working on *Ervilia* I found it impossible to distinguish *E. subcancellata* from *E. rostratula*. Bermuda was the source of the first part (Sta. 33, *Challenger* Collections) of the syntype material from which Smith described *E. subcancellata,* and much of the subsequent *Ervilia* material from Bermuda has been deposited in museum collections as either *E. subcancellata* or *E. rostratula.*

In Bermuda, living specimens of *Ervilia* were found only at Ferry Reach. Empty valves were collected at other localities in the Bermuda Islands. The group of right valves in Figure *5* was selected from a sample taken at Shelly Bay to demonstrate how rostration of the posterior margin increases as the clams increase in size. Smaller specimens accord with descriptions and figures of *E. subcancellata*; larger specimens resemble typical specimens of *E. rostratula.* Therefore, I conclude that Smith based his description on small specimens, and Rehder based his on large specimens of the same species. Distribution of the synonymized *E. subcancellata* has been determined by sorting out museum material showing significant rostration of the posterior margin.

Diagnosis: Smaller than *Ervilia nitens* or *E. concentrica.* Distinct rostration of the posterior margin producing a

---

[4] American Museum of Natural History, New York City, N. Y.

more marked trigonal shape (shells with a relatively greater height). Concentric ridges present but not prominent, radiating striae especially prominent on the posterior portion but usually visible anteriorly as well.

Distribution: Florida (U. S. A): Palm Beach (ANSP); Lake Worth (ANSP, MCZ, USNM); Pompano (MCZ); Miami (USNM); Biscayne Bay (MCZ); Upper Matecumbe Key (USNM); Little Duck Key (MCZ, USNM); Grassy Key (ANSP, MCZ); Boot Key (MCZ); Bahia Honda Key (USNM); Key West (ANSP, USNM); Dry Tortugas (USNM); Marco (ANSP); Turtle Harbor (US NM); Tampa Bay (USNM). Bermuda: North Rock (ANSP); Richardson's Inlet (MCZ); Castle Roads (MC Z); Bailey's Bay (MCZ); Shelly Bay (MCZ); Spanish Point (ANSP); Ferry Reach (MCZ). Bahama Islands: Hopetown, Great Abaco Island (MCZ); Cat Cay (US NM), South Bimini (USNM), Bimini Islands; Andros Island (MCZ); Nassau, New Providence Island (MCZ); Long Island (MCZ); Turks Island (MCZ). Cuba: Los Arroyos (USNM); Habana Harbor (USNM); Habana (MCZ); Banes (MCZ). Puerto Rico (USNM). Virgin Islands: St. Thomas (MCZ). Antigua (MCZ, US NM). Grenada (ANSP). Grand Cayman (USNM). Jamaica (MCZ). Brasil: Areia Branca (ANSP), Cabo de São Roque (USNM), and Natal (ANSP), Rio Grande do Norte; São Sebastiao (USNM), São Paulo.

NOTES on LIVING *Ervilia subcancellata*

The living specimens of *Ervilia subcancellata* collected at Ferry Reach, Bermuda, were studied in laboratory tanks and dishes at the Bermuda Biological Station. The substratum at the collecting site was fine sand consisting of coral fragments and broken shell with occasional larger pieces of coral. This substratum material was sifted in the water through a U. S. Standard Screen, mesh no. 12 with an opening of 1.6 mm. The retained material, containing the specimens, was taken to the laboratory for careful examination which ultimately yielded 10 live specimens. Each specimen was placed into a separate dish or small tank filled with seawater and unsifted substratum from the collecting site. Their behavior and gross anatomy were observed.

A relaxed living specimen is illustrated in Figure 6. The foot was slender and very active, and was often extended for as much as $1\frac{1}{2}$ times the length of the shell. The ventral margin of the foot had a well-defined groove. Presumably, this groove secretes the mucous strands for attachment to substratum particles. When a specimen was allowed to burrow into the sand while in the laboratory and removed several hours later, there usually was a string of particles attached to the mucous strands extending from the anteroventral part of the animal (Figure 7c). Additional attachment in the substratum may possibly be provided by the many papillae which extend outward from the mantle margins (Figure 7a). These papillae have expanded terminal portions not unlike echinoderm tube feet and are arranged in the alternatingly repetitive pattern shown diagrammatically in Figure 7b. The papillae may also be tactile as they are withdrawn quickly if disturbed.

As shown in Figures 6 and 7, the dorso-posterior excurrent siphon is the longer of the 2 siphons and has no papillae surrounding the distal opening. The more ventral incurrent siphon is equipped with a number of long papillae. During normal pumping and feeding activity these papillae curve inward over the siphon opening (Figure 7d) presumably preventing entry of suspended particles or organisms. Tactile irritation of the siphon papillae caused immediate withdrawal of the siphons. Figure 7d shows a diagrammatic cross-section of the substratum adjacent to a specimen of *Ervilia subcancellata* in normal buried position. Arrows indicate typical observed water flow when pumping or feeding was underway. Suspended matter in the water and discharge of fecal material facilitated detection of water flow.

Muscle tracts (not shown in the illustrations) were visible in the walls of both siphons. They presumably effect the rapid siphon withdrawal observed. Stomach contents were not examined, but considering the orientation of *Er-*

Explanation of Figures *4, 5*

Figure *4*: *Ervilia subcancellata*. Holotype of *Ervilia rostratula*, US NM 517059. Lake Worth, Florida. Length 4.5 mm, height 3.3 mm; a, exterior, right valve; b, interior, right valve; c, exterior, left valve; d, interior, left valve.

Figure *5*: Right valves of *Ervilia subcancellata* selected from a sample taken at Shelly Bay, Bermuda, 23 August, 1966, and arranged to show the increasing degree of rostration as larger size is attained. Smaller specimens resemble Smith's *E. subcancellata*, and larger specimens resemble Rehder's *E. rostratula*. Lengths: a, 2.7 mm; b, 3.8 mm; c, 5.5 mm; d, 6 5 mm; e, 7.6 mm.

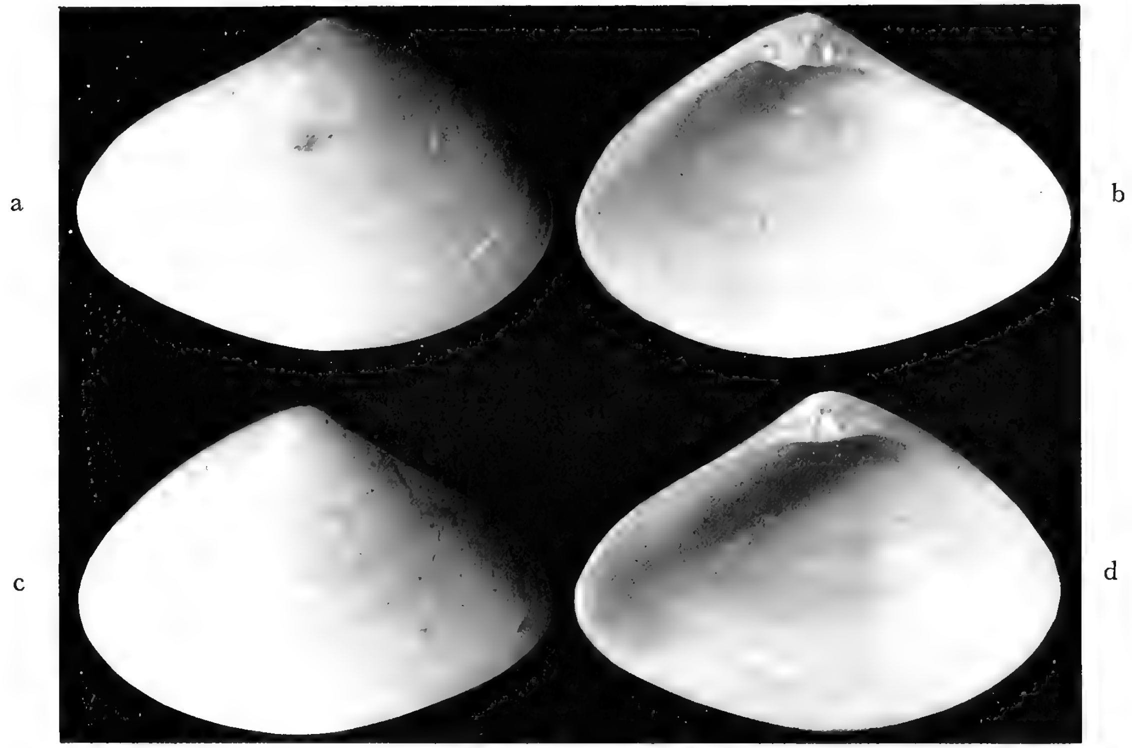


Figure *4*

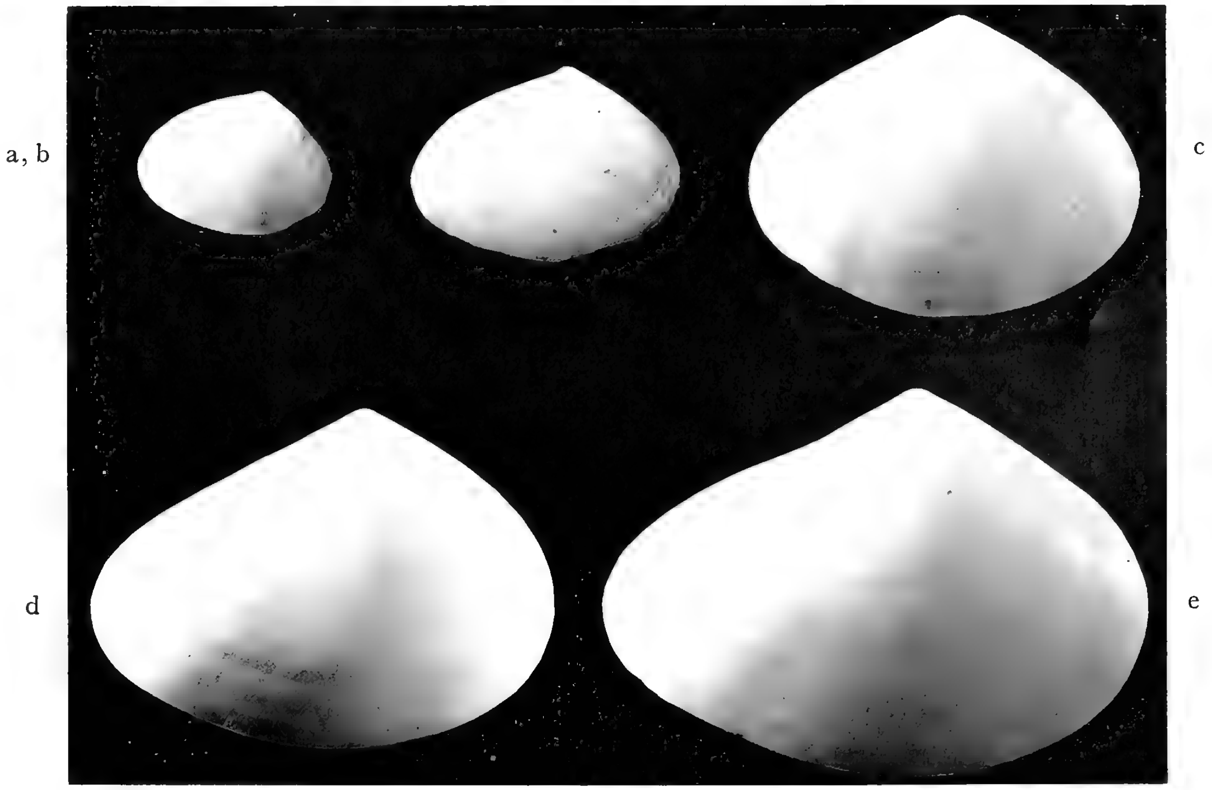


Figure *5*

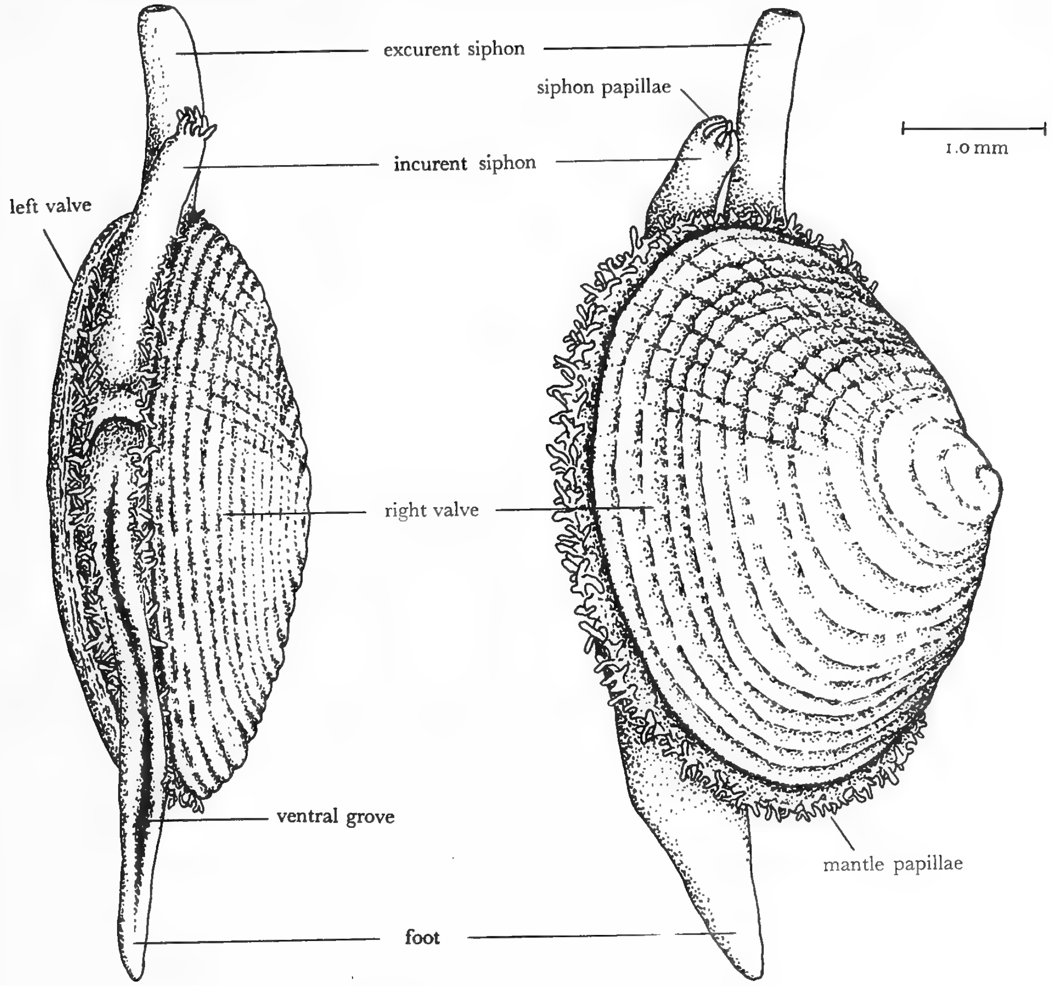


Figure 6

External appearance and structure of *Ervilia subcancellata.*
Right figure: right lateral aspect showing foot and siphons extended. Left figure: ventral aspect with foot and siphons similarly extended. Note presence of groove in ventral margin of foot and well-developed papillae on mantle periphery.

vilia subcancellata specimens in the substratum during these laboratory studies, I assume this pelecypod to be a filter feeder. Moreover, studies on several other members of the family Mesodesmatidae reveal filter-feeding life modes: Rapson (1952, 1954) described the Toheroa, *Amphidesma ventricosum,* of New Zealand as a filter feeder, and Coscaron (1959) demonstrated a similar life mode for *Mesodesma mactroides* of the beaches of Argentina and Brasil. My own continuing studies on the western North Atlantic representatives, *M. arctatum* and *M. deauratum,* also indicate similar feeding habits.

A specimen placed in a dish of seawater with suitable substratum would remain completely still for some time, but eventually the siphons appeared and, shortly after, the

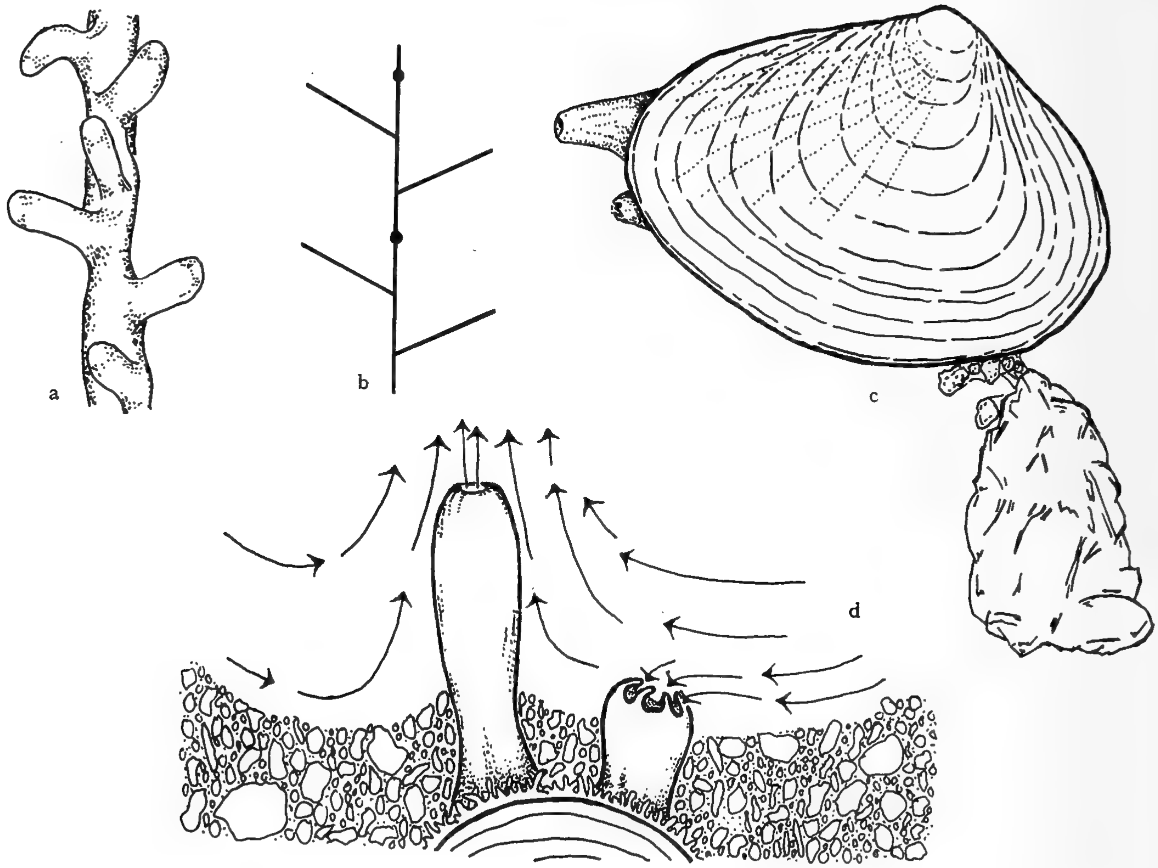


Figure 7

Observed features of *Ervilia subcancellata.*

a, edge of mantle periphery showing arrangement of mantle papillae; b, diagram of the repetitive positioning of mantle papillae: The vertical line represents the axis of the mantle fold with the plane of the mantle perpendicular to that of the paper. Solid circles on the mantle axis represent papillae projecting directly toward the viewer. Papillae projecting to the sides are represented by diagonal lines to left and right; c, view of specimen of *E. subcancellata* extracted from substratum with particles attached, presumably by mucous strands secreted by foot; d, general pattern of water flow adjacent to excurrent siphon (taller) and incurrent siphon (shorter) while pumping/feeding is underway.

foot protruded. At first the foot felt out the substratum with several fast jabs, then was inserted between nearby sand particles. Subsequently the clam quickly pulled itself erect, several convulsive tugs drawing it partway into the substratum. After a pause of from several seconds to several minutes, 3 to 4 stronger tugs pulled the clam virtually out of sight, only the siphons remaining visible. Usually specimens burrowed only to a depth that still permitted extension of the free ends of the siphons above the substratum surface, but occasionally, when disturbed, the entire clam and siphons disappeared. However, when the siphons were again extended, they easily displaced the sand and reappeared at the bottom of a small pit formed during initial penetration of the substratum.

When preparing to dig in, the clam forced out a jet of water between the dorsal edge of the foot and the anterior adductor muscle concurrently effecting a quick closing of the valves. The valves reopened almost immediately. The sudden water current usually forced some of the finer material away from the burrowing site.

The observed burrowing pattern of *Ervilia subcancellata* seems quite similar to the sequence attributed to the freshwater clam *Margaritifera margaritifera* by TRUEMAN (1968) and later generalized for burrowing bivalves by STANLEY (1970). Particularly interesting is the appearance of water currents from the mantle margin during adduction of the valves. As noted for *E. subcancellata,* this sudden flow of water removes finer sediment particles from the burrowing area. In *M. margaritifera,* according to Trueman, valve adduction (closing) is rapid and corresponds with expansion (dilation) of the foot and forced expulsion of water from the mantle cavity. Concurrently, the siphons are closed. The burrowing behavior pattern and sequence of events of *E. subcancellata* appear to be closely similar. It is altogether possible that valve adduction, foot expansion and expulsion of mantle cavity water are behavioral patterns commonly held by most pelecypod mollusks burrowing in relatively coarse, loose substratum.

In the laboratory containers, *Ervilia subcancellata* burrowed into and moved about in the substratum. Regardless of where the mollusks initially entered the sand material they eventually came to rest along the side of the dish or against a larger particle or rock in the substratum. This consistently repeated pattern suggested that *E. subcancellata* tends to position itself adjacent to larger rocks or coral fragments, possibly to attain some slightly greater degree of protection in its natural habitat.

ACKNOWLEDGMENTS

Drs. K. J. Boss, MCZ; J. Rosewater, USNM; R. T. Abbott, formerly ANSP; and N. D. Newell, AMNH are thanked for loans of museum material. Special thanks are due to Dr. N. Tebble, formerly of the British Museum (Natural History), for information on the Smith syntypes of *Ervilia subcancellata.* Drs. W. J. Clench, K. J. Boss and A. Gismann are thanked for their careful review of the manuscript and their many helpful suggestions.

Literature Cited

COSCARON, S.
1959. La "Almeja Amarilla" (*Mesodesma (T.) mactroides* Deshayes) de la costa de la provincia de Buenos Aires. Agro Publ. Techn. Ano 1, no. 3: 66 pp.
DALL, WILLIAM HEALEY
1896. On the American species of *Ervilia.* The Nautilus **10** (3): 25 - 27 (2 July 1896)
DAVIS, JOHN D.
1967. *Ervilia concentrica* and *Mesodesma concentrica*: clarification of synonymy. Malacologia **6** (1/2): 231 - 241 (31 December)
FORBES, EDWARD & SYLVANUS HANLEY
1853. A history of British Mollusca and their shells.. vol. 1: 486 pp.; 64 plts. J. van Voorst, London
GOULD, AUGUSTUS ADDISON
1862a. Descriptions of new genera and species of shells. Proc. Boston Soc. Nat. Hist. **8**: 280 - 284 (February 1862)
1862b. Otia conchologica: Descriptions of shells and mollusks from 1839 to 1862. Gould & Lincoln, Boston, iv+256 pp.
HOLMES, F. S.
1860. Post-Pleiocene fossils of South Carolina. Russel & Jones, Charleston, S. C. 122 pp.; 28 plts.
JOHNSON, RICHARD I.
1964. The Recent Mollusca of Augustus Addison Gould. U. S. Nat. Mus. Bull. **239**: v+1 - 182; plts. 1 - 45
MONTAGU, GEORGE
1808. Supplement to Testacea Britannica with additional plates. London, England, 183 pp.; plts. 17 - 30
RAPSON, A. M.
1952. The Toheroa, *Amphidesma ventricosum* Gray (Eulamellibranchiata), development and growth. Austral. Journ. Marine Freshw. Res. **3**: 170 - 198
1954. Feeding and control of Toheroa *Amphidesma ventricosum* Gray (Eulamellibranchiata) populations in New Zealand. Austral. Journ. Marine Freshw. Res. **5**: 486 - 512
REHDER, HARALD ALFRED
1943. New marine mollusks from the Antillean region. Proc. U. S. Nat. Mus. **93** (3161): 187 - 203
SMITH, EDGAR ALBERT
1885. Report on the Lamellibranchiata collected by H. M. S. *Challenger* during the years 1873-76. Part 35: 341 pp.
STANLEY, STEVEN M.
1970. Relation of shell form to life habits in the Bivalvia (Mollusca). Geol. Soc. Amer. Mem. **125**: i - xiii+1 - 296; plts. 1 - 40; figs. 1 - 48 (December 1970)
THIELE, JOHANNES
1935. Handbuch der systematischen Weichtierkunde. **Bd. 2**: 779 - 1154; illust. Jena, Gustav Fischer
TRUEMAN, E. R.
1968. The locomotion of the freshwater clam *Margaritifera margaritifera* (Unionacea : Margaritanidae). Malacologia **6** (3): 401 - 410 (30 June 1968)
TURTON, WILLIAM
1822. Conchylia Dithyra Insularum Britannicarum: The bivalve shells of the British Isles. 279 pp.; 20 plts. M. A. Nuttall, London

The Northwest American Semelidae

BY

EUGENE V. COAN

Research Associate, Department of Geology

California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

(2 Plates; 7 Text figures)

INTRODUCTION

THIS IS THE SECOND ARTICLE based on research conducted while I was a graduate student at Stanford University, the Tellinidae having been discussed in an earlier paper (COAN, 1971). The main purpose of the present account is to put on record data on the systematics of the northwest American Semelidae, though not in as much detail as was possible in the case of the Tellinidae. The present survey also permitted the review of data on the geographic and geologic distribution and habitats of members of this family. These aspects are summarized at the end of the article.

The major previous accounts on this family in northwestern America were those of DALL (1915), GRANT & GALE (1931), and BURCH (1945a-1945c).

The detailed "Introduction," "Acknowledgments," and "Methods" sections of my earlier paper need not be repeated here, although special thanks are extended to Drs. Myra Keen, Warren Addicott, and Kenneth Boss who reviewed the present manuscript, and to Mr. Barry Roth who prepared the illustrations. The following abridged comments on format and abbreviations will permit the present paper to stand alone.

(1) The applicable synonymous species-level names are listed in chronological order, with the name to be used cited first and "first revisions," if any, indicated. Under each name are listed accounts published using those names and also accounts of type material pertinent to each. These works are listed in chronological order with major changes in generic allocation indicated in brackets above the account in which they were first employed. It is to be assumed that nearly all subsequent accounts used the same name combination. Other nomenclatural comments are included in brackets after the account to which they refer.

The works listed do not represent a complete catalogue of literature but are the major accounts concerning living and fossil northwest American material, particularly those containing previously unpublished information or taxonomic innovations. Not included are books written largely for amateurs or general works on marine biology.

Numbers following dates (as 1851: 27) are page numbers.

(2) The type material pertinent to the valid name and its synonyms is discussed. Measurements given are of the greatest lengths of type specimens. When type material is no longer extant the dimensions from original accounts or of original illustrations are given. (In most early accounts the illustrations were usually printed at natural size, though this was rarely stated.) Photographs of type specimens or of original illustrations are included.

(3) Type localities of the various nominal species are given. The original collector is also cited, and sometimes major collections are mentioned when this clarifies the history or location of the specimens.

(4) A nomenclatural commentary may be given to explain nomenclatural complications not made clear in the synonymy or in the discussion of type material.

(5) Description. A short diagnosis of each species is given that emphasizes distinguishing characters. Most features of internal shell morphology are not discussed in detail but are illustrated with line drawings.

(6) Geographic Distribution and Ecology. The end-points of the distribution are given, together with reference to the source. The intermediate distributional data from between these end-points are summarized.

The sources of habitat information on each species other than from museum labels are indicated. I mention also the approximate number of lots examined.

(7) Geologic Distribution and Biogeography. The final section under each species is a summary of paleontologic records from published accounts. I have not listed all Pleistocene records, but generally have given only the end-points of their distributions and indicated the published accounts that form their bases. This is followed by notes on what seem to be related fossil species from earlier than the Pleistocene and related species in the Panamic province.

References are included under "Literature Cited" for all genera, species, and papers mentioned.

Conventions, symbols, and abbreviations used are as follows:

ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania
Berry collection – The private collection of Dr. S. Stillman Berry, Redlands, California
BM(NH) – British Museum (Natural History), London, England
CAS – California Academy of Sciences, San Francisco, California
ex (Conrad) MS – from the manuscript name of (Conrad)
ICZN – International Commission on Zoological Nomenclature, or International Code of Zoological Nomenclature (Stoll *et al.*, 1964)
LACM – Los Angeles County Museum of Natural History, Los Angeles, California
m – meter(s)
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
mm – millimeter(s)
not, not of – as in the case of homonyms or misidentifications
pair – the two valves of one specimen
SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California
SDNHM – San Diego Natural History Museum, San Diego, California
SU – Stanford University, Stanford, California
UCLA – University of California at Los Angeles, California
USNM – United States National Museum, Smithsonian Institution, Washington, District of Columbia

SYSTEMATIC ACCOUNT

Semelidae Stoliczka, 1870

Keen (1969) recognized both the Semelidae and the family Scrobiculariidae H. & A. Adams, 1856, but a preliminary survey of pertinent literature suggests that such a division may be untenable. There are no clear-cut points of distinction between the two groups. If this proves to be true, a petition to the International Commission on Zoological Nomenclature to give precedence to the name "Semelidae" might be in order.

There are a number of accounts on the functional anatomy of European species of the genera *Abra* and *Scrobicularia,* and a review of many of these can be found in Yonge (1949). Our knowledge of the soft parts of the two genera known to be represented in northwest America, *Semele* and *Cumingia,* is limited to the following: a description of the anatomy of *Semele solida* (Gray, 1828) by Schröder (1916), discussions of the mantle currents in *Semele decisa* (Conrad, 1837) by Kellogg (1915) and Stasek (1963), a discussion of the heart and pericardial gland of *Semele sinensis* (A. Adams, 1854) [now known as *S. cordiformis* (Holten, 1802)] by White (1942) and a brief description of the anatomy of *Cumingia* by Deshayes (1857).

The familial and generic classification of these genera is much in need of review, and this would be an excellent project for someone to undertake.

Semele Schumacher, 1817

[Type species: *Semele reticulata* Schumacher, 1817,
= *Tellina proficua* Pulteney, 1799; by monotypy]

Into the genus *Semele* are placed species with medium-sized to large shells. They are equilateral or longer anteriorly and are variously sculptured. Most are brightly colored. The resilium is located in an elongate depression on the hinge plate. Lateral teeth are present, generally most prominent in the right valve. There are anterior to the resilium two weak cardinal teeth in each valve which are nearly equal in size. The pallial sinus is not confluent with the ventral pallial line and ascends obliquely.

An insufficient number of generic taxa are as yet proposed to divide west American species meaningfully into subgenera. It appears that *Semele incongrua* Carpenter, 1864, and allied Panamic species might be placed into the subgenus *Amphidesma* Lamarck, 1818 [type species: *A. variegata* Lamarck, 1818; by subsequent designation of Children, 1822]. *Semele rupicola* Dall, 1915, and its

Galápagos Island homologue might fit into *Elegantula* de Gregorio, 1884 [type species: *Semele fazisa* de Gregorio, 1884=*Amphidesma striatus* Reeve, 1853; by monotypy].

Semele decisa (Conrad, 1837)

(Figures *1* to *3* and 14)

Amphidesma decisum Conrad
- Conrad, 1837: 239; plate 19, figure 2 [as *A.* "*decisa*"]
- Reeve, 1853: plate 4, figure 24

[*Semele*]
- Carpenter, 1857a: 213
- Carpenter, 1857b: 195, 228, 231, 303, 351
- Carpenter, 1864b: 536, 540, 640 [1872: 22, 26, 126]
- Gabb, 1869: 94
- Arnold, 1903: 165 - 166
- Dall, 1915: 25
- I. Oldroyd, 1925: 179
- Grant & Gale, 1931: 376, 908; plate 14, figures 13a, 13b
- Burch, 1945a: 17, 19 (text figure); 1945b: 17
- Hertlein & Strong, 1949: 242
- Keen, 1966: 171

Amphidesma rubrolineatum Conrad [first revision herein]
- Conrad, 1837: 239; plate 18, figure 11 [as *A.* "*rubro-lineata*"]

[*Semele*]
- Carpenter, 1857a: 212 [as a synonym of *S. simplex* (Adams & Reeve, 1850)]
- Carpenter, 1857b: 163, 195, 232, 303, 351
- Carpenter, 1864b: 536, 640 [1872: 22, 126]
- Dall, 1915: 27 - 28
- Keen, 1966: 171

Semele rubrotincta Carpenter, "*ex* Conrad MS" [a misspelling for *Amphidesma rubrolineatum*]
- Carpenter, 1857b: 284, 352

Type Material:

Amphidesma decisum – BM(NH) Nuttall collection 1861.5.20.137, holotype, pair, 49mm. Conrad's stated measurement of 127mm is too large. Figure *1*.

Amphidesma rubrolineatum – Lost (Carpenter, 1857a; Keen, 1966). The original figure measures 25 mm. Figure *2*.

Type Localities:

Amphidesma decisum & *A. rubrolineatum* – "In the vicinity of" San Diego, California; T. Nuttall, in "deep water."

Nomenclatural Commentary:

Carpenter (1857a, 1857b), following an opinion of Hugh Cuming, suggested that Conrad's *Semele rubrolineata* might be a synonym of *Amphidesma simplex* Adams & Reeve, 1850 and that the latter might be from California rather than the original "China Sea." Later, however, he speculated that *S. rubrolineata* might represent young *S. decisa* (Carpenter, 1864b). This last opinion seems correct. The original illustrations and photographs of the type specimens (BM(NH) 3 unnumbered syntypes) of *Semele simplex* show that the shell of this presumably Asian species is more elongate, and according to the original description is golden within and has an overall rosy color. Young *S. decisa* (Figure *3*) have rosy rays, as mentioned in Conrad's description of *S. rubrolineata.* Conrad's illustration is poor, but I can see no reason to doubt his locality, nor is there reason to doubt the original locality of *S. simplex.* The action of a "first reviser" is needed (ICZN Article 24a).

Carpenter (1857a) discussed Gould's suggestion that *S. decisa* might prove identical to *S. rosea* (Sowerby, 1833b). However, the latter is distinct in having regular concentric sculpture and a pink color within. It occurs from southern Mexico to Peru.

Description:

Large (to 94 mm); rounded; right valve more inflated; heavy; longer anteriorly in young to equilateral [illegible] adult; rounded anteriorly; truncate postero-ventrally; antero-dorsal margin slightly concave near beaks, with a weakly developed lunule; postero-dorsal margin relatively straight, detectably beveled; sculpture of heavy, irregular concentric undulations and granular striae arranged in a somewhat radial pattern, most pronounced posteriorly; periostracum thin, generally worn off in adult and present only as dorsal and ventral fragments; externally with a light purplish tinge, darker between concentric undulations, and sometimes with reddish radial rays, particularly near beaks and in juvenile specimens; hinge area tinged purple both externally and internally; conspicuously punctate within, purple; pallial sinuses large, upturned. Other internal details as in Figure 14. Juvenile specimens smoother, with a more abrupt postero-dorsal slope than those of the next species.

Geographic Distribution and Ecology:

Coal Oil Point (SBMNH 23476) and Santa Rosa Island (Fitch, in correspondence), Santa Barbara County, California, to Cabo San Lucas, Baja California Sur (CAS 17663a), with many intermediate records. A specimen at

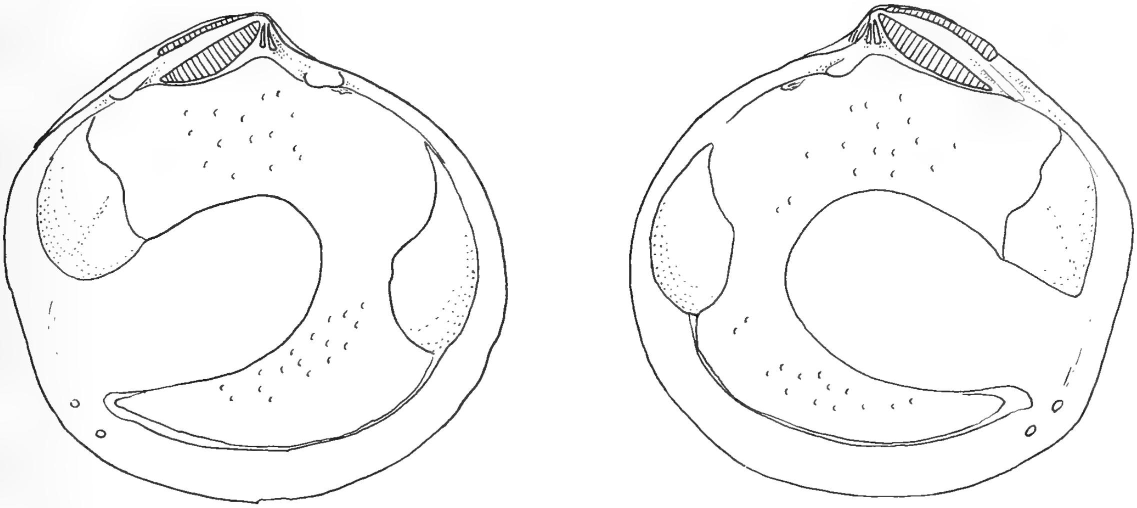


Figure 14

Semele decisa

internal view of valves, MCZ 86934, San Diego, California; 78.5 mm

Harvard University (MCZ 233099) labeled "Puerto Peñasco," Sonora, probably represents an error in labeling. This species is found in protected intertidal areas among rubble but sometimes in sand to 46 m (Burch, 1945a).

Material seen:
109 lots.

Geologic Distribution and Biogeography:

This species is well represented in the late Pleistocene, with records from Tomales Bay, California (Dickerson, 1922; Weaver, 1949; Addicott, 1966), to Bahía Magdalena, Baja California Sur (Jordan, 1936), with many intermediate localities. It is known from the early Pleistocene of San Pedro, California (Arnold, 1903; Clark, *in* Natland, 1957). There are records from southern Californian formations transitional between the Pliocene and the Pleistocene and from the Pliocene of the Los Angeles basin.

There are no described fossil species in northwest America that resemble *Semele decisa.* On the other hand, it is one of a group of large species of *Semele,* the rest of which occur in the Panamic province. In fact, it is apparently homologous to *Semele punctata* (Sowerby, 1833b), known from the Recent (Keen, 1971) and the Pleistocene (Hertlein & Strong, 1939) of the Galápagos Islands. The latter differs in being smaller, more elongate, more rounded posteriorly, more flattened; the pallial sinus is more rounded and less dorsally directed; the sculpture is proportionately heavier, with more elongate radial pustules, essentially constituting radial sculpture. The beaks often have an orange flush, as opposed to the purple of the Californian species. I suggest that these two species represent isolated populations of what was once one species, perhaps in the Pliocene.

I know of no similar Asian or Caribbean species.

Its establishment in Tomales Bay in the Pleistocene, north of its present northern limit, may have been the result of larval settlement in one of the warm interglacial periods, although it may have remained for a time after its introduction. (It could also represent a relict population of a once wider distribution for which evidence is not yet known.)

Semele rubropicta Dall, 1871

(Figures *4* and 15)

Semele rubropicta Dall
Dall, 1871: 144 - 145, 160; plate 14, figure 10
Dall, 1915: 26
I. Oldroyd, 1924: 56, 212; plate 22, figure 10
I. Oldroyd, 1925: 180; plate 43, figure 10
Dall, 1925: 36, 37; plate 18, figures 1, 2
Grant & Gale, 1931: 376
Burch, 1945a: 17; 1945b: 17; 1945c: 30

Amphidesma rubrolineatum Conrad, of authors, not of Conrad
[not Conrad, 1837: 239; plate 18, figure 11]

[*Semele*]
Carpenter, 1864b: 627 [1872: 113]

Type Material:

USNM 101960, **lectotype** herein, left valve, 39.8 mm; USNM 678001, **paralectotype**, right valve, evidently not the same specimen as lectotype; ANS P 51749, probable paralectotype, right valve, 39.4 mm. The latter was probably that figured and measured (39.3 mm) by Dall (1871); however, its broken condition, its present lack of exact data, and the fact that Dall (1925) illustrated the here-chosen lectotype have decided the selection made. Figure *4*.

Type Locality:

Soquel [Capitola], California; W. H. Dall, on "beach."

Nomenclatural Commentary:

None necessary.

Description:

Medium-sized (to 50 mm); ovate-elongate; equivalve; average in thickness for size; markedly longer, rounded anteriorly; only slightly truncate posteriorly; antero-dorsal margin slightly concave near beaks forming a weak lunule, convex distally; postero-dorsal margin weakly convex, slightly beveled; sculpture of concentric undulations, predominating in southern populations, and radial striae, most prominent in northern populations; periostracum thin, more adherent than in other species, but sometimes present only as dorsal and ventral fragments; externally with a pinkish hue, red radial rays, and a purplish tinge on hinge; internally smooth, white; pallial sinus large. Other internal details as in Figure 15. Juveniles are more covered with periostracum (particularly northern specimens) and are more elongate than those of the preceding species.

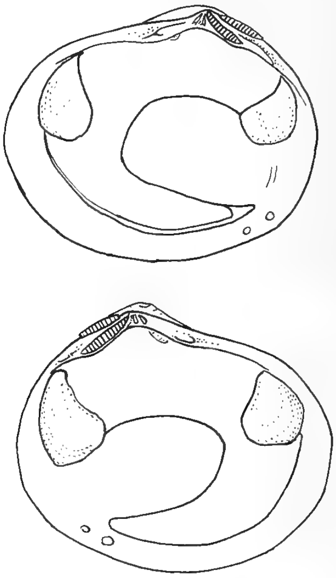


Figure 15

Semele rubropicta

internal view of valves, MCZ 60100, Eagle Island, Puget Sound, Washington; 52 mm

Geographic Distribution and Ecology:

Craig, Prince of Wales Island, Alaska (UCLA 20522), to the Strait of Juan de Fuca, Washington (MCZ 68842), with several intermediate localities, including throughout Puget Sound; Bodega Bay, California (Pacific Marine

Explanation of Figures *1* to *5*

Figure *1*: *Semele decisa*. Holotype of *Amphidesma decisum*, BM (NH) Nuttall collection 1861.5.20.137; 49 mm

Figure *2*: *Semele decisa*. Original figure of *Amphidesma rubrolineatum*; 25 mm

Figure *3*: *Semele decisa*, USNM 590481, Mission Bay, San Diego, California; 26 mm

Figure *4*: *Semele rubropicta*, lectotype (herein), USNM 101960; 39.8 mm

Figure *5*: *Semele rupicola*, lectotype (herein), USNM 272099; 19 mm

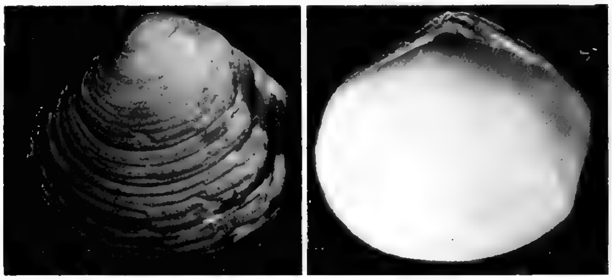


Figure *1*

Figure *2*

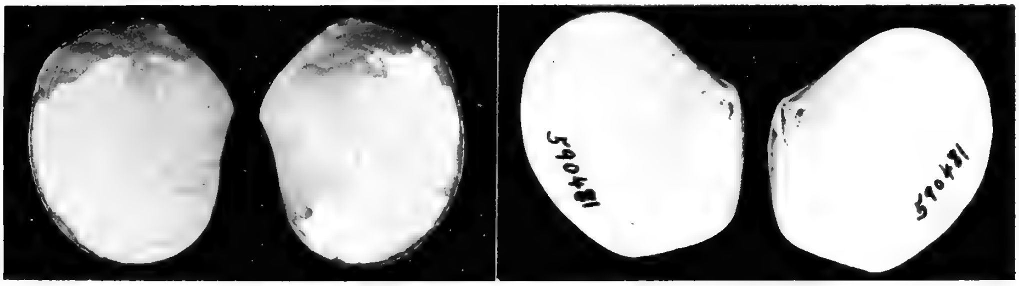


Figure *3*

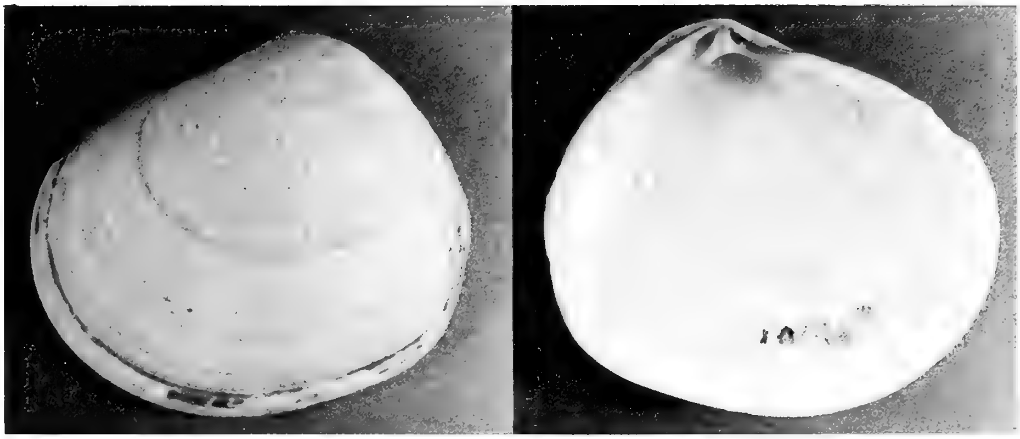


Figure *4*

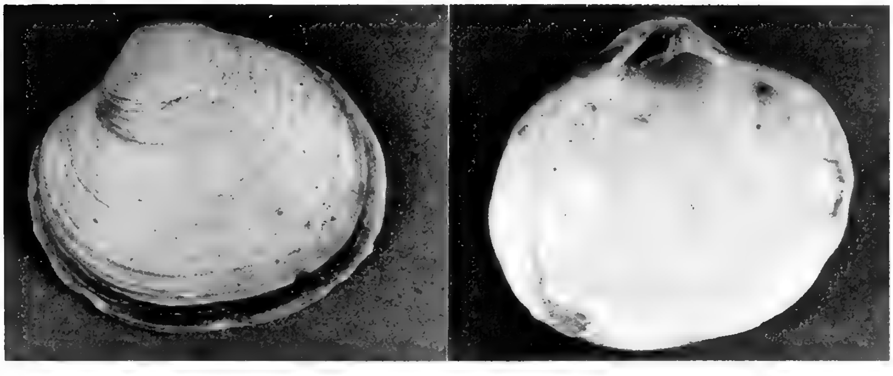


Figure *5*

Station collection), to Isla Natividad, Baja California Sur (LACM 72-117), with several intermediate localities. This species is not yet known from between northern Washington and Bodega Bay. A specimen (SDNHM 15261) labeled "Guaymas" probably represents an error in labeling. Occurrence is from the intertidal area to 91 m, on a variety of bottom types, most often on coarse sediments (Burch, 1945a; Smith & Gordon, 1948; Quayle, 1960). Kirsop (1922) found it to occur in numbers of 78 per m² in 21 to 25 m.

Material seen:
91 lots.

Geologic Distribution and Biogeography:

In the late Pleistocene, the species is known from Cayucos, California (Valentine, 1958), to Bahía Magdalena, Baja California Sur (Jordan, 1924, 1936), with a number of intermediate records. There are records in the early Pleistocene of the San Pedro area, California (T. Oldroyd, 1925; Clark, 1931; Burch, 1947), as well as several in the Pliocene of California.

The lack of specimens from the late Pleistocene from north of Cayucos suggests that living northern populations may represent a settlement during an interglacial period. However, unlike the occurrence of *Semele decisa* in Tomales Bay in the late Pleistocene, the immigration of *S. rubropicta* into the Puget Sound area was apparently successful, the species perhaps having been protected by the warmer temperatures of that area. Gene flow between northern and southern populations is not yet proven, but the morphological differences are not yet sufficient to regard the two populations as subspecies. The problem invites further study.

Semele rubropicta seems more closely related to fossil species of the northwest American area than to any Recent Panamic species. It seems especially close to *S. fausta* Nomland, 1917, from the Pliocene of central California. Other related species may be *S. sylviaensis* Weaver, 1912, from the Miocene and Pliocene of Washington; *S. vancouverensis* Clark & Arnold, 1923, from the Oligocene of Vancouver Island; and *S. reagani* Dickerson, 1917, from the Oligocene of Washington.

Semele rupicola Dall, 1915

(Figures 5 and 16)

Semele rupicola Dall
Dall, 1915: 26
I. Oldroyd, 1925: 180; plate 11, figures 9, 10
Burch, 1945a: 17; 1945b: 17
Keen, 1958: 200 - 201; text figure 495

Amphidesma rupium Sowerby, of authors, in part, not of Sowerby
[not Sowerby, 1833b: plate 1, figure 12]

[*Semele*]
Carpenter, 1864b: 611, 640, 684 [1872: 97, 126, 170]

Type Material:

USNM 272099, **lectotype** herein, left valve, 19 mm; USNM 663892, **paralectotype**, smaller left valve. The lot selected is the only one in the USNM with the name "*Semele rupicola*" written on it, and we can be reasonably certain that Dall examined this lot prior to naming the species. There is no material in the USNM from Santa Cruz, California, the only specific locality mentioned by Dall (1915). Figure 5.

Type Locality:

Santa Barbara, California; W. H. Dall.

Nomenclatural Commentary:

Early records of this species were of its Galápagos relative, *Semele rupium* (Sowerby). Misidentified, light-colored young specimens of this species account for Californian Recent (Dall, 1915, based on USNM 109039) and Pleistocene (Kanakoff & Emerson, 1959) records of *S. striosa* (C. B. Adams, 1852a). The latter, now relegated to the synonymy of *S. bicolor* (C. B. Adams, 1852a), occurs from the Gulf of California to Panama and is more regular in shape (Keen, 1971).

Description:

Medium-sized (to 53 mm); ovate to rounded, but frequently deformed by its nestling habit; equivalve or nearly so; heavy for size; rounded, slightly produced anteriorly; longer, generally weakly truncate posteriorly; antero-dorsal margin somewhat concave near beaks forming a weak lunule; postero-dorsal margin rounded, somewhat beveled; sculpture of irregular concentric lamellar ridges and fine radial striae; periostracum dark, worn off in adult and present only as ventral fragments; exterior not conspicuously colored; punctate within, red around margins, occasionally with an orange hue; pallial sinuses relatively small. Other internal details as in Figure 16. Juveniles are more regular in outline, without conspicuous concentric sculpture.

Geographic Distribution and Ecology:

South Farallon Island, California (CAS 32813); Monterey, California (SU 4361, 21330), to Cabo San Lucas, Baja California Sur (USNM 663892), with numerous intermediate records. It occurs from the inter-

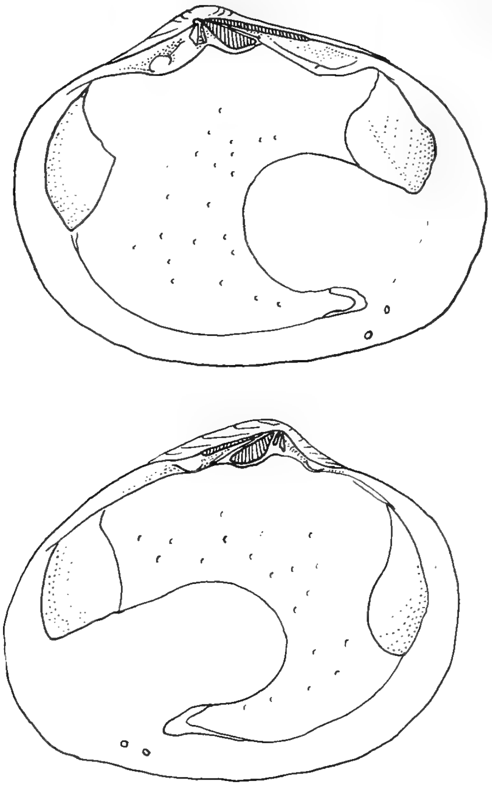


Figure 16

Semele rupicola

internal view of valves, MCZ 176237, San Diego, California; 32.6 mm

tidal area to 27 m, perhaps as deep as 46 m, nestling in rock crevices and among *Mytilus* (Burch, 1945a; Smith & Gordon, 1948).

Material seen:

87 lots.

Geologic Distribution and Biogeography:

In the late Pleistocene, this species has been recorded from Cayucos, California (Valentine, 1958), to Rosario, Baja California Norte (Valentine, 1957). It has also been recorded in the early Pleistocene of San Pedro, California (Valentine & Meade, 1961).

The biogeographic relationships are similar to those of *Semele decisa*. Ancestral species are unknown on the West Coast, but a homologous form is present on the Galápagos Islands, *S. rupium* (Sowerby), known from both the Pleistocene (Hertlein & Strong, 1939) and the Recent (Keen, 1971). *Semele rupium* seems to differ from *S. rupicola* in being more quadrate, having heavier radial sculpture and a more orange hue internally, but additional material should be studied to provide a more detailed comparison.

Semele incongrua Carpenter, 1864

(Figures 6, 7 and 17)

Semele incongrua Carpenter

Carpenter, 1864b: 611, 640 [1872: 97, 126]
Carpenter, 1865-1866: 208 - 209 [as *S. "incungrua"*]
Dall, 1915: 27
I. Oldroyd, 1925: 181; plate 11, figures 12, 13
Grant & Gale, 1931: 377
Burch, 1945a: 18; 1945b: 17
Hertlein & Strong, 1949: 248 - 249
Palmer, 1958: 16, 27, 38, 48, 110 - 111, 338 - 339; plate 14, figures 7 - 10

Semele pulchra montereyi Arnold

Arnold, 1903: 166 - 167, 392; plate 15, figures 3, 3a
Grant & Gale, 1931: 377
Burch, 1945a: 18

Type Material:

Semele incongrua – USNM 663888, **lectotype** herein, pair, 14.5 mm; Redpath Museum, **paralectotypes**. The USNM specimen also bears the California State Collection number 1061. Figure Figures 6 and 17.

Semele pulchra montereyi – USNM 162526, holotype, right valve, 18.7 mm. Figure 7.

Type Localities:

Semele incongrua – Catalina Island, California; J. G. Cooper, 73 to 110 m.

Semele pulchra montereyi – "Deadman Island," San Pedro, California; Lower San Pedro formation, early Pleistocene; R. Arnold.

Nomenclatural Commentary:

Arnold's subspecies, proposed as a "variety" of *Semele pulchra* (Sowerby, *in* Broderip & Sowerby, 1832), presumably by mistake, was described as being more oval, thicker, with less angular and more anteriorly placed beaks. It was synonymized with *S. incongrua* by Dall (1915). Grant & Gale (1931) listed it as a distinct Pleistocene subspecies, but they did not give any reasons for so regarding it. Burch (1945a) suggested that the name could also be applied to a northern Recent subspecies. Hertlein & Strong (1949) indicated that the fossil subspecies might be separable in being more rounded and in having more pronounced sculpture.

Each of the points of distinction advanced by Arnold (1903) and by Hertlein & Strong (1949) are within the range of variation of mature specimens.

Description:

Small (to 25 mm); ovate-elongate; left valve somewhat more inflated; thin; longer, rounded anteriorly; rounded posteriorly; antero-dorsal margin beveled to form a lunule; postero-dorsal margin rounded; sculpture of concentric lamellar ridges, more conspicuous in right valve, and fine radial striae in the interstices; periostracum not evident; purplish tinge near beaks, sometimes with purplish radial rays; smooth internally, with purplish rays; pallial sinus large. Other internal details as in Figure 17.

Geographic Distribution and Ecology:

Monterey, California (USNM 204038 and many other lots) to Isla San Benito, Baja California Norte (SDNHM 28842), with many intermediate records. It has been taken from 9 to 192 m, in fine to coarse sand and nestling in borer holes in shale (Burch, 1945a; Smith & Gordon, 1948).

Material seen:

66 lots.

Geologic Distribution and Biogeography:

In the late Pleistocene, this species has been reported only from Newport Bay, California (Bruff, 1946). In the early Pleistocene it is known from Santa Barbara, California (Arnold, 1907a, 1907b) and from the San Pedro area, California (Arnold, 1903; T. Oldroyd, 1925; Clark, 1931; Burch, 1947; Valentine & Meade, 1961). The relative scarcity of late Pleistocene records may be due to the fact that offshore deposits are better represented in the early Pleistocene of southern California; this is an offshore species.

It is similar to the Panamic *Semele venusta* (Reeve, 1853, *ex* A. Adams MS), which occurs from Acapulco, Guerrero, Mexico, to Colombia (Keen, 1971). The shell of this Panamic species is larger, heavier, with more prominent beaks, and is more smoothly sculptured, with more rounded concentric lamellae. The pallial sinus in *S. venusta* is more pointed, and the shell is more conspicuously colored, with a dark purple hue and even darker Λ-shaped lines.

Semele incongrua has not been reported from the Pliocene. It may be related to *S. morani* Anderson & Martin, 1914, from the Miocene of central California and perhaps to *S. gayi* Arnold, 1908, from the Oligocene or Miocene of central California.

Semele pulchra (Sowerby, *in* Broderip & Sowerby, 1832)

(Figures *8* to *11* and 18)

Amphidesma pulchrum Sowerby, *in* Broderip & Sowerby
Sowerby, *in* Broderip & Sowerby, 1832: 57
Sowerby, 1833b: plate 17, page 1, figure 2 [1841: page 7]
Reeve, 1853: plate 1, figure 2

[*Semele*]
Carpenter, 1857b: 188, 280, 303

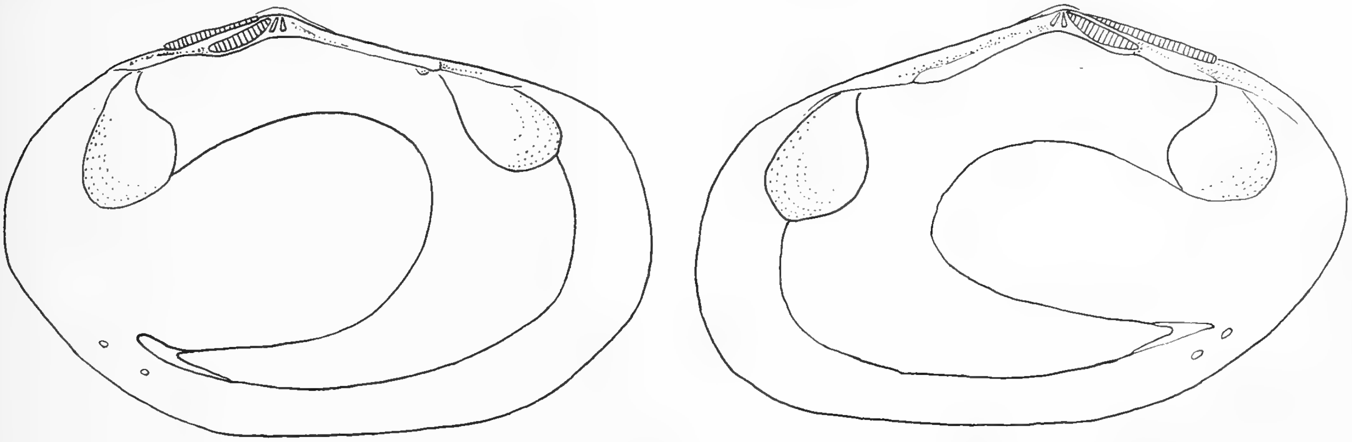


Figure 17

Semele incongrua

internal view of valves, USNM 663888, lectotype (herein); 14.5 mm

Carpenter, 1864a: 367 [1872: 203]
Carpenter, 1864b: 537, 553, 592, 611, 640, 668 [1872: 23, 39, 78, 97, 126, 154]
Arnold, 1903: 166, 392; plate 15, figures 1, 1a
Dall, 1915: 27
I. Oldroyd, 1925: 181
Grant & Gale, 1931: 377
Burch, 1945a: 18; 1945b: 17
Hertlein & Strong, 1949: 246, 258; plate 1, figure 15
Keen, 1958: 198 - 199, text figure 492
Olsson, 1961: 368 - 369, 538; plate 65, figure 5
Keen, 1971: 253 - 254; text figure 641

Semele quentinensis Dall
Dall, 1921: 22
Dall, 1925: 26, 36; plate 8, figure 4
Grant & Gale, 1931: 377
Hertlein & Strong, 1949: 246 - 247, 258; plate 1, figure 10
Keen, 1958: 198 - 199; text figure 494
Keen, 1971: 253 -254; text figure 643

Type Material:

Amphidesma pulchrum – BM(NH) without registry number, **lectotype** herein, pair, about 31 mm; **paralectotypes**, two smaller pairs. Figure *8*.

Semele quentinensis – USNM 333114, **lectotype** herein, right valve, 13.8mm; USNM 64516, **paralectotypes**, 4 valves. The lectotype selected is that figured by Dall (1925). Figure *9*.

Type Localities:

Amphidesma pulchrum – Bahía de Caráquez, Ecuador; H. Cuming.

Semele quentinensis – Bahía San Quíntin [as "San Quentin"], Baja California Norte; late Pleistocene [as "late Pliocene or early Pleistocene"]; C. R. Orcutt.

Nomenclatural Commentary:

Hertlein & Strong (1949) considered *Semele pulchra* and *S. quentinensis* to be two separable species, with overlapping distributions from Nicaragua to Costa Rica. *Semele quentinensis* was said to be more elongate, more evenly rounded dorsally, thinner and more lightly colored.

I have illustrated two lots in addition to the type material demonstrating that some of these points of distinction do not hold. A specimen from San Diego, California (USNM 601034) (Figure *10*) is markedly rounded, more so than the type of *Semele pulchra,* while a specimen from Panama (USNM 73494) (Figure *11*) is almost as elongate as the type specimen of *S. quentinensis*.

A review of material in several collections suggests that there is one continuously occurring species, the differences seemingly being clinal.

Description:

Small (to 31 mm); ovate to ovate-elongate; equivalve; average in thickness; longer anteriorly to equilateral in some specimens; rounded anteriorly; weakly truncate posteriorly; antero-dorsal margin relatively straight, with a beveled lunule; postero-dorsal margin straight to slightly convex, with a beveled escutcheon; sculpture of fine, rounded concentric ribs and radial striae on the anterior end (occasionally with a few radial ribs on posterior end); periostracum not evident; externally with a purplish flush on beaks in Californian specimens, but with more color evident in Panamic material; smooth within, with a purplish or yellowish hue; pallial sinus relatively large. Other details as in Figure 18.

Geographic Distribution and Ecology:

Point Mugu, California (Burch, 1945a); Redondo Beach, California (SU 53220), to Zorritos, Peru (Olsson, 1961), with fairly numerous intermediate records. A lot at the Academy of Natural Sciences of Philadelphia (ANSP 51756) from Monterey, California, may either represent an error in labeling or the result of larval settlement in an especially warm year. It is found intertidally to 46 m. Burch (1945a) records it from 15 cm in sand in bays and also from among rubble along the outer coast.

Material seen:

62 northwest American lots.

Explanation of Figures *6* to *13*

Figure *6*: *Semele incongrua,* lectotype (herein), USNM 663888; 14.5 mm

Figure *7*: *Semele incongrua.* Holotype of *Semele pulchra montereyi,* USNM 162526; 18.7 mm

Figure *8*: *Semele pulchra.* Lectotype (herein) of *Amphidesma pulchrum,* BM(NH) without registry number; about 31 mm

Figure *9*: *Semele pulchra.* Lectotype (herein) of *Semele quentinensis,* USNM 333114; 13.8 mm

Figure *10*: *Semele pulchra,* USNM 601034, Mission Bay, San Diego, California; 24.3 mm

Figure *11*: *Semele pulchra,* USNM 73494, Panama; 26 mm

Figure *12*: *Cumingia californica,* original figure; 31.8 mm

Figure *13*: *Cumingia californica.* Lectotype (herein) of *Cumingia densilineata,* USNM 333115; 30.7 mm

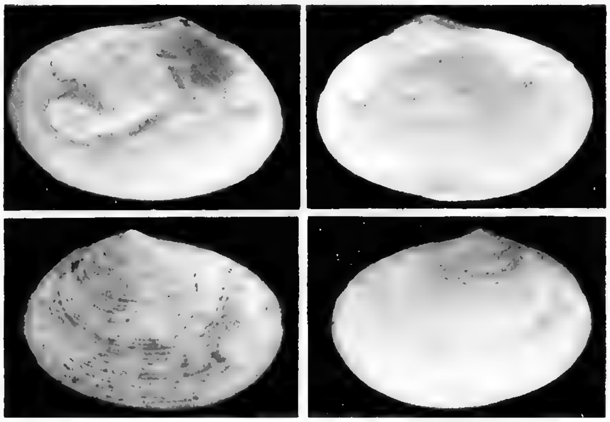


Figure *6*

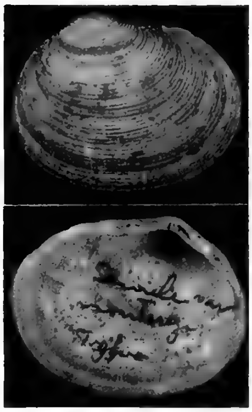


Figure *7*

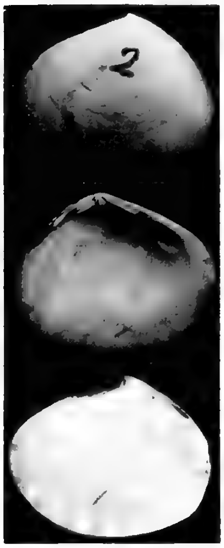


Figure *8*

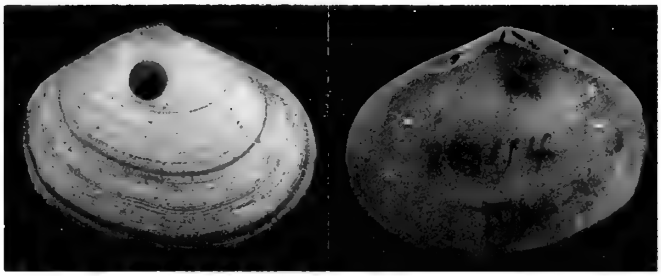


Figure *9*

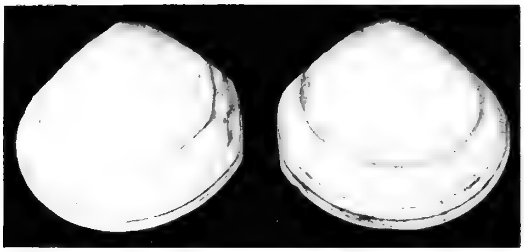


Figure *10*

Figure *11*

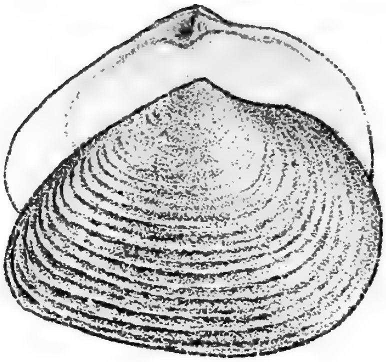


Figure *12*

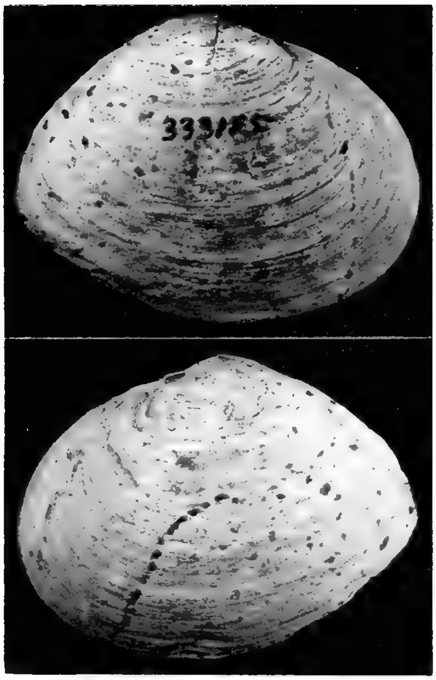


Figure *13*

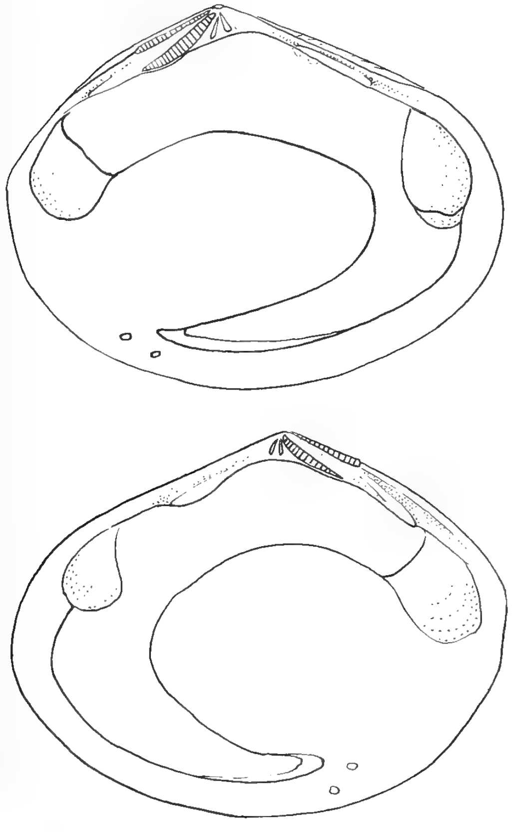


Figure 18

Semele pulchra

internal view of valves, MCZ 210445, San Diego, California; 20 mm

Geologic Distribution and Biogeography:

This species has been reported in the late Pleistocene from Anacapa Island, California (Valentine & Lipps, 1963), to Bahía Magdalena, Baja California Sur (Jordan, 1936), with many intermediate records. It has been recorded in the early Pleistocene only from the San Pedro, California, area (Schenck, 1945; Burch, 1947).

Semele pulchra is closest to other living Panamic species, such as *S. guaymasensis* Pilsbry & Lowe, 1932; *S. pacifica* Dall, 1915; and *S. verrucosa* Mörch, 1860. The differences among them are discussed by Keen (1971).

Cumingia Sowerby, 1833a

[Type species: *Cumingia lamellosa* Sowerby, 1833a; by subsequent designation of Gray, 1847]

Into the genus *Cumingia* are placed species with small to medium-sized shells. They are equilateral to longer anteriorly and are rounded anteriorly and angular posteriorly. Their outline is often irregular due to a nestling habit, and they are smooth or sculptured with concentric lamellae. The shells are white, and the resilium is large and projecting. Two small cardinal teeth and two large lateral teeth occur in each valve; the latter are particularly prominent in the right. The pallial sinus is partly confluent with the pallial line.

Cumingia californica Conrad, 1837

(Figures *12, 13* and 19)

Cumingia californica Conrad

Conrad, 1837: 234; plate 17, figure 12
Carpenter, 1857a: 213
Carpenter, 1857b: 195, 231, 234, 245, 304, 351, 353
Carpenter, 1857c: 30
Carpenter, 1864b: 540, 640 [1872: 26, 126]
Gabb, 1869: 94
Dall, 1900: 1001
Arnold, 1903: 167
Burch, 1945a: 19; 1945b: 17
Hertlein & Strong, 1949: 251
Keen, 1966: 171

Cumingia lamellosa Sowerby, of authors, in part, not of Sowerby

[not of Sowerby, 1833a: 34]
Dall, 1916: 28
I. Oldroyd, 1925: 182
Grant & Gale, 1931: 378, 911, 920; plate 14, figure 23; plate 19, figure 1

Cumingia densilineata Dall

Dall, 1921: 22
Dall, 1925: 15, 36; plate 8, figure 5; plate 11, figure 2
Jordan, 1926: 244, 248 - 249; plate 25, figures 1, 3, 5

Type Material:

Cumingia californica – Lost (Keen, 1966), but Conrad's figure is sufficient to identify the species; 31.8 mm (Conrad, 1837). Figure *12*.

Cumingia densilineata – USNM 333115, **lectotype** herein, pair, figured by Dall (1925: plate 11, figure 2), 30.7 mm; USNM 348044, **paralectotypes**, 3 valves. The location of the specimen figured by Dall on his plate 8, figure 5, is a mystery. Figure *13*.

Type Localities:

Cumingia californica – near Santa Barbara, California; T. Nuttall, in "salt marshes" (probably in error, as the species occurs among rocks on the outer coast).

Cumingia densilineata – Bahía San Quintín, Baja California Norte; late Pleistocene [as "late Pliocene or early Pleistocene"]; C. R. Orcutt.

Nomenclatural Commentary:

For several years workers incorrectly synonymized the Californian species with the Panamic *Cumingia lamellosa.* The differences between these species are discussed below. Dall (1900) synonymized *C. similis* Adams, 1850, with *C. californica.* An examination of the type specimens of the former (BM(NH), without registry number) indicates that it is a synonym of the Panamic *C. lamellosa*; this view was followed by Keen (1971).

Dall described *Cumingia densilineata* as differing from *C. californica* in having more closely-set, regular sculpture and a posterior end with straighter dorsal and ventral margins. Jordan (1926) found his specimens to differ in being thinner and more delicate and illustrated an unusually thin valve (CAS Geology Type collection 1845).

Some live-collected specimens of *Cumingia californica* closely resemble the type material of *C. densilineata.* Indeed, the type lot of the latter contains both thick and thin specimens. I can see no justification at the present time to regard this material as representing a distinct species or subspecies.

A juvenile specimen of *Cumingia californica* (USNM 15579) is responsible for the Californian record of "*Tellina lamellata* Carpenter, 1857c." The type specimen of the latter, described from Mazatlán, Mexico, proved to be a juvenile *Semele* (Keen, 1968, 1971).

Description:

Medium-sized (to 36 mm); ovate-trigonal, but generally conforming to nestling site; equivalve; heavy; approximately equilateral to somewhat longer anteriorly; rounded anteriorly; pointed, narrowly truncate posteriorly; antero-dorsal margin convex with a small concavity forming a weak lunule; postero-dorsal margin straight to slightly convex, conspicuously beveled to form an escutcheon; sculpture of heavy, concentric lamellae, more or less evenly distributed over surface; white outside, with remnants of dark periostracum ventrally; white within with light radial striae within. Other internal details as in Figure 19.

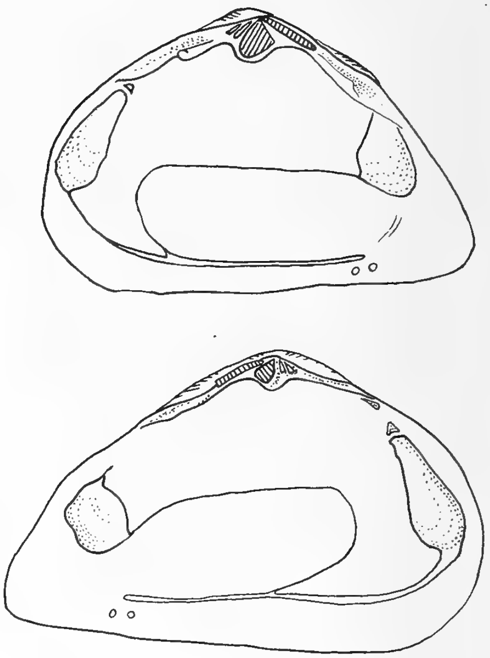


Figure 19

Cumingia californica

internal view of valves, MCZ 176003, Cayucos, California; 31.5 mm

Geographic Distribution and Ecology:

Crescent City, California (USNM 74188); Monterey, California (USNM 74218 and many other lots) to Bahía San Juanico, Baja California Sur (Berry collection 31639). Newcombe's (1893) record from British Columbia is certainly in error, and the one lot from Crescent City is doubtful and needs confirmation. There are many lots and localities between Monterey and Bahía San Juanico. It occurs from the intertidal area to 64 m, nestling among rocks, in crevices, in holes of dead boring clams, and among attached animals on piers. It is also found on gravel bottoms in deeper water (Burch, 1945a; Smith & Gordon, 1948).

Material seen:

118 lots.

Geologic Distribution and Biogeography:

There are several records in the late Pleistocene from Cayucos, California (Valentine, 1958), to Bahía Magdalena, Baja California Sur (Jordan, 1936). It is also known from the early Pleistocene of Santa Barbara (Dibblee, 1966) and the San Pedro area (Arnold, 1903; T. Oldroyd, 1925; Burch, 1947; Valentine & Meade, 1961), California. There are no related West American fossil species.

This species is closest to the common Panamic *Cumingia lamellosa* Sowerby, 1883a, which differs in being smaller, thinner, more irregular in shape, and in having proportionately fewer, more lamellar concentric ribs. It also has a more projecting chondrophore which is conspicuous even in young specimens. Juvenile specimens of *C. californica* are smoother, heavier, more regular in shape, and the chondrophore is hardly projecting at all. The ranges of the two species are not yet known to overlap on the outer coast of Baja California Sur.

OTHER SPECIES

A few other specific names were encountered during this study which have not yet been discussed.

(1) *Semele flavescens* (Gould, 1851) [described in *Amphidesma*] was based on a specimen supposedly from "San Diego, California." This is evidently in error, probably the result of the mixing of Lieutenant T. P. Green's specimens. Green also brought specimens to Gould from several localities on the west coast of Mexico (Johnson, 1964). This species is characteristic of the Panamic province and has not been recorded from north of Bahía Magdalena, Baja California Sur (Burch, 1945a; Hertlein & Strong, 1949; Keen, 1971). Californian specimens at Stanford University (SU 188/2) cited by Grant & Gale (1931) prove to be young *S. decisa*. Hertlein & Strong (1949) mention a Dall record from "Catalina Island, California." I cannot find Dall's published account or USNM specimens that might have formed its basis, although there are USNM specimens of *S. decisa* from Catalina Island, California, as well as an Isla Santa Catalina in the Gulf of California.

(2) *Semele californica* (Reeve, 1853, *ex* A. Adams MS) [described in *Amphidesma*] was reported from San Pedro, California, by Williamson (1892). This species is also Panamic and does not occur north of Bahía Magdalena, Baja California (Keen, 1971).

(3) *Semele pacifica* Dall, 1915, was recorded at the time of its description from "Catalina Island, California." This record was based on a specimen (USNM 73921), which is clearly labeled as having come from Isla Santa Catalina, Gulf of California.

(4) There is a specimen of *Semele guaymasensis* Pilsbry & Lowe, 1932, at Harvard University (MCZ 105544) labeled as having been collected in 46 m off Redondo Beach, California, by Dr. Thomas Burch. This species is not reported by Burch (1945a - 1945c) nor is it present in other collections from the same source. There are no records of it from outside the Gulf of California (Keen, 1971). The label with the specimen, listing it as *"Semele incongrua,"* is therefore probably in error, perhaps the result of mixing in shipment.

(5) *Theora (Endopleura) lubrica* Gould, 1861, described from Japan, has been collected in Anaheim Bay, southern California, by personnel of the California Department of Fish and Game. Insufficient data are available to ascertain whether this species has become firmly established.

(6) It is only a matter of time before deepwater members of the genus *Abra* are found off the northwest American coast (F. Bernard, personal communication). *Abra californica* Knudsen, 1970, was described from off Baja California Sur in about 3500 m, and other species have been recorded in the northern Atlantic (Knudsen, 1970).

ECOLOGY

The ecological information about the species is summarized in the following Table:

Table 1

Species	Depth range meters	Bottom type	Coastal exposure
Semele decisa	0 - 46	sand to rubble	semi-protected
Semele rubropicta	0 - 91	various, mostly coarse	semi-protected
Semele rupicola	0 - 27 (?64)	rock	exposed
Semele incongrua	9 - 192	fine to coarse sand	protected, offshore
Semele pulchra	0 - 46	sand to rubble	generally protected
Cumingia californica	0 - 64	rock and rubble	exposed

As can be seen, most species occur in coarse sediments or nestle among or in rocks. Only one species is characteristic of an offshore environment.

The abundance of species is reflected in their frequency in collections:

Table 2

Species	Number of lots seen
Cumingia californica	118
Semele decisa	109
Semele rubropicta	91
Semele rupicola	87
Semele incongrua	66
Semele pulchra	62

BIOGEOGRAPHY

In my previous paper on the Tellinidae (Coan, 1971), I defined the molluscan provinces mentioned here as follows:

Aleutian – Eastern Aleutian Islands to Cape Flattery, Washington

Oregonian – Cape Flattery, Washington, to Point Conception, California

Californian – Point Conception, California, to Punta Eugenio, Baja California Sur

Panamic – Punta Eugenio, Baja California Sur, to Punta Aguja, northern Peru

The following table demonstrates the predominance of members of the Semelidae in warmer waters, in contrast to the Tellinidae.

Table 3

<table>
<tr><th>Aleutian</th><th>Oregonian</th><th>Californian</th><th>Panamic</th></tr>
<tr><td colspan="3">3. <i>Semele rubropicta</i></td><td></td></tr>
<tr><td></td><td colspan="2">2. <i>Semele incongrua</i></td><td></td></tr>
<tr><td></td><td colspan="3">3. <i>Semele rupicola</i>
3. <i>Cumingia californica</i></td></tr>
<tr><td></td><td></td><td colspan="2">2. <i>Semele decisa</i>
2. <i>Semele pulchra</i></td></tr>
</table>

In this table, the following abbreviations are used:
2. species occurring in 2 provinces
3. species occurring in 3 provinces

Distributions in the late Pleistocene are substantially the same as those in the Recent fauna, and most minor differences can probably be explained by lack of information, but there are two interesting exceptions. *Semele decisa,* like *Leporimetis obesa* in the Tellinidae (Coan, 1971), occurs in the late Pleistocene in Tomales Bay, California, evidently as an isolate that died out since the Pleistocene. On the other hand, *Semele rubropicta* has evidently extended its distribution into Puget Sound since the Pleistocene.

Semele rubropicta evidently has a long fossil history on this coast, with an ancestry probably dating from the Oligocene. *Semele incongrua* may also have a long ancestry, but shows affinities to species in the Panamic province. Both *S. decisa* and *S. rupicola* are closely related to species occurring in the Galápagos Islands, and their arrivals in northwest America date from the Pliocene and the Pleistocene respectively. *Semele pulchra* is mainly a Panamic species, and is related to other species in that province. *Cumingia californica* may be related to Panamic species of *Cumingia,* and it may represent an early Pleistocene isolate.

Literature Cited

[All works cited in the text, including sources of taxonomic units are listed. Volume, bulletin, monograph, memoir, professional paper, and special paper numbers are in bold face; series numbers, in parentheses, precede volume numbers; supplementary information, such as secondary methods of listing volumes, part numbers, and parenthetical statements, are given in brackets. Plates, portraits, text figures, maps, and charts are listed, but not tables. Exact publication dates are given when possible.]

Adams, Arthur
1850. Description of new species of the genus *Cumingia,* with some additonal generic characters. Proc. Zool. Soc. London (for 1850) **20** [prt. 18] (202): 24 - 25; plt. 8 (part) (12 November 1850)
1854. Descriptions of new species of *Semele, Rhizochilus, Plotia,* and *Tiara* in the Cumingian collection. Proc. Zool. Soc. London (for 1853) **23** [prt. 21] (153-154): 94 - 99 (25 July 1854)
Adams, Arthur & Lovell Augustus Reeve
1850 [1848-1850]. Mollusca. *In*: A. Adams, ed., The zoology of the voyage of H. M. S. *Samarang,* under the command of Captain Sir Edward Belcher, . . . during the years 1843-1846. London (Reeve, Benham, Reeve) x+87 pp.; 24 plts. [pp. 1-24 (November 1848); pp. 25-44 (May 1850); pp. 45-87 (August 1850)] [collation: Sherborn, 1922: cxi]
Adams, Charles Baker
1852a. Catalogue of shells collected at Panama, with notes on synonymy, station and habitat, ... Lyc. Nat. Hist. New York, Ann. **5:** 229 - 296 (June); 297 - 549 (July) reprinted:
1852b. Catalogue of shells collected at Panama, with notes on their synonymy, station, and geographical distribution. New York (Craighead) viii+334 pp. [see also Turner, 1956]
Adams, Henry & Arthur Adams
1856 [1853-1858]. The genera of Recent Mollusca; arranged according to their organization. London (van Voorst) **1:** xi+484 pp.; **2:** 66 pp.; **3** (atlas): 138 plts. (collation: **2:** 661)
Addicott, Warren Oliver
1966. Late Pleistocene marine paleoecology and zoogeography in central California . U. S. Geol. Sur. Prof. Paper **523C:** 21 pp.; 4 plts.; 5 text figs.

Anderson, Frank Marion & Bruce Martin

1914. Neocene record in the Temblor Basin, California, and Neocene deposits of the San Juan District, San Luis Obispo County. Proc. Calif. Acad. Sci. (4) **4:** 15 - 112; plts. 1 - 10 (30 December 1914)

Arnold, Ralph

1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Calif. Acad. Sci. Mem. **3:** 420 pp.; 37 plts. (27 June 1903) [dating: Hertlein (1964)]

1907a. New and characteristic species of fossil mollusks from the oil-bearing Tertiary formations of southern California. Proc. U. S. Nat. Mus. **32** (1545): 525 - 546; plts. 38 - 51 (15 June 1907)

1907b. Geology and oil resources of the Summerland district, Santa Barbara County, California. U. S. Geol. Surv. Bull. **321:** vii+93 pp.; 17 plts.; 1 text fig. (September 1907)

1908. Descriptions of new Cretaceous and Tertiary fossils from the Santa Cruz Mountains, California. Proc. U. S. Nat. Mus. **34** (1617): 345 - 390; plts. 31 - 37 (8 August 1908)

Bartsch, Paul, Harald Alfred Rehder & Beulah E. Shields

1946. A bibliography and short biographical sketch of William Healey Dall. Smithson. Misc. Coll. **104** (15): 1 - 96; 1 portr. (30 January 1946)

Boss, Kenneth J., Joseph Rosewater & Florence A. Ruhoff

1968. The zoological taxa of William Healey Dall. U. S. Nat. Mus. Bull. **287:** 427 pp.

Broderip, William John & George Brettingham Sowerby 1st

1832. [Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming]. (one section only) Proc. Zool Soc. London (for **1832**) [prt. 2] (17): 50 - 61 (5 June 1832)

Bruff, Stephen C.

1946. The paleontology of the Pleistocene molluscan fauna of the Newport Bay area, California. Univ. Calif. Publ., Bull. Dept. Geol. Sci. **27** (6): 213 - 240; 12 text figs. (21 August 1946)

Burch, Beatrice LaRue

1947. Comparison of the molluscs of three Pleistocene beds with the Recent fauna of Los Angeles County, California. Min. Conch. Club South. California **73:** 1 - 18 (September 1947)

Burch, John Quincy (ed.)

1945. Superfamily Tellinacea (and Solenidae). *In*: Distributional list of the West American marine mollusks from San Diego, California, to the Polar Sea. Part I: Pelecypoda. Min. Conch. Club South. Calif. [1945a: no. **43:** 3 - 33 (January); 1945b: no. **45:** 3 - 21 (index, corrections and additions) (March); 1945c: no. **46:** 30 (corrections and additions) (March)]

Carpenter, Philip Pearsall

1857a. Monograph of the shells collected by T. Nuttall, Esq., on the Californian coast, in the years 1834-5. Proc. Zool. Soc. London (for **1856**) [prt. 24] (314): 209 - 224; (315): 225 - 229 (26 January 1857)

1857b. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Brit. Assoc. Adv. Sci. Rprt. **26** (for 1856): 159 - 368; plts. 6 - 9 + 4 pp. (pre 22 April) [dating: Carpenter, 1857c: iv]

1857c. Catalogue of the collection of Mazatlan shells, in the British Museum, collected by Frederick Reigen, . . . London (British Museum). iv+ix - xvi+552 pp. (Preface by J. E. Gray) (1 August). Warrington (Oberlin) edition: viii+xii+552 pp., with author's preface, published simultaneously [dating: Carpenter, 1872: xi; Sherborn, 1934] [reprinted by Paleo. Res. Inst. Ithaca, New York, 1967]

1864a. Review of Prof. C. B. Adam's 'Catalogue of the Shells of Panama,' from the type specimens. Proc. Zool. Soc. London (for **1863**) (3): 339 - 369 (April 1864) [reprinted in Carpenter (1872) (B): 173 - 205 (also pp. 1 - 31)]

1864b. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Brit. Assoc. Adv. Sci., Rprt. **33** (for 1863): 517 - 686 (post 1 August) [reprinted in Carpenter, 1872 (A): 1 - 172] [dating: Carpenter, 1872]

1865-1866 [1864-1866]. Descriptions of new marine shells from the coast of California. Parts I - III. Proc. Calif. Acad. Sci. **3:** 155 - 159 (July 1864); 175 - 176 (December 1864); 177 (January 1865); 207 to 208 (post 4 September 1865); 209 - 224 (February 1866)

1872. The mollusks of western North America. Embracing the second report made to the British Association on this subject, with other papers; reprinted by permission, with a general index. Smithson. Inst. Misc. Coll. **10** (252): xii+325 pp. + pp 13 - 121 (December 1872)

Children, John George

1822 [1822-1823]. Lamarck's genera of shells. Quart. Journ. Sci. Lit. Arts (London) **14** (27): 64 - 87; plts. 3, 4 (October 1822); **14** (28): 298 - 322; plts. 5, 6 (January 1823); **15** (29): 23 - 52; plts. 2, 3 (April 1823); **15** (30): 216 - 258; plts. 7, 8 (July 1823); **16** (31): 49 - 79; plt. 5 (October 1823); **16** (32): 241 - 264; plt. 6 (December 1823, as "January 1824") [see also Kennard, Salisbury & Woodward, 1931]

Clark, Alex

1931. The cool-water Timms Point Pleistocene horizon at San Pedro, California. Trans. San Diego Soc. Nat. Hist. **7** (4): 25 - 42; 1 map; 1 chart (19 December 1931)

1957. see under Natland, 1957

Clark, Bruce Lawrence & Ralph Arnold

1923. Fauna of the Sooke Formation, Vancouver Island . . . with a description of a new coral by T. Wayland Vaughan. Univ. Calif. Publ. Bull. Dept. Geol. **14** (5): 123 - 234; plts. 15 - 42 (6 Nov. 1923)

Coan, Eugene Victor

1971. The northwest American Tellinidae. The Veliger **14** (Suppl.): 1 - 63; plts. 1 - 12; 30 text figs. (15 July 1971)

Conrad, Timothy Abbott

1837. Descriptions of new marine shells from Upper California, collected by Thomas Nuttall, Esq. Journ. Acad. Nat. Sci. Philadelphia **7** (2): 227 - 268; plts. 17 - 20 [see also Keen, 1966] (21 November 1837)

Dall, William Healey

[see also Bartsch, Rehder, & Shields, 1964; and Boss, Rosewater, & Ruhoff, 1968]

1871. Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. Amer. Journ. Conch. **7** (2): 93 - 160; plts. 13 - 16 (2 November 1871)

1900. Contributions to the Tertiary fauna of Florida with especial reference to the Silex beds of Tampa and the Pliocene beds of the Caloosahatchie River including in many cases a complete revision of the generic groups treated and their American Tertiary species. Trans. Wagner Free Inst. Sci. **3** (5): [Teleodesmacea: *Solen to Diplodonta*]: i - x+949 - 1218; plts. 36 - 47 (December 1900)

1915. Notes on the Semelidae of the west coast of America, including some new species. Proc. Acad. Nat. Sci. Philadelphia **67:** 25 - 28 (2 March 1915)

1916. Checklist of the Recent bivalve mollusks (Pelecypoda) of the northwest coast of America from the Polar Sea to San Diego, California. Los Angeles (Southwest Mus.) : 44 pp.; 1 port. (28 July 1916)

1921. New shells from the Pliocene and early Pleistocene of San Quentin Bay, Lower California. The West Amer. Scient. **19** (3): 21 - 23 (15 June 1921)

1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. Proc. U. S. Nat. Mus. **66** (2554): 1 - 41; plts. 1 - 36 (22 September 1925)

Deshayes, Gérard Paul

1857. Note sur l'animal des *Cumingia*. Journ. Conchyl. **5** [(2) **1**] (3): 278 - 282; plt. 8 (prt.) (January 1857)

Dibblee, Thomas Wilson, Jr.

1966. Geology of the central Santa Ynez Mountains, Santa Barbara County, California. Bull. Calif. Div. Mines & Geol. **186:** 99 pp.; 4 plts.; 25 text figs.

Dickerson, Roy Ernest

1917. Climate and its influence upon the Oligocene faunas of the Pacific coast, with descriptions of some new species from the *Molophorus lincolnensis* zone. Proc. Calif. Acad. Sci. (4) **7** (6): 157 - 192; plts. 27 - 31 (31 July 1917)

1922. Tertiary and Quaternary history of the Petaluma, Point Reyes and Santa Rosa quadrangles. Proc. Calif. Acad. Sci. (4) **11** (19): 527 - 601; plts. 17 - 41 (10 July 1922)

Gabb, William Moore

1869 [1866-1869]. Paleontology of California **2:** Section 1 [Tertiary invertebrate fossils]. . Geol. Surv. Calif. 124 pp.; 18 plts. [part 1 (Descriptions of new species) pp. 1 - 38; plts. 1 - 13 (1866); part 2 (Descriptions of new species, cont.) pp. 39 - 64; plts. 14 - 18 (probably early 1869); part 3 (Synopsis of the Tertiary invertebrate fossils of California) pp. 65 - 124 (probably early 1869)] [dating: Stewart, 1927]

Gould, Augustus Addison

[concerning his publications and types, see Johnson, 1964]

1851. [Descriptions of a number of California shells collected by Maj. William Rich and Lieut. Thomas P. Green, United States Navy, ...] Proc. Boston Soc. Nat. Hist. **4** (6): 87 - 93 (November 1851)

1861. Descriptions of shells in the North Pacific Exploring Expedition under Captains Ringgold and Rogers. (one section only) Proc. Boston Soc. Nat. Hist. **8** (1): 14 - 32 (March 1861)

Grant, Ulysses Simpson, IV & Hoyt Rodney Gale

1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Nat. Hist. **1:** 1036 pp.; 32 plts.; 15 text figs. (3 November 1931)

Gray, John Edward

1828. Spicilegia zoologica; or, Original figures and short systematic descriptions of new and unfigured animals, prt. 1 London, (Treüttel, Würtz & Co.) & Strand (Wood) pp. 1 - 8; plts. 1 - 6 (July 1828)

1847. A list of the genera of Recent Mollusca, their synonyms and types. Proc. Zool. Soc. London (for **1847**) [prt. 15] (178): 129 - 219 (November 1847)

Gregorio, Antonio de

1884. Studi su talune conchiglie Mediterranee viventi e fossili, con una rivista del gen. *Vulsella.* Bull. Soc. Mal. Ital. **10:** 36 - 288; plts. i - v

Hertlein, Leo George

1964. Note concerning the date of issue of Arnold's monograph on the Pliocene and Pleistocene of San Pedro. The Veliger **6** (3): 172 (1 January 1964)

Hertlein, Leo George & Archibald McClure Strong

1939. Marine Pleistocene mollusks from the Galapagos Islands. Proc. Calif. Acad. Sci. (4) **23** (24): 367 - 380; plt. 32 (20 July '39)

1949. [Families Semelidae and Donacidae]. *In*: Mollusks from the west coast of Mexico and Central America, part 8. Eastern Pacific Expeditions, New York Zool. Soc., prt. 41. Zoologica **34** (4): 239 - 258; plt. 1 (30 December 1949)

Holten, Hans Severin

1802. Enumeratio systematica conchyliorum beat. J. H. Chemnitz ... quae publica auctione venduntur die ... [vi]+88 pp. Havniae (K. H. Scidelini) [concerning this work, see Winckworth, 1943]

Iredale, Tom

1922. Book notes. Proc. Malacol. Soc. London **15** (2/3): 78 - 92 (December 1922)

Johnson, Richard Irwin

1964. The Recent Mollusca of Augustus Addison Gould. U. S. Nat. Mus. Bull. **239:** 182 pp.; 45 plts. (28 July 1964)

Jordan, Eric Knight

1924. Quaternary and Recent molluscan faunas of the west coast of Lower California. Bull. South. Calif. Acad. Sci. **23** (5): 145 - 156 (25 October 1924)

1926. Expedition to Guadalupe Island, Mexico, in 1922, no. 4: Molluscan fauna of the Pleistocene of San Quintin Bay, Lower California. Proc. Calif. Acad. Sci. (4) **15** (7): 241 - 255; plt. 25; 1 text fig. (26 April 1926)

1936. The Pleistocene fauna of Magdalena Bay, Lower California. Contrib. Dept. Geol. Stanford Univ. **1** (4): 103 - 173; plts. 17 - 19 (13 November 1936)

Kanakoff, George Paul & William Keith Emerson

1959. Late Pleistocene invertebrates of the Newport Bay area, California. Contrib. Sci. Los Angeles County Mus., no. **31:** 1 -47; 5 text figs. (14 October 1959)

Keen, A. Myra

1958. Sea shells of tropical West America: marine mollusks from Lower California to Colombia. i - xi+624 pp.; 10 col. plts.; 1700 text figs. Stanford Univ. Press, Stanford, Calif. (5 Dec. 1958)

1966. West American mollusk types at the British Museum (Natural History). I. T. A. Conrad and the Nuttall collection. The Veliger **8** (3): 167 - 172; 1 text fig. (1 January 1966)

1968. West American mollusk types in the British Museum (Natural History). IV. Carpenter's Mazatlan collection. The Veliger **10** (4): 389 - 439; plts. 55 - 59; 171 text figs. (1 April 1968)

1969. [Superfamily Tellinacea]. pp. 613 - 643 *in*: L. R. Cox, *et al.*, eds., Mollusca **6:** Bivalvia *in* R. C. Moore, ed., Treatise on Invertebrate Paleontology, part N: xxxviii + 1224 pp.; illust. Geol. Soc. Amer. & Univ. Kansas.

1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv+1064 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

Kellogg, James L.

1915. Ciliary mechanisms of lamellibranchs. Journ. Morphol. **26** (4): 625 - 701; 72 text figs. (December 1915)

Kennard, Alfred Santer, Albert Edward Salisbury & Bernard Barham Woodward

1931. The types of Lamarck's genera of shells as selected by J. G. Children in 1823. Smithson. Misc. Coll. **82** (17)[3113]: 40 pp. (11 July 1931)

Kirsop, Frances Mullis

1922. Preliminary study of methods of examining the life of the sea bottom. Univ. Wash., Publ. Puget Sound Biol. Sta. **2** (64): 129 - 139; plts. 20 - 23

Knudsen, Jørgen

1970. The systematics and biology of abyssal and hadal Bivalvia. Galathea Rprt. **11:** 241 pp.; 20 plts.; 132 text figs. (6 Nov. 1970)

Lamarck, Jean Baptiste Pierre Antoine de Monet de

1818 [1815-1822]. Histoire naturelle des animaux sans vertèbres ... Paris (Verdière, Deterville, and "chez l'auteur") 7 vols. [**5:** 612 pp. (25 July 1818)] [dating: Iredale, 1922]

Mörch, Otto Andreas Lowson

1860. Beiträge zur Molluskenfauna Central-Amerika's. Malak. Blätter **7:** 66 - 96 (July 1860); 97 - 106 (August 1860)

Natland, Manley Leonard

1957. Paleoecology of West Coast Tertiary sediments. *In*: H. S. Ladd, ed., Treatise on marine ecology and paleoecology 2 [Paleoecology]. Geol. Soc. Amer., Mem. **67** (2): 543 - 571; 5 plts.; 2 text figs. (25 March 1957)

Newcombe, Charles Frederick

1893. Report on the marine shells of British Columbia. Bull. Nat. Hist. Soc. British Columb. (for **1893**): 31 - 72

Nomland, Jorgen O.

1917. The Etchegoin Pliocene of middle California. Univ. Calif. Publ., Bull. Dept. Geol. **10** (14): 191 - 254; plts. 6 - 12; 2 text figs. (19 April 1917)

Oldroyd, Ida Shepard

1924. The marine shells of Puget Sound and vicinity. Univ. Wash., Publ. Puget Sound Biol. Sta. **4:** 272 pp.; 49 plts. (March 1924)

1925. The marine shells of the west coast of North America **1** (Pelecypoda). Stanford Univ. Publ., Univ. Ser. Geol. Sci. **1** (1): 247 pp.; 57 plts. (September 1925) [dating: Keen, 1971, p. 1006]

Oldroyd, Thomas Shaw

1925. The fossils of the Lower San Pedro fauna of Nob Hill cut, San Pedro, California. Proc. U. S. Nat. Mus. **65** (22) [2535]: 1 - 39; plts. 1 - 2 (16 January 1925)

Olsson, Axel Adolf

1961. Mollusks of the tropical eastern Pacific particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). Ithaca, New York (Paleo. Res. Inst.) 574 pp.; 86 plts. (10 March 1961)

Palmer, Katherine Evangeline Hilton Van Winkle

1958. Type specimens of marine Mollusca described by P. P. Carpenter from the West Coast (San Diego to British Columbia). Geol. Soc. Amer., Mem. **76:** viii+376 pp.; 35 plts. (8 December 1958)

Pilsbry, Henry Augustus & Herbert Nelson Lowe

1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929-31. Proc. Acad. Nat. Sci. Philadelphia **84:** 33 - 144; plts. 1 - 17; 7 text figs.; 2 photogr. (21 May 1932)

Pulteney, Richard

1799. Catalogues of the birds, shells, and some of the more rare plants of Dorsetshire. From the new ... edition of Hutchins's History of that country. London, 92 pp.; 1 port. (pre 2 July 1799)

Quayle, Daniel Branch

1960. The intertidal bivalves of British Columbia. Brit. Columb. Provinc. Mus. Handb. no. **17:** 104 pp.; illust. (July 1960)

Reeve, Lovell Augustus

1853. Monograph of the genus *Amphidesma. In*: Conchologica Iconica; or, Illustrations of the shells of molluscous animals **8:** 7 plts.; 1 p. index [plts. 1 - 4 (October 1853); plts. 5 - 7 & index (November 1853)]

Reynell, Alexander

1910. Further notes on the dates of issue of the parts of Sowerby's *Conchological Illustrations.* Proc. Malacol. Soc. London **9** (3): 212 - 213 (26 September 1910)

Schenck, Hubert Gregory

1945. Geologic application of biometrical analysis of molluscan assemblages. Journ. Paleo. **19** (5): 504 - 521; plts. 66 - 67; 3 text figs. (4 October 1945)

Schröder, Otto

1916. Beiträge zur Anatomie von *Amphidesma.* Jenaische Zeitschr. f. Naturw. **54** (1): 101 - 132; 13 text figs. (21 July 1916)

Schumacher, Chrétien Fréderic

1817. Essai d'un nouveau système des habitations des vers testacés. Copenhagen (Schultz) [iv]+287 pp.; 22 plts. (post 1 March 1817)

Shaw, Henry Otho Nicholson

1909. On the dates of issue of Sowerby's "Conchological Illustrations," from the copy preserved in the Radcliffe Library, Oxford. Proc. Malacol. Soc. London **8** (6): 333 - 340 (5 October 1909)

Sherborn, Charles Davies

1909. On "The Conchological Illustrations," by George Brettingham Sowerby, Jun., London, 1832-41, and the "Descriptive Catalogue of Shells," by John Edward Gray, 1832. Proc. Malacol. Soc. London **8** (6): 331 - 332 (5 October 1909)

1922 [1902-1933]. Index animalium ... Section **1:** lix+1195 pp.; Section **2:** cxxxvi+7056+cxlvii+1098

1934. Dates of publication of catalogues of natural history (post 1850) issued by the British Museum. Ann. Mag. Nat. Hist. (10) **13** (74): 308 - 312 (February 1934)

Smith, Allyn Goodwin & Mackenzie Gordon, Jr.

1948. The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. Proc. Calif. Acad. Sci. (4) **26** (8): 147 - 245; plts. 3 - 4; 4 text figs. (15 December 1948)

Sowerby, George Brettingham (1st of name)

1833a. [Characters of new species of Mollusca and Conchifera, collected by Hugh Cuming]. (one part only) Proc. Zool. Soc. London (for 1833) **3** [prt. 1] (1 - 3): 34- 38 (17 May 1833)

Sowerby, George Brettingham (2nd of name)

1833b. [1832-1841]. The conchological illustrations; or, Coloured figures of all the hitherto unfigured Recent shells, ... London, (Sowerby) [200 plates in 200 parts, each with its own text, paginated separately and usually also reissued in 1841] [parts 17 - 19 (*Amphidesma*): 10 figs.; pp. 1 - 2 (7 - 8 in 1841): pre 8 March 1833] [concerning this work see Sherborn, 1909, Shaw, 1909, and Reynell, 1910]

Stasek, Charles Robert

1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. The Veliger **6** (2): 91 - 97; 5 text figs. (1 October 1963)

Stewart, Ralph Bentley

1927. Gabb's California fossil type gastropods. Proc. Acad. Nat. Sci. Philadelphia **78**: 287 - 447; plts. 20 - 32 (3 January 1927)

Stoliczka, Ferdinand

1870 [1870-1871]. Cretaceous fauna of southern India. 3. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. ... Mem. Geol. Surv. India, Paleontologica Indica (6). xxii+538 pp.; 50+4 plts. [pp. 1 - 222; plts. 1 - 12 (1 September 1870); pp. 223 - 408; plts. 13 - 28 (1 March 1871); pp. 409 - 537+i - xxii; plts. 29 - 50 (1 August 1871)]

Stoll, Norman Rudolph, *et al.*

1964. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. London (Intl. Trust Zool. Nomencl.) xx+176 pp.

Turner, Ruth Dixon

1956. The eastern Pacific marine mollusks described by C. B. Adams. Harvard Univ., Mus. Comp. Zool. Occ. Papers on Mollusks **2** (20): 21 - 135; plts. 5 - 21 (22 September 1956)

Valentine, James William

1957. Late Pleistocene faunas from the northwestern coast of Baja California, Mexico. Trans. San Diego Soc. Nat. Hist. **12** (16): 289 - 308; 6 text figs. (25 September 1957)

1958. Late Pleistocene megafauna of Cayucos, California, and its zoogeographic significance. Journ. Paleo. **32** (4): 687 - 696; 2 text figs. (22 July 1958)

Valentine, James William & Jere Henry Lipps

1963. Late Cenozoic rocky-shore assemblages from Anacapa Island, California. Journ. Paleo. **37** (6): 1292 - 1302; 3 text figs. (14 December 1963)

Valentine, James William & Robert F. Meade

1961. Californian Pleistocene paleotemperatures. Univ. Calif. Publ., Bull. Dept. Geol. **40** (1): 1 - 46; 4 text figs. (14 July 1961)

Weaver, Charles Edwin

1912. A preliminary report on the Tertiary paleontology of western Washington. Bull. Wash. Geol. Surv. **15**: 80+iii pp.; 15 plts.

1949. Geology of the coast ranges immediately north of the San Francisco Bay region, California. Geol. Soc. Amer. Mem. **35**: ix+242 pp.; 14 plts. 2 text figs. (20 October 1949)

White, Kathleen M.

1942. The pericardial cavity and the pericardial gland of the Lamellibranchia. Proc. Malacol. Soc. London **25** (2): 37 - 88; 41 text figs. (28 August 1942)

Williamson, Mattie Burton

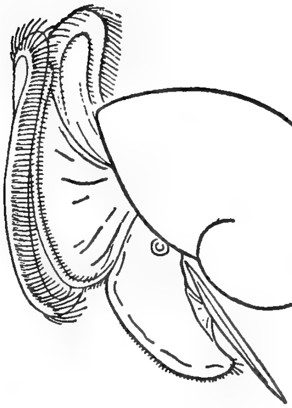
1892. An annotated list of the shells of San Pedro Bay and vicinity. (With a description of two new species by W. H. Dall.) Proc. U. S. Nat. Mus. **15** (898): 179 - 220; plts. 19 - 23 (2 August 1892)

Winckworth, Ronald

1943. Holten's systematic list of the shells of Chemnitz. Proc. Malacol. Soc. London **25** (4): 146 - 150; plt. 5 (10 September 1943)

Yonge, Charles Maurice

1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. Philos. Trans. Roy. Soc. London (B) **234** (609): 29 - 76; 29 text figs. (5 September 1949)



Mantle Changes in the Pearl Oyster *Pinctada maxima* Induced by the Pea Crab *Pinnotheres villosulus*

BY

TREVOR G. DIX

School of Biological Sciences, James Cook University of North Queensland, Townsville, Australia [1,2]

(1 Plate)

CHENG (1967) REVIEWED the numerous studies of the general biology and relationships of pinnotherid crabs associated with bivalve molluscs. Damage to or erosion of the bivalve's gills has been observed repeatedly and PEARCE (1966) revealed that "... constant irritation by the crab dactyls caused a blister or cyst-like formation ..." on the mantle of *Modiolus modiolus* (Linnaeus, 1758), a condition McDERMOTT (1962) had reported for *Anomia simplex* Orbigny, 1845, infested by *Pinnotheres,* and STAUBER (1945) for a few specimens of *Ostrea* (= *Crassostrea*) *virginica* Gmelin, 1791 infested by *P. ostreum* (Say, 1817).

These observations apparently have not been extended by microscopical studies. Current interest in invertebrate pathology and in the etiology of invertebrate tumors (PAULEY, 1969) prompted an investigation of the histology of mantle swelling induced by pinnotherid crabs. Adult *Pinnotheres villosulus* Guerin, 1830, induce pronounced mantle swelling in the pearl oyster *Pinctada maxima* (Jameson, 1901) and provided material for the present study.

METHODS AND MATERIALS

General observations and notes on the incidence of pea crabs and induced mantle thickenings were made in conjunction with other studies on 126 *Pinctada maxima* collected in the Torres Straits, North Queensland, between December 1969 and November 1970. Further material for histological work was collected in 1971.

Most histological specimens were fixed at the collection site while some in 1971 were airfreighted to Townsville and maintained in the sea there until fixation. Excised thickened pallial mantle from 15 pearl oysters was fixed in Davidson's fluid (SHAW & BATTLE, 1957) or formol calcium (PEARSE, 1960). Fixed tissues were routinely dehydrated, Paraplast embedded, sectioned at 6 - 8 µm and stained using (1) Ehrlich's haematoxylin and eosin; (2) the connective tissue techniques of Masson's trichrome for collagen and muscle, Gomori's aldehyde fuchsin for elastin, Gordon and Sweet's method for reticulin (DRURY & WALLINGTON, 1967) and Mallory's PTAH method for muscle (LUNA, 1960); (3) the mucosubstance techniques, PAS and alcian blue/chlorotine fast red (PEARSE, 1960).

A previous study of mantle histology (DIX, in press) furnished normal material for comparison.

RESULTS

General Observations: In each parasitised pearl oyster a pinnotherid crab was always found clinging firmly to one mantle lobe and facing inwards in the anterior part of the mantle cavity near the foot, gills and palps of the bivalve (Figure *1*). No more than one crab was found in a pearl oyster and most of the crabs were female. Associated with the crab was a conspicuous firm lump of thickened mantle; this was up to 1 cm thick and was always found on the mantle ventral to the crab. The lump was slightly concave to partially accommodate the crab and the mantle immediately beneath the crab was wrinkled rather than the normal smooth (Figure *2*). Gill or palp erosion was not evident in any of the pearl oysters with crabs.

Pea crabs with associated mantle lumps were common in the pearl oysters as 67½% of the 126 bivalves examined had one pinnotherid or mantle lump or both. Mantle lumps without were found in 7.1%, indicating that the association may not be permanent. However, crabs without associated mantle lumps were never observed although presumably this must occur early in the association; it is noted that no juvenile pearl oysters were examined.

---

[1] Supported by the Cape York Pearling Company postdoctoral research fellowship in marine biology.

[2] Present address: Sea Fisheries Division, Department of Agriculture. P. O. Box 192B, Hobart 7001, Australia.

Figure *1*

Figure *2*

Figure *3*

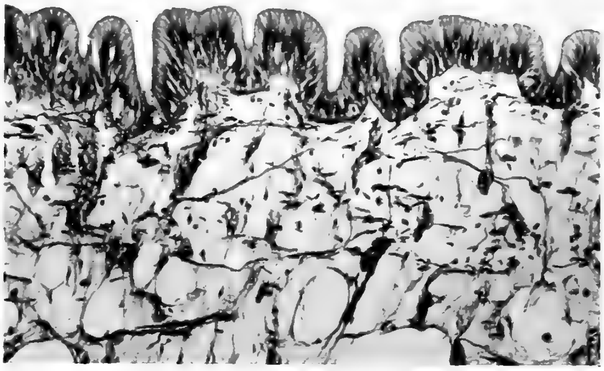


Figure *4*

Figure *1*: *Pinnotheres villosulus* in the mantle cavity of *Pinctada maxima*. The crab (c) was always found in this region, near the foot (f), palps (p), and gills (g). The pronounced lump (mt) is evident adjacent to the crab. Note the absence of gill erosion and the normal marginal mantle (m). Scale line = 0.5 cm

Figure *2*: Mantle with crab removed showing thickening (mt) and the wrinkled mantle where the crab was situated. Scale line = 1.0 cm

Figure *3*: Stroma of the mantle thickening showing numerous irregularly arranged muscle fibers (mf) in a collagenous matrix (co) next to a muscle band (mb). Masson's trichrome; ×200

Figure *4*: Inner pallial mantle epithelium from beneath a pinnotherid crab. Note the tall columns of epithelial cells and numerous subepithelial secretory cells (ss). Haematoxylin and eosin; ×280

Microscopical Observations: Normal structure was evident in the marginal mantle and in the outer (shell) epithelium and associated secretory cells of the pallial mantle near the crabs. However, considerable changes were found in the stroma and in the inner epithelium.

In the normal mantle, strong bands of longitudinal muscles extend into the pallial mantle from the inner and outer marginal mantle folds; a strong central core of transverse fibers is found also. Together, these muscle bands normally occupy most of the pallial mantle stroma, the rest being collagenous connective tissue with sparsely scattered muscle fibers.

Displacement and replacement of these muscle bands was marked in the pinnotherid-thickened mantle. A single longitudinal band near the outer edge of the stroma constituted most of the aggregated fibers. The rest of the thickening consisted of very numerous, irregularly orientated single muscle fibers in a collagenous connective tissue matrix (Figure *3*). The fibers, some of which branched from fibroblast-like cells, were readily distinguishable by Masson's trichrome and Mallory's PTAH staining. Aldehyde fuchsin staining failed to show elastic fibers although mammalian lung controls gave positive results. Reticulin fibers also were not demonstrated although this test was positive in similarly fixed pearl oyster ovary.

Blood spaces were scattered irregularly through the stroma of the thickened mantle but hemocyte infiltration of connective tissue was little if any greater than normal.

The inner epithelium of the pallial mantle normally consists of a single layer of ciliated, pigmented cells about 10 - 12 μm high. Both granular acidophilic and basophilic mucous secretory cells occur but they are scattered between the epithelial cells and do not occur subepithelially.

While the inner epithelium in close contact with the pinnotherid crab was ciliated and pigmented, the single layer of cells formed more uniform columns higher than normal (19 - 26 μm) (Figure *4*). Epithelial secretory cells were absent but abundant subepithelial mucous cells opened through the epithelium. These stained with Ehrlich's haematoxylin and alcian blue and were PAS-positive.

DISCUSSION

Mantle lumps showed remarkably little variation in shape and location and were always found in pearl oysters with pea crabs. There is no cause to doubt a direct causal relationship between the crab and associated mantle modifications although examination of juvenile pearl oysters and specimens with experimentally introduced pea crabs might disclose aspects of the development of the lumps on the mantle.

The pinnotherid has very sharp dactyls which firmly grip the mantle and probably cause irritation. Formation of the non-inflammatory, fibrous thickening, abundant mucous cells and a modified inner mantle epithelium are clear responses to the crab's presence. These modifications may ensure that the pearl oyster is able to continue at least some of its normal mantle processes as no abnormalities of the shell or the shell-secreting outer mantle epithelium were seen in the region of the crab.

In superficial appearance and histology of the stroma, the mantle lumps show some similarity to certain molluscan neoplasms reviewed by Pauley (1969). By indicating one way in which a fibrous tumor-like swelling can arise in a mollusc, the present study may help interpret some true neoplasms and also add to the general pathological responses of molluscs.

ACKNOWLEDGMENTS

I wish to thank Mr. A. Summers for help with the histology, Dr. C. G. Alexander for criticism, and Messrs. H. Lamont and R. Yeldwyn for photographic assistance. Dr. J. Lucas helped with identification of the pinnotherid crab.

Literature Cited

Cheng, Thomas Clemant
1967. Marine molluscs as hosts for symbioses. Adv. Mar. Biol. **5**: 1 - 424

Dix, Trevor George
(in press) Histology of the mantle and pearl sac of the pearl oyster *Pinctada maxima* (Lamellibranchia). Journ. Malacol. Soc. Aust.

Drury, Roger Anderson Brownsward & E. A. Wallington
1967. Carleton's histological technique, 4th ed.; Oxford Univ. Press: 432 pp.

Luna, Lee G.
1960. Manual of histologic staining methods of the Armed Forces Institute of Pathology, 3rd ed.; McGraw-Hill, New York, 258 pp.

McDermott, John Joseph
1962. The incidence and host-parasite relations of pinnotherid crabs (Decapoda, Pinnotheridae). Proc. 1st Natl. Coastal Shallow Water Res. Conf. October 1961: 162 - 164 (February 1962)

Pauley, Gilbert B.
1969. A critical review of neoplasia and other tumor-like lesions in molluscs. Nation. Cancer Inst. Monogr. **31**: 509 - 539

Pearce, Jack B.
1966. The biology of the mussel crab, *Fabia subquadrata*, from the waters of the San Juan Archipelago, Washington. Pacif. Sci. **20** (1): 3 - 35 (January 1966)

Pearse, Anthony Guy Everson
1960. Histochemistry. Theoretical and applied. 2nd ed. Churchill, London: 998 pp.

Shaw, Barbara L. & Helen I. Battle
1957. The gross and microscopic anatomy of the digestive tract of the oyster, *Crassostrea virginica* (Gmelin). Canad. Journ. Zool. **35**: 325 - 347

Stauber, Leslie Alfred
1945. *Pinnotheres ostreum*, parasitic on the American oyster, *Ostrea* (*Gryphaea*) *virginica*. Biol. Bull. Mar. Biol. Lab., Woods Hole, **88**: 269 - 291

A Recent *Oreohelix*

(Gastropoda : Pulmonata)

from Baja California Sur, Mexico

BY

WALTER B. MILLER

Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721

(1 Plate; 1 Text figure)

In December 1970, the author made a general field survey of land snail distribution in Baja California, Mexico, from Tijuana to Cabo San Lucas. The expected helminthoglyptids were found in the north and central regions and the urocoptids and bulimulids in the central and southern regions. Quite unexpected, however, and heretofore unreported, were two flat, helicoid species from the region of San Bartolo, south of La Paz. One was *Oreohelix*-like, while the other resembled *Hendersoniella* but without its twisted aperture. As no live animals of either could be found at that time, they remained unidentifiable.

During a subsequent trip, in October 1971, the *Oreohelix*-like snail was again found, this time at San Javier, west of Loreto, well to the north of San Bartolo and La Paz. Many live specimens were collected and subsequent dissection revealed that it was indeed a new species of *Oreohelix* of the subgenus *Radiocentrum*; it is described below. The *Hendersoniella*-like species was not found at San Javier and its elucidation must await the procurement of live animals from San Bartolo.

Oreohelix (Radiocentrum) ***exorbitans*** W. B. Miller, spec. nov.

(Figures *1* to *3* and 4)

Description of Holotype: Shell very depressed, discoidal, acutely carinate, widely umbilicate, the umbilicus contained about 3 times in the diameter; thin, with a dark-brown periostracum and no trace of color bands. Embryonic shell of $1\frac{3}{4}$ whorls, with a median, raised, spiral ridge, sculptured with strong, retractive, radial ribs upon which are superimposed several fine spiral threads. Post-embryonic whorls also with the median, raised, spiral ridge on the upper surface, as well as the dense radial rib striae; spiral threads becoming more prominent on both the upper and lower surfaces. Body whorl with a prominent, hollow, gutter-like, peripheral carina; the upper surface with a continuation of the median, raised, spiral ridge as well as a secondary ridge nearer to the suture; lower surface with 3 angular, spiral ridges; both surfaces also have dense rib striae and faint, raised spiral threads. The last part of the body whorl descends slightly in front. Aperture polygonal; peristome thin, not expanded, the margins nearly straight between the angles formed by the spiral ridges and the gutter-like, peripheral carina; upper and basal margins converge and are joined by a thin, adnate, parietal callus. Thin, triangular, periostracal processes, matted with a thick coat of dirt, project at right angles from the shell above the radial ribs, giving it an extensive fringe along the periphery and the spiral ridges.

Shell Measurements: The holotype has a diameter of 11.5 mm, a height of 3.9 mm, and an umbilicus of 4.1 mm; it has $4\frac{1}{2}$ whorls.

Animal and Genitalia: The animal has a dark-gray body wall and a light-gray mantle collar. The radula has 22·1·22 teeth, the central unicuspid, the laterals with a small ectocone, and the marginals bicuspid; the transition from laterals to marginals is gradual and indistinct. The jaw is arcuate, orange-colored, without plaits or ribs, its surface vertically, finely striate (aulacognathous). The genitalia (Figure 4) are typical for the subgenus *Radiocentrum.* There is a club-shaped penis with a particularly distinct, short, pointed, tubular appendix near the insertion of the epiphallus. There is also a well-developed albumin gland, typical of this oviparous subgenus, and a curved, saccular

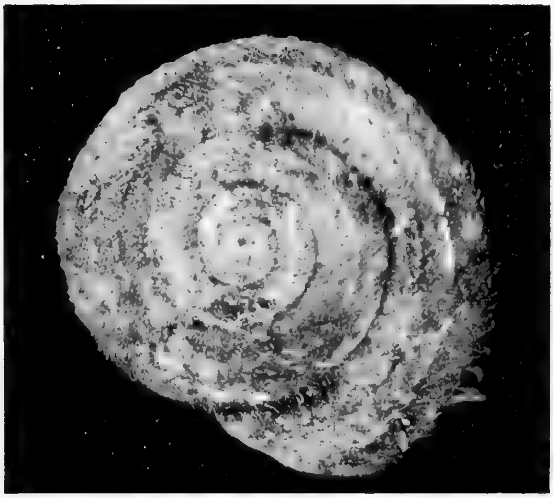


Figure *1*

Figure *2*

1 cm

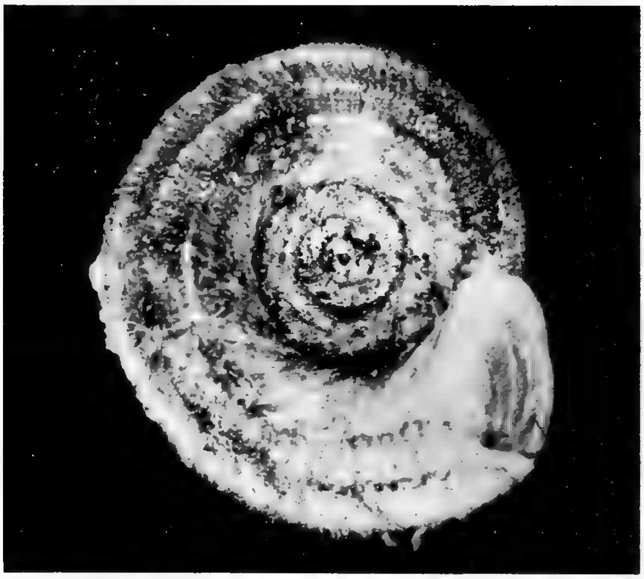


Figure *3*

Oreohelix (Radiocentrum) ***exorbitans*** W. B. Miller, spec. nov.
Holotype, California Academy of Sciences, Geology Type Collection
No. 53267. San Javier, Baja California Sur, Mexico
Scale in millimeters

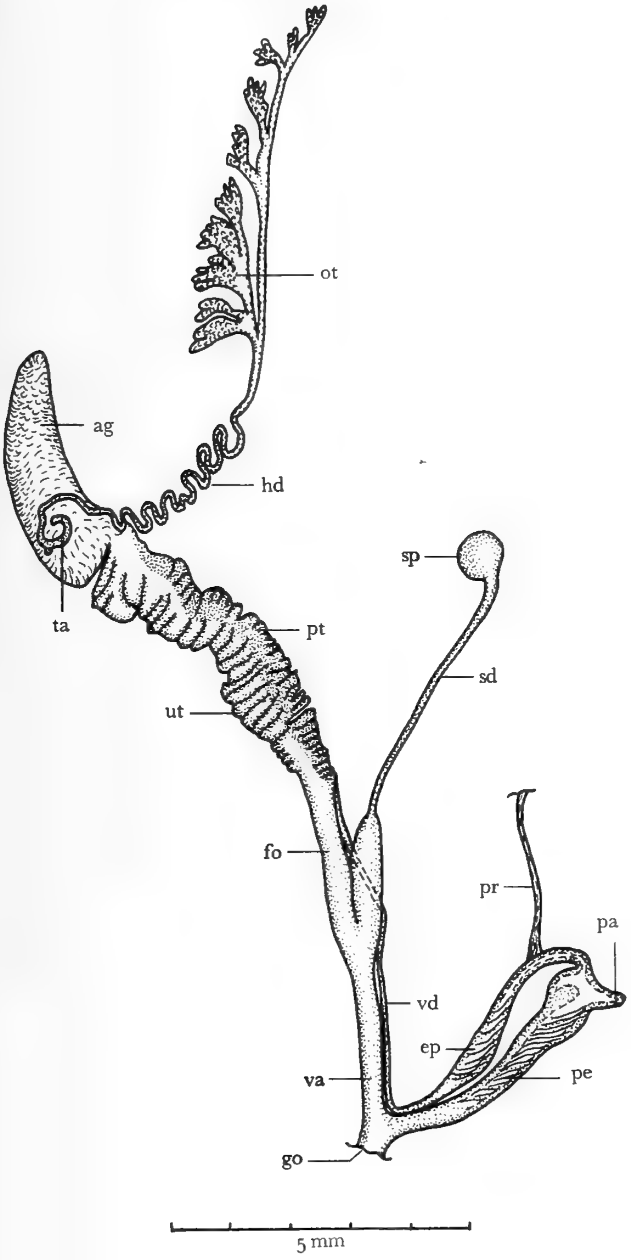


Figure 4

Oreohelix (Radiocentrum) ***exorbitans*** W. B. Miller, spec. nov. Genitalia of holotype; drawing made from projection of stained whole mount. Scale in millimeters

ag – albumin gland ep – epiphallus fo – free oviduct
go – genital orifice hd – hermaphroditic duct
ot – ovotestes pa – penial appendix pe – penis
pr – penial retractor pt – prostate sd – spermathecal duct
sp – spermatheca ta – talon ut – uterus va – vagina
vd – vas deferens

talon. The lower fourth of the spermathecal duct is swollen approximately 3 times the diameter of the upper duct.

Type Locality: Sierra de la Giganta, Baja California Sur, Mexico, at Mission San Javier, in lava rock slides immediately south of the mission; elevation from 400 to 450 m. San Javier is approximately 37 km, by road, southwest of Loreto, at 25°47′ N Lat. and 111°31′ W Long., the southwesternmost known locality for the genus.

Disposition of Specimens: Holotype deposited in the California Academy of Sciences, Geology Type Collection No. 53267. Paratypes in the Invertebrate Museum, Department of Biological Sciences, University of Arizona; Academy of Natural Sciences of Philadelphia; U. S. National Museum; Delaware Museum of Natural History; Florida State Museum at the University of Florida; and the collections of Wendell O. Gregg, Munroe L. Walton, Artie L. Metcalf, and the author.

Remarks: Approximately 200 paratypes were collected, of which about 35 were alive. The largest shell measures 12.9 mm in diameter with an umbilicus of 4.6 mm. Seven of the paratypes are larger than 12.0 mm in diameter. Small mature shells cannot be distinguished from immature shells since the last part of the body whorl does not always descend in front; hence the diameter of the smallest mature paratype could not be determined. The spire varies from completely flat or slightly sunken to slightly elevated. A few large shells tend to be scalariform.

The radulae showed variability in shape as well as numbers of teeth. In one specimen, the central tooth was distinctly tricuspid and the outer marginals had bifid ectocones; numbers of teeth varied from 23·1·23 to 20·1·20.

The most distinguishing characteristics of this species are the very flat spire and the very wide umbilicus. It most closely resembles *Oreohelix (Radiocentrum) ferrissi* Pilsbry, 1915, from the Big Hatchet Mountains of New Mexico; it differs from that species in having a much wider umbilicus which is contained about 2.8 times in the diameter while *O. ferrissi* has an umbilicus which is contained about 4 times in the diameter.

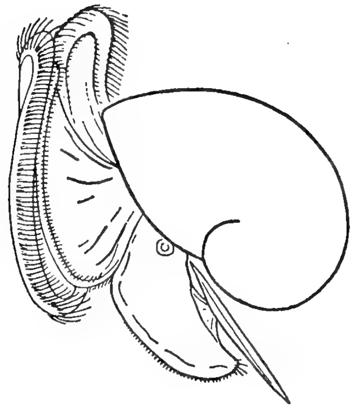
The finding of a Recent population of *Oreohelix* in Baja California Sur represents an enormous range extension for the genus. It is apparently a disjunct isolate. The nearest reported populations of *Oreohelix*, to the author's knowledge, are *O. (Radiocentrum) labrenana* Pilsbry, 1948, and *O. (R.) caenosa* Pilsbry, 1948, in the Sierra Madre Occidental of Chihuahua near Colonia Juarez, about 580 km northeast of San Javier, and *O. (R.) almoloya* Drake, 1949, from southwestern Chihuahua near Jimenez, about 630 km from San Javier.

An interesting development of finding *Radiocentrum* in Baja California is the renewed interest in rediscovering

Oreohelix (Radiocentrum) avalonensis Pilsbry, 1905, on Santa Catalina Island, California, where Hemphill originally collected it and where it has not been found again by later collectors, including Pilsbry and the author. The molluscan fauna of Santa Catalina Island is more closely related to that of Baja California than to that of the adjacent mainland, and *O. avalonensis* can now be added more credibly to the list of relicts from a probable earlier Mexican origin.

ACKNOWLEDGMENTS

I wish to thank Dr. W. O. Gregg for the loan of paratypes of *Oreohelix ferrissi* and *O. almoloya*; Dr. J. C. Bequaert for the critical review of this manuscript; and my laboratory assistant, Margaret Magerle, for the photographs of the holotype.



Notes on *Cypraea cinerea* Gmelin and *Cyphoma gibbosum* (Linnaeus) from the Caribbean Sea and Description of their Spawn

BY

KLAUS BANDEL

Institute of Paleontology of the University Bonn, Germany

(2 Text figures)

INTRODUCTION

In shallow water areas with abundant coral-growth in the region of Santa Marta, Colombia and of Curaçao, Netherlands Antilles, *Cypraea cinerea* Gmelin, 1791 is the most common species of the genus *Cypraea.* Usually the brownish mauve to light orange-brown shell is hidden under a blackish-gray to dark brown mantle with gray specks and many smooth, small tubercules. In more or less the same habitat sea-fans are to be found and living on them are usually 2 or 3 *Cyphoma gibbosum* (Linnaeus, 1758). The rich cream-orange to pure-white shell usually is covered almost completely with the translucent, opaque mantle with dark orange spots surrounded by a brown rim. Both species are cypraeans, one belonging to the family Cypraeidae, the other to the family Ovulidae.

Descriptions of cypraeacean spawn are found in Vayssière (1923), Lebour (1932), Ostergaard (1950), Natarajan (1958), Theodor (1967), and D'Asaro (1969).

METHODS

Egg masses were collected by the author while working in the Instituto Colombo Aleman (ICAL) in Santa Marta, Colombia from fall 1970 to spring 1972 and while visiting the Caraibisch Marien-Biologisch Instituut (Carmabi) in Curaçao, Netherlands Antilles in July 1971.

Adult specimens were kept in aquaria with sea-water running 12 hours a day in the laboratory of the ICAL in Santa Marta for over a year. Egg masses were kept in dishes until hatching of the young. Water was exchanged in these dishes daily or every other day and temperature of the water was that of the airconditioned laboratory (air between 25° and 27° C). Egg capsules and masses were measured and drawn from freshly laid living material in the laboratory, afterwards fixed in 70% alcohol.

Cypraea cinerea Gmelin, 1791

(Figure 1)

In aquaria *Cypraea cinerea* were fed with tunicate and sponge crusts on rocks and oysters which were collected in the sea below the institute. The animals grew and lived a long time but did not spawn.

In the sea spawn was found in June 1971 in 60 cm depth on the underside of a flat stone in the little bay of Taganilla, a part of the bay of Santa Marta and in July 1971 on the underside of a dead *Acropora palmata* near the Carmabi Institute in Curaçao in about 1 m water depth.

On both egg masses a breeding female was sitting, covering her spawn with her foot.

The egg mass is a rounded oval cluster of club-shaped capsules, tightly glued to each other. One cluster had the dimensions of 2 cm length, 1.5 cm width and 0.5 cm height. The cluster is composed of 4 layers of capsules. Each egg mass contains about 400 individual capsules.

The oothecae are somewhat variable in shape. The walls are translucent, colorless and smooth. Each capsule contains about 200 - 300 white embryos, which swim in an opaque, albuminous liquid. The foot of the capsule has a round sole, which in the lowest layer of the egg mass is glued to the substrate (surface of rock or coral). Inside of the egg mass an ootheca is glued to the top of a capsule of the layer below, mainly onto the escape aperture. The escape aperture is on the upper end of the ootheca, mostly in an extended lobe. The oothecae are 2 to $2\frac{1}{2}$ mm high, about 1 mm wide and a little under 1 mm thick.

All embryos undergo development and hatch as long-term planktotrophic veligers.

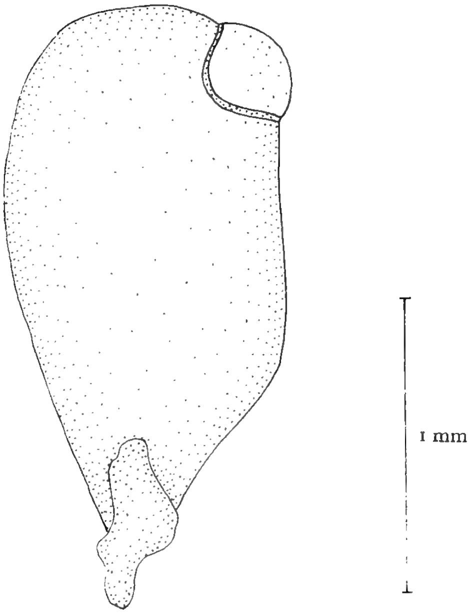


Figure 1

Ootheca of *Cypraea cinerea* Gmelin, 1791. Lateral View.

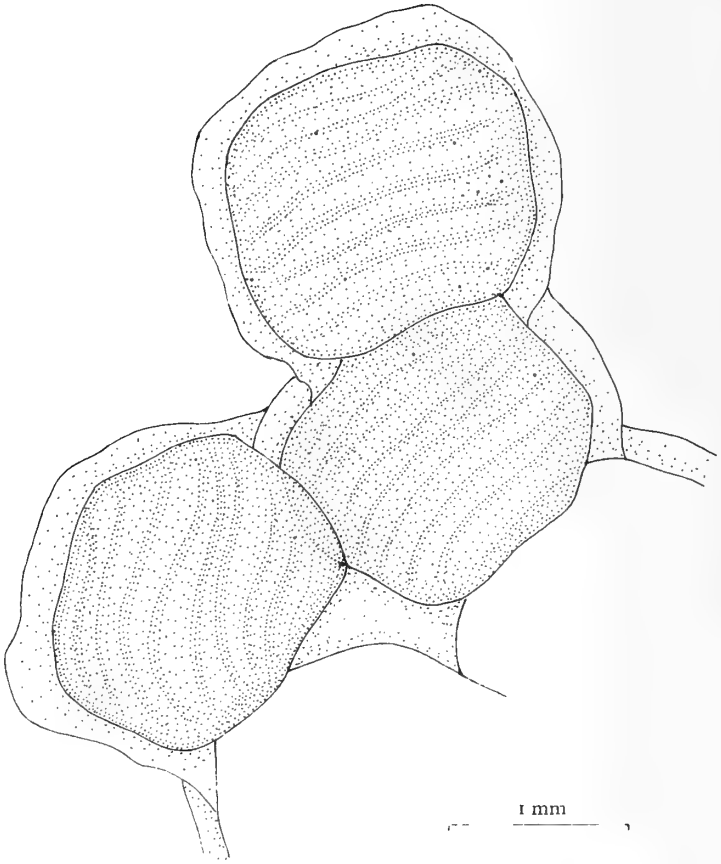


Figure 2

Ootheca of *Cyphoma gibbosum* (Linnaeus, 1758) with the rim membranes which provide attachment to the substrate and the convex upper walls. Inside of the freshly deposited capsules the embryos are concentrated in curved rows, discernible through the transparent walls.

Cyphoma gibbosum (Linnaeus, 1758)

(Figure 2)

On rocky bottom in clear waters of the bays near Santa Marta sea-fans (gorgonians) are common and on them *Cyphoma gibbosum.* On most of the larger fans in areas, where little collecting of shells for souvenirs is done by local fishermen, 1 - 4 animals can be found, mostly more than one per fan. Specimens collected below the ICAL in Santa Marta were kept in aquaria and fed weekly with living sea-fans. *Cyphoma gibbosum* eats the flesh of these Anthozoa and due to this chews off all purple parts of the sea-fan branches, leaving only the internal black skeleton.

Cyphoma gibbosum scattered in all parts of the aquarium will find freshly introduced sea-fans within a very short time and start feeding on them. They even reach sea-fans through free water, letting themselves down from some projection on their own mucus secreted by the foot.

Fresh spawn can be found throughout the year on sea-fans in the habitat of *Cyphoma gibbosum.* The transparent rows are very difficult to detect on free-living gorgonians.

Well fed *Cyphoma gibbosum* specimens in the aquaria spawn from time to time. Usually the first spawning animal induces spawning in all other females in one aquarium, and one or more communal egg masses are produced. Copulation takes place up to 4 days before spawning and is continued while spawning. In the aquaria females attach egg masses to the walls and also to dead and living sea-fans. The spawn of one single female contains 4 to 34 capsules, with an average of 18 capsules.

The ootheca are arranged in lines and nets, when attached to the cellular structure of sea-fans; and in clusters, when attached to the walls of the aquaria.

Communal egg masses in the aquaria had up to 120 capsules. This is probably an unusually large mass, for free-living animals show a less close settlement.

Oothecae of *Cyphoma gibbosum* are transparent, colorless and smooth (except for very fine microscopical lines) structures, which are somewhat variable in shape. The basal outline of each capsule shows roughly the shape of a rectangle with rounded angles. No escape aperture is existent. Both walls of the cushion-like ootheca are fused at the sides, forming a clear membrane, which surrounds the whole capsule and attaches the capsule to the substrate or the neighboring rim membrane of another capsule. If attached by the rim and hanging free in the holes of a sea-fan the capsular walls are both convex. When attached to the walls of the aquarium or the axis of a sea-fan, the basal capsular wall is flat or concave, but attachment to the substrate is only made by the rim. One capsular rim only overlaps onto the rim of the next capsule, but never onto the capsular walls.

The average dimensions of the capsules are: length 2 mm, width 1.7 mm, height 0.3 - 0.5 mm.

Individual oothecae contain 250 to 500 embryos with an average of about 300.

The embryos in just produced oothecae are concentrated in longitudinally curved rows, giving the capsule a striped appearance. On the 5th day of development the rows have disintegrated and the formerly white embryos have grown to colorless, round, and in the internal cavity of the capsule rotating larvae. On the 8th day a completely colorless veliger, with a transparent larval shell, is seen swimming around in the capsule and on the 9th day a pink pigment in the shell marks a color change. On the 10th to 11th day the capsular walls disintegrate and pink, long-term planktotrophic veligers hatch.

DISCUSSION

Cypraea cinerea produces egg masses which are very similar to those of *C. spurca acicularis* Gmelin, 1791, described and figured by D'Asaro (1970) and two other cypraeids as described by Vayssière (1923) and Ostergaard (1950). Breeding continues until hatching takes place, as Ostergaard (1950) has shown for *C. isabella* Linnaeus, 1758 and *C. helvola* Linnaeus, 1758.

Theodor (1967) describes the life of *Simnia spelta,* an ovulid, which just like *Cyphoma gibbosum,* feeds on the flesh of anthozoans and also fixes mimetic eggs around the branches of gorgonian colonies in the Mediterranean Sea.

The oothecae are similar in size and form to those of *Cyphoma gibbosum.* Thiriot-Quiévreux (1967) states that a color change prior to hatching occurs in the larval shell of *Simnia spelta* (Linnaeus, 1758). Similar capsules are also produced by *Jenneria pustulata* (Lightfoot, 1786) (D'Asaro, 1969) and *Simnia patula* (Pennant, 1777) (Lebour, 1932). The major differences of these capsules in comparison with *Cyphoma gibbosum* capsules is the existence of an escape aperture and of pustulate wall structures in the former.

SUMMARY

The egg masses and oothecae of *Cypraea cinerea* Gmelin and *Cyphoma gibbosum* (Linnaeus) are figured and described for the first time and some data are given on the ecology of both species in the sea and on keeping them in aquaria.

Literature Cited

D'Asaro, Charles
1969. The egg capsules of *Jenneria pustulata* (Lightfoot, 1786), with notes on spawning in the laboratory. The Veliger **11** (3): 182 - 184: 1 text fig. (1 January 1969)
1970. Egg capsules of prosobranch mollusks from South Florida and the Bahamas and notes on spawning in the laboratory. Bull. Marine Sci. **20:** 414 - 440
Lebour, Marie V.
1932. The larval stages of *Simnia patula.* Journ. Mar. Biol. Assoc. U. K. **18** (1): 105 - 115; 2 plts.; 1 text fig.
Natarajan, A. V.
1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proc. Indian Acad. Sci. **B. 46:** 170 - 228
Ostergaard, Jens Mathias
1950. Spawning and development of some Hawaiian marine gastropods. Pacif. Sci. **4:** 75 - 115; 42 text figs. (April 1950)
Theodor, Jacques
1967. Contribution à l'étude des gorgones (VI): La dénudation des branches des gorgones par des mollusques prédateurs. Vie et Milieu Arago **18:** 73 - 78
Thiriot-Quiévreux, Catherine
1967. Observations sur le développement larvaire et postlarvaire de *Simnia spelta* Linné (Gastéropode Cypraeidae). Vie et Milieu Arago, Ser. A: Biol. marine **18** (**1 A**): 143 - 151; 3 plts. (Oct. 1967)
Vayssière, Albert Jean Baptiste Marie
1927. Recherches zoologiques et anatomiques sur les mollusques de la famille des Cypraeidés. 2me partie. Ann. Mus. Hist. Nat. Marseille, Zool. **21:** 133 - 184; plts. 24 - 28

Scanning Electron Micrographic Study of the Dorsal Integument of the Land Slug *Lehmannia poirieri* (Mabille, 1883)

BY

JOHN A. ARCADI

Department of Biology, Whittier College, Whittier, California 90608

AND

NORMAN HODGKIN

Department of Pathobiology, University of California, Irvine, California 90712

(2 Plates)

THE HISTOLOGY OF THE integumentary structures of the slug, *Lehmannia poirieri* (Mabille, 1883), and the snail, *Helix* sp., has been studied by several observers (ARCADI, 1963; CAMPION, 1961; ZILL, 1924).

The surface of the integument has not been previously studied in detail, particularly with the scanning electron microscope. It is our purpose to present such a study of the slug integument. Specimens were obtained in Whittier, California, in February and March, 1970. The slugs were fixed by plunging them into 4% glutaraldehyde buffered to pH 6.8 and cooled to 0° C. Other specimens were freeze substituted according to a modified technique of FEDER & SIDMAN (1958), using isopentane cooled with liquid nitrogen to − 155° C.

The dorsal integument was excised, mounted on a stub and shadowed with a gold-palladium alloy. The tissue was then viewed under 1×10^{-5}Torr in a Cambridge "Stereoscan" Mark D2 scanning microscope.

The orifices of what we presume to be mucous glands are visualized with mucus exuding from them (Figure *1*). Slightly smaller orifices were noted in a lattice-like arrangement (Figure *2*). Around a large orifice (Figure *3*) are seen slight roughening or projections that may be the microvilli seen with the transmission electron microscope noted in an unpublished work by Arcadi. Smooth smaller orifices are also seen (Figure *4*). Under low power, peculiar ridges (Figure *5*) are seen, the significance of which is not known at present.

This then is the first known presentation of scanning electron microscope studies of the dorsal integument of the slug showing openings of mucus-producing gland cells.

Explanation of Figures *1* to *3*

Figure *1*: Three stomata with a stoma open and a small amount of mucus exuding from an orifice. Note the protuberances that may well be so-called microvilli. ca. × 200

Figure *2*: Lattice-like arrangement of orifices of mucous cell glands. ca. × 100

Figure *3*: A large mucous gland orifice exuding its secretion with the smaller ridge segments of microvilli. ca. × 10000

Explanation of Figures *4*, *5*

Figure *4*: Smaller orifice with many adjacent structures which appear to be villi similar to those in Figure *1*. Further studies will reveal the nature of these structures. × 100

Figure *5*: Peculiar ridges seen in the dorsal integument of the slug are shown under low power magnification. They are seen consistently and therefore we consider them a physiological expression of the integument. × 200

Figure *1*

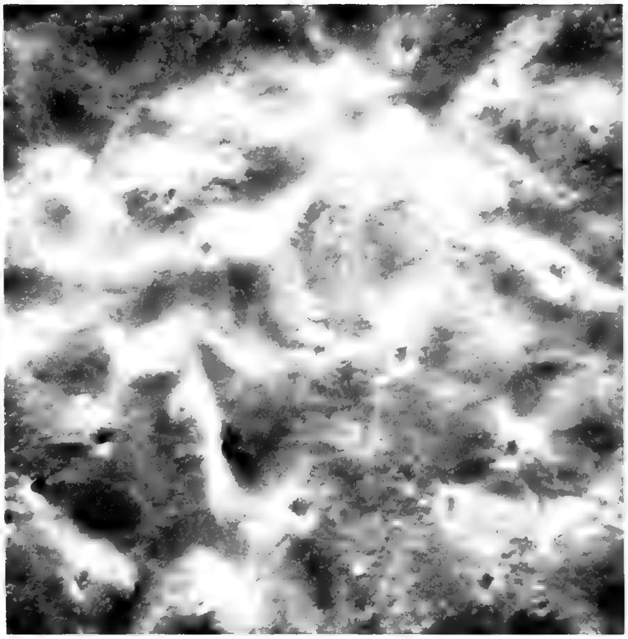


Figure *2*

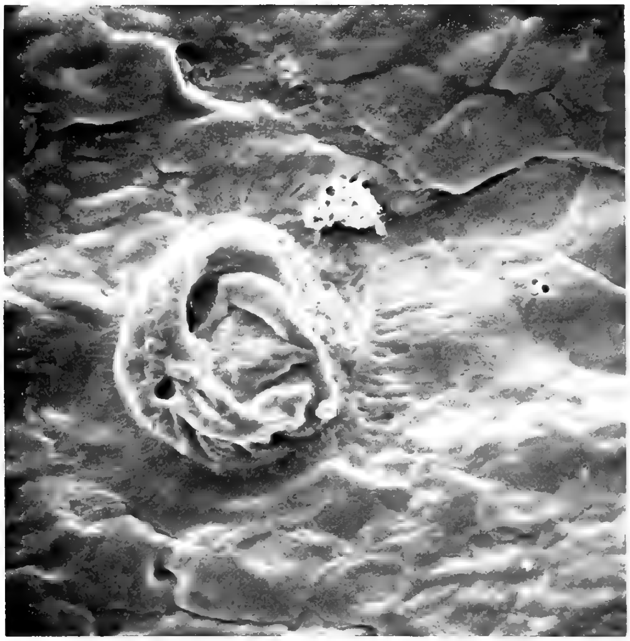


Figure *3*

All scanning work was done at Micrographics Laboratory in Newport Beach, California.

SUMMARY

The gold-palladium alloy shadowed dorsal integument of the slug, *Lehmannia poirieri* (Mabille, 1883), was viewed under a Cambridge scanning electron microscope after fixation in glutaraldehyde, or freeze substitution. Orifices of mucus-producing cells have been seen and demonstrated, and peculiar ridges in the integument are noted for the first time.

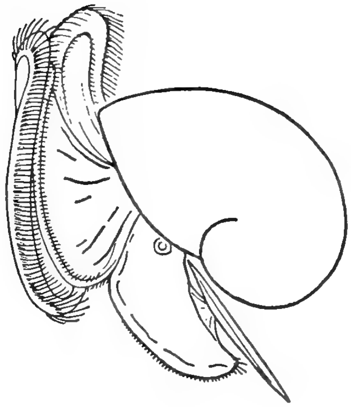
Literature Cited

Arcadi, John Albert
1963. Some mucus-producing cells of the garden slug (*Lehmannia poirieri*). Ann. N. Y. Acad. Sci. **106:** 451 - 457

Campion, Mary
1961. The structure and function of the cutaneous glands in *Helix aspersa.* Quart. Journ. Microsc. Sci. **102:** 195 - 216; 4 figs.

Feder, Ned & Richard L. Sidman
1958. Methods and principles of fixation by freeze-substitution. Journ. Biophys. Biochem. Cytol. **4:** 593 - 611; 4 plts.; 18 text figs.

Zill, Reinhold
1924. Die subepithelialen Hautdrüsen von *Helix pomatia* und einigen anderen Landgehäuseschnecken. Zeitschr. Anat. Entwickl'gsgesch. (1) **71:** 1 - 40; 22 drawings



Zoogeography and Ecology of Seven Species of Panamic-Pacific Scaphopoda

BY

M. S. McFADIEN

School of Oceanography, Oregon State University, Corvallis, Oregon 97331

(2 Plates; 3 Text figures)

INTRODUCTION

Literature on the Scaphopoda is largely taxonomic, based on shell morphology. Internal anatomy has been examined by Pelseneer (1889, 1906). Other morphological and developmental studies include those by Lacaze-Duthiers (1857), Sars (1861), Kowalevsky (1883) and Wilson (1904).

Certain aspects of functional morphology have been investigated by Yonge (1937), Morton (1959), and Dinamani (1964a, 1964b). A few generalized notes on distribution and ecology of Eastern Tropical Pacific species have been given by Pilsbry & Sharp (1897), Keen (1958), and Emerson (1951, 1956, 1958). There has been little work done on the scaphopod fauna of the Panamic Province and Gulf of California. Biogeography, ecology, and biology of the species from these waters are virtually unknown.

This study presents new data and combines these data with other available information to better understand certain ecological parameters and the distributions of seven Panamic Province scaphopod species including: *Cadulus austinclarki* Emerson, 1951; *C. panamensis* Pilsbry & Sharp, 1897; *Dentalium inversum* Deshayes, 1826; *D. oerstedii* Mörch, 1860; *D. sectum* Deshayes, 1826; *D. splendidum* Sowerby, 1832; and *D. innumerabile* Pilsbry & Sharp, 1897.

METHODS AND MATERIALS

Field data for this study were obtained during Stanford Oceanographic Expedition 20 (September 14 to November 30, 1968) and from the scaphopod collections of the Academy of Natural Sciences of Philadelphia (ANSP) and the American Museum of Natural History. Additional environmental data for the Eastern Tropical Pacific shallow waters and Gulf of California were found in oceanographic literature.

Stanford Oceanographic Expedition 20 collections: The cruise was undertaken as a broad inquiry into the biological oceanography of the Eastern Tropical Pacific. Both shallow-water and abyssal stations were included. This study includes data gathered from the shallow-water stations, beginning at the mouth of the Guayas River off Ecuador, and extending to near Acapulco, Mexico (Figure 1).

Scaphopods were collected using an epibenthic sled and a modified box dredge. A plankton net was incorporated into the box dredge to collect small organisms such as scaphopods. The sled collected approximately 3 times as much mud as the dredge. A more detailed account of dredging methods is given by Pearse in the mimeographed cruise report of Stanford Oceanographic Expedition 20 (1968).

All macroscopic organisms were sieved from the sediments using a No 32 Tyler series screen (mesh size 0.485 mm). All mollusks were preserved in 75% ethanol.

Scaphopods were identified following Pilsbry & Sharp (1897), Keen (1958), and Emerson (1951, 1956, and 1962). Identifications were confirmed by comparisons with specimens identified by earlier workers and type specimens from the collections of the Academy of Natural Sciences of Philadelphia and the American Museum of Natural History.

Sediments were sampled primarily with a Shipek Sediment Sampler (Hydro Products, Div. of Dillingham Corp., San Diego, California) and analyzed for grade size by a modification of the method used by M. G. (personal communication). This method is based on the theory given by Emery (1938) and similar in technique to the method of Southward (1965).

Hydrographic data were taken with Nansen casts near the sites of dredging. Additional hydrographic data were found in publications of the Inter-American Tropical Tuna Commission (1958, 1963, 1966, 1967), Muromstev (1963), Reid *et al.* (1965), Sverdrup and staff (1943),

Figure 1

Approximate locations of collecting sites for expeditions included in this study.

■ = SOE 20 × = other expeditions

and the United States Department of Commerce - Coast & Geodetic Survey Publications 31-3 (1967) and 31-4 (1968).

Data from Museum Collections: Several expeditions were represented in the scaphopod collections of the two museums consulted in this study. Collecting sites for these expeditions are shown in Figure 1.

Various techniques were used to collect scaphopods on the various expeditions. The Orange-Peel grab and the Puritan dredge were used predominantly.

Several collectors and museum workers classified the scaphopods collected on these expeditions. Misidentifications of specimens in the museums were corrected by the author and the shells recatalogued before tabulating the data for this study [1].

Sediment data for the dredging sites were collected where possible. The sediment classifications are general, no grade analyses having been done on these cruises. Also, many decisions on type sediment sampled during these expeditions may have been based on samples retrieved in dredge nets where sieving of fine particles may have occurred, resulting in an erroneous decision.

Other sediment data were found in BYRNE & EMERY's study (1960). Although these data were not collected concurrently with the scaphopods studied in the present research, the data represent grade-analyzed samples at specific locations and an overall analytical picture of the Gulf of California.

Hydrographic data were noted for dredging sites given in the various expedition reports. Additional data were found in the same publications listed above, as well as in RODEN (1958).

RESULTS

Stanford Oceanographic Expedition 20: A total of 21 shallow-water dredging attempts were made between the mouth of the Guayas River off Ecuador to near Acapulco, Mexico. Ten of these attempts were successful in collecting scaphopods. Original station data are tabulated in McFADIEN (1969).

Specimens included 7 identified species, 1 subspecies, and 2 undetermined species.

Data from Museum Collections: A total of 160 collections were studied in the museums. Each of the collections was used for plotting the geographical distributions of different species. Basic data on all specimens are tabulated in McFADIEN (1969).

Sediment grade data available from the Robert Parker (Scripps) collections and the Puritan American Museum Expedition were integrated with the Stanford Oceanographic Expedition 20 data to study the correlation between sediment grades and scaphopod species distributions.

The Robert Parker (Scripps) collections included hydrographic data from collecting sites (PARKER, 1964). These data and those of SOE 20 were combined to investigate correlations between temperature, salinity, oxygen and the species distributions.

DISCUSSION

Compilation and analysis of the data in this study indicate certain ecological parameters, probable latitudinal ranges and general zoogeography for the species considered.

Ecological Parameters: On the basis of temperature, oxygen, and salinity (bottom-water), as well as depth and sediment grade data illustrated in Figure 2, the 7 species studied appear to demonstrate varied adaptations to different shallow water zones.

The zones considered are littoral, infralittoral, circalittoral, and epibathyal as diagrammatically defined by HEDGPETH (1957) and modified by PÉRES (1957). Definition of lagoon and estuarine environments is more difficult

---

[1] The following series were found to be mixed and were re-catalogued by the author at the Academy of Natural Sciences of Philadelphia:

156413 *Dentalium splendidum*	156413 *Dentalium splendidum* 316204 *Dentalium inversum*
300597 *Dentalium semipolitum*	300597 *Dentalium semipolitum* 316205 *Dentalium splendidum?*
312128 *Dentalium inversum*	312128 *Dentalium inversum* 316206 *D. (Laevidentalium)* sp.

Explanation of Figure 4

Figure 4a: *Cadulus panamensis* Pilsbry & Sharp, 1897. ANSP 316155 × 10.7

Figure 4b: *Cadulus austinclarki* Emerson, 1951. ANSP 316136 × 10.7

Figure 4c: *Dentalium inversum* Deshayes, 1826. ANSP 316152 anterior half × 11.4

Figure 4d: *Dentalium inversum*, posterior half × 11.4

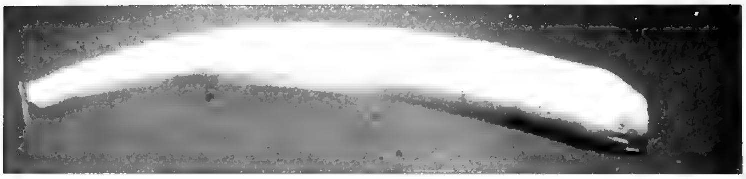


Figure 4 a

Figure 4 b

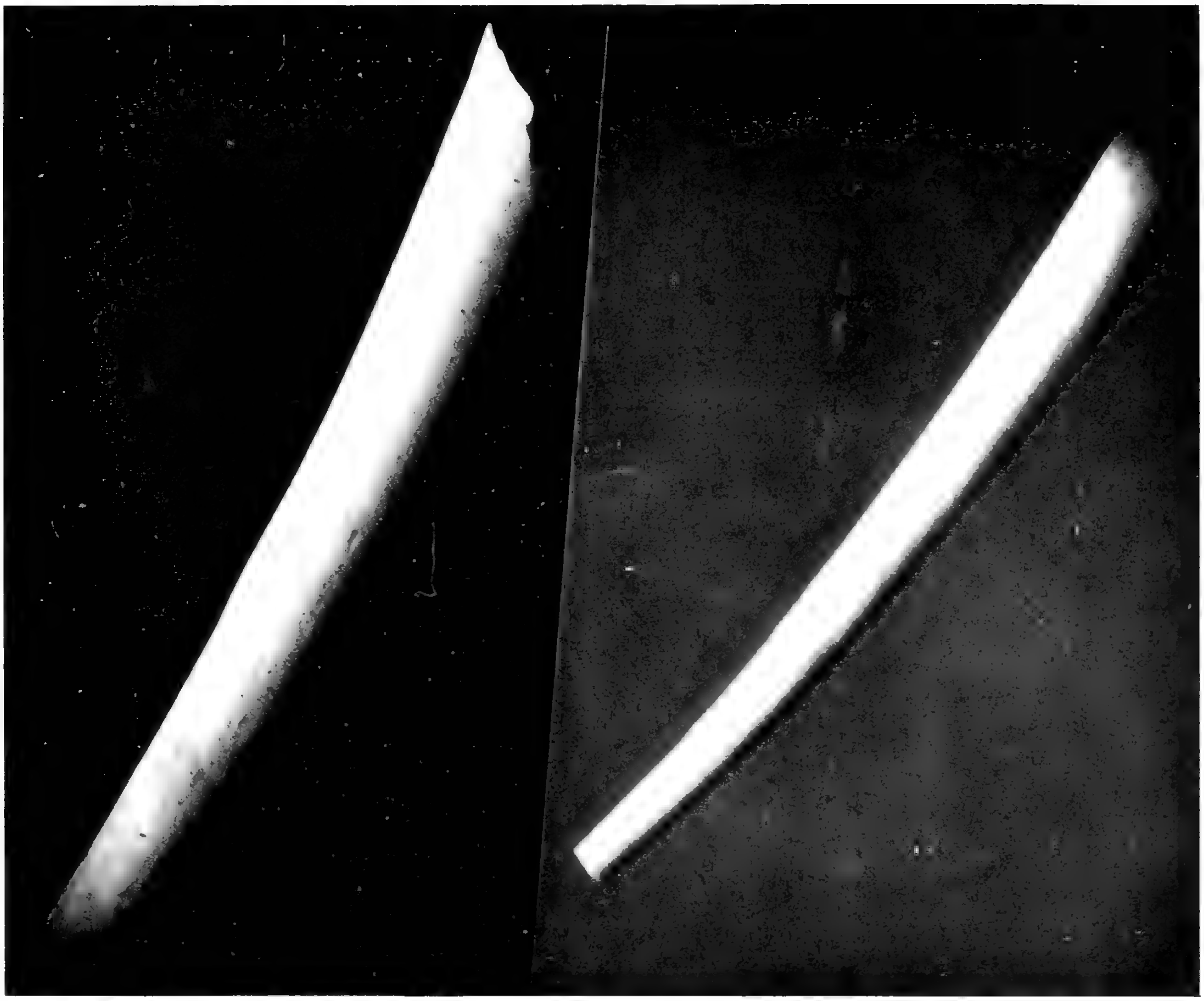


Figure 4 c

Figure 4 d

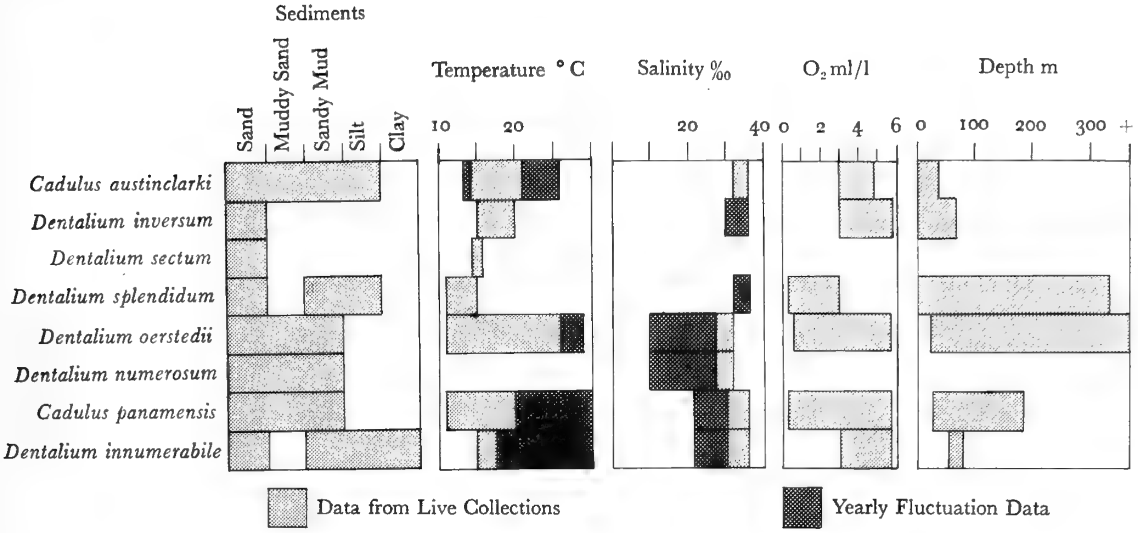


Figure 2

Tolerance ranges of seven scaphopod species, compiled from data collected concurrently with live scaphopod collections, and yearly fluctuations at sites of live animal collections

because of ambiguity of existing terms among various authorities; however, lagoons and tidal flats are considered in accordance with Emery & Stevenson (1957). Estuaries are zoned in accordance with Carriker's (1967) illustration of zonation and classification of estuaries.

I have defined biotic categories for the scaphopods studied as follows:

restricted: those species found in one or possibly two closely related bathymetric or ecological zones
tolerant: those species occurring in several, but not a wide variety of, bathymetric or ecological zones
broadly tolerant: those species present in many or all bathymetric or ecological zones considered

Figure 3 demonstrates the zones in which the individual species might be found as well as the range of habitats for each species.

Latitudinal Distributions: Although certain geographical areas were more heavily sampled than others, this research encompasses shallow coastal waters from Guayaquil, Ecuador, to San Diego, California and the coastal areas of the Gulf of California.

The text below describes possible latitudinal extensions and variations from past distributional descriptions. In the past, collection of empty shells has sometimes been used to determine geographical range; however, such shells neither confirm nor deny the existence of those species for a given area. When dredging, many empty and broken shells are collected for each living animal retrieved, but these may illustrate nothing more than wash-up, without existence of the living animal in that region, or they may suggest a sampling error where live animals exist but were not collected. Thus, sites where live animals were collected and sites where empty shells were collected are differentiated.

Cadulus panamensis Pilsbry & Sharp, 1897

(Figure 4a)

Conspecific with *Cadulus perpusillus* Sowerby, 1832 (Emerson, 1971).

The range of this species, according to live collections, extends from off Guayaquil, Ecuador (02°22′ S), north in the Gulf of California to Cabo Lobos (29°39′12″ N) and Punta San Fermin (30°05′ N). Collection of shells ex-

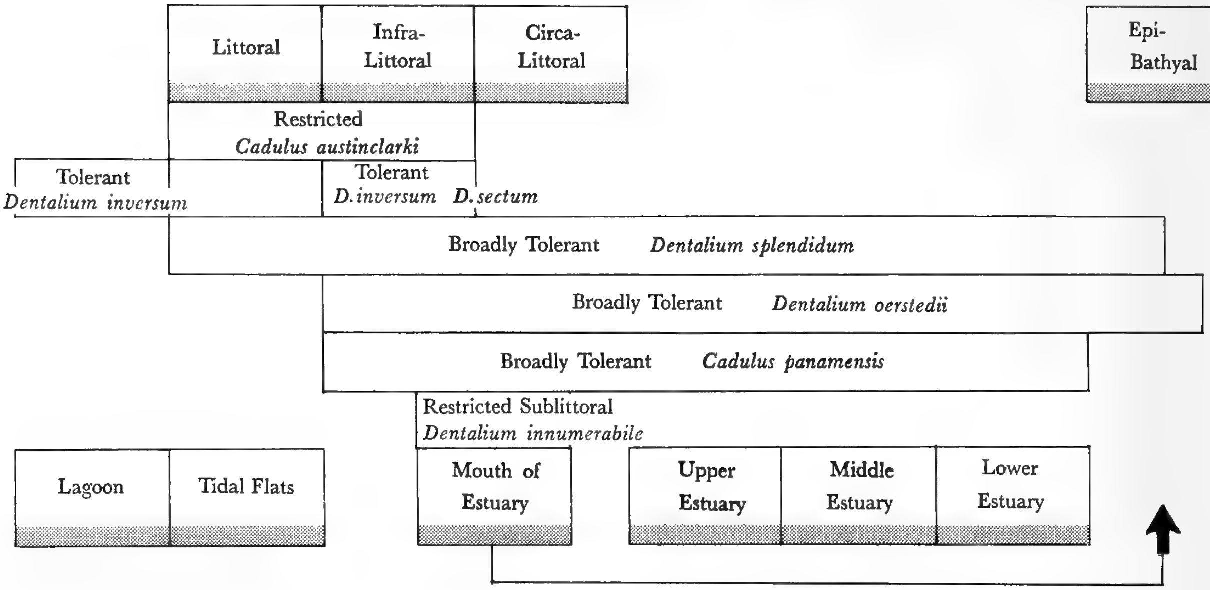


Figure 3

Zonal intergradation and biotic categories of species

tends north in the Gulf to San Felipe (about 32° N) and to San Diego, California. This latitudinal distribution extends farther south than Keen's (1958) indication to Panama.

Cadulus austinclarki Emerson, 1951

(Figure 4b)

This species has been collected live at widely separated points from Guayaquil, Ecuador to Angeles Bay (27°10′ N). Paucity of collections and the widely separated collection points may be due to either small populations of the species or sampling error. Previous data indicate that the species ranges to the outer coast of Baja California (Keen, 1958), but does not extend as far south as my data indicate.

Dentalium inversum Deshayes, 1826

(Figures 4c, 4d)

Collection data indicate the range of this species to be from San José, Guatemala (13°39′ N) to the Lagoons of Tiburon (29°08′ N)4 in the Gulf of California and San Ignacio (26°08′ N) on the oceanic side of Baja California. Empty shells have been collected farther north in the Gulf off Puerto Peñasco (about 31° N). The specimens available that were collected off Guayaquil were not listed as collected live. However, collection of the shells at least near Guayaquil indicates this might be part of the latitudinal range of *Dentalium inversum.*

Dentalium sectum Deshayes, 1826

(Figure 5a)

This species has been collected live from San José, Guatemala to at least San Marcos Island (27°10′ N). This is a southern extension compared to Keen's (1958) suggestions.

Dentalium innumerabile Pilsbry & Sharp, 1897

(Figure 5b)

This species has been collected live from its type locality in Panama Bay to Islas Tres Marias (21°28′ N) and

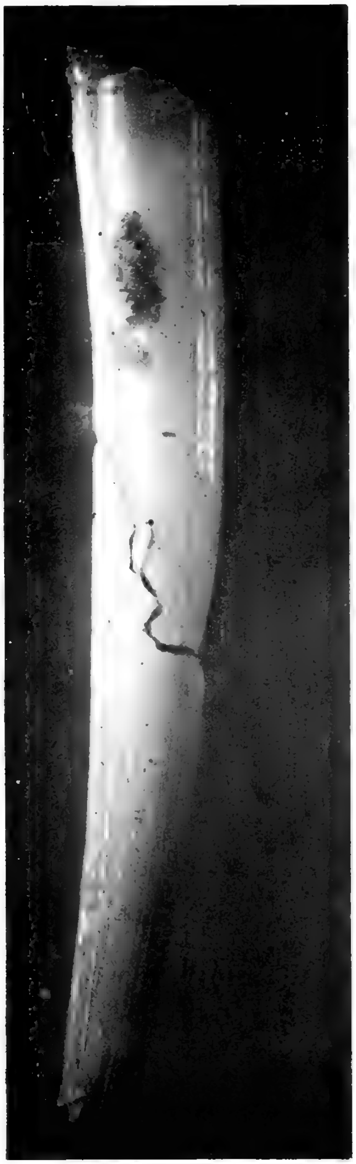


Figure 5a

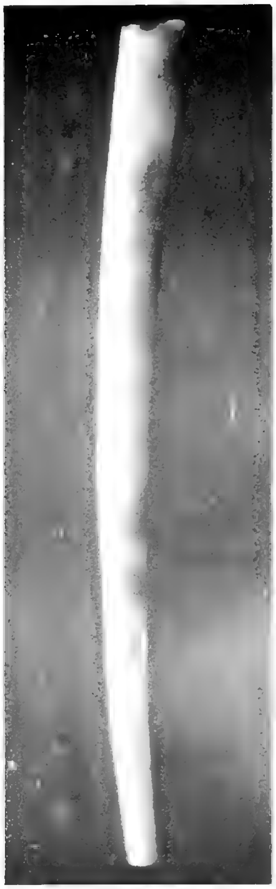


Figure 5b

Figure 5c

Figure 5a: *Dentalium sectum* Deshayes, 1826. ANSP 316153. × 10.7
Figure 5b: *Dentalium innumerabile* Pilsbry & Sharp, 1897. ANSP 316145 × 10.7
Figure 5c: *Dentalium oerstedii* Mörch, 1860. ANSP 316146. × 13.6

Coronados Island (26° N) in the Gulf of California. This range corresponds with that given by Keen (1958).

Dentalium splendidum Sowerby, 1832

This species has been collected live from Bahía Chocos, Colombia (03°48′ N) to Gonzaga Bay (29°45′ N), Baja California and off San Ignacio on the oceanic side of the Baja California Peninsula. Keen (1958) indicates the species extends to Ecuador. My data suggest extension of its range to the outer coast of Baja California, not previously indicated. Shell collections indicate a possible range to 30° N in the Gulf of California.

Dentalium oerstedii Mörch, 1860

(Figure 5c)

This species has been collected live from Bahía Chocos, Colombia, north to Cabo Teboca, Mexico (29°54′ N), and Angel de la Guarda Island (29°04′ N) in the Gulf of California. Shells have been collected on the oceanic side of the Baja California Peninsula as far north as San Ignacio. Keen (1958) indicates the species is found near the Galápagos Islands also.

Dentalium oerstedii numerosum Pilsbry & Sharp, 1897

Live collections have been made from Bahía Chocos, Colombia, north to Mazatlán, Mexico (23°12′ N), and off Consag Rock (30°54′ N) in the Gulf of California. This range extends considerably south compared to Keen's (1958) range to Lower California.

Zoogeographical Implications: Those species which tolerate the lowest temperatures tend to have confirmed or possible latitudinal ranges extending from the tropics into the warm temperate regions (Table 1).

Table 1 demonstrates the zoogeography known to date of the 7 species studied and is based on the data presented earlier in this paper.

It appears that *Dentalium splendidum, D. oerstedii* and *Cadulus panamensis,* as broadly tolerant species inhabiting the greatest variety of environments, demonstrate the greatest latitudinal ranges. *Dentalium inversum* and *D. sectum* may be conspecific, and *D. oerstedii* and *D. oerstedii numerosum* may well prove to be more closely related than subspecies on the basis of overlap, although there are still insufficient quantitative data to make a final decision. The other 4 species, including the closely related *D. inversum* and *D. sectum,* as well as *C. austinclarki* and *D. innumerabile,* although widely distributed, appear

Table 1

Summary of Zoogeography of Seven Scaphopod Species
(given in order of ranges north for Californian tropical and warm temperate species)

Species	Ecological Zones	LTT[1] (° C)	Faunal Province	Littoral Province
Dentalium innumerabile	sublittoral	15.0	Panamic Californian	tropical
Cadulus austinclarki	littoral, infralittoral, estuary mouth	13.3	Panamic Californian	tropical
Dentalium sectum	infralittoral, estuary mouth, lower estuary	15.0	Panamic Californian	tropical
Dentalium inversum	lagoon, infralittoral, estuary mouth, lower estuary	15.0	Panamic Californian	tropical warm temperate
Dentalium splendidum	tidal flat, sublittoral, epibathyal, all estuaries	11.0	Panamic Californian	tropical warm temperate
Dentalium oerstedii	sublittoral, epibathyal, all estuaries	11.0	Panamic Californian	tropical warm temperate
Cadulus panamensis	sublittoral, all estuaries	11.0	Panamic Californian	tropical warm temperate

---

[1] Lowest Temperature Tolerated

more restricted latitudinally to warmer waters than do the more tolerant species. This last observation appears especially clear when correlated with known temperature tolerances.

SUMMARY

A survey of ecological preferences and zoogeography of 7 scaphopod species was undertaken. The species studied were *Cadulus austinclarki* Emerson, 1951; *C. panamensis* Pilsbry & Sharp, 1897; *Dentalium inversum* Deshayes, 1826; *D. sectum* Deshayes, 1826; *D. oerstedii* Mörch, 1860; *D. splendidum* Sowerby, 1832; and *D. innumerabile* Pilsbry & Sharp, 1897; and one subspecies, *D. oerstedii numerosum* Pilsbry & Sharp, 1897.

The range of *Cadulus panamensis* is extended farther south to Guayaquil, Ecuador. The range of *C. austinclarki* is extended south to Guayaquil, Ecuador; that of *Dentalium sectum* south to San José, Guatemala; and that of *D. oerstedii numerosum* south to Bahía Chocos, Colombia.

Studies imply that *Dentalium splendidum, D. oerstedii,* and *Cadulus panamensis* are capable of inhabiting a variety of environments with respect to temperature, oxygen, salinity, depth, and sediment grades. *Dentalium inversum, D. sectum, C. austinclarki,* and *D. innumerabile,* although widely distributed, are more latitudinally restricted to warm waters.

Dentalium sectum and *D. inversum* may be conspecific and *D. oerstedii* and *D. oerstedii numerosum* may be more closely related than subspecies. Further research is needed, however, to determine accurately such systematic relationships.

ACKNOWLEDGMENTS

This research was supported by NSF Grants GB 6870 and GB 6871, as well as the Jessup Scholar Grant at the Academy of Natural Sciences of Philadelphia. I am indebted to Drs. R. Tucker Abbott and Robert Robertson, as well as the remainder of the staff of the Department of Mollusks at the ANSP for their encouragement and suggestions. I am also grateful to Dr. W. K. Emerson for assistance in identifying certain specimens.

Much of the field work could not have been accomplished without the help of Dr. John Pearse and JoAnne Aiello, and I express special thanks to both for their tireless energies. Completion of this paper could not have been possible without the research space afforded me at Hopkins Marine Station, and I thank Dr. Donald P. Abbott for his review of the manuscript.

Finally, Dr. E. H. Wheeler, Jr., Chief Scientist, and Bruce Robison, Teaching Assistant on the RV *Te Vega* Cruise, deserve a most sincere note of appreciation for their assistance with field research and critical reviews of the manuscript, as well as for their general support and encouragement of the research.

Literature Cited

Bennett, Edward B.
1963. An oceanographic atlas of the Eastern Tropical Pacific Ocean, based on data from Eastropic Expedition, October-December 1955. Inter-Amer. Trop. Tuna Comm. Bull **8** (2): 31 - 165; 53 figs.
1966. Monthly charts of surface salinity in the Eastern Tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm. Bull. **11** (1): 1 - 44; 12 figs.
Byrne, John V. & K. O. Emery
1960. Sediments of the Gulf of California. Bull. Geol. Soc. Amer. **71** (7): 983 - 1010; 2 plts.; 14 figs. (July 1960)
Carriker, Melbourne Romaine
1967. Ecology of estuarine benthic invertebrates: a perspective. pp. 442 - 487 *In*: George H. Lauff, ed., Estuaries. Amer. Assoc. Adv. Sci., Washington, D. C., 757 pp.; illust.
Cromwell, Townsend
1958. Thermocline topography, horizontal currents and "ridging" in the Eastern Tropical Pacific. Inter.-Amer. Trop. Tuna Comm. Bull. **3** (3): 133 - 164; 6 figs.
Dinamani, P.
1964a. Feeding in *Dentalium conspicuum.* Proc. Malacol. Soc. London **36** (1): 1 - 5; 1 fig. (April 1964)
1964b. Burrowing behavior of *Dentalium.* Biol. Bull. **126** (1): 28 - 32; 1 fig.
Emerson, William Keith
1951. A new scaphopod mollusk, *Cadulus austinclarki,* from the Gulf of California. Journ. Wash. Acad. Sci. **41** (1 : 24 - 26; 2 figs. (15 January 1951)
1956. A new scaphopod mollusk, *Dentalium (Tesseracme) hancocki,* from the Eastern Pacific. Amer. Mus. Novit. **1787:** 1 - 7; 1 fig. (28 September 1956)
1958. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 1. General account. Amer. Mus. Novit. **1894:** 1 - 25; 9 figs. (22 July 1958)
1962. A classification of the scaphopod mollusks. Journ. Paleont. **36** (3): 461 - 482; 5 plts. 2 text figs.
1971. *Cadulus (Gadila) perpusillus* (Sowerby, 1832), an earlier name for *C. (G.) panamensis.* The Nautilus **84** (3): 77 - 81
Emery, Kenneth O. & R. E. Stevenson
1957. Estuaries and lagoons. pp. 673 - 750; 3 plts.; 30 text figs. *In* Joel W. Hedgpeth, ed., Treatise on marine ecology and paleoecology. I. Ecology. Mem. Geol. Soc. Amer, **67** (1): 1296 pp.
Hedgpeth, Joel Walker
1957. Classification of marine environments. pp. 17 - 28 *In*: Joel W. Hedgpeth, ed., Treatise on marine ecology and paleontology. I. Ecology. Mem. Geol. Soc. Amer. **67** (1): 1296 pp.
Keen, A. Myra
1958. Sea shells of tropical West America: marine mollusks from Lower California to Colombia. i - xi + 624 pp.; 10 col. plts.; 1700 text figs. Stanford Univ. Press, Stanford, Calif. (5 Dec. 1958)
Kowalevsky, A.
1883. Étude sur l'embryogénie du Dentale. Ann. Mus. Hist. Nat. Marseille, Zool. **1** (7): 54 pp.; 8 plts.
Lacaze-Duthiers, Felix Joseph Henri de
1857. Histoire de l'organisation et du développement du Dentale. Ann. Sci. Nat. Zool. **4** (6-7): 5 - 51; 3 plts.; 13 figs.
McFadien, Margaret Smith
1969. Zoogeography and ecology of seven species of Eastern Pacific Scaphopoda. M. A. thesis, West Chester State College; 74 pp.; 22 figs.
Morton, John Edward
1959. The habits and feeding organs of *Dentalium entalis.* Journ. Mar. Biol. Assoc. U. K. **38:** 225 - 238; 5 figs.
Muromtsev, A. M.
1963. The principal hydrological features of the Pacific Ocean. 417 pp.; 177 figs. Jerusalem (Israel Program for Scient. Transl.)

PARKER, ROBERT H.

1964. Zoogeography and ecology of some macro-invertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico. Vidensk. Medd. Dansk Naturh. Foren **126**: 1 - 178; 29 figs.; 15 plts. (17 February 1964)

PELSENEER, PAUL

1889. Recherches morphologiques et phylogénétiques sur les mollusques archaiques. Mém. cour. Acad. R. Belg. **57**

1906. Mollusca. 355 pp.; 301 figs. *In*: E. RAY LANKESTER, ed., A treatise on zoology, part V. Adam & C. Black, London

PÉRES, J. M.

1957. Le problème de l'étagement des formations benthiques. Rec. Trav. Stat. Mar. Endoume **21** (12): 4 - 21

PILSBRY, HENRY AUGUSTUS & B. SHARP

1898. Scaphopoda. (1) **17** (65): 1 - 80; plts 1 - 9 [11 May 1897] *In*: G. W. TRYON, Jr., ed., Manual of Conch., **17**; Acad. Nat. Sci. Phila.

REID, JOSEPH L., ROBERT S. ARTHUR, EDWARD B. BENNETT, eds.

1965. Ocean observations of the Pacific: 1959. 901 pp.; Univ. Calif. Press, Berkeley

RODEN, GUNNAR

1958. Oceanographic and meteorological aspects of the Gulf of California. Pacif. Sci. **12** (1): 21 - 45; 19 figs. (January 1958)

SARS, M.

1861. Om *Siphonodentalium vitreum* en ny Slaegt og art af Dentalidernes Famile. Christiana (Univ. progr.)

SOUTHWARD. A. J.

1965. Life on the sea-shore. 153 pp.; 8 plts.; 51 figs. Harvard Univ. Press, Cambridge, Mass.

SVERDRUP, H. U. and staff

1943. Oceanic observations of the Scripps Institution in 1939. Rec. Observ., SIO **1** (2): 65 - 160; 4 figs.

U. S. DEPARTMENT OF COMMERCE /Coast and Geodetic Survey

1967. Surface water temperature and density, Pacific Coast. 85 pp. Rockville, Md. (C+GS Publ. 31-3, 2nd ed.)

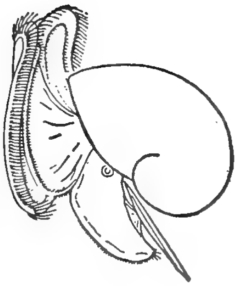
1968. Density of seawater at tide stations, Pacific Coast. Rockville, Md. (C+GS Publ. 31-4, 5th ed.)

WILSON, EDMUND B.

1904. Experimental studies in germinal localization. 1. The germ region in the egg of *Dentalium*. 2. Experiments on the cleavage mosaic in *Patella* and *Dentalium*. Journ. Exp. Zool. **1**: 197 - 268; figs.

YONGE, CHARLES MAURICE

1937. Circulation of water in the mantle cavity of *Dentalium entalis*. Proc. Malacol. Soc. London **22** (6): 333 - 337; figs.



Additional Notes on Cephalopods from Northern California

BY

ROBERT R. TALMADGE[1]

IN 1967 I BRIEFLY DISCUSSED the status of 10 species of cephalopods collected along the coast of northern California, between the 40th and 42nd parallels. In that discussion I mentioned that many of the species were pelagic and that probably in due time additional species would be found in this area. The following data are presented to record such additional species.

Vampyroteuthis infernalis Chun, 1903

A. G. SMITH (1971) reported on 2 specimens of this species that I had deposited in the collection of Invertebrate Zoology at the California Academy of Sciences in San Francisco and that had been taken by the M. V. *Ina* off northern California. I can now add 2 additional records from the same general region, one taken in 380 fathoms, and one in the very unusual depth of slightly less than 100 fathoms by the *Lynda Dawn* near Crescent City, Del Norte County, California. Both specimens are in the Talmadge collection, Eureka, California.

Calliteuthis dofleini (Pfeffer, 1912)

A single specimen of this squid species reached me through the courtesy of the crew of the dragboat *Ina*. The specimen, a female in good condition, lacked only the tips of the 2 club arms. The body was firm and not distorted. This specimen, taken in nearly 400 fathoms of water off the study area, was deposited in the Invertebrate Collection of the California Academy of Sciences, San Francisco.

It is quite probable that this species has been taken several times along the west coast of North America, but has been unreported. BERNARD (1970) refers the species to *Histioteuthis,* and lists it as being "Pelagic, 48° : 50° N" on the coast of British Columbia, Canada. I follow Voss (1963) who uses *Calliteuthis* instead of *Stigmatoteuthis* as does AKIMUSHKIN (1963) for the species. Regardless of generic placement, the single specimen appears to be the first recorded from northern California.

Dosidicus gigas (d'Orbigny, 1835)

There is a specimen of this species, reputedly taken off the northern Californian coast at Humboldt State College in Arcata, California. However, as the data were so incomplete and as out-of-region material was mixed in with the teaching collection, I have hesitated to record the species from this area. Recently, Dr. William Shapeero of the College of the Redwoods asked me to check out the identification of a medium-sized squid that had been given to the college. The specimen proved to be a female of the species under discussion, somewhat distorted, but with the horny, toothed rings on the suckers of both the arms and the clubs quite noticeable. Later, in conversation with Captain Jim Riley of the M. V. *Ina,* which had furnished the specimen, I learned that this was one of several such squid taken off Trinidad, Humboldt County, California in approximately 340 fathoms. Captain Riley stated that such squid appear from time to time in large numbers, but that their occurrence is definitely sporadic with no apparent migration periods.

Literature Cited

AKIMUSHKIN, I. I.
1963. Cephalopods of the seas of the U. S. S. R. Acad. Nauk U. S. S. R. Transl. Israel Program Scientif. Transl., Jerusalem iii - viii + 1 - 223; illust.

BERNARD, FRANK R.
1970. A distributional checklist of the marine Mollusca of British Columbia; based on faunistic surveys since 1950. Syesis 3: 75 - 94

SMITH, ALLYN GOODWIN
1971. Note on an unusual Pacific Coast cephalopod. The Veliger 14 (1): 131 (1 July 1971)

TALMADGE, ROBERT RAYMOND
1967. Notes on cephalopods from northern California. The Veliger 10 (2): 200 - 202 (1 October 1967)

VOSS, GILBERT L.
1963. Cephalopods of the Philippine Islands. Bull. U. S. Nat. Mus. 234: 1 - 180; 4 plts.; 36 text figs.

---

[1] Field Associate, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, California 94118

A Note on the Anatomy of the Circumesophageal Ganglion Complex of Several Doridacean Nudibranchs

BY

L. DONALD PARTRIDGE, Jr.

Department of Physiology and Biophysics, University of Washington, Seattle, Washington 98105

(2 Text figures)

INTEREST IN THE ELECTRICAL PROPERTIES of large identifiable neurons has led to detailed studies of the nervous systems of many gastropods. In the process of mapping large neurons within the circumesophageal ganglion complex of several doridacean nudibranchs (*Archidoris montereyensis* (Cooper, 1862), *Anisodoris nobilis* (MacFarland, 1905), and *Austrodoris odhneri* (MacFarland, 1966)), I have found a disagreement in the standard literature concerning the locations of the pedal and pleural ganglia. ALDER & HANCOCK (1845: plt. II) (see Figure 1A) and HANCOCK & EMBLETON (1852: plt. XVI) (see Figure 1B) show the circumesophageal ganglion complex of *Doris tuberculata* to consist of centrally located dorsal cerebral ganglia, pleural (brachial) ganglia lying more caudal and somewhat ventral, and most laterally and ventral to these, the pedal ganglia. These early works show nerves from the most lateral ganglia (labelled pedal) coursing to the foot while most of those from the ganglia labelled as pleural (brachial) run to the mantle. MACFARLAND (1966: plt. 36) (see Figure 1D) interchanges the positions of the pedal and pleural ganglia, placing the pleural most lateral and ventral and the pedal most caudal. This report discusses staining and electroanatomical approaches to establishing the identity of these two ganglia.

Specimens of *Archidoris* or *Austrodoris* were obtained inter- or subtidally from the waters around San Juan Island, Washington. Animals were pinned to a wax-bottomed dish under cold sea water. A midline dorsal incision was made in the mantle from between the rhinophores to the circumanal gill plume. The mantle was pinned open and the viscera, except for the esophagus and buccal mass, were removed. This procedure left intact the central nervous system and the major nerves to the mantle and foot. The nerves were stained for easy identification by the application of a solution of methylene blue in sea water to the preparation. The epineural sheath enclosing the ganglion complex was removed after it had been softened by application of pronase.

Camera lucida drawings and photographs of the ganglia and major nerves were made at various magnifications. Single nerves were carefully lifted onto bipolar hook electrodes and stimulated with single 0.1 sec, 40 V pulses, while the animal was observed for gross muscular contractions.

Examination of preparations vitally stained with methylene blue allowed nerves to be traced to fine terminal branches. The large nerve (no. 2, Figure 1C) which runs caudally from the ganglion lying most laterally and ventrally to the others appeared to send numerous branches to the region of the foot. The major caudal trunk (no. 1 or no. 3, Figure 1C) from the most caudal ganglion innervated only the lateral aspects of the animal, presumably the mantle.

Major nerve trunks from the two more laterally lying ganglia were stimulated to determine further their regions of termination. Stimulation of nerves labelled 1 and 3 in Figure 1C caused contraction of the mantle while stimulation of the nerve labelled 2 produced a discrete contraction of muscles of the foot. These observations are consistent with the ganglion naming scheme used by Hancock and co-workers.

A final bit of inferential evidence in favor of the large, most posterior ganglia being pleural instead of pedal comes from observing cells in ganglia with the epineural sheath removed. One might expect from the cell mapping of pleural and pedal ganglia in *Tritonia* (WILLOWS & HOYLE, 1967) that the cell locations in the two pedal ganglia would be very symmetrical while those in the two pleural ganglia would be asymmetrical. Cells are quite asymmetrically located in these two posterior ganglia in *Archidoris* and *Austrodoris* – most strikingly a large white cell can be observed in the left but not in the right ganglion.

The early drawings of the central nervous system of *Doris tuberculata* (Cuvier, 1805), presented by Hancock & Embleton (1852) thus appear accurately to represent that observed in the species of doridacean nudibranchs studied here. That is, the conically shaped cerebral ganglion lies most rostrally sending nerves to the buccal mass, rhinophore, mouth, eye, oral tentacles and the cerebrobuccal connective. Lying most caudally are the oval pleu-

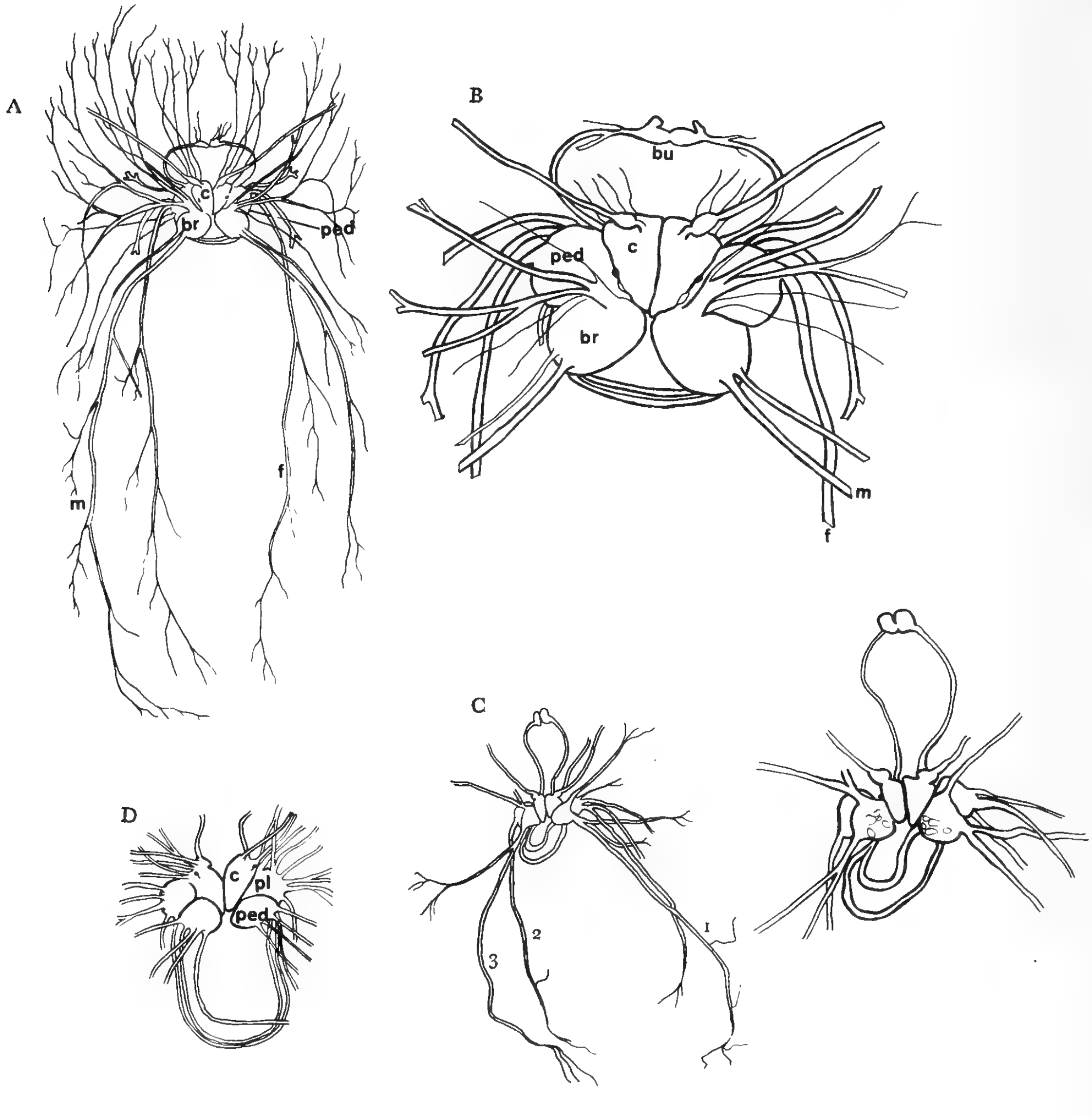
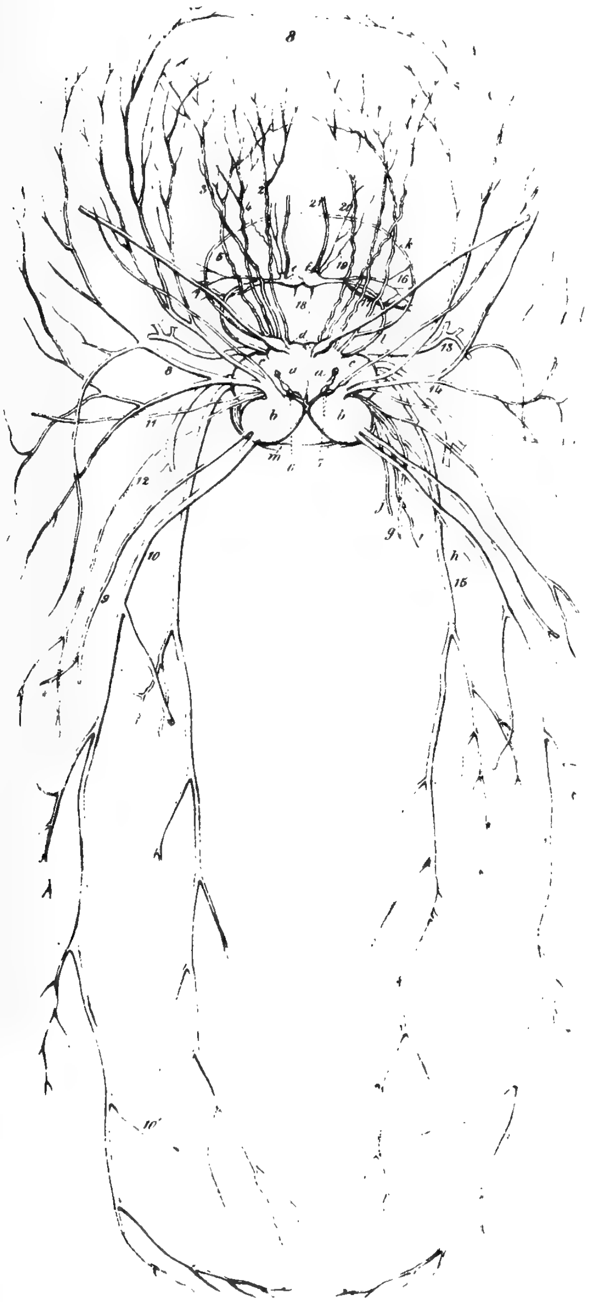


Figure 1

A. Drawing of the central nervous system of *Doris tuberculata*; after plate XVI in Hancock & Embleton (1852). B. Circumesophageal ganglion complex of *Doris tuberculata*; after plate I in Alder & Hancock (1845). C. Camera lucida drawing of a vitally stained preparation of *Austrodoris odhneri*. Drawing on the right is $2\frac{1}{2}\times$ the magnification of that on the left. Nerves labelled 1, 2, and 3 are discussed in the text. D. Circumesophageal ganglion complex of *Austrodoris odhneri*; after plate 36 in MacFarland (1966). Abbreviations used throughout this figure: c – cerebral ganglion; pl – pleural ganglion; ped – pedal ganglion; br – brachial (pleural) ganglion; bu – buccal ganglion; m – nerve to mantle; f – nerve to foot



ral ganglia from which course nerves principally to the mantle. Finally, lying somewhat ventral to these other two ganglia are the pedal ganglia, the nerves of which innervate the foot. Because of the need for such a drawing by those involved in studies on these animals and because of the inaccessibility of this published figure, it is reproduced here as Figure 2.

ACKNOWLEDGMENTS

I am indebted to Professor R. L. Fernald, Director of the Friday Harbor laboratories, for making available the facilities of the laboratories, to Dr. C. F. Stevens, Dr. D. Gardner, and D. Attwood for advice and assistance and to C. Eaton for providing specimens. This investigation was supported by USPHS grants GM00260 and NS05934.

Literature Cited

Alder, Joshua & Albany Hancock
1844-1855. A monograph of the British nudibranchiate Mollusca, with figures of all the species. London, Ray Soc. prts. 1 - 7: 438 pp.; 84 plts.

Alder, Joshua & Dennis Embleton
1852. On the anatomy of *Doris.* Philos. Trans. Roy. Soc. (London) 142: 443 - 461; 18 plts. (4 March 1852)

MacFarland, Frank Mace
1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. 6: xvi+546 pp.; 72 plt. (8 April 1966)

Willows, Arthur Owen Dennis & Graham Hoyle
1967. Correlation of behavior with the activity of single identifiable neurons in the brain of *Tritonia.* Symp. Neurobiol. Invert. Hung. Acad. Sci. (1967): 443 - 461; 10 figs.

(← adjacent column)

Figure 2

Reproduction of figure 8 of plate XVI in Hancock & Embleton (1852), showing the central nervous system of *Doris tuberculata.* a – cerebral ganglion. b – pleural ganglion. c – pedal ganglion. d – olfactory ganglion. e – buccal ganglion. f – gastroesophageal ganglion. 1 – olfactory nerves. 2 – nerves supplying upper portion of channel of mouth and lip. 3 – nerves to oral tentacles. 4 and 5 – to the sides and lower portions of channel of mouth and lip. 6 – optic nerves, each having at its origin a small ganglion. 7 – statocysts. 8 and 9 – nerves supplying anterior portions of mantle. 10 – nerves to posterior portions of same. 10′ – to ganglia of the stomatogastric system. 11 and 12 – nerves to side of body. 13, 14, and 15 – nerves to foot. 16 and 17 – nerves to buccal mass. 18 – nerves to radula. 19 – nerves to salivary glands. 20 – nerves to top of esophagus. 21 – nerves passing down esophagus and united to two large ganglia of the stomatogastric system. g, h, i, and j – nerves from visceral ganglion. l – cerebro-buccal connective. m – pedal commissure

Additions to the Opisthobranch Mollusk Fauna of Marin County, California, with Notes on Their Natural History

BY

TERRENCE M. GOSLINER[1]

AND

GARY C. WILLIAMS[2]

(1 Map)

INTRODUCTION

In a previous article (Gosliner & Williams, 1970) we set out to list all species of opisthobranch mollusks from Marin County, California, observed from the summer of 1966 through the summer of 1969. Since then, 4 species not previously mentioned have been collected, and another 4 species have been reported from Marin County in the literature. These additional data bring the total number of opisthobranchs observed in Marin County to 75. Observations were made from August, 1969 through May, 1972. As in our preceding paper, an asterisk (*) before a species name denotes an extension of its known range.

New records of previously listed species are as follows:

Anisodoris nobilis (MacFarland, 1905)

Rocky subtidal
Fort Cronkhite, Marin County; Van Damme Cove, Mendocino County

Discodoris heathi MacFarland, 1905

Rocky subtidal
Van Damme Cove, Mendocino County

Hermaeina smithi Marcus, 1961

Mudflats
Drake's Estero, Marin County

Hermissenda crassicornis (Eschscholtz, 1831)

Mudflats
Drake's Estero, Marin County

Phyllaplysia taylori Dall, 1900

Zostera beds
Hog Island, Tomales Bay, Marin County

New records of Marin County opisthobranchs are as follows:

Acanthodoris hudsoni MacFarland, 1905

Rare, rocky intertidal
Duxbury Reef
Vancouver Island, British Columbia, to Gaviota, Santa Barbara County, California

Alderia modesta (Lovén, 1844)

Common, mudflats, found on the xanthophyte *Vaucheria*
Schooner Bay, Drake's Estero
San Juan Islands, Washington, to Elkhorn Slough, California; Europe

Dendronotus iris Cooper, 1862

Seasonally common, mudflats
Lawson's Landing, Tomales Bay
Vancouver Island, British Columbia, to Coronados Islands, Lower California

---

Permanent addresses:
[1] 859 Butterfield Road, San Anselmo, California 94960
[2] 267 Oak Manor Drive, Fairfax, California 94930

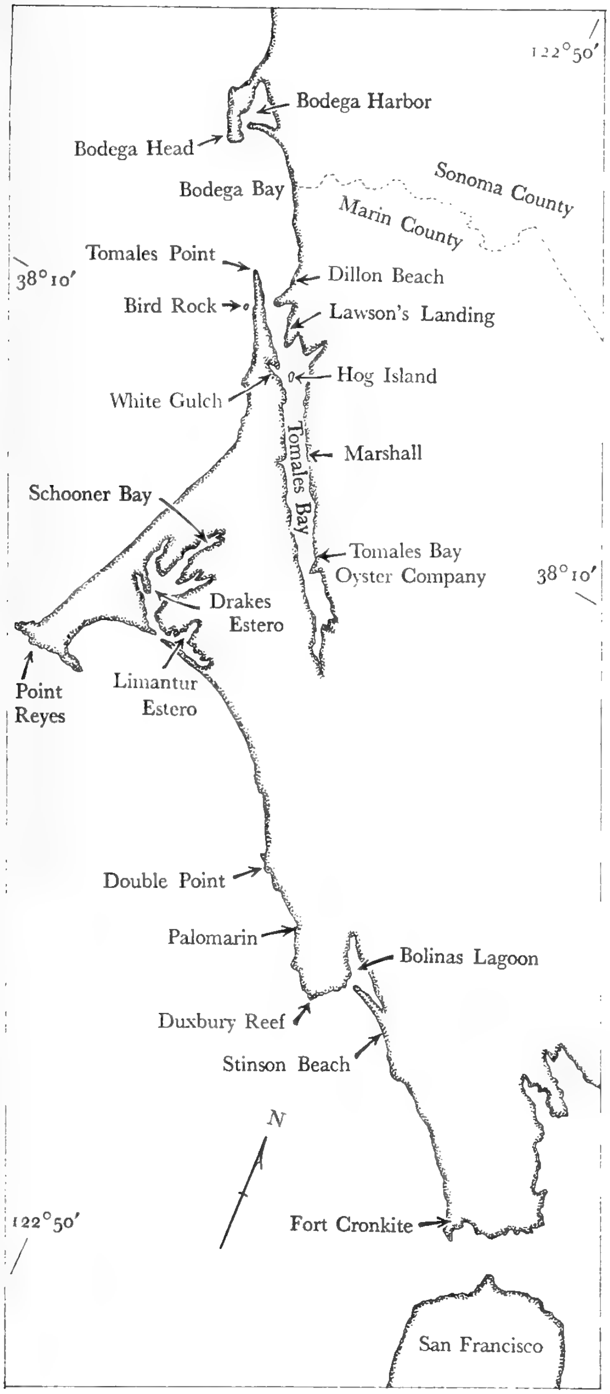


Figure 1

* *Trinchesia virens* (MacFarland, 1966)

Rare, rocky intertidal
Duxbury Reef
Duxbury Reef to San Luis Obispo
(Monterey to San Luis Obispo)

Natural history and habitat of previously unrecorded species:

Dendronotus iris Cooper, 1862

Several animals of *Dendronotus iris* were found at low tide at Lawson's Landing, Tomales Bay, on July 5, 1970. Individuals were found in small pools or along the water's edge, crawling along blades of the eelgrass *Zostera marina* Linnaeus or on the mudflat surface. Numerous egg masses were also present.

It is our opinion that the animals found had migrated from the deeper regions of the bay where their primary food source (as reported by Wobber, 1970), the burrowing anemone, *Cerianthus,* is commonly dredged. The intertidal region seems to provide a more suitable habitat for spawning. Personal communication with Dr. Gordon L. Chan of the College of Marin's Bolinas Marine Station has revealed that this species has been observed in previous years during the month of July, exhibiting essentially the same behavior. Animals were kept in an aquarium where they frequently exhibited a swimming behavior of rapid lateral bending of the body. Farmer (1970) has noted such behavior in this species as well as in other members of the genus.

Acanthodoris hudsoni MacFarland, 1966

During the midsummer of 1970 several individuals of this phanerobranch dorid were found at Duxbury Reef

GEOGRAPHICAL LOCATIONS

Tomales Bay (mouth)	38°14′ N	122°58′ W
Lawson's Landing	38°14′ N	122°57′ W
White Gulch	38°11′ N	122°57′ W
Hog Island	38°11′ N	122°56′ W
Marshall Boat Works	38°10′ N	122°53′ W
Tomales Bay Oyster Company	38°07′N	122°51′ W
Schooner Bay	38°05′ N	122°56′ W
Drake's Estero	38°03′ N	122°56′ W
Duxbury Reef	37°53′ N	122°42′ W
Fort Cronkhite	37°50′ N	122°33′ W

in low zone tide pools. Prior to these occurrences we had not observed this species in 4 years of collecting.

Trinchesia virens (MacFarland, 1966)

One individual of this minute aeolid was observed in June, 1970 on the rhodophyte *Iridea* sp. at Duxbury Reef. The species had previously been recorded from Pacific Grove, California (MacFarland, 1966) and from Pismo Beach, California (Long, 1969). The record from Marin County constitutes a northern range extension of slightly more than 100 miles (160 km).

Alderia modesta (Lovén, 1844)

On March 13, 1972, we observed 17 individuals of this small sacoglossan at the northern sector of Schooner Bay, Drake's Estero, on the Point Reyes National Seashore. All of the animals observed were on the xanthophyte *Vaucheria* sp. The species has been reported from many stations along the Pacific coast of North America by Hand & Steinberg (1955).

Species which have been recorded from Marin County by other authors but were omitted in our earlier paper are:

Armina californica (Cooper, 1862)
in Marcus, 1961

Rare, subtidal
White Gulch, Tomales Bay
Vancouver Island, British Columbia, to the Gulf of Panama

Elysia hedgpethi Marcus, 1961

Rare, intertidal mudflats
Tomales Bay Oyster Company mudflats
San Juan Island, Washington, to Bahía de los Angeles, Gulf of California (Mexico)

Polycera hedgpethi Marcus, 1964

Rare, bay boat landings
Marshall Boat Works, Tomales Bay
Tomales Bay to the Gulf of California

Tritonia exsulans Bergh, 1894
in Marcus, 1961

Rare, subtidal
Tomales Bay
Vancouver Island, British Columbia to Lower California, Mexico; Florida; Japan

Literature Cited

Farmer, Wesley Merrill
1970. Swimming gastropods (Opisthobranchia and Prosobranchia). The Veliger 13 (1): 73 - 89; 20 text figs. (1 July 1970)

Gosliner, Terrence M. & Gary C. Williams
1970. The opisthobranch mollusks of Marin County, California. The Veliger 13 (2): 175 - 180; 1 map (1 October 1970)

Hand, Cadet & Joan Emily Steinberg
1955. On the occurrence of the nudibranch *Alderia modesta* (Lovén, 1844) on the central Californian coast. The Nautilus 69 (1): 22 - 28; 1 fig. (July 1955)

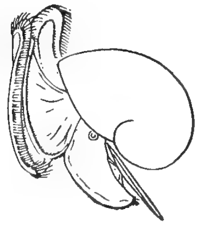
Long, Steven J.
1969. Records of *Trinchesia virens*, *Trinchesia fulgens*, and *Placida dendritica* from San Luis Obispo County, California. The Tabulata 2 (4): 9 - 12; 2 figs. (1 October 1969)

MacFarland, Frank Mace
1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. 6: xvi+546 pp.; 72 plt. (8 April 1966)

Marcus, Ernst
1961. Opisthobranch mollusks from California. The Veliger 3 (Supplmt. I): 1 - 85; plts. 1 - 10 (1 February 1961)
1964. A new species of *Polycera* (Nudibranchia) from California. The Nautilus 77 (4): 128 -131; 4 figs. (April 1964)

Roller, Richard A.
1970. A supplement to the annotated list of opisthobranchs from San Luis Obispo County, California. The Veliger 12 (4): 482 - 483 (1 April 1970)

Wobber, Don R.
1970. A report on the feeding of *Dendronotus iris* on the anthozoan *Cerianthus* sp. from Monterey Bay, California. The Veliger 12 (4): 383 - 387; plts. 55 - 57 (1 April 1970)



Oxidation of C^{14}-Glucose by the Aestivating Snail *Pila globosa* (Swainson)

BY

S. RAGHUPATHI RAMI REDDY [1]

AND

R. RAMAMURTHI

Department of Zoology, Sri Venkateswara University, Tirupati, Andhra Pradesh, India

INTRODUCTION

THE INDIAN APPLE-SNAIL *Pila* provides an interesting case for the study of aestivation. In summer months when the ponds, streams and paddy fields inhabited by this snail dry up, it retires into deeper layers of the mud, withdraws its body into the shell, closes the shell aperture with the operculum and enters into a state of dormancy until the advent of rain (PRASHAD, 1925; SAXENA, 1955; MEENAKSHI, 1956a, 1964). It has been reported that this snail can aestivate for one year or more if the conditions in the environment demand. Based on manometric experiments and on the ability of the snail to aestivate in plastimould for several months, MEENAKSHI (1956b, 1956c, 1957) concluded that the aestivating *Pila virens* does not consume oxygen. She also reported progressive depletion of the glycogen reserves and accumulation of lactic acid in tissues during aestivation, followed by a repayment of oxygen debt during revival in the post-aestivation period. On the basis of these observations, Meenakshi concluded that metabolism in the aestivating *Pila virens* is entirely anaerobic. On the other hand, COLES (1968) has recently reported that the related species *P. ovata* from Africa is aerobic during aestivation and shows measurable oxygen consumption in manometric experiments. We report here that the aestivating *Pila globosa* (Say, 1822) oxidizes C^{14}-glucose to $C^{14}O_2$ and hence is aerobic.

MATERIAL AND METHODS

Snails aestivating for 3 months in dry mud in large wooden boxes in the laboratory (SAXENA, 1956) were used in the experiments. A small hole was drilled into the operculum of the aestivating snail and 1 microcurie of U-C^{14}-glucose was injected into the foot of the snail through this hole with a Hamilton microsyringe. Immediately a little plasticene was applied to the hole to prevent any oozing out of fluids, and sealed with melted wax. The CO_2 liberated by 4 such snails was trapped in 50 ml of saturated KOH as described by HU (1958) and BERGREEN, MEENAKSHI & SCHEER (1961). The CO_2 in 2 ml aliquots of KOH taken at daily intervals for 5 days was precipitated as $BaCO_3$. After repeated washing, the precipitate was suspended in 95% ethanol and plated on stainless steel planchets for counting of radioactivity on thin window GM counters (Atomic Energy Commission, Trombay, India).

RESULTS AND DISCUSSION

The experiment was repeated thrice and the results of a typical experiment given in Table 1 show that there is significant radioactivity in $BaCO_3$ precipitates. It is evident from these results that the aestivating snail is putting out $C^{14}O_2$ and thus has the potentiality to oxidize glucose to CO_2. These results also suggest that lactic acid, which according to MEENAKSHI (1956a, 1956b, 1957) accumulates in the snail tissues during aestivation, is not the only end product of glucose metabolism in the aestivating *Pila globosa*.

---

[1] Present address: Department of Zoology, University of Poona, Poona-7, Maharashtra, India

Table 1

$C^{14}O_2$ output by aestivating snails injected with C^{14}-glucose

Days after injection	cpm/2ml KOH [1]
1 day	1199
2 days	1267
3 days	1785
4 days	1972
5 days	2109

Probably pyruvate resulting from the glycolysis of glucose in the aestivating snail is partly reduced to lactate and partly oxidized to CO_2 and water via the Krebs' cycle. It is also possible that some glucose in the aestivating snail is channeled through the hexose monophosphate shunt pathway resulting in the production of labeled CO_2. Thus the output of $C^{14}O_2$ suggests that the aestivating *Pila globosa* is aerobic. The activity of respiratory enzymes is reduced by 50 to 60% only in the tissues of aestivating *Pila globosa* (REDDY, 1967). Thus it is likely that metabolism in the aestivating *P. globosa*, though at a depressed level, is at least partially aerobic as shown by COLES (1968) in the case of *P. ovata*. The failure of MEENAKSHI (1956a, 1957) to measure any oxygen consumption in aestivating *P. virens* may be due to the reason that the mercury manometers she used are not sensitive enough to detect the minute gaseous exchange occurring in the snail during this torpid state.

MEENAKSHI (1956a, 1957, 1964) considers that the shell of *Pila* does not permit gaseous exchange and the closure of the shell opening with the operculum during aestivation is airtight. *Pila globosa* loses weight during aestivation; this weight loss is too high to be explained in terms of the depletion in the nutritional reserves of the body and hence should be due to water loss (REDDY, 1965). The related species *P. ovata* respires, though at a reduced rate, during aestivation (COLES, 1968). SPEEG & CAMPBELL (1968) reported that the shell of the terrestrial snails *Otala lactea* and *Helix aspersa* permits diffusion of gaseous ammonia. These reports as well as the output of $C^{14}O_2$ by the aestivating *P. globosa* reported here suggest that either the shell of this snail is pervious to gases or the closure of the shell opening with the operculum during aestivation is not air-tight, or both. Hence we suggest that this snail aestivates both under aerobic and anoxic conditions metabolizing glucose to lactic acid when oxygen is not available as during burial in the plastimould (MEENAKSHI, 1956a, 1956b, 1956c, 1957, 1964) and at least partially to CO_2 when oxygen is available in the environment. Further experiments on the pathways of glucose metabolism in active and aestivating snails should be of interest.

SUMMARY

Aestivating *Pila globosa* injected with C^{14}-glucose produced $C^{14}O_2$. Metabolism in this snail during aestivation is at least partly oxidative and not entirely anaerobic as claimed by other workers.

ACKNOWLEDGMENTS

S. Raghupathi Rami Reddy was a Scientist's Pool Officer of the Council of Scientific and Industrial Research (New Delhi) during the course of this work. We thank Prof. K. S. Swami of the Department of Zoology for facilities and encouragement and Prof. J. Bhimasenachar of the Department of Physics for radioactive counting facilities.

Literature Cited

BERGREEN, P. W., V. R. MEENAKSHI & B. T. SCHEER
1961. The oxidation of glucose by crustaceans. Comp. Biochem. Physiol. **2**: 218 - 220
COLES, G. C.
1968. The termination of aestivation in the large freshwater snail *Pila ovata* (Ampullaridae): 1. Changes in oxygen uptake. Comp. Biochem. Physiol. **25**: 517 - 522
HU, A. S. L.
1958. Glucose metabolism in the crab *Hemigrapsus nudus*. Arch. Biochem. Biophys. **75**: 387 - 395
MEENAKSHI, V. R.
1956a. Studies on the physiology of *Pila virens* (Lamarck) with special reference to aestivation. Doct. Dissert. Annamalai Univ., India
1956b. The physiology of hibernation in the apple-snail *Pila virens* (Lamarck). Curr. Sci. (India) **25**: 321 - 322
1956c. Seasonal variation in the glycogen and fat content in the apple-snail *Pila virens* (Lamarck). Journ. Zool. Soc. India **8**: 57 - 62
1957. Anaerobiosis in the South Indian apple snail *Pila virens* (Lamarck) during aestivation. Journ. Zool. Soc. India **9**: 62 - 71
1964. Aestivation in the Indian apple snail *Pila*. 1. Adaptation in natural and experimental conditions. Comp. Biochem. Physiol. **11**: 379 - 386
PRASHAD, BAINI
1925. Anatomy of the common Indian apple-snail *Pila globosa*. Mem. Indian Mus. **8**: 91 - 153
REDDY, S. R. R.
1965. Some biochemical studies on the snail *Pila globosa* with particular reference to aestivation. Doct. Dissert. Sri Venkateswara Univ., India.
1967. Respiratory enzymes during aestivation of the Indian apple-snail *Pila globosa*. Life Sci. **6**: 341 - 345
SAXENA, B. B.
1956. Some observations on the ecology and behaviour of the common Indian apple-snail *Pila globosa* (Swainson). Journ. Bombay Nat. Hist. Soc. **53**: 733 - 736
SPEEG, K. V. & J. W. CAMPBELL
1968. Formation and volatilization of ammonia gas by terrestrial snails. Amer. Journ. Physiol. **214**: 1392 - 1402

---

[1] corrected for the background counts

Nomenclatural Notes on West Coast *Odostomia*

(Gastropoda : Pyramidellacea)

BY

JAMES X. CORGAN

Austin Peay State University
Clarksville, Tennessee 37040

SEVERAL HUNDRED pyramidellacean gastropods of the odostomiid stock have been described from the West Coast of North America and they are a continuing source of nomenclatural confusion. This note seeks to clarify some objective, nomenclatural problems in West Coast *Odostomia.*

Odostomia cypria Bartsch, 1912

Odostomia (Evalea) cypria (Dall & Bartsch) BARTSCH, 1912a: 282; plt. 37, fig. 9
Odostomia (Evalea) cypria (Dall & Bartsch) BARTSCH, 1912b: 336
Odostomia (Evalea) cypria DALL & BARTSCH, 1913: 142; plt. 10, fig. 4

Odostomia cypria was first described by BARTSCH (1912a: 282) and is known only from the holotype. At the time of Bartsch's study, this specimen was unnumbered and in the collection of the Geological Survey of Canada. It is now number 1607 in the collection of The National Museum of Canada.

In the first publication of the name *Odostomia (Evalea) cypria,* BARTSCH (1912a) attributed authorship to Dall & Bartsch, without indication of a date or place of publication. This treatment was repeated by BARTSCH (1912b: 336). The species was then described as new in a subsequent paper (DALL & BARTSCH, 1913) which BARTSCH (1912a: 261) had noted as a work in press. Wording of this second description is identical with that of the first and illustrations are the same.

All known citations of *Odostomia cypria* attribute authorship to Dall & Bartsch. DALL (1921: 132) attributed authorship to DALL & BARTSCH, 1910. He then correctly identified the journal, page, and plate of the original publication by BARTSCH (1912a). Confusion with an earlier article (DALL & BARTSCH, 1910) is apparent. This erroneous 1910 citation is repeated in virtually every major nomenclator of the West Coast fauna.

Under Article 50 of the International Code of Zoological Nomenclature, the person who publishes a manuscript name is, normally, cited as author of the name. It thus seems that authorship is by BARTSCH (1912a: 282).

Odostomia hypatia Bartsch, 1912

Odostomia (Evalea) hypatia (Dall & Bartsch) BARTSCH, 1912a: 282; plt. 37, fig. 5
Odostomia (Evalea) hypatia (Dall & Bartsch) BARTSCH, 1912b: 336
Odostomia (Evalea) hypatia DALL & BARTSCH, 1913: 143; plt. 10, fig. 5

The history of the name of the name *Odostomia hypatia* is similar to that of *O. cypria,* discussed above. The holotype and only known specimen is now number 1606 in the collection of The National Museum of Canada. The name was first published by BARTSCH (1912a: 282) and Bartsch should be cited as author of the name.

Odostomia skidegatensis Bartsch, 1912

Odostomia (Evalea) skidegatensis BARTSCH, 1912a: 284; plt. 35, fig. 7
Odostomia (Evalea) skidegatensis Bartsch: BARTSCH, 1912b: 341
Odostomia (Evalea) skidegatensis DALL & BARTSCH, 1913: 143; plt. 10, fig. 1

Bartsch is the author of the specific name and publication was by BARTSCH (1912a). The original description records 7 specimens. Three, from a locality in Skidegate Inlet, are listed as cotypes. One is USNM 220116 and the other two were unnumbered specimens in the Geological Survey of Canada collection. Later, BARTSCH (1912b: 341) listed the two Canadian specimens as the only cotypes. The diagnosis and comments of BARTSCH (1912a) are repeated without change in DALL & BARTSCH (1913).

Canadian specimens are now lot 1609 in the National Museum of Canada collection. The larger cotype is cleaner and most resembles the original illustration. It is here designated the **lectotype** of *Odostomia skidegatensis* Bartsch, 1912. *Odostomia cassandra* Bartsch (1912: 285) has a similar nomenclatural history. A lectotype was selected by CORGAN (1969).

Odostomia cookeana Bartsch, 1910

Odostomia (Evalea) cookeana Bartsch, 1910: 138; plt. 11, fig. 7
Odostomia (Evalea) cookeana Bartsch, Bartsch, 1912a: 283; plt. 37, fig. 8

Dall (1921: 132) and most later students of West American faunas cite this species as published by Bartsch in 1912. The page and place of publication are, generally, correctly recorded. Confusion with Bartsch (1912a) is apparent.

Bartsch based the description of this species on two specimens and never designated either as type. Oldroyd (1927: 488) states "Type in United States National Museum, no. 208427." This statement is apparently an adequate designation of a lectotype.

Odostomia washingtonia Bartsch, 1920

Odostomia (Amaura) washingtonia Bartsch, 1920: 571
Odostomia (Amaura) washingtona Bartsch, 1927: 20; plt. 4, fig. 10

In each of the original descriptions, cited above, the newly introduced form is explicitly termed a new species and the single letter difference in spelling of specific names is not a *lapsus calami*. The second name appears more than once in the article that established it, descriptions differ in wording, and there is a minor difference in measurement of the holotype. Descriptions are independent of each other and the names are not homonymous.

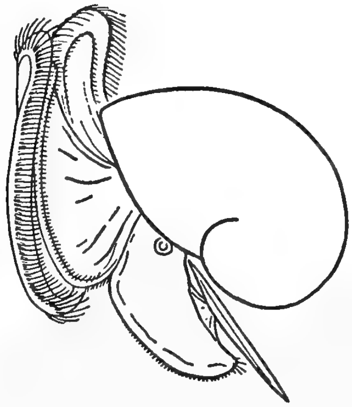
Bartsch created two nominal species. Each name is founded on the same specimen, USNM 334390, collected from the Washington Coast. *Odostomia washingtona* Bartsch, 1927, is thus a junior objective synonym of *O. washingtonia* Bartsch, 1920. The holotype is the only known specimen.

ACKNOWLEDGMENTS

Dr. Arthur H. Clarke, National Museum of Canada, and Dr. Joseph Rosewater, U. S. National Museum, granted access to specimens in their charge. Library expenses were, in part, paid by an Austin Peay State University Tower Fund Faculty Research Grant.

Literature Cited

Bartsch, Paul
1910. New marine shells from the Northwest Coast of America. The Nautilus **23** (11): 136 - 138; prt. of plt. 11
1912a. Additions to the West American pyramidellid mollusk fauna with descriptions of new species. Proc. U. S. Nat. Mus. **42** (1903): 261 - 289; plts. 35 - 38 (17 May 1912)
1912b. A zoogeographic study based on the pyramidellid mollusks of the West Coast of America. Proc. U. S. Nat. Mus. **42** (1906): 297 - 349 (15 June 1912)
1920. The Caecidae and other marine mollusks from the northwest coast of America. Journ. Wash. Acad. Sci. **10** (20): 565 - 572
1927. New West American marine mollusks. Proc. U. S. Nat. Mus. **70** (11): 36 pp.; 6 plts.
Corgan, James Xavier
1969. *Odostomia cassandra* Bartsch. The Nautilus **83** (2): 71 - 72
Dall, William Healey
1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. U. S. Nat. Mus. Bull. **112**: 1 - 217; plts. 1 - 22 (24 February 1921)
Dall, William Healey & Paul Bartsch
1910. New species of shells collected by Mr. John Macoun at Barkley Sound, Vancouver Island, British Columbia. Mem. 14-N, Canad. Mines, Geol. Surv. Branch, pp. 5 - 22; plts. 1, 2
1913. New species of mollusks from the Atlantic and Pacific Coasts of Canada. Victoria Memor. Mus. Bull. **1**: 139 - 146; plt. 10
Oldroyd, Ida Shepard
1927. The marine shells of the West Coast of North America. Stanford Univ. Publ. Geol. Sci. **2** (2): 298 - 601; plts. 23 - 64



NOTES & NEWS

Status of *Obeliscus clavulus* A. Adams, 1854

BY

JAMES X. CORGAN

Austin Peay State University
Clarksville, Tennessee 37040

In current literature, the name *Pyramidella (Pharcidella) moffati* Dall & Bartsch, 1906, is used for a West American marine gastropod that was first described as *Obeliscus clavulus* A. Adams, 1854. Dall & Bartsch (1906: 323) proposed *P. moffati* as a replacement name. In their very reasonable interpretation, the name *Obeliscus clavulus* A. Adams, 1854, was considered to be preoccupied by *Obeliscus clavulus* Beck, 1837. Actually, the nomenclatural problem is fairly complex.

Adams' species was initially assigned to the marine gastropod genus *Obeliscus* Humphreys, 1797 (A. Adams, 1854: 811; plt. 171, fig. 33). In the original description of Beck's species, it was assigned to the land gastropod genus *Obeliscus* Beck, 1837 (Beck, 1837: 62). Thus, two species bearing the same trivial name, *clavulus*, were assigned to two different, but homonymous, genera.

Under Article 57c of the current International Code of Zoological Nomenclature, the name *Obeliscus clavulus* A. Adams, 1854, is not preoccupied by *Obeliscus clavulus* Beck, 1837, since the two species were not, and never have been, assigned to the same genus. No replacement name is needed and the name *Pyramidella (Pharcidella) moffati* Dall & Bartsch, 1906, should be ranked as an unnecessary junior objective synonym of *Obeliscus clavulus* A. Adams, 1854.

Dall & Bartsch (1906: 323) referred *Obeliscus clavulus* A. Adams to *Pyramidella (Pharcidella)*. In the most recent commentary on *Pharcidella* Dall, 1889, it was ranked as a subgenus of *Longchaeus* Mörch, 1875 (Bartsch, 1955: 9). Following this interpretation, the species should be cited as *Longchaeus (Pharcidella) clavulus* (A. Adams, 1854). The species is referable to *Longchaeus*, but an assignment to the subgenus *Pharcidella* does not seem prudent. The characteristics of *Pharcidella* Dall, 1889, are poorly understood since the type species, *Pyramidella (Pharcidella) folinii* Dall (1889: 334), has never been illustrated or described in detail. A brief synonymy is given below.

Longchaeus clavulus (A. Adams, 1854)

Obeliscus clavulus A. Adams, 1854: 811; plt. 171, fig. 33
Pyramidella (Pharcidella) moffati Dall & Bartsch, 1906: 323 (unnecessary replacement name).

Literature Cited

Adams, Arthur
1854. Monographs of the genera *Eulima, Niso, Leiostraca, Obeliscus,* (1855) *Pyramidella,* and *Monoptygma*. *In*: Sowerby, Thes. Conch. **2:** 793 - 826; plts. 169 - 172 [publ. date *fide* Kuroda & Habe, 1952, p. 101]

Bartsch, Paul
1955. The pyramidellid mollusks of the Pliocene deposits of North St. Petersburg. Florida. Smithson. Misc. Coll. **125** (2): 102 pp. 18 plts. (5 May 1955)

Beck, Henrik Henriksen
1837. Index molluscorum praesentis aevi musei principis augustissimi Christiani Frederici. Fasc. prim. et secund. Mollusca gastraeopoda pulmonata. Hafniae, 124 pp.

Dall, William Healey
1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U. S. Coast Survey steamer "Blake," ... XXIX. Report on the Mollusca. — Part II. Gastropoda and Scaphopoda. Bull. Mus. Comp. Zool. **18:** 1 - 492; plts. 1 - 40 (January-June 1889)

Dall, William Healey & Paul Bartsch
1906. Notes on Japanese, Indo-Pacific, and American Pyramidellidae. Proc. U. S. Nat. Mus. **30** (1452): 321 - 369; plts. 17 - 26 (9 May)

Kuroda, Tokubei & Tadashige Habe
1952. Check list and bibliography of the Recent marine Mollusca of Japan. pp. 1 - 210; 2 maps; Tokyo, Japan (4 April 1952)

Odostomia minutissima Dall & Bartsch, 1909 a Synonym of *Odostomia raymondi* Dall & Bartsch, 1909

BY

JAMES X. CORGAN

Austin Peay State University
Clarksville, Tennessee 37040

Though the name *Odostomia (Evalea) minutissima* Dall & Bartsch, 1909, is preoccupied, it is currently used for a minute marine gastropod known from several Recent and Pleistocene localities in California and Baja California (*e. g.*: Dall & Bartsch, 1909: 211 - 212; Jordan, 1929: 246). Review of the United States National Museum collection suggests that the name *O. minutissima* Dall

& Bartsch, 1909, is a synonym of *Odostomia (Evalea) raymondi* Dall & Bartsch, 1909. This second name was proposed for two specimens dredged off Catalina Island, California.

In small individuals of *Odostomia minutissima,* the aperture is rather oval and becomes rhombic in older, larger shells. In the holotype of *O. raymondi,* the aperture is broken but appears quite oval and Dall & Bartsch (1909: 212) considered this a prime difference between the two nominal species. Actually, the holotype of *O. raymondi* has a poorly repaired break about one quarter volution before the aperture and secretion of the last quarter of the body whorl was, apparently, abnormal.

The type of *Odostomia raymondi* differs from representative *O. minutissima* in three characters that do not involve the aperture. The suture rises and falls in a pattern that resembles a sine wave while the suture of *O. minutissima* is a simple, incised line. In the type of *O. raymondi* the last three whorls have a tendency to balloon, becoming distinctly convex, while the whorls of *O. minutissima* are flat-sided. Finally, the holotype of *O. raymondi* is larger than any known *O. minutissima,* about 15% longer and comparably broader at 6 volutions.

Differences between the holotype of *Odostomia raymondi* and representative *O. minutissima* are not believed to be taxonomically significant. The retention of a juvenile character-like apertural shape, the ineffective repair of shell breakage, coiling irregularities, a ballooning of whorls, and large size are standard conchological manifestations of parasitism in gastropods (*e. g.*: Rothschild, 1936). The two nominal species seem identical in protoconch characters, in protoconch-teleoconch relationship, in all elements of sculpture, and in general growth form. Minor differences in size, in details of whorl profile, and in apertural shape seem to be normal individual variations in health. The two names are, thus, interpreted as synonyms. As the synonymy given below indicates, the name *Odostomia minutissima* Dall & Bartsch, 1909, is preoccupied and the name *Odostomia raymondi* Dall & Bartsch, 1909, should be used for this species.

Odostomia raymondi Dall & Bartsch, 1909

Not *Acteon minutissimus* Murdoch, 1900: 316; plt. 20, fig. 5 [referred to *Odostomia* by all, or most, modern students of the New Zealand fauna (e. g. Laws, 1940: 200)]

Odostomia (Evalea) minutissima Dall & Bartsch, 1909: 211; plt. 25, fig. 4

Odostomia (Evalea) raymondi Dall & Bartsch, 1909: 212; plt. 25, fig. 9

ACKNOWLEDGMENTS

Travel expenses to examine the U. S. National Museum collection were partially paid by an Austin Peay State University Tower Fund research grant. Dr. Joseph Rosewater, U. S. National Museum, did much to facilitate this study.

Literature Cited

Dall, William Healey & Paul Bartsch
1909. A monograph of West American pyramidellid mollusks. U. S. Nat. Mus. Bull. **68:** xii+258 pp.; 30 plts. (13 December 1909)
Jordan, Eric Knight
1926. Molluscan fauna of the Pleistocene of San Quentin Bay, Lower California. Proc. Calif. Acad. Sci. (4) **15** (7): 241 - 255; plt. 25; 1 text fig. (26 April 1926)
Laws, Charles R.
1940. Review of the Tertiary and Recent Neozelanic pyramidellid molluscs. No. 6. The genus *Odostomia.* Trans. Roy. Soc. New Zealand **69:** 191 - 209; plts. 16 - 18 (May 1940)
Murdoch, R.
1900. Descriptions of some new species of Pliocene Mollusca from the Wanganui District, with notes on other described species. Trans. New Zealand Inst. **32:** 216 - 221; plt. 20
Rothschild, Miriam
1936. Gigantism and variation in *Peringia ulvae* Pennant, 1777, caused by infection with larval trematodes. Journ. Mar. Biol. Assoc. (n. s.) **20:** 537 - 546

Comments on Vokes' Paper

BY

MICHAEL D. HUBBARD

Department of Biological Science
Florida State University, Tallahassee, Florida 32306

The recent paper by Vokes (1972) deserves comment as part implies an erroneous interpretation of the International Code of Zoological Nomenclature and the rest may lead to subsequent confusion. While staying out of the taxonomic debate between Vokes and Cernohorsky I would like to discuss the conclusions of Vokes in her paper.

Quoting from Vokes "Article 20 states: 'If an existing genus-group name has been modified by substituting *-ites, -ytes* or *-ithes* for the original termination, the modified name if applied only to fossils is not available, except for the purposes of the Law of Homonymy' (*i. e.,* it would preoccupy a subsequently proposed genus of the same name)." Nowhere in Article 20 or elsewhere in the Code is it stated that this name is identical to or a homonym of the name from which it is modified. Therefore *Murex* and *Muricites, Pecten* and *Pectinites,* etc., are not homonyms and should not be treated as such. Since *Murex* and *Muricites* are neither homonyms nor identical (on the basis of nomenclature), *Murex aculeatus* Lamarck, 1822, is not a homonym of *Muricites aculeatus* Schlotheim, 1820. The same applies to the other examples quoted by Vokes.

The problem of secondary homonymy is indeed a vexing one. MAYR (1969) mentions the concept of the "actuality principle" whereby there is a strong trend to sanction renaming only where two specific names are nominally congeneric (secondary homonyms in actuality) at the time of discovery of the potential homonymy. Thus if no confusion results from retaining the specific names, it seems provident not to change one if they are not congeneric at the time.

Literature Cited

MAYR, ERNST
1969. Principles of systematic zoology. New York (McGraw-Hill) xi+428 pp.; illust.

VOKES, EMILY HOSKINS
1972. Note on secondary homonymy. The Veliger 15 (2): 102 (1 October 1972)

(with additional comments by a referee and the editor)

REFEREE'S COMMENTS

The rationale for Article 20 of the International Code on Zoological Nomenclature, concerning genus-group names ending in *-ites,* must seem obscure to zoologists who have not had to deal with the paleontological literature of the early 19th century. There was even a proposal at the ICZN Colloquium in 1958 not to include it in the Code. However, when the matter was explained by paleontologists present, the provision was adopted.

In pre-Darwinian days, when the geologic time-scale was only just beginning to be set in order, relative ages of fossils (or "petrifactions," as they were usually called) could hardly even be guessed at. Workers tended to name their fossil finds in terms of modern genera, but to make clear that they were speaking of a petrifaction, not a modern specimen, they would use a special ending, derived from the Greek word for stone, "*lithos*" (λιθος), as an indication that this was a fossil member of the stated genus. A species would be cited as "*Pectinites x-us*" rather than as the more cumbersome "*Pecten x-us,* fossil specimen." In a list that would comprise both fossil and Recent forms, the generic name and the derived *-ites* names might be used interchangeably. In the 1940's paleontologists brought to the attention of the International Commission this peculiar usage, and a procedure for dealing with it was incorporated in the tentative code that was published in 1953 as the "Copenhagen Decisions." Later, in 1958, Professor J. C. Bradley compiled from this and the previous Rules a draft code that was used by the 1958 Colloquium. From this stems the official (1961) version of our present Code. In the Bradley draft, the intent is more clear-cut than it is in the final published version, for the committee charged with drawing up the wording of the final Code was also charged to condense, and in this case there was some loss of clarity. The Bradley draft, which was published in the Bulletin of Zoological Nomenclature, vol. 14, part 1/6, 1957, reads (p. 57):

"Forms of generic names intended for palaeontology -- If an established generic name is subsequently modified by changing its original termination to "*-ites,*" "*-ytes,*" or "*-ithes,*" whether preceded by a consonant or not, and if there is no clear evidence that this was done with any intent to establish a distinct genus (subgenus) and if an included species was based on a fossil, the modified form of the generic name shall have no status of availability, except that it shall enter into homonymy." There was a further explanation by Prof. Bradley: "Paleontologists have sometimes changed an established generic name in the manner indicated in order to signify that it was being used in reference to a fossil species."

Thus, under the Code the "*-ites*" names would in one sense be comparable to an incorrect subsequent spelling, without nomenclatural status but remaining nomenclaturally equivalent to the original generic name from which derived. However, because they are categorized as entering into homonymy (Article 56-b), they would preempt use of such a combination of letters for a generic name later proposed. In effect, when reading an old paleontological list, one would read "*Pecten*" for "*Pectinites,*" but no one can now validly propose as a new generic name *Pectinites.*

EDITOR'S COMMENTS

We cannot see that any useful purpose would be served if this debate about secondary homonymy were carried on further in "The Veliger." It would appear to us that it might be desirable for the various protagonists to enter into direct personal correspondence and, if and when they come to a complete agreement, to petition the International Commission to reword the pertinent provisions of the Code in a less ambiguous way. It is true that some provisions of the Code are open to different interpretations; this probably is intentional because of the assumption that different circumstances may require different approaches and that taxonomists would use their best judgment when applying the "Rules" and "Recommendations."

Soviet Contributions to Malacology in 1971

BY

KENNETH J. BOSS

AND

MORRIS K. JACOBSON

In continuing this series of lists of Soviet publications (see Boss, 1969, The Veliger **12:** 226 - 227; Boss & Jacobson, 1970 & 1971, *Ibid,* **13:** 199 - 202; **14:** 437 - 440), we are supported by comments of colleagues who have found the references useful. Since the papers listed are only those which are included in the section on Invertebrate Zoology of the Referativnyy Zhurnal for the respective year, there is both a considerable time lag and a possibility for omission. Sometimes the Soviet abstracters will overlook a 1970 book in the 1970 abstracts.

Herein we list all those Soviet articles abstracted in the Referativnyy Zhurnal for the year 1971. We have omitted reference to papers published in the Bulletin of the World Health Organization (Byul. Vsemiri. Organiz. Zdrayookhr) since they consist of Russian translations of Western originals. Subheadings dividing the abstracts into special sections have been retained.

Increased research activity can be noted in areas which are poorly known malacologically. For example, several papers on Armenian mollusks were published last year and new species were described in widely different taxa by Soviet malacologists.

Special remarks must be accorded Starobogatov's book on fresh-water mollusks (see General category). Readers who note Starobogatov's contributions to malacology will be at once astounded by the diversity and volume of his work. In recent publications he has treated the fresh-water mollusks of all continental bodies of water in the world, revised the classification of the Bivalvia, over-named the mollusk fauna of the Caspian Sea and commented on the nomenclature of several families.

The book contains three main sections plus an extensive bibliography. In part one he lists all the families and genera with representatives in fresh-water. Large scale maps showing the distribution of some taxa are provided. The extent of this compilation reflects the taxonomic difficulties encountered in the study of fresh-water mollusks. The number of nominal generic level taxa in the Rissoacean prosobranchs is so large as to indicate that the description of a new genus of this group of snails is probably unwarranted. The morass of names is enough to keep the serious worker concerned with biological and evolutionary phenomena away from these largely minute fresh-water prosobranchs, which is unfortunate since they are intrinsically interesting.

Although much of Starobogatov's list may be found in Wenz-Zilch's *Handbuch der Paläozoologie* or in Moore's *Treatise on Invertebrate Paleontology,* Starobogatov does offer a direct access to the molluscan groups having invaded fresh waters. Even professional malacologists will be surprised at the number of groups having fresh-water representatives which are usually considered to be exclusively marine.

Part 2 provides some generalizations about the distribution of fresh-water mollusks. Contemporary patterns are assessed in light of probable historical factors. Kinds of dispersal are discussed as modes of overcoming natural extrinsic barriers. And finally a section is provided which deals with the similarities and differences in the distribution of various taxonomic groups.

Part 3 regards the faunas of nine different regions (oblasti) which Starobogatov recognizes as natural zoogeographic units. These include: Palearctic, Ponto-Caspian, Baikalian, Sino-Indian, Ethiopian, Tanganyikan, Nearctic, Neotropical and Australian. As Boss is preparing a paper on the fresh-water mollusks of ancient lakes, he has had several relevant sections translated, and Starobogatov has provided quite complete analyses. However, he unnecessarily complicates nature by burying everything in an unrealistic plethora of names. For example, in a separate work, Logvinenko and he (1968, Mollusks [*in*] Atlas of the Invertebrates of the Caspian Sea, pp. 308 - 385, 407 - 410) have described so many Rissoacean snails from the Caspian Sea as to be ludicrous. No recognition of a modern species concept is apparent; the shells are mere stamps, named and illustrated by simple outline drawings. That Starobogatov (p. 228) dislikes revisionary work which seeks to treat faunas in terms of evolutionary systematics is evident in his remarks amout Leloup's superb monograph of the fauna of Lake Tanganyika: 'one should note in two of the latter comparatively detailed résumés (Leloup's paper), that there appears a marked tendency to lump species together . . . '

In the final section of the book, an epilogue which could not be fitted into the three main portions, he sketches an outline of the classification of the Rissoaceans, largely reflecting the frequently overlooked and elegant paper by Kozhov (1951. On the morphology and history of the Baikalian endemic mollusks of the family Baicaliidae. Trudy Baik. limnol. St. Akad. Sci. USSR, **13:** 93 - 119).

Further, a list of new taxa of fresh-water bivalves is appended. Over a dozen new subfamilies or tribes are established and over 40 new generic level names introduced. Although the names are valid, one can question their utility. Many, if not most, may, hopefully, fall into the synonymic oblivion they deserve.

The book is nevertheless an important compilation of an immense literature and constitutes a valuable resource for any library. A complete English translation is being initiated by Professor J. B. Burch of the University of Michigan.

Abbreviations and symbols we have used are:

ES – English Summary
ZEBP – Zhurnal Evolyutsionnoi biokhimii i Fiziologii (Journal of evolutionary biochemistry and physiology)
ZZ – Zoologicheskii Zhurnal (Zoological Journal)

Mr. Victor M. Lessiovski of the United Nations aided us in the translation of certain obscure words. Mrs. G. Dent carefully typed the manuscript.

GENERAL

Akramovsky, N. N.
1970. The biocenotic relationships of Armenian mollusks and the role of these organisms in the cycling of matter and energy. Zool. Sbornik Akad. Nauk, Armenian SSR **15**: 150 - 214 (Armenian and English summaries)

Anonymous (no author listed)
1971. Mollusks. The directions, methods, and results of their study. 4th Soviet (Congress) for the study of mollusks. Leningrad, 158 pp.

Eretl, L. Ya.
1970. A Pacific Ocean squid and the basic methods of its utilization. Izv. Tikho-okeansk. nauch.-issled. inst. rybn. Khoziaistva i okeanogr. **74**: 250 - 255

Gorokhov, V. V.
1971. Molluscicides and ecological prerequisites for their application. Sbornik rabot. po gelmintol. Moscow, Kolos, 100 to 101

———
1971. Procedures for research on new molluscicides and the calculations of their effectiveness. Profilaktika Zabolev. Zhivotnykh. Vologda, 105 - 106

Ioganzen, B. G.
1971. Scientific methodological conference on the study of freshwater mollusks of Siberia. Biol. vnutr. vod. Inform. Byul. No. **10**, 6 - 7

Kafanov, A. I. & Ya. I. Starobogatov
1971. *Pettancylus petterdi* in the USSR and autointroduction of aquarial mollusks in natural water bodies of the USSR. ZZ **50** (6): 933 - 935 (ES)

Leshko, Yu. V.
1971. The mollusks of the middle current of the Pechará and their significance in the feeding of fish. Trudy Komifil. Akad. Nauk SSSR, No. **22**, 97 - 105

Logvinenko, B. M. & O. P. Kodolova
1971. On the possibility of distinguishing univalve species by comparing electrophoregrams of water-soluble proteins. ZZ **50** (6): 923 - 925 (ES)

Mikulich, L. V. & L. P. Kozak
1971. An experiment in the maintenance of the Pacific Ocean squid under artificial conditions. Ekologiya **3**: 94 - 96

Minichev, Yu. S.
1971. On the fauna, ecology and systematics of the Retusidae (Opisthobranchia, Cephalaspidea) of Posset Bay in the Sea of Japan. Issled. Fauny Morei, Leningrad, Nauka **8** (16): 230 - 241

———
1971. *Tritonia primorjensis* sp. n. (Gastropoda, Opisthobranchia), a suitable subject for neurophysiological and biophysical investigations. ZZ **50** (2): 282 - 284 (ES)

Nikolova, V.
1970. Slugs and the possibilities of counter measures taken against them. Rast. Zashchita **18** (12): 21 - 25 (Bulgarian)

Savchuk, M. Ya.
1971. The mollusk *Mya* – a new productive goal of the Black Sea. Rybnoe Khoziaistvo, No. **8**, 20 - 22

Shikov, E.
1971. Land mollusks of the Kalinin region as potential intermediate hosts of helminths. Uchenye Zapiski Kalinin. gosudarstvennogo pedagog. inst. **89**: 149 - 154

Shileyko, A. A.
1971. Malacology: deceptive resemblance and the nature of differences. Methods of teaching about species diversity of the mollusks. Priroda, No. **7**, 75 - 80

Starobogatov, Ya. I.
1970. The molluscan fauna and the zoogeographical zonation of the continental water reservoirs of the earth. Nauka, Leningrad, 372 pp.

MORPHOLOGY

Aizeishtadt, T. B.
1971. Cytomorphologic investigations of the follicles in the ovaries of cuttlefish. II. The secretory function of the follical epithelium. Tsitologiya **13** (8): 956 - 964 (ES)

Anonymous (no author listed)
1971. Statocysts in gastropod mollusks, in bivalve or lamellibranch mollusks and in cephalopod mollusks. [*in*] Probl. Kosmich. Biol., Leningrad, Nauka, 86 - 103, 104 - 125, 125 - 139, respectively.

Burdenko, V. T. & A. I. Nadvodnyuk
1971. Conduction paths in the buccal ganglia of the grapevine snails. Elektrofiziol. issled. neironov. Kishinev, Akad. Nauk Moldavian SSR, 36 - 42

Chukhchin, V. D.
1970. Functional morphology of *Rapana*. Nauk Dumka, Kiev, 1 - 139; 83 plts.

———
1970. The method of feeding and the functional morphology of the digestive system of several tropical gastropod mollusks of the family Strombidae. Ecol.-Morph. invest. benthic organisms. Nauk Dumka, Kiev, 76 - 89

———
1970. A comparative investigation of the anatomy and histo-

logy of the digestive system of several mollusks of the superfamily Cypraeacea with the distinctive nature of their food. Ecol.-Morph. invest. benthic organisms. Nauk Dumka, Kiev, 89 - 102

Drozdova, T. V., A. V. Karyakin & V. A. Krasnova
1971. The chemical composition and infrared spectrum absorption of the organic matrix of the shell of the cuttlefish *Sepia pharaonis.* ZEBP **7** (4): 350 - 356 (ES)

Ivanova, L. M.
1970. Weight measurement indices and biomass of species of mollusks in the Central Caspian. Trudy molodykh uchenykh. Vses. nauch-issled. inst. morsk rybn. Khoziaistva i okeanogr. **3**: 93 - 107 (ES)

Kondrat'ev, G. P.
1970. On the correlation of weight and linear measurements of the body of some mollusks. Vopr. Fiziol. i Populayats. Ekol. Saratov, Saratov Univ. 56 - 60

Logvinenko, B. M. & Ya. I. Starobogatov
1971. The curvature of the frontal section fold as a systematic index in bivalve mollusks. Nauchnye dokl. vysshei shkoly biolog. nauki, No. 5, 7 - 10

Minichev, Yu. S.
1970. The evolution of the circulatory system of the lower Opisthobranchia. Issled. po evolyuts. morfologii bespozvonochnykh. Leningrad Univ., 101 - 113

Minichev, Yu. S. & L. V. Slavoshevskaya
1971. Features of the evolution of the renopericardial complex in terrestrial pulmonata. ZZ **50** (3): 350 - 360 (ES)

Mitrofanov, V. M. & Yu. B. Morev
1970. The morphology of the foot tissue of mollusks – intermediate host of protostrongilids. Trudy Kirg. inst. Ser. Zoovet. **15** (3): 68 - 71

Sadykhova, I. A.
1970. On the allometrics of growth of *Crenomytilus grayanus* (Dunker) of Peter the Great Bay. Trudy molodykh uchenykh. Vses. nauch. issled. inst. morsk. rybn. Khoziaistva i okeanogr. **3**: 108 - 117 (ES)

Skirkyavichene, Z. Yu.
1971. The regularity of increase in the weight of *Dreissena.* 2. The influence of the season of the year. Trudy Lietuvos TSR Mokslu Akad., Vilna. Biol. Inst. DARBAI (V) No. 2 (52): 91 - 97 (Lithuanian and English summaries)

Terent'ev, P. V.
1970. The geographical variation of the shells of large ponds. Vestnik Leningrad. Univ. **21**: 146 - 154 (ES)

Zuev, G. V. & Yu. V. Chmovzh
1971. The ecological morphology of the brain of the Argentinian squid. Nauchnye dokl. vysshei shkoly biolog. nauki, No. 1, 15 - 19

SYSTEMATICS AND FAUNISTICS

Akramovsky, N. N.
1970. The zoogeographical aspect of the Recent molluscan fauna of Armenia and the zoogeographical regions of the Republic. Aiastani gensapanakan antes. Biol. Zhur. Armenii **23** (11): 118 - 127

———
1970. A new Recent species of freshwater mollusk from Armenia, *Gabbiella araxena* Akramovsky (Gastropoda : Prosobranchia : Bithyniidae). Aikakan SSR Gitytyunneri Akademia Zekuitsner. Dokl. Akad. Nauk Armenian SSR **51** (4): 255 - 257 (Armenian summary)

———
1971. A short catalog of the Recent molluscan fauna of Soviet Armenia. Aiastani gensapanakan antes. Biol. Zhur. Armenii **24** (6): 3 - 12 (Armenian summary)

Bonadysenko, A. P., V. S. Konyushko, V. A. Radkevich & T. M. Romenko
1970. The gastropods of the lakes of the Tiosto groups. Poozer'ya. 1, Minsk, Belorussk. Univ., 154 - 166

Burch, J. B., G. K. Lindsay & P. T. Loverde
1971. A comparative study of some Polish and American Lymnaeidae: an assessment of phylogenetic characters. ZZ **50** (8): 1158 - 1168 (ES)

Filippova, Yu. A.
1970. Distribution of masses of species of cephalopod mollusks in the epipelagic zone in the Indian Ocean. Trudy molodykh uchenykh. Vses. nauch.-issled. inst. morsk. rybn. Khoziaistva i okeanogr. Vyp. **4**, 42 - 52 (ES)

Golikov, A. N. & O. A. Skarlato
1971. On the molluscan fauna of Posset Bay in the Sea of Japan. Issled. Fauny Morei, Leningrad, Nauka **8** (16): 188 - 205

Gvozdev, M. A.
1970. On the mollusk fauna of Central Kuito Lake. Materialy Mezhvyz Konferentsii, Leningrad, 94 - 96

Izzatullaev, Z.
1970. The tropical mollusk *Pupoides coenopiotus* (Hutton) in the USSR. Akhboroti Akad. Fankhon RSS Tochikistan Shu'ban Fankhon Biol. Izv. Akad. Nauk Tadzhikistan SSR. Otd. Biol. **3**: 82 - 83 (Tadzhik summary)

———
1970. Materials for the study of land mollusks of the Gissarsky mountain ridge and contiguous regions of Tadzhikistan. Izv. Akad. Nauk Tadzhikistan SSR. Otd. Biol. **239**: 79 - 86 (Tadzhik summary)

Kodolov, L. S.
1970. On the squid of the Behring Sea. Trudy Vses. nauch.-issled. inst. morsk. rybn. Khoziaistva i okeanogr. **65**: 429 - 435

Krivosheina, L. V. & Ya. I. Starobogatov
1970. A contribution to the taxonomy of *Anodonta* (Bivalvia, Unionidae) of Siberia and adjacent regions of Kazakhstan. ZZ **49** (9): 1327 - 1333 (ES)

Krakatitsa, T. F.
1970. New findings of *Rapana* (Gastropoda, Muricidae) in the Karkinitsky and Djarylgachsky Bays of the Black Sea. ZZ **49** (8): 1247 - 1248 (ES)

Lazareva, A. I.
1971. On the systematics of the molluscan gastropod genus *Falsicingula* Habe (Prosobranchia, Rissoidea). ZZ **50** (5): 768 - 770 (ES)

Moskalev, L. I.
1970. The gastropod mollusks of the genus *Collisella* (Prosobranchia, Acmaeidae) of the outlying Asiatic seas of the Pacific Ocean. Trudy Inst. Okeanol. Akad. Nauk SSSR **88**: 174 - 212 (ES)

Nesis, K. N.
1971. The squid *Gonatus fabricii* (Licht.) in the central Arctic Basin. Gidrobiol. Zhur. **7** (1): 93 - 96

Pirogov, V. V.
1970. On the presence of new species of mollusks of the genus *Pyrgula* Christ. et Jan. in the mouth (near delta) of the Volga River. Trudy Astrakhan gosudarstvennogo Zapovednik. Vyp. **13**: 249 - 253

Roginskaya, I. S.
1971. *Arctadalaria septentrionalis* gen. n., sp. n. (Onchidorididae), a new nudibranchiate mollusc from the Laptev Sea. ZZ **50** (8): 1154 - 1157 (ES)

Shileyko, A. A.
1970. Volume, systematics, and phylogeny of the group *Perforatella – Zenobiella – Chilanodon* (Pulmonata, Helicidae). ZZ **49** (9): 1306 - 1321 (ES)

———
1971. A comparative anatomical investigation of some Ariantinae (Pulmonata, Helicidae). ZZ **50** (7): 990 - 1001 (ES)

Slavoshevskaya, L. V.
1971. A new aberrant opisthobranch mollusk from the Sea of Japan. Issled. Fauny Morei Leningrad Nauka **8** (16): 206 - 220

Starobogatov, Ya. I.
1970. Mollusks of the family Unionidae in the delta of the Volga. Trudy Astrakhan gosudarstvennogo Zapovednik, **13**: 226 - 248

Taktakishvili, I. G.
1970. Of the phylogenetic development of the genus *Arcicardium* Fischer (Mollusca, Bivalvia). Soobshch. Akad. Nauk Gruz SSR **59** (1): 229 - 232 (Georgian and English summaries)

Yablokov, A. V. & A. V. Valetzky
1971. On changes in the range of the sinistral form of *Eulota lantzi* in Zailiisky Alatau during recent decades. ZZ **50** (3): 436 - 438 (ES)

Yaroshenko, M. F. & F. B. Gontya
1970. The mollusks of the reservoirs of the lower Dniester. Kishinev, Akad. Nauk Moldavian SSR, 65 - 73

BIOLOGY AND ECOLOGY

Gontya, F. A.
1970. Some problems in the ecology of freshwater mussels in the Dniester. Biol. protsessy v mor. i Kontinent. vodoemakh. Kishinev. Akad. Nauk Moldavian SSR, 85 - 86

Katkov, M. V.
1971. On the survival of Planorbidae (Pulmonata) and the preservation of trematode larvae in drying reservoirs. ZZ **50** (4): 584 - 586 (ES)

Khokhutkin, I. M.
1971. Polymorphism and the population boundary in terrestrial mollusks of the genus *Bradybaena*. Ekologiya No. 4, 73 - 80

Kiseleva, G. A.
1970. The settling and metamorphosis of the larvae of the rock-boring mollusks *Pholas dactylus* Linne. Ecol.-morph. invest. benthic organisms. Nauk Dumka, Kiev, 102 - 113

Minichev, Yu. S.
1971. On the biology of some species of Pyramidellidae (Gastropoda) in the Posset Bay in the Sea of Japan. Issled. Fauny Morei, Leningrad, Nauka **8** (16): 221 - 229

Mitropol'sky, V. I.
1970. Observations on the life cycle of *Pisidium henslowanum* (Sheppard) (Mollusca, Lamellibranchia). Biol. vnutr. vod. Inform. Byul. No. 6, 23 - 26

Sadykhova, I. A.
1970. The formation and composition of colonies of *Crenomytilus grayanus* (Dysodonta, Mytilidae). ZZ **49** (9): 1408 - 1410 (ES)

Shevtsov, G. A.
1970. Some notes on the squids of the Peruvian current and adjacent waters. Izv. Tikho-okeansk. nauch.-issled. inst. rybn. Khoziaistva i okeanogr. **69**: 90 - 93

Vovk, A. N.
1971. Some notes on the biology and distribution of *Loligo vulgaris* L. in the waters of Southwest Africa. Trudy Upr. Kadrov i Uchebn. Zavedenii Moskva rybn. Khosiaistva SSSR, **25**: 49 - 59

Zuev, G. V.
1970. Ecological peculiarities of the reproduction of *Sepia pharaonis* Ehrenberg and its distribution in the north western portions of the Indian Ocean. Ecol. morph. invest. benthic organisms. Nauk Dumka, Kiev, 113 - 121

PHYSIOLOGY

Alyakrinskaya, I. O.
1971. Some adaptations of *Mytilus galloprovincialis* (Bivalvia) and *Planorbis corneus* (Gastropoda) to the absence of water. ZZ **50** (5): 648 - 656 (ES)

Anonymous (no author listed)
1971. On some observations on the perception of stimuli on gravity receptors in cephalopods. Probl. Kosmich. Biol., Leningrad, Nauka, 475 - 477

Berger, V. Ya.
1971. A study of the functional basis of euryhalinity in several White Sea littoral mollusks. Ekol. mor. organizmov., Moskva, Univ. 4 - 5

Berger, V. Ya., V. V. Lukanin & V. N. Lapshin
1970. The respiration of several White Sea littoral mollusks in the process of acclimatization to variations in the surrounding salinity. Ekologiya **5**: 68 - 72

Govardovsky, V. I.
1971. Some properties and the dynamics of the endolymph in the statocysts of cephalopod mollusks. ZEBP **7** (4) 410 - 416

Grigor'eva, G. M. & S. S. Tkachenko
1971. Cholinesterase in the hemolymph of gastropod mollusks. ZEBP **7** (3): 254 - 261 (ES)

Khlebovich, V. V. & O. I. Olontseva
1970. The variation of the concentration of free amino acids in the tissues of the mussel *Mytilus edulis* in the dependence on the salinity of the external surroundings. Doklady Akad. Nauk SSSR **195** (2): 493 - 495

Konev, A. D. & V. M. Burtseva
1970. The variation of thermal stability of the entire organisms

and their cells in causal relation to the temperature maintenance of mollusks. Ekologiya 6: 80 - 88

Korobtsov, G. N. & D. A. Sakharov
1971. The role of surrounding ions in the realization of neural and hormonal influence on the ciliary action in molluscan larvae. ZEBP 7 (3): 238 - 240

Korzhuev, P. A. & I. O. Alyakrinskaya
1971. Sampling the hemocyanin in the hemolymph of *Rapana thomasiana* from the Black Sea. ZEBP 7 (4): 427 - 428 (ES)

Kovaleva, A. A.
1970. The level of gas exchange of several bivalve and gastropod mollusks. Vopr. Fiziol. i Populyats. Ekol. Saratov. Univ. 1: 31 - 37

Lukomskaya, N. Ya. & S. N. Nistratova
1970. Pharmacological characteristics of the chlorinoreceptives of the heart of *Anodonta* sp. ZEBP 6 (5): 527 - 535 (ES)

Manokhina, M. C. & L. V. Kuz'mina
1971. Distribution of biogenic monoamines in the central nervous system of the opisthobranch mollusk *Tritonia* sp. from the Pacific Ocean. ZEBP 7 (4): 357 - 361 (ES)

Petrov, V. N. & L. M. Belova
1970. The restoration of the lost function and development of the degenerative process in the closed ganglia of mollusks after partial injury. Vestnik Khar'kov. Univ., Ser. Biol. 39 (2): 66 - 70

Shakhmaev, N. K.
1969. On the problem concerning the correlation of magnesium and ascorbin in acidity. Vopr. Obshch. i Prikl. Khimii. Chelyabinsk 2: 80 - 83

Shirokolobov, V. N.
1971. Salinity variation in the mantle liquids of mussels and dependence on the condition of its maintenance. Gidrobiol. Zhur. 7 (1): 75 - 78

Shyl'man, G. E. & C. A. Goromosova
1970. A study of fat and glycogen in the flesh of cephalopod mollusks. Nauk Dumka, Kiev, 77 - 80

Stadnichenko, A. P.
1970. Variations of the white spectrum of the blood of *Viviparus contectus* (Millet, 1813) (Gastropoda, Prosobranchia). Parazitologiya 4 (5): 484 - 488 (ES)

Turpaeva, E. P., I. N. Soldatova & R. G. Simkina
1970. Intensity of metabolism of bivalve mollusks in the Black Sea. ZZ 49 (10): 1571 - 1572 (ES)

Usov, A. I., M. D. Martynova & N. K. Kochetkov
1970. Use of agar (discelectrophoresis) in the detection of species in mollusks of the genus *Littorina*. Doklady Akad. Nauk SSSR, 194 (2): 455 - 457

Verzhbinskaya, N. A. & M. V. Savina
1971. Evolution of the glycolytic system in typical mollusks. ZEBP 7 (4): 337 - 345 (ES)

Zuev, G. V.
1970. Reliability and the brain of cephalopod mollusks. Ecol.-morph. invest. benthic organisms. Nauk Dumka, Kiev, 121 - 135

Council of Systematic Malacologists

The following news release, of interest to many of our readers, was received too late for inclusion in our January issue.

Whereas the Phylum Mollusca is exceeded in living diversity only by the Phylum Arthropoda and flowering plants;

Whereas the existing collections of mollusks in North American museums number between 25,000,000 and 40,000,00 specimens;

Whereas the management of these collections presents problems that are not shared with collections of other phyla;

Whereas the services of malacology to society can be improved through definition of goals and priorities in malacological research and collection management;

The undersigned systematists, representing major malacological collections in North America, have organized a "Council of Systematic Malacologists."

The purposes of this organization shall be:

1) To prepare recommendations concerning standards and techniques of collection management for malacological resources;
2) To define the goals and priorities of malacology.

Membership shall be open to all professional persons in the Americas who use or manage systematic malacological resources. Membership shall be expanded through announcements in specialist journals and at relevant meetings.

Periodic meetings shall be held in adjunct with scheduled scientific meetings or as needed to confer on common problems.

A temporary steering committee has been formed to organize and promote an effective representative group for malacology in the Americas. This committee consists of:

Alan Solem, Chairman
George M. Davis
Arthur H. Clarke
James H. McLean

Working subgroups have been appointed to prepare recommendations concerning:

1) Compatible EDP and curatorial programs for use by malacologists in collection management and research;
2) Articulation of national goals for malacological research;
3) Coordination of specimen acquisition policies for malacological collections;
4) Preparation of position papers outlining priority programs for malacology.

Preliminary reports shall be circulated to the undersigned and other interested parties prior to a formal meeting open to a wide participation by malacologists.

signed:

George M. Davis, Academy of Natural Sciences of Philadelphia
Robert Robertson, Academy of Natural Sciences of Philadelphia
R. Tucker Abbott, Delaware Museum of Natural History
Alan Solem, Field Museum of Natural History
James H. McLean, Los Angeles County Museum of Natural History
Kenneth J. Boss, Museum of Comparative Zoology, Harvard University
Arthur H. Clarke, Jr., National Museum of Canada
Joseph Rosewater, National Museum of Natural History
George E. Radwin, Natural History Museum, San Diego
David H. Stansbery, Ohio State University
J. B. Burch, University of Michigan

Conchologists of America

The first convention of this new organization was held October 13 - 15, 1972 at Middletown, Rhode Island.

The organization was formed to unite shell collectors and clubs in the United States and to promote conservation and interest in shell collecting; the emphasis will be placed on conchology rather than malacology.

Officers elected at the initial meeting are:

President: Mrs. Bette Rachlin, Brookline, Mass.
Vice-President: Mr. Kirk Anders, Fort Lauderdale, Fl.
Secretary/Treasurer: Mrs. Dorothy Janowsky,
946 Ralph Avenue
Brooklyn, N. Y. 11236

Interested persons may obtain further information by writing to Mrs. Janowsky.

Announcing

the publication, on January 31, 1973, of a supplement to Volume 15:

A Systematic Revision
of the Recent Cypraeid Family Ovulidae

by Crawford Neill Cate

116 pages and 51 plates, 4 of them in color

Price: $15.00 plus handling charges as follows: $0.75 for addresses in the United States of America; $1.40 for all other addresses; residents of California please add the appropriate amount for State Sales Tax.

Important Notices

If the address sheet of this issue is **PINK**, it is to indicate that **your** dues remittance had not arrived at the time the mailing was **prepared** (*i. e.*, by March 1, 1973). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc. by April 15, 1973. However, in view of the extremely slow postal service, members should not be alarmed by this notice as their remittances may be received between the first of March and the date of mailing this issue. Surface mail in the United States may take several weeks - there is no longer any air-lift program; from overseas addresses we must allow a minimum of 6 weeks for surface mail.

The **pink sheet** is intended only as a reminder and we resort to this means to save on postage charges.

It is with great regret that we must announce the following increases in Membership Dues and Subscription Rates. effective with volume 16:

Membership Dues are US$12.00; to this we must add US$1.50 for members living in Canada, Mexico, Brazil, and all Spanish speaking countries (postally known as PUAS-countries); for members in all other foreign countries, the postage charge will be US$2.00. The basic subscription rate is set at US$25.00; to this must be added the same postage charges as for members.

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$6.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US$12.00 for all foreign addresses (including PUAS).

Because of the peculiar rate-fixing policies of the Postal Service (the so-called "temporary rates" which may be put in effect without advance notice, pending a final decision by the Rate Fixing Commission) we must reserve the right to ask our members and subscribers for additional payment for postage charges; however, because of the rather high cost such an extra collection would cause, we expect to absorb any but unbearable increases. That such increased charges may have to be reflected in future price schedules is evident.

It is general knowledge that in spite of the optimistic statements made in the propaganda disseminated by the U. S. Postal Service, the service continues to deteriorate. Regrettably, however, the United States of America is not alone in this respect. Evidence is accumulating in our offices to the effect that irregularities occur in other countries as well; to our surprise, Japan is one of these. Since we have designed a system which makes it impossible to omit mailing copies of our journal to any member or subscriber who is paid up, and because of the regulations pertaining to the second class mailing permits, we know that if a copy does not reach the addressee, the fault lies with the postal system of the country or area of destination. Our complaints to the local Post Office can bear no fruit in such cases. We must request our members and subscribers to inquire at their local post offices if their copies do not arrive. We cannot replace lost copies free of charge and, unless the journal were mailed by insured post, the Post Office will not indemnify the injured party. The losses we have sustained in the past years have been mounting steadily, and not in proportion to our increased circulation.

REGARDING POSTAL SERVICE

We must call the attention of our Members and Subscribers to the fact that we mail our journal on the date stated on the cover of a particular issue. After we have delivered the journal to the Post Office, our control ends. Delays in delivery seem to become more and more common. Needless to say that we regret this very much; we had hoped that when the salaries of the Postal Workers were increased, the service would improve. However, this seems not to be the case.

In view of the ever increasing difficulties in the postal service, it is essential that members and subscribers not only give us prompt and early notice of address changes, but that proper arrangement for forwarding of our journal be made with the local post office (at the old address). We are not able to replace lost copies free of charge but must charge single copy rates. There will, of course, be only the usual charge of $1.00 for re-forwarding a copy *IF* it has been returned by the post office to us. We also must urge our members and subscribers to place written complaints with the U. S. Post Office Department in case of loss, as every copy of our journal carries our guarantee for return postage. Thus, destruction of a copy of our journal by postal employees constitutes gross negligence and the person concerned deserves an official reprimand, at least.

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. Post Office 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.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of $2.50 (to reimburse us for the expenses involved in redeeming them) and at $0.95 per $1.00 face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Endowment Fund

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

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

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

THE CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.
announces

Backnumbers of

THE VELIGER

and other publications

Volumes 1 through 8: out of print

Volume 9: $22.- Volume 10: out of print
Volume 11: $24.- Volume 12: $28.-
Volume 13: $24.- Volume 14: $28.-
Volume 15: $28.-

Supplement to Volume 3: $6.-* plus $-.75 handling charge
[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;

Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

[The two parts are available separately at $3.- each plus a handling charge of $-.75 or as indicated above. If purchased separately, each part is subject to the California State sales tax if mailed to California addresses.]

Supplement to Volume 7: $2.-* plus $-.60 handling charge
[Glossary of A Thousand-and-One Terms used in Conchology, compiled by WINIFRED H. ARNOLD]

Supplement to Volume 11: $5.-* plus $-.75 handling charge.
[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Vol. 14: $5.-* plus $-.75 handling charge
[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 15: $15.-* plus handling charges as follows: $0.75 for addresses in the United States of America; $1.40 for all other addresses.
[A systematic Revision of the Recent Cypraeid Family Ovulidae by CRAWFORD NEILL CATE]

Items marked with * are subject to sales tax in the State of California; residents of that State please add the appropriate amount to their remittances.
Prices subject to change without notice.

Send orders with remittance to:

Mrs. Jean M. Cate, *Manager,* Post Office Drawer R, Sanibel, Florida 33957. Please make checks payable to C. M. S., Inc.

Shipments of material ordered are generally made within two weeks after receipt of remittance.

Subscription to Volume 16: $25.- domestic; $26.50 in Canada, Mexico, Central and South America, Spain and Spanish Morocco; $27.- in all other foreign countries.

{We are pleased to announce that we have completed arrangements with Kraus Reprint Co. to reprint those of our publications that are out of print. Inquiries regarding the availability and price(s) of desired items should be addressed to:

Kraus Reprint Co.
Route 100
Millwood, N. Y. 10546

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first working day of the month following receipt of the remittance. The same policy applies to new members.

Affiliate Membership for the fiscal year July 1, 1973 to June 30, 1974 has been set at $12.-. Postage for members in Canada, Mexico, Central and South America, Spain and Spanish Morocco $1.50; for members in any other foreign country $2.- additional.

Effective January 1, 1967 there will be an initiation fee of $ 2.- for persons joining the Society.

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.

Supplements

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

Requests to be placed on this special mailing list should be sent to the Manager, Mrs. Jean M. Cate, Post Office Drawer R, Sanibel, Florida 33957.

General Notices

Moving?

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

change of address – $1.-
change of address and re-mailing of a returned issue – $2.-.

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.

California Malacozoological Society, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

Contributions to the C. M. S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes). Bequests, legacies, gifts, devices are deductible for Federal estate and gift tax purposes under section 2055, 2106, and 2522 of the Code. The Treasurer of the C. M. S., Inc. will issue suitable receipts which may be used by Donors to substantiate their respective tax deductions.

BOOKS, PERIODICALS, PAMPHLETS

Life Between Tidemarks on Rocky Shores

by T. A. Stephenson & Anne Stephenson. xii + 425 pages; 227 illustrations. Clothbound $15.00; paperbound $6.95. W. H. Freeman and Company, 660 Market Street, San Francisco, California 94104

The senior author died in 1961, after having spent many years performing the research which is the basis of this book. Throughout these explorations and field studies he was accompanied by his equally competent wife, who undertook the task of putting into book form the results of their labors.

It may be said that the Stephensons, while perhaps not the first, were certainly the most determined proponents of the need of the study of life in the intertidal area as a whole, as a phenomenon that includes both animals and plants. The book, if it did nothing else, makes this thesis convincingly clear.

Through the years of their studies the authors have made, in numerous publications, many valuable contributions to a rational approach to the study of ecology. Possibly the best known of these contributions is their division of the intertidal zone, an approach differing fairly radically from that of Ricketts whose work was confined to the Pacific coast of North America. The Stephensons, however, had long-term close contact with several areas in different parts of the world and short-term contact with most of the others. It is a danger, of course, that with experience based on a long-term study of one particular area, the student is tempted to extrapolate on possibly insufficient evidence obtained in a short visit. Then, too, the long-term student of the Pacific coast of North America might come to conclusions quite at variance with those of a student visiting the area for but a few months; and to compound the difficulties - conditions today are vastly different from those that obtained at the time of the visit by the Stephensons. No one should be surprised by this, since it is well known that pollution and human population pressures have taken a tragic toll among the forms inhabiting the intertidal region.

Despite these limitations, the book is important and very valuable for its presentation of the similarities and differences in various parts of the world at the time the authors studied them.

RS

Shells

Photographs by Andreas Feininger; text by William K. Emerson. 295 pages. The Viking Press, Inc. 625 Madison Avenue, New York, N. Y. 10022. $27.50. November 2, 1972.

This coffee-table-sized book will receive, no doubt, a varied reception, ranging from enthusiastic acceptance without critical appreciation to out-of-hand rejection.

To do the book justice, it is necessary to consider the aim of the photographer on the one hand and that of the author of the accompanying text on the other. The photographer is well known for his artistic interpretations with a photographic camera of various subjects. In this light, his presentation here can only be called superb. Mr. Feininger quite frankly and very obviously is not interested in shells from the point of view of the malacologist or conchologist, but entirely from that of the artist. And that he does his work exceedingly well, no one can deny.

On the other hand, the serious malacologist may consider that some of the illustrations are inappropriate to the subjects photographed. We concur with this latter view only in our moments when we consider the book as a scientific, not an artistic document. In fact, we would rather find this book on the coffee-tables than quite a few others we have seen there.

Dr. Emerson, of the American Museum of Natural History, is a well-known malacologist and an able writer. His critical approach to the scientific aspects of malacology cannot be disregarded. We found his presentation highly readable and reliable as to factual details. That part of the book, starting on page 235, is, in our opinion, a very acceptable approach to the teaching some fundamentals of molluscan classification to the lay public. For, after all, coffee-table "text" books are intended for the browsing layman. In this section Dr. Emerson will no doubt "catch" the interest of many persons who startle the trained malacologist or conchologist with the most peculiar questions about the mollusks.

We would like to recommend that "Shells" replace most of the tomes now on coffee-tables – even children can enjoy it.

RS

Malacological Review

volume 5; 1972. Edited by J. B. Burch and others.
Subscription: $5.00 for volume 6. P. O. Box 801, Whitmore Lake, Michigan 48189.

The present issue is number 2 of the volume and contains a research article by S. K. Wu: Comparative studies on a polyploid series of the African snail genus *Bulinus.* This well illustrated and equally well documented article comprises pages 95 to 164. Two brief communications precede the resolution adopted by the Unitas Malacologica Europaea, which is deeply concerned with conservation and encourages observations and photographic recording of living mollusks, discouraging the actual collection - with the necessary killing - of specimens.

In view of the pressures on all animal communities, such a resolution deserves widest adoption and strict implementation not only in Europe but all over the world.

The usual features of this valuable publication complete the volume.

RS

Catalog of Specimens in the Type Collection of the Department of Geology, California Academy of Sciences
Brachiopoda

by Barry Roth. Occ. Pap. Calif. Acad. Sci., no. 102, 18 pp.; December 27, 1972.

Many malacologists include the brachiopods in their studies. For them, as well as for the students specializing on this interesting group, the catalog forms an indispensable tool. The work is well organized and easy to use. It is hoped that Mr. Roth will be able to follow, in the near future, with a similar list, pertaining, however, to the gastropods and bivalves.

RS

Corrections to the List of European Malacologists 1971

by Oliver E. Paget. Naturhistorisches Museum, Vienna.

While the list originally was intended, at least apparently so, for the members of the European Malacological Union, it is of great help to malacologists everywhere. The present 3-page mimeographed list brings the addresses up to date; it also contains the names of those who have died since the issuance of the original roster.

Dr. Paget has rendered a valuable service to malacology.

RS

Molluscan Digest

volume 3, number 1, January 1, 1973
edited by Jack W. Brookshire, 2962 Balboa Avenue, Oxnard, California 93030.

With this issue, Mr. Steven J. Long announces his resignation from the journal.

This issue is devoted, aside from editorial notes and a list of current events, to an index of all authors cited in the first two volumes of M. D. Following authors' names are listed the citation numbers used in M. D. This compilation should prove useful to the owners of a set of Molluscan Digest.

RS

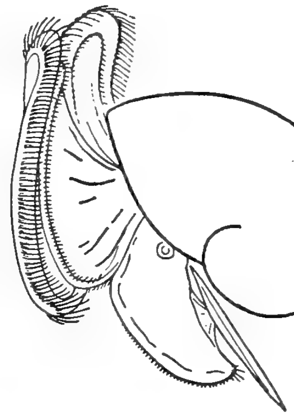
Catalog of Dealer's Prices for Marine Shells

by Tom Rice, Port Gamble, Washington 98364
third edition, May 1, 1972. Retail price: $3.00

of Sea and Shore

volume 3, number 4. Subscription rate: $3.50 per year. This journal continues to increase the number of color illustrations; it includes, among articles of a wide interest to the amateur shell collector, some sound observations on molluscan life and also timely warnings about various dangers lurking in often unsuspected areas. Numerous advertisements from shell dealers all over the world and from other business enterprises may prove useful to many collectors.

RS



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.

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 other 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, may be published in the column "NOTES and NEWS"; in this column will also appear notices of meetings of regional, national and international malacological organizations, such as A. M. U., U. M. E., W. S. M., etc., as well as news items which are deemed of interest to our Members and subscribers in general. Articles on "METHODS and 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, and 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, not exceeding 8½" by 11", at least double spaced and accompanied by a clear carbon or photo 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.

EDITORIAL BOARD

EDITOR-IN-CHIEF

ASSOCIATE EDITOR