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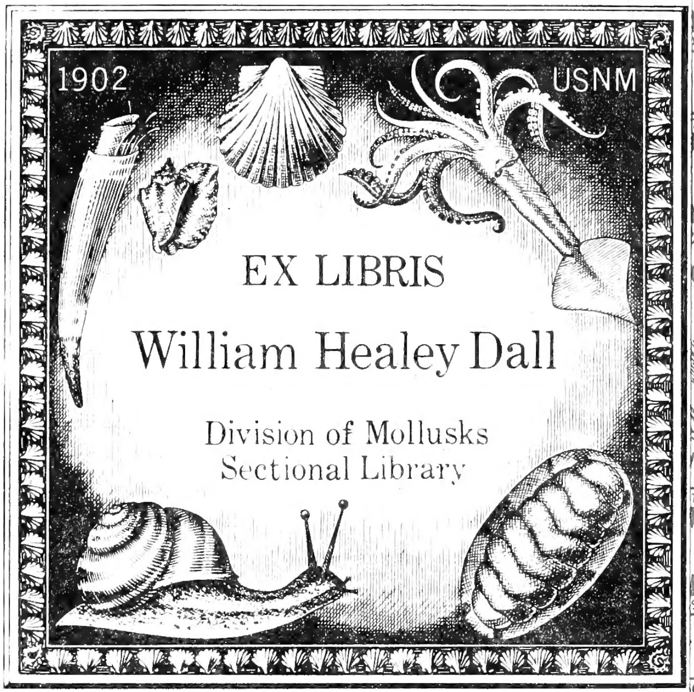

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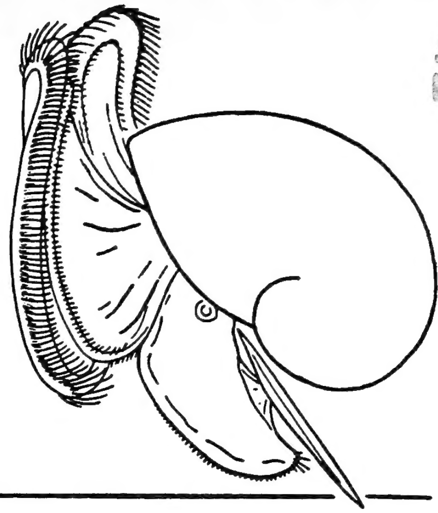

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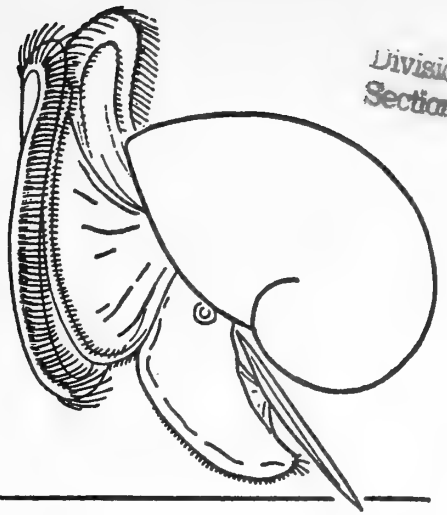

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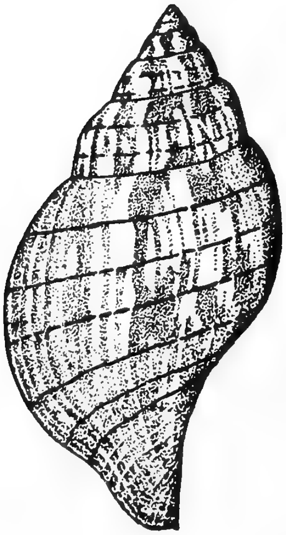


Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

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

The Anatomy and Functional Morphology of the Reproductive System in the Opisthobranch Mollusk *Phyllaplysia taylori* Dall, 1900

BY

ROBERT D. BEEMAN

Marine Biology Department, San Francisco State College, San Francisco, California 94132

(5 Plates; 13 Text figures)

INTRODUCTION

Hermaphroditism evidently is one of the basic features of the opisthobranch mollusks. As might be expected in such a large, diverse, and morphologically flexible group, an immense array of anatomical patterns seems to have arisen to cope with the many functional problems involved where both sex roles are carried out simultaneously in the same individual.

Some information on these systems was included in the large opisthobranch literature which had developed by the early part of the twentieth century, but the total picture of opisthobranch reproduction was very confusing. Most of these older papers treated the reproductive system only from a taxonomic or strictly anatomical viewpoint. Considerations of function were often very limited or were based on speculation rather than on critical observation and experimentation. Ghiselin (1964, 1965) rendered an invaluable service by drawing together information on opisthobranch reproduction from both older and newer literature in an attempt to logically reconstruct the phylogeny of the opisthobranchs. The variety and complexity of the reproductive system provided a pivot point for that study; thus, probable homologies and functions of reproductive structures were stressed. That survey points out the need for much additional study of form and function within specific groups.

The scarcity of functional information in the older papers is due only in part to the rarity of a functional anatomy perspective. It was also due to a lack of techniques for satisfactorily studying living processes. In 1957 the technique of labeling newly replicated deoxyribonucleic acid by tritiated thymidine was introduced (Taylor *et al.,* 1957). The site of origin and the subsequent movements of cells so labeled can be detected by autoradiography. Phase-contrast microscopy also provides a valuable modern tool for observing living material. Electron microscopy adds new dimensions to the study of fixed material. In the present study such new techniques have been applied to old unanswered questions of opisthobranch reproductive function.

The order Anaspidea (the "sea-hares") (defined by Beeman, 1968a) is especially interesting for its complex, incompletely divided reproductive tracts which are probably close to the ancestral patterns of its clade. Despite several papers relating to reproduction in this group, many gaps and conflicts remained. The early accounts, sometimes colorful and often grossly inaccurate, of Pliny (60 A. D.), Cuvier (1803), and others have been reviewed by Mazzarelli (1891, 1893a), Eales (1921), Winkler (1957), and Linton (1966). Most of the study of anaspidean reproduction has been concerned with *Aplysia,* the large sea-hare. Such study had its serious start with the masterful work of Mazzarelli (1891, 1893a). The memoir on *Aplysia* by Eales (1921) is a key work of the early twentieth century. Lloyd (1952) presented one of the few good studies of opisthobranch reproductive anatomy, but her treatment of a single anaspidean (*Aplysia punctata* Cuvier, 1803) was superficial; many of her comments were based on mistaken notions of gamete routing. Winkler (1957) added limited, primarily speculative, information on reproduction in *A. californica* Cooper, 1863. Hopefully, my recent studies of aplysid reproductive biology (Beeman, 1966, 1968a, 1970a, 1970b, 1970c) have helped to resolve many of the key questions concerning the reproduction of these animals. Thompson & Bebbington's (1969) report on reproductive anatomy and function in *Aplysia* independently added support and details to some of these studies and provided the first transmission electron microscopy of the mature aplysid sperm.

The present paper is a modification and expansion of my previous work on reproductive structure and function (Beeman, 1966). This study is basically an attempt to elucidate the reproductive anatomy and functional morphology of the anaspidean *Phyllaplysia taylori*. This is a small, bright green, striped sea-hare (Figures 1 and 2) abundant on the marine angiosperm *Zostera marina* Linnaeus, 1758 in the bays and estuaries of the northeastern Pacific Ocean. There has been relatively little known about it or any other member of the sub-family Dolabriferinae.

Only McCauley (1960), Marcus (1961), and MacFarland (1966) have provided any information, previous to my studies, on the reproductive system of *Phyllaplysia taylori*. These reports are very limited and contain severe conflicts. MacFarland's (1966) post-humous memoir contains the most accurate work ever published on the reproductive system of this species, but its coverage of individual organs is brief and many sections were obviously never completed for the published manuscript. It contains no information on function.

The present report is divided into two parts, one on the anatomy and histology, and another on the functional morphology, each with its own methods and materials section.

I. ANATOMY AND HISTOLOGY OF THE REPRODUCTIVE SYSTEM

METHODS AND MATERIALS

Animals for anatomical study were taken directly from Elkhorn Slough, Monterey County, California (36°48′ N; 121°47′15″ W) or from populations obtained at the slough and maintained in large cement tanks in a greenhouse or out-of-doors at Hopkins Marine Station, Pacific Grove, California. These tanks, held at 14° - 16° C by running seawater, provided very favorable conditions, including rich growths of sessile diatoms for food.

Much of the anatomical study was done on fresh or relaxed live specimens. Most were relaxed by a one-hour immersion in a magnesium chloride solution isotonic with seawater. The succinylcholine relaxation procedure of Beeman (1968a, 1968b) was occasionally used for extremely rapid relaxation; this method was especially useful in the functional morphology study to observe internal functions in progress.

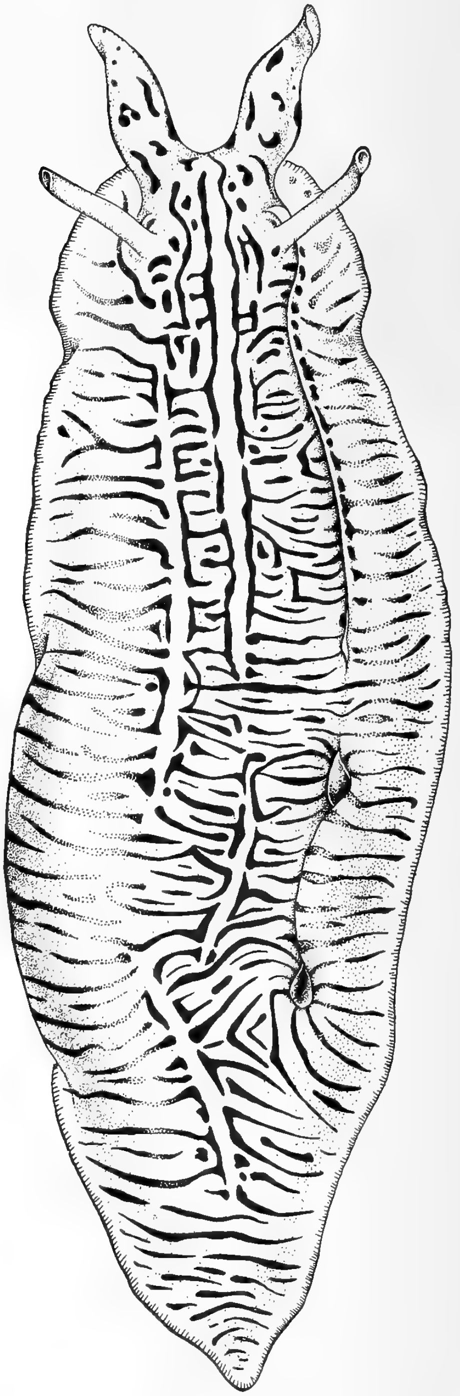


Figure 1

Phyllaplysia taylori

Dorsal aspect of a 4.5 cm individual, from life (from Beeman, 1968a)

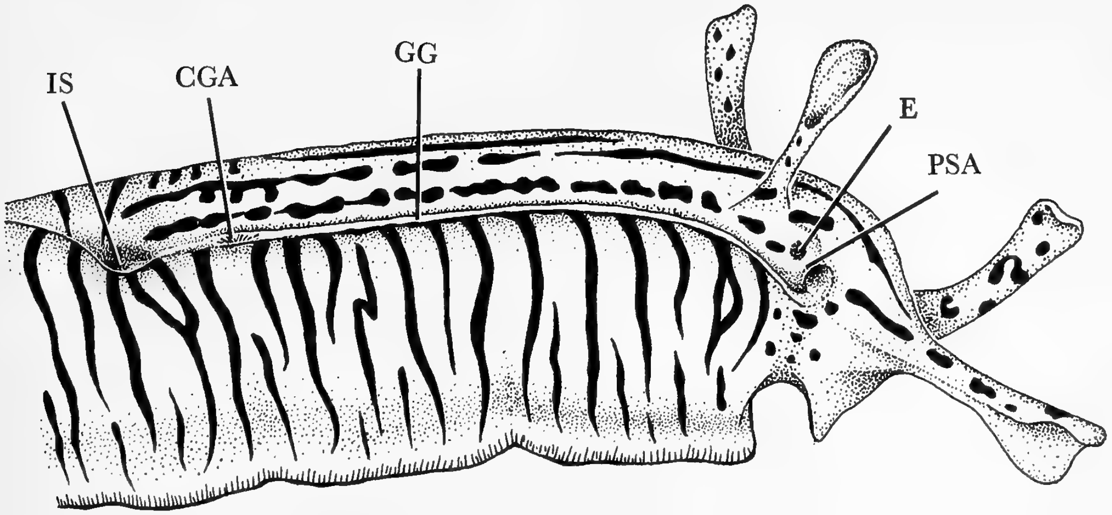


Figure 2

Phyllaplysia taylori

Right lateral aspect of a 4.5 cm individual, from life. The labial lappet is directly ventrad from the penial sheath aperture (Modified from Beeman, 1968a)

Note: Legend abbreviations for all figures are on the foldout near the end of this article.

Methyl green stain was extremely useful in the dissection work. This stain, originally suggested for *in toto* staining of nudibranch mucous glands (Racovitza after Lee, 1928), colors just the mucoid secretory areas and is thus especially useful in contrasting parts of the female gland mass. Methyl green worked best on material fixed in ethyl alcohol or seawater Bouin's solution. Fixed animals were transferred to 70% ethyl alcohol and allowed to remain overnight after the addition of several drops of a stock solution of 1% methyl green in 50% ethyl alcohol.

Animals to be fixed were given a rapid intra-hemocoelic injection of seawater Bouin's fixative into the anterior left quarter of the animal. This afforded almost instant fixation of the nervous system and muscles, thus eliminating most contraction artifact and providing minimal disturbance which might affect the position of gametes. Animals thus killed were fixed overnight in seawater Bouin's solution under refrigeration.

Paraffin sections were cut at 2μ to 20μ; most examinations were made on 7μ slices. Most non-autoradiographic specimens were stained in Kessel's modification of Mayer's Haemalum (Clifford Grobstein, pers. comm., 1962) and counterstained in Galigher's Triosin. Several preparations were stained in Mallory's Triple Stain or Mallory Heidenhain's Azan Stain (Humason, 1962). Autoradiograms (discussed in the functional morphology section) stained with both Mayer's Haemalum and Celestine Blue B, without any counterstaining, were especially useful for examination of many cellular features. The periodic acid-Schiff reaction (PAS) was used to demonstrate 1:2 glycol groups or equivalent amino or alkylamino derivatives (Mowry, 1963). Complete or partial serial sections were prepared of 240 animals, ranging in fixed weight from 0.1 mg to 15.1 g.

Material for scanning electron microscopy was fixed in 70% ethyl alcohol, dehydrated through an ethanol series, and cemented to aluminum disks. These disks were vapor coated with gold on a rotary shadowing stage in a Varian vacuum evaporator, affixed to specimen stubs with silver paint, and examined in a Cambridge Stereoscan scanning electron microscope.

TERMINOLOGY AND GENERAL FEATURES

The terminology used in this study mainly follows that of Ghiselin's 1965 comparative study of opisthobranch reproductive systems. It should be noted, however, that Ghiselin uses structural names, not in reference to function, but to inferred homologies. Some terms have been anglicized for the sake of consistency. The "external seminal groove" of his study is here called the external genital groove since it carries both semen and ova. There is some question that his choice of "membrane gland" is a happy substitute for what is often referred to as the "covering gland" by prosobranch workers (Fretter & Graham, 1962, etc.). However, it is a far better term than "winding gland," an inaccurate term without functional or comparative value which has been used regularly by students of anaspideans. "Ampulla" is retained as a name for a structure which is almost certainly homologous to the ampulla or seminal vesicle of male prosobranchs and which is represented in female prosobranchs only by a corresponding but unmodified segment of the gonoduct. Ampulla is a term well known to opisthobranch workers and is an improvement over seminal vesicle considering that the structure here has a female as well as a male role. I have also followed the concept, used by Ghiselin and others, of dividing the gonoduct into pallial and coelomic regions. This concept seems to be supported by Thompson's 1962 study of nudibranch ontogeny, if ectodermal origin is accepted as evidence of pallial origin.

Comparing the terminology used here to that of other authors, one finds the situation has not changed completely since Bruel (1904) wrote of the contradictions and tangles which were involved in the naming of various vesicles. Ghiselin's work has helped to clarify terminology for the reproductive systems of opisthobranchs as a group, and the present work gives synonyms at several points where possible confusion may arise in the anaspideans. Further discussions of terminology, old and new, are available in Mazzarelli (1891) and Pruvot-Fol (1960).

The general association of the reproductive organs of *Phyllaplysia taylori* is shown in Figures 3, 4, and 5. Starting posteriorly, a large ovotestis empties into the coelomic gonoduct which consists of the ampulla and its pre- and post-ampullar ducts. The post-ampullar duct leads to the fertilization chamber, focal point of the female gland mass and beginning of the pallial gonoduct. The female gland mass is composed of the albumen, membrane, and mucous glands. The pallial gonoduct consists of the common genital duct and its associated organs. The common genital duct connects the above 3 pallial glands to the outside. This outgoing tube is incompletely divided into 2 ducts, the pallial spermoviduct and the copulatory duct. Three chambers open into the common genital duct: the seminal receptacle, the copulatory bursa, and the atrium. The common genital duct opens externally as the common genital aperture. The external genital groove runs forward along the right external body surface from this aperture to the penis ensheathed within the right side of the head.

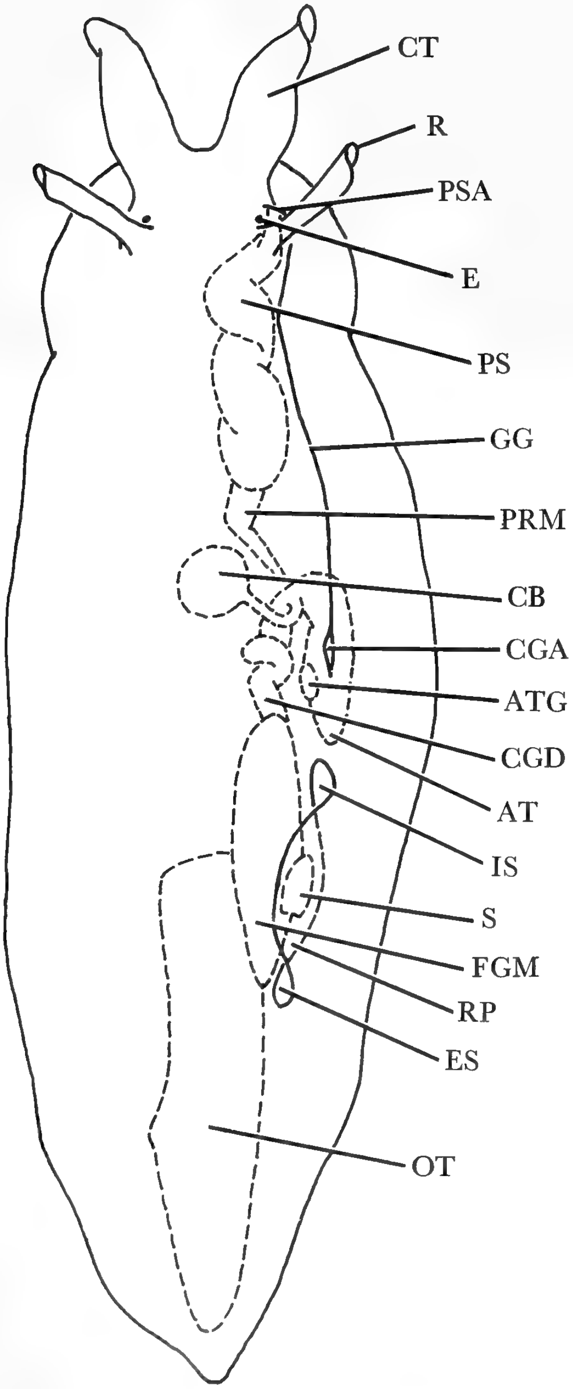


Figure 3

Phyllaplysia taylori

Semi-diagrammatic outline indicating main external features and reproductive system

(Modified from Beeman, 1968a)

OVOTESTIS

Most references to the dolabriferean ovotestis have been made in connection with taxonomic studies; authors have especially noted whether the organ was lobate or non-lobate, a feature which probably depends to some degree on the state of preservation and the extent of dissection. The term "ovotestis" is preferred to its synonym, "hermaphroditic gland," as there is no evidence of glandular secretion. Lūsis (1961) suggests that development of most of the hermaphroditic reproductive system in the pulmonate *Arion* is independent of the ovotestis, as development of other reproductive structures proceeds normally even if growth of the ovotestis is retarded. Other reports, also from outside the opisthobranchs, give conflicting conclusions from meager evidence. Laviolette, in a very short 1956 review, states that there is some evidence of hormonal control by the gastropod gonad.

In mature specimens the ovotestis is the largest of the reproductive organs and second largest organ in the body, being exceeded only by the digestive gland. It is roughly cone-shaped and extends for about $\frac{1}{3}$ of the body length, from a narrow posterior tip which fills the rear of the hemocoel to a blunt anterior end (Figure 3). Anteriorly, the left side is strongly indented by the rounded surface of the digestive gland.

The lobate nature of the ovotestis is made visible upon slightly spreading the organ (Figure 4). The numerous lobes are completely independent, being bound together only by a covering membrane and by the converging branches of the pre-ampullar duct. The branches join to form the main pre-ampullar duct which leads forward from the ovotestis to become the ampulla.

The color of the ovotestis is visible through the ventral surface of the living animal. The organ is quite greenish in most specimens, greenish-yellow in animals with large oocytes, greenish-yellow with yellow spots when oocytes are ripe, and white (and shrunken) in starved individuals. The thin membrane which encloses it often has longitudinal brown stripes of a color similar to that on the exterior of the animal.

Except for the simple squamous epithelia which ensheath the individual lobes and the entire organ, almost every cell of the ovotestis appears generative. A definite germinal epithelium does not exist; both sperm and ova in the last stages of gametogenesis could be found attached directly to the simple bounding membrane, while gametocytes of similar, less, or no visible differentiation form groups along this membrane and within the lobe. This observation on the lack of a germinal epithelium agrees with that of Mazzarelli (1891) for *Aplysia,* but his finding that all the gametocytes differentiate at the same time and thus provide only one breeding season does not agree with the situation in *Phyllaplysia taylori.* There appears to be a decreasing reserve of undifferentiated gametocytes throughout the life of the animal.

Each lobe of the ovotestis is composed of numerous acini, each acinus simultaneously containing a mixture of all stages of male and female cells after the onset of sexual maturation (at about 20 mg body weight). The oocytes are somewhat more common on the periphery, but this tendency is by no means as well developed as in my sections of *Aplysia californica* ovotestis where the great majority of the oocytes is found toward the outside. The lumen of each acinus is filled with the tails of developing sperm, finished gametes, cell fragments, and amebocyte-like cells.

Very early oocytes and spermatocytes could not be distinguished from one another. Oogenesis as such was not studied, though measurements of oocyte diameter were made in connection with growth studies. No division of oocytes was observed in the ovotestis. Oocyte yolk granules show a strongly positive PAS reaction. Details of spermatogenesis in *Phyllaplysia taylori* were presented by Beeman (1970a). Oogenesis was nicely reported for *Aplysia* by Thompson & Bebbington (1969).

COELOMIC GONODUCT

The coelomic gonoduct, referred to by some authors as the ampulla or little hermaphroditic duct, is a single tube leading from the ovotestis to the fertilization chamber. Ghiselin's (1964) convenient subdivision of the duct into 3 regions, a pre-ampullar portion, an ampulla proper, and a post-ampullar portion, is accepted for the present work.

1. Pre-ampullar Portion (PRA)

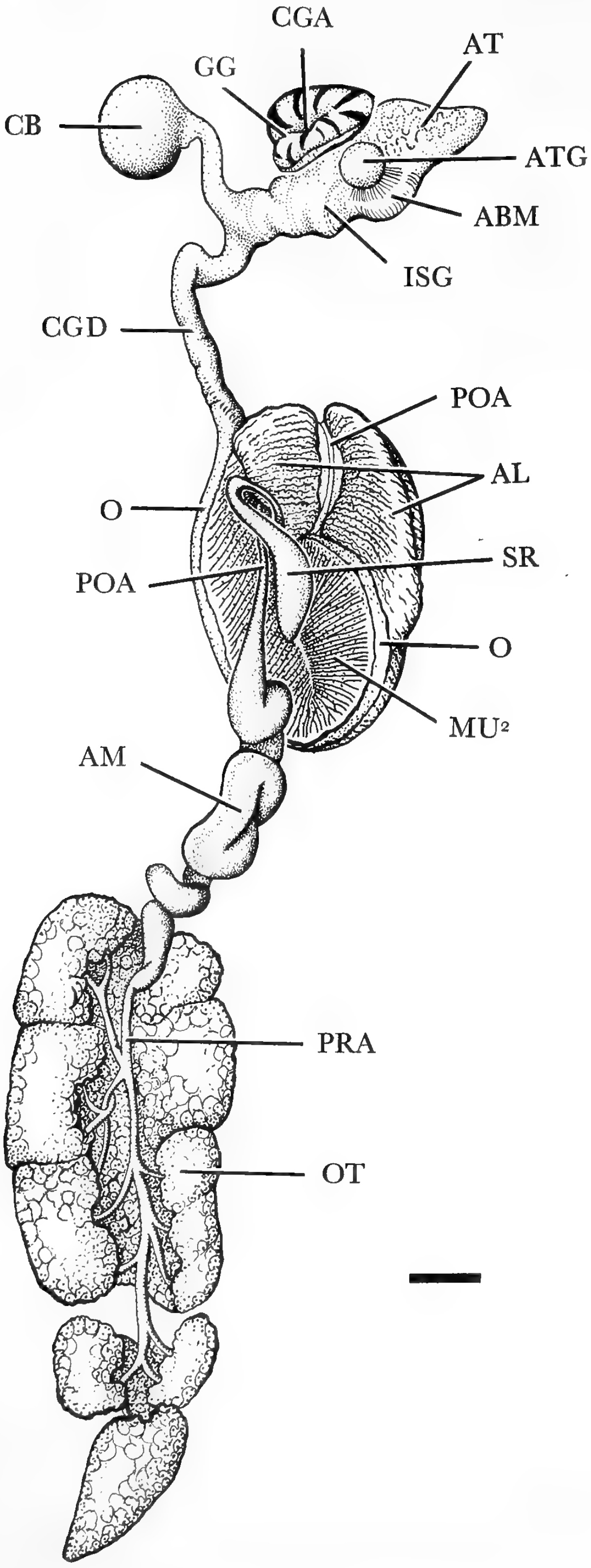
The pre-ampullar portion consists of tiny tubules which converge from the individual lobes of the ovotestis and unite into a single, larger, relatively straight tube which extends anteriorly to about the anterior end of the ovotestis (Figure 4). The thin wall of this tube is little more than a squamous or cuboidal epithelium. The forward end dilates to become the ampulla proper.

2. Ampulla Proper (AM)

The main body of the ampulla is a large, highly convoluted tube (Figure 4). Cuboidal cells, slightly larger on one side of the tube, form a lining externally bounded by sparse connective tissue or muscle fibers and a very thin squamous layer. The tube is generally distended by sperm and oocytes or separate masses of each. The ampulla has a glistening pearly appearance which is due to reflection of light by contained sperm. A distinct band of cilia is centered on the area of the larger cuboidal cells. The cilia cover an increasing part of the internal circumference until the completely ciliated lining of the post-ampullar portion is reached. Distally the ampulla tapers rapidly to become the post-ampullar duct at about the point where it has traversed half of the female gland mass (Figures 4, 36).

3. Post-Ampullar Portion (POA)

The post-ampullar portion or duct leads forward from the ampulla, runs along the left face of the female gland mass, moves over its forward edge to the right face, arches up and over the ventral lobe of the albumen gland, and disappears into the left side of the female gland mass to join the fertilization chamber (Figures 4, 5, 6, *10* (E)). Before it starts the arch over the albumen gland, it becomes very narrow; the lumen may have a diameter no greater than that needed for the passage of oocytes in single file. The tube is completely lined with columnar cells bearing very strong cilia as tall as the cells. A small swelling, erroneously called the fertilization chamber by Marcus (1961), is often evident as the duct slips between the common genital duct and the anterior lobe of the albumen gland (Figure 36). An interesting structure, here designated as the post-ampullar gland (Figures *10*, 36), starts just forward of this point. This gland begins with a few columnar lining cells which are greatly enlarged to form a narrow glandular strip along the wall of the duct. This glandular strip is composed of 2 types of cells, both completely PAS negative. The most obvious are wide columnar cells with basal nuclei and rounded, spreading glandular heads which narrow abruptly before reaching the lumen. Between these are other cells with slender bases against the basement membrane and enlarged distal regions which contain the nuclei. The distal ends of these cells bear strong cilia and are expanded to form what appears to be a solid ciliated surface on the glandular area. This alternate arrangement of thick glandular cells with basal nuclei and thin cells with expanded ciliated



(<— adjacent column)

Figure 4

Phyllaplysia taylori

Left aspect of the internal reproductive organs
Scale line roughly represents 2 mm

(E) Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

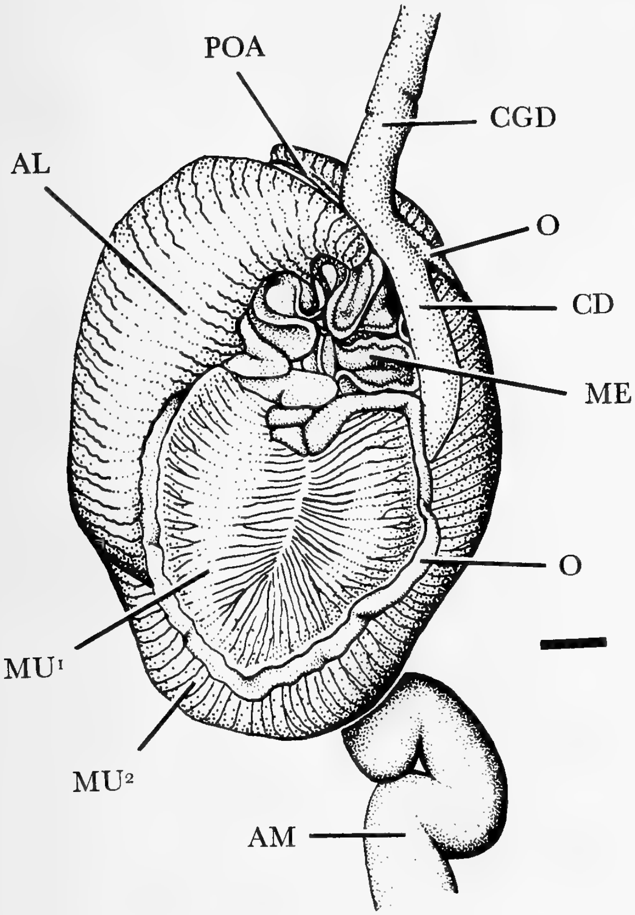


Figure 5

Phyllaplysia taylori

Right aspect of the female gland mass. Dorsal edge is to the left in this drawing
Scale roughly represents 1 mm

tips and distal nuclei is characteristic of many of the glandular areas of the gastropod reproductive tract. It was observed by MAZZARELLI (1891) in *Aplysia* and is nicely represented in his figures 35 and 45, Plate III, for the membrane gland.

The width of the post-ampullar gland increases distally until it lines the complete circumference of the post-ampullar duct except for a narrow groove which is reflected against the side of the tube. The gland stains heavily with methyl green, a mucous stain. In stained preparations the color terminates just as the post-ampullar duct enters the fertilization chamber. Cells of similar morphology, but not staining with methyl green, continue through the chamber into the common genital duct.

There is surprising variation in the accounts of ciliation in anaspidean ampullae. MAZZARELLI (1891) notes some cilia in *Aplysia*. EALES (1921) reports that the ampulla of *Aplysia punctata* is unciliated until it constricts to form the post-ampullar duct. MARCUS & MARCUS (1957) state that cilia occur in both of these parts of the coelomic gonoduct in *A. brasiliana* RANG, 1828, *A. dactylomela* RANG, 1828, and *A. juliana* QUOY & GAIMARD, 1832. THOMPSON & BEBBINGTON (1969) report that $\frac{1}{3}$ - $\frac{1}{2}$ of transverse sections of the ampullae of *A. depilans* GMELIN, 1791, *A. fasciata* POIRET, 1789, and *A. punctata* are ciliated. MCCAULEY (1960) and WINKLER (1957) in their major studies of the anatomy of *Phyllaplysia taylori* and *A. californica*, respectively, made no mention of cilia in the coelomic gonoduct. MACFARLAND (1966) indicates, in what are probably the most careful previously published observations on the reproductive system of *P. taylori*, that the ampulla is lined with cilia "throughout the greater part of its extent."

PALLIAL GONODUCT

Pallial gonoduct is the term used by GHISELIN (1964, 1965) and many others for the reproductive organs intervening between the fertilization chamber and the common genital aperture. It has been assumed that the pallial gonoduct arose originally as a simple epidermal groove or tube which has since evolved complexities and specializations in both structure and function. Although logical, there is as yet little evidence beyond that provided by comparative anatomy to support this assumption.

In anaspideans, the pallial gonoduct is considered to consist of the common genital duct, which in turn gives rise to the female gland mass at its proximal end, the copulatory bursa further distad, and finally the expansion which forms the atrium and atrial gland, before it becomes the external genital groove at the common genital aperture.

1. Female Gland Mass (FGM)

a. Topology

No part of the anaspidean reproductive system has given rise to more confusion than the female gland mass. This term refers to the distinct unit formed by the albumen gland, membrane gland, and mucous gland. The complexity of the association of these organs makes it imperative to consider them as a unit before dealing with them individually.

In most anaspideans the female gland mass is an olive-shaped unit stemming from the proximal part of the pallial gonoduct at its junction with the coelomic gonoduct. Figures 3 and 4 show that in *Phyllaplysia taylori* its position is similar, but the mass is laterally more flattened; the right side bulges convexly against the left wall of the gill cavity, while on the left side the mass is generally concave due to its cramping against the rounded surface of the digestive gland. The common genital duct, the tubular portion of the pallial gonoduct, runs forward from its ventral edge.

The fertilization chamber, shown in Figures 36 and 37, is the structural and functional focal point of the female gland mass. It connects directly to the common genital duct, the 3 glands of the female gland mass, and the seminal receptacle and thus should be considered with them as part of the pallial gonoduct.

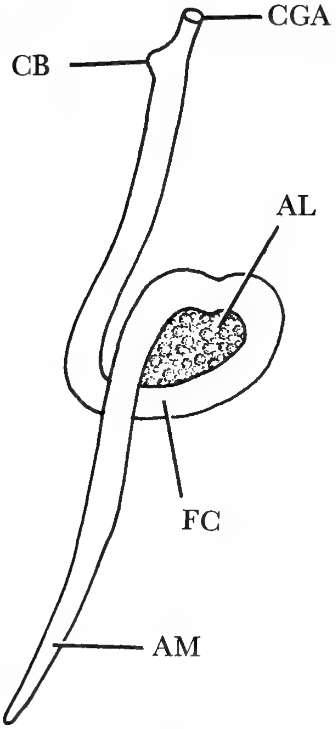


Figure 6

Juvenile condition of the reproductive system in *Aplysia punctata* Modified from Mazzarelli, 1893a. Not to scale

Figure 4 shows the left face of the female gland mass with the seminal receptacle and the anterior part of the ampulla nestled in its concave surface. The ventro-posterior surface is occupied by the translucent white secondary lobe of the mucous gland. The albumen gland, closely matching the mucous gland in texture but of a slightly yellower cast, fills the anterior region. The descending loop of the post-ampullar duct marks the albumen gland into ventral and dorsal parts. Dissecting away the ventral part exposes the junction of the descending loop of the post-ampullar duct with the fertilization chamber (Figure 36).

Careful dissection and reconstruction of serial sections have shown that the female gland mass of *Phyllaplysia taylori* is basically 3 sacculations with all their internal surfaces continuous with each other in the area of the fertilization chamber (Figure 36). Each of these 3 pockets develops into a gland whose wall is then folded into increasingly complex patterns. No part of the mass is a true tube separate from the rest of the pallial gonoduct. The "tubes" that have been reported previously are the internal edges of folds.

While the ontogeny of the female gland mass has not been followed, it is possible to visualize how this system may develop. Figure 6 is a modification of Mazzarelli's (1893) sketch of the hermaphroditic system in a juvenile *Aplysia punctata*. It simply shows a single tube running from the ovotestis to the common genital aperture; the middle of this tube is thrown into a loop within which the albumen gland is found. With some imagination, one can think of one side of the above loop giving off 2 pockets at the fertilization chamber point. One of these pockets would be the membrane gland which then secondarily develops a tortuous folding. The other pocket would be the mucous gland secondarily turning anteriorad in a manner which results in a small right primary lobe and a large left secondary lobe. These processes would result in pockets of the shape suggested by Figures 35 (MU^1 and MU^2) which shows the routes taken by eggs around the internal edges of these folds of the adult.

The seminal receptacle and albumen gland also open into the fertilization chamber. They are merely arched blind outpocketings. The albumen gland fits in the large dorsal groove between the 2 lobes of the mucous gland (Figure 36).

It is evident that evagination and infolding of simple tube linings, even to a quaternary order, are basic mechanisms by which the organs of the female gland mass and, as shown later, the other reproductive organs in this anaspidean are formed.

b. General Discussion

The fertilization chamber is not only the focal point of form and function of the female gland mass; it is also the center of controversy and of conflicting and partly or wholly erroneous reports. There are only 3 original figures of the reproductive system of *Phyllaplysia taylori* in the literature. MacFarland (1966) shows only an external view of the system, McCauley's (1960) figure shows an incorrect arrangement of the organs, but correctly indicates most of the connections to the fertilization chamber. McCauley evidently believed that all of these connections were tubes and that the chamber did not connect directly to its mucous gland. Marcus (1961), despite reference to McCauley's paper, gives a completely erroneous diagram. The slight swelling in the ascending limb of the post-ampullar duct is labeled as the fertilization chamber, whose only exit is into a tubular membrane gland, which in turn connects to a tube running along the female gland mass to the common genital duct. No connections to what should be the albumen and mucous gland are indicated. Marcus & Marcus (1957b) seem to show a similar arrangement in *P. engeli* Marcus, 1955, except here they indicate the seminal receptacle, where "the alien spermatozoa are heaped without any order," attached near the "fertilization chamber" rather than high on the common genital duct. The authors state that the "acidophil albumen and basophil mucous gland communicate with the *sperm*oviduct [emphasis mine] by several connections." Both these latter papers indicate that the only connection between the ampulla and the common genital duct is through a single tube which follows a long course around the female gland mass and has occasional connections with it (Figure 34).

It is not now possible to predict the extent to which the folded arrangement of the female gland mass of *Phyllaplysia taylori* will be found to apply to other anaspideans. The condition may be widespread. The routes in this mass may have formed into true tubes in some species; however, since folds in *P. taylori* have been repeatedly called tubes, the existence of such "tubes" in other anaspideans is highly suspect.

The folded nature of the membrane gland has been reported previously by Guiart (1901) for *Aplysia punctata,* and by Marcus & Marcus (1957a) for *A. brasiliana, A. dactylomela,* and *A. juliana.* Interpretation of the membrane gland as a "winding gland" of convoluted tubules seems to be an error that has long persisted. Mazzarelli's (1891) description, many features of which can be traced to Cuvier (1803), refers to this gland as "twisted like a ball of thread." This view has been maintained by MacFarland (1909, 1918), Eales (1921), Winkler (1957), McCauley (1960), and others.

The primary and secondary folding of the mucous gland has not been reported previously. As noted above, all previous authors who have dealt with *Phyllaplysia taylori* have considered this gland to be a tube. Mazzarelli (1891), Guiart (1901), Eales (1921), and Thompson & Bebbington (1969) clearly show it as a tube in *Aplysia punctata.* This is difficult to believe, for (as noted later), the female gland mass of this species has a special similarity to that of *P. taylori.* MacFarland's 1918 work on *Dolabella* mentions the "plication of the walls of this duct," but this refers to the tertiary folding within the gland.

It is now difficult to apply the classic descriptive terms "monaulic," "diaulic," etc. to *Phyllaplysia taylori*'s complex single-tube pallial gonoduct. Ghiselin (1965) has reminded opisthobranch workers that the word "aulic" refers to a tube, and thus words coined from it should refer only to the number of reproductive tubes. Using as a model Eale's (1921) diagram of the *Aplysia punctata* reproductive system, which clearly portrays a tubular female gland mass, Ghiselin has coined the term "oodiaulic" to apply to the reproductive systems of the Anaspidea, the Cephalaspidea of the family Diaphanidae, and the Sacoglossa. Ghiselin (*loc. cit.*) defines the oodiaulic condition as "a variation of the ancestral form in which the nidamental glands have, to a greater or lesser degree, acquired a separate, closed channel by a division of the pallial gonoduct." From a strictly morphological viewpoint, *P. taylori* is monaulic, though perhaps it could be considered as presumptively or functionally diaulic. If Ghiselin's term "oodiaulic" is to be applied, it should be used only with the clear understanding of the slight extent to which the nidamental glands can be considered to have a "separate closed channel."

c. Phylogenetic Significance

The importance of the arrangement of the organs in the female gland mass has been much neglected. This is partly due to a poor understanding of its anatomy. Its complexity makes it an exceedingly difficult area to dissect, to interpret in serial sections, and to illustrate, while its glandular nature and high mucus content pose special problems to one making histological preparations for study. Most anaspideans have ovoid-shaped female gland masses which have evidently undergone greater compaction than that of *Phyllaplysia taylori,* and which present an external banding which probably reflects further internal complication. The complete internal arrangement of such a female gland mass has never been satisfactorily worked out. Mazzarelli (1891) shows external views and a sketchy diagram of the internal arrangement for this type of female gland mass in *Aplysia limacina* Linnaeus, 1758 and *A. depilans* Gmelin, 1791. Anderson (1933) and Winkler (1957) do the same for *A. californica.* Marcus & Marcus (1957a) show a similar unit for *A. cervina* Dall & Simpson, 1902, *A. brasiliana, A. dactylomela,* and *A. juliana.*

It is here proposed that the type of female gland mass found in *Aplysia californica* be called the "banded-ovoid type" and the homologous but very different appearing mass in *Phyllaplysia taylori* be called the "flat-pocket" type. It must be emphasized that these are terms of convenience only; the bands of the banded-ovoid type may indeed represent parts of extended pockets, but this is not externally apparent and has not been well confirmed internally.

It is interesting to note the occurrence of the different female gland mass types in the anaspideans. As would be expected, other *Phyllaplysia* species seem to have the flat-pocket type. The very sketchy figures of MARCUS & MARCUS (1957b) and MAZZARELLI (1893b), for *P. engeli* and *P. lafonti* (FISCHER, 1870) respectively, indicate this. PRUVOT-FOL's (1954, 1960) exceedingly poor diagram of *Petalifera petalifera* (RANG, 1828) suggests a similarity to *Phyllaplysia*. GUIART's (1901) diagram of *Notarchus punctatus* PHILIPPI, 1836 and MACFARLAND's (1918) diagram of *Dolabella agassizii* MACFARLAND, 1918 also suggest the flat-pocket type. The female gland mass of *Dolabrifera* has not been adequately figured; PRUVOT-FOL's (1960) diagram of the reproductive system of an unspecified *Dolabrifera* is meaningless.

Most interesting comparisons can be made between *Phyllaplysia taylori, Aplysia punctata,* and *Akera bullata* MÜLLER, 1776. MAZZARELLI's (1891) and EALES' (1921) figures for *Aplysia punctata* show external and internal features which very strongly suggest that the female gland mass is of the flat-pocket type, and is perhaps even simpler than that of *P. taylori.* INGIER's (1906) work on *Akera bullata* lacks diagrammatic or functional layouts of the reproductive system, but her excellent drawings of gross anatomy and serial sections show features amazingly similar to those of *P. taylori.* The albumen gland even fits between the lobes of the mucous gland in the same manner. *Akera,* although very probably divergent in several ways from the ancestral anaspideans, is generally accepted as an anaspidean with many primitive features (GUIART, 1901; BOETTGER, 1954; BEEMAN, 1968a; etc.). This suggests that the flat-pocket type of female gland mass is more primitive than the banded-ovoid type. As far as presently is known, all species of *Aplysia* other than *A. punctata* have the banded-ovoid type. It would be interesting to know if *A. parvula* GUILDING *in* MÖRCH, 1863, the only other member of the subgenus *Pruvotaplysia* to which *A. punctata* belongs, has the flat-pocket type of female gland mass. EALES (1960) did not mention any reproductive features in establishing this subgenus, but she considers all of the characters listed as features of the subgenus to be primitive ones. If both *P. taylori* and *A. punctata* are presumptively oodiaulic, they are closer to each other in reproductive structure than either species is to other *Aplysia* species.

The features of the individual organs of the female gland mass can now be considered separately. It should be noted that many authors, such as PRUVOT-FOL (1960) and MACFARLAND (1966), do not recognize a distinction between membrane gland and mucous gland.

2. Albumen Gland (AL)

The "albumen" gland of *Phyllaplysia taylori* is a large, yellowish-white caecum extending from the fertilization chamber. Its anterior end forms most of the forward part of the female gland mass; its posterior section fits between the dorsal edges of the 2 mucous gland lobes. Most of its external features are discussed in the preceding section and illustrated in Figures 4, 5, *26,* and 36. Its position and connection have been noted correctly by almost every author except MARCUS (1961).

The large, irregularly-shaped lumen often has a large secondary fold running along its dorsal and anterior edge (Figure 36). The walls are composed of thin, longitudinal, tertiary folds which extend into the lumen as sharp-edged ridges. These folds are composed of broadly columnar, strongly PAS-positive, unciliated cells. The elliptical basal nuclei are about $\frac{1}{4}$ the height of the cells; each contains a single distinct nucleolus. The upper $\frac{2}{3}$ of each cell are densely filled with secretion granules. A dense connective tissue fills the thin spaces between the folds and the squamous epithelium which forms a simple, tight sheath over the entire organ.

The gland narrows sharply as it enters the fertilization chamber. As noted by MACFARLAND (1966), this neck is lined with a low ciliated endothelium. The cilia, averaging 11μ, are up to twice the height of the cells which bear them. MACFARLAND also reports large nerve cells "projecting into this epithelium at intervals."

3. Membrane Gland (ME)

This small gland forms the right-anterior section of the female gland mass (Figures 5, *26,* 36). Its spatial arrangement and associations with the remainder of the gland mass have been discussed above. The tangled external appearance caused by its secondary folding has led many authors to call it the "winding gland." Others have referred to it as a special part of, or have failed to distinguish it from, the mucous gland. It has many structural and histological resemblances to the mucous gland and may only be a specialized part of that organ. Like the mucous gland it is moderately PAS positive. The membrane gland differs from the mucous gland primarily in its position and in its highly convoluted folding. Its entrance is formed by a fold which gives the impression of a tube leaving the fertilization chamber (Figure 36).

Methyl green staining reveals vividly that the membrane gland is not uniformly glandular. The proximal, anterior region stains darkly while the distal, posterior folds do not stain (Figure 5). A tortuous line of unstained tissue indicates the edge of the oviducal groove. This edge is composed of cuboidal cells with very powerful cilia 2 to 3 times the height of the cells.

The endothelium lining the glandular anterior region of the membrane gland has the same arrangement of glandular and ciliated cells described for the post-ampullar gland. The cilia are up to twice the height of the cells which bear them. Ciliation is less dense away from the groove. Toward the non-staining posterior region of the membrane gland, the ciliated and glandular cells become sparser. The oviducal groove continues from this area into the primary lobe of the mucous gland.

4. Mucous Gland (MU)

The mucous gland is a semi-translucent white organ which forms the greater part of the female gland mass (Figures 4, 5, 36). Due to its complex folding, discussed in the preceding section, it forms 2 unequal, connected lobes, the smaller being visible on the left side. Since the smaller lobe is the first in the sequence out of the membrane gland, it is here designated as the primary mucous gland lobe (MU^1); the larger lobe is thus the secondary lobe (MU^2).

A strongly ciliated groove follows the inside edges of the gland (Figure *13*). This is an extension of the oviducal groove from the membrane gland. After following the double U-shaped route indicated by Figures 35 and 36, the oviduct leaves the gland and becomes part of the spermoviduct of the common genital duct. The oviducal groove in the mucous gland is composed of a simple ciliated columnar endothelium. A group of special gland cells, resembling those of the post-ampullar gland but strongly PAS-positive, are present along one of the inner sides of the open groove.

The oviducal groove opens along its entire course on one side to the non-ciliated, glandular region which comprises the bulk of the mucous gland. The glandular region is composed of third and fourth order folds which form ridges running diagonally to the oviducal groove. The cells are only moderately PAS-positive. When the cells are not secreting, the general histology resembles that of the membrane gland. Cell structure and staining properties differ from those of the albumen gland. Methyl green stains the mucous gland green or blue-green; it leaves the albumen gland white in alcoholic solutions. Two cell types are found in the walls of the mucous gland. The larger cells are columnar with occasional vacuoles near the base and large spherical nuclei about halfway up the cell body. The smaller cells possess nuclei about ½ the diameter of those in the larger cells; the cells are broad distally and apparently have slender basal extensions. During the secretory phase the vacuoles expand to almost fill the large cells and swell the cells several fold.

Connective tissue bearing blood sinuses lined with squamous cells fills the small spaces under the folded epithelium lining the mucous gland. The entire organ is encased in the usual sheath of very thin squamous epithelium.

5. Seminal Receptacle (SR)

The seminal receptacle is a blind sac. While it opens into the fertilization chamber in *Phyllaplysia taylori,* this is not the case in all anaspideans. My dissections of *Aplysia californica* show that its sole opening is at a point over ½-way up the common genital duct in that animal. Positional variations of this type are the basis for a long-standing dispute in the literature. A connection between the seminal receptacle and the fertilization chamber in aplysids was first reported by Cuvier (1803) and this duct later came to be known as the "duct of Cuvier." This term was then used in reference to aplysids in which the seminal receptacle opened at a point very near the fertilization chamber and thus "duct of Cuvier" was virtually synonymous with the term "seminal receptacle duct." Mazzarelli (1891) figured the seminal receptacle duct of a "generalized" aplysid as opening into the proximal region of the common genital duct. He used the term "duct of Cuvier" to refer, not to the seminal receptacle duct, but to a hypothetical connection between the seminal receptacle duct and the fertilization chamber. However, MacFarland (1909) continued to consider "duct of Cuvier" as synonymous with seminal receptacle duct and he applied the former term even to a seminal receptacle duct which opened into the common genital duct far from the fertilization chamber. The resulting confusion led Marcus & Marcus (1957) to declare that there was a "serious discrepancy between MacFarland's and our observations" concerning *Aplysia cervina.* Actually the figures of Marcus & Marcus (*op. cit.*) and MacFarland (*op. cit.*) agree perfectly on this point. The term "duct of Cuvier" has only caused continued confusion and it should be abandoned by malacologists.

The point at which the duct of the seminal receptacle opens into the pallial gonoduct varies in different anaspideans. This also raises a question as to whether the organs referred to as seminal receptacles are really homologous structures throughout the anaspideans and other opisthobranchs.

The internal structure of the seminal receptacle is shown in Figures *27, 28, 29,* 30 and 31. A very thin outer sheath covers a thick underlying muscular layer. This, in turn, is lined with a single unciliated columnar endothelium. Variations in the height of the endothelium form longitudinal ridges and furrows adjacent to the lumen. The nuclei lie basally in the endothelial cells and are about ½ the height of the shorter cells. Scanning electron microscopy reveals that inner tips of these endothelial cells are rounded, equipped with microvilli, and secrete material into the lumen.

If the gastropod seminal receptacle is defined as the female region containing oriented sperm (*e. g.*, Ghiselin, 1965), this structure fits the definition well. Figure *29* shows sperm packed in parallel rows in the furrows of the receptacle. The tips of these sperm are embedded into the endothelial cells. The development of the muscle coat and the endothelial ridges diminishes as the receptacle narrows to form its arched duct.

6. Common Genital Duct (CGD)

The common genital duct (= large or wide hermaphroditic duct) is a tubular continuation of the pallial gonoduct from the fertilization chamber and the pallial oviduct to the common genital aperture (Figures 4, 5, and 36). Externally it appears as a single duct in *Phyllaplysia taylori,* but it is actually composed of 2 distinct and parallel ducts, the pallial spermoviduct and the copulatory duct (= vaginal channel), plus an intervening space. These 2 ducts are incompletely separated by 2 infolded ridges of the lining endothelium, here called the spermoviduct fold and the copulatory fold (Figures *15* and 36). Thompson & Bebbington (1969) also found this duct to be incompletely divided in *Aplysia punctata, A. fasciata,* and *A. depilans.* This arrangement evidently does not occur in all anaspideans. In some species of *Aplysia* much of the proximal part of the common genital duct is reported to be completely divided (*cf.* Marcus & Marcus, 1957a, fig. 16). Functionally and phylogenetically, the divided pattern is probably a more advanced condition.

The spermoviduct fold is the largest of the internal folds and vertically divides the common genital duct throughout its proximal part. Its free edge is either broad or recurved toward the copulatory duct. At the level of the copulatory bursa duct (Figure 4), the spermoviduct fold is pressed against the inner wall of the common genital duct to form an internal seminal groove which makes 2 counter-clockwise turns and then reverses for ½ of a clockwise turn as the common genital duct coils tightly between the copulatory bursa duct and the atrium. These turns are partly visible on the outside of the system (Figure 4). The internal seminal groove then avoids the lumen of the atrium and makes 2 clockwise turns before it reaches the exterior at the common genital aperture.

A third fold, here called the egg-string guide, is prominent at the proximal end of the pallial gonoduct, but tapers out and disappears before the level of the entrance of the copulatory bursa duct. This blunt fold is found in the wall of the spermoviduct. A true continuation of the pallial oviduct from the female gland mass (Figures *13* and *26*) can be followed within the spermoviduct (Figure *15*) until this small fold fades out.

The copulatory bursa duct enters the pallial gonoduct where the latter becomes tightly coiled. Internally the copulatory bursa duct enters the copulatory duct (Figure *23*), but it is at this point that the above-mentioned seminal groove begins and part of the space of this spermoviduct merges into the copulatory duct.

The copulatory duct is more distinct in its entire route. Proximally it forms a caecum slightly below the fertilization chamber (Figure *26*) and then extends as a duct distad, forming the atrium by great expansion of one side; and finally it opens to the exterior by a short duct surrounded by the final coils of the internal seminal groove. This opening of the copulatory duct and the modified spermoviduct to the outside of the body is the common genital aperture. The seminal groove continues anteriorad from this aperture as the external genital groove.

The histology of the ducts helps to define their extent, especially in cross-section. The same special endothelium of broad, columnar secretory cells and slender, distally expanded ciliated cells described for the post-ampullar gland and the membrane gland also lines the spermoviduct. This tissue matches what Ghiselin (1965) has referred to as the "prostate." It will be referred to here as the spermoviduct gland. In typical cross-section views (Figure *15*), this special endothelium starts near the oviduct side of the spermoviduct fold and extends to the base of the copulatory fold. Its ciliary and secretory nature is most strongly developed in the oviduct region of the spermoviduct (Figure *14*). In one specimen, the glandular cells were 100μ long and 10μ wide, while the ciliated cells, also 100μ long, were only 1 or 2μ wide for most of their length. Such cells have been well illustrated by Mazzarelli (1891) and Lloyd (1952). The cells become lower and more cuboidal toward the base of the copulatory fold.

The spermoviduct gland represents a continuation of the oviducal gland tissue; the cells are similar histologically, and are also strongly PAS positive. The spermoviduct gland becomes restricted distad to the internal seminal groove, and finally disappears about the level of the atrium. The remainder of the common genital duct, mostly copulatory duct, is lined with columnar-cuboidal ciliated cells. A few greatly expanded, highly basophilic cells are found in the region of the egg-string guide.

The entire common genital duct is encased in a circular layer of smooth muscle. The thickness of this muscular coat diminishes distally except for special development near the atrium and common genital aperture. A simple squamous epithelium covers the outside of the tube.

7. Copulatory Bursa (CB)

The copulatory bursa is an almost perfectly spherical organ connected to the upper part of the common genital duct by a thin muscular tube (Figures 4 and *24*). Tissue layers present include the usual thin outer epithelium, a middle layer of connective tissue and muscle, and a lining of columnar endothelium (Figure *25*). This sphere is capable of great expansion but, unlike the atrium, it possesses no special folds to accommodate this.

The endothelial cells lining the organ are very distinctive. The entire cell shows a strong pattern of longitudinal fibers; these are especially well developed in the upper and lower quarters of the cell body which seem to be devoid of all other structures and which stain a pale mixture of red and blue in hematoxylin and eosin preparations. The fibers are especially dense proximally, and form a distinctive basal band in which visible cell boundaries are lacking. This band resembles the basal fibrillar apparatus which Wilson (1925) referred to as tonofibrillae and described as having a skeletal support function within tissues. The center ½ of these cells is less dense and takes a much more definite basophilic stain. A very distinctive elongate nucleus occurs in the lower region of this section. A clear vacuole, which appears to be part of the nucleus, is apparent at its basal end. This vacuole is enlarged beyond the width of the nucleus in a few cells, is about nuclear width in the majority of cells, and is apparently discharged in others. From 1 to 4 clear vacuoles are usually evident in the upper part of the basophilic region. Some of these vacuoles coalesce; a very few seem to be discharging through the dense upper quarter of the cell to the lumen of the bursa.

The bursa is rarely empty. Usually it contains a strange, layered mixture consisting of granules, spermatozoa in various stages of breakdown, amorphous material, and yellow-red to dark-red oil droplets (Figure *23*). The amorphous material frequently forms large, rounded, densely packed nodules.

The copulatory bursa duct is a muscular tube lined with a simple cuboidal endothelium bearing cilia 2 or 3 times the cell height. The nature of its connection to the common genital duct has been discussed in the section on that duct.

8. Atrium (AT)

The atrium or genital atrium is a large expansion of the posterior side of the copulatory duct near the common genital aperture (Figure 4). It is a loosely walled sac with a posterior tip, often curved ventrally.

The outer wall is a muscular layer with a thin squamous epithelial covering. The inner surface is an enormously convoluted columnar endothelium (Figure *11*). A "cuticle" covers the lumen surface of the cells. This layer is about ¼ to ⅓ the height of the cells, with occasional areas which are very much thicker or thinner. Due to the presence of this layer it is not possible to discern if this surface shares the ciliary cover found in almost all of the rest of the common genital duct. The lumenal endothelial cells are entirely basophilic except for a slightly eosinophilic basement membrane. The lumen ends of the cells are expanded. The nuclei are central and elongate. A clear vacuole-like structure is occasionally seen next to the basal end of the nucleus.

The duct from the atrial gland enters the left side of the atrium. The internal genital groove bypasses the atrium at the anterior end of the lumen.

Two muscular bands close the 2 main atrial openings. A very heavy muscular semi-circular band, here called the atrium basal muscle (ABM), is found on the copulatory duct at its proximal, anterior entrance. A sphincter encircles the short portion of the common genital duct which forms the distal, dorsal exit of the atrium.

The development of the atrium is highly variable among different anaspideans. A small swelling where the copulatory bursa duct joins the common genital duct is designated as the "lateral pocket, or bursa seminalis" by Eales (1921) and referred to as the "clustered gland" by Marcus & Marcus (1957a). Thompson & Bebbington (1969) refer to a similar swelling in *Aplysia fasciata* and *A. punctata* and an extended glandular area in *A. depilans* as a prostate gland. These structures are probably homologous with the atrium of *Phyllaplysia taylori*, as their walls bear a glandular tissue which seems to be identical with that of the atrial gland in my material.

A similar small swelling is shown as the "réservoir séminal" for *Akera bullata* by Guiart (1901). This is evidently the same structure that Ingier (1906) labels the "Prostatadrüse." The large organ which MacFarland (1918) calls the "seminal receptacle" in *Dolabella agassizi* matches the description and illustration of the atrium in *Phyllaplysia taylori.* It is obvious that knowledge of this organ leaves much to be desired.

9. Atrial Gland (ATG)

The atrial gland in *Phyllaplysia taylori* is a distinct ovoid organ attached to the left side of the anterior, proximal end of the atrium (Figure 4). Its single duct connects directly with the atrial lumen near the atrium basal muscle. In living animals, the yellowish color of the gland contrasts with the greenish-white of the atrial walls.

The atrial gland can be recognized instantly in sections by its compact clusters of acini entirely lined with basophilic glandular cells (Figure *12*). There are typically 3 rows of these acini encircling and opening into a central lumen. A thin layer of connective tissue surrounds the acini and a simple squamous outer epithelium covers the outside of the organ.

The acini are lined with a simple endothelium of large columnar cells with spherical basal nuclei each containing 1 or 2 distinct nucleoli. The upper halves of these cells are expanded and contain numerous clear, coalescing secretory vacuoles. Cilia, as long as the cells, line all of the internal ducts and part of the main duct to the atrium. The cells of this main duct are distinctly different from those of the gland; they are very much smaller, non-secretory, and grade from columnar to cuboidal in shape.

The atrial gland is often confused with the atrium itself by authors dealing with other anaspidean species.

EXTERNAL GENITAL GROOVE (GG)

The external genital groove is a continuation of the pallial spermoviduct, and extends along the outer body wall from the common genital aperture to the tip of the penis. The groove is not homogeneous throughout, but possesses 2 distinct regions. The first runs along the right dorsal surface of the animal from the common genital aperture to the opening of the penial sheath near the right rhinophore (Figure 3). A flap extending from the dorsal left edge of the open groove forms this region into a functional duct. Most of the circumference of the duct is lined with a simple, strongly ciliated epithelium of cuboidal to columnar cells. The nucleus is central in each cell. Occasional glandular cells similar to those in the PAS-positive mucous glands of the skin occur. The second section of the external genital groove runs into the penial sheath, along its wall, and then along the glans penis (Figures *19, 20,* and *21*). Cross-sections of the glans penis show that this section of the groove forms a duct by inrolling of the groove and an expansion of its bottom. The groove is lined with very small cuboidal cells; those along the bottom of the groove bear cilia 2 or 3 times their height.

PENIS (P)

The penis of *Phyllaplysia taylori* (Figure *19*) is composed of the penial sheath (termed preputium by some authors) and the glans penis (termed penis by most authors). The sheath is obviously a tubular inpocketing of the outer body wall surface; it even has fine parallel stripes for about $\frac{1}{3}$ of its extent which match the pigment of the dorsal stripes. When inrolled, the sheath projects into the hemocoel along the brain; it opens to the surface by the penial sheath aperture under the right eye. The glans penis rests coiled within the sheath, attached to the latter at its inner end. The glans is a flattened organ with the genital groove running along one edge. Powerfully muscular, the glans is composed mainly of crossbedded erectile tissue. Both the sheath and the glans are armed with cuticular-tipped spines. These spines are considered to have taxonomic

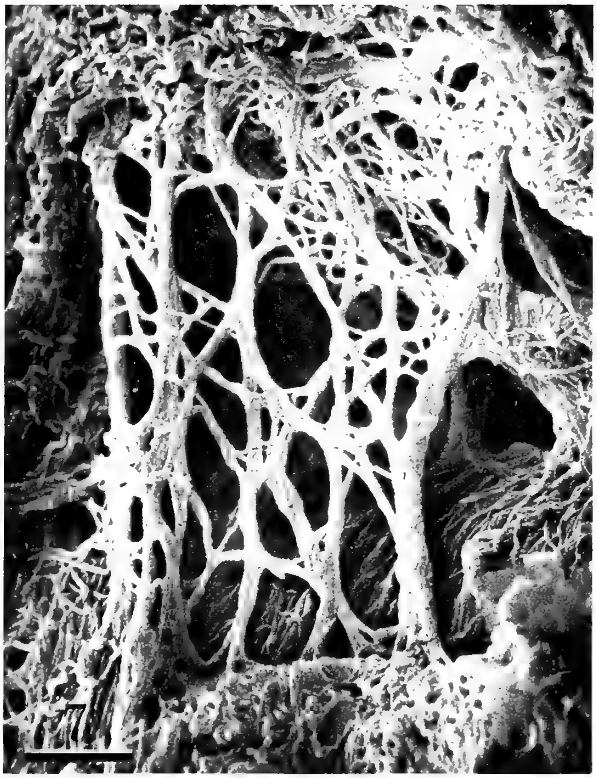
Plate Explanation

Figure *7*: Scanning electron micrograph of ampullar contents in *Phyllaplysia taylori.* The seminal mass has been gently teased apart.
20° beam angle Scale line represents 10μ

Figure *8*: Same area as Figure 7 but at higher magnification. Note the parallel bundles of sperm filaments. Arrow indicates the anterior tip of one spermatozoon
Scale line represents 2μ

Figure *9*: Sperm bundles and one oocyte in the post-ampullar duct. Mayer's haemalum and triosin. Scale line represents 25μ

Figure *10*: A seminal strand fixed while moving in the post-ampullar duct along the ciliated surface of the post-ampullar gland
Haematoxylin and eosin Scale line represents 8μ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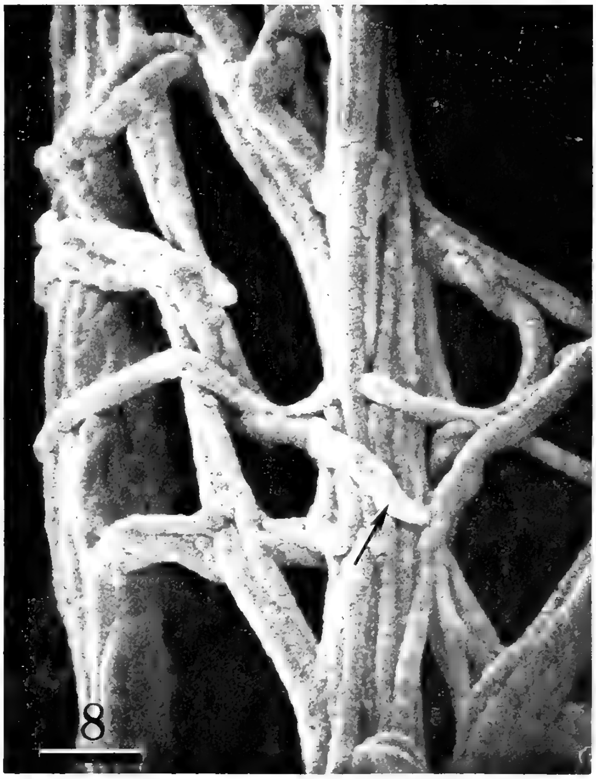
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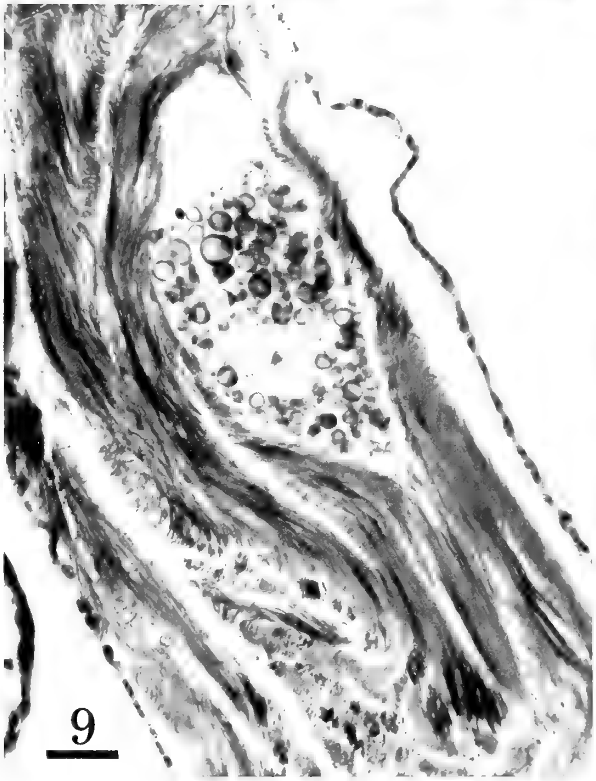
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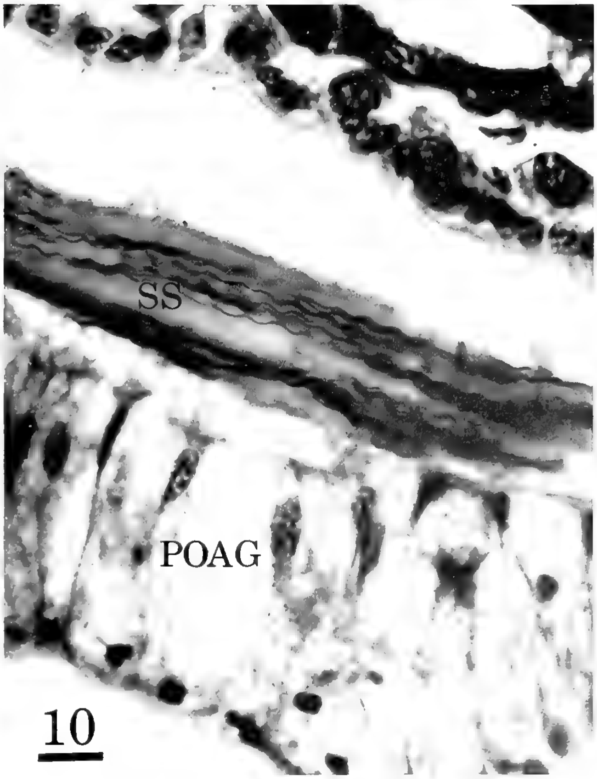

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importance. A powerful penis retractor muscle, originating on the hemocoel floor near the genital atrium, is inserted into the base of the glans penis (Figures 3 and *20*). In contrast to many other opisthobranchs, no prostate is associated with the penis. If a prostatic function exists it may be carried out by the post-ampullar gland or the spermoviduct gland.

Ghiselin (1964) has pointed out that the position of the penis on the side of the head is probably a primitive condition. He feels that the original position of the opening of the pallial gonoduct was inside the mantle cavity, and that the forward position of the penis is an evolutionary response to conditions where the gonoduct opening was blocked by the shell. The retention of the penis in this position in the anaspideans is not surprising, as members of the group show numerous primitive features; some even retain a well-developed shell (*e. g., Akera*). The possession by the sacoglossans of a penis lying in a similar position but equipped with a closed ejaculatory duct may represent a higher development of this pattern; it supports the idea that all or part of the Sacoglossa arose from an ancestral stock near the anaspidean line.

II. FUNCTIONAL MORPHOLOGY OF THE REPRODUCTIVE SYSTEM

The reproductive system of an anaspidean such as *Phyllaplysia taylori* may contain, simultaneously, the following: female gametes at various stages of development ranging from oogonia to fertilized eggs borne in the egg string; endogenous male gametes ranging from spermatogonia to morphologically mature sperm; and exogenous sperm received as a result of copulation. Some of these may be present simultaneously in such areas as the fertilization chamber and common genital duct. For even an elementary understanding of reproductive function in the animal one must know: the morphology of the reproductive tract; the paths of movement of the 3 categories of gametes present (which requires the ability to distinguish exogenous from endogenous sperm); and the events which occur in each part of the reproductive tract. The morphology is covered in the first section of this paper; function is considered below.

METHODS AND MATERIALS

Animals used in functional morphology studies were freshly obtained from Elkhorn Slough. After the start of experimentation they were kept in the large outdoor seawater tanks, previously described, at Hopkins Marine Station. Living animals and fresh or fixed and sectioned tissues were used. Most of the relaxation, microdissection, fixation, and microtechnique methods were described in the anatomy section.

Tritiated thymidine autoradiography was a very useful method for distinguishing exogenous from endogenous sperm and for determining the translocations of labeled sperm. Monesi (1962), Lima-de-Faria & Borum (1962), and others have found that the most mature germ cells that can incorporate this label are the primary spermatocytes and primary oocytes in premeiotic DNA synthesis. Thus spermatozoa bearing this label must have acquired it at their point of origin, the ovotestis. The subsequent movement of such labeled sperm can be detected by autoradiography. Details of my autoradiographic experiments to determine the exchange and storage of sperm within *Phyllaplysia taylori,* and an outline of some highlights of the following results, have been previously reported (Beeman, 1970c).

MOVEMENT AND STORAGE OF ENDOGENOUS SPERM

There is a steady movement of spermatozoa from the lumen of the ovotestis lobes to the ampulla. While the exact mechanism of this movement is not clear, several methods can be postulated. 1) The sperm may move out by their own actions. If this occurs, it must be by groups of sperm rather than by individual ones, for the size and organization of sperm clumps in the ampulla indicate that sperm temporarily remain in the parallel groups in which they developed in the ovotestis. 2) The sperm could be moved out by the pressure created by the increasing volume of sexual products in the ovotestis. 3) The sperm may be moved out by contraction of the ovotestis wall or body wall. There is no evidence to indicate that the ovotestis is capable of any active contraction.

After the sperm is gathered by the tiny tubules of the pre-ampullar duct (Figure 4), it is stored in the ampulla. The increasing volume of sperm greatly distends the ampulla. The pearly white ampulla filled with sperm is visible through the ventral body wall in most animals at most times. While the sperm in a given bundle show a parallel orientation, the bundles themselves stored in the ampulla are oriented at random (Figures *7*, *8*, *9*, and 36). Unlabeled sperm in the ampulla are replaced by labeled sperm within 30 days after injection of tritiated thymidine. Allowing for spermiogenesis time (*ca.* 10 days, Beeman, 1970a), this would indicate that sperm, in animals allowed to copulate, remained in the ampulla less than 20 days (Beeman, 1970c). Various impurities such as yolk particles, single oocytes, abnormal sperm, and amebocytes are occasionally seen mixed with the sperm (Figure *9*).

Winkler (1957), who diagrams and discusses the copulatory bursa as a seminal vesicle (*cf.* my Figure 33) in *Aplysia californica,* nevertheless shows the ampulla distended with stored sperm in his photograph of the gross anatomy of the reproductive system. Winkler's diagram, at this point only, follows that of Eales (1921) for *A. punctata* (Figure 32). Guiart (1901) felt that the seminal receptacle in *A. punctata* was a seminal vesicle. However, most authors dealing with anaspideans indicate that the ampulla is the location of endogenous sperm storage. Even on the basis of the present radiolabeling alone, I am convinced that the ampulla is the only true seminal vesicle in *Phyllaplysia taylori,* and the same seems highly likely in all other anaspideans as well.

Peristaltic waves of contraction often seen in dissections of *Phyllaplysia taylori* force the ampullar sperm into the post-ampullar duct. As the spermatozoa are forced further into the narrowing post-ampullar duct ciliary action is added to the muscular action and the sperm are aligned into a distinct seminal thread or strand in which sperm bundles now show parallel orientation (Figure *10*). The post-ampullar gland cells evidently secrete mucoid material which serves to fill the interstices of, and bind together, this thread of parallel packed sperm; it may also serve to lubricate its passage. Thus the post-ampullar gland very likely has a prostatic function.

The seminal strand (Figures *10, 16, 26,* and 36) is a very distinct structure by the time it reaches the fertilization chamber. This cohesiveness of the thread allows the endogenous sperm to be moved by strong ciliary action across the edge of the fertilization chamber to the axial edge of the spermoviduct fold with little chance of mixing with other sexual products (Figure 36). Folds in the wall of the fertilization chamber also seem to have a valve-like action in helping to guide the various sexual products (Figure *26*). Vivisections, and the contrast of labeled exogenous and unlabeled endogenous sperm *in situ* in sections of fixed animals, showed clearly that the relatively tough seminal strand is not an artifact caused by the contraction of an encasing tube, and that it is a purely endogenous structure. Having established this by autoradiography and vivisection it became possible to use the easily recognized features of the endogenous seminal thread as a morphological label to supplement or replace the radio-labeling. This was one of the most valuable results of the study for it provided a means of confirming some of the results obtained with radiolabeled animals through using unlabeled individuals, and permitted the gathering of information not available from the radiolabeled series.

I have not seen oocytes or clumps of yolk particles, both of which are mixed with the sperm in the ampulla, in the seminal thread or exogenous sperm. They are evidently excluded as the thread is formed, and comprise part of the debris which ciliary action sweeps through the fertilization chamber into the female gland mass duct; here it forms some of the material in the "pseudo-egg-strings" that some vivisected animals are seen to produce. It is not clear where these pseudo-eggstrings are eliminated. I have seen this material carried up to the spermoviduct by ciliary action and loosely piled in the outer regions of the common genital duct. It seems likely that this material is normally taken into the copulatory bursa, agglutinated, and partially destroyed. The formation of pseudo-eggstrings suggests that the separation of male and female functions in the fertilization chamber is at least partially mechanical without associated chemical or nervous mechanisms.

Mazzarelli (1891) did not find a direct connection between the fertilization chamber and the common genital duct; however, he represented such a connection by the dotted line in his generalized diagram of the *Aplysia* reproductive system. His belief that such a duct existed and served only for exogenous sperm led him to deduce and to state clearly that endogenous sperm follow the same route as the eggs through "l'oviduttodeferente," by which he meant both the oviduct groove running through the female gland mass and the spermoviduct running up the common genital duct. This point was corrected by Eales (1921), who evidently based her conclusions on anatomical deduction, but her diagram (*cf.* my Figure

Plate Explanation

Figure *11*: A section of the genital atrium of *Phyllaplysia taylori.* Mayer's haemalum and eosin.

Figure *12*: A section of the atrial gland of *Phyllaplysia taylori.* Mayer's haemalum and eosin.

Figure *13*: A section of the mucous gland of *Phyllaplysia taylori,* showing the folds of secretory tissue and the oviduct. Haematoxylin and triosin.

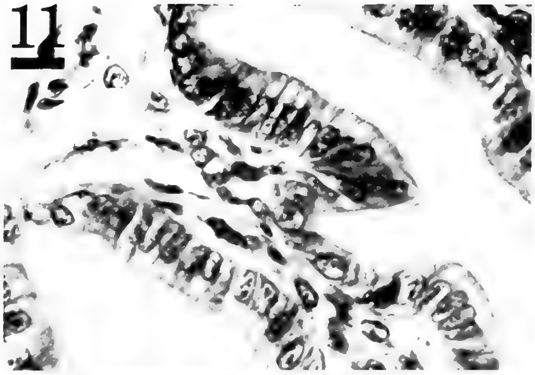
Figure *14*: A section from the common genital duct of *Phyllaplysia taylori,* showing the strong cilia of the copulatory duct. Mallory's triple stain.

Figure *15*: A cross-section of the common genital duct of *Phyllaplysia taylori.* Haemalum and triosin.

Figure *16*: Similar to Figure *15*, but showing the ciliary contact between the tip of the spermoviduct fold and the seminal strand.

Figure *17*: A cross-section of the common genital duct of *Phyllaplysia taylori* killed while the egg-string was moving up the spermoviduct. Mayer's haemalum.

Scale lines: 10μ in Figures *11, 14, 16*; 100μ in Figures *12, 13, 15, 17*.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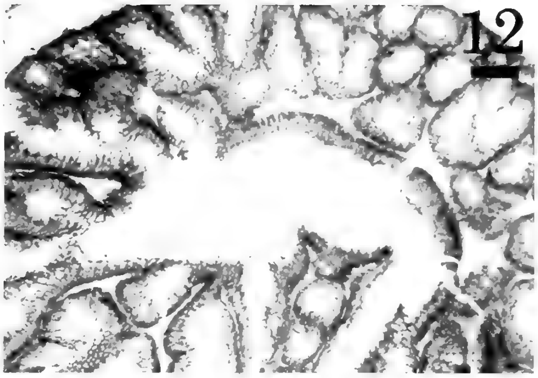
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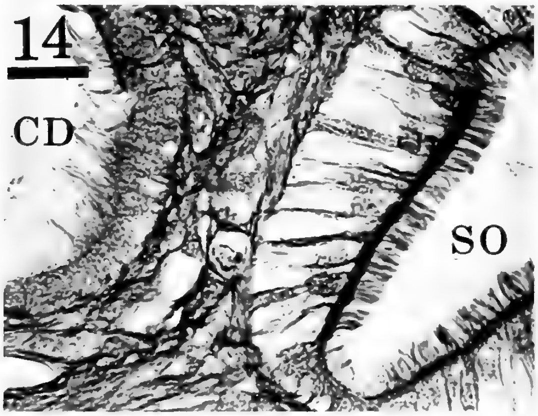
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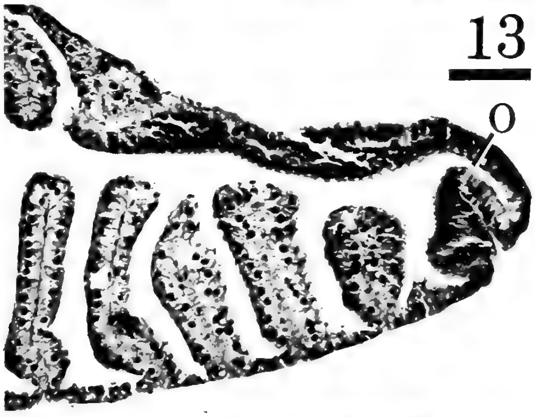
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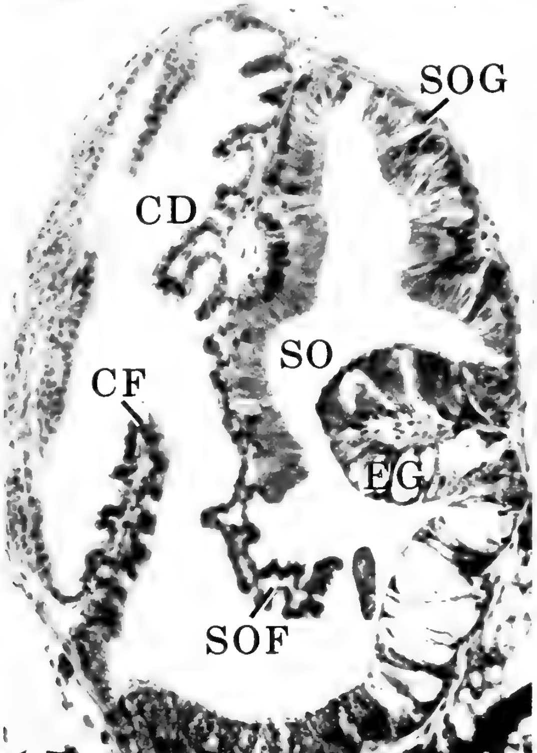
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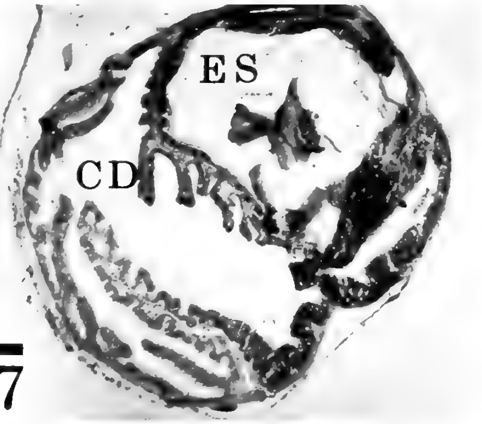
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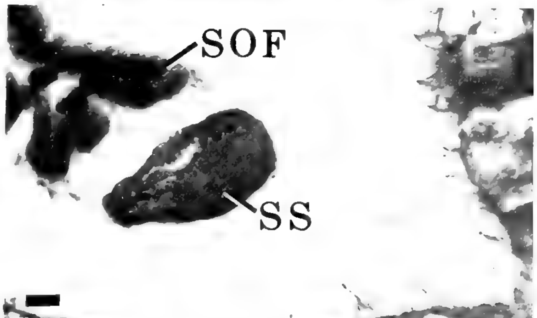
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32) shows the endogenous sperm moving from the fertilization chamber to the copulatory duct instead of to the spermoviduct. She may have been misled by some of MAZZARELLI's drawings, which are confusing since he was not able to distinguish clearly between exogenous and endogenous sperm.

The seminal strand typically moves up the spermoviduct attached to the tip of the spermoviduct fold (Figures *15, 16,* and 36). In action, this tip is held against the spermoviduct wall near the outer edge of the egg guide fold; the concave tip and the curving surface of the wall form a tube which encloses the seminal thread. Only ciliary action could be involved in the propulsion of the thread at this point. Examination of Figure *15* shows that muscular action could only be applied laterally and this would have the effect of bending the spermoviduct fold rather than applying forward motion to the thread. The common genital duct can be seen through the body wall in the intact animal. Although fully capable of powerful muscular action, the common genital duct did not show any waves or upward contraction when I watched it in several different animals during copulation.

The spermoviduct gland appears to contain a variety of different gland cells. Only the oviducal region of this gland has a strongly positive PAS reaction; the region where the seminal thread contacts the glandular wall is PAS negative. Some of the cells appear clear in hematoxylin and eosin preparations (Figure *15*); possibly these cells provide lubrication for the seminal thread.

A distinct change occurs at the level of the copulatory bursa duct. The spermoviduct gland tapers to an end at about this point and the tip of the spermoviduct fold becomes less distinct. A lateral outgrowth, which encloses the penis tip of the mate, develops on the spermoviduct fold. This deepens the apparent position of the seminal thread in the spermoviduct (Figure *22*). At about this point the spermoviduct becomes the internal seminal groove and the spermoviduct gland fades out. The seminal thread moves deep into this groove and follows its tortuous route to the common genital aperture.

It must be stressed that in being moved from the fertilization chamber to the common genital aperture, the outgoing seminal thread has normally completely bypassed the seminal receptacle, the copulatory bursa, the copulatory duct, the atrium, and the atrial gland (Figures 36 and 37). Emerging from the common genital aperture, the seminal thread merely continues forward along the external body wall, carried in the bottom of the external genital groove (Figure *21*). Ciliary action propels the thread directly to the tip of the penis which is extended in copulation.

COPULATION

Copulation normally occurs between 2 animals facing in opposite dirctions on the surface of *Zostera* leaves. The animals crawl toward each other and each bends to the right so that their right anterior quadrants overlap. The penis of each is now projected and inserted into the common genital aperture of the mate. The usual arrangement is the reciprocal exchange of sperm between the 2 individuals, but one-way transfers and mating triangles are occasionally seen.

Copulation in *Phyllaplysia taylori* was observed to occur in the field throughout the year. Individual *Phyllaplysia* were observed to copulate repeatedly over a period of months in study tanks. The smallest copulating animal observed was 13 mm (66 mg) and this is probably not much above the minimum size.

The glans penis is projected as the penis sheath is everted by hydrostatic pressure within the hemocoel. The everted sheath forms a tubular basal section of the functional penis, with the penis retractor muscle extending into and up this tube to its insertion on the base of the glans (Figure *20*).

After insertion, the penis is twisted and undergoes pulsations within the copulatory duct until its tip reaches a point just internal to that where the copulatory bursa duct joins the copulatory duct. A loop of the penis may invade the entrance of the copulatory bursa duct, but the tip of the penis bypasses this opening and goes deeper into the copulatory duct (Figures *18, 22, 23*; point "T" on Figure 37). The penis is now exceedingly well anchored in the copulatory duct by the following mechanisms: 1) The sphincter of the common genital aperture grasps the penis at its base. 2) The hollow base of the penis has been greatly expanded by hydrostatic pressure to form a bulbous anchor in the cavity of the atrium. Even thus expanded, the walls of the atrium are still much folded and pleated. 3) The penis forms an elbow-like angle within the atrium. This provides both anchorage and a base for the thrust of the glans into the tight, coiled section of the copulatory duct between the atrium and the copulatory bursa duct (Figures 4 and *22*). 4) The penial spines are pressed into the female tract by muscular and hydrostatic action (Figure *20*). 5) Points within the female tract are pressed against the penis. 6) The very powerful atrium basal muscle (Figure 4) clamps the base of the glans on the inward side of the atrium. Lesser muscular contraction is also evident in the coiled section of the common genital duct. 7) The complex configurations of the coiled section of the copulatory duct provide the final anchorage for the penis (Figure *22*).

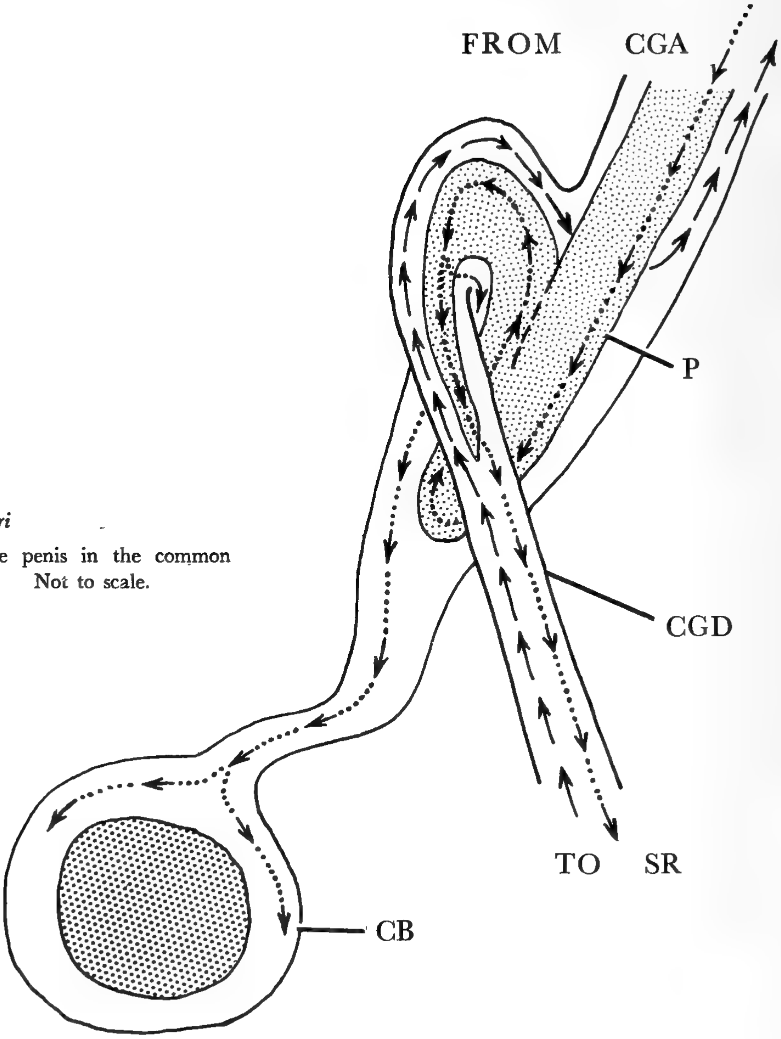


Figure 18

Phyllaplysia taylori

Diagram showing the placement of the penis in the common genital duct during copulation. Not to scale.

Plate Explanation

Figure *19*: The penis and opened penial sheath of *Phyllaplysia taylori*. The genital groove is visible on the inner surface of the sheath. Several penial spines are evident near the junction of the sheath and the coiled glans. From life. Scale line represents 250μ.

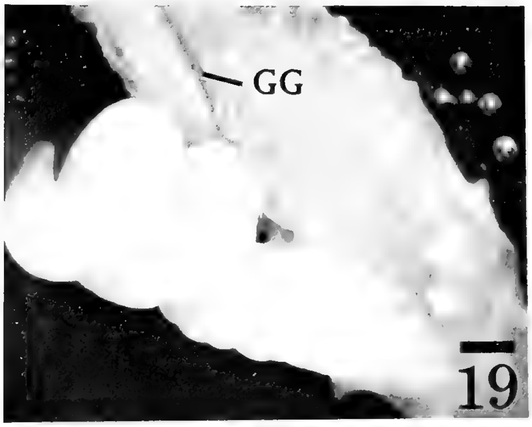
Figure *20*: Cross-section of the penis of *Phyllaplysia taylori* killed during copulation. Mayer's haemalum and triosin. Scale line represents 100μ.

Figure *21*: Enlarged view of the genital groove of the above specimen, showing ciliary transport of the seminal mass. Scale line represents 12μ.

Figure *22*: Section of *Phyllaplysia taylori* killed during copulation. All the coils of the glans penis are contained within the tightly spiraled copulatory duct; a deeper continuation of this is marked. Exogenous sperm is being poured into this animal, while the endogenous sperm is moving out as a seminal thread. Haemalum and triosin. Scale line represents 75μ.

Figure *23*: A section of the common genital duct, at the level of the copulatory bursa duct, of a *Phyllaplysia taylori* killed during copulation. Exogenous sperm was moving from the penis tip both laterally into the copulatory bursa duct and downward in the copulatory duct toward the seminal receptacle. Endogenous sperm is moving as a seminal strand up the spermoviduct. Mayer's haemalum and triosin. Scale line represents 90μ.

Figure *24*: Exogenous sperm pouring into the copulatory bursa of the specimen of Figure *23*. The arrow indicates a "tail" which marks the point where semen, probably from a former copulation, stopped flowing into the bursa. Note the yolk granules within the older, darker, contained mass. Mayer's haemalum and triosin. Scale line represents 80μ.



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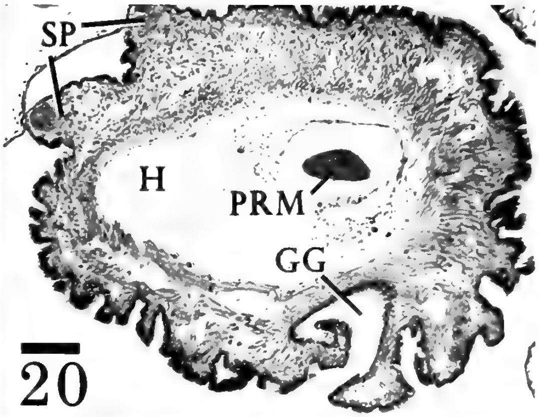

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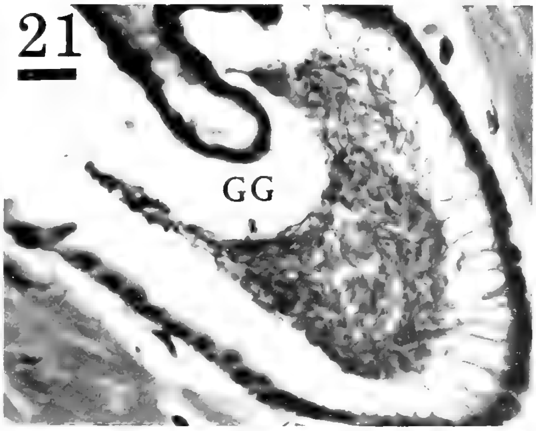

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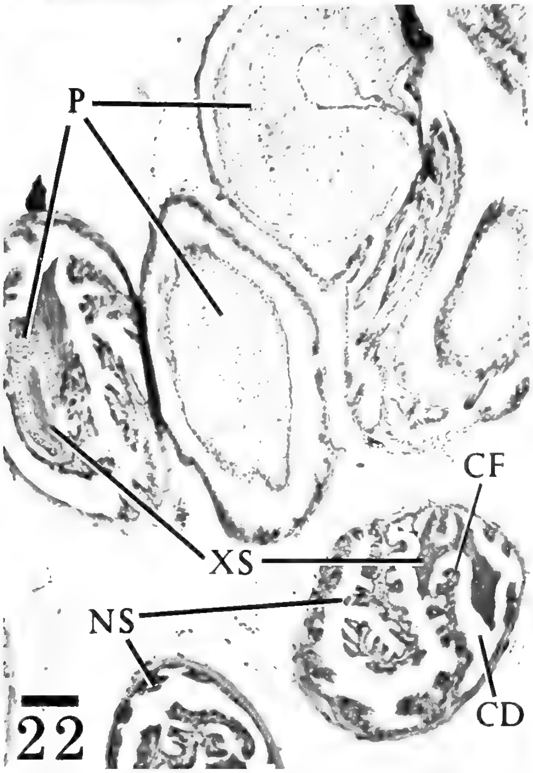

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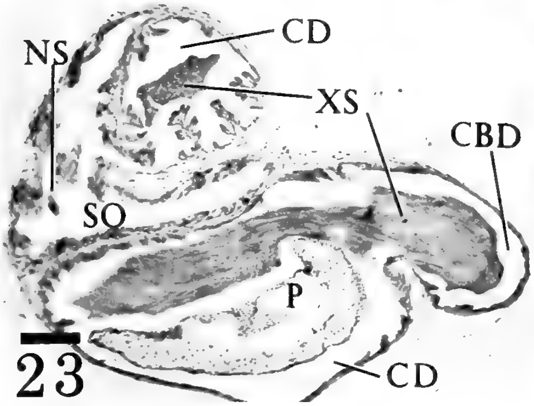
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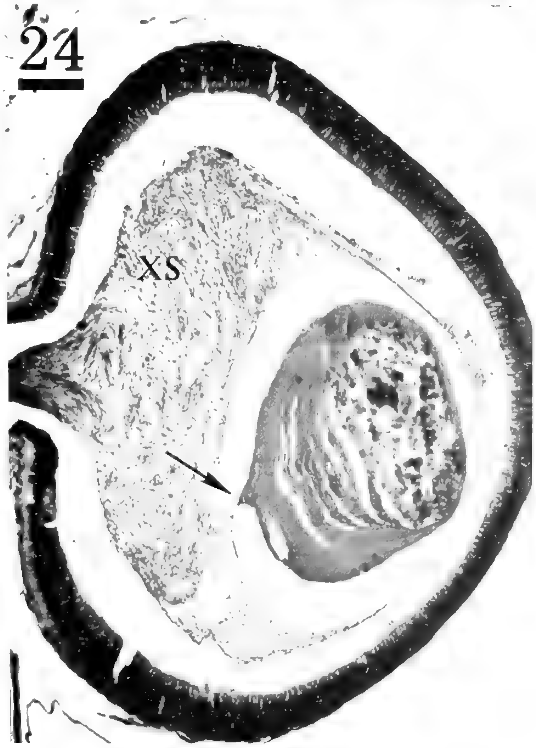

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The lumen of the atrial gland is filled with a weakly staining secretion during copulation. This secretion can be seen to extend out of the atrial gland and surround the passing penis. After copulation the vacuoles of the atrial gland cells appear to be discharged and the entire gland has shrunken.

The penis continues to pulsate during copulation. This may help to keep the penis anchored or it may help in the transport of sperm, either by directly forcing the seminal fluid or by keeping its channel clear despite its many convolutions and compressions.

Copulation is a very extended process. It usually lasts 2 or 3 hours but often continues for more than 4 hours. It is usually a continuous process, but I have seen partners mate for a period, separate, wander about, and then rejoin. The end of copulation is often not a synchronous process. One may withdraw and move about, dragging the still connected partner around for up to 30 minutes.

The long copulations and the elaborate mechanisms for maintaining copulatory contact are probably necessary considering the slow transport of sperm cells by cilia. It doesn't matter if part of the propulsion is later seen to be muscular, for there are at least sections of the tract where a thin seminal strand is moved only by ciliary means, and the speed at these points determines the upper limit of the transfer rate.

The purpose of copulation, of course, is the transfer of semen into a mate. This was typically evidenced by the decrease in size of the ampulla in both partners, clearly visible through their ventral body walls. However, reciprocal copulations were observed in which one partner had an empty ampulla when copulation commenced. Post-copulation dissection revealed that such a partner passed no semen to its mate. Not infrequently other copulations were discontinued when one partner had transferred his semen, while the mate had not yet finished.

The functional morphology of copulation in an anaspidean has not previously been described in detail. However, one aspect, of considerable functional import, has been the subject of dispute. This concerns the final placement of the penis tip. MAZZARELLI (1891) believed that in *Aplysia punctata* the tip was diverted toward the copulatory bursa duct by a fold in the copulatory duct. EALES (1921), working on the same species, crudely demonstrated that the penis penetrated deeper, towards the seminal receptacle, by dissecting out a penis which had been severed at its base during copulation. What degree of artifact was present in her experiment is debatable; the penis is not as well anchored in most *Aplysia* as in *Phyllapysia* and the severe stimulus of severing may have caused unknown changes in penis position or length. LLOYD (1952) found that such severing even caused the ejection of the inserted penis in the nudibranch *Archidoris*. The present observations on *P. taylori* consistently showed the penis at the position shown in Figures 18, *22*, *23*, and 37, regardless of the method of fixation or killing, so long as it was very rapid. THOMPSON & BEBBINGTON (1969) reported ejection problems when copulating *A. fasciata* or *A. punctata* were plunged into boiling Bouin's fluid, but they indicate a similar penis penetration for *A. depilans*.

It seems clear that the atrial gland is involved with the lubrication of the penis; it could be considered analogous to the vestibular glands of the human female. The "bursa seminalis" is an organ at the base of the copulatory bursa duct in *Aplysia punctata* which is obviously homologous to the atrial gland of *Phyllaplysia taylori*. The location of this "bursa seminalis" led EALES (1921) to deduce that its function was the agglutination of seminal debris which was then drawn up into the copulatory bursa. The different position of the atrial gland in *Phyllaplysia*, at a point removed from direct contact with exogenous semen, would argue against this. LLOYD (1952, p. 93) suggested that it may contribute prostatic secretion to the outgoing endogenous sperm in *A. punctata*, perhaps even capacitating them. This followed from her erroneous assumption that the endogenous sperm must travel past this organ on the "right side" (copulatory duct) "if they are to avoid the female accessory glands." THOMPSON & BEBBINGTON (1969) also reported that prostatic secretions from similar glands are added to outgoing endogenous sperm.

The atrium is seen to be a relatively passive female structure involved in the anchoring of the hydrostatic bulb of the penis. A similar but much more distinct structure in *Akera* is designated as a "réservoir séminal" by GUIART (1901), and another in *Dolabella* is called the "seminal receptacle" by MACFARLAND (1918). These unfortunate terms are the result of giving anatomical structures functional names before their function has actually been determined.

MOVEMENT AND STORAGE OF EXOGENOUS SPERM

The distinctness of the seminal strand is lost as the semen is moved into a mate during copulation. The dissolution of the incoming seminal strand may be due to the distance it has traveled without "prostatic" action, to the pulsating of the penis during copulation, to substances produced within the penis, or to substances present in the copulatory duct. Three observations argue against the last-named suggestion. First, the strand appears to be loosening even before it is discharged from the penis. Second, accidental tangles of endogenous seminal strands in the atrial area during copulation are not broken up until after copulation. Third, the normal endogenous seminal strand of the animal receiving exogenous sperm is not affected, though it passes through the same area. However, it is well protected from the copulatory duct by folds and perhaps by a mucus seal.

Whatever the reason for breakup of the incoming seminal strand, the breakup itself seems to aid in the movement of sperm from the discharge area. Weak muscular waves move down the common genital duct from the common genital aperture towards the seminal receptacle. These contractions evidently supplement the action of the rather moderately developed cilia of the copulatory duct in moving semen inward. It is interesting to remember that, in the same tube, less than a millimeter away, an endogenous seminal strand is moving in the opposite direction. As previously noted, this outgoing thread is moved by powerful cilia, in an anatomical arrangement which is unaffected by the inward contraction waves.

An abundance of semen is passed into a mate during a typical copulation. Near the end of, and immediately after, copulation in *Phyllaplysia taylori,* exogenous semen fills the copulatory duct below the atrium (Figure *23*). This seminal mass has started into the copulatory bursa and the seminal receptacle (Figures *23, 24, 26,* and 37). This has been confirmed by vivisections, dissections, and autoradiography. A few mated animals did not have sperm in the copulatory bursa. The sperm are completely unoriented in either seminal receptacle or copulatory bursa at this time.

As noted earlier (Beeman, 1970c), labeled exogenous sperm are seen to get barely around the tip of the copulatory fold, and are completely absent from the spermoviduct of unlabeled animals (Figure *22*).

Stained sections of the exogenous semen in the copulatory duct reveal many oval to pointed-oval nuclei without distinct cell boundaries scattered among the elongated sperm heads. Phase-contrast preparations suggest that these objects are amebocytes.

The bulk of the exogenous semen in the copulatory duct is moved into the recipient's seminal receptacle within 2 hours after copulation. A few sperm are left stuck in a viscous material which now lines the duct. A few of these sperm are coiled apparently in the epithelium of the duct walls; it is possible that they are being phagocytized. Within 5 hours after copulation the 10% of the exogenous sperm which have penetrated most deeply into the seminal receptacle have become oriented with their heads buried into the receptacle lining (Figure *27*). Sperm orientation was not observed ectad from the middle of the seminal receptacle. Several hours after copulation, large, irregularly shaped, clear areas, containing no sperm, were present in the center and upper end, but never the bottom, of the seminal receptacle (Figure *27*). The exogenous sperm are maintained in the oriented position in the seminal receptacle until oviposition.

The exogenous semen, if any, which was deposited in the copulatory bursa is left stranded there. It is then compacted, and perhaps digested; no sign of phagocytosis by the walls of the copulatory bursa wall was observed. Examination of Figure *24* shows at least 2 almost concentric sperm masses, an outer one composed of fresh exogenous sperm just added by copulation, and an older inner one which has been compacted and partially destroyed. The new mass has pushed the old one in and surrounded it; the area on the old mass which was formed in the copulatory bursa duct persists as a small "tail." The origin of the older mass is not definitely known. The simplest assumption is that it represents overflow of exogenous sperm from a former copulation, but the presence

Plate Explanation

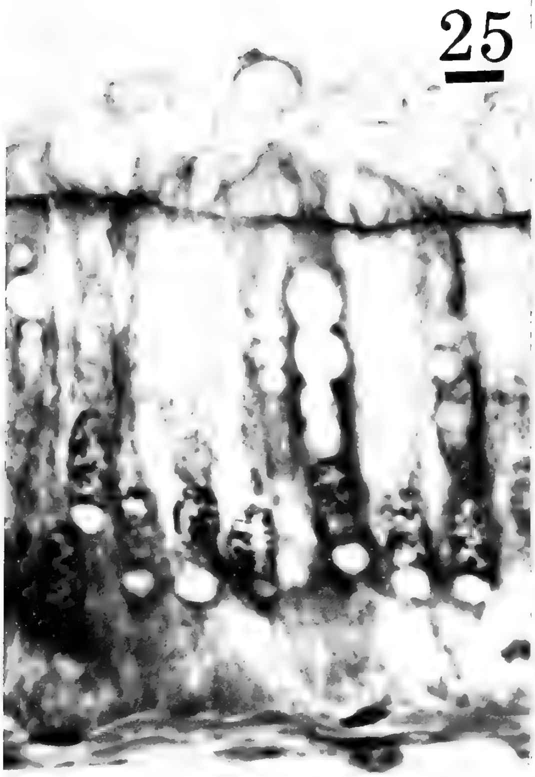
Figure *25*: Columnar endothelium of the copulatory bursa wall in *Phyllaplysia taylori.* Mayer's haemalum and triosin. Scale line represents 60µ.

Figure *26*: An angled sagittal section of the female gland mass of a *Phyllaplysia taylori* killed during copulation. Exogenous sperm was moving down the copulatory duct, up the seminal receptacle duct, and into the seminal receptacle. Endogenous sperm was coming up the post-ampullar duct, passing into a loop of the same duct into the fertilization chamber area, and then continuing up the common genital duct as a seminal strand. The oviduct and membrane gland are inactive in this phase. Mayer's haemalum and eosin. Scale line represents 75µ.

Figure *27*: Longitudinal section of a seminal receptacle of a *Phyllaplysia taylori* killed 5 hours after copulation. Note the beginning of orientation of the exogenous sperm and the presence of clear areas of seminal fluid. Scale line represents 60µ.

Figure *28*: A section of the seminal receptacle wall of *Phyllaplysia taylori* killed before exogenous sperm became oriented. Mayer's haemalum and triosin. Scale line represents 12µ.

Figure *29*: As in Figure *28,* but now the exogenous sperm have become oriented and attached to the specialized endothelial lining of the seminal receptacle. Scale line represents 20µ.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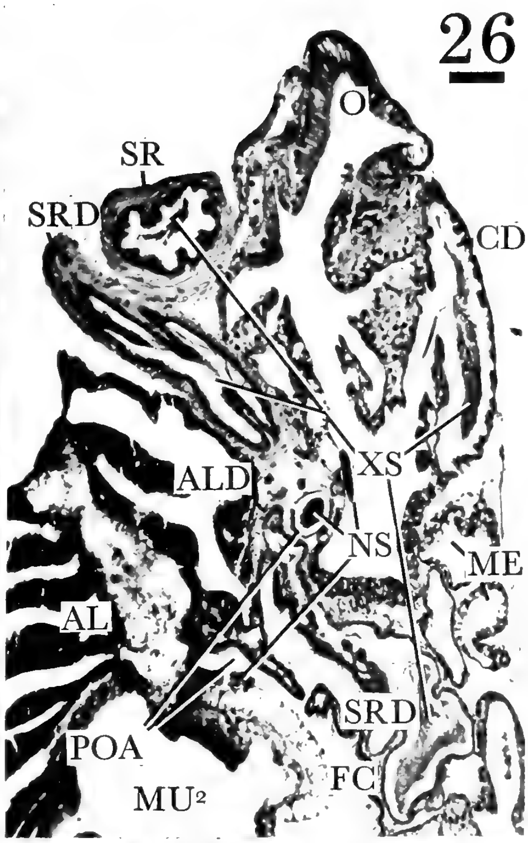
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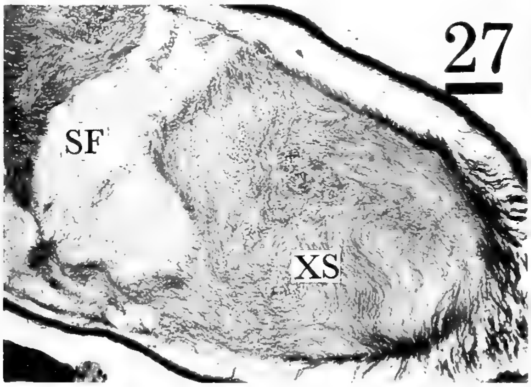
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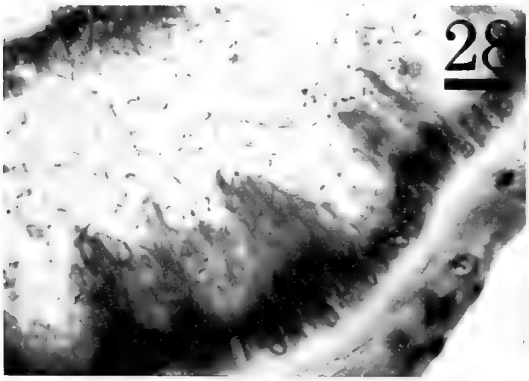
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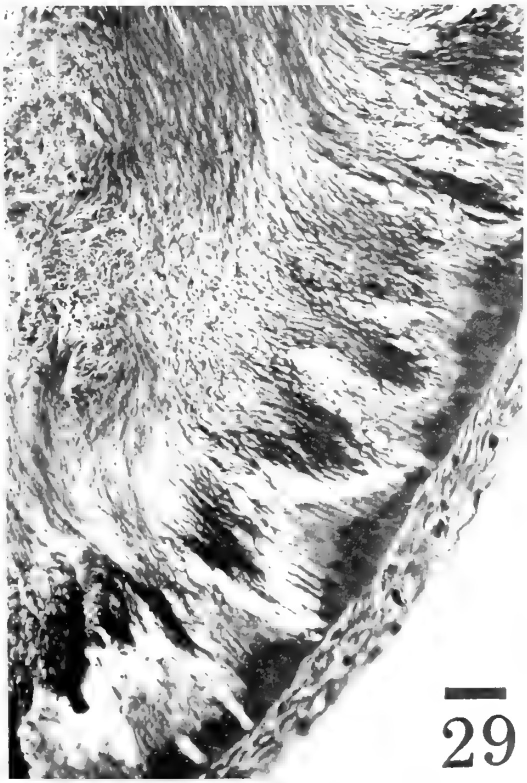
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of yolk granules in the center of the old mass indicates that at least some endogenous material is present.

As Ghiselin (1964) has remarked, opisthobranch workers have largely overlooked muscular action as a factor in moving materials in the gonoduct. The relation of muscular action to sperm movement discussed above (and to egg string movement to be discussed later) is therefore of special interest. I agree with Ghiselin that speculations, such as those by Thompson (1961), Lemche (1956), and Eales (1921), invoking the movement of opisthobranch sperm over relatively long distances by means of their own motility, are questionable. The sperm of *Phyllaplysia taylori* are certainly motile; those from the ovotestis, ampulla, seminal receptacle, and to a lesser extent the copulatory bursa, exhibit strong lashing and twisting movements. It is very likely that these are functionally involved in short-range movements such as orientation and fertilization, but the presence of the muscular movements and ciliated tracts already described make it unnecessary to postulate directed swimming movements of sperm over greater distances in the reproductive system.

A number of general discussions of sperm reception must be considered. Mazzarelli (1891) believed that the sperm in *Aplysia* are ejaculated and forced to flow entirely into the copulatory bursa. He stated that exogenous sperm leave the seminal material in the bursa and then pass down the copulatory duct to accumulate in the seminal receptacle. Eales (1921) felt that the seminal discharge and purification both occur in the copulatory duct of *A. punctata*. She suggested the sperm then move to the seminal receptacle and the debris is swept into the copulatory bursa. Her modification of Mazzarelli's scheme is schematically diagrammed in Figure 32. Eales' conclusions have served as a model for most later discussions of anaspidean reproductive function. McCauley's (1960) discussion and drawing of the reproductive system of *Phyllaplysia taylori* agree with her model almost completely. However, his morphological study included only side references to the reproductive functions; the discussion and diagram are therefore very incomplete on this point.

Marcus (1961a) has published the only diagram of the reproductive system of *Phyllaplysia taylori* in which the routes for gametes can be traced (see the anatomy section for my many objections to the anatomical relationships indicated by this diagram). Marcus did not discuss reproductive function in *P. taylori*. I have attempted to illustrate Marcus' ideas in a schematic diagram (Figure 34); this presents his concept of *P. taylori*'s anatomy and incorporates his comments (Marcus & Marcus, 1957a) on reproductive function in *Aplysia cervina* insofar as these are consistent with his diagram of *P. taylori*. It must be emphasized that Marcus might have shown these matters quite differently had he actually worked on reproductive function in *P. taylori*. Although lacking a definitive way to distinguish between endogenous and exogenous sperm, Thompson & Bebbington (1969) report sperm routings in 3 species of *Aplysia*, which are similar to the radiolabeling results in *P. taylori*.

Many of the main points of agreement and difference between my work and that of others can be most easily seen by comparing the schematic diagrams of Figures 32, 33, 34, and 37. The copulatory bursa and seminal receptacle require special discussion which is deferred until the movement and deposition of ova has been discussed.

EGG-STRING PRODUCTION AND MOVEMENT

1. Movement of Oocytes

Several hours to days normally elapse between copulation and oviposition in *Phyllaplysia taylori*. Preparatory to oviposition groups of oocytes accumulate in the lumen of the ovotestis lobes as they are shed from the ovotestis walls. They move, evidently by ciliary action, singly into the dendritic channels of the pre-ampullar duct being propelled along the ciliary band of the ampulla and then neatly bypass masses of sperm stored in the ampulla. This ciliary propulsion gradually results in oocytes filling the anterior region of the ampulla.

Egg-string production begins with the ciliary movement, perhaps with some muscular assistance, of the loose oocytes stored in the ampulla into a more or less single-file train up the post-ampullar duct. This passage is so narrow that only the single-file arrangement of the still unconnected oocytes is possible at most points, but several can be seen at one time in the small bulge of this duct. The post-ampullar duct arches over the albumen gland and slowly delivers the oocytes by ciliary action to the fertilization chamber. Development of the oocytes up to this point has been halted at metaphase of the first meiotic maturation division.

2. Fertilization

Within 3 hours after copulation the seminal receptacle is packed and distended with sperm; the more distal material is brownish. As ciliary action passes the loose, single oocytes through the fertilization chamber, the entire seminal receptacle exhibits vigorous constriction and dilation. Peristaltic waves start at the base of the receptacle neck and push sperm down the duct and into the fertilization chamber. This wave triggers a reverse wave which then quickly and progressively closes the lumen of the duct. This process is repeated every few seconds. Oocytes and exogenous sperm are mixed as the oocytes continue in a loose association through the fertilization chamber.

3. Egg-String Formation and Oviposition

The routing of the egg-string in the female gland mass can best be followed by considering the following discussion in conjunction with Figures 35, 36, and 37.

As fertilization proceeds, the albumen gland discharges its secretion into the fertilization chamber by an undetermined mechanism. An irregular line of eggs covered with a loose mush of albumen results and is slowly moved into the membrane gland by ciliary action. The limited opening of the membrane gland forces the ova (which are still independent of each other) to again become almost single-file. An indistinct strand of eggs, heavy with their loose albumen coverings, then starts moving by ciliary action through the complex sacculations of the membrane gland. The first sacculations start to smooth the albumen coats of the ova. The strand is too large to enter the tiny groove which follows the distal margins of these flattened sacculations, but its movement seems to be aided by the well-developed cilia present there. Soon after the strand has entered the first portion of the membrane gland (the region which stains darkly with methyl green) the strand begins to look more compact and to glisten. A distinct and coherent egg-string is gradually developing, covered with a membrane-like film. The egg-string is slowly rotated by ciliary action as it moves along the oviducal route; each egg, within a flattened ovoid of albumen, is individually wrapped in the membrane, and the membrane between adjacent ova becomes spirally twisted. This mechanism of wrapping the eggs supports the observations of Ghiselin (1965) who, Thompson & Bebbington (1969) claimed, was in error. The egg-string continues to move through the spiraled and reverse-spiraled sacculations, into the final and apparently non-glandular section of the membrane gland. From here the egg-string continues along the increasingly more distinct oviducal groove into the primary lobe of the mucous gland, still moved by ciliary action alone. The string compresses slightly as it enters the mucous gland so that for a short span it is 2 or 3 eggs across and thus flattened, and about 3 times as wide as thick.

The egg-string is now moved along the double U-shaped oviducal groove, which marks the edge of the mucous gland, first along the small U of the primary lobe, then straight through the female gland mass to the large U of the secondary lobe. Mucus, secreted by the large, non-ciliated, secretory part of this gland, moves peripherally to the oviducal groove and is added in layers to the rotating egg-string. The egg-string thus gains diameter as it passes and shortly after entering the mucous gland it becomes round in cross-section again. Secretory cells found directly in the oviducal groove perhaps serve to lubricate the string's passage.

The finished egg-string contains eggs which are quite uniform; they have a diameter of about 110μ (100μ to 116μ) in fixed sections, and a nucleus of about 25μ across. The addition of the membrane and albumen had increased the diameter of the egg-string to about 220μ (200μ to 250μ) and the addition of mucus brings the total diameter to about 540μ (515μ to 610μ).

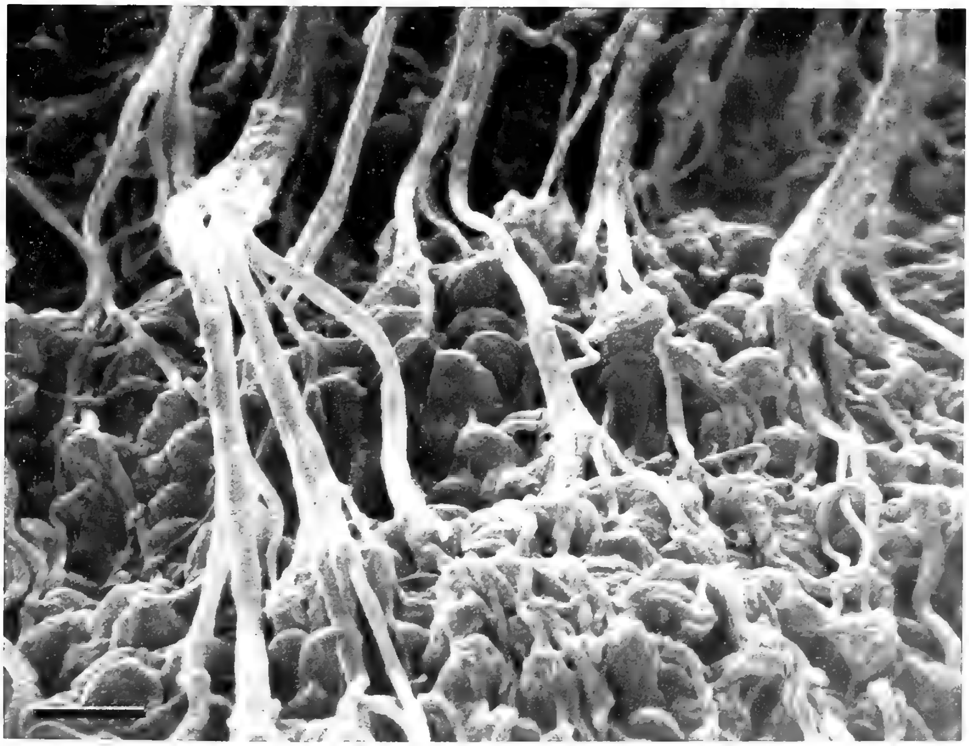
A mucus seal between the tip of the spermoviduct and the axial, weakly ciliated side of the egg guide turns most of the oviducal groove of the spermoviduct into a true tube during egg passage (Figure *17*). Within this tube the egg-string is carried forward by powerful cilia. The secretory cells lining the oviducal groove are obviously highly active during this phase. Several functions, or combinations of functions, are possible for this secretion. Suggestions include egg-string lubrication (Mazzarelli, 1891) and treatment of the egg-string with bacteriostatic materials (C. B. vanNeil, pers. comm., 1966). Fretter & Graham (1962) report that similar glands in prosobranchs aid ova in sticking to the substrate. Before the spermoviduct gland is referred to as a "prostate" it should be noted that it is here more involved with the egg-string than with the semen.

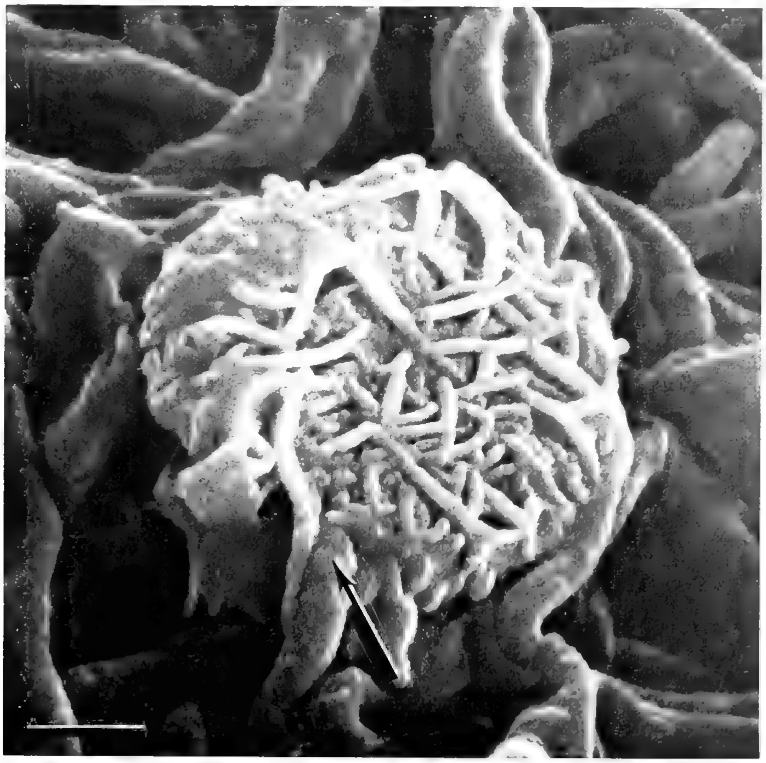
The spermoviduct narrows into an internal seminal groove at the level of the copulatory bursa duct. The seminal groove, which prior to copulation carries the endogenous seminal thread, spirals around the wall of the common genital duct above this point. The egg-string, in contrast, travels directly through the cavity around which the internal seminal groove coils; it simply follows the shortest possible duct to the common genital aperture. The cavity along which the egg-string travels also serves as the outer part of the copulatory duct. Simultaneous copulation and egg-laying have not been observed in

Plate Explanation

Figure *30*: Scanning electron micrograph of the lumen surface in the seminal receptacle of *Aplysia californica*. Oriented bundles of sperm filaments project upward into the lumen. The anterior ends of these exogenous sperm spread over, between, and into the rounded heads of the endothelial cells. Scale line represents 5μ. 20° beam angle, 20 kv.

Figure *31*: Scanning electron micrograph similar to Figure *31*, but at higher magnification. The lumenal end of an endothelial cell, with exposed microvilli and associated secretions, fills the center of this micrograph. The anterior end of the spermatozoon marked by the arrow is buried into this endothelial cell. Scale line represents 1μ. 20° beam angle, 30 kv.





Phyllaplysia taylori. However, I have seen it occur among *Aplysia californica,* and how the two processes can go at once here is something of a mystery.

After leaving the common genital aperture the egg-string is moved forward by ciliary action along the ventral side of the external genital groove. It is roofed by, but not wrapped in, the left flap of this groove. The open edge of the groove is sealed with mucus; even the base of the right rhinophore may be "glued" to the top of the foot. The egg-string goes directly past the penial sheath aperture and swings left under the right lappet to the point of the mouth. Only Hoffman (1932 - 1940, p. 239) seems to have previously considered the function of these labial lappets. The lips, lappets, and anterior edge of the foot serve to press the egg-string to the substrate, normally a *Zostera* leaf. The animal then moves its head alternately from side to side, continuously laying down the egg-string. An egg-packet or nidosome is formed by the application of the egg-string in a flat tight zig-zag of parallel rows which run at right angles to the animal's main body axis. The egg-string is applied to the nidosome at the edge closest to the animal, through a temporary notch formed in the foot's leading edge by the retraction of the mouth region. The animal slowly moves backward as the nidosome is laid down. The projecting edges of the foot smooth down the most recently laid 6 to 8 rows of eggs while each new row is added. Successive rows are about $\frac{1}{2}$ mm in width; the diameter of the finished egg-string is very slightly compressed between similar segments of the string which parallels itself on either side.

Nidosomes varied in size from 4 mm squares to packets roughly 20×50 mm laid by obese animals reared in the outdoor tanks. Each compartment of the egg-string contains one larva, and oily droplets and small clumps of extra cells of enigmatic origin. One animal may produce several nidosomes in a month.

The chemical nature of the egg-string was not considered in this study. Ghiselin (1964) has reported histochemical tests on egg-strings of several opisthobranchs and has reviewed the work of several previous workers. He noted that the "albumen" is probably a variable mixture of galactogen and protein and that it should not be confused with a similar term used by authors for certain proteinaceous secretions. The mucus is reported as "probably a variety of acid mucopolysaccharides" and it is suggested that the membrane is similar but may contain more protein. It should also be noted that the term "mucus" and the prefix "muco" are used in most invertebrates only as physiological terms for adhesive, gel-like secretions; this usage does not imply the presence of amino sugars (*cf.* Stacey & Barker, 1962).

The route of the egg-string in anaspideans has evidently been more often deduced than followed. Nevertheless, previous authors, although often confused about the anatomy of the organs involved, have been in fairly general agreement as to the main route taken (*cf.* Figures 32, 33, 34, and 37).

4. Anaspidean Egg-Strings

Thorson (1946) described the egg-string for *Aplysia punctata.* Ostergaard (1950) added notes on Hawaiian animals that he referred to as *Notarchus striatus* Quoy & Gaimard. *Dolabrifera olivacea* Pease, *Aplysia grandis* (Pease), *A. bipes* (Pease), and *A. elongata* (Pease). *Aplysia* species apparently always produce a loose, tangled egg-string which often has more than one ovum per compartment. I have noticed several ova per compartment in *Aplysia californica* egg-strings. Thompson & Bebbington (1969) report 50 to 60 ova per compartment in 3 British species of *Aplysia.* The *Notarchus* mentioned by Ostergaard also deposits a tangled string, but there is only one ovum per compartment. His report of *Dolabrifera* indicates an egg-string like that of *Phyllaplysia taylori* but lacking the fine orientation of deposited rows. *Phyllaplysia taylori*'s ability to encapsulate single eggs and the neat construction of its nidosome are thus not matched by many anaspideans. Control of these processes may be lost in older individuals; I dissected an 80 mm long "senile" animal which had its mucous gland jammed with an egg-string containing as many as 8 unfertilized ova per compartment.

GENERAL DISCUSSION

That the greater part of *Phyllaplysia taylori*'s reproductive system is a continuous cavity divided only by foldings may impress some as a crude and inefficient arrangement. The studies presented here indicate that, despite gross anatomical appearances, the system functions with efficiency and precision, and may be under little selective pressure favoring further modification.

Two elements of the reproductive system remain whose role requires further discussion: the seminal receptacle and the copulatory bursa.

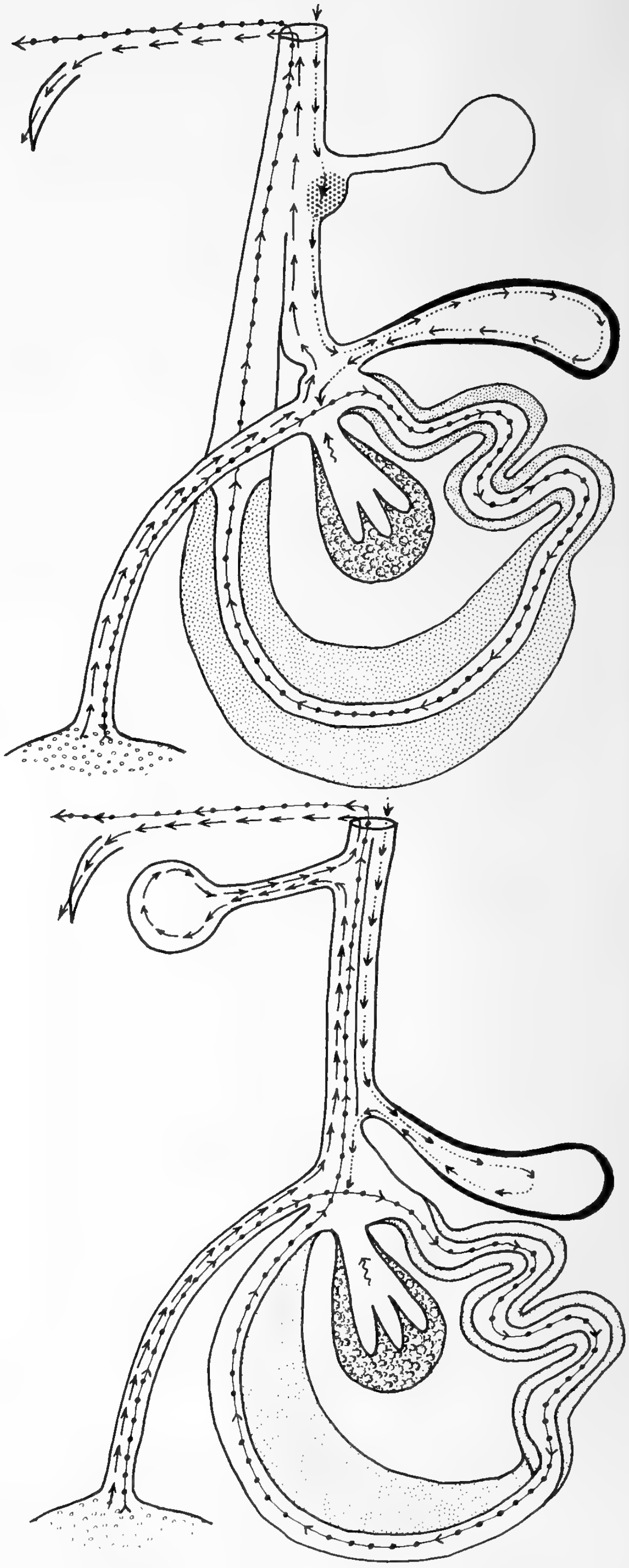
1. Seminal Receptacle

The problem of homology is of immediate concern when comparing different opisthobranchs with respect to almost any structure, and the seminal receptacle is no exception. Lloyd (1952) stated that although some opisthobranchs lack a copulatory bursa, all have a seminal receptacle. Thompson (1961) then carefully figured the reproductive system of the well-known nudibranch *Tritonia* with a copulatory bursa, but with no seminal receptacle. However, the "bursa copulatrix" of his paper is virtually identical in gross anatomy, histology, and function with the seminal receptacle of the present discussion. Until many more embryological details are known for the reproductive system, it seems sensible to accept Ghiselin's (1964) suggestion that the homologies of such organs be inferred on functional and logical as well as morphological bases. Thus the seminal receptacle is that female organ in which masses of exogenous sperm are stored with their heads oriented peripherally and closely associated with the lining endothelium.

The results of the present study leave little doubt that only exogenous sperm is found in the seminal receptacle of *Phyllaplysia taylori* and that this is received almost directly during copulation. There seems to be no transfer of material from the copulatory bursa to the seminal receptacle in this animal. That the seminal receptacle is at least the final vessel for exogenous sperm storage is one of the few functional points on which almost all opisthobranch students agree. The orientation of the sperm, however, is seldom mentioned (cf. Figures *29* and 37).

Ghiselin (1964) considers the primitive point of attachment of the duct of the seminal receptacle to be at or near the interior end of the pallial gonoduct, where exogenous spermatozoa could easily contact the uncoated eggs. *Phyllaplysia taylori* would thus be considered to show the primitive condition. As noted in the anatomy section, there is considerable variation among various anaspidean species as regards the exact point where the seminal receptacle duct joins the pallial gonoduct. An interior position favors the fertilization process while a more exterior position places the receptacle where it can better receive sperm during copulation. The latter consideration may be the more critical of the two, especially in the larger species, for the upper position is found more often, especially in anaspideans such as *Aplysia californica,* whose reproductive system seems generally more advanced than that of *Phyllaplysia* (see anatomy section).

The oriented attachment of the sperm to the endothelial lining of the seminal receptacle has never been explained adequately, but it might be significant in at least 3 ways. First, the oriented arrangement suggests a neat, efficient and simple mechanism for separating sperm and seminal fluid. The sperm attach and then muscular action expels the loose seminal material into the gonoduct for disposal in the gonoduct, the copulatory bursa, or out the common genital aperture. I have repeatedly observed large, translucent, cell-free masses in the upper lumen of



the seminal receptacle (Figure 27). This does not agree with Lloyd's (1952, p. 70) statement that only pure sperm is found in the opisthobranch seminal receptacle. The clear masses may represent extracted seminal material, but I have not actually seen the masses discharged. Mazzarelli (1891) stated that separation of incoming sperm from its accompanying seminal fluid occurred in the copulatory bursa; Eales (1921) suggested it must occur in the copulatory duct. Second, the attachment to the endothelial lining may serve a nutritive function for the exogenous sperm. The sperm may remain in this sac for at least several days after copulation. The receptacle at least stores and protects the exogenous sperm and may well nourish them for the storage reserves in sperm are necessarily small. Third, the exogenous sperm may be capacitated here; that is, rendered capable of fertilization. The problem of self-sterility is a basic one for hermaphroditic animals, especially those that use common ducts. The self-sterility of the hermaphroditic tunicate *Ciona* is reported to be due to chorion and egg membrane factors (Morgan, 1923; Reverberi, 1933; Minganti, 1948). Bretschneider (1948) describes a process in the pulmonate *Limnaea stagnalis* Say, 1818 which is almost undoubtedly related to sperm capacitation. The endogenous sperm of this mollusk cannot fertilize the ova. An orange-yellow pigment is added to incoming exogenous sperm in the seminal receptacle and this exogenous sperm is formed into little colored balls. The sperm in these balls are now able to fertilize the ova. Protandry has been mentioned as a self-sterility mechanism but Ghiselin (1964) feels that it is not important in opisthobranchs, with the possible exception of some pteropods. Eales (1921) suggests that the eggs of *Aplysia* do not "ripen" until they reach the fertilization chamber. I agree with Lloyd (1952) that this mechanism is too risky to be probable; also it does not suggest any mechanism by which fertilization would be limited to exogenous sperm. As noted by Lemche (1956), and others, it is far more likely that maturity of the sperm is the key factor. Lloyd also suggests that capacitation may be accomplished by the atrial gland as endogenous sperm move out of the animal. In *Phyllaplysia taylori,* as previously noted, this is anatomically impossible. However, Lloyd (1952) and Thompson (1961) suggest that the most likely site for capacitation is the seminal receptacle, and with this I certainly agree. Unfortunately, experimental evidence to support this viewpoint is still lacking. Preliminary attempts (Thompson & Bebbington, 1969) to induce capacitation in *Aplysia* have failed, but these studies produced the very interesting report that endogenous sperm can fertilize an animal's own oocytes if these sperm have first been placed in another animal by copulation. Thus there is no intrinsic block between endogenous sperm and oocytes.

In summary, the available evidence, and deduction suggest 5 functions for the seminal receptacle in *Phyllaplysia taylori,* all of which involve exogenous sperm:
1) to receive the semen in copulation; 2) to remove the seminal fluid; 3) to store, and perhaps maintain, the sperm; 4) to capacitate them; and 5) to discharge them for the fertilization process.

Note: Figures 32 to 34 are comparative schematic diagrams stylized from previous reports of anaspidean reproductive systems. They should be compared with the labeled Figure 37 which represents the findings of the present study. Homologous structures have identical tones. Not to scale.

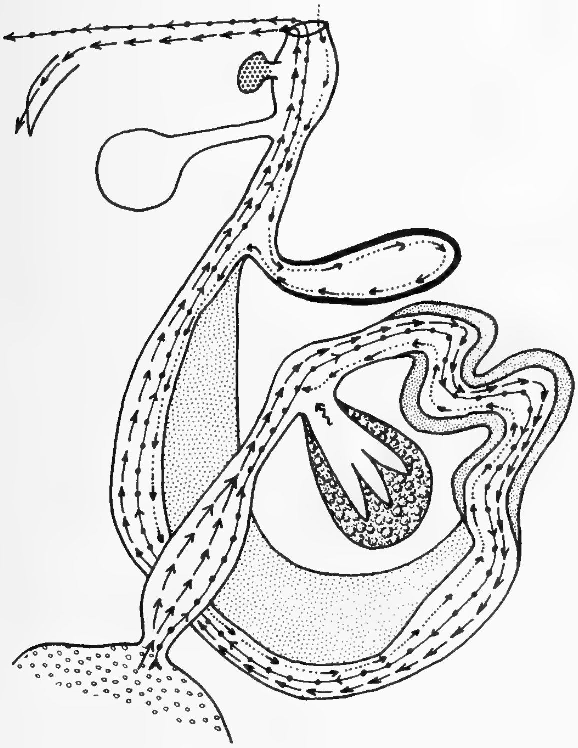


Figure 34

Phyllaplysia taylori,

after Marcus, 1961, and Marcus & Marcus, 1957

(⟵ on facing page)

Figure 32

Aplysia punctata, after Eales, 1921

Figure 33

Aplysia californica, after Winkler, 1957

2. Copulatory Bursa

The copulatory bursa has been one of the most enigmatic of anaspidean structures. **Mazzarelli** (1891) thought that it received the full discharge of exogenous sperm at copulation, purified it, and passed it on to the seminal receptacle. **Eales** (1921) felt that the bursa gathered debris which was drawn up from exogenous semen placed in the copulatory duct. **Winkler** (1957) reported that the copulatory bursa was full of "concentrated" seminal fluid in "breeding specimens which had not been permitted copulation for several days" and suggested that the organ served as a vesicle for endogenous sperm storage.

Lloyd (1952) reviewed the possible roles of the copulatory bursa in opisthobranchs, but added little that was new. **Thompson & Bebbington** (1969) reported that this organ destroyed "stray" ova and sperm, but they were not able to determine if the male gametes were endogenous, exogenous, or both.

The histology of the wall of the copulatory bursa (Figure *25*) suggests a secretory role, a point also observed by **Fodera** (1915). The relation of the secretion to the contents of the bursal lumen is not clear; it may be involved in their digestion, as is suggested by the condition of the older sperm mass in Figure *24*. The presence of labeled sperm within the copulatory bursa of unlabeled animals during this study has established that at least part of the contents of the copulatory bursa in *Phyllaplysia taylori* is exogenous semen.

There also is little doubt that some of the granules in the bursa are yolk granules from oocytes. They have the same size and appearance, stain the same with triosin, Mallory's triple stain, Azan, light green SF, and haemalum stains, and they have the same strongly positive PAS reaction. A red, or reddish-brown, oily material, perhaps similar to that noted by **Brüel** (1904) in the copulatory bursa of the sacoglossan *Caliphylla* is found in the bursas of *Phyllaplysia taylori* exceeding about 15 mm in length; it has not been identified. As previously noted, no sign of phagocytosis by the cells lining the copulatory bursa was ever observed. If material does pass through the bursa wall, it does so in a form not visible with a light microscope. It is possible that the bursa contents are just stored; *Phyllaplysia* has such a short life span that this organ just might serve wholly or partially as a waste receptacle. (I once found a 30 cm long *Aplysia californica* that had a copulatory bursa swollen to 4 cm in diameter!)

The position of the copulatory bursa is a key point. **Ghiselin** (1964) believes that its primitive position in opisthobranchs was near the genital opening, but he could see no functional reason why it should not be connected to the upper end of the pallial gonoduct. In either position it would serve to receive the penis in copulation, an arrangement known to occur widely in prosobranchs (**Fretter & Graham**, 1962). **Ghiselin** notes that the bursa is found in such an outer position among opisthobranchs with a long, undivided gonoduct except in those with reproductive systems that must, on other grounds, be considered specialized (*Acteon,* several sacoglossans). **Lloyd** (1952) reports that a copulatory bursa is absent in the opisthobranchs *Alderia, Eubranchus, Idulia,* and *Eolidina.* **Fretter & Graham** (1962, p. 368) note a similar lack in many monotocardian prosobranchs. **Lloyd** correlates the absence of the bursa with the proximity of the seminal receptacle to the surface and with longer penes, arrangements that would allow sperm to be placed directly in the "receptacular duct." The situation in *Phyllaplysia taylori,* and especially in *Aplysia californica,* argues against this hypothesis. *Aplysia californica* has a seminal receptacle and a penis highly modified for direct contact with it, and yet the copulatory bursa is well developed and obviously in heavy use. The position of the bursa in *P. taylori* results in its receiving some of the overflow of exogenous semen. The copulatory transfer of an over-abundance of semen has obvious value in assuring the impregnation of a mate of unknown capacity and need. However, the bursa's exceedingly high point of connection in some anaspideans (almost at the common genital aperture in *A. californica*) suggests that it is not just a convenient sac for catching exogenous seminal overflow or for gathering internal wastes which would be difficult to discard in other ways. (The copulatory bursa in *A. californica* also does not receive the penis in copulation; its duct is too high and too narrow for such a role.) Thus, while the external position of the copulatory bursa may be an ancestral condition, there seems to be a selective functional advantage to maintaining, and even developing the external position in many derived lines. This has evidently occurred in the anaspideans.

It seems probable that the copulatory bursa in anaspideans is now serving a modified role, perhaps a nutritive one, both in intake and recycling of materials of high physiological value. Digestion and translocation of the absorbed substances could involve lining cells or amebocytes or both. Ova fragments and exogenous semen are trapped in the bursa. It is likely that glandular wastes and endogenous semen are also added. The endogenous sperm could be of "old stock" from the top of the ampulla or abnormal, underdeveloped sperm masses. I have seen sperm masses in the bursa which looked like the groups that would be cast loose accidentally if an oocyte under them in the ovotestis was shed. It was not possible to trace labeled endogenous sperm in a labeled animal to test this hypothesis.

The above arrangement would have definite reproductive value. Considering the low likelihood of many anaspideans, but probably not *Phyllaplysia taylori,* meeting their own kind in nature, it should be of considerable selective advantage that they be able to successfully impregnate each other at every copulation opportunity. The intake and recycling of critical materials from unused exogenous and endogenous sperm, and fragments of eggs, would allow a large production of fresh gametes without undue physiological expense.

The idea of digestive activity by the copulatory bursa has been suggested by previous authors. LEMCHE (1956) mentioned "possible chemical action" by secretions from the wall cells in the cephalaspidean, *Cylichna.* The destruction of gametes within this organ has led THOMPSON & BEBBINGTON (1969) to propose naming it the "gametolytic gland." This seems to be an excellent suggestion but perhaps its adoption should wait until the homologies with other so-called "copulatory bursas" are better understood.

The idea that the copulatory bursa helps to keep the gonoduct clear is unconvincing; this function could better be met by discharging material to the outside. LLOYD (1952) suggested the absorption of proteins from the copulatory bursa and FRETTER & GRAHAM (1962) report a special "ingesting gland" in the prosobranch *Nucella* which they suggest helps to maintain "an efficient stock of sperm." Such mechanisms would join a list of devices which may help to assure adequate reproduction in anaspideans: hermaphroditism (TOMLINSON, 1966), possible detection of mates by highly developed rhinophores, the several mechanisms by which copulating individuals are anchored together, extended copulations, transfer of surplus semen, storage of exogenous semen, the special egg coverings, extended breeding periods, early and continued fecundity, and often the production of enormous numbers of eggs.

SUMMARY

This simultaneously hermaphroditic system is composed of the ovotestis, coelomic gonoduct, pallial gonoduct, external genital groove, and penis. The coelomic gonoduct consists of the ampulla and its pre- and post-ampullar portions. The coelomic gonoduct connects to the fertilization chamber, beginning of the pallial gonoduct and focal point of structure and function for the female gland mass. This mass (traversed only by the egg-string) is not a separate tube but consists of 3 complexly folded outpocketings, one each for the albumen gland, membrane gland, and mucous gland. The pallial gonoduct consists of the common genital duct and its associated organs. Leading from the fertilization chamber to the external genital groove, the common genital duct appears single externally but is divided incompletely within to form the copulatory duct and spermoviduct. The seminal receptacle enters the copulatory duct at the fertilization chamber; the copulatory bursa enters it much higher.

Endogenous sperm are stored in the ampulla. At copulation they are formed into a coherent seminal strand in the post-ampullar duct and are moved by ciliary action through the fertilization chamber and **up** the common genital duct, mainly following the spermoviduct fold; in this position the seminal strand is anatomically independent of muscular waves which simultaneously help to move exogenous sperm **down** this duct. The endogenous sperm strand leaves the common genital duct at the common genital aperture and is moved along the external genital groove to the penis which is extended by hydrostatic pressure.

Copulation is reciprocal. Several mechanisms which insure long copulation contact compensate for the slow ciliary transfer of sperm. The penis tip reaches down the copulatory duct to just below the junction of the copulatory bursa duct. The seminal strand is dissolved as it issues from the penis, thus releasing the now exogenous sperm. Most exogenous semen is moved directly into the seminal receptacle by muscular and ciliary transport. Surplus semen flows into the copulatory bursa.

Yolk granules, exogenous semen, and possibly immature or aged endogenous sperm enter the copulatory bursa and are destroyed there. This bursa serves as a waste receptacle and may aid in removing materials of high physiological value from surplus gametes.

Within 5 hours after copulation some of the exogenous sperm have become oriented with their heads buried into the endothelium of the seminal receptacle. Several functions involving exogenous sperm only are suggested for this receptacle: reception in copulation, removal of seminal fluid, storage and perhaps maintenance, capacitation, and discharge for fertilization.

Oocytes are moved past endogenous sperm stored in the ampulla and through the post-ampullar duct into the fertilization chamber. Here they receive exogenous sperm forced from the seminal receptacle and acquire a loose coat of albumen. The ova now pass into the tortuously folded membrane gland where the albumen is smoothed and further secretions coat each egg and bind the eggs into a linear egg-string. Carried along and continually rotated by cilia, this egg-string is coated with thick mucous layers in the mucous gland and is transported up the spermoviduct and along the external genital groove to the animal's lips which apply it to the substrate.

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Figure 35

Routes of the gametes through the female gland mass region of *Phyllaplysia taylori*

Not to scale

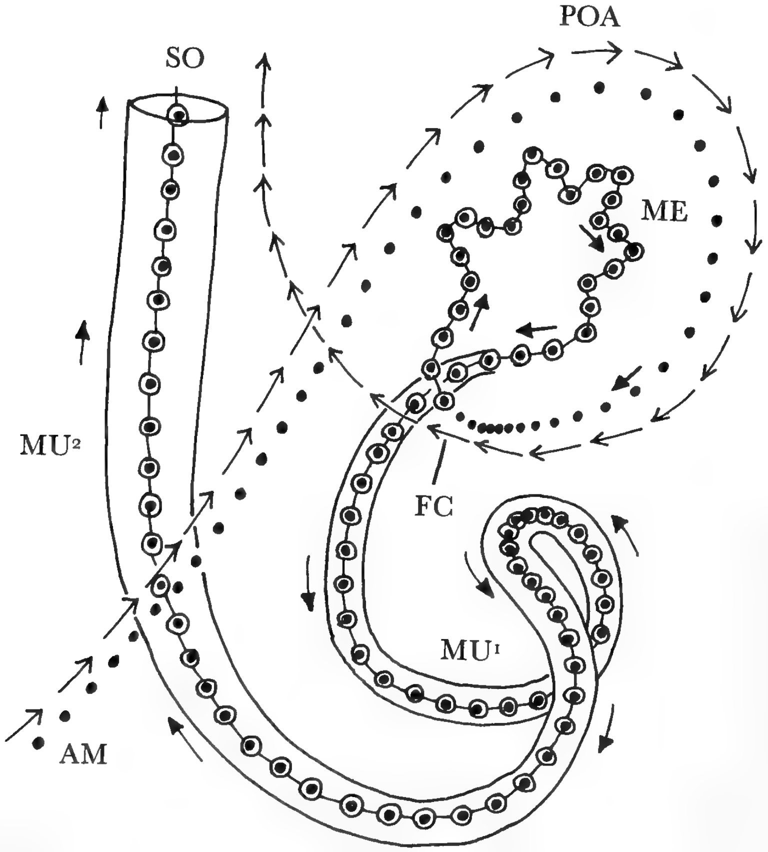
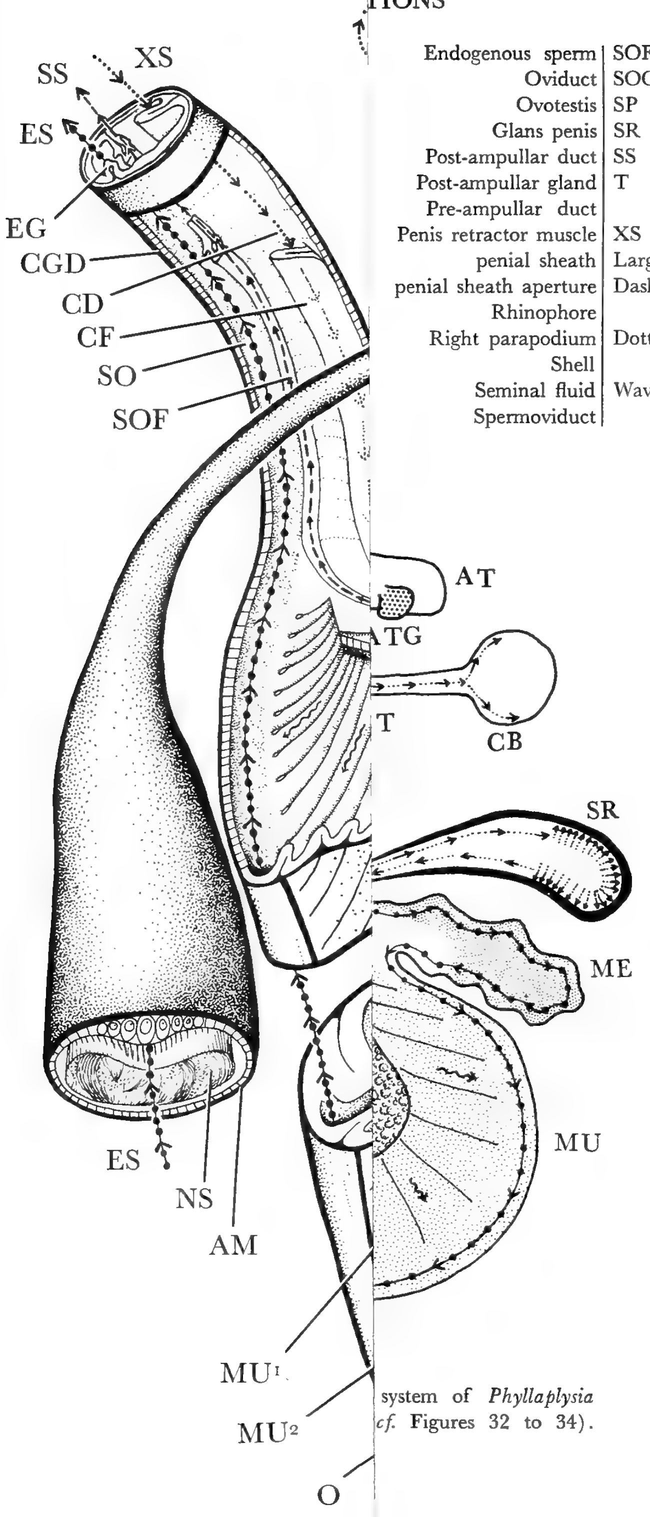


Figure 36

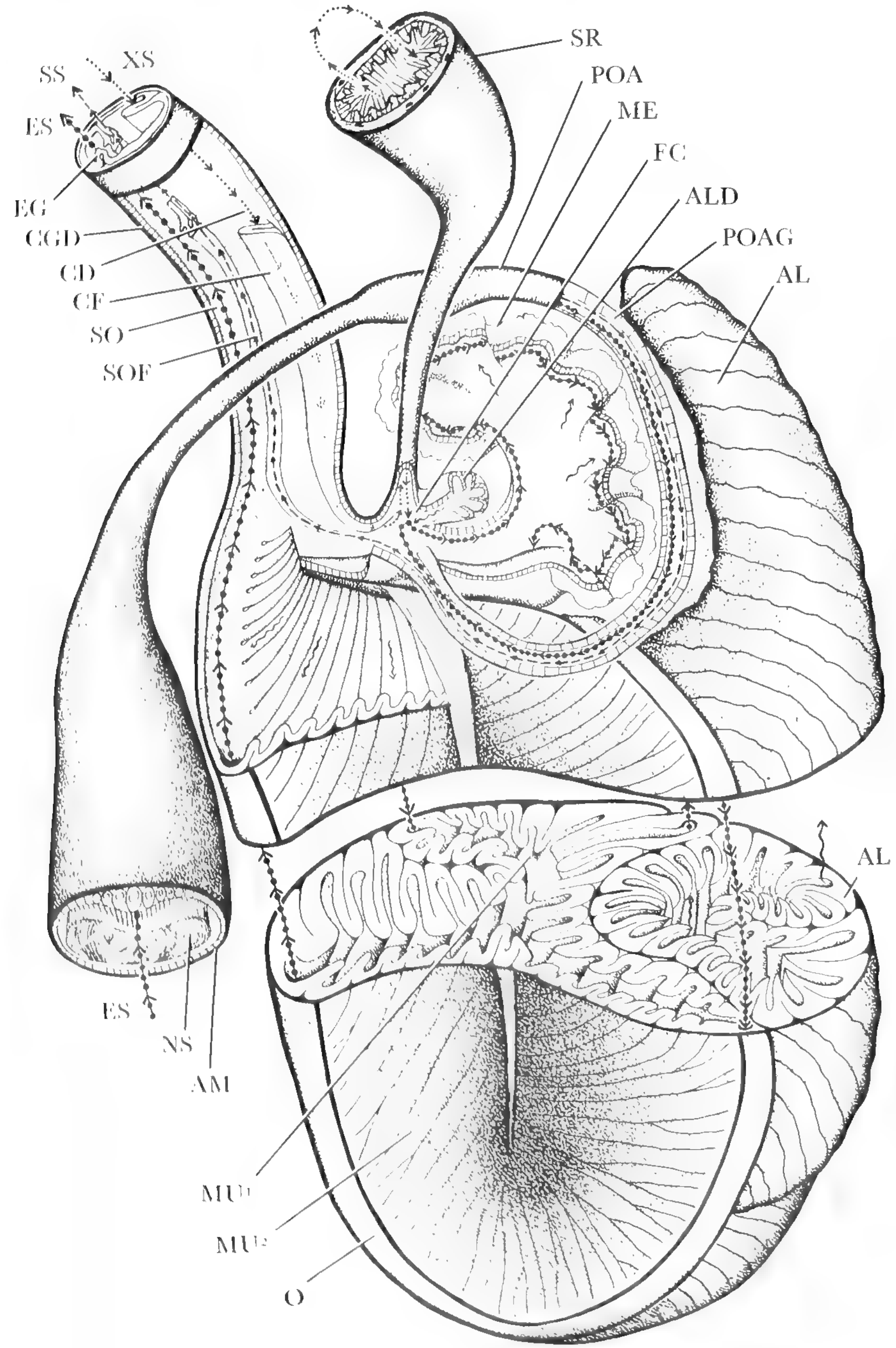
Simplified functional diagram of the female gland mass area in *Phyllaplysia taylori*. The seminal receptacle has been reflected and transected. The ampulla has been moved to the ventral side and transected. The ventral lobe of the albumen gland has been removed. Not to scale. (on facing page ⟶)

TIONS

Endogenous sperm	SOF	Spermoviduct fold
Oviduct	SOG	Spermoviduct gland
Ovotestis	SP	Penial spines
Glans penis	SR	Seminal receptacle
Post-ampullar duct	SS	Seminal strand
Post-ampullar gland	T	Location of penis tip in copulation
Pre-ampullar duct		
Penis retractor muscle	XS	Exogenous sperm
penial sheath	Large dots	Oocytes or eggs
penial sheath aperture	Dashed arrows	Endogenous sperm
Rhinophore		
Right parapodium	Dotted arrows	Exogenous sperm
Shell		
Seminal fluid	Wavy arrows	Secretions
Spermoviduct		



system of *Phyllaplysia*
cf. Figures 32 to 34).



LEGEND ABBREVIATIONS

ABM	Atrial basal muscle
AC	Acini
AL	Albumen gland
ALD	Albumen gland duct
AM	Ampulla
AT	Atrium
ATG	Atrial gland
CB	Copulatory bursa
CBD	Copulatory bursa duct
CD	Copulatory duct
CF	Copulatory fold
CGA	Common genital aperture
CGD	Common genital duct
CT	Cephalic tentacle
E	Eye
EG	Egg-string guide
EGS	Egg-string
ES	Exhalent siphon
FC	Fertilization chamber
FGM	Female gland mass
GG	Genital groove
H	Hemocoel
IS	Inhalent siphon
ISG	Internal seminal groove
ME	Membrane gland
MU¹	Mucous gland, primary lobe
MU²	Mucous gland, secondary lobe
NS	Endogenous sperm
O	Oviduct
OT	Ovotestis
P	Glans penis
POA	Post-ampullar duct
POAG	Post-ampullar gland
PRA	Pre-ampullar duct
PRM	Penis retractor muscle
PS	penial sheath
PSA	penial sheath aperture
R	Rhinophore
RP	Right parapodium
S	Shell
SF	Seminal fluid
SO	Spermoviduct
SOF	Spermoviduct fold
SOG	Spermoviduct gland
SP	Penial spines
SR	Seminal receptacle
SS	Seminal strand
T	Location of penis tip in copulation
XS	Exogenous sperm
Large dots	Oocytes or eggs
Dashed arrows	Endogenous sperm
Dotted arrows	Exogenous sperm
Wavy arrows	Secretions

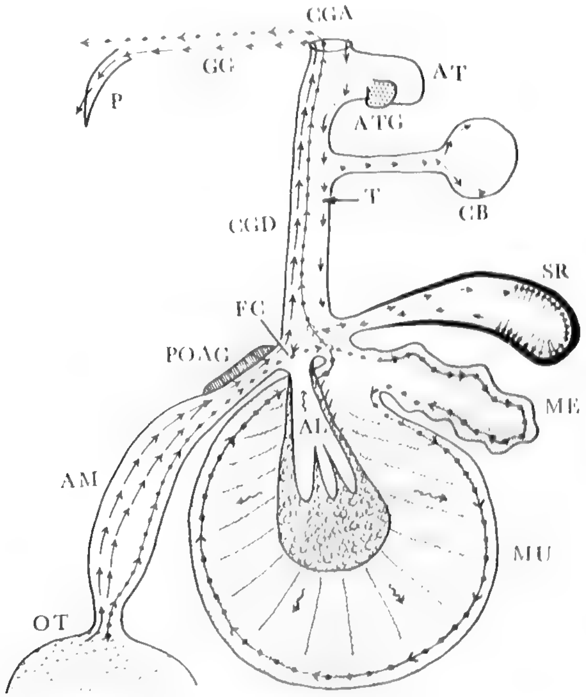


Figure 37

Schematic diagram of the reproductive system of *Phyllaplysia taylori* according to the present study (*cf.* Figures 32 to 34).

{Editor's Note: Dr. M. Ghiselin kindly called our attention to the fact that the reprints of his paper "Reproductive function and the phylogeny of opisthobranch gastropods" published in volume 3, no. 3 of Malacologia bore the publication date 1965; however, this number was not published until May, 1966. Unfortunately this information was received after the current number of The Veliger was in page proof. All citations to Ghiselin (1965) in this article should read: Ghiselin (1966).}

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An Aberrant *Cryptomphalus (Helix) aspersa* (MÜLLER) from Southern California

BY

T. W. FISHER

Department of Entomology, Division of Biological Control
University of California, Riverside, California 92502

(1 Plate)

FREAKS OF NATURE probably will remain of enigmatic interest to collectors and biologists alike. The hobbyist values them because they may be strikingly different from the "norm". The biologist, noting the obvious, wonders "why" and may offer a choice of explanations, most of which now-a-days end with mutterings to the effect that somehow the genetic code became garbled.

The specimen herein described was handed to me moribund by an acquaintance, Mrs. John Cook of Sunnymead, Riverside County, on January 31, 1969. She obtained it from a neighbor, Mr. Tom Noonan, who found it in his garden at 11885 Davis Street. I immediately asked Mr. Noonan to look for other brown garden snails with pulled-out spires, but despite a flurry of neighborhood interest accompanied by a few submitted normal specimens, none was forthcoming.

With the hope that this individual would recover and lay some eggs it was placed in a terrarium in the laboratory. Unfortunately, it did not become active and was dead 48 hours later. During preparation of the specimen, it was noted that the liver appeared to extend to the penultimate whorl, and no ova were detected. The shell is dextral, 35 mm high and 16 mm across the aperture. The embryo cap and the following 2 whorls are light tan and whitish in color. Brown color bands, characteristic of *Cryptomphalus (Helix) aspersa* (MÜLLER, 1776), appear on the light brown 2 main body whorls.

Of passing interest is the fact that a sinistral aberrant of this species was reported 39 years ago by BASINGER (1931: figure 3) who also was a member of this University of California research division.

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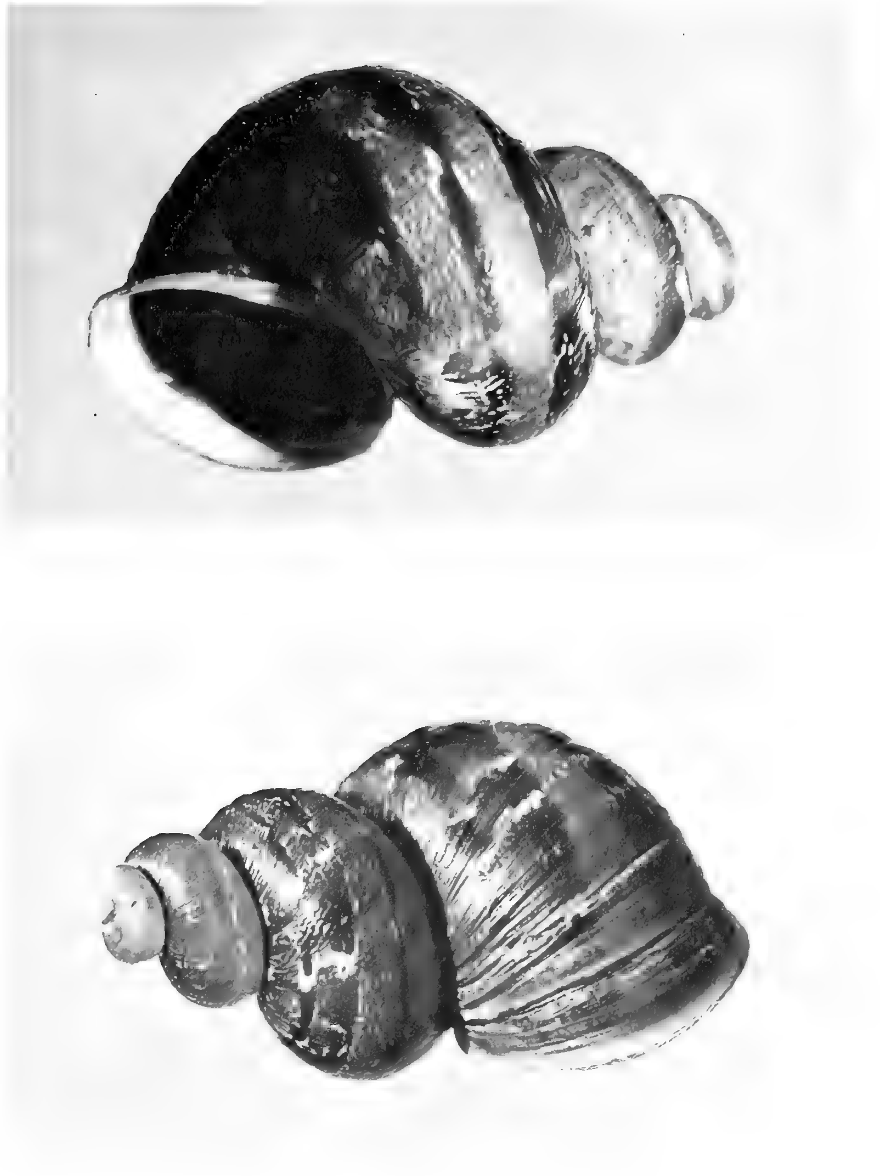

Two aspects of the aberrant *Cryptomphalus aspersa* (Müller, 1776)
from southern California

Occurrence of the Spirochaete Genus *Cristispira* in Western Canadian Marine Bivalves

BY

F. R. BERNARD

Fisheries Research Board of Canada, Biological Station, Nanaimo, British Columbia, Canada

INTRODUCTION

THE PRESENCE OF A LARGE cristaferous unicellular organism in the digestive tract of molluscs has been known since CERTES (1882) reported it in *Ostrea edulis* LINNAEUS, 1758. CERTES (1891) considered it a trypanosome. LAVERAN & MESNIL (1901) suggested it was a bacterium, while PERRIN (1906) placed it among the Protozoa on the basis of the complex cytological organization. SWELLENGREBEL (1907) first recognized the spirochaete affinities and was followed by GROSS (1910) who erected the genus *Cristispira* to contain those forms characterized by an encircling crista and the relatively large size. NOGUCHI (1921) reported upon the distribution of the genus in molluscs collected at Woods Hole, Massachusetts, and DIMITROFF (1926) reviewed the literature to that date. BERKELEY (1959) first recorded the genus from Western Canada in the large clam *Saxidomus giganteus* (DESHAYES, 1841).

METHOD

As many individuals as possible of 63 species of bivalves collected throughout the year from the intertidal to 1700 meters were examined for the presence of *Cristispira*. Examination was made as quickly as possible; in no case more than 10 minutes after collection. One valve was removed and a hypodermic needle inserted dorsally into the stomach and a small amount of stomach contents aspirated. The digestive system was then dissected and duplicate smears taken from the stomach, crystalline style (if present), the style pouch or mid-gut, and the hind-gut. One set of smears was examined at once by means of transmitted and oblique illumination. The second set was fixed in absolute alcohol and stained in Giemsa solution. The distribution of *Cristispira* within the substance of the style of *Saxidomus giganteus* was determined by sectioning frozen styles.

RESULTS

Twelve of the 62 species examined contained *Cristispira*. All of these were suspension feeders, generally belonging to stomach type V (PURCHON, 1960). All those with *Cristispira* were intertidal dwellers excepting *Diplodonta orbella* which was collected in 10 m. Some species including *Entodesma saxicola* were found to host *Cristispira* in intertidal situations, but solitary representatives collected by means of SCUBA in 10 - 20 m were invariably free of the spirochaete. A similar situation exists in *Compsomyax subdiaphana*; examination of 79 specimens from various localities in the northern portion of the Strait of Georgia in 60 - 200 m failed to yield *Cristispira*, but in shallower water more southern representatives of the species were hosts (pers. comm., Dr. R. G. B. Reid, University of Victoria). Commercial and natural beds of the Pacific oyster (*Crassostrea gigas*) are frequent hosts; however, no individuals collected from the head of Pendrell Sound contained *Cristispira*.

Considerable variation in infection sites may be demonstrated. In *Saxidomus* the area of maximum infestation is in the style pouch and consequently adhering to the crystalline style. In winter the stomach is often completely free but in summer small isolated numbers of *Cristispira* may be present. In *Tresus* the stomach is the chief site and numbers may be found in the intestine and large numbers in the pallial cavity. Earlier papers suggest that the spirochaete is present within the style substance. Careful sectioning of frozen styles showed that in no case had *Cristispira* penetrated the style but merely formed a coating on the surface. Adhering *Cristispira* can also be removed by washing the complete style in saline solution and blotting dry.

Numbers of *Cristispira* present vary seasonally, being much more abundant in summer when concentration in the order of 8×10^6 per ml stomach contents may be reached in *Tresus.*

Cristispira are variable in outline and until a culture technique is perfected, it may be prudent to avoid amendments or additions to the nomenclature. Classifications based solely upon external morphology are open to doubt as various histological procedures such as fixation and staining radically alter the appearance. The 7th edition of Bergey (1957) lists 3 species which adequately cover the morphological varieties present in British Columbia marine clams. The results of examination are listed in Table 1 and representatives of each occurrence have been assigned to one of 3 groups; this does not imply any systematic affinity but merely a general group with characters in common.

Type	Similar to	Size	Characteristic
	Cristispira		
δ	*C. balbianii* (Certes, 1882)	40 - 140μ	Obtuse ends
β	*C. anodontae* (Kysselitz, 1906)	44 - 88μ	Pointed ends
α	*C. pinnae* (Gonder, 1908)	10 - 60μ	Blunt ends

DISCUSSION

Berkeley (1959) reported that the crystalline style of *Saxidomus giganteus* contained a large population of *Cristispira* except at the distal end which impinges against the gastric shield where food is broken down and subjected to enzymatic action of the disintegrating style. Previously Berkeley (1933) had demonstrated that one of the products of the oxidizing action of the crystalline style upon plankton was probably glucosone. Berkeley (1962) carried out experiments which showed that plankton extracts were toxic to *Cristispira* suspensions in 60 to 90 minutes and further investigated the toxicity of glucosone. The results showed that addition of 0.5% glucosone to an active suspension of *Cristispira* in sea water held at 5° C rendered inactive all the spirochaetes in approximately one hour. Glucosone has been shown to be toxic to many animals (Becker & Day, 1953). Dean (1958) reported that extracts of style caused rapid dissolution of *Cryptomonas,* though some algae including *Isochrysis* remained unaffected after 72 hours. The lysolytic activity of the style is transitory and present only during active disintegration. Lavin (1946) first reported cellulolytic activity in the styles of *Mactra* and *Mya.* Newell (1953) supported the contention and demonstrated similar activity in *Ostrea edulis* and *Mytilus edulis,* suggesting that cellulosis might be associated with the presence of *Cristispira.* No *Cristispira* has been found in *Bankia setacea,* which would appear to cast doubts upon Newell's suggestion. There is no direct correlation of the occurrence of the spirochaete and species of bivalve, though it appears that closely grouped intertidal populations are the most frequently infected.

The interesting situation where *Cristispira*-free populations of *Crassostrea gigas* and *Venerupis japonica* occupy the head of Pendrell Sound might be explained by the pronounced halocline present in these waters. The summer months are characterized by surface waters of relatively low salinity (10‰ - 20‰) which could have an inhibitory effect upon *Cristispira.* Clams and oysters from the mid region of the Sound demonstrated an infection percentage of 20 - 50, while at the mouth and surrounding areas virtually 100% of susceptible bivalves are infected. A contributing factor might be found in the precipitous walls of the Sound, which offer few suitable habitats for interstitial bivalves which could act as a *Cristispira* reservoir. No difference in conditions between the infected and *Cristispira*-free bivalves could be found, an indication that the spirochaete is not an obligative part of the gut fauna. The presence or absence of *Cristispira* appears to have little effect upon the well-being of the host and should probably be regarded as a commensal organism.

ACKNOWLEDGMENTS

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Table 1

Occurrence of *Cristispira*
in Western Canadian Marine Bivalvia

Species	Depth (m)	Number examined	Number positive	Type
Acila castrensis (Hinds, 1843)	146	25	0	
Astarte alaskensis Dall, 1903	180	2	0	
Astarte esquimalti Baird, 1863	23	6	0	
Bankia setacea (Tryon, 1963)	Int.	28	0	
Cardiomya californica (Dall, 1886)	275	14	0	
Cuspidaria pectinata (Carpenter, 1864)	180	3	0	
Cardita ventricosa Gould, 1850	165	6	0	
Chlamys rubida (Hinds, 1845)	110	14	0	
Chlamys hericius (Gould, 1850)	110	9	0	
Clinocardium nuttallii (Conrad, 1837)	Int.	27	25	δ, α
Compsomyax subdiaphana (Carpenter, 1864)	60-200	79	0	
Crassostrea gigas (Thunberg, 1793)	Int.	25	25	δ, α
(Pendrell Sound)	Int.	10	0	
Cuspidaria apodema Dall, 1916	1700	2	0	
Cyclopecten carlottensis Bernard, 1968	1650	1	0	
Diplodonta orbella (Gould, 1851)	10	2	2	
Entodesma saxicola (Baird, 1863)	10	6	0	
Entodesma saxicola (Baird, 1863)	Int.	4	4	δ, β
Gari californica (Conrad, 1849)	18	2	0	
Gari californica (Conrad, 1849)	Int.	14	0	
Glycymeris subobsoleta (Carpenter, 1864)	90	50	0	
Hiatella arctica (Linnaeus, 1767)	40	6	0	
Hinnites multirugosus (Gale, 1928)	20	4	0	
Kellia suborbicularis (Montagu, 1804)	40	2	0	
Lucinoma annulata (Reeve, 1850)	114	18	0	
Lyonsia pugetensis Dall, 1913	Int.	2	2	β, α
Macoma brota Dall, 1916	35	4	0	
Macoma calcarea (Gmelin, 1791)	65	12	0	
Macoma inflatula Dall, 1897	40	6	0	
Macoma nasuta (Conrad, 1837)	Int.	3	0	
Macoma secta (Conrad, 1837)	25	5	0	
Modiolus modiolus (Linnaeus, 1758)	Int.	4	0	
Modiolus capax (Conrad, 1837)	50	5	0	
Mya arenaria Linnaeus, 1758	Int.	3	0	
Mytilimeria nuttallii Conrad, 1837	Int.	2	0	
Mytilus californianus Conrad, 1837	Int.	14	0	
Mytilus edulis Linnaeus, 1758	Int.	35	0	
Nemocardium centifilosum (Carpenter, 1864)	95	8	0	
Nucula carlottensis Dall, 1897	280	4	0	
Nuculana cellulita (Dall, 1896)	750	3	0	
Ostrea lurida Carpenter, 1864	Int.	25	21	δ, β, α
Pandora bilirata Conrad, 1855	365	11	0	
Pandora filosa (Carpenter, 1864)	410	2	0	
Pandora grandis Dall, 1877	250	10	0	
Panope generosa Gould, 1850	Int.	1	1	β, α
Pecten caurinus Gould, 1850	105	5	0	
Pododesmus cepio (Gray, 1849)	Int.	3	0	
Poromya beringiana (Dall, 1916)	750	1	0	
Poromya tenuiconcha Dall, 1913	1385	3	0	
Propeamussium davidsoni (Dall, 1897)	825	6	0	
Protothaca staminea (Conrad, 1837)	Int.	25	24	δ, β, α
Saxidomus giganteus (Deshayes, 1839)	Int.	37	37	δ, β, α
Serripes groenlandicus (Bruguière, 1789)	52	2	0	
Siliqua patula (Dixon, 1789) [1]	Int.	5	0	
Solemya agassizii Dall, 1908	350	8	0	
Solen sicarius Gould, 1850	Int.	1	0	
Tellina carpenteri Dall, 1900	20	4	0	
Tellina salmonea (Carpenter, 1864)	75	15	0	
Thyasira bisecta (Conrad, 1849)	170	2	0	
Thyasira disjuncta (Gabb, 1866)	200	27	0	
Tresus capax (Gould, 1850)	Int.	2	2	β, α
Tresus nuttallii (Conrad, 1837)	Int.	5	5	β, α
Venerupis japonica (Deshayes, 1841)	Int.	25	22	δ, β, α
Yoldia ensifera Dall, 1897	420	22	0	
Yoldia thraciaeformis (Storer, 1838)	100	5	0	
Zirfaea gabbi (Tryon, 1863)	Int.	47	0	

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[1] Berkeley (1959) lists *Siliqua patula* as being host to *Cristispira*. This is an error of identification and the record should be referred to *Solen*.

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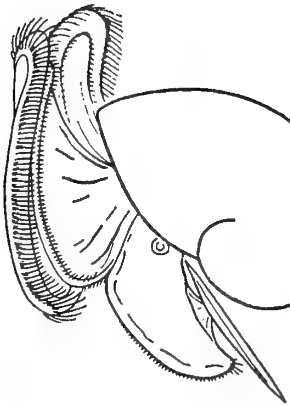

Egg Capsules of Some Prosobranchs from the Pacific Coast of Panama[1]

BY

CHARLES N. D'ASARO

Institute of Marine and Atmospheric Sciences, University of Miami, Florida 33149[2]

(6 Text figures)

INTRODUCTION

OOTHECAE OF MARINE PROSOBRANCHS, especially those produced by the larger neogastropods, are often conspicuous in the littoral zone. With the exception of the following, previous publications on gastropods contain few references to prosobranch oothecae and development in tropical marine habitats: AMIO (1963; in part), ANDREWS (1935), D'ASARO (1970), GOHAR & EISAWY (1967a, 1967b), KNUDSEN (1950), KOHN (1961a, 1961b), LAURSEN (1958), LEBOUR (1945), NATARAJAN (1958), OSTERGAARD (1950), RISBEC (1921, 1932, 1935), STRUHSAKER (1966). THORSON (1940), and assorted papers on individual species. Molluscan diversity and abundance in tropical regions have been noted often as KEEN (1958) does for the Panamic faunal province, but rarely is information on reproduction included. Therefore, the purpose of this report is to add information on the life histories of certain Panamic species, including several important to aquaculturists and other scientists.

METHODS

The report is based on specimens collected by Dr. F. M. Bayer of the Institute of Marine and Atmospheric Sciences, University of Miami. Adult prosobranchs were transported to the Institute's laboratories in Miami, Florida, where they were maintained in aquaria with circulating sea water for over six years. During this period spawn was obtained from *Anachis fluctuata, Anachis varia, Bursa caelata* (=*corrugata*) (BRODERIP, 1833), *Jenneria pustulata* (LIGHTFOOT, 1786), *Muricanthus radix* (GMELIN, 1791), and *Vitularia salebrosa.* Egg masses from *Bursa corrugata* and *Jenneria pustulata* were described previously (D'ASARO, 1969a, and 1969b). *Muricanthus radix* produced several egg masses which were distinctly abnormal; therefore, they were not described. The remaining material is examined in this report.

Specimens were preserved in 10% sea-water formalin. Illustrations were prepared by the author from camera lucida drawings of fixed material. Terminology used in the descriptions is the same as that used by D'ASARO (1970). Averages are based on five or more samples. The systematic arrangement follows KEEN (1958). A summary of the data is presented in Table 1.

Vitularia salebrosa (KING & BRODERIP, 1832)

(Figures 1a and 1b)

Oothecae from this species were collected from Venado Island in the Bay of Panama on December 24, 1965 attached to the nacreous interior of a pelecypod shell. Mature animals spawned in the laboratory from October through January. Egg masses were deposited on the glass sides of aquaria close to the surface film. In several instances capsules were placed above the surface film and consequently did not develop normally. The spawn forms a flat sheet irregular in outline with the oothecae arranged lineally at 1 mm intervals. Adjacent capsules in a row are usually oriented in the same direction as indicated by the almost continuous apical sutures. A mass may contain from 50 to 400 capsules with an average of 190. Communal spawning does occur in the restricted environment of a 60 liter aquarium where only limited space is avail-

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[1] Contribution No. 1175 from the Institute of Marine and Atmospheric Sciences, University of Miami. This investigation was conducted under the auspices of the U. S. Public Health Service (GM 125-41-02), H8179.

[2] Present address: Department of Biology and Marine Sciences, The University of West Florida, Pensacola, Florida 32504.

Table 1

A Summary of Data on the Spawn of Panamanian Prosobranchs

Species	Average Number Capsules/Mass	Average Number Eggs/Capsule	Average Number Eggs/Mass	Capsular Dimensions H - W - T (mm)	Type of Development[3]
Vitularia salebrosa	190	520	99 000	2.0 - 2.5 - 2.1	pv
Anachis fluctuata	98(2)	24	2 400	1.7 - 0.9 - 0.7	pv
Anachis varia	17[4]	78	–	3.5 - 1.6 - 1.4	pv
Melongena patula	29(1)	–	–	53.0 - 50.0 - 2.0	–
Fasciolaria salmo	106(3)	1 900	201 000[5]	18.0 - 13.0 - 6.0	dd
Conus ximenes mahogani	34	1 100	37 000	7.0 - 7.0 - 1.0	pv

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[3] dd - direct development; pv - planktonic veliger

[4] incomplete

[5] includes nurse eggs

able near the surface film. No direct information is available on breeding habits in the natural habitat; however, one egg mass from Venado Island included spawn from another muricid.

The opaque, white capsules are columnar with rounded apices and flared out bases, and are roughly ellipsoid in cross-section (Figures 1a and 1b). Apically, each structure is marked by a central, transparent escape-aperture (Figure 1b). A distinct suture, interrupted only by the escape-aperture, divides the capsule into equal halves in a plane with the long axis of the ellipse and extends into the basal membrane on both sides. During spawning, the basal membranes are fused into a common, transparent sheet which holds the mass together. Variations in color from white to a light pinkish-brown are due to progressive development of the embryo's light brown protoconch and scattered, pigmented granules in the tissues. The average capsular dimensions are: height, 2.0 mm; width (at the base), 2.5 mm; thickness, 2.1 mm. The number of embryos per capsule varies from 380 to 650 with an average of 520. Embryos are nourished by capsular albumen. No nurse eggs are involved. This species, which was reared in the laboratory for two weeks, has a long-term planktotrophic veliger stage.

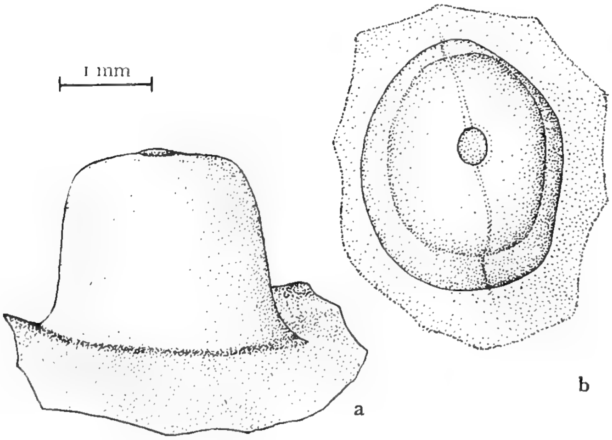

Figure 1

Egg Capsules of *Vitularia salebrosa*

a: lateral view including a portion of the basal membrane
b: apical view

Anachis fluctuata (Sowerby, 1832)

(Figures 2a, 2b, and 2c)

Adult specimens were collected from Venado Island on December 24, 1965 and maintained in aquaria. On March 24, 1967 two egg masses were produced by these animals. The flat, irregular masses, arranged in rows containing 5 to 11 units, were attached to the aquarium glass near the bottom and contained 94 and 101 capsules.

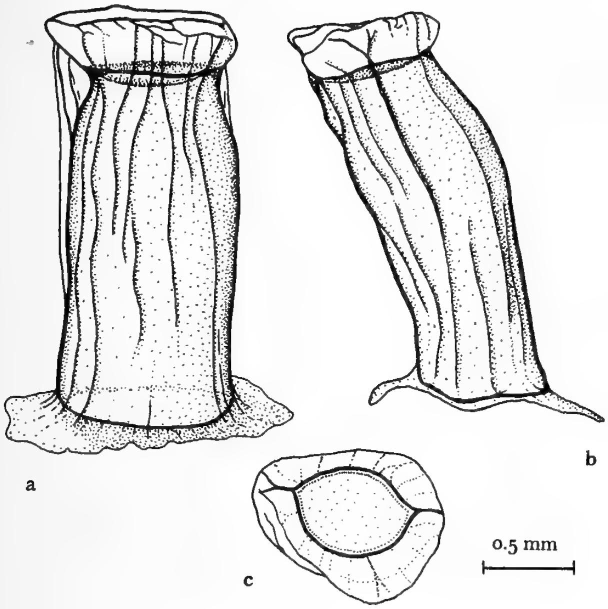

Figure 2

Egg Capsules of *Anachis fluctuata*

a: convex side (tilted toward the viewer)
b: view of the apical plate only
c: lateral view of a tilted capsule

Anachis fluctuata has transparent oothecae which are roughly columnar, marked by multiple, uneven, longitudinal ridges on all sides, and have a wide, collar-like membrane surrounding the apical plate (Figures 2a and 2b). The normally convex sides may be flat or even concave. Most longitudinal ridges extend into the apical membrane and occasionally the basal membrane. On both sides, a single extension of a longitudinal ridge forms a distinct keel bridging the constricted area at the apex (Figure 2a). One keel is usually larger. Laterally, the capsules appear tilted (Figure 2b). The apical plate, which is roughly ovate and slightly wider than the body of the capsule, is outlined by a suture forming the escape-aperture (Figure 2c). There is no peduncle. The oothecae are connected by a continuous basal membrane. Average capsular dimensions are: height, 1.7 mm; width (of the capsule), 0.9 mm; width (of the apical membrane), 1.1 mm; thickness, 0.7 mm. The capsules contained between 17 and 27 embryos, averaging 24. Embryos hatch as advanced veligers which remain in the plankton for only a short period.

Anachis varia (Sowerby, 1832)

(Figures 3a and 3b)

Egg masses and spawning adults were collected from Venado Island on December 24, 1965, under rocks exposed at low tide. The field sample obviously represents a fragmentary egg mass, since only 17 oothecae attached to a shredded basal membrane were included.

The transparent, yellowish oothecae are roughly vasiform, flattened, heavily ribbed and have a raised, apical escape-aperture (Figures 3a and 3b). Three uneven, longitudinal ribs, a large central and two laterals, mark the widest sides. These may appear singular or multiple. In the latter case, the ribs are often constructed of slightly separated, nearly parallel ridges (Figure 3a). A section of the apical plate containing the escape-aperture is elevated and surrounded by a very narrow, transparent membrane raised from the surface. In most cases, the oval exit is covered by an opaque membrane. In addition, the apical plate has sharp ridges extending around the periphery and occasionally from the apertural ridge to the intersection of a lateral ridge. Other randomly placed, low folds may occur. No distinct peduncle is present; however, supporting ribs in the area connect the lateral ribs to the basal membrane. The average capsular dimensions are: height, 3.5 mm; width, 1.6 mm; thickness, 1.4 mm.

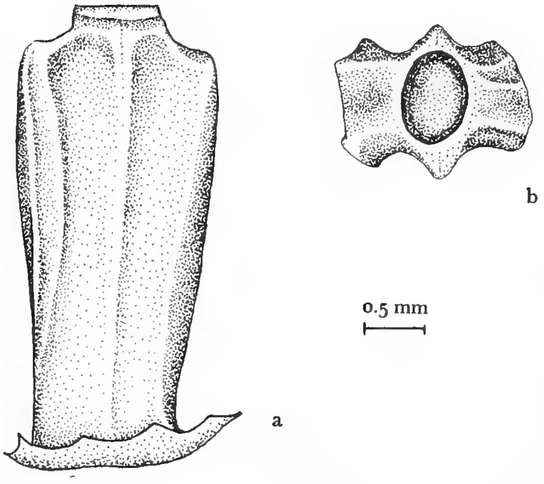

Figure 3

Egg Capsules of *Anachis varia*

a: lateral view including a portion of the basal membrane
b: apical view

Oothecae in the fragmentary mass contained an extremely uniform number of embryos, averaging 78. The enclosed embryos appear to be typical of species with planktotrophic veligers.

Melongena patula (Broderip & Sowerby, 1829)

(Figures 4a and 4b)

Several fragmentary egg masses collected on August 28, 1965 at Venado Island were identified by the collector as *Melongena patula.* Morphologically, the oothecae resemble the egg capsules of *M. corona* (Gmelin, 1791) from South Florida (Clench & Turner, 1956) which are proportionally thicker but do not have serially fused peduncles. The extreme size of the Panamanian oothecae is indicative of a large prosobranch like *M. patula* which may be 10 inches long (Keen, 1958). A total of 29 capsules from a single mass was examined.

Oothecae of this species are flat, opaque, membranous envelopes entirely lacking sculpture (Figure 4a). The edges, where the membranes fuse, are thin and almost knife sharp. There is no apical plate. Instead, the envelope's border corresponding to the apex is unevenly indented (Figures 4a and 4b). A narrow suture in the fused membrane at the base of the deepest indentation forms the escape-aperture. Each capsule has a solid peduncle with two supporting ribs on opposite sides placed at right angles to the envelope's plane (Figure 4b). These supports extend only a short distance toward the apex as distinct ridges. Adjacent ribs are fused, connecting the capsules in a chain spaced about 6 mm apart. The oothecae have the following average dimensions: height, 5.3 cm; width, 5.0 cm; thickness (at the base), 0.2 cm. No embryos were present in the material examined.

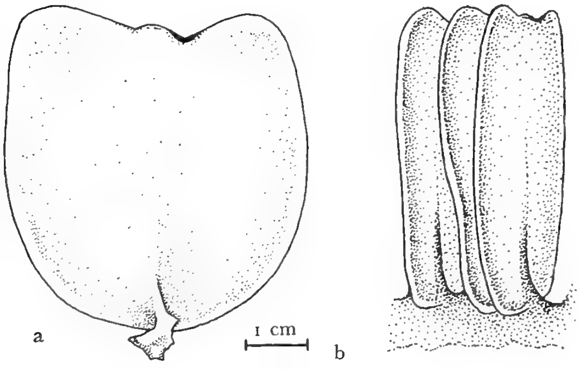

Figure 4

Egg Capsules of *Melongena patula*

a: view of the flat side with the apical suture accentuated
b: three capsules shown in lateral view

Fasciolaria salmo (Wood, 1828)

(Figures 5a, 5b, 5c, and 5d)

Three large egg masses of this common species were collected from barnacle covered rocks on mud and sand flats around Venado Island on December 24, 1965. There was no direct evidence indicating the number of individuals involved during spawning. The masses are layered and compartmented with the largest containing 4 layers. Each capsule is oriented facing in the same direction as others in a given layer. However, adjacent groups are often situated at various angles or face the opposite direction. Two possible explanations can be given to account for this variation. *Fasciolaria salmo* could be an intermittent spawner pausing frequently, or more likely, it is a communal spawner. Behavioral patterns of this type were noted in the genus by Gohar & Eisawy (1967). According to Keen (1958), the animals are 4 to 5 inches long. At this size they should be able to produce egg masses containing a maximum of 150 capsules. Since the larger clusters examined contained approximately 225 oothecae, considerably more than expected from a 5-inch specimen, communal spawning probably occurs. The masses contained 24, 70, and 225 capsules. Clusters within each contained from 18 to 54, averaging 40.

Fasciolaria salmo has vasiform capsules which are characteristic and typical of the genus. The opaque oothecae have flattened or slightly convex sides, one side having a few low ridges or none and the other is divided into two sections by a sharp keel (Figures 5a, 5b, and 5c). Often low ridges appear on either side of the keel (Figure 5c). Sharp ribs line the lateral edges of the capsules and are continuous with the peduncle (Figure 5b). The apical plate is surrounded by a thickened rib with a sharp edge which flares over the concave side as a large membranous lappet giving the apical region the shape of a conventionalized heart with a raised area where indented (Figure 5d). An oval escape-aperture, covered by an opaque membrane, is situated close to the border of the keeled side. Sutures extend from opposite sides of the oval to the membranous flap (Figure 5d). The peduncle is solid, and typically has supportive ribs. As expected, the basal membranes are fused. Average capsular dimensions are:

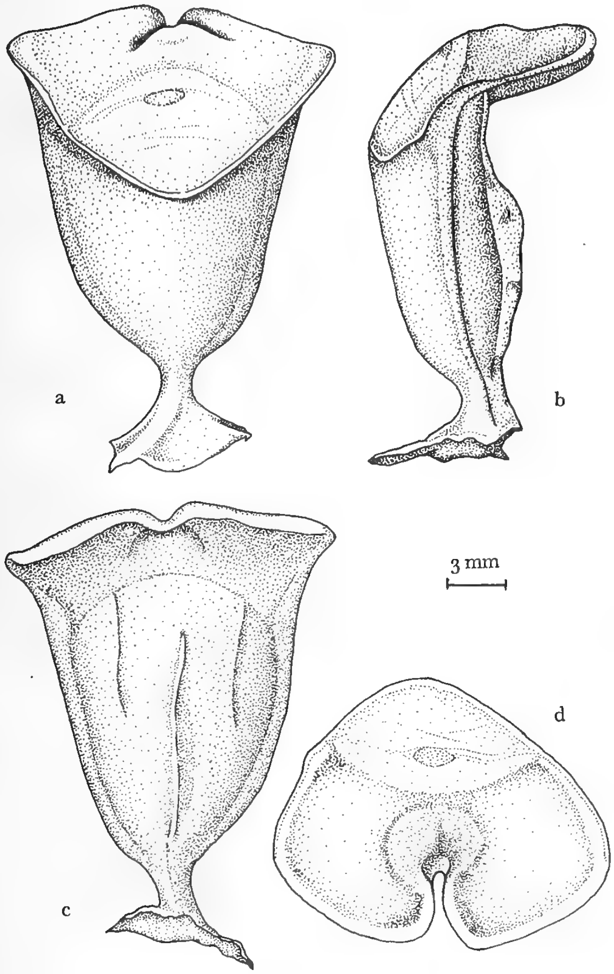

Figure 5

Egg Capsules of *Fasciolaria salmo*

a: view of the smooth, convex side
b: view of the ribbed side showing the keel in lateral view
c: view of the keeled side
d: apical view

height, 1.8 cm; width (capsule), 1.3 cm; width (membranous flap), 1.5 cm; thickness, 0.6 cm. The number of embryos per capsule ranges from 1800 to 2100, averaging 1900. Since the spawn was collected shortly after oviposition, it was not possible to estimate the number of viable embryos. Nurse eggs are common in this genus; therefore, most eggs are expected to be of that type. Direct development is most probable.

Conus ximenes mahogani Reeve, 1843

(Figures 6a, 6b, and 6c)

Two egg masses were collected from sand flats around Venado Island on December 24, 1965. Both were attached to the sand surface of polychaete tubes. In the collector's opinion, *Conus ximenes mahogani* is most probably the spawner since it is especially common in the area. Capsules are generally arranged lineally about 1 mm apart. All spawn present on a given polychaete tube, even if several small masses were included, was considered the production of a single female. The author has observed spawning cones, which normally produce discrete egg masses, depositing isolated egg clusters near a large central mass. The spawn contained 29 and 39 capsules.

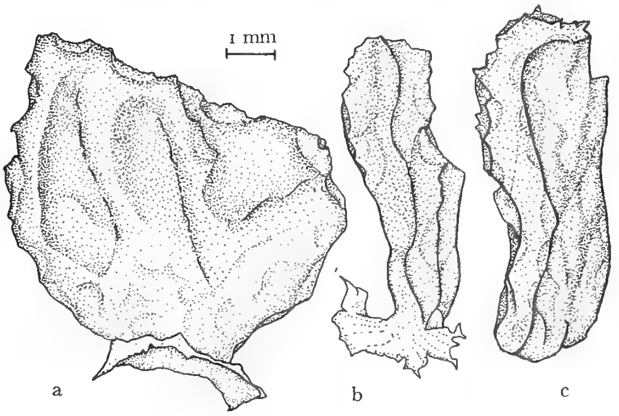

Figure 6

Egg Capsules of *Conus ximenes mahogani*

a: view of the flattened, ridged side

b: lateral view

c: apical view of the sigmoid plate and part of one side

Conus ximenes mahogani has flattened, vasiform capsules with irregularly corrugated and crenulated surfaces (Figures 6a and 6b). The abbreviated peduncles are positioned somewhat off center with the edge opposite the peduncular region being longer. Sculpturing on the sides is patterned only in that there are usually one or more poorly defined ridges running from the central apical region to the peduncle (Figure 6a). Most capsules have a crenulated apical plate with a roughly sigmoid shape (Figure 6c). No definite escape-aperture was observed. Basal membranes are narrow and often discrete. Average capsular dimensions are: height, 7.0 mm; width, 7.0 mm; thickness, 1.0 mm. The capsules contain from 970 to 1300 embryos with an average of 1100. This species has a planktotrophic veliger.

DISCUSSION

Prosobranch adaptability is again demonstrated by the spawning habits of *Vitularia salebrosa.* This species easily adjusts to a new environment and even to strange food-organisms, requiring only the proper temperature, a hard substrate, and abundant food to produce large egg masses. Finding the proper food remains a problem in spawning some species in the laboratory. For example, specialized carnivores like certain cypraeaceans accept a limited number of colonial ascidians as food and require the food organisms in which to deposit egg capsules.

Columbellids present an interesting example of the caenogenetic variations which often appear in the Prosobranchia. *Anachis fluctuata,* for example, has roughly columnar, ridged oothecae with a wide, collar-like apical membrane. This type is not common to the family or even to the genus. As Thorson (1940) noted, 5 or more different types are found in *Columbella* alone, ranging from stalked structures to semi-globular oothecae with one or more collar-like membranes around the apical region. *Anachis* has a similar range in structural types. Egg capsules of *A. avara* described by Scheltema (1963) are conical and unribbed. *Anachis varia* has roughly vasiform, flattened and heavily ribbed oothecae without distinct peduncles. The columnar structure of the oothecae of *A. fluctuata* also differs and most resembles that of members of the genus *Columbella* with a similar collar-like membrane. In general, these variations indicate that the columbellids are in a state of evolutionary flux, especially when compared to more stable, large groups like the conids or strombids, each having many species with very similar oothecae.

Many similarities exist between the oothecae of *Melongena patula* from Panama and *M. corona* from South Florida and the Gulf of Mexico. Spawn from *M. corona* examined by the author and others (Clench & Turner, 1956) has proportionately thicker capsules and unfused peduncles attached to flat basal membranes. In *M. patula,* ribs on either side of the peduncles fuse to each other as well as to the basal membrane. The resulting structure is somewhat similar to the central rib of xancid spawn (D'Asaro, 1970) and probably is formed in a similar manner.

Oothecae deposited by *Fasciolaria salmo* differ significantly from other fasciolarids in having a large, indented lappet extending from the apical plate. By comparing spawn from the fasciolarids of Florida and the Caribbean, it is possible to establish that the lappet is homologous with the expanded apical rib or ridge found in these species.

Of the 5 species examined in this report, *Conus ximenes mahogani* produced comparatively the least variable spawn. The oothecae are typically conid in their linear arrangement and general shape. The best references for comparative data on the Conidae are by Kohn (1961a and 1961b).

ACKNOWLEDGMENTS

The egg masses examined herein were collected in Panama or obtained from laboratory reared specimens from the same location by Dr. F. M. Bayer of the Institute of Marine and Atmospheric Sciences, University of Miami. The author is greatly indebted to Dr. Bayer for allowing him to study and report on the collections.

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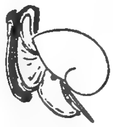

Comparisons Among Growth Characteristics of Two Species of Sea Mussel, *Mytilus edulis* and *Mytilus californianus*

BY

J. R. E. HARGER

Department of Biological Sciences, University of California at Santa Barbara[1]

(11 Text figures; 11 Tables)

INTRODUCTION

THIS PAPER DEALS WITH growth characteristics of two species of sea mussel, *Mytilus edulis* LINNAEUS, 1758 and *Mytilus californianus* CONRAD, 1837, in the waters of Southern California (Santa Barbara).

Mytilus edulis has a world-wide distribution, being present in both northern and southern hemispheres (STUBBINGS, 1954). On the west coast of North America it is commonly found in quiet waters, such as bays, sloughs, etc., but may also occur in considerable numbers on exposed and semi-exposed shores.

Mytilus californianus seems to be endemic to the west coast of North America, with a range extending from the Aleutian Islands to Isla Socorro, Mexico (SOOT-RYEN, 1955). It occurs sparsely within harbors (together with *M. edulis*), but is confined principally to exposed coasts.

Considerable overlap between extremes of exposure and shelter exists in the distribution of the two species and striking examples of populations resulting from this overlap occur on open coast pier pilings in Southern California. Such a situation is found at Ellwood Pier (property of Signal Oil and Gas Company), located some 14 miles west of Santa Barbara on an open sandy shore. Constructed on steel girders, this pier extends approximately $\frac{1}{2}$ mile into the sea, from the shallow surf zone out to a depth of some 40 feet. Intertidal regions of the pilings support enormous clumps of sea mussels consisting of both *Mytilus edulis* and *M. californianus* (HARGER, 1968).

My interest in the biology of these mussels was initially stimulated by the sight of the two species growing together in the same clumps, and, hence, seeming to circumvent the "competitive exclusion principle" (HARDIN, 1960).

Most of the detailed experimental work designed to evaluate the effects of competition between two species of animals having similar ecological requirements have been studies performed in the laboratory. DEBACH (1966) says "almost without exception where two species compete for identical food in the same habitat (laboratory universe), one species displaces the other completely within relatively few generations."

The co-occurrence of large numbers of *Mytilus edulis* and *M. californianus* within the same clump seemed in violation of the above statement, particularly as the limited amount of intertidal piling available for colonization indicated that space must sometimes be limiting to these animals.

The following information relating to growth characteristics of *Mytilus edulis* and *M. californianus* has been gathered as a by-product of experiments originally set up to investigate interactions between the two mussel species.

GENERAL METHODS

Mussels used in the experiments were placed in wire mesh cages suspended intertidally at various heights from the cross-girders at Ellwood Pier or from marina floats in Santa Barbara Harbor. The cages were cylindrical in shape (diameter 7 inches or 7.78 cm, height $8\frac{1}{2}$ inches or 21.5 cm) and constructed from galvanized hardware cloth. Components (wire sections, etc.) used in cage construction were laced together with braided nylon cord and the entire unit was coated with epoxy resin. This coating served to give rigidity to the nylon binding and at the same time to cut down any leaching of zinc ions which might affect enclosed mussels. A log normal distribution of mussel lengths was chosen to represent mature mussel populations, since this was similar to the distribution of *Mytilus californianus* within clumps on Ellwood Pier (Harger, 1968). The mussels used ranged in length from 2.5 cm up to 10 cm (for size classes and frequencies, see Table 1). *Mytilus californianus* individuals occurring within clumps are often much larger than 10 cm, but this tends to be the upper size limit for *M. edulis*. A log normal distribution most accurately mimics that of *M. californianus* in natural clumps (Harger, 1968), and although the distribution of *M. edulis* tends to be normal, or bimodal normal if both juveniles and adults are present, it seemed advisable to use an identical size distribution for both species in order to be sure of eliminating any effects which might arise as the result of size differences.

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[1] Present address: Department of Zoology, University of British Columbia, Vancouver 8, British Columbia.

Table 1

Lognormal distribution used to construct experimental mussel populations. Cages containing both *Mytilus edulis* and *Mytilus californianus* received equal representation to make a total of 90 individuals

Size Class	N
2.5 – 3.5 cm	12
< 3.5 – 5.0 cm	32
< 5.0 – 6.5 cm	24
< 6.5 – 8.0 cm	14
< 8.0 – 10.0 cm	8
Total:	90

Cages containing populations of mature mussels were constructed from $\frac{1}{2}$-inch (1.27 cm) aperture hardware cloth and a total of 90 mussels was placed within each cage (equal numbers of the two species for mixed populations). Individual mussels used in the experiments were marked in the following manner: after drying, a small patch was scoured on the shells with sandpaper, code numbers were written on the roughened surface in white ink, and a small drop of clear epoxy resin was placed over the symbols and allowed to harden overnight.

The maximum length of each animal was recorded in centimeters (accurate to 2 decimal places), between the anterior hinge and the posterior siphon regions at the commencement and conclusion of the experiment. (Mussels were removed from water for approximately 12 to 24 hours for marking, etc., and mortality ranged between 10 and 15% as a result of this process.)

All mussels used in the experiments were taken from clumps at Ellwood Pier no more than one day before marking. Before and immediately after marking the animals were kept in running (non-recirculating) sea water. Laboratory containers were well aerated and mussels spent a maximum of 3 days between removal from the pier clumps and replacement at the pier within experimental cages.

METHODS USED TO RECORD SEASONAL FLUCTUATIONS IN GROWTH

Coe & Fox (1942) and Coe (1945) reported that growth of both *Mytilus californianus* and *M. edulis* fluctuated seasonally at Scripps Pier (La Jolla, Southern California). To monitor similar variations at Santa Barbara two replicate cages containing mixed populations of marked *M. edulis* and *M. californianus* were placed at each location where long term competition experiments were run. These positions were the top, middle, and bottom of the mussel clumps at Ellwood Pier and beneath the marina floats in Santa Barbara Harbor. Growth was recorded from the mussels in these cages throughout the year. From these data the mean growth increment of mussels falling within each of 9 size classes at the beginning of each 2-month time period was calculated. Initially, measurements were made at intervals of one month, later this was increased to 2 months to minimize disturbance effects. Data obtained from the monthly recordings were corrected to the longer interval; but the resulting values are probably higher than they would otherwise have been since the effect of removing mussels from the water and measuring them tends to prevent individuals from inhibiting each other's growth (see later).

METHODS USED IN OBTAINING LONG TERM GROWTH INFORMATION FROM ARTIFICIAL "MATURE" MUSSEL POPULATIONS

To investigate the possible effects of competition between *Mytilus edulis* and *M. californianus* an experiment using a 3-way factorial design was set up involving 2 species, 3 intertidal levels, and 4 treatments. The top intertidal level corresponded to the top of the mussel clumps occurring on Ellwood Pier pilings (Harger, 1968) (about 2 feet or 60 cm below the highest tides), the middle level to the middle of the clumps and the bottom level (just exposed at the lowest tides) to the bottom of the clumps. The 4 treatments consisted of different arrangements of mussels within the cages: Treatment 1 consisted of surrounding one species in the center of the cage by the other species; Treatment 2 the reverse; Treatment 3 consisted of mixing individuals of both species as evenly as possible; and Treatment 4 of *M. edulis* or *M. californianus* alone. This experiment was initiated before I was aware of behavioral differences which exist between the two species (HARGER, 1968). Briefly, *M. edulis* individuals react to pressure imposed upon them by crawling against such pressure, whereas *M. californianus* react slowly or not at all. Thus, the first 3 treatments probably became identical since *M. edulis* tended to arrange itself on outer surfaces of the caged clumps. Only cages containing pure *M. californianus* and pure *M. edulis* (3 replicates each) were run at the mid-intertidal level. All other treatments within the design were replicated 5 times.

An extension of this experiment consisted of setting up 2 replicates of the following 3 treatments: evenly mixed *Mytilus edulis* and *M. californianus;* pure *M. edulis;* and finally, pure *M. californianus* in Santa Barbara Harbor. Cages were here suspended from marina floats in such a way as to be approximately one foot (30 cm) below the water surface at all times.

The complete experiment was started during August, 1965; at Ellwood Pier, 3 of the aforementioned 5 replicates were left in the sea for 6 months before removal (including all the mid-tidal cages) and the remaining 2 replicates were withdrawn after one year.

The first 3 replicates were removed after 6 months because the cages were in danger of being washed off the pier by heavy storms experienced by the area at that time. Rather than risk losing a great part of the experiment I elected to analyze $\frac{3}{5}$ of it at that point (3 cages were lost).

METHODS USED IN OBTAINING GROWTH INFORMATION FROM JUVENILE MUSSEL POPULATIONS

To study the effect of competition between juvenile mussels (1.5 to 2.5 cm long) the following experiment involving 3 treatments, each replicated twice, was set up:
a) pure *Mytilus edulis* (200 individuals); b) pure *M. californianus* (200 individuals); c) *M. edulis* mixed evenly with *M. californianus* (100 individuals of each species). In this experiment individual animals were not marked, but all were measured at the start and at each inspection. The cages containing them were plastic kitchen colanders (10 inches or 25.4 cm in diameter) placed face to face and lashed together round the edges. The maximum diameter of holes in the colanders was $\frac{1}{4}$ inch (0.63 cm). All cages were first suspended from Ellwood Pier in October, 1965 at the low intertidal position only. The first 3 inspections were made at intervals of one month. Thereafter, in order to reduce effects of disturbance that might influence the outcome of the experiment, the interval was increased to 2 months for the next 2, and to 4 months for the last 3 inspections. In all, a total of 19 months growth was recorded. A further experiment using juvenile mussels was set up during January, 1966 which was designed to check growth and the effects of competition in both rough and calm water. The 2 locations used for this experiment were Ellwood Pier (rough water) and Santa Barbara Harbor (calm water). The experimental populations (200 individuals) were set up in wire hardware cloth cages ($\frac{1}{4}$ inch or 0.63 cm aperture) and positioned in the same manner as previously reported, at the pier (lowest level) and the harbor. In the harbor the 3 treatments (pure *M. edulis;* pure *M. californianus*; and both in even proportion) were the same as reported for the previous experiment, together with a parallel set at Ellwood Pier. Two additional treatments (*M. edulis* and *M. californianus* mixed in the ratio of 3:1 and the reverse) were also used at the latter site. These were designed to investigate the effect of differing initial proportions of the 2 species on the outcome of the competitive process. A checking interval of 4 months allowed time for undisturbed growth.

RESULTS

SEASONAL GROWTH CHARACTERISTICS OF *Mytilus edulis* AND *Mytilus californianus*

Figures 1, 2, 3, and 4 show the bimonthly growth characteristics for 3 size classes (4 - 5 cm, 5 - 6 cm, 6 - 7 cm) of both species of mussels throughout the period November, 1965 to January, 1967 from the bottom, middle, and top positions at Ellwood Pier and from Santa Barbara Harbor. As individual mussels initially present within the 4 - 5 cm size class grew, they passed through and were recorded within the larger size classes at different times. This method of presenting growth data allows the effect of the increasing size of individual organisms to be eliminated from the seasonal pattern without having to set up separate new populations throughout the year. A complete record of smaller size classes (below 4 cm) was not obtained since most small mussels passed into the larger size classes before the experiment was over. Size classes larger than 6 - 7 cm showed a growth pattern similar to that of the 6 - 7 cm class.

At Ellwood Pier, both *Mytilus edulis* and *M. californianus* in cages set in the low position showed a period of "slow" growth between December, 1965 and March, 1966

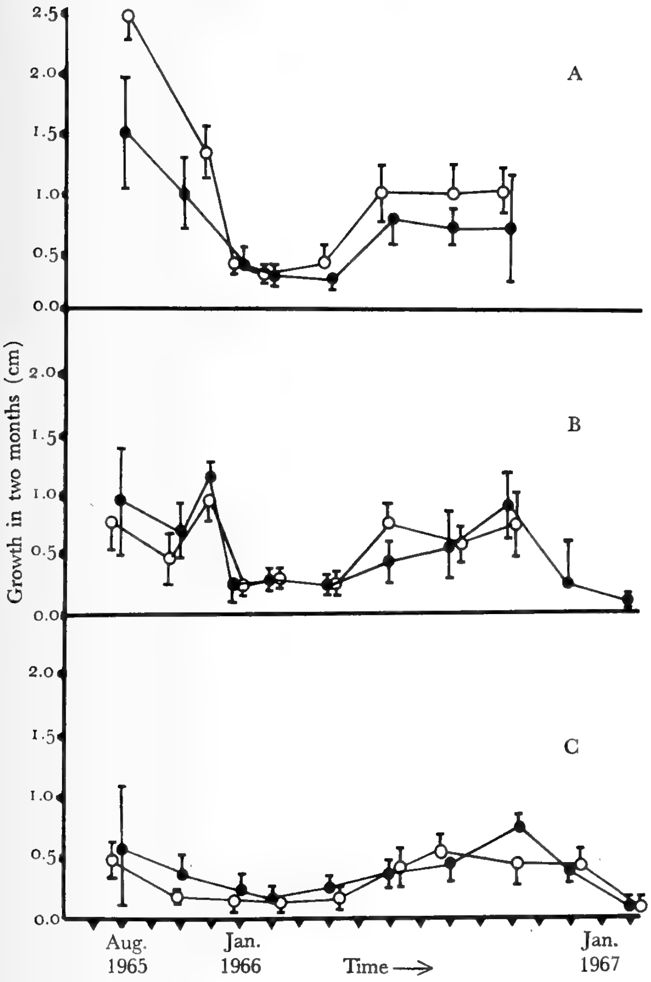

Figure 1

Growth fluctuations for mussels set in cages at the low position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period August, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

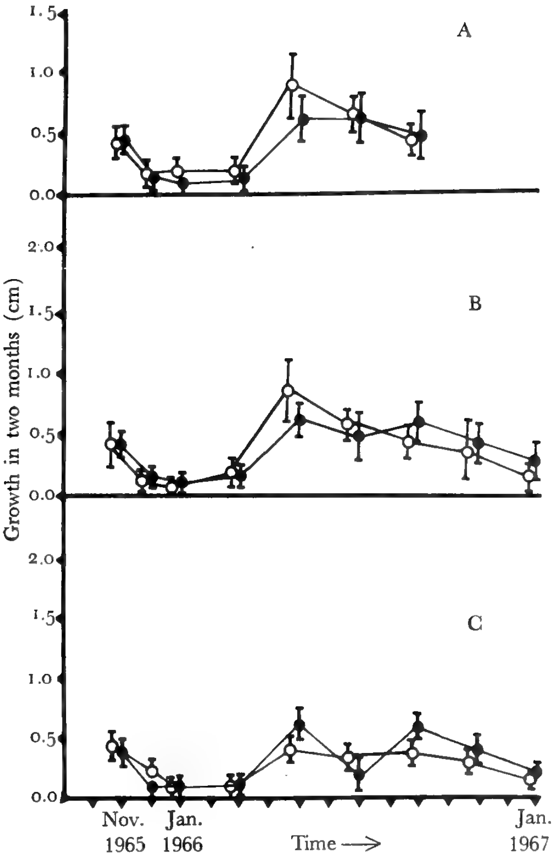

Figure 2

Growth fluctuations for mussels set in cages at the middle position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

for all recorded size classes. This was repeated between November, 1966 and January, 1967 (Figure 2). Both periods of slow growth occurred during winter months when water temperature was at its lowest (Figure 5) and when frequent heavy seas occurred, both of which may have limited growth. Maximum growth occurred during the warmer summer months. Similar growth patterns were exhibited by mussels in cages placed in the intertidal region, that is at the middle and the top of the mussel clumps (Figures 2, 3).

In the low cages growth of *Mytilus edulis* within the smaller (4 - 5 cm) class exceeded that of *M. californianus* of the same size class at all times except during the coldest months when both species showed equal growth (Figure 1). In the middle cages, small *M. edulis* individuals grew more than *M. californianus* but only for the first 6 months of the year, whereas in the upper cages growth of *M. californianus* was always greater than that of *M. edulis*. Growth of the larger *M. californianus* size classes for the most part exceeded that shown by *M. edulis* of similar size except for the 5 - 6 cm size class at the middle and lower levels during the summer months (Figures 1, 2, 3).

In Santa Barbara Harbor, growth of *Mytilus californianus* was lower than that of *M. edulis* for all size classes. Here fluctuations in the seasonal growth pattern for both species were almost non-existent, unlike the situation at Ellwood Pier (Figure 4). This might suggest that it was not low water temperature *per se* that caused low winter growth rates at Ellwood Pier (surface water temperatures were similar in both places throughout the year), but some associated phenomenon such as food scarcity or wave action. Within the harbor wave action was very slight during severe winter storms, whereas the Pier re-

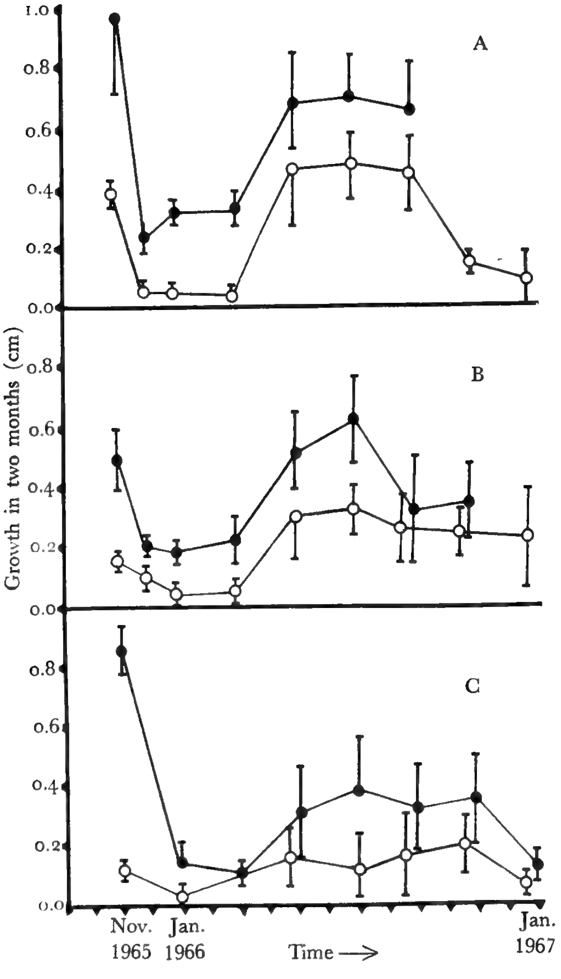

Figure 3

Growth fluctuations for mussels set in cages at the top position, Ellwood Pier (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; < 6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

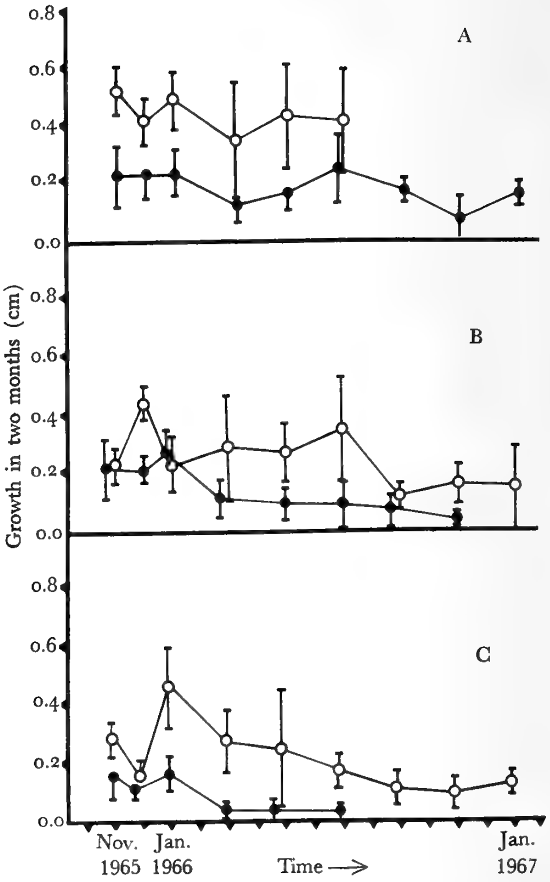

Figure 4

Growth fluctuations for mussels set in cages at Santa Barbara Harbor (see text)

The mean growth increment for each of three size classes, A, B, and C (< 4 - 5 cm; < 5 - 6 cm; <6 - 7 cm) is recorded at bimonthly intervals for the period October, 1965 to January, 1967. *Mytilus edulis* is represented by open symbols and *Mytilus californianus* by closed symbols. Twice the standard error of the mean is represented by a bar on each side of the symbol. (Some symbols are displaced for clarity.)

ceived an extensive pounding on such occasions. Although I have shown (Harger, 1967) that growth of *M. edulis* is inhibited by wave action, this was not demonstrated for *M. californianus* (at least for the moderate wave action at which the investigation was undertaken).

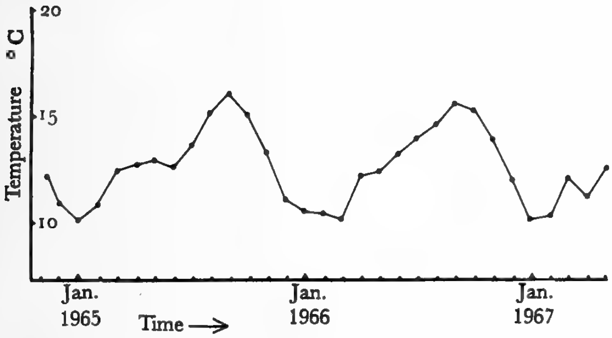

Figure 5

Mean monthly surface water temperatures from Santa Barbara Harbor. Readings were taken daily at midday.

GROWTH OF MUSSELS IN EXPERIMENTS INVOLVING "MATURE" POPULATIONS

Growth patterns of *Mytilus edulis* during both the 6 and 12 month immersion intervals were similar, this being true also for *M. californianus.* The following comments mainly concern results obtained from the 12 month interval with the understanding that no differences of importance are apparent between the 2 sets of data (more growth was of course recorded for the longer interval).

Results obtained from populations which were permitted to grow undisturbed for 12 months indicate that *Mytilus edulis* and *M. californianus* possess different growth characteristics. Figures 6 and 7 show growth curves for both species from the top and bottom intertidal positions. These curves were constructed by sorting all the mussels (each species separately) alive at the end of the 12 month period into 1 cm size classes based on the measurements made at the beginning of the experiment. The mean growth increment was then calculated for each group, and a cumulative growth curve based on the year's growth for each individual size class was then made up. For convenience, it was assumed that the mean size of any group at the start of the year corresponded to the mid point of each size class, *i. e.,* for the class 2 - 3 cm this would be $2\frac{1}{2}$ cm. The resulting curve indicates the expected growth pattern the mussels would show over a number of years if all years corresponded in weather conditions, etc., to that in which the measurements were made. The data from which the curves were constructed are recorded in Tables 1 and 2 (Appendix).

Since mussels from all the different treatments have been grouped together to provide the data on which

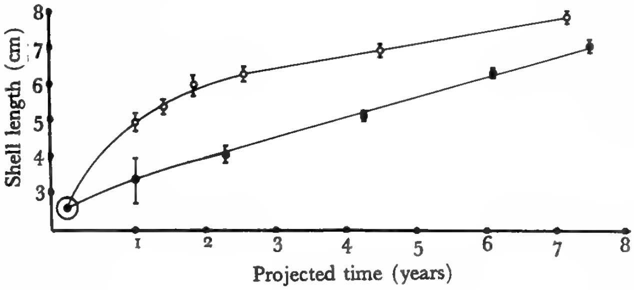

Figure 6

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at the top position, Ellwood Pier (see text). Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 1 in the Appendix.)

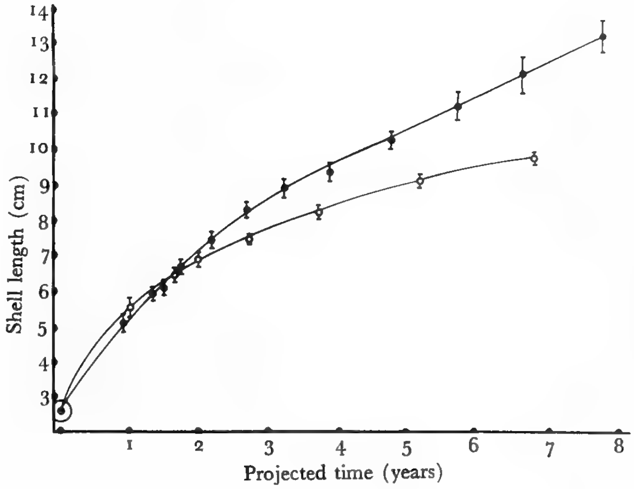

Figure 7

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at the bottom position, Ellwood Pier (see text). Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 2 in the Appendix.)

these curves are based it is probable that these results are representative of the growth that would occur in heterogeneous natural populations.

At the lowest level *Mytilus edulis* grew slightly more than *M. californianus* for approximately the first year, *i. e.*, until *M. edulis* reached a length of 5 - 5½ cm; thereafter, growth of *M. edulis* fell off and almost ceased by the time the mussels had reached a length of 10 cm or so. Growth of *M. californianus* did not fall off appreciably until individuals had reached at least 15 cm (2 to 3 years). Growth rate exceeded that of *M. edulis* increasingly after a length of about 6 cm had been reached. At the high level, growth of *M. edulis* of all sizes was always exceeded by that of *M. californianus*.

The curves for mussels growing in the low posititon are similar to those recorded by Coe (1945) at La Jolla, California, except that considerably higher growth for both *Mytilus edulis* and *M. californianus* was obtained at La Jolla than at Santa Barbara. This, overlooking the possible effects of temperature and differing geographical conditions, was most probably due to the difference in culture techniques. Coe's technique consisted in keeping mussels submerged and out on wire trays; this obviously avoids any effects of intraspecific competition and so maximum growth would be recorded. An effect such as this is apparent when growth of mussels from the disturbed populations (those used to obtain seasonal fluctuations) is compared with growth from the long term undisturbed populations. For instance, the 3 to 4 cm size class for *M. californianus* growing in the bottom cages at Ellwood Pier showed a mean annual increase of 3.08 cm ±0.48 cm for the disturbed cages and 2.33 cm ± 0.12 cm for the undisturbed cages. A similar trend is present in the other sizes and is also to be found in *M. edulis*. This difference presumably arose because of effects of intraspecific and interspecific competition were continually reduced in the disturbed populations by the bi-monthly inspections which served to rearrange mussels.

THE EFFECT OF INTERTIDAL EXPOSURE ON GROWTH OF

Mytilus edulis AND *Mytilus californianus*

Cages were set out at top, middle, and bottom intertidal positions for the 6 month period only. Discussion of the effects of intertidal position on growth will therefore be confined mainly to data obtained during this time interval.

Because small mussels exhibit a growth pattern which differs from that of large mussels, each population has been divided into 2 groups. The first is comprised of all those mussels originally smaller than 4 cm, and the second, those larger than 5 cm. Mussels between 4 and 5 cm are not included in order that a clear distinction between the growth patterns exhibited by small and large mussels can be made.

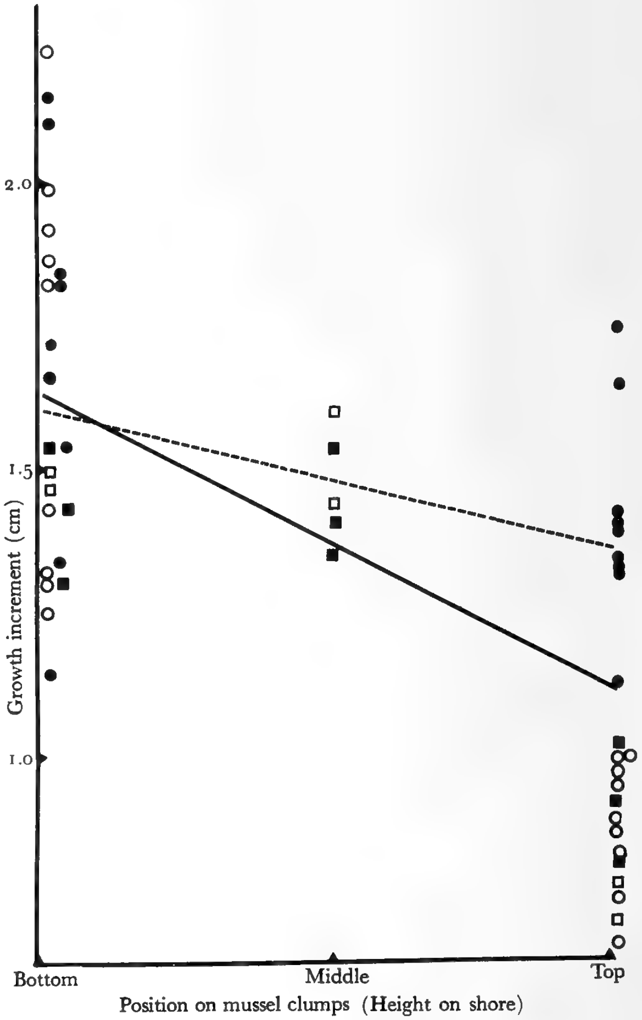

Figure 8

Mean growth increment per cage for mussels initially under 4 cm in length, plotted against height of cage (*i. e.*, height on shore). The mussels were allowed to grow undisturbed for 6 months (August, 1965 to February, 1966). ○ represent *Mytilus edulis* from cages in which both species occurred. □ represent *Mytilus edulis* from pure clumps. ● represent *Mytilus californianus* from mixed clumps and ■ represent *Mytilus californianus* from pure clumps. *Mytilus californianus* is represented by the dashed regression line and *Mytilus edulis* by the solid line. The regression coefficients for the two lines are significantly different from each other ($P < 0.001$), see Table 3.

(a) Mussels Initially Under 4 cm

Growth of smaller mussels is shown in Figure 8. Here, mean growth increment for each cage has been plotted against height on shore. There was no significant difference between the growth of the 2 species at the lower or middle positions, but the growth of *Mytilus edulis* in the top position was markedly lower than that of *M. californianus* (Table 2). The slopes of the regression lines which relate height on pilings to growth increment are significantly different from one another (Table 3), which suggests that with increasing tidal exposure time growth of smaller *M. edulis* individuals is inhibited to a greater extent than is that of *M. californianus*.

Table 2

Comparison between the growth increment of small individuals of *Mytilus edulis* and *Mytilus californianus* contained within adult populations in upper cages at Ellwood Pier for the period August, 1965 to February, 1966. All measurements were obtained from mussels initially between 2.5 cm and 4.0 cm in length. (In this and following Tables 3 asterisks {***} indicate a significant difference, $p < 0.001$)

Group	M	SD	SS	F 1,340
Mytilus edulis	0.83	0.43	166	
Mytilus californianus	1.23	0.64	176	46.66***

M = mean; SD = standard deviation; SS = sample size

Table 3

Comparison between the slopes of the regression lines relating growth increment of *Mytilus edulis* and *Mytilus californianus* individuals initially less than 4 cm in length, growing within adult populations at Ellwood Pier, to intertidal level. The dependent variable is growth increment and the independent variable is intertidal level (top, middle, bottom positions, see text). Growth occurred between August, 1965 and February, 1966. All measurements were in centimeters

Group	SS	Regression equation	Sl	F 1,814
Mytilus edulis	371	$y = 1.64 - 0.133X$	–0.133	
Mytilus californianus	447	$y = 1.60 - 0.063X$	–0.063	15.67***

SS = sample size; Sl = slope

(b) Mussels Initially Over 5 cm

Results obtained from larger mussels are quite clear. First, growth of *Mytilus edulis* at all 3 heights is signifi-

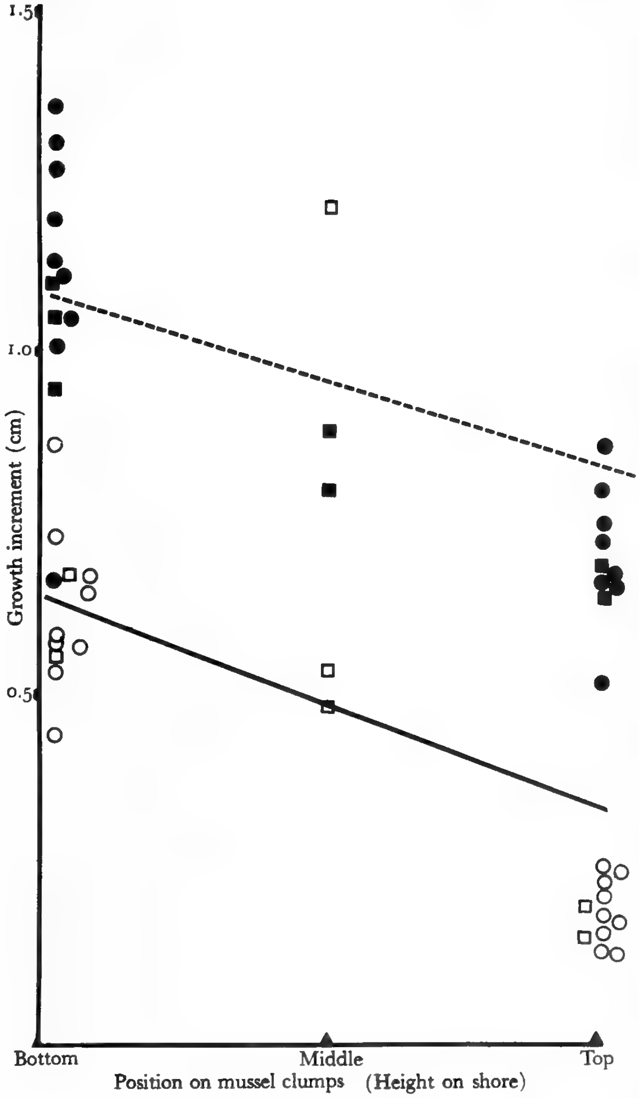

Figure 9

Mean growth increment per cage for mussels initially over 5 cm in length, plotted against height of cage (*i. e.*, height on shore). The mussels were allowed to grow undisturbed for 6 months (August, 1965 to February, 1966). ○ represent *Mytilus edulis* from cages in which both species occurred. □ represent *Mytilus edulis* from pure clumps. ● represent *Mytilus californianus* from mixed clumps and ■ represent *Mytilus californianus* from pure clumps. *Mytilus californianus* is represented by the dashed regression line and *Mytilus edulis* by the solid line. The lines are not significantly different from each other in slope, but are so in position (y intercept), $p < 0.001$.

cantly less than that of *M. californianus* (Figure 9). Figure 9 shows that for large individuals growth of both species is adversely affected to the same degree by the increased exposure associated with increased height on the shore (this was not the case for the smaller mussels).

Cages left suspended in place for one year yielded similar growth results to those reported for the 6 month period. For the smaller mussels (originally 4 cm and less), the overall relationship between the 2 species remained as before, *i. e.,* there was no significant difference between the growth of either species in cages set at the bottom level, but as before, the growth of *Mytilus edulis* in the top cages was far less than that for *M. californianus.* One difference from the 6 months' growth was that over a year's time *M. californianus* grew as much at the upper as at the lower levels.

GROWTH CHARACTERISTICS OF MATURE POPULATIONS OF MUSSELS IN SANTA BARBARA HARBOR

When both species were grown in Santa Barbara Harbor for 12 months, growth of *Mytilus edulis* was greater than that of *M. californianus* for both small and large mussels (Figure 10).

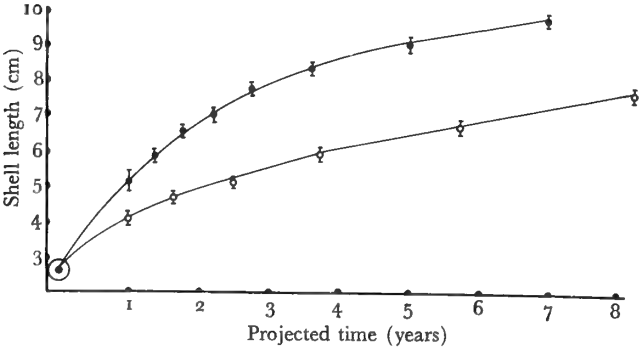

Figure 10

Projected growth curves for *Mytilus edulis* (open symbols) and *Mytilus californianus* (closed symbols), based on data obtained from undisturbed populations of mussels at Santa Barbara Harbor. Growth occurred between August, 1965 and August, 1966. Twice the standard error of the mean for each size class (see text) is represented by a bar on each side of the symbol. (Data used to construct these curves may be found in Table 3 in the appendix.)

COMPARISON BETWEEN GROWTH CHARACTERISTICS OF MATURE POPULATIONS AT ELLWOOD PIER AND SANTA BARBARA HARBOR

Growth of smaller mussels (2 - 4 cm) from mature pure species populations in the harbor, when compared with that of mussels from similar treatments at the low positions on the Pier indicated that *Mytilus californianus* populations at the Pier grew faster than those in the harbor; no significant difference could be detected between the *M. edulis* populations from the two locations. Larger *M. edulis* at the Pier, however, grew at a faster rate than those in the harbor (Table 4). After *M. edulis* has reached 6 - 7 cm (2 to $2\frac{1}{2}$ years) in the harbor, growth rate falls off markedly (Figure 10). (The data used to construct these curves are recorded in Table 3, Appendix.)

Table 4

Itemized comparison of the growth increment shown by small size classes (part of adult populations) of *Mytilus edulis* at Santa Barbara Harbor (calm water) and at the bottom position (see text), Ellwood Pier (rough water). Populations were immersed from August, 1965 to February, 1966

SANTA BARBARA HARBOR

SC	SS	MGI	SD
2 - 3 cm	13	2.41	0.48
> 3 - 4 cm	62	1.82	0.69
> 4 - 5 cm	38	1.49	0.75
> 5 - 6 cm	40	0.72	0.59

ELLWOOD PIER

SC	SS	MGI	SD
2 - 3 cm	15	2.99	0.60
> 3 - 4 cm	98	2.44	0.62
> 4 - 5 cm	85	1.91	0.77
> 5 - 6 cm	92	1.35	0.61

Note: larger size classes (> 4 cm) exhibit a greater increase at Ellwood Pier than at Santa Barbara Harbor.

SC = size class; SS = sample size; MGI < mean growth increment; SD = standard deviation

An equivalent decrease in growth rate occurs at the Pier when a length of between 9 and 10 cm has been reached (perhaps 6 years old) (Figure 6). (The maximum size reached by natural populations of *M. edulis* in the harbor appears to be around 6 cm, whereas 8 - 9 cm is quite common for mature mussels at the Pier.

In the harbor, *Mytilus edulis* maintains a higher growth rate than *M. californianus* until it reaches a length of about 6 cm at about 2 to 2½ years of age (Figure 10); after this the rate drops and becomes less than that of *M. californianus* of equivalent size. At Ellwood Pier, the growth of *M. edulis* exceeds that of *M. californianus* until a length of 5 cm is reached after 1 year (Figure 6). (It must, however, be remembered that *M. californianus* does not normally occur in harbors.)

SUMMARY OF GROWTH CHARACTERISTICS OF MATURE MUSSEL POPULATIONS

(1) At Ellwood Pier (rough water), populations of *Mytilus californianus* grew faster than those of *M. edulis* (although at low intertidal levels small individuals of *M. edulis* grow faster than *M. californianus* of equivalent size).
(2) In Santa Barbara Harbor (quiet water), *Mytilus edulis* populations showed more growth than *M. californianus* populations.
(3) Growth of both species is reduced at high intertidal levels from that shown at low intertidal levels. Growth of small individuals of *Mytilus edulis* decreases much more sharply from low to high intertidal levels than that of *M. californianus*. Growth of large mussels of both species is reduced by the same degree from low to high intertidal levels.
(4) The greatest overall growth for both species occurred at Ellwood Pier.

GROWTH PATTERNS OF MUSSELS OBTAINED FROM COMPETITION EXPERIMENTS INVOLVING JUVENILES

(A) Ellwood Pier

At the first inspection of the experiment set in September, 1965 it was discovered that most *Mytilus edulis* individuals in the mixed species cages had crawled to the outside of the mussel clumps.

From Figure 11 it can be seen that initially the growth rate of small *Mytilus edulis* (as estimated by the slopes of the lines connecting the means) is greater than that of small *M. californianus*. This relationship holds for the first 6 to 7 months only, until *M. edulis* has reached a mean length of between 4½ and 5 cm, and *M. californianus* has reached about 3½ cm. Thereafter the growth rate of *M. californianus* is greater.

Although all treatments should have originated with mussels of a similar size, the initial (October, 1965)

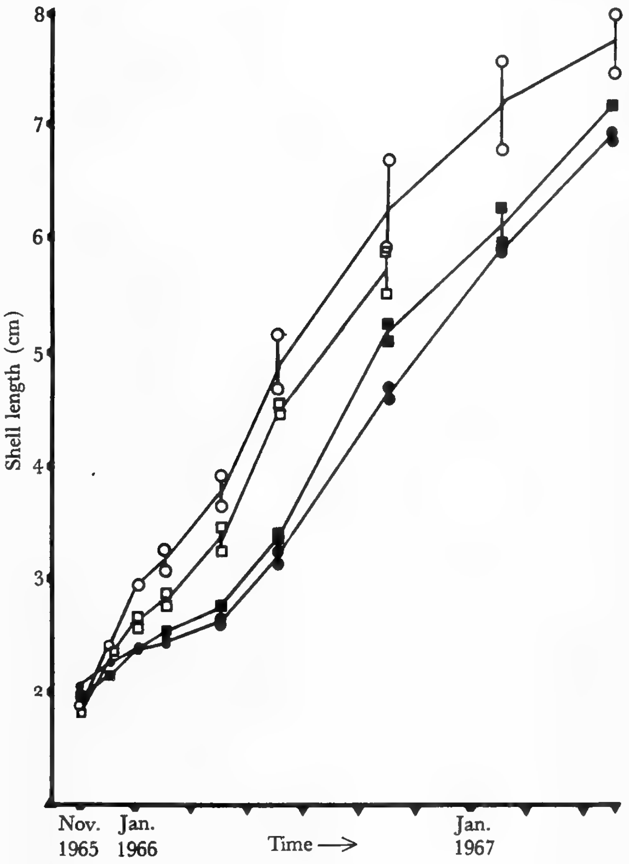

Figure 11

Progressive growth of juvenile mussels from cages set at the bottom position at Ellwood Pier (see text)

The mean length of *Mytilus edulis* growing in cages containing *Mytilus californianus* is represented by ○ and from cages containing *Mytilus edulis* only by □. *Mytilus californianus* from mixed clumps is represented by ● and from pure clumps by ■. Each symbol represents the mean length of the mussels in one cage. From December, 1965 the mean length of the *Mytilus edulis* populations is always significantly greater ($p < 0.001$) than the *Mytilus californianus* populations. From January, 1966 *Mytilus edulis* growing with *Mytilus californianus* are larger than *Mytilus edulis* growing by themselves ($p < 0.001$). From April, 1966 *Mytilus californianus* growing by themselves are larger than *Mytilus californianus* growing in conjunction with *Mytilus edulis* ($p < 0.05$).

Mytilus edulis populations were significantly smaller than the *M. californianus* populations. After one month's growth, however, all the *M. edulis* populations, taken together, were significantly larger than the *M. californianus* populations ($P < 0.001$).

Populations of juvenile mussels first set out at Ellwood Pier during January, 1966 showed the same trends as outlined for those initiated in September, 1965.

(B) Santa Barbara Harbor

Within the experiment started in January, 1966 growth of the *Mytilus edulis* populations was at all times greater than that of *M. californianus.* For the first 4 months the populations of *M. edulis* in the harbor grew faster than those at the Pier (Table 5). During this time the growth of *M. californianus* was also greater in the harbor than at Ellwood Pier (Table 6). This relationship was reversed for both species by the end of the second 4-month period (Tables 7 and 8), *i. e.,* growth was greater at Ellwood Pier than at the harbor. During this second period large numbers of *M. edulis* recruits settled within the harbor cages and their presence undoubtedly influenced the growth of the resident mussels.

Table 5

Comparison between populations of juvenile *Mytilus edulis* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). Populations were initially not significantly different from each other in mean length of individuals. Growth occurred between 25 January, 1966 and 22 May, 1966. All measurements were made in centimeters

Group	M	SD	SS	F 1,551
Santa Barbara Harbor	3.91	0.62	225	
Ellwood Pier	3.29	0.53	328	158.18***

M = mean; SD = standard deviation; SS = sample size

As previously stated, the harbor seas are normally quite calm; this apparently allows silt, detritus, and fecal matter to settle inside mussel clumps growing there. Such deposits accumulate and form a glutinous mud core inside clumps (Harger, 1968), often smothering centrally located mussels. Mortality due to this mechanism after one year resulted in 31/200 and 7/100 *Mytilus californianus* individuals surviving in the pure and mixed cages. The survival of *M. edulis* was 117/200 and 65/100 from the pure and mixed cages, respectively. Over a similar time interval there was no significant difference in survival of the 2 species in cages set at the low position at Ellwood Pier. Presumably this was because constant wave action at that location tended to wash any accumulating silt out of the clumps. In fact, the amount of silt accumulating in cages set at the pier was negligible (Harger, 1968).

If one compares growth of juvenile mussels from "mature" undisturbed populations with those which developed initially within "juvenile populations" (Figures 7 and 11) over a period of one year it can be seen that growth is greater among the latter mussels. This seems to be due to 2 factors: first the periodic disturbances (measuring, etc.) experienced by the juvenile populations

Table 6

Comparison between populations of juvenile *Mytilus californianus* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). Populations were initially not significantly different from each other in mean length of individuals. Growth occurred between 25 January, 1966 and 22 May, 1966. All measurements were made in centimeters

Group	M	SD	SS	F 1,665
Santa Barbara Harbor	2.99	0.58	207	
Ellwood Pier	2.53	0.46	460	122.51***

M = mean; SD = standard deviation; SS = sample size

Table 7

Comparison between populations of juvenile *Mytilus edulis* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). These populations were initially placed in the water during 25 January, 1966, at which time there was no difference in mean length of individuals comprising them. After a period of four months' immersion (22 May, 1966), the populations in the harbor yielded individuals of a larger mean size than at the Pier (see Table 5); this difference was reversed after a further four months' growth (19 September, 1966). All measurements were made in centimeters

Group	M	SD	SS	F 1,494
Santa Barbara Harbor	4.83	0.78	212	
Ellwood Pier	5.24	0.88	284	29.66***

M = mean; SD = standard deviation; SS = sample size

Table 8

Comparison between populations of juvenile *Mytilus californianus* after growth at Santa Barbara Harbor (quiet water) and the low position (see text) at Ellwood Pier (rough water). These populations were initially placed in the water during 25 January, 1966, at which time there was no difference in mean length of individuals comprising them. After a period of four months' immersion (22 May, 1966), the populations in the harbor yielded individuals of a larger mean size than at the Pier (see Table 6); this difference was reversed after a further four months' growth (19 September, 1966). All measurements were made in centimeters

Group	M	SD	SS	F 1,486
Santa Barbara Harbor	3.69	0.64	75	
Ellwood Pier	4.11	0.88	413	15.46***

M = mean; SD = standard deviation; SS = sample size

leading to the release of oppressed individuals with subsequent growth promotion; second, perhaps some form of growth inhibition being imposed upon juveniles through competition with adults. Both probably play some part since growth of juveniles from mature but disturbed populations (see text previously) was found to be greater than that from undisturbed mature populations, but less than that of the disturbed juvenile populations.

Over long time periods (6 months to one year), when the artificial growth curves (prepared from growth increment data obtained from mussels grown without disturbance for one year) from the harbor are compared with those from the low pier position it is apparent that both species grow at a lower rate within the harbor. The growth curve for *Mytilus californianus* in the harbor (compare with Pier) is markedly depressed and is entirely below that of *M. edulis*.

CONCLUSION

The almost exclusive domain of *Mytilus edulis*, harbors and estuaries, does not seem to be the place where it is able to grow best. The crawling behavior of *M. edulis* probably insures that most *M. californianus* juveniles will be eliminated from a mixed species clump in quiet locations since silt will tend to accumulate and smother the inside mussels, which will always be *M. californianus* in such situations. In disturbed situations, however, continual wave action insures that suffocation of *M. californianus* by silt in the presence of *M. edulis* does not take place. Here the greater growth capacity of *M. californianus* enables these animals to push themselves clear of *M. edulis* in mixed species clumps. The smaller *M. edulis* are then usually incorporated within the clump matrix and crushed by their stronger competitors.

ACKNOWLEDGMENTS

This work forms part of a Ph. D. dissertation submitted at the University of California at Santa Barbara wherein all data not reported directly in this paper can be found. I wish to thank Dr. Joseph H. Connell for guidance and criticism. Additionally I owe much to Dr. D. E. Landenberger and Dr. J. Stimson for their constant criticism. Finally I wish to acknowledge the use of shore line facilities belonging to Signal Oil and Gas Company at Ellwood, without which, in view of current population densities in Southern California, this research could not have been undertaken.

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APPENDIX

Table 1

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) at the top position (see text) at Ellwood Pier. These data were used to construct the curves in Figure 6

Mytilus edulis

SC	SS	MGI	SE
2 - 3 cm	26	1.60	0.10
< 3 - 4 cm	65	1.17	0.08
< 4 - 5 cm	85	0.67	0.05
< 5 - 6 cm	78	0.43	0.03
< 6 - 7 cm	62	0.23	0.03
< 7 - 8 cm	27	0.20	0.05
< 8 - 9 cm	10	0.07	0.02
< 9 - 10 cm	15	0.05	0.02

Mytilus californianus

SC	SS	MGI	SE
2 - 3 cm	17	2.55	0.15
< 3 - 4 cm	93	2.33	0.06
< 4 - 5 cm	94	1.98	0.06
< 5 - 6 cm	85	1.51	0.06
< 6 - 7 cm	62	1.24	0.06
< 7 - 8 cm	45	0.86	0.07
< 8 - 9 cm	15	0.51	0.08
< 9 - 10 cm	17	0.29	0.07

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean

Table 2

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) at the bottom position (see text) at Ellwood Pier. These data were used to construct the curves in Figure 7

Mytilus edulis

SC	SS	MGI	SE
2 - 3 cm	15	2.99	0.16
< 3 - 4 cm	98	2.45	0.06
< 4 - 5 cm	85	1.92	0.08
< 5 - 6 cm	92	1.35	0.06
< 6 - 7 cm	61	0.94	0.05
< 7 - 8 cm	31	0.74	0.08
< 8 - 9 cm	22	0.63	0.07
< 9 - 10 cm	18	0.30	0.05

Mytilus californianus

SC	SS	MGI	SE
2 - 3 cm	19	2.70	0.16
< 3 - 4 cm	100	2.66	0.08
< 4 - 5 cm	90	2.27	0.09
< 5 - 6 cm	89	1.99	0.09
< 6 - 7 cm	65	1.86	0.09
< 7 - 8 cm	43	1.48	0.12
< 8 - 9 cm	24	0.85	0.12
< 9 - 10 cm	18	0.72	0.09

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean

Table 3

Growth increment data for 1 cm size classes (original measurements) for *Mytilus edulis* and *Mytilus californianus* after one year's development (August, 1965 to August, 1966) in Santa Barbara Harbor. These data were used to construct the curves in Figure 10

Mytilus edulis

SC	SS	MGI	SE
2 - 3 cm	13	2.42	0.13
< 3 - 4 cm	62	1.82	0.09
< 4 - 5 cm	38	1.49	0.12
< 5 - 6 cm	40	0.73	0.09
< 6 - 7 cm	30	0.47	0.07
< 7 - 8 cm	20	0.38	0.06
< 8 - 9 cm	11	0.26	0.08
< 9 - 10 cm	9	0.11	0.02

Mytilus californianus

SC	SS	MGI	SE
2 - 3 cm	4	0.85	0.30
< 3 - 4 cm	34	0.52	0.07
< 4 - 5 cm	48	0.58	0.08
< 5 - 6 cm	46	0.83	0.07
< 6 - 7 cm	40	0.57	0.06
< 7 - 8 cm	26	0.55	0.08
< 8 - 9 cm	12	0.58	0.09
< 9 - 10 cm	11	0.34	0.07

SC = size class; SS = sample size; MGI = mean growth increment; SE = standard error of mean

Calotrophon, A New World Muricid Genus

(Gastropoda : Muricacea)

BY

JAMES H. McLEAN

Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007

AND

WILLIAM K. EMERSON

American Museum of Natural History
Seventy-ninth Street and Central Park West, New York, New York 10024

(1 Plate; 6 Text figures)

INTRODUCTION

In one of his later papers William H. Dall in 1919 briefly described *Tritonalia turrita* as a new muricacean species from the west coast of Baja California, Mexico, but unfortunately he did not illustrate it; the lectotype is here figured for the first time. The taxon has mostly remained an enigma, although specimens that are now known to represent the species were used as bases for the proposal of two other specific names – *Calotrophon bristolae* Hertlein & Strong, 1951, and *Hertleinella leucostephes* Berry, 1958, each being made type of a new generic unit. On the west coast of Florida there is a common muricacean species of similar aspect that also has been a source of perplexity as to its proper placement generically – *Murex ostrearum* Conrad, 1846 (better known as *Urosalpinx floridana* Conrad, 1869). It was made the type species of *Pseudosalpinx* Olsson & Harbison, 1953, although later workers have taken scant notice of the available name. It is our conviction that Dall's *T. turrita* and Conrad's *M. ostrearum* are congeneric and that the earliest valid generic name for the complex is *Calotrophon* Hertlein & Strong, 1951.

Abbreviations for museums mentioned in the text are as follows:

AHF	Allan Hancock Foundation, University of Southern California (on loan to LACM)
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
CAS	California Academy of Sciences, San Francisco
LACM	Los Angeles County Museum of Natural History
SDNHM	San Diego Museum of Natural History
USNM	United States National Museum Washington, D. C.

SYSTEMATIC ACCOUNT

Calotrophon Hertlein & Strong, 1951

Calotrophon Hertlein & Strong, 1951, p 87. Type species by OD, *Calotrophon bristolae* Hertlein & Strong, 1951

Pseudosalpinx Olsson & Harbison, 1953, p. 254 (as subgenus of *Cantharus* Röding, 1798). Type species by OD. *Urosalpinx floridana* Conrad, 1869 [= *Murex ostrearum* Conrad, 1846, *fide* Dall, 1902; Johnson, 1934; Abbott, 1954]

Hertleinella Berry, 1958, p. 95. Type species by OD, *Hertleinella leucostephes* Berry, 1958

Diagnosis: Shell solid, fusiform, periostracum lacking, surface with a thin, white, chalky layer; whorls shouldered, axial sculpture of strong ribs, spiral sculpture of raised imbricate ridges; canal of moderate length, open, siphonal fasciole broad, columella smooth, concave, outer lip lirate within, lirations terminating as denticles at or near the edge of the lip. Nuclear whorls $1\frac{1}{2}$, rounded.

Operculum with a terminal (apical) nucleus and a broad marginal inner callus, outer surface with a shallow groove. Rachidian plate of radula with 5 simple cusps; lateral plate cuspidate; marginal plate wanting.

A character of taxonomic importance in the Muricacea that has evidently not previously been noticed in the shells of *Calotrophon ostrearum* and *C. turritus* is the presence of a thin, white chalky surface layer. Overcleaned or naturally abraded specimens show traces of the chalky layer and this white film is evident in the illustrations of both species (see Plate). Such chalky layers are characteristic of *Aspella, Dermomurex, Trialatella, Favartia,* and *Takia* and are present in some species of *Typhis* and *Trophon* (*sensu lato*).

The radular dentition of *Calotrophon ostrearum* was illustrated previously by Radwin & Wells (1968, fig. 6). A new radular drawing of *C. ostrearum* (Figure 15) is presented here for comparison with that of *C. turritus* (Figures 8, 9), representing specimens from the west coast (Figure 8) and southeastern coast (Figure 9), respectively, of Baja California, Mexico. The operculum is similar in *C. turritus* (Figure 10) and *C. ostrearum* (Figure 16); it is of the muricoid type, with a terminal (or apical) nucleus. Some muricacean species with similar radular characters are now placed in the Trophoninae, which, however, appears to be an unnatural group, at least on the basis of the opercular morphology. The Austral-Antarctic "typical" species of Trophoninae are known to have a purpuroid operculum (lateral nucleus), whereas the American boreal species have a "fusoid" operculum (apical nucleus), as Dall (1902, pp. 533 - 550) noted in a review of the New World species of this subfamily. The radular characters of *Calotrophon,* moreover, are not typically trophonine, owing to the absence of 2 secondary cusps at the outer extremity of the rachidian plate, and they are closer to those of the Muricinae. *Calotrophon* appears to be related to such genera as *Aspella, Dermomurex, Takia* and *Attiliosa.* Subfamily classification of these genera is as yet unsettled. Therefore, we are tentatively assigning *Calotrophon* to the Muricinae, pending the re-evaluation of the subfamily placement of these genera and the American species now placed in the Trophoninae.

Olsson & Harbison (1953, p. 254) proposed the subgeneric name *Pseudosalpinx* and tentatively placed this taxon in the genus *Cantharus* Röding, 1798, which they allocated to the Muricidae rather than the Buccinidae. They noted that the type species of *Pseudosalpinx, Urosalpinx floridana* Conrad, 1869 (= *ostrearum* Conrad, 1846), has a muricoid operculum, whereas the operculum of the type species of *Urosalpinx* Stimpson, 1865, is purpuroid. They stated: "Tentatively, we are associating *Pseudosalpinx* with *Cantharus* pending more complete knowledge of the soft parts of its Recent species."

In addition to the type species, Olsson & Harbison referred the following nominal species to *Pseudosalpinx*: *Cantharus (P.) perplexus* Olsson & Harbison, new species, from the Plio-Pleistocene of Florida, and *C. (P.) multangula* (Philippi, 1849), a western Atlantic species with a fossil record dating from the Pliocene. Examination of the holotype and paratype of *Cantharus perplexus* has led us to the conclusion that this taxon was based upon robust specimens of *Calotrophon ostrearum. Cantharus multangulus* was subsequently shown by Rorertson (1957), on the basis of radular, opercular, and shell characters, to be referable to *Cantharus* (*sensu lato*) of the Buccinidae.

Jung (1969, p. 494; plt. 50, figs. 7 - 9) described "*Calotrophon (?) hutchisoni,* n. sp." from the late Miocene of Trinidad, but his taxon has "four elongate denticles near the base" of the inner lip, a character not noted in recognized species of *Calotrophon.* Jung, however, anticipated us in pointing out the resemblance of *Pseudosalpinx* to *Calotrophon.*

The genus *Bedeva* Iredale, 1924 (type species, *Trophon hanleyi* Angas, 1867; Australia), has a shell morphologically similar to that of *Calotrophon.* The shell (Wenz, 1941, p. 1105; fig. 3138) has the proportions, the siphonal fasciole and denticles in the outer lip, and the radular rachidian plate (Thiele, 1929, p. 292; fig. 317) has 5 cusps as does that of *Calotrophon.* However, examination of specimens from South Australia (SDNHM 37931) shows that the operculum of *Bedeva hanleyi* possesses a median fold and a lateral nucleus (Figure 17) and that the shell lacks a chalky surface layer. The 2 taxa, therefore, are not considered to be closely related.

Calotrophon turritus (Dall, 1919)

(Plate figures *1* - *7*; Text figures 8 - 10)

Tritonalia turrita Dall, 1919, p. 336 (*ex*-Stearns MS)

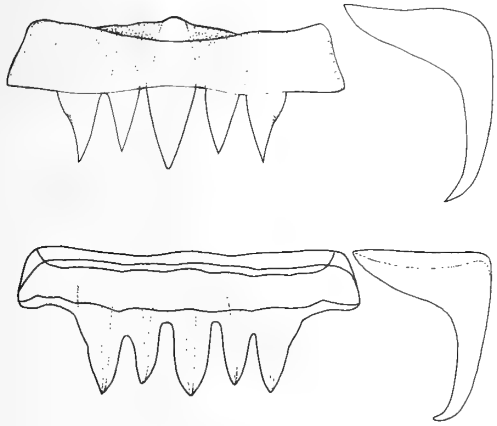
Calotrophon bristolae Hertlein & Strong, 1951, p. 87, pl. 2, fig. 2; Jung, 1969, p. 494

Trophon (Calotrophon) bristolae (Hertlein & Strong). – Keen, 1958, p. 364, fig. 373

Hertleinella leucostephes Berry, 1958, p. 95. – Vokes, 1964, p. 29

Diagnosis: Shell attaining a length of 43 mm, heavy, whitish, surface chalky, axial sculpture of 7 - 10 ribs, crossed by 7 - 10 narrow, raised, scaly, dark brown or black spiral cords, cords usually lacking or very weak on shoulder. Aperture ovate, canal open, siphonal fasciole well developed, mature outer lip with 4 - 5 strong denticles.

Type Material and Type Localities: Lectotype (here designated), *Tritonalia turrita* Dall, USNM 34517 (Figure *1* (E)), paralectotype, USNM 635623, type locality: San Quintín Bay, Baja California. Holotype, *Calotrophon bristolae* Hertlein & Strong, 1951, CAS 9612 (Figure *2*), 1 paratype, CAS 17764; 1 paratype, SDNHM 12297; type locality: Gorda Banks, southern Gulf of California (23°01′ N; 109°29′ W), 60 fathoms. Holotype, *Hertleinella leucostephes* Berry, 1958, Stanford University 8654 (Figure *3*), paratype, Berry Collection 13939; type locality: 2 miles north of Cedros Village, Cedros Island, Baja California, 10 fathoms.



Figures 8a, 8b

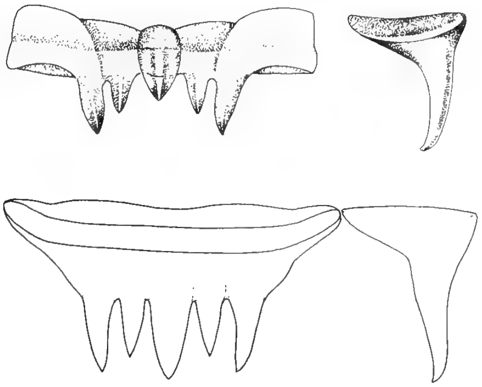
Calotrophon turritus (Dall)

Asuncion Island, Baja California, LACM 67-66, radular dentition
8a: rachidian tooth and one lateral tooth, indicating relative size of teeth; antero-dorsal view
8b: rachidian tooth and one lateral tooth, anterior view
(all greatly enlarged)

All radular slides and drawings are through the courtesy of Dr. G. E. Radwin and Mr. Anthony D'Attilio

Distribution: Cedros Island, Baja California, to Arena Bank, off the southeastern tip of Baja California, Mexico. Although the stated type locality of *Tritonalia turrita* is San Quintín Bay, approximately 200 miles north of Cedros Island, we believe that the record needs verification since recent shore collecting in the San Quintín Bay vicinity and diving by McLean at nearby San Martin and San Geronimo Islands has not yielded the species.

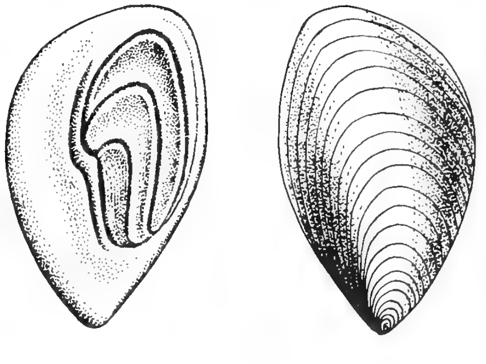
Material Examined: In addition to type material the following localities in Baja California are represented: USNM 265246, northeast end Cedros Island, 2 beach-worn specimens; LACM 67-64, off Cedros Village pier, 1 specimen, 60 feet, mud bottom; LACM 67-65, 1 mile north of Cedros Village, 9 specimens (subsequently lost), 15 - 25 feet, gravel and boulder bottom; AMNH 157183, off Cedros Village in 11.5 - 16.5 fathoms, 1 specimen; LACM-AHF 1260-41, Dewey Channel, opposite Point



Figures 9a, 9b

Calotrophon turritus (Dall)

Arena Bank, Gulf of California, CAS 17715, radular dentition
9a: rachidian tooth and one lateral tooth; antero-dorsal view
9b: rachidian tooth and one lateral tooth, anterior view
(all greatly enlarged)



Figures 10a, 10b

Calotrophon turritus (Dall)

Asuncion Island, LACM 67-66; operculum
10a: inner surface 10b: outer surface (greatly enlarged)

(E) Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Eugenio, 1 broken specimen, 23 - 26 fathoms (Figure *4*); LACM 67-66, east anchorage, Asuncion Island, 3 specimens, 25 - 50 feet, gravel bottom (Figure *5*); USNM 111141, off Magdalena Bay, 1 specimen, 36 fathoms (Figure *6*); LACM-AHF 618-37, San Jaime Bank off Cape San Lucas, 1 worn specimen, 75 fathoms; LACM-AHF 1118-40, Inner Gorda Bank, 1 specimen, 59 - 78 fathoms (Figure *7*); CAS 17715, Arena Bank, Gulf of California, 3 specimens, 50 fathoms.

Variation: Specimens from shallow water in the more northern localities are large and heavy and have dark spiral banding, while the specimens from deeper water on the offshore banks at the eastern tip of Baja California show lighter banding and the shells are not as robust. The number and spacing of the dark spiral cords is highly variable, as indicated in the illustrations.

Remarks: The subsequent descriptions of the taxa *Calotrophon bristolae* and *Hertleinella leucostephes* resulted chiefly from the failure of DALL to illustrate his *Tritonalia turrita*, which would have enabled recognition of the more strongly marked specimens in the northern part of the range. VOKES (1964, p. 29) indicated the equivalence of *Hertleinella leucostephes* and *Tritonalia turrita*, but she relegated these taxa to *Cantharus* (family Buccinidae).

Calotrophon ostrearum (CONRAD, 1846)

(Plate figures *11* - *14*; Text figures 15, 16)

Murex ostrearum CONRAD, 1846, p. 25. – TRYON, 1880, p. 136 (copy CONRAD description)
Muricidea ostrearum (CONRAD). – DALL, 1902, p. 505, fig. 2 (with *U. floridanus* in syn.)
Muricopsis ostrearum (CONRAD). – ABBOTT, 1954, p. 211, fig. 47g (copy of DALL's 1902, fig. 2). – PERRY & SCHWENGEL, 1955, p. 155, pl. 31, fig. 218. – RADWIN & WELLS, 1968, p. 72, fig. 6 (radula), fig. 20g
Urosalpinx floridanus CONRAD, 1869, p. 106, pl. 12, fig. 4. – TRYON, 1880, p. 153, pl. 39, fig. 486
Muricidea floridana (CONRAD). – DALL, 1884, p. 326. – DALL, 1889, p. 212
Cantharus floridana (CONRAD). – OLSSON & HARBISON, 1953, p. 254, pl. 37, figs. 2, 2a ("type lot")
Muricidea floridana attenuata DALL, 1890, p. 149
Cantharus (Pseudosalpinx) perplexus OLSSON & HARBISON, 1953, p. 255, pl. 37, figs. 1, 1a

Diagnosis: Shell attaining 30 mm in length, brownish with a chalky white surface layer, axial sculpture of 7 - 8 strong ribs, crossed by strong, scaly spiral cords, weakly developed on the shoulder, aperture ovate, canal open, siphonal fasciole well developed, interior dark mauve colored, mature outer lip with 6 - 7 elongate, lighter colored denticles.

Type Material and Type Localities: Syntypes, *Murex ostrearum*, depository not known; type locality: Tampa Bay, Florida. Lectotype, *Urosalpinx floridana* CONRAD, 1869, ANSP 36551 (here designated), 2 paralectotypes, ANSP 316873; type locality: Tampa Bay, Florida. Holotype, *Cantharus perplexus* OLSSON & HARBISON, 1953, ANSP 19028, paratype, ANSP 19028a; type locality: St. Petersburg, Florida, Plio-Pleistocene.

Distribution: Florida, Biscayne Bay, and Key West to Tampa Bay. Not uncommon on oyster beds at low tide and to depths of 35 fathoms. Numerous specimens are represented in museum collections.

Variation: Shallow water specimens have the aperture dark mauve colored and are not strongly spinose (Figures *11*, *13*). Specimens from offshore, dredged in 25 fathoms, are slightly larger than those from shallow water and show a more pronounced development of the peripheral spines (see Figure *14*). In these specimens the aperture is white, tinged with pink.

Plate Explanation

Figures *1* to *7*: *Calotrophon turritus* (DALL, 1919)

Figure *1*: Lectotype, *Tritonalia turrita* DALL, USNM 34517
Figure *2*: Holotype, *Calotrophon bristolae* HERTLEIN & STRONG, CAS 9612
Figure *3*: Holotype, *Hertleinella leucostephes* BERRY, Stanford University 8654
Figure *4*: LACM-AHF 1260-41, Dewey Channel, opposite Point Eugenio, Baja California, 23 - 26 fathoms
Figure *5*: LACM 67-66, Asuncion Island, Baja California, 25 - 50 feet
Figure *6*: USNM 111141, off Magdalena Bay, Baja California, 36 fathoms
Figure *7*: LACM-AHF 1118-40, Inner Gorda Bank, Baja California, 59-78 fathoms

Figures *11* to *14*: *Calotrophon ostrearum* (CONRAD, 1846)

Figure *11*: Lectotype, *Urosalpinx floridanus* CONRAD, ANSP 36551
Figure *12*: Holotype, *Cantharus (Pseudosalpinx) perplexus* OLSSON & HARBISON, ANSP 19028
Figure *13*: LACM A.52, Tampa Bay, Florida
Figure *14*: AMNH 100637, Southwest of Egmont Key, Florida, 25 fathoms

(all figures × 2)

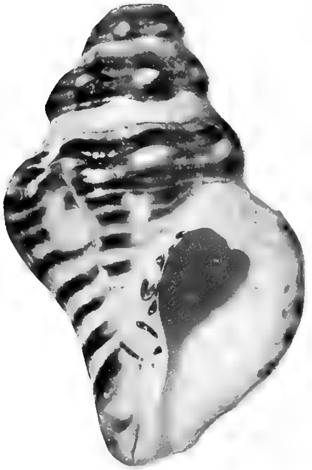


Figure 1

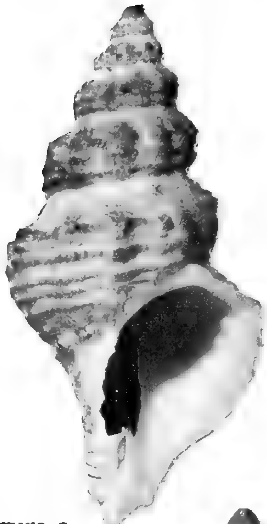


Figure 2

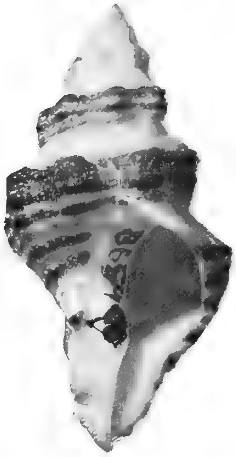


Figure 3

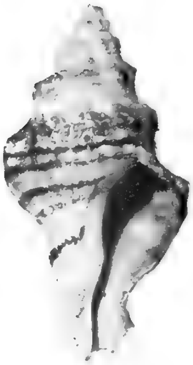


Figure 4

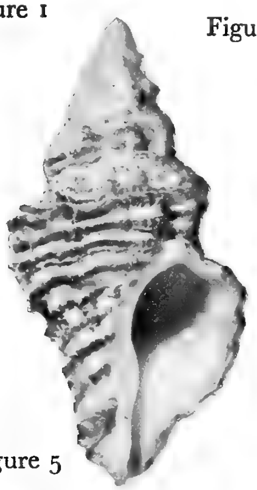


Figure 5

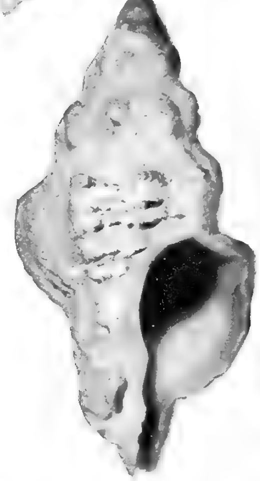


Figure 6

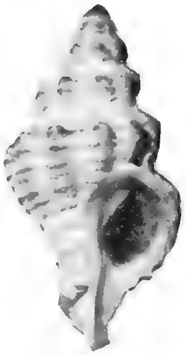


Figure 7

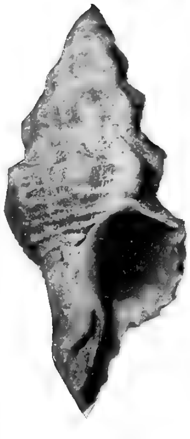


Figure 11

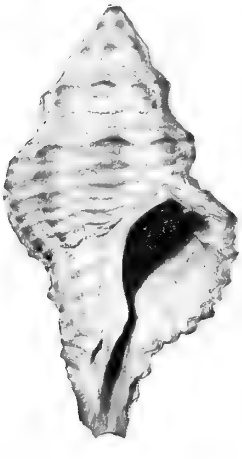


Figure 12

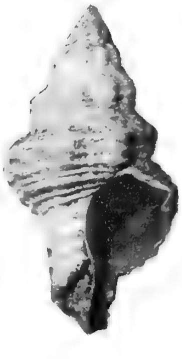


Figure 13

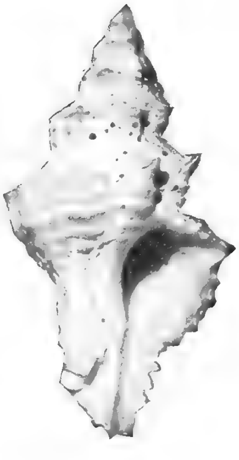
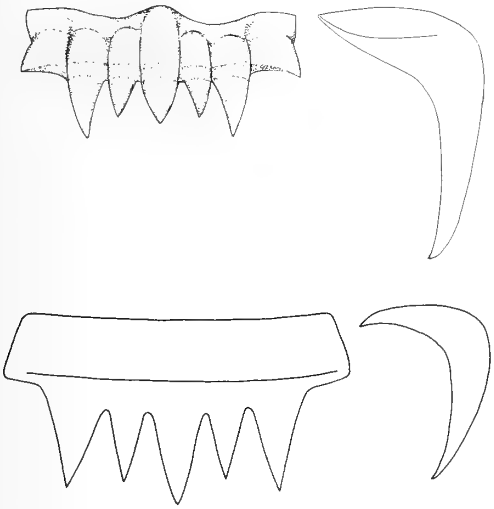


Figure 14

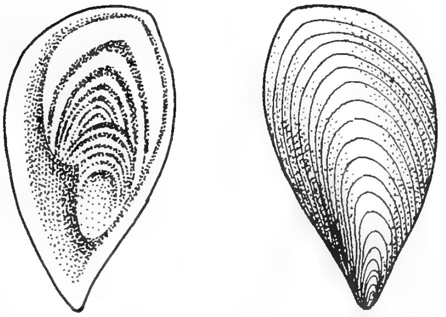
Remarks: Lots of this species in old collections are frequently mixed with *Urosalpinx perrugata* (Conrad, 1846), which it superficially resembles. Conrad's *U. perrugata* has a shell possessing spiral cords on the shoulder, a yellow to rosy brown aperture, and lacks the white chalky layer. The operculum has a lateral nucleus.



Figures 15a, 15b

Calotrophon ostrearum (Conrad)

off Peninsula Point, Franklyn County, Florida, radular dentition
15a: rachidian tooth and one lateral tooth, indicating relative size of teeth; antero-dorsal view
15b: rachidian tooth and one lateral tooth, anterior view
(all greatly enlarged)



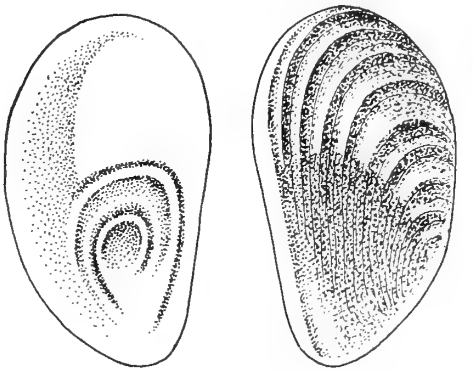
Figures 16a, 16b

Calotrophon ostrearum (Conrad)

Estero Island, Florida; operculum
16a: inner surface 16b: outer surface (greatly enlarged)

Conrad's unillustrated species, "*Murex*" *ostrearum*, was not recognized as a senior synonym of "*Urosalpinx*" *floridana* until Dall (1902, p. 505) indicated its priority. In the absence of the type material of "*Murex*" *ostrearum*, we are following Abbott (1954, p. 211) in accepting Dall's synonymy.

Dall (1890, p. 149) proposed the varietal name *Muricidea floridana attenuata* for a slender specimen that he referred to this variable species from the Pliocene Caloosahatchee formation of Florida. We have not seen type material of Dall's *M. attenuata*, and Boss, Rosewater, & Ruhoff (1968, p. 37) do not cite typological specimens in the collection of the U. S. National Museum.



Figures 17a, 17b

Bedeva hanleyi (Angas)

South Australia, SDNHM 37931; operculum
17a: inner surface 17b: outer surface (greatly enlarged)
All opercular drawings are by Mr. Anthony D'Atillio

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Two New Species of Janolidae from Toyama Bay, Japan

(Gastropoda : Nudibranchia)

BY

KIKUTARÔ BABA

Osaka Kyoiku University, Tennoji, Osaka, Japan

AND

TAKEO ABE

Takaoka Senior High School, Takaoka, Toyama-ken, Japan

(3 Text figures)

INFORMATION CONCERNING the family Janolidae (Arminacea, Pachygnatha) has been greatly increased thanks to the latest works by BURN & MILLER, 1969 and MILLER, 1970. Thus it has become rather easier for us to identify the janolid specimens which had been collected some years ago by the members of the Biological Club, Takaoka Senior High School, from Toyama Bay and its vicinity, and placed at our disposal for study. Two new species are proposed below:

1. *Janolus toyamensis* BABA & ABE, spec. nov.

(Japanese name: Koyanagi-umiushi)

Holotype (Figure 1): Collected from the shore of Nakata, Toyama Bay (Japan Sea coast of Honshu Island, Japan), on August 4, 1960; 1 specimen.

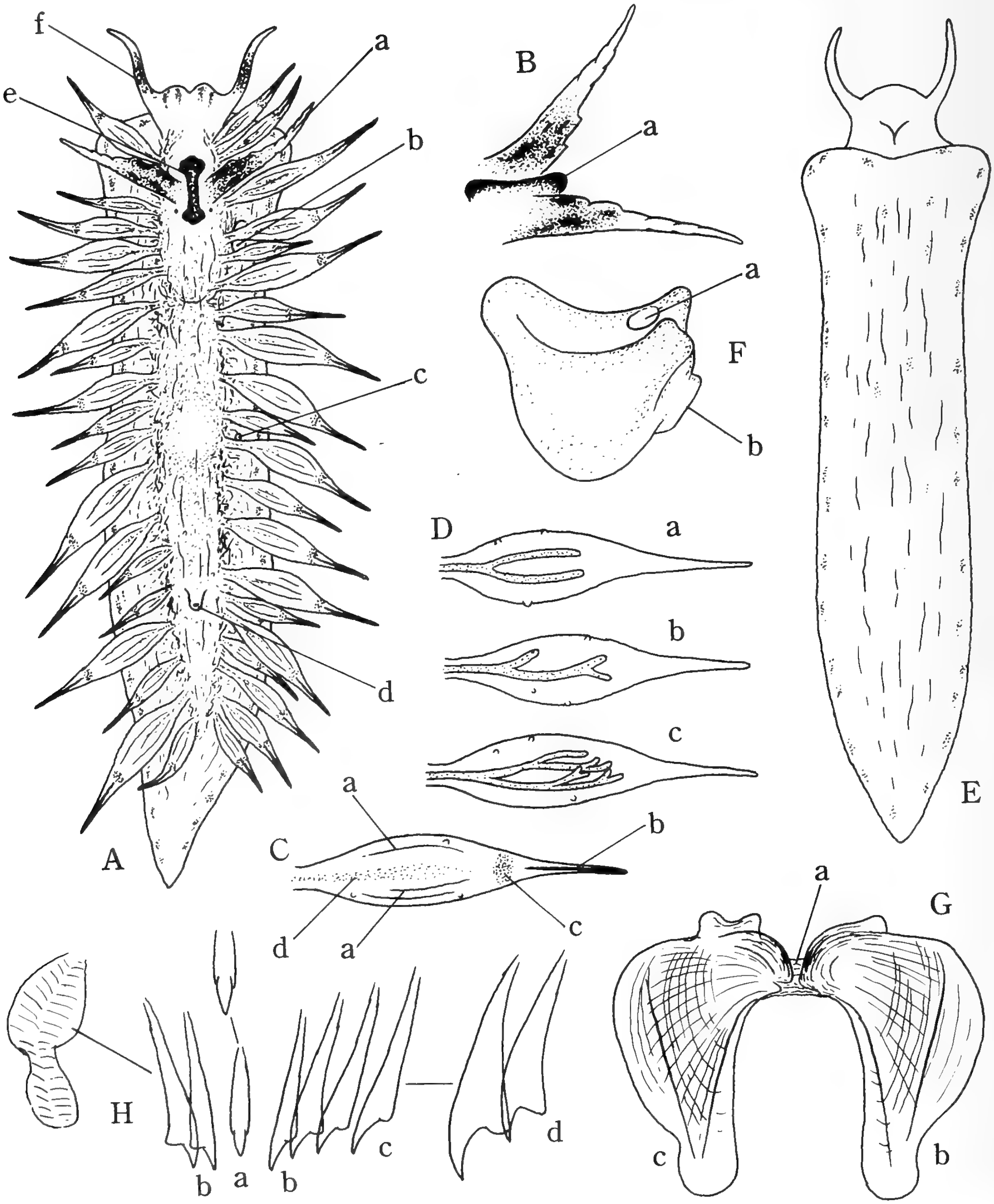
When living, the animal is about 10 mm in length. Oral tentacles short, linear. Rhinophores stouter, each showing a slight indication of perfoliations on the upper half (lamellae not marked on this animal). With an inter-rhinophorial crest. Deciduous branchial papillae irregularly set in 1 - 2 longitudinal rows on back margins. They are fusiform, sparsely and indistinctly tuberculated, and exceedingly elongated to form each a tapering tip. Anus in median dorsal line, posterior; genital orifice below and behind the right rhinophore; nephroproct below the middle of the pericardial prominence on the right side. Bare space of back covered sparsely with minute tubercles. Foot broad, corners rounded. No tail crest.

General integument of body translucent ashy yellow; on the back, sides, sole and branchial papillae it is scattered with short longitudinal lines of opaque white. There are some additional spots of dark brown on the sides and foot brim. Each of the cephalic structures is dark brown below. Inter-rhinophorial crest black. The branchial papillae are marked each with a chrome-yellow spot a short distance below the apex which, in turn, is conspicuously tinged with reddish brown. The liver diverticulum within the papillae is dark green.

Jaws approximately equal, united by a ligament, yellowish brown in colour, each plate, though incised slightly at the hinge end in the present material, having no serial denticulations whatever. The radula is slightly yellowish and has the formula $20 \times 10 - 20 \cdot 1 \cdot 10 - 20$. The central is unicuspidate, the laterals are hooked, and all are quite smooth. The liver diverticula of the branchial papillae are sometimes simple, but more often they are branched. Genitalia not determined.

Paratypes: Collected from the shore of Cape Echizen-misaki, Fukui (Japan Sea coast of Honshu Island), on August 14, 1966; 2 specimens. These paratypes appear to be slightly larger in size than the holotype (the length of the two paratypes after preservation measured about 10 mm each). According to a coloured drawing taken from life by Mr. Haruo Izumi, there are pinnate formations on the length of the rhinophores, and the inter-rhinophorial crest assumes a vertically lobate appearance. When examining the preserved material it was noticed that there occurred more thickly set tubercles on the back and branchial papillae than in the holotype.

Additional datum: An additional collection of this new species was made from the shore of Okazaki, Tsuruga Bay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(Japan Sea coast of Honshu Island) on July 30, 1955. The animal was represented by a coloured drawing only, made by Abe.

Remarks: According to the synopsis of the genera of the family Janolidae (= Antiopellidae) by Burn & Miller, 1969, the present new species appears to be a member of *Janolus* Bergh, 1884, by having (1) a crest between the rhinophores, (2) scattered tubercles on the branchial papillae, and (3) a non-denticulated edge on the jaw-plates, as evidence for generic assignment. This new species is especially distinct from the previously known members of the genus in the shape of the branchial papillae and in the coloration of the body.

2. *Janolus mirabilis* Baba & Abe, spec. nov.

(Japanese name: Karajishi-umiushi)

Holotype (Figures 2, 3): Collected from the shore of Abugashima, Toyama Bay (Japan Sea coast of Honshu Island) on August 17, 1958; 1 specimen.

Living animal about 7 mm in length. Rhinophores distinctly perfoliated above. There is a crest between the 2 rhinophores. Branchial papillae falling off easily. According to a coloured sketch made from life these papillae are covered with acutely pointed tubercles near the tip, and they stand in a single row on the antero-lateral margins of the body. A small number of papillae are found also on the postero-lateral margins of the body. The bare space of the back is covered with minute tubercles. Anus

(<— on facing page)

Figure 1

Janolus ***toyamensis*** Baba & Abe, spec. nov.
(Holotype)

A: Animal from above; length 10 mm
a - rhinophore b - genital orifice c - nephroproct
d - anus e - inter-rhinophorial crest f - oral tentacle
B: Paired rhinophores from right side
a - inter-rhinophorial crest
C: A branchial papilla
a - opaque white lines b - reddish brown apex
c - chrome-yellow spot d - dark green liver diverticulum
D: Different aspects (a - c) of the liver branching in the branchial papillae
E: Animal from below, showing opaque white lines on the sole
F: Pharyngeal bulb from right side
a - oesophagus b - mouth
G: Paired jaw-plates from outside (× 15)
a - ligament b - left jaw c - right jaw
H: Transverse row of radula (× 320)
a - central tooth b - 1st lateral c - 4th lateral d - 18th lateral
(figures by K. Baba)

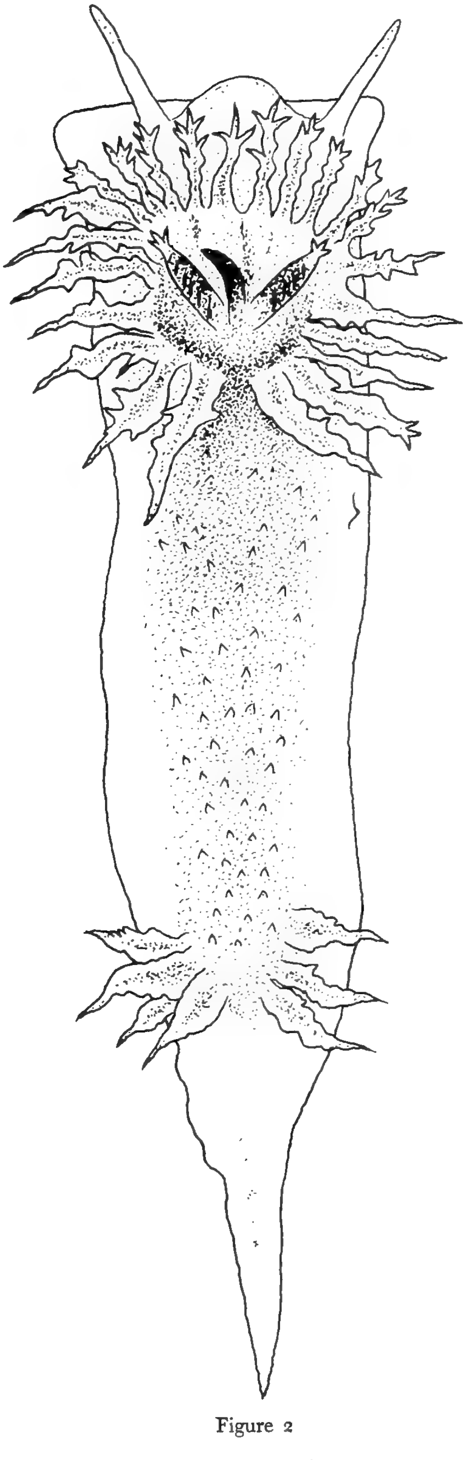

Figure 2

Janolus ***mirabilis*** Baba & Abe, spec. nov.
(Holotype)

Animal from above (adapted from the original drawing made by Mr. Seigoro Takahashi); length 7 mm

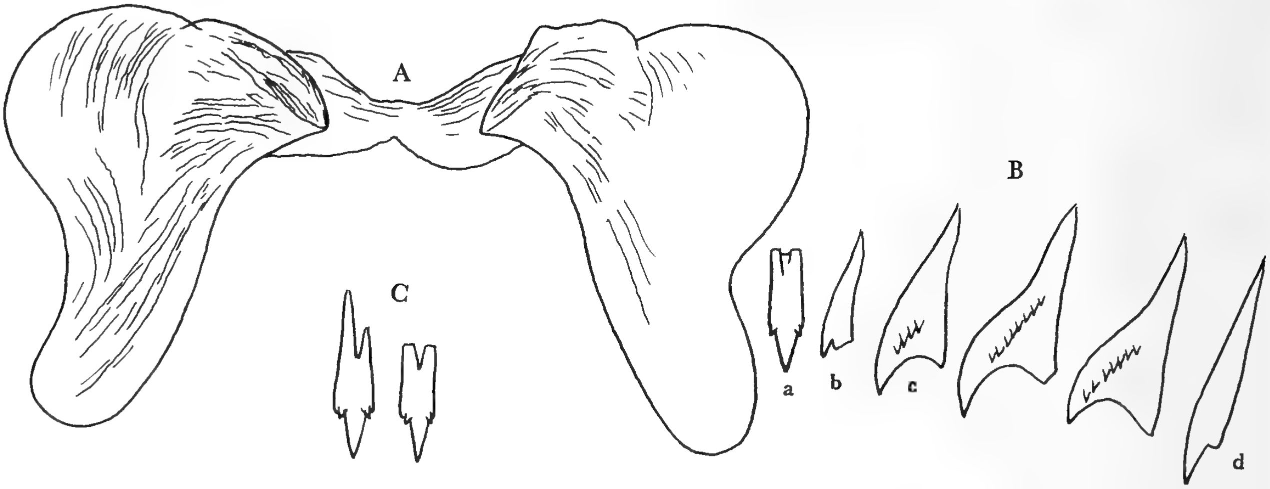

Figure 3

Janolus mirabilis Baba & Abe, spec. nov.
(Holotype)

A: Paired jaw-plates from outside (× 70)
B: Half-row of radula (× 700)
C: Different aspects of centrals
a - central tooth b - 1st lateral c - 2nd lateral d - 5th lateral
(figures by K. Baba)

near the rear end of the mantle in the median line. Genital orifice on the right side below the anterior end of the pericardial prominence. Nephroproct not determined. Foot broad with rounded corners. No tail crest.

General integument of body translucent ashy yellow, and the back is tinged with dark brown. Rhinophores dark brown below, opaque white at tip. Inter-rhinophorial crest black. Branchial papillae tipped with opaque white; the liver diverticulum within the papillae yellowish. Tip of oral tentacles whitish. Tail and sole spotted here and there with opaque white.

Jaws very large in proportion to the size of the body, yellowish brown in colour, and not provided with serial denticles. Radula greatly reduced in size. Formula about $20 \times 5 \cdot 1 \cdot 5$. Teeth colourless. The central with 1 denticle on each side of the median cusp. The first 3 laterals with 7 - 10 serrulations each, the rest smooth. Genitalia not determined.

Remarks: The present new species, though more or less astonishing in the family Janolidae in the external appearance of the animal, was referred to *Janolus* by the combination of the following characters of the genus: (1) the presence of an inter-rhinophorial crest, (2) the possession of tuberculated branchial papillae, and especially (3) the absence of serial denticles on the edge of the jaw-plates. In the previously recorded species of *Janolus* the radular teeth are sometimes smooth and sometimes denticulated.

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Some Associates of *Tresus nuttallii* (Conrad, 1837)

(Pelecypoda : Mactridae)

BY

WILLIAM E. STOUT

Marine Science Center, Oregon State University, Newport, Oregon 97365

The horse-neck, or gaper clam *Tresus nuttallii* (Conrad, 1837), a byssate, infaunal suspension feeder, is found in bays, where it is most abundant, and in the more quiet sheltered areas along the outer coast from the Straits of Georgia, British Columbia, to Scammons Lagoon, Baja California (Addicott, 1963).

Tresus nuttallii is easily recognized by its large shell, which extends 20 cm in length and 15 cm in height and is covered with a brown periostracum in life, its pronounced posterior gape, and elongated siphon with dark, wrinkled skin, with two leather-like siphonal plates.

According to Swan & Finucane (1952) the siphonal plates which are present in both *Tresus capax* (Gould, 1850) and *T. nuttallii,* tend to be much heavier and harder in *T. nuttallii* than in *T. capax.* In *T. capax* the periostracum is constantly being sloughed off whereas in *T. nuttallii* it is retained as a tough, externally smooth membrane. This sloughing or shedding action evidently prevents barnacles and other organisms from growing as large on *T. capax.*

Quayle (1941), Swan & Finucane (1952), and Marriage (1954) noted the presence of barnacles and marine plants on the siphonal plates of *Tresus nuttallii;* however, no mention was made of any other organisms. Anderson & Bourne (1960) noted the presence of the nematode *Pontonema vacillatum* Leidy, 1855, along the mantle and in the folds of the "neck skin" of a large percentage of soft shell clams (*Mya arenaria* Linnaeus, 1758) collected at Campobello Island, Bay of Fundy.

COLLECTING SITE AND METHODS

All bivalves were collected from South Humboldt Bay, Humboldt County, California, and were taken with shovels, placed in individual plastic tubes and transferred to the laboratory for processing. The attached algae were removed from the plates and placed in specimen jars to which 2 - 3% formalin was added. The siphonal plates were removed from the bivalve, placed in specimen jars to which $MgCl_2$ (73.2 g/l tap water) was added to relax the associated fauna, fixed in 10% formalin for 2 to 3 days, and then transferred to 70% ethanol for storage. The associated fauna was removed from the plates and forwarded to specialists for identification.

RESULTS AND DISCUSSION

Fifty species representing 10 animal phyla and several plant divisions were found associated with the siphonal plates (Table 1). There are 3 types of sites where the organisms are found: (1) On the exterior of the plates, *e. g.* sponges, hydroid Cnidarians, Entoprocts, barnacles, tubes of the sabellid polychaete *Schizobranchia insigna* Bush, 1904, and the species of algae; (2) on the attached algae and hydroids, *e. g.* gammarid and caprellid amphipods, pycnogonids, and copepods; and (3) among the sand grains and detrital material which accumulates between the lamellae of the plates, *e. g.* nemerteans, nematodes, sipunculoids, gastropod and pelecypod mollusks, cumaceans, isopods, tanaidaceans, foraminiferans, and the nereid *Platynereis bicaniculata* (Baird, 1863).

The siphonal plates of *Tresus nuttallii* apparently provide increased surface area for diatoms and a suitable attaching surface for other algae and several sedentary animals which probably benefit from their position near the feeding or respiratory currents of the bivalve; *e. g.* entoprocts, barnacles, and hydroids.

The entoproct *Myosoma spinosa* was found attached to the siphonal plates near the siphonal opening. Entoprocts are ciliary feeders, consuming organic particles and small plankton. Suspended food particles, carried toward the siphon of the bivalve, no doubt pass between the tentacles of the entoprocts, providing them with food.

Barnacles were the most conspicuous animals found on the siphonal plates, sometimes covering the entire sur-

Table 1

Species associated with the siphonal plates
of the horse-neck or gaper clam
Tresus nuttallii (Conrad, 1837)

Protozoa	*Elphidium tumidum* Natland, 1938
	Elphidiella hannai (Cushman & Grant, 1927)
Porifera	several spicules found
Cnidaria	
Hydrozoa	*Clytia* sp.
	Perigonimus repens (Wright, 1858)
	Calycella syringa (Linnaeus, 1767)
Nemertina	*Malacobdella grossa* (Müller, 1776)
Entoprocta	*Myosoma spinosa* Robertson, 1900
Nematoda	*Anticoma* sp.
	Enoplus sp.
	several specimens of the subfamily Oncholaiminae
Sipunculoidea	*Phascolosoma agassizii* Keferstein, 1866
Mollusca	
Gastropoda	*Odostomia (Evalea)* cf. *O. (E.) quadrae* Dall & Bartsch, 1910
	Alvania sp.
Pelecypoda	*Modiolus rectus* (Conrad, 1837)
	Mytilus edulis Linnaeus, 1758
	Protothaca staminea (Conrad, 1837)
	Transennella tantilla (Gould, 1852)
	Psephidia lordi? (Baird, 1863)
	Macoma irus (Hanley, 1845)
Annelida	
Polychaeta	*Schizobranchia insignis* Bush, 1904
	Sabella media (Bush, 1904)
	Arctonoe sp.
	Platynereis bicaniculata (Baird, 1863)
	Polydora sp.
Arthropoda	
Isopoda	*Munna ubiquita* Menzies, 1952
Pycnogonida	*Achelia* sp.
Copepoda	*Paranthessius panopeae* Illg, 1949
Cirripedia	*Balanus crenatus* Bruguière, 1789
Tanaidacea	*Leptochelia dubia* (Krøyer, 1842)
Cumacea	*Leptocuma* sp.
	Cumella? sp.
Amphipoda	
Caprellidea	*Caprella laeviuscula* Mayer, 1903
	Caprella californica Stimpson, 1856
	Tritella laevis Mayer, 1903
Gammaridea	*Aoroides columbiae* Walker, 1898
	Photis brevipes Shoemaker, 1942
	Anisogammarus pugettensis (Dana, 1853)
	Ampithoe lacertosa (Bate, 1858)
	Allorchestes angustus Dana, 1854
	Pontogeneia inermis (Krøyer, 1838)
	Photis californica? Stout, 1913
	Melita dentata (Krøyer) Sars, 1895
	Corophium acherusicum (Costa, 1857)
Rhodophyta	*Polysiphonia paniculata* Montagne, 1842
	Platythamnion pectinatum Kylin, 1925
Chlorophyta	*Ulva lobata* (Kützing) Setchell & Gardner, 1920
	Enteromorpha intestinalis (Linnaeus) Link, 1820
	Enteromorpha Linza (Linnaeus) J. G. Agardh, 1883
Phaeophyta	*Ectocarpius Parksii* Setchell & Gardner, 1924
	Giffordia sp.
Chrysophyta	*Navicula comoides* (J. G. Agardh) Hustedt, 1962

face and masking the presence of other associates. The presence of barnacles is probably due to the lack of other attachment sites in the area. I did not determine whether the presence of the associates was due to attracting substances in the water from the host or the nature of the substratum, or both.

The hydroid *Clytia bakeri* Torrey, found commonly on the shells of *Donax gouldii* Dall, 1921 near the end of the siphon, may be found in a similar position on the pismo clam, *Tivela stultorum* (Mawe, 1823), or occasionally even on the tip of the spire of *Olivella* (Dales, 1966). *Clytia* sp. was found near the end of the siphon of *Tresus nuttallii.* It may be that this species of hydroid is found on the plates purely for want of another suitable substratum. Hydroids and algae are important members of the *Tresus* association as they provide food, shelter and materials for tube building for several species.

Fry (1965) has shown that the pycnogonid *Rhynchothorax australis* Hodgson is adapted to feed on hydroid polyps and demonstrated a strong preference for association with the hydroid *Eudendrium tottoni* Stechow. The major preference was three times as strong as the animal's preference for association with any other kind of potential food. Another pycnogonid, *Ammothea striata,* is known to feed on the hydroid *Ophiodissa arborea* (Allman). The pycnogonid *Achelia* sp. was collected in the hydroid *Clytia* sp.

In addition to serving as a site of attachment for several organisms, the siphonal plates, with their associated flora and fauna, serve as a sediment trap, providing food and material for tube building. The gammaridean amphipods *Photis brevipes* and *Corophium acherusicum* build tubes upon surface objects such as shells. *Anisogammarus pugettensis* grazes upon deposit material. MILLS (1967) has shown an *Ampelisca* association which regulates algae and sedimentation in localized patches. The main food materials of the amphipods were diatoms, unicellular algae and detritus.

The association of the caprellid amphipods with the algae is probably for two reasons: (1) attachment; and (2) feeding. SAUNDERS (1966) has shown that caprellids, in addition to eating live animal matter, *e. g.* hydroids, also consume plant matter, primarily sessile diatoms. All caprellid amphipods were found clinging to the algae and hydroids which are commonly covered with protozoans and diatoms (*Navicula comoides,* a diatom, was found epiphytic on *Enteromorpha linza*).

Juveniles of the following bottom-dwelling forms were found in the sand grains and detrital material entrapped between the lamellae of the siphonal plates: *Modiolus rectus, Mytilus edulis, Protothaca staminea, Transennella tantilla,* and *Alvania* sp. According to KEEN (personal communication) the juvenile pelecypods are probably only accidentally associated with the clams. Several *Odostomia (Evalea) cf. O. (E.) quadrae* DALL & BARTSCH, 1910, were found in the sediments. The odostomias are carnivorous gastropods that either feed directly on the mantle tissue of the mollusk or that locate themselves where they can tap the incoming food streams of the host. One *Evalea* has been demonstrated by THORSON (1961) to be the associate of *Trichotropis cancellata.* It is not known if the *Odostomia* found during this study is feeding on *Tresus* or at least getting its food from its association with the bivalve.

The nemertean *Malacobdella grossa,* which is known to occur in the mantle cavity of several bivalves (*Cyprina, Pholas, Mya,* and *Tresus*) was found among the sand grains and detrital material which accumulates between the lamellae of the plates.

The sipunculoid *Phascolosoma agassizii* was found in the same situation. Sipunculoids are all bottom dwellers, found in a variety of habitats including sand or mud. These sediments usually contain foraminiferans, crustaceans, and polychaetes. AWATI & PRADHAN (1935) found ciliates, foraminiferans, small turbellarians, tiny crustaceans, polychaete larvae, and other small animals in the intestine of the sipunculoid *Dendrostoma signifer.*

SUMMARY

The siphonal plates of the horse-neck, or gaper clam, *Tresus nuttallii* (CONRAD, 1837), are the site of attachment for several species of plants and animals, provide increased surface area for diatoms and a suitable surface for other algae and several sedentary animal species, and, with their associated flora and fauna, serve as a sediment trap, providing food and material for tube building organisms.

Fifty species representing 10 animal phyla and several plant divisions were found associated with the siphonal plates.

There are 3 types of sites where the organisms are found:

(1) On the exterior of the plates;
(2) on the attached algae and hydroids; and
(3) among the sand grains and detrital material which accumulates between the lamellae of the plates.

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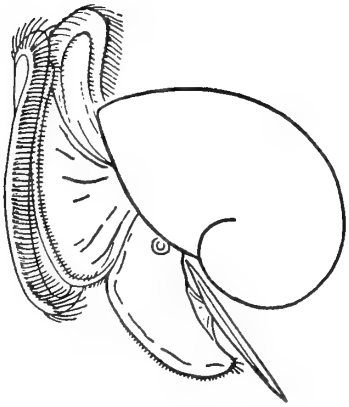

New Eastern Pacific Subgenera of *Turbo* LINNAEUS, 1758 and *Astraea* RÖDING, 1798

BY

JAMES H. McLEAN
Los Angeles County Museum of Natural History
900 Exposition Boulevard, Los Angeles, California 90007

IN THE COURSE OF REVIEWING the tropical eastern Pacific species of Turbinidae, the need for one new subgenus of *Turbo* LINNAEUS, 1758, and one of *Astraea* RÖDING, 1798, has been recognized. Both of these genera are large cosmopolitan groups in tropical and subtropical areas of the world. Subgenera in each are based upon sculpture of the mature shell and the morphology of the calcareous opercula. In many of the available taxa, the opercular differences are striking, and no doubt some will eventually come to be treated as full genera, following review on a worldwide scale.

The available generic taxa in these two groups are diagnosed and many of the type species are illustrated in the Treatise on Invertebrate Paleontology (MOORE, ed., 1960).

Chaenoturbo McLEAN, subgen. nov.
(of *Turbo* LINNAEUS)

Type Species: *Turbo mazatlanicus* PILSBRY & LOWE, 1932 (p. 87; plt. 9, fig. 6).

Diagnosis: Mature shell relatively small, openly umbilicate. The two keels of the juvenile shell are weakly stellate. Surface of operculum granular, central area raised relative to the flat shelf-like area along the outer margin, the marginal area evenly sloping to the summit adjacent to the columella; a deep central pit is bordered by a broad, spirally descending cord making two turns.

Discussion: The operculum of *Turbo mazatlanicus* has not previously been described. This is an uncommon species, generally known from beachworn specimens collected at Mazatlan, Mexico. Seven lots are represented in the Los Angeles Museum, ranging from the Cape San Lucas area of Baja California south to Port Utria, Colombia, with operculate specimens on hand from the Tres Marias Islands and Cuastecamate Cove, Jalísco, Mexico. Living specimens occur on rocky bottoms offshore at depths of 20 - 50 feet.

The open umbilicus of mature shells of *Turbo mazatlanicus* differentiates this species from all other New World turbos. Juvenile shells of most turbinids are umbilicate (ROBERTSON, 1957, p. 319), but the only other subgeneric taxon listed by MOORE (1960, p. 268) as umbilicate in the mature shell is *Subninella* THIELE, 1929 (*Lunatica* RÖDING, 1798, is erroneously so listed). The type species of *Subninella*, the Australian *T. undulatus* GMELIN, 1791, is a moderately large, low-spired form with rounded whorls and a convex operculum. The granular, deeply pitted operculum of *T. mazatlanicus* is not similar to that of any other New World subgenus of *Turbo* (*Callopoma* GRAY, 1850; *Halosephus* REHDER, 1943; *Marmorostoma* SWAINSON, 1829; *Taeniaturbo* WOODRING, 1928). On the opercular distinction plus that of the umbilicate shell, the monotypic ***Chaenoturbo*** is regarded as coordinate in rank with the other above mentioned taxa.

The prefix *chaeno-* is derived from the Greek verb χαιηω, meaning to gape, open, and referring in ***Chaenoturbo*** to the open umbilicus.

Megastraea McLEAN, subgen. nov.
(of *Astraea* RÖDING)

Type Species: *Trochus undosus* WOOD, 1828.

Diagnosis: Shell exceptionally large, exceeding 100 mm in height; periostracum thick, forming raised lamellae. Outer face of operculum bearing 3 (or 4, counting the small, upper marginal rib) raised, spinose ridges.

Discussion: Two subtropical species of the Californian province comprise the Recent members of this subgenus of *Astraea* RÖDING, 1798: the familiar *A. undosa*, and the less well known *A. turbanica* (DALL, 1910), as synonyms of which I regard *A. petrothauma* BERRY, 1940, and *A.*

rupicollina Stohler, 1959. Not until 1959 with the description of *A. rupicollina* were fully mature living specimens of *A. turbanica* discovered near the Coronado Islands south of San Diego on the outer coast of Baja California (Stohler, 1959, p. 425). Dall's species (Dall, 1910, p. 134) was based upon an immature specimen from the Magdalena Bay area (see Keen, 1958, p. 263, fig. 75), and Berry's taxon was based upon Lower Pleistocene specimens from Los Angeles County (Berry, 1940, p. 10; plt. 2, figs. 2, 3). Recently collected material from a number of localities along the outer coast of Baja California now provides the basis for arriving at the above synonymy; comparison of this material with type material of the 3 taxa clearly indicates that a single species is represented. Woodring (1946, p. 63) anticipated this synonymy in treating Berry's taxon as a subspecies of Dall's taxon. Mature specimens of *A. turbanica* are easily separated from *A. undosa.* They are generally larger than *A. undosa,* have 2 peripheral carinations rather than one, and the lowermost ridge of the operculum is curved and nearly lacking spines, in contrast to that of *A. undosa,* in which it is uncurved, thick, and spiny. *Astraea gradata* Grant & Gale, 1931, from the middle Pliocene of Los Angeles County (Grant & Gale, 1931, p. 818; plt. 31, figs. 1, 3, 5, 8, 9) is also referable to ***Megastraea.***

Astraea undosa was considered by early workers to be referable to the subgenus *Pomaulax* Gray, 1850, but the type species of *Pomaulax* is *Trochus japonicus* Dunker, 1845 (see Keen, 1956, p. 6; Moore, 1960, p. 266), a Japanese species having a smooth, convex operculum. *Pomaulax* is now in use for the Californian species *A. gibberosa* (Dillwyn, 1817). The subgenus *Uvanilla* Gray, 1850, type species *Trochus unguis* Wood, 1828, comprises a group of tropical eastern Pacific species of medium size, having 2 granulose (rather than spiny) ridges on the operculum. On the basis of size, periostracal, and opercular differences, ***Megastraea*** is regarded as coordinate in rank with *Uvanilla.*

The prefix *meg-* is derived from the Greek adjective *μεγασ* and means large, an appropriate designation for this group of the largest species of *Astraea.*

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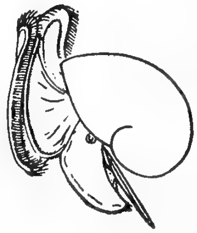


Swimming Gastropods (Opisthobranchia and Prosobranchia)

BY

WESLEY M. FARMER

Department of Zoology, Arizona State University, Tempe, Arizona 85281

(20 Text figures)

INTRODUCTION

In looking for information about swimming gastropods, it became evident that clarification of the classification of the methods of swimming was necessary. Most authors have treated swimming behavior superficially, without a close look at the various types of swimming in the class Gastropoda. However, more attention has been given to individual species of late. For example, any number of gastropods has been described as undulating; yet there are at least 6 different ways of swimming. In this paper 3 of the undulators have been placed in a different category.

This is not the first attempt to categorize swimming in gastropods. Pelseneer (1935) outlined the swimming types for members of the phylum Mollusca, including Pelecypoda, pelagic species, and veligers. Pruvot-Fol (1954) also discusses locomotion in gastropods (pelagic species). These works have been useful in establishing swimming types for this paper.

A system of classification for 9 different forms of swimming is presented; the terms are defined. The knowledge regarding the swimming in *Coryphella cynara* and *Nembrotha eliora* is expanded. Introduced to the literature is a new swimmer, *Olivella zanoeta.* In Table 2 are listed 47 species of swimming opisthobranchs and 8 species of swimming prosobranchs.

It is not fully known why most of the swimming gastropods do swim. There is speculation that in many cases it is an escape response although the predator as yet is unknown. However, swimming is an escape response for *Nembrotha eliora* (from the predatory nudibranch *Roboastra* sp.) and for *Olivella biplicata* (from the echinoderm *Pisaster brevispinus*).

MATERIALS AND METHODS

A single lens reflex camera and a strobe light were used to stop the action of swimming gastropods. Motion pictures were obtained with a Super 8 Bauer C2A camera. Illustrations were made from various exposures.

The effectiveness of the motion picture camera has proven its worth. Rates of swimming or motion can be obtained from the known speed of the filmed animal. The shape of soft structures is recorded in different successive frames during the swimming motion.

In order to study the swimming of *Aplysia,* I filmed the 8 drawings in figure 22 of Pruvot-Fol (1954) and found that it appeared to be swimming backwards. This is not apparent from the illustrations. By reversing the drawings and filming, the animal appeared to be swimming forward (Figure 1).

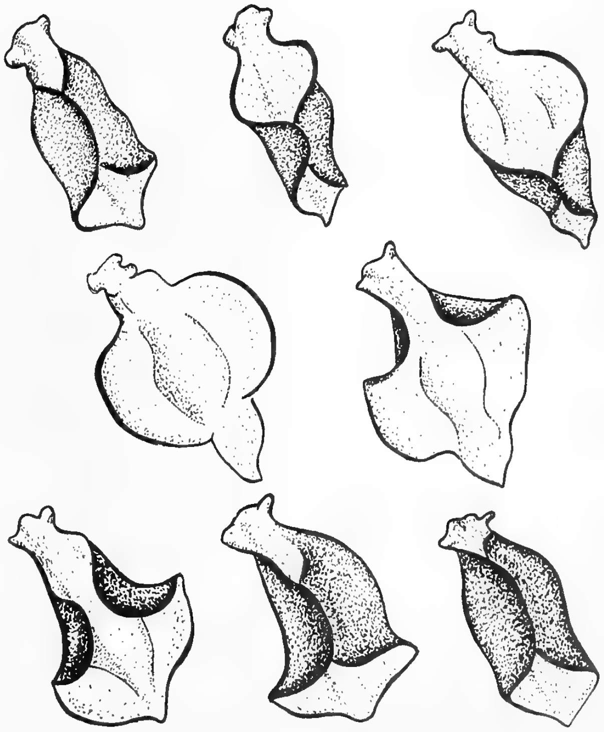


Figure 1

The swimming of *Aplysia* is redrawn from Pruvot-Fol, 1954, in proper sequence

There are several motion picture films of swimming opisthobranchs. Researchers as Pruvot-Fol, Tokioka & Baba, Risbec, Thompson & Slinn, Morton & Holme, Hurst, Haefelfinger & Kress have employed the motion picture film to obtain sequential drawings of the animal in the process of swimming. Figures 1, 16, 17 and 18 are from some of their reports and have been redrawn here to illustrate types of swimming.

SWIMMING GASTROPODS

The methods of swimming have been partially defined in the literature. For example: gastropods that "undulate" are many; however, the structure used and the method of undulating vary greatly. I will expand on and define some of the methods of swimming for various members of the opisthobranchs and prosobranchs. Pelagic forms, such as the pteropods and veligers, are not considered in this paper. Of the species included, the opisthobranchs outnumber the prosobranchs by 6 to 1.

Table 1

Swimming Classification

Type of Swimming	Table 2 abbreviations	Swimming example
1. Flapping structures (paired)		
A. Notal	nf	2, 3, 4
B. Parapodial	pf	1
C. Metapodial	mf	19, 20
2. Undulation (single structure)		
A. Entire body	ub	3
B. Foot	uf	16
C. Propodial	upro	17, 18
3. Lateral bending of the body	lb	5 - 10
4. The "breast stroke" movement	bs	11 - 15
5. Jet propulsion	jp	21

1. Flapping

Flapping through the water is interpreted as the use of 2 lateral structures that are waved up and down to provide propelling surfaces, moving the animal generally forward in the water. These structures are the notum or mantle, the parapodium and the metapodium.

A. Notal

The mantle edge of opisthobranchs has a progressive wave synchronous or asynchronous one side with the other.

B. Parapodial

Parapodial swimming is similar to notal swimming except that the structures fold over the top of the body when the animal is at rest. Its apparent initial thrust would be a downward stroke.

C. Metapodial

The metapodium of some prosobranchs is used to move the animal through the water. These flaps of tissue normally ride over the shell when the animal is crawling. When the animal swims, these structures move up and down at the sides. The metapodium arises ventrally. Metapodial swimming is similar to parapodial swimming.

2. Undulation

Undulation is defined as an up and down motion forming a progressive wave on the vertical plane through the body of the animal. The structure performing this is the propodium, the entire body, or just the foot. The animal may be upside down or right side up.

A. Entire body

In this method the dorsal surface and ventral surface provide the areas to push against the water and to move the animal forward. At least one dorid nudibranch uses this method of swimming.

B. Foot

Some prosobranchs use only the posterior $\frac{3}{4}$ of the foot which is "waved" for propulsion through the water. The anterior part of the foot is apparently of little use.

C. Propodium

The propodium of some prosobranchs is used to great advantage in propelling the animal through the water. In this case the anterior part of the animal is used in swimming, while the posterior part merely trails. Motion of the propodium is up and down.

3. Lateral bending of the body

By far more nudibranchs fall into this category than into any other. The head and tail rapidly approach each other, first on one side and then on the other. This process is repeated for some time with the flattened sides providing the propelling surfaces. Usually the animal moves upward with either the foot or back uppermost.

Table 2

Swimming Opisthobranchs and Prosobranchs

(see Table 1 for explanation of abbreviations under swimming types)

	Swimming Type	Reference
CEPHALASPIDEA		
Philinacea		
Gastropteridae		
Gastropteron bicornutum Baba & Tokioka, 1965	pf	Baba & Tokioka, 1965
Gastropteron cinereum Dall, 1925	?	Tokioka & Baba, 1964
Gastropteron flavum Tokioka & Baba, 1965	pf	Baba & Tokioka, 1965
Gastropteron fuscum Baba & Tokioka, 1965	pf	Baba & Tokioka, 1965
Gastropteron japonicum Tokioka & Baba, 1965	?	Tokioka & Baba, 1964
Gastropteron pacificum Bergh, 1893	pf	Bertsch, 1969
Gastropteron rubrum (Rafinesque, 1814)	pf	Haefelfinger & Kress, 1967a
Gastropteron sibogae Bergh, 1905	?	Tokioka & Baba, 1964
Gastropteron sinensis A. Adams, 1861	pf	Tokioka & Baba, 1964
Gastropteron viride Tokioka & Baba, 1964	?	Tokioka & Baba, 1964
Sagaminopteron ornatum Tokioka & Baba, 1964	pf	Tokioka & Baba, 1964
ASCOGLOSSA		
Elysiacea		
Elysiidae		
Elysia pilosa Risbec, 1928	pf	Risbec, 1928
ANASPIDEA		
Aplysiacea		
Akeratidae		
Akera O. F. Müller, 1776		Morton, 1967
Akera bullata O. F. Müller, 1776	pf	Haefelfinger & Kress, 1967b
Aplysiidae		
Aplysia Linnaeus, 1767		Pruvot-Fol, 1954
Aplysia depilans Gmelin, 1791	pf	Haefelfinger & Kress, 1967b
Aplysia fasciata Poiret, 1789	pf	Haefelfinger & Kress, 1967b
Aplysia punctata Cuvier, 1803	pf	Haefelfinger & Kress, 1967b
Notarchus Cuvier, 1817		Pruvot-Fol, 1954
Notarchus punctatus Philippi, 1836	jp	Haefelfinger & Kress, 1967b
NOTASPIDEA		
Pleurobranchacea		
Pleurobranchidae		
Pleurobranchus (membranaceus) tuberculatus Meckel, 1808	nf	Thompson & Slinn, 1959
Oscanius tuberculatus Meckel, 1808	nf	Martin, 1966
Euselenops luniceps (Pace, 1901)	nf	Pelseneer, 1935
NUDIBRANCHIA		
Doridoidea		
Cryptobranchia		
Hexabranchidae		
Hexabranchus aureomarginatus Ostergaard, 1955	nf	Neu, 1932
Hexabranchus imperialis, possibly *H. marginalis*	nf	Haefelfinger & Kress, 1967b
Hexabranchus marginatus Quoy & Gaimard, 1833	ub, nf	Edmunds, 1968 Risbec, 1928 Vicente, 1963
Hexabranchus tinkeri Ostergaard, 1955	nf	Ostergaard, 1955
Hexabranchus sanguineus (Rüppell & Leuckart)	nf	Gohar & Soliman, 1963
Phanerobranchia		
NONSUCTORIA		
Polyceridae		
Nembrotha eliora Marcus, 1967	lb	Lance, 1968
Plocamopherus F. S. Leuckart, 1828		Pruvot-Fol, 1954
Triopa fulgurans Risbec, 1928	lb	Risbec, 1925

Table 2 [continued]

	Swimming Type	Reference
Dorididae		
Archidoris nubilosa	nf	Kay, pers. comm.
Goniodoridinae		
Trapania velox (Cockerell, 1901)	lb	Cockerell, 1901
DENDRONOTACEA		
Dendronotidae		
Dendronotus giganteus O'Donoghue, 1921	lb	Haefelfinger & Kress, 1967b
Dendronotus iris Cooper, 1863	lb	Bertsch, pers. comm.
Dendronotus nanus Marcus, 1967	lb	Marcus, 1967
Dendronotus albus MacFarland, 1966	lb	Long, pers. comm.
Dendronotus frondosus (Ascanius, 1774)	lb	Long, pers. comm.
Dendronotus subramosus MacFarland, 1966	lb	Long, pers. comm.
Bornellidae		
Bornella (Gray) Adams & Reeve, 1848		Risbec, 1928
Bornella digitata Risbec, 1953	lb	Risbec, 1953
Scyllaeidae		
Scyllaea pelagica (Linnaeus, 1758)	lb	Pruvot-Fol, 1954
Tritoniidae		
Melibe leonina (Gould, 1852)	lb	Hurst, 1968
Melibe pilosa Pease,	lb	
Chioraera dalli Heath, 1917	lb	Heath, 1917
Fimbria fimbria (Bohadsch, 1761)	lb	Pruvot-Fol, 1954
Marionia tethydes Delle Chiaje, 1828	lb	Haefelfinger & Kress, 1967b
AEOLIDOIDEA		
Pleuroprocta		
Flabellinidae		
Coryphella (Flabellinopsis) iodinea (Cooper, 1862)	lb	MacFarland, 1966
Coryphella cynara Marcus, 1967	bs	Marcus, 1967
Flabellina telja Marcus, 1967	lb	Marcus, 1967
Phyllobranchillidae		
Phyllobranchillus orientalis Kelaart, 1858	bs	Risbec, 1953
Eolidoidea		
Aeolidiidae		
Aeolidiella alba Risbec, 1928	bs	Pruvot-Fol, 1954
ARCHAEOGASTROPODA		
Trochacea		
Trochidae		
Solariella nektonica Okutani, 1961	uf	Okutani, 1961
MESOGASTROPODA		
Viviparacea		
Ampullariidae		
Ampullarius	upro	Pelseneer, 1935
Naticacea		
Naticidae		
Polinices josephinus (Risso, 1838)	upro	Ziegelmeier, 1958
NEOGASTROPODA		
Stenoglossa		
Volutacea		
Olividae		
Olivella biplicata (Sowerby, 1825)	mf	Edwards, 1969
Olivella zanoeta (Duclos, 1835)	mf	
Olivella verreauxii (Ducros, 1857)	mf	Wilson, 1969
Oliva tehuelchana (d'Orbigny, 1841)	mf	Wilson, 1969
Ancillista cingulata (Sowerby, 1830)	upro	Wilson, 1969

4. The "breast stroke" movement

As the human swimmer uses his extremities, these nudibranchs use their cerata to "stroke" the water, rowing themselves into the water column. The animal moves forward.

5. Jet propulsion

Water is taken into the peribranchial cavity formed by the joined parapodia, and forced out through a small opening, causing the animal to move in the opposite direction.

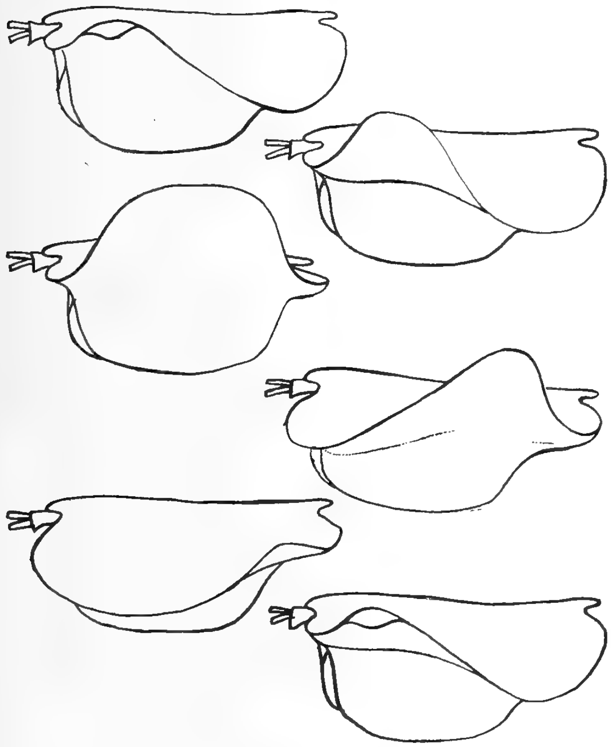


Figure 2

The swimming of *Pleurobranchus tuberculatus* after Thompson & Slinn, 1959

SWIMMING OPISTHOBRANCHS

Swimming by opisthobranchs has been well documented by earlier investigators. Many of the early observations concerned the manner an opisthobranch used as a means of locomotion. More recently, Risbec, Pruvot-Fol, Thompson & Slinn, Haefelfinger & Kress, Baba, Tokioka, Martin, Edmunds, Hurst, Craig, Wilson & Vicente have given excellent descriptions, with illustrations, of the manner of swimming which the animal exhibited.

There are 47 species listed in Table 2, that have been reported as having the ability to swim. Much of the classification follows Taylor & Sohl (1962).

Information as to the rate of swimming is scattered. Comparisons with other opisthobranchs can be found in Table 3. The size of animals with swimming locomotion ranges from a few millimeters in *Gastropteron* to over 40 cm in *Aplysia*.

Dr. George E. Radwin (personal communication) observed several hundred aplysids (propably *Aplysia dactylomela* Range, 1828) swimming near the surface under night lights in Florida. Dr. Alison Kay (personal communication) has reported seeing *Hexabranchus tinkeri*, *H. aureomarginatus* and *Archidoris nubilosa* swim. Ostergaard (1955) says of the Hexabranchids "Swimming is effected by vigorous transverse flextions [sic] of the body and undulating movements of the broad, thin cloak, which serves as fins" (Figures 3, 4).

Cockerell (1901) says of *Thecacera velox* (now *Trapania velox*) "... very active when swimming with an undulating motion at the surface of the water." I worked with this species and tried unsuccessfully to induce it to swim.

By far a majority of swimming species apparently use lateral bending of the body as an auxiliary method of locomotion (Figures 5 - 10). Of the Nudibranchia, most members of the suborders Eolidoidea and Dendronotoidea employ this method. A few limaciform members of the suborder Doridoidea also use this method of swim-

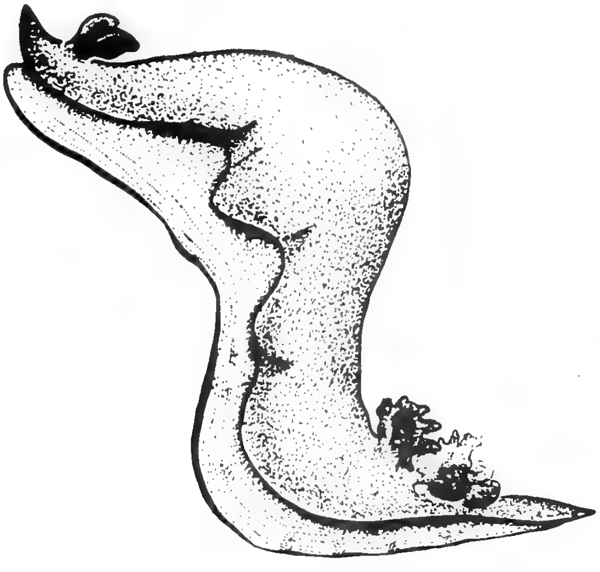


Figure 3

Hexabranchus marginatus in the process of swimming redrawn from Edmunds, 1968

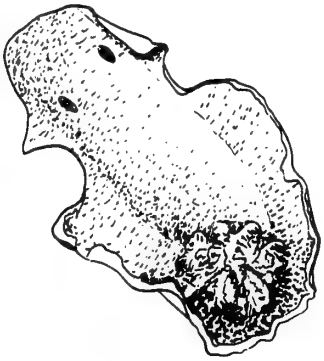


Figure 4

Hexabranchus sanguineus swimming. Redrawn from Gohar & Soliman, 1963

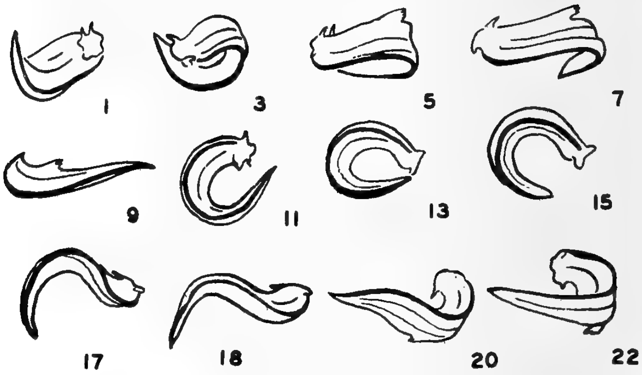


Figure 6

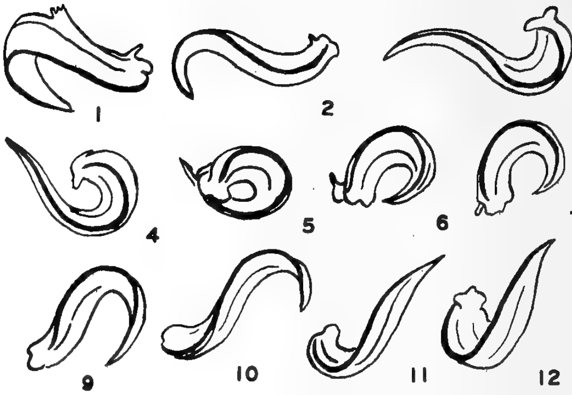


Figure 7

Figures 6 and 7

Nembrotha eliora actively swimming by lateral bending of the body. Numbers are those of motion picture frames in sequence.

ming, *i. e., Nembrotha eliora* (Figures 6, 7), a nonsuctorian nudibranch.

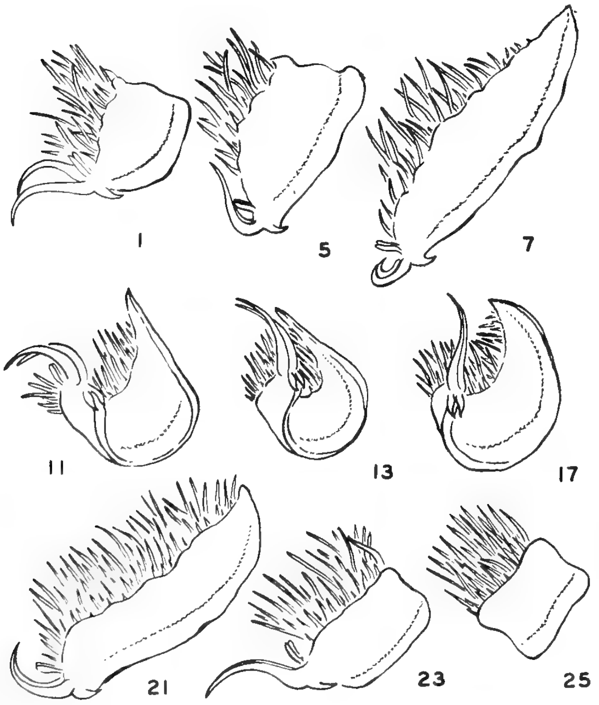


Figure 5

Coryphella iodinea swimming by lateral bending of the body. Numbers are those of motion picture frames in sequence.

Heath (1917) says of *Melibe leonina* "... body is strongly flexed from side to side." MacFarland (1966) says of *Coryphella iodinea* "... swims freely by doubling the body laterally from side to side until head and tail meet ..." A good example of this is seen in Figure 5. Lance (1968) reported *Nembrotha* "... swimming ... by undulating its body from side to side ..."

Hurst (1968) writes "*Melibe leonina* just prior to swimming folds the whole foot longitudinally so that the right and left halves of the sole meet. The body becomes laterally compressed while the dorsal papillae elongate and flatten. In this manner the animal presents maximal surface area for swimming." Hurst reports that the rate and degree of bending determine the speed of progress. The hood of *Melibe* plays no major part in propulsion. Hurst stresses that the animal swims upside down.

A slight variation of the usual method was reported by

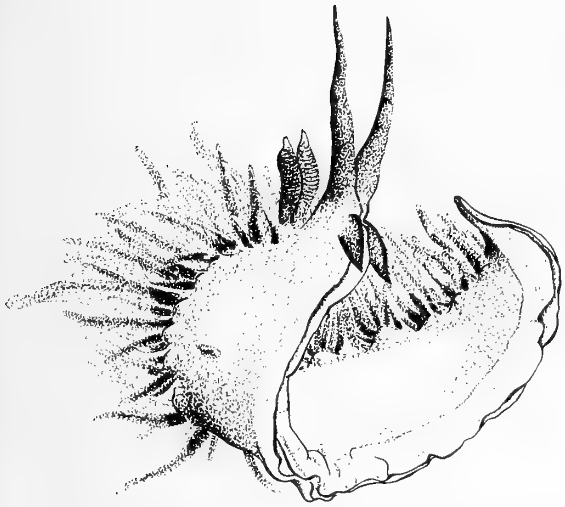


Figure 8

Coryphella iodinea swimming

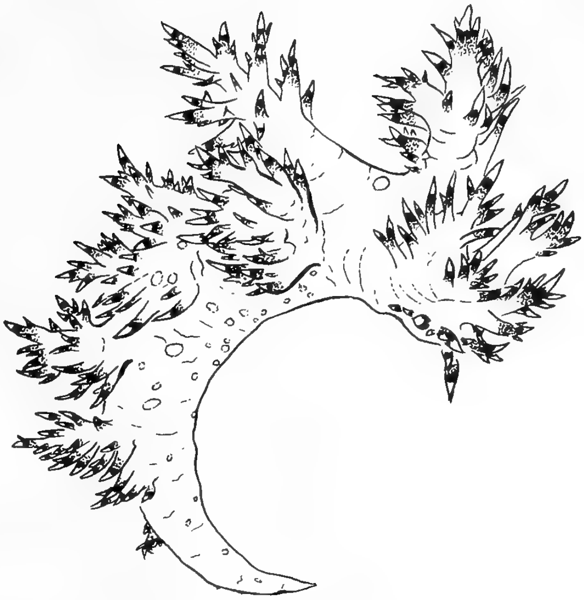


Figure 10

Dendronotus nanus swimming by lateral bending of the body

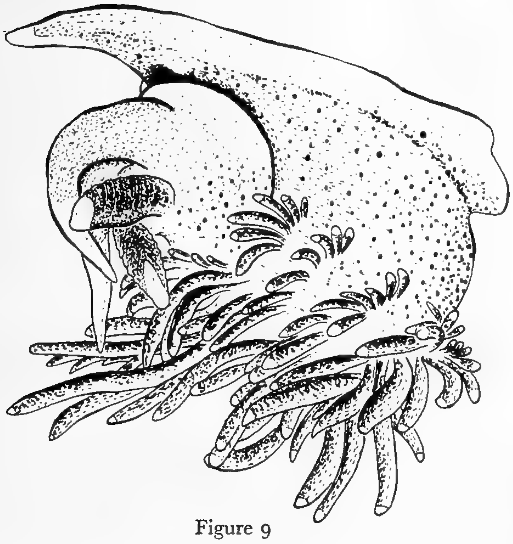


Figure 9

Flabellina telja swimming by lateral bending of the body

Agersborg (1923) for *Dendronotus giganteus.* "It swims by bending the anterior end of the body sideways, forming a wave-like twist in the side of the body wall like that in a blade of a propeller. This wave passes gradually toward the posterior end and disappears when the animal makes the next stroke to the opposite side. When the animal makes a stroke to the right the posterior two thirds is bent so as to form an angle of 45° with the anterior one third. But the posterior part of the body also rotates about 45° from the vertical plane, so that the left side with the foot forms a large wave which sweeps posteriorly, while the anterior part of the body, in front of the wave, is kept vertical."

The lateral bending of the body in *Nembrotha eliora* is slightly different from that utilized by other species in this method of swimming. There is a degree of momentum along the axis of the animal in the direction of the head. A rapid flexing brings the body into a circular position at which continued motion takes place around the circle. At times when the animal passes from one side of the stroke to the other, the body takes on an "S" form, the head initiating the stroke while the tail lags slightly (Figure 6 [18] and Figure 7 [2, 10]). In other species, the tail and head apparently travel at approximately the same speed, meeting at the same time on the other side of the stroke (Figure 5 [13]), without going through the "S" form. *Nembrotha* has a pivot point about $\frac{3}{4}$ of the way back from the head, while the pivot point on others is about at the center of the body. *Nembrotha* makes about $1\frac{1}{2}$ strokes per second. At 18 frames per second the animal went from a tight coil to the other side and back again, amounting to 90 strokes per minute. It swims with foot dorsal or ventral. This action in *N. eliora* is definitely an escape response, for when this species comes in contact with the predacious nudibranch (which, for now, will be called *Roboastra* sp.), there is an immediate reaction to move the head away with a fast jerk, free its hold on the substrate, and rapidly swim. I observed the predatory nudibranch try to eat one of the swimming nudibranchs, and also observed 3 being eaten. When *Nembrotha* was in the buccal envelope of *Roboastra,* it tried to escape by rapidly moving from side to side as if trying to swim. Because of the off-center pivot point and the forward momentum after a stroke, it would be to the advantage of *Nembrotha* to have this additional characteristic to escape from the sac-like cavity and "screw" its way out of the buccal envelope. When *Nembrotha* fails to escape, there is visible evidence of its presence in the head of *Roboastra* because of its movements.

The breast stroke movement is effected by the cerata of *Aeolidiella alba* (Figure 11), *Coryphella cynara* (Figure 12), and *Phyllobranchillus orientalis* (Figure 13). These are the only species known at this time to swim in this manner.

Risbec (1953) says of *Aeolidiella alba* "The crawling motion is sometimes augmented by the movements of the cirri." This is particularly remarkable with *A. alba* which proceeds by jerks while all the cerata thrust abruptly backward, beating the water vigorously. The animal is 6 mm long, with short blunt cerata. Apparently the swimming motion augments the crawling and is probably a combination of swimming and crawling.

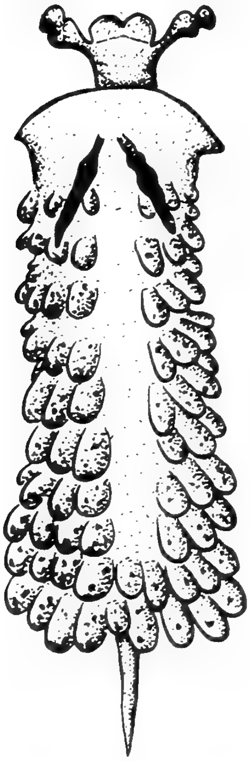


Figure 11

Aeolidiella alba. Cerata are used by this species for swimming, after Risbec, 1953

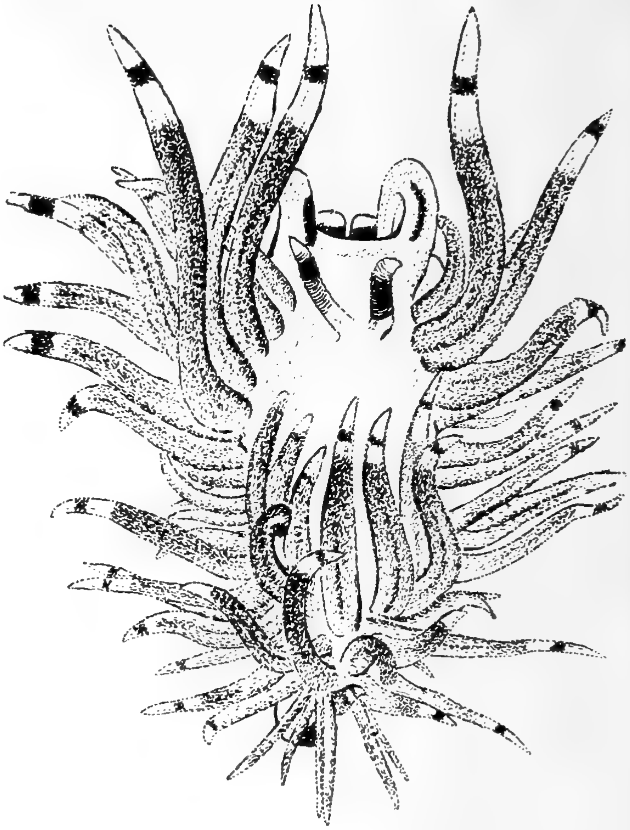


Figure 12

Dorsal aspect of *Coryphella cynara* actively swimming with cerata

Risbec (1928) says of *Phyllobranchillus orientalis* "The papillae of it are, in fact, very motile and serve for locomotion." The animal is about 4 cm in length. Risbec (1953) figures and discusses the animal further (see Figure 13).

Coryphella cynara has only recently been recognized as a swimmer. It has great strength and stamina when it swims and can remain in the water column for periods greater than 45 minutes without noticeably resting. There is apparently a lack of fatigue in the muscles moving the

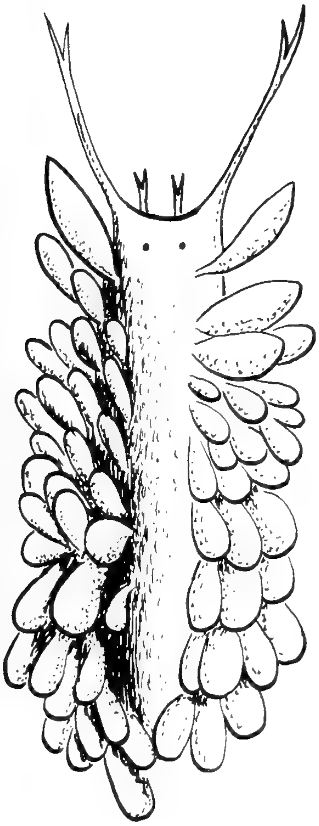


Figure 13

Phyllobranchillus orientalis swims with cerata, after Risbec, 1953

cerata. This could be due to the fact that the cerata are also respiratory in function and the rapid movement through the water hyper-oxygenates the inner fluids which bathe the muscles, removing fatigue-producing by-products.

The species lives in the upper Gulf of California and apparently is an occasional visitor to the shallow water from deeper areas. *Coryphella cynara* is a carnivore and has been observed eating *Hermissenda crassicornis* in captivity (Lance, pers. comm.). Because it ventures into the

(adjacent column ⟶)

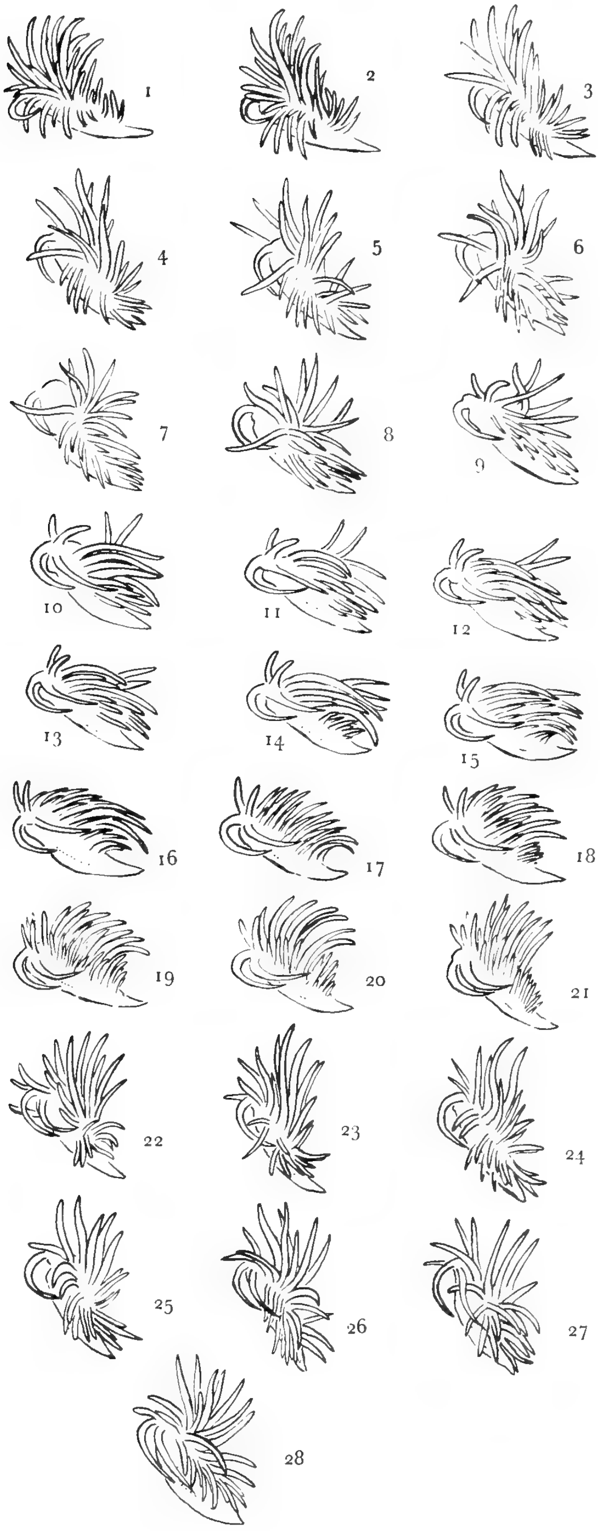


Figure 14

Sequence of *Coryphella cynara* swimming

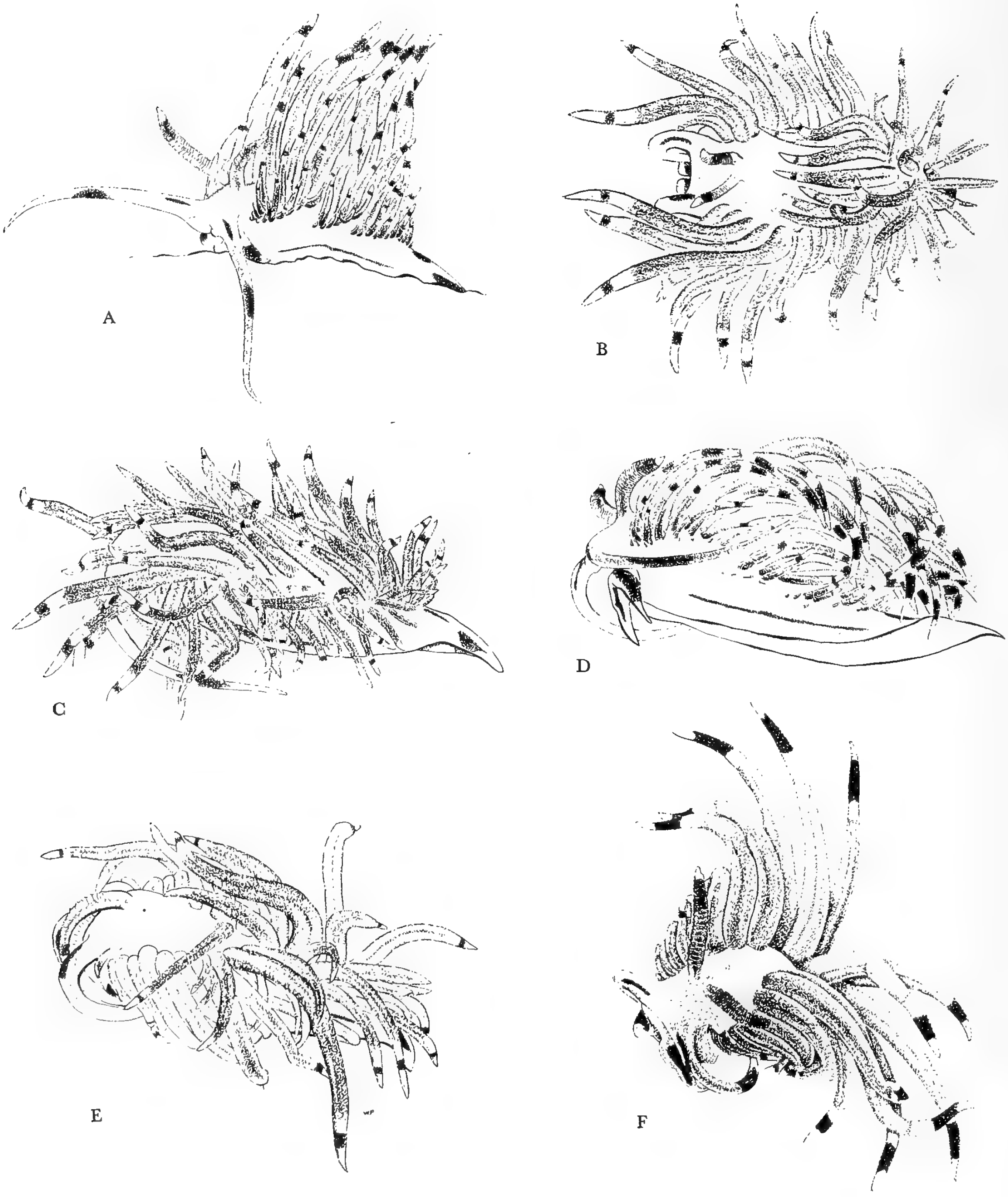
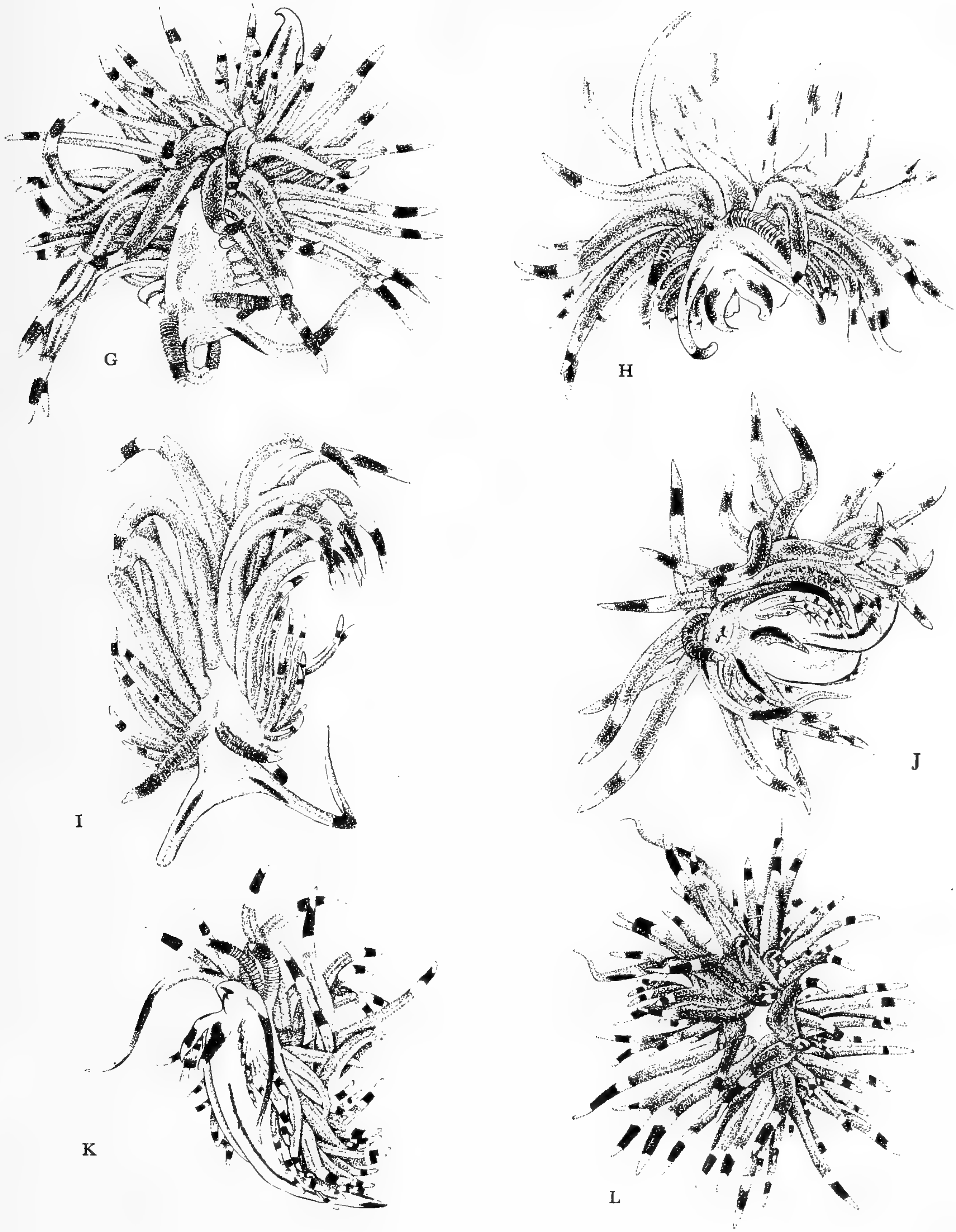


Figure 15

Coryphella cynara

A: actively crawling – B to L: actively swimming


G
H
I
J
K
L

upper water it may feed to a great extent on organisms in the water column, as salps, jellyfish, siphonophores; but this is only speculation.

Marcus & Marcus (1967) quote L. Pardy as saying, "Only a single specimen of this swimming nudibranch was found. It was lying on the sand at low tide line. It swims with a 'breast stroke', moving the cerata in horizontal plane along the side of the body in unison and extended. On the return stroke the cerata are collapsed, but return along the same plane."

With this first account in mind, I will expand the data. Mrs. Eva Schroeder of Phoenix, Arizona, called my attention to a specimen of *Coryphella cynara* collected by Mrs. Carol Skoglund in the Cholla Bay area, Sonora, Mexico. It was obtained on April 13, 1968 at a very low tide of –6 feet, among rocks at the water's edge. The animal was 25 mm long, 7 mm wide, and 8 mm high. The distance across the cephalic tentacles was 32 mm. It had striking purple markings on the side and back of the foot as well as on the cephalic tentacles and cerata (Figure 15 A).

The cerata were used in unison in the "rowing movement," like the "breast stroke" of swimmers, to propel the animal upward and forward or along a horizontal plane. It appeared that all the cerata were brought into play for the backward stroke, for they spread out as they were brought forward in a bowed manner with the tips of the cerata pointing posteriorly (Figure 15 B). With a swift movement nearly all cerata moved back and downward, the last ones completing the stroke first, then the middle ones, and lastly the anterior cerata, the tips of the cerata coming to rest under the foot (Figures 14, 15 F). During this motion the foot was folded straight down the center into a hatchet-like edge or slightly apart (Figure 15 K). There was no sideward movement of the body. It appeared the motion was entirely in the cerata. The rhinophores tended to move about with the currents when the animal was swimming (Figure 15), while the oral tentacles were apparently folded under the animal. I observed the animal swimming 150 consecutive strokes in 3 minutes 21 seconds, or about 0.75 strokes per second (44.1 strokes per minute).

The Conchological Club of Southern California made a dredging trip on a shrimp boat out of San Felipe, Baja California, Mexico, June 27 through June 29, 1968. Mrs. Joyce Gemmell of San Felipe reported the collections in a club news letter and stated that Don Cadien identified *Coryphella cynara* and *C. iodinea* that were dredged in 126 feet of water at 10:30 a. m. in the vicinity of Consag Rock off San Felipe. Two specimens were given to Mr. J. R. Lance. A 28 mm long specimen was less strikingly colored than the specimen from Cholla Bay. Later, with the animal in a one-gallon aquarium, I made the following observations.

Beginning with a swimming nudibranch, I kept a record of the number of strokes the animal made, and the elapsed time until it settled to the bottom of the aquarium. The temperature of the water was 26° C. Observation lasted from 1:17 p. m to 2:02:30 p. m. It had swum 2 100 strokes during the 45½ minutes of observation or 0.77 strokes per second. It began swimming again at 2:18 and stopped at 2:45 p. m. The animal swam without initial prodding and without touching bottom. It swam more slowly than the Cholla Bay animal probably because of its larger size.

Pruvot-Fol (1954) describes the jet propulsion method of swimming for *Notarchus* " ... a sharp recoil to expel water contained in the peribranchial sac formed by the joined parapods ... " In my observations on *Notarchus* in the Gulf of California I saw no swimming by this method.

DISCUSSION

Some species are capable of remaining in the water column for some time, such as *Pleurobranchus tuberculatus* and *Coryphella cynara,* and possibly others. In the case of *P. tuberculatus* (Figure 2) the two lobes are not synchronous in their action; "that of one side undergoes its recovery stroke at the precise time when the other is in the phase of effective beat" (Thompson & Slinn, 1969). In *C. cynara* there is synchronous action with the cerata, each side in balance with the other (Figure 15 B). Here all cerata are poised for the backward thrust, the posterior ones already in this process. Synchronous beating also occurs in *Akera* and *Gastropteron.*

It is not known why opisthobranchs swim in the various manners discussed. Some are weak swimmers and once in the water column are carried by the currents. *Coryphella cynara* is considered a strong swimmer and has efficient means of swimming.

Many opisthobranchs have no apparent direction to their swimming, such as the lateral body benders. On the other hand, animals using notal and parapodial methods of swimming have more control of the direction of their movement.

Swimming in many cases, as in that of *Nembrotha eliora,* is an escape response while in others it is apparently merely a means of moving from one place to another. This applies particularly to *Melibe leonina,* which is commonly found in kelp beds where it seems advantageous to be able to swim from one kelp frond to another, if the animal is dislodged.

SWIMMING PROSOBRANCHS

There are 8 species, representing 3 orders, of swimming prosobranchs.

Solariella nektonica, an archaeogastropod, is about 7 mm in greatest dimension; it has been recorded from 31°35'18" N, 130°06'30" E. When the animal swims, the foot expands to 2 - 3 times its usual dimensions and the shell is kept on the upper side. When movement is suspended and the animal is ready to descend (see Figure 16), the shell is downward.

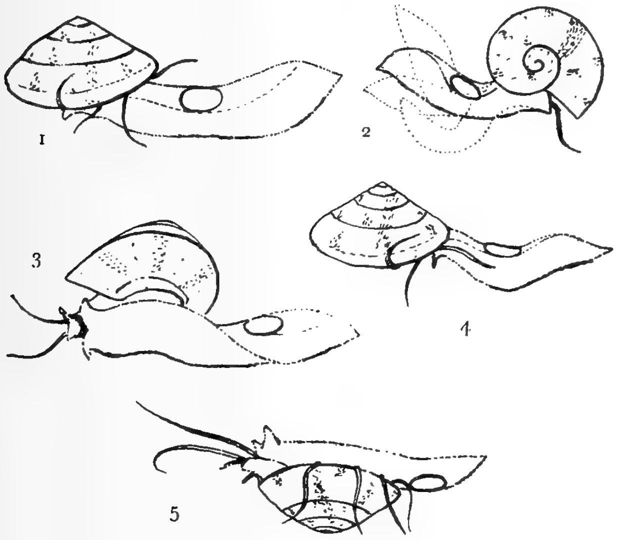


Figure 16

Movement of swimming in *Solariella nektonica.*

1 to 4: Movement of swimming – 5: animal descends when swimming is suspended, after Okutani, 1961

"The expanded posterior part of the foot is twisted at a right angle, thus it becomes like the tail of a tadpole in appearance and in function. This gastropod swims in a rather straight direction, controlling the swimming by itself. It is not considered to be a demented movement." (Okutani, 1961).

Ampullarius, according to Pelseneer (1935), swims by using quick movements of the snout and cephalic appendages. *Polinices josephinus* is reported by Ziegelmeier (1958) to swim by thrashing the extended propodium (see Figures 17, 18). Ziegelmeier's film was taken at 16 frames per second. At this speed one swimming motion or "stroke" takes 33 frames or 2 seconds. This species can swim with the shell dorsal or ventral to the foot.

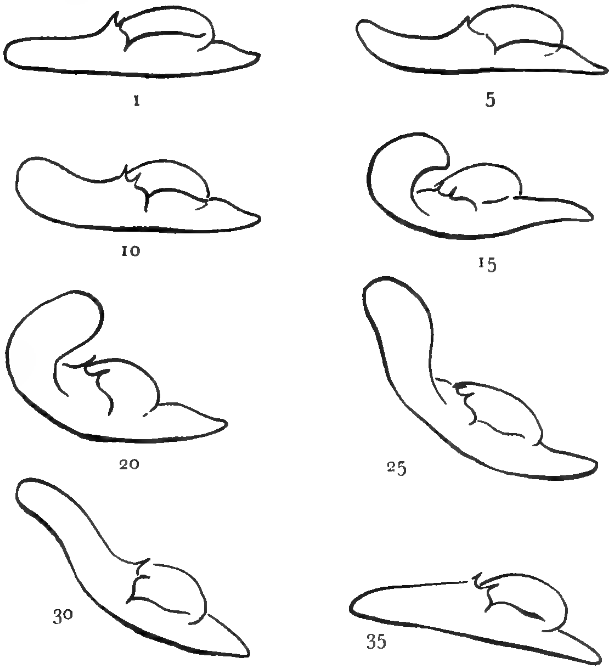


Figure 17

Polinices josephinus, a swimming prosobranch in normal position. Filmed at 16 frames per second; after Ziegelmeier, 1958

Edwards (1969) writes that *Olivella biplicata,* in an escape response to *Pisaster* will rear up on the hind portion of its foot, withdrawing the propodium and throwing the parapodia forward; frequently the snail will flip over backwards. The snail pumps the expanded metapodium violently up and down, lifting the animal off the substrate and carrying it away some 5 - 10 cm in a form of upside-

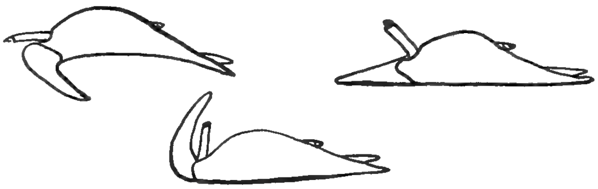
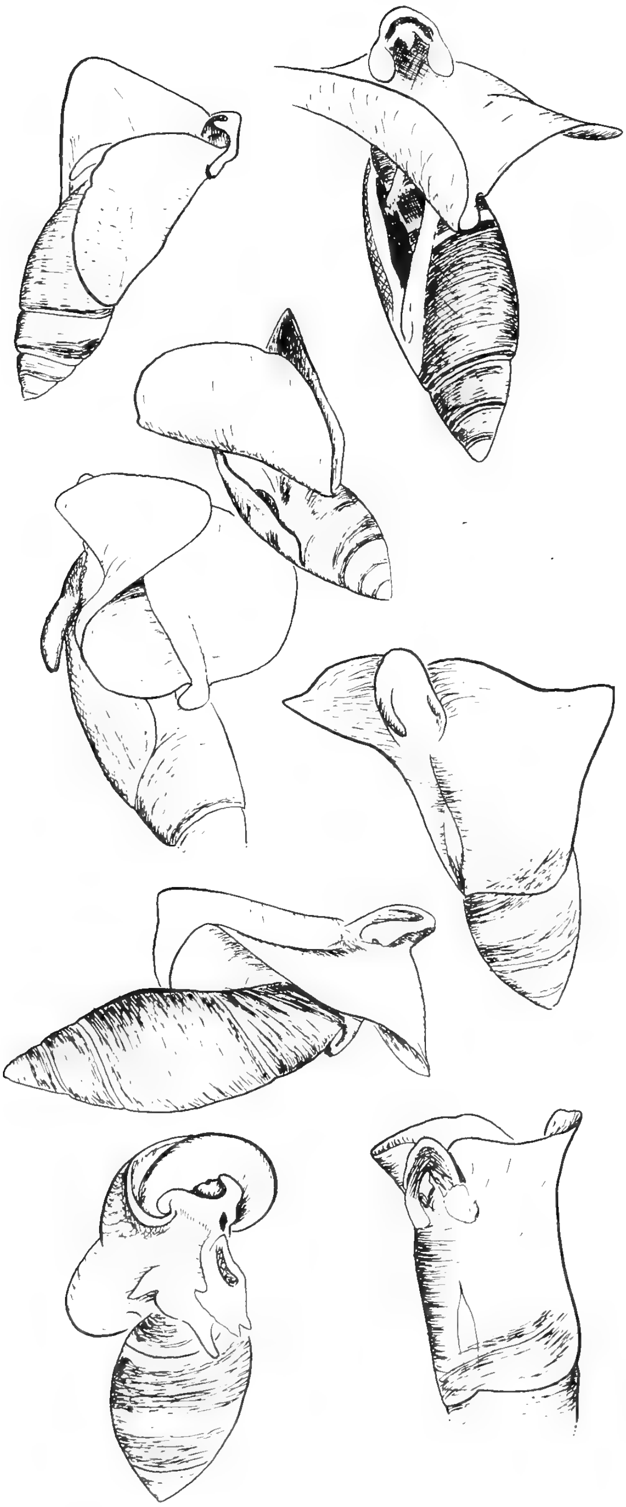


Figure 18

Ancillista cingulata utilizes the propodium in swimming, after Wilson, 1969



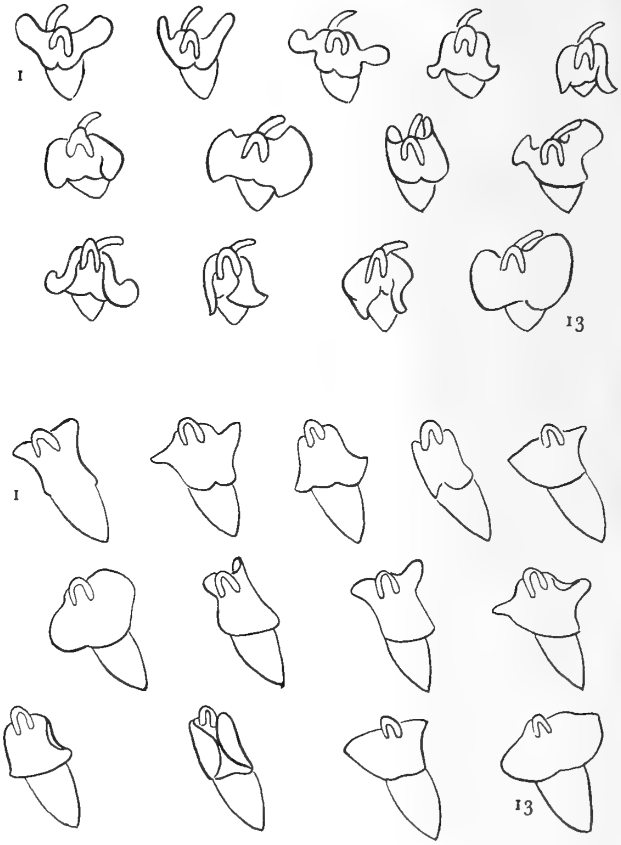


Figure 20

Olivella zanoeta; swimming rate is 240 strokes per minute. Two sequences are represented here

down swimming. This metapodial swimming response is qualitatively distinct from any previously reported escape behavior by a gastropod. It is effected by holding the parapodia close to the sides of the shell, especially at the anterior end, so the vigorous down beats of the large, horizontally extended metapodium force water down and back, lifting the gastropod up and propelling it forward.

WILSON (1969) reports on the swimming behavior of *Oliva tehuelchana, Olivella verreauxii* and *Ancillista cingulata.* The 2 former swim by the lateral wing-like flaps

(← adjacent column)

Figure 19

Olivella zanoeta filmed with a single lens reflex camera with strobe light to stop the action of the metapodium. Bottom of tank, relative to animal, is down of the metapodium, the latter utilizes the propodium. The metapodium characteristically folds over and covers the shell in members of the Olividae.

The propodium is used as the primary swimming organ in *Ancillista cingulata* with the metapodium trailing. *Ancillista* swims in a jerky manner reminiscent of the random swimming movements of scallops (Wilson, 1969). "The propodium repeatedly flapped backwards from the horizontal plane, first dorsally and then ventrally at regular intervals of slightly more than one second. Each movement threw the animal forward a distance varying between 5 and 15 cm. The ventral beat appeared to be the most effective. The shell was uppermost, but 'barrel-rolls' were frequent. This activity continued for 45 seconds, during which time the propodium flapped 35 times. Swimming did occur spontaneously." Wilson concluded that the behavior was an escape response.

Olivella zanoeta is a swimmer from the Gulf of California. The movements of the metapodia are very rapid, causing the snail to move about in a somewhat irregular manner. Motion pictures of its swimming behavior did not stop the action of the metapodium when taken at 24 frames per second. However I could determine from individual frames that the animal has a swimming rate of 240 strokes per minute. This was evident from 6 frames of the sequence (Figures 19, 20).

DISCUSSION

The prosobranchs utilize the foot, propodium and metapodium type of undulation to propel themselves through the water. The family Olividae has apparently the most swimming members. Because of the nature of the escape response of *Olivella biplicata,* it may be assumed that the other species of swimming Olividae might in fact be trying to escape from predators commonly found in their habitats.

Table 3

Swimming Rates and Duration

Species	Swimming Type	Strokes per Minute	Duration
		Opisthobranchs	
Akera bullata	pf	120	up to ½ hour
Coryphella cynara	bs	44	
		46	over 45 minutes
Dendronotus giganteus	lb	45	—
Nembrotha eliora	lb	90	few seconds
Pleurobranchus tuberculatus	un	55 - 60	may be several hours
		Prosobranchs	
Ancillista cingulata	upro	46	45 seconds
Olivella zanoeta	mf	240	few seconds
Polinices josephinus	upro	30	—

CONCLUSION

Swimming gastropods use a variety of structures to effect swimming: the notum, parapodium, metapodium, propodium, and foot. The entire body can be used in a horizontal or vertical plane. Some species use a combination of 2 types of swimming: the entire body and the notum. Some use the cerata in a "breast stroke" rowing movement and one group utilizes the parapodia to form an opening through which to expel water.

If motion pictures are utilized to a greater extent, more variation in the different methods of swimming may become evident. Special care needs to be taken in acquiring additional data on rate, duration, and circumstances promoting swimming. Tables 1, 2, and 3 summarize much of what is known about swimming gastropods.

Several aplysids were not included, however, as the literature refers to swimming structures rather than to actual swimming.

Coryphella cynara possesses remarkable stamina in its swimming. However, as yet I do not know why this benthic nudibranch shows this behavior. The long swimming duration, I can theorize, may be related to the quest for food or to breeding behavior.

Nembrotha eliora shows a swimming behavior that is an escape reaction from its prime predator, *Roboastra* sp. Both are benthic species and apparently abundant in water 45 - 90 feet deep. *Roboastra* attains a length of up to one foot and more and is very swift in capturing the smaller *N. eliora* in its buccal envelope. *Nembrotha eliora* seems to sense the presence of *Roboastra* from several centimeters away and will avoid it by crawling away from it almost at a right angle.

The method of swimming of *Coryphella iodinea* is illustrated for the first time. Selected examples from the literature are used to illustrate the different types of swimming listed in Table 1.

ACKNOWLEDGMENTS

I would like to thank Dr. Dwight W. Taylor for his constructive remarks and introduction to the prosobranchs. Mrs. Carol Skoglund and Mr. H. Schroeder were very helpful; Mrs. Susan Kreml assisted by translating some French references. Dr. Alison Kay, Mr. Steven J. Long and Mr. James R. Lance offered additional data or specimens. Mr. Boris Innocenti provided a number of *Nembrotha eliora* and *Roboastra* sp. Hans Bertsch and Gladys Lytle critically read the manuscript. Much appreciation goes to my wife for her aid and support while this paper was being prepared.

ADDENDUM

It has been brought to my attention that perhaps more pelagic nudibranchs should be considered, including Steinberg's (1956) report on *Cephalopyge trematoides* (Chun, 1889). Steinberg has observed it swimming but does not mention how it swims. Being a pelagic species, *C. trematoides* most probably is a floater with its movements augmented by some swimming effort.

Gordon Robilliard (pers. comm.) has observed 4 other species of swimming opisthobranchs. *Cumanotus beaumonti* uses its cerata, *Tritonia gilberti* swims by dorsal-ventral flexings, *Dendronotus dalli* by lateral bending of the body and *Coryphella longicaudata* by lateral bending, while also twisting in a screwshape from front to back.

Richard A. Roller (pers. comm.) observed *Tritonia gilberti* in an escape response from the sun-star, *Pycnopodium helianthoides.*

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Commensal Activity as a Function of Age in Two Species of California Abalones

(Mollusca : Gastropoda)

BY

JOHN C. HANSEN

Moss Landing Marine Laboratories, Moss Landing, California 95039

(2 Plates; 2 Text figures)

INTRODUCTION

THE PURPOSE OF THIS STUDY was to determine the value of commensal activity as a function of relative age in shells of two species of California abalones. The vacant shells of two species of California abalones (Haliotidae), *Haliotis rufescens* SWAINSON, 1822 and *H. cracherodii* LEACH, 1817 were chosen for this study for their abundance in a large size range (2.1 cm to 21.0 cm) at the location of collection, the beaches of Año Nuevo Island, 63 km south of San Francisco in San Mateo County, California. Because of the large number of shells of all sizes required for this type of study, shells of animals that had died of natural causes were used rather than a collection of shells of living animals.

The red abalone, *Haliotis rufescens,* is primarily a sublittoral species and is the largest and commercially most important species of California haliotids. The black abalone, *Haliotis cracherodii,* is somewhat smaller than the red abalone and is found living in the eulittoral and shoal sublittoral areas.

Two of the most common animals that live commensally on the shells of many marine gastropods are *Clione celata* GRANT, var. *californiana* DE LAUBENFELS, 1932, a boring sponge (Porifera), and *Penitella conradi* VALENCIENNES, 1846, a piddock or boring clam. *Cliona celata californiana,* a member of the family of lime-boring sponges, the Clionidae, is yellow in color and lives commensally on the shells of a number of species of mollusks and cirripeds. This sponge bores a vast network of tunnels in its host's shell to increase surface area for attachment (MACGINITIE & MACGINITIE, 1949). The sponge borings can greatly reduce shell strength. I have found that the infection by *C. celata californiana* invariably begins in the protoconch area of gastropods and in the umbonal area of bivalves. These are the oldest and most weathered areas of the shells and are therefore the most vulnerable to the initial attack by the sponge. The sponge then spreads from these initial areas and often reduces the host shell to a fragile skeleton. Typical infestations by *C. celata californiana* on shells of *Haliotis rufescens* are shown in Figures *1*a, *1*b, and *2*a, *2*b [E]. In Figure *1*a infection had begun in the protoconch area at the top of the shell. The infection had spread from the protoconch area in Figure *1*b. It appears as stippling near the top of the shell. Nearly 50% of the shell surface in Figure *2*a shows evidence of infection. At this stage much of the identity of the shell surface has been lost. Figure *2*b shows the severity of an advanced stage of infection by boring sponges. The brick-red prismatic layer has been completely destroyed on the upper half of the shell and the borings are well into the nacreous inner layer.

A number of mollusk species have similar responses to the activity of *Cliona celata californiana.* Some highly infected shells of *Haliotis rufescens, Hinnites multirugosus*

Plate Explanation

A typical process of shell infection by *Cliona celata californiana* on *Haliotis rufescens.* Infection invariably begins in the protoconch area (Figure *1* a) and spreads over the surface of the shell (Figures *1* b, *2* a, *2* b)

[E] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

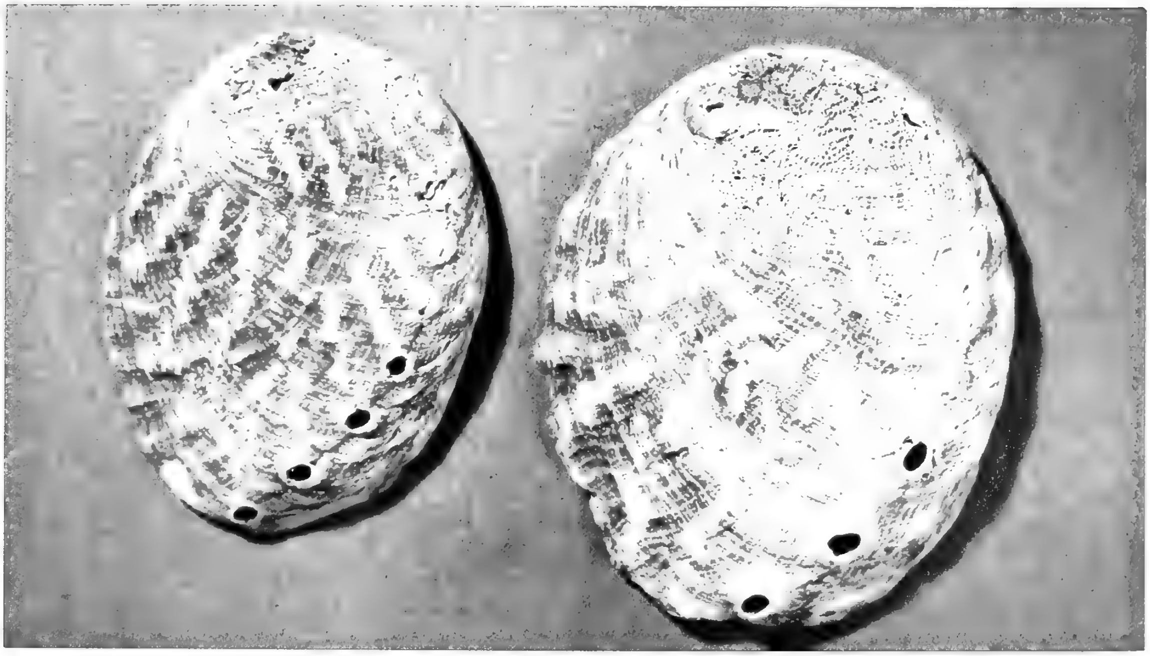

Figure *1* a 5 cm Figure *1* b

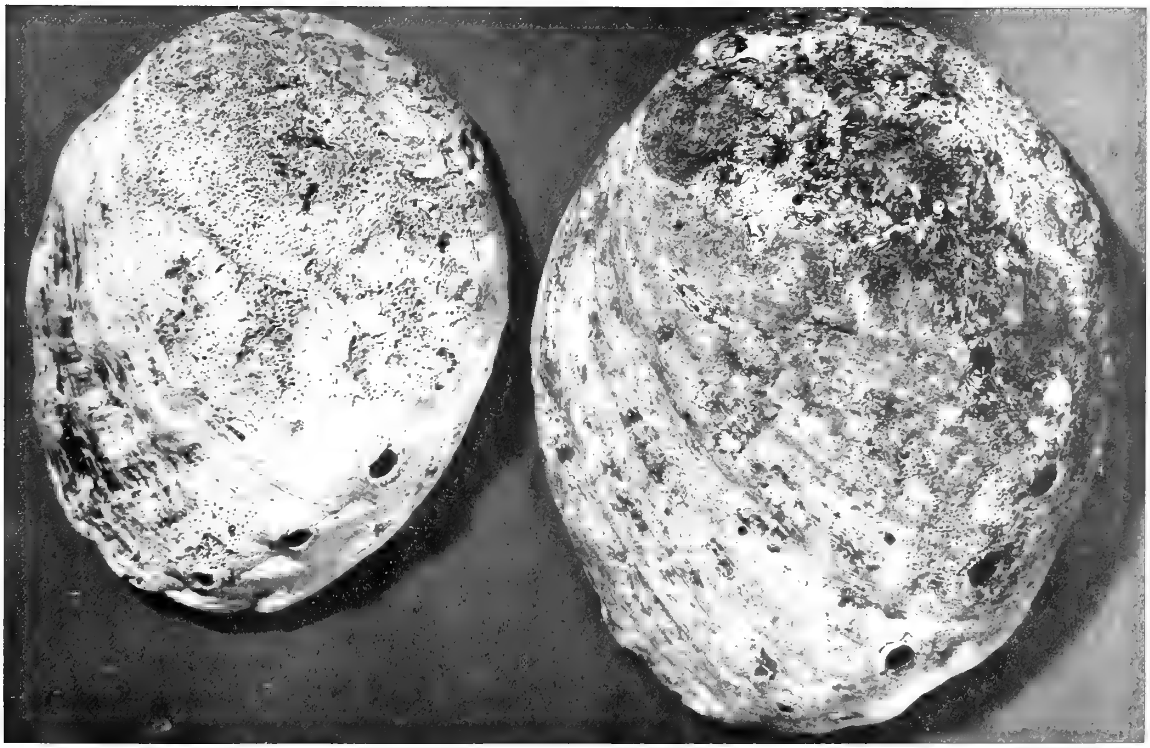

Figure *2* a 5 cm Figure *2* b

Gale, 1928 and *Mytilus californianus* Conrad, 1837 were found to be up to 5 times thicker than similar shells with less infection.

The piddock, *Penitella conradi,* belongs to a group of rock and shell borers of the family Pholadidae. This piddock bores into the shells of a number of marine mollusk species, including *Mytilus californianus, M. edulis* Linnaeus, 1758, most species of *Haliotis, Astraea undosa* Wood, 1828, and others.

In *Haliotis* species the piddock always enters the shell from the outside and bores at right angles to the shell surface (Cox, 1962). As it bores into the abalone shell and approaches the inner surface, a layer of nacre is secreted over the affected area by the mantle. As the piddock continues to bore, successive layers of nacre continue to coat the area. Eventually, a rounded bulge or blister pearl is formed on the inner surface of the shell (Oliver, 1916). Figures *3*a, *3*b show typical blister pearl formations on the inner surface of shells of *H. rufescens.* In Figure *3*a, the dark ring at the bottom of the shell was caused by one *Penitella conradi* individual that bored completely through the shell while the abalone was living. In this instance, *P. conradi* may have been the cause of death. Complete penetration was found in only 3% of the shells examined in this study. All other infections by *P. conradi* appeared as those in Figure *3*b.

Abalone shells are occasionally hosts to a third group of shell borers, the polychaetous annelids of the family Polydoridae. The polydorid burrows are distinguished from those of the boring sponge and the boring piddock by the characteristic ○○-shaped opening to the burrow. Polydorid burrows occur in only 12% of the shells discussed in this paper. Figures *4*a, *4*b, and *4*c show polydorid burrows exposed on shells of *Haliotis cracherodii.* Notice that the polydorid burrows have also begun in the area of the protoconch (Figure *4*a) and have subsequently spread to other areas of the shell (Figures *4*b, *4*c).

MATERIALS AND METHODS

A total of 90 shells of *Haliotis rufescens* and 165 of *H. cracherodii* were used in this study. Five parameters of each shell were measured: maximum diameter (anteroposterior axis), minimum diameter (lateral axis), shell height (dorso-ventral axis), number of borings by *Penitella conradi,* and percentage of surface area of each shell infected by *Clione celata californiana.* The polydorid polychaete activity was not included because of the low frequency of occurrence.

The shell dimensions were measured with a device consisting of two flat parallel boards mounted vertically on a surface calibrated in millimeters. One of the boards remained stationary, while the other could slide freely across the calibrated surface.

The borings of *Penitella conradi* were counted by examination of the outer surface of the shell and the conspicuous blister pearls on the inner surface The percentage of the surface area of each shell infected by *Cliona celata californiana* was determined by placing a 1.25 mm mesh grid over the shell surface. By counting the squares over the entire shell and the squares over the infected area only, dividing the latter number by the former and multiplying the result by 100, the percentage of infected area was obtained. A re-examination of these procedures revealed an error of less than 5%.

RESULTS AND DISCUSSION

Commensalism is a very common occurrence in the marine environment but is seldom studied in relation to phenomena such as growth and aging. The age-dating of abalones by shell characteristics has long been a problem confronting malacologists and conchologists. The growth rate of abalones has been found to be primarily a function of their distribution. Throughout the geographical range of *Haliotis rufescens,* for example, there are what are known as "fast-growing" and "slow-growing" areas (pers. comm. by Ebert). This means that the ages of two comparably sized shells from two different areas are not necessarily the same.

An additional complicating factor involved with age-dating abalones is the cessation of growth during gonadal maturation. The resumption of growth activity after spawning is then directed at building either shell increment or body mass, but not simultaneously. The order and extent of these activities are primarily on an individual basis (pers. comm. by Montgomery).

Sakai (1960) described growth rings corresponding to annual gonad maturation in *Haliotis discus hannai* Ino, 1952. However, the first spawning season of the young abalone and the growth increments established before that time varied with local conditions.

The percentages of occurrence of *Penitella conradi* and *Cliona celata californiana* on shells of *Haliotis rufescens* and *H. cracherodii* are listed in Table 1. These data indicate a nonpreference of *C. celata californiana* to either *H. rufescens* or *H. cracherodii,* and a significant preference of *P. conradi* for shells of *H. rufescens.*

Table 1

FREQUENCY OF COMMENSALS

Commensal	Frequency of Occurrence on *Haliotis rufescens*	*Haliotis cracherodii*
Cliona celata californiana	81%	79%
At least 50% of shell surface infected by *Cliona celata californiana*	32%	20%
Penitella conradi	42%	25%
Polydorid polychaetes	11%	12%

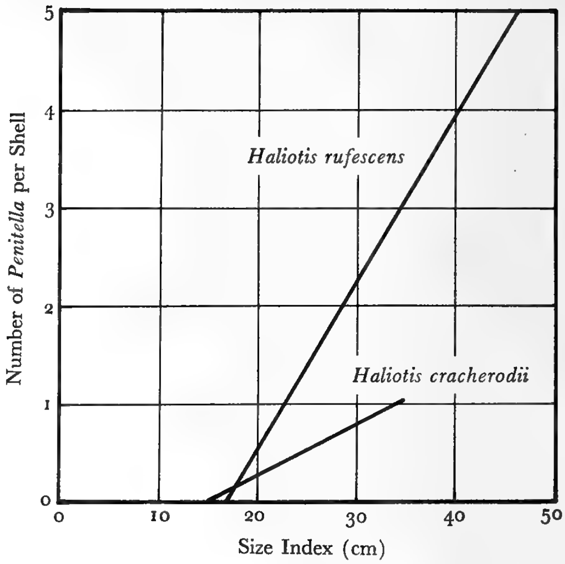

Figure 5

Regression lines of numbers of *Penitella conradi* against the size index of *Haliotis rufescens* and *Haliotis cracherodii*

Infection by *Penitella conradi*

Meredith (1968) reported *Penitella conradi* found in the lower 2 feet of a 7 foot intertidal mussel bed. Since *P. conradi* was not found in the upper 5 feet of the mussel bed, the upper limit to the vertical distribution of *P. conradi* must be in the lower intertidal zone. The vertical distribution of *Haliotis cracherodii* extends well above the lower intertidal zone. Therefore, individuals above the lower intertidal zone should be free from attack by *P. conradi*. This observation was confirmed by field investigations at Año Nuevo Island, Pigeon Point (San Mateo County) and Point Pinos (Monterey County). The frequency data, therefore, should show a significant preference of *P. conradi* for *H. rufescens,* a sublittoral species.

Figure 5 is a comparison of the mean infection rates of *Penitella conradi* with shell size of *Haliotis rufescens* and *H. cracherodii*. The size index, derived from the sum of the maximum diameter, the minimum diameter, and the height for each shell, was found by far the best criterion on which a number of shells of either species of abalone could be sorted on a scale indicative of successive ages.

Individuals of both *Haliotis cracherodii* and *H. rufescens* smaller than size index 15 had no signs of attack by *Penitella conradi*. Beyond this size, the regression of the number of *P. conradi* per shell increased linearly with increasing shell size index. The 95% confidence limits established on the regression analysis of these data indicated a significant difference existed between the regression lines of the two species of abalones. The difference was attributed to the lack of *P. conradi* on individuals of *H. cracherodii* from above the lower intertidal zone.

Infection by *Cliona celata californiana*

The regressions of the shell surface areas infected by *Cliona celata californiana* are shown in Figure 6 as functions of shell size index of *Haliotis rufescens* and *H. cracherodii*. Again, no infection was evident below size index 15. In either case of infection by *C. celata californiana,* the regression of infected shell area was a logarithmic progression with the abalone shell size index. This relationship indicated that the infected area was the result of the initial attachment and subsequent proliferation of a

Plate Explanation

Figure 3: Infection by *Penitella conradi* on *Haliotis rufescens*. A black ring marks the shell (Figure 3a) where *P. conradi* had bored through the nacreous shell layer of the living abalone, a variation from the more common blister pearl (Figure 3b)

Figure 4: Successive ages of *Haliotis cracherodii* (Figures 4a, 4b, 4c, respectively) show burrows of polydorid polychaetes centered around the protoconch area

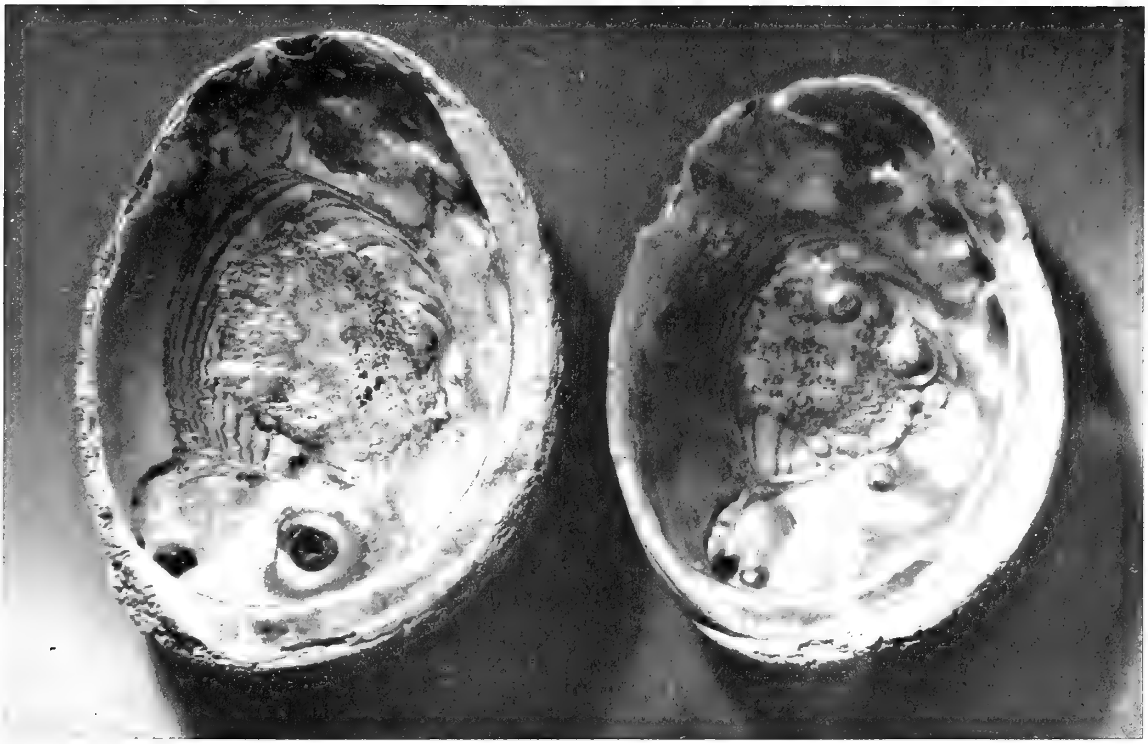

Figure 3 a

5 cm

Figure 3 b

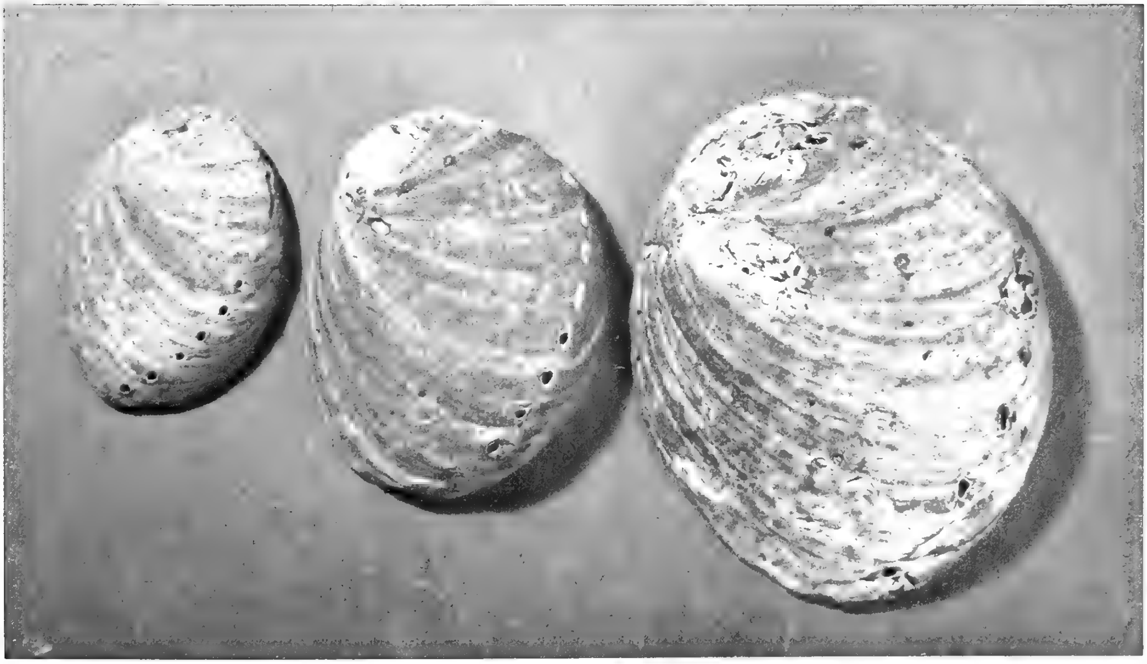

Figure 4 a

5 cm

Figure 4 b

single individual rather than a number of attacks by different individuals, as Figure 5 had indicated. Figure 5 is the result of simple linear regression analyses which required no data transformations to logarithms, probits, logits, etc. Since both *C. celata californiana* and abalones grow in size over a period of time, the percentage of the shell area depends upon which member of the commensal relationship grows more rapidly. While the abalones are successively adding shell increments, the percentage of shell area infected with *C. celata californiana* will decrease or at least increase more slowly. But when the abalone shell growth increments decrease or cease, due to senescence or a number of other factors, the percentage of the shell area infected by *C. celata californiana* increases more rapidly. Therefore, *H. cracherodii,* with a smaller maximum size than *H. rufescens,* also had a more rapid rate of infection than *H. rufescens.*

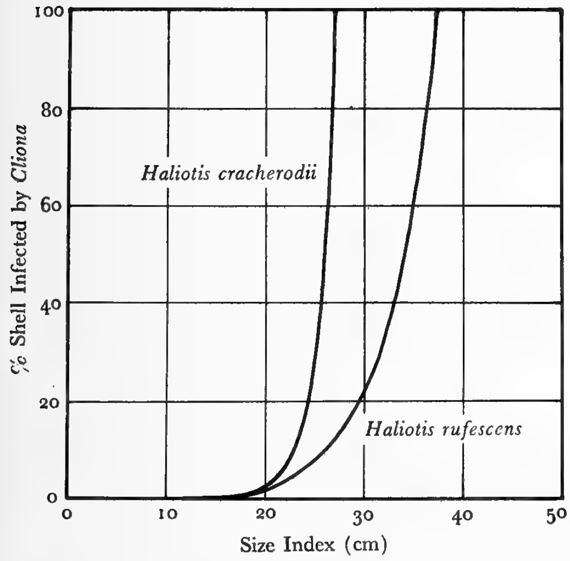

Figure 6

Regression lines of % shell infection by *Cliona celata californiana* against the size index of *Haliotis rufescens* and *Haliotis cracherodii*

CONCLUSIONS

Direct, positive correlations have been shown to exist between shell size of *Haliotis rufescens* and *H. cracherodii* and the rate of infection of these shells by the commensals, *Cliona celata californiana* and *Penitella conradi.* The means by which shell sizes were compared, the shell size index, was also a good estimate of relative ages of haliotids. Therefore, a correlation of commensal activity with the size index was also a good correlation with relative age.

The nature of the correlations with shell size index differed with both species of shell commensals. Infection rates of *Penitella conradi* were linear progressions with shell size index; whereas, corresponding rates of infection by *Cliona celata californiana* were logarithmic progressions.

The rate of infection differed with both *Haliotis* species. *Penitella conradi* was more commonly found on shells of *H. rufescens* than on shells of *H. cracherodii* due to the higher intertidal range of the latter, which conflicts with an upper limit of the lower intertidal for *P. conradi.* The range of *H. rufescens,* which is primarily sublittoral, better corresponds with the vertical range of *P. conradi.*

The results of this study have several possibilities for practical applications. For example, the vitality of haliotid populations of different areas may be measured in relation to each other not only by the size and shape of their shells, but also by the activities of their shell commensals. Also, the characteristics of the commensal relationships studied here may be applicable to other mollusks and to other similar symbiotic relationships.

ACKNOWLEDGMENTS

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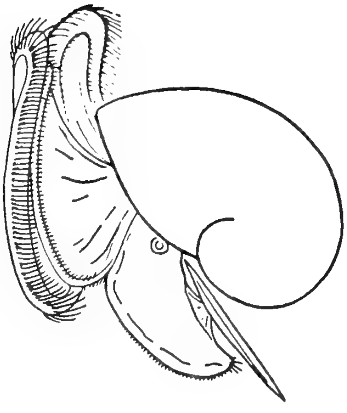

An Ecological Study of Two Sympatric Species of *Fasciolaria*

(Mollusca : Gastropoda)

in Alligator Harbor, Florida[1,2]

BY

FRED ETHAN WELLS, Jr.

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

(1 Plate; 9 Text figures)

INTRODUCTION

Two species of tulip shells, *Fasciolaria hunteria* (Perry, 1811), the banded tulip, and *F. tulipa* Linnaeus, 1758, the true tulip, occur along the southeastern coast of the United States. These species are members of the neogastropod family Fasciolariidae and are found from Beaufort, North Carolina, on the Atlantic coast southward to southern Florida. Their distribution then follows the Gulf of Mexico westward to Texas, where *F. distans* Lamarck, 1847, replaces *F. hunteria*. *Fasciolaria tulipa* ranges southward along the Mexican coast and is found throughout the Caribbean Sea. Both *F. hunteria* and *F. tulipa* are present locally in Alligator Harbor, Franklin County, Florida. Another member of the Fasciolariidae, the horse conch, *Pleuroploca gigantea* (Kiener, 1840) is present but is not included in the present study. Except for the taxonomic descriptions, little is known about either species. Until recently they were thought to be of no commercial importance, but in a report on prey selection H. Wells (1958) found *F. hunteria* to be a predator of the commercially important Virginia oyster, *Crassostrea virginica* (Gmelin, 1791). *Fasciolaria hunteria* prefers the drill *Urosalpinx cinerea* (Say, 1822) as a prey species over the Virginia oyster (H. Wells, *op. cit.*), and thus could be important in decreasing oyster predation by the drills. In a previous study of oyster predators in Alligator Harbor, Menzel & Nichy (1958) did not discuss *F. hunteria*.

The theoretical problems arising from a sympatric distribution of two closely related species make the biology of *Fasciolaria hunteria* and *F. tulipa* fertile ground for investigation. This study was undertaken to analyze the habitats, population structure, mating habits, predators, escape responses, and aspects of the anatomy of the two species in relation to the mechanisms that allow them to live sympatrically.

MATERIALS AND METHODS

Observations of *Fasciolaria hunteria* and *F. tulipa* were made both in the field and in the laboratory from January to April, 1969. Laboratory experiments were intended to supplement the field observations rather than substitute for them. Population studies were conducted along the docks of the old Florida State University marine laboratory and along the southern portion of the Bay Mouth Bar. All individuals found in these areas were measured, marked, and returned to the site of collection. Measurements of length and width of individuals less than 130 mm long were made with a steel caliper to the nearest 0.1 mm, while individuals over 130 mm long were measured with a wooden ruler to the nearest 1 mm. Marking was done initially in the manner described by Hathaway (1957). A file was used to scrape incrustations and the periostracum off the body whorl of the shell. Plastic model airplane paint, which dries in about 10 minutes, was used to num-

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[1] Presented to the Department of Biological Science, The Florida State University in partial fulfillment of the requirements for the degree of Master of Science. This research was supported by a Graduate Traineeship granted by the National Science Foundation.

[2] Present address: Department of Zoology, McGill University, Montreal, Canada

ber the shells, after which the animals were returned to the collection site. After it became apparent in both the field and in the laboratory that the paint would flake off certain individuals, subsequent markings were made by notching the lip of the shell with a file. This method of marking fails to maintain a differentiation of individuals but variations in the number and location of notches were used on different trips. The notch is permanent and can be identified on the old lip even after the shell has grown.

Physical data recorded on each collecting trip included date; collecting times; time and depth of low tide; salinity; temperatures of sand, water, and air; water and general atmospheric conditions. Salinities were determined by using the titration method described by Strickland & Parsons (1960). Because of the extreme difficulty of locating individuals in several feet of water, most collecting was done at low tide.

Salinities in the laboratory aquaria varied from 32.7 to 37.4 parts per thousand, and temperatures varied from 13.5° C to 21.0° C. Salinities encountered on collecting trips ranged from 27.8 to 33.8 ppt and temperatures from 8 °C to 15° C.

Sex ratios were determined by boiling the specimens and then removing them from the shells. In neogastropods sex can be easily determined by the presence or absence of the penis on the right side just behind the head. In some instances sexing was done on live individuals placed upside down in an aquarium. As the animal emerged to right itself, the presence or absence of the penis was readily observable. This method was of limited use because of the tendency of animals to remain upside down for several hours before attempting to right themselves. In one instance a specimen of *Fasciolaria hunteria* remained overturned for more than 12 hours before finally righting itself.

Radulae were prepared in a manner modified from the methods presented by Magelhaes (1948) and Mahoney (1966). After an animal was removed from the shell the proboscis was dissected out and placed in a concentrated aqueous solution of sodium hydroxide for several hours. The radula was then transferred to a fresh solution of sodium hydroxide to remove any remaining tissues, flattened between 2 slides, which were bound together, and allowed to dehydrate in 70% ethanol for 10 minutes. The radula was immersed in solutions of 5% oxalic acid and 1% potassium permanganate for 5 minutes each, then stained in Orange-G. The radula was then dehydrated completely, cleared in xylene and mounted in Euparal.

PHYSICAL DESCRIPTION OF ALLIGATOR HARBOR

Alligator Harbor on the northwest coast of Florida is bounded on the north by the mainland and on the south by Alligator Point, which has a continuous land connec-

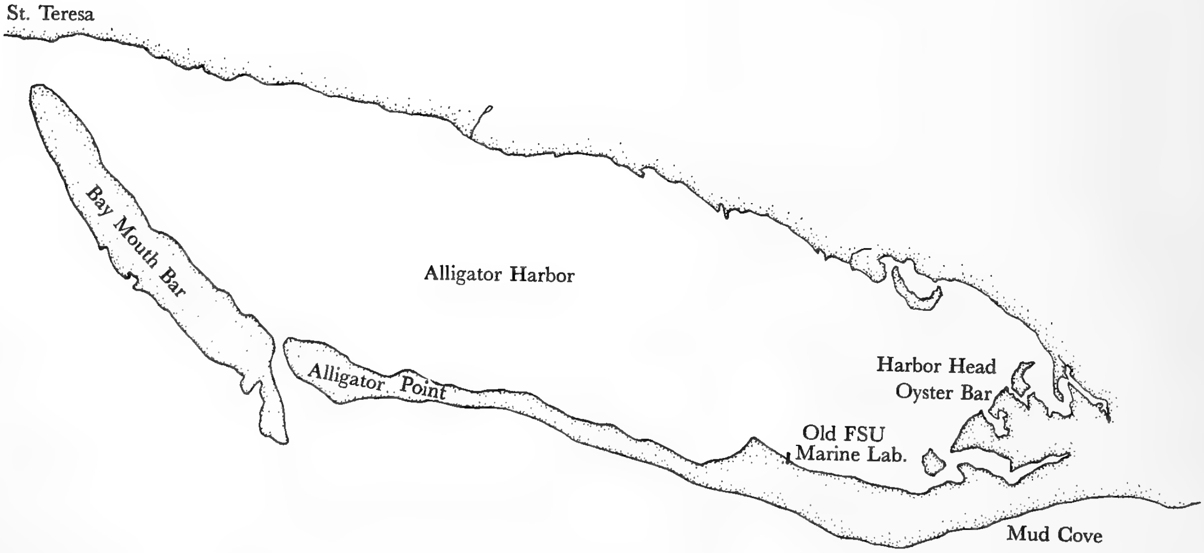

Figure 1

Map of Alligator Harbor

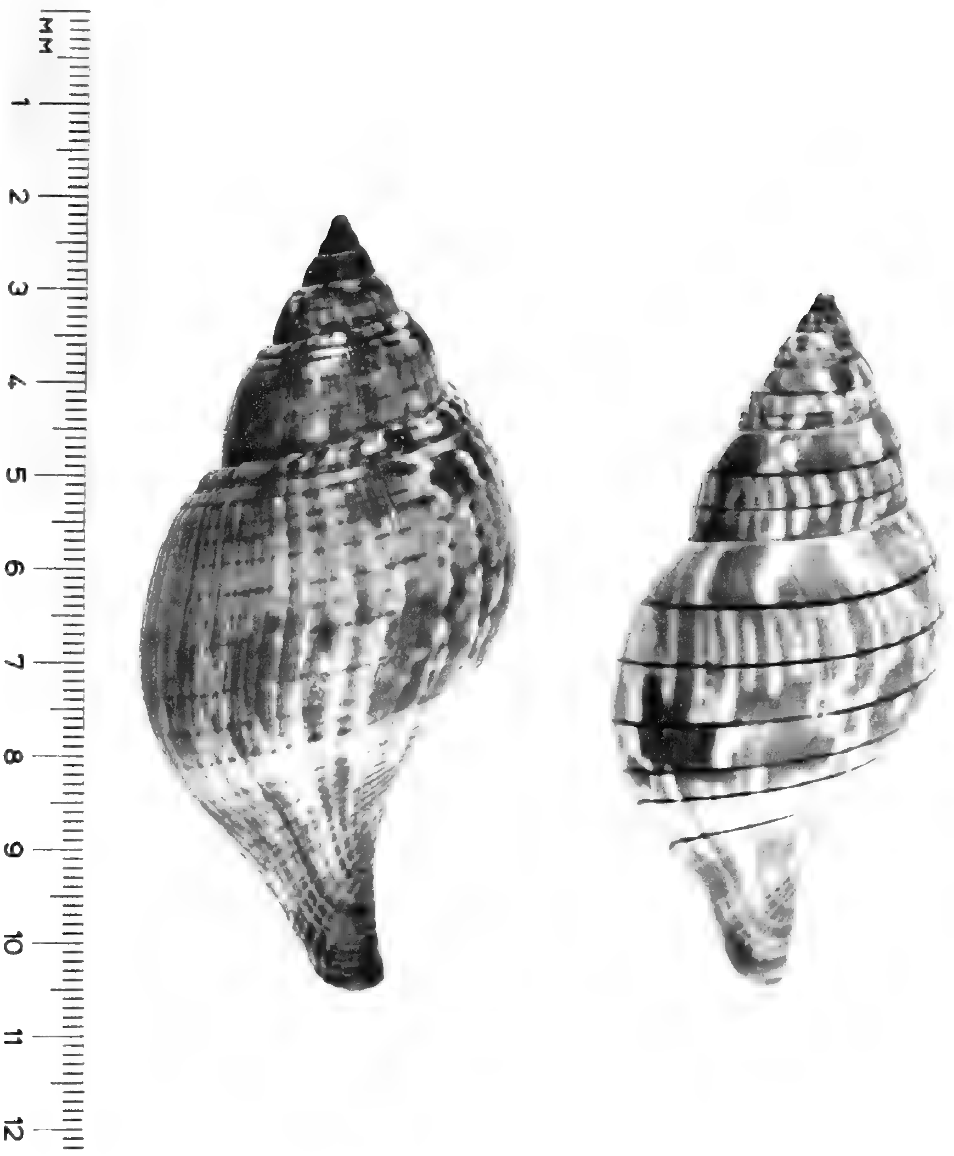
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Figure 2

Photograph of shells of *Fasciolaria hunteria* (right) and *Fasciolaria tulipa* (left). Scale nearest the shells is in inches

tion with the mainland at the east end of the harbor (Figure 1). The marine laboratory of the Florida State University was located at Alligator Harbor for many years, but has recently been moved 8 miles west to Turkey Point. Alligator Harbor is a neutral estuary 4 miles long and 1½ miles wide with no major rivers or streams entering the harbor to dilute the sea water (Olson, 1955). Salinities seldom vary by more than 3 ppt over the entire harbor surface, and normally range between 30 and 34 ppt. Although greater fluctuations are not uncommon, there are no known seasonal or annual variations in salinity. Many of the salinity variations that do occur are attributed to tidal mixing of harbor water with the adjacent Gulf water (Olsen, *op. cit.*).

Alligator Harbor is uniformly shallow with an average depth of 1.2 m and a maximum depth of 3 m at mean low water, except for one hole with a depth approaching 6 m. Although the normal tidal range is only 0.58 m, the vertical distance between high and low water levels may approach 2 m on some spring tides.

Despite its small size and the lack of significant freshwater inflows, Alligator Harbor offers several types of habitats. The harbor bottom is composed of sand or sandy mud. Salt marshes with localized oyster reefs occurring in the east end of the harbor are drained by two small tidal creeks and their tributaries. The oyster reefs are found primarily along the edges of the salt marshes and the mouths of the tidal creeks, and extend from slightly above mean low water to about ½ m above mean low water (Nichy 1957). Most of the oysters in Alligator Harbor are *Crassostrea virginica* with a mean length of 50 - 60 millimeters. Oysters are also found adjacent to the docks of the old Florida State University marine laboratory.

Alligator Harbor is bordered by sandy beaches interspersed with muddy areas. The harbor mouth is closed by Bay Mouth Bar, a typical sand bar, except for natural channels at St. Teresa and Alligator Point. Although Bay Mouth Bar is completely submerged at high tide, substantial portions largely overgrown with *Thalassia testudinum* and *Diplantheria wrightii* are uncovered at low tide. The bar supports a diversified fauna which includes at least 40 species of mollusks.

OBSERVATIONS

Shell Anatomy

General Shape: To conduct an ecological study of this type, one must be able to recognize the species being studied and become aware of traits that reflect adaptations to different niches. For this reason, a detailed analysis of the shells of *Fasciolaria hunteria* and *F. tulipa* was made. As can be seen in Figure *2*, [E] the shells of both *F. hunteria* and *F. tulipa* are fusiform with moderately long anterior siphonal canals. Both species are dextral and remarkably similar in shape. Shells of young individuals of the two species resemble each other so closely that they cannot be distinguished by any characteristic other than coloration.

There is a marked difference in the maximum size of *Fasciolaria hunteria* and *F. tulipa*, but growth rates are not known for either species. A sample of 206 individuals of *F. hunteria* had an average length of 59.3 mm, with the largest being 85.5 mm (Table 1). Abbott (1954) reported the length of *F. hunteria* as 50 to 100 mm. Wells (1958) used specimens ranging in size from 47 to 103 mm, with most individuals measuring between 75 and 90 mm in length. The maximum lengths reported by Abbott and

Table 1

Comparison of Shell Dimensions of *Fasciolaria hunteria* and *Fasciolaria tulipa*

Characteristic	*Fasciolaria hunteria*	*Fasciolaria tulipa*
Shell Length:		
Number of specimens	206	39
Maximum length (mm)	85.5	148
Minimum length (mm)	34.8	107.4
Mean length (mm)	59.3	128
Shell Width:		
Number of specimens	71	39
Maximum width	40.0	72.8
Minimum width	22.8	50.2
Mean width	29.3	59.6
Length to Width Ratio		
Number of specimens	71	39
Maximum L/W ratio	2.16	2.23
Minimum L/W ratio	1.78	1.91
Mean L/W ratio	1.94	2.07
Operculum Dimensions:		
Number of specimens	38	11
Mean operculum length	24.3	61.7
Mean operculum width	11.4	27.9
Mean operculum length to shell length ratio	0.45	0.44

[E] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Wells are much greater than the maximum found in the local population. Johnson (1919) recorded the length of *F. hunteria* as 65 to 85 mm, which is similar to the lengths obtained for the Alligator Harbor population. Thirty-nine adult individuals of *F. tulipa* averaged 128.4 mm in length, with the largest specimen measuring 162 mm. This exceeds the length of 75 to 125 mm given by Abbott (*op. cit.*), but is much smaller than the maximum of 200 mm reported by Johnson (*op. cit.*). As could be expected, the shells differ in thickness. Shells of adult *F. hunteria* average 0.3 mm, while the larger *F. tulipa* shells average 0.5 mm in thickness at the lip. Immature specimens of *F. tulipa* have the same thickness as shells of *F. hunteria* of the same size.

Sculpturing: Growth lines are not easily distinguished, especially in younger individuals, and both species are completely lacking in shell spines. *Fasciolaria hunteria* has 4 to 8 primary black lines on the body whorl that are secreted by correspondingly lined tissues on the underlying mantle. This is more variable than was indicated by either Johnson (1919) or Hollister (1957). The latter reported that there are 6 primary spiral lines, while the former reported 5 or 6, which is in accord with the findings of the present study, accounting for 93% of the total number of individuals. Although the lines are equidistant in most cases, some lines on a few specimens are twice as far apart as the adjacent pairs of lines, indicating that one line was not formed. While only 2 primary lines remain visible in the early whorls, adults have the same number of primary lines as they had as juveniles. Many shells have secondary lines that are not continuous to the aperture and are not as fully formed as the primary lines. Adult individuals with more primary lines have a greater average length than individuals with fewer primary lines (Figure 3), which suggests that they were initially larger. The number of lines present in a juvenile individual cannot be used to accurately predict the adult size of the individual because of the significant overlap in the lengths of individuals with varying numbers of lines.

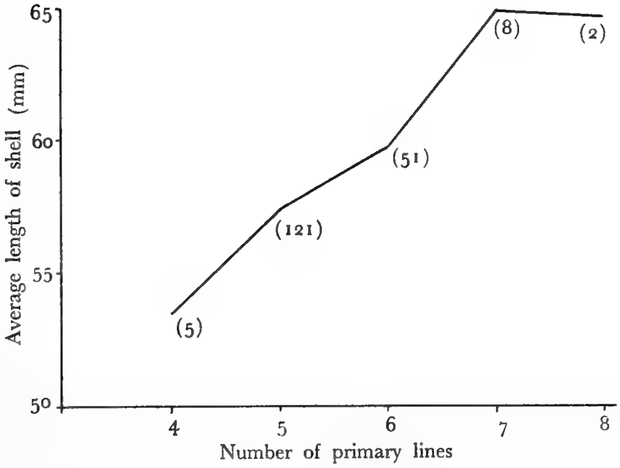

Figure 3

Graph of length of shell vs. number of primary lines in *Fasciolaria hunteria*. Numbers in parentheses indicate number of individuals

Shells of adult *Fasciolaria tulipa* have 25 to 39 spiral black lines which, unlike those of *F. hunteria*, are interrupted at frequent intervals. The first several lines near the body suture are grooved, but the remaining lines are not. Lack of shells with intermediate numbers of lines and the poor condition of many due to encrustations prevented any correlation between the number of lines and the length of shell being made in *F. tulipa*. The lines of adult *F. tulipa* extend on small teeth past the lip margin, giving the lip a notched appearance (Table 2).

Five to 8 ribs are found on the siphonal canal of *Fasciolaria hunteria* just below the primary lines; 15 to 20 ribs are present over the siphonal canal of *F. tulipa*, and there are about 75 small ribs on the inner surface of the lip of adult individuals of both species. A ridge on the body whorl just under the shoulder of *F. hunteria* forms one side of a groove containing the anal canal (Hollister, 1957).

Table 2

Comparison of Shells of *Fasciolaria hunteria* and *Fasciolaria tulipa* from Alligator Harbor

Description	*Fasciolaria hunteria*	*Fasciolaria tulipa*
Thickness of shell (mm)	0.3	0.5
Primary lines	4-8	25-39
Character of lines	Solid	Interrupted
Lines extend on ridges	No	Yes
Siphonal ribs	5-8	15-20
Ridge for anal canal	Present	Absent
First lines grooved	No	Yes
Primary color	Gray	Brown

Coloration: Differences in the color of the shells of *Fasciolaria hunteria* and *F. tulipa* are readily noticed. The background color of both the lip and the whorl is whitish

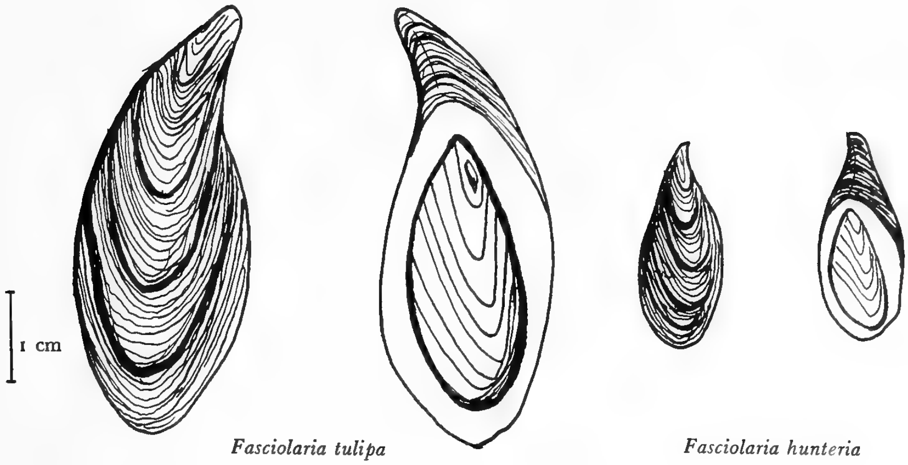

Figure 4

Comparison of the opercula of *Fasciolaria hunteria* and *Fasciolaria tulipa*

in both species. The presence of black spiral lines has already been mentioned. Shells of *F. hunteria* are blotched with gray, while those of *F. tulipa* are splotched with brown, and are often covered with encrustations. Abbott (1954) mentioned a rare albino form of *F. hunteria* and a mahogany variety of *F. tulipa,* but neither was encountered in this study.

Periostracum and Operculum: The brown periostracum of both species is so thin that its presence is not easily determined, especially in *Fasciolaria tulipa* when the shell is encrusted. The uncalcified operculum is secreted by and borne on the dorsal surface of the metapodium (Hyman, 1968). The opercula are pointed anteriorly and rounded posteriorly (Figure 4), with different patterns on the dorsal and ventral surface of each operculum. The ventral side of the operculum has a large muscle scar where it is attached to the foot, whereas the margin of the operculum remains free and unattached to the foot. Growth lines are readily seen on the modified concentric pattern of the operculum. The operculum serves a protective function by completely closing the aperture when the animal retreats into its shell. The operculum can also be used as a weapon. Hollister (1957) reported that it functions as a claw, but did not describe how this is done. The present author found that the animal often extends itself completely when being held in the hand. A rapid contraction of the foot can bring the pointed anterior end of the operculum into sharp contact with the unsuspecting hand, causing the shell to be dropped. Randall (1964) noticed a similar defense mechanism in the queen conch, *Strombus gigas* Linnaeus, 1758.

Radulae

Radulae vary widely among the various groups of prosobranchs, and are consequently of great taxonomic importance. Hollister (1954) demonstrated a direct correla-

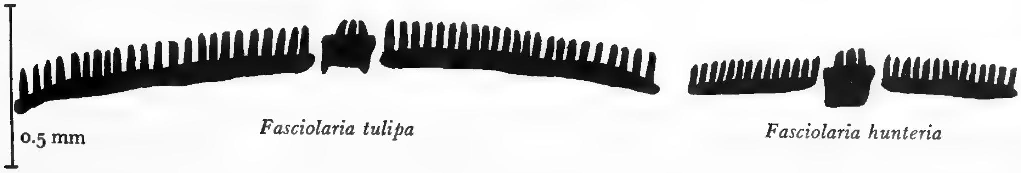

Figure 5

Radular teeth of *Fasciolaria*

tion between the number of cusps on the lateral teeth of the radula and the size of the shell in *Fasciolaria tulipa* and *F. gigantea* (=*Pleuroploca gigantea*). He also showed that at any particular size, *F. tulipa* has a larger number of cusps on the lateral teeth. The number of these cusps also increases with the length of the shell in *Busycon carica* Gmelin, 1791, and *B. contrarium* Conrad, 1867, but the increase is not as great as in *Fasciolaria* (Hollister, 1954). Of the two species of *Busycon*, specimens of the same size have the same number of cusps on the lateral teeth.

The present author investigated the radulae of *Fasciolaria hunteria* and *F. tulipa* in order to better understand the feeding habits of the two species. Like most neogastropods, the carnivorous *Fasciolaria* have a reduced number of radular teeth, with only a tricuspid central tooth flanked on each side by a lateral tooth (Figure 5). There are no marginal teeth. Maes (1966) reported sexual dimorphism in the central tooth of *Nassa*. The 3 cusps of the central tooth of *Nassa* are of the same size in the female, but the central cusp is elongated in the male and dominates the tooth. No dimorphism of this type was found in either *F. hunteria* or *F. tulipa*.

The lateral teeth of *Fasciolaria hunteria* have between 8 and 17 cusps; those of *F. tulipa* have 15 to 34 cusps in the adult. The radular formula of a typical adult *F. hunteria* is 0 · 16/1 · 3/1 · 16/1 · 0 and that of an adult *F. tulipa* is 0 · 30/1 · 3/1 · 30/1 · 0. The number of lateral cusps increases directly with the length of the shell in a straight line relation in each species (Figure 6), not a curved one as Hollister (1954) indicated on his graph for *F. tulipa*. Individuals 120 mm long have about twice as many cusps on the lateral teeth as those individuals 60 mm long. There is some variation in the number of cusps found in individuals of a given size, as is indicated on Figure 5. Maes (1967) reported a similar phenomenon in *Pleuroploca*, and found that individuals with thicker shells have more cusps than individuals of equal size with thinner shells. Thus, at a given size older individuals have more cusps on the lateral teeth than the younger individuals (Mayes, *op. cit.*).

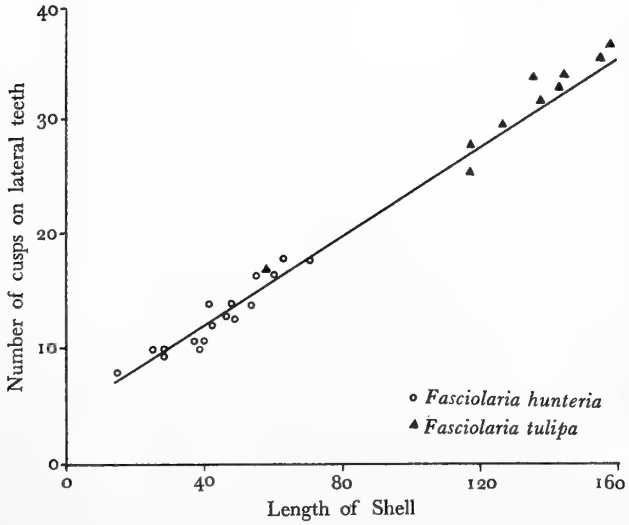

Figure 6

Graph of length of shell vs. number of cusps on the lateral teeth

The total number of teeth on a radula of an adult *Fasciolaria hunteria* varies from 225 to 265, while the larger *F. tulipa* has 300 to 350 teeth. This is similar to the 270 - 450 radular teeth reported for 3 species of *Busycon* (Magalhaes, 1948). *Busycon* is a large carnivorous gastropod related to the Fasciolariidae, so the close parallel between the number of teeth in *Busycon* and *Fasciolaria* is not unexpected.

A bifurcation in the lateral cusp of a *Fasciolaria hunteria* was found. A similar abnormality was reported by Magalhaes (1948) in one of the *Busycon* radulae studied. In most cases the number of cusps on the lateral teeth opposite a given central tooth are equal, but in some instances one of the lateral teeth has one more cusp than its opposite member.

Because it has been difficult to study a radula in a living animal, conclusions on radular growth must be drawn from preserved radulae. The teeth are formed in a radular sac and move forward to replace the old teeth as they are worn away. The radula also increases in both length and width as the animal grows. The medial cusp of the lateral tooth is the largest (Figure 5), and the most lateral cusp is the smallest of the cusps on the tooth. In no case has an intermediately placed cusp been larger than the medial cusp. Maes (1967) found that the additional cusps of the lateral teeth in *Pleuroploca* are are added at the margin. As the radula moves forward the new cusps that are formed become progressively larger until the cusp has reached full size and new cusps have been formed along the margin of the radula.

Distribution of *Fasciolaria* in Alligator Harbor

As can be seen in Figure 7, *Fasciolaria hunteria* occurs in small groups along the margins of Alligator Harbor, from Bay Mouth Bar in the west to Harbor Head Oyster Bar in the east in association with the oyster bars. As a result, the local distribution of *F. hunteria* is spotty (Figure 7). There are many areas in the harbor where *F. hunteria* does not occur since, with the exception of Bay Mouth Bar, this species is found in Alligator Harbor only in areas immediately adjacent to oyster reefs, and has not been found on the sandy patches between oyster clumps. Most of the oysters in Alligator Harbor are found on piers, concrete walls, or other artificial substrata along the margins of the harbor, and at the reef at the east end of the harbor. Since the southern portion of the harbor has been most modified by man, most of the habitats suitable for *F. hunteria* occur there. Of 50 individuals collected in a survey of the piers of the old marine laboratory, 46% were on oysters, 42% were within 30 cm of the nearest oyster, and only 12% were more than 30 cm from the nearest oyster. The maximum distance separating *F. hunteria* from the adjacent oysters was 180 cm. Many of the oyster reefs in Alligator Harbor are found at the harbor head, but it is interesting to note that *F. hunteria* is rare in that area despite its affinity for oysters. A possible explanation is that *Urosalpinx perrugata* Conrad, 1846, a principal food of *F. hunteria* on oyster reefs, is lacking in the harbor head area, but it is also possible that the factor preventing *Urosalpinx* from getting a foothold there also keeps *F. hunteria* out.

Living specimens of *Fasciolaria tulipa* in Alligator Harbor were found only on Bay Mouth Bar, except for 2 individuals found in a grass flat on the north shore. Dead shells were found near the docks of the old marine laboratory, near the Harbor Head Oyster Bar, and near the piers along the southern margin of the harbor, but extensive investigations of these areas have not revealed a single living individual, so it appears likely that the shells were introduced into these areas after the animals died. *Fasciolaria tulipa* is widely distributed in the subtidal areas surrounding Bay Mouth Bar and the waters off St. Teresa, as was evidenced in collections made on snorkeling trips to those areas. *Fasciolaria tulipa* is found in association with beds of *Diplantheria* and *Thalassia*. Neither plant species forms beds in the harbor itself.

Bay Mouth Bar is the only area of Alligator Harbor where *Fasciolaria hunteria* and *F. tulipa* are truly sympatric. About 80% of the *F. hunteria* collected on the bar came from the sandy areas of the southern end. *Fasciolaria tulipa* is distributed throughout the grass beds that cover most of the bar, but does not occur in the sandy areas. *Fasciolaria tulipa* and *F. hunteria* have been found as close as 5 feet apart on the grass flats.

Population Characteristics

Andrewartha & Birch (1954) described 3 conditions necessary for successful mark and recapture experiments. The marked individuals must be distributed homogeneously among the unmarked individuals of the population such that the marked specimens are not clumped together in a small portion of the study area. The marked individuals must have the same chance of being recaptured as the unmarked individuals, and there must be no movement of the population to or from the study area. Individuals of *Fasciolaria hunteria* found at the old marine laboratory and on Bay Mouth Bar were marked with notches on the lip of the shell. Recaptures were not attempted until at least one week after marking to allow the marked individuals to distribute themselves throughout the population. Since there was no way to observe the marking until the snail was in the collector's hand, marked

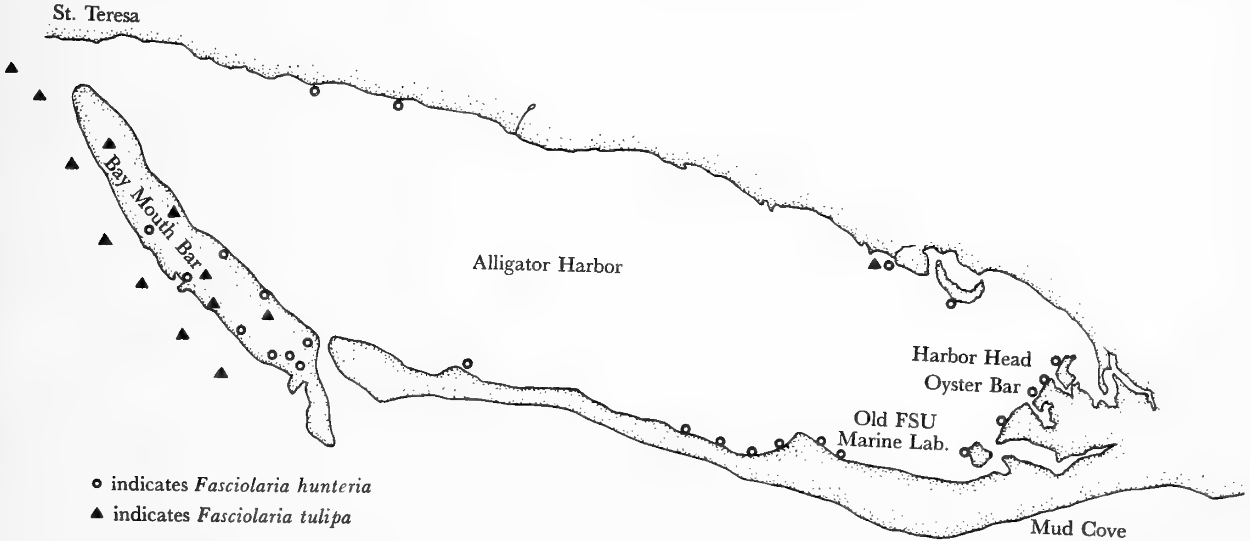

Figure 7

Distribution of *Fasciolaria* in Alligator Harbor animals had the same chance of being collected as the unmarked ones. Because no marked individuals were found in areas other than the one in which releases were made, it appears that *F. hunteria* limits its movement to the area immediately adjacent to the oyster reef on which it lives. Most individuals of *F. hunteria* living along a concrete wall 600 m from the marine laboratory were removed in July, 1968. Despite the relative proximity of the marine laboratory population, no repopulation of the wall had occurred by April 1969. The tendency of individuals to remain in a small home area is not due to an inability of *F. hunteria* to traverse the sandy areas between oyster outcrops because this species has been observed to move forward at a rate of up to 10 cm/minute on sand by means of retrograde monotaxic muscular waves on the sole of the foot.

If P is the population size in number of individuals, M the number of marked individuals, N the total number of individuals subsequently recaptured and R the number of marked individuals recovered, then $P = NM/R$ (Andrewartha & Birch, 1954). Using this formula for obtaining population size, the marine laboratory population of *F. hunteria* was estimated at 132 individuals, and the Bay Mouth Bar population at 720 individuals. The estimates were based on a small number of returns, and more work would have to be done to establish a better estimate. The lack of recaptures is a problem often encountered in mark and recapture experiments.

The relatively small number of *Fasciolaria tulipa* present on Bay Mouth Bar prevented a mark and recapture experiment on this species. The population density of *F. tulipa* was determined in the manner described by Nichy (1956). The investigator walked in a straight line and recorded the number of individuals found within reach of either arm. Thus, a corridor was made along the bar, and the number of individuals encountered divided by the length of the corridor gave an estimate of the density of the population. A small error was introduced by the inability of the investigator to locate buried specimens. The density of the *F. tulipa* population on the bar in early March was estimated at 0.0011 individuals per square meter, or one *F. tulipa* for every 917 m² on the bar surface. The population on the bar was just beginning to increase from the winter low when the estimate was made. According to the graph of the relative population sizes of snails on Bay Mouth Bar over the year presented by Paine (1963), the density of the *F. tulipa* population would be expected to increase to 3 or 4 times the density in March by early summer.

The age distribution of the members of a population is an important characteristic influencing both natality and mortality (Odum, 1953). A rapidly expanding population has a larger proportion of younger individuals than an older one. Figure 8 is a graph of the length vs. frequency of individuals from the populations on Bay Mouth Bar and at the old marine laboratory. There are very few small individuals of either *Fasciolaria hunteria* or *F. tulipa*, indicating that the populations are static. The smaller specimens are found in protected areas such as old shells, or between the valves of the pen shell, *Atrina*. The young often feed on the remains of dead *Atrina* and the tidbits left on the inside of the valves of the bay scallop *Aequipecten irradians* (Lamarck, 1847) after a predator has eaten most of the bivalve and abandoned the prey.

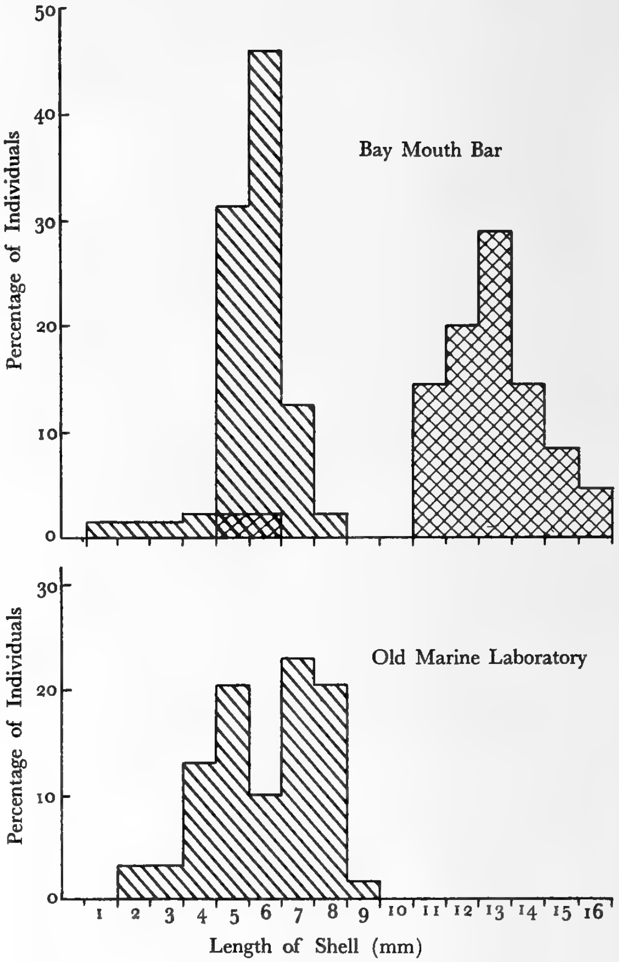

Figure 8

Graph of length of shell vs. percentage of individuals in population Graphs at left are for *Fasciolaria hunteria;* graph at upper right is for *Fasciolaria tulipa*

In his paper on trophic relations on Bay Mouth Bar, Paine (1963) presented graphs of the frequency of several size classes of both *Fasciolaria hunteria* and *F. tulipa,* but the graphs are not as detailed as Figure 8. The general outlines of PAINE's graphs indicate that the *Fasciolaria* populations have remained fairly stable since PAINE studied the bar in 1959 and 1960. A major difference in the 2 sets of graphs is the lack of extremely large individuals of both species on the bar now compared to the number present in 1960. Although PAINE studied the bar over an entire year, the differences in the graphs are not due to differences in the time of year at which they were made. The lack of large individuals may be due to the activity of collectors, who generally select the largest specimens available. The population of *F. hunteria* at the marine laboratory is similar in structure to the Bay Mouth Bar population, but there is a somewhat larger proportion of extremely large individuals and of very small ones.

Sexual Characteristics

Mating Habits: I observed the mating position of both species of *Fasciolaria* on numerous occasions. The female lies passively in the sand with her body in the normal upright posititon (Figure 9). The male is upside down with the axis of his shell almost at right angles to that of the female. Using his foot as a lever, the male presses his shell into close contact with the female in such a way that there is a slight overlap of the shells in the outer lip area. In this position the siphonal canals are oriented in almost the same direction except that the siphonal canal of the male is inverted. With the 2 individuals in this position the male is able to insert his penis into the vagina of the female.

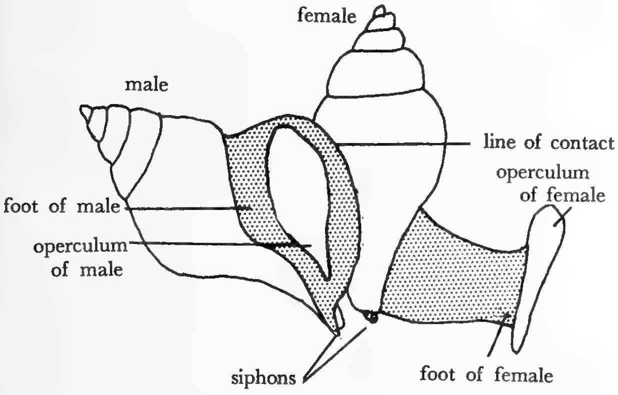

Figure 9

Mating position of *Fasciolaria,* viewed from above

The mating position is maintained for periods of up to 125 minutes, during which neither snail moves. HATHAWAY (1957) reported that *Melongena corona* GMELIN, 1791, which has a similar mating stance, remained in copulation for 90 to 100 minutes. A mating pair of *Fasciolaria hunteria* was placed in a glass fingerbowl to facilitate study. The transfer had little effect on either individual, and the mating position was maintained. After 50 minutes the female extended her foot in preparation for crawling and became generally active at the termination of mating. Separation was rapid and complete, after which the female crawled away while the male regained his normal crawling position.

A total of 25 matings of *Fasciolaria hunteria* and 4 of *F. tulipa* was observed in the field and in the laboratory during the study period. Individuals of both sexes of both species mated up to 3 times during a single week, indicating that individuals may mate more than once in a season. Animals were observed mating in the field during both day and night hours from the end of January until observations were terminated at the end of March. Some of the pairs were observed mating subtidally, but the majority was uncovered by the receding tides. Although both species normally burrow into the substratum when the falling tides expose them, those uncovered during copulation do not terminate their mating to seek refuge in the sand.

Sexual Dimorphism of the Shell: During this study a total of 151 specimens of *Fasciolaria hunteria* was sexed and measured to determine the sex ratio and to investigate the possibility of sexual dimorphism in shell length. Females of *F. hunteria* averaged 60.4 mm long, while males measured 57.6 mm, but despite the consistency of the difference in the various samples, statistical tests revealed no significant difference in the average lengths of the male and female shells.

Males of *Fasciolaria tulipa* averaged 124.0 mm in length, while the females had a mean length of 145.3 mm. This difference is statistically significant ($p < 0.001$), revealing a sexual dimorphism in the length of the shells of *F. tulipa.*

Sex Ratios: Of the 151 specimens of *Fasciolaria hunteria* sexed, 47% were females and 53% were males. Sex ratios of the samples therefore approximated the 1:1 ratio, except for one sample at the old marine laboratory that had 1 female and 8 males. Samples taken at the same location before and after the aberrant sample all approximated the expected proportion of half male and half female. The sex ratio for 18 individuals of *F. tulipa* collected during the study was exactly 1:1.

Activity Rhythms

Fasciolaria hunteria is primarily a nocturnal species, although a few individuals can be found on the sand during the daytime. Several collecting trips were made to the old marine laboratory at different hours to gather the data presented in Figure 10. Weather, tidal, and water conditions were similar on the various trips, and animals encountered were left in their habitat so that the number of individuals found on later trips was not lessened by earlier removal of part of the population. The number of specimens collected per hour averaged 16.7 for the night trips and only 2.4 for the day trips. Most of the snails collected at night were on oysters, actively feeding, or copulating. Individuals found during the day were invariably partially buried in the sand with the upper portions of the shell visible.

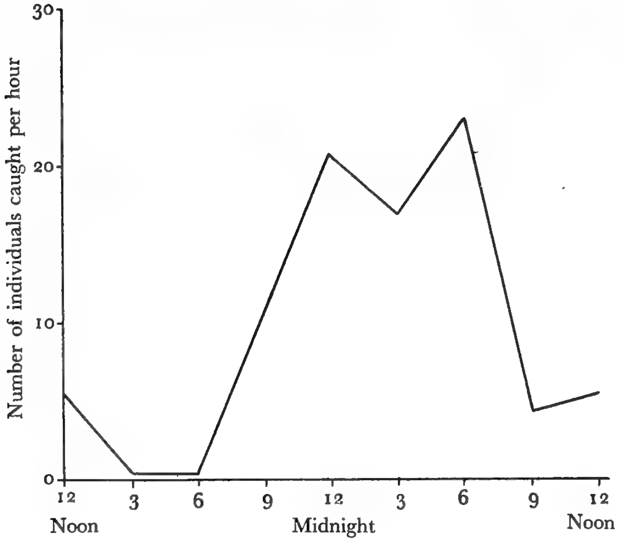

Figure 10

Number of *Fasciolaria hunteria* caught per hour at the old Marine Laboratory

Tidal Rhythm: *Fasciolaria hunteria* frequently climbs piers and searches for food among the attached oysters when the tide is in. Individuals exposed to the air as the water level drops fall from the oysters to the sand below and burrow into the substratum. *Fasciolaria hunteria* on Bay Mouth Bar also burrow into the sand as the receding tide exposes them. In both areas there are a few individuals that remain above the sand after the tide has receded. Snails below the tide level, and those in the tide pools, are not exposed to the air and remain active throughout the low tide period at night, but individuals of this species are not active during the day. Copulating pairs ignore the exposure and continue mating. As the tide returns, the sand containing the burrowed snails is again under water and the animals rapidly emerge and resume their normal activity.

Fasciolaria tulipa is widely distributed in the subtidal areas adjacent to Bay Mouth Bar, and has been collected in waters up to 10 feet deep. This larger species is not normally subject to frequent tidal exposure and tends to have a much more uniform activity pattern than *F. hunteria.* None of the animals found subtidally was even partially buried in the substratum, and all were actively moving or feeding. The number of individuals exposed by minus tides on Bay Mouth Bar is quite small when compared to the population as a whole, but when *F. tulipa* is exposed, it also burrows into the sand.

Seasonal Rhythms: Paine (1963) found *Fasciolaria hunteria* to be present on Bay Mouth Bar at all times of the year. The populations within the harbor are also present at all times, and are not subject to wide seasonal variations. *Fasciolaria tulipa* is present on Bay Mouth Bar in large numbers during the spring, but the numbers decline by August (Paine, *op. cit.*). Paine attributed the decrease in the number of *F. tulipa* on the bar to an increase in the number of predatory *Pleuroploca gigantea.* Only isolated individuals of *F. tulipa* are found on Bay Mouth Bar during the winter months.

Predators and Escape Responses

Paine (1963) reported that both *Fasciolaria hunteria* and *F. tulipa* are tertiary consumers and are at the top of the food web at Bay Mouth Bar. In this position *Fasciolaria* is relatively free of predators. Paine found *F. tulipa* to be cannibalistic; similarly, I found *F. hunteria* to prey on members of its own species. The large gastropod *Pleuroploca gigantea* feeds on the 2 species of *Fasciolaria* (Paine, 1963b), a process requiring a long period of time. Under aquarium conditions, one *P. gigantea* 11.9 cm took over 30 hours to consume a specimen of *F. hunteria* 5.8 cm long. *Murex fulvescens* Sowerby and *Melongena corona* both feed on *F. hunteria,* but do not normally occur in the same habitat as *F. hunteria.*

Shoup (1968) reported that both *Fasciolaria* species are consumed by crabs of the genus *Calappa,* and shells with the distinctive breakage pattern have been found in

Alligator Harbor. The stone crab *Menippe mercenaria* (Say, 1818) is a predator of *F. hunteria* in oyster environments and on Bay Mouth Bar. One individual of *Pagurus pollicaris* Say, 1817, was observed attacking a *F. hunteria* in the field, but the attack was not repeated in the laboratory.

Sting rays weighing up to 40 pounds are common in Alligator Harbor during the summer, but are absent during the winter months. The rays, which feed to a large extent on mollusks, appear to be major predators of *Fasciolaria* on Bay Mouth Bar.

Three types of defensive reactions are demonstrated by *Fasciolaria hunteria* upon encountering an individual of *F. tulipa*: withdrawal into the shell, active avoidance, and a flipping motion that is a modification of the righting response. Gore (1966) found a similar escape response pattern in *Nassarius vibex* Say, 1817, elicited by *F. hunteria, F. tulipa* and the sea star *Luidia alternata* Say, 1817. Withdrawal into the shell by *Fasciolaria* can be elicited by a variety of mechanical and visual stimuli. In both *F. hunteria* and *F. tulipa* the operculum completely seals off the aperture, preventing a predator from reaching the animal inside.

Fasciolaria hunteria exhibits the full spectrum of escape responses when stimulated by the presence of *F. tulipa* in the laboratory. Withdrawal into the shell has already been described. Four 10 to 15 gallon capacity aquaria were maintained in the laboratory, 2 with a 4-inch layer of sand on the bottom and 2 with a bare slate bottom. Individuals of both species were able to bury themselves completely in the sand. Ten *F. hunteria* were placed in tanks 1 and 2 with sandy bottoms, and 12 were placed in tanks 3 and 4 with the slate bottoms. Four *F. tulipa* were put in tank 2, and 3 were included in tank 4. The results of observations made over a 1-week period are given in Table 3. No difference was found between data collected during the day and at night. *Fasciolaria tulipa* remained on the bottom or burrowed into the sand, but rarely climbed the sides of the aquaria. The individuals of *F. hunteria* were on the bottom of tank 4 only 16.4% of the time, while those in tank 3, without *F. tulipa* on the bottom, were on the bottom 99% of the time. Since this difference was statistically significant, it was concluded that the climbing by *F. hunteria* was an avoidance response to the predatory *F. tulipa*. Similar results were obtained in the aquaria with sandy bottoms. While only 53.6% of the *F. hunteria* in tank 1 were buried, 94.5% of those in tank 2 burrowed into the sand. Almost $\frac{2}{5}$ of the *F. hunteria* that did venture out of the sand in tank 2 climbed the sides of the aquarium in the avoidance response found in tank 4. In several instances *F. hunteria* that ventured too near *F. tulipa* were captured and eaten. From the data obtained, it appears that *F. hunteria* actively avoids *F. tulipa* by burrowing if a choice between burrowing and fleeing is present. If no choice is available the *F. hunteria* climbs the aquarium walls as an escape response from the predator.

Table 3

The Position of *Fasciolaria hunteria* on the Walls of the Aquaria, on the Bottom, or Burrowed into the Sand in Relation to the Presence of *Fasciolaria tulipa*

			Percentage of *Fasciolaria hunteria*		
Tank	Substratum	*Fasciolaria tulipa*	on walls	on bottom	buried
1	Sand	0	22.4	24.0	53.6
2	Sand	4	3.5	2.0	94.5
3	Slate	0	1.0	99.0	–
4	Slate	2	83.6	16.4	–

The righting response of the 2 species of *Fasciolaria* is modified into the flipping escape response seen in *F. hunteria*. An understanding of the righting response will make the mechanics involved in the escape response easier to visualize. The righting action of both species may be divided into 3 sequential steps similar to those described by Clark (1964). The overturned snail contracts the circular muscles of its foot, thrusting the foot outward from the columella. In 29 of the 31 righting responses witnessed, the foot was extended around the inner lip and the columella of the shell. In the remaining cases the foot was extended over the outer lip of the shell. Individuals unable to reach the substratum by the first method chosen made a second attempt from the other side of the shell.

Differences were observed in the righting responses taking place on a solid or sand substratum. A specimen of *Fasciolaria* on a solid surface extends the anterior portion of the foot until it contacts the substratum and creates a suction with the help of a mucous secretion. The longitudinal foot muscles contract to pull the shell over. The foot is unable to establish a firm grip on a sandy substratum, however, and in this situation the snail extends and twists the distal portion of its foot so that the pointed anterior tip of the operculum is facing the substratum. A rapid contraction of the foot muscles drives the operculum into the substratum where it serves as an anchor. When the longitudinal foot muscles contract, the shell is pulled over, rather than the foot being pulled loose.

The initial attempt at righting the shell was successful in 55% of the 31 rightings investigated, and 19% of the 31 rightings were successful on the second try. *Fasciolaria* unable to right themselves after repeated attempts resort to a more active method. The foot is rapidly extended in the manner described, but when the substratum is reached the foot is quickly extended by a kicking motion, which often lifts the entire shell and body off the substratum and throws the animal a distance of 3 or 4 cm. This process is repeated until the animal happens to fall in the normal upright position.

A modification of the rapid righting response described above is used in the escape response of *Fasciolaria hunteria*. The flipping response is begun in the presence of *F. tulipa* and continues until the *F. hunteria* is some distance away. *Fasciolaria hunteria* in aquaria have been observed crawling about on the shells and opercula of *F. tulipa* without indicating an attempt to escape. However, a specimen of *F. hunteria* approaching the anterior portion of the foot of *F. tulipa* initiated the escape response before physical contact was made, indicating a possible chemical or visual mediation of the response. Individuals trapped beneath the foot of *F. tulipa* respond immediately and continue to flip until the 2 species are no longer in contact.

DISCUSSION

The primary concern of this paper has been the investigation of the ecological similarities and differences of *Fasciolaria hunteria* and *F. tulipa,* and the manner in which these ecological characteristics reflect upon the theoretical problems arising from the sympatric distribution of these two morphologically and phyletically closely related species. Cain (1953) limited the field of consideration of sympatry to an area in which the breeding ranges of the two species overlap. Although the two species of *Fasciolaria* share a wide geographical range, the area in which the two species are truly sympatric is limited, at least in Alligator Harbor.

Fasciolaria hunteria and *F. tulipa* are truly sympatric in Alligator Harbor only on Bay Mouth Bar. Since individuals of both species have been observed copulating on the bar at the same times of the year, their breeding ranges are also sympatric in this limited area, and there is no physical barrier to interbreeding. However, when the two species do come together *F. hunteria* is selectively eaten by *F. tulipa* (Paine, 1963), unless an escape response is effective in removing the smaller tulip from contact with the larger *F. tulipa.* This would prevent crossbreeding from occurring when individuals of the two species encounter each other.

Harper *et al.* (1961) found 3 factors to be necessary for the continued coexistence of closely related species. All species must be able to tolerate the physical and biological hazards of the environment. The related species must be able to maintain the genetic differences between them. Harper *et al.* (*op. cit.*) also cited 3 genetic conditions which can result when closely related species coexist. First, the breeding behavior may prevent hybrids from being formed. In the second situation hybrids are produced by crossmatings, but the progeny is sterile. Finally, fertile hybrids result from crossmatings between the 2 species. The reproductive characteristics of the *Fasciolaria* populations in Alligator Harbor fit the first case. The 2 species are closely related: the shells are almost identical in shape and structure, the opercula are identical, and the structure of the radula in *F. hunteria* is not distinguishable from that of *F. tulipa* of the same size. Differences in coloration and size are the most important external distinguishing characteristics separating *F. hunteria* from *F. tulipa.* Although 30 mating pairs were observed, no interspecific matings were encountered in either the field or in the laboratory. No intermediate forms resembling hybrids were found among the 295 live individuals of *F. hunteria* or the 18 live individuals of *F. tulipa* collected during the study.

Paine (1962) pointed out that to coexist, potential competitors each must utilize some aspect of the common environment more effectively than the other. Paine (*op. cit.*) also noted that if this were not the case, competitive pressures would lead to the exclusion or encourage modification of the less well adapted species. Differences in distributional patterns, the fact that *Fasciolaria hunteria* is primarily intertidal in Alligator Harbor and *F. tulipa* is subtidal, and differences in daily activity patterns all lessen the contact and competition between the 2 species. Hairston (1959) claimed that food is the only resource that 2 competing species cannot share. Paine (1963) presented feeding data for *F. hunteria* and *F. tulipa,* and also (Paine, 1962) reported a feeding diversification in 2 sympatric *Busycon* species on Bay Mouth Bar. A similar diversification in the feeding habits of *Fasciolaria* is evident from the feeding data reported in Paine's (1963) paper. Bivalves comprised about the same portion of the diet of the 2 species, with *F. hunteria* feeding on the smaller bivalves. The majority (58%) of the prey of *F. tulipa* encountered by Paine was other gastropods, compared with only 13% for *F. hunteria.* Polychaete worms accounted for 41% of the diet of *F. hunteria,* but none was included in the feeding observations of *F. tulipa.* Paine concluded that the feeding differences in the 2 *Fasciolaria* were due to the difference in size of the 2 species. While both species are catholic feeders, the ability of *F. tulipa* to attack and consume larger prey than *F. hunteria,* and the larger species' corresponding disinterest in small potential prey, results in an important ecological diversification between the two species.

While *Fasciolaria hunteria* and *F. tulipa* share a sympatric distribution in the geographical sense, they occupy different ecological niches. Furthermore, the evolution of an escape response in *F. hunteria* initiated by *F. tulipa* would prevent any attempt at genetic intermixing in these species.

SUMMARY

1. The ecology of 2 closely related species of the neogastropod genus *Fasciolaria* was studied in Alligator Harbor, Florida, to determine the similarities and differences in their ecology, as it relates to their sympatric distribution. Particular emphasis was placed on the mechanisms that allow the two species to live sympatrically.
2. The shells of *Fasciolaria hunteria* and *F. tulipa* were studied and compared. *Fasciolaria tulipa* is larger, averaging 128 mm in length, while *F. hunteria* averages 59.3 mm. *Fasciolaria hunteria* has 4 to 8 solid primary lines, with a direct correlation between the number of lines and the length of the shell, while *F. tulipa* has 25 to 39 interrupted primary lines.
3. The radulae of the two species are remarkably similar, and increases in length, width, and the number of cusps on the lateral teeth of the radulae were correlated with increases in the length of the shell. The radulae of *Fasciolaria* have one central tooth flanked on each side by a lateral tooth. There are no marginal teeth.
4. *Fasciolaria hunteria* is distributed along the margin of Alligator Harbor wherever there are oyster outcrops. *Fasciolaria tulipa* occurs intertidally in the harbor on Bay Mouth Bar only, but the species is common in the subtidal waters surrounding the bar and off St. Teresa. The two species are sympatric on Bay Mouth Bar and in restricted areas of the north shore of the harbor.
5. The Alligator Harbor populations of both species are adult and stable. *Fasciolaria hunteria* is the more common of the two species, since 295 live individuals were encountered in the study and only 18 live specimens of *F. tulipa* were found.
6. Fertilization occurs internally in both species and copulation times may exceed 2 hours. Female individuals of *F. tulipa* tend to have larger shells than males, but no dimorphism of this type was found in *F. hunteria*. Both species have a 1 : 1 ratio of males to females.
7. *Fasciolaria hunteria* is nocturnal and is thought to be most active just before and after low tides; both species are present in Alligator Harbor throughout the year, but *F. tulipa* occurs intertidally only during the summer months.
8. *Fasciolaria hunteria* exhibits an escape response to *F. tulipa* that includes withdrawal into the shell, active avoidance, and a flipping response. Active avoidance by burrowing into the substratum is the preferred escape response.
9. *Fasciolaria hunteria* and *F. tulipa* are sympatric in the geographical aspect of the term, but they do not share the same distribution in Alligator Harbor. Diversification in the ecological niches occupied by the two species further lessens contact between them.

ACKNOWLEDGMENTS

I would like to extend my sincere thanks and appreciation to my friend and major professor, Dr. C. R. Stasek, for the assistance and encouragement he gave during the course of my graduate studies and the preparation of this thesis. Dr. R. W. Menzel and Dr. W. D. Herrnkind served as members of my advisory committee, and were very helpful in critically evaluating the manuscript. Mr. R. W. Miller accompanied me on many of the collecting trips.

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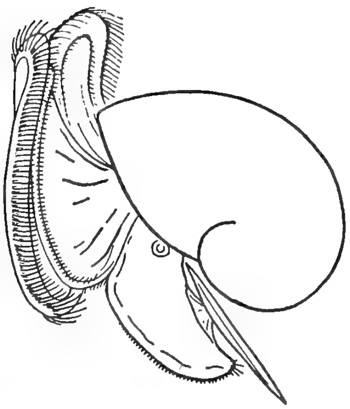

The Date of Publication of GOULD's "Descriptions of Shells from the Gulf of California"

BY

EUGENE V. COAN

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

AN ARTICLE IMPORTANT to West American malacology by GOULD appeared in the Boston Journal of Natural History in 1853. There has been question about the date of publication of the 32 species described in this article, 18 of the 50 species discussed having been validated in GOULD, 1851.

This paper appeared in the third issue of the Journal (article no. XXIV: pp. 374 - 408; plts. 14 - 16). Internal evidence (an 1853 date on the issue cover; October 1853 signature dates at the bottoms of pp. 377, 385, 393, and 401; and a January 17, 1853, writing date at the end of the previous article) require that it be dated October 1853.

Copies in the United States National Museum and the Academy of Natural Sciences of Philadelphia indicate that this work was also issued separately. The printing was from the original article, but the title was reset without the article number, and the pages were renumbered. There are no signature indications with dates at the bottom of pages; there is no indication of publisher or publication date.

First mention of GOULD's paper was by CARPENTER (1857: 225 - 228), who evidently had only the separate and assumed that it had been published in 1855. GOULD (1862), reviewing the article in his "Otia," indicated that it had been published in April 1852. This date may have been taken in error from a previous signature date in the Journal and was probably responsible for the "April 1852" note on the National Museum copy and for DALL's (1909:204) comment, "also issued in advance of the Journal, separately, April, 1852." However, the fact that the separate is in the Journal type together with the fact that the previous Journal article was only completed in January 1853 indicate an 1852 date is unlikely.

Thanks are extended to Drs. A. Myra Keen, Joseph Rosewater, and Robert Robertson, and to Mr. Richard I. Johnson for their help in working out this matter.

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NOTES & NEWS

Additional Remarks on Studies of Cenozoic Marine Mollusks of the Pacific Coast[1]

BY

WARREN O. ADDICOTT
U. S. Geological Survey, Menlo Park, California 94025

It has been brought to my attention that certain studies on Cenozoic marine mollusks of the west coast of North America were omitted or incorrectly reported in a recently published summary of investigations (Addicott & Kanno, 1969). The purpose of this note is to emend the record. Studies initiated after early 1969 are not included.

TAXONOMIC STUDIES

Barry Roth (California Academy of Sciences, San Francisco, California 94118) is making a biogeographic study of west American species of Marginellidae in collaboration with Eugene V. Coan (% Department of Geology, Stanford University, Stanford, California 94305). Roth has completed a manuscript on central American species of *Noetia.*

The systematic treatment of Tertiary mollusks of the Canal Zone and adjoining areas of Panama by Wendell P. Woodring (U. S. National Museum, Washington, D. C. 20560) has not been completed as suggested in the earlier summary. Two additional parts of U. S. Geological Survey Professional Paper 306 dealing with classes of mollusks other than gastropods are planned.

BIOSTRATIGRAPHIC STUDIES

Victor A. Zullo (California Academy of Sciences, San Francisco, California 94118) and J. Wyatt Durham (University of California, Berkeley, California 94720) are completing a manuscript on Pliocene and early Pleistocene molluscan faunas of coastal northwestern California and southwestern Oregon. Zullo has recently published reports on late Pleistocene mollusks from southwestern Oregon.

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[1] Publication authorized by the Director, U. S. Geological Survey

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Dolabrifera dolabrifera (Rang, 1828): Range Extension to the Eastern Pacific

BY

HANS BERTSCH
Las Cruces Marine Station, Baja California, Mexico[1]

(1 Text figure)

During the summer of 1969, I was doing research at the Las Cruces Marine Station, Baja California, on the opisthobranch fauna of the region. A live specimen of *Dolabrifera dolabrifera* (Rang, 1828), collected on July 9, 1969, from underneath a rock in about 5 feet of water, in Las Cruces Bay (24°13′ N; 110°05′ W; 20 miles E of La Paz, Baja California, in the southern Gulf of California), was given to me by Mr. Jerry Devlin. This opisthobranch gastropod is taxonomically placed in the order Anaspidea, family Aplysiidae, subfamily Dolabriferinae (Beeman, 1968: 94).

The animal measured 38 mm in length, 18 mm in width, and 10 mm in height when not moving. It closely matched the descriptions of *Dolabrifera dolabrifera* given by Engel & Hummelinck (1936: 29 - 43) and Kay (1964: 184 - 185). A color transparency of the living animal (see Figure 1) was sent to Dr. Kikutarô Baba, who has collected this species in Japan (Baba, 1937: 216). He kindly confirmed my identification of the animal.

The published range of this species is worldwide throughout circum-tropical and circum-subtropical marine waters, with the exception that it has not previously been recorded from the American Pacific coast (Marcus & Marcus, 1963: 10 - 11; Marcus & Burch, 1965: 244; Marcus & Marcus, 1967: 38 - 39; Work, 1969: 680; comprehensive locality data and synonymy of the species are given by Engel & Hummelinck, *loc. cit.*, and Kay,

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[1] Permanent address: Franciscan School of Theology, 1712 Euclid Avenue, Berkeley, California 94709

loc. cit.). This is the first reported occurrence of *Dolabrifera dolabrifera* in eastern Pacific waters.

The specimen was kept alive in an aquarium for a week. During this time it usually remained attached to the glass wall near a corner of the rectangular tank. It adhered quite tenaciously to the glassy substrate. Only once (July 16, at 8:30 in the evening) was it observed freely crawling around in the aquarium without any prior stimulation having been applied to the animal. When the animal was greatly disturbed, it exuded a whitish fluid from its mantle cavity.

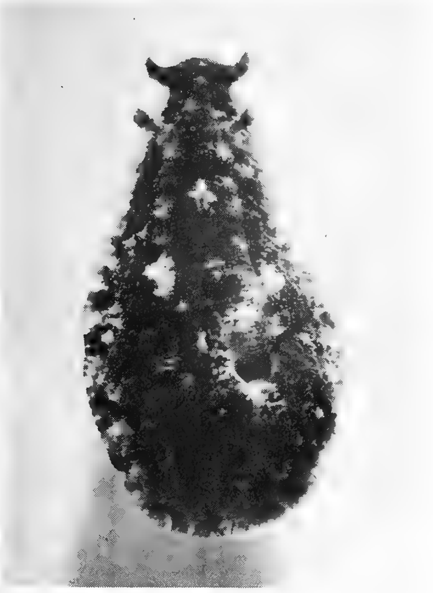

Figure 1

Dolabrifera dolabrifera (Rang, 1828)

photograph by Hans Bertsch

Tests were conducted to measure the speed of travel of *Dolabrifera dolabrifera*. Removing the animal from its position in the aquarium and placing it in another container would induce it to crawl. Locomotion was by the extension-contraction method, *i. e.*, alternately extending its anterior portion forward (at which time it measured 43 mm long) and then pulling up the rest of the body (in the contracted phase its length measured 37 mm). Engel & Hummelinck (1936: 32) speak of the animal's ability to contract itself into a ball-shaped form ("zu einer Kugel"), but they do not specifically indicate that this behavior is used by *D. dolabrifera* while crawling. The speed of the animal averaged slightly more than 17 cm per minute (Engel & Hummelinck, *loc. cit.*, gave a speed of locomotion of about 20 cm/min).

The preserved specimen has been placed in the collection of the California Academy of Sciences (CASIZ no. 417). I am very grateful to Mr. Devlin and Dr. Baba, and also to Mr. Hugh C. Bertsch, Rev. Alberic A. Smith, and Miss Virginia Raisch for their assistance and support.

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California Malacozoological Society, Inc.

Affiliate Membership for the fiscal year July 1, 1970 to June 30, 1971 has been set at $8.-. Postage for members in Canada, Mexico, Central and South America $1.-, for members in any other foreign country $1.50 additional. Send for Membership Application blanks to the Manager of the Society in Los Angeles.

On the Authorship of Part V of Eschscholtz's "Zoologischer Atlas," 1833

BY

JAMES H. McLEAN

Los Angeles County Museum of Natural History
900 Exposition Boulevard, Los Angeles, California 90007

{Editor's Note: In reviewing the "Handbook" by Dr. J. H. McLean, we noticed that he credited Rathke with the authorship of some limpets which heretofore had always been credited to Eschscholtz. As we were convinced that there must be good and sufficient reasons for this change, and as we were not aware of any publication in which the reasons were given, we inquired of Dr. McLean on what basis he had made the changes. Upon receiving his explanation, we decided that this was of such general importance that the reasons for the necessary changes should be published promptly, in order that an apparent error not be perpetuated. Upon our urging, though exceedingly reluctantly, Dr. McLean submitted at last the following report.}

THE FIRST REPORTED species of northeastern Pacific acmaeid limpets were collected by Johann Friedrich Eschscholtz at Sitka, Alaska, according to CARPENTER, (1857, p. 172). Although Eschscholtz published some new molluscan species in parts I - IV of the "Zoologischer Atlas" (1829 - 31), the new species of *Acmaea* were not published until 1833 in Part V of the "Atlas" by Martin Heinrich Rathke, "from the author's MSS," according to CARPENTER. Recent authors have overlooked CARPENTER's remarks and have credited the limpets solely to Eschscholtz.

STORER (1925, pp. 47 - 48) discussed the problem of authorship of the salamanders also described in Part V of the "Atlas." He showed that diagnoses of several of the species in the text were followed by the letter "E", an indication taken to mean that Eschscholtz had contributed that portion of the text, while other descriptions written in an entirely different style lacked such a reference to Eschscholtz. Those names with the "E" appended were credited to Eschscholtz by STORER and those bearing no reference to Eschscholtz were credited to Rathke. The acmaeid descriptions of Part V have no reference to Eschscholtz, and the lack of such credit is construed as indicating that Rathke is fully responsible for the work. There is no evidence that Eschscholtz even suggested the names. In my dissertation on the northeastern Pacific limpets (McLEAN, 1966), and the more recent handbook (McLEAN, 1969) I credit to RATHKE the acmaeid species and *Diodora aspera,* the only northeastern Pacific mollusks so affected.

The genus *Acmaea* was first proposed without species in 1830 in the appendix by ESCHSCHOLTZ *in* KOTZEBUE's "Voyage Around the World," published in German, English, and Dutch (see GRANT, 1937, p. 10). Validation of the generic name has been established by the ICZN (Opinion no. 344, 1955) as ESCHSCHOLTZ *in* RATHKE (1833, p. 16).

I am indebted to Dr. S. Stillman Berry of Redlands, California, who, on the basis of study of his personal copy of the "Atlas," originally suggested to me that Rathke should correctly be given as the author of the acmaeid species. He also brought the precedent set by Storer to my attention.

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First Symposium of Brazilian Paleontology

The Academia Brasileira de Ciências is organizing the first symposium of Brazilian Paleontology to be held in Rio de Janeiro, Brasil, from September 20 to 25, 1970.

We quote from a bulletin of information just received: ". . . Original papers presented will be published in a Supplement Volume of the Anais of the Academy.

In order to prepare the agenda, the titles and abstract of original papers (or other communications) to be presented at the Symposium should reach the Secretary of the Academy by 31 July, 1970 (Secretaria da Academia Brasileira de Ciências, Caixa Postal 229, ZC-00, Rio de Janeiro, GB, Brasil).

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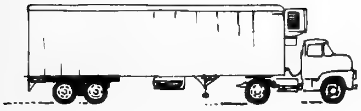

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BOOKS, PERIODICALS, PAMPHLETS

The Genus *Miltha* (Mollusca:Bivalvia) in the Australian Cainozoic

by Nellie H. Ludbrook. Transact. Roy. Soc. South Australia, vol. 93, pp. 55 - 63; plts. 1 - 5; 1969.

This paper contains a discussion of the genus *Miltha* (family Lucinidae) and its occurrences including 4 species and one subspecies from the late Cenozoic of southern and western Australia. Two of these forms, *M. flindersiana* Singleton & Woods and *M. f. dennanti* Wilkins, were described previous to this paper. Three species are described here for the first time: *M. hamptonensis,* Pleistocene, *M. lindsayi,* late Pliocene, and *M. nullarborensis,* of early Miocene age.

It is an interesting coincidence that this paper dealing with *Miltha* in Australia and one by Vokes dealing especially with Neogene species of this genus in Florida both appeared in the latter part of the same year (see H. E. Vokes: "Observations on the genus *Miltha* (Mollusca: Bivalvia) with notes on the type and the Florida Neogene species." Tulane Stud. Geol. Paleont. vol. 7, no. 3, pp. 93 - 126; 7 figs; 3 in text; 29 December 1969).

LGH

Malacological Review.

P. O. Box 801, Whitmore Lake, Michigan 48189. 187 pp.; illust. Subscription $5.-. Vol. 1 for 1968, received in 1969.

This new publication, in addition to a number of original papers brings, as an interesting and useful innovation, facsimile reproductions of the tables of contents of a number of leading journals in the field of malacology.

The original papers in this, the first, volume include:
The reproductive anatomy and chromosome number of *Quickia spura* (Gould) (Stylommatophora: Heterurethra: Succineidae) by C. M. Patterson (pp. 1 - 13; illust.).
Erinna newcombi of Hawaii and *Limnaea onychia* of Japan by J. B. Burch (pp. 15 - 30; illust.).
Notes on Hawaiian Lymnaeidae by J. P. E. Morrison (pp. 31 - 33).
Morphological features of Liberian *Bulinus* and *B. truncatus* of Egypt: a pictorial essay on snails of three subgenera (Planorbidae: Basommatophora) by Harold J. Walter (pp. 35 - 89; illust.).
Histogénèse des mucocytes de la glande et de la sole pédieuses d'*Arion rufus* (Stylommatophora: Arionidae) by D. Binot & M. Chetail (pp. 91 - 102 illust.).
Sur les variations de *Littorina saxatilis.* Exemple de distribution d'une variété donnée by E. Fischer-Piette & J.-M. Gaillard app. 103 - 118; 1 table; 2 maps).
A new species of the genus *Cycloteuthis* (Cephalopoda: Oegopsida) by J. A. Filippova [*Cycloteuthis akimushkini*] (pp. 119 - 124; illust.).
Molluscan organ culture by C. J. Bayne (pp. 125 - 135).

RS

The Echo:

Abstracts and Proceedings of the Second Annual Meeting of the Western Society of Malacologists, Pacific Grove, California, June 18 - June 21, 1969

Judith Terry Smith, editor. Stanford, Calif.: pp. 1 - 84; photograph and map. March 9, 1970. Price $2.50 plus $-.50 mailing charge; available from Secretary, Western Society of Malacologists, 3846 East Highland Avenue, Phoenix, Arizona 85018.

In this, its second year of actual issue, **The Echo** becomes a valid publication under Article 8 of the International Code of Zoological Nomenclature, which requires that "a work when first issued must . . . be obtainable by purchase or free distribution." The one previous issue (dated 1968, issued March 1969) was distributed only to members of the Western Society of Malacologists.

Neat photo-offset reproduction and $8\frac{1}{2} \times 11$ - inch page size are used. The abstracts included cover a wide variety of topics, mainly related to the eastern Pacific region. A useful bibliography of works on taxonomic procedure, a list of periodicals containing malacological articles, and a biography of Philip Pearsall Carpenter are among the useful "extras" contained. The format adopted by the present editor seems flexible enough to include even full-length articles in future issues, adding to the publication's value.

The Membership Directory, accurate as of October 1969, was five months outdated at The Echo's date of publication. Since one purpose of this type of publication is to facilitate communication between workers, the defect is unfortunate.

Wording of the publication's title varies between the cover and the title-page, and also between the two issues. No volume or issue number is given, so to cite clearly articles appearing in The Echo one should probably use an extended form of the title – as above, taken from the 1970 cover. By whatever name, The Echo promises to be a useful and informative periodical.

AGS

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

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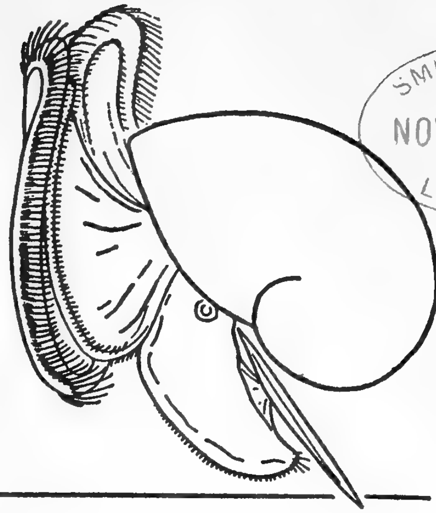

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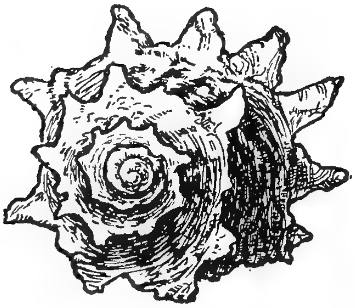

Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

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

Reproductive Biology and Shell Site Preference in *Hipponix conicus* (SCHUMACHER)

(Gastropoda : Hipponicidae)

BY

HELENE M. LAWS

South Australian Museum, Adelaide 5000

(1 Plate; 5 Text figures)

THE BONNET LIMPET, *Hipponix conicus* (SCHUMACHER, 1817) is found commonly on the surface of other gastropod shells over a very wide geographic range from East Africa, through the Indo-Pacific to Japan, the Hawaiian Islands and the Tuamotu Archipelago. In Australia it is found from Western Australia to Victoria and Tasmania as a common commensal on the shells of the haliotids *Haliotis ruber* LEACH, 1814, *H. improbulum* IREDALE, 1924 and *H. laevigata* DONOVAN, 1808 and on *Pleuroploca* and *Pterynotus*. The observations which follow were made on *Hipponix conicus* individuals taken from series of *Haliotis improbulum* collected at Port Willunga during 1963, and at West Island during 1964-1965, and from specimens of *H. laevigata* and *H. improbulum* collected at Flinder's Island and Reef Heads in June and July, 1968. Museum specimens of *Pleuroploca australasia* (PERRY, 1811) and *Pterynotus triformis* (REEVE, 1845) were used for recording the distribution of *Hipponix conicus* on these gastropods.

BEHAVIOUR AND MORPHOLOGY

In South Australian specimens of *Hipponix conicus* the shell is brown externally and sometimes on the interior lip, and the interior may be white or white with a central area of brown. The animal is relatively immobile on the surface of the host, the shell margin assumes the contours of the host surface, and the host shell becomes eroded beneath each individual. *Hipponix conicus* is, however, capable of a limited amount of movement at any stage of life. HARTLEY (1958) illustrated eroded tracks on the surface of *Haliotis ruber* showing that the limpets move slowly, the rate being determined by the rate of growth of the host shell since mature *Hipponix* are almost invariably found at the haliotid shell margin. Similar eroded tracks were found on South Australian host haliotids (Figure *3*) [E] and Figure *4* shows a track produced by a male on the surface of a female, such as was reported by CERNOHORSKY in 1968 for a Pacific male. In a few cases on South Australian host shells, especially when a sharp decrease in epifauna showed that the host had made sudden and rapid growth, the *Hipponix* individuals failed to "keep up" and were found in a row at a distance from the host shell margin. In Figure *3* the large female has not quite kept pace with the *Haliotis* margin.

The animals of *Hipponix conicus* were cream in color with blue-black tentacles and proboscis. As has previously been noted for *H. antiquatus* (LINNAEUS, 1767) by YONGE (1953), *H. conicus* is not a ciliary feeder as are related members of the Capulidae and Calyptraeidae, but searches for food particles by lifting the anterior margin of the shell and groping about with the extensible and very mobile proboscis.

The radula is similar to that figured by CERNOHORSKY (1968) for Fijian specimens but the first lateral cusp of the median tooth is more prominent and overlaps the basal plate; in addition the central tooth has at least 5, and sometimes even 7 lateral cusps and the denticles of the marginal teeth may be more pronounced.

Reproduction in *Hipponix conicus*

Hipponix conicus has been reported to be a protandrous hermaphrodite (CERNOHORSKY, 1968), thus showing a reproductive pattern comparable to that which has long been known for the members of the related families

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[E] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Capulidae and Calyptraeidae (CONKLIN, 1897; COE, 1942, 1944; ORTON, 1909).

Observations on the position occupied by the sexual stages were made using the series of specimens collected at Port Willunga in June, July and August of 1963. The position and size of individuals on the haliotid shells were recorded and if they were 2 mm or more in length their sex was determined by microscopic examination of pieces of gonadal tissue to check for the presence of developing or mature sperm or ova. In individuals less than 2½ mm in length, and in those between 2½ and 16 mm which were more than 3 mm away from females, no developing sperm or ova could be found. With the exception of one large male which was 17 mm long, all specimens over 16 mm were females. All in the 2½ - 16 mm range which were in contact with, or within 3 mm of a female, were males (Figures 2 and 7). It appears that the presence of a female induces adjacent individuals to develop as males, and that isolated individuals do not spontaneously become males. Mature females may be solitary but the fact that no solitary males were found suggests that these females had not passed through a functional male phase, although some did possess a rudimentary penis.

The gonad of the male (Figure 8) was white and the penis large and elongate and capable of extension well beyond the margin of the male shell, as was observed for *Hipponix antiquatus* by YONGE (1960). Many of the males situated on females had eroded a channel in the edge of the female shell (Figures 5 and 6) allowing communication between the two. The erosion of the female shell shows that the notches are made from the male side (Figure 6). It was not uncommon for a female to carry two males and have a shell notch for each one. Males were usually attached on the right anterior margin of the female shell. This position is the one closest to the opening of the oviduct, and the shell notch would allow copulation to occur without the margins of the male and female shells being raised. Such communication channels were never observed between a female and an adjacent male.

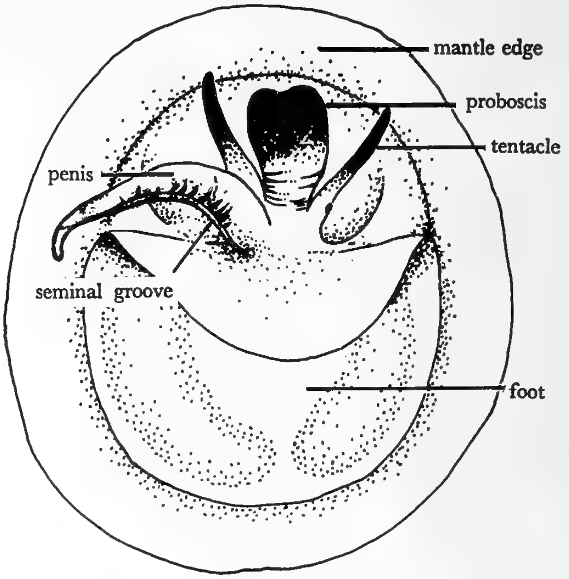

Figure 8

Male *Hipponix conicus*: ventral view with the anterior foot membrane turned back to show the head region

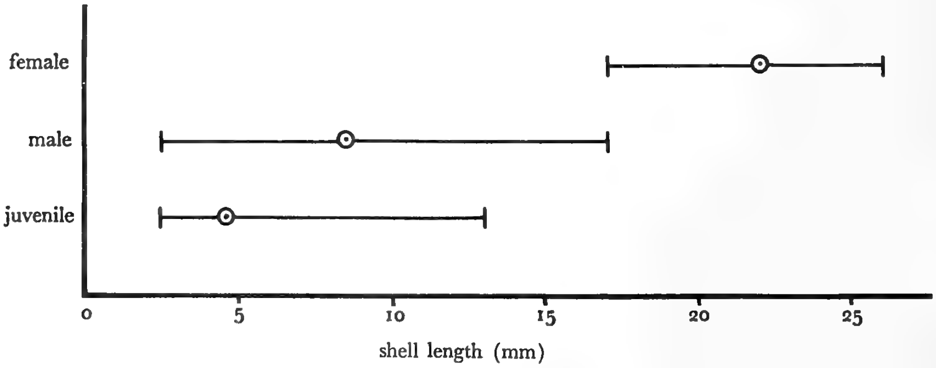

Figure 7

Shell length (mean and range) of juvenile, male and female individuals of *Hipponix conicus*

In mature females (Figure 9) the gonad is a rich yellow in color and a rudimentary penis may be present. Eggs are deposited in 5 to 10 elongate brood sacs which lie in the left side of the mantle cavity and are attached to the left anterior part of the foot. From 9 to 24 embryos develop in each sac and the whole brood is at the same stage of development. A number of females were solitary, there being no scars to indicate where a male might have previously been; some of these solitary females had brood sacs with developing embryos.

Juveniles are released when about 1 mm in length. They settle on the haliotids, particularly round the anterior margin, and the young shell is smooth until it is about 3 mm long when the ribbing characteristic of an adult shell begins to develop. The young individuals are red-brown and clearly show the spiral protoconch; with increasing size the protoconch is eroded off the top of the shell.

During 1964 - 1965 over a period of 16 months, females from the West Island collections were checked for the presence of brood sacs. Samples ranged in size from 4 to 12 individuals and the resulting picture of the reproductive cycle can only be regarded as approximate. The results do show, however, that *Hipponix conicus* breeds throughout the year and they suggest that there is a peak of reproductive activity in the late winter (Figure 10). Three collections at Port Willunga in June, July and August of 1963 support the suggestion of a late winter reproductive peak as does a single collection of 12 females from Reef Heads in August, 1968.

Position of *Hipponix conicus* on the Host Shell

On *Pleuroploca* and *Pterynotus* no site seems to be particularly favored. In a few cases the host may carry an

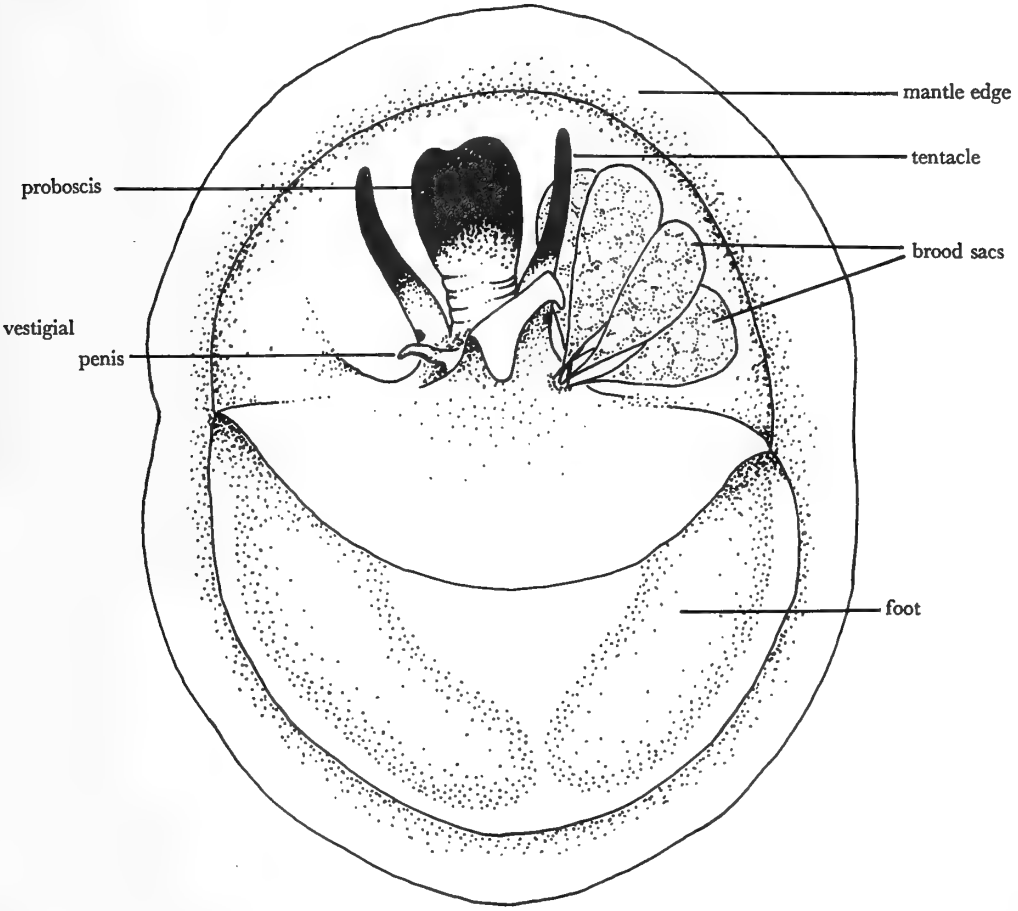

Figure 9

Female *Hipponix conicus*: ventral view with the anterior foot membrane turned back to show head region and spawn

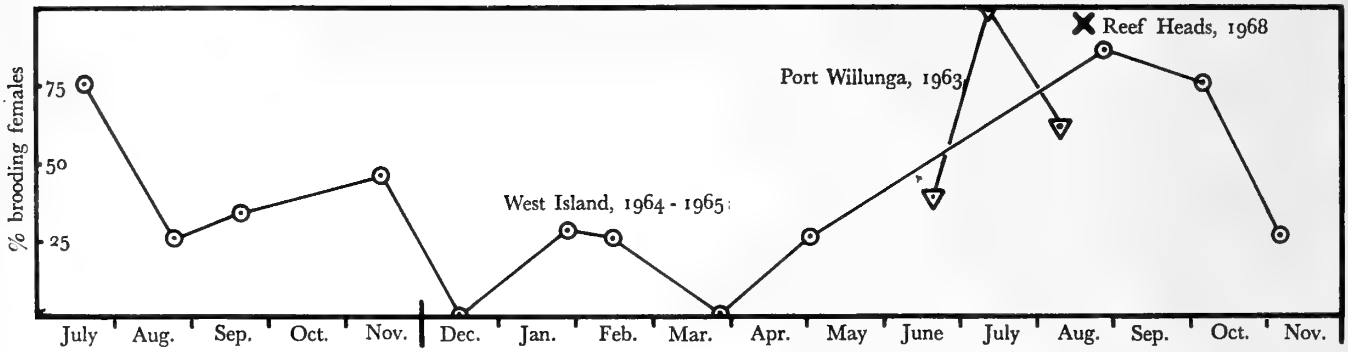

Figure 10

The annual reproductive cycle shown by brooding females

almost complete covering of *Hipponix* (Figure *1*); this whelk even had juvenile specimens attached to its operculum.

The distribution of *Hipponix conicus* individuals on haliotids showed a definite pattern. In order to record the distribution, the number of *Hipponix* on each of 6 sectors of the haliotid shell was counted (see Figure 11). Three size classes of bonnet limpet were recorded separately: $<$ 5 mm long, 5 - 16 mm, and $>$ 16 mm. All females were in the $>$ 16 mm group. In this way the distribution on haliotid shells was established for 54 *Haliotis improbulum* shells (761 *Hipponix conicus*) from West Island, and for 8 *Haliotis laevigata* shells (840 *Hipponix conicus*) from Flinder's Island. The results are shown in Figure 11. The anterior and right-hand margins are the only places on *Haliotis improbulum* where females and their attendant males occur. Only juveniles were found on other sectors of the shells; greater numbers and wider distribution of the smaller size class containing juveniles suggests that individuals are progressively lost as they increase in size. On *Haliotis laevigata* female distribution showed a peak on the front and right-hand margins of the shell although some were found in all other sectors. Three *Haliotis improbulum* shells collected with the *H. laevigata* at Flinder's Island had limpets present only on sector IV, comparing with the more restricted distribution seen on the West Island shells. For all size classes of bonnet limpet, distribution was less restricted on *Haliotis laevigata* than on *H. improbulum*.

It was noted that on the Flinder's Island shells the central parts of the shell which are not used by *Hipponix conicus* with the exception of occasional juveniles, were occupied by the related hipponicid limpet *Antisabia foliacea* (Quoy & Gaimard, 1835).

DISCUSSION

Consecutive hermaphroditism has been recorded among the Mesogastropoda in the families Scalidae, Ianthinidae, Capulidae, Calyptraeidae (Fretter & Graham, 1962) and the Hipponicidae (Yonge, 1960; Cernohorsky, 1968). It has been studied in particular detail in *Crepidula*

Plate Explanation

Figure *1*: Large numbers of *Hipponix conicus* on *Pleuroploca australasia*.

Figure *2*: *Haliotis improbulum* bearing a large female *Hipponix conicus* individual with a male situated on her anterior shell margin and another (completely covered with a bryozoan colony) adjacent to her; all other individuals were juvenile.

Figure *3*: The track eroded on the surface of a *Haliotis improbulum* shell by a solitary advancing female which has not quite reached the haliotid's anterior margin.

Figure *4*: A female *Hipponix conicus* bearing a smaller male. Erosion of the ribbing on the female shell marks the path of movement by the male.

Figure *5*: The interior view of a large female shell which carries two male individuals at the anterior margin (the lower margin in the figure); each male has formed a communication notch in the margin of the female shell.

Figure *6*: The dorsal view of the female shell of figure *5* showing erosion of the shell by the males (the male shells have been removed).

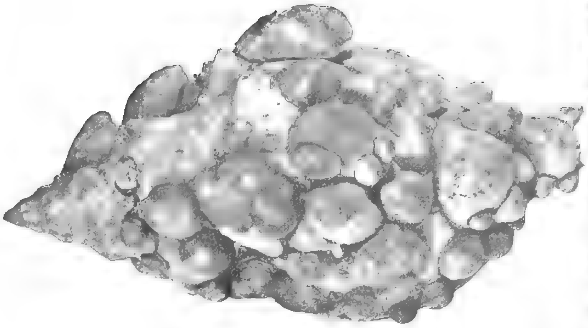

Figure 1

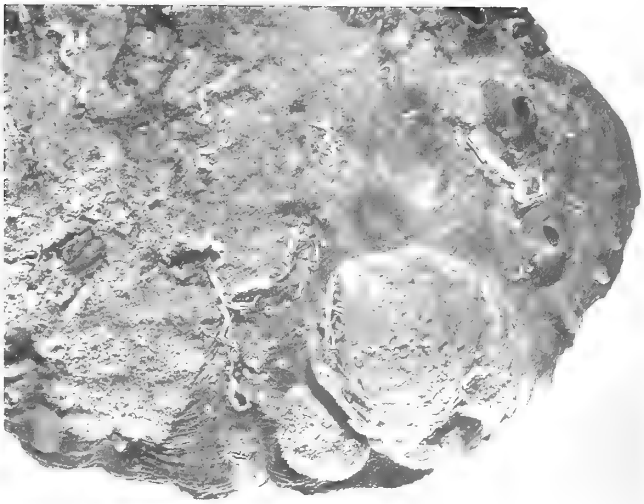

Figure 2

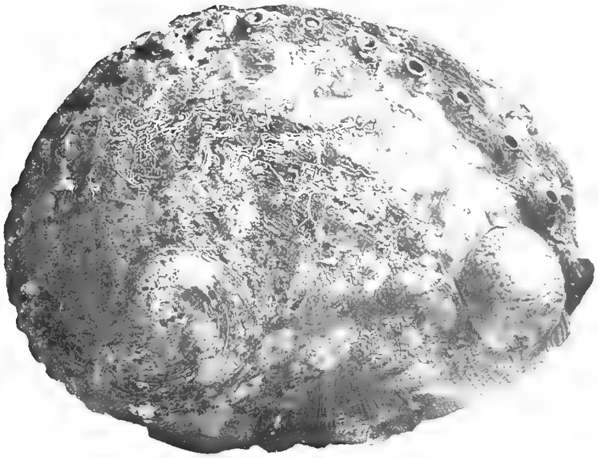

Figure 3

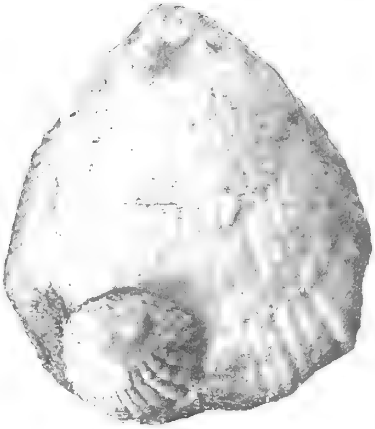

Figure 4

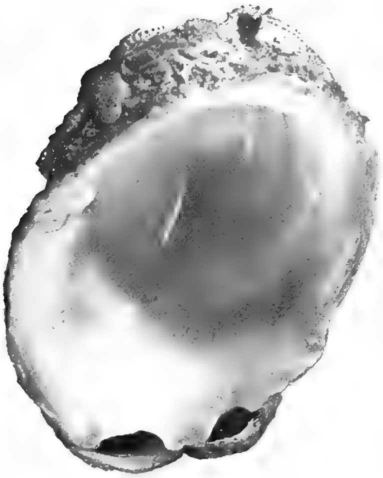

Figure 5

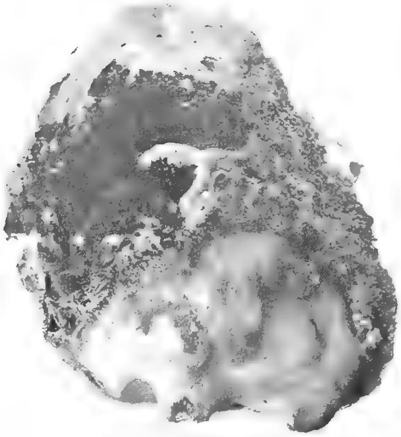

Figure 6

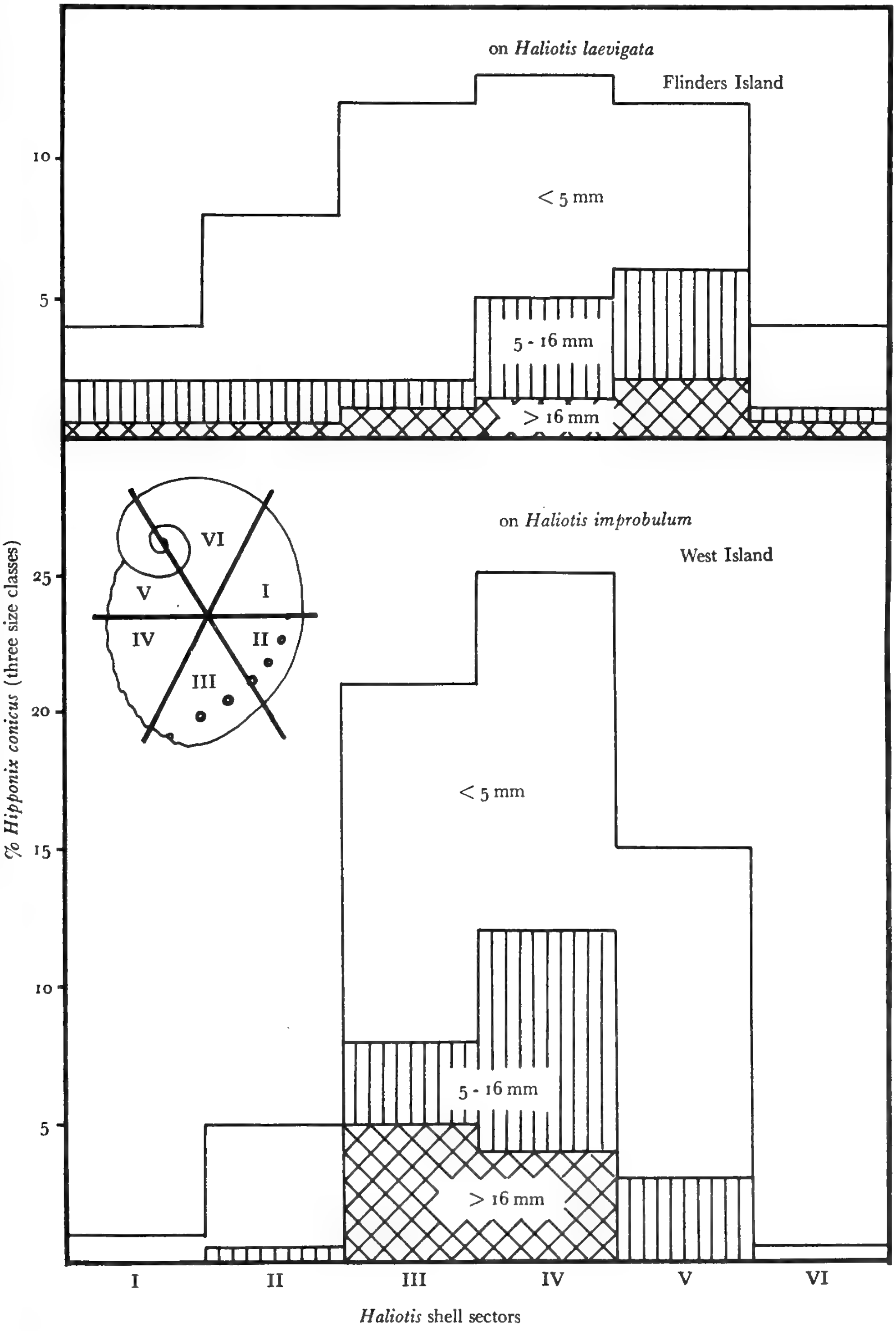

Figure 11

The distribution of *Hipponix conicus* individuals on *Haliotis* shells because of the economic importance of members of this genus as competitors for food and space in oyster beds. *Crepidula fornicata* (Linnaeus, 1758) is a protandrous hermaphrodite, the individuals associating in chains with older large females at the base of the chain, transitional individuals in the middle and small younger males at the top (Gould, 1947; Coe, 1948, 1953). Transition from male to female phase occurs at different times in different individuals. Gould (1919) concluded that the presence of a mature female influences associated juveniles to develop as males. If a juvenile settles alone on a rock rather than joining a colony, the male phase may be brief or even lacking, or it may persist until a younger individual settles on it inducing the change to the female phase. In the Japanese *C. aculeata* (Gmelin, 1791) and *C. walshi* (Reeve, 1859) (Ishiki, 1936) small juveniles settling beside a large female may become and remain male and may eventually grow to be as large. Solitary males become hermaphrodite and if several juveniles settle together, one becomes female directly and the others become male. In contrast, in *Calyptraea,* the sex change occurs at a definite stage of the life cycle (Fretter & Graham, 1962, after Pelligrini).

The very great size overlap observed in juveniles and males of *Hipponix conicus* and the fact that males were found only in association with females suggests that in this species, as in *Crepidula,* sexual development is affected by the proximity of other individuals. The absence of isolated males indicates that females develop directly, but on the other hand some females had a rudimentary penis suggestive of a prior male phase or at least of male potentialities. For South Australian *H. conicus* the question of protandry remains unanswered. Cernohorsky (1968) recorded hermaphrodite individuals of intermediate size among specimens from the Pacific Islands indicating protandry, but he does not state on what characters his decision of hermaphroditism was based. Yonge (1960), describing the males of *H. antiquatus* recorded "that the animals were protandric hermaphrodites" basing his conclusion on the smaller size of the males. This in itself is not conclusive evidence of protandry.

Hipponix conicus shows a preference for the right anterior shell margin of *Haliotis improbulum;* on *H. laevigata* there is a similar preference although on this species the site tolerance is broader. It has been suggested (Wilcynski, 1955) that the chains of individuals characteristic of *Crepidula* are primarily feeding units, rather than breeding associations as has been previously thought, creating a strong feeding current which benefits all members of the chain. Although *Hipponix* is a particle feeder, individuals will still benefit from a water current bringing food particles and I suggest that the position of *H. conicus* individuals on haliotids enables them to gain maximum advantage from any food particles carried in by the haliotid's afferent respiratory current. Feeding activities of the host haliotid may free particles of algae into the water current. The broader site tolerance of the bonnet limpet on *Haliotis laevigata* needs explanation. *Haliotis improbulum* is found on rocky reefs; *H. laevigata* also occurs on rocks but it prefers areas of flatter reef with sandy patches, where there is a greater amount of suspended matter in the water (S. Shepherd, pers. comm.). Under these conditions *Hipponix conicus* is able to reach maturity at any site on a *Haliotis laevigata* shell although it prefers the anterior and right-hand edges.

Comparison with Cernohorsky's descriptions (1968) of *Hipponix conicus* revealed a number of differences in spawn, radula and animal color between South Australian and Pacific populations (see Table 1). In the light of this, a study of the anatomy and spawning habits of *Hipponix conicus* throughout its range would be of interest.

Table 1

Comparison of Pacific and South Australian *Hipponix conicus*

	Pacific [1]	South Australia
shell	white or white and brown	brown
proboscis	brownish-grey	blue-black
tentacles	yellowish with lateral or distal purple-brown or purple	blue-black
radula – median tooth	four lateral cusps	5 - 7 lateral cusps, the first overlapping the basal plate
spawn	36 brood sacs	5 - 10
embryos per sac	ca. 300	9 - 24
developmental stages in spawn mass	various	all the same

[1] from Cernohorsky, 1968

SUMMARY

Hipponix conicus (Schumacher) occurs on the shells of *Haliotis, Pleuroploca* and *Pterynotus* in South Australia. On *Haliotis, Hipponix conicus* individuals > 16 mm in length are females, those $2\frac{1}{2}$ - 16 mm and on or adjacent to mature females are males, while those $< 2\frac{1}{2}$ mm and all which are < 16 mm long but are isolated from females, are juvenile. Males situated on a female erode a communication notch in her shell margin. Too little evidence is

available to decide whether these *Hipponix* populations show protandrous hermaphroditism; absence of actual hermaphrodites and of any isolated males suggests that direct development of females may occur. Spawn is brooded under the female shell and is present at all seasons of the year although there is probably a peak of reproductive activity in the late winter (July - August).

Hipponix conicus prefers the anterior margin of *Haliotis* shells and I suggest that this position enables the bonnet limpets to gain maximum advantage from food particles carried by the haliotid's afferent respiratory current.

ACKNOWLEDGMENT

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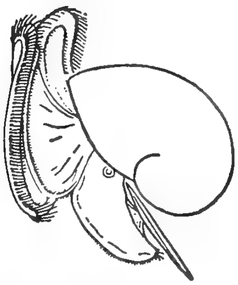

The pH Tolerance of Embryos and Larvae of the Coot Clam, *Mulinia lateralis* (SAY)[1,2]

BY

ANTHONY CALABRESE

Bureau of Commercial Fisheries, Biological Laboratory, Milford, Connecticut 06460

(2 Text figures)

INTRODUCTION

ESTUARIES ARE A MAJOR HABITAT of bivalve mollusks and are one of the most complex environments found in nature. The coot clam, *Mulinia lateralis* (SAY, 1822), is an ecologically important member of the estuarine fauna because it serves as food for many inshore species of animals, such as the scup, *Stenotomus chrysops* (LINNAEUS), and other fishes (VERRILL, 1873); the starfish, *Asterias forbesi* (DESOR, 1848), and the oyster drills, *Eupleura caudata* and *Urosalpinx cinerea* (SAY, 1822) (C. L. MACKENZIE, Jr., personal communication); and the greater scaup duck, *Aythya marila,* and the lesser scaup duck, *Aythya affinis* (CRONAN, 1957). Of the many interacting factors – biological, chemical, and physical – that affect bivalves in these waters, pH has received less attention than any other major variable.

In laboratory experiments LOOSANOFF & TOMMERS (1947) found that adult American oysters, *Crassostrea virginica* (GMELIN, 1791), kept in sea water at pH 4.25 remained open, on an average, 76% of the time, but pumped only 10% as much water as did the controls at pH 7.75. The pumping rate of oysters kept at pH 6.75 and 7.00 initially was greater than that of the control animals, but later decreased to less than that of the controls. PRYTHERCH (1928), who took pH measurements at several stations in Milford Harbor and the Milford area of Long Island Sound, found that it ranged from 7.2 - 8.4 during the day and suggested that oysters, *C. virginica,* spawned at pH 7.8 - 8.2 in these waters. On this basis he concluded that low pH inhibited oyster spawning and that oysters in Milford Harbor spawned at high tide because this was the only tidal stage at which the pH was between 7.8 and 8.2. CALABRESE & DAVIS (1969) found that the minimum and maximum pH levels at which American oysters were capable of spawning were 6.0 and 10.0, but that eggs and sperm released at pH 6.0 and 10.0 lost their viability within 2 - 4 hours, due to a combination of pH effects and aging.

KORRINGA (1941), quoting GAARDER (1932) and GAARDER & SPÄRCK (1932), stated that larvae of the European oyster, *Ostrea edulis* (LINNAEUS, 1758), died when the pH level in their oyster polls exceeded 9.0. CALABRESE & DAVIS (1966), who studied the effect of pH on embryonic development and survival and growth of larvae of *Crassostrea virginica* and the hard clam, *Mercenaria mercenaria* (LINNAEUS, 1758), found that some oyster larvae survived throughout a pH range from 6.00 - 9.00 but that satisfactory growth was limited to a pH range from 6.75 to 8.75. Some clam larvae survived between pH levels of 6.25 - 9.00, but growth of these larvae was satisfactory only within the pH range from 6.75 to 8.50.

Although the pH of oceanic waters ranges from 7.5 to 8.5, the pH levels in bays and estuaries may decrease to 7.0 or lower, due to dilution and production of H_2S (SVERDRUP *et al.,* 1942). Such bodies of water constitute a major habitat of bivalves, and DAVIS & CALABRESE (1964) suggested that these regions may be exceedingly important also as nursery grounds for the larval stages. Since bivalve larvae must encounter, at times, a wide range of pH in their natural habitat, it seems possible that success or failure of recruitment in some areas may be determined by such exposure.

The present study was designed to determine the pH tolerance of the embryonic and larval stages of coot clams under experimental conditions.

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[1] Part of a dissertation submitted to the Graduate Faculty of the University of Connecticut in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Contribution No. 60 from the Marine Research Laboratory, University of Connecticut.

METHODS

Methods for maintaining oysters, *Crassostrea virginica*, in spawning condition and obtaining fertilized eggs throughout the year and for spawning other species of bivalves and rearing their larvae were described by Loosanoff & Davis (1963). To determine the effect of pH on embryonic development of *Mulinia lateralis*, 12 000 to 15 000 fertilized eggs were placed into each of a series of 1-liter polypropylene beakers containing filtered, ultraviolet-treated sea water (salinity 27 ± 0.5‰) and test conditions were established. In 3 experiments fertilized eggs were placed in the beakers and the pH of duplicate cultures was adjusted with HCl or NaOH to levels ranging from 5.75 to 9.25 at 0.25-unit intervals. One pair of cultures maintained at the pH of the laboratory sea water (7.30 - 7.80) served as controls. All cultures were kept at ambient room temperature (21 ± 1°C). To determine the effect of pH on embryonic development, the larvae from each culture were collected on a stainless steel screen of mesh size small enough to retain them, after 48 hours at the experimental conditions. The larvae were resuspended in a 250-ml graduated cylinder and, after thorough mixing to assure random distribution of the larvae, a 4-ml quantitative sample was removed and preserved in 5% neutral formalin. The samples were examined under a compound microscope and the number of normal larvae that had developed was counted. The percentage of embryos developing to normal straight-hinge larvae at each pH level was calculated as a percentage of the maximum number developing normally in any pair of cultures in that experiment. The percentages reported in this study are the averages of the results in the 3 experiments.

Three additional experiments were run to determine the effect of various pH levels on the survival and growth of larvae. In each experiment a known number of larvae (usually 10 000 to 14 000), which had been reared to the 48-hour straight-hinge stage under normal conditions, were placed into each of the series of 1-liter beakers and the different pH levels established as above. The sea water in all cultures was changed 3 times a week to eliminate metabolic waste products and experimental conditions were reestablished. Supplemental algal food, consisting of *Isochrysis galbana*, *Monochrysis lutheri*, and *Chlorella* sp. (580) (Indiana University Collection No. 580), was added to each beaker daily, following the procedures of Davis & Guillard (1958). When food was added on days that the sea water was not changed, the pH was readjusted following the addition of food. In all larval experiments 50 mg/l of Sulmet were added to all cultures to prevent possible disease-induced mortality which might obscure the effects of the factor being tested. (Sulmet, sodium sulfamethazine, is a trade name of American Cyanamid Co. Mention of trade names does not imply endorsement of the product by the Bureau of Commercial Fisheries.) In all experiments the cultures were kept in a constant-temperature bath at 25 ± 1° C. Experiments were terminated when larvae in the fastest growing cultures reached setting size (6 - 8 days). Quantitative samples were taken from each culture at the termination of an experiment in a similar manner as for experiments with embryos. The number of larvae that had survived the experimental treatment was counted and 100 (if available) were measured to the nearest 5μ with an ocular micrometer in a compound microscope. The number of larvae surviving and the increase in mean length were calculated as a percentage of the maximum number surviving and maximum increase in mean length, respectively, in any one pair of cultures within that experiment. The method for determining the number of larvae surviving or the percentage of bivalve embryos developing into normal straight-hinge larvae is considered accurate to approximately ± 10% (Davis, 1958).

Since prior experience suggested that buffers were not adequate for maintaining desired pH levels for long periods of time (Calabrese & Davis, 1966), it was necessary to readjust the pH at approximately 12-hour intervals. The pH was measured with a line-operated, solid-state pH meter having a readability of 0.02 pH unit and a repeatability of 0.01 pH unit. The range and average pH for each initial pH established are shown in Figure 1.

EFFECT OF pH ON EMBRYONIC DEVELOPMENT

The percentage of *Mulinia lateralis* embryos developing normally, within the pH range from 7.25 to 8.25, did not vary significantly (Table 1 and Figure 2), but pH 7.75 appeared to be the optimum for such development. The percentage of fertilized eggs that developed normally was reduced to 59.5 at pH 7.00 and 61.8 at pH 8.50. Embryonic development decreased precipitously below pH 7.00 and above pH 8.50; only 26.5% and 5.1% of the embryos developed normally at pH 6.75 and 8.75, respectively. At pH 6.25 and pH 9.00 few or no embryos developed into shelled larvae.

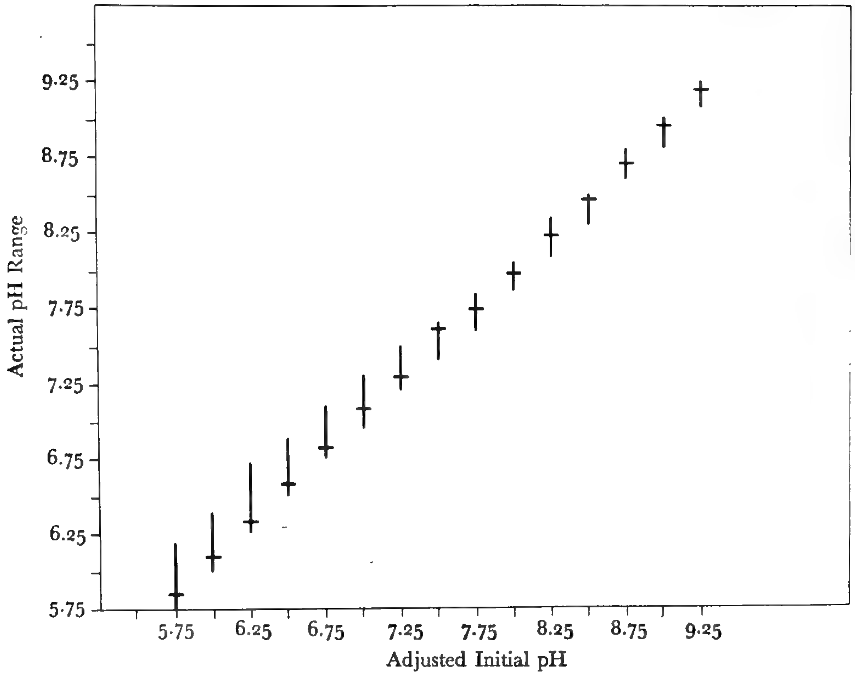

Figure 1

Maximum range of pH (vertical bar) and average pH (horizontal bar) for each initial pH. The "adjusted initial pH" was established at the beginning of each experiment and readjusted to this level at 12-hour intervals, by the addition of HCl or NaOH

EFFECT OF pH ON SURVIVAL

Survival of larvae increased sharply from 14.2% at pH 6.00 to 65.1% at pH 6.25, was about normal (70% or more of maximum) throughout the range from pH 6.50 to 8.75, and decreased sharply from 83.8% at pH 8.75 to 20.2% at pH 9.00 (Table 1 and Figure 2). No larvae survived at pH 9.25. Thus, the larvae were able to survive throughout a much wider pH range than the embryos.

EFFECT OF pH ON GROWTH

The pH range for satisfactory growth (70% or more of maximum) was 7.00 to 8.50 (Table 1 and Figure 2). Therefore, the range for normal growth was slightly narrower than the pH range of 6.50 to 8.75 for satisfactory survival. The maximum increase in mean length occurred at pH 7.25. The percentage increase in mean length varied only slightly within the pH range from 7.00 to 8.50, but below pH 7.00 and above 8.50 the rate of growth decreased rapidly.

IMPLICATION FOR DISTRIBUTION AND SURVIVAL IN NATURE

Embryonic development of *Mulinia lateralis* occurred within the pH range from 6.25 to 8.75, and some larvae survived from 5.75 to 9.00. The pH range for a satisfactory percentage of embryos to develop, however, was 7.25 to 8.25 and for survival of larvae it was 6.50 to 8.75. Even though a substantial percentage (65.1) of larvae was able to survive at pH 6.25, growth was negligible and good growth was not attained until pH 6.75 was reached. A significant percentage (83.8) of larvae survived at pH 8.75 and showed fair growth (50.4%). CALABRESE & DAVIS (1966) reported that *Mercenaria mercenaria* and *Crassostrea virginica* embryos developed normally within

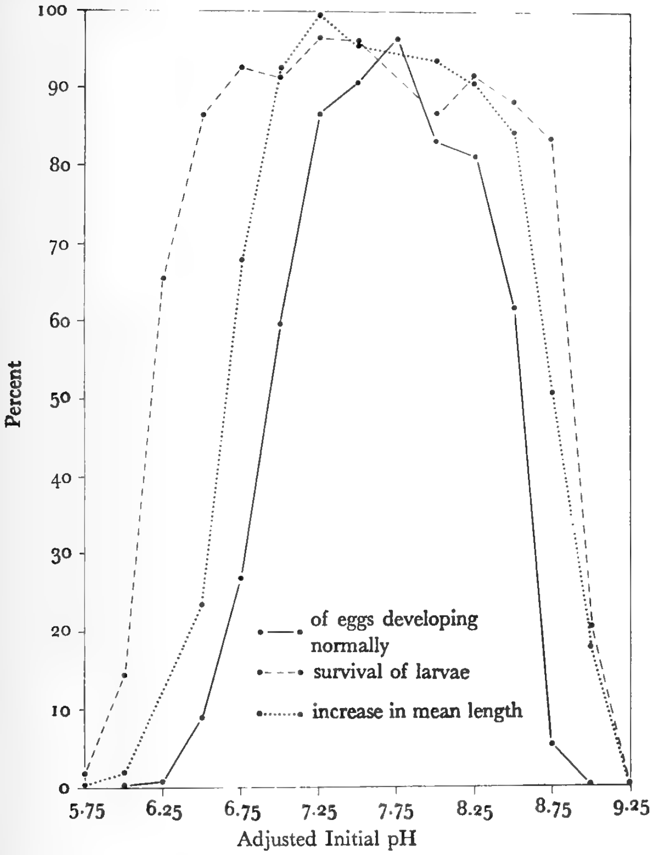

Figure 2

The pH tolerance of embryos and larvae of *Mulinia lateralis,* as indicated by percentage of embryos that developed normally, percentage of larvae that survived, and percentage increase in mean length of larvae

the pH range 7.00 - 8.75 and 6.75 - 8.75, respectively; thus, *Mulinia lateralis* embryos appear to be less tolerant to pH variations than either of these 2 species. *Mulinia lateralis* larvae attain maximum growth at a pH level lower than that reported for larvae of either *Mercenaria mercenaria* (pH 7.50 - 8.00) or *C. virginica* (pH 8.25 - 8.50), as reported by Calabrese & Davis (*op. cit.*). It can be concluded, therefore, that for successful recruitment of *Mulinia lateralis* the pH of the waters that form their principal habitat is limited primarily by the pH range for embryonic development; this range must not fall below 7.25 nor rise above 8.25.

Table 1

Percentage Development of *Mulinia lateralis* Embryos, Larval Survival, and Increase in Mean Length of Larvae at Various pH Levels[3]

pH	Percentage development of embryos	Percentage survival of larvae	Percentage increase in mean length of larvae
5.75	0.0	1.8	0.0
6.00	0.0	14.2	1.7
6.25	0.4	65.1	3.8
6.50	9.4	86.4	23.8
6.75	26.5	92.8	67.7
7.00	59.5	91.3	92.7
7.25	86.9	96.6	99.9
7.50	90.9	96.0	95.8
7.75	95.7	91.4	94.5
8.00	83.1	86.7	93.9
8.25	81.3	91.6	90.7
8.50	61.8	88.3	84.2
8.75	5.1	83.8	50.4
9.00	0.0	20.2	17.2
9.25	0.0	0.0	0.0

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[3] Development, survival, and increase in mean length are expressed as percentage of the greatest development, survival, and increase in mean length at any pH within that experiment. Figures are averages for duplicate cultures at each pH level in all 3 experiments.

Laboratory experiments have shown that high concentrations of silt can lower the pH of sea water to 6.40 (Calabrese & Davis, 1966), or below the lower limit for normal development of embryos of the coot clam. It is apparent, therefore, that heavy silting, or any pollution that can change the pH of sea water, could cause failure of recruitment of these clams.

SUMMARY

Some embryos of *Mulinia lateralis* developed into normal larvae from pH 6.25 to 8.75, but development was satisfactory (70% or more of maximum) only within the range from 7.25 to 8.25, and was highest at 7.75. Some larvae survived from pH 5.75 to 9.00, but survival was satisfactory (70% or more of maximum) only within the range from 6.50 to 8.75, and was highest at 7.25 to 7.50. Larvae grew satisfactorily within the pH range from 7.00 to 8.50; pH 7.25 was the optimum for growth.

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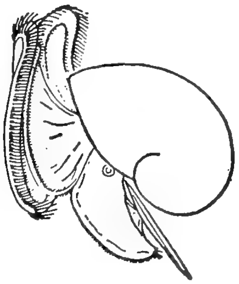

The Relationship between the Number of Varices and Total Shell Length in Some New Zealand Cymatiidae

(Gastropoda : Prosobranchia)

and its Ecological Significance

BY

J. H. LAXTON

Department of Zoology, University of Queensland, Brisbane, Australia 4067

(1 Plate; 6 Text figures)

MEMBERS OF THE MOLLUSCAN family Cymatiidae exhibit an extreme form of discontinuous growth (LAXTON, 1970). Individuals of a species may grow rapidly, adding half a whorl to their shells in a few weeks, after which shell growth ceases for periods ranging from a month to as long as two or more years. A flared lip or varix, bordering the shell aperture, is laid down at the end of each growth period. These varices are partially buried by succeeding whorls and provide a permanent, visible record of the number of growth stages taken by an animal to produce its shell. Varix production in the cymatiids studied is neither an annual nor seasonal phenomenon, and is in no way indicative of the age of an individual. MACKENZIE (1960) reached the same conclusion regarding varix production in the muricid gastropod *Eupleura caudata*.

For a particular cymatiid species, the distribution of varices on the shell appears to be regular, with the angle between one varix and the next more or less constant. Thus, within a species, shells with the same number of varices may be expected to have approximately the same total length provided the spiral pattern of the shells remains constant throughout growth.

The distribution of varices was examined for 13 species of Recent New Zealand cymatiids. Both inter- and intra-specific variations were examined and an attempt was made to link intra-specific differences to environmental conditions, especially food availability.

MATERIALS AND METHODS

The shells of 13 species of New Zealand cymatiids were examined and the total shell length, number of varices, the position of the first varix and the angle between successive varices (measured about the protoconch), were recorded for each individual. For each of the common species {*Mayena australasia* (PERRY, 1811), *Monoplex australasiae* PERRY, 1811, *Cabestana spengleri* (PERRY, 1811), *Charonia rubicunda* (PERRY, 1811) and *Ch. capax* FINLAY, 1926} several populations from different habitats were analysed separately.

The rarer species {*Austrosassia parkinsonia* (PERRY, 1811), *Cabestanimorpha exarata* (REEVE, 1844), *Argobuccinum ranelliformis tumidum* (DUNKER, 1802), *Ranella olearium* (LINNAEUS, 1758), *Cymatoma tomlini* POWELL, 1955, *Annaparenna verrucosa* (SOWERBY, 1825), *Cabestana waterhousei segregata* POWELL, 1933, and *Fusitriton laudandum* FINLAY, 1926} were examined from shells in private and museum collections. Supplementary observations were made on live material whenever it became available.

Estimates of the abundance of simple ascidians, upon which some of the commoner species feed, were made by measuring the percentage cover using a 1/10 m^2 quadrat.

RESULTS

Three distinct growth patterns can be recognised, and these are characterised by *Mayena australasia, Cabestana spengleri* and *Monoplex australasiae* (see Plate).

Mayena australasia

In *Mayena australasia* the first varix is formed approximately half a whorl from the protoconch and subsequent

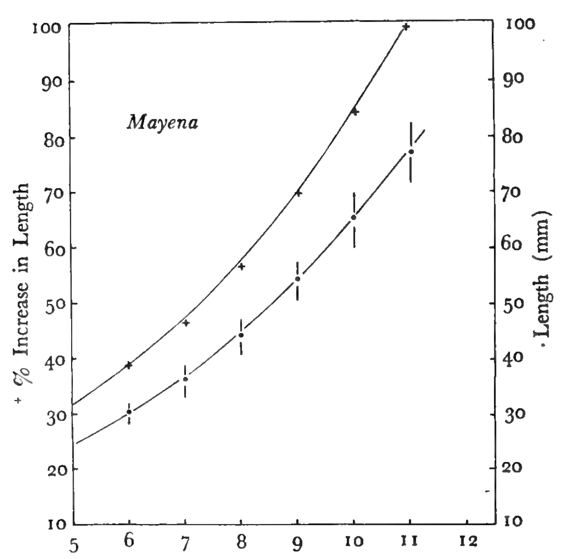

Figure 1

Percentage increase in shell length per varix (+) and mean length and standard deviation (●) plotted for each varix number in *Mayena australasia*

varices are laid down at regular intervals until the adult size is reached. Figure 1 shows the mean shell length and standard deviation for varices 5 - 12 in the *M. australasia* sampled. Animals with less than 5 varices were not found in sufficient numbers to be included in the analysis. Variations between individuals for each varix number is small, giving a regular increase in length with the addition of each new varix. No significant deviation from this pattern is noticeable when individual populations are analysed, so data have been pooled to give Figure 1. When the angle between each successive varix and the next is plotted as an angle frequency diagram for each varix (Figure 2), the most frequent value is in the region of 180° with a total range of 150° - 240°. Length frequency data plotted on the same diagram for varices 6 - 10 correspond closely to the shape of the angle frequency histograms for a particular varix. This indicates that the variation in length for each varix is generated by slight differences in the angles between varices, producing slightly longer or shorter shells.

Charonia capax, Ch. rubicunda, Annaparenna verrucosa, Austrosassia parkinsonia, Argobuccinum ranelliformis tumidum, Fusitriton laudandum, Ranella olearium and *Cymatoma tomlini* are other cymatiid species found in New Zealand waters which exhibit an apparently similar growth pattern.

Table 1

The relationship between abundance of simple ascidians on the substrate and the ratio of animals with 5 : 4 : 3 : 2 whorls before the first varix, in the population of *Cabestana spengleri*. The ascidian species at Ahipara is unidentified and at the remaining localities *Microcosmus kura* Brewin is the dominant ascidian.

Area	Locality	Ratio of 5 : 4 : 3 : 2 whorl animals	% of 5 & 4 whorl animals	% cover of ascidians
Exposed West Coast				
	Ahipara	0 : 43 : 10 : 0	81.1	60 – 70
West Coast Harbour				
	Mill Bay	3 : 56 : 1 : 0	98.3	50 – 60
	Mill Bay (Fringe)	0 : 0 : 3 : 0	0.0	0.5
East Coast Harbour				
	Parengarenga (Te Hapua)	3 : 12 : 5 : 0	75.0	40 – 50
Whangarei Heads				
	McDonald Bank	0 : 13 : 0 : 0	100.0	50 – 60
	McLeod Bay (N)	0 : 29 : 3 : 0	78.3	30 – 40
	McLeod Bay (S)	0 : 7 : 5 : 0	58.3	10
	Taurikura	0 : 10 : 11 : 0	47.6	10
	Reotahi	0 : 2 : 5 : 0	40.0	5 – 10
	Urquhart's Bay	0 : 3 : 10 : 0	23.0	2

The correlation coefficient between the percentage of 5 & 4 whorl animals in the population and the percentage cover of ascidians in the area is 0.98

Cabestana spengleri

In *Cabestana spengleri* there is considerable variation in the position of the first varix. It may be laid down either 2, 3, 4 or 5 whorls from the protoconch.

Populations of *Cabestana spengleri* have been analysed in 3 groups based on broad habitat differences. They are:

(**a**) The Mill Bay population – which lives on silty, ascidian covered, low-tidal rocks in the relatively sheltered west coast Manukau Harbour.

(**b**) The Ahipara population – which lives intertidally on an exposed rocky shore in the far North (Figure 3).

(**c**) A North Island East Coast population – which consists of a number of groups of animals living both intertidally and in shallow water. Animals from the Whangarei Harbour area are not included in this group but were analysed separately (Table 1).

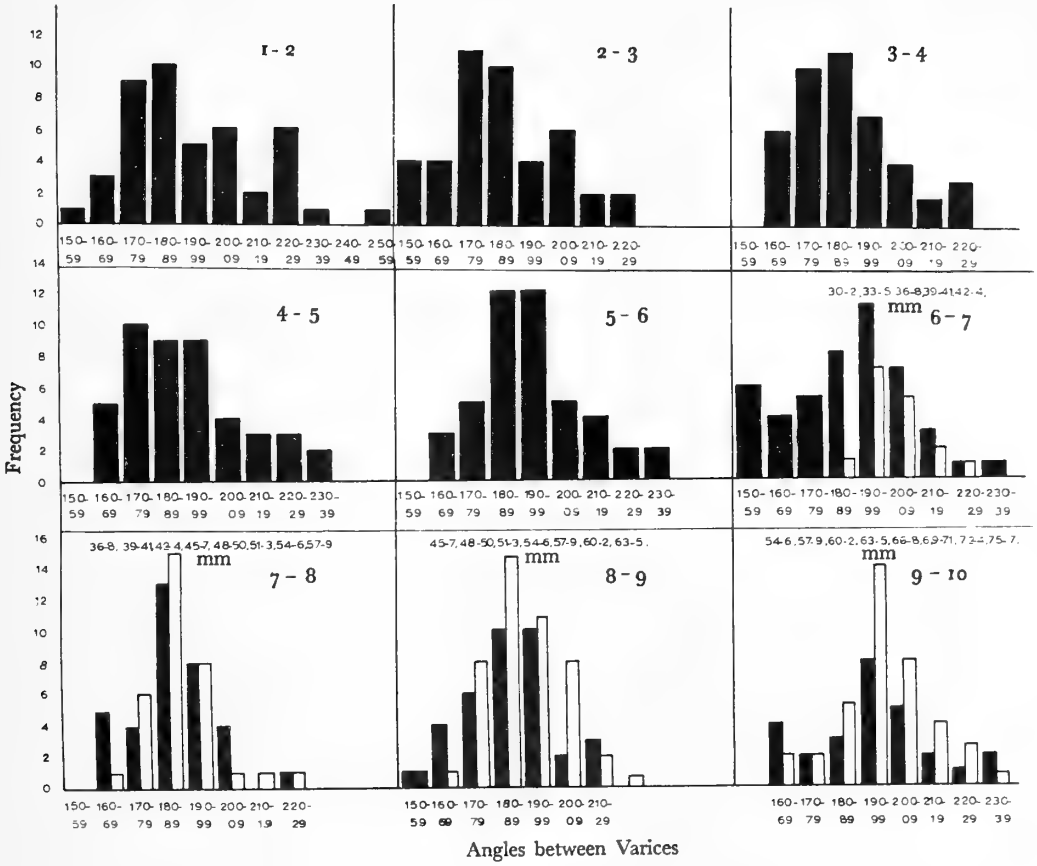

Figure 2

Angle frequency histograms (black blocks) and corresponding length frequency histograms (white blocks – varices 6 - 10) for each varix in *Mayena australasia*

Figure 4 shows the relationship between the varix number and total shell length for the 3 populations. There is little difference between the Mill Bay and Ahipara populations, but considerable variation exists between these and the North Island East Coast population. The percentage increase in length for each varix added (Figure 5), however, is practically the same in both groups, the only difference being the length reached by the juveniles before the first varix is secreted. The reason for there being only 3 varices present on the shells of adult *Cabestana spengleri* from Ahipara (Figure 4) is that sexual maturity is reached at a smaller size than in animals from Mill Bay, due to the limited amount of ascidian food available to support a relatively dense population (LAXTON, 1970a).

Angle frequency data for the first 3 varices of the Mill Bay population and the North Island East Coast population (Figure 6) show that the most common angle between one varix and the next lies between 180° and 210° with a total range of 160° to 260°. Length frequency histograms have the same general shape as the angle frequency graphs showing, again, that small differences in the angles between one varix and the next cause the observed variations in shell length for each varix number within a population. Thus, the shell length at which the first varix is laid down in *Cabestana spengleri* determines the final shell length for a given number of varices, since the angle between each two varices is more or less constant.

Since *Cabestana spengleri* grows rapidly without any major interruption until the first varix is secreted, large amounts of food (simple ascidians) must be required to sustain this growth rate. In Table 1, the ratio of animals

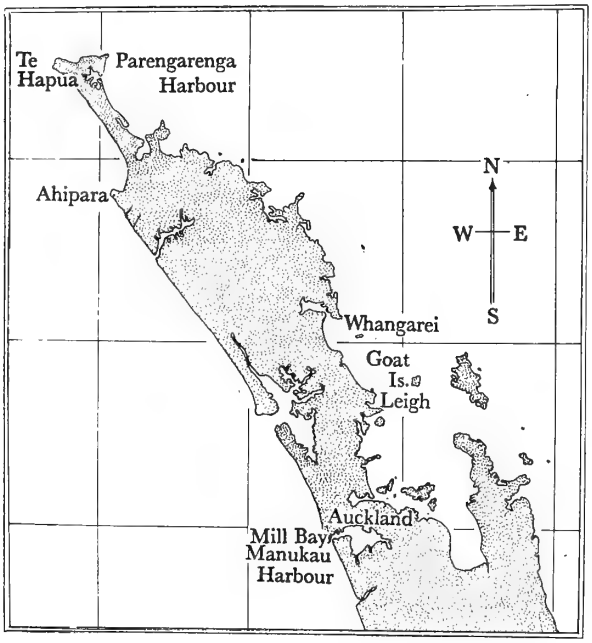

Figure 3

Map of Northland, New Zealand showing the study areas

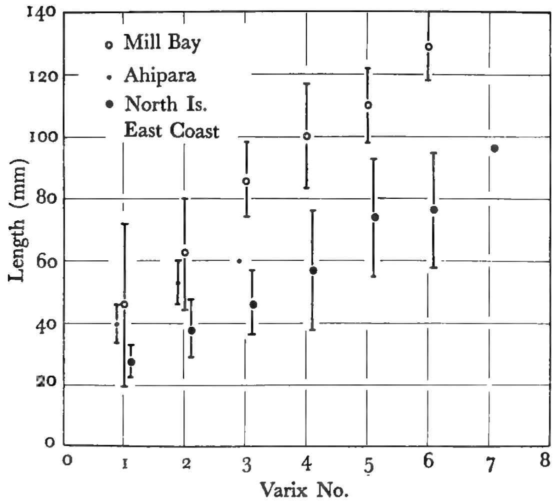

Figure 4

Mean shell length and standard deviation plotted against varix number for 3 populations of *Cabestana spengleri* in Northland, New Zealand

with either 2, 3, 4, or 5 whorls before the first varix and the percentage cover of ascidians on the substrate are shown for several areas in Northland, New Zealand (Figure 3).

Cabestana waterhousei segregata is another New Zealand cymatiid with a growth pattern apparently similar to that of *Cabestana spengleri.*

Monoplex australasiae

The growth pattern of *Monoplex australasiae* is different from that of the other 2 already described. This species is unusual because by the time adult size has been reached only a single labial varix has been formed. Growth is still discontinuous, but instead of a solid calcareous varix being laid down at the end of each growth period, a horny fringe of periostracum is secreted. The distance between fringes is irregular and indicative of the growth rate; short ones indicate a slow rate while longer ones denote rapid growth.

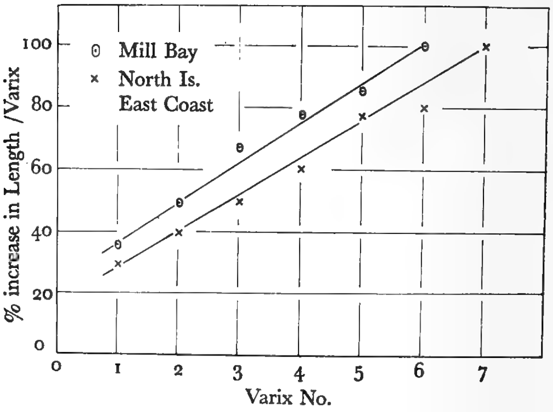

Figure 5

Percentage increase in length per varix plotted against varix number for the Mill Bay and the North Island East Coast populations of *Cabestana spengleri*

The labial varix may be formed 3, 4, 5 or 6 whorls from the protoconch, depending on the amount of available food in the area in which the animal is living. In a small number of older individuals a second varix, added some years after the first, may be present, showing that growth may be resumed under favourable conditions. There is considerable variation in the angle between the first and second varix from animal to animal, unlike both *Cabestana spengleri* and *Mayena australasia.*

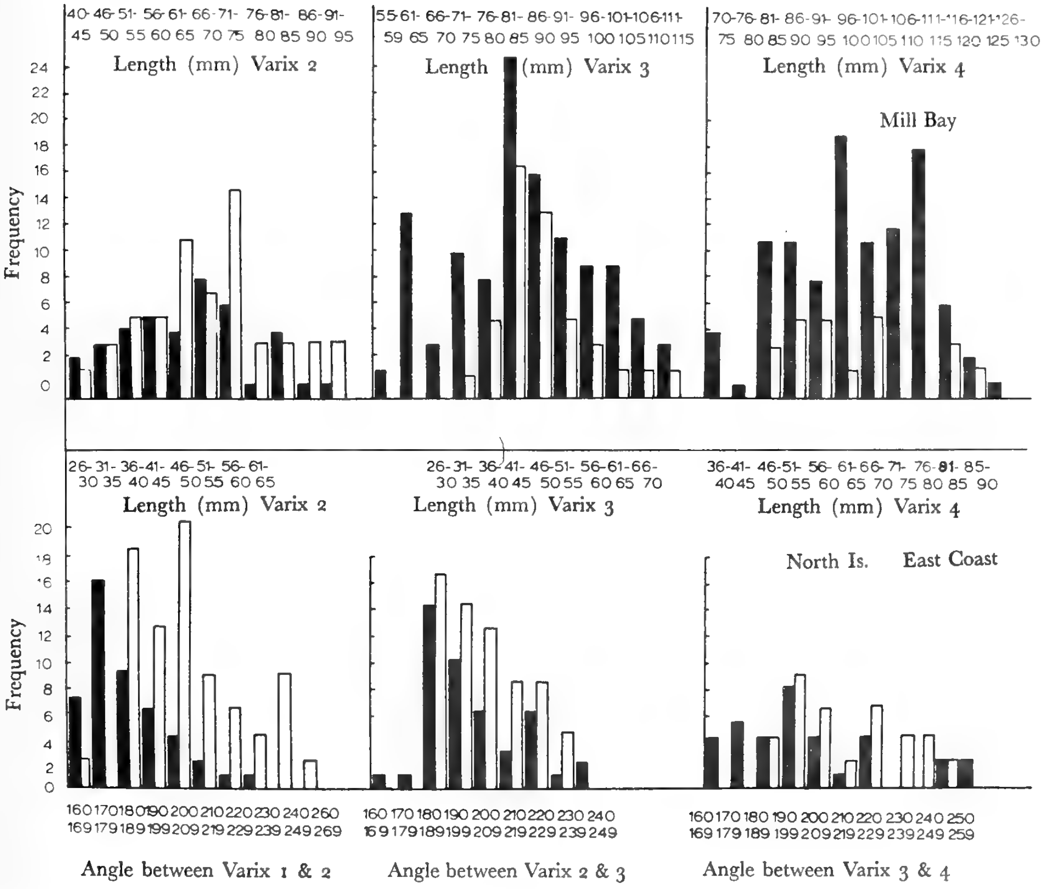

Figure 6

Angle frequency histograms (black blocks) and corresponding length frequency histograms (white blocks) plotted for the first 3 varices of the Mill Bay and North Island East Coast populations of *Cabestana spengleri*

Cabestanimorpha exarata apparently exhibits a similar growth pattern although a second varix is more common.

DISCUSSION

According to HUXLEY (1932), "The majority of animals show unlimited growth; they continue growing, though usually at a constantly diminishing rate, until they die,..." Although many molluscs also show indeterminate growth, some families of prosobranch gastropods have determinate growth. Members of the Strombidae and Cypraeidae (FRANK, 1969) and probably the Struthiolariidae, Cerithiidae, Cassidae and some Volutidae grow continuously until adult size is reached, after which there is no further increase in size. The varix producing families Bursidae, Cymatiidae and Muricidae also exhibit a determinate growth pattern, upon which their system of discontinuous growth has been superimposed.

In the majority of cymatiids studied, growth ceases after a certain size has been reached and this is followed by an adult phase of constant size and long duration.

Three distinct types of growth pattern have been described for the Cymatiidae which impose varying degrees of restriction on the animals. In the first type, illustrated by *Mayena australasia,* the shell growth pattern is rigorously controlled, providing little opportunity for the animal to adapt to environmental changes. The first varix is laid down close to the protoconch and subsequent varices are formed at approximately half-whorl intervals. This means that *M. australasia* cannot respond readily to an increased food supply by substantially increasing its growth rate, apart from varying the angle of shell added before the next varix is secreted. Some individuals have been observed to grow through nearly twice the normal angle during one growth period while the succeeding angles remained constant. This can be interpreted as a response to increased food supply during that particular phase of growth. The only other way available for *M. australasia* to respond to increased food supply is to add two half-whorls in succession. There is still a delay, however, while the varix is formed and the shell is partially thickened, before shell growth can be resumed.

The shell growth pattern of *Cabestana spengleri* is more flexible and susceptible to environmental influences. The first varix is laid down at varying distances from the protoconch depending on the amount of available food during the early stages of growth. Table 1 shows that the proportion of animals with 5 and 4 whorls before the first varix increases as the percentage cover of simple ascidians, and hence the amount of available food, increases. It is also noticeable that in a heavily populated region like Mill Bay, where the abundance of ascidians is reduced towards the fringes of the area, the ratio of 5:4:3:2 whorled animals changes markedly. There is a greater proportion of 2- and 3-whorled animals towards the periphery of the population. Animals from these fringe areas are responsible for the large standard deviations calculated for the lengths up to the first 2 varices when the population is considered as a whole (Figure 4).

Growth following the laying down of the first varix is subject to the same restrictions as in *Mayena australasia,* with subsequent varices being laid down at half-whorl intervals.

In Foveaux Strait, at the southern tip of New Zealand, *Cabestana spengleri* reaches a very large size. This is due to a slow, rather than rapid initial growth rate. Usually there are only 3 whorls before the first varix. This means that the shell length by the time the 7th varix is secreted is considerably less than that of a 7-varix northern specimen with 4 or 5 whorls before the varix. Under these circumstances an 8th half-whorl may be added, producing a shell of about 190 mm. It is unlikely that a northern 4- or 5-whorl animal could add an 8th varix because the resulting shell would be in excess of 230 mm. This is some 40 mm greater than the largest *Cabestana spengleri* recorded for the New Zealand region.

A latitudinal or temperature effect could be involved (Frank, 1969) whereby an animal may grow slowly, but become larger and older near the edge (colder) of its distribution. This implies that the growth rate of *Cabestana spengleri* increases with rising water temperature the further north it occurs, and that growth ceases at a smaller size. While this may be partly true, there are some notable exceptions. For example, in Northern New Zealand, tiny individuals occur with only 2 whorls before the first varix, indicating a slow initial growth rate. These animals are often heavily encrusted and eroded suggesting that they are considerably older than their size indicates. An important feature of the areas in which these small animals live is the paucity of ascidian food. Thus, although temperature may influence the growth rate, it is the abundance of food in the area which permits this rate to be realised.

Further possible evidence that food affects the growth rate comes from the following observation. When a growing *Cabestana spengleri* which had just commenced growing was removed from its food supply, the half-whorl in the process of secretion was completed but no further growth occurred. When the animal was returned to its natural food supply some months later, feeding was intense and within a month a further half-whorl was added to the shell.

Shell growth in *Monoplex australasiae* is subject to none of the morphological restrictions of the preceding two species. Growth may continue as long as there is available food. Whenever a temporary halt in growth occurs, a fringe of periostracum is laid down quickly (complete within two days) and growth may be resumed immediately, if necessary. Even after a calcareous varix has been added to the shell, further unrestricted growth is still possible if conditions permit.

Plate Explanation

Figure *7*: Dorsal view of the shells of *Mayena australasia, Cabestana spengleri,* and *Monoplex australasiae* illustrating the different types of growth pattern

Figure *8*: Aperture views of the same 3 animals (arrows indicate the position of the first varix)

Erratum: On the facing Plate read Figure 7 instead of Figures 1, 2, and 3, and Figure *8*, instead of Figures 4, 5, and 6.

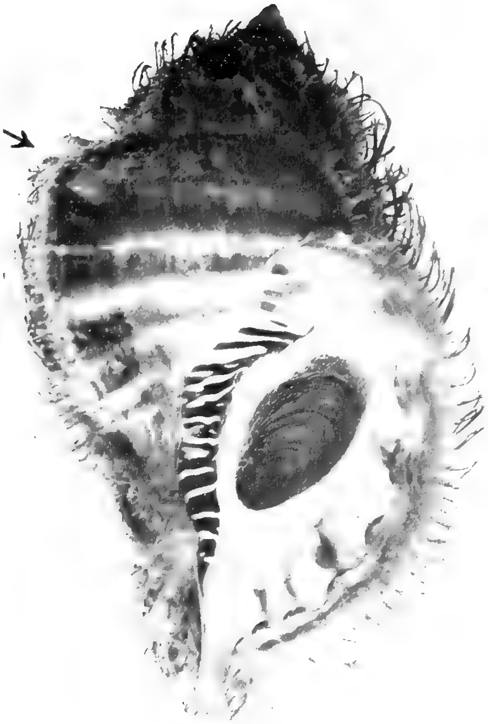

Figure 1

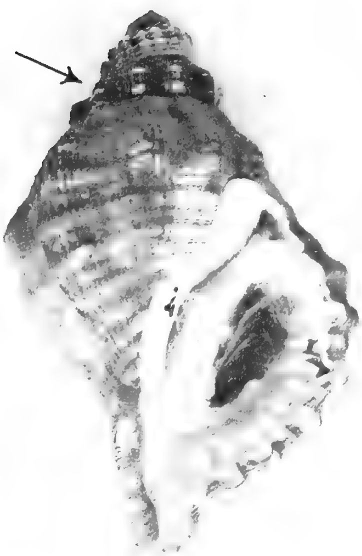

Figure 2

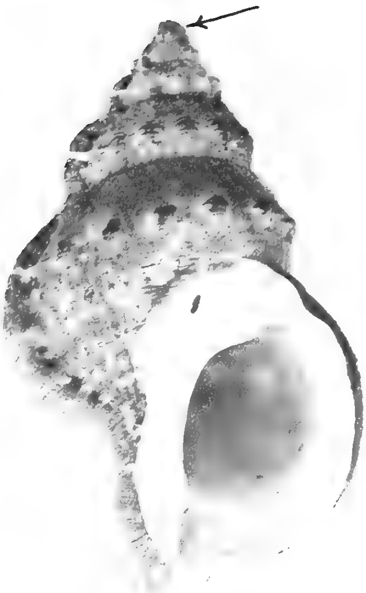

Figure 3

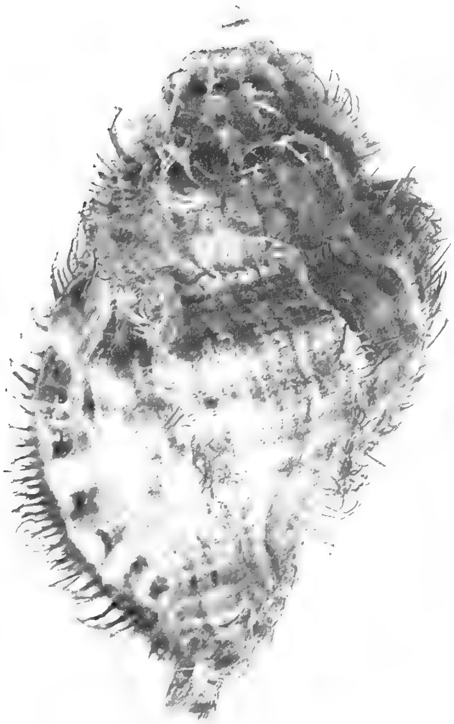

Figure 4

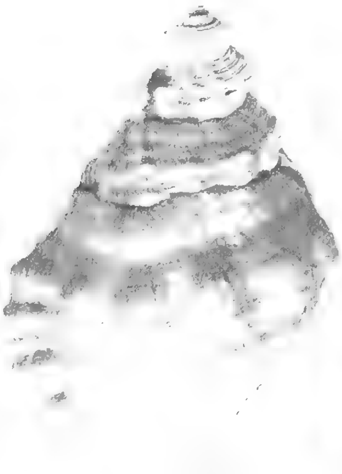

Figure 5

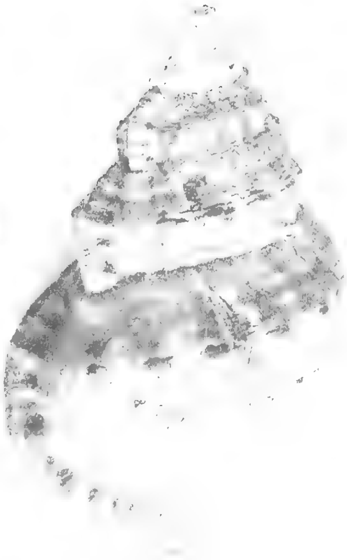

Figure 6

As has been pointed out already, the distance between fringes of periostracum varies in *Monoplex australasiae,* indicating changes in the growth rate. The cause of this changing rate is obscure and does not appear to be correlated with changes in food supply. In an area like Mill Bay, where ascidian food is super-abundant, animals with widely varying distances between fringes occur alongside individuals where the distances are extremely regular. As has been suggested (Laxton, 1970a), periodic halts to shell growth may be necessary in rapidly growing animals because shell growth exceeds tissue growth to such an extent that a balance can only be restored by temporarily halting shell secretion. This does not, however, explain why the distances between fringes varies in some individuals and remains constant in others.

In *Mayena australasia,* and other cymatiids with a similar growth pattern, determinate growth, coupled with the rigid system of varix production, renders the animals incapable of substantially altering their growth rate in response to changes in the food supply. In *Cabestana spengleri* and *Monoplex australasiae,* however, there is a progressive move away from determinate growth towards a form of indeterminate growth. In *Monoplex australasiae,* this form of indeterminate growth has been arrived at by modification of the original cymatiid determinate pattern, possibly via an intermediate stage similar to the one now seen in *Cabestana spengleri.* This increased flexibility allows considerable alteration of the growth pattern to take advantage of favourable conditions.

The question now arises: what is the cause of the halt in shell growth resulting in the formation of a varix? It is not seasonal nor confined to the breeding period although feeding ceases, at least in the females, while the eggs are laid and incubated (Laxton, 1969). In *Mayena australasia* the females go without food for the entire 3 months of their breeding season. *Cabestana spengleri, Monoplex australasiae* and *Mayena australasia* are carnivores which graze on simple ascidians (Laxton, 1970b), which generally occur, at least in some of the localities studied, in super-abundant supply over the entire year. Thus, a varying food supply does not cause the discontinuous growth. The only cymatiid species in which food is limited are *Charonia capax* and *Ch. rubicunda* which feed spasmodically on a variety of echinoderm species. Growth does not, however, appear to be linked to periods immediately following feeding. Specimens of *Charonia* which have been provided (for long periods) with regular meals of starfish in quantities far in excess of that normally consumed in nature do not appear to alter their growth pattern. While growth ceased when the growing *Cabestana spengleri* was removed from its food supply, it was not until the half-whorl in the process of being secreted had been finished. In fact, *C. spengleri* could not be induced to cease shell secretion at any stage other than when about 180° had been added. The only time that angles between varices substantially less than 180° were observed was in the last varix of very old, probably senile animals in which the shell had become grossly deformed.

This suggests that the growth pattern may be genetically controlled in cymatiids rather than a result of environmental or behavioural rhythms. Relaxation of this rigid control has allowed *Cabestana spengleri* and *Monoplex australasiae* greater freedom to respond to changes in conditions. It must be remembered, however, that this freedom can only be exercised in *Cabestana spengleri* during the period prior to the laying down of the first varix, since subsequent growth takes place in half-whorl additions.

The actual adaptive significance of discontinuous growth in the Cymatiidae remains unknown as it does not appear to be connected with any natural cycle but it does permit the animals to grow very quickly when conditions are favourable.

Monoplex australasiae is distributed widely throughout the Pacific region and has successfully colonised an extremely wide range of habitats ranging from the most exposed to the most sheltered coasts. It also occurs on soft and rocky shores and extends into deeper off-shore waters. A greater variety of food organisms is consumed by *Monoplex australasiae* (simple ascidians, bivalves and possibly some worms) than any of the other cymatiid species studied. The flexible growth pattern may have contributed, at least in part, to this species' success at colonising new ecological situations made available to it through its long-lived free-swimming larval period.

Thus, within this family, the type of shell growth may have had a profound effect on the success and adaptability of the member species.

ACKNOWLEDGMENTS

I wish to thank Dr. A. W. B. Powell for permitting me to examine collections in the Auckland Museum, and members of the Conchology Section of the Auckland Museum for making their private collections available. I am also grateful to Mr. S. L. Smith for making some of the apparatus used in this study and I wish to thank Mr. W. Stablum for taking and preparing the plates. Sincere thanks are due to Dr. J. F. Grassle for discussion and criticism of the manuscript and to Mr. D. J. Gravatt for reading and correcting the script.

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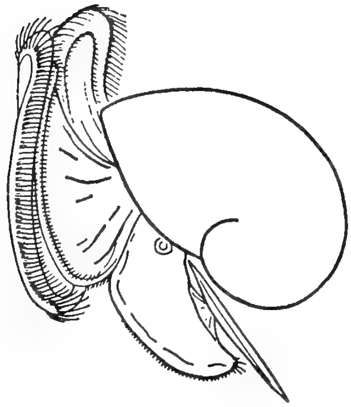

The *Nerita ascensionis* Species Complex in the South Atlantic

(Gastropoda : Prosobranchia)

BY

GEERAT J. VERMEIJ

(1 Plate)

In the summer of 1969 James W. Porter and I had the opportunity to visit Ilha Fernando de Noronha, a volcanic island of about 17 square kilometers at 3°52′S, 32°26′W, some 200 miles off the coast of Ceará, northeast Brazil. During our stay, molluscs were collected in connection with my investigation into the functional shell morphology of high-tidal gastropods and into marine biogeographical problems associated with isolated oceanic islands. Examination of the material has revealed several taxonomic problems, one of which, concerning the *Nerita ascensionis* species complex, is discussed in this paper.

I wish to thank James W. Porter for his assistance in the field work, and the government of the Federal Territory of Fernando de Noronha for permission to visit the island and for its cooperation during our stay. I am further indebted to Dr. Kenneth J. Boss and Mr. Robert J. Bullock for their assistance while I was studying the collections at the Museum of Comparative Zoology, Harvard University.

SYSTEMATICS

The genus *Nerita* is represented at Fernando de Noronha by a single species, which occurs abundantly along the entire shoreline from the intertidal zone to somewhat above high tide line. Smith (*in* Ridley, 1890) and Lopes & Alvarenga (1955), in their respective compilations of molluscs from the island, list the species as *N. ascensionis* Gmelin, 1791. Matthews & Rios (1967) list *N. fulgurans* Gmelin, 1791 from the island, but this record is of very doubtful validity because of the considerable gross similarity between *N. fulgurans* and *N. ascensionis* (see below).

Nerita ascensionis is also recorded from the type locality (Ascension Island) and from the island of Trindade ("South Trinidad"), off southeast Brazil (Smith, 1881, 1890b), but is not known from St. Helena (Smith, 1890a; Colman, 1946) or the mainland coast of Brazil (Lopes & Alvarenga, 1955). An examination of specimens from the 3 islands from which *N. ascensionis* is known reveals some small but consistent differences in the shell between populations. On the basis of these differences, the 3 populations are here separated as 3 subspecies of one oceanic South Atlantic species. It must be remembered, however, that the mutual allopatry or near allopatry of the populations precludes a more objective assignment of their taxonomic rank at this time. The rank "subspecies" is given to these populations only to point out the close relationships between them, and because the magnitude of the differences is small.

The following names are introduced here:

Ascension Island population: *Nerita (Theliostyla) ascensionis ascensionis* Gmelin, 1791
Fernando de Noronha population: *Nerita (Theliostyla) ascensionis* ***deturpensis*** Vermeij, subspec. nov.
Trindade population: *Nerita (Theliostyra) ascensionis* ***trindadeensis*** Vermeij, subspec. nov.

Nerita (Theliostyla) ascensionis ***deturpensis*** Vermeij, subspec. nov.

Description: Shell thin but strong, moderately depressed (height:length ratios from 0.70 to 0.77 in shells greater than 20.0 mm wide), greatest linear shell diameter (width) up to 30.4 mm; spire low, consisting of 3 - 4 whorls, often considerably corroded. External shell surface black, sculptured with 14 - 18 weak to moderately strong spiral ribs which are strongest near the suture; sometimes the ribs may disappear during ontogeny, so that the shell becomes smooth or nearly so in later stages of growth. Parietal area plane to somewhat concave, smooth to very weakly pustulose, bright light orange in color; edge of parietal area with 2 rather weak median teeth, the posterior one being the more strongly developed. Aperture proper (opening between outer lip and edge of parietal area) quite wide; outer lip somewhat thickened within, with about 16 very weak teeth, which are generally absent in young specimens; the posteriormost of these teeth is much the largest, but is still poorly developed in comparison to other members of the subgenus; no large anterior tooth on outer lip. Operculum calcareous, thin; outer surface very slightly convex, brownish in color, with numerous darker-colored pustules.

Types: Holotype – MCZ No. 262991. Width 24.8 mm, length 17.4 mm, height 13.8 mm.

Type Locality: Praia da Atalaia, south coast of Ilha Fernando de Noronha, collected 28 June 1969 by J. W. Porter and the author.

Paratypes: MCZ No. 262992, from the type locality; Yale Peabody Museum No. 15818, Baía de Sueste, south coast of Ilha Fernando de Noronha, collected 27 June 1969 by J. W. Porter and the author. Measurements of the paratypes are given in Table 1.

Table 1

Measurements of the Paratypes of *Nerita ascensionis* ***deturpensis*** Vermeij, subspec. nov.

Width (mm)	Length (mm)	Height (mm)	Locality
22.4	16.5	12.3	Sueste
21.5	16.1	12.4	Sueste
20.5	14.5	11.4	Sueste
20.0	14.1	11.0	Sueste
25.5	17.5	14.3	Atalaia

This subspecies is named after DETURP (Departamento de Turismo e Relações Publicas), where James W. Porter and I were guests during our stay on Fernando de Noronha.

Nerita ascensionis ***deturpensis*** differs from the typical *N. a. ascensionis* in having much weaker spiral ribs and in the markedly more brilliant light orange of the parietal area. In *N. a. ascensionis,* furthermore, the outer lip never possesses teeth, and the spiral ridges are invariably strong and rugose. The teeth at the edge of the parietal area are somewhat more strongly developed than in the typical *N. a. ascensionis.*

Nerita (Theliostyla) ascensionis ***trindadeensis*** Vermeij, subspec. nov.

This subspecies is very similar to *Nerita ascensionis* ***deturpensis,*** but teeth on the outer lip are barely developed, and are in any case never as strong as in the populations from Fernando de Noronha. The parietal area is colored a very pale light orange, being similar in this respect to typical *N. a. ascensionis.*

Types: Holotype – MCZ No. 262990; width 24.2 mm, length 17.4 mm, height 13.0 mm.

Type Locality: Trindade Island.

Paratypes: MCZ No. 216920, from the type locality. Measurements of selected paratypes are given in Table 2.

Discussion: Table 3 and Figure *1* [(E)] summarize the differences between the 3 subspecies of *Nerita ascensionis.* From these it is evident that the population from Trindade is morphologically much closer to that from Fernando de Noronha than either is to the typical *N. a. ascensionis.*

Nerita ascensionis stands somewhat apart from other species in the subgenus *Theliostyla* by the absence or very slight development of pustules on the parietal area. In this respect the species appears to be most closely related to the West African *N. atrata* Gmelin, 1791 which is, however, generally without spiral ornament. Of the 4 western Atlantic species in the genus *Nerita* (Russell, 1941), *N. fulgurans* Gmelin, 1791 most closely resembles *N. ascensionis.* It differs from the latter species,

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[(E)] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Plate Explanation

Figure 1

Comparisons between *Nerita ascensionis ascensionis* and *Nerita ascensionis* ***deturpensis***

a: *Nerita ascensionis ascensionis,* ventral view
b: *Nerita ascensionis ascensionis,* dorsal view
c: *Nerita ascensionis* ***deturpensis,*** holotype, ventral view
d: *Nerita ascensionis* ***deturpensis,*** paratype (Atalaia), dorsal view

Figure 2

Ventral view of holotype of *Nerita ascensionis* ***trindadeensis***

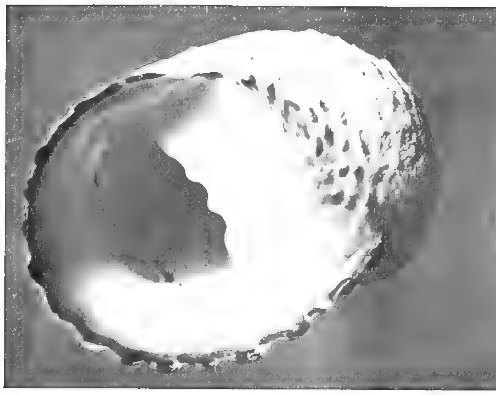

Figure 1a

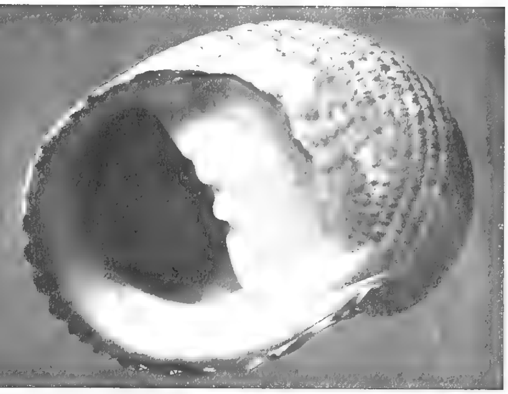

Figure 1c

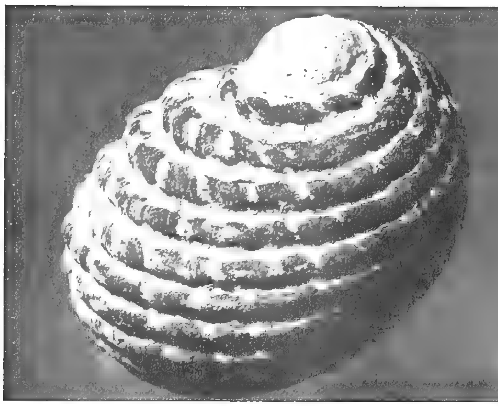

Figure 1b

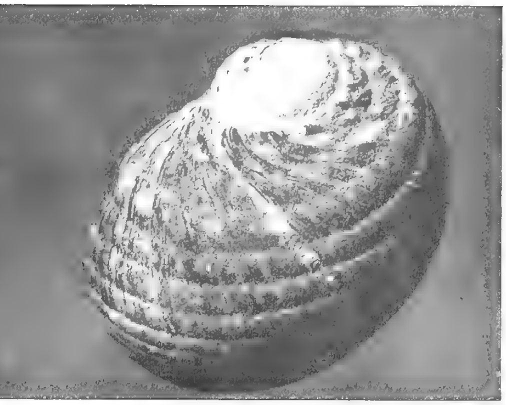

Figure 1d

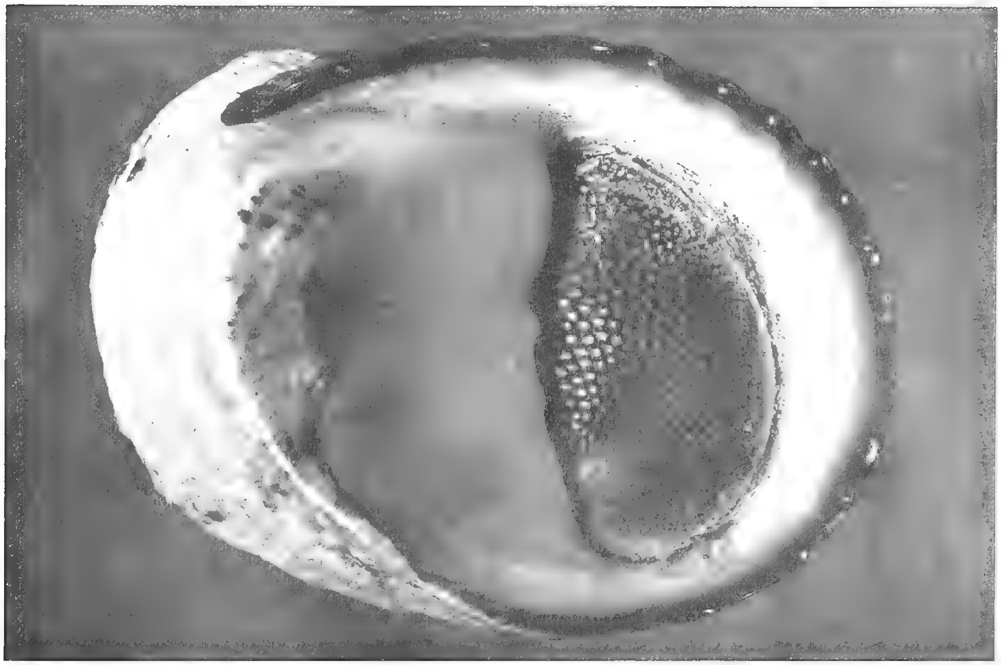

Figure 2

Table 2

Measurements of Selected Paratypes of *Nerita ascensionis* ***trindadeensis*** Vermeij, subspec. nov.

Width (mm)	Length (mm)	Height (mm)
27.0	20.0	15.1
22.7	16.6	11.7
22.5	16.7	21.7
22.4	16.2	12.6
20.0	15.7	10.7

however, in possessing a lower spire, more numerous spiral ridges, more strongly toothed outer lip, strongly pustulose parietal area, a bluish white to gray operculum, and different external coloration. *Nerita ascensionis* differs from spirally ribbed specimens of *N. peloronta* Linnaeus, 1758 by possessing a lower spire, light orange rather than red parietal area, much weaker median parietal teeth, thinner and more generally pustulose brownish rather than brightly-colored operculum, and a black rather than grayish-yellow outer surface with black and red markings.

ADDITIONAL OBSERVATIONS on *Nerita ascensionis* ***deturpensis*** Vermeij, subspec. nov.

Very little appears to be known about the biology of even the most abundant intertidal molluscs inhabiting the South Atlantic islands. This state of affairs is partly attributable to the scant attention that the islands themselves, particularly Trindade, have received. It therefore seems pertinent to include some observations on the *Nerita* population of Fernando de Noronha.

Nerita ascensionis ***deturpensis*** is characteristic of both intertidal and supralittoral fringe rocky surfaces. In the intertidal, the snails are generally found singly, and co-occur with the common limpets *Acmaea noronhensis* Smith, 1890 and *Siphonaria* cf. *S. alternata* (Say, 1827), and a small species of *Nodilittorina* with weakly developed blunt nodules. At and slightly above high tide line, *Nerita* is most commonly encountered singly beneath boulders or aggregated in large numbers (> 50) on shaded rock walls or in crevices. At this level the snails share the habitat with large individuals of *Nodilittorina* and with the locally common *Siphonaria pectinata* (Linnaeus, 1758). In contrast to certain other species of *Nerita,* such as the Panamic *N. (Ritena) scabricosta* Lamarck, 1822 and *N. (Theliostyla) funiculata* Menke, 1851, the form from Fernando de Noronha avoids immersion in small splashpools or tidepools.

Different levels of the shore are inhabited by specimens of different size. At Ponta de São António, on the eastern tip of the island, 26 specimens collected from intertidal surfaces washed by surf had a mean width of 14.6 mm, with a range of 13.2 mm to 18.0 mm. On a nearby rock wall, none of the specimens collected from just above the high tide line were smaller than 19.7 mm, and the mean width was 26.4 mm. Similar size gradients, with small individuals inhabiting low shore levels and large individuals occurring higher up, were observed at Praia da Atalaia and Baía de Sueste on the south coast, and Praia da Quixaba on the north coast.

The variable expression of the spiral sculpture alluded to in the description appears to be related to the presence or absence of sand scouring. At Praia da Quixaba, a sandy beach fronting the open ocean with intertidal rock outcroppings along its length and a high cliff at its eastern end, both intertidal and supralittoral fringe specimens have reduced spiral ridges. This is also true of the 26 intertidal individuals collected at Ponta de São António on severely sand-scoured rocks; 8 of the specimens were, in fact, almost completely smooth except for 3 or 4 very faint spiral ridges near the suture. The large specimens from just above high tide line at the same locality have the spiral ridges well developed relative to other populations from the island; these snails, however, were collected from a cliff behind a beach of basalt boulders, where they are free from sand abrasion.

Table 3

Summary of Differences Between Three Subspecies of *Nerita ascensionis*

Character	*Nerita ascensionis ascensionis*	*Nerita ascensionis* ***deturpensis***	*Nerita ascensionis* ***trindadeensis***
Spiral ridges	strong	weak to moderately strong	weak to moderately strong
Outer lip teeth	absent	weak in adults, absent in young	very weak or absent
Parietal area	very pale light orange	bright light orange	very pale light orange

Reduction of spiral ridges may enhance resistance to sand abrasion in that relatively less surface area is presented upon which the forces associated with abrasion can act than if the ridges were strong. Any loss in shell strength that may accompany spiral ridge reduction is thus probably offset by the advantage of minimizing the surface through which environmental forces act.

The coast of Fernando de Noronha consists mostly of sand beaches alternating with rocky cliffs and headlands. Small outcrops of volcanic rocks are characteristic of the sandy beaches, and these provide ample living space for intertidal organisms. Assuming that initial colonization resulted from transport of a propagule of *Nerita ascensionis ascensionis* from the southeast, via the westward-drifting Equatorial Current, one can imagine that any variants with poorly developed spiral ridges in the initial population would be selected for in view of the widespread occurrence of sand scouring. In this connection it would be interesting to know something about the physical regimes of the intertidal zone at Trindade, where the sculptural aspect of *N. a.* ***trindadeensis*** is very similar to that in the subspecies from Fernando de Noronha. If, during the history of the two islands, erosional activity causes a coast dominated by high cliffs to be transformed into one with sandy beaches and alternating headlands, then one could expect a temporal change in the sculptural aspect of the resident *Nerita,* if sculpture is indeed a function of sand abrasion.

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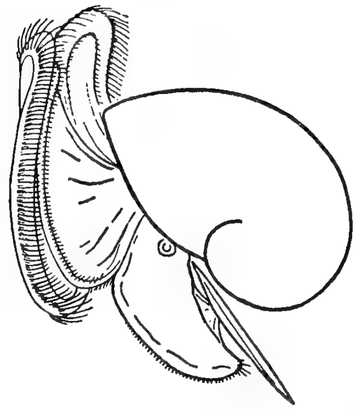

Morphometry of Two Species of the Squid Family Ommastrephidae

BY

JOHN H. WORMUTH

(3 Text figures; 2 Tables)

INTRODUCTION

It is common practice in cephalopod taxonomy to record certain morphological measurements from specimens. Each measurement is usually divided by the dorsal mantle length to give a ratio, sometimes referred to as an index. In recent years, due to the greater frequency of oceanic cruises and improved sampling techniques, enough specimens of some oceanic species have been collected to examine the variability of these measurements and ratios for a large range of sizes.

It has been shown that these ratios can change as the mantle length increases (Haefner, 1964; Spencer, 1969). Two interpretations of this type of analysis have been made. Haefner (1964) suggests that his data provide "useful information for specific identification and classification of most size groups of both *Loligo pealei* and *Lolliguncula brevis*" while Spencer (1969) concludes that the differences in relative growth patterns and gross morphology (of the fins) are indicative of the degree to which the fins are responsible for maintenance of vertical position and locomotion at slow speeds in the two species he examined.

When morphometric data for two other species of oegopsid squid were analyzed in the same manner as those previously mentioned, the weaknesses of that type of analysis were apparent. This paper presents an alternative method of analysis of three selected characters of *Symplectoteuthis oualaniensis* (Lesson, 1830) and *S. luminosa* Sasaki, 1915. The character measurements are used to calculate "best" fit curves which are fit to the values. The biological meaning of the curves is discussed with respect to isometric and allometric types of growth. These growth patterns are shown to be occasionally indistinct.

METHODS

Data were obtained for 439 specimens of *Symplectoteuthis oualaniensis* and 82 specimens of *S. luminosa.* All specimens of the former species have the dorsal light organ described in Clarke (1963). Measurements were recorded to the nearest 0.5mm with an average error of 0.5mm. The specimens used in this study were collected on various cruises in the Pacific and Indian Oceans by the Scripps Institution of Oceanography. The morphological characters examined in this paper are: dorsal mantle length (ML), mantle width (MW), fin length (FL) and fin width (FW). A description of these measurements is found in Haefner (1964). In my study MW was always measured at the mantle opening. Of the eight characters presented in Spencer (1969), these showed the largest changes with respect to mantle length.

The data were examined in several ways. For purposes of comparison the method of Haefner (1964) and Spencer (1969) was used. This process converts the data to ratios which are averaged within 10mm ML intervals. In addition, the range and 95% confidence limits on the mean were calculated within each interval. This was done to reflect the number per interval and their variability. When this was done it became apparent that a better type of analysis must be found if any conclusions were to be drawn from the data.

After consulting Marr (1955) on the use of ratios as opposed to measurements, it was decided that the original variates would be more useful. The MW, FL and FW measurements were plotted against ML for both species. For the remainder of the paper these three combinations will be referred to as pairs. Linear and quadratic regression equations were calculated for each pair. The measurements were then transformed to logarithms and both types of regression were used again. For each pair of each species there were four equations as possible fits to the data. For reasons which will be discussed later the linear equations were chosen as the "best" curves and were fit to the data.

RESULTS

The method used by Haefner (1964) and Spencer (1969) has two serious faults. It makes no allowance for having different numbers of individuals in each interval and it does not reflect the variability of ratio values within each interval. These weaknesses can be corrected as mentioned above. When this was done with my data it was clear that any interval with 2 or 3 individuals had very wide confidence limits associated with it as seen in Figure 1. Curve fitting for these graphs seemed inappropriate.

The original variates proved easier to work with. In all pairs, each of the four possible regression equations accounted for a statistically highly significant ($p < .005$) amount of the variability in the measurements. Most of the equations which accounted for the greatest percentage of the total variability involved logarithmic transformations of the data, but they were not much better fits than the linear ones as seen in Table 1.

DISCUSSION

One would expect inherent variability in the data due to differences at three levels: the species, the population and the individual levels. Due to the difficulty in obtaining large single population samples or maintaining live individuals over long periods of time, nothing was done about this nonmeasurement error. The graphs in Figure 1 show that the ratios tend to change most rapidly in juveniles, but are not constant in adults. The taxonomist should be cautioned in using ratios as diagnostic tools since they can be size dependent. The graphs strongly suggest that a reversal in the direction of change of a character ratio in larger individuals such as observed in the FW/ML ratio of *Gonatopsis borealis* by Spencer (1969) is not a real phenomenon. It is probably an error due to a combination of the inherent variability previously mentioned and the small numbers of larger individuals examined. A very good discussion of the advantages of using measurements over ratios is given in Marr (1955) and examples of the use of ratios in the literature are discussed. The maximum amount of information is present in measurements. Conversion to ratios and subsequent averaging over intervals not only obscures the variability, but produces curves that appear difficult to fit.

Table 1

Percentage of the total variability removed by each type of regression equation (SS(regression)/SS(total) ×100)

Symplectoteuthis oualaniensis	MW on ML	FL on ML	FW on ML
Type I (linear)	95.5	98.1	95.2
Type II (exponential)	96.0	98.4	96.1
Type III (quadratic)	95.5	98.2	95.6
Type IV (log quadratic)	96.5	98.6	96.7

Symplectoteuthis luminosa	MW on ML	FL on ML	FW on ML
Type I (linear)	96.1	99.4	98.4
Type II (exponential)	97.3	99.3	98.6
Type III (quadratic)	96.7	99.4	98.5
Type IV (log quadratic)	97.9	99.3	98.6

Although equations of type IV (see Table 1) generally accounted for the greatest amount of variability, they were not much of an improvement on type I which are plotted in Figure 2. The fact that there was little distinction between linear and exponential types of equations was most surprising at first. The contrast between linear (isometric) and exponential (allometric) growth in fish was examined and found to be as poor. The curve fitting analysis of this paper was used to calculate "best" fit equations for some measurements of striped marlin given in Morrow (1952). Morrow had concluded that sword length and body depth grew isometrically while the dorsal fluke of the caudal fin showed negative allometry. The analysis showed that sword length, body depth and the dorsal fluke of the caudal fin plotted against standard length were all equally well fitted by either linear or exponential equations. Linear equations removed an average of 44.9% of the total variability while exponential ones averaged 44.7%. In this example, then, the two types of growth

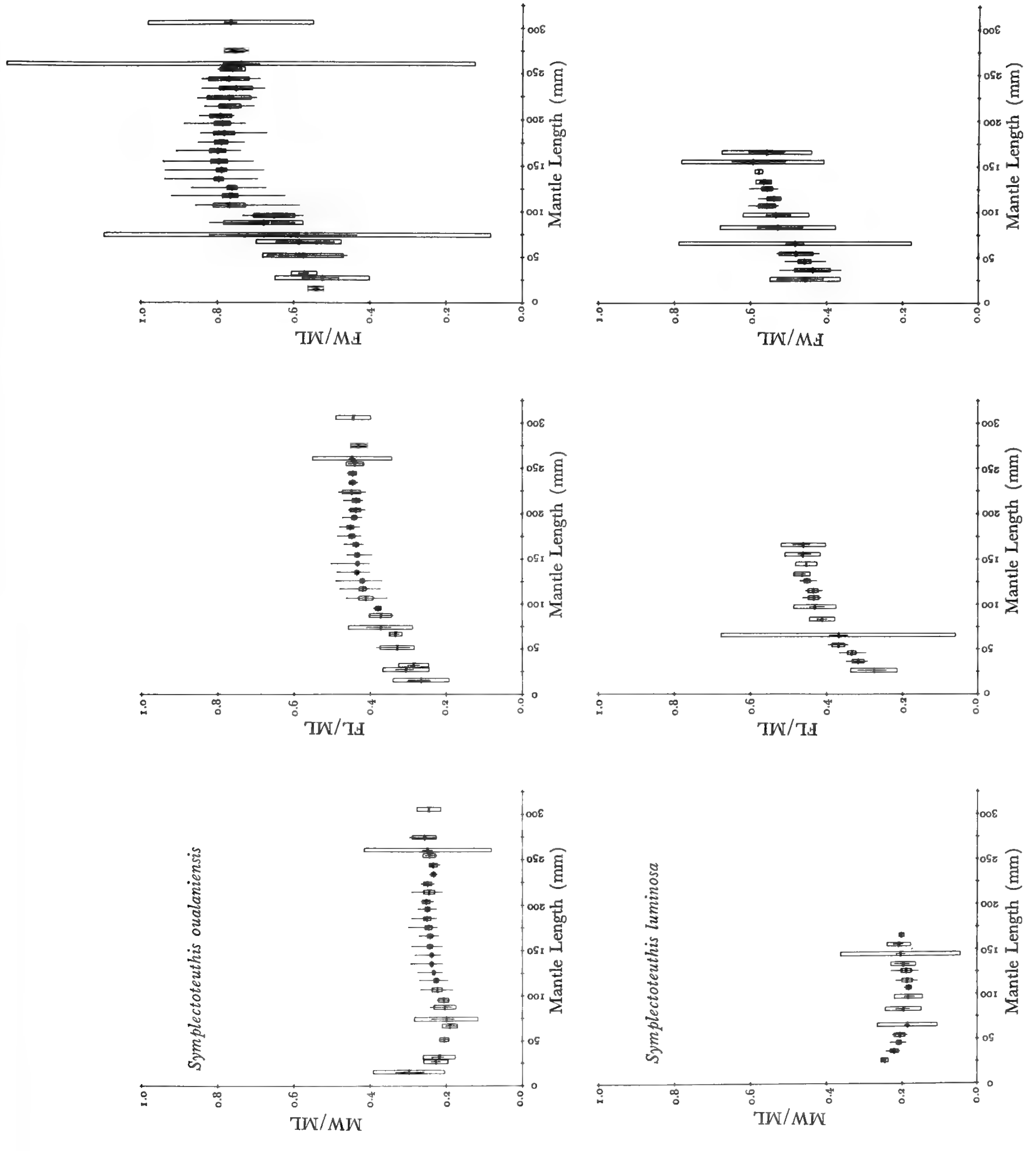

Figure 1

Interval means, ranges and associated 95% confidence limits on the means. The means are represented by the crosses in the centers of the rectangles. The vertical lines inside the rectangles represent the range of values. The height of the rectangles represents the 95% confidence limits on the means (their width has no meaning).

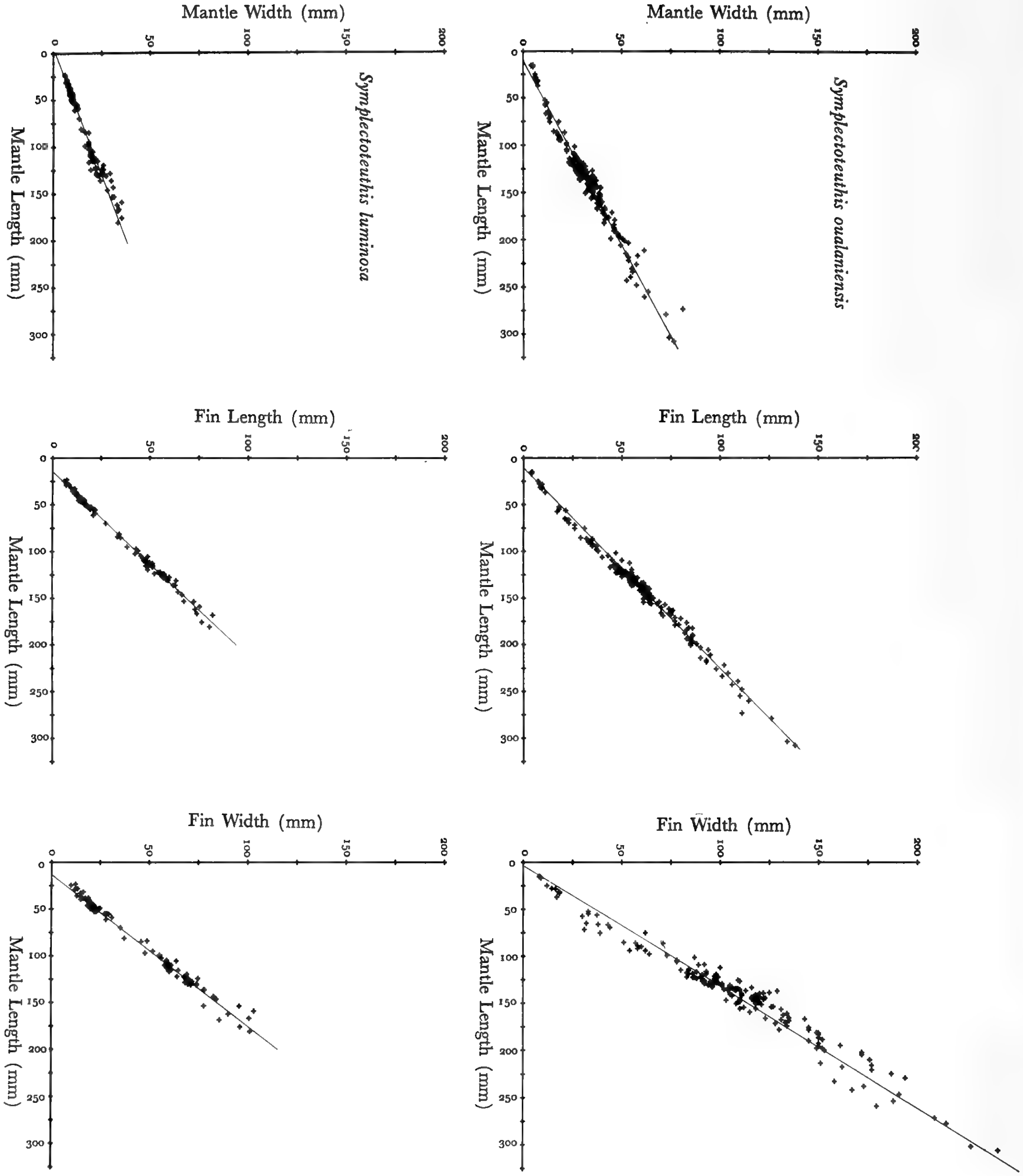

Figure 2

The original variates and their calculated linear equations.

were statistically indistinguishable. A similar situation was found when measurement data of yellowfin tuna (Schaefer, 1948) were analyzed in the same manner. Schaefer stated that head length grows linearly with respect to total length. The curve fitting analysis showed that the exponential equations give as good a fit as the linear ones (99.2% of the total variability v. 99.3% respectively).

A similar analysis applied to two other species in the family Ommastrephidae, *Dosidicus gigas* (d'Orbigny, 1835) (218 specimens) and *Ommastrephes bartramii* (Lesueur, 1821) (96 specimens) with fin shapes very similar to *Symplectoteuthis oualaniensis*, agree in the overall trends shown in this paper. In some cases an exponential equation fit "best" while in other cases the linear ones fit "best" (see Table 2). The general trends of the two species presented in Figure 2 agree. Their fin shapes (Figure 3) are very similar to those examined by Spencer (1969). The differences he observed and attributed to different fin shapes must be peculiar to the two species he examined, not the fin shapes.

Table 2

Percentage of the total variability removed by each type of regression equation (SS(regression)/SS(total) ×100)

Dosidicus gigas	MW on ML	FL on ML	FW on ML
Type I (linear)	97.1	99.1	98.0
Type II (exponential)	98.1	97.2	99.0
Type III (quadratic)	97.3	99.1	99.2
Type IV (log quadratic)	98.7	99.4	99.0

Ommastrephes bartramii	MW on ML	FL on ML	FW on ML
Type I (linear)	94.4	97.7	95.8
Type II (exponential)	94.4	97.7	96.2
Type III (quadratic)	94.4	98.1	96.3
Type IV (log quadratic)	94.4	97.9	96.7

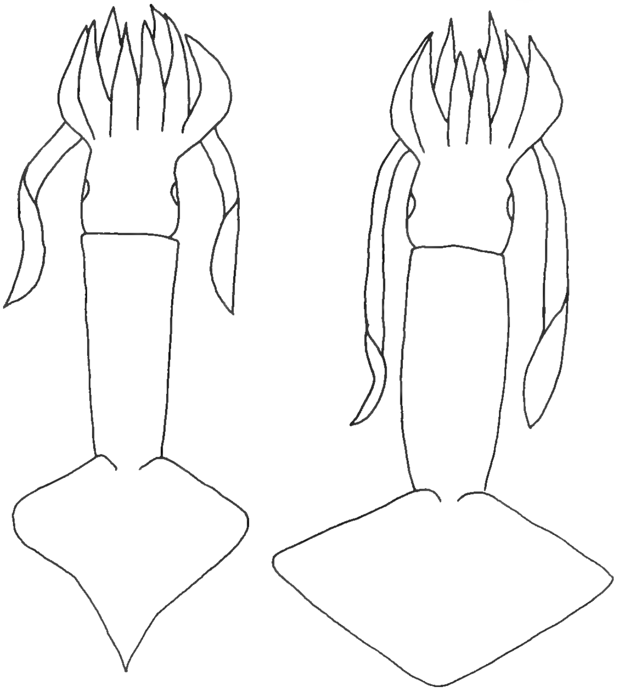

Figure 3

External morphology of *Symplectoteuthis oualaniensis* (right) (170mm ML) and *S. luminosa* (left) (160mm ML).

If the calculated curves for any character pair are compared for the two species of *Symplectoteuthis* discussed here, they are sufficiently distinct for taxonomic identification as also found by Haefner (1964) with ratio curves. When the observed points are compared, however, the variability around the calculated curves is more than enough to obscure this distinction and make the identification impossible by means of MW and FL. Using FW and ML, the distinction is satisfactory beyond 100mm ML while below this it would be questionable. If the reader desires a quantitative separation, the use of discriminant functions is suggested (Fisher, 1958), however there are usually qualitative characters which permit a faster specific separation than the type of data presented in this paper.

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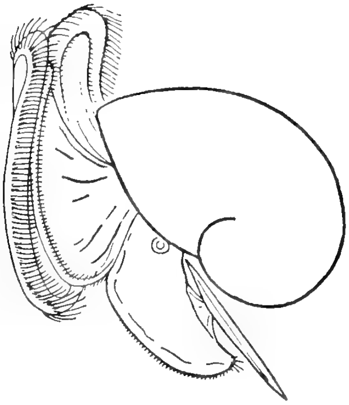

Modiolus demissus: A New Host for the Oyster Crab *Pinnotheres ostreum* in Virginia[1]

BY

PAUL A. SANDIFER[2]

AND

WILLARD A. VAN ENGEL

Virginia Institute of Marine Science, Gloucester Point, Virginia 23062

Pinnotheres ostreum SAY, 1817, COMMONLY PARASITIC in the oyster *Crassostrea virginica* (GMELIN, 1791), also may infest the jingle shell *Anomia simplex* ORBIGNY, 1845, and the edible mussel *Mytilus edulis* LINNAEUS, 1758 (MCDERMOTT, 1961, 1962). A fourth host, the ribbed mussel *Modiolus demissus* (DILLWYN, 1817) should now be added to the list of bivalves parasitized by this crab.

Mussels were collected from intertidal mussel beds at Sandy Point in the lower York River, Virginia (37°16′N, 76°33′W), from November, 1968, through June, 1969. Of 747 *Modiolus demissus* collected, 136 (18.2%) contained *Pinnotheres ostreum*. All of the crabs were small (0.71 to 3.15 mm carapace width) pre-hard and hard-stage (Stage I) crabs. No developmental stages later than the hard stage were seen. Gill erosions similar to those caused by young *P. ostreum* in *Crassostrea virginica* (CHRISTENSEN & MCDERMOTT, 1958) were often associated with the presence of the crabs in *M. demissus*.

Crabs were found in the mussels during all months except January, when no samples were taken. The majority of the crabs apparently overwintered in the pre-hard stages and reached the hard stage in May. Following the molt to the hard stage, the crabs apparently left the mussels in June. MCDERMOTT (1961, 1962) reported a similar emigration of *Pinnotheres ostreum* from *Mytilus edulis* at the hard stage. He (personal communication) has also found pre-hard and hard-stage, but never mature, female *P. ostreum* in *Modiolus demissus* in Delaware Bay.

The phenomenon of invasion of a "primary" host followed by movement from that host, presumably in search of some "secondary" host, is not unique to *Pinnotheres ostreum* among the Pinnotheridae. Similar behavior has been described for the European mussel crab *P. pisum* (PENNANT, 1777) (CHRISTENSEN, 1958) and the west coast mussel crab *Fabia subquadrata* DANA, 1851 (PEARCE, 1966). In all three species the apparent emigration occurs at the hard stage, which is morphologically adapted for a free-living existence and for invasion of a second host. The reasons for these emigrations, however, are obscure. CHRISTENSEN's (1958) observations suggest that in the area in which he worked *P. pisum* is selectively attracted to *Spisula solida* (LINNAEUS, 1758) at the invasive stage and to *Modiolus modiolus* (LINNAEUS, 1758) at the hard stage. This does not seem to be the case with *P. ostreum* and *F. subquadrata*, both of which commonly occur in their secondary, as well as their primary, hosts at the invasive stage. PEARCE (1966) did not believe that the primary hosts of *F. subquadrata* were large enough to accommodate the adult female crabs. Primary host size, however, cannot explain the failure of *P. ostreum* to reach maturity in *Mytilus edulis* and *Modiolus demissus*. *Pinnotheres ostreum* reaches maturity in *Anomia simplex* (MCDERMOTT, 1961, 1962) which has a smaller mantle cavity than do the mussels; *Mytilus edulis* commonly contains adults of *P. pisum* (comparable in size to *P. ostreum*) in European waters; and *Modiolus modiolus* (comparable in size to *Modiolus demissus*) accommodates adults of the large pinnotherid, *F. subquadrata*. Other facets of host biology, such as differences in pumping rates and mucus secretions, as well as requirements and tolerances of the crabs, must be considered in any attempt to ascertain the reasons for these emigrations.

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[2] Recipient of an NDEA Title IV Graduate Fellowship during the study.

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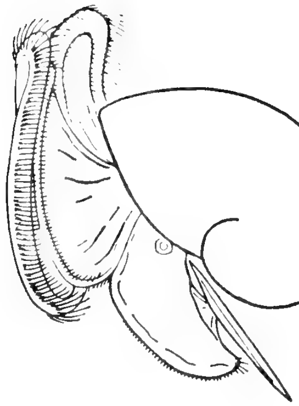

The Effect of Species Composition on the Survival of Mixed Populations of the Sea Mussels *Mytilus californianus* and *Mytilus edulis*

BY

J. R. E. HARGER

Department of Biological Sciences, University of California at Santa Barbara[1]

(5 Text figures)

In the course of an investigation into the nature of competitive interaction between the sea mussels *Mytilus californianus* Conrad, 1837 and *M. edulis* Linnaeus, 1758 on the coast of Southern California (Santa Barbara) (Harger, 1968), it became apparent that the immediate outcome of such an interaction depended in large part on the ratio of the two species concerned.

Several authors in the past have envisaged situations wherein the coexistence of ecological homologues would be permitted. For instance, Hutchinson (1957) claims that coexistence might occur if the advantage of one species over the other is constantly reversed by habitat variations; however, Klomp (1961) considers that this could occur only if habitat variations were dependent on the numerical ratio of the species involved, and this seems improbable.

It is proposed that within this system of interacting mussels inhabiting the intertidal region at least one effect of environmental variation is directly dependent on the numerical ratio of the species involved and that furthermore, the advantage possessed by each species over the other may be reversed by habitat variations (e. g. *Mytilus edulis* may be washed off by heavy seas, thus permitting formerly imprisoned *M. californianus* to grow. A period of calm weather may permit re-domination by *M. edulis*).

This paper deals with the effect of a physical environmental variable (wave action) on the survival of mixed populations of mussels.

METHODS

a. Relationship of Mussel Size to Environmental Conditions

Mussel clumps growing in intertidal beds on the shore adjacent to Ellwood Pier, 14 miles north of Santa Barbara, during 1964 - 1967 were composed principally of *Mytilus californianus*; individuals of *M. edulis* occurring there were quite small, usually between 2 and 4 cm in length (measured between the umbo and siphon regions), whereas *M. californianus* sometimes attained a length of up to 20 cm. The shore itself is gently sloping, containing large projecting boulders in some places and extensive lines of slanting reefs in others. The situation here differed markedly from the pier (see Harger, 1968 for a description of Ellwood Pier and associated mussel populations) in that wave impact on the shore was much greater than that experienced on the pier pilings (Harger, 1967). At the outer end of the pier, under normal (non-storm) conditions, waves take the form of unbroken swells which rush past the pilings, creating a tremendous swirling and pushing, but little else. At the shore, on the other hand, all the kinetic energy contained in these swells is expended in the space of a few feet as the waves break. For this reason, and because measurement showed the shore to experience heavier wave action than the pier pilings (Harger, 1967) the former was classified as being more exposed than the latter.

To account for the presence of small *Mytilus edulis* only on the shore, I supposed that wave action either limited growth of the mussels such that individuals would not exceed 4 cm in length, or that the force of the waves simply removed any larger than this. (The maximum size attained by *M. edulis* within clumps attached to Ellwood Pier is 8 - 9 cm).

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[1] Present address: Department of Zoology, University of British Columbia, Vancouver 8, British Columbia.

The following experiment was designed to investigate the problem. Artificial clumps of mussels were set out on the sea shore by confining individuals inside rectangular hardware-cloth cages ($\frac{1}{2}$ inch [1.27 cm] mesh). The cages were screwed tightly to seaward rock faces, thus confining a one-mussel thick layer in such a way as to prevent individuals being washed around by wave action. After a period of 3 weeks the cages were removed, leaving the surviving mussels firmly attached by byssal threads to the rock surface. Three size classes of mussels were used – large (9 - 10 cm), medium (7 - 8 cm), and small (5 - 6 cm) – together with 3 treatment groups within each size class – pure *Mytilus californianus*, pure *M. edulis*, and a mixture containing equal proportions of both species. The treatments involving the smallest size class were replicated twice, whereas the medium and large sizes were represented by one sample per treatment. The mussels were marked and measured individually (see Harger, 1967 for a description of the marking method) before the experiment was initiated.

b. Relationship Between Species Composition and Population Survival

Carpinteria reef is an extensive outcropping of rock occurring south of the city of Santa Barbara. In profile, the reef presents a steep seaward face approximately 10 feet (3 m) high behind which, and depressed by about 3 feet (1 m), the broad mass of the reef extends horizontally for a distance of about 100 yards (92 m). Due to protection by the front face, and because the reef itself tends to be flat, wave impact over the top of the rock is much reduced. Certainly the area is less exposed than Ellwood Shore.

During December, 1965, an intense storm was experienced in the Santa Barbara area. Prior to the storm the surface of Carpinteria reef was largely dominated by a thick sheet of mussels comprised mainly of *Mytilus edulis*. The storm stripped most of these animals from the reef and drastically altered the composition of the mussels in the remaining clumps. Areas within the original bed which were comprised principally of *M. edulis* were the ones lost, leaving groups composed mainly of *M. californianus*.

Table 1 indicates the relative proportions of the 2 species commonly present within the original mussel population as well as the highest proportions of *Mytilus edulis* which could be found after the storm. The proportion of *M. edulis* to *M. californianus* in the samples collected after the storm was much lower than in those collected before.

Table 1

Proportion of *Mytilus edulis* within natural beds of mussels at Carpinteria Reef before and immediately after a severe storm in December, 1965

	N	Proportion of *Mytilus edulis*
Before storm, December 1965	530	94%
	400	93%
After storm, December 1965	293	40%
	267	30%
	308	55%

The ratio of the component species within a clump, then, seems to have considerable importance in determining the resultant clump stability. To investigate this hypothesis a series of artificial mussel clumps was constructed containing the 2 species of mussels in the following proportions: *Mytilus californianus* to *M. edulis* – 1.0 : 0.0; 0.33 : 0.66; 0.5 : 0:5; 0.66 : 0.33; and finally 0.0 : 1.0.

Each ratio was represented by 3 separate clumps, one of which was comprised of small mussels (4 - 5 cm), the second of medium-sized mussels (6 - 7 cm), and the third of large mussels (9 - 10 cm). As far as possible, the mass of each clump was kept at about 1250 gr except for clumps of small mussels which averaged 600 gr.

Mussels forming each clump were placed in cheesecloth bags through the center of which was inserted a 20-inch (50 cm) length of 3-inch (7.6 cm) by $\frac{1}{2}$-inch (1.2 cm) redwood stake. The bag was then tied and stapled securely to the top and bottom of the stake in such a way that the mussels were pressed firmly against each other and against the center (Figure 1). An iron weight was lashed to the top end of the stake to insure the clump would not float in the water and each assemblage was suspended from a cross girder on Ellwood pier so that it hung just below low water.

RESULTS

The results of the experiment conducted on Ellwood shore are presented as survival curves in Figures 2, 3, and 4. Populations of pure *Mytilus californianus* survived well in

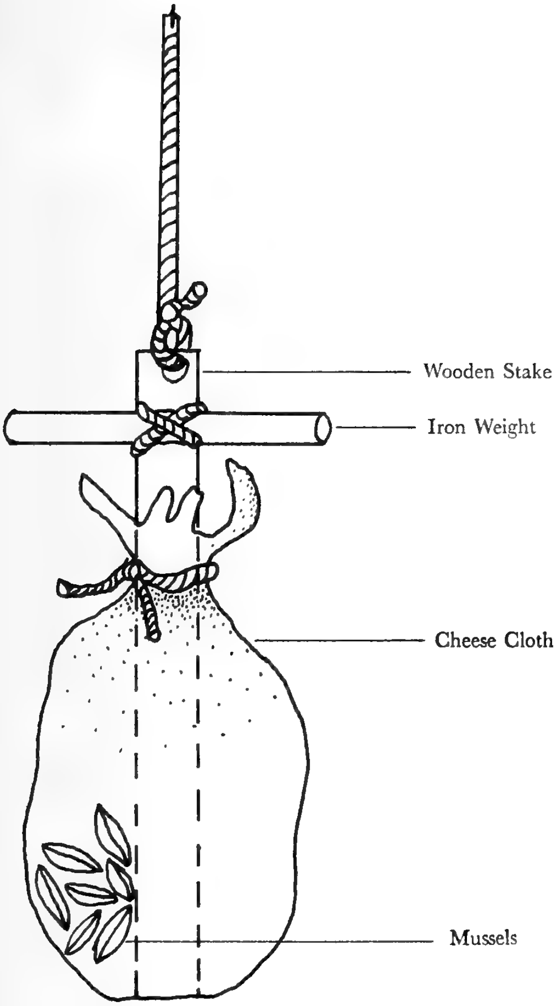

Figure 1

Artificial mussel clump constructed inside cheesecloth bag

all 3 size classes, whereas populations of pure *M. edulis* suffered highest mortality. Large *M. edulis* survived for less than 2 weeks before the animals were ripped from the rock face and pounded to pieces prior to removal of the cage. Medium-sized *M. edulis* fared a little better, lasting for 3 months before the last individual was dislodged. Small *M. edulis* lasted for 5 months and were finally eliminated through snail predation (*Thais emarginata* (Deshayes, 1839) and *Acanthina spirata* (Blainville, 1832)).

Survival of the mixed populations was consistent for all 3 size classes. In each case, individuals of *Mytilus californianus* from the mixed populations disappeared faster than from populations of *M. californianus* growing alone. For the large and medium size classes, the survival of *M. edulis* was improved as a result of association with *M. californianus*. Survival amongst the small mussels, however, was not improved, probably because the principal mortality factor operating on these mussels was predation by the carnivorous snail *Thais emarginata,* not wave impact. Both medium (7 - 8 cm) and small (5 - 6 cm) *M. edulis* showed growth over the period as did all classes of *M. californianus.*

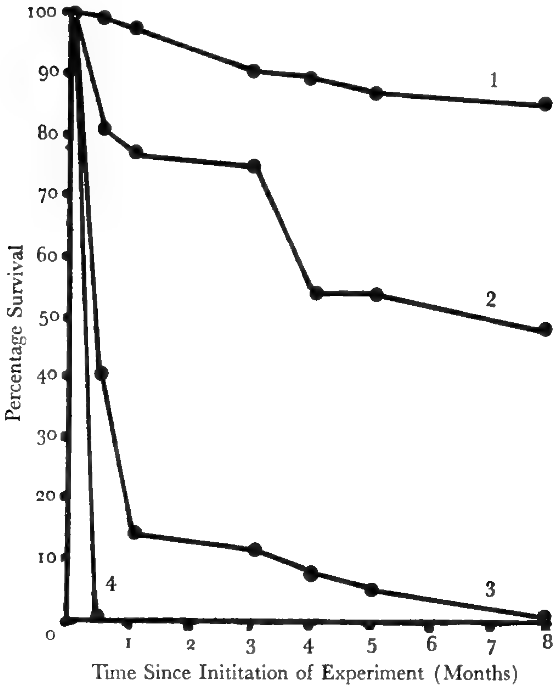

Figure 2

Survival curves of large mussels (8 - 10 cm) on Ellwood Shore Curve 1 represents *Mytilus californianus* alone. Curve 2 represents *Mytilus californianus* growing in association with *Mytilus edulis.* Curve 3, *Mytilus edulis* growing in association with *Mytilus californianus,* and Curve 4, *Mytilus edulis* alone.
Curves 2 and 3 were obtained from mussels growing in the same clump. Each clump originally contained 100 mussels. The experiment was started in January, 1966

This experiment indicates, among other things, that the safe upper size limit for *Mytilus edulis* in an exposed location depends to some extent on the presence of *M. californianus.* It is logical to assume that this upper limit will vary in accordance with amount of exposure, *i. e.,* wave impact.

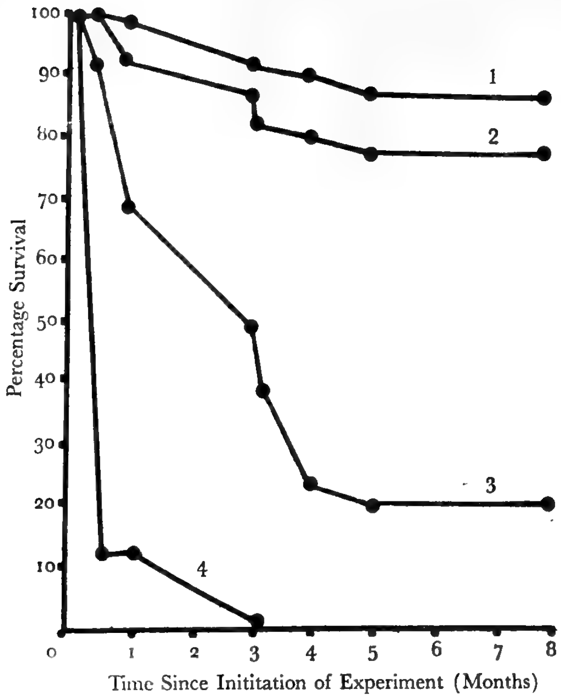

Figure 3

Survival curves of medium mussels (5 - 6 cm) on Ellwood Shore Curve 1 represents *Mytilus californianus* alone. Curve 2 represents *Mytilus californianus* growing in association with *Mytilus edulis,* Curve 3 *Mytilus edulis* growing in association with *Mytilus californianus,* and Curve 4, *Mytilus edulis* alone.

Curves 2 and 3 were obtained from mussels growing in the same clump. Each clump originally contained 78 mussels

As has been previously stated, the upper size limit for *Mytilus edulis* occurring in clumps at Ellwood pier is 8 - 9 cm. Larger individuals (up to 15 cm) can however be found growing in clumps of mussels attached below the low tide level to zinc electrode cables, which do not touch the sea floor. Such clumps are consequently protected from wave action and are at the same time not susceptible to predation by starfish (*Pisaster ochraceus* (Brandt, 1835) or *P. giganteus* (Stimpson 1857)), which occur beneath the pier (Landenberger, 1967).

A large sample of mussel shells gathered from the sea bed directly below the pier contained no *Mytilus edulis* larger than 7 cm. This perhaps indicates that wave action tends to dislodge this species from clumps formed in the intertidal region of the pilings once this size is reached.

The experiment utilizing artificial clumps at Ellwood Pier yielded the following results.

After 2 weeks the cloth bags rotted away and exposed the clumps to wave action, between March, 1966 to May, 1966. During this time the weather was mild with no severe winds. At the end of this period the clumps were taken in and the numbers of individuals of each species present recorded. Figure 5 indicates that clumps which had contained a high proportion of *Mytilus edulis* lost a high proportion of mussels. No difference due to size was apparent. This last result is a little surprising since clumps containing only small *M. edulis* (3 - 4 cm) can frequently be found growing on projecting pieces of iron, broken electrode cables, etc. Such clumps are usually broken up by wave action when the mussels reach 4 - 5 cm in length. This leads to the conclusion that the artificial clumps were not as firmly formed as natural associations would have been.

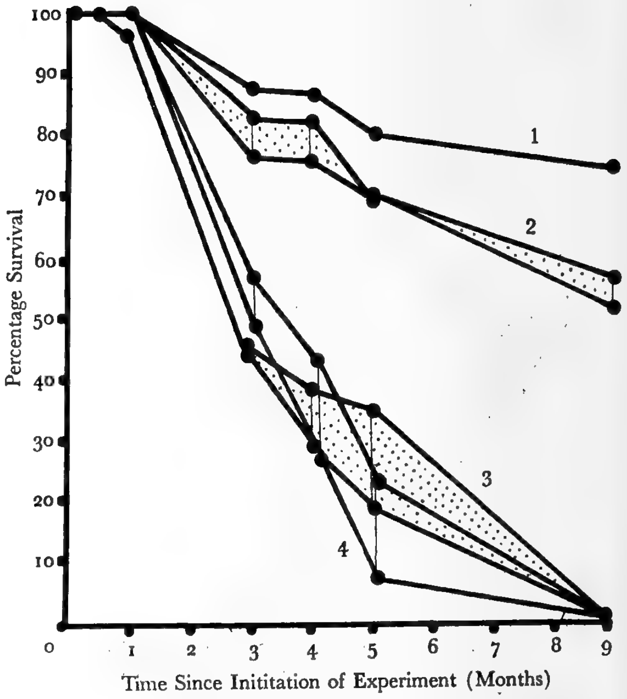

Figure 4

Survival curves of small mussels (3 - 4 cm) on Ellwood Shore Curve 1 (two replicates) represents *Mytilus californianus* alone. Curve 2 (two replicates) represents *Mytilus californianus* growing in association with *Mytilus edulis,* Curve 3, (2 replicates), *Mytilus edulis* growing in association with *Mytilus californianus,* and Curve 4 (2 replicates) *Mytilus edulis* alone

Curves 2 and 3 were obtained from the same two clumps. Each clump originally contained 68 mussels

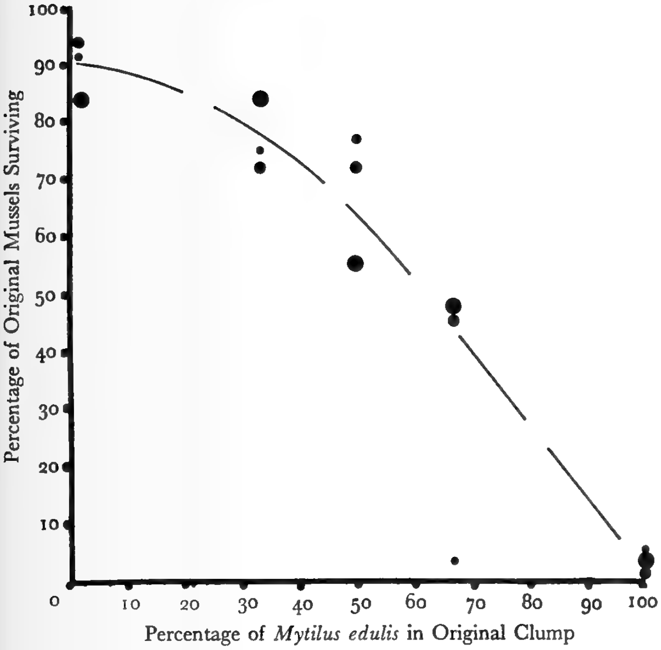

Figure 5

Relationship between the proportion of *Mytilus edulis* in the original artificial "cheesecloth" clumps and survival of both species (*i. e., Mytilus edulis* and *Mytilus californianus*). The clumps were suspended at Ellwood Pier, below low water, from March, 1966 until May, 1966. Small dots represent small mussels (4 - 5 cm) from original clumps comprised of 60 individuals. Medium dots represent "medium mussels" (6 - 7 cm) from original clumps containing 48 individuals. Large dots represent large animals (8 - 9 cm) from original clumps containing 24 individuals

The following conclusions emerge from these 2 exposure experiments:

1. Clumps of *Mytilus californianus* containing *M. edulis* are "weaker" than are similar clumps comprised only of *M. californianus.*
2. Survival of *Mytilus edulis* is increased in regions experiencing heavy wave impact if individuals of *M. californianus* are also present (this protection undoubtedly is a result of the stronger web of byssal threads which *M. californianus* weaves; *M. edulis* weakens this web wherever it occurs within a mixed species mat).
3. Small individuals of *Mytilus edulis* are better able to withstand the forces resulting from wave impact than are larger animals.
4. *Mytilus californianus* survives strong wave impact at all sizes.

The last two points are supported by the fact that small specimens of *Mytilus edulis* are able to attach to rocks almost as strongly as similar-sized *M. californianus.* Individuals longer than 5 cm, however, are more weakly attached than *M. californianus* of equivalent size (Harger, 1967).

DISCUSSION

From the foregoing evidence it seems reasonable to conclude that the effect a storm has on a population consisting of both *Mytilus edulis* and *M. californianus* depends on both the proportional representation of the two species and the size of the constituent individuals. Since clumps are progressively weakened by an increasing concentration of *M. edulis,* it follows that populations wherein this species is numerically dominant (over *M. californianus*) will be most susceptible to wave action.

In the Santa Barbara region heavy storms occur only during winter months, but they do not occur each year. It is thus possible for *Mytilus edulis* to build up heavy populations in protected and semiprotected regions (Ellwood Pier pilings and Carpinteria reef). Such populations usually flourish at the expense of *M. californianus* since *M. edulis* individuals always maneuver themselves so as to cover their competitors (Harger, 1968). In extremely quiet situations this results in the underlying *M. californianus* being smothered by silt. In areas, such as Carpinteria reef, large amounts of sand become deposited amongst the mussels with essentially the same effect; underlying mussels are smothered by oxygen-poor, heavily reduced material. This characteristic also adds to the progressive deterioration in clump stability caused by dominance and subsequent growth of *M. edulis.* Inclement weather may then eliminate large areas of *M. edulis,* leaving only *M. californianus*-dominated populations and juvenile *M. edulis. Mytilus edulis* is never entirely eliminated from such situations because the extreme spatial heterogeneity of the intertidal region ensures that some areas, behind rocks, etc., are always protected from direct wave action and, in addition, the juvenile mussels are capable of withstanding heavy seas (I have found small (2 - 3 cm) *M. edulis* growing in the intertidal region at Point Mugu, Ventura County, California, an external exposed region).

Areas stripped of mussels by storm action are soon colonized by barnacles and small mussels (particularly *Mytilus edulis*), thus setting the cycle in motion again.

The balance between the 2 species is interesting because the presence of *Mytilus californianus* seems always to enhance survival of *M. edulis* in the face of wave action. The growth pattern of *M. californianus* is, however, such that if *M. edulis* does not succeed in smothering its competitor at an early stage, it is itself incorporated into the clump matrix and crushed (Harger, 1967). As far as *M. californianus* is concerned, the presence of *M. edulis* always serves to weaken the clump structure.

In conclusion, it seems evident that the effect a storm has on mussel populations (of any particular size) varies according to the proportions of the 2 species making up the association.

ACKNOWLEDGMENT

This work forms part of a Ph. D. program carried out under the guidance of Dr. J. H. Connell. My thanks are due to Dr. D. E. Landenberger and Dr. J. Stimson for constant and persistent criticism. Thanks are also due to Signal Oil and Gas Company, whose property at Ellwood was made available for the purpose of ecological research.

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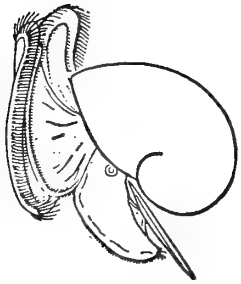
CORRECTION

Figures 6 and 10 were inadvertently mutually misplaced on pages 49 and 52, respectively, in the article by the same author, published in no. 1 of the current volume. We apologize for any inconvenience this may have caused.

The Editor.



On *Pecten (Amusium) condoni* HERTLEIN from the West Coast of North America[1]

BY

KÔICHIRÔ MASUDA
Miyagi University, Sendai, Japan

AND

WARREN O. ADDICOTT
U. S. Geological Survey, Menlo Park, California 94025

(1 Plate)

INTRODUCTION

AMONG THE TERTIARY PECTINIDAE of the west coast of North America *Pecten (Amusium) condoni* HERTLEIN is potentially of significance in interregional correlation because of its limited geological range and close affinity to certain fossil pectinids of northern Japan.

Pecten (Amusium) condoni was first described by HERTLEIN (1925) based upon specimens from the Montesano Formation of FOWLER (1965) of western Washington. However, as pointed out by GRANT & GALE (1931), its interior characteristics which are considered to be most definitive for reference to *Amusium* have remained unknown. Thus, the subgeneric classification of this species has remained uncertain. The fact that *Amusium* is now restricted to low-latitude, tropical or subtropical areas in the Pacific casts some doubt on the initial subgeneric assignment of this species as it occurs in an assemblage of cool temperate aspect. Moreover, all of the other Tertiary records of *Amusium* or *Amusium*-like pectinids from the middle latitudes of the marginal eastern North Pacific are in warm-water assemblages of pre-late Miocene age that occur no farther north than central California.

Numerous specimens preserved in the Department of Geology of Stanford University and at the U. S. Geological Survey in Menlo Park, California, were studied by the writers. Examination of these specimens has led the writers to consider this species to be referable to the genus *Yabepecten* MASUDA, 1963, based upon *Pecten tokunagai* YOKOYAMA, 1911, from Japan. Accordingly, this is the first recognition of the occurrence of the genus in the eastern North Pacific. This article includes a redescription of this species based upon the holotype, topotypes, and other specimens from the Montesano Formation and a discussion of its relationship with other species from the northern Pacific region.

PECTINIDAE

Pectininae

Yabepecten MASUDA, 1963

Yabepecten condoni (HERTLEIN, 1925)

(Figures *1*, *3* to *9*)

1925. *Pecten (Amusium) condoni* HERTLEIN. Southern California Acad. Sci. Bull., **24** (2): 41; plt. 4, figs. 8, 9
1931. *Pecten (Amusium) condoni* HERTLEIN. GRANT & GALE, San Diego Soc. Nat. Hist. Mem. **1**: 232
1967. *?Miyagipecten alaskensis* MACNEIL. U. S. Geol. Survey Prof. Paper **553**: 45; plt. 6, figs. 4, 5

Type Specimen: Stanford University Type Coll. No. 15.

Description: The following description is based upon specimens preserved in the collections of Stanford University and of the U. S. Geological Survey, Menlo Park, California.

Shell medium in size, rather thin, smooth, compressed, nearly orbicular in outline, equilateral except for auricles,

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[1] Publication authorized by the Director, U. S. Geological Survey

subequivalve; valves radiately ribbed and forming an angle of about 100° at apex.

Right valve with 20 to 25 faint, low, flatly rounded, inconspicuous radial ribs crossed by fine concentric growth lines; radial ribs obscure near beak but tending to become more distinct towards ventral margin, much broader than their very shallow interspaces, rarely divided into two unequal riblets by shallow furrow; auricles medium in size, subequal, anterior one with wide and shallow byssal notch, a few faint, fine radial threads and concentric lines; posterior auricle truncated behind at obtuse angle and with concentric lines; interior surface smooth. Left valve with fine, low radial ribs, fine concentric growth lines and a fine microsculpture network; radial ribs much narrower than their shallow interspaces, somewhat distinct at upper part but tending to become somewhat broader and more obscure towards ventral margin.

Hinge with simple cardinal crura, wide and shallow resilial pit with rather distinct lateral ridges in right valve and auricular crurae which terminate distally in an obscure rounded oblong denticle.

Remarks: These morphological characters indicate that this species should be assigned to the genus *Yabepecten.*

Yabepecten condoni is closely related to *Y. tokunagai* (Yokoyama) (Figure 2) from the early Pliocene of northern Japan (Masuda, 1962, 1963). The right valve can usually be distinguished from *Y. tokunagai* by its radial ribs, which are always broader than their interspaces; the left valve differs in being moderately inflated. Nevertheless, the right valves of these species are sometimes rather difficult to distinguish from each other.

Miyagipecten saromensis Hasimoto & Kanno, 1958, from the Miocene Chirai Formation of Hokkaido, Japan, also resembles *Yabepecten condoni,* but it can be distinguished by the smaller number of radial ribs on the right valve, which are also less distinct, and by the rather distinct ribs provided with intercalary threads on the left valve.

Miyagipecten alaskensis MacNeil, 1967, an early Pliocene species from the upper Yakataga Formation, Malaspina District, Alaska, is doubtfully included with the present species, as indicated by a comparison with the type specimens, both of which are very poorly preserved and fragmental.

Type Locality: Loc. No. 148 (Stanford University, NP 244) at dam No. 35, west fork of the Wishkah River, Grays Harbor County, Washington (SE¼NW¼ sec. 35, T. 21 N., R. 7 W.). Upper part of the lower member of the Montesano Formation of Fowler (1965). Early Pliocene (?).

Age of the Montesano Formation of Fowler (1965): The age and correlation of the Montesano Formation of Fowler (1965), in terms of the Pacific coast mega-invertebrate chronology (Weaver *et al.*, 1944), is doubtful because no definitive biostratigraphic study of the formation has ever been made. Although specialists in larger invertebrates include the lowermost part in the late Miocene, they place the bulk of the formation in the early Pliocene because of faunal similarity with the early Pliocene Empire Formation of coastal Oregon (Weaver, 1945; Youngquist, 1961; Addicott, 1966). Preliminary study of extensive collections from the Montesano Formation made by Gerald A. Fowler suggests that there is, indeed, a faunal change between assemblages from near the base of the formation and those from stratigraphically higher parts. This change seems to occur stratigraphically below the *Yabepecten* localities, and for this reason these localities are here tentatively considered to be of early Pliocene age. It is noteworthy that the most recent studies of benthonic Foraminifera from the Montesano Formation (Fowler, 1965; Rau, 1967) have considered the

Plate Explanation

(All figures natural size)

Figure *1.* *Yabepecten condoni* (Hertlein). Right valve, USNM No. 646455. USGS loc. M3039. Montesano Formation, Pliocene.

Figure *2.* *Yabepecten tokunagai* (Yokoyama). Right valve, USNM No. 646456. Hamada Formation, Pliocene. Aomori Prefecture, Northern Japan.

Figure *3.* *Yabepecten condoni* (Hertlein). Right valve, SUPTC No. 22340. Stanford Univ. loc. NP244. Montesano Formation, Pliocene.

Figure *4.* *Yabepecten condoni* (Hertlein). Left valve, SUPTC No. 22340. Stanford Univ. loc. NP244. Montesano Formation, Pliocene.

Figure *5.* *Yabepecten condoni* (Hertlein). Right valve, USNM No. 646457. USGS loc. M2991. Montesano Formation, Pliocene.

Figure *6.* *Yabepecten condoni* (Hertlein). Right valve, SUPTC No. 22340. Stanford Univ. loc. NP249. Montesano Formation, Pliocene.

Figure *7.* *Yabepecten condoni* (Hertlein). Hinge area of left valve, USNM No. 646458. USGS loc. M3039. Montesano Formation, Pliocene.

Figure *8.* *Yabepecten condoni* (Hertlein). Right valve, USNM No. 646459. USGS loc. M2991. Montesano Formation, Pliocene.

Figure *9.* *Yabepecten condoni* (Hertlein). Left valve, USNM No. 646460. USGS loc. M2991. Montesano Formation, Pliocene.

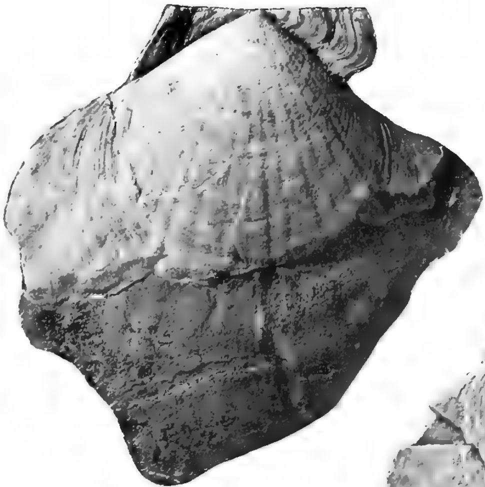


Figure 1

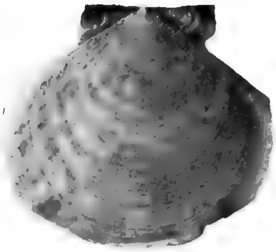


Figure 2

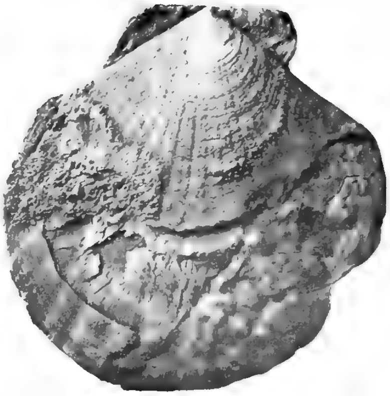
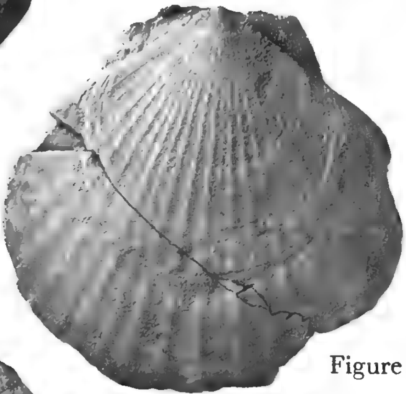


Figure 3



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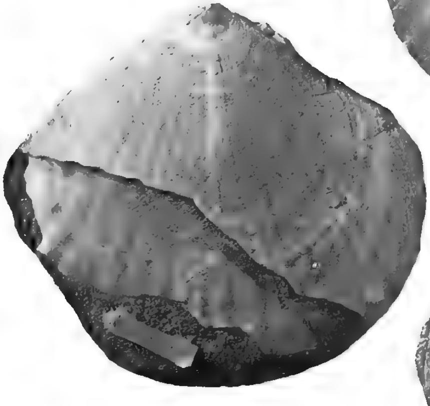

Figure 5

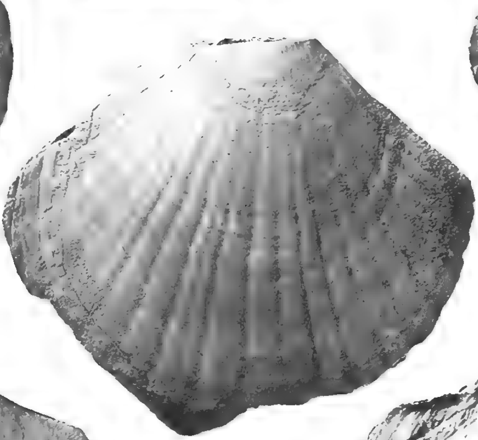

Figure 6

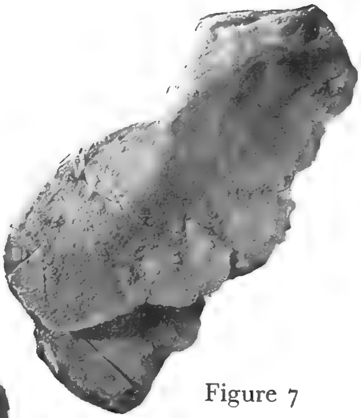

Figure 7

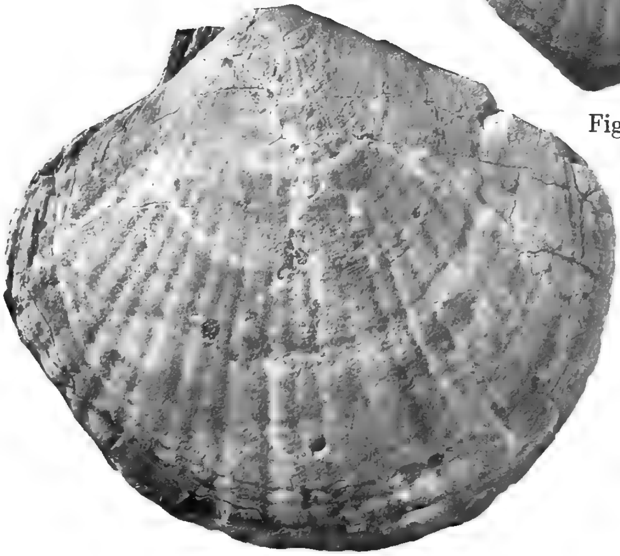

Figure 8

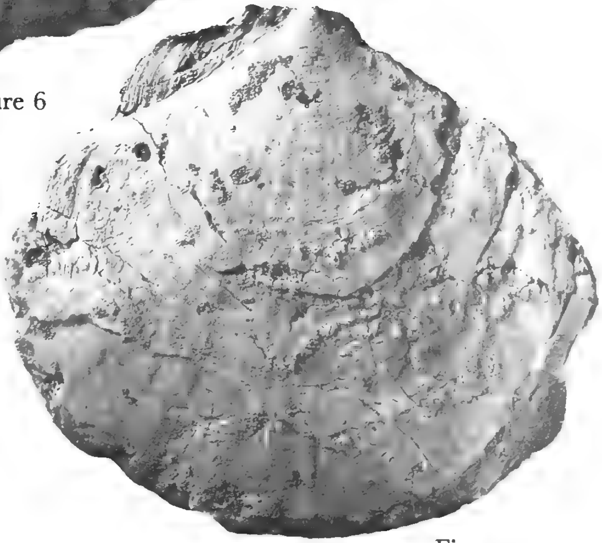

Figure 9

greater part, or all, of the formation to be of late Miocene age.

Keen's (1954) belief that mollusks from the type locality of *Pecten condoni* (NP-244) and from a nearby locality (NP-243) were of middle Miocene age seems to have been influenced by reconnaissance mapping by Weaver (1937) that showed both localities as included in the Astoria Formation. Recent geologic mapping and biostratigraphic studies of this area (Fowler, 1965; Rau, 1967) show that these localities are in the Montesano Formation and are of post-middle Miocene age.

Associated Fauna: The following mollusks occur with *Yabepecten condoni* at U. S. Geological Survey locality M2991 near the top of the lower part of the Montesano Formation on the middle fork of the Wishkah River, Grays Harbor County, Washington: *Calyptraea* sp., *Fusitriton* cf. *F. oregonensis* (Redfield), *Cyclocardia* sp., and *Lucinoma* cf. *L. acutilineata* (Conrad). The assemblage is suggestive of a cool, shallow-water depositional environment.

Distribution: Upper part of the lower member of the Montesano Formation of Fowler (1965), western Washington: Stanford Univ. loc. NP 244 and NP 249; USGS loc. M2991 and M3039. Upper part of the Yakataga Formation, southeastern Alaska: USGS loc. M1321(?).

REMARKS

The genus *Yabepecten* was established by Masuda (1963, p. 149 - 150) based upon the early Pliocene scallop, *Pecten tokunagai* Yokoyama, 1911. As Masuda has noted, the genus *Yabepecten* is related to the genus *Patinopecten*, but *Patinopecten* can be distinguished from *Yabepecten* by its distinct rectangular radial ribs in the right valve, deep byssal notch, much more conspicuous auricular crura, and large, thick shell. Other similar genera from Japan, such as *Fortipecten, Mizuhopecten*, etc., can be easily distinguished from the present one because they lack auricular crura.

Insofar as known, *Yabepecten tokunagai* (Yokoyama) is restricted to the early Pliocene of northern Japan (Japan Sea Borderland of Masuda, 1962). Judging by the associated fauna, the early Pliocene formations of northern Japan were deposited under cool to cold conditions. The occurrence of *Y. condoni* (Hertlein) in the Montesano Formation of western Washington and its doubtful occurrence in the upper part of the Yakataga Formation in Alaska are both of probable early Pliocene age. It is evident from the associated fauna that *Y. condoni* may also have lived under relatively cool conditions in the eastern Pacific. Therefore, it seems that *Yabepecten* was a cool to cold water inhabitant.

As noted above, the genus *Yabepecten* is known only from rocks of probable early Pliocene age along the west coast of northern America and from the early Pliocene of northern Japan. It seems likely, therefore, that the ancestral stock originated in the northern Pacific or Arctic and that it was not an immigrant from East Asia. Possibly it migrated from the Arctic sea through the Bering Strait into the northern Pacific at the beginning of the early Pliocene. Because there is insufficient evidence at present, further investigation is necessary to determine its origin.

The genus *Yabepecten* was of rather widespread geographic occurrence in cool or cold water molluscan faunas during the early Pliocene, being recorded from northern Japan and now from the west coast of North America as far south as western Washington. The genus became extinct by the end of the early Pliocene. Owing to its brief geologic record and widespread distribution, it is of considerable significance in circum-North Pacific faunal correlation. It seems probable that the genus will eventually be found in the Neogene sequence of Kamchatka.

ACKNOWLEDGMENTS

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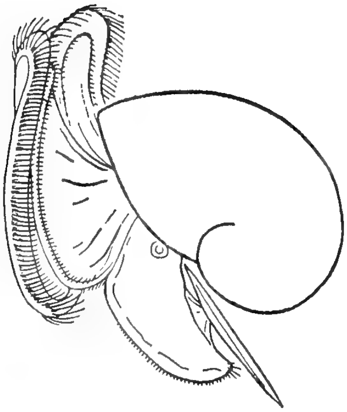

The Survival of the Daughter Sporocysts of *Microphallus pygmaeus* (LEVINSEN, 1881)

(Trematoda: Microphallidae)

in a Chemically Defined Medium

BY

DAVID PASCOE, ROY J. RICHARDS AND BRIAN L. JAMES

Department of Zoology, University College, Swansea, Glamorgan, Great Britain

(3 Text figures)

INTRODUCTION

IN ANOTHER PAPER, RICHARDS, PASCOE & JAMES (1970) have discussed recent work on the cultivation of the intramolluscan stages of the Digenea and have compared the oxygen uptake, reduced weight, metabolic rate and length of the daughter sporocysts of *Microphallus pygmaeus* (LEVINSEN, 1881) in two non-nutrient media, namely artificial and natural sea water, with that in a nutrient medium, namely the tissue culture medium 199 (MORGAN *et al*, 1950), modified to suit the osmotic, ionic and nutritional requirements of a parasite from a marine mollusc. Artificial and natural sea water were used because of their osmotic and ionic similarity to the haemocoelic fluid of the intertidal molluscan host.

The survival of the daughter sporocysts in the same media at various temperatures is compared in this paper.

MATERIALS AND METHODS

The constituents, preparation and sterilization procedures for the media are given by RICHARDS, PASCOE & JAMES (1970).

The daughter sporocysts were teased from the haemocoel of the digestive gland of several host winkles, *Littorina saxatilis tenebrosa* (MONTAGU, 1803) var. *similis* (JEFFREYS, 1865) *sensu* JAMES, 1968a and washed thoroughly in fresh filtered sea water. Only mature daughter sporocysts containing fully formed metacercariae were used in the experiments but these included small sporocysts, measuring 0.25 - 0.5 mm long and containing 10 - 35 metacercariae, of the form of *Microphallus pygmaeus* from juvenile winkles, and large sporocysts, measuring 0.6 - 1.2 mm long and containing 40 - 150 metacercariae, of the form from adult winkles. Both forms are described by JAMES (1968b).

Nine covered dishes were set up, each containing 10 large and 10 small sporocysts in 5 ml of natural sea water (3 dishes), artificial sea water (3 dishes) or modified medium 199 (3 dishes).

Three dishes, one of each medium, were maintained at 20°C, 3 at 10°C and 3 at 4°C.

The medium in each dish was changed periodically and the sporocysts examined with the light microscope at irregular intervals, of between 2 and 7 days, for up to 120 days.

RESULTS

The body wall (tegument and subtegument) of the healthy sporocysts immediately after removal from the host is extremely thin, transparent and very slightly contractile. The contained metacercariae, seen clearly through the sporocyst wall rolled up in a characteristic posture (JAMES, 1968b), are also transparent and contractile.

When the temperature is 20°C, and sometimes also at the lower temperatures, no apparent indication of degeneration occurs, *in vitro,* until the sporocyst wall ruptures and liberates the metacercariae. More frequently, however, the first indication of degeneration at the lower temperatures is that one or more of the contained metacercariae become inactive, opaque, granular in appearance and are apparently dead. The number increases progressively until all contained metacercariae are dead. During this period, usually before all contained metacercariae are dead, the body wall of the sporocyst may burst or itself become immobile, opaque and granular. After the body wall becomes opaque, further observation of the contained metacercariae can be made only by dissection of the sporocyst.

Thus, in the graphs (Figures 1 - 3), the relative capacity of the media to maintain the sporocysts is assessed by plotting the number of intact, contractile, transparent sporocysts which remained, on each day on which observations were made. Other criteria for assessing the media, such as the first appearance of opaque, immobile metacercariae within the sporocysts or the continuing occurrence of healthy transparent, active metacercariae within immobile opaque sporocysts, are described in the text. The results obtained from the small and large sporocysts are grouped in the graphs (Figures 1 - 3) but, wherever necessary, considered separately in the text.

At 20°C, the metacercariae are extremely active, continually expanding and contracting within the sporocysts, in all media. The sporocysts, however, are inactive and survive for only a short time (Figure 1). Every sporocyst in artificial and natural sea water bursts, liberating the metacercariae, by 4 to 6 days. Those in the nutrient medium usually survive for no longer, most having burst by day 6. One small sporocyst, however, survived for 16 days before rupturing. Before bursting and after 2 days in the nutrient medium, the sporocysts progressively secrete a mucus-like substance which adheres them to each other and to the side of the culture dish. The large sporocysts rupture before the small in all media at 20°C.

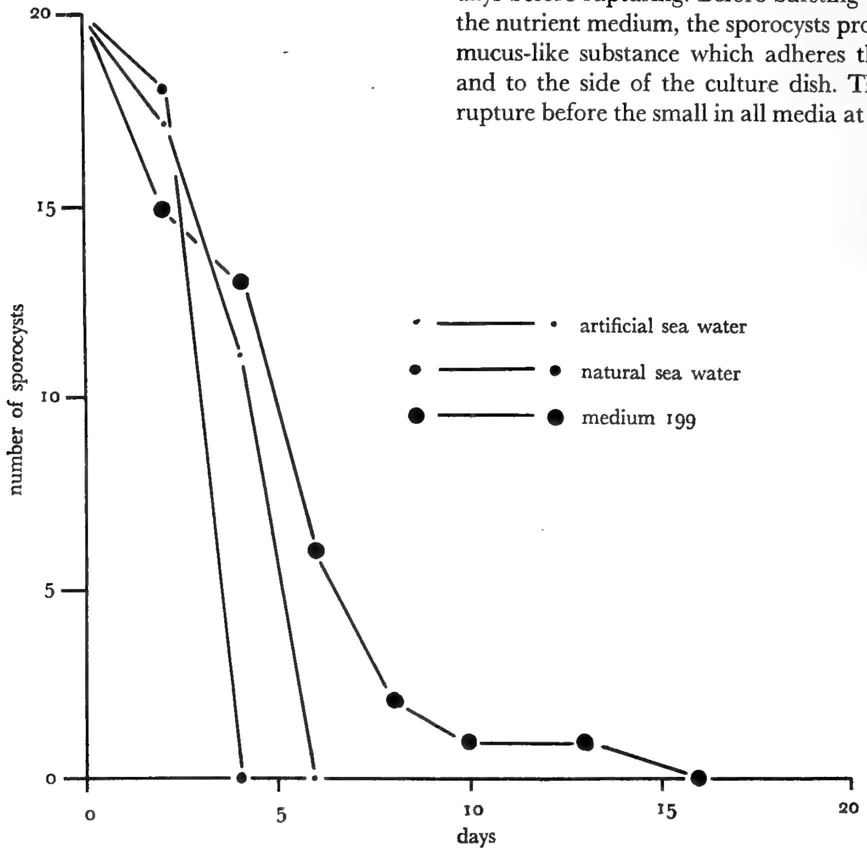

Figure 1

Variations in the number of intact, contractile and transparent daughter sporocysts of *Microphallus pygmaeus* remaining in natural sea water, artificial sea water and modified medium 199 with days, *in vitro* at 20°C

At 10°C, the sporocysts survive longer (Figure 2) than those in the corresponding media at 20°C (Figure 1).

In artificial and natural sea water about half of the contained metacercariae are immobile, opaque and granular by day 4 in the small sporocysts but not until day 8 in the large sporocysts. Thereafter, the number of opaque metacercariae increases, until the sporocyst walls burst or become immobile and opaque, from day 4 to 13 in the small sporocysts and from day 10 to day 16 in the large sporocysts. On dissection, however, the opaque sporocysts were seen to contain some apparently healthy metacercariae until day 18 in the small sporocysts and until day 21 in the large sporocysts.

The sporocysts survive for a considerable period in the nutrient medium at 10°C (Figure 2). The first apparent change, occurring after 4 to 8 days, is the secretion of the adhesive mucus-like substance. The behaviour of the sporocysts is also unusual in that the body walls are extremely contractile. Immobile, opaque granular metacercariae first appear in the small sporocysts on day 18 but not until day 21 in the large sporocysts. The body wall bursts or becomes opaque and immobile in the small sporocysts first on day 21 and in the large sporocysts on day 24. The number increases progressively until all small sporocysts are affected by day 30 and all large sporocysts by day 56 (Figure 2). On dissection, the opaque small sporocysts were seen to contain healthy metacercariae until day 70 and the large sporocysts until day 120.

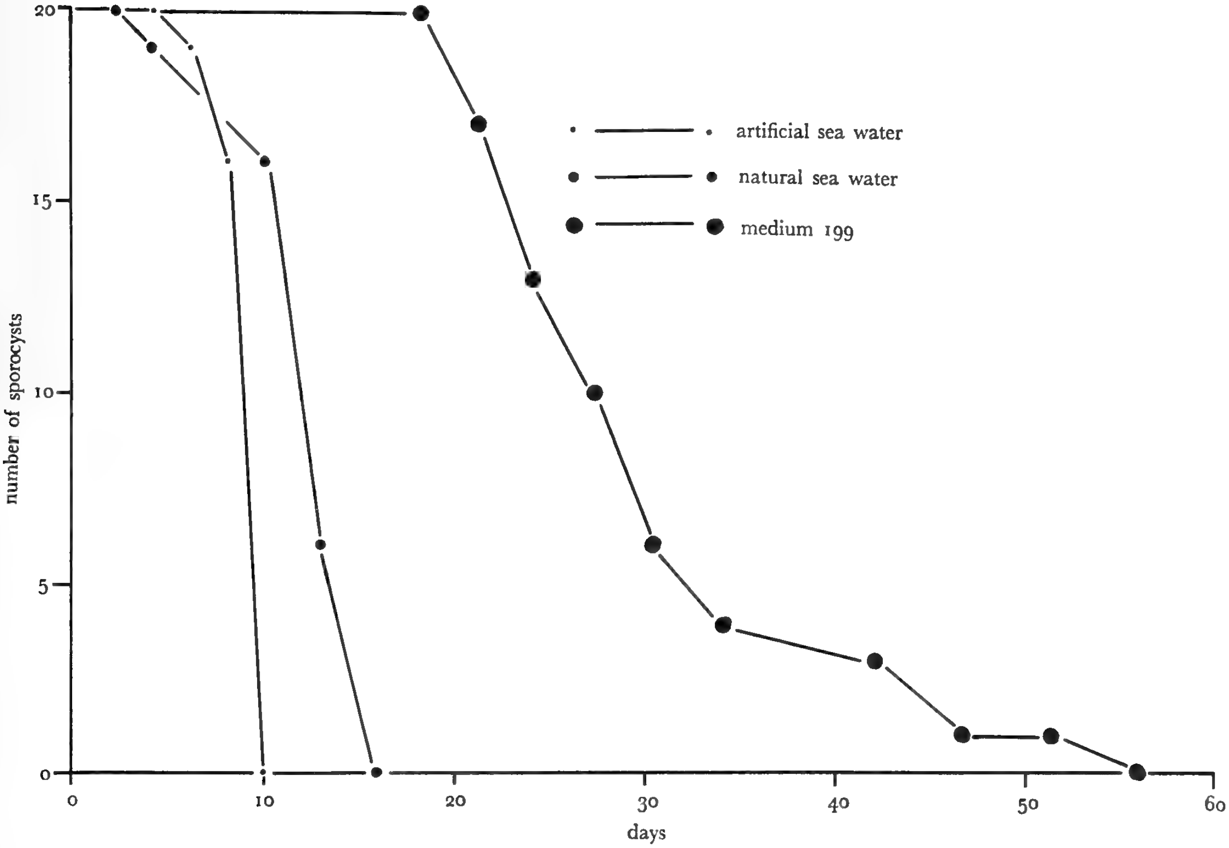

Figure 2

Variations in the number of intact, contractile and transparent daughter sporocysts of *Microphallus pygmaeus* remaining in natural sea water, artificial sea water and modified medium 199 with days, *in vitro* at 10° C

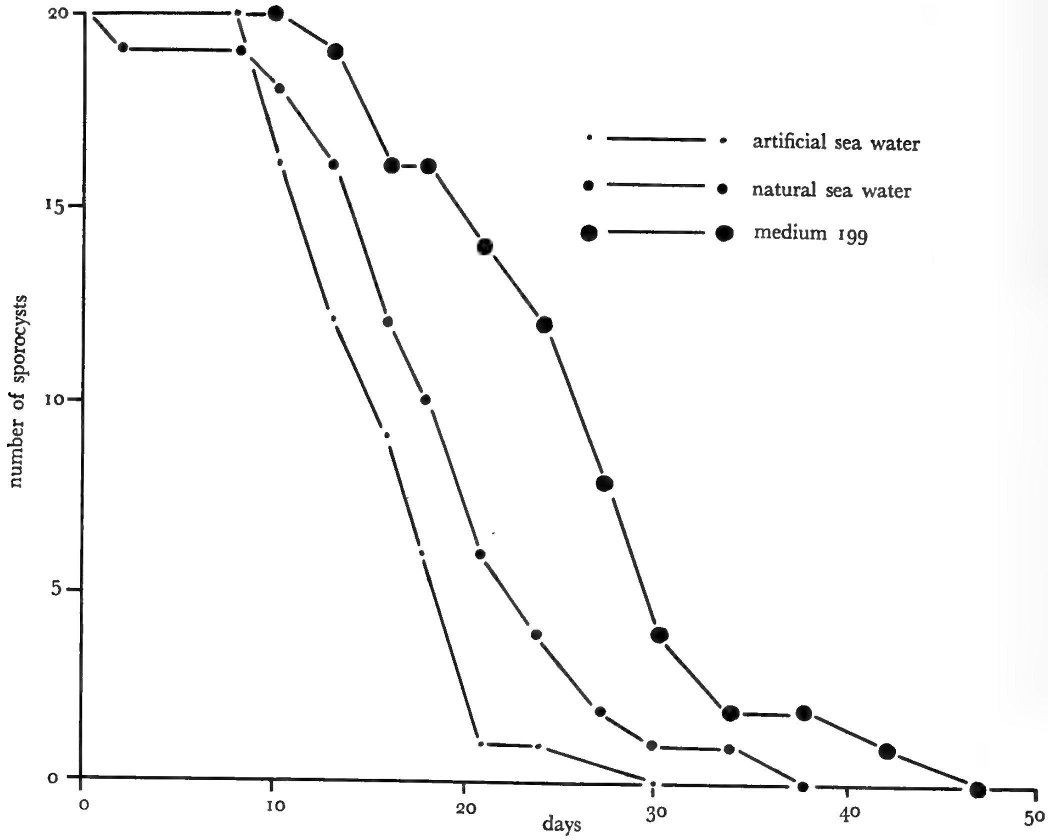

Figure 3

Variations in the number of intact, contractile and transparent daughter sporocysts of *Microphallus pygmaeus* remaining in natural sea water, artificial sea water and modified medium 199 with days, *in vitro* at 4° C

At 4°C (Figure 3), the sporocysts in artificial and natural sea water degenerate less rapidly and survive longer than at 10°C (Figure 2). In contrast, the sporocysts in the nutrient medium at 4°C degenerate more rapidly and do not survive as long as those at 10°C.

In artificial and natural sea water at 4°C, some opaque, granular, immobile metacercariae occur within all small sporocysts by day 6 and in all large sporocysts by day 10. The body wall bursts or becomes opaque and immobile first on day 10 in the small sporocysts and on day 13 in the large sporocysts in artificial sea water but on day 2 and day 16 respectively in natural sea water. The number increases progressively until all small sporocysts are affected by day 16 and all large sporocysts by day 30 in artificial sea water but by day 21 and 38 respectively in natural sea water. All sporocysts, dissected as soon as they became opaque, contained immobile, opaque metacercariae only.

In the nutrient medium, opaque, granular metacercariae first appear much earlier (on day 8) and increase in number more rapidly at 4°C than at 10°C in both small and large sporocysts. The secretion of an adhesive mucus-like substance occurs within 4 days and the first small sporocysts burst or become opaque and immobile on day 12 and the first large sporocysts on day 21, earlier than at 10°C. The number increases progressively until all small sporocysts are affected by day 27 and all large sporocysts by day 47. All sporocysts dissected as soon as they became opaque and immobile contained dead metacercariae only.

DISCUSSION

The results confirm earlier work (Richards, Pascoe & James, 1970) which indicated that the chemically defined nutrient medium supports the daughter sporocysts of *Microphallus pygmaeus* better than the non-nutrient media. The large sporocysts, for example, may remain healthy, as far as can be determined from the observations described here and from the measurements of oxygen uptake and reduced weight (Richards *et al, op. cit.*), in the nutrient medium for a period which compares favourably with the life span, *in vivo* (James, 1965). The health of these sporocysts is confirmed by the fact that metacercariae, removed from their body cavities, are able to develop, *in vitro,* into egg-bearing adults. The conditions required to bring about this development are described briefly by James (1970).

The nutrient medium is not ideal, however, as indicated by the eventual appearance and progression of degenerative changes and by variations in the reduced weight and oxygen uptake (Richards, Pascoe & James, 1970). Nevertheless, in spite of considerable degeneration, the occurrence of apparently healthy metacercariae within the body cavity, suggests that the sporocyst wall may still be alive and functional after 4 months (120 days) at 10°C. The metacercariae survive for a much shorter period, when liberated from the sporocyst. The considerable increase in the secretion of the mucus-like substance, probably acid mucopolysaccharide, by the sporocysts in the nutrient medium, as compared with that within the mollusc (James & Bowers, 1967), may be a stress reaction which requires further investigation. It is possible, however, that this reaction may occur *in vivo,* to adhere the sporocysts to each other and to the vertebrate host intestine in order to prevent them from passing through before the metacercariae are liberated. The ultrastructure and oxygen uptake of the body wall of the sporocysts, after considerable periods in the nutrient medium, is being examined in order to determine accurately changes in morphology and activity.

The life cycle of the parasite suggests possible explanations for the effect of temperature on the survival of the sporocysts, *in vitro.* Work being carried out in this department (see James, 1970) indicates that, when the bird final host eats infected winkles, the sporocysts escape from the host tissue in the crop or gizzard and that the temperature (about 37°C), stimulating the contained metacercariae to expand and contract vigorously, contributes to the rupture of the sporocyst wall. This occurs, within an hour or so of infection, usually in the duodenum of the host. The liberated metacercariae then develop into adults.

Thus, at 20°C, *in vitro,* the metacercariae are extremely active causing the sporocyst wall to rupture because the temperature approaches that found in the final host. The large sporocysts rupture before the small because they contain more metacercariae and have a relatively thinner body wall. The similarity in the survival of the sporocysts in the nutrient and non-nutrient media at 20°C (Figure 1), suggests that they are not absorbing nutrients at this temperature. Thus, autolysis, which will occur even when exogenous nutrients are present, accelerates the rupture of the sporocyst wall and the liberation of the metacercariae, *in vitro* and *in vivo.* Progressive autolysis and the increasing activity of the metacercariae may also account for the shape of the curves (Figure 1) obtained at 20°C.

The sporocysts survive longer in the non-nutrient media at 4°C than at 10°C, probably because the utilization of their stored food reserves (Richards, 1970) is slower when the metabolic rate is lower.

The fact that the sporocysts remain healthy and survive longer in the nutrient medium at 10°C than at 4°C indicates that the former is closer to the optimum temperature of the parasite. This is consistent with the known climatic conditions experienced by the host winkle (James, 1968a).

It is possible that the shorter survival of the small sporocysts, as compared with the large, in all media at 4°C and 10°C, may be due to their having less food reserves, as a result of occurring in juvenile hosts, than the large sporocysts which occur in adult hosts. This indicates also that, even in the nutrient medium 199, prolonged survival depends on the utilization of endogenous reserves. The probable normal distribution of the frequency of death (Figures 2, 3), provides some support for this suggestion.

SUMMARY

The daughter sporocysts of *Microphallus pygmaeus* (Levinsen, 1881) remain healthy and survive longer in a chemically defined nutrient medium, namely medium 199 modified to suit the osmotic, ionic and nutritional requirements of a parasite from a marine mollusc, than in non-nutrient media at 4°C and 10°C. At 20°C, however, survival is similar in the nutrient and non-nutrient media. The sporocysts of the large form of *M. pygmaeus* from adult *Littorina saxatilis tenebrosa* (Montagu, 1803) remain healthy and survive longer in all media at 4°C and 10°C but do not fare as well at 20°C as the small form from juvenile winkles. The reasons for these variations are discussed.

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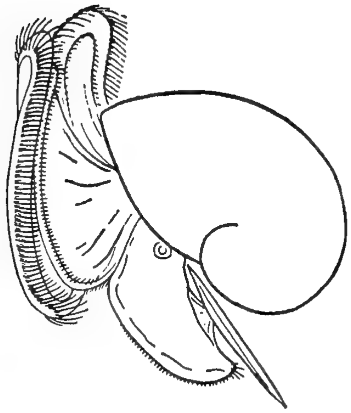

Responses of *Gemma gemma* to a Catastrophic Burial

(Mollusca: Pelecypoda)

BY

ERIC SHULENBERGER

Department of General Biology, University of Kansas, Lawrence, Kansas 66044

(6 Text figures)

INTRODUCTION

Gemma gemma (Totten, 1834) IS A SMALL ovoviviparous marine clam of the family Veneridae. On the east coast of the United States it occurs in concentrations as high as 300 000 per square meter and is an important item in the diets of many birds, crabs, and bottom-feeding fish (Sellmer, 1959). *Gemma gemma* also occurs in large numbers in the uppermost sediments on the tidal flat of the delta of Walker Creek, Tomales Bay, California. This population has been used in the present study.

Within the estuarine environment at Walker Creek, *Gemma gemma* is subjected to sudden variations in physical parameters: repeated exposure to drying during the tidal cycle, wide variations in temperature, both seasonal and daily changes in salinity with variations in the runoff from Walker Creek, and catastrophic burial under various types of sediment.

Burial may take place in a number of ways. First, the tidal flat may receive a large influx of suspended material from Walker Creek due to heavy winter rainfall. Second, the already-established bottom sediments may be reworked by tidal or wind-and-wave action. Finally, sudden burial may result from earthquake, mudslide, or other like phenomena.

Armstrong (1965), working with 10 species (not including *Gemma gemma*), concluded that no clams artificially buried in aquaria or 5-gallon cans showed any ability to elevate. Bradley & Cooke (1959) reported some simple burial experiments on *G. gemma* but did not investigate burrowing rates.

To an animal as small as *Gemma gemma* (2 - 5 mm long as adults) sudden burial under several centimeters of sediment would appear to be a major catastrophe. The present study investigates its ability to burrow upwards in response to catastrophic burial under 2 types of sediment.

MATERIALS AND METHODS

Animals: At low tide on 31 July 1969, 1442 specimens were obtained from 2 sites in Walker Creek delta; a 1.41 mm mesh sieve was used to collect the animals. A large proportion of the *Gemma gemma* population is of such a size as to pass through this mesh (Jackson, 1968; Welch, 1969); the sieve was chosen so as to collect adult animals only. The sites had a combined surface area of less than one-half square meter and were sampled to a depth of about 2 cm. In the experiments only clams of from 2 to 4 mm in length were used.

The 2 collection sites were selected as representative of areas where catastrophic burial might occur. The seaward site has a sandy substrate that is subject to tidal and wind-and-wave disturbances, particularly at low tide. The shoreward site has a silty substrate and receives heavy inputs of suspended material from Walker Creek. Animals from the 2 sites were combined at random in the experiments.

Sediment: Substrate samples were taken from both collection sites and were analyzed for particle size. Over 85% (wet weight) of the silty sample passed through a 63μ sieve. Nearly 90% (wet weight) of the sandy sediment was found to be between 105 and 500μ in diameter, with greatest concentration between $150 - 350\mu$.

Sediments used for burying the animals were 'sand' ($105 - 500\mu$) and 'silt' (less than 63μ). No attempt was made to further narrow the sediment size ranges because more thorough sorting does not appear to occur naturally in the area. The sediments were kept in running sea water until use.

Equipment: Three aquaria were built of redwood and single-strength window glass; inside dimensions were 39 cm wide by 29 cm high, and 0.6 cm thick (Figure 1).

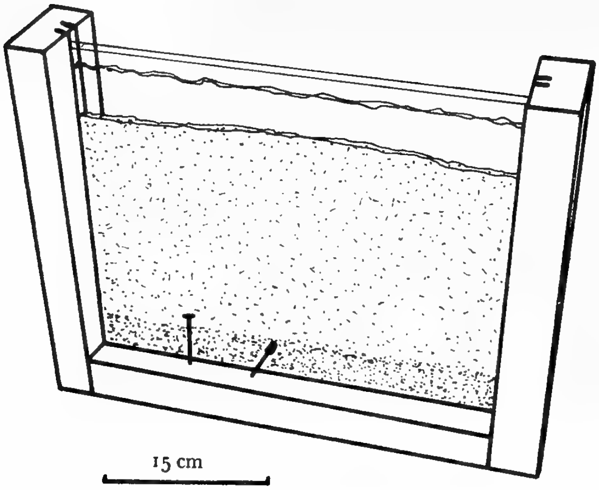

Figure 1

One of three special aquaria
(Note original - compacted - substrate, overlying sediment layer, marker nails)

A dental x-ray unit was used to photographically record the animals' positions. In order to have observed them visually the aquaria would have had to be so narrow as to provide a much more unnatural habitat due to warming and confinement.

All x-ray-records were made on one of 3 types of film:
Kodak "Blue Brand Medical X-ray Film" BBA-59;
Kodak "Blue Sensitive Medical X-ray Film" SB-9;
Kodak "No-Screen Medical X-ray Film".
Nails driven into the aquaria frames provided position-referencing images on the negatives.

Experimental Procedure: X-ray exposure was determined initially by trial-and-error. Basic settings for most exposures were:
X-ray tube filament current, 3 mA;
Exposure time, $1\frac{3}{8}$ seconds;
Aquarium-to-projector distance, 50 cm.
The film was held in standard magnesium-front x-ray film holders during exposure.

All film was developed for 5 minutes at 20°C in General Electric "Supermix" x-ray film developer and fixed for 5 - 10 minutes in "Supermix" speed-type x-ray fixer. All film was treated with Kodak "Photo-Flo" and air-dried.

X-rays were examined by transmitted light. *Gemma gemma* stand out clearly, as do the sediment-water interface and the interface between the original substrate and added sediment. The clams were numbered on each x-ray film; all individuals could be identified (by position) in consecutive x-ray photographs and their progress recorded.

No *Gemma gemma* individuals were x-rayed more than 10 times, for a 13.8 second maximum total exposure to low-intensity x-ray radiation, and animals were changed at the end of each experiment so that possible radiation damage would not interfere with their performance. I encountered no literature on the effects of radiation on mollusks.

At all times except when making an x-ray record the aquaria were supplied with a steady circulation of sea water at 15 - 17°C. With the exception of the last 3 experiments, all were conducted with sea water of 33‰ salinity.

In each experiment an aquarium was filled with sea water and 3 to 4 cm of sand was placed in it as original substrate. This layer was compacted by jiggling and tapping the aquarium until no further settling could be observed. Twenty-three to 28 *Gemma gemma* were selected and arranged on the substrate at intervals of about 1 cm to provide a large sample, avoid crowding, and make the x-ray records easy to interpret. The animals were allowed 30 minutes to burrow into the substrate. Any that failed to burrow to siphon depth within this time were removed to be certain that all animals used were alive at the start of the experiment.

A given depth of the type of sediment desired was then deposited on the animals by allowing it to drift down through the water. The aquarium was tapped lightly after each addition of sediment to help settle the added material and release trapped air. This compaction never approached that of the original substrate.

Immediately after the addition of sediment the aquarium was disconnected from the sea water system and carried to the x-ray apparatus, the film and aquarium were positioned, the exposure made, and the aquarium was returned to the wet laboratory and reconnected to the sea water system within 3 minutes of disconnection. The temperature of the aquarium did not change measurably during this interval.

X-ray records were made frequently for the first several hours, usually every hour or hour and a half; 2 or 3 more were made at approximately 9 to 12 hour intervals thereafter. Each negative was developed immediately following exposure, to be certain of having obtained a usable picture, and each was permanently numbered.

The experiment was terminated when either 20% of the animals had reached the surface or 3 days had elapsed. No attempt was made to wait until all of the clams had reached the surface. Upon termination the animals were recovered by rinsing the sediment through a 1 mm sieve. Recovered *Gemma gemma* were dropped onto sand 2 cm deep in a small dish and placed in running sea water. Clams which had burrowed to siphon depth within 4 or 5 hours were counted as being alive. Those which had remained on the surface and had given no indication of motion were counted as being dead, as were all animals which were obviously dead (*i. e.,* with shells agape). Survival percentages were calculated from these observations, not from the number of animals that attained the surface.

An attempt was made to determine if the clams' burrowing and survival rates varied with changes in salinity. Aquaria were supplied with brackish water at 16½‰ salinity from a large reservoir vessel in which sea water and Dillon Beach tap water had been mixed in equal volumes. Despite its chlorine content, tap water was used because of the unavailability of a 200-liter-per-day source of de-ionized or distilled water or rainwater. The size of the reservoir vessel was such that the amount of water in it acted as a thermal buffer and prevented temperature changes greater than 1°C in the aquaria.

The x-ray records made during each experiment were arranged in sequence and a vertical line was inked on each through a marker-nail image. This line served as a reference from which to measure lateral distances. Sequential measurements of each animal's depth and lateral position were made to the nearest mm. The depth recorded was the distance from the uppermost point on the clam's shell to the sediment-water interface above it. Lateral distances were measured from the left-hand-most point on the animal's image to the lateral reference line.

RESULTS

Behavioral Observations: On 6 August 1969, 20 *Gemma gemma* were recovered after 79 hours of burial under 20 cm of sand and placed on sand 2 cm deep in running sea water. First movement of the first animal, consisting of opening of the shell and a brief protrusion of the foot occurred at 1.8 minutes. After 3.3 minutes this animal had buried itself to siphon depth and another was half buried. Several animals were observed to bury themselves to siphon depth within 2 minutes of their first motion. After 12 minutes, 18 *G. gemma* had re-established themselves at siphon depth.

In burrowing into a sandy substrate, *Gemma gemma* goes through a definite sequence of motions. First the foot protrudes, tests the substrate, and is withdrawn. The foot is then re-extended, its tip is forced into the sand, and the animal raises itself in one rapid motion to a posterior-up position. The clam then buries itself by means of 10 to 15 rocking motions at about 10-second intervals. Each rocking motion takes ½ second and consists of a dorsal-ventral swing of about 25° in the plane established by the edges of the valves. The initial swing of each motion forces the anterior end ventrally; the second brings it back.

Twenty-five *Gemma gemma* were allowed to burrow into 2 cm of sand and were left in running sea water overnight in a darkened room. Furrows were observed in the surface of the sand 10 hours later; they were 1 to 2 mm wide, up to 2 mm deep and up to 5 cm long. A buried *G. gemma* was found at one end of each furrow. No such furrows were produced during daylight hours.

Data: Summarized results are presented in Figures 2 to 6. A change in depth (Δd) between successive x-ray exposures was figured for each animal. A mean Δd was calculated from all Δds obtained from 2 consecutive x-ray records. Knowing the elapsed time between the x-ray exposures, a 'mean rate of climb' for all animals measured was calculated. The fastest 25% of the animals measured were also noted, and a 'mean rate of climb fastest 25%' was calculated. An overall mean Δd was figured for each experiment by comparison of the first and last negative in the series, and from this an 'overall mean rate of climb' was figured for the entire duration of each experiment. Lateral movement was measured by comparison of the first and last x-ray negatives in each series, and a 'mean lateral movement' was calculated. This is an approximation, since it was impossible to observe lateral movement perpendicular to the plane of the x-rays. From the mean lateral movement and the overall mean Δd, a mean angular deviation from a vertical path was calculated for each experiment. In the lateral movement calculations the net lateral movements of individual animals were summed without regard to their directions.

DISCUSSION

Survival: Adult *Gemma gemma* are able to survive burial in either sand or silt for periods of more than 100 hours. In sand, survival rates were at or near 100% at all burial depths and at both 33‰ and 16½‰ salinities. In silt under seawater, the survival rate dropped to 58%. No brackish water experiments were conducted with silt (Figure 2).

The difference in survival between burial in sand and burial in silt is considerable (Figure 2). In the silt experiment it is possible that only those animals which had already reached the surface would have survived in a natural situation, and that others (alive but still buried at

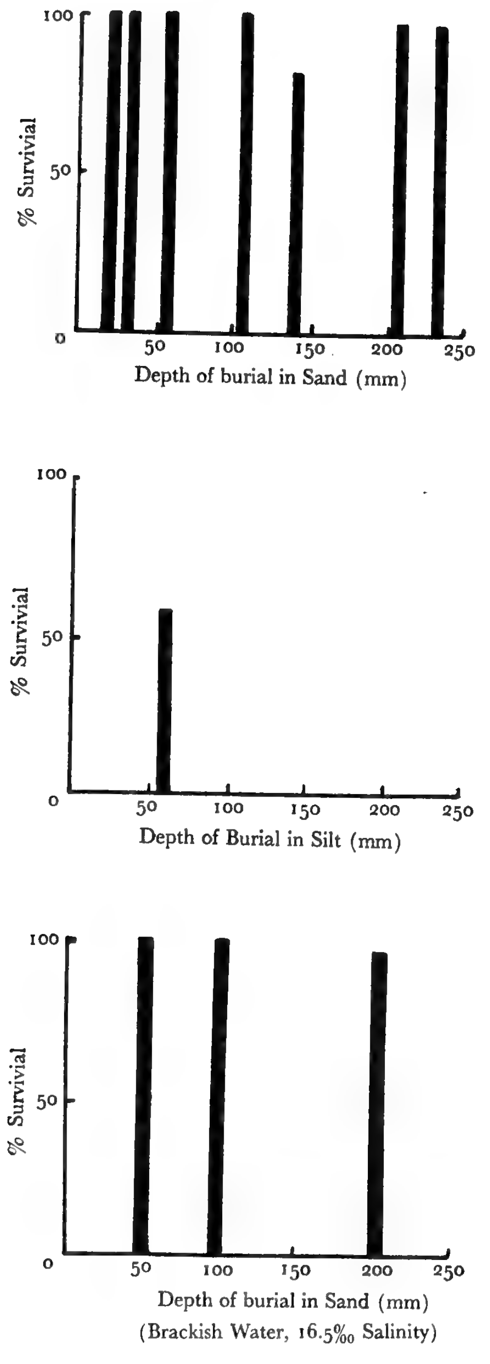

Figure 2

Survival rates

(Top two with seawater at 33‰ salinity; all at 15 - 17° C)

termination) would have perished; this would have given a survival rate of 46% instead of 58%.

Twenty-eight *Gemma gemma* were exposed to 16½‰ salinity (with chlorine) for 2 days, then accidentally left buried under 200 mm of damp (not saturated) sand at room temperature for 4 more days. Surprisingly, 27 survived.

In 3 experiments with brackish water at 16½‰ salinity, *Gemma gemma* failed to burrow upwards through sand. Despite this, survival under 50, 100, and 200 mm of sand was 96% or better. More work is needed on the clams' survival under changing temperature and salinity.

Bradley & Cooke (1959) reported on some simple burial experiments with *Gemma gemma*. They did not investigate burrowing rates, nor did they define their term "recovered", although it appears to mean those animals which returned to the surface, rather than those which survived. Their data were as follows:

Table 1

At depth of --	Date planted	Date recovered	Number planted	Number recovered [1]
2 inches				
test clams	Aug 30	Sept 1	10	10
control clams	Aug 30	Sept 1	10	[2] 10
4 inches				
test clams	Sept 1	Sept 3	10	7
control clams	Sept 1	Sept 3	10	10
8 inches				
test clams	Sept 3	Sept 5	10	5
control clams	Sept 3	Sept 5	10	10

[1]: feeding

[2]: at surface, half emerged

No further elaboration of terms was contained in the paper.

Gemma gemma possesses between 8 and 12 fine tentacles on the tip of the incurrent siphon (Sellmer, 1959), which are loosely interdigitated and may function as a sieve to keep out sand. It is possible that, in burrowing through sand, *G. gemma* is able to obtain oxygen from interstitial water which has been filtered through these tentacles. It is probable that the tentacles are incapable of filtering silt-sized particles and that the animals' ctenidia become fouled if they attempt to utilize interstitial water from silt. This, coupled with the viscous nature of silt, may account for the difference in survival rates between silt and sand burials.

Additional evidence is available that *Gemma gemma* is able to utilize interstitial water from sand. In many x-ray pictures a short, tubular structure is visible at the posterior end of some animals. If not a siphon, this may represent a small, water-filled void, perhaps created by the excurrent water from the clam.

ARMSTRONG (1965), working with *Mya arenaria* LINNAEUS, 1758, *Siliqua patula* (DIXON, 1788) and *Macoma nasuta* (CONRAD, 1837), among others, obtained high

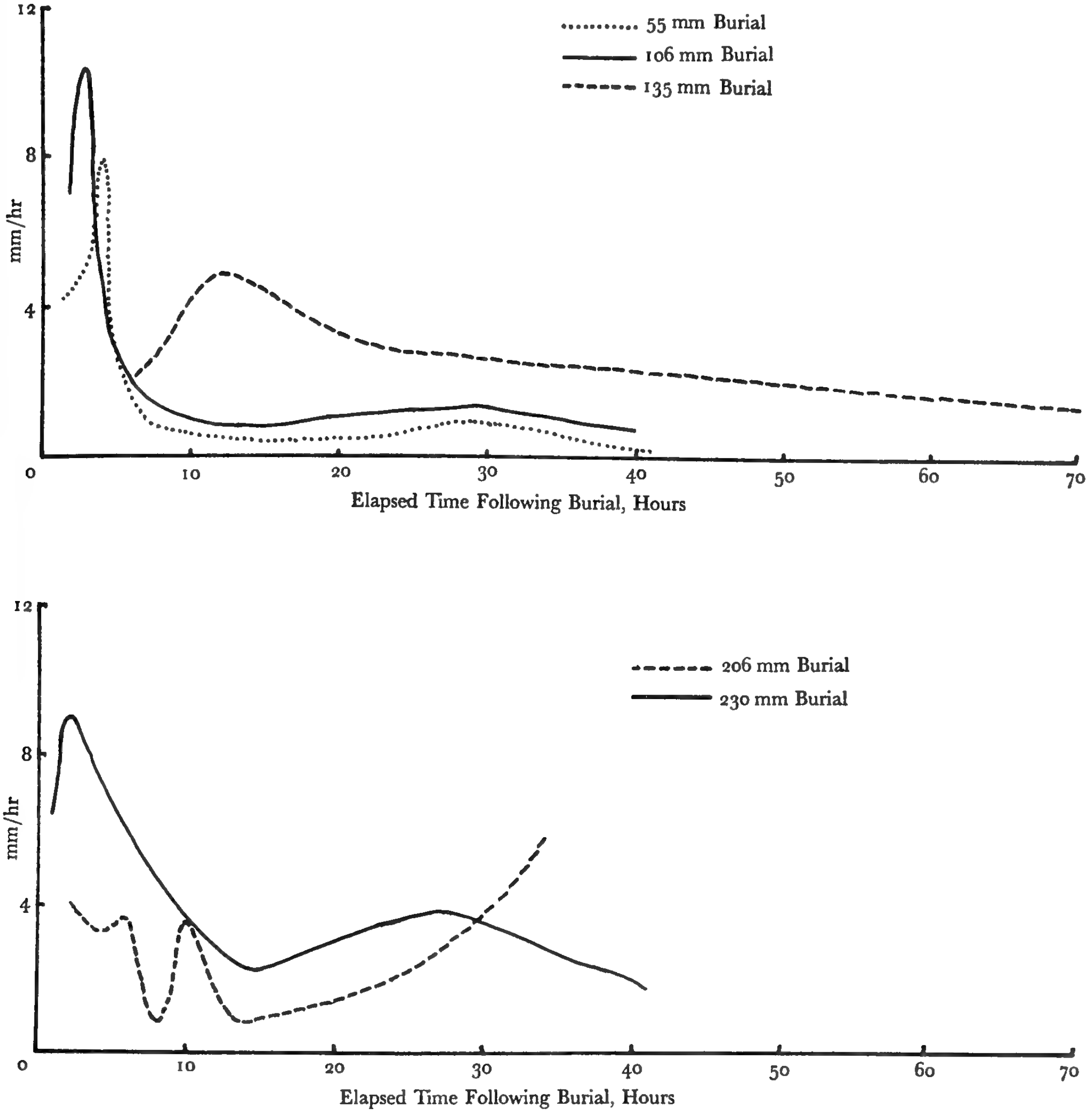

Figure 3

Mean rates-of-climb for all animals measured in each experiment (On 2 identical sets of axes for clarity; all burials in sand, under seawater at 33‰ salinity and at 15 - 17°C) mortalities with burials as shallow as 10 cm of sand and found that none of these species was capable of any elevation when artificially buried. Recent work by **Kranz** (personal communication) has shown that *Mya arenaria* is capable of burrowing up through at least 8 cm of sand and that *S. patula* is capable of extricating itself from burial in up to 30 cm of sand. **Kranz** also indicates that *Macoma nasuta* is capable of burrowing upwards through

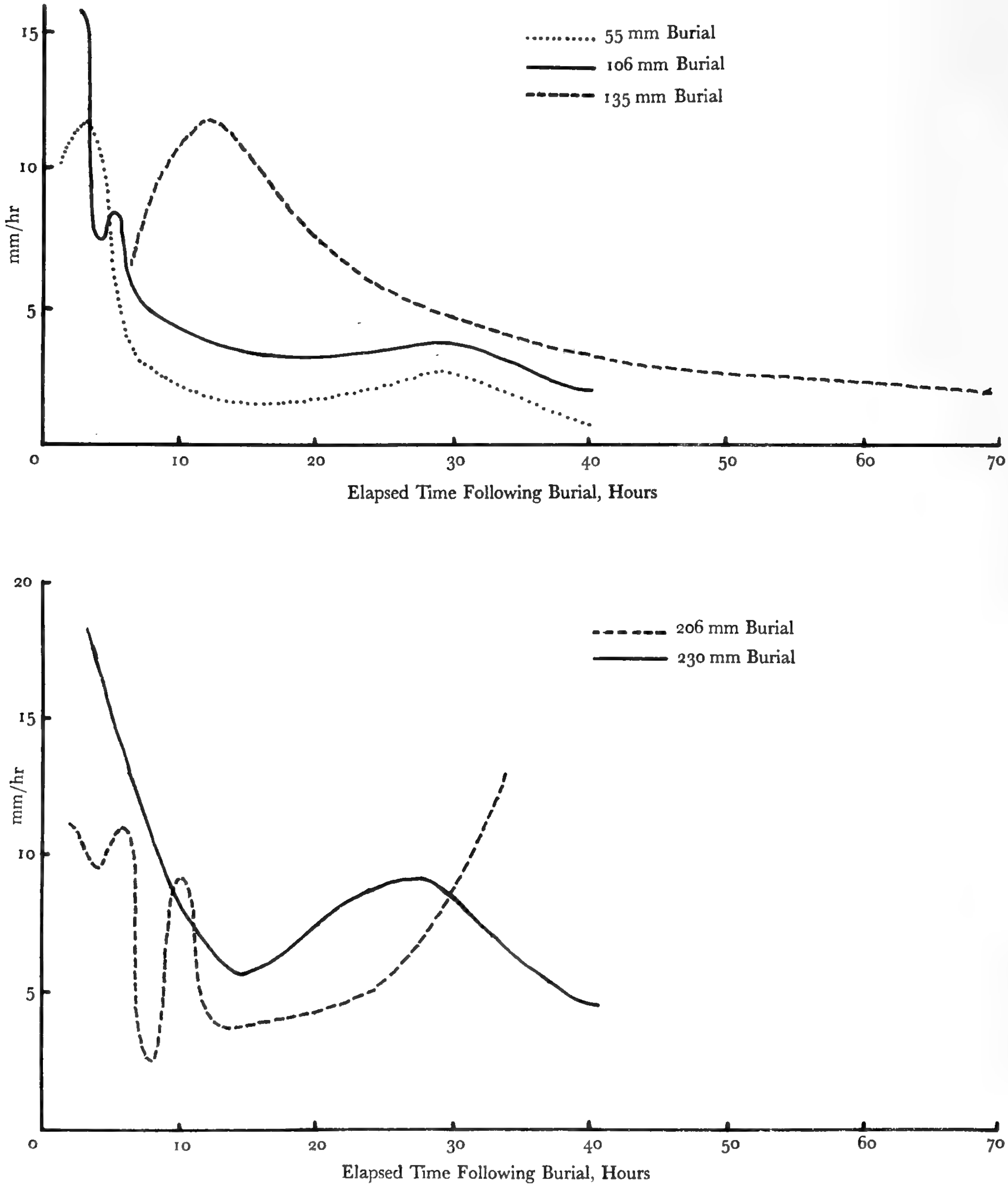

Figure 4

Mean rates-of-climb for fastest 25% in each experiment
(On 2 sets of axes for clarity; all burials in sand under seawater
at 33‰ salinity and at 15 - 17° C)

36 cm of sand in 18 hours, and his experiments with *M. nasuta* were terminated when over 80% of the test animals returned to the surface through 40 cm of sand. These findings cast considerable doubt on the validity of ARMSTRONG's conclusions.

All of the species with which ARMSTRONG and KRANZ worked are considerably larger than *Gemma gemma*; 'body size vs. sediment particle size' ratio in relation to burrowing ability deserves further investigation.

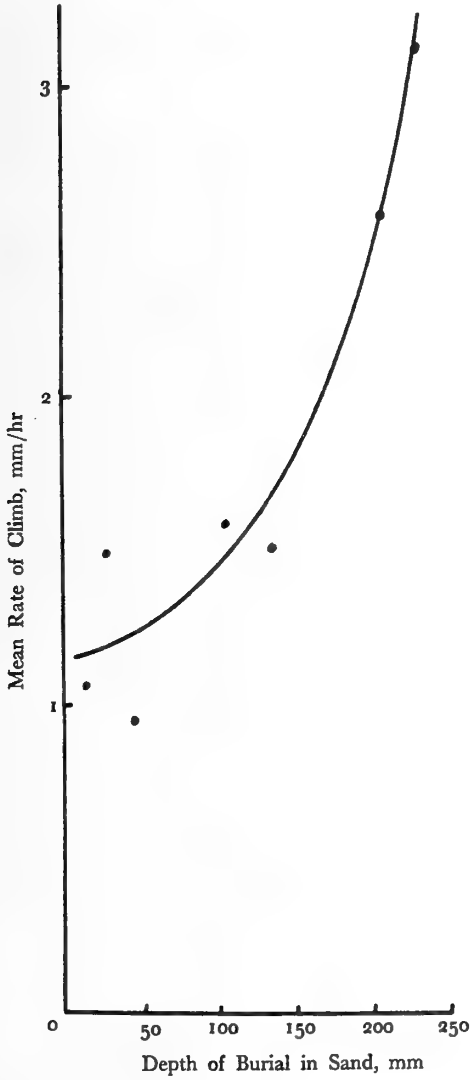

Figure 5

Mean overall vertical burrowing rate of all animals measured in each experiment

Rates of Climb: Graphs for both 'mean rate of climb' and 'mean rate of climb, fastest 25%' (Figures 3 and 4) show that the data for 55, 106, and 230 mm burial in sand all have remarkably similar forms despite the different depths. All 3 begin at high rates of climb shortly after burial (individual rates of over 35 mm/hour were recorded), and all reach peaks within 5 hours. Rates of climb then decrease sharply, and minima occur in the 14 to 17 hour period. In all 3 cases *Gemma gemma* exhibits a resurgence of climbing activity at 25 to 28 hours after the first peak; this period is nearly equal to one tidal cycle, but no attempt has been made to correlate these data with that cycle.

Burials at 135 and 206 mm deviate from this pattern. Data for the 135 mm burial curve are sketchy and it is probable that this group actually exhibited the same pattern of activity as did those buried in 55, 106, and 230 mm of sand. Results from the 206 mm burial are puzzling; particularly striking is the strong upsurge in activity at the end of the experiment.

Animals buried under sand and kept in brackish water simply failed to burrow upwards significantly within the time span of the experiments. Whether failure to burrow was due to the change in salinity, the chlorine content of the tap water, or some other factor was not determined.

Gemma gemma exhibits a sharp increase in digging rate as burial depth in sand increases (Figure 5); similar investigations might be made on its behavior in silt. This implies that *G. gemma* is capable of sensing the depth to which it has been buried.

Deviations from the Vertical in Burrowing: The deeper *Gemma gemma* is buried the more nearly vertical its path becomes (Figure 6). Time and energy expenditure are minimal if the animal burrows straight up; in all but the shallowest of burials this is what *G. gemma* did.

SUMMARY

Gemma gemma is able to cope successfully with catastrophic burial in up to 230 mm of sand and 57 mm of silt. Large percentages survive burial for up to 6 days under a variety of conditions. Rates of upward burrowing appear to follow a definite and possibly cyclic pattern, and the rates increase as burial depth increases. The animals burrow nearly vertically, more so with greater depth.

Among unanswered questions, two are of particular interest: whether *Gemma gemma* utilizes interstitial water while buried, and what are the maximum sustained rates of deposition with which the clam can cope.

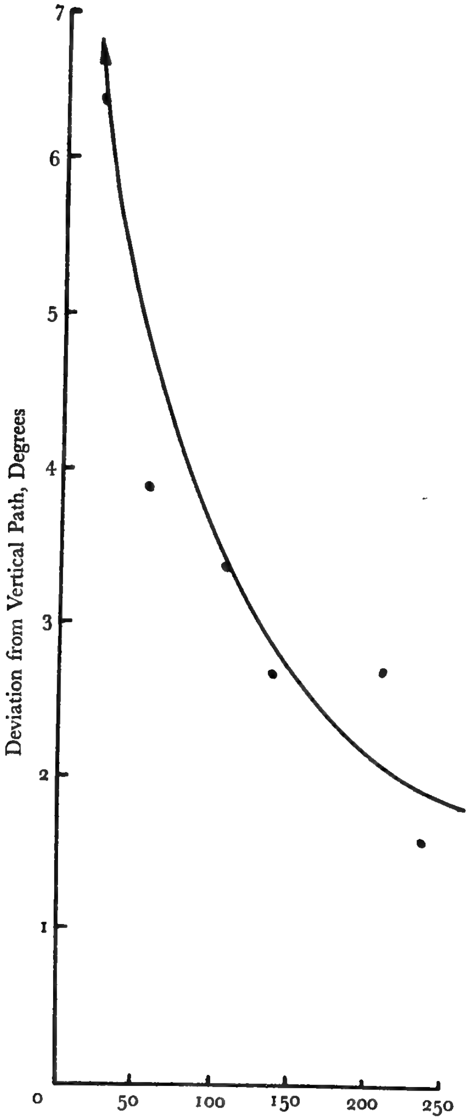

Figure 6

Mean deviation from vertical path

ACKNOWLEDGMENTS

I wish to thank Dr. Edmund H. Smith, Director, and the staff of Pacific Marine Station, Dillon Beach, California, with whose support and at whose facilities this research was conducted. My thanks also go to Mr. Dave Montgomery for his continual help, and to Mr. Peter Kranz for aid and advice in the execution of the experiments. Special thanks go to Dr. Eugene Coan for his considerable editorial assistance.

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Observations on Opisthobranchs of the Gulf of California

BY

HANS BERTSCH[1]

AND

ALBERIC A. SMITH[2]

Las Cruces Marine Station, Baja California, Mexico

INTRODUCTION

THE SOUTHERN PART of the Gulf of California exhibits a tropical fauna that is still largely unknown. Owing to the ruggedness of the Baja California peninsula, the isolation of the region, and the smallness of the human population, this region has remained fairly inaccessible to collectors. The Las Cruces Marine Station, under the direction of Dr. Rita Schafer of Immaculate Heart College, Los Angeles, California, and sponsored by Mr. and Mrs. Bing Crosby, operates during the summer near La Paz, Baja California, to provide research facilities to broaden the knowledge of the animal and plant life of this section of the Gulf. During a recent study at the station, in July, 1969, we found substantially new data for a number of species of opisthobranchs. In this paper we report on a range extension and predator-prey relationships of *Navanax inermis,* and the presence of *Onchidiella binneyi* in the southern Gulf of California.

Navanax inermis (Cooper, 1862)

SYNONYMY AND REFERENCES

Strategus inermis Cooper, 1862: 202 - 203

Navarchus inermis (Cooper). Cooper, 1863a: 8. Cooper, 1863b: 58. Bergh, 1893: 133 - 134; plt. 8, fig. 14. Bergh, 1894: 214 - 217; plt. 10, fig. 13; plt. 11, figs. 2 - 5.

Chelidonura inermis (Cooper). Bergh, 1900: 212. Bergh, 1905: 42 - 43

Aglaja sp. Pruvot-Fol, 1954: 50, fig. 8, g.

Navanax inermis (Cooper). Pilsbry, 1895: 131. Pilsbry, 1895-96: 57 - 58; plt. 15, figs. 89 - 93. Dall, 1921: 64. MacFarland, 1924: 390. Johnson & Snook, 1927: 255, 485 - 486; plt. 8, fig. 1; text fig. 494. Oldroyd, 1927: 49. MacGinitie, 1930: 68. Thiele, 1931: 395. MacGinitie, 1935: 737. Smith & Gordon, 1948: 179. MacGinitie & MacGinitie, 1949: 256, 313, 371 - 372, 374, 376 - 377, 380 - 381. Marcus, 1961: 7 - 8; plt. 1, figs. 14 - 16. Paine, 1963: 1 - 9. Steinberg, 1963: 116. Paine, 1965: 603 - 619. Lance, 1966: 71. MacFarland, 1966: 9 - 11; plt. 2, figs. 1 - 3; plt. 6, figs. 10, 11; plt. 7, figs. 21 - 23. Marcus & Marcus, 1967: 19, 149 - 151, 238; fig. 8 (of part II). Beondé, 1968: 376. Ricketts & Calvin, 1968: 300, 322-323, 513. Sphon & Lance, 1968: 80. Lance, 1969: 35. Roller & Long, 1969: 427. Bertsch & Smith, 1970: 19

DISTRIBUTION

The recorded range of *Navanax inermis* is from Elkhorn Slough, near Monterey, California (36°50′ N; 121°47′ W), to Laguna Manuela, Baja California (28°11′ N; 114°04′ W), and in the Gulf of California from Puerto Peñasco (31°17′ N; 113°35′ W) to Kino Bay, Sonora, Mexico (28°48′ N; 111°55′ W).

The new localities of the following specimens collected by the authors constitute a range extension of *Navanax inermis* over 250 miles southward to the southwestern end of Isla Cerralvo:

1) SW corner Isla Cerralvo (24°09′ N; 109°50′ W).
July 2, 1969; one specimen, 22 mm long; dredged from sandy bottom, about 30 feet deep. Inside of a dead pelecypod shell that was heavily encrusted with algae, tunicates and bryozoans.

2) Las Cruces Bay (24°13′ N; 110°05′ W).
July 4, 17, and 21, 1969; 3 specimens, 9 mm, 34 mm, and 29 mm long, respectively; 2 specimens found under rocks in 5 to 10 feet of water; a 3rd found during a dawn low tide on top of a rock, crawling amid algae, in 1 foot of water.

3) NW Isla Cerralvo (24°22′ N; 109°56′ W).
July 16, 1969; one specimen; under rocks, 10 feet of water.

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[1] Permanent address: Franciscan School of Theology, 1712 Euclid Avenue, Berkeley, California 94709

[2] Permanent address: St. Elizabeth's High School, 1530 34th Avenue, Oakland, California 94601

4) Isla Espíritu Santo (24°31′ N; 110°22′ W).
One specimen, juvenile; 38 feet deep, at night with SCUBA, by Don Wobber (identified by Lawrence Andrews). This specimen is in the collection of the California Academy of Sciences and has not been reported previously.

PREDATOR-PREY RELATIONSHIPS

The diet preference of *Navanax inermis* for *Bulla gouldiana* Pilsbry, 1895, and *Haminoea virescens* (Sowerby, 1833) has been well documented (Johnson & Snook, 1927, p. 486; MacGinitie & MacGinitie, 1949, p. 372; Paine, 1963, pp. 1 - 9; 1965, pp. 603 - 619). The *N. inermis* we caught July 16 from NW Isla Cerralvo was kept alive in an aquarium. Later that day it excreted a shell of *Haminoea* cf. *H. angelensis* Baker & Hanna, 1927, which it had eaten in the field.

One specimen of *Navanax inermis* (obtained July 17) was fed a *Lamellaria inflata* (C. B. Adams, 1852). The *L. inflata* was placed in the same tank with *Navanax* at 9:00 p. m., was eaten sometime during the night, and its shell was excreted at 2:00 p. m. the following day. Although *Navanax* is known to feed on some prosobranchs (Paine, 1963, p. 5), this is the first recorded predation (laboratory fed) on *Lamellaria*.

The only anaspidean Paine (1963, p. 5) recorded as part of the diet of *Navanax inermis* is *Aplysia californica* Cooper, 1863. However, in the laboratory we observed feeding attempts on *Stylocheilus longicauda* (Quoy & Gaimard, 1824), the most common opisthobranch we found in the Las Cruces region in July. During the first observation, *Stylocheilus* touched the cephalic region of *Navanax*. *Stylocheilus* contracted violently, jerked the anterior half of its body up and down several times, pulled back slightly and then crawled forward quite rapidly (in relation to its normal speed of crawling). It did this by extending its anterior portion, then pulling up the rest of the body. This extending-contracting motion was so great, that during the contracted phase the mid-ventral region was arched above the substrate, not in contact with the surface on which the animal was crawling. The second observation involved a 34 mm *Navanax* and a 19 mm *Stylocheilus*. Again *Stylocheilus* exhibited a vehement escape reaction. When the tips of *Navanax*'s head shield touched the anterior end of *Stylocheilus*, the prey lifted up its head and actually turned a somersault, flipping over backwards to escape. Shortly afterwards, the predator approached the mid-lateral region of *Stylocheilus* and attempted to ingest it. Eversion of the buccal mass was observed as *Navanax* unsuccessfully tried to suck in its food. *Navanax* later came upon the *Stylocheilus* from behind and touched the tail of the *Stylocheilus*. Its prey pulled in its tail quickly and contracted it towards the main part of its body.

The large size of *Stylocheilus* in comparison with that of *Navanax* (Paine, 1965, p. 605, discusses the relative size of prey that a *Navanax* can swallow whole) and its escape reactions resulted in its not being eaten by *Navanax* during the observed feeding attempts.

Onchidiella binneyi (Stearns, 1893)

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DISTRIBUTION

Onchidiella binneyi is commonly found throughout the northern half of the Gulf of California. Although Keen (1958, p. 512) states it can be found "throughout the Gulf of California," the only published locality records, as far as we have been able to ascertain, are between Puerto Peñasco (31°17′ N; 113°35′ W) and Bahía San Francisquito (28°26′ N; 112°54′ W).

On the dawn low tide of July 6, 1969, the senior author collected 16 specimens of *Onchidiella binneyi* from the upper middle tide zone in Las Cruces Bay (24°13′ N; 110°05′ W). They were congregated under submerged rocks in groups of 3 - 5 individuals. This is a range extension of approximately 275 miles into the southern extreme of the Gulf of California.

ACKNOWLEDGMENTS

Our month's research trip was made possible by the financial assistance of Mr. Hugh C. Bertsch. We gratefully acknowledge his kind generosity.

We were aided in our field collecting by Mr. Jerry Devlin, Dr. Rita Schafer, and Sr. Philomene Breemans. Our thanks are also given to Mr. Gale Sphon, who identified the shelled gastropods consumed by *Navanax*, and to Mr. Allyn G. Smith and Dea Beach who provided us with specimen data from the California Academy of Sciences.

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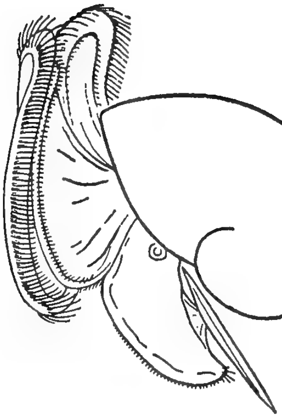


The Opisthobranch Mollusks of Marin County, California

(Gastropoda)

BY

TERRENCE M. GOSLINER

859 Butterfield Road, San Anselmo, California 94960

AND

GARY C. WILLIAMS

267 Oak Manor Drive, Fairfax, California 94930

(1 Map)

INTRODUCTION

In Northern California the collection of opisthobranch mollusks has been limited to very few areas. Collections have been made primarily from Monterey and Dillon Beach. Some data have been published from San Francisco Bay and Moss Beach in San Mateo County, but these data were obtained from rather isolated observations over very short periods of time.

From the summer of 1966 to the summer of 1969, research and collecting have been done along the entire Marin County coast line with central focus on Duxbury Reef, Bolinas. Several different environments are present in Marin County and have been explored. These include the rocky granite shore of Tomales Point and Bird Rock, the *Zostera* mud flats of Limantour and Tomales Bays, the rugged outer coast of Point Reyes, the soft shale reefs of Double Point, Palomarin, and Duxbury Reef, and the mud flat, wharf environment of Bolinas Lagoon. Collecting was also done at Fort Barry, Sausalito wharfs, and the Marina (San Francisco Yacht Harbor in San Francisco County). Collecting at these locations was done during all seasons, but with primary emphasis on the summer months.

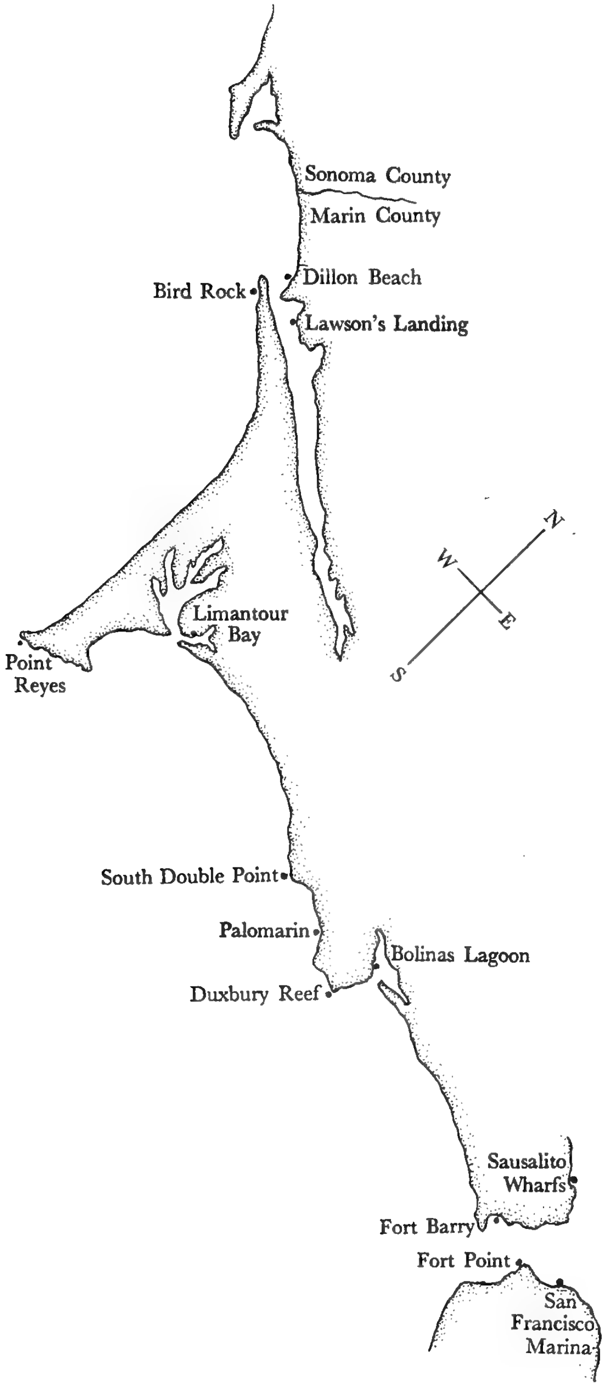
During this period, 67 species of opisthobranchs have been collected in Marin County, 20 of which represent range extensions, and one new species which is presently being described by the authors.

Range extensions are designated by an asterisk (*) and new species by two asterisks (**). This follows the format set up by Lance (1961), which has been used widely since. The general organization of this paper follows that of Sphon & Lance (1968) and Roller & Long (1969).

The authors would like to convey their appreciation to Mr. Richard A. Roller of San Luis Obispo for his helpful suggestions in preparing the manuscript.

GEOGRAPHICAL LOCATIONS

Location	Latitude North	Longitude West
Van Damme Cove	39°16′	123°47′
Bodega Bay	38°18′	123°03′
Dillon Beach	38°14′	122°58′
Bird Rock (Tomales Point)	38°14′	123°00′
Limantour Bay	38°01′	122°55′
Double Point	37°56′	122°45′
Palomarin Reef	37°55′	122°44′
Duxbury Reef	37°53′	122°42′
Bolinas Lagoon	37°54′	122°41′
San Francisco Bay	37°47′	122°27′
Moss Beach	37°32′	122°31′
Monterey Bay	36°37′	121°53′
Pismo Beach	35°09′	120°38′
Laguna Beach	33°32′	117°44′
Point Loma	32°40′	117°14′
Coronados Islands	32°24′	117°14′
Bahía de Los Angeles	28°55′	113°32′
Point Eugenia	27°51′	115°12′


Sonoma County
Marin County
Dillon Beach
Bird Rock
Lawson's Landing
N
W
E
S
Limantour Bay
Point Reyes
South Double Point
Palomarin
Bolinas Lagoon
Duxbury Reef
Sausalito Wharfs
Fort Barry
Fort Point
San Francisco Marina

Acanthodoris lutea MacFarland, 1925

Frequent. Intertidal.
Duxbury Reef, Palomarin
Dillon Beach to Point Loma

Acanthodoris nanaimoensis O'Donoghue, 1921

Frequent. Intertidal.
Duxbury Reef, Palomarin
Vancouver Island to Shell Beach

Acanthodoris rhodoceras Cockerell & Eliot, 1905

Frequent. Intertidal, mud flats
Duxbury Reef, Bolinas Lagoon
Dillon Beach to Coronados Islands

Acteon punctocaelatus (Carpenter, 1864)

Common. Mud flats
Tomales Bay, Limantour Estero, Bolinas Lagoon
Alaska to Baja California

Aegires albopunctatus MacFarland, 1905

Common. Intertidal.
Duxbury Reef, Palomarin
Vancouver Island to Coronados Islands; Baja California

Aeolidia papillosa (Linnaeus, 1761)

Frequent. Intertidal, mud flats
Duxbury Reef, Bolinas Lagoon
Cosmopolitan

Aglaja diomedea (Bergh, 1894)

Common. Mud flats
Tomales Bay, Limantour Estero
Alaska to Morro Bay

Aglaja ocelligera (Bergh, 1894)

Common. Mud flats
Limantour Estero, Tomales Bay
Alaska to Santa Barbara

* *Ancula pacifica* MacFarland, 1905

Frequent. Intertidal.
Duxbury Reef
Duxbury Reef to Point Loma
(Moss Beach to Point Loma)

Anisodoris nobilis (MacFarland, 1905)

Rare. Intertidal.
Duxbury Reef, Bird Rock, Point Reyes
Vancouver Island to Coronados Islands

Antiopella barbarensis (Cooper, 1863)

Frequent. Intertidal, mud flats, bay boat landings
Bolinas Lagoon, Duxbury Reef, Double Point, San Francisco Yacht Harbor
Vancouver Island to Bahía San Quintín

Aplysia californica Cooper, 1863

Rare. Mud flats
Bolinas Lagoon
Humboldt Bay to Baja California

Archidoris montereyensis (Cooper, 1862)

Common. Intertidal.
Duxbury Reef, Sausalito
Alaska to San Diego

Berthella californica (Dall, 1900)

Rare. Intertidal.
Duxbury Reef
Crescent City to San Diego

Cadlina flavomaculata MacFarland, 1905

Rare. Intertidal.
Duxbury Reef
Vancouver Island to Point Eugenia

Cadlina luteomarginata MacFarland, 1905

Frequent. Intertidal.
Duxbury Reef
Vancouver Island to Point Eugenia

* *Cadlina modesta* MacFarland, 1966

Common. Intertidal.
Duxbury Reef, Palomarin
Palomarin to La Jolla

* *Catriona alpha* (Baba & Hamatani, 1963)

Rare. Intertidal.
Duxbury Reef, Double Point
Double Point to San Diego; Japan
(Monterey Bay to San Diego; Japan)

Corambe pacifica MacFarland & O'Donoghue, 1929

Common, seasonally. On *Zostera*
Limantour Estero
Vancouver Island to San Diego

* *Coryphella pricei* MacFarland, 1966

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Monterey Bay
(Monterey Bay)

Coryphella trilineata O'Donoghue, 1921

Common. Intertidal.
Bolinas Lagoon, Duxbury Reef, Palomarin, Bird Rock
Vancouver Island to Coronados Islands

Cumanotus beaumonti (Eliot, 1908)

Rare. Mud flats
Bolinas Lagoon

* *Dendronotus diversicolor* Robilliard, 1970

Rare. Intertidal.
Duxbury Reef, Bird Rock
San Juan Island to Duxbury Reef
(San Juan Island, Victoria)

Dendronotus frondosus (Ascanius, 1774)

Common. Intertidal, mud flats
Duxbury Reef, Bolinas Lagoon
Cosmopolitan

Dendronotus subramosus MacFarland, 1966

Frequent. Intertidal.
Duxbury Reef, Palomarin, Bird Rock
Humboldt Bay to Newport Bay

* *Diaphana californica* Dall, 1919

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Coronados Islands
(San Pedro to Coronados Islands)

Diaulula sandiegensis (Cooper, 1862)

Common. Intertidal, bay boat landings
Sausalito, Duxbury Reef, Palomarin, Double Point, Point Reyes, Bird Rock
Japan to Cape San Lucas

Dirona albolineata COCKERELL & ELIOT, 1905

Rare. Intertidal.
Duxbury Reef, Point Reyes
Puget Sound to San Diego

Dirona picta MACFARLAND *in* COCKERELL & ELIOT, 1905

Common. Intertidal, bay boat landings
San Francisco Yacht Harbor, Sausalito, Fort Point, Duxbury Reef
Dillon Beach to Point Loma

Discodoris heathi MACFARLAND, 1905

Frequent. Intertidal.
Duxbury Reef
Vancouver Island to Laguna Beach

Doridella steinbergae (LANCE, 1962)

Rare. Bay boat landings
San Francisco Yacht Harbor
San Juan Islands to Coronados Islands

* *Doriopsilla ? albopunctata* (COOPER, 1863)

Rare. Intertidal.
Duxbury Reef
Van Damme, Mendocino County to Point Eugenia
(Salt Point to Point Eugenia)

** *Doris* spec.

Rare. Intertidal.
Duxbury Reef, Bird Rock

* *Doto columbiana* O'DONOGHUE, 1921

Frequent. Intertidal.
Duxbury Reef, Palomarin
Vancouver Island to Duxbury Reef
(Vancouver Island to Dillon Beach)

Doto amyra MARCUS, 1961

Rare. Intertidal.
Duxbury Reef
Dillon Beach to Monterey Bay

* *Doto kya* MARCUS, 1961

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Shell Beach
(Moss Beach to Shell Beach)

Doto wara MARCUS, 1961 (?)

Common. Intertidal.
Duxbury Reef, Palomarin
Dillon Beach to Monterey Bay

* *Eubranchus rustyus* (MARCUS, 1961)

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Bahía de los Angeles
(San Francisco Bay to Bahía de los Angeles)

Fiona pinnata ESCHSCHOLTZ, 1831

Rare. Pelagic
Limantour Estero
Cosmopolitan

Flabellinopsis iodinea (COOPER, 1862)

Rare. Intertidal, subtidal to 20 feet
Duxbury Reef, Bird Rock
Vancouver Island to Coronados Islands

* *Hermaeina oliviae* MACFARLAND, 1966

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Monterey Bay
(Monterey Bay)

Hermaeina smithi MARCUS, 1961

Frequent. Intertidal.
Duxbury Reef
San Juan Islands to San Diego

Hermissenda crassicornis (ESCHSCHOLTZ, 1831)

Common. Intertidal, mud flats, bay boat landings
San Francisco Yacht Harbor, Sausalito, Duxbury Reef, Bolinas Lagoon, Palomarin, Double Point, Limantour Estero, Tomales Bay, Bird Rock
Alaska to Point Eugenia

Hopkinsia rosacea MACFARLAND, 1905

Rare. Intertidal.
Duxbury Reef, Palomarin
Coos Bay to Point Loma

Laila cockerelli MACFARLAND, 1905

Frequent. Intertidal.
Duxbury Reef
Vancouver Island

Melibe leonina (GOULD, 1853)

Frequent, seasonally. On *Zostera*
Limantour Estero
Alaska to La Paz Bay

Okenia plana BABA, 1960

Frequent. Bay boat landings
San Francisco Yacht Harbor
San Francisco Bay; Japan

* *Onchidella borealis* DALL, 1871

Rare. Intertidal.
Duxbury Reef
Alaska to Duxbury Reef
(Alaska to Dillon Beach)

Onchidoris bilamellata (LINNAEUS, 1767)

Common, seasonally. Mud flats
Bolinas Lagoon
Alaska to Morro Bay

Onchidoris hystricina (BERGH, 1878)

Common. Intertidal, mud flats
Bolinas Lagoon, Duxbury Reef, Palomarin
Alaska to Point Loma

Phyllaplysia taylori DALL, 1900

Common. On *Zostera*
Limantour Estero, Tomales Bay
San Juan Islands to San Diego

Placida dendritica (ALDER & HANCOCK, 1843)

Common. Bay Boat Landings
Fort Barry Docks
San Francisco Bay to Newport Bay
(Fort Barry to Pismo Beach)

* *Polycera atra* MACFARLAND, 1905

Common. Bay boat landings, mud flats
San Francisco Yacht Harbor, Sausalito, Limantour Estero,
Limantour Estero to Coronados Islands
(San Francisco Bay to Coronados Islands)

Precuthona divae MARCUS, 1961

Frequent. Intertidal.
Duxbury Reef, Palomarin, Double Point, Point Reyes
Dillon Beach to Santa Barbara

Rostanga pulchra MACFARLAND, 1905

Common. Intertidal.
Duxbury Reef, Palomarin, Bird Rock
Vancouver Island to Chile

* *Spurilla oliviae* (MACFARLAND, 1966)

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Santa Barbara
(Monterey Bay to Santa Barbara)

Stiliger fuscovittata LANCE, 1962

Common. Bay boat landings
San Francisco Yacht Harbor, Fort Barry, Sausalito
San Juan Islands to San Diego; Bahía de Los Angeles

* *Trinchesia abronia* (MACFARLAND, 1966)

Common. Intertidal.
Duxbury Reef, Palomarin
Palomarin to Pismo Beach
(Monterey Bay to Pismo Beach)

* *Trinchesia albocrusta* (MACFARLAND, 1966)

Frequent. Intertidal.
Duxbury Reef, Palomarin
Palomarin to Santa Barbara
(Monterey Bay to Santa Barbara)

* *Trinchesia flavovulta* (MACFARLAND, 1966)

Common. Intertidal.
Duxbury Reef, Palomarin
Palomarin to Shell Beach
(Monterey Bay to Shell Beach)

Trinchesia fulgens (MACFARLAND, 1966)

Rare. Intertidal.
Duxbury Reef
Duxbury Reef to Pismo Beach

* *Trinchesia lagunae* (O'DONOGHUE, 1926)

Common. Intertidal.
Duxbury Reef, Palomarin
Palomarin to Rosarito Beach
(Monterey Bay to Rosarito Beach)

Triopha carpenteri (STEARNS, 1873)

Common. Intertidal.
Duxbury Reef, Palomarin
Vancouver Island to San Diego

* *Triopha grandis* MacFarland, 1905

Common, seasonally. Mud flats
Limantour Estero
Limantour Estero to Catalina Island
(Santa Cruz to Catalina Island)

Triopha maculata MacFarland, 1905

Common. Intertidal.
Duxbury Reef, Bird Rock
Bodega Bay to San Diego

Triopha spec.

Common. Intertidal.
Duxbury Reef, Palomarin

Tritonia festiva (Stearns, 1873)

Rare. Intertidal.
Duxbury Reef, Bird Rock
Vancouver Island to Coronados Islands

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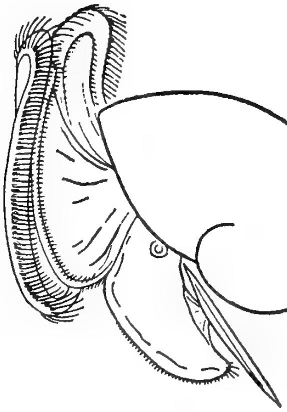

A New Species of Japanese Ovulidae

BY

CRAWFORD N. CATE

12719 San Vicente Boulevard, Los Angeles, California 90049

(1 Text figure)

AMONG TWENTY-TWO LOTS of Ovulidae received from Professor Masao Azuma was a shell which proved to be new to science and which is described herewith.

Primovula ***azumai*** CATE, spec. nov.

(Figure 1)

Shell of medium size for the genus, ovate, thinly formed, sub-translucent; terminals well produced, sharply, pointedly so in back, squarely so in front; dorsum roundly inflated centrally, sloping sharply to either terminal, saddle-like; dorsum numerously, very distinctly, transversely incisedly striate; base inflatedly ovate, narrowing abruptly and thickly to the front; a short, elevated, double-knobbed funiculum at the rear; base striate, with a longitudinal, narrow callus the length of the central base; columella fairly broad, striate, noticeably depressed, deepening toward the front, becoming a well developed fossula; a well formed adaxial carinal ridge outlines both; aperture narrow, slightly curving; outer lip thick, rounded, semi-dentate, with large, poorly formed teeth; color a deep, rich honey-yellow to yellow-brown, with carinal ridge, tip of funiculum, and teeth a lighter color.

Length, 9.6 mm; width, 4.4 mm; height, 3.9 mm.

Type Locality: 1 - 2 km off Kirimezaki, Kii Peninsula, Japan, in 20 - 30 fathoms; leg. M. Azuma, 13 February 1970.

Holotype: Azuma collection, No. 14826.

The photograph is by Bertram Draper, the processing by Takeo Susuki.

This new species was taken from lobster nets set in deep water off the Kii Peninsula in central Japan. I take pleasure in naming it in honor of Professor Masao Azuma, who has contributed so much to our knowledge of the Recent Japanese Ovulidae, and with whom I have enjoyed working.

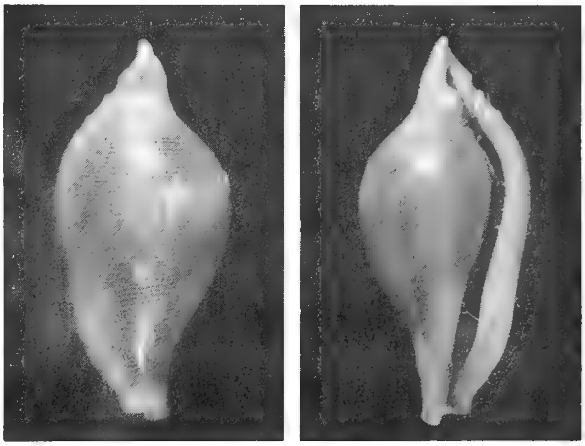

Figure 1

Primovula ***azumai*** CATE, spec. nov.

Holotype; Azuma no. 14826 × 6

Some Comments on CERNOHORSKY's "Muricidae of Fiji" (The Veliger, 1967)

BY

EMILY H. VOKES

Tulane University, New Orleans, Louisiana 70118

ALTHOUGH AN OVERLONG interval has passed since the appearance of W. O. Cernohorsky's paper on the Muricidae of Fiji - Part I, Subfamilies Muricinae and Tritonaliinae (1967), I have become so distressed at certain aspects of it, as I have tried to use it, that I feel compelled to point out some items of disagreement between that author and myself. In general his paper is so useful that workers on the Pacific faunas will find it indispensable. Were it a paper that soon would sink into oblivion I would not be concerned, but I consider that the following observations should be placed on record for the benefit of those who will be relying upon Cernohorsky in their own work.

The following list is arranged in sequence of appearance of the disputed points in CERNOHORSKY (1967).

1. CERNOHORSKY does not accept my (VOKES, 1964) explanation of *Murex pecten* MONTFORT, 1810, (= *M. tribulus* LINNAEUS, 1758) as type of *Murex*, but uses instead subsequent designation of GRAY, 1847. His objection is that *M. pecten* is not synonymous with *M. tribulus* LINNAEUS. However, *M. pecten* of MONTFORT is synonymous with *M. tribulus* of LINNAEUS, but not of subsequent authors who have restricted the polyspecific *M. tribulus* of LINNAEUS to that species today known as *M. tribulus*. *Murex pecten* of MONTFORT, 1810, which = *M. pecten* of LIGHTFOOT, 1786, is that shell also known as *M. triremis* (PERRY, 1811) and *M. tenuispina* LAMARCK, 1822. I readily concede that I overlooked the Lightfoot name and should have indicated that the type species of *Murex* is *M. tribulus* LINNAEUS (as *M. pecten* MONTFORT = *M. pecten* LIGHTFOOT). *Murex pecten* MONTFORT is a homonym but is also a synonym of *M. pecten* LIGHTFOOT, both taking their name from the "Venus Comb" as this shell was known (*Le rocher peigne de Venus,* as stated by MONTFORT, 1810, p. 619). CERNOHORSKY's second objection to this type designation is that the name *Murex pecten* was not one of the originally included nominal species. However, the ICZN Code (Art. 69a-iv) states: "If an author designates ... as type species a nominal species that was not originally included, and if, but only if, at the same time he synonymizes that species with one of the originally included species, his act constitutes designation of the *latter* as type- species of the genus." [Italics mine.] Inasmuch as MONTFORT lists "*Murex tribulus* Linn. et Gmel. sp. 2" as his first reference it would certainly seem that the necessary qualifications had been met by MONTFORT.

2. The species *Murex scolopax* DILLWYN, 1817, and *M. nigrispinosus* REEVE, 1845, are not synonyms of *M. tribulus* as given in the synonymy of that species. *Murex scolopax* is a larger, smoother shell and may be distinguished from *M. tribulus* by the development of a large flared anal channel, which is buttressed upon the previous whorl, and which remains completely visible on the shell after the aperture has progressed to the next resting stage (*i. e.*, varix). This residual flared lip is well shown in both MARTINI, vol. 3, fig. 1052, and in CHEMNITZ, vol. 11, fig. 1819, the figures upon which this species is based. In addition to this unmistakable difference, the nature of the aperture is different in the two forms, *M. scolopax* having only a thin lip, crenulated into each of the varical spines. These varical spines are fewer in number in *M. scolopax* than in *M. tribulus,* that species having several small intercalary spines in addition to the major three.

Murex nigrispinosus REEVE, although it may be only a subspecies of *M. tribulus,* should certainly be given at least that distinction. It is a coarse, massive shell, and the tips of the spines are very dark. It is probably confined to the Philippine Islands. REEVE's figure (1845, plt. 20, fig. 79) is an excellent representation of the form.

Both of the above-mentioned species may be distinguished from *Murex tribulus* s. str. by the nature of the nuclear whorls. These three different types of embryonic shells were discussed and well figured by BAKER (1890, pp. 66 - 69) in a paper that should be closely studied by every student of muricine taxonomy. From Baker's observations (which I have verified independently with my own identifications), it may be seen that otherwise similar appearing species can be separated immediately by embryonic differences. One of the more striking examples of this scientific aid is found in the two species *M. tribulus* and *M. ternispina* Lamarck. Placed in synonymy by almost every author, and reasonably so on the basis of superficial shell morphology, the 2 forms have completely different nuclear types. I first encountered this in shells thought to be *M. tribulus* from the Gulf of Suez. When I realized the difference in the embryonic shell I then began trying to identify the species and through Baker discovered the species to be *M. ternispina* (at least as figured by Kiener, who is presumed to have had Lamarck's shell before him). In passing it may also be noted that the shell figured by Kiener (1842, plt. 4, fig. 1; plt. 5, fig. 1) as *M. crassispina* Lamarck is an excellent representation of *M. scolopax,* although Lamarck's original references included illustrations of both *M. tribulus* and *M. scolopax.* Lamarck (or Kiener) did a very good job of separating the frequently confused species of the *M. tribulus* group. *Murex tribulus, M. crassispina* (= *M. scolopax*), *M. ternispina,* and *M. tenuispina* (= *M. pecten*), are indeed all valid species.

3. Cernohorsky mentions several species of *Chicoreus* that have been synonymized with *C. brunneus* (Link, 1807). It is not clear from his discussion whether he agrees or disagrees with these assignments, but as he does not include them in his synonymy it must be concluded that he does not consider any of them to be synonyms of *C. brunneus.* The first of these is *Murex australiensis* A. Adams, 1854. The specimen so labeled in the British Museum (Natural History), which may or may not be the type, is only a light-colored variant of *C. brunneus. Murex huttoniae* Wright, 1878, is a brilliant orange-colored variety of *C. brunneus,* but no more. However, *M. penchinati* Crosse, 1861, is a different species. The type of this species is in the British Museum (Natural History) and is a small shell (about 45 mm in height) with two small equisized intervarical nodes in contrast to the one very large node of *C. brunneus.* It is a bright pink color. The shell usually figured in modern books and sold by shell dealers as *"Murex penchinati"* is not that species but is *M. trivialis* A. Adams, 1854, a species that more nearly resembles *M. brunneus* than does *M. penchinati,* but which is nevertheless another valid species.

4. As much as I too would like to save the name *Murex aculeatus* Lamarck, 1822, it is a secondary homonym of *Aranea aculeata* Perry, 1811. That Lamarck's species is now placed in the genus *Chicoreus* does not alter the fact that it was originally named in the genus *Murex.* As *Aranea* Perry is unequivocally a synonym of *Murex* s. str. the homonymy is incontestable. Cernohorsky states (p. 117) that Perry's figure is a *"Bolinus* species of the genus *Murex* s. str.," but if one examines the figure given by Perry (1811, plt. 46, fig. 2) it can be observed, as bad as the picture is, that there are no varices visible on the portion of the shell between the left-hand edge (as seen in the figure) and the aperture of the shell. *Bolinus,* which has 5 or more varices, always has varices visible in this area, whereas *Murex* s. str. with only 3 varices, does not show any. Perry's figured shell distinctly shows 3 varical spines, not 2, and also lacks the flaring inductura of *Bolinus.* As weird as the figure is, it probably is meant to represent *Murex carbonnieri* (Jousseaume) from the Red Sea, not too far off from the "African Seas" of Perry. Presumably it was this latter locality assignment that led Cernohorsky to his *Bolinus* conclusion.

Unfortunately, even if Perry's species could be shown to be a *Bolinus,* and that subgenus elevated to a separate genus, it would not save the Lamarckian name, for there is a *Muricites aculeatus* Schlotheim, 1820, and according to the Code (Art. 20) the name is considered a homonym of *Murex aculeatus.* Only an appeal to the Commission could conserve this name.

5. The species *Purpura capucina* Röding, 1798, is based on two references. The first is "Tour. d'Auverg. 1073." This is clarified somewhat by Chemnitz, who adds "FAVANNE, Catal. rais. p. 218, no. 1073. Tab. 4, fig. 1073," in his discussion of *"Murex monachus capucinus"* (1795, vol. 11, p. 123). The work in question is actually an anonymous catalogue of an anonymous collection. The complete title is "Catalogue systématique et raisonné, ou description du magnifique cabinet, appartenant ci-devant à M. le C. de [Compte de la Tour d'Auvergne]. Par. M. de [Favanne de Montcervelle]." The figure in question may be intended to be a specimen of *"Murex monachus capucinus"* but as such it would leave much to be desired and, on the basis of the illustration alone, seems to be a specimen of *Murex triqueter* Born rather than *"capucinus."* The other illustrations on this same plate are in general very well done and completely undistorted and it seems unreasonable to make an exception for figure no. 1073.

The second reference of Röding is "Martini 3. t. 105. f. 994." The adjacent figure 993, which is *"Murex capucinus* Lamarck" of authors was **not** cited. We might conclude that Röding was attempting to discriminate between the two figures cited by Gmelin for his *"Murex* *ramosus* var." The shell shown in figure 994 is not *M. capucinus* Lamarck, nor of authors (if they are indeed different), but is the 4-varixed species named *Murex quadrifrons* Lamarck, 1822. Unless we make the unjustified assumption that Röding's "994" was a typographical error, it would seem undeniable that Röding's *Purpura capucina* is a composite species, combining *Murex triqueter* and *Murex quadrifrons*. In the interest of stability it seems most logical to declare it a *species dubium* and continue to use the presently accepted names for the 3 species: *triqueter, quadrifrons,* and *capucinus* Lamarck.

I can appreciate what Cernohorsky is attempting to do in trying to conserve the name *Murex capucinus* for the shell long known by that name, but I feel it is unnecessary. The species *Murex capucinus* Lamarck, 1822, is involved in the philosophical debate of whether the illustration cited by an author as a "type figure" is to have precedence over a subsequently discovered type specimen. In this case Lamarck cited the well done, easily recognizable figures of Chemnitz, vol. 11, figs. 1849, 1850, and the shell there illustrated was known by the name *M. capucinus* for almost 100 years. In 1915 Hedley announced that he had examined Lamarck's "type specimen" and it was not the shell usually thought of as *M. capucinus* but was another species, probably *M. torrefactus* Sowerby. From Lamarck's (1822, p. 164) statement: "Longueur de mon plus grand individu, 4 pouces, 9 lignes" it is evident that there was more than one specimen in the type lot, hence what Hedley saw could not be the **holotype**, but at least one of Lamarck's shells probably was *M. torrefactus,* or some other similar species, as the size he gives is much larger than any specimen known of *M. capucinus*. Since there was evidently more than one specimen in Lamarck's type lot, an attempt should be made to locate the other specimens and from them a lectotype should be chosen, which would match the Chemnitz illustrations. Should this prove impossible, as it well may, then the next course is to choose a neotype or to designate the Chemnitz figure as the "type figure" and pursue the matter no further. Lamarck stated that the varices of *M. capucinus* are "subdepressis, scabris," and this would seem to be an indication that the shell in question was really the *M. capucinus* of authors rather than *M. torrefactus,* for the varices of the latter do not fit this description.

Inasmuch as *capucina* Röding was described as "*Purpura* (not *Purpura* of authors), the type of which has been selected as *Murex trunculus,* making it a synonym of *Hexaplex* (or of *Truncularioppsis,* should the reader not agree with my synonymization of the two latter taxa) and *capucinus* was described as "*Murex*" there is no problem of primary homonymy. Should one choose to restrict the Röding name *capucina* to the Favanne figure, which was the first cited, it would become a junior synonym of *Naquetia triqueter* (Born, 1778) and, as such, be a secondary senior homonym of *Naquetia capucina* (Lamarck). If the name is restricted to the Martini figure it then becomes a senior synonym of *Chicoreus quadrifrons* (Lamarck) and serves little purpose other than to engender confusion. However, if at the same time, as was suggested by Cernohorsky, *capucinus* Lamarck were also to be placed in *Chicoreus,* then again secondary homonymy would occur. All of these problems can be avoided by allowing *Purpura capucina* Röding to lie undisturbed among the *nomina oblita* and *species dubia,* to which it rightfully belongs. Should secondary homonymy become unavoidable, then *Murex permaestus* Hedley, 1915, is available.

As mentioned above, Cernohorsky would place "*Murex*" *capucinus* Lamarck in the genus *Chicoreus*. I am still of the opinion, which I expressed in 1964, that *capucinus* is more akin to *Naquetia* than to *Chicoreus*. The disagreement as to whether Favanne's illustration is meant to be *capucinus* or *triqueter* would tend to corroborate that decision. The question as to whether *Naquetia* should be a subgenus of *Chicoreus* or of *Pterynotus* is less easily decided. *Naquetia* is intermediate between *Pterynotus* and *Chicoreus* and has characters of both. A good case could be made for making *Naquetia* a subgenus of either *Chicoreus* or *Pterynotus*. I have weighed the evidence and decided in favor of *Pterynotus,* but this is a matter of personal choice. Paleontologically the affinities of *Naquetia* lie with *Pterynotus* rather than with *Chicoreus*. There is a lower Oligocene species from the Crimea, "*Murex*" *williamsi* Sokolov *in* Kliushnikov, 1958 (unfortunately preoccupied by *Murex williamsi* Maury, 1925), that is virtually identical with *Naquetia amanuensis* (Couturier, 1907), from the western Pacific. Inasmuch as the *Chicoreus* line does not appear until the Miocene epoch, or several million years later, while *Pterynotus* is one of the most ancient of the muricine line, it seems evident that *Naquetia* is derived from a *Pterynotus* ancestor and as such is better placed with that group. [*Naquetia amanuensis* is frequently confused with *N. triqueter* and has been figured as such by both Cernohorsky, 1967, plt. 15, fig. 15, and by Vokes, 1968, plt. 13, figs. 3, 4]. Cernohorsky states (p. 125) that "*Murex triqueter amanuensis* Couturier appears to be a smaller, more slender and elongated variant which occurs sporadically in Fiji and the Philippine Islands, and which is of no racial significance," but according to Anthony D'Attilio of the San Diego Natural History Museum, the two forms differ in distribution, with *N. triqueter* being more common in the Indian Ocean area and *N. amanuensis* in the western Pacific. The two overlap in the Philippines. It is hoped that Mr. D'Attilio will publish his information soon and eliminate the confusion surrounding these two distinct species.

6. Cernohorsky applies the name *Purpura carneola* Röding, 1798, to the shell generally known as *Murex torrefactus* Sowerby, 1841. If this were simply a case of "whether 'tis nobler" to resurrect a *nomen oblitum* or not this would be only a matter of conscience. However, I can see no justification for the stated synonymy. Röding's *P. carneola* is based on 2 Martini figures (vol. 3, figs. 995, 996). Of these 2 figures, one (fig. 995) is definitely the same as *Murex saulii* Sowerby, 1841, and the second (fig. 996) probably is the same. Neither is *M. torrefactus.* The most striking features of the 2 figures cited and of *M. saulii* are the pink aperture and the light brown color. Therefore, if Cernohorsky wishes to apply the name *Chicoreus carneolus* to Sowerby's *M. saulii* I have no objections other than the ethics of using a *nomen oblitum,* a problem that is far from being satisfactorily resolved. But I cannot accept his using it for *M. torrefactus.*

Cernohorsky justifies usage of the Röding name on the grounds that if he did not, then the next older name *Purpura elongata* Link, 1807, would have to be used, making the point that it could not qualify as a *nomen oblitum* as it was used by Tomlin & Winckworth in 1935. As Link's species is based on the same Martini figures as *P. carneola* it must also be a synonym of *M. saulii* and not of *M. torrefactus,* in spite of Tomlin and Winckworth's assertion of the latter synonymy. The third Martini figure (fig. 997), which Cernohorsky states is an undeterminable species of *Chicoreus,* probably also represents the light-colored *M. saulii* lending further authority to the identity of the species in question. *Purpura rosana* Schumacher, 1817, is another name for the same species, also based on the Martini figures 995 - 997.

Triplex abortiva Perry, 1811, is the second *nomen oblitum* introduced by Cernohorsky in the synonymy of his *carneola-torrefactus.* It is possible that Perry's figure is meant to be the same species as *Chicoreus torrefactus* (with Perry's figures all things are possible) but the illustrated shell is much smaller than an adult specimen of *C. torrefactus* (67 mm as compared to about 100 mm for an adult *C. torrefactus*). Perry's figures, in general, are of the same size as the species portrayed or even somewhat larger. I would certainly hesitate to replace the well-known name *torrefactus* with a *nomen oblitum* of such dubious identity.

7. The erroneous citation of *"Murex (Chicoreus) raciniatus* Sowerby" of Azuma, 1960, is included by Cernohorsky in the synonymy of *Chicoreus laciniatus* (Sowerby), but not the *"laciniatus"* as figured by the two other authors he mentions in his discussion of the species. However, the Japanese species figured by these three authors is not *C. laciniatus,* but is a completely different shell. It is not to be referred to *Chicoreus* but is an undescribed species very near *Murex barclayi* Reeve and is a *Naquetia.* D'Attilio (1966, p. 4, fig. 2) recognized this fact and cited his specimen as *"Naquetia* cf. *laciniatus"* with a reference to the Habe, 1961, figure of the species. According to Cernohorsky the "degenerate fronds" of the Japanese shell have prompted authors to place the species in *Naquetia* but the truth of the matter is that it is misidentification of a species of *Naquetia* as *Chicoreus laciniatus* that has caused the problem.

8. *Murex monodon* Sowerby, 1825, is included *"in pars"* in the synonymy of *Chicoreus ramosus* (Linnaeus), on the basis of Sowerby's reference to Martini, vol. 3, fig. 980. However, this latter reference is clearly a typographical error, for what Sowerby actually cited in the Tankerville Catalogue (1825, App., p. 19) was: "Martini Conch. Cabin. III t. 105, f. 987, 980." As Cernohorsky states, figure 980 appears on plate 102, not 105, while on plate 105 there are two excellent figures of *M. monodon*: figures 987 and 988. Furthermore, in the Conchological Illustrations (1841), Sowerby corrected the reference to read "Martini, iii. t. 105, f. 987-8." In view of this rather obvious typographical error it seems injudicious to confuse the uninitiated by suggesting that there was ever any connection in Sowerby's mind between *monodon* and *ramosus.* In his discussion Cernohorsky attempts to explain this inclusion, but I do not feel that it has any place in his synonymy.

The problem of the identity of *Murex ramosus* of authors was discussed in some detail by me in a previous paper (Vokes, 1964, p. 8) and it was concluded that Lamarck had satisfactorily restricted the name *ramosus* to the species figured by Martini, vol. 3, figs. 980, 981. Cernohorsky's suggestion that the name *Purpura incarnata* Röding, 1798, should perhaps replace the name *ramosus* seems an unnecessary and undesirable solution.

9. *Murex phyllopterus* Lamarck, 1822, is not a synonym of *M. pinnatus* Swainson, 1822, as suggested, but is another species subsequently named *Murex rubridentatus* Reeve, 1846. It is scarcely a justification to say that the description given by Lamarck fits *M. pinnatus* for Lamarck says "labro margine dentato," a statement that would expressly exclude the non-denticulated *pinnatus* from consideration. The illustration given by Kiener (1842, plt. 24, fig. 1) is an excellent representation of the species. Reeve's illustration of *M. rubridentatus* (1846,

plt. 36, fig. 186) shows a specimen somewhat less elaborately flanged but otherwise identical. Cernohorsky's contention that *M. phyllopterus* was described without figure citation, while technically correct, is somewhat misleading in that LAMARCK (1822, p. 164) stated that this species "a été figuré dans dessins posthumes et inédits de Chemnitz," and KIENER (1843, p. 103) cites SCHUBERT & WAGNER (1829, vol. 12, continuation of Chemnitz), plt. 219, fig. 3042, 3043. These figures were reproduced in the 1878 edition of the Conchylien-Cabinet, by KÜSTER, plt. 18, fig. 1, 2, under the name *M. phyllopterus* Lamarck, and are also excellent representations of the species.

Cernohorsky suggests that *Murex pinnatus* SWAINSON, 1822, may well be a secondary homonym of *Triplex pinnata* PERRY, 1811, as the latter appears to him to be a species of *Pterynotus*. I am certain that Perry's illustration (1811, plt. 7, fig. 5) is the same as *Murex foliatus* GMELIN, 1791, and thus is a *Ceratostoma* rather than a *Pterynotus*. As the two genera are placed in different subfamilies, there is little likelihood of even the worst of "lumpers" placing the two species in the genus *Murex* s. l. Regrettably, Cernohorsky is completely correct in stating that *Purpura alata* RÖDING, 1798, is an older name for *Murex pinnatus* SWAINSON. Again an appeal should be made to the Commission to conserve the well-known *pinnatus* and declare *Purpura alata* RÖDING to be a *nomen oblitum*.

10. *Murex uncinarius* LAMARCK, 1822, is placed by Cernohorsky unequivocally in the synonymy of *Pterynotus elongatus* (LIGHTFOOT, 1796) because of the queried reference by Lamarck to the Martini figures that do represent the latter species. However, the size quoted by Lamarck – 11 lignes (= 25 mm) – is exactly right for the species now known as *uncinarius*; but only about $\frac{1}{3}$ the size of an adult *elongatus*. In the description, LAMARCK (1822, p. 166) stated that the color is "albido-fulva [whitish-yellowish brown], which agrees with the color of *M. uncinarius* but not *P. elongatus*, which is always a dead white. The varices are described as "alis inferne dentatis: lateralibus antice divisis" [wings dentate below: laterals divided anteriorly], which again agrees with the digitations of the varices of *M. uncinarius*, whereas *P. elongatus* has a solid wing-like flange. But perhaps the single most telling point in Lamarck's description is the statement: "Ses ailes latérales seules ont antérieurement des crochets qui le rendent fort remarquable." Certainly the reference to the hooks on the varices alone would be sufficient to recognize the species from Lamarck's description. When one examines MARTINI, vol. 3, figures 1034, 1035, it is easy to understand why Lamarck might have thought they could be the species he had. They are poorly done and there is a definite "hook" shown on one of the spines of the spire whorls (as in Cernohorsky's figure 13). But to place Lamarck's well described species in the synonymy of *P. elongatus* in spite of all the evidence to the contrary, solely on the basis of this reference of which Lamarck expressed doubt, is unacceptable.

I would like to take this opportunity to add that, although I previously (VOKES, 1964, p. 27) placed both *Murex capensis* SOWERBY, 1841, and *M. mitriformis* SOWERBY, 1841 (incorrectly spelled "*mitraeformis*" by VOKES, 1964, and by CERNOHORSKY, p. 123) in synonymy with *M. uncinarius*, I have since received specimens of *M. mitriformis* from the Natal Museum, through the courtesy of Dr. A. C. Van Bruggen, and I can readily see that I was in error in synonymizing this species with *"Murex" uncinarius*. It is also a *Poropteron* but may be distinguished by its higher spire, lighter color, and by the presence of 5 varical digitations rather than 4 as seen in *P. uncinarius*. As Cernohorsky indicates, this name is preoccupied (but not by *Murex mitraeformis* BROCCHI, 1814, rather by *M. mitriformis* WOOD, 1828) and a new one is necessary. I do not feel that this is the place to propose it. *"Murex" capensis* is, however, a synonym of *P. uncinarius*, due to Sowerby's having also been misled by Lamarck's queried reference as was Cernohorsky.

11. Although generic assignment is always a matter of personal opinion, I cannot agree with the placement of *Murex noduliferus* SOWERBY, 1841, in the genus *Poirieria*, The presence of the denticulations on the inner and outer lips, to me, indicates placement in *Muricopsis*. The numerous fine spiral lines and associated spinelets seem a most un-*Poirieria*-like attribute.

12. The specimen illustrated as *Favartia tetragona* (BRODERIP, 1833) (plt. 15, fig. 20) bears only a generic resemblance to Broderip's species. True *F. tetragona* is a high spired shell that has been placed in synonymy with *F. brevicula* (SOWERBY, 1834) by many authors and, as a result, the two species have been confused by other authors. REEVE (1845, plt. 26, fig. 118) figured a specimen of *F. brevicula* under the name *Murex tetragonus*, placing *M. breviculus* in synonymy, and stated "I cannot discover any specific difference between the *Murices tetragonus* and *breviculus*; it is a species in which the growth is more pyramidal in some examples than in others, but the sculpture is invariable [sic] the same." KIENER (1842) figured both species adequately (*M. breviculus* – plt. 4, fig. 2; *M. tetragonus* – plt. 5, fig. 2), noting that the two species are very close but that *M. breviculus* is shorter than *M. tetragonus*. HABE (1961, plt. 27, fig. 9) figured a shell as *Favartia tetragona*, but in the 1964 English edition of the same book correctly identified the species as *F. brevicula.* The shell that Cernohorsky has figured as *F. brevicula* is correctly identified; however, the one he calls *F. tetragona* is not that species, but is, in my opinion, *"Murex" cyclostoma* SOWERBY, 1841, described from the Philippine Islands and well figured in the Conchological Illustrations (1841, plt. 194, fig. 95).

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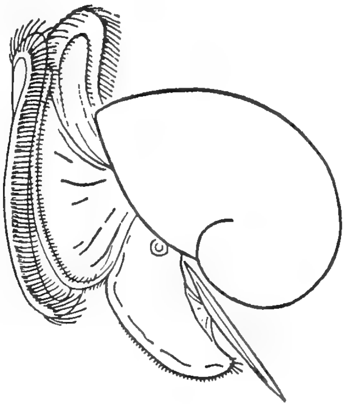

New Gastropod Taxa from Tropical Western America

BY

DONALD R. SHASKY[1]

734 West Highland Avenue, Redlands, California 92373

(1 Plate; 2 Text figures)

INTRODUCTION

During the past decade and a half I have collected extensively in the Panamic region of the Eastern Pacific. My collecting localities range from Magdalena Bay, Baja California, throughout the Gulf of California and the West Mexican mainland southward to Panama and Ecuador.

This paper offers for validation two new columbellid genera and 9 gastropod species, most of which I have personally collected from the above mentioned region.

A companion paper, in which I am describing 10 new turrid species, is now in press.

Abbreviations for type repositories mentioned in the text are as follows:

AHF	Allan Hancock Foundation (collection on loan to LACM)
AMNH	American Museum of Natural History New York, N. Y.
ANSP	Academy of Natural Sciences, Philadelphia
CAS	California Academy of Sciences, San Francisco
LACM	Los Angeles County Museum of Natural History
SDNHM	San Diego Natural History Museum
SU	Stanford University Collection, Stanford, California
USNM	United States National Museum Washington, D. C.

Macrarene spectabilospina Shasky, spec. nov.

(Figures *1* and *2*)

Diagnosis: Shell similar to *Macrarene farallonensis* (A. G. Smith, 1952), but more spinose and with deeply impressed square pits on either side of the main basal carina.

Description: Shell of medium size, depressed, turbinate, of pale brown color; nucleus of one partially submerged smooth whorl; the 3½ remaining whorls highly sculptured; suture a deeply submerged canal; axial ribs about 16 initially, dwindling to about 12; the ribs begin as low rounded ridges increasing rapidly in strength and becoming rather precipitous; the ribs separated by deep wide troughs; ribs noded at the shoulder then continue on to terminate in recurved channeled spines; the troughs between the ribs are filled with fine orthocline growth lines; spiral sculpture of 2 undulating, rather weak carinae; the adapical carina forming weak webs between the nodes of the shoulder and the abapical carina forming much stronger webs between the spines; on the base of some specimens, primarily the immature ones, a weak rib reappears at the abapical root of the spines and on the more mature specimens the ribs are obsolete except near the umbilicus; the base of the body whorl is surrounded by a very strong spiral cord that disappears into the umbilicus; this cord is crossed by equally strong but short ribs forming deep rectangular pits on either side; aperture round, pearly, smooth; operculum concave, multispiral, with 5 calcareous beads and chitinous bristles at the margin. Dimensions of the holotype: height 10.1 mm, diameter 14.1 mm.

Type Locality: Gulf of Tehuantepec, Chiapas, Mexico, 15°08′ N; 93°23′ W, 82 m, rocky bottom, San Juan Expedition station N-13, 10 July 1963, 6 specimens, collected by Donald Shasky.

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[1] Research Associate in Invertebrate Zoology, Los Angeles County Museum of Natural History.

Type Material: Holotype, LACM 1409; single paratypes, AMNH, CAS, SDNHM, USNM, Shasky Collection.

Referred Material: Shasky Collection, station D-2, Gulf of Tehuantepec, Oaxaca, Mexico, 15°56′ N; 95°32′ W, 52 m, rocky bottom, 1 specimen.

Discussion: *Macrarene* ***spectabilospina*** is the most spinose species of the genus described to date. Its closest affinity is with *M. farallonensis* from the central California coast. *Macrarene farallonensis* differs principally in lacking the deeply impressed square pits on either side of the main basal carina.

The species name is derived from the Latin *spectabilis,* showy, and *spina,* spine or thorn.

Lapsigyrus ***myriosirissa*** SHASKY, spec. nov

(Figure *3*)

Diagnosis: A non-shouldered *Lapsigyrus* with many more spiral threads and axial riblets than the type species of the genus, *L. contrerasi* (JORDAN, 1936).

Description: Shell minute, white, 6-whorled; nucleus glassy, semitransparent, helicoid, of 2½ whorls; spiral sculpture of thin threads with 11 on the penultimate and 18 on the body whorl; the 5 terminal threads on the base are about twice as strong as the preceding threads; minute axial riblets fill the channels between the threads with resultant innumerable, very minute squarish pits; suture indistinct; aperture large, pyriform, and with a shallow posterior canal at the apex; columella angled about 45° in relation to the longitudinal axis; outer lip varicose, smooth within. Dimensions of holotype: height 3.3 mm, diameter 1.5 mm.

Type Locality: Punta Tiburon, Mazatlan, Sinaloa, Mexico, 23°12′30″ N, 106°26′30″ W, one hermit crab specimen collected at low tide by Donald Shasky, 22 December 1962.

Type Material: Holotype, LACM 1410.

Discussion: The genus *Lapsigyrus* was erected by BERRY (1958, p. 92) for *Alvania contrerasi* JORDAN, 1936, a Pleistocene fossil from Magdalena Bay, Baja California. BERRY has reported *L. contrerasi* in Recent siftings from the vicinity of Puerto Peñasco, Sonora, Mexico. I have collected 2 dead specimens of *L. contrerasi* from 20 m in Olas Altas Bay, Mazatlan, Sinaloa, Mexico.

Lapsigyrus contrerasi is distinctly shouldered on the first 2 postnuclear whorls, while *L.* ***myriosirissa*** is not shouldered. It further differs from *L. contrerasi* by having about twice as many spiral threads and much finer and more numerous axial riblets. The name of the new species is derived from the Greek *myrios,* numberless, and *siros,* pit.

Lapsigyrus milleriana (HERTLEIN & STRONG, 1951) from Ballena Bay, Costa Rica, appears to be a junior synonym of *L. contrerasi.*

Coralliophila ***macleani*** SHASKY, spec. nov.

(Figure *4*)

Diagnosis: A variable species similar in morphology and habitat to *Coralliophila caribaea* ABBOTT, 1958, from the Caribbean Sea and the Gulf of Mexico. *Coralliophila* ***macleani*** differs from *C. caribaea* by having tabulate whorls and a proportionally larger body whorl.

Description: Shell medium sized, white, rather globose; protoconch of 3½ mammillate whorls that are usually eroded smooth on larger specimens but occasional juvenile specimens show numerous, very fine microscopic riblets and one or two spiral threads; subsequent whorls 4, tabulate; these rapidly expand so that the body whorl is more than ⅔ of the height of the shell; sculpture variable, most specimens with delicately scalloped spiral cords of varying strength, the strongest at the shoulder; fully mature specimens have 7 cords on the tabulate portion of the body whorl; individual specimens vary as to strength of axial ribbing, which is usually present on the early whorls but frequently disappears on the body whorl; ribs vary in number from 13 to 15 on the penultimate whorl; when axial ribs are present on the body whorl the sculpture becomes rather nodose; suture impressed; aperture broadly trigonal, glistening white; outer lip crenulate, widely flaring, with situs aberrations not unusual; columella straight, extending into a short, open siphonal canal that may be straight, bent, or recurved; umbilicus, when present, a shallow pit; operculum corneous, yellowish-brown to dark brown, with nucleus excentrically placed. Dimensions of holotype: height 17.6 mm, diameter 12.0 mm, height of aperture 13.0 mm.

Type Locality: Saladita Bay, Guaymas, Sonora, Mexico, 27°53′15″ N, 110°59′ W, 3 - 4 m on the bases of white gorgonid sea whips, December 1958, and December 1959, 21 specimens, collected by Donald Shasky.

Type Material: Holotype, LACM 1411; 1 paratype, LA CM 1412; single paratypes, AMNH, ANSP, CAS, SDN HM, SU, and USNM; 13 paratypes, Shasky Collection.

Referred Material: LACM H3935, Adair Bay, Sonora, 1 specimen; LACM 66-12, Cape San Lucas, Baja California, 25 - 100 feet, 10 specimens; Shasky Collection: Norse Beach, Puerto Peñasco, Sonora, 6 specimens; west side, Venado Island, Mazatlan, Sinaloa, Mexico, 3 - 10 m, 7 specimens.

Discussion: *Coralliophila* ***macleani*** is so variable that a composite description would confuse the reader. The apertural variations are undoubtedly due to its rather sedentary existence on the base of its gorgonid host. The largest specimen observed measures 24.3 mm in height (Shasky Collection, Puerto Peñasco). The outer lip is frequently quite thin and sometimes fractures as the shell is removed from the host.

It is my pleasure to name this species for Dr. James H. McLean, Curator of Invertebrate Zoology, Los Angeles County Museum of Natural History.

Anachis ***berryi*** SHASKY, spec. nov.

(Figure *5*)

Diagnosis: Closest to *Anachis gracilis* (C. B. ADAMS, 1852) and *A. rehderi* (HERTLEIN & STRONG, 1951). *Anachis gracilis* is a chunkier and much more striate shell than *A.* ***berryi***. *Anachis rehderi* differs by having a subsutural cord and an outer lip lacking the adapical notch and the denticles.

Description: Shell small, slender, 8-whorled; protoconch of 2 glassy, smooth, slightly inflated whorls; sculpture of postnuclear whorls, except the body whorl, of axial ribs that are lightly noded just below the suture and again about $\frac{1}{3}$ of the length of the ribs below the suture; axial ribs number about 22; faint spiral threads commence in the middle of the body whorl and become stronger abapically; suture a shallow, undulate groove; outer lip shallowly notched abapically to the suture, and with 3 strong denticles and one or 2 lirae abapically to the notch, the adapical tooth the strongest; columella with 2 or 3 very faint lirae; canal short and recurved; color light yellowish-tan with scattered triangular brown blotches; dimensions of holotype: height 9.2 mm, diameter 3.3 mm.

Type Locality: El Pulmo Reef, Baja California, Mexico, 23°26′ N, 109°25′ W, 1 - 3 m, rocky bottom, 23 - 25 April 1965, 40 specimens, collected by Donald Shasky.

Type Material: Holotype, LACM 1413; 2 paratypes, LACM 1414; 2 paratypes each, AMNH, ANSP, CAS, SDNHM, SU, USNM; 25 paratypes, Shasky Collection.

Referred Material: LACM 66-7, South side, Cabo Pulmo, 2 specimens; LACM 65-13, East Anchorage, Maria Cleophas Island, Tres Marias Islands, Mexico, 5 specimens.

Discussion: Sufficient comparison has been made under the diagnosis.

This species is named in honor of Dr. S. Stillman Berry, of Redlands, California, whose depth of knowledge and friendly assistance have frequently been used by this struggling author.

Radwinia SHASKY, gen nov.

(Figure 11)

Radwinia is proposed as a new columbellid genus characterized by a smooth 3-whorled protoconch; by centrally inflated, noded whorls; a sharply varicose, unnotched, denticulate outer lip; a faintly lirate columella; and a short well-differentiated, backward curved anterior canal.

Type Species: ***Radwinia tehuantepecensis*** **SHASKY**, spec. nov.

Radular Description (Figure 11[E]): Each transverse radular row consists of a single rachidian plate, flanked on each side by a single lateral tooth. The rachidian plate is simple, subrectangular, and is gently bent at the ends. There are no cusps and no apparent cutting edge.

The lateral teeth have a sickle-like form. The tooth is oriented in a single plane, with a main shaft, bearing a large primary cusp distally. Proximally there is a broad deep bight followed by a sharply hooked secondary cusp. Most proximally, following a smaller gap, there is a narrow extension of the main shaft with a smaller sharp spur-like cusp. A notable thickening extends along the proximal edge of the main shaft for $\frac{3}{4}$ of its length. Another thickening is apparent on the proximal spur and extends proximally to the end of the extension of the main shaft.

The rachidian plate resembles those of other columbellid genera. The lateral teeth resemble those of many species of the buccinid genus *Phos*. Only the extended main shaft, its attached spur, and the thickening of these areas are unique to the lateral teeth of this genus and species.

Discussion: Genera related to ***Radwinia*** are *Nassarina* DALL, 1889; *Cigclirina* WOODRING, 1928; and *Zanassarina* PILSBRY & LOWE, 1932. ***Radwinia*** has a 3-whorled nucleus while *Nassarina* has but $1\frac{1}{2}$ nuclear whorls. *Nassarina bushii*, the type species of the genus, has fine spiral striations on the last portion of the nucleus while the entire

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[E] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Radwinia nucleus is smooth. From *Zanassarina*, ***Radwinia*** differs by the absence of an anal notch and by having a well-differentiated anterior canal. ***Radwinia*** does not have the fine reticulate sculpture of *Cigclirina*; furthermore, *Cigclirina* has an anal notch.

The new genus is named for Dr. George Radwin, curator of mollusks at the San Diego Museum of Natural History. His work with the Columbellidae will hopefully, in time, provide answers to many of the unresolved problems within this family.

Radwinia tehuantepecensis SHASKY, spec. nov.

(Figures *6* and 11)

Diagnosis: An elongate shell unlike any other West American Columbellid.

Description: Shell small, brown, elongate fusiform, 10-whorled; protoconch conical, smooth, 3-whorled; axial ribs extend from suture to suture, but are not continuous; axial ribs 13 or 14 on late whorls; 3 strong spiral cords cross over the central part of the whorls and one weak spiral thread crosses adapically to the suture; there are 10 or 11 spiral cords and threads on the body whorl; the intersections of axial ribs with the spiral cords are nodose, with squarish pits between; nodes whitish; suture an indistinct groove; pillar sculptured with closely spaced opisthocline spiral threads; body whorl strongly varicose near the outer lip; outer lip with 4 or 5 denticles within; columella faintly lirate; anterior canal open, recurved. Dimensions of holotype: height 8.7 mm, diameter 2.8 mm.

Type Locality: Between San Simeon and Puerto Madero, Gulf of Tehuantepec, Chiapas, Mexico, 30 - 55 m, July 1961, 6 specimens, collected by Carlos Carballo, Jr.

Type Material: Holotype, LACM 1415; single paratypes, CAS, SDNHM, SU, USNM, and Shasky Collection.

Discussion: The placement of this genus and species is not certain. Radular affinities for both Columbellidae and Buccinidae are indicated. The aperture is distinct from any of the species within the *Anachis, Nassarina, Zanassarina, Cigclirina* group of columbellids.

Special thanks are due to Dr. George Radwin for the radular preparation and description, and to Mr. Anthony D'Attilio for the radular drawing.

Ruthia SHASKY, gen. nov.

(Figure 12)

Ruthia is proposed as a new columbellid genus for elongate shells with a trochoid nucleus of 2 or 3 whorls; somewhat flattened postnuclear whorls with noded axial ribs, which extend from suture to suture; an oval aperture with a lirate outer lip, which may or may not have a faint anal notch; a smooth columella; and a short anterior canal. Type species: ***Ruthia mazatlanica*** SHASKY, spec. nov.

Radular Description (Figure 12): The radula is columbelloid. Each transverse row consists of a single rachidian plate, flanked on each side by a single lateral tooth. The rachidian plate is simple, subrectangular and gently bent at the ends, imparting a roughly crescent-like appearance to it. There are no cusps or other outstanding features. As in the radulae of other columbellid species, the rachidian plate appears to be largely non-functional, as there is no apparent cutting edge.

The lateral teeth are considerably more complex. Each tooth has 2 distinct axes, essentially at right angles to

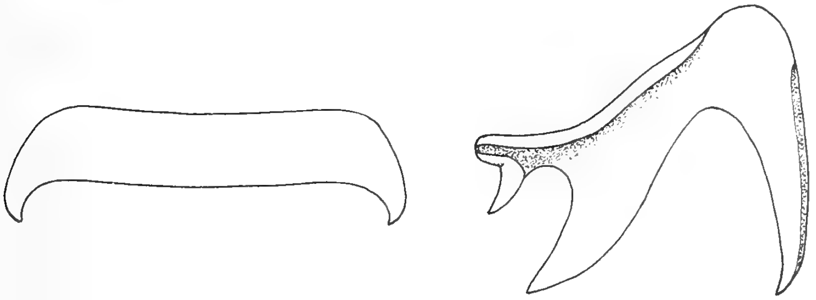

Figure 11

Radula of ***Radwinia tehuantepecensis*** SHASKY, spec. nov., paratype.
Left, rachidian tooth; right, lateral tooth. Greatly enlarged.
Drawn by Anthony D'Attilio.

each other. The main axis is curved in a sickle-like manner and has, in addition to the primary, distal cusp, 2 smaller, slightly bent, proximal cusps. If the major axis is seen from the side, allowing the most complete view of the cusps, the minor axis projects out of the plane in view and is seen in a severely foreshortened aspect. It bears no cusps or other features and is generally rectangular. An attempt to understand the entire structure of the tooth with only the major axis in focus imparts a superficially sigmoid appearance to it.

Discussion: ***Ruthia*** has characters of the buccinid genera *Phos* Montfort, 1810, and *Strombinophos* Pilsbry & Olsson, 1941, and the fossil columbellid genus *Strombinella* Dall, 1896. Since ***Ruthia*** is a columbellid, comparisons with the buccinids will not be made here. *Strombinella* has a subsutural collar similar to the terebrid subgenus *Strioterebrum*. This is lacking in ***Ruthia***. Immature specimens of ***Ruthia*** or specimens with the outer lip broken could be confused with the turrid genus *Clavus* Montfort, 1810.

Ruthia is named in honor of Ruth Shasky, my wife and longsuffering partner on many collecting trips. Her patience and continued encouragement are especially appreciated.

Ruthia mazatlanica Shasky, spec. nov.

(Figure 7)

Diagnosis: A small elongate brown-shelled species similar to the following species, but with one more nuclear whorl, and several other differences which are noted later.

Description: Shell small, turriculate, dark greyish-brown, 10-whorled; nucleus smooth, trochoid, 3-whorled; postnuclear whorls flattened, the first with 8 axial ribs, the second with 7, and succeeding whorls with 6 except on the body whorl which has a 7th rudimentary rib next to the terminal rib; terminal rib very strong, producing a varix; ribs extend from suture to suture, but are usually offset; ribs tapered, with abapical portion the wider; ribs, except on the last whorl, with 2 dark cream-colored nodes; body whorl with 6 to 8 similarly colored nodes, most being interconnected with spiral threads; suture a shallow, undulate groove; aperture oval; columella smooth; outer lip with a slight outward flare, and with 6 lirae within, the adapical the strongest; anterior canal short, open; anal notch lacking; operculum chitinous, brown, unguiculate. Dimensions of holotype: height 12.4 mm, diameter 3.9 mm, height of aperture 3.9 mm.

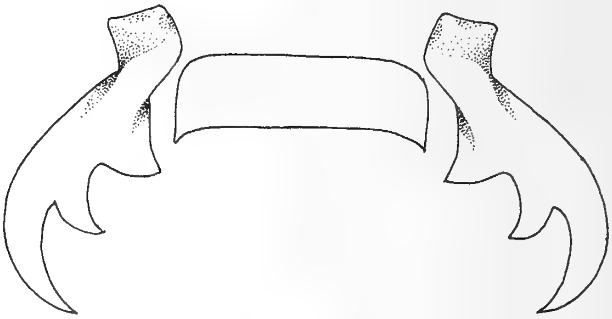

Figure 12

Radula of ***Ruthia ecuadoriana*** Shasky, spec. nov., holotype. Center, rachidian tooth; left and right, lateral teeth. Greatly enlarged. Drawn by Anthony D'Attilio.

Plate Explanation

Figures *1, 2*: ***Macrarene spectabilospina*** Shasky, spec. nov. Holotype, LACM 1409. Gulf of Tehuantepec, Mexico. Height 10.1 mm, diameter 14.1 mm. × 4.0

Figure *3*: ***Lapsigyrus myriosirissa*** Shasky, spec. nov. Holotype LACM 1410. Mazatlan, Mexico. Height 3.3 mm, diameter 1.5 mm. × 13

Figure *4*: ***Coralliophila macleani*** Shasky, spec. nov. Holotype, LACM 1411. Guaymas, Mexico. Height 17.6 mm, diameter 12.0 mm. × 2.6

Figure *5*: ***Anachis berryi*** Shasky, spec. nov. Holotype, LACM 1413. El Pulmo, Baja California. Height 9.2 mm, diameter 3.3 mm. × 6.5

Figure *6*: ***Radwinia tehuantepecensis*** Shasky, spec. nov. Holotype, LACM 1415. Gulf of Tehuantepec, Mexico. Height 8.7 mm, diameter 2.8 mm. × 8.3

Figure *7*: ***Ruthia mazatlanica*** Shasky, spec. nov. Holotype USNM 567103. Mazatlan, Mexico. Height 12.4 mm, diameter 3.9 mm. × 4.7

Figure *8*: ***Ruthia ecuadoriana*** Shasky, spec. nov. Holotype, LACM-AHF 1417. Cape San Francisco, Ecuador. Height 14.6 mm, diameter 4.8 mm. × 4.0

Figure *9*: ***Columbella socorroensis*** Shasky, spec. nov. Holotype, LACM 1418. Socorro Island, Mexico. Height 18.7 mm, diameter 9.2 mm. × 2.6

Figure *10*: ***Strombina (Cotonopsis) mendozana*** Shasky, spec. nov. Holotype, LACM 1419. Gulf of Fonseca, El Salvador. Height 22.5 mm, diameter 9.1 mm. × 2.6

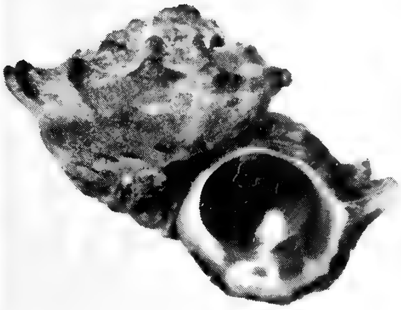

Figure 1

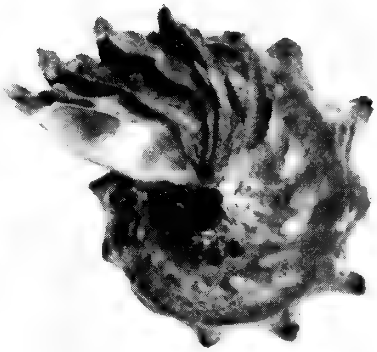

Figure 2

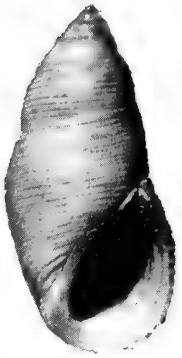

Figure 3

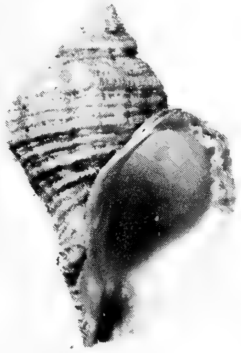

Figure 4

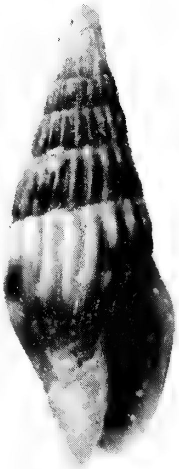

Figure 5

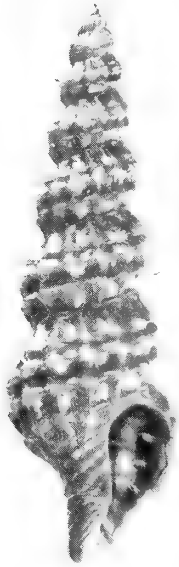

Figure 6

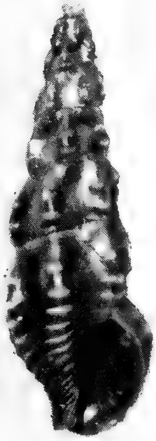

Figure 7

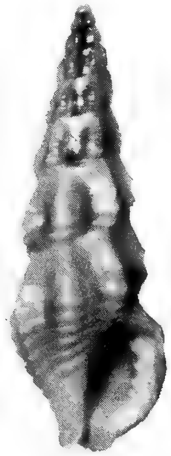

Figure 8

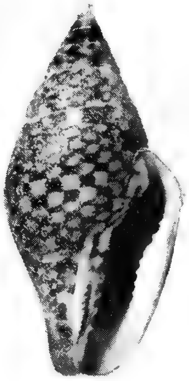

Figure 9

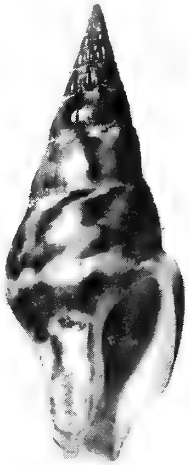

Figure 10

Type Locality: Between Azada Island and Pala Point, Mazatlan, Sinaloa, Mexico, 23°11′ N, 106°27′ W, 3 - 4 m, gray sand, 11 - 16 April 1940, 2 specimens collected by Russell Hawkins, Jr.

Type Material: Holotype, USNM 567103; 1 paratype, 679563. Additional paratype, USNM 567008, east of Azada Island, 3 - 4 m, Hawkins. Twenty-three paratypes (hermit crab shells) from east side of Chivos Island, Mazatlan, 26 December 1962 and 19 December 1964, collected by Ruth, Mike, and Donald Shasky, single specimens distributed as follows: AMNH, ANSP, CAS, LA CM, SDNHM, SU, and USNM; 16 paratypes, Shasky Collection.

Referred Material: Helen DuShane Collection (Whittier, California), Los Angeles Bay, near Tenacatita Bay, Jalisco, Mexico, 11 m, 1 specimen.

Discussion: The ribs of the holotype are offset more than on most specimens. For comparison see the discussion under the following species.

Azada and Chivos Islands are no longer separate islands. Older maps show Pala Point, on the mainland, separated from Creston Island with Azada Island in between. Because of extensive filling between Pala Point and Creston Island, Azada Island no longer exists and Creston Island is now shown as Creston Point. The sportfishing fleet docks on the harbor side of where Azada Island used to be. Chivos Island, directly across the harbor channel, is still listed on modern maps as an island, but it is connected on the east side to the mainland by a wide breakwater.

It is doubtful that ***Ruthia mazatlanica*** could be found living in the harbor channel; however, shallow dredging on the southeast side of Chivos Island and in the sand between the boulders north of where Azada Island was probably would produce additional live specimens.

Ruthia ecuadoriana Shasky, spec. nov.

(Figures *8* and 12)

Diagnosis: Similar to *Ruthia mazatlanica*, but distinguished by its larger size, yellow color, 2 rather than 3 nuclear whorls, and other sculptural differences.

Description: Shell small, yellow, turriculate, 9-whorled; nucleus smooth, trochoid, 2-whorled; early postnuclear whorls flattened, later whorls somewhat inflated; first postnuclear whorl with 8 and succeeding whorls with 7 axial ribs, except on the body whorl where there is a much smaller rib adjacent to the terminal rib; terminal rib strong, forming a labial varix; ribs tapered with abapical portion wider; ribs extend from suture to suture, but are slightly offset on some whorls; ribs of early whorls with 2 nodes, but increasing to 3 nodes on the penultimate whorl; penultimate whorl nodes are connected between the ribs with faint spiral threads; on the body whorl the ribs are crossed with about 9 spiral threads that are strongest where they cross the ribs; suture an undulate groove; aperture oval; outer lip varicose and with an outward flare; inner lip with 6 lirae, the adapical the strongest; abaxial to the strong lira there is a very shallow depression for an anal notch; anterior canal short, open; columella smooth. Dimensions of holotype: height 14.6 mm, diameter 4.8 mm, height of aperture 5.2 mm.

Type Locality: Off Cabo San Francisco, Ecuador, 0°39′30″ N, 80°06′30″ W, 4 m, mud and rock bottom, R/V *Velero* III station 214-34, 11 February 1934, 1 specimen.

Type Material: Holotype, LACM-AHF 1417.

Discussion: The differences between the 2 species of ***Ruthia*** are as follows:

Table 1

	Ruthia mazatlanica	***Ruthia ecuadoriana***
Number of whorls	10	9
Height of shell	12.4 mm	14.6 mm
Color	Dark grey-brown with yellowish nodes	Solid yellow
Shape of post-nuclear whorls	Flattened throughout	Penultimate and body whorl somewhat inflated
Number of axial ribs	Six ribs with 7th short rib on body whorl	Seven ribs with 8th short rib on body whorl
Nodes on ribs	Two nodes throughout	Three nodes on ribs of penultimate whorl
Spiral threads of body whorl	Weak	Stronger
Anal notch	Lacking	Shallow depression

The radular mount and description is by Dr. George Radwin, and the radular drawing by Mr. Anthony D'Attilio, both of the San Diego Natural History Museum.

Columbella socorroensis Shasky, spec. nov.

(Figure *9*)

Diagnosis: A *Columbella* similar to *C. luteola* Kiener. *Columbella socorroensis* is more elongate, with axial ribs on the early whorls, and a callus whose adapical point is angled adaxially.

Description: Shell medium size, ovate, 10-whorled; protoconch of 3 smooth conical whorls; next 3 succeeding whorls have about 18 axial riblets which are keeled at both ends; remaining whorls smooth except over the pillar and anterior end of the body whorl which are crossed by fine spiral threads; suture slightly canaliculate; aperture elongate, bluish-white, but with color and pattern of body whorl partially visible; outer lip thickened within by a ridge of 12 to 14 lirae; on the adapical end of the columella at the suture is a thickened, usually bifid, callus whose adapical point is directed adaxially; the central and abapical portions of the columella have 5 to 7 lirae; canal short, open; color a rich chocolate brown interspersed with bluish-white squares, rectangles, or amorphic designs. Dimensions of holotype: height 18.7 mm, diameter 9.2 mm.

Type Locality: Braithwaite Bay, Socorro Island, Revillagigedo Islands, Mexico, 18°42′45″ N, 110°56′50″ W, 2 m, rocky bottom, 11 August 1965, 7 specimens, collected by Donald Shasky.

Type Material: Holotype, LACM 1418; single paratypes, AMNH, CAS, SDNHM, USNM; 2 paratypes, Shasky Collection.

Referred Material: AHF 128-34, Braithwaite Bay, Socorro Island, 3 specimens; AHF 130-34, Braithwaite Bay, 2 specimens; AHF 140-34, Sulphur Bay, Clarion Island, Revillagigedo Islands, Mexico, 1 specimen.

Discussion: It is my opinion that Reeve's figure for *Columbella luteola* Kiener almost certainly represents the same species as *C. aureomexicana* (Howard, 1963). Mrs. Howard's observation as to color was very close to that of Kiener's when she originally named her taxon *C. aureola.*

The presence of axial ribs on the early whorls, its more elongate form, the angled bifid callus, and the color and pattern all help to distinguish *Columbella socorroensis* from *C. luteola.*

Socorro Island, of the Revillagigedo group, is approximately 410 miles WNW of Manzanillo, Colima, and 240 miles SSW of Cabo San Lucas, Baja California.

It was my privilege to accompany the Mexican Naval transport *"Papaloapan"* on one of its trips with supplies for the garrison on Socorro. My trip was arranged by Vice Admiral Jorge Lang Islas through the office of Dr. Agustin Ayala-Castañares, Director of the Instituto de Geologia, Universidad Nacional de Mexico.

Strombina (Cotonopsis) mendozana Shasky, spec. nov.

(Figure *10*)

Diagnosis: This new species is a member of a complex made up of *Strombina edentula* Dall, 1908, *S. deroyae* Emerson & D'Attilio, 1969, and another as yet unnamed form from off Panama. From *S. edentula* it is distinguished by its smaller size and the presence of numerous lirae in the outer lip. *Strombina deroyae,* which is 50 - 60 mm in length, has a much longer anterior canal, a narrower, more ovate aperture, a more lirate outer lip, and a strong anal plait.

Description: Shell medium size, 10-whorled; nucleus smooth, of about 1½ whorls; the first 5 or 6 post-larval whorls sculptured with about 20 axial ribs that extend the length of the whorl; the penultimate and body whorls are essentially smooth except for faint, slightly opisthocyrt growth lines; the thin, tan periostracum appears on the body whorl in fine feathered rows corresponding to the growth lines; suture somewhat undulate; just anterior to the central bulge of the body whorl and extending to the terminus of the anterior canal are fine spiral threads; aperture elongate, of white to violet color; outer lip thin-edged with 6 to 10 lirae within; a varicose ridge about 2 mm exterior to the outer lip margin runs the length of the body whorl; columella smooth, except near the suture, where there is a single oblique plica; anterior canal open, short, recurved; operculum chitinous, brown, unguiculate; color of most specimens is white with straight or zigzag bands of brown and a white band about the center of the body whorl; a single specimen from the type lot is virtually a solid yellow and another yellowish-brown. Dimensions of holotype: height 22.5 mm, diameter 9.1 mm.

Type Locality: Gulf of Fonseca, El Salvador, 15°57′ N, 95°32′ W, 33 - 73 m, October 1960, 28 specimens, collected by Capt. Xavier Mendoza von Borstel.

Type Material: Holotype, LACM 1419; 1 paratype, LACM 1420; single paratypes, AMNH, ANSP, CAS, SDNHM, SU, and USNM; 20 paratypes, Shasky Collection.

Referred Material: Shasky Collection, Station D-2, Gulf of Tehuantepec, Oaxaca, Mexico, 52 m, 4 specimens. Three additional lots are in the LACM collection, dredged by George Willett in 1938 from Chamela, Banderas, and Tenacatita Bays, 27 to 73 m.

Discussion: For additional remarks on the species of *Cotonopsis* the reader is referred to the paper by EMERSON & D'ATTILIO, 1969.

This new species is named for Capt. Xavier Mendoza von Borstel of Mexico City, who was the first to bring it to my attention.

ACKNOWLEDGMENTS

A number of individuals have given invaluable assistance in the preparation of this paper. First and foremost is Dr. James H. McLean of the Los Angeles County Museum of Natural History. His suggestions, textual criticisms, and the photography are most appreciated. Dr. George Radwin and Mr. Anthony D'Attilio of the San Diego Natural History Museum have previously been mentioned for their radular preparations, descriptions, and drawings. Dr. S. S. Berry of Redlands, California, provided valuable references. Other courtesies have been extended by Dr. Myra Keen, Dr. William Emerson, Capt. Xavier Mendoza von Borstel, Dr. Agustin Ayala-Castañares, Dr. Antonio Garcia-Cubas, and Mr. Eugene Bergeron.

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METHODS & TECHNIQUES

A Compact Aquarium Unit for Macrophotography

BY

J. SHERMAN BLEAKNEY

Department of Biology
Acadia University, Wolfville, Nova Scotia

(1 Plate; 2 Text figures)

THE USUAL laboratory arrangement for photographing many species of marine invertebrates consists of a rather large glass aquarium supported several inches above a black background. This somewhat cumbersome setup and modifications of it are well illustrated in BLAKER's (1965) "Photography for Scientific Publication", but none of these answered my problem of a portable, unbreakable aquarium that could be conveniently packed and transported with camera and accessory lenses.

The final unit design is depicted in Figure 1 and consists basically of a small rectangular acrylic plastic aquarium tank with a lengthwise pocket beneath, and a narrow vertical pocket at one end. The "ventral" pocket raises the tank so that a suitable background can be inserted into this space beneath the tank. I carry a variety of coloured and textured cloths, as well as black velvet, cemented to file cards and cut to fit this lower chamber. With this series of backgrounds a specimen can be photographed first with standard black velvet and then other cards can quickly be substituted. The vertical pocket holds a reflector of aluminum foil taped to a file card. It serves to soften the deep shadows created by the flash unit which is aimed horizontally through the depth of water from the opposite side of the tank (Figure 2). Depending upon the specimen being photographed or the effect desired, the

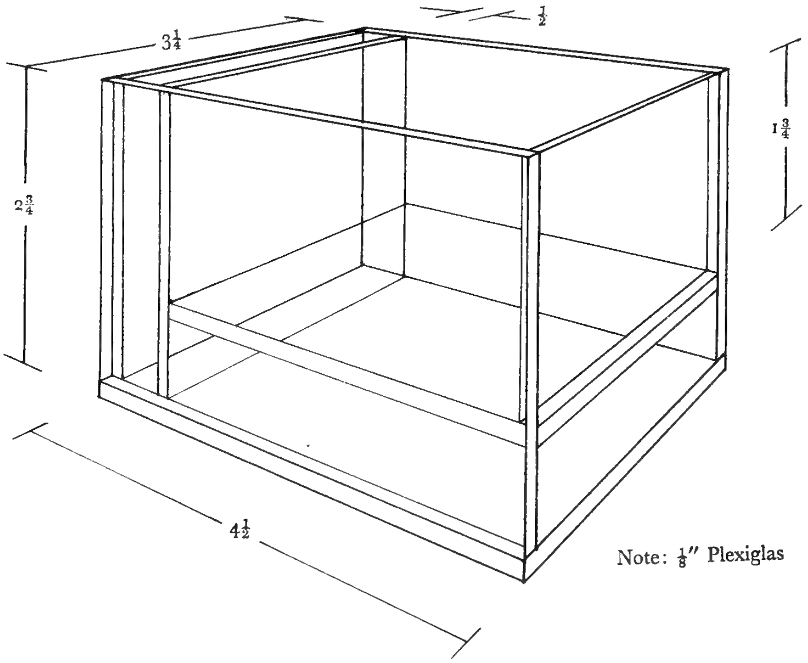
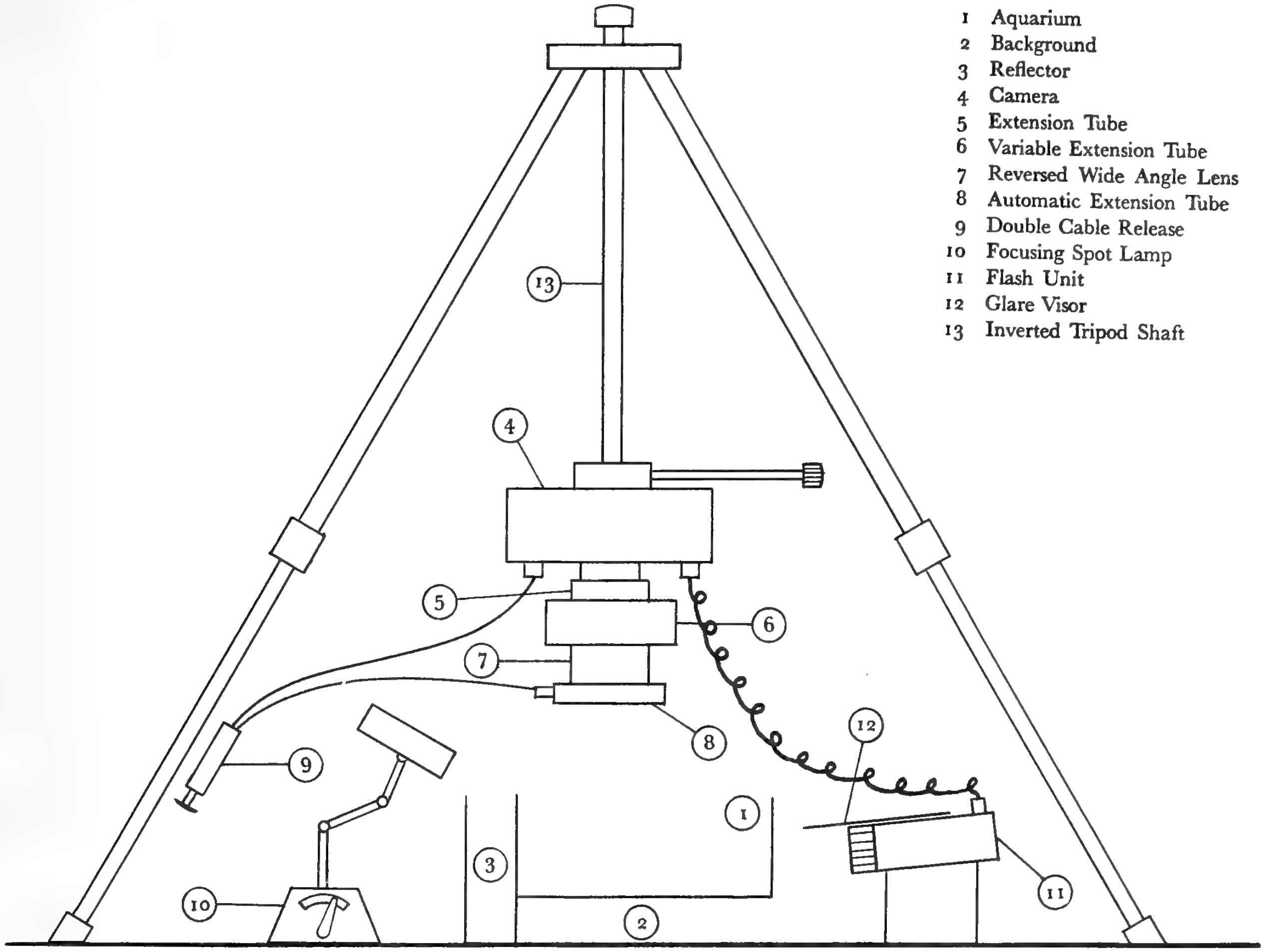


Figure 1

Aquarium unit with a ventral pocket for insertion of background colors, and a vertical pocket to house flash reflectors



1 Aquarium
2 Background
3 Reflector
4 Camera
5 Extension Tube
6 Variable Extension Tube
7 Reversed Wide Angle Lens
8 Automatic Extension Tube
9 Double Cable Release
10 Focusing Spot Lamp
11 Flash Unit
12 Glare Visor
13 Inverted Tripod Shaft

Figure 2

Diagram of macrophotography arrangement using aquarium-background-reflector unit

reflector unit can be quickly changed from aluminum to white paper or omitted entirely.

This basic combination of (a) camera and flash unit, (b) focusing lamp, and (c) aquarium-background-reflector unit can be conveniently set up in a few moments; an important advantage when working with captive sensitive nudibranchs. On a sunny day in the field the focusing lamp and flash unit are not necessary. The aquarium material is durable clear acrylic, but will scratch; however, as photographs are taken through the water surface this disadvantage is of no consequence. If one plans to photograph animals over a wide range of sizes, a nesting set of 2 or 3 units can be made, in which one entire unit fits neatly into the tank of the next unit.

This aquarium unit was devised for opisthobranch photography, but is suitable for any sessile, slow moving, or preserved organism. My own system is to place freshly caught nudibranchs in a refrigerator and add the aquarium unit and a jar of filtered sea water from the same bay. Specimens and aquarium and sea water are brought to the camera and transferred to the chilled tank. Focusing is done by moving the tripod legs using both hands, one of which holds the double cable release and a switch (or blackout card) for the focusing lamp. After each specimen is photographed the tank is washed out with sea water and wiped with a paper towel to remove any mucous trails. Many species produce substances which elicit either an active avoidance response or a contraction and inactivity response from other species if added to the same water immediately afterwards. I have found it nearly impossible to obtain photographs of normally active nudibranchs unless the aquarium is emptied and cleaned after each species has been photographed. With such a small aquarium unit this can be accomplished very quickly. If lens, tubes or film need changing, then the entire aquarium unit with specimens can be placed in the refrigerator during that period to keep the water chilled.

The most versatile and convenient combination of lenses and accessories that I have found for our generally small North Atlantic nudibranchs is a 58 mm camera lens, a reverse 35 mm wide angle lens, a variable extension tube (0 - 30 mm) and a standard set of extension tubes. The variable extension tube is excellent for zooming down on parts of one specimen and conversely for enlarging the field of view to include 2 specimens in one frame, or a specimen plus its spawn.

Colour reproductions of two species photographed by the above technique (Figures *3* and *4*) are presented not for their beauty, but because of contrast with hand executed illustrations in standard references. The *Acteon tornatilis* (Linnaeus, 1758) diagrams in Hyman (1967), Graham & Fretter (1964), and Pruvot-Fol (1954), bear poor structural and pattern resemblance to this average specimen from South Wales. The first colour illustration of *Alderia modesta* (Lovén, 1844) from our east coast is the peculiar figure 227, plate XVI in Gould & Binney (1870). The drawing of a Californian specimen in Hand & Steinberg (1955) is accurate, but again based on average sized specimens of 5 to 8 mm and does not have the unexpected proportions found in large 14 mm specimens common in Nova Scotia. Note that cerata of the right side are in a contraction phase and the left ones are expanded. The rhythmical contraction of the rows of cerata substitutes for an atrophied heart.

The author is indebted to Dr. Henning Lemche and Mr. James Lance for their initial encouragement and helpful suggestions towards more successful photography of living nudibranchs. This technique was developed in connection with a study of Nova Scotia nudibranchs supported by a National Research Council of Canada Grant.

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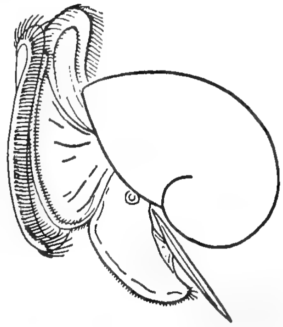

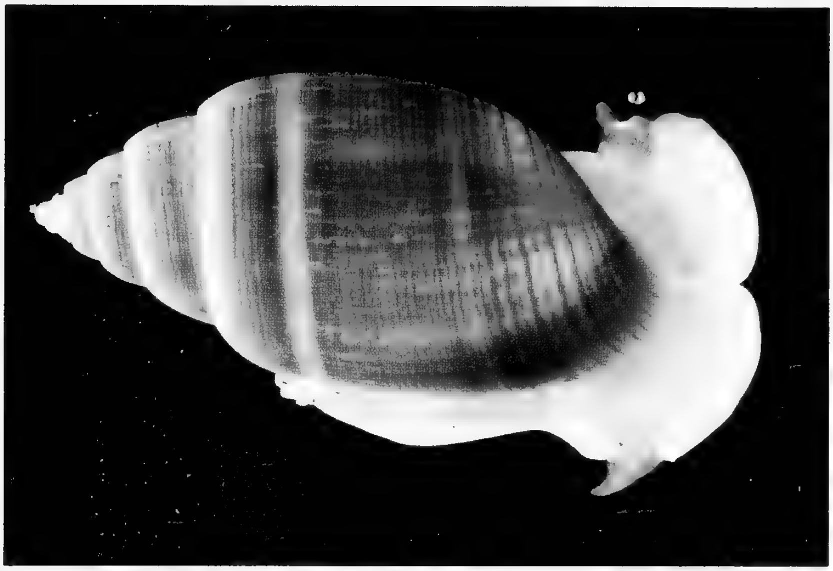

Figure 3

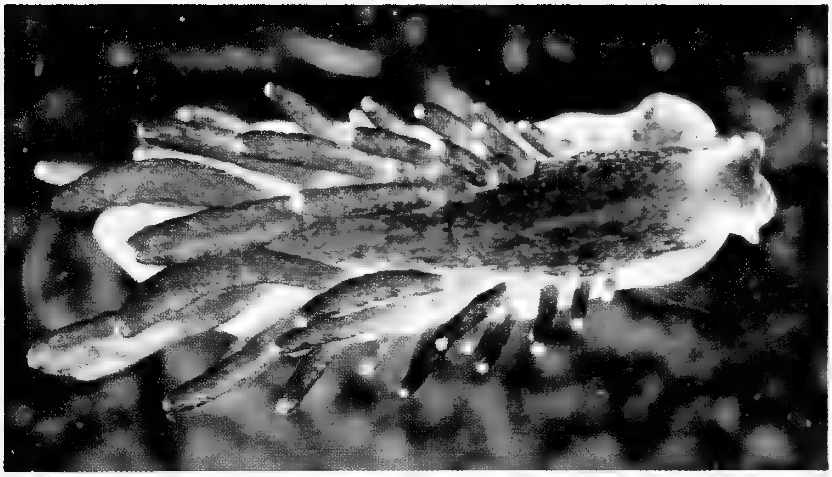

Figure 4

Figure 3

Acteon tornatilis collected by T. E. Thompson, September 26, 1967 at Rhossili Bay, Gower, Wales. Size 15 mm

Figure 4

Alderia modesta collected by J. S. Bleakney, March 1969, Canning salt marsh, Minas Basin, Nova Scotia. Size 14 mm

NOTES & NEWS

Soviet Contributions to Malacology

BY

KENNETH J. BOSS

Museum of Comparative Zoology, Harvard University
Cambridge, Massachusetts 02138

AND

MORRIS K. JACOBSON

American Museum of Natural History,
New York, N. Y. 10024

Soviet publications in malacology continue to constitute a little known portion of the world's scientific literature until they are translated into western languages or cited in the Zoological Record. Last year Boss (The Veliger 12 (2): 226 - 227) provided a list of Russian malacological papers extracted from the section on Invertebrate Zoology of the Referativnyy Zhurnal, which contains the monthly abstracts published by the Government Committee of the Soviet Ministry of the USSR for Science and Technology.

We have reviewed the 12 issues of the Referativnyy Zhurnal for the year 1969 and translated the titles of Soviet articles contained therein. Several book-length items as well as individual articles appear to be important contributions to zoology. It is is interesting to note that there is a trend to greater productivity in some of the outlying Republics in the Soviet Union.

We have not located all the journals or even the titles for them since some are not available in any American library; thus, we have provided complete citations when we could, or have given the abbreviations as they appeared in the Referativnyy Zhurnal. Abbreviations and symbols we have used are:

ZZ	Zoologicheskii Zhurnal (Zoological Journal)
BWHO	Byul. Vsemiri. Organiz. Zdravookhr. (Bulletin of the World Health Organization)
PBI	Physiology and biochemistry of the Invertebrates. Leningrad, Science [Press] Fiziologiya i biokhimiya bespozvonochnikh. Leningrad. Nauka.
ES	English Summary

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Comment on a Nomenclatural Matter in Mitridae

BY

A. MYRA KEEN

Stanford University, Stanford, California 94305

The following letter was sent to the Editor of the Hawaiian Shell News on December 24, 1969 but has not as yet been published. The problem which it points up is one that should be given some discussion; therefore the letter is being released here.

Editor, Hawaiian Shell News
2777 Kalakaua Avenue
Honolulu, Hawaii 96815

Dear Sir:

I notice in the lead article of the December "Hawaiian Shell News" [vol. 12, no. 12] an unfortunate nomenclatural usage in a paper by W. O. Cernohorsky entitled, "The taxonomy of Hawaiian and Indo-Pacific Mitridae, Part I." I am hoping that if there is a similar usage in the next part of his paper it can be pruned out before publication. He attributes authorship of *Mitra golischi* and *M. lipara* to Jean Cate. Perhaps in his own mind he was thinking of this as a short-cut way of referring to her discussion of these names. Actually both names were *nomina nuda* from a Dall manuscript, and she was careful to leave them as such. She did not under the International Code of Zoological Nomenclature validate the names, for she made clear that she regarded them as synonyms. Under Article 11 (d) of the Code, a name published in synonymy has no status. Cernohorsky points out a figure by Dietrich and Morris[1] for one of these species; they cited it as *Strigatella golischi* Dall. At first glance it might appear that Dietrich and Morris had validated the name, but again under the Code it remains a *nomen nudum*. The Code, Article 13 (A) (i) requires a statement of characters differentiating the taxon. This neither Dietrich and Morris nor Jean Cate gave. To attribute the Dall nude names to either subsequent author is apt to cause confusion.

I call this to your attention because I feel a personal interest in this matter, having been one of Mrs. Cate's advisers when she was preparing her report on the Dall miters. Her paper, which is not cited by Cernohorsky but which may form part of the bibliography for his second part was: "Review of Dall's Hawaiian mitrids . . " The Veliger, vol. 6, no. 1, pp. 23-42, 4 pls., 1963.

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[1] Dietrich, Richard V., and Percy A. Morris. "Mollusks from Kwajalein," The Nautilus, vol. 67, no. 1, pp. 13-18, 1 pl., July, 1953.

Note on *Micrarionta harperi* (Bryant, 1900)

BY

ALLYN G. SMITH

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

Recent work on the accessioning of California desert snails into the collection of the California Academy of Sciences required a review of specimens of the rare *Micrarionta harperi* (Bryant, 1900). Fortunately, 4 syntypes of this species were in the Henry Hemphill Collection and are now in the Academy's possession. These are Hemphill's original no. 8676A and now California Academy of Sciences Geology Type Collection nos. 5367 - 5370, inclusive. CASG no. 5367 has been illustrated by Berry (1922, Proceedings of the Academy of Natural Sciences, of Philadelphia, vol. 74, p. 94, plt. 10, figs. 5 - 8) and is hereby designated as the lectotype of the species; the remaining 3 shells become lectoparatypes.

In 1937, Bartsch described a subspecies, *orcuttiana,* collected by Charles Russell Orcutt in "the Colorado desert" without a more specific locality. In the California Academy collection there are 6 separate lots of *M. harperi orcuttiana* and one in my private collection, as follows:

Mountain Springs, San Diego Co., California. CASG no. 42651 (*ex* Willett Coll.). Five adult shells and 3 subadults. Some collected alive or only recently dead. This is by far the best available set.

2½ mi. E of Mountain Springs. CASG no. 42652 (*ex* Willett Coll.). Two dead, bleached adults.

Mountain Springs. CASG no. 22641. G D. Hanna, coll., 1921. One adult; 6 subadults; all dead and bleached.

Mountain Springs. CASG no. 22833. G D. Hanna, coll. One adult; 4 subadults; all dead and bleached with some shells broken.

Mountain Springs. CASG no. 22834. G D. Hanna, coll. One adult; 2 subadults; dead and bleached.

Mountain Springs. A. G. Smith coll. 14 May 1926, AGS no. 2896. One adult; 2 subadults; dead and bleached.

3 mi. E of Jacumba, San Diego Co., California. CASG no. 42653. Stanley C. Williams and V. F. Lee, colls., 7 July 1969. Two adults and 2 subadults; all shells in good condition.

A recent, thorough discussion of both the species and the subspecies is presented in Pilsbry, 1939 (Monographs of the Academy of Natural Sciences of Philadelphia no. 3, vol. 1, pt. 1, pp. 253 - 256). This and comparison of the above listed shells identified as *Micrarionta harperi orcuttiana* with those from the original lot of *M. harperi* fails to establish any consistent size or sculptural characters that separate the two. Thus, *M. harperi orcuttiana* (Bartsch, 1900) should be treated as a synonym of its parent species, *M. harperi* (Bryant, 1900).

ABOUT 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.

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CALIFORNIA MALACOZOOLOGICAL SOCIETY, Inc.

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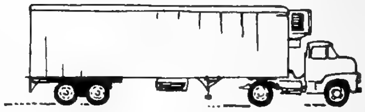
In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology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



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W. S. M.

At the third annual meeting of the Western Society of Malacologists, held at Stanford University, the following officers were elected:

Dr. Eugene Coan, *President*
Mrs. Beatrice L. Burch, *First Vice President*
Dr. Warren O. Addicott, *Second Vice President*
Mrs. Mary D'Aiuto, *Secretary*
Mr. Ralph Fox, *Treasurer*
Mr. Barry Roth and Dr. James H. McLean, *Councillors at Large*

Other Council Members are the Past Presidents:

Mr. David K. Mulliner
Dr. William K. Emerson
Dr. A. Myra Keen

The fourth Annual Meeting will be held at Asilomar, Pacific Grove, California, from June 16th to June 19th, 1971. Detailed plans for that meeting will be announced at a later date.

U. M. E.

Fourth European Malacological Congress

The Fourth European Malacological Congress will be held in Geneva, Switzerland, from September 7 to 11, 1971. It will follow a one-day meeting of museum curators in charge of molluscs, devoted to the discussion of curatorial problems and collaboration. The meetings will take place in the new Museum of Natural History and, eventually, also in the nearby University buildings. All malacologists are cordially invited.

Accommodations will be arranged by the Tourist office in hotels and the student hostel.

Congress fee is Swiss Fr. 30.- (about $7.-) for members and corresponding members of U. M. E.; S.Fr. 40.- (*ca.* $9.-) for non-members, and S.Fr. 15.- (*ca.* $3.50) for students and accompanying persons.

Persons interested and not having received the circulars are asked to contact the president, Dr. E. Binder, for more detailed information.

Address: IV European Malacological Congress
Museum of Natural History
CH - 1211 Geneva 6, Switzerland

BOOKS, PERIODICALS, PAMPHLETS

New Records of Mytilidae from the northern South West African Coast

by Brian Kensley & Mary-Louise Penrith. Ann. South African Mus. vol. 57, prt. 2, pp. 15 - 24; figs. 1 - 5. April 1970.

Six species of Mytilidae are reported from the northern coast of South West Africa from about 18° to 27° South Latitude. Three species are discussed of which 2 are illustrated. Especially interesting is the report of 3 species heretofore recorded only from South America. These are *Modiolus carvalhoi* Klappenbach, originally from Brazil; and *Semimytilus algosus* (Gould) from the west coast of South America, and *Aulacomya magellanica* (Chemnitz) from the same area and ranging to the Magellanic region.

LGH

Malacological Review.

P. O. Box 801, Whitmore Lake, Michigan 48189. Vol. 2 for 1969 (received in June 1970): 214 pp., illust. Subscription $5.-. (issued in 2 separate parts)

In Part 1 of this volume there is one paper (102 pages), by Harold J. Walter. The title of this work is "Illustrated biomorphology of the *"angulata"* lake form of the basommatophoran snail *Lymnaea catascopium* Say." The second part contains a paper by S.-K. Wu on "Some chitons from Taiwan" reporting on six species of chitons, of which four are new to Taiwan. Three so-called "brief communications" include: J. B. Burch, The chromosome number of *Bulinus sericinus* from Ethiopia; J. H. McLean, New species of tropical eastern Pacific Gastropoda [21 new taxa are described]; and J.-J. van Mol, Malacologists interested in Africa. Pages 131 to 136 are devoted to a presentation of the titles of papers given at the Proceedings of the Society for Experimental and Descriptive Malacology, held in 1969. Abstracts of 5 of the papers are included, with a note where other papers will be published *in extenso*. The very useful facsimile reproduction of the tables of contents of a number of the leading journals in the field of malacology is continued.

This reviewer would welcome a prominently displayed statement as to the exact publication dates of both parts, a bit of information that might prove important in later decisions as to the priority of new taxa described in this publication.

Considering the general trend of printing costs, the price of this volume is remarkably low and it is to be hoped that many amateur malacologists as well as the professionals will subscribe to this Review.

RS

Collecting Seashells

by Kathleen Yerger Johnstone. Grosset & Dunlap, Inc., New York, N. Y. 198 pp., 6 color plts., halftone and line drawing illustr. $5.95. 1970.

The enthusiasm of the author of this beautifully illustrated book is highly contagious. It is difficult to pick out any one part of the book as the "best;" however, to this reviewer, chapter 5 "Shell Names" would be worth the price of the book all by itself. In fact, it would be a good thing if this chapter were to be read and discussed at least once a year at all shell clubs.

While the book is supposedly written by an amateur, it is quite obvious that in this case the "amateur" is a very advanced and knowledgable one, distinguished from many professional malacologists perhaps only by the fact that the author collects and studies shells without being paid for this activity. It is certain that almost all other amateurs and many professionals can benefit from the many handy hints and suggestions in this volume.

RS

Catálogo de los Moluscos marinos del Uruguay (Parte III).

by Alfredo Figueiras & Omar E. Sicardi. Comunicaciones de la Sociedad Malacológica del Uruguay, vol. 2, nos. 16 - 17, pp. 355 - 378; plts. 3, 4 (pp. 377, 378). April/October, 1969.

This is a continuation of a catalog of the marine mollusks of Uruguay. It contains Pelecypoda of the order Eulamellibranchia, suborder Heterodonta.

LGH

Type Specimens of Fossil Invertebrata in the Los Angeles County Museum of Natural History, Exclusive of Paleoentomology

by Edward C. Wilson & Donald E. Bing. Contr. in Sci., Los Angeles County Mus. Nat. Hist., No. 181: 20 pp. 27 February 1970.

Type Specimens of Recent Invertebrates (except Arachnida and Insecta) in the San Diego Natural History Museum

by Edward C. Wilson & George L. Kennedy. Trans. San Diego Soc. Nat. Hist., vol. 14, no. 19, pp. 237 - 280. 17 November 1967.

Type Specimens of Fossil Invertebrates in the San Diego Natural History Museum

by Edward C. Wilson. Trans. San Diego Soc. Nat. Hist., vol. 14, no. 9, pp. 97 - 132. 29 April 1966.

These three publications form an important contribution to the source material available in California. Such inventories are very desirable as they obviate much correspondence. The presence of an occasional misspelling of genus or species names, however, may somewhat impair the otherwise great value of the work.

RS

A Sheller's Directory of Clubs, Books, Periodicals and Dealers

by T. C. Rice, Port Gamble, Washington, 52 pp., mimeographed. $1.-

This second edition is expanded and corrected, according to the introduction. The booklet may prove useful to the beginning as well as to the advanced shell collector.

RS

Statement of Ownership, Management, etc.

of "The Veliger," published quarterly on the first day of July, October, January, and April, at Berkeley, California, as required by the Act of August 24, 1912. Publisher: California Malacozoological Society, Inc. Editor: Rudolf Stohler. Owner: California Malacozoological Society, Inc., a non-profit, educational corporation. Bondholders, mortgagees, and security holders: none.

(signed) R. Stohler, *Editor.*

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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.

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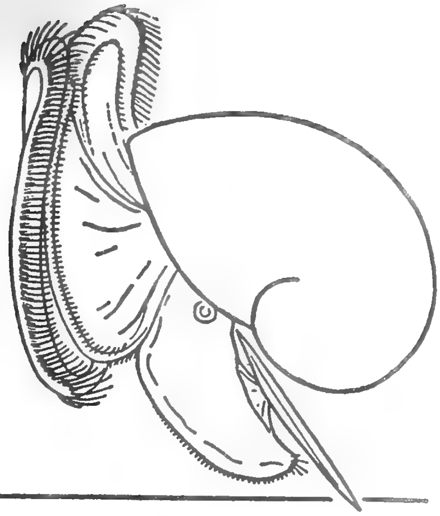

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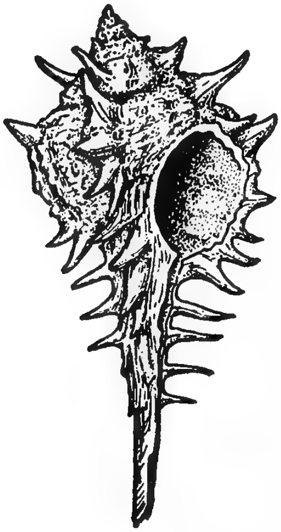


Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

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

Mouse Ascites Fluid as a Source of Antibody Against Molluscan Antigens

BY

GEORGE M. DAVIS

AND

SETSUKO SUZUKI

Malacology Section, Department of Medical Zoology, 406 Medical Laboratory, USAHCZ; APO San Francisco 96343

(4 Plates; 4 Text Figures; 21 Tables)

INTRODUCTION

UTILIZATION OF IMMUNOLOGICAL TECHNIQUES as applied to molluscan systematics has recently increased. This trend is seen in studies on Lymnaeidae (TRAN VAN KY *et al.*, 1962; MORRILL *et al.*, 1964), Planorbidae (TRAN VAN KY *et al.*, 1962; MICHELSON, 1966a,b; WRIGHT & KLEIN, 1967; BURCH, 1968), Hydrobiidae (DAVIS, 1968a), Pleuroceridae (DAVIS, 1968b, 1969), and Pelecypoda (FISHER, 1969). These studies have involved precipitating antigen-antibody systems in ring-tests, Ouchterlony diffusion plates, acrylamide and agar gel immunoelectrophoresis.

A problem exists in producing quantities of antisera for studies involving small gastropods. With whole-body extracts excluded for the reasons stated by DAVIS & LINDSAY (1967) it is difficult to procure adequate protein to induce antibody production at a desired level using snails of the size of most Hydrobiidae or smaller. From 28 to 212 mg protein have been used to hyperimmunize one rabbit (DAVIS, 1969) with maximum yields of 100 ml of antiserum (pooled from two successive bleedings). With *Oncomelania hupensis nosophora* foot muscle extract, this amount of protein may involve 400 to 2000 snails respectively. It may take four rabbits to obtain one which will produce excellent antiserum; i.e., a total investment of 1600 to 8000 snails.

MUNOZ (1957) reported production of specific antibody of high titer in large amounts of peritoneal fluid by injecting mice with albumin antigens mixed with Freund's adjuvant. HERRMANN & ENGLE (1958) coupled viral immunization with Sarcoma 180 cell-induced ascites to produce large volumes of peritoneal fluid with high titer antibody. KASEL *et al.* (1959) utilized a bacterial-adjuvant mixture to provide a high titer viral antibody. LIEBERMAN *et al.* (1961) showed that mice strains varied in potential to produce ascitic fluid when inoculated intraperitoneally with *Staphylococcus aureus*—incomplete Freund's adjuvant mixtures. SARTORELLI *et al.* (1966) used Sarcoma 180/TG in addition to human serum albumin, globulin and viral antigens to prepare hyperimmune ascitic fluid in mice.

The purpose of this paper is to present data showing that high titer antibody may be routinely produced in large volumes of mouse ascitic fluid when mice are injected intraperitoneally with snail antigens. Methodology is presented on how to obtain maximum yields of ascitic fluid using Sarcoma 180 cells coupled with Freund's complete adjuvant. Methods for determining the quality of the ascites are given. Antibodies (quality and quantity) in mouse ascitic fluid are compared with those in hyperimmune rabbit serum by comparing the antigen-antibody precipitating systems of 10 snail taxa with the homologous anti-*Semisulcospira libertina* systems. Specificity of antibodies in rabbit serum and ascitic fluid is analyzed and discussed. The pertinence of these findings relative to molluscan systematics and analyses of molluscan genetic systems is discussed.

MATERIALS AND METHODS

1. Source of Snails:

Eleven species of prosobranch snail were utilized in this study. These are listed systematically in Table 1.

Table 1

Systematic arrangement of snails utilized in this study together with the collection localities and date of lyophilization of foot-muscle extracts.

	Systematic arrangement	Locality where collected	Date of lyophilization
	ORDER ARCHAEOGASTROPODA		
S. Family	Neritacea		
Family	Neritidae		
1)	*Clithon retropictus* (v. Martens)	Japan, Honshu, Shizuoka Pref., Shimoda	19 December 1968
	ORDER MESOGASTROPODA		
	Archaeotaenioglossa		
	Viviparidae		
2)	*Sinotaia histrica* (Gould)	Japan, Honshu, Saitama Pref., Yagyu	12 September 1968
	Rissoacea		
	Hydrobiidae		
3)	*Oncomelania hupensis nosophora* (Robson)	Japan, Honshu, Yamanashi Pref., Kofu Valley	25 April 1967
	Cerithiacea		
	Potamididae		
4)	*Batillaria multiformis* (Lischke)	Japan, Honshu, Kanagawa Pref., Manazuru	12 July 1969
	Cerithiidae		
5)	*Clypeomorus humilis* (Dunker)	Japan, Honshu, Kanagawa Pref., Manazuru	12 July 1969
	Pleuroceridae		
6)	*Semisulcospira libertina* (Gould)	Japan, Honshu, Shizuoka Pref., Shimoda	6, 9 June 1969 6, 15 August 1969
7)	*Semisulcospira niponica* (Smith)	Japan, Honshu, Shiga Pref., Lake Biwa	2 June 1969
	Thiaridae		
8)	*Brotia costula episcopalis* (Lea)	Malaysia, W. Malaysia, Selangor, Ulu Langat	31 March 1969
9)	*Stenomelania crenulata* (Deshayes)	India, Madras State, S. Arcot Dist., Coleron River	
10)	*Melanoides tuberculatus* (Müller)	Japan, Okinawa, Motobu-cho, East of Higashi	11 April 1968
11)	*Thiara scabra* (Müller)	Japan, Okinawa, Onna-Son, West of Atsuta	15 April 1968

2. Mice and Rabbits:

The strain of mouse used was 406 Inbred Swiss Albino. The animals were 18 to 23 g virgin female and/or male. Rabbits were 6 to 7 lb. virgin females of an albino strain (406 Inbred).

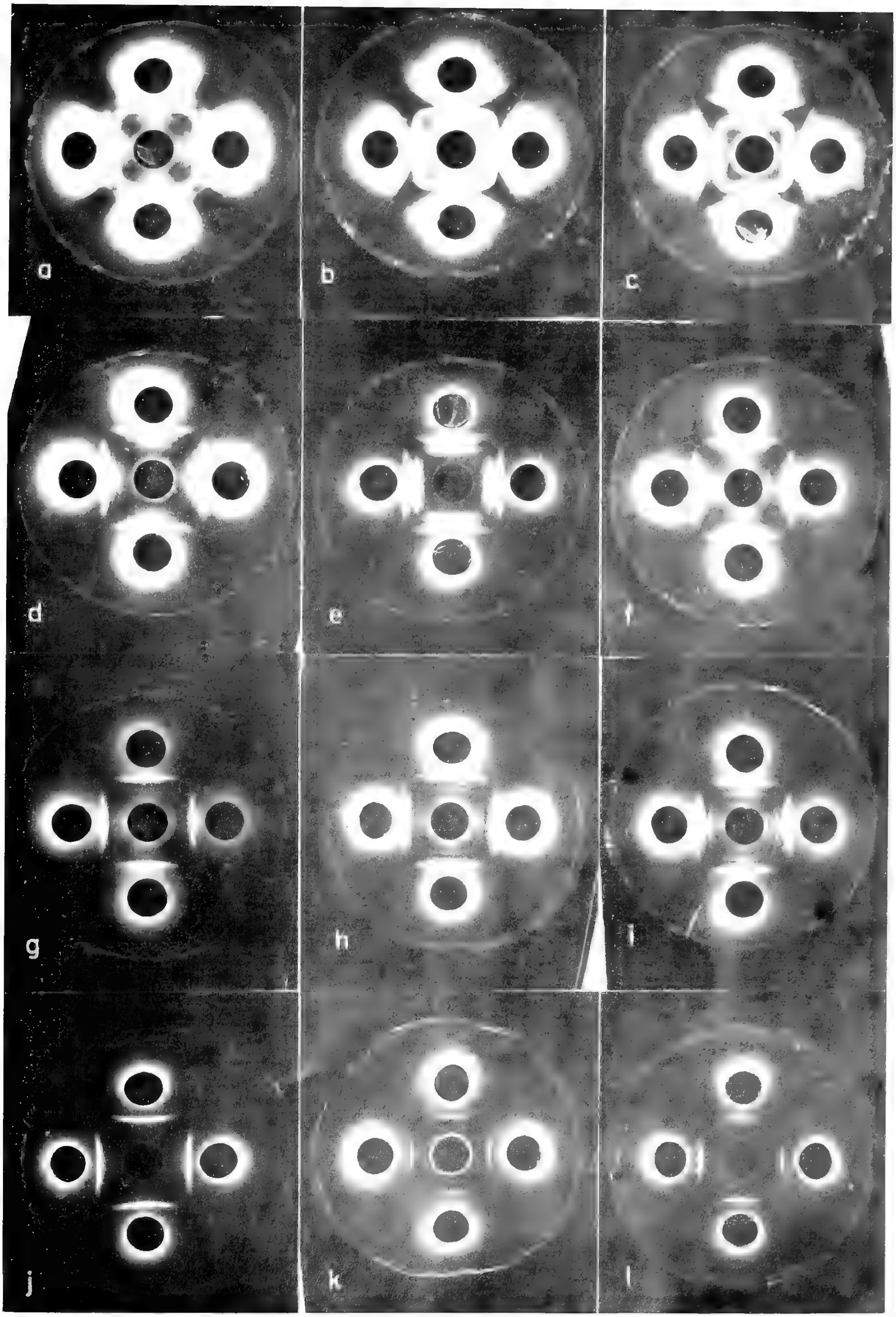
3. Preparation of Extracts:

Davis & Lindsay (1964) initiated the use of foot-muscle extracts for biochemical studies of Mollusca. Such extracts have subsequently been used by Davis (1967), Davis & Lindsay (1967), Davis (1968a,b, 1969), and Burch (1968) in electrophoretic or immunological studies, or both. Freshly cut foot muscle, trimmed of epidermis as well as pockets of dense green pigment (where these existed) was homogenized (300 mg blotted wet weight per 2.0 ml Carriker's 1946 saline) first by using a motor-driven tissue grinder with a teflon-tipped pestle. The homogenate was then transferred to a 5.0 ml micro cup and homogenized for 60 seconds at 50,000 rpm (Sorvall microhomogenizer).

Plate Explanation

Figure *1*.

Determination of the quality of immune ascitic fluid using micro-Ouchterlony double diffusion methods. a-e are "strong"; f-i are "medium," while j-n are "weak." The strength of reactions in a, b is much greater than reactions seen to date with rabbit sera with titers of 1:1024. Such "strong" ascitic fluid can be diluted 1:2 with saline (0.45%) to obtain optimal results in experiments.


a
b
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All operations were carried out at 2–5°C maintained by use of ice baths. The final homogenate was centrifuged at 3000 rpm (1500 × g) for five minutes and the supernatant was decanted; the sediment was centrifuged again at 4000 rpm (2600 × g) for five minutes. The supernatants were combined.

Protein contents of pooled extracts were initially determined using the Biuret reaction (*fide* Kabat & Mayer, 1961). The standard curve was made using crystalline bovine albumin (clinical pathology standard). Subsequently, the Folin-reagent test was used (Daughaday *et al.*, 1952) and a standard protein solution of crystalline bovine albumin was used with each test. The latter procedure proved more desirable as only 0.1 ml extract was needed contrasted with 1.0 ml for the former test. A Bausch and Lomb Spectronic 20 spectro-photometer was used.

Extracts were used immediately, or lyophilized in 1.0 ml units and stored until used (–20°C). Lyophilized extracts were reconstituted with distilled water.

4. Immunological Procedures:

A. Production of Antiserum—Antisera were produced in rabbits against antigens in freshly prepared or lyophilized extracts from *Semisulcospira libertina.* Control sera were obtained prior to intravenous (ear route) injections of extracts following the schedule given in Table 2. Bleeding from the ear (modified method of Nace & Spradlin, 1962) was conducted on two consecutive days starting on the third or fourth day after the last injection of extract. After the first bleeding each rabbit was injected with 25 ml physiological saline. Bleeding on the second day was initially by ear, then by heart puncture. After clotting and centrifugation, sera from all bleedings for one rabbit were pooled. Titers were determined by interfacial ring test and a twofold dilution series of antigen where a volume of antigen equal to that of antiserum was layered over the latter in a glass capillary tube (1.85 × 72.5 mm). The tubes were maintained at 23° ± 2°C and examined for the precipitin band at 30 and 60 minutes. The antisera used were "excellent" as defined by Davis (1968b, 1969). Sera were, for the majority, frozen and stored at –20°C until used.

B. Production of Ascitic Fluid—Injection and ascites collection schedules for mice are presented in tabular form (Tables 3–16) for each of eight experiments conducted for the purpose of establishing the best method of producing large volumes of mouse ascitic fluid with high titer antibody. The experiments show the effects of different techniques and injection time schedules on the volume of ascites produced. Freund's complete adjuvant was used (Difco Laboratories, Detroit, Michigan) by mixing thoroughly with an equal volume of either extract or Cariker's saline. Sarcome 180 cells were used in Experiments 4 to 8 to induce ascites production. The cell line was obtained from the Department of Virology, 406 Medical Laboratory, and maintained by injecting several mice each week with 0.5 ml of a 10% suspension of cells obtained from the previous week's injected mice. In Experiments 5 through 8, 0.5 ml of a 10% suspension in phosphate buffered saline were injected intraperitoneally.

Table 2

Schedule for intravenous injection of five rabbits with freshly prepared or lyophilized foot-muscle extract of *Semisulcospira libertina* and the quantity and titers of sera obtained.

	Fresh extract			Lyophilized extract	
Day	A	B	C	D	E
1	2 mg	2 mg	2 mg	2 mg	2 mg
2	2	2	2	2	2
3	2	2	2	2	2
4	2	2	2	2	2
5	2	2	2	2	2
6	2	2	2	2	2
7	—	—	—	2	2
Rest	3 weeks	3 weeks	3 weeks	3 weeks	3 weeks
1	2 mg	2 mg	2 mg	2 mg	2 mg
2	2	2	2	2	2
3	2	2	2	2	2
4	2	2	2	2	2
5	2	2	2	2	2
6	2	2	2	2	2
7	—	—	—	2	2
Total injected	24 mg	24 mg	24 mg	28 mg	28 mg
10[2]	b[1]	b	b	—	—
11[2]	b	b	b	b	b
12[2]	—	—	—	b	b
Volume serum obtained	90 ml	100 ml	90 ml	90 ml	80 ml
Titer:					
30 min	1/512	1/512	1/512	1/256	1/256
60 min	⋝1/1024	⋝1/1024	⋝1/1024	1/512	1/512

[1] Bleed

[2] Pool sera from two days bleeding

Mice were "tapped" (paracentesis of the literature) with an 18 gauge needle whenever the mice appeared swollen. The volume per mouse per tap (one t-unit) was recorded. The ascitic fluid was allowed to clot at room temperature for 30 minutes and under refrigeration for an additional 30 to 60 minutes. Each "t-unit" was centrifuged at 4000 rpm (2600 × g) for 10 minutes. It was evident after the fifth experiment that this procedure was not satisfactory as clotting was not complete as evidenced by further clotting after several days when the ascitic fluid was unfrozen from –20°C storage. In Experiments 7 and 8 (also used, in part, in Experiment 6 as discussed below), freshly drawn rabbit blood was added to each "t-unit" (one part rabbit blood to two parts ascitic fluid). The resulting clot cleared the ascites of all clotting elements. The dilution with rabbit blood (serum) did not seem to alter the strength or number of precipitating antigen-antibody systems.

Poor results, using the interfacial ring test to determine titer, caused us to abandon this technique for ascitic fluid. Subsequently, the worth of each "t-unit" for immunological studies was determined by micro-Ouchterlony double diffusion plates (five-hole system discussed in Davis, 1968a, 1969). Each "t-unit" was characterized as strong, medium or weak depending on the number of precipitation systems clearly observed in the diffusion plates in the homologous reaction. In this system, "t-units" with three or more clearly discerned systems were considered strong, those with two clearly discerned systems with or without other poorly resolved systems were classed as medium while zero or one clearly discerned system with or without poorly resolved ones were classed as weak. Pools were made of the strong and medium "t-units" but the weak units were discarded. In Experiment 6, the "strong" "t-units" were pooled and then divided into two groups only one of which received whole rabbit blood (R). Immunoelectrophoretic experiments were conducted using these "R" and "No-R" "strong" ascites pools to discern if different results would be obtained.

C. Immunoelectrophoresis—The procedures used were those given in detail by Davis (1968b, 1969). Over 50 immunoelectrophoretic experiments were conducted using more than 600 slides. The extracts were adjusted to a protein concentration of 6 mg/ml. All taxa of snails were compared with the homologous precipitin systems of *Semisulcospira libertina.* Immunoelectrophoretic experiments, where the homologous reactions were not as clear as the established patterns for a given serum, were discarded and those experiments were repeated. In this series of comparisons no studies with absorbed sera were conducted. Results were recorded in terms of the number of precipitin systems in the homologous reactions, number of systems in the heterologous reactions and number of systems "unique" to the homologous systems. In addi-

Plate Explanation

Figure 2.

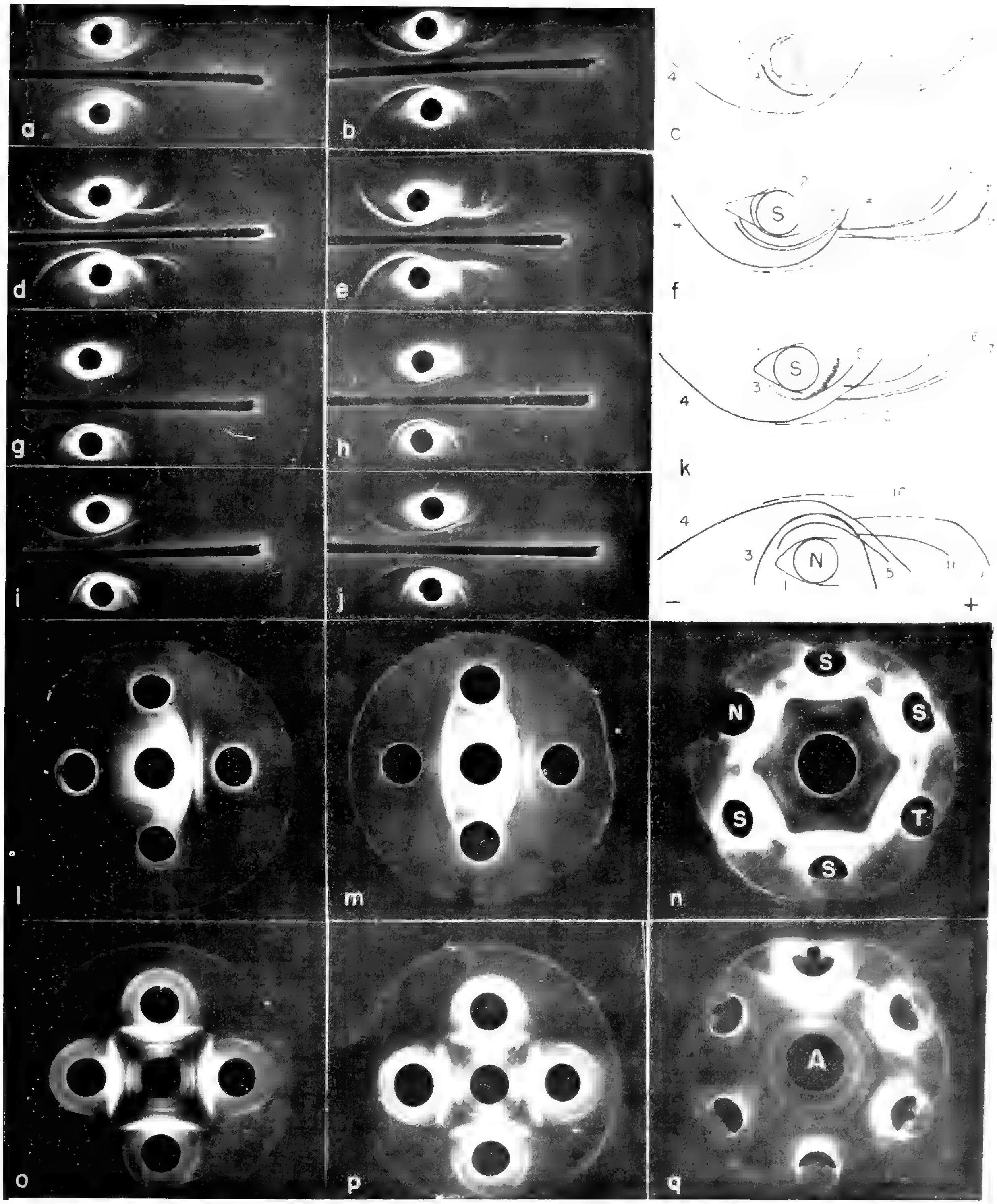
Immunoelectrophoretic and micro-Ouchterlony double diffusion results with immune ascitic fluid and rabbit antisera.

a-k Results of concentrating immune ascitic fluid. The antigens in both wells in a to f are from *Semisulcospira libertina.* In g to k the upper well contained antigen from *S. libertina* (S) while the lower well contained antigen from *S. niponica* (N). a) "Medium" ascitic fluid from Experiment 8, unconcentrated (41 mg/ml protein). b) Ascitic fluid in "a" concentrated by vacuum dialysis (53 mg/ml). c) Diagrammatic presentation of precipitin systems in "a" and "b"; bands 1, 2 are artifacts found in using the control sera. All bands are strengthened by the concentration, and bands 5 and 7 were made observable. d) "Strong" ascitic fluid from Experiment 8, unconcentrated (52 mg/ml). e) The same (d) concentrated by vacuum dialysis (79 mg/ml). f) The diagrammatic presentation is given for reactions in "d" and "e." Band 4 is notably strengthened by concentration. Bands 3 and 5 are too dense, causing lack of clarity of the systems. Bands 6 and 8 are made evident by the concentration. g) Unconcentrated "medium" immune ascitic fluid from one mouse in Experiment 5. h) Fluid in "g" lyophilized and reconstituted to original volume with distilled water. i) Vacuum dialysis of fluid in "g" to half the original volume. j) Fluid in "g" lyophilized and reconstituted to half the original volume with distilled water. k) diagrammatic presentation of reactions g, h, i, j. Concentration resulted in bands 6, 7 and 11 becoming clearly discerned and making band 10 observable. There were no differences in the results between different methods for concentrating the ascitic fluid. Note that band 3 is clearly delineated in the heterologous reaction while blurred in the homologous reaction.

l-n Results of initial experiments with mouse ascitic fluid containing antibodies in micro-Ouchterlony double diffusion systems. l) Antigens in center well, ascitic fluid (from Experiment 1) full strength in right well, other wells filled with control ascitic fluids from three different mice. m) Center well with antigens (6 mg/ml-protein); right well, ascites (from Experiment 1) half strength; left well, ascites quarter strength; upper and lower wells, rabbit antisera full strength. There were five bands in common and one very pronounced band unique to the ascites systems. n) Center well with ascites (from Experiment 1) half strength. Outer wells with antigens (6 mg/ml-protein). S, *S. libertina* antigens; T. *S. trachea* antigens (*S. trachea* is a synonym of *S. libertina;* see Davis, 1968b); N, *S. niponica* antigens. The ascitic fluid is "strong" and yielded seven precipitin systems. No qualitative differences between antigens were noted.

o-q Micro-Ouchterlony double diffusion system with three different rabbit antisera with interfacial ring test titers of 1:1024. In q, there was a serial dilution of antigens (twofold) with a protein concentration of 6 mg/ml in the upper well. Seven precipitin systems resulted. A = antiserum.

[DAVIS & SUZUKI] Figure 2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tion to using five different rabbit sera, eight pools of ascitic fluid from Experiments 5 through 8 (Tables 11–16) were employed.

D. Concentration of Ascites Fluid—Vacuum dialysis (described handily by Clausen, 1969) was used to concentrate "medium" pools of Experiment 5 using S&S Collodion Bags No. 100 (Schleicher & Schuill, Inc., Keene, N.H., U.S.A.) which retain proteins $\geqq$ 70,000 mol wt. Dialysis was against physiological saline. The capacity of the bags is 8 ml and the ascites was concentrated to approximately half volume. For comparison with vacuum dialysis, sera were lyophilized and reconstituted with ½ volume of distilled water, reconstitution with original volume (control 1); or used unaltered (control 2). Results of concentrating the ascitic fluid were checked by immunoelectrophoresis.

RESULTS

1. The relative quality of immune ascitic fluid.

It was found that the interfacial ring test did not give an adequate indication of titer relative to the excellent results with this test using rabbit sera. Low titers of 1:32 and 1:64 were obtained although the strength of precipitating systems in gel diffusion indicated a strength comparable to 1:512 or 1:1024 using rabbit antisera. As a result, the quality of the immune ascitic fluid was determined by assessing the number and strength of antigen-antibody precipitating systems in five-well micro-Ouchterlony double diffusion plates. As shown in Figure *1*, a to e are the result of using "strong" ascitic fluid and compare favorably with results using rabbit sera with titers $\geqq$ 1:512 (compare with Figure *2*, o-p; likewise compare Figure *2*, n with Figure *2*, o-q). Results with some "strong" ascitic fluids (Figure *1*, a-b) indicate quantities of antibody far in excess of that found in any rabbit serum to date; i.e., with titers greatly in excess of 1:1024. "Medium" ascites yielded results as shown in Figure *1*, f-i, while "weak" ascites yielded results comparable to those shown in Figure *1*, j-l.

2. Utility and methodology of concentrating hyperimmune fluid.

There was no observed difference in the immunoelectrophoretic results of concentrating hyperimmune ascitic fluid using vacuum dialysis, or lyophilization and reconstitution to half the original volume with distilled water. When these procedures were done using "medium" ascitic fluid (Figure *2*, g-k), bands 6, 7 and 11 became clearly discernible and band 10 appeared. With these concentrating techniques it was found that the heterologous reaction (involving *Semisulcospira niponica* extract) lacked band 7 (Figure *2*, k).

In another case (Figure *2*, a-c), concentration of "medium" ascitic fluid from Experiment 8 by vacuum dialysis increased the protein concentration from 41 mg per ml to 53 mg per ml with the result that all bands were strengthened and bands 5 and 7 became evident. When "strong" ascitic fluid from the same experiment was similarly concentrated (from 52 mg per ml to 79 mg per ml) bands 6 and 8 were made evident. However, bands 3 and 5 became too dense and thus lost clarity.

In subsequent immunoelectrophoretic experiments, ascites from Experiment 5 was concentrated by lyophilization and reconstitution with distilled water to one-half the original volume.

Table 3

Injection schedule for eight male mice in a pilot experiment to obtain high titer ascitic fluid. The antigen was from *Semisulcospira libertina*.

	Experimental group (4 mice)			Control group (4 mice)		
Day of injection	Material injected	mg Protein injected/ mouse	ml Fluid injected	Material injected	mg Protein injected/ mouse	ml Fluid injected
1	a + ad	1.1	1.0	s + ad	0	1.0
14	s + ad	0	0.5	s + ad	0	0.5
28	a + ad	1.1	0.6	s + ad	0	0.6

a = lyophilized antigen
ad = adjuvant
s = saline

3. Results of initial Experiments 1–5.

(Tables 3–12)

Experiments 1 through 5 represent progressive steps toward establishing procedures now routinely used to produce large volumes of high quality precipitating immune ascitic fluid. As a result of Experiment 1, it was evident that high titer ascitic fluid could be obtained. As shown in Figure *2*, l-n, five to seven strong precipitin systems resulted in the homologous reaction even when the ascitic fluid was cut to half concentration. Compare the strength of reaction in Figure *2*, n with that in Figure *2*, q, where rabbit serum (Table 2, with a titer $\geqq$ 1:1024 at 60 min.) was tested for precipitating properties (antigen full concentration at top well).

Table 4

Record on the volume of ascitic fluid produced in the pilot experiment outlined in Table 3.

Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
		Experimental group		
42	3	1	1.5	1.5
52	3	1	10.0	10.0

Total ml produced—11.5
% of mice producing—33
Accumulative production per producing mouse (average)—11.5

Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
		Control group		
42	4	4	26.5	6.6
52	4	0	0	0

Total ml produced—26.5
% of mice producing—100
Accumulative production per producing mouse (average)—6.6

In Experiment 2 (Tables 5, 6) particulate antigens were injected on days 1 and 15. The result was poor production of ascitic fluid with only 7 ml maximum accumulative production per producing mouse (maximum in the experimental group) which ended on the 35th day after the first injection. After three weeks many mice became

Table 5

Experiment 2. Injection schedule for 20 male and 19 female mice of the experimental group and 10 each of males and females of the control group. The freshly prepared antigen was from *Oncomelania hupensis nosophora.*

	Experimental group			Control group		
Day of injection	Material injected	mg Protein injected/ mouse	ml Fluid injected	Material injected	mg Protein injected/ mouse	ml Fluid injected
1	wa + ad	3.8	2.0	s + ad	0	2.0
15	wa + ad	3.8	2.0	s + ad	0	2.0

wa = fresh whole foot extract (uncentrifuged, antigen)
ad = adjuvant
s = saline

Table 6

Record of volume of ascitic fluid produced in Experiment 2.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Experimental group				
28	18	7	33	4.7	19	5	15	3.0
35	15	9	19	2.1	11	2	1	0.5

Total ml produced—52 (♀) 16 (♂)
% of original 19 mice producing (maximum)—47.4 (♀) 25.0 (of 20 original ♂)
Accumulative production (ml) per producing mouse—6.8 (♀) 3.5 (♂)

Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Control group				
28	10	6	37	6.2	10	5	22	4.4
35	6	4	26	6.5	8	2	7	3.5

Total ml produced—63 (♀) 29 (♂)
% of original 10 mice producing (maximum)—60 (♀) 50 (♂)
Accumulative production (ml) per producing mouse—12.7 (♀) 7.9 (♂)

Table 7

Experiment 3. Injection schedule for 15 males and females of the experimental group and five each of males and females of the control group. The antigen was from *Semisulcospira libertina.*

	Experimental group			Control group		
Day of injection	Material injected	mg Protein injected/ mouse	ml Fluid injected	Material injected	mg Protein injected/ mouse	ml Fluid injected
1	fa + ad	2.5	1.0	s + ad	0	1.0
15	fa + ad	2.5	1.0	s + ad	0	1.0
29	fa + ad	2.5	1.0	s + ad	0	1.0

fa = freshly prepared extract (antigen)
ad = adjuvant
s = saline

swollen as if producing ascites. However, palpation indicated that a hard mass had developed in the abdominal cavity. By day 35, several mice developed gross abdominal abscesses. Necropsy and histological examination indicated proliferating fibrous tissue along with a chronic inflammatory response of the liver, intestine and colon. The gross amount of fibrous tissue was correlated with little to no ascitic fluid production. As a result, work with particulate antigens was dropped.

Experiment 3 was similar to Experiment 1 in terms of schedule of injection. However, fresh antigen was used and antigen was injected on day 15. The total yield of ascitic fluid was very low in the experimental group and significantly higher in the control group. Production of ascites by experimental animals after day 43 was extremely poor. The ascitic fluid produced was "strong" (seven of eight experimental animals).

Experiment 4 was initiated to test Sarcoma 180 relative to producing a large volume of ascitic fluid (Table 9). The injection schedule was somewhat similar to that in Experiment 2. Lyophilized antigen was used. Sixty per-

Table 8

Record of the volume of ascitic fluid produced in Experiment 3.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Experimental group				
28	15	5	3.2	0.6	14	2	3.5	1.8
43	12	3	10.5	3.5	12	3	7.3	2.4
50	11	0	0	0	11	0	0	0
60	8	0	0	0	11	3	8.3	2.7

Total ml produced—13.7 (♀) 19.1 (♂)
% of original 15 mice producing (maximum)—33 (♀) 20.0 (♂)
Accumulative production (ml) per producing mouse—4.1 (♀) 6.9 (♂)

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Control group				
28	5	2	3.3	1.7	5	2	3.8	1.9
43	5	2	13.0	6.5	5	3	14.0	4.7
50	5	1	14.5	14.5	5	4	17.6	4.4
60	4	2	12.0	6.0	4	3	15.0	5.0

Total ml produced—42.8 (♀) 50.4 (♂)
% of original 5 mice producing (maximum)—40 (♀) 80 (♂)
Accumulative production (ml) per producing mouse—28.7 (♀) 16.0(♂)

cent of the mice produced ascites and a comparatively large volume was collected (58 ml and 120.5 ml from experimental females and males respectively) on the 22nd day after the first injection (Table 10). Of 23 mice producing enough ascites to test by micro-Ouchterlony diffusion procedures, only four produced weak bands, the others were precipitin system negative.

As a result of Experiment 4, the schedule of Experiment 1 (Table 3), which resulted in high quality ascitic fluid, was coupled with a Sarcoma 180 injection eight days after the last injection with antigen. As shown in Table 12, the results were highly satisfactory. Greater amounts of ascitic fluid would have been obtained if tapping had been continued beyond 42 days. As seen in Table 17, 63 percent of the ascites producing females and 60 percent of the males of Experiment 5 yielded usable hyperimmune fluid.

4. Females were superior producers.

Experiment 5 was repeated twice (Experiments 6, 7) to determine if, indeed, the inoculation schedule in Experiment 5 resulted in: 1) females producing more ascites than males, 2) production equal to or greater than 25 ml per producing mouse, 3) more females producing high titer ascites than males, 4) more than 40 percent of the ascites producing mice yielding "strong" or high quality immune precipitating fluid (see Table 17).

As seen in Figure 6, the accumulative average per initial mouse (i.e., ml per mouse in terms of number of mice at the beginning of each experiment) for the three experiments clearly shows that females produced twice the volume yielded by males (experimental and control groups). The difference in volume production by males and females is not due to increased mortality rates for males. After day 54, too few mice remained to give a reliable trend per time period.

The difference in volume produced by males and females is attributed to: 1) Fewer males produce ascites than females. The average number of mice producing ascites in each of the three experiments, considering all "tap" periods, was 9.4 for females and 6.6 for males (experimental groups) and 4.7 vs. 3.0 (control groups). 2) Of the producing mice, females actually did produce more. The accumulative production for producing mice summed up for the three experiments was 138.2 ml for females and 93.2 ml for males (experimental groups) and 129.4 ml vs. 79.1 ml (control groups).

As shown in Table 17, columns 6–8, there was little difference in the percent of mice producing strong and medium ascites. Females produced more "strong" ascites than males (58% vs. 43%). In only one experiment (No. 5) did mice produce ascites which, throughout several "taps," yielded fluid with no demonstrable precipitating antibodies; these involved only male mice.

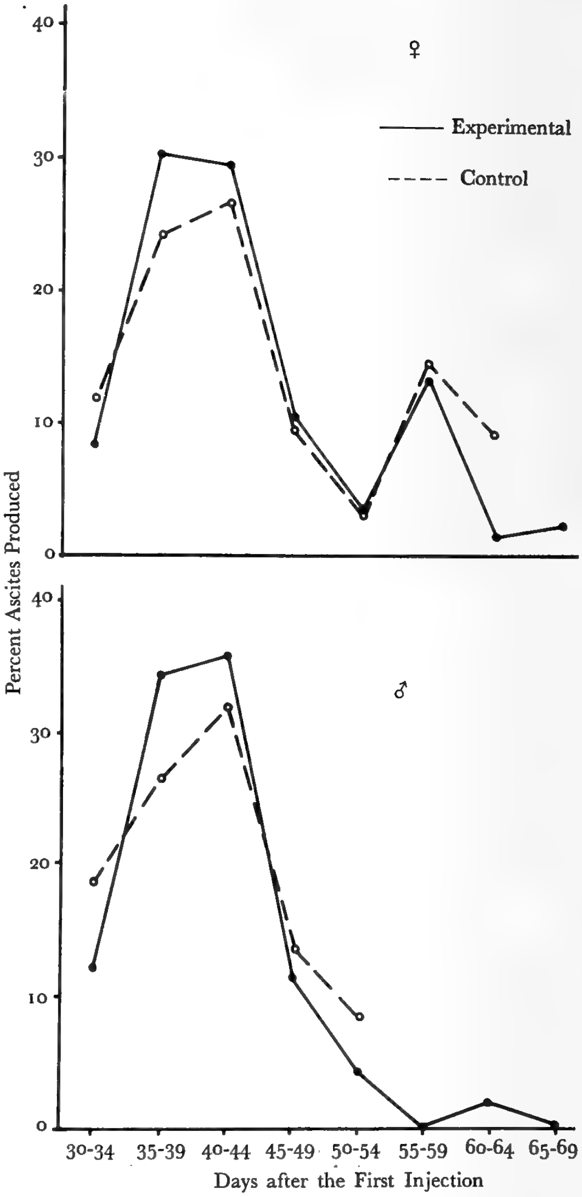


Figure 3

The percentage of ascites produced by mice per unit time following the first injection in Experiments 5 to 7.

5. Time frame for peak production of ascitic fluid, mouse mortality and relative quality of the ascites produced.

As shown in Figure 3, peak production occurred between 35 and 44 days after the first injection when the schedule used in Experiments 5–7 was employed. This pattern was the same for experimental and control groups as well as the sexes. When the mortality of male and female mice was considered (Figure 4), it was seen that 50 percent mortality occurred about 50 days after the first injection. During the period of peak production there was 20 to 30 percent mortality.

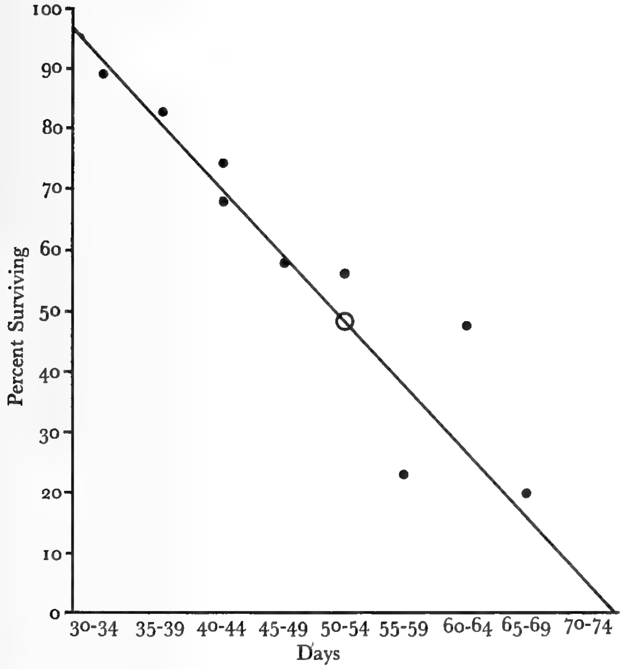


Figure 4

The average percent of experimental male and female mice surviving after the day of the first injection and when Sarcoma 180 was used in Experiments 5 to 7.

About 30 percent of the tap-units produced between days 30 and 34 had no demonstrable precipitating antibodies and an additional seven percent were weak and thus discarded (Figure 5). In the period of peak volume production (days 35 to 44), over 40 percent of the tap-units were "strong" while 21 to 22 percent were weak and had to be discarded.

6. Maximum performance of individual mice.

As shown in Table 18, the greatest volume of ascitic fluid produced by one mouse in one "tap" was 28 ml. The greatest accumulative volume yielded by one mouse was 78 ml. The beneficial effect of using Sarcoma 180 is immediately apparent as seen in the table.

7. The effect of Sarcoma 180 on ascites production; a definitive test.

The results of Experiments 5 to 7 showed that female mice produced more ascitic fluid than males. Experiment 8 was initiated to test the effect of Sarcoma 180 on the volume of ascitic fluid produced. As seen in Table 16, over twice the volume of ascitic fluid is produced in the experimental group when mice receive Sarcoma 180 compared with those not receiving the Sarcoma. In addition, the accumulative production per producing mouse is three times as great. Production using antigen (experimental) is greater than production without antigen (control) in terms of accumulative production per producing mouse. Results with control group C showed that the use of Sarcoma 180 alone, in one injection, resulted in an accumulative production nearly equal to that produced in control group A where mice received saline, adjuvant and Sarco-

Table 9

Experiment 4. Injection schedule for 20 male and female mice of the experimental group and five each of males and females of the control group. The antigen was from *Semisulcospira libertina* and Sarcoma 180 was used.

	Experimental group			Control group		
Day of injection	Material injected	mg Protein injected	ml Fluid injected	Material injected	mg Protein injected	ml Fluid injected
1	a + ad	2.0	0.7	s + ad	0	0.7
16	a + ad + sar	2.0 + sar	0.7	s + ad + sar	0 + sar	0.7

s = lyophilized antigen
ad = adjuvant
sar = Sarcoma 180
s = saline

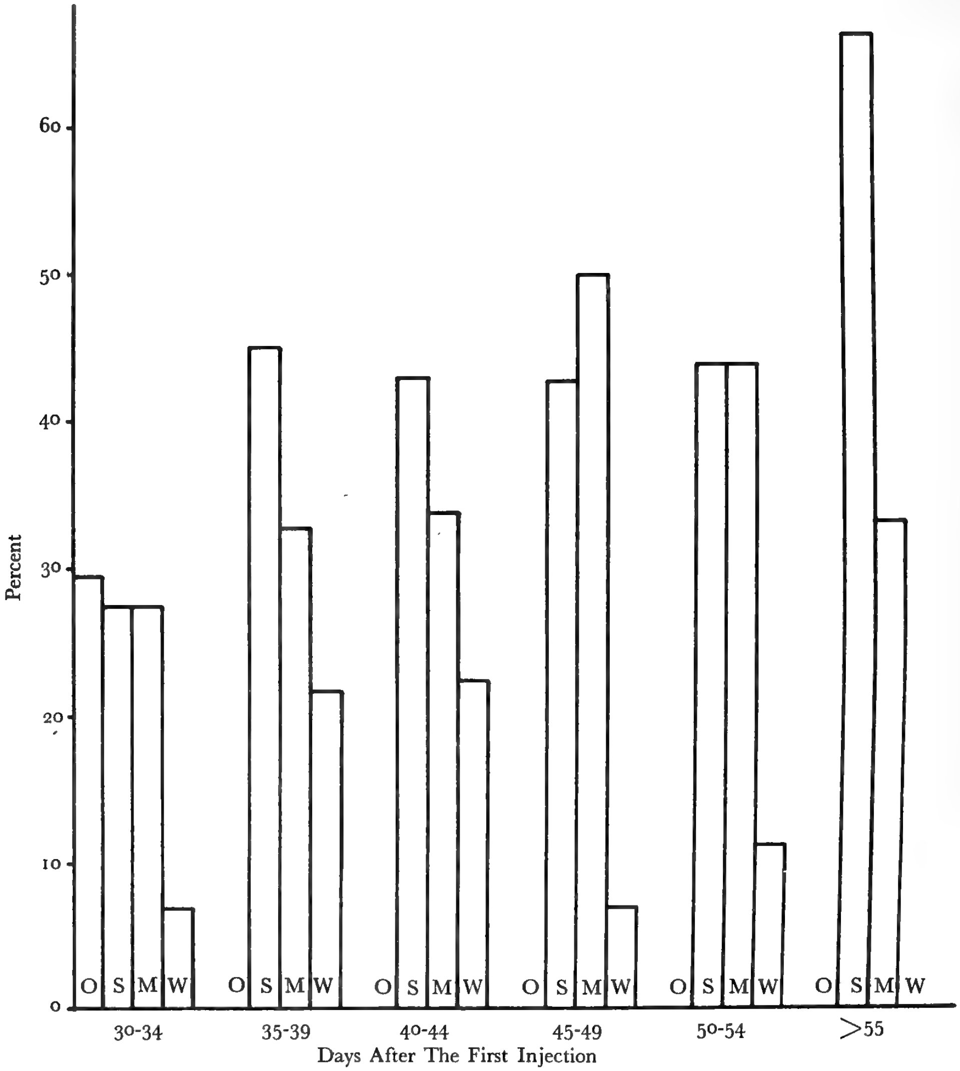


Figure 5

The percent of mice at each time period producing ascitic fluid which lacked demonstrable precipitating antibodies (o), or had strong (s), medium (m) or weak (w) precipitating antibodies. Males and females from Experiments 5 through 7 were used.

ma 180 in a four-shot series. This amount is about half the production when antigen is coupled with Sarcoma 180.

8. Comparing rabbit antisera and mouse ascitic fluid in terms of numbers of discernible precipitating antigen-antibody systems and specificity.

Five rabbit antisera and eight different pools of hyperimmune ascitic fluid are compared in Table 20 in terms of the average number of precipitin systems of the homologous reaction counted from stained slides after the immunoelectrophoretic experiments. It was evident that the same average number of antigen-antibody precipitin systems (arcs or bands) could be obtained using either rabbit or mouse hyperimmune sera (fluids). The greatest average number was 9.3 using rabbit serum and 9.2 using

Table 10

Record of the volume of ascitic fluid produced in Experiment 4, a pilot experiment using Sarcoma 180.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Experimental group				
22	14	10	58	5.8	14	15	120.5	8.0

% of original mice producing (maximum)—50 (♀) 75 (♂)

				Control group				
22	3	3	7.5	2.5	4	3	20.5	6.8

% of original mice producing (maximum)—60 (♀) 60(♂)

ascitic fluid. The greatest range (acceptable variation) for both was 7 (8) to 11 (12).

The crudest level of comparison between snail taxa was used to determine the minimum level of specificity of the 13 different hyperimmune sera (fluids). The number of bands in the heterologous reaction was subtracted from the number of bands of the homologous reactions. The remainder was converted to percentage of bands in the homologous reaction "unique" or remaining to the homologous reaction. Taxa were ranked by decreasing affinity to *Semisulcospira libertina* (i.e., decreasing number of pre-

Table 11

Experiments 5 to 7. Injection schedule for 20 male and female mice of the experimental group and 10 of each sex in the control group. The antigen was from *Semisulcospira libertina* and Sarcoma 180 was used.

	Experimental group			Control group		
Day of injection	Material injected	mg Protein injected	ml Fluid injected	Material injected	mg Protein injected	ml Fluid injected
1	a + ad	1.1[1]	0.5	s + ad	0	0.5
14	s + ad	0	0.5	s + ad	0	0.5
28	a + ad	1.1	0.5	s + ad	0	0.5
36[2]	sar	sar	0.5	sar	sar	0.5

a = lyophilized antigen
ad = adjuvant
s = saline
sar = Sarcoma 180

[1] 1.0 in Experiments 6 and 7, respectively

[2] Days 32 and 35 in Experiments 6 and 7, respectively

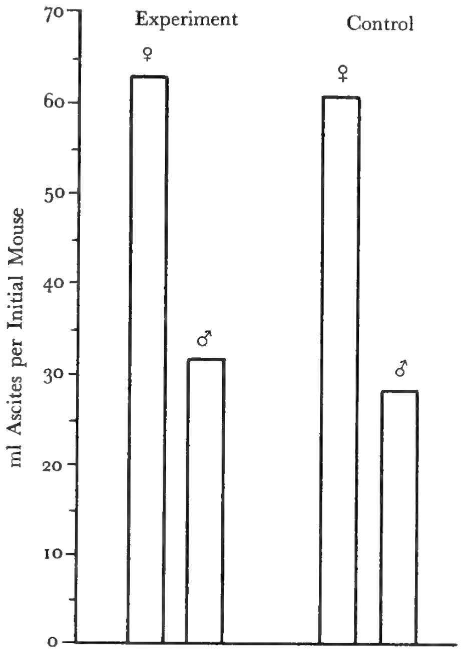


Figure 6

The sum of the average production of ascites produced per initial (= total volume divided by total number of mice initially injected) mouse in Experiments 5 through 7. Divide by three to obtain the average production per mouse per experiment.

Table 12

Record of the volume of ascitic fluid produced in Experiment 5, using Sarcoma 180.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Experimental group				
32	19	12	54	4.5	20	9	26	2.9
36	19	13	71	5.5	19	10	46	4.6
38	19	11	62	5.6	19	8	42	5.3
40	16	8	48	6.0	17	12	65	5.4
42	14	12	66	5.5	11	9	57	6.3

Total ml produced—301 (♀) 236 (♂)
% of original 20 mice producing (maximum)—65 (♀) 60 (♂)
Accumulative production (ml) per producing mouse—27.1 (♀) 24.5 (♂)

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
				Control group				
32	10	0	0	0	10	0	0	0
36	10	4	21	5.3	10	2	7	3.5
38	9	3	19	6.3	7	2	13	6.5
40	8	4	24	6.0	6	2	9	4.5
42	7	7	36	5.1	3	3	7	2.3

Total ml produced—100 (♀) 36 (♂)
% of original 10 mice producing (maximum)—70 (♀) 30 (♂)
Accumulative production (ml) per producing mouse—22.7 (♀) 16.8 (♂)

cipitin bands relative to the number in the homologous reaction). As seen in Table 19, there is fairly good agreement between results using rabbit antisera and hyperimmune ascitic fluid in ranking taxa on the average percent of precipitin systems "unique" to the homologous reactions. There was a slight amount of difference in ranking *Batillaria multiformis* (37%), *Melanoides tuberculatus* (37%) and *Thiara scabra* (34%) under results with ascitic fluid relative to results with rabbit sera. As one would suspect, the taxon having closest affinity to *Semisulcospira libertina* is another species of the same genus, *S. niponica.*

An accumulative percent index was constructed by adding up the percentages in each column (i.e., for each serum or fluid) representing those bands "unique" to the homologous reaction in the analysis of each snail taxon. The greatest value represents, in a relative comparative manner, that serum or fluid which was most specific; i.e., yielded the greatest number of antigen-antibody systems "unique" to the homologous reaction. The sera (fluids) are ranked in Table 20 (columns 2-3) in terms of specificity thus determined. As seen in Table 20, the three most specific hyperimmune fluids were from ascitic fluid pools 6s-r, 8m, 7m (accumulative percent indices of 592, 564, 560 respectively, as seen in Table 19). It is thus evident that the greatest specificity of reaction was obtained using hyperimmune mouse ascitic fluid. It is noteworthy that only in cases involving ascitic fluid were differences between *S. libertina* and *S. niponica* detected. Ascitic fluid led rabbit sera on overall average (493 vs. 470, Table 19, columns 7 and 16) in terms of specificity as determined by the accumulative percent index.

Prints of immunoelectrophoretic results are given in Figures 7 and *8*. These are representative of 130 sets of reactions involving more than 600 slides. The prints are ar-

Table 13

Record of the volume of ascitic fluid produced in Experiment 6, using Sarcoma 180.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
Experimental group								
34	19	19	232	12.2	14	11	91	8.3
37	16	14	134	9.6	13	9	71	7.9
40	16	11	107	9.7	12	7	44	6.3
44	10	8	127	15.9	8	1	6	6.0
56	7	2	35	17.5	2	0	0	0
Total ml produced—635 (♀) 212 (♂) % of original 20 mice producing (maximum)—95 (♀) 55 (♂) Accumulative production (ml) per producing mouse—64.9 (♀) 28.5 (♂)								
Control group								
34	10	10	79	7.9	7	5	34	6.8
37	10	7	49	7.0	7	5	30	6.0
40	10	9	64	7.1	7	6	32	5.3
44	6	5	35	7.0	6	5	23	4.0
56	3	2	25	12.5	1	0	0	0

Total ml produced—252 (♀) 119 (♂)
% of original 10 mice producing (maximum)—100 (♀) 50 (♂)
Accumulative production (ml) per producing mouse—41.5 (♀) 22.1 (♂)

ranged to represent a series ranging from greatest genetic affinity to *Semisulcospira* to least affinity. The results in Tables 19 and 20 were obtained from an analysis of all of these slides.

DISCUSSION

Wagner & Rasanen (1967) prepared precipitating immune ascites to a variety of vertebrate antigens and obtained excellent results in immunoelectrophoretic experiments. They stated that 10 mice were roughly equal to one rabbit in terms of producing hyperimmune serum. They found that precipitate bands obtained using mouse ascites corresponded favorably with those produced with corresponding immune rabbit sera. The results of this paper, using molluscan antigens, agree fairly well with these authors.

In this laboratory we have invested a minimum of 24 mg protein to immunize one rabbit. The process takes 39 days and the maximum yield was 100 to 125 ml serum. The same production can be obtained using eight to nine female mice and investing 16 to 18 mg protein. This is based on the fact that the average production throughout an experiment, in terms of the initial number of female mice injected, was 19.3 ml (and thus mortality has been accounted for) and over 75 percent of the fluid produced would be strong or medium quality and thus useful. As Wagner and Rasanen pointed out, "for total failure in immunization, up to ten [8–9] individual mice, in lieu of one rabbit, have to be lost . . ."

The use of whole rabbit blood to help clot the freshly drawn ascitic fluid makes up for the volume of ascites lost due to clotting and, in fact, increases the final volume of fluid. The rabbit serum does not affect the results as determined by the number and density of precipitate arcs

Table 14

Record of the volume of ascitic fluid produced in Experiment 7, using Sarcoma 180.

	Females				Males			
Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
Experimental group								
35	17	9	103	11.4	19	2	16	8.0
38	14	4	28	7.0	18	6	37	6.2
43	13	9	91	10.1	18	7	61	8.7
49	12	8	61	7.6	16	6	62	10.3
52	9	4	30	7.5	14	4	16	4.0
60	6	3	11	3.6	13	2	4	2.0
Total ml produced—324 (♀) 196 (♂) % of original mice producing (maximum)—45 (♀) 35 (♂) Accumulative production (ml) per producing mouse—47.2 (♀) 39.2 (♂)								
Control group								
35	10	4	50	12.5	10	1	8	8.0
38	10	4	37	9.3	10	1	5	5.0
43	10	5	70	14.0	9	6	55	9.2
49	9	5	40	8.0	8	5	55	11.0
52	8	4	22	5.5	4	1	7	7.0
60	7	2	32	16.0	4	0	0	0

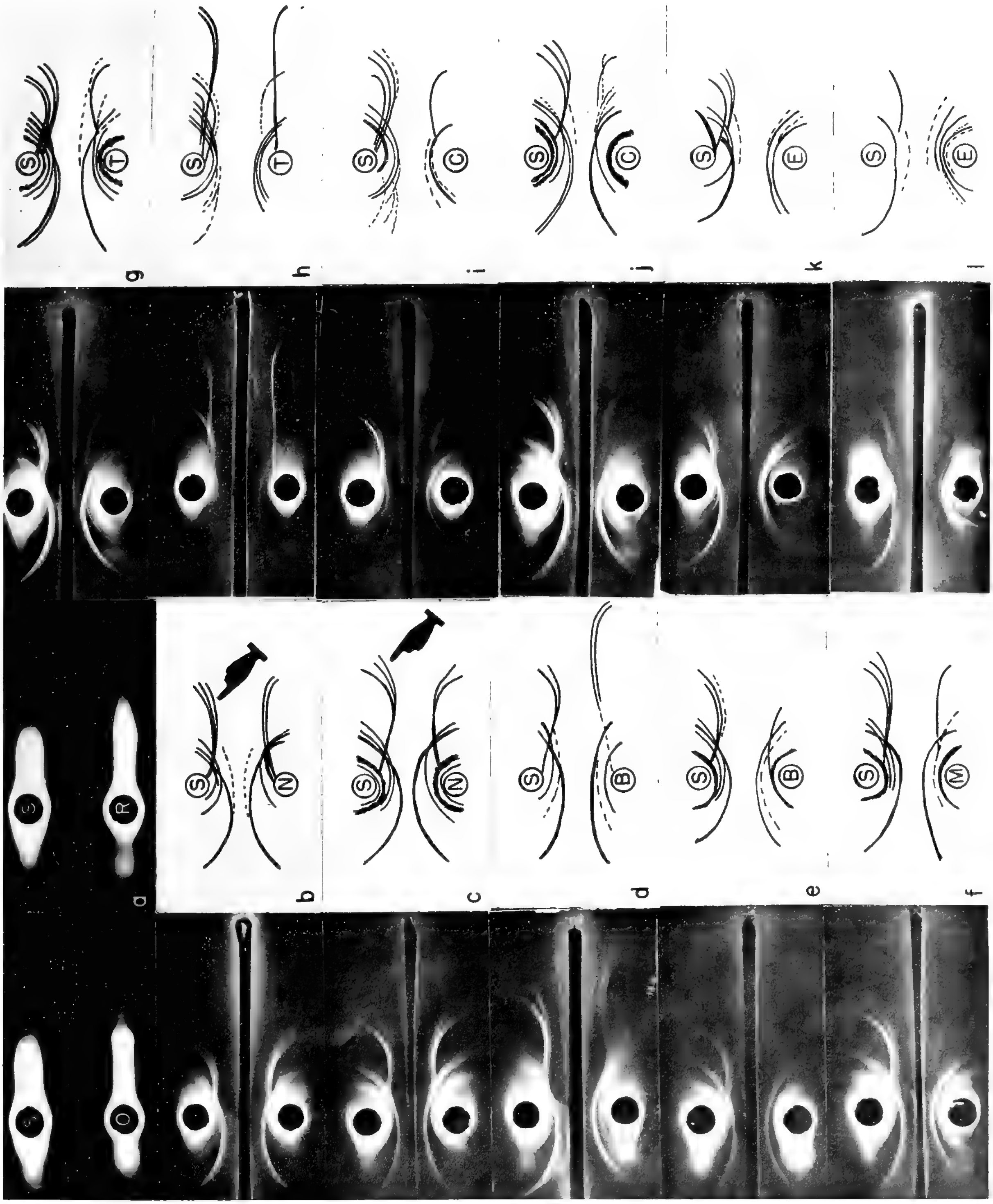
Total ml produced—251 (♀) 130 (♂)
% of original 10 mice producing (maximum)—50 (♀) 60 (♂)
Accumulative production (ml) per producing mouse—65.3 (♀) 40.2 (♂)

Plate Explanation

Figures *7*, *8*.

Representative prints of the immunoelectrophoretic results chosen from 130 sets of reactions involving 11 taxa of snails and 13 different sera (or ascites). The prints are arranged to represent a series ranging from greatest genetic affinity to *Semisulcospira* (Figure *1*, b-c) to least affinity (Figure *2*, j-l). The drawn patterns are presented because photographic reproduction of the precipitin systems is often not adequate to make faint precipitin systems visible in print. From Figure *2*, d one can see two bands at the well of the homologous reaction(s) when control ascitic fluid was used. These two bands are artifacts and were not considered in the analysis of the slides. Depending on the experiment there were zero to three such bands. Results in Figure 7a show the migration pattern of the protein in the electric currents at 60 minutes. The greatest bulk of the protein traveled eight to 12 mm from the anodal edge of the well while some protein traveled 18 to 20 mm from the edge of the well (anodally). Hyperimmune fluid was used as follows: Figure 7b, 6s-nr; *7*c, 6s-r; *7*d, 6s-nr; *7*e, 6s-r; *7*f, 6s-r; *7*g, 6s-r; *7*h, D; *7*i, B; *7*j, 6s-r; *7*k, 6s-r; *7*l, 5c; Figure *8*a, 7m; *8*b, 6s-r; *8*c, C; *8*d, 6-cont; *8*e, 7s; *8*f, 6s-r; *8*g, 6s-r; *8*h, 8m; *8*i, C; *8*j, A; *8*k, 6m; *8*l, 6s-r.

The pointers in Figure 7b and 7c indicate the one precipitin system unique to the homologous reaction, thus indicating a difference between *Semisulcospira libertina* and *S. niponica*. B, *Batillaria multiformis*; C, *Stenomelania crenulata*; E, *Brotia costula episcopalis*; H, *Clypeomorus humilis*; I, *Sinotaia histrica*; M, *Melanoides tuberculatus;* N, *Semisulcospira niponica;* O, *Oncomelania hupensis nosophora*; R, *Clithon retropictus*; S, *Semisulcospira libertina;* T, *Thiara scabra.*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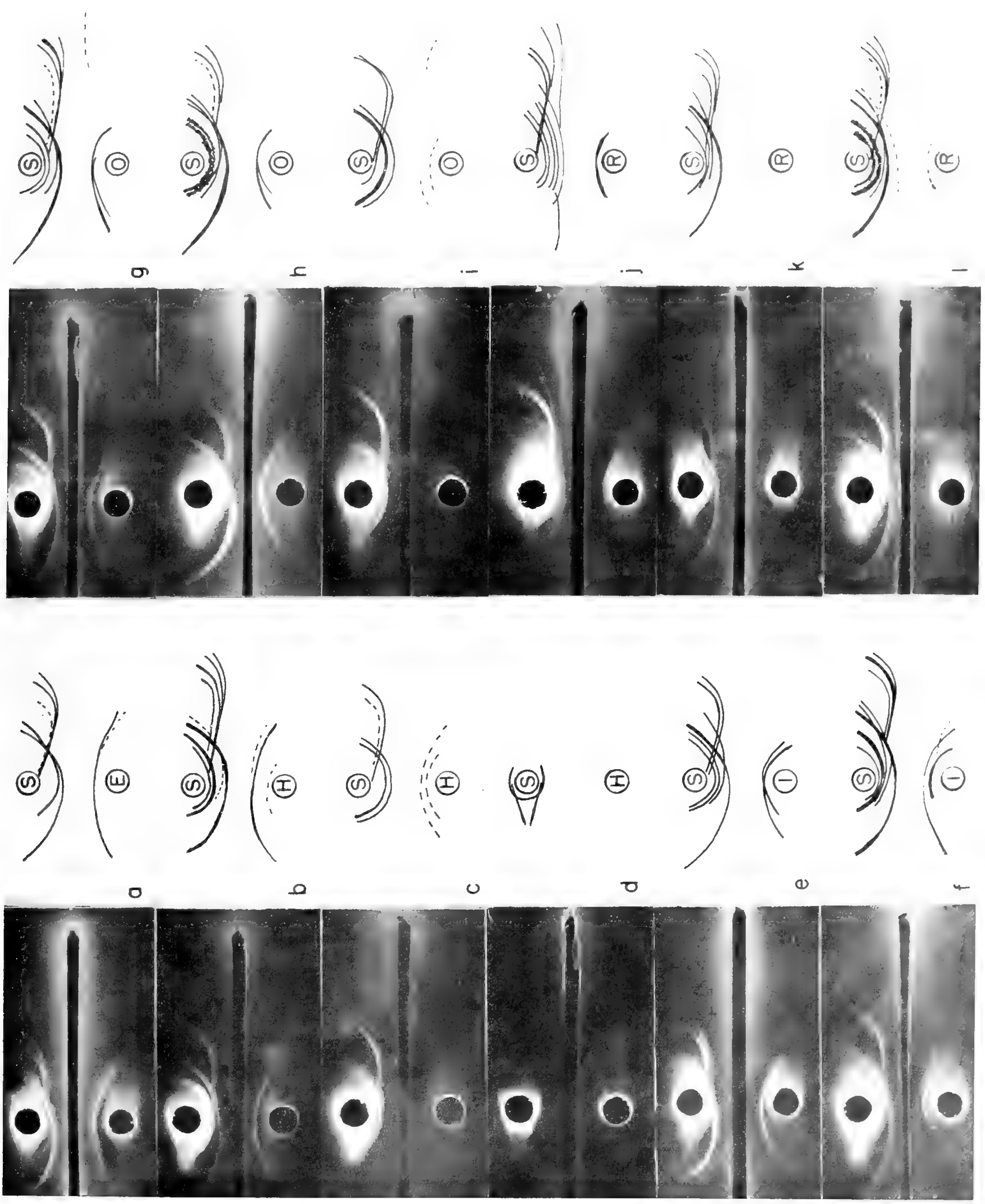
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Table 16

Record of the volume of ascitic fluid produced in Experiment 8.

Day tapped	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse	No. mice living	No. mice producing	ml Ascites collected	Average production per producing mouse
		Experimental group A (with Sarcoma)				Experimental group B (without Sarcoma)		
35	16	7	70	10.0	14	10	71	7.1
39	14	9	86	9.6	13	11	42	3.8
44	13	11	113	10.3	12	6	17	2.8
46	9	3	3	6.0	12	0	0	0
49	9	7	49	7.0	12	7	12	1.7
57	5	4	34	8.5	11	4	10	2.5
66	4	3	14	4.7	9	0	0	0

Total ml produced—384 (A) 152 (B)
% of original 25 mice producing—44 (A) 44 (B)
Accumulative production (ml) per producing mouse—56.1 (A) 17.9 (B)

		Control group A (with Sarcoma)				Control group B (without Sarcoma)		
35	9	3	22	7.3	7	1	4	4.0
39	9	8	49	6.1	7	3	4	1.3
44	9	7	47	6.7	6	2	5	2.5
46	6	0	0	0	6	0	0	0
49	6	5	42	8.4	6	1	3	3.0
57	5	2	25	12.5	6	1	4	4.0
66	4	0	0	—	—	—	—	—

Total ml produced—185 (A) 20 (B)
% of original 10 mice producing (maximum)—80 (A) 30 (B)
Accumulative production (ml) per producing mouse—41.0 (A) 14.8 (B)

		Control group C (only Sarcoma)		
44	9	7	40	5.7
46	9	2	11	5.5
49	9	7	48	6.9
57	8	4	22	5.5
66	7	4	35	8.8

Total ml produced—156
% of original 10 mice producing (maximum)—90
Accumulative production (ml) per producing mouse—32.4

Table 15

Experiment 8. Injection schedule for 25 female mice in each of two experimental groups, only one of which was given Sarcoma 180. There were three control groups of 10 females each. The antigen was from *Semisulcospira libertina*.

Day of injection	Material injected	mg Protein injected	ml Fluid injected	Material injected	mg Protein injected	ml Fluid injected
	Experimental group A			Experimental group B		
1	a + ad	1.2	0.5	a + ad	1.2	0.5
14	s + ad	0	0.5	s + ad	0	0.5
28	a + ad	1.2	0.5	a + ad	1.2	0.5
35	sar	sar	0.5	—	—	—
	Control group A[1]			Control group B		
1	s + ad	0	0.5	s + ad	0	0.5
14	s + ad	0	0.5	s + ad	0	0.5
28	s + ad	0	0.5	s + ad	0	0.5
35	sar	sar	0.5	—	—	—

a = lyophilized antigen
ad = adjuvant
s = saline
sar = Sarcoma 180

[1] Control group C received only Sarcoma 180, 0.5 ml, on day 35

Table 18

Production of ascitic fluid by individual mice in experiments with *Semisulcospira libertina* foot-muscle antigen.

Experiment No.	Experimental: Greatest volume (ml) for one mouse at one tap	Experimental: Greatest total volume (ml) for one mouse	Control: Greatest volume (ml) for one mouse at one tap	Control: Greatest total volume (ml) for one mouse
		No Sarcoma 180 used		
1	10.0 (♂)	11.5 (♂)	8.0 (♂)	8.0 (♂)
3	6.5 (♀)	6.5 (♀)	11.0 (♀)	36.0 (♂)
8	7.4 (♀)	17.0 (♀)	4.0 (♀)	14.7 (♀)
		With Sarcoma 180		
4	15.0 (♀)	15.0 (♀)	8.5 (♀)	8.5 (♀)
5	10.0 (♀)	31.0 (♀)	9.0 (♀)	17.0 (♀)
6	28.0 (♀)	78.0 (♀)	23.0 (♀)	60.0 (♀)
7	20.0 (♀)	50.0 (♀)	25.0 (♀)	55.0 (♀)
8	17.0 (♀)	69.0 (♀)	20.0 (♀)	64.0 (♀)

Table 17

The percentage of mice producing ascitic fluid of varying quality in Experiments 5 through 8.

Experiment No.	No. mice at start	No. dead before producing ascites	% Not producing of those living at least two "tap" periods	% Producing ascites with no precipitin systems	% Mice producing ascites of quality: S	M	W
5 (♀)	20	1	21.1	0	42.1	21.1	15.7
6 (♀)	20	1	0	0	94.7	5.3	0
7 (♀)	20	3	11.8	0	47.0	17.6	23.5
8 (♀)	25	10	6.7	0	46.7	20.0	26.7
		Av. 3.8	Av. 9.9	Av. 0	Av. 57.6	16.0	16.5
5 (♂)	20	0	0	10	35.0	25.0	30.0
6 (♂)	20	6	14.3	0	71.4	7.1	7.1
7 (♂)	20	1	31.6	0	21.1	31.6	15.8
		Av. 2.3	Av. 15.3	Av. 3.3	Av. 42.5	21.2	17.6

S = strong M = medium W = weak

Table 19

The average percent of precipitin systems remaining after the number in the heterologous reactions were subtracted from the number of homologous reactions. Taxa are ranked by increasing percentages (decreased genetic affinity).

	Percent of precipitin systems unique to the homologous reactions														
	Rabbit sera pools						Ascitic fluid pools								
Taxa	D	E	A	B	C	Average	8s†	8m	7s	7m	6s-nr	6s-r	6m	5c	Average
Semisulcospira libertina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Semisulcospira niponica	0	0	0	0	0	0	0	0	13	0	13	30	0	0	7
Batillaria multiformis	25	25	11	29	38	26	29	60	39	40	38	43	40	13	37
Melanoides tuberculatus	29	25	0	50	60	33	25	60	43	50	0	60	17	40	37
Thiara scabra	44	38	22	38	29	34	38	60	13	40	13	40	20	50	34
Stenomelania crenulata	29	50	22	45	80	45	33	40	29	60	25	45	50	43	41
Brotia costula episcopalis	43	63	63	36	71	55	71	60	75	60	38	56	40	0	50
Clypeomorus humilis	44	50	75	67	67	61	67	67	38	50	63	78	86	60	64
Sinotaia histrica	57	75	67	73	60	66	67	60	57	60	67	75	67	80	67
Oncomelania hupensis nosophora	67	75	71	67	60	68	57	57	63	100	64	78	67	60	68
Clithon retropictus	57	88	90	92	83	82	88	100	86	100	75	87	86	80	88
Totals = accumulative % index	395	489	421	497	548	470	475	564	446	560	396	592	473	426	493

†Numbers indicate experiments from which fluids were obtained.

s = strong (excellent)
m = medium (good)
r = with rabbit serum
nr = with rabbit serum
c = concentrated by vacuum dialysis

of the homologous reaction. However, as shown in Table 19, ascites 6s-nr (no rabbit blood) was much less specific than the same fluid with rabbit blood added (6s-r), as determined by the accumulative percent index. The reason for this difference is not known.

Concentrating hyperimmune fluid is decidedly beneficial in accentuating weak precipitin arcs and thus is best used with "medium" strength ascitic fluid. It does not matter if concentration is accomplished by vacuum dialysis or lyophilization. Concentration by lyophilization is more convenient as the ascitic fluid is conveniently stored in a small area when lyophilized and numerous units of ascites can be lyophilized simultaneously.

Immune precipitating ascitic fluid has yielded up to 11 precipitin arcs in immunoelectrophoretic experiments and these have been obtained from 17 percent of the individual ascites producing efforts. In the case of rabbit sera, 11 to 12 precipitin systems have resulted from nine percent of the rabbits. About 25 percent of the rabbits have yielded poor sera. No rabbit serum tested to date has yielded strength of antibody (titer) equal to that routinely obtained from mouse ascitic fluid (greatly in excess of 1:1024). The ascitic fluid has greater specificity. It was determined that the use of Sarcoma 180 definitely causes an increase in volume of ascites produced and immunoelectrophoretic tests have shown that this procedure does not affect the quality of the ascitic fluid in terms of the production of precipitin systems relative to precipitin systems obtained using ascitic fluid where Sarcoma 180 was not used.

Specificity, as determined in this paper, is considered to be the minimal degree of specificity because no consideration was given to the amount of non-specific reactions or homology of precipitin arcs. Only the number of arcs and the difference in number between homologous and heterologous reactions was considered. It is obvious, from Figure 7, d, l, etc., that there was often an asymmetry between the homologous and heterologous reactions. Clarification of such asymmetry and homology depends upon absorption studies (general discussion, Kabat & Mayer, 1961; also, Davis, 1968b, 1969). Such absorption studies are beyond the scope of this paper, which is to provide data on the utility of mouse ascitic fluid in immunological studies involving molluscan antigens.

Table 20

Sera ranked according to the degree of specificity they exhibited as derived from the accumulative percent index of Table 19 and the average number of precipitin systems produced by each serum.

Source of sera	Specificity of sera as ranked 1–10	Serum (fluid)	Average no. precipitin systems	Range
Rabbit	4	C	6.0	4–8
	5	B	9.3	7–12
	6	E	7.1	7–8
	13	D	7.9	7–12
	11	A	8.7	6–11
Ascites	1	6s-r	9.2	7–11
	2	8m	5.5	5–7
	3	7m	4.8	4–6
	7	8s	6.9	6–8
	8	6m	6.2	5–9
	9	7s	7.4	7–8
	10	5c	5.3	5–7
	12	6s-nr	8.4	8–11

In ranking taxa in Table 19, it was evident that general results of genetic relatedness to *Semisulcospira libertina* based on fewer differences between the homologous and heterologous reactions were generally the same using rabbit sera and mouse ascitic fluid. The one area of disagreement in results between rabbit and mouse hyperimmune fluid involved the ranking of *Batillaria multiformis, Melanoides tuberculatus* and *Thiara scabra*, which have closely grouped average percent values as listed under ascitic fluid (Table 19). When the taxa are ranked according to average percent values using the three most specific immune precipitating fluids (Table 21), a different arrangement within the Cerithiacea occurs which is very slight relative to the reference pleurocerid species, *S. libertina*. In making such ranking, the necessity for using several different sera becomes obvious, as seen in the body of Table 19. In comparing Tables 1 and 19, it is seen that the immunological results compare favorably with classical systematic structure. 1) *Clithon* of the Archaeogastropoda is farthest removed from *Semisulcospira* of the Mesogastropoda. 2) Next, the Archaeotaenioglossa and Rissoacea are farther removed from *Semisulcospira* than are genera and families of the Cerithiacea of which *Semisulcospira* is a member. 3) The closest genetic relationship is between two species of the same genus; i.e., between *S. libertina* and *S. niponica*.

Within the Cerithiacea, representatives of four currently recognized families were studied. Two (Potamididae, Cerithiidae) are marine and two (Pleuroceridae, Thiaridae) are fresh water. Concerning the latter two, past literature has most commonly included them in the family "Melaniidae." Morrison (1954) considered the "family of melanians, in the broad sense, . . . [to be] a biological absurdity." He considered the snails grouped in the Melaniidae to consist of the families Pleuroceridae, Melanopsidae and Thiaridae which evolved from ancestors common to the marine families Cerithiidae, Modulidae and Planaxidae, respectively. This is further discussed in Davis, 1969. It is of considerable interest that, on the basis of overall results, the Potamididae appears more related to the Pleuroceridae than the Cerithiidae and that the representatives of the Thiaridae and Potamididae are more closely allied to the Pleuroceridae than the representative of the Cerithiidae. These preliminary results suggest that the Cerithiidae (if *Clypeomorus* may be considered a basic representative of the family) may be far removed from the relationships suggested by Morrison (1954). This question of relationships is open to fruitful investigation relative to the phylogeny of so-called melanian snails.

Table 21

Species ranked according to increasing average percentages of precipitin arcs remaining to the homologous reaction, using the three most specific fluids.

Taxa	Average percentage
Semisulcospira libertina	0
Semisulcospira niponica	10
Thiara scabra	47
Batillaria multiformis	48
Stenomelania crenulata	48
Melanoides tuberculatus	57
Brotia costula episcopalis	59
Clypeomorus humilis	65
Sinotaia histrica	65
Oncomelania hupensis nosophora	78
Clithon retropictus	96

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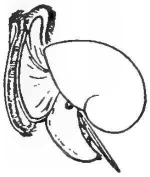

Some Paleogene Mud Pectens of the Genus *Propeamussium* from Alaska and California

BY

WARREN O. ADDICOTT

U. S. Geological Survey, Menlo Park, California 94025

(1 Plate)

INTRODUCTION

THIS REPORT IS BASED on a study of a collection of Paleogene *Propeamussium* from the Aleutian Islands of the marginal North Pacific Ocean. The pectinids were collected from the northern part of Adak Island (Lat. 176° 54′ W; Long. 51°54′ N) by D. W. Scholl and H. G. Greene of the U. S. Geological Survey in 1968. The material is from a rock unit once thought to be of Paleozoic age based upon identification of supposed specimens of the plant *Annularia* (COATS, 1956). Preliminary study of the small mud pectens and associated marine microfossils clearly indicated a Tertiary age (SCHOLL *et al.*, 1969). Initial identification of these specimens as *Propeamussium* cf. *P. stanfordensis* (ARNOLD) led to a tentative middle Tertiary age assignment inasmuch as this species was originally recorded from rocks of Miocene age at the type locality (ARNOLD, 1906). Subsequent discovery of Eocene Foraminifera and fish remains in additional samples from Adak Island by R. L. PIERCE (*in* SCHOLL *et al.*, 1969) called for re-examination of the stratigraphic occurrence of *P. stanfordensis*. And indeed, recent geologic mapping (DIBBLEE, 1966; PAMPEYAN, 1969) of the central California area from which

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[1] Publication authorized by the Director, U. S. Geological Survey

Plate Explanation

Propeamussium (Propeamussium) ***leohertleini*** ADDICOTT, spec. nov.

(All figured specimens are from USGS loc. M3892)

Figure *1*. USNM 646439. Left valve of deformed articulated specimen with part of the right anterior ear exposed. Height 11.8 mm; length 12.8 mm

Figure *2*. USNM 646440. Right valve. Height 11 mm; length 10.5 mm

Figure *7*. USNM 646441. Immature left? valve. Height (incomplete) 5.4 mm; length 5.6 mm

Figure *9*. USNM 646442. Exterior of left valve. Height 8.1 mm; length (incomplete) 7 mm

Figure *12*. USNM 646443. Left? valve. Height 10.6 mm; length 10.9 mm

Figure *13*. USNM 646444. Holotype, right valve. Height 10.7 mm; length 10.4 mm. Fragment of left valve; hinge measures 5 mm in length

Propeamussium (Parvamussium) stanfordensis (ARNOLD)

Figure *3*. USNM 646445. USGS loc. 5749. Right valve (above) 10.4 mm in height and 10.1 mm in length; left valve (below) 13.6 mm in height and 12.5 mm in length

Figure *5*. USNM 646446. USGS loc. M1492. Left valve (above) 7.8 mm in height and 8 mm in length; right valve (below) 9 mm in height and 8.1 mm in length

Figure *8*. USNM 646447. USGS loc. 5749. Right valve (above) 9 mm in height and 8.6 mm in width. Incomplete valve (below) 10.7 mm in width

Figure *10*. USNM 646448. USGS loc. 5749. Right valve. Height 10.9 mm; length 9.6 mm

Propeamussium spec. nov. ?

Figure *4*. USNM 646449. USGS loc. M4108. Height (incomplete) 10.8 mm; length 12.8 mm

Propeamussium (Propeamussium) interradiatum (GABB)

Figure *6*. USNM 646450. USGS loc. 5742. Right valve. Height 16 mm; length 17.1 mm

Figure *11*. USNM 646451. USGS loc. 5742. Incomplete right valve. Height 16.3 mm

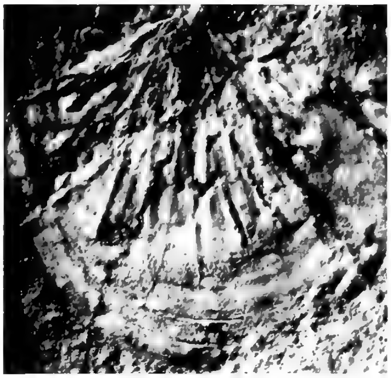
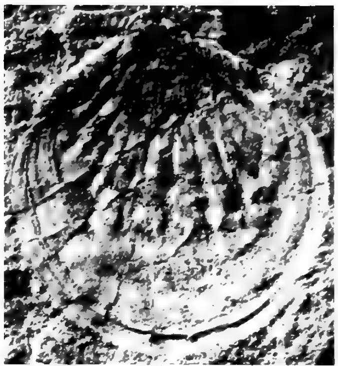


Figure *1*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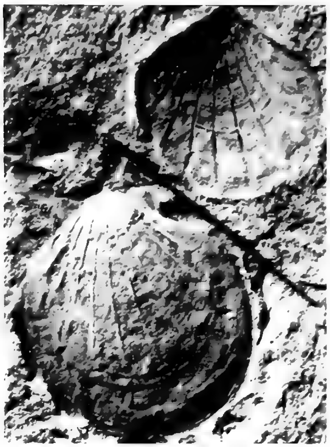
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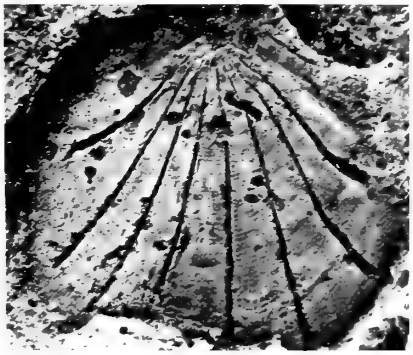
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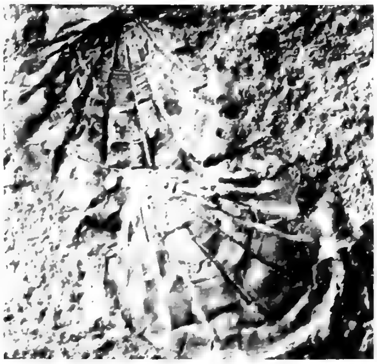


Figure *5*

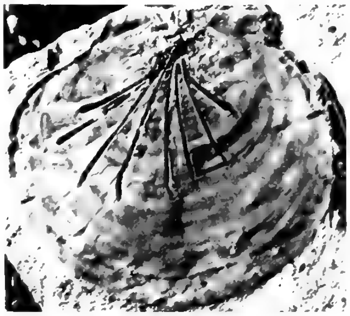


Figure *6*

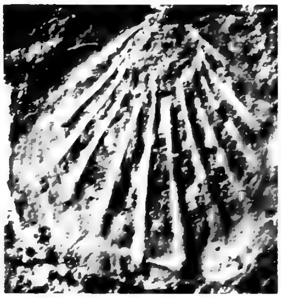
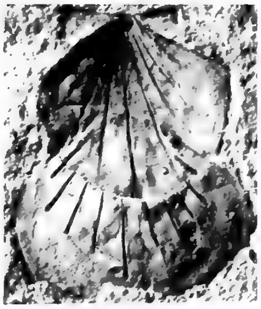


Figure *7*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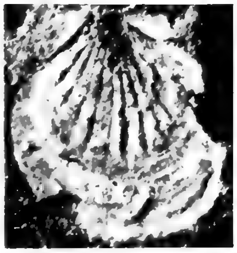
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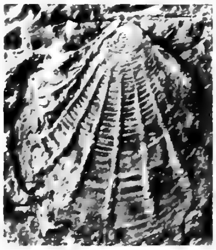
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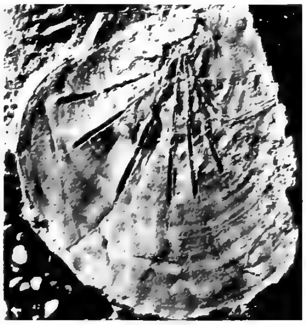
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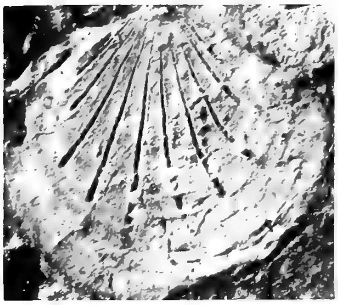
Figure *12*

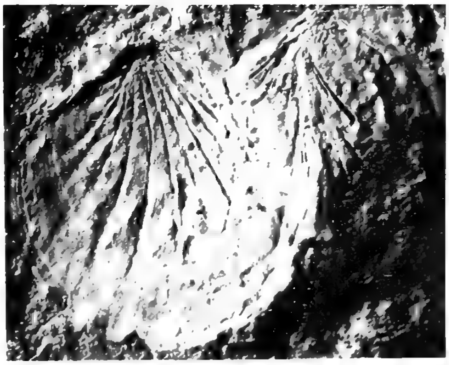
Figure *13*

this species was originally collected (Lat. 37°30′N) indicates that the type material came from rocks of Eocene rather than middle Miocene age.

The recently discovered material from the Aleutian chain includes three different mud pectens – two species of *Propeamussium* and a very poorly preserved, specifically indeterminate *Delectopecten*. This is the first Tertiary record of *Propeamussium (Propeamussium)* from Alaska, the few previous Alaskan records of this genus having been reclassified as *Polynemamussium* by MacNeil (1967) [*Polynemamussium* = *Propeamussium (Parvamussium)* of Grau (1959)]. It is also the earliest Tertiary record of the genus from the rim of the North Pacific, the oldest previously recorded occurrence being from rocks of late Oligocene age in Kamchatka – *Propeamussium* cf. *P. pillarensis* (Slodkewitsch, 1938).

The purpose of this note is to describe the early Tertiary species from Alaska and to clarify the stratigraphic and chronologic occurrence of *Propeamussium stanfordensis* in California. The *Propeamussium* from exposures on Adak Island is indeed very similar to *P. stanfordensis* (Arnold), as previously indicated (Scholl *et al.*, 1969). It differs, however, in the configuration of the right anterior ear and in minor sculptural detail. This taxon is here named *P. leohertleini*. Another *Propeamussium* represented by a single poorly preserved specimen from a stratigraphically higher locality on Adak likewise seems to be undescribed, but is not named here. Generic classification of species treated herein is based upon Grau (1959).

SYSTEMATIC PALEONTOLOGY

Propeamussium de Gregorio, 1884

(Propeamussium) de Gregorio, 1884

Propeamussium (Propeamussium) leohertleini Addicott, spec. nov.

(Figures *1, 2, 7, 9, 12, 13*)

1969. *Propeamussium* cf. *P. stanfordensis* (Arnold). Scholl, Greene, Addicott, and others, Amer. Assoc. Petroleum Geologists Bull. 53: 459

Description: Small, thin-shelled with equal auricles. Valves circular, equidimensional with similar external sculpture. Surface of right valve almost smooth; extremely fine pattern of faint concentric undulations discernible on some specimens. Right anterior auricle with weak byssal notch reflected by curvature of growth lines. Interior with 10 slightly curved ribs extending nearly ¾ of distance toward the margin. Left valve with almost equally faint but more strongly delineated sculpture of regular concentric growth lines. Interior with 10 ribs slightly curved extending nearly ¾ of distance from beak to margin.

Type: U. S. National Museum 646444, a right valve.

Dimensions of holotype: height 10.7 mm, length 10.4 mm

Type Locality: USGS Cenozoic locality M3892. About ¼ mile northwest of Mitchell Field air strip on point projecting into east shore of Lake Andrews, northern part of Adak Island, Aleutian Islands, Alaska. Andrew Lake Formation of Scholl *et al.* (1970), middle or late Eocene.

Discussion: *Propeamussium leohertleini* occurs in the lower part of the Andrew Lake Formation at localities about 200 m (M3891) and 350 m (M3892) above the base. It is associated with a small assemblage of benthonic foraminifers considered by R. L. Pierce (*in* Scholl *et al.*, 1970) to be provincially of late Eocene age [Narizian Stage of Mallory (1959)].

Seven of the 16 specimens from the type locality have 10 internal ribs; the remainder from this locality and from nearby M3891 are incompletely preserved. Many of the latter are crushed, articulated valves on which the internal ribs are intermeshed and, in some cases, deformed (Figure *1*). The delicate surface sculpture of concentric growth lines and undulations is discernible on only a few of the specimens; it appears to be crisper on the left valves. Clear-cut radial sculpture was not detected on any of the specimens.

As previously indicated (Scholl *et al.*, 1969) this species is very similar to *Propeamussium stanfordensis* (Arnold), a late Eocene species from central California (Figures *3, 5, 8, 10*). It differs from that species, and from the similar early Eocene species *P. mideocenicum* Vokes, 1939 from California, principally in lacking a well-defined byssal notch. The left valve of *P. mideocenicum* can be differentiated from this species by its prominent, sharp external ribs (12 on two of the syntypes: UCMP 15584 and 15586). Further, but minor, differences from the California species are the relatively shorter internal ribs and the prominent, but very fine, growth striae of *P. leohertleini*.

Propeamussium interradiatum (Gabb, 1869, p. 199; plt. 33, figs. 98, 98a), the common Eocene species of this genus from California, differs from *P. leohertleini* in having a relatively smooth exterior and fewer internal ribs – 8 rather than 10 (Figures *6, 11*).

This species is named for Leo G. Hertlein, Curator Emeritus at the California Academy of Sciences, in recognition of his contributions to the study of Tertiary and Quaternary monomyarian pelecypods.

Occurrence: Andrew Lake Formation (middle or upper Eocene), Adak Island, Aleutian Islands, Alaska. USGS Cenozoic localities M3891, M3892, M4108.

Propeamussium spec. nov.?

(Figure *4*)

A single specimen of a *Propeamussium* from float collected near the top of the Andrew Lake Formation (Scholl *et al.*, 1970) on the northern part of Adak Island, Aleutian Islands, Alaska, appears to be distinct from known species of Tertiary age along the margins of the North Pacific. Although represented by a single incomplete valve, the sculpture, strong internal ribbing, and auricles (incompletely preserved) indicate reference to *Propeamussium.*

Propeamussium spec. nov.? is distinguished from *P.* ***leohertleini*** spec. nov., which also occurs in the Andrew Lake Formation, by its fewer radial ribs – 8 rather than 10 – and the fact that these ribs extend almost to the edge of the disk.

The length of the internal ribs, extending almost to the margin, and the prominent concentric microsculpture likewise distinguish this specimen from the common Eocene species *Propeamussium interradiatum* (Gabb) from California.

Occurrence: Float block from northwest shore of Clam Lagoon, Andrew Lake Formation (middle or upper Eocene), Adak Island, Aleutian Islands, Alaska. USGS Cenozoic loc. M4108.

(Parvamussium) Sacco, 1897

Propeamussium (Parvamussium) stanfordensis (Arnold)

(Figures *3, 5, 8, 10*)

1906. *Pecten (Propeamusium) stanfordensis* Arnold, U. S. Geol. Survey Prof. Paper **47**: 91 - 92; plt. 23, fig. 4

1909. *Pecten (Propeamusium) stanfordensis* Arnold. Branner, Newsome, and Arnold, U. S. Geol. Atlas, Santa Cruz Folio [no. 163]: illust. II, fig. 51

?1939. *Propeamussium mideocenicum* Vokes, New York Acad. Sci. Annals **38**: 55 - 56, in part; plt. 3, fig. 4 (not figs. 2 and 3)

Type: Stanford Univ. Paleontol. Type Coll., no. 12, a left and a right valve.

Type Locality: "... buff colored Miocene [Eocene] shale in a small ravine on the Burke [now Webb] ranch one-third mile south [west] of Los Trancos Creek near Stanford University, San Mateo County" (Arnold, 1906, p. 92). A more detailed description (Keen & Bentson, 1944) fixes this locality in a small east-flowing tributary to Los Trancos Creek, about ½ mile west of Felt Lake [in rocks of Eocene age mapped as Butano(?) Sandstone by Dibblee (1966) and Pampeyan (1969)].

Discussion: *Propeamussium stanfordensis* is reconsidered here in light of the revision of its stratigraphic occurrence – from middle Miocene to upper Eocene – and the availability of additional material from near the type locality for figuring. One of the specimens figured herein, a virtual topotype (Figure *5*) has a much better preserved external surface showing relatively strong, regularly spaced concentric undulations.

Arnold (1906, p. 92) originally classified the stratigraphic occurrence of this species as middle Miocene, apparently believing the light-colored shale exposure from which it was collected to be part of the Monterey Shale. Consequently, subsequent treatments of Tertiary *Propeamussium* (Slodkewitsch, 1938; Weaver, 1942) have considered species, and phylogenies, in the context of a Neogene stratigraphic occurrence of this taxon. A doubtful identification of this species from lower Tertiary rocks in the Aleutian Islands (Scholl *et al.*, 1969) is now believed to represent a different species, described herein as *P.* ***leohertleini***. The occurrence of a similar species in lower Tertiary strata led to re-examination of the type locality of *P. stanfordensis* near Stanford University in central California. It was found that the type locality is in an area of upper Eocene rather than middle Miocene rocks, according to recent geologic mapping and related micropaleontologic studies.

Two of the specimens of *Propeamussium stanfordensis* figured in this report (Figure *5*) can be regarded as topotypes. They are from a locality on the north wall of the same drainage from which the holotype was collected by Ralph Arnold, possibly on strike from his locality. They occur with a diverse foraminiferal assemblage of late Eocene Narizian age according to M. C. Israelsky (in written communication to E. H. Pampeyan, April 16, 1963; USGS microfossil locality Mf707). The occurrence is about 45 m stratigraphically below the base of middle Miocene rocks in a unit mapped by Dibblee (1966) and by Pampeyan (1969) as Butano(?) Sandstone and by Page & Tabor (1967) as unnamed Eocene rocks.

Study of the recently collected specimens from USGS Cenozoic loc. M1452 (Figure *5*) indicates that the anterior ear of the right valve has a rather strong byssal notch that is reflected in the curvature of the growth lines. Moreover, the internal ribs extend almost to the margins of the valves. Accordingly, placement in the subgenus *Parvamussium* is clearly indicated.

One of the early Eocene specimens of *Propeamussium mideocenicum* Vokes, 1939, UCMP 15585 from the Arroyo Hondo Shale Member of the Lodo Formation in the San Joaquin basin, California, might be *P. stanfordensis*. The ears, number and configuration of internal ribs, and size of this syntype are similar to *P. stanfordensis*. The other syntypes (both left valves) are quite distinct; they probably represent an entirely different species than *P. stanfordensis* judging by the occurrence of external ribbing and by the fact that these ribs are much more numerous than on the right valve – 12 instead of 9.

It seems doubtful that *Propeamussium stanfordensis* represents young specimens of the well-known Eocene species *P. interradiatum* (Gabb) as was suggested by Grant & Gale (1931). The shorter, consistently fewer internal ribs – 8 rather than 10 or more – and the weaker, much finer concentric sculpture of *P. interradiatum* (Figures *6, 11*) permit differentiation. The ears are incompletely preserved on the lectotype of *P. interradiatum* (Stewart, 1930, p. 123). Whereas the ears and the length of the internal ribs on one of the original hand-drawn illustrations representing a left valve of *P. interradiatum* (Gabb, 1869, plt. 33, fig. 98) indicate reference to *Propeamussium (Propeamussium)*, the other illustration of a portion of the dorsal margin of a right valve (figure 98a) indicates a deep byssal notch and an extremely narrow right anterior ear. These features are not characteristic of *Propeamussium*; they suggest that the figures are of entirely different taxa. It is noteworthy that specimens in the collection from USGS loc. 5742 (basal part of the Kreyenhagen Shale near Cantua Creek, Fresno County, California) are here regarded as conspecific with *P. interradiatum*, compare closely with Stewart's lectotype (1930, plt. 8, fig. 10), and have a very shallow byssal notch and a broad anterior ear indicative of assignment to *Propeamussium (Propeamussium)*.

Occurrences: Late Eocene: Butano(?) Sandstone of Dibblee (1966), Palo Alto quadrangle, California (unnumbered Stanford Univ. locality, USGS loc. M1492); near the base of the Kreyenhagen Shale, Cantua Creek area, Fresno County, California (USGS loc. 5749); near Idria, San Benito County, California (USGS loc. 5743); Aldwell? Formation, Clallam County, Washington (USGS loc. M4149).

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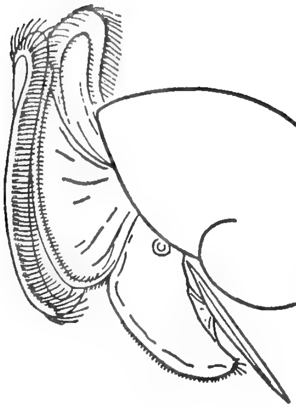

Niche Differences in the Intertidal Limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in Central California

BY

STONER B. HAVEN

Department of Zoology, University of California, Berkeley, California, 94720[1]

(10 Text figures)

INTRODUCTION

THE GASTROPOD GENUS *Acmaea* is of particular ecological and evolutionary interest because of its unusually large number of sympatric species on the west coast of North America. In central California, 16 species are found in the rocky intertidal zone (LIGHT *et al.*, 1954; FRITCHMAN, 1960). Some of these are rigidly stenotopic, living only on a single algal or gastropod species, while others are more eurytopic and utilize a variety of algal foods over a broad vertical range. However, general ecological studies (particularly TEST, 1945; also HEWATT, 1937; SHOTWELL, 1950; RICKETTS & CALVIN, 1968; FRITCHMAN, 1960, 1961) have shown that nearly all of the species occupy niches that are non-overlapping in at least one important dimension: vertical range, microhabitat preference, or food preference. Thus these limpets seem to conform to the classical requirement of ecological separation for the coexistence of closely related species.

The present study (HAVEN, 1966) was prompted by an apparent exception in the upper intertidal zone, where two closely related species (TEST, 1946) are abundant: *Acmaea digitalis* RATHKE, 1833 and *A. scabra* (GOULD, 1846). Although comments in the literature have suggested ecological differences between them, they have been considered to occupy roughly the same niche (TEST, 1945): both graze on the microscopic encrusting algal film on the relatively bare rocks of the upper intertidal and splash zones and their vertical ranges are broadly overlapping. They coexist over a large geographic distance, from Baja California to southern Oregon. *Acmaea digitalis* ranges from Unalaska Island to Guadalupe Island, off northern Baja California; *A. scabra* from southern Oregon to Cape San Lucas, Baja California (FRITCHMAN, 1962; JESSE, 1968b). (Range limits need better documentation, particularly in the south; some publications erroneously list *A. scabra*'s northern limit as Puget Sound).

This paper reports studies on the distribution and abundance of *Acmaea scabra* and *A. digitalis* in relation to microhabitat, undertaken to detect areas of niche separation which might be expected in view of the species' abundant and apparently stable coexistence. Results of field experiments on competition between *A. scabra* and *A. digitalis* will be reported in another paper (HAVEN, in prep.).

In the past surprisingly little quantitative information has been published on microdistribution and population dynamics of west North American *Acmaea*. Recently, however, the situation has changed with the appearance of FRANK's (1964, 1965a, 1965b) demographic study of *A. digitalis*; FRITCHMAN's (1961-1962) work on reproductive cycles; a class study including several papers on *A. scabra* and *A. digitalis* (ABBOTT *et al.*, 1968); and population studies on *A. scabra* (SUTHERLAND, 1969) and on several species including *A. scabra* and *A. digi-*

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[1] Present address: Department of Biological Sciences, Simon Fraser University, Burnaby 2, British Columbia, Canada

talis (Stimson, 1968). Other recent papers involving *A. scabra* and *A. digitalis* include those of Castenholz (1961) on grazing effects, Galbraith (1965) on homing, and Glynn (1965) on the *Endocladia-Balanus* association. Niche segregation among sympatric congeneric species, although less frequently studied than in terrestrial organisms, has been demonstrated in several groups of benthic marine organisms including gastropods (Kohn, 1959; Paine, 1962, 1963), bivalves (Pearce, 1965), amphipods (Bowers, 1964; Croker, 1967), crabs (Jeffries, 1966) and polychaetes (Mangum, 1964). The broad subject of competition, niche relationships, coexistence and exclusion has been thoroughly reviewed by Hutchinson (1965) and Miller (1967).

METHODS

To study microhabitat differences between *Acmaea scabra* and *A. digitalis,* limpet populations were sampled by means of transect censuses. The censuses were designed to test for the effects of angle of slope of substrate, intertidal height, and amount of wave action. Locations for the transects were selected by surveying the shore and choosing sites at which one or more of these factors were isolated as well as possible from other environmental variables. For example, one group of transects was located where several horizontal, vertical, and intermediate rock surfaces at varying intertidal heights were closely juxtaposed to each other within a small area (Mission Point).

Each transect was a linear strip of square quadrats, 20 × 20 cm. Limpets were either counted *in situ* or collected for later counting and measuring. Transects in a given area were tied together vertically by hand levelling, and their approximate heights above tidal datum (mean lower low water) were determined by measuring from water level at low tide, usually averaging several measurements from different days.

Transect censuses were made at 9 locations from Point Lobos (Monterey County) north to Moss Beach (San Mateo County) in central California. Observations were made at numerous additional sites from southern Monterey County (near Lucia) north to Sonoma County (Fort Ross). The transects reported in detail in this paper are from the Monterey Bay area: Mission Point (between Carmel beach and the mouth of the Carmel River); Point Pinos (Monterey Peninsula); and Hopkins Marine Station of Stanford University (Mussel Point, Pacific Grove). Site descriptions and photographs showing the exact locations of the transects are given in Haven (1966).

To study temporal population variations in relation to microhabitat, 9 permanent quadrats, each in a different microhabitat, were maintained at Hopkins Marine Station from September 1963 to January 1966. Quadrat size was 20 × 20 cm; boundaries were located with chisel marks. Limpets in the quadrats were counted once or twice per month (occasionally at longer intervals). To provide information on the amount and timing of recruitment in relation to microhabitat, 3 arbitrary size classes of limpets were separated: animals less than 4 mm in greatest shell length (the smallest limpets found were ca. 2 mm); animals 4 to 7 mm long; and individuals greater than 7 mm. Intertidal heights of the quadrats were determined from a nearby bench mark. Photographs and descriptions of the quadrat sites are given in Haven (1966).

The notorious intraspecific variability of the shell in *Acmaea* species calls for comment on species identification. *Acmaea scabra* and *A. digitalis* can usually be identified *in situ* by their diagnostic shell characters: for *A. digitalis,* heavy ribs, apex anterior with concave surface in front, convex surface behind; for *A. scabra,* heavy ribs with spines, apex more central, surfaces more plane, and shell edge more irregular (illustrations in Light *et al.,* 1954; Ricketts & Calvin, 1968). However, all shell characters vary greatly and may be obliterated because of erosion from boring organisms (Bonar, 1936) and other causes, both environmental and genetic (Test, 1945, 1946). The more irregular shell edge in *A. scabra* results from this species' homing behavior (Hewatt, 1940), which is generally lacking in *A. digitalis* (see Discussion). Fortunately, any questionable individuals can readily be identified by the presence (*A. scabra*) or absence (*A. digitalis*) of dark spots on the side of the foot and on the head. For example, some high intertidal *A. scabra* have shell profiles similar to *A. digitalis,* and if strongly eroded are virtually indistinguishable except for these spots. No individuals were found that could be interpreted as genetic intermediates between *A. scabra* and *A. digitalis.*

The intertidal zonation scheme of Ricketts & Calvin (1968) is used in this paper, recognizing, however, that the relationships between individual species distributions and the generalized "zones" is complex and needs more detailed study. The zones, defined both biologically and by tidal levels by Ricketts & Calvin, were recognized in the field only by biological criteria:

Zone 1 (covered by higher high tides and splash). Largely bare rock covered with a microalgal film, with scattered zone 2 barnacles and algae in the lower part; *Acmaea digitalis* and *A. scabra* were the dominant animals along with *Littorina planaxis* Philippi, 1847 (ranges much higher) and *L. scutulata* Gould, 1849 (commoner in zone 2).

Zone 2 (upper limit at mean high water level). Dominated by barnacles (*Balanus glandula* Darwin, 1854, and others) and macroalgae (*Endocladia, Pelvetia,* and others); biota more diverse and variable than in zone 1; *Acmaea scabra* and *A. digitalis* reached their lower limits here.

Zone 3 (algal cover of *Iridaea, Egregia,* etc.; mussel beds with strong wave action) and **Zone 4** (below mean lower low water; dominated by the kelp *Laminaria,* etc.) were of little concern in this study.

Most of the transects and quadrats fall in the "protected outer coast" wave-exposure classification of Ricketts & Calvin. Although a few (e. g., the outermost Point Pinos transects) were on "open coast," no data were obtained from totally exposed rock surfaces.

HABITAT DIFFERENCES:

TRANSECT SURVEYS

Differences in the distribution and abundance of *Acmaea scabra* and *A. digitalis* with respect to angle of slope of

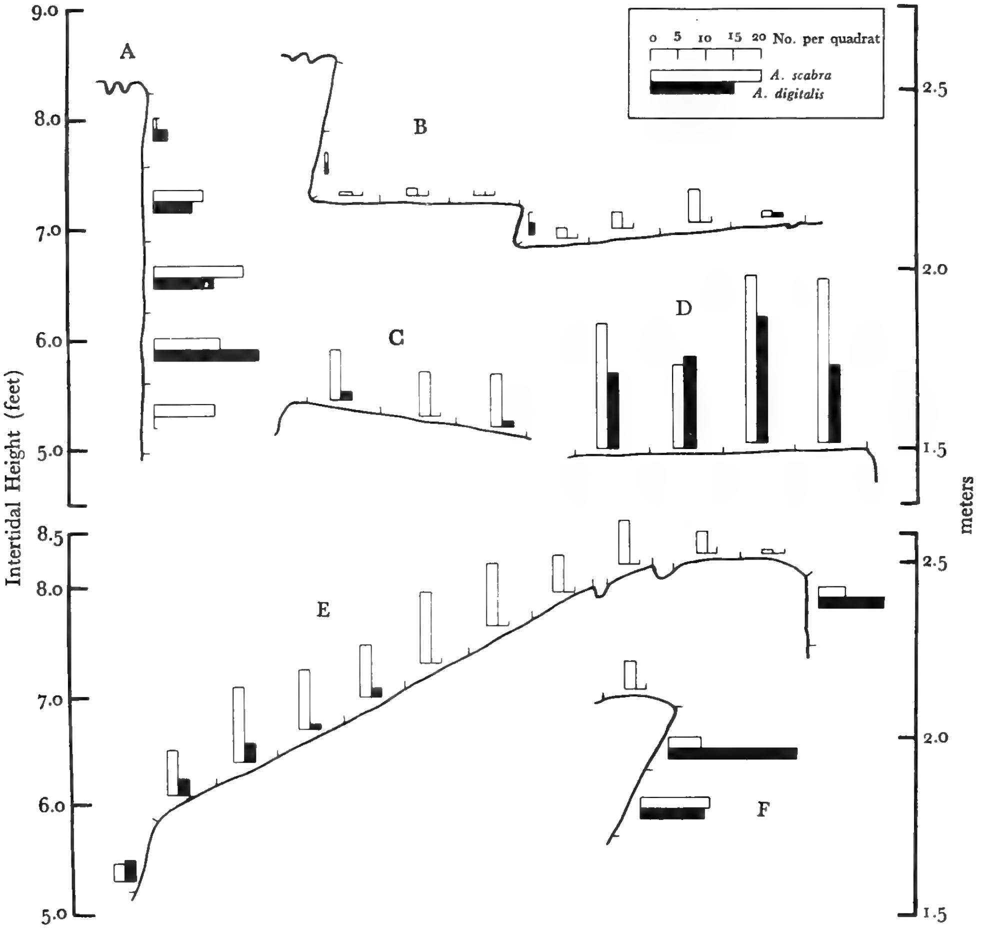

Figure 1

Results of transect censuses at Mission Point. Solid lines are profiles of the rock surfaces; quadrat size is 20×20 cm. Transect D is effectively in zone 2; others are in zone 1 the substrate, vertical intertidal height, and amount of wave action were demonstrated by the results of the transect censuses (Figures 1 - 3). In the following discussion, individual transects are referred to by figure number and letter.

Angle of slope, zone 1

On the largely bare rocks of zone 1, limpet populations were correlated with angle of substrate slope as follows:

Horizontal and gently sloping surfaces (slope less than about 25°): *Acmaea scabra* was by far the dominant species (1B, 1C, 1F; 2D; 3C, 3E, 3L). *Acmaea digitalis* was either absent or much less numerous than *A. scabra.* The few *A. digitalis* that did occur were usually restricted to small crevices or depressions (e. g., 1B), whereas *A. scabra,* although showing this tendency to some extent, was more randomly dispersed over smooth, exposed parts of the surface.

Vertical and overhanging surfaces (slope steeper than about 75°): Both species were usually present, but relative abundance varied considerably. Much of this variation was correlated with vertical intertidal height and wave action (see below). Large populations of *Acmaea digitalis* occurred only on these steeply sloping surfaces, frequently but not always outnumbering *A. scabra* (1A, 1B, 1E, 1F; 2A - 2D; 3A, 3E, 3F, 3J - 3L). However, there was no general tendency for *A. scabra* to be less numerous on vertical than on adjacent horizontal rocks; in fact the reverse was sometimes true (e. g., 1A, 1B).

Intermediate slopes: Frequently *Acmaea digitalis* occurred only at low levels (e. g., in zone 2), leaving *A. scabra* as the dominant species at higher levels (1E). However, interactions with other factors, particularly wave action, made limpet distribution on intermediate slopes difficult to predict.

On irregular rock surfaces, populations of the two species often appeared to be randomly interspersed, but upon close examination were seen to show differential distribution with respect to angle of slope. Even when there was a relatively small or localized change in the angle of slope of a rock, *Acmaea digitalis* tended to be restricted to the steeper surface.

Angle of slope, zone 2

In contrast to the absence of *Acmaea digitalis* from horizontal rocks in zone 1, both *A. digitalis* and *A. scabra* were common on zone 2 horizontal rocks that supported

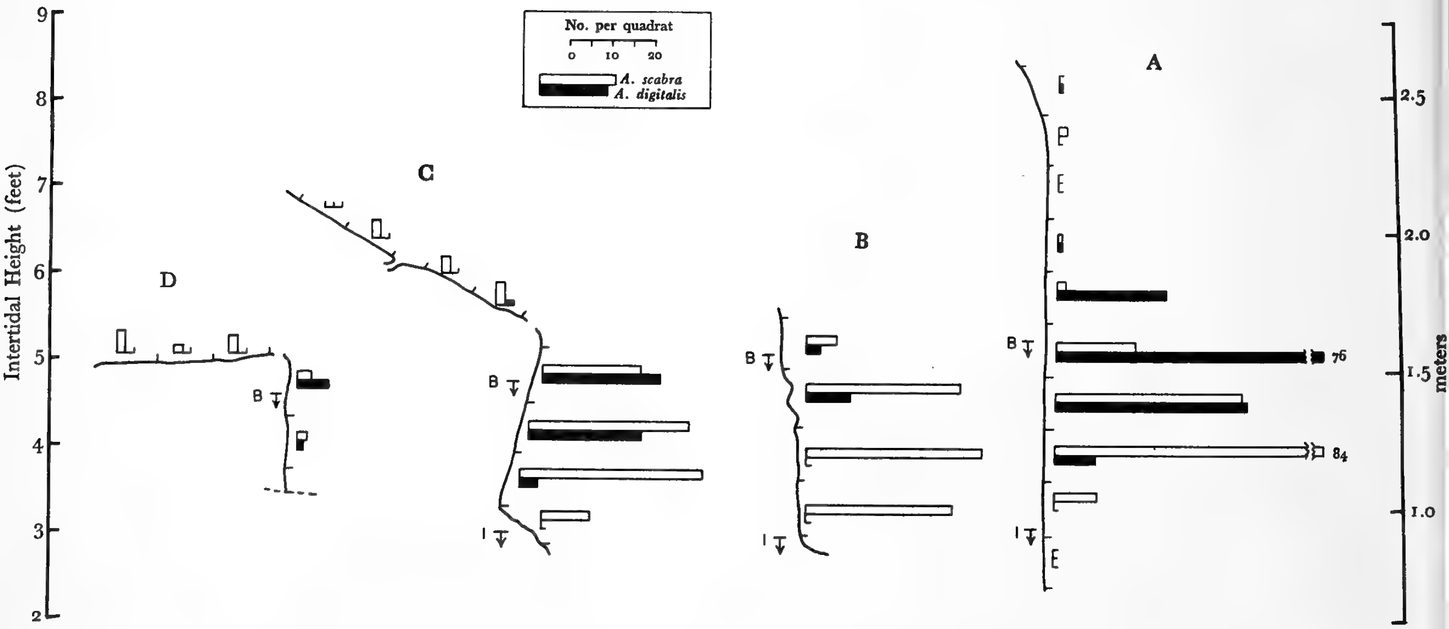

Figure 2

Results of transect censuses at Hopkins Marine Station. Wave action increases from left to right. B = dense barnacles (zone 2); *I* = *Iridaea* (zone 3)

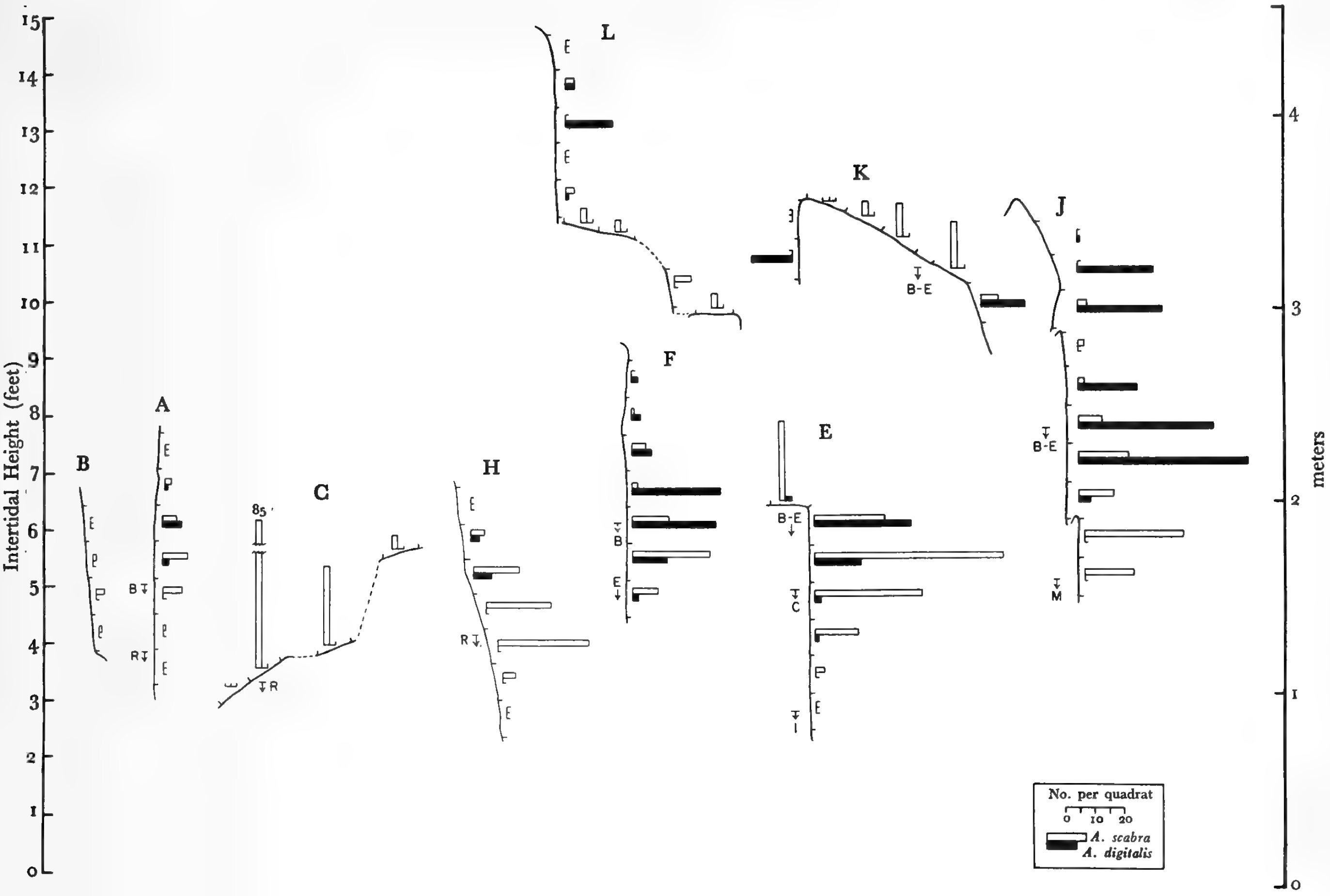

Figure 3

Results of selected transect censuses at Point Pinos. Wave action categories: very light – B; light – A, C, H; moderate – F; heavy – E, J, K, L. B = dense barnacles (zone 2); E = *Endocladia* (zone 2); I = *Iridaea* (zone 3); R = assorted red algae (zone 3); C = encrusting coralline algae; M = mussel beds (*Mytilus*)

dense barnacle and algal populations. This is illustrated by comparing transects 1C and 1D. Although they were on adjacent rocks differing only slightly in slope and intertidal height, 1C was effectively in zone 1 and 1D in zone 2. There were only scattered barnacles on 1C, whereas 1D was densely covered with barnacles of several species. Observations on a rising tide showed that 1D received more water coverage than 1C (1D was covered earlier and for longer periods by waves and retained water runoff better); this occurred because 1D was located closer to the incoming waves and because its barnacle cover significantly increased water retention. *Acmaea scabra* was the dominant limpet on 1C, whereas both *A. scabra* and *A. digitalis* were common (including large individuals of both species) on 1D. The much higher population densities of both species on 1D were due to an abundance of small individuals; larval settlement was generally greater in zone 2 than in zone 1 (see "Temporal Variations").

Experiments at Mission Point

An experiment was carried out at Mission Point in July, 1959, to test whether survival or behavior of transplanted *Acmaea digitalis* was correlated with the distributional patterns shown by the transect censuses (transplanting of *A. scabra* was unsuccessful because of the irregular shell edge resulting from this species' homing behavior). Groups of 10 *A. digitalis* were transplanted from a vertical surface (1A) to 3 horizontal surfaces (1B, 1C, 1D), and, as a control, for a short distance on the vertical surface. Another 10 *A. digitalis* were removed from the bottom of the intermediate slope (1E) to the top, where only *A. scabra* occurred. Within 1 to 3 days, all the *A. digitalis* transplanted to zone 1 horizontal rocks dominated by *A. scabra* (1B, 1C) had moved to adjacent vertical surfaces or into sheltered cracks. In contrast, the *A. digitalis* transplanted to the zone 2 horizontal surface dominated by barnacles, and with both *A. digitalis* and *A. scabra* common (1D), remained within the barnacle-covered area as long as observations were continued (2 weeks). The *A. digitalis* transplanted to the top of the intermediate slope all moved down to their previous level or laterally into deep vertical cracks within 1 to 5 days. *Acmaea digitalis* in the control group moved only within a 1 foot radius on the vertical rock, and losses during the 2 week period did not exceed 40% in any of the groups.

Another experiment was carried out during a brief visit to the same site in April, 1964. At this time, extensive patches of the macroscopic alga *Porphyra* were found in both zones 1 and 2 (this is probably a common occurrence in winter and spring). Large individuals of both *Acmaea digitalis* and *A. scabra* were found under the *Porphyra* in places where only *A. scabra* were found in the absence of algal cover in the original transect censuses (e. g., the upper part of the intermediate slope 1E, and the horizontal surface 1F). All *Porphyra* was removed (in early morning) from a 20 × 40 cm area within a *Porphyra* patch in the former area (1E). This exposed 14 *A. digitalis* and 18 *A. scabra,* which were marked with fingernail polish. By the same afternoon (after the intervention of only one high tide), all 18 *A. scabra* were still within the cleared area, whereas of the *A. digitalis,* 4 were in the cleared area, 8 were under adjacent *Porphyra* cover (maximum distance moved, 25 cm), and 2 were not found. On several subsequent visits to this site, all in summer or early fall, *Porphyra* patches were absent and distribution of *A. digitalis* was the same as that shown by the transects.

Intertidal height

Although the vertical intertidal ranges of *Acmaea scabra* and *A. digitalis* overlapped broadly, some vertical separation of their populations was indicated by the transects. Data for vertical rock surfaces are diagrammed in Figure 4. The upper limits of the two species were quite variable. However, the commonest situations were for *A. digitalis* to range significantly higher than *A. scab-*

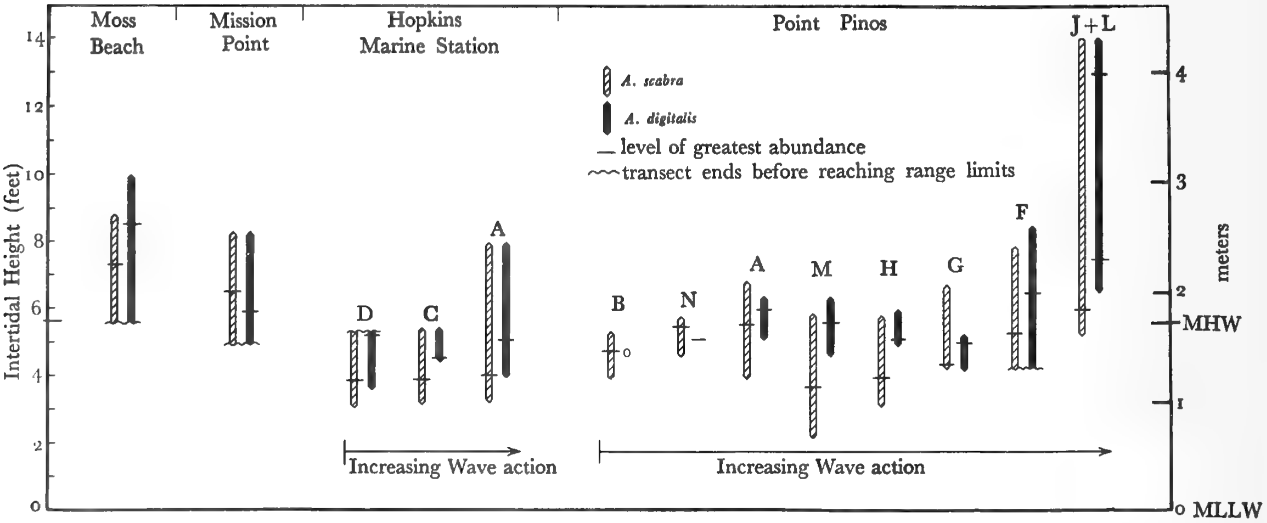

Figure 4

Vertical intertidal ranges and levels of maximum population density for *Acmaea scabra* and *Acmaea digitalis* on vertical rocks. Data taken from the transect censuses *ra,* or for both species to have virtually the same upper limit. Only occasionally did *A. scabra* extend higher than *A. digitalis*; in many of these cases the absence of *A. digitalis* at higher levels appeared to be related to small decreases in angle of slope or to random effects resulting from low population density. (As stated previously, *A. scabra* ranged higher than *A. digitalis* on intermediate slopes, and *A. digitalis* was rare or absent on horizontal surfaces above zone 2.) The lower vertical limit of *A. scabra* was nearly always below that of *A. digitalis,* but the amount of difference was quite variable. The lower limit of *A. digitalis* was generally in upper or mid zone 2, that of *A. scabra* in lower zone 2; a few *A. scabra* occasionally occurred among *Iridaea* or other algae in zone 3.

Another aspect of vertical separation was that the maximum population density of *Acmaea digitalis* often occurred at a higher intertidal level than that of *A. scabra* (Figure 4). This was true chiefly on relatively smooth vertical rocks that extended throughout the vertical ranges of both species (2A, 2B, 2C; 3A, 3E, 3F, 3J). Where the vertical range was large or the rock surface irregular, population density was sometimes polymodal with respect to vertical height but still with the peak density of *A. digitalis* higher than that of *A. scabra* (3J - 3L). The few exceptions to this relationship among the transects may be attributable to such factors as small population size (Figure 4, Point Pinos N) or insufficient extension of the vertical surface (1A).

Dispersion

Dispersion was not specifically studied, but it should be noted that although both species were usually more or less contagiously dispersed, *Acmaea digitalis* generally had a more aggregated dispersion than *A. scabra. Acmaea digitalis* often occurred in dense aggregations, particularly on vertical surfaces, whereas *A. scabra* rarely did so. However, *A. digitalis* was by no means always densely aggregated; most of the transects were located where dispersion was more uniform. Dispersion of both species often seemed related to protection from desiccation or wave shock, but the factors controlling dispersion, especially those determining whether or not *A. digitalis* was densely aggregated, need further detailed study.

Wave action

The effects of wave action were documented mainly by the Point Pinos transects, located along an inlet that exhibited a pronounced (though not uniform) wave action gradient. Ranking of the transects according to strength of wave action was based on their position in the inlet (photographs in Haven, 1966) and on direct observations of waves. The exact rank of some intermediate transects may be wrong, but the grouping into "heavy," "moderate," light," and "very light" wave action categories is doubtless valid (Figure 5). A less pronounced wave action gradient was shown by the Hopkins Marine Station transects (Figure 2).

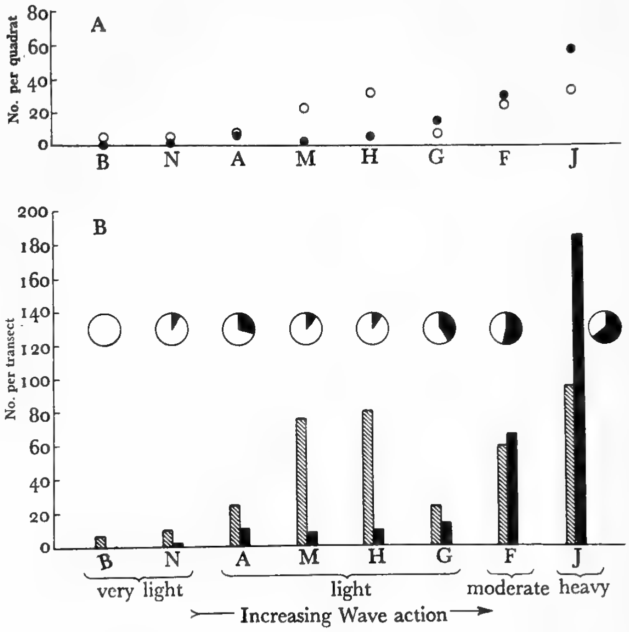

Figure 5

Abundance of *Acmaea scabra* and *Acmaea digitalis* in relation to wave action on vertical rocks at Point Pinos, as indicated by (A) maximum population density and (B) total numbers (bars, absolute; circles, percent) per transect. Solid – *Acmaea digitalis*; hatched or clear – *Acmaea scabra.* Letters identify the transects

One effect of increasing wave action was to expand the vertical ranges of both *Acmaea scabra* and *A. digitalis* (Figures 2, 4). However, no differential effect on the two species was evident. As expected for splash zone species, the upper limits were elevated much more than the lower limits, which were raised only where surf was strongest.

A relationship between wave action and abundance of the two species on vertical rocks at Point Pinos is shown in Figure 5. Numbers of *Acmaea digitalis* increased greatly with increasing wave action, as reflected both by maximum population density along a transect

(Figure 5A) and by total numbers per transect (Figure 5B). *Acmaea scabra* exhibited this tendency to a lesser degree, but its abundance was poorly correlated with wave action. The net result was that the relative abundance of *A. digitalis* increased with increasing wave action (Figure 5B). *Acmaea digitalis* was absent or scarce where waves were light but became the dominant species where surf was strong. The wave-correlated increase in total numbers of limpets per transect were due both to lengthening of vertical ranges as the splash zone expanded, and to higher population densities at optimum levels within the transects.

Transect 3H is an example of a common but poorly understood situation on vertical rocks in which *Acmaea scabra* extended much farther below *A. digitalis* into zone 2 than usual. This generally occurred in the absence of dense barnacle and macro-algal cover in zone 2, which in turn seemed to occur mainly where wave action was light. Under these conditions, the highest population densities and often the largest individuals of *A. scabra* were found below the lower limit of *A. digitalis*, thus maximizing vertical separation between the two species.

The occurrence of both *Acmaea digitalis* and *A. scabra* on zone 2 horizontal rocks was restricted to areas of moderate to strong wave action where these rocks were densely covered with barnacles and macro-algae. In areas protected from surf, barnacles may be scarce or absent and these rocks populated only by *A. scabra*, as in zone 1 (e. g., 3C).

In connection with wave action, some distributional relationships beween *Acmaea scabra* and *A. digitalis* and the large owl limpet *Lottia gigantea* Sowerby, 1834 may be noted. *Lottia* was largely restricted to areas of heavy surf, where it generally occupied a fairly narrow band along the upper edges of mussel beds. At Pacific Grove, surfaces inhabited by *Lottia* often supported a distinctive dark algal film and were virtually devoid of barnacles, larger algae, and other organisms (cf. Stimson, 1970). The lower limit of *Acmaea digitalis* usually coincided with the upper limit of these *Lottia* areas. *Acmaea scabra*, however, ranged farther down and was the only *Acmaea* species commonly found in *Lottia* territories (other zone 2 limpets such as *A. pelta* Rathke, 1833 and *A. scutum* Rathke, 1833 were found less frequently). At Santa Barbara, California, Stimson (1970) found that *Lottia* push off their territories individuals of *Acmaea* which they encounter. For unknown reasons, *A. scabra* may be relatively unaffected by this behavior of *Lottia*. *Acmaea scabra* was also by far the commonest limpet found living on *Lottia* shells. Rarely was a *Lottia* found without one or two *A. scabra* on it, and I have found as many as 5 *A. scabra*, each with a home scar, on a single *Lottia*. *Acmaea pelta* and *A. paradigitalis* Fritchman, 1960, but only rarely *A. digitalis*, were also found on *Lottia*.

Size-frequency distribution

The size-frequency structure of *Acmaea scabra* and *A. digitalis* populations, although quite variable, differed with respect to microhabitat and appeared to contribute to microhabitat separation between the species. From the size-frequency data obtained at the transect sites and elsewhere, samples have been selected to illustrate some commonly observed patterns correlated with angle of slope and intertidal height (Figures 6 and 7).

For both species, regardless of microhabitat, the smallest individuals were most numerous at the lowest intertidal heights (mainly zone 2), reflecting the pattern of larval settlement (see also "Temporal Variations").

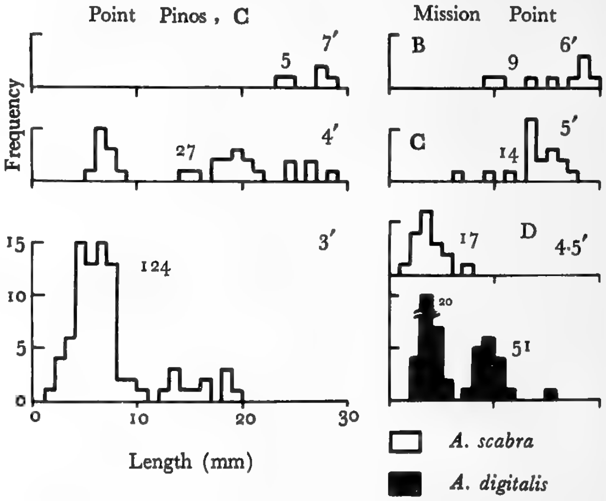

Figure 6

Size-frequency distributions from populations of *Acmaea scabra* and *Acmaea digitalis* on horizontal surfaces (data from the transect censuses). Each distribution is from one 20 × 20 cm quadrat whose intertidal height in feet is given; small numbers give population density (number per quadrat)

The larger size classes, which account for most of the biomass and reproductive output, are better indicators of the relative success of the two species in particular microhabitats. Both *Acmaea scabra* and *A. digitalis* are capable, under suitable conditions, of reaching about the same maximum length (the largest *A. scabra* collected in the

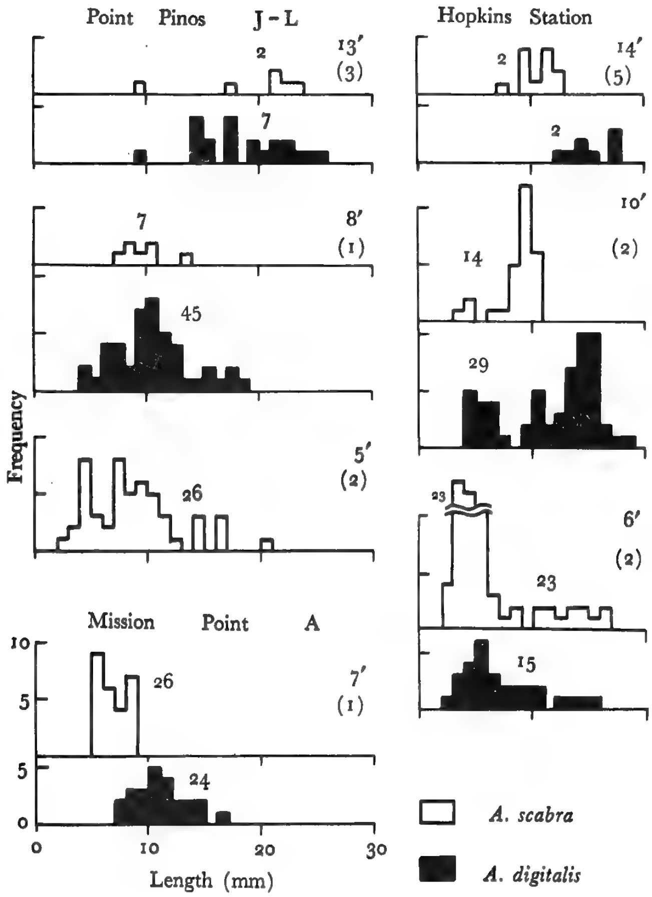

Figure 7

Size-frequency distributions from populations of *Acmaea scabra* and *Acmaea digitalis* on vertical rocks (Point Pinos and Mission Point data from the transect censuses; Hopkins Marine Station data from site of competition experiment no. 3). The number of quadrats is given in parentheses under the intertidal height for each distribution; small numbers give population density at each site (mean number per quadrat)

present study was 35 mm, the largest *A. digitalis* 30 mm, maximum shell diameter).

The largest individuals of *Acmaea digitalis* were generally found at high intertidal levels (zone 1) on vertical surfaces (Figure 7). The size-frequency distribution of *A. digitalis* on vertical surfaces showed a shift towards larger sizes with increasing intertidal height.

The largest *Acmaea scabra* were generally found at high levels (zone 1) on horizontal surfaces (Figure 6). *Acmaea scabra* on horizontal surfaces also showed a shift towards larger sizes with increasing intertidal height, either in the absence of *A. digitalis* or with *A. digitalis* present only in zone 2.

The size distribution of *Acmaea scabra* showed some noteworthy features on vertical surfaces where both species were present (Figure 7). The maximum size of *A. scabra* was smaller than that of *A. digitalis* within the zone where *A. digitalis* was most numerous, whereas the largest *A. scabra* occurred below and sometimes above this zone. In the Hopkins Marine Station samples, the maximum size of *A. scabra* decreased markedly upwards from the 6 foot level (at and below the lower limit of *A. digitalis*) to the 10-foot level (where *A. digitalis* was commonest), and then increased slightly at the 14-foot level (above the main *A. digitalis* population; at the upper limit of *A. scabra*). Maximum sizes of *A. scabra* and *A. digitalis* were about equal at the lower level (*A. scabra* slightly larger), whereas at the higher levels maximum size of *A. scabra* was much less than that of *A. digitalis*. The large *A. scabra* disappeared very quickly (within ca. 1 foot) above the lower limit of *A. digitalis*. The Point Pinos samples showed a similar pattern, except that the lowest quadrats were completely below the lower limit of *A. digitalis*, and there was a greater increase in the maximum size of *A. scabra* at the highest level (at the upper limits of both species). In the Mission Point sample, maximum size of *A. scabra* was, as usual, smaller than *A. digitalis*, in contrast to the much larger *A. scabra* occurring on adjacent horizontal surfaces (Figure 6).

HABITAT DIFFERENCES:

TEMPORAL VARIATIONS

Population fluctuations of *Acmaea scabra* and *A. digitalis* (and other associated species) in the fixed 20 cm square quadrats at Hopkins Marine Station are shown in Figures 8 and 9. Initially, limpet populations in the 9 quadrats, each in a different microhabitat, were as would be predicted from the transect census results. During the 20 - 29 month period of observations, the populations of each quadrat showed a characteristic pattern of fluctuation, but in most cases retained the initial pattern of relative abundance of *A. scabra* and *A. digitalis*.

Population size of "adult" *Acmaea scabra* (greater than 7 mm) was less variable than that of *A. digitalis* in most of the quadrats. This was due to the homing behavior exhibited by *A. scabra* but not by *A. digitalis*. Successive counts of *A. scabra* recorded the same individuals except for usually low rates of recruitment and mortality, whereas numbers of *A. digitalis* were strongly influenced by movements of individuals into and out of the quadrats. However, the data did not indicate whether or not population size of *A. digitalis* was more variable than that of *A. scabra* over an area large enough to eliminate the local effects of movements.

Quadrats 1 - 3 illustrated the effects of angle of slope in zone 1 (quadrats 1 and 2 were on nearby vertical rocks, 1 higher than 2; 3 was on a horizontal rock between them, just above 2). The vertical quadrats 1 and 2 supported good populations of *A. scabra* and *A. digitalis* throughout the study, whereas the horizontal quadrat 3 supported only *A. scabra* except for a single *A. digitalis* present for 2 months.

Quadrat 4 at first was typical of barnacle-covered horizontal rocks in zone 2. Both *Acmaea digitalis* and *A. scabra* were common; recently settled individuals (2 - 4 mm) were nestled among and inside barnacle tests. Barnacle cover (mainly large *Balanus glandula*) was about 70%. Most adult *A. digitalis* were found among the barnacles, whereas *A. scabra* also occurred in bare places. By early 1965 it was evident that the barnacle population was declining, due mainly to predation by the snail *Thais emarginata* (Deshayes, 1839). The decline of *A. digitalis* in the quadrat was closely correlated with the disappearance of barnacles. By November, 1965 only a small patch of dead barnacle tests remained, among which the 5 remaining *A. digitalis* were clustered. By January, 1966, all the barnacle tests were gone, and no *A. digitalis* were found in the quadrat nor elsewhere on the surrounding horizontal surface, from which all large barnacles had also disappeared. In contrast, moderate numbers of *A. scabra* remained.

Quadrat 5 (vertical; adjacent to and just below quadrat 4) overlapped the vertical boundary between the high and low species of *Acmaea*. Usually *A. digitalis*, *A. scabra*, and *A. paradigitalis* occupied the upper one third to two thirds of the quadrat, whereas *A. limatula* Carpenter, 1864 occupied the lower one third to two thirds along with a few *A. pelta* and *A. scutum*. Much of the considerable variability in numbers of *A. digitalis*, *A. paradigitalis*, and *A. limatula* was due to vertical movements of limpets into and out of the quadrat. Although not studied in detail, these movements may be related to tidal and weather factors. For example, in September, 1965 *A. limatula* moved up into the quadrat, *A. paradigitalis* and *A. digitalis* up out if it, following an unseasonable storm accompanied by heavy wave action. An anomalous feature of this quadrat in view of the transect results was the scarcity of *A. scabra*. Despite a moderate sized initial population of small individuals, there was never more than 1 individual after October, 1964.

Quadrats 6 - 9 illustrated population variations on a steeply sloping surface. These quadrats effectively formed a single vertical series with quadrat 6 the highest (quadrat 9 was the same height as quadrat 8 but, being laterally displaced, received more wave coverage; thus quadrat 9 was effectively lower than quadrat 8 – in zone 2 – while quadrats 8, 7, and 6 were in zone 1). The numbers of both *Acmaea scabra* and *A. digitalis* were consistently greatest in quadrat 9 and declined upwards. However, *A. scabra* declined faster than *A. digitalis*: in quadrat 8 its number reached zero on one occasion and quadrats 7 and 6 were essentially above its range. Two

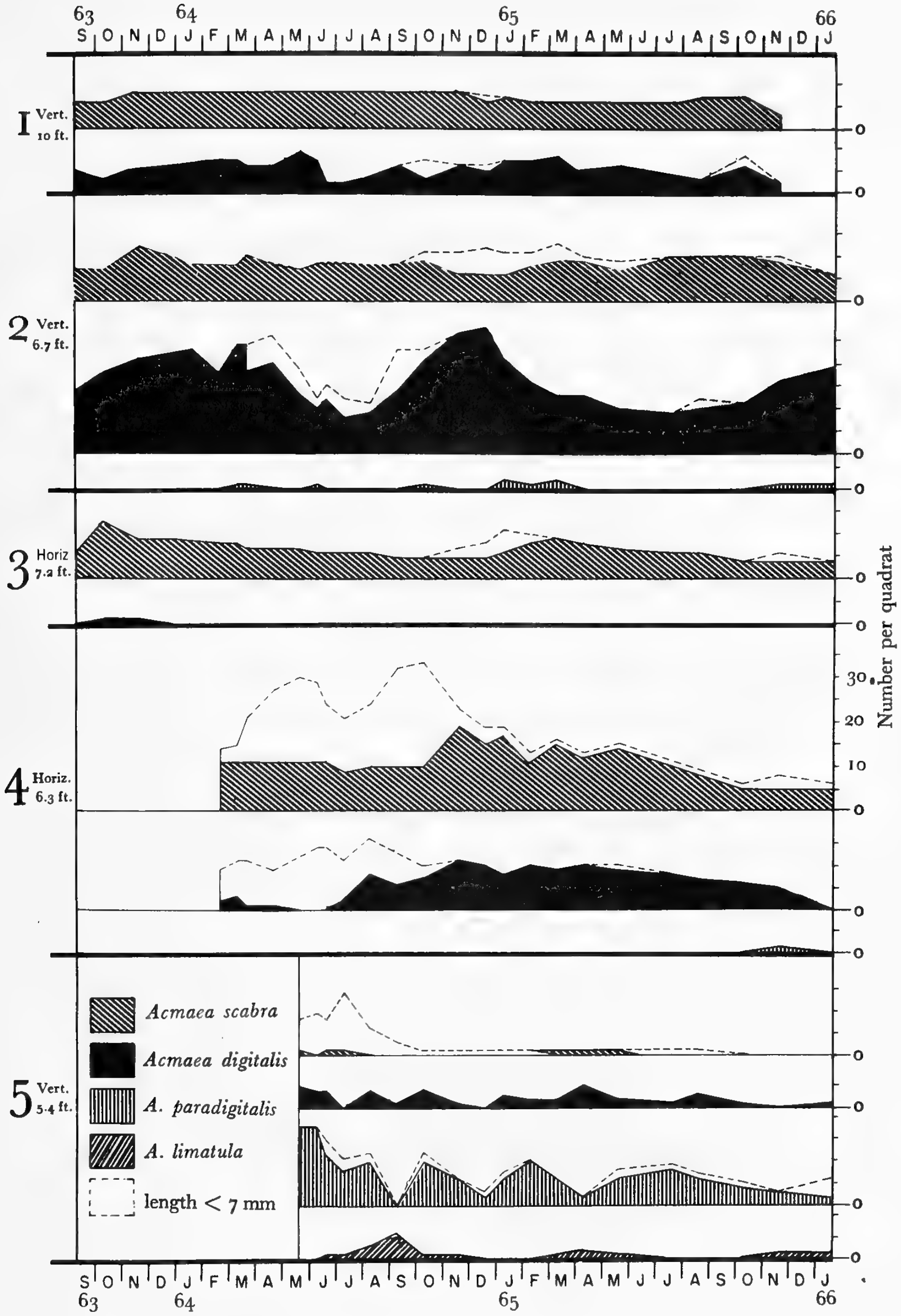

Figure 8

Population fluctuations in fixed quadrats 1 - 5. Slope and intertidal height are given for each quadrat; quadrat size is 20 × 20 cm. Dotted lines indicate individuals less than 7 mm long for all species (beginning March 1964 in quadrats 1 - 3)

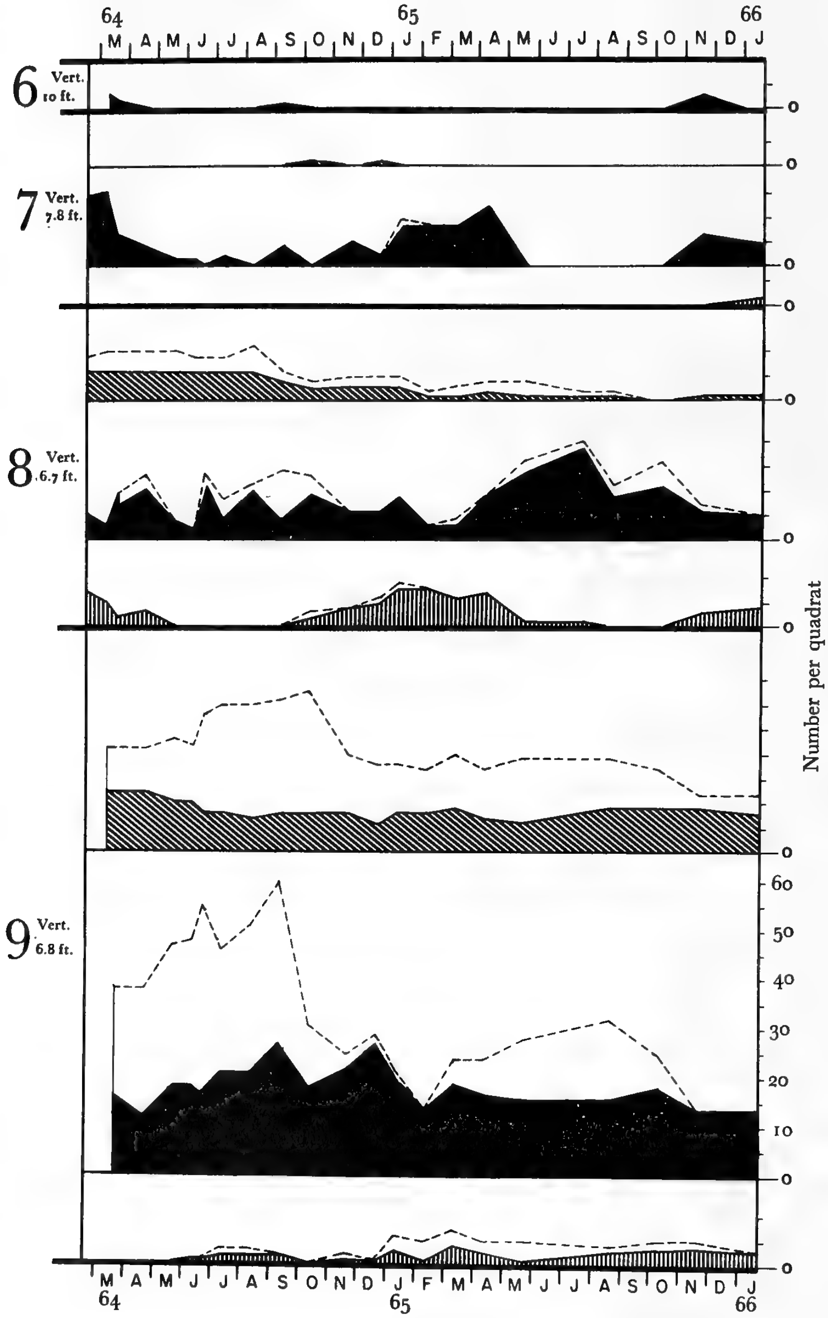

Figure 9

Population fluctuations in fixed quadrats 6 - 9. Explanation as in Figure 8 young individuals (less than 4 mm) were found in quadrat 7 on separate dates but disappeared within a month; none occurred in quadrat 6. *Acmaea digitalis,* although declining upwards, was the dominant species at higher levels: it usually outnumbered *A. scabra* in quadrat 8 and was virtually the only species in quadrats 7 and 6.

Variability in population density of *Acmaea digitalis* increased at higher levels. Although marked animals were not followed, much of this variability was clearly due to vertical and horizontal movements, both short-term and seasonal. Quadrat 7 showed the most pronounced seasonal pattern, with *A. digitalis* scarce or absent in summer but common in winter. That this was due in part to vertical movements (down in summer, up in winter) is supported by the reciprocal pattern shown (at least in 1965) about a foot below in quadrat 8. *Acmaea digitalis* in quadrat 2 also showed pronounced seasonal fluctuations attributable to movements. Likewise, the seasonal pattern of *A. paradigitalis* in quadrat 8 was due to vertical movements: when the limpets were absent from the quadrat (summer), large numbers were observed immediately below the quadrat, and vice versa. Quadrat 6, occupied only occasionally by *A. digitalis,* was not only the highest quadrat but also the least steeply sloping and the most protected from wave action. *Acmaea digitalis* presumably moved to this area only when conditions were particularly favorable (strong wave action, cool weather, etc.). It is noteworthy that on the outer face of this rock, which was directly exposed to incoming waves, large populations of both *A. scabra* and *A. digitalis* remained all year up to the same vertical level as quadrat 6; likewise, both species persisted in quadrat 1, at the same height as 6 but steeper and receiving more wave action.

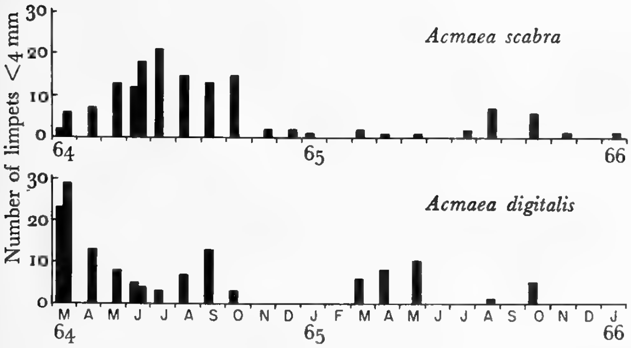

Figure 10

Recruitment of *Acmaea scabra* and *Acmaea digitalis* as indicated by abundance of limpets with length less than 4 mm. Data are summed from the 9 fixed quadrats

The relative contribution of small (2 - 7 mm), recently recruited individuals to the total population varied considerably among the quadrats. In general, recruitment was greatest at low intertidal levels for both species. This agrees with the size-frequency data presented earlier. Large numbers of small limpets occurred only in quadrats 9 (vertical) and 4 (horizontal), both of which were in zone 2. The upwards decrease in recruitment is shown by comparing these with quadrats 8-7-6 (vertical) and 3 (horizontal). It should be pointed out that the distribution and abundance of immediately post-settlement limpets (less than 2 mm long) is unknown.

The approximate timing of recruitment is shown in Figure 10, in which numbers of 2 - 4 mm individuals are pooled from all the quadrats. Recruitment occurred through most of the year, but was generally least during the winter months, and for unknown reasons was much less in 1965 than in 1964. Peaks in recruitment of *Acmaea scabra* and *A. digitalis* appeared to come at different times, usually in spring for *A. digitalis* and in summer and early fall for *A. scabra.* However, Figures 8 and 9 show that the timing and amount of recruitment varied considerably between the quadrats.

DISCUSSION

The transect data support the conclusion that populations of *Acmaea scabra* and *A. digitalis,* despite considerable spatial overlap, show significant differences in distribution and abundance with respect to microhabitat. To summarize the principal differences, in zone 1 *A. scabra* is dominant on horizontal or gently sloping surfaces; *A. digitalis* is largely restricted to vertical or overhanging rocks. Although *A. scabra* also occurs on vertical rocks, separation between the two species on these surfaces results from (a) the higher upper vertical limit of *A. digitalis* on some rocks, especially where this is magnified by seasonal upward movements of *A. digitalis;* (b) the higher vertical position of maximum population density of *A. digitalis;* (c) the increasing relative abundance of *A. digitalis* with increasing wave action; and (d) reduced individual size in *A. scabra.* In zone 2, although both species occur on horizontal surfaces in the presence of dense barnacle cover (moderate to strong wave action), *A. scabra* extends lower than *A. digitalis* regardless of slope.

Generalization of these habitat differences between *Acmaea scabra* and *A. digitalis* must take into account the great physical and biotic heterogeneity of the intertidal environment, and the inherent limitations of the sampling methods, such as possible bias in site selection, influence of habitat factors other than those tested, and possible alteration of limpet distribution by movements at high tide. Extensive observations at the study areas and elsewhere indicate at least that the habitat differences observed represent widespread rather than unusual local situations, and that they have considerable predictive value, particularly in the Monterey Peninsula area but also as far north as Sonoma County.

Previously published statements on microhabitat distribution of *Acmaea scabra* and *A. digitalis* have been based mainly on observational evidence, with some quantitative data available from general community studies. Some of these statements are supported by the present results, others are not, but a detailed comparison is not warranted (Hewatt, 1937; Test, 1945, 1946; Shotwell, 1950; Fritchman, 1961; Frank, 1965a; Glynn, 1965; Ricketts & Calvin, 1968).

The size-frequency data generally reinforce the transect evidence for microhabitat separation. The occurrence of the largest individuals of each species in different habitats – zone 1 horizontal rocks for *Acmaea scabra,* zone 1 vertical rocks for *A. digitalis* – implies that differential distribution between the two species would be even more pronounced on a biomass than on a numerical basis. Of particular interest is the reduced maximum size of *A. scabra* compared to *A. digitalis* on zone 1 vertical rocks where both species are abundant, especially since *A. scabra* is larger (i. e., about the same maximum size as *A. digitalis*) below and sometimes above the main *A. digitalis* population on these rocks. This hinted that interspecific competition might be occurring in this area of population overlap, an hypothesis which was confirmed by results of field experiments (Haven, in prep.).

Population fluctuations through time did not appear to be sufficiently great or irregular to alter the general pattern of microhabitat separation between *Acmaea scabra* and *A. digitalis.* In fact, the fixed quadrat data indicate a surprising temporal consistency in limpet population characteristics within very small areas (400 cm^2). As in the descriptive model of Andrewartha & Birch (1954), temporal population variability is greatest toward the extreme distributional limits; much of this variation, however, shows a discernable pattern, for example the seasonal vertical movements of *A. digitalis.* The one example of a major change in relative abundance – the disappearance of *A. digitalis* in quadrat no. 4 correlated with the decline of barnacles – is consistent with transect results which indicate that *A. digitalis* occurs on zone 2 horizontal rocks only in the presence of barnacle (or algal) cover. Of course, observations extending over many generations would be required to assess longterm numerical and distributional stability. Information on population dynamics is now available for *A. digitalis* in Oregon (Frank, 1965a), *A. scabra* at Bodega Bay, California (Sutherland, 1969), and both species at Santa Barbara, California (Stimson, 1968).

A demonstration of ecological differences in coexisting, closely related species can be approached from several points of view with respect to explanatory hypotheses and biological significance. One is a comparative autecological approach, which leads to explanations in terms of morphological, physiological, or behavioral adaptations of each species in relation to its environment (e. g., tolerance limits to physical factors). Other approaches are those of population and community ecology, which may focus on the population dynamics of individual species in order to explain distribution and abundance, as in the studies just cited, or, as in the present study, may be concerned with the role of competition and other species interactions (in an evolutionary perspective) in determining niche relationships and community dynamics in groups of species utilizing the same environmental resources.

To take the comparative autecological approach, the question can be asked, to what extent are the habitat differences between *Acmaea scabra* and *A. digitalis* explainable by differences in the morphological, physiological, or behavioral adaptations of each species. Since behavioral differences are clearly important, the evidence on these needs to be reviewed.

Acmaea scabra usually shows precise homing behavior, returning to exactly the same orientation on the same spot after each feeding foray at high tide. This was first demonstrated at Pacific Grove by Hewatt (1940) and confirmed by Brant (1950, unpublished) in probably the most thorough study to date on homing in limpets; Brant found, for example, that in 298 marked *A. scabra* whose movements at high tide were mapped for 24 days, 98.7% of 691 movements away from home scars terminated in return to the home sites. Jessee (1968a) found homing equally persistent at high and low intertidal levels and regardless of size above 6 mm. Observations in the present study, including mapping of limpets in the competition experiments, demonstrated homing in most *A. scabra* in zone 1 (Haven, unpublished). Villee & Groody (1940) concluded from a study in San Mateo County, California, that *A. scabra* does not show homing behavior; many individuals were never observed away from their homesites, which often were deep pits in soft rock. However, most of their data were based on periodic low tide observations; continuous observations during high tides might reveal movements and homing in these *A. scabra.*

Acmaea digitalis, on the other hand, generally does not exhibit precise homing behavior, as clearly shown by VILLEE & GROODY (1940); most individuals are found at different spots at successive low tides. FRANK (1965a) demonstrated seasonal vertical movement in *A. digitalis* in Oregon, upward in winter when greater wave action wets the higher levels, and downward in summer; also, there was a general upward movement with increasing age. FRANK (1964) also showed statistically that *A. digitalis,* while not homing precisely, has a home range, more restricted laterally than vertically. The fixed-quadrat and size-frequency data in the present study are consistent with the above results. *Acmaea digitalis* appears to show the same seasonal and vertical movements in California as in Oregon, except that the magnitude of these movements seems quite variable, depending on the extent of vertical surface available and the amount of variability in wave action. Recently at Pacific Grove, MILLARD (1968) demonstrated daily movements and considerable membership change in a group of *A. digitalis* clusters; and MILLER (1968) showed that *A. digitalis* moves upward at higher high tides and downward at lower high tides, and moves up or down within 24 hours of the onset or decline of heavy surf. This correlation of movements with surf conditions was also observed in the present study. Despite its well documented movements, there is some evidence for homing in *A. digitalis*: MILLER (1968) found about 25% homing at Pacific Grove, GALBRAITH (1965) found 54% homing in a sample of 26 in southern California, and in the present study a few *A. digitalis* were found with irregular shell edges precisely fitting the rock surface, indicating that homing had occurred. Further study is needed to ascertain any spatial or temporal pattern in the occurrence of homing in *A. digitalis.*

In summary, although homing behavior appears to be labile both within species and within individuals, one can conclude that, at least around Pacific Grove, *Acmaea scabra* is largely a homing species, *A. digitalis* largely a non-homing species. These behavioral differences can now be incorporated into hypotheses to explain the distributional differences between the two species.

First, active behavioral habitat choice appears to be the proximate cause of much of the observed distributional pattern of *Acmaea digitalis.* This is supported by the published evidence just cited and in the present study by the Mission Point experiments and the fixed quadrat data. Habitat choice behavior is probably much less important as an immediate cause of distribution in *A. scabra,* although occasional changes of home by adults and movements by pre-homing young individuals may play a role. For both species, the role of behavioral habitat choice in settling larvae is unknown.

A further hypothesis postulates differential resistance to desiccation, related to behavior, in *Acmaea scabra* and *A. digitalis.* Desiccation is widely recognized as a prime limiting factor in the high intertidal and splash zones; its importance for *A. scabra* and *A. digitalis* has been emphasized by TEST (1945, 1946), and its influence on other limpet species has been well studied (e. g., SEGAL & DEHNEL, 1962; DAVIES, 1969).

This hypothesis states first that *Acmaea scabra,* because of its homing behavior, has a greater resistance to desiccation than *A. digitalis.* Homing behavior allows the shell edge of *A. scabra* to grow precisely to fit small irregularities in the rock surface at the home site, whereas the shell of *A. digitalis,* although crenulated because of ribs, is generally much less irregular in outline and does not fit any particular spot on the rock precisely. This difference is obvious upon comparing series of shells from the same area (except where rock surfaces are exceptionally smooth) and is also clearly visible *in situ*: small gaps between *A. digitalis* shells and the rock surface contrast with the exact fit of *A. scabra* to minute surface irregularities. The implication is that a tighter fit between shell and rock may give *A. scabra* greater water retention ability and therefore greater resistance to desiccation. The hypothesis assumes secondly that on the average, horizontal or gently sloping surfaces experience greater desiccation than vertical or overhanging rocks because (1) solar radiation hits horizontal rocks at a steeper angle of incidence and is therefore more intense per unit area, and (2) the frequency and duration of shading decrease as rock slopes approach the horizontal. Reduced runoff rate may compensate for stronger insolation on horizontal rocks (FRITCHMAN, 1961), but my observations suggest that most "horizontal" rocks have sufficient slope to assure rapid runoff unless barnacle or algal cover is present.

The desiccation hypothesis was initially formulated to account for the dominance of *Acmaea scabra* on zone 1 horizontal rocks and the restriction of *A. digitalis* to zone 1 vertical rocks (the occurrence of the more tolerant *A. scabra* in both habitats is consistent). It is further supported by the occurrence of *A. digitalis* on zone 2 horizontal rocks in the presence of barnacle or algal cover, whose water retaining abilities are readily observable; the close correlation between the disappearance of *A. digitalis* and barnacles in fixed quadrat no. 4 (horizontal, zone 2) points to the necessity of barnacle cover despite the greater tidal coverage in zone 2. Similar evidence of lesser resistance to desiccation in *A. digitalis* than in *A.*

scabra is the appearance of *A. digitalis* on zone 1 horizontal and intermediate surfaces in the presence of algal cover, and its behavioral restriction to this cover as shown by the Mission Point experiments. Also consistent with the desiccation hypothesis are the relatively more aggregated dispersion and greater restriction to sheltered crevices and depressions in *A. digitalis,* and the increasing relative abundance of *A. digitalis* with increasing wave action, assuming that greater wave action reduces desiccation by increasing the frequency and duration of water coverage by waves and spray. The hypothesis would predict that *A. digitalis* should be relatively more abundant on north- than south-facing rocks, and should be progressively more restricted to steeper or more overhanging surfaces in more severely desiccated habitats (such as generally south-facing shores or shores protected from wave action but not from insolation). Observations at some sites bear out these predictions, but substantiating data are needed.

Temperature, either *per se* or as a primary cause of desiccation, needs also to be considered. *Acmaea scabra,* being a more southerly species, would be expected to tolerate higher temperatures than *A. digitalis.* Thus, high temperature stress should differentially affect habitat distribution of *A. scabra* and *A. digitalis* in the same direction as desiccation. Recent experiments by Hardin (1968) indicate that *A. scabra* does have a higher lethal temperature than *A. digitalis* and also experiences higher microhabitat temperatures. Test (1945) states that the northerly distribution of *A. scabra* is correlated with pockets of warmer water, and Fritchman (1961) discusses relationships between temperature, reproduction, and distribution in the two species. Segal & Dehnel (1962) observed *A. limatula* lifting its shell off the rock, probably for evaporative cooling. The apparent conflict between this process and the proposed function of tight shell fit for water retention in *A. scabra* needs to be investigated.

Some habitat differences between *Acmaea scabra* and *A. digitalis* are not consistent with the hypothesis that *A. scabra* is more resistant than *A. digitalis* to desiccation or high temperatures. Most important of these is the relatively lower position of *A. scabra* in the intertidal zone as indicated by the lower vertical position of (a) its peak population density, (b) its lower range limit, and (c) sometimes its upper range limit. In addition, *A. scabra* is commonly found permanently submerged in tide pools whereas *A. digitalis* is not.

This apparent paradox may be explained partly by a further hypothesis involving behavior. *Acmaea digitalis* may thrive at high levels because it can change its position, seeking out particularly sheltered spots when necessary and occupying the highest levels only in winter, when tides are highest, or at other times when desiccation is minimal due to reduced insolation or greater wave coverage or both. *Acmaea scabra,* with its homing behavior, cannot go higher than a permanently tolerable level (i. e., regularly submerged by tides), being unable to move away when conditions become adverse. This view is supported by the fixed quadrat results, particularly the sporadic occupation by *A. digitalis* of the highest quadrats, and is consistent with the previously cited information on movements in *A. digitalis.* Another hypothesis is that *A. digitalis* is better adapted than *A. scabra* to tolerate or even to require aerial conditions (e. g., for respiration), given that desiccation is not too severe. This could account for the tide pool distribution of *A. scabra* and for the fact that *A. digitalis* does not extend as low vertically as *A. scabra* – an explanation supported by some recent experiments. Kingston (1968) demonstrated that the limpet mantle fold functions in aerial respiration and has a greater blood capacity in *A. scabra* and *A. digitalis* than in lower *Acmaea* species; Baldwin (1968) found that under damp and aerial conditions *A. digitalis* has a much higher respiratory rate than *A. scabra,* whereas *A. scabra* has the higher rate when submerged.

In general, it appears that during the adaptive radiation of the genus *Acmaea* on the North American west coast, both *A. scabra* and *A. digitalis* became adapted to occupy the higher intertidal and splash zones by evolving the necessary abilities to tolerate greater extremes of aerial exposure and desiccation than were encountered by species occupying lower levels (Test, 1945, 1946). However, *A. scabra* and *A. digitalis* followed different strategies in doing so, and this contributed to their microhabitat separation: *A. scabra* adopted homing behavior, enabling it to occupy the most severely desiccated microhabitats (e. g., zone 1 horizontal rocks) but only if permanently tolerable, whereas *A. digitalis* followed a strategy of active behavioral regulation of its distribution, allowing it to occupy temporarily favorable habitats but restricting it largely to surfaces (e. g., vertical rocks) somewhat protected from desiccation. This view, although oversimplified and subject to further testing and modification, suggests that the microhabitat differences between *A. scabra* and *A. digitalis* can be partly accounted for, in terms of proximate causes, by the responses of each species to the physical environment.

Turning to a community ecological viewpoint, the role of interspecific competition is of principal concern (predation and other biotic influences are not discussed here because of lack of evidence). Fundamental questions regarding interspecific competition include (1) what is its role as a proximate (demographic) factor affecting the microhabitat differences between *Acmaea scabra* and *A. digitalis,* (2) what is its role as a selective pressure favoring evolutionary divergence – i. e., the evolution of the above-mentioned adaptive differences, and (3) do the observed niche differences prevent competitive exclusion, and are they therefore a necessary condition for the stable coexistence of *A. scabra* and *A. digitalis.*

The classical approach to competition based on the exclusion or Gause's principle says (among other things) that stably coexisting species must exhibit significant niche differences with respect to their shared resources. *Acmaea scabra* and *A. digitalis* can no longer be considered an exception to this generalization. Their niches are partly non-overlapping in the two principal dimensions in which competition can occur – space and food. Spatial separation is directly demonstrated by the transects; and although *A. scabra* and *A. digitalis* eat the same type of food (encrusting microalgae), they utilize different parts of the total food resource by virtue of their spatial separation. They are thus consistent with the other species of the genus *Acmaea* in showing pronounced niche segregation (Test, 1945). In central California, *A. scabra* and *A. digitalis* are separated from all but three of their congeners at least by differences in vertical intertidal range. Of the three, two have specialized niches (*A. persona* Rathke, 1833 is restricted to caves or other extremely shaded sites, *A. fenestrata* (Reeve, 1855) to the bases of rocks situated in sand), and the third, *A. paradigitalis* shows some differences (Fritchman, 1960) but needs more study with respect to overlap with *A. scabra* and *A. digitalis* (Haven, 1966). Niche segregation among coexisting, ecologically similar or closely related species has been demonstrated in the other groups of marine benthic invertebrates which have been studied (citations given in the introduction).

However, niche segregation does not necessarily imply the existence of, nor a causal role for, interspecific competition or competitive exclusion (Hutchinson, 1965; Birch, 1957). It is therefore desirable to have direct evidence for the occurrence of competition. Such evidence was obtained by field exclosure experiments with *Acmaea scabra* and *A. digitalis*; the two species compete for food where their niches overlap on zone 1 vertical rocks. Further discussion of competition will be deferred to the paper reporting these results (Haven, in preparation); in general they indicate a proximate demographic role for competition and support the view that the niche differences are a necessary condition for the coexistence of *A. scabra* and *A. digitalis.*

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Marine Fouling and Boring Organisms at 100 Feet Depth in Open Water of Monterey Bay

BY

EUGENE C. HADERLIE

Department of Oceanography, Naval Postgraduate School, Monterey, California 93940

(3 Figures, 2 Tables)

INTRODUCTION

Continuous studies on the fouling and boring organisms of Monterey Harbor and the open water of Monterey Bay down to depths of 50 feet have been underway since 1966. The initial results of these investigations have been published (Haderlie, 1968a; 1968b; 1969). In June, 1967, a study was initiated on the organisms that attach to or drill into test panels exposed to the marine environment of the open water of Monterey Bay at depths of 100 feet. The present paper summarizes the results of this investigation which extended over a 33 month period from June 1, 1967, to March 1, 1970. At the present time additional studies are being conducted at water depths of 200 feet and the results of these investigations will be reported in time.

As in previous studies, the primary objective of the investigation reported on here was to obtain information on the kinds of marine organisms that settle on or bore into test panels exposed to the marine environment. In addition it was hoped to learn something about the season or seasons of settlement, to determine preference for substrate, and to determine rate of growth and longevity of different organisms.

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AREA OF STUDY

The initial site chosen for this study was on the southern edge of the firing range approximately 1 nautical mile off Fort Ord in 100 feet of water (Figure 1). From the beginning it was apparent that swell and wave action would make it difficult to keep the arrays securely moored and in place. Monterey Bay is open to the Pacific and the area off Fort Ord receives the full impact of long period swell from the open ocean. None-the-less, it was possible to keep at least some arrays in place for a period of 9 months from June 1, 1967, until the end of February, 1968, when all except one array with Short Term panels attached were lost to storm waves. In anticipation of this difficulty, a new site was chosen in January, 1968, which was nearer the southern end of the Bay where some protection is afforded by the northerly projecting Monterey Peninsula. This new site was 1 nautical mile due north of Del Monte Beach in 100 feet of water (Figure 1). A complete set of arrays were planted off Del Monte immediately after the loss at the Fort Ord site occurred in late February, and a new series of collections began. There is, therefore, no break in the record of data. Although some losses due to winter storms were sustained, sufficient spare arrays were deployed at the Del Monte site to give continuous records for two full years.

The bottom of the Bay at both sites is sandy and relatively firm and flat. The water is clean and free of obvious pollutants. Due to lack of time and facilities, no physical parameters at the depth of the test panels were measured. For the first 20 months of the study surface temperatures were measured once a month at the test site and these varied from lows of 11.0° C recorded in December to highs of 16.0° C recorded in late summer and early fall. Previous studies in the southern end of the Bay (Bolin

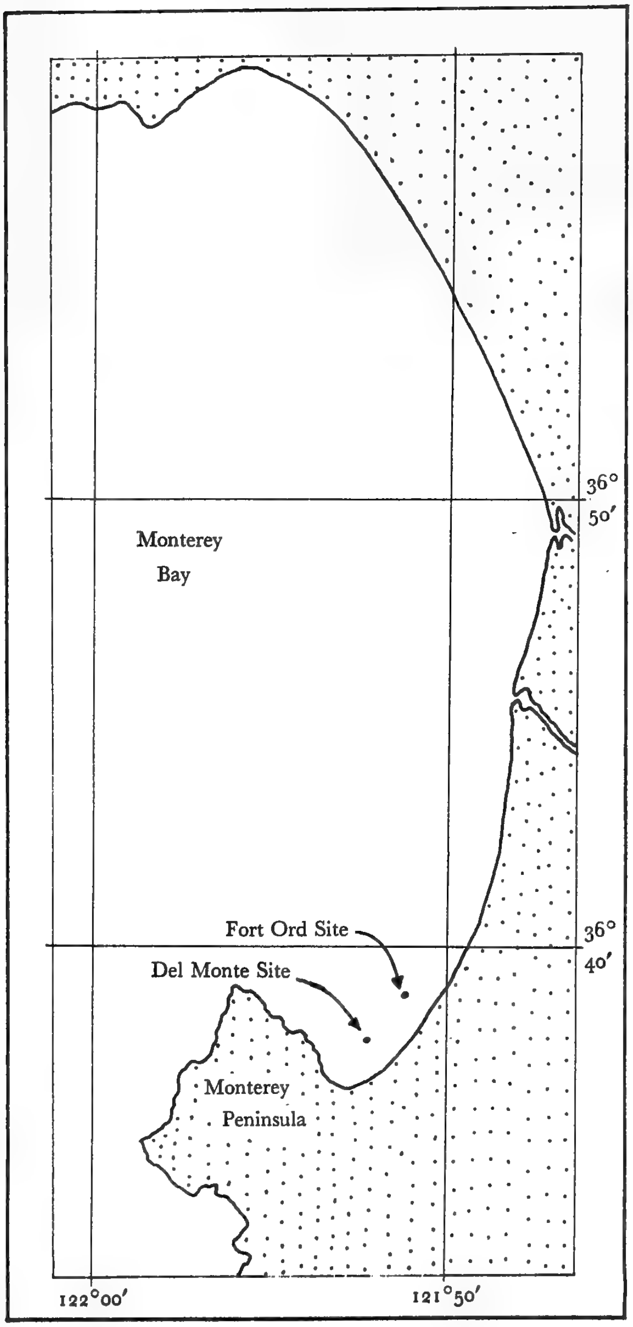


Figure 1

Map of Monterey Bay showing sites of fouling arrays off Fort Ord and Del Monte Beach

and Abbott, 1963) have shown that surface salinities are relatively constant during most years with averages ranging from 32.8 ‰ to 33.8 ‰. The tide at the sites of this study has a maximum range of 8 feet during springs and a mean range of 3.5 feet. Very little is known regarding current patterns in this part of the Bay, but the currents seem to be sluggish. Winter storms, however, can create considerable turbulence.

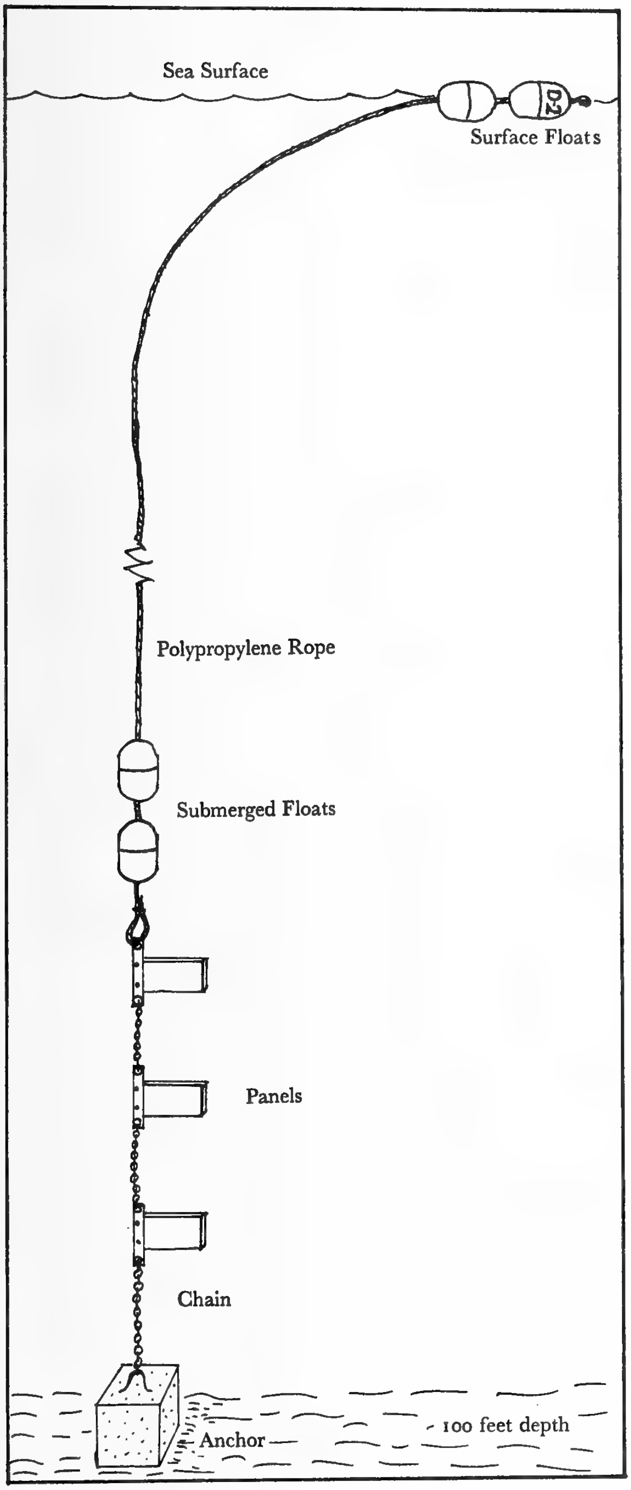
MATERIALS AND METHODS

For many years the Naval Oceanographic Office has been conducting surveys of boring and fouling organisms in coastal waters of the world. In these studies standard test surfaces are employed at all sites so that results are comparable (De Palma, 1966). Similar test panels have been and are being employed in Monterey Bay.

In this investigation each test panel employed consisted of one piece of 1/4 inch thick black asbestos board (Johns-Manville Colorlith) and one piece of 3/4 inch thick flat sawn and planed douglas fir lumber. Each piece measured 6 inches by 12 inches and the two were attached back to back with brass screws. Previous studies by many workers have shown that black asbestos board is an effective collector of most fouling organisms. The wooden part of the test panel was employed primarily to collect wood boring organisms, but it also collected foulers and by comparing these with the population settling on the asbestos board it was possible to determine substrate preference for certain fouling organisms. These panels were of such size as to be handled easily in the field and the laboratory, yet were large enough to present a reasonable surface area for the settlement of organisms.

The panels were arrayed as shown in Figure 2. This arrangement was somewhat different from that employed previously (De Palma, 1966; Haderlie, 1968b) for in earlier work in Monterey Bay at the 50 foot level it was found that the polypropylene rope often failed at points of panel attachment due to abrasion and chafing. In the present study, therefore, the panels were not attached directly to the rope. On the end of each panel a bar of stainless steel measuring 8 inches × 1 inch × 1/4 inch was secured with stainless steel bolts. This bar had holes in each of the ends. Panels were fastened together by shackles in this attachment bar and an 18 inch length of 1/4 inch galvanized chain.

The mooring system consisted of an anchor made of a clump of concrete weighing 175 pounds in which a galvanized eye-bolt was embedded for securing the buoyant



(← adjacent column)

Figure 2

Sketch of fouling array

array. From the anchor a 2 foot length of chain extended to the attachment bar of the lowest panel. In the work reported on here at depths of 100 feet, 3 panels were attached to each array. From a shackle on the attachment bar of the upper panel a 3/8 inch length of 3-strand black polypropylene rope extended upward to the water's surface. To keep the panels in a vertical orientation and to prevent their rubbing together, two plastic toggle floats (5 inches by 9 inches "Butyrate") were attached to the line immediately above the panels. These floats kept the panels vertical and the connecting chains taut, yet the panels were free to rotate and like flags could align themselves with the direction of water movement. The polypropylene rope above these bottom floats was slack and being slightly positively buoyant tended to float upward. At the upper end of the rope two additional toggle floats were secured and these were used for locating and recovering the arrays. Sufficient scope of rope was used to insure that the upper floats were not pulled under at high tide nor during normal wave action. Even if the upper floats were pulled under by an exceptionally high wave, however, the total buoyancy of the floats was insufficient to lift the heavy anchor off the bottom. The anchors on the arrays off Fort Ord were buried due to sand shifts and this made recovery of the arrays difficult and in a few cases impossible. Off Del Monte Beach this was never a problem. Most of the losses at both sites was due to corrosion weakening the chains or shackles which broke and allowed the arrays to drift away. The galvanized hardware, therefore, had to be replaced periodically, usually after about six months submergence. Some arrays were lost due to fishing vessels running over the floats at night and breaking them or cutting the polypropylene ropes. During the last two years of the project off Del Monte Beach a total of 18 arrays with 3 panels each were planted and 11 of these were recovered. Except for the loss of an array containing a panel that was meant to collect settlers during the month of November, 1967, the record of data for the entire 33 month period of study is continuous and unbroken.

Two series of test exposures were used in this investigation at 100 feet depth. Short Term panels were exposed on the first of every month and recovered the first of the following month for the entire period. These panels provided data on the season of settlement of different animals up to one month after settlement, and gave information on the nature of the pioneer fouling communities at dif- throughout the year, the rate of growth during periods ferent times of the year. A second series of panels called Long Term panels was exposed for one month and for cumulatively longer periods of time up to 12 months. The entire year-group of these panels was exposed at the same time; one was removed at the end of one month, a second at the end of two months, and so cumulatively up to 12 months. The Long Term panels exposed at the Fort Ord site remained in the water for a maximum of only 9 months (June, 1967, through February, 1968) before the arrays at this site were lost. At the Del Monte Beach site, however, panels exposed in March, 1968, remained in place for periods up to 12 months when a new series was planted that remained for up to another year until March 1, 1970.

Arrays used in this study were planted and recovered using a hydrographic winch on a 63 foot hydrographic research vessel. On the first of each month throughout the study period one of the arrays was lifted to the surface and appropriate panels removed. One month following the initial planting an array would be raised and one panel removed; this was used as the first of the Short Term panels, but also served as a one-month panel of the Long Term series. Before replanting the array a new Short Term panel was attached. At the beginning of the next month this Short Term panel was removed and another new one attached. At the same time a Long Term panel that had now been exposed for 2 months was removed. This routine of removing one Short Term panel and one Long Term panel and adding one new Short Term panel continued monthly throughout the year.

On raising the arrays the panels were out of the water for only a short time. Panels removed for study and laboratory analysis were immersed in a tub of sea water and were kept in sea water until the analysis in the laboratory was completed. As the panels were taken to the laboratory immediately after returning to port, the time involved from recovery at sea until analysis was begun rarely exceeded 2 hours. The animals on the panels were therefore all alive and active and this made analysis and identification much easier.

In the laboratory the panels were immersed in enamel pans full of cold sea water and the panel surface carefully surveyed with a binocular stereoscopic microscope (×7 to ×30 magnification). This procedure made possible the discovery of small forms such as protozoans and the newly settled stages of barnacles and serpulid worms and the early stages of wood borers. This technique also made it possible to locate and identify many of the non-sedentary or loosely attached organisms that are often a characteristic part of the fouling community but which are often lost if panels are preserved in any way before they are analyzed. During the analysis of each panel, after identification of the foulers the numbers and size of each species were recorded. This procedure was carried out on both the asbestos and the wood surfaces. On the wood a special effort was made to search for evidence of wood borers. Following the analysis of each of the Long Term panels the asbestos side was scraped clean of all fouling growth and the scrapings were oven dried at 100° C until the weight was constant. The results are shown on the bottom line of Table 2 and are expressed as grams of dry weight of tissue and shell per panel side (0.5 sq. ft.). The amount of growth on the Short Term panels was usually so slight that this procedure of scraping and weighing was not carried out. The results of the weight analysis on the Long Term panels should provide a rough statistical measure of the concentration and size of organisms and an index to the productivity of the environment for the specific period of exposure. In practice, however, this is not possible, for on many of the panels exposed for several months it was obvious that the mass of barnacles, for example, had become so great that they had broken off in large slabs. In other cases most of the weight of the scraping was made up of the dead shells of barnacles that had been there for several months. In rough weather some of the fouling growth was accidentally broken off the panels during recovery operations. A combination of all these factors resulted in the rather meaningless weight figures given in Table 2, particularly for the older panels.

The wooden part of each test panel was not scraped but was dried and saved as a reference. In many of the older panels, however, there was little or no wood left due to the activities of wood borers.

At each 3 month interval, after the last panel was removed from an array, the entire array—floats, polypropylene rope, chain and anchor—was recovered and analyzed for the more obvious macroscopic fouling organisms. The upper floats after being in the water for several months usually carried heavy growths of a variety of algae such as *Polysiphonia acuminata* Gardner, 1927; *Ulva linza* Linnaeus, 1753; and *Enteromorpha* sp.; and were commonly fouled with the barnacle *Lepas anatifera* (Linnaeus, 1758). The upper parts of the polypropylene ropes also were fouled with the algae noted above but also often carried small specimens of *Macrocystis pyrifera* Agardh, 1820. The dominant fouling organisms on the ropes, however, were massive growths of *Obelia* sp. and the soft ectoproct *Bowerbankia gracillis* O'Donoghue, 1926. Associated with the organisms on the ropes were numerous nudibranchs, especially *Hermissenda crassicornis* (Eschscholtz, 1831) and *Dendronotus frondosus* (Ascanius, 1774) and skeleton shrimps (*Caprella californica* Stimpson, 1857). The lower floats were sometimes covered with the acorn barnacle *Balanus crenatus* Bruguière, 1789, and occasionally also carried a few specimens of the barnacle *Balanus tintinnabulum* (Linnaeus, 1758). Also commonly attached to the lower floats were sedentary polychaetes such as *Chitinopoma groenlandica* (Mörch, 1863) and the rock oyster *Pododesmus cepio* (Gray, 1850). The concrete anchors were all fouled with *Balanus crenatus* and *Chitinopoma groenlandica* and often carried dozens of nudibranchs, mainly *Acanthodoris brunnea* MacFarland, 1905.

THE FOULING COMMUNITY

1. Discussion of Organisms Settling on Short Term Panels and Substrate Preference

During the 33 months of this study a total of 28 different kinds of animals settled on or bored into the test panels exposed for monthly periods throughout the year at a depth of 100 feet (Table 1). This number of animal species settling is less than was found on panels exposed at 50 feet depth in an earlier study (Haderlie, 1968b) where 32 species were recorded. With the exception of two rare hydroids, no species were found settling at 100 feet depth that were not also found at 50 feet. As can be seen from Table 1 some organisms settled during practically every month of the year while others settled seasonally or rather erratically.

The dominant and most consistent foulers settling on the Short Term panels were serpulid worms (*Chitinopoma groenlandica*), acorn barnacles (*Balanus crenatus*), and hydroids (*Obelia* sp.). Other species were less abundant and encountered less frequently. The following discussion will review briefly the most common organisms of each major group listed in Table 1. Where there appears to be data supporting substrate preference these will be discussed also.

Protozoa:

The only protozoan that was regularly found on the one-month panels was the suctorian *Ephelota gemmipara*. This organism was commonly associated with the hydroid *Obelia* sp. where it attached to the perisarc of the hydroid colonies, but was also often found covering the shells of barnacles and also on the wooden and asbestos surfaces totally independent of other attached organisms. The colonial ciliate *Zoothamnium* sp. was seen only once, on a panel submerged during January, 1967. Foraminiferans were also rare on the Short Term panels.

Coelenterata:

Obelia sp. settled sporadically during most of the months of this investigation and often during late summer and early fall would be one of the dominant organisms on the Short Term panels. In a period of one month the colonies were usually not more than 1 cm tall, but on one panel submerged during August, 1967, the *Obelia* growth all over the panel was a dense mass with individual stalks being up to 5 cm tall. On a panel removed after being in the water during March, 1968, the lush growth of *Obelia* had gonangia filled with medusae. Other hydroids were encountered only rarely and usually in small numbers. One of these, *Clytia* sp., released masses of tiny medusae when the panel on which it was growing was removed to the laboratory after being submerged during June, 1967.

Platyhelminthes:

Two species of flatworms were recorded from these panels, but only *Notoplana acticola* was found on more than one occasion. As will be seen below, flatworms were more abundant and varied on the Long Term panels.

Ectoprocta:

Ectoprocts, which are the dominant fouling animals in Monterey Harbor, are much less common in deeper water of the Bay. Only one species was found to have settled on the Short Term panels at 100 feet depth, and this was found only once.

Annelida:

Although four species of annelids were recorded from the one-month panels, only *Chitinopoma groenlandica* was common and it proved to be one of the most consistent settlers observed. In earlier papers (Haderlie, 1969; Smith and Haderlie, 1969) this serpulid was referred to as *Chitinopoma occidentalis* (Bush, 1904). In a recent publication by Hartman (1969) this species is referred to as *Chitinopoma groenlandica* (Mörch, 1863) and will be so designated in this paper. Small specimens of *Chitinopoma* 2–3 mm long were found to have settled during most months of the year. December–February were periods of minimal settling. May–September seemed to be the months of maximum settling and often hundreds of small tubes up to 7 mm long could be found on a panel face.

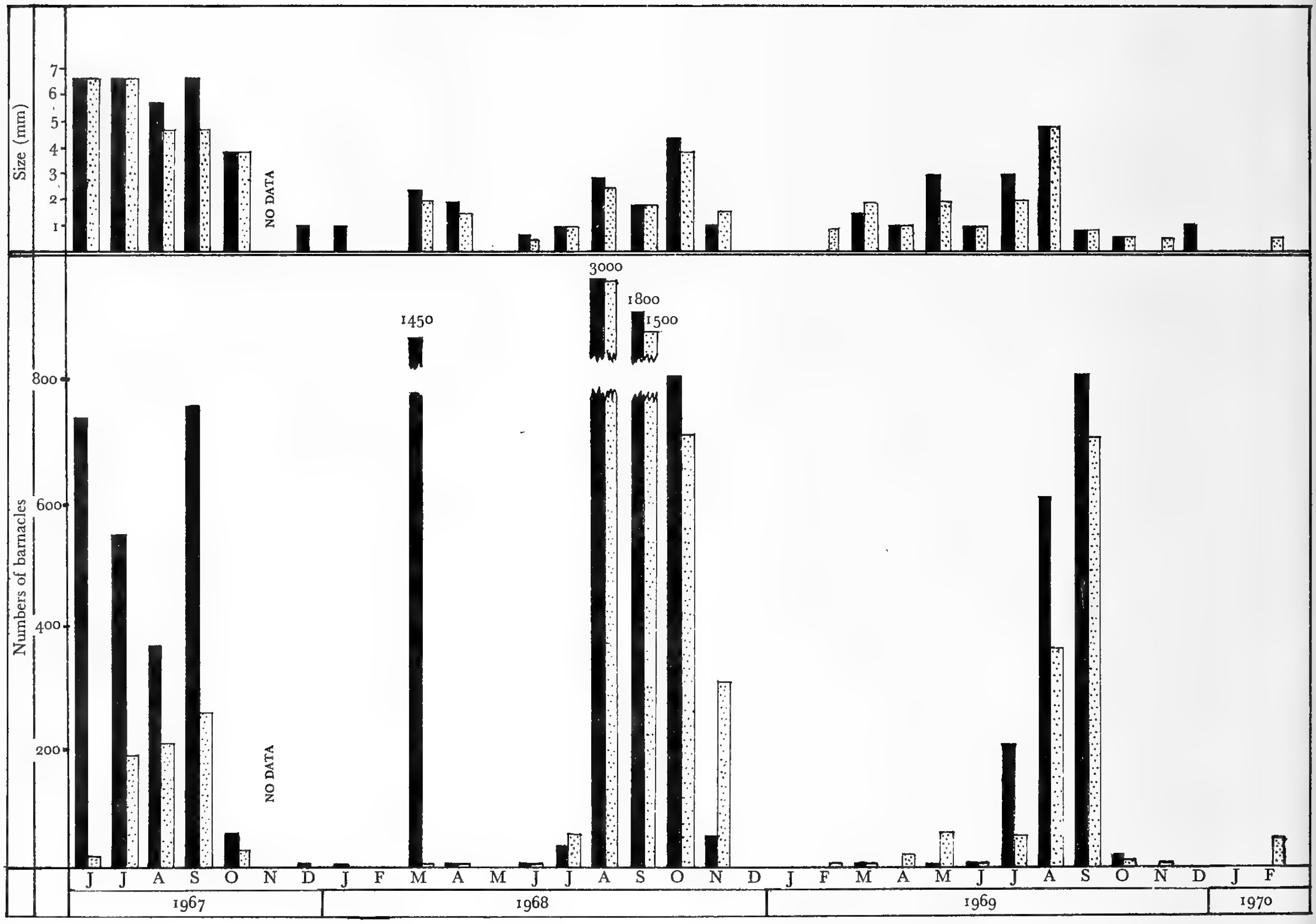


Figure 3

Numbers and sizes of *Balanus crenatus* settling on Short Term Panels

During September, 1968, *Chitinopoma* settled in numbers of 10/sq. inch on an asbestos panel. The worms seemed to prefer asbestos to wood as a settling surface, and on asbestos they showed no particular tube orientation. On the wood panels, however, the tubes were nearly all lined up with the grain of the wood.

Arthropoda:

Free-moving and tube-dwelling amphipods and an occasional small crab were seen on the Short Term panels,

Explanation to Table 1

Symbols used at head of columns indicate:

A = Asbestos board panel
W = Wooden panel

Symbols used in columns indicate:

1 = species present in numbers from 1 to 10 individuals or colonies per panel side
2 = species present in numbers from 11 to 20 individuals or colonies per panel side
3 = species present in numbers upward from 20 individuals or colonies per panel side

Species	1969																1970			
	May		June		July		Aug		Sept		Oct		Nov		Dec		Jan		Feb	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																				
Rosalina columbiensis (Cush														1						
Ephelota gemmipara (Hartw	3	3	3	3	3	3	3	3			3	3	3	3						
Zoothamnium sp.																				
Coelenterata:																				
Clytia sp.																				
Hydractinia sp.																				
Syncoryne mirabilis (Agassiz																				
Obelia sp.					1	1	3	2		2	1				2	2				1
Platyhelminthes:																				
Notoplana acticola (Boone,																				
Pseudocerous sp.									1											
Ectoprocta:																				
Celleporella hyalina (Linna													1							
Annelida:																				
Chitinopoma groenlandica (	2	2	3	3	3	3	3	2	3	3	1	1	2	1				1		1
Platynereis agassizi (Ehlers,																				
Polydora brachycephala Ha									2											
Sabellaria cementarium Mo																				
Arthropoda:																				
Balanus crenatus Bruguière	1	3	1	1	3	3	3	3	3	3	2	2		1	1					3
Lepas anatifera (Linnaeus,																				1
Caprella californica Stimpso													1			1				
Caprella sp.																				
Corophium insidiosum Cra																				
Loxhorynchus sp.																				
Mollusca:																				
Dendronotus albus MacFarl																				
Dendronotus frondosus (As																				
Hermissenda crassicornis (E							1	1												
Trinchesia albocrusta (Mac	1																			
Acanthodoris brunnea Mac					1		3	3	2											
Triopha grandis MacFarlan																				
Pododesmus cepio (Gray, 18																				
Bankia setacea (Tryon, 1863		1										3				3		3		3

Table 1

List of Species, and of Panels where Organisms Settled in Short Term Series

Species	1967 June		July		Aug		Sept		Oct		Nov		Dec	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:														
Rosalina columbiensis (Cushman, 1925)											No data, panel lost	No data, panel lost		
Ephelota gemmipara (Hartwig, 1876)					3	3	3	3	3	3			3	3
Zoothamnium sp.														
Coelenterata:														
Clytia sp.	3	3				1								
Hydractinia sp.					1	2								
Syncoryne mirabilis (Agassiz, 1862)														
Obelia sp.					3	3	3	3	2	2			2	2
Platyhelminthes:														
Notoplana acticola (Boone, 1929)			1				2		2	1				
Pseudoceros sp.														
Ectoprocta:														
Celleporella hyalina (Linnaeus, 1767)														
Annelida:														
Chitinopoma groenlandica (Mörch, 1863)	2		1		1		1	1	1					
Platynereis agassizi (Ehlers, 1868)			1											
Polydora brachycephala Hartman, 1936					1		3							
Sabellaria cementarium Moore, 1906													1	
Arthropoda:														
Balanus crenatus Bruguière, 1789	3	2	3	3	3	3	3	3	3	3			1	
Lepas anatifera (Linnaeus, 1758)														
Caprella californica Stimpson, 1857							2		3					
Caprella sp.			1											
Corophium insidiosum Crawford, 1937														
Loxorhynchus sp.			1		1									
Mollusca:														
Dendronotus albus MacFarland, 1966					2									
Dendronotus frondosus (Ascanius, 1774)	1				2	2								
Hermissenda crassicornis (Eschscholtz, 1831)			1	1	2	2	3		1					
Trinchesia albocrusta (MacFarland, 1966)					2	2				1				
Acanthodoris brunnea MacFarland, 1905					2	2			2	1				
Triopha grandis MacFarland, 1905														
Pododesmus cepio (Gray, 1850)			1		1		1			1				1
Bankia setacea (Tryon, 1868)														3

Species	1968 Jan		Feb		Mar		Apr		May		June		July		Aug		Sept		Oct		Nov		Dec	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																								
Rosalina columbiensis (Cushman, 1925)																								
Ephelota gemmipara (Hartwig, 1876)	3	3	3	3										2							3	3		
Zoothamnium sp.	3	3																						
Coelenterata:																								
Clytia sp.																								
Hydractinia sp.																								
Syncoryne mirabilis (Agassiz, 1862)																						1		
Obelia sp.					3	3	2				1	1	3	3	1	1						1		
Platyhelminthes:																								
Notoplana acticola (Boone, 1929)					1	1																		
Pseudoceros sp.																								
Ectoprocta:																								
Celleporella hyalina (Linnaeus, 1767)																								
Annelida:																								
Chitinopoma groenlandica (Mörch, 1863)					1		1	1	3	2	3	3	3	3	3	3	3	3	3	3	3	3	2	2
Platynereis agassizi (Ehlers, 1868)																								
Polydora brachycephala Hartman, 1936																								
Sabellaria cementarium Moore, 1906																								
Arthropoda:																								
Balanus crenatus Bruguière, 1789	1				3	1	1	1			1	1	3	3	3	3	3	3	3	3	3	3		
Lepas anatifera (Linnaeus, 1758)																								
Caprella californica Stimpson, 1857																								
Caprella sp.																								
Corophium insidiosum Crawford, 1937																								
Loxorhynchus sp.																								
Mollusca:																								
Dendronotus albus MacFarland, 1966																								
Dendronotus frondosus (Ascanius, 1774)																								
Hermissenda crassicornis (Eschscholtz, 1831)																					1			1
Trinchesia albocrusta (MacFarland, 1966)																	1							
Acanthodoris brunnea MacFarland, 1905																			2	2				
Triopha grandis MacFarland, 1905																				1				
Pododesmus cepio (Gray, 1850)																								
Bankia setacea (Tryon, 1868)		2		3				1		2		2		1										2

Species	1969 Jan		Feb		Mar		Apr		May		June		July		Aug		Sept		Oct		Nov		Dec		1970 Jan		Feb	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																												
Rosalina columbiensis (Cushman, 1925)																						1						
Ephelota gemmipara (Hartwig, 1876)					3	3	3	3	3	3	3	3	3	3	3	3			3	3	3	3						
Zoothamnium sp.																												
Coelenterata:																												
Clytia sp.																												
Hydractinia sp.																												
Syncoryne mirabilis (Agassiz, 1862)																												
Obelia sp.					1		1	1					1	1	3	2		2	1				2	2				1
Platyhelminthes:																												
Notoplana acticola (Boone, 1929)																												
Pseudoceros sp.																	1											
Ectoprocta:																												
Celleporella hyalina (Linnaeus, 1767)																					1							
Annelida:																												
Chitinopoma groenlandica (Mörch, 1863)		1			2	1			2	2	3	3	3	3	3	2	3	3	1	1	2	1				1		1
Platynereis agassizi (Ehlers, 1868)																												
Polydora brachycephala Hartman, 1936																	2											
Sabellaria cementarium Moore, 1906																												
Arthropoda:																												
Balanus crenatus Bruguière, 1789				1	1	1	1	2	1	3	1	1	3	3	3	3	3	3	2	2		1	1					3
Lepas anatifera (Linnaeus, 1758)																												1
Caprella californica Stimpson, 1857																					1			1				
Caprella sp.																												
Corophium insidiosum Crawford, 1937																												
Loxorhynchus sp.																												
Mollusca:																												
Dendronotus albus MacFarland, 1966																												
Dendronotus frondosus (Ascanius, 1774)																												
Hermissenda crassicornis (Eschscholtz, 1831)	1						1								1	1												
Trinchesia albocrusta (MacFarland, 1966)					1	1			1				1		3	3	2											
Acanthodoris brunnea MacFarland, 1905																												
Triopha grandis MacFarland, 1905																												
Pododesmus cepio (Gray, 1850)																												
Bankia setacea (Tryon, 1868)		3				3				1										3				3		3		3

but the only arthropod encountered regularly was the acorn barnacle *Balanus crenatus.* In terms of numbers of individuals settling this species was clearly the dominant fouling organism at 100 feet depth. Small barnacles were seen on the panels during every month of the year at one time or another but, as can be seen in Table 1, January was clearly a period of minimal settling during most years and December and February were also low periods. Figure 3 presents these data in more detailed form and also shows the maximum size attained by the barnacles during any one month. The size recorded was that achieved at the time the panel was removed and depending on settling time the barnacles could be of any age from a few hours to one month. It appears, however, that *Balanus crenatus* can grow to a maximum size of 7 mm diameter in one month during the summer at 100 feet depth. During the summer months *Balanus crenatus* must grow most rapidly during the first few weeks or months, for the largest specimens ever observed on Long Term panels were 12 mm in diameter, and these were on panels exposed for 3 months from June 1 to September 1, 1967. Figure 3 also illustrates that periods of maximum settlement were also, in general, periods of maximum growth. Asbestos board was preferred to wood as a substrate in most cases, although exceptions exist. Also, maximum sizes achieved were, as a whole, greater on asbestos board than on wood. A curious exception to the above occurred in November, 1968, when 6 times as many barnacles settled on the wood as on the asbestos board and achieved a greater size on the wood.

During most of the time this study was in progress at the 100 foot level a similar study closer inshore at depths of 50 feet was also proceeding (Haderlie, 1968b, and unpublished data). During any one month at the 50 foot level *Balanus crenatus* never achieved a size greater than 4.5 mm. It is also interesting to compare settling times at the two depths at sites that were only about ½ mile apart. In 1967 the maximum settlement period at 50 feet was during August (900 settled per panel surface), whereas in July and September far fewer settled (from 1–5 barnacles per panel surface) and in June none settled. One half mile further out in the Bay, however, at 100 feet depth, June and September were periods of maximum settlement (over 700 per panel surface) whereas August had about half this number. Another strange anomaly occurred in March, 1968. No barnacles settled on panels at 50 feet during the month, yet 1450 settled on the asbestos panel at 100 feet. In August, 1968, only 50 barnacles settled on a panel at 50 feet, yet 3000 settled on a similar panel at 100 feet.

The foregoing discussion illustrates the difficulty of predicting settling time and growth rates of fouling organisms when one has data for only a short period of time or from one depth. It is obvious that several years' data from various depths must be collected before the variations can be appreciated and predictions made.

Mollusca:

The only mollusks commonly encountered on the Short Term panels were a variety of nudibranchs. Of these *Hermissenda crassicornis* and *Acanthodoris brunnea* were the most abundant. A common boring mollusk (*Bankia setacea*) will be considered later.

2. Discussion of Organisms Settling on Long Term Panels

The Long Term panels which were exposed for cumulative periods of from 1 month to 12 months collected a greater variety of fouling organisms than the Short Term panels. A total of 57 species of animals identified at least to genus were recorded over a period of 33 months. Table 2 summarizes the data from the Long Term panels. Panels were initially exposed at the beginning of June, 1967, at the Fort Ord site and it was intended that they stay down for periods of up to one year. However, as explained earlier, after 9 months the arrays at this site were all lost and the first period of study of Long Term panels thus terminated on March 1, 1968. A new series was then exposed in 100 feet of water at the Del Monte Beach site and some of these remained in place for one year. A third series was exposed at the same site on March 1, 1969, and collected specimens for an additional full year.

Table 2 (bottom line) also presents data on the total biomass that collected on panels exposed for varying times. These data are not reliable as measures of total growth or productivity, however, for as the fouling growth increased in thickness the weight of the mass often caused slabs of growth to break away and be lost. This explains why the observed weight of fouling growth on one panel may be far less than that observed on a panel exposed for a shorter period of time.

As before, each of the major groups represented and the most abundant organisms within each group will be discussed.

Protozoa:

As in the case of the Short Term panels, the suctorian *Ephelota gemmipara* was the only protozoan regularly seen. It was most abundant on panels carrying a growth of *Obelia,* but was also seen independent of the hydroid, especially on the edges of the panels where it formed a fuzzy growth. A foraminiferan, *Rosalina columbiensis,* was seen only occasionally. This scarcity of benthic foraminiferans settling on panels in the open water of the Bay is in contrast to the relatively great numbers and varieties observed on panels exposed in the water of Monterey Harbor (Haderlie, 1969).

Porifera:

The sponge *Leucosolenia eleanor* occurred only on panels that had been exposed for 6 months or longer, and occasionally formed large tangled masses of tubes. Two other sponges, *Leuconia heathi* and *Rhabdodermella nuttingi,* were of rare occurrence.

Coelenterata:

Obelia sp. was the only hydroid encountered regularly. It was exceedingly abundant on many panels and especially so on the polypropylene ropes that extended from the panels upward to the floats at the sea surface. Associated with the *Obelia* colonies were such organisms as the suctorian *Ephelotà gemmipara,* nudibranchs such as *Hermissenda crassicornis* and the skeleton shrimp *Caprella californica.* The gonangia on *Obelia* colonies were often full of medusae after exposures of one or two months.

On one occasion a single small sea anemone was found on one panel that had been exposed for 11 months. Although this animal was completely white in color it was obviously *Corynactis californica.*

Platyhelminthes:

At one time or another four different species of flatworms were encountered on the Long Term panels. Usually there were only a few worms per panel, but occasionally up to 20 could be found. Some of these, particularly *Pseudocerous* sp., were often found curled up in the larger dead shells of *Balanus crenatus,* and in general the greater the number of dead barnacles the greater the number of flatworms. Although no flatworm was seen feeding off a living barnacle, the possibility exists that such predation does occur.

Ectoprocta:

Bryozoans are the dominant fouling organisms in Monterey Harbor, but in the open waters of the Bay they are represented by fewer species and individual colonies. On the Long Term panels at 100 feet depth a total of 7 species was recorded but usually only one or two colonies were found on a single panel. Only in the case of *Tubulipora tuba* did numbers approach those found in the shallower water, and these appeared only on panels that had been submerged for several months. This species of *Tubulipora* was incorrectly identified and was called *Tubulipora pacifica* Robertson, 1910, in earlier papers dealing with fouling in Monterey Bay (Haderlie, 1968a, 1968b, 1969; Smith and Haderlie, 1969).

Two additional species of bryozoans, *Phidolopora pacifica* and *Schizoporella unicornis,* were encountered quite often on older panels. In both cases the colonies of these forms were bright orange in color. These two have not been reported previously from fouling studies in shallower water of the Bay and harbor, but *Phidolopora,* at least, is well-known from natural rock outcrops on the bottom of Monterey Bay and is occasionally seen in deep, sheltered pools in the low intertidal.

Nemertea:

Nemertean worms are of infrequent occurrence on fouling panels at all depths in Monterey Bay. During the course of this study only 4 individual worms were encountered representing 2 species.

Annelida:

A total of nine species of polychaetes were encountered on the Long Term panels. Most of these were seen only occasionally, but three species were relatively common. *Chitinopoma groenlandica* was found on practically every panel examined and often in numbers in excess of 20 per panel. This was to be expected since these worms settle at 100 feet during most months of the year, apparently have relatively long individual life spans, and the calcareous tubes, once attached to a solid substrate, do not break off easily. On asbestos board panels in the water from March to July *Chitinopoma* with tubes up to 2 cm long were often the dominant fouling organisms. The mature

Explanation to Table 2

Date at head of double columns indicates time panel was removed from the water

Symbols used at head of columns indicate:

A = Asbestos board panel
W = Wooden panel

Symbols used in columns indicate:

1 = species present in numbers from 1 to 10 individuals or colonies per panel side

2 = species present in numbers from 11 to 20 individuals or colonies per panel side

3 = species present in numbers upward from 20 individuals or colonies per panel side

Species	Series 3, Exposed March 1, 1969																	
	1 Jul		1 Aug		1 Sept		1 Oct		1 Nov		1 Dec		1 Jan 1970		1 Feb		1 Mar	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																		
Rosalina columbiensis (Cushman, 1925)																		
Ephelota gemmipara (Hartwig, 1876)					3	3												
Porifera:																		
Leucosolenia eleanor Urban, 1905											3				2		3	
Leuconia heathi (Urban, 1905)																		
Rhabdodermella nuttingi Urban, 1902																		
Coelenterata:																		
Clytia sp.																		
Obelia sp.			3	2		3	3											
Corynactis californica Carlgren, 1936																		
Platyhelminthes:																		
Notoplana acticola (Boone, 1929)																		
Stylochus sp.																		
Kaburbakia excelsor Bock, 1925																		
Pseudocerous sp.			2	2	2		2	2										
Ectoprocta:																		
Tubulipora tuba (Gabb and Horn, 1862)																		
Celleporella hyalina (Linnaeus, 1767)																		
Cryptosula pallasiana (Moll, 1803)																		
Callopora circumclathrata (Hincks, 1881									1									
Phidolopora pacifica (Robertson, 1908)											1		1		1			
Schizoporella unicornis (Johnston, 1847)									1				1				1	
Crisia sp.																		
Nemertea:																		
Cerebratulus sp.																		
Amphiporus bimaculatus Coe, 1901																		
Annelida:																		
Nereis sp.																		
Halosydna brevisetosa Kinberg, 1855																		
Sabellaria cementarium Moore, 1906	1						1								1		1	
Cistenides brevicoma (Johnson, 1901)												**Panel destroyed by borers**		**Panel destroyed by borers**		**Panel destroyed by borers**		**Panel destroyed by borers**
Crucigera zygophora Johnson, 1901																		
Serpula vermicularis Linnaeus, 1767													1		1		1	
Chitinopoma groenlandica (Mörch, 1863	1					3	3	3		3	2		2		2		3	
Spirorbis sp.																		
Polydora brachycephala Hartman, 1936		1			2		1	1	1									
Arthropoda:																		
Balanus crenatus Bruguière, 1789	3	3	3	3	3	3	3	3	3	3								
Balanus flos Pilsbry, 1916																		
Balanus tintinnabulum (Linnaeus, 1758)							1		1	1	1		1		1		1	
Balanus concavus Pilsbry, 1916	1			1														
Balanus aquila Pilsbry, 1916									3		1		1		1		1	
Loxhorynchus sp.					1		1											
Cancer sp.																		
Cirolana sp.																		
Caprella californica Stimpson, 1857			2	2			3				3		3		2		2	
Corophium insidiosum Crawford, 1937																	2	
Mollusca:																		
Dendronotus albus MacFarland, 1966																		
Dendronotus frondosus (Ascanius, 1774)																		
Hermissenda crassicornis (Eschscholtz, 18			1	1		1												
Trinchesia albocrusta (MacFarland, 1966					1													
Acanthodoris brunnea MacFarland, 1905	3	2	1	1	2	3	3	3	3	3	2		2		1			
Triopha sp.																		
Coryphella triliniata O'Donaghue, 1921							1		1									
Hiatella arctica (Linnaeus, 1771)		1					1	1							1		1	
Pododesmus cepio (Gray, 1850)									1		1		1				2	
Hinites sp.																		
Bankia setacea (Tryon, 1863)		3		3		3		3		3								
Echinodermata:																		
Eupentacta quinquesimeta (Selenka, 186																		
Cucumeria piperata (Stimpson, 1864)							1											
Ophiothrix spiculata LeConte, 1851																		
Chordata (Tunicata):																		
Styela montereyensis (Dall, 1872)																		
Styela truncata Ritter, 1901															1		1	
Corella sp.																		
Dry Weight (g) of Fouling Growth	107.3		100.6		39.6		128.6		140.0		20.5		15.0		14.5		14.0	

Table 2

List of species, and of Panels where Organisms Settled in Long Term Series

Series 1, Exposed June 1, 1967

Species	1 Jul 1967		1 Aug		1 Sept		1 Oct		1 Nov		1 Dec		1 Jan 1968		1 Feb		1 Mar	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																		
Rosalina columbiensis (Cushman, 1925)																		
Ephelota gemmipara (Hartwig, 1876)					3							3		3				
Porifera:																		
Leucosolenia eleanor Urban, 1905																		
Leuconia heathi (Urban, 1905)																		
Rhabdodermella nuttingi Urban, 1902																		
Coelenterata:																		
Clytia sp.	3	3																
Obelia sp.										2			3					1
Corynactis californica Carlgren, 1936																		
Platyhelminthes:																		
Notoplana acticola (Boone, 1929)				1				1	2	2								
Stylochus sp.							2	1										
Kabusbakia excelsor Bock, 1925																		
Pseudoceros sp.																		
Ectoprocta:																		
Tubulipora tuba (Gabb and Horn, 1862)																		
Celleporella hyalina (Linnaeus, 1767)																		
Cryptosula pallasiana (Moll, 1803)														1				
Callopora circumclathrata (Hincks, 1881)																		
Phidolopora pacifica (Robertson, 1908)																		
Schizoporella unicornis (Johnston, 1847)																		
Crisia sp.																		
Nemertea:																		
Cerebratulus sp.							1		1									
Amphiporus bimaculatus Coe, 1901																		
Annelida:																		
Nereis sp.											3							
Halosydna brevisetosa Kinberg, 1855			1									1						
Sabellaria cementarium Moore, 1906									2	1	1	2	1	1	2	1	1	1
Cistenides brevicoma (Johnson, 1901)					1													
Crucigera zygophora Johnson, 1901																		
Serpula vermicularis Linnaeus, 1767																		
Chitinopoma groenlandica (Mörch, 1863)	2		2	2	2	1	3	2	3	2	3	3	3	3	3		3	
Spirorbis sp.																		
Polydora brachycephala Hartman, 1936			1		2					2								
Arthropoda:																		
Balanus crenatus Bruguière, 1789	3	2	3	3	3	3	3	3									1	1
Balanus flos Pilsbry, 1916																		
Balanus tintinnabulum (Linnaeus, 1758)																		
Balanus concavus Pilsbry, 1916																		
Balanus aquila Pilsbry, 1916																		
Loxorhynchus sp.																		
Cancer sp.				1														
Cirolana sp.										1								
Caprella californica Stimpson, 1857									2	2				1				
Corophium insidiosum Crawford, 1937																		
Mollusca:																		
Dendronotus albus MacFarland, 1966						1												
Dendronotus frondosus (Ascanius, 1774)	1		1	1	1													
Hermissenda crassicornis (Eschscholtz, 1831)			1	1	2			1		1	1	1						
Trinchesia albocrusta (MacFarland, 1966)			1	1	1													
Acanthodoris brunnea MacFarland, 1905				1	3	1	2	3			2							
Triopha sp.																		
Coryphella trilineata O'Donoghue, 1921																		
Hiatella arctica (Linnaeus, 1771)							1		2	3	2	2						
Pododesmus cepio (Gray, 1850)					1		1	1	1	1	2	2	1		3	2		1
Hinnites sp.																		
Bankia setacea (Tryon, 1863)										1	[illegible]	3		3		3		3
Echinodermata:																		
Eupentacta quinquesemita (Selenka, 1867)																		
Cucumaria piperata (Stimpson, 1864)																		
Ophiothrix spiculata LeConte, 1851																		
Chordata (Tunicata):																		
Styela montereyensis (Dall, 1872)															1			
Styela truncata Ritter, 1901											1							
Corella sp.																		
Dry Weight (g) of Fouling Growth	3.5		92.9		122.1		223.3		40.1		64.6		60.2		40.5		[illegible]	

Series 2, Exposed March 1, 1968

Species	1 Apr		1 May		1 Jun		1 Jul		1 Aug		1 Sept		1 Oct		1 Nov		1 Dec		1 Jan 1969		1 Feb		1 Mar	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																								
Rosalina columbiensis (Cushman, 1925)								3		3			1	1										
Ephelota gemmipara (Hartwig, 1876)									3	3	3	3									3	3		
Porifera:																								
Leucosolenia eleanor Urban, 1905													1	1	2	2	1		2	2	1	2		1
Leuconia heathi (Urban, 1905)																			1				1	
Rhabdodermella nuttingi Urban, 1902																			1					
Coelenterata:																								
Clytia sp.																								
Obelia sp.	3	3	3		3	3		2				2							2	2	2		2	2
Corynactis californica Carlgren, 1936																						1		
Platyhelminthes:																								
Notoplana acticola (Boone, 1929)	1	1							1															
Stylochus sp.						1																		
Kabusbakia excelsor Bock, 1925															2									
Pseudoceros sp.																			1					
Ectoprocta:																								
Tubulipora tuba (Gabb and Horn, 1862)							1	1	2	1	1		2	2					2		1	1	1	1
Celleporella hyalina (Linnaeus, 1767)					1							1												
Cryptosula pallasiana (Moll, 1803)																								
Callopora circumclathrata (Hincks, 1881)									1										1	1		1	1	1
Phidolopora pacifica (Robertson, 1908)																			1	1	1		1	
Schizoporella unicornis (Johnston, 1847)									1				1	1					1		1			1
Crisia sp.																							1	
Nemertea:																								
Cerebratulus sp.																								
Amphiporus bimaculatus Coe, 1901																							1	1
Annelida:																								
Nereis sp.																								
Halosydna brevisetosa Kinberg, 1855															1									
Sabellaria cementarium Moore, 1906					1		2		1	1	1						1							1
Cistenides brevicoma (Johnson, 1901)																								
Crucigera zygophora Johnson, 1901																							2	2
Serpula vermicularis Linnaeus, 1767																							1	
Chitinopoma groenlandica (Mörch, 1863)	1		3	3	3		3	1	3	2	3	3	3	2	1		2		3	3	2		3	2
Spirorbis sp.							1																	
Polydora brachycephala Hartman, 1936													2											
Arthropoda:																								
Balanus crenatus Bruguière, 1789	3	1	3	3	3	3	1	2			3	3	3	3	3	3								
Balanus flos Pilsbry, 1916																							1	
Balanus tintinnabulum (Linnaeus, 1758)																								
Balanus concavus Pilsbry, 1916																								
Balanus aquila Pilsbry, 1916																								
Loxorhynchus sp.																								1
Cancer sp.			1												1									
Cirolana sp.																								
Caprella californica Stimpson, 1857																			3					3
Corophium insidiosum Crawford, 1937															3								1	
Mollusca:																								
Dendronotus albus MacFarland, 1966																								
Dendronotus frondosus (Ascanius, 1774)			1	1	1	1																	1	
Hermissenda crassicornis (Eschscholtz, 1831)			1	1	1	1						1							1	1			1	
Trinchesia albocrusta (MacFarland, 1966)			1	1		2														1			1	
Acanthodoris brunnea MacFarland, 1905			2	2	3	3					1		1		3	3	3	1						
Triopha sp.																			1					
Coryphella trilineata O'Donoghue, 1921																							1	
Hiatella arctica (Linnaeus, 1771)																1							1	1
Pododesmus cepio (Gray, 1850)							1						1	1	1	1			1				1	1
Hinnites sp.																				1				
Bankia setacea (Tryon, 1863)						3		3		3		3		3		3		3		3		3		3
Echinodermata:																								
Eupentacta quinquesemita (Selenka, 1867)											1													
Cucumaria piperata (Stimpson, 1864)																								
Ophiothrix spiculata LeConte, 1851																1								
Chordata (Tunicata):																								
Styela montereyensis (Dall, 1872)																								
Styela truncata Ritter, 1901																							1	
Corella sp.															1				1				1	
Dry Weight (g) of Fouling Growth	0.7		21.0		3.1		[illegible]		1.0		[illegible]		23.0		[illegible]		[illegible]		[illegible]		5.0		11.0	

Series 3, Exposed March 1, 1969

Species	1 Apr		1 May		1 Jun		1 Jul		1 Aug		1 Sept		1 Oct		1 Nov		1 Dec		1 Jan 1970		1 Feb		1 Mar	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Protozoa:																								
Rosalina columbiensis (Cushman, 1925)																								
Ephelota gemmipara (Hartwig, 1876)	3	3			3	3					3	3												
Porifera:																								
Leucosolenia eleanor Urban, 1905																	3				2		3	
Leuconia heathi (Urban, 1905)																								
Rhabdodermella nuttingi Urban, 1902																								
Coelenterata:																								
Clytia sp.																								
Obelia sp.	1		1	1					3	2		3	3											
Corynactis californica Carlgren, 1936																								
Platyhelminthes:																								
Notoplana acticola (Boone, 1929)				2	2	1																		
Stylochus sp.																								
Kabusbakia excelsor Bock, 1925																								
Pseudoceros sp.									2	2	2		2	2										
Ectoprocta:																								
Tubulipora tuba (Gabb and Horn, 1862)																								
Celleporella hyalina (Linnaeus, 1767)																								
Cryptosula pallasiana (Moll, 1803)																								
Callopora circumclathrata (Hincks, 1881)															1									
Phidolopora pacifica (Robertson, 1908)																	1		1		1			
Schizoporella unicornis (Johnston, 1847)															1				1				1	
Crisia sp.																								
Nemertea:																								
Cerebratulus sp.																								
Amphiporus bimaculatus Coe, 1901																								
Annelida:																								
Nereis sp.																								
Halosydna brevisetosa Kinberg, 1855																								
Sabellaria cementarium Moore, 1906							1						1								1		1	
Cistenides brevicoma (Johnson, 1901)																								
Crucigera zygophora Johnson, 1901																								
Serpula vermicularis Linnaeus, 1767																			1		1		1	
Chitinopoma groenlandica (Mörch, 1863)	2	1	3	1	3	1	1					3	3	3		3	2	Panel destroyed by borers	2	Panel destroyed by borers	2	Panel destroyed by borers	3	Panel destroyed by borers
Spirorbis sp.																								
Polydora brachycephala Hartman, 1936			1					1			2		1	1	1									
Arthropoda:																								
Balanus crenatus Bruguière, 1789		1	3	3	3	3	3	3	3	3	3	3	3	3	3	3								
Balanus flos Pilsbry, 1916																								
Balanus tintinnabulum (Linnaeus, 1758)													1		1	1	1		1		1		1	
Balanus concavus Pilsbry, 1916				1	1		1			1														
Balanus aquila Pilsbry, 1916															3		1		1		1		1	
Loxorhynchus sp.											1		1											
Cancer sp.																								
Cirolana sp.																								
Caprella californica Stimpson, 1857									2	2			3				3		3		2		2	
Corophium insidiosum Crawford, 1937																							2	
Mollusca:																								
Dendronotus albus MacFarland, 1966																								
Dendronotus frondosus (Ascanius, 1774)																								
Hermissenda crassicornis (Eschscholtz, 1831)					1	1			1	1		1												
Trinchesia albocrusta (MacFarland, 1966)	1	1		1							1													
Acanthodoris brunnea MacFarland, 1905					2	2	3	2	1	1	2	3	3	3	3	3	2		2		1			
Triopha sp.																								
Coryphella trilineata O'Donoghue, 1921			1	1									1		1									
Hiatella arctica (Linnaeus, 1771)								1					1	1							1		1	
Pododesmus cepio (Gray, 1850)					1										1		1		1				2	
Hinnites sp.																								
Bankia setacea (Tryon, 1863)		3		3		3		3		3		3		3		3								
Echinodermata:																								
Eupentacta quinquesemita (Selenka, 1867)																								
Cucumaria piperata (Stimpson, 1864)													1											
Ophiothrix spiculata LeConte, 1851																								
Chordata (Tunicata):																								
Styela montereyensis (Dall, 1872)																								
Styela truncata Ritter, 1901																					1		1	
Corella sp.																								
Dry Weight (g) of Fouling Growth	0.1		[illegible]		[illegible]		[illegible]		100.6		[illegible]		[illegible]		100.0		30.5		15.0		11.5		14.0	

worm tubes are easy to identify for they invariably have a distinct keel running the full length of the tube which ends with a characteristic spine or tooth overhanging the aperture. The operculum of the living worm is also distinctive in having a thick horny terminal plate which is often coated with sand or debris. These worms were also common on the concrete anchors that held the arrays in place. The maximum size attained by *Chitinopoma* was 4 cm tube length on a panel exposed for 12 months.

Sabellaria cementarium was relatively common on the panels. The sandy tubes of this species were most often observed wedged in between barnacles. Some of the tubes were over 4 cm in length. The spionid *Polydora brachycephala* was also seen quite regularly on panels with a heavy growth of other foulers in which the tubes of *Polydora* were entwined.

The serpulid *Crucigera zygophora* was seen only once during this entire study when from 15–20 of these worms were found on both the wood and asbestos parts of a panel recovered in March, 1969, after a year of exposure.

Arthropoda:

The common sub-tidal acorn barnacle *Balanus crenatus* was clearly the dominant fouling organism in terms of total biomass and numbers of individuals encountered on the Long Term panels exposed at 100 feet depth. In making the counts of these barnacles that are summarized in Table 2 only living barnacles were counted. This accounts for the blanks that are found in the table. For example, during the first part of this study living barnacles were found on all panels exposed from June through September, 1967, but by the first of November all were dead and no new live ones appeared until February, 1968. The panels during this latter period none-the-less carried a heavy load of dead barnacle shells as indicated by the weight of the total biomass shown at the bottom of Table 2. Barnacles or barnacle shells invariably accounted for most of the weight of fouling growth on panels exposed for more than a few months.

During the second year of study a heavy settlement of *Balanus crenatus* occurred in March, 1968 (see Figure 3), and as this was the beginning month of a new long term series, most of the panels were colonized by barnacles and these remained alive and grew on most of the panels until the first part of December, 1968, when it was found that all barnacles were dead. Again no new living barnacles were found on the panels until March, 1969. In one Long Term panel removed on August 1, 1968, after being exposed for 5 months, all the barnacles were dead. The dead shells of these, or the bases if the upper wall plates had broken off, measured up to 7 mm in diameter and covered 95% of the asbestos panel. Other Long Term panels of the same age attached to the same array carried mainly live barnacles. This illustrates that occasionally some catastrophe can overtake an isolated population and wipe it out. Possibly some predator moved over this panel and killed all the barnacles while not attacking nearby panels with similar populations.

During the third year of the study similar observations were made. The Long Term panels exposed in March, 1969, carried extensive populations of living *Balanus crenatus* for many months but by December they were all dead and no new ones appeared. This study would indicate, therefore, that at 100 feet depth the maximum lifetime of an individual *Balanus crenatus* is about 9 months.

In regard to maximum size achieved by *Balanus crenatus,* only rarely was a living barnacle found with a basal diameter exceeding 10 mm (12 mm was the largest size recorded) and these large forms were normally found on panels where the barnacles were not overly crowded. On many Long Term panels the barnacles had settled so thickly that when they had grown to have a basal diameter of about 2 mm they were all touching one another and additional growth in diameter became impossible. These then grew in height and became tall tubular forms. It was not unusual to find panels completely covered with barnacles having basal diameters of 2 mm but varying in height. The tallest of these were over 20 mm high, being tubular and thin for much of their height then expanding to a maximum diameter of 5 mm at the top. In gross morphology these barnacles grown in very crowded conditions are not at all the typical shape normally associated with acorn barnacles.

One of the objectives of this study was to determine if possible the breeding season of the dominant fouling organisms. Figure 3 indicates the time of settling of *Balanus crenatus,* but this gives no information on time of release

One of the objectives of this study was to determine if ever larvae were released by adult barnacles while the panels they were attached to were being examined microscopically in the laboratory. This was first observed on a panel originally exposed on June 1 and removed on August 1, 1967. After two months the panel was covered with tall, tubular barnacles and many of these were releasing clouds of nauplii. *Balanus crenatus* can therefore become reproductively mature and release larvae at an age of 2 months or less during the summer at 100 feet depth. A similar release of larvae was observed on a panel removed October 1, 1967, after being in the water 4 months. In panels originally exposed in March, 1969, larvae were observed being released on July 1 (4 months exposure), on August 1 (5 months exposure) and again on October 1 (7 months exposure). These observations in the laboratory may not coincide with events in the sea, however, for it is known that the release of barnacle larvae can be triggered by environmental conditions and the increase in water temperature that occurred when panels were recovered may have stimulated the release of nauplii.

The large red and white striped barnacle *Balanus tintinnabulum* was found in relatively small numbers on several of the older Long Term panels during the last year of this study. The maximum size of these was 30 mm in basal diameter. This species was also occasionally found on the lower floats of the arrays.

Three other acorn barnacles were recorded on the Long Term panels at 100 feet depth that had never been encountered before in fouling studies in shallower water of the Bay. *Balanus flos* was found on only one panel that had been exposed for 12 months and was recovered in March, 1969. Three large individuals measuring 30 mm in basal diameter and 15 mm in height were found clustered together in one corner of the asbestos board panel. The barnacles were characterized by having parietes that were slightly pink in color and which formed a sharp, crenulated, flaring orifice. The appendages of the living animals were pink and the tergoscutal flaps were of a brilliant yellow coloration.

Balanus aquilla was found only on panels exposed for 8 months or more during the last year of this study. Usually only from 1 to 5 individuals were found on any one panel, but on one panel removed on November 1, 1968, after 8 months exposure, there were 25 individuals clumped together in one corner. The largest of these was 25 mm in basal diameter, but on older panels in the water 12 months the largest *Balanus aquilla* was 35 mm in diameter. The walls of these barnacles showed well developed ribs. On the panel mentioned above that was removed on November 1, 1968, the largest specimen of *Balanus aquilla* released thousands of nauplii into the sea water as the panel was being examined in the laboratory.

Balanus concavus (referred to as *Balanus concavus pacificus* by CORNWALL, 1951) was encountered on 4 different panels exposed from 2 to 4 months during the spring and summer of 1969. Only one or two individuals were found on any one panel and the largest encountered was 15 mm in basal diameter. In all cases the barnacles were of smooth conical shape with a diamond-shaped orifice and with delicate pink stripes in the lateral wall plates. The scuta were distinctly striated. The living animals had yellow appendages and yellow and black tergoscutal flaps.

The only other arthropods encountered fairly regularly were skeleton shrimps (*Caprella californica*). These were particularly abundant on the polypropylene ropes and on panels that had heavy growths of *Obelia*.

Mollusca:

A variety of nudibranchs was encountered on the Long Term panels, but any one species was usually represented by only one or two individuals on any one panel. An exception was *Acanthodoris brunnea*. This small, relatively flat and extremely sluggish animal was found on most of the panels examined and often in numbers of from 20 to nearly 100 per panel. The maximum length recorded was 10 mm. This nudibranch was found in small numbers on panels at 50 feet depth in earlier studies, but has not been seen on panels exposed in the harbor at depths down to 25 feet. On panels at the 100 foot level *Acanthodoris brunnea* was usually found only on panels with sizable populations of living, mature acorn barnacles (*Balanus crenatus*). Occasionally, however, sizable numbers were found on panels where the barnacles had all recently died. In no case were these ever seen in a position where they might appear to be feeding on the barnacles, but the suspicion is there that they are predatory on the barnacles for often very little else was found on the panels except dozens of these nudibranchs and hundreds of acorn barnacles. *Acanthodoris brunnea* was also exceedingly abundant on the concrete anchors that had a covering of acorn barnacles. A group of 15 adult *Acanthodoris* were observed depositing strings of white eggs on a panel recovered on December 1, 1968, after being in the water 9 months.

The jingle *Pododesmus cepio* was also a fairly common mollusk on the panels. The largest individual ever seen was about 30 mm in diameter and all the larger jingles carried numerous tubes of the serpulid *Chitinopoma groenlandica* on the upper valves.

The molluscan borer *Bankia setacea* will be considered later.

Echinodermata:

Echinoderms are not abundant in the fouling community at any depth in Monterey Bay. During this study only two species of sea cucumbers and one species of brittlestar were encountered, each represented by a single individual.

Chordata:

Among the ascidians *Styela truncata* and *Styela montereyensis* were each represented on the Long Term panels by a few individuals. A third ascidian encountered proved to be an undescribed species of the genus *Corella.* The animal in life was globular, semitransparent and about 15 mm in diameter. Small golden flecks were embedded in the tunic. In one specimen on a panel recovered on January 1, 1969, there was a large flatworm curled up in the atrial cavity. The worm was basically cream colored with a white margin and large purple spots on the dorsum. Its tentacles were wine red. The worm is probably a member of the genus *Pseudocerous.*

WOOD BORING ORGANISMS

The shipworm *Bankia setacea* was the only wood borer encountered during this study at depths of 100 feet. In earlier studies at depths of 50 feet and in the harbor area the gribble *Limnoria quadripunctata* Holthuis, 1949, was seen regularly on wooden panels, yet in the present investigation this species was never recorded.

Data collected during the 33 months of this study indicate that *Bankia setacea* is a very common borer in wood at 100 feet depth in Monterey Bay and in investigations now underway at 200 feet depth it seems to be equally abundant, especially near the bottom. At both of these depths douglas fir panels ¾ inch thick are usually riddled with *Bankia* burrows after 6 months exposure and the wood usually crumbles and falls completely away from attachment fittings after about 9 months. It would appear that no untreated soft wood lying on the bottom of Monterey Bay down to depths of 200 feet would remain intact for over a year.

Short Term panels exposed for 1 month periods throughout the course of this study collected shipworms and data from these panels gave information on settling time and initial growth rates of *Bankia setacea* at 100 feet depth. As can be seen from Table 1, this shipworm settled during December, 1967; during the months January, February, April, May, June, July and December, 1968; during January, March, May, October and December, 1969; and during January and February, 1970. No settlement in June, 1967, is indicated in Table 1, but this probably was not the case for at that time the very small initial settling stages of *Bankia setacea* were not recognized as such by the investigator and may have been overlooked. Long Term panels removed later during 1967 harbored mature *Bankia,* therefore a settlement must have taken place in early summer.

The above indicates that settlement can occur from October through July, but in all cases the months of most active settlement was from December through June. This is the same period of intense settlement recorded at the 50 foot level in Monterey Bay (Haderlie, 1968b). This is also the period of minimum water temperatures in the Bay.

A panel removed on December 1, 1967, after being in the water since June harbored 50 or more large *Bankia.* After recovery this panel was temporarily placed in an aquarium with circulating sea water and within a short period of time many of the shipworms were releasing milky clouds into the water. The clouds proved to be sperm; no eggs were released as far as could be determined. A Short Term panel removed after being in the water during December, 1967, carried over 100 recently settled *Bankia* ranging in size from small spherical bodies 0.2 to 0.3 mm in diameter possessing two siphonal apertures separated by a calcareous bridge to slightly larger forms possessing short siphons. Another panel removed on February 1, 1969, after being exposed 1 month carried a similar population of over 100 newly settled shipworms. A similar situation was observed on a panel exposed during December, 1969.

The first series of Long Term panels was immersed in June, 1967, and the second and third series in March, 1968, and March, 1969, respectively. Times of initial submergence therefore occurred during months when *Bankia setacea* settle in Monterey Bay. It is not surprising, then, that all Long Term wooden panels exposed at 100 feet depth ultimately carried infestations of shipworms. The reason that Table 2 indicates no *Bankia* recorded during the initial months of exposure in the summer and fall of 1967 and again in the first two months of exposure in 1968 was that early stages of this shipworm are often not very obvious and many settle on the cross sectional ends of the panels that are difficult to examine microscopically. The fact that panels a month or two later carried large mature shipworms indicates that they were present but not detected earlier.

Table 2 also indicates no *Bankia* in wooden panels recovered from December, 1969, to March, 1970. The reason for this was simply that there were no wooden panels left after December for the shipworms had totally destroyed the panel and it had crumbled away. In previous years this had not occurred, for although starting in about October of each year the panels were practically completely riddled internally, they none-the-less had sufficient superficial wood left to remain attached to the asbestos board backing.

The evidence indicates, therefore, that wooden panels at 100 feet depth are heavily penetrated with little structural strength left after 4 months and totally destroyed in approximately 7 to 8 months after being infested with *Bankia setacea.* In panels riddled with the burrows of shipworms, few living borers could be found after about

8 months of submergence. In most cases, primarily due to crowding, the bore holes were only about 5–7 mm in diameter and 10–15 cm long.

SUMMARY

(1) Over a 33 month period extending from June 1, 1967, to March 1, 1970 a series of test panels were exposed to the marine environment in open water of Monterey Bay at a depth of 100 feet.

(2) Test surfaces consisted of panels of douglas fir and asbestos board attached back to back and suspended vertically in the water.

(3) Two series of panels were used; Short Term panels were exposed at the beginning of each month and recovered the first of the following month, while Long Term panels were exposed for cumulatively longer periods up to 12 months.

(4) A total of 28 different kinds of animals settled on or bored into the Short Term panels. The most conspicuous species were hydroids (*Obelia* sp.), acorn barnacles (*Balanus crenatus*) and serpulid worms (*Chitinopoma groenlandica*).

(5) A total of 57 species of animals was recorded from the Long Term panels at 100 feet depth. The same hydroids, barnacles and serpulids were the dominant fouling organisms as those found on the Short Term panels. The shipworm *Bankia setacea* was important as a borer and was so abundant as to destroy many of the Long Term wooden panels.

(6) The acorn barnacle *Balanus crenatus* was the dominant organism in terms of total number of individuals and biomass on any one panel. The major period of settlement at 100 feet for this barnacle was found to be from July through November with August and September being months of most intense settlement.

(7) *Bankia setacea* was an important wood borer at depths of 100 feet, and the period of settlement was found to be from October through July with most intense settlement in December and January. Wooden panels were completely destroyed by *Bankia* after being exposed for 7–8 months.

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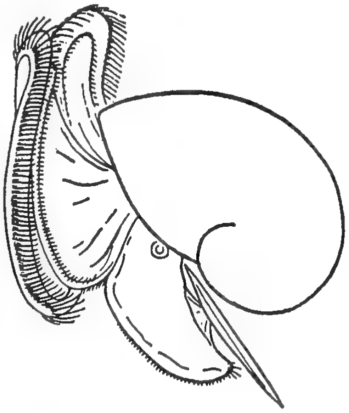

Sixteen New Species and One New Genus of Japanese Ovulidae

BY

MASAO AZUMA

1-42 Kamiyoshihara, Nishinomiya, Hyogo, Japan 662

AND

CRAWFORD N. CATE

12719 San Vicente Boulevard, Los Angeles, California 90049

(2 Plates; 8 Text figures)

DURING THE COURSE of the preparation of a revision of the molluscan family Ovulidae by the junior author, Masao Azuma, Nishinomiya, Hyogo, Japan, sent a group of ovulid specimens to be identified. There were 22 lots of shells, consisting mostly of a single specimen each. It was a curious assortment, representing several genera, and, surprisingly, most of the shells appeared to be new to science. Since this work overlapped the larger revision of the family in several instances, it was decided to make a joint effort of both workers of describing the new taxa.

The excellent drawings of radulae and soft parts, and their descriptions, are the work of Masao Azuma. Identification of the host species is that of Dr. Huzio Utinomi of Kyoto University and the Seto Marine Laboratory. Descriptions of the shells are by Crawford N. Cate. All specimens were taken by lobster nets from deep water, 2 - 5 km west of the Kii Peninsula, Central Japan, during late 1969 and early 1970. The photographs are by Bertram C. Draper, their processing by Takeo Susuki.

1. *Prionovolva (Prionovolva)* ***aenigma*** AZUMA & CATE spec. nov.

(Figure *1*)

Shell small, roundly pyriform; terminals produced, curved left, semi-pointed in back, rounded, slightly recurved in front; dorsum smooth, glossy, except that surface shows evidence of breaks, cracks, and repairs; base ovate, smooth, glossy, tapering sharply, thickly (ridge-like) to the front; a small triangular elevated eruption of callus forming a funiculum on rear base; columella smooth, very broad (extending from interior adaxial carinal ridge out to a noticeable central ridge on base), deepening, converging to the front to form a shallow fossula (a circular injury is also visible on columella); aperture crescent shaped, broad, becoming exceedingly broad to the front; outer lip semi-circular, thick, though barely shouldered above, with inward plane of lip flattened and numerously dentate with 14 fairly well formed large teeth; shell basically a honey-ivory color with 4 broad bands of deep rose extending over the dorsum from the outer lip shoulder, across the base and columella, to the interior adaxial carinal ridge.

Holotype: Azuma collection, no. 14826A.
Length 5.0 mm; width 3.5 mm; height 2.8 mm

Type Locality: 1 - 2 km off Kirimezaki, Kii Peninsula, Japan; leg. M. Azuma.

The name of this new species is based on its original confusion with *Ovula hervieri* HEDLEY, 1899, in the literature (see AZUMA, 1970, **28** (4): 179; text fig. 1, spec. 2 from left). It differs from the Hedley species very distinctly by being more rounded and globular in shape (rather than sub-pyriform); by lacking the significant, incised dorsal striae over all – by being smooth, glossy; by having a differently shaped funicular projection; by a greater number of labial teeth, differently formed and constituted, on the inner edge; and by a different arrangement of shell colors. Future work on these animals, however, may eventually prove to closely relate them subspecifically.

2. *Prionovolva (Prionovolva)* ***nebula*** Azuma & Cate spec. nov.

(Figure *4*)

Shell small, evenly ovate, humped, solid; terminals only barely produced, with rear projection somewhat curving left and fairly sharply pointed, beaked; dorsum dull, subglossy, with fine transverse incised lines emanating limitedly from either terminal, central dorsum without striation; base ovate, smooth, inflated, narrowing as a thick ridge to the front; a large triangular elevated funiculum on the rear base; columella broad, smooth, conspicuously concavely depressed, broadening and deepening in front as a fossula; aperture broad, evenly curving; outer lip thick, broad, with a central longitudinal ridge, which causes adaxial plane of lip to slope inward at a sharp angle; outer portion of lip thickly rounded, shouldered above; teeth (22) even, well developed, the length of adaxial lip plane, some of which cut the lip edge centrally in the manner of the genus; shell color dorsally light beige with 3 longitudinal, very irregular color bands of reddish-brown; funiculum, outer lip, and teeth off-white.

Holotype: Azuma collection, no. 14826B.
Length 6.6 mm; width 4.0 mm; height 3.5 mm

Type Locality: Off Minabe, Japan; leg. M. Azuma, 6 January 1969.

The name is derived from the Latin noun *nebula,* meaning cloud, fog.

3. *Pseudosimnia (Diminovula)* ***incisa*** Azuma & Cate spec. nov.

(Figure *3*)

Shell small, solid, narrow, ovate; terminals produced, blunt in front, rounded in back; dorsum sub-glossy, evenly rounded, with numerous transverse incised striae over all; base ovate, smooth, sub-glossy, narrowing thickly to the front; a thick, multi-knobbed funiculum covers adapical end of base; columella broad, deep, curving, deepening into a long, concave fossula, both of which are outlined adaxially by a thick, longitudinal carinal ridge; aperture broad, curving; outer lip broad, rounded, roundly shouldered above, with numerous large, though weakly formed teeth; dorsal shell color light grey over all with irregularly sized large diffused punctations of bright orange; base light grey; adaxial carinal wall, funiculum, outer lip and teeth milk-white; terminal canals orange.

Holotype: Azuma collection, no. 14843.
Length 5.2 mm; width 2.7 mm; height 2.4 mm

Type Locality: 3 - 4 km off Hinomisaki, Kii Peninsula, Japan; 50 - 70 fathoms.

The name is derived from the Latin adverb *incise,* meaning cut into, grooved, incised.

4. *Primovula* ***virgo*** Azuma & Cate, spec. nov.

(Figures *2* and 17 [(E)])

Shell large for the genus, elongate, broadening subcentrally, where it is angularly shouldered; terminals blunt, open, narrowing gently to the front and back; dorsum sub-glossy, with numerous transverse incised striae over all; base rhomboidly-ovate, smooth, glossy, narrowing constrictedly to the front; a large, thick crenular funiculum covers entire adapical triangle of base area; columella smooth, broad, depressed, with a long, low longitudinal ridge adaxially, which outlines a deepened fossular area; aperture straight, widening in front; outer lip broad, thick, rounded, with very weak teeth along ⅔ of its length, some of which are lengthened

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[(E)] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

Plate Explanation

Figure *1*: *Prionovolva* ***aenigma*** Azuma & Cate, spec. nov. Holotype
Aza. 14826A × 12

Figure *2*: *Primovula* ***virgo*** Azuma & Cate, spec. nov. Holotype
Aza. 14841 × 3½

Figure *3*: *Pseudosimnia* ***incisa*** Azuma & Cate, spec. nov. Holotype
Aza. 14843 × 10

Figure *4*: *Prionovolva* ***nebula*** Azuma & Cate, spec. nov. Holotype
Aza. 14826B × 9

Figure *5*: *Primovula* ***colobica*** Azuma & Cate, spec. nov. Holotype
Aza. 14848 × 4⅔

Figure *6*: *Primovula* ***horimasarui*** Azuma & Cate, spec. nov.
Holotype Aza. 14842 × 5

Figure *7*: *Primovula* ***myrakeenae*** Azuma & Cate, spec. nov.
Holotype Aza. 14847 × 5½

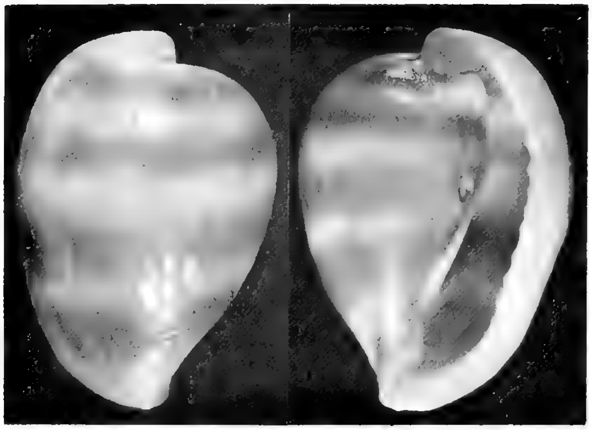


Figure 1

Prionovolva ***aenigma***

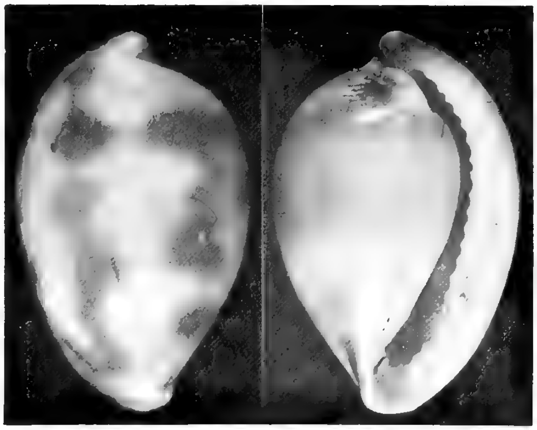


Figure 4

Prionovolva ***nebula***

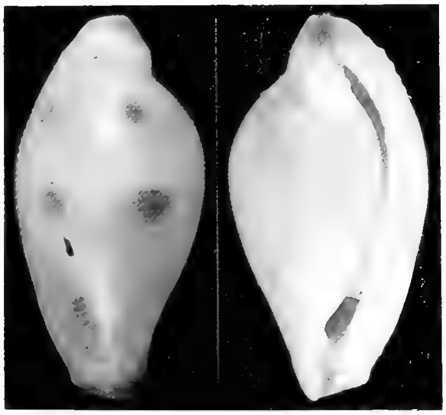


Figure 3

Pseudosimnia ***incisa***

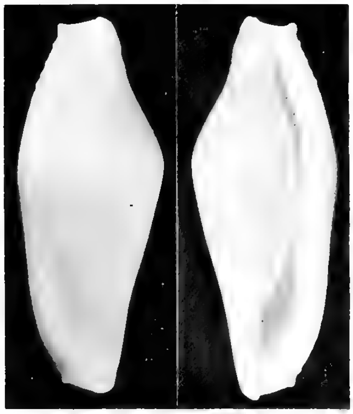


Figure 2

Primovula ***virgo***

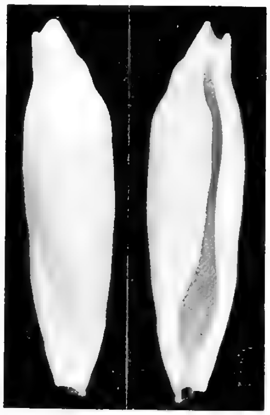


Figure 6

Primovula ***horimasarui***

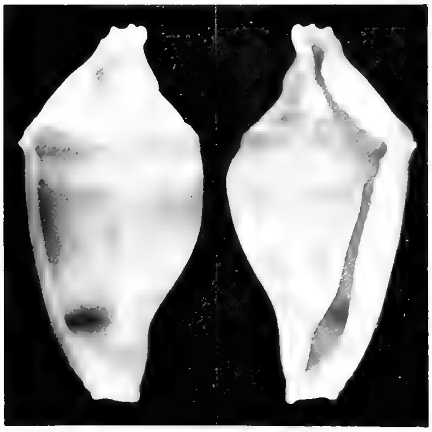


Figure 5

Primovula ***colobica***

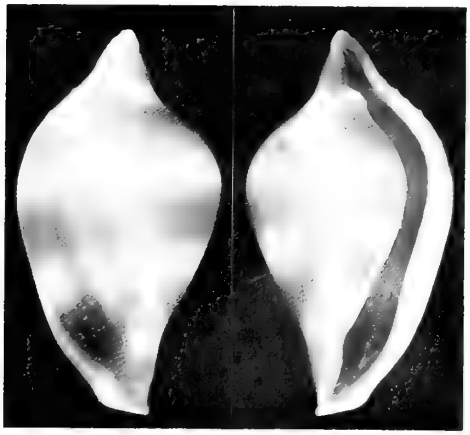


Figure 7

Primovula ***myrakeenae***

photographs by Bertram C. Draper

to reach outer lip edge in back; color milk-white over all. Length 14.2 mm; width 5.5 mm; height 4.4 mm

Radula: Radula of taenioglossate type; formula 2 · 1 · 1 · 1 · 2. The central tooth is rounded, rectangular in shape, with a moderate central cusp and 7 minute denticles on both sides, the innermost of which is the smallest. The lateral teeth are rather cactus leaf-shaped, the outer base of which is very slender, projected backwards and the inner base with a minute cusp; the frontal has a large cusp that is slightly curved within; near frontal edge are 3 obsolete minute denticles.

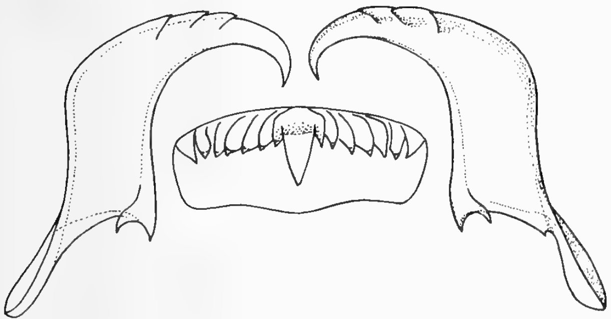


Figure 17

Radula of *Primovula virgo* Azuma & Cate, spec. nov.

Holotype: Azuma collection, no. 14841. Collected by Mr. Shingo Habu, 20 March 1970.
Length 14.2 mm; width 5.5 mm; height 4.4 mm

Type Locality: 3 - 4 km off Hinomisaki, Kii Peninsula, Japan; living on a host capitulum of *Solenocaulon chinense* Kükenthal, at a depth of 50 - 70 fathoms.

5. *Primovula horimasarui* Azuma & Cate, spec. nov.

(Figure 6)

Shell long, narrow, bluntly-lanceolate, with a sinistral twist of terminal area adapically, causing a low dorsal ridge in same area, in same direction; terminals open, bluntly angled; dorsum sub-glossy, numerously finely transversely incisedly striate over all; base long, narrow, centrally ridged longitudinally, smooth, glossy, narrowing and obliquely angling right front and back; no funicular swelling adapically; columella without depression, a continuation of the base slanting adaxially, with only a very slight concavity in the fossular area, outlined by an interior longitudinal ridge that disappears on the columella centrally; aperture narrow, twisting, with a long widening in front due to constriction of base and outer lip; outer lip thick, broadly shouldered above, angling flatly inward; no indication of teeth; color milk-white over all, except that interior carinal ridge is deep pink.

Holotype: Azuma collection, no. 14842.
Length 10.4 mm; width 2.5 mm; height 2.1 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan; in 30 - 50 fathoms; leg. Masaru Hori, 6 January 1969.

The species is named in honor of Mr. Masaru Hori, who collected the shell.

6. *Primovula colobica* Azuma & Cate, spec. nov.

(Figure 5)

Shell fairly large, sub-bulbous, rhomboid, angularly elevated sub-centrally, with numerous transverse, incised striae (these are disturbed centrally by shell wound); terminals acutely produced, blunt in front, squarely beaked in back, with 3 protruding tooth processes; base inflated, ovate, faintly striate, tapering sharply to the front; funiculum on rear base thickened, triangular, undulating eruption of nacreous callus; columella wide, only slightly depressed, faintly striate, then deepening, with the aid of interior wall, to form a significant fossula; outer lip narrowly thickened, with numerous large, weak teeth most of its length; color light beige (ivory) over all, except that dorsum and base are variably 3-banded with bright orange; terminal canals deep orange.

Holotype: Azuma collection, no. 14848.
Length 10.6 mm; width 5.0 mm; height 4.3 mm

Type Locality: Off Kirimezaki, Kii Peninsula, Japan, in 30 - 50 fathoms; leg. M. Azuma.

The name is derived from the Latin *colobicus*, meaning mutilated.

7. *Primovula myrakeenae* Azuma & Cate, spec. nov.

(Figure 7)

Shell small, bulbously inflated, rhomboidly pyriform, thinly formed, sub-translucent; terminals extended, somewhat pointed in back, blunt in front; dorsum glossy, although having wavy, transversely incised striae all over, which are intercepted longitudinally by incremental growth lines; base pyriformly ovate, roundly inflated, tapering sharply, narrowly adapically, transversely striate to adaxial edge within; there is a small, subcircular, upraised, multi-knobbed funiculum on rear base; aperture fairly broad, curving; columella follows natural curve of base, striate, though indistinctly outlined by a ridge within, with a deepening in the fossula area;

outer lip somewhat thickened, rounded, with large, rudimentary, widely separated teeth on rear half of lip edge, front half without teeth; color bright red-brown with 3 bands of light grey and a yellowing of the red brown on the adapical terminal beak.

Holotype: Azuma collection, no. 14847.
Length 9.7 mm; width 5.2 mm; height 4.4 mm

Type Locality: Off Nada, Kii Peninsula, Japan, in 30 to 50 fathoms; leg. M. Azuma.

This species is named in honor of Dr. A. Myra Keen, Curator of Mollusca, Emeritus, Stanford University, Stanford, California.

8. *Primovula* ***mucronata*** Azuma & Cate, spec. nov.

(Figure *8*)

Shell small, angularly ovate, thin, translucent; terminals sharply produced, more so adapically; dorsum smooth, glossy, except that transverse, incised striae emanate restrictedly from either terminal, with more numerous lines at the rear; base ovate, with more numerous incised striae than above, covering most of the ventral surface; funiculum a narrow, thickened, uneven elevation on the rear base; columella rounded, striate, without depression; fossula only barely recognizable; aperture long, curving; outer lip rounded, thickened, with numerous large, short, weak teeth on inner edge; color basically light grey-white over all, with large red-brown, elongate clouds on dorsum, especially on the right side; both terminal beaks yellow, except tip of adapical beak which is white; terminal channel yellow in front, brown in back.

Holotype: Azuma collection, no. 14845.
Length 9.7 mm; width 4.2 mm; height 3.6 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, in 30 - 50 fathoms; leg. M. Azuma, 20 March 1969.

The name is derived from the Latin *mucronatus*, signifying sharp, pointed, a striking character of the adapical terminal beak.

9. *Primovula* ***tosaensis*** Azuma & Cate, spec. nov.

(Figures *9* and 18)

Shell small, long, narrow, broadening and enlarged sub-centrally, thinly formed, translucent, sub-glossy, with transverse, widely separated incised striae over all; terminals narrowing to the front and back, almost beaked adapically; base narrow, elongately-ovate, uncalloused, transversely striate; posterior funiculum long, thick, curiously twisting obliquely to form a second dextral canal opening; columella rounded, striate, without depression, and with a longitudinal low carinal wall adaxially; fossula long, shallowly trenched, with an upraised triangular wall within; aperture long, narrow, enlarging openly in front due to constriction of outer lip; outer lip fairly thick, rounded, only slightly crenate toward the rear; color bright light grey over all, except that funicular tip and columellar carinal wall are white; base wall of front and rear canal bright lavender-red, with bright canary yellow enveloping the terminals.

Radula: Radula of taenioglossate type, formula 2 · 1 · 1 · 1 · 2. Central tooth rounded, rectangular in shape, with a moderate central cusp and 5 minute denticles on both sides, the innermost of which is the smallest. Lateral

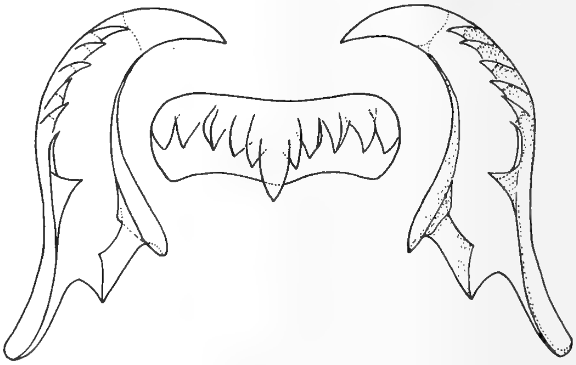


Figure 18

Radula of *Primovula* ***tosaensis*** Azuma & Cate, spec. nov.

Plate Explanation

Figure *8*: *Primovula* ***mucronata*** Azuma & Cate, spec. nov.
Holotype Aza. 14845 × 6
Figure *9*: *Primovula* ***tosaensis*** Azuma & Cate, spec. nov. Holotype Aza. 14840 × 4
Figure *10*: *Phenacovolva* ***tayloriana*** Azuma & Cate, spec. nov.
Holotype Aza. 1739A × 5
Figure *11*: *Phenacovolva* ***kiiensis*** Azuma & Cate, spec. nov.
Holotype Aza. 1737 × 2½
Figure *12*: *Phenacovolva* ***improcera*** Azuma & Cate, spec. nov.
Holotype Aza. 1739B × 5
Figure *13*: *Phenacovolva* ***yoshioi*** Azuma & Cate, spec. nov.
Holotype Aza. 1750 × 1⅔
Figure *14*: *Kuroshiovolva* ***shingoi*** Azuma & Cate, spec. nov.
Holotype Aza. 14839 × 4
Figure *15*: *Pseudosimnia (Diminovula)* ***fulguris*** Azuma & Cate, spec. nov. Holotype Aza. 14844 × 9
Figure *16*: *Primovula* ***fumikoae*** Azuma & Cate, spec. nov.
Holotype Aza. 1036 × 5½

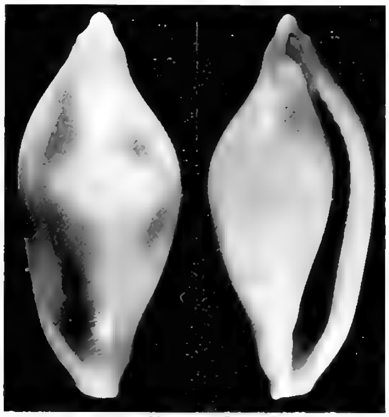


Figure *8*

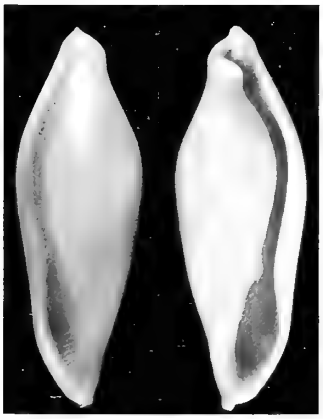


Figure *9*

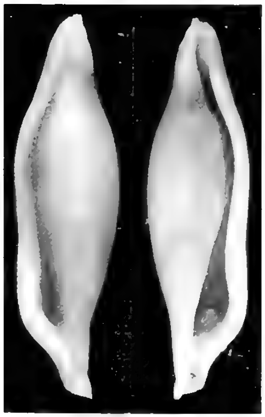
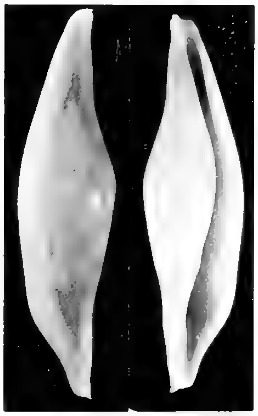


Figure *10*



Figrue *11*

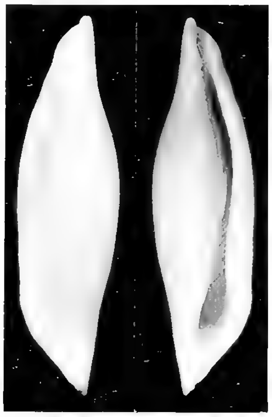


Figure *12*

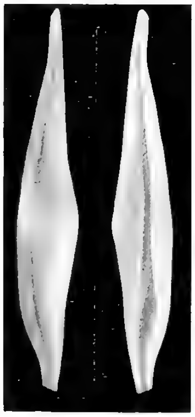


Figure *13*

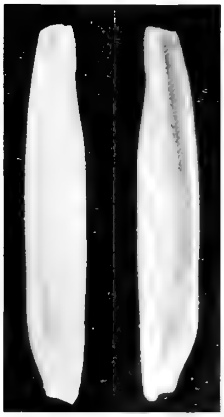


Figure *14*

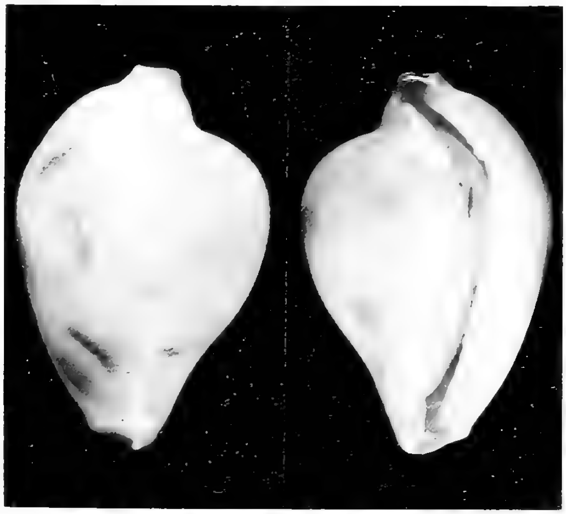


Figure *15*

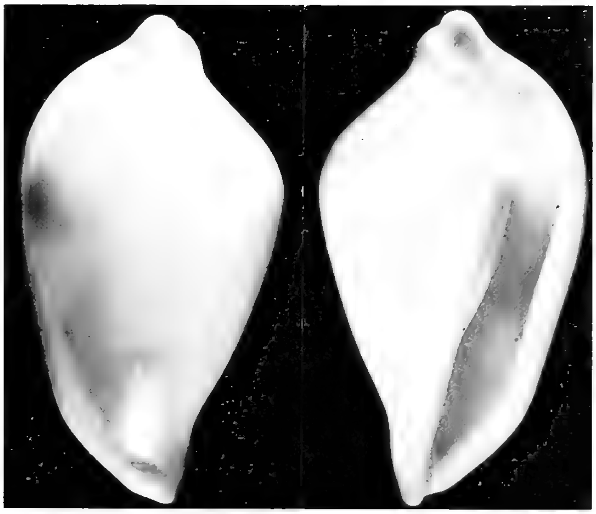


Figure *16*

photographs by BERTRAM C. DRAPER

teeth rather cactus leaf-shaped, the base of which is slender, projected backwards, its frontal with a large cusp that is slightly curved within and the outer side of it with 7 minute denticles, the base one of which is the largest.

Holotype: Azuma collection, no. 14840.
Length 11.5 mm; width 4.0 mm; height 3.3 mm

Type Locality: 2 km off Kirimezaki, Kii Peninsula, Japan, in 30 - 40 fathoms; leg. M. Azuma, 21 March 1970.

10. *Phenacovolva* ***tayloriana*** Azuma & Cate, spec. nov.

(Figure *10*)

Shell small, long, narrow, thin, translucent; terminals thin, knife-like on edges, open, though blunt at ends, taperingly produced, narrowly so to the rear, square in front; dorsum sub-glossy, with numerous fine, transverse incised striae, which become almost obsolete centrally; base smooth, glossy, elongately ovate, narrowing considerably in front, with hardly any funicular swelling in back; columella smooth, glossy, rounded, without depression; fossula barely existent; aperture long, narrow, twisting, widening in front due to acute angling of the outer lip; outer lip long, narrow, twisting, thick, rolled, smooth; dorsal color pale yellow-brown, darkening on the adapical terminal collar; terminal tips pale translucent grey; base and canals yellow-brown; outer lip off-white.

Holotype: Azuma collection no. 1739A.
Length 11.8 mm; width 3.2 mm; height 2.8 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, in 30 fathoms; leg. M. Azuma, 15 February 1970.

Discussion: This new species may be mistaken for another new species, *Phenacovolva* ***improcera,*** described below, but a close examination of their shells reveals that this species is differently and less striate dorsally; the outer lip is not as laterally constricted inward and squarely and acutely angled in front; it differs also by being conspicuously more delicate and translucent; by a different contour of the base and a more twisting outline of the outer lip; the color is also a separating feature.

This species is named in honor of Dr. John D. Taylor, Department of Mollusca, British Museum (Natural History), London.

11. *Phenacovolva* ***kiiensis*** Azuma & Cate, spec. nov.

(Figure *11*)

Shell of medium size, narrowly elongate, reflexed, almost lanceolate, attenuating sharply to either end of shell; terminal endings square and open at ends; dorsum smooth, glossy, without striation; base narrow, ovate, smooth, glossy, tapering narrowly to either end; columella rounded, smooth, glossy, without depression; no funiculum adapically and only a faint raised adaxial wall to suggest a fossula; aperture only slightly curving, broadening to the front because of lip and body constriction; outer lip edge thickened, rounded, and smooth, without shoulder above; shell color rich orange-beige dorsally, overlaid with a fairly broad, diffused yellow line the length of outer lip margin, which connects at either end with a line of small, solid, looping circles of yellow color over most of the central length of the dorsum (clearly visible under a microscope); base beige; funiculum and interior of shell deeper orange; outer lip edge stark white.

Holotype: Azuma collection no. 1737.
Length 20.9 mm; width 5.5 mm; height 4.4 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, in 20 - 30 fathoms; leg. M. Azuma, 15 February 1970.

12. *Phenacovolva* ***improcera*** Azuma & Cate, spec. nov.

(Figure *12*)

Shell small, long, narrow, almost translucent, subglossy; terminals tapering, with angling edges, open; dorsum rounded, inflated centrally, with fine transverse incised striae over all; base smooth, narrowly ovate, constricted in front, with a very weak funicular thickening in back; columella broad, shallowly depressed, striate, with a very shallow fossular area in front; aperture long, very narrow, open in front; outer lip roundly smooth, with an undulating curvature; color milk-white over all, with a faint olive-brown darkening at the terminal tips.

Holotype: Azuma collection no. 1739B.
Length 11.7 mm; width 3.1 mm; height 2.6 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, in 30 - 50 fathoms; leg. M. Azuma, 15 February 1970.

The species name is derived from the Latin *improcerus,* meaning small, short, undersized.

13. *Phenacovolva yoshioi* Azuma & Cate, spec. nov.

(Figures *13* and 19)

Shell fairly large, long, narrow, lanceolate, solid; terminals long, attenuate, narrow, especially in back where they become blunt-ended; dorsum glossy, roundly, evenly humped, broadening noticeably centrally, and numerously transversely incisedly striate over all; base long, narrow, tapering to either end with a curious sharply angled outer edge centrally, which becomes the summit of a longitudinal base ridge; base slopes flatly, angling sharply downward and inward to a long, low, adaxial carinal ridge; there is no funicular process; columella long and narrow, without special character except that it deepens weakly to form a shallow fossula; aperture long, very narrow, widening in front due to constriction of base and lip; outer lip long, narrow, roundly thickened, smooth; color milk-white, with a broad, distinct lemon-yellow line on the dorsal periphery of the sides and terminals, below which it darkens to a pale butter-yellow; ventral terminal beaks milk-white; base and outer lip of different intensities of yellow; columella lemon yellow to brownish the length of the adaxial carinal ridge; carinal ridge stark white.

Radula: Radula of taenioglossate type, formula 2 · 1 · 1 · 1 · 2. The central tooth of a rather obsolete rectangular form, concave at the center of the frontal margin, with a large sharp central cusp and 6 minute denticles on both sides, the outermost of which is the smallest. Lateral teeth rather cactus leaf-shaped, the outer base of which is projected backward, and in the frontal margin is a large cusp, curved within, outer side of which has 3 obsolete minute denticles.

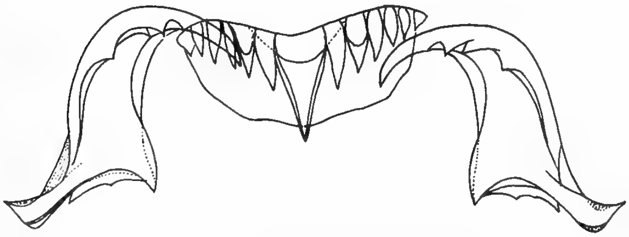


Figure 19

Radula of *Primovula yoshioi* Azuma & Cate, spec. nov.

Holotype: Azuma collection no. 1750.
Length 29.7 mm; width 4.8 mm; height 3.8 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, in 20 - 30 fathoms; leg. Yoshio Azuma, 15 February, 1970.

The species is named for Yoshio Azuma who collected the shell.

Kuroshiovolva Azuma & Cate, gen. nov.

Shells of this genus are very small, long, fragile, narrow, flattened with an evenly open, straight aperture and squarely blunt, open terminals.

The slight constriction of the outer lip removes the genus from any relationship with the genus *Simnia* Risso, 1826.

Type Species: ***Kuroshiovolva shingoi.***

14. *Kuroshiovolva shingoi* Azuma & Cate, spec. nov.

(Figures *14*, 20, 21, 22, and 23)

Shell small, long, rectangularly narrow, translucent; terminals open, square at ends; dorsum smooth, glossy, except that very fine longitudinal incremental growth lines are visible under the microscope (no transverse dorsal striation); base long, exceedingly narrow, rounded, smooth, glossy, with very slight constriction in front; no funicular swelling in back; columella smooth, glossy, rounded, without other characters; fossula narrow, concave, boat-shaped; aperture straight, narrow; outer lip thickened, though very narrow and smooth; shell color milk-white over all.

Radula: Radula of taenioglossate type, formula 2 · 1 · 1 · 1 · 2. Central tooth an inverted trapezoid in shape with a large, sharp central cusp and 2 minute denticles on

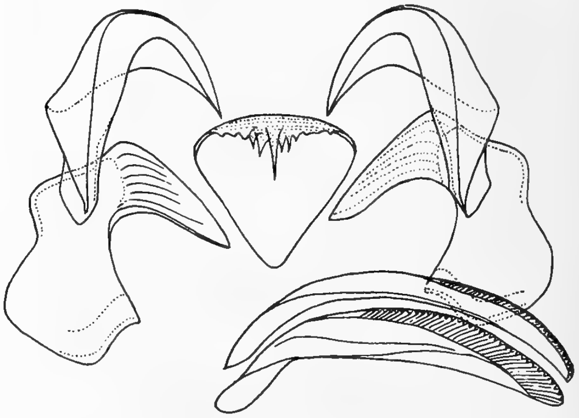


Figure 20

Radula of *Kuroshiovolva shingoi* Azuma & Cate, spec. nov.
Paratype No. 1 (♀)
a central tooth; lateral teeth of 2 pairs; and a marginal tooth

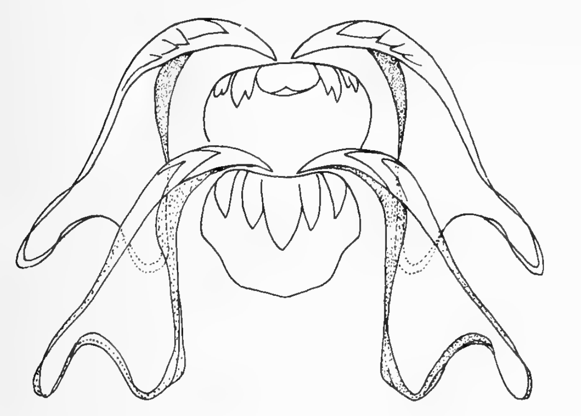


Figure 21

Radula of *Kuroshiovolva shingoi* Azuma & Cate, spec. nov.
a) anterior part of radular ribbon; b) middle part of radular ribbon

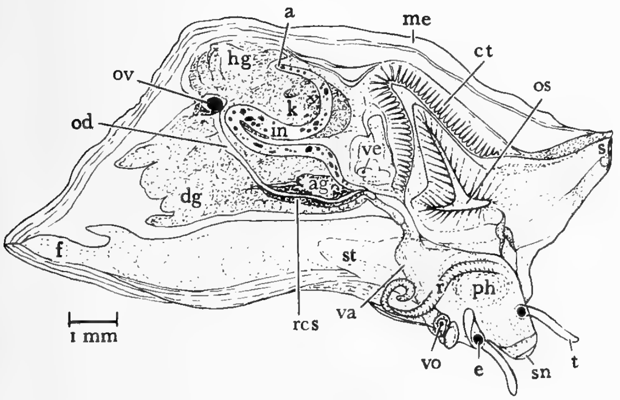


Figure 22

Kuroshiovolva shingoi Azuma & Cate, spec. nov.
Paratype No. 1 (♀) dissected to show contents of mantle cavity from the right

a – anus
ag – albumen gland
ct – ctenidium
dg – digestive gland
e – eye
f – foot
hg – hypobranchial gland
iko – opening of kidney
in – intestine
k – kidney
me – mantle edge
od – oviduct
os – osphradium
ov – ovary
p – penis
ph – pharynx
pna – penial aperture
pr – prostate gland
r – radular sac
rcs – receptaculum seminis
s – siphon
sn – snout
st – stomach
t – tentacle
va – vagina
ve – ventricle
vd – vas deferens
vo – vaginal opening

both sides, the outer of which is the smaller. Lateral teeth triangular leaf-shaped, the base of which is slender and projected backward; the frontal has a large cusp that is slightly curved within, the outer side with 2 - 4 minute denticles.

The radula of paratype no. 1 (♀): Central triangular in shape with a sharp, prickly central cusp and 2 - 3 minute denticles on both sides, of which the outermost is the smallest. Lateral teeth sickle-shaped, the frontal edge curved inward, Marginal teeth slightly frontal, leaf-shaped, the frontal to outer side with numerous minute denticles.

Holotype: Azuma collection no. 14839.
Length (♂) 13.3 mm; width 2.3 mm; height 1.7 mm

Type Locality: 2 - 4 km off Hinomisaki, Kii Peninsula, Japan, in 70 - 80 fathoms living on *Plumarella cristata* Kükenthal & Gorzawski; leg. Shingo Habu, 10 February 1970.

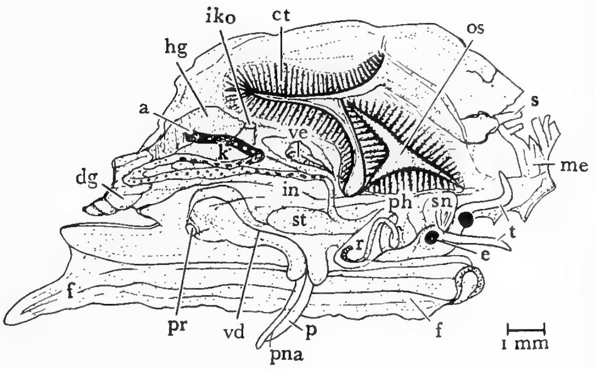


Figure 23

Kuroshiovolva shingoi Azuma & Cate, spec. nov.
Type (♂), dissected to show contents of mantle cavity from the right

There are 3 paratypes:

1. 26.5 mm; 4.0 mm (♀) Azuma collection 14910.
2. 11.0 mm; 2.0 mm; Cate collection C3884.
3. 17.0 mm; 2.0 mm; Shingo Habu collection.

15. *Pseudosimnia (Diminovula) fulguris* Azuma & Cate, spec. nov.

(Figures *15* and 24)

Shell small, bulbously, inflatedly pyriform, solidly formed; terminals gently produced, more so in back where the terminal is squarely beaked; dorsum elevated, roundly inflated sub-centrally, with transversely incised striation over all; base pyriformly inflated, striate, though less conspicuously so than dorsally, and narrowing sharply to the front; a thick, elevated, triangularly knobbed funiculum outlines left rear canal to dual left and forward terminal openings; columella broad, concavely depressed, deepening toward the front to form a large, distinct fossula; aperture broad, curving; outer lip broad, heavily thickened, rounding inwardly, with thick, large, poorly formed teeth; color of dorsum light grey, with curious lightning-like slash marks of brilliant dark orange; terminals solid orange on their edges; base lighter grey; outer lip and fossula white.

Radula: Radula of taenioglossate type, formula 2 · 1 · 1 · 1 · 2. Central tooth a rounded rectangle in shape with large central cusp and 2 - 3 minute denticles on both sides, the innermost of which is the smallest. Lateral teeth very slender and long, spoon-shaped, the frontal with a large cusp that is slightly curved within, outer side of frontal edge bears 4 minute denticles, the middle one the largest and minutely projected backwards.

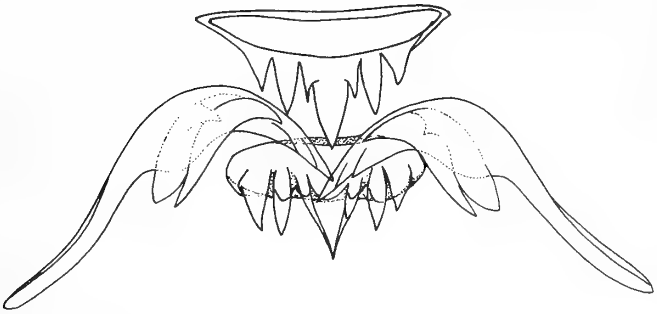


Figure 24

Radula of *Pseudosimnia (Diminovula) fulguris* Azuma & Cate spec. nov.

Holotype: Azuma collection no. 14844.
Length 6.9 mm; width 4.3 mm; height 3.8 mm

Type Locality: 2 - 3 km off Kirimezaki, Kii Peninsula, Japan, living on *Alcyonium gracillimum* Kükenthal; leg. M. Azuma, 15 February 1969.

The name of this species is derived from the Latin noun *fulgur,* meaning lightning.

16. *Primovula fumikoae* Azuma & Cate, spec. nov.

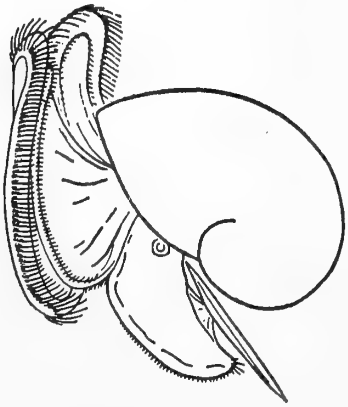
(Figure *16*)

Shell of medium size, pyriformly-rhomboid, humped, angled centrally; terminals somewhat pointed, less so in front; dorsum sub-glossy, though very faintly lined with longitudinal growth lines; fine transverse incised striae extend restrictedly from either end, central dorsum smooth; base narrow, rhomboidly-ovate, glossy, tapering abruptly and thickly to the front; thick, low, spiralling funiculum outlines the oblique canal opening; columella smooth, noticeably flat, broad, deepening narrowly, concavely to form a shallow fossula, which is defined by a short adaxial ridge; aperture broad, open, curving rather abruptly both front and back; outer lip edge roundly thickened, shouldered above, numerously, finely dentate within; dorsal shell color very light beige-brown, with a lighter, almost off-white band over the angle of the dorsum; base, outer lip, teeth, canals off-white; a short bright orange line extends over the margin of both terminal collars.

Holotype: Azuma collection no. 1036.
Length 13.0 mm; width 7.0 mm; height 5.8 mm

Type Locality: Off Tosa, Japan, in 80 - 100 fathoms; leg. Fumiko Azuma.

This species is named for Miss Fumiko Azuma, the daughter of the senior author, who collected the species.



The Influence of Water Temperature on the Morphology of *Leptopecten latiauratus* (Conrad, 1837)

BY

GEORGE R. CLARK II

Department of Geology, University of New Mexico, Albuquerque, New Mexico 87106

(1 Plate)

INTRODUCTION

Characteristics of living organisms are commonly divided into two groups: inherited and acquired. Taxonomists classify different forms of life by comparing characteristics, and their success is largely dependent upon the recognition and separation of acquired characteristics from genetic.

It is nearly a truism that no two species will occupy the same environmental niche. Differences between closely related animals with the same life habits can usually be attributed to minor differences in genetic character. However, when differences appear between two groups of closely related animals **not** occupying the same ecologic niche their origin is not easy to establish. In such a case it is usually assumed that differences in genetic character have dictated different environmental requirements. But there is no theoretical reason why such differences could not be acquired rather than genetic, and be dictated by, rather than dictating, the environment. This situation could continue only if both groups remained in a common gene pool; but since most marine invertebrates have a pelagic larval stage this is not a serious limitation.

While conducting a series of experiments on the periodicity of formation of growth lines in scallop shells (Clark, 1968, 1969), I found that many, if not all, of the morphological differences between two supposed subspecies of scallops can be shown to be influenced by the environment. Although I am continuing investigations along these lines, I thought my preliminary results might be of sufficient interest to justify a brief report and a few speculations.

INVESTIGATIONS

Two subspecies of *Leptopecten latiauratus* (Conrad, 1837), *L. l. latiauratus* and *L. l. monotimeris* (Conrad, 1837), are found in the Southern California area. These two forms are quite different in both morphology and ecology.

The basic morphological differences are in prominence of ribs, number of ribs, presence of concentric ridges (growth lines), obliquity of shell, ratio of length of hinge line to length of shell, and shell thickness. Most of these differences can be seen between specimen 0380 (*Leptopecten latiauratus latiauratus*) and specimen 0542 (*Leptopecten latiauratus monotimeris*) in the accompanying Plate.

The ecological differences are equally striking. Grau (1959) notes of *Leptopecten l. latiauratus*: "Bathymetric range: Recorded in 1 foot (minus tide) to 125 fathoms. Ecological data: Found attached to rocks or pilings in shallow water; in deeper water on rock, shale, gravel or sand bottoms, often attached to calcareous algae." (p. 110) and of *L. l. monotimeris*: "Bathymetric range: Apparently (from available data) never more than a few feet below the surface. Ecological data: Usually attached by byssus to seaweed or eel grass, less frequently to pilings, bottoms of boats, calcareous algae or rocks" (op. cit., p. 113).

Leptopecten latiauratus monotimeris is the most abundant scallop in the area where I conducted my experiments (Kerckhoff Marine Laboratory, Corona del Mar, California). During some seasons of the year these small animals enter the laboratory seawater system as larvae and appear by the hundreds in the aquaria. Despite their abundance they are of little use for periodicity studies for they form no growth ridges.

Leptopecten latiauratus latiauratus, which does form growth ridges, is not so readily available. However, on 22 July 1967 I obtained 15 specimens of this form from a depth of about 60 meters in waters off Santa Catalina Island, California. I established these in an aquarium at Kerckhoff Marine Laboratory to test the periodicity of their growth lines.

Twelve of the 15 specimens had approximately doubled in size by 1 September; the other 3 did not grow. However, the new growth was unsuitable for growth line counts because in most specimens it lacked growth lines. Moreover, this new growth appeared to have changed in other aspects from a morphology characteristic of *Leptopecten l. latiauratus* to one more characteristic of *L. l. monotimeris.* In the Plate, specimens 0542 and 0586 are normal *L. l. monotimeris.* Specimen 0380 is the only specimen (of 12) of *L. l. latiauratus* which retained its characteristic features in the new growth. Three specimens, like 0372, gradually changed character, and 8 specimens, like 0369 and 0373, changed abruptly from a morphology characteristic of *L. l. latiauratus* to a morphology characteristic of *L. l. monotimeris.*

This strongly suggests that much of the morphological differences between the two subspecies is due to environmental factors. But which factors might be involved? Several possibilities are suggested by the conditions of this experiment, as the environments at the collection site and at the laboratory differ in several important ways.

One obvious difference in environment is pressure. There is approximately 6 atmospheres more pressure at the 60 m depth of the collection site than in the aquarium at the laboratory. It is not known whether pressure differences can cause such morphological changes, although Bé (1965) notes that structural changes in the tests of certain planktonic foraminifera correlate with depth. It has also been shown that a number of organisms, notably among the plankton, is sensitive to small pressure changes and uses them to regulate the behavior (Knight-Jones & Morgan, 1966; Digby, 1967).

The amount of illumination present at the collecting site is not known, but I have noted while diving nearby in 25 m that the water is unusually clear and the bottom is well illuminated. I would estimate that the differences in illumination between the collecting site and the laboratory are slight, although the duration of daylight would be less at depth.

The temperature is much lower at the collecting point than in the laboratory. In July, the bottom temperature at 60 m is probably about 12° C and the surface temperature is about 17° C at the collecting site. The seawater temperature in the laboratory varied from 18° C to 22° C during the experimental period.

Many other factors, such as plankton concentration, turbidity levels, oxygen concentration, current velocities, etc., probably differ between the two environments but cannot be easily evaluated.

In another experiment, several specimens of *Leptopecten latiauratus monotimeris* were grown under artificially varied conditions of light and dark. No differences in morphology were noted between specimens grown in continuous light, continuous dark, and alternate periods of light and darkness. In addition, many hundreds of specimens settled from larvae in the sea table in the dark laboratory during this period, and except for a very few hours spent their entire lives in an environment of absolute darkness. These appeared in no way

Plate Explanation

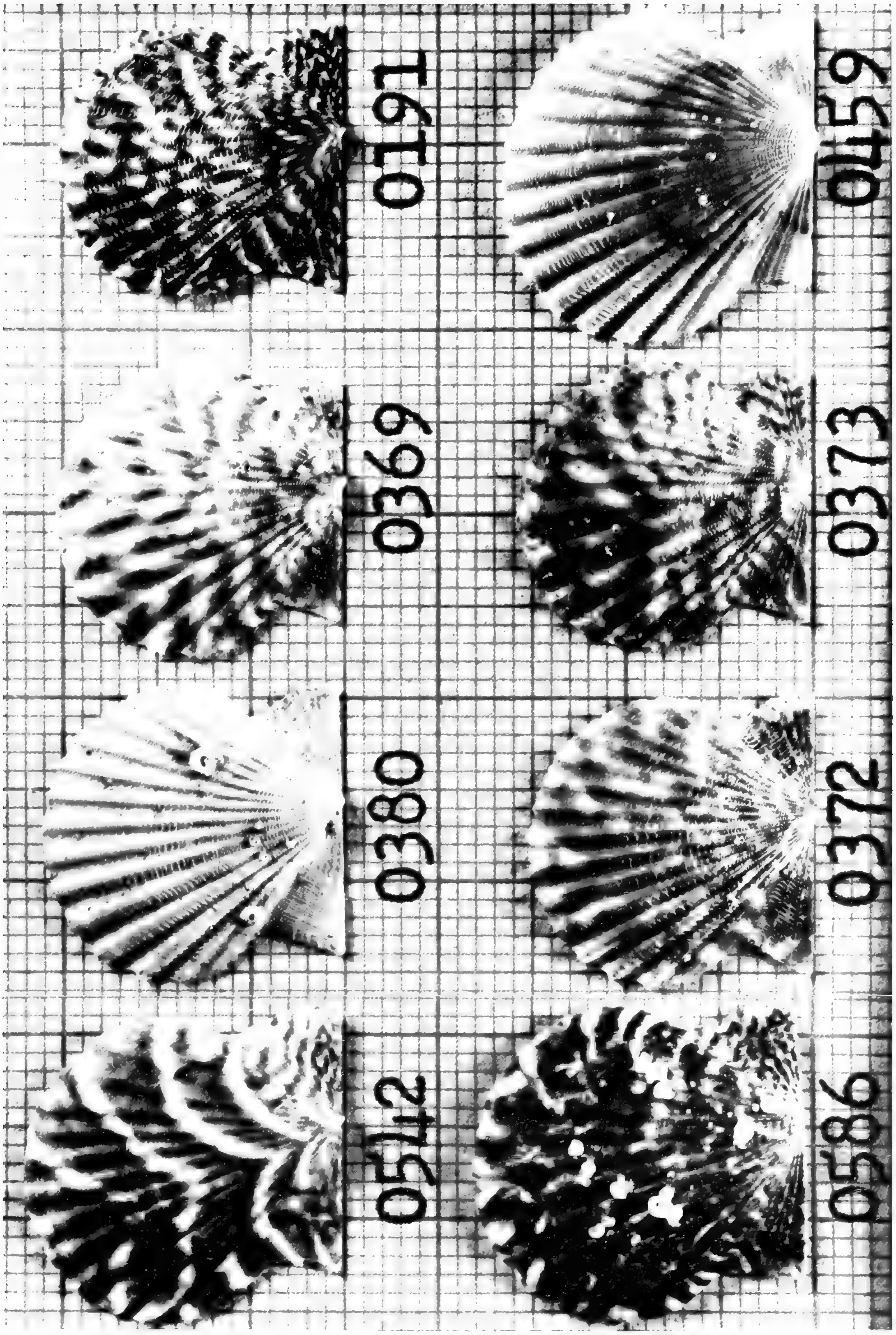
Specimens 0542 and 0586: Examples of *Leptopecten latiauratus monotimeris,* collected at Kerckhoff Marine Laboratory, Corona del Mar, California.

Specimens 0380, 0372, 0369, and 0373: Examples of *Leptopecten latiauratus latiauratus,* collected at Santa Catalina Island, California, as juveniles and then grown at Kerckhoff Marine Laboratory. Size when collected was approximately one-third the size at death. Note that this older portion of the shell is characterized by closely spaced growth lines in each instance. This is a feature of *L. l. latiauratus.* Specimen 0380 has retained this surface sculpture in the new growth added at Kerckhoff Laboratory. Specimen 0372 retains the growth lines in a portion of its new growth, but the most recent growth is free of such sculpture. Specimens 0369 and 0373 shift abruptly from a growth habit with concentric sculpture to one without it. Their most recent growth appears more characteristic of *L. l. monotimeris* in other respects as well.

Specimen 0191: Example of *Leptopecten latiauratus monotimeris* collected at Kerckhoff Marine Laboratory during the winter.

Specimen 0459: Example of *Leptopecten latiauratus latiauratus* collected in 10 meters of water at Corona del Mar during the summer and grown in Kerckhoff Marine Laboratory until the next spring. The first 3 to 4 mm of growth was prior to collecting; the next portion, lacking growth lines, was added during the summer and fall, when water temperatures in the laboratory were high; the outer portion, with numerous growth lines, was added during the winter when water temperatures were low.

Scale: Grid lines are 1 mm apart


0542
0380
0369
0191
0586
0372
0373
0459

morphologically different from other individuals from the same spatfall which settled in other locations in the laboratory near exterior windows.

In an intensive review of my records, I found that specimens of *Leptopecten latiauratus monotimeris* grown at Kerckhoff Laboratory when seawater temperatures ranged from 17° C to 25° C all exhibited features characteristic of that subspecies. However, in examining some 200 specimens of *L. l. monotimeris* which I had collected at various times at the laboratory, I found 15 specimens with some features (notably growth lines) of *L. l. latiauratus*. Usually these features were restricted to juvenile portions of the shells. My records showed that all these had been collected in the winter months, when seawater temperatures ranged from 14° C to 16° C. Specimen 0191 (see Plate) is one of these 15 specimens. However, other specimens collected at the same time were normal *L. l. monotimeris*.

Additional evidence was provided by a single specimen of *Leptopecten latiauratus latiauratus* collected in 10 m of water at Corona del Mar in September 1967. This individual added growth without ridges until mid-October, then stopped growing until about mid-January, when it began growing again with typical *L. l. latiauratus* features. Temperatures in the laboratory in September and October were about 19° C to 22° C; in January they were about 14° C to 16° C. This specimen is 0459 in the Plate.

Another clue to the cause of morphological differences may be in the geographic range of the two subspecies. Grau (1959) notes that the northern limit of *Leptopecten latiauratus monotimeris* is Monterey Bay, while *L. l. latiauratus* extends further north to Point Reyes (pp. 110 and 113). Too much significance should not be attached to this, however, for the difference in surface temperature, winter or summer, is less than one degree Centigrade (Ricketts & Calvin, 1952, pp. 348 - 349). The southern limit for both forms is Cape San Lucas, Baja California (although *L. l. latiauratus* extends northward again in the Gulf of California, while *L. l. monotimeris* does not) (Grau, op. cit., pp. 110 and 113).

DISCUSSION

Although far from definitive, these observations do strongly suggest that the difference in temperature is the major cause of the differences in morphology. This effect would not be unique; Ericson (1959) noted that the coiling direction in a species of planktonic foraminifera depends on the temperature. Also, it is possible that the effect noted by Bé is due to the temperature rather than the pressure changes involved.

Apart from the question of the exact conditions responsible for the morphological differences, these observations have implications for the taxonomy of the group. Recent workers (Abbott, 1954; Grau, 1959) consider *latiauratus* and *monotimeris* to be subspecies, but some of the earlier taxonomists felt that the two forms were environmental varieties. For example, Dall (1898, p. 710), in speaking of the variety *fucicolus* (now *monotimeris*) says: "This form lives attached by the byssus to the giant kelp of the Californian coast, and the absence of shock, due to the floating situs, is probably correlated with the obsolescence of the ribs and posterior sinus. Intergradations with the type are not at all rare." Grant & Gale (1931, p. 205) say of the variety *monotimeris*: "This variety lives in great abundance attached by its byssus to kelp. Its situs accounts for its special characters. Mrs. I. S. Oldroyd has informed the writers that the normal variety, although not so common, is found attached to worm tubes at low tide level near San Pedro."

From my own observations I can add that *Leptopecten latiauratus monotimeris* has a strong inclination to move upward. The animal climbs with surprising agility with its foot, which is attached to a smooth surface, pulls up the shell to the point of attachment, spins a byssal thread as a temporary anchor, and extends upward to a new point of attachment. This procedure is repeated until the animal reaches the top of the object it is climbing, the surface of the water, or a major obstruction. If several hundred animals are put in the bottom of a small aquarium, the majority moves to the uppermost portion of the aquarium walls within a few hours. The animals live there crowded so closely together that many form misshapen shells. Moreover, in some circumstances they seem unable to move downward; in several instances where stoppages in the drain temporarily raised the water level, the animals which moved up in response to this were stranded and died when the stoppage was cleared and the water level returned to its former position.

This behavior pattern might be the reason for the environmental distribution of the two subspecies. In the absence of any evidence to the contrary (such as different breeding periods), let us assume that the two forms are genetically identical. At breeding times the larvae of both groups are widely distributed in the coastal waters of Southern California. Upon settling, the young *Leptopecten latiauratus* find themselves in a wide variety of environments. Following their instincts, they climb upward on any surface available. Those animals which reach the surface will often die from exposure when tidal fluctuations leave them stranded; the exceptions are those on kelp or other floating objects. These develop the morphological characteristics of *Leptopecten latiauratus monotimeris.* The rest, unable to reach the surface, develop the morphological characteristics of *Leptopecten latiauratus latiauratus.* Although highly speculative, this model may be worthy of further investigation.

Regardless of what answers are finally found for the questions raised in this discussion, there seems to be little doubt that environmental factors can have a profound influence on the morphological characteristics of the shell of a bivalved mollusk.

ACKNOWLEDGMENTS

This study formed a part of my doctoral research at California Institute of Technology under the guidance of Heinz A. Lowenstam. Research space at Kerckhoff Marine Laboratory was provided by the Division of Biological Sciences, California Institute of Technology. This research was supported by NSF grant GB-6275.

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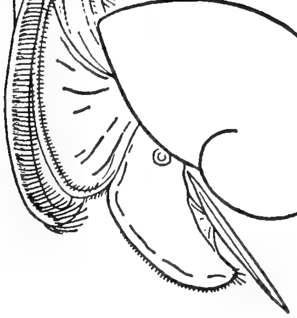

On the Function of the Digestive Gland in *Nassarius*

(Gastropoda: Prosobranchia)

BY

N. McLEAN

Department of Zoology, San Diego State College, San Diego, California 92115

(1 Plate)

THE DIGESTIVE GLAND of mollusks is generally considered to be an organ in which absorption of ingested food occurs. Recently MARTOJA (1961a and b, 1964) has reported that in the carnivorous European neogastropod *Nassarius reticulatus* (LINNAEUS, 1758), the digestive gland is not an organ of absorption. Neither food, nor reagents ingested with food, appear in the lumina of the glandular tubules, and there is no sign of apical absorption by the cells of the tubules. Food is absorbed through the epithelia of the stomach and intestine, and only then is delivered to the cells of the gland for further processing. The observations reported here indicate that in three American species of *Nassarius*, ingested reagents, and probably food, enter the ducts of the digestive gland from the stomach and then proceed into the lumina of the tubules of the gland where absorption occurs.

METHODS

Nassarius fossatus (GOULD, 1850) and *N. tegula* (REEVE, 1853) were collected from bays in San Diego, California. *Nassarius obsoletus* (SAY, 1822) was obtained by air express from the Marine Biological Laboratory, Woods Hole, Massachusetts. Animals were starved for from 1 to 14 days, and then were fed on flesh of the mussel, *Mytilus edulis* LINNAEUS, 1758, thoroughly mixed with reagents (colloidal graphite, carmine powder, rice starch grains, titanium dioxide powder) identifiable in the light microscope. After definite periods of digestion, specimens either were shelled and fixed without dissection, or were shelled and dissected before fixation, or were immersed in liquid nitrogen before shelling and fixation. Fixatives employed were 10% formalin in sea water, Bouin's fluid, formalin-ethanol-acetic, and SUSA. Paraffin sections were taken at 4 to 10μ, and stained in Lugol's iodine or in Mayer's hemalum.

RESULTS

The digestive gland in *Nassarius* is a large acinous structure, the tubules of which are furnished with lumina that communicate through ducts with the stomach. The glandular cells separate the lumina from the blood (Figure *1*). Material may enter the glandular cells apically from the lumina, or basally from the blood. In 104 of the 153 animals examined, the reagents utilized were found in the tubule lumina (Figure *1*). In considerable numbers of animals, the reagents were present in the lumina in quantity 30 min. or less after ingestion. Colloidal graphite, the reagent usually employed, was found within the cells of the digestive gland tubules in 43 specimens of the 3 species. The reagent ordinarily was concentrated apically (Figure *2*), although cells which contained graphite distributed throughout their length were often seen. Generally the graphite appeared in the cells from 30 to 45 min. after it was found in the tubule lumina. Carmine was observed within the cells of a few specimens. Titanium dioxide powder and rice starch grains were fed to a few animals, and while not seen within the tubule cells, were in each case to be found within the lumina of the tubules. At times the reagents were seen in small quantities in the blood spaces within the digestive gland; but since there was never an indication of a basal absorption by the glandular cells (i. e., a basal intracellular concentration of the reagent), I regarded the occasional occurrence of the reagents in the blood spaces as an artifact induced during dissection or other tissue processing.

In 49 animals, the reagents ingested were not found within the tubule lumina. Some of these specimens were fixed after very short periods of digestion, and it is assumed that sufficient time for the materials to reach the lumina had not elapsed. In other cases it was evident from inspection of sections of the stomach contents that the amount of reagent ingested was small when compared with the quantity of food taken in, and it is reasonable to suggest that the sections taken showed regions of the digestive gland to which only food had been delivered.

DISCUSSION

It is possible that on occasion the stomach contents may be forced into the entrances of the main ducts of the digestive gland by spasmodic muscular contractions during fixation (Owen, 1956); however, I do not consider the occurrence of ingested materials in the lumina of the many tubules in such a large number of animals to be an artifact. In a number of cases liquid nitrogen was employed as an immobilizing agent prior to fixation, and I do not consider it likely that during or after such treatment, spasmodic muscular contractions could occur to such an extent that they would produce the observed phenomena.

It is reasonable to assume that when ingested reagents are found in the lumina of the tubules, they have been accompanied there by food, and that a subsequent apical concentration of the reagents indicates that food has been absorbed from the lumina. Absorption of material from the lumina by the tubule cells, with subsequent apical concentration, is a common occurrence in mollusks (Fretter, 1937, 1939; Graham, 1932, 1938; McLean, 1970; Morton, 1955a, 1955b; Oldfield, 1955; Owen, 1955; Vonk, 1924); and it is generally accepted that absorption of ingested reagents shows a pathway for the uptake of food. It is conceivable that the absorption of extraneous material such as graphite is an excretory device; but the common occurrence of extracellular digestion in carnivorous gastropods (Owen, 1966) suggests that soluble materials derived from the food are to be found in the glandular lumina along with the ingested reagents. It is likely, therefore, that in such a region of active absorption some uptake of food does occur.

Martoja (1961a, 1961b, 1964) has shown that in *Nassarius reticulatus* materials are absorbed at the level of the stomach and intestinal epithelia. It appears that in the 3 species investigated here, uptake of food also occurs in the tubule cells of the digestive gland.

ACKNOWLEDGMENTS

I thank Dr. Mary E. Clark for a critical reading of the manuscript, Dr. Daniel L. Lindsley for the use of photographic equipment, and Dr. George E. Radwin for helpful comments. This work was supported in part by a grant from the San Diego State College Foundation.

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Plate Explanation

Nassarius fossatus (Gould, 1850)

Figure 1: Tubule of the digestive gland. Mayer's haemalum. B, blood space; L, lumen of the tubule; arrow, ingested carmine in the lumen, 18 minutes after feeding (× *ca.* 400)

Figure 2: Cells of a tubule. Mayer's haemalum. L, lumen of the tubule; arrows, ingested colloidal graphite concentrated in apical regions of cells, 75 minutes after feeding (× *ca.* 1 200)

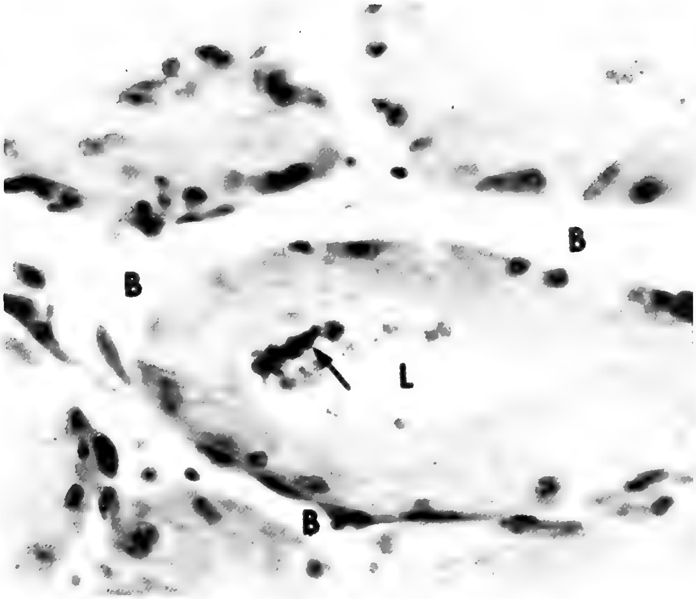

Figure *1*

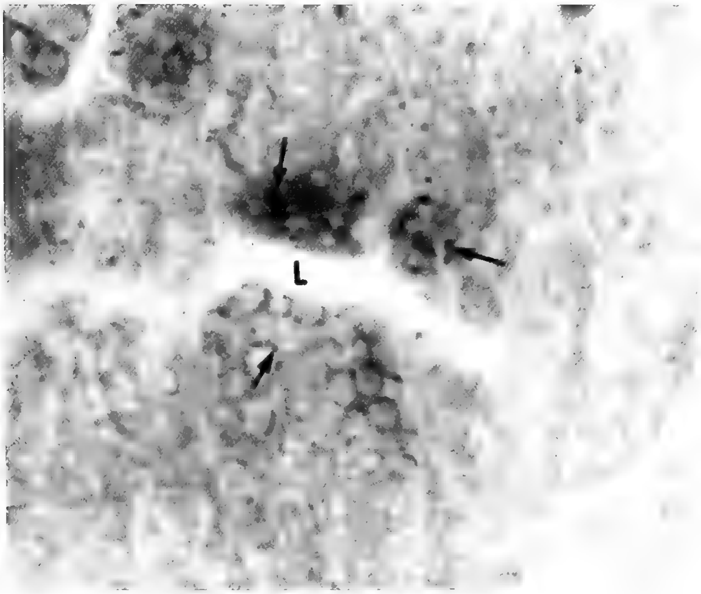

Figure *2*

Orientation of the Bivalve *Anadara trapezia* (Deshayes) Relative to Water Currents

BY

A. K. O'GOWER

AND

PATRICIA I. NICOL

School of Zoology, University of New South Wales, Kensington, New South Wales, Australia

(1 Text figure)

INTRODUCTION

Although reports on the orientation of birds and the analyses of such orientation are extensive (Batschelet, 1965), while the orientation of palmate algae, gorgonians, barnacles, gastropod molluscs and fish to water currents is documented (Charles, 1961; Dinamani, 1964; Overholser, 1964; Theodor & Denizol, 1965; Weaver, 1963), few records are available on the orientation of bivalve molluscs to water currents (Morton, 1962). During a study on the ecological genetics of *Anadara trapezia* (Deshayes, 1840) (Nicol & O'Gower, 1967; O'Gower & Nicol, 1968) a correlation was noted between the orientation of this relatively immobile bivalve mollusc and the strength and direction of flow of water currents in the environment.

METHODS

Using the hinge line of the bivalve as the origin, the angular orientation of samples of 100 individuals was measured in 15° sectors with an underwater compass. The animals were systematically sampled from populations in restricted, circumscribed areas within the four selected localities, and the rate of water flow was measured at each site by timing a float past two markers. The four localities were selected on the basis of their current flow patterns, as follows:

1. **Mallacoota Inlet:**
   The sampling site was a sand flat at the edge of the channel connecting the small coastal lake to the Pacific Ocean, hence, although the site was exposed to a semi-diurnal mixed tide, under conditions of heavy rain there was a seawards flow of brackish water over several tidal periods.
2. **Gunnamatta Bay**, a northern inlet off Port Hacking:
   The sampling site was exposed to a semi-diurnal mixed tide, but with heavy coastal surfs small wavelets run from south to north, being either: deflected, north east swells; or direct, wind generated southerly waves.
3. **Smith's Lake**, a small coastal lake which is opened to the sea at irregular intervals to relieve flooding:
   Sampling site A was a sand spit where the summer, wind-induced, current flow was from the north east and the winter, wind-induced current was from the south west. Sampling site B was a small, island-sheltered bay lacking current flow.

The significance of the orientations was determined using the Chi-square test as a goodness-of-fit to a circular distribution (k, the number of groups, being 12, Batschelet, 1965).

To determine whether orientation was fortuitous or in response to current flow, 30 *Anadara trapezia* were placed in each of two closed aquaria for a five day period. One of the aquaria lacked any current flow, the other had a circular, anticlockwise current flow.

RESULTS

The compass bearing orientations of samples of *Anadara trapezia* are presented as polar wedge diagrams (Gum-

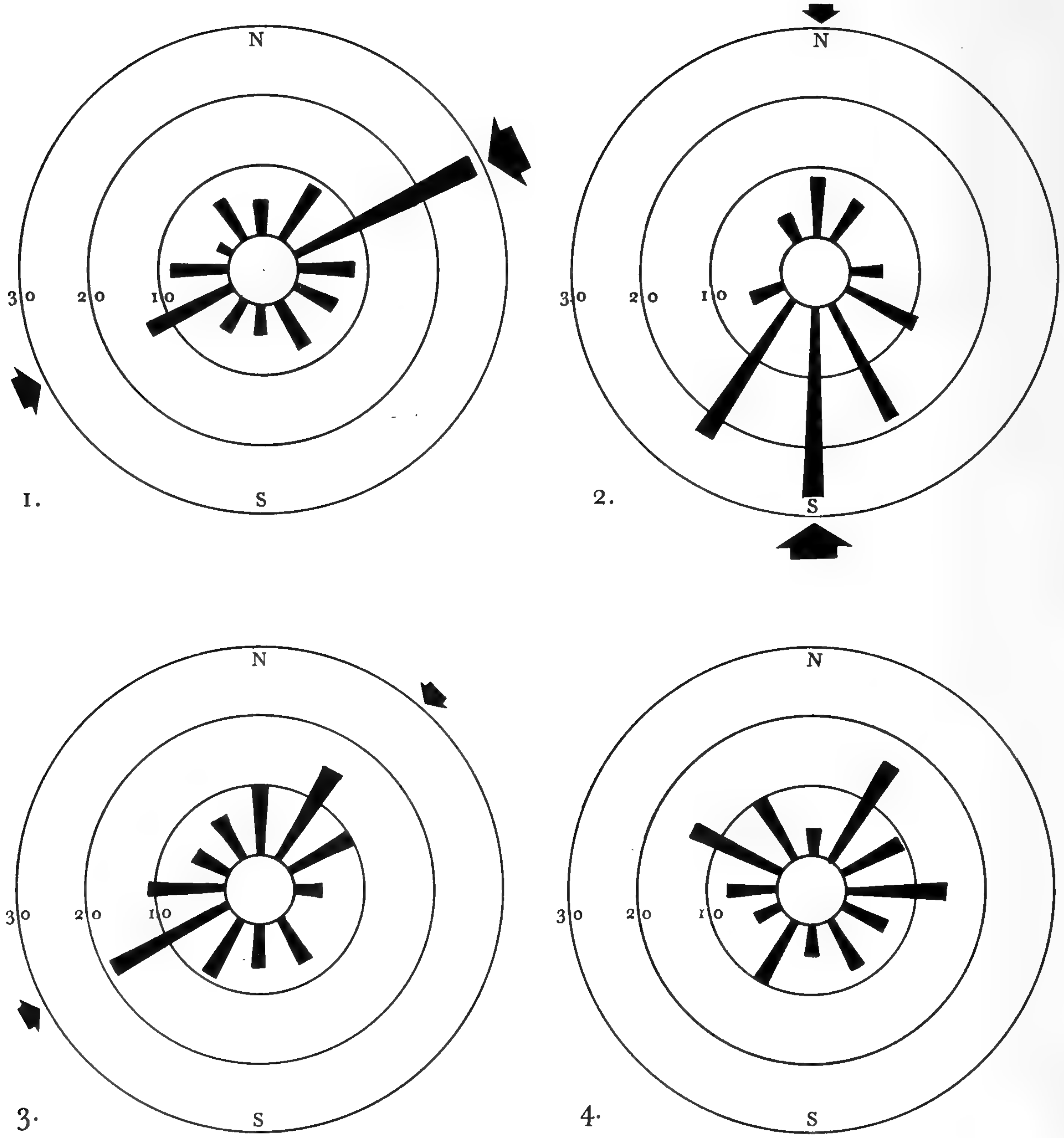

Figure 1

Angular orientation of *Anadara trapezia* from four localities:

1. Mallacoota Inlet 2. Gunnamatta Bay 3. Smith's Lake A 4. Smith's Lake B Current directions are indicated by arrows, whose size indicate the relative volumes of water involved.

Table 1

Compass quadrant orientation of *Anadara trapezia,* percentages of animals lying on their sides, maximum rate and direction of water current and Chi-square value ($n = 12$) and probability for randomness of orientation of samples from four selected localities

Locality	Current			Orientation						
	Rate (ft/min)	Direction	Side %	N-E	E-S	S-W	W-N	Total	X^2	P
Mallacoota Inlet Victoria	54.5	N. E. – W. S. W.	0	45	17	26	13	101	59.75	< 0.001
Gunnamatta Bay New South Wales	26.6	N. – S.	2	11	57	26	6	100	120.08	< 0.001
Smith's Lake A New South Wales	5.4	N. E. – W. S. W.	10	27	13	38	21	99	31.55	< 0.001
Smith's Lake B New South Wales	–	–	36	37	19	21	28	105	19.23	< 0.05

BEL *et al.,* 1953) in Figure 1 and the numbers of animals orientated in each of the compass quadrants and the maximum rate and direction of current flow for each of the four selected localities are given in Table 1. It will be noted that using the Chi-square test on the data in Figure 1 orientation was random for only one locality, Smith's Lake, Area B and that with decrease in current flow, there was an increase in the percentage of animals lying on their sides (Table 1) rather than half buried in the substratum.

In the aquarium lacking water currents 21.2% of the animals moved, but orientation was random. In the aquarium with a circular water current of approximately 30 cm/sec, 87.2% of the animals moved and 56.4% orientated in the direction of the current flow.

DISCUSSION

As *Anadara trapezia* is relatively immobile and cannot rapidly flush water across its gills, as it actively orientates into water currents (see Results, above), and as there is a positive relationship between the strengths and directions of water currents and the orientation of this mollusc in its natural environment (Table 1), it is probable that correct orientation would assist respiration, feeding and sanitation, while at the same time such orientation should lessen the chances of accidental dislodgment. The former hypothesis is an interesting challenge, while to support the latter hypothesis, it has been observed that *A. trapezia* suffers heavy mortalities in certain localities due to stranding, after the molluscs have been dislodged from the substratum by the action of wind-generated waves on the algae which have grown on their shells.

It is most unlikely that the latitudinal cline in haemoglobin polymorphism of *Anadara trapezia* (O'GOWER & NICOL, 1968) is correlated with either accidental dislodgment or orientation for respiration, feeding or sanitation; however, it is likely that accidental dislodgment strongly influences the abundance of this mollusc in certain localities, while correct orientation for respiration, feeding or sanitation should effect considerable savings in the expenditure of energy in these functions. The sensory mechanisms used by bivalves to detect such water currents obviously differ from those used by more active animals (WEAVER, 1963), but how such mechanisms operate with *A. trapezia* is at present unknown, and such a problem is worthy of further investigation. It seems probable that, unlike other active bivalves (MORTON, 1960, 1962), behaviour to currents will not involve visual stimuli but could involve tactile and gravity stimuli.

SUMMARY

The orientation of the bivalve *Anadara trapezia* (DESHAYES, 1840) is correlated with the direction and strength of tidal or wind-driven water currents both in the natural environment and under experimental conditions. Such orientation is probably associated with survival and with various physiological functions.

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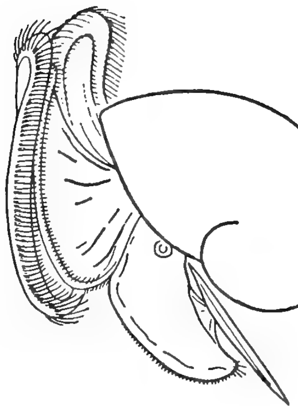

The Ecology of *Macoma inconspicua* (BRODERIP & SOWERBY, 1829) in Central San Francisco Bay.

Part II. Stratification of the *Macoma* Community within the Substrate

BY

MARILYN T. VASSALLO

Department of Biological Sciences, California State College at Hayward [1]

(6 Text figures)

INTRODUCTION

IN MAY AND JUNE of 1967 core samples were taken from a mud flat located $\frac{1}{2}$ mile north of the San Mateo Bridge in east central San Francisco Bay. Both the stratification within the substrate and the vertical distribution of the *Macoma inconspicua* (BRODERIP & SOWERBY, 1829) (= *M. balthica* LINNAEUS, 1758) community were studied.

The present paper reports the results of the stratification study.

MATERIALS AND METHODS

A core sampler with a cross-section of 9.7 cm × 9.7 cm and a length of 21 cm was used to take a total of 63 samples. The apparatus and method of taking the samples are described in earlier papers (VASSALLO, 1969 and in press).

Stratification was determined by cutting the mud core at 1 cm intervals. From one corner of each layer a 3 cm by 3 cm subsample was sieved through an 0.297 mm mesh under running water and then the rest of that layer was sieved through an 0.5 mm mesh. This procedure was modified for the upper 2 cm by sieving the rest of the layer through an 0.297 mm mesh.

The lengths of *Macoma inconspicua* and *Mya arenaria* LINNAEUS, 1758 were recorded as the animals were taken from each layer.

RESULTS AND DISCUSSION

Coelenterata:

Since only two specimens were taken with the core sampler, the stratification of *Flosmaris grandis* HAND & BUSHNELL, 1967 is not shown in Figure 9. Three additional specimens were dug from the mud flat with a shovel. The bases of the anemones were located 17 to 25 cm beneath the surface. None of the specimens penetrated to a depth beyond 25 cm. A thick layer of dense clay begins at this depth in the mud. On the mud flats adjacent to Bay Farm Island in northern San Francisco Bay, the majority of the specimens were attached 30 to 46 cm beneath the surface (HAND & BUSHNELL, 1967).

Annelida:

The cirratulid polychaete *Tharyx parvus* BERKELEY, 1929, inhabited the upper $5\frac{1}{2}$ cm of mud (Figure 1). It was most abundant between 2.0 and 5.0 cm. JONES (1961) found the major portion of the *Tharyx parvus* population at Point Richmond (in the northern part of the bay) to occur within this region. He found that a small percentage of the population occurred from 5.0 to 10.0 cm below the surface.

The polychaetes *Mediomastus californiensis* HARTMAN, 1944; *Marphysa sanguinea* MONTAGU, 1804; and *Neanthes succinea* (FREY & LEUKART, 1847) were distributed relatively evenly through the mud. In comparison with the errant polychaetes *Marphysa* and *Neanthes*, *Mediomastus* (Sedentaria) moves relatively slowly through the mud. Possible variation of the distribution in the mud with tide level was reported by JOHNSON

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[1] Present address: Department of Biology, University of Victoria British Columbia, Canada

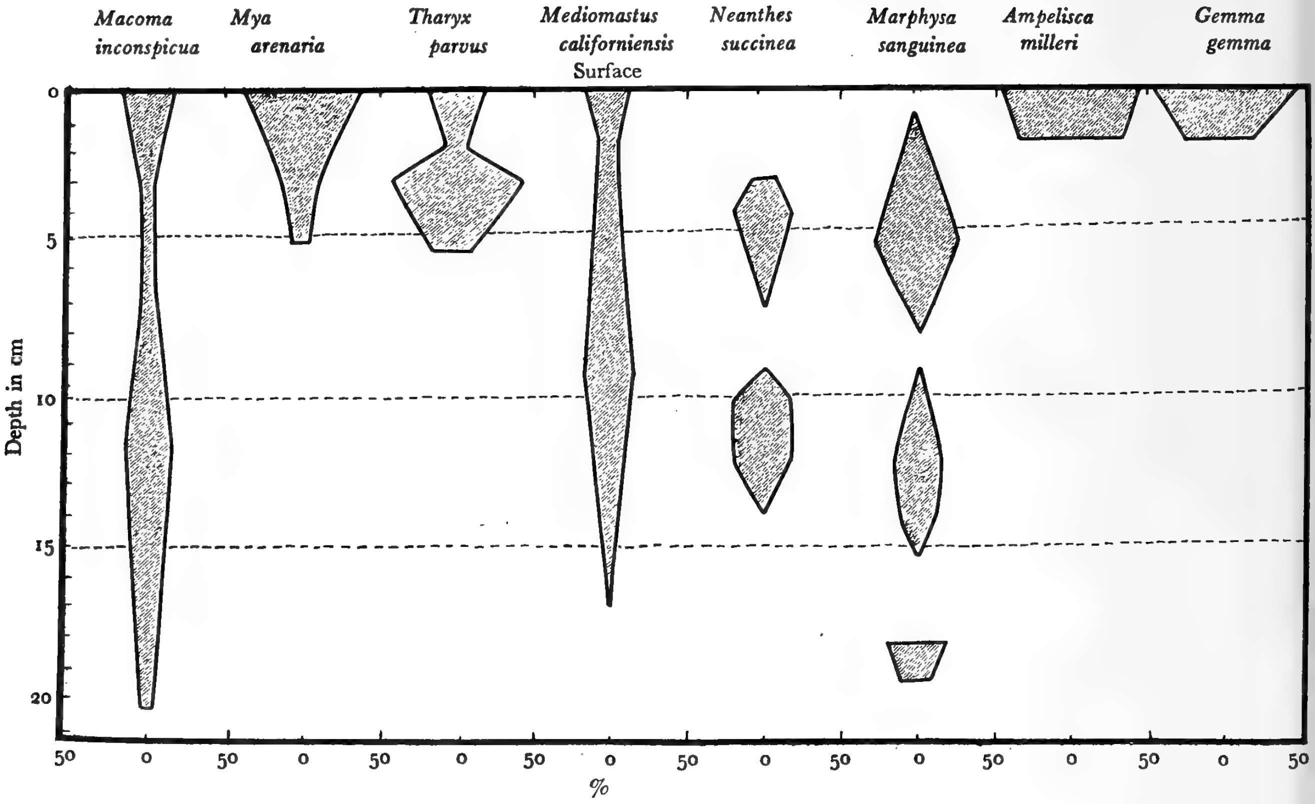

Figure 1

Per cent distribution of eight populations plotted against depth in centimeters

(1967). He reported that the distribution of the infauna of Lawsons Flat in Tomales Bay does not appear to fluctuate with tide level. With the exception of one member of the Nephtyidae, all of the polychaetes were members of the Sedentaria.

Vader (1964) found significant movements by *Nereis diversicolor* towards the surface of the mud as the tide flat is immersed. This species is closely related to *Neanthes succinea* (Frey & Leukart, 1847) (Hartman, 1936).

In the Salton Sea, Carpelan & Linsley (1961) report that *Neanthes succinea* spends most of its life in the mud and on the surface of the mud. The burrows of *N. succinea* in the San Francisco Bay mud flats communicate to the surface. It seems likely that *Neanthes* may also migrate to the surface when the tide is in.

Mollusca:

Mya arenaria was found to a depth of 5.5 cm. The majority of the individuals were small (Figure 2). Figure 3 suggests that distribution within the mud is related to size. However, there are not enough large individuals in the population to determine such a relationship.

The numbers of *Macoma inconspicua* were relatively uniform from the surface to the lower strata. However, the distribution of the large and small *Macoma* differed. There was a definite correlation between size and depth down to a depth of 7 to 10 cm ($r = 0.88$). From 8 to 20 cm there was a correlation of 0.34 (Figure 4).

The size frequency distribution of *Macoma* is shown in Figure 5.

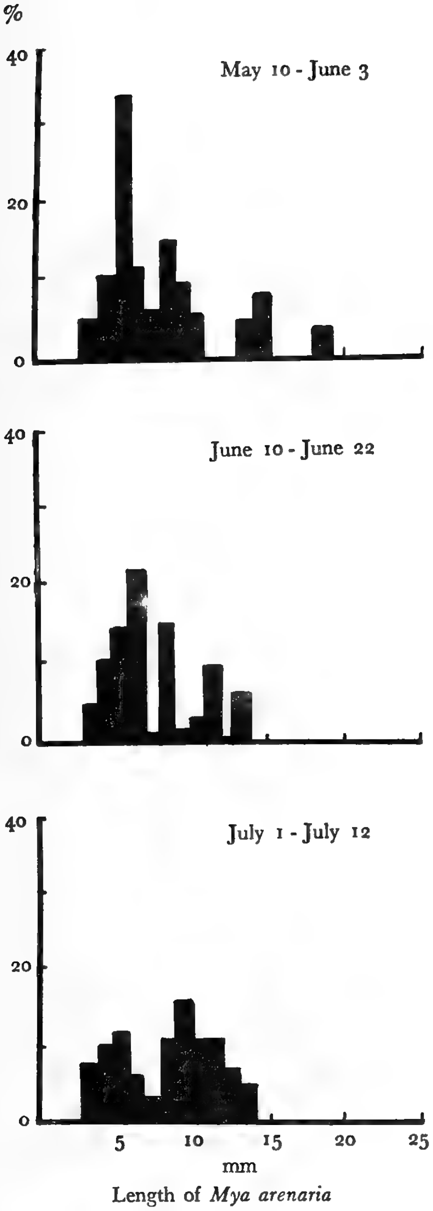

Figure 2

Frequency distribution of the length of *Mya arenaria*

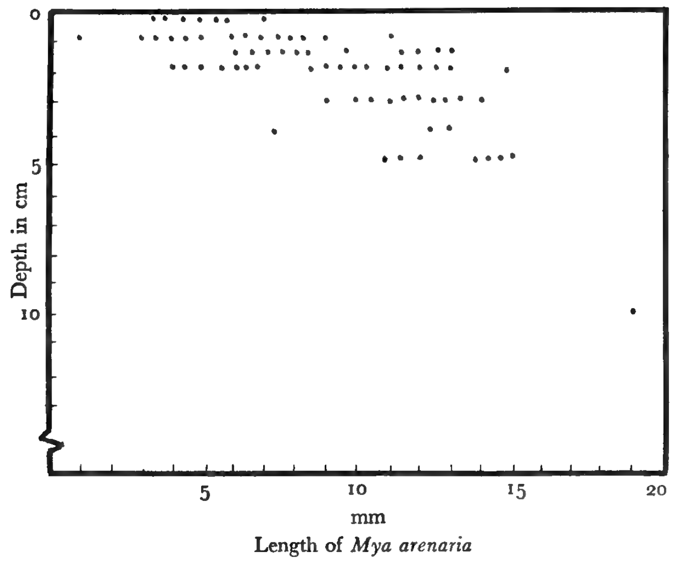

Figure 3

Stratification of *Mya arenaria* within the mud

In the laboratory specimens of *Macoma inconspicua* were placed on the surface of mud filled into milk cartons and allowed to burrow. After a week, the depth to which they had burrowed was measured. The distribution was similar to that found in the field (Figure 6).

The depth to which a *Macoma* can burrow may be limited by siphon length. Laboratory results tend to support this theory. However, the correlations appear to extend only to a depth of 7 to 10 cm. Beyond this point there does not appear to be a marked relationship between depth and size.

Burrowing within the mud may provide protection against wave action and predation in direct ratio to depth down to a given level beyond which the animal is safe. MATTHIESSON (1960) has shown that specimens of *Mya arenaria* up to 15 mm in length are susceptible to extensive dislodging by surf action. Burrowing deep may also provide protection from predators. In a study of migratory shorebirds on a mud flat south of and across the bay from the present study area, RECHER (1963) found that *Macoma* and *Mya* formed 3% to 4% of the diet of black-bellied plovers, dowitchers and willets. The pelecypods constituted 6% of the diet of the marbled godwit. Thousands of shorebirds have been observed, in a single day, feeding on the mud flat currently studied.

The bill lengths of the marbled godwit, dowitcher and willet are approximately 8 to 13 cm, 5 to 6 cm and $5\frac{1}{2}$ to

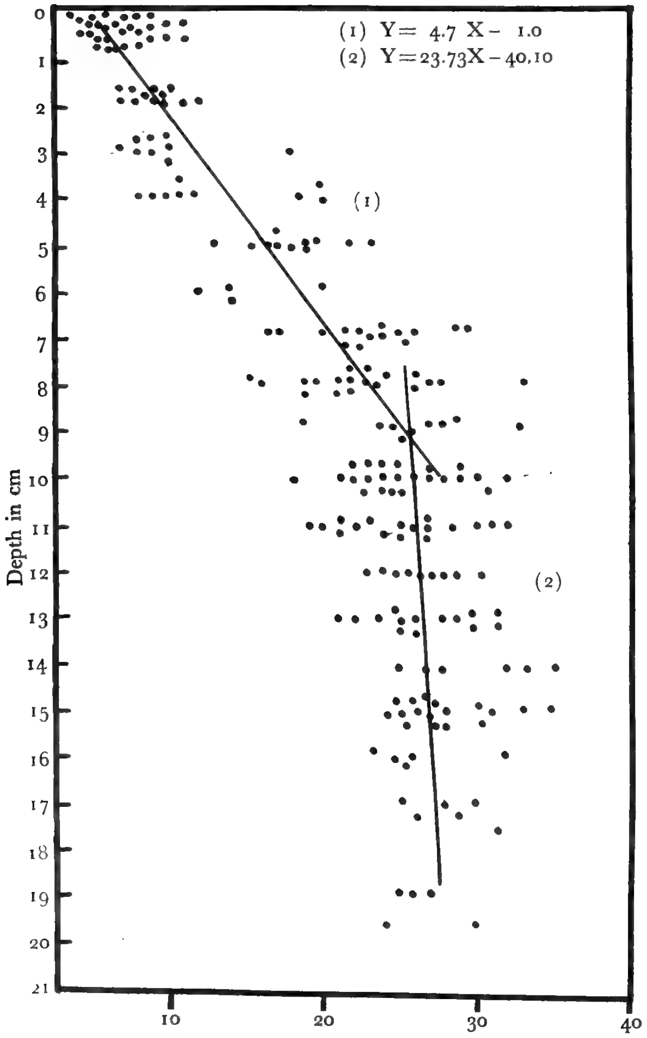

Figure 4

Stratification of *Macoma inconspicua* observed in the field. 'Y' refers to the horizontal axis and was determined from points taken on an eye-fitted curve

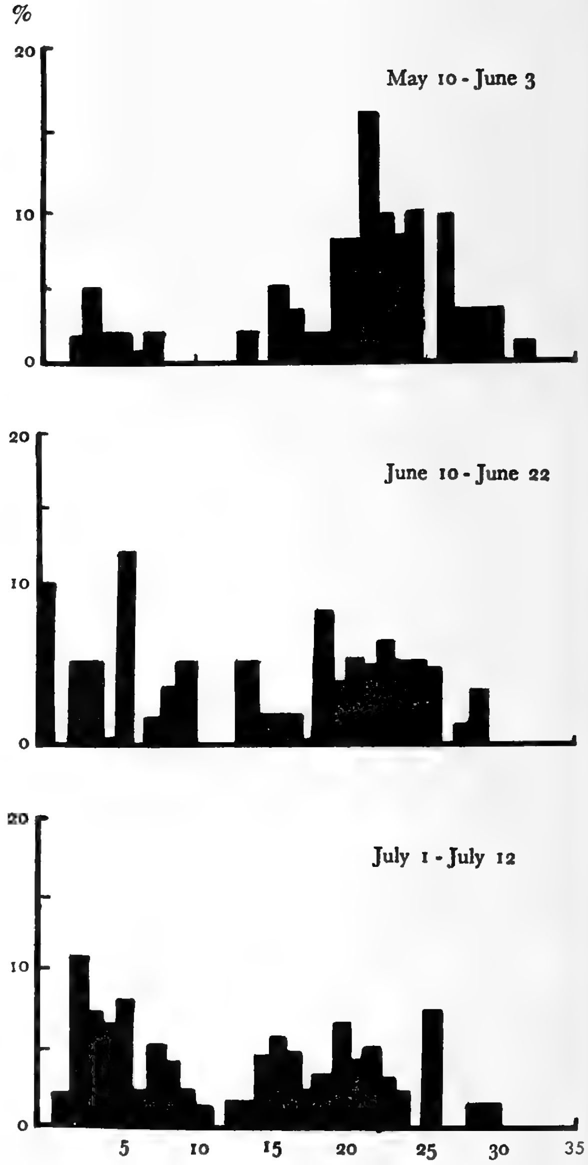

Figure 5

Frequency distribution of the length of *Macoma inconspicua*

7 cm respectively (FORBUSH, 1912). They feed on the mud flat by probing into the mud with their long bills, while plovers take food primarily from the mud surface. RECHER'S (1963) work indicates that remnants of pelecypods are found in shorebirds' stomachs. That shorebirds do, in fact, remove whole clams from the mud and swallow them has not been clearly established.

If they are taking clams, their predation is limited to the length of their bills, the greatest depth to which they

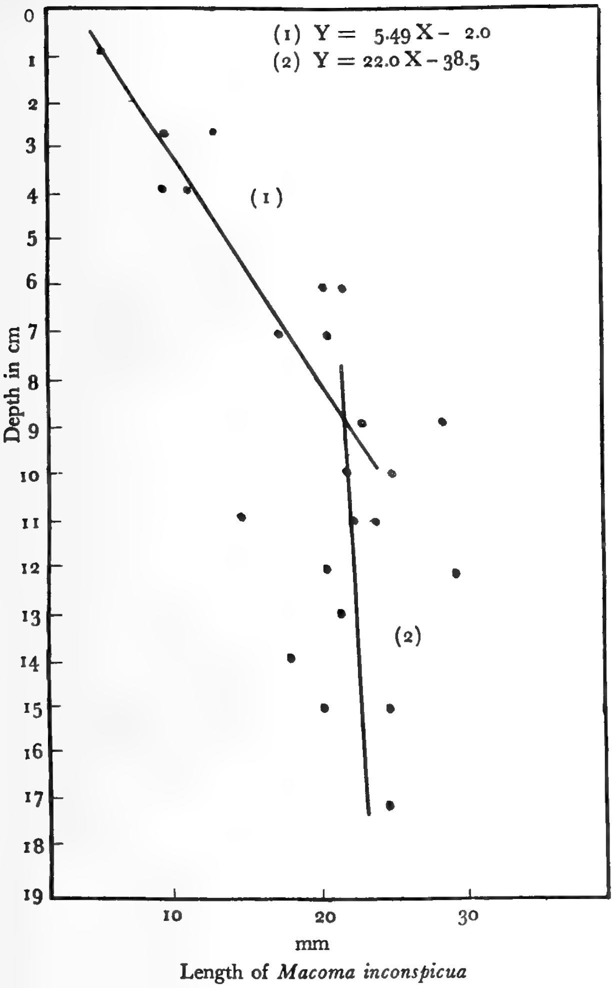

Figure 6

Stratification of *Macoma inconspicua* in the laboratory

can probe being about 13 cm. The blind probing would be more effective in taking larger animals than smaller ones. This might explain the absence of large *Macoma* in the upper strata.

Fraser (1932) reported that *Macoma inconspicua* occurs in immense numbers in the upper 3 or 4 cm of mud. The clams were small (1 to 1½ cm). Beanland (1940) stated that the upper one inch of mud contained a representative fauna. She did not indicate the size range of *Macoma inconspicua.* Whether migratory shorebirds frequent the area she studied is not known to this author.

Arthropoda:

The tubes of *Ampelisca milleri* Barnard, 1954, extended to a depth of 2½ cm. The size distribution of the population was not studied. Jones (1961) found that *A. milleri* extend to a depth of about 3 cm.

SUMMARY

1. The stratification within the substrate of a mud flat community was studied.
2. The numbers of *Macoma inconspicua* were relatively uniform from the surface down to a layer of clay 25 cm beneath the surface.
3. The distribution of large and small *Macoma* differed.
4. It is suggested that the smaller *Macoma* are limited to the upper layers by the length of their siphon. The low correlation of length of *Macoma* to depth below 13 cm indicates that there may be other factors involved.
5. Previous studies of the distribution of *Macoma* and studies on the feeding of shorebirds do not contradict the suggestion that large individuals of *Macoma* may be absent from the upper layers due to predation by shorebirds.

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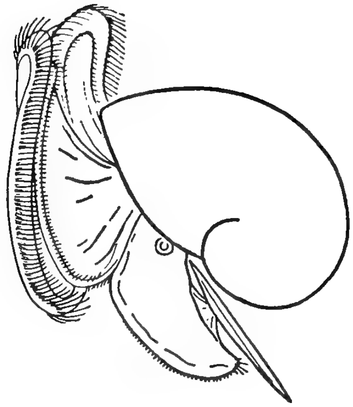

Cellulase from the Crop of *Aplysia vaccaria* WINKLER, 1955

BY

ROBERT L. KONINGSOR Jr.

University of California, Davis, California 95616[1]

AND

DON HUNSAKER II

Department of Zoology, San Diego State College, San Diego, California 92115

(4 Text figures)

INTRODUCTION

THE OPISTHOBRANCH MOLLUSK *Aplysia vaccaria* WINKLER, 1955, is a strict herbivore; thus it would be benefited if only a small percentage of the cellulose passing through its digestive tract could be utilized.

Few animals have been shown to be capable of digesting cellulose, and it appears to be very useful to plants as a structural polysaccharide for this reason. GORTNER (1949) states that "cellulose is the most widely distributed skeletal polysaccharide and the most abundant and chemically resistant of all substances elaborated by living cells."

YONGE (1926) stated that *Aplysia* digests cellulose, but he gave no evidence nor did he cite any particular species. The only other literature we found that refers to cellulases of *Aplysia* was STONE & MORTON (1958). According to these authors, a weak cellulase was found in *Aplysia punctata* CUVIER, 1803 by HOWELLS in 1942.

MATERIALS AND METHODS

All *Aplysia vaccaria* used in this study were collected at Bird Rock, La Jolla, California (Lat. 32°49′ N; Long. 117°17′ W). They were packed in damp seaweed in plastic buckets with a small amount of sea water while being transported to the laboratory. Special care was taken not to expose the *Aplysia* to extreme sunlight while they were confined in a small volume of sea water.

Since *Aplysia vaccaria* is found very low in the intertidal zone, numbers of *Aplysia* sufficient for experimentation could be collected only when the tidal level was 0.5 feet or more below mean sea level. Few *Aplysia* could be found during turbulent surf conditions when the tide was changing, but they were often found grazing in the quietly receding waters an hour or so before low tide and about 30 minutes after the incoming tide had covered the area.

When the *Aplysia* could not be dissected within a few hours after being collected, they were kept in 20-gallon capacity aquaria filled with sea water. The water in these aquaria was continuously filtered and aerated.

Dissection of the *Aplysia* was necessary to remove fluid from the crop. Pipettes and syringes were tried unsuccessfully. WINKLER'S (1961) dissection method was used, then the circumesophageal nerve cords were cut and the ganglia extirpated.

Fluid was removed from the crop by pinching off the esophagus, severing it, then draining the crop contents into a beaker. The fluid portion was decanted into centrifuge tubes. Finer particles were removed by centrifugation at 29 000 g on a Model HT International centrifuge for 30 minutes.

Disintegration of Paper

A 6 ml sample of crop fluid obtained from 4 freshly collected *Aplysia vaccaria* which had been fed *Ulva* sp. was placed in a soft glass digestion tube along with a strip of Whatman No. 1 chromatography paper. The manufacturers of this paper state that it is 100% cellulose. No Pyrex glassware was used for holding incubation mixtures, since PICKFORD & DORRIS (1934) have pointed out that some enzymes, i. e., trypsin and amylase, are inhibited by Pyrex glassware. Five drops of toluene were added as a bacteriostat.

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[1] Permanent address: P. O. Box 477, Dixon, California 95620

A similar tube containing 6 ml of distilled water instead of crop fluid was also prepared. This tube also contained 5 drops of toluene and a strip of chromatography paper.

Both tubes were observed after 48 and 72 hours of incubation at room temperature (26° C), and the condition of the paper was noted.

Glucose Production from Paper

To determine whether or not cellulose is actually degraded to glucose by the crop fluid of *Aplysia vaccaria,* the following experiment was performed.

Fluid removed from the crops of freshly collected *Aplysia vaccaria* was centrifuged and placed into soft glass digestion tubes as follows:

Tube *T* contained 2 ml of crop fluid and a strip of chromatography paper. Tube *B* was prepared identically to tube *T* except that the crop fluid had been boiled for 10 minutes in a water bath. Tube *C* contained 2 ml of distilled water and a similar strip of chromatography paper. Tube *D* contained 2 ml of crop fluid, but no paper. Three drops of toluene were added to each tube as a bacteriostat, and each tube was stoppered with cotton. All tubes were incubated at room temperature (26° C) for 10 days.

The paper strips were removed from tubes *T, B,* and *C*. All tubes were centrifuged at 2 800 g for 10 minutes. The supernatants of the 4 tubes were tested for glucose using Glucostat reagent (Worthington Biochemical Corporation). The relative amounts of glucose present were indicated by the optical densities measured on a Model 15 Cary spectrophotometer at 400 mμ.

Determination of Optimal pH

In order to determine whether the glucose production observed was due to an enzymatic reaction or acid hydrolysis, an attempt was made to determine the optimal pH of the reaction.

Crop fluid of *Aplysia vaccaria* was obtained and centrifuged in a similar manner to that used in the preceding experiments.

Two sets of 10 non-Pyrex digestion tubes were prepared as follows. One ml of citrate-phosphate buffer prepared according to McIlvaine (1921) was added to each tube so that 2 identical series of 10 tubes were obtained. The 10 pH's tested were 2.2, 3.1, 4.1, 4.5, 5.1, 5.5, 6.0, 6.4, 7.0, and 7.9. These pH values were measured with a Beckman pH meter; all were within 0.2 of the pH expected from McIlvaine's formula. Identical strips of Whatman No. 1 chromatography paper were added to each tube. One ml of crop fluid was then added to each tube, and the paper was immediately removed from one series of 10 tubes. Four drops of toluene were added to each tube as a bacteriostat. The contents of all tubes were thoroughly mixed by rotating the tubes between the palms of the hands and then allowed to settle. After the toluene had separated and risen to the top, 0.3 ml of the fluid below the toluene was immediately assayed for glucose with Glucostat reagent. Glucose standards and a reagent blank were also assayed. All tubes were stoppered with cotton to prevent evaporation and locked in a dark cabinet. Care was taken to be sure no paper was exposed above the level of the toluene.

After 72 hours of incubation at room temperature (26° C), the contents of all tubes were again assayed for glucose in the same manner. Since the paper had started to disintegrate, the paper was removed, and the tubes were centrifuged at 2 800 g for 10 minutes before the assay was performed. After the assay, fresh paper strips were added. The tubes were restoppered with cotton and locked in a dark cabinet.

After another 72 hours of incubation, a total incubation time of 144 hours, the paper was removed, the tubes were recentrifuged, and the assay was repeated.

The entire experiment was repeated twice to obtain the values shown in Figures 2, 3, and 4.

RESULTS

Disintegration of Paper

After 48 hours of incubation, there was very little difference between the appearances of the paper strips, but by 72 hours of incubation, the paper in the tube containing crop fluid had disintegrated. The fibers had separated, and individual fibers were no longer distinct to the naked eye. Microscopic examination revealed some fibers similar in appearance to the original fibers, but about half as long. There was no observable change in the appearance of the paper strip in distilled water even after a week of incubation.

Similar results were obtained when the experiment was repeated 2 months later.

When *Ulva* sp. was substituted for paper in the above experiment, the results were inconclusive. *Ulva* in crop fluid disintegrated after 48 hours, but so did *Ulva* placed in a 50:50 mixture of sea water and McIlvaine's (1921) citrate-phosphate buffer at a pH of 5.5. *Ulva* sp. did not disintegrate in sea water or distilled water.

Glucose Production from Paper

The relative amounts of glucose present in each tube as indicated by the optical densities are shown in Figure 1. The optical density of the mixture prepared from tube *T* (crop fluid, paper, and toluene) and assayed with Glucostat was far higher than that of any of the control tubes.

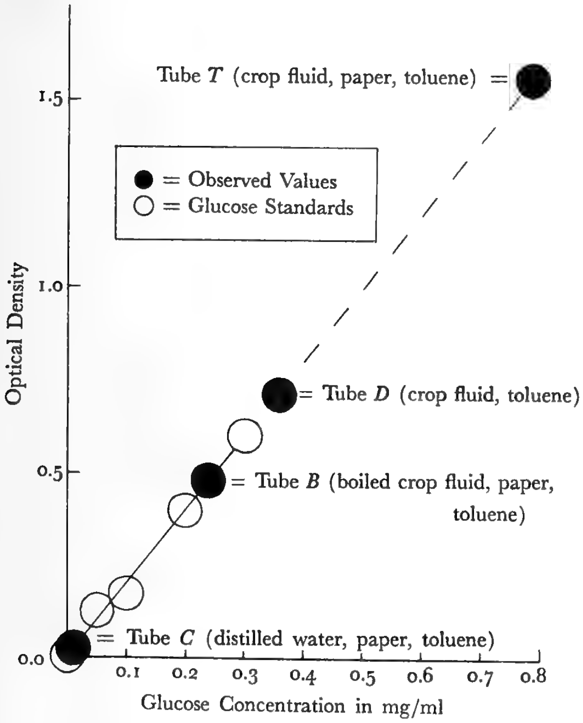

Figure 1

Glucose produced from filter paper substrate as indicated by optical density of glucostat

The low optical density of the mixture prepared from tube *B* (boiled crop fluid, paper, and toluene) suggests that glucose was not produced in that tube. A precipitate (probably denatured proteins) was observed during the boiling process. The absence of this precipitate from the mixture may account for the optical density being lower than that for the mixture prepared from tube *D*.

Glucose present in tube *C*, which contained distilled water instead of digestive fluid, appears negligible.

Since 2 of the observed optical densities were beyond the range of the standards for which Glucostat reagent is known to give a straight line relationship between glucose and optical density, no attempt was made to convert optical density to amount of glucose. Nevertheless, it is reasonable to state that the amount of glucose in tube *T* exceeded 0.30 mg per ml.

Determination of Optimal pH

Figures 2 through 4 graphically portray the results of this experiment. The optical density as measured on the spectrophotometer is an index of the amount of glucose present in each tube. The color of the crop fluid may also have contributed insignificantly to the optical density, but it would have been the same in all tubes, and only one-tenth of the assay mixture read by the spectrophotometer was crop fluid. Most of the points which did not fall near the curve of average values were affected by turbidity differences in the incubation mixtures. However, the spectrophotometer could not differentiate between optical density and turbidity differences. As a result, the curves for the 3 individual trials are a bit more irregular than optical density differences alone would warrant.

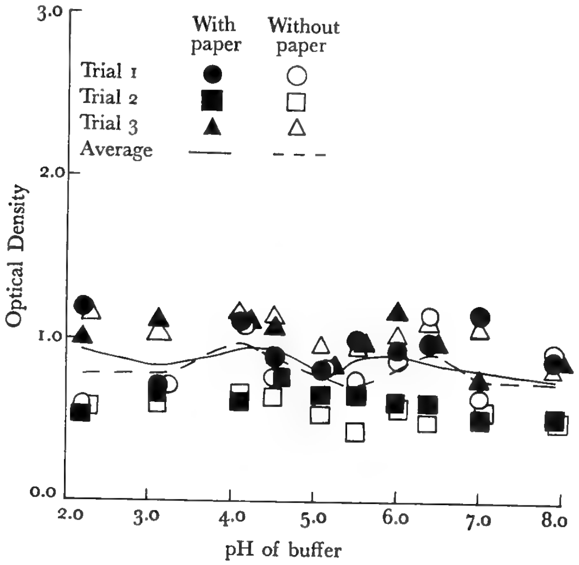

Figure 2

Optical density as an index of glucose present at T_0 (zero days of incubation)

The symbol T_0 indicates results obtained prior to any incubation period. Those results obtained after 3 days of incubation were labeled T_3. Results of assays made after 6 days of incubation were labeled T_6. Average values for the 3 trials are connected by a solid line curve

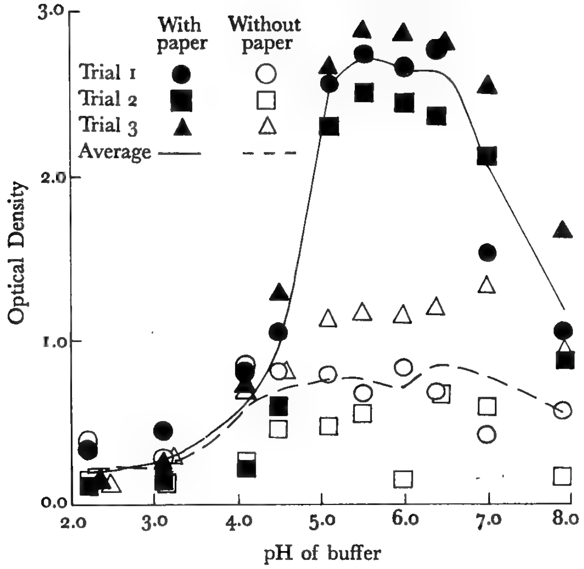

Figure 3

Optical density as an index of glucose present at T_3 (three days of incubation)

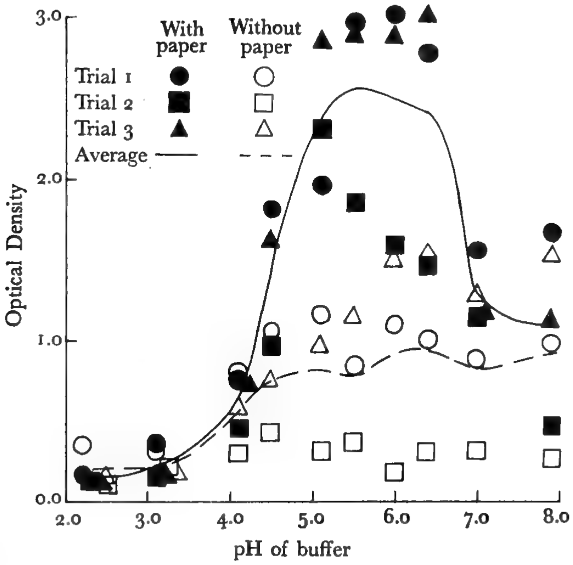

Figure 4

Optical density as an index of glucose present at T_6 (six days of incubation)

for the tubes with paper and by a dotted line curve for the tubes without paper.

It can readily be seen that there was no consistent difference between the curves at T_0. A pH optimum of about 5.5 was observed for the results taken at T_3 and T_6, 3 days and 6 days of incubation, respectively.

SUMMARY

The observation that chromatography paper disintegrates in crop fluid of *Aplysia vaccaria* does not prove that this animal is capable of utilizing the cellulose from its diet as a food source; however, it does suggest that more refined experiments should be performed to investigate the possibility that the opisthobranch may indeed possess this remarkable power.

Glucose Production from Paper

The results of this experiment do indicate that *Aplysia vaccaria* has the ability to convert paper (100% cellulose) to glucose, a source of energy utilized by most organisms. Since the boiled crop fluid in tube *B* did not yield a higher glucose reading than crop fluid alone (tube *D*), it suggests that the reaction is enzymatic. Apparently, boiling inactivates the enzyme or enzymes involved by denaturing them.

Determination of Optimal pH

The optimal pH of 5.5 observed for the production of glucose is good evidence that an enzyme or enzyme system is involved. If acid hydrolysis of the cellulose chains were the cause, one could expect the most glucose to be produced at the lowest pH's tested.

The pH optimum of 5.5 is a value consistent with other cellulases' pH optima. Parnas (1961) found one pH optimum of 5.75 for a cellulase from the crop of the snail *Levantina hierosolma* Boiss. He found another pH optimum of 5.6 for a cellulase from the hepatopancreas of the same snail. Lasker & Giese (1956) found cellulase pH optima of 4.0, 6.0, and 7.7 for the silverfish *Ctenolepisma lineata*. A pH optimum of 5.28 was determined for a cellulase of the terrestrial snail *Helix* by Karrer & Illing (1925).

Obviously a herbivorous mollusk that can convert cellulose to glucose has a distinct advantage over any competitors who lack this ability. *Aplysia vaccaria* seems to possess this ability. As yet, it is not proven that the cellulase is endogenous to *A. vaccaria,* i. e., the cellulase may be an extracellular enzyme produced by a bacterial symbiont, but we do not believe this to be the case, on the basis of some preliminary bacterial studies.

Perhaps studies of other herbivorous mollusks will indicate that the phenomenon of cellulose digestion is not as unusual among the Mollusca as present knowledge indicates.

ACKNOWLEDGMENTS

This graduate study was done at San Diego State College. We would like to thank Dr. Frank Ratty for the use of his laboratory facilities, and express our special thanks to Dr. Norman McLean for his assistance and advice.

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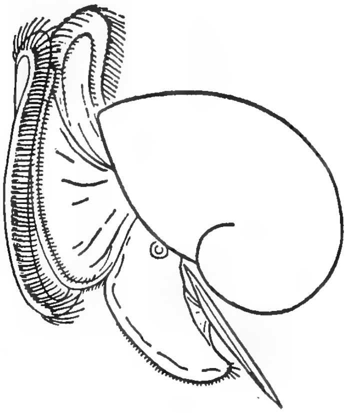

On the Identity of *Conus cedonulli* Linnaeus, 1767

BY

V. ROGER DUNN

4727 27th Avenue South, Gulfport, Florida 33711

(1 Plate)

HISTORY

In the tenth edition of the Systema Naturae Linnaeus named and described *Conus ammiralis* and three infra-specific forms, giving as locality "O. Americae meridionalis." From these descriptions, however, *ammiralis* was recognized as a now well-known Indo-Pacific species. In the 12th edition of the Systema he added a fourth form (*C. ammiralis cedo-nulli* Linnaeus, 1767) and again gave the habitat as "O. Americae meridionalis." His brief description was insufficient in itself to define the form and he cited but one figure (Seba, 1758, vol. 3, plt. 48, fig. 8). The hypotype of this figure was a specimen originally in the cabinet of Johan Bernard de la Faille of The Hague, Holland, and known as "*Cedo Nulli*" as early as 1718. Its present whereabouts are unknown.

Hwass in Bruguière (1792, p. 602) boosted *cedonulli* to specific rank and re-described it but failed to attribute it to any author. However, he also named and described 9 infra-specific forms and included *Conus ammiralis cedo-nulli* Linnaeus and its description in his synonymy of variety A (*Conus cedonulli amiralis* Hwass in Bruguière, 1792). All varieties were given Caribbean localities and 7 were named for them.

Lamarck (1822, p. 447) accepted Hwass' revision but credited *cedonulli* as a separate species to Bruguière. Linnaeus was mentioned only as using the name as a "variety." Through most of the 19th century conchologists recognized *Conus cedonulli* as a valid Caribbean species, although they often credited it to Bruguière, Hwass, or Lamarck.

But Tryon (1884, vol. 6, p. 28) merely listed "*Cedonulli* Hwass" as a synonym of "*nebulosus* Solander" (probably *nebulosus* Hwass = *Conus regius* Gmelin, 1791) and this could well be true of Tryon's specimen, for *regius* was often polished and sold as *cedonulli.*

Clench (1942, Johnsonia no. 6, pp. 3 - 7) divided *cedonulli* of Hwass and Lamarck between *Conus regius* and *C. dominicanus* Hwass, 1792 and said these were "long confused with *C. cedonulli* and *C. ammiralis* – both Indo-Pacific."

Dodge (1953, p. 27) says that Hwass' forms of *Conus cedo-nulli* were based on a specimen of *C. regius* and that the real *cedonulli* is an Indo-Pacific shell.

Kohn (1963, Journ. Linn. Soc. **44**, no. 302, p. 762) says he agrees with Linnaeus that *cedonulli* is a variety of *Conus ammiralis* and (1968, Journ. Linn. Soc. **47**, no. 313, p. 450) that he considers all of Hwass' varieties of *cedonulli* to be conspecific with *Conus insularis* Gmelin, 1791.

Finally, Dance (1966, p. 232) publishes Seba's type figure of "*Cedo Nulli*" and says it is probably the *architalassus* Lightfoot form of *Conus ammiralis.*

DISCUSSION

I am greatly indebted to Mr. G. W. Nowell-Usticke of St. Croix, Virgin Islands for the opportunity to study and photograph an extraordinary specimen in his collection of the *Conus cedonulli* of Hwass, here shown as Figure *1,* and I am grateful to Mr. S. Peter Dance for reproducing Seba's figure of *cedonulli* Linnaeus, shown as Figure *2,* which I otherwise might never have seen. Seba

Plate Explanation

Figure *1*: *Conus cedonulli* Linnaeus. St. Vincent, Windward Islands (Nowell-Usticke collection). × 1

Figure *2*: *Conus ammiralis cedonulli* Linnaeus. Type figure from Seba, vol. 3, plt. 48.

Figure *3*: *Conus ammiralis* Linnaeus. Philippines. × 1.3

Figure *4*: *Conus ammiralis* Linnaeus. Aori Island, New Hebrides. × 3.0

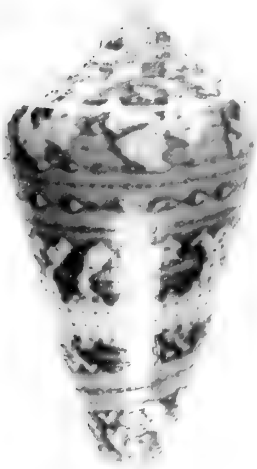

Figure *1*

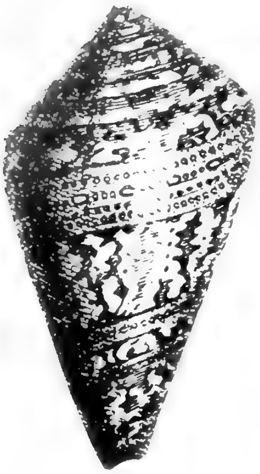

Figure *2*

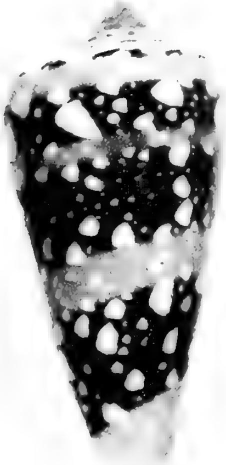

Figure *3*

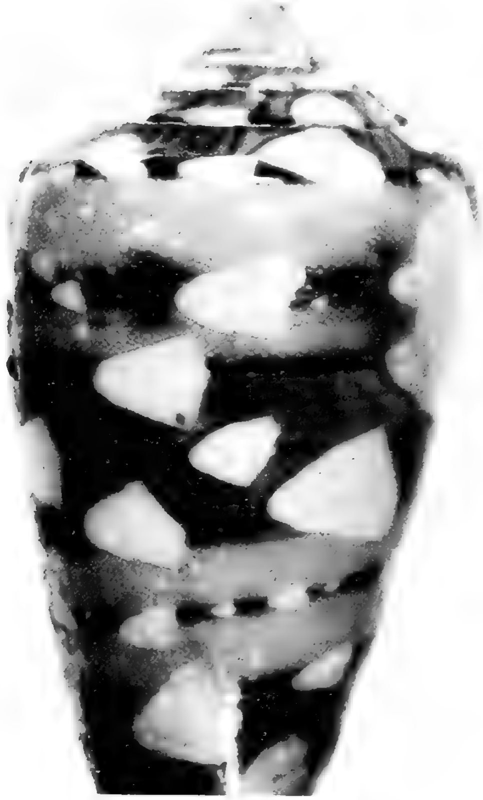

Figure *4*

published this figure in reverse and upside down; so for better comparison I have re-reversed it. Other figures are of *Conus ammiralis* LINNAEUS from my own collection.

At first glance I was satisfied that the SEBA figure supported the *Conus ammiralis* identification, but further study made this less and less convincing. Indeed it finally appeared that the figure contained only one feature characteristic of *ammiralis* – the sharp delimitation of the bands on the body whorl – and Usticke's remarkable specimen showed that feature to be less than conclusive. All else supported HWASS' determination.

Conus ammiralis has only nearly imperceptible concentric sculpture on the spire but prominent radiating dark lines in patches of lighter color, and the whorls are slightly concave – not convex. The spire pattern never extends over the shoulder. Instead there is invariably a yellow band of fine reticulations at the shoulder, and any coarser markings in it are random – not aligned as beads on a string. The dark panels usually show still darker lines, on which there may be a slight bead effect, but this is obscured by the larger white markings that are shaped like crude arrowheads – not clouds.

The above definition applies to all forms of *Conus ammiralis* with which I am familiar, including the *architalassus* form of SOLANDER in LIGHTFOOT (1786, p. 189), distinguished only by being pustulate, and the shell listed by KIENER (p. 135, pl. 21, fig. 1c) as *ammiralis*, form *blainvilli* VIGNARD and by MARSH (pl. 21, fig. 19) as *Conus architalassus* SOLANDER.

None of the above applies to SEBA's figure, but the exact opposite does apply – to it and to the traditional Caribbean *Conus cedonulli*. *Cedonulli* does not have the radiating dark lines of *C. ammiralis* on the spire, but only a random pattern of white and brown splotches, and its spire whorls are mostly convex. The spire pattern does extend over the shoulder, and there is no band of reticulations. The bands on the body whorl consist of white figures which are cloudlike, and these figures may appear elsewhere in the shell, but do not resemble arrowheads. The entire body whorl is normally encircled by fine lines carrying small white figures like beads on a string.

Mr. Nowell-Usticke reports (personal communication) that the specimen shown here as Figure *1* was selected from near 100 dredged at St. Vincent, and that only one other approached it in pattern.

CONCLUSION

SEBA's figure is of an unusual specimen but is matched well by the Nowell-Usticke shell shown as Figure *1*. *Conus cedonulli* LINNAEUS, 1767 should be restored to its rightful position as a valid Caribbean species.

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Cypraea cervus and *Cypraea zebra* in Florida - One Species or Two?

BY

M. ELLEN CROVO

2915 South West 102nd Avenue, Miami, Florida 33165

(1 Plate; 1 Map)

INTRODUCTION

Two NOMINAL SPECIES of large *Cypraea* occur in Florida waters. These are *C. cervus* LINNAEUS, 1758, and *C. zebra* LINNAEUS, 1758 (= *C. exanthema* LINNAEUS, 1767). Since both are often found together or occupying the same general ecological niche, it has been suggested that they might represent a case of sexual dimorphism of a single species (WARMKE & ABBOTT, 1951, p. 92). This account will show they are two distinct species, easily differentiated by morphological shell characters as well as by important structural modification of their radulae. *Cypraea zebra* is evidently geologically older, for a closely similar species, *C. cervinetta* KIENER, 1843, occurs in the Panamic-Pacific region. *Cypraea cervus* evidently was a more recent development, because it has no corresponding form in the Pacific.

Collecting Localities

Due to the great popularity of cowries among shell collectors, undisturbed localities were hard to find, but a small colony of *Cypraea cervus* was located in depths of 5 - 8 feet, in June 1966, 300 yards N E of Soldier Key, Upper Florida Keys. Here some collecting was done, but all females that were brooding clusters of egg capsules were left undisturbed. These were all *C. cervus*. Thirteen specimens were collected and examined for determination of sex. This group consisted of 9 females and 4 males. Since none of the females contained eggs in any stage of development, it is believed that spawning took place at an earlier date.

Two small areas on the Florida Keys, Whale Harbor and Channel Five, were intensely concentrated on over a period of 2 years. In Table 1 are shown the numbers of males and females of both species from these 2 localities. All specimens were fully mature.

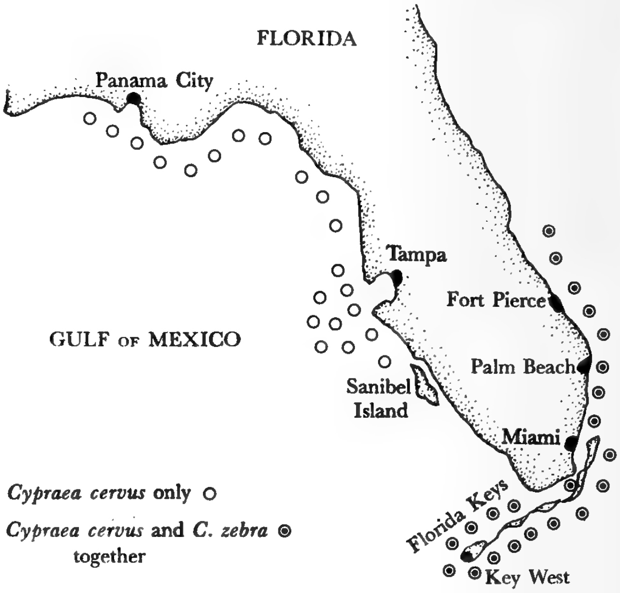

Table 1

Locations Florida Keys	*Cypraea cervus* ♀♀	 ♂♂	*Cypraea zebra* ♀♀	 ♂♂
Channel Five	3	1	18	11
Whale Harbor	33	27	14	8
Totals	36	28	32	19

In addition, specimens collected from many other localities were examined for determination of sex, and both males and females were found in both species.

Differences of the Shells

There did not seem to be any discernible characteristic in shell structure which would distinguish the males from the females in either species. Neither the dimensions of the shells nor width of the aperture had any noticeable relationship to the sex of the mollusk; nor did the number of labial or columellar teeth. Some shells had more teeth on the lip, while others had more on the columella. However, the study showed that *Cypraea cervus* has, on the average, approximately 15% more teeth on the lip than does *C. zebra*. The average number of teeth on the columella is the same in both species. These averages were based on the examination of 20 randomly selected specimens of each species. The shells of *C. zebra* are more slender and elongate than those of *C. cervus*.

Ranges

In Florida the two species occur sympatrically in the Dry Tortugas, along both sides of all the Florida Keys, and northward along the southeast coast to Palm Beach County and possibly as far north as the vicinity of Fort Pierce. The usual habitats are patch reefs, and around rocks and bridge abutments where there is a flow of clear, unpolluted sea water. In some areas both species may be found living among roots of the red mangrove trees.

On the southwest coast of Florida only worn shells of *Cypraea cervus* have been collected (PERRY & SCHWENGEL, 1955, p. 147). *Cypraea cervus* was taken fairly commonly during the recent "Hourglass" survey, off the Tampa Bay area in depths ranging from 60 to 120 feet on bottom characterized by limestone outcrops, sparse living coral, and sponge (W. Lyons, personal communication). The species also ranges northward to Panama City, Florida (WORK, 1969, p. 625).

Mr. Lyons stated "No *Cypraea zebra* were taken, nor have I seen the species from any other collections in the Gulf of Mexico." Regarding the Sanibel Island area, Mrs. Elsie Malone (personal communication) stated, "We do not know of anyone who has collected *Cypraea zebra* in this area nor have we examined any specimens that have been found on this coast." *Cypraea zebra,* to the exclusion of *C. cervus,* ranges southward from the Florida Keys to Brazil.

Food of the *Cypraea*

Cypraea are nocturnal feeders, hiding in crevices and under rocks during daylight hours. They graze over algae and sponge covered rocks, scraping off food by means of a strong radula within a stout proboscis. Individuals gather whatever food is in the immediate path rather than choose it selectively. This may be observed closely in a tank of sea water, where the radula may be clearly seen in action scraping algae from the glass. Studies of the stomach contents showed *Cypraea* to be omnivorous rather than herbivorous as previously assumed.

Contents of the foregut of *Cypraea cervus* consisted of the following: quantities of fine calcareous sediment; abundant green and red filamentous algae and a few small fragments of the calcareous alga *Halimeda*; a few sand grains and a considerable number of sponge spicules, mostly oxeas; a few keratose sponge fibers, probably from a rather delicate species of *Dysidea*; several minute tubes of polychaete worms, probably sabellids; a fair number of several species of Foraminifera; a few specimens of two species of harpacticoid copepods; several ostracods; a few small fragments of a delicate, encrusting bryozoan and several fragments of a "moss type" bryozoan; and one nearly dissolved gastropod shell which appeared to be a species of *Rissoina* still containing part of the animal.

The foregut of *Cypraea zebra* contained the following: hydroids; Foraminifera; the gastropod *Tricolia*; calcareous worm tubes of the serpulid polychaetes *Salmacina dysteri* HUXLEY and *Dexiospira spirillum* LINNAEUS; a minute clam; a few fragments of a sponge, probably a *Haliclona* species; filamentous algae; and several minute gastropod egg capsules with embryonic shells inside. It is evident that approximately the same diet is enjoyed by both species.

Juvenile *Cypraea* are sometimes much larger than mature specimens found in the same area. Certain juveniles may find a small area of plentiful food, which is conducive to very rapid growth before the outer lip turns in and maturity is reached. Others may not find as rich a feeding ground, and thus growth is slower. It is the writer's belief that maturity comes at a determined age, and the ultimate size of a specimen is regulated by the food supply available. There is a small area in the Florida Keys in which both *C. cervus* and *C. zebra* are very seldom found larger than 2½ to 3 inches in length. At this particular locality, the general appearance of the bottom suggests impoverishment, and there is only sparse vegetation.

Radulae

The taenioglossate radula of *Cypraea* has 7 rows of teeth. The radulae of *C. cervus* and *C. zebra* are much alike but can be readily distinguished, as may be seen from a close examination of the Figures *4* and *5*. The most marked feature shown by *C. cervus* is its split lateral tooth, while in *C. zebra* this tooth is solid.

Egg Capsules

Both *Cypraea cervus* and *C. zebra* have been observed brooding clusters of egg capsules during the months from early January to late June. Several females collected during February, March, and April contained unreleased egg masses. Specimens collected later than April rarely held unreleased eggs.

Egg capsules are generally attached to the under sides of rocks. When first laid, the capsule mass is a creamy white, deepening to a light lavender color, then gradually to a dark purplish brown just before release of the veligers. Each capsule contains approximately from 100 to 1500 minute eggs, the number of capsules and number of eggs per capsule depending on the size of the mother. On March 7 and 8, 1966, a *Cypraea cervus* held in a large tank produced egg capsules over which she sat protectively and over which she worked her proboscis regularly to keep them clean and free of growths and sediment. The foot became extremely enlarged during this period of brooding and completely covered the egg cluster. Free swimming veligers were escaping from the capsules on March 26 and 27, after a total period of 19 days. The veligers were approximately 0.1 mm in size. All were lost in the filter system.

Development of the Shell

Upon completion of their free-swimming stage, the veligers settle to the bottom and metamorphose into juvenile *Cypraea*. Those that settle in favorable areas, where food is plentiful, grow rapidly. The shell progresses through an elongate, very thin and fragile bulla stage.

As the mollusk reaches full size, the outer lip turns inward, after which teeth form along the lip and columellar wall. No formation of sex organs was apparent in any of the examined specimens that had not begun forming apertural teeth. This would suggest that full size and maturity come with formation of these teeth. After this stage shell growth ceases. The mantle then continues to add layers of glossy shell material, first over the teeth and base of the shell, then gradually over the sides and dorsum, except at the line where the mantle lobes meet, intermittently releasing pigments in a spotted pattern, first at the outer edge of the base, then dorsally. The shell is now fully mature. Further mantle action consists of additional layers of shell material being repeatedly laid over the outer surface, thus thickening the shell to the point of callousing over the spire.

Shells cut at different stages of growth revealed considerable difference in thickness. Old shells are very thick and heavy. Examination of numerous cut *Cypraea* shells would discredit a theory that *Cypraea* dissolves the old shell and remains soft and helpless while growing a larger shell (Joyce Allan, 1959, p. 3). It is possible that the opisthobranchs *Aplysia* and *Bursatella* have been mistaken for naked specimens of *Cypraea*. Perfect nuclei and earlier bulla stages were obvious in all sectioned shells. No evidence was noted of any of the interior of the shells having been dissolved.

CONCLUSION

The examination of 69 specimens of *Cypraea zebra* showed a ratio of 25 males to 44 females. The examination of 111 specimens of *C. cervus* showed a ratio of 49 males to 52 females. Although in part the ranges of the two species are identical, in some areas one may occur without the other, but males and females are found in both species in either of the two situations.

The difference noted in radular studies and the obvious difference in the shape of the shells convince the writer that *Cypraea cervus* and *C. zebra* are two distinct species.

ACKNOWLEDGMENTS

Several persons contributed to the success of the study in the following ways: Dr. R. Tucker Abbott of the Delaware Museum of Natural History suggested that the author complete this study and encouraged preparation of this manuscript; Lt. Col. Corinne E. Edwards aided in

Plate Explanation

Figure *1*: *Cypraea cervus* Linnaeus. Length 73 mm; width 47 mm [natural size]

Figure *2*: Spire and apertural views of nepionic shells of *Cypraea zebra*. × 80

Figure *3*: *Cypraea zebra* Linnaeus. Length 75 mm; width 37 mm [natural size]

Figure *4*: Radula of *Cypraea cervus*. Showing central and right lateral and marginal teeth. ×60

Figure *5*: Radula of *Cypraea zebra*. Showing central and right lateral and marginal teeth. × 52

Figure *6*: Mass of egg capsules of *Cypraea cervus*. Diameter 70 mm [natural size]

Figure *7*: *Cypraea cervus* shell sectioned to show progressive bulla stages.

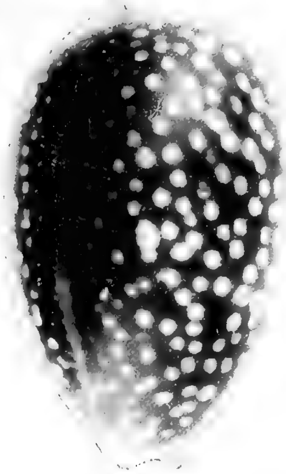

Figure 1

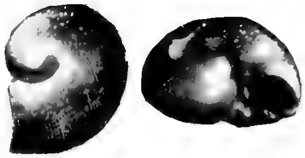

Figure 2

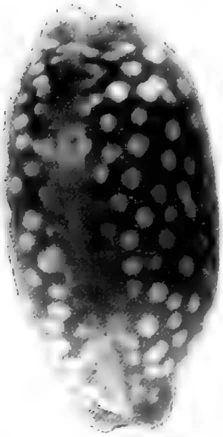

Figure 3

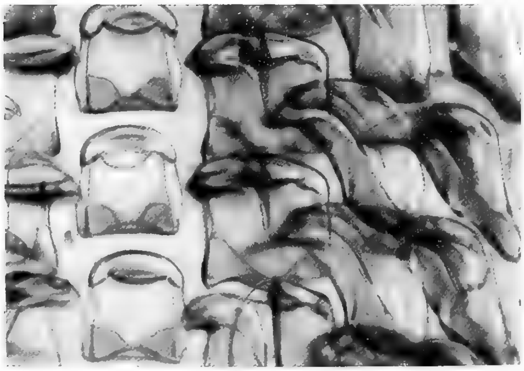

Figure 4

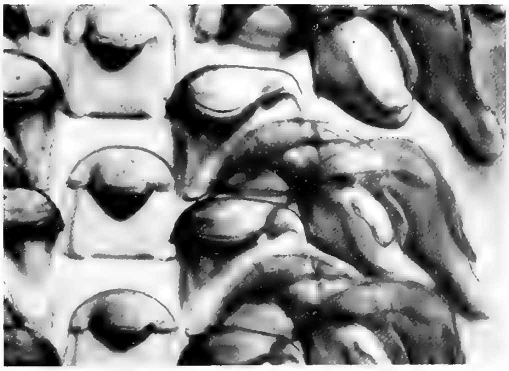

Figure 5

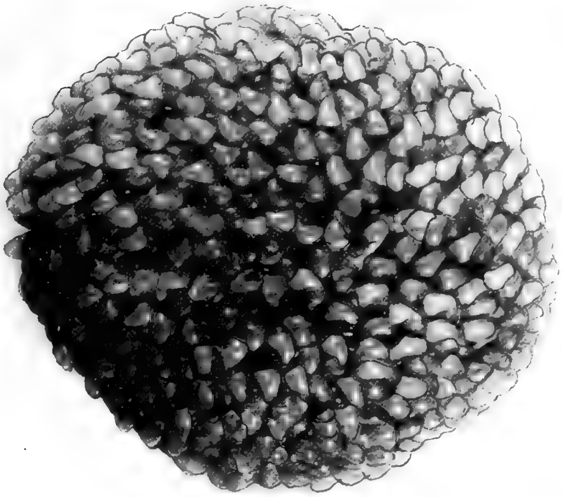

Figure 6

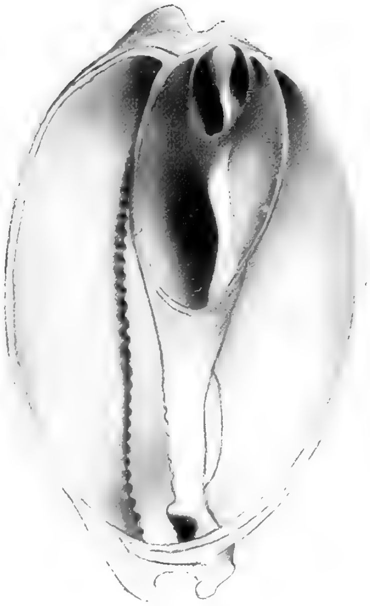

Figure 7

the collecting, cleaning, sexing, measuring, and counting the apertural teeth of nearly 200 specimens; Mr. Paul Shank kindly assisted with collecting and sectioning shells of *Cypraea*; Dr. Donald R. Moore, of the University of Miami's School of Marine and Atmospheric Sciences, identified microscopic contents of the foregut of *C. zebra* and confirmed the author's determination of male and female animals of the two species; Mr. Robert C. Work, of the School of Marine and Atmospheric Sciences, examined and identified microscopic contents of the foregut of *C. cervus,* and critically read this manuscript; Mr. Axel A. Olsson contributed his excellent photography, suggestions and information on radulae; Mr. William G. Lyons, of the Florida Board of Conservation, and Mrs. Elsie Malone aided in range determination. Further aid in the collection of specimens, during 1966 through 1968, was given by Mr. Lawrence E. Crovo.

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NOTES & NEWS

Two New Supraspecific Taxa in the Gastropoda

BY

A. MYRA KEEN

Department of Geology, Stanford University
Stanford, California 94305

Two NAMES NEEDED in the classification of eastern Pacific gastropods are here published in advance of a revised edition of "Sea Shells of Tropical West America."

VERMETIDAE

Tripsycha KEEN, 1961

Eualetes KEEN, subgen. nov.

Type Species: *Vermetus centiquadrus* VALENCIENNES, 1846

Diagnosis: Cream-colored to brown shells of moderate to large size, with whorls cemented to substrate throughout, tending to have regular, tight spirals, the outer edge of each whorl appressed; whorls not forming a hollow cone as in *Tripsycha, s. s.,* but coiled more like those of *Petaloconchus (Macrophragma),* which CARPENTER picturesquely described as being like a *Turritella* squeezed sideways. The contour of the aperture may be affected by the appressing of the outer edge of each turn to the substrate, and it may become semilunar in outline. Nuclear whorls of about two turns, more globose than in *Tripsycha s. s.*; operculum as large as aperture, concave, brown, with several volutions, the edge of each one slightly upturned but not forming a spiral lamina such as occurs in *Petaloconchus,* the volutions sometimes seeming to be dichotomous because of occasional heavier growth striae.

Discussion: The subgeneric name is chosen to implement what was evidently Carpenter's purpose in proposing *Aletes.* His description of this genus in the "Mazatlan Catalogue" (CARPENTER, 1857b) cites the operculum and thus applies to the species here selected as type of ***Eualetes***. Unfortunately, Carpenter allocated a new species that he was describing to this genus, and the paper in which it was named appeared in print a few months in advance of the Catalogue (CARPENTER, 1857a). The latter species, *Aletes squamigerus,* is inoperculate and is, as he later realized, a *Serpulorbis.* The term "eu-aletes" means "the true aletes," *αλετες* being the Greek word for "wanderer" – an appropriate term for irregularly coiled shells.

The type species, *Tripsycha (**Eualetes**) centiquadra,* seems to be characteristic of the northern part of the Panamic province, from the Gulf of California to southern Mexico. A second species in the subgenus has as yet been taken only in the Panama area. This is *T. (E.) tulipa* (CHENU, 1843). The species is not well known, even under its three synonymous names: *Vermetus angulatus, V. panamensis,* and *V. effusus* CHENU, 1844. Type specimens of *V. effusus,* from "Amérique" and *V. panamensis,* from Panama, are in the Paris Museum collection. The type specimen for *V. tulipa* is lost. The name, however, has priority, and illustrations of all four forms can readily be matched with material from Panama Bay collected by Eugene Bergeron. This vermetid is evidently not uncommon on islands of Panama Bay, the shells rivalling in size some *Serpulorbis* from other areas.

MURICIDAE

Aspellinae KEEN, new subfamily

Shells with rather inconspicuous varices, two to six in number, rarely with spines; sculpture generally subdued, the shell surface in many with a thin chalky layer; operculum muricoid, with an apical nucleus; radula with the central tooth having three larger cusps, two smaller cusps between. The narrow anterior canal is short to moderate in length in most species, the aperture smooth to dentate within. Type genus, *Aspella* MÖRCH, 1877.

This subfamily shows some relationship to both the Muricinae and Ocenebrinae, differing in less scaly sculpture and in the frequent occurrence of a superficial chalky layer. Other genera that may be assigned to **Aspellinae** include *Attiliosa, Calotrophon, Favartia, Eupleura,* and *Phyllocoma.*

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Range of *Gastropteron pacificum* BERGH, 1893

BY

EVELINE MARCUS

Caixa Postal 6994, São Paulo, Brasil

IN RECENT PAPERS in the Veliger (BERTSCH, 1969, **11**: 432; ROLLER, 1970, **12**: 483) the range of *Gastropteron pacificum* BERGH, 1893, includes the Galápagos Islands. BERTSCH refers to MACFARLAND, 1966, who (p. 4) indicates that "the species has also been taken off San Francisco and along the west coast of Central America from the Gulf of California to the Galapagos Islands by the U. S. S. Albatross in 1881." I did not find any other reference to these localities in BERGH's publications (1893, 1894), nor did TOKIOKA & BABA (1964) in their careful review of the genus *Gastropteron* mention the Galápagos. I suppose that the title of BERGH's second paper: "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," has brought about this error, which should not creep into further lists. BERGH in his introduction (1894: 125) explained that due to the small number of opisthobranchs furnished by the Albatross Expedition February to May 1891 he took the occasion to insert several related forms collected by Dall mainly from the Pacific. However, none of these forms came from the Galápagos, and, in fact, on pp. 202-203, BERGH clearly states: "Von dieser neuen Art fand sich eine Anzahl von (13) Individuen, bei Unalaschka (Aleutischen Inseln) von Dall in August 1874 aus einer Tiefe von 9–15 Faden (auf Steinboden) gefischt." This statement might also be adduced to fix the type locality for the species. The southernmost known occurrence is Point Loma, San Diego, San Diego County, California (BERTSCH, 1969: 432, no. 1).

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The Occurrence of *Ancula pacifica* MACFARLAND in San Francisco Bay

BY

DAVID W. BEHRENS

San Francisco State College, San Francisco, California

ON APRIL 30, 1970, ONE LIVING specimen of *Ancula pacifica* MACFARLAND, 1905 was collected on a piling at the Oyster Point Municipal Marina, South San Francisco, California (37°39′47″ N Lat.; 122°22′50″ W Long.). It was found on an assemblage of filamentous diatoms, *Melosira* sp. The specimen measured 11 mm in length and 2 mm at its widest point. On May 12, 1970, Robert Case and I collected 7 living specimens on the floats at the San Francisco Municipal Marina (37°48′31″ N Lat.; 122°26′28″ W Long.). At least 5 more specimens were observed but not collected. All were found on clusters of *Mytilus edulis* LINNAEUS, 1758 and a few were near a yellow bryozoan. The smallest specimen was 7 mm in length and 1 mm at its widest point; the largest was 16 mm in length and 2 mm wide. Identification was confirmed by Mr. Allyn G. Smith and Miss Joan E. Steinberg. All specimens are in the collection of the California Academy of Sciences in San Francisco.

Ancula pacifica has been reported to be a rare nudibranch (MacFarland, 1905, 1966; Johnson & Snook, 1927; Steinberg, 1963). I believe it should be noted that *Ancula pacifica* is relatively common in San Francisco Bay during the early summer months.

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Egg Capsule and Early Veliger

of *Charonia tritonis* (Linnaeus)

BY

CARL J. BERG, Jr.

Department of Zoology, University of Hawaii
Honolulu, Hawaii 96822

(1 Text figure)

A female triton, *Charonia tritonis* (Linnaeus, 1758), was collected off Oahu, Hawaii, October 5, 1969. It was kept with other tritons and observed copulating during the day on three occasions in October. Egg capsules were collected from sides of the holding tank on February 1, 1970 and again on March 7, 1970. On this latter date the triton was transferred to a 100-gallon capacity aquarium to protect the egg capsules from damage by other tritons. Eighty-eight egg capsules were laid in 10 separate clusters between March 12 and 18. The capsules were attached to the sides of the aquarium by flattened, irregular bases and were often joined at their bases forming groups of as many as 24 capsules.

Each egg capsule is approximately 25 mm long, 9 mm wide at the greatest diameter, and 5 mm wide at the stalk (Figure 1). Light orange, ellipsoid eggs (450μ by 600μ) are visible through the wall of the egg capsule and the gelatinous layer which lines the capsule.

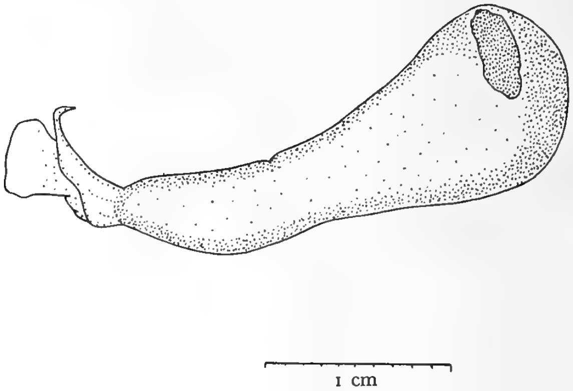

Figure 1

Empty Egg Capsule of *Charonia tritonis* with the Opening through which the Veligers escaped

Swimming veligers escape through an opening in the rounded end of the capsule (Figure 1) 6 to 8 weeks after the laying of the eggs. The light brown, translucent protoconch consists of one smooth whorl at hatching. Shells range in size from 768μ to 934μ at greatest diameter. The veliger has a white foot and a quadrilobed velum. Two black eye spots are present. From 2 capsules, 1140 and 1447 veligers at different stages of development were recorded, respectively.

All my attempts to raise veligers past metamorphosis have failed to date, although some veligers were maintained for 30 days. The oldest veligers crawled on their foot, even though they had 4 elongated velar lobes and the start of what might become 5th and 6th lobes.

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[1] Contribution No. 360, Hawaii Institute of Marine Biology of the University of Hawaii, Honolulu, Hawaii 96822

The Occurrence of *Urosalpinx cinerea* (SAY) in Newport Bay

BY

VERNON L. HUMAN

2421 Clement Avenue, Venice, California 90291

ON NOVEMBER 20, 1969, EIGHT SPECIMENS of *Urosalpinx cinerea* (SAY, 1822) were collected intertidally in upper Newport Bay, California. A more thorough investigation on November 23, 1969 disclosed a colony of approximately 200 specimens, ranging in length from 10 to 39 millimeters. Specimens were found as high as the mid-tide level on a −0.8 tide, but were larger and more numerous along the water's edge. Although the species is known from northern California (HANNA, 1966, p. 47), this collection apparently represents the first published record of *Urosalpinx* in Newport Bay.

The locality is adjacent to the Back Bay Road, 1.3 miles from its junction with Jamboree Road. Specimens occur on the undersurfaces, and less commonly on the vertical sidesurfaces, of rocks resting on a gently sloping sandy silt substrate. The rocky area is about 100 feet in length and is truncated at both ends by sandy mudflats. A moderate amount of shore fishing takes place at the site, which suggests that *Urosalpinx* may have been introduced with purchased fish bait. I have not observed this gastropod elsewhere in Newport Bay.

A scattering of small specimens of *Ostrea lurida* CARPENTER, 1864, might be sufficient to satisfy the food requirements of *Urosalpinx,* but *Mytilus edulis* LINNAEUS, 1758, is much more common. The burrowing pelecypods *Protothaca staminea* (CONRAD, 1837) and *Chione* spp. also occur abundantly.

A single clutch of eggs, apparently referable to *Urosalpinx,* was observed on a rock undersurface.

Appreciation and thanks are due to Dr. James H. McLean, Los Angeles County Museum of Natural History, for identification of specimens and to Mr. Boris Savic, who assisted in the collection of specimens and in the population survey.

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GENEROSITY OF SAN DIEGO SHELL CLUB

During the year 1970, the San Diego Shell Club has again sent a generous contribution to the California Malacozoological Society. This donation was used to help defray the cost of illustrations of a paper published during the year and both, the Society and the author, express their appreciation to the San Diego Shell Club.

Important Notices

At a Special Meeting of the Regular Membership, it was decided to keep Membership Dues and Subscription rates at the current level despite the ever increasing printing cost and postage fees. At the same time we take this opportunity to remind our members that Membership renewals are due to reach us on or before April 15, 1971; after that date a re-instatement fee of $1.00 will be due in addition. Statements will be mailed at about the same time as this issue.

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. If it is any consolation to our readers, we might mention that we have had some rather unpleasant experiences ourselves: an Air Mail Special Delivery letter to Los Angeles took 2 weeks!

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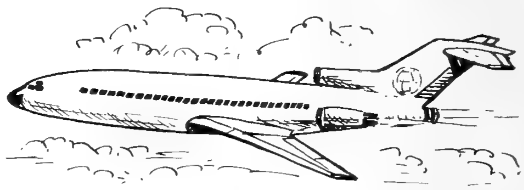

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We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

BOOKS, PERIODICALS, PAMPHLETS

West American Freshwater Mollusca, 1: Bibliography of Pleistocene and Recent Species

by Dwight W. Taylor. San Diego Soc. Natural History Memoir 4; 73 pp.; 1 frontispiece. Available from the Librarian, San Diego Nat. Hist. Museum, P. O. Box 1390, San Diego, CA 92112, at $5.00. (30 June 1970)

This extremely carefully prepared and, apparently, fairly complete, compilation of the titles covering the field indicated in the title, is a "must" for the working library of serious students of freshwater mollusks, be they from western America or from elsewhere.

While 51 pages of the book are taken up by the alphabetically arranged bibliography proper, there are lists of the references arranged according to geographical distribution, and topics such as archaeology and parasitology.

It is true, the work does not read like a Sherlock Holmes story, but it is apt to make a successful sleuth for the pertinent literature of even a beginner in the field.

RS

Malacological Review, Volume 3

P. O. Box 801, Whitmore Lake, Michigan 48189. 102 pp.; illust. Subscription $5.00. (1970)

In addition to the continuing presentation of facsimile reproductions of the tables of contents of the leading journals in malacology throughout the world, all published during the calendar year 1969, this volume also contains three original papers. These are:

An immuno-cytological study of *Bulinus* s. s. (Basommatophora: Planorbidae) by J. B. Burch & G. K. Lindsay (pp. 1 - 18; 5 figs.).

Cytological studies of Indian mollusks: Chromosomes of some opisthobranchs from Porto Novo, South India by R. Natarajan (pp. 19 - 23; 7 figs.).

Morphological and cytological studies of the succineid genus *Quickia* from India by C. M. Patterson (pp. 25 to 36; 20 figs.).

Of further assistance to the active worker in the field of malacology is the list of books and pamphlets, as well as separate papers, published outside of the regular journals. This list comprises about 200 titles of articles published in 1969 and early 1970.

As we have stated in respect to an earlier volume of this publication, the price of $5.00 is a modest sum to pay for the multitude of up-to-date titles that can be gleaned.

RS

Fossil Mollusks of Oahu, Hawaii Islands

by Sadao Kosuge. Bulletin of the National Science Museum (Tokyo), vol. 12, no. 4, pp. 783 - 794, plts. 1 - 7. December 20, 1969.

This paper reports 191 species of fossil mollusks of Pleistocene age from raised coral reefs on Oahu, Hawaii. Of these, 4 are extinct; 7 are not known to be living in Hawaii; 6 are rarely found living in Hawaii but are common in other Indo-Pacific waters; 5 are endemic to Hawaii.

Many of the species represented in the faunal list by fossils only and others rarely found living in Hawaii, now thrive in warmer waters around other island groups in the Indo-Pacific. From this it is inferred that the marine waters around Hawaii were warmer when the coral reefs were formed and accompanied by the molluscan species reported in the present paper.

LGH

Prosobranquios Marinos Nuevos para la Fauna de Cuba (Mollusca: Gastropoda)

by Hortensia Sarasúa. Poeyana, Instituto de Biologia, La Habana, Cuba, Serie A, Number 72, pp. 1 - 20; figures 1 (A - D), 2 (A - D), 3 (A - D), 4 (A - D). April 30, 1970.

Fifty species of marine gastropods are reported and discussed in this paper and of these 38 are believed to be new to the fauna of Cuba; 16 species are illustrated.

LGH

Proceedings of the Third European Malacological Congress Vienna 1968

in Malacologia, vol. 9, no. 1; pp. 1 - 338; plates, text figs. publ. by Department of Molluscs of the Natural History Museum, Vienna and the Institute of Malacology, Ann Arbor, Michigan. Price $4.00. (November 1969)

This volume contains not only the business proceedings of the third European Malacological Congress, but also complete articles and abstracts of papers presented by the participants at the Congress. The book is excellent in its format and of great interest not only to the many malacologists who were unable to attend, but also to those fortunate enough to be able to attend. This is so because the presentation had to be divided into various groups or sections on account of the great number of papers to be presented and the limited time available for the Congress.

And as yet nobody has found a way of being present in three or four different places at the same time, not even the malacologists!

The price of $4.00 is a modest sum, not only considering production costs, but also because of the wealth of very valuable information on current research presented.

RS

The Distribution of *Paragonimus westermani* in Japan

by Myron G. Radke & George M. Davis.
Bio-medical reports of the 406 Medical Laboratory. No. 17; 103 pp.; 23 plts.; numerous tables.
(November 1969)

This paper deals with the human lung fluke in Japan. The work is divided into 3 sections; section 1 deals with the geographic location of reported cases of infected snails, crabs, and human beings; section 2 with the difficulties of locating infected snails in river systems; section 3 with the identity of the snail species reported to be the first intermediate host of the parasite.

RS

Nouvelles Données sur les Veneridae (Mollusques Lamellibranches) du Brésil

by E. Fischer-Piette, M. Kempf and A.-M. Testud.
Bulletin du Muséum National d'Histoire Naturelle, 2ᵉ Série, vol. 41, no. 6, pp. 1543 - 1553, figs. 1 - 4. 1969 (issued June 26, 1970).

Twenty-three species of the family Veneridae are reported and discussed in this paper. These are chiefly from the region between Maceió and Belém along the north coast of Brasil. One new species, *Gouldia altenai* (p. 1543, fig. 3) is described from near Maceió, 9°37′ S Lat., 35°35′ W Long.

The species described as *Transenpitar keenae* by Fischer-Piette & Testud, 1967, is relegated to the synonymy of *Transenpitar americana* (Doello-Jurado, 1951), (originally described as *Sunetta americana* Doello-Jurado).

LGH

ARGAMON

Journal of the Israel Malacological Society

In July 1970 the first issue of this new journal was issued. It contains a number of papers, some of them printed in the Hebrew language (with English abstracts), others in English (with Hebrew abstracts). The Society is desirous of establishing contacts with individuals and organizations with similar pursuits. Details may be obtained from the Israel Malacological Society, P. O. Box 9216, Haifa, Israel.

RS

Kelp Habitat Improvement Project

Annual Report, 1 July, 1968 — 30 June, 1969.
by Wheeler J. North and others. W. M. Keck Laboratory of Environmental Health Engineering, California Institute of Technology. 142 pp.; illust.

This publication is in the nature of a progress report on the continuing studies of the re-establishing of the kelp beds that flourished about 60 years ago off Point Loma in San Diego County and that were, by the late 1950s, almost completely wiped out. Much valuable information on many factors affecting the plants has been and continues to be presented in these annual reports. The role of sewage and other pollutants and their effects on the sea urchin populations are studied. And though the kelp beds have made a remarkable comeback, the original status is as yet far from being attained. Much food for thought can be found in these pages by all who are concerned about the marine environment.

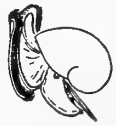
RS

Catalogue of Australian Tertiary Mollusca (except Chitons)

by Thomas A. Darragh. Memoirs of the National Museum of Victoria, no. 31, pp. 125 - 212. May 18, 1970.

This useful catalog contains an up-to-date list of all species of mollusks (except chitons) which have been described from marine strata of Tertiary age in Australia. Species (followed by the genus) are listed alphabetically with a reference to the original publication, the locality from which they came and the modern genus to which each species is believed to be referable. A list of pertinent references is included.

LGH



THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

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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.

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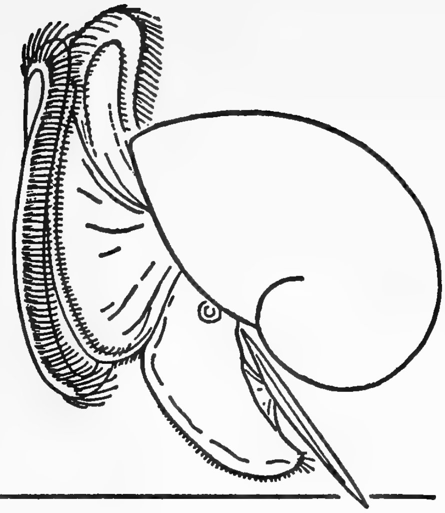

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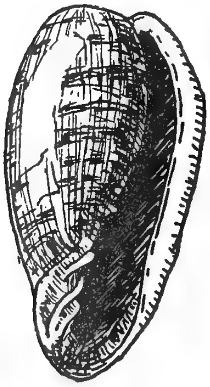


Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

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

HAROLD HANNIBAL (1889 - 1965) with a Review of his Molluscan Research

BY

DWIGHT W. TAYLOR

Natural History Museum, San Diego, California 92112

AND

ALLYN G. SMITH

California Academy of Sciences, San Francisco, California 94118

(5 Plates)

HAROLD HANNIBAL SPENT a meteoric career in Tertiary paleontology, and in studying living and fossil freshwater mollusks, during the early years of this century. His brilliant early work was tragically cut short, and he passed more than half his life in a mental institution only a few miles from his birthplace. Today he is remembered mainly through colorful stories dating from the period of his illness. We have combined a summary of the species he described and new illustrations of the type specimens with a short account of his life.

The virtual lack of contemporaries who knew Hannibal, the absence of personal records in his surviving field notebooks, and the few scientific contacts that he had, force a biographer to rely almost entirely on the published record and on the letters preserved in the files of the U. S. National Museum. For the rest we have only second-hand stories, his specimens and books at Stanford University, and a few bald circumstantial records. Our account of his work is thus partly inference and personal evaluation.

Harold Briggs Hannibal was born at Bay Tree Farm near the present town of Alviso, Santa Clara County, California, on November 27, 1889. Of his early life we have no record, and depend on the implications of his knowledge and interests shown in letters beginning in 1907, when he was not yet 18 and then in his senior year at San Jose High School. We quote extensively from his letters for two reasons: to let him speak for himself to the modern reader, and to record some of his observations and locality information that are otherwise inaccessible.

ACKNOWLEDGMENTS

Opportunity to borrow and study both notebooks and specimens is due to A. M. Keen, Department of Geology, Stanford University, and J. W. Durham, Museum of Paleontology, University of California. Photographs are by K. Sakamoto, U. S. Geological Survey, Menlo Park, California. Joseph Rosewater, U. S. National Museum, made available copies of Hannibal's letters. L. G. Hertlein, California Academy of Sciences, and A. M. Keen discussed the allocation of some of Hannibal's marine species based on poorly preserved material. Dorothy Radbruch, U. S. Geological Survey, Menlo Park, advised on the stratigraphic position of some fossil localities in the Berkeley Hills, California.

EARLY LIFE AND WORK

Hannibal's first scientific discovery was the freshwater mussel named in his honor by William Healey Dall: *Gonidea angulata haroldiana* DALL, 1908. Perhaps this is what turned him definitely toward freshwater mollusks, for he already had greater familiarity with the marine fauna (letter to Dall, 22-X-1907). At any rate, he turned to freshwater species – fossil and living – with prodigious energy. He graduated from high school in January, 1908; within three years he had **published** five papers, including the summary of western freshwater mollusks in Keep's "West coast shells." After another two years he had published a thorough treatment of the southern California fauna, and his "Freshwater Mollusca of the Californian Province." This in addition to school work at Stanford University, field studies in geology as well as the living fauna, and a paper in paleobotany. One wonders if he ever slept. But by the end of 1912, at the age of 23, Hannibal had most of his writings behind him. Perhaps in part he simply burned himself out.

In the fall of 1907 Hannibal sent some freshwater mussels to the U. S. National Museum for identification. This led to correspondence with W. H. Dall to whom Hannibal wrote in the earliest letter we have seen:

> "I am deeply interested in palaeontology and am about to take up some work suggested by Dr. J. P. Smith on the Santa Clara lake beds around this valley. I expect to work more or less in connection with S. S. Berry of Stanford Univ. who is working on the living Pulmonates.
>
> "On account of lack of material and poor identification of what there is I find it will be necessary to send specimens to you for identification at least to start in with for while I am more or less familiar with the generic characters of marine shells, I have no comparative collection or any work on the fresh water except Keep, W. A. S. [West American shells]" (22-X-1907).

In December, 1907, Dall wrote Hannibal that the mussels were a new variety to be named *haroldiana*. The local excitement is shown by a note in the San Jose (California) Times, December 12: "High School Lad is Conspicuously Honored." Dall's description was published the following month, January 28 (Dall, 1908). That spring Hannibal began to search elsewhere for "his" variety as well as other mussels:

> "I have extended the distribution of my variety to the following:
>
> Coyote Creek, San Jose to S. F. Bay
> Guadaloupe Creek, San Jose to Sta. Clara
> Quito Creek, or Campbells Creek, Sta. Clara to S. F. Bay
>
> Above these towns there is no water in the creeks in summer as that is as far up as the artesian belt extends. From Sta. Clara to the bay in the Guadaloupe there is sewage (no septic tanks either) and my variety being particular about its food died out. Tho' my father remembers when he used to make soup and chowder from them when a boy." (Hannibal to Dall, 24-IV-1908).
>
> "I have another geographic variety of *Gonidea angulata* very triangular about 3 in. long with hinge teeth in adult, somewhat more angular than mine rather thin shelled and slender from the Pacheco (Pass) Creek between Santa Clara & San Benito Counties. The habitat is almost identical also the associated species *Anodonta nuttalliana* var.
>
> "I have also collected *Margaritana margaritifera* in the San Lorenzo River on a special trip to the locality on learning it occurred there from an old paper sent me by Dr. Stearns [R. E. C. Stearns]. Both the purple and orange forms occur but the latter predominates. It is not a very common species, two hours collecting at Felton and Boulder only yielding 14 specimens." (Hannibal to Dall, 7-VII-1908).

In this letter too Hannibal mentions some specimens of *Lyonsia* that were evidently what Dall (1915) later described as *Lyonsia californica haroldi.*

In the fall of 1908 Hannibal entered Stanford University. He wrote concerning his extracurricular work:

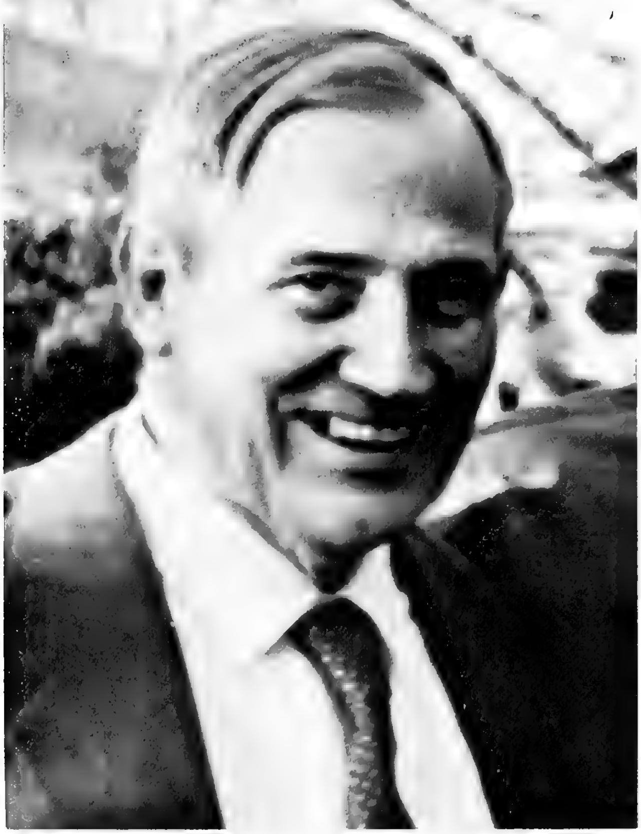
> "I am working strictly on fresh water shells and fossils when not assisting in the palaeontology laboratory where I am arranging and labeling the collection of the late Miss Annie Laws which has been loaned the department by her heirs. When that is done there is the department collection of shells and the Delos Arnold collection so I will have enough to do as long as I am here." (Hannibal to Dall, 26-X-1908).

No notebooks or itineraries are available for Hannibal's collecting in southern California, but evidently this work occupied him in parts of 1909-1910. He published a summary of the freshwater mollusks, and of the land mollusks jointly with H. M. Edson (Hannibal, title 8). Perhaps Hannibal also collected fossils during this tour of southern California, but if so, we have no record.

During the summer of 1911 Ralph Arnold commissioned Harold Hannibal to collect fossils and make stratigraphic studies along the northwestern Pacific Coast. This was the first of several such mutually profitable ventures, leading to a substantial stratigraphic work by Arnold and Hannibal in 1913 (Hannibal bibliography, no. 11). Although Hannibal planned to describe the collections together with Arnold, untimely illness prevented this work. The only published results of these trips by Hannibal are a few fossil freshwater species (Hannibal bibliography, no. 9).

This first trip for Arnold is more carefully documented than later ones, perhaps because Hannibal wanted to prove he spent his sponsor's money prudently. Here is the first page from his expense account of 1911:

Preliminary	Notebook, pencils, erasers, etc.	$1.00
	Pair of bike tires and supplies	13.00
	For $100 worth of travelers checks	.50
June 5	Fare San Jose to S. F. [San Francisco]	1.50
	Fare S. F. to San Rafael	1.00
	Photo supplies	.90
	Meals	1.15
	Room	.50
June 6	Fare S. R. to Calistoga	1.60
	Meals	1.50
	Baggage by stage	.50
	Room	.25
June 7	Meals	1.50
	Room	.25
	Freight on box fossils	1.00



Yours Respectfully
Harold Hannibal.

June 8	Meals	1.50
	Room	.35
June 9	Fare Ukiah to Sherwood	2.00
	Meals	1.50
	Bicycle repairs	1.35
	Baggage by stage	1.30
June 10	Meals	1.50
	Room	.50
	Freight on box spec.	1.00
June 11	Meals	1.65
	Room	.50
June 12	Meals	1.55
June 13	Meals	1.50
	Packing boxes and paper	.60

Hannibal numbered serially the localities at which he collected Recent mollusks on this 1911 trip, beginning with number 1 on June 5, and ending with number 96 on August 26, 1911. Some sample entries follow:

> 1. Drain from N end RR tunnel 1 mi N of San Rafael, ½ mi S of Forbes. *Segm.[entina] dilat.[ata]* & *Physa.* [June 5, 1911]
>
> 25. Third watertrough about 8 mi. N of Harris 3 mi S of Vances house. *Corneocyclas.* [June 11, 1911]
>
> p. 8
>
> 47. Collect *Goniobasis* clinging to sea cliffs wet from seep water ½ mi SE of Cape Blanco. [June 23, 1911]

The localities at which Hannibal collected can practically all be located precisely on modern topographic maps by following his notebook and tracing the itinerary. This much cannot be said for many subsequent collectors, or even for a substantial amount of present-day publications. Thus his collections are of value by modern standards, and of course particularly where later cultural changes have eliminated the former molluscan fauna. The high quality of these basic data recorded by Hannibal is one of the standards by which we rate him high as a malacologist.

This 1911 field trip produced a multitude of stratigraphic and paleontologic data. Hannibal's correspondence with Dall shows the exchange of numerous ideas on identity of fossils and the classification and nomenclature of both fossils and formations. In reply to a letter from Dall, Hannibal wrote (7-III-1912) from Seattle, Washington:

> "I surely appreciate your admonition in regard to caution. Up in this country where one scratches around in the devil's club [a kind of spiny shrub] and fallen fir logs for a creek that has trenched down through the glacial drift and the fossils when one gets them look more than half the time like they had been hit by a steam roller at high-speed, geological work is something that isn't polite to mention in public."

In early 1912 Hannibal was completing his largest work, "A synopsis of the Recent and Tertiary freshwater Mollusca of the Californian Province." The only pre-publication mention in Hannibal's letters is included in correspondence to Dall (7-III-1912):

> "I am just finishing up the last of a general paper on the west coast fresh water forms straightening out the worst of the nomenclature and describing a number of new forms and decided to take a hand in the Pleuroceridae mess. You know what it is! Pilsbry seems to have given it up in disgust and no one else has had the gall to attempt it. I have plenty of material and have been able to get the species and genera in good shape – compared with what they were before at least. . . ."

The *Synopsis* was submitted for review to some of the faculty in the Department of Geology at Stanford University, and so came – unbeknownst to Hannibal – to S. S. Berry. Dr. Berry recalls that he thought the paper contained some original and suggestive insights, even a few inspired ideas. Yet there were serious flaws, too, and he recommended that the paper not be published in its present form. Nevertheless it appeared soon, and with no substantial revision, in the *Proceedings of the Malacological Society of London.* Two features of Hannibal's paper appeared – and still appear – largely unwarranted: the sweeping union of many species under a single name, and the undocumented assertion that water chemistry is responsible for the nominal "species."

Shortly after the *Synopsis* appeared in print, H. A. Pilsbry published a savagely critical review in the Nautilus (volume 26, page 71). He called the *Synopsis* a fantastic farce, and violated good taste as well as good judgment in roundly damning it. One might suppose that Hannibal would have been furious, hurt, or somehow affected strongly. And yet in a letter to Paul Bartsch not long after he sounds quite mild:

> "Am much obliged for the papers and will return the compliment shortly with a copy of the one that Pilsbry recently made notorious. Personally I think that our Philadelphia friend will regret that he did not wait till I "played my other hand" to use a sporting expression. I certainly never intended to shoot all my ammunition in this one paper and if he had read it carefully he might have noticed it." (24-XII-1912).

A more balanced review of Hannibal's *Synopsis* than that by Pilsbry appeared in the Pomona College *Journal of Entomology and Zoology* for 1913. Written by Fordyce Grinnell, Jr., an entomologist, not a mollusk specialist, this note shows how someone who evidently knew Hannibal at second hand, or perhaps had met him personally, regarded the work:

> "The author of this paper, a young and very enthusiastic Stanford student, has covered a good portion of the Pacific Coast from San Diego to Seattle, with his bicycle, in search

> of shells; investigating every puddle, pool, pond, lake, ditch, stream and river in his trips. He has collected material in large quantities and then studied it in the laboratory; so from training and experience he is more capable of writing on the fresh water shells of this coast than anyone. This, the most extensive of his published papers, is full of original ideas, and numerous suggestions. He first gives the boundaries of the California province in detail, then the composition of the fauna as found in the paleontological history of the region; thirdly, the classification employed; fourthly, the new term *Syntonia* is explained in detail; then lastly taking up most of the paper, the synopsis of species, in which the groups from the superfamily to species are defined. There is a full bibliography and synonymy for the genera and species; a table showing the Evolutionary Cycle of the Unionoideae, and a summary and range in time of the California fauna, and concluding remarks.
>
> "Of course, a student with such radical ideas, a progressive, could not escape the fire of one or more of the conservative men; and this is just what happened in a recent number of The Nautilus. If you wish to smile, just look it up!"

Although keeping a strong interest in freshwater species, Hannibal devoted his field work and research from 1912 on primarily to marine Tertiary paleontology and stratigraphy. Probably this was due in part to the sponsorship of Ralph Arnold, who employed or subsidized him as a collector. Hannibal made headquarters at the University of Washington during most of 1912, and went on short field excursions to points on Vancouver Island as well as coastal Washington. He returned to Stanford in October, 1912, and seemingly did no more field work outside of California. He wrote to Dall (29-IV-1913):

> "Expect to work northern California this year and perhaps as far south as San Louis [sic] Obispo using a motorcycle to travel with. Of course I will watch out for the festive mollusk that inhabits the beaches and rocks.'

Evidently about 1914 came the first of Hannibal's serious mental disturbances, that were to force him into an institution. After a lapse in correspondence Hannibal wrote Dall (23-VIII-1916, dated at home instead of, as usual, Stanford University):

> "Have been drifting through a case of remittent brain fever the last two years and not doing much scientific work. Hope to get back into it this winter, however ...
>
> "Have just learned from Dr. [J. O.] Snyder that of La Honda, Pescadero and San Lorenzo Rivers in which an isolated colony of *Margaritana* var. *falcata* occurs – the nearest other points being Merced Falls, and Long Valley Creek, Lake Co., La Honda and Pescadero Creeks contain no fluviatile fishes and San Lorenzo River only three minnows. It appears that this species utilizes one or more of the migratory Salmonidae or Cottidae as a host for the glochidia, presumable the former from the peculiarities of the distribution of *Margaritana*. There seems to be a chance that these colonies were originally established by glochidia brought from more northern streams by the open sea route.
>
> "Conditions are rather indifferent for research work at Stanford this year. Dr. Wilbur had a good deal of success at the medical school but since he became president it has been a mad scramble for credits and an increased tendency to interfere in student affairs. Instead of a big man like Jordan or Branner who is unapproachable or a man with ideals like Wilbur they need a business man like Arnold who commands the friendship and respect of students and faculty and can gum-shoe around and get ideas from Tom, Dick, and Harry and have his sails set when the wind blows.
>
> "I suppose Mrs. Oldroyd must be back at Stanford by this time but I haven't been there for several weeks. I couldn't quite make out what she was doing but she seems to have got some cases to house the shell collections which was more than I was able to do."

Recurrent mental problems gradually forced Hannibal's scientific work to a close. After the large paper by Arnold and Hannibal in 1913 (Hannibal bibliography, no. 11) his scientific publications consist of only a few short notes.

After a long lapse during which he apparently did not communicate with any scientific colleague, Hannibal corresponded at some length with G Dallas Hanna of the California Academy of Sciences. The letters are a mixture

Plate Explanation

Figures *1, 5, 8*: *Pisidium catherinae* (Hannibal, 1912b), Miocene, Holotype, SU 5816 × 10

Figure *2*: *Sphaerium mecki* (Hannibal, 1912b), Miocene. Holotype, SU 450 × 3

Figures *3, 4, 7, 10*: *Plesielliptio transpacifica* (Arnold & Hannibal, *in* Hannibal, 1912b), Eocene × 1

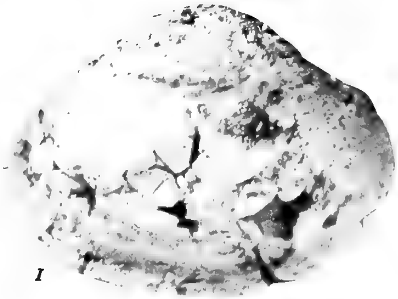
3, 4: Holotype, SU 454

7, 10: Paratype, SU 453

Figure *6*: *Sphaerium andersonianum* Hannibal, 1912b, Pliocene. Holotype, SU 299 × 3

Figures *9, 11, 13, 15*: "*Sphaerium*" *rogersi* Hannibal, 1912b, Eocene. Holotype, SU 457 × 3

Figures *12, 14*: "*Margaritifera*" *herrei* Hannibal, 1912b, Eocene. Holotype. SU 452 × 1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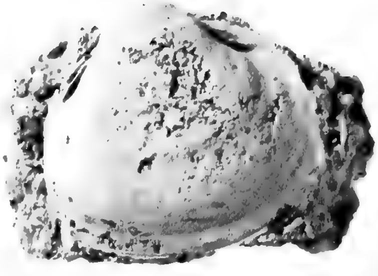
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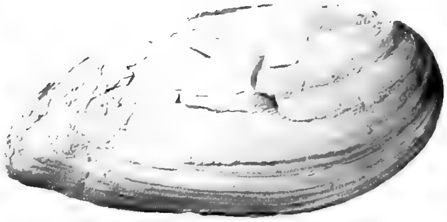
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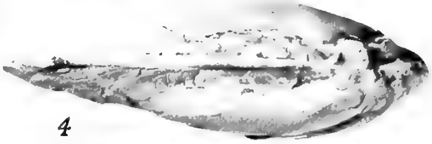
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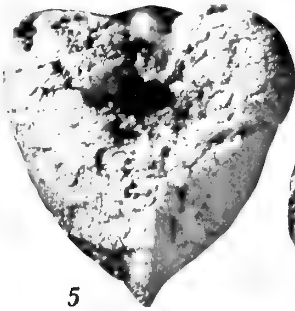
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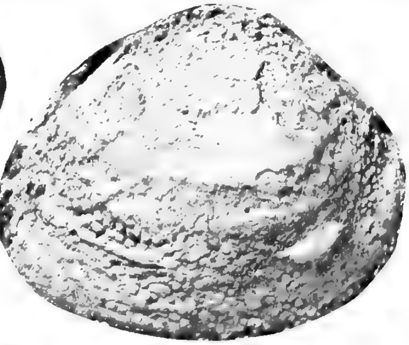
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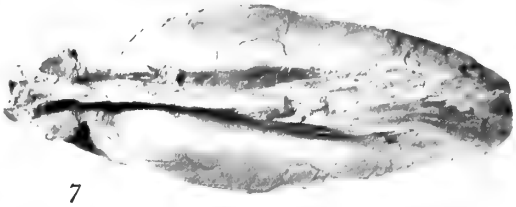
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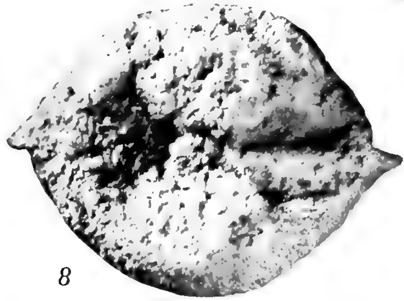
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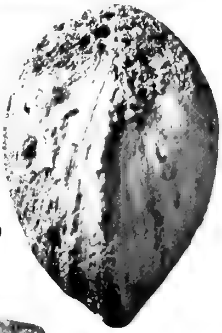
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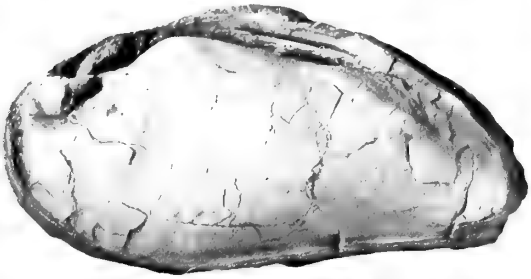
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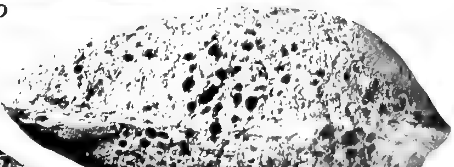
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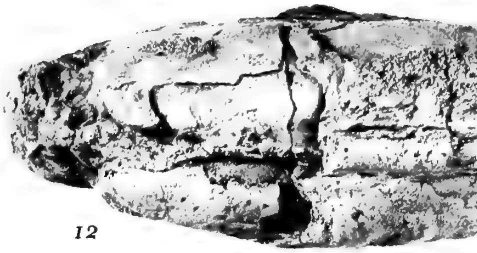
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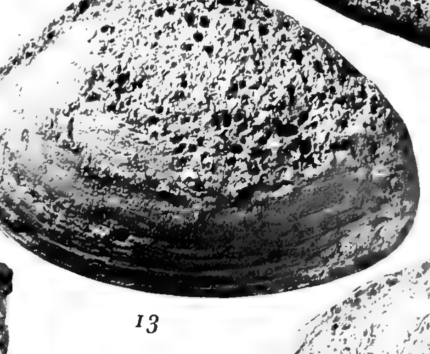
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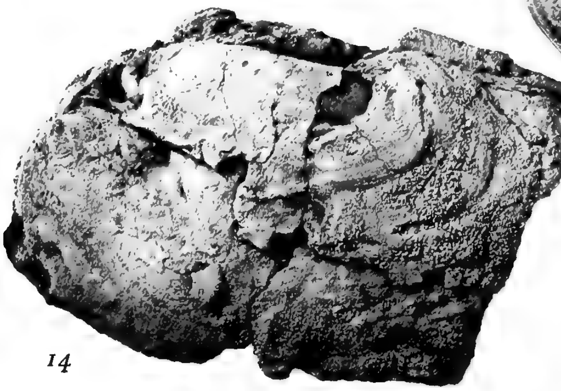
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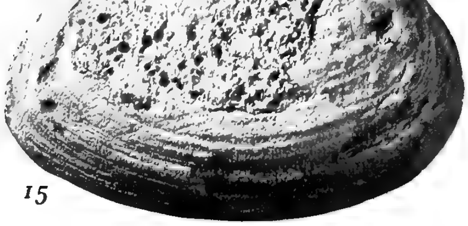
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of lucid memories of early collecting and research, together with sad fantasies about the current world. This exchange of letters terminated with Hannibal's death on December 17, 1965. He is survived by a sister, Edna-Ann Hannibal Wagoner, and by a half-brother, Arthur Alton Hannibal.

The collection of freshwater mollusks, the library, and a few notebooks that Hannibal left are housed in the Department of Geology, Stanford University. We have found all of the type specimens that he described, and illustrated most of them herein.

A PARTIAL APPRAISAL

Harold Hannibal's ability and energy are indicated partly by the diversity of the fields in which he worked. He published papers dealing with vertebrate paleontology, paleobotany, and marine Tertiary stratigraphy, besides his principal efforts in the classification and distribution of fossil and living freshwater mollusks. Most of this work appeared within five years after he was graduated from high school, so one can scarcely fault his industry. As to the quality of Hannibal's work we have tried to appraise only his efforts in nonmarine mollusks: their classification and distribution.

The basic data that Hannibal collected and published remain valuable and detailed in spite of possible different interpretations. One can find readily where he collected, and the specimens he left are in good order, clearly labeled. All of his type specimens survive.

In the description of new species one cannot rate Hannibal quite so high. He gave 29 names to species and varieties. About one-fourth of these appear superfluous. Further, a few were sadly misclassified. The "ancylid snail" *Zalophancylus morani* turned out to be the mold of a fish vertebra. *Gonidea hemphilli* and *Sphaerium rogersi* are not freshwater species but belong to entirely different, marine families of clams. The photographs of the new forms were mostly inadequate even when published originally – a major stimulus for preparation of our present paper.

Out of 12 new genera and subgenera that Hannibal proposed, nearly half have not proved useful to later workers. Only the fish vertebra, *Zalophancylus,* could be called an outright blunder. The other needless names apply to groups that others have ranked lower than did Hannibal.

Of 11 family or subfamily names proposed by Hannibal only about one-fourth survive. Some have vanished because of later nomenclatural changes. Most of the useless names were proposed for groups that were founded on too few characters to survive further research, or that were interpreted by Hannibal as phylogenetic units in his "ontogenetic classification."

The zoogeographic treatment of the West American fauna that Hannibal published in 1912 remains a high-water mark. Subsequently the tide has receded, so far as quality of work is concerned. From Dall (1905a, b) Hannibal took the idea of grouping the freshwater mollusks into drainage "Systems." These were drainages, or groups of drainages, with a generally similar fauna. Thus in the "Californian Province" there were the Yukon System, Coast Range System, Inland Empire System, Los Angeles System and the like.

To this scheme one can contrast the molluscan provinces described by Henderson (1931). An obvious difference is the neat coincidence of some of Henderson's "provincial" boundaries with the political boundaries of states – the southwestern edge of Nevada, the southern edge of Utah and Colorado, and the like. More seriously, Hannibal's earlier discussions and characterizations of the aquatic fauna were not even mentioned. The fundamental reason why Hannibal's earlier work is likely to prove more lasting than Henderson's classification was well stated by Dall (1905b): "The distribution of water animals is carried on by different means from those influential in the dispersal of terrestrial forms, and any discussion which combined the two without distinction would be liable to contain errors of fact and deduction." Just as Henderson failed even to mention Hannibal's work, so too he did not cite Dall's paper or advance justification for establishing "provinces" for both terrestrial and aquatic forms.

A final question remains: What led to Hannibal's illness? We have no satisfactory answer. In his published works and unpublished letters prior to the first mental troubles we see no evidence of derangement. His views are original, and often unacceptable, but evidently reasoned. Leo G. Hertlein has repeated to us a story heard from the late J. P. Smith, one of Hannibal's teachers at Stanford. Thrown from his motorcycle on a rough road, Hannibal fell on his head. Only thereafter did his first mental problems appear, then gradually worsen and eventually force him to leave the field of science that he had begun to till so energetically.

SUMMARY of NEW MOLLUSCAN NAMES

Hannibal proposed altogether 52 new names for Mollusca, from family to variety. We have summarized the current taxonomic standing of these, provided new illustrations of most of the type specimens, and relocated a number of type localities in the light of stratigraphic studies and topographic maps available since Hannibal's work.

In the following list Hannibal's names are cited as he proposed them. The grouping by family is modern, and shows the order in which we discuss the names. References to illustrations indicate those type specimens figured herein.

PELECYPODA

Margaritiferidae	
herrei, Margaritana	Figures *12, 14*
Amblemidae	
Limnobasilissa	
Unionidae	
Arnoldina	
Migranaja	
Pleurobeminae	
Propterinae	
transpacifica, Unio	Figures *3, 4, 7, 10*
Sphaeriidae	
andersonianum, Sphaerium	Figure *6*
catherinae, Sphaerium	Figures *1, 5, 8*
Corneocycladidae	
meeki, Corneocyclas	Figure *2*
tremperi, Corneocyclas	
Hiatellidae	
hemphilli, Gonidea	Figures *38, 39*
Veneridae?	
rogersi, Sphaerium	Figures *9, 11, 13, 15*

GASTROPODA

Valvatidae	
calli, Valvata	Figures *47, 48, 51, 52*
whitei, Valvata	Figures *45, 46, 50*
Viviparidae	
andersoniana, Lioplax	Figures *32, 33*
Callina	
Cipangopaludina	
turneri, Viviparus	Figures *27-29, 31*
washingtonianus, Viviparus	Figures *26, 30*
Bithyniidae	
Bulimidae	
Pleuroceridae	
Ellipstomidae	
Gyrotominae	
olequaensis, Ambloxus	Figures *22, 23*
Thiaridae	
drakei, Pachychilus	Figures *41, 42*
Hydrobiidae	
binneyana, Cincinnatia	
Heathilla	
modoci, Fluminicola	Figures *16, 17*
williamsi, Pyrgulopsis	Figures *18-21, 24, 25*
Latiidae	
Latiinae	
Lancidae	
Fisherola	
klamathensis, Lanx	
lancides, Fisherola	Figure *34*
Lancinae	
Walkerola	
Lymnaeidae	
Acellinae	
cooperi, Lymnaea	Figures *36, 37, 40*
lawsoni, Pachychilus	Figures *43, 44*
sanctijosephi, Lymnaea, cubensis var.	Figure *35*
stearnsi, Lymnaea	
Ancylidae	
Kincaidilla	
Laevapecinae	
morani, Zalophancylus	
Planorbidae	
Brannerillus	
cordillerana, Helisoma	Figures *57, 58, 60, 61*
mojavensis, Planorbis	
Neoplanorbinae	
Perrinilla	
physispira, Brannerillus	Figures *49, 53*
sanctaclarae, Carinifex	Figures *54-56, 59*

In the following summary of names proposed by Hannibal, the entry is divided usually into two parts. The first paragraph includes such objective data as original reference, illustration, and type locality. Later paragraphs include such modern or revisionary data as subsequent illustration of Hannibal's material, current stratigraphic

Plate Explanation

Figures *16, 17*: *Lithoglyphus turbiniformis* (Tryon, 1865), Recent. Holotype of *Fluminicola modoci* Hannibal, 1912b, SU 5777 × 10

Figures *18, 19*: *Savaginius percarinatus* (Pilsbry, 1934), Pliocene. Paratype of *S. williamsi* (Hannibal, 1912b), SU 466 × 5

Figures *20, 21*: *Savaginius perditicollis* (Pilsbry, 1934), Pliocene. Paratype of *S. williamsi* (Hannibal, 1912b), SU 465 × 5

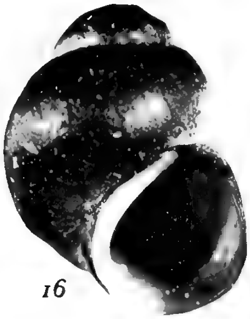
Figures *22, 23*: *Juga olequaensis* (Hannibal, 1912b), Eocene. Holotype, SU 459 × 3

Figures *24, 25*: *Savaginius williamsi* (Hannibal, 1912b), Pliocene. Holotype, SU 461 × 5

Figures *26, 30*: *Bellamya washingtoniana* (Arnold & Hannibal, *in* Hannibal, 1912b), Eocene. Holotype, SU 462 × 3

Figures *27, 29, 31*: *Bellamya turneri* (Hannibal, 1912b), Pilocene.
27, 31: Holotype, UCMP 12216 × 1½
28, 29: Paratype, SU 5902 × 1½

Figures *32, 33*: *Campeloma andersonianum* (Hannibal, 1912b), Eocene. Holotype, SU 463 × 3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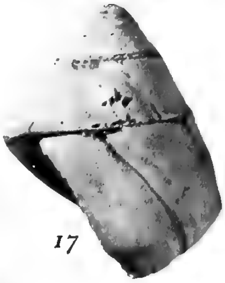
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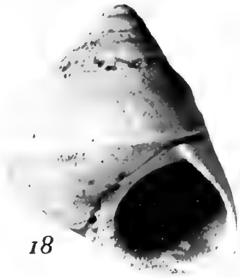
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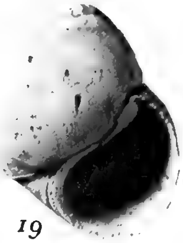
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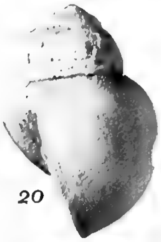
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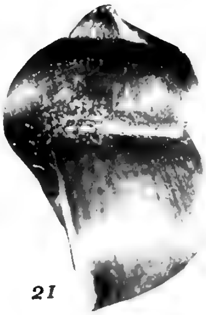
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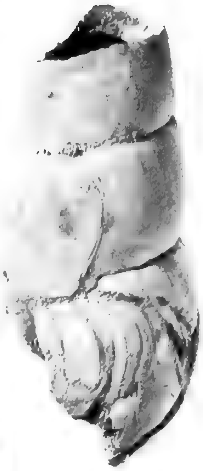
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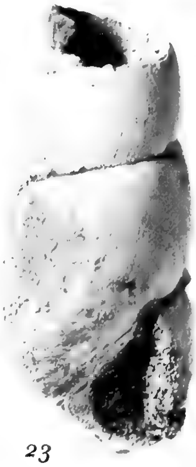
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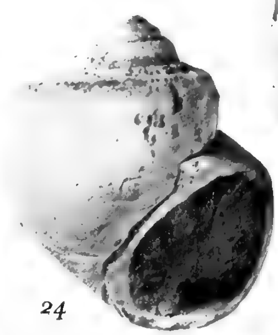
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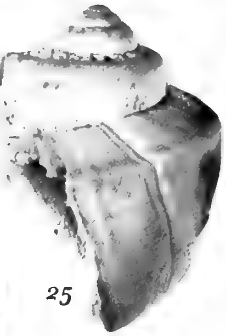
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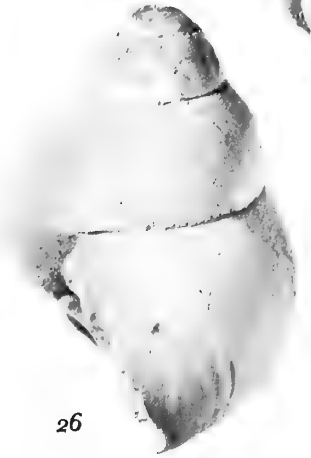
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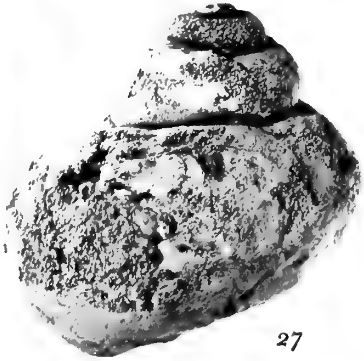
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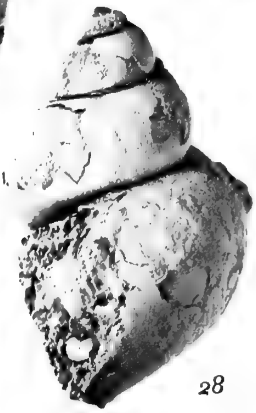
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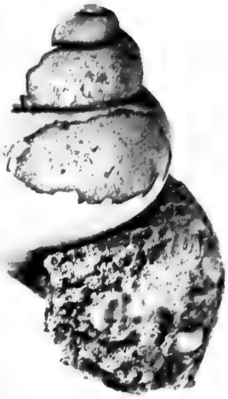
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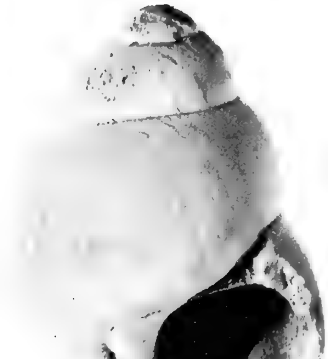
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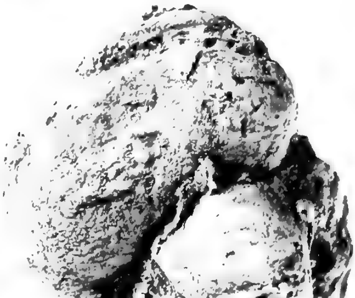
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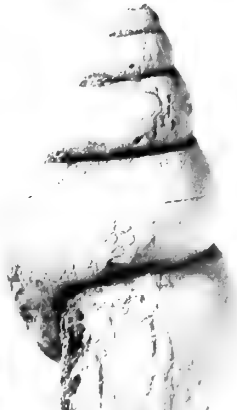
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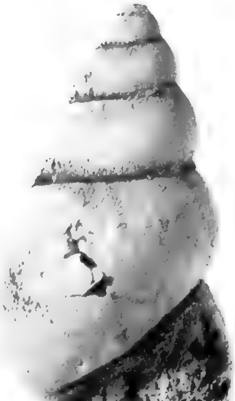
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classification of the formation from which the type material came, and current taxonomic standing of Hannibal's name.

MARGARITIFERIDAE

herrei Hannibal, 1912, *Margaritana*. Proc. Malac. Soc. London **10:** 121; plt. 7, fig. 17. One-fourth mile above Carnegie Pottery plant, in cut along Western Pacific Railway, Corral Hollow, Tesla, California; W. H. Ochsner, H. Hannibal.

Holotype SU 452; Figures *12, 14*. The locality is in the Tesla Formation, of Middle Eocene age, as mapped by HUEY (1948), in the NE ¼ sec. 33, T. 3 S., R. 4 E., San Joaquin County, California. The type is poorly preserved, but may be *Margaritifera* (now preferred to *Margaritana*) or *Plesielliptio*. Same locality as *Campeloma andersonianum*. Hannibal's notebooks indicate that he collected here January 3, 1911.

AMBLEMIDAE

Limnobasilissa Hannibal, 1912. Proc. Malac. Soc. London **10:** 127. Proposed as subgenus of *Gonidea*. No later author has found this name useful.

UNIONIDAE

Arnoldina Hannibal, 1912. Proc. Malac. Soc. London **10:** 128. Proposed as genus of Unionidae, Anodontinae. Later authors have generally not maintained the group as valid, though MODELL (1964) ranked it as a genus of Unionidae, Rectidentinae. Anatomical investigations might indicate the name could be used for a genus or subgenus, but surely *Arnoldina* was instituted prematurely.

Migranaja Hannibal, 1912. Proc. Malac. Soc. London **10:** 124. Proposed as genus of Unionidae, Unioninae. Nomenclatorially this name has fallen as a synonym of *Potomida* Swainson, 1840, of the Unionidae. Yet the American fossil that Hannibal dealt with is now classified in *Margaritifera*, of the Margaritiferidae. Both in taxonomy and nomenclature Hannibal's work in this instance was hasty.

Pleurobeminae Hannibal, 1912. Proc. Malac. Soc. London **10:** 118, 120. Proposed as subfamily of Quadrulidae. No later author has retained this group. The name as used by MODELL (1964) refers to a widely different assemblage.

Propterinae Hannibal, 1912. Proc. Malac. Soc. London **10:** 118, 120. Proposed as subfamily of Lampsilidae. No subsequent writer has found this group useful.

transpacifica Arnold & Hannibal, 1912, *Unio*. Proc. Malac. Soc. London **10:** 123; plt. 7, figs. 18a, b. Bluffs along Olequa Creek at shoals, 1½ miles above Little Falls, Washington; H. Hannibal.

Holotype SU 454; paratype SU 453; Figures *3, 4, 7, 10*. Classified as *Plesielliptio transpacifica* (Arnold & Hannibal) by TAYLOR (in press). Hannibal's notebooks indicate that he collected in the Little Falls area from July 25 to August 2, 1911, and that is presumably when he obtained material of this species. The locality is in rocks now classified as Cowlitz Formation, of late Eocene age; the species was not listed by WEAVER (1943).

SPHAERIIDAE

andersonianum Hannibal, 1912, *Sphaerium*. Proc. Malac. Soc. London **10:** 132; plt. 6, fig. 11. Badland Hills, one mile east of Sand Hollow, Oregon; R. B. Moran.

Holotype SU 299, Figure *6*. Probably an earlier name for *Sphaerium malheurense* Henderson & Rodeck, 1934. Probably from the lower and middle Pliocene Grassy Mountain Formation as described by KITTLEMAN *et al.* (1965).

catherinae Hannibal, 1912, *Sphaerium*. Proc. Malac. Soc. London **10:** 132; plt. 7, fig. 20. Hill near Hawthorne on the Belmont stage-road, Nevada.

Holotype SU 5816, Figures *1, 5, 8*. Probably an earlier name for *Pisidium leslieae* Firby, 1966, and a species of *Pisidium* (s. s.).

The type locality is evidently within the "beds near Hawthorne" where BUWALDA (1914: 351) found an assemblage of mollusks like that in the Esmeralda Formation of Stewart and Ione Valleys, Nevada. *Pisidium catherinae* (Hannibal), *Sphaerium meeki* (Hannibal), and *Perrinilla cordillerana* (Hannibal) were all described from the "hill near Hawthorne on the Belmont stage-road." Two of these were recorded by BUWALDA in the Esmeralda Formation of Ione and Stewart Valleys. All three appear to have been described as new by FIRBY (1966) from the upper Miocene-lower Pliocene Esmeralda Formation of Ione and Stewart Valleys, without comparison with Hannibal's species or discussion of Buwalda's identifications.

CORNEOCYCLADIDAE Hannibal, 1912. Proc. Malac. Soc. London **10:** 133. Proposed as a family of "Cyrenoideae," that is, Corbiculacea in the current sense, in substitution for the prior name Pisidiidae which Hannibal considered unavailable. *Sphaerium* and *Pisidium* have generally been classified together in the SPHAERIIDAE by later authors.

meeki Hannibal, 1912, *Corneocyclas*. Proc. Malac. Soc. London **10:** 135; plt. 6, fig. 12. Hill near Hawthorne on the Belmont stage-road, Nevada.

Holotype SU 450, Figure 2. Classified as *Sphaerium meeki* (Hannibal) by Herrington & Taylor (1958); probably an earlier name of *S. stewartensis* Firby, 1966. Same locality as *S. catherinae*, in the Esmeralda Formation.

tremperi Hannibal, 1912, *Corneocyclas.* Proc. Malac. Soc. London**10:** 137; plt. 7, fig. 22. Bluff Lake Cienaga, San Bernardino Mountains, California; H. Hannibal.

Holotype SU 5805. Figured by Taylor & Herrington, (1962). Ranked as a subjective synonym of *Pisidium ventricosum* form *rotundatum* Prime, 1852 (Taylor & Herrington, 1962; Herrington, 1965).

Hiatellidae

hemphilli Hannibal, 1912, *Gonidea.* Proc. Malac. Soc. London **10:** 128; plt. 7, fig. 19. Water-tunnel, head of Telegraph Canyon, Berkeley Hills, California.

Holotype SU 455, Figures *38, 39.* The posteriorly concave dorsal margin and flared posterior end of the poorly preserved type show it is not one of the Unionacea known as Tertiary fossils from western North America. It is at least close to *Panope abrupta* (Conrad), known from rocks as old as middle Miocene, and still living from Washington to Baja California. Clark (1915) reported the species (under the name of *Panope generosa* Gould) from the San Pablo group in the region of Mount Diablo, east of the Berkeley Hills. The reference of *Gonidea hemphilli* to *Panope abrupta* is thus plausible even though Hannibal's type is so poorly preserved that identification must remain uncertain. Moore (1963) provided numerous references and discussed the synonymy of *Panope abrupta.*

The stratigraphic horizon of the type can be limited on the basis of inferred marine environment. D. H. Radbruch, U. S. Geological Survey, Menlo Park, suggested that a likely sources of the specimen is a marine tongue at the base of the otherwise nonmarine Orinda Formation (lower Pliocene).

Veneridae?

rogersi Hannibal, 1912, *Sphaerium.* Proc. Malac. Soc. London **10:** 131; plt. 7, fig. 21. One-fourth mile above Carnegie Pottery plant, in cutting along Western Pacific Railway, Corral Hollow, Tesla, California; W. H. Ochsner, H. Hannibal.

Holotype SU 457, Figures *9, 11, 13, 15.* The locality is in the Tesla Formation, of middle Eocene age, as mapped by Huey (1948), in the NE ¼ Sec. 33, T. 3 S., R. 4 E., San Joaquin County, California. Hannibal's notebook indicates that he collected here January 3, 1911. The available geographic data would indicate the locality is the same as that of *Margaritifera? herrei* and *Campeloma andersonianum.* Yet those two are both strictly freshwater genera, whereas "*Sphaerium*" *rogersi* clearly does not belong to a genus normally inhabiting fresh water. Possibly the species are from slightly different horizons, or perhaps, as in the genus *Corbula,* "*S.*" *rogersi* is a freshwater species of a typically marine genus.

Without knowing the hinge one can scarcely fit "*Sphaerium*" *rogersi* into modern classification with any conviction. Yet in form, size, and sculpture it is certainly much like *Macrocallista domenginica capayana* Vokes, 1939, from a correlative horizon.

Valvatidae

calli Hannibal, 1910, *Valvata.* Nautilus **23:** 107. Near Summer Lake, Oregon; F. M. Anderson.

Holotype SU 472, Figures *47, 48, 51, 52.* Also figured by Hanna (1963). Ranked as a valid species probably of Blancan age by Taylor (1966).

whitei Hannibal, 1910, *Valvata.* Nautilus **23:** 107. Near Summer Lake, Oregon; F. M. Anderson.

Plate Explanation

Figure *34*: *Fisherola nuttallii* (Haldeman, 1841), Recent. Holotype of *Fisherola lancides* Hannibal, 1912b, SU 5851 × 10

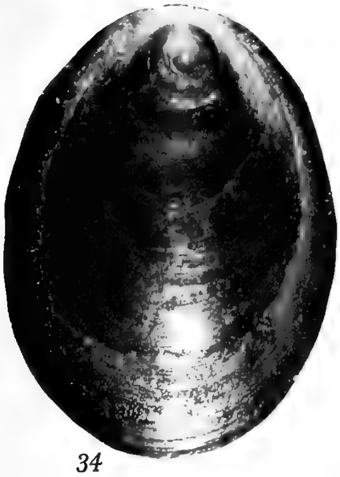
Figure *35*: *Bakerilymnaea bulimoides* (Lea, 1841), Recent. Holotype of *Lymnaea cubensis sanctijosephi* Hannibal, 1911, SU 6625 × 5

Figures *36, 37, 40*: *Fossaria cooperi* (Hannibal, 1912b), Recent.
36, 37: Holotype, SU 5815 × 5
40: Paratype, SU 5814 × 5

Figures *38, 39*: "*Gonidea*" *hemphilli* Hannibal, 1912b, Pliocene. Holotype, SU 455 × 2

Figures *41, 42*: "*Pachychilus*" *drakei* Arnold & Hannibal, *in* Hannibal, 1912b, Eocene. Holotype, SU 458 × 2

Figures *43, 44*: *Lymnaea lawsoni* (Hannibal, 1912b), Miocene. Holotype, SU 200 × 3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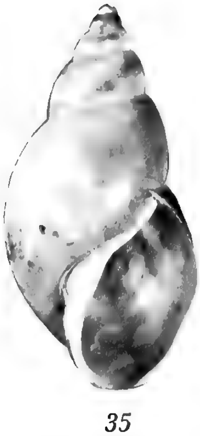
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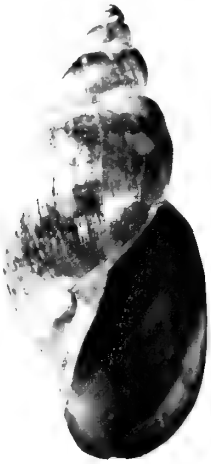
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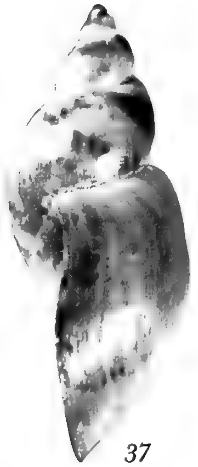
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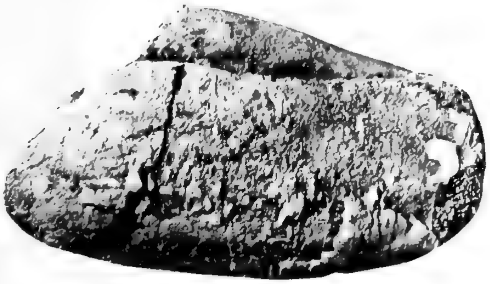
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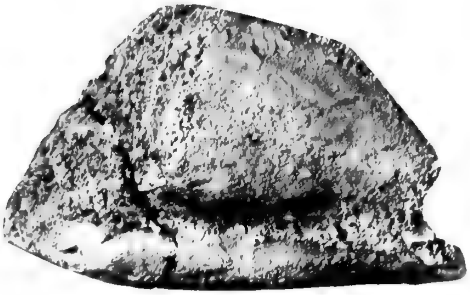
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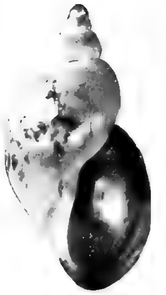
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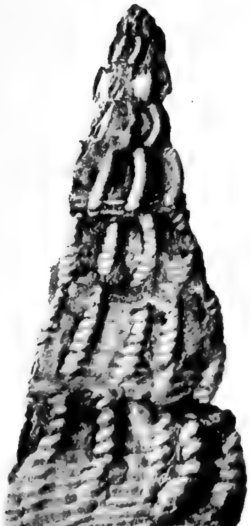
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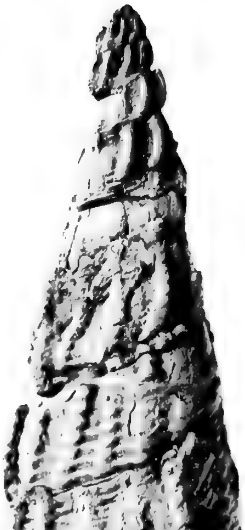
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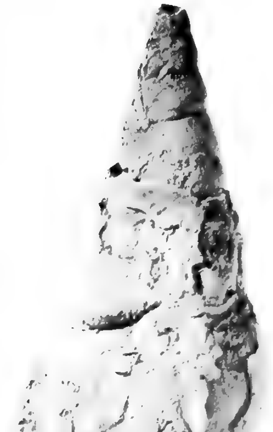
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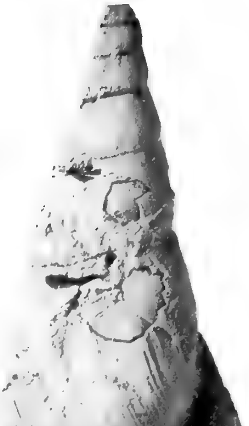
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Holotype SU 473; Figures *45, 46, 50*. Also figured by HANNA (1963). Ranked as a valid species probably of Blancan age by TAYLOR (1966).

VIVIPARIDAE

andersoniana Hannibal, 1912, *Lioplax*. Proc. Malac. Soc. London **10:** 196; plt. 8, fig. 33. Corral Hollow, near Tesla, California; cut along Western Pacific Railroad, ¼ mile above Carnegie Pottery plant; H. Hannibal.

Holotype SU 463; Figures *32, 33*. The locality is in the Tesla Formation, of middle Eocene age, as mapped by HUEY (1948), in the NE ¼ sec. 33, T. 3 S., R. 4 E., San Joaquin County, California. Classified as *Campeloma andersonianum* (Hannibal) by TAYLOR (in press). Same locality as *Margaritifera? herrei*. Hannibal's notebook indicates that he collected here January 3, 1911.

Callina Hannibal, 1912. Proc. Malac. Soc. London **10:** 193. Proposed as a subgenus of *Viviparus*. No later student of Viviparidae has considered this worthy of subgeneric rank.

Cipangopaludina Hannibal, 1912. Proc. Malac. Soc. London **10:** 194. Proposed as subgenus of *Idiopoma*. The group was distinguished by ANNANDALE (1920, under the synonymous name *Lecythoconcha*) by features of shell, operculum, and anatomy. Modern usage is not consistent. In a recent work (ZILCH, 1955) *Cipangopaludina* is treated as a genus in the Bellamyinae.

turneri Hannibal, 1912, *Viviparus*. Proc. Malac. Soc. London **10:** 193; plt. 8, fig. 31. Near coal mine, Silver Peak Range, Nevada; H. W. Turner.

Holotype UCMP 12216; paratypes SU 5901, 5902; Figures *27-29, 31*. Classified as *Bellamya (Paludotrochus) turneri* (Hannibal) by TAYLOR (in press). The locality is in the upper Miocene-lower Pliocene Esmeralda Formation.

washingtonianus Arnold & Hannibal, 1912, *Viviparus*. Proc. Malac. Soc. London **10:** 194; plt. 8, fig. 32. Bluffs along Olequa Creek above shoals 2 miles north of Little Falls; Washington; H. Hannibal.

Holotype SU 462; Figures *26, 30*. Same locality as *Juga olequaensis*. Classified as *Bellamya (Paludotrochus) washingtoniana* (Arnold & Hannibal) by TAYLOR (in press). Hannibal's notebooks indicate that he collected in the Little Falls area from July 25 to August 2, 1911, and that is presumably when he obtained material of this species. The locality is in rocks now classified as Cowlitz Formation, of late Eocene age (WEAVER, 1943).

BITHYNIIDAE

Bulimidae Hannibal, 1912. Proc. Malac. Soc. London **10:** 183. Proposed as a replacement for Bithyniinae. Hannibal regarded *Bythinia* as nomenclaturally unavailable, but subsequently Opinion 475 of the International Commission on Zoological Nomenclature validated *Bithynia* and rejected *Bulimus*.

PLEUROCERIDAE

Ellipstomidae Hannibal, 1912. Proc. Malac. Soc. London **10:** 167 - 168. Proposed as family of "Melanoideae," that is, Cerithiacea in a broad modern sense. Hannibal gave no criteria for rank, or diagnosis. The genera included have otherwise been classified in Pleuroceridae, Pleurocerinae.

Gyrotominae Hannibal, 1912. Proc. Malac. Soc. London **10:** 167. Proposed as subfamily of Pleuroceridae. Later writers have not found the group useful, and have included it in Pleurocerinae.

olequaensis Arnold & Hannibal, 1912, *Ambloxus*. Proc. Malac. Soc. London **10:** 178; plt. 8, fig. 27. Bluffs along Olequa Creek above shoals 2 miles north of Little Falls, Washington.

Holotype SU 459; Figures *22, 23*. Also figured by WEAVER (1943, plt. 75, fig. 14). Classified as *Juga olequaensis* (Arnold & Hannibal) by TAYLOR (in press). Hannibal's notebooks indicate that he collected in the Little Falls area from July 25 to August 2, 1911, and that is presumably when he obtained material of this species. The locality is in rocks now classified as Cowlitz Formation, of late Eocene age (WEAVER, 1943).

THIARIDAE

drakei Arnold & Hannibal, 1912, *Pachychilus*. Proc. Malac. Soc. London **10:** 183; plt. 8, fig. 26. Bluffs along Olequa Creek at bend below Little Falls, Washington; H. Hannibal.

Holotype SU 458; Figures *41, 42*. Also figured by WEAVER (1943, plt. 75, fig. 13). Hannibal's notebooks indicate that he collected in the Little Falls area from July 25 to August 2, 1911, and that is presumably when he obtained material of this species. The locality is in rocks now classified as Cowlitz Formation, of late Eocene age (WEAVER, 1943).

HYDROBIIDAE

binneyana Hannibal, 1912, *Cincinnatia*. Proc. Malac. Soc. London **10:** 190. New name for *Paludina obtusa* Lea

(1841), *non* Troschel (1837). Classified as *Fontigens binneyana* (Hannibal) by Morrison (1947).

Heathilla Hannibal, 1912. Proc. Malac. Soc. London **10:** 186. Proposed as subgenus of *Fluminicola,* the latter regarded as a synonym of *Lithoglyphus* by Taylor (1966). No subsequent author has found this group of taxonomic value.

modoci Hannibal, 1912, *Fluminicola.* Proc. Malac. Soc. London **10:** 187; not plt. 8, fig. 30. Fletcher's Spring, south end of Goose Lake, California; H. Hannibal.

Holotype SU 5777; Figures *16, 17.* Ranked as a synonym of *Lithoglyphus turbiniformis* (Tryon, 1865) by Taylor (1966).

williamsi Hannibal, 1912, *Pyrgulopsis.* Proc. Malac. Soc. London **10:** 189; plt. 8, fig. 29. Martin and Dudley's well, SE ¼ sec. 32, T. 26 S., R. 21 E., Lost Hills oil field, California; W. Williams.

Holotype SU 461; Figures *24, 25*; paratypes SU 465, 466; Figures *18 - 21.* Classified as *Savaginius williamsi* (Hannibal) by Taylor (1966). The horizon from which the type specimens came is now referred to the upper part of the San Joaquin Formation, of late Pliocene age (Taylor, 1966 and references therein).

LATIIDAE

Latiinae Hannibal, 1912. Proc. Malac. Soc. London **10:** 147. Proposed as subfamily of Ancylidae. As generally classified the Latiidae include only one genus, *Latia.* The other groups included by Hannibal belong to other families.

LANCIDAE

Fisherola Hannibal, 1912. Proc. Malac. Soc. London **10:** 151. Proposed as a genus of Ancylidae. Ranked as a genus of Lancidae by Morrison (1955), but as a subgenus or lower category within *Lanx* by some others.

klamathensis Hannibal, 1912, *Lanx.* Proc. Malac. Soc. London **10:** 149; plt. 8, fig. 25. Government Irrigation Dam, Upper Klamath Lake, Oregon; E. Applegate, H. Hannibal.

Holotype SU 5849, paratype SU 5850. Ranked as a valid species by Morrison (1955).

lancides Hannibal, 1912, *Fisherola.* Proc. Malac. Soc. London **10:** 152; plt. 8, fig. 35. Snake River, Washington; Henry Hemphill.

Holotype SU 5851; Figure *34.* Probably a junior synonym of *Fisherola nuttallii* (Haldeman, 1841).

Lancinae Hannibal, 1914. Nautilus **28:** 24. Proposed as subfamily of "Laevapecidae," without adequate foundation. The group Lancinae of Walker (1918), and Lancidae of Pilsbry (1925) correspond essentially to the probable scope intended by Hannibal.

Walkerola Hannibal, 1912. Proc. Malac. Soc. London **10:** 149. Proposed as a subgenus of *Lanx.* Ranked as a "section or subgenus" of *Lanx* by Morrison (1955).

LYMNAEIDAE

Acellinae Hannibal, 1912. Proc. Malac. Soc. London **10:** 138. Proposed as subfamily of Lymnaeidae. No subsequent author has found this group useful.

cooperi Hannibal, 1912, *Lymnaea.* Proc. Malac. Soc. London **10:** 143; plt. 6, figs. 13 a - c. Spring, Wrights, Santa Cruz Mountains, California; H. Hannibal.

Holotype SU 5815; Figures *36, 37, 40.* Wrights is a former settlement in the NW ¼ sec. 23, T. 9 S., R. 1 W., Santa Clara County. Probably a valid species of the *Fossaria obrussa* group.

lawsoni Hannibal, 1912, *Pachychilus.* Proc. Malac. Soc. London **10:** 183; plt. 8, fig. 23. Near Bald Peak, Berkeley Hills; H. Hannibal.

Holotype SU 200; Figures *43, 44.* Evidently Hannibal collected the type material of this species March 29, 1911. His notebook entry for that date reads: "Roy Leach and three U. C. [University of California] fellows walk to Bald Peak and return to U. C." The stratigraphic unit from which the type came is uncertain on account of lack of precision of the original locality. Hannibal ascribed the species to the "Contra Costa lake beds." Although Firby (1967) reviewed previous reports of mollusks from the Pliocene Siesta Formation (including the obsolete

Plate Explanation

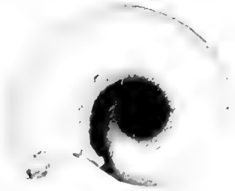
Figures *45, 46, 50*: *Valvata whitei* Hannibal, 1910, Pliocene. Holotype, SU 473 × 5

Figures *47, 48, 51, 52*: *Valvata calli* Hannibal, 1910, Pliocene. Holotype, SU 472 × 5

Figures *49, 53*: *Brannerillus physispira* Hannibal, 1912b, Pliocene. Holotype, SU 460 × 10

Figures *54 - 56, 59*: *Helisoma sanctaeclarae* (Hannibal, 1909), Pliocene. Holotype, SU 451 × 5

Figures *57, 58, 60, 61*: *Vorticifex cordilleranus* (Hannibal, 1912b), Miocene. Holotype, SU 464 × 3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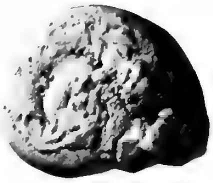
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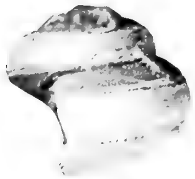
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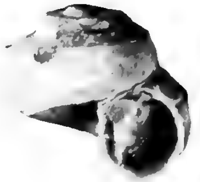
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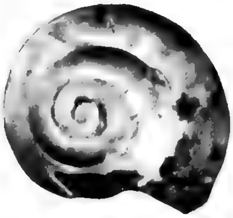
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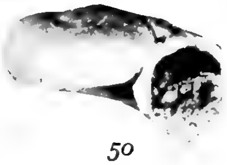
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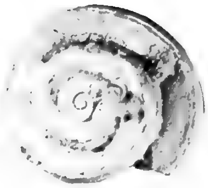
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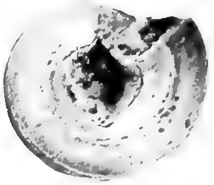
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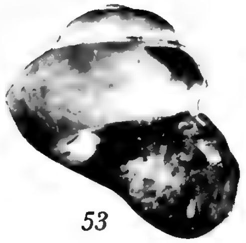
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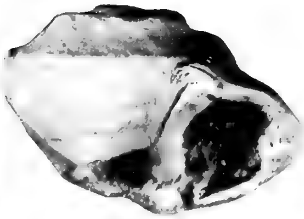
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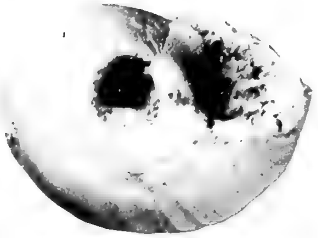
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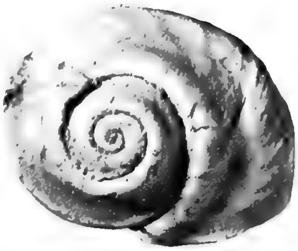
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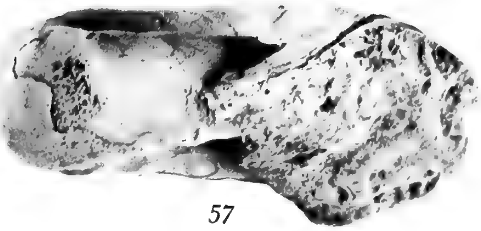
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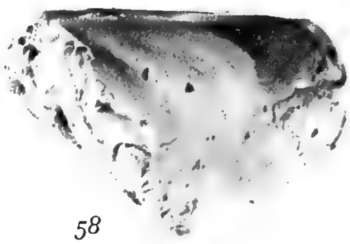
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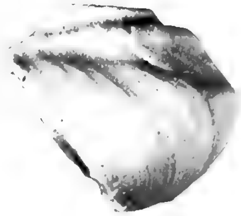
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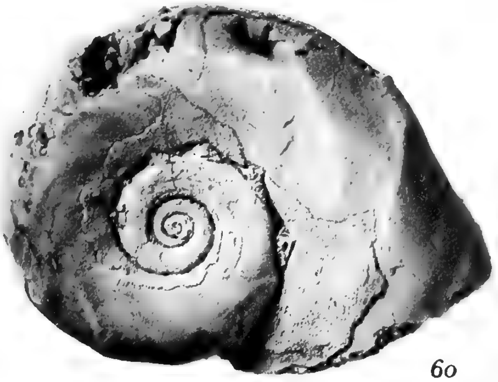
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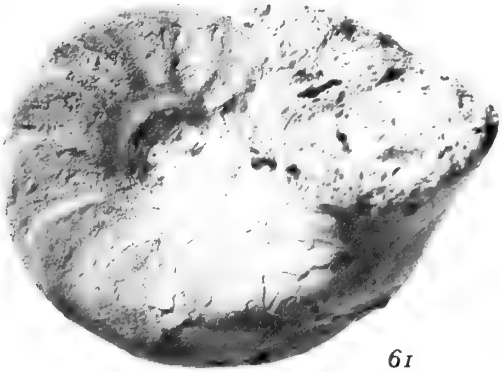
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"Contra Costa lake beds") he did not mention Hannibal's species.

The restudy of "*Pachychilus*" *lawsoni* revealed surprisingly that the type is one of the subgenus *Lymnaea (Stagnicola),* and one of the *L. palustris* group as classified by F. C. BAKER (1911). The species is closely similar to, and indeed might well be another name for *L. mohaveana* Taylor, 1954, from the upper Miocene Barstow Formation in southern California. This affinity could be taken as evidence that *L. lawsoni* is from a stratigraphic unit below the Siesta Formation.

sancti-josephi Hannibal, in KEEP, 1910, *Lymnaea cubensis* var. West coast shells: 309; plt. 3, fig. 6. Artesian Belt near San Jose, California.

Holotype SU 6625; Figure *35*. The original label specifies the locality more precisely as Calabazas Slough between Alviso and Lawrence. We believe this is a synonym of the common local species *Bakerilymnaea bulimoides* (Lea, 1841).

stearnsi Hannibal, in BAKER, 1911, *Lymnaea.* Spec. Publ. Chicago Acad. Sci. **3:** 102. New name for *Limnaea maxima* Stearns, 1906, *non* Collins, 1872.

An objective synonym of *Lymnaea mascallica* Cossmann, 1907, proposed earlier as a substitute for Stearns' preoccupied name. The further synonymy remains uncertain, pending a review of the fossil material of *Bulimnea* and its relation to the sole living species of the genus, *Bulimnea megasoma* (Say, 1824).

ANCYLIDAE

Kincaidilla Hannibal, 1912. Proc. Malac. Soc. London **10:** 148. Proposed as subgenus of *Gundlachia.* HUBENDICK (1964) ranked the name as a synonym of *Ferrissia* (s. s.).

Laevapecinae Hannibal, 1912. Proc. Malac. Soc. London **10:** 147. Proposed as subfamily of Ancylidae, but including groups now classified as Ancylidae and Lancidae. BURCH (1962) maintained a subfamily Laevapecinae in the Ancylidae, though HUBENDICK (1964) recognized no subfamily categories.

Zalophancylus morani Hannibal, 1912. Proc. Malac. Soc. London **10:** 152; plt. 6, fig. 15. Badland Hills, one mile east of Sand Hollow, Oregon; R. B. Moran.

Holotype SU 2. Same locality as *Sphaerium andersonianum.* Later interpreted as the mold of a fish vertebra (HANNA, 1925).

PLANORBIDAE

Brannerillus Hannibal, 1912. Proc. Malac. Soc. London **10:** 191. Proposed as genus of Amnicolidae (Hydrobiidae), but classified in the Planorbidae by TAYLOR (1966).

cordillerana Hannibal, 1912, *Helisoma.* Proc. Malac. Soc. London **10:** 161; plt. 6, fig. 16; plt. 8, fig. 34. Hill near Hawthorne on the Belmont stage-road, Nevada.

Holotype SU 464; Figures *57, 58, 60, 61.* Classified as *Perrinilla cordillerana* (Hannibal) by BAKER (1945). Probably an older name for *Vorticifex stewartensis* Firby, 1966.

This species was described from the same locality as *Pisidium catherinae* and *Sphaerium meeki,* in the Esmeralda Formation of late Miocene to early Pliocene age.

mojavensis Hannibal, 1912, *Planorbis.* Proc. Malac. Soc. London **10:** 157; plt. 8, figs. 24a, b. Near Barstow, Mojave Desert, California; J. C. Merriam, C. L. Baker.

Holotype UCMP 34178?, paratypes SU 5460, UCMP 34179-34182, uncat.; S. S. Berry collection 8924. Classified as *Planorbula mojavensis* (Hannibal) by TAYLOR (1954). The species is known only from the upper Miocene Barstow Formation in the Barstow Hills, San Bernardino County, California.

Neoplanorbinae Hannibal, 1912. Proc. Malac. Soc. London **10:** 147. Proposed as subfamily of Ancylidae. ZILCH (1959-1960) maintained a family Neoplanorbidae that is essentially Hannibal's group, whereas WALKER (1923) treated it as a subfamily of Ancylidae. Most recently TAYLOR & SOHL (1962) included it in the Planorbidae.

Perrinilla Hannibal, 1912. Proc. Malac. Soc. London **10:** 159. Proposed as subgenus of *Helisoma.* Ranked as a genus of Planorbidae, Helisomatinae by BAKER (1945).

physispira Hannibal, 1912, *Brannerillus.* Proc. Malac. Soc. London **10:** 191; plt. 8, fig. 28. Marl "reefs" near mouth of gulch south of Medallion One Canyon, east flank of Kettleman Hills, California; H. Hannibal.

Holotype SU 460; Figures *49, 53.* The locality is in the basal part of the Tulare formation, upper Pliocene, but we have been unable to trace the location of "Medallion One Canyon" precisely. Hannibal's notebook indicates that he collected in the Kettleman Hills area from December 28, 1910 to January 1, 1911. The species was ranked as valid by TAYLOR (1966), *sanctaeclarae* Hannibal, 1909, *Carinifex*. Nautilus **23:** 40. Near Los Gatos limestone quarry, Los Gatos, Santa Cruz Mountains, California.

Holotype SU 451; Figures *54-56, 59*. Also figured by Hannibal (1912b, plt. 6, figs. 14a, b). Ranked as a valid species of *Helisoma (Carinifex)* by Taylor (1966).

A letter from Hannibal to Dall (22-X-1907) describes an occurrence of fossils that may be the type locality:

> "I am sending to you for identification after which you may deposit in the museum in my name some Pulmonates from the Santa Clara Lake beds (Pliocene) here.
>
> "Topmost lacustrinal horizon, S. C. Lake bed, old Carson rd., Panorama Ranch, Mr. Snell owner, Foster Rd., Los Gatos, Santa Clara Co., Cal., alt. 500± ft. The material I send is just as I dug it out except that it was in my lab. washed on a no. 40 screen. The lower horizons of the fossiliferous portion of the bed are a hard marl and chalk. The bed is 100 ft thick but excepting the upper 25 ft is barren clay, sand, and gravel partly indurated. The fossils in the bed are almost solely the species I send ... ."

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A New Muricid Gastropod from Western Australia

BY

ANTHONY D'ATTILIO

Department of Marine Invertebrates, Natural History Museum, San Diego, California 92112

AND

WILLIAM E. OLD, Jr.

Department of Living Invertebrates American Museum of Natural History
Seventy-ninth Street and Central Park West, New York, New York 10024

(1 Plate; 1 Text figure)

Some time ago, Dr. Barry Wilson, Curator of Mollusks, at the Western Australian Museum, Perth, Western Australia, submitted a portion of the Museum's collection of muricid gastropods for examination. The collection consists of shells obtained by the Western Australian-Hawaiian Expedition, material from their own collecting trips, and specimens received from other sources. Among the material is a distinctive new species which is described below.

Haustellum Schumacher, 1817

Type species: *Murex haustellum* Linnaeus, 1758 by tautonymy.

Radular dentition herein illustrated, Figure 3. Operculum with centrally situated nucleus.

*Haustellum **wilsoni*** D'Attilio & Old, spec. nov.

Description: Shell club-shaped with a moderately short canal; with 7 rounded whorls (protoconch in Paratypes "B" and "E" consists of 2 polished rounded whorls); whorls deeply and widely channeled below the suture; 3 varices on first 4 or 5 whorls, which follow one another axially with slight irregularity; varices thick, strongly rounded and reflected; varices may be excavated on the trailing edge. Sculpture on surface consisting of nodulose axial ribbing, usually 5 ribs between each varix, and of low spiral cords, about 10 on the body whorl; between the nodulose cords, finer intercalating non-nodulose striae are present; about 5 or 6 similar cords on spire but more elevated and pronounced than those on later whorls. The

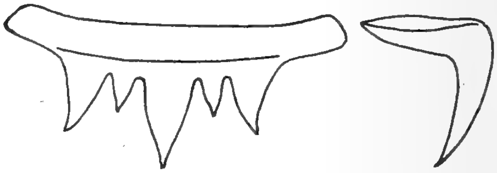

Figure 3

Radular characters of the central tooth and a lateral tooth of *Haustellum haustellum* (Linnaeus, 1758). Greatly enlarged. Drawing by Anthony D Attilio

Plate Explanation

*Haustellum **wilsoni*** D'Attilio & Old, spec. nov.

Figure *1*, a and b: Paratype "A" (AMNH no. 154655) Jurien Bay, West Australia

Figure *2*, a and b: (Inset Figure 2c): Holotype (WAM N/3981) Jurien Bay, West Australia, in craypot at 35 - 40 fathoms.
Figure 2c: Apical view of Holotype. All Figures × 1

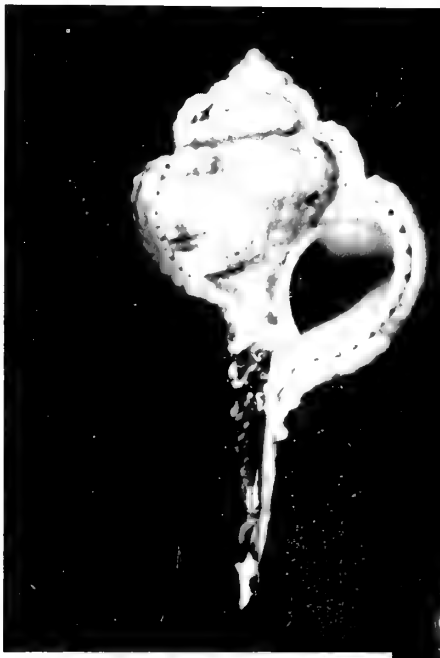

Figure 1a

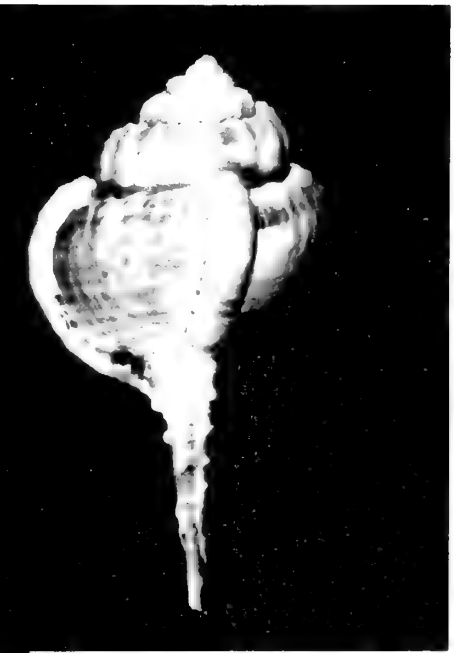

Figure 1b

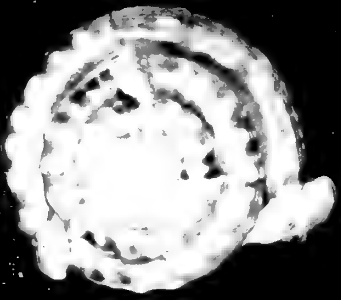

Figure 2c

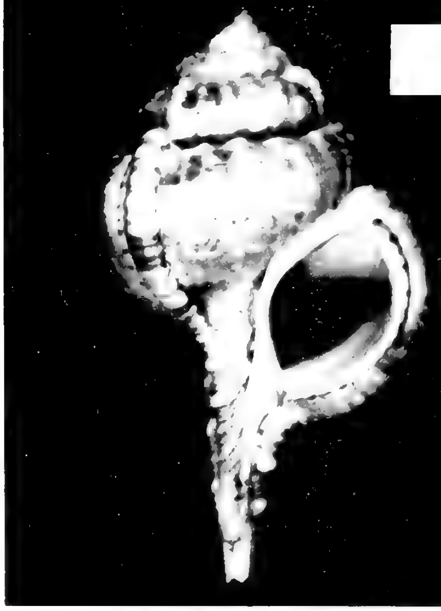

Figure 2a

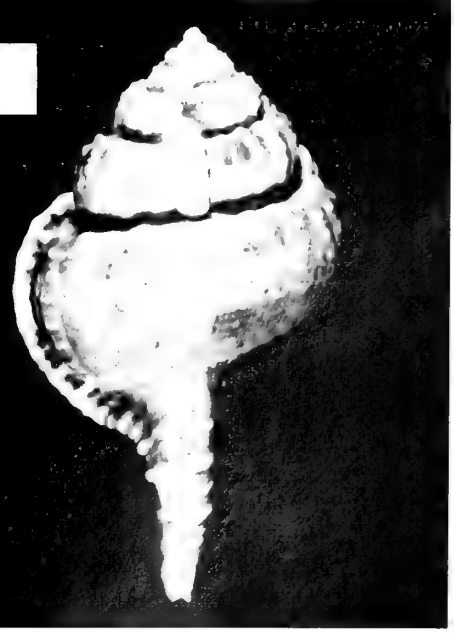

Figure 2b

photographs courtesy American Museum of Natural History

surface of the shell is finely malleated from the interaction of axial and spiral sculpture. Shell is pinkish brown with the nodes of a paler whitish hue and there are faint indications of 3 spiral bands of darker brown pigment evenly distributed on the body whorl, and a single band of brown on the shoulder of the spire.

Aperture is ovate, white, placed diagonally to the axis of the shell; outer lip has lirations within, which correspond to the external cords; the inner lip is adherent above; the margin of the lip is detached from shell and well elevated; below it arises distantly from the shell and is rolled outward. Outer lip is white in color on the exterior, and ornamented with about 12 red-brown dots. Additional dots may also be seen within the proximal portion of the anterior canal, and on earlier varices, where they appear as "stitching".

Opercular characters and soft parts are unknown. The specimens examined, including the holotype, were dead shells with hermit crab inhabitants, obtained by prawn fishermen, by skin diving, or shore collecting.

Holotype: Depository, Western Australian Museum, Perth, no. WAM N/3981. Collected off Jurien Bay, Western Australia, by C. Lazarich on the vessel *Martha,* in 1958 or 1959.

Type Locality: Jurien Bay, Western Australia.

Paratype "A": Depository, American Museum of Natural History, no. 154655. Collected at Jurien Bay, Western Australia, by E. Parkin, on 29 December 1967.

Paratypes: Six additional paratypes, "B" through "G" were collected at localities ranging from Dunsborough, near Cape Naturaliste in the south, to Beagle Island off the central coast of Western Australia (see Table 1). These paratypic specimens are deposited in the collections of the Western Australian Museum, Perth.

Discussion: The new species may be easily distinguished from *Haustellum haustellum* (Linnaeus, 1758) by the lack of the deep posterior notch in the aperture. In *H. haustellum* and *H. longicaudum* (Baker, 1891), the notch is deep and constricted almost to a key-hole shape. Some authors, including Vokes (1964) and MacNeil (1960) have considered this notch to be characteristic of the genus *Haustellum.* Also, in both of these species the nucleus of the operculum is centrally located and surrounded by concentric growth rings. ***Haustellum wilsoni*** spec. nov. lacks this notch, as do several similarly shaped muricid species, including *Murex multiplicatus* Sowerby, 1895, from Northwest Australia, and *M. hirasei* Hirase, 1915, from deep water in the Western Pacific. The latter species was referred to *Haustellum* by Vokes (1964), but both of these species possess opercula with terminally situated nuclei. Both species seem better placed in the subgenus *Tubicauda.*

Haustellum wilsoni spec. nov. may be distinguished from *Murex (Tubicauda) tweedianus* McPherson, 1962 (= *M. espinosus* McPherson, 1959, *non* Hutton, 1886), of eastern Australia, by its larger size, channeled suture, and lack of any of the low spines present on the varices of *M. tweedianus.* It should be noted that *M. tweedianus* displays a well-developed anal notch, when viewed from above. This species also has an operculum with a terminal nucleus.

The opercular and radular characters of the new species are not known. Considering the unique shell characters possessed by the species, its placement in *Haustellum* s. s. must be considered tentative until additional anatomical data become available.

Table 1

Haustellum wilsoni D'Attilio & Old, spec. nov.

Specimen	Collection	Size	Locality	Collector	Date
Holotype	WAM N/3981	76 mm+	Jurien Bay, in craypot in 35-40 fms., between Jurien Bay and Green Head, Western Australia	C. Lazarich on *Martha*	1958 or 1959
Paratype A	AMNH 154655	73.5 mm+	Jurien Bay, Western Australia	E. Parkin	29 December 1967
Paratype B	WAM N/5366	70 mm+	in craypot, Beagle Island, Western Australia	Poole Bros.	April 1962
Paratype C	WAM N/5367	64 mm+	in craypot, approx. 15-20 fms., Beagle Island, Western Australia	Poole Bros.	November 1962
Paratype D	WAM N/3955	65 mm+	Beagle Island, Western Australia	Poole Bros.	1964
Paratype E	WAM N/2641	58.5 mm+	with hermit crab, 5 fms., Hall's Bank, Gage Roads, Fremantle, Western Australia	Barry Wilson	2 February 1963
Paratype F	WAM N/2148	58 mm+	Leighton Beach, near Perth, Western Australia	Barry Wilson	June 1955
Paratype G	WAM N/2987	45 mm+	54ft., 3 miles off Dunsborough, Western Australia, "under stones and coral"	Barry Wilson	1954

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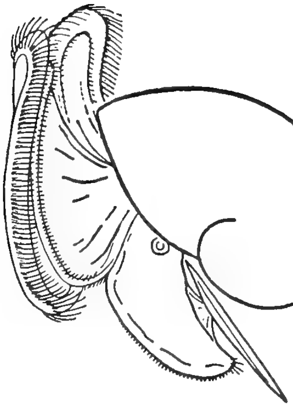

Oviposition, Fecundity, and Larval Development of Three Sacoglossan Opisthobranchs from the Northumberland Coast, England

BY

FU-SHIANG CHIA[1]

Dove Marine Laboratory and Department of Zoology, University of Newcastle upon Tyne, England

(4 Plates)

INTRODUCTION

ALONG THE NORTHUMBERLAND COAST, three species of sacoglossan opisthobranchs, *Limapontia capitata* (MÜLLER, 1773), *L. depressa* (ALDER & HANCOCK, 1862) and *Acteonia cocksi* ALDER & HANCOCK, 1848, are to be found. Although their distribution is restricted (GASCOIGNE, 1952, 1956), a large number of specimens can be secured from localities not far from the Dove Marine Laboratory.

A number of papers have been published on various aspects of the reproductive biology of these species. Notable are those of PELSENEER (1899) and COLGAN (1911, 1912) on the development of *Acteonia cocksi*; THORSON (1946) on the larval morphology of *Limapontia capitata*; GASCOIGNE (1956) on the reproductive system and mating behaviour of *L. capitata* and *A. cocksi*, and MILLER (1962) on the reproductive cycle of *A. cocksi* and *L. capitata*. More recently, SEELEMANN (1967) described the larval development and metamorphosis of *L. depressa*. Scattered information on opisthobranch development has been summarized and tabulated by THOMPSON (1967). Despite these studies, knowledge of developmental chronology and fecundity of these species is still lacking or fragmentary at best. The present paper describes laboratory observations on their oviposition, fecundity, and larval development.

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This study was supported by a research grant from the Natural Environment Research Council. I thank Dr. T. Gascoigne who introduced me to these beasties and who has never failed to lend me his enthusiasm throughout the course of this study. I thank also Dr. R. L. Fernald for reading the manuscript.

COLLECTION

Limapontia capitata and *Acteonia cocksi* were collected from shallow rocky pools at the north side of the Cullercoats Bay or from those at St. Mary's Island. In these pools, there is plenty of green algae, *Cladophora* or *Cladophora* and *Enteromorpha*, upon which the animals feed. Since both opisthobranch species are similar in size and color, it is difficult to distinguish them in the field without the aid of magnifying glasses. However, behaviorally, *A. cocksi* are usually seen crawling on the substratum whereas *L. capitata* are found on the algae.

In the laboratory the animals were kept in small finger bowls and provided with a few branches of *Cladophora*, at a temperature of 10 - 14° C. However, they can survive equally well at room temperature (19 - 21° C) and in one half of the salinity of normal sea water.

Limapontia depressa was collected from the salt marshes at Alnmouth where it is flooded only during spring tides. They usually aggregate into small clusters on the bed of *Vaucheria*, which is their major food. The color of this animal varies from lemon yellow to green and black, matching well with that of their environment. In the laboratory they were kept in finger bowls with a layer of *Vaucheria* on coarse sand. More information on the collection is summarized in Table 1.

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[1] Present address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada

Table 1

DATA OF COLLECTION

Date	Locality	Species	Number of Animals Collected	Average Length (in mm) of the Animals
April 1969				
2	Cullercoats	*Limapontia capitata*	17	3.1
2	St. Mary's	*Acteonia cocksi*	2	3.9
		Limapontia capitata	25	3.4
8	St. Mary's	*Acteonia cocksi*	14	4.2
11	Alnmouth	*Limapontia depressa*	110	4.5
16	St. Mary's	*Limapontia capitata*	79	4.3
		Acteonia cocksi	51	4.7
May 1969				
15	Alnmouth	*Limapontia depressa*	170	?
22	Cullercoats	*Limapontia capitata*	numerous	1.2

OVIPOSITION AND FECUNDITY

The three sacoglossans are hermaphroditic and fertilization is by hypodermic impregnation (GASCOIGNE, 1956). One copulation is apparently sufficient to fertilize the eggs of several spawn masses within the breeding season.

Limapontia capitata:

Two days after capture, the animal began to lay eggs. The eggs are enclosed in a sausage-like jelly mass which is attached either on the algae or on the glassware. The size of the spawn mass varies depending on the number of eggs it contains. A large spawn mass with 500 eggs is about 0.7 mm in diameter and 2 mm long, while a small spawn mass with less than 50 eggs is spherical and ½ mm in diameter. The jelly material is homogeneously transparent, adhesive on the surface and usually covered with debris in the natural habitat. In large spawn masses the eggs are spirally arranged into regular rows but this is not so in small spawn masses. The eggs do not attach to each other nor the jelly mass envelope; they are suspended free in a fluid in the lumen of the jelly. Upon damage to the jelly, the eggs usually flow out freely. An individual egg is enclosed in a capsule which is about 100μ in diameter, whereas the egg itself is only 82μ in diameter. The fluid inside the capsule is either transparent or with suspended granular material (albumen). This material, however, does not serve any essential function as the eggs without albumen develop equally well. The egg is yellowish in color and is perfectly spherical, although the capsule in most cases is oval in shape. Most of the capsules contain only one egg, but up to 4 eggs in one capsule have been observed occasionally.

In order to study the fecundity, 20 animals collected on April 2nd from St. Mary's Island were placed in one finger bowl with 150 ml sea water and some *Cladophora*. The culture dish was maintained at the temperature of 10 to 13° C and was examined daily. Spawn masses were removed, and the number of spawn masses and the number of eggs of each spawn mass was counted and recorded. After one month in captivity, the animals were getting smaller and fed less actively and most of them died in the second month.

Table 2

RECORD OF EGG-LAYING BY 20 ANIMALS OF *Limapontia capitata* WITHIN A MONTH

Date	Number of Egg Masses	Number of Eggs per Spawn Mass		Total Number of Eggs
		Range	Mean	
April				
4	2	244-720	482	964
5	7	250-700	382	2674
6	0			
7	8	180-600	362	2896
8	6	140-705	393	2358
9	0			
10	10	38-300	177	1770
11	5	105-180	124	620
12	3	108-163	134	402
13	10	65-170	114	1140
14	3	58-184	132	396
15	6	57-166	106	636
16	7	31-142	108	756
17	3	56-125	95	285
18	6	66-134	91	546
19	4	53-131	86	344
20	3	61-113	95	285
21	3	75- 85	81	243
22	7	45-114	76	532
23	1	63	63	63
24	1	71	71	71
25	0			
26	9	41- 93	67	603
27	0			
28	8	34- 68	44	352
May				
3	6	49- 65	55	330
Total	118			18 266

Table 2 shows that among the 118 spawn masses, the highest number of eggs per spawn mass is 720 and the lowest is 31. In general, the larger spawn masses were laid during the first 5 days after capture, and getting smaller and smaller thereafter. It further shows that each animal spawned on an average of 6 times during one month and that the average number of eggs laid by each animal is about 913.

Acteonia cocksi:

The spawn mass of *Acteonia cocksi* is essentially similar to that of *Limapontia capitata.* The eggs are, however, much larger than those of *L. capitata* and consequently there are only a few eggs in each mass. The egg capsule is oval in shape and measures $350\mu \times 550\mu$. The egg itself is spherical, yellow to orange in color and measures 200μ in diameter. There is always a granular and milky coloured albuminous material inside the capsule. It is likely that this is a dehydrated material which will be hydrated later to expand the egg capsule to give more room for locomotion to the developing embryo. This conclusion is supported by the observation that all albumen granules become liquefied at gastrula stage and in the meantime the egg capsule enlarges about 40% of its original size.

Table 3

RECORD OF EGG-LAYING BY 14 ANIMALS OF *Acteonia cocksi* WITHIN A MONTH

Date	Number of Egg Masses	Number of Eggs per Spawn Mass		Total Number of Eggs
		Range	Mean	
April				
12	1			19
14	3	10-20	15	46
15	3	17-26	21	63
16	4	7-23	17	68
17	1			10
22	1			2
23	5	6-17	9	45
26	2	5- 6	5	11
28	2	5-10	8	15
May				
3	3	4- 7	6	17
10	4	3- 6	4	17
12	2	4- 6	5	10
Total	31			323

Among all the spawn masses I have examined, there was always one egg per capsule. The egg laying records of 14 animals collected on April 8 are given in Table 3, which shows that these animals laid 31 spawn masses or 323 eggs within a month. In other words, each animal laid only an average of 2 spawn masses or 23 eggs. As in *Limapontia capitata,* the animals were getting smaller and smaller after one month in captivity, and all died in the second month.

Limapontia depressa:

The spawn mass of *Limapontia depressa* differs from that of *L. capitata* and *Acteonia cocksi* in several ways. First, the jelly mass appears to be lamellated, thinner, and more elastic. Secondly, the jelly mass tapered at one end (the end last out from the oviduct) into a fine point which bends into a hook. In most cases, the spawn mass lies parallel to the animal and since both are about the same colour, one often mistakenly interprets this as a mating pair. In the culture dish 2 or 3 spawn masses are often seen close by one animal, suggesting that one animal may lay more than one spawn mass within 24 hours. As in the other 2 species already described, there is again no clear preference as to where the egg mass is deposited; egg masses are found both above and underneath the algal layer as well as on the glassware or on the sand grains.

A large spawn mass, 2×5 mm in size, contains about 950 eggs and a small spawn mass of 0.5×1 mm in size contains only 73 eggs. The egg capsule, 120μ in diameter, contains in most cases only one egg, 80μ in diameter, but occasionally up to 4 eggs per capsule were found. Many egg capsules also contain granular albumen but this has apparently little nutritional value, as those eggs without albumen develop equally well.

Seventy animals collected on April 11, 1969 were placed in a small finger bowl on a layer of *Vaucheria.* The finger bowl was kept in high humidity but the animals were not immersed in water. The egg laying record of these animals within one month is summarized in Table 4. This table shows that the animals began to lay eggs 5 days after capture and within one month a total of 346 egg masses were deposited. Although I did not count the eggs in every spawn mass, it was estimated that the average number of eggs per spawn mass was about 450. This means that on the average each animal laid 5 spawn masses or 2250 eggs. This is more than double the number of eggs produced by each *Limapontia capitata.*

Table 4

RECORD OF EGG-LAYING BY 70 ANIMALS
OF *Limapontia depressa* WITHIN A MONTH

Date:	April								May			
	11	16	18	20	22	24	26	28	3	5	10	12
Number of Spawn Masses laid	0	2	9	34	59	70	50	34	35	20	23	0

EFFECT OF LIGHT ON OVIPOSITION

During my observations on the oviposition of *Limapontia capitata* and *Acteonia cocksi,* the culture dishes were examined twice a day, once at about 10 o'clock in the morning and once at about 5 o'clock in the afternoon. All the spawn masses, with a few exceptions, were collected in the morning. Since the detailed chronology of the early development is known, the precise time of egg laying can be estimated from the stages of development. In this way it is discovered that most of the spawn masses were laid in the morning between about 6 and 9 o'clock. This led me to suspect that the change of illumination, switching from dark to light, might be responsible for inducing the spawning, which is the case for many invertebrates (see Kume & Dan, 1968). To test this observation, animals of both species, collected on April 16, 1969, were studied experimentally by subjecting 15 animals of each species to 3 conditions: constant light, constant dark, and normal day light cycles as control. The light and dark experimental groups were again exposed to normal day light cycles after 3 days. The result shows that continuous light or dark tends to repress the spawning, but the spawning frequency did not increase after returning to normal conditions. Hence, the egg laying behaviour in these species may be associated with the change of illumination, but artificial induction of spawning by control of light was not successful.

LARVAL DEVELOPMENT

As noted earlier, the larval morphology of these species is already known. This section presents information only on the chronology of development which has not been established in detail previously.

The morphology of developmental stages of *Limapontia capitata* and *L. depressa* is almost identical under laboratory conditions. The major events of development are summarized in Table 5 and illustrated in the accompanying 2 Plates. It is noted that it takes 12 days for *L. capitata* and 10 days for *L. depressa* to reach the hatching larval stage at the temperature of 10 - 14° C. At room temperature (19 - 21° C) the time was shortened to 8 days for *L. capitata* and to 7 days for *L. depressa.*

In contrast to that of *Limapontia,* the development of *Acteonia cocksi* is direct and a planktotrophic larva is lacking; the major developmental events are summarized in Table 6 and illustrated in 2 additional Plates accompanying this paper.

It is interesting to record that after hatching, the juveniles of *Acteonia cocksi* do not crawl away from the jelly mass; instead, they remain inside and feed actively on the egg capsules as well as on the inner layer of jelly mass. Two to 3 days pass before they begin to feed on the algae. At no stage of development is a larval shell observed.

Plate Explanation

Development of *Limapontia capitata*

Figure *1*: One and 2-cell stages showing polar bodies (pl. b.)
Figure *2*: 4-cell stage
Figure *3*: 4-cell stage, showing the presence of albumen (a)
Figure *4*: 16-cell stage, showing micromeres (mi) and macromeres (ma)
Figure *5*: Gastrula with polar bodies (pl. b.) and open blastopore (bl. p.)
Figure *6*: Veliger larvae before hatching

Plate Explanation

Development of *Limapontia depressa*

Figure *7*: One-cell stage showing polar bodies (pl. b.)
Figure *8*: One- and 2-cell stages
Figure *9*: 4-cell stage
Figure *10*: 8-cell stage, showing micromeres (mi) and macromeres (ma)
Figure *11*: Blastula, flattened along A - V axis
Figure *12*: Gastrula with open blastopore (bl. p.)
Figure *13*: Young veligers
Figure *14*: Veliger just before hatching

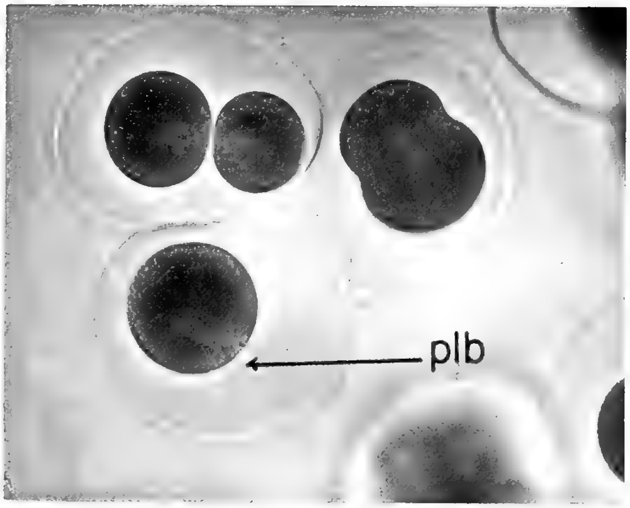


Figure *1*

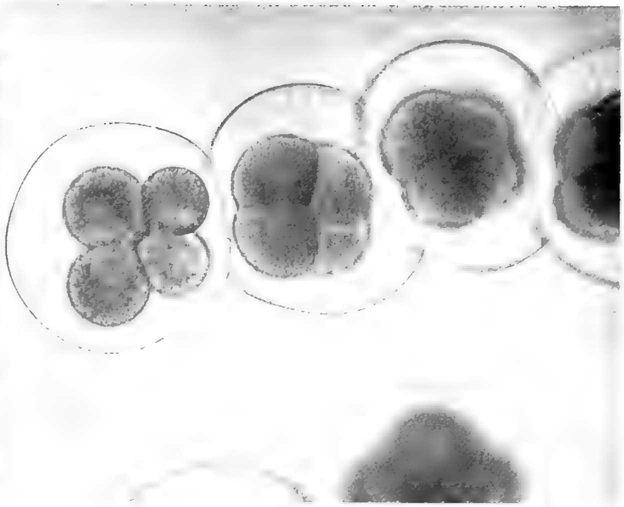


Figure *2*

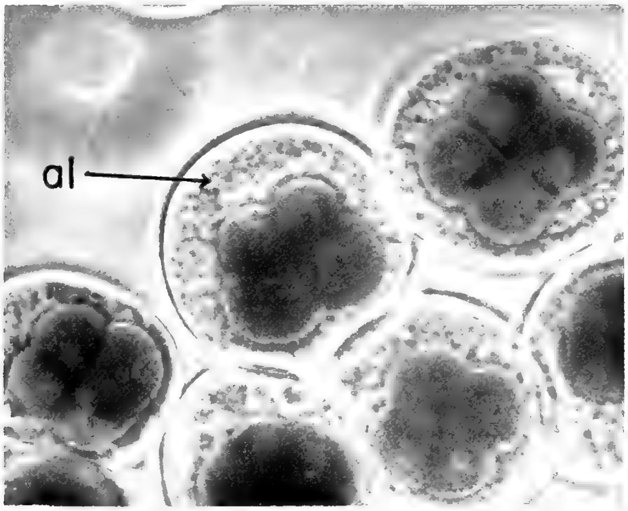


Figure *3*

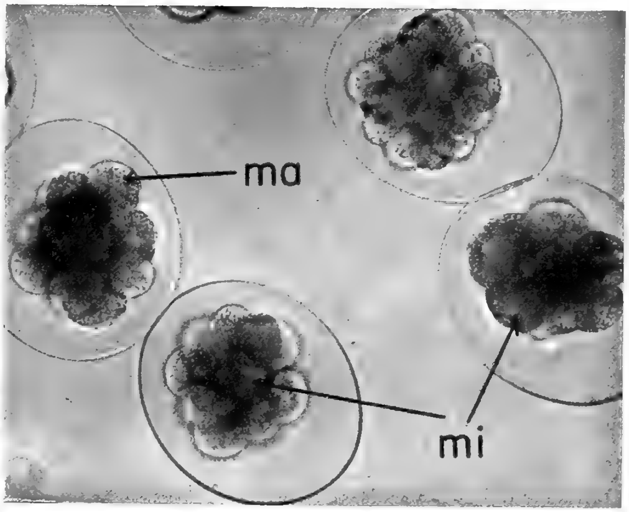
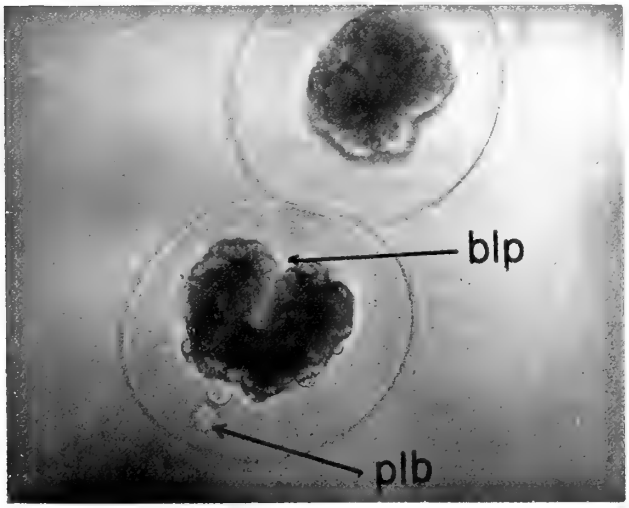


Figure *4*



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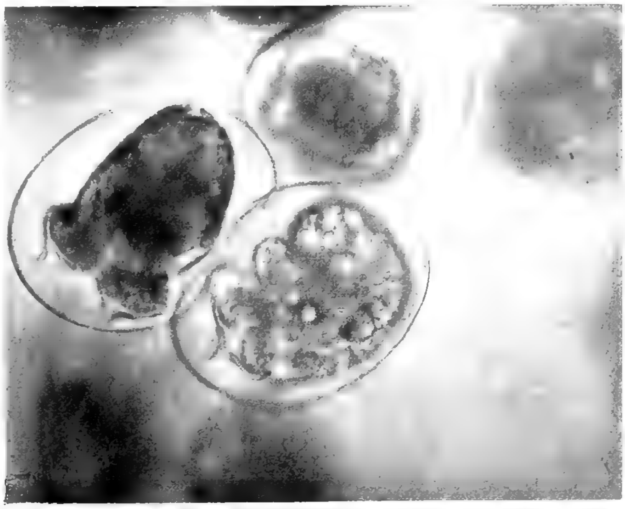

Figure *6*

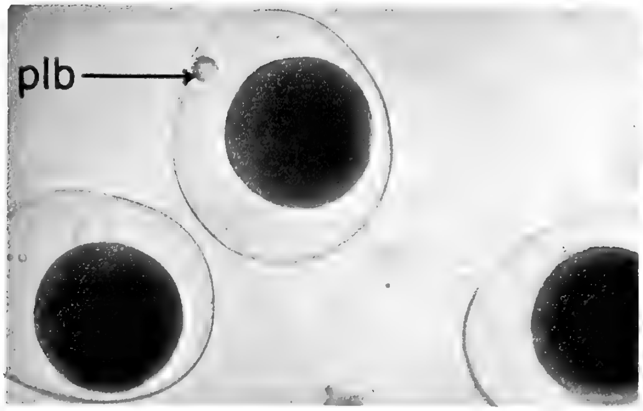

Figure 7

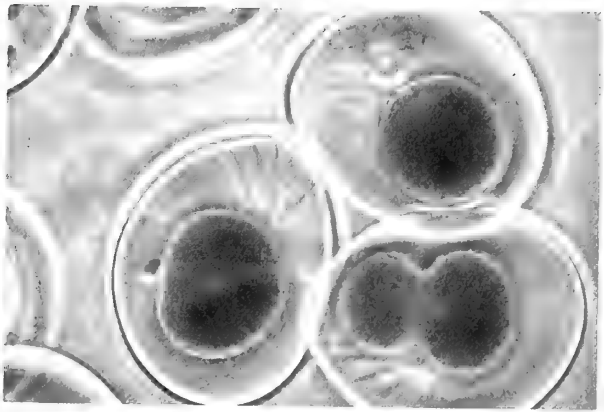

Figure 8

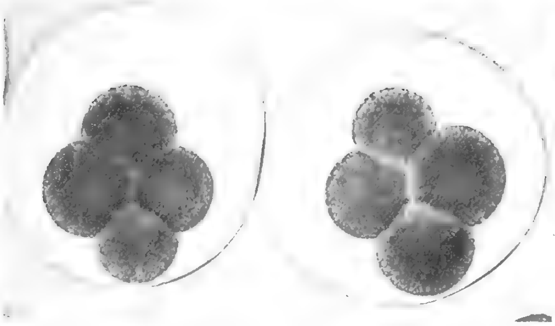

Figure 9

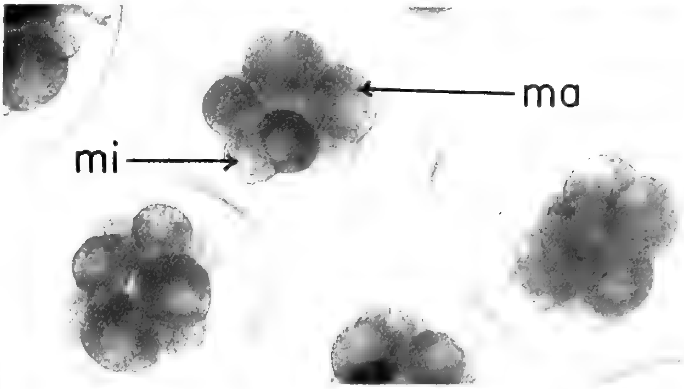

Figure 10

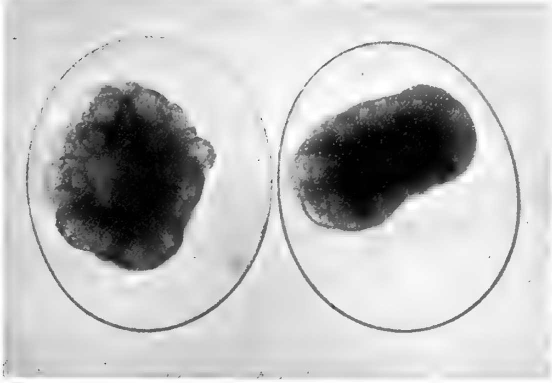

Figure 11

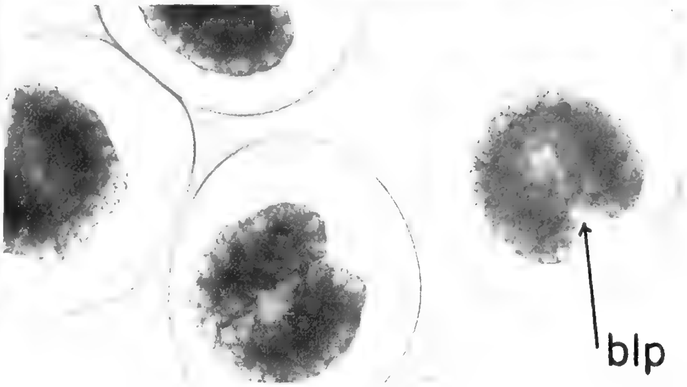

Figure 12

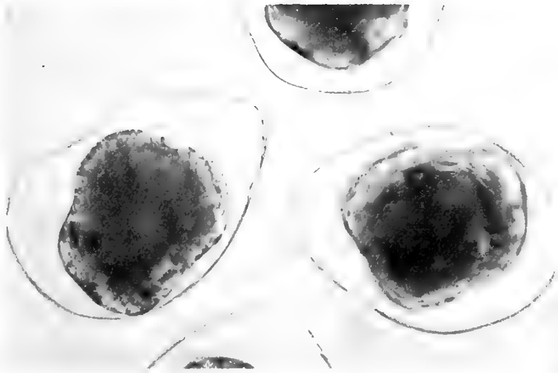

Figure 13

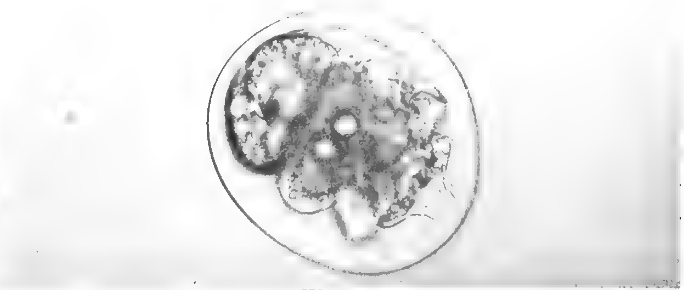

Figure 14

Table 5

CHRONOLOGY OF DEVELOPMENT OF *Limapontia capitata* AND *Limapontia depressa* AT THE TEMPERATURE OF 10 TO 14° C

Developmental Stages	Time *Limapontia capitata*	 *Limapontia depressa*
Freshly spawned eggs with intact germinal vesicle	0	0
Formation of first polar body	8 hours	6 hours
Formation of second polar body	10 hours	9 hours
Completion of first cleavage	18 hours	12 hours
Completion of second cleavage	25 hours	15 hours
Young blastula	2 days	2 days
Blastula	3 days	2 days
Gastrula with open blastopore	4 days	3 days
Young veliger with velum rudiments	5 days	4 days
Veliger, moving by rotating	6 days	4 days
Veliger with well developed shell and gut	7 days	5 days
Veliger with well developed ciliated foot and operculum; moving by rocking back and forth	8 days	6 days
Veliger with retractable velum	9 days	7 days
Hatching; hatched veliger 120 μ long	11 days	8 days
Hatching completed from one egg mass	12 days	10 days

Table 6

CHRONOLOGY OF DEVELOPMENT OF *Acteonia cocksi* AT THE TEMPERATURE OF 10 TO 14° C

Time	Developmental Events
0 hours	Freshly spawned eggs with intact germinal vesicle
10 hours	Formation of first polar body
15 hours	Formation of second polar body
19 hours	Completion of first cleavage
24 hours	Completion of second cleavage
3 days	Morula, blastula
3 days	Blastula flattened along animal-vegetal (A-V) axis
4 days	Gastrula with open blastopore
5 days	Gastrula, blastopore moves
	Ventral side, albumen begins to liquidate
6 days	Blastopore closed
8 days	Young veliger with velum rudiments
9 days	Young veliger with velum rudiments, rotate by cili-
12 days	Appearance of statocyst
	ary movement
15 days	Velum more pronounced, appearance of eye spot
17 days	Velum reduced in size; appearance of black pigment on the ventral body surface; metamorphosis begins
20 days	Appearance of black pigment on dorsal body surface; Velum absorbed, foot well developed, muscular movement evident, visceral mass still yolky
22 days	Young slugs inside the egg capsule, changing shape by muscular movement
24 days	Hatching from the egg capsule
25 days	Hatching from egg capsule completed in same spawn mass; 1 mm in length of the newly hatched slug

LARVAL HATCHING IN *Limapontia depressa*

The salt marshes at Alnmouth, where *Limapontia depressa* was collected, is covered by water only during the spring tide. Laboratory observations show that embryos develop normally whether they are in moist air or water. However, the fully developed veligers do not hatch when the culture is in moist air only. For example, the larvae would hatch on the 10th day when they were cultured in either full-strength or half-strength sea water at the temperature of 10 - 14° C, but they would not hatch even after 21 days when cultured in moist air. If, on the other hand, when the larvae are cultured in moist air for more than 11 days and then transferred to water they would hatch within 12 hours. This means immersion in water is essential for hatching.

DISCUSSION

Although the egg production recorded in this paper was obtained in the laboratory, it is unlikely to differ much from that in the natural habitat. In all cases, the animals were collected at the beginning of April, which is the beginning of the spring breeding season. Prior to that date, no spawn masses were found in the natural habitat. Thus, it is improbable that some of them had already produced spawn masses before being brought to the laboratory. It was observed that after one month of egg laying in the laboratory the feeding activity of the animals was greatly reduced or stopped, and, as a consequence, they shrank in size and soon died. Thus, the spawning period of any individual does not likely last over one month.

According to GASCOIGNE (1956) the breeding season of *Limapontia capitata* and *Acteonia cocksi* at Cullercoats is also in April. However, MILLER (1962) reported that *L. capitata* and *A. cocksi* begin to lay eggs in February at Port Erin and suspected that they may reproduce throughout the year with a maximum reproduction in April to June. THORSON (1946) recorded veligers of *L. capitata* throughout the year in Danish waters.

The total egg production per individual during the breeding season [913 for *Limapontia capitata,* 23 for *Acteonia cocksi,* and 2250 for *L. depressa*] seems low, but considering the size of the animal the number may not be as low as one first thought. In a related species, *Alderia modesta* (LOVÉN, 1844), according to SEELEMANN (1967), one animal can produce 1000 eggs per day through the warm season. This is indeed a very high fecundity considering that *Alderia modesta* is about the same size as the three sacoglossans discussed in this paper.

The fact that *Acteonia cocksi* and *Limapontia capitata* are two closely related species which live in similar habitats, but at the same time have contrasting modes of development, is indeed intriguing. *Limapontia capitata,* undergoing indirect development, produces about 30 times more eggs than *A. cocksi* which undergoes direct development. The egg of *A. cocksi* is, however, about 2.7 times greater in diameter than that of *L. capitata.* If we calculate the fecundity in terms of total egg protoplasm produced by each species, this value for *L. capitata* is

$$\frac{4\pi\times0.041^3}{3}\times913 = 0.2637\text{ ml}$$

whereas for *A. cocksi* the total egg protoplasm is

$$\frac{4\pi\times0.100^3}{3}\times23 = 0.09638\text{ ml}$$

That means that *L. capitata* produces about 2.7 times more egg protoplasm than does *A. cocksi.* If the two types of development are equally successful, then it follows that the indirect development is more expensive. There are flaws, of course, in this analysis. First, we are comparing two species (although they are closely related), and, secondly, we do not know the organic contents in terms of energy storage of these two types of eggs. It nevertheless presents itself as a hypothesis capable of being tested.

Limapontia depressa, because of its habitats which are flooded only during spring tides, and because of its indirect development, faces a serious problem of dispersal. It was noted that the veligers of *L. depressa* will not hatch unless covered with water; this is certainly a necessary adaptation. This is not true, however, for *Alderia modesta,* because, according to SEELEMANN (1967) "the larvae will hatch regardless of the water level. Thus a considerable number die because they do not reach the water."

It should be pointed out that the small size and the great tolerance of temperature and salinity variations of these species make them ideal material for laboratory studies, particularly at places where there is no adequate sea water system. All of them would lay eggs under seemingly very unfavourable conditions and the spawn masses be easily examined under a microscope. Interesting features such as spiral cleavage, gastrulation, typical veliger larvae of *Limapontia* and modified veligers of *Acteonia* can be demonstrated to students in embryology classes. In the case of *A. cocksi,* because they undergo direct development, I see no difficulty in rearing them through generations, thus establishing laboratory clones.

SUMMARY

1. The total number of eggs produced by each animal within one month (April to May) in the laboratory is 913 for *Limapontia capitata,* 23 for *Acteonia cocksi,*

Plate Explanation

Development of *Acteonia cocksi*

Figure *15*: One-cell stage, showing the region where polar bodies (pl. b.) are formed. Note the abundance of albumen
Figure *16*: 2-cell stage
Figure *17*: 4-cell stage
Figure *18*: 16-cell stage
Figure *19*: Gastrula with open blastopore (bl. p.). Note the albumen is liquefied and egg capsule expanded
Figure *20*: Ventral view of the modified lecithotrophic veliger with velum (v)

Plate Explanation

Development of *Acteonia cocksi*

Figure *21*: Lateral view of a veliger
Figure *22*: Juvenile *Acteonia cocksi,* just after hatching
Figure *23*: Veliger stage showing the eye (e) and statocyst (s). The larva was slightly pressed under a cover slip
Figure *24*: Higher magnification of the eye showing the pigment (p) and lens (l). The larva was squashed under a cover slip

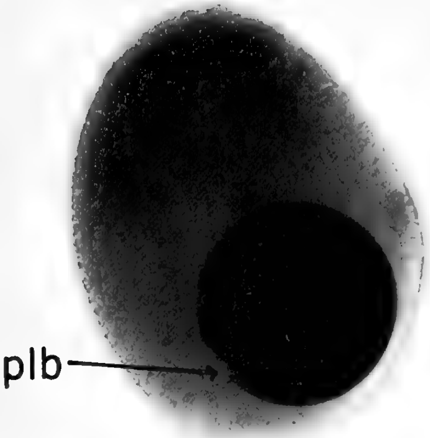

Figure 15

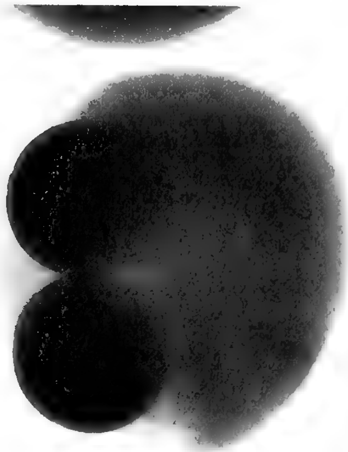

Figure 16

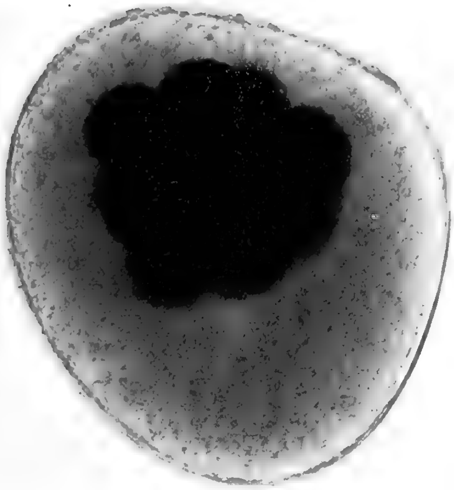

Figure 17

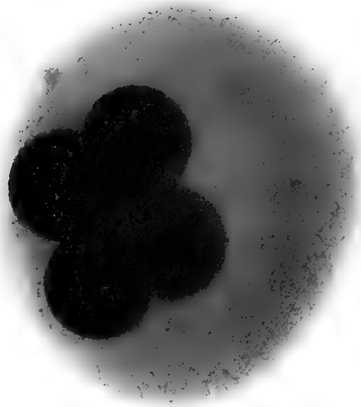

Figure 18

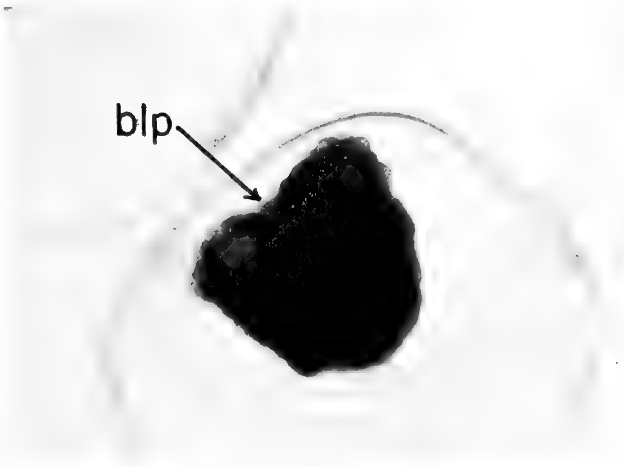

Figure 19

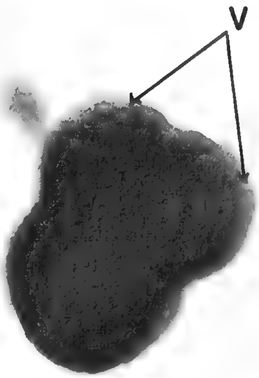

Figure 20

Figure 21

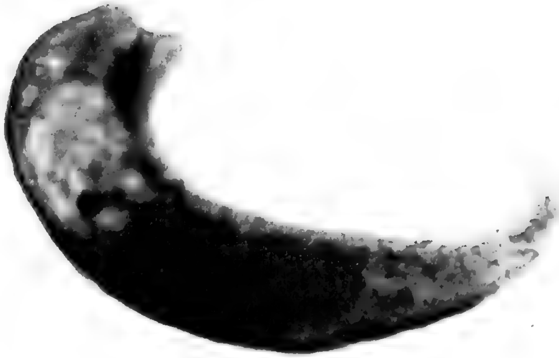

Figure 22

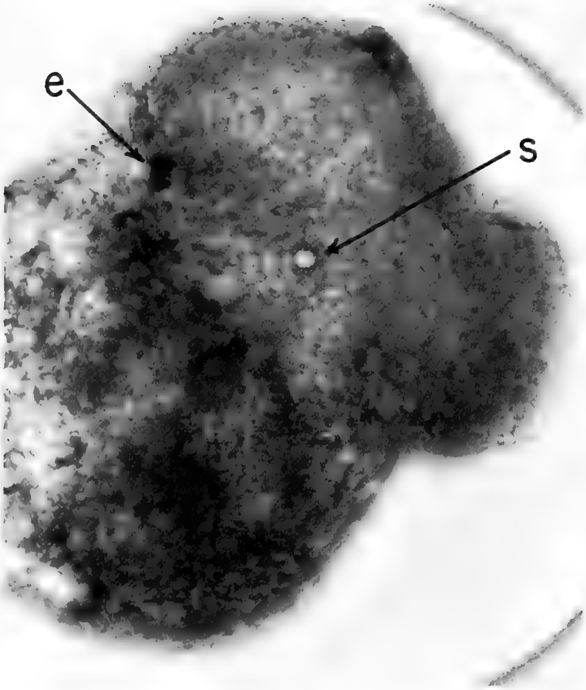

Figure 23

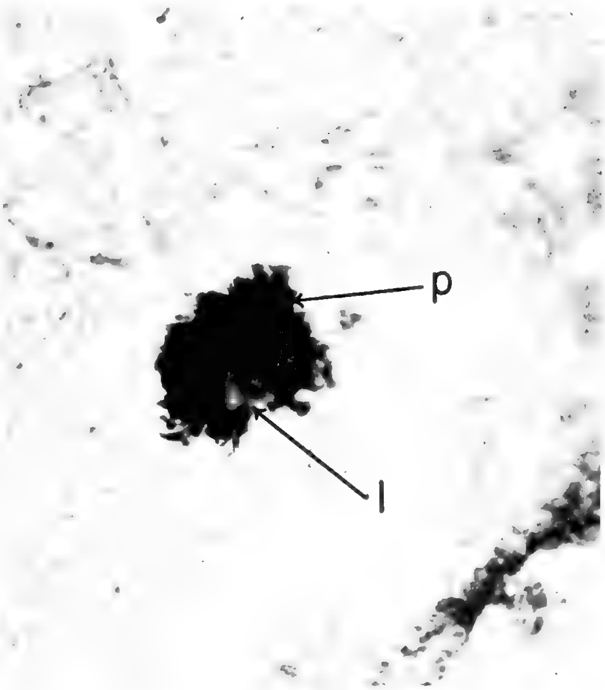

Figure 24

and 2250 for *Limapontia depressa.*

2. The development from egg laying to hatching of the veliger takes 12 days for *Limapontia capitata* and 10 days for *L. depressa* at the temperature of 10 - 14° C. At room temperature (19 - 21° C) the development to hatching shortens to 8 days for *L. capitata* and 7 days for *L. depressa.*
3. The development of *Acteonia cocksi* is direct, in which the modified veliger larvae are lecithotrophic and hatch from the egg capsule as juvenile adults. It takes 23 days to hatching at the temperature of 10 - 14° C.
4. Tables of chronological events of all three species are presented.
5. The effect of light on oviposition in *Limapontia capitata* and *Acteonia cocksi* and the delaying of hatching in *L. depressa* when cultured in moist air were studied experimentally and discussed.

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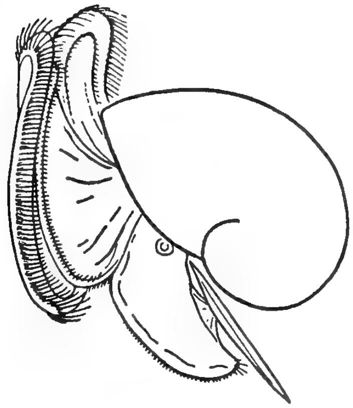


Description of *Pleurobranchus semperi* (Vayssière, 1896) from Osaka Bay, Middle Japan

(Gastropoda : Notaspidea)

BY

KIKUTARÔ BABA

Osaka Kyoiku University, Tennoji, Osaka, Japan

AND

IWAO HAMATANI

Tennoji Senior High School attached to Osaka Kyoiku University, Tennoji, Osaka, Japan

(1 Text figure)

In August 1957 we were fortunate enough to collect and observe two live specimens of an enormously sized pleurobranchid from the bed of *Zostera marina* in the shallow water of Tannowa fishery harbour, Osaka Bay, Japan. They were each provided dorsally with prominent polygons consisting of compounded tubercles, and owing to this unusual configuration of the back, a specific name *Pleurobranchus semperi* (Vayssière, 1896) was proposed by the senior author (Baba, 1969, p. 191) to be applicable to them. Both *Oscaniella lugubris* Bergh, 1905 (this species appeared in Usuki, 1969, p. 5 under the generic name of *Pleurobranchus*) and *Susania karachiensis* White, 1946 are regarded here as junior synonyms of *P. semperi.* The aim of the present paper is to make comments on the various characters of our specimens so far as they are useful in supporting the above identification as correct.

The three principal genera that appeared in the taxonomic history of the family Pleurobranchidae (subfamily Pleurobranchinae in the sense of Burn, 1962) are shown briefly as follows (cf. Burn, *op. cit.*, p. 131):

1. *Pleurobranchus* Cuvier, 1804
   = *Oscaniella* Bergh, 1897
   Type: *Pleurobranchus peroni* Cuvier, 1804
   Shell very small, situated in the anterior part of the mantle (see Pilsbry, 1896, plt. 74, figs. 88, 89)
2. *Oscanius* Leach, 1847
   Type: *Pleurobranchus tuberculatus* Meckel, 1808
   Shell very large, occupying the greater part of the length of the mantle (see Pilsbry, 1896, p. 214)
3. *Susania* Gray, 1857
   Type: *Pleurobranchus testudinarius* Cantraine, 1835
   Shell very small (see Pilsbry, 1896, p. 213), and posterior in position (see Marcus & Marcus, 1962, p. 468)

The interrelationship between these three genera is rather puzzling (cf. Burn, *op. cit.*, p. 131), and the value of the formation of a tiny shell in the taxonomy of the Pleurobranchidae is questioned by Macnae (1962, p. 169). It is the genus *Pleurobranchus* of Thompson (1970, p.

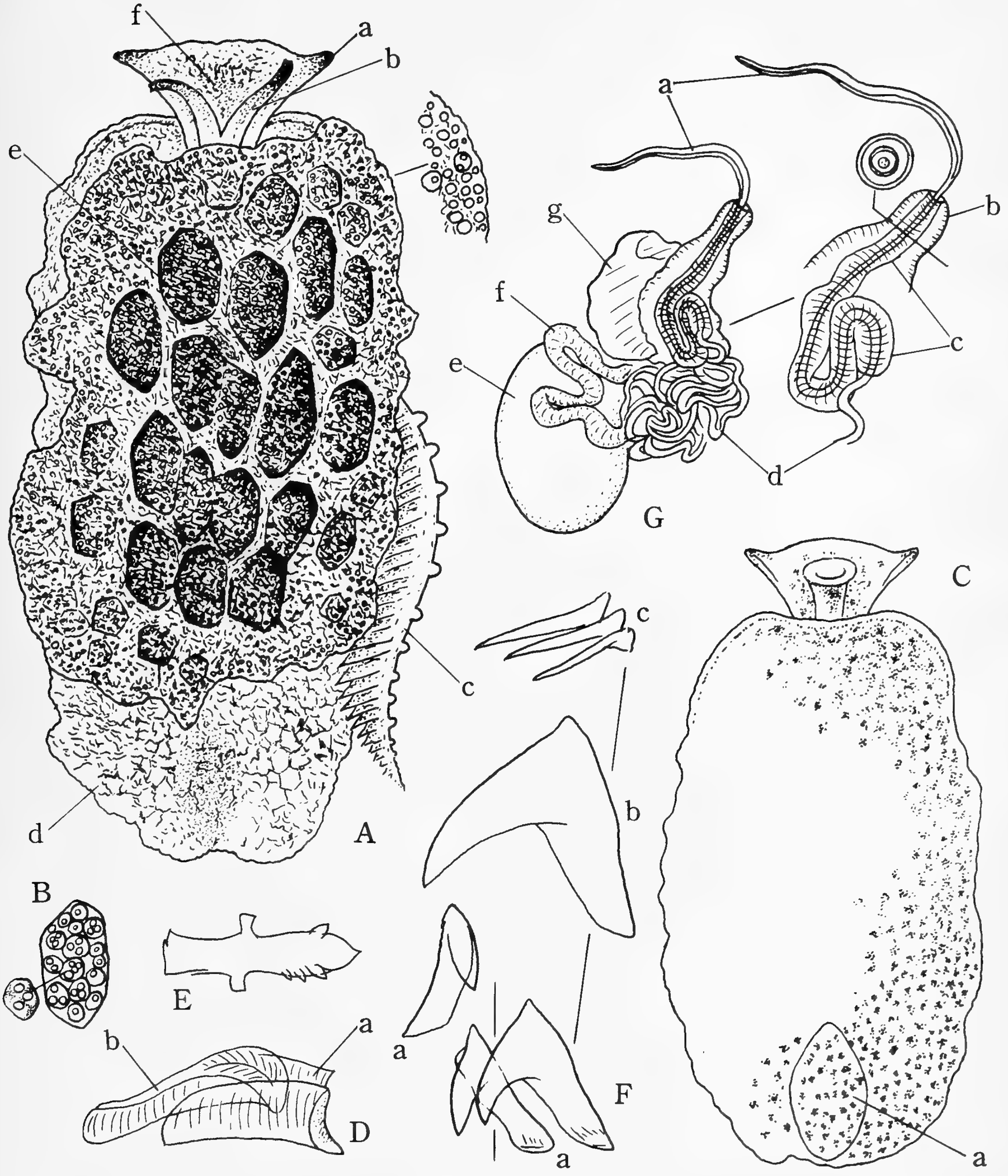
Figure 1

(on facing page ⟶)

Pleurobranchus semperi (Vayssière, 1896)

(Specimen no. 1)

A: Animal from above; length 10 cm
a – cephalic tentacle b – rhinophore c – gill d – tail
e – location of internal shell f – cephalic veil
B: Compounded polygon of mantle
C: Animal from below
a – pedal gland
D: Paired jaw-plates (a) and a radular ribbon (b)
E: Element of jaw-plate (× 100)
F: Right half-row of radula (× 260)
a – innermost laterals b – 100th lateral c – outermost laterals
G: Part of genitalia
a – penis proper b – outer penial sac c – inner penial sac
d – muscular part of vas deferens e – prostatic gland mass
f – prostatic part of vas deferens
g – membranous flap attached to protruded penial sac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179) that covers all of the species of *Pleurobranchus* (s. s.), *Oscanius* and *Susania* extensively.

Pleurobranchus semperi (Vayssière, 1896)

(Japanese name: Zenigata-fushiera-gai)

Oscanius semperi Vayssière, 1896, pp. 134-135; plt. 4, fig. 1 – Philippines
Pleurobranchus semperi, Baba, 1969, p. 191 (list only) – Japan
Oscanius sp. Bergh, 1905, plt. 2, fig. 2 (figure only)
Oscaniella lugubris Bergh, 1905, pp. 60-61; plt. 11, figs. 18-22 – 'Saleh-Bai'
Pleurobranchus cf. *lugubris*, Marcus, 1965, p. 271 (list only) – Palau Island; Usuki, 1969, p. 5; plt. 1, fig. 9 (list only) – Sado Island
Susania karachiensis White, 1946, pp. 55-56; figs. 7-10 – Karachi

Material: Specimen no. 1: Tannowa, Osaka Bay, 27 August 1957
Specimen no. 2: Tannowa, Osaka Bay, 28 August 1957

Total length of body, extended, 10 cm. Mantle sinuated behind rhinophores. Decalcified shell about 16 mm long is found in front of the middle of the mantle length in the preserved animal (see also Bergh, 1905, p. 60). The median part of the back is occupied by larger or smaller polygonal elevations which are each composed of closely set tubercles partly fused together (see also Vayssière, 1896, plate 4, figure 1; Bergh, 1905, plate 2, figure 2; Bergh, 1905, p. 60). Minute tubercles are also scattered around the margin of the mantle. Gill rachis provided with a double row of knobs. A membranous flap is present on the anterior margin of the protruded penial sac. Anus opens at the posterior end of the gill membrane. A large pedal gland is on the sole near the posterior end.

The general ground colour of the body is yellowish brown; the dorsal polygons, themselves being coloured chocolate brown, are mostly accentuated around the periphery by a narrow line of blackish brown respectively. Moreover, there are fine reticulations of blackish brown scattered everywhere on the upper surface of the mantle, including that of the polygons (see also Vayssière, 1896, p. 134 and plt. 4, fig. 1; Bergh, 1905, plt. 2, fig. 2). The dorsal polygons may sometimes be bounded by an additional line of opaque white. The corners of the cephalic veil and the distal end of the rhinophores are chocolate brown; gill yellowish brown; foot above boldly reticulated with blackish brown; tail above intensively coloured dark brown in the median line; sole covered by dark brown mottles. The whole animal after preservation assumes a dirty blackish brown hue as stated by Bergh (1905, p. 60).

The jaw elements are ensate, with usually 1 - 2 (rarely 3) denticles on either side. Radular formula 75×100-120·0·100-120. All the lateral teeth are simply hamate. The penial sac consists of double walls (or it may be said that there is an inner penial sac protected by an outer one). The penis proper is flagelliform, having a narrow groove over its length. It is unarmed. The male duct forms a prostatic gland mass and a prostatic vas deferens. There are a spermatheca and a spermatocyst which latter is seemingly bilobed (?) in constitution (see also Marcus & Marcus, 1970, p. 158).

Additional data: Additional localities in Japan of the species are: Sagami Bay (The Biological Laboratory, Imperial Household, collector), Sado Islands (Drs. Yoshiharu Honma and Itaru Usuki, collectors) and Toyama Bay (Mr. Takeo Abe, collector).

SUMMARY

1. *Oscanius semperi* Vayssière, 1896 is recorded from Japan. It is described anatomically under the comprehensive generic name *Pleurobranchus* Cuvier, 1804.
2. The species *Pleurobranchus semperi* is especially characterized by the possession dorsally of mostly large-sized and compounded polygons which are well defined from each other. Based on this peculiar configuration of the mantle surface the species *Oscaniella lugubris* Bergh, 1905 and *Susania karachiensis* White, 1946 are regarded as synonyms of *P. semperi.*
3. *Pleurobranchus semperi* (Vayssière, 1896) is found thus to be distributed widely in the Indo-Pacific. In Japan it comes from Sagami Bay, Osaka Bay, Sado Islands, and Toyama Bay.

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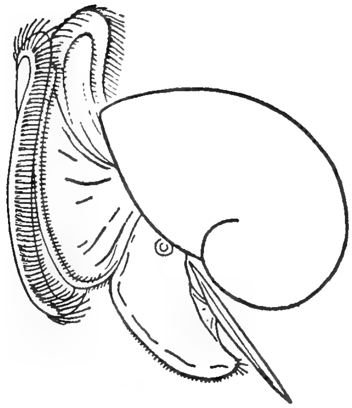

Dimyidae in Japan and Its Adjacent Areas

BY

TADASHIGE HABE

National Science Museum, Tokyo, Japan

(1 Plate; 2 Text figures)

THE DIMYIDAE CONSTITUTE a small family in the bivalves, including only one genus and several existing species, of which two have been reported from Japan, namely, *Dimya radiata* KURODA, 1928 with *D. radiata takii* KURODA, 1928 and *D. lima* BARTSCH, 1913. Recently through the courtesy of Dr. H. A. Rehder of the U. S. National Museum, the writer has received the paratype specimens of two Philippine *Dimya*, *D. filipina* and *D. lima,* both described by BARTSCH in 1913, to be compared with the Japanese forms. After critical observations the writer concludes that *D. radiata* and *D. radiata takii* are synonyms of *D. filipina* BARTSCH and *D. lima* reported by him is a new species, named ***D. japonica*** herewith and closely allied to *D. molokaia* DALL, BARTSCH & REHDER, 1938.

The writer wishes to extend sincere thanks to Dr. H. A. Rehder for his warmhearted cooperation.

Dimya ROUALT, 1848

1848 *Dimya* ROUALT, Mem. Soc. Geol. France (2) 3: 470
(Type species: *Dimya deshayesiana* ROUALT, by M)
1936 *Dimyarina* IREDALE, Rec. Austr. Mus. 19: 269
(Type species: *Dimya corrugata* HEDLEY, by OD)

The shell is small, usually ovate to subquadrate in shape, but varies in shape because of the sessile life, pearly white, in some species with brown radial rays and inequivalved. The right valve attaches to the substrata and is larger and deeper than the slightly convex free left valve, and tightly embraces it. The hinge has two crenulated ridges and a small socket between them, in which the internal ligament is situated. The interior is also pearly and has two muscle scars, the anterior being narrowly elongate and the posterior roundly ovate, connecting with a simple pallial line.

Three Japanese and Philippine species are distinguished by the following key:

Shell attached to the substrate by the broad surface of the right valve, with brown radial rays on the left valve .... *Dimya filipina* BARTSCH, 1913
Shell attached to the substrate by the broad surface of the right valve, without brown radial rays on the left valve .... *Dimya lima* BARTSCH, 1913
Shell attached to the substrate by the umbonal portion of the right valve, without brown radial rays on the left valve .... ***Dimya japonica*** HABE, spec. nov.

Dimya filipina BARTSCH

(Figures 1, 2; Plate Figures *5-8*)

1913 *Dimya filipina* BARTSCH, Proc. U. S. Nat. Mus. 45: 305; plt. 28, figs. 1 - 4
1928 *Dimya radiata* KURODA, Venus 1: 14; plt. 1, fig. 11
1932 *Dimya radiata takii* KURODA, Venus 3, App.: 111; plt, 53, fig. 1
1961 *Dimya radiata,* HABE, Col. Illust. Shells Japan 2:: 117; plt. 53, fig. 1
1964 *Dimya radiata,* HABE, Shells West. Pacif. Col. 2: 173; plt. 53, fig. 1
1965 *Dimya radiata,* HABE, Encycl. Fauna Jap. 2: 236, no. 884

The valves are rather thick, variable in shape depending on the nature of the substrate to which the shell adheres,

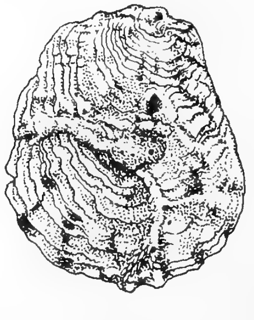

Figure 1

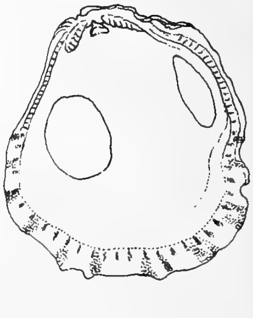

Figure 2

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[1] Supported by a grant from the Kaiseikai Science Foundation

but are usually rounded ovate in shape. The upper, left valve is smaller than the lower, right valve, convex and thick, silvery white with brown radial rays of various size and usually marking the coarse lamellated growth lines. The right valve is rather deeply concave, made so by the raised marginal area.

Holotype: Height 11.0 mm, length 12.0 mm, and breadth 5.0 mm (right valve); height 9.0 mm, length 10.0 mm and breadth 1.0 mm (left valve).

Paratype: Specimen donated by the U. S. National Museum (USNM 246281) and preserved in the National Science Museum, no. NSMT-Mo 37294): Height 10.7 mm, length 10.5 mm and breadth 3.2 mm (right valve) (Plate Figures *7, 8*).

Height 8.5 mm, length 8.5 mm, breadth 2.1 mm (right valve of paratype specimen) (Plate Figures *5, 6*).

Height 13.8 mm, length 16.2 mm, and breadth 4.1 mm (right valve, collected from Kii Channel between Honshu and Shikoku).

Height 18.0 mm, length 15.0 mm, breadth 6 mm (right valve collected from Tomioka, Amakusa, Kyushu).

Height 15.0 mm, length 18.5 mm (right valve of type specimen of *Dimya radiata* KURODA, attached to *Amusium japonicum*).

Height 21.0 mm, length 22.5 mm (right valve of type specimen of *Dimya radiata takii* KURODA, attached to *Malleus albus*).

Type locality: Off Anima Sola Island, the Philippines (Lat. 13°20′ N; Long. 123°14′15″ E; about 192 m deep).

Distribution: Philippines (type locality only) and Japan (Amakusa, Kyushu; Kii Channel and Sagami Bay, Honshu; 20 - 60 m deep).

Remarks: *Dimya radiata* is merely a smooth form of this species attaching to the smooth surface of the saucer scallop, *Amusium japonicum* (GMELIN, 1791). *Dimya radiata takii* agrees quite well with the paratype specimens of this species preserved in the National Science Museum of Tokyo.

Dimya lima BARTSCH

(Plate Figures *3, 4*)

1913 *Dimya lima* BARTSCH, Proc. U. S. Nat. Mus. 45: 306; plts. 27, 28, figs. 5, 6

The valves are thin, roundly ovate in shape and narrowly erect at the ventral margin, showing a dished appearance, pearly white. The upper, left valve is nearly flat and possesses weakly marked growth lines; there are many narrow distinct riblets on its surface uniting the surface sculpture of the file shell, *Acesta bartschi* THIELE, 1920 (= *Acesta smithi* BARTSCH, 1913, *non* SOWERBY, 1888) to which the lower, right valve broadly adheres. The lower, right valve is also flat and very thin at the place of attachment.

Height 13.5 mm, length 15.5 mm (type specimen attached to *Acesta bartschi* THIELE).

Height 17.8 mm, length 18.9 mm, breadth 3.0 mm (conjoined valves of paratype specimen donated by the U. S. National Museum, USNM 256978 and preserved in the National Science Museum, no. NSMT-Mo 37295) (Plate Figure *3*).

Height 17.3 mm, length 16.4 mm, breadth 2.7 mm (conjoined valves of paratype specimen collected from off Point Origon, Philippines) (Plate Figure *4*).

Type Locality: Off Balicasag Island, the Philippines (Lat. 9°27′15″ N; Long. 123°31′48″ E, about 790 m deep).

Distribution: Indonesia (Lat. 5°26′06″ S; Long. 132°32′05″ E; 397 m deep) and Philippines (about 152 - 790 m deep).

Dimya japonica HABE, spec. nov.

(Plate Figures *9 - 19*)

1951 *Dimya* sp. HABE, Gen. Jap. Shells 1: 68; figs. 130, 131
1958 *Dimya lima*, HABE, Jap. Journ. Malac. (Venus) 19: 178, 182; figs. 7, 8 (non BARTSCH, 1913)
1958 *Dimya lima*, HABE, Publ. Seto Mar. Biol. Lab. 6: 262; plt. 11, fig. 21
1961 *Dimya lima*, HABE, Col. Illust. Shells Jap. 2: 117; plt. 53, fig. 2
1964 *Dimya lima*, HABE, Shells West. Pacif. Col. 2: 173; plt. 53, fig. 2
1965 *Dimya lima*, HABE, Encycl. Fauna Jap. 2: 25, 236

The valves are thin but rather solid, pearly white without any colored rays, usually obliquely subquadrate in shape with the dorsal margin straight. The upper, left valve is somewhat convex at the umbonal portion and reflexed and radially wrinkled at the marginal area; the lamellated growth lines are distinctly marked. The lower valve, attached to the substrate by the umbonal portion, is deeply concave, tightly embracing the upper, left valve, and sculptured with the radial wrinkles. The interior of the left valve is smooth and highly polished, pearly white and slightly crenulated at the margin by the radial wrinkles on the outer surface. The anterior muscle scar is narrow and elongate and the posterior is roundly ovate, and the pallial line is situated distant from the margin.

The right valve is also distinctly crenulated at the marginal portion. The hinge has two very weak ridges and a socket between them.

Height 11.4 mm, length 11.9 mm, breadth 2.1 mm (left valve of type specimen preserved in the National Science Museum, NSMT-Mo 37296) (Plate Figures *14, 15*).

Height 13.5 mm, length 13.0 mm, breadth 5.3 mm (right valve of paratype specimen preserved in the National Science Museum, NSMT-Mo 38622) (Plate Figure *10*).

Height 12.5 mm, length 11.8 mm, breadth 4.4 mm (right valve of paratype specimen preserved in the National Science Museum, NSMT-Mo 38622) (Plate Figure *11*).

Type Locality: Tomioka, Amakusa, Kumamoto Pref., Kyushu.

Distribution: Kyushu, Shikoku and Honshu (north to Boso Peninsula on the Pacific coast and Oga Peninsula, Akita Pref., on the Japan Sea coast), 20 - 600 m deep.

Remarks: This new species, attached to the shells of various species, is very common even in the shallow waters in Japan. This is easily recognized by the subquadrate shell with the distinctly straightened dorsal margin and with the rather small umbonal portion for attachment on its right valve. According to Dr. H. A. Rehder (personal communication), this new species has a larger and thinner shell with the more cup-shaped attached right valve than *Dimya molokaia* Dall, Bartsch & Rehder, 1938. Moreover, the former has the more elongate and narrower anterior adductor muscle scar.

Finally, the Recent species of the genus *Dimya* are listed as follows:

Dimya argentata Dall, 1886. Loc. West Indies
Dimya californiana Berry, 1936. Loc. Gulf of California
Dimya corrugata Hedley, 1902. Loc. South-Eastern Australia
Dimya coralliotis Berry, 1944. Loc. California
Dimya filipina Bartsch, 1913. Loc. Philippines and Japan
Dimya japonica Habe, 1971 Loc. Japan
Dimya lima Bartsch, 1913. Loc. Indonesia and Philippines
Dimya lima Habe (non Bartsch), 1958. Loc. Japan.
This is *Dimya japonica* Habe described herewith.
Dimya mimula Dall, Bartsch & Rehder, 1938. Loc. Hawaii
Dimya molokaia Dall, Bartsch & Rehder, 1938. Loc. Hawaii
Dimya radiata Kuroda, 1928. Loc. Japan
This is a synonym of *Dimya filipina* Bartsch
Dimya radiata takii Kuroda, 1932. Loc. Japan
This is a smooth form of *Dimya filipina* Bartsch

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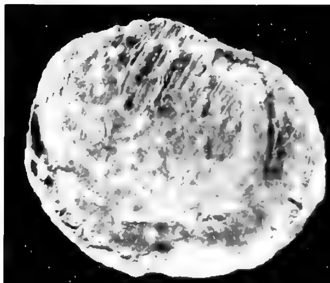
Plate Explanation

Figure *3*: Paratype specimen (conjoined valves) of *Dimya lima* Bartsch (height 17.8 mm; length 18.9 mm; breadth 3.0 mm)
Figure *4*: Paratype specimen (left valve) of the same species (height 17.3 mm; length 16.4 mm; breadth 2.7 mm)
Figures *5, 6*: Paratype specimen (right valve) of *Dimya filipina* Bartsch (height 8.5 mm; length 8.5 mm; breadth 2.1 mm)
Figures *7, 8*: Paratype specimen (right valve) of the same species (height 10.7 mm; length 10.5 mm; breadth 3.2 mm)
Figure *9*: Paratype specimen (right valve) of *Dimya japonica* spec. nov. (height 12.5 mm; length 11.5 mm; breadth 4.0 mm)
Figure *10*: Paratype specimen (right valve) of the same species (height 13.5 mm; length 13.0 mm; breadth 5.3 mm)
Figure *11*: Paratype specimen (right valve) of the same species (height 12.5 mm; length 11.8 mm; breadth 4.4 mm)
Figure *12*: Paratype specimen (right valve) of the same species (height 12.0 mm; length 12.4 mm; breadth 4.7 mm)
Figure *13*: Paratype specimen (right valve) of the same species (height 14.5 mm; length 14.2 mm; breadth 4.3 mm)
Figures *14, 15*: Type specimen (left valve) of the same species (height 11.4 mm; length 11.9 mm; breadth 2.1 mm)
Figures *16, 17*: Paratype specimens (left valve) of the same species (height 12.2 mm; length 11.4 mm; breadth 2.0 mm)
Figures *18, 19*: Paratype specimen (left valve) of the same species (height 11.8 mm; length 11.8 mm; breadth 2.1 mm)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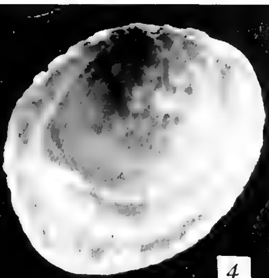
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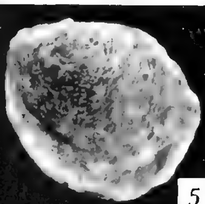
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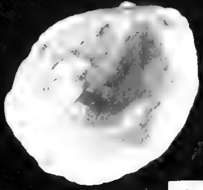
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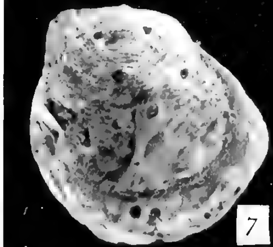
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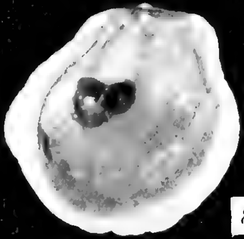
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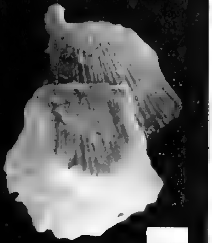
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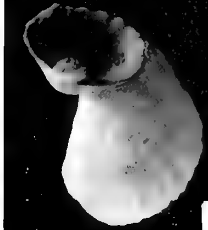
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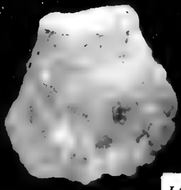
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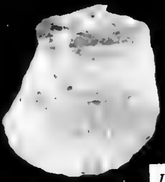
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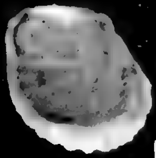
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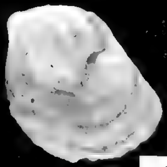
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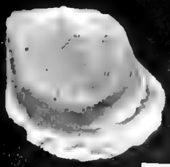
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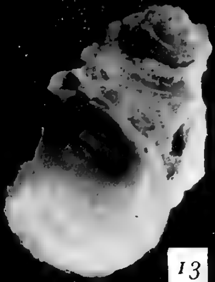
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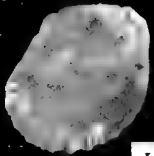
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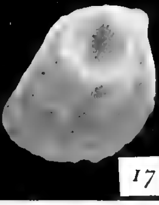
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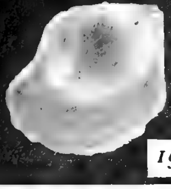
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Tritoniidae from the North American Pacific Coast

(Mollusca : Opisthobranchia)

BY

T. E. THOMPSON

Zoology Department, University of Bristol, U. K.

(3 Text figures)

INTRODUCTION

TRITONIID NUDIBRANCHS are common in the shallow coastal waters of the western United States and Canada. They have been employed with notable success in experiments on the functioning of the central nervous system by American neurophysiologists (WILLOWS & HOYLE, 1967; WILLOWS, 1968), and closely related forms have been studied in the U. S. S. R. (SAKHAROV, 1966). Despite the importance of the family, confusion surrounds the taxonomy of the North American species.

The opportunity to collect and study live American tritoniids, some of which are the largest known nudibranchs, arose during a visit to the Friday Harbor laboratories of the University of Washington in July and August, 1969. Previous workers had often been hampered by the necessity to work from preserved material only. Thanks to the kindness of Dr. A. O. D. Willows and Mr. G. A. Robilliard, collections of freshly dredged and hand-collected tritoniids were available at Friday Harbor. Furthermore, tritoniid collections in the California Academy of Sciences were generously lent by the Associate Curator of Invertebrate Zoology, Mr. A. G. Smith. Spirit material was sent by Dr. F. R. Bernard of the Nanaimo Biological Station (British Columbia, Canada). The British Museum (Natural History), containing specimens from C. H. O'Donoghue's Vancouver collections, provided helpful corroborative material. Finally, Dr. Henning Lemche kindly sought out and sent to me a specimen of *Tritonia diomedea* from the R. Bergh collections in the Copenhagen Universitetets Museum.

HISTORICAL RÉSUMÉ

The following tritoniid species have been recorded in the coastal areas from California to Alaska.

1. *Limax tetraquetra* PALLAS, 1788; Kurile Islands (PALLAS); Victoria, British Columbia (O'DONOGHUE, 1926); California (MACFARLAND, 1966).
2. *Tritonia palmeri* COOPER, 1863; San Diego, California.
3. *Lateribranchaea festiva* STEARNS, 1873; Monterey, California.
4. *Tritonia diomedea* BERGH, 1894; Shumagin Island, Alaska (BERGH).
5. *Tritonia exsulans* BERGH, 1894; Point Año Nuevo, California (BERGH); Vancouver Island (O'DONOGHUE, 1926).
6. *Tritonia gigantea* BERGH, 1904; Alaska.
7. *Sphaerostoma undulata* O'DONOGHUE, 1924; Vancouver Island.
8. *Duvaucelia gilberti* MACFARLAND, 1966; Monterey and San Francisco, California.

It was certain that some of these names should be merged in synonymy, but subsequent authors have not found it easy to decide which are the 'good' species.

O'DONOGHUE (1926) worked with tritoniids from Canadian Pacific waters for some years and concluded that the species should be arranged as follows.

Sphaerostoma MACGILLIVRAY, 1843; type *S. jamesoni* MACGILLIVRAY (= *Tritonia hombergi* CUVIER, 1803).

1. *S. diomedia* (BERGH, 1894)
2. *S. exsulans* (BERGH, 1894)
3. *S. gigantea* (BERGH, 1904)
4. *S. palmeri* (COOPER, 1863)
5. *S. tetraquetra* (PALLAS, 1788)
6. *S. undulata* O'DONOGHUE, 1924

There are several reasons why this list is unsatisfactory. (A) O'Donoghue apparently misunderstood STEARNS' (1873) paper describing *Lateribranchaea festiva*, and considered this to be a phanerobranch dorid. In fact, as STEINBERG (1961) has pointed out, O'Donoghue's description of his new species *Sphaerostoma undulata* seems rather close to Stearns' description of *L. festiva*. To check this, I examined the types of *S. undulata* in January 1970 (British Museum [Natural History] 1953.6.30.36-7) and can state with confidence that these two species are one and the same, the older name, *L. festiva*, taking precedence.

(B) *Sphaerostoma gigantea* is almost certainly a synonym of *S. tetraquetra,* the latter name having priority.

(C) *Sphaerostoma palmeri* was so poorly described by COOPER (1863) and by COCKERELL & ELIOT (1905) that it must be set aside as a *nomen dubium.*

(D) O'Donoghue's inclusion of *Sphaerostoma diomedea* in his list for Vancouver Island appears to be unjustified, for the following reasons. First, O'DONOGHUE'S (1921) description of his specimens leaves little doubt that they were in reality *Lateribranchaea* (= *Tritonia*) *festiva* STEARNS. Second, two specimens labelled by O'Donoghue '*Sphaerostoma diomedia*' (British Museum [Natural History] 1953.6.30.40.40-41) were examined in January 1970. One proved to be the dorid *Triopha carpenteri* (STEARNS, 1873); the other was a 3 cm *L. festiva.* In this context, it may be noted that, in his 1921 paper, O'Donoghue introduced a mis-spelling of Bergh's species *diomedea* (incorrectly rendered *diomedia*) which has proved persistent (O'DONOGHUE, 1926; SAKHAROV, 1966).

More recently, MACFARLAND (1966) published a rather different arrangement of the species.

Duvaucelia RISSO, 1826; type *D. gracilis* RISSO, 1826.

1. *D. diomedea* (BERGH, 1894)
2. *D. exsulans* (BERGH, 1894)
3. *D. festiva* (STEARNS, 1873)
   = *Sphaerostoma undulata* O'DONOGHUE, 1924
   = *Tritonia reticulata* BERGH, 1881 (from Japan)
4. *D. gilberti* spec. nov.
5. *D. palmeri* (COOPER, 1863)
6. *D. tetraquetra* (PALLAS, 1788)
   = *Tritonia gigantea* BERGH, 1904

While MacFarland had gone some way towards correcting errors in O'Donoghue's taxonomy, he did not go far enough and, indeed, created a major further difficulty by his introduction of a new species, *Duvaucelia gilberti.* This new species approached very closely the description of *Tritonia diomedea* given by BERGH (1894) from Alaska, yet MacFarland did not apparently examine any specimens of the older species in order to evaluate the supposed differences. These differences concern the shape of the median and lateral teeth of the radula and of the cutting edges of the mandibles (all of which involve subjective judgments) and the shape of the penis (which Bergh had not described adequately in any case). The penis of *D. gilberti* was said by MacFarland to be elongate, clubbed at the end, with a raised ring below the club. In the case of the penis of *Tritonia diomedea,* Bergh states that 'die kurz kegelformige [sic], dicke Glans tief zurückgezogen, 5 mm. lang' (meaning that the short, conical, thick penis is 5 mm long and deeply withdrawn). This description seemed to imply that the penis had not been fully dissected out by Bergh. This was checked out by examining one of Bergh's original specimens (locality: California) in the Copenhagen Museum. The body measured 30 mm in length, preserved. The jaws were examined and proved to lack marginal denticulations, contrary to MACFARLAND'S (1966) assertion, and to BERGH'S (1894) own description of a larger individual from Shumagin Bay, Alaska. It is clear that the character of the jaw-edge is variable. The penis of the Copenhagen specimen was dissected out and proved to be 3 mm in length, having a terminal club and a subterminal elevated ridge, similar to MacFarland's description of *D. gilberti.* These facts lead to the conclusion that *D. gilberti* MACFARLAND, 1966 and *Tritonia diomedea* BERGH, 1894 are one and the same species, the older name having priority.

DIAGNOSTIC FEATURES OF THE VALID SPECIES

Tochuina ODHNER, 1963;
type *Limax tetraquetra* PALLAS, 1788

1. *Tochuina tetraquetra* (PALLAS, 1788) (Figure 1)
   = *Limax tetraquetra* PALLAS, 1788
   = *Doris tetraquetra,* GMELIN, 1791
   = *Tritonia tetraquetra,* O'DONOGHUE, 1922
   = *Tritoniopsilla tetraquetra,* ODHNER, 1936
   = *Tritoniopsis tetraquetra,* MARCUS, 1961
   = *Duvaucelia tetraquetra,* MACFARLAND, 1966
   = *Tritonia gigantea* BERGH, 1904
   = *Sphaerostoma gigantea,* O'DONOGHUE, 1926

Material examined: numerous adult specimens taken alive, San Juan Islands, July-August 1969.

Body length up to 30 cm, weight 1400 gr alive. Colour pale yellow, with a faint tinge of pink on the dorsum. The dorsal mantle is divided by shallow grooves into raised polygonal areas, many of which have a central mamilla; these elevations are especially well developed on the dorsal surface of the oral veil, which is large, slightly divided along the anterior margin, but not grossly bilobed. Rhinophore sheaths are somewhat open anteriorly. Hundreds of small, rather uniform gill tufts arise from the mantle edge on either side. The sides of the foot bear numerous long, soft, conical papillae.

The anal and genital openings lie on the right side; the nephroproct lies up to 2 cm in front of the anus. The penis is flagelliform. The central tooth of the radula is unicuspidate.

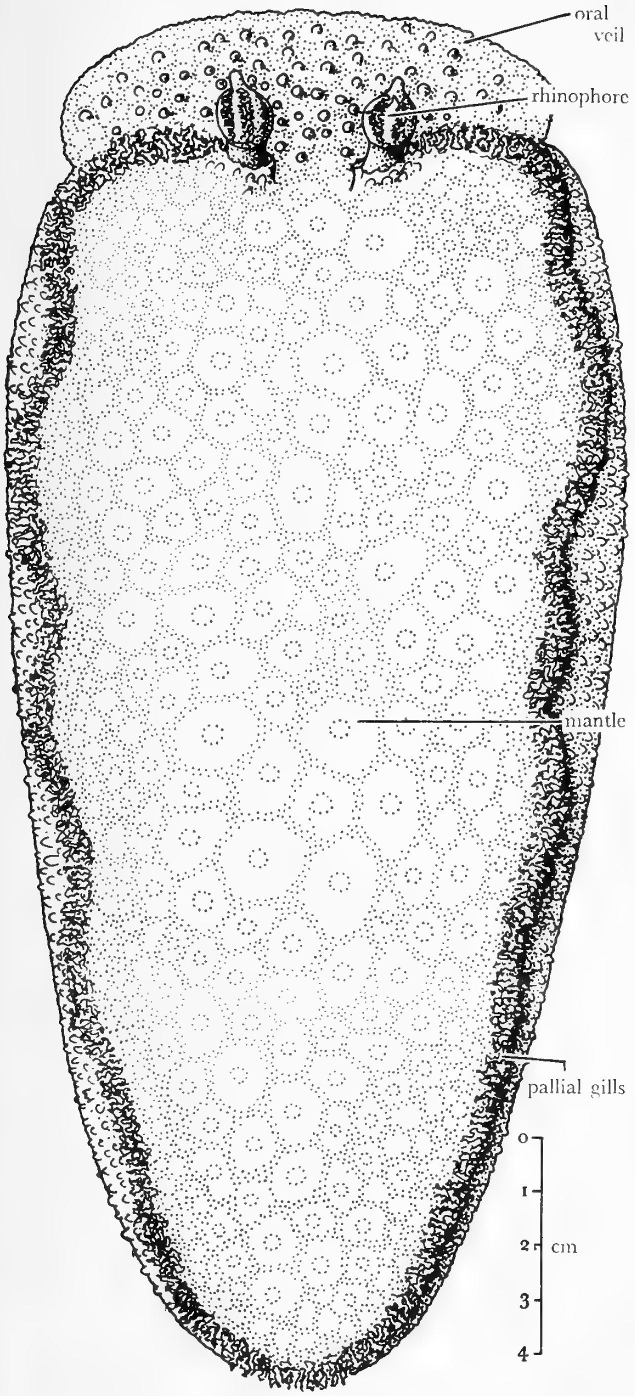

Figure 1

Tochuina tetraquetra (Pallas, 1788)

San Juan Island specimen, 30 cm in length, drawn from life

This is the largest known species of tritoniid (indeed, the largest nudibranch), and feeds upon the sea-pen *Ptilosarcus guernii.*

It is recorded from the Kurile Islands (Pallas, 1788), Unalashka (Bergh, 1879), Victoria, B. C. (O'Donoghue, 1926), Monterey Bay, California (Marcus, 1961), Pacific Grove and San Francisco, California; Alaska (MacFarland, 1966), North Japan (Baba, 1969b), as well as from the San Juan Islands.

Tritonia Cuvier, 1798;

type *Tritonia hombergi* Cuvier, 1803
(validated in I. C. Z. N. Opinion no. 667)

2. *Tritonia diomedea* Bergh, 1894 (Figure 2)
= *Sphaerostoma diomedia,* O'Donoghue, 1926
= *Duvaucelia gilberti,* MacFarland, 1966
= *Tritonia gilberti,* Willows, 1968
= *Tritonia exsulans,* Marcus, 1961
?= *Tritonia diomedia,* Sakharov, 1966

Material examined: (A) Numerous adult and juvenile specimens taken alive sublittorally, San Juan Islands, July-August 1969. (B) Single specimen 9 cm in length (preserved) from the California Academy of Sciences, collector R. Pool, locality 3 miles SE of Chimney Rock, off Drake's Bay, California, 29 fathoms, October 1963. (C) Single specimen 5 cm in length (preserved) from the Nanaimo Biological Station (B. C., Canada), locality Departure Bay, British Columbia, December 1969. (D) Single specimen 13 cm in length (preserved) from the Nanaimo Biological Station (B. C., Canada), collector D. B. Quayle, locality Green Inlet, British Columbia, 50 fathoms, June 1962. (E) Single specimen 3 cm in length (preserved) from the Copenhagen Universitetets Museum, identified by R. Bergh, locality California.

Body-length up to 22 cm, weight 500 gr alive. Colour delicate rosy pink, darkening in the largest specimens. The dorsal mantle is rather smooth, but with faint mamillae especially towards the rear and between and in front of the rhinophores. The oral veil is slightly bilobed, with up to 14 simple digitate papillae projecting from the anterior edge on each side. These papillae have a tendency to be alternately dorsally and ventrally directed. The frontal margin is chalk-white and a white line runs up from this margin to join the white rim of the rhinophore sheath on each side. The rhinophore lamellae are brownish, the tip of each tentacle chalk-white. From the mantle edge on each side of the body arise numerous branched gills; in a large specimen there may be on each side 7 - 8 major gills, and 20 - 24 smaller plumes. The sides of the foot are faintly mamillate.

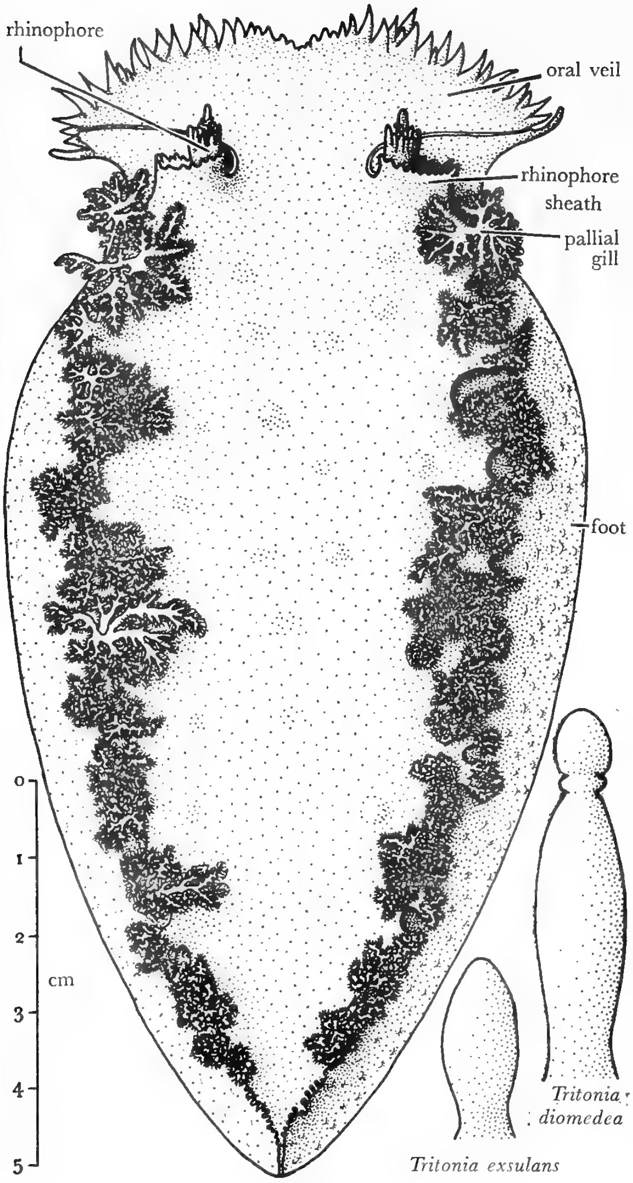

Figure 2

Tritonia diomedea Bergh, 1894

San Juan Island specimen, 15 cm in length, drawn from life. Inset: Drawings of the penis of preserved specimens of *Tritonia diomedea* and *Tritonia exsulans*

In the alimentary canal, the oral tube and the oesophagus sometimes exhibit red-brown pigmentation, but this fades and disappears after some years in preservative.

The anal and genital openings lie on the right side; the nephroproct is situated immediately above the anus. The penis is elongated, rather slender, with a subterminal raised ridge and a terminal swollen club. The central tooth of the radula is tricuspidate. The radula formulae of two specimens were determined. In an 8 cm individual the formula was $49 \times 56 \cdot 0 \cdot 56$, whereas the formula for a 16 cm individual was $65 \times 89 \cdot 1 \cdot 89$.

This species feeds upon the sea-whip *Virgullaria.* It is able to swim (by dorso-ventral flexions of the whole body) if alarmed.

It is recorded from the Shumagin Islands, Alaska (Bergh, 1894), from Vancouver Island (O'Donoghue, 1926) and from Monterey and San Francisco, California (MacFarland, 1966), as well as the San Juan Islands.

3. *Tritonia exsulans* Bergh, 1894 (Figure 2)

= *Sphaerostoma exsulans,* O'Donoghue, 1926
= *Duvaucelia exsulans,* MacFarland, 1966
not = *Tritonia exsulans,* Marcus, 1961, which = *T. diomedea* Bergh, 1894

Material examined: (A) Single specimen 55 mm in length (preserved) from the California Academy of Sciences, collector T. Skogsberg, identified by F. M. MacFarland, locality 'off Pacific Grove, California', summer, 1932. (B) Single specimen 90 mm in length (preserved) from the California Academy of Sciences, collected Hanna, Smith and Chapman, locality 'off oil tanks', Monterey Bay, California, on sand dollar bed, May 1945. (C) Single specimen 62 mm in length (preserved) from the California Academy of Sciences, F. M. MacFarland collection, locality Bering Sea U. S. S. *Albatross* station 4777, 43 - 52 fathoms, September 1906. (D) Single specimen 90 mm in length (preserved) from the California Academy of Sciences, locality "off the Oregon coast", 1260 m, R/V Yaquina Cruise 6606, June 1966. (E) Single specimen 90 mm in length (preserved) from the California Academy of Sciences, locality "off the Oregon coast", 1200 m, R/V Yaquina Cruise 6501, January 1965. (F) Three specimens, 20 - 34 mm in length (preserved) from the California Academy of Sciences, locality "off the Oregon coast", 1000 m, R/V Acona Cruise 6408, August 1964.

In external appearance, this species resembles *Tritonia diomedea* very closely. Dissection is necessary to distinguish the two species, *T. exsulans* having a short, squat, conical penis. This feature is the only one I have found reliable. The pigmentation of the oral canal and oesophagus is extremely variable in both *T. exsulans* and *T. diomedea*; similarly the shapes of the radula teeth and mandibular borders vary widely. Distinguishing features of the penis are shown in Figure 2. It should be noted that the ring of 40 penial spines described by MacFarland (1966) has been seen in *T. exsulans* by no other author. If it can be shown that these two types of penis intergrade, *T. exsulans* and *T. diomedea* should be merged (the latter name having page priority). The radula formulae of two of the specimens were determined. In a 55 mm individual, the formula was $49 \times 110 \cdot 1 \cdot 110$; in the largest individual it was $64 \times 104 \cdot 1 \cdot 104$.

Apart from the localities mentioned above, this species has been recorded from Vancouver Island (O'Donoghue, 1921), Alaska and Japan (MacFarland, 1966).

4. *Tritonia festiva* (Stearns, 1873) (Figure 3)

= *Lateribranchaea festiva* Stearns, 1873
= *Tritonia reticulata* Bergh, 1881
= *Sphaerostoma undulata* O'Donoghue, 1924
= *Duvaucelia festiva,* MacFarland, 1966

Material examined: (A) Numerous adult and juvenile specimens taken alive sublittorally San Juan Islands July-August 1969. (B) British Museum (Natural History) 1953.6.30.40.40-41, presented by C. H. O'Donoghue, Vancouver Island, 10 - 25 fathoms, single specimen 3 cm in length (preserved). (C) British Museum (Natural History) 1953.6.30.36 - 37, presented by C. H. O'Donoghue, type specimens of *Sphaerostoma undulata* O'Donoghue, 1924.

Body-length up to 70 mm. Colour translucent white or orange with pink or brown tinting dorsally. There is a characteristic but rather variable pattern of chalk-white lines along the mantle rim, under each gill tuft and along the margin of the oral veil; there are also usually two wavy white lines down the middle of the dorsum. These white markings are absent in rare individuals. The rhinophore sheaths and clubs are white and a white line often connects the two sides. The edges of the foot are white. The body-surface is rather smooth. The oral veil bears up to 12 blunt frontal papillae; it is not markedly bilobed. From the mantle edge on each side arise up to 16 pinkish gill plumes.

The anal and genital openings lie on the right side; the nephroproct is situated immediately above the anus. The penis is short, squat and almost barrel-shaped. The central tooth of the radula is tricuspidate. In a 65 mm specimen from the Friday Harbor area the radula formula was $50 \times 81 \cdot 1 \cdot 81$.

Tritonia festiva is able to swim (by dorso-ventral flexions) if alarmed.

It is recorded from Monterey Bay (Stearns, 1873), Japan (Bergh, 1881; Baba, 1969a) and from Vancouver Island (O'Donoghue, 1924), as well as the San Juan Islands.

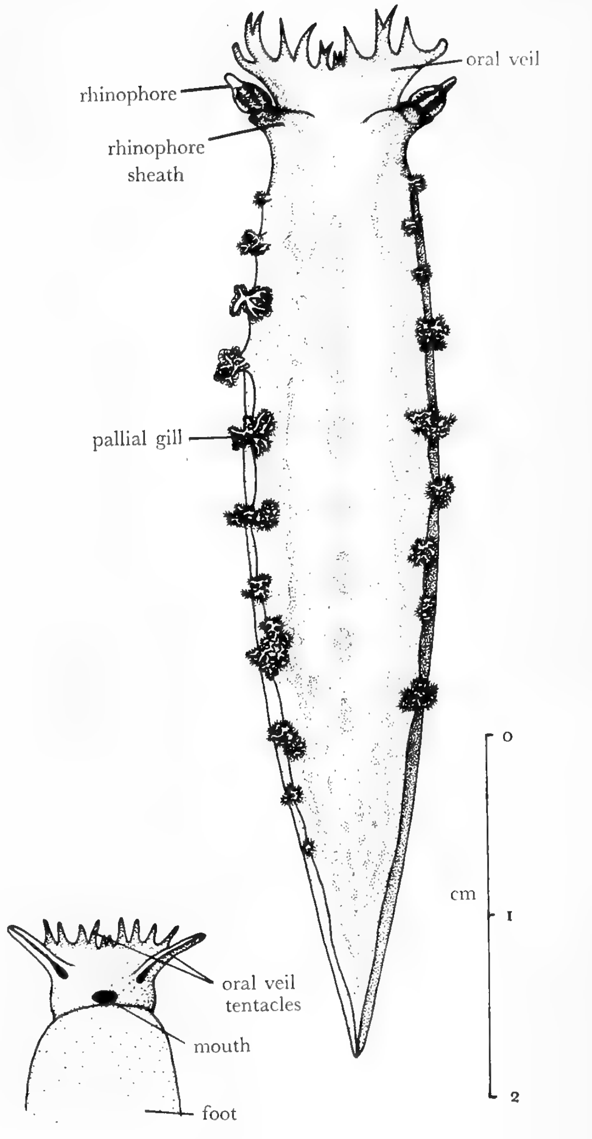

Figure 3

Tritonia festiva (Stearns, 1873)

(A): San Juan Island specimen, 55 mm in length, drawn from life.
(B): Under side of the head of another specimen, 35 mm in length, drawn from life

KEY FOR THE IDENTIFICATION OF PACIFIC NORTH AMERICAN SPECIES

1. Nephroproct a short distance anterior to the anus; body length up to 30 cm .... *Tochuina tetraquetra* (Pallas) (Figure 1)

   Nephroproct close above the anus; body length below 20 cm 2

2. Mantle bears chalk-white streaks, rarely lacking; body length to 7 cm; penis short, barrel shaped .... *Tritonia festiva* (Stearns) (Figure 3)

   Mantle pinkish, not marked as above; body length to 22 cm; penis conical or elongated, not barrel shaped 3

3. Penis elongated, with terminal bulb and subterminal ridge .... *Tritonia diomedea* Bergh (Figure 2)

   Penis squat, conical .... *Tritonia exsulans* Bergh (Figure 2)

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Effect of Temperature on Egg Capsule Deposition in the Mud Snail, *Nassarius obsoletus* (Say)

BY

A. N. SASTRY

Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881

(2 Text figures)

INTRODUCTION

Temperature, food and light affect the reproductive activity of marine invertebrates (Barnes, 1963; Loosanoff & Davis, 1952; Sastry, 1963, 1966, 1968). It has been suggested that the pattern of annual reproductive activity for a species may be a genetically controlled response to the environment and that variation in geographically separated populations can either be induced as the phenotypic response of a single genotype or else be truly genetic (Sastry, 1970).

The mud snail, *Nassarius obsoletus* (Say, 1822) has a wide geographical distribution ranging from the Gulf of St. Lawrence to northern Florida on the east coast of North America, resulting in many geographically separated populations exposed to different temperatures (Abbott, 1954; Schroeder, 1966). The period of egg capsule deposition varies among the separate populations (Jenner, 1956). The present study examines the reproductive activity of *Nassarius* throughout the year and the effect of various temperatures on the deposition of egg capsules.

MATERIALS AND METHODS

The snails were collected at monthly intervals on a sand-mud flat in the vicinity of the Duke University Marine Laboratory, Beaufort, North Carolina. The reproductive condition of the monthly samples was determined by microscopic examination of the gonadal tissue. Only adult females (14.5 - 25.0 mm) and males (15.0 - 21.1 mm) were examined. The gonads were classified as developing, mature or neutral. Developing gonads were those with spermatocytes and spermatids or oocytes.

During October, December and January, a large number of snails was collected and females exposed without food to 10°, 15°, 20°, 25° and 30° C in the laboratory. The photoperiod was set for 12 hours of light and 12 hours of darkness. The time from collection until deposition of egg capsules was recorded for each temperature group.

OBSERVATIONS

Reproductive Cycle

Males: Spermatozoa were observed from January through May. The gonads were neutral from June to the end of September. The copulatory organ was reduced to a short papilla but regenerated with the onset of spermatogenesis. Jenner & Chamberlin (1956) found good correlation between the reduction of copulatory organ and the cessation of seasonal reproductive activity. Spermatogonia and spermatocytes appeared in October. During November and December spermatozoa were observed as well. With the development of spermatozoa, the gonads turned from their neutral brown to purple.

Females: The reproductive condition of females in the monthly samples is shown in Figure 1. Oocytes in the vitellogenesis growth phase and a few eggs were observed in January. Mature eggs were predominant from February through May. During this period the animals shed the eggs freely when they were removed from their shells. The gonads were neutral from June through September. Oogenesis began in October, with the oocytes entering cytoplasmic growth phase during November and the vitellogenesis growth phase in December. The gonads, brown in the neutral condition, became cream white on maturity.

Egg capsule deposition: In the field there were large numbers of egg capsules between the end of February

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[1] Aided by NSF Grant GB-1356. The research work was done at the Duke University Marine Laboratory, Beaufort, North Carolina.

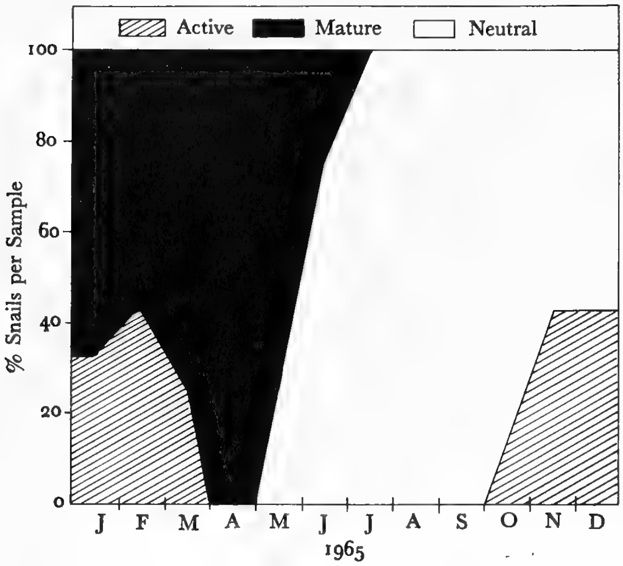

Figure 1

The gonad condition of *Nassarius obsoletus* females in the monthly samples

and May. A few egg capsules, however, appeared as early as late December, when the water temperatures were slightly higher than normal. During the winter the snails usually burrowed into the substratum or aggregated in shallow tide pools where the water was slightly warmer than below the tide mark. The colder temperatures in the winter may have been responsible for the delay in deposition of egg capsules until February, since the animals were already in a mature state by the end of December.

Effect of Temperature on the Deposition of Egg Capsules

Snails collected in October did not deposit egg capsules at any of the experimental temperatures in the laboratory. Snails collected in December deposited the egg capsules, but only at intermediate temperatures. No egg capsules were deposited at the extremes of 10° and 30° C. Snails collected in January deposited egg capsules at all the experimental temperatures. The time required for deposition of eggs shows a direct correlation with temperature (Figure 2). It also appears that the time required for the deposition of egg capsules decreases the closer the population is to the time of deposition in the natural habitat. From February through May, snails brought to the laboratory deposited their egg capsules readily.

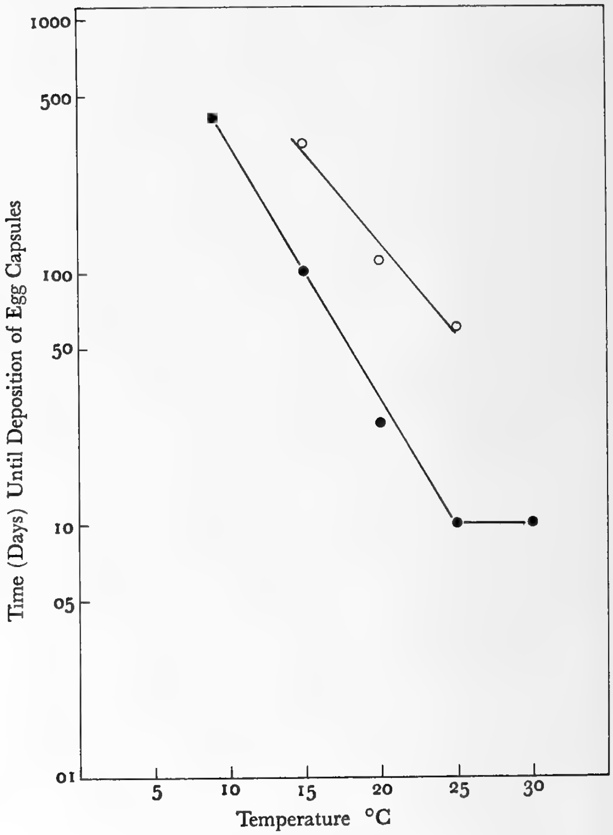

Figure 2

Days until deposition of egg capsules for snails maintained at different temperatures

○——○ December collection ●——● January collection

DISCUSSION

In the annual reproductive cycle of *Nassarius obsoletus,* deposition of egg capsules occurs from the end of February through May at Beaufort, North Carolina. A neutral period in the summer is followed by gametogenesis in the fall. Although the population developes mature gametes by the end of fall, the deposition of egg capsules is delayed until late February. This delay in deposition may be due to low winter temperatures. Egg capsules seem to be deposited in winter when the temperature is slightly warmer than usual. Apparently, there is a minimum temperature which must be exceeded before the deposition of egg capsules can begin.

The egg capsules are deposited within a range of temperatures. Within this range, the time required for deposition seems to correlate with the temperature to which the snails have been exposed. Deposition seems to occur, however, only after the oocytes have reached the vitellogenesis growth phase. Sastry (1966) reported that in the bay scallop, *Aequipecten irradians* (Lamarck, 1819) the time required for oocyte growth to maturation and spawning was directly influenced by the temperature to which the scallops had been exposed. It was also reported (Sastry, 1968) that oocyte growth began when the environmental temperatures exceeded a certain minimum and food was available.

Scheltema (1967) reported that gametogenesis in geographically separated populations of *Nassarius* from Cape Cod, Massachusetts, and Beaufort, North Carolina, is completed by the end of fall but that the period of egg capsule deposition and the neutral period are different. The variation in the period of egg capsule deposition for populations between Booth Bay Harbor, Maine and Mayport, Florida is reported to correlate with the temperature distribution along the Atlantic Coast (Jenner, 1956). It appears that the population differences in the period of egg capsule deposition and neutral period are related to the time when the required environmental temperature is reached in different parts of the range. Variation in reproductive activity, therefore, appears to be environmentally induced response within the genetic limits of this species.

SUMMARY

1. In the annual reproductive cycle of *Nassarius obsoletus* at Beaufort, North Carolina, the period of egg capsule deposition occurs from the end of February through May.
2. The time until deposition seems to be regulated by the water temperature.
3. The variation in geographically separated populations appears to be influenced by the time when the required temperatures for gametogenesis, egg capsule deposition and neutral period develop in different locations. Hence, the variation in geographically separated populations probably reflects environmentally induced reponse of the same genotype.

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Mesodon leatherwoodi, A New Land Snail from Central Texas

BY

W. LLOYD PRATT

Collections Department, Fort Worth Museum of Science and History, Fort Worth, Texas 76107

(1 Plate)

On 2 May 1965 a series of an apparently undescribed *Mesodon* was collected during a visit to a locality in western Travis County, Texas. In August of the same year Tony L. Burgess and James H. Turner made a second trip to obtain more material of the form herein described as a new species. The specific epithet is given in memory of Robin Lee Leatherwood, Jr., a promising student of field biology who died of leukemia at the age of 16, the day after the species was first collected.

Mesodon (Mesodon) ***leatherwoodi*** Pratt, spec. nov.

(Figures *1, 2*)

Holotype: United States National Museum no. 701581, Figure *1*, collected during August, 1965, in talus at the base of limestone cliffs deeply shaded by oak-elm forest in West "Cave," a canyon formed by the collapse of a cave system at the Pedernales River crossing of the Bee Caves - Cypress Mill Road, 3 miles north and 11⅓ miles west of Bee Caves, Travis County, Texas.

Diagnosis: A member of the *Mesodon binneyanus* group, distinguished by the combination of open umbilicus, obsolescent spiral sculpture, straight upper lip, flattened spire, and small size (diameter less than 19 mm).

Description of the Holotype: Shell depressed helicoid, whorls 4⅛ (measured along suture), greatest diameter 17.6 mm, height 8.5 mm; spire depressed, forming angle of 150°; periphery subangular, becoming rounded on the last ½ of the body whorl; umbilicus open, diameter 2.2 mm; suture deeply impressed, descending slightly to the aperture; aperture oblique, lunate, plane of aperture at an angle of 40° to the axis; peristome sharp-edged, thickening towards inner edge, upper margin straight, expanded at periphery, the expansion gradually increasing to reflection on the basal margin; thin, fragile columellar margin expanded to cover about ⅓ of the umbilicus (often broken away in the series at hand); a very weak parietal tooth (present in 10 of 29 specimens); moderately strong radial striae, continuing unweakened onto the base; spiral sculpture virtually obsolete, absent above except for traces on the last ¼ whorl, stronger below, discernable with some difficulty at 30× magnification; shell translucent, light brown, peristome white.

Paratypes: Numbers 94V-1490 and 94V-1491 in the collection of the Fort Worth Museum of Science and History, no. 0098A in the collection of the Dallas Museum of Natural History, and no. 1200 in the author's collection.

Extreme diameters 14.8 mm and 18.4 mm, mean 16.7 mm ($N = 29$).

DISCUSSION

Mesodon ***leatherwoodi*** is most similar to *M. roemeri*. It is distinguished from *M. roemeri* by the smaller size, more depressed spire, more angulate periphery, and obsolescent spiral sculpture. The periphery is higher in *M.* ***leatherwoodi***, about ⅓ the height of the body whorl below the suture; whereas in *M. roemeri* the periphery is at about the middle of the whorl. The suture is more deeply impressed in *M.* ***leatherwoodi***. Although umbilicate specimens occur in many populations of *M. roemeri*, the columellar expansion of the peristome covers ½ or more of the umbilicus and is thicker and more durable than in

Plate Explanation

Figure *1*: *Mesodon* ***leatherwoodi*** Pratt, spec. nov. Holotype, U. S. National Museum no. 701581. West Cave, Travis County, Texas. Scale slightly less than ×2, actual diameter 17.6 mm

Figure *2*: *Mesodon* ***leatherwoodi*** Pratt, spec. nov. Paratype Dallas Museum of Natural History No. 0098A. West Cave, Travis County, Texas. Figures 2a, 2b, and 2c ×2; Figure 2d ×1

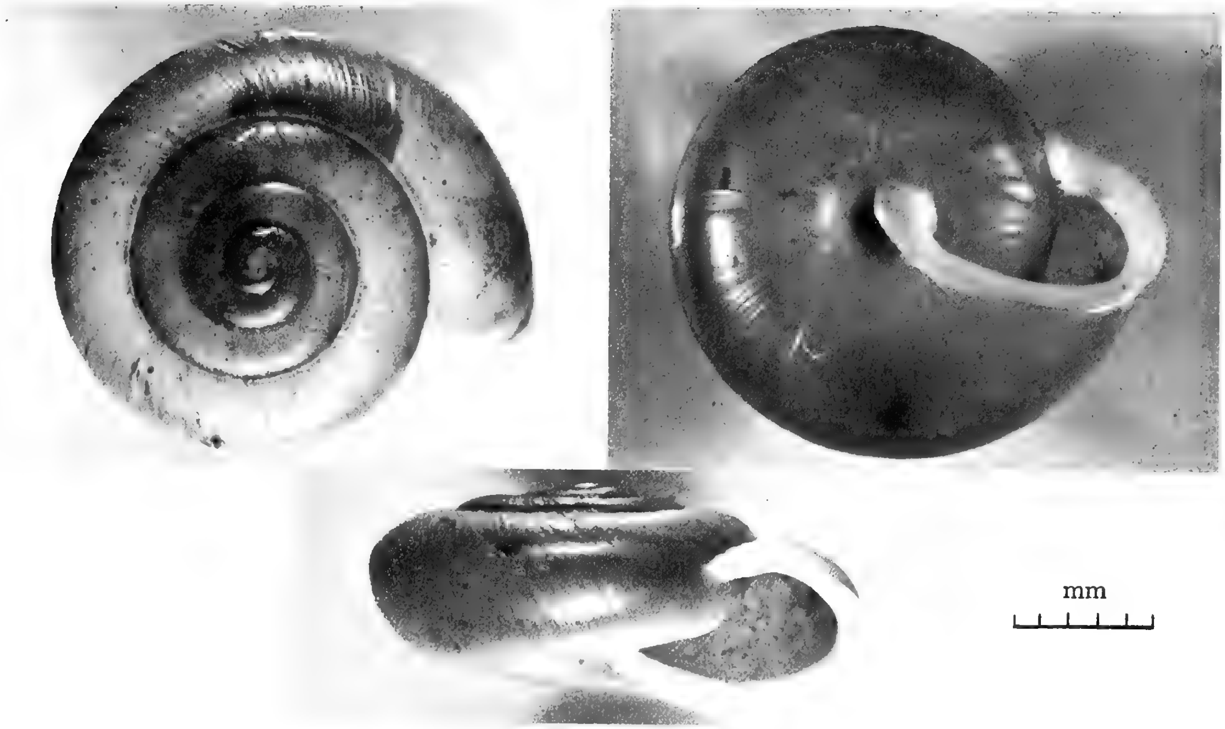


Figure *1*

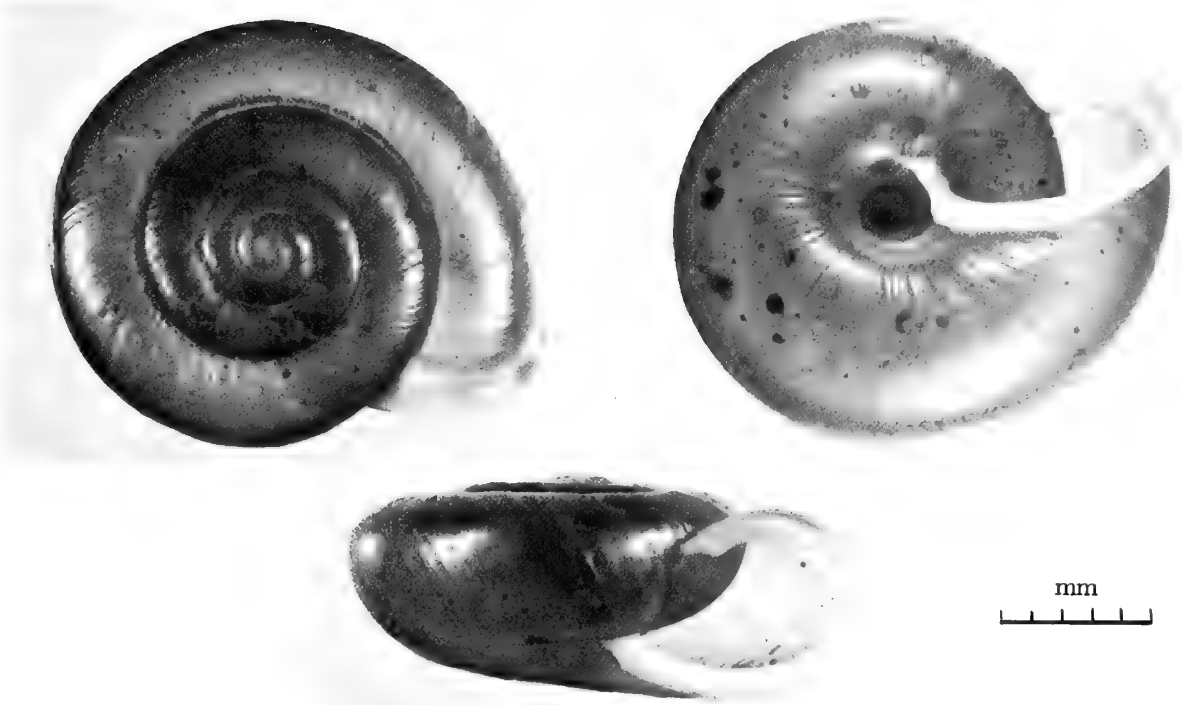


Figure *2*

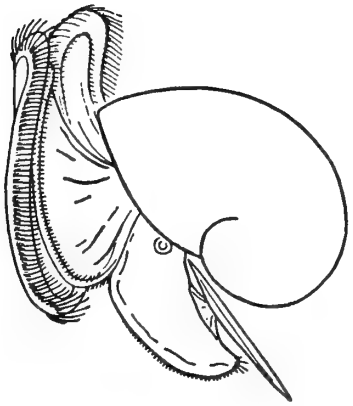
M. leatherwoodi. In central Texas populations of *M. roemeri* most specimens have the umbilicus closed. In ***M. leatherwoodi*** the columellar expansion covers $\frac{1}{3}$ or less of the umbilicus and is so thin and fragile that it is often broken away. ***Mesodon leatherwoodi*** also differs from *M. roemeri* in habits; *M. roemeri* is characteristically found under rocks and under and in rotten logs. Although such cover is abundant in West Cave. ***M. leatherwoodi*** was found only in talus at the foot of sheer limestone walls. *Mesodon roemeri* is apparently absent from the immediate region.

REMARKS

West Cave proper is a small remnant at the head of a sheer-walled box canyon formed by the collapse of a cave system. The surrounding uplands are covered by oak-juniper woodland grading into oak-hackberry woodland in the valleys. There is a single line of Bald Cypress *(Taxodium distichum)* along each bank of the Pedernales River. Very large Bald Cypress and Sycamore *(Platanus occidentalis)* grow along a small stream on the floor of the canyon and in a small amphitheater at its head. Talus slopes extending to the banks of the stream below the amphitheater support a closed canopy oak-elm forest. *Mesodon* ***leatherwoodi*** is found in leaf mold collected in talus, and less commonly, in rock crevices at the base of the canyon walls in the amphitheater and along the north wall. Associated species include *Helicina orbiculata* (SAY, 1818), *Helicodiscus eigenmanni* PILSBRY, 1900, *Glyphyalinia indentata* (SAY, 1823), *Euglandina singleyana* (W. G. BINNEY, 1892), *Holospira roemeri* (PFEIFFER, 1848), *Polygyra texasiana* (MORICAND, 1833), *P. mooreana* (W. G. BINNEY, 1857), and *Praticolella berlandieriana* (MORICAND, 1833).

ACKNOWLEDGMENTS

Dr. E. P. Cheatum critically reviewed this paper, and I am grateful for his comments. Mrs. Aubyn Kendall, Curator of Collections, Fort Worth Museum of Science and History, reviewed the grammar and construction. I am especially indebted to Richard W. Fullington, of the Dallas Museum of Natural History, who made the photographs illustrating this paper.



The *Intritacalx*, an Undescribed Shell Layer in Mollusks

BY

ANTHONY D'ATTILIO

AND

GEORGE E. RADWIN

Natural History Museum, San Diego, California 92112

(1 Plate; 1 Text figure)

IN THE COURSE OF WORK on the taxonomy and evolution of muricid gastropods, we have noted a peculiar feature of the shell surface. It differs from the underlying shell in being flat white in color, much softer, and, in many cases, with intricate sculpture which may not correspond to that of the underlying shell. For this surface layer we have coined the term **intritacalx**, a name which reflects some of the unique features of this structure: intrita - crumbly; calx - chalk.

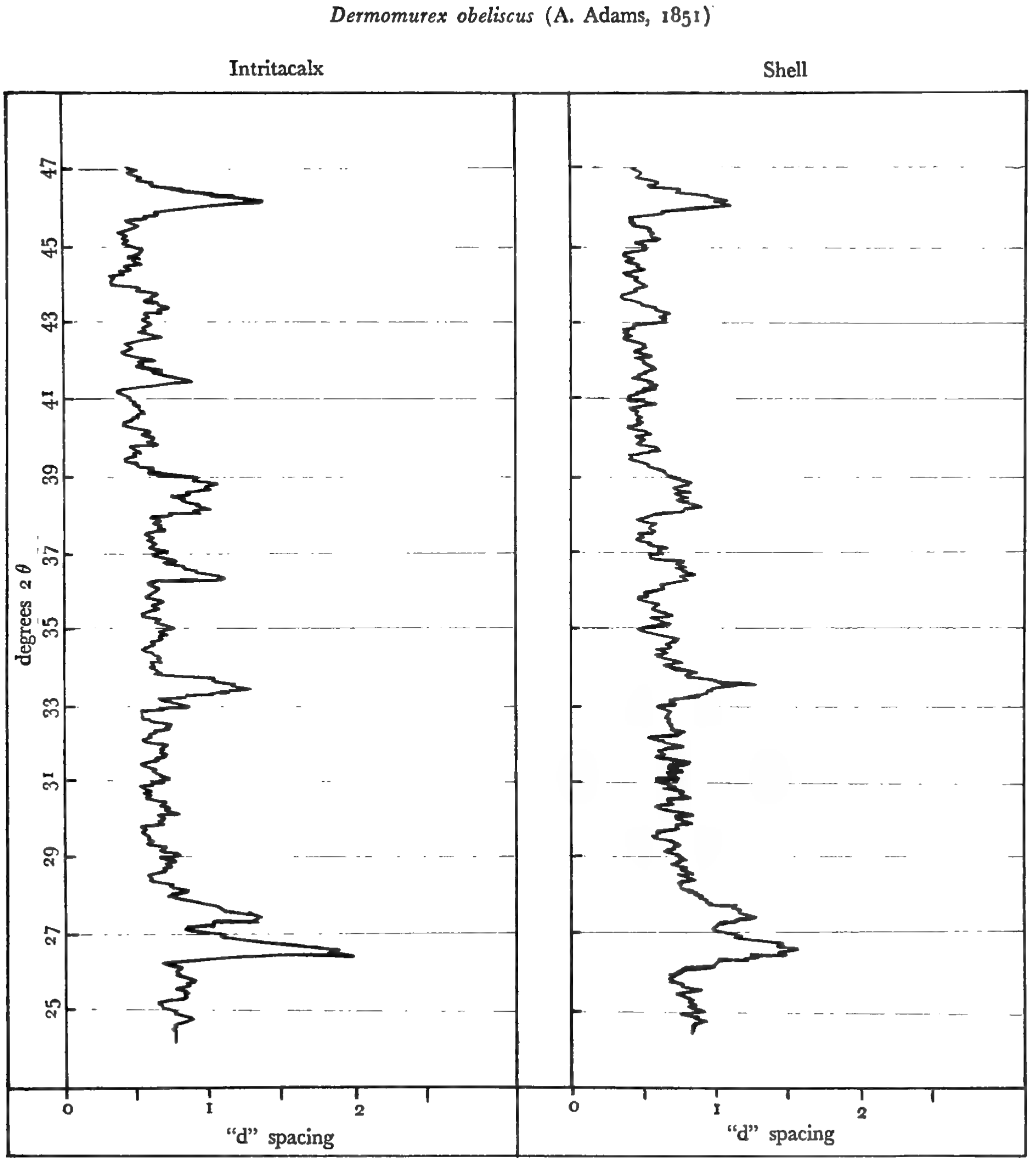
A great deal of work has been done on the deposition and mineralogy of molluscan shells (BØGGILD, 1930; CLARK & WHEELER, 1922; TRAVIS, FRANÇOIS, BONAR & GLIMCHER, 1967; TAYLOR & KENNEDY, 1969; KENNEDY, TAYLOR & HALL, 1969). In none of these papers, nor in any pertinent secondary references on the subject, have we found any comment which indicates an awareness of this surface layer.

A few of the malacologists who have studied the Muricidae and were aware of this structure have made only cursory mention of a peculiar color, texture, or microsculpture (HARRY, 1969; KEEN, 1958; KURODA, 1953; MCLEAN & EMERSON, 1970; VOKES, 1970). Some authors have commented that species of *Aspella* were generally "... worn-looking but had bright underlying color patterns." They apparently did not realize that the specimens in question had the intritacalx partially worn away, and that the bright color pattern was in the underlying shell. Other workers were under the misapprehension that the white, limy coating was an extraneous encrustation or deposit, or due to deterioration of the shell from weathering. Although the intritacalx occurs most frequently in the Muricidae, it is also present in other gastropod and in bivalve groups.

The differences between the intritacalx and the underlying shell suggested that its chemical or physical nature might differ from typical molluscan shell matter. Results of X-ray diffraction tests showed that chemically the intritacalx is made up of calcium carbonate ($CaCO_3$), essentially indistinguishable from the typical molluscan shell. Physically the intritacalx is composed of varying proportions of aragonite and calcite, the two crystalline forms of calcium carbonate found in mollusk shells. The relative amount of aragonite and calcite in the intritacalx of a given shell is in the same proportion as that of the underlying shell (Figure 1). The hardness of molluscan shells is principally dependent on the presence and amount of organic binding material, termed conchiolin. Presumably, the softness of the intritacalx is due to a sparsity of conchiolin (TRAVIS & GONSALVES, 1969).

We have studied the intritacalx in 4 families of gastropods (Muricidae, Bursidae, Cancellariidae, Turritellidae) and two families of bivalves (Mactridae, Pholadidae). In most instances it is deposited in the form of simple axial growth striae, differing from the underlying shell only in hardness and color. Where the intritacalx is deposited in axial lamellae, it is not only softer than the underlying shell but also may not correspond to the shell sculpture underlying it. The most unusual form taken by the intritacalx is found in the genera *Aspella, Typhisopsis, Tripterotyphis,* and related groups, and in the Bursidae. In these groups it is deposited in intricate patterns which are either much exaggerated reflections of the sculpture of the shell beneath it or are completely unrelated to it. The patterns are commonly reticulate, as in *Dermomurex* and *Bursa* (Figures 6, 8), but other, more complex patterns are found in other groups (e. g. *Aspella, Typhisopsis*).

In *Typhisopsis coronata* (Broderip, 1833) (Figure 7), the intritacalx is laid down as growth striae. In the most recently deposited section, the layer is continuous and uninterrupted. At a slightly earlier point in the growth of



Dermomurex obeliscus (A. Adams, 1851)

Figure 1

Dermomurex obeliscus (A. Adams, 1851)
X-ray diffraction patterns of the shell and intritacalx

the shell, shortly behind the outer apertural lip, roughly semicircular depressions are found, most deeply imprinted opposite to the direction of growth. These depressions are sparsely and randomly scattered over the surface. The density of these features increases toward the earlier whorls until, on the third or fourth whorl previous to the growing edge, the entire surface is covered with depressions. The pattern may occur throughout the genus, but sufficient material has not been available to investigate this possibility.

In *Tripterotyphis lowei* (Pilsbry, 1932) (Figure 2) the intritacalx is deposited in the form of numerous scalloped or frilled laminae covering the entire shell surface. The embayments in the scalloped edges are raised from the surface and the projections are appressed to the shell. There are also comparatively large pits in a single row, aligned with each varix, imparting the appearance of a coarsely stitched seam to the postvarical area.

Another, more intricate type of intritacalx is found in the Panamic *Aspella* sp. (*cf. A. pyramidalis* (Broderip, 1833)) (Figure 4) and in several other species of *Aspella*. Under low magnification there appears to be a pattern of exceedingly fine axial grooves. Under higher magnification (100×) the grooves can be seen to be lined with pits which appear as tunnel openings. These openings seem to penetrate the intritacalx at a shallow angle. The tunnels do not extend as far as the next axial groove in the direction of growth.

In *Gracilimurex bakeri* (Hertlein & Strong, 1951) (Figure 5) and *Takia inermis* (Sowerby, 1841) the intritacalx is laid down as axial growth striae with broad, shallow, wide-spaced, spiral depressions crossing them. A specimen with a partially eroded surface shows that the intritacalx erodes more noticeably in these depressed areas. When a section at right angles to the direction of growth is viewed, it is apparent that the intritacalx is undermined with tunnels following the spiral sculpture. The intritacalx between the spiral furrows is continuous from its outer surface to the shell below and thus erosion in this region is not as quickly evident.

A simpler form of intritacalx is found in the genera *Calotrophon* and *Favartia* (Figure 3). The chalky surface here is deposited in the form of lamellae, best developed in the shoulder region. The surface is unrelated to the sculptural elements of the underlying shell.

The simplest form of intritacalx is found in *Austrotrophon, Boreotrophon, Maxwellia, Poirieria, Turritella, Cancellaria,* and other genera. In all of these groups we have found the intritacalx occurring as a series of simple growth striae following the periodic increments of the underlying shell. In species in these and other groups we have, on many occasions, found the intritacalx underneath a thin, yellow, parchment-like periostracum.

In conclusion, we believe that the intritacalx is of potentially great taxonomic importance in the groups in which it occurs. This is particularly true in the genera *Aspella, Dermomurex, Typhisopsis* and *Tripterotyphis.* In each of these groups the sculpture of the intritacalx is characteristic and constant. It is also of value at the species level, especially in *Aspella.* In this genus, species from widely separated geographical regions have often been confused and considered conspecific on the basis of worn shells. The distinctive details of the intritacalx of *Aspella* species are helpful in separating them.

On the basis of the foregoing we suggest that:

1: As the intritacalx is mineralogically similar to or identical with the underlying shell, its softness is probably due to a sparsity of organic binding matter.

2: Since the shell is deposited by the mantle, it is not unreasonable to assume that the intritacalx is also laid down by the mantle.

3: We believe that the intritacalx is deposited synchronously with the underlying shell, an assumption strengthened by its deposition, in many cases, immediately under a periostracum.

The intricacy of pattern and structure (as in those species whose intritacalx is undermined with tunnels) may prove of interest in determining the possible functional morphology of this chalky surface layer.

ACKNOWLEDGMENTS

We would like to express our appreciation to Dr. Richard W. Berry, Department of Geology, San Diego State College, for assistance in X-ray diffraction analysis and for other helpful suggestions. We also thank Mr. Arnold Ross, San Diego Museum of Natural History, and Dr. Willian K. Emerson, the American Museum of Natural History, for reading and criticizing drafts of this paper.

Plate Explanation

Intritacalx Patterns – Schematic Representation

Figure 2: *Tripterotyphis lowei* (Pilsbry, 1931) – normal view ca. 800×

Figure 3: *Calotrophon ostrearum* (Conrad, 18?) – composite view normal and cross-sectional ca. 50×

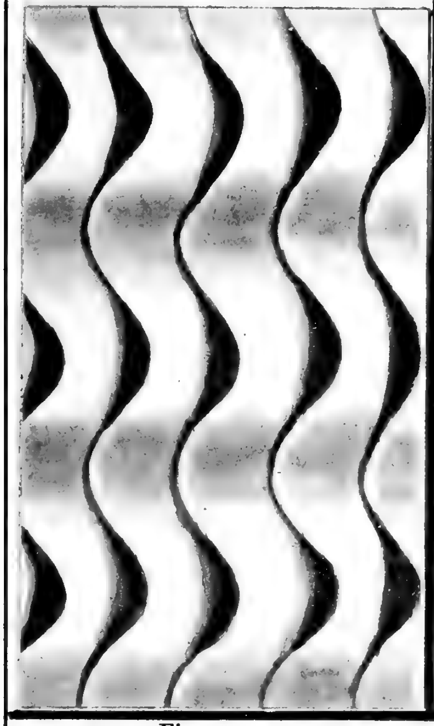
Figure 4: *Aspella* cf. *A. pyramidalis* (Broderip, 1833) – normal views upper: 630×; lower: 900×

Figure 5: *Gracilimurex bakeri* (Hertlein & Strong, 1951) – Composite view, normal and cross-sectional ca. 70×

Figure 6: *Dermomurex obeliscus* (A. Adams, 1851) – normal view ca. 200×

Figure 7: *Typhisopsis coronata* (Broderip, 1833) – normal views left: ca. 125×; right: ca. 75×

Figure 8: *Bursa calcipicta* Dall, 1908 – normal view, ca. 85×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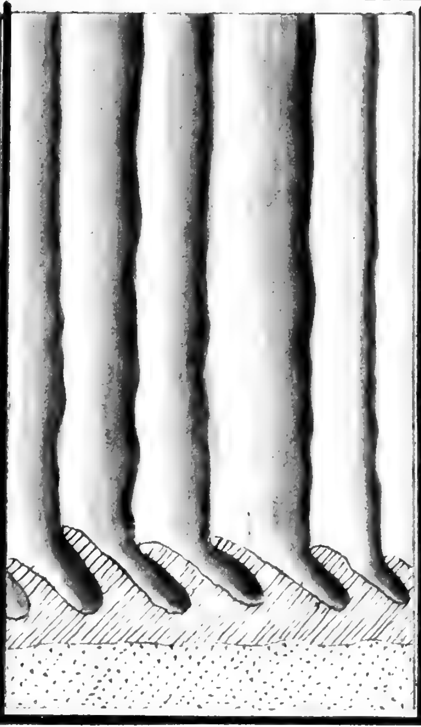
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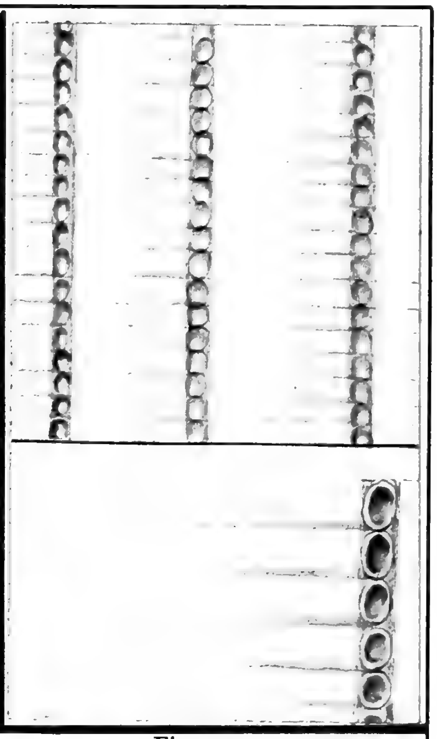
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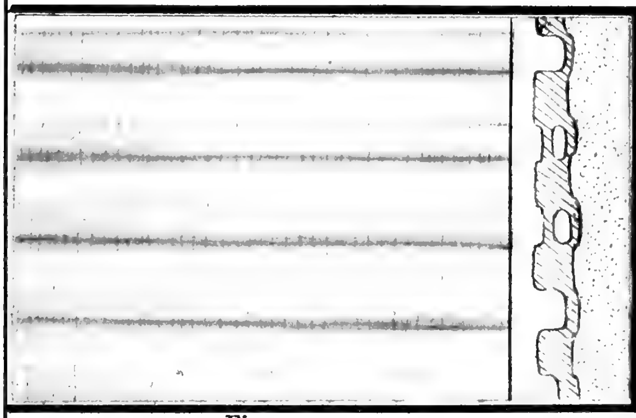
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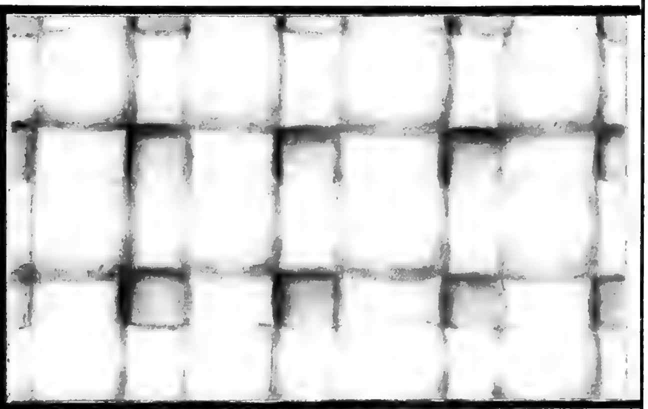
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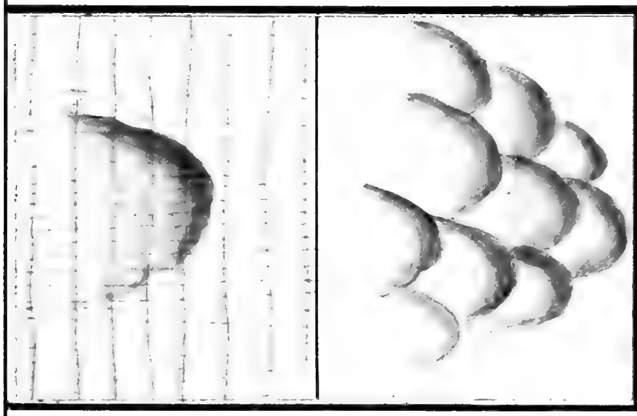
Figure 7

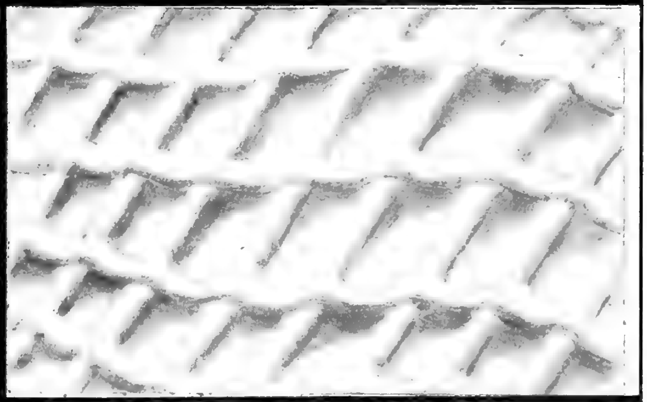
Figure 8

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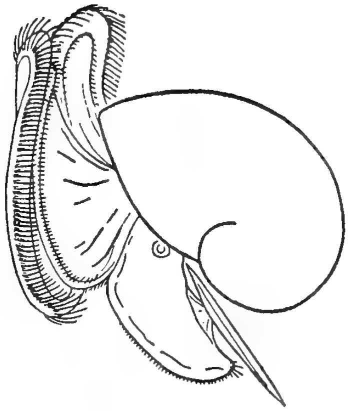

Reproductive Biology of *Thais emarginata* (Deshayes, 1839) and *Thais canaliculata* (Duclos, 1832)

BY

ROY S. HOUSTON

Pacific Marine Station, Dillon Beach, California 94929

(1 Plate; 5 Text figures)

INTRODUCTION

Thais emarginata (Deshayes, 1839) and *Thais canaliculata* (Duclos, 1832) are two common Pacific coast muricid gastropods. *Thais emarginata* is found in semi-protected rocky areas from Alaska to Baja California, while *T. canaliculata* occurs in quiet bays from Alaska to Monterey Bay, California (Ricketts & Calvin, 1966). Both species occur on rocks and jetties where they can be seen feeding upon barnacles and young mussels. Despite the abundance of these species their reproductive biology has not been examined.

Reproductive studies of muricids in relationship to environmental factors are almost non-existant. Work on the biology of *Thais lapillus* (Linnaeus, 1758) by Moore (1938) constitutes the bulk of the literature in this regard.

Other work has been directed towards the commercially important oyster drills such as the mating and spawning in *Eupleura caudata* (Say, 1822) and *Urosalpinx cinerea* (Say, 1822) (Hargis, 1961; Carriker, 1955; Manzi, 1970) and spawning behavior in *Tritonalia japonica* (Dunker, 1860) (Chapman & Banner, 1949).

In the present study, the following aspects of the reproductive biology of *Thais emarginata* and *T. canaliculata* are presented: Relationship of gonadal development to environmental factors; histological changes in the reproductive organs during the gametogenic cycle; spawning behavior; and morphology of the egg capsules.

METHODS AND MATERIALS

Ten individuals of each species were collected at bimonthly intervals for 13 months. *Thais emarginata* was sampled from the Second Sled Road area just north of the Pacific Marine Station, while *T. canaliculata* was collected on the jetty at Nick's Cove in upper Tomales Bay (Figure 7). Since the females were gregarious, half of each sample was collected in sparsely populated areas so that both males and females would be sampled. The snails were then taken to the Pacific Marine Station where shell measurements, establishing sex ratios, and preparation for sectioning were undertaken.

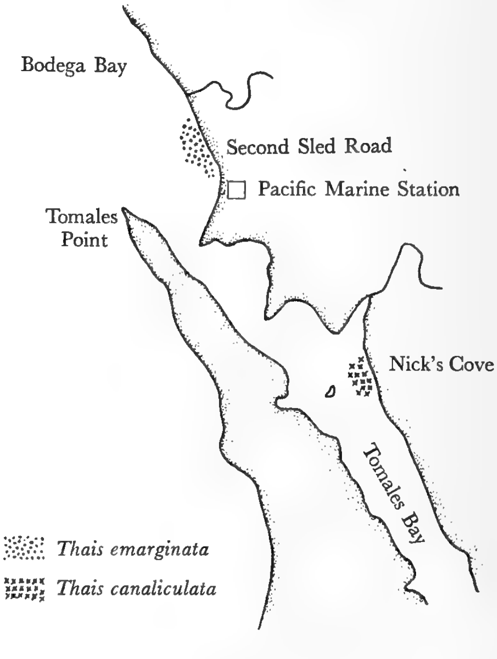

Figure 7

Collecting areas in Tomales and Bodega Bays

Length of the shell was determined by measuring with vernier calipers the distance between the shell apex and the tip of the anterior siphonal canal. Sex determination was first attempted by using the live sex technique formulated by Hargis (1957). However, this method proved impractical because it was time consuming. Therefore, sex was determined by removing the soft parts from the shell with the aid of a vise, and examining the reproductive system.

The gonads, along with various other structures of the reproductive system, were fixed in Bouin's fluid. Using standard histological techniques, the tissue was infiltrated with paraffin (melting point 52.5° C), sectioned at 10μ, stained with Harris' Hemalum, Alcian blue, and counterstained with Eosin B. Alcian blue was used for the identification of mucous cells.

Hydrographic data were monitored at both collecting stations. These included surface water temperature and surface salinity. Tide tables were interpolated in determining periodicity.

RESULTS

It is appropriate to discuss maturation of each species separately because of the difference in their reproductive biology.

Thais emarginata

Spermatozoa were present in all of the males of *Thais emarginata* throughout the sampling program. The testes consisted of many tubules each containing ripe sperm with their heads attached to the epithelial walls, and the tails extending into the lumina. Each tubule is surrounded by a thin layer of connective tissue. The seminal vesicles were densely packed with spermatozoa.

Throughout the year there were no histological changes in the prostate gland. The lumen appears as a ciliated dorso-longitudinal slit. Occasionally, blind diverticula were seen projecting into the lobes of the gland. Similar results have been observed in other neogastropods (Fretter, 1941).

Qualitative observations showed that females spawned throughout the year with most active spawning lasting from late November through February. This is similar to the spawning habits of *Thais lapillus,* mentioned by Costello *et al* (1957), Colton (1916), Moore (1938) and Pelseneer (1935). Ripe females were collected from early March until the middle of May (about 10%) whereas the other 90% of the samples showed little gametic activity. Ovaries sectioned from ripe females were packed with mature ova, while the other females showed follicle cells which contained vast amounts of connective tissue with a few immature oocytes lining the follicular walls (Figure *1* [E]).

Maturation of the gametes took place from late spring through September simultaneously with the disappearance of follicular connective tissue. In some cases mature ova were present. By the end of September nearly 70% of the females sampled had gonads packed with mature ova. Also a few cells in earlier stages of gametogenesis were present on the follicular walls (Figure *2*). By late November mass spawning had commenced.

During this period the females congregated in large clusters of 20 or more. After spawning, the snails moved from the immediate area leaving behind large masses of egg capsules.

Histological changes within the female reproductive system accompanied gametogenesis. When gametic activity was at its lowest level, there was no differentiation with respect to staining in regions of the subepithelial gland cells of the capsule gland. As the gonad ripened, the medial regions (mr) of the capsule gland lost their homogeneous staining qualities and became differentiated (Figure *3*). This differentiation was probably due to increased activity in the gland cell (sg). The ingesting gland changed conspicuously during gametogenesis. In females with little gametic activity the gland was devoid of sperm and appeared as an irregular structure containing numerous blind tubules (t) lined with epithelial gland (eg) cells (Figure *4*). In ripe and newly spawned females, however, the gland is packed with dark masses of spermatozoa (Figure *5*). Upon closer examination it appeared that the epithelial cells were actully ingesting the sperm.

Histological changes in the albumin gland were not seen.

It is interesting to note that a sperm sac (sc) is located within the capsule gland (cp). This sac runs parallel to the ventral channel (vc) and is filled with sperm, arranged in an orderly fashion with their heads attached to the walls (Figure *6*). In addition, there is a continuous opening (ov) between the sac and the ventral channel. A complete description of the reproductive systems of both *Thais emarginata* and *T. canaliculata* will appear in another report (Houston, in preparation).

Thais canaliculata

As in *Thais emarginata, T. canaliculata* males were ripe throughout the year.

[E] Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

During gametogenesis no histological changes were observed in the prostate gland. However, the general shape of the gland is different from that of *Thais emarginata.*

Contrary to *Thais emarginata, T. canaliculata* exhibited definite maturation and spawning seasons. From June to December females exhibited little gametic activity. Gonadal sections showed that the follicles contained much nutritive tissue with a few immature eggs lining the follicular wall. However, in January and February there was a rapid increase in gametic activity, characterized by a marked reduction of connective tissue within the follicles. By the 11th of March, 80% of the females sampled contained ripe ova. Gonadal sections showed follicle cells expanding with mature ova. By the 24th of March spawning was observed in the field.

The most active period of spawning extended from the 24th of March through the 19th of May. There was no sporadic spawning throughout the year as was the case for *Thais emarginata.*

Throughout the gametogenic and spawning periods sections were made of the capsule, ingesting, and albumin glands. Histological and structural changes were similar to those observed in *Thais emarginata.* No sperm sac as that found in *T. emarginata* was observed in *T. canaliculata.*

Sex and Shell Measurements

In addition to observing histological changes of gonads, sex and shell measurements were recorded for each species. Of the total sample of 252 *Thais emarginata,* 144 were female and 108 were male. Three of the females were morphological hermaphrodites. Of 252 *T. canaliculata,* 113 were female and 139 were male. There were no hermaphrodites found in *T. canaliculata.*

In both species the females were longer than the males, which suggests that sexual dimorphism may exist in these animals. Average lengths for *Thais emarginata* were 18.9 mm for females and 17.8 mm for males. Respective lengths for *T. canaliculata* were 26.5 and 24.8 mm.

Spawning Behavior and Egg Capsule Morphology

Spawning was observed in the laboratory as well as in the field. Both *Thais emarginata* and *T. canaliculata* display a similar spawning behavior. Prior to depositing egg capsules, the females twist and move in a contorted fashion. As the egg capsules are deposited, they are sur-

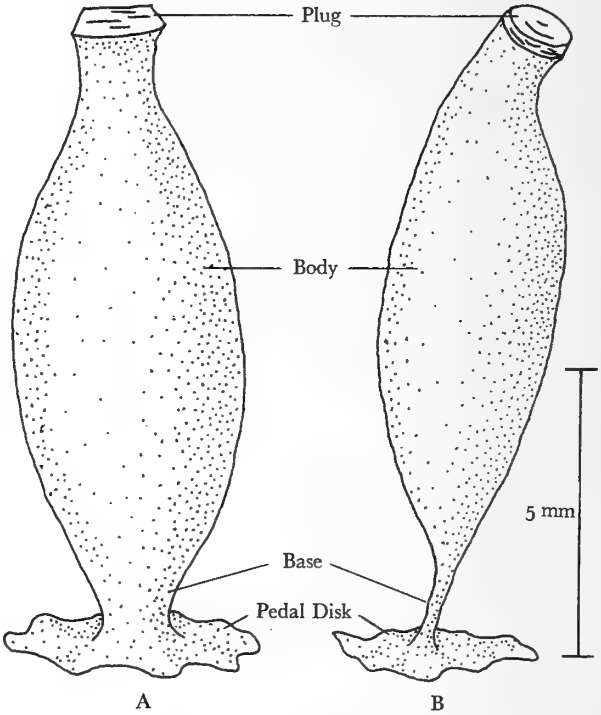

Figure 8

Egg capsule morphology of (A) *Thais emarginata* and (B) *Thais canaliculata*

Plate Explanation

Figure *1*: Section through an ovary of a female *Thais emarginata* in a state of low gametic activity

Figure *2*: Section through ripe ovary of a female *Thais emarginata*

Figure *3*: Section through a differentiated capsule gland of a female *Thais emarginata*

lc – lumen of capsule gland; mr – medial region
sg – subepithelial gland cells

Figure *4*: Section through an empty ingesting gland of a female *Thais emarginata*

al – albumin gland; cp – capsule gland;
eg – epithelial gland cells; t – tubules

Figure *5*: Section through a full ingesting gland of a female *Thais emarginata*

cp – capsule gland sp – sperm

Figure *6*: Section through sperm sac of a female *Thais emarginata*

ov – opening of sperm sac into ventral channel
cp – capsule gland; sp – sperm; vc – ventral channel

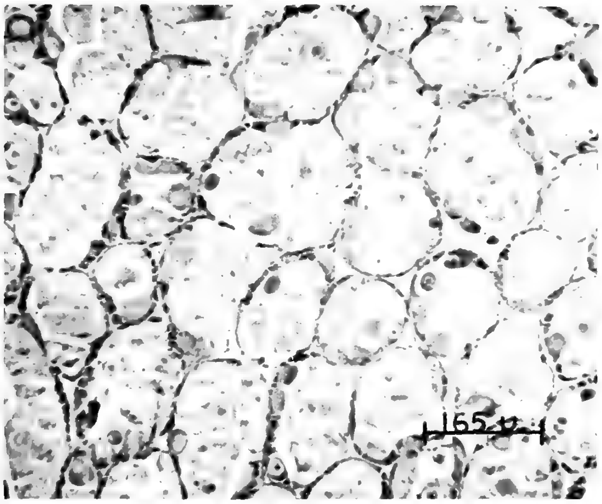

Figure *1*

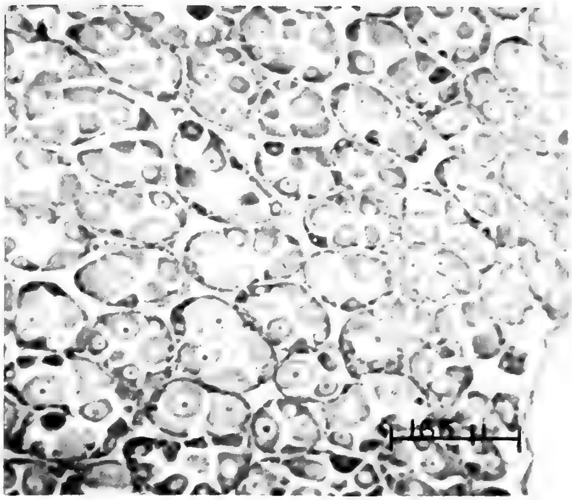

Figure *2*

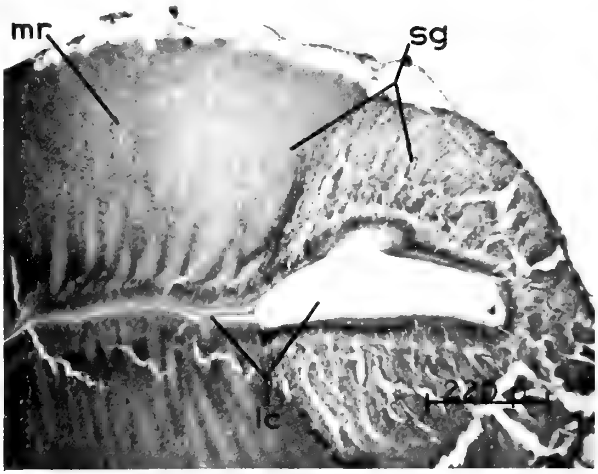
mr
sg
lc
220 µ

Figure *3*

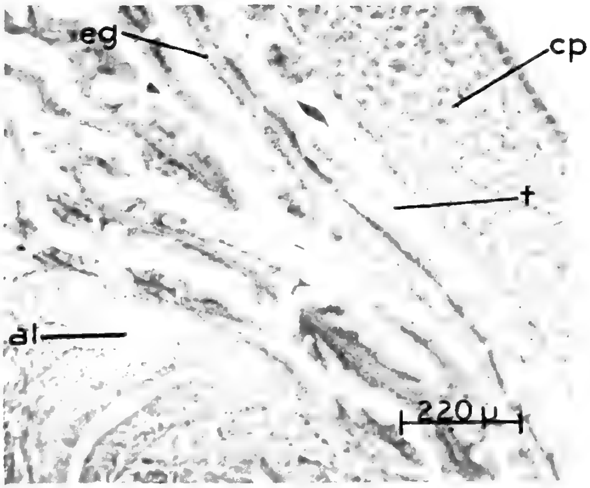
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Figure *4*

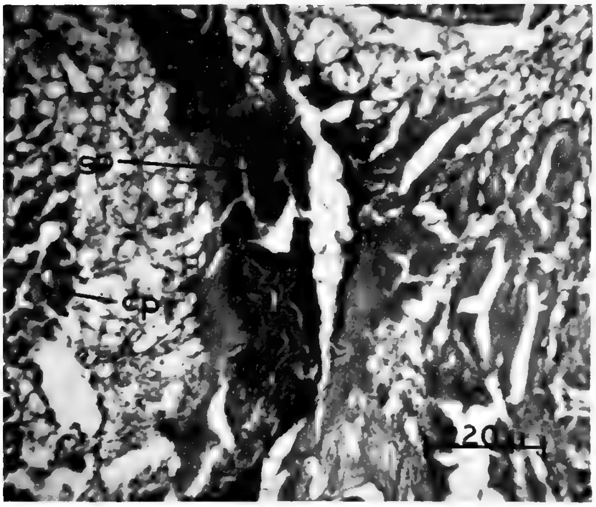

Figure *5*

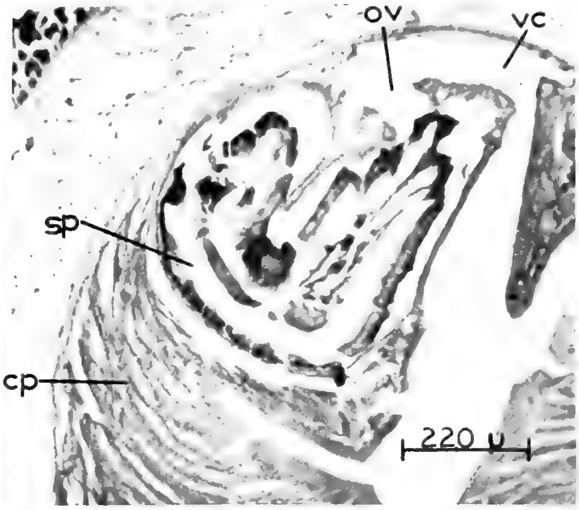
ov
vc
sp
cp
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Figure *6*

rounded by the epipodial palps and caressed or rubbed by the cephalic tentacles. The epipodial palps then constrict the base of the capsule and deposition is completed.

Capsule deposition was more rapid in *Thais emarginata* than in *T. canaliculata.* On the average, *T. emarginata* would deposit one capsule every 30 minutes, as opposed to an average of one capsule every hour for *T. canaliculata.* Individual females of *T. emarginata* would lay 8 or 9 capsules, with one female depositing 31; *T. canaliculata* females would average 6 capsules.

Morphologically the capsules of *Thais emarginata* are vase shaped with a short constricted base joining a flat pedal disk. The plug on the top of the capsule is a transparent gable-shaped covering (Figure 8).

As shown in Figure 8, the body of the capsule of *Thais canaliculata* assumes a different shape, with a narrow stalk that joins the pedal disk. The cylindrical-shaped plug at the top of the capsule is a separate hollow chamber.

Egg numbers were determined by opening the capsules and counting the eggs under a dissecting microscope. The number of eggs per case was about the same in both species (200 - 300).

Development in both *Thais emarginata* and *T. canaliculata* is direct with the young adults emerging through the opening on top of the capsule. It was observed that only a small percentage of eggs would actually develop into juveniles: 5% for *T. emarginata* and 3% for *T. canaliculata.* The remaining unfertilized eggs served as food for the developing embryos or larvae. This occurs in other neogastropods (Ankel, 1936a; Ganeros, 1958; Hancock, 1956; Kohn, 1961, and Hargis, 1961).

Hydrographic Observations

Surface water temperature, surface salinity, and daylength were plotted to exemplify the seasonal trends which

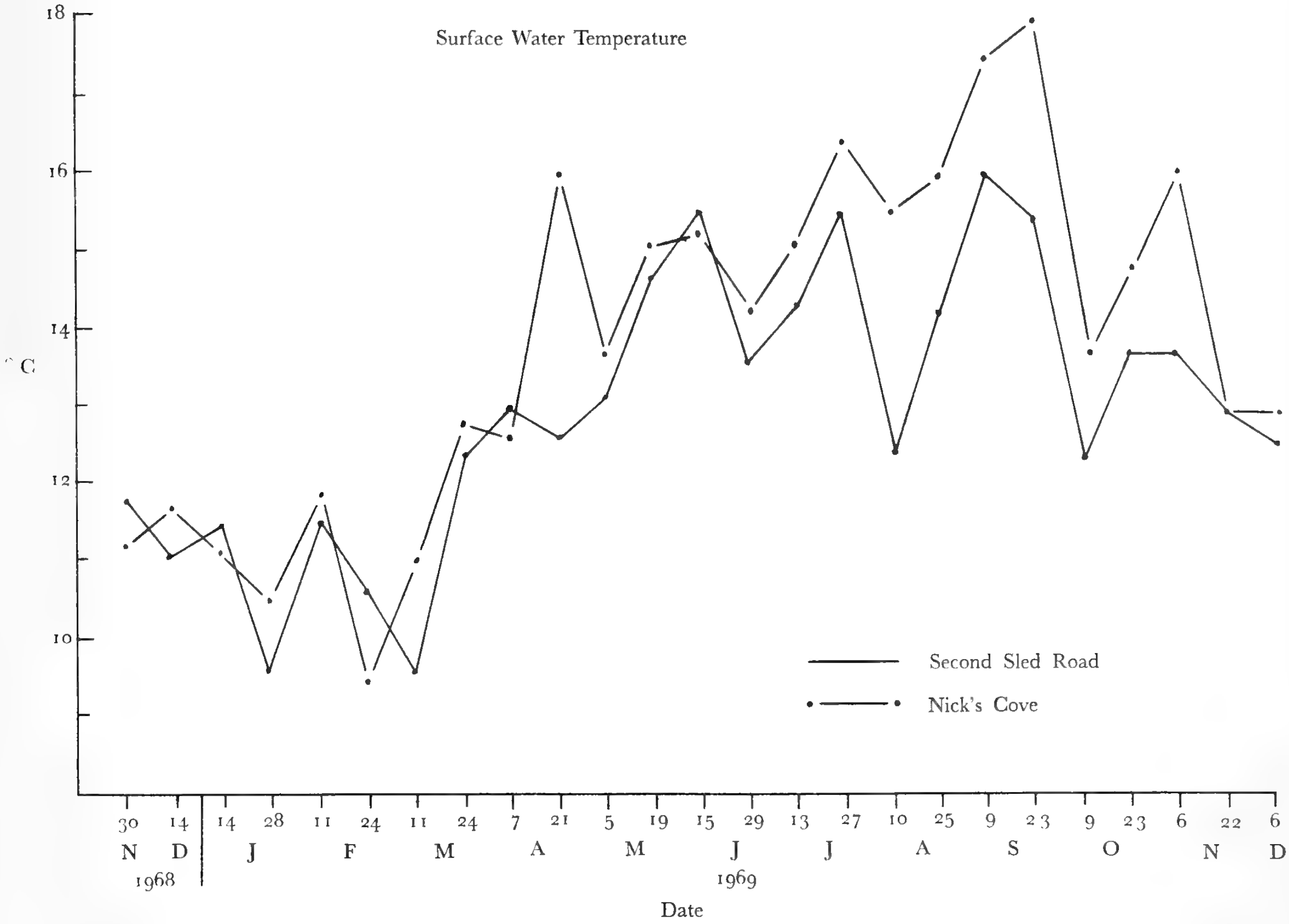

Figure 9

Seasonal trends in surface water temperature occurred (Figures 9, 10, and 11). Kinne (1963; 1964) has indicated there may be a relationship of maturation in invertebrates to changes in temperature and salinity.

In general, the seasonal trends in water temperature were the same for Nick's Cove and Second Sled Road (Figure 9). However, the water temperatures at Nick's Cove were 1° to 3° higher than at Second Sled Road. This is because the bay water was protected by adjacent land masses, and thereby subjected to local climatic conditions for longer periods than the water at Second Sled Road. There was also less mixing with offshore water at Nick's Cove. In November, a cooling trend began which lasted until the middle of January. From January through the second week in March, water temperatures remained relatively stable (9.5° - 11.8° C). Temperatures rose with maximum readings of 18° C for Nick's Cove, and 16° C for Second Sled Road in late summer and early fall.

Salinity trends were also similar for both areas (Figure 10). There was a sharp drop in salinity during the winter months. This was the result of precipitation and fresh water runoff. During February 1969 the salinity at Nick's Cove was 14.5‰, which was almost twice as low as that recorded at Second Sled Road (25.2‰). This was largely due to the runoff from adjacent Walker Creek. On the other hand, most of the runoff at Second Sled Road was carried away by the longshore currents or mixed with offshore water. In early March there was a sudden increase in salinity, which continued to rise slowly until midsummer when the highest readings were recorded (34.0‰ for Second Sled Road, and 33.8‰ at Nick's Cove). During this time the salinity remained steady until the fall when storms caused a slow steady decline.

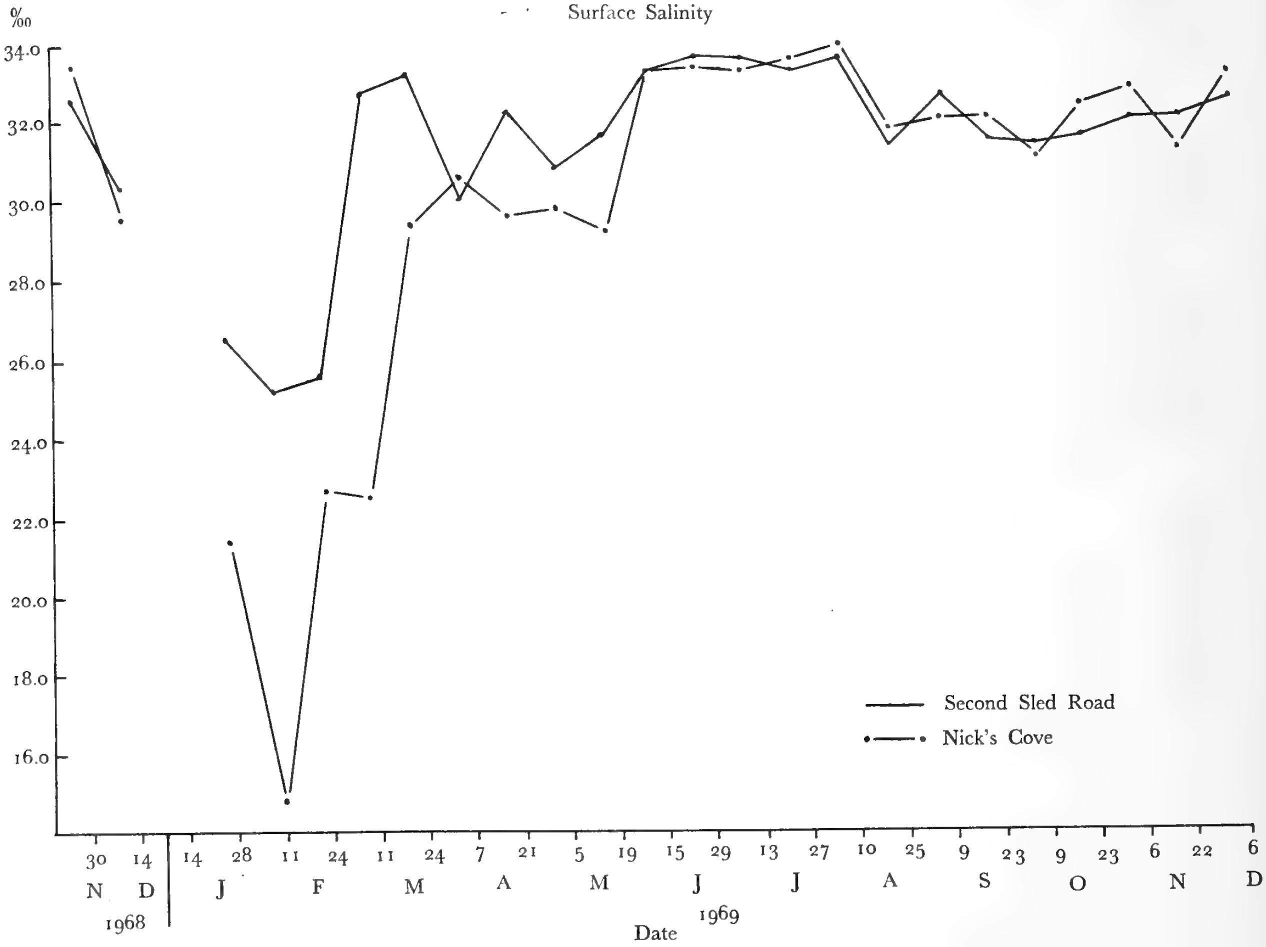

Figure 10

Seasonal trends in surface salinity

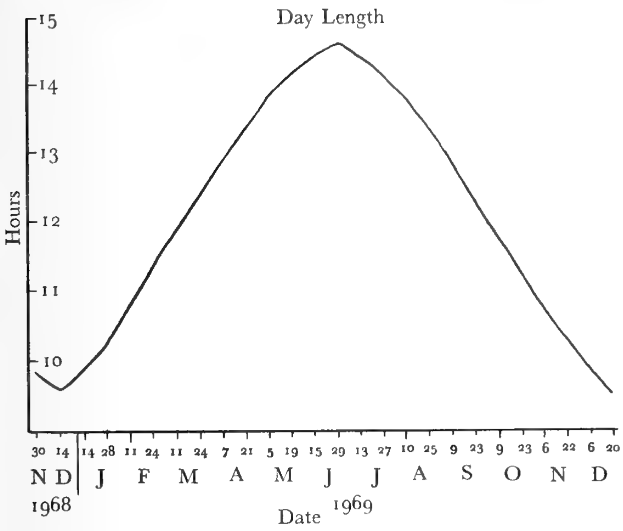

Figure 11

Seasonal changes in daylength

DISCUSSION

Environmental factors that initiate and control gametogenesis and spawning in mollusks are not well known. Loosanoff (1945; 1958) has shown that water temperature affects gametogenesis and spawning in oysters. Maturation of gametes occurs after sustained exposure to relatively high temperatures. Gametogenesis in the opisthobranch *Aplysia* has also been shown to be stimulated by elevated temperatures (Smith & Carefoot, 1967).

Contrary to the cited studies, data compiled in this investigation do not support the hypothesis that water temperature is directly correlated with gametogenesis and spawning in *Thais emarginata*.

The water temperatures at Second Sled Road exhibit a definite warming trend from late spring through the summer. During this time over 75% of the females sampled showed an increase in gametic activity. By September and early October the maximal temperatures of 16° C are obtained, and the follicles are packed with ripe ova. By late November mass spawning was observed and continued throughout the colder months until February when minimal temperatures of 9.5° C were recorded. However, observations showed that sporadic spawning occurs throughout the year. At least one ripe female was found in over 90% of the samples collected. Therefore, in this species, gametogenesis and spawning appear to be independent of water temperature. These results agree with other studies involving faunae which inhabit exposed or semi-exposed rocky intertidal areas. A 10-year study by Giese (1959) showed that gonadal development in the chiton *Katharina tunicata* (Wood, 1815) only occasionally showed a correlation with seasonal changes in water temperature. Monroe & Boolootian (1965) suggested that water temperature alone does not stimulate spawning in the chiton *Mopalia muscosa* (Gould, 1846). According to Orton (1956), hydrographic factors can hardly stimulate spawning in the limpet *Patella vulgata* Linnaeus, 1758, because different populations will spawn simultaneously in areas with varying hydrographic conditions. In addition, Giese (1969) pointed out that gonadal changes in the black abalone *Haliotis cracherodii* Leach, 1817 showed no correlation with seasonal changes in water temperature.

Thorson (1946) suggests that long spawning seasons for *Nassarius reticulatus* (Linnaeus, 1758) and *Akera bullata* (Müller, 1776) are due to their distribution over a considerable vertical range. Consequently, the critical temperature for spawning at different depths would be reached at different times. This does not apply to *Thais emarginata* because of its narrow vertical range (about 2 feet).

The gametogenic cycle is quite different for *Thais canaliculata* in that definite seasonal trends exist. Gametic activity occurs from January until the middle of March when water temperature is coldest. At this time the ovaries of 80% of the females examined were ripe.

It is apparent that water temperature does not directly affect gametogenesis because it occurs when temperatures are relatively stable (Figure 9). There is a correlation between water temperature and spawning. During the latter part of March, when temperatures began to warm up, mass spawning occurs. Peak spawning occurs through May until the warming trend starts to level off. At this time there is a marked decrease in spawning even though slight increases in water temperature occur throughout the summer. By this time, sections of all of the gonads collected, were devoid of mature ova, indicating that the females were spent. Loosanoff (1942; 1965) demonstrates the effect of temperature upon spawning for *Crassostrea virginica* (Gmelin, 1791) in Long Island Sound where climatic conditions are different from those in California.

There does not appear to be a relationship between salinity and gametogenesis, because there was almost 4 months of continuous precipitation from late 1968 through January 1969. It is difficult to assess if the extremely low salinities encountered from January through March affected the gametogenic and spawning periods of either species. The trends from high to low salinities, however, are almost in phase with seasonal fluctuations in water temperature (Figures 9 and 10).

Photoperiod is not correlated with gametogenesis and spawning in *Thais emarginata* because sporadic spawning was observed throughout the year. However, photoperiod may affect gametogenesis and spawning in *T. canaliculata*. Increased gametic activity started soon after the increase in daylength. By the time there were approximately 12 hours of daylight, 80% of the females collected were ripe. The period of most active spawning continued from the end of March through May, with a sudden decrease in activity during the period of maximal daylength.

Giese (1969) determined that the period of most rapid gonadal growth in *Haliotis cracherodii* started when daylength was at its maximum and continued through September as daylength decreased. However, his data do not clearly substantiate a direct relationship between photoperiod and gametogenesis. He suggests the possibility that photoperiod may initiate the gametogenic cycle. Then after spawning, if daylength is still greater than the minimum, gametogenesis will again be initiated.

Lunar periodicity has been suggested to stimulate spawning. Grave (1922) has shown this relationship for the chiton *Chaetopleura apiculata* (Say, 1830). The oyster *Ostrea edulis* Linnaeus, 1758 lays more eggs between full and new moons than between new and full, although it is uncertain whether it is the phases of the moon or some other parameter (Korringa, 1947).

It was previously mentioned that both *Thais emarginata* and *T. canaliculata* feed upon barnacles and small mussels. From laboratory observations it was noticed when both barnacles and mussels were placed in the same pans with either species, that the snails would first consume the barnacles and then the mussels. Therefore, the primary diet of either species consists of barnacles. It was observed that *Balanus glandula* Darwin, 1854 sets during the same period in which *T. canaliculata* spawns (Mrs. Sondra Smith, personal communication). If the timing is right, when the young snails hatch they will be able to feed upon the newly set barnacles. More work is needed in this area before a conclusive relationship can be established.

Control of gametogenesis and spawning may be indirectly correlated with environmental conditions. Loosanoff & Davis (1952) propose that gametogenesis could be affected only indirectly by environmental parameters which would act on an internal regulating system. Regulating systems affecting gametogenesis have been described in cephalopods (Wells & Wells, 1959). Such regulating systems were not examined in the present study.

It has been shown that this study and the previous work has been concerned with organisms that occur in two different environments: the rocky intertidal and the protected bay areas. Each one of these areas has its own set of variables which may be entirely different from one another. The point that should be emphasized is that direct correlation of environmental factors to gametogenesis and spawning has arisen from studies on bivalves in protected bays, as opposed to those conducted on chitons and gastropods in coastal rocky intertidal regions.

An excellent example is in Long Island Sound where Loosanoff (1942) found wide temperature fluctuations to be directly correlated to gametogenesis and spawning in *Crassostrea virginica*. On the other hand, Orton (1956) has suggested that there may be a correlation between waveshock and the onset of spawning in *Patella vulgata*, which occurs on the rocky coast of the British Isles. In addition, Hedgpeth & Gonor (1969) have shown that internal temperatures in marine invertebrates are different from surface water temperatures taken synoptically. Mussel populations that were exposed for 6 hours in early summer have mean internal temperatures ranging from 19° C to 24° C, and often from 27° C to 31° C. On the other hand, surface water temperatures ranged between 10° C and 12° C.

In conclusion, a vast amount of work and thought should be directed towards improved instrumentation and experimental design when working with physiological processes of intertidal organisms in relation to environmental factors.

Various glands and structures within the reproductive system undergo cyclic changes during gametogenesis. It was noticed in both *Thais emarginata* and *T. canaliculata* that the staining properties of the capsule gland changed with periods of gametic activity. Bayne (1968) has shown histochemically that egg capsules of prosobranch gastropods are composed of several layers. These layers are constructed from different compounds of glycoproteins and mucopolysaccharides. Since differentiation in the gland occurs during periods of high gametic activity, it is possible that these different staining patches are gland cells specific to the different secretions that compose an egg capsule. As the ovary ripens, these gland cells become active in preparation for the formation of the capsules. After spawning the gland cells become inactive, and the gland assumes its homogeneous staining quality.

In ripe females there is increased activity in mucous cells that are in proximity to the ventral channel. Since there is no musculature within the capsule gland, these mucous cells, with the help of cilia, may aid in the removal of the egg capsules from the gland. The twisting movements of the female during deposition may also aid in the removal of the capsules.

As described earlier, the ingesting gland appears to be cyclic in accordance with gametogenesis and spawning. In females which have recently spawned the presence of sperm balls within the lumen of the gland suggests that sperm remaining after fertilization are resorbed. Spermatozoa were actually seen being ingested by epithelial gland cells in *Thais emarginata*. These observations agree with those of FRETTER (1941). MARCUS & MARCUS (1962) have observed sperm ingestion within the bursa copulatrix and gonopericardial duct in columbellids that do not have a separate ingesting gland. Sperm ingestion has also been observed in similar glands of other prosobranchs (FRETTER, 1941; SMITH, 1967).

In *Eupleura caudata* and *Urosalpinx cinerea,* HARGIS & MACKENZIE (1961) argue that if sperm left over from one mating are not completely resorbed, then they are viable for the next spawning period. They also suggest that sperm ingestion would be a way of disposing of "sick" sperm which would otherwise penetrate ripe ova and block the passage of viable sperm. On the other hand, FRETTER (1941) suggests the possibility that ingested sperm serve as nourishment for the adult.

Since the males of both species are always ripe, there are no seasonal variations in the prostate gland.

The existence of an anterior sperm sac in *Thais emarginata* may account for the sporadic spawning noted throughout the year. Retention of sperm would enable females to fertilize and deposit capsules without ever coming in contact with a male again. It was previously mentioned that spawning rates and number of capsules deposited for an individual female were greater for *T. emarginata* than for *T. canaliculata*. These higher rates may possibly be attributable to the presence of the sperm sac because the retention of sperm would increase the production of fertilized ova, which in turn would require a greater number of egg capsules.

Observations by MARCUS & MARCUS (1962) point out that in some species of columbellids the bursa copulatrix is divided into two sacs. One side serves as a site for ingestion, as mentioned earlier, while the other is used for sperm storage. A similar case is known from the Rissoidae (JOHANNSON, 1957).

It is noted that 1.2% of the population of *Thais emarginata* are morphological hermaphrodites. They are functional females with a rudimentary male system containing a small penis and the anterior portion of the penial duct. In *Lora turricula* (MONTAGU, 1803), SMITH (1967) found different stages of hermaphroditism existing within a population.

FRETTER & GRAHAM (1964) suggest that genetic changes and environmental conditions are two criteria for hermaphroditism in a population. The "gene dispersal model" for hermaphroditism is stated by GHISELIN (1969). He says that the genetic environment of a population may be affected by limitations upon gene dispersal. For example, if there is a greater number of one sex, the number of viable crosses would be decreased, thereby lowering the variability within a population. Hence, simultaneous hermaphroditism would equalize the sexes, thereby increasing the effective population size. This may possibly explain why the sex ratio in *Thais emarginata* is more or less stabilized.

MURRAY (1964) points out that in addition to hermaphroditism, multiple matings and sperm storage will maximize the effective population variability. This would explain the functional importance of the anterior sperm sac. If multiple matings occur, the female will have sperm from different males in her sperm sac. The resulting embryos, collectively, would then contain a wide variety of hereditary factors. HARGIS (1961) has suggested this for *Urosalpinx cinerea* and *Eupleura caudata.*

It was previously stated that the external shape of the egg capsules is different for *Thais emarginata* and *T. canaliculata.* FRETTER & GRAHAM (1962) state that in neogastropods the shape of the cavity of the ventral pedal gland resembles that of the egg capsules. In these species there was no difference observed in the shape of the glands. In *Torvamurex territus* (REEVE, 1845) the capsules are vase-shaped (MURRAY, 1964) as opposed to lens-shaped capsules in the oyster drill *Bedeva hanleyi* (ANGAS, 1867) (HEDLEY, 1916).

Egg capsules of *Thais emarginata* and *T. canaliculata* contain large numbers of eggs of which only 3 to 5% developed into adults. On opening the capsules it was noted that most of the eggs had fused into a yolk mass on which the developing larvae fed. Nurse egg feeding is known for *T. lapillus* (COSTELLO *et al,* 1957) and other neogastropods (FRETTER & GRAHAM, 1962). On the other hand, MURRAY (1964) noted that the Australian muricid *Torvamurex territus* deposits 9 to 25 eggs per capsule, all of which develop into adults.

According to THORSON (1950), prosobranchs with wide zoogeographical ranges tend to have brood protection and direct development, or both, in colder waters, and free-swimming larvae in warmer waters. He has shown this to be the case for *Thais haemastoma* (LINNAEUS, 1767). Since the zoogeographical range of *T. emarginata* is so great, it would be interesting to test Thorson's hypothesis on populations of this species that occur along the coast of Baja California.

SUMMARY

1. *Thais emarginata* spawns throughout the year with the most active spawning period from late November through February. From September to early November 70% of the females collected were ripe. However, ripe females were collected throughout the entire sampling program. Changes in gametic activity showed no direct correlation with water temperature, salinity, or photoperiod.

2. *Thais canaliculata* exhibited a definite gametogenic and spawning period. In January and February 80% of the females contained ripe ova, with peak spawning occurring from the end of March through the middle of May. There was no direct correlation between gametogenesis and changes in water temperature because gonadal development occurred when temperatures were relatively stable. Increasing temperatures, however, appear to affect spawning. In addition, photoperiod may influence spawning, for active spawning occurred during periods of increasing day length.

3. During the gametogenic cycle histological changes were noted in the capsule and ingesting glands of both species. As gametic activity increased, different glandular areas became differentiated with respect to staining. Also, it appeared that sperm ingestion was taking place in females that had just spawned. Sections made of female *Thais emarginata* revealed the presence of an anterior sperm sac within the capsule gland. Also, 3 morphological hermaphrodites were collected.

4. Egg capsules differ in their morphology for each species. Development is direct with the young hatching out through an opening on top of the capsule.

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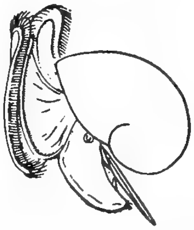

Criteria for Categorizing Feeding Types in Bivalves

BY

ROBERT G. B. REID

Department of Biology, University of Victoria, Victoria, British Columbia, Canada

THE PROBLEM OF SUBDIVIDING groups of organisms according to criteria other than phylogenetic relationships necessarily involves arbitrary divisions. This is so for categories of feeding types in the bivalves, and as POHLO (1969) points out confusion ensues if the arbitrary criteria are ill-chosen.

If a bivalve feeds on suspended particles it is called a suspension feeder, whether the particles are planktonic in origin, or are stirred-up deposit particles, and if a bivalve orientates its siphon to take up material at or near the surface of the substrate it is called a deposit feeder, although it may take up suspended particles also. Since both types of food are likely to be ingested at some time or another is the distinction worth perpetuating?

Both Pohlo and myself (REID & REID, 1969) use the behaviour of the inhalant siphon as the chief criterion for classification of feeding types, but I believe that this matter deserves a more exhaustive consideration. The feeding of a bivalve involves several stages: 1. siphon behaviour, which can determine the uptake of suspended material, deposited material, or both; 2. pallial sorting activities, which can reject the majority of particles drawn in through the inhalant siphon; 3. gastric processes which may reject particles on the basis of size, density or indigestibility. If categorization is to be based on a single criterion it should be the type of food from which the animal derives the bulk of its nutritional requirements. However, all three feeding stages deserve attention.

There are three possible food sources for these molluscan microphages: phytoplankton, detritus, and the microflora and microfauna found growing on the surfaces, and in the fissures of organic and inorganic particles. Since bivalves are unable to distinguish between detritus and its associated microorganisms this leaves us with only two categories: those animals which depend mainly on phytoplankton, and those which depend mainly on deposit materials and their associated microorganisms. These two categories correspond with what have been called in the past suspension feeders and deposit feeders respectively. However, in our work on the genus *Macoma* (REID & DUNNILL, 1969; REID & REID, 1969), which seems to run the whole gamut of feeding behaviour and food sources found in the Tellinacea, we further divided the deposit feeders into two categories: those which ingest fine deposits only, and those which ingest sand grains and presumably derive their food from the microorganisms associated with the sand grains. Finding an apt name for the latter category has so far eluded me. The feeding characteristics of these three groups are as follows:

Suspension Feeders – siphons project from the substrate; pallial sorting mechanisms accept particles up to 100μ; stomach contents characteristically green or brown from the preponderance of phytoplankton, though in winter months are colourless and have same constituents as the deposit feeders.

Fine Deposit Feeders – siphons lie along the surface of the substrate and the tip of the inhalant siphon may bend over to touch the surface and take up clumps of deposit material; pallial sorting mechanisms reject most particles more than 20μ; stomach contents are mainly small particles of organic debris and silt, together with small phytoplankton.

Sand Grain Feeders – inhalant siphon describes circles, with the tip touching the substrate and taking up sand grains and deposit material; pallial sorting mechanisms accept particles up to 300μ and more; stomach contents are mainly large sand grains, together with phytoplankton; stomach has large embayment protected by an extension of the crystalline style; gastric esterases and proteases are stronger than in the other two groups (REID & DUNNILL, 1969, and unpublished work).

NOTES

1. I use the expression "pallial sorting mechanisms" in the broad sense, since in our work on *Macoma* (REID & REID, 1969) we found no specific differences in the ciliary sorting mechanisms and concluded that the specific differentiation in the size of particles accepted was based on

the quality or quantity of the mucus secreted, although there may be differences in the ciliary sorting mechanisms of the Tellinacea as a whole.

2. The inclusion of the enzymatic characteristic in the sand grain feeders is justified on the basis of *Macoma secta* (Conrad, 1837) only, and it would be most interesting to see if this applies in the cases of the other sand grain eaters in the Tellinacea. It is postulated that the proteases particularly aid in the release of the colonies of microorganisms from the surfaces of the sand grains.

3. The large extension of the gastric shield is found in many of the other Tellinaceans (Yonge, 1949).

The use of any single criterion as a basis for feeding types is open to the kind of criticism put forward by Morton (1960), and reported by Pohlo (1969): "the difference in feeding habits is not great, for surface deposits are stirred into suspension and deposit feeders imbibe suspended material." However, by considering all the factors concerned in feeding there emerge three types. Two of these types are the suspension feeders and the fine deposit feeders. The main distinction between them is that the gastric contents of the former are composed of phytoplankton during those months when it is available. The other distinctions, such as size of particles accepted, and mucus quality, are more matters of degree. However, all warrant the division into two categories. The third type "sand grain eaters" is distinctive in all respects.

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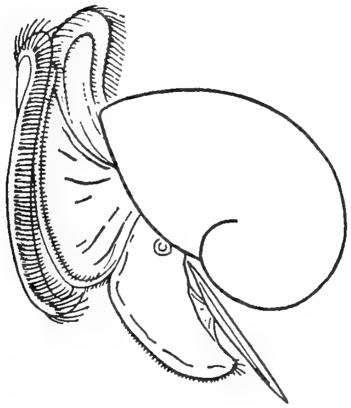

Composition of Uterine Fluid of *Viviparus bengalensis* and its Utility for the Brooding Young

BY

D. BALAKRISHNA RAO, M. C. VENKATA SUBBAIAH, P. VENKATESWARA RAO

AND

K. S. SWAMI

Department of Zoology, Sri Venkateswara University, Tirupati (A. P.), India

(2 Tables)

The banded pond snail *Viviparus bengalensis* (Lamarck) is ovoviviparous and broods the young in the uterine brood chamber up to the crawling stage. Embryos of all stages may be obtained from this chamber throughout the year. This chamber is observed to contain a viscous fluid (uterine fluid) in which hatched as well as unhatched embryos are bathed. Moreover, live young ones could be collected in large numbers from the adults kept for aestivation in dry sand for more than three months. Live young ones collected from active adults when kept buried in pure acid-washed sand could not survive for more than 24 hours, while they could survive in water without food for a few days only. Since the young ones could live inside the aestivating adults for more than three months, it is felt that the uterine fluid provides the required moisture and help in the nutrition of the young. With this in view, the constituents of uterine fluid have been estimated (Table 1).

The animal is removed from the shell with the least possible injury, blotted free of moisture, and the brood chamber is punctured. The fluid oozing out of the rather large puncture is collected with a micropipette or syringe, diluted with glass-distilled water to a known volume and used for estimations.

Galactogen was estimated by the Orcinol sulphuric acid reaction, and the level was read from the graph prepared by measuring the corresponding quotient values for the mixed solutions (Bruckner, 1953). Glycogen was determined colorimetrically by the method of Kemp *et al.* (1954). Protein content of the fluid was estimated with the folin phenol reagent (Lowry *et al.*, 1951). Inorganic phosphorus was determined by the method of Fiske & Subbarao, 1925, using 1, 2, 4-aminonaphtholsulfonic acid as reducing agent. Sodium, potassium and calcium were estimated by flame photometry using Kipp's H45-392, Holland flame photometer, while magnesium was determined colorimetrically as magnesium-Erichrome black T soluble complex (Smith, 1955). Lipid in chloroform-ethanol extracts of the fluid and total solids in the fluid were determined gravimetrically.

Galactogen, which is known to be a staple reserve food (Wilbur, 1966) for developing molluscan embryos, is found to be the major uterine constituent. Besides this, the uterine fluid seems to be rich in glycogen and protein. The fat content is low. Evidently the young snails in the brood chamber must be thriving on galactogen, glycogen, and protein. Of the other constituents (Table 1) estimated sodium and calcium are in appreciable quantities, while

Table 1

Composition of Uterine Fluid (mg/ml)

S. No.:	pH	Total Solids	Protein	Fats	Glycogen	Galactogen	Calcium	Inorganic Phosphorous	Sodium	Potassium	Magnesium
Mean	8.7	287.27	15.25	0.0127	2.633	25.10	0.445	0.0030	0.860	0.190	0.013
S. D.	–	±4.479	±0.0322	±0.00083	±0.0058	±2.05	±0.00055	±0.00006	±0.00081	±0.0000024	±0.0000458

magnesium and inorganic phosphorus are not. This may be due to the important role calcium and sodium may play in maturation, cleavage, and gastrulation and the maintenance of the colloidal structure of the egg cortex (Raven, 1958).

It is observed that on aestivation the quantity of the fluid and its total solids decrease considerably with time (Table 2) and the embryos are found sticking closely together in the uterine brood chamber, suggesting the possibility of the utilization of uterine fluid during aestivation. It is further observed that no unhatched embryo could be recovered from the uterine chamber of 50 animals kept under aestivation for three months. All these studies indicate that embryos develop, hatch and grow at the expense of uterine fluid, even inside the aestivating adults. The pH of the uterine fluid (Table 1) at 8.7 seems to favour such development and growth of the young.

Table 2

Total Solids (mg/ml)

State	Mean	S. D.
Active Life	287.27	± 4.479
Aestivation Period	213.00	±17.600

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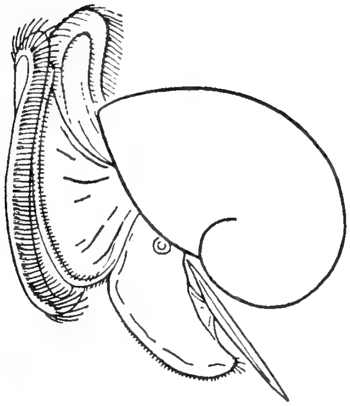

Additions and Corrections to Two Recent Articles on Ovulidae

(Gastropoda)

BY

CRAWFORD N. CATE

12719 San Vicente Boulevard, Los Angeles, California 90049

In two recent articles describing a total of 17 new species of Ovulidae (Cate, 1970; Azuma & Cate, 1971), the paragraphs containing the discussions of the various species, and their respective comparisons with other related species, were inadvertently omitted due to several unfortunate circumstances. I therefore offer them herewith, with my apologies, in order to validate the new species in conformance with the International Code on Zoological Nomenclature (ICZN Art. 13a (i)).

Another error, as yet unexplained, occurred in the preparation of the first plate accompanying the paper by Azuma & Cate. A corrected plate accompanies this issue of the Veliger and it is suggested that this plate be substituted for the misnumbered plate.

To Cate, 1970: A new species of Japanese Ovulidae. The Veliger **13** (2): 181, Figure 1.

Primovula azumai Cate, 1970 most closely resembles *P. mariae* (Schilder, 1941); however, *P. azumai* is less rhomboid, more roundly ovate; it has a more pointed adapical terminal beak which lacks projecting teeth; it is bulbously rounded dorsally, without the transversely angled dorsal ridge of the Schilder species, and finally, *P. azumai* has a rich, honey-yellow color instead of being entirely white.

To Azuma & Cate, 1971: Sixteen new species and one new genus of Japanese Ovulidae. The Veliger **13** (3): 261 - 268; figures *1* through *16*.

1. *Prionovolva (Prionovolva) aenigma* Azuma & Cate, 1971 (Figure *1*) appears to be most closely related to *Ovula hervieri* Hedley, 1899, but it differs from that species significantly by its more rounded form, rather than being subpyriform; by lacking the typical overall dorsal striation of *O. hervieri,* being smooth and glossy instead; by possessing a differently formed funicular projection on the rear base; by having a greater number of teeth on the outer lip, and by a different arrangement of its color pattern.

2. *Prionovolva (Prionovolva) nebula* Azuma & Cate, 1971 (corrected Figure *4*) appears to most closely resemble *P. nipponensis* (Pilsbry, 1913), but clearly differs from that species by its more elongately narrow shell, by its more narrowly projecting adapical terminal beak, by a flatter plane on the outer lip, by the more developed teeth on the outer lip, and by possessing a distinct dorsal color pattern.

3. *Pseudosimnia (Diminovula) incisa* Azuma & Cate, 1971 (Figure *3*) may be compared with *P. punctata* (Duclos, 1831) as its most closely related form, but it differs from *P. punctata* in that it is much more slender with more elongate terminal processes, a straighter aperture, a crenate funiculum, and its teeth at the rear of the outer lip project beyond the periphery of the lip; also, the dorsal spotting of *P. incisa* is less distinct than that of *P. punctata.*

4. *Primovula virgo* Azuma & Cate, 1971 (corrected Figure *2*) most closely resembles *P. verconis* (Cotton & Godfrey, 1932) among its congeners, but is larger, with a prominent funicular process that is apparently lacking in *P. verconis*; *P. virgo* has a deeply incised dorsum, which seems to be lacking in the worn type specimen of *P. verconis,* and in *P. virgo* the peripheral teeth on the outer lip are lengthened into distinct projections.

5. *Primovula horimasarui* Azuma & Cate, 1971 (corrected Figure *6*) somewhat resembles *P. depressa* (Sowerby 3rd, 1875), but differs by being smaller, lacking in dorsal color, by having a more contorted aperture with the inner line of the outer lip more acutely angled; by possessing an angled funicular ridge on the rear base, and its terminal beaks project at a different angle than those of *P. depressa.*

6. *Primovula colobica* Azuma & Cate, 1971 (corrected Figure *5*) seems to resemble *P. mariae* (Schilder, 1941)

very closely, and may eventually, upon the discovery of additional specimens, be considered as a subspecies of *P. mariae*. However, despite the mutilation of the type specimen of *P. colobica* it seems to differ from *P. mariae* in the following respects: it has a more pyriform shell outline, the outer lip teeth are not lengthened, it has a more rigid, elevated and narrowed abapical base, it has a broader, more flattened fossular flange, and a much more colorful shell.

7. *Primovula myrakeenae* Azuma & Cate, 1971 (Figure *7*) is rather closely related to *P. azumai* Cate, 1970, but *P. myrakeenae* has a much broader, more bulbous shell form, less tortuous terminal beaks, and is much less prominently striate dorsally; it also has a broader, more curved aperture, less developed outer lip with finer, weaker teeth; also the color patterns of the two species are different.

8. *Primovula mucronata* Azuma & Cate, 1971 (Figure *8*) may be compared with *P. azumai* Cate, 1970, but it is more narrowly ovate and elongate; it lacks the central dorsal striae; it has a straighter and more even aperture, more simple terminal beaks, more numerous teeth on the full length of the outer lip, which lacks the angles and constrictions present in *P. azumai*; the basic color of the shell is different and so, also, is its color pattern.

9. *Primovula tosaensis* Azuma & Cate, 1971 (Figure *9*) most closely resembles *P. inflexa* (Sowerby 2nd, 1832), but differs from that species by being a smaller, less ovate, narrower form with a less sharply formed, inflected funiculum; by having the base constricted in front; it also has a much narrower aperture with an angled and serpentine edge to the outer lip, and is a solid grey color dorsally.

10. *Phenacovolva tayloriana* Azuma & Cate, 1971 (Figure *10*) possesses some of the morphological aspects of *P. recurva* (A. Adams & Reeve, 1848) but *P. tayloriana* is a much smaller species, with a more ovate, less angled dorsum in the central portion; it has shorter, broader, more open terminal canals and aperture, and it has a more prominent thickening of the outer lip.

11. *Phenacovolva kiiensis* Azuma & Cate, 1971 (Figure *11*) most closely resembles *P. subreflexa* (A. Adams & Reeve, 1848), but *P. kiiensis* has narrower and more recurved terminal beaks; it has a less angled outer lip and a broader aperture, and a different combination of shell colors.

12. *Phenacovolva improcera* Azuma & Cate, 1971 (Figure *12*) has many of the shell characteristics of *P. angasi* (Reeve, 1865), but it is much smaller; it has a striate, rather than glossy, polished dorsum; it has sharper and more pointed terminal ends, with a less constricted base in front; and the color is a different shade of white, often with brown terminal tips.

13. *Phenacovolva yoshioi* Azuma & Cate, 1971 (Figure *13*) may be compared with *P. piragua* (Dall, 1889), but appears to differ from that species by having a distinct dorsal striation over the entire dorsum instead of only faint striations at the terminal ends; it has a more flattened base and a narrower aperture; the adapical terminal beak is more recurved, and the shell is more colorful, with a different combination of shell colors than those in *P. piragua*.

14. *Kuroshiovolva shingoi* Azuma & Cate, 1971 (Figure *14*) is so unusual in form that it was necessary to erect a new genus for it; therefore it is difficult to single out any other ovulid species with which to make a comparison. Perhaps it can best be compared with the form of the razor clams, or *Ensis* species, although of course it is not a pelecypod. There is no constriction of the outer lip, as seen in the other species of Ovulidae.

15. *Pseudosimnia (Diminovula) fulguris* Azuma & Cate, 1971 (Figure *15*) very closely resembles *P. florida* Kuroda, 1958, but when viewed under magnification it seems different in the following respects, the similar dorsal pattern notwithstanding: *P. fulguris* has longer, more squarely blunt terminal beaks; a broader, more flattened outer lip with less numerous, larger and more weakly formed teeth; it has a broader, more convex columellar-fossular channel, and is transversely striate dorsally, with broader and deeper sculptured lines.

16. *Primovula fumikoae* Azuma & Cate, 1971 (Figure *16*) somewhat resembles *P. rhodia* (A. Adams, 1854); however, it differs by being larger and broader; it has a more angled dorsal hump; it lacks the constriction of the abapical base, and it has a narrower outer lip with weak, poorly formed teeth.

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METHODS & TECHNIQUES

The Construction of a Collecting Device for Small Aquatic Organisms and a Method for Rapid Weighing of Small Invertebrates [1]

BY

KERRY BRUCE CLARK

Marine Research Laboratory
University of Connecticut, Noank, Connecticut 06340

(1 Text figure)

WHILE STUDYING the changes in populations of nudibranchs, I have frequently had to collect and obtain dry weights of many small animals. To facilitate this, I have devised two techniques which I feel may be helpful to others working with small invertebrates. One technique is the construction of a suction device used for the rapid collection of small aquatic organisms; the other is a method of rapidly weighing small objects.

I consider that nudibranch biologists have, in the past, placed too much reliance upon length as an indicator of size, probably because length is normally an easier measurement to obtain, as well as being non-destructive of the animal where only a few are available. It is my hope, therefore, that the techniques presented here, by enabling the collector to obtain greater numbers of animals, and lessening the labor involved in weighing, will encourage others to benefit from the greater precision resulting from the use of dry weight as a measurement.

The collecting device, intended primarily for use with SCUBA, utilizes suction to entrap clinging, floating, or swimming organisms. Its design was inspired by several other collection devices, including the "slurp gun" of tropical fish collectors and the "Acadian SOCK" (BLEAKNEY, 1969). The most important feature of the collector is the use of two simple one-way valves, which create great efficiency and speed of action. The valves may be obtained as components of a polyethylene gasoline siphon pump, which costs about $1.25 and is available in most hardware, boating or automobile supply stores. The other materials required are a soft-walled 250 or 500 ml capacity polyethylene sample bottle with a 22 mm diameter threaded neck, obtainable from any biological or chemical supply department; plastic window screening or similar fine plastic mesh; a plastic "T" or "Y" tubing connector, or a "quick-disconnect" tubing connector (available from most laboratory supply houses); and an extremely sticky adhesive, "Touch'N'Glue," which is available at most hardware stores. This material is an adhesive used commercially to bond plasterboard and paneling to walls, and is the only substance I have found that will successfully bond polyethylene.

CONSTRUCTION

(Figure 1)

As shown in Figure 1A, the siphon may be disassembled into three sections: a rear part, connected to a length of $\frac{1}{4}$ inch polyethylene tubing, which may be discarded; the squeeze bulb, which contains one valve (A) where it is joined with the tubing connector; and the outlet or nozzle of the siphon, which contains the second valve (B). The nozzle may be unscrewed from the squeeze-bulb and is used essentially intact. A circle of plastic window screen, 22 mm in diameter, is inserted into the threaded end of the nozzle as far as the "shoulder" of the nozzle and cemented in place. When dry, this assembly will thread directly onto the neck of the bottle and will constitute the outlet valve of the collector bottle.

The rear section of the siphon may be pulled away from the squeeze-bulb to reveal valve "A", which is press-fitted into the squeeze-bulb and may easily be pried free. The assembly of this valve to the collector spout will depend upon the type of tubing connector used (see Figure 1B). The preferred type is one-half of a "quick-disconnect" snap-apart tubing connector which has a broad rim allowing the positioning and cementing of the intake nozzle assembly from the outside of the bottle. Alternatively, one arm of a "T" or "Y" tubing connector may be cut off and used as the spout. Either type of spout is cemented directly to the valve, making certain that no adhesive touches the flap of the valve and that the valve will open **inward** when assembly is completed. This intake nozzle assembly should be allowed to dry before assembly of the collector is completed.

To complete the collector, a hole of the appropriate size is drilled or cut one inch from the shoulder of the bottle. If the snap-apart type connector is used, adhesive is spread around the rim of the nozzle assembly and the valve portion pressed into the bottle. If the other type of connector is used, adhesive is added at the juncture of the valve and the nozzle, and the assembly is dropped through the neck of the bottle and pulled through the hole with

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[1] Contribution No. 70 of the Marine Research Laboratory, University of Connecticut, Noank, Connecticut 06340

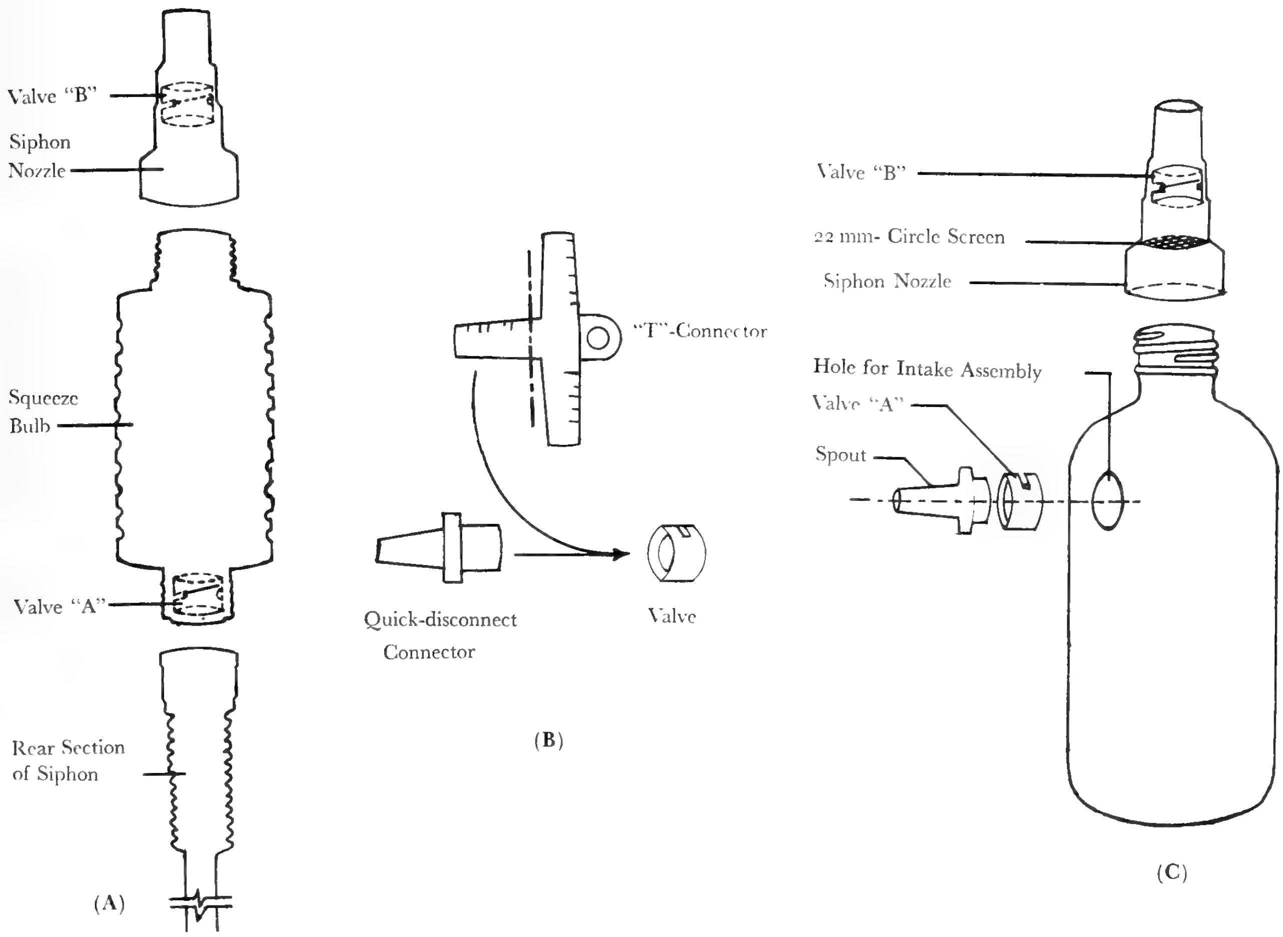
Valve "B"
Siphon Nozzle
Squeeze Bulb
Valve "A"
Rear Section of Siphon
(A)
"T"-Connector
Quick-disconnect Connector
Valve
(B)
Valve "B"
22 mm- Circle Screen
Siphon Nozzle
Hole for Intake Assembly
Valve "A"
Spout
(C)

Figure 1

(**A**) View of three parts of gasoline siphon pump, showing location of one-way valves

(**B**) Assembly of intake nozzle from two types of tubing connectors

(**C**) Construction of completed collector

forceps. After drying overnight, the collector is ready for use.

USE

This device is used in essentially the same way as the 'Acadian SOCK', but one may suck animals into the bottle as rapidly as desired because of the one-way movement of water through the bottle. The walls of the bottle are squeezed together, forcing water through the top of the bottle, and when released, spring rapidly apart, pulling the animal harmlessly into the bottle along with the influx of water. As new animals are added to the bottle the retaining screen prevents expulsion of previously captured specimens.

DISCUSSION

The functions and utility of this device do not completely overlap those of the 'SOCK'. The use of the adhesive provides a structurally weaker bond than that of plexiglas joints, with the result that the collector is not quite as sturdy as the 'SOCK', though it is easily reparable. The maximum size of animals which may be collected is limited by the diameter of the valve opening, 11 mm, so that somewhat larger animals may be taken with the 'SOCK'. The translucent polyethylene does not permit detailed observation of the animals as does the 'SOCK', and some possibility of damage to animals contacting the screen exists, although I have never observed such damage during use of the collector. In practice, most animals settle quickly to the bottom of the bottle.

This collector does, however, have several advantages. Only the simplest, most economical and readily obtainable tools and materials are required for its construction. Efficiency and speed of action are maximal. The through-flow of water ensures that internal conditions of the bottle will not become harmful to the animal, as through anoxia or metabolite build-up. The device requires somewhat less dexterity than does the 'SOCK'.

This collection device may be modified somewhat to suit the organisms to be collected. The retaining screen may be made from finer grades of mesh, including plankton netting, to retain very small organisms. The diameter of the spout may be changed by using variously-sized nozzles to most efficiently collect an animal of a given size, although no advantage is gained by using a diameter larger than the inside diameter of the valve. I have found this device to be very gentle in action, and have even been able to collect, completely unharmed, such delicate animals as the medusae of *Obelia, Sarsia,* and *Aurelia,* which are frequently damaged by plankton nets.

The weighing technique uses small aluminum foil cups, which can be rapidly constructed, preweighed, and stored until needed.

CONSTRUCTION

An 8″ by 12″ sheet of aluminum foil is folded repeatedly, each time in half, to produce a block of foil about 1½″ square and containing 32 foil layers. This foil block is then trimmed with scissors to a circle 1″ in diameter, to yield a stack of 32 1″ foil disks. After peeling the layers apart, each disk is given a one- or two-digit identification number. The number should be scribed with a blunt probe or needle in the center of the **dull** side of the foil disk to ensure maximum legibility. This operation is best performed upon a firm, but not hard surface, such as a piece of cardboard, to prevent tearing the foil. Each disk is then molded into a small cup by centering the numbered portion of the foil, dull side up, over a piece of fire-polished ⅜″ glass tubing, and pressing the edges of the foil down around the walls of the tubing. The cup may then be removed from the tubing, and the identifying number should be readily legible on the bottom of the cup. The process of molding the cup is easier if the glass tubing is supported by a base made from a large rubber stopper. After briefly baking the cups to remove moisture and oils from handling, the cups may be pre-weighed. The entire process of manufacture and pre-weighing will require less than one minute per cup.

USE

A nudibranch, or other small marine organism, should be blotted to remove the accompanying salt water, as there may be sufficient dissolved salts in the accompanying water droplet to give an erroneous weight. Nudibranchs, and many other invertebrates, secrete mucus as they die; this mucus serves to cement the animal to the cup and prevent loss of the material. The cups should be baked at 110° C at least overnight before reweighing, to ensure thorough removal of all water from the tissues of the animal. As the surface area of the dried animal is usually very small, it is normally unnecessary to keep the cups in a desiccator while weighing, if only one set of cups is removed from the oven and weighed at one time. The weight gain is undetectable over a half-hour period if a semi-micro balance (sensitivity 10^{-5} gram) is used. If nudibranchs less than one millimeter in length are to be weighed, it is necessary to weigh several in one cup and to compute an average dry weight, unless one has access to a balance having a sensitivity of greater than 10^{-5} gram. The dry weight of such small animals, from 5×10^{-6} to 1×10^{-5}, are near the limits of precision of most laboratory balances. After determination of the dry weight, the nudibranch may be stored in the cup, and the radula and jaws may be later extracted by boiling in potassium hydroxide solution, as described by Fritchman (1960).

DISCUSSION

The use of small, lightweight, disposable cups provides several advantages. Cost is negligible, while minimal labor and skill are necessary for production. The small volume of the cups allows storage of many cups in a small space. For example, a set of cups may easily be stored in a 5″ finger bowl, and finger bowls stacked. In this way several hundred cups may be made and pre-weighed at one time, and stored dust-free until needed.

The mass of an individual cup should be between 0.01 and 0.05 g, depending upon the area of the foil disk and the brand of foil used. This small weight permits the use of the direct optical readout alone to weigh the cup and its contents, if such a balance is available. Even if an older, two-pan balance lacking optical readout must be used for weighing, the variability of weight between cups of a single lot is low enough that only the finest weight increments need be changed. Most moderately-sized nudibranchs, up to 5 cm length, and many other invertebrates, will be small enough (between 1×10^{-5} and 9×10^{-2} g) that their weights may also be measured directly by optical readout. These factors shorten the weighing process considerably. A further time saving is attained by the small mass of the cups as a result of faster damping of the swinging of the balance pans. The low mass of the cups also lessens the possibility of damaging the balance through erroneous weighing technique, such as failure to lock the pan arresting mechanism before addition or removal of a cup, or dropping a cup onto the balance pan accidentally This technique might therefore be especially useful where it is necessary for relatively unskilled personnel, such as undergraduate students, to use precision balances.

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1969. A simplified vacuum apparatus for collecting small nudibranchs. The Veliger **12** (1): 142 - 143; 1 text fig. (1 July 1969)

Fritchman, Harry K., II
1960. Preparation of radulae. The Veliger **3** (2): 52 - 53 (1 October 1960)

Application to Molluscan Ultrastructure Research of the Balzers 360M Freeze-Etching Plant

BY

T. E. THOMPSON

Zoology Department, University of Bristol, U. K.

(1 Plate; 1 Text figure)

Interest in research into the ultrastructure of molluscs shows no sign of slackening, and, indeed, there are still countless problems which only the electron microscope can solve. But existing methods for investigating the spatial relationships at the ultrastructural level of cells and of sub-cellular structures have at least two major disadvantages.

1. Chemical fixation results in unpredictable, sometimes capricious, damage to the specimen.
2. Cytological three-dimensional reconstruction is difficult even when serial sectioning has been mastered.

The technique of freeze-etching, devised by Dr. H. Moor as an adjunct to transmission electron-microscopy of biological and medical materials, offers an interesting and rewarding alternative to the older preparative methods.

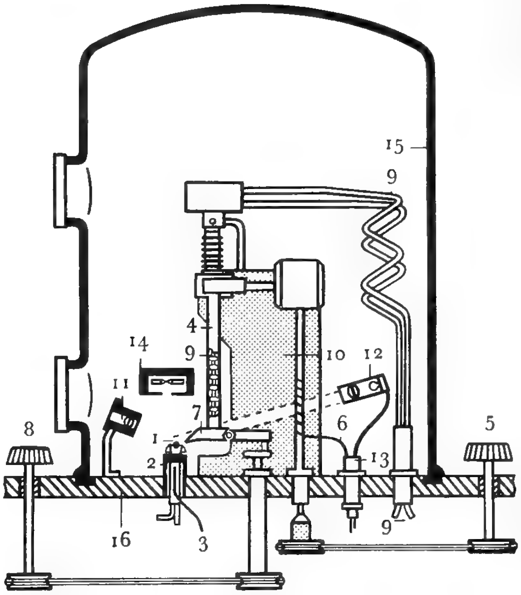

Figure 1

Diagram showing basic features of the vacuum chamber of the Moor freeze-etching apparatus

1. Specimen holder
2. Cold specimen table
3. Temperature sensing device
4. Microtome arm
5. Mechanical microtome advance
6. Thermal microtome advance
7. Cutting head
8. Microtome drive
9. Liquid nitrogen supply and exhaust device
10. Microtome stand
11. Observation lens
12. Light sources
13. Power lead-in
14. Carbon evaporation device
15. Vacuum chamber hood
16. Base plate

Dr. Moor's technique is novel in this respect: it is a purely physical preparation of the specimen, thus providing a useful check on preparative methods which involve chemical fixation.

Figure 1 shows the vacuum and coating chamber of the Balzers 360M Freeze-etching Plant, supplied and installed at Bristol by agents for Balzers Aktiengesellschaft für Hochvakuumtechnik und dünne Schichten, FL-9496 Balzers, Principality of Liechtenstein.

A brief outline of the method is necessary for appreciation of the results which can be obtained. Living, unfixed biological material for freeze-etching is first cooled rapidly in liquid nitrogen before being placed on the cold specimen table (1). The metal hood of the vacuum chamber (15) is now lowered and clamped, and the chamber evacuated (5 - 12 minutes). The specimen is then struck repeatedly by a cooled razor edge (7) which is operated and advanced by external manual controls (5 and 8). Each stroke of the razor produces a new fracture-surface, which tends to follow the natural surfaces of the individual specimen. It is possible to study surfaces of membrane and other cell systems which are otherwise inaccessible. The fracture-surface becomes etched by a process of low-temperature sublimation in the vacuum chamber, and a replica of this etched surface is then produced by coating with, for instance, platinum.

After coating, the specimen can be raised to room temperature and pressure. The biological material is now dissolved away (using sodium hypochlorite solution followed by concentrated sulphuric acid) and discarded. It is the platinum replica which is carefully washed and floated on to a copper grid and in due course examined in the transmission electron microscope. Electron micrographs obtained in this way have a three-dimensional quality which is strikingly reminiscent of micrographs from a scanning electron microscope (Thompson & Hinton, 1968) (but of course far better resolution is possible using a transmission electron microscope). This three-dimensional appearance is not spurious, and genuinely allows a rapid, accurate appreciation of spatial relationships. The micrographs presented here (Figures *2* and *3*) illustrate this point rather clearly. They enable an immediate understanding of the shape of some of the components of the pulmonate sperm tail. It would be exceedingly laborious to build up such a clear picture of this kind of cell by reconstruction of serial sections through fixed material embedded in resin. It would certainly take many days, compared with 4 to 6 hours to obtain good micrographs of freeze-etched material.

Defects of the freeze-etching method are few. 1. The plant is expensive, costing about the same as a transmission electron microscope. 2. Certain organelles do not survive the preparation well. The β fibrils of flagella, for instance, become difficult to discern. 3. The Balzer 360M is a bulky apparatus, weighing approximately 500 kg. But the future is bright, with new models under development (some recently exhibited at the Micro 70 meeting held in Imperial College, London). Certainly, research workers planning projects in molluscan and other ultrastructure will want to examine the implications of freeze-etching in planning their work.

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NOTES & NEWS

New Opisthobranch Records for the Eastern Pacific

BY

GALE G. SPHON

Los Angeles County Museum of Natural History
Los Angeles, California 90007

The three taxa discussed here are of interest because they represent new records for the eastern Pacific.

Plate Explanation

Transmission electron micrographs of freeze-etch-replicas of autosperms of pulmonate molluscs

Figure 2: Several sperm-tails from the vesicula seminalis of *Planorbarius corneus* (Basommatophora)

Figure 3: Part of the tail of a spermatozoon from the seminal vesicle of *Helix pomatia* (Stylommatophora)

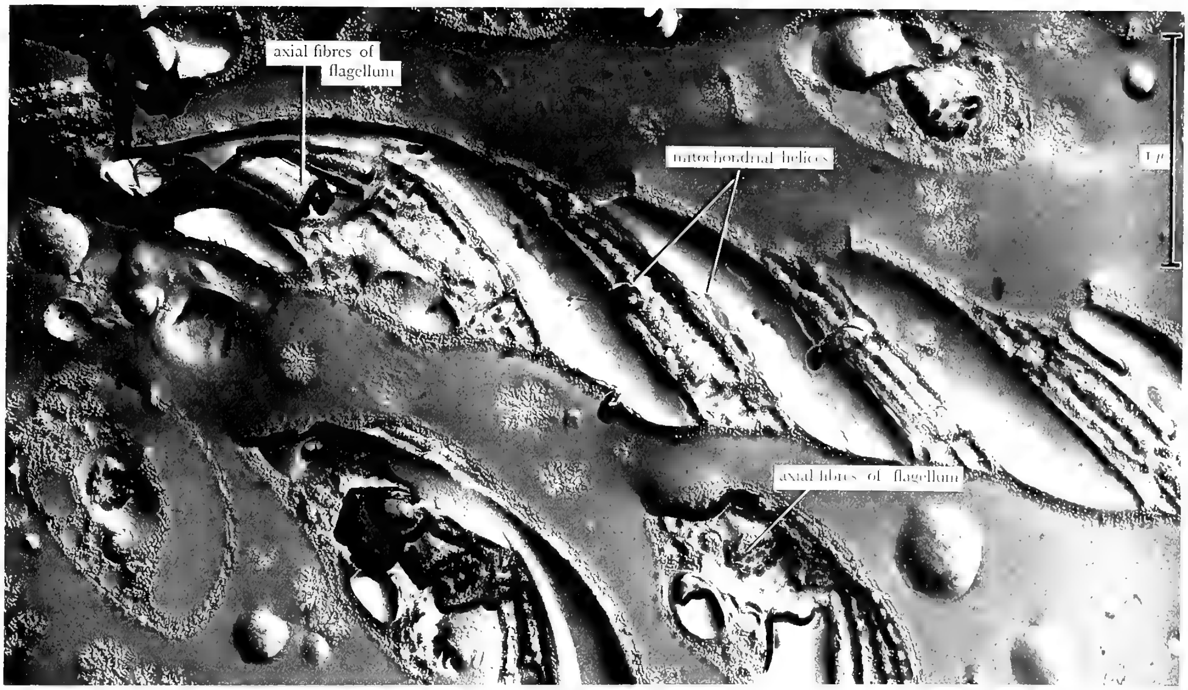
axial fibres of flagellum
mitochondrial helices
1 μ
axial fibres of flagellum

Figure 2

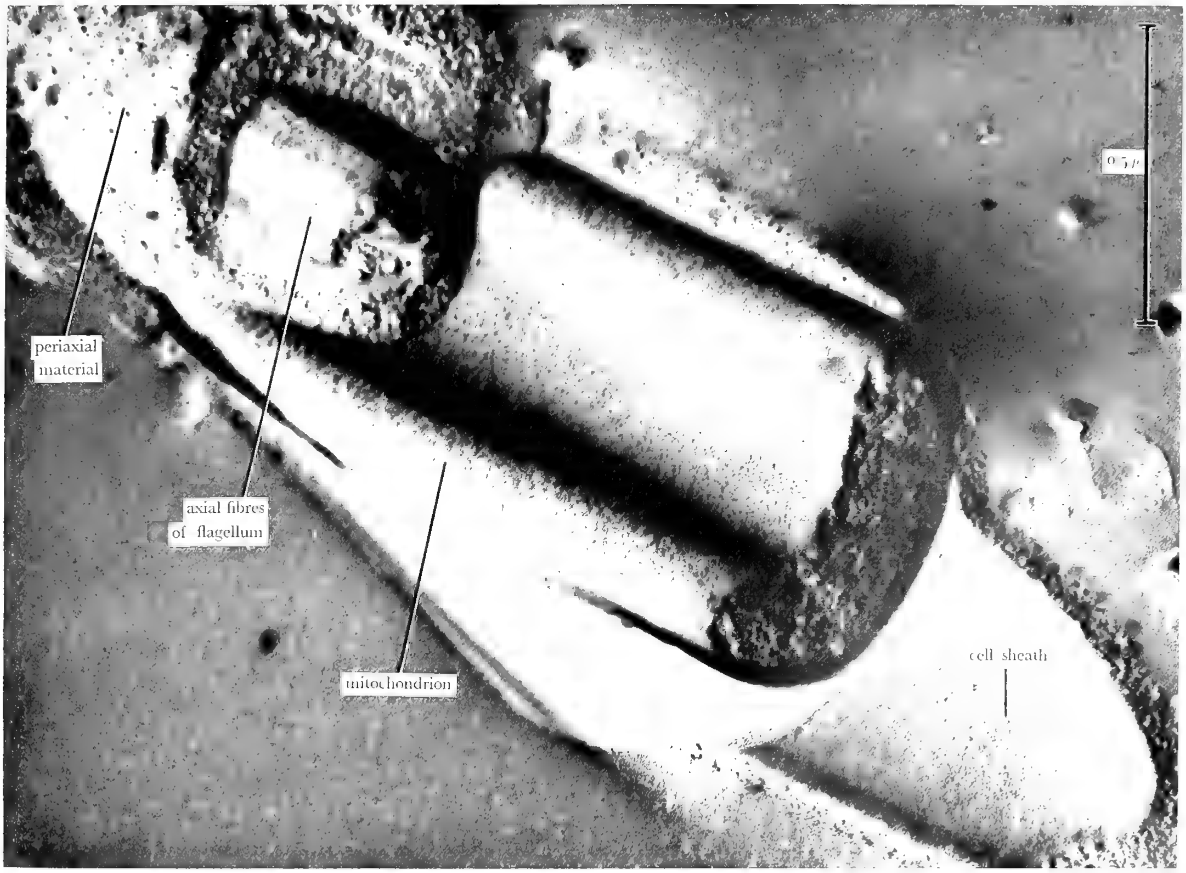
0.5 μ
periaxial material
axial fibres of flagellum
mitochondrion
cell sheath

Figure 3

Lobiger souverbii Fischer, 1856, was first collected in the eastern Pacific by Faye Howard and myself in 1961 at Santa Cruz, Nayarit, Mexico, and again in January 1970 at the same locality. This species has been reported from Hawaii (Kay, 1964) and from the Caribbean (Warmke & Abbott, 1961). *Lobiger souverbii* apparently lives exclusively on the green alga *Caulerpa* which is restricted to tropical waters.

Aeolidella takanosimensis (Baba, 1937) was originally described from Japan, but for a number of years it has been taken seasonally at the docks of one of the yacht basins in San Diego, California. On at least two occasions specimens have also been taken from the Palos Verdes Peninsula, Los Angeles County, California.

Spurilla alba (Risbec, 1928) was originally described from New Caledonia as *Aeolidella alba.* It has been reported by Burn (1966) from New South Wales and Queensland, Australia. More recently, Edmunds, (1969) reported the species from Tanzania, Africa. In January, 1970 I collected one specimen from Punta Mita, Nayarit, Mexico. The specimen compares favorably with both Risbec's original description and the later description of Edmunds (1969). A photograph was sent to Dr. Edmunds who has confirmed the identification of the species.

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Note on *Planorbis mysarus* Mabille, 1895

BY

G DALLAS HANNA

AND

ALLYN G. SMITH

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

(3 Text figures)

In a discussion of land and freshwater mollusks from Baja California described by Jules Mabille in 1895 (Hanna & Smith, 1968) mention was made of the fact that the type specimens of several of his species could not be

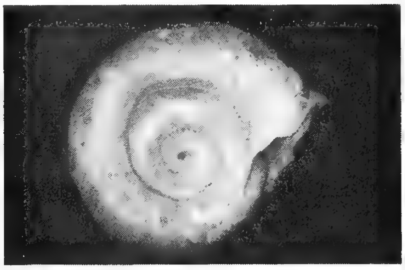

Figure 1

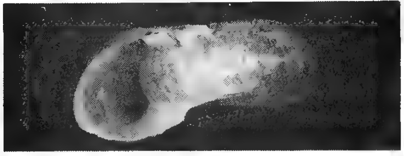

Figure 2

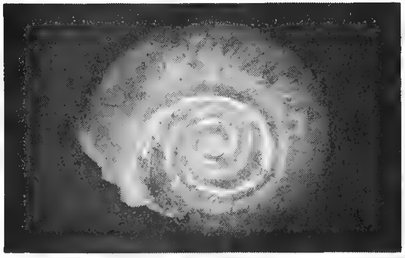

Figure 3

Figure 1	Figure 2	Figure 3
Dorsal View	Side View	Ventral View

Holotype of *Planorbis mysarus* Mabille, 1895
Maximum diameter, 21.5 mm; height, 9.5 mm; maximum diameter aperture, 9.5 mm. Photographs courtesy of Dr. H. Chevallier, Muséum National d'Histoire Naturelle, Paris

located in the Paris Museum of Natural History. One of these was *Planorbis mysarus*. Subsequent search by Dr. H. Chevallier of the Malacological Laboratory of the Paris Museum has resulted in the discovery of a syntype of *P. mysarus* with the label: "Planorbis mysarus Mab. = Pf. – Basse Californie – type; à partir d'une altitude de 800 m." An accompanying label by Louis Germain reads: "*Planorbis tumidus* Pfeiffer, échantillon déformé."

Through the courtesy of Dr. Chevallier, we are now able to illustrate Mabille's species for the first time (Figures 1 - 3).

Placement of *Planorbis mysarus* in the synonymy of *P. tumidus* Pfeiffer, 1839, by Germain (1921) has been reviewed recently by Dr. Dwight W. Taylor (unpublished manuscript), who considers it to be a synonym of *Planorbella tenuis* (Dunker, 1850).

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A. M. U.

Pacific Division

Dr. G. Bruce Campbell, Chairman of the Pacific Division, called an executive board meeting on December 13, 1970 at Whittier, California. Other board members present were: Dr. James H. McLean, Vice-Chairman; Dr. A. Myra Keen (chairman, 1964); and Mr. Gale G. Sphon (chairman, 1967). The board discussed various plans for clarifying the status of the Pacific Division and reviewed the assets, which were found to consist principally of several exhibit cases and a gavel. The board worked out a plan for distribution of these assets to the Western Society of Malacologists and to the American Malacological Union, pending acceptance by both organizations. The current officers tendered their resignations, effective as of the date of final distribution of the assets. It should be pointed out that under the proposed new constitution of the American Malacological Union, the Pacific Division can be reactivated at any time by petition of a group of AMU members residing on the West Coast.

Western Society of Malacologists

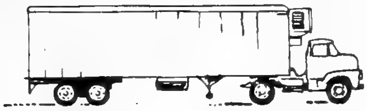
The fourth annual meeting of the Western Society of Malacologists will be held at Asilomar, Pacific Grove, California, from June 16th to June 19th, 1971. Symposia and contributed papers will be presented on a wide spectrum of malacological topics.

Inquiries about the meeting should be made no later than May 15th and should be directed to the Secretary, Mrs. Mary D'Aiuto, 804 Fielding Drive, Palo Alto, California 94303. Applications for membership in the W. S. M. should be sent to the Treasurer, Mr. Ralph O. Fox, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Dues are $2.50 for Regular Members and $1.00 for students.

Executive Board members for the year are: President Dr. Eugene V. Coan; First Vice-President Mrs. Beatrice L. Burch; Second Vice-President Dr. Warren O. Addicott; Secretary Mrs. Mary D'Aiuto; Treasurer Mr. Ralph O. Fox; Members-at-Large Mr. Barry Roth and Dr. James H. McLean; the three most recent Past Presidents are Mr. David K. Mulliner, Dr. William K. Emerson and Dr. A. Myra Keen.

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, 1970). 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, 1970.



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.

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.

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Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first 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, 1970 to June 30, 1971 has been set at $8.-. Postage for members in Canada, Mexico, Central and South America $1.-, for members in any other foreign country $1.50 additional. Send for Membership Application blanks to the Manager of the Society in Los Angeles.

ABOUT 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, 12719 San Vicente Boulevard, Los Angeles, California 90049.

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.

At a Special Meeting of the Regular Membership, it was decided to keep Membership Dues and Subscription rates at the current level despite the ever increasing printing cost and postage fees. At the same time we take this opportunity to remind our members that Membership renewals are due to reach us on or before April 15, 1971; after that date a re-instatement fee of $1.00 will be due in addition.

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.

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Endowment Fund

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

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

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

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.

Change in Format

A GRADUAL CHANGE IN THE FORMAT of our journal has taken place during the current year. The reasons are to enable us to hold back such papers for which authors have not returned, within the time specified, their corrected galley proofs or have made excessive author's corrections. By no longer numbering our plates, it is now possible to postpone the publication of a paper to which a plate has been assigned. We are hoping by this measure to further reduce errors, either of a typographical or of a factual nature; we have had some extremely unfortunate experiences in this regard.

Another change that we hope will assist in avoiding possible confusion will be initiated with volume 14 (although 2 papers already in galley proofs will not conform) by setting in Capitals and SMALL CAPITALS only the names of authors in connection with a literature citation. Other names, including the names of authors of taxa will be set in regular type; for example, we will no longer cite *Calliostoma ligatum* (GOULD, 1849), but *Calliostoma ligatum* (Gould, 1849). On the other hand, a citation of GOULD, 1849 would be to a literature reference. We hope that this will also assist the beginning student to avoid making erroneous assumptions, i. e. that the author whose work on a particular species is cited is the author of the species. For example, *Calliostoma ligatum* (ABBOTT, 1954) should no longer mistakenly be interpreted that Abbott established this taxon, but rather that in his book in 1954 he discussed this species.

BOOKS, PERIODICALS, PAMPHLETS

Lista preliminar de Lamelibranquios de Chile

by CECILIA OSORIO Y NIBALDO BAHAMONDE. Museum Nacional de Historia Natural (Santiago), Boletin 31, pp. 185 - 256; April 1970.

This paper contains a list of the Pelecypoda of Chile, chiefly compiled from the earlier literature. Fifty-one families are included. Species with their ranges are cited, although some of the ranges are now believed to be less extensive. Synonyms are listed (pp. 208 - 243) and a bibliography and index are included.

LGH

Kelp Habitat Improvement Project

Annual Report, 1 July, 1969 - 30 June, 1970. W. M. Keck Laboratory of Environmental Health Engineering, California Institute of Technology; 78 pp.; 23 figures.
With an appendix: Final Report, Marine Waste Disposal and Sea Urchin Ecology. 93 pp.; 42 figures.

The first part of this report gives a detailed account of the continuing study of the various factors involved in the possible restoration of the kelp beds off Point Loma and vicinity, San Diego County, California. Here the beds of *Macrocystis* as "recently" as 1911 were luxuriant and supported a rich population of fishes and many types of invertebrates. By the year 1956 the apparently inexorable disappearance of the kelp caused an intensive study of the problem to be begun, with the aim of eventual restoration of the kelp habitat. The various progress reports published annually - the present being the latest in the series - have detailed the efforts made and shown the varying degrees of success. During the course of these studies attention was attracted to the effect of the ever increasing quantities of sewage discharged into the ocean. The appendix shows with startling clarity that the sewage has an unexpectedly strong influence on the normal cycle. The normal cycle is an alternation between an invasion of the kelp beds by sea urchins with an eventual reduction of the amount of kelp to a point which causes the sea urchin populations to decrease. Then the kelp beds can recover until, eventually, the sea urchin population increases again. The large quantities of sewage, however, seem to be able to maintain the sea urchin populations at a level which makes it impossible for the young kelp plants to get a sufficiently strong start and thus the normal cycle is broken.

It seems to this reviewer that such studies are of utmost importance and it can only be hoped that such reports will find their way into the hands of legislators who will recognize the message implied and who will sponsor, without fear, such legislation as is necessary to at last help to save the last resource of mankind - the ocean.

RS

The Living Volutes

by CLIFTON STOKES WEAVER & JOHN ELEUTHÈRE DUPONT Monograph Series No. 1, Delaware Museum of Natural History, Greenville, Delaware, 1 October 1970.

xv+375 pp.; 78 plates in full color; 44 text figures; 13 distributional maps. Cloth bound. Obtainable from the Delaware Museum for $55.00.

This handsome book, 9¼ by 12¼ inches, is the result of many years of intensive and extensive collecting of the rare, very rare and not so rare volutes. With what can only be called loving care, the various species have been photographed in natural colors. To this reviewer, of special interest are the portraits of the living animals, showing the extended foot with its special color patterns. For most if not all species distributional maps are included.

Each species is discussed as completely as is possible; synonymies are given, followed by a paragraph concerning the type of the species; the type locality, if known; the range; the habitat; the dimensions of a typical shell; a description of the shell; a description of the animal and of the radula, where known, and of the operculum in many cases; and a final paragraph of discussion completes the rather complete treatment of each species.

Aside from a very few typographical errors, which in any work of this size, are unavoidable, this book avoids some of the annoying shortcomings of other recent books of a similar nature: this work is easy to use as the reader is referred back to the correct text page page from the plate or to the correct figures from the text; the maps are easy to interpret. All in all, this is a fine example of what can be achieved by a serious amateur.

While the cost of the book appears to be rather high - in these days of tight budgets very few individuals have an excess 55 dollars lying around - the price must be judged as very reasonable considering the large number of excellent color plates. It might be expected that many shell clubs would wish to acquire a copy for their library and thus make the work accessible to many collectors who otherwise would be prevented from ever enjoying the beauty of these creatures.

RS

Journal of the Malacological Society of Australia

Volume 2, Number 1, 17 August 1970.

This journal has adopted a vastly improved format as compared to the issues comprising volume 1. It is well illustrated with clear typography and contains 11 papers by various authors. The emphasis is, as before, on molluscan articles dealing with species at home in Australia, New Zealand and "neighboring" islands. If we understand the arrangement correctly, this journal is sent to the members of the Malacological Society of Australia. Membership dues are Austr.$ 4.50 per year, a low enough price for the journal considering today's printing costs.

RS

On the Ecology of the Caribbean Chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: Density, Mortality, Feeding, Reproduction, and Growth

by PETER W. GLYNN. Smithsonian Contributions to Zoology 1970, No. 66: 21 pages; 10 figures; 9 tables. Available from Superintendent of Documents, U. S. Government Printing Office, Washington, D. C. 20402; price 35 cents.

This well documented study indicates, among other things, that the two chiton species studied show rapid growth and early attainment of sexual maturity. Because some earlier work, which indicated slow growth and maturing, has been cited extensively in the literature, the author gives a critical discussion of all data now available on growth and reproduction in chitons.

RS

Catalogo de los Moluscos marinos Bonaerenses

by ZULMA J. AGEITOS DE CASTELLANOS (Colaboró: DELICIA F. DEAMBROSI; illustrador: JORGE E. AGEITOS). Anales de la Comision de Investigacion Cientifica (La Plata), Vol. 8, pp. 9 - 364; plts. 1 - 26, 1967 (1970).

This catalog deals with the marine mollusks of the Buenos Aires Province of Argentina. It is based in great part on collections in the Museo Argentino de Ciencias Naturales Rivadavia and Museo de La Plata.

Two hundred and eighty-six species are distributed in 65 genera of Gastropoda, 2 of Polyplacophora, 2 of Scaphopoda, 11 of Cephalopoda, and 71 of Pelecypoda. Each species discussion is accompanied by a description, synonymy, range, and habitat. A key to the species of each genus is included. Of the species 258 are illustrated on 26 plates. A list, only, of Pteropoda is given. A bibliography and index add to the usefulness of this paper.

LGH

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.

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