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IN MEMORIAM
PAUL S. GALTSOFF
(1887–1979)

ERRATUM

Vol. 18, p. 320, Table 1, line 2: for "Les valeurs en concernent . . ." read "Les valeurs en caractères gras [boldface] concernent. . . ."

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BIOLOGICAL RESULTS OF THE UNIVERSITY OF MIAMI DEEP-SEA EXPEDITIONS. 130. THE SYSTEMATICS AND ZOOGEOGRAPHY OF THE GASTROPOD FAMILY TROCHIDAE COLLECTED IN THE STRAITS OF FLORIDA AND ITS APPROACHES

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ABSTRACT

Fifty-four species of molluscs in the family Trochidae are reported from the Straits of Florida in depths of 180 m or more. The following new taxa are described: *Echinogurges,* n. gen. (type-species *Trochus* (*Margarita*) *clavatus* Watson); *Mirachelus clinocnemus,* n. sp.; *Solariella* (*Solariella*) *multirestis,* n. sp.; *Microgaza rotella inornata,* n. subsp. *Microgaza vetula* Woodring is reported from the Recent fauna for the first time. The radula of *Microgaza rotella rotella* Dall is described and illustrated for the first time and indicates that *Microgaza* is in the subfamily Solariellinae. Each species, except those in the genera *Gaza, Calliostoma* and *Lischkeia,* is fully described and illustrated with photographs, and synonymies and distributions are given. A zoogeographic analysis indicates that the trochid fauna is a tropical deep-sea assemblage.

INTRODUCTION

The molluscan fauna of the Straits of Florida has been extensively, if sporadically, sampled, beginning with the BLAKE expeditions (1877–78, 1878–79, 1880) and continuing to 1972, when the R/V GERDA was retired from service by the University of Miami. The identification of species from this area has been based primarily on the work of William Healey Dall (1881, 1889, 1927a,b). The majority of his work was excellent, but he often worked with scanty collections and inadequate literature, and mistakes and discrepancies often appeared. Despite this, subsequent authors have generally accepted Dall's opinions uncritically, especially in the archaeogastropod family Trochidae. Since Dall, several descriptive works and a few faunal lists have included species found in the Straits, but except for a study of *Gaza* (Clench & Abbott, 1943) and a monograph of the genus *Calliostoma* (Clench & Turner, 1960), no critical work has been attempted involving trochids found in the Straits. Since the GERDA collections were rather rich in trochids, this study was selected to fill a considerable gap in the systematic literature of the Trochidae.

This study treats those species of Trochidae which have been taken in depths greater than 180 m in the Straits of Florida and deals with the systematics and zoogeography of this rather important group. The depth limitation eliminates 11 shallow-water species from consideration in the systematic account, but for the sake of completeness, 10 of these are included in the zoogeographic considerations.

LITERATURE REVIEW OF STRAITS TROCHIDAE

In the first hundred years after Linnaeus's 10th edition of *Systema Naturae* was published, 8 species of trochids assignable to the Straits fauna were described. Linnaeus (1758), Born (1778), Lamarck (1822) and Arthur Adams (1854) each described 1 species, and Gmelin (1791) and C. B. Adams (1845, 1850) contributed 2 species apiece. All 8 are shallow water species, and only 2 (*Calliostoma jujubinum* Gmelin and *C. pulchrum* C. B. Adams) can be included in this study.

The first deep water trochid to be attributed to the Straits area *per se* was *Solariella amabilis* (Jeffreys, 1865), a name Dall used for *Solariella pourtalesi* Clench & Aguayo, 1938. *S. amabilis* is now known to be strictly an Eastern Atlantic form. Watson (1879, 1886), in working up the CHALLENGER gastropods, reported 14 new Western Atlantic species, of which 7 are found in the Straits (in 1886 he added a fifteenth, *Margarites euspira* Dall, 1881). Verrill (1880) reported on the molluscs collected by the FISH HAWK and included 3 new Western Atlantic trochid species, of which 1, *Solariella lamellosa* (Verrill & Smith, 1880) is also found in the Straits.

In working up the molluscs of the BLAKE and ALBATROSS expeditions, William Healey Dall was primarily responsible for laying the groundwork on which most of the Western Atlantic molluscan research is based. In his preliminary report on the BLAKE collections (1881) Dall recognized 24 species of Trochidae, 19 of which were new and 14 which are now known from the Straits. His 1889 paper, the comprehensive report on the Caribbean molluscs from the BLAKE expeditions, added 13 new species, and 34 of the 45 trochids discussed are found in the Straits. A preliminary report on the ALBATROSS expedition of 1887–1888 listed 10 species, 5 now recorded from the Straits. Finally, 2 papers on ALBATROSS material from off southern Georgia (Dall, 1927a, 1927b) produced 29 species of which 23 were new and 10 occur in the Straits.

A series of papers by Clench & Aguayo (1938, 1939, 1940, 1941, 1946) introduced 11 new species of trochids, mostly in the genus *Calliostoma,* and 7 of the species were taken in the Straits. Papers by Schwengel & McGinty (1942) and Schwengel (1951) added 2 new shallow water species of *Calliostoma,* and Clench & Abbott (1943) treated 3 species of *Gaza* known from the Straits area. Rehder (1955) redescribed *Turcicula imperialis* Dall, and discussed the relationships of *Turcicula* to *Lischkeia, Bathybembix,* and *Calliotropis.*

Clench & Turner (1960) produced a comprehensive monograph of the Western Atlantic *Calliostoma,* and included a section dealing with species which were originally described as *Calliostoma,* but are doubtfully in that genus, or assigned to some other genus entirely. In all, they dealt with 56 species of which 23 are known from the Straits area. Finally, Bayer (1971) reviewed 59 species of molluscs from the tropical West Atlantic and included 8 species of trochids (five from the Straits).

A few lists of molluscs have been published which include species of the Straits fauna. The most important are Dall's (1885, 1889b) and Johnson's (1934). A work which is helpful only as a list is Abbott (1974). Another useful work is Pilsbry (1889) in the *Manual of Conchology,* in which he compiled the original descriptions and citations for as many trochid species as possible on a worldwide basis, and brought together most of the illustrations then available.

MATERIALS AND METHODS

Material for this study came from collections made by a variety of ships. The bulk of these collections is deposited at the University of Miami and the U.S. National Museum, with a lesser amount of material in the Museum of Comparative Zoology, Harvard University. The major portion of the collections was made aboard the USCGS BLAKE (1877–1880), the U.S. Fish Commission Ship ALBATROSS (1883–1887), John Henderson's yacht EOLIS (1910–1917), the ATLANTIS (1938–1939), and the R/V GERDA of the University of Miami (1962–1972). Additional specimens from the Caribbean were obtained by the State University of Iowa Expedition to Barbados and Antigua (1918) with the launch EOLIS jr, and by the University of Miami aboard the R/V JOHN ELLIOTT PILLSBURY.

The collecting gear used by the expeditions is quite varied. The BLAKE and ALBATROSS used primarily the beam trawl and a modified beam trawl known as the BLAKE trawl, which fished equally well on either side. Several types of dredges were also used upon occasion aboard the BLAKE and ALBATROSS. John Henderson, aboard the EOLIS and EOLIS jr used, almost exclusively, a small box-type dredge. The ATLANTIS used 10-ft and 14-ft BLAKE trawls and 35-ft, 52-ft and 60-ft otter trawls. The GERDA employed several types of gear, primarily the 10-ft otter trawl or "try net." A 16-ft otter trawl was used briefly from the GERDA, but was soon discarded since it was rather unwieldy aboard the GERDA and it merely caught larger quantities of species taken by the try net. Several types of dredges were employed, including a box dredge, pipe dredge and triangular dredge, but their use was discontinued primarily for reasons of economy. They did not obtain large enough collections to warrant the time and energy expended. An accidental bottoming of a 6-ft Isaacs-Kidd Midwater Trawl obtained a rather rich collection of small molluscs. For a detailed description of the GERDA and her gear, see Devany (1969) and Staiger (1970). The PILLSBURY worked primarily in the Caribbean Sea, using the 10-ft and 40-ft otter trawls, and occasionally a 5-ft BLAKE trawl.

The dredges are, without doubt, the best gear for obtaining the minute molluscs, including those which burrow shallowly. However, the area sampled is necessarily small, and in deep-sea surveys, they are inadequate. The BLAKE and beam trawls are better, but still somewhat uneconomical for extensive use in the deep-sea. Therefore, since the 1930's, most work has been done with the otter trawl. The limitation on the otter trawls is that, although capturing the larger organisms adequately, the very small organisms are often washed through the mesh of the net and only part are retained. It is difficult to make any assumptions as to the relative abundance of individuals at any station. The small molluscs are also frequently overlooked in sorting the catch, and unless the debris and sediment are saved and sorted under magnification, many specimens could be lost.

For the literature used in identifying the specimens, see Literature Review section. In addition to the primary literature, many smaller, less comprehensive papers were consulted to verify identifications, check synonymies, and compile distributional data. Types of several species were kindly loaned by Dr. Kenneth J. Boss of the MCZ. Finally, two trips were made to the USNM to examine the types of all the Western Atlantic trochids deposited there, and to compare many of the RSMAS specimens with material in the USNM collections. In addition to the Jeffreys collection, the USNM collections contain most of the material from the BLAKE and ALBATROSS expeditions, the entire Henderson collection, as yet largely unidentified, and the State University of Iowa Expedition collections. These afforded numerous lots of material from the Straits of Florida and the Caribbean.

A WILD M-5 binocular dissecting microscope was used for examination of all specimens and a camera lucida attachment was used for preliminary drawings of many of the smaller species and comparison with similar species. A WILD M-20 compound microscope was used for examination of radular preparations.

Radulae were removed by soaking the specimen in hot KOH to dissolve the tissue. They then were washed and mounted in Euparal on a microscope slide. Shell measurements were made with dial calipers graduated in tenths of millimeters. All measurements are given in millimeters and depths are in meters.

All photographs were taken with a PENTAX SP II 35 mm SLR camera using KODAK Panatomic-X film. A bellows attachment and 2x teleconverter were used when photographing specimens less than 10 mm in height. A ROLLEI E-27 strobe unit was used for primary lighting and a white card reflector was placed behind the specimen for fill-in lighting.

Measurements given in the descriptions are the total height of the specimen unless otherwise noted.

Abbreviations used in the paper are as follows:

RSMAS—Rosenstiel School of Marine and Atmospheric Science
USNM—U.S. National Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University
ANSP—Academy of Natural Sciences, Philadelphia
UMML 30-0000—University of Miami Marine Lab. gastropod accession number
G-0000—R/V GERDA Station number
P-0000—R/V PILLSBURY Station number
OT—Otter Trawl
IKMT—Isaacs-Kidd Midwater Trawl
J-S—Johnson-Smithsonian Deep-Sea Expedition to the Puerto Rico Deep in 1933
SUI—State University of Iowa Barbados-Antigua Expeditions, 1918.

The synonymies cited in the Species Account are, for the most part, complete. Some minor lists have been omitted, and recent popular and semi-popular guides and identification manuals have not been included with the exception of Abbott's *American Seashells* (1974). This was included since most of the species treated here are listed, and the work enjoys a very wide following, both amateur and professional. With the exception of species of *Calliostoma* and *Gaza,* all species have been redescribed and figured since the species are poorly known and the original descriptions were often inadequate or misleading, and relatively inaccessible without an extensive literature search. Types of almost all species were traced and examined. Those which were not examined are noted under *Types* section on the species description.

The *Material Examined* sections of the species descriptions are in abbreviated form, consisting of a vessel or expedition station number followed by the number of specimens in the lot and the museum accession number of the lot. Miscellaneous collections, such as those by the EOLIS, are accompanied by complete data. Complete data for the abbreviated notations are included in the Appendix.

Area of Study.—For the purposes of this study, the Straits of Florida are defined as follows: bounded on the north by 27°30′N, on the east by the Bahamas or 78°30′W, on the west by the Florida peninsula and out to 83°30′W, and on the south by the northern coast of Cuba. The approaches to the Straits are the Yucatan Channel, Nicholas Channel, Santaren Channel, and the Northwest Providence Channel. This is a somewhat arbitrary demarcation, selected primarily to agree with previous studies of the fauna of the Straits (Robins, 1968; Devany, 1969; Staiger, 1970; Cairns, 1973; Messing, 1975). In these reports, the various physical, geological and hydrographical aspects of the Straits have been extensively summarized. Therefore, only the following brief description of the area is presented:

The Straits of Florida are an arcuate, sloping trough, separating the Florida Plateau from the Bahama Platform and Cuba, and forming the bed of the Florida Current. The thalweg of the trough descends from a northern sill located about 27°25′N at a depth of just over 700 m. The slope is at first slight (0.4 m/km), descending to a broad, flat plateau with a depth of 860–878 m just north of the Cay Sal Bank. In the Cay Sal area the thalweg assumes a much steeper gradient (up to 5 m/km), descending to about 2800 m at its junction with the extreme southeastern Gulf of Mexico. The axis of the Straits from Cay Sal to the Gulf of Mexico extends roughly to the west. Here the bottom topography also becomes very rugged.

The Yucatan Channel separates Cuba and Yucatan and permits the passage of water from the northwestern Caribbean Sea into the Gulf systems and the Florida Current. The southeastern Straits is divided into 2 subsidiary channels, the Nicholas and Santaren Channels, by the Cay Sal Bank. To the southeast these 2 channels merge to form the Old Bahama Channel which separates Cuba and the Bahama Platform. The Northwest Providence Channel enters the Straits from the northeast, dividing the Bahamas Platform into the Great and Little Bahama Banks. To the north of the Straits, the Blake Plateau extends to the northeast and descends gradually to a depth of about 1500 m, from whence the bottom drops suddently to the floor of the Atlantic (about 3700 m).

Detailed descriptions of the various physiographic features of the Straits are presented in Jordan & Stewart (1961), Jordan et al. (1964), Kofoed & Malloy (1964) and Malloy & Hurley (1970). Summaries of the hydrography of the Straits may be found in Wennekens (1959), Devany (1969) and Cairns (1973). Messing (1975) gave an extensive summary of all aspects of the oceanography of the Straits.

SYSTEMATICS

The higher classification used in this study is primarily based on that of Thiele (1929) and modified by Keen (1960) and McLean (1971).

Phylum MOLLUSCA
- Class GASTROPODA Cuvier, 1797
  - Subclass Prosobranchia A. Milne-Edwards, 1848
    - Order Archaeogastropoda Thiele, 1925
      - Suborder Trochina Cox & Knight, 1960
        - Superfamily Trochacea Rafinesque, 1815
          - Family Trochidae Rafinesque, 1815
            - Subfamily Margaritinae Stoliczka, 1868
              - Genus *Margarites* Gray, 1847
              - Genus *Calliotropis* Seguenza, 1903
              - Genus *Lischkeia* Fischer, 1879
              - Genus *Euchelus* Philippi, 1847
              - Genus *Mirachelus* Woodring, 1928
              - Genus *Echinogurges* gen. nov.
            - Subfamily Umboniinae Pilsbry, 1886
              - Genus *Gaza* Watson, 1879
            - Subfamily Calliostomatinae Thiele, 1924
              - Genus *Calliostoma* Swainson, 1840
              - Genus *Dentistyla* Dall, 1889
            - Subfamily Solariellinae Powell, 1951
              - Genus *Solariella* S. V. Wood, 1842
              - Genus *Microgaza* Dall, 1881

Subfamily Margaritinae Stoliczka, 1868

Genus **Margarites** Gray, 1847

Margarita Leach, 1819: 464 (*non* Leach, 1814).
Margarites Gray, 1847b: 268.
Eumargarita Fischer, 1885: 825.
Valvatella Melville, 1897: 472 (*non* Gray, 1857).

Type-species.—Trochus helicinus Fabricius, 1780; by original designation, Gray, 1847b: 268.

Diagnosis.—Shell small, usually nacreous, conical or rather depressed, smooth or spirally striate, with rounded whorls, usually umbilicate. Radula rhipidoglossate; rhachidian with a single, laterally serrate cusp; laterals 4 to 6, serrate on the outer edges; marginals numerous, similar in size and form to the laterals.

Subgenus **Bathymophila** Dall, 1881

Bathymophila Dall, 1881: 102; 1889a: 378; 1889b: 162.—Pilsbry, 1889: 306.—Johnson, 1934: 73.—Abbott, 1974: 37.

Type-species.—Margarita euspira Dall, 1881; by monotypy, Dall, 1881: 102.

Diagnosis.—Shell with or without a subsutural row of nodules; columella broad, flattened, granular in young specimens; umbilicus closed by callus.

Margarites (Bathymophila) euspira
(Dall, 1881)
Figs. 1,2

Margarita (?) *euspira* Dall, 1881: 44.
Margarita (Bathymophila) euspira: Dall, 1881: 102; 1889a: 378, pl. 32, fig. 8; 1889b: 162, pl. 32, fig. 8 (listed only; fig. from 1889a).—Pilsbry, 1889: 306, pl. 51, fig. 24; pl. 47, figs. 1–3 (description from Dall, 1881; figs. from Dall, 1889a and Jeffreys, 1883).
Margarita (Bathymophila) euspira var. *nitens* Dall, 1881: 102.
Trochus (Oxystele) euspira: Jeffreys, 1883: 98, pl. 20, fig. 6.—Watson, 1886: 68.
Trochus (Oxystele) euspira var. *coronata* Jeffreys, 1883: 99.
Margarites (Bathymophila) euspira: Johnson, 1934: 73 (listed only).
Margarites (Bathymophila) euspirus: Abbott, 1974: 37, fig. 237 (listed only; fig. from Dall, 1889a).

Description.—Shell small (attaining a height of about 7 mm), bluntly conical, polished, white with an underlying iridescence, of about 6 rounded whorls. Protoconch small, glassy, of about 1½ whorls. First 2 whorls with 6 to 8 strong spiral cords which generally become obsolete on later whorls; cord nearest the suture often persisting as a row of obscure to prominent nodules. Whorls following the 2nd generally smooth and polished, with only fine growth lines. Base rounded; umbilicus open in young specimens, filled by columellar callus in mature specimens. Aperture obliquely ovate; outer lip thin and simple; columella thick, flattened, broad at its base, with a small obscure tubercle above a shallow subterminal hollow.

Holotype.—Not traced.

Type-locality.—BLAKE sta. 2, 23°14′N, 82°25′W, off Havana, Cuba, 1472 m.

Material examined.—Blake, sta. no. unrecorded, Yucatan channel, 1170 m; 1, MCZ 7576; 5, MCZ 7577.

Geographic distribution.—This is an amphi-Atlantic species which occurs in the Eastern Atlantic in Vigo Bay off northern Portugal and in the Western Atlantic in the southern Straits of Florida, the Yucatan Channel, and the Virgin Islands.

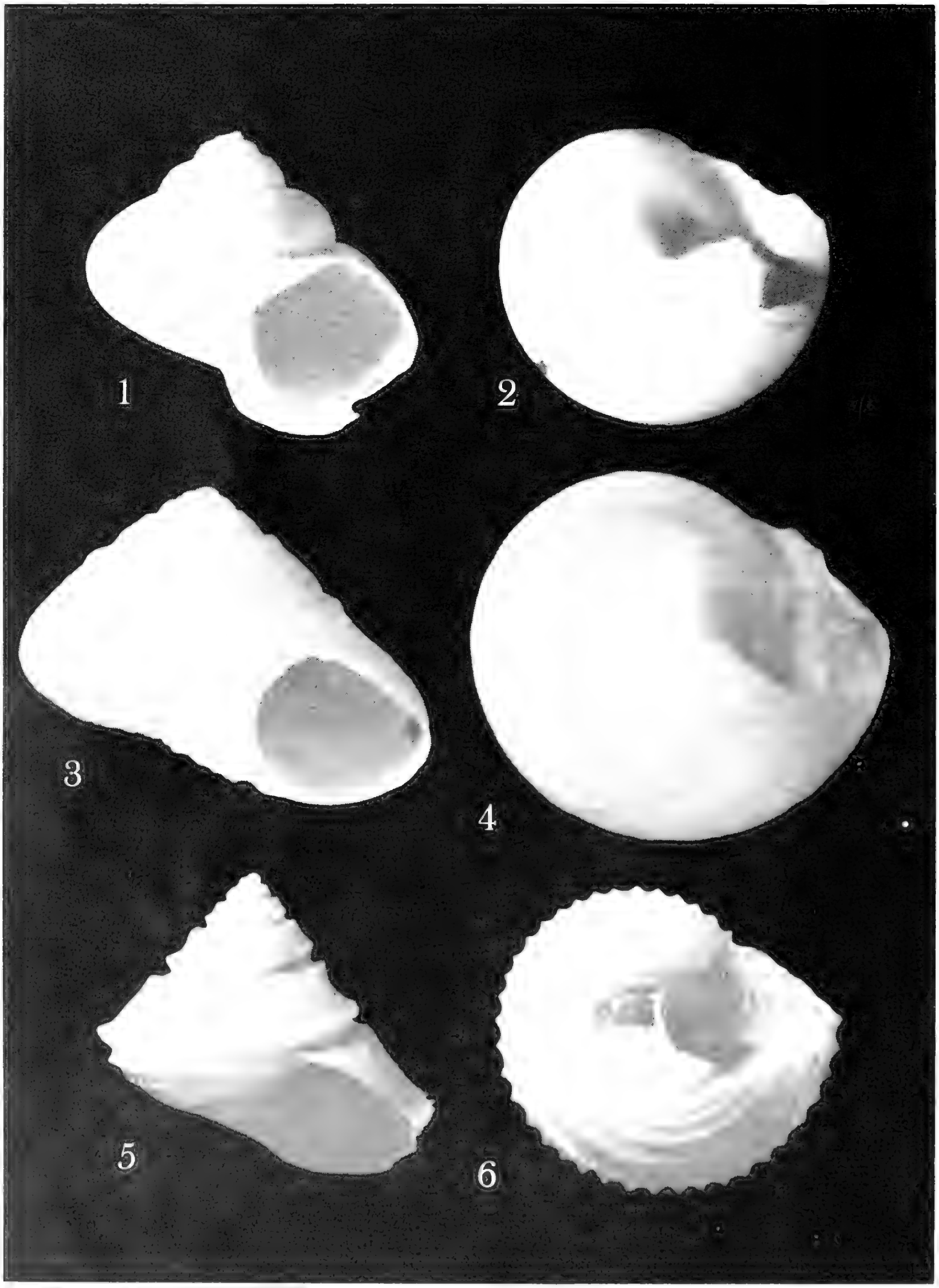
Bathymetric range.—Known in the Eastern Atlantic from 1353 to 2003 m, and in the Western Atlantic from 713 to 1472 m.

Remarks.—This species is rather variable in sculpture. The usual form is devoid of any sculpture other than the row of obscure beads at the suture. Some forms exhibit spiral cords over the whole shell, some have a strongly coronated subsutural cord (variety *coronata* Jeffreys, 1883), and others are lacking the subsutural band entirely (variety *nitens* Dall, 1881). The relationships of this species are unclear at present. It appears to be closest to the *"Umbonium" bairdi* of Dall, which is not an *Umbonium*. *M. euspira* also bears a superficial resemblance to *Solariella lubrica* Dall (*q.v.*), but they are not closely related. Whether or not *M. euspira* belongs in *Margarites* must await examination of the radula.

Margarites (Bathymophila) bairdi
(Dall, 1889)
Figs. 3,4

Umbonium bairdii Dall, 1889a: 359, pl. 21, figs. 6, 6a; 1889b: 160, pl. 21, figs. 6, 6a (listed only; figs. from 1889a).—Pilsbry, 1889: 457, pl. 60, figs. 5, 6 (description and figs. from Dall, 1889a).—Johnson, 1934: 74 (listed only).—Abbott, 1974: 40, fig. 270 (listed only; fig. from Dall, 1889a).

Description.—"Shell small, depressed conic, white, polished, externally porcellanous, internally slightly nacreous; nucleus globular, dextral; whorls five or more. Radiating sculpture of occasional faint impressed incremental lines; spiral sculpture of occasional microscopic striae, and a single strap-like band appressed to the suture, and bearing numerous flattish squarish nodules or elevations, which coronate the whorls; periphery rounded, base rounded, depressed in the centre, which is nearly filled with a mass of white callus having a very finely granular surface. Aperture ovate, margin simple, thin, oblique." (Dall, 1889a: 359.)



FIGS. 1–6. 1–2. *Margarites (Bathymophila) euspira* (Dall): BLAKE sta. off Yucatan, h = 4.9 mm, d = 5.6 mm. 3–4. *Margarites (Bathymophila) bairdi* (Dall) (holotype): ALBATROSS sta. off "Florida Reefs," h = 3.9 mm, d = 5.3 mm. 5–6. *Calliotropis (Calliotropis) ottoi* (Philippi): USNM 179612.

Holotype.—USNM 95064, from an unspecified ALBATROSS Station off the Florida Reefs.

Type-locality and *Material examined.*—ALBATROSS (sta. number unspecified), off the Florida Reefs; 1, USNM 95064 (holotype).

Geographic distribution.—Known only from the Straits of Florida and the Yucatan Channel.

Bathymetric range.—366 to 1170 m.

Remarks.—Several workers have commented that this species is probably not an *Umbonium,* an opinion with which I agree. *U. bairdi* appears to have an affinity with *Margarites (Bathymophila) euspira* Dall, at least in external shell characters. Both have spiral cords on the first whorls, the subsutural row of beads in *U. bairdi* is quite similar to that exhibited by *M. euspira,* especially the coronated forms, and the peculiar columellae are remarkably alike. The granulated surface of the columella of *bairdi* is also present in immature specimens of *euspira. U. bairdi* differs from *M. euspira* primarily in having a more conical shape with the sutures rather indistinct and not strongly impressed, having weaker spirals on the first whorl, and having the columella slightly different. The similarities of the 2 species lead me to believe that they should be congeneric.

Genus **Calliotropis** Seguenza, 1903

Calliotropis Seguenza, 1903: 462.
Solariellopsis Schepman, 1908: 53 (*non* Gregorio, 1886).
Margarita (partim), Auctt. (*non* Gray, 1847a).
Solariella (partim), Auctt. (*non* S. V. Wood, 1842).

Type-species.—*Trochus ottoi* Philippi, 1844; by original designation, Seguenza, 1903: 462.

Diagnosis.—Shell small to moderate in size, thin, iridescent, inflated, widely umbilicate, sculptured with spiral rows of sharp tubercles. Radula with rhachidian, 3 subequal laterals and 1 rudimentary lateral, and 12 to 21 rather small marginals.

Remarks.—*Calliotropis* was erected by Seguenza for the fossil trochid *Trochus ottoi* Philippi (Figs. 5, 6). *C. regalis* (Verrill & Smith) (Figs. 7, 8) has been considered a synonym of *ottoi* since shortly after its description. However, as Rehder & Ladd (1973) have pointed out, the 2 are very closely related but entirely distinct species. The numerous marginal teeth of the radula show it to be in the Margaritinae rather than in the Solariellinae where many of its species have been placed as recently as 1974 (Abbott, 1974). *Calliotropis* recently has been considered a subgenus of *Lischkeia* Fischer, 1879, but the large, rather heavy shell, umbilical callus, and reflected inner lip of the latter seem to be sufficient characters for generic separation.

Subgenus **Solaricida** Dall, 1919

Solaricida Dall, 1919: 361.—Keen, 1960: 1262.—McLean, 1971: 331.

Type-species. — *Solariella (Solaricida) hondoensis* Dall, 1919; by monotypy, Dall, 1919: 361.

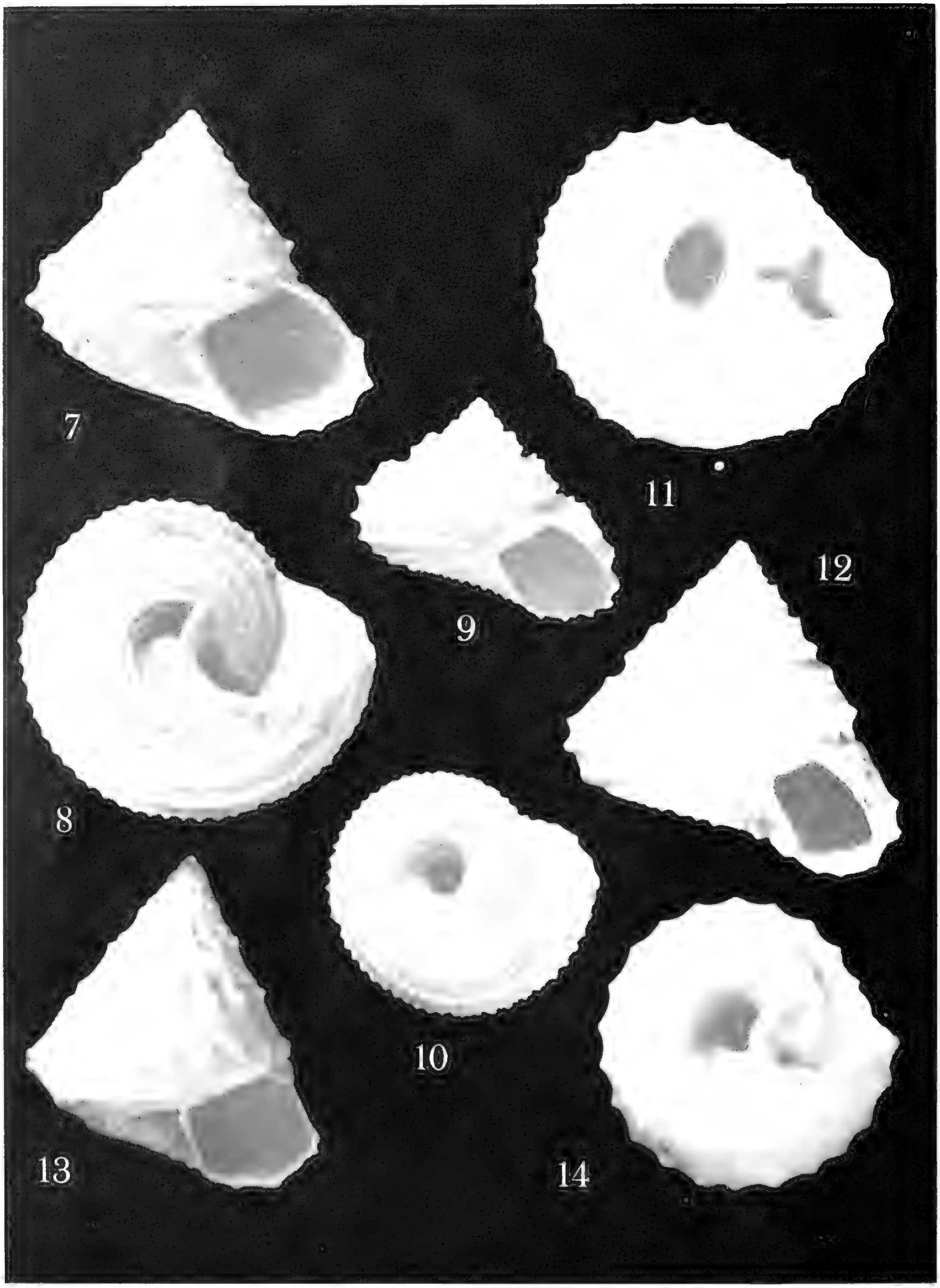
Diagnosis.—Shell generally more inflated than *Calliotropis s. s.,* with a wider and deeper umbilicus.

Calliotropis (Solaricida) aeglees

(Watson, 1879)
Figs. 11,12

Trochus (Margarita) aeglees Watson, 1879: 704; 1886: 81, pl. 5, fig. 10.
Trochus (Margarita) ottoi: Jeffreys, 1883: 98 (*partim*).
Margarita (Solariella) aegleis: Dall, 1889a: 379 (*partim*); 1889b: 164 (*partim*; listed only).—Pilsbry, 1889: 315, pl. 66, figs. 18, 19 (*partim*; description from Watson, 1879; figs. from Watson, 1886).
Solariella (Machaeroplax) aegleis aegleis: Johnson, 1934: 71 (*partim*?; listed only).
Solariella aegleis aegleis: Abbott, 1974: 41 (*partim*; listed only).

Description.—Shell small (attaining a height of about 5 mm), broadly conical, of about 6 whorls, white with an underlying nacreous lustre. Protoconch small, prominent, glassy, of about 1½ whorls. First whorl with strong axial riblets which disappear on later whorls. Sculpture on later whorls of spire consisting of 2 spiral rows of rounded, axially produced tubercles. There is no connection between the tubercles of 1 row and those of the other, but an obscure spiral cord connects the tubercles of each individual row. Upper row very close to the suture line and separated from the second row by a fairly broad, flat area. Body whorl bears a third carina just below the second and forms the whorl periphery. Distance between the lower 2 carinae about half that between the upper 2, giving



FIGS. 7–14. 7–8. *Calliotropis (Calliotropis) regalis* (Verrill & Smith): USNM 44681. 9–10. *Calliotropis vaillanti* Fischer: USNM 94958. 11–12. *Calliotropis (Solaricida) aeglees* (Watson (syntype): CHALLENGER-24, h = 6.9 mm, d = 7.3 mm. 13–14. *Calliotropis (Solaricida) lissocona* (Dall) (holotype): BLAKE-47, h = 5.6 mm, d = 5.2 mm.

the whorl a sloping contour. Base rounded, narrow, with 3 spiral cords. Outer spiral obscurely beaded, the middle 1 smoothish, and the inner set with strong rounded tubercles, forming the umbilical margin. Spaces between the basal cords concave with rather strong radial plications which continue up into the umbilicus. Umbilicus very wide but sharply constricted within, deep. Aperture oblique, rounded, quadrangular; lips thin, inner lip reflected slightly. Columella thin, concave above and below a blunt tooth which is the termination of a spiral ridge extending into the aperture.

Holotype.—None selected. The syntype series is in the British Museum (Natural History), cat. nos. 87.2.9.311-314, and 1 syntype is in the USNM, cat. no. 118787; all are from CHALLENGER sta. 24.

Type-locality.—CHALLENGER sta. 24, 18°38′30″N, 65°05′20″W, off Culebra Island, Virgin Islands, 713 m.

Material examined.—Straits of Florida: G-1008; 1, UMML 30-8044.—G-1096; 1, UMML 30-8036.—Caribbean: J-S sta. 67; 13, USNM 429422.—J-S sta. 93; 2, USNM 429539.—CHALLENGER sta. 24; 1, USNM 118787 (syntype).

Geographic distribution.—Known only from the Straits of Florida near Cay Sal Bank, off the Dry Tortugas, and from off Puerto Rico and the Virgin Islands.

Bathymetric range.—*C. aeglees* occurs in rather deep water, from 350 to 732 m.

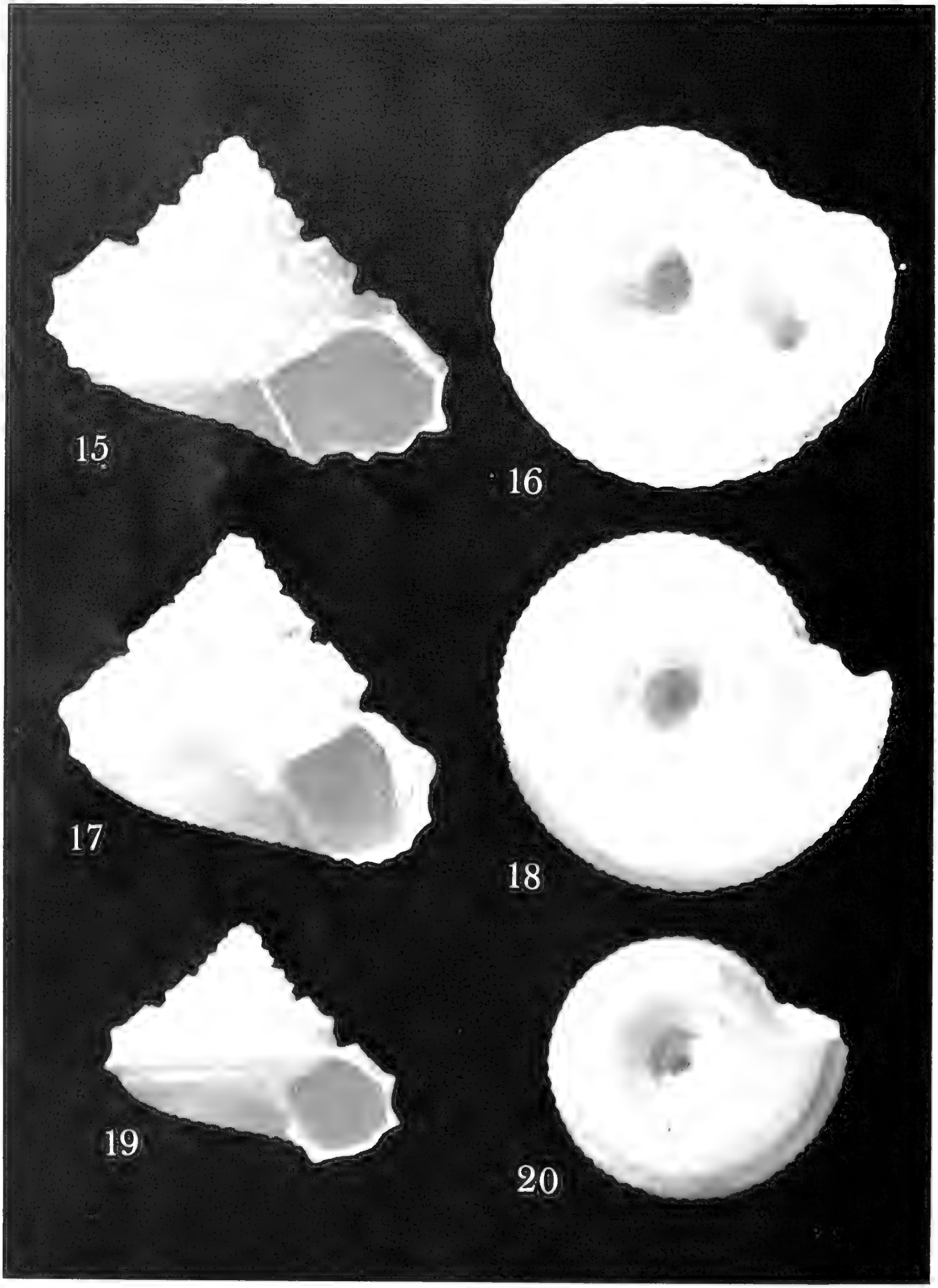
Remarks.—There has been an extraordinary amount of confusion surrounding this species. In 1879, Watson described *C. aeglees, Trochus lima* (=*C. rhina* Watson, 1886), *Echinogurges clavatus* and *E. rhysus* as *Trochus (Margarita)* species. Dall (1881) reported *aeglees* from the BLAKE dredgings and included *Solariella lamellosa* as a synonym. This was a mixed lot consisting primarily of specimens of *S. lamellosa, S. pourtalesi* Clench & Aguayo, and probably some specimens of *Calliotropis calatha* (Dall), *C. rhina,* and *E. clavatus,* all of which he considered merely forms of one another. In 1883, J. G. Jeffreys placed *aeglees* into synonymy with *C. ottoi* (Philippi), a Pliocene fossil from Italy. Watson (1886) disagreed with Dall's opinion (1881) that *S. lamellosa* was synonymous with *aeglees,* and he also expressed doubt that Jeffreys' identification of *aeglees* with *C. regalis* (Verrill & Smith) was correct. Dall, in the meantime, had obtained the Jeffreys collection, and, on the basis of this additional material, modified his earlier views somewhat. He removed *S. lamellosa* and *S. pourtalesi* (as *S. amabilis* Jeffreys) from synonymy with *aeglees,* but added a new variety, *lata* (=*C. calatha* Dall). This variety was introduced as a *nomen nudum,* and an examination of his specimens reveals another mixed lot. Along with *aeglees,* Dall mentioned 2 lots of fossils from the Tertiary of Belgium and 2 from Italy, and a specimen taken by the TALISMAN expedition. There seems to have been a transposition of labels of the fossil lots which Dall was unable to straighten out, and as a result, he was faced with a problem in assigning names to the specimens. Apparently the labels of a lot of *Trochus peregrinus* Libassi (USNM94960, not 94952) and a lot of "*Solarium" turbinoides* Nyst (=*Solariella maculata* S. V. Wood; USNM 94952, not 94960) were transposed before Dall examined them. He decided that *peregrinus* was the same as his variety *lata.* They are closely related, but definitely not conspecific. He continued to believe, however, that *rhina, clavatus, rhysus,* and his "wide form" *lata* were all varieties of *aeglees.* One factor which probably contributed to Dall's confusion was the rather poor quality of the illustrations of each species in the CHALLENGER report (Watson, 1886). The specimen from the TALISMAN, labeled *"Trochus ottoi"* by Jeffreys, is an Eastern Atlantic species, *Calliotropis vaillanti* (Fischer) (Figs. 9, 10), although later in his discussion of *ottoi,* Dall stated that he had never seen a specimen of this species. All works since Dall (1889) have followed his opinions uncritically, neither noticing that the variety *"lata"* was a *nomen nudum,* nor that this form is the same as *C. calatha* Dall.

C. aeglees differs from *calatha* in having (1) the spire more conical than scalar; (2) the subsutural carina abutting the suture rather than separated from it by a narrow shelf; (3) the mid-whorl carina lower on the whorl; and (4) the tubercles of all 3 carinae more equal in size, less prominent, and more rounded than in *calatha.*

As redefined here, *C. aeglees* has a far more restricted range than previously supposed, and is rather rare, especially when compared to the number of specimens of *calatha* available.

Calliotropis (Solaricida) calatha
(Dall, 1927)
Figs. 15–20, 23–26

Margarita (Solaricida) aegleis var. *lata* Dall, 1889a: 380 (*partim*); 1889b: 164 (listed



FIGS. 15–20. 15–16. *Calliotropis (Solaricida) calatha* (Dall) (syntype): ALBATROSS-2415, h = 4.1 mm, d = 5.0 mm. 17–18. *Calliotropis (Solaricida) calatha* (Dall) ("var. *lata*" Dall): G-1312, h = 4.7 mm, d = 6.3 mm. 19–20. *Calliotropis (Solaricida) calatha* (Dall): G-1008, h = 4.5 mm, d = 5.9 mm.

only).—Johnson, 1934: 71 (listed only). All are *nomina nuda.*

Solariella calatha Dall, 1927a: 128.—Johnson, 1934: 72 (listed only).—Abbott, 1974: 41 (listed only).

Solariella aegleis aegleis: Abbott, 1974: 41 (*partim*; listed only).

Description.—Shell attaining a height of 9 to 10 mm, broadly conical, carinated, spire high or slightly depressed, widely umbilicate, highly sculptured, of about 6 whorls, white with an underlying nacreous lustre. Protoconch small, prominent, glassy, of 1½ whorls. Spire bearing 2 (occasionally 3) carinae set with numerous sharp, axially produced tubercles; another similar carina becomes visible on the body whorl. Tubercles of each carina connected by a fine spiral thread; number of tubercles on lower 2 carinae may vary greatly in a series of specimens, but usually is about 60 on the last whorl. Upper carina separated from the suture by a narrow shelf and bears about 20 to 30 sharp tubercles. Periphery of the whorl may be formed by either or both of the lower 2 carinae. Middle carina lies slightly closer to lower carina than to subsutural carina. Occasional specimens may have another carina intercalated below the subsutural one. Base with 3 to 4 finely beaded cords, the innermost of which is somewhat stronger and more coarsely beaded and defines the umbilical margin. Surface of the whorls between the spiral sculpture may be smooth (except for fine growth lines) to highly corrugated axially. Umbilicus very wide, deep, and strongly constricted within; walls slightly concave, axially rugose, and often with fine spiral cords. Aperture strongly oblique, ovate; lips thin, inner lip slightly reflected over the umbilicus. Columella strongly arched, slightly thickened, usually ending in a strong, blunt tooth, below which the lip is concave, rounding into the basal lip. Periostracum thin, brown.

Holotype.—None selected. Syntype series is in the USNM, cat. no. 108424, 13 specimens from ALBATROSS sta. 2415.

Type-locality.—ALBATROSS sta. 2415, 30°44′N, 79°26′W, 805 m.

Material examined.—ALBATROSS sta. 2415; 13, USNM 108424 (syntypes).—ALBATROSS sta. 2668; 18, USNM 108121.—Straits of Florida: G-1312; 1, UMML 30-8091.—Off Fowey Rocks, Miami, Rush Coll., 850 m; 1, USNM 83034.—G-289; 1, UMML 30-8100.—G-1018; 2, UMML 30-8047.—G-1008; 1, UMML 30-8045.—EOLIS sta. 329 off Sambo Reef, 247 m; 1, USNM 450557.—G-1015; 1, UMML 30-8035.—G-967; 1, UMML 30-8034.—BLAKE sta. 2; 1, USNM 94955.—Yucatan Channel: BLAKE, sta. no. unrecorded, near Cape San Antonio, Cuba, 1170 m; 1, USNM 94954.—Caribbean: P-604; 4, UMML 30-8101.—P-605; 2, UMML 30-8102.—P-607; 2, UMML 30-8103.—Off Cour del Padre, Cuba, 1166 m; 4, USNM 94956.—P-1225; 5, UMML 30-8104.—J-S sta. 67; 4, ex USNM 429422.—J-S sta. 94; 2, USNM 429923.—P-919; 5, UMML 30-8105.—P-929; 2, UMML 30-8106.—P-905; 4, UMML 30-8107.—BLAKE sta. 230; 1, USNM 94957.—P-861; 9, UMML 30-8108.—P-846; 1, UMML 30-8109.—P-754; 2, UMML 30-8110.

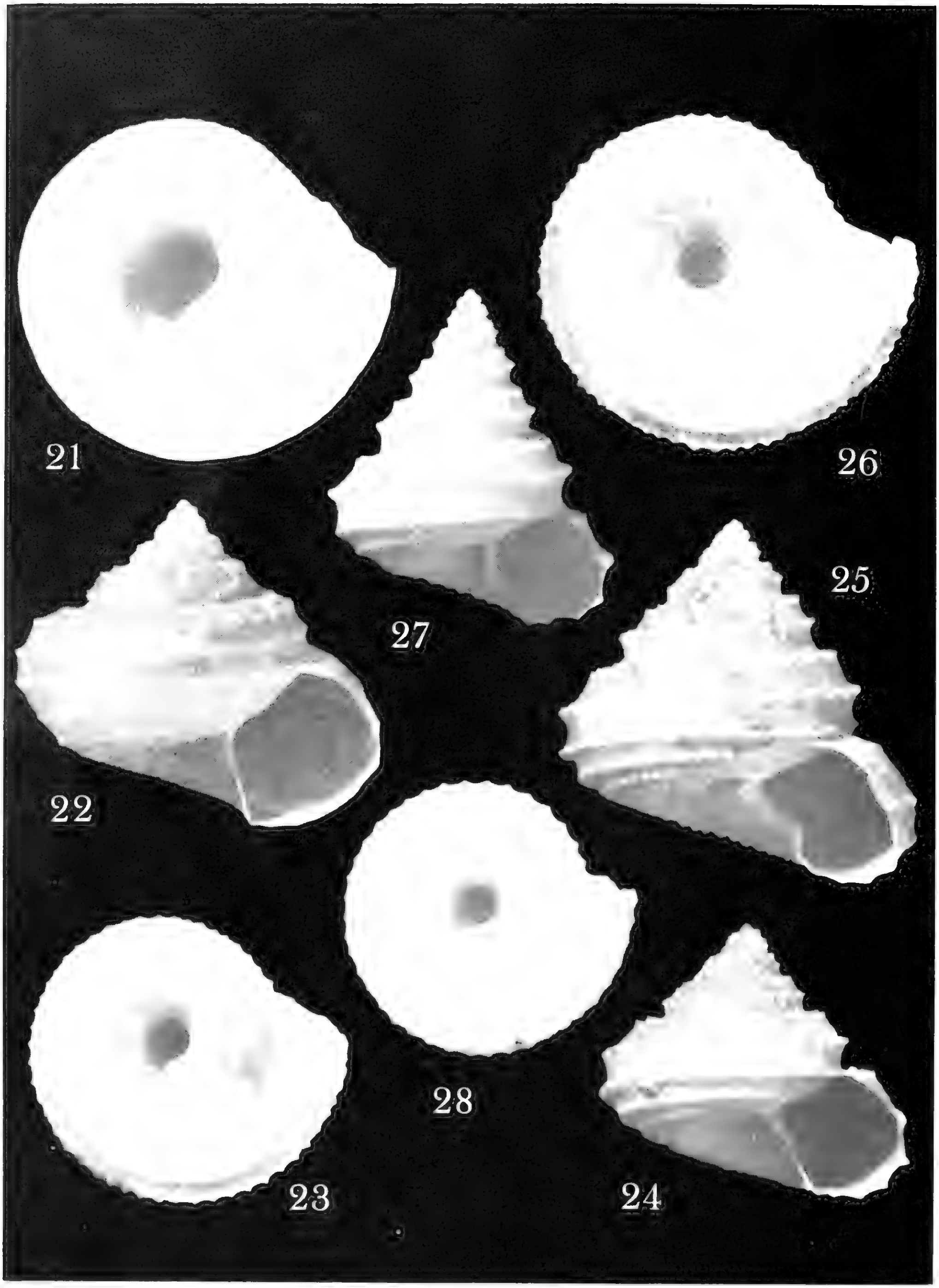
Geographic distribution.—From off Georgia south through the Straits of Florida and the Yucatan Channel, and throughout the Caribbean.

Bathymetric range.—The possible range is 18 to 1574 m, but specimens are generally found in about 500 to 1000 m. The station which records 18 meters as the shallowest depth (P-861) spanned a total depth range of 726 meters (18–744 m); otherwise the species is found almost exclusively in depths exceeding 500 m.

Remarks.—See *Remarks* section under *C. aeglees.* This species has been cited under the name *"Solariella" aegleis lata* since Dall's mention of the name in 1889. This was a *nomen nudum* and has never been validated, so the name cannot stand for the species. However, examination of the specimens of "*lata*" and *C. calatha* (Dall, 1927) in the USNM has revealed that the two are conspecific, and the species therefore takes the later name.

This is an extremely variable species, not only over its whole range, but within individual populations. The elevation of the spire, the distinctness of the axial sculpture, the number of tubercles on the carinae, and the width of the umbilicus are all involved in the variation. As different as any two specimens seem, there appears to be a "connecting link" throughout a long series of specimens. It is at present impossible to separate any of the forms satisfactorily into even subspecies since there is no consistent pattern in the variation either geographically or bathymetrically.

Two specimens are worthy of note. One specimen from G-23 (25°32′N, 79°44′W, 477–238 m, UMML 30-8024) and 1 from P-741 (11°47.8′N, 66°06.8′W, 1052–1067 m,



FIGS. 21–28. 21–22. *Calliotropis (Solaricida) actinophora* (Dall) (holotype): ALBATROSS-2751, h = 7.4 mm, d = 8.4 mm. 23–24. *Calliotropis (Solaricida) calatha* (Dall): P-605, h = 6.75 mm, d = 7.7 mm. 25–26. *Calliotropis (Solaricida) calatha* (Dall): P-846, h = 9.1 mm, d = 9.2 mm; 27–28. *Calliotropis (Solaricida) rhina* (Watson): G-966, h = 7.0 mm, d = 6.0 mm.

UMML 30-6808) are possibly specifically distinct. They have peripheral carinae with extremely closely-set, scalelike tubercles, a rather narrow, vertically-walled umbilicus, and slightly more elevated spire, but because *C. calatha* is so variable and the specimen from off Cour del Padre, Cuba (USNM 94956) approaches this form, I am reluctant to erect a separate taxon for these shells until more material is available for study.

Calliotropis (Solaricida) rhina
(Watson, 1886)
Figs. 27,28

Trochus (Margarita) lima Watson, 1879: 703 (*non* Philippi, 1844).

Trochus (Margarita) rhina Watson, 1886: 80, pl. 5, fig. 1 (*nom. nov.* for *T. (M.) lima* Watson, 1879).

Margarita (Solariella) aegleis var. (?) *rhina*: Dall, 1889a: 380; 1889b: 164 (listed only).—Pilsbry, 1889: 316, pl. 64, figs. 51, 52 (description from Watson, 1879; figs. from Watson, 1886).

Solariella (Machaeroplax) aegleis rhina: Johnson, 1934: 71 (listed only).

Solariella aegleis aegleis: Abbott, 1974: 41 (*partim*; listed only).

Description.—Shell attaining a height of more than 10 mm, conical, spire rather extended, carinated, widely umbilicate, of 6½ to 7 whorls, white with an underlying iridescence. Protoconch smooth, glassy, prominent, of about 1½ whorls. There are 2 carinae on the spire with a third becoming apparent on the body whorl; these are set with many sharp, conical tubercles. Upper carina separated from the suture by a narrow, flat shelf; tubercles are strongest on this carina and are connected by a fine spiral cord. Below the subsutural carina are 2 stronger carinae forming the periphery, the lower of which defines the base. These carinae have about twice as many, finer tubercles as the subsutural carina. Base rounded, with 3 or 4 finely beaded spiral cords, the innermost of which defines the umbilicus. Axial sculpture of strong lamellar ribs on the first postnuclear whorl, but thereafter of only fine growth lines, which may become stronger near the umbilicus and ascend into the umbilicus. Umbilicus rather wide, deep, with convex walls which may bear 1 or 2 fine spiral cords. Aperture slightly oblique, ovate; outer lip thin and angled by the carinae; inner lip thin and slightly reflected; columella smooth, straight, rounding to meet the outer lip. Periostracum rather heavy, brown.

Holotype.—None selected. The syntypes are probably in the British Museum (Natural History). Watson mentioned 1 specimen in particular as "an almost exceptionally fine specimen from Station 78" which probably should be chosen as lectotype.

Type-locality.—CHALLENGER sta. 78, 37°26′N, 25°13′W, off San Miguel, Azores in 1829 m, herein restricted.

Material examined.—ALBATROSS sta. 2384; 1, USNM 93812.—Straits of Florida: G-190; 1, UMML 30-7748.—G-23; 1, UMML 30-8039.—G-368; 1, UMML 30-8027.—G-1106; 1, UMML 30-8096.—G-126; 1, UMML 30-8040.—G-966; 1, UMML 30-8093.—G-439; 1, UMML 30-6971.—BLAKE sta. 2; 2, USNM 94950.—P-605; 6, UMML 30-8111.—P-607; 5, UMML 30-8112.—ALBATROSS sta. 2150; 2, USNM 93855.—P-1255; 4, UMML 30-8113.—P-1256; 3, UMML 30-8114.—P-1261; 6, UMML 30-8115.—CHALLENGER sta. 24; 1, *ex* USNM 118787.—P-988; 3, UMML 30-8116.—P-919; 1, UMML 30-8117.—P-904; 1, UMML 30-8118.—P-861; 3, UMML 30-8119.—P-754; 2, UMML 30-8120.—P-766; 1, UMML 30-8121.

Geographic distribution.—*C. rhina* is an amphi-Atlantic species; it is recorded from off the Azores in the Eastern Atlantic, and the Gulf of Mexico, the Straits of Florida and Caribbean.

Bathymetric range.—As in *C. calatha,* the possible depth range is from only 18 m to over 1800 m. Disregarding the 18 m record (since the station covered a vertical distance of 726 m), the species is usually taken in depths of 500 to 800 m.

Remarks.—*C. rhina* is very closely related to *C. aeglees* (Watson) and *C. calatha* (Dall), but it is much more elevated than either of those two species. It is much less sculptured than *calatha,* the aperture is less oblique, and the columella never has the tooth as in *calatha. C. rhina* is an extremely widespread deep-sea Atlantic species and its characters are remarkably conservative throughout its occurrence, which is in sharp contrast to *calatha.*

Calliotropis (Solaricida) lissocona
(Dall, 1881)
Figs. 13,14

Margarita lissocona Dall, 1881: 41.
Margarita (Solariella) lissocona: Dall, 1889a: 381, pl. 21, figs. 8, 8a; 1889b: 164, pl. 21, figs. 8, 8a (listed only; figs. from 1889a).—Pilsbry, 1889: 322, pl. 48, figs. 23, 24 (description from Dall, 1881; figs. from Dall, 1889a).
Solariella (Machaeroplax) lissocona: Johnson, 1934: 72 (listed only).
Solariella lissocona: Abbott, 1974: 41, fig. 288 (listed only; fig. from Dall, 1889a).

Description.—Shell attaining a height of 6.3 mm, conical, highly iridescent, carinate, umbilicate, of about 6 whorls. Protoconch small, glassy, of a little more than 1 whorl. Just below the suture is a spiral row of small conical beads connected by a fine thread. From this the whorl slopes flatly to the peripheral carina which is formed by a double row of beads similar to those of the subsutural row. The beads of a single row are connected by a fine spiral thread, and the beads of 1 row are semi-fused with their counterparts in the other. Base somewhat convex with 2 strong, sharp, undulate spiral cords in the middle and a strongly beaded cord defining the umbilical margin. Axial sculpture of strong riblets on the first 2 post-nuclear whorls, and thereafter only of fine growth lines. Umbilicus rather wide, deep, strongly constricted within. Aperture subquadrate; outer lip thin, simple; inner lip thin and very slightly reflected; columella slightly oblique, a little arched, ending in an obscure tooth from which the lip curves into the basal lip. Fresh specimens with traces of a brown periostracum.

Holotype.—USNM 214282, from BLAKE sta. 47.

Type-locality.—BLAKE sta. 47, 28°42′N, 80°40′W, off the Mississippi Delta, in 587 m.

Material examined.—Gulf of Mexico: BLAKE sta. 47; 1, USNM 214282 (holotype).—ALBATROSS sta. 2398; 1, USNM 93839.—Straits of Florida: G-967; 1, UMML 30-8122.—Caribbean: P-776; 2, UMML 30-8123.

Geographic distribution.—Known from 2 stations in the northern Gulf of Mexico, 1 in the Straits of Florida near the Marquesas Islands, and 1 in the southern Caribbean off Colombia.

Bathymetric range.—From 408 to 587 m.

Remarks.—This is a beautiful species, apparently most closely related to *C. aeglees* (Watson) from which it differs in being smaller; the peripheral carina is composed of a double row of tubercles more closely apposed than in *aeglees,* and the columella has only a very slight thickening rather than the strong tooth of *C. aeglees. C. lissocona* is a rare, although seemingly rather widespread, species and it will probably turn up in other parts of the Caribbean in depths of about 500 m.

Calliotropis (Solaricida) actinophora
(Dall 1890)
Figs. 21,22

Margarita (Solariella) actinophora Dall, 1890: 353, pl. 12, figs. 8, 11.
Solariella actinophora: Abbott, 1974: 41, fig. 295 (listed only; fig. from Dall, 1890).

Description.—Shell attaining a height of 9 mm, thin, inflated, spire depressed, umbilicate, of 5–6 whorls, highly nacreous when fresh, otherwise white. Protoconch small, glassy, protuberant, of about 1½ whorls. Whorls of the spire with 3 fine, sharp spiral threads; the upper is very fine and very close to the suture; the second is often the strongest and placed just above mid-whorl; the third may be as strong as the second and is just above the succeeding suture. A fourth spiral, hidden by the suture on the spire, forms the periphery of the last whorl. Spiral sculpture is crossed at regular intervals by axial ribs which are of the same character as the spirals. Axials are continuous on the first 3 whorls, forming a reticulate pattern with the spirals; otherwise, the axials are restricted to sharp, close-set plications radiating a short distance from the suture and likewise from the umbilicus. The beading of the upper 2 spirals is coarsest, with the beading becoming much finer on the lower spirals. Base tumid, usually with 3 rather weak, beaded spiral cords between the periphery and a strongly tubercled inner cord which bounds the umbilicus. Umbilicus wide, deep, walls nearly vertical with axial corrugations. Aperture rounded; outer lip thin, simple; inner lip thin, very slightly reflected; columella straight, thin, with a weak to strong tooth at the middle in mature specimens. Periostracum thin, olive-brown.

Holotype.—USNM 96468, from ALBATROSS sta. 2751.

Type-locality.—ALBATROSS sta. 2751, 16°54′N, 63°12′W, south of St. Kitts, Lesser Antilles, in 1257 m.

Material examined.—Straits of Florida: G-824; 1, UMML 30-7701.—G-1111; 1, UMML 30-8037.—G-1112; 2, UMML 30-8038.—G-129; 1, UMML 30-8026.—G-366; 1, UMML 30-8124.—G-375; 1, UMML 30-8029.—G-374; 3, UMML 30-8028.—G-128; 9, UMML 30-8125.—G-965; 6, UMML 30-7761.—G-964; 3, UMML 30-7743; 7, UMML 30-8033.—G-449; 2, UMML 30-6976.—G-448; 2, UMML 30-8126.—G-963; 10, UMML 30-7694.—G-960; 5, UMML 30-8032.—G-959; 1, UMML 30-8031.

Geographic distribution.—The Gulf of Mexico, the Bahamas and the Straits of Florida, south through the Antillean arc, and South America from Tobago to the Rio de la Plata, Argentina.

Bathymetric range.—This species has a possible depth range of 21 to 1863 m, but is generally rather rare in depths less than 1000 m, and rather common between 1000 and 1500 m.

Remarks.—*C. actinophora* has been rather rare in most collections, and has been overlooked in the literature to a great extent. Since its description in 1890, it has been cited only in the semi-technical book *American Seashells* (Abbott, 1974). However, the various ships from RSMAS have taken this species throughout the Caribbean area. It is closely related to *C. infundibulum* (Watson, 1879), a much larger, more elevated species which is also found in the Western Atlantic. *C. actinophora* was taken by the ALBATROSS at station 2764 off the Rio de la Plata in 11½ fathoms (21 m). I am very reluctant to accept the depth here since *actinophora* is rarely taken in depths much shallower than 1000 m, and other species collected at this station occur normally at great depths themselves (e.g., *Seguenzia trispinosa* Watson, 1879).

Genus **Lischkeia** Fischer, 1879

Lischkeia Fischer, 1879: 419.
Margarita (partim): Auctt. (*non* Leach, 1814).
Calliostoma (partim): Pilsbry, 1889: 332.

Type-species.—*Trochus moniliferus* Lamarck, 1816; by original designation, Fischer, 1879: 419.

Diagnosis.—Shell large, elevated trochoid, sculptured by nodulous spiral ribs, umbilicus partly or wholly covered by a thin callus, columella arched and smooth, base flattened to slightly convex.

Subgenus **Turcicula** Dall, 1881

Turcicula Dall, 1881: 42; 1889a: 376; 1889b: 162; 1908: 348; 1909: 98.—Fischer, 1885: 827.—Pilsbry, 1889: 330.—Cossmann, 1918: 254, 263.—Taki & Otuka, 1942: 93.—Rehder, 1955: 222.—Abbott, 1974: 39.

Type-species.—*Margarita (Turcicula) imperialis* Dall, 1881; by monotypy, Dall, 1881: 42.

Diagnosis.—Shell rather thin, sutures deep, sculpture of spiral rows of nodules and axial vermiculate lamellar growth ridges, outer lip reflexed at maturity, umbilicus covered.

Remarks.—This genus is represented by a single species from the Caribbean. The placement of *Turcicula* has been a matter of conjecture since it was first proposed, and will remain so until a specimen with soft parts is available for study. However, in view of the obvious similarities of *Lischkeia monilifera* and *Turcicula imperialis,* I prefer to retain *Turcicula* as a subgenus of *Lischkeia.*

Lischkeia (Turcicula) imperialis (Dall, 1881)
Figs. 29,30

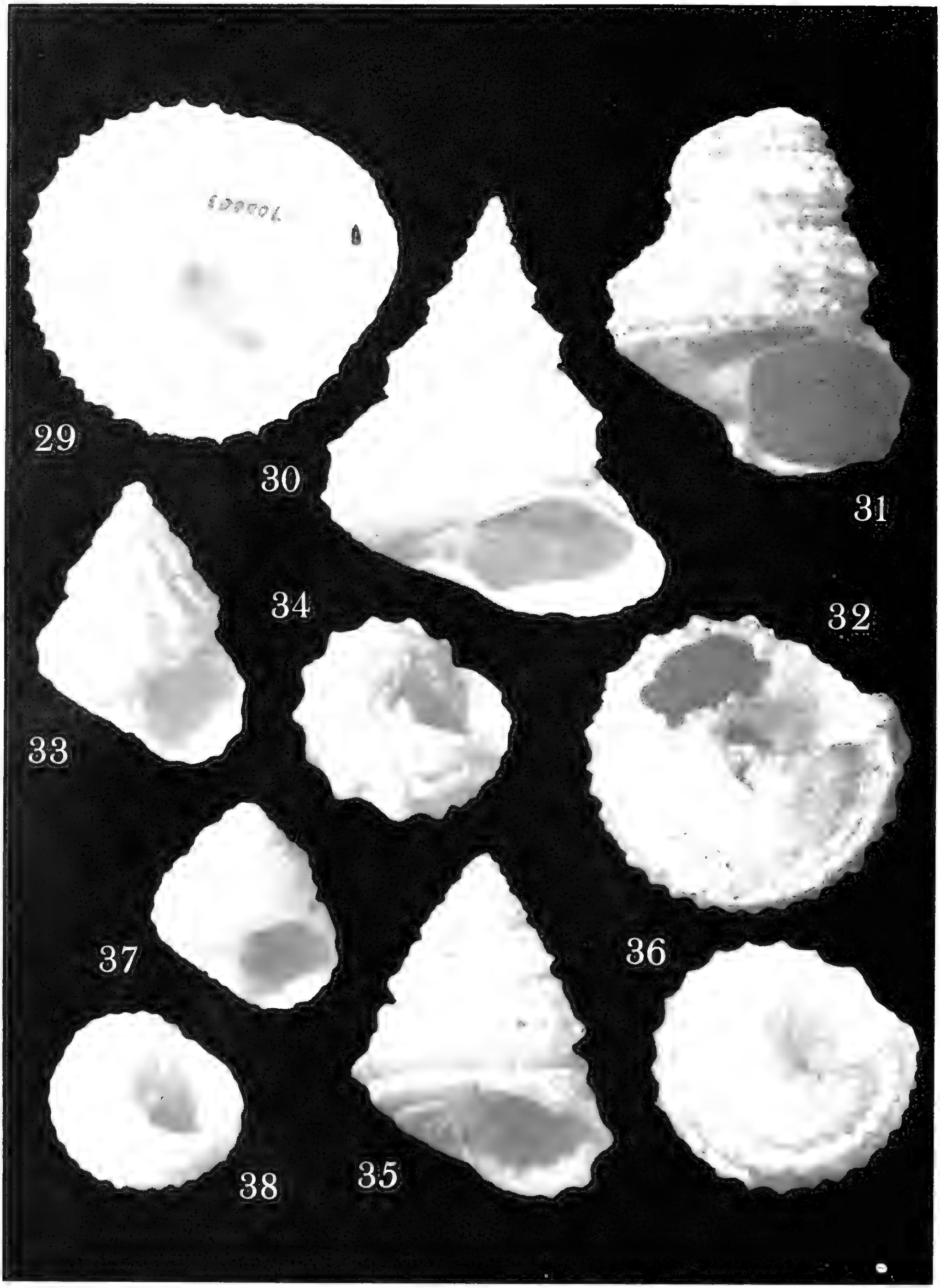
Margarita (Turcicula) imperialis Dall, 1881: 42; 1889a: 376, pl. 22, figs. 1, 1a; 1889b: 162, pl. 22, figs. 1, 1a (listed only; figs. from 1889a).—Pilsbry, 1889: 330, pl. 49, figs. 29, 30 (description from Dall, 1881; figs. from Dall, 1889a).
Turcicula imperialis: Johnson, 1934: 70 (listed only.)—Rehder, 1955: 223, pl. 12, figs. 1–9.—Keen, 1960: I256, figs. 163 (12a,b).
Lischkeia deichmannae Bayer, 1971: 121, fig. 5.
Lischkeia (Turcicula) imperialis: Abbott, 1974: 39, fig. 262.
Calliostoma (Turcicula) imperialis: Humphrey, 1975: 60, pl. 5, fig. 12.

Description.—See Rehder, 1955; Bayer, 1971.

Holotype.—MCZ 7575, from off Cuba, 366 m.

Material examined.—ALBATROSS sta. 2349; 1, USNM 94968.—G-897; 1, UMML 30-7727.—P-889; 1, USNM 700003 (holotype of *L. deichmannae*).

Geographic distribution.—From the southern Straits of Florida off Cuba, Arrowsmith Bank off Yucatan, south and east to the Lesser Antilles.



FIGS. 29–38. 29–30. *Lischkeia (Turcicula) imperialis* (Dall) (holotype of *L. deichmannae* Bayer): P-889, h = 55.0 mm, d = 44.5 mm. 31–32. *Lischkeia (Turcicula) imperialis* (Dall): ALBATROSS-2349, h = 15.0 mm, d = 12.0 mm (immature specimen with spire and body whorl broken). 33–34. *Mirachelus clinocnemus* Quinn, n. sp.: SUI-18, h = 3.4 mm, d = 2.6 mm. 35–36. *Mirachelus corbis* (Dall): G-56, h = 4.6 mm, d = 3.7 mm. 37–38. *Euchelus guttarosea* Dall: EOLIS-315, h = 2.5 mm, d = 2.4 mm.

Bathymetric range.—Prior to 1975 this species was known from depths of 55–91 to 403 m indicating a relatively deep habitat. Humphrey (1975) reported a specimen taken on a beach on Barbados, so perhaps the species inhabits depths considerably shallower than previously believed.

Remarks.—This species was known only from 2 broken and immature specimens until Rehder (1955) reported a mature specimen taken near St. Vincent, Lesser Antilles. In the same paper he redescribed *imperialis* in light of the new material, reviewed the history and supposed relationships of *Turcicula,* and concluded that it was of generic standing. Bayer (1971) based his *L. deichmannae* on an almost perfect specimen of *imperialis* and noted its striking similarity to the type species of *Lischkeia, L. monilifera.* It is this similarity which prompts me to follow Wenz (1938) in placing *Turcicula* as a subgenus of *Lischkeia.*

Genus **Euchelus** Philippi, 1847

Euchelus Philippi, 1847a: 20.
Monodonta (partim): Auctt.
Trochus (partim): Auctt.

Type-species.—Trochus quadricarinatus Holten, 1802; by subsequent designation, Herrmannsen, 1847: 430.

Diagnosis.—Shell solid, turbinate, with spiral beaded cords; umbilicus open or closed; aperture ovate, outer lip thickened, lirate within; columella thickened, with a tooth at its base.

Euchelus guttarosea Dall, 1889
Figs. 37,38

Euchelus guttarosea Dall, 1889a: 382, pl. 33, fig. 7; 1889b: 164, pl. 33, fig. 7 (listed only; fig. from 1889a).—Johnson, 1934: 73 (listed only).—Abbott, 1974: 38, fig. 258.
Euchelus (Euchelus) guttarosea: Pilsbry, 1889: 443, pl. 51, fig. 21 (description and fig. from Dall, 1889a).

Description.—Shell small (attaining a height of about 6 mm), solid, imperforate, with about 5 rounded, highly sculptured whorls. Protoconch depressed, small, glassy, of about 1½ whorls. Spiral sculpture consists of 3 strong cords on the spire with a 4th appearing on the body whorl and forming the whorl periphery; smaller, intercalary spirals are usually present; base with 4 to 7 slightly nodulous cords. Axial sculpture on the first post-nuclear whorl of fine, sharp retractive riblets, becoming stronger on the later whorls; these form strong nodules on the spirals, and with the spirals form a strong reticulate pattern on the whorls. Aperture ovate, thickened within, with 7 to 8 strong lirations ending in strong denticles; columella short, straight, thickened, with a strong tooth near its base. Color white, often with discrete spots of red on the major spirals.

Holotype.—USNM 54774, from Nassau, New Providence Island, Bahamas.

Material examined.—Bahamas: Nassau, New Providence Is.,; 1, USNM 54774 (holotype).—Straits of Florida: EOLIS sta. 329, off Sambo Reef, 247 m; 1, *ex* USNM 438325; 12, USNM 450556.—EOLIS sta. 330, off Sambo Reef, 220 m; 1, USNM 450559.—EOLIS sta. 333, off Key West, 201 m; 1, USNM 450534. —BLAKE sta. no. unrecorded, off Havana, Cuba, 823 m; 1, USNM 95047.

Geographic distribution.—The Bahamas, southeast Florida, and south through the Antilles to Barbados.

Bathymetric range.—This species, like all the others of the genus, is primarily a shallow water species, occurring below the 100 m level only as dead shells. Deeper records are usually in the vicinity of a sharp drop-off, and shells are washed down the slope to as deep as 823 m.

Remarks.—The shells from deep water are all dead and few exhibit the rose-colored patches often seen in the shallow water forms. Whether this is due to wear of the shell is hard to say, but many of the fresher specimens from deeper water are pure white, indicating that perhaps there is a population in deeper water which never develops the coloration of some shallow water forms.

Genus **Mirachelus** Woodring, 1928

Mirachelus Woodring, 1928: 434.—McLean, 1970: 118.—McLean, 1971: 311.

Type-species.—Calliostoma corbis Dall, 1889; by original designation, Woodring, 1928: 434.

Diagnosis.—"Shell small, conical, imperforate, inner layer nacreous. Aperture subquadrangular. Outer lip, as viewed from above, slanting backward from suture. Basal lip almost straight. Outer and basal lips lirate within aperture. Columella vertical, bearing a tooth-like inflation near base. Parietal wall covered with thin wash of callus. Sculpture reticulate." (Woodring, 1928).

Remarks.—This genus has been considered by most recent workers to be a subgenus of either *Solariella* S. V. Wood, 1842, or *Euchelus* Philippi, 1847. McLean (1970) described a species from the Eastern Pacific whose dentition showed a close relationship with *Euchelus,* but the differences in shell sculpture and radular details indicate that *Mirachelus* should be separated at the generic level. While examining material of *M. corbis* in the collections of the USNM, I discovered a form which seems to be specifically distinct from *corbis,* and it is herein described.

Geographic distribution.—Western Atlantic: the southern Straits of Florida, the Gulf of Mexico, and south to the Lesser Antilles.—Eastern Pacific: the Galapagos Islands and Cocos Island.

Bathymetric range.—Known from 165 to 1426 m.

Mirachelus corbis (Dall, 1889)
Figs. 35,36

Calliostoma tiara: Dall, 1881: 45 (*partim*).
Calliostoma corbis Dall, 1889a: 365, pl. 33, fig. 1; 1889b: 162, pl. 33, fig. 1 (listed only; fig. from 1889a).—Pilsbry, 1889: 381, pl. 48, fig. 7 (description and fig. from Dall, 1889a).—Johnson, 1934: 69 (listed only).
Mirachelus corbis: Woodring, 1928: 434.
Solariella (Mirachelus) corbis: Clench & Turner, 1960: 79 (listed only).
Euchelus (Mirachelus) corbis: Keen, 1960: I250 (listed only).—Abbott, 1974: 39, fig. 259 (listed only; fig. from Dall, 1889a).

Description.—Shell small (attaining a height of about 5 mm), solid, compactly conical, carinate, highly sculptured, imperforate, of about 6 whorls. Protoconch small, glassy, of 1 whorl. Spiral sculpture of a very strong peripheral cord and a slightly weaker subsutural cord, usually with 1 or 2 similar cords intercalated between; another cord, on which the suture is formed, lies just under the periphery and defines the base; base with 5 (rarely 4) cords which are slightly excavated along their outer edges. First 1 or 2 whorls with thin axial ribs; axial sculpture on remaining whorls of strong, oblique ribs, which nodulate the spirals and form deep, squarish pits between the spirals; axials not as strong on the base, but nodulate the basal spirals. Base convex, terraced by the spiral sculpture, imperforate. Aperture rounded, thickened within, strongly lirate; lips thin, outer lip crenulated; columella short, thickened, with a blunt tooth in the middle.

Holotype.—MCZ 7562, from off Havana, Cuba.

Type-locality.—Off Havana, Cuba, in 823 m (BLAKE sta. 51?).

Material examined.—Straits of Florida: G-56; 1, UMML 30-5519.—EOLIS sta. 329, off Sambo Reef, 247 m; 12, USNM 450566.—EOLIS sta. 330, off Sambo Reef, 220 m; 1, USNM 450559.—EOLIS sta. 332, off Sambo Reef, 210 m; 1, USNM 450560.—EOLIS sta. 333, off Key West, 201 m; 1, USNM 450534.—EOLIS sta. 325, off Sand Key, 174 m; 1, USNM 450530.—EOLIS sta. 319, off Western Dry Rocks, 165 m; 1, USNM 450567.—BLAKE sta. ?, off Havana, Cuba, 823 m; 1, MCZ 7562 (photograph of holotype, courtesy of Barbara Steger).—BLAKE sta. 20; 2, USNM 95023.—Caribbean: ALBATROSS sta. 2135; 1, USNM 93907.—SUI sta. 116, off English Harbor, Antigua, "deep"; 4, USNM 500229.—SUI sta., off Barbados, "deep"; 1, USNM 500222.

Geographic distribution.—Straits of Florida from off Miami to Key West, the Gulf of Mexico, and south to Barbados.

Bathymetric range.—From 165 to 1426 m.

Remarks.—This compact little species seems to be widely distributed throughout the Caribbean and appears to be rather rare. It is a larger and more finely sculptured species than *M. clinocnemus* n. sp., and occurs in deeper water. It is most commonly taken in depths of 200 to 300 m while *clinocnemus* is rarely found in more than 150 m.

Mirachelus clinocnemus Quinn, n. sp.
Figs. 33,34

Description.—Shell small (attaining a height of about 4.5 mm), solid, conical, of about 6 whorls. Protoconch small, polished, white, of 1½ whorls. Spiral sculpture of 2 very strong, subequal cords, forming a square periphery; shell constricts sharply beneath the periphery to the base which has 4 (rarely 3 or 5) rather strong cords. Axial sculpture of strong, retractive, widely spaced ribs; each rib begins as a nodule at the suture and continues across the peripheral cords, forming strong nodules; axials weak on the base, but bead the spirals. Suture indistinct, obscured by the subsutural nodules. Base convex, often with an umbilical chink. Aperture subcircular, thickened within by a layer of nacre; lips thin, outer lips crenulated by the external sculpture; columella short, straight, thickened, with an obscure tooth in the middle, often completely closing the umbilical chink. Operculum thin, brown, corneous, multispiral. Radular formula ~15.4.1.4.~15. Rhachidian with a broad base and bearing a strong central cusp with 3 sharp lateral cusps on each side; laterals all similar, each with a strong central cusp and 6 lateral cusps; marginals in two series: inner series of 5 very strong, large, sickle-shaped teeth, inner 2 dentate on both edges, outer 3 dentate only on outer side, all overhanging the central part of radula; outer series of about 10 weaker teeth directed outward, outer edges of teeth may be minutely dentate. Radula less than 0.2 mm total width and 1.5–2.0 mm long.

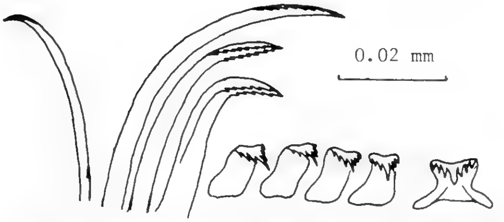


FIG. 89. Partial radular row showing rhachidian, laterals, first three marginals and one marginal from the outer series.

Holotype.—USNM 500731, from off Pelican Island, Barbados.

Type-locality.—Off Pelican Island, Barbados, 146 m (taken by the State University of Iowa Expedition of 1918, sta. 13).

Paratypes.—29 specimens, USNM 711106, with same data as holotype.

Material examined.—EOLIS stations in the Straits of Florida: 157, off Miami Bell Buoy, 40 m; 1, USNM 450514.—Off Fowey Light: 76, 73 m; 1, USNM 450489.—78, 55 m; 2, USNM 450476.—79, 64 m; 3, USNM 450487.—90, 80 m; 1, USNM 450478.—148, 70 m; 1, USNM 450486.—150, 64 m; 3, USNM 450483.—329, off Sambo Reef, 247 m; 4, USNM 438224.—101, off Sand Key, 70 m; 1, USNM 450528.—321, off Western Dry Rocks, 119 m; 1, USNM 450569.—BLAKE sta. 36; 2, USNM 126796.—Antigua: SUI sta. 115, off English Harbour, 220 m; 4, USNM 500744.—Barbados: SUI sta. 3, off Pelican Is., 137–146 m; 54, USNM 500723.—SUI sta. 13, off Pelican Is., 146 m; 30, USNM 500731 & 711106 (1 holotype and 29 paratypes).—SUI sta. 18, off Pelican Is., 73 m; 6, USNM 500726.—SUI sta. 21, off St. Matthais Church, 110 m; 4, USNM 500740.—SUI sta. 25, off Pelican Is., 146 m; 2, USNM 500727.—SUI sta. 26, off Pelican Is., 137 m; 29, USNM 500728.—SUI sta. 27, off Pelican Is., 146–165 m; 8, USNM 500729.—SUI sta. 29, off Lazaretto, 165–183 m; 2, USNM 500732.—SUI sta. 31, off Lazaretto, 146–165 m; 2, USNM 500734.—SUI sta. 44, off Pelican Is., 165–183 m; 7, USNM 500725.—SUI sta. 47, off Pelican Is., 46–132 m; 8, USNM 500730.—SUI sta. 48, off Lazaretto, 172 m; 1, USNM 500733.—SUI sta. 51, off Pelican Is., 60 m; 7, USNM 500724.—SUI sta. 54, off Cable Station, 60 m; 2, USNM 500735.—SUI sta. 67, off Telegraph Station, 91–110 m; 4, USNM 500736.—SUI sta. 78, off Payne's Bay Church, 64–137 m; 4, USNM 500739.—SUI sta. 79, off Telegraph Station, 55–128 m; 8, USNM 500737.—SUI sta. 80, off Telegraph Station, 73–137 m; 8, USNM 500738.—SUI sta., number unrecorded, 146 m; 12, USNM 500743.—SUI sta., number unrecorded, 146 m; 3, USNM 500742.—SUI sta., position and depth unrecorded; 1, USNM 500741.—Brazil off Chui, Rio Grande do Sul, 166 m, 17 Jan. 1972; 1, Museu Oceanográfico do Rio Grande No. 17. 318.

Geographic distribution.—From off Miami, south and west along the Florida Keys to off Key West, and the Lesser Antilles to Barbados; Rio Grande do Sul, Brazil.

Bathymetric range.—Known from 46 to 247 m. This species is concentrated in depths of less than 150 m and is only occasionally taken in greater depths. It probably does not form a part of the molluscan fauna in the Straits below 150 m.

Remarks.—This is the 3rd known species in the genus *Mirachelus,* and the second reported from the Western Atlantic. Specimens of this species have been in the collections of the USNM for many years as *M. corbis* (one lot was labeled by Dall as *corbis*). *M. clinocnemus* can easily be distinguished from *corbis* by the square periphery formed by two subequal spiral cords, not one as in *corbis,* the absence of spiral cords above the peripheral ones, 4 basal cords (5 in *corbis*), and generally smaller size. *M. clinocnemus* is generally a small, compact species, but there are forms which have the spire somewhat extended. The umbilical chink varies from open to completely covered by the columella.

The radula of *M. clinocnemus* is similar to that illustrated by McLean (1970) for *M. galapagensis* but has 4 lateral teeth and differently shaped and stronger inner marginals. The radula of *M. corbis* is unknown.

Genus **Echinogurges** Quinn, gen. nov.

Margarita (partim), Auctt. (*non* Leach, 1814).
Solariella (partim), Auctt. (*non* S. V. Wood, 1842).
Calliotropis (partim), Auctt. (*non* Seguenza, 1903).

Type-species.—Trochus (Margarita) clavatus Watson, 1879: 705; herein designated.

Gender.—Masculine.

Diagnosis.—Shell small (about 5 mm), trochoid, acutely conical with an extended spire, base rounded, umbilicate; shell nacreous under an external chalky layer, sculptured by spiral rows of tubercles and/or axial riblets.

Remarks.—This genus seems to be rather well-defined, although apparently closely related to *Calliotropis*. At least 1 species (*E. clavatus*) has been considered a juvenile of *C. aeglees* (Watson). Shells of *Echinogurges* can be distinguished from *Calliotropis* by their much smaller size, the base rounding smoothly into the umbilicus without an umbilical keel, and their much more acutely conical shape. To my knowledge, no living specimens of this genus have been obtained, so radular characters are, as yet, unavailable to aid in placing it. Whatever its relationships, the genus seems distinct enough to warrant generic separation.

Geographic distribution.—Amphi-Atlantic, found in the Eastern Atlantic off Portugal, and in the Western Atlantic off Georgia, the Straits of Florida and the Lesser Antilles. It probably occurs throughout the Caribbean.

Bathymetric range.—538 to 1723 m.

Echinogurges clavatus (Watson, 1879)
Figs. 43,44

Trochus (Margarita) clavatus Watson, 1879: 705; 1886: 82, pl. 5, fig. 8.
Margarita (Solariella) aegleis var. (?) *clavata*: Dall, 1889a: 380; 1889b: 164 (listed only). —Pilsbry, 1889: 318, pl. 66, figs. 98, 99 (description from Watson, 1879; figs. from Watson, 1886).—Johnson, 1934: 71 (listed only).
Margarita (Solariella) clavata: Dall, 1890: 352.
Solariella aegleis aegleis: Abbott, 1974: 41 (*partim*).

Description.—Shell small, attaining a height of 6 mm, conical, with an extended spire, umbilicate, of about 6½ whorls, highly nacreous when fresh. Protoconch small, glassy, prominent, of about 1½ whorls. There are 3 sharp spiral cords on the spire and a fourth appearing on the body whorl; each cord is set with sharp, axially produced tubercles. The upper spiral is just below the suture, the second at about mid-whorl, and the third about mid-way between the second and fourth, on which the suture forms; the second and third are at the periphery of the whorl. Axial sculpture of fine, sharp riblets whose intersections with the spirals produce the nodulations. Base rounding smoothly into the umbilicus with 5 or 6 beaded spiral cords. Umbilicus deep and constricted within to a narrow pore. Aperture almost circular; lips thin; inner lip slightly reflected; columella arched and rounding smoothly into the outer lip.

Syntypes.—Syntypes are in the British Museum (Natural History).

Type-locality.—Watson's original description included 8 specimens from CHALLENGER sta. 24 and 120, but he was uncertain that the 2 from sta. 120 were the same species. Until the type-series can be examined a final decision cannot be made as to the type-locality, but I would expect that it should be CHALLENGER sta. 24, 18°38′30″N, 64°05′30″W, off Culebra Island, Virgin Islands, 713 m.

Material examined.—Bahamas: CI-356; 4, UMML 30-8130.—Straits of Florida: G-23; 3, UMML 30-8078.—G-965; 1, UMML 30-8043. —BLAKE sta. 2; 1, USNM 94951.—ALBATROSS sta. 2751; 4, USNM 95398; 3, USNM 330740.—ALBATROSS sta. 2754; 1, USNM 96877.

Geographic distribution.—The Straits of Florida, the Bahamas, and the Lesser Antilles. *E. clavatus* probably occurs throughout the Antillean arc.

Bathymetric range.—Taken in depths of about 1400 to 1600 m throughout its range.

Remarks.—*E. clavatus* has been long regarded as either a form or a young specimen of *Calliotropis aeglees* (Watson), *C. calatha* (Dall), or *C. rhina* (Watson). It differs from these species in being much smaller and more elevated, in having the base round smoothly into the umbilicus, and in having a prickly aspect to the sculpture. *E. clavatus* seems to be closest to *E. anoxius* (Dall) and *E. rhysus* (Watson). *E. clavatus* can easily be separated from *anoxius* and *rhysus* by having 2 carinae at the periphery rather than one. It is much more highly sculptured than *E. rhysus,* some specimens approaching the sculpture of *anoxius,* but not as coarse as in that species.

Echinogurges anoxius (Dall, 1927)
Figs. 41,42

Solariella anoxia Dall, 1927a: 129.—Abbott, 1974: 41 (listed only).
Solariella (Machaeroplax) anoxia: Johnson, 1934: 72 (listed only).

Description.—Shell small (attaining a height of about 4 mm), acutely conical, with an extended spire, obscurely carinate, highly sculptured, umbilicate, of abut 5½ whorls. Protoconch small, glassy, prominent, of about 1½ whorls. There are 3 major angulations (1 hidden by the suture on the spire) which are almost too obscure to be termed carinae. One lies just below the suture, another is at mid-whorl, and the third, on which the suture is formed, defines the base. Fine spiral cords may or may not be present in the intercarinal spaces. Axial sculpture of strong, close-set ribs which are somewhat oblique above the periphery, from which they descend vertically across the base and into the umbilicus. Intersections of the axial and spiral sculpture result in sharp conical tubercles. Base convex with 3 to 5 spiral cords, rounding into the umbilicus. Umbilicus constricting within to a narrow central pore. Aperture rounded, almost circular; lips thin; columella arched, thin, rounding smoothly into the outer lip.

Syntypes.—USNM 108142, from ALBATROSS sta. 2668.

Type-locality.—ALBATROSS sta. 2668; 30°58′30″N, 79°38′30″W, in 538 m.

Material examined.—ALBATROSS sta. 2668; 9, USNM 108142 (syntypes).—ALBATROSS sta. 2415; 1, USNM 108420; 4, USNM 108421.—Straits of Florida: G-23; 1, UMML 30-8097.

Geographic distribution.—Known only from 2 stations off southern Georgia and 1 off Miami, Florida.

Bathymetric range.—From 538 to 805 m.

Remarks.—This species looks very much like *E. clavatus* (Watson) but is more strongly sculptured and has only a single peripheral carina rather than a double one, and is much smaller. The spiral sculpture varies in that the fine cords between the carinae may or may not be present. The forms with no intermediate spirals approach the appearance of *E. rhysus* (Watson), but the strong axial sculpture is still present, while it is almost totally lacking in *rhysus.*

Echinogurges rhysus (Watson, 1879)
Figs. 39,40

Trochus (Margarita) rhysus Watson, 1879: 706; 1886: 83, pl. 5, fig. 4.—Dall, 1889a: 380 (name only).
Margarita (Solariella) rhysus: Pilsbry, 1889: 324, pl. 66, figs. 9, 10 (description from Watson, 1879; figs. from Watson, 1886).
Non Solariella rhyssa Dall, 1919: 360.

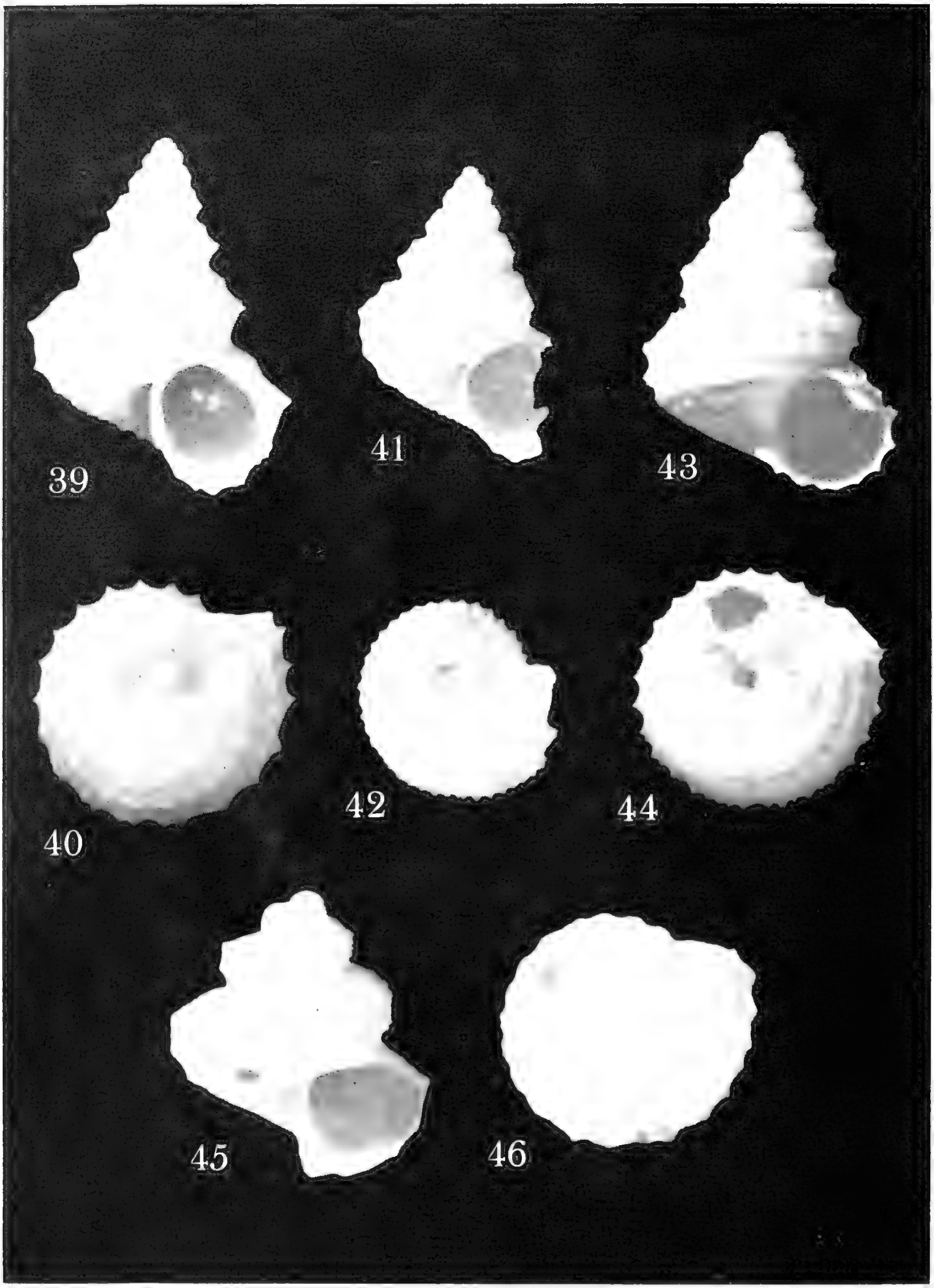
Description.—Shell small (attaining a height of 4.6 mm), conical, with an extended spire, carinate, umbilicate, of about 5½ whorls, nacreous when fresh. Protoconch small, prominent, glassy, of about 1½ whorls. Spiral sculpture of 3 carinae set with sharp, axially produced tubercles; only 2 of the carinae are visible on the spire. The upper carina is just beneath the suture, the second is at mid-whorl and forms the whorl periphery, and the third, on which the suture is formed, defines the base. Base with 4 smooth to finely beaded cords. Axial sculpture of sharp riblets on the first 2 whorls, becoming obsolete on the following whorls where they are indicated by the tubercles on the spiral sculpture. Base convex under the sculpture, rounding into the umbilicus, which constricts within to a narrow central pore. Aperture subcircular; lips thin; inner lip slightly reflected; columella concave, thin, rounding smoothly into the outer lip.

Syntypes.—Two syntypes are in the British Museum (Natural History).

Type-locality.—None selected. The 2 specimens representing the syntype series were collected at 2 different CHALLENGER stations. One was taken at station II off Portugal (38°10′N, 09°14′W) and the other was taken off the Virgin Islands. Considering the confusion regarding identification of species in this genus, there is a good chance that the 2 specimens referred to *E. rhysus* may represent 2 different species. It is therefore necessary to examine the syntypes and choose a lectotype before a type-locality can be defined.

Material examined.—ALBATROSS sta. 2415; 1, *ex* USNM 108421.—ALBATROSS sta. 2654; 5, USNM 330606.—Straits of Florida: G-368; 2, UMML 30-8054.—G-1106; 1, UMML 30-8095.—G-130; 1, UMML 30-8041. —G-859; 1, UMML 30-8163.

Geographic distribution.—Apparently amphi-Atlantic: reported from off Portugal (CHALLENGER sta. II), and known in the Western Atlantic from off northeastern Flor-



FIGS. 39–46. 39–40. *Echinogurges rhysus* (Watson): G-1106, h = 4.0 mm, d = 3.1 mm. 41–42. *Echinogurges anoxius* (Dall) (syntype): ALBATROSS-2668, h = 3.8 mm, d = 2.9 mm. 43–44. *Echinogurges clavatus* (Watson): G-965, h = 4.2 mm, d = 3.0 mm. 45–46. *Echinogurges tubulatus* (Dall) (holotype): ALBATROSS-2668, h = 3.7 mm, d = 3.5 mm.

ida, the Straits of Florida, and off Sombrero, Virgin Islands.

Bathymetric range.—From 805 to 1723 m.

Remarks.—*E. rhysus* has long been overlooked as is evident from the short synonymy. The last worker to mention this species in the scientific literature seems to have been Pilsbry in 1889, although his treatment was merely a literature compilation, adding nothing new. This species had been reported only from off Portugal and the Virgin Islands by Watson, so the present material represents a substantial extension of its range.

Occasional specimens of *rhysus* have fine intercalary spirals in the intercarinal spaces and some have traces of the axial sculpture persisting onto the last whorl, particularly below the peripheral carina.

Echinogurges tubulatus (Dall, 1927)

Figs. 45,46

Solariella tubulata Dall, 1927a: 130.

Description.—Shell small, conical, carinate, umbilicate, white, of about 3 whorls. Protoconch rather large, smooth, of about 1½ to 2 whorls. Spiral sculpture of 2 strong carinae, forming a wide, square periphery, and a somewhat weaker 1 defining the base. Space between the suture and the upper carina wide, rather flat, with fine prosocline growth lines; between the 3 carinae there are numerous strong axial cords which nodulate the spirals. Base slightly convex, usually with 4 very faint spiral threads; umbilicus narrow, microscopically rugose. Aperture subcircular, slightly angulated by the spiral sculpture; lips thin; inner lip slightly reflected; columella thin, slightly arched.

Syntypes.—Syntype series of 2 specimens; USNM 108109, from ALBATROSS sta. 2668.

Type-locality.—ALBATROSS sta. 2668, 30°58′30″N, 79°38′30″W, in 538 m.

Material examined.—ALBATROSS sta. 2668; 2, USNM 108109 (syntypes).—ALBATROSS sta. 2415; 7, USNM 108415.—Straits of Florida: G-23; 1, UMML 30-8079.

Geographic distribution.—Known only from off southeastern Georgia and the Straits of Florida off Miami.

Bathymetric range.—538 to 805 m.

Remarks.—This is a very well-marked species, with its characteristic flat shoulder and square periphery separating it immediately from any other species. It seems to fit best in *Echinogurges*, but whether it really belongs here must await examination of soft parts.

The specific name *tubulata* is evidently a mistake for Dall's originally intended name "*tabulata*," which is a much more appropriate name. However, only a label in the type lot indicates this and it is impossible to determine whether the published spelling was a typographical error or a mistake by Bartsch who published the paper after Dall's death. Under the rules of nomenclature, *tubulatus* must stand as the specific name.

Subfamily Umboniinae Pilsbry, 1886

Genus **Gaza** Watson, 1879

Gaza Watson, 1879: 601; 1886: 93.
Callogaza Dall, 1881: 49 (*partim*).

Type-species.—*Gaza daedala* Watson, 1879; by monotypy.

Diagnosis.—"Shell turbinate to depressed turbinate, rather thin, generally highly opalescent. Umbilicus deep, rather wide and partially or completely covered by a columellar pad or callus. Operculum corneous, multispiral, thin and colored a pale amber." (Clench & Abbott, 1943.)

Remarks.—*Gaza* is a beautiful and very distinct genus of trochids. It is restricted to deep water and possesses a thin, highly nacreous shell which readily separates it from other genera. It has been considered rather rare, but recent collections, especially in the Gulf of Mexico and southern Caribbean, have shown that *Gaza* is not uncommon, and may even be abundant in areas of mud and sand bottom in depths of 400–600 m. Like many other trochids, species of *Gaza* probably feed primarily on detrital material and possibly on minute infaunal organisms, such as benthic foraminifera.

Geographic distribution.—The few species known seem to be distributed in deep tropical waters, probably circumtropical, although I can find no species attributed to the Indian Ocean.

Bathymetric range.—Exclusively deep water, from about 200 to over 1000 m, with the exception of *G. (Callogaza) sericata* Kira from Japan, which occurs in rather shallow water (less than 200 m).

Subgenus **Gaza** Watson, 1879

Diagnosis.—Characters of the genus; sculpture of fine spiral lirations or smooth;

shell rather large, generally 20–40 mm in diameter; shell of one color, usually a straw or ivory.

Gaza (Gaza) superba cubana Clench & Aguayo, 1940

Gaza superba cubana Clench & Aguayo, 1940: 81, pl. 15, fig. 3.
Gaza (Gaza) superba cubana: Clench & Abbott, 1943: 3, pl. 3, figs. 1, 2.
Gaza (Gaza) superba: Abbott, 1974: 49, fig. 375a (listed as form of *G. superba*; figs. from Clench & Abbott, 1943).

Description.—See Clench & Abbott, 1943.

Holotype.—MCZ 135151, from ATLANTIS sta. 3448.

Type-locality.—ATLANTIS sta. 3448, off Sagua la Grande, 23°21′N, 79°56′W, in 695 m.

Material examined.—Straits of Florida: G-524; 1, UMML 30-7751.—G-917; 1, UMML 30-7677.—G-357; 1, UMML 30-6022.—G-815; 1, UMML 30-7560.—G-130; 1, UMML 30-8135.—G-111; 1, UMML 30-8089.—S. of Cozumel, Yucatan: P-602; 11, UMML 30-8136.

Geographic distribution.—The Northwest Providence Channel south through the Straits of Florida and Yucatan Channel.

Bathymetric range.—From 329 to 1089 m.

Remarks.—Clench & Abbott (1943) suggested that this form is specifically distinct from *G. superba* (Dall), but Abbott (1974) indicated that he considered it to be an infrasubspecific form of *superba.* I have not, as yet, been able to examine enough specimens of either species to enable me to resolve the problem. The few specimens I have seen and an examination of the ranges of the 2 forms indicates to me at least a separation at the subspecific level, and pending further research, I am leaving *cubana* as a subspecies of *superba. G. superba* differs from *cubana* in being larger, more inflated, and higher-spired. *G. superba* occurs throughout the Caribbean area and extends up into the northern Gulf of Mexico, while *cubana* is restricted to the Straits of Florida and the Yucatan Channel as far as is now known. *G. superba cubana* also seems to prefer the insular margin of the Straits, but occurs along the continental coast of southeastern Yucatan.

Gaza (Gaza) fischeri Dall, 1889

Gaza fischeri Dall, 1889a: 355, pl. 37, fig. 6; 1889b: 160, pl. 37, fig. 6 (listed only; fig. from 1889a).
Gaza fischeri: Pilsbry, 1889: 158, pl. 49, fig. 37 (description and fig. from Dall, 1889a).—Johnson, 1934: 73 (listed only).—Clench & Aguayo, 1938: 380.—Clench & Abbott, 1943: 4, pl. 3, figs. 3–5.—Abbott, 1974: 49, fig. 376 (listed only; figs. from Clench & Abbott, 1943).

Description.—See Dall, 1889a; Clench & Abbott, 1943.

Lectotype.—Selected by Clench & Abbott (1943), MCZ 7543, from BLAKE sta. 221.

Type-locality.—BLAKE sta. 221, off St. Lucia, 13°54′55″N, 61°06′05″W, 772 m.

Material examined.—Straits of Florida: G-918; 1, UMML 30-7678.—G-190; 1, UMML 30-8005.—G-226; 1, UMML 30-5711.—G-289; 2, UMML 30-5960.—G-365; 5, UMML 30-6024.—G-362; 4, UMML 30-6023.—G-130; 1, UMML 30-5526.

Geographic distribution.—The Straits of Florida and the Gulf of Mexico, and from Cuba south throughout the Caribbean Sea.

Bathymetric range.—From 600 to 1021 m.

Remarks.—This species is readily separated from the others in the comma-like axial plications on the early whorls and an umbilical pad which completely covers the umbilicus. The spiral sculpture is coarser than in *Gaza superba* or *G. superba cubana,* and there is a series of short radial plications around the umbilical margin (usually hidden by the umbilical pad) which are not present in the other species. *G. fischeri* appears to be the most common species of *Gaza* in the Western Atlantic although future trawling along the Caribbean coast of Central America may show one of the other species to be more common.

Subgenus **Callogaza** Dall, 1881

Callogaza Dall, 1881: 50; 1889a: 356.—Clench & Abbott, 1943: 5.

Type-species.—*Callogaza watsoni* Dall, 1881; by subsequent designation, Dall, 1889a: 356.

Diagnosis.—Differs from *Gaza s. s.* in having stronger spiral sculpture, a distinctly shouldered whorl, a mottled color pattern (not a uniform color as in *Gaza*), and in generally being smaller.

Gaza (Callogaza) watsoni (Dall, 1881)

Margarita filogyra Dall, 1881: 42.
Callogaza watsoni Dall, 1881: 50.
Gaza (Callogaza) watsoni: Dall, 1889a: 356, pl. 22, fig. 7, 7a; pl. 24, fig. 2, 2a; 1889b: 160, pl. 22, fig. 7, 7a; pl. 23, fig. 1, 1a; pl. 24, fig. 2, 2a (listed only; figs. from 1889a).
Gaza (Callogaza) watsoni: Pilsbry, 1889: 158, pl. 49, figs. 25–28; p. 48, figs. 11, 12 (description from Dall, 1881 & 1889a; figs. from Dall, 1889a).—Johnson, 1934: 73 (listed only).—Clench & Abbott, 1943: 5, pl. 2, figs. 3, 4.—Abbott, 1974: 49, fig. 377 (listed only; fig. from Dall, 1889a).
Gaza watsoni: Clench & Aguayo, 1938: 381.

Description.—See Dall, 1881 and 1889a; Clench & Abbott, 1943.

Holotype.—MCZ 7544, from BLAKE sta. 12.

Type-locality.—BLAKE sta. 12, off Havana, Cuba, 24°34′N, 83°16′W, 66 m (not 177 fms as reported by Dall, 1881 & 1889; 117 fms, as reported by Clench & Abbott, 1943, is a misprint).

Material examined.—BLAKE sta. 12; 1, MCZ 7544.—BLAKE, sta. no. unrecorded, off Bahia Honda, Cuba, 402 m; 2, MCZ 7546 (paratypes of *Margarita filogyra*).—BLAKE sta. no. unrecorded, Yucatan Channel, 1170 m; 1, MCZ 7545 (holotype of *M. filogyra*); 1, MCZ 7547 (paratype of *M. filogyra*).—G-897; 2, UMML 30-7725.

Geographic distribution.—*G. watsoni* occurs around Cuba, south through the Antillean arc, and Brazil off the Para River.

Bathymetric range.—Known from 66–1170 m, but primarily inhabits depths greater than 250 m.

Remarks.—*G. watsoni* is a very distinctive species and cannot be confused with any of the other known Western Atlantic species. *Margarita filogyra* was described from immature specimens of *watsoni.* Dall, acting as first revisor in 1889, chose *watsoni* over *filogyra* as the species name. Fortunately, no subsequent author has attempted to revive *filogyra* and the name *watsoni* has been accepted. Only one other species of this subgenus seems to be known at present, *G. (C.) sericata* Kira, from Japan. However, *sericata* is a relatively shallow water form, living in 100–200 m.

Subfamily Calliostomatinae Thiele, 1924

Genus **Calliostoma** Swainson, 1840

Calliostoma Swainson, 1840: 218, 351
Conulus Nardo, 1840: 244 (*non* Leske, 1778)
Ziziphinus Gray, 1840: 147 (*nomen nudum*); 1843: 237
Stylotrochus Seguenza, 1876: 186 (*non* Haeckel, 1862).
Fluxina Dall, 1881: 51.
Manotrochus Fischer, 1885: 827.
Jacinthinus Monterosato, 1889: 79.
Ampullotrochus Monterosato, 1890: 145.
Dymares Schwengel, 1942: 1.

Type-species.—*Trochus conulus* Linnaeus, 1758; by subsequent designation: Herrmannsen, 1846: 154.

Diagnosis.—Shell trochoid, spire conical, base generally flattened, umbilicate or imperforate; interior of shell nacreous, exterior sculptured and calcareous, with nacreous sheen often showing through. Aperture rounded or oblique, smooth or lirate within, outer lip thin, base of columella thickened. Sculpture usually of smooth or beaded spiral cords. Operculum thin, corneous, circular, multispiral.

Remarks.—Swainson (1840) introduced the name *Calliostoma* without any designation of a type-species. His mention of *Trochus zizyphinus* as an example of the genus has been considered by some subsequent authors as monotypy. However, Swainson later in the same work (p. 351) listed 7 additional species with *Trochus zizyphinus* under *Calliostoma,* obviously not considering it a monotypic genus. I therefore agree with Woodring (1928) and Olsson (1971) that this does not constitute monotypy and that the subsequent designation of *Trochus conula* Martyn (=*T. conulus* Linnaeus) by Herrmannsen (1846) should stand.

The classification of *Calliostoma* has depended greatly on differences in shell morphology, especially the presence or absence of an umbilicus. This character has been used not only at the subgeneric level, but also to separate genera. However, Clench & Turner (1960) discarded this approach in favor of subgeneric groupings using jaw morphology and radular characters, since some species are umbilicate when young and become imperforate with maturity. They based their study on the jaws and radulae of 20 North Atlantic species, but since these characters have been recorded for so few species from other geographic areas, we must await further work along these lines to determine whether these groupings are valid.

What little is known of the natural history of this genus has been summarized by Clench & Turner (1960). Most authors have considered species of *Calliostoma* to be strict herbivores or detrital feeders. Perron (1975), in a study of 3 shallow-water species of *Calliostoma,* established that at least some members of the genus are carnivorous, feeding on hydroids. It is still probable that deep-water species are primarily detrital feeders but may be opportunistic predators of hydroids.

Geographic distribution.—*Calliostoma* is widely distributed in tropical and temperate waters. As strictly defined it does not seem to enter Arctic or Antarctic waters, being replaced in the Antarctic by closely related genera such as *Photinula* Adams & Adams and *Photinastoma* Powell (Powell, 1951). The *Calliostoma* fauna of the western North Atlantic is rich, probably comprised of about fifty species.

Bathymetric range.—From the intertidal zone to over 2000 m. The deepest Atlantic record is 2330 m for *Calliostoma suturale* (Phillipi) collected west of Morocco by the TALISMAN. In the western North Atlantic *C. occidentale* (Mighels & Adams) was taken alive in 1792 m by the BLAKE off Georges Bank, and several species were collected by the BLAKE in 1472 m in the Straits of Florida off Havana, Cuba.

Subgenus **Calliostoma** Swainson, 1840

Type-species.—*T. conulus* Linnaeus, 1758, by subsequent designation; Herrmannsen, 1846: 154.

Diagnosis.—Shells generally imperforate, marked with axial flames of reddish brown or unicolored. Sculptured with beaded cords, occasional species are found having these cords beaded only on the early whorls. Aperture subquadrate. Radula with a denticulate central tooth, five rather uniform lateral teeth, the first marginal tooth broad, the succeeding marginals becoming more attenuate, and having numerous, fine denticles. Jaw subcircular with their anterior ends broadly rounded and with a short fringe.

Calliostoma (Calliostoma) pulchrum
(C. B. Adams, 1850)

Trochus pulcher C. B. Adams, 1850: 69.—Dall, 1889a: 366.—Clench & Turner, 1950: 331, pl. 40, fig. 7.

Calliostoma pulcher: Dall, 1889b: 162 (listed only).—Pilsbry, 1889: 375.

Calliostoma veliei Pilsbry, 1900: 128.

Calliostoma (Calliostoma) pulchrum: Clench & Turner, 1960: 17, pl. 3, fig. 3; pl. 14.—Abbott, 1974: 42, fig. 306.

Description.—See Clench & Turner, 1960.

Holotype.—MCZ 156356, from Jamaica.

Type-locality.—Jamaica.

Geographic distribution.—North Carolina, Florida, the Bahamas, Cuba, the Gulf of Mexico and the northern Caribbean.

Bathymetric range.—This species is not uncommon in depths of less than 2 m to about 150 m, with only 1 specimen taken in greater depths (Pourtalès, collected at an unspecified locality in the Straits of Florida, 366 m, USNM 83382).

Remarks.—See *Remarks* under *C. roseolum. C. pulchrum* seems to prefer depths of less than 150 m, with the 1 exception of the Pourtalès specimen. This is probably merely a fortuitous occurrence. The specimen was dead when collected and, because of the precipitous nature of much of the Straits area, the specimen might easily have been carried to this depth by currents or perhaps a fish.

Calliostoma (Calliostoma) roseolum
Dall, 1881

Calliostoma roseolum Dall, 1881: 45; 1889b: 162, pl. 24, figs. 6, 6a (name only, figures taken from Dall, 1889a).—Pilsbry, 1889: 373, pl. 49, figs. 35, 36 (description from Dall, 1881; figures from Dall, 1889a).—Johnson, 1934: 70 (name only).

Calliostoma apicinum Dall, 1881: 46; 1889b: 162, pl. 24, figs. 3, 3a (name only, figures from Dall, 1889a).—Pilsbry, 1889: 379, pl. 60, figs. 1, 2 (description from Dall, 1881; figures from Dall, 1889a).—Johnson, 1934: 69 (name only).

Calliostoma (Calliostoma) roseolum: Dall, 1889a: 366, pl. 24, figs. 6, 6a.—Clench & Turner, 1960: 19, pl. 4, fig. 3; pl. 15.—Abbott, 1974: 43, fig. 307.

Calliostoma (Calliostoma) apicinum: Dall, 1889a: 366, pl. 24, figs. 3, 3a.

Description.—See Clench & Turner, 1960; Dall, 1889a.

Holotype.—MCZ 7563, from BLAKE sta. 11.

Type-locality.—BLAKE sta. 11, 24°43′N, 83°25′W, off Havana, Cuba, 68 m.

Record.—BLAKE sta. 56 (23°09′N, 82°21′W, off Havana, Cuba, in 320 m).

Geographic distribution.—North Carolina, both sides of Florida, west to Mexico, and the Lesser Antilles.

Bathymetric range.—From 13 to 320 m.

Remarks.—This species can be distinguished from *C. pulchrum* by being proportionally higher, more coarsely sculptured (especially on the base), and generally having less color. Like *C. pulchrum, C. roseolum* is a relatively shallow water species, occurring commonly in depths of less than about 150 m. The BLAKE station in the Straits (see above) and an unspecified BLAKE station off Barbados in 100 fms (183 m) are the only records of this species from 100 fms or more. Again, these may be no more than accidental occurrences since both records are near very steep slopes down which the shells may have fallen or been carried by currents.

Calliostoma (Calliostoma) yucatecanum
Dall, 1881

Calliostoma yucatecanum Dall, 1881: 47.
Calliostoma (Eutrochus) yucatecanum: Dall, 1889a: 370, pl. 24, figs. 4, 4a; 1889b: 162, pl. 24, figs. 4, 4a (name only, figures from Dall, 1889a).—Pilsbry, 1889: 407, pl. 48, figs. 19, 20 (description from Dall, 1881; figures from Dall, 1889a).
Calliostoma (Leiotrochus) yucatecanum: Johnson, 1934: 70 (name only).
Calliostoma (Astele) agalma Schwengel, 1942: 1, fig. 1.
Calliostoma (Calliostoma) yucatecanum: Clench & Turner, 1960: 27, pl. 4, fig. 4; pl. 8, fig. 4; pl. 19.—Abbott, 1974: 43, fig. 309.

Description.—See Dall, 1889a; Clench & Turner, 1960.

Holotype.—MCZ 7567, BLAKE (station number not recorded) from the Yucatan Strait in 1170 m.

Material examined.—Off Cay Sal Bank: G-984; 1, UMML 30-8004.—BLAKE, station number not recorded, Yucatan Strait, 1170 m; 1, MCZ 7567 (holotype).

Geographic distribution.—North Carolina, Florida and the Gulf of Mexico south to Yucatan.

Bathymetric range.—From 9 to 1170 m; see *Remarks.*

Remarks.—The GERDA specimen represents an extension of the previously known geographic range of this species. Clench & Turner (1960) suggested that *C. yucatecanum* might be found in this general area despite the absence of the species in the extensive dredgings of the EOLIS. In addition to predicting this range extension, they cast doubt on the depth record for the holotype (1170 m). All other records for the species fall between 9 and 64 m and there is no record of a BLAKE station of 1170 m in the Yucatan Strait in the published station data for the BLAKE (Peirce & Patterson, 1879; Smith, 1889). The GERDA specimen does not necessarily confirm a deep habitat for this species. It was dead when collected and was taken in an area where, because of the steep slope, the shell could easily have washed out into deeper water after death. Consequently, I doubt that *C. yucatecanum* lives in depths much exceeding 90 m.

Calliostoma (Calliostoma) echinatum
Dall, 1881

Calliostoma echinatum Dall, 1881: 47; 1889a: 364, pl. 21, figs. 2a, 5; 1889b: 162, pl. 21, figs. 2a, 5 (name only, figures from Dall, 1889a).—Pilsbry, 1889: 377, pl. 49, figs. 40, 41 (description from Dall, 1881; figures from Dall, 1889a).—Johnson, 1934: 69 (name only).—Clench & Turner, 1960: 55, pl. 36.—Abbott, 1974: 46, fig. 336.

Description.—Shell attaining 10 mm in height, conical, with extended spire, imperforate, highly sculptured, with 7½ slightly convex whorls. Color light tan, with faint axial flammules of deep pink regularly arranged around the periphery. Protoconch of 1½ whorls, smooth and polished, whitish. First whorl with low axial ridges beaded by 2 spiral cords, giving a cancellate aspect to the whorl. The axials persist on the second whorl but disappear afterward. Number of spirals increase by intercalation from the initial 2 to 11 at the aperture. Spirals generally alternate in size, the body whorl having 6 major tubercled cords with weak smooth cords in the spaces between the majors. A cord at, or just above, the periphery is especially strong on the early whorls, giving the spire a pagoda-like appearance, but becoming less conspicuous on the later whorls. In addition to the major spiral sculpture, there are microscopic incised spiral lines on the first 3 whorls. Base slightly convex, imperforate, with 13 spiral cords which are more undulate than beaded. Aperture subquadrate, thickened in adults by a grooved layer of nacre. Outer lip thin and slightly crenulated by the external sculpture. Columella white, slightly arched and twisted, truncate anteriorly. Operculum and animal unknown.

Holotype.—USNM cat. no. 214270, from BLAKE sta. 62.

Type-locality.—BLAKE sta. 62, off Havana, Cuba, 146 m.

Material examined.—Northern Straits of Florida: G-636; 1, UMML 30-7996.—Cay Sal: G-986, 1, UMML 30-7997.—Southern Straits of Florida: BLAKE sta. 62, off Havana, Cuba, 146 m; 1, USNM 214270 (holotype).—Virgin Islands: J-S Exp. sta. 10, 18°29′20″N, 66°05′30″W, 220–293 m, 2 Feb. 1933, 9′ tangle; 1, USNM 429727.—J-S Exp. sta. 104, 18°30′40″N, 66°13′20″W, 146–220 m, 8 March 1933, oyster trawl; 1, USNM 430055.

Geographic distribution.—Off the NW corner of the Great Bahama Bank, Cay Sal, the northern coast of Cuba and the Virgin Islands.

Bathymetric range.—From 87 to 293 m.

Remarks.—The 2 GERDA specimens are only the 4th and 5th specimens collected of this rare species. Other than the holotype are 2 specimens collected by the Johnson-Smithsonian Expedition in 1933. All 5 records are in the Greater Antilles, but the species may be found in the future farther south in the Antillean arc.

The holotype of *echinatum* is a young specimen 5.4 mm high and the GERDA specimens are both mature, measuring 10 mm high. Since these are mature, I have chosen to redescribe the species. This species is very similar to *C. roseolum* Dall. With maturity *echinatum* assumes the rounded periphery and convex base of *roseolum. C. echinatum* can be easily distinguished from *roseolum* by its sharp, conical beading above the periphery, having the cords alternating in strength, and the smoothish basal cords. On the basis of its extreme conchological similarity to the group of *roseolum,* I am assigning *echinatum* to *Calliostoma* (*s. s.*). This allocation cannot be confirmed until the radula and jaws have been described.

Subgenus **Elmerlinia** Clench & Turner, 1960

Type-species.—*Trochus jujubinus* Gmelin, 1791; by original designation, Clench & Turner, 1960: 29.

Diagnosis.—"Shell perforate in all known species, marked with axial flames of reddish brown or nearly unicolored. Sculpture with beaded cords. Aperture subquadrate with the columella arched and truncated at the base. Radula with a central tooth having serrate or denticulate margins, 6 lateral teeth, 4 of which are denticulate, the 2 outer laterals plate-like or with extremely slender cusps. First 2 marginal teeth narrow with rather large denticulations; remaining marginal teeth long and finely denticulate. Jaws long, with the anterior ends sharply rounded and with a long fringe at the anterior margin." (Clench & Turner, 1960).

Calliostoma (Elmerlinia) jujubinum
(Gmelin, 1791)

Trochus jujubinus Gmelin, 1791: 3570.—Philippi, 1847b: 37, pl. 7, figs. 8, 9; pl. 13, fig. 5.—Fischer, 1875: 80, pl. 18, fig. 2 (*non* Röding, 1798).

Trochus lunatus Röding, 1798: 82.

Trochus perspectivus 'Koch' Philippi, 1843: 32, pl. 1, fig. 5 (*non* Linnaeus, 1758; *non T. perspectivus* A. Adams, 1864).

Trochus tampaensis Conrad, 1846: 26, pl. 1, fig. 35.

Zizyphinus jujubinus: Reeve, 1863: fig. 12.

Eutrochus alternatus Sowerby, 1874: 719, pl. 59, fig. 5.

Calliostoma (Eutrochus) jujubinum: Dall, 1889a: 369; 1889b: 162 (listed only).—Pilsbry, 1889: 404, pl. 40, fig. 16.

Calliostoma (Eutrochus) jujubinum tampaensis: Dall, 1889a: 369; 1889b: 162 (listed only).

Calliostoma (Eutrochus) jujubinum rawsoni Dall, 1889a: 369; 1889b: 162 (listed only).—Pilsbry, 1889: 405.

Calliostoma (Eutrochus) jujubinum var. *perspectivum*: Pilsbry, 1889: 405, pl. 66, figs. 35, 36.

Calliostoma (Leiotrochus) jujubinum jujubinum: Johnson, 1934: 70 (listed only).

Calliostoma (Leiotrochus) jujubinum perspectivum: Johnson, 1934: 70 (listed only).

Calliostoma (Leiotrochus) jujubinum rawsoni: Johnson, 1934: 70 (listed only).

Calliostoma (Elmerlinia) jujubinum: Clench & Turner, 1960: 31, pl. 5, fig. 2; pl. 9, fig. 1; pl. 21.—Abbott, 1974: 44, fig. 312; pl. 2, fig. 312.

Description.—See Clench & Turner, 1960.

Holotype.—The figures representing the type of *T. jujubinus* Gmelin are numbers 1612 and 1613 on Plate 167 of Chemnitz (1781).

Type-locality.—Gmelin originally gave the locality as cited by Chemnitz: "ad insulam S. Mauritii, et in mari Americam australem alluente." Clench & Turner (1960) restricted the type-locality to St. Croix, Virgin Islands.

Material examined.—Northern Straits of Florida: G-984; 1, UMML 30-8003.

Geographic distribution.—Florida, Texas south to Colombia, and the Bahamas south throughout the West Indies.

Bathymetric range.—From the intertidal zone to 192 m.

Remarks.—*Calliostoma jujubinum* is another shallow-water species, probably the most common *Calliostoma* in the Western Atlantic. This species evidently does not form a part of the fauna found deeper than 180 m as the GERDA specimen might indicate. This specimen was taken at the same station as reported for *C. yucatecanum* (off Cay Sal Bank) and was most likely transported artificially to deep water with *C. yucatecanum* (see also *Remarks* under *C. yucatecanum*). *C. jujubinum* otherwise does not occur below 150 m.

Subgenus **Kombologion** Clench & Turner, 1960

Type-species.—*Calliostoma bairdi* Verrill & Smith, 1880; by original designation, Clench & Turner, 1960: 37.

Diagnosis.—"Shell usually imperforate, though generally with an umbilical depression. Sculpture consists of numerous beaded cords which may cover the entire surface or be formed only at the whorl periphery or above the base. Radula with 5 to 7 nearly uniform lateral teeth, the first and second marginal teeth rather long and not too dissimilar to the remaining marginal teeth. Outermost marginal teeth non-serrated. Jaws rounded, the anterior ends rather broadly rounded and having a very short edge of fringe along the anterior margin." (Clench & Turner, 1960.)

Calliostoma (Kombologion) psyche
Dall, 1889

Calliostoma psyche Dall, 1878: 61 (*nom. nud.*); 1880: 45 (*nom. nud.*).

Calliostoma (Calliostoma) bairdii psyche Dall, 1889a: 364.

Calliostoma bairdii psyche: Pilsbry, 1889: 376.

Calliostoma (Kombologion) psyche: Clench & Turner, 1960: 39, pl. 7, fig. 1; pl. 25.

Calliostoma (Kombologion) bairdii psyche: Abbott, 1974: 44, fig. 316.

Calliostoma subumbilicatum 'Dall' Abbott, 1974: 44.

Description.—See Clench & Turner, 1960.

Lectotype.—Selected by Clench & Turner (1960) is in the MCZ, cat. no. 224572, collected by Pourtalès.

Type-locality.—Off the Florida Reefs in 183 to 366 m.

Material examined.—Northern Straits of Florida: off Palm Beach, 146–165 m, Thompson & McGinty coll.; 3, USNM 666964.—EOLIS sta. 346, ESE of Fowey Rocks, 238 m; 3, USNM 438136.—EOLIS sta. 358, off Fowey Rocks, 229 m; 3, USNM 438142.—EOLIS sta. 360, off Fowey Rocks, 183 m; 1, USNM 438146.—EOLIS sta. 361, off Fowey Rocks, 137–183 m; 10, USNM 438145.—EOLIS sta. 368, off Ajax Reef, 146–183 m; 2, USNM 438166.—G-847; 7, UMML 30-7609.—G-606; 1, UMML 30-7416.—Southern Straits of Florida: G-483; 2, UMML 30-7987.—G-484; 2, UMML 30-6993.—G-432; 6, UMML 30-7591.—G-459; 3, UMML 30-6048.—EOLIS sta. 330, off Sambo Reef, 220 m; 2, USNM 438173.—EOLIS sta. 331, off Sambo Reef, 216 m; 2, USNM 438175.—EOLIS sta. 15, 8 km S of Sand Key, 183 m; 2, USNM 438153.—EOLIS sta. 323, off Sand Key, 201 m; 7, USNM 438158.—BLAKE, station number unrecorded, off Sand Key, 234 m; 1, USNM 95003.—Off Dry Tortugas, 229 m, collected by J. A. Weber; 1, USNM 696741.

Geographic distribution.—From off North Carolina south along the east coast of Florida, the Florida Keys, and then north along the west coast of Florida to about Tarpon Springs.

Bathymetric range.—From 26 to 443 m. This species seems to prefer depths of about 150 to 200 m.

Remarks.—This species is extremely similar to *C. bairdii* Verrill & Smith. The resemblance is striking enough for most authors to consider *C. psyche* merely a subspecies of *C. bairdii*. However, Clench & Turner (1960) separated *C. psyche* as a distinct species using several characters: *C. psyche* is smaller, proportionately wider, more finely sculptured, with more color and an external sheen. In addition, the radula of *C. psyche* has six lateral teeth and that of *C. bairdii* has seven. I have seen a specimen of what I believe to be *C. psyche* from the Gulf of Mexico (in the collection of Donna Black) which is larger than the largest recorded *C. bairdii*, so the size may not be of prime importance. The other differences seem to be fairly constant, especially the radular differences, and on this basis I must agree with Clench & Turner that *C. psyche* is a distinct and valid species.

C. psyche seems to prefer the lower shelf and upper slope areas of the continental margin. There are no records of its occurrence along the insular margin of the Straits area (along the Bahamas or Cuba). This may be due to the extreme steepness of the insular margin which affords little or no horizontal area on which to live and feed. Most deep-water calliostomas live on mud bottoms where presumably they feed on detritus.

Calliostoma (Kombologion) hendersoni Dall, 1927

Calliostoma hendersoni Dall, 1927b: 7.
Calliostoma (Leiotrochus) hendersoni: Johnson, 1934: 70 (listed only).
Calliostoma (Kombologion) hendersoni: Clench & Turner, 1960: 43, pl. 7, fig. 4; pl. 11, fig. 2; pl. 28.—Bayer, 1971; 121, fig. 4 (right).—Abbott, 1974: 44.

Description.—See Clench & Turner, 1960.

Holotype.—USNM 333703; from EOLIS sta. 331.

Type-locality.—EOLIS sta. 331, off Sambo Reef, Florida, 216 m.

Material examined.—Southern Straits of Florida: G-598; 2, UMML 30-7990.—G-813; 3, UMML 30-7531.—G-482; 1, UMML 30-6987.—G-134; 1, UMML 30-5530.—G-837; 1, UMML 30-7994.—G-866; 1, UMML 30-7618.—G-132; 3, UMML 30-7995.—G-839; 1, UMML 30-7566.—OREGON sta. 1349 (24°03′N, 80°30′W, 274 m; 2, H. Bullis). —EOLIS sta. 331, off Sambo Reef, 216 m; 1, USNM 333703.

Geographic distribution.—*C. hendersoni* is found only along the Florida Keys, from off Alligator Reef (Bayer, 1971) to SE of Key West.

Bathymetric range.—This species has a possible depth range of 133 to 288 m, but seems to be found most frequently near 200 m.

Remarks.—This adds 3 more records (G-132, G-589, G-837) to those reported by Bayer (1971), all within the established range of the species. A specimen from off Alligator Reef (TURSIOPS sta. 10, position not recorded, 133–154 m, 23 June 1966, UMML 30-7982) increases the known size of the species from 19.5 mm (height), 23 mm (width), to 23 mm (height), 27.5 mm (width).

The umbilicus of this species is rather narrow and usually open, but the specimen from G-866 has the umbilicus filled with callus, leaving only a pit-like umbilical depression. Abbott (1974) suggests that this is only a form of *C. psyche*. However, *C. hendersoni* can easily be distinguished from *C. psyche* by its generally open umbilicus, smooth basal cords and completely different radula (see Clench & Turner, 1960: pl. 7, figs. 1 & 4). The two species are also found in the same geographical area (the Florida Keys) and the same depth range (about 200 m). I must therefore consider *C. hendersoni* a distinct species.

Calliostoma (Kombologion) schroederi Clench & Aguayo, 1938

Calliostoma (Calliostoma) schroederi Clench & Aguayo, 1938: 377, pl. 23, fig. 3.
Calliostoma (Kombologion) schoederi: Clench & Turner, 1960: 45, pl. 7, fig. 2; pl. 11, fig. 1; pl. 29.—Bayer, 1971: 118, fig. 3.—Abbott, 1974: 45, fig. 329 (listed only).

Description.—See Clench & Aguayo, 1938; Clench & Turner, 1960.

Holotype.—MCZ 135002; from ATLANTIS sta. 2981.

Type-locality.—ATLANTIS sta. 2981, 22°48′N, 78°48′W, off Punta Alegre, Camaguey, Cuba, 412 m.

Material examined.—Northwest Providence Channel: G-915; 1, UMML 30-7627.

Geographic distribution.—From off the NW corner of Little Bahama Bank (Matanilla Shoal) south through the Bahamas to the Old Bahama Channel off Camaguey, Cuba.

Bathymetric range.—From 265 to 439 m is the possible range, but the minimum is probably about 300 m.

Calliostoma species not assigned to subgenera

Calliostoma sapidum Dall, 1881

Calliostoma sapidum Dall, 1881: 46; 1889b: 162, pl. 21, figs. 2, 4 (name only, figures from 1889a).—Pilsbry, 1889: 378, pl. 49, figs. 38, 39 (description from Dall, 1881; figures from Dall, 1889a).—Johnson, 1934: 70 (name only).—Clench & Turner, 1960: 53, pl. 34, fig. 2.—Abbott, 1974: 46, fig. 334 (listed only).
Calliostoma (Calliostoma) sapidum: Dall, 1889a: 364, pl. 21, figs. 2, 4.

Description.—See Clench & Turner, 1960.

Holotype.—USNM 214271, from BLAKE sta. 2.

Type-locality.—BLAKE sta. 2, 23°14′N, 82°25′W, off Havana, Cuba, 1472 m.

Material examined.—Southern Straits of Florida: BLAKE sta. 2, 23°14′N, 82°25′W, off Havana, Cuba, in 1472 m; 1, USNM 214271 (holotype).

Geographic distribution.—Off Tampa, Florida, northern Cuba, Barbados and Antigua.

Bathymetric range.—From 121 to 1472 m.

Remarks.—This species, on conchological grounds, seems to belong in the subgenus *Calliostoma,* but until a specimen with soft parts is found, this is mere speculation. It seems to be closest to *C. pulchrum* (C. B. Adams), but is smaller and has a stronger, more heavily beaded peripheral cord.

Calliostoma torrei Clench & Aguayo, 1940

Calliostoma (Calliostoma) torrei Clench & Aguayo, 1940: 79, pl. 14, fig. 5.
Calliostoma torrei: Clench & Turner, 1960: 59, pl. 40.—Abbott, 1974: 46 (listed only).

Description.—See Clench & Aguayo, 1940; Clench & Turner, 1960.

Holotype.—MCZ 135165, from ATLANTIS sta. 1985.

Type-locality.—ATLANTIS sta. 1985, 23°13′N, 81°22′W, off Matanzas, Cuba, 704 m.

Record and distribution.—Known only from the holotype.

Remarks.—This appears to be the largest of all Western Atlantic species of *Calliostoma.* The holotype is 41 mm high and 36 mm wide and only *C. sayanum* Dall is close to this size.

Calliostoma cubanum Clench & Aguayo, 1940

Calliostoma (Calliostoma) cubanum Clench & Aguayo, 1940: 78, pl. 16, fig. 4.
Calliostoma cubanum: Clench & Turner, 1960: 61, pl. 43.—Abbott, 1974: 45 (listed only).

Description.—See Clench & Aguayo, 1940; Clench & Turner, 1960.

Holotype.—MCZ 135163, from ATLANTIS sta. 3474.

Type-locality.—ATLANTIS sta. 3474, 23°18′N, 80°46′W, off Cardenas, Cuba, 896 m.

Record and distribution.—Known only from the holotype.

Remarks.—This species is known only from a single, damaged specimen. It is, however, a very distinctive species and can be confused with no other.

Calliostoma atlantis Clench & Aguayo, 1940

Calliostoma (Calliostoma) atlantis Clench & Aguayo, 1940: 81, pl. 15, fig. 4.
Calliostoma atlantis: Clench & Turner, 1960: 62, pl. 44.
Calliostoma (Kombologion) atlantis: Abbott, 1974: 45 (listed only.)

Description.—See Clench & Aguayo, 1940; Clench & Turner, 1960.

Holotype.—MCZ 135164, from ATLANTIS sta. 3306.

Type-locality.—ATLANTIS sta. 3306, 23°04′N, 82°37′W, off Mariel, Pinar del Rio, Cuba, in 603 m.

Record and distribution.—Known only from the holotype.

Remarks.—This beautiful species is distinctive in being almost devoid of sculpture. It most nearly resembles *C. torrei* Clench & Aguayo, *C. cubanum* Clench & Aguayo, and *C. amazonica* Finlay, and bears a superficial resemblance to *C. schroederi* Clench & Aguayo.

Calliostoma jeanneae Clench & Turner, 1960

Calliostoma jeanneae Clench & Turner, 1960: 65, pl. 47, figs. 1, 2.—Abbott, 1974: 46 (listed only).

Description.—See Clench & Turner, 1960.

Holotype.—MCZ 228370, from ATLANTIS sta., station number unrecorded, off Havana, Cuba.

Record and distribution.—Known only from the holotype.

Remarks.—This species is like *C. atlantis* Clench & Aguayo in having very little sculpture, but this lack of sculpture and distinctive shape make *C. jeanneae* unlike any other in the Western Atlantic.

Calliostoma sayanum Dall, 1889

Calliostoma (Eutrochus) sayanum Dall, 1889a: 370, pl. 33, figs. 10, 11; 1889b: 162, pl. 33, figs. 10, 11 (name only, figures from

Dall, 1889a).—Pilsbry, 1889: 407, pl. 60, figs. 7, 8 (description and figures from Dall, 1889a).

Calliostoma (Leiotrochus) sayanum: Johnson, 1934: 70 (name only).

Calliostoma sayanum: Clench & Turner, 1960: 68, pl. 50, figs. 1–3.—Abbott, 1974: 45, fig. 320.

Description.—See Dall, 1889a; Clench & Turner, 1960.

Holotype.—USNM 61240, from ALBATROSS sta. 2594.

Type-locality.—ALBATROSS sta. 2594, 35°01′N, 75°12′W, SE of Cape Hatteras, North Carolina, 293 m.

Material examined.—Northern Straits of Florida: G-854; 1 damaged specimen, UMML 30-7610.

Remarks.—Northern Straits of Florida: off Palm Beach in 135 m, T. McGinty coll.—Southern Straits of Florida: off Sand Key Light, Key West, in 119 m, T. McGinty coll.—OREGON sta. 1009, 24°34′N, 83°34′W, about 74 kilometers W of Tortugas, 366 m, H. Bullis.

Geographic distribution.—From off Cape Hatteras, North Carolina to off the Dry Tortugas, Florida Keys.

Bathymetric range.—From 119 to 366 m.

Remarks.—*C. sayanum* is a large and very striking species. It resembles *C. springeri* Clench & Turner, but it is larger, more inflated, and has coarser sculpture and a narrower umbilicus.

Calliostoma bigelowi Clench & Turner, 1960

Calliostoma bigelowi Clench & Turner, 1960: 72, pl. 53, figs. 1, 2.—Abbott, 1974: 46, fig. 341 (listed only).

Description.—See Clench & Turner, 1960.

Holotype.—MCZ 135003, from ATLANTIS sta. 2963C.

Type-locality.—ATLANTIS sta. 2963C, 22°07′N, 81°08′W, off Bahía de Cochinos, Cuba, 375 m.

Record.—Southern Straits of Florida: ATLANTIS sta. 2999, 23°10′N, 81°29′W, off Matanzas, Cuba, in 265–421 m.

Geographic distribution.—The north and south coasts of Cuba.

Calliostoma brunneum (Dall, 1881)

Fluxina brunnea Dall, 1881: 52; 1889a: 273, pl. 22, figs. 6, 6a; 1889b; 148 pl. 22, figs. 6, 6a (name only, figures from Dall, 1889a).—Tryon, 1887: 16 (name only).—Johnson, 1934: 101 (name only).

Calliostoma (Astele) tejedori Aguayo, 1949: 94, pl. 4, fig. 7.

Calliostoma tejedori: Clench & Turner, 1960: 73, pl. 54, figs. 1, 2.

Calliostoma brunneum: Merrill, 1970a: 32.—Abbott, 1974: 46 (listed only).

Description.—See Dall, 1881; Clench & Turner, 1960.

Holotype.—MCZ 7463, from BLAKE sta. 2.

Type-locality.—BLAKE sta. 2, 23°14′N, 82°25′W, off Havana, Cuba, 1472 m.

Material examined.—Northern Straits of Florida: G-636; 1, UMML 30-7992.—Cay Sal: G-986; 2, UMML 30-7993.—Southern Straits of Florida: BLAKE, station number unrecorded, off Havana, Cuba, in 146 m; 1, USNM 94897.

Record.—Arenas de la Chorrera, near Havana, Cuba. This is a pile of construction sand dredged from 5–27 m off Santa Fe, near Havana.

Geographic distribution.—From the NW corner of the Great Bahama Bank south to Cuba, Jamaica, and Barbados.

Bathymetric range.—From 5–27 m to 1767 m.

Remarks.—*C. brunneum* was described by Dall in 1881 as the only species in the genus *Fluxina.* In 1889 he added a second species, *F. discula* (probably a *Basilissa*), and placed the genus in the Solariidae (=Architectonicidae). A specimen of this species was found in a pile of construction sand near Havana, and Aguayo (1949) correctly assigned it to *Calliostoma,* but he did not realize that his new species, *tejedori,* was conspecific with *F. brunnea.* The 2 species remained unquestioned until Merrill (1970a) examined the type of *F. brunnea* while researching the Atlantic Architectonicidae. He recognized that *tejedori* was the same as *brunnea* and synonymized *Fluxina* with *Calliostoma.*

This is a distinctive species, resembling in shape *C. bigelowi* and *C. springeri* Clench & Turner, but has very little sculpture on the body whorl and a brownish-red umbilicus. The only other species in the Western Atlantic with a colored umbilicus is *C. barbouri* (q.v.), but the 2 species are completely different in shell shape and sculpture.

Calliostoma cinctellum Dall, 1889

Calliostoma (Eutrochus) cinctellum Dall, 1889a: 372, pl. 32, figs. 1, 4; 1889b: 162, pl.

32, figs. 1, 4 (listed only; figs. from 1889a). —Pilsbry, 1889: 409, pl. 49, figs. 31, 32 (description and figs. from Dall, 1889a).— Clench & Turner, 1960: 80 (name only; generic placement questioned).

Calliostoma (Leiotrochus) cinctellum: Johnson, 1934: 70 (listed only).

Basilissa cinctellum: Abbott, 1974: 38, figs. 244 (listed only; fig. from Dall, 1889a).

Description.—See Dall, 1889a.

Holotype.—USNM 214274, from BLAKE sta. 101.

Type-locality.—BLAKE sta. 101, off Morro Light, Havana, Cuba, in 320–457 m.

Material examined.—BLAKE sta. 101; 1, USNM 214274 (holotype).

Geographic & bathymetric range.—Known only from the holotype.

Remarks.—This is a very striking and beautiful species. Dall, in his original remarks (1889a), stated that *cinctellum* "recalls *Basilissa* in its general appearance." Clench & Turner (1960) more directly suggested that the species was indeed a *Basilissa*. Abbott (1974) followed Clench & Turner and placed *cinctellum* in his list of *Basilissa* species. Dall, again in his original description, gave a careful account of the jaws and radula: "Jaws separate, squarish, composed of small horny obliquely set rods, whose lozenge-shaped end-sections reticulate the surface. . . . The rhachidian and (on each side) five laterals have broad simple bases with a pear-shaped outline; the cusps, which might be compared to the stem of the pear bent over, are extremely narrow and long and symmetrically serrate on each side with 4–6 serrations. The major uncinus is stout and has a large four-toothed ovate cusp; there are about twenty more slender uncini with scythe-like cusps serrate on the outer edge; outside of these are two or three of a flat form, like a section of a palm-leaf fan from handle to margin with four riblets, and the distal edge with three or more indentations. They (the uncini) are smooth, thinner toward the distal end, and have no distinct shaft." This description shows marked differences from the radula of *Basilissa alta*: "rhachidian with a triangular cusp finely denticulated on the sides, a wide lateral with an inwardly directly triangular cusp denticulated on both sides, and several (6 or 7) marginals, flat and rather narrow, denticulated along most of the outer edge but on the inner edge only near the tip" (Bayer, 1971: 124, fig. 7). Therefore, the radula of *cinctellum* differs from that of *Basilissa* in the number and structure of both the laterals and marginals. However, the radula of *cinctellum* corresponds quite closely to that of *Calliostoma s. s.* as defined and figured by Clench & Turner (1960). Examination of the holotype of *cinctellum* revealed no shell characters which would indicate that the species belongs in *Basilissa,* and on the basis of the radula, I prefer retaining the species in *Calliostoma s. l.* On conchological grounds, this species is very similar to *C. echinatum,* but differs in having a wider, more angular shell with flat whorls and an umbilicus (see also *C. echinatum*).

Calliostoma circumcinctum Dall, 1881

Calliostoma circumcinctum Dall, 1881: 44; 1889a: 364, pl. 22, figs. 3, 3a; 1889b: 162, pl. 22, figs. 3, 3a (listed only; figs. from 1889a).—Pilsbry, 1889: 376, pl. 49, figs. 33, 34 (description from Dall, 1881; figs. from Dall, 1889a).—Johnson, 1934: 69 (listed only).—Clench & Turner, 1960: 80 (listed only).—Abbott, 1974: 46 (listed only.)

Description.—See Dall, 1881.

Holotype.—MCZ 7558, from BLAKE sta. 2.

Type-locality.—BLAKE sta. 2, off Havana, Cuba, 23°14′N, 82°25′W, in 1472 m.

Material examined.—Yucatan Channel: G-897; 1, UMML 30-7716.—BLAKE, sta. number unrecorded, 1170 m; 1, USNM 95020.

Geographic distribution.—Off Havana, Cuba and the Yucatan Channel.

Bathymetric range.—This species has a possible depth range of 210–1472 m, but the 2 deep records (1170 and 1472 m) were both taken near steep escarpments. The GERDA specimen was collected alive between 200 and 300 m, indicating that the specimens collected by the BLAKE were carried to deeper water after death.

Remarks.—This is a very distinctive species, possessing sharp, lamellar spiral keels which immediately separate it from any other species of *Calliostoma.*

Calliostoma barbouri Clench & Aguayo, 1946

Calliostoma barbouri Clench & Aguayo, 1946: 89, text fig.—Clench & Turner, 1960: 67, pl. 49, figs. 1–3.—Abbott, 1974: 43, fig. 311.

Description.—See Clench & Aguayo, 1946; Clench & Turner, 1960.

Holotype.—MCZ 178128, from Havana, Cuba.

Type-locality.—From Havana, Cuba, in construction sand in Arenas de la Chorrera, dredged in 5–27 m near Havana.

Material examined.—Straits of Florida: G-984; 1, UMML 30-8001.—G-985; 1, UMML 30-8000.—Lesser Antilles: P-912; 1, UMML 30-8132.

Geographic distribution.—Cay Sal Bank, northern Cuba and the Lesser Antilles.

Bathymetric range.—This species has been taken as deep as 230 m, but the Cuban records indicate that it is really a rather shallow water species.

Remarks.—*C. barbouri* appears to be closely related to *C. javanicum* and *C. jujubinum,* and possibly *C. hassler* Clench & Aguayo. The character of *barbouri* which sets it apart from all these species is the presence of a brownish-red colored umbilicus. In this, *barbouri* resembles *C. brunneum,* but the shell shape of the two species is totally dissimilar. On the basis of shell morphology, I suspect that *barbouri* should probably be placed in the subgenus *Elmerlinia* with *javanicum* and *jujubinum.*

Genus **Dentistyla** Dall, 1889

Dentistyla Dall, 1889a: 373; 1889b: 162.—Pilsbry, 1889: 411.—Johnson, 1934: 70.—Abbott, 1974: 41.

Type-species.—*Margarita asperrima* Dall, 1881, by subsequent designation, Keen, 1960: I258.

Diagnosis.—Shell rather thin, conical, base slightly convex, usually umbilicate; exterior sculptured by spiral rows of close-set conical or rounded nodules, interior nacreous; aperture subquadrate, somewhat oblique, sometimes thickened within; columella straight, thickened, often with a strong tooth in mature specimens.

Remarks.—*Dentistyla* was erected as a subgenus of *Calliostoma* for the species *asperrima, dentifera* and *sericifila.* Since that time, however, the species have been variously assigned to other genera, and *Dentistyla,* if used, was generally accepted at the subgeneric level, either of *Calliostoma* or *Solariella. Dentistyla* is a very distinctive group, however, and the characters do not fit any other described group, although they most closely resemble those of *Calliostoma.* I think that the peculiar nodulous sculpture and presence of a columellar tooth are sufficient to separate the group at the generic level, retaining it within the Calliostomatinae.

Geographic distribution.—*Dentistyla* occurs from North Carolina south through the Straits of Florida to the extreme southern Gulf of Mexico, and the Caribbean Sea.

Bathymetric range.—Known from 66–914 m.

Dentistyla asperrimum (Dall, 1881)
Figs. 49,50

Margarita asperrima Dall, 1881: 40 (*partim*).

Calliostoma (Dentistyla) asperrimum: Dall, 1889a: 373; 1889b: 162 (listed only).—Pilsbry, 1889: 411 (description from Dall, 1881).—Johnson, 1934: 70 (listed only). Not *Calliostoma asperrimum* Guppy & Dall, 1896: 323 (=*guppyi* Woodring, 1928).

Calliostoma asperrimum: Woodring, 1928: 433.

Solariella (Dentistyla) asperrima: Clench & Turner, 1960: 79.—Abbott, 1974: 41 (listed only).

Astele (Dentistyla) asperrima: Keen, 1960: I258.

Description.—Shell attaining a height of 8.5 mm, conical, somewhat turreted, carinate, umbilicate, highly sculptured, of about 7 whorls. Protoconch small, glassy, of about 1 whorl. Spiral sculpture of 2 major nodulous cords, of which the lower forms the peripheral carina; between the major cords may be intercalated 1 or 2 similar but weaker cords. Below the periphery the whorl constricts sharply to a circumbasal cord which may be smoothish or finely beaded; base with 3 or 4 smoothish to finely beaded cords with 1 strongly beaded cord at the margin of the umbilicus. Axial sculpture of fine threads which are visible between the spirals, and the intersections of spirals and axials result in the nodulations. Base rounded; umbilicus narrow, axially rugose, sometimes with a very fine spiral thread near the marginal cord. Aperture oblique, subquadrate, somewhat thickened within; lips thin, outer lip crenulate, inner lip slightly reflected; columella straight, thickened, with a strong tooth in mature specimens. Periostracum thin, brownish.

Holotype.—MCZ 7568, from BLAKE sta. 12.

Type-locality.—BLAKE sta. 12, 24°34′N, 83°16′W, in 66 m.

Material examined.—Straits of Florida: Pourtalès Plateau, off the Florida Keys, 366 m, Nutting coll.; 2, USNM 107502.—BLAKE sta. 12; 2, USNM 95055 (paratype).—BLAKE sta. 20; 2, USNM 95056.—Yucatan Channel: G-947; 1, UMML 30-7733.—Caribbean: J-S sta. 102; 1, USNM 430365.—P-610; 3, UMML 30-8133.

Geographic distribution.—The southern Straits of Florida, the Yucatan Channel, and the Antillean arc.

Bathymetric range.—Known from 66 to 914 m, but probably occurs primarily in depths of 200 to 400 m.

Remarks.—This species is very closely related to *D. dentiferum* Dall and *D. sericifilum* Dall. Dall himself had difficulty separating *asperrimum* and *dentiferum.* He originally included both forms under *"Margarita" asperrima.* In 1889 he separated *dentifera* as a variety of *asperrima.* Only one specimen was designated as *dentifera* and the others left as *asperrima.* In examining the lots in the USNM, I discovered that the specimens were, for the most part, immature, and both species were present in several of the lots. *D. asperrimum* can be distinguished from *dentiferum* by its narrower umbilicus, whose walls have at most 1 spiral thread and often none, and its coarser sculpture. In mature shells, the nacreous thickening within the aperture is smooth, not lirate as in *dentiferum.* The *Antillachelus vaughani* Woodring, 1928, seems to be *D. dentiferum,* not *asperrimum* as suggested by Clench and Turner (1960).

Dentistyla dentiferum (Dall, 1889)
Figs. 47,48

Calliostoma (Dentistyla) asperrimum var. *dentiferum* Dall, 1889a: 373, pl. 23, figs. 7, 8; 1889b: 162, pl. 23, figs. 7, 8 (listed only; figs. from 1889a).—Pilsbry, 1889: 411, pl. 60, figs. 10, 11 (diagnosis and figs. from Dall, 1889a).

Basilissa (Ancistrobasis) near *costulata* Dall, 1903: 1585 (listed only).

Antillachelus dentiferum: Woodring, 1928: 433.

Antillachelus vaughani Woodring, 1928: 433, pl. 36, figs. 12–14.

Euchelus (Antillachelus) dentiferus: Keen, 1960: I250, fig. 161(6).—Abbott, 1974: 39, 41, fig. 260 (listed only).

Solariella (Dentistyla) dentifera: Clench & Turner, 1960: 79.

Calliostoma cf. *corbis*: Rice & Kornicker, 1965: 117, pl. 1, fig. 9.

Description.—Shell attaining a height of 8 mm, conical, carinate, umbilicate, highly sculptured, of about 7 whorls. Protoconch small, glassy, of about 1 whorl. Spiral sculpture of 2 major beaded cords, the lower of which forms the peripheral carina; from 1 to 3 similar cords are intercalated between, often becoming subequal to the primaries. Below the peripheral cord the whorl is sharply constricted to a beaded circumbasal cord; base rounded with 5 to 7 beaded cords, of which the innermost is strongest and defines the umbilicus. Axial sculpture of sharp riblets whose intersections with the spirals form the nodulations. Umbilicus moderate, axially striate, usually with one to three rather strong nodulous spiral cords. Aperture oblique, subquadrate, thickened within by nacre in which there are numerous sharp lirations; lips thin, outer lip somewhat crenulated, inner lip slightly reflected; columella straight, oblique, usually with a strong swelling or blunt tooth.

Holotype.—USNM 95059, from BLAKE sta. 299.

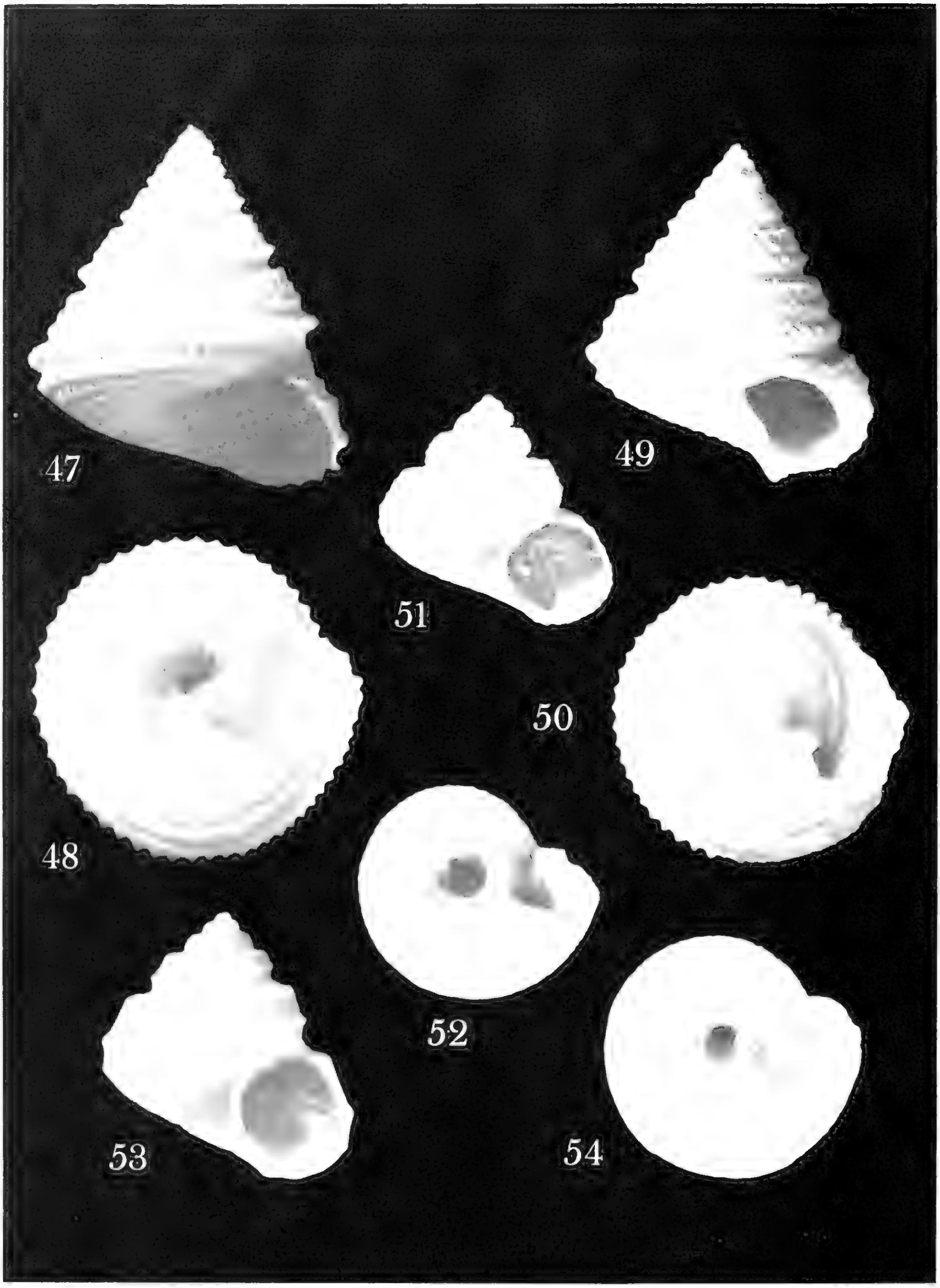
Type-locality.—BLAKE sta. 299, 13°05′N, 59°39′40″W, off Barbados, in 256 m.

Material examined.—ALBATROSS sta. 2602; 1, USNM 95054.—Straits of Florida: G-1011; 1, UMML 30-7635.—EOLIS sta. 329, off Sambo Reef, 247 m; 1, USNM 438325.—EOLIS sta. 320, off Western Dry Rocks, 146 m; 1, USNM 450568.—BLAKE sta. 20; 2, *ex* USNM 95056.—Kornicker sta. 1328, 21°50′N, 92°30′W, 168 m; 4, USNM 667860.—Caribbean: BLAKE, sta. no. unrecorded, off Barbados, 183 m; 1, USNM 95057.—BLAKE sta. 299; 1, USNM 95059 (holotype); 1, USNM 95098 (paratype).

Geographic distribution.—From off North Carolina, south through the Straits of Florida, the Campeche Bank, and the Lesser Antilles; it probably occurs throughout the Caribbean.

Bathymetric range.—From 146 to 311 m.

Remarks.—(See also *Remarks* section under *D. asperrimum* Dall.) This species is remarkably similar to *D. asperrimum. D. dentiferum* can be separated from *asperrimum* by its wider umbilicus with strong spiral sculpture within, its finer beading, more numerous basal cords, and especially by the presence of sharp lirations within the aperture. The external sculpture may be visible within the apertures of juveniles of both species as Clench & Turner observed, but in mature specimens there are grooves cut into the nacreous lining of *dentiferum* which are



FIGS. 47–54. 47–48. *Dentistyla dentiferum* (Dall): G-1011, h = 5.9 mm, d = 5.5 mm. 49–50. *Dentistyla asperrimum* (Dall): P-610, h = 7.5 mm, d = 6.8 mm. 51–52. *Solariella (Solariella) amabilis* (Jeffreys) "var. *affinis*" (Friele): PORCUPINE-61, h = 5.3 mm, d = 5.5 mm. 53–54. *Solariella (Solariella) amabilis* (Jeffreys): "off British Isles," h = 6.0 mm, d = 6.0 mm.

not related to the external sculpture. Specimens in USNM lots 95054, 95057 and 95058 were all identified as *asperrimum,* but in fact contained both species, and lot 95056 had *asperrimum, dentiferum,* and the turbinid *Homalopoma linnei* (Dall).

Subfamily Solariellinae Powell, 1951

Genus **Solariella** S. V. Wood, 1842

Margarita.—Auctt. (*partim; non* Leach, 1814).
Solariella S. V. Wood, 1842: 531.—Auctt. (*partim*).
Machaeroplax Friele, 1877: 311.—Sars, 1878: 136.
Calliotropis.—Auctt. (*partim*).

Type-species.—Solariella maculata S. V. Wood, 1842; by monotypy.

Diagnosis.—Shell small, generally less than 10 mm high, trochoid, with tubular whorls, usually widely umbilicate, umbilicus often bounded by a strong nodulous keel. Sculpture of spiral cords and collabral striae, or almost smooth. Radula short, broad, with few (10 or less) marginals.

Remarks.—Solariella was erected by S. V. Wood for a fossil species, *S. maculata,* from the Crag Formation of England. Friele (1877) based *Machaeroplax* on his *M. affinis* (*ex* Jeffreys MS) (Figs. 51, 52). *M. affinis* is merely a strongly lirate variant of *S. amabilis* (Jeffreys) (Figs. 53,54), and the range of characters exhibited by the varieties of *S. amabilis* bridges the gap between the forms resembling *S. lacunella, S. iris,* etc., and those of the *S. lamellosa* type. I am therefore following Thiele (1929) in regarding *Machaeroplax* as a junior subjective synonym of *Solariella s. s.*

Solariella, since being separated from the catch-all *Margarita* (=*Margarites* Gray, 1847), has in turn been used as a depository of miscellaneous species. Many of the species assigned to *Solariella* can be placed in *Calliotropis, Dentistyla* or *Microgaza.*

Geographic distribution.—Worldwide, in all oceans.

Bathymetric range.—Known from less than 50 m to well over 2000 m.

Solariella (Solariella) lacunella (Dall, 1881)
Figs. 55–58

Margarita maculata Dall, 1881: 43 (not S. V. Wood, 1842).
Margarita lacunella Dall, 1881: 102.
Margarita (Solariella) lacunella: Dall, 1889a: 381, pl. 21, figs. 1, 1a; 1889b: 164, pl. 21, figs. 1, 1a (listed only; figs. from 1889a).—Pilsbry, 1889: 322, pl. 51, figs. 32, 33 (description from Dall, 1881; figs. from Dall, 1889a).
Margarita (Solariella) lacunella depressa Dall, 1889a: 382; 1889b: 164 (listed only).—Pilsbry, 1889: 323 (from Dall, 1889a).
Solariella (Machaeroplax) lacunella lacunella: Johnson, 1934: 71 (listed only).—Abbott, 1974: 40, fig. 274.
Solariella (Machaeroplax) lacunella depressa: Johnson, 1934: 71 (listed only).

Description.—Shell attaining a height of about 8.5 mm, rather thin, depressed-conical, inflated, of about 7 whorls. Protoconch small, glassy, of 1–1½ whorls. Spiral sculpture of numerous subequal cords (usually 15–18 on the last whorl); inner 2 basal cords strong, usually strongly beaded, and separated from each other by a rather deep, narrow channel; there are usually 5 or 6 strong, beaded cords on the walls of the moderately wide umbilicus. Axial sculpture of fine plications radiating from the suture which crenulate or finely bead the upper 2–5 spirals, otherwise visible in the spiral interspaces as fine threads. Suture at the bottom of a channel formed by the overhanging periphery and the upper spiral cord. Aperture subcircular, thickened within by a layer of nacre; lips thin, crenulated by the sculpture, inner lip slightly flared. Color ivory to yellowish-white, with a slight nacreous sheen in some specimens, variously marked above with splotches and flammules of straw or reddish-brown.

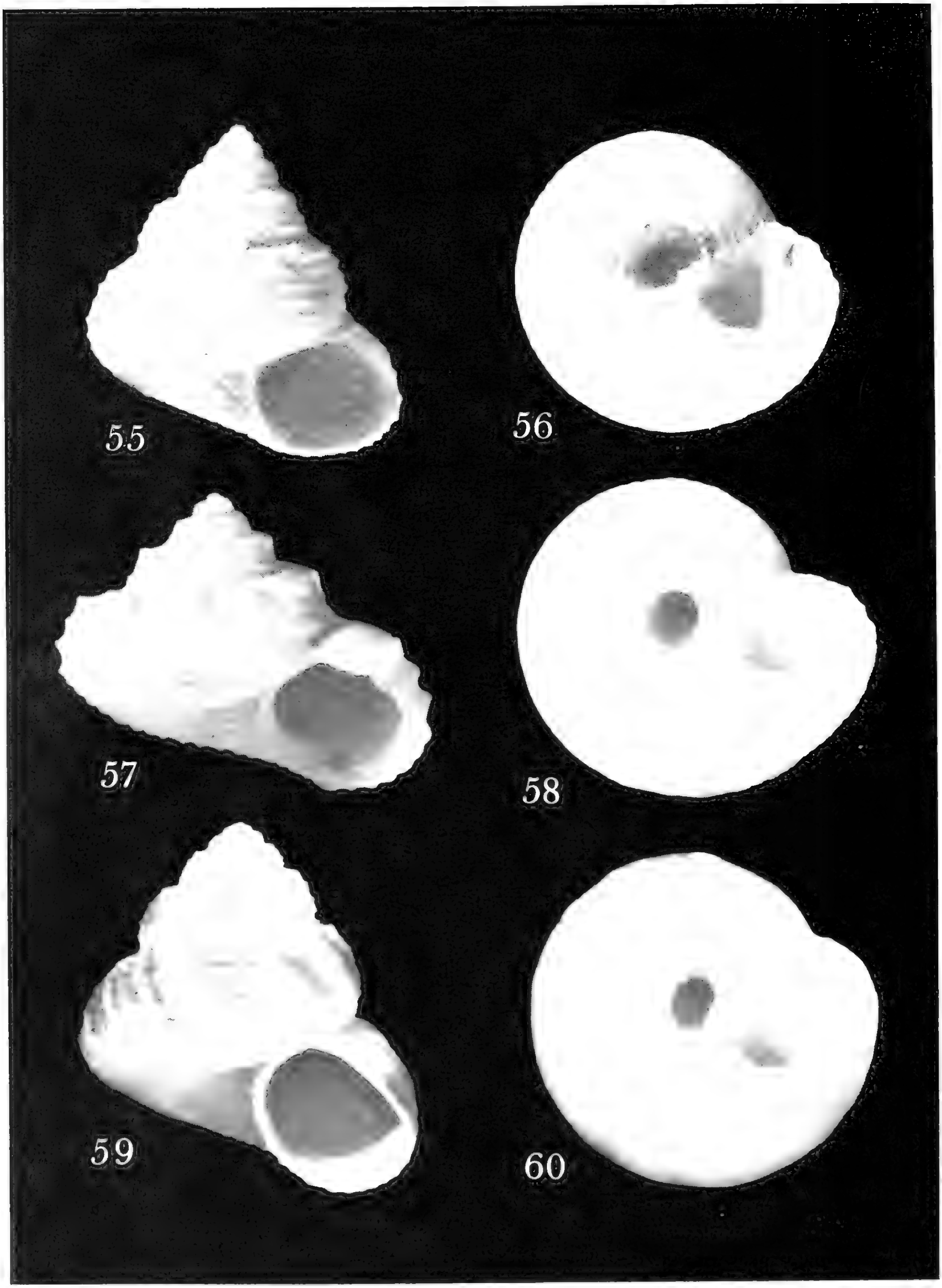
Holotype.—USNM 333705, from BLAKE sta. 2.

Type-locality.—BLAKE sta. 2, 23°14′N, 82°25′W, off Havana, Cuba, 1472 m.

Material examined.—Straits of Florida: EOLIS sta. 310, off Government Cut, Miami, 216 m; 2, USNM 438313.—EOLIS sta. 360, off Fowey Rocks; 183 m; 39, USNM 438386.—EOLIS sta. 153, 5½ km SE of Fowey Rocks, depth not recorded; 64, USNM 438352.—BLAKE sta. 2; 1, USNM 333705 (holotype).—Many lots from shallower depths in the Straits and many from the Lesser Antilles.

Geographic distribution.—From off North Carolina south through the Straits of Florida, the Gulf of Mexico, and the Antillean Arc to St. Lucia and Barbados.

Bathymetric range.—S. lacunella occurs commonly in depths from 20 to 150 m, with



FIGS. 55–60. 55–56. *Solariella (Solariella) lacunella* (Dall) (holotype): BLAKE-2, h = 8.7 mm, d = 8.3 mm. 57–58. *Solariella (Solariella) lacunella* (Dall) ("var. *depressa*" Dall, holotype): BLAKE-22, h = 3.7 mm, d = 4.8 mm. 59–60. *Solariella (Solariella) multirestis* Quinn, n. sp. (holotype): P-874, h = 11.8 mm, d = 11.5 mm.

occasional specimens known down to 1472 m, but most of the deeper records are for dead-collected material.

Remarks.—This is primarily a shallow-water species and does not form a major part of the molluscan fauna below 200 m. The variety described by Dall as *depressa* is known only from the holotype and appears to be merely a freak morphological variant and should not be considered at the subspecific rank.

Solariella (Solariella) multirestis
Quinn, n. sp.
Figs. 59,60

Description.—Shell large for the genus, reaching 11.8 mm, spirally striate, umbilicate, ivory-colored with axial flammules of light brown, iridescent when fresh, of 6 tubular whorls. Protoconch small, glassy, slightly depressed, of about 1½ whorls. Spiral sculpture above of 4 or 5 major cords with 1–3 intercalary cords between each pair; between the suture and the upper cord is a narrow shelf, on which there are several fine spiral threads on the later whorls. Axial sculpture of, on the early whorls, fine ribs which become restricted to the subsutural shelf on later whorls, and finally disappear on the final whorl. Base convex, with about 6 strong, subequal spiral cords and a spiral of strong beads bounding the umbilicus; umbilicus rather wide, very deep; walls convex with about 10 finely beaded spiral cords. Aperture subcircular, thickened within by a layer of nacre; lips thin, simple, inner lip slightly reflected; columella smooth, arched, not thickened. Operculum and radula unknown.

Holotype.—USNM 711107, from PILLSBURY sta. 874.

Type-locality.—P-874, 13°11.2′N, 61°05.3′W, off St. Vincent, Lesser Antilles, 156–201 m, 6 July 1969, 5′ BLAKE trawl.

Other material.—One specimen from G-974, 24°22′N, 80°57′W, SE of Sombrero Light, Florida Keys, 251–252 m, 3 February 1968,10′ OT, UMML 30-7697; this specimen is in poor condition but is here considered this species.

Geographic and bathymetric distribution.—See under Types.

Remarks.—This is one of the most striking of the species in the *S. lacunella-S. iris* complex.It can be distinguished readily from the others in this group by its finer, more numerous spiral cords, more numerous intraumbilical cords, striking coloration, and larger size. The 2 records of this species indicate that it probably is widely distributed throughout the Caribbean area, and may be present in other collections as *S. lacunella.*

Solariella (Solariella) tubula Dall, 1927
Figs. 65,66

Solariella tubula Dall, 1927a: 129.—Johnson, 1934: 72 (listed only).—Abbott, 1974: 41 (listed only).

Description.—Shell small (attaining about 4 mm in height), depressed-conical, whorls tubular and inflated, umbilicate, white, of about 3 whorls. Protoconch small, glassy, of about 1½ whorls. Spiral sculpture varies: the shell may be entirely smooth, it may be covered completely by spiral striations, or it may be somewhere in between; there is usually an umbilical keel, and the umbilicus often has a few spirals within; there may be a sharp or rounded subsutural ridge shouldering the whorl. Axial sculpture, when present, consists of numerous equal and equally spaced plications radiating from the suture, and is most distinct on the early whorls; on specimens with a sharp subsutural ridge, the axials finely serrate the ridge. Umbilicus rather wide and funicular. Aperture circular, lips thin and simple.

Syntypes.—USNM 108140, 154 specimens from ALBATROSS sta. 2668.

Type-locality.—ALBATROSS sta. 2668, 30°58′30″N, 79°38′30″W, 538 m, 5 May 1886, large beam trawl.

Material examined.—ALBATROSS sta. 2668; 154, USNM 108140 (syntypes); 5, USNM 108134.—ALBATROSS sta. 2415; 27, USNM 108422.—ALBATROSS sta. 2644; 1, USNM 330533.

Geographic distribution.—Known only from off southern Georgia and the Straits of Florida off Miami.

Bathymetric range.—353 to 805 m.

Remarks.—This is the smallest species of *Solariella* in the Straits area and probably in the Western Atlantic. Its small size probably accounts for its seeming rarity since it would generally pass through the mesh of most sampling gear other than a dredge, and if taken might easily be overlooked in the debris. It is a rather variable species, but can be mistaken for no other species of *Solariella* in the Western Atlantic.

Solariella (Solariella) lamellosa
(Verrill & Smith, 1880)
Figs. 61,62

Margarita lamellosa Verrill & Smith, 1880: 391, 397.—Verrill, 1880: 378; 1882: 530, pl. 57, fig. 38.—Watson, 1886: 82.

Margarita aegleis: Dall, 1881: 40 *(partim)*.

Margarita (Solariella) lamellosa: Dall, 1889a: 379; 1889b: 164, pl. 63, fig. 98 (list only; figure from Verrill, 1882).—Pilsbry, 1889: 315, pl. 57, fig. 14 (description from Verrill & Smith, 1880; figure from Verrill, 1882).

Margarita (Solariella) amabilis: Dall, 1889a: 378 (*partim*); 1889b: 164 (*partim*; listed only).

Solariella calatha: Dall 1927a: 128 (*partim*).

Solariella tiara: Dall, 1927a: 130.

Solariella lamellosa: Johnson, 1934: 71 (listed only).

Solariella (Machaeroplax) lamellosa: Abbott, 1974: 40, fig. 275.

Description.—Shell attaining a height of about 9 mm, thin, bluntly conical, carinate, umbilicate, of 6 to 7 whorls. Protoconch small, glassy, slightly depressed, of about 1 whorl. There are 2 spiral carinae on the spire with a 3rd appearing on the body whorl; the subsutural carina bears strong, rounded tubercles and tabulates the whorl; the 2nd carina is just below mid-whorl, and forms the periphery; the 3rd carina, on which the suture is formed, defines the base; a row of strong tubercles circumscribes the umbilicus; there may or may not be fine spiral threads in the spaces between the carinae and within the umbilicus. Axial sculpture of thin ribs on the first 2 whorls, becoming obsolete thereafter, remaining only as tubercles on the upper 2 carinae; shell otherwise with fine growth lines. Base flattened, smooth or spirally striate; umbilicus wide, deep, and somewhat restricted within. Aperture subcircular, angulated by the carinae; lips thin and simple; columella concave, not thickened.

Holotype.—USNM cat. no. 44738, from ALBATROSS sta. 871.

Type-locality.—ALBATROSS sta. 871, off Martha's Vineyard, 210 m.

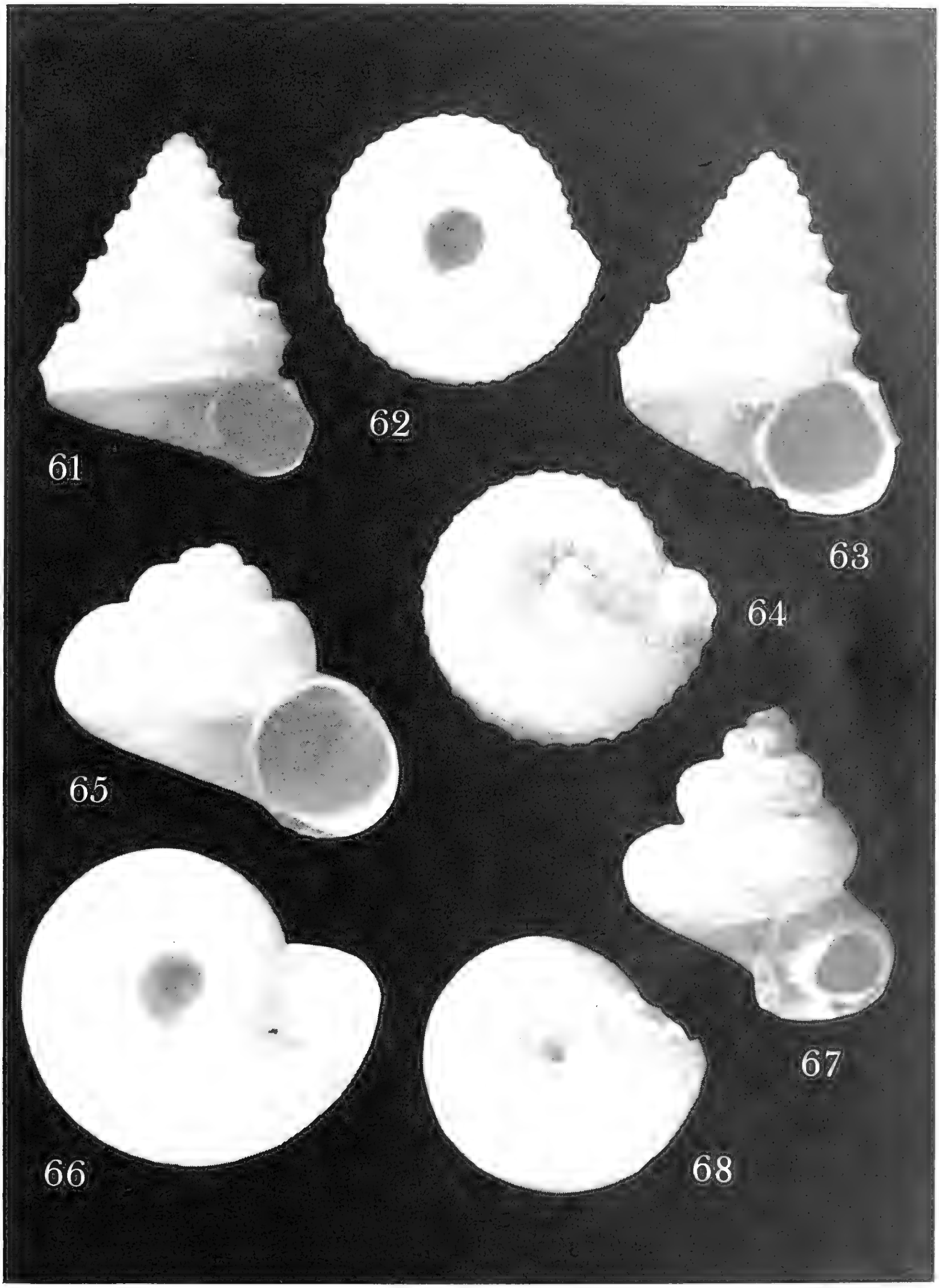
Material examined.—Straits of Florida: G-300; 2, UMML 30-8051.—G-4; 1, UMML 30-8025.—G-830; 1, UMML 30-7565.—ALBATROSS sta. 2644; 7, USNM 94946; 4, USNM 330559.—G-23; 2, UMML 30-8099.—EOLIS sta. 115, off Government Cut, 183 m; 1, USNM 438406.—EOLIS sta. off Fowey Rocks: 153; 1, *ex* USNM 438352.—303; 11, USNM 438431.—305; 4, USNM 438434.—306; 10, USNM 438435.—340; 14, USNM 438438.—348; 2, USNM 438437.—349; 2, USNM 438439.—360, 14, *ex* USNM 438349.—361; 100, USNM 438444.—377; 12, USNM 438451.—378; 5, USNM 438456.—EOLIS sta. 368, off Ajax Reef, 146–185 m; 5, USNM 438459.—EOLIS sta. 339, off Ragged Key, 183 m; 7, USNM 438400.—G-857; 2, UMML 30-8042.—G-834; 1, UMML 30-7538.—G-1035; 1, UMML 30-7914.—G-970; 8, UMML 30-7770.—G-969; 1, UMML 30-8063.—G-968; 1, UMML 30-7644.—G-967; 6, UMML 30-8062.—G-1099; 1, UMML 30-8065.—G-861; 1, UMML 30-8058.—EOLIS sta. 302; 1, USNM 438416.—EOLIS sta. 323; 19, USNM 438415.—Schmitt sta. 69 off Dry Tortugas, 455–655 m; 5, USNM 421840.—BLAKE sta. 2; 4, USNM 94947.—BLAKE sta. 21; 4, USNM 94948.

Geographic distribution.—From off North Carolina south through the Straits of Florida, and the Antillean Arc to Barbados.

Bathymetric range.—Living examples of the species have been taken from 25 to 600 m, and dead specimens are known down to 1472 m.

Remarks.—This species has had a rather confused history, primarily as a result of Dall's work. At first Dall assigned specimens of *S. lamellosa* and *S. pourtalesi* Clench & Aguayo to *Calliotropis aeglees* (Watson) (Dall, 1881). In 1889 he separated these 2 species from *C. aeglees,* regarding *S. lamellosa* as a distinct species. He did not consistently recognize *S. lamellosa,* especially young specimens, and placed some of these along with most of his specimens of *S. pourtalesi* with the Eastern Atlantic species *S. amabilis* (Jeffreys) (see also *S. pourtalesi* Clench & Aguayo). Juvenile specimens of *lamellosa* were also present in lots reported by Dall (1927a) as *S. calatha,* and, in the same paper, he listed a specimen of *lamellosa* as *S. tiara* (Watson). Clench & Aguayo (1939) finally separated *S. pourtalesi* as a distinct species, but did not recognize that some of the USNM lots of *pourtalesi* were mixed, containing *lamellosa* as well.

S. lamellosa is very closely related to *S. amabilis* and *S. pourtalesi. S. lamellosa* presents a neater appearance than either *amabilis* or *pourtalesi* since the sculpture is sharper and the shell is more acutely angulated. The umbilicus is also wider in *lamellosa* than in the other 2 species, making the base very narrow. *S. lamellosa* is one of the commonest species in the Straits area in depths



FIGS. 61–68. 61–62. *Solariella (Solariella) lamellosa* (Verrill & Smith): G-967, h = 8.3 mm, d = 7.0 mm. 63–64. *Solariella (Solariella) pourtalesi* Clench & Aguayo: P-747, h = 9.1 mm, d = 7.6 mm. 65–66. *Solariella (Solariella) tubula* (Dall) (syntype): ALBATROSS-2668, h = 3.7 mm, d = 4.7 mm. 67–68. *Solariella (Micropiliscus) constricta* Dall (syntype): ALBATROSS-2145, h = 3.6 mm, d = 3.1 mm.

greater than 200 m, but is primarily an inhabitant of depths of 50 to 150 m throughout its range.

Solariella (Solariella) pourtalesi
Clench & Aguayo, 1939
Figs. 63,64

Margarita (Solariella) amabilis: Dall, 1889a: 378 (*partim*); 1889b: 164 (*partim*; listed only).—Pilsbry, 1889: 313 (*partim*) (*non Trochus amabilis* Jeffreys, 1865.)
Solariella pourtalesi Clench & Aguayo, 1939: 190, pl. 28, fig. 2.—Abbott, 1974: 41.

Description.—Shell large for the genus, reaching height of 10.3 mm, rather thin, bluntly conical, carinate, umbilicate, of about 6½ whorls. Nucleus small, inflated, glassy, of about 1½ whorls. Spiral sculpture of 2 pustulose carinae, 1 just below the suture, shouldering the whorl, and the other about midwhorl, forming the periphery; a 3rd carina, on which the suture is formed, is thread-like, smoothish, and circumscribes the base; fine spiral threads may be present in the intercarinal spaces and on the base; a strongly tuberculate cord borders the rather wide, funicular umbilicus. Axial sculpture of lamellar ribs on the second and third whorls and prominent, irregular growth lines. Aperture subcircular; lips thin, simple, inner lip slightly flared over the umbilicus; columella arched, not thickened.

Holotype.—MCZ 135108, from ATLANTIS sta. 2993.

Type-locality.—ATLANTIS sta. 2993, 23°24′N, 80°44′W, 1061 m, 15 March, 1938, 14′ Blake trawl.

Material examined.—G-693; 20, UMML 30-8053.—G-366; 3, UMML 30-8053.—G-365; 2, UMML 30-8052.—G-1107; 1, UMML 30-8139.—G-1106; 2, UMML 30-8046.—G-368; 1, UMML 30-8092.—G-446; 1, UMML 30-8140.—G-375; 2, UMML 30-8056.—G-859; 1, UMML 30-8141.—G-374; 4, UMML 30-8055.—G-128; 1, UMML 30-8142.—G-129; 6, UMML 30-8048.—G-964; 1, UMML 30-7744; 2, UMML 30-8061.—G-965; 11, UMML 30-7760.—G-1112; 2, UMML 30-8066.—G-960; 18, UMML 30-8060.—G-959; 1, UMML 30-8059.—BLAKE sta. 2; 2, USNM 94947.—Off Havana, 1873 m, Henderson coll.; 1, USNM 438225.—BLAKE, sta. no. unrecorded, Yucatan Channel, 1170 m; 3, USNM 168774.

Geographic distribution.—From the Northwest Providence Channel south through the Straits of Florida and the Yucatan Channel, and southeast through the Lesser Antilles.

Bathymetric range.—This species occurs in deep water from 275 to 2350 m.

Remarks.—This is a rather common species in depths greater than 1000 m. In the northern Straits the species occurs in somewhat shallower depths, about 650–1000 m, but the record of 275–293 m (G-693) seems suspect. The station data seem to be correct, so perhaps the specimens were mislabeled. Dall originally identified the species as *S. amabilis* (Jeffreys) (see also *S. lamellosa* (Verrill & Smith) referring to a rather overdrawn illustration of *amabilis* in Jeffrey's work. He also identified 1 specimen as *Calliotropis rhina* (Watson). Clench & Aguayo (1939), in working up the ATLANTIS material, finally recognized *pourtalesi* as a separate species. Even though *pourtalesi* is superficially rather similar to *C. rhina,* it seems most closely allied to *S. lamellosa (q. v.),* differing in being larger, more coarsely sculptured, and with a relatively narrow umbilicus.

Subgenus **Suavotrochus** Dall, 1924

Suavotrochus Dall, 1924: 90.

Type-species.—*Solariella lubrica,* Dall, 1881; by monotypy.

Diagnosis.—Shell small, iridescent, smooth or nearly so, umbilicate.

Solariella (Suavotrochus) lubrica
(Dall, 1881)
Figs. 68–74.

Margarita lubrica Dall, 1881: 44.
Margarita (Solariella) lubrica: Dall, 1889a: 392, pl. 21, figs. 9, 9a; 1889b: 164, pl. 21, figs. 9, 9a (listed only; figs. from 1889a).—Pilsbry, 1889: 324, pl. 51, figs. 25, 26 (description from Dall, 1881; figs. from Dall, 1889a).
Margarita (Solariella) lubrica var. *iridea* Dall, 1889a: 382; 1889b: 164 (listed only).—Pilsbry, 1889: 324 (from Dall, 1889a).
Solariella (Suavotrochus) lubrica: Dall, 1924: 90.
Solariella (Machaeroplax) lubrica lubrica: Johnson, 1934: 72 (listed only).
Solariella (Machaeroplax) lubrica iridea: Johnson, 1934: 72 (listed only).
Solariella (Solariella) lubrica lubrica: Abbott, 1974: 41, fig. 290 (listed only; fig. from Dall, 1889a).

Solariella (Suavotrochus) lubrica iridea: Abbott, 1974: 41, fig. 290a.

Description.—Shell small (reaching a height of 5.5 mm), bluntly conical, smooth, brilliantly nacreous when fresh, otherwise white, of about 5 whorls. Nucleus small, glassy, with very fine spiral striations, of about 1–1¼ whorls. Whorls inflated, smooth, with a strong subsutural ridge which breaks up into elongate beads on the last 2 or 3 whorls; the beads are crossed by 2 fine spiral threads, giving the beads a squarish cross-section. Whorl rounds smoothly into the base, at the center of which is a moderate, funicular umbilicus. A ridge composed of 1 or 2 spiral threads encircles the umbilicus in most specimens; ridge beaded by strong axial plications which originate within the umbilicus and extend a short distance onto the base. Aperture circular; lips thin and simple; inner lip slightly flared over the umbilicus. Operculum thin, corneous, multispiral.

Holotype.—USNM 95061, from BLAKE sta. 2.

Type-locality.—BLAKE sta. 2, 23°14′N, 82°25′W, 1472 m.

Material examined.—ALBATROSS sta. 2644;1, USNM 95063; 1, USNM 95063a; 2, USNM 330549.—EOLIS sta. off Fowey Rocks: 346; 238 m; 1, USNM 450491.—347, 220 m; 2, USNM 438292.—348; 201 m; 2, USNM 450490.—349, 183–274 m; 1, USNM 450493.—EOLIS sta. 372, 183 m; 1, USNM 450503.—EOLIS sta, 339, off Ragged Key, 183 m; 1, USNM 438289; 1, USNM 450554. —G-1095; 6, UMML 30-7931.—G-1096; 5, UMML 30-8088.—G-967; 2, UMML 30-8086. —Schmitt sta. 69 off Tortugas, 455–655 m; 1, USNM 421842.—BLAKE sta. 2; 1, USNM 95061 (holotype).

Geographic distribution.—From the Straits of Florida off Miami, south throughout the Caribbean, and the Gulf of Mexico.

Bathymetric range.—From 155 to 1472 m. *S. lubrica* probably inhabits depths of about 200 to 500 m.

Remarks.—This species is somewhat variable in the strength of its sculpture. Dall (1889a) described the variety *iridea* from off Cape Florida for a form which is somewhat more inflated than the typical form, and is almost devoid of all sculpture. However, other specimens from the same locality show intergrades which indicate that this variety is nothing more than a morphological variant. The occurrence of *S. lubrica* at BLAKE sta. 2 (1472 m) is probably not indicative of a normal existence at that depth. As with other species recorded from that station, *S. lubrica* probably lives in considerably shallower water and was moved down the steep slope of the northern Cuban coast after death.

Subgenus **Micropiliscus** Dall, 1927

Micropiliscus Dall, 1927a: 130.

Type-species.—*Solariella (Micropiliscus) constricta* Dall, 1927; by monotypy.

Diagnosis.—Shell small, spirally striate, umbilicate, with a large brown carinate protoconch.

Solariella (Micropiliscus) constricta
Dall, 1927
Figs. 67,68

Solariella (Micropiliscus) constricta Dall, 1927a: 130.

Description.—Shell small (reaching a height of about 4 mm), turbinate, umbilicate, of about 3 whorls. Protoconch large, conical, brown, smooth with 1 or 2 spiral carinae just above the suture, of about 2 whorls; there is a sharp, flaring varix separating the protoconch and teleoconch. Spiral sculpture of fine, weak, subequal spiral threads over the whole surface of the shell. Axial sculpture of fine growth lines; some specimens have a series of small, axially elongated pits radiating out from the suture, giving the whorl a puckered aspect. Base rounded, not set off from the rest of the whorl; umbilicus small and pore-like, without a carina. Aperture subcircular; lips thin and simple.

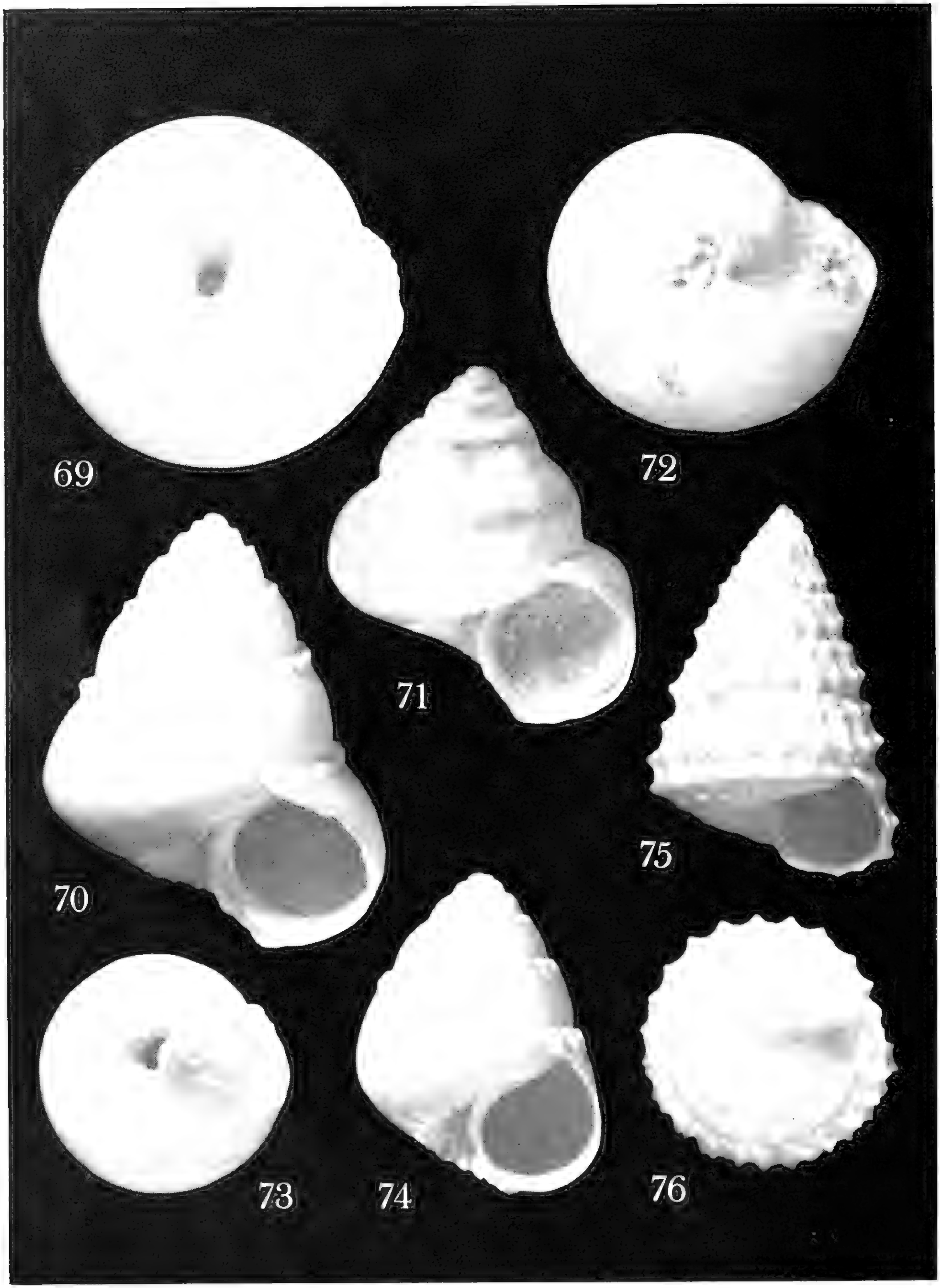
Syntypes.—A series of 11 specimens in 2 lots is in the USNM, cat. nos. 108414a and 108414b, from ALBATROSS sta. 2415.

Type-locality.—ALBATROSS sta. 2415, 30°44′N, 79°26′W, 805 m, 1 April 1885, large beam trawl.

Material examined.—ALBATROSS sta. 2415; 5, USNM 108414a; 6, USNM 108414b (syntypes).—EOLIS sta. 370, off Ajax Reef, 128–165 m; 2, USNM 450572.—EOLIS sta. 344, off Key West, 183 m; 1, USNM 450536. —EOLIS sta. 338, off Sand Key, 156 m; 1, USNM 450526.

Geographic distribution.—This species is known only from off southern Georgia and the Straits of Florida off Miami and Key West.

Bathymetric range.—Known from 128–164 to 805 m.



FIGS. 69–76. 69–70. *Solariella (Suavotrochus) lubrica* (Dall): G-1089, h = 5.5 mm, d = 4.6 mm. 71–72. *Solariella (Suavotrochus) lubrica* (Dall) ("var. *iridea*" Dall, holotype): ALBATROSS-2644, h = 5.2 mm, d = 4.8 mm. 73–74. *Solariella (Suavotrochus) lubrica* (Dall) (holotype): BLAKE-2, h = 4.7 mm, d = 4.0 mm. 75–76. "*Solariella*" *tiara* (Watson): G-289, h = 6.6 mm, d = 4.7 mm.

Remarks.—*S. constricta* is a very distinctive species since it is the only species in the group which has a large brown protoconch. The shell ornamentation varies only slightly in that the spiral striations are often slightly stronger at the whorl periphery and the subsutural pits may or may not be present.

Solariella species *incertae sedis*

"Solariella" tiara (Watson, 1879)

Figs. 75,76

Trochus (Ziziphinus) tiara Watson, 1879: 696; 1886: 60, pl. 6, fig. 4.
Calliostoma tiara: Dall, 1880: 45; 1881: 45 (*partim*); 1889a: 365; 1889b: 162 (listed only).—Pilsbry, 1889: 380, pl. 17, fig. 29.—Johnson, 1934: 70 (listed only).
Margarita scabriuscula Dall, 1881: 41.
Margarita (Solariella) scabriuscula: Dall, 1889a: 379, pl. 21, figs. 10, 10a; 1889b: 164, pl. 21, figs. 10, 10a (listed only; figs. from 1889a).—Pilsbry, 1889; 330, pl. 51, figs. 28, 29 (description from Dall, 1881; figs. from Dall, 1889a).
Solariella scabriuscula: Johnson, 1934: 71 (listed only).—Abbott, 1974: 41, fig. 280 (listed only; fig. from Dall, 1889a).
Solariella (Machaeroplax) tiara: Johnson, 1934: 72 (listed only).
Solariella tiara: Clench & Turner, 1960: 78 (major synonymy only).—Abbott, 1974: 41 (listed only).

Description.—Shell small, thin, spire rounded conical, of 6 to 7 whorls. Protoconch bulbous, glassy, of 1 whorl. Spiral sculpture of, on the spire 2, on the last whorl 3 carinae, each set with numerous strong, conical tubercles. The upper carina is separated from the suture by a narrow flat area and is on the same level as the suture, the second is just below mid-whorl and forms the periphery, and the third, on which the suture forms, defines the base, Base with 3 to 4 spiral cords whose sculpture ranges from weakly undulate to fairly distinctly beaded; the innermost cord is strongly beaded and bounds the umbilical depression. Axial sculpture of sharp riblets on the first 2 whorls persisting on later whorls as low ridges between the carinae, irregularly connecting tubercles on adjacent carinae. Otherwise, there are fine, crowded, irregular growth lines over the whole surface. Base flatly rounded, with a shallow central depression, at the center of which is a small umbilical pore which is reduced to a chink in most specimens. Aperture subrectangular, slightly thickened within; lips thin, inner lip slightly reflected; columella thickened, sometimes more so in the middle, forming an obscure tooth.

Syntypes.—Series of three specimens is in the British Museum (Natural History), cat. nos. 87.2.9.218-220, from CHALLENGER sta. 56.

Type-locality.—CHALLENGER sta. 56, off Bermuda, 32°04′45″N, 64°59′35″W, in 1966 m.

Material examined.—G-23; 1, UMML 30-8098.—G-815; 1, UMML 30-8143.—G-289; 1, UMML 30-8050.—G-966; 1, UMML 30-8094.—Gulf of Mexico: BLAKE sta. 44; 1, USNM 214281 (holotype of *Margarita scabriuscula*).

Geographic distribution.—Known from Bermuda, the Straits of Florida, the Gulf of Mexico, and the Caribbean, especially the Antilles.

Bathymetric range.—This species has been taken in depths of 400–1966 m. It seems to be most frequent in the 600–800 m range.

Remarks.—As can be seen in the synonymy, this species has been cited frequently since its description. However, no one has compared specimens of *tiara* with the holotype of *scabriuscula,* the only known specimen of that species. Instead, authors subsequent to Dall merely quoted from the literature. In trying to identify specimens from the Straits, I examined the holotype of *scabriuscula* and compared it with a photograph of one of the syntypes of *tiara*; I found no characters on which to base a separation at the specific level. A subsequent examination of specimens taken by the PILLSBURY from the Caribbean supported my belief that the two species are in fact the same. This species has been placed in the genus *Solariella* by most authors since Dall, but in my opinion, it does not belong there at all. I can find no described group in which *tiara* fits, and so assign it to a "genus uncertain" rank.

Genus **Microgaza** Dall, 1881

Microgaza Dall, 1881: 50; 1889a: 357; 1889b: 160.—Dall, in Guppy & Dall, 1896: 323.—Pilsbry, 1889: 11, 160.—Cossmann, 1918: 258.—Woodring, 1928: 435.—Johnson, 1934: 74.—Thiele, 1929: 48.—Keen, 1960: I262.—Abbott, 1974: 42.

Type-species.—*Callogaza (Microgaza) rotella* Dall, 1881: 51; by monotypy.

Diagnosis.—Shell small, circular, depressed, deeply umbilicate, highly iridescent when fresh. Aperture subquadrate, lips thin, columella straight and simple. Sculpture of umbilical plications extending out onto the base and sometimes pustulations or plications at the suture. Operculum thin, corneous, circular, multispiral.

Remarks.—*Microgaza* was introduced as a subgenus of *Callogaza* Dall, 1881, for *M. rotella* Dall, 1881. In 1889 he relegated *Callogaza* to subgeneric rank under *Gaza* Watson, 1879, and kept *Microgaza* as a subgenus, placing it in *Gaza*. The first usage of *Microgaza* at the generic level was by Dall (1885) in his list of eastern American molluscs. Cossmann (1918) described a fossil species from the European Miocene as *Microgaza,* but Woodring (1928) expressed doubt that it was actually in this genus. Woodring in the same paper described a new subspecies of *rotella, vetula,* and erected a new subgenus to accommodate his *M. cossmanni. M. cossmanni* is fossil and *vetula* was first reported as a fossil, but the GERDA has obtained 6 specimens of *vetula* to bring the total number of living forms known to 3 (including 1 subspecies).

The systematic position of *Microgaza* has long been unsettled. Dall's original placement of *Microgaza* in *Callogaza* and then *Gaza* was followed in turn by Cossmann (1918), who included it under *Eumargarita* Fischer, 1885 (=*Margarites* Gray, 1847), Thiele (1929), who synonymized it with *Solariella* Wood, 1842, and Keen (1960), who placed it as a subgenus of *Solariella.* Examination of the radula of *Microgaza rotella rotella* indicates a close relationship with *Solariella.* The radular ribbon is rather short and broad with relatively few rows of teeth. The rhachidian is broad and rounded posteriorly with a very strong cusp bearing two denticles on each side. The admedians and second laterals are similar to each other, each with an inwardly directed triangular cusp, denticulate only on the outer edge. The third lateral is very strong and broad with a rather weak, inwardly directed cusp. The few marginals (6–8 per half-row) are large and sickle-shaped, overhanging the three laterals. Radular formula is 8-6.3.1.3.6-8 (see figure below).

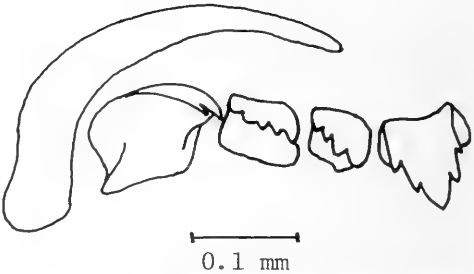


FIG. 90. Part of a half-row of the radula of *Microgaza rotella rotella* showing the rhachidian, the three laterals and the inner marginal.

Microgaza rotella rotella (Dall, 1881)
Figs. 77,78

Callogaza (Microgaza) rotella Dall, 1881: 51.
Microgaza rotella: Dall, 1885: 170; 1889b: 160, pl. 22, figs. 5, 5a (listed only).—Dall, in Guppy & Dall, 1896: 323.—Woodring, 1928: 435.—Abbott, 1974: 42.
Gaza (Microgaza) rotella: Dall, 1889a: 357, pl. 22, figs. 5, 5a.—Pilsbry, 1889: 160, pl. 48, figs. 5, 6 (description from Dall, 1881; figs. from Dall, 1889a).—Johnson, 1934: 74 (*partim*; listed only). Dautzenberg, 1900: 71.

Description.—"Shell depressed, with five whorls, somewhat flattened above and below; nucleus small, translucent white, and with the two first whorls smooth or marked only by faint growth-lines; remainder of the whorls with a narrow puckered band revolving immediately below the suture, on which the shell matter is as if it were pinched up into slight elevations at regular intervals, about half a millimeter apart. In some specimens, outside of this band an impressed line revolves with the shell; remainder smooth, shining or with evanescent traces of revolving lines impressed from within and strongest about the rounded periphery; base rounded toward the umbilical carina over which it seems to be drawn into flexuously radiating well-marked plications (about thirty-two on the last turn) which disappear a third of the way toward the periphery; walls of the umbilicus concave, overhung by the carina, turns of the shell so coiled that the part of each whorl uncovered by its successor forms a narrow spiral plane ascending to the apex like a spiral staircase or screw thread. Pillar straight, thin, with no callus; aperture rounded except at the angle of the umbilical carina; margin thin, sharp, not reflected or thickened; no callus on the body whorl in the aperture; shell whitish or greenish; nacre less brilliant in dead or deep-water specimens; with zigzag brown lines variously transversely disposed and disappearing on the base." (Dall, 1881.)

Lectotype.—MCZ 7548, from BLAKE sta. 2. The paralectotype from this station is MCZ 288095 and 7 more from Barbados are MCZ 7550.

Type-locality.—Here restricted, BLAKE sta. 2, 23°14′N, 82°25′W, in 1472 m.

Material examined.—Straits of Florida: G-606; 2, UMML 30-7418.—G-451; 1, UMML 30-8009.—G-1035; 4, UMML 30-7913.—EOLIS sta. 322, off Sand Key, 210 m; 2, USNM 437998.—EOLIS sta. 323, off Sand Key, 201 m; 1, USNM 437999.—EOLIS sta. 344, off Key West, 183 m; 1, USNM 438004.—EOLIS sta. 333, off Key West, 201 m; 3, USNM 438005.—EOLIS sta. C, S. of Key West, 183 m; 1, USNM 438007.—BLAKE sta. 2; 1 MCZ 7548 (lectotype) 1 MCZ 288095 (paralectotype).—Barbados: BLAKE sta., number unrecorded, 183 m; 7, MCZ 7550 (paralectotypes). Many lots from the EOLIS in shallower water in the Straits, and from the SUI expedition to Barbados.

Geographic distribution.—The southeastern Gulf of Mexico, the Straits of Florida occasionally as far north as Key Largo, Cuba and south through the Antillean arc.

Bathymetric range.—The possible range is 46 to 1472 m, but most commonly occurring in 100 to 200 m.

Remarks.—This is a beautiful species occurring rather commonly in depths less than 200 m. *Microgaza rotella rotella* is the southern form of this species, occurring occasionally as far north as Key Largo. The area from roughly Key Largo to off Miami is the transitional area between the 2 subspecies, with intermediate forms occurring commonly. North of Miami the subspecies *inornata* is found exclusively, and south of Key Largo only true *rotella* is taken. This indicates that true geographic subspecies are involved and not mere individual or population variation. The distinguishing character of true *rotella* is the presence of a row of elongate beads just below the suture line. The other subspecies, *inornata,* lacks these pustules; however, the name *"inornata"* seems never to have been introduced validly into the literature. I herein do so:

Microgaza rotella inornata
Quinn, n. subsp.
Figs. 74,80

Microgaza rotella: Dall, 1889a: 357 (*partim*); 1889b: 160 (*partim*); listed only).—Pilsbry, 1889: 160 (*partim*).

Microgaza rotella inornata Dall, in Guppy & Dall, 1896: 323.—Woodring, 1928: 435. Both are *nomina nuda.*

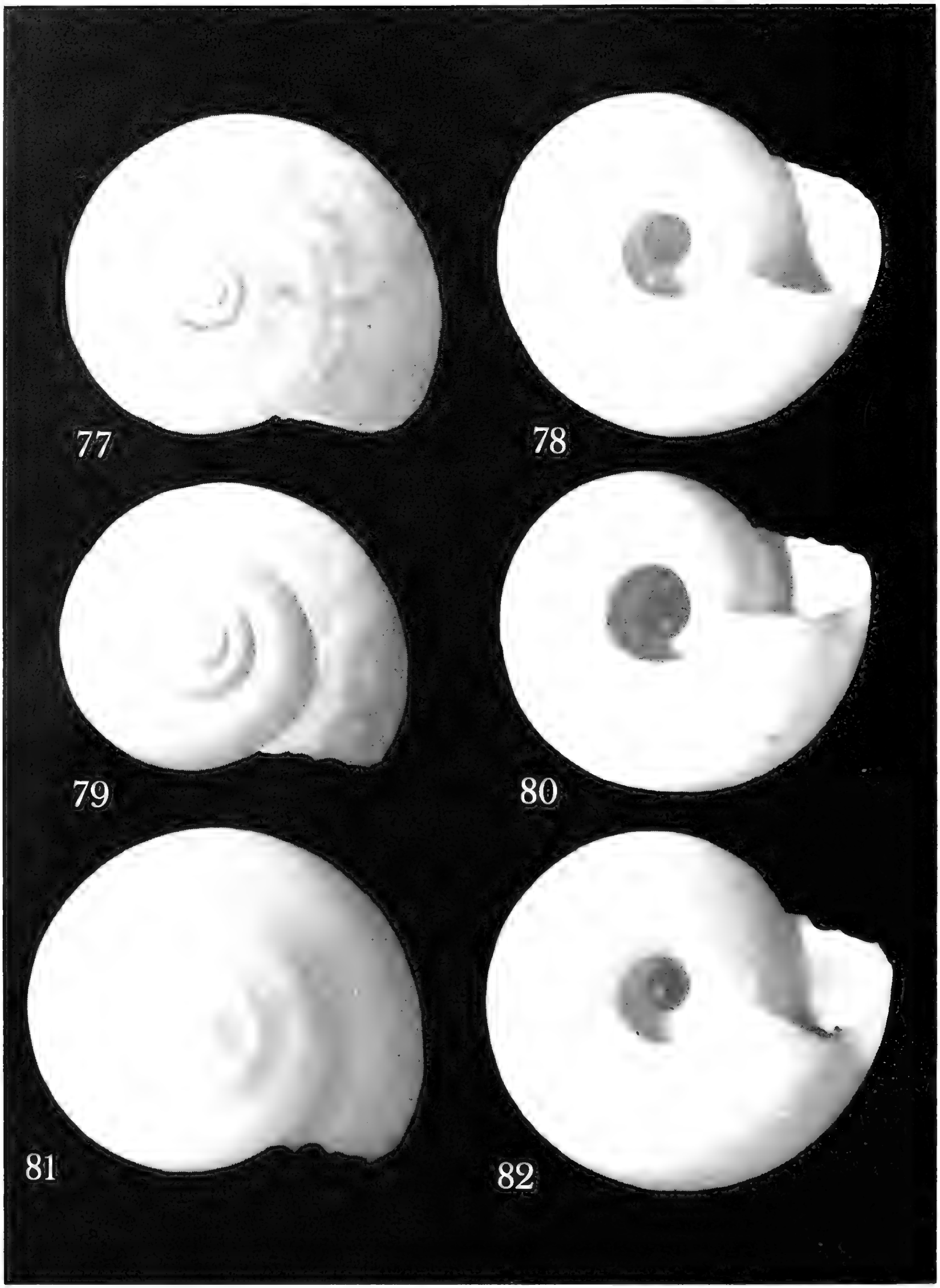
Microgaza rotella form *inornata*: Abbott, 1974: 42 (name invalid under Article 45e (ii), International Code of Zoological Nomenclature, 1964).

Holotype.—USNM 94101, from ALBATROSS sta. 2311.

Type-locality.—ALBATROSS sta. 2311, 32°55′N, 77°54′W, off South Carolina, in 144 m.

Description.—Shell depressed, whitish with irregular zigzag splotches of brown on the upper surface of the whorls, highly iridescent, of about 5 whorls. Nucleus small, white, polished, of 1½ whorls. Post-nuclear whorls with faint spiral lines near the periphery. A series of radial grooves around the umbilicus crenulates the umbilical keel. Occasional specimens may have a fine smooth cord just beneath the suture on the third and fourth whorls, but most specimens lack this character. Umbilicus wide, deep, with slightly concave walls, giving the umbilicus the aspect of a spiral ramp. Aperture subquadrate, outer lip thin, simple; columella straight, thin, not reflected, forming a sharp angle with the base.

Material examined.—ALBATROSS sta. 2602; 1, USNM 94993.—ALBATROSS sta. 2592; 1, USNM 329455.—ALBATROSS sta. 2417; 1, USNM 87574.—ALBATROSS sta, 2311; 1, USNM 94101 (holotype).—ALBATROSS sta. 2312; 2, USNM 93659.—ALBATROSS sta. 2313; 6, USNM 94126.—ALBATROSS sta. 2314; 1, USNM 322960.—Burry coll., 24 km E of Delray Beach, 503–549 m; 1, USNM 620314.—EOLIS sta. 189, E of Cape Florida, 122 m; 16, USNM 438009.—EOLIS stations off Fowey Rocks: 165, 143 m; 2, 438039.—169, 128 m; 11, 438038.—174, 106 m; 3, 438037.—181, 130 m; 1, 438036.—182, 137 m; 1, 438041.—183, 146 m; 5, 438040.—186, 124 m; 2, USNM 438016.–305, 201 m; 1, USNM 438021.—346, 238 m; 1, USNM 438020.—351, 165 m; 14, USNM 438019.—352, 165 m; 13+, USNM 438018.—353, 155 m; 3, USNM 438017.—354, 146 m; 30, USNM 438022.—355, 128 m; 12, USNM 438028.—356, 101 m; 32, USNM 438027.—358, 229 m; 1, USNM 438026.—360, 183 m; 2, USNM 438025.—361, 137–183 m; 44, USNM 438029.—362, 174 m; 20, USNM 438024.—363, 155 m; 1, USNM 438023.—364, 137–165 m; 24, USNM 438034.—373, 128–165 m; 27, USNM 438033.—374, 155 m; 18, USNM 438032.—



FIGS. 77–82. 77–78. *Microgaza rotella rotella* (Dall) (lectotype): BLAKE sta. off Havana, Cuba, h = 3.8 mm, d = 6.5 mm. 79–80. *Microgaza rotella inornata* Quinn, n. subsp.: G-280, h = 3.7 mm, d = 6.3 mm. 81–82. *Microgaza vetula* Woodring: G-984, h = 3.8 mm, d = 6.8 mm.

375, 137–165 m; 16, USNM 438031.—382, 128 m; 3, USNM 438030.—Sta. no unrecorded, 91 m; 2, USNM 438036.—EOLIS sta. off Ragged Key: 192, 137 m; 3, USNM 438015. —193, 146 m; 12, USNM 438011.—194, 155 m; 1, USNM 438010.—339, 183 m; 2, USNM 438014.—365, 137 m; 1, USNM 438013.—366, 137–165 m; 19+, USNM 438012.—350, off Triumph Reef, 128–165 m; 49, USNM 438044.—368, off Ajax Reef, 146–183 m; 2, USNM 438043.—369, depth unrecorded; 2, USNM 438047.—370, off Ajax Reef, 128–165 m; 4, USNM 438042.—376, off Caesar's Creek, 165 m; 19, USNM 438046.—G-857; 1, UMML 30-8012.—G-606; 2, UMML 30-8011.

Geographic distribution.—From Cape Hatteras, North Carolina, south to about Miami, Florida.

Bathymetric range.—The possible depth range of this form is 91 to 549 m, but the normal range is probably about 120 to 180 m.

Remarks.—See also *Remarks* section under *M. rotella rotella.* The name *"inornata"* has been used since 1896 when Dall first mentioned it. This appears to be a manuscript name for which Dall never published a diagnosis, description, or figure. As such the name stands as a *nomen nudum,* and, since no one has validated it since, merely listing the name, I have corrected the oversight. I have retained *"inornata"* since it is an appropriate name and it will serve nomenclatural stability best.

Microgaza vetula Woodring, 1928
Figs. 81,82

Microgaza rotella: Dall, in Guppy & Dall, 1896: 323 (*partim*); Dall, 1903: 1585 (*partim*).
Microgaza rotella var. *inornata* Dall, 1903: 1585 (*fide* Woodring, 1928; listed only).
Eumargarita (Microgaza) rotella Dall subsp.: Cossmann, 1918: 258, pl. 9, figs. 9, 10.
Microgaza (Microgaza) rotella vetula Woodring, 1928: 435, pl. 37, figs. 1–3.

Description.—Shell depressed, porcellaneous, white, of about 5 whorls. Nucleus small, white, of about 1 whorl. First postnuclear whorl microscopically spirally striate, 2nd whorl with a series of flexuous axial riblets. Sculpture on following whorls of a low spiral cord which bears low beads and adjoins the suture. Fine spiral threads are present on the periphery of the whorls. Base smooth except for a series of grooves radiating out from the umbilicus and crenulating the umbilical keel. Umbilicus deep, not extremely wide, margin sharp, walls sharply angled back from the margin, exposing part of the base of the preceding whorl. Umbilical wall bears one to three fine spiral threads. Aperture subquadrate, lips thin and simple; columella thin, straight, inclined, forming a sharp angle with the basal lip.

Holotype.—USNM 369570.

Type-locality.—Bowden Formation, Jamaica, Miocene.

Material examined.—Straits of Florida: G-984; 3, UMML 30-7798.—G-985; 1, UMML 30-7815.—G-986; 2, UMML 30-7831.

Geographic distribution.—Recent specimens known only from the Straits of Florida near the Cay Sal Bank; found as a fossil in the Miocene of Jamaica (Bowden Formation).

Bathymetric range.—From 119 to 192 m.

Remarks.—This is the first record of this species from the Recent fauna. It was evidently a common species during the Miocene of Jamaica, and was described from there as a subspecies of *M. rotella.* Superficially, *vetula* looks like a small bleached *rotella,* but the two may be distinguished easily by *vetula's* smaller size, presence of axial riblets on the second whorl, smaller umbilicus with its walls retreating from the margin more sharply than in *rotella,* and spiral threads on the umbilical walls of *vetula.* These characters are distinctive and consistent, so I feel justified in separating *vetula* and *rotella* at the specific level.

Genus **Basilissa** Watson, 1879

Basilissa Watson, 1879: 593; 1886: 96.—Dall, 1889a: 383.—Pilsbry, 1889: 15, 419. —Cotton, 1959: 189.—Keen, 1960: 250.—Bayer, 1971: 123.—Abbott, 1974: 39.

Type-species.—*Basilissa superba* Watson, 1879, by subsequent designation: Cossmann, 1888: 335.

Diagnosis.—Shell usually small, trochoid, deeply umbilicate, carinate, highly nacreous. Aperture subquadrate, lips thin; outer lip with a wide, fairly deep sinus near the suture, and another, narrower sinus near the periphery of the basal lip, resulting in a claw-like projection of the lip at the periphery. Operculum circular, thin, concave, multispiral.

Remarks.—This genus has traditionally been included in the Trochidae, and indeed, species of *Basilissa* bear a strong resemblance to some members of the family, particularly some of the Calliostomatinae. As noted by Dall (1889a) and Bayer (1971) the nacreous shells and peculiar sinuses in the outer lip of *Basilissa* are quite similar to those in *Seguenzia*. Bayer further stated: "*Seguenzia costulata* (*sic,* error for *S. carinata* Jeffreys) differs from *Basilissa* only in having a stronger columellar fold and more deeply sinuate lip, thus forming a transition between the genera as already noticed by Dall" (Bayer, 1971: 123). The radulae of *Basilissa* and *Seguenzia* as described by Thiele (1929) are very similar, again indicating a close relationship. Therefore, even though I am including *Basilissa* in this report on the Trochidae, I believe that it belongs in the family Seguenziidae with *Seguenzia* and *Thelyssa* Bayer, 1971.

Geographic distribution.—Probably cosmopolitan in tropical and temperate waters.

Bathymetric range.—Primarily a deep water genus, occurring in 200–2000 m, although records of *B. costulata* are of less than 100 m.

Subgenus **Basilissa** Watson, 1879

Type-species.—*Basilissa superba* Watson, 1879, by subsequent designation: Cossmann, 1888: 335.

Diagnosis.—Shell thin, finely sculptured, aperture not thickened.

Basilissa (Basilissa) alta Watson, 1879

Figs. 83,84

Basilissa alta Watson, 1879: 597; 1886: 100.—Dall, 1881: 48; 1889a: 384; 1889b: 164 (listed only).—Pilsbry, 1889: 419, pl. 36, fig. 5.—Johnson, 1934: 73 (listed only).—Bayer, 1971: 123, fig. 6, D-G; fig. 7.

Seguenzia delicatula Dall, 1881: 48.

Basilissa alta var. *oxytoma* Watson, 1886: 100, pl. 7, fig. 8e.—Pilsbry, 1889: 421, pl. 36, fig. 4.

Basilissa alta var. *delicatula*: Dall, 1889a: 384, pl. 22, figs. 2, 2a; 1889b: 164 (listed only).—Pilsbry, 1889: 421, pl. 48, figs. 3, 4.—Johnson, 1934: 73 (listed only).

Description.—See Watson, 1879 and 1886.

Holotype.—None selected. Syntypes are in the British Museum (Natural History), nos. 87.2.9.351 and 87.2.9.352, from CHALLENGER sta. 24.

Type-locality.—CHALLENGER sta. 24, off Culebra Island (Virgin Islands), 18°38′30″N, 65°05′30″W, in 713 m.

Material examined.—G-365; 1, UMML 30-8144.—G-370; 1, UMML 30-8145.—G-478; 1, 30-8146.—G-185; 1, UMML 30-8147.—BLAKE sta. 43; 1, USNM 94941.—G-959; 5, UMML 30-8148.—G-960; 7, UMML 30-8149.—G-963; 1, UMML 30-7692.—G-964; 1, UMML 30-8150; 2, UMML 30-7764.—G-965; 5, UMML 30-7759.—G-966; 1, UMML 30-8151.—G-967; 3, UMML 30-8152.—G-1099; 1, UMML 30-8018.—G-1112; 1, UMML 30-8022.

Geographic distribution.—Tongue of the Ocean, Bahamas, the Straits of Florida, the Gulf of Mexico, and south through the Antilles to Ceara, Brazil.

Bathymetric range.—Known from 348–1864 m, but occurs primarily in the 500–1500 m range.

Remarks.—This species exhibits a considerable variation in the strength of the surface sculpture of the shell. However, since this variation may be found in specimens of the same population, it is preferable to consider the varieties *oxytoma* and *delicatula* as infrasubspecific forms of *alta.*

Basilissa (Basilissa) discula (Dall, 1889)

Figs. 87,88

Fluxina discula Dall, 1889a: 273, pl. 23, figs. 5, 6; 1889b: 148, pl. 23, figs. 5, 6 (listed only).—Bayer, 1971: 129, fig. 8.

Planitrochus disculus: Abbott, 1974: 39 (listed only).

Description.—"Shell small, whitish, polished, of about five whorls, the base of the immersed nucleus looking exactly like a dextral nucleus; surface marked by the fine flexuous incremental lines, which do not interrupt the polish, and by faint occasional indications of spirals; upper surface of the whorls concave near the sutures, elsewhere flattened, so that the sutural junction is slightly elevated; periphery sharply carinated, base moderately rounded, not impressed near the carina; umbilicus moderate, scalar, its walls smooth and vertical; umbilical margin carinate, an impressed line just outside the carina; aperture wide, margins thin, columella straight, a little thickened, a wash of callus on the body; apparently little if any notch at the end of the umbilical carina." (Dall, 1889a: 274).

Holotype.—USNM 508721, from BLAKE sta. 180.

Type-locality.—BLAKE sta. 180, off Dominica, 15°29′18″N, 61°34′40″W, in 1796 m.

Material examined.—Bahamas: CI-356, 24°28.3′N, 77°29.5′W, 1597 m; 1, UMML 30-8157.—Straits of Florida: G-967; 1, UMML 30-8158.—G-1106; 1, UMML 30-8019.—G-960; 1, UMML 30-8159.—Lesser Antilles: BLAKE 180; 1, USNM 508721 (holotype).—P-604; 3, UMML 30-8160.

Remarks.—The considerable rarity of this beautiful species has no doubt led most workers to overlook it. Merrill (1970a), in synonymizing *Fluxina* with *Calliostoma* (see *Remarks* under *Callistoma brunneum*), did not even mention it, although he tentatively assigned *discula* to *Basilissa* in his dissertation (Merrill, 1970b). Bayer (1971) further discussed the similarities of the characters of *discula* and those of *Basilissa,* but declined to formally assign the species to *Basilissa* until more material was availble for study. Abbott (1974) placed *discula* in the extinct Silurian genus *Planitrochus* Perner, 1903. He was in error here since *Planitrochus* does not have the distinct sinuses in the outer lip which are evident in *discula*. For the present, then, I feel that *discula* best fits the characters of *Basilissa,* and until radular characters are known, I prefer keeping *discula* in *Basilissa.*

Basilissa (Basilissa) rhyssa Dall, 1927

Basilissa (Ancistrobasis) rhyssa Dall, 1927a: 121.—Johnson, 1934: 73 (listed only).

Basilissa rhyssa: Abbott, 1974: 38 (listed only).

Description.—Shell small, turbinate, strongly carinate, of about 6 whorls. Nucleus small, glassy, somewhat depressed. Whorls of spire with a single carina or shoulder about ⅓ down the whorl; body whorl periphery formed by an extremely acute, capelike carina which is hidden by the suture in the earlier whorls. Axial sculpture of low, flexuous ribs which modulate the whorl shoulder and extend down only as far as the peripheral carina. Base slightly convex and smooth except for very fine growth lines. Umbilicus moderate, bounded by a spiral cord. Aperture quadrangular, lips thin and with the typical *Basilissa* sinuses.

Syntypes.—Series of 3 specimens is in the USNM, cat. no. 108145, from ALBATROSS sta. 2668.

Type-locality.—ALBATROSS sta. 2668, off Fernandina, Florida, 30°58′30″N, 79°38′30″W, in 538 m.

Material examined.—ALBATROSS sta. 2415; 23, USNM 108395.—ALBATROSS sta. 2668; 3, USNM 108145 (syntypes).—BLAKE sta. 2; 2, USNM 214284.—BLAKE sta., Chicago Academy of Sciences, position unrecorded in the Yucatan Channel; 1, USNM 168769.

Geographic distribution.—From off southern Georgia south through the Straits of Florida to the Yucatan Channel.

Bathymetric range.—Known from 538–1472 m, but the true depth range for the species is problematical since all records are for dead shells. At least 1 station (BLAKE 2) had many rather shallow-water species which had obviously been transported down the steep slope of the northern Cuban escarpment.

Remarks.—This is a very distinctive species, the angulated whorls and capelike peripheral carina separating it immediately from all other known *Basilissa* species. Dall (1927) assigned *rhyssa* to the subgenus *Ancistrobasis* Dall, 1889, but that subgenus is characterized by a relatively heavy shell, with the aperture thickened and toothed within. *B. rhyssa* exhibits none of these characters and placement in *Ancistrobasis* seems unwarranted.

Subgenus **Ancistrobasis** Dall, 1889

Type-species.—*Basilissa costulata* Watson, 1879; by monotypy.

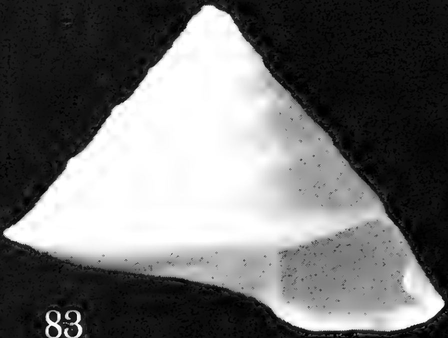
Diagnosis.—Shell solid, slightly depressed, highly sculptured; aperture thickened within and provided with strong lirations forming denticles at the aperture; columella with a strong terminal tooth.

Basilissa (Ancistrobasis) costulata
Watson, 1879
Figs. 85,86

Basilissa costulata Watson, 1879: 600; 1886: 103, pl. 7, fig. 11.—Dall, 1881: 48.

Basilissa (Ancistrobasis) costulata: Dall, 1889a: 384; 1889b: 164 (listed only).—Pilsbry, 1889: 426, pl. 36, fig. 3.—Johnson, 1934: 73 (listed only).—Abbott, 1974: 37 (listed only).

Basilissa (Ancistrobasis) costulata var. *depressa* Dall, 1889a: 384, pl. 23, figs. 4, 4a; 1889b): 164, pl. 23, figs. 4, 4a (listed only; figs. from 1889a).—Pilsbry, 1889: 428, pl. 60, figs. 14, 15 (description from Dall,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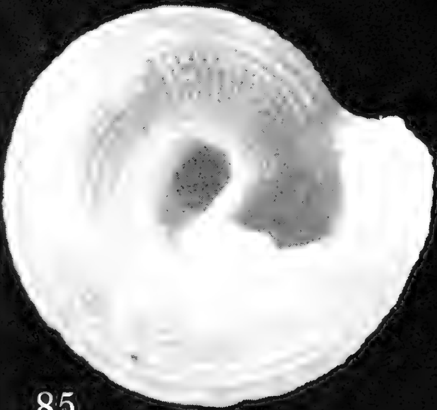
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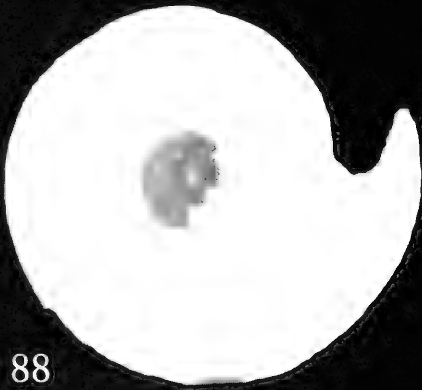
88

FIGS. 83–88. 83–84. *Basilissa (Basilissa) alta* Watson: CI-356, h = 4.7 mm, d = 6.1 mm. 85–86. *Basilissa (Ancistrobasis) costulata* Watson ("var. *depressa*"Dall): EOLIS-146, h = 4.2 mm, d = 6.1 mm. 87–88. *Basilissa (Basilissa) discula* (Dall): G-967, h = 2.9 mm, d = 6.6 mm.

1889a).—Johnson, 1934: 73 (listed only).—Abbott, 1974: 37.

Description.—See Watson, 1879; Dall, 1889a.

Holotype.—None selected. Syntype series of 3 immature specimens is in the British Museum (Natural History), cat. nos. 87.2.9.355-357, from CHALLENGER sta. 24.

Type-locality.—CHALLENGER sta. 24, off Culebra Island, Virgin Islands, 18°38′30″N, 65°05′30″W, in 713 m.

Material examined.—Straits of Florida: BLAKE sta. no. unrecorded, off Sand Key, in 27 m; 1, USNM 94945.—EOLIS sta. 146, off Key West, 179 m; 3, USNM 435753.—Yucatan Channel; BLAKE, sta. no. unrecorded, 1170 m; 3, USNM 94944.—G-897; 1, UMML 30-7717.

Geographic distribution.—From off southern Georgia through the Straits of Florida to the Yucatan Channel, the northern Gulf of Mexico, and the Virgin Islands.

Bathymetric range.—Recorded from 27–1170 m, establishing the species as the shallowest known species of the genera.

Remarks.—This is a very uncharacteristic species of *Basilissa.* Its heavy shell and strongly armed aperture, combined with its strong, coarse sculpture, make *costulata* a very easy species to recognize. There does not seem to be enough difference between *costulata s. s.* and *depressa* to warrant separation.

ZOOGEOGRAPHY

Faunal affinities.—From the study of a single family from so restricted an area as the Straits of Florida, it is somewhat dangerous to make broad generalizations or unqualified comparisons with the worldwide fauna. The results discussed herein are mostly indications, suggestive as they might seem. However, it is of value to discuss the apparent relationships of the Straits trochid fauna with respect to the worldwide fauna as well as the Western Atlantic trochids.

At the generic level, the Straits Trochidae seem to show a strong affinity with the other tropical areas of the world. Five genera (36%) can be considered circumtropical, and 3 more (21%) are cosmopolitan in tropical and temperate waters. That these genera are, for the most part, depauperate in the Western Atlantic, and that there are three more genera which are restricted to the Western Atlatnic, is to be expected when one considers the climatic changes during the late Miocene (Ekman, 1953). Even when the genera which have no species occurring deeper than 180 m (*Tegula* and *Cittarium*) are eliminated from the analysis, the results remain virtually unchanged.

The 54 species (including subspecies) with maximum recorded depths of greater than 180 m fall into 5 divisions: Tropical West Atlantic, Temperate, Northwest Atlantic, Amphi-Atlantic and Endemic Straits. The largest of these is the Tropical West Atlantic component with 27 species (50%) indicating that the Straits area is within the tropical domain of the Western Atlantic, although at the northern edge. As is to be expected for a marginal region, there is also a rather strong influence from the warm temperate area to the north. In the Straits, the Temperate Northwest Atlantic component forms 18.5% (10 species) of the total. These species are fairly common from Cape Hatteras to the northern parts of the Straits, a few species occurring as far south as Key West, and 3 species (*Calliostoma pulchrum, C. yucatecanum,* and *C. psyche*) are also known from the eastern Gulf of Mexico.

TABLE 1. List of Tropical West Atlantic Trochidae.

Calliostoma echinatum
Calliostoma jujubinum
Calliostoma schroederi
Calliostoma sapidum
Calliostoma brunneum
Calliostoma barbouri
Solariella multirestis
Solariella pourtalesi
Solariella lubrica
Calliotropis aeglees
Calliotropis calatha
Calliotropis lissocona
Calliotropis actinophora
Echinogurges clavatus
Dentistyla asperrima
Microgaza rotella rotella
Microgaza vetula
Mirachelus corbis
Mirachelus clinocnemus
Gaza fischeri
Gaza watsoni
Euchelus guttarosea
Basilissa alta
Basilissa discula
Basilissa costulata
Lischkeia imperialis
"Solariella" tiara

TABLE 2. List of Temperate Northwest Atlantic Trochidae.

Calliostoma pulchrum
Calliostoma yucatecanum
Calliostoma psyche
Calliostoma sayanum
Solariella tubula
Solariella constricta
Echinogurges anoxia
Echinogurges tubulatus
Microgaza rotella inornata
Basilissa rhyssa

Four species (8%) may be termed Western North Atlantic, their ranges extending from the Carolina capes south through the Antillean arc. Species included are *Calliostoma roseolum, Solariella lacunella, Solariella lamellosa,* and *Dentistyla dentifera.*

The Amphi-Atlantic and Endemic Straits components comprise three species each (6%). *Margarites euspira, Calliotropis rhina,* and *Echinogurges rhysus* are known from the eastern Atlantic as well as the West Indies. Those species known only from the Straits of Florida are: *Calliostoma hendersoni, Margarites bairdi,* and *Gaza superba cubana.*

In examining the affinities of the shallow-water trochids, all species whose depth ranges fell either wholly or in part in the 0–180 m range were included. With this restriction, 26 species can be included, some of which also occur deeper than 180 m. These species fall into 3 groups: Tropical West Atlantic, Temperate Northwest Atlantic and Western North Atlantic. The shallow water forms show a very great tropical influence with 18 species (69%) assignable to the Tropical West Atlantic fauna. The Temperate Northwest Atlantic component contributes 4 species (15%) and the Western North Atlantic component comprises 3 species (12%), both significant contributions, although not very strong when compared to the tropical influence.

Eight species, all in the genus *Calliostoma (torrei, cubanum, atlantis, jeanneae, bigelowi, cinctellum, circumcinctum* and *orion*), were not relegated to a faunal group since all are known only from one or two specimens near Cuba. They may well belong in the tropical element, so the Tropical West Atlantic components could be as strong as 63% for the Jeep water forms and 73% for the shallow water species.

Ninety-five percent of the total trochid fauna of the Straits of Florida (65 species) is restricted to the Western North Atlantic, but most of the genera are rather widespread. This can be explained by applying the principles advanced by Ekman (1953). After the Atlantic basin had become a substantial feature, the original Tethyan fauna of the Atlantic was severely decimated by the late Miocene climatic cooling. When water temperatures once again reached tropical nature, the relict fauna reinvaded the Wesern North Atlantic and resulted in a unique fauna which was isolated on the east by the still widening Atlantic, and on the west by the Isthmus of Panama. Species such as *Solariella lacunella, S. lamellosa, Margarites euspira* and *M. bairdi* are probably remnants of the cooler water species which moved into the tropical areas during the glacial periods and were flexible enough to adapt to the elevated water temperatures of the post-Miocene period. From this we see a fauna that is 100% endemic in the shallow water species and 94% endemic in the deep water species.

Bathymetric analysis.—The Straits trochid fauna appears to fall into the bathymetric zones proposed by Ekman (1953) with some modification of the limits set for the bathyal zone. The littoral, or shelf, fauna extends from the tidal area down to about 150–180 m in the Straits. This is somewhat shallower than the 200 m boundary used by Ekman (1953), Bruun (1957) and Voss (1967), but in the trochid fauna at least there is a distinct break in the species composition occurring in the 150–180 m depths. The littoral trochid fauna of the Straits is composed of 26 species, and is dominated by the genus *Calliostoma* (14 species, 54%). Fifteen species which are here allocated to the littoral zone are also known from deeper than 180 m, but almost all of these records are probably fortuitous occurrences and only one species (*Solariella lamellosa*) can be considered a true inhabitant of both the littoral and bathyal zones. One other species, *Calliostoma psyche,* is known from shallow water in the northern part of its range, but has not been taken in the littoral of the Straits area.

The bathyal zone extends down to about 2000 m, or to about the 4°C isotherm. The majority of the trochid species in the Straits (39 species, 60%) are to be found in this zone. There seems to be a slight break at about 1000 m. This break is not a distinct change in species composition, but rather a rapid diminution in the number of species found at that depth. This may be an indication of a true faunal break as suggested by Ekman (1953). However, it may be an artificial break introduced by the fact that only the southwestern part of the Straits off Cuba is deeper than 1000 m and has been less thoroughly sampled than the shallower areas. Here, then, I am terming the depths from 180–1000 m the upper bathyal, and those from 1000–2000 m the lower bathyal. Only 3 species occur exclusively in the lower bathyal of the Straits: *Margarites euspira, Calliotropis actinophora* and *Echinogurges clavatus.*

Only 1 species (*Solariella pourtalesi*) is known from abyssal depths in the Straits, occurring as deep as 2350 m.

TABLE 3. Trochidae of the Lower Bathyal Zone.

Solariella pourtalesi
"Solariella" tiara
Margarites bairdi
Margarites euspira
Echinogurges clavatus
Echinogurges rhysus
Calliotropis actinophora
Gaza superba cubana
Gaza fischeri
Gaza watsoni
Basilissa alta
Basilissa discula
Basilissa rhyssa
Basilissa costulata

TABLE 4. Trochidae of the Upper Bathyal Zone.

Calliostoma psyche
Calliostoma hendersoni
Calliostoma schroederi
Calliostoma sapidum
Calliostoma sayanum
Solariella lamellosa
Solariella lubrica
Solariella multirestis
Solariella constricta
Solariella tubula
Solariella pourtalesi
"Solariella" tiara
Lischkeia imperialis
Dentistyla asperrima
Dentistyla dentifera
Mirachelus corbis
Calliotropis aegleis
Calliotropis rhina
Calliotropis calatha
Calliotropis lissocona
Echinogurges anoxia
Echinogurges rhysus
Echinogurges tubulatus
Gaza superba cubana
Gaza fischeri
Gaza watsoni
Basilissa alta
Basilissa costulata
Basilissa discula
Basilissa rhyssa

We see here a striking increase in the number of trochid species with increasing depth, at least to about 1000 m. Hickman (1974) noted this trend in a survey of the Tertiary and Recent faunal assemblages of the Pacific coast of North America. She also found that the increase in the number of species resulted in a disproportionate increase in the percent composition of the total fauna. There are indications that this holds true in the Straits area, but since it is very difficult to determine the total number of prosobranch species found in the Straits, it is impossible to quantify this trend at present. We can get a little better idea of the relative numbers of individuals and the importance of the trochids in this respect. Okutani (1968) reported that *Bathybembix aeola* (Watson) was the most numerous species in the bathyal fauna of Sagami Bay. The collections of the GERDA indicate the same importance of trochids in the bathyal fauna of the Straits, at least with respect to gross number of specimens. Of the almost 1800 specimens collected by the GERDA in the Straits, 342 (19%) are trochids, second in number only to the Turridae (385 specimens, 21.5%).

TABLE 5. List of Littoral Trochidae.

Calliostoma pulchrum
Calliostoma roseolum
Calliostoma yucatecanum
Calliostoma echinatum
Calliostoma jujubinum
Calliostoma brunneum
Calliostoma barbouri
Calliostoma fascinans
Calliostoma javanicum
Calliostoma adelae
Calliostoma euglyptum
Calliostoma marionae
Calliostoma orion
Calliostoma sarcodum
Solariella lucunella
Solariella lamellosa
Microgaza rotella rotella
Microgaza rotella inornata
Microgaza vetula
Mirachelus clinocnemus
Euchelus guttarosea
Lischkeia imperialis
Cittarium pica
Tegula fasciata
Tegula lividomaculata
Tegula excavata

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APPENDIX: STATION DATA

Ship	Sta. no.	Date	Position	Depth (m)	Gear
GERDA	4	5/4/62	25°49′N, 79°59.5′W	256	OT[1]
GERDA	23	6/20/62	25°32′N, 79°44′W	768	IKMT[1]
GERDA	56	8/28/62	25°31′N, 79°20′W	458	Lyman Dredge
GERDA	126	6/20/63	24°03′N, 81°49′W	805–741	OT
GERDA	128	6/20/63	23°49′N, 81°37′W	1391–1464	10′ OT
GERDA	129	6/20/63	23°46′N, 81°15′W	1281	10′ OT
GERDA	130	6/21/63	23°59′N, 81°10′W	1021	10′ OT
GERDA	132	6/21/63	24°26′N, 80°49′W	288	10′ OT
GERDA	134	6/21/63	24°30′N, 80°51′W	191	10′OT
GERDA	190	7/4/63	25°57′N, 78°07′W	732–896	OT
GERDA	226	1/23/64	24°40′N, 80°04′W	803	6′ OT
GERDA	289	4/3/64	24°11′N, 81°36′W	594–604	10′ OT
GERDA	300	4/5/64	26°16′N, 79°30′W	640	10′ OT
GERDA	357	8/25/64	25°28′N, 79°31′W	842	6′OT
GERDA	362	9/15/64	24°11′N, 81°39′W	631	10′OT
GERDA	365	9/15/64	24°11′N, 81°37′W	672	10′ OT
GERDA	366	9/15/64	24°12′N, 81°17′W	679–709	10′ OT
GERDA	368	9/15/64	24°03′N, 81°10′W	961–1016	16′ OT
GERDA	374	9/17/64	23°50′N, 81°37′W	1208–1241	16′ OT
GERDA	375	9/17/64	23°54′N, 81°27′W	1153–1190	16′ OT
GERDA	432	11/28/64	24°19′N, 82°29′W	188–199	10′ OT
GERDA	439	11/29/64	24°14′N, 82°29′W	583–565	10′ OT
GERDA	446	11/30/64	23°57′N, 82°32′W	988–1071	10′ OT
GERDA	448	12/1/64	23°54′N, 82°21′W	1135–1184	10′ OT
GERDA	449	12/1/64	23°55′N, 82°05′W	1373–1428	10′OT
GERDA	451	1/22/65	25°02′N, 80°11′W	199	10′ OT
GERDA	459	1/24/65	24°20′N, 82°52′W	187–192	10′ OT
GERDA	482	1/26/65	24°31′N, 80°51′W	205	2.5′ Scal. Dr.[1]
GERDA	483	1/27/65	24°30′N, 80°28′W	443	10′ OT
GERDA	484	1/27/65	24°33′N, 80°25′W	403	10′ OT
GERDA	524	3/3/65	26°17′N, 78°41′W	513–715	10′ OT
GERDA	598	4/15/65	24°47′N, 80°26′W	183	2.5′ Scal. Dr.
GERDA	606	4/15/65	25°18′N, 80°04′W	183	Brattstrom Dr.
GERDA	611	4/15/65	25°25′N, 80°05′W	119	Brattstrom Dr.
GERDA	636	6/30/65	26°04′N, 79°13′W	87	2.5′ Scal. Dr.
GERDA	693	7/21/65	26°34′N, 78°26′W	275–293	10′OT
GERDA	813	6/21/67	24°35′N, 80°37′W	201	Scallop Dr.
GERDA	815	6/22/67	24°08′N, 79°48′W	618	10′ OT
GERDA	824	7/7/67	25°37′N, 80°02′W	187–220	10′ OT
GERDA	830	7/7/67	25°40′N, 79°59′W	342	10′ OT
GERDA	834	7/10/67	25°15′N, 80°10′W	86–79	10′ OT
GERDA	837	7/11/67	24°29′N, 80°59′W	193	10′ OT
GERDA	839	7/11/67	24°23′N, 80°52′W	239	10′ OT
GERDA	847	8/2/67	25°49′N, 80°03.5′W	201–137	10′ OT
GERDA	854	8/25/67	25°27′N, 80°02′W	221	Pipe Dr.
GERDA	857	8/25/67	25°22′N, 80°03′W	194–186	10′ OT
GERDA	859	8/29/67	23°54′N, 81°57′W	1161–1200	10′ OT
GERDA	861	8/29/67	24°08′N, 81°36′W	514–558	10′ OT
GERDA	866	8/29/67	24°28′N, 81°09′W	187	10′ OT
GERDA	897	9/10/67	20°59′N, 86°24′W	293–210	10′ OT
GERDA	915	9/26/67	25°54′N, 78°12′W	439	10′ OT
GERDA	917	9/26/67	25°59′N, 78°12′W	658–704	10′ OT
GERDA	918	9/26/67	26°03′N, 78°05′W	814	10′ OT
GERDA	923	9/28/67	24°02′N, 77°34′W	1554–1573	10′ OT
GERDA	947	1/27/68	21°13′N, 86°25′W	284–247	Triangular Dr.
GERDA	959	1/31/68	23°25′N, 82°35′W	1830	10′ OT
GERDA	960	1/31/68	23°30′N, 82°26′W	1692–1697	10′ OT
GERDA	963	2/1/68	23°41′N, 82°16′W	1441–1454	10′ OT

APPENDIX (continued)

Ship	Sta. no.	Date	Position	Depth (m)	Gear
GERDA	964	2/1/68	23°46′N, 81°51′W	1390–1414	10′ OT
GERDA	965	2/1/68	23°45′N, 81°49′W	1394–1399	10′ OT
GERDA	966	2/2/68	24°10′N, 82°22′W	553–558	10′ OT
GERDA	967	2/2/68	24°15′N, 82°26′W	499–503	10′ OT
GERDA	968	2/2/68	24°17′N, 82°34′W	499–503	10′ OT
GERDA	969	2/2/68	24°18′N, 82°33′W	269–402	10′ OT
GERDA	970	2/2/68	24°24′N, 82°08′W	512	10′ OT
GERDA	974	2/3/68	24°22′N, 80°57′W	250–252	10′OT
GERDA	984	3/5/68	24°05′N, 80°20′W	192	Triangular Dr.
GERDA	985	3/5/68	24°06′N, 80°12′W	119	Triangular Dr.
GERDA	986	3/5/68	24°05′N, 80°19′W	189	10′ OT
GERDA	1008	6/14/68	24°03′N, 79°36′W	540–576	10′ OT
GERDA	1011	6/14/68	23°43′N, 79°32′W	291–311	10′ OT
GERDA	1015	6/15/68	23°34′N, 79°17′W	525–516	10′ OT
GERDA	1018	6/15/68	24°07′N, 79°28′W	556	10′ OT
GERDA	1035	2/26/69	24°34.7′N, 80°58.6′W	254–358	10′ OT
GERDA	1095	4/28/69	24°20′N, 82°56.5′W	229–274	10′ OT
GERDA	1096	4/28/69	24°19′N, 82°55′W	329–366	10′ OT
GERDA	1099	4/28/69	24°12.5′N, 82°50′W	622	10′ OT
GERDA	1106	4/29/69	24°02′N, 81°30′W	1706–1723	10′ OT
GERDA	1107	4/29/69	24°05′N, 81°20′W	1556–1709	10′ OT
GERDA	1111	4/30/69	23°51.9′N, 80°42.7′W	1080–1089	10′ OT
GERDA	1112	4/30/69	23°44′N, 81°14′W	2276–2360	10′ OT
GERDA	1312	3/31/71	26°38.4′N, 79°02.5′W	527–505	10′ OT
PILLSBURY	413	7/18/66	09°01.5′N, 76°53′W	1281–963	40′ OT
PILLSBURY	585	5/23/67	21°02′N, 86°29′W	567–570	10′ OT
PILLSBURY	598	3/15/68	21°07′N, 86°21′W	155–205	10′ OT
PILLSBURY	604	3/17/68	18°58′N, 87°28′W	970–988	Box Dr.
PILLSBURY	605	3/17/68	18°50.1′N, 87°31.5′W	695–772	10′ OT
PILLSBURY	606	3/17/68	18°45′N, 87°33′W	466–649	10′ OT
PILLSBURY	607	3/17/68	18°30′N, 87°37′W	715–787	10′ OT
PILLSBURY	610	3/18/68	17°02′N, 87°38.4′W	296–329	10′ OT
PILLSBURY	747	7/24/68	11°46′N, 67°05.7′W	1174–1108	10′ OT
PILLSBURY	754	7/26/68	11°36.9′N, 68°42′W	684–1574	10′ OT
PILLSBURY	776	7/29/68	12°13.3′N, 72°50′W	408–576	10′ OT
PILLSBURY	846	7/2/69	11°37.8′N, 60°37.4′W	658–1126	10′ OT
PILLSBURY	861	7/4/69	12°42′N, 61°05.5′W	18–744	10′ OT
PILLSBURY	874	7/6/69	13°11.2′N, 61°05.3′W	156–201	5′ Blake Tr.
PILLSBURY	903	7/9/69	13°44′N, 61°03.1′W	231–430	Triangular Dr.
PILLSBURY	904	7/9/69	13°45.5′N, 61°05.7′W	201–589	Scallop Dr.
PILLSBURY	905	7/9/69	13°46.3′N, 61°05.4′W	384–963	Scallop Dr.
PILLSBURY	919	7/12/69	16°05.3′N, 61°19.3′W	683–733	5′ Blake Tr.
PILLSBURY	929	7/15/69	15°29.5′N, 61°11.5′W	457–503	5′Blake Tr.
PILLSBURY	988	7/23/69	18°29.3′N, 63°24.6′W	686–723	5′ Blake Tr.
PILLSBURY	1225	7/6/70	17°42.5′N, 77°58′W	457–558	10′ OT
PILLSBURY	1255	7/14/70	17°18′N, 78′32′W	622–823	10′ OT
PILLSBURY	1256	7/14/70	17°27′N, 78°10′W	521–658	10′ OT
PILLSBURY	1261	7/15/70	17°13′N, 77°50′W	595–824	10′ OT
PILLSBURY	1262	7/15/70	17°21.4′N, 77°34.8′W	805–1089	10′ OT
PILLSBURY	1309	12/5/70	25°44.5′N, 79°50.0′W	311	10′ OT
COLUMBUS ISELIN	356		24°28.3′N, 77°29.5′W	1597	40′ OT
BLAKE	2		23°14′N, 82°25′W	1472	
BLAKE	12		24°34′N, 83°16′W	66	
BLAKE	20		23°02.5′N, 83°11′W	402	

APPENDIX (continued)

Ship	Sta. no.	Date	Position	Depth (m)	Gear
BLAKE	21		23°02′N, 83°13′W	525	
BLAKE	36		23°13′N, 89°16′W	154	
BLAKE	43		24°08′N, 82°51′W	620	
BLAKE	44		25°33′N, 84°35′W	986	
BLAKE	47		28°42′N, 84°40′W	587	
BLAKE	62		off Havana	146	
BLAKE	230	2/20/1879	13°13.3′N, 61°18.8′W	848	
BLAKE	299	3/10/1879	13°05′N, 59°39.7′W	256	
ALBATROSS	871		off Martha's Vineyard	210	
ALBATROSS	2135	2/27/1884	19°55′58″N, 75°47′07″W	457	Tangle bar
ALBATROSS	2150	4/9/1884	13°34′45″N, 81°21′10″W	699	Dredge & Tangle bar
ALBATROSS	2311	1/5/1885	32°55′N, 77°54′W	144	Large Blake Trawl
ALBATROSS	2312	1/5/1885	32°55′N, 77°54′W	161	Large Blake Trawl
ALBATROSS	2313	1/5/1885	32°53′N, 77°53′W	181	Large Blake Trawl
ALBATROSS	2314	1/5/1885	32°43′N, 77°51′W	291	Large Blake Trawl
ALBATROSS	2384	3/3/1885	28°45′N, 88°15′30″W	1719	Large Blake Trawl
ALBATROSS	2398	3/14/1885	28°45′N, 86°26′W	415	Large Blake Trawl
ALBATROSS	2415	4/1/1885	30°44′N, 79°26′W	805	Large Blake Trawl
ALBATROSS	2417	4/2/1885	33°18′30″N, 77°07′W	174	Large Blake Trawl
ALBATROSS	2594	10/17/1885	35°01′N, 75°12′W	293	Large Blake Trawl
ALBATROSS	2602	10/18/1885	34°38′30″N, 75°33′30″W	227	Large Blake Trawl
ALBATROSS	2644	4/9/1886	25°40′N, 80°00′W	353	Blake Dredge
ALBATROSS	2654	5/2/1886	27°57′30″N, 77°27′30″W	1207	Large Blake Trawl
ALBATROSS	2668	5/5/1886	30°58′30″N, 79°38′30″W	538	Large Blake Trawl
ALBATROSS	2751	11/28/1887	16°54′N, 63°12′W	1257	Large Blake Trawl
ALBATROSS	2754	12/5/1887	11°40′N, 58°33′W	1609	Large Blake Trawl
JOHNSON-SMITHSONIAN EXPEDITION	10	2/2/33	18°29′20″N, 66°05′30″W	220–293	9′ Tangle
JOHNSON-SMITHSONIAN EXPEDITION	67	2/23/33	18°30′12″N, 65°45′48″W	329–512	4′ Dredge
JOHNSON-SMITHSONIAN EXPEDITION	93	3/2/33	18°38′00″N, 65°09′30″W	640–732	3′ Dredge
JOHNSON-SMITHSONIAN EXPEDITION	94	3/2/33	18°37′45″N, 65°05′00″W	549–860	3′ Dredge
JOHNSON-SMITHSONIAN EXPEDITION	102	3/4/33	18°50′30″N, 64°43′00″W	165–914	35′ OT
JOHNSON-SMITHSONIAN EXPEDITION	104	3/7/33	18°30′40″N, 66°13′20″W	146–220	Oyster Trawl
ATLANTIS	1985		23°13′N, 81°22′W	704	
ATLANTIS	2963C	2/25/38	22°07′N, 81°08′W	375	35′ OT
ATLANTIS	2993	3/15/38	23°24′N, 80°44′W	1061	14′ Blake Trawl
ATLANTIS	2999	3/17/38	23°10′N, 81°29′W	265–421	10′ Blake Trawl

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[1] IKMT = Isaacs-Kidd Midwater Trawl; OT = Otter Trawl; Scal. Dr. = Scallop Dredge.

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APPAREIL GÉNITAL DE *CARINARIA LAMARCKI* (GASTROPODA HETEROPODA); STRUCTURE ET AFFINITÉS

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RÉSUMÉ

L'étude de *Carinaria lamarcki*, menée au moyen de méthodes histologiques, a permis de donner une première description de l'appareil génital femelle, de compléter les données antérieures relatives au mâle et de comparer cette espèce représentative des Carinariidae à d'autres types de Mésogastropodes.

L'appareil génital femelle est entièrement inclus dans la masse viscérale. L'ovaire, tubuleux et ramifié, se prolonge par un oviducte proximal à allure de gonade indifférenciée puis par un oviducte distal, simple conduit cilié. Le réceptacle séminal, qui fait suite, en est séparé par une valvule. Après avoir donné naissance à un caecum, il forme des circonvolutions, aborde les glandes annexes par leur extrémité antérieure et conflue avec elles en un carrefour commun à l'ensemble. Il est tapissé de hautes cellules dont l'aspect se modifie au contact des spermatozoïdes. La glande de l'albumine et la glande de la coque sont accolées latéralement l'une à l'une à l'autre. Chacune est refermée en caecum à l'arrière et s'ouvre à l'avant sur la cavité palléale. Leur tissu est formé d'un épithélium cilié doublé de faisceaux de cellules glandulaires. Les deux glandes sont sillonnées par des gouttières ciliées où s'opère le tri des oeufs au cours de l'élaboration des enveloppes puis du cordon ovigère. Une bourse copulatrice multifide se rattache au vagin. Cet appareil génital femelle présente plusieurs caractères anatomiques et histologiques identiques à ceux de *Pterotrachea.*

La spermatogénèse est caractérisée par des "cellules nourricières" au sens de Reinke (1912), qui ne contractent des rapports avec les spermatozoïdes que dans la vésicule séminale. L'appareil génital mâle ne diffère de celui des autres Mésogastropodes que par une migration de la prostate à l'intérieur de la masse viscérale. La prostate est formée de nombreux tubules débouchant sur une cavité unique; elle est traversée ventralement par le canal déférent qui s'ouvre dans la cavité palléale.

INTRODUCTION

L'appareil génital des Carinaires est très mal connu. Les seules données concernant la femelle résultent des observations de Gegenbaur (1855) qui, en examinant des animaux par transparence, reconnut l'ovaire, l'oviducte, le pore génital et deux organes annexes, l'un glandulaire, l'autre en ampoule. Les illustrations de Tesch (1949) et de Fretter & Graham (1962) n'apportent aucun complément à ce schéma. Les connaissances relatives au mâle sont plus avancées. Selon Tuzet (1936), la spermatogénèse est double mais la lignée atypique est abortive. Les voies génitales internes comportent une prostate (Gabe, 1965) et, comme chez les autres Hétéropodes, un appendice glandulaire est associé au pénis (Leuckart, 1853; Gegenbaur, 1855; Gabe, 1965). Enfin, les oeufs sont pondus en chapelets (Gegenbaur, 1855) et il existerait des spermatophores (Van der Spoel, 1972).

Or les Hétéropodes, auxquels appartiennent les Carinariidae, comportent deux autres familles, Atlantidae et Pterotracheidae, qui diffèrent sensiblement l'une de l'autre par l'organisation de leur appareil génital (Gabe, 1951, 1965, 1966; Thiriot-Quiévreux & Martoja, 1974, 1976) tout en présentant certains points communs avec les Mésogastropodes benthiques, en particulier les Littorines (Martoja & Thiriot-Quiévreux, 1975). Nous avons donc cherché à situer les Carinaires dans cet ensemble en étudiant l'appareil génital femelle de *Carinaria lamarcki* et en complétant les données relatives au mâle.

MATÉRIEL ET MÉTHODES

Toutes les Carinaires ont été récoltées à bord du Korotneff dans le plancton de la région de Villefranche-sur-Mer (Méditerranée occidentale) à l'exception d'un mâle juvénile qui provient d'une campagne océanographique effectuée par le N.O. Knorr (Woods Hole Oceanographic Institution) en Atlantique Nord.

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Les animaux ont été fixés *in toto* par le mélange de Halmi, soit directement, soit après mise en attente dans du formol salé. Ils ont été inclus à la paraffine, coupés et étalés en séries complètes.

Les méthodes suivantes ont été utilisées, seules ou combinées entre elles (voir Martoja & Martoja, 1967, pour l'exposé des techniques):

—coloration à l'azan de Heidenhain; trichrome de Prenant, variante de Gabe (topographie générale);
—Coloration au bleu de toluidine (répartition des acides nucléiques, métachromasie);
—réaction à l'acide periodique—Schiff (APS) (détection des composés oxydables par l'acide periodique et notamment des glucides);
—coloration au bleu alcian à pH 3,2, coloration de Ravetto au bleu alcian à pH 0,5-jaune alcian à pH 2,5 (étude des mucines acides sulfatées et carboxylées);
—réaction à l'alloxane—Schiff (détection globale des protéines).

L'étude anatomique a été réalisée à partir de reconstitutions graphiques de coupes sériées par les procédés de reconstruction projective et d'isolement graphique (voir Gabe, 1968 pour le détail des méthodes).

RÉSULTATS

Anatomie Microscopique

1. Nomenclature et topographie générale

La nomenclature de l'appareil génital des Gastéropodes diffère selon les auteurs et selon la position systématique des animaux. Le choix en devient donc difficile dès que l'organisation s'écarte d'un schéma classique. La terminologie de Ghiselin (1965), basée sur la morphologie fonctionnelle et applicable aux Prosobranches ou aux Euthyneures, devrait éliminer ces difficultés. Toutefois le découpage des glandes annexes femelles en trois unités ne correspond pas ici aux données anatomiques et le terme d'oviducte utilisé pour le canal de ponte des formes diauliques prête à confusion avec l'acception traditionnelle.

Nous inspirant de plusieurs auteurs (Fretter & Graham, 1962; Ghiselin, 1965; Franc, 1968), nous proposons pour *Carinaria* les désignations suivantes:

1° **pour l'appareil génital mâle,** spermiducte (= gonoducte coelomique) lui-même divisé en spermiducte prévésiculaire, vésicule séminale et spermiducte post-vésiculaire; prostate (= glande annexe = gonoducte palléal des Mésogastropodes à cavité palléale normalement développée); gouttière spermatique; appareil copulateur composé d'un pénis et d'un appendice glandulaire;

2° **pour l'appareil génital femelle,** oviducte proximal et oviducte distal (= gonoducte coelomique) caractérisés par leur structure histologique; réceptacle séminal et bourse copulatrice identifiés par la disposition des spermatozoïdes; glande de l'albumine et glande de la coque (= glandes annexes = gonoducte palléal des autres Mésogastropodes), définies d'après le trajet des oeufs; vagin et canal de ponte.

Les Carinaires sont gonochoriques. Dans les deux sexes, la gonade occupe la région dorsale du "nucleus," terme ancien qui désigne, dans ce groupe, la masse viscérale; les organes annexes sont situés à la base et le gonoducte coelomique traverse la glande digestive sur toute sa hauteur. Le spermiducte effectue un parcours légèrement oblique et s'accole à l'extrémité postérieure de la prostate. Le pore génital s'ouvre au fond et à droite de la cavité palléale. Une gouttière spermatique le relie à l'appareil copulateur, appendu sur le flanc droit du corps, au-dessous du nucléus. L'oviducte prend une direction presque horizontale, s'élargit en un réceptacle séminal et aborde les glandes annexes par leur extrémité antérieure; comme dans quelques autres espèces (voir Creek, 1951), la dénomination de réceptacle séminal s'appuie ici sur une donnée fonctionnelle. Une bourse copulatrice est rattachée au vagin. Le pore génital dédoublé est situé comme l'orifice mâle, au fond et à droite de la cavité palléale. Il se prolonge par deux gouttières jusqu'au sommet d'une papille qui n'existe pas chez le mâle.

2. Appareil génital mâle (Fig. 1)

L'emplacement du testicule est délimité par la paroi du corps, la glande digestive, l'intestin et le rein. Sa forme est celle d'une lentille biconvexe très régulière. Du centre de sa face ventrale émerge un court spermiducte prévésiculaire qui se dilate progressivement chez l'adulte pour faire place à une vésicule séminale. Celle-ci est un long tube, large et distendu qui, sous l'effet de la réplétion, peut décrire deux ou trois circonvolutions dans sa

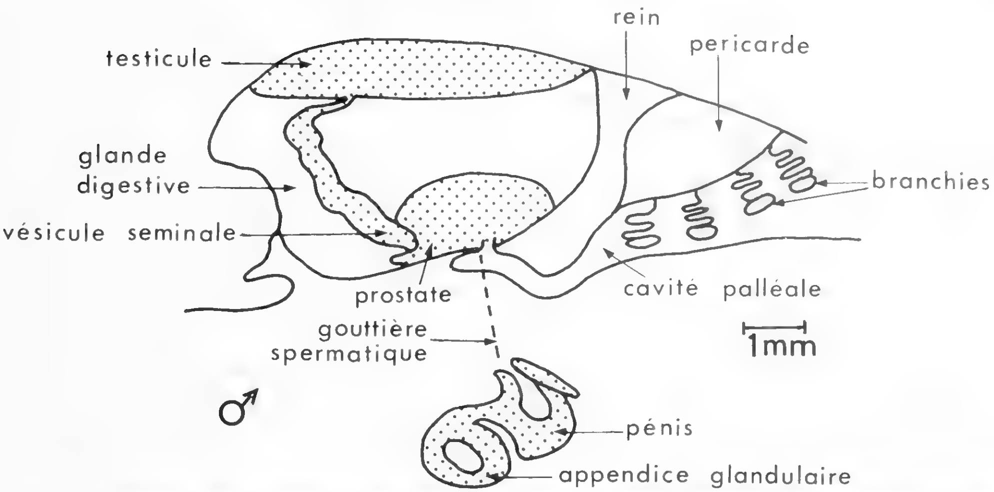

FIG. 1. Organisation de l'appareil génital mâle. Le "nucléus" (= masse viscérale) est représenté en coupe sagittale. Les connexions et orifices sont arbitrairement ramenés dans un même plan.

partie terminale. Le spermiducte post-vésiculaire est très court et englobé dans une échancrure latérale de la prostate. Il y débouche au niveau du tiers postérieur en formant une valvule. Chez l'animal impubère, aucune particularité anatomique ne permet d'identifier la future vésicule séminale: la division du spermiducte en trois segments repose donc uniquement sur des bases fonctionnelles, ce que confirme l'examen histologique.

Réduite chez le jeune, la prostate atteint chez l'adulte des dimensions voisines de celles du testicule. C'est une glande oblongue, pointue à l'avant, bifide à l'arrière, les deux branches de la fourche enserrant les circonvolutions distales de la vésicule séminale. Avant la maturité génitale, elle se présente comme un sac vide, à peine lobé. A la puberté, les invaginations de la paroi qui délimitaient les lobes se multiplient et progressent à l'extérieur et à l'intérieur de l'organe. Ce processus aboutit à la formation de tubes jointifs rayonnant autour d'une cavité centrale restreinte par rapport à celle de l'animal impubère.

L'orifice génital se présente comme une fente transversale bordée de deux lèvres. La lèvre antérieure est raccordée au toit de la cavité palléale. La lèvre postérieure se prolonge par deux bourrelets tégumentaires saillants et parallèles qui délimitent la gouttière spermatique et réalisent la jonction entre la prostate et le pénis. A ce dernier, est accolé un appendice glandulaire, dépourvu de connexion anatomique avec le reste du système génital, doté d'un orifice unique et indépendant.

3. Appareil génital femelle (Fig. 2)

Par son emplacement, sa forme et son volume, l'ovaire est identique au testicule. Le départ de l'oviducte se situe, de la même façon, au centre de sa face ventrale.

L'oviducte est un conduit étroit, de calibre uniforme qui, après avoir traversé la glande digestive, longe la face dorsale de la glande de l'albumine sans s'y raccorder. Il dépasse l'extrémité antérieure de cette glande et débouche, en formant une valvule, dans un segment dilaté qui fonctionne comme réceptacle séminal. Cette dilatation est piriforme et un caecum effilé s'en détache à proximité de la valvule. Son diamètre diminuant peu à peu, le réceptacle séminal devient un long tube qui s'enroule en un peloton serré situé en avant des glandes annexes. La partie terminale du tube se dégage de la masse des circonvolutions, se dirige vers l'arrière, s'enfonce dans une dépression latérale de la glande de l'albumine et fusionne avec un canal qui, à ce niveau, est commun aux deux glandes annexes. L'oviducte proximal, l'oviducte distal et le réceptacle séminal sont identifiables dès le stade impubère, contrairement aux segments du gonoducte mâle.

La glande de l'albumine et la glande de la coque sont grossièrement fusiformes. Elles sont disposées côte à côte et leur grande axe est parallèle à celui de l'animal. Chacune s'ouvre à l'avant et se referme en caecum à l'arrière. Elles ne sont tout à fait indépend-

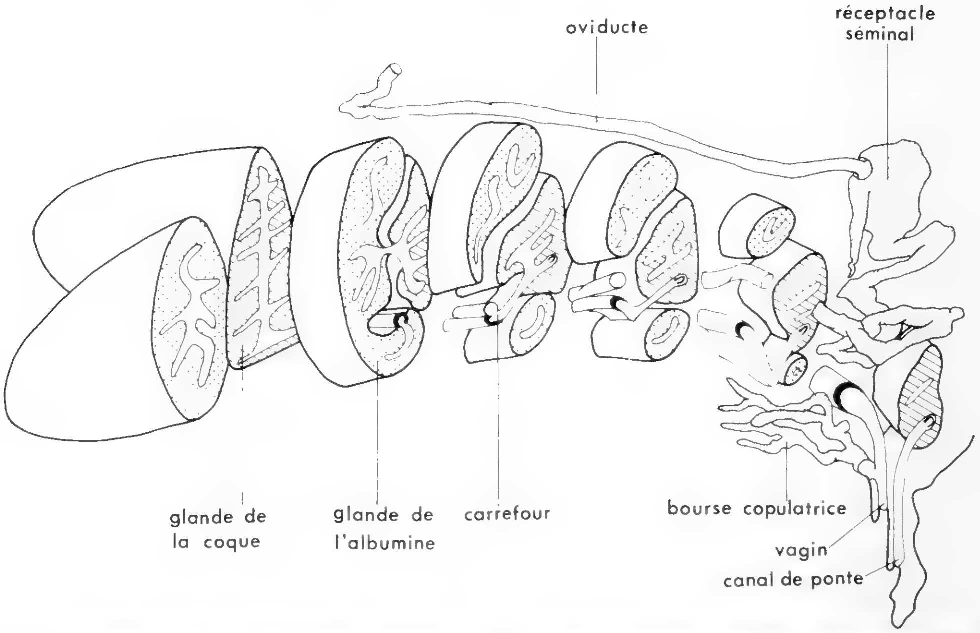

FIG. 2. Diagramme des voies génitales femelles. Pour la clarté du schéma, quelques modifications ont été apportées: plus d'importance a été donnée à la région du carrefour; les deux glandes annexes ont été séparées dans leur zone antérieure; les circonvolutions du réceptacle séminal ont été dissociées des diverticules de la bourse copulatrice.

antes l'une de l'autre que dans leur région postérieure. Dans leur région antérieure, elles sont à la fois imbriquées et desservies par un canal unique aplati dorso-ventralement et muni de deux gouttières ciliées latérales, diamétralement opposées. La gouttière gauche correspond à la glande de la coque; la gouttière droite correspond à la glande de l'albumine et reçoit le réceptacle séminal, d'où l'existence d'un carrefour où se rejoignent les divers segments. En se plissant et en se subdivisant, le canal commun donne naissance à des fentes qui se prolongent vers l'arrière et forment les cavités des glandes. Les deux gouttières ciliées se subdivisent de la même façon si bien que ces cavités sont sillonnées par de multiples gouttières parallèles. En avant du carrefour, le canal s'incurve en un V de plus en plus fermé puis se scinde en deux conduits où s'engagent les gouttières latérales. Le conduit gauche, issu de la glande de la coque, devient un canal de ponte. L'autre, plus court, constitue un vagin. A quelque distance de l'orifice génital, un diverticule multifide, qui joue le rôle de bourse copulatrice, se rattache au vagin; ses caeca sont intimement mêlés aux circonvolutions du réceptacle séminal mais n'ont aucune communication avec elles.

Une telle organisation implique qu'une partie des spermatozoïdes reçus du conjoint et les oeufs, aux divers stades de leur maturation, empruntent les mêmes voies, le tri en étant assuré par les gouttières ciliées du canal commun et des cavités qui en dérivent. A l'intérieur de chaque glande, les oeufs accomplissent un parcours complexe qui part du carrefour et y revient. Quant aux spermatozoïdes, ils sont répartis entre deux réservoirs dont l'un est intégré au tractus génital et l'autre, anatomiquement individualisé. Il serait intéressant de savoir s'ils se divisent d'emblée en deux lots ou si tous passent par la bourse copulatrice pour y acquérir leur capacitation, par exemple, avant de s'engager dans le réceptacle séminal. La disposition topographique permet seulement de constater que les oeufs ne peuvent rencontrer les spermatozoïdes emmagasinés dans la bourse copulatrice.

Histologie

1. Appareil génital mâle

Les travaux de Tuzet (1936) et de Gabe (1965) comportent la description complète de la spermatogénèse et du système génital mâle. Nous n'envisageons donc ici, que quelques points qui, selon nos observations, doivent être reconsidérés.

a) **Spermatogénèse:** certains secteurs des tubes séminifères sont occupés par des cellules différentes des cellules germinales (Fig. 3D). Ces éléments se distinguent des spermatozoïdes bien avant la puberté, non seulement par leur noyau plus gros et plus clair mais par leur cytoplasme plus abondant et nettement APS-positif. Chez l'adulte, leur noyau ne s'est pas modifié mais leur cytoplasme s'est accru: elles sont ellipsoïdes, mesurent 10 µm sur 8 environ et sont pourvues d'un noyau sphérique parfaitement normal d'environ 6 µm de diamètre. La chromatine dessine un réseau lâche et il y a

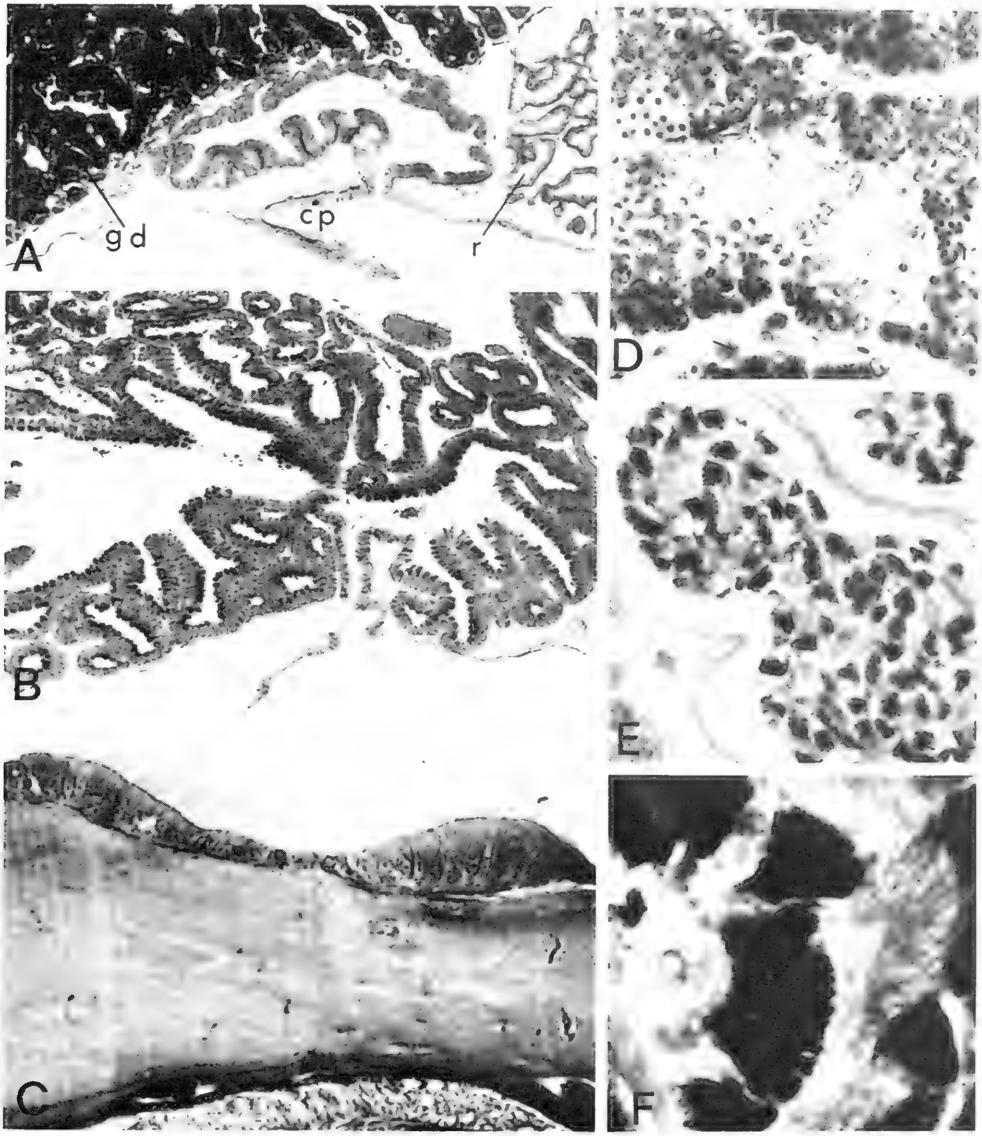

FIG. 3. Appareil génital mâle. A. Coupe sagittale de la prostate d'un mâle infantile (APS-hématoxyline, ×75) (cp, cavité palléale; gd, glande digestive; r, rein). B. Coupe sagittale de la prostate d'un mâle adulte (même technique; même grandissement). C. Gouttière spermatique (Bleu alcian-APS-hématoxyline; ×560). D. Coupe de testicule (APS-hématoxyline; ×560). Remarquer au centre, les "cellules nourricières." E. Coupe de vésicule séminale (APS-hématoxyline; ×150). F. Groupe de spermatozoïdes entourant une "cellule nourricière" dans la vésicule séminale (APS-hématoxyline; ×1400).

un ou deux petits nucléoles. Après réaction à l'APS, le cytoplasme est coloré en rose pâle et contient quelques minuscules grains très rouges. La paroi elle-même est fortement réactive et, de ce fait, très visible.

Les cellules ellipsoïdes suivent le même trajet que les spermatozoïdes et parviennent intactes dans les voies génitales. Dans le spermiducte prévésiculaire, elles sont mêlées aux spermatozoïdes qui, eux-mêmes, forment des pelotons. Dans la vésicule séminale, une organisation précise s'établit: tous les spermatozoïdes se regroupent en faisceaux autour des éléments en question, la tête dirigée vers eux (Fig. 3E). A partir de ce moment, les noyaux des cellules ellipsoïdes deviennent vésiculeux, les grains intracytoplasmiques se résorbent et la paroi cellulaire perd son caractère APS-positif (Fig. 3F). Aucune image de cytolyse complète n'a, toutefois, été observée. Sans doute en raison d'un transit rapide, ni ces cellules, ni les spermatozoïdes n'ont été vus dans la prostate. Il ne nous a donc pas été possible de déterminer à quel moment cesse leur association. Seuls les spermatozoïdes ont été retrouvés dans les voies génitales des femelles fécondées.

b) **Voies génitales:** une valvule, constituée aux dépens de la zone terminale du spermiducte post-vésiculaire, est interposée entre ce segment et la prostate. A ce niveau, les cellules épithéliales deviennent plus hautes et sont dépourvues des grains de pigment noir très abondants dans le reste du spermiducte; leur ciliature est aussi plus développée. L'épithélium repose sur une basale très épaisse et plissée et, surtout, il est entouré d'un important manchon de fibres conjonctives qui n'a d'équivalent ni autour du spermiducte proprement dit, ni autour des tubes prostatiques.

Au stade juvénile, la paroi du sac prostatique est faite d'un épithélium simple, non cilié (Fig. 3A). L'approche de la puberté se manifeste d'abord au niveau des noyaux qui, alternativement, s'allongent ou au contraire s'arrondissent, Les premiers grains de sécrétion n'apparaissent que plus tard. La prostate de l'adulte est une glande ramifiée (Fig. 3B). Chaque tube est constitué d'un épithélium pseudo-stratifié comportant des cellules ciliées peu visibles et de grandes cellules glandulaires dont les caractères ont été décrits par Gabe. Les sécrétions déversées par les tubes sont collectées dans une cavité centrale où s'ouvrent ventralement d'une part la valvule spermiductaire, d'autre part la fente qui débouche sur la cavité palléale. Entre les deux s'étend une gouttière qui représente le canal déférent. Les cellules ciliées y deviennent prépondérantes par rapport aux cellules glandulaires; elle est doublée extérieurement d'une tunique conjonctive prolongeant le manchon de la valvule. Dans l'épithélium qui borde la fente, les cellules ciliées restent très développées et les cellules glandulaires caractéristiques des tubes prostatiques sont remplacées par des mucocytes. Sur le plan fonctionnel, il paraît évident que les spermatozoïdes sont draînés de la valvule à la fente, par la canal déférent, sans circuler dans les tubes glandulaires où, d'ailleurs, on n'en trouve jamais. C'est durant ce court trajet qu'ils se mêleraient aux sécrétions prostatiques.

La gouttière spermatique est délimitée par deux bourrelets édifiés à partir de l'épithélium de surface. Chacun est formé de hautes cellules pourvues d'une ciliature très développée (Fig. 3C).

2. Appareil génital femelle

a) **Ovaire:** comme le testicule, l'ovaire (Fig. 4A) est dépourvu de thèque conjonctive mais ne présente pas la moindre imbrication avec les tissus voisins. Comme le testicule également, il est constitué de tubes convergeant en direction d'un point médio-ventral. Les tubes sont séparés par de nombreuses cellules conjonctives libres chez l'animal impubère alors qu'ils sont jointifs chez l'adulte. Chaque tube comporte une *tunica propia* sur laquelle repose l'épithélium germinatif. Le déroulement de l'oogénèse est conforme au schéma classique (voir Raven, 1972). Il y a lieu de noter seulement que toute activité mitotique des oogonies semble cesser chez l'animal parvenu au stade de l'ovulation, qu'il n'existe pas de cellules folliculaires mais quelques petites cellules coniques qui pourraient être des cellules nourricières et que l'oocyte en prévitellogénèse est doté d'un "corps vitellin" important; la nature de ce dernier reste à préciser.

Lors de l'ovulation, l'oocyte est une cellule légèrement amiboïde d'une cinquantaine de μm de diamètre, peu chargée en vitellus. La vésicule germinative, au contour dentelé, renferme un unique nucléole hétérogène comportant une sphère dense excentrique. Les plaquettes vitellines sont très petites et leur réactivité à l'égard de l'APS est particulièrement intense.

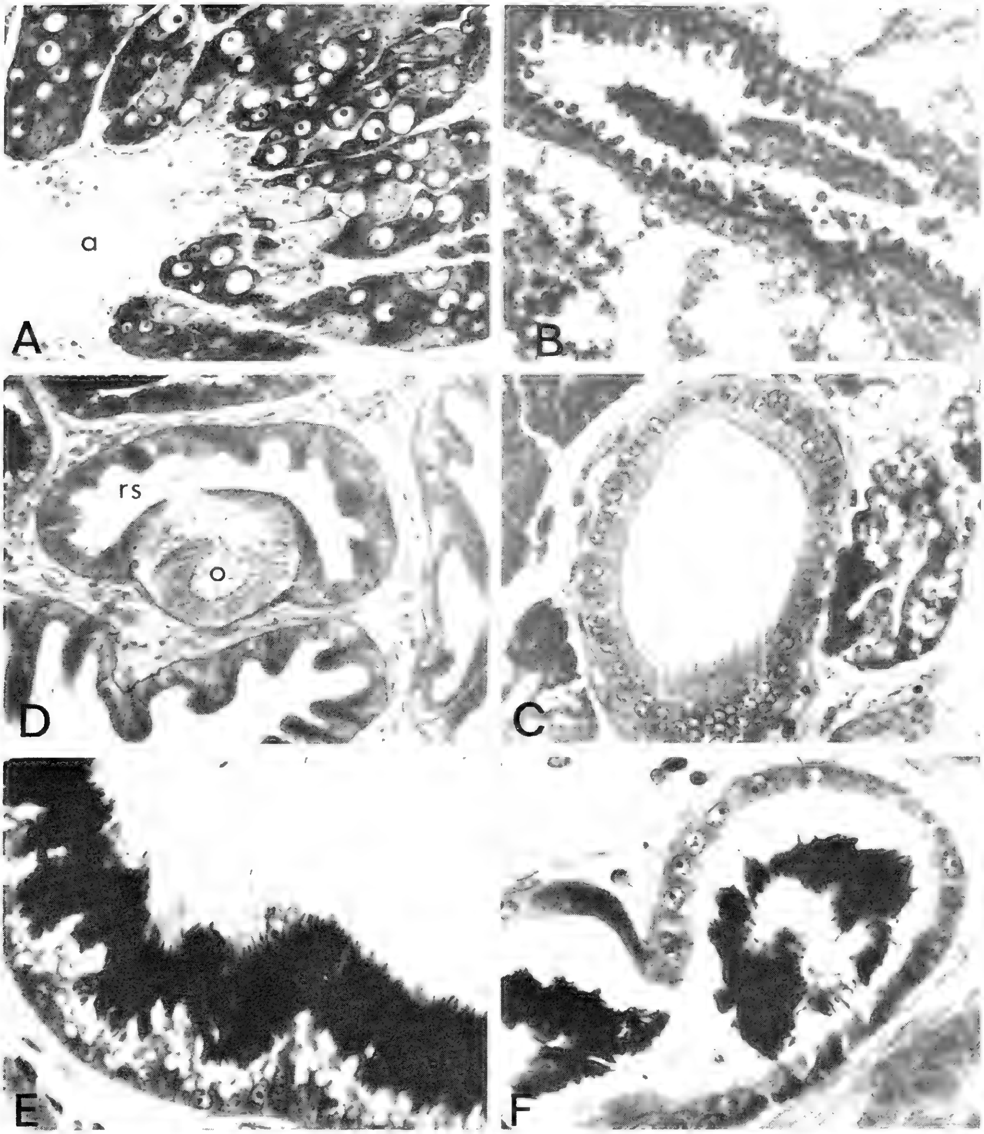

FIG. 4. Appareil génital femelle. A. Coupe de l'ovaire (trichrome de Prenant-variante de Gabe; ×140) (a, artère génitale). B. Oviducte proximal (APS-hématoxyline; ×400). C. Oviducte distal (trichrome de Prenant-variante de Gabe; ×400). D. Valvule séparant l'oviducte distal (o) du réceptacle séminal (rs) (APS-hématoxyline; ×200). E. Réceptacle séminal (trichrome de Prenant-variante de Gabe; ×560). Remarquer l'agencement des spermatozoïdes le long de la paroi. F. Bourse copulatrice (APS-hématoxyline; ×560). Remarquer l'agencement différent des spermatozoïdes.

b) **Oviducte:** l'examen histologique impose de diviser l'oviducte en deux segments. L'oviducte proximal est constitué d'une musculeuse externe assez importante qui s'épaissit peu à peu à partir de l'ovaire, d'une tunique conjonctive moyenne et d'une rangée continue de cellules internes (Fig. 4B). Celles-ci ne sont pas ciliées. Elles sont arrondies et, de ce fait, disjointes. Caractérisées par un rapport nucléoplasmique très élevé, elles ressemblent de près aux gonocytes si bien que ce segment semble en réalité n'être qu'un prolongement inactif de l'ovaire.

Sans aucune transition, l'oviducte proximal fait place à l'oviducte distal dont la structure est différente (Fig. 4C). Les fibres musculaires moins nombreuses et les fibres conjonctives, au contraire plus nombreuses, sont mêlées. Cette tunique musculo-conjonctive entoure un épithélium cylindrique cilié banal. Les cellules à allure de gonocytes disparaissent totalement.

Selon toute vraisemblance, le mode de propulsion des oeufs change à partir de l'oviducte distal, les courants ciliaires prenant le relai du péristaltisme qui, d'après l'allure de la musculeuse, se manifesterait dans l'oviducte proximal.

c) **Réceptacle séminal:** l'oviducte pénètre à l'intérieur du réceptacle séminal et les épithelium des deux segments s'accolent par leur base pour former une valvule (Fig. 4D). Le tissu conjonctif n'entre pas dans la constitution de cette dernière qui est donc très différente de la valvule prostatique.

La paroi du réceptacle séminal, faite d'une tunique musculo-conjonctive et d'un épithélium, entoure une lumière très vaste au contour festonné. L'épithélium est, en effet, marqué de plis très réguliers formés par l'allongement de certains groupes de cellules. Mise à part leur différence de hauteur, toutes ces cellules sont identiques. Elles portent une courte ciliature et sont dépourvues de sécrétions figurées. Chez le jeune, leur zone apicale renferme de petits grains de pigment noir qui ne sont plus visibles chez l'adulte. Au contact des spermatozoïdes, les cellules épithéliales subissent des modifications qui se traduisent, sur pièces fixées, par l'apparition de "vacuoles" (Fig. 4E). Le caecum présente une structure proche de celle de l'organe principal. Toutefois, la lumière en est plus réduite. Enfin, dans le prolongement rectiligne qui rejoint le canal commun, il n'y a plus de plis épithéliaux. Les cellules cubiques, très régulières, ne renferment ni inclusions ni "vacuoles" mais portent une ciliature très développée (Fig. 6B).

Chez la femelle fécondée, les spermatozoïdes sont alignés perpendiculairement à l'épithélium du réceptacle séminal. Les têtes sont dirigées vers celui-ci et sont en contact étroit avec lui. De tels alignements sont rares dans le prolongement rectiligne qui apparaît plutôt comme une région de transit. Quant au caecum, il reste constamment vide. Au moment de la ponte, les oeufs traversent le réceptacle séminal. Les images les montrant entourés de spermatozoïdes libres dans la lumière s'observent surtout dans le prolongement rectiligne et c'est probablement à ce niveau que s'opère la fécondation (Fig. 6B).

d) **Bourse copulatrice:** la bourse copulatrice (Fig. 5B) diffère sensiblement du réceptacle séminal. Dans la tunique musculo-conjonctive qui entoure le canal principal et les canaux secondaires de cet organe ramifié, les fibres musculaires sont beaucoup plus nombreuses qu'autour du réceptacle séminal. Cette tunique est plus réduite à l'extrémité borgne des diverticules. L'ensemble est tapissé d'un épithélium cilié (Fig. 4F). Selon les individus, les cellules sont aplaties ou, au contraire, étirées en hauteur mais, en aucun cas, on ne remarque ni sécrétions, ni "vacuoles" signalétiques de réactions cellulaires.

Les spermatozoïdes se trouvent soit en désordre dans la cavité, soit à proximité de l'épithélium. Leur alignement est alors moins rigoureux que dans le réceptacle séminal et surtout, il ne s'établit aucun contact entre eux et la paroi de l'organe.

e) **Glandes annexes:** les deux volumineuses glandes annexes ne sont séparées des tissus voisins par aucune thèque conjonctive. Elles offrent, sur coupes, un aspect massif, leurs cavités étant réduites à d'étroites fentes dont la disposition est extrêmement précise (Figs. 5A à C). En section transversale, la lumière de la glande de la coque est bipectinée par rapport à un axe dorsoventral; des fentes limitées par un simple épithélium alternent avec des fentes associées du parenchyme glandulaire. L'organisation de la glande de l'albumine apparaît mieux en section sagittale. Les fentes, symétriques par rapport à un axe longitudinal, sont alternativement courtes et longues; toutes sont associées à du parenchyme glandulaire. Les extrémités de toutes les fentes sont différenciées pour former des gouttières ciliées. Chez les femelles fixées en période de ponte, c'est à l'intérieur de ces gouttières que se trouvent la majorité des oeufs (Fig. 6).

Plusieurs tissus concourent à l'édification des glandes annexes. Ils sont les mêmes dans les deux cas. Leur répartition dans l'espace est différente mais également rigoureuse. Comme pour les fentes, il existe une symétrie et une périodicité remarquables.

L'épithélium pavimenteux forme le canal commun et certaines fentes de la glande de la coque. Il borde l'axe longitudinal de la glande de l'albumine et l'axe vertical de la glande de la coque. Ses cellules ont environ 5 μm de

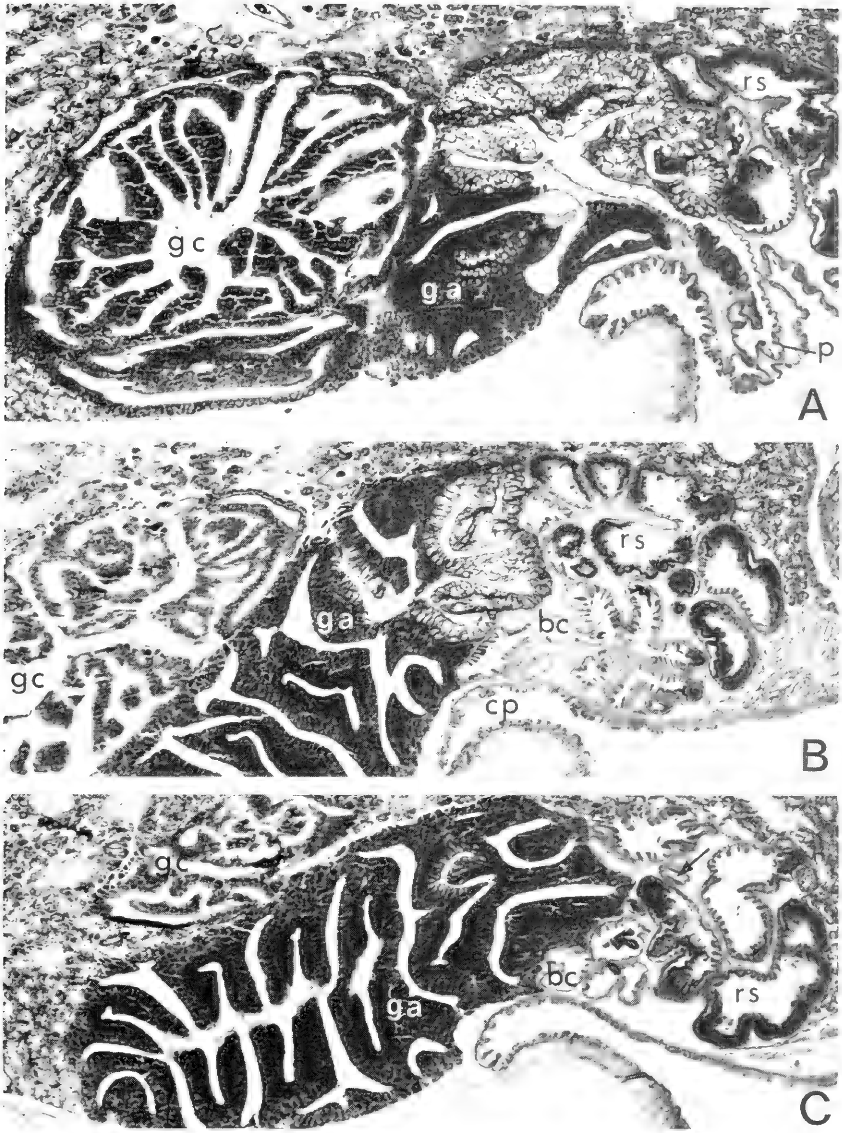

FIG. 5. Appareil génital femelle. A, B, C. Coupes parasagittales de la base de la masse viscérale (bleu alcian-APS-hématoxyline; ×35) (bc, bourse copulatrice; cp, cavité palléale; ga, glande de l'albumine; gc, glande de la coque; p, papille; rs, réceptacle séminal).

haut, reposent sur une basale bien visible, portent une ciliature assez longue mais peu dense et renferment parfois de minuscules grains naturellement colorés en ocre. Cet épithélium se distingue très tôt des autres régions: chez l'animal impubère, il est cubique, non cilié et doublé d'une basale très épaisse.

Le tissu glandulaire borde toutes les fentes dans la glande de l'albumine et la majorité d'entre elles dans la glande de la coque.

Avant la puberté, ce tissu est représenté par un épithélium simple, cylindrique non cilié, riche en cellules toutes identiques et caractérisées par une très haute teneur en ARN. Ultérieurement, certaines cellules deviennent piriformes et s'étirent de telle sorte que la partie renflée qui contient le noyau s'enfonce sous la couche cellulaire superficielle tandis que l'apex garde le contact avec la lumière. Chez l'adulte, le tissu glandulaire est formé d'un épithélium cilié associé à des faisceaux de cellules sous-jacentes; celles-ci sont pourvues de prolongements qui traversent l'épithélium et déversent leurs sécrétions directement dans la lumière (Fig. 6C et D).A l'échelle cellulaire les éléments glandulaires se présentent sous deux aspects. Certaines cellules glandulaires ont un volumineux noyau et un ergastoplasme très développé. Les sécrétions, indécelables dans le corps cellulaire au microscope photonique, ne sont visibles que dans le prolongement cytoplasmique, sous forme de petits grains toujours individualisés, fortement APS-positifs et dépourvus de protéines histochimiquement

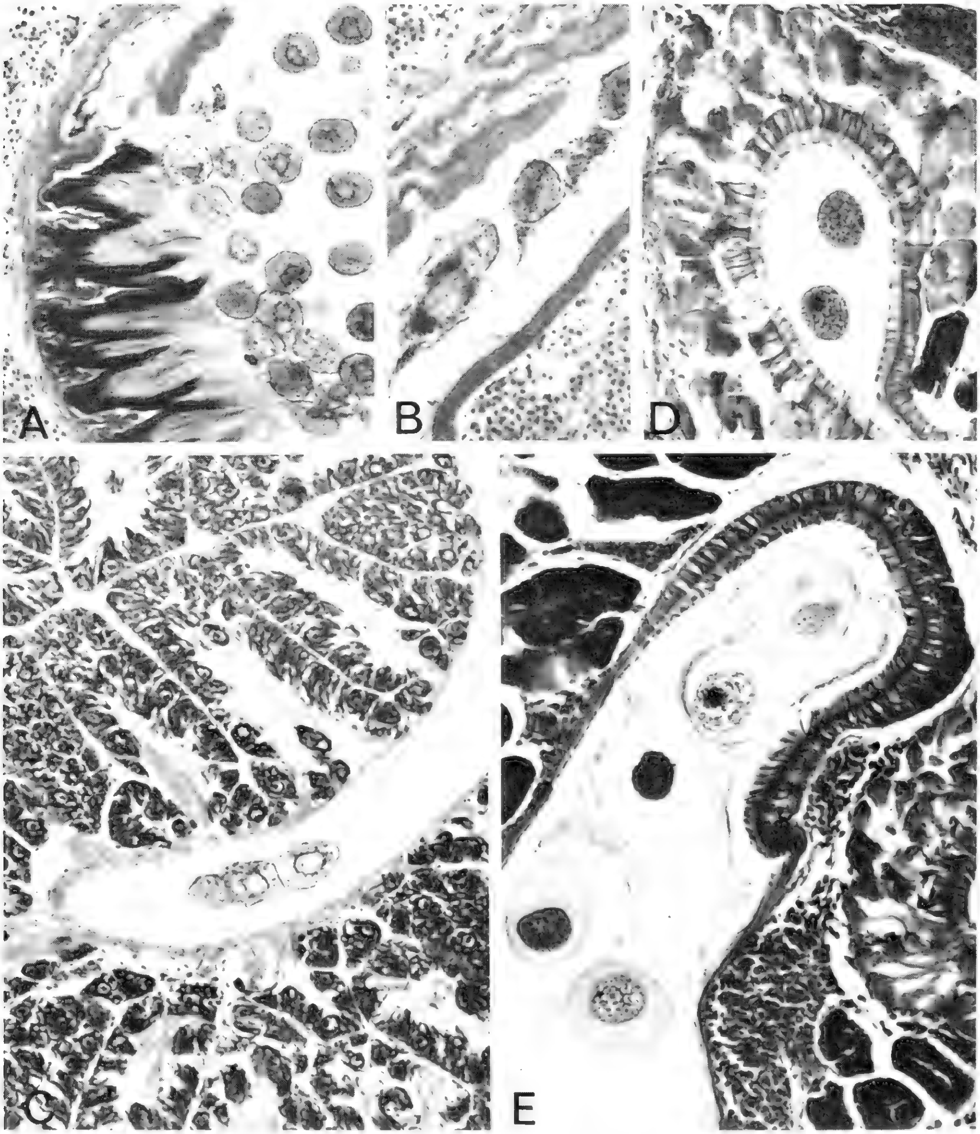

FIG. 6. Evolution de l'oeuf dans les voies génitales femelles (A à E, trichrome de Prenant-variante de Gabe; ×140). A. Oocytes traversant la zone dilatée du réceptacle séminal après l'ovulation. B. Oocytes entourés de spermatozoïdes dans le segment rectiligne du réceptacle séminal. C. Oeufs fécondés abordant la zone muqueuse de la glande de l'albumine. D. Oeufs pourvus de leurs enveloppes dans la zone muqueuse de la glande de la coque. E. Cordon ovigère dans la zone dorsale de la glande de la coque.

décelables. Ceux de la glande de l'albumine sont légèrement carboxylés. Les autres cellules glandulaires ont un noyau plus réduit, souvent frippé. Le cytoplasme est masqué par les sécrétions qui occupent à la fois le corps cellulaire et le prolongement. Ces sécrétions ont, dans les deux glandes, une allure spongieuse ou floconneuse; elles sont faiblement APS-positives et riches en groupements sulfatés. Il s'agit donc de mucoytes typiques élaborant des mucines très acides.

Les gouttières ciliées résultent d'une modification des cellules épithéliales qui deviennent plus hautes (30 à 40 μm sur les bords, 20 μm au fond de la concavité) et qui acquièrent une puissante ciliature (15 μm) (Fig. 6E). Lorsqu'elles sont coupées transversalement, les gouttières ont toujours un contour arrondi bien qu'elles ne soient doublées d'aucune assise conjonctive. La plupart sont entourées de faisceaux de cellules glandulaires mais celles qui prolongent les épithéliums pavimenteux, dans la glande de la coque, sont presque partout constituées d'un épithélium simple.

Enfin des fibrocytes et des cellules amiboïdes comblent les espaces laissés libres par les autres tissus. Chez les animaux de grande taille, ces éléments deviennent extrêmement abondants.

Les oeufs s'engagent d'abord dans les plis muqueux de la glande de l'albumine. Leur aspect y est identique à celui des oocytes contenus dans l'oviducte ou le réceptacle séminal (Fig. 6D). Dans les autres plis de cette glande, les grains de sécrétions viennent s'accoler individuellement autour de chaque oeuf; ils conflueront plus tard en une masse homogène aux limites imprécises. Dans la glande de la coque, trois phénomènes se produisent successivement: les sécrétions diffuses, élaborées au moins en partie dans la glande de l'albumine, se condensent si bien que l'épaisseur de l'enveloppe se réduit de 30 μm à 7 μm environ; ensuite, une très fine pellicule intensément colorable se dépose à son tour sur cette première enveloppe (Fig. 6C); enfin, une sécrétion lâche et floconneuse enrobe plusieurs oeufs alignés, les solidarisant ainsi en chapelets (Fig. 6E). Les aspects correspondant aux phases de l'élaboration des membranes s'observent à tous les niveaux de la glande de la coque, ce qui traduit la complexité du trajet parcouru par les oeufs. Il en résulte que, en l'absence d'étude histochimique détaillée, le lieu d'édification des différentes enveloppes de l'oeuf n'a pu être précisé.

f) **Papille:** la papille n'est qu'une excroissance banale soutenue par un tissu conjonctif lâche et recouvert d'un tégument identique à celui de la cavité palléale (Fig. 5A). Les deux gouttières qui sillonnent sa surface sont revêtues d'un épithélium cylindrique cilié, doublé d'assez nombreuses fibres conjonctives associées en réseau.

DISCUSSION

Appareil génital mâle

Certaines de nos observations sur le déroulement de la spermatogénèse et la structure des voies génitales diffèrent de celles de nos devanciers. Ainsi, la notion de lignée atypique abortive introduite par Tuzet (1936) doit être nuancée. En effet, les cellules distinctes de la lignée germinale typique contractent des rapports particuliers avec les spermatozoïdes. Le fait que ces rapports ne s'établissent que dans la vésicule séminale impose également de les distinguer des cellules de Sertoli bien connues chez divers Gastéropodes. Les cellules ellipsoïdes de la Carinaire sont, en réalité, très comparables à celles qui ont été décrites sous le nom de "nurse-cells" chez *Littorina* spp. par Reinke (1912) puis Linke (1933). L'interprétation de ces cellules "nourricières" est loin d'être évidente comme le montre l'analyse de Roosen-Runge (1977). Leur extrême rareté parmi les Mollusques accentue l'intérênt d'une similitude entre la Carinaire et les Littorines.

C'est certainement à des défectuosités du matériel examiné qu'il faut attribuer certains points de la description de Gabe (1965) que nous ne confirmons pas et qui concernent la structure de la prostate, la position de l'orifice génital et la gouttière spermatique. Cette description repose, en effet, sur l'observation de coupes parasagittales (Gabe, 1965: 1035) alors que l'examen de coupes sagittales est indispensable à la compréhension du système. Les rectifications que nous apportons montrent que l'appareil génital mâle de *Carinaria lamarcki* présente une organisation tout à fait classique de Prosobranche Mésogastropode. La persistance de caractères primitifs comme l'ouverture de la prostate sur la cavité palléale et la présence d'une gouttière spermatique également ouverte le rapproche d'un type bien connu, par exemple chez les Littorines. Seule apparaît inhabituelle la position de la prostate à l'intérieur de la masse viscérale et non au toit de la cavité palléale. Cette migration peut être due à la réduction de la cavité palléale, caractéristique des Carinariidae. Néanmoins, il est remarquable que l'organe soit séparé du spermiducte par une valvule alors que ce dispositif est inséré d'ordinaire entre le spermiducte et le segment rénal des voies génitales, comme le souligne Purchon (1968). Des recherches embryologiques devraient donc déterminer si la prostate des Carinaires est bien l'homologue du gonoducte palléal des autres Prosobranches. La structure de cette prostate est d'ailleurs assez rare et rappelle, dans une certaine mesure, celle de *Bythinia* où les tubes prostatiques s'ouvrent séparément dans un canal unique (Lilly, 1953). Enfin, l'appareil copulateur, tel qu'il est décrit par Gabe (1965) et que nous l'avons observé nous-mêmes, présente plusieurs points communs avec celui des Littorines. Ce rapprochement avait déjà été fait pour d'autres Hétéropodes (Martoja & Thiriot-Quiévreux, 1975).

Appareil génital femelle

La morphologie de l'ovaire, le déroulement de l'oogénèse sont conformes au schéma classique (voir Raven, 1972) et l'aspect de l'oviducte proximal appuie l'opinion de Linke (1933) selon laquelle cette zone du tractus génital ne serait, chez les Prosobranches, qu'un segment indifférencié de la gonade.

L'organisation des voies génitales proprement dites est, au contraire, très particulière à plusieurs égards. Le gonoducte "palléal" a, comme chez le mâle, subi une migration vers la masse viscérale mais, ici, les relations topographiques entre les divers segments s'en trouvent modifiées par rapport au type Prosobranche. Ainsi, l'ensemble oviducte-réceptacle séminal est situé en avant des glandes annexes et les aborde par leur extrémité antérieure. La position de l'orifice génital à l'avant de ces glandes étant conservée, chacune se termine en caecum vers l'arrière et les oeufs doivent parcourir un ou plusieurs allers et retrours à travers leurs cavités. D'autre part, les deux glandes sont accolées et même imbriquées sur une certaine longueur, ce qui nécessite le tri des produits génitaux par des gouttières spécialisées. Or, chez les Prosobranches, les divers segments sont habituellement alignés et les oeufs progressent régulièrement de l'un à l'autre dans le sens postéro-antérieur; c'est sur ce modèle simple qu'est construit le tractus génital des Atlantidés (Thiriot-Quiévreux & Martoja, 1974). Ceci correspond à l'évolution phylogénique de la lignée des Hétéropodes qui présente différents degrés d'adaptation à la vie pélagique, les Atlantidés étant les plus primitifs. Par sa complexité et la position de ses connexions, l'appareil génital femelle n'est pas sans évoquer l'organisation de certains Opisthobranches (voir Ghiselin, 1965), le gonochorisme constituant toutefois une différence essentielle.

D'autres caractères anatomiques retiennent l'attention sans être aussi exceptionnels. L'absence de canal gono-péricardique, fréquente ches les Mésogastropodes, est constante chez les Hétéropodes qu'il s'agisse d'Atlantidae (Thiriot-Quiévreux & Martoja, 1974, 1976), de *Pterotrachea* (Gabe, 1951) ou de *Firoloida* (Gabe, 1966). La tendance a la diaulie notée chez *Carinaria* existe également dans certaines espèces d'Atlantidae où le réceptacle séminal est pourvu d'un orifice propre. Quant aux réservoirs à spermatozoïdes, le nombre et la position en sont très variables chez les Prosobranches (Johansson, 1956, 1957) et cette variabilité se manifeste au sein même des Hétéropodes. *Carinaria* possède à la fois une bourse copulatrice et un réceptacle séminal alors que les autres Hétéropodes possèdent seulement un réceptacle séminal. Chez *Carinaria,* ce dernier n'est qu'un segment de l'oviducte; une disposition analogue a été signalée dans trois espèces de Littorinoidea (voir Creek, 1951) et chez les Pterotracheidae (Gabe, 1951, 1966). La ressemblance avec cette dernière famille est accentuée par la présence d'une valvule. Enfin, l'existence d'un caecum sans signification fonctionnelle apparente et qui représente peut-être un organe vestigial, se limite à *Carinaria* et *Pterotrachea.*

Du point de vue de l'anatomie microscopique, la symétrie et la périodicité qui caractérisent la répartition des catégories cellulaires dans les glandes annexes, semblent peu communes. Leur structure histologique est, en revanche, très classique. On sait que ces glandes annexes consistent ou bien en un épithélium simple doublé d'éléments glandulaires sous-jacents, ou bien en un épithélium pseudostratifié contenant lui-même les cellules glandulaires. Celles de *Carinaria* correspondent au premier type, comme celles de *Pterotrachea*; ces deux genres s'opposant aux Atlantidae et à *Firoloida* qui appartiennent au second type. De même, la paroi du réceptacle séminal est assez proche de celle de *Pterotrachea* mais différente de l'épithélium cubique banal des autres Hétéropodes. Néanmoins, nous n'y avons observé aucune image menant à croire qu'elle soit le siège d'une phagocytose et l'activité cellulaire que traduit l'existence de vacuoles au contact de spermatozoïdes pourrait être en rapport avec un rôle nourricier.

CONCLUSION

L'appareil génital mâle de *Carinaria* conserve un caractère primitif. Son organisation est celle d'un Mésogastropode, l'originalité résidant en une migration de la glande annexe vers la masse viscérale. L'appareil génital femelle est, lui, beaucoup plus modifié, une migration analogue entraînant un bouleversement des connexions anatomiques par rapport au type Mésogastropode.

Parmi les Hétéropodes, c'est avec *Pterotrachea* que *Carinaria* présente le plus de points communs mais les particularités de sa spermatogénèse le rapprochent du genre *Littorina.*

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ABSTRACT

GENITAL APPARATUS OF *CARINARIA LAMARCKI* (GASTROPODA HETEROPODA): STRUCTURE AND AFFINITIES

Micheline Martoja and Catherine Thiriot-Quiévreux

A histological study of *Carinaria lamarcki* provides the first description of the female reproductive system and some new data on the male reproductive system. This species which is representative of Carinariidae is compared with some other types of mesogastropods.

The whole female reproductive system is enclosed in the visceral mass. The ramified tubular ovary extends to form a gonad-like proximal oviduct and is followed by a ciliated distal oviduct and a receptaculum seminis. The oviduct is separated from the receptaculum by a valve and a caecum protrudes from the receptaculum near the valve. The receptaculum seminis comes into contact with the anterior part of the two associated glands and extends posteriorly to fuse with their common duct. Its epithelium is columnar cells which change when in contact with spermatozoa. The albumen gland and the capsule gland are side by side. Their ducts are closed posteriorly and, anteriorly, discharge to the mantle cavity by way of the vagina and egg-laying duct respectively. Their ciliated epithelium is underlaid by bundles of gland cells. The ducts have ciliated gutters where egg-capsules and egg-strings are elaborated. A branched bursa copulatrix is connected to the vagina. The female genital system has several anatomical and histological characters similar to *Pterotrachea.*

Spermatogenesis is characterized by "nurse-cells" according to Reinke's (1912) meaning; spermatozoa attach to them in the seminal vesicle only. The male reproductive system resembles that of the other mesogastropods except that the prostate gland is within the visceral hump. The prostate is made of many tubules branching from a single lumen. The vas deferens traverses the prostate ventrally and opens to the mantle cavity.

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FORM AND FUNCTION IN *TRISIDOS* (BIVALVIA) AND A COMPARISON WITH OTHER BURROWING ARCOIDS

Michael J. S. Tevesz[1] and Joseph G. Carter[2]

ABSTRACT

Trisidos Röding, 1798, is unique among the Arcoida in the marked twisting of the posterior portions of the shell around the hinge axis. Studies of live *T. yongei* Iredale, 1939, show that this twisted shell is adaptive for slow, shallow burrowing and byssal attachment in moderately physically rigorous sedimentary environments.

Analysis of the functional morphology of *Trisidos* and other modern arcoids suggests that arcoid burrowers may have evolved three distinct morphologic strategies as a compromise between burrowing efficiency and minimal resistance to ventilating currents at the shell margins and within the mantle cavity. Inflated shells with projecting umbos (e.g., *Anadara* and *Noetia*) allow for spacious lateral mantle cavities but offer minimal shell streamlining. Laterally compressed and subcircular shells (e.g., *Limopsis* and *Glycymeris*) are moderately streamlined and offer a wide margin for ventilating currents. The third morphologic strategy, represented only by *Trisidos,* combines streamlining of the shell anterior with posterior twisting, which again permits more efficient ventilation of the mantle cavity. Another adaptive advantage is conferred by this twisting and also by the anteroposteriorly compressed form of other burrowing arcoids. These features allow the slow-burrowing animals to more quickly achieve a "low-profile" life position and thus avoid adverse effects of current scour.

While preventing extreme specialization, the morphological limitations of arcoids have tended to preserve their evolutionary potential to make repeated transitions from infaunal to epifaunal life habits and back. The versatility of the pedal-byssal apparatus has probably played a role in this respect.

Data concerning hinge dentition and shell morphology suggest that *Trisidos* evolved from a morphologically less specialized representative of the Arcinae similar to the modern *Barbatia. Barbatia* was preadapted for the evolution of a shallow burrowing life habit because of its relatively efficient ligament and streamlined shape, features initially evolved as adaptations for epifaunal nestling.

INTRODUCTION

The bivalve order Arcoida is an ancient group within the subclass Pteriomorphia, whose fossil record dates back to early Paleozoic time. Arcoids are generally characterized by ecological conservatism, as evidenced by their never having evolved cementing, swimming, or even deeply burrowing forms. On the other hand, their numerous fossil and Recent species represent a number of distinct adaptations for "primitive" shallow burrowing, epifaunal or semi-infaunal nestling, and, in one instance (*Litharca*), hard substratum boring.

Perhaps none of the morphological adaptations developed by the Arcoida is more unusual and striking than the posterior shell twisting in the genus *Trisidos* Röding, 1798. In some species of *Trisidos* the posterior commissure plane has rotated in the course of evolution almost 90° relative to the shell anterior (Fig. 1). Despite the uniqueness of this shell form, its functional significance has not been fully analyzed.

In this paper we provide ecological observations on one of the more highly twisted of the *Trisidos* species (*T. yongei* Iredale, 1939) from Queensland, Australia, and using this information, attempt to interpret the evolution of this genus from a functional point of view. These observations of *Trisidos* and other burrowing arcoids provide new insights into the conservative nature of adaptive radiation within the ancient order Arcoida.

MATERIALS AND METHODS

Live *T. yongei* was dredged at depths of 2–4 m below the mean tidal level off the leeward (western) side of Magnetic Island, Queensland, Australia, in April of 1973. Magnetic Island lies within the Indo-Polynesian Province as delimited by Briggs (1974),

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and is situated between the Australian mainland and the Great Barrier Reef. The life habits of four individuals of *T. yongei* were observed on their native substratum. Ciliary current patterns and particle transport were observed by removing one shell valve and the corresponding mantle lobe, and then by introducing carmine or carborundum particles into the mantle cavity. Soft parts were studied from dissections of fresh material.

Additional data on shell form and habitat for other arcoids were obtained from a variety of literature sources, and from the collections at the Yale Peabody Museum (New Haven, Conn.), the National Museum of Natural History (Washington, D.C.), and the American Museum of Natural History (New York).

COMPARATIVE ANATOMY AND LIFE HABITS

Shell form

Although all fossil and Recent species of *Trisidos* are characterized by posterior shell twisting, this feature is particularly emphasized in the Australian species *T. yongei.* Especially striking here is the angularity of the posterior margin, which is set off from the more anterior parts of the shell by an umbonal to posteroventral angular deflection (Figs. 1 and 3a). In fossil species of *Trisidos,* e.g., *T. fajumensis* (Oppenheim, 1906), Eocene, Egypt; *T. yatsuoensis* Fujii, 1961, Miocene, Japan; *T. prototortuosum* Noetling, 1901, Tertiary, India), and in the Recent *T. tortuosa* (Linné, 1758), Indo-Pacific, the posterior twisting and angularity are less pronounced. As is evident from the localities listed here, modern and fossil *Trisidos* are restricted to the Indo-Pacific Region. Only one species, *T. tortuosa,* is represented by both Recent and fossil material (e.g., Tertiary of Mozambique, Moura, 1969).

Aside from its posterior twisting, *T. yongei* and other species of this genus are typically arcid in their shell form and hinge dentition.

Soft parts

The soft parts of *T. yongei* likewise resemble those of other modern arcids except for minor differences directly related to posterior twisting. For example, the left and right valve adductor muscle attachment scars in *T. yongei* are about equal in size, but only the left one is subquadrate in shape. Also correlated with twisting is an unusual elongation of the attachment surface of the left-valve posterior pedal retractor muscle.

These observations differ slightly from those by Ghosh (1924) for *T. tortuosa.* In this species, the left-valve adductor muscle attachment scar is triangular and smaller than in the right valve. Ghosh (1924) also noted that abdominal sense organs are absent in *T. tortuosa* and that esophagus and stomach are distinct. However, these two latter observations were subsequently contradicted by Heath (1941). Additionally, Heath mentions the following four general differences between *Trisidos* and most other arcoids: 1) the right abdominal sense organ is larger than the left; 2) the esophagus and stomach are difficult to distinguish; 3) the alimentary canal penetrates the heart; and 4) the labial palps show large, undulating folds in addition to the more typically arcoid smaller ridges.

In conclusion, except for the labial palp and alimentary canal features, most of the distinguishing anatomical features of *Trisidos* can be directly related to its evolution of shell twisting and the resulting inequivalve condition.

Mantle cavity currents and particle sorting

As in many burrowing arcoids, water for respiration and feeding enters the mantle cavity at the posteroventral shell margin through apertures formed by the local and temporary appression of the mantle lobes. This appression also defines a posterodorsal aperture for the exhalant current. Particles trapped by the gills are sorted, and either rejected by a posteriorly-directed gill ciliary tract, or accepted for further sorting and ingestion by anteriorly-directed ciliary feeding tracts. Particle rejection tracts are located on the mantle and foot as well as on the gills. These ciliary feeding and rejection tracts do not differ appreciably from the common arcoid pattern as developed in *Arca* and *Glycymeris* (Atkins, 1936), *Anadara* (Lim, 1966), *Noetia* and *Barbatia* (Tevesz, personal observations), *Limopsis,* and to some extent, *Philobrya* and *Lissarca* (Tevesz, 1977). Rejected particles are removed from the mantle cavity by being bound in mucus strings and ejected through the inhalant aperture by sudden valve contraction.

Life habits

Specimens of *T. yongei* were found living in a muddy, fine to medium sand substratum containing abundant fragmental shell material. The environment where the collections were made was subject to the effects of tidal currents and wave activity. Nevertheless, the area was protected on one side by the nearby mainland and on the other side by Magnetic Island and the more distant Great Barrier Reef, so the general environment in which *T. yongei* lived is properly termed moderately physically rigorous. This is somewhat similar to the environment inhabited by *T. tortuosa* (Ghosh, 1924). Ghosh cited a note from the Director of the Biological Station at Ennor (Madras, India) indicating that *T. tortuosa* "is fairly numerous in certain parts of Palk Bay between 4½ to 6½ fathom lines on a bottom of dirty muddy sand, and is not found in crevices." This information is important, since it confirms our observation that *Trisidos,* unlike other representatives of its subfamily Arcinae, is typically a burrower (rather than a nestler or rock-borer).

Specimens of *T. yongei* left in a laboratory tank on their native substratum for several hours showed an integrated burrowing activity consisting of the following sequence: 1. The foot emerges anteroventrally, probes the substratum, and anchors itself in the sediment. 2. Although initially lying with the anterior commissure plane more or less horizontal, *T. yongei* assumes a vertical orientation of this commissure plane as the anterior of the shell penetrates the substratum. Because the shell posterior is torted approximately 90° relative to the anterior, its posterior commissure plane therefore assumes a more or less horizontal position relative to the sediment-water interface. 3. A slow sequence of extension, expansion, and contraction of the foot pulls the shell diagonally downward into the substratum until the shell is shallowly buried with only the shell posterior exposed. The posterior commissure is then horizontal to and only a few millimeters above the sediment-water interface. Sequential positions of the shell during this burrowing sequence are illustrated in Fig. 1.

Once the animal is sufficiently buried in the substratum, it attaches to larger sediment particles (especially shell debris) by means of an exceptionally long byssus. The byssus fibers may attain a length of up to one half the length of the shell. This burrowing sequence may take several hours to complete, since it is commonly interrupted.

Because of the valve inequality and the horizontal position of the posterior shell margins, the longer, uppermost left valve forms a slightly projecting shelf above the shorter right valve. In terms of its semi-infaunal life habit, *Trisidos* is unique among modern representatives of the subfamily Arcinae. Other modern members of this subfamily are either epibyssate (*Arca* and *Barbatia*) or endolithic (*Litharca*: Frizzell, 1946). According to Thomas (1978), some fossil species of *Barbatia* were endobyssate.

MORPHOLOGICAL COMPARISONS WITH OTHER ARCOIDA

A number of arcoids are known to be burrowers or are inferred burrowers on the basis of their shell form. These include the modern Limopsidae and Glycymerididae (Limopsacea), certain Noetiidae and Anadariinae (Arcacea), and the largely fossil Cucullaeidae (Arcacea) (Stanley, 1970; Tevesz, 1977; personal observations). The family Cucullaeidae is represented by a single surviving genus, *Cucullaea,* which is almost certainly a shallow burrower, but whose life habits are otherwise little known. The presumed ancestral arcoid superfamily Cyrtodontacea and some Parallelondontidae (early Arcacea) are likewise inferred to have been burrowers (Pojeta, 1971; Stanley, 1972).

Modern arcoid burrowers naturally comprise three morphologic groups defined by lateral compression and umbonal projection. Group I burrowers show laterally inflated shells with strongly projecting umbos, as in *Anadara* and *Noetia* (Fig. 2a). Group II burrowers are laterally compressed, dorsoventrally expanded, and show relatively subdued umbos, as in *Limopsis* and *Glycymeris* (Fig. 2b). Group III burrowers are morphologically similar to the epifaunal nestler *Barbatia* and are intermediate in terms of lateral compression (in the shell anterior) and umbonal projection. Group III burrowers are represented only by *Trisidos.*

An interesting aspect of the form of these modern burrowing arcoids is that none of them have evolved a streamlined morphology, i.e., a form that is at the same time both laterally *and* dorsoventrally compressed. This is unusual because a streamlined form enhances burrowing efficiency (Stanley, 1970) and thus might confer survival-related advantages to these burrowing arcoids.

This lack of streamlining further documents observations made by Thomas (1976) regarding the morphological and ecological limitations of arcoids. Thomas cogently argued that the weak duplivincular ligament of most arcoids is a major cause of this conservatism.

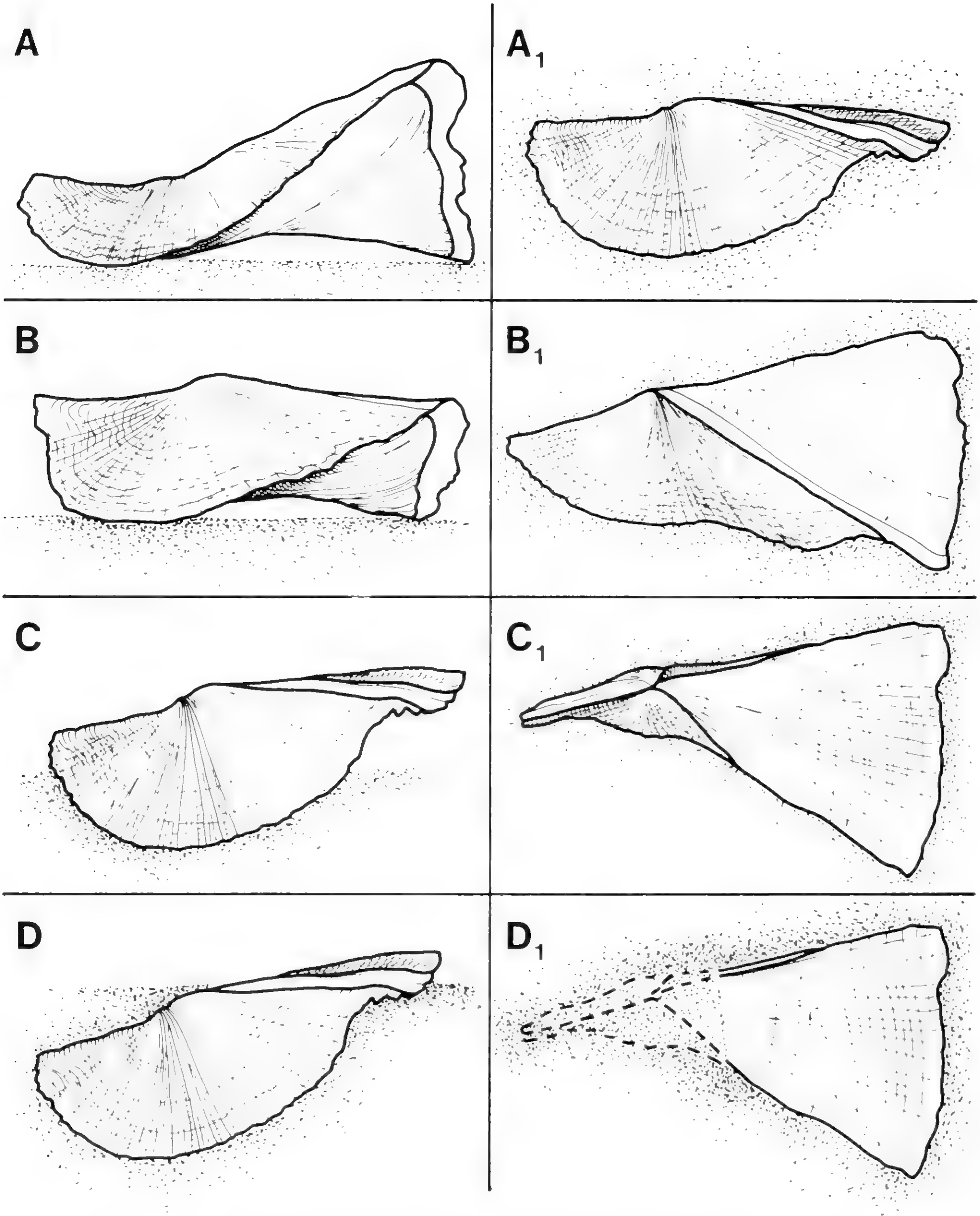

FIG. 1. Sequential shell orientations of live *Trisidos yongei* during burrowing. A–D = side view; A_1–D_1 = corresponding top view; A,A_1 = prior to burrowing; B,B_1 = burrowing; C,C_1 = burrowing; D,D_1 = usual life position.

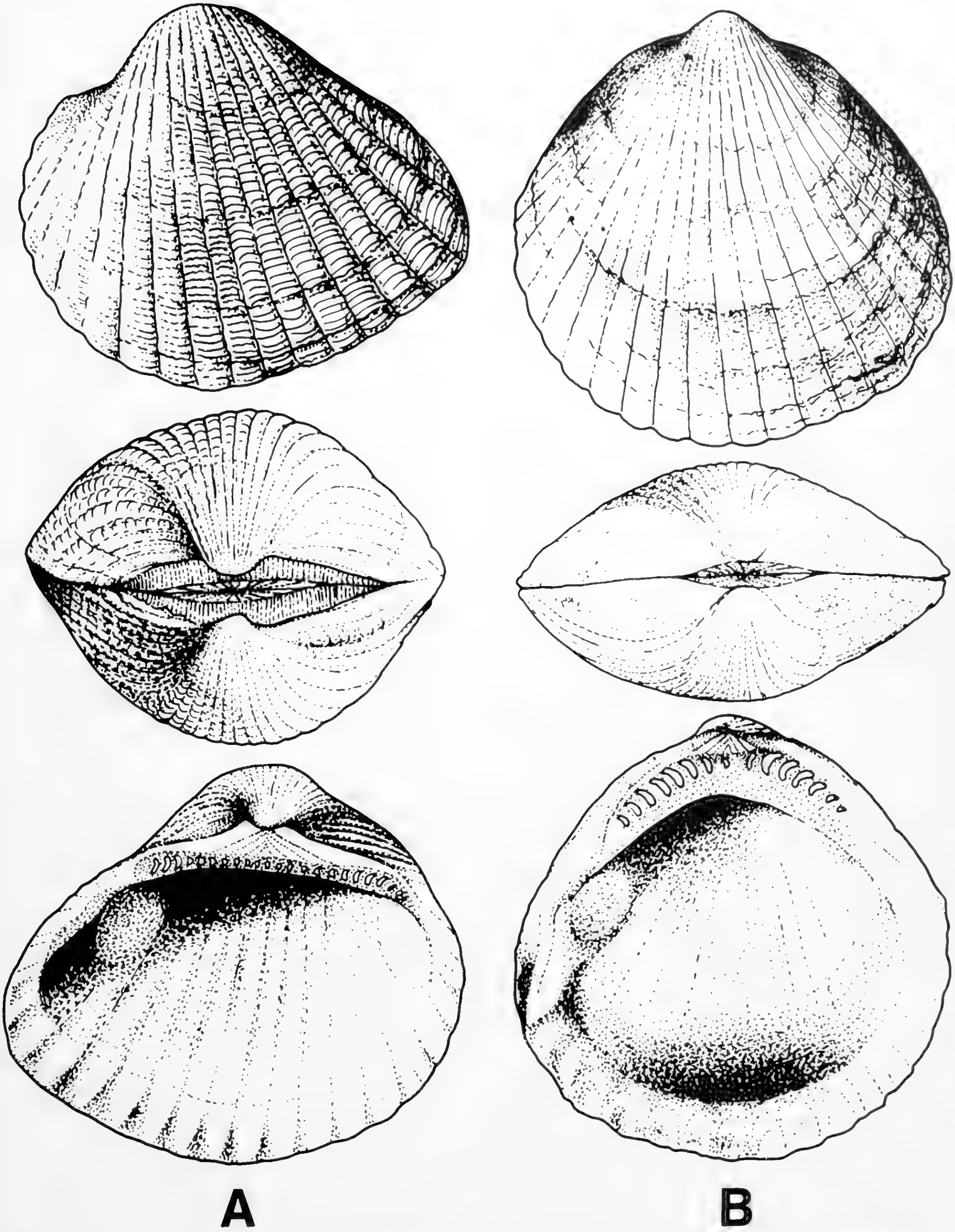

FIG. 2. Genera representing two morphologic groups of burrowing arcoids. Exterior and interior views of left valves and dorsal views of articulated valves for: A) *Anadara* (Group I); and B) *Glycymeris* (Group II). Respective actual lengths = 57 mm and 24 mm.

LIMITATIONS ON THE EVOLUTION OF SHELL FORM IN BURROWING ARCOIDS

Mantle cavity ventilation

We offer the working hypothesis that in addition to the ligament, factors relating to improving mantle cavity ventilation and minimizing frictional resistance of water currents within the mantle cavity may have influenced shell form in burrowing arcoids.

Group I forms typically live with the anterior portion of the shell buried in the substratum, so the substratum precludes freedom of circulation of an anteroventral inhalant mantle current. This current must therefore be restricted to the shell posterior, or at least to the posteroventral shell margin, thereby increasing frictional resistance at these mantle margins. Possibly to ease the resultant frictional resistance on the mantle currents, Group I burrowers have inflated their valves and increased the depth of their umbonal cavity. This significantly increases the volume of the lateral mantle cavities, thereby reducing the frictional resistance of their circulating water currents.

In contrast, Group II arcoids have partially streamlined their shells by increasing their lateral compression and by reducing the prominence of their umbos. But lateral compression decreases the volume of the lateral mantle cavities, thereby increasing frictional resistance on the interior mantle currents. Consequently, these species may have retained a non-streamlined sub-circular lateral profile in order to increase the area of anterior inhalant and anterior and posterior exhalant currents (see Atkins, 1936). Because Group II burrowers are commonly found in coarser sediments (such as gravels) than Group I burrowers, they can potentially utilize more of their mantle margins for mantle cavity ventilation, thereby not only reducing the frictional resistance of these currents entering the shell, but also likely promoting circulation within the mantle cavity.

Trisidos combines features of Group I and Group II burrowers. Its twisted form creates a lateral expansion of the mantle cavity in the posterior portion of the shell. Moreover, the posterior margin is expanded and elevated above the substratum (but at a low angle). This allows for spacious areas of mantle margin that are free from the substratum and which may be utilized for mantle cavity ventilation.

As noted previously, the ligamental hypothesis of Thomas (1976) adequately explains why arcoids have generally been unsuccessful in evolving active burrowers ecologically comparable to those in certain veneroid superfamilies. But this ligamental hypothesis fails to explain why arcoids have evolved and maintained throughout their long evolutionary history two major morphologic groups among their burrowing forms, neither of which is characterized by a totally streamlined shell form that would minimize, rather than aggravate, the limitation of their weak duplivincular ligament on burrowing efficiency. Nor does the ligamental hypothesis account for the fact that the one burrowing arcoid genus with total shell streamlining in its anterior, i.e., *Trisidos,* has not maintained this streamlined profile in its posterior. Because of the structure of duplivincular ligaments, maximum ligament efficiency is obtained in arcoids with a short interumbonal distance and, consequently, with strong lateral compression. Arcoids with a short interumbonal distance are capable of maintaining proportionally more ligamental lamellae attached between the two shell valves as the ligamental areas separate during shell growth. On the basis of considerations of burrowing efficiency, one might expect that burrowing arcoids would generally be dorsoventrally compressed for streamlining and laterally compressed for both streamlining and ligament strength, i.e., morphologically similar to certain epifaunal *Barbatia.*

This hypothesis makes no assumption regarding comparative pumping efficiencies of arcoid filibranch versus more complex veneroid eulamellibranch gills. The ventilation hypothesis assumes only that, in connection with the anatomy and burrowing habits peculiar to arcoids, relatively free access to mantle ventilating currents can be adaptively advantageous, and can therefore partially influence the shell morphology of arcoid burrowers. The possibility remains that eulamellibranch gills offer greater potential than filibranch gills for the evolution of mantle fusion, siphon formation, and deeper and more streamlined burrowers. But analysis of the evolutionary significance of gill type between arcoid and veneroid bivalves must take into consideration a wide range of variables, including efficiency of particle sorting, size and shape of the mantle cavity and gills, and possibly other factors in addition to pumping efficiency. Such comparisons between the Arcoida and Veneroida are beyond the scope of the present paper.

Stability in physically rigorous environments

Inasmuch as burrowing arcoids are typically limited in their burrowing rate and tend to occupy current-swept sediments (Thomas, 1975, 1976) their long exposure during reburrowing may be an additional factor influencing the evolution of posterior twisting in *Trisidos* and a highly compressed valve to valve profile in burrowers such as *Glycymeris*. Trueman (1966, 1968a, b) and Trueman et al. (1966) showed that bivalves with extensive mantle fusion can build up relatively high water pressures within the mantle cavity. This water, expelled as jets from the pedal aperture, aids the foot in burrowing by loosening underlying sediments. In bivalves lacking an extensively fused mantle, water jets are not used as effectively, and the burrowing rate is generally slower. Largely unfused mantle margins characterize the modern burrowing arcoids, and arcoids correspondingly require considerable time to assume their final infaunal life positions (i.e., with the posterior shell margin protruding only slightly, if at all, above the sediment surface; Stanley, 1968; 1970; Tevesz, personal observations). In this context, and especially because *Trisidos* is a slow burrower with an elongate shell in physically rigorous environments, its twisted posterior may be adaptive for reducing the hazard of current scour around the shell during burrowing as well as in its normal life position. Similarly, the compressed profile of *Glycymeris* results in reducing the exposure of the shell during burrowing, thereby minimizing current scour.

EVOLUTION OF *TRISIDOS*

As shown in Fig. 3, the epifaunal arcoid *Barbatia* is morphologically similar to *Trisidos* in terms of its lateral compression and moderately projecting umbos. These genera are likewise similar in their obliquely oriented hinge teeth, radial external ribbing, and in some *Trisidos* species, in their beaded external ornament. *Trisidos* differs from *Barbatia* primarily only in its twisted shell posterior, the absence of a prominent ventral gape (compared to some epifaunal *Barbatia*), and associated minor changes in internal anatomy (see above). Since *Barbatia* has a long fossil record prior to the Eocene appearance of *Trisidos* (Newell: N252–N254, in Cox et al., 1969), it is reasonable to assume that it is ancestral to *Trisidos*.

Epifaunal *Barbatia* might be considered preadapted for the evolution of a burrowing life habit because of its streamlined, wedge-shaped anterior and relatively subdued ornament. It may also be preadapted because its closely spaced umbos make possible a relatively strong duplivincular ligament (Thomas, 1976). A strong ligament would be

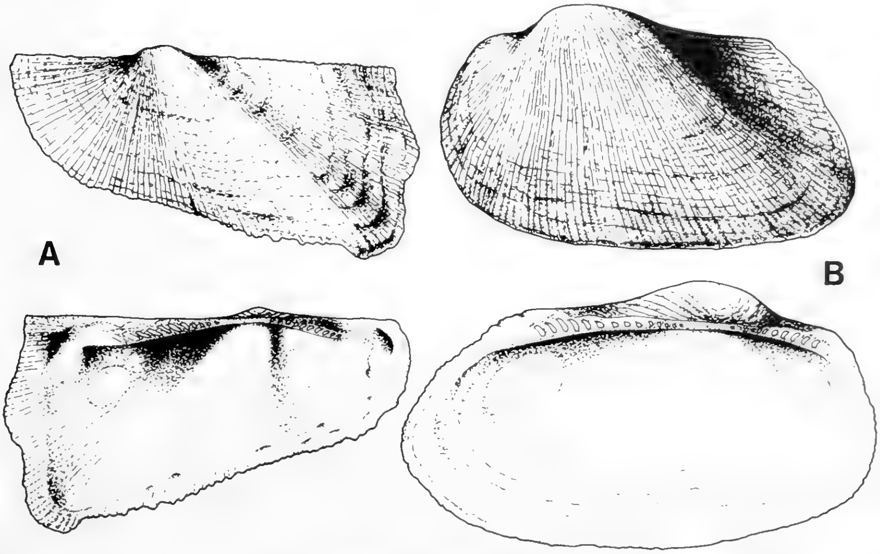

FIG. 3. Comparative shell features of *Trisidos* and *Barbatia*. Exterior and interior views of left valve for: A) *Trisidos yongei* Iredale. Australia. B) *Barbatia novaezelandiae* Smith. New Zealand. Respective actual lengths = 36 mm and 41 mm.

advantageous for pressing the shell valves against the burrow walls, especially in a species lacking fused mantle margins. Unlike the burrowing arcoids, *Barbatia* may have been able to evolve such shell streamlining because its epifaunal life habit imposes few restrictions on the area of its shell margin utilized for ventilating currents. As noted by Bretsky (1976), *Barbatia* utilizes its ventral shell margin for maintaining the inhalant mantle current, thereby leaving the entire posterior shell margin for the exhalant current. *Barbatia* is occasionally found nestling in cryptic habitats, but its inhalant area is still generally sufficiently elevated above the substratum to allow for free circulation of water currents. The laterally compressed form of *Barbatia* is clearly advantageous in connection with its habit of nestling in crevices, and its moderate dorsoventral compression is likewise advantageous for concealing the shell in this ecological setting.

But according to the ventilation hypothesis elaborated above, the evolution of infaunal burrowing in an arcoid with the shell morphology of *Barbatia* would be accompanied by problems of mantle cavity ventilation. Reduced ventilation may have resulted in connection with its laterally compressed mantle cavity when the ventilating currents became restricted to the posterior shell margins, i.e., above the sediment-water interface. In their evolution of burrowing life habits, the hypothesized descendants of *Barbatia* might have solved the mantle ventilation problem by evolving greater lateral inflation of the valves and a deeper umbonal cavity (as in *Anadara*), or by evolving a rounded lateral profile (as in *Glycymeris*). But these two alternatives require major remodeling of the shell. The ancestors of *Trisidos* evidently followed an evolutionary pathway involving greater economy of change, i.e. simple twisting in the shell posterior. This twisting was accomplished, as noted above, with minimal change in internal anatomy and with retention of both lateral and dorsoventral streamlining in the shell anterior. While increasing the area of the posterior shell margin elevated above the sediment-water interface and while increasing the internal volume of the posterior mantle cavity, the posterior twisting in *Trisidos* also improved the stability of the shell by creating a low profile in its living position.

It is interesting to speculate that the hypothesized change from epifaunal nesting to infaunal burrowing in the evolutionary history of *Trisidos* may have greatly influenced the nature and amount of suspended sediment entering its mantle cavity. In addition to bringing its inhalant area close to the sediment-water interface, the unique burrowing habit of *Trisidos* caused its inhalant and exhalant currents to lie in a similar position relative to a horizontal plane along the sediment surface. Consequently, these two currents may be less efficiently separated in *Trisidos* than in its hypothesized epifaunal ancestors.

SUMMARY AND CONCLUSIONS

As noted by Thomas (1976), the weak arcoid ligament has apparently limited evolutionary specialization by arcoids for both deep burrowing and permanent epibyssate attachment, because it limits valve gape in burrowing and anterior reduction. It is presently proposed that problems of mantle ventilation and shell stability in the context of slow burrowing have additionally imposed restrictions on the evolution of streamlined *shallow* burrowers in this order. But Thomas (1976) also noted that the inherent limitations on arcoid evolution have nevertheless permitted arcoids to make repeated transitions from epifaunal to infaunal modes of life and back. For example, according to Stanley (1972), the early Arcoida demonstrate a general evolutionary trend from ancestral burrowing to epifaunal life habits. Within the Arcacea, the Arcidae apparently evolved at an epifaunal grade of evolution and later reverted to the infaunal habit in many species. Later, certain infaunal Arcidae re-radiated back to the epifaunal habit, e.g., in the origin of *Arcopsis*. The infaunal Limopsidae (Limopsacea) likewise radiated into the epifaunal habit with the origin of the Philobryidae (Tevesz, 1977).

The invasion of a new adaptive zone is often accompanied by high-level taxonomic diversification (Simpson, 1953; Valentine, 1973). Arcoids exemplify this trend because their evolutionary life habit transitions are frequently accompanied by the appearance of new taxonomic categories, even at the superfamily level (Pojeta, 1971; Tevesz, 1977). In this respect, the ecologically versatile pedal apparatus of arcoids may have played a major role in their preadaptation for the evolution of both burrowers and epifaunal species. In addition to providing a powerful burrowing organ, it can afford firm byssal attachment in the epifaunal forms. The versatility of this pedal apparatus possibly compensated for their limitations in ligament strength, thereby allowing for their evolutionary persistence and for much of their ecological diversity.

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Note added in proof:

After this paper was accepted for publication, G. McGhee (*Lethaia,* 1978, 11: 315–329) published a paper concerning the theoretical implications of shell twisting in *Trisidos* and other bivalves. The reader is referred to this paper for this theoretical treatment.

MALACOLOGIA, 1979, 19(1): 87–101

CYCLE DE DEVELOPPEMENT, CROISSANCE ET FECONDITE DE CINQ POPULATIONS DE *LYMNAEA CATASCOPIUM CATASCOPIUM* (GASTROPODA, LYMNAEIDAE) AU LAC SAINT-LOUIS, QUEBEC, CANADA[1]

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RESUME

En suivant l'évolution de la structure démographique de cinq populations de *Lymnaea catascopium catascopium,* le Lymnaeide le plus important au lac Saint-Louis, Québec, nous avons pu définir son cycle de développement, et évaluer sa croissance et sa fécondité. Cette espèce présente deux types de développement, l'un simple avec une seule génération par année et une seule période de reproduction effective (au printemps), l'autre plus complexe avec deux générations par année et deux périodes de reproduction en juin-juillet puis d'août à novembre. Ces différences fondamentales dans le cycle de développement peuvent être mises en relation avec la nature des eaux du lac: les eaux dures et alcalines du fleuve St-Laurent et les eaux douces et neutres de la rivière des Outaouais. La croissance des individus est de type sigmoïde et présente des variations annuelles intraspécifiques qui s'expliquent plutôt par des différences dans la nature trophique des milieux que par des variations des composantes physico-chimiques. *L. catascopium catascopium* dépose deux types de pontes et est sexuellement mature à une taille inférieure à 10 mm. Sa fécondité estimée sur la période du 18 juin 1970 au 23 novembre 1971 varie de 3380 oeufs à 43674 oeufs selon les populations. Au laboratoire, chaque spécimen dépose de 273 à 690 oeufs à 15°C et 226 à 365 oeufs à 20°. Les résultats de notre étude laissent aussi entrevoir des implications évolutives en relation avec la nature des milieux d'eau douce.

INTRODUCTION

Les Lymnaeidae, comme la plupart des pulmonés d'eau douce présentent un grand potentiel de variation à la fois au point de vue morphologique et au point de vue écologique (Hubendick, 1951; Hunter, 1961a, b; Walter, 1968, 1969; Hunter, 1972, 1975). Au Canada, la distribution et l'anatomie des Lymnaeidae est bien connue (Clarke, 1973) mais aucune étude ne traite de la dynamique de population de ces mollusques. C'est ce dernier aspect que nous avons étudié sur cinq populations de *Lymnaea catascopium catascopium* Say, (1817), au lac Saint-Louis, Québec, où les mollusques benthiques constituent un des groupements les plus importants de la zone littorale (Magnin, 1970). Nous étudierons le cycle de développement, la croissance et la fécondité de ces populations situées dans des biotopes aux caractéristiques physico-chimiques et trophiques différentes.

MILIEU D'ETUDE

Le lac Saint-Louis (45°15′N et 73°40′W) est un élargissement du fleuve Saint-Laurent situé au sud de l'île de Montréal. Les stations échantillonnées peuvent être classées en trois types correspondant aux trois grandes masses d'eau du lac déjà décrites par Brundritt (1963), Pageau & Lévesque (1968) et Magnin (1970): les stations 3 et 6 situées dans les eaux vertes et dures du fleuve Saint-Laurent, les stations 2 et 10 dans les eaux brunes et douces de la rivière des Outaouais et la station 9 dans les eaux constituées par un mélange des deux eaux précédentes. Le Tableau 1 indique les valeurs moyennes et extrèmes des paramètres physico-chimiques de l'eau à chacune des stations d'échantillonnage en 1970 et 1971. Les variations saisonnières de la température et la durée de période avec glace sont très semblables dans les différentes stations (Fig. 1). Les stations d'échantillonnage présentent aussi des différences dans les facteurs biotiques du milieu. Les algues benthiques sont surtout représentées par les algues vertes filamenteuses (*Cladophora*) dans les stations 3 et 6 du fleuve Saint-Laurent, par les Diatomées dans les stations 2 et 10 de la rivière des Outaouais et par les algues bleues

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[1] Texte adapté et extrait d'une partie d'une thèse de Ph.D. soutenue au département des Sciences biologiques de l'Université de Montréal (Pinel-Alloul, 1975).

TABLEAU 1. Moyenne annuelle et valeurs extrèmes (entre parenthèses) des paramètres physico-chimiques des eaux à chaque station d'échantillonnage.

Paramètres	Années	Sta. 3	Sta. 6	Sta. 2	Sta. 10	Sta. 9
pH	1970	7.9 (7.0–8.5)	8.2 (7.2–8.8)	7.1 (6.8–7.9)	7.0 (6.6–7.7)	7.7 (7.0–8.6)
	1971	8.0 (7.2–8.7)	8.3 (7.7–9.1)	7.0 (5.8–7.7)	7.4 (6.9–7.9)	7.9 (7.1–9.1)
O_2 dissous mg/l	1970	11 (9–14)	13 (10–16)	10 (7–12)	9 (6–10)	11 (9–14)
	1971	10 (6–14)	13 (8–17)	9 (7–12)	10 (8–11)	10 (9–12)
Alcalinité mg/l	1970	85 (64–90)	78 (68–105)	22 (16–30)	21 (10–30)	27 (20–40)
	1971	82 (68–98)	79 (65–88)	30 (19–42)	26 (18–40)	43 (30–68)
Dureté totale mg/l	1970	105 (95–120)	102 (90–120)	27 (20–35)	29 (25–35)	37 (30–55)
	1971	104 (85–125)	107 (95–123)	35 (25–55)	32 (25–40)	57 (35–100)
Dureté en calcium mg/l	1970	80 (70–90)	73 (60–85)	20 (15–25)	21 (20–55)	27 (20–40)
	1971	81 (70–100)	83 (75–95)	24 (20–35)	21 (15–30)	46 (30–90)

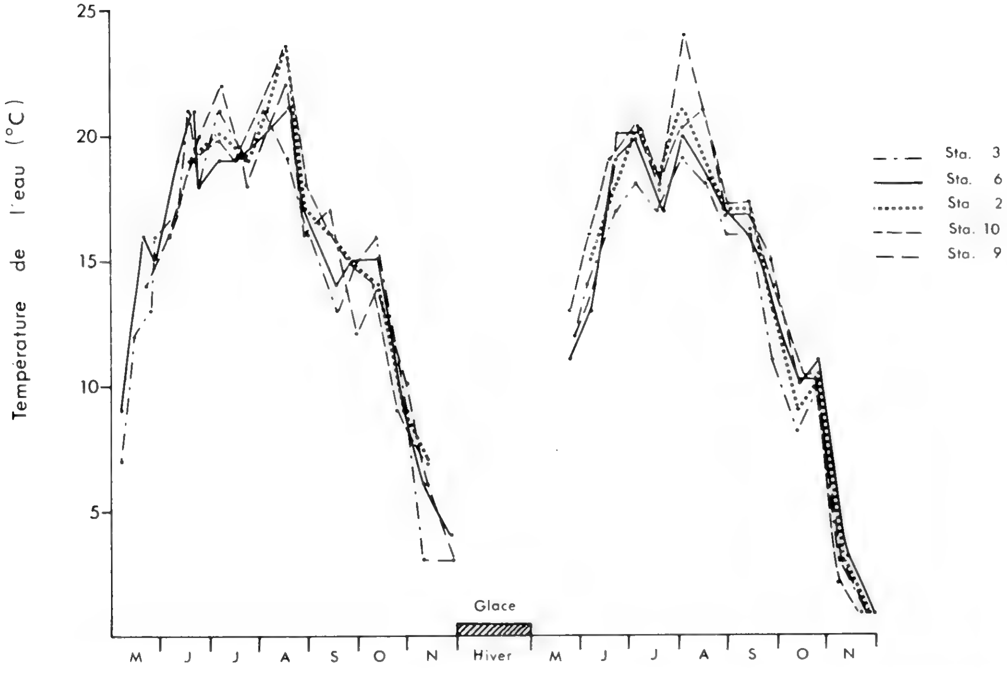

FIG. 1. Variations saisonnières de la température de l'eau aux différentes stations d'échantillonnage en 1970 et 1971.

dans les eaux mixtes de la station 9. La faune malacologique présente aussi un aspect différent dans les différentes stations: les Bithynies (Prosobranches) prédominent dans les eaux du fleuve Saint-Laurent et dans les eaux mixtes tandis que les Lymnées et les Planorbes (Pulmonés) sont plus abondantes dans les eaux de la rivière des Outaouais.

MATERIEL ET METHODES

L'échantillonnage fut effectué en 1970 et 1971, des mois de mai à novembre inclusivement, selon la méthode des quadrats (Zhadin, 1954; Heurteaux & Marazanof, 1965; Marazanof, 1969; Finnish IBP-PM Group, 1969; Houp, 1970). Tous les quinze jours, nous fixions dans chacune des stations quatre quadrats d'un mètre carré d'où nous retirions avec précaution toutes les roches mobiles. Hors de l'eau, nous détachions tous les mollusques et pontes qui y adhéraient et les roches étaient ensuite lavées et nettoyées dans un seau d'eau afin de recueillir les plus petits spécimens. Finalement nous prélévions manuellement les mollusques présents sur le fond de chaque quadrat et sur les roches immobilisées dans la vase. Si l'on tient compte de la surface totale des roches, la surface échantillonnée est supérieure à un mètre carré et elle varie en fonction de la grandeur des roches. Diverses techniques d'estimation des surfaces recouvertes de roches ont déjà été décrites (Hunter, 1953; Calow, 1972). Mais comme l'indique Hunter (1961a), l'estimation des abondances par surface fixe de substrat, quelle que soit sa nature, est justifiée si l'on analyse les résultats sur une base comparative, ce que nous nous proposons de faire précisément.

Au laboratoire, les mollusques et les pontes récoltées étaient fixés à l'alcool à 70% additionné de glycérine, triés, comptés et mesurés (distance de l'apex de la coquille au bord distal du péristome) aux grossissements 6X et 12X d'une loupe binoculaire munie d'une chambre claire. L'analyse de la structure des populations a été faite selon la méthode déjà décrite par Pinel-Alloul & Magnin (1971).

La taille à la maturité sexuelle fut estimée par la taille moyenne des individus au début de leur période de reproduction. La fécondité des Lymnées de chaque population fut estimée par la formule:

$$(1) \qquad F = \sum_{i=1}^{k} N_i \times O_i$$

dans laquelle N_i est le nombre de pontes récoltées et O_i le nombre moyen d'oeufs par ponte à chaque date d'échantillonnage i, k étant le nombre d'échantillonnages effectuées au cours de la période de reproduction. Nous avons aussi estimé au laboratoire la fécondité des Lymnées des populations des stations 2, 6 et 9, représentant chacune un des types de biotope du lac. Les élevages ont été faits aux températures de 15°C et 20°C sous une photopériode: 12–12.

RÉSULTATS

Cycle de développement et structure des populations

Au lac Saint-Louis, *Lymnaea catascopium catascopium* présente deux types de cycle de développement: un type simple avec une seule génération par année aux stations 3, 6 et 9 (Fig. 2) et un type plus complexe avec deux générations par année aux stations 2 et 10 (Fig. 3).

En suivant les variations de la structure en taille des populations des stations 3, 6 et 9 (Fig. 2), nous constatons que la distribution des spécimens est bimodale en juin et juillet 1970 et 1971, ce qui témoigne de la coexistence de deux cohortes à cette période de l'année. Les représentants de la cohorte de 1969 constituent la totalité de la population à la fin mai 1970 puis disparaissent à la fin juin (station 9) ou au début juillet (stations 3 et 6) après avoir donné naissance à une nouvelle génération (cohorte 1970). Au printemps 1971, le même phénomène se reproduit, la cohorte 1970 engendrant la nouvelle génération de 1971; nous remarquons cependant que les individus de la cohorte 1970 survivent plus longtemps que ceux de la cohorte 1969 aux stations 3 et 6.

En plus d'indiquer les effectifs de chaque échantillon (N), la Figure 2 rapporte aussi les nombres de pontes récoltées (n) à chaque date d'échantillonnage. Exception faite en 1971 à la station 6, il se succède deux périodes de ponte chaque année, mais, seule la période de ponte printannière coïncide avec l'apparition d'une nouvelle génération. La période de ponte estivale n'est suivie que de l'apparition de quelques individus. Les pontes printannières de 1970 et 1971 sont déposées par les individus des cohortes 1969 et 1970 qui ont survécu durant l'hiver; les pontes récoltées en août, septembre et octobre sont probablement produites par certains individus

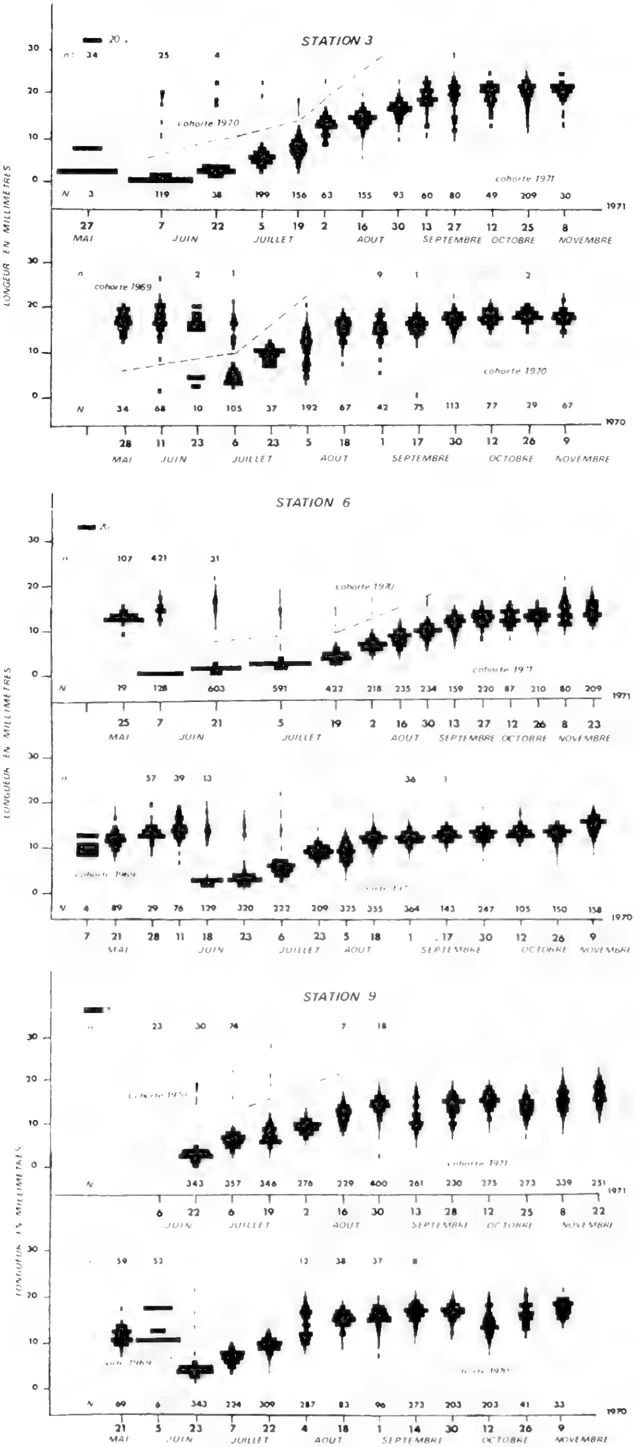

FIG. 2. Structure en taille des populations de *L. catascopium catascopium* aux stations 3, 6 et 9. N: effectif des échantillons; n: nombre de pontes.

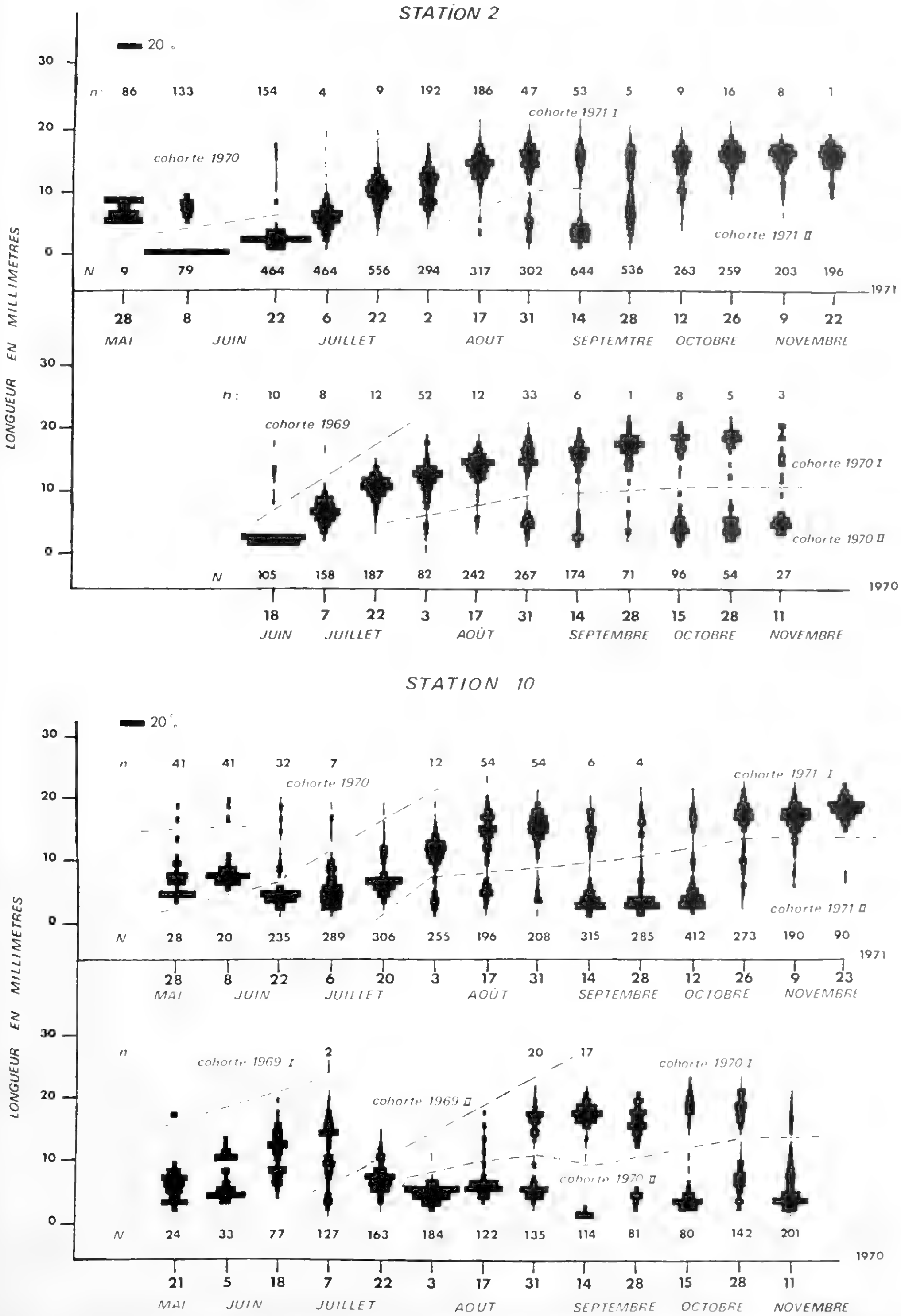

FIG. 3. Structure en taille des populations de *L. catascopium catascopium* aux stations 2 et 10. N: effectif des échantillons; n: nombre de pontes.

des cohortes 1970 et 1971, nés au printemps de la même année et qui ont atteint leur maturité sexuelle.

La Figure 3 illustre la structure des populations des stations 2 et 10 qui ont un cycle de développement à deux générations par année. A chaque date d'échantillonnage, la distribution en taille des spécimens est généralement bimodale. La première génération (I) est engendrée par les survivants des cohortes de l'année précédente et apparaît en juin ou juillet (le 8 juin 1971 et le 18 juin 1970 à la station 2; le 22 juin 1971 et le 7 juillet 1970 à la station 10). La deuxième génération (II) est engendrée par les individus matures de la génération printannière associés à quelques survivants des cohortes de l'année précédente et apparaît durant tout l'été et l'automne, depuis le mois d'août jusqu'au mois de novembre. La génération printannière (I) coexiste avec la génération estivale (II) jusqu'à l'hiver et même parfois jusqu'au printemps suivant (station 10, printemps 1970).

A la station 2, nous avons récolté des pontes à chaque date d'échantillonnage (n dans la Figure 3). Nous pouvons discerner deux pics de pontes, correspondant chacun avec l'apparition d'une nouvelle génération. La ponte printannière déposée en mai et juin par les individus des cohortes de l'année précédente est très nette en 1971 mais l'est beaucoup moins en 1970, la période d'échantillonnage ayant débuté plus tard. La ponte d'été-automne déposée par les individus de la génération printannière (I) très intense en août est de plus en plus faible jusqu'en novembre. A la station 10, les deux périodes de pontes sont bien définies en 1971; toutefois, la ponte d'été-automne ne se poursuit pas jusqu'en novembre et les deux périodes de pontes ne se chevauchent pas comme à la station 2.

Croissance des individus des différentes cohortes

Les courbes de croissance des générations I des cohortes de 1970 et 1971 (Fig. 4) sont

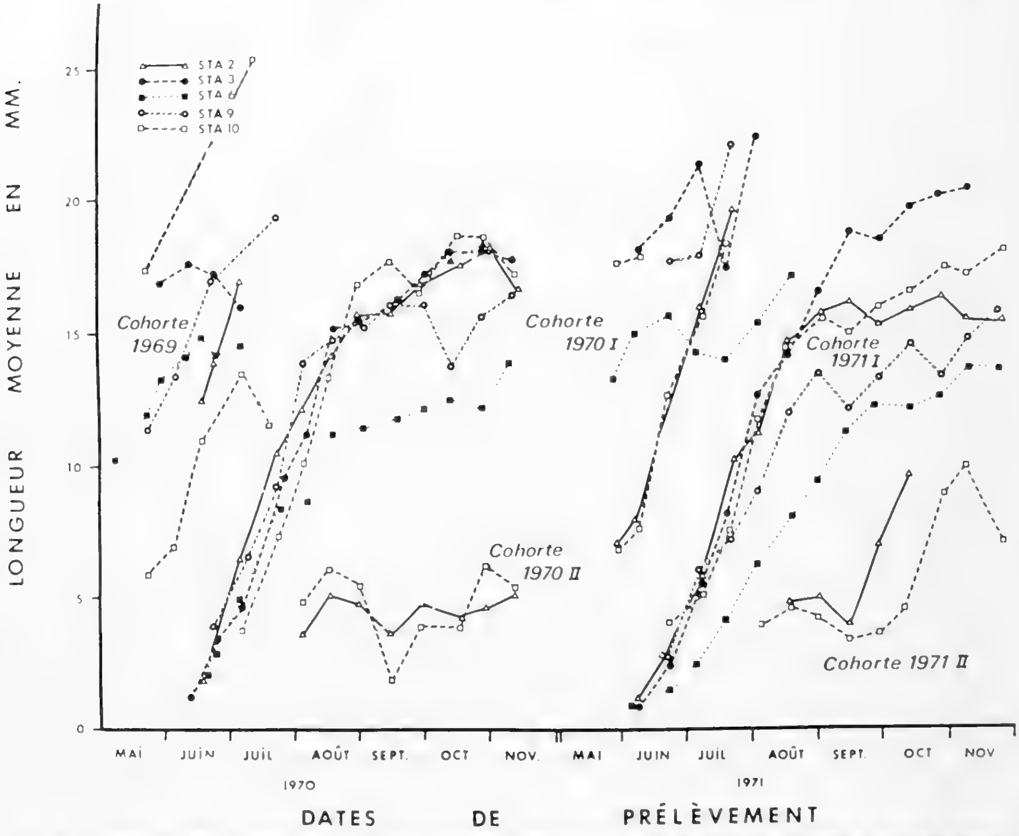

FIG. 4. Croissance en longueur des *L. catascopium catascopium* des différentes cohortes à chaque station d'échantillonnage en 1970 et 1971.

de type sigmoïde caractérisé par une phase de croissance rapide (juin à la fin août) suivie d'une phase de croissance lente (septembre à novembre); à la mi-août, soit deux mois après leur naissance les individus des générations printannières (I) de 1970 ont en effet déjà effectué 80% de leur croissance à la station 2 et environ 70% de leur croissance aux stations 3, 6, 9 et 10. Il leur faut ensuite de 2 mois (stations 2 et 10) à 10 mois (stations 3, 6 et 9, incluant la période d'hibernation) pour effectuer le reste de leur croissance. Signalons aussi que la brusque diminution de croissance à la mi-août coïncide avec le commencement de la ponte d'été-automne, période à laquelle certains individus nés au printemps ont atteint la taille de la maturité sexuelle. Une analyse de variance et un test de Student indiquent que les tailles moyennes atteintes en septembre par les générations printanières des stations 2, 6 et 10 ne sont pas significativement différentes en 1970 et 1971 ($\alpha = 0.05$). A la station 3, par contre, les individus sont significativement plus grands en 1971 (18.4 mm) qu'en 1970 (15.9 mm) et à la station 9, ils sont significativement plus petits en 1971 (13.2 mm) qu'en 1970 (15.9 mm) ($\alpha = 0.01$). Les mêmes tests montrent qu'en septembre 1970, il n'y a pas de différence significative de tailles chez les individus des stations 2, 3, 9 et 10 ($\alpha = 0.05$). Par contre, en septembre 1971 les tailles atteintes dans les différentes stations sont toutes significativement différentes, se classant ainsi par ordre décroissant: stations 3, 10, 2, 9 et 6.

Les courbes de croissance des individus des cohortes d'été-automne (II) des stations 2 et 10 sont plus difficiles à interpréter (Fig. 4). Durant les premiers mois de leur existence, les lymnées grandissent mais ce phénomène n'est pas mis en évidence par la variation de leur longueur moyenne, cette moyenne étant constamment diminuée par l'apparition de nouvelles recrues dans la population. Nous pouvons cependant constater que le tiers de la croissance de ces individus s'effectue avant la période d'hibernation (26% à la station 2, 34% à la station 10) et que les deux autres tiers s'effectuent au printemps suivant sur une période de deux mois environ.

Les comparaisons entre les tailles moyennes atteintes en septembre et celles atteintes au printemps suivant indiquent que les individus des cohortes printanières (I) n'effectuent aucune croissance hivernale mais que ceux des cohortes d'été-automne (II) continuent à grandir durant l'hiver ($\alpha = 0.01$).

Reproduction et fécondité

La taille à la maturité sexuelle, estimée par la taille moyenne des individus de chaque cohorte au début de leurs périodes de pontes (mai-juin; août-septembre) varie entre 6.9 mm (station 10, cohorte 1970 II, le 28 mai 1971) et 17.8 mm (station 3, cohorte 1970 I, 7 juin 1971) (Tableau 2). Au laboratoire, nous avons noté que le plus petit spécimen ayant déposé des pontes provenait de la station 2 et mesurait 8.15 mm. Il semble donc que les *L. catascopium catascopium* du lac Saint-Louis puissent atteindre la maturité sexuelle à une taille inférieure à 10 mm. Nos resultats indiquent aussi que les individus des populations à cycle de développement simple (station 3, 6 et 9) atteignent généralement la maturité sexuelle à une plus grande taille que ceux des populations à cycle de développement plus complexe avec deux générations par année (stations 2 et 10).

La densité des pontes des lymnées (nb/m^2) varie au cours de la saison (Fig. 5). Les pontes déposées entre août et novembre 1970 proviennent des individus des générations printanières de l'année et elles sont les plus nombreuses aux stations 2 et 9 (environ 10 par mètre carré). Les pontes déposées en juin et durant la premièe quinzaine de juillet de 1971 proviennent des individus de la génération d'été-automne de 1970 aux stations 2 et 10 et des survivants de la génération printanière de 1970 aux stations 3, 6 et 9. Le nombre de pontes printanières est très fort aux stations 2 et 6 (respectivement 64 et 80 au m^2 les 8 et 22 juin 1971). Le second pic de ponte en 1971 (août-septembre) est très réduit ou inexistant aux stations 3, 6 et 9, mais il est, par contre, plus important aux stations 2 et 10 où il représente alors la principale et unique période de pontes des individus nés au printemps.

L. catascopium catascopium produit deux types de pontes: la plupart, dites typiques, sont longues et étroites (12 mm et plus de longueur sur 2 à 3 mm de largeur) et en forme de croissant; les autres plus rares, dites atypiques, sont rondes ou légèrement ovoïdes et de petites dimensions (2 à 3 mm de longueur sur 2 mm de largeur). Ces pontes peuvent contenir de 5 à 175 oeufs. En moyenne, une ponte de *L. catascopium catascopium* contient 44 oeufs à la station 2,

TABLEAU 2. Tailles à maturité sexuelle des *L. catascopium catascopium,* estimés par la longueur moyenne des individus de chaque cohorte au début de leurs périodes de reproduction.

Station	Cohorte	Date	Taille moyenne (mm) ± erreur standard
2	1969 II	18 juin 1970	12.59 ± 2.14
	1970 I	3 août 1970	12.13 ± 0.55
	1970 II	28 mai 1971	6.97 ± 0.89
	1971 I	2 août 1971	11.02 ± 0.29
3	1969 I	23 juin 1970	17.12 ± 1.46
	1970 I	1 sept. 1970	15.19 ± 0.85
	1970 I	7 juin 1971	17.84 ± 2.26
	1971 I	13 sept. 1971	18.65 ± 0.72
6	1969 I	28 mai 1970	13.24 ± 0.91
	1970 I	1 sept. 1970	11.30 ± 0.13
	1970 I	25 mai 1971	13.08 ± 0.62
9	1969 I	21 mai 1970	11.40 ± 0.41
	1970 I	4 août 1970	13.87 ± 0.34
	1970 I	22 juin 1971	17.50 ± 1.62
	1971 I	15 août 1971	11.70 ± 0.26
10	1969 I et II	7 juil. 1970	13.11 ± 0.70
	1970 I	3 août 1970	10.07*
	1970 II	28 mai 1971	6.86 ± 1.09
	1971 I	3 août 1971	11.55 ± 0.24

*un seul spécimen.

TABLEAU 3. Fécondité des *L. catascopium catascopium* des cohortes de chaque population en 1970 et 1971.

Station	Cohortes	Période de reproduction	Nombre d'oeufs déposés
2	1969 II	18 juin—7 juil. 1970	490
	1970 I	22 juil.—11 nov. 1970	4874
	1970 II	28 mai—7 juil. 1971	13827
	1971 I	22 juil.—23 nov. 1971	24483
			Total: 43674
3	1969 I	18 juin—7 juil. 1970	151
	1970 I	31 août—15 oct. 1970	262
		28 mai—18 juin 1971	2946
	1971 I	14 sept. 1971	21
			Total: 3380
6	1969 I	28 mai—18 juin 1970	3294
	1970 I	31 août—14 sept. 1970	423
		28 mai—18 juin 1971	24240
	1971 I	—	—
			Total: 27957
9	1969 I	28 mai—6 juin 1970	5046
	1970 I	5 août—14 sept. 1970	3558
		6 juin—7 juil. 1971	7815
	1971 I	17 août—31 août 1971	1038
			Total: 17457
10	1969 II	7 juil. 1970	94
	1970 I	31 août—14 sept. 1970	1435
	1970 II	28 mai—7 juil. 1971	5426
	1971 I	5 août—28 sept. 1971	4468
			Total: 11423

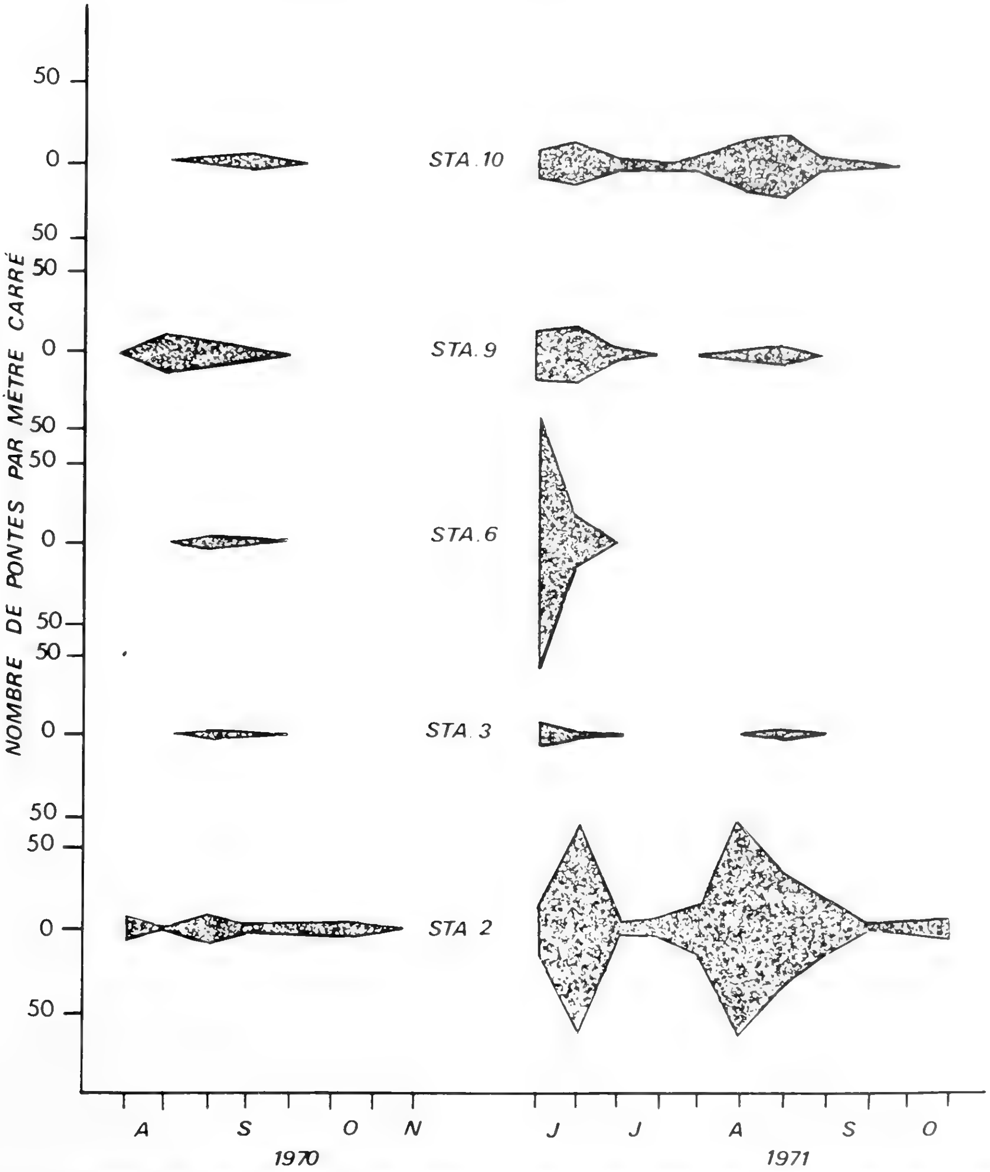

FIG. 5. Variation de la densité (nb/m²) des pontes de *L. catascopium catascoium* d'août à novembre 1970 et de juin à octobre 1971 dans chaque station d'échantillonnage.

43 oeufs à la station 3, 37 oeufs à la station 6, 49 oeufs à la station 9 et 38 oeufs à la station 10. Au laboratoire les pontes déposées par les Lymnées contenaient de 5 à 100 oeufs; les nombres moyen d'oeufs par ponte étaient de 29 (15°C) et 24 (20°C) pour les Lymnées de la stations 2; de 20 (15°C) et 25 (20°C) pour celles de la station 6 et de 69 (15°C) pour celles de la station 9.

La variation du nombre d'oeufs par ponte est très forte dans toutes les populations; ceci suggère que cette valeur n'est pas un critère de la fécondité des organismes et que celle-ci serait plutôt estimée par le nombre total d'oeufs déposés. Compte tenu de ces critères, nous avons estimé la fécondité des individus de chaque génération, à chaque année et dans chacune des populations par le nombre total d'oeufs déposés sur 4 m² au cours de la ou des périodes de reproduction de chaque génération, connaissant la durée de la période de reproduction, le nombre de pontes et le nombre moyen d'oeufs par ponte à chaque date d'échantillonnage. Les résultats (Tableau 3) indiquent que la fécondité des populations de Lymnées diffèrent d'une année à l'autre et d'une station à l'autre. Un plus grand nombre de pontes a été récolté en 1971; ceci est probablement dû au fait que nous avons eu, en 1970, une plus grande difficulté à repérer les pontes sur les roches. Parmi les populations qui ont un cycle avec deux générations per année, celle de la station 2 est plus féconde que celle de la station 10. Parmi les populations qui ne produisent qu'une seule génération par année, si nous comparons seulement les résultats obtenus pour la génération printanière (I) de la cohorte de 1970 dont nous avons observé les deux périodes de pontes, ce sont les individus de la station 6 qui sont les plus féconds (24663 oeufs); viennent ensuite ceux de la station 9 (11373 oeufs) et finalement ceux de la station 3 qui sont très peu féconds (3208 oeufs).

Au laboratoire, la fécondité des *L. catascopium catascopium* varie de 273 à 690 oeufs par individu à 15°C et de 226 à 365 oeufs par individu à 20°C. Ces données sont basées sur toute la période de vie des organismes, celle-ci variant de 48 à 150 jours selon les individus. Seuls les résultats obtenus chez les individus en provenance de la station 6 permettraient de supposer que la fécondité des individus est plus forte à 20°C (365 oeufs par spécimen) qu'à 15°C (273 oeufs par spécimen). A partir des résultats obtenus au laboratoire, nous avons estimé la relation entre la fécondité et la taille des organismes d'une part et celle entre la fécondité et le nombre d'oeufs moyen par ponte. Il en ressort que la fécondité des organismes n'est pas plus forte chez les gros spécimens que chez les plus petits ($r = 0.266$; $\alpha = 0.05$) et que le nombre moyen d'oeufs par ponte n'est pas plus faible chez un spécimen qui dépose beaucoup de pontes que chez un autre qui en dépose peu ($r = -0.158$; $\alpha = 0.05$).

DISCUSSION

Les variations de températures entre les milieux ne peuvent induire les différences fondamentales observées dans le cycle de développement des Lymnées car, comme nous l'avons vu, elles sont très faibles. Il semble, par contre, que l'on puisse mettre en corrélation la nature chimique des eaux et le type de cycle annuel des Lymnées: les populations qui présentent un cycle de développement avec une seule génération par an se situent dans les eaux dures du fleuve Saint-Laurent (stations 3 et 6) ou en eau mixte (station 9) tandis que celles qui ont un cycle de développement avec deux générations par année se situent dans les eaux douces de la rivière des Outaouais (stations 2 et 10).

Plusieurs auteurs ont signalé les effets de la nature physico-chimique et biotique du milieu sur la biologie des mollusques d'eau douce (Williams, 1964, 1970; Dussart, 1973, 1976). Harrison et al. (1970) ont mis en évidence l'action du bicarbonate de calcium sur la dynamique de populations du Planorbidé *Biomphalaria pfeifferi.* Hunter (1961a, b), Eisenberg (1970) et Stanczykowska et al. (1971) ont montré que les conditions trophiques entrainent aussi des modifications dans la biologie et particulièrement dans les types de développement de diverses espèces de mollusques. L'avantage d'un cycle de développement avec une seule génération par année, où les jeunes recrues ne font pas compétition avec leurs géniteurs pour la nourriture, est en effet évident. Nos propres recherches sur la nutrition de *L. catascopium catascopium* semblent confirmer cette hypothèse: la qualité du régime alimentaire des spécimens des stations 3 et 6 était en effet beaucoup plus faible que celles des individus des stations 2 et 10 (Pinel-Alloul & Magnin, sous presse).

Parmi les autres Lymnaeidae, le type de développement le plus simple avec une seule génération par année est le plus commun en zones tempérées nordiques (McCrawn, 1961; Noland & Carriker, 1946; De Coster & Persoone, 1970; Morrison, 1932; Herrington, 1947). En Angleterre, cependant *L. peregra* et *L. palustris* présentent les deux types de développement (Hunter 1961b, 1975). On a signalé aussi d'autres variations dans les cycles de développement: trois générations par an chez *L. truncula*ta (Walton & Jones 1926), un cycle bisannuel avec une génération à tous les deux ans chez *L. stagnalis* (Berrie, 1965; Pinel-Alloul 1975). La majorité des Pulmonés ont un cycle de développement simple mais le cycle avec deux générations par année semble très courant chez les Physidés (De Wit, 1955; Hunter, 1961b; Clampitt, 1970; Lacasse-Joubert, 1970) et, il existe aussi chez les Ancylidae (Burky, 1971) et chez les Planorbidae (Achard, 1973).

L'oviposition printanière a lieu lorsque la température de l'eau est d'environ 12 à13°C; en automne des pontes ont été récoltées jusqu'en novembre à des températures de 9 à 10°C. Boerger (1972, 1975) indique que la ponte chez *Helisoma trivolvis, H. campanulatum* et *H. anceps* ne se déclenche qu'à des températures supérieures à 10°C, quelle que soit la photopériode. Le succès de la ponte d'été-automne ne semble pas devoir être lié à l'action limitante de la température, car, aux stations 3 et 6, les températures mesurées en août et septembre 1970 et 1971 sont comparables à celles observées aux stations 2 et 10 et elles sont toujours supérieures à 10°C (Fig. 1). Il serait plutôt relié à des différences dans l'âge et la taille à la maturité sexuelle. Les individus des populations à cycle simple atteignent généralement la maturité sexuelle à une taille plus grande que ceux des populations avec un cycle à deux générations par année; ils deviennent donc matures plus tard à l'automne quand la température de l'eau baisse et pour la plupart d'entre eux la saison de reproduction se trouve ainsi reportée au printemps suivant. La même observation a été faite sur des populations de *L. peregra* de Loch Lomond, Ecosse (Hunter 1961b); il semble que cette différence dans la taille à la maturité sexuelle soit reliée à la fois aux facteurs physiques (température), trophiques (qualité du régime alimentaire) et génétiques.

Chez les populations qui ne produisent qu'une seule génération par année, le développement de cette génération requiert environ 12 mois (juin à mai-juin de l'année suivante), mais dans les populations avec un type de développement à deux générations par année, la majorité des individus de la génération printanière vivent moins de six mois. Le même phénomène a été observé chez d'autres pulmonés d'eau douce (Geldiay, 1956; Hunter, 1961b; Achard, 1973). Dans les régions plus chaudes que le Québec, la période de recrutement de la génération printanière est plus longue: de mars à août chez les *L. peregra* d'Ecosse (Hunter 1961b), d'avril à août chez les *Ferrissia rivularis* de l'état de New York (Burky, 1971).

Lacasse-Joubert (1970), Clampitt (1970) et Achard (1973) ont aussi observé l'étalement de la période d'éclosion des générations d'été-automne chez des populations de Physes et de Planorbes. Ce phénomène laisse supposer que les individus de la génération printanière n'atteignent pas tous en même temps la maturité sexuelle et qu'ils se reproduisent de façon échelonnée aussi longtemps que la température du milieu le permet, bien qu'ils soient nés sur une période de temps assez courte (environ 15 jours). Ceci est probablement la conséquence des variations individuelles de la croissance des individus que l'étalement des histogrammes de fréquence des longueurs met en évidence (Figs. 2 et 3).

Le schéma de croissance n'est pas le même pour tous les individus. La croissance des individus de la génération printanière (I) suit une courbe sigmoïde typique des mollusques d'eau douce (Crabb, 1929; Baily, 1931; Sitaramaiah, 1966). La croissance des individus de la génération d'été-automne (II) (stations 2 et 10) est difficile à préciser par suite de l'étalement de la période de recrutement des jeunes; il semble toutefois qu'elle soit faible en automne et beaucoup plus rapide au printemps. Ces résultats sont comparables à ceux obtenus par Clampitt (1970) et Lacasse-Joubert (1970), sur des populations de Physes, qui ont un cycle de développement avec deux générations par année.

Nos résultats font aussi ressortir l'action de la température ambiante sur la croissance des individus, ce qui a été maintes fois observé chez d'autres Gastéropodes (Vaughn, 1953; Duncan, 1959; Pinel-Alloul, 1969; Lacasse-Joubert, 1970; Achard, 1973; Calow, 1973). Dans le milieu naturel, nous remarquons en effet que les individus nés au printemps (génération I) et qui survivent à la période d'hibernation, reprennent leur croissance au printemps suivant à une vitesse supérieure à celle de l'automne.

Nous avons aussi noté que la croissance des individus des générations II se poursuit faiblement durant l'hiver tandis que celle des individus des générations I est pratiquement nulle. Ces résultats sont comparables à ceux obtenus par Lacasse-Joubert (1970) sur *Physa gyrina* du lac Saint-Louis et Calow (1973) sur *Planorbis contortus* à Leeds en Angleterre. Il semble que cet arrêt de croissance soit directement contrôlé par la température car ces deux auteurs ont ramené en hiver des spécimens du milieu naturel (≃ 0°C) au laboratoire (18°C) et ceux-ci ont recommencé à croître et à se reproduire. Par contre, Hunter (1961b) rapporte que *L. peregra* continue de croître durant l'hiver au Loch Lomond (Ecosse) et Clampitt (1970) fait la même observation pour *Physa gyrina* et *P. integra* au lac Okboji (Iowa).

Parmi les facteurs susceptibles d'entraîner des variations annuelles dans la croissance des organismes on pense d'abord à la température. Or nous avons vu que les variations de la température sont assez semblables au cours des mois de juillet et août durant lesquels s'effecture surtout la croissance des mollusques. On remarque aussi qu'à la station 3 les Lymnées sont plus grandes en 1971 qu'en 1970 alors que la température de l'eau était généralement plus élevée en 1970 qu'en 1971, Achard (1973) a fait exactement les mêmes observations sur les variations annuelles de la croissance d'*Helisoma trivolvis* récoltés en même temps et aux mêmes stations. Il semblerait donc que les variations annuelles de la croissance des individus seraient dues plus aux conditions trophiques du milieu qu'à la température.

Au laboratoire, le plus petit spécimen sexuellement mature mesurait environ 8 mm (station 2). D'après Walter (1969), le système reproducteur de *L. catascopium* a une structure adulte chez les individus de 10 à 11 mm au lac Houghton, Michigan; le sperme est présent dans la glande hermaphrodite des spécimens de 8 mm et les ovules matures dans ceux de 11 mm. A partir d'observations effectuées sur le cycle de développement, Kevan (1942) estime que la taille moyenne des *L. catascopium catascopium* sexuellement matures est de 13 mm en Angleterre. Au lac Saint-Louis, elle varie de 6.9 à 17.8 mm. Les individus en provenance des populations à cycle vital avec une seule génération par année (stations 3, 6 et 9) atteignent généralement la maturité sexuelle à une taille plus grande que ceux des populations avec un cycle vital à deux générations par année (stations 2 et 10). La même constatation a été faite par Hunter (1961b) sur les populations de *L. peregra* du Loch Lomond, Ecosse. Walter (1969) a aussi observé deux types de pontes chez une population de *L. catascopium catascopium* au lac Houghton (Michigan), mais en Angleterre, Kevan (1942) n'a récolté que des pontes typiques (10 à 15 mm de longueur sur 5 à7 mm de largeur). Ce phénomène semble s'étendre à d'autres espèces de Lymnaeidae; Hunter (1961a) signale la même chose pour *L. peregra* en Ecosse et émet l'hypothèse qu'il s'agit peut-être là d'un mélange de deux races physiologiques.

La grande variation du nombre d'oeufs par ponte pourrait signifier que cet indice n'est pas un critère de la fécondité des *L. catascopium catascopium*. Van der Steen (1967), après des études au laboratoire sur la reproduction de *L. stagnalis stagnalis*, mentionne aussi que le nombre d'oeufs par ponte ("capsule size") et la fécondité sont des variables indépendantes de la reproduction.

Les résultats de nos élevages en laboratoire, ont mis en évidence que la température n'a pas une influence déterminante sur le nombre moyen d'oeufs par ponte de *L. catascopium catascopium*, ce qui avait déjà été observé chez *L. stagnalis stagnalis* par Van der Steen (1967).

Les estimations de fécondité faites en laboratoires (226 à 690 oeufs/Lymnée) s'accordent avec celles rapportées pour d'autres Pulmonés: *Lymnaea peregra* pond de 315 à 1155 oeufs au cours de sa période de reproduction en milieu naturel (Hunter, 1961a) et de 200 à 300 oeufs en captivité (Boycott, 1936); *Physa gyrina* pond de 200 à 300 oeufs par mois durant son pic de reproduction et un total de 700 à 1000 oeufs au cours de sa période de reproduction (Clampitt, 1963) mais sa fécondité peut aussi être plus faible: 272 oeufs/individu (De Witt 1954b). Nous n'avons pas obtenu de corrélation positive entre la taille des organismes et leur fécondité contrairement à ce qu'a obtenu De Witt (1954a) sur *Physa gyrina*.

Au lac Saint-Louis, *Lymnaea catascopium catascopium*, qui présente déjà un fort potentiel de variations morphométriques (Clarke, 1973), fait preuve aussi d'une grande plasticité écologique dans son cycle de développement, sa croissance et sa fécondité. De nombreux travaux font d'ailleurs mention de ce phénomène chez d'autres Pulmonés (Clampitt, 1963; Geldiay, 1956; Hunter, 1961b; Lacasse-Joubert, 1970; Burky, 1971; Achard, 1973), mais, ce potentiel de variation serait plus élevé chez les Lymnaeidae et les Physidae que chez les Planorbidae et les Ancylidae.

D'après Hunter (1961b), cette plasticité écologique s'expliquerait par les processus d'évolution des mollusques pulmonés dans les milieux d'eau douce qui sont souvent transitoires et caractérisés par une isolation à court terme et à petite échelle. Ces organismes n'auraient pas eu le temps d'atteindre une spéciation définitive; la sélection à laquelle ils auraient été soumis aurait produit seulement des génotypes présentant une grande flexibilité phénotypique et une grande capacité d'adaptation.

CONCLUSION

Notre étude montre que les différents paramètres qui régissent la dynamique des populations de *Lymnaea catascopium catascopium* au lac Saint-Louis sont sujets à de très fortes variations:

—le Lymnaeide presente deux types de développement qui peuvent être mis en corrélation avec la nature chimique des eaux: les populations qui présentent un cycle de développement avec une seule génération par an se situent dans les eaux dures du Saint-Laurent (stations 3 et 6) ou en eau mixte (station 9); celles qui ont un cycle de développement avec deux générations par années se situent dans les eaux douces de la rivière des Outaouais (stations 2 et 10). Ces différences dans le cycle de développement s'accompagnent de variations dans l'intensité et la durée des périodes de pontes, dans la composition de la population hibernante et dans la longévité des individus.

—La croissance des individus nés au printemps suit une courbe sigmoïde typique des mollusques d'eau douce mais elle est sujette à des variations annuelles et entre les populations.

—*L. catascopium catascopium* peut être mature à une taille inférieure à 10 mm et la maturité sexuelle est plus tardive dans les populations à cycle de développement avec une seule génération par année. Il y a deux pics de pontes: en juin et juillet puis d'août à novembre et les pontes contiennent en moyenne de 37 à 49 oeufs.

—La fécondité des populations diffèrent d'une année à l'autre et d'une station à l'autre; parmi les populations qui ont un cycle avec deux générations par année, celle de la station 2 est plus féconde que celle de la station 10; parmi les populations qui produisent une seule génération par anné, celle de la station 6 est la plus féconde, vient ensuite celle de la station 9 et finalement celle de la station 3.

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ABSTRACT

LIFE CYCLE, GROWTH AND FECUNDITY OF FIVE POPULATIONS OF *LYMNAEA CATASCOPIUM CATASCOPIUM* (GASTROPODA, LYMNAEIDAE) IN LAKE SAINT-LOUIS, QUEBEC, CANADA

Bernadette Pinel-Alloul and Etienne Magnin

In following the demography of five populations of *Lymnaea catascopium catascopium,* the commonest lymnaeid in Lake Saint-Louis, Quebec, we have studied its life cycle, growth and fecundity. This species has two kinds of development, one simple with a single generation per year and a single period of successful reproduction (in spring), the other more complex with two generations per year and two periods of reproduction (June-July and August-November). These fundamental differences in the life cycle can be related to water chemistry: the hard, alkaline waters of the St. Lawrence River and the soft and neutral waters of the Outaouais River. The growth of individuals fits a sigmoid curve and shows intraspecific and annual variations which can be explained by differences in the trophic nature of the habitat rather than by physicochemical variations. *L. catascopium catascopium* lays two kinds of egg masses and is sexually mature at a length less than 10 mm. Its fecundity estimated for the period 18 June 1970 to 23 November 1971 varied from 3,380 to 43,674 eggs depending on the population. In the laboratory, each animal laid 273 to 690 eggs at 15° C and 226 to 365 eggs at 20°. The results of our study have evolutionary implications in relation to the nature of fresh-water habitats.

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PHYLOGENETISCHE ASPEKTE DER RADULAMORPHOGENESE VON GASTROPODEN

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ZUSAMMENFASSUNG

In verschiedenen Pulmonatenfamilien wurde die Morphogenese der Embryonalradula untersucht.

1. Das für die Lungenschnecken typische, gleichmässige Zahnmuster liegt ontogenetisch erst sekundär vor. Zuerst werden 2 laterale Zahn-Längsreihen angelegt (edistiches Stadium). Nach Auftreten weiterer lateralen Längsreihen sitzen die Zähnchen in 2 getrennten Arealen. Erst mit der Ausbildung von Mittelzähnen entsteht ein einheitliches Areal mit dem typischen Zahnmuster der Pulmonaten.

2. Die primär distiche, bzw. bilaterale Anordnung der Zähnchen in der Embryonalradula gleicht auffallend dem in den niederen Molluskenklassen der Caudofoveata und Solenogastres vorherrschenden Zahnmuster. Daraus wird gefolgert, dass in der Morphogenese der Gastropodenradula Anklänge an eine phylogenetisch ursprünglichere Radulaform hervortreten.

EINLEITUNG

Sterki (1893) fand bei verschiedenen Landpulmonaten eine gesetzmässig ablaufende Radulamorphogenese mit einem auffälligen Formwechsel zwischen Jugend- und Adultzähnen. Entsprechendes beschreibt Richter (1961) bei den prosobranchiaten Atlantiden. In dieser Familie besitzen die evoluierteren Arten spezialisierte, einspitzige Adultzähne. Die frühontogenetisch ausgebildeten Zähne rekapitulieren die mehrspitzigen Zahnmorphen ursprünglicherer Atlantiden-Arten.

Mit Hilfe einer Quetschmethode, die es gestattet, serienweise gute Radulapräparate von Embryonen herzustellen, wurden Radulamorphogenesen und Radulawachstum in einer ganzen Reihe von Pulmonatenfamilien untersucht (Rittmann, 1973; Schier, 1975; unveröffentlicht). In dieser Arbeit interessiert speziell die am frühesten fassbare Radula des Pulmonatenkeimes. An ihr zeigen sich Besonderheiten des Zähnchenmusters, die einer phylogenetischen Interpretation unterzogen werden sollten. Sie betreffen Überlegungen zum Aussehen einer phylogenetisch ursprünglichen Mollusken-Radula, wie sie schon mehrfach, zuletzt von Salvini-Plawen (1972) sowie Minichev & Sirenko (1974) angestellt wurden.

MATERIAL UND METHODEN

Haltung der Versuchstiere

Helix pomatia (Helicidae). Freilandkäfig, Futter: Salat, Karotten. Eientwicklung bei 15°C und 12/12 Gleichtag.

Limax flavus (Limacidae). Zucht: siehe Kerth & Krause (1969).

Lymnaea stagnalis (Lymnaeidae). Zucht bei 25°C, 12/12 Gleichtag, Futter: Frischer Salat.

Biomphalaria glabrata (Planorbidae). Zucht bei 25°C, 12/12 Gleichtag. Futter: Frischer Salat.

Planorbarius corneus (Planorbidae). Zucht bei 21°C, 16/8 Langtag. Futter: Salat, Teichdetritus, Wasserpflanzen.

Physa fontinalis (Physidae). Adulti stammen vom Neusiedler See. Zucht bei 15°C, 12/12 Gleichtag. Futter: moderndes Pflanzenmaterial vom Teichboden.

Ancylus fluviatilis (Ancylidae). Zucht bei 15°C, 12/12 Gleichtag. Futter: Steinaufwuchs vom Bachgrund.

Quetschpräparation der Embryonalradula

Die den Gelegen entnommenen Eier werden von ihrer Hülle befreit. Verdünnte HCl wird auf den Embryo aufgetropft, um die

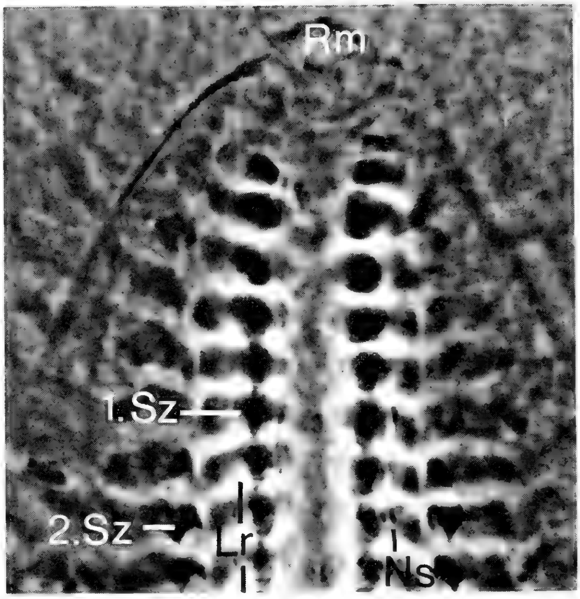

ABB. 1. *Planorbarius corneus.* Vorderende der Embryonalradula. Innere Seitenzahn-Längsreihen zuerst entstanden. 10. Tag, 1400 × Phako (Phasenkontrast). Lr, Längsreihe; Ns, Nebenspitzen; Rm, Radulamembran; Sz, Seitenzahn.

Schale aufzulösen. Anschliessend 5 min Mazerieren mit 5% KOH. Der mazerierte Embryo wird unter dem Deckglas in heisser Glycerin-Gelatine kräftig gequetscht. Die winzige Radula liegt fast immer schön ausgebreitet. Altersangaben in Tagen nach Eiablage.

BEFUNDE ZUR EMBRYONALRADULA

Entstehung des Zähnchenmusters

Bei den untersuchten Pulmonaten tritt eine Radula im Quetschpräparat erstmals 5–12 Tage nach Eiablage auf. Die Radulabildung beginnt mit der Sezernierung eines terminalen Membranabschnittes (Abb. 1). Hinter diesem folgen in Längs- und Querreihen angeordnete Zähnchen. Hintereinander liegende Querreihen entstehen zeitlich nacheinander (Isarankura & Runham, 1968; Kerth & Krause, 1969).

Bei allen untersuchten Arten ausser *Ancylus* entsteht die Pulmonaten-Radula auf dieselbe Weise. Zuerst erscheint ein Paar Zahn-Längsreihen: die 1. Seitenzähne beiderseits der Radulamedianen (Abb. 1). Weitere Seitenzahn-Längsreihen treten auf beiden Seiten gleichmässig ausserhalb der schon vorhandenen hinzu. Erst wenn 1–3 Paare lateraler Längsreihen angelegt worden sind, erscheinen in der Radulamedianen die Mittelzähne.

Die Embryonalradula ist an ihrem Vorderende zuerst distich, d.h. es existieren nur 2 Längsreihen. Nach Auftreten weiterer lateraler Längsreihen liegen die Zähnchen zunächst meist in zwei median deutlich getrennten Arealen. Dies trifft zu für *Helix, Lymnaea, Planorbarius, Biomphalaria, Physa* (Abb. 2a–e). Bei ihnen treten die Mittelzähne später als bei den anderen untersuchten Arten auf. Erst durch das Erscheinen der Mittelzähne entsteht eine einheitliche zahnbesetzte Fläche (Abb. 2c). Von da an weitet sich das Zähnchenmuster aus, indem ständig neue Querreihen am Radulahinterende und neue Längsreihen an den Radularändern hinzukommen. So entsteht das grossflächige, gleichmässige Zahnmuster der Lungenschnecken. Zur histologischen Basis der Musterbildung vergleiche Kerth & Hänsch (1977).

Nur bei *Ancylus* entsteht das Zähnchenmuster der Embryonalradula anders. Auf einer schmalen Membran liegen 2 Zähnchenareale hintereinander (Abb. 3a, b; I, II). Das vordere (I) besteht aus 2 Längsreihen mit je etwa 10 hakenförmigen Dentikeln (Abb. 3c). Dahinter (im Bild: darunter) folgt ein Areal (II) mit dem normalen

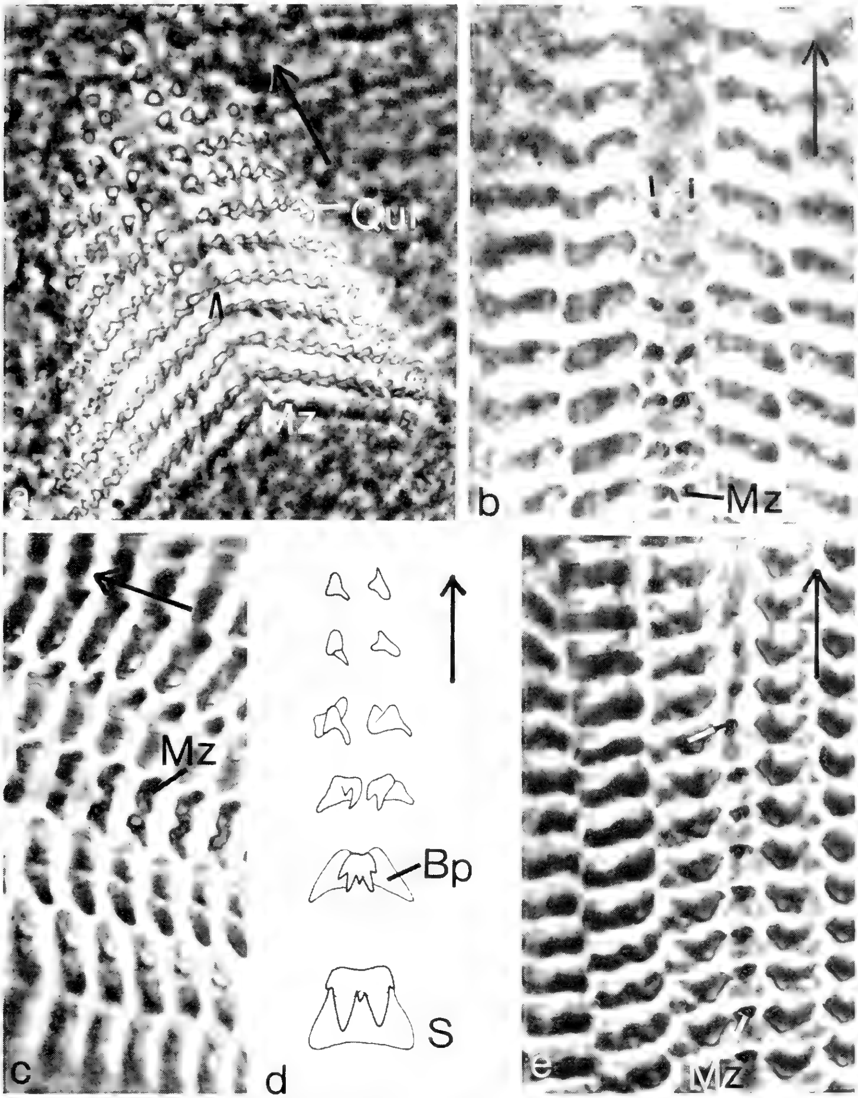

ABB. 2. Primäre Zahnordnung der Embryonalradula. Vordere Querreihen sind älter als hintere. Pfeil zeigt stets zum Radulavorderende. (a) *Physa fontinalis.* Am Radulavorderende sitzen die Zähne in 2 lateralen Arealen. Einheitliche zahnbesetzte Fläche erst nach Ausbildung des Mittelzahnes. (8. Querreihe, Marke !). 12. Tag, 480 × Phako. Mz, Mittelzahn; Qur, Querreihe. (b) *Planorbarius corneus.* Paarige Mittelzahn-Höcker (Marken !). 10. Tag, 1200 × Phako. (c) *Planorbarius corneus.* Nach Ausbildung der Mittelzähne liegt ein geschlossenes Zähnchenareal vor, 10. Tag, 1200 × Phako. (d) *Planorbarius corneus.* Morphogenese des Mittelzahnes. Bp, Basalplatte; S, Zahnform zum Schlüpfzeitpunkt. (e) *Lymnaea stagnalis.* Singuläre Mittelzahn-Höcker (Marke), 9. Tag, 1200 × Phako.

Zähnchenmuster. Die beiden Dentikelreihen sind zuerst entstanden. Sie haben einen grösseren Zwischenabstand als Längsreihen des hinteren Areals. Ausserdem sitzen ihre Zähnchen in grösserem Abstand hintereinander. Das Zähnchenmuster des Areals (II) entsteht später und in der oben beschriebenen, üblichen Weise. Zur Schlüpfzeit ist die Region (I) bereits abgebaut worden.

Zahnmorphogenese in den Längsreihen

Laterale Reihen. In den lateralen Längsreihen der Embryonalradula erkennt man bei allen untersuchten Arten ausser *Physa* die

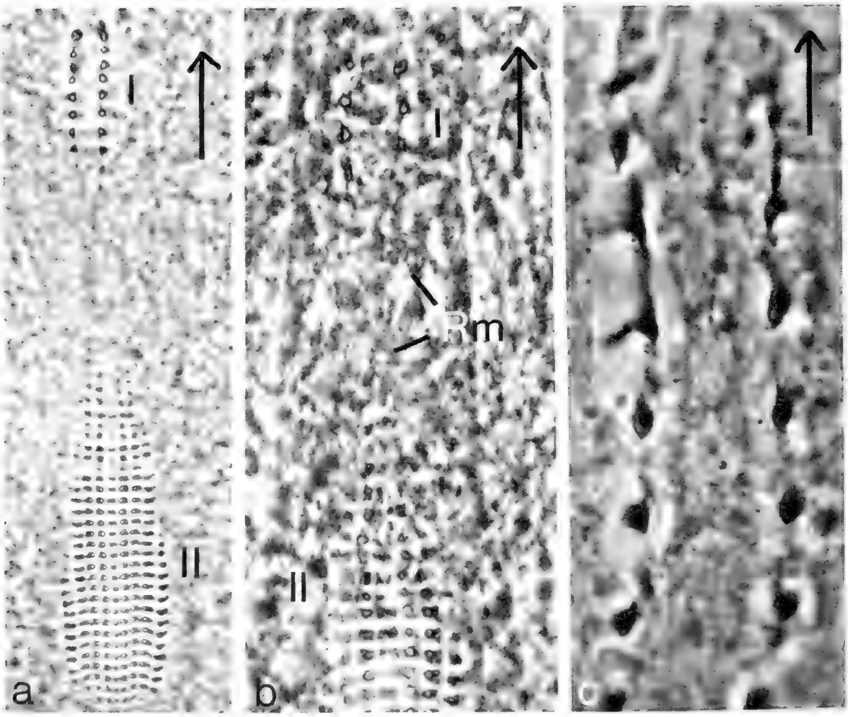

ABB. 3. *Ancylus fluviatilis*. Embryonalradula, 13. Tag. (a) Vorderer Radulaabschnitt (I) mit nur 2 Längsreihen. Dahinter normales Zähnchenareal der Embryonalradula (II). 246 × Phako. (b) Areal (I) und (II) auf der gemeinsamen Radulamembran. 480 × Phako. (c) Hakendentikel des vorderen Radulaabschnittes. 1400 × Phako.

schon von Sterki (1893) bei verschiedenen Pulmonaten gefundene auffällige Änderung der Zahnform. Hinter den vordersten kleinen Höckern folgen mehr- bis vielspitzige (echinate) Zähnchen mit völlig anderem Umriss als bei Zähnen eines adulten Tieres (Abb. 1, Ns). Die Adulti der untersuchten Arten besitzen in den entsprechenden Längsreihen nur noch ein- bis dreispitzige Zähne. Der Formübergang zeigt sich an Zähnen, die in der späten Embryonal- und frühen Postembryonalentwicklung gebildet werden. Nur *Physa* ist eine Ausnahme. Bei ihren gesägten Zähnen erhöht sich während der Ontogenese die Zahl der Schneidendentikel ständig.

Mittelzahn-Reihe. Nur bei *Helix* und *Lymnaea* erscheinen die Mittelzähne sofort als singuläre Gebilde (Abb. 2e). Bei den anderen Arten treten im medialen Radulabereich zuerst paarige Höcker auf (Abb. 2b). Dann erscheinen fusionierende Höcker und später wird ein einheitlicher Mittelzahn sezerniert. (Der definitive Mittelzahn von *Physa* ergibt sich aus einer weiteren Fusion mit dem rechts und links angrenzenden Seitenzahn.)

DISKUSSION

Die phylogenetisch ursprüngliche Molluskenradula

Die Vielfalt der heutigen Molluskenradulae reflektiert Anpassungen an die verschiedenen Formen des Nahrungserwerbs. Überlegungen, wie eine ursprüngliche Radula ausgesehen haben könnte, konzentrieren sich auf vergleichend morphologische und embryologische Befunde an den in vielen Merkmalen primitiven Molluskengruppen der Caudofoveata, Solenogastres, und Polyplacophora.

Die Meinungen gehen weit auseinander. Boettger (1955) hält eine median zweigeteilte Radula für ursprünglich. Salvini-Plawen (1972) legt sich auf eine ungeteilte, einheitliche Radula als Basisform bei den Weichtieren fest.

Innerhalb der niedersten Molluskenklassen

Caudofoveata und Solenogastres ist die distiche Radula (mit 2 Zahn-Längsreihen) vorherrschend. Nierstrasz (1909) sieht sie für beide Gruppen als phylogenetisch ursprünglich an. Salvini-Plawen (1972) hält dagegen die distiche Bezahnung für abgeleitet. Er stellt eher eine Radula mit vielen Dentikel-Längsreihen an die Molluskenbasis. Minichev & Sirenko (1974) nehmen nach embryologischen Untersuchungen an, dass die Polyplacophora ursprünglich eine Radula mit einer Zahn-Längsreihe besassen. Aus den Radulaformen bei primitiven Schnecken-Familien schliessen sie, dass für die Gastropoda eine Radula mit vielen Längsreihen und einheitlicher, flächiger Bezahung ursprünglich ist.

Radulamorphogenese der Pulmonaten

Frühontogenetische Befunde liegen nunmehr zu 5 Stylommatophoren- und 4 Basommatophorenfamilien vor (mit Sterki, 1893, und Schnabel, 1903). Die Embryonalradula durchläuft zuerst ein distiches Stadium. Nachdem weitere laterale Längsreihen auftreten, besitzt sie zwei deutlich getrennte Zähnchenareale. Erst mit dem Erscheinen der Mittelzähne vereinigen sich die bilateralen Areale zu einer einheitlichen Fläche. Dieser Fusionsvorgang wird bei mehreren Spezies auch in der Entstehung der Mittelzähne deutlich. *Das typische, sehr einheitliche Zähnchenmuster der Pulmonaten liegt also ontogenetisch erst sekundär vor.*

Abweichende Befunde von Sterki an 3 verschiedenen Stylommatophoren sind nicht sehr aussagekräftig. Aus seinen Abbildungen geht deutlich hervor, dass er damals die vordersten, winzigen Zahnhöcker der Embryonalradula übersehen hat.

Am aufälligsten ist die primär distiche Bezahnung bei *Ancylus* ausgeprägt. Bevor das typische Pulmonatenmuster erscheint, liegt ein ganz anderer "Radulatyp" vor. Seine Hakendentikel erinnern an Solenogastresverhältnisse. Damit gibt es bei den Lungenschnecken eine Parallele zur Opisthobranchia-Gattung *Polycera.* Dort entsteht ebenfalls vor dem definitiven Radula-Areal eine Region mit distichen Hakendentikeln (Präradula, Pruvot-Fol, 1926). Auch der prosobranchiate *Viviparus* bildet seine Zahn-Längsreihen nach dem Pulmonatenschema aus. Erst wenn alle Lateralreihen angelegt sind, erscheinen die Mittelzähne (Schnabel, 1903).

Die von Sterki (1893) beschriebenen, nur frühontogenetisch gebildeten echinaten Zähne sind in fast allen untersuchten Pulmonatenfamilien gefunden worden.

Phylogenetische Aspekte der Radulamorphogenese

In Untersuchungen und Diskussionen über Radulaevolution spielen Rekapitulationsphänomene in der Radulamorphogenese eine wichtige Rolle (Richter, 1961; vergleiche Einleitung dieser Arbeit; Salvini-Plawen, 1972, Minichev & Sirenko, 1974). Generell dürfen Rekapitulationen bei kritischer Beurteilung durchaus als existent angesehen werden (Rensch, 1960; Mayr, 1967).

Es stellt sich nun die Frage, ob auch in der Embryonalradula der Pulmonaten phylogenetische Reminiszensen hervortreten. Der Übergang von der primär distichen bzw. bilateralen Bezahung zur geschlossenen flächigen ist nicht funktionell- durch Ernährungsumstellung-bedingt. Er ist vollzogen, bevor sich das Scheidenlumen zur Mundhöhle öffnet (Schnabel, 1903; Cumin, 1972). Man darf deshalb bei aller Vorsicht im ontogenetisch primär distichen beziehungsweise bilateral-zweiteiligen Zähnchenmuster ein phylogenetisches Relikt erblicken. Es scheint nicht auf die Pulmonaten beschränkt zu sein, sondern wird auch bei den diesbezüglich kaum bearbeiteten Proso- und Opisthobranchia angetroffen.

Aus der Radulamorphogenese der Gastropoda kann geschlossen werden, dass der phylogenetische Weg zu den heutigen Schneckenradulae über ein distich-bilaterales Stadium der Bezahnung gelaufen ist. Ob man damit einen Schlüssel zur Radula der Molluskenbasis gefunden hat, ist nicht zu entscheiden. Jedenfalls sprechen die embryologischen Befunde bei Schnecken gegen die Auffassung von Minichev & Sirenko (1974) zur phylogenetisch ursprünglichen Radula an der Gastropodenbasis.

Ein distiches, beziehungsweise bilateral-zweiteiliges Zahnmuster ist bei den Solenogastres und Caudofoveata vorherrschend (Salvini-Plawen, 1969; Götting, 1974).Beide Gruppen werden von Salvini-Plawen (1972) trotz deutlicher Spezialisierungen überzeugend in den Umkreis der Stammesbasis gestellt. Mit der Rekapitulierung eines heute nur bei diesen niedersten Weichtierklassen anzutreffenden Zahnmusters tritt bei den

Gastropoda offenbar ein genetisch fixiertes, phylogenetisch sehr altes Molluskenmerkmal zutage.

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ABSTRACT

PHYLOGENETIC ASPECTS OF RADULA MORPHOGENESIS OF GASTROPODS

Klaus Kerth

The embryonic morphogenesis of the radula was investigated in several pulmonate families.

1. The uniform tooth pattern, typical for pulmonates, arises ontogenetically as a secondary phenomenon. When the radula begins to be secreted, two longitudinal rows of lateral teeth appear (distichous phase). In the following stage further rows of lateral longitudinal rows are added, and the teeth are arranged in two separate areas. When the central teeth are finally secreted, both patches are united into a uniform area, the typical tooth pattern in pulmonates.

2. The primary distichous, or bilateral, arrangement of teeth in the pulmonate radula conspicuously resembles the predominant tooth pattern in the lower mollusc classes of Caudofoveata and Solenogastres. Therefore it is concluded that the radula morphogenesis of gastropods reveals vestiges of a phylogenetically more primitive organ.

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NON-PELAGIC REPRODUCTION OF SOME ANTARCTIC PROSOBRANCH GASTROPODS FROM SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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ABSTRACT

The eggs of ten species of Antarctic marine prosobranch gastropods are described from Signy Island, South Orkney Islands. All the species are oviparous and develop non-pelagically, with young emerging as crawling juveniles. Two species utilise "nurse eggs" as food for a single embryo, whereas in the remaining species the majority of eggs in the mass or capsule develop successfully. Egg development in six of the species was followed by monthly inspection of the sub-littoral over a two year period, and in four of these the recruitment of juveniles was monitored by quantitative sampling. The reproductive patterns of six species are constructed from these data.

Spawning was largely asynchronous in most species, and spawning and development periods were prolonged. Periods during which juveniles emerged from the egg masses or capsules were also lengthy and did not specifically coincide with the austral summer, though there may have been increased recruitment of juveniles over this period. The significance of non-pelagic development is discussed, and egg-size, fecundity, juvenile size at emergence, and seasonality of reproduction examined in relation to the Antarctic marine environment.

INTRODUCTION

The benthic marine invertebrate faunas of both the Arctic and Antarctic show a strong tendency towards non-pelagic development. The Echinodermata (Einarsson, 1948), Polychaeta (Curtis, 1977), Lamellibranchia (Ockelmann, 1958), Crustacea and Gastropoda (Thorson, 1935, 1936, 1950), are all good examples of Arctic groups in which the majority of species whose reproduction is known develop without a pelagic larval stage. In the Antarctic, the echinoderms, lamellibranchs, crustaceans, and polychaetes have adaptations similar to those of their Arctic counterparts (Thorson, 1936, 1950; Soot-Ryen, 1951; Dell, 1964, 1972; Bone, 1972; Bregazzi, 1972; Thurston, 1972; White, 1970). The Antarctic gastropods have been assumed to follow suit, but for many years the only evidence of non-pelagic development in this class was the absence of gastropod larvae in the plankton of high southern latitudes (Simroth, 1911; Mackintosh, 1934). Gastropod eggs were mentioned in some early taxonomic accounts (e.g. Melvill & Standen, 1898; Strebel, 1904–1907) and short notes on eggs and egg masses have appeared more recently (Hedgpeth, 1964, Gibson et al., 1970). Thorson (1950) examined, but did not describe, the egg capsules of 16 species of prosobranch gastropods from the "Discovery" collections, and determined from the capsules that the species all seemed to have non-pelagic development. Such isolated observations support the assumption that the majority of Antarctic gastropods develop without pelagic larvae, but there are few detailed studies to confirm this conclusion. The most pertinent are Simpson's (1977) account of the reproduction of four littoral species at Macquarie Island in the sub-Antarctic (54°38′S 158°53′E), and Seager's work on *Philine gibba* Strebel, 1908, at South Georgia (54°16′S 36°30′W) (personal communication).

This paper outlines the life histories of eight prosobranch gastropod species from the littoral or immediate sub-littoral zones of Signy Island, South Orkney Islands (60°43′S 45°38′W). The eggs and young of each species are described for the first time, establishing that their development is non-pelagic. The young of six species are known to emerge from attached egg masses or capsules as crawling juveniles, and this is inferred for the remaining two from the state of their well-developed encapsulated embryos. In addition a description of the eggs of two unidentified gastropod species is included, since both illustrate the use of "nurse eggs" as a food source for developing embryos.

MATERIALS AND METHODS

The eggs and young of six prosobranch species were studied in detail in the sub-littoral from April 1975 to March 1977. The species were: *Margarella antarctica* (Lamy, 1905), *Pellilitorina setosa* (Smith, 1875), *P. pellita* (Martens, 1885), *Laevilacunaria antarctica* Martens, 1885, *Laevilacunaria (Pellilacunella) bennetti* (Preston, 1916) and an unidentified *Trophon*, species A. The eggs of *Trophon minutus* Melvill & Standen, 1907, and two unidentified species, were found infrequently during this time. The eggs of *Laevilitorina (Corneolitorina) coriacea* (Melvill & Standen, 1907) were examined on a few occasions in the littoral zone.

All sub-littoral observations and collections were made by SCUBA diving, particularly in an area around Billie Rocks, Borge Bay, on the east coast of the island (Fig. 1). The substrate consists of small rocks and stones set in gravel, with areas of exposed bedrock, sand and gravel. The bottom slopes gently from an almost bare shore-line to about 12 m depth, where there is a fairly abrupt transition to a flat, muddy-sand bottom. The slope bears a varied, and often lush, flora of macro-algae, characterised by mature *Himantothallus grandifolius, Desmarestia anceps, D. menziesii* and *Ascoseira mirabilis* plants. These overlie a rich understorey of Rhodophyceae including *Plocamium secundatum, Pseudophycodrys* sp., *Cystoclonium obtusangulum, Gigartina apoda,* and *Leptosarca simplex.* Approximately 35 species of prosobranchs are found in the first 12 m of the sub-littoral. The variety of macroalgae communities and the secretive locations afforded by the substrate provide numerous sites for the deposition of egg masses and capsules.

The developmental state of eggs found in the sub-littoral was assessed by external examination each month, and assigned to one of three broad categories: 1. *Recently laid.* Ova uncleaved, or in the early stages of development. 2. *Developing.* Embryos well advanced in their development, with an obvious shell. 3. *Emerging.* Juveniles in the process of emerging, or young of newly-emerged size found in the sub-littoral. No attempt was made

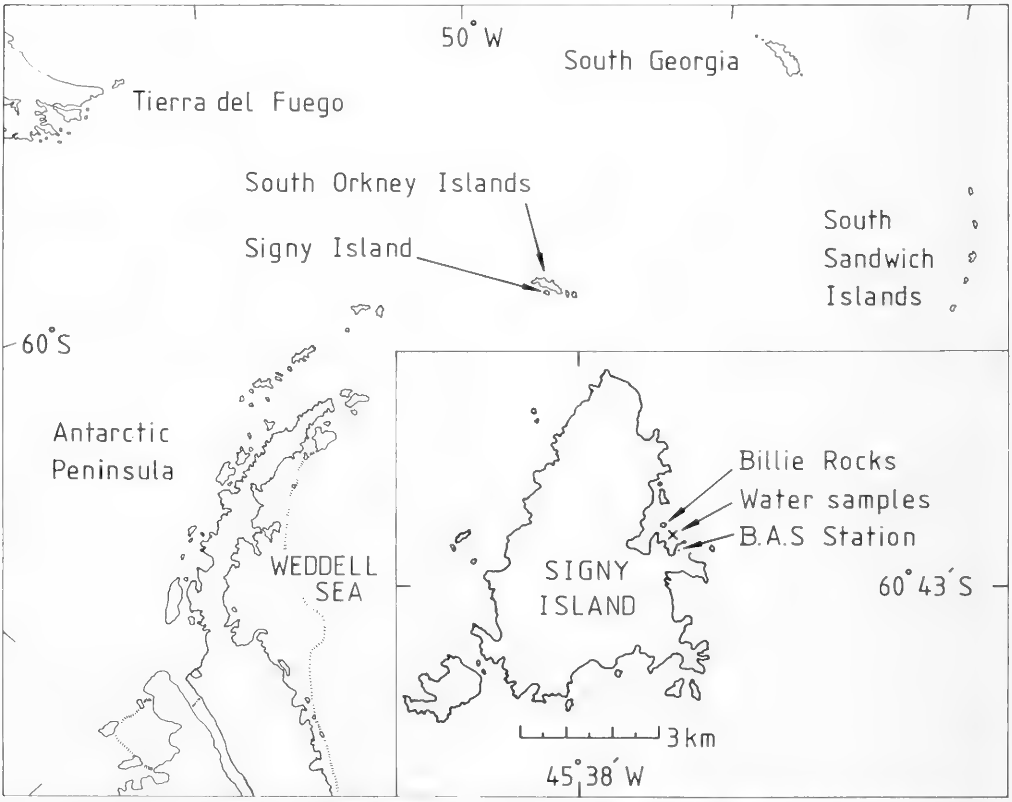


FIG. 1. The location of the South Orkney Islands. Inset, an outline map of Signy Island showing the position of Billie Rocks, the water sampling site at the mouth of Factory Cove, and the British Antarctic Survey Station.

to quantify the states of development at any particular date; the presence or absence of each state was simply recorded.

Spawning was not observed in any species and eggs were primarily identified by comparing their juveniles with adult specimens. Large collections of prosobranchs were obtained in the course of monthly quantitative sampling using an air-lift suction device built after the design of Hiscock & Hoare (1973) fitted with a bag of mesh size 0.5 mm. In the six most extensively studied species the collections furnished a progressive size series, from newly-emerged to adult, from which the identification of their eggs and juveniles could be confirmed. The monthly samples were also used to monitor the emergence of *Pellilitorina setosa, P. pellita, Laevilacunaria antarctica* and *L. bennetti.* The juveniles of these species were considered large enough to be adequately collected by the sampling technique, and for accurate periods of emergence to be derived from these data.

Additional information on size at emergence and development times was obtained from laboratory maintained eggs. In the first year, June 1975–April 1976, individual egg masses were kept in small jars of seawater in aquaria cooled by circulating seawater at ambient temperature. The jars were inspected every day and newly emerged young removed; the seawater in the jars was changed weekly. An improved method was used in the second year, May 1976–March 1977. Single egg masses were suspended in aquaria from glass rods, with seawater at ambient temperature circulating freely around them. Masses were again checked daily and juveniles removed.

The individual fecundity of *Margarella antarctica* was investigated by counting the eggs in a series of fresh, mature ovaries. The shell was measured, then carefully cracked, and the whole body removed. The ovary was separated form the rest of the body tissue, and gently macerated on a slide to spread the eggs into a thin layer. The eggs were then counted. The proportion of *M. antarctica* body devoted to the ovary was examined in a second series of specimens. Ovary and body tissue were extracted as described, dried separately at 65°C to constant weight, then weighed to 0.1 mg.

Adult shells, and large egg masses and egg capsules were measured to the nearest 0.1 mm with a sliding vernier caliper. Smaller masses and capsules, individual eggs, ova, and shelled embryos, were measured with an eyepiece micrometer. Measurements were also taken from scale drawings made by camera lucida. The standard measurement for the size of adult and juvenile shells was their height, from apex to the lowest point on the body whorl. *Margarella antarctica* and *Laevilacunaria antarctica* have broad-based shells, so the standard measurement of size for these species was the maximum shell diameter, measured across the body whorl, perpendicular to the columellar axis.

The terminology in the descriptions below follows that adopted by Thorson (1935) and Lebour (1937). The *egg* consists of the ovum surrounded by the egg membrane, albuminous layer, egg covering, and gelatinous sheath. The egg diameter is measured across the gelatinous sheath. Many such eggs laid together and covered by further gelatinous layers constitute an *egg mass.* The term *egg capsule* denotes a protective outer case, containing a fluid in which eggs freely float.

DESCRIPTION OF EGGS AND YOUNG

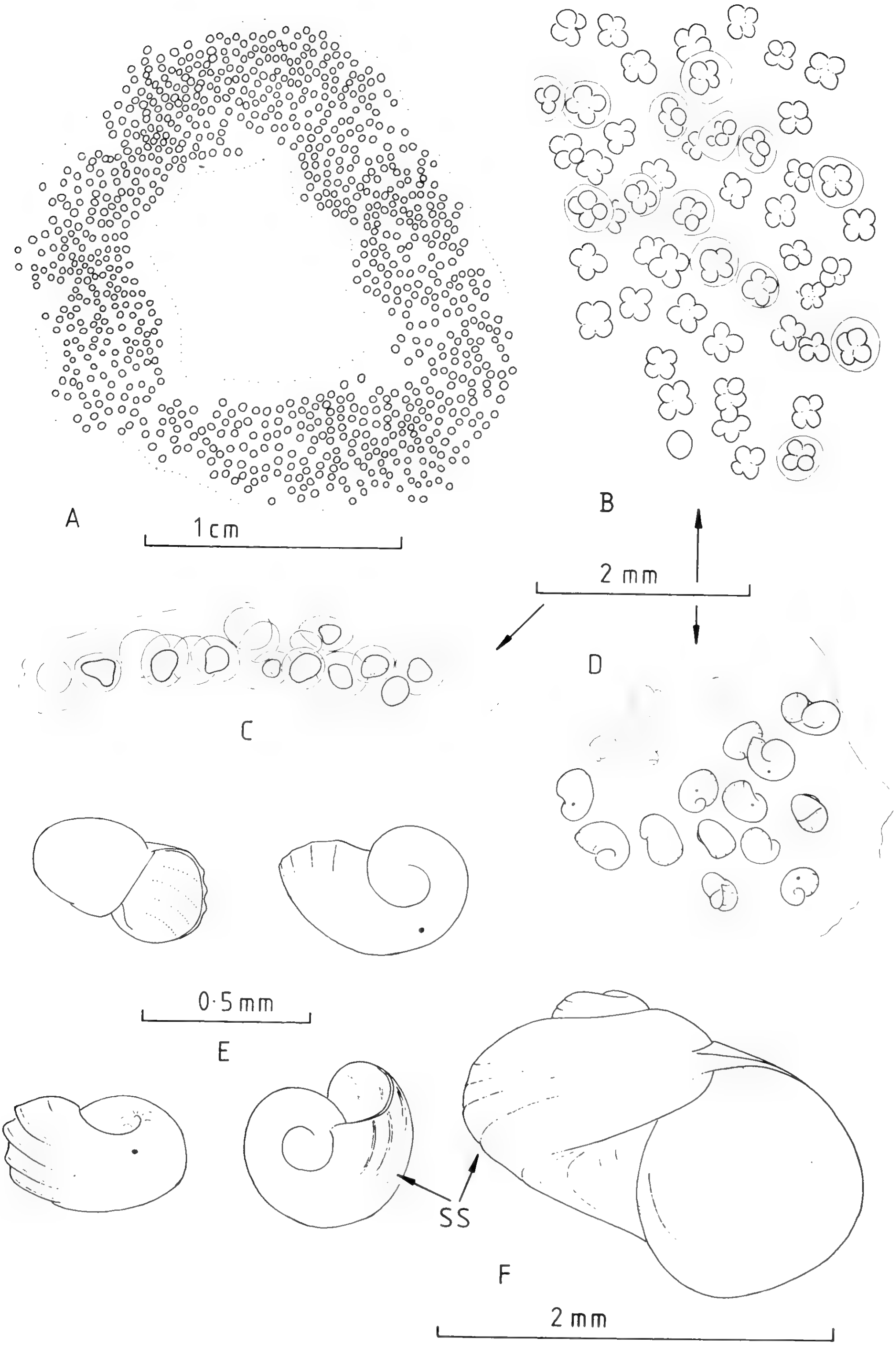
Order ARCHAEOGASTROPODA
Family TROCHIDAE

Margarella antarctica

Margarella antarctica was conspicuous in the sub-littoral where adults attained a maximum shell diameter of 12.8 mm. Gonads were rarely seen in individuals less than 7.5 mm in diameter and probably only animals more than 9.0 mm in diameter were mature.

Margarella antarctica egg masses were found exclusively on the underside of stones and small rocks from 4 m to at least 10 m below mean low water (MLW). The eggs were embedded in a clear gelatinous matrix laid as a ribbon 2.5–5.0 mm wide, 0.6–0.8 mm thick, cemented to the rock in a rough circle about 20 mm in diameter (Fig. 2A–D). Eggs were 0.4–0.5 mm in diameter, with a spherical, bright yellow ovum approximately 0.3 mm in diameter.

The eggs were characteristically laid in compound, overlapping masses, presumably the result of several individuals congregating and spawning at a favourable site. Individual fecundity was estimated in September 1976, i.e. just before the beginning of the spawning period. Fig. 3 shows the relationship between


A
1 cm
B
2 mm
C
D
0·5 mm
E
SS
F
2 mm

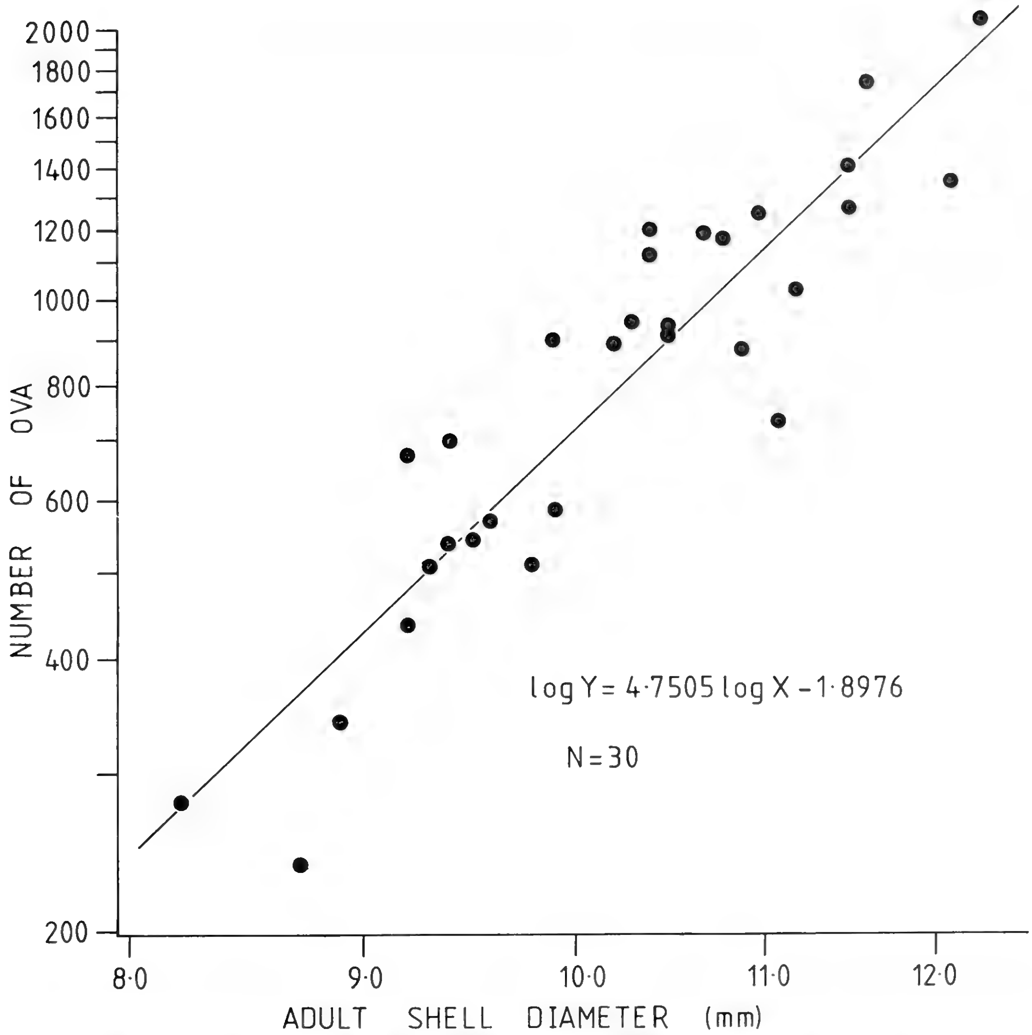


FIG. 3. *Margarella antarctica.* Relationship between the shell diameter and the number of mature ova in the ovary. Both scales are logarithmic.

adult shell size and the number of ova. Two complete, single, discrete masses found in the sub-littoral closely agreed with this estimation. The masses contained 874 and 728 eggs, and from Fig. 3 might have been the entire spawn of females about 10.5 mm in diameter, or certainly not less than half that of an individual about 12.0 mm in diameter.

Recently laid eggs were found each month from September to February, and shelled embryos were observed in masses collected in March and May. In May and July newly-emerged juveniles were found crawling over masses examined within 1 hr of their collection in the sub-littoral. It is clear that periods of spawning and emergence were extended, with development times probably in excess of three months.

The young emerged as tiny crawling juveniles, with almost transparent opercula. The shell, of 1–1½ whorls, was off-white and bore fine spiral striae on the lower part of the body

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FIG. 2. *Margarella antarctica.* A. Complete, recently laid egg mass, containing 874 eggs. B. Developing eggs. C. Cross-section of the egg ribbon. D. Shelled embryos within the gelatinous matrix. E. Views of the protoconch; note the spiral striations. F. An older juvenile, with striations still discernible. SS, spiral striations.

whorl similar to those seen on older individuals up to about 4.0 mm in diameter (Fig. 2E–F). The mean maximum shell diameter of 42 juveniles found crawling over masses in May 1976 was 0.56 mm (s.d. ± 0.03 mm).

Comparison with the other Signy prosobranchs which develop non-pelagically shows that *M. antarctica* lays many more eggs, the majority of which appeared to develop successfully. *Margarita cinerea* in northeast Greenland is similarly adapted, depositing masses of 200–700 eggs, each about 0.5 mm in diameter, from which juveniles with a basal diameter of at least 0.5 mm emerge (Thorson, 1935). Most of the eggs develop successfully.

The diminutive juveniles of *Margarella antarctica* are very vulnerable when newly-emerged, and mortality in the first few months of life must be high. High mortality is compensated by the increased fecundity of *M. antarctica,* and this was reflected in the proportion of the tissue weight devoted to the ovary in September 1976. In Fig. 4 the dry ovary weight, expressed as a percentage of the whole body dry tissue weight, is plotted against shell diameter. Two clusters of points are seen, showing a clear distinction between "ripe" and "unripe" ovaries, with a few at an intermediate stage. Examination of the ovaries before drying showed that the "unripe" ovaries were not being confused with the post-spawning ovaries of mature females. The ripe ovary may constitute up to 46% of the whole-body dry tissue weight in September, and most of this will be lost on spawning. Fig. 4 also confirms the observation that few females less than 9.0 mm in diameter were mature.

Order MESOGASTROPODA
Family LITTORINIDAE

Pellilitorina setosa and **P. pellita**

Pellilitorina setosa and *P. pellita* were common on macro-algae in the sub-littoral and adults attained shell heights of 17.4 mm and 17.8 mm respectively. Gonads were rarely distinguished in animals less than about 10.5 mm high, and only individuals more than

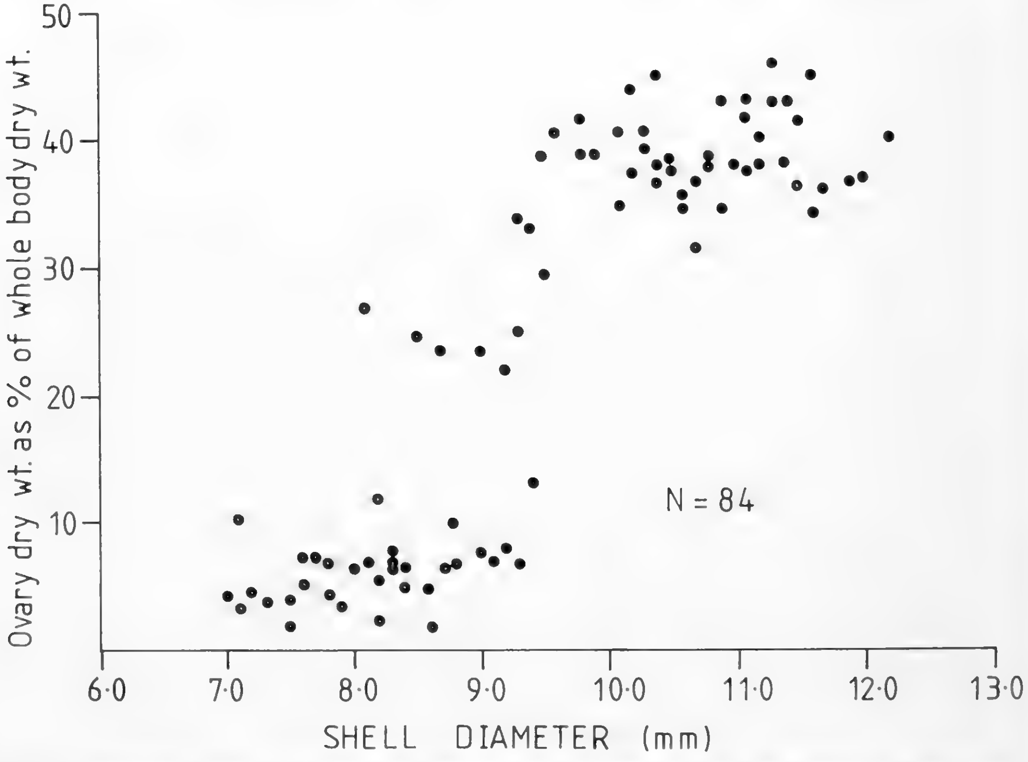

FIG. 4. *Margarella antarctica.* Relationship between shell diameter, and dry ovary weight as a percent of the total body tissue dry weight.

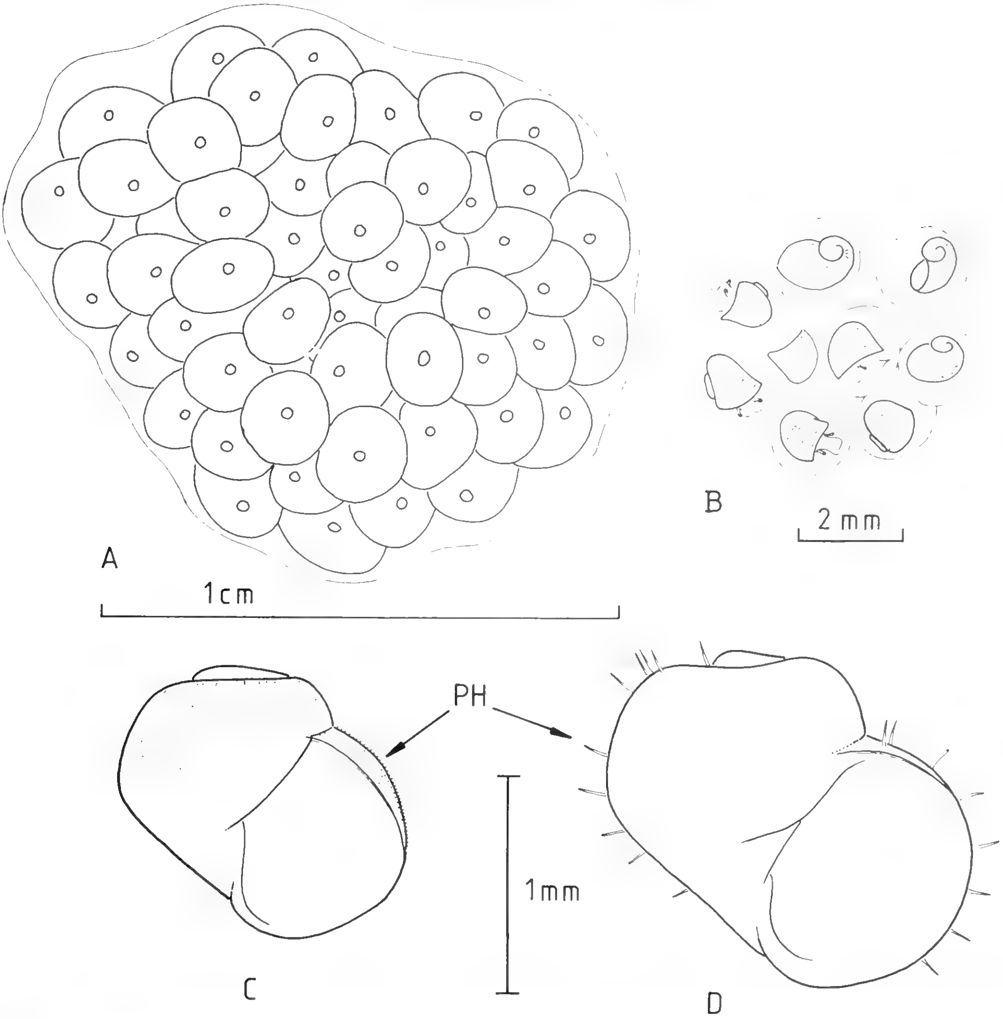

FIG. 5. *Pellilitorina* species. A. Recently laid *Pellilitorina* sp. egg mass. B. Developing *Pellilitorina setosa* embryos. C. Apertural view of *P. setosa* protoconch. D. Apertural view of *P. pellita* protoconch. PH, periostracal hairs.

about 13.0 mm high may have been fully mature. *Pellilitorina setosa* and *P. pellita* of this size were at least 3 years old.

The newly laid egg masses of the 2 species were indistinguishable and the following description is applicable to both. Masses were usually found cemented onto algae from 2 m to at least 10 m below MLW, the fronds of *Gigartina, Pseudophycodrys* and *Leptosarca* being particularly favoured. The mass initially appeared as a flattened ball of spherical, clear eggs embedded in an almost transparent gelatinuous matrix which rendered the mass quite firm (Fig. 5A–B). The eggs were deposited in a tight circle, with the last often laid on top of the first, giving the mass a characteristic bulbous appearance. The eggs were not an integral part of the matrix and were easily dissected from it. Eggs were 1.5–1.75 mm in diameter, with a spherical, pale yellow ovum 0.25 mm in diameter. The mean number of eggs in 27 masses collected during July–August 1976 was 40 (s.d. ± 10), with a range of 23–60 eggs per mass. The typical dimensions of a mass containing 40 eggs were, maximum diameter 11.0 mm; minimum diameter 9.0 mm; thickness 4.5 mm.

Egg masses in all stages, from recently laid to those with shelled embryos, were found throughout the year. *Pellilitorina pellita* juveniles of newly-emerged size were collected in sub-littoral samples in all months of the year except May. *Pellilitorina setosa* of newly-emerged size were found in January to March, July, September, October and December. Emergence was observed in the laboratory maintained masses of both species from June to March. Both *P. setosa* and *P. pellita* spawned asynchronously throughout the year and juveniles were correspondingly recruited in low numbers nearly every month. Development times were prolonged; the longest period of laboratory maintenance before successful emergence commenced was 7 months for *P. setosa* eggs and 6 months for *P. pellita* eggs.

The young emerged as crawling juveniles with opercula, escaping through several small holes in the upper surface of the mass. The individuals of any one mass emerged singly or in low numbers over a period of many days, probably because the young had to digest the jelly matrix to escape. Individuals near the surface therefore escaped more readily than those deeper in the mass. In the laboratory, *P. setosa* masses took from 25 to 56 days for all juveniles to emerge.

The emergent young of the 2 species were readily distinguished from each other. *Pellilitorina setosa* juveniles had a pale brown shell of 1½ whorls, with a periostracum bearing numerous columns of very fine short hairs, identical to those of the adult (Fig. 5C). The mean height of 391 individuals emerging from 9 laboratory masses in the first year was 1.34 mm (s.d. ± 0.06 mm). *Pellilitorina pellita* juveniles had a darker brown shell of 1½ whorls and were a little larger, the mean height of 107 individuals emerging from 6 laboratory masses in the first year being 1.40 mm (s.d. ± 0.08 mm) (Fig. 5D). The periostracal hairs of *P. pellita* juveniles were consistently longer and less numerous than those of *P. setosa,* and were identical to the hairs on the unabraded adult *P. pellita* shell.

Laevilacunaria antarctica

Laevilacunaria antarctica was abundant on macro-algae in the sublittoral, where adults attained a maximum shell diameter of 7.1 mm. Gonads were not found in animals less than 4.0 mm in diameter and probably only individuals more than 5.0 mm in diameter were fully mature. *Laevilacunaria antarctica* of this size were at least 2 years old.

Laevilacunaria antarctica eggs were always found on algal fronds, especially those of *Ascoseira, Leptosarca* and *Pseudophycodrys*, from 2 m to at least 15 m below MLW. Even though both species of *Desmarestia* bore many young and adult *L. antarctica,* egg masses were never found on these algae; their narrow fronds were apparently unsuitable for the deposition of eggs, and adult *L. antarctica* descended to the lower-storey algae to spawn.

The eggs formed a single layer of roughly rectangular cells each approximately 1.0 by 0.8 mm, deposited in a characteristic oval or elongated-oval mass. The cells were well defined, and each contained a spherical, pale yellow ovum 0.15 mm in diameter (Fig. 6A–B). Fifty-nine masses examined in August 1976 contained from 9 to 47 eggs, with a mean of 22 (s.d. ± 7) eggs per mass. The typical dimensions of a mass with 22 eggs were, length 5.5 mm; width 4.0 mm; thickness 1.1 mm.

The field observations of *L. antarctica* egg masses were the most complete of all the species studied, and revealed the following sequence. Recently laid egg masses were present from January to October and those with shelled embryos from May to November. Juveniles of newly-emerged size were found in sub-littoral samples each month from June to February. The juveniles of laboratory maintained masses from both years also emerged in all months from June to December.

The development times of egg masses collected in the sub-littoral and maintained in the laboratory were prolonged. In the first year *L. antarctica* masses collected with cleaving ova took from 81 to 169 days before emergence commenced, whereas those collected with shelled embryos took from 3 to 62 days. In the second year, recently laid cleaving eggs took from 66 to 102 days before emergence commenced, and those with shelled embryos from 7 to 93 days. These observations show the imprecision of a subjective assessment of an egg mass's developmental stage, but they are nonetheless consistent with the estimated development time of about 150 days which is deduced below.

The young emerged as crawling juveniles with opercula, escaping *en masse,* or within a few days of each other, through a split in the upper surface of the mass which often followed the sutures between the cells. The juvenile shell, of 1½ whorls, was dark red-brown, smooth and shiny (Fig. 6E). There was a characteristic shoulder on the body whorl

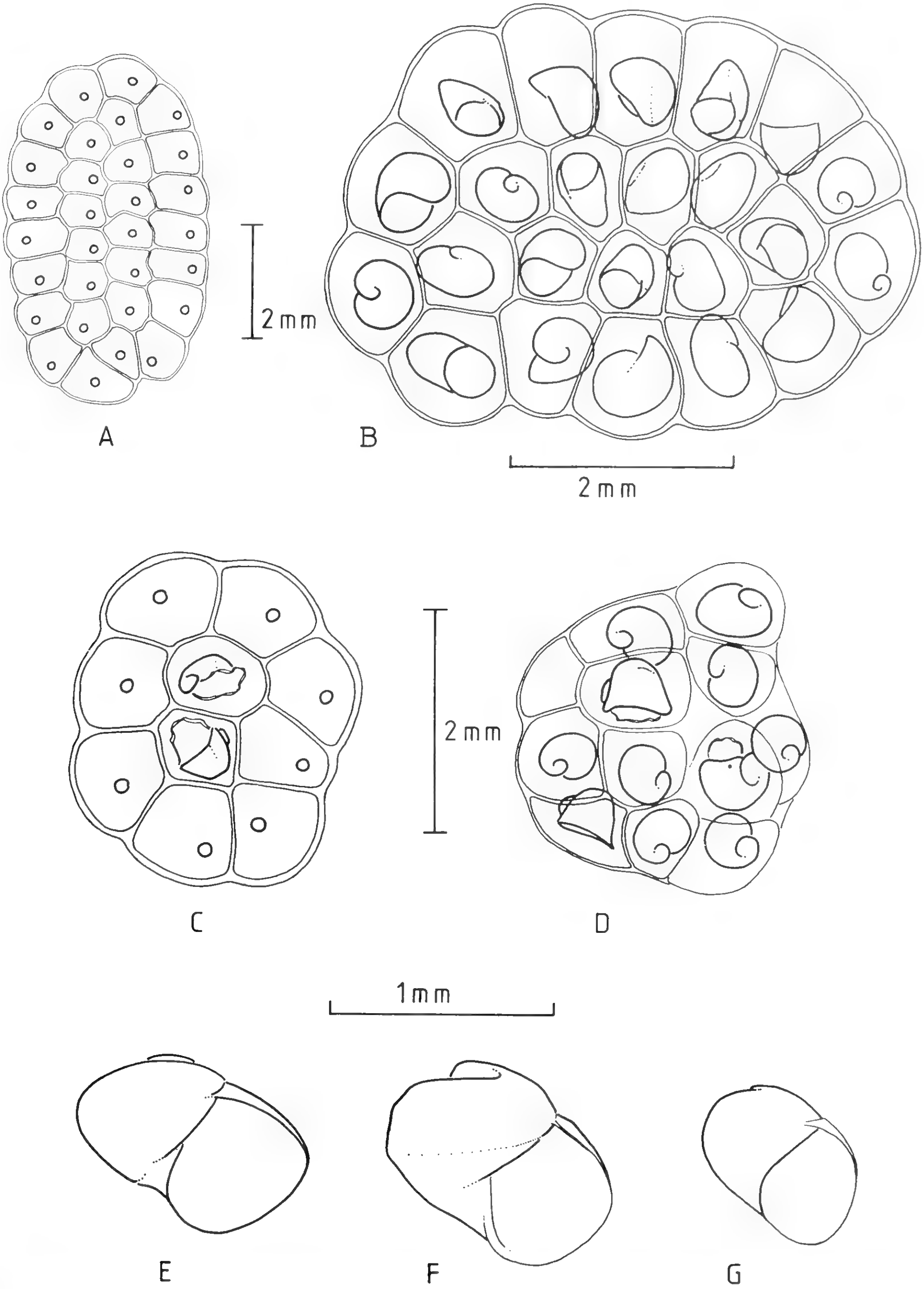

FIG. 6. *Laevilacunaria* and *Laevilitorina* species. A. Recently laid *Laevilacunaria antarctica* egg mass. B. Well-developed *L. antarctica* shelled embryos within their cells. C. *Laevilacunaria (Pellilacunella) bennetti* egg mass, with 2 shelled embryos and 8 infertile eggs. D. A fragment of *Laevilitorina coriacea* egg mass conglomeration, containing a single layer of eggs with well-developed shelled embryos. E. Apertural view of *Laevilacunaria antarctica* protoconch. F. Apertural view of *L. bennetti* protoconch. G. Apertural view of *Laevilitorina coriacea* shelled embryo, extracted from the egg mass.

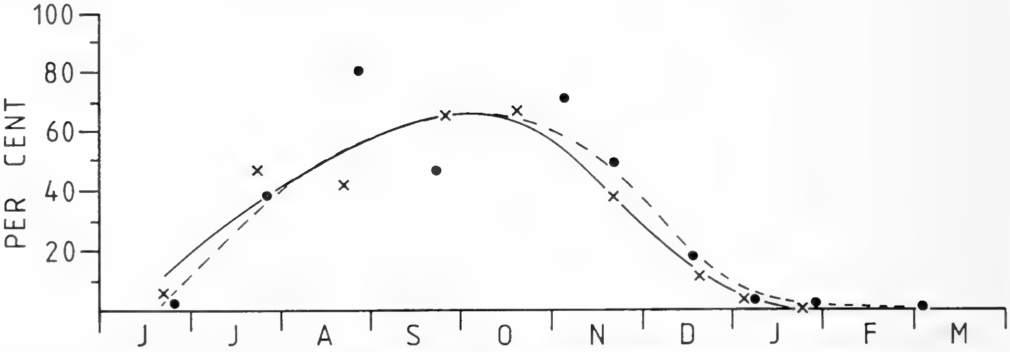

FIG. 7. *Laevilacunaria antarctica* recruitment. The percentage of newly-emerged juveniles in the population each month over a 2 year period. ---- ● ---- Juveniles of 1975. ——— × ——— Juveniles of 1976.

which distinguished it from the protoconch of *Laevilacunaria (Pellilacunella) bennetti* (Fig. 6F). The mean maximum shell diameter of 525 individuals emerging from 28 laboratory masses in the first year was 0.97 mm (s.d. ± 0.06 mm), and that of 443 individuals from 27 masses in the second year was 0.98 mm (s.d. ± 0.06 mm). Although periods of spawning and emergence were lengthy *L. antarctica* did show seasonal periodicity in reproduction, the evidence for which is as follows.

The size of newly-emerged *L. antarctica* is known from juveniles which emerged from laboratory maintained egg masses, and from juveniles collected in the sub-littoral while in the process of emerging (324 individuals found from July to October 1976, mean maximum shell diameter of 0.94 mm s.d. ± 0.08 mm). Individuals with a maximum shell diameter of 1.1 mm or less are therefore considered to be newly-emerged. Since *L. antarctica* develops non-pelagically, an indication of the number of eggs completing development each month may be given by the number of juveniles recruited into the population. Recruitment was followed in the size-frequency histograms derived from the monthly samples. Fig. 7 shows the number of newly-emerged juveniles expressed as a percentage of the total *L. antarctica* sample each month. Recruitment has a roughly normal distribution from June to February, reaching a peak around the end of September in both years. This may be termed the "mean date of emergence." There is no recruitment over the period March to June. Although emergence continues into the summer, the bulk of juveniles have entered the population by spring. Recruitment in *L. antarctica* is therefore seasonal, albeit extending over 7 or 8 months of the year.

A value for the time required to complete development can be obtained if it is assumed that the rate at which egg masses are deposited during the spawning period (Jan. to Oct.) has a distribution similar to the rate of recruitment. If this assumption is correct, a "mean spawning date" in May is derived. The interval between the "mean spawning date" and the "mean date of emergence" is approximately 150 days, and may be a reasonable estimate of the development time.

Laevilacunaria (Pellilacunella) bennetti

Laevilacunaria bennetti was common in the sub-littoral where adults attained a height of 5.5 mm. Their eggs were found cemented to the fronds of *Ascoseira, Leptosarca* and *Pseudophycodrys* and were easily confused with smaller *L. antarctica* masses. *Laevilacunaria bennetti* masses were circular or oval, 3–4 mm in diameter and 1.0 mm thick, composed of 10–20 eggs laid as a single layer of cells similar to those of *L. antarctica*. The cells were well defined, slightly distorted rectangles about 0.8 mm by 0.7 mm, and each contained a spherical, pale yellow ovum about 0.3 mm in diameter (Fig. 6C).

Because of the difficulty in distinguishing between *L. bennetti* and *L. antarctica* masses, observations on known *L. bennetti* masses were few. Recently laid masses were found from June to August, and those with shelled embryos from June to September. Newly-emerged juveniles were present in the sub-littoral from June to December. The general pattern was similar to that of *L. antarctica*, with lengthy periods of spawning and emergence. Development times were also prolonged; 2 masses maintained in the laboratory took 3 and 4 months respectively before successful emergence commenced.

The young emerged as crawling juveniles with opercula. In the few examples observed all the individuals in the mass escaped within a few days of each other, through an irregular hole in the upper surface. The juvenile shell, of 1½ whorls, was dark brown, smooth and dull, with an angular body whorl (Fig. 6F). The mean height of 34 individuals that emerged from laboratory maintained masses in the first year was 0.77 mm (s.d. ± 0.17 mm).

Laevilitorina (Corneolitorina) coriacea

Laevilitorina coriacea is a littoral species and its eggs were always found cemented to the sheltered underside of rocks in tidal pools. A discrete egg mass attributable to one female was never seen. The egg masses of several individuals were invariably found in overlapping conglomerations, so that it was impossible to measure the size of, or count the eggs in, any single mass. Fig. 6D illustrates a fragment of a "compound" mass in which there is only a single layer of 12 eggs. The eggs were approximately 0.6 mm in diameter with a spherical, pale yellow ovum 0.2 mm in diameter.

Masses in all stages of development, from recently laid to those with shelled embryos, were found in December and again in March, on both occasions with many adult *L. coriacea* clustered over and around them. Few observations were undertaken in summer and no search was made during the winter months, but it is suggested that the *L. coriacea* spawning period begins in spring and that emergence is completed before the littoral zone freezes again in the autumn.

Newly-emerged juveniles were not found, but well-developed shelled embryos were seen in some egg masses. The protoconch, of about 1 whorl, was light brown and smooth, and approximately 0.6 mm high (Fig. 6G). Development was therefore non-pelagic and the young emerged as crawling juveniles.

Order NEOGASTROPODA
Family MURICIDAE

Trophon Species A

Trophon species A is a carnivore which was common in the sub-littoral where adults attained a height of 32.8 mm. *Trophon* species A is a new species and will be formally described from the adult type in a forthcoming British Antarctic Survey Scientific Report by Oliver & Picken.

The eggs of *Trophon* species A were deposited in capsules which were always found cemented in sheltered locations on rocks and stones, from 2 m to at least 15 m below MLW. Between 15 and 25 spherical, bright yellow eggs approximately 0.8 mm in diameter were loosely held within a tough, dull-yellow or buff, hemispherical capsule, about 7.5 mm in diameter and 3.0 mm high. There was a characteristic pattern of fine striae running around the capsule concentrically (Fig. 8A). A semi-transparent membrane covered the bottom of the capsule adjacent to the rock surface.

Capsules were found only occasionally and the data for spawning periods and development are consequently incomplete. Eggs which appeared recently laid were found in May, August to October, and December. Capsules containing shelled embryos were collected in May, July, October and February, and juveniles in the process of emerging were found in May and July. Periods of spawning and emergence were therefore extended and overlapping, and probably largely aseasonal.

The young emerged as crawling juveniles with opercula, escaping through a single hole at the top of the capsule. The juvenile shell, of 1½–2 whorls and about 1.5 mm high, was very pale brown, with fine lamellae on the leading edge of the body whorl (Fig. 8B). These were the first signs of the lamellae seen on the unabraded adult shell.

Trophon minutus

Trophon minutus was present in low numbers in the sub-littoral, and adults attained a height of 9.1 mm. *Trophon minutus* eggs were deposited in small hemispherical capsules about 2.5 mm in diameter and 1.0 mm high, cemented to stones. The few specimens examined contained either 4 or 6, spherical, bright yellow eggs approximately 0.4 mm in diameter (Fig. 8D–E). The capsules were slightly opaque, very faintly marked with concentric striae, and there was a clear area at the apex through which the juveniles probably emerged. Because of their small size, capsules were not seen in the sub-littoral but only discovered while examining monthly samples microscopically. Field observations are therefore lacking and little can be said about peri-

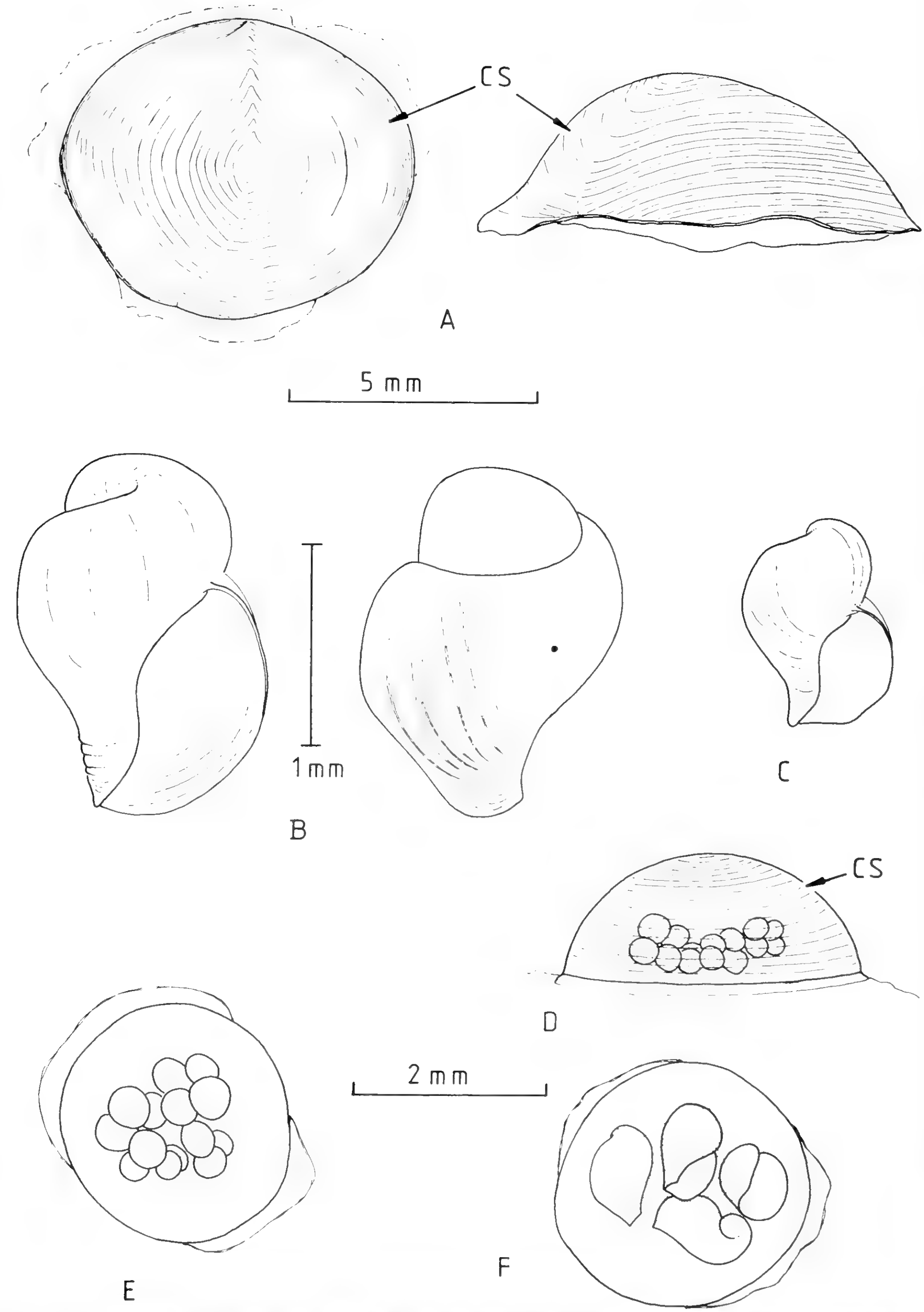

FIG. 8. *Trophon* species. A. *Trophon* species A, apical and anterolateral views of the egg capsule. B. Apertural and dorsal views of *Trophon* species A protoconch, showing the fine lamellae. C. Apertural view of *T. minutus* shelled embryo, extracted before emergence from the egg capsule. D. *T. minutus,* lateral view of the egg capsule attached to a chip of stone. E. Apical view of *T. minutus* capsule, with 4 cleaving eggs. F. Apical view of *T. minutus* capsule with 4 shelled embryos. CS, concentric striae.

ods of spawning or emergence. Newly-emerged juveniles were not found, but shelled embryos were seen moving in one capsule (Fig. 8F). The protoconch was pale yellow, about 1.0 mm high, and the embryo had an obvious foot and operculum (Fig. 8C). Development was non-pelagic and the young emerged as crawling juveniles.

The eggs of two unidentified prosobranch species

Two further types of egg capsule were discovered while examining monthly samples microscopically. Some capsules of both types contained numerous recently laid eggs, whereas others were filled by a single shelled embryo. The specimens examined therefore strongly suggested that the majority of eggs initially laid in the capsules were "nurse eggs," which were consumed by the embryo as it developed. The use of nurse eggs by Antarctic prosobranchs has not been previously reported. The embryos of both species undoubtedly emerged as crawling juveniles. Both types of capsule remain unidentified, and have been deposited at the National Museum of Wales, Cardiff, United Kingdom, as part of a small collection of Antarctic prosobranch egg masses and capsules.The capsules are identified here by their voucher numbers.

Type 1. NMW 79.1Z.1

The capsules were oval, about 1.3 mm long, 0.9 mm wide and 0.7 mm thick, and virtually transparent (Fig. 9A). One capsule contained approximately 350 eggs, each 0.09 mm in diameter, and others were completely filled by a single shelled embryo (Fig. 9B). The pale brown protoconch, of 1½–1¾ whorls, was approximately 1.0 mm high. The capsule and protoconch may have been those of *Prosipho* species A (order Neogastropoda, family Buccinulidae), which was common to the sub-littoral from 2 m to 12 m below MLW. *Prosipho* species A is a new species and will be formally described in a forthcoming British Antarctic Survey Scientific Report by Oliver & Picken. The protoconch NMW 79.1Z.1 was very similar to the apices of older specimens of *Prosipho* species A (Fig. 9C).

Type 2. NMW 79.1Z.2

A distinctive small goblet-like capsule which was found attached to algal strands by a short, broad-based peduncle. The capsule had an oval top, maximum diameter 0.9 mm; minimum diameter 0.6 mm, and with the peduncle stood 1.1 mm high. Some capsules contained about 200 recently laid eggs, each about 0.07 mm in diameter (Fig. 9D–E). One specimen was found with a developing embryo and about 80 nurse eggs, whereas the remaining capsules contained a single pale brown shelled embryo of about 1 whorl, 0.8 mm high, with no nurse eggs (Fig. 9F).

DISCUSSION

The ten species of Antarctic prosobranch gastropods whose egg masses or capsules were studied at Signy Island are all oviparous. The embryos of each species develop without a free pelagic larval stage, and emerge as crawling juveniles. Powell (1960) lists approximately 500 prosobranch species from the Antarctic and sub-Antarctic biogeographical provinces (Powell, 1960, 1965); the reproduction of 17 of the species is now known, and only 3 have a pelagic larva (Table 1). If the species with a wholly sub-Antarctic distribution are eliminated, namely *Nacella (Patinigera) macquariensis* (Finlay, 1927), *Cantharidus coruscans* (Hedley, 1916), *Diacolax cucumariae* Mandahl-Barth, 1946, and *Macquariella hamiltoni* (Smith, 1898), 13 remain with only 1, *Nacella (Patinigera) concinna* (Strebel, 1908) having a pelagic development.

There is clearly a predominance of non-pelagic development in the Antarctic prosobranchs studied to date, and this is to be anticipated from the literature on the reproduction of the benthic marine invertebrates of both polar regions. The prosobranchs were cited by Thorson (1936) as a particularly good example of the trend towards non-pelagic development in Arctic invertebrates, and they are apparently an equally good example of this tendency in the Antarctic. Thorson (1950) attributed the evolution of similar modes of reproduction in polar marine invertebrates to the comparable conditions in the coastal waters, the key factors being the low temperature and short periods of phytoplankton production. He thought that in such situations there would be a strong selective pressure for the adoption of some form of non-pelagic development, either by means of egg capsules, brood protection or viviparity. Vance (1973) suggested that lecithotrophic larvae would be favoured in conditions of poor food

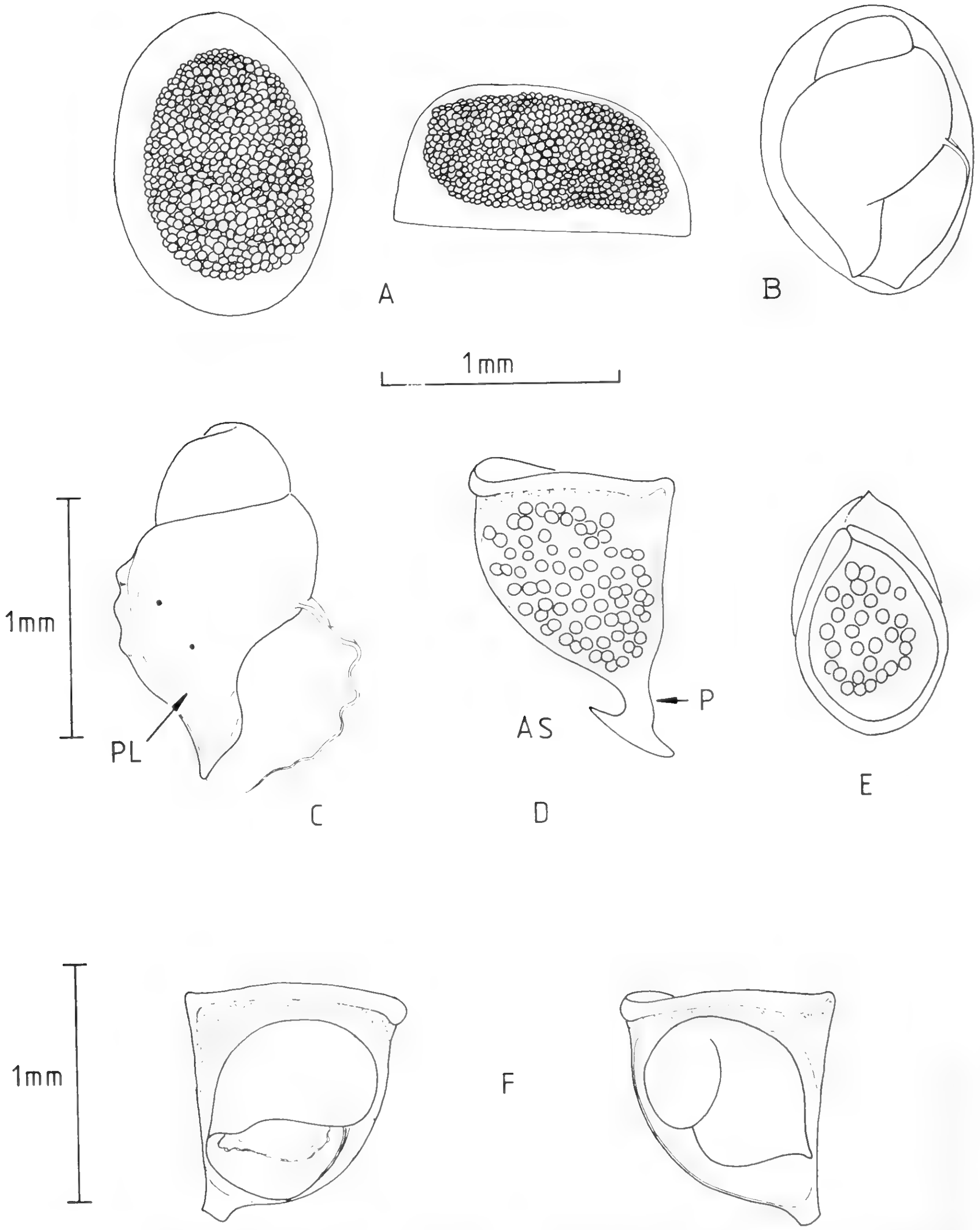

FIG. 9. Two unidentified egg capsules. A. NMW 79.1Z.1, apical and lateral views of a recently laid capsule, filled with nurse eggs. B. NMW 79.1Z.1, apical view of a capsule containing a single shelled embryo. C. A young *Prosipho* species A, showing a protoconch similar to that of the encapsulated embryo in B, above. D and E. NMW 79.1Z.2, lateral and apical views of the egg capsule filled with nurse eggs. F. NMW 79.1Z.2, lateral views of a capsule containing a single shelled embryo. The peduncle is broken in this specimen. PL, demarcation of the protoconch outer lip; AS, algal strand; P, peduncle.

TABLE 1. The reproduction of Antarctic and sub-Antarctic prosobranchs. The allocation of each species' type-locality and range to the Antarctic or sub-Antarctic biogeographical provinces follows Powell's (1965) definition of these regions.

Species	Source	Distribution	Development
Nacella (Patinigera) concinna	Shabica (1971, 1976)	Antarctic & sub-Antarctic	Pelagic
Nacella (Patinigera) macquariensis	Simpson (1972)	Sub-Antarctic	Pelagic
Cantharidus coruscans	Simpson (1977)	Sub-Antarctic	Pelagic
Margarella antarctica	This paper	Antarctic	Non-pelagic
Margarites refulgens	Arnaud (1972)	Antarctic & sub-Antarctic	Non-pelagic
Pellilitorina setosa	This paper	Antarctic & sub-Antarctic	Non-pelagic
Pellilitorina pellita	This paper	Antarctic	Non-pelagic
Laevilacunaria antarctica	This paper	Antarctic	Non-pelagic
Laevilacunaria bennetti	This paper	Antarctic	Non-pelagic
Laevilitorina coriacea	This paper	Antarctic	Non-pelagic
Laevilitorina caliginosa	Simpson (1977)	Antarctic & sub-Antarctic	Non-pelagic
Macquariella hamiltoni	Simpson (1977)	Sub-Antarctic	Non-pelagic
Diacolax cucumariae	Mandahl-Barth (1946)	Sub-Antarctic	Non-pelagic
Trophon species A	This paper	Antarctic	Non-pelagic
Trophon minutus	This paper	Antarctic	Non-pelagic
Two unidentified species	This paper	Antarctic?	Non-pelagic

TABLE 2. Comparisons of the egg size, fecundity and size of newly-emerged juveniles of some Arctic and Antarctic prosobranchs which develop non-pelagically.

Species	Locality	Diameter (mm)	Number	Juvenile (mm)	Source
Margarella antarctica	Antarctic	Egg 0.45–0.50	200–2,000/ovary	0.56 diam.	This paper
Margarita cinerea	Arctic	Egg 0.50	200–700/mass	>0.50 diam.	Thorson (1935)
Laevilacunaria antarctica	Antarctic	Ova 0.15	9–47/mass	0.97 diam.	This paper
Laevilacunaria bennetti	Antarctic	Ova 0.30	10–20/mass	0.77 height	This paper
Laevilitorina coriacea	Antarctic	Ova 0.20	?	>0.60 height	This paper
Laevilitorina caliginosa	Antarctic	Ova 0.18	9–16/ovary	?	Simpson (1977)
Littorina obtusata	Arctic	Ova 0.25	90–150/mass	?	Lebour (1937)
Pellilitorina setosa	Antarctic	Ova 0.20	23–60/mass	1.34 height	This paper
Pellilitorina pellita	Antarctic	Ova 0.20	23–60/mass	1.40 height	This paper
Trophon species A	Antarctic	Egg 0.80	15–25/capsule	1.50 height	This paper
Trophon minutus	Antarctic	Egg 0.40	4–6/capsule	>1.00 height	This paper
Trophon muricatus	N. temperate	Egg 0.48	5–8 capsule	>0.64 diam.	Lebour (1936)
Trophon clathratus	Arctic	?	9–12/capsule	1.00 height	Thorson (1940)
Trophon truncatus	Arctic	Egg 0.40	?	1.20 height	Thorson (1946)
Trophon geversianus	Falkland Is.	Egg 0.23–0.30	74–112/capsule	2.50 height	Melvill & Standen (1898)

availability and low water temperature. He further proposed that low temperatures, by increasing the development time, would confer an advantage on non-pelagic development. Mileikovsky (1971) reviewed the relationships between types of development in benthic invertebrates and environmental and ecological factors, and Simpson (1977) discussed several salient points with particular reference to sub-Antarctic molluscs. Two aspects of the reproductive adaptations of the Antarctic prosobranch gastropods at Signy Island will be considered further, the first being egg size and fecundity.

Species which develop without a pelagic larval stage produce fewer, larger eggs than those with a pelagic development (Thorson, 1950; Mileikovsky, 1971; Spight, 1976). This may be a more efficient use of energy than the production of numerous pelagic larvae (Chia, 1970; Vance, 1973), an important consideration if the resources available for reproduction were limited. Large eggs will give rise to larger juveniles (Amio, 1963), which will generally have a better chance to survival than smaller juveniles (Smith & Fretwell, 1974; Spight, 1976). In the Northern Hemisphere, Thorson (1936, 1950) showed that Arctic species of lamellibranchs, crustaceans and gastropods produced larger eggs than more southerly species. There are no such data for the Southern Hemisphere prosobranchs, but comparisons between Arctic and Antarctic species of the same or closely related genera may be valid. The available examples show that Arctic and Antarctic species lay eggs of aproximately the same size, and in numbers of the same order of magnitude. Their juveniles are also of equivalent sizes (Table 2).

The Antarctic prosobranch species so far studied do not utilise nurse eggs to the same extent as Arctic prosobranchs. Only 2 of the 13 Antarctic species produce nurse eggs, whereas 15 of the 30 Arctic prosobranchs discussed by Thorson (1936) show this mode of reproduction. This may reflect a tendency towards the use of nurse eggs in the genera found in the Arctic, rather than a particular characteristic of Arctic as opposed to Antarctic reproduction.

The second important aspect of any reproductive adaptation is the timing of gametogenesis and spawning, and consequently of the release of young into the sub-littoral. Marked seasonality of reproduction is common in Arctic and Antarctic invertebrates (Giese & Pearse, 1974), with most benthic species taking advantage of the elevated summer production levels. Thorson (1936) derived reproductive cycles for 15 species of sub-littoral Arctic prosobranchs from periodic examinations of their egg masses. He concluded that the majority of reproduction took place during the summer, and that embryonic development was generally completed within this period.

Fig. 10 shows the reproductive patterns of the eight identified prosobranch species from Signy Island. This synopsis is compiled from two year's observation, and follows the probable periods of spawning, development and emergence of each species over one year. Periods of spawning and emergence are prolonged in most species, and the emergence of juveniles does not specifically coincide with the summer.

Maritime conditions are obviously relevant to the reproductive patterns of gastropods in the littoral and immediate sub-littoral zones of the Antarctic. Signy Island lies well within the Antarctic Convergence and coastal conditions are highly seasonal. The annual cycle of maritime events, outlined below, were remarkably similar for the two years of this study and belie the fact that conditions often vary greatly from year to year.

The sea was free of fast-ice from about November to June, and there was a pronounced phytoplankton bloom in December–January when the level of incident light was highest. Seawater temperature at a depth of 6 m in Borge Bay reached a maximum of about +1°C towards the end of January. Sea-ice formed late in May, thickening to more than 1 m through the winter. Light levels were lowest in August–September, and seawater temperature reached a minimum of −1.8°C in September. The sea-ice remained firm over the main study area throughout both winters, though there were temporary areas of open water within 1 km during the second winter. The sea-ice broke out rapidly at the end of October in both years.

White (1977) showed that the onset and duration of fast-ice cover at Signy Island was highly variable from one year to the next, and surmised that this must lead to irregularities in the summer primary production. He proposed a hypothesis of possible reproductive adaptations for Antarctic marine invertebrates where the timing of reproduction was largely controlled by the degree to which adults or young were dependent on the summer production. Most Signy prosobranchs appear to be relatively independent of the elevated summer production levels, though the patterns shown in Fig. 10 are open to a variety of interpretations. All the species except *Trophon* are herbivorous and probably graze the epiphytic algae covering rocks and macro-algae fronds. It is not known if their diet, or the amount of food available, changes with the seasons. Any interpretation of the seasonality of reproduction in the light of White's hypothesis would therefore be open to criticism without evidence from feeding studies. Bearing this reservation in mind, the reproductive periodicity of each species is outlined below, and some speculations on timing offered. The evidence at this stage suggests that neither adults nor young of any species are totally dependent on the summer production, variable as it is in onset and duration, but rather that the young of some winter-emerging species are able to benefit from the increased production whenever it occurs.

The data for *Trophon* species A, *T. minutus* and *Laevilitorina coriacea* have been briefly discussed already and are insufficient for further analysis. *Margarella antarctica* egg masses were not easily found and newly-emerged juveniles were too small to be quantitatively collected in samples. The incomplete data indicate spawning from late winter to summer, with emergence in autumn and early winter. The mature ovaries of *M. antarctica* constituted between 30% and 46% of the whole body dry tissue weight, and it seems unlikely that *M. antarctica* would spawn more than once a year. Spent adults probably begin gametogenesis during summer and autumn,

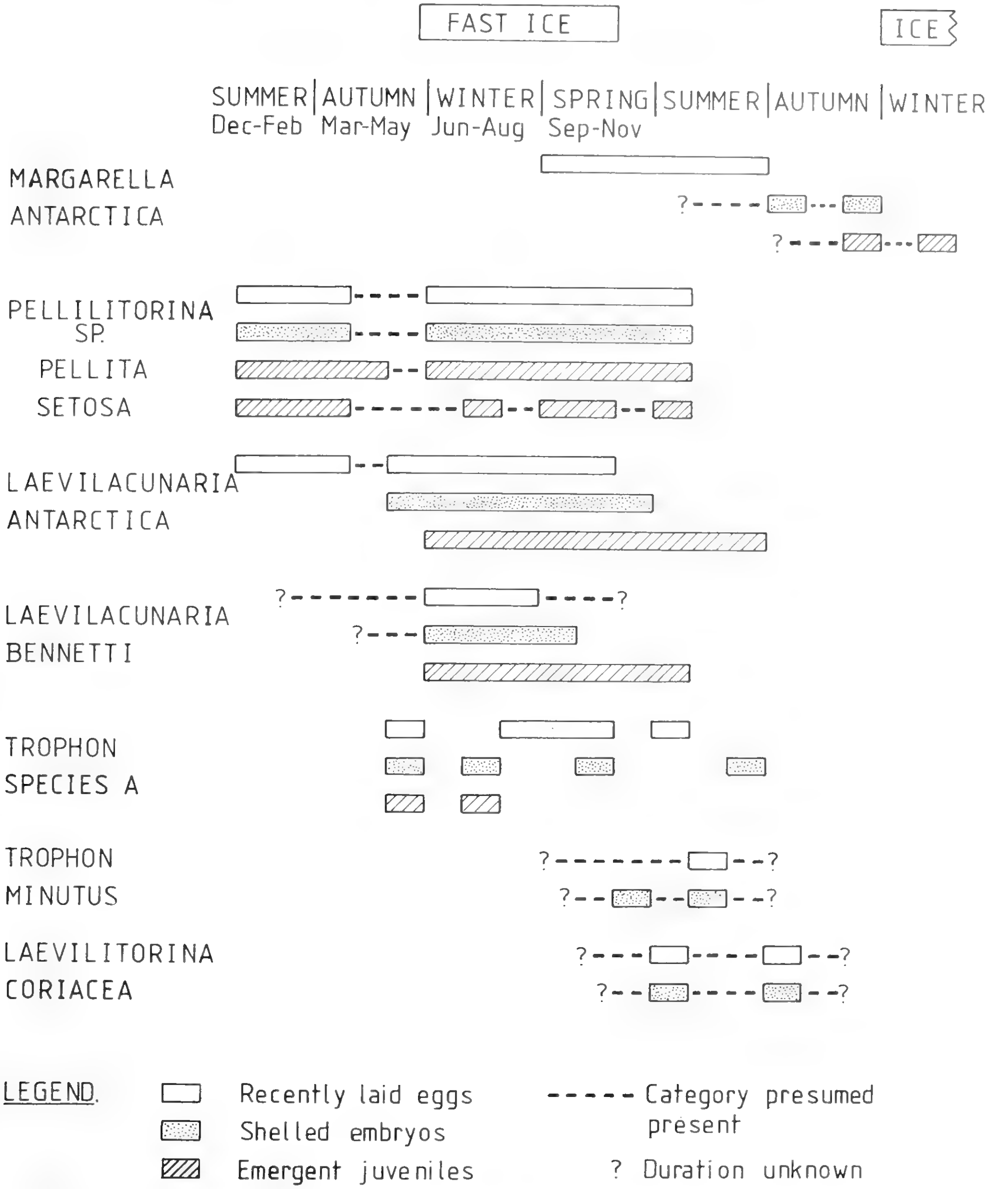

FIG. 10. Synopsis of the reproductive patterns of eight Antarctic prosobranchs from Signy Island.

possibly benefiting from the increased summer production, in preparation for spawning in the following spring-summer.

The reproductive periodicity of *Pellilitorina setosa, P. pellita, Laevilacunaria antarctica* and *L. bennetti* is better known, and in each species the data for both years agree closely. Fig. 10 is probably an accurate summary of the reproductive pattern. *Pellilitorina setosa* and *P. pellita* spawn throughout the year, and qualitative observations of their egg masses will not reveal seasonal fluctuations in spawning. Possible fluctuations may be registered as changes in the rate of juvenile recruitment during the year, but the interpretation of such data is complicated by variations in the total numbers sampled each month. Both the *Pellilitorina* species appear to recruit juveniles at a steady, low rate more or less throughout the year. There may be some increase in the number of newly-emerged young in both populations during the spring and summer months.

Laevilacunaria antarctica and *L. bennetti* show seasonality of reproduction the most clearly. *Laevilacunaria antarctica* spawns from January to October, and *L. bennetti* probably spawns over the same period. Both species have periods of emergence extending from mid-winter to mid-summer, but in *L. antarctica* at least, a definite seasonal recruitment to the population can be demonstrated (Fig. 7). The majority of *L. antarctica* and *L. bennetti* juveniles emerge during the winter and early spring, and will therefore be present in the sub-littoral when food becomes more plentiful in the summer.

The effect of the summer primary production can be seen in the first year's growth of juvenile *L. antarctica* (Fig. 11). The sigmoid curve is interpreted as follows. During the first three or four months of the period of emergence

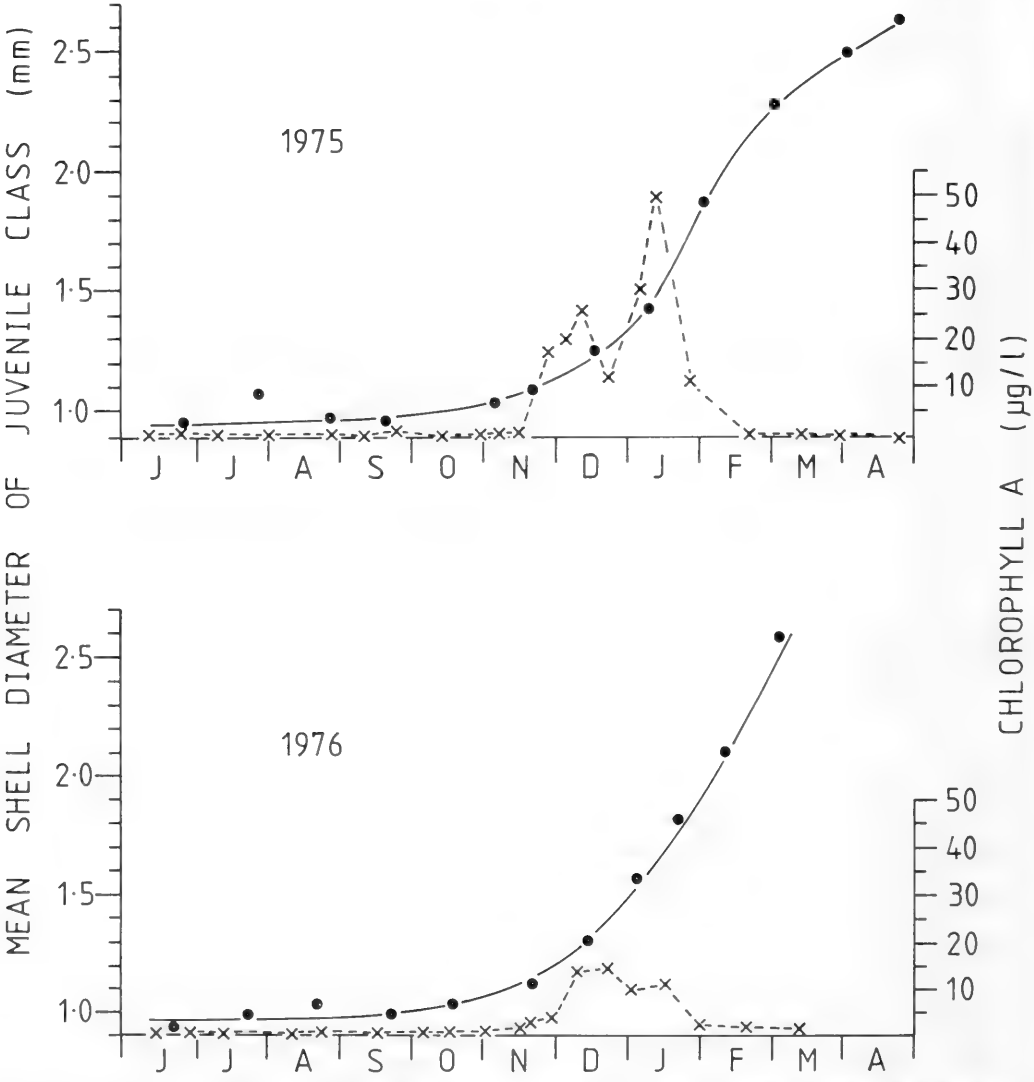

FIG. 11. *Laevilacunaria antarctica*. The first year's growth of juveniles in relation to the phytoplankton bloom. ——— ● ——— mean diameter of the juvenile class. – – – – × – – – – concentration of chlorophyll a. (The chlorophyll a data are from Brook 1975, 1976. Water samples were taken from 6 m depth at the mouth of Factory Cove, approximately 250 m from Billie Rocks.)

there is little increase in the mean size of juveniles. Young emerging in mid and late winter do not grow appreciably in their first few months of benthic life. The mean size of the class begins to increase in October–November, and the period of fastest growth extends from December to February. The elevated summer growth rate is probably due to the greater abundance of food, possibly enhanced by the higher seawater temperatures of the shallow sub-littoral during this time. The correlation between elevated primary production and the accelerated growth rate of *L. antarctica* juveniles is shown in Fig. 11. The decline of the growth rate in autumn coincides with the reduction in primary production at this time of year.

In the polar environment reproduction without pelagic development is apparently a more efficient adaptation for the majority of benthic invertebrates. Reproduction with non-pelagic development is common but by no means universal, and Mileikovsky (1971) has pointed out that polar species which have retained pelagic development are often among the most widespread and dominant members of the fauna. The occurrence of non-pelagic development has important implications. The absence of pelagic larvae which can be transported by oceanic currents reduces a species' ability to colonise new territory and expand its geographic range. It restricts the rate at which populations will be re-established after being eliminated by some local catastrophe, and reduces the gene-flow between separated populations. These consequences of non-pelagic development are all seen in the sub-littoral invertebrate fauna of the Antarctic, where many species have a restricted range and species endemism is high. Local, nearshore, prosobranch populations are maintained by the production of relatively few, highly viable juveniles, which emerge directly into the most favourable habitat alongside the adults. It seems that dispersion is largely achieved by the chance transport of adults or egg masses attached to macroalgae, and this may explain why many of the shallow sub-littoral prosobranchs have ranges restricted to the Palmer Peninsula and the islands of the Scotia Arc.

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COURTSHIP OF LAND SNAILS OF THE GENUS *PARTULA*

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ABSTRACT

The land snails of the genus *Partula* inhabiting the island of Moorea in French Polynesia form a closely related group with some members only partially reproductively isolated from each other. This paper describes the mating behavior of the two most widely distributed and distinctive species. The study provides a basis for the evaluation of the role of behavior as an isolating mechanism in *Partula*.

Partula suturalis and *P. taeniata* are ovoviviparous hermaphrodites normally reproducing by cross-fertilization but occasionally resorting to self-fertilization. Courtship is non-reciprocal with one partner acting as a male and the other as a female.

Courtship can be described in five stages: 1. Foreplay consists of curving turns, the form differing according to species, and *pursuit*. 2. Early courtship takes the form of *shell wandering* by the male on the shell of the female. The pattern of *shell wandering* is species-specific. 3. Late courtship consists of the *probing* of the body of the female by the penis of the male. *Shell wandering* separates bouts of *probing*. Late courtship may include *biting, kissing, head entwining, shell twirling, head prodding,* or *touching tentacles*. 4. Copulation takes place after prolonged *probing*. Tentacles are withdrawn. Copulation may be very brief or may extend for more than an hour, according to species. 5. Reversal often follows copulation, with the two partners exchanging roles for a second complete courtship.

The details of courtship differ in the two species. Whether the differences are sufficiently great to serve as isolating mechanisms has not been determined.

Of particular interest is the behavior of pairs of *P. suturalis* of opposite chirality. The male partner carries out the courtship as if the female were of his own type, with the result that *probing* is directed to the side of the head away from the genital opening. It is suggested that this behavior may result in partial reproductive isolation of dextral and sinistral animals.

INTRODUCTION

The land snails of the genus *Partula* make up a conspicuous part of the fauna of the volcanic islands of Polynesia. These animals are remarkable not only for a rich polymorphism in the color and form of the shell but also for a pattern of speciation that has resulted in extensive sympatry of similar species.

Knowledge of the distribution and variation of *Partula* is based on the studies of Professor H. E. Crampton during the early decades of this century (Crampton, 1916, 1925, 1932). His account of the island of Moorea in the Society Islands (Crampton, 1932) is especially thorough, describing in detail the relationships among the species found there. More recently Clarke and Murray have re-examined the Moorean *Partulae*. They have worked out the genetics of the polymorphism in two of the species (Murray & Clarke, 1966, 1976a, b), described the pattern of variation in natural populations (Clarke, 1968; Clarke & Murray, 1969, 1971), and discussed the evidence for incomplete speciation in two pairs of species (Murray & Clarke, 1968; Schwabl & Murray, 1970).

According to Crampton there are eleven species of *Partula* on Moorea (Crampton, 1932; Crampton & Cooke, 1953). Two of these have subsequently been removed to the genus *Samoana* (Kondo, 1973). Although it is difficult to decide how many of the remaining nine should be considered "good" species, it is common for as many as four distinct forms to occur sympatrically. This is the case for *Partula suturalis, P. taeniata, P. mooreana,* and *P. mirabilis* in the central part of the island and for *P. suturalis, P. taeniata, P. tohiveana,* and *P. mirabilis* farther east. There are indeed slight differences of ecological preference, but without any question the opportunity for interspecific hybridization exists.

Under these circumstances it is of interest to investigate possible mechanisms that might be responsible for the maintenance of reproductive isolation. To this end we have observed the mating behavior of two of the species, *Partula suturalis* and *P. taeniata*. Since these two species appear to be the most distinct morphologically and ecologically, as well as being the most widely distributed on Moorea, they may be expected to exhibit the greatest differences in behavior of all the

Moorean species. In addition, *P. suturalis* is unusual in displaying true chiral polymorphism. Populations in some areas are all dextral, others are all sinistral, while still others are amphidromic. It has been suggested that differences in chirality may function as an interspecific isolating mechanism in *Partula,* and indeed there is some evidence for a restriction of random mating between dextral and sinistral *P. suturalis* in nature (Clarke & Murray, 1969). Descriptions of the mating behavior of these species and morphs will serve as a basis for the comparative study of other species and for the investigation of mating behavior in interspecific crosses.

MATERIALS AND METHODS

Origin of the Animals. Collections of *Partula* from Moorea were made by Bryan Clarke and James Murray in the summers of 1962, 1967, and 1968. Snails used in this study were obtained either directly from these collections or as offspring of genetic crosses established from the 1962 samples. Collecting localities are shown in Fig. 1.

Maintenance of Animals. snails were maintained as described by Murray & Clarke (1966). They were kept in plastic boxes lined with moistened toilet paper and were fed a diet of oatmeal, lettuce, and powdered natural chalk.

Breeding Biology. Partula suturalis and *taeniata* are ovoviviparous hermaphrodites. Self-fertilization is possible but occurs only rarely (Murray & Clarke, 1966, 1976a, b). The genitalia of *Partula* are asymmetrical. In dextral individuals the genital opening is on the right side of the body; in sinistrals it is on the left.

Selection of Animals for Study. Individuals were chosen for mating on considerations of maturity, health, shell condition, and origin. Maturity can be judged by the development of a reflected lip to the shell. Health and general physical condition are indicated by activity and willingness to feed. Since the shell is the "stage" on which courtship occurs, only animals with shells free from malformations were chosen.

For each trial, individuals were selected on

FIG. 1. A map of Moorea, French Polynesia, showing the valleys of origin of the animals used in this study. Apootaata is a division of the inner part of Faatoai.

the basis of: 1) species, 2) valley of origin, 3) previous mating experience, and 4) for *P. suturalis,* direction of coil. Since we wished to use only individuals with no hint of hybrid ancestry, localities where snails show evidence of hybridization with other species were avoided. In four cases, however, we were forced to use animals from Faamaariri (see Table 1), where hybridization with *P. aurantia* is a possibility. In the initial studies of animals born in nature, individuals from the same local valley were paired in order to detect intraspecific variation. In trials with laboratory reared animals, pairs with previous mating experience and proven fertility were used in most instances. A few matings were set up with virgin animals, isolated from birth. In *P. suturalis* the direction of coil was taken into consideration. Individuals of the same chirality were used initially, and then observations were extended to mixed pairs.

Preparation of Animals for Observation. From the experience of the genetic program, it appears that isolation increases the readiness of individuals to court and that a short period of aestivation in dry conditions stimulates activity when moisture is restored. Hence the animals were maintained in isolation and without moisture for at least a week prior to the trials, except in those cases where the effect of isolation was being tested. Since attempts to stimulate courtship by reducing illumination were unsuccessful, no special efforts were made to control illumination during the trials.

Observation. In single-pair matings, partners were placed in a clear polystyrene box (11.5 × 11.5 × 3.3 cm) on a freshly moistened paper substrate. All the actions of the animals were recorded. A clock and stopwatch were used to keep time. Photographs of various stages of courtship were made with a 35 mm camera. The observing room had overhead lighting, and the temperature ranged from 18 to 21°C. Observations were carried out both during the day and in the evening.

In group matings, 4 to 12 individuals were placed in a larger polystyrene box (19 × 13.9 × 9 cm) with a moistened paper substrate. Half of the animals were physically isolated prior to the trials; the other half were kept together. In one trial involving virgins tested as a group, all animals were previously isolated. Prior aestivation was enforced for all the animals. In group trials each shell was marked with an identifying number written with a waterproof felt-tipped pen. The animals showed no visible reaction to the ink.

Tables 1 and 2 list the histories of animals used in this study and the type of test in which they were used.

Analysis. Each successful mating was analyzed to characterize the component movements. Matings of similar type were then compared to establish the typical sequence of events. Diagrams of the movements of male-acting animals were made for each courting pair and were used to analyze elements of the courtship. Examples are shown in Figs. 2–3.

RESULTS

Partula suturalis

Description of Courtship

Of 41 trials conducted with *P. suturalis,* 25 produced useful results, the remainder showing either complete inactivity (if so, trials were terminated after 30 minutes) or random exploratory behavior (if so, trials were terminated after 120 minutes). In order to organize the description, courtship has been divided into five stages: Foreplay, Early Courtship, Late Courtship, Copulation, and Reversal. Table 1 summarizes the behavioral elements recorded in each of these stages.

Foreplay. Foreplay is defined by frequent meetings, departures, and temporary shell mountings, sometimes including *pivoting* and *pursuit. Pivoting* consists of a series of C- and S-shaped turns made by a pair. The animals are positioned at right angles to one another and turn sequentially so that one animal moves into a curve as the other moves out. On approaching one another, there is usually some contact of tentacles or shells. *Pursuit* consists of circling turns toward one animal made by its partner without reciprocation.

Foreplay usually takes the following form. After wandering about the box, A and B meet. A mounts the shell of B and moves from lip to apex. A then dismounts and the pair begin to separate. *Pursuit* or *pivoting* follows. In *pursuit* B continues on a straight path while A approaches with C- and S-shaped turns. On contact A will mount B. A may follow the slime trail of B. In *pivoting* both animals make sequential turns until they touch, when mounting or separation will follow.

Early Courtship. Early Courtship is defined by shell mounting followed by *shell wander-*

TABLE 1. A list of courtships observed in *Partula suturalis*, showing the origins of the animals, the conditions of the tests, and the elements of courtship occurring in each test.

Preparation						Foreplay			Early Courtship			Late Courtship													
														Probing											
Origin of animals	Number of animals	Time of test	Virgin	Isolated	Dried	Pivots	Repeated meetings	Frequent mounts	Shell wandering	Testing the lip	Female to top	Hanging position	Head-aligned position	Foot	Body stalk	Head-genital aperture	Male biting	Female biting	Head entwining	Head turning	Shell twirling	Head prodding	Kissing	Copulation	Reversal
Dextrals, laboratory reared, tested in pairs																									
Faatoai × Maramu / Faamaariri	2	PM	+	+	–	–	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dextrals from nature, tested in pairs																									
Faataofe	2	PM	–	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Faataofe	2	PM	–	+	+	–	–	–	+	+	+	+	+	+	+	+	+	–	+	+	+	+	–	–	–
Faataofe	2	PM	–	+	+	–	–	–	+	+	+	+	+	+	+	+	+	–	+	+	+	+	–	–	–
Faataofe	2	PM	–	+	+	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+	–	+	–	–	–
Dextrals from nature, tested as groups																									
Maramu	8	AM	–	+	+	1	5	5	5	–	5	–	1	–	–	–	1	1	1	–	–	3	–	–	–
Maramu	8	PM	–	+	+	1	1	1	5	1	2	1	2	1	1	1	1	1	1	1	1	1	1	–	–
Faataofe	10	PM	–	+	+	–	3	3	9	4	4	5	1	1	2	4	4	2	–	3	3	2	3	1	1
Sinistrals, laboratory reared, tested in pairs																									
Faatoai / Fareaito	2	PM	–	+	–	–	–	–	+	–	+	+	–	+	–	+	?	?	?	?	?	?	?	+	+
Faatoai / Fareaito	2	AM	–	+	–	+	+	+	+	–	+	+	+	+	–	+	–	–	+	+	–	–	–	+	+
Faatoai / Fareaito	2	PM	–	+	–	–	–	–	+	+	+	+	+	+	–	+	+	–	–	+	–	–	–	+	+
Faatoai	2	PM	–	+	–	–	–	–	+	+	+	+	+	+	+	+	+	–	–	+	+	–	–	–	–
Faatoai	2	AM	–	+	–	–	–	–	+	+	+	+	+	+	–	+	+	–	+	+	+	+	–	+	+

Faatoai Fareaito	2	PM	−	+	−	−	+	+	+	+	+	+	+	+	−	+	+	−	+	+	+	−	−	−	−
Faatoai	2	PM	−	+	−	−	−	−	+	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−
Faatoai × Fareaito Faatoai	2	PM	−	+	+	−	−	−	+	+	+	+	−	+	−	+	−	−	−	−	−	−	−	−	−
Sinistrals from nature, tested in pairs																									
Maharepa	2	PM	−	+	+	+	+	+	+	+	+	+	−	+	−	+	+	−	+	+	−	−	−	−	−
Maharepa	2	AM	−	+	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Maharepa	2	AM	−	+	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Sinistrals from nature, tested as groups																									
Faatoai	6	AM	−	+	+	5	11	7	7	1	7	1	−	−	−	1	−	−	1	1	1	−	−	−	−
Maharepa	6	PM	−	+	+	−	5	5	2	2	2	2	1	2	−	2	1	−	−	1	1	1	−	−	−
Faatoai	6	AM	−	+	+	2	2	2	3	−	3	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Faatoai	6	PM	−	+	+	−	1	1	1	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Faatoai	6	PM	−	+	+	2	3	2	4	−	2	2	1	1	1	2	−	−	1	1	1	−	−	−	−
Maharepa	9	PM	−	+	+	1	1	1	4	4	2	4	4	4	−	4	4	4	−	4	4	−	−	4	1
Dextral/sinistral pairs,laboratory reared																									
Faatoai S Faamaariri D	2	PM	+ −	+	−	+	+	+	+	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Faamaariri S Opunohu D	2	PM	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Opunohu D Faatoai × Fareaito S	2	PM	+	+	−	+	+	+	+	−	−	−	−	−	−	−	+	−	+	+	−	+	−	−	−
Opunohu S Faamaariri D	2	PM	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+	+	+	−	−	−
Faatoai × Fareaito S Opunohu D	2	AM	+	+	−	+	+	+	+	−	+	−	−	−	−	−	−	−	−	+	+	+	−	−	−
Dextral/sinistral groups from nature																									
Faataofe D	4	AM	−	+	+	−	1	1	3	−	1	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Maherepa S	4					−	1	1	1	−	1	1	1	1	−	1	1	−	−	1	1	1	−	−	−
Faataofe D	4	AM	−	+	+	−	−	−	2	−	1	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Faatoai S	4					1	1	−	2	−	2	−	−	−	−	−	−	−	−	−	−	−	−	−	−

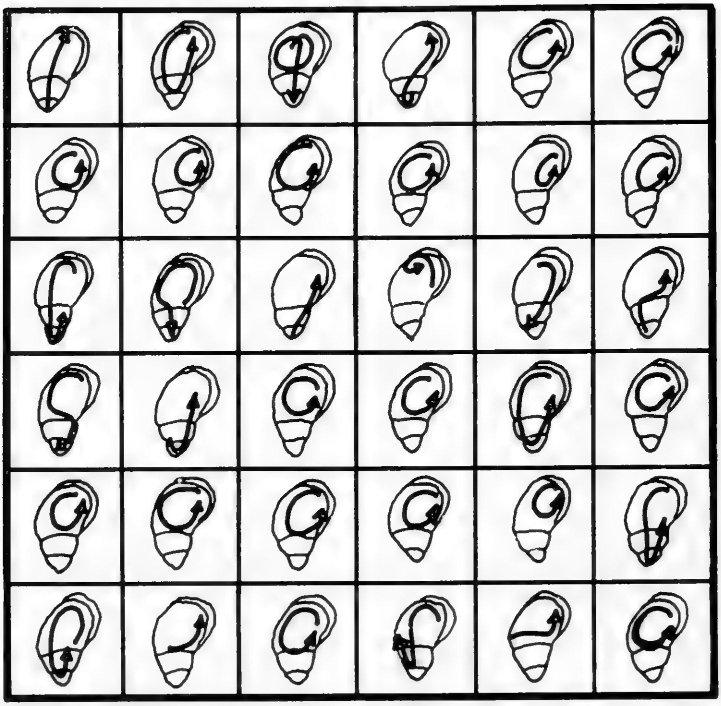

FIG. 2. An ideogram of *shell wandering* during Early Courtship of *Partula suturalis*. The outline of the shell represents the female-acting animal. The directed line shows the path of the male in a typical, continuous sequence of movements.

ing. At this stage, sex roles become differentiated, the male-acting animal (called simply the male hereafter) mounting the shell of the female-acting animal (called the female). *Shell wandering* describes the movement of the male on the shell of the female. The male moves from the point of boarding to the opposite end of the shell and back, describing a generally circular pattern, either clockwise or counter-clockwise. The direction appears to be random at first; but as *shell wandering* progresses, a dextral male tends to settle into a counter-clockwise pattern (Fig. 2), and a sinistral male tends to move clockwise. As the male enters the *lip quadrant* (that section of the shell bounded by the lip, the suture, and the midline), the penis is everted. At this time the male may pass his head or his penis along the edge of the shell, a movement that we have called *testing the lip*. During these events the female moves toward the top of the mating chamber and either remains stationary or moves slowly in half or quarter turns.

A typical sequence of events is as follows. As the male approaches the female there is usually some body contact, often involving the tentacles. The male then mounts the shell of the female at any convenient place and begins *shell wandering* (Fig. 4a, c). Whenever the circling motion brings him into the *lip quadrant*, the penis begins to appear, reaching its full extension as the male passes the center of the lip. At this point he may *test the*

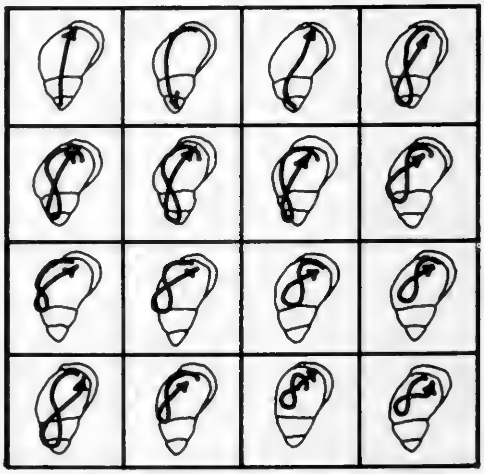

FIG. 3. An ideogram of *shell wandering* during Early Courtship of *P. taeniata*.

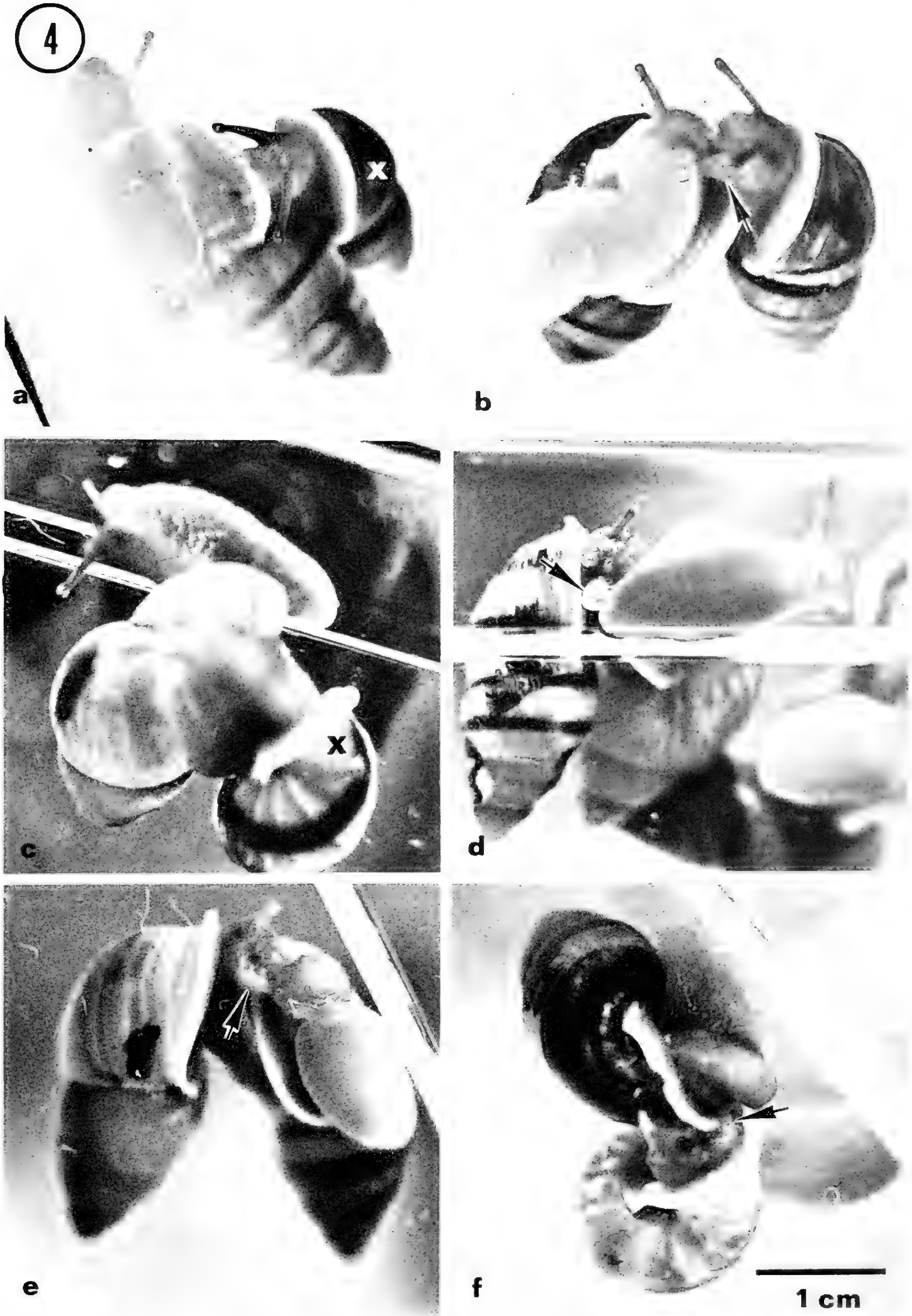

FIG. 4. Courtship of *P. suturalis* of like coil. Sinistral: (a) Early Courtship: *shell wandering,* with male (X) at the lip moving into a *hanging position.* (b) Late Courtship: *probing,* penis (arrow) near genital aperture of the female. Dextral: (c) Early Courtship: *shell wandering,* with male (X) moving in counter-clockwise direction, (d) Late Courtship: *probing,* penis (arrow) at rear of foot of female. (e) and (f) Copulation: two views showing the position of head, tentacles, and penile bridge (arrows).

lip and then turn away to continue wandering. The female climbs to the top of the chamber and proceeds along a crooked course.

Late Courtship. Late courtship is defined by the assumption of the *hanging position* or *head-aligned position* by the male. The male commences *probing* of the female with the everted penis. In the *hanging position* the male is positioned so that his foot is parallel to the lip and his head is projected slightly over the lip of the shell of the female. In the *head-aligned position* the male is at the center of the lip with his head and foot parallel to that of the female. *Probing* consists of a series of stroking, swirling, or jabbing movements made by the extended penis directed toward the skin of the female. The probes are directed toward the foot, body stalk, or head/genital aperture and are powerful enough to leave temporary indentations on the skin.

Other movements made in late courtship by the male or female include *biting, head entwining, kissing, shell twirling,* and *head prodding.* Both partners may engage in *biting.* The male bites along the head, body stalk, or foot of the female, The female bites the head or foot of the male. The bitten animal reacts suddenly by pulling or turning away or by retracting into the shell. In *head entwining* the heads of the male and female touch and encircle one another. During this movement *kissing*, consisting of mutual mouth contact and visible working of the radulae, may occur. *Kissing* differs from *biting* in that no sudden reaction occurs. *Shell twirling* is a movement by the female involving a clockwise and counter-clockwise rotation of the shell, the foot remaining stationary. *Head prodding,* by the male, occurs when he is along the lip and consists of pushing his head into the aperture between the shell and body of the female, thus prodding her body stalk or the side of her foot.

In a typical late courtship, the male moves along the lip into the *hanging position* and commences *probing* (Fig. 4b). The everted penis is placed on the female for several seconds, lifted slightly, and then replaced. After two to five seconds of concentrated probing, the male usually lifts the organ higher and retracts it slightly. Then probing resumes. The entire bout of probing may last as long as 20 minutes at a time, with every exposed portion of the female receiving attention (Fig. 4d). After the bout, the penis is retracted, and the male returns to *shell wandering.* As he reaches the *lip quadrant,* the penis is everted; and he may begin another bout of *probing* or continue *shell wandering.* The numbers of wanderings and probing are quite variable. Occasionally the male will move into the *head-aligned position*, probing closer to the genital region. *Biting* and *head entwining* may occur at any time during late courtship. *Head prodding* and *kissing* are rarely observed.

During late courtship the female is not wholly passive. She often moves in slow C- or S-shaped turns (Fig. 4b). She may bite the male or twirl her shell. She may turn her head to engage in *head entwining.* During the most intense probing, she curves her foot so that the genital aperture is at the top of the curve.

The series of late courtship movements may be repeated many times until copulation occurs.

Copulation. At some point during the probing, the tip of the male organ is inserted into the female tract (Fig. 4f). The penis becomes thinner and more transparent. A more opaque white "thread" (probably the penis retractor muscle) within the organ can be seen to extend from the male to the female. Pulsations along the penis can be seen. At this stage the animals are stationary with tentacles withdrawn, and they may be partially retracted into their shells. The male is in the *hanging position.* The female arches her head off the substrate to curl it around the head or penis of the male (Fig. 4e, f). Copulation persists for 5 to 65 minutes.Then the white thread can be seen to be withdrawn first, followed by the penis itself.

Reversal. The male dismounts and the two animals separate. Sex roles may then be reversed and courtship may resume. The second courtship is almost as long as the first and follows the same course leading to copulation.

Comparative Mating Behavior

Wild and Laboratory Reared Animals. The mating behavior of animals reared in the laboratory was indistinguishable from that of snails obtained from the wild.

Single Pairs and Group Trails. Courtship patterns in group trials did not differ from those exhibited by single pairs. The principal effect of the group trials was that courting pairs were often disturbed by other animals. This led to the formation of *mating chains* involving three to five animals (Fig. 6a). Common chains included two males courting one female, or a male courting the male of another pair. If two males court one female, then there is compe-

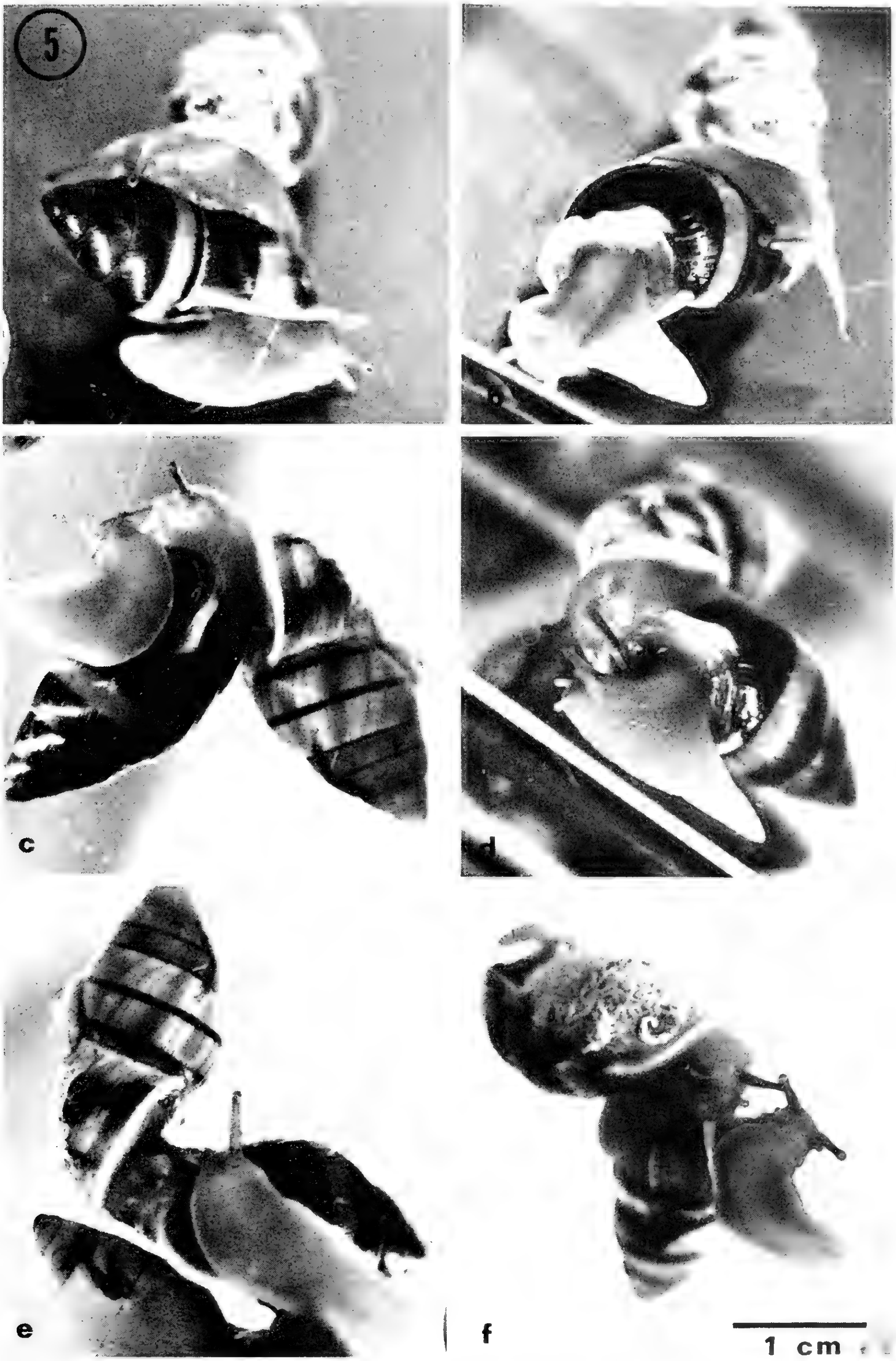

FIG. 5. Courtship of a dextral by a sinistral *P. suturalis*. (a) and (b) Early Courtship: *shell wandering*. (a) The sinistral male moves to the apex from the lip. (b) The same male describes a clockwise circle by continually turning right and is shown returning to the umbilicus rather than the suture of the shell. (c) through (f) Late Courtship: *probing*. (c) Sinistral male at umbilicus probing the left side of the female. (d) Female adjusts shell, shifting the male closer to the genital aperture on right. (e) Female repositions male by turning her head. (f) Female turns her head and shell to place the male closer to her right side.

tition for the correct probing position; and one male is usually displaced toward the umbilicus where he may continue to probe. Eventually one male dismounts, either the original male or the intruder. If a male begins to court an animal that has already begun courtship as a male, then the latter usually reverses roles and behaves as a female.

In the group trials all animals had been induced to aestivate, but half the animals in each trial had been individually isolated. The subsequent trials showed no great disparity between isolated and non-isolated animals, although there is a suggestion in the data that isolated animals tend to assume the role of male.

Animals from Different Origins. Animals of the same chirality from different valleys showed no detectable differences in behavior. Dextrals from Faataofe, Maramu, and laboratory broods had very similar courtships as did sinistrals from Faatoai, Maharepa, and laboratory broods. Courtship of dextrals was a mirror-image of that of sinistrals. Each directed probing to the side of the head appropriate to females of its own chirality, right for dextrals and left for sinistrals.

Virgin and Non-Virgin Animals. No difference could be detected in the courtship of virgin and non-virgin animals.

Courtship of Mixed Dextral and Sinistral Pairs

Since chirality may function as an isolating mechanism in nature, the behavior of dextral/sinistral crosses in *P. suturalis* is of special interest. That mating can occur has been established by laboratory breeding (Murray & Clarke, 1966, 1976b), but it appears that in natural populations mating is not random with respect to chirality (Clarke & Murray, 1969). In these trials most of the animals were taken from populations in which only dextrals or only sinistrals are found. However, three animals were from polymorphic populations (Faamaariri), and two were sinistral offspring of dextral/sinistral crosses. Table 1 shows the types of crosses, the mating activity, and the elements of behavior that were displayed.

Foreplay. Pivoting and *pursuit* were carried out as described above. The directions of the C- and S-shaped turns were not related to the type of coil of the animals.

Early Courtship. The predominating direction of *shell wandering* depends on the chirality of the courting male. Dextral males move in counter-clockwise circles; sinistral males, in clockwise circles. These movements lead the male to approach the "wrong" side of the lip, placing him near the umbilicus (Fig. 5a, b).

Late Courtship. The male continues courtship as if the female were of the same chirality. The *hanging position* of males in these crosses was at the umbilicus. *Probing* was directed to the side opposite the genital aperture of the female (Fig. 5c). *Shell wandering* separated bouts of probing.

The female in these trials was not passive; she frequently turned her head and displayed *shell twirling, head entwining,* and *biting.* These movements appeared to be directed toward aligning her genitalia with those of the male (Fig. 5d–f).

Two late courtships were observed. Two other pairs displayed many of the patterns of courtship without probing. Copulation was never witnessed in these trials.

In group tests, where four animals of each coil were placed together, the opportunity for dextral/dextral and sinistral/sinistral pairings also existed. Of the 23 mountings that were observed, 12 were between like pairs and 11 involved dextrals and sinistrals. Although the numbers are small, there is no indication of assortative mating.

Comparison with Monomorphic Trials. From the mixed trials it appears that the behavior of the males does not differ from that observed in monomorphic trials. The male courts as if the female were identical to himself. The behavior of the female in mixed trials, however, is different. She apparently employs normal movements of courtship in a special manner to facilitate copulation by the male.

Partula taeniata

Description of Courtship

Of 22 trials conducted with *P. taeniata,* 17 produced useful results, the remainder showing either complete inactivity (if so, trials were terminated after 30 mintues) or random exploratory behavior (if so, trials were terminated after 120 mintues). As in *P. suturalis,* the description of the courtship of *P. taeniata* has been divided into five stages: Foreplay, Early Courtship, Late Courtship, Copulation, and Reversal. Table 2 summarizes the behavioral elements recorded in each of the stages.

Foreplay. Foreplay is defined by frequent meetings and departures, *dances,* and *pursuit.* Mounting occurs often during meetings but not during the dance. *Dances* consist of

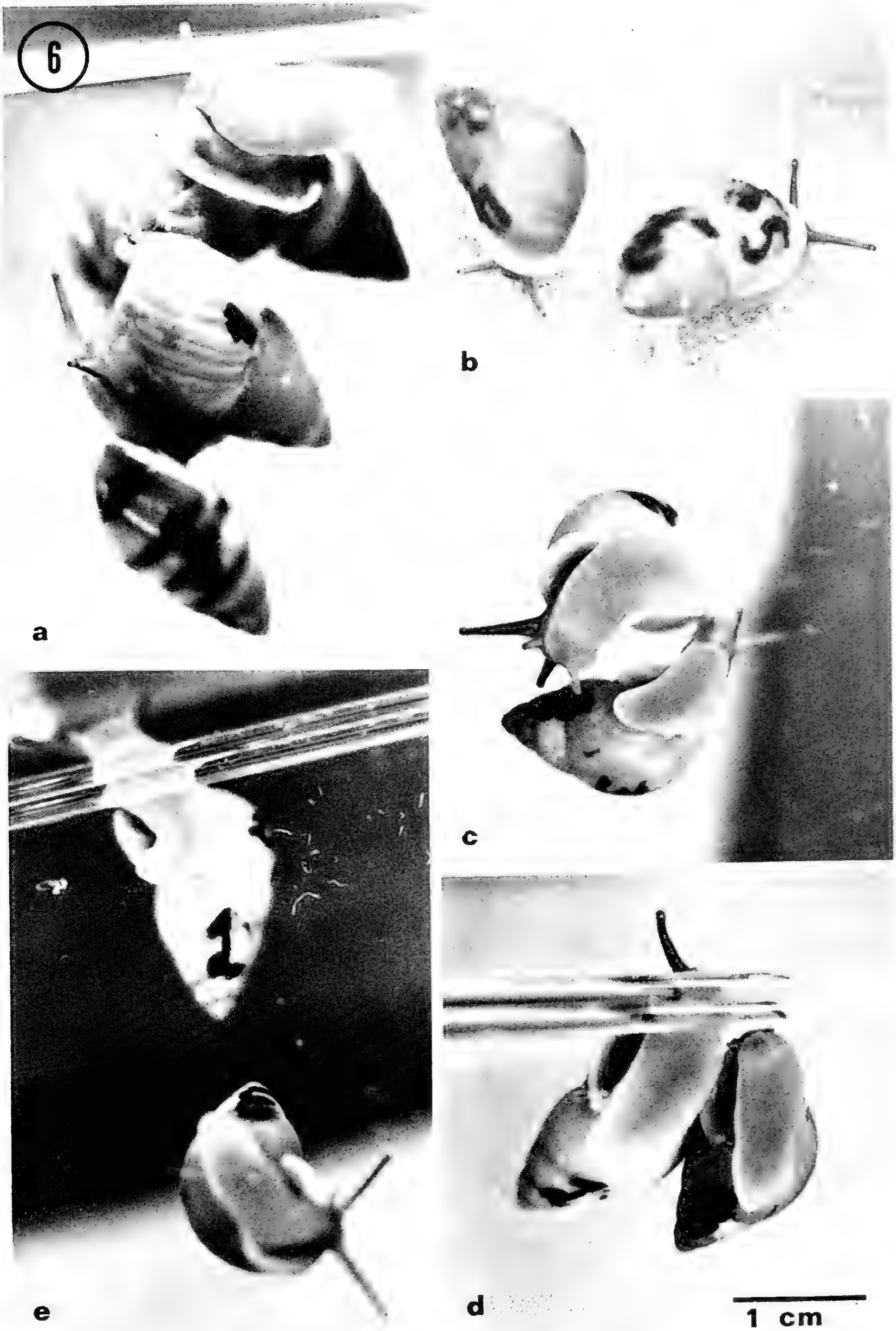

FIG. 6. (a) Mating chain of *P. suturalis.* (b) through (e) Foreplay of *P. taeniata.* (b) *Dance,* showing turns by both animals. (c) *Dance,* different view and type of turn. (d) *Dance,* pair touch side-by-side while passing. (e) *Pursuit.*

TABLE 2. A list of courtships observed in *Partula taeniata*, showing the origins of the animals, the conditions of the tests, and the elements of courtship occurring in each test.

Preparation						Foreplay			Early Courtship			Late Courtship														
														Probing												
Origin of animals	Number of animals	Time of test	Virgin	Isolated	Dried	Dances	Repeated meetings	Frequent mounts	Shell wandering	Testing the lip	Female to top	Hanging position	Head-aligned position	Foot	Body stalk	Head-genital aperture	Male biting	Female biting	Head entwining	Head turning	Shell twirling	Head prodding	Kissing	Touching tentacles	Copulation	Reversal
Laboratory reared animals, tested in pairs																										
Roroie × Apootaata	2	PM	–	+	–	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Roroie × Apootaata	2	PM	–	+	–	+	+	+	+	+	+	–	+	–	–	+	–	+	+	+	+	+	–	+	+	–
Roroie × Apootaata	2	PM	–	+	–	+	+	+	+	+	+	–	+	–	–	+	–	+	+	+	+	–	–	+	+	+
Faatoai	2	PM	–	+	–	+	+	+	+	+	+	–	+	–	–	+	–	+	+	+	+	–	–	+	–	–
Faatoai × Fareaito	2	AM	–	+	–	+	+	+	+	+	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Roroie × Apootaata	2	PM	–	+	+	–	–	–	+	+	+	–	+	–	–	+	–	+	+	+	+	+	–	+	–	–
Laboratory reared animals, tested as groups																										
Faatoai, Urufara, Roroie, & Roroie × Apootaata	5	PM	+	+	+	2	8	8	4	2	4	–	1	–	1	1	–	1	1	3	1	1	–	2	1	–
Animals from nature, tested as groups																										
Maharepa	8	AM	–	+	+	3	6	3	4	2	2	–	2	–	–	2	–	1	1	1	3	1	–	2	1	–
Faatoai	12	AM	–	+	+	1	4	2	10	1	9	–	8	–	–	7	4	6	5	8	6	2	4	6	5	2
Faatoai	12	AM	–	+	+	–	5	5	10	6	9	–	9	–	–	8	–	7	3	7	7	–	–	7	3	2
Maharepa	12	PM	–	+	+	–	1	1	4	1	1	–	4	–	–	4	–	2	–	2	1	–	1	–	1	–
Faataofe	12	PM	–	+	+	–	7	7	12	3	8	–	7	–	–	7	3	4	1	4	3	1	2	–	3	–
Faamaariri	12	AM	–	+	+	1	3	3	2	–	1	–	1	1	–	1	–	1	1	2	–	–	2	1	1	–
Animals from nature (mixed valleys), tested as groups																										
Faatoai	6	AM	–	+	+	–	2	2	7	4	5	–	6	–	–	4	–	2	–	5	3	1	1	2	2	–
Maharepa	6					–	1	1	5	1	5	–	5	–	–	5	2	5	2	5	–	–	3	–	5	2
Faatoai	10	PM	–	+	+	–	2	2	5	–	2	–	5	–	–	5	–	4	1	5	–	–	–	–	3	2
Faataofe	10					–	3	3	8	–	7	–	8	–	–	8	1	5	–	8	1	–	–	–	5	4
Faatoai	6	PM	–	+	+	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maharepa	6					–	3	3	9	4	7	–	3	–	–	3	2	–	1	1	3	1	1	–	–	–
Faatoai	6	AM	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maharepa	6					–	2	2	9	2	8	–	6	–	–	6	3	5	–	5	5	3	–	–	1	–

almost synchronous straight or curved movements. As they approach each other, one animal gently bumps the side of the other with its head. The two then pass side to side, touching shells as they pass. Pursuit consists of circling turns made by one animal toward another.

In a typical foreplay sequence, the pair approach, facing one another, and move into the *dance.* Animal A approaches B diagonally. A bumps B, and as they pass, their shells touch. A then turns to follow B, while B also turns toward A (Fig. 6b). Making C- and S-shaped turns, the pair approach again (Fig. 6c). B bumps A, and they touch shells in passing (Fig. 6d). After a prolonged dance the pair usually separate. One may follow the other in pursuit (Fig. 6e). The pursuing animal may mount the shell of the other. He then either dismounts or proceeds to the next stage of courtship.

Early Courtship. Early courtship is defined by shell mounting followed by *shell wandering.* In *shell wandering* the male moves around the shell of the female in a figure of eight pattern (Figs 2, 7a–e).

In a typical early courtship sequence, the male mounts the shell of the female, usually at the lip or the apex. *Shell wandering* follows, bringing the male to the *lip quadrant* (bounded by the lip, the midline, and the suture). As he moves toward the center of the lip, penis eversion occurs. He may *test the lip* by passing his head or penis along the lip. *Shell wandering* is then resumed. During this sequence of events the female usually climbs to the top of the mating chamber.

Late Courtship. Late courtship begins when the male assumes the *head-aligned position* at the center of the lip (Fig. 7f) and begins *probing* the head and genital area of the female. Figure of eight *shell wandering* usually occurs before and after a series of probes with the everted penis. The male may also engage in *biting, kissing,* and *head prodding.* The female may respond by *biting, shell twirling,* turning her head, or moving in C-shaped turns. *Head entwining* or *touching tentacles* involve both partners.

Touching tentacles takes place while the male is in the *head-aligned position.* One optic tentacle of the male and one of the fe-

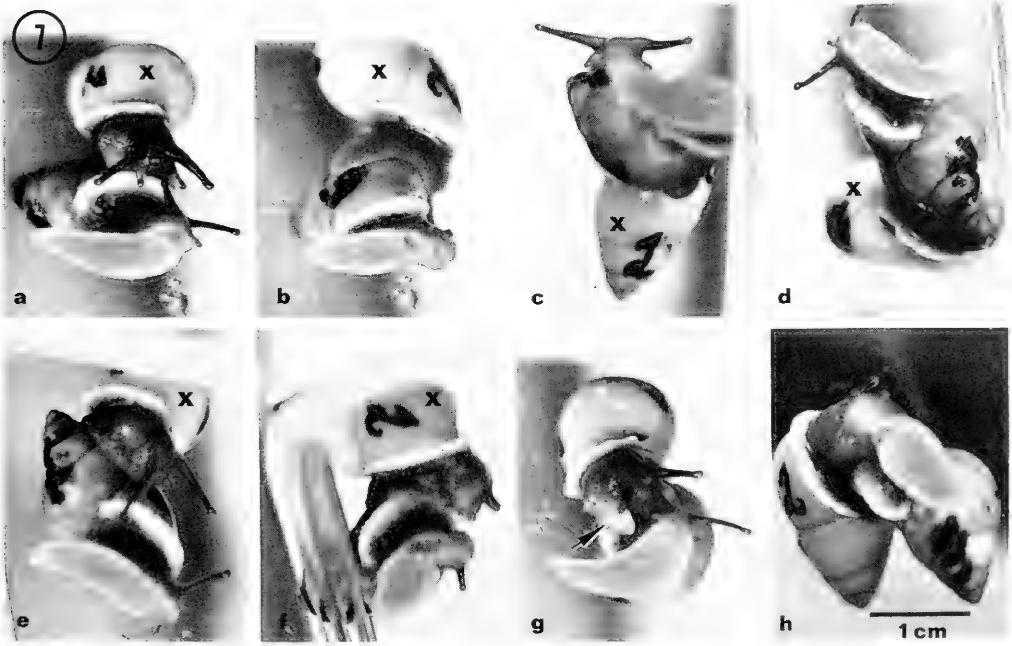

FIG. 7. Courtship of *P. taeniata.* (a) through (f) Early Courtship: *shell wandering* sequence describing a figure of eight (X designates male throughout the sequence). (a) Male in *head-aligned position.* (b) Male turning away toward apex of female shell. (c) Female has rotated her shell. (d) Male at apex of shell. (e) Male has turned at the apex and moves toward the lip. (f) Male has returned to the *head-aligned position* and the female curves her head. (g) Late Courtship: *Probing.* (h) Copulation.

male touch, adhere briefly, and then separate. The other terms are as defined in the description of late courtship in *P. suturalis*.

In a typical sequence, the male moves to the center of the lip of the female and assumes the *head-aligned position*. He everts his penis and begins *probing* the head and genital area of the female (Fig. 7g). The movements vary from gentle strokes to strong jabs and may be continued for a few seconds to several minutes. After a bout of *probing* the male resumes *shell wandering* that may extend to the apex as in early courtship or may be confined to the body whorl of the shell. *Biting, kissing,* and *head prodding* may accompany the principal movements.

The female is usually moving in slow C- and S-shaped turns. She turns her head to present her genital area to the male and may twirl her shell and bite the male about the head and everted penis. The pair may engage in *head entwining* and *touching tentacles*.

Copulation. At some time during *probing*, the male inserts the penis into the female aperture (Fig. 7h). Copulaton is brief, averaging only 75 seconds. During copulation both animals retract their tentacles. The female turns her head, arching over the male's head so that her mouth comes in contact with the inserted penis. She bites the organ and the top of the male's head, often causing him to retract into his shell, leaving only the penis exposed. After copulation the male quickly moves straight ahead off the shell. The female, her head still turned and arched, licks her genital aperture, where a mucous secretion is often seen.

Reversal. The female, after licking her aperture, may follow and mount the departing male and begin *shell wanderng*. Alternatively the pair may separate and later undertake a reversed courtship. Reversal was observed following 13 of 33 successful copulations. Once successful mating of both individuals has occurred, courtship between the two ceases. Even though they may subsequently meet and briefly mount, no *shell wandering* occurs. On the other hand multiple copulation with several different animals is common. During one observation period one individual was observed to copulate with four different animals. In another test one individual was involved in four courtships with two animals, behaving as a male and female toward each. The two male courtships were unsuccessful, the first female courtship resulted in a completed copulation, while the second female courtship ended when a spermatophore was extruded after copulation.

Comparative Mating Behavior

Wild and Laboratory Reared Animals. The mating behavior of animals reared in the laboratory was indistinguishable from that of snails obtained from the wild.

Single-Pair and Group Trials. In group matings the movements took place as in the single-pair matings, but the timing was often modified. With single pairs foreplay, especially the *dance,* was usual and often prolonged. In group matings this stage was abbreviated or absent.

In group trials mating pairs seemed to attract other animals. The formation of *mating chains* interfered with the courtship and prevented reversal. Over all, single pairs were more successful in bringing courtship to the point of copulation.

Animals from Different Origins. No differences were detected in the courtship of animals from different valleys. Animals from Faatoai, Faataofe, Faamaariri, and Maharepa showed essentially the same behavior. Matings between animals from different valleys did not show any unusual features. In mixed group trials there was no detectable tendency for snails of the same origin to mate preferentially with one another. However, the data do not permit statistical analysis since the observations are not independent.

Virgin and Non-Virgin Animals. There was no apparent difference in the courtship of virgins and non-virgins.

Comparative Mating Behavior of *P. suturalis* and *P. taeniata*

The mating behavior of *P. suturalis* and *P. taeniata* is very similar. The differences between the species are subtle and are summarized in Table 3.

The foreplay of both species includes meeting, mounting, and circular turns involving body contact. The timing, however, is different. *Pivoting* in *P. suturalis* involves sequential turns, while the *dance* of *P. taeniata* consists of almost simultaneous movements. Body contact is always sidelong in *P. taeniata* but is variable in *P. suturalis*. Shell mounting does not occur during the *dance* of *P. taeniata*.

The *shell wandering* movements of the two species in early courtship are rather different.

TABLE 3. A comparison of the elements of courtship in *Partula suturalis* and *P. taeniata*.

	P. suturalis	*P. taeniata*
Foreplay:		
1. Timing of movements	Sequential	Simultaneous
2. Body contact	Variable	Sidelong
3. Shell mounting	Present	Absent in dance
Early Courtship:		
1. Shell wandering	Circular	Figure of eight
2. Penis eversion	At umbilicus	At center of lip
Late Courtship:		
1. Probing	Entire body	Genital aperture and top of head
2. Touching tentacles	Absent	Present
Copulation:		
1. Duration	Long	Short
2. Female activity	Passive	Actively bites
3. Post-copulatory licking	Absent	Present
Reversal:	Delayed	Rapid

P. suturalis follows a generally circular pattern; *P. taeniata* moves in a figure of eight. Penis eversion occurs later in *P. taeniata* beginning only when the male arrives at the center of the lip.

The *probing* in late courtship differs in detail in the two species. *P. suturalis* probes the foot, head, genital area, and body stalk of the female, gradually concentrating on the genital aperture. *P. taeniata* directs its probing much more to the genital aperture and the top of the head. The female controls the area to be probed by revolving her shell (and hence the male). *P. taeniata* seems to require more precise alignment before it begins probing.

Copulation differs in the two species mainly in duration. In *P. suturalis* copulation has been observed to last for up to 65 minutes, but the longest duration for *P. taeniata* was 2 minutes. In addition, the female of *P. taeniata* is more active during copulation, biting the penis and head of the male. The post-copulatory licking of the genital aperture has only been observed in *P. taeniata*. Separation and subsequent meeting is usual in *P. suturalis*.

DISCUSSION

Relation to Courtship in Other Pulmonates

In most of the stylommatophoran pulmonates that have been studied so far, courtship and copulation are reciprocal, both animals acting as males and females at the same time (Fretter & Graham, 1964). The non-reciprocal mating behavior of *Partula* is therefore unusual in at least two significant aspects: role recognition and reversal.

By the time that early courtship has begun, separate male and female behavior patterns have become apparent. The results of this study suggest that the events of foreplay are important in the establishment of these roles; and that if the differentiation is not successfully accomplished, courtship is broken off. Four lines of reasoning support this hypothesis.

First, prolonged foreplay is common in single-pair trials when partners have been isolated for a long time. Since the chance of an animal encountering an animal of opposite tendency is reduced in single-pair as opposed to group trials, and since there is a tendency for isolated animals (at least in *P. suturalis*) to behave as males, the extended foreplay can be interpreted as the result of trying to resolve the problem of similar inclination.

Second, the behavior of two individuals in foreplay is essentially the same. Moreover it is similar to that of other stylommatophorans with reciprocal courtship. The series of turns so typical of foreplay in *Partula* has also been described by Webb for numerous species (1954a, *Ashmunella*; 1942, *Helminthoglypta*; 1948b, *Stenotrema*; 1952a, *Monadenia*; 1952b, *Cepolis*). Gerhardt (1933, 1934, 1935) used the term *Kreis* to describe the turning movements of the *Vorspiel* in the slugs *Limax, Agriolimax,* and *Arion*. The animals form circles, break out of them, and then reform the circles. Herzberg & Herzberg (1962) mention a *preliminary maneuvering stage* before the courtship of *Helix aspersa*. The similarity of foreplay in *Partula* to the early stages of reciprocal courtship in other pulmonates suggests that at this stage sexual roles are not yet determined. What the proximate factor causing the differentiation could be remains to be discovered.

Third, foreplay may be abbreviated or absent from the courtship of *Partula*. Many pairs proceed directly to early courtship, suggesting that when role differentiation is already established, foreplay is unnecessary.

Finally, pairs often break off contact after foreplay, suggesting that the problem of differentiation has not been resolved.

Once sexual roles have become established during foreplay, the behavior of the two animals in a non-reciprocal courtship is very different. The male is considerably more active than the female. The difference becomes apparent when the male mounts the shell of the female and begins *shell wandering* and *probing.*

Shell mounting appears to be an important element of non-reciprocal courtship and is found whenever this type of behavior occurs (*Strophocheilus,* Wiswell & Browning, 1967; *Oreohelix,* Webb, 1951; *Lymnaea,* Barraud, 1957). In contrast, partners engaging in reciprocal courtship approach one another head-on with both animals on the substrate (Fretter & Graham, 1964).

The movements of *shell wandering,* so prominent in early and late courtship, probably function in orientation. After mounting the shell the male explores its surface in order to align himself with the genital aperture of the female. Then after a period of *probing* during which he changes his position on the lip, a reorientation becomes necessary. Similar movements are performed by other pulmonates with non-reciprocal courtships (*Oreohelix,* Webb, 1951; *Lymnaea,* Barraud, 1957). In reciprocal courtship, reorientation on the substrate is accomplished by what appear to be the same sorts of movements (*Ashmunella,* Webb, 1954a; *Monadenia,* Webb, 1952a; *Helminthoglypta,* Webb, 1942; *Cepolis,* Webb, 1952b).

Probing appears to have a dual function. Probes directed toward the genital aperture probably serve to orient the penis to the opening of the female. Probing is also stimulatory. In other pulmonates this stimulation may be accomplished with the penis itself, as in *Partula (Strophocheilus,* Wiswell & Browning, 1967; *Lymnaea,* Barraud, 1957), or with special stimulatory organs (*Arion,* Meisenheimer, 1921; *Cepaea,* Taylor, 1914). Some doubt has been cast on the role of these organs by the work of Lind and Jeppeson. They have pointed out that successful courtship often takes place in *Helix pomatia* without the discharge of the love dart (Lind, 1976) and even after complete extirpation of the dart sac (Jeppeson, 1976). Lind (1976) suggests that while the firing of the dart may be stimulatory to the actor it may even inhibit the recipient. This interpretation supports their general thesis that mating behavior in *Helix* is not a series of reflex responses. Instead it is driven by an internal program that is subject only to orientation and synchronization by the partner's behavior (Lind, 1976; Jeppeson, 1976).

One component of male behavior in *Partula, testing the lip,* appears to be unique. We suggest that the function of this movement is to detect whether the prospective partner is adult, since the reflected lip only develops with the attainment of sexual maturity. Dissections show that the internal genitalia are immature prior to the development of the reflected lip.

The role of the female in the non-reciprocal mating pattern is generally passive. In *Partula* the usual female response during courtship is her movement to the top of the mating chamber. In nature we have observed *P. taeniata* courting on the underside of leaves up to two meters from the ground. Climbing during courtship has also been observed in nature for *Limax* (Gerhardt, 1933) and in the laboratory for *Monadenia* (Webb, 1952a), *Mesodon* (Webb, 1954b), and *Cepolis* (Webb, 1952b).

Both male and female partners engaged in mouth movements. The mouth contacts take two forms, *biting* and *kissing,* both of which are probably stimulatory. Radular biting seems to be common among pulmonates (*Helix,* Meisenheimer, 1907; Lind, 1976; *Triodopsis,* Webb, 1948a; *Oreohelix,* Webb, 1951; *Monadenia,* Webb, 1952a; *Ashmunella,* Webb, 1954a; *Mesodon,* Webb, 1954b). Mutual lip contact is not as frequently observed but does occur (*Helix,* Lind, 1976).

Two reciprocal elements present in non-reciprocal courtship are *head entwining* and retraction of the tentacles at copulation. Although the significance of *head entwining* is unknown, it does occur in other pulmonates (*Helix,* Meisenheimer, 1921; *Haplotrema,* Webb, 1943). Retraction of the tentacles by both partners has also been observed frequently (*Helix,* Szymanski, 1913; *Limax,* Adams, 1898; *Monadenia,* Webb, 1952a; *Cepaea,* personal observation).

The presence of a mucoid secretion after copulation has been noted in *Limax* (Adams, 1898), *Monadenia* (Webb, 1952a), *Cepolis* (Webb, 1952b), and *Lymnaea* (Barraud, 1957). In *Limax* as in *Partula* the secretion is eaten.

Non-reciprocal courtship requires not only the existence of separate roles, but also their reversal. If both animals of a pair are to receive sperm they must at some time change the nature of their roles. Reversal has also been reported for other snails with non-reciprocal behavior (*Lymnaea* (Barraud, 1957; *Polygyra,* Archer, 1933).

Overall, the courtship of *Partula* is most similar to that of *Lymnaea* (Barraud, 1957). In *Lymnaea* there are also two probing positions very similar to the *hanging* and the *head-*

aligned positions of *Partula*. Since *Lymnaea* is rather distantly related to *Partula,* the close similarity is probably due to convergence.

Courtship as an Isolating Mechanism

Although many of the elements of the mating behavior of *Partula* are found in other pulmonates, *Partula* courtship is distinctive. In addition there are subtle differences between the behavior of *P. suturalis* and *P. taeniata.* The two species differ in the form of *dancing* and *pivoting,* in the pattern of *shell wandering,* in the location of *probing,* and in the duration of copulation. The next stage in the study of these species will be to determine whether these differences are of sufficient magnitude to account for the reproductive isolation between the species in nature.

The mirror-image differences in the behavior of dextral and sinistral *P. suturalis* are of particular interest, since the distribution of these forms in nature suggests that chirality is related to interspecific reproductive isolation (Clarke & Murray, 1969). Mixed pairs are certainly capable of crossing and producing viable, fertile offspring (Murray & Clarke, 1966, 1976b). Nevertheless there appears to be some degree of assortative mating in natural populations (Clarke & Murray, 1969). The behavioral studies have shown that this may result simply from the disturbing effects of reversed courtship. Successful copulation between mixed pairs was not observed in this study.

In one respect our results may not be typical of mixed courtships in nature. Most of the animals were derived from populations that are either wholly dextral or wholly sinistral. It is possible that courtship and copulation might have been more successful if more animals from polymorphic populations had been used. However, since those populations that coexist with closely-related species are normally monomorphic for the opposite coil, it is likely that mating behavior is a factor in enforcing reproductive isolation between species.

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AN ANALYSIS OF COPULATION IN *BULINUS (PHYSOPSIS) GLOBOSUS* (GASTROPODA: PLANORBIDAE)[1]

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ABSTRACT

Copulation in *Bulinus (Physopsis) globosus* is unilateral, one member of a pair acting as male only and one acting as female only during a single mating. Copulation usually lasts 40–90 minutes. Pre-insertion stages, from the time a male has attached to the shell of the female until the insertion of the ultrapenis, account for 21.2% of total copulatory time. The ejaculatory period, from the time of insertion of the ultrapenis until withdrawal, accounts for 69.7%, and post-withdrawal stages, from withdrawal of the ultrapenis until the male leaves the female's shell, account for 9.1% of total copulatory time.

Sperm are placed at the posterior end of the uterus, at the outlet to the oviduct, and can reach the carrefour region while the snails are *in copula.* A copulatory plug, which contains entrapped sperm at its posterior end, is found to fill the uterine lumen following copulation. The copulatory plug and sperm are removed from the uterus to the spermatheca three to five hours following copulation. The plug is of "springy" consistency and does not prevent insertion or insemination of the plug-containing female by a second male.

INTRODUCTION

Sexual reproduction in many freshwater pulmonates may occur by either self- or cross-fertilization. Although many freshwater pulmonates can reproduce by self-fertilization, the preference for allosperm over autosperm is well documented in studies using genetic markers (e.g., Cain, 1956; Wu, 1972; Richards, 1973). Cross-fertilization involves copulation, and there have been a number of studies describing in some detail aspects of copulation of various freshwater species (de Larambergue, 1939; Noland & Carriker, 1946; Malek, 1952; Horstmann, 1955; Barraud, 1957; Boray, 1964; Pace, 1971).

Bulinine vector snails of human schistosomiasis have not been studied intensively in regard to copulation, however. Some aspects of copulation have been shown for *Bulinus contortus* (= *truncatus*) (Brumpt, 1928; de Larambergue, 1939), and Kuma (1975) has given an overview of copulatory behavior for *Bulinus (Physopsis) globosus.* Bulinine snails are particularly interesting with regard to copulation because of the copulatory organ, which, due to the structural differences from the copulatory organs of other freshwater snails, is termed an ultrapenis (Hubendick, 1955). The method of eversion of the ultrapenis is described for a number of bulinine species (de Larambergue, 1939; Hubendick, 1948; Demian, 1960; Wu, 1972).

Sperm exchange, although important, may not be the only function of copulation in freshwater pulmonates. It has been suggested that snails which have acted as females will oviposit at a younger age than isolated (i.e., self-fertilizing) snails (e.g., Boycott et al., 1930; Noland & Carriker, 1946; DeWitt, 1954; Horstmann, 1955; DeWitt & Sloan, 1958, 1959) and that copulatory plug formation and inducement of reciprocation are other aspects of the copulatory act (Rudolph, 1979).

The present study examines two aspects of copulation in *Bulinus (Physopsis) globosus* (Morelet), copulatory behavior and copulatory plug formation, in order to begin determination of the role of copulation in the sexual reproduction of this important snail vector of *Schistosoma haematobium.*

MATERIALS AND METHODS

Albino *Bulinus (Physopsis) globosus* snails were used from stocks maintained at The Uni-

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versity of Michigan and at Ain Shams University, Cairo, Arab Republic of Egypt. The parental snails of these stocks were collected in Lourenço Marques, Mozambique, and maintained in laboratory culture since 1960. Snails were raised in community, but were isolated for at least one day prior to observation of copulation. Snails were normally placed together in pairs, but occasionally three or four were placed together.

Paraffin sections were made of reproductive tracts during and after copulation of snails which acted as females. Two pairs of snails *in copula* were killed by immersion in boiling water, the ultrapenis of the male-acting snails severed, and the reproductive tracts of the female-acting snails dissected out and fixed. Reproductive tracts of other female-acting snails were removed and fixed at 0, 15 and 30 minutes and two, three, four and five hours following copulation. Tissues were fixed in Heidenhain's Susa, dehydrated and cleared in ethyl alcohol and xylene and embedded in paraffin. Sections were made at 6 μm and stained with hematoxylin-eosin. Other observations were made by dissection of live snails.

Voucher specimens were deposited in the Museum of Zoology, The University of Michigan. Shell specimens are UMMZ 250035, and alcohol specimens are UMMZ 250036.

RESULTS

Freshwater pulmonate snails are hermaphroditic, and are capable of acting as either male or female or both. The term male will hereafter refer to the male-acting snail and the term female to the female-acting snail.

The timed intervals for the copulatory phases reported below, unless otherwise stated, were determined at water temperatures of 20–22°C and are from copulations in which insertions of the ultrapenis occurred. Timed observations were made at other temperatures and observations were also made during copulations which were not timed. Copulation occurred at water temperatures of 16–25°C, but no attempt was made to observe below or above these temperatures. Not all phases were observed on all copulations, many times due to unfavorable positioning of the snails.

Copulatory behavior

Crawling on shell to initiate copulation. After reunion into pairs, the interval between reunion and the first crawling by the male on the shell of the female which led to copulation ranged from 10 to 131 minutes ($n = 20$, mean $= 47.9$, S.D. $= \pm 32$). The male attaches directly to the female's shell without any courtship. Crawling on shells which did not lead to copulation was frequently observed, and union into pairs did not always lead to copulation. Snails would also twist or pivot the shell, sometimes violently, when another snail attached, in apparent attempts to prevent attachment. This twisting did not discourage a male which was to copulate. The male held on, and the female soon stopped the twisting motion.

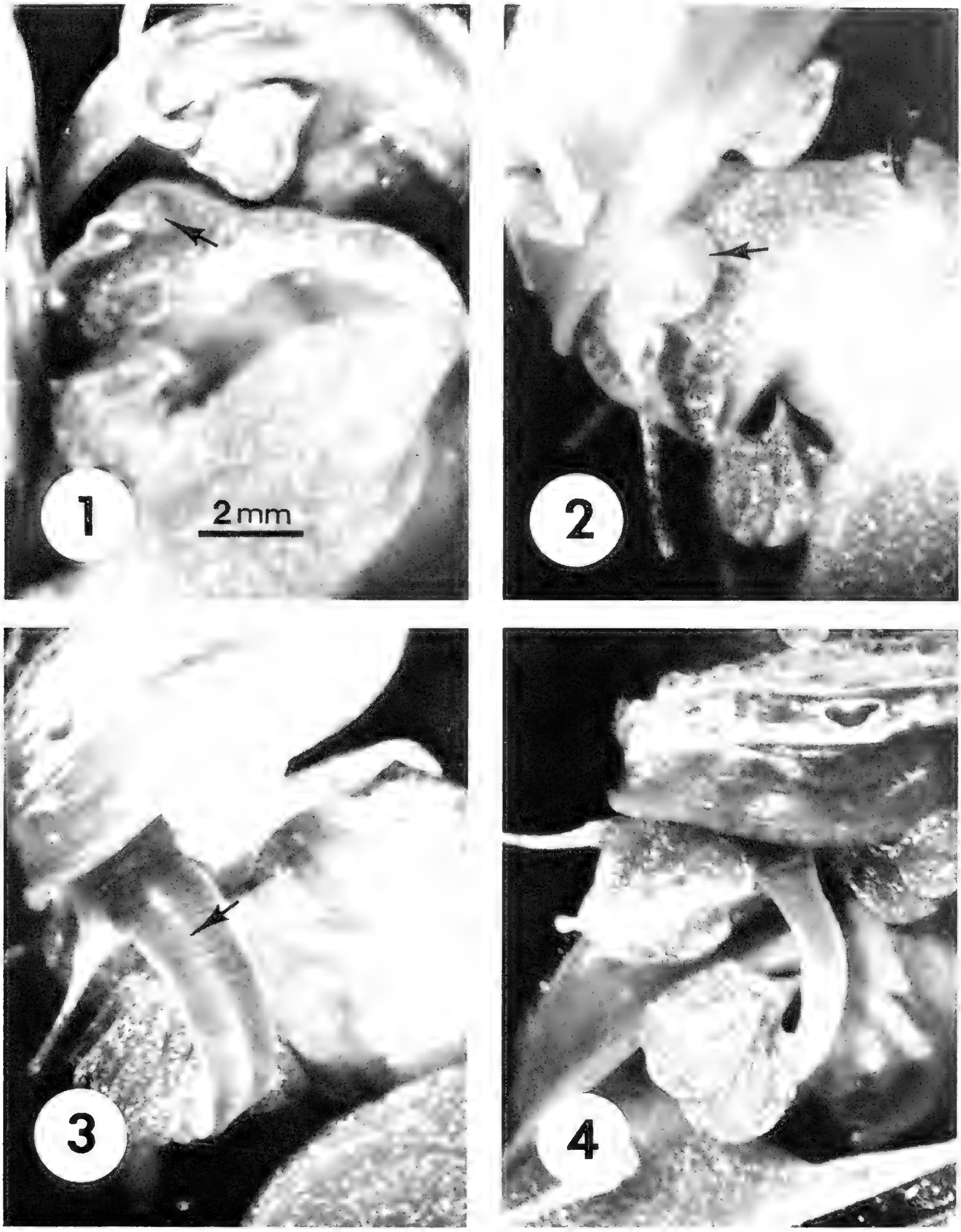
Moving into position. After attaching to the female's shell, the male moves to the copulatory position. The male may move over the female's shell in a circular manner from the female's right to left, or may move directly to the copulatory position. This, in part, depends on whether first contact with the female's shell is made at the anterior or posterior end, or from the side. Final movement to the copulatory position is always from the apex of the shell toward the aperture. Thus a male attaching to the female's shell at the anterior end will move to the apex and then slowly crawl anteriorly on the left side to the copulatory position. However, a male attaching to the apex of the shell may move directly to the copulatory position or may circle in the above manner. The interval from the time of first male crawling to its assumption of the copulatory position was two to eight minutes ($n = 13$, mean $= 4.3$, S.D. $= \pm 1.6$).

The position of the male is at the left margin of the female's shell, its head at the level of the female pseudobranch and the posterior end of the male foot generally overlapping the apex of the female's shell. The male holds tightly to the shell with its compacted foot (see Figs. 3 and 4).

Preputial bulge. The first bulge of the preputium occurs after the male is in the copulatory position (Fig. 1). The interval after having moved into position was less than three minutes ($n = 14$, mean $= 1.8$, S.D. $= \pm 0.9$). In many cases the preputial bulge occurred in less than one minute.

Preputial eversion. First eversion of the preputium (Fig. 2) is also relatively rapid, taking three and one-half minutes or less ($n = 16$) from the time of appearance of the bulge.

Preputium under female's shell. Total eversion and placing the preputium under the shell of the female is generally a continuous



FIGS. 1–4. Phases of copulation of *Bulinus (Physopsis) globosus.* All figures are to the same scale. Fig. 1. Preputial bulge (arrow) after the male is in the copulatory position. Fig. 2. First eversion of the preputium (arrow). Fig. 3. Preputium under the shell of the female before insertion; ultrapenis visible through the preputial wall (arrow). Fig. 4. Ejaculatory stage; after insertion of the ultrapenis.

motion. The interval between the beginning of eversion and placing the preputium under the female's shell is two minutes or less (n = 15).

In many instances the first eversion was an unmeasurable continuation of the bulge, or the total eversion and placing the preputium under the shell was a continuation of the first eversion. The total time from preputial bulge to placing the preputium under the shell was less than four minutes (n = 15, mean = 2.1, S.D. = ± 0.9).

Ultrapenis insertion. After the preputium is placed under the female's shell, the male proceeds to insertion. Insertion was judged to have occurred when the ultrapenis, visible as a white stripe through the preputial wall, disappeared and the preputium became rounded and light red, in contrast to the broad, flattened, dark red preputium exhibited prior to insertion (Figs. 3 and 4). The interval from placing the preputium under the female's shell to insertion was from 2 to 20 minutes (n = 21, mean = 6.8, S.D. = ± 5.5). Other observations showed that even longer times may be required (up to 103 minutes) or that insertion may never be successful. Extended periods with everted preputia were usually associated with retraction and re-eversion of the preputium, and probing motions, and it was fairly obvious that the male was having difficulty with insertion. Moving out of the copulatory position and back can also occur.

While the ultrapenis is inserted, the male is tightly attached to the female's shell, and the male's tentacles are contracted and often slightly crossed. The male's preputium loops ventral to the female's extended pseudobranch (Fig. 4). During the period that the ultrapenis was inserted, the female usually did not move or moved only slowly, but rapid gliding movement by females also occurred.

Withdrawal. Withdrawal was determined by the reappearance of the ultrapenis and immediate removal of the preputium from the genital pore of the female. The interval between insertion and withdrawal was 24 to 63 minutes (n = 21, mean = 38.6, S.D. = ± 11.6).

Moving off copulatory position. After withdrawal, the preputium is inverted and the male usually moves from the copulatory position. The interval from withdrawal to the first movement from the copulatory position for 17 snails was one-half to five minutes (mean = 3.2, S.D. = ± 1.2). Two other males remained in the copulatory position for an extended time period (28 and 40 minutes), and two further males remained in position 136 and 139 minutes and then reinserted their ultrapenes. Remaining in the copulatory position for an extended time was observed in non-timed copulations as well. Preputial bulging and eversion could occur during these extended periods, in addition to the reinsertions described above.

Copulations in which the male remained in the copulatory position as stated above were at first considered as unsuccessful copulations. However, subsequent dissection or sectioning of two females from copulations in which the male remained in position but did not, or was not allowed, to reinsert showed sperm and other material present in the female reproductive tract of the female.

Moving off shell. After the first movement from the copulatory position by the male, it usually moves directly off the shell of the female. After the male has left the female's shell, it shows no further interest in the female. The interval for 16 snails to move from the shell after moving from the copulatory position was one to six minutes (mean = 2.8, S.D. = ± 1.7). Another snail stayed on the shell 19 minutes. Two other males moved back into the copulatory position and remained there for 107 and 144 minutes and then were removed. It is possible that a male could remain longer than 144 minutes, since this snail was removed forcibly and the experiment terminated.

Inversion of roles. Copulation in which the female acted as male to either the male or a third snail occurred in three cases of 44 copulations observed at all temperatures. Others occurred in non-timed observations. They always occurred after the male had moved from the female's shell. In the timed observations, intervals from the departure of the male until the female crawled onto the shell to initiate copulation were two, 23 and 42 minutes. Males can act as females after acting as males.

Female receptivity. In non-timed observations, it was seen that the failure of the male to copulate successfully can be due to the female (also see Second Copulations, below). The female behaved in two ways to prevent successful insertion by the male—by holding its shell tightly against its body and by using its foot to fill the aperture of the shell. The female, in the latter case, turned its foot around so that the head region was in the posterior region of the aperture. The male could not place its extended preputium near the female's genital pore, and it also appeared that the female actively repelled the preputium of the male with its foot and head region while in that position.

Summary of copulation in Bulinus (Physopsis) globosus. Copulaton is unilateral, one snail acting as male and one as female during a single meeting between two snails. There is no reciprocation, although females may be able to function as males shortly after having functioned as females. Since nearly all observations were made using only two snails, there was little opportunity to observe multiple unilateral copulations (i.e., chain copulations, as defined by Rudolph, 1979). However, I have observed chain copulations by these snails in community aquaria.

Total time of copulation is considered to last from the time the male crawled onto the female's shell until the male departed. Five copulations which showed extended pre-insertion or post-withdrawal stages lasted 89, 190, 205+, 215+ and 231 minutes. However, copulations usually did not show extended pre-insertion or post-withdrawal stages. Such copulations lasted 41–86 minutes (n = 13, mean = 57.2, S.D. = ± 13.1). Observations of all stages in ten of these 13 copulations showed that pre-insertion stages (from first crawling until the ultrapenis was inserted) accounted for an average of 21.2% of total copulation time. The ejaculatory stage (from insertion of the ultrapenis until withdrawal) accounted for 69.7% of total copulation time, and post-withdrawal stages for 9.1% of total copulation time (Table 1).

Female Reproductive Tract of Female Snail

Sections and dissections showed that immediately following copulation the female reproductive tract of the female contained sperm, situated at the posterior end of the uterus, extending into the chambers of the post oviduct (terminology of Walter, 1968) and the oviduct. The uterine lumen also contains a mass of material. This mass extends to the vagina, filling the lumen of the uterus, and the sperm in the uterus are captured or embedded in the material of the mass (Figs. 5 and 6). The material forms a mass which is not rigidly compact, but rather somewhat soft and "springy" in consistency. Part of the material which immediately surrounds the sperm is basophilic, while the remainder is eosinophilic. Dissections of females showed that the material adheres somewhat to the uterine walls.

Sperm were present at the level of the carrefour region 30 minutes after insertion but before withdrawal of the ultrapenis, as well as in snails fixed immediately, 15 and 30 minutes following copulation.

Sperm are passed to the female before the mass of material found in the uterus, and are deposited at the proximal end of the uterus (ovotestis as reference point for proximal and distal) at the outlet to the oviduct. It was not determined whether any material is passed along with the sperm.

The sperm and mass of material persist in the uterus apparently unaltered for at least two hours following copulation. By three hours

TABLE 1. Time and percentage of total time of the stages of copulation of *Bulinus (Physopsis) globosus.*

	Pre-insertion		Ejaculatory		Post-withdrawal		
Snail	Minutes	%	Minutes	%	Minutes	%	Total time minutes
1	9	22.0	28	68.3	4	9.8	41
2	14	33.3	24	57.1	4	9.5	42
3	7	15.9	31	70.5	6	13.6	44
4	7	14.6	33	68.8	8	16.7	48
5	13	26.5	33	67.3	3	6.1	49
6	13	24.1	39	72.2	2	3.7	54
7	11	18.3	44	73.3	5	8.3	60
8	15	22.1	48	70.6	5	7.4	68
9	15	21.7	48	69.6	6	8.7	69
10	15	17.4	63	73.3	8	9.3	86
Mean	11.9		39.1		5.1		56.1
S.D.	± 3.2		± 11.8		± 2.0		± 13.8
Mean %		21.2		69.7		9.1	

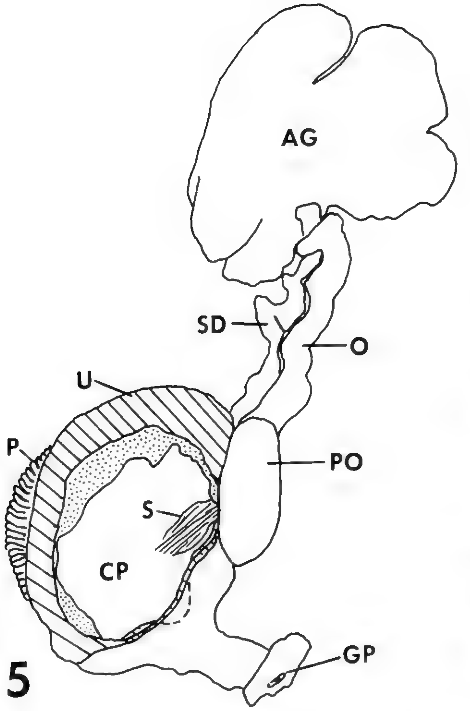


FIG. 5. Diagrammatic dorsal view of the female reproductive system of *Bulinus (Physopsis) globosus* immediately following copulation. The surface of the uterus has been removed to show the position of the copulatory plug and sperm. Hatched area represents the cut surface of the uterus. Abbreviations: AG = albumen gland; CP = copulatory plug; GP = female genital pore; O = oviduct; P = prostate; PO = post oviduct; S = sperm; SD = sperm duct; U = uterus.

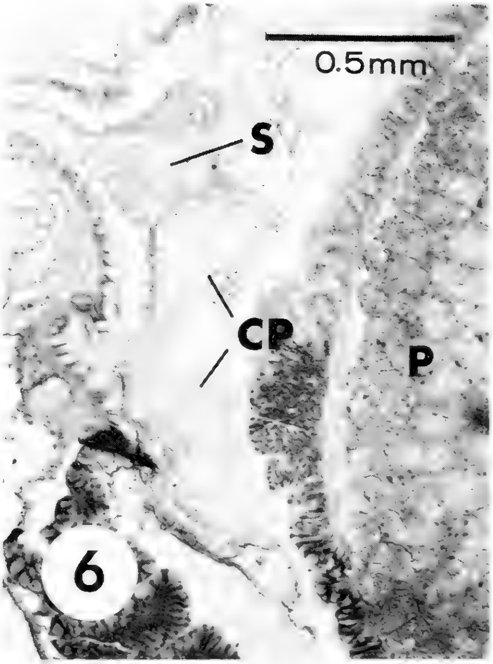


FIG. 6. Section of the uterus of a female *Bulinus (Physopsis) globosus* immediately following copulation. See Fig. 5 for abbreviations.

following copulation, the mass and associated sperm have been displaced either anteriorly into the vaginal region or are removed entirely to the spermatheca. Reproductive tracts are empty four and five hours following copulation, and sperm and associated material are recognizable in the spermatheca. In fact, no sperm can be observed anywhere except in the spermatheca at four and five hours.

The mass of material which fills the uterine lumen is probably composed primarily of secretions from the male reproductive tract of the male snail, although participation by the female reproductive tract of the female snail can not be ruled out. The method of its removal to the spermatheca is not clear.

Second Copulations

Females were allowed to be mated by a second male to determine whether the mass of material which fills the uterine lumen from the first mating can function to prevent a second copulation. Of seven attempts, three males were completely unable to insert the ultrapenis and moved off the female's shell. This lack of success was due, however, to female non-receptivity as described above, even though the female had been completely receptive to copulation by the first male. Three other males were able to insert their ultrapenes but with difficulty, due to female non-receptivity, and with extended phases with everted preputia. These three were able to insert at one, one and three-fourths and two and one-half hours following the withdrawal by the first male. One further snail met with no resistance and was able to insert its ultrapenis 15 minutes following the first copulation. These results indicate that insertion is not prevented by the presence of the material from a previous copulation plugging the uterus.

Males, except the one which inserted one hour following the first copulation, were allowed to finish. Histological observations on reproductive tracts of females from the second copulations with insertion times of one and three-fourths hours and two and one-half hours following withdrawal of the first male showed evidence of two sperm groups, but it could not be determined to which male partner the sperm belonged. In both instances, one sperm group was present at the oviducal outlet and was organized as if it were recently placed. The other group was not as well organized and was in the uterus and vagina, distal to the above group of sperm. In the female in which second intromission occurred 15 minutes after the withdrawal of the first male, the sperm groups appeared to be such that one mass was at the outlet to the post oviduct, the position sperm are normally placed. The second mass was in the uterus, close to the first mass and distal to it. The female from the second copulation with insertion one hour following withdrawal of the first male was dissected approximately 20 minutes following insertion by the second male. The ultrapenis of this second male was in the normal position, inserted between the mass of material in the uterus and the uterine wall.

The indications are that it may be possible for the second male to ejaculate its sperm at the proper position, especially one and one-half to two hours following withdrawal of the first male, since, by this time, the material in the uterus from the first copulation may be more easily moved than immediately after copulation. Even in a second copulation which occurred 15 minutes following withdrawal of the first male, it is possible that the first sperm group is pushed from its normal position by the ultrapenis of the second snail, which then placed its own sperm at the normal position. It is not possible to determine the relationships between two copulations in regard to the contents of the uterus following the second copulation, since it is not possible to distinguish between the products of the two copulations.

DISCUSSION

Copulation in *Bulinus (Physopsis) globosus* is found in the present study to be unilateral, confirming the observation made by Kuma (1975) on the same species. The present behavioral observations show that the stages prior to intromission and following withdrawal of the ultrapenis are relatively rapid. The longest phase is while the snails are *in copula,* during which ejaculation of spermatozoa and other material, presumably composed of secretory products from the male reproductive system of the male snail, occurs. Unilateral copulation is shared by the other bulinine snails *Bulinus contortus* (= *truncatus*) and *Pyrgophysa forskali* (de Larambergue, 1939).

Kuma (1975) also stated that copulation in *Bulinus (Physopsis) globosus* lasted between one and two hours. The present study shows that copulation usually lasted from about 40 to 90 minutes, in general agreement with Kuma. The objective of this study was to determine the temporal relationships during copulation in *B. (P.) globosus.* Of particular interest is that even though a male could be in the copulatory position for extended periods, these extended periods were primarily in the phase when intromission is attempted and in post-withdrawal phases. The phase of insertion appears to be the most critical. If insertion is not effected, even after an extended period of attempting insertion, the snail will move off the shell and copulation will be unsuccessful. The interval when the snails were actually *in copula* was reasonably uniform, and after intromission had occurred, ejaculation was probably assured. This was also the longest phase of copulation, undoubtedly due to the importance of exchanging sperm and male secretory products.

Details of copulation, such as unilaterality, "coagulum" or plug formation and rapidity with which the ejaculated sperm reach the upper portions of the female reproductive tract of the female, are very similar to that which occurs in *Bulinus contortus* (= *truncatus*) (de Larambergue, 1939).

The importance (to the snail) of the mass found in the female reproductive tract of the female is not entirely clear. Rudolph (1979) has interpreted the mass found in the vagina of *Stagnicola elodes* (Lymnaeidae) as a copulatory or mating plug. A similar structure to that of *Stagnicola* was described for *Lymnaea stagnalis* (Horstmann, 1955) and de Larambergue (1939) reported a mass in *Bulinus contortus* (= *truncatus*) similar to the one found in *Bulinus (Physopsis) globosus.* Two functions which were ascribed to a copulatory plug (Parker, 1970), prevention of sperm leakage and prevention of a second insemination of the same female by a second male, appeared to be feasible for the plug in *Stagnicola.*

Neither of these two functions appear likely for the copulatory plug of *Bulinus (Physopsis) globosus.* Due to the placement of the sperm at the proximal end of the uterus at the outlet to the post oviduct, sperm leakage from the female gonopore appears to be unlikely. The mechanism by which sperm are transported to the carrefour region is not clear. Bulinine snails do not contain a ciliated groove in the oviduct as is found in lymnaeids. There does not seem to be agreement as to whether the oviduct contains any ciliation in bulinine snails. Stiglingh et al. (1962) reported oviducal ciliation in *B. tropicus* and Hamilton-Attwell & Van Eeden (1969) reported sparse ciliation in *B. depressus,* but Wright (1957) did not find cilia in the oviduct of *B. (P.) jousseaumei* and I found none in *B. (P.) globosus* in the present study. It is fairly clear that if ciliation is present, it is sparse. If peristaltic muscular pressure or active movement by the sperm themselves are mechanisms which move the sperm through the oviduct in *B. (P.) globosus,* it is possible that the plug functions to prevent sperm leakage from the oviduct itself, preventing backflow of sperm ascending the oviduct into the uterus. However, sperm reach the carrefour before the male has withdrawn, so sperm leakage appears to be of small concern.

A second function described for a copulatory plug, that of preventing successive copulations or inseminations of the same female by two different males, is not shown by the plug of *Bulinus (Physopsis) globosus.* A second successful insertion of the ultrapenis and subsequent ejaculation of sperm can occur while there is plug material present in the female reproductive tract of the female, even as soon as 15 minutes following the first copulation, possibly due to the rather soft consistency of the plug. However, determination of the origin of the sperm present in the female after two successive copulations was not possible. The possibility still exists that the passage into the oviduct is successfully blocked and that sperm from the second copulation cannot pass those from the first. Thus, although successful insemination is possible, successful fertilization may not be. After clearing of the female reproductive tract, of course, there appears to be no physical barrier to the sperm of a second male. This would imply that sperm which have reached a storage site and are then left unprotected by a copulatory plug may have some other advantage over sperm which arrive later, if they are to be used preferentially. The possibility also exists that mixing of sperm from two males could occur or that sperm from a later copulation are used preferentially.

Whatever its function(s), the rapidity with which the sperm reach the carrefour region may be important in determining the effective existence of a copulatory plug. Since sperm in *Bulinus (Physopsis) globosus* can already be at the carrefour region before the male withdraws, the maintenance time of a plug may not need to be as long as in a species in which sperm are deposited in the vaginal region, and thus proportionally have further to travel. In *Lymnaea stagnalis,* for example, sperm reach the carrefour region about two hours after copulation (Horstmann, 1955), and the effective existence of the copulatory plug of *Stagnicola elodes* appears to be about two to three hours (Rudolph, 1979).

It is probable that, in *Bulinus (Physopsis) globosus,* the material found in the uterus has other functions in addition to or instead of the two mentioned above. Further studies in the area of the fate of the sperm from a second copulation, both while the uterus is full of material and after it has been cleared, await the use of genetic markers or radioactively labeled sperm.

The present study is a basic step in evaluating the function of the male reproductive system in *Bulinus (Physopsis) globosus.* Study of sexual reproduction in freshwater snails has long been weighted toward the female reproductive system and its products, the eggs, with good reason. However, studies on the functioning of the male system and its influence on reproduction may yield insight into, as yet, unexplored methods of snail control.

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ANATOMY OF *CHIONE CANCELLATA* AND SOME OTHER CHIONINES (BIVALVIA: VENERIDAE)[1]

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ABSTRACT

Chione cancellata (Linnaeus), *Chione undatella* (Sowerby), and *Chione paphia* (Linnaeus) are anatomically very similar, although their lineages diverged before the end of the Miocene. Except for differences ascribable to greater size, *Mercenaria mercenaria* (Linnaeus) is in soft anatomy similar to the smaller chionines. *Mercenaria* and *Chione* diverged by the Late Oligocene; soft anatomy is fairly conservative. *Austrovenus stutchburyi* (Gray) of New Zealand, although superficially similar to the cancellate American chionines, differs from them in complex characters, and is probably not closely related to them. Lack of intermediate fossils supports this interpretation.

INTRODUCTION

To begin to elucidate relationships among genera assigned to the Chioninae (Keen, 1951, 1969), I examine the anatomy of five common and fairly widespread species usually put in this subfamily of venerid bivalve mollusks. *Chione cancellata* and *C. undatella* represent the nominate subgenus on the American Atlantic and Pacific coasts, respectively. Caribbean *C. paphia* represents the once-prosperous subgenus *Panchione*. The fourth species usually aligned with *Chione* is *Austrovenus stutchburyi* of New Zealand, Pliocene to Recent. The large and commercially important American chionine, *Mercenaria mercenaria,* lives on the eastern and Gulf coasts, as well as in other parts of the world where it has been introduced.

The contentions I particularly wish to address are those of Frizzell and Marwick. In his reclassification of the Veneracea, to which the species discussed here belong, Frizzell (1936) rejected classification based solely on soft parts as inapplicable to fossils, and the processes of obtaining this sort of information as too costly and time-consuming. He further stated that conchological characters and character states are numerous enough to provide the many combinations on which to base a satisfactory classification. He failed to consider the point that combinations mathematically possible might not be biologically viable, and that certain highly adaptive combinations may evolve in several different lineages in response to similar circumstances. Marwick (1927) dismissed such convergences as uncommon, "because so many coincidences are involved." On the basis of shell morphology, especially sculpture, Marwick stated that *Austrovenus stutchburyi* of New Zealand is closely related to American chionines of both east and west coasts. I wish to show that characters of soft anatomy and shells, together with evidence from the fossil record, do provide enough clues for the construction of a phylogenetic classification which can accommodate convergence in shell characters.

MATERIALS

The numbers and provenance of specimens dissected are herein listed. All were sexually mature.

Chione (Chione) cancellata (Linnaeus): 1, Bimini Lagoon, Bahamas; 3, western Virginia Key, Biscayne Bay, Fla.; 8, Bear Cut, Virginia Key, Biscayne Bay, Fla.

Chione (Chione) undatella (Sowerby): 9, San Diego, Cal., Hassler Expedition.

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[1] This paper is a revision of a chapter in a dissertation submitted in partial fulfillment of the Degree of Doctor of Philosophy in the Department of Geological Sciences, Harvard University, Cambridge, Massachusetts.

Chione (Panchione) paphia (Linnaeus): 7, Enseada das Palmas, São Paulo, Brazil.

Mercenaria mercenaria (Linnaeus): 8, market; 1, Buzzards Bay, Mass.

Austrovenus stutchburyi (Gray): 7, Auckland Harbour, New Zealand.

METHODS

For most of this work I used an inexpensive binocular microscope suitable for examining relatively large objects; only occasionally had I access to a dissecting microscope. Most structures studied are, therefore, those visible through a relatively poor optical system. Except for *Chione paphia,* the animals were not relaxed. *Chione undatella, C. paphia* and *Austrovenus stutchburyi* were preserved in 80–90% ethyl alcohol; the other species were preserved in commercial isopropyl alcohol. Because they are believed useful in establishing relationships (Ansell, 1961), and because there is a body of literature about them, I pay particular attention to the stomach and siphons. Lack of general information prompted attention to the nervous system.

Unless otherwise indicated, the scale line represents 1 mm. Arrows point anteriorly. Widely spaced canted lines indicate severed edges. All shells are shown at the same scale.

KEY TO ABBREVIATIONS ON FIGURES

aa	anterior aorta
ac	anal canal
ad	dorsal aorta
ama	anterior adductor muscle
amp	posterior adductor muscle
an	anus
ap	posterior aorta
at	acceptance tract
au	auricle
aum	muscle fibres in auricle
ba	bulbus arteriosus
bk	beak
ca	collecting area
cpc	cerebropedal connective
ct	connective tissue
cta	anterior cardinal tooth
ctax	ctenidial axis
ctc	central cardinal tooth
ctp	posterior cardinal tooth
cvc	cerebrovisceral connective
dbi	inner demibranch
dbo	outer demibranch
dboe	extension of outer demibranch
ddv	digestive diverticulum
dgl	digestive gland
dp	dental platform
dvse	distal valve of excurrent siphon
es	escutcheon
f	foot
fg	food groove
fn	fenestra
gc	cerebral ganglion
gd	gonad
gdt	gonoduct
gp	pedal ganglion
gpr	gonopore
gs	gastric shield
gss	subsidiary siphonal ganglion
gv	visceral ganglion
in	intestine
ir	interlocking ridge
is	interlocking slot
kil	inner limb of kidney
kol	outer limb of kidney
lg	ligament
ln	lunule
lpd	dorsal labial palp
lpm	longitudinal pallial muscle
lpv	ventral labial palp
m	mouth
ma	anterior margin
md	dorsal margin
mdn	marginal denticle
mf1	first mantle fold
mf2	second mantle fold
mf3	third mantle fold
mf4	fourth mantle fold
mg	midgut
mgo	opening into midgut
mp	posteror margin
mv	ventral margin
nam	nerve to adductor muscle
nbm	nerve to body mantle
nct	ctenidial nerve
ned	nephridioduct
nep	nephridiopore
nes	nephrostome
nlp	nerve to labial palp
nn	nerve to kidney
np	pedal nerve
npa	anterior pallial nerve
npav	anteroventral pallial nerve
npp	posterior pallial nerve
nppv	posteroventral pallial nerve
npr	pedal retractor nerve
nse	nerve to excurrent siphon
nsi	nerve to incurrent siphon
nsm	nerve to shell mantle
nsr	siphonal retractor nerve

nst	nerve to statocyst
nvm	nerve to anterodorsal visceral mass
ny	nymph
oe	oesophagus
oeg	oesophageal gland (?)
orc	commarginal ornamentation
orr	radial ornamentation
osdv	opening between stomach and digestive diverticulum
pcc	pericardial cavity
pfs	partial flap over siphons
pgl	pedal gland
pgld	duct of pedal gland
pgls	slit of pedal gland
pgr	periostracal groove
pl	pellicle
pll	pallial line
pls	pallial sinus
plt	posterior lateral tooth
pm	pallial muscle
prma	anterior pedal retractor muscle
prmp	posterior pedal retractor muscle
pvse	proximal valve of excurrent siphon
pvsi	proximal valve of incurrent siphon
s	stomach
sa	sorting area
saa	scar of anterior adductor muscle
sap	scar of posterior adductor muscle
se	excurrent siphon
sh	shelf of stomach
si	incurrent siphon
sm	shell mantle
soc	supraoesophageal commissure
spra	scar of anterior pedal retractor muscle
sprp	scar of posterior pedal retractor muscle
srm	siphonal retractor muscle
st	statocyst
t	tentacle
ty	typhlosole
tyma	major typhlosole
tymi	minor typhlosole
vl	valve between auricle and ventricle
vn	ventricle
wc	water chamber
wt	water tube

PREVIOUS WORK

Although many workers have examined details of its anatomy and physiology, Kellogg (1910), Belding (1912), Woodruff (1938), Miner (1950), Pierce (1950), and Barnes (1974) offer only figures and slight discussion of the general anatomy of *Mercenaria mercenaria* or the quahog. Indeed, the same figure, variously modified, appears in most of these works. Carriker (1961) discusses fully the larval and juvenile phases of the quahog; D'Asaro (1967) and LaBarbera & Chanley (1970) studied the development of larval *Chione cancellata,* Moore and López (1969) its ecology, Paine (1963) its enemies. Stanley (1970) comments on the burrowing habits and functional morphology of many species, including *C. cancellata, C. paphia* and *M. mercenaria.* Dissections of several other venerids are sufficiently detailed for comparison (Ansell, 1961; Nielsen, 1963; Narchi, 1972). Information on the anatomy of *C. undatella* and *A. stutchburyi* is lacking. Brown et al. (1956) studied cycles of activity in the quahog, and Comfort (1957) listed this clam as living as long as 40 years (but see Farrow, 1972; Loesch & Haven, 1973). Particulars of anatomy garnered from other works appear in their due places.

Chione cancellata prefers muddy sand stabilized by marine plants (McNulty, 1961; McNulty et al., 1962) in the shallow subtidal zone. Examination of Bird's (1970) tables and maps shows that this species tolerates salinities as low as about 18‰. *Chione cancellata* prefers sheltered embayments. It occurs from about Beaufort, North Carolina southward to about Rio de Janeiro, and in the Gulf of Mexico. *Chione paphia* is occasionally found in the Florida Keys, but is common in the Caribbean and southward to southern Brazil. It lives in clean gravelly carbonate sand without plants at depths of about 10 to 55 fathoms (Stanley, 1970; Rios, 1970). *Mercenaria mercenaria* lives in the intertidal and shallow subtidal zones, buried in gravelly sand and gravelly muddy sand (Stanley, 1970). The quahog ranges from the Gulf of St. Lawrence to Florida. *Chione undatella* lives in tidal creeks (Macdonald, 1969) and in protected beaches, from southern California to Payta, Peru (Keen, 1971). *Austrovenus stutchburyi* usually lives in moderately firm sands in the shallow subtidal zone, although a few large animals live in soft flocculent muds; it prefers embayments with fairly strong currents (Paul, 1966), and is uncommon in poorly aerated sediments (Powell, 1937). It is found all around New Zealand (Penniket, 1970). All are shallow-burrowing suspension feeders. The presence of polydorid polychaetes, plant attachments, and even small corals on their posterior margins shows that *C. cancellata* and *A. stutchburyi* live not quite fully buried. *A. stutchburyi* is often extensively eroded in this area.

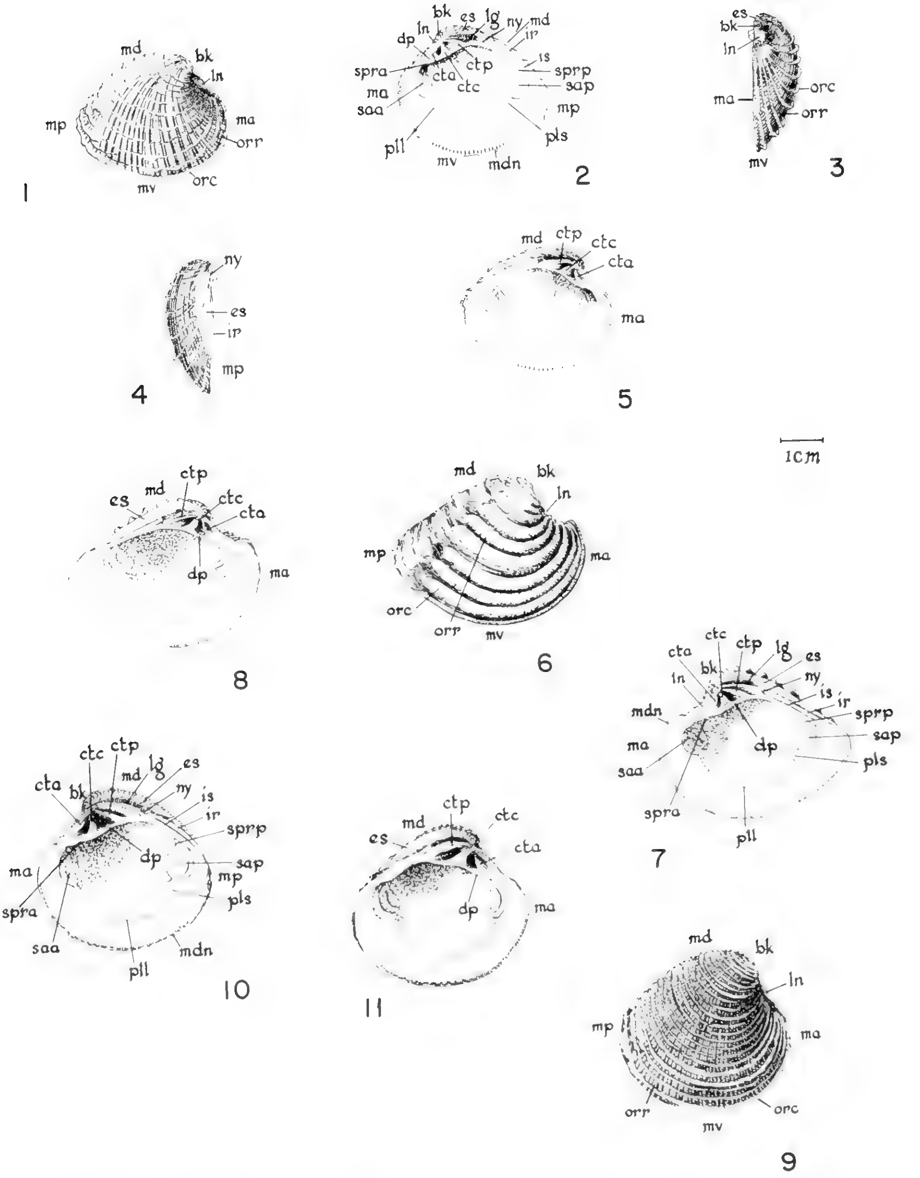
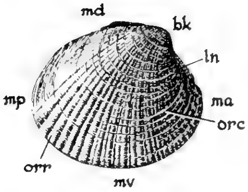


FIG. 1. *Chione cancellata*, exterior of right valve. FIG. 2. *Chione cancellata*, interior of right valve. FIG. 3. *Chione cancellata*, anterior end of left valve. FIG. 4. *Chione cancellata*, posterior end of left valve. FIG. 5. *Chione cancellata*, interior of left valve. FIG. 6. *Chione paphia*, exterior of right valve. FIG. 7. *Chione paphia*, interior of right valve. FIG. 8. *Chione paphia*, interior of left valve. FIG. 9. *Chione undatella*, exterior of right valve. FIG. 10. *Chione undatella*, interior of right valve. FIG. 11. *Chione undatella*, interior of left valve.



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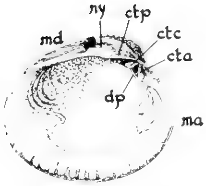

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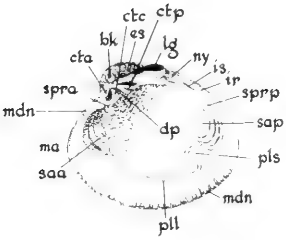

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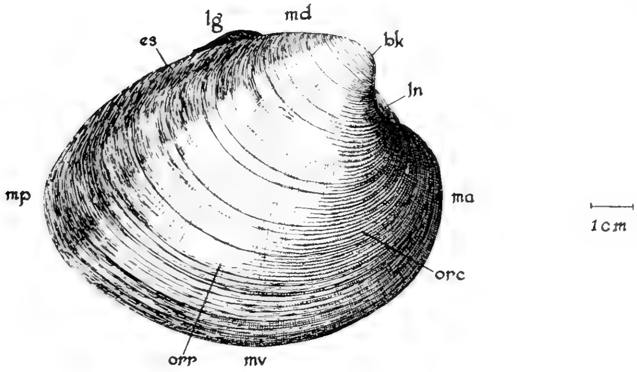

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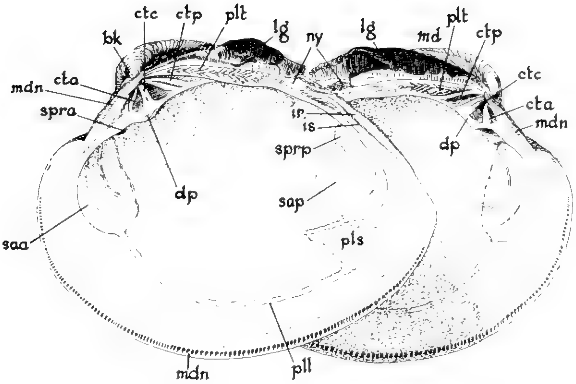
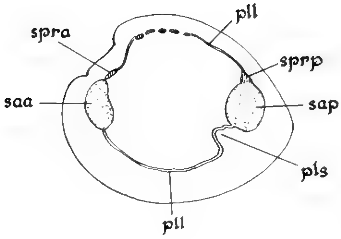


FIG. 12. *Austrovenus stutchburyi*, exterior of right valve. FIG. 13. *Austrovenus stutchburyi*, interior of right valve. FIG. 14. *Austrovenus stutchburyi*, interior of left valve. FIG. 15. *Mercenaria mercenaria*, exterior of right valve. FIG. 16. *Mercenaria mercenaria*, interior of right and left valves.



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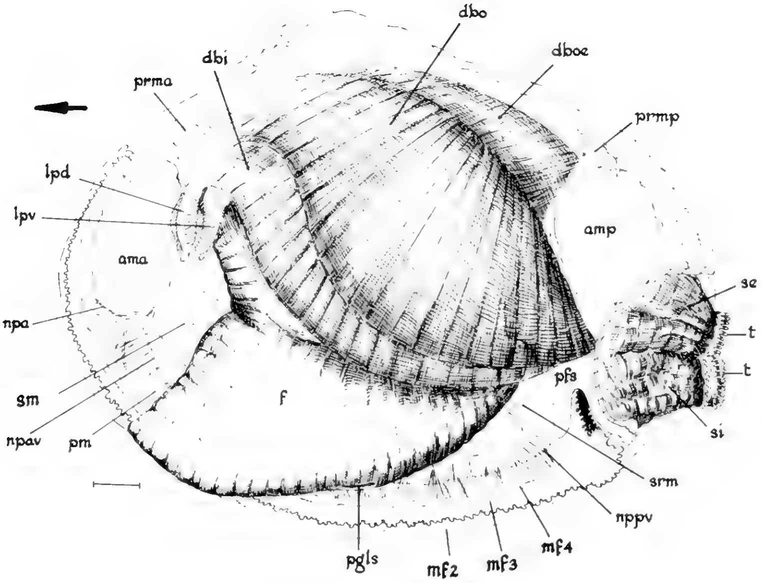

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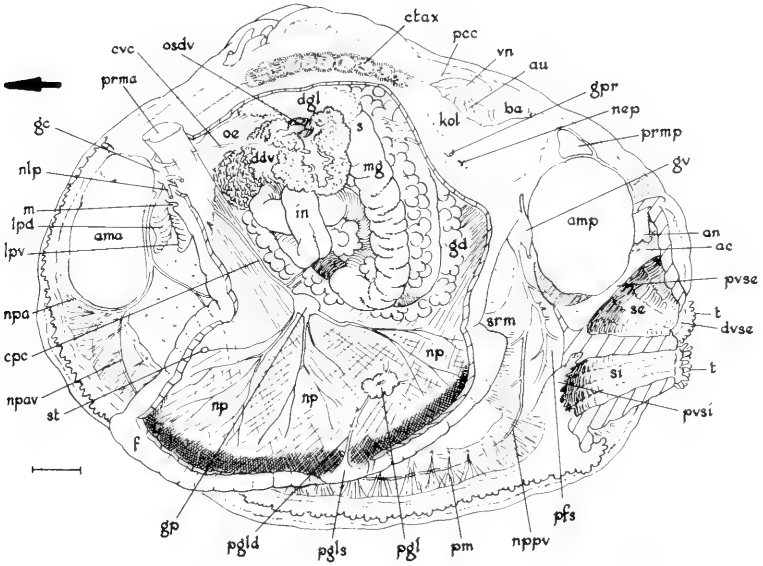
FIG. 17. Muscle scars in venerid bivalves. FIG. 18. Chionine anatomy, shell removed.



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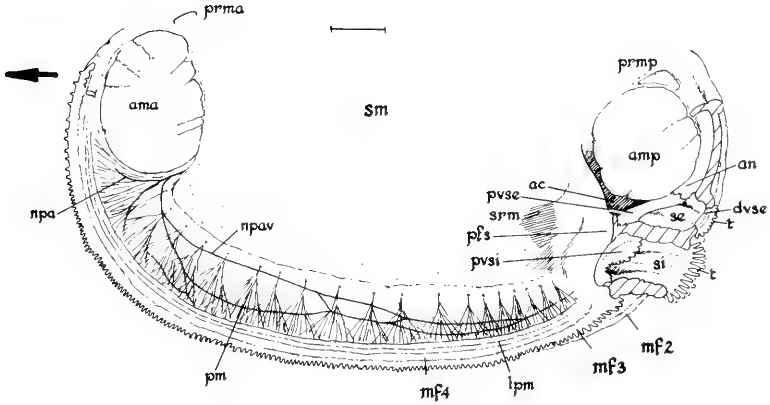

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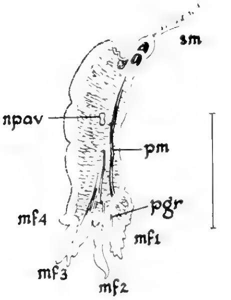
FIG. 19. Chionine anatomy, mantle and body wall removed. FIG. 20. Mantle of *Chione cancellata.*



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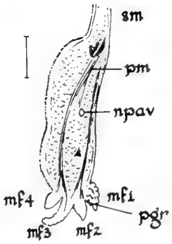

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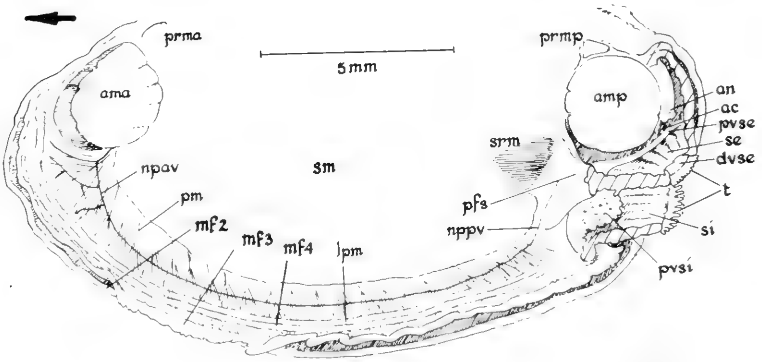

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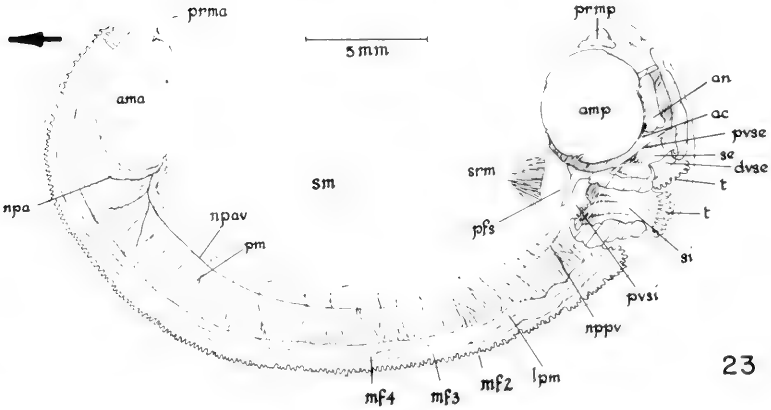

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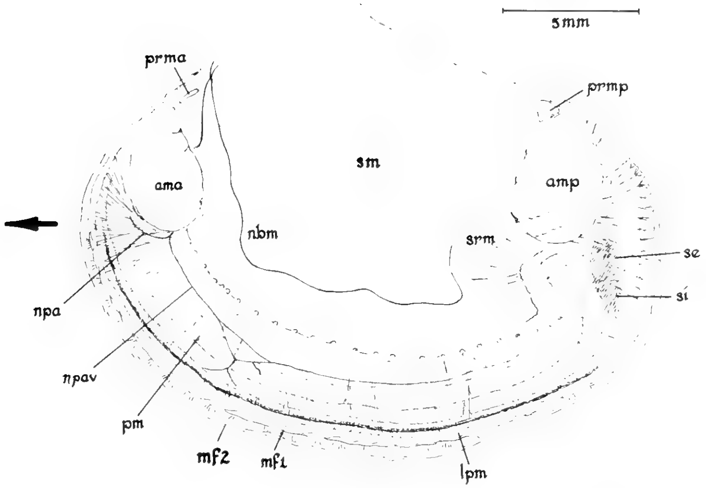
FIG. 21. Midventral cross section of mantle edge, *Chione cancellata*. FIG. 22. Mantle of *Chione paphia*. FIG. 23. Mantle of *Chione undatella*. FIG. 24. Midventral cross section of mantle edge, *Chione undatella*.



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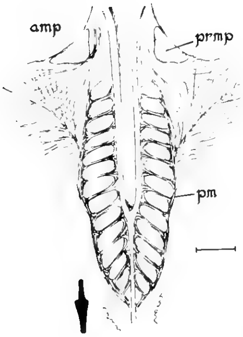

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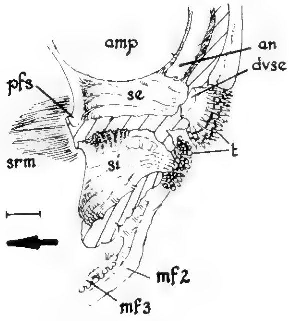

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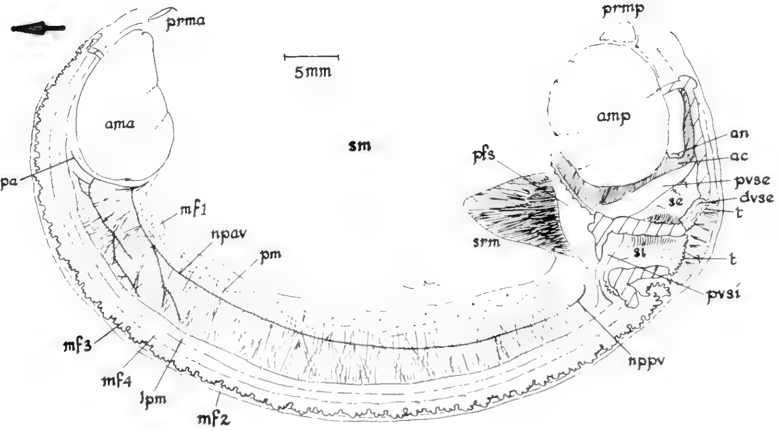
FIG. 25. Mantle of *Austrovenus stutchburyi.* FIG. 26. Dorsal edge of mantle, *Austrovenus stutchburyi.* FIG. 27. Section of siphons, *Austrovenus stutchburyi.*



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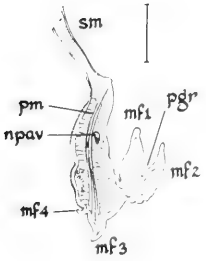

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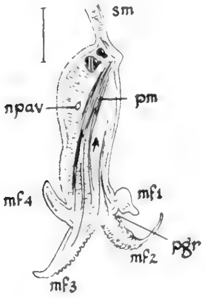

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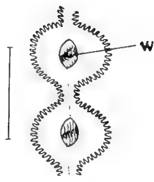
FIG. 28. Midventral cross section of mantle edge, *Austrovenus stutchburyi.* FIG. 29. Mantle of *Mercenaria mercenaria.* FIG. 30. Midventral cross section of mantle edge, *Mercenaria mercenaria.*



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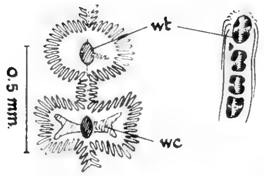

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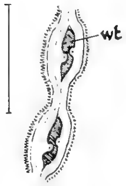

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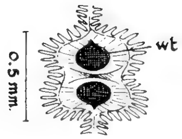

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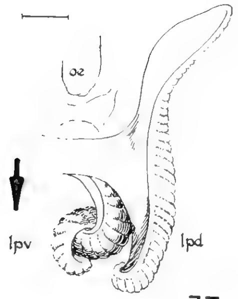

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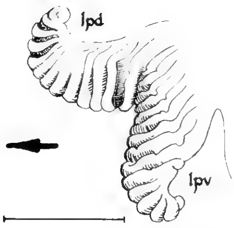

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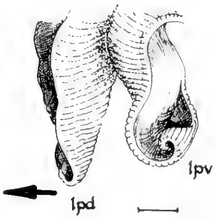

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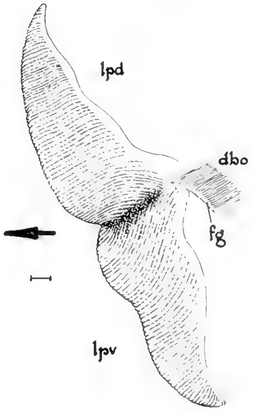

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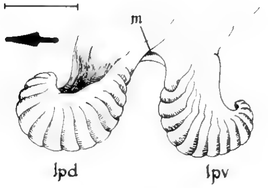

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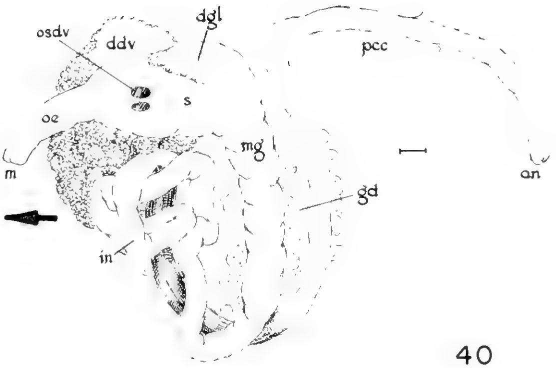
FIG. 31. Cross section of gill plica, *Chione cancellata.* FIG. 32. Cross section of gill plica, *Chione undatella.* FIG. 33. Cross section of gill plica and structure of water tube, *Austrovenus stutchburyi.* FIG. 34. Cross section of gill plica, *Mercenaria mercenaria.* FIG. 35. Labial palps of *Chione cancellata.* FIG. 36. Labial palps of *Chione paphia.* FIG. 37. Labial palps of *Chione undatella.* FIG. 38. Labial palps of *Austrovenus stutchburyi.* FIG. 39. Labial palps of *Mercenaria mercenaria.*



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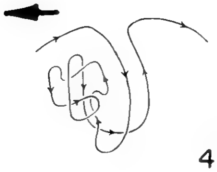

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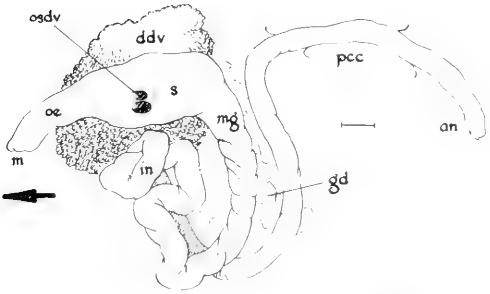

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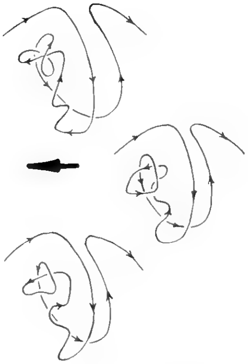

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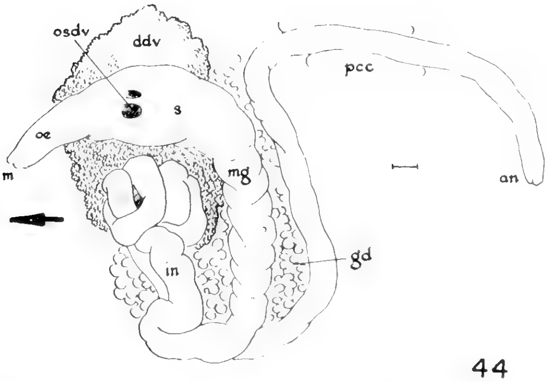

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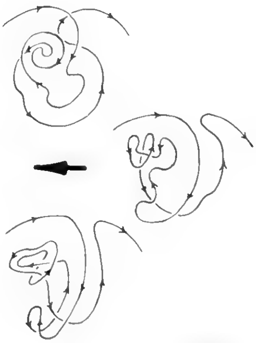

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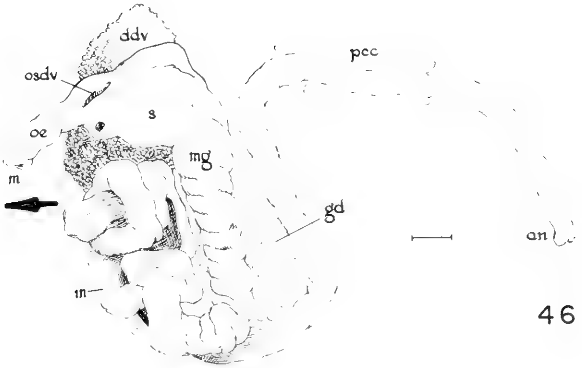
FIG. 40. Digestive system, *Chione cancellata*. FIG. 41. Scheme of digestive system, *Chione cancellata*. FIG. 42. Digestive system, *Chione paphia*. FIG. 43. Scheme of digestive system, *Chione paphia*. FIG. 44. Digestive system, *Chione undatella*. FIG. 45. Scheme of digestive system, *Chione undatella*.



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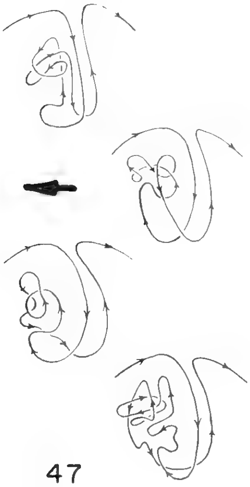

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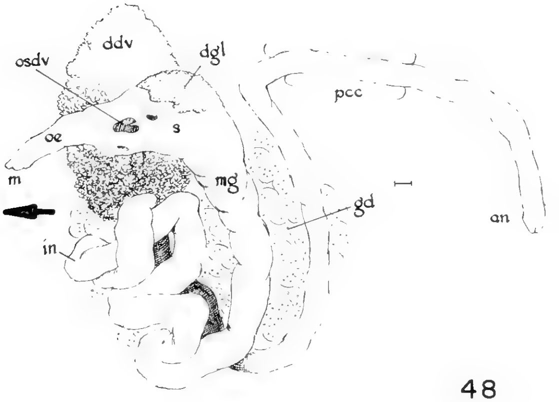

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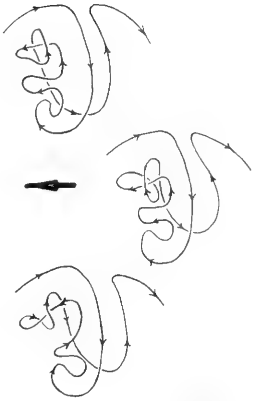

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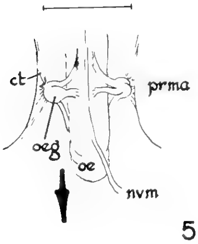

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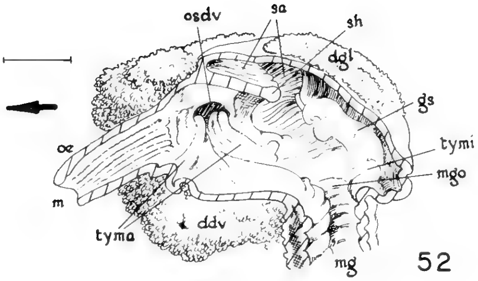
FIG. 46. Digestive system, *Austrovenus stutchburyi.* FIG. 47. Scheme of digestive system, *Austrovenus stutchburyi.* FIG. 48. Digestive system, *Mercenaria mercenaria.* FIG. 49. Scheme of digestive system, *Mercenaria mercenaria.* FIG. 50. Oesophageal glands (?) of *Chione paphia.* FIG. 51. Dorsal and ventral aspects of oesophageal gland (?) of *Chione undatella.*



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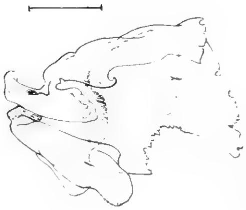

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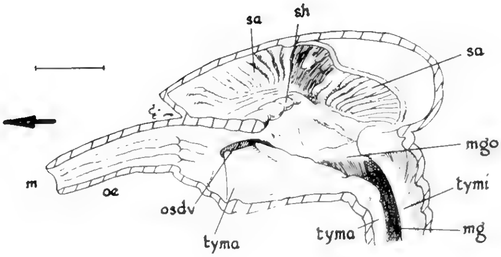

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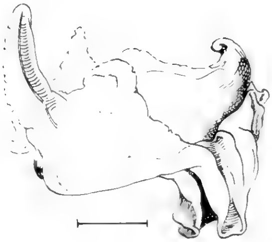

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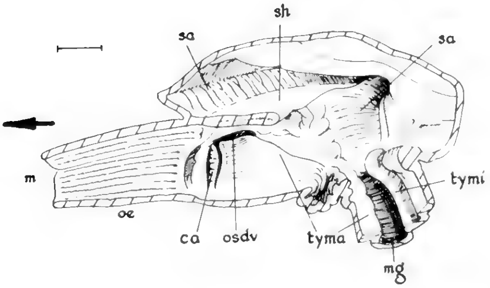

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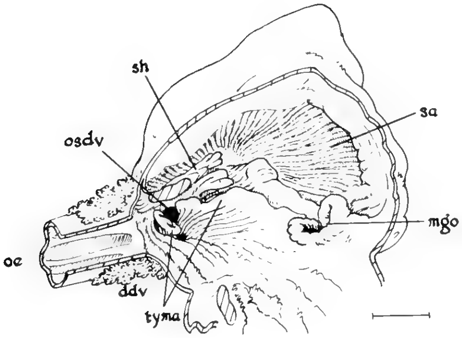
FIG. 52. Stomach, *Chione cancellata.* FIG.53. Stomach, *Chione paphia.* FIG. 54. Stomach, *Chione undatella.* FIG. 57. Gastric shield, *Chione undatella.* FIG. 58. Gastric shield, *Austrovenus stutchburyi.* FIG. 59. Gastric shield, *Mercenaria mercenaria.*



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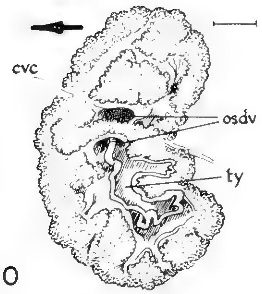

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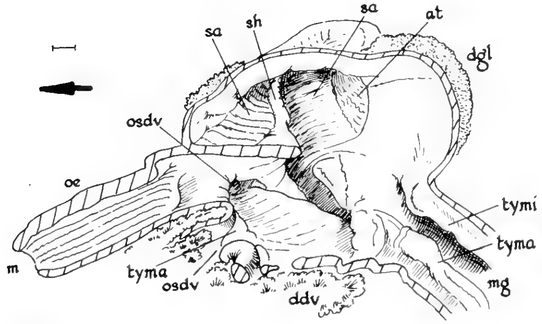

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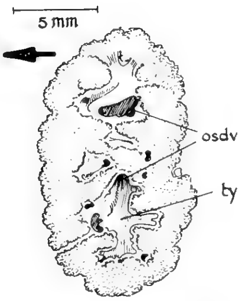

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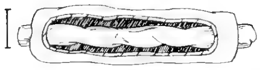

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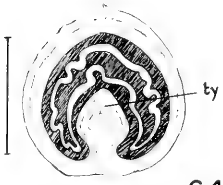

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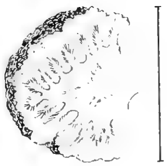

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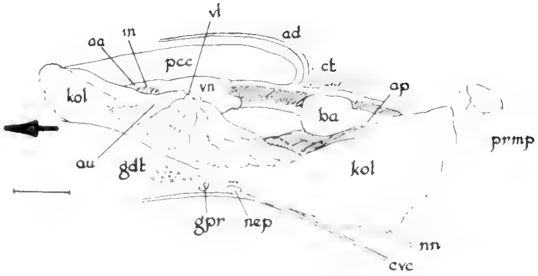
FIG. 55. Stomach, *Austrovenus stutchburyi.* FIG. 56. Stomach, *Mercenaria mercenaria.* FIG. 60. Digestive diverticulum, *Austrovenus stutchburyi.* FIG. 61. Digestive diverticulum, *Mercenaria mercenaria.* FIG. 62. Detail of digestive diverticulum, *Chione cancellata.* FIG. 63. Detail of intestine just anterior to heart, *Mercenaria mercenaria.* FIG. 64. Cross section of intestine in gut loop, *Mercenaria mercenaria.*



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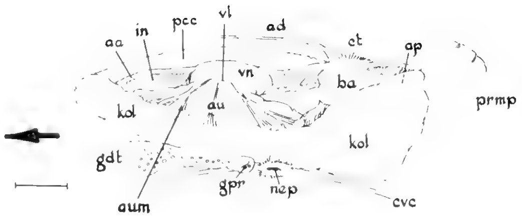

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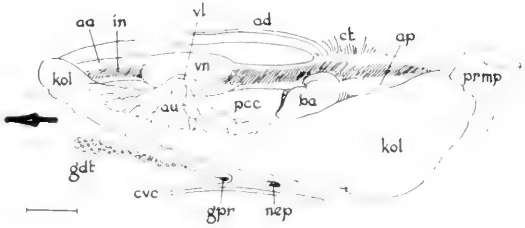

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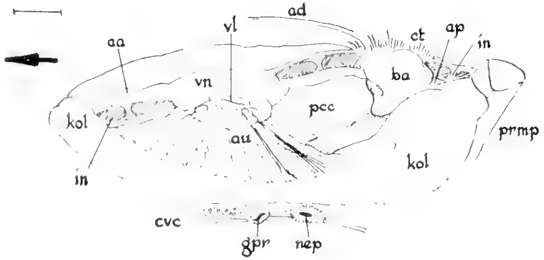

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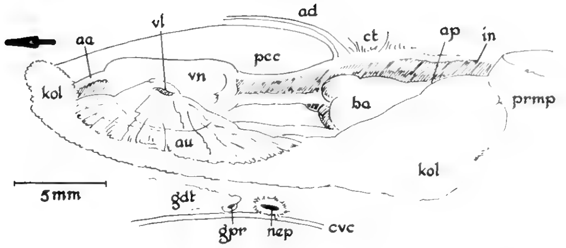
FIG. 65. Heart, *Chione cancellata.* FIG. 66. Heart, *Chione paphia.* FIG. 67. Heart, *Chione undatella.* FIG. 68. Heart, *Austrovenus stutchburyi.*



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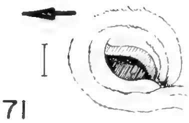

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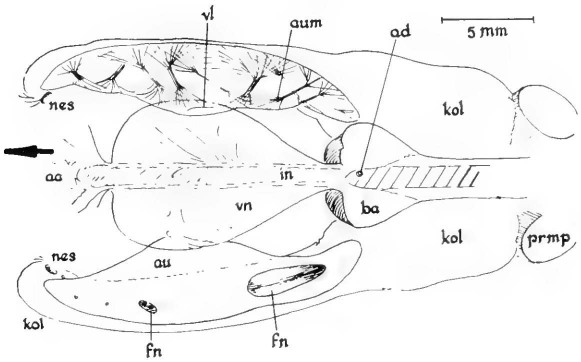

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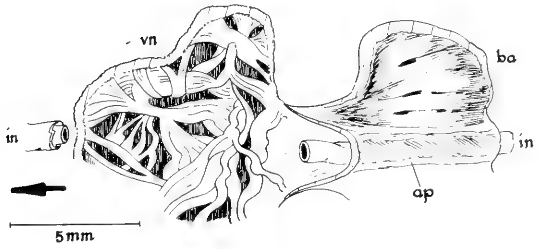

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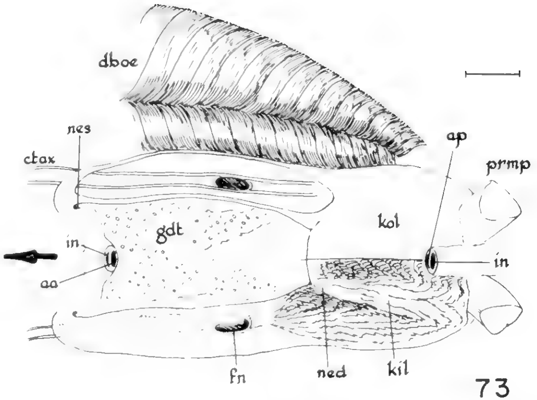
FIG. 69. Heart, *Mercenaria mercenaria.* FIG. 70. Dorsal aspect of heart, *Mercenaria mercenaria.* FIG. 71. Lateral aspect of valve between auricle and ventricle, *Mercenaria mercenaria.* FIG. 72. Interior of ventricle and bulbus arteriosus, *Mercenaria mercenaria.*



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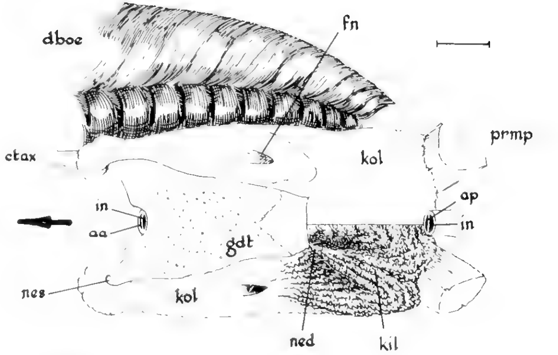

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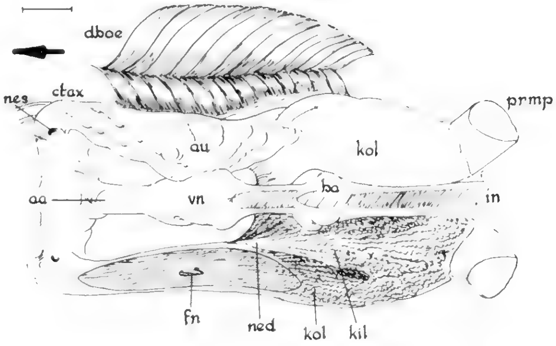

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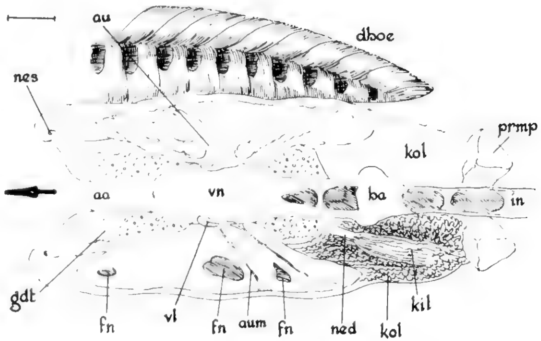

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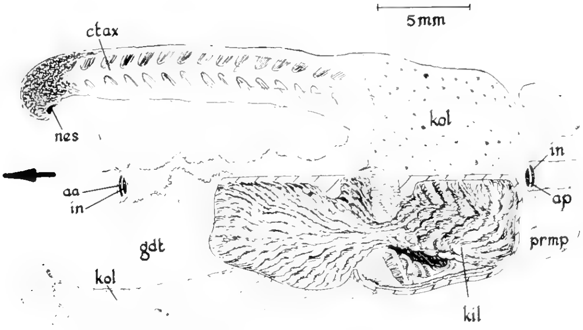
FIG. 73. Kidney, *Chione cancellata*. FIG. 74. Kidney, *Chione paphia*. FIG. 75. Kidney, *Chione undatella*. FIG. 76. Kidney, *Austrovenus stutchburyi*.



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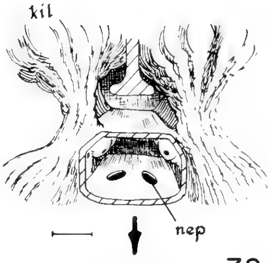

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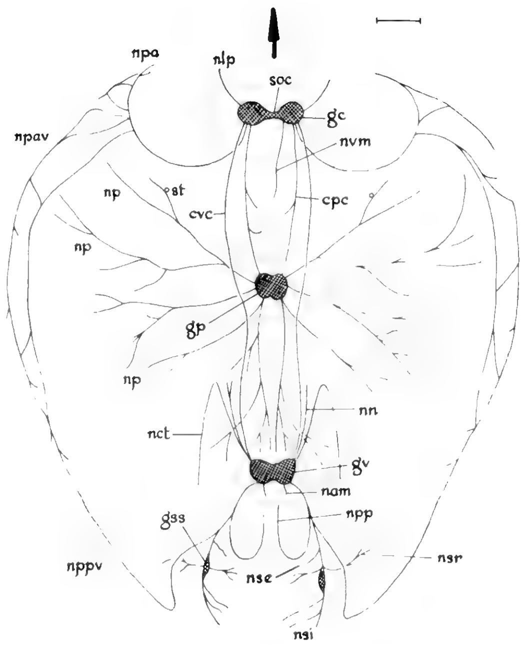
FIG. 77. Kidney, *Mercenaria mercenaria.* FIG. 78. Chamber between kidneys and mantle cavity, *Mercenaria mercenaria.*



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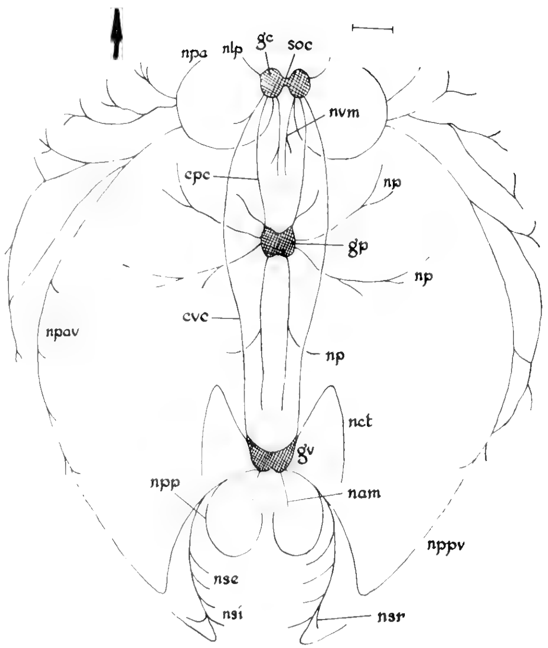

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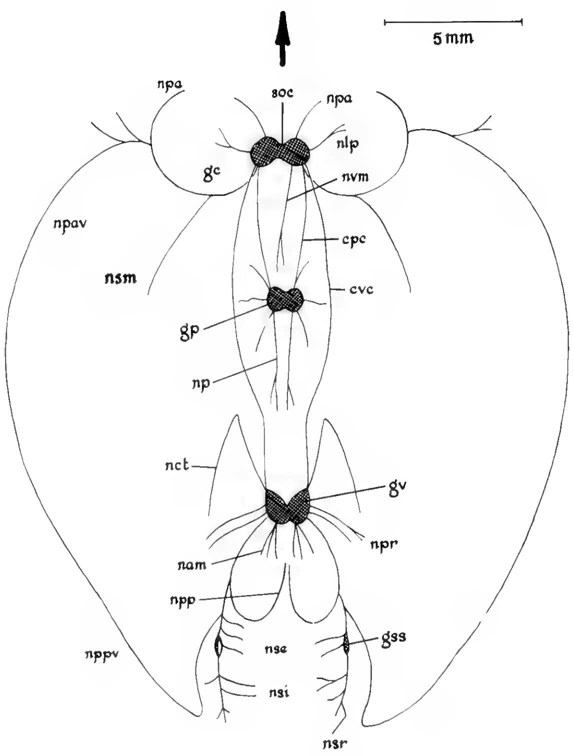
FIG. 79. Scheme of nervous system, *Chione cancellata*. FIG. 80. Scheme of nervous system, *Chione paphia*.



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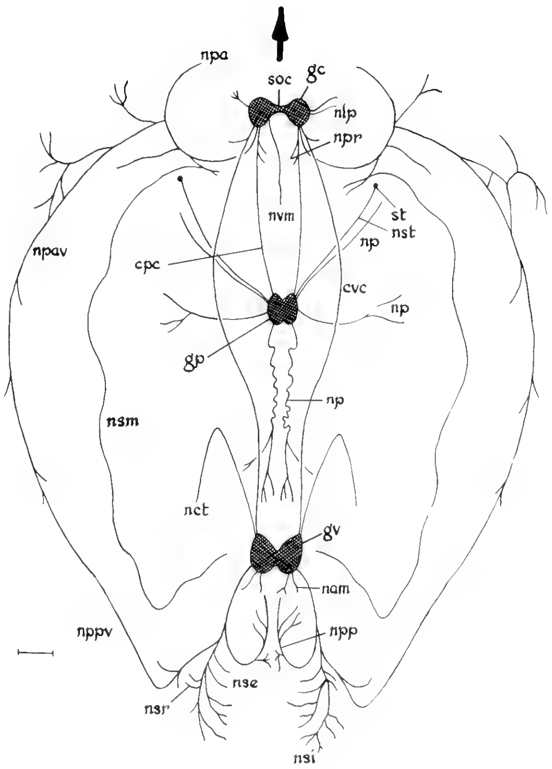

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FIG. 81. Scheme of nervous system, *Chione undatella*. FIG. 82. Scheme of nervous system, *Austrovenus stutchburyi*.

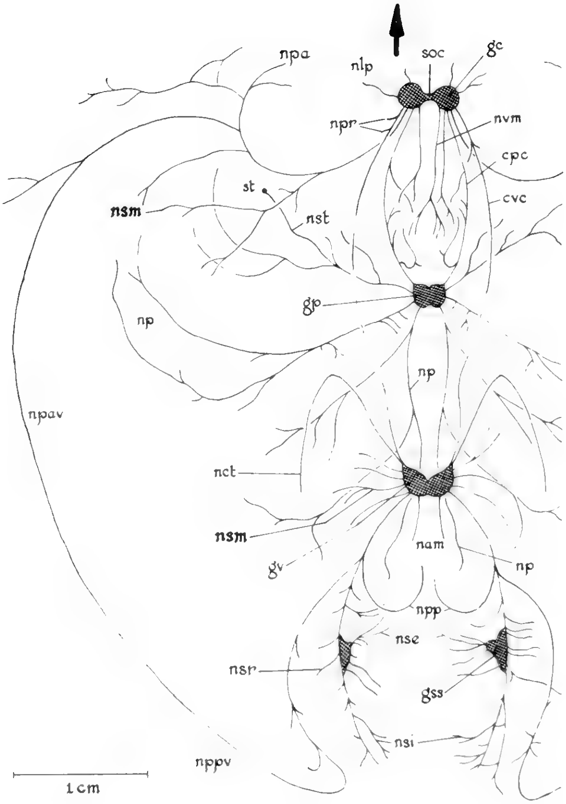

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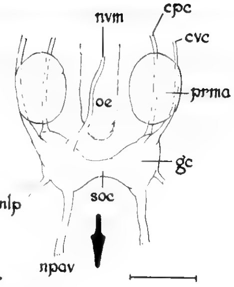
FIG. 83. Scheme of nervous system, *Mercenaria mercenaria*.



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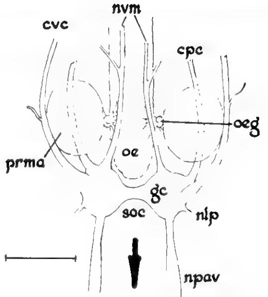

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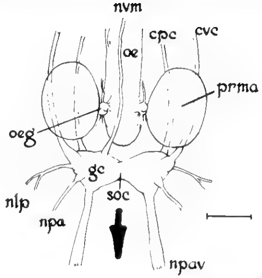

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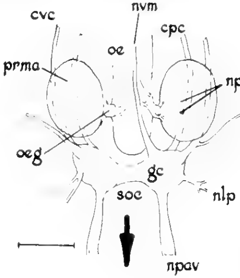

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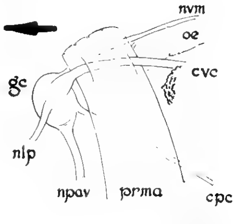

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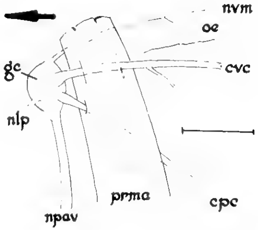

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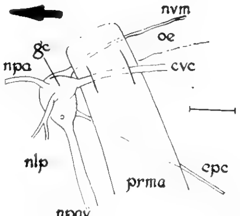

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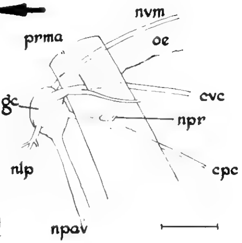

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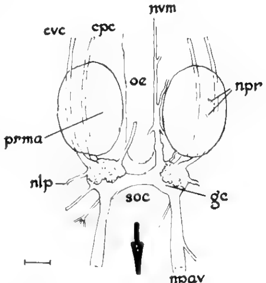

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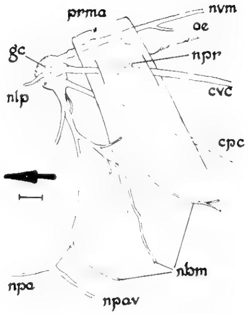

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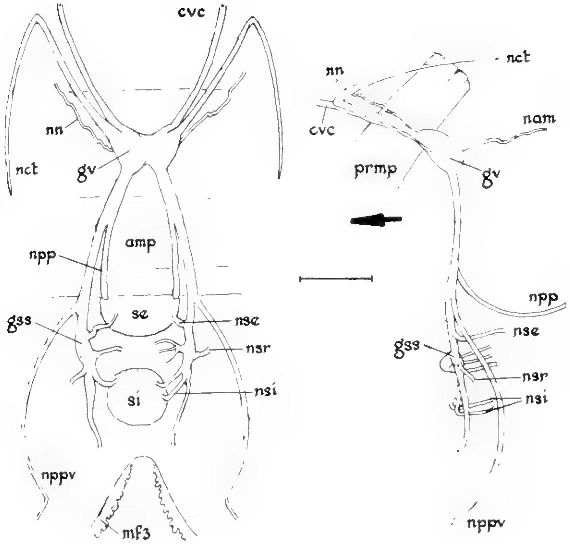
FIG. 84. Anterodorsal aspect of cerebral nervous system, *Chione cancellata*. FIG. 85. Lateral aspect of cerebral nervous system, *Chione cancellata*. FIG. 86. Anterodorsal aspect of cerebral nervous system, *Chione paphia*. FIG. 87. Lateral aspect of cerebral nervous system, *Chione paphia*. FIG. 88. Anterodorsal aspect of cerebral nervous system, *Chione undatella*. FIG. 89. Lateral aspect of cerebral nervous system, *Chione undatella*. FIG. 90. Anterodorsal aspect of cerebral nervous system, *Austrovenus stutchburyi*. FIG. 91. Lateral aspect of cerebral nervous system, *Austrovenus stutchburyi*. FIG. 92. Anterodorsal aspect of cerebral nervous system, *Mercenaria mercenaria*. FIG. 93. Lateral aspect of cerebral nervous system, *Mercenaria mercenaria*.



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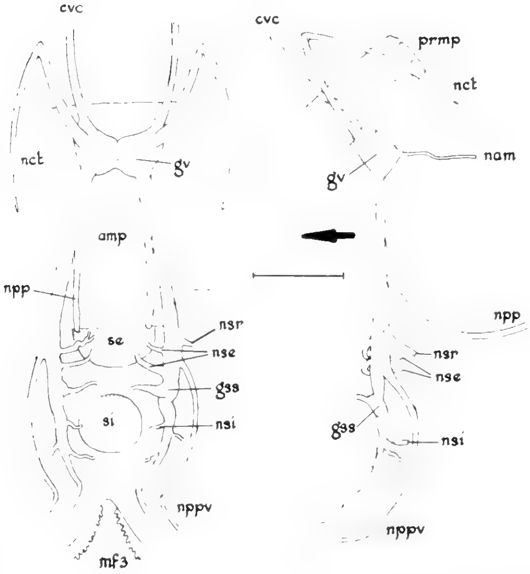

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FIG. 94. Anterior and lateral aspects of visceral nervous system, *Chione cancellata*. FIG. 95. Anterior and lateral aspects of visceral nervous system, *Chione paphia*.

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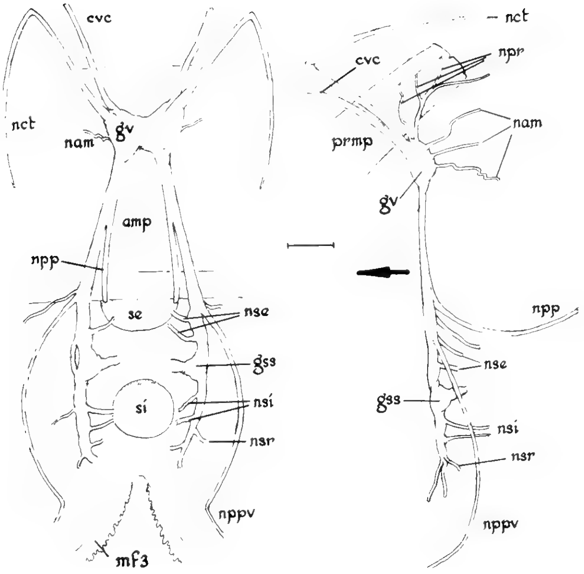

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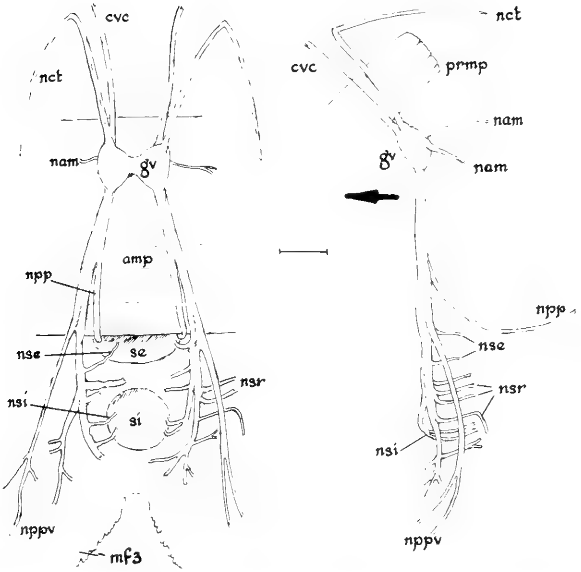

FIG. 96. Anterior and lateral aspects of visceral nervous system, *Chione undatella*. FIG. 97. Anterior and lateral aspects of visceral nervous system, *Austovenus stutchburyi*.

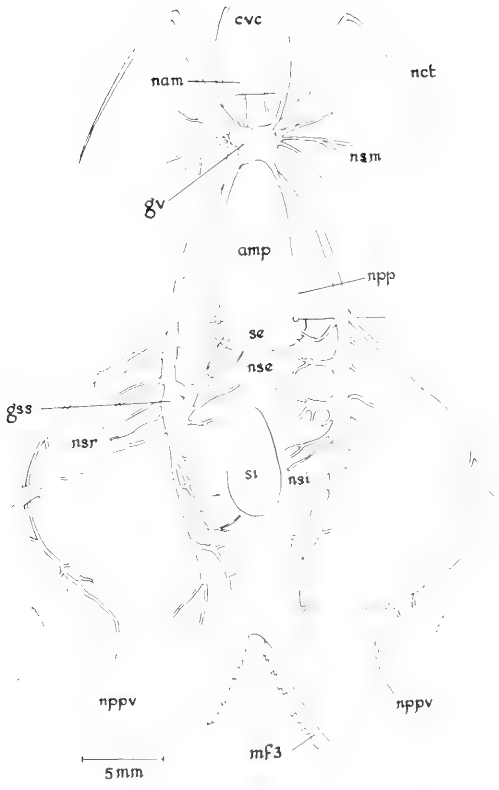

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FIG. 98. Anterior aspect of visceral nervous system, *Mercenaria mercenaria*.

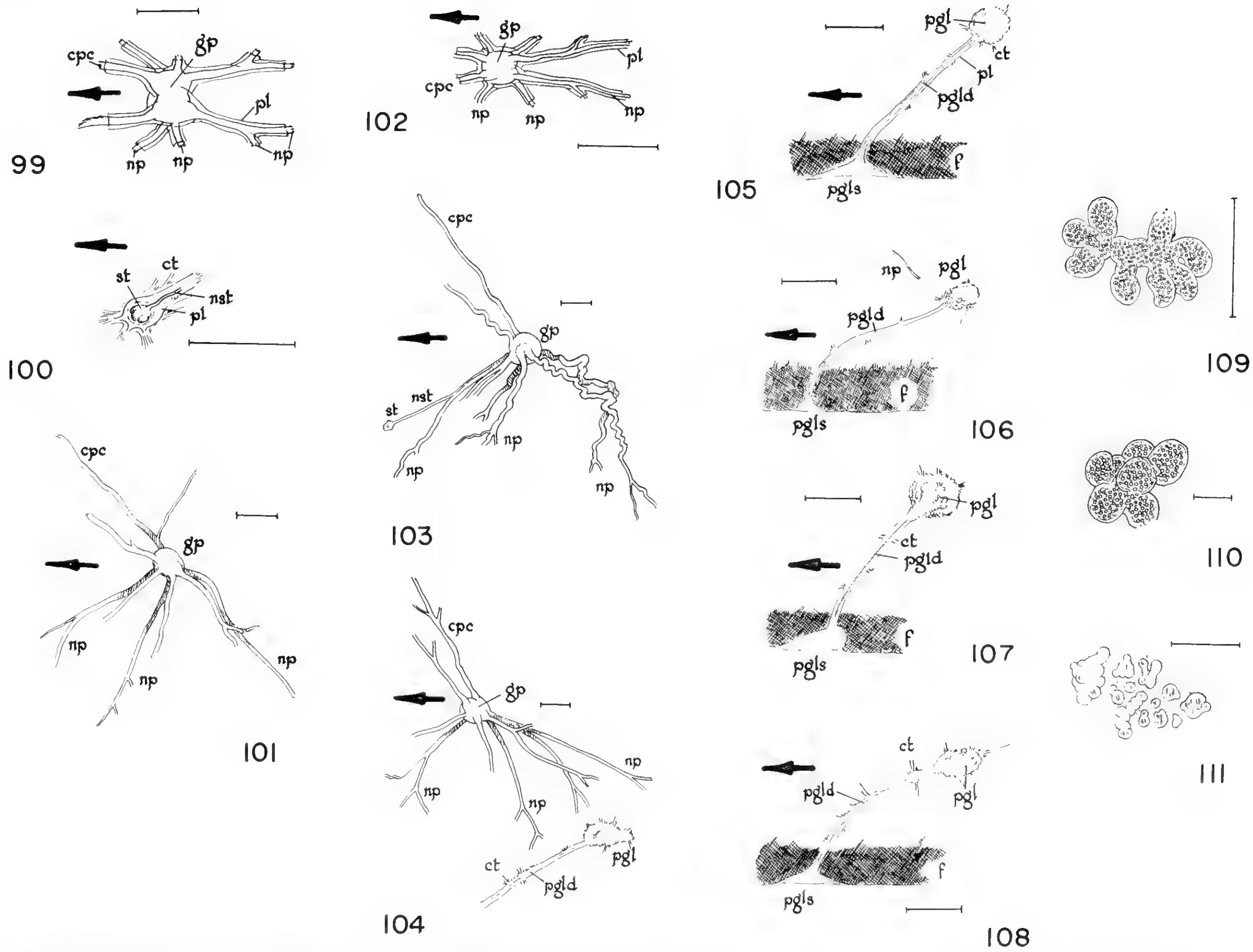

FIG. 99. Pedal ganglia, *Chione cancellata*. FIG. 100. Statocyst, *Chione cancellata*. FIG. 101. Pedal nervous system, *Chione paphia*. FIG. 102. Pedal ganglia, *Chione undatella*. FIG. 103. Pedal nervous system, *Austrovenus stutchburyi*. FIG. 104. Pedal nervous system and pedal gland, *Mercenaria mercenaria*. FIG. 105. Pedal gland, *Chione cancellata*. FIG. 106. Pedal gland, *Chione paphia*. FIG. 107. Pedal gland, *Chione undatella*. FIG. 108. Pedal gland, *Austrovenus stutchburyi*. FIG. 109. Ripe ovarian follicles, *Austrovenus stutchburyi*. FIG. 110. Ripe ovarian follicles, *Mercenaria mercenaria*. FIG. 111. Unripe follicles, *Mercenaria mercenaria*.

SHELL

Shell structure of the species discussed here has been studied by Barker (1964), Oberling (1964), and Taylor et al. (1973). This last work reveals differences among species which may be of taxonomic value. Shells of *Chione paphia* and *Mercenaria mercenaria* have the same structure. The outer layer is composite prismatic, the middle layer is cross-lamellar becoming homogeneous inward, and the inner layer is homogeneous. Between the middle and inner layers is the prismatic pallial myostracum, thin in *M. mercenaria.* Unlike most members of the Chioninae and Venerinae studied, *C. undatella* lacks the outer prismatic layer. The shell of *Austrovenus stutchburyi* is composed of an outer cross-lamellar layer which becomes homogeneous inward, a prismatic pallial myostracum, and an inner layer which is complex cross-lamellar to homogeneous. The shell structure of *C. cancellata* as described by Barker (1964) seems to resemble that of *C. paphia* and *M. mercenaria.* The shells of all venerids studied are aragonitic. According to Barker, the outer and middle shell layers of *C. cancellata* and *M. mercenaria* contain little conchiolin, but the inner shell layer is rich in it.

All species are equivalve, rounded-trigonal to ovate, robust, and fairly inflated (Figs. 1–16). A robust shell tends to protect a clam from smaller predators who gain access to the soft parts by chipping away the shell (Paine, 1963). Observation of thousands of specimens shows that *Chione cancellata* is variable in elongation and inflation. Some specimens, such as *C. c. mazyckii* Dall (1902), are quadrate. *C. undatella* is so variable in outline and sculpture that it has received many names (Verrill, 1870; Keen, 1971). *Mercenaria mercenaria* and *C. paphia* are posteriorly somewhat rostrate. More robust specimens of *C. paphia* are somewhat more inflated. Of the five species, *Austrovenus stutchburyi* is usually the most inflated. All are prosogyrate with the beak subcentral to well anterior. All have a strong external ligament seated in well-developed nymphs posterior to the beak. In very young venerids the ligament is internal until about the fortieth day of life, when it begins to pass by allometric growth to the exterior (LePennec, 1973). The ligament in juvenile *C. ulocyma* Dall, a close fossil relative of *C. paphia,* followed this same sequence (LaBarbera, 1974).

All five species have radial and commarginal sculpture. *Chione cancellata, C. undatella* and *Austrovenus stutchburyi* (Figs. 1, 9, 12) have cancellate sculpture consisting of thin, erect, commarginal lamellae crossing less-pronounced radial ribs which become more numerous with growth by splitting and intercalation. The commarginal ridges of *A. stutchburyi* are comparatively low. In the American species, the commarginal lamellae form broad flanges at their posterior ends. Such flanges are lacking in *A. stutchburyi.* Strong commarginal sculpture retards burrowing but promotes stability of the animal once buried (Stanley, 1970). *C. paphia* (Fig. 6) has broad reflected lirae which abruptly attenuate to flanges on the posterior slope. This species is a very slow burrower (Stanley, 1970). *C. paphia* and many of its extinct relatives, such as *C. burnsii* Dall and *C. ulocyma* Dall (Palmer, 1927, 1929), have at the anterior end of every other lira a scoop-shaped process which may aid in burrowing. In *C. paphia,* radial sculpture is restricted to shallow notches in the ventral surfaces of the lirae. *Mercenaria mercenaria* (Fig. 15) has subdued sculpture, consisting of crowded narrow commarginal ridges at the anterior end of the shell. On the ventral surfaces of the ridges are faint radial incisions. Growth lines are obvious, especially on the disc and posterior slope, and on the ventral portions of larger animals. Fine radial ribs within the fabric of the shell are expressed at the surface as fine radial lines. Adult quahogs rely on their mass to maintain their position in the substratum, but juveniles have erect commarginal ridges for anchorage (Pratt & Campbell, 1956). Stanley (1970) found adult quahogs to be rapid burrowers, but Trueman (1975) considers them slow burrowers who settle into excavations made by forcible ejection of water from the mantle cavity. Layers in the shells of *C. cancellata* and *Mercenaria mercenaria* thought to be daily growth increments are thicker in animals from warmer waters (Barker, 1964). The sequence of thick daily increments deposited in spring and summer to thin increments laid down in autumn and winter is well seen in *A. stutchburyi* (Coutts, 1970).

The lunule in all species is cordiform. In the American species it is surrounded by a sharply incised line (Fig. 3). In *Austrovenus stutchburyi* an abrupt change from fine radial ribs on the lunule to much coarser ribs on the anterior slope delimits the lunule. The cancellate American species also have radial ribs on the lunule. The lunule of *Chione paphia* is without ornament; that of *Mercenaria mercenaria* bears more or less obsolete commarginal ridges. The lunule varies from slightly pouting in the cancellate forms, to flat in *M. mercenaria,* to slightly impressed and sinuous in *C. paphia.*

All species have escutcheons. In the four American species the left half is smooth, strongly impressed, with a sharp dorsal margin where it joins the disc (Figs. 4, 8, 11); the right half is somewhat rounded and crossed by evident growth lines and the posterior ends of the commarginal lamellae (Figs. 2, 7, 10). The escutcheon is proportionally broader in *Chione* than in *Mercenaria.* In *Austrovenus* this feature is rather narrow, rounded, and only slightly impressed (Figs. 13, 14). Marwick (1927) noted that the escutcheon of *A. stutchburyi* is less well defined than that of its supposed American relatives, but that the ancestor of *A. stutchburyi* had a fairly well-defined escutcheon.

Chione paphia and *C. cancellata* are cream-colored, with chevrons or maculae or rays, or some combination of these, in pale orange or brown. The lunule is often pigmented. The escutcheon bears diagonal brown stripes, broader and fewer on the left side. In general, specimens of *C. cancellata* from the United States bear fine brown or orange chevrons, whereas those from the Caribbean have maculae and rays. *C. undatella* is commonly off-white without markings, although a number of colored forms exist (Verrill, 1870; Dall, 1902). *Austrovenus stutchburyi* is also off-white without markings. *Mercenaria* is usually pale brown or grey, but the color morph *M. m. notata* (Say, 1822) bears brown chevrons (Clench, 1928). All species are covered by a thin yellow or tan periostracum.

Each species has three radiating cardinal teeth below the umbo of either valve; the formula is R101010/L010101. The teeth of the three small American species (Figs. 2, 5, 7, 8, 10, 11) are robust and not bifid, or only slightly so. Four cardinal teeth in *Austrovenus stutchburyi* and *Mercenaria mercenaria* are patently bifid (Figs. 13, 14, 16). In addition to cardinal teeth, *M. mercenaria* has large interlocking rugose areas between the posterior cardinal teeth and the nymphs. This paired structure probably functions as additional teeth in preventing shear between the valves and in securing proper occlusion. The dentition of the four American species merges ventrally into the robust dental platform before reaching its ventral edge; in *Austrovenus* the teeth extend almost undiminished in height to the edge of the relatively small dental platform. LePennec (1973) discusses the development of larval dentition in several European venerids. The juvenile dentition of fossil *Chione ulocyma* Dall (LaBarbera, 1974) resembles that of *Venus striatula (=Chamelea gallina),* another member of the Chioninae, more closely than it does that of species of *Venerupis,* a member of the Tapetinae. Details of the morphogenesis of dentition may provide clues to phylogenetic relationships.

The adductor scars are large and subequal in size (Fig. 17). The small oval scar of the anterior pedal retractor is separate from that of the anterior adductor, and is in a pit under the anterior edge of the dental platform. The triangular posterior pedal retractor scar is confluent with the anterodorsal edge of the posterior adductor scar. The ventral pallial line runs nearly parallel to the ventral margin. The pallial sinus of *Chione undatella* and *C. cancellata* is shallow and dorsally directed whereas those of the other species are deeper and anteriorly directed. The dorsal pallial line extends from the dorsal edges of the pedal retractor scars into the umbonal cavity, where it is punctuated by several small discrete scars.

Along the posterodorsal margin is an overlap device which permits this part of the margin to remain closed while the rest is open for feeding or burrowing (Figs. 2, 5, 7, 8, 10, 11, 13, 14, 16). The edge of the left escutcheonal margin fits into a groove in the edge of the right valve, and is overlapped by a sinuous extension of the right valve. This overlap device is best developed in the small American chionines.

All species have denticles on the interior face of the lunular, anterior, and ventral margins, becoming obsolete or absent at the posterior end. In the cancellate forms denticles correspond to external radial ribs, and sockets to interradial grooves. The marginal denticles of *Chione paphia* and *Mercenaria mercenaria* seem to correspond to radial structures within the fabric of the shell. Kennedy, Taylor & Hall (1969) find that a radial rib on the underside of each radially arranged first-order composite prism of the outer shell layer forms a denticle at the margin. *Austrovenus stutchburyi* lacks the outer layer of composite prisms and the radial structure which it forms in the fabric of the shell; its marginal denticles are related directly to external sculpture. Stanley (1970) suggests that marginal denticulation helps prevent rotational shear between valves during burrowing. As denticles do not engage when the shell is open, as it must be during burrowing, this explanation of the function of the denticles cannot be correct. It is probable that Rudwick (1964) is correct in supposing that zigzag margins, such as these with denticles, reduce the effective aperture so as to exclude pests and sand grains.

Both *Chione cancellata* and *Austrovenus stutchburyi* are strongly pigmented inside, most commonly purple. *C. cancellata* rather often is orange, pink, or red inside. Around some Caribbean islands this species is white inside with a brown or purple macula near the posterior end; these same shells are often less inflated than usual, and have distant commarginal ridges and dark brown blotches outside. *C. paphia* is usually pale pink or orange inside. *Mercenaria mercenaria* is most commonly purple at the posterior end, but some specimens are entirely white inside. *C. undatella* is white inside, with the teeth and pallial sinus tinted purple.

SOFT ANATOMY

The relationships of organs are shown in Figs. 18 and 19.

The bilobed mantle (Figs. 20, 22, 23, 25, 29) attaches to the valves along the pallial line, and is pierced by the adductor and pedal retractor muscles. Each lobe has inner and outer walls, and secretes the inner shell layer, within the pallial line (Neff, 1972b). This part of the shell supplies calcium to neutralize succinic acid produced by anaerobiosis when the valves are closed; when the valves are open and aerobiosis resumes, the inner shell layer is restored (Crenshaw & Neff, 1969). Between the pedal retractors parallel bundles of muscle extend from the shell mantle a few millimeters to the pallial line and small scars in the umbonal cavity, to suspend the mantle and viscera (Fig. 26). Within the ventral margin bundles of muscles radiate ventrally from the pallial line, interlace, and penetrate the mantle folds. At the posterior end, these muscles control the siphons. The siphonal retractor muscles of *Austrovenus stutchburyi* seem relatively weakly developed. There seems to be a longitudinal band of muscle just dorsal to the innermost mantle fold. Nerves from the visceral and cerebral ganglia serve the mantle. All four species examined for this character have four mantle folds (Figs. 21, 24, 28, 30). *Chione paphia* probably has this number, which seems typical of venerids (Yonge, 1957; Ansell, 1961; Narchi, 1971). At the anterior end of the large pedal gape, the first and second folds fuse, as do the third and fourth. At the posterior end of the pedal gape, the first and second folds continue along the edge of the shell, and the third and fourth folds fuse to form the siphons.

Along the ventral margin the configuration of the four folds varies among the species. In the American species distinct vacuities, probably blood vessels, pass longitudinally just ventral to the line of attachment to the shell. *Austrovenus stutchburyi* alone of the species examined has a possibly glandular patch of tissue beneath the medial surface of the mantle just dorsal to the fourth mantle fold. This structure occurs in *Protothaca* also. Hillman & Shuster (1966) suggest that the fourth mantle fold is derived from the inner surface of the third mantle fold and from the dorsally adjacent part of the mantle surface. Yonge (1957), followed by Ansell (1961), suggests that the fourth fold is the former third fold, and that the second and third folds are the separated surfaces of the former second fold. If the fourth fold was derived in the manner supposed by Hillman & Shuster, the sensory function of the former second fold was assumed by the remnant of the former third fold; in Yonge's model, the functions of the former second fold were retained by the two derivative folds. Hillman & Shuster do not consider this aspect of the derivation of the fourth fold. Nor is there any guarantee that this fold originated in the same way in all species possessing it. The inner surface of the first mantle fold contains several kinds of cells which secrete the various layers of the protein-rich periostracum (Neff, 1972a) and the phenolic substrate which when oxidized tans the periostracum (Hillman, 1961). Hillman (1964) found that the fourth, innermost fold secretes mucus which probably aids the expulsion of pseudofeces.

The siphons, the third and fourth mantle folds fused, are complete. The conical valve in the tip of the excurrent siphon and the inner row of tentacles on the incurrent siphon represent the fourth fold; the ring of tentacles on the excurrent sipon and the outer ring of tentacles on the incurrent siphon represent the third fold (Yonge, 1957; Ansell, 1961). All tentacles are simple. *Austrovenus stutchburyi* seems to have two rows of tentacles on the excurrent siphon. Only in this last species are the tips of the siphons appreciably separate. The cream color of the flesh, the white patches visible through it, and the brown flecks on it may serve to camouflage the siphons against a light granular background. In very young *Mercenaria* the siphons are relatively long (Carriker, 1961), but in adults they are short. The four American species have in the proximal ends of their siphons the partial flap to which the posterior tips of the gills attach, and valves, considered typical of venerids (Ansell, 1961). The ventral portion of the partial flap, also known as the siphonal membrane, can be raised to admit freely the incoming water, or lowered to direct the water ventrally toward the edge of the mantle cavity just anterior to the siphons where pseudofeces accumulate, so as to suspend this rejected material prior to its expulsion from the mantle cavity via the incurrent siphon (Kellogg, 1915). *Austrovenus stutchburyi* has the partial flap, but lacks the valves (Fig. 27). The valves in the incurrent siphons of the American species are more or less frilly on their free edges, and drop forward from the roof and sides of the siphons. They probably control the volume of incoming water and aid in the expulsion of pseudofeces. *Chione cancellata* is quite capable of ejecting forcibly sand grains deliberately introduced into its incurrent siphon. The valves in the excurrent siphon resemble human inferior vocal chords, with the slot-shaped aperture tending dorsoventrally. They delimit the anal canal. They probably increase the efficiency with which wastes and gametes are expelled. Siphonal musculature of *Venus verrucosa,* probably fairly closely related to the American chionines, consists of a clearly defined outer layer of "circular" muscles, a main body of longitudinal muscles with irregularly arrayed "circular" muscles among them, and a very poorly defined inner layer of "circular" muscles (Duval, 1963). The so-called circular muscles are, as Duval explains, in clockwise and counterclockwise helices.

The eulamellibranch gills extend from a point between the labial palps, along the ventral edge of the pericardium, to the dorsal edge of the partial flap. The inner demibranch is considerably broader than the outer, which sends a supra-axial extension over the pericardial wall (Fig. 18). Stasek (1963) has determined that the anterior ends of the gills of venerids other than the very smallest are inserted into the distal oral groove, to which they are fused. There is a food groove along the ventral edge of the inner demibranch; whether there is such a groove at the edge of the outer demibranch is uncertain. Kellogg (1915) studied the movement of particles on the gills, mantle, visceral mass, and palps of *Mercenaria mercenaria, Chione fluctifraga* and *C. succincta (=C. californiensis).* Foster-Smith (1978) examined detailed relationships between gills and palps, and movement of particles on the palps of several species, including some venerids. As turbidity of the water increases, the proportion of material which is accepted declines, and the material rejected is moved ventrally and posteriorly on the mantle to a collection site at the rear of the mantle cavity near the base of the incurrent siphon, through which it is periodically ejected.

In cross-section, the plicae of the gills (Figs. 31–34) vary greatly from species to species. In *Mercenaria mercenaria, Chione undatella* and *Austrovenus stutchburyi* each plica has one water tube, supported by rings of tissue. In *C. undatella* the gill filaments are broader on the lateral surface of the gill.

Two pairs of triangular, rather small labial palps, dorsal and ventral, surround the mouth (Figs. 35–39). The palps of the left side are shown in the figures. In the three small American species the rugae on the palps are coarse and few; in the other two species they are numerous and fine. In *Chione undatella* a lappet extends from the palps posteriorly between the demibranchs.

The general plan of the digestive system and the configuration of the gut loop are similar in all five species (Figs. 40–49). This system and the gonads are supported by numerous bundles of fibers, said to be muscular (Ansell, 1961).

In the anterodorsal edge of the foot is the oval mouth, closely surrounded by the labial palps. *Chione undatella, C. paphia* and *Austrovenus stutchburyi* have small paired globular structures adjacent to the dorsal side of the oesophagus, between the heads of the anterior pedal retractors (Figs. 50, 51). These bodies apparently are not part of the nervous system, and may be oesophageal glands (Stenta, 1906). Some species of venerids possess salivary glands in the bases of the labial palps (Berner, 1938); if any of the species examined here have such glands, I failed to find them. Even in so highly advanced a group of bivalves as the venerids there are yet traces of the primitive form having a head. The contention of Yonge (1953) that loss of the head entailed loss of all associated buccal, radular, and oesophageal structures is not correct. The oesophagus is lined with longitudinal epithelial rugae, closely spaced and fine in *C. cancellata, C. undatella* and *Mercenaria mercenaria,* but coarse in *C. paphia.* In *A. stutchburyi* these rugae are of various widths, and separated by thin-walled areas seemingly devoid of tall epithelial cells.

The general structure of the stomach (Figs. 52–56) is similar among all venerids so far examined, although there are many differences in detail (Graham, 1949; Purchon, 1960; Ansell, 1961; Dinamani, 1967; Narchi, 1971, 1972). A narrow collecting area (circular tract of Ansell, 1961) borders the proximal end of the oesophagus, evident in *Chione undatella* (Fig. 54). A shelf divides the anterior end of the globose stomach into a dorsal hood and a larger ventral portion. A large sorting area extends from the upper opening into the left digestive diverticulum, across the dorsal surface of the shelf, around the right side of the stomach, and onto the floor. The sorting ridges are fine in all species but *C. paphia.* The dextral extension of the stomach is anterodorsal in *Austrovenus stutchburyi* (Fig. 55) and in some species of *Protothaca,* but posterolateral in the American species. The acceptance tract on the posterior wall of the stomach is evident in *Mercenaria* (Fig. 56). A somewhat rugose area, bounded anteriorly by the major typhlosole, crosses the anterior floor between the ventral openings into the digestive diverticula. In *Austrovenus* there is a small rugose gap in the major typhlosole between the posterior sorting area and the opening into the right digestive diverticulum. A thin gastric shield (Figs. 57–59) covers the roof and most of the left interior wall of the stomach. Kubomura (1959) has shown that the gastric shield of *Meretrix meretrix,* another venerid, is composed of an outer layer, seemingly scleroprotein, probably collagen, and of an inner layer, probably of chitin. The outer layer contains appreciable amounts of amylase. In addition to its supposed abrasive, protective, and digestive functions (Owen, 1974; Kubomura, 1959), the shield with its two prongs projecting through the upper and lower openings into the left digestive diverticulum probably helps prevent the collapse of the stomach. The shield of *Mercenaria mercenaria* (Fig. 59) has an additional rib-strengthened process which crosses the posterior floor of the stomach. In *C. cancellata* and *M. mercenaria* a yellow spongy mass, supposedly a digestive gland, is closely appressed to the external roof of the stomach (Figs. 52, 56). This tissue is in the position said to be occupied by the pericardial gland (Kato, 1959).

The green to brown digestive diverticula (or midgut glands) surround the anterior end of the stomach and communicate with that organ through an opening near the right side of the oesophagus, one or more openings near the left side of the oesophagus, one large opening at the left end of the shelf, and in some cases by another small opening at the left end of the shelf, posterior to the large opening. Lobes of the major typhlosole pass through the perioesophageal opening, and a similar extension of the sorting area on the shelf forms a large lobate caecum from the large upper opening. Extending distally from the lobes of the typhlosoles are ever-finer tubules which lead to sacs in which digestion occurs. The configuration, histology, and function of these structures has been discussed by Nakazima (1956) and Owen (1955, 1966). Owen (1974) suggested that in some bivalves digestion in the diverticula is both intra- and extracellular. A parasitic copepod, *Pseudomyicola spinosus* (Raffaele & Monticelli), often lives in the digestive diverticula of *Austrovenus stutchburyi* (see Humes, 1968).

The midgut (posterior part of the stomach, according to Ansell, 1961) is divided longitudinally by the posterior part of the major typhlosole and by the minor typhlosole into the style sac on the left and the intestine on the right. The whitish translucent crystalline style, when present, projects well into the lumen of the stomach. The intestine receives wastes from the digestive diverticula and supposedly rejected material from the sorting areas. Owen (1966) said nothing of the functions of the intestine, in conformity with the view that the intestine serves only to mold its contents into fecal pellets or rods. Such a view does not explain the increased length of the gut with increased depth, and probably increased paucity of nutrients (Allen & Sanders, 1966). Reid (1968) and Purchon (1971) produced evidence that digestion occurs in the midgut, increasing the efficiency of the use of ingested material. Stewart & Bamford (1976) found that the midgut of *Mya arenaria,* in the same general group of bivalves as venerids based on stomach structure, does indeed absorb soluble nutrients. They further found that digestion is cyclic and synchronous with the tidal cycle in this intertidal and shallow subtidal animal, and that the crystalline style disintegrates when the animal is not actively feeding. Whether venerids have such cycles is not known, but the presence of the style in some animals, and its absence in others preserved in the same way for the same length of time suggests that these clams have cyclic digestion. None of the work done so far deals with possible digestion in the gut loop. In all species examined here, the gut loop is on the left side of the visceral cavity, and the posterior end of the intestine passes through the pericardial cavity where it supports the heart and aortae, passes dorsal to the posterior adductor, and ends as the anus in the anal canal of the American species, in the excurrent siphon of *Austrovenus stutchburyi*. That digestion occurs in this post-midgut section of the intestine is suggested by the presence of a prominent typhlosole and a thick epithelium, as in *Mercenaria* (Figs. 63, 64). The structure of the intestine (rectum) of *M. mercenaria* and *Chione cancellata* has been described in detail by Jegla & Greenberg (1968a,b). These workers conclude that, because the "important and mandatory function" of the intestine is the molding and expulsion of feces, the intestine in all its complexity is nonadaptive. It is clear that more work on this organ is needed before anyone can make such startling and all-encompassing statements.

The circulatory system is similar in all five species (Figs. 65–70). The pericardial wall is thin ventrally and laterally, but thickens dorsally and merges with the hinge mantle. Narain (1976) suggested that firm support of the pericardium by adjacent tissue is integral to the maintenance of circulation. The lateral auricles (atria) communicate with the medial ventricle via openings fitted with valves (Fig. 71) preventing retrograde flow of the blood. The thin-walled auricles, crossed by bundles of possibly muscular fibers, receive blood from the outer limbs of the kidneys via one or more fenestrae. Numerous bundles of muscles, many of which originate around the openings from the auricles, cross the lumen of the ventricle (Fig. 72). In *Venus (=Chamelea) gallina* similar fibers originate a short distance from these openings (Brunet & Jullien, 1936). In *Katelysia marmorata* these fibers are smooth (Joshi & Bal, 1976b). In the bulbus arteriosus are longitudinal sheets which appear to be muscular. Hersh (1957) found muscle fibers in the bulbus, but did not consider the primary function of this structure muscular. He suggested that the variety of glandular cells indicated a secretory function. Hersh did not find a valve between the bulbus and anterior part of the posterior aorta. In *K. marmorata* there is such a valve (Joshi & Bal, 1967b). The anterior aorta passes anteriorly dorsal to the intestine, supplies sinuses near the anterior end of the stomach, and continues ventrally along the anterior wall of the visceral cavity. Nielsen (1963), Joshi & Bal (1967b) and Brand (1972) traced a similar vessel into the tip of the foot, and found several derivative vessels to the stomch, intestine, and gonad. A fine aorta from the vicinity of the bulbus serves the hinge mantle. In *K. marmorata* this area is served by a vessel arising from the anterior aorta (Joshi & Bal, 1967b). The posterior aorta, having passed into the anterior end of the bulbus, by which it is interrupted in *Mercenaria,* continues posteriorly ventral to the intestine. This aorta supplies large, poorly defined sinuses on the anterior face of the posterior adductor, and penetrates the posterior edge of the mantle. Duval (1963) found in short-siphoned species, such as these, four longitudinal siphonal haemocoels, dorsal, ventral, and lateral. Longitudinal vacuities in the ventral edge of the mantle are probably blood vessels. It is assumed that the flow of blood in these species resembles that in *Anodonta anatina* (L.) (Brand, 1972).

I was unable to find with certainty the pericardial glands, although tissue labelled as digestive glands in *Chione cancellata* and *Mercenaria mercenaria* (Figs. 40, 48) and the pale brown anastomose tissue at the posterior end of the pericardium of *C. paphia* (Fig. 26) may be this organ. In some other venerids, this paired gland lies in the umbonal cavity, near the blood sinuses of the visceral hump (Kato, 1960), or in the mantle near the heart (not necessarily a position different from that cited by Kato), or on the auricles (White, 1942). White considered these glands to empty the wastes extracted from the blood into the pericardial cavity, but Kato found evidence that they pass nitrogenous wastes to the gills and mantle, which in turn pass them into the water in the mantle cavity.

The pale brown kidney lies along the ventral edges of the pericardium and on the anterior faces of the posterior pedal retractor muscles (Figs. 73–77). Kato (1959) reports that the kidneys of Japanese venerids excrete nitrogenous wastes and granules of melanin.

The thin-walled outer limbs contain greater or lesser amounts of spongy tissue, usually most evident at their anterior ends. The nephrostomes are in the anteroventral corners of the pericardial cavity, as in *Anodonta* (Potts, 1967), not in the posteroventral corners, as in British venerids (Ansell, 1961). Between the kidney and the auricles are fenestrae, one on either side in *Chione,* three in *Austrovenus,* and one large and several small in *Mercenaria.* The posterior portion of the outer limb is lined on all sides by anastomosing ridges of spongy tissue in which are often embedded small dark-brown calculi of fairly high refractive index. These calculi may be inexcretable wastes stored as solids (Strohl, 1914), or perhaps melanin granules (Kato, 1960). The ridges of spongy tissue converge on the posterior wall of the kidney and continue anteroventrally as the inner limb, which empties into the suprabranchial cavity via the nephridiopore. In *Mercenaria* wastes empty into a small chamber in the midline, dorsal to the exterior nephridiopores (Fig. 78). This chamber is perhaps a bladder to hold wastes when the shell is closed. The two sides of the kidney communicate by a passage along the floor of the organ. Connections between the kidney and the gills were impossible to find with the microscope used.

The nervous system (Figs. 79–83) is pale yellow, and enveloped by a thin pellicle. There are three pairs of ganglia, cerebral, visceral, and pedal, their connectives, and many derivative nerves. The visceral system is the most complex.

The cerebral ganglia (Figs. 84–93) lie just anterior to the heads of the anterior pedal retractor muscles, among a mass of tough connective tissue, and are joined by a short, thick supraoesophageal commissure. The bright yellow caps of these ganglia in *Mercenaria* (Figs. 92, 93) may be incompletely fused pleural ganglia. Small nerves pass laterally into the labial palps. In some animals fine nerves are seen to pass dorsal to the adductor muscle into the anterior edge of the mantle. From one or both ganglia a nerve extends posteriorly along the oesophagus to the viscera. Perhaps this nerve supplies the tiny fibers in the intestine observed by Jegla & Greenberg (1968b). The main nerves from the cerebral ganglia descend the posterior face of the adductor muscle, and send fine nerves into the shell mantle, and probably into the adductor itself. Near the ventral edge of the muscle, one branch of the nerve runs anteriorly into the edge of the mantle, and the other branch runs posteriorly among the radial muscles of the mantle. This anteroventral pallial nerve sends numerous branches to the mantle folds. Posteriorly it becomes the posteroventral pallial nerve from the visceral complex.

The cerebrovisceral connective courses from the laterodorsal corner of the cerebral ganglion, passes just within the lateral face of the pedal retractor muscle and among the colliculi of the digestive diverticulum, crosses the gonad, runs past the ventral edges of the gonopore and nephridiopore, leaves the visceral mass anterior to the main body of the posterior pedal retractor muscle, and joins the laterodorsal corner of the visceral ganglion. In some cases this connective sends fine nerves to the anterior pedal retractor. The closely fused visceral ganglia (Figs. 94–98) are affixed to the anterior face of the posterior adductor by connective tissue and a thin covering membrane. A large nerve runs anteriorly into the base of the gill, and seems to send fibers into the plicae. The visceral ganglion sends a fine nerve to the kidney. This nerve has been traced in other venerids to the auricle and ventricle (Carlson, 1905; Phillis, 1966). Slender nerves leave the dorsal edge of the ganglion to serve the pedal retractor and shell mantle. Another, larger nerve passes posteriorly into the adductor muscle. A short distance ventral to the ganglion the main descending nerve sends a branch into the posterior end of the mantle. Near the ventral edge of the adductor the main nerve splits: a small nerve tends posteriorly into the excurrent siphon; a fairly large branch descends among the siphonal retractor muscle fibers and turns anteriorly in the edge of the mantle; and the largest branch runs ventrally along the bases of the siphons. This latter branch sends many nerves into the siphons and siphonal retractor muscle. At the level of the junction of the siphons is a subsidiary ganglion in the American species, only slightly developed in small specimens of *Chione paphia.* In all cases there seems to be a nerve connecting the two sides of the siphonal complex at the junction of the siphons. Ventrally the siphonal complex extends almost into the edge of the mantle, and terminates. Duval (1963) notes that species with short siphons, such as these and some other venerids, have irregularly arrayed nerves in the siphons.

The cerebropedal connective runs from the posterior face of the cerebral ganglion ventrally through the pedal retractor, to which in many cases it sends fine nerves, and joins the anterior end of the pedal ganglion. The pedal ganglia (Figs. 99, 101–104) are extensively fused and lie just anteroventral to the ventral turn of the midgut, from which they are separated by a thin screen of transverse muscles. In *Mercenaria* the connective sends tiny nerves dorsally among the splayed fibers of the pedal retractor muscle lining the visceral cavity. Three pairs of nerves innervate the foot. The anterior pair extends anteriorly and somewhat laterally to innervate the anterior part of the foot. The middle pair passes ventrally and medially to the central part of the foot. One branch of these nerves closely approaches the pedal gland. The posterior pair runs a short distance posteriorly from the ganglia and divides, with one branch plunging ventrally and the other continuing posteriorly to the posterior part of the foot. All three pairs branch several times as they extend toward the edge of the foot. Ansell (1961) records only two pairs of pedal nerves, the anterior and middle. In *Katelysia marmorata,* an anterior pair of pedal nerves innervates the sides of the foot, and a posterior pair sends branches into the anterior and posteror ends of the foot (Joshi & Bal, 1967a). Nielsen (1963) states that the posterior nerves from the pedal ganglia innervate the intestine; I did not find such a relationship. Structures believed to be statocysts (Fig. 100) are visible in some animals in the anterior edge of the foot at the ends of tiny nerves extending from the pedal ganglia approximately parallel to the anterior pedal nerve. The statocyst nerve is said to arise from the cerebral ganglion (Pelseneer, 1906). Some of these structures contained a tiny yellow stone, presumably the statolith. I did not find statocysts near the pedal ganglia; Nielsen also failed to find them in this position.

The pedal gland (Figs. 104–108) is situated in the midline of the foot among the crossed fibers of the pedal retractors. In juveniles this organ is byssiferous (Belding, 1912; Carriker, 1961; D'Asaro, 1967). Barrois (1885) stated that among venerids, only tapetinids retain this byssiferous gland in the adult. Boutan (1895) noted that *Venus (=Pitar) rudis* loses the byssal gland during ontogeny. Nielsen (1963) found a pedal gland in adult *Katelysia,* in which the function is unknown. Adult *Venerupis pullastra,* a nestler, retains a functional byssal gland (Mahéo, 1969). This gland is byssiferous in the adults of the small venerid clam, *Transennella* (Narchi, 1970). Ladd (1951) collected *Chione grus* (Holmes) apparently attached to sea grass. The collections of the Museum of Comparative Zoölogy contain hundrds of adult specimens of this small chionine taken from buoys; almost certainly these animals were byssally attached. I have found the structure in *Protothaca* as well. The pedal gland is white, rather globular, and mammilate on its inner surface. A narrow, pellicle-covered duct leads anteroventrally to a slot in the edge of the foot. In all five species the gland is rather small, and not anchored by the broad band of muscle to be expected if this organ were byssiferous. In the adults of larger species this gland may secrete mucus to lubricate the tip of the foot during burrowing. In adult *Gemma gemma* this organ secretes a mucilaginous substance which aids in crawling (Sellmer, 1967). Trueman (1975) noted that a foot coated with mucus-glued sand grains has a superior grip on the substratum during burrowing. Yonge (1962) regarded the presence of the byssal apparatus in some burrowing adults as the probable retention of a structure advantageous to juveniles, and therefore neotenous or paedomorphic.

Follicles of the ripe gonad (Figs. 109, 110) occupy all the space in the visceral cavity around the digestive system (Fig. 19). Tributary ducts from the follicles gradually converge posterodorsally to form the gonoduct, which passes beneath the pericardium to empty via a discrete gonopore into the suprabranchial cavity. Most animals examined were ripe females with stalked and free ova filling the follicles and ducts. The ova are about 0.3 mm in diameter. The gonads of an adult specimen of *Mercenaria* of undetermined sex (Fig. 111) consists of tough yellow tissue through which are scattered seemingly unconnected clusters of pale yellow follicles. Moore & López (1969) found that *Chione cancellata* is sexually mature by the time it is about 15 mm long, and the animals are then clearly male or female. The sex ratio is probably 1:1. Young *M. mercenaria* are bisexual with strong male predominance (Loosanoff, 1936). At the age of about 10 months, the animals become definitive males or females, and become functional about a year later. A few adults are functional hermaphrodites, but change of sex does not seem to occur in adults. Both *M. mercenaria* and *C. cancellata* have 19 pairs of chromosomes (Menzel, 1968). Sexual development of the other species has not been studied.

DISCUSSION

The differences in both shell and soft parts among the five species are summarized in Table 1; in Table 2 the number of differences between any two species are summed. These differences and others not easily represented in this form are discussed in turn.

Taylor (1973) suggested that the primitive structure of the shells of most heterodonts, including lucines and venerids, consists of an outer layer of composite prisms, a middle cross-lamellar layer, the pallial myostracum, and an inner layer of complex cross-lamellae. He supposes that in the course of evolution the outer prismatic layer is lost, and that the other layers becomes progressively homogeneous. He suggested that homogeneous layers of tiny crystals are inexpensive to form. The repeated solution and redeposition of the inner layer in intertidal and shallow subtidal clams (Crenshaw & Neff, 1969) would probably require such economy of effort. If Taylor's evolutionary sequence be correct, then *Austrovenus stutchburyi* is more advanced than the eastern American chionines in lacking the outer layer of composite prisms, but less advanced in retaining some complex cross-lamellae in the inner layer. In this scheme, *Chione undatella* is the most advanced. Taylor & Layman (1972) showed that composite prisms are particularly resistant to pinpoint stress. This array of material forms the sculpture of the three eastern American species. If the function of commarginal sculpture is resistance against disinterment, then it is advantageous for this sculpture to be formed of material resistant to the pinpoint stress of impinging sand grains. Taylor noted (1973) that the very earliest lucines, much older than the oldest venerids, had the outer composite-prismatic layer, and assumes that this structure is primitive in venerids as well. It may be, however, that this layer evolved separately in venerids, and is relatively new, rather than primitive. It seems to be true that this layer can be secondarily lost. If, as Stanley (1970) maintained, sculpture is advantageous to the possessor, and if, as Taylor suggested, the outer layer (which forms the sculpture) is primitive, then one would expect the early venerids to have been sculptured, and that the sculptured condition and the shell layer which gives rise to it to have been retained by most later generations of venerids. Examination of the vast literature shows that fossil venerids were generally devoid of sculpture from their beginning in the mid-Mesozoic until some time in the Eocene, when pitarines, a western Tethyan group, developed commarginal or even zigzag sculpture. *Mercenaria,* and through *Mercenaria, Chione* are almost certainly descended from Middle Eocene *Rhabdopitaria* of the American Gulf Coast (Stenzel, 1955). *Mercenaria* has had this outer layer since its first appearance in the Middle Oligocene. *Chione undatella,* a descendent of *Mercenaria,* seems to have lost this layer. Taylor, Kennedy & Hall (1973) noted that some species of venerids are variable in their possession of the outer layer, but do not mention whether *C. undatella* is one of these species. That the sculpture-bearing Venerinae are probably very

TABLE 1. Anatomical differences among *Chione cancellata, Chione undatella, Chione paphia, Mercenaria mercenaria,* and *Austrovenus stutchburyi.*

	C.c.	*C.u.*	*C.p.*	*M.m.*	*A.s.*
Posterior flanges	+	+	+		
No posterior flanges				+	+
Lunule sharply defined	+	+	+	+	
Lunule poorly defined					+
Escutcheon well defined	+	+	+	+	
Escutcheon poorly defined					+
Cardinal teeth simple	+	+	+		
Cardinal teeth bifid				+	+
Teeth merge with platform	+	+	+	+	
Teeth extend to edge of platform					+
Pallial sinus shallow, ascending	+	+			
Pallial sinus deeper, anterior			+	+	+
Tips of siphons fused	+	+	+	+	
Tips of siphons separate					+
Valves in siphons	+	+	+	+	
No valves in siphons					+
Subsidiary ganglia	+	+	+	+	
No subsidiary ganglia					+
Palp rugae coarse	+	+	+		
Palp rugae fine				+	+
Oesophageal rugae close	+	+	+	+	
Oesophageal rugae distant					+
Stomach sac posterolateral	+	+	+	+	
Stomach sac anterodorsal					+
1 fenestra/auricle	+	+	+		
More than 1 fenestra/auricle				+	+

TABLE 2. Sums of anatomical differences between any two species.

Species	*C.c.*	*C.u.*	*C.p.*	*M.m.*	*A.s.*
Chione cancellata	0				
Chione undatella	0	0			
Chione paphia	1	1	0		
Mercenaria mercenaria	5	5	4	0	
Austrovenus stutchburyi	13	13	12	8	0

closely related to the Chioninae is suggested by shell structure, internal anatomy, and possible fossil intermediates of Late Oligocene and Early Miocene age (see also Fischer-Piette, 1975).

It is possible that the absence of the composite prismatic layer in *Austrovenus stutchburyi* is primitive. The projecting posterior tips of this species are often so worn as to expose the pigmented inner layer. The American species are almost never abraded in this way. Although Taylor & Lyman (1972) asserted that both cross-lamellae and composite prisms resist erosion, in these cases composite prisms are superior to cross-lamellae.

Radial sculpture may have arisen directly in some instances by exaggeration of the radial composite prisms, which also form ventrally the marginal denticles. *Rhabdopitaria* has both the composite prismatic layer and the denticles, but not the radial sculpture (Stenzel, Krause & Twining, 1957). Middle Oligocene *Mercenaria mississippiensis* has the commarginal sculpture typical of young Recent *Mercenaria,* fairly well developed marginal denticles, but only hints of radial sculpture. In forms intermediate between *Mercenaria* and *Chione,* seemingly coeval with *M. mississippiensis,* and in Late Oligocene species of *Chione,* radial sculpture consists of riblets which are mere extensions of the marginal denticles onto the ventral surfaces of the commarginal ridges. These riblets probably acted as brackets or supports for the somewhat thin commarginal lamellae in their function as anchors against disinterment. By the Middle Miocene these radial elements became continuous across the interlamellar space, as in *Chione chipolana* Dall. (For this and other fossil American chionines, see Dall, 1903, and Palmer, 1927, 1929.) Recent *Chione pubera* (Valenciennes) and *C. intapurpurea* (Conrad) retain the older mode of radial sculpture. The radial ribs of *Austrovenus stutchburyi* seem to involve most of the thickness of the shell, and probably arose in a manner different from that suggested for *Chione* and *Mercenaria. Chione undatella* has radial sculpture, despite the absence, or loss, of the outer shell layer; presumably the next layer has been pressed into service.

It seems likely that sculpture can be formed from a variety of crystalline arrays, usually from the outermost prismatic layer among the Chioninae and Venerinae, and is sufficiently adaptive to have arisen independently in separate lineages. It also seems clear that *Austrovenus stutchburyi* represents a stage in the structural evolution of the shell different from that exemplified by the American chionines.

Posterior flanges are evident in many American chionines, fossil and living, and in some venerids of the Miocene deposits of the Vienna Basin and Pliocene deposits of Italy, but are absent in *Austrovenus stutchburyi.* These flanges are adjacent to that part of the margin near which the siphons protrude, and may protect the siphons from abrasion and bites. Carter (1967) suggests that spines in this position on *Hysteroconcha,* a pitarine, and on *Hecuba,* a donacid, discourage predators.

Austrovenus stutchburyi alone of the five species lacks a well-defined lunule. Every American chionid, of whatever epoch, has a well-defined lunule surrounded by an incised line. In this respect, *Austrovenus* more closely resembles species in the Tapetinae, Meretricinae, and Circinae. The function of a well-defined lunule is unknown. Ansell (1961) suggests that a flat lunule, like that of *Mercenaria,* may aid in burrowing. Cox (1969) noted that the lunule on the outside of the shell corresponds to the track of the growing anterodorsal hinge structures on the inside, and is composed of the same shell layer as the dentition. The way in which this relationship might affect the degree of definition of the lunule is unclear.

All American chionines have well-defined impressed escutcheons, usually relatively broad in the smaller species. *Austrovenus* resembles such tapetines as *Venerupis* and *Katelysia* in its weakly defined escutcheon. The overlap device of living American chionines is well developed; in some extinct species this structure seems rather weak. In a general way, those species with poorly developed overlap devices were short-lived, or restricted in range, or both; those species with this structure well developed were longer-lived, or more widespread, or both. Toward the end of the Miocene, polydorid polychaetes invaded the shells of many species of *Chione.* In this same span of time, many species became extinct. It is tempting to see a causal relationship between these trends. Most of the specimens of *A. stutchburyi* from Auckland Harbour were infested with polydorids. This clam also has a rather weak overlap device, and lives with the posterior end of the shell projecting from the substratum, an open invitation to the polydorid pests. *Austrovenus* *stutchburyi* existed in the Pliocene (Powell, 1934), when its escutcheon was better defined (Marwick, 1927). The overlap device is weak to absent in many species of *Protothaca,* in most tapetines (see Fischer-Piette & Métivier, 1971), and in most venerids before the Oligocene.

Bifidity of teeth may represent an increase in the number of effective teeth from a few basic elements. Additional dental processes may distribute shearing stress more evenly and so prevent fracture, especially in species with relatively slight teeth, such as *Austrovenus stutchburyi,* and in species with relatively massive shells, such as *Mercenaria mercenaria.* Lateral teeth or tooth-like structures would serve the same end. All eastern American species of *Chione,* living and extinct, are of small or medium size, and have simple teeth. Occasional specimens of *C. pubera* (Valenciennes), the largest living Atlantic species of this genus, have an extra tooth in the right valve anterior to the cardinal teeth. All species of *Mercenaria* are, as adults, of medium to large size and massive; they and *Rhabdopitaria* and a few other, small, Middle Eocene pitarines of the Gulf Coastal Plain have a rugose area adjacent to the nymphs and some cardinal teeth bifid. On the Pacific coast, where until recently *Mercenaria* has been absent, many species of *Chione,* especially those of the subgenus *Chionopsis,* are as large as the quahog and have bifid cardinal teeth. Any relationship between angle of rotation during burrowing (Stanley, 1970) and number of dental prominences is hard to discern. The sample is small, however, and further research might reveal some such relationship.

The extension of the teeth almost undiminished to, and even beyond, the edge of the dental platform is unknown in American species of *Chione,* although it occurs commonly in *Protothaca* (Keen, 1971) and in some tapetines (Fischer-Piette & Métivier, 1971). In *Chione* and *Mercenaria* the teeth merge gradually ventrally into the edge of the rather robust dental platform. In this character, *Austrovenus* resembles *Protothaca.*

Stanley (1970) provides information on 18 species as to size and direction of the pallial sinus, and as to depth and attitude in the sediment. Those species with shallow pallial sinuses, and presumably short siphons, all live with their posterior tips within 2 cm of the surface of the substratum, or even projecting from it. Those species with deep sinuses live more than 1 or 2 cm below the surface, many within more or less permanent burrows. There seems not to be any correlation between attitude in the substratum and direction of the sinus.

In addition to the partial flap at the proximal ends of the siphons, many venerids, including the four American species discussed here, have paired membranes in the excurrent siphon and a curtain-like valve in the incurrent siphon. These structures presumably aid the closer regulation of the flow of water into and out of the mantle cavity. *Gemma gemma* (Totten) (Sellmer, 1967) and some species of *Protothaca* have only the valve in the excurrent siphon. *Austrovenus* entirely lacks valves in the siphons. The four American species have subsidiary ganglia at the bases of their siphons, probably for finer, more integrated control of the siphons. *Austrovenus* lacks subsidiary ganglia. Perhaps the separation of the tips of siphons in *Austrovenus* increases control of excurrent flow. Ansell (1961) considers separation of the tips of the siphons as a specialization for life in very turbid, shallow waters. Some of the American species live in waters seemingly as shallow and turbid as those inhabited by *Austrovenus,* yet have fully joined siphons. It seems likely that once a lineage of clams had evolved structures so adaptive as internal siphonal valves, it would not then lose them; *Austrovenus* and its ancestors probably never had these valves.

Coarseness and number of rugae on the labial palps, and size of the palps relative to the area of the gills seem related to turbidity of the environment. According to Ansell (1961), animals in turbid waters have relatively large palps with many and large rugae capable of considerable muscular activity and of creating complex ciliary currents. Ansell found that species of *Venerupis* living in turbid water have large palps with many small ridges, and venerids of the sublittoral zone have simple palps. The arcid *Anadara anomala* Reeve lives in sand and has relatively small palps with some 43 thick, broad rugae, whereas *Anadara cuneata* (Reeve) inhabits mud and has relatively large palps with some 150 long, slender rugae (Lim, 1966). *Chione cancellata* and *C. undatella* live in shallow, turbid water, but have the small palps with few rugae expected of species in deeper, less turbid water. The palps of *Mercenaria mercenaria* and *Austrovenus stutchburyi,* although rather small, have the many ridges postulated for dwellers in turbid water. *C. paphia* lives in deeper, clearer water, and, as predicted, has small palps with few large ridges. Work on ciliary currents on the palps of these species might show closer adaptation to turbidity than the size of palps and number of ridges might suggest.

The significance of the size and spacing of the longitudinal ridges in the oesophagus is unknown. Perhaps they are related to the quantity and size of particles accepted.

All species examined have type-V stomachs (Purchon, 1960). There is a difference in shape, however. In the four American species the dextral extension of the stomach is lateral and slightly posterior to its junction with the main part of the stomach, but in *Austrovenus,* as in *Protothaca,* this extension is somewhat anterodorsal to the rest of the stomach. Among venerids there are variations of shape and detail within the type-V stomach which may be useful in determining relationships at levels lower than the superfamilial and familial, and in exploring adjustments between stomach structure and the kinds and sizes of materials accepted. Gut contents of all five species consisted of grey mud and algal cells. The ridges of the sorting areas in *Chione paphia,* like the rugae on the palps and in the oesophagus, are coarse, perhaps to deal with a relatively broad array of particle sizes in the clearer, deeper waters.

The significance of the number of fenestrae between the outer limb of the kidney and the auricle is not known. Each of the three species of *Chione* has one such opening; *Mercenaria* has one large fenestra in the same position as that in *Chione* and several much smaller ones anterior to it. *Austrovenus stutchburyi* and *Neotrigonia margaritacea,* both about the size of the small chionines, have three and two fenestrae, respectively. The number of fenestrae is not dependent solely on size.

CONCLUSIONS

It is evident from Table 2 that the three species of *Chione* are very similar to one another in both soft and hard parts. Because it has robust commarginal ridges, *C. paphia* is assigned by all workers to a subgenus different than the nominate subgenus, to which *C. cancellata,* the type, and *C. undatella* belong. The fossil evidence is ambiguous, but suggests that *C. paphia* is more closely related to species of the subgenus *Panchione* Olsson (1964) than to those of *Lirophora* Conrad. *Chione undatella* seems to lack the structures identified as oesophageal glands in the other three small species, and is alone in having a lappet extending from the labial palps to the gills. Oligocene and Miocene fossils, as well as anatomy, show that the three small American species are closely related.

Mercenaria mercenaria differs from the small American chionines in fewer than half of the characters considered, even though their lineages diverged before the Late Oligocene. Two of these differences, the dentition and the number of openings between the kidney and the auricle, are probably functions of the greater adult size of *Mercenaria,* which lives well below the surface of the substratum with only the tips of its siphons protruding from the substratum. *Chione,* with its shallow sinus and well-developed flanges, lives with the posterior tip of the shell projecting from the sediment. Differences in the size of rugae on the labial palps seem related to differences in size and volume of particles ingested. In complex characters, such as the shape of the escutcheon, degree of definition of the lunule, configuration of the stomach, possession of valves in the siphons, and in other, perhaps simple characters, such as complete fusion of the siphons and possession of subsidiary siphonal ganglia, *Mercenaria* resembles *Chione.* The resemblance of *Chione,* especially the Oligocene species from the Gulf Coastal Plain, and juvenile *Mercenaria* with its commarginal lamellae and similar shell structure suggests that *Chione* arose from *Mercenaria* by neoteny. Soft anatomy appears to be conservative.

Austrovenus stutchburyi differs from like-sized *Chione* in almost all 13 characters, simple and complex. In some characters it resembles *Mercenaria,* but in many conchological characters it resembles equally well *Protothaca* and some members of the Tapetinae. The differences of anatomy, particularly the stomach, dentition, and siphons, and the lack of fossil intermediates indicate that *Austrovenus* does not belong to the genus *Chione,* and may not belong to the Chioninae. It seems more likely that the similarity of *Austrovenus* to *Chione* in sculpture is the result of convergent evolution of very different lineages adapting to a shallow infaunal mode of life in shifting substrata in the intertidal and shallow subtidal zones.

Finally, this work suggests that soft anatomy, details of the structure and configuration of the shell, and the fossil record together can provide enough information for the detection of phylogenetic relationships, and for the construction of a taxonomic scheme reflecting those relationships.

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MULTIVARIATE ANALYSIS OF DESERT SNAIL DISTRIBUTION IN AN ARIZONA CANYON

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ABSTRACT

Multiple discriminant analysis and principal component analysis were found quite useful in interpreting distributions of two land snails in a desert canyon in Arizona. Snail presence and abundance in small, arbitrarily chosen sites can be accurately predicted from five environmental variables: elevation, slope angle, slope aspect, percent vegetational cover, and substrate type. Though correlation among the environmental variables was high, vegetational cover was found to account for most of the variance in snail presence. Independent of vegetation, slope aspect, slope angle, and elevation were not demonstrated to affect the presence of snails. The two snail species commonly found living in the canyon, *Discus cronkhitei* and *Sonorella baboquivariensis cossi,* differ significantly in their preference of slope angle and substrate. It is suggested that *Sonorella* was found more commonly on steep rocky slopes because it requires rocks for shelter. *Discus,* a much smaller snail, can find adequate shelter in loosely packed humus and thus inhabits shallower slopes where humus accumulates.

INTRODUCTION

Boycott (1934) suggested that the major factors influencing habitat selection by land snails are shelter (protection from desiccation and predation) and availability of lime. More recent work has emphasized a third important consideration, food availability. There is evidence of correlation between snail abundance and both the amount of calcium and organic matter in soil samples (Burch, 1955). In the western U.S.A., many land snails are more often found associated with certain deciduous trees than with pines or grasses, implying that the litter from deciduous trees serves as food (Karlin, 1961). Grime & Blythe (1969) found two species of snails inhabiting opposite slopes of the same pass and feeding on different plants, but they suggested that climatic rather than vegetational differences were responsible for the separation. Differences in the sites of activity of several land snails have been interpreted as adaptations facilitating coexistence (Cameron, 1978).

Perhaps the major difficulty in all of these studies has been that of dealing with environmental variables often unmeasured or correlated with each other. Cover, moisture, food, lime, competition and predation are surely only a few of the factors potentially influencing the local distribution of land snail populations. In this investigation I examine the abundance of individuals of two snail species in quadrat samples from a canyon in southern Arizona. Since rainfall is quite low in the area, measures reflecting cover, moisture, and temperature should account for a large part of the variance in snail distribution observed. The importance of unmeasured factors such as lime were not addressed by this study.

How accurately can snail presence at a small site in the desert be predicted from altitude, slope angle, slope aspect, percent vegetational cover and substrate? Which of these variables is most important in explaining the variance? Do the two species differ in their local distributions, and if so, which variables seem best correlated to these differences? I have employed multivariate analysis to address these questions. If multivariate statistical techniques can be demonstrated useful in the relatively simple desert environment, their application to more complex sets of distributions or to environments where important variables are more difficult to identify will seem promising.

METHODS

Arch Canyon is located in Organ Pipe Cactus National Monument, Arizona, about

TABLE 1. Environmental variables measured at each site.

Variable	Mean	Standard deviation	Maximum	Minimum
Altitude (feet (meters))	3160 (963)	230(70)	3700 (1128)	2700 (883)
Slope aspect (degrees)	73	66	180	0
Slope angle (degrees)	21	12	50	0
Substrate type (coded)	4.4	1.6	6	1
Vegetational cover (%)	56	29	100	0

21 km from the Mexican border (32°02′ N, 112°42′ W). Its mouth at 2560 ft (780 m) altitude is well within the limits of the Sonoran Desert, and cacti comprise a large portion of the vegetation, but at the top of the canyon (4000 ft., 1219 m) shrubs and trees dominate. On 5 to 10 January, 1978, quadrat samples 4 m^2 each were made at 129 arbitrarily chosen sites in the canyon. Smaller sample areas might have permitted better estimation of the actual environment experienced by the snails, but a sample size of at least 4 m^2 was dictated by the scarcity of individuals.

Measurements of five environmental variables were made at each site (Table 1). Altitude was estimated to the nearest 50 ft (15.2 m) from a topographic map. Slope aspect was determined to the nearest 45° on a scale from 0° to 180°, evaluating both east and west at 90°. I measured slope angle with an inclinometer set on a meter stick lying flush with the ground and oriented upslope. Substrate type was scored on a scale from 1 to 6, with 1 designating solid rock; 2, coarse cobble (diameter more than 25 cm); 3, fine cobble (diameter less than 25 cm); 4, sand; 5, dirt; and 6, humus. Vegetational cover was estimated to the nearest 25%. Notice that the distributions of these variables at best only approximate normality, for each variable is broken into a small number of discrete values. The results of my analyses are therefore only approximations.

Each quadrat was thoroughly searched for snails by turning rocks and sorting through humus. The two snail species commonly found living were the helminthoglyptid *Sonorella baboquivariensis cossi* Miller and the endodontontid *Discus cronkhitei* (Newcomb). *Sonorella* was occasionally observed in the morning actively foraging on the surface, but *Discus* was only seen lying dormant in sheltered areas. Forty individuals of *Sonorella* were found in 21 quadrats, while 59 *Discus* inhabited 32 quadrats. Rocks were replaced and all snails returned to the quadrats after sampling.

The multivariate analytical methods I used will be briefly described by example. Each of my 129 sample sites can be imagined as a point plotted in five dimensional space, where the axes are measures of the five environmental variables. Using factor analysis, new axes (factors) running through this five dimensional space can be described. In principal component analysis, a type of factor analysis, the axes are generally uncorrelated with one another and chosen to maximize the variance explained. Thus if correlation among the original variables is high, the data can be expressed in much fewer than 5 axes with little loss of information. In discriminant function analysis, the axes chosen are those that maximize the separation of two or more groups of points. Thorough discussions of these techniques are given by Morrison (1967), Harman (1967), and Pielou (1969).

RESULTS AND DISCUSSION

Principal component analysis is a useful tool for simplifying complex data sets and identifying latent regularities. It has been used extensively in vegetational studies (e.g., Austin, 1968; Peet & Loucks, 1977) where each collection site is characterized by its species composition. I applied principal component analysis based on the correlation matrix of the five environmental variables

TABLE 2. Correlations among environmental variables. Elements of the matrix above the diagonal are simple correlation coefficients, while those below the diagonal are partial correlation coefficients.

	Altitude	Aspect	Angle	Substrate	Cover
Altitude	1.00	−.236**	.177	−.026	.000
Aspect	−.192*	1.00	−.306**	−.085	−.097
Angle	.104	−.313**	1.00	−.268**	−.196*
Substrate	−.026	−.085	−.200*	1.00	.795**
Cover	.023	−.037	.011	.780**	1.00

*Significant at the 95% confidence level.
**Significant at the 99% confidence level.

(BMDP4M, Dixon, 1977) to the 129 sample sites. Factors were rotated orthogonally to maximize the variance.

Both simple and partial correlation coefficients (all other variables held constant) are presented in Table 2. There is a very high positive correlation between cover and substrate, demonstrating that those sites with high vegetational coverage tend to have dirt and humus below. There is also an inverse correlation between substrate and slope angle, reflecting the tendency of dirt and humus to collect in flat areas and the tendency for rocks to be exposed on steeper slopes. The correlation between cover and slope angle disappears in the partial correlation analysis, suggesting that this correlation is secondary to the one between substrate and slope angle. The high correlations between slope angle and slope aspect, and between slope aspect and altitude reflect peculiarities of Arch Canyon. The canyon's north-facing slope is dissected by several steep washes, and at high elevations the canyon itself steepens and turns toward the south making south-facing sites rare. Hence higher elevations and higher slope angles both tend to have lower (more northerly) slope aspects.

Two principal components had eigenvalues greater than one, and together they accounted for 67.5% of the total variance. The factor loadings on these two principal components (PC's) are presented in Table 3, and the 129 sample sites are plotted by their factor scores in Fig. 1. Notice that substrate and cover are very highly loaded on PC 1 and relatively unimportant in PC 2, while slope aspect and altitude are highly correlated with PC 2 but not with PC 1. Fig. 1 shows that snail-containing sites had uniformly high PC 1 scores but occupied the range of PC 2. This suggests that snails can be found at almost all elevations and all slopes within the canyon, but they localize at places with high vegetational cover and humus.

To verify this result, I employed stepwise discriminant function analysis (BMDP7M, Dixon, 1977) on the 41 snail-containing sites versus the 88 sites without snails. Strahler (1978) used a similar technique to investigate the relationship between woody plant species and underlying rock type. Percent cover and substrate were the only two variables with any power to identify snail-containing sites, and once the cover variable was entered into the function, the discriminating power of substrate was rendered insignificant. Table 4 shows the

TABLE 3. Factor loadings on the first 2 principal components in analysis of 129 sample sites.

	PC 1	PC 2
Altitude	−.123	−.630
Slope aspect	.013	.799
Slope angle	−.489	−.579
Substrate	.924	−.176
Cover	.901	−.231
Eigenvalue	1.92	1.45
% variance explained (cumulative)	38.4	67.5

TABLE 4. F ratios for environmental variables in discriminant function analysis of snail presence.

	At outset of stepwise procedure	After first step
Vegetational cover	52.27	entered
Substrate	42.84	2.62
Slope angle	3.76	.76
Slope aspect	3.38	2.14
Altitude	1.42	1.99
Degrees of freedom	1 and 128	1 and 127

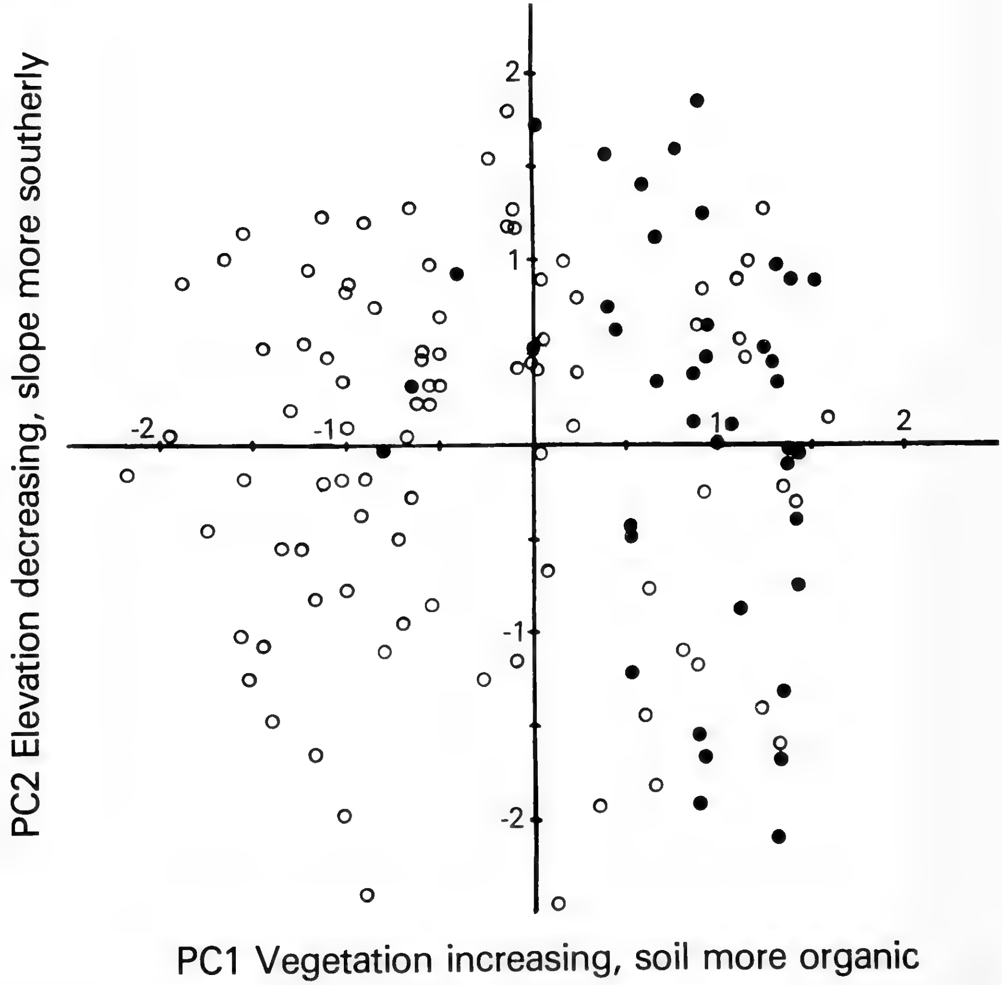

FIG. 1. Principal component analysis of environmental variables at 129 sample sites. Darkened points are samples that contained snails.

F ratios for the five variables at the outset of the discriminant function analysis and the F ratios of the four remaining variables after "cover" was entered in the first step of the procedure. On the basis of vegetational cover alone snail presence can be predicted in all sites with 78% accuracy (Fig. 2). Altitude, slope angle, and slope aspect were not demonstrated to have any significant influence on the presence of snails at small sites in Arch Canyon.

Stepwise discriminant analysis was also used to identify differences in the distributions of *Sonorella* and *Discus* within the canyon. The occurrence of each species in any particular site was weighted by its abundance at that site. Discriminant analysis has been used widely in studies of community structure (M'Closkey, 1976; Dueser & Shugart, 1978). Green (1971, 1972) used multiple discriminant analysis to determine the factors important in separating the habitats of 10 species of freshwater bivalves. Harner & Whitmore (1977) have proposed methods to calculate niche overlap from discriminant function scores. They used the program BMDO7M to rank 10 environmental variables by their ability to discriminate between bird species pairs.

I obtained a discriminant function significant at the 99% confidence level (F=13.4, d.f.= 2, 97) capable of classifying 72% of the cases correctly. The F ratios for variables not in-

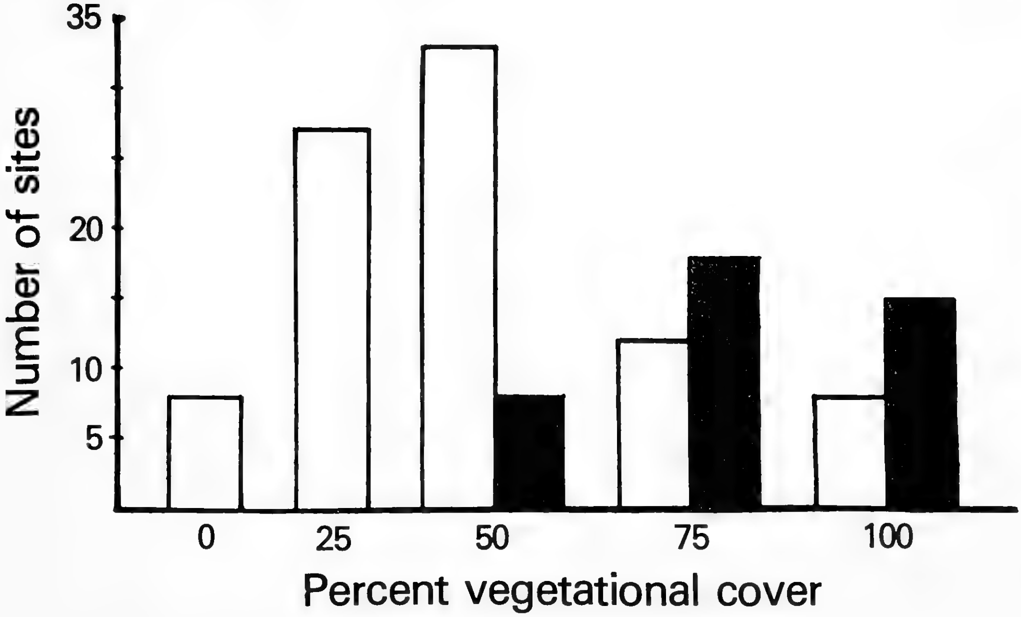

FIG. 2. Histogram showing the 129 sample sites categorized by their percent vegetational cover. Snail-containing sites are darkened.

TABLE 5. F ratios in discriminant function analysis of *Discus* and *Sonorella* distribution.

	At outset of stepwise procedure	After first step	After second step
Slope angle	20.25	entered	entered
Substrate	10.71	5.56	entered
Slope aspect	8.13	.27	.41
Altitude	5.51	.95	.40
Vegetational cover	.11	.08	.92
Degrees of freedom	1, 99	1, 98	1, 97

cluded in the function are listed for each step in Table 5. Slope angle was the best discriminator between the two species. Fig. 3 shows that *Sonorella* is found on significantly steeper slopes than *Discus* ($P < .001$, Mann-Whitney U test). One likely explanation for the differing abundances of the two species on different slope angles involves the great difference in their sizes. An average *Sonorella* has a shell 19 mm in diameter while a typical *Discus* has a shell only 4 mm across. Thus *Discus* can find adequate shelter during dry periods in interstitial spaces of the humus that collects in flat areas, but *Sonorella* requires rocks more common on steeper slopes. In the course of this survey, individuals of *Sonorella* were indeed found most frequently under rocks, while *Discus* was most often encountered while sifting through deep, loosely packed humus.

Table 5 shows that the substrate variable also had significant discriminating power even after "angle" was entered into the function (*Discus* scores higher, as expected). It is important to notice, however, that the cover variable had no discriminating power, even though cover and substrate are very highly correlated (Table 1). Cover, it has been demonstrated, is a good predictor for the presence of both species. But apparently *Discus* is to be expected where the vegetation grows in flat areas so that humus accumulates, while *Sonorella* is most common in the few places where vegetation grows on steep-

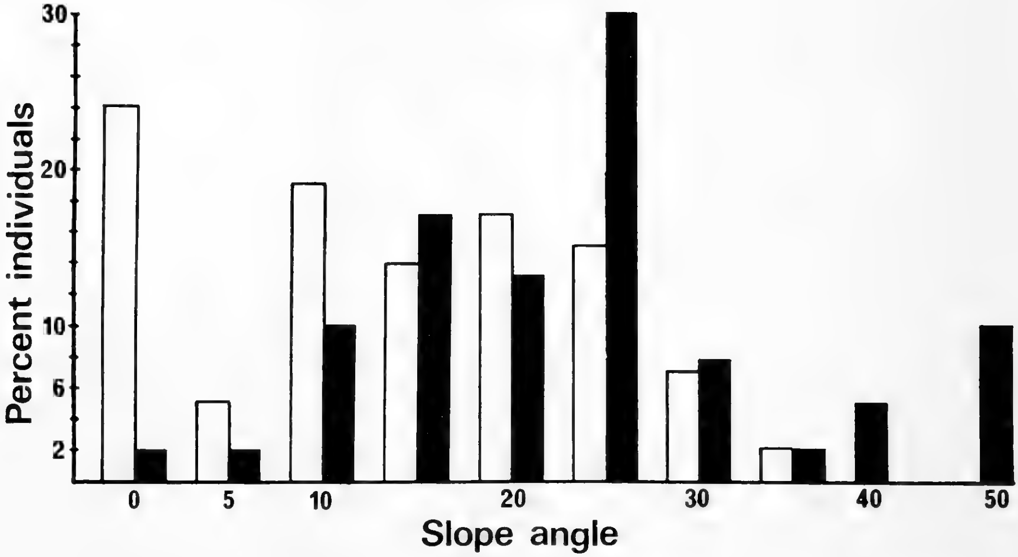

FIG. 3. Abundance of *Discus* and *Sonorella* at sites of varying slope angle. *Sonorella* is darkened and *Discus* is left unshaded.

er slopes and humus does not collect, leaving rocks and cobble exposed. Differences of this nature decrease the probability that individuals of different species occur at the same site, and thus could reduce competition.

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RESUMEN

ANALYSIS MULTIVARIADO DE LA DISTRIBUCION DE LOS CARACOLES DEL DESIERTO EN UN CAÑON DE ARIZONA

Robert T. Dillon, Jr.

El análisis discriminatorio múltiple y el análisis de componentes principales resultaron bastante útiles para interpretar la distribución de dos especies de caracoles en un cañón desértico. En sitios pequeños, elegidos al azar, es posible predecir con precisión la presencia y abundancia de las especies a partir de las siguientes variables ambientales: altitud, ángulo de la pendiente, orientación de la pendiente, porcentaje de cobertura vegetal y tipo de substrato. Aunque la correlación entre las variables ambientales fue alta, la cobertura vegetal explicó la mayor parte de la varianza en la presencia de las especies. La orientación y ángulo de la pendiente, y la altitud, no afectan la presencia de las especies cuando se les considera en forma independiente de la vegetación. Las dos especies que viven en el cañón, *Discus cronkhitei* y *Sonorella baboquivariensis cossi,* difieren significativamente en sus preferencias en substrato y ángulo de la pendiente. Se sugiere que *Sonorella* fue encontrada más frecuentemente en pendientes rocosas inclinadas debido a que requiere la protección de las rocas. *Discus,* una especie mucho más pequeña, puede encontrar abrigo adecuado en humus suelto y así habitar en pendientes más leves, donde el humus se puede acumular.

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MOLLUSCAN DISTRIBUTION PATTERNS ON THE CONTINENTAL SHELF OF THE MIDDLE ATLANTIC BIGHT (NORTHWEST ATLANTIC)

David R. Franz[1] and Arthur S. Merrill[2]

ABSTRACT

A zoogeographic analysis of the inner continental shelf fauna of the Middle Atlantic Bight (Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, U.S.A.) is presented based on the geographical and depth distributions of 184 mollusk species collected by the R/V DELAWARE II in 1960 (Cruise 60-7). The Middle Atlantic Bight fauna contains fewer than 4% of species endemic to this zone, and is composed of a mixture of northern and southern species. The former comprises two faunal groups: an *Arctic-Boreal* group containing species which extend northward into arctic waters, and a *Boreal* group, which reaches northern limits near the south of Labrador. Species of both faunal groups reach their southern limits in the Middle Atlantic zone.

The faunal component of predominantly southern species is designated the *Transhatteran* faunal group, a term which emphasizes the capability of these species to transgress the ecological barrier of Cape Hatteras.

Many arctic-boreal and boreal species exhibit *submergence* south of Cape Cod, i.e. they track cold isotherms into the deeper shelf waters. Species showing submergence tend to be amphiatlantic in distribution. Endemic boreal species generally do not show submergence in the Middle Atlantic Bight, and are thus more tolerant of warm summer temperatures which characterize the inshore waters of this area. Transhatteran species do not show submergence, although they are variable in their depth distributions.

INTRODUCTION

The molluscan fauna of the Middle Atlantic Bight of the United States is reasonably well known, and Coomans (1962) has recently reanalyzed this fauna in the framework of provincial zoogeography. The continental shelf zone bounded on the north by Cape Cod, Massachusetts, and on the south by Cape Hatteras, North Carolina, is the Virginian Subprovince (Dana, 1853; Johnson, 1934; Hazel, 1970) which, together with the Carolinian Subprovince to the south, comprise a major molluscan province, the Transatlantic Province (Woodward, 1851–1856; Johnson, 1934). The molluscan fauna of the Virginian Subprovince lacks a significant endemic component (Coomans, 1962) and is best characterized as a zone supporting a mixed fauna of cold-tolerant "boreal" species, which range southward into the zone, and warm-tolerant southern ("Transatlantic") species which extend northward into the zone (Stephenson & Stephenson, 1954; Coomans, 1962; Powell & Bousfield, 1969).

The marine environment of the shallow continental shelf of the Virginian zone is subjected to extreme seasonal temperature fluctuations (Sanders, 1973) which are partially ameliorated at increasing depth. Consequently species which are eliminated by temperature conditions in the shallow shelf—either by seasona extremes or by severe thermal instability—may survive in deeper water. For "boreal' species, which extend southward into the Virginian Subprovince, this phenomenon has been called *boreal submergence* (Ekman, 1953). Likewise, warm-water species which extend northward into the Virginian zone survive by virtue of warm summer conditions which prevail over the inner shelf and estuarine areas. The successful co-occurrence of both warm- and cold-tolerant species is made possible by their respective abilities to reproduce during the summer and winter periods, and to survive extreme temperatures during their non-reproductive periods (Hutchins, 1947).

In this paper we propose an operational classification of the molluscan fauna of the Virginian Subprovince based on the analysis of the extended geographical ranges and maximum depth limits of species. Depth distribution patterns in the study area are presented

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and analyzed for selected species within each of the faunal groups. Our data indicate that faunal groups which share similar geographic ranges may also share similar patterns of depth distribution in the Middle Atlantic Bight. Both the geographical ranges and depth distribution patterns reflect differing thermal adaptive modes, which may be correlated with the different origins of each of the faunal groups.

METHODS AND MATERIALS

In May, 1960, the Bureau of Commercial Fisheries[3] initiated a cruise of the R/V DELAWARE II (Cruise 60-7) in the Middle Atlantic Bight from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. One hundred and thirteen stations were sampled at depths of 26 to 146 m (see Merrill & Franz, in preparation, in which the distributions of all invertebrate species are graphed along with station locations and depths). While the primary purpose of the cruise was to collect data on the distribution and abundance of sea scallops, *Placopecten magellanicus* (Gmelin), samples of other macroinvertebrates were taken at each station. Additionally, a 76.2 cm (30 in.) Digby Dredge with 12.7 mm (½ in.) liner was towed at all stations to collect biota associated with the scallops. These collections were frozen on board, later thawed, sorted, identified and tabulated ashore as time allowed.

A total of 184 species of mollusks identified from these collections were used in the following analysis. In addition, four species of thecosomatous pteropods were collected. Some material collected in deeper waters included non-living mollusks which today live in estuarine and nearshore waters. These have been determined to be of Holocene age, deposited during a period when sea levels were lower than today (see papers by Merrill, Emery & Rubin, 1965; Merrill, Davis & Emery, 1978). Range extensions of mollusks based on this cruise were published recently (Merrill, Bullock & Franz, 1978).

There are several advantages in basing a zoogeographic analysis on data from a single cruise rather than on distributional data published in general works such as Abbott (1954, 1974) or faunal compilations such as Dall (1889b) or Johnson (1934). In the present study, our analysis is based on a list of 184 taxa, all but 8 of which were identified to species. In addition to few taxonomic problems, we were not confronted with the problem of dealing with large numbers of poorly known species with questionable distributional records. The main advantage, however, lies in the accurate depth and latitudinal information which, in the present study, are combined to produce depth distributions for selected species among several zoogeographic groups. However, there are limitations in the use of cruise data. In this study, shallow stenobathic and/or intertidal species were either not represented or under-represented because no dredge samples were taken at depths less than 26 m. Likewise, some small species were probably not collected due to the systematic sampling scheme, and the use of a dredge liner with relatively large screen size of 12.7 mm. However, the near-shore component of the molluscan fauna has been easier to acquire in the past so that these species and their patterns of distribution are better understood. Published information on the near-shore distribution of species have been combined with the off-shore results of the present study to provide a reliable summary of the depth and latitudinal limits of many species inhabiting the Middle Atlantic Bight. When grouped into zoogeographic categories, the few inaccuracies which may be present do not significantly detract from the general conclusions discussed below.

In determining distribution, we have consulted the usual literature of which the major sources are indicated by an asterisk in the References section. This information has been used to supplement our own work in the Middle Atlantic area. Thus, the DELAWARE II Cruise 60-7, on which this report is based, yielded close to 200 mollusk species (including cephalopods) from the Middle Atlantic Bight. At the same time, transect studies undertaken off South Carolina produced an additional 300 species. As a result of these studies, over 100 new latitudinal ranges and some 20 significant new depth ranges have been added to the literature (Merrill & Petit, 1965, 1969; Merrill, Bullock & Franz, 1978). Additional information relative to the critical area of Cape Hatteras was obtained through cooperation with colleagues at Duke University Marine Laboratory and the Institute of Marine Sciences of the University of North Carolina, Morehead City, North Carolina (cf. Cerame-Vivas & Gray,

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[3] Now the National Marine Fisheries Service.

TABLE 1. Zoogeographic composition of the 184 species collected by the R/V DELAWARE (Cruise 60-7).

Appendix		No.	%
1	Northern species with distributions predominantly north of Cape Cod, MA	42	22.8
2	Species *endemic* to the Middle Atlantic zone	7	3.8
3	Southern species with northern limits north of Cape Cod	22	12.0
4	Southern species with northern limits at or south of Cape Cod	60	32.6
5	Southern species with northern limits in NC	38	20.7
6	Cosmopolitan and/or eurybathic species	7	3.8
7	Unidentified species including specimens too worn or fragmented to be identified	8	4.3
	Totals	184	100.0

1966, for distributional patterns of shelf invertebrates north and south of Cape Hatteras and Porter (1974) for distribution patterns of invertebrates in North Carolina coastal waters). The collections at the National Museum of Natural History (USNM) and the Museum of Comparative Zoology (MCZ) at Harvard University have been consulted as well as the extensive research collections of the National Marine Fisheries Service at Woods Hole, Massachusetts. The mollusk materials collected during the DELAWARE II Cruise 60-7 have been accessioned into the mollusk collection at the MCZ.

RESULTS

The general geographical and depth distributions of the 184 species are shown in Appendices 1–7 in the following zoogeographic categories: 1—Northern species with southern limits north of Cape Hatteras, NC; 2—Species endemic to the Middle Atlantic Bight; 3—Southern species ranging south of Cape Hatteras with northern limits north of Cape Cod, MA; 4—Southern species with northern limits in the Middle Atlantic Bight at or south of Cape Cod; 5—Southern species with northern limits in North Carolina; 6—Cosmopolitan and/or eurybathic species; 7—Unidentified species.

The relative proportions of these zoogeographic groups are shown in Table 1. About 23% of the Mollusca are northern species which range predominantly north of Cape Cod, but which reach their southern limits in the Middle Atlantic Bight. Only seven species (< 4%) are endemic to the Middle Atlantic zone between Cape Cod and Cape Hatteras. Roughly 12% is composed of warm-water species with northern limits north of Cape Hatteras (Appendix 3); and 33% are southern species with northern limits in the Middle Atlantic Bight at or south of Cape Cod (Appendix 4). The last major component is a group of warm-water species, comprising 21%, which reach their northern limits in North Carolina.

DISCUSSION

Zoogeographic Categories and Extended Geographic Ranges

The faunal analysis shown in Table 1 indicates that the shelf Mollusca of the Middle Atlantic Bight form two major components: (a) predominantly northern species whose ranges extend south of Cape Cod, and thus into the Middle Atlantic zone (Appendix 1); (b) predominantly southern species which range north of Cape Hatteras. Most of the latter reach their northward limits at or south of Cape Cod although a significant proportion extends further northward, to the Gulf of St. Lawrence or Newfoundland (Appendices 3 and 4).

Only seven species collected in this survey appear to be endemic to the Middle Atlantic zone (Appendix 2). In some cases, the taxonomic status is uncertain, and it is likely that the ranges of others will eventually be extended by further collecting. Thus, Coomans' (1962) contention that the "Virginian" subprovince (the coastal zone between Cape Cod and Cape Hatteras) lacks a zoogeographically significant level of endemic mollusks is supported by this study.

Analysis of the extended ranges of the northern species (Appendix 1) in the northwest Atlantic indicates that this group contains two elements: *boreal* species, which reach their northern limits in Labrador or south; and *arctic-boreal* species, which extend poleward into arctic waters (as defined by Dunbar, 1954). Of the species listed in Appendix 1, approximately 69% are boreal, and 31% arctic-boreal.

Although the precise northern limits of some species are poorly known, it is likely that the actual poleward limit of many boreal species is related to the interface between arctic and subarctic water masses as defined by Dunbar (1954). These thermal boundaries occur on the southeast coast of Baffin Island and in the region of the Davis and Hudson Straits. Complex thermal and other ecological barriers operate in these areas to affect the poleward distribution of many species. These include maximum summer temperatures of 2–8°C, and extremely reduced summer salinities in shallow water due to the melting of ice.

Analysis of Appendix 1 shows that the arctic-boreal and boreal components differ quantitatively in their extended geographical distributions. About 85% of arctic-boreal species are amphiatlantic (occurring on both sides of the North Atlantic) as compared to only 21% of boreal species. Furthermore, nine of the 13 arctic-boreal species (69%) also occur in the North Pacific as compared with only one of 28 (3.5%) of boreal species. These differences in northern species suggest differences in paleobiogeography, and are discussed in a companion paper (Franz & Merrill, 1980).

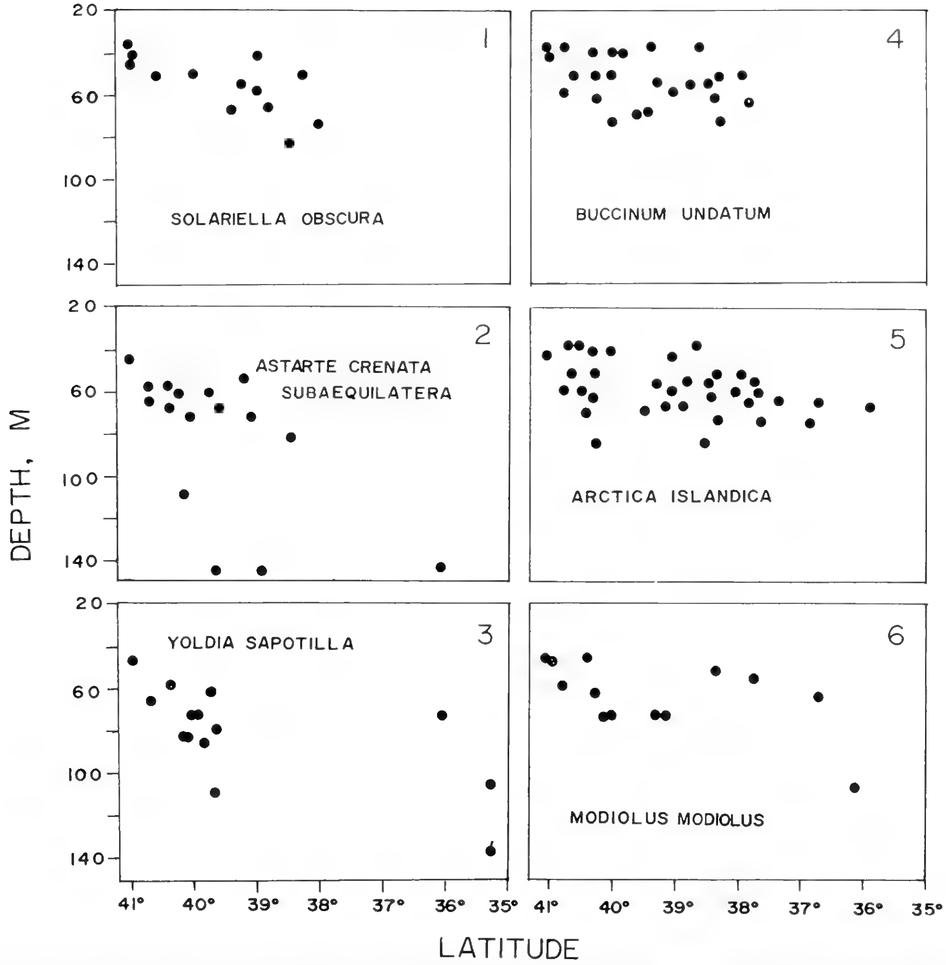
The fauna of group (b), southern species with northern limits north of Cape Hatteras, is designated *transhatteran* in recognition of the ability of these species to transgress the Cape Hatteras thermal barrier, and to maintain populations in the thermally unstable shallow waters of the Northwest Atlantic. As seen in Appendix Groups 3 and 4 of Table 1, these are species which range southward to Florida, the Gulf of Mexico, and in many cases into the Caribbean and to Brazil. This is essentially an endemic temperate/subtropical fauna. Thus, it is evident that transhatteran species provide the major endemic component in the geographical zone between Cape Cod and Florida, i.e. the "Transatlantic Province" of Woodward (1851–56) and Johnson (1934). The two terms are unambiguous however. The Transatlantic faunal province is defined as a geographical zone (Hazel, 1970); the transhatteran fauna refers to a group of species unique in their endemicity and in their distribution across the Cape Hatteras faunal barrier.

Depth Distributions

The known depth ranges of the 184 species collected by the R/V DELAWARE are included in Appendices 1–6. Depth ranges, as such, convey only limited information on depth preferences of benthic species, so that generalizations based on these data must be considered tentative at best. Table 2 shows the depth distributions for each of the faunal groups represented by Appendices 1, 3, 4, and 5. For each faunal group the percentage of species with maximum depths falling within five categories from < 10 m to > 200 m are listed. These data suggest several tentative generalizations. A large majority (80%) of the northern species of Appendix Group 1 (Table 2) have depth ranges which extend into deeper waters, i.e. greater than 100 m. Thus, the capacity of this fauna, as a whole, to live in relatively deep waters is correlated with the amphiatlantic characteristic of the group, and especially the arctic-boreal component as noted above. Furthermore, the combination of

TABLE 2. Depth distribution of faunal groups.

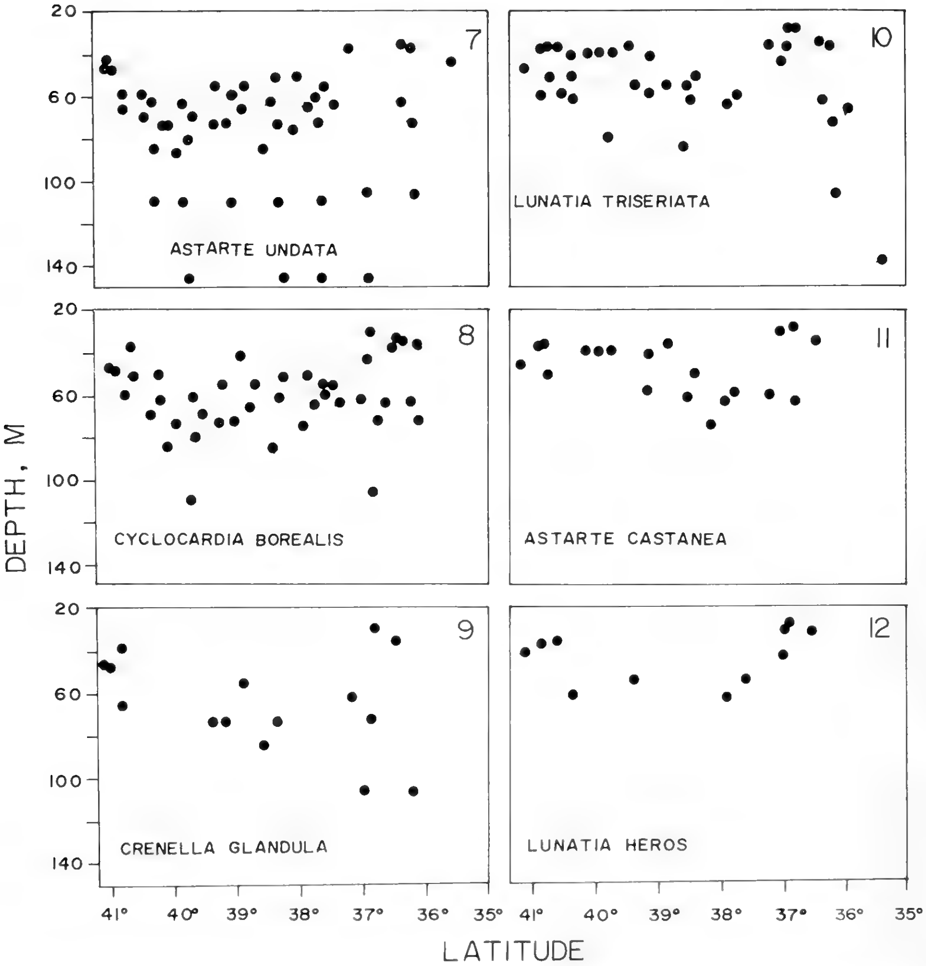
Appendix	1		3		4		5	
	Northern species		Southern species extending north of Cape Cod		Southern species extending to or south of Cape Cod		Southern species extending north to NC	
Maximum depth (m)	No.	%	No.	%	No.	%	No.	%
10		0	4	21.0	1	1.7		0
10–50	3	7.1	4	21.0	12	21.0	4	10.8
51–100	5	11.9	7	36.8	14	24.6	8	21.6
101–200	16	38.0	1	5.3	11	19.3	16	43.2
200+	18	42.8	3	15.8	19	33.3	9	24.3
Totals	42		19		57		37	



FIGS. 1–6. Depth distribution patterns of six species collected from the Middle Atlantic Bight. All of these species are predominantly northern in distribution but extend south of Cape Cod into the Middle Atlantic zone. All show *submergence* as indicated by increasing minimum depth with decreasing latitude. All points based on living material. Figs. 1–3 (*Solariella obscura, Astarte crenata subaequilatera, Yoldia sapotilla*) are arctic-boreal; Figs. 4–6 (*Buccinum undatum, Arctica islandica, Modiolus modiolus*) are boreal. All but *Yoldia sapotilla* are amphiatlantic.

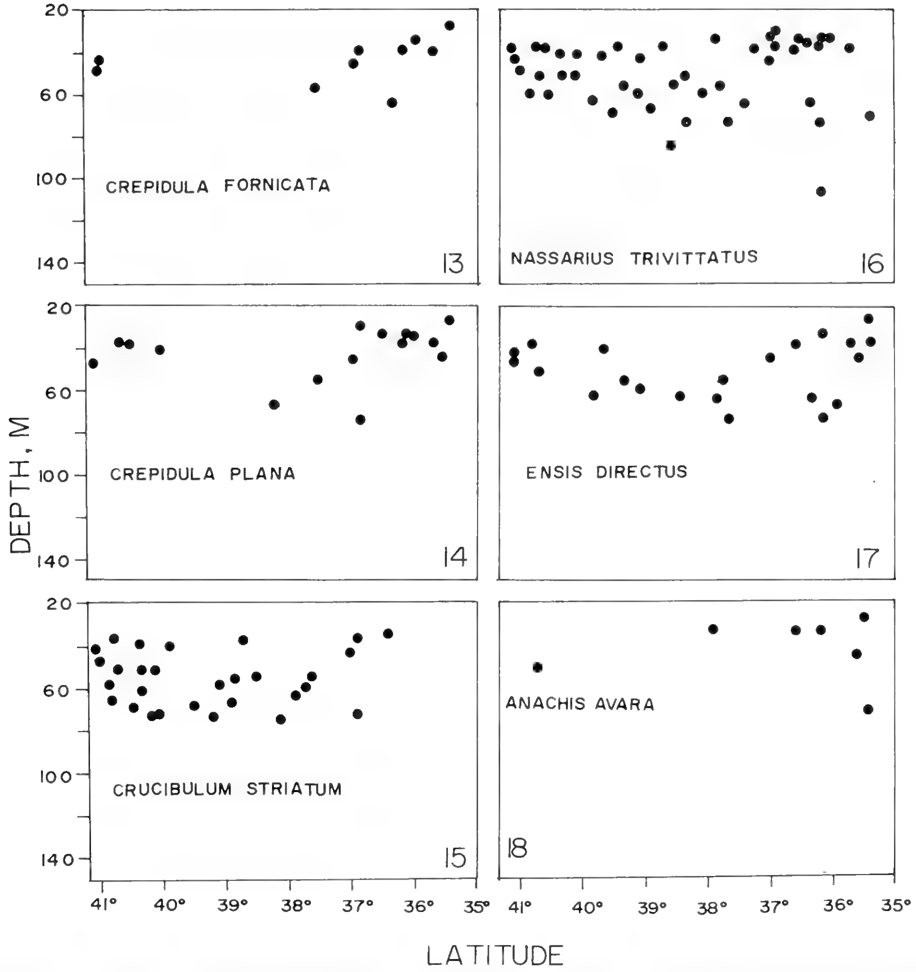
northern geographical distributions and the capacity to live at greater depths suggests that these species should occur in deeper waters farther south, a phenomenon referred to by Ekman (1953) as *submergence* (boreal and tropical submergence). Submergence is usually considered to reflect a degree of cold stenothermy, at least to some critical life function.

A large proportion (67%) of the warm temperate/subtropical species represented in Appendix Group 5 (Table 2) also have maximum depth ranges greater than 100 m. Thus, this group and the arctic-boreal faunal group, both of which extend only marginally into the middle Atlantic zone, are able to do so by virtue of their capacities to live in deeper water. The latter (Appendix Group 1 species in Table 2) extend into the Middle Atlantic Bight by tracking cold isotherms into deeper water; the former (the warm-temperate/subtropical species of Appendix Group 5, Table 2) extend northward by tracking warm isotherms on the continental shelf off north Carolina. Winter temperatures inshore north of Cape Hatteras are too cold for the survival of such species.



FIGS. 7–12. Depth distribution patterns of six endemic boreal species collected from the Middle Atlantic Bight shown in order of decreasing depth limits: Fig. 7 *Astarte undata,* Fig. 8 *Cyclocardia borealis,* Fig. 9 *Crenella glandula,* Fig. 10 *Lunatia triseriata,* Fig. 11 *Astarte castanea,* Fig. 12 *Lunatia heros.* The first three species range northward to Labrador; the remainder reach northern limits at or south of the Gulf of St. Lawrence. Note the absence of submergence in the Middle Atlantic zone.

The dominant fauna of the Middle Atlantic zone is represented by Appendix Groups 3 and 4 (Table 2). As noted above, both are transhatteran in distribution. The Group 3 species are found predominantly in shallow water, with 42% restricted to less than 50 m and 79% generally found in waters less than 100 m. The combination of transhatteran zoogeography and shallow depth distributions suggest that the capacity of this faunal group to range north of Cape Cod is correlated with warm summer temperatures which develop in the shallow bays and estuaries of the Gulf of Maine and southeastern Canada (Ganong, 1890). Indeed, this group does contain the highest proportion of shallow sublittoral species (21% with maximum depths less than 10 m—Table 2), and includes the most characteristic estuarine molluscan fauna of the Middle Atlantic and New England regions. Group 4 differs from Group 3 in lacking a large proportion of shallow species; only 21% are restricted to waters less than 50 m. Evidently these temperate shelf species are unable to maintain populations at the cool summer temperatures which develop at their normal depth range north of Cape Cod. As noted earlier, we combine the species of Groups 3



FIGS. 13–18. Patterns of depth distribution of transhatteran species in the Middle Atlantic Bight. The first five species (Figs. 13–17): *Crepidula fornicata, C. plana, Crucibulum striatum, Nassarius trivittatus* and *Ensis directus,* reach northern limits in shallow and estuarine waters north of Cape Cod. The last species (Fig. 18), *Anachis avara,* is restricted to relatively shallow waters south of Cape Cod.

and 4 into a single faunal unit—the transhatteran—of which the Group 3 species can be considered as only the very shallow shelf and estuarine component, i.e. outliers of the main transhatteran fauna, most of which reach northern limits at or south of Cape Cod.

The depth distributions of selected species based on DELAWARE cruise data from the Middle Atlantic Bight are presented in Figs. 1 to 18. Species were selected based on the completeness of available data, and to represent the faunal groups defined above. Figs. 1–6 show the pattern for six northern species selected from Appendix 1. All are widely distributed, cold-water amphiatlantic species, and all show submergence with decreasing latitude. The pattern for *Solariella obscura* is somewhat anomalous in that it was not collected in the deeper stations, although this species has been collected from very deep water (Clarke, 1962). *Astarte crenata subaequilatera* and *Yoldia sapotilla,* are also arctic-boreal with great depth ranges. Submergence is clearly illustrated by the increasing minimal depth of collection with decreasing latitude. The remaining species, *Modiolus modiolus, Buccinum undatum* and *Arctica islandica,* are predominantly amphiatlantic boreal in distribution although *M. modiolus* and *B. undatum* are known to extend marginally into arctic waters (Ockelmann, 1958; Macpherson, 1971). In the Middle Atlantic zone, these species are limited to relatively shallow depths, and each shows definite submergence. It is clear that submergence does not necessarily imply wide depth distributions since both *B. undatum* and *A. islandica* are restricted to depths generally less than 100 m in the Middle Atlantic Bight. Thus, the southward distribution of arctic-boreal and boreal species on the shelf depends on their depth limitations. Deep ranging species may occur as far south as Cape Hatteras in the deep shelf (or even further in the case of the eurybathal *Astarte crenata subaequilatera*). Shallow boreal species such as *Modiolus modiolus* and *Buccinum undatum* are constrained in their seaward distribution by unsuitable depths (or depth-related ecological factors) and shoreward by critical warm summer temperatures.

Figs. 7–12 illustrate patterns of depth distribution of six *endemic* boreal species (also from Appendix 1) placed in order of decreasing depth limits in the Middle Atlantic zone. The first three, *Astarte undata, Cyclocardia borealis,* and *Crenella glandula,* range north to Labrador; the remaining three, *Lunatia triseriata, Astarte castanea,* and *Lunatia heros,* reach northern limits in Nova Scotia and/or the Gulf of St. Lawrence. Note that none of these endemic boreal species exhibits marked submergence in the study area, as compared with the amphiatlantic species shown in Figs. 1 to 6. This implies that the endemic boreal species are less sensitive to warm summer nearshore temperatures in the Middle Atlantic Bight.

The capacity of certain endemic boreal species to range significantly farther poleward than others is puzzling. As more data become available on the depth, thermal and latitudinal limits of boreal endemic species, it may be possible to determine if the northward extension of species is correlated with its depth range in the Middle Atlantic Bight. Shallow species adapted to the thermal environment of the shallow shelf of the Middle Atlantic Bight may be constrained by cold temperatures which occur at comparable depths in and north of the Gulf of St. Lawrence. Alternately, relatively eurybathal species, adapted to the variable thermal environment encountered over a greater depth range in the Middle Atlantic shelf, may be better adapted to extend their ranges northward on the Canadian Atlantic shelf.

Figs. 13–18 illustrate the patterns of depth distribution for six transhatteran species. The first five: *Crepidula fornicata, C. plana, Crucibulum striatum, Nassarius trivittatus,* and *Ensis directus,* range north of Cape Cod (see Appendix 3). Note that each occurs in waters of moderate to shallow depths (< 85 m) and, indeed, these five species are examples of transhatteran forms which extend north of Cape Cod in shallow bays, estuaries and coastal waters. The last species, *Anachis avara,* reaches its northern limits near Cape Cod (Appendix 4). An epibenthic predator restricted to relatively shallow depths (< 90 m), its northern range limits may be determined by cold summer temperatures on the shallow continental shelf north of Cape Cod.

None of the other species of Appendix 4, i.e. transhatteran species with northern limits at or south of Cape Cod, was collected in enough abundance, or over a wide enough latitudinal range, to plot in the form shown in these figures. This may seem surprising since many of the species listed in Appendix 4 are important components of the fauna of the Middle Atlantic Bight (e.g. *Busycon canaliculatum, B. carica, Mitrella lunata, Nassarius vibex, Anadara ovalis, A. transversa, Lyonsia hyalina, Macoma tenta, Tellina versicolor,* etc.). However. it must be remembered that Cruise 60-7 was primarily initiated to survey populations of sea scallops in commercial quantities. For this reason, collecting stations were restricted to sites deeper than 26 m since sea scallops are largely prevented from occupying shallow sublittoral habitats due to summer warming. North of Cape Hatteras, the species listed above are most abundant in shallow inshore waters and would consequently be underrepresented in the R/V DELAWARE samples. Not surprisingly, many of the species of Appendix 4 appear more frequently in the DELAWARE cruise stations from the southern end of the Middle Atlantic zone. Thus, as more data become available, we may find in these species a depth distribution pattern more appropriately characterized as "boreal emergence," i.e. a tendency for these species to be restricted to shallower waters north of Cape Hatteras.

The transhatteran faunal groups of Appendices 3 and 4 comprise the major molluscan component of the American Atlantic coast. This fauna is complex and ancient and undoubtedly contains a diversity of adaptive strategies as regards thermal requirements, thermal tolerance limits and depth distributions. Depth distribution patterns are not always related to temperature; and we are rarely able to completely partition the various environmental factors affecting the depth distribution of a species. However, the critical role of temperature in structuring depth patterns is indisputable in many species, and probably significant in most. We believe that as more depth distribution data become available over the entire latitudinal ranges of continental shelf species, we will have a valuable tool for interpreting and evaluating the faunal distinctions proposed in this and earlier papers.

Molluscan zoogeographers have rarely considered the origins of faunal groups as major determinants of distribution *within* marine faunal provinces. It is possible that groups of species with similar paleogeographical histories may share similar physiological requirements and tolerances—which may be reflected in similar distribution patterns. For example, our data show that the amphiatlantic boreal species are more vulnerable to warm summer temperatures—as indicated by boreal submergence—than are the endemic boreal species. Perhaps this is related to the origin of the endemic component from Cenozoic American ancestors, with long histories in the Middle Atlantic zone. The amphiatlantic boreal species, on the other hand, may be derived from ancestors in the eastern Atlantic or North Pacific—boreal regimes of much less thermal variability than the Northwest Atlantic. The relationships between the distribution patterns and possible origins of faunal groups in the Northwest Atlantic are discussed further in a subsequent paper (Franz & Merrill, 1980).

CONCLUSIONS

Based on an analysis of the geographical and depth distributions of 184 molluscan species collected by the R/V DELAWARE II Cruise 60-7 in the Middle Atlantic Bight, the following generalizations are suggested:

(1) Fewer than 4% of the species appear to be endemic to the Middle Atlantic zone; and the percentage may well be lower should their taxonomic status and distribution be modified by further study.

(2) The fauna contains two major groups of species. The first is made up of predominantly northern species whose ranges extend south of Cape Cod, and thus into the study area. This group contains two components—*arctic-boreal* and *boreal*—which differ in their latitudinal limits, and in the proportions of amphiatlantic and endemic species.

(3) The second major group consists of predominantly southern species which range north of Cape Hatteras, and thus into the Middle Atlantic zone. This fauna is designated the *transhatteran* fauna in this paper.

(4) A significant proportion of transhatteran species reach their northern limits north of Cape Cod, and occur northward to the Gulf of St. Lawrence. These are mostly shallow stenobathic forms which live in shallow bays and estuaries.

(5) The majority of transhatteran species reach northern limits at or south of Cape Cod.

(6) Many of the arctic-boreal and boreal species of the northern fauna show *submergence* in the Middle Atlantic zone, i.e. they "track" cold isotherms into the deeper shelf waters of the Middle Atlantic Bight. Species showing submergence tend to be amphiatlantic in distribution. Boreal species endemic to the Northwest Atlantic do not show submergence in the Middle Atlantic Bight. These differences are related to the ability of species to tolerate summer temperatures in the shallow shelf zone, and may reflect differences in the origins of the endemic and amphiatlantic faunal groups.

(7) Transhatteran species, while variable in depth distributions, do not show submergence in the Middle Atlantic Bight. As the major faunal element of the Transatlantic faunal province, transhatteran species show great diversity in depth and thermal tolerance patterns. Further analysis of the depth distribution patterns of these species over their entire geographical ranges may reveal interesting zoogeographical patterns.

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APPENDIX 1. Northern species (distributed primarily north of Cape Cod).

Species	Geographical range in the NW Atlantic	Extended range*	Faunal group*	Depth range (m)	Time of appearance
Alvania areolata Stimpson, 1851	Gulf of St. Lawrence to NJ	—	B	18-238	Pleistocene
Buccinum undatum Linné, 1758	Frobisher Bay to VA	AA	B	1-73	Pliocene
Colus islandicus (Gmelin, 1791)	Cumberland Sound to off VA	AA, NP	AB	37-3107	Pleistocene
Colus pubescens (Verrill, 1882)	Arctic Canada to SC	AA	AB	33-1170	
Colus pygmaeus (Gould, 1841)	Gulf of St. Lawrence to NC	—	B	2-1170	Pleistocene
Colus stimpsoni (Mörch, 1867)	Labrador to NC	—	B	1-2000	Pleistocene
Cylichna linearis Jeffreys, 1867	Off VA	AA	B	?	
Lunatia heros (Say, 1822)	Gulf of St. Lawrence to NC	—	B	1-435	Miocene
Lunatia pallida (Broderip & Sowerby, 1829)	Pond Inlet (Baffin Island) to NC	AA,NP	AB	10-2275	Pleistocene
Lunatia triseriata (Say, 1826)	Gulf of St. Lawrence to NC	—	B	1-115	Miocene
Natica clausa Broderip & Sowerby, 1829	Hudson Strait to NC	AA,NP	AB	1-2800	Pleistocene
Oenopota bicarinata (Couthouy, 1838)	Baffin Island to NY	AA,NP	AB	1-768	
Oenopota harpularia (Couthouy, 1838)	Baffin Island to Rhode Island	AA,BP	AB	11-820	
Philine quadrata (S. Wood, 1839)	Labrador Sea to NC	AA	AB	6-2222	
Polinices immaculatus (Totten, 1835)	Gulf of St. Lawrence to NC	—	B	10-200	Pleistocene
Solariella obscura (Couthouy, 1838)	Hudson Strait to off VA	AA,NP	AB	4-2587	
Turbonilla polita (Verrill, 1872)	Maine to NJ	–	B	37-73	
Anomia squamula Linné, 1758	Labrador to NC	AA	B	1-640	Miocene
Arctica islandica (Linné, 1767)	Newfoundland to NC	AA	B	9-165	Pliocene
Astarte castanea (Say, 1822)	Nova Scotia to NC	—	B	10-120	Pleistocene
Astarte undata Gould, 1841	Labrador to NC	—	B	5-190	
Cerastoderma pinnulatum (Conrad, 1831)	Labrador to NC	—	B	12-200	
Crenella glandula (Totten, 1834)	Labrador to NC	—	B	6-110	
Cyclocardia borealis (Conrad, 1831)	Labrador to NC	—	B	4-457	Miocene
Cyrtodaria siliqua (Spengler, 1793)	Labrador to Rhode Island	—	B	10-165	
Megayoldia thraciaeformis (Storer, 1838)	Greenland to NC	—	AB	10-480	
Mesodesma arctatum (Conrad, 1830)	Labrador to NY	AA,NP	AB	1-12	
Modiolus modiolus (Linné, 1758)	Labrador to off NJ	AA	B	1-146	Pliocene
Musculus niger (Gray, 1824)	Baffin Bay to NC	AA,NP	AB	1-110	
Mya arenaria Linné, 1758	Labrador to NC	AA,NP	B	1-10	Miocene
Pandora gouldiana Dall, 1886	Gulf of St. Lawrence to NC	—	B	1-183	Pliocene
Periploma leanum (Conrad, 1831)	Nova Scotia to NC	—	B	6-30	Pliocene
Periploma papyratium (Say, 1822)	Labrador to NJ	—	B	11-2295	
Pitar morrhuanus Linsley, 1848	Gulf of St. Lawrence to NC	—	B	18-110	
Placopecten magellanicus (Gmelin, 1791)	Labador to NC	—	B	1-200	Miocene
Spisula solidissima (Dillwyn, 1817)	Labrador to NC	—	B	1-130	Miocene
Thracia conradi Couthouy, 1838	Labrador to NY	—	B	3-62	
Thracia septentrionalis Jeffreys, 1872	Greenland to NY	—	AB	9-113	
Xylophaga atlantica Richards, 1942	Gulf of St. Lawrence to NC	—	B	1-3718	
Yoldia limatula (Say, 1831)	Nova Scotia to NC	—	B	2-90	Pliocene
Yoldia sapotilla (Gould, 1841)	Arctic Seas to NC	AA,NP	AB	1-250	
Zirfaea crispata (Linné, 1758)	Labrador to Delaware	AA	B	1-75	Pliocene

*AA = amphiatlantic, i.e. species which occur on both sides of the North Atlantic.
NP = North Pacific, i.e. species which occur both in the NW Atlantic and in the North Pacific. Most such species are also amphiatlantic.
AB = Arctic-boreal (as defined in the text).
B = Boreal (as defined in the text).

APPENDIX 2. Species endemic to the Middle Atlantic zone (Cape Cod to Cape Hatteras).

Species	Geographical range	Depth range (m)
Crenella fragilis Verrill, 1885	VA to NC	110-140
Marginella borealis Verrill, 1884	S. of MA to NC	64-180
Odostomia dealbata (Stimpson, 1851)	MA to NY	6-73
Odostomia smithii Verrill, 1880	S. of MA	155-267
Palliolum subimbrifer (Verrill & Bush, 1897)	MA to NC	37-667
Philippia n. sp.	VA to NC	106-146
Turbonilla elegantula (Verrill, 1882)	MA to NC	26-110

APPENDIX 3. Southern species with northern limits.

Species	Geographical range	Faunal group*	Depth range (m)	Time of appearance
Acteocina canaliculata (Say, 1822)	NS to Fla., Texas & W.I.	TH	1-8	Pliocene
Crepidula fornicata (Linné, 1758)	S.E. Canada to Fla., Texas	TH	1-88	Miocene
Crepidula plana Say, 1822	S.E. Canada to Texas, Brazil, Bermuda	TH	1-66	Miocene
Crucibulum striatum Say, 1824	NS to both coasts of Fla.	TH	6-346	Pliocene
Ilyanassa obsoleta (Say, 1822)	Gulf St. Lawrence to N.E. Fla.	TH	0-2	Pliocene
Nassarius trivittatus (Say, 1822)	Newfoundland to N.E. Fla.	TH	1-90	Miocene
Natica pusilla Say, 1822	Maine to Fla., Gulf states to Brazil	TH	1-130	
Turbonilla interrupta (Totten, 1835)	Gulf St. Lawrence to W.I.	TH	1-35	
Crassostrea virginica (Gmelin, 1791)	Gulf St. Lawrence to Gulf Mex.; W.I.	TH	1-40	Pliocene
Cumingia tellinoides (Conrad, 1831)	NS to Fla.	TH	1-90	Miocene
Ensis directus Conrad, 1843	Labrador to Fla.	TH	1-73	Pliocene
Gemma gemma (Totten, 1834)	NS to Fla., Texas, Bahamas	TH	1-30	
Lucinoma filosa (Stimpson, 1851)	Newfoundland to N. Fla., Gulf States	TH	30-965	Pleistocene
Mercenaria mercenaria (Linné, 1758)	Gulf St. Lawrence to Fla., Gulf Mex.	TH	1-6	Miocene
Mulinia lateralis (Say, 1822)	Maine to N. Fla., Texas	TH	1-8	
Nucula proxima Say, 1822	NS to Fla., Texas; Bermuda	TH	1-90	Miocene
Petricola pholadiformis (Lamarck, 1818)	Gulf St. Lawrence to Texas; S. to Uruguay	TH	0-20	Pliocene
Tellina agilis Stimpson, 1857	Gulf St.Lawrence to GA	TH	1-88	Pliocene
Thyasira trisinuata Orbigny, 1842	NS to S. Fla, W.I.; Alaska to San Diego, CA	TH	27-350	
Illex illecebrosus (Lesueur, 1821)	Newfoundland to N. Fla.	TH	Pelagic	
Loligo pealeii Lesueur, 1821	NS to Fla., Texas, Venezuela; Bermuda	TH	Pelagic	
Rossia tenera (Verrill, 1880)	NS to Texas; N. Europe	?	Pelagic	

*TH = transhatteran.

APPENDIX 4. Southern species with northern limits in the Middle Atlantic zone at or south of Cape Cod.

Species	Geographical range	Faunal group*	Depth range (m)	Time of appearance
Anachis avara (Say, 1822)	MA to E. Fla., Texas	TH	1-88	
Aplysia willcoxi Heilprin, 1886	Cape Cod to Fla. (both coasts), Texas to Brazil; Bermuda	TH	0-?	
Busycon canaliculatum (Linné, 1758)	MA to St. Augustine, Fla.	TH	1-40	Pliocene
Busycon carica (Gmelin, 1791)	MA to E. Fla.	TH	1-70	Pliocene
Busycon contrarium (Conrad, 1840)	NJ to Fla., Gulf States	TH	1-37	Pleistocene
Cadulus carolinensis Bush, 1885	VA to Fla., Texas	Th	5-183	
Calliostoma bairdii Verrill & Smith, 1880	MA to Fla.	TH	37-465	
Diodora tanneri Verrill, 1883	Off Delaware Bay to Barbados	?	75-730	

APPENDIX 4. (Continued)

Species	Geographical range	Faunal group*	Depth range (m)	Time of appearance
Epitonium championi Clench & Turner, 1952	MA to SC	TH	1-70	
Epitonium dallianum (Verrill & Smith, 1880)	NJ to Fla.	?	70-350	
Epitonium pourtalesi (Verrill & Smith, 1880)	NJ to off Barbados	?	80-1100	
Hyalina veliei (Pilsbry, 1896)	VA to Fla.	TH	1-37	
Inodrillia dalli (Verrill & Smith, 1882)	MA to Gulf Mex.	TH	35-267	
Kurtziella cerina (Kurtz & Stimpson, 1851	MA to Fla.; Yucatan	TH	3-55	Pleistocene
Marginella roscida Redfield, 1860	NJ to E. Fla.	TH	18-241	Miocene
Mitrella lunata (Say, 1826)	MA to Fla., Texas to Brazil; Bermuda	TH	1-88	Pliocene
Nassarius acutus (Say, 1822)	VA to Fla., Texas		10-110	Pliocene
Nassarius vibex (Say, 1822)	MA to Fla., Gulf States, W.I.	TH	1-37	Pliocene
Odostomia cancellata Orbigny, 1842	VA to NC; Cuba	?	26-33	
Olivella mutica (Say, 1822)	NJ to Fla., Bahamas	TH	1-146	
Polinices duplicatus (Say, 1822)	MA to Fla., Gulf States	TH	1-58	Miocene
Pyramidella unifasciata Forbes, 1843	NJ to Gulf Mex.	TH	35-2966	
Sinum perspectivum (Say, 1831)	NJ to Fla., Texas, W.I., Brazil, Bermuda	TH	25-70	
Stilifer stimpsoni Verrill, 1872	MA to E. Fla.		1-2295	
Teinostoma cryptospira Verrill, 1884	NJ to W.I.		18-275	
Terebra dislocata (Say, 1822)	MD to Fla., Texas, W.I., Brazil; Redondo Beach CA to Panama	TH	1-116	Pliocene
Turbonilla reticulata (C. B. Adams, 1850)	VA to W.I.	?	33	
Turritella exoleta (Linné, 1758)	VA to W.I., Brazil	TH	1-183	Pliocene
Abra lioica Dall, 1881	MA to S. Fla., W.I.	TH	11-1573	
Aequipecten glyptus (Verrill, 1882)	S. of Mass. to Fla., Texas	TH	125-425	
Aequipecten phrygium (Dall, 1886)	MA to Fla., W.I.	TH	70-1450	
Anadara ovalis (Bruguière, 1789)	MA to Texas, W.I., Brazil	TH	1-14	Miocene
Anadara transversa (Say, 1822)	MA to Fla., Texas	TH	1-37	Miocene
Anomia simplex Orbigny, 1842	MA to Fla., Texas, Brazil; Bermuda	TH	1-70	
Argopecten gibbus (Linné, 1758)	MD to Fla., Texas, Brazil; Bermuda	TH	18-366	
Barnea truncata (Say, 1822)	MA to Texas; Brazil; amphi-atlantic—Senegal to Gold Coast	?	1-55	
Corbula contracta Say, 1822	MA to Fla., W.I., Brazil	TH	1-115	Pliocene
Corbula swiftiana C. B. Adams, 1852	MA to Fla., Texas, W.I.	TH	11-823	
Crassinella lunulata (Conrad, 1834)	MA to Fla., Texas; Brazil; Bermuda	TH	2-110	Pliocene
Cyclopecten nanus Verrill & Bush, 1897	VA to Fla., Texas, Puerto Rico, Brazil	TH	40-538	
Cyrtopleura costata (Linné, 1758)	MA to Texas; Brazil	TH	0-4	Pliocene
Dinocardium robustum (Lightfoot, 1786)	VA to N. Fla., Mexico	TH	3-37	
Divaricella quadrisulcata (Orbigny, 1842)	MA to S. Fla., W.I., Brazil	TH	2-95	
Dosinia discus (Reeve, 1850)	VA to Fla., Texas, Bahamas	TH	1-49	
Laevicardium pictum (Ravenel, 1861)	VA to Brazil; Bermuda	TH	12-155	
Limopsis sulcata Verrill & Bush, 1898	MA to Fla., Gulf States, W.I.	TH	10-650	
Lyonsia hyalina Conrad, 1831	NS to SC	TH	1-70	Miocene
Macoma tenta (Say, 1834)	MA to S. Fla., Brazil; Bermuda		1-157	
Mercenaria campechiensis (Gmelin, 1791)	NJ to Fla., Texas; Cuba	TH	1-36	Miocene
Myrtea lens (Verrill & Smith, 1880)	MA to Brazil	TH	5-850	
Noetia ponderosa (Say, 1822)	VA to Florida, Texas	TH	1-126	Pliocene
Nuculana acuta (Conrad, 1831)	MA to Texas, W.I., Brazil	TH	12-410	Miocene

APPENDIX 4. (Continued)

Species	Geographical range	Faunal group*	Depth range (m)	Time of appearance
Ostrea equestris Say, 1834	VA to Texas, W.I., Brazil	TH	1-146	
Pandora inflata Boss & Merrill, 1965	NJ to Fla. (both coasts)	TH	48-165	
Pandora trilineata Say, 1822	VA to Fla., Gulf Mex.	TH	2-44	
Parvilucina multilineata (Tuomey & Holmes, 1857)	NJ to Fla. (both coasts), Brazil	TH	?	Pliocene
Pecten raveneli Dall, 1898	VA to Fla., Texas, W.I.	TH	17-75	
Pleuromeris tridentata (Say, 1826)	VA to Fla.	TH	1-227	Miocene
Tellina tenella Verrill, 1874	MA to Fla., Gulf States	TH	1-70	
Tellina versicolor DeKay, 1843	RI to S. Fla., Texas, W.I.	TH	3-70	

*TH = transhatteran

APPENDIX 5. Southern species with northern limits in North Carolina.

Species	Geographical range	Depth range (m)
Crepidula aculeata (Gmelin, 1791)	NC to Fla., Texas, Brazil; Bermuda; Central Calif. to Chile	0-?
Cyclichnella bidentata (Orbigny, 1841)	NC to Fla., Texas; Brazil	1-366
Distorsio clathrata (Lamarck, 1816)	NC to Texas, Caribbean, Brazil	9-227
Granulina ovuliformis (Orbigny, 1841)	NC to Fla. (both coasts), W.I.	2-950
Marginella eburneola Conrad, 1834	NC to Fla. (both coasts), W.I.	1-1100
Nassarius albus (Say, 1826)	NC to Fla., Texas, W.I. to Brazil	1-110
Niso aeglees Bush, 1885	NC to Texas, W.I. to Brazil	13-196
Oliva sayana Ravenel, 1834	NC to Gulf States	1-130
Olivella floralia (Duclos, 1853)	NC to Fla. (both coasts), W.I. to Brazil, Bermuda	1-100
Phalium granulatum (Born, 1778)	NC to Texas, Brazil; Bermuda	1-66
Terebra concava Say, 1827	NC to Fla., Texas to Brazil	18-37
Tonna galea (Linné, 1758)	NC to Texas, W.I. to Brazil; Mediterranean, Indo-Pacific	1-42
Trivia maltbiana Schwengel & McGinty, 1942	NC to Fla., Caribbean	1-100
Abra aequalis (Say, 1822)	NC to Texas, W.I.; Brazil	1-140
Aequipecten muscosus (Wood, 1828)	NC to Fla., Texas to Brazil; Bermuda	1-165
Atrina rigida (Lightfoot, 1786)	NC to S. Fla., Caribbean	1-75
Chione cancellata (Linné, 1767)	NC to Fla., Texas, W.I.; Brazil	1-110
Chione grus (Holmes, 1858)	NC to Fla., Texas	1-138
Chione intapurpurea (Conrad, 1849)	NC to Texas, W.I., Brazil	1-86
Chione latilirata (Conrad, 1841)	NC to Fla., Texas	18-227
Diplodonta soror C. B. Adams, 1852	NC to Texas, W. I.	26
Diplodonta verrilli Dall, 1899	NC to Fla., Texas	22-55
Ervilia concentrica (Holmes, 1860)	NC to Fla. (both coasts) to Brazil; Bermuda	1-227
Eucrassatella speciosa (A. Adams, 1852)	NC to Fla. (both coasts), W.I.	6-183
Laevicardium laevigatum (Linné, 1758)	NC to Fla. (both coasts), W.I. to Brazil, Bermuda	1-137
Lucina nassula (Conrad, 1846)	NC to Fla., Texas; Bahamas	1-366
Lucina radians (Conrad, 1841)	NC to Fla., W.I.; Bermuda	10-155
Pandora arenosa (Conrad, 1848)	NC to Texas; Mexico	11-37
Pitar fulminatus (Menke, 1828)	NC to Fla., W.I., Brazil; Bermuda	1-115
Plicatula gibbosa Lamarck, 1801	NC to Fla., Texas, W.I., Brazil; Bermuda	22-140
Semele bellastriata (Conrad, 1837)	NC to Fla.,Texas, W.I., Brazil; Bermuda	18-116
Strigilla mirabilis (Philippi, 1841)	NC to Texas, Caribbean, Brazil; Bermuda	1-55
Tellina aequistriata Say, 1824	NC to Texas, Brazil	1-55
Tellina alternata Say, 1822	NC to Fla., Texas	1-128
Tellina squamifera Deshayes, 1855	NC to Fla., Texas	1-229
Tellina sybaritica Dall, 1881	NC to Fla., Brazil; Bermuda	1-110
Varicorbula operculata (Philippi, 1848)	NC to Fla., Texas, W.I., Brazil	18-460
Dentalium eboreum Conrad, 1846	NC to Fla., Texas, W.I.	3-200

APPENDIX 6. Cosmopolitan and/or eurybathic species.

Species	Geographical range	Depth range (m)
Astarte crenata subaequilatera Sowerby, 1854	Arctic Ocean to off Fla., N.Europe, N. Pacific	40-783
Cuspidaria obesa (Lovén, 1846)	Arctic Ocean to W.I., N.Europe, Mediterranean	18-4450
Cuspidaria rostrata (Spengler, 1793)	Arctic Ocean to W.I.	64-3100
Hiatella arctica (Linné, 1767)	Arctic Ocean to W.I., N. Europe	2-183
Limatula subauriculata (Montagu, 1808)	Greenland to Puerto Rico, Alaska to Mexico, N.E. Europe	10-1800
Macoma balthica (Linné, 1758)	Arctic Ocean to off GA; N. Europe	1-400
Poromya granulata (Nyst & Westendorp, 1839)	Arctic Ocean to W.I.; Mediterranean	25-2640

APPENDIX 7. Unidentified species.

Species	Stations
Alvania sp.	A-7
Inodrillia sp.	4-3 A24; 3-2 A31; 4-5 A-1; 5 A-4; 6-7 A-5
Neaeromya sp.	8-1, 8-7-10; 3-3
Prunum sp.	4-3; 7-8 A-9
Puncturella sp.	A-8
Vitrinella sp.	7-6 A-13
Astarte sp.	1-2; 6-5 A-18; 5-4; 7-6 A-15
Rossia sp.	??

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THE ORIGINS AND DETERMINANTS OF DISTRIBUTION OF MOLLUSCAN FAUNAL GROUPS ON THE SHALLOW CONTINENTAL SHELF OF THE NORTHWEST ATLANTIC

David R. Franz[1] and Arthur S. Merrill[2]

ABSTRACT

An analysis of the extended geographical ranges, and endemicity, of the most prominent gastropod and bivalve species of the shallow (≤ 150 m) continental shelf of the northwest Atlantic is presented. Three faunal groups, the *Arctic-Boreal, Boreal* and *Transhatteran,* broadly overlap in the zone between Cape Hatteras, North Carolina, and northern Labrador. The hypothesis that these faunal groups differ in their origins and paleoecology is examined. The hypothesis is supported for the *Arctic-Boreal* and *Transhatteran* faunal groups. The former consists of Pliocene trans-arctic migrants into the North Atlantic; the latter comprises species which are derived from the Miocene/Pliocene Atlantic fauna. The *Boreal* faunal group is of mixed origins, including trans-arctic migrants, species of Atlantic origins and species of Miocene American progenitors.

Paleo-oceanographic factors are discussed in relation to the probable Pliocene emergence of the endemic boreal component; and the glacial environment of the northwest Atlantic shelf zone is described as it relates to the probable survival of boreal species during the Pleistocene. Information on Holocene range adjustments is reviewed, and evidence on the re-establishment of boreal species is presented.

The overlapping faunal groups of the northwest Atlantic shelf are discussed within the framework of the traditional marine provinces of this zone. Traditional biotic provinces between Labrador and North Carolina lack predictive value for continental shelf mollusks because of the broad overlapping nature of the faunal groups.

INTRODUCTION

The marine molluscan fauna of the shallow continental shelf (≤150 m) off the northwestern Atlantic between Cape Hatteras, North Carolina, and Labrador can be viewed as three overlapping faunal groups (Powell & Bousfield, 1969; Clarke, 1969). The "Transhatteran" faunal group as defined by Franz & Merrill (1980) comprises predominantly shallow shelf and estuarine species which are distributed both north and south of Cape Hatteras, and which are endemic to the American Atlantic coast. The "Boreal" faunal group contains both endemic and amphiatlantic species which are distributed between Cape Hatteras and Labrador, although many species in this group have narrower ranges within this zone. The third faunal group, the "Arctic-Boreal," is made up of predominantly pan-arctic-boreal species which extend into Arctic waters at the northern end of their ranges, but which reach their southern limits on the American coast south of Newfoundland.

Groups of species with similar geographical ranges obviously share similar limitations. Since the American coast is punctuated by well known geographical/thermal barriers—which form the basis for traditional zoogeographic classifications—it might be argued that the faunal groups noted above merely reflect groups of species whose only relationship is their common environmental requirements. Alternately, the existence of well-defined faunal groups may be accounted for by determinants unrelated to the present geography and marine climate (Valentine, 1973). Among these determinants, Tertiary species diversity, Tertiary faunal migrations, Quaternary paleoecology, and especially Holocene events and faunal movements must also be considered to account for the present patterns of distribution.

In this paper, we provide an analysis of these faunal groups, with particular emphasis on the boreal faunal component. We argue that these faunal groupings are not to be considered as merely correlates of the existing

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marine environment, nor the products, only, of thermal/geographic barriers. Rather, these groupings have clearcut Tertiary origins, and we suggest that their present distribution patterns are the result of environmental conditions in the Pleistocene, and especially the Holocene. Finally, we present our views supporting the abandonment of traditional provincial constructs for this faunal area.

METHODS

In this paper, our goal is to re-examine the geographical ranges of the most numerically and ecologically prominent mollusks of the northwest Atlantic continental shelf, and to classify these data so as to reveal patterns which may be related to the origins of faunal groups. The decision to restrict this analysis to numerically and ecologically important species is necessitated by the considerable lack of information on the distributions of many less well known northwest Atlantic species.

The zone of primary concern in this study is the continental shelf of the northwest Atlantic between northern Labrador (60°N) and Cape Hatteras, North Carolina (35°N). In general, we have not considered species which occur predominantly in the deep continental shelf (>150 m) and continental slope, even though some of these may extend into the shallow shelf zone. Likewise, species with primarily high arctic distributions are not treated even though some of these reach their southern limits on the Labrador coast.

Species included in this analysis (listed in Appendices 1–5) have been assigned to zoogeographic categories (Franz & Merrill, 1980) as follows: Arctic-Boreal gastropods (Appendix 1), Arctic-Boreal bivalves (Appendix 2), Boreal gastropods (Appendix 3), Boreal bivalves (Appendix 4), Transhatteran gastropods and bivalves (Appendix 5). The assignment of species to one of these faunal categories has been based on the extended geographical ranges of each species, as indicated by published sources, including Dall (1903), Johnson (1934), Thorson (1941), Madsen (1949), Ockelmann (1958), Macpherson (1971), Abbott (1974), Clarke (1974) and Porter (1974). Other sources of published information are listed in an earlier paper (Franz & Merrill, 1980).

RESULTS

Several aspects of the macrodistribution of the arctic-boreal and boreal groups based on Appendices 1–4 are summarized in Table 1. The transhatteran group is not included since all of these species are restricted in their distribution to the northwest Atlantic. The arctic-boreal fauna is ubiquitous—81% of these species are amphiatlantic, only 8% are endemic to the northwest Atlantic and the

TABLE 1. Macrodistribution of Northwest Atlantic Arctic-Boreal and Boreal Mollusks.

	Gastropods		Bivalves		Total	
ARCTIC-BOREAL FAUNA	No.	%	No.	%	No.	%
Endemic to the NW Atlantic	2	4.8	4	12.5	6	8.1
Amphiatlantic	36	85.7	24	75.0	60	81.1
Amphiatlantic/Pacific	27	75.0	22	91.7	49	81.7
Amphiatlantic but not Pacific	9	25.0	2	8.3	11	18.3
Pacific but not NE Atlantic	4	9.5	4	12.5	8	10.8

Total: Gastropods—42
Bivalves —32

	Gastropods		Bivalves		Total	
BOREAL FAUNA	No.	%	No.	%	No.	%
Endemic to the NW Atlantic	13	59.1	20	69.0	33	64.7
Amphiatlantic	9	40.9	9	31.0	18	35.3
Amphiatlantic/Pacific	2	22.2	4	44.4	6	33.3
Amphiatlantic but not Pacific	7	77.8	5	55.6	12	66.6
Pacific but not NE Atlantic	0	—	0	—	—	

remaining 11% occur both in the north Pacific and northwest Atlantic. The boreal fauna, on the other hand, shows a much higher level of endemic species (65%), the remaining 35% being amphiatlantic. Of the 18 amphiatlantic boreal species, 12 (67%) are restricted to the Atlantic as compared to only 18% of the amphiatlantic arctic-boreal species. In contrast to the arctic-boreal group, all of the boreal species with north Pacific distributions are also amphiatlantic, i.e. there are no boreal species which occur in the Pacific and the northwest Atlantic which do not also occur in the northeast Atlantic.

The distributions of the three faunal groups in the zone between Cape Hatteras (35°N) and northern Labrador (60°N) are shown in Fig. 1. In constructing these curves, we have assumed that all species are geographically continuous within appropriate habitats throughout their ranges.

Northern Limits of Transhatteran Species

Transhatteran species decline sharply in the Cape Cod area. Over 80% of a sample of 35 transhatteran bivalve species collected by the R/V DELAWARE extended northward to Cape Cod (41° – 42°N); but north of Cape Cod this drops to about 30% (Fig. 1). North of the Gulf of St. Lawrence (48°N), the remnants of this faunal group rapidly disappear. Indeed, transhatteran species north of Cape Cod are generally confined to shallow bays and estuaries where warm summer temperatures allow reproductive success (Ganong, 1890).

Southern Limits of the Boreal and Arctic-Boreal Faunal Groups

The Cape Cod area (latitude 41° – 42°N) is a major environmental barrier to the southward distribution of arctic-boreal species (Fig. 1). Although about 25% of arctic-boreal spe-

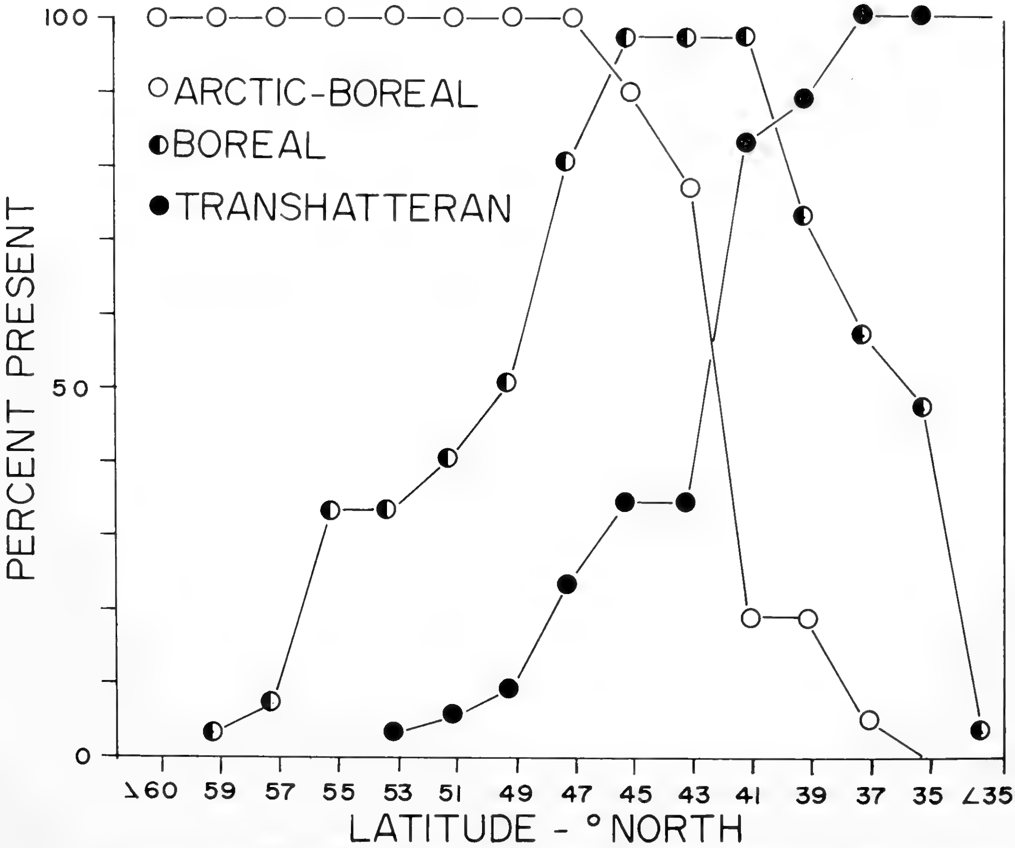

FIG. 1. The geographical distributions of three faunal groups of bivalves occupying the inner continental shelf of the Northwest Atlantic between Cape Hatteras (35°N) and Northern Labrador (60°N). The ordinate indicates the percent of all species in each faunal group present at latitudes between 35° and 60°N. These curves are based on the geographical ranges of species listed in appendices 2 and 4 and 5.

cies range south of Cape Cod, these exhibit marked "boreal submergence" as they track cold isotherms into deeper water (Franz & Merrill, 1980).

The majority of boreal species (ca. 70%) extend south of Cape Cod, some continuing to Cape Hatteras, North Carolina (Fig. 1). The amphiatlantic boreal species show boreal submergence in this zone, a tendency much less evident among the endemic boreal species (Franz & Merrill, 1980).

Geographical Limits of the Boreal Faunal Group

The latitudinal limits of the boreal group (Fig. 1) occur within the zone between Cape Hatteras and Labrador although, as noted later, a few boreal species may establish viable populations farther north. Fig. 1 also illustrates the optimal success of the boreal group in the geographic zone in which both the arctic-boreal and transhatteran groups exhibit severe declines in representation.

DISCUSSION

Range Limits of the Boreal Faunal Group

Unlike the arctic-boreal and transhatteran groups, which are highly amphiatlantic and exclusively endemic respectively, the boreal group contains an endemic and amphiatlantic component. The distributions of these components for gastropods and bivalves are shown in Figs. 2 and 3. Although 46% of endemic boreal gastropods range as far south

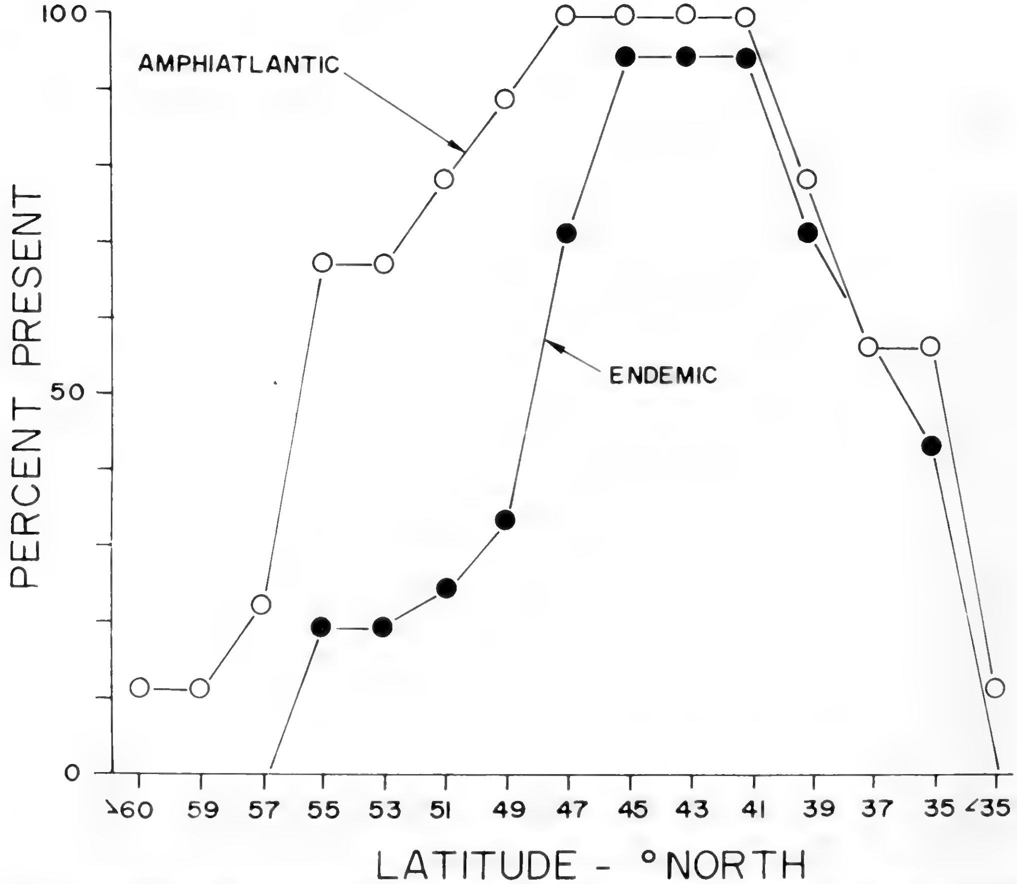

FIG. 2. Frequency distribution of the endemic and amphiatlantic components of boreal gastropod species (based on appendix 3).

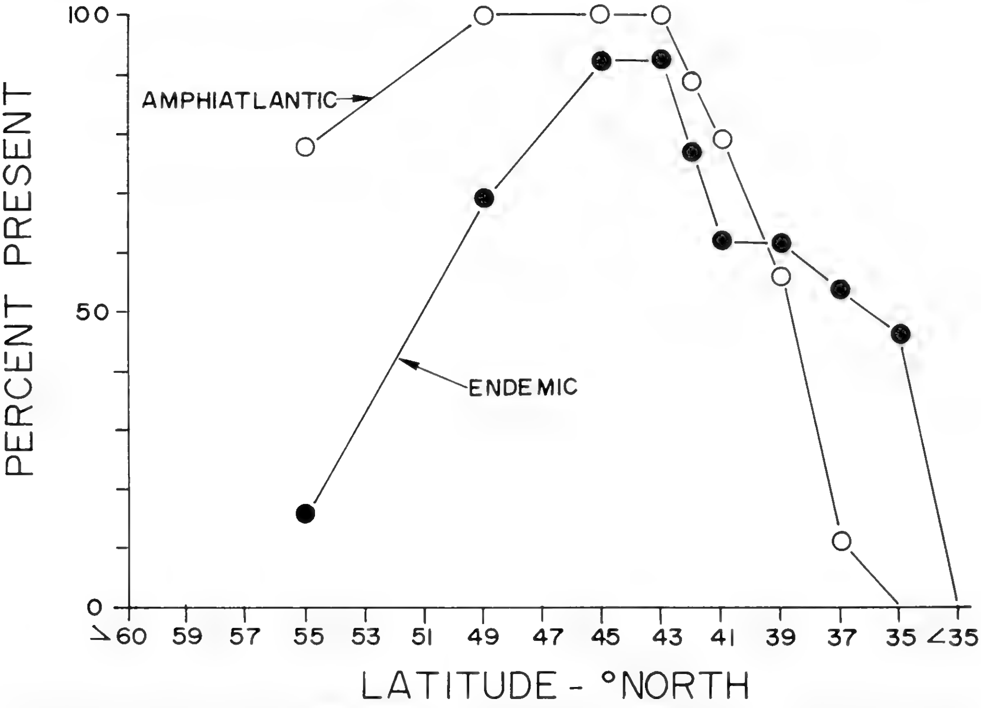

FIG. 3. Frequency distribution of the endemic and amphiatlantic components of boreal bivalve species (based on appendix 4).

as Cape Hatteras as compared with 11% of amphiatlantic species, neither component maintains permanent populations south of Cape Hatteras. For bivalves, both the endemic and amphiatlantic components are very similar, with no species extending south of Cape Hatteras. The optimal geographic ranges of both components coincide (31° – 47°N). However, for both gastropods and bivalves, a significantly larger proportion of amphiatlantic species reach their northern limits on the Labrador coast as compared with endemic species; and the endemic component is clearly skewed toward the southern end of the range. On the average, endemic species of bivalves have a range of 16 degrees of latitude as compared with 22 degrees for the amphiatlantic group. Endemic gastropods range over about 11 degrees of latitude, compared to about 14 degrees for the amphiatlantic component.

There may be significant differences between boreal gastropods and bivalves (Fig. 4). Note that a greater proportion of the amphiatlantic gastropods reach their northern limits in Labrador (55° – 60°N) than bivalves, due largely to the high degree of eurytopy among littoral gastropods, particularly the littorines, *Lacuna* and *Nucella*. Jackson (1974) also emphasized that shallow, infaunal mollusks (bivalves) were more eurytopic and had wider geographical ranges than sublittoral species. In the endemic bivalves (Fig. 4), a somewhat larger proportion reach their northern limits on the Labrador coast than gastropods, but the validity of this observation needs further confirmation because the precise northern limits of some of these species are not known. It is likely, however, that some of the endemic predaceous gastropods represented by this graph are linked trophically to the productive, shallow "fishing banks" (Grand Banks, Georges Banks) off northern New England.

Marine Climate and the Distribution of Arctic Boreal and Boreal Species

The poleward range limits of boreal species are generally thought to be correlated with the subarctic/arctic oceanographic interface, which, as discussed by Dunbar (1951, 1954, 1968), occurs on the eastern coast of Baffin Island, and in the area of the Hudson Strait.

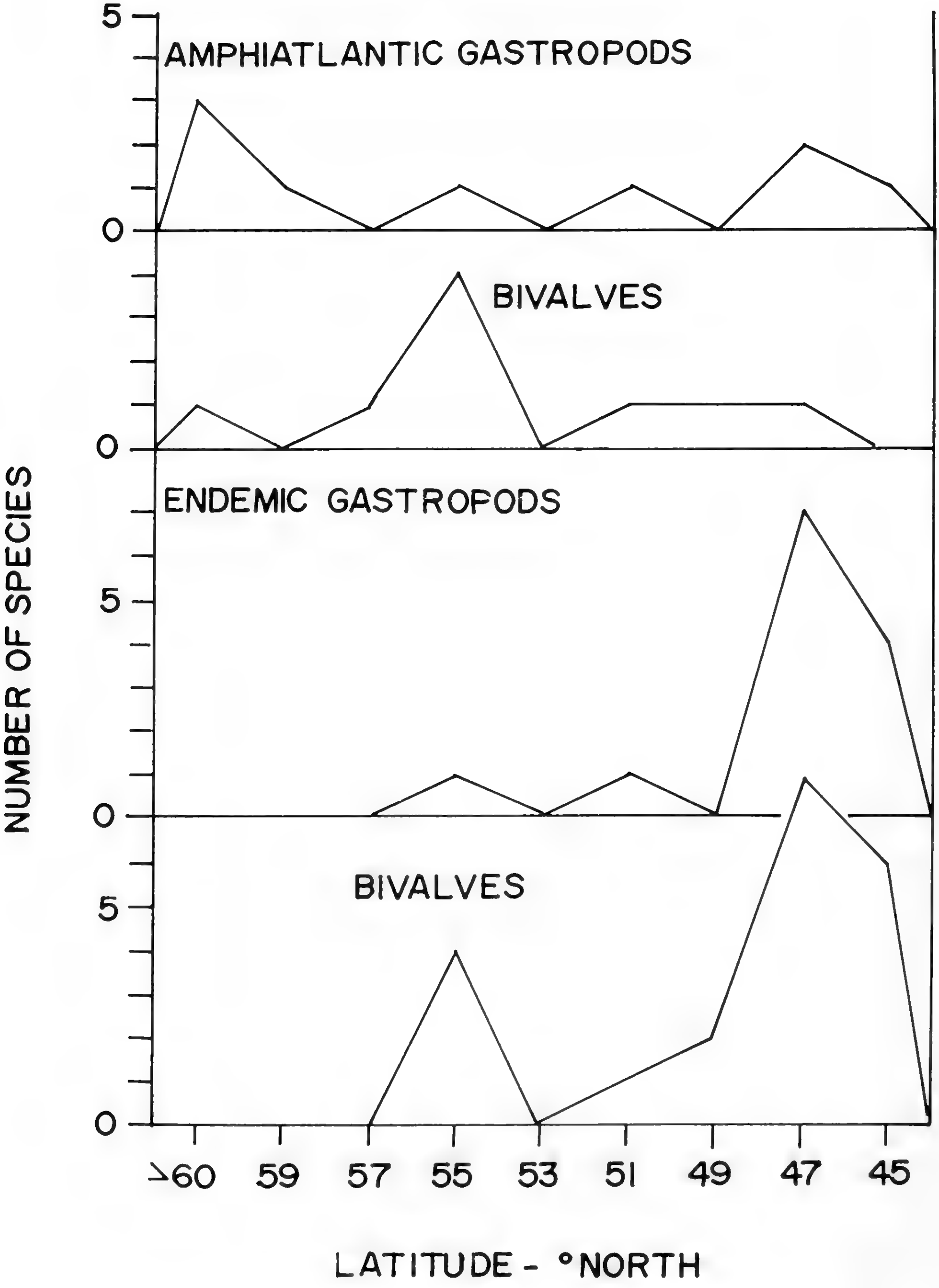

FIG. 4. Frequency distribution of the northern limits of the endemic and amphiatlantic components of boreal gastropods and bivalves (based on species listed in appendices 3, 4).

Southward, including the southeastern coast of Baffin and the entire coast of Labrador to the Grand Banks (as well as western Greenland), subarctic oceanic conditions prevail to a depth of about 200 m. Such waters are characterized by summer temperatures usually above 2°C, vertical thermal instability, and long periods free of ice during the summer months. Arctic conditions prevail to the north and west, with summer surface temperatures normally in the 1 – 2°C range (up to 8° in Hudson Bay) while temperatures in deeper water range from −1 to −2°C (Andrews, 1972).

The arctic/subarctic marine interface marks the poleward limits of the more cold-tolerant of boreal species, and the boundary is particularly dramatic for littoral species, as reported by Ellis & Wilce (1961) on the southeast coast of Baffin Island (66°N). The relative roles of temperature, reduced salinity and sea ice are not easily distinguishable in these areas. One boreal species which extends poleward beyond the subarctic boundary areas is *Mytilus edulis* which has been found in Hudson Bay, and as far north as Pond Inlet, northeast Baffin Island (Ellis & Wilce, 1961).

The relationship between boreal, arctic-boreal and arctic species and the arctic/subarctic marine climatic zones is particularly striking in West Greenland where thermal gradients are gradual, and the subarctic mixed zone extends farther northward due to the warming influence of the West Greenland Current (Ellis, 1960). On this coast, for example, boreal opisthobranch mollusks occur as far northward as Upernivik at 73°N (Lemche, 1941).

Origins of the Faunal Groups

Scarlato (1977) hypothesized that the optimum temperature for survival, and especially reproduction, is precisely fixed within faunal groups, and that these thermal characteristics are "stimulated by the condition under which the corresponding groups of species originated . . ." (Scarlato, 1977). This hypothesis can be restated for application to the northwest Atlantic faunal groups as follows: The three major, overlapping groups (arctic-boreal, boreal, transhatteran) comprise sets of species with similarities in thermal limits, thermal requirements, and thermal adaptive strategies which reflect similarities in the origins of these species in space and time.

The Arctic-Boreal Faunal Group

Scarlato's hypothesis finds strong support in the arctic-boreal group. The Pacific origin of this fauna via the Arctic Ocean is emphasized in the works of Soot-Ryen (1932), Ekman (1953), Nesis (1961), MacNeil (1965), Durham & MacNeil (1967), Strauch (1972), and Briggs (1974). Einarsson, Hopkins & Doell (1967) have shown that the Bering Strait opened during the late Pliocene or early Pleistocene and that transarctic migrations of Pacific species into the Atlantic may have taken place one-half to one million years prior to the first glaciation.

Einarsson (1964) indicates the probable fate of the majority of these transarctic migrants during the subsequent glacial periods. Of eighteen Pacific species known from the early Pleistocene *"Cardium groenlandicum"* zone of the Tjörnes beds of Iceland, only seven are part of the present Icelandic fauna, all arctic or arctic-boreal species. By inference, eurybathyic arctic-boreal species probably survived by maintaining populations, at depth, in the north Atlantic Basin, while shallow arctic-boreal and boreal species probably became extinct (as in Iceland) or survived by extending their ranges southward into glacial refugia.

Thus, the existing, largely pan-arctic-boreal fauna comprises a set of species which migrated from the Pacific during the late Pliocene to early Pleistocene and which survived the glacial episodes in the North Atlantic either in glacial refugia (boreal and boreal-arctic shallow species) or, in the case of predominantly arctic species, in the subpolar arctic sea.

Nesis (1961) has suggested that species which are distributed both in the north Pacific and northwest Atlantic, but do not occur east of Greenland, may have migrated into the northwest Atlantic via the Canadian Archipelago during the post-glacial climatic optimum (PGCO). Presumably, their continued eastward dispersal has been blocked by the East Greenland depth barrier (Clarke, 1973). The species included by Nesis are: *Amicula vestita, Neptunea lyrata decemcostata, Yoldia myalis, Megayoldia thraciaeformis, Cardita granulata,* and *Spisula polynyma.* Ockelmann (1954) believes that *Megayoldia myalis* originated in the Atlantic Ocean and migrated into the North Pacific. *Neptunea lyrata decemcostata* occurs in deposits of

Sangamon Interglacial age in the Northwest Atlantic (Clarke, Grant & Macpherson, 1972) and in lower Pleistocene deposits in Iceland and is considered to have migrated into the Atlantic via the Arctic during the late Pliocene Beringian transgression (Nelson, 1978). *Cardita granulata* occurs in Miocene deposits from Maryland (Dall, 1904). Therefore, these two species at least are not Holocene transarctic migrants. The migration of shelf species form the Pacific to the Atlantic in late glacial times is highly questionable. Even assuming that the Arctic Ocean was free of pack ice during the post-glacial climatic optimum, reduced surface salinity would have been a barrier to the dispersal of boreal species. As pointed out by Herman (1974) salinity reductions during these ice-free periods probably assume greater ecological importance for the survival of invertebrates than the very modest temperature increases. In the case of the species indicated by Nesis, it is difficult to accept that thermal conditions suitable to the establishment of these species were present on the Arctic continental shelf north of Canada during the Holocene.

Boreal Faunal Group

Approximately 35% of boreal species are amphiatlantic, of which about half have fossil and/or Recent distributions in the North Pacific. Some of these are considered to be of Pacific origin, and to have migrated into the Atlantic via the Arctic at one or more times since the Pliocene. Among these species are *Mya arenaria, Macoma balthica, Mytilus edulis* and *Neptunea despecta* (Durham & MacNeil, 1967). Boreal species of Atlantic origin which are thought to have migrated from the Atlantic to the Pacific include *Chlamys islandica, Thyasira flexuosa, Yoldia myalis* and *Yoldia limatula* (Durham & MacNeil, 1967).

There remains an important residue of amphiatlantic species which apparently evolved in the Atlantic and have survived through the Pleistocene even though the genera are, in some cases, known to be of Pacific origin. These include *Littorina littorea, L. obtusata, Nucella lapillus, Buccinum undatum, Anomia squamula, Arctica islandica,* and *Zirfaea crispata.* All except *L. littorea* occur in Pleistocene interglacial deposits in the northwest Atlantic (Richards, 1962; Clarke, Grant & Macpherson, 1972) indicating that this subset of the amphiatlantic boreal fauna lived in the northwest Atlantic during the Pleistocene, prior to the Wisconsin glaciation. The origins of these species need to be examined on an individual basis. Some are probably derived from Tertiary progenitors in the North Pacific (e.g. *Zirfaea crispata, Nucella lapillus, Buccinum undatum*). Others may be derived from Tethyan Atlantic ancestors, e.g. *Cyrtodaria siliqua.* According to Nesis (1965) this species entered the northwest Atlantic in the Pliocene via shoals between Norway and Greenland. The northeast Atlantic and arctic populations are thought to have become extinct during the Pleistocene. A similar mechanism may account for amphiatlantic distributions of other boreal species during the Pleistocene, as well as presently existing amphiatlantic distributions, if it is assumed that populations were maintained on both shores of the north Atlantic during glacial times. Below, we discuss holocene environmental conditions in the boreal zone during glacial maxima, and suggest the unlikelihood of survival of at least some boreal species. It is known, however, that boreal species were present in northeastern Atlantic refugia during the last glacial period. For example, in the western Mediterranean, species such as *Arctica islandica, Modiolus modiolus, Buccinum undatum* and *Chlamys islandica* have been recovered from submerged beds at 90–340 m. These have been dated using ^{14}C at between 31,500 to 9,800 B.P. (Froget, Thommeret & Thommeret, 1972). The occurrence of these and other boreal species in Wisconsin glacial deposits off the American coast have not been recorded, as far as we know, although these species occur in postglacial deposits (e.g. Wagner, 1970).

The remaining, and largest, component of boreal species is the endemic northwest Atlantic group, which comprises about 65% of the total boreal fauna. One of these species, *Yoldia limatula,* has a fossil record in the Gulf of Alaska (lower Pleistocene, Upper Yagataga Formation, Allison, personal communication) but is considered to have migrated from the Atlantic. A second species, *Cyclocardia borealis* is closely related to North Pacific congeners (Soot-Ryen, 1932) but is probably of Atlantic origin. The remaining endemic boreal species—by far the major component—are closely related to Miocene faunal elements of the American Atlantic coast.

In summary, it is clear that the boreal faunal group in the northwest Atlantic contains species of varying origins in space and time. We have distinguished four components: (1) Boreal species derived from the North Pacific via transarctic migration. This component is closely allied with the arctic-boreal fauna; (2) Boreal species, derived from the Atlantic, which migrated into the Pacific via the Arctic Ocean, and presently maintain populations in both the North Pacific and North Atlantic. (3) Atlantic species, amphiatlantic in distribution, which originated in the North Pacific. In either case, these are species with long histories in the Atlantic. (4) Boreal endemic species derived from American Miocene ancestors (e.g. *Placopecten magellanicus, Cerastoderma pinnulatum, Pandora gouldiana,* etc.

Transhatteran Fauna

The third major faunal element in the northwest Atlantic is the transhatteran group of generally temperate and frequently estuarine species which occur both north and south of Cape Hatteras. As noted above (see also Franz & Merrill, 1980) most of these species reach their northern limits at or south of Cape Cod although some occur farther north to Nova Scotia or to the Gulf of St. Lawrence. These species are derived from the Miocene fauna of the American Atlantic coast. Dall (1904) indicated that 10–20% of Maryland Miocene species have survived to the present (based on the Choptank, Calvert and St. Mary's formations) including ubiquitous and abundant species such as *Littorina irrorata, Crepidula fornicata, C. plana, Neverita duplicata, Lunatia heros, Mercenaria mercenaria, Laevicardium mortoni* and *Thracia conradi.* Likewise, approximately 23% of the 116 mollusk species identified by Bailey (1977) from the Chowan River deposits in North Carolina (Pliocene: Yorktown formation) occur as Recent species in the northwest Atlantic. The probable lineages of many Recent species from Miocene/Pliocene ancestors have been suggested by various authors although careful analyses such as those of Gardner (1943) on the *Placopecten* complex and Clarke (1965) and Waller (1969) on the *Argopecten* complex are generally lacking.

Paleo-oceanographic Developments in Relation to the Evolution of Endemic Boreal and Transhatteran Species

Strauch (1972) has shown that many Recent boreal mollusks derived from temperate, eurythermal Cenozoic ancestors evolved in the Pliocene and Pleistocene in response to changing climatic conditions, new migration routes or geographic isolation. We believe that this paradigm will also explain the origins of most of the endemic boreal species as well as those transhatteran species which at present extend well northward in the northwest Atlantic. The conditions which may have prevailed at the time of appearance of these species are summarized as follows:

The onset of northern hemispheric continental glaciation (3–2.5 million years ago) and the development of the Labrador Current System significantly altered the thermal environment of the northwest Atlantic continental shelf (Berggren & Hollister, 1977). Prior to this, a warm Gulf Stream flowing northward around Newfoundland and into the Labrador Sea created the subtropical to warm-temperate marine environment which prevailed at the time of deposition of the Yorktown formation of Virginia and North Carolina (Hazel, 1971). Molluscan species in Miocene deposits from New Jersey to Florida clearly indicate warm-temperate to subtropical conditions (Dall, 1904; Richards, 1968) with little evidence for a significant faunal barrier associated with Cape Hatteras (Hecht, 1969; Hecht & Agan, 1972) although ostracod biofacies studied by Hazel (1971) do converge at Cape Hatteras.

The advent of the Labrador Current System had the effect of displacing the Gulf Stream seaward (to roughly its present position) and, in conjunction with northern hemispheric cooling, initiating the highly seasonal thermal conditions which now characterize the marine environment of the northwest Atlantic continental shelf.

The displacement of the Gulf Stream (to its present position) set the stage for the geographical and ecological separation of molluscan populations on either side of Cape Hatteras. At this time, and in the following Pleistocene period, natural selection favoring cold tolerance and eurytopy acted on the surviving Miocene stocks in the zone north of Cape Hatteras. In some cases, selection operated to enhance the cold tolerance of already existing species, thus increasing their ability to survive both severe winter temperatures and great seasonal variability. As a consequence, these species retained their ability to exist north of Cape Hatteras. In other cases, selection would have produced new species specifically adapted to the harsh condition of the Northwest Atlantic (represented by the endemic component of the boreal species listed in Appendices 3 and 4).

The specific conditions under which this speciation occurred, rates and specific times of speciation, the relative roles of thermal cooling, increasing seasonal variability, and geographic isolation as causative factors in speciation remain to be worked out for most of the species of this endemic boreal group. The evolution of morphologically distinct subspecies with converging geographic ranges near Cape Hatteras (e.g. *Spisula solidissima solidissima* and *S. s. raveneli*) and the well-known tendency of American endemic temperate species to produce "physiological races" (e.g. *Crassostrea virginica, Urosalpinx cinerea*) may represent different evolutionary outcomes to the complex environmental challenges of this and subsequent periods.

The Glacial Environment and Boreal Distributions

Little is known of the fate of boreal species, and to a lesser extent arctic-boreal species in the northwest Atlantic during the last glacial maximum. *Chlamys islandica, Macoma balthica, Arctica islandica, Buccinum undatum, Modiolus modiolus* and perhaps other amphiatlantic boreal species probably survived in refugia in the northwest Atlantic. Unfortunately, the glacial shorelines which might contain the evidence for the survival of such species are located far at sea, near the edge of the continental shelf; since living populations of many of the species in question live at these same depths, it becomes difficult to distinguish fossil and Recent specimens.

The reconstruction of environmental conditions during the Wisconsin glacial maximum in the north Atlantic (McIntyre et al., 1976) does permit some speculation on the probability of survival of these species in the northwest Atlantic. At 18,000 B.P., considered to be the time of the last glacial maximum, very sharp ocean thermal gradients were present at 42°N. North of this there existed a relatively small, subpolar sea bordered on three sides by continental glaciers and solid pack ice. Seasonal sea temperatures ranged from 0° to 10°C in summer; and 0° to −2°C in winter. Summer conditions in shallow water south of 42°N were dominated by dilution from melting sea ice; the counter-clockwise gyre of surface currents most likely transported sea ice along the American coast in winter and early spring.

Cape Hatteras operated then, as today, in deflecting the Gulf Stream eastward; but the North Atlantic Drift did not occur. Rather, the Gulf Stream flowed directly eastward across the Atlantic. Summer sea temperatures at Cape Hatteras ranged from 10°C in February to 20° in August. South of Cape Hatteras, isotherms rapidly approached existing conditions, indicating that Cape Hatteras was then, as today, a severe thermal barrier to the southward penetration of arctic-boreal and boreal species.

The water temperatures of the shallow shelf between 35° and 42°N (Cape Hatteras to Cape Cod) varied from roughly 0° − 10°C in winter, and 10° – 20°C in summer (McIntyre et al., 1976). These would seem to be suitable temperatures for the survival and reproduction of most boreal species. However, the seaward displacement of glacial shorelines caused a significant reduction in the actual shelf space available for colonization (Emery & Garrison, 1967). Sharp latitudinal thermal gradients in this zone, superimposed on a much reduced shelf, must have imposed a further constraint on habitat space since it is likely that only segments of this reduced boreal zone would have been thermally acceptable for reproduction at any given time during the short summer season. Furthermore, it is also likely that drifting pack ice, followed by severe dilution due to melting, characterized the littoral zone in spring and early summer.

These environmental constraints imposed by glacial conditions would have put a premium on certain adaptive characteristics: the ability to complete reproduction over a wide temperature range, the ability to disperse rapidly, the ability to withstand reduced salinity and severe winter temperatures, and in the case of littoral species, to maintain populations in sublittoral habitats which would be less affected by sea ice and meltwater. These adaptive characteristics largely define the life strategies of most existing boreal endemic mollusks.

It is significant that the most prominent estuarine and shallow-shelf mollusks occurring today in the zone between Cape Hatteras and Newfoundland are species with long evolutionary histories in the Atlantic, and with adaptive strategies favoring survival in shallow, variable and/or estuarine conditions (e.g., amphiatlantic species such as *Mytilus edulis, Macoma balthica, Littorina littorea,* transhatteran species of Miocene ancestry including *Crassostrea virginica, Urosalpinx cinerea, Neverita duplicata, Tellina agilis,* or boreal-endemic species of Miocene ancestry, e.g. *Lunatia heros, Spisula solidissima, Astarte undata, Placopecten magellanicus* and *Argopecten irradians*). All are capable of surviving thermal and salinity stress, of reproducing over a relatively wide thermal range, and dispersing rapidly (r-strategists in the parlance of evolutionary ecology). During the Pleistocene, these traits would have permitted such species to use portions of this boreal zone during glacial periods, and rapidly extend their ranges during interglacials, i.e. to track suitable thermal and salinity conditions northward with the gradual retreat of the ice pack. This is illustrated by the fossil distributions of the boreal bivalve *Mesodesma arctatum.* As reported by Merrill, Davis & Emery (1978) this species evidently extended its range southward to at least as far as Cape Hatteras during the glacial maximum, and contracted northward during the Holocene, leaving fossil evidence of its former presence in deposits associated with specific Holocene shorelines. Other boreal species including *Astarte undata, Cyclocardia borealis, Placopecten magellanicus* and the arctic boreal *Clinocardium ciliatum* have been collected from core samples at a depth of 146 m off New Jersey (Ewing, Ewing & Fray, 1960).

The absence of endemic boreal rocky shore species is not, however, accounted for by the severe glacial conditions in this zone. While there are endemic littoral mollusks which presently occur in the boreal zone, all are transhatteran in distribution, and none is restricted entirely to the littoral environment. Consequently, none would have been endangered by glacial conditions north of 35°N. On the other hand, populations of some eurytopic amphiatlantic boreo-littoral species may very well have been excluded by these conditions during glacial maxima.

Holocene Range Adjustments

The disappearance of sea ice and the final disintegration of the great Laurentide Ice Sheet, accompanied by massive marine transgressions, signaled a period of intense faunal migration and range extension which, to a degree, is continuing to the present time. Worldwide warming began about 14,000 B.P. and the Laurentide Ice Sheet disintegrated dramatically about 8,000 B.P. (Bryson et al., 1969).The fiords of eastern Labrador were ice free by 9,000 B.P., and Hudson Bay was open by about 8,000 B.P. The Foxe Basin is thought to have been ice free (Andrews, 1972) although this point is controversial (Clark, 1971). Extensive, shallow seas of marine to brackish water occupied the St. Lawrence basin (Dionne, 1977) and the Ottawa and St. Lawrence Valleys (the Champlain Sea) as well as southwestern Maine from about 11,500 to 7,000 B.P. (Wagner, 1970; Bloom, 1960, 1963). The warming trend continued until about 4,600 B.P., with a peak about 6,000 B.P., the so-called post-glacial climatic optimum (PGCO). Evidence suggests that in the Canadian arctic, the marine optimum lagged behind the terrestrial PGCO, occurring about 3,500 B.P. (Andrews, 1972).

Evidence for the Re-Establishment of Boreal Species

While post-glacial species movements remain largely unknown, information is available on the colonization of several formerly glaciated areas by marine mollusks, and some inference can be drawn concerning the times and routes of migration. This information is provided mainly by aggregations of marine shells in raised deposits at many sites in the Canadian Arctic, West Greenland, the Canadian Atlantic coast and New England. These collections usually contain a mix of arctic-boreal and boreal species, indicating a rapid re-colonization of the shallow shelf by boreal species. The mechanisms of colonization and the origins of these species remain speculative.

Two sources of re-colonizing populations are possible: boreal species may have dispersed from glacial refugia in the northwest Atlantic; or, species originating on the European coast could have dispersed westward via the Faeroe Islands, Iceland, and southwest Greenland. The latter source is less likely for species lacking an efficient larval or adult dispersal mechanism but has been suggested for benthic amphipods by Bousfield (1973). This mechanism, i.e. westward dispersal of larvae via surface currents, is suggested by Kraeuter (1974) to account for the dispersal of *Littorina littorea* and is supported indirectly by studies of larval distribution by Mileikovsky (1968) and Scheltema (1977). Proof of the trans-Atlantic movement of boreal species does not exist at present, but the possibility is supported by several lines of evidence. The post-glacial recolonization of Iceland was effected by the westward migration of European species (Thorson, 1941; Einarsson, 1964), and lusitanian-boreal species such as *Emarginula fissura* and *Acmaea virginea,* which presently reach their western limits in Iceland (Thorson, 1941), have been reported from Holocene raised deposits in West Greenland (Laursen, 1950). The extinction of these less cold-tolerant boreal species in Greenland supports the argument that at least some boreal species extended westward in post-glacial times as far as Greenland, and that subsequent extinctions may be correlated with thermal deterioration following the end of the PGCO. This has also been suggested to account for the disjunct amphiatlantic distribution of the less cold-tolerant boreal amphiatlantic nudibranchs (Franz, 1970, 1975). If the presently-existing boreal amphiatlantic fauna survived the glacial period in refugia in the northwest Atlantic, the poleward movement of these species in the Holocene would present few problems. As suggested below, the available evidence supports this for some boreal species, but is equivocal for others, particularly the shallow shore component.

Evidence from Early Holocene Transgression Faunas

The Champlain Sea transgression is believed to have lasted from about 11,500 to between 9,000 and 8,000 B.P. (Wagner, 1970). During this period, the thermal environment improved from essentially arctic conditions at the beginning (Cronin, 1976, 1977) to temperate conditions at the end, corresponding to the PGCO for this area (about 9,000 years B.P.) (Schnitker, 1977). Fossil mollusks indicative of the early arctic-subarctic condition include *Portlandia arctica, Nuculana pernula, Polinices pallidus, Mya truncata, Buccinum hancocki, Nuculana tenuisulcata, Buccinum terrae-novae, Serripes groenlandicus, Buccinum plectrum* and *Natica clausa.* Transhatteran and boreal endemic fossils such as *Haminoea solitaria, Crassostrea virginica, Yoldia limatula* and *Lyonsia hyalina* mark the terminal, temperate phase of the Champlain Sea.

The amphiatlantic boreal component of the Champlain Sea fauna includes *Macoma balthica, Mytilus edulis, Mya arenaria, Neptunea despecta, Nucula tenuis* and *Chlamys islandica.*

Raised deposits containing a mixture of arctic-boreal species from southwestern Maine (the Presumscot Formation) are thought to date from 11,000 to 7,000 B.P. (Bloom, 1960). The boreal component of this fauna includes endemic species such as *Astarte undata, Cerastoderma pinnulatum, Mesodesma arctatum,* and *Spisula solidissima*; and the amphiatlantic species *Chlamys islandicus, Macoma balthica, Buccinum undatum* and *Neptunea lyrata decemcostata.* The paleoecology of the Presumscot fauna—like the early Champlain Sea—implies subarctic conditions comparable, as suggested by Bloom (1960), to the present marine climate of Labrador.

It seems highly probable that all of the amphiatlantic species noted above from the Champlain Sea and Presumcot formations were present in the northwest Atlantic during the Wisconsin glacial period. *Macoma balthica* is a highly eurythermal estuarine species (although it does not occur in Arctic waters per se). *Mytilus edulis,* as noted by Andrews (1972), is not restricted to intertidal environments although it prefers shallow water; although generally subarctic-boreal in distribution, it has occurred recently as far north as North Baffin Island. *Chlamys islandica* is an active species which presently lives on the West Greenland (north to Disco Island) and Labrador coasts, and southward to the Gulf of Maine and Buzzards Bay. *Mya arenaria* is similar to *Macoma balthica* in its present distribution, being tolerant of estuarine conditions and subarctic temperatures. Both *Neptunea despecta* and *Nucula tenuis* exhibit "boreal submergence." *Neptunea* ranges from 10 m to 1203 m (Thorson, 1941) and *Nucula tenuis* occurs in very deep water as far south as Florida. Since *Neptunea despecta* lacks a pelagic larval stage, it seems likely that both of these species maintained populations in the northwest Atlantic during the glacial periods.

Fossil representatives of *Mytilus edulis, Macoma balthica* and *Chlamys islandica* in post-glacial deposits on Baffin Island (Andrews, 1972) and west Greenland (Laursen, 1950) are considered to indicate the existence of a warmer marine environment corresponding to the PGCO at 4,000–3,000 B.P. The co-occurrence of these species in post-glacial deposits in west Greenland, the Canadian Arctic and the Champlain Sea suggests that these species may already have been present in the northwest Atlantic, and were able to disperse northward early in the Holocene.

Buccinum undatum is not present in the

Champlain Sea deposits, although it does occur in raised deposits in west Greenland dated at 7,730 B.P. (Sugden, 1973) and Maine (Bloom, 1960). Since this species is known from Pleistocene deposits from Labrador to New Jersey (Richards, 1962) including mid-Wisconsinan deposits (e.g. Sankaty Head, Nantucket: Wagner, 1977) and lacks a pelagic larval stage, it is likely that it also survived the Wisconsin glacial period in the northwest Atlantic.

Little is known of the origins, modes and times of movement of other boreal amphiatlantic species which are not represented in the early Holocene transgression faunas (e.g. *Arctica islandica, Modiolus modiolus, Anomia squamula, Zirfaea crispata*). Records of *Modiolus* and *Arctica* from Sankaty Head (Nantucket) and Tobaccolot Bay (Gardiners Island, New York) are considered to be of late Sangamonian or mid-Wisconsinan age (Gustavson, 1976) but their fate during the glacial maximum and their subsequent patterns of migration are unknown.

The Shore Fauna

As noted earlier, drifting sea ice and seasonal fluctuations in salinity and temperature in the Middle Atlantic zone would have provided stringent conditions for littoral species during glacial maxima. Major adaptive traits conferring survival value during this period would include: a) short annual reproductive period, b) eurythermal reproduction, and c) vertical mobility. Thus, species which were able to complete reproduction during the relatively short summers and to reproduce over a wide temperature range would be more successful in utilizing the much-reduced boreal zone. Also, survival over the long, harsh winters and spring periods of drifting sea ice and reduced salinity would have been enhanced by the ability to move vertically out of the littoral zone.

Of the common amphiatlantic littoral species (excluding nudibranchs which were discussed by Franz, 1975), the following probably survived the recent glacial maximum in the northwest Atlantic: *Littorina saxatilis, Nucella lapillus* and *Acmaea testudinalis.*

Littorina saxatilis presently occurs from New Jersey to the Canadian Arctic (Macpherson, 1971) and in post-Pleistocene deposits in Hudson Bay, James Bay, Newfoundland, and Quebec (Richards, 1962). Wisconsinan records of this species and *Nucella lapillus* exist from Connecticut and Long Island. *Nucella* is also known from the Salmon River (Nova Scotia) beds of mid-Wisconsinan age (Wagner, 1977). Both of these species can move into deeper water to avoid winter ice: *L. saxatilis* from 0–94 m and *N.lapillus* from 0–55 m (Thorson, 1941). This implies the possibility of the continued existence of these species during glacial times. *Acmaea testudinalis* presently occurs from the Canadian Arctic (Macpherson, 1971) and on the American coast south to New Jersey. Although predominantly a littoral form, it survives deeper water down to 40 m (Macpherson, 1971). Rapid dispersal is facilitated by a planktonic veliger larva.

The available evidence suggests that the following common littoral species may not have survived the last glacial maximum and were probably re-introduced in the Holocene: *Littorina littorea, Littorina obtusata* and *Lacuna vincta.* At present, *Littorina littorea,* in its southward range expansion on the American coast, shows a predilection to occur freely on sand and marsh grass; *Lacuna vincta* is most abundant on *Laminaria* in the sublittoral. But both species are ecologically linked to the littoral and/or shallow sublittoral zones and both are unlikely to have been able to survive winter and early spring conditions in the boreal zone during glacial maxima. At present, *L. littorea* has a disjunct amphiatlantic distribution. It is absent in Iceland, the Faeroes and West Greenland, but occurs in northern Europe and the American coast from the Gulf of St. Lawrence to Maryland (Wells, 1965). *L. littorea* has been found in the Salmon River (Nova Scotia) deposits of presumed mid-Wisconsinan age (Wagner, 1977), and younger specimens from Nova Scotia, New Brunswick and Newfoundland have been dated to at least 1000 AD (Clarke & Erskine, 1961; Bird, 1968). It seems most likely that *L. littorea* dispersed via planktonic eggs and larvae into the northwest Atlantic during the PGCO, as suggested by Kraeuter (1974).

Littorina obtusata offers basically the same problems as *L. littorea* except that it has been recognized as characteristic of the Canadian Maritime and New England fauna throughout historical times and has not undergone a significant recent range extension. It is reported from the Sankaty Head deposits (Nantucket) (Clarke, Grant & Macpherson, 1972), which are considered of late Sangamonian (Richards, 1962; Clarke et al., 1972) or mid-Wisconsinan age (Wagner, 1977). According to Thorson (1941), this species may occur to a depth of 150 m but is generally associated with seaweeds (*Fucus, Ascophyllum*) in the intertidal zone. Since the egg masses are deposited on seaweed, the Holocene dispersal could be accounted for by rafted *Fucus* or some other means of natural dispersal. Populations presently occur in Iceland and southwest Greenland, suggesting the probable reintroduction of this species in the Holocene. This may also apply to *Lacuna vincta,* which does not occur in pre-Wisconsin deposits in North America. Its egg masses, which are also laid on *Laminaria* and *Fucus,* release planktonic veligers, unlike the eggs of *L. obtusata,* which undergo direct development.

The final answers to the continued presence of all of these species during glacial maxima must be sought individually for each; perhaps the submerged shorelines of the American Atlantic coast will yield this information in coming years. What is certain, however, is that range expansions continue to occur, as indicated by recent rapid range modification of *Littorina littorea* (Clarke & Erskine, 1961; Wells, 1965; Clarke, 1971; Kraeuter, 1974), and *Rangia cuneata* (Hopkins & Andrews, 1970).

Zoogeography

The thrust of this study has been, first, to identify groups of species which share similarities in range and thermal requirements; second, to examine the total geographical distributions of these groupings; and finally, to consider the possibility that these groups reflect common origins in time and place. This approach is similar to Petersen's (1977) analysis of North Sea bivalves. But what relationship, if any, exists between this approach and the traditional analysis of zoogeographic provinces? In theory, as most recently discussed by Valentine (1973), zoogeographic provinces are geographic areas which support faunas of relatively consistent taxonomic composition. Adjacent provinces are separated by geographical/thermal (or other ecological) barriers; but there is disgreement as to the degree of consistency required in the recognition of distinct provinces. Obviously, provinces defined in this way cannot overlap. But biologists often invert this conception of zoogeographic provinces so that a province is defined as the area occupied by a unique fauna—perceived either as some critical level of endemicity or by some other distinctive characteristic (e.g. the geographic region characterized by the presence of hermatypic corals). Zoogeographic provinces so defined can overlap if there is geographical overlap between two adjacent unique faunas. As noted by Hazel (1970), this dichotomy is partly to blame for the confusion in the zoogeographic terms applied to the northwest Atlantic region and in the meanings of these terms. Some malacologists, e.g. Abbott (1957), have proposed non-overlapping zoogeographic provinces in the classical mode; but many other workers (Stephenson & Stephenson, 1954; Coomans, 1962; Powell & Bousfield, 1969; Franz, 1970) have recognized the significance of the overlapping of broad faunal groups, particularly in the "Virginian" province (bounded by Cape Hatteras and Cape Cod).

Fig. 5 shows the relationships between the faunal groups and the traditional, non-overlapping provinces as recently discussed by Hazel (1970). Clearly, the characteristic molluscan fauna associated with each province corresponds to the three faunal groups studied in this paper; i.e. the dominant fauna of the Syrtensian Province is the arctic-boreal; the fauna of the Nova Scotian Province refers primarily to the boreal; and the fauna of the Virginian province refers primarily to the Transhatteran faunal group. But the traditional provinces fail as predictive tools because each province contains two or three overlapping faunal groups of very different overall thermal strategies and origins.

Of course, the perception of the validity of biotic provinces, no matter how defined, is affected by the taxonomic groups used in the analysis. The ostracods studied by Hazel (1970) show relatively high proportions of endemic species north of Cape Hatteras, thus allowing a stronger correlation between the classically defined provinces and faunal groups. But the zoogeographic patterns in shallow water gammaridean amphipods observed by Bousfield (1973) and Watling (personal communication) and for polychaetes by Kinner (1977) seem very similar to the patterns for shelf mollusks discussed in this paper.

Ecological barriers to distribution, particularly thermal/geographic barriers, are important in all zoogeographic treatments; in the present study, Figs. 1–3 illustrate this role in the case of Cape Hatteras and Cape Cod. It is possible, however, that the role of barriers in preventing species transgressions has been

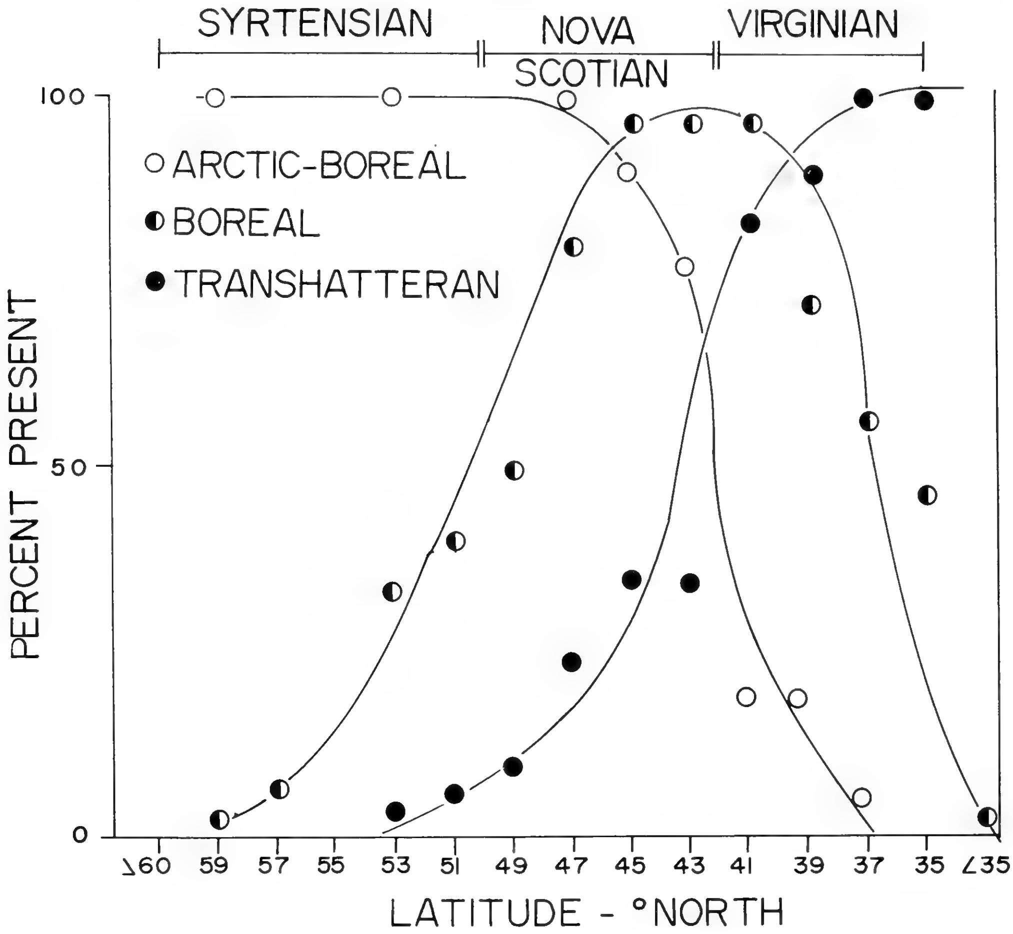

FIG. 5. The geographical distribution of faunal groups (from Fig. 1) in relation to traditional biogeographic provinces (based on Hazel, 1970).

overemphasized, with too little emphasis on the species which are able to disregard such barriers. This problem is exemplified by Hecht's analysis of molluscan distribution on the Atlantic coast from Newfoundland to Florida (Hecht, 1969). His phenograms, based on q-mode cluster analyses, indicated three groupings with boundaries at Cape Cod and Cape Hatteras. He interpreted these data as evidence supporting the concept of three faunal provinces. However, these data also support an alternative conclusion not considered by Hecht, viz. that the entire area between Newfoundland and Florida is an area of overlap between four faunal groups, with boreal species extending south of Cape Cod, arctic-boreal species largely limited by the Cape Cod thermal barrier, subtropical species largely limited by the Cape Hatteras Barrier, and temperate-endemic (transhatteran) species extending both north and south of Cape Hatteras. Clearly, Cape Cod and Cape Hatteras are important geographical and ecological barriers to the distribution of many species, but the faunal provinces defined by such barriers alone combine groups of species with different overall thermal capacities, origins and histories.

CONCLUSIONS

The molluscan fauna of the inner continental shelf ($\leq$ 150 m) of the northwest Atlantic between Cape Hatteras and Labrador consists of three broadly overlapping species groups which differ in their thermal requirements, limits, and adaptive strategies. The arctic-boreal faunal group, which prevails north of Newfoundland, is composed almost entirely of amphiatlantic and North Pacific species which reach their southern limits on the American coast near Cape Cod (although some continue farther south in deeper water). The boreal faunal group, a mixture of endemic and amphiatlantic species, overlaps the arctic-boreal north of Cape Cod. Between Cape Cod and Cape Hatteras, boreal species decline in importance, with most reaching their southern limits on the continental shelf north of Cape Hatteras. The transhatteran faunal group consists of species entirely endemic to the northwest Atlantic, all of which continue south of Cape Hatteras, and the majority of which reach their northern limits between Cape Hatteras and the Gulf of St. Lawrence.

The ecological and biogeographical homogeneity of the arctic-boreal fauna reflects the Pacific origin of these species via the Arctic Ocean during the late Pliocene to early Pleistocene. The boreal fauna comprises three groups of differing origins: Pliocene trans-arctic migrants; amphiatlantic species with long histories in the Atlantic; endemic species derived from American Miocene ancestors. The latter may have evolved from warm-temperate progenitors at the time of the development of the Labrador Current system (3 m.y. ago). The transhatteran fauna consists of species conspecific with or derived from warm-temperate American Miocene species. Thus, Scarlato's hypothesis, that major biogeographic groups reflect thermal conditions at the time of their origins, is supported in the above analysis for the arctic-boreal and transhatteran faunal groups. Their thermal charcteristics and biogeography on the American coast are correlated with their origins in space and time. On the other hand, the boreal group is clearly an artificial aggregation containing species of mixed origins.

The distributions of arctic-boreal species in the Northwest Atlantic in late glacial times was probably characterized by severe dislocations and perhaps local extinctions. Transhatteran species tracked appropriate thermal gradients southward during glacial maxima and the evidence indicates that suitable conditions for these species continued to exist south of Cape Hatteras throughout the Pleistocene. Arctic-boreal species survived the late glacial period in the Northwest Atlantic by tracking appropriate thermal gradients northward during warmer interglacial periods; and the reverse during periods of thermal deterioration.

Boreal species on the American coast were probably forced southward into the zone bounded approximately by Cape Hatteras and Cape Cod (35° – 42°N) during glacial maxima. Evidence indicates that environmental conditions in this zone may have been unsuitable for the continued survival of some boreal, and especially the more stenotopic boreo-littoral species. Populations of these species may have been re-established in the northwest Atlantic during the PGCO (marine hypsithermal period) via West Greenland, Iceland and northern Europe.

The three faunal groups—because of their overlapping geographical distributions—are not completely reconcilable with traditional zoogeographic constructs for this region. In particular, the geographical zone between Cape Hatteras and the Gulf of St. Lawrence, a zone encompassing two adjacent marine provinces (Virginian, Nova Scotian) contains all three faunal groups in varying proportions. The role of thermal/geographic barriers in defining biogeographic regions, and in separating faunal groups, has been over-emphasized in the northwest Atlantic where enormous seasonal thermal fluctuations allow the co-existence of several distinct faunal groups.

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APPENDIX 1. Arctic-Boreal Gastropods of the northwest Atlantic.

Species	Endemic northwest Atlantic	Amphi-Atlantic	North Pacific	Pacific origin[1]
Puncturella noachina (Linné, 1771)		+	+	
Acmaea testudinalis (Müller, 1776)		+		
Lepeta caeca (Müller, 1776)		+	+	
Margarites helicinus (Phipps, 1774)		+	+	+
Margarites olivaceus (Brown, 1827)		+	+	
Margarites costalis (Gould, 1841)		+	+	+
Margarites groenlandicus (Gmelin, 1791)	+			
Solariella obscura (Couthouy, 1838)		+	+	?
Lacuna vincta (Montagu, 1803)		+	+	+
Littorina saxatilis (Olivi, 1792)		+		
Alvania brychia (Verrill, 1884)		+		
Cingula aculeus Gould, 1841		+		
Skeneopsis planorbis (Fabricius, 1780)		+		
Tachyrhynchus erosus (Couthouy, 1838)			+	+
Acirsa borealis (Lyell, 1857)			+	+
Epitonium greenlandicum (Perry, 1811)		+	+	+
Trichotropis borealis Broderip & Sowerby, 1829		+	+	+
Aporrhais occidentalis Beck, 1836		+		
Velutina velutina (Müller, 1776)		+	+	+
Velutina plicatilis (Müller, 1776)		+	+	+
Velutina undata (Brown, 1839)		+	+	+
Marsenina glabra (Couthouy, 1832)		+	+	
Lunatia pallida (Broderip & Sowerby, 1829)		+	+	+
Amauropsis islandica (Gmelin, 1791)		+	+	+
Natica clausa Broderip & Sowerby, 1829		+	+	
Boreotrophon clathratus (Linné, 1758)		+	+	+
Mitrella rosacea (Gould, 1841)		+	+	
Buccinum glaciale Linné, 1761			+	+
Buccinum scalariforme Möller, 1842		+	+	+
Buccinum plectrum Stimpson, 1865			+	+
Colus islandicus (Gmelin, 1791)		+	+	
Colus pubescens (Verrill, 1882)	+			
Colus spitzbergensis (Reeve, 1855)		+	+	
Volutomitra groenlandica (Möller, 1842)		+	+	
Admete couthouyi (Jay, 1839)		+	+	+
Propebela turricula (Montagu, 1803)		+	+	+
Propebela pingelii (Möller, 1842)		+		
Oenopota harpularia (Couthouy, 1838)		+	+	+
Oenopota pyramidalis (Ström, 1788)		+	+	?
Oenopota bicarinata (Couthouy, 1838)		+	+	
Oenopota decussata (Couthouy, 1839)		+		
Oenopota incisula (Verrill, 1882)		+		

[1] Following Durham & MacNeil, 1967.

APPENDIX 2. Arctic-Boreal pelecypods of the northwest Atlantic.

Species	Endemic northwest Atlantic	Amphi-Atlantic	North Pacific	Pacific origin[1]
Nucula delphinodonta Mighels & Adams, 1842		+		
Nucula tenuis Montagu, 1808		+	+	?
Nuculana pernula (Müller, 1771)		+	+	
Nuculana minuta (Fabricius, 1776)		+	+	?
Nuculana tenuisulcata (Couthouy, 1838)	+			
Yoldia amygdales Valenciennes, 1846		+	+	
Yoldia sapotilla (Gould, 1841)	+			
Yoldia myalis (Couthouy, 1838)			+	?
Megayoldia thraciaeformis Storer, 1838			+	+
Crenella decussata (Montagu, 1808)		+	+	+
Crenella faba (Müller, 1776)	+			
Modiolus modiolus (Linné, 1758)		+	+	+
Musculus niger (Gray, 1824)		+	+	+
Musculus discors (Linné, 1767)		+	+	+
Kellia suborbicularis (Montagu, 1803)		+	+	+
Turtonia minuta (Fabricius, 1780)		+	+	
Astarte elliptica (Brown, 1827)		+	+	
Astarte montagui (Dillwyn, 1817)		+	+	
Astarte borealis (Schumacher, 1817)		+	+	
Serripes groenlandicus (Bruguière, 1789)		+	+	+
Clinocardium ciliatum (Fabricius, 1780)		+	+	+
Spisula polynyma (Stimpson, 1860)			+	+
Macoma calcarea (Gmelin, 1791)		+	+	+
Liocyma fluctuosa (Gould, 1841)		+	+	+
Mya truncata Linné, 1758		+	+	+
Panomya arctica (Lamarck, 1818)		+	+	+
Lyonsia arenosa Möller, 1842		+	+	+
Pandora glacialis Leach, 1819		+	+	+
Thracia myopsis Möller, 1842		+		
Thracia septentrionalis Jeffreys, 1872	+			
Cuspidaria glacialis (G. O. Sars, 1878)		+	+	
Periploma fragile (Totten, 1835)			+	

[1] Following Durham & MacNeil, 1967.

APPENDIX 3. Boreal gastropods of the northwest Atlantic.

Species	Endemic northwest Atlantic	Amphi-Atlantic	North Pacific	Pacific origin[1]
Calliostoma occidentale (Mighels & Adams, 1842)		+		
Lacuna pallidula (da Costa, 1778)		+		
Littorina littorea (Linné, 1758)		+		
Littorina obtusata (Linné, 1758)		+		
Alvania areolata Stimpson, 1851	+			
Hydrobia totteni Morrison, 1954	+			
Omalogyra atomus (Philippi, 1841)		+		
Bittium alternatum (Say, 1822)	+			
Couthouyella striatula (Couthouy, 1839)	+			
Polinices immaculatus (Totten, 1835)	+			
Lunatia heros (Say, 1822)	+			

APPENDIX 3. (Continued)

Species	Endemic northwest Atlantic	Amphi-Atlantic	North Pacific	Pacific origin[1]
Lunatia triseriata (Say, 1826)	+			
Nucella lapillus (Linné, 1758)		+		+
Buccinum undatum Linné, 1758		+	+	
Colus stimpsoni (Mörch, 1867)	+			?
Colus ventricosus (Gray, 1839)	+			
Colus pygmaeus (Gould, 1841)	+			
Neptunea lyrata decemcostata (Say, 1836)	+			
Neptunea despecta (Linné, 1758)		+		
Propebela elegans (Möller, 1842)		+	+	
Propebela gouldii (Verrill, 1882)	+			
Propebela sarsii (Verrill, 1880)	+			

[1] Following Durham & MacNeil, 1967.

APPENDIX 4. Boreal pelecypods of the northwest Atlantic.

Species	Endemic northwest Atlantic	Amphi-Atlantic	North Pacific	Pacific origin[1]
Nucula atacellana Schenck, 1939	+			
Yoldia limatula (Say, 1831)	+	f	f	
Solemya borealis Totten, 1834	+			
Mytilus edulis Linné, 1758		+	+	+
Crenella glandula (Totten, 1834)	+			
Thyasira flexuosa (Montagu, 1803)		+	+	
Chlamys islandica (Müller, 1776)		+	+	
Palliolum striatum (Müller, 1776)		+		
Placopecten magellanicus (Gmelin, 1791)	+			
Anomia squamula Linné, 1758		+		
Cyclocardia borealis (Conrad, 1831)	+		f	
Astarte undata Gould, 1841	+			
Astarte castanea (Say, 1822)	+			
Cerastoderma pinnulatum (Conrad, 1831)	+			
Mesodesma arctatum (Conrad, 1830)	+			
Mesodesma deauratum (Turton, 1822)	+			
Siliqua costata Say, 1822	+			
Macoma balthica (Linné, 1758)		+	+	+
Arctica islandica (Linné, 1767)		+		
Pitar morrhuanus Linsley, 1848	+			
Mya arenaria Linné, 1758		+	f	+
Cyrtodaria siliqua (Spengler, 1793)	+			
Zirfaea crispata (Linné, 1758)		+		+
Xylophaga atlantica Richards, 1942	+			
Pandora inornata Verrill & Bush, 1898	+			
Pandora gouldiana Dall, 1886	+			
Thracia conradi Couthouy, 1838	+			
Periploma papyratium (Say, 1822)	+			
Periploma leanum (Conrad, 1831)	+			

[1] Following Durham & MacNeil, 1967.
f = fossil.

APPENDIX 5. Transhatteran mollusks collected on R/V DELAWARE Cruise 60-7, 11–21 May, 1967.

Gastropoda
- *Stilifer stimpsoni* Verrill, 1872
- *Crucibulum striatum* Say, 1824
- *Crepidula fornicata* (Linné, 1758)
- *Neverita duplicata* (Say, 1822)
- *Natica pusilla* Say, 1822
- *Sinum perspectivum* (Say,1831)
- *Anachis avara* (Say, 1822)
- *Mitrella lunata* (Say, 1826)
- *Busycon carica* (Gmelin, 1791)
- *Busycon canaliculatum* (Linné, 1758)
- *Nassarius vibex* (Say, 1822)
- *Ilyanassa obsoleta* (Say, 1822)
- *Marginella roscida* Redfield, 1860
- *Kurtziella cerina* (Kurtz & Stimpson, 1851)
- *Cylichnella canaliculata* (Say, 1822)
- *Cylichnella bidentata* (Orbigny, 1841)

Bivalvia
- *Nucula proxima* Say, 1822
- *Nuculana acuta* (Conrad, 1831)
- *Anadara transversa* (Say, 1822)
- *Anadara ovalis* (Bruguière, 1789)
- *Noetia ponderosa* (Say, 1822)
- *Limopsis sulcata* Verrill & Bush, 1898
- *Aequipecten glyptus* (Verrill, 1882)
- *Aequipecten phrygium* (Dall, 1886)
- *Argopecten gibbus* (Linné, 1758)

Bivalvia (Continued)
- *Anomia simplex* Orbigny, 1842
- *Crassostrea virginica* (Gmelin, 1791)
- *Myrtea lens* (Verrill & Smith, 1880)
- *Lucinoma filosa* (Stimpson, 1851)
- *Divaricella quadrisulcata* (Orbigny, 1842)
- *Thyasira trisinuata* Orbigny, 1842
- *Astarte crenata subaequilatera* Sowerby, 1854
- *Crassinella lunulata* (Conrad, 1834)
- *Dinocardium robustum* (Lightfoot, 1786)
- *Spisula solidissima* (Dillwyn, 1817)
- *Ensis directus* Conrad, 1843
- *Tellina agilis* Stimpson, 1857
- *Tellina versicolor* DeKay, 1843
- *Tellina tenella* Verrill, 1874
- *Macoma tenta* (Say, 1834)
- *Abra lioica* (Dall, 1881)
- *Mercenaria mercenaria* (Linné, 1758)
- *Mercenaria campechiensis* (Gmelin, 1791)
- *Dosinia discus* (Reeve, 1850)
- *Gemma gemma* (Totten, 1834)
- *Petricola pholadiformis* (Lamarck, 1818)
- *Corbula contracta* Say, 1822
- *Corbula swiftiana* C. B. Adams, 1852
- *Barnea truncata* (Say, 1822)
- *Cyrtopleura costata* (Linné, 1758)
- *Pandora gouldiana* Dall, 1886
- *Pandora inflata* Boss & Merrill, 1965

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A RECONSIDERATION OF SYSTEMATICS IN THE MOLLUSCA (PHYLOGENY AND HIGHER CLASSIFICATION)

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ABSTRACT

A reconsideration of phylogenetic interrelations in molluscs with respect to several more recent studies on different groups of various taxa leads to a somewhat revised presentation of presumed molluscan evolution. Taking into consideration not only the quantitatively predominant shelled groups, adequately documented as fossils, but allowing also for the minor, yet comparative-anatomically equivalent aplacophoran molluscs, the synorganizationally relevant characters and organ systems reflect distinct anagenetic pathways. This analysis evidences a homogeneous frame of continuous evolution along a phylogenetic main line of archimolluscs—Placophora—Conchifera, and an early sidebranch of Scutopoda. Four essential steps of progressive differentiation are obvious which separate a) the Scutopoda (Caudofoveata) from the Adenopoda (all other molluscs), b) the Solenogastres from the shell-bearing adenopods (Testaria), c) the Placophora from the Conchifera, and d) the conchiferan groups among each other; herein, the Placophora and Solenogastres are synapomorphously tied together in contrast to the merely symplesiomorphous characters in Solenogastres and Caudofoveata ("Aplacophora"). A correspondingly modified higher classification is proposed.

INTRODUCTION

Increase in the knowledge of comparative anatomy and increase in the number of species frequently cause systematic problems. This is especially obvious when a major group of organisms is thoroughly studied and revised, or when some aberrant organization is introduced and/or brought to general knowledge. Since systematics should—as far as possible—coincide with the respective relationships of different organization with an adequate classification (to get a 'natural' system), all taxa within a group as well as the higher taxa should be arranged according to equivalent morphological or other quality—but not with respect to quantity (of species, etc.) or scientific importances (actual or seeming). In the endeavour to present phylogenetic relationships, only monophyletic groups can be classified together; this, however, can only seldomly be confirmed within a linear system (cf. Mayr, 1974). Therefore, a compromise must be accepted which intervenes between evidenced phylogenetic course and usable praxis.

Such systematic discrepancies and problems have more recently been raised in various aspects and levels within the Mollusca, and especially with regard to differences in zoological and paleontological points of view. Most molluscan classifications suffer from domination by the—generally well-investigated—conchiferan groups, which are sometimes even uniquely regarded as "true" molluscs (cf. Fretter & Graham, 1962, etc.). This often results also in the proposition to accept purely conchiferan conditions as ancestral for molluscan organization: the Conchifera—or even the mere Gastropoda—are misinterpreted so as to represent the organizational standard for all Mollusca (cf. e.g. Yonge, 1947; compare also Runnegar & Pojeta, 1974; Yochelson, 1978). Respective to these conditions, the present contribution tries to present and discuss those various discrepancies for the higher taxa within all molluscs, and to synthesize them for a classification that is adequate phylogenetically as well as for practical systematics.

CAUDOFOVEATA AND SOLENOGASTRES

Several more recent studies (S. Hoffman, 1949; Boettger, 1955; Salvini-Plawen, 1969, 1972) have especially dealt with the organization of the so-called aplacophoran molluscs, resulting in the evidence that they constitute "two long-separate lines" (Stasek, 1972: 40) which diverged at the basic level of archimolluscan organization. When thoroughly compared in their organ systems, the Caudofoveata (the former Chaetodermatina/ Chaetodermomorpha / Chaetodermoidea) and the Solenogastres (also Neomeniina/ Neomeniomorpha/Neomenioidea) are similar primarily in the symplesiomorphous mantle structure and muscle systems, as well as in the convergently reduced true gonoducts. The alimentary tract in Caudofoveata could be derived from the more primitive one in the Solenogastres (the latter having the most conservative configuration within all mollusca; cf. Salvini-Plawen, 1969, 1972, 1979). All other organ systems (foot, mantle cavity, reproductive system, also nervous system and circulatory system), however, are not synorganizationally derivable from each other in both groups, consequently resulting in the cognition of early convergence of both evolutionary lines.

The Caudofoveata already deviated at the most primitive level of common molluscan organization in adapting to a burrowing way of life. The elaboration of the cerebrally-innervated section of the ventral gliding surface to the actual pedal shield, the reduction of the other gliding surface with the mid-ventral fusion of the lateral mantle rims, and the elaboration of the body wall musculature to a hydrostatic muscular tube are distinct results of that adaptation. The differentiation of the strong longitudinal musculature in the anterior body (including the regression of other muscle systems) must be understood with respect to the antagonistic body fluid for burrowing locomotion in the sediment. And the feeding on microorganisms resulted in a brushing radula of the distichous type (and later on a forceps-like seizing organ), as well as in the separation of a ventral midgut gland including, in higher members only, the differentiation of a protostyle and a gastric proto-shield (primitive stomach; cf. Salvini-Plawen, 1979).

The Solenogastres are conservative members of the alternative evolutionary line within those early molluscs which proceeded in a gliding-creeping locomotion upon the ventral surface, but having already differentiated a peripedal mantle cavity, a rudimentary head (snout), and the pedal gland. They are still provided with the primitive mantle cover and—owing to their early preference for feeding as predators on Cnidaria—with the original configuration of a pouched midgut (and serial dorsoventral muscle bundles). The narrowing of the whole body including the foot, the partial reduction of the mantle cavity and its partial internalization are adaptations to a winding-wriggling manner of muco-ciliary locomotion on secondary hard bottoms (also coral reefs, littoral, etc.). The manifold modifications of the monoserial radula and/or the differentiation of a pharyngeal sucking-pump are further adaptations for feeding on Cnidaria (cf. Salvini-Plawen, 1979).

The most obvious evidence for these divergent evolutionary pathways in the Caudofoveata and the Solenogastres comes from the comparative analysis of the pedal system and the mantle cavity. Solenogastres, Placophora and Conchifera possess a ventrally-innervated foot and a distinct pedal gland associated with it; on the contrary, the Caudofoveata are only provided with a cerebrally-innervated pedal shield structurally almost identical to the foot of other molluscs. The presence of mucous glandular cells like those along the pedal groove in the Solenogastres (cf. S. Hoffman, 1949), the lack of mantle folds (Fig. 3), and the cerebral innervation of the pedal shield (Salvini-Plawen, 1972) contradict its interpretation as secondarily re-established pedal organ, but positively indicate its primitive condition. The ventrally-innervated section of the ancestral gliding surface in the caudofoveatan line has been reduced from posterior to anterior (as is still obvious in some species of *Scutopus*), so that the mantle edges are midventrally fused (Fig. 3). The mantle cavity coincides in its terminal position with that statement, and it has medially inverted pallial grooves with mucous tracts and with ventrolateral (!) openings of the pericardial outlets (cf. S. Hoffman, 1949; Salvini-Plawen, 1972). That configuration, as well as the total lack of further portions of the mantle cavity essentially serve to contrast the whole organ system of the Caudofoveata to that in the Solenogastres (and other molluscs), both of which cannot be derived from each other.

Also the gonopericardial system of both Caudofoveata and Solenogastres can in no case be derived from each other. Findings in *Phyllomenia* and further arguments (cf. S. Hoffman, 1949; Salvini-Plawen, 1970b, 1972, 1978) clearly indicate that the forerunners of the Solenogastres possessed both pericardioducts as well as gonoducts; the latter, however, are now predominantly in secondary connexion by their upper portion with the pericardium (the lower portions then being reduced). The pericardioducts open into the spawning ducts, i.e. the internalized posterior-lateral sections of the mantle cavity provided

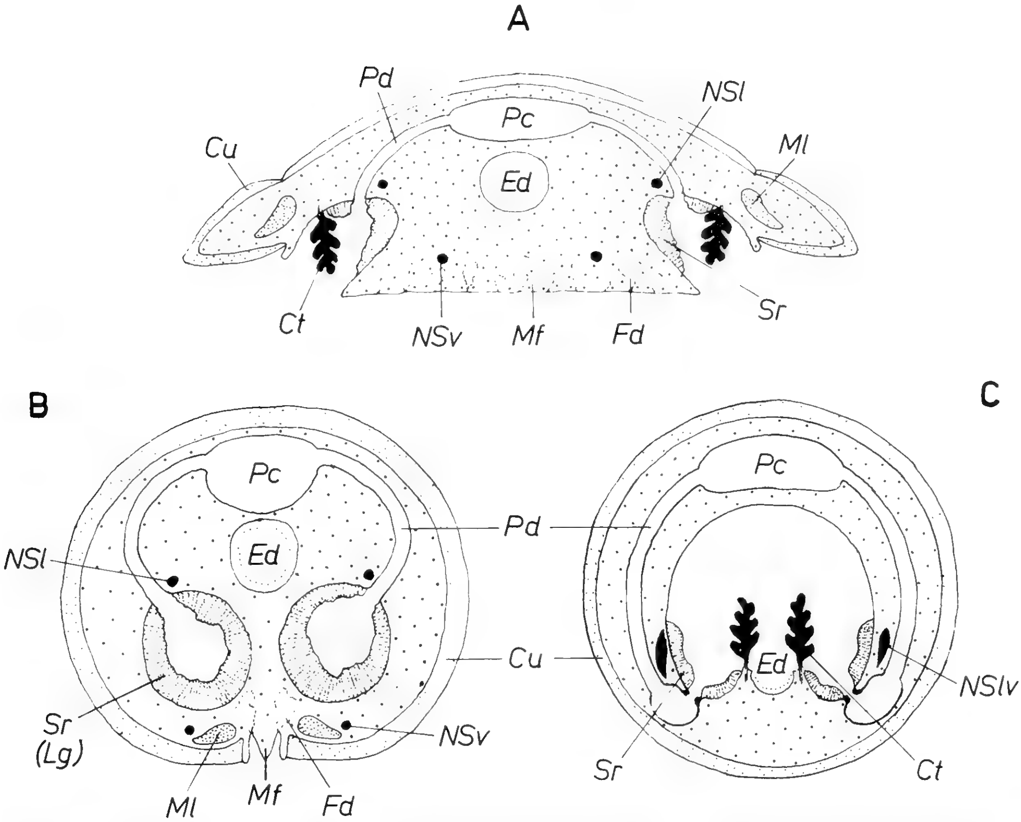

FIG. 1. Comparative arrangement of the pallio-pericardial system in A Placophora-Lepidopleuridae, B Solenogastres, and C female Caudofoveata (after Salvini-Plawen, 1972). *Ct* ctenidium, *Cu* mantle-cuticle, *Ed* hind gut, *Fd* sole glands, *Lg* spawning duct, *Mf* foot, *Ml* longitudinal muscle, *NSl/NSv/NSlv* lateral and ventral nerve cords, *Pc* pericardial cavity, *Pd* pericardioduct, *Sr* mucous tract.

with the mucous tracts (S. Hoffman, 1949; cf. Fig. 1). In contrast, the pericardioducts in the Caudofoveata open into ectodermal glandular ducts (cf. Fig. 1) which, owing to their configuration as well as to their structure, neither belong to the pericardioducts nor to the mantle cavity (into which they open ventrolaterally by means of a narrow opening with strong sphincter). Since there are no real gonoducts in the Caudofoveata, these glandular ducts may possibly constitute the altered lower portions of the original gonoducts (cf. Salvini-Plawen, 1972: 251 ff.).

Such outlined conditions, and properties in further organ systems synorganizationally considered in Caudofoveata and in Solenogastres (cf. Salvini-Plawen, 1972; Salvini-Plawen & Boss, 1980), cannot be derived from each other and hence obligatorily prove the basically independent evolutionary differentiation of both groups from an ancestral organization common to all molluscs (see Figs. 3–5).

Following knowledge of the "diphyletic Aplacophora" (Stasek, 1972: 19),[1] the Caudofoveata (Boettger, 1955) have been separated from the solenogastrid aplacophorans and raised to the rank of an independent class, equivalent to Solenogastres and Placophora (Salvini-Plawen, 1967, 1968b, 1975). The some 65 described species are grouped in three families (Salvini-

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[1] Although Stasek (1972: 19 & 40) is well aware of the "long-separate," "diphyletic" aplacophoran molluscs, he takes this knowledge not into account and inexplicably classifies both groups again under one single taxon. There are no comments here on the mis-conceived interpretation by Scheltema (1978) as concerns commonly inherited (symplesiomorphous) and phylogenetically specialized (apomorphous) characters.

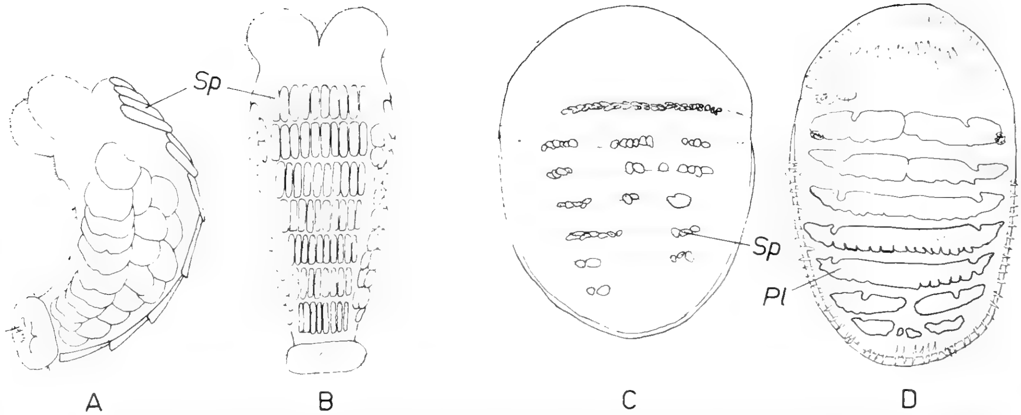

FIG. 2. Differentiation of the mantle cover in just metamorphosed individuals of *Nematomenia banyulensis* (Solenogastres; A lateral, B dorsal view) and of *Middendorffia caprearum* (Placophora; C and D two successive stages) (after Pruvot and Kowalevsky from Salvini-Plawen, 1972). *Pl* shell plates in formation through coalescence of the juxtaposed scaly bodies *Sp* arranged in seven transverse rows.

Plawen, 1968b, 1975) within the single order Chaetodermatida Simroth (emended by Smith, 1960).

Precisely defined by the term Solenogastres (Gegenbaur, 1878: 139; *solen* = tube, groove, and *gaster* = venter, 'belly'), these numerically predominant aplacophoran organisms with a ventrally-innervated foot narrowed to a groove persist as a distinct class; the unfamiliar terms Telobranchiata (Koren & Danielssen, 1877) and Ventroplicida (Boettger, 1955) hence can be disregarded. A comprehensive analysis of the 180 Recent species (Salvini-Plawen, 1978) brought about the establishment of four orders (Pholidoskepia, Neomeniomorpha, Sterrofustia, and Cavibelonia) within two higher levels of organization (supraorders Aplotegmentaria and Pachytegmentaria).

The long ignored investigation of aplacophoran molluscs, their seemingly small numbers, their lack of a shell, and their worm-like shape unfortunately led to a misunderstood interpretation until a few years ago in regarding them either as vaguely mollusk-like or as aberrant Mollusca. Only a few authorities (e.g. H. Hoffmann, C. R. Boettger), according to their general knowledge, took a neutral point of view independent of hypertrophic information on Conchifera and evaluated the molluscan organizations comparatively according to differentiated quality. As a consequence of the more recent organizational-evolutionary elucidations, neither the superficially similar appearance of Caudofoveata and Solenogastres, nor their seemingly hidden manner of living in being exclusively distributed in marine habitats of greater depths can serve as arguments for conservative under-estimation: The taxon Aplacophora (Ihering, 1876) had to be abandoned, since it artificially unites two basically different, diphyletic evolutionary lines which merely coincide by some ancestral (symplesiomorphous) characters but by no single commonly-acquired (synapomorphous) property.

PLACOPHORA

In considering the (Poly-)Placophora, one condition has generally not been taken sufficiently into account, viz. the ontogenetic differentiation of initially only seven shell plates (cf. summary in Smith, 1966). That peculiarity is underlined by the predominant 'abnormality' in adults, i.e. the formation of only seven plates (cf. H. Hoffmann, 1929/30: 173; Taki, 1932). A further particularity is met within the Solenogastres, where the metamorphosed stage of *Nematomenia banyulensis* (a member of the most conservative Pholidoskepia) is provided dorsally with seven transverse rows of juxtaposed scaly bodies; this coincides exactly with an occasional condition in the Placophora (Fig. 2), where the formation of the plates results from the coalescence of calcareous granulations arranged in seven transverse rows.[2] Finally, the record of fossil Placophora with seven plates, described as

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[2] "formation des plaques par la coalescence de granulations calcaires" (Kowalevsky, 1883: 33).

Septemchiton (Bergenhayn, 1955; Sanders, 1964), must be emphasized. This seven-plated condition shows that the placophoran stock originated in organisms which differentiated only seven primordial calcareous plates, presumably through coalescence of the formative anlagen (the isolated-intracellular centers of calcification) of juxtaposing bodies provided with a basal quinone-tanned organic layer ("cup"; cf. S. Hoffman, 1949; Beedham & Trueman, 1967, 1968; Carter & Aller, 1975); the same stock also gave rise to the Solenogastres. The Septemchitonida, therefore, are either the direct successors of that primitive stock, or they form an evolutionary line arising by paedomorphy. In either case, however, it appears necessary to separate the order Septemchitonida within a special subclass, for which the term Heptaplacota is proposed.

The comprehensive revision of the Placophora by Bergenhayn, (1930, 1955, 1960) included fossil as well as Recent members and resulted in a homogeneous system that is largely accepted (cf. Smith, 1960, Van Belle, 1975). With the separation of the Septemchitonida as a special subclass Heptaplacota, the main line constitutes the (hypothetical) Eoplacophora (Pilsbry, 1893; see Bergenhayn, 1955: 39), more or less identical with the subclass Loricata including Bergenhayn's orders Chelodida, Lepidopleurida, Ischnochitonida (= Chitonida), Acanthochitonida, and Afossochitonida[3]). Only the Chelodida are hence included with the supraorder Palaeoloricata and contrasted to the other orders = Neoloricata; the latter, however, do not form a monophyletic group but have, according to Bergenhayn (1960: 176), a diphyletic root within the Chelodida. The Neoloricata constitute therefore an artificial group to be avoided. Starobogatov & Sirenko (1975) discuss in a short article the classification within the Neoloricata and reclassify them in accepting the articulamentum-bearing orders Scanochitonida nov., Lepidopleurida including Bergenhayn's Afossochitonidae, and Chitonida including Ischnochitonina and Acanthochitonina; the dubious *Llandeilochiton* is omitted (cf. also Van Belle, 1975), and the Palaeoloricata anyway remain identical with the order Chelodida.

The first term given for the chitons as an independent group was that of Ducrotay-Blainville in 1819 as Polyplaxiphora; it was amended in 1821 to Polyplacophora by Gray. It was, however, Ihering, (1876) who introduced the group in a comparative point of view with respect to the molluscs; accordingly his—also familiar, and even simpler—term Placophora may be preferred, even more so since there is no problem in confusing the group.

TRYBLIDIIDA AND BELLEROPHONTIDA: GALEROCONCHA

Early Cambrian univalve molluscs have long been a cause for scientific debate whether planispiral shells belong to untorted (exogastric) or torted (endogastric-gastropod) organization (cf. Runnegar & Jell, 1976; Berg-Madsen & Peel, 1978). Recent investigations (Rollins & Batten, 1968, and others) have shown that the exogastric tryblidiids already possessed a marked shell sinus, since *Sinuitopsis acutilira* (Hall) with its three pairs of symmetrical muscle scars, as well as other similarly organized species unequivocally must be regarded as untorted-exogastric. The sinus in *Sinuitopsis* therefore proves that this shell character (and even the shell slit) has been evolved adaptively long before gastropod torsion took place. Thus there is no further argument in favour of considering the Bellerophontida, provided with a sinus and/or shell-slit and with one symmetrically-arranged pair of dorsoventral muscle bundles (cf. Knight, 1947), as belonging to the gastropods; the sinus or slit merely demonstrates the symmetrical (paired) arrangement of the pallial organs (cf. also Fretter, 1969).

Pojeta & Runnegar (1976: 24 ff.) likewise discuss most arguments and come to the conclusion that the Bellerophontida as well as the Helcionellacea were untorted organisms with an exogastric shell (cf. also Runnegar & Jell, 1976). The symmetrical arrangement of one single pair of muscle scars in adults, however, might also be due to regulative migrations of the muscles during larval development (compare Scissurellidae, and cf. Crofts, 1937, 1955); but additional conditions refute the arguments of Knight (1947, 1952); Cox & Knight, (1960); Berg-Madsen & Peel (1978); and also Stasek (1972):

a) Gastropod torsion occurs in two phases, and loss of equilibrium in the pelagic larva after the first phase because of the heavier

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[3] The suffix -ina generally designates a suborder, whereas for orders the ending -ida should be used (cf. also Starobogatov & Sirenko, 1975).

main bulk of the visceral mass at the left side automatically causes an asymmetry of the whole pallio-visceral complex of the larva including the covering shell: only the left set of pallial organs develops (cf. Fretter, 1969) and the shell becomes asymmetrical before (!) the second phase of torsion begins (cf. Crofts, 1937: 242 f, 259). Since that asymmetrical growth is independent of the (endogastric) coiling of the visceral hump, every shell of torted animals principally demonstrates an asymmetrical condition in the larvae (cf. Fretter & Graham, 1962: 447); this however, is not the case within the Bellerophontida.

b) The growth of a more coiled shell in the plantigrade stage of metamorphosing archaeogastropods with differential regulative processes causes a posterior overweight (right side of the post-torsional visceral hump with shell) which is compensated by dextral helicoid growth and thus appears to be an indirectly-caused consequence of torsion. Planispiral coiling can therefore generally be considered as proof of an untorted condition (comp. also most Nautiloida, Ammonoida, etc.); only rarely is symmetry secondarily reached, e.g. in some exceptional gastropods such as *Caecum,* several Omalogyridae, and others.[4])

c) Many operculum-bearing gastropods show some very distinct adaptive structures at the shell-aperture in relation to the respective operculum—in contrast to all known Bellerophontida with a more or less symmetrical, homogeneously formed and wholly regular, wide holostomous aperture. This coincides with the negative record of opercula in bellerophontid beds, indicating that the operculum is obviously an evolutionary attribute of the torted condition, the more since its functional secretion takes place asymmetrically (!) by glands at the post-torsional right side of the posterior pedal ectoderm (compare also Crofts, 1937: 240; 1955: 738).

Summing up earlier arguments (cf. Pojeta & Runnegar, 1976) and the above presented additional arguments, we may positively state that the majority of organisms assigned to the Bellerophontida were untorted animals with a planispiral, exogastric shell. Consequently they have to be separated from the torted Gastropoda and classified closer to the cap-shaped tryblidiids, as already realized by Simroth (1904) and Wenz (1940) and as also discussed by Salvini-Plawen (1972: 272 f). Wenz classified the Tryblidiacea and Bellerophontacea together within the subclass Amphigastropoda, but without separation from the gastropods (the diagnostic definition of the latter, therefore, becoming inaccurate). Today there is no doubt that the Gastropoda are defined by torsion (and presence of an operculum), and that the untorted groups have to be arranged as a distinct class outside the gastropods. Hence, the term Galeroconcha may be suitable to include Tryblidiida and Bellerophontida, since 'Monoplacophora' is (as a synonym) unequivocally tied to the cap-shaped or orthoconic Tryblidiida (= Tryblidiacea Wenz)[5] and contrasted to the Bellerophontida (= Bellerophontacea Wenz). The class Galeroconcha is defined to consist of fossil and Recent laterally-symmetrical and untorted Conchifera with a cap-shaped to (exogastrically) planispiral shell, devoid of a siphon and covering the whole body, and with symmetrically-paired dorsoventral muscle bundles which may be fused; it includes the two orders (subclasses) Tryblidiida (Monoplacophora) and Bellerophontida (Bellermorpha) (cf. Salvini-Plawen, 1972: 272).

Findings of Recent tryblidiids (*Neopilina*) have led not only to a reactivation of the annelid-theory (derivation of the molluscs from segmented coelomates) which has since been totally refuted by Boettger (1959), Vagvolgyi (1967), Salvini-Plawen (1968a, 1969, 1972), Stasek (1972), Trueman (1976) and others; it also resulted in an increased interest in the whole group, followed, however, by some taxonomic confusion and nomenclatorial misinterpretation (cf. Cesari & Guidastri, 1976; Berg-Madsen & Peel, 1978; Yochelson, 1978). On the one hand, there is a peculiar misuse of the taxon and term Monoplacophora (by Runnegar & Jell, 1976, even assigned to Knight, 1952); most obvious, however, is the trend toward a hypertrophical classification of the fossil genera and families (cf. Knight & Yochelson, 1958; Starobogatov, 1970; Golikov & Starobogatov, 1975, and others) which does not correspond to the degree of morphological differences that are present. Similarly, neither the classification of

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[4] The protoconchae in Tryblidiina are mostly bulbous and uncoiled (cf. Menzies, 1968: 7); the slight larval (pretorsional-) dextral coiling in *Neopilina galatheae* therefore has nothing to do with the helicoid coiling in plantigrade (postlarval) gastropods.

[5] "man könne die Tryblidiacea geradezu als Monoplacophora bezeichnen" (Wenz, 1940: 5, citing Odhner); compare also Yochelson, 1978.

TABLE 1. Classification of the Galeroconcha.

Classis GALEROCONCHA nov. (pro "Amphigastropoda" Simroth in Wenz, 1940)

Ordo **Tryblidiida** Wenz, 1938 (= **Monoplacophora** Odhner in Wenz, 1940)
  Subordo Tryblidiina Pilsbry, 1899
  Subordo Cyrtonellina Knight & Yochelson, 1958
  Subordo Archinacellina Knight, 1956

Ordo **Bellerophontida** Ulrich & Scofield, 1897 (= **Belleromorpha** Naef, 1911)
  Subordo Sinuitopsina Starobogatov, 1970
  Subordo Helcionellina Wenz, 1938
  Subordo Bellerophontina McCoy, 1851

some more closely related genera or families in orders, nor a subdivision of the newly defined class Galeroconcha into two subclasses appears to be adequate and hence justified; as evidenced by Yochelson (1967), Pojeta & Runnegar (1976), Runnegar & Jell (1976), or Berg-Madsen & Peel (1978), the morphological variation does not exceed the level of two orders.

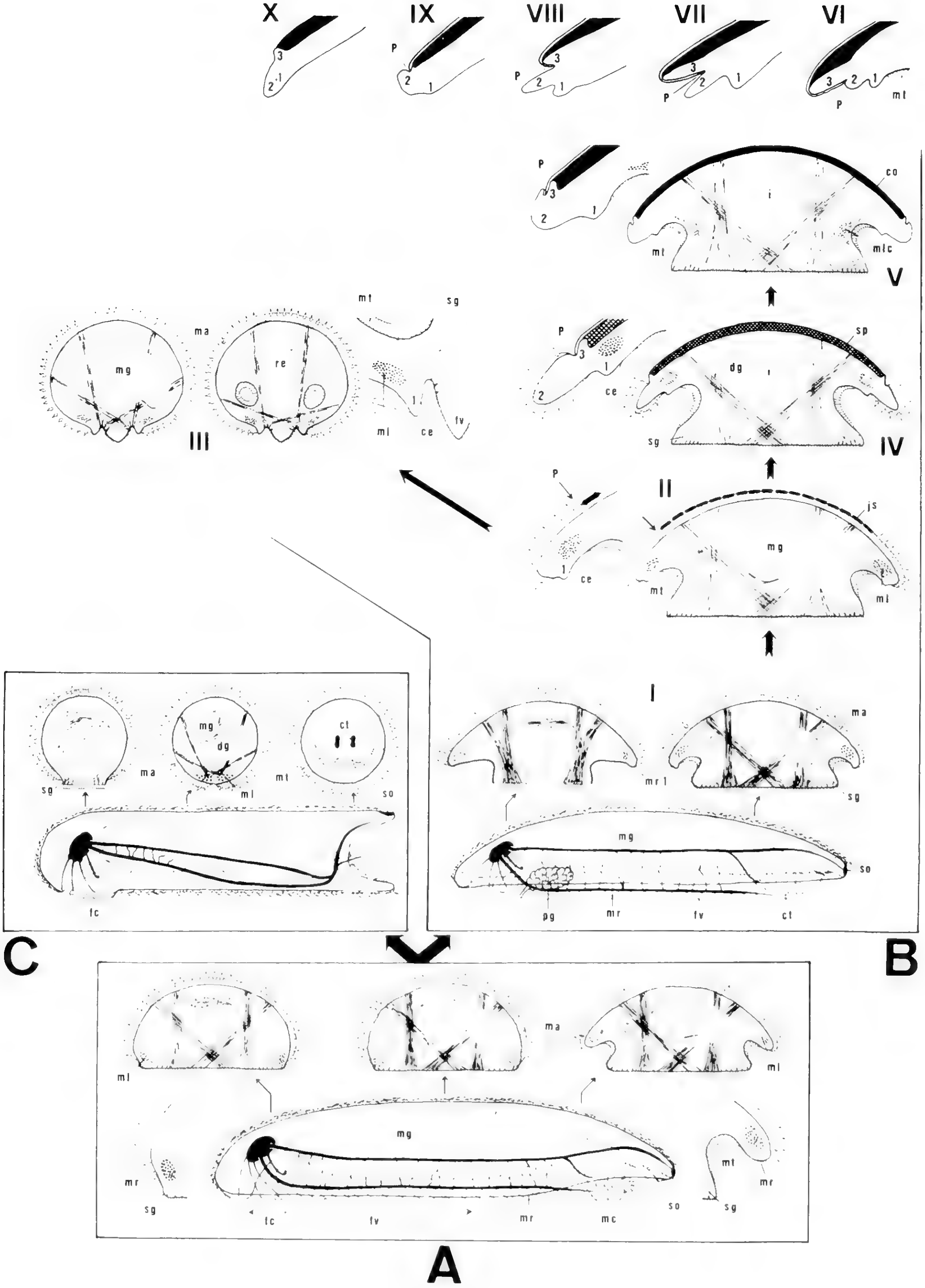
With the new concept of Galeroconcha, the classification of Horný (1965) can also be abandoned: his Tergomya are identical with the Tryblidiina (see Table 1), and his Cyclomya are partly incorporated within the Bellerophontida (cf. also Pojeta & Runnegar, 1976; Runnegar & Jell, 1976). To avoid further confusion, we retain the general outline of both orders as presented by Knight & Yochelson (1960), Yochelson (1967), and Berg-Madsen & Peel (1978), which is predominantly based upon the configuration of the concha. Some uncertainty remains only with a few cyrtoconic members, and the position of the Archinacellina as well as Helcionellina still needs confirmation (cf. Knight & Yochelson, 1960; Yochelson et al. 1973; Golikov & Starobogatov, 1975; Pojeta & Runnegar, 1976; Yochelson, 1978); the Multifariida Byalyi can be recognized as a separate family within the Sinuitopsina, and the Kirengellida Rozov obviously belong to the Tryblidiina close to *Scenella* (cf. Runnegar & Jell, 1976; Berg-Madsen & Peel, 1978).

The classification of the Galeroconcha, including the Tryblidiida (with cap-shaped to cyrtoconic concha, mantle cavity generally peripedal) and the Bellerophontida (with exogastrically-planispiral concha generally provided with a midposterior sinus or slit, mantle cavity generally confined to the posterior body), can be summarized as in Table 1.

Finally, it should be pointed out that despite agreement with Runnegar in considering the Bellerophontida to be untorted organisms and hence with an exogastric visceral sac, there is disagreement in two major phylogenetic points of view. First, as extensively demonstrated by Salvini-Plawen (1972), nowhere discussed by Runnegar, the ontogenetic as well as comparative-anatomical condition in the Placophora unequivocally evidences their interconnecting organizational level between the aplacophoran and conchiferan grades (compare also Figs. 3–5). Therefore, the hypothesis of a secondary subdivision of the concha as evolving to seven or eight plates in Placophora (Runnegar & Pojeta, 1974; Pojeta & Runnegar, 1976) has to be rejected. Moreover, the cap-shelled (limpet-shaped) Tryblidiina must be considered ancestral to the other conchiferans. This is supported by further arguments concerning the comparative analysis of Placophora and *Neopilina* (cf. Salvini-Plawen, 1969; 1972). Consequently, the tergomyan Tryblidiina are the primitive stock when compared with other Galeroconcha. Secondly, the functional synorganization of comparative anatomy confirm the evolutively close relationship between the Bellerophontina and the origin of Gastropoda as presented below. Consequently, there is full agreement with the critique of Berg-Madsen & Peel (1978: 123) as concerns the phylogenetical role of Pelagiellacea emphasized by Runnegar.

GASTROPODA

The principal diagnostic criterion for the Gastropoda is torsion (cf. also Yochelson, 1967, and others), supplemented by the presence of an operculum and the lack of the (post-torsional) left gonad. According to the arguments discussed above, the Bellerophontida are not considered to be torted and are thus separated from the gastropods. There is, however, distinct evidence that—in contrast to Runnegar & Jell (1976) or Runnegar & Pojeta (1974)—some Bellerophontina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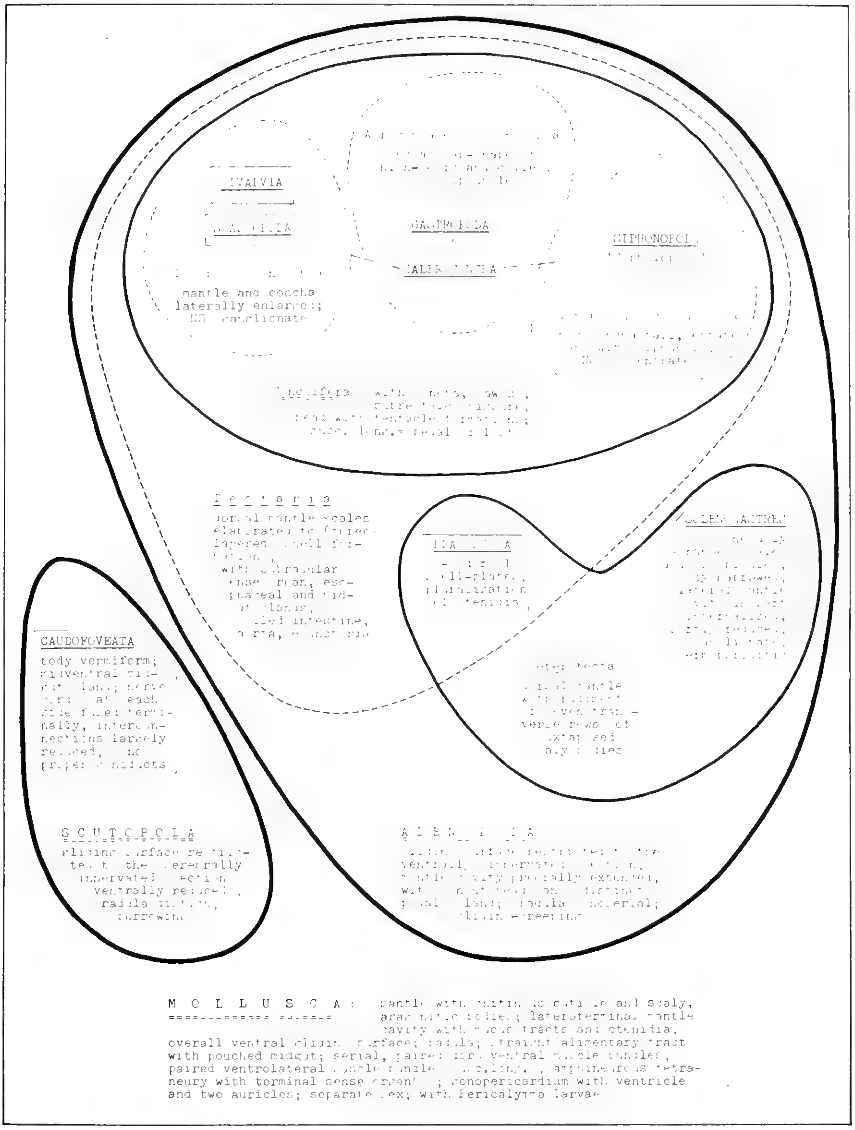
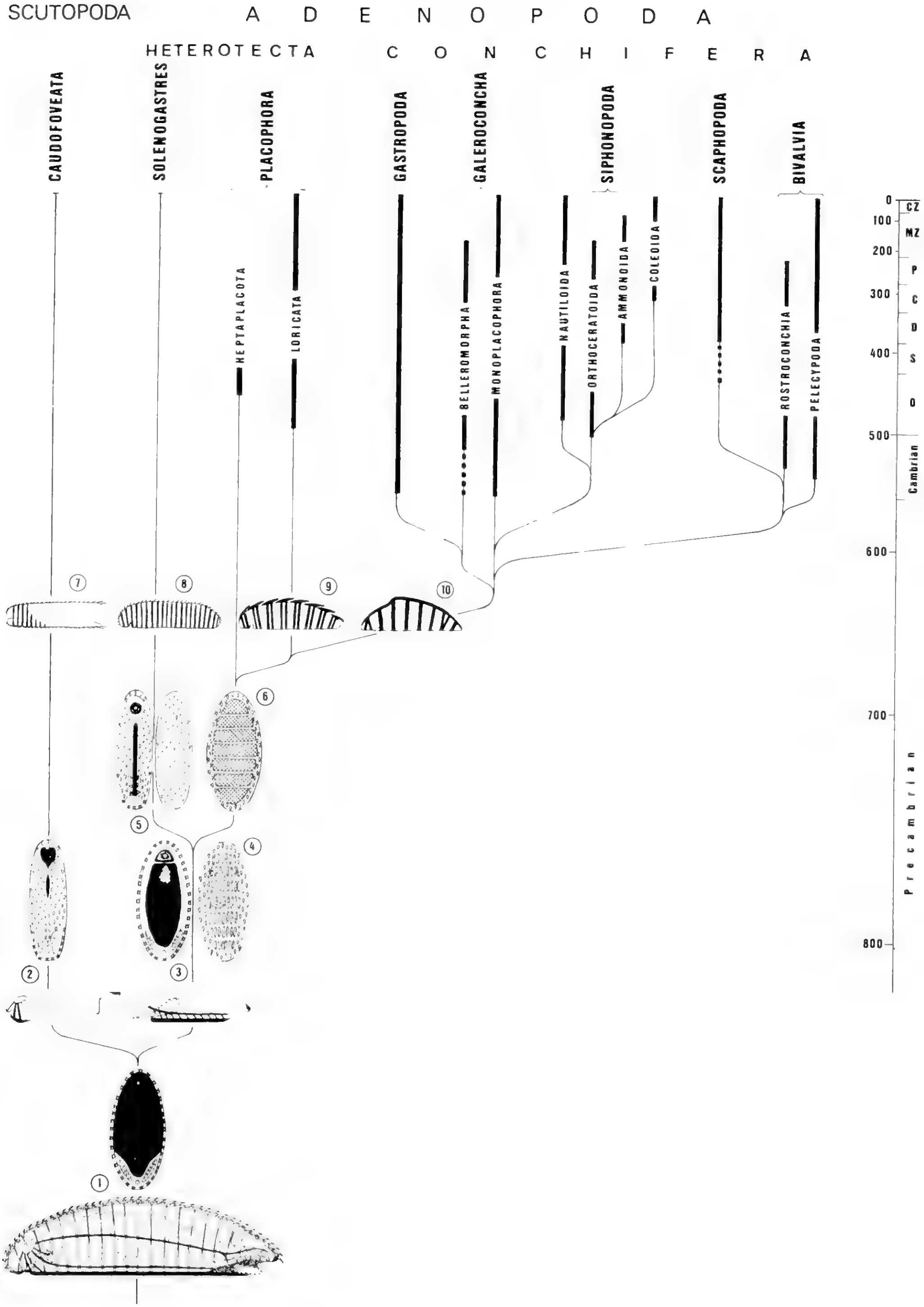


FIG. 4. Anagenetic relations of the molluscan classes by means of commonly-acquired (synapomorphous) main features indicated for the levels (encircled).

←

FIG. 3. Scheme of the evolutionary pathways in Mollusca (predominantly with respect to the mantle, the mantle cavity, the locomotory surface, the dorsoventral as well as longitudinal muscle systems, and in A, B_I, C the main nervous system). A ancestral Mollusca; B Adenopoda; C Scutopoda (Caudofoveata). I ancestral Adenopoda; II ancestral Heterotecta; III Solenogastres; IV Placophora; V ancestral Conchifera; VI Galeroconcha (*Neopilina*); VII Bivalvia; VIII Siphonopoda (*Nautilus*); IX Gastropoda (*Haliotis*); X Scaphopoda. *1* inner fold of mantle edge (= *mr*), *2* middle fold of mantle edge, *3* outer fold of mantle edge; *ce* cuticularized cilia-epithelium of mantle cavity, *co* concha, *ct* ctenidium, *dg* midgut gland, *fc* cerebrally innervated section of locomotory surface (in C: pedal shield), *fv* ventrally innervated section of locomotory surface (in B: foot), *i* intestine, *js* juxtaposed scaly calcareous bodies, *ma* scales- and cuticle-bearing mantle, *mc* mantle cavity, *mg* midgut, *ml* musculus longitudinalis, *mlc* musculus (long.) circularis, *mr* mantle rim (= *1*), *mt* mucous tract, *p* periostracal groove, *pg* pedal gland, *re* rectum, *sg* sole glands, *so* terminal sense organ, *sp* shell plate.


SCUTOPODA
ADENOPODA
HETEROTECTA
CONCHIFERA
CAUDOFOVEATA
SOLENOGASTRES
PLACOPHORA
GASTROPODA
GALEROCONCHA
SIPHONOPODA
SCAPHOPODA
BIVALVIA
HEPTAPLACOTA
LORICATA
BELLEROMORPHA
MONOPLACOPHORA
NAUTILOIDA
ORTHOCERATOIDA
AMMONOIDA
COLEOIDA
ROSTROCONCHIA
PELECYPODA
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were direct phylogenetic and morphological forerunners of the Gastropoda, initially merely separated by the shift of the pallio-visceral complex into an anterior position.

This process of torsion proper was probably not due to a spontaneous mutation (cf. Crofts, 1955; Fretter & Graham, 1962) which would demand the postulation that at least two reproducing individuals simultaneously underwent an identical and dominant mutation to be spread in the population; with respect to the condition in lower gastropods, it was much more probably because of two different gradual adaptive processes, (a) to regulate stabilization of the larval equilibrium and (b) to regulate balancing posture in the plantigrade stage (cf. Crofts, 1955: figs. 9–10; Ghiselin, 1966: 347; Minichev & Starobogatov, 1972; Underwood, 1972). Larvae of exogastrically coiled animals (but not of cap-shaped tryblidiids as speculated by Stasek, 1972) show already in early stages a prominent visceral mass with the shell rudiment; it thus disturbs the axial equilibrium as well as the balance in the case of directional swimming. That effect is now ontogenetically compensated by the reestablishment of equilibrium relative to the direction of the larva's movement carried out by the developmental acceleration of the right larval shell muscle running obliquely to the head-foot: its contraction causes the first (and true) phase of torsion (90°) in relation to the foot (but not in relation to the axis of equilibrium), swinging the visceral mass into the right position for the larva's balancing posture in the pelagic zone relative to the propelling ciliary apparatus. The genetic fixation of such a precocious acceleration (tachymorphous heterochrony) for larval equilibrium consolidated torsion of 90°; it directly resulted in the mere development of the (post-torsional) left set of pallial organs including the retractor (cf. Fretter, 1969), since the respiratory water currents enter (left-) frontally and leave toward the (frontal) right.

That quasi-monotocardian condition is not altered before the beginning plantigrade stage of the metamorphosing larva, in which the balancing posture relative to the substratum and the axial divergence of about 90° (palliovisceral bulk versus body axis) is regulated by differential growth processes—shifting the mantle cavity into rather an anterior position (second phase of approximately another 90°; cf. Crofts, 1937, 1955). The mantle/shell sinus or slit already existing appears to be a prerequisite for the survival of such torted animals in not shedding their waste products towards the inhalant currents. The regulative growth also includes the development of the right pallial organs and right dorsoventral retractor muscle.

The process of torsion and its consequences may herewith be summarized as:

—The pretorsional presence of a planispirally coiled visceral hump with a midposterior shell-sinus or slit (compare Bellerophontina);

—regulative shifting of the heavy visceral mass of the larvae towards an arrangement of equilibrium for their balancing posture in the pelagic environment, and the adaptive dominant development of the right larval, dorsoventral retractor muscle;

—positively selective, genetic stabilization of the precociously accelerated development

FIG. 5. Diagram of the phylogenetic radiation of the Mollusca (black bars indicate fossil records; time-scale in millions of years, logarithmic). (1) Hypothetical archi-mollusc (main organization, and ventral view) with overall ventral gliding surface (black), posterio-lateral mantle cavity, scale-bearing mantle, straight midgut pouched laterally, serial dorsoventral muscle bundles, gonopericardial system, and main nervous system with terminal sense organ(s). (2) Evolutionary branch of burrowing Scutopoda (lateral and ventral) with cerebrally-innervated section of locomotory surface (= pedal shield, black) and reduction of its ventrally-innervated section. (3) Evolutionary branch of gliding-creeping Adenopoda (lateral and ventral) with ventrally-innervated section of locomotory surface (= foot, black) including the pedal gland, with rudiment of head, and with peripedal-preoral mantle cavity. (4) Level of primitive Heterotecta (dorsal view), dorsal mantle with seven transverse rows of juxtaposed scaly bodies. (5) Level of Solenogastres (ventral and dorsal) with narrowed body and foot, mantle cavity reduced to preoral sensory pit (atrial sense organ) and to internal tubes (spawning ducts); adult mantle cover altered again to homogeneous arrangement of scales. (6) Level of early Placophora (= Heptaplacota; dorsal view) with consolidation of juxtaposed scaly bodies to seven shell plates. (7) Regressive dorsoventral musculature in Caudofoveata. (8) Serial arrangement of dorsoventral musculature in Solenogastres; compare (1). (9) Serial arrangement of dorsoventral musculature in recent Placophora, concentrated according to the eight shell plates ($8 \times 2 = 16$). (10) Primitive Conchifera with further concentration of the placophoran dorsoventral musculature (9) according to the homogeneous concha (see *Neopilina*).

of that right larval retractor: establishment of the first phase of torsion (90°);
—the predominant development of the pretorsional right (or: the retarded development of the pretorsional left) pallial organs due to respiratory currents (quasi-monotocardian stage);
—regulation of the divergent axial and balance conditions between the visceral hump and the head-foot respective to plantigrade movement by differential growth processes in metamorphosing animals: second phase of torsion[6] of approximately another 90°; this regulation includes and is combined with
—the development of the second (posttorsional right) set of pallial organs including the retractor muscle, the mantle/shell sinus/slit enabling the now paired inhalant respiratory current to be directed symmetrically from the latero-frontal areas towards the anterio-medio-dorsal area.

Starting from such a possible torsion process of two different adaptive phases which fully corresponds to the developmental patterns, Recent gastropods appear to belong to different lines having achieved pallial asymmetry independently (water currents, ctenidia, etc.):

1) The most conservative stock—also with respect to shell structure (cf. MacClintock, 1967)—possesses paired pallial organs (Zeugobranchia) and paired dorsoventral retractor bundles in the adults: Scissurellidae, Fissurellidae, Haliotidae;
2) The predominance of the posttorsional right retractor muscle and helicoid coiling result in the loss of the left retractor muscle: Pleurotomariidae;
3) The hypertrophy of the right retractor muscle and helicoid coiling leads to the suppression of the left retractor as well as to the right set of pallial organs: Trochacea;
4) The reason for the change in water currents and the abandonment of the right set of pallial organs remains enigmatic (cf. Yonge, 1947: 493, Golikov & Starobogatov, 1975: 190 f), since both retractor muscles are obviously retained and are united posteriorly (cf. Smith, 1935: 122 & fig. 25 with Crofts, 1955: 730 & fig. 19; but compare also Dodd, 1957): Patellacea;
5) The hypertrophy of the (posttorsional) right excretory-genital duct causes the pronounced asymmetry with the loss of the right set of pallial organs: Neritacea (paired retractor muscles retained);
6) The asymmetry of the pallial organs is due to a paedomorphous retention of the larval asymmetry (first phase of torsion, 90°) prior to regulation in the plantigrade stage. Owing to a long-lasting, planktotrophic larval life, the development of the right pallial organs as well as of the right retractor was more and more retarded; the period of formative potency to regulate the symmetry of the pallial organs was missed and the potency finally lost, so that the larval 'quasi-monotocardian' condition was preserved also in the post-metamorphic stage: Monotocardia, Pulmonata, Gymnomorpha, Opisthobranchia. The second phase of torsion during the early plantigrade stage thus merely comprises the differential growth to regulate the condition of balance and axes, but not the symmetrization of the pallial organs; occasional atavistic conditions may occur (e.g. paired retractor muscles in *Rissoella, Lamellaria, Trivia, Velutina,* or the larvae of *Acteon*; cf. Fretter & Graham, 1962; Bebbington & Thompson, 1968).

Among these lines with differently caused asymmetry, in accordance with other characters (cf. Yonge, 1947; Cox, 1960a) the groups (1) and (2) form one branch, as do the more advanced Trochacea (3); all three lines, however, are characterized by the predominance of the (posttorsional) right retractor muscle, and they retain the right excretory organ. The latter character is also maintained in the Patellacea (4) which, however, have a special organization, combining certain conservative traits with advanced ones, unlike other archaeogastropods (cf. Golikov & Starobogatov, 1975): Thus the odontophore and the complexity of the radula musculature may be a conservative character (cf. Graham, 1964: 326; 1973: 343), as the ctenidium appears to be; in contrast, the rudimental coiling of the shell without sinus or slit together with other characters point to an advanced level, at least adaptively removed from the common origin as far as the Trochacea are concerned, but with special properties.—On the other hand, the Neritacea (5) as well as all other

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[6] It must be pointed out that neither this second phase nor the detorsion in Opisthobranchia and Gymnomorpha are true rotation processes, but are due to regulative growth processes (cf. also Brace, 1977).

(monophyletic ?) gastropods (6) show the left excretory organ retained; in the Monotocardia, etc., the loss of the right set, however, obviously is due to an inhibitory discontinuation during development (abandonment of the regulative symmetrization in the pallial organs), whereas in the Neritacea a special condition of the reproductive system shows quite different evolutionary pathways.

Additionally, both the Neritacea and Patellacea are characterized by a conservative morphology of their ctenidium: In contrast to Yonge (1947: 495 ff) we cannot regard these organs as derived from a condition almost identical to that in zeugobranch gastropods. The merely basal attachment of the ctenidium, its lack of skeletal rods, as well as its short and stoutish lamellae, these characters rather prove a primitive, i.e. conservatively retained condition when compared with the ctenidia in Caudofoveata, Placophora, and also *Neopilina*; the same holds good even for the Valvatacea. Thus, also in this respect, both groups appear to be early offshots from the common gastropod stock, not yet having undergone in their ctenidia those alternations typical for the main lines (the skeletal rods, for example, are supports for mechanical needs, being analogous not only to those in Siphonopoda = Cephalopoda but also in Bivalvia).

Summing up the evolutionary pathways within early gastropods (cf. also Cox, 1960a; Golikov & Starobogatov, 1975), there appear to exist two main lines (1–3) and (6), as well as two early side-branches (4) and (5). In accordance with Yonge (1947) and Golikov & Starobogatov (1975), respectively, both the latter groups have to be admitted a more separate status[7] within the Archaeogastropoda. Hence, the order Archaeogastropoda would be classified adequately in three suborders, viz. the Vetigastropoda (nov.), the Docoglossa = Patellina, and the Neritopsina; the new taxon Vetigastropoda (no former term available) is defined by the dominant presence of the (posttorsional) right dorsoventral retractor muscle as well as the right excretory organ and by bilamellate ctenidia with skeletal rods, and it includes the Macluritoidea, Pleurotomarioidea, Cocculinoidea, Trochoidea, and Murchisonioidea (?) (cf. Cox, 1960; Cox & Knight, 1960). Despite the emphasis of Golikov & Starobogatov (1975), the other gastropods (line 6 above)—even if possibly polyphyletic—might better be classified in Caenogastropoda (including Mesogastropoda and Neogastropoda), Pulmonata, Gymnomorpha, and Opisthobranchia.

As is generally accepted and repeatedly evidenced by developmental patterns, the groups of Opisthobranchia underwent convergent, gradual so-called detorsion, thus secondarily regaining euthyneury in different degrees by regulative differential growth (cf. Brace, 1977). This is, however, not the case in the still "prosobranch" Pulmonata, the so-called euthyneury of which results from the extreme concentration of the nervous system. Hence, the Euthyneura are not a monophyletic group (cf. also Minichev, 1972) and the pair of taxa Streptoneura/Euthyneura should be dropped. Within the Pulmonata, in contrast to earlier opinion (cf. Boettger, 1954), there are three orders to be recognized (Archaeopulmonata, Basommatophora, Stylommatophora). As accurately elaborated by Morton (1955) and Van Mol (1967), the Ellobiidae and Otinidae have to be separated as a special group, the basic Archaeopulmonata; that classification has already been accepted in the textbook by Götting (1974).

The Opisthobranchia, the monophyly of which—rooted in early, sediment-ploughing cephalaspideans (cf. Brace, 1977)—is becoming more and more weakened (cf. Robertson, 1974), are variously classified in five to nine or even more orders (cf. Morton, 1963, etc.); an arrangement in seven orders stands—according to recent knowledge—critical estimation: 1) The Pyramidellimorpha. 2) The Cephalaspidea, divided into the main group Bullomorpha and into the Thecosomata as suborders (cf. Boettger, 1954); herein the Philinoglossoidea and Acochlidioidea simply constitute two differently evolved bullomorphan family groups (but no separate suborders or even orders; cf. Salvini-Plawen, 1973b). 3) The Anaspidea, divided into Aplysiomorpha and Gymnosomata (suborders). 4) The Saccoglossa (Sacoglossa emend., Ascoglossa, Monostichoglossa). 5) The Notaspidea. 6) The Nudibranchia, con-

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[7] The separation of the Neritacea as an order distinct from the Archaeogastropoda appears not to be justified (as done by Yonge, 1947; Morton & Yonge, 1964; Franc, 1968), nor is the arrangement of the Patellacea as Cyclobranchia in contrast to Scutobranchia and Pectinibranchia (as done by Golikov & Starobogatov, 1975). Moreover, there is no organizational justification to hypertrophize the taxonomic rank of more or less constant family groups (as do Cox & Knight, 1960 or Golikov & Starobogatov, 1975).

fined to the suborders Dendronotina, Arminina, and Aeolidiina. 7) The Anthobranchia (= Doridacea) which are comparative-anatomically well-separated from the former group(s) (cf. Ghiselin, 1965; Minichev, 1970; Brace, 1977: 51 f).

The systematically greatly contested, shell-less Onchidiacea and Soleolifera (Veronicellacea) doubtlessly constitute a natural relationship (cf. H. Hoffmann, 1925; Van Mol, 1967). The more conservative Onchidiidae still retain a modified pallial cavity (the "cloaca"), and the so-called lung-cavity clearly represents an additional, new formation, not derivable from tissues of the pallial cavity (cf. Fretter, 1943, also H. Hoffmann, 1925: 324–326). Other characters ostensibly identical to those in Pulmonata (eye-tentacles, lamellate excretory organ, innervation of the penis, etc.) likewise have been demonstrated to be analogous (cf. Plate, 1893; Boettger, 1952; Morton, 1955; Van Mol, 1967; Salvini-Plawen, 1970a; Minichev, 1975; Starobogatov, 1976). Whereas some features (procerebrum and cerebral glands, paired albumen gland) point to a close root with the Archaeopulmonata (or simply to an identical environment of origin ?), the nervous system combined with the mutual position of the mantle cavity and the likewise detorted female genital opening clearly demonstrate a pre-pulmonate offshot; further characters, i.e. the so-called detorsion, vacuolated cells (so-called larval kidneys), and so-called anal kidneys, in their turn evidence a distinct relation with (Prosobranchia and) primitive Opisthobranchia. Accordingly, the group cannot be included as an order (variously named Ditremata, Teletremata, Systellommatophora, or Gymnophila; cf. Salvini-Plawen, 1970a) into one of the existing subclasses; it serves to represent an evolutionary line (subclass) per se separate from the Opisthobranchia as well as from Pulmonata (cf. Stringer, 1963, Morton, 1963; Salvini-Plawen, 1970a; Minichev, 1975). With the inclusion of the formerly enigmatic Rhodopacea, Salvini-Plawen, (1970a) proposed the term Gymnomorpha for the proper unit of the three reclassified groups (the—later—term Opisthopneumona chosen by Minichev, 1975, is a misnomer, since neither the Rhodopidae, nor the Rathousiidae or several Onchidiidae are opisthopneumonous). In accordance with Minichev (1975), the three groups within the Gymnomorpha may tentatively be classified as orders.

BIVALVIA

A most confusing situation is found within the bivalves as concerns the supraspecific classification. The many different systems which were formerly and/or are actually in use strikingly demonstrate the precarious systematic situation. The lasting uncertainty of relationships between family groups is once more indicated by the over-estimation of certain characters (cf. Nevesskaya et al., 1971; Pojeta, 1971, and others) which in no way correspond to actual comparative-anatomical differences when compared with other molluscan groups. Most of these discrepancies are due to there being knowledge of only one or a few special characters, and that little effort has been made to judge pathways from the point of view of functionally synorganized alteration; more recent investigation (cf. Yonge, 1953, 1962; Stanley, 1972) have demonstrated the high degree of convergences and the need for thorough comparative analysis.

The adaptation of some tryblidiid predecessors of the Bivalvia to soft bottoms, correlated with the elaboration of inherited cerebrally-innervated labial organs (cf. Drew, 1901: 353, 373; Allen & Sanders, 1969; Lemche & Wingstrand, 1959: 23 f), simultaneously resulted in the narrowing of the foot and the lateral compression of the body. The reduction of the buccal mass clearly points to the probability that mucociliary feeding by the labial palps gradually replaced the original mode of feeding, since ctenidian filter-feeding per se would not seem suitable to replace radular feeding at that early level of evolution (although the latter is adequate for occasional transport of food; cf. Stasek, 1965). Thus, the ancestors of all Recent bivalves might have been provided with enlarged labial flaps (palps) singling out microorganisms and organic material from the currents entering from the anterior during ploughing in the sediment. That evolutionary level may be represented by the extinct Rostroconchia. The bent condition of the mid-dorsal mantle area finally led to the partition of the shell gland in an early ontogenetical stage (comp. Prodissoconch I) and resulted in the development of the two valves as well as in their subsequent functional equipment (adductors, hinge).

The evolutionary differentiation found in (Recent) bivalves is basically expressed by four developmental lines: two lines of the

Protobranchia s. l., the Lamellibranchia s. str., and the Septibranchia s. str. The protobranch groups retained the primitive state of bivalve organization with an anterior inhalent current, with pallial mucous tracts (hypobranchial gland), with predominant mucus-ciliary feeding by means of the labial flaps, with only a few orifices of the midgut glands, and with slightly modified ctenidia (cf. Yonge, 1939, 1959; Owen, 1959; Purchon, 1959). The ctenidiobranch and ctenodont Nuculacea retained further those primitive adult characters and larval features (Pericalymma-larva; cf. Salvini-Plawen, 1973a), but improved the labial flaps for deposit-feeding by adapting specialized palps with a tentacular appendage. On the other hand, the Solemyacea are adapted for filter-feeding of suspended material (cf. Yonge, 1953, 1959; Allen & Sanders, 1969) with respectively enlarged, foliate (plain-faced) ctenidia and with simplified labial palps.

The most successful line includes the lamellibranch bivalves (sensu Yonge, 1959, 1962; Purchon, 1959; Morton, 1963), characterized by the successive alteration of the ctenidia to filter-feeding. It may be presumed that the origin of those (monophyletic ?) groups occurred by invading the littoral (primary hard bottoms) characterized by variation of salinity (tidal zone): Both the paedomorphous retention of the byssus (cf. Yonge, 1962) and the development of protonephridia (not existing in all other molluscs except limnic gastropods; cf. Salvini-Plawen, 1969, 1972: 287 f & 353) positively support that probability (cf. also Stanley, 1972), as does the thorough adaptation from deposit- towards filter-feeding itself. Rudimentarily present in ctenidiobranch bivalves (cf. Stasek, 1965), the enlargement of the gills by elongation of the axis and the laterally connected as well as ventrally-bent multiplied lamellae resulted in the filibranch level of organization; further specialization along that adaptive line finally led to the eulamellibranch condition. Especially that advanced level includes a high radiation of specialized groups which underwent two predominant, polyphyletic trends: the byssal attachment gave rise to different anisomyarian and monomyarian conditions in epifaunal forms, whereas the preference of (primary or secondary) infaunal habits resulted in the fusion of the mantle edges and the formation of siphons (cf. Yonge, 1953, 1962; Morton, 1963; Kauffman, 1969; Stanley, 1972); that radiation is also obvious in the different types of hinge-dentition (cf. Newell, 1965; Nevesskaya et al., 1971), some of which likewise might be polyphyletic as, e.g. the taxodont type (cf. Pojeta & Runnegar, 1974).

A special situation is found in the septibranch condition. The investigations of Nakazima (1967), of Allen & Turner (1974), and of Bernard (1974) convincingly demonstrate that the Verticordiacea principally belong to the Anomalodesmata (= Desmodonta), the lamellibranch gills of which, however, are gradually replaced by their own lateral attachment-membranes increasingly forming a septum; as in the case of the ctenidia of other bivalves, that septum is also innervated by the visceral ganglion. In contrast to that condition, the septum in the Poromyacea and Cuspidariacea is innervated by the cerebral ganglion (cf. Bernard, 1974: 5, 18), which proves it not to be homologous with the verticordiacean septum. There are no vestiges of ctenidia in Cuspidariacea-Poromyacea and the origin of their septum is obscure. Purchon (1956, 1963; cf. also Nevesskaya et al., 1971) emphasized the unity of the septibranch stomach (including Verticordiacea: Gastrodeuteia) and its possible relationship to the Protobranchia (Gastroproteia). The analysis of the Verticordiidae demonstrates, however, that such characters of the alimentary canal are obviously in close correlation with the food (cf. Allen & Turner, 1974: 516 f), and their reliance on phylogenetic patterns is dubious. Hence, the structural relation of Cuspidariacea-Poromyacea to the Protobranchia with respect to the stomach becomes questionable, as it does so concerning most other (generally polyphyletic) characters; up to now there is no synorganized character confirming a closer relationship either to the protobranchs s. l. or to the lamellibranchs s. str.

In transferring the evolutionary pathways outlined above to a systematic arrangement, there is clear evidence that the bivalves should be subdivided into four major taxa, i.e. the two protobranch groups, the lamellibranchs s. str., and the septibranchs s. str.; this coincides with the paleontologic situation underlined by Newell (1969: 212 ff), that the Protobranchia s. l. are not a homogeneous group and can be united no longer within a single taxon. In contrast to the polyphyletic radiation within the lamellibranch line (s. str.), the gill structure reflects not only the levels of organization, but also major, synorganizationally monophyletic groups; hence the gills prove to

TABLE 2. Classification of the Bivalvia.

Classis BIVALVIA Linné, 1758

I. Subclassis PELECYPODA Goldfusz, 1820

1. Superordo **Ctenidiobranchia** nov. (= **Palaeotaxodonta** Korobkov, 1954)
   - Ordo **Nuculida** Dall, 1889 (= **Ctenodonta** Dechaseaux, 1952, in Nevesskaya et al., 1971)
2. Superordo **Palaeobranchia** Iredale, 1939 (= **Cryptodonta** Neumayr, 1883, in Newell, 1965)
   - Ordo **Solemyida** Dall, 1889 (= **Lipodonta** Iredale, 1939)
   - Ordo **Praecardiida** Newell, 1965
3. Superordo **Autobranchia** Nevesskaya et al., 1971 (ex **Autolamellibranchia** Grobben, 1894)
   - Ordo **Pteriomorpha** Beurlen, 1944 (= **Filibranchia** Pelseneer, 1889, plus **Pseudolamellibranchia** Pelseneer, 1889)
     - Subordo Mytilina Rafinesque, 1815 (= Isofilibranchia Iredale, 1939)
     - Subordo Arcina Stoliczka, 1871 (= Eutaxodonta Grobben, 1892 = Pseudoctenodonta Dechaseaux, 1952 = Neotaxodonta Korobkov, 1954)
     - Subordo Pteriina Newell, 1965
       - Superfamilia Pterioidea Newell, 1965 (incl. Pinnoidea)
       - Superfamilia Limoidea D'Orbigny, 1846
       - Superfamilia Ostreoidea Ferussac, 1882
       - Superfamilia Pectinoidea Adams & Adams, 1857
   - Ordo **Palaeoheterodonta** Newell, 1965
     - Subordo Lyrodesmatina Scarlato & Starobogatov, 1971
     - Subordo Trigoniina Dall, 1889
     - Subordo Unionina Stoliczka, 1871
   - Ordo **Heterodonta** Neumayr, 1883
     - Subordo Venerina Adams & Adams, 1856
     - Subordo Myina Stoliczka, 1870 (= Adapedonta Cossmann & Peyrot, 1909)
   - Ordo **Anomalodesmata** Dall, 1889
     - Subordo Pholadomyina Newell, 1965 (incl. Verticordioidea Stoliczka)
4. Superordo **Septibranchia** Pelseneer, 1888/1906
   - Ordo **Poromyida** Ridewood, 1903
       - Superfamilia Poromyoidea Dall, 1886
       - Superfamilia Cuspidarioidea Dall, 1886

II. Subclassis ROSTROCONCHIA Cox, 1960

- Ordo **Ribeiriida** Kobayashi, 1933
- Ordo **Ischyriniida** Pojeta & Runnegar, 1976
- Ordo **Conocardiida** Neumayr, 1891

be the most adequate single character reflecting evolutionary pathways and may well serve as superordinal taxobases. The difficulties arise, however, with the classification within the possibly polyphyletic lamellibranch group (s. str.) since, according to the frequent convergences, an undisputed natural grouping has not yet convincingly been presented (cf. e.g. Cox, 1960b; Morton, 1963; Newell, 1965, 1969; Nevesskaya et al., 1971; Pojeta, 1971, 1975, and others). At the present state of our knowledge, the most adequate arrangement of its groups and of the hinged bivalves in general appears to be the classification[8] as summarized in Table 2.

Pojeta et al. (1972) elevated the former Conocardioidea (Bivalvia) to a separate class Rostroconchia Cox,[9] characterized by a univalved protoconch and a bivalved concha without ligament, hinge teeth, and adductor muscles; subsequently (Runnegar & Pojeta, 1974) enlarged by the Ribeiroidea (formerly Crustacea-Conchostraca), that group in any case ranges very close to the Bivalvia, and may represent a more primitive evolutionary level of bivalve organization. We doubt, how-

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[8] With respect to the largely uniform general organization of the Bivalvia, the four main groups of Pelecypoda should be ranked as superorders (but not as subclasses; cf. also Nevesskaya et al., 1971: 155).

[9] Authorship of Rostroconchia must be assigned to Cox (1960b), but not to Pojeta et al. (1972), since there is only elevation of rank without change of contents. Similarly, the term Caudofoveata remains assigned to Boettger (1955) and not to Salvini-Plawen (1967) who elevated the group to the status of an independent class.

ever, whether the characters mentioned are prominent enough to justify the status of a separate class: The univalved larval shell is likewise present (though in a more advanced evolutionary stage) in typical hinged Bivalvia with the Prodissoconch I, and the degree of calcification per se seems to be a very vague argument; the lack of a typical hinge as well as of adductors appear simply to constitute primitive characters (as is the lack of an articulamentum in the placophoran Chelodida). Since the differences between the hinged Bivalvia and the Rostroconchia do not appear more prominent than do those between the placophoran Heptaplacota and Loricata, for example (compare also univalved and bivalved gastropods; cf. also Yochelson, 1978), we merely accord the rank of subclass to the Rostroconchia as opposed to the hinged bivalves or Pelecypoda. As monographically presented by Pojeta & Runnegar (1976), the subclass Rostroconchia is subdivided in three orders, the Ribeiriida, Ischyriniida, and Conocardiida.

CEPHALOPODA = SIPHONOPODA

In re-establishment of the findings of Ihering (1877: 250–269) and Dietl (1878: 100–108), Young's recent investigations (1965: 8–10; 1971: 1, 11) likewise confirm the innervation of the head-tentacles or arms to be in fact cerebral (and not pedal): The pedal-complex sensu lato consists of two structurally different sections with different interconnections with other parts of the central nervous mass. The frontal (= brachial) section receives its connectives directly from the cerebral ganglia; in contrast, the hind (= infundibular) section of the complex is truly pedal (innervating the funnel) and is connected with the magnocellular (= lateral) region, which in turn is linked with the cerebral (= supraesophageal) nerve mass. Despite the secondary topographic fusion of the brachial and infundibular/pedal masses, there is distinct separation as concerns the nerve bundles and their innervation areas. The pedal gland (funnel gland, funnel organ) fully corresponds with that evidence since it is situated in direct connexion with and in a frontal position of the adenopod foot (= funnel). In accordance with that (reestablished) elucidation, the term 'Cephalopoda' clearly is erroneous and should be abandoned in favour of Siphonopoda (Lankester, 1877, nec G. O. Sars, 1878).

In consideration of the evolutionary systematic condition within the Cephalopoda/Siphonopoda, there are striking differences concerning the classification mainly due to the radiating fossil branches. Whereas the Coleoida[10] have been recently dealt with thoroughly by Mangold-Wirz & Fioroni (1970), extinct groups are subject to considerable controversy. This becomes immediately evident within the Coleoida when comparing the analyses of Jeletzky (1966) and Teichert (1967); both authors, however, coincide in the separation of the Aulacocerida and Phragmoteuthida as distinct groups, which is likewise accepted by Fioroni (1974). The Coleoida (= Endocochlia of Schwartz, 1894 = Dibranchiata of Owen, 1826), including the Belemnites, are generally accepted as having evolved from Bactritites (= Michelinoceratites). Since Erben (1964, 1966) was able to demonstrate that the ammonites likewise evolved from Bactritites (originating within the Orthocerida-Sphaerorthoceridae according to Ristedt, 1968), he supported an earlier suggestion concerning the contradictory structure of the siphon and of septa in ammonites and nautiloids respectively. The group known under the vague term of Ectocochlia (or Tetrabranchiata) could therefore no longer be upheld, and the closer relationship of the Ammonoida and Coleoida has been manifested. This has subsequently been supported by the elucidation of some internal, partly soft structures in early ammonities (cf. Kolb, 1961; Close, 1967; Lehmann, 1966; 1967a, b, 1976; Zeiss, 1968; Reyment, 1972a, b), indicating that the ammonites presumably were provided with a radula, an ink-sac, a fairly low number of arms, and sexual dimorphism, as have the Coleoida. Lehmann (1967a) consequently proposed a new classification of the class: Angustiradulata (Ammonoida and Coleoida) and Lateradulata (Nautiloida s.l). This latter radula with 13 longitudinal rows of teeth is merely known in the Recent *Nautilus* and a close relative *Palaeocadmus* (cf. Solem & Richardson, 1975), but nothing is known so far about the radulae of distantly related groups; moreover, there is some indication that *Nautilus* itself represents a specialized form even within the

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[10] Following Recommendation 29A of the International Code of Zoological Nomenclature, the taxonomic ending "-oidea" should uniformly be restricted to superfamilies (family groups); accordingly, a change of the subclass endings to "-oida" is proposed.

Nautiloida sensu lato (cf. Ihering, 1881; H. Hoffmann, 1937; Flower, 1955; Lehmann, 1967b; Mangold-Wirz & Fioroni, 1970). Lehmann's proposition, therefore, merely holds good for his own Angustiradulata.

A subdivision of the class into only two taxa (as proposed by Lehmann) is neither morphologically nor phylogenetically satisfactory (cf. Donovan, 1964; Teichert, 1967; Mangold-Wirz & Fioroni, 1970). As stated by Flower (1955) and Teichert (1967), the primitive orthoconic groups and groups closely related to them differ considerably from the Nautiloida s. str. Likewise, orthoconic Endocerida (including Intejocerina), Actinocerida, and Discosorida, even if their organizations are more distinctive, cannot be regarded as representing ranks of subclasses since many of their features are repeated within other groups (cf. Teichert, 1967: 204), and since they appear merely to be smaller offshoots of the primitive Ellesmerocerida (cf. Flower, 1955; Donovan, 1964; Teichert, 1967). All these more or less closely related groups may consequently be united in one separate subclass, Orthoceroida (see Table 4).

MOLLUSCA

This presentation so far demonstrates that increase in knowledge implies alterations and even revisions of our understanding of phylogenetic pathways, and hence of systematic representation. This reflexion of permanent systematic flux also concerns the molluscs as a whole when emphasizing the evolutionary morphologically qualitative importance of organizations irrespective of quantitative contents (compare: Gastropoda with Scaphopoda, etc.).

Based upon an extensive study of the lower molluscs, Salvini-Plawen (1972) also did a comparative analysis of molluscan organization in general, especially with respect to phylogenetic pathways from the zoological (neontological) point of view; simultaneously, Stasek (1972) presented a study coming to similar conclusions in general outline, differing in detail, however, owing to his emphasis on the advanced groups only.

As summarized in Figs. 3–5, the evolutionary radiation within the Mollusca is not a weighted one, but dominates along the line of mantle(-foot)-differentiation culminating with the Siphonopoda (cephalopods); this condition also contributed to the under-estimation of the lower molluscs. The earliest confirmable evolutionary branching already took place at the level of very primitive molluscan organization, still characterized by an overall ventral gliding surface, by a merely circum-posterior mantle cavity, and by an aculiferan mantle cover (chitinous cuticle with embedded aragonitic scaly bodies; cf. Degens et al., 1967: 640; Beedham & Trueman, 1968; Salvini-Plawen, 1969, 1972; Peters, 1972; Stasek, 1972; Carter & Aller, 1975; Trueman, 1976; Salvini-Plawen & Boss, 1980). The preference and subsequent adaptation of some populations to sediment-burrowing habits finally resulted in the Recent Caudofoveata, during their course of which the locomotory surface was restricted to its cerebrally-innervated section, i.e. the pedal shield. That evolutionary line of Scutopoda, including only the Caudofoveata, is contrasted phylogenetically to the Adenopoda: Selective pressure upon the improvement of food-uptake by the organisms while steadily gliding by means of cilia led to the individualization of a snout. The trend to release the oral region from its earlier locomotory function induced the extension of the posterio-lateral mantle grooves towards the anterior to unite preorally. Additionally, the locomotory surface hence confined to the purely ventrally-innervated section, i.e. the foot, was subsequently supported in its function by the selection of an anterior accumulation of a distinct follicular gland. That pedal gland, innervated by the first nerves of the ventral/pedal system, proves itself to be a genetically well-established differentiation (cf. Salvini-Plawen, 1972: 304 ff). In its interdependent evolutionary synorganization with a peripedal-preoral mantle cavity it distinctly defines the phylogenetic branch of Adenopoda, including all (Recent as well as extinct) molluscan groups except the Caudofoveata.

Two adenopodan groups, the Solenogastres and Placophora, not only share the still primitive aculiferan mantle cover; they are also synapomorphously tied together by the rudiment of seven transverse rows of calcareous bodies in the larvae (see Fig. 2) which distinctly prove the monophyletic origin of both groups within the Adenopoda. Their later differentiation of the mantle cover demonstrates, however, the subsequent specific deviation: re-disintegration of the cover of spicules in the Solenogastres, and consolidation of the juxtaposed bodies to seven shell plates in early Placophora (Heptaplacota).

The ancestral, common character of transverse rows of middorsal scales in both Solenogastres and Placophora, as well as the subsequent tendency to consolidate these juxtaposed scaly elements to become homogeneous formations, is likewise obvious in the solenogastre *Nematomenia (?) protecta*: the scaly mantle cover of this species is characterized "by three peculiar shields at the dorsal side of the head, which are clearly formed by coalescence of several juxtaposed small scales; apparently about 10 small scales have been united by lateral fusion, so that the original separation is merely indicated by a number of indentations at the posterior rim. I always find three such shields, the anteriormost of which is located close to the anterior end of the animal and partly imbricates the immediately subsequent second shield. The third shield, on the other hand, is separated from the middle one by a small number of ordinary scales" (translated from Thiele, 1913: 39).

Placophora with eight (!) plates, however, must be considered ancestral to the Conchifera. Since these placophorans bend and roll up ventrally—effected by the primitive character of a longitudinal muscle bundle close to each mantle edge, likewise present in Solenogastres and even in Caudofoveata—not prior to the prevention of that bending (probably by living in an undisturbed environment) the centers of plate-formation concentrated and fused to create a single, homogeneous concha; Fig. 3 demonstrates the respective synorganized alterations (cf. Salvini-Plawen, 1972; Haas, 1972 *versus* Beedham & Trueman, 1967; Stasek & McWilliams, 1973). This fusion was followed by concentration of the dorsoventral (shell-pedal) muscle bundles from 16 to 8, and by further elaboration (jaws, statocysts, subrectal commissure). The recent tryblidiid *Neopilina* characteristically demonstrates a far-reaching 'connecting link'-configuration in combining characters of both Placophora and Conchifera (dorsoventral musculature, esophageal and digestive glands, slender intestine, subradular organ; cf. Boettger, 1959; Salvini-Plawen, 1972, and others).

In regard to the radiation within the Conchifera, unanimous opinion seems to exist from the zoological as well as from the paleontological point of view that the Bivalvia (including the Rostroconchia) and the Scaphopoda represent a somewhat closer relationship, mainly due to the developmental configuration of the mantle-shell (cf. Salvini-Plawen, 1972: 312; Pojeta & Runnegar, 1976: 43; and others). On the other hand, the Tryblidiida, Bivalvia and Scaphopoda have retained the peripedal mantle cavity of the typical Adenopoda, and the merely single pair of ctenidia in Bivalvia may therefore serve additionally to indicate that these organs are secondarily pluralized in Placophora and *Neopilina*. In contrast, in Bellerophontida partim and in Gastropoda, as well as in Cephalopoda/Siphonopoda, the mantle cavity is confined to the (morphologically) posterior body in connexion with the increase of cephalization and the heightening of the shell. That condition clearly demonstrates that gastropods and siphonopods were derived from advanced, high-cyrtoconic Galeroconcha in contrast to bivalves and scaphopods originating in more primitive, cap-shaped galeroconchs. The closer ancestral relationship of Cephalopoda/Siphonopoda and Bellerophontida-Gastropoda (cf. also Yochelson et al., 1973) might also be indicated by the possible homology of the eyes (cf. Salvini-Plawen & Mayr, 1977), presumably differentiated already in the more advanced galeroconchs. There is no substantiated reason, however, to join the three groups systematically into one supertaxon, and the reverse tendency by Mangold-Wirz & Fioroni (1970) and Fioroni (1974) to classify the siphonopods as separate from all other Conchifera is based merely upon present day differences; it disregards, however, the not-at-all extraordinary phylogenetic point of view, according to which there is continuous evolution and radiation (cf. Yochelson et al., 1973; Erben, 1964, 1966; Ristedt, 1968, and others).

According to that analysis, one could certainly subdivide the Conchifera with respect to possible evolutionary pathways (see Fig. 4), and classify them, e.g. as Ventropoda or Archaeoconcha (Galeroconcha and Gastropoda), Siphonoconcha (Siphonopoda/Cephalopoda), and Loboconcha (Bivalvia and Scaphopoda); this grouping would be more adequate than a subdivision into Cyrtosoma and Diasoma as proposed by Runnegar & Pojeta (1974) which, in addition, relies on a partially imagined or even incorrect character (Tryblidiida; Scaphopoda). All these attempts are mere supposition, since they still appear to be more or less contestable speculations. The Conchifera are a phylogenetically as well as morphologically compact group ancestrally tied to the Galeroconcha, and subdivision of them at our present state of knowledge is not justified.

In consideration of the widely substantiated, comparative-anatomical as well as evolutionary levels within the molluscan organization, only three essential evolutionary steps are conspicuous: (1) The restriction of the ventral locomotory surface to the ventrally-innervated section combined with beginning cephalization and the preoral extension of the mantle cavity; this evolutionary differentiation separates the Adenopoda from the Scutopoda. (2) The elaboration of a shelled mantle cover (Placophora) correlated with the beginning concentration of the dorsoventral musculature, and accompanied by the specific differentiation of the alimentary canal s. l. (esophageal and midgut glands, slender and winding intestine, subradular sense organ; differentiation of the pericardioducts as excretory organs ?); that evolutionary step within the Adenopoda separates the Placophora and Conchifera from the Solenogastres. (3) The establishment of a homogeneous concha, accompanied by the differentiation of the jaws, the statocysts, the subrectal commissure, and the cerebrally-innervated tentacle formations (preoral tentacles and velum in *Neopilina,* cephalic tentacles in Gastropoda, palps in Bivalvia, captacula in Scaphopoda, arms in Cephalopoda/Siphonopoda; cf. Lemche & Wingstrand, 1959; Allen & Sanders, 1969; Grobben, 1886; Gainey, 1972; and others); these synapomorphies separate the Conchifera.

An adequate classification would have to reflect the above steps (Fig. 4) systematically; this, however, would also result in an unjustified over-accentuation of the Solenogastres. In an endeavour not to hypertrophize the specialist's own group, it must be stated that the Solenogastres are quite distinct from the Caudofoveata (see Adenopoda versus Scutopoda), but within the Adenopoda they constitute merely an early side branch. The close relationship of the Placophora and Solenogastres, synapomorphously tied together by the rudiments of seven transverse rows of juxtaposed spicules (see Figs. 2–3), justifies including both groups under one taxon for which the appropriate term Heterotecta may be coined (defined as Adenopoda without concha and characterized by the developmental rudiment of seven transversely arranged rows of juxtaposed calcareous bodies at the middorsal mantle; these bodies have different fates). Such a classification also appears more adequate in regard to the morphological weight of the phylogenetically most successful Conchifera, as well as concerning the reasonable subdivision of the Adenopoda solely into two groups, i.e. to separate the Conchifera from the collectively more primitive Placophora and Solenogastres. Consequently, the systematic grouping of the Mollusca results as compiled in Fig. 5 and Table 3.

OTHER TAXA

The Scaphopoda do not need special discussion. Their somewhat close relationship to the Bivalvia has been mentioned above. Emerson (1962) as well as Palmer (1974a, b) have reclassified the group, Palmer (1974a) introducing two orders Dentaliida and Siphonodentaliida (compare footnotes 3 and 10).

There are several terms and taxa associated with the molluscs still to be discussed shortly. The familiar term Aplacophora (Ihering, 1876) has already been dealt with; it must be dropped due to the diphyletic origin of the Caudofoveata and Solenogastres.

The term Amphineura (Ihering, 1876) was originally created because of the seemingly similar nervous systems in Aplacophora and Placophora; more recently, many scientists tend to confine the term to the Placophora. Since neither the Solenogastres, nor the Caudofoveata still possess a truly amphineural nervous system (i.e. two separate pairs of medullary cords (= without ganglia formation) provided with irregular ventral as well as lateroventral interconnexions), this condition is still represented only in Placophora and—although already more specialized—also in *Neopilina.* Other configurations only reflect the general tetraneury typical of all Mollusca.

The term Aculifera (Hatschek, 1891) is more adequate when considering the aplacophoran and polyplacophoran groups—as originally introduced and as used by Salvini-Plawen (1968b, 1969, 1972); it has been misleadingly limited by Stasek (1972; and copied by Pojeta & Runnegar, 1976) to the aplacophoran groups. This taxon, however, shares with the 'Aplacophora' disregard of the evolutionary branching into Scutopoda and Adenopoda, thus including three different groups having conservatively retained the symplesiomorphous character of the mantle cover with cuticle and aragonitic bodies.

TABLE 3. Higher classification within molluscs.

	Subphylum	Infraphylum/Superclassis	Classis
current grouping (Götting, 1974; Lehmann, 1976)	Aculifera		Caudofoveata Solenogastres Placophora
	Conchifera		Monoplacophora Gastropoda Bivalvia Scaphopoda Cephalopoda
corrected version	Scutopoda		Caudofoveata
	Heterotecta		Solenogastres Placophora
	Conchifera		Galeroconcha Gastropoda Siphonopoda Bivalvia Scaphopoda
phylogenetically adequate classification	Scutopoda		Caudofoveata
	Adenopoda	Heterotecta	Solenogastres Placophora
		Conchifera	Galeroconcha Gastropoda Siphonopoda Bivalvia Scaphopoda

The enigmatic Late Cambrian *Matthevia* still remains one of the 'problematica' with molluscan affinities (cf. Yochelson, 1978). Yochelson (1966) reviewed recent records and erected a new class for the genus; on the other hand, Runnegar & Pojeta (1974) suggest that the two, co-occurring, somewhat unequal and massive shells with two tapering cavities each represent the conical values of a primitive chiton. Disregarding the evidence for a very different evolution of the Placophora (see Figs. 3 & 5) than that speculated by Runnegar & Pojeta, it remains here to stress (1) that the placophoran plates "in no way resemble the hard pieces of *Matthevia*" (Yochelson, 1966: 8) even when compared with Chelodida, and (2) that the conical internal cavities of the shells separated by a strong septum are situated in succession but not in juxtaposition. If compared to Placophora, both the latter characters point to highly specialized features, the paired dorsoventral muscle bundles being then concentrated apically (in contrast to Tryblidiida and Placophora). The strange reconstruction of *Matthevia* by Yochelson (1966), however, raises a question as to how such organisms should have been adaptively selected; in contrast to the opinion of Yochelson, the reconstructed condition is not streamlined (compare *Patella, Ancylus,* etc., which press their anterior shell margin to the bottom), and the animal cannot retract into the small cavities (which are, additionally, filled by "powerful muscles")—and the size of the organisms is purely speculative. Is it not possible that the soft parts of the body greatly exceed the shell(s) (analogously to Bivalvia-Pholadoidea or -Clavagelloidea)?

The Stenothecoida with their two symmetrical and unequal hingeless valves must be placed incertae sedis until more information can be offered in favour of a distinct relationship to another group (within or even outside of the molluscs; cf. also Yochelson, 1978). While Yochelson's reconstruction (1969) is not quite satisfactory as concerns a 'mollusk,' the interpretation of Runnegar & Pojeta (1974: 316) as "bivalved monoplacophorans, with the lower valve formed by the sole of the foot" appears to be pure speculation.

TABLE 4. Classification of the Mollusca proposed herein (+ = extinct).

- Phylum *MOLLUSCA* Cuvier, 1795
  - Subphylum *SCUTOPODA* Salvini-Plawen, 1978
    - Classis CAUDOFOVEATA Boettger, 1955
      - Ordo **Chaetodermatida** Simroth, 1893
  - Subphylum *ADENOPODA* Salvini-Plawen, 1971
    - Infraphylum/Superclasssis HETEROTECTA nov.
      - Classis SOLENOGASTRES Gegenbaur, 1878
        - Superordo **Aplotegmentaria** Salvini-Plawen, 1978
          - Ordo **Pholidoskepia** Salvini-Plawen, 1978
          - Ordo **Neomeniomorpha** Pelseneer, 1906 (emend.)
        - Superordo **Pachytegmentaria** Salvini-Plawen, 1978
          - Ordo **Sterrofustia** Salvini-Plawen, 1978
          - Ordo **Cavibelonia** Salvini-Plawen, 1978
      - Classis PLACOPHORA Ihering, 1876
        - + Subclassis HEPTAPLACOTA nov.
          - Ordo **Septemchitonida** Bergenhayn, 1955
        - Subclassis LORICATA Schumacher, 1817
          - + Ordo **Chelodida** Bergenhayn, 1943
          - + Ordo **Scanochitonida** Starobogatov & Sirenko, 1975
          - Ordo **Lepidopleurida** Thiele, 1910
          - Ordo **Chitonida** Thiele, 1910
    - Infraphylum/Superclassis CONCHIFERA Gegenbaur, 1878
      - Classis GALEROCONCHA nov.
        - Ordo **Tryblidiida** Wenz, 1938 = **Monoplacophora** Odhner in Wenz, 1940
        - + Ordo **Bellerophontida** Ulrich & Scofield, 1897 = **Belleromorpha** Naef, 1911
      - Classis GASTROPODA Cuvier, 1795
        - Subclassis PROSOBRANCHIA Milne-Edwards, 1848
          - Ordo **Archaeogastropoda** Thiele, 1925
            - Subordo Vetigastropoda nov.
            - Subordo Docoglossa Troschel, 1866
            - Subordo Neritopsina Cox, 1960
          - Ordo **Caenogastropoda** Cox, 1960
            - Subordo Mesogastropoda Thiele, 1925
            - Subordo Neogastropoda Thiele, 1929
        - Subclassis PULMONATA Cuvier, 1817
          - Ordo **Archaeopulmonata** Morton, 1955
          - Ordo **Basommatophora** Keferstein, 1864
          - Ordo **Stylommatophora** Schmidt, 1855
        - Subclassis GYMNOMORPHA Salvini-Plawen, 1970
          - Ordo **Onchidiida** Rafinesque, 1815
          - Ordo **Soleolifera** Simroth, 1908 = **Veronicellida** Gray, 1840
          - Ordo **Rhodopida** Fischer, 1883
        - Subclassis OPISTHOBRANCHIA Milne-Edwards, 1848
          - Ordo **Pyramidellimorpha** Fretter, 1979
          - Ordo **Cephalaspidea** Fischer, 1883
          - Ordo **Anaspidea** Fischer, 1883
          - Ordo **Saccoglossa** Ihering, 1876 (= **Ascoglossa** Bergh, 1879)
          - Ordo **Notaspidea** Fischer, 1883
          - Ordo **Nudibranchia** Ducrotay-Blainville, 1814
          - Ordo **Anthobranchia** Férussac, 1819
      - Classis BIVALVIA Linné, 1758
        - Subclassis PELECYPODA Goldfusz, 1820
          - Superordo **Ctenidiobranchia** nov.
            - Ordo **Nuculida** Dall, 1889
          - Superordo **Palaeobranchia** Iredale, 1939
            - Ordo **Solemyida** Dall, 1889
            - + Ordo **Praecardiida** Newell, 1965
          - Superordo **Autobranchia** Nevesskaya et al., 1971
            - Ordo **Pteriomorpha** Beurlen, 1944
            - Ordo **Palaeoheterodonta** Newell, 1965

TABLE 4 (Continued).

      - Ordo **Heterodonta** Neumayr, 1883
      - Ordo **Anomalodesmata** Dall, 1889
    - Superordo **Septibranchia** Pelseneer, 1888/1906
      - Ordo **Poromyida** Ridewood, 1903
  - + Subclassis ROSTROCONCHIA Cox, 1960
      - Ordo **Ribeiriida** Kobayashi, 1933
      - Ordo **Ischyriniida** Pojeta & Runnegar, 1976
      - Ordo **Conocardiida** Neumayr, 1891
- Classis SCAPHOPODA Bronn, 1862
      - Ordo **Dentaliida** Palmer, 1974
      - Ordo **Siphonodentaliida** Palmer, 1974
- Classis SIPHONOPODA Lankester, 1877 = CEPHALOPODA Schneider, 1784
  - + Subclassis ORTHOCERATOIDA Kuhn, 1940
      - Ordo **Ellesmerocerida** Flower, 1950
      - Ordo **Orthocerida** Kuhn, 1940
      - Ordo **Ascocerida** Kuhn, 1949
      - Ordo **Discosorida** Flower, 1950
      - Ordo **Endocerida** Teichert, 1933
      - Ordo **Actinocerida** Teichert, 1933
  - Subclassis NAUTILOIDA Lamarck, 1812
      - + Ordo **Oncocerida** Flower, 1950
      - Ordo **Nautilida** Agassiz, 1847
      - + Ordo **Tarphycerida** Flower, 1950
  - + Subclassis AMMONOIDA Lamarck, 1812
      - Ordo **Bactritida** Shimanskij, 1951
      - Ordo **Goniatitida** Hyatt, 1884
      - Ordo **Ammonitida** Agassiz, 1847
  - Subclassis COLEOIDA Bather, 1888
      - + Ordo **Aulacocerida** Jeletzky, 1965
      - + Ordo **Belemnitida** Zittel, 1885
      - Ordo **Sepiida** Naef, 1916
      - + Ordo **Phragmoteuthida** Jeletzky, 1964
      - Ordo **Teuthida** Naef, 1916
      - Ordo **Vampyromorpha** Grimpe, 1917
      - Ordo **Octobrachia** Boettger, 1952 (pro **Octopoda** Leach, 1817)

The following taxa are considered to include Mollusca dubiosa: Hyolitha, Tentaculita, Agmata and Jinonicellina. There is need of much more information whether the Hyolitha (cf. Marek & Yochelson, 1964, 1976; Runnegar et al., 1975; Yochelson, 1978), the Tentaculita (cf. Blind, 1969; Runnegar et al., 1975), the Agmata (*Volborthella, Salterella*; cf. Yochelson, 1977b; Glaessner, 1976), and the Jinonicellina (cf. Runnegar, 1977; Yochelson, 1977a; Pokorny, 1978) are actually of molluscan organization or rather belong to other shelled organisms (compare, e.g., Glaessner, 1976 for the 'Agmata'). With respect to the hyoliths, we doubt the interpretation given by Runnegar et al. (1975) concerning the position of the muscle bundles, the insertions of which are preserved on both the operculum and cone; such strong bundles indicate the need for strenuous performance and correspondingly the need for rigid structures of insertion, but not connective tissue. Moreover, and in addition to the critique by Marek & Yochelson (1976), in firmly shelled organisms (and in contrast to deformable tube-dwelling bodies like sipunculids or some polychaetes) pressure upon the body fluid can easily be exercised by circular musculature; only the retraction of the body needs compact musculature. Since muscle bundles from the dorsal to the ventral side of the shell itself serve no purpose whatsoever, the bundles might have inserted either at a compact organ (i.e. radula bolster, cartilage-like structures, and other) or rather—and more likely—at the operculum with its five pairs of muscle scars (cf. Yochelson, 1974; compare also the rudists = Hippuritoidea).

FINAL DISCUSSION AND PROPOSAL

The Mollusca constitute one of the best defined groups within the animal kingdom and are distinguished by several synorganized characters original to the phylum, viz. the dorsal integument secreting chitinous cuticle and/or calcareous formations = the aplacophoran/polyplacophoran/conchiferan mantle; a respiratory mantle cavity with ctenidia, mucous tracts and body outlets; the ventral body surface serving for locomotion by means of cilia and mucous glands as well as partly of dorsoventral musculature; the gono-pericardial complex and an open circulatory system; a series of paired dorsoventral muscle bundles and—primitively—a pair of longitudinal muscle bundles along the margin causing the animal to roll up; the radula; and the tetraneury associated with a pallial sense organ (terminal sense organ, osphradia).

Owing to the fact that most molluscs produce fossilizable hard structures, we fortunately are able to study a great deal of molluscan phylogeny by means of these shell formations within different levels and groups. That condition, however, largely suppresses the importance and morphologically equivalent significance of other groups of molluscs of which no fossils have been handed down. Supported by the overwhelming quantitative dominance of the shell- (especially concha-) bearing molluscs, that discrepancy as concerns the comparative importance of different molluscan groups has become nearly inexcusable. In consideration of phylogenetic reconstruction and the endeavour to trace evolutionary pathways, two essential reflexions should always be taken into account: (1) Any adaptive alteration of a character is tied at any time to anatomical and functional interdependence on syn-organization; (2) a close, monophyletic relationship, i.e. the common descendant from an ancestral organization, is only substantiated by new character(s) acquired in common (syn-apomorphies), whereas the common retention of conservative characters (syn-plesiomorphies) merely demonstrate a more general relationship within a superior frame. Thus, many speculations and (mis-)interpretations, about *Neopilina* for example, could have been avoided under these premises, as well as the revival of the taxon 'Aplacophora' (cf. Scheltema, 1978).

In consideration of the evolutionary pathways within the Mollusca, there are four essential steps of progressive differentiation (Scutopoda/Adenopoda, Solenogastres/Testaria, Placophora/Conchifera, and radiation of Conchifera); since the Caudofoveata and Solenogastres are only tied together by symplesiomorphies, and since the Solenogastres-Placophora, as well as the Placophora-Conchifera are each tied by synapomorphies, the phylogenetic lines are obvious (Figs. 3–5). Transposed to usable linear system (cf. also Mayr, 1974), these conditions may be rendered by the final proposal as presented in Table 4.

SUMMARY

A reconsideration of systematic problems in the Mollusca raised by various recent studies results in the discussion of phylogenetic pathways and in the presentation of a correspondingly modified higher classification (as summarized in Fig. 5 and Table 4):

1) The original, common organization of Mollusca, characterized by an overall ventral gliding surface and a posterior-lateral mantle cavity, according to further way of life differentiated along two basic evolutionary lines: a) the burrowing Scutopoda with the locomotory surface restricted to the cerebrally-innervated section (Caudofoveata only); b) the continuing gliding-creeping Adenopoda with the locomotory surface confined to the ventrally-innervated section, with the differentiation of a rudimentary head, with a preorally extended mantle cavity, and with a distinct pedal gland (Solenogastres, Placophora, and Conchifera).
2) Within the Adenopoda, both the Solenogastres and Placophora are monophyletically (synapomorphously) interconnected by the rudimental mantle differentiation of seven middorsal, transversely arranged rows of juxtaposed calcareous bodies (cf. Fig. 2). Accordingly, the Septemchitonida are raised to a separate subclass Heptaplacota, and both Solenogastres and Placophora are classified together as Heterotecta, separated from the Conchifera.
3) Within that classification, the Caudofoveata constitute an isolated, early separated group (Scutopoda) interconnected to the Solenogastres and/or other molluscs merely by the conservative presence of ancestral (symplesiomorphous) characters. Placophora and Conchifera are interconnected by several synapomorphous characters; herein, the organization of *Neopilina* constitutes a connecting link.
4) No sufficient characters are obvious to serve for justified supraclasses within the Conchifera.
5) A reconsideration of the torsion process leads to the presumption that the two separate torsional phases reflect different evolutionary adaptations. Correlative to

that interpretation, the Bellerophontida (Belleromorpha) are considered to have been untorted organisms and are hence reclassified together with the Tryblidiida (Monoplacophora) within the new taxon Galeroconcha, and the pallial asymmetry of the higher gastropods other than Archaeogastropoda is regarded to be a paedomorphous character.

6) Onchidiacea, Soleolifera, and Rhodopacea are demonstrated to represent a separate line (subclass Gymnomorpha) distinct from both the Pulmonata as well as the Opisthobranchia. The Doridacea must be separated from the Nudibranchia as a separate order Anthobranchia.
7) The Rostroconchia are regarded as a subclass of the Bivalvia, and the hinged, pelecypod Bivalvia may phyletically be grouped in four lines according to way of life (feeding, differentiation of gills); the Poromyida must be classified as a separate group (Septibranchia).
8) The recent confirmation that the arms of cephalopods are cerebrally-innervated organs favours the term Siphonopoda for the class. The various early lines of fossil Siphonopoda (cephalopods) are classified within the taxon Orthoceroida and set apart from Nautiloida, Coleoida, and Ammonoida.
9) Other taxa, groups, and terms are briefly discussed, with special emphasis on the avoidance of hypertrophy of systematic categories which are not justified comparatively.

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ZUSAMMENFASSUNG

EINE NEU-BEURTEILUNG DES SYSTEMS DER MOLLUSKEN (PHYLOGENIE UND GROSZ-GRUPPIERUNG)

Luitfried v. Salvini-Plawen

Eine Analyse verschiedener Unstimmigkeiten, welche durch in jüngerer Zeit durchgeführte Beiträge hinsichtlich phylogenetischer Zusammenhänge und systematischer Groszgruppierung entstanden, führt zur Darlegung neuerer Vorstellungen zum stammesgeschichtlichen Entwicklungsablauf innerhalb der Mollusken und zu einem entsprechend modifizierten System (vgl. Fig. 5 und Tabelle 4):

1) Die ursprüngliche, gemeinsame Molluskenorganisation, welche u.a. durch eine die gesamte Ventralfläche einnehmende Gleitsohle und einen posterio-lateralen Mantelraum gekennzeichnet war, spaltete sich entsprechend der Lebensweise in zwei Entwicklungslinien auf: a) in die grabenden Scutopoda mit Einschränkung des Lokomotionsorganes auf den cerebral innervierten Abschnitt (nur Caudofoveata), und b) in die weiterhin gleitend-kriechenden Adenopoda mit Einschränkung der Lokomotionsfläche auf den ventral innervierten Abschnitt, mit der beginnenden Differenzierung eines Kopfabschnittes, mit einem sich praeorad ausdehnenden Mantelraum, und mit der Ausbildung einer distinkten Fuszdrüse (Solenogastres, Placophora, Conchifera).
2) Innerhalb der Adenopoda sind die Solenogastres und Placophora durch die monophyletische (synapomorphe) Ausbildung von sieben Querreihen nebeneinanderliegender Kalkkörper in der Mantelmitte verbunden (vg. Fig. 2). Dementsprechend werden die Septemchitonida als eine eigene Unterklasse Heptaplacota abgetrennt, und Solenogastres wie Placophora werden zusammen als Heterotecta den Conchifera gegenübergestellt.
3) Innerhalb dieses Gesamtrahmens stellen die Caudofoveata daher eine isolierte Gruppe dar (Scutopoda), welche mit den Solenogastres und/oder anderen Mollusken nur durch konservativ erhaltene (symplesiomorphe) Merkmale verbunden sind. Placophora und Conchifera sind durch mehrere synapomorphe Merkmale verbunden; *Neopilina* stellt hierbei eine vermittelnde Brückenorganisation dar.
4) Innerhalb der Conchifera lassen sich bisher keine ausreichenden Verbindungen erkennen, welche die Errichtung von Überklassen rechtfertigen würden.
5) Eine Analyse der Torsionsvorgänge führt zu der Annahme, dasz die ontogenetische Zweiphasigkeit auf zwei evolutiv verschiedene Anpassungsprozesse zurückzuführen sind. Entsprechend dieser Aufschlüsselung werden die Bellerophontida (Belleromorpha) als untortierte Organismen aufgefasst und zusammen mit den Tryblidiida (Monoplacophora) im Rahmen einer Klasse Galeroconcha neu eingereiht, wie auch die Asymmetrie des Mantelraumkomplexes bei den Schnecken mit Ausnahme der Archaeogastropoda als eine Paedomorphie interpretiert wird.
6) Onchidiacea, Soleolifera und Rhodopacea lassen sich als eine eigene, von Pulmonata wie Opisthobranchia unabhängige Entwicklungslinie feststellen (Unterklasse Gymnomorpha). Die Doridacea sind als eigene Ordung Anthobranchia von den Nudibranchia abzutrennen.
7) Die Rostroconchia werden als eine Bivalvia-Unterklasse (und nicht als eigene Klasse) aufgefasst. Die mit Schlosz versehenen pelecypoden Bivalvia können entsprechend ihrer Lebensweise (Ernährung, Kiemendifferenzierung) in vier Entwicklungslinien gruppiert werden; die Poromyida sind hierbei als eigene Gruppe zu führen (Septibranchia).
8) Die in jüngerer Zeit bestätigten Befunde, dasz die Fangarme der 'Cephalopoden' rein cerebral-innervierte Organe darstellen geben der Bezeichnung Siphonopoda für die Klasse den Vorzug. Die verschiedenen, frühen Entwicklungslinien fossiler Siphonopoden werden als eine Unterklasse Orthoceroida zusammengefasst und so den Nautiloida, Coleoida und Ammonoida gegenübergestellt.
9) Einige weitere Taxa und Gruppenbezeichnungen werden diskutiert, wie darauf hingewiesen wird, eine vergleichend nicht gerechtfertigte Hypertrophie systematischer Gruppen zu vermeiden.

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CHROMATOPHORE ARRANGEMENTS OF HATCHLING LOLIGINID SQUIDS (CEPHALOPODA, MYOPSIDA)

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ABSTRACT

The color, location and number of chromatophores were studied as a basis for identifying hatchlings of three western Atlantic loliginid squids (*Loligo plei, Loligo pealei* and *Lolliguncula brevis*) and one eastern Pacific species (*Loligo opalescens*). Counts of chromatophores were made on the head and mantle of the squid hatchling, and the mean number and frequency distribution were calculated to establish a standard number of chromatophores for each area. Lines drawn to connect specific groups of chromatophores formed rows and shapes that were used to describe a specific arrangement for each species. Comparisons among the species indicate that all four are distinguishable by their characteristic chromatophore arrangements at hatching. *Loligo opalescens* and *Lolliguncula brevis* are the most easily identifiable species, while *Loiigo plei* and *Loligo pealei* are more difficult to distinguish.

INTRODUCTION

Neritic squids of the family Loliginidae are increasingly important worldwide as neurophysiological research models (Rosenberg, 1973; Arnold et al., 1974; Matsumoto, 1976) and as commercial fisheries resources (Voss, 1973; Okutani, 1977; Rathjen et al., 1979). While this importance has resulted in a better understanding of the biology of some loliginid species, most studies have been concerned with adult animals; relatively little is known about the hatchlings. In particular, little information exists on the distinguishing characteristics of the hatchlings. Historically, chromatophore coloration and patterning in cephalopods have not been used as a means of identification because the delicate skin is easily abraded during capture and colors fade in preservation. However, recent works (e.g. Holmes, 1940; Wolterding, 1971; Packard & Hochberg, 1977; Hanlon, 1978; Hanlon & Hixon, in press) have shown that skin patterning is species-specific in several cephalopods and is useful in the identification of live animals. While some workers (Joubin, 1892; Naef, 1921–1928) have suggested the importance of chromatophores for the identification of hatchlings, only Fioroni (1965) and Hall (1970) have attempted species-specific descriptions of chromatophores of hatchlings.

We believe that chromatophores, one of the basic elements of cephalopod skin patterning (as defined by Packard & Hochberg, 1977), provide a basis for identification of squid hatchlings. In this paper we describe and compare four New World species: the tropical arrow squid *Loligo (Doryteuthis) plei* Blainville, 1823, the common squid *Loligo pealei* Lesueur, 1821 and the brief squid *Lolliguncula brevis* (Blainville, 1823), all from the western Atlantic; and the California market squid *Loligo opalescens* Berry, 1911 from the eastern Pacific. Other noteworthy references that describe or illustrate chromatophores of late embryonic or post-hatching stages of these species are: *Loligo plei* (LaRoe, 1967: 176); *Loligo pealei* (Brooks, 1880: pl. 3, fig. 18; Verrill, 1881: 320 and pl. XLI; Arnold, 1965: 31; 1971: 277); *Lolliguncula brevis* (LaRoe, 1967: 186; Hall, 1970: 746, 766; and Hunter & Simon, 1975: 50, fig. 15); *Loligo opalescens* (Berry, 1912: 297 and pl. XLIII; Fields, 1965: 60; Okutani & McGowan, 1969: 11). Because the primary interest of these studies was either morphological or embryological and not specifically about chromatophores, the chromatophore arrangements depicted may be inexact.

Collectively the three western Atlantic species range from Nova Scotia (45°N latitude) southward throughout the Gulf of Mexico and Caribbean Sea to Argentina (45°S); *Loligo opalescens* ranges from British Columbia in the eastern Pacific (50°N) to the tip of Baja California (22°N). These myopsid squids live on the continental shelf from the shore to depths greater than 200 m. They all have relatively small telolecithal eggs, are of a similar small size at hatching and become planktonic after hatching.

Because the generic status of *Loligo plei* is uncertain we use *Doryteuthis* as a subgeneric designation (see discussion in Cohen, 1976). To avoid confusion in the text the abbreviation *L.* is used only for the three species of the genus *Loligo.* In all references to *Lolliguncula* the genus is given in full.

MATERIALS AND METHODS

Wild-caught adult *L. plei, L. pealei* and *Lolliguncula brevis* captured by dipnets and bottom trawls in the northern Gulf of Mexico south of Galveston, Texas were maintained separately by species in circular, 2 m diameter, 1000 l closed-system seawater tanks (Hanlon et al., 1978). Mating and egg laying were observed in captivity thus insuring positive identification of each species of hatchling. Egg mops were removed from the oyster shell substrate and segregated into 64 l rectangular aquaria within the original 1000 l tank (for details see Hanlon et al., 1979). Development occurred at 21 to 23°C for these species with salinities ranging from 32°/∞ to 37°/∞ for the two Atlantic *Loligo* species and 22.5°/∞ to 24°/∞ for *Lolliguncula brevis. L. opalescens* eggs were collected by divers in Monterey Bay, California and shipped to Galveston in insulated, sealed plastic bags filled with oxygen and seawater at a temperature of 12.5°C and a salinity of 36°/∞. These eggs were hatched in the 1000 l tanks at 15°C and a salinity of 36°/∞.

Live hatchlings zero to five days posthatching were randomly chosen and transferred by pipette to small petri dishes where they were examined under a stereomicroscope at 50×. Excess water was removed to restrict movement of hatchlings. Both dorsal and ventral surfaces were observed by carefully manipulating the squids with surgical forceps. A representative drawing was made of each species at 25× with the aid of a camera lucida. The color and placement of each chromatophore for twenty individual hatchlings were plotted on this outline. The results described here are based on squids from the same brood, but additional observations of photographs and live hatchlings from other broods supplemented the descriptions of the twenty specific individuals.

The color of an individual chromatophore varies according to the degree of expansion. Retracted or slightly expanded chromatophores appear as prominent "dots" on a squid hatchling and are darker in color and more discrete than expanded chromatophores. Since chromatophores of hatchlings are most commonly retracted or only slightly expanded, our descriptions and drawings are based on chromatophores in this state. Colors were standardized according to *A Dictionary of Color* (Maerz & Paul, 1950). Chromatophores of hatchlings may be broadly divided into two categories of color: reds, ranging from Flaming maple (Maerz & Paul, 1950: pl. 4, no. L-5) to Domingo brown (ibid.: pl. 8, no. L-9); and yellows, ranging from Lemon yellow (ibid.: pl. 10, no. K-3) to Caramel (ibid.: pl. 12, no. F-10). Standards of color are assigned for each species, but due to intraspecific variability of color these standards should not be considered definitive. A considerable interspecific overlap of color occurs; therefore, color alone is not used as a distinguishing character. For these reasons, and for brevity, we refer only to a generalized classification of chromatophores as red or yellow. Furthermore, it is understood that in the text the words red or yellow refer to a single chromatophore of that color and not to the total hue of the animal.

A model arrangement of chromatophores was derived for each species. A standard number of chromatophores in a given anatomical area was determined on the basis of the mean number of chromatophores and their frequency distribution. Descriptions of arrangements of chromatophores are based, in part, on lines drawn to connect chromatophores that create geometric shapes and rows. Although this organization is arbitrary, it establishes order and defines some of the most stable and distinct elements of the arrangement of chromatophores.

The following sequence for collection of data was used for each region of the hatchling, and color, placement and numbers of chromatophores were recorded: (1) Dorsal head, (2) Dorsal mantle, (3) Ventral head, (4) Ventral mantle, (5) Total number of chromatophores and (6) Dorsal mantle length (ML; measured from anterior margin to posterior tip of mantle, calculated at 25×).

The red chromatophores of the ventral mantle were categorized according to the arrangements defined by Fioroni (1965): irregular (chromatophores not ordered in rows in any direction), transverse rows, longitudinal rows and regular (chromatophores both in transverse and longitudinal rows that, when joined by lines, form a grid). If rows occurred their number was recorded.

Observations of the hatchlings were made in an anterior to posterior direction assuring consistent technique. This procedure is especially helpful for species in which transverse rows occur on the ventral mantle, since the first three rows generally are the straightest and easiest to "read"; additional rows often are less clear-cut and may require arbitrary decisions concerning individual placement.

For statistical analyses, a nonparametric Kruskal-Wallis test was used to establish differences among the four species for selected single classification parameters. The sum of squares simultaneous test procedure (STP) was then used to compare these differences at a .01 level of significance (Sokal & Rohlf, 1969: 387).

RESULTS

Descriptions of arrangements of chromatophores: The drawings in Fig. 1 show the dorsal and ventral model arrangement of chromatophores for each species. The standard numbers (and ranges) of chromatophores for each species used in these descriptions are compiled in Table 1. Fig. 2 is a photograph of a live hatchling to complement Fig. 1.

Loligo plei: L. plei has a standard number of 82 chromatophores of which 16 are dorsal and 66 ventral (Fig. 1A). Red chromatophores appear Cardinal (Maerz & Paul, 1950: pl. 5, no. L-5) and yellows are Chrome o^P (ibid.: pl. 10, no. K-12). Mean mantle length of *L. plei* at hatching is 1.5 mm.

Nine yellow chromatophores occur on the dorsal surface of the head and five on the mantle. The five anteriormost chromatophores on the head form an inverted "V" between the eyes, with the apex at the base of the first pair of arms. The four remaining chromatophores on the head occur in a transverse curved row at the posterior end of the head. The five yellow chromatophores on the dorsal mantle form a pentagon when joined by lines, with its apex located posteriorly between the fins. Two red chromatophores are centered dorsally within the pentagon on each side of the ink sac.

Ventrally there are 31 chromatophores on the head and 35 on the mantle. The ventral surface of each tentacle has five chromatophores arranged in a row, alternating red (3) and yellow (2). Each fourth arm has two red chromatophores. A transverse row of three yellow chromatophores runs between the base of the fourth pair of arms and the eyes. Directly between the eyes is a pair of red chromatophores, and posteror to each eye is a pair of yellow chromatophores. Four red chromatophores form a trapezium on each side of the posterior end of the head when connected by lines. Twenty red chromatophores are arranged in five transverse rows on the ventral mantle. Yellow chromatophores are located in three areas: short rows of three posterior and lateral to row 1, intermixed with row 3, and one at each end of rows 4 and 5.

Loligo pealei: Of the standard 97 total chromatophores 19 are dorsal and 78 are ventral (Fig. 1B). Red (Cardinal) and yellow (Chrome O^P) chromatophores are the same color as those of *L. plei.* Mean mantle length of *L. pealei* is 1.6 mm at hatching. Nine chromatophores appear on the dorsal surface of the head and ten on the dorsal mantle. Those on the head occur in an inverted "V" and a transverse row similar to *L. plei.* The eight yellow chromatophores on the dorsal mantle form a tear-drop shape when connected by lines, with two red chromatophores on the mantle centrally located on each side of the ink sac.

The arrangement on the ventral surface of the head consists of alternating red (3) and yellow (3) chromatophores on the tentacles, two red chromatophores on each fourth arm and a transverse row of three yellow chromatophores at the base of the fourth pair of arms. The arrangement is completed with two red chromatophores between the eyes, a pair of yellow chromatophores posterior to each eye, and a trapezium formed by four red chromatophores on each side of the base of the head. This arrangement is identical to *L. plei* with the exception of an extra yellow chromatophore at the tip of each tentacle. The ventral surface of the mantle has 27 red chromatophores assembled in six transverse rows. Eighteen yellow chromatophores on the mantle occur in association with rows 1, 3, 5 and 6 in locations similar to those described for *L. plei.*

Lolliguncula brevis: Lolliguncula brevis has a standard number of 93 chromatophores (12 dorsal and 81 ventral) (Fig. 1C; Fig. 2). Red chromatophores appear Brazil brown (Maerz

TABLE 1. Comparison of chromatophore arrangements and mantle lengths of squid hatchlings—standard numbers and (range) based upon twenty individuals of each species. The standard numbers correspond to the model diagrams of Fig. 1.

	Loligo plei	*Loligo pealei*	*Lolliguncula brevis*	*Loligo opalescens*
Dorsal head and mantle chromatophores				
No. yellow	14 (12 - 17)	17 (14 - 18)	12 (12 - 14)	14 (11 - 17)
No. red	2 *	2 *	0 *	12 (10 - 15)
Total no.	16 (14 - 16)	19 (16 - 19)	12 (12 - 14)	26 (22 - 30)
Ventral head chromatophores	31 (30 - 32)	33 (31 - 36)	31 (30 - 32)	34 (31 - 38)
Ventral mantle chromatophores				
No. yellow	15 (12 - 17)	18 (16 - 21)	11 (10 - 13)	6 (4 - 11)
No. red	20 (15 - 23)	27 (21 - 32)	39 (36 - 44)	34 (30 - 39)
Total no.	35 (28 - 40)	45 (38 - 50)	50 (47 - 57)	40 (37 - 48)
Ventral mantle red chromatophore arrangement	Transverse rows	Transverse rows	Transverse rows	Irregular
No. transverse rows	5	6	7	n/a
No. red chromatophores/row				
Row 1	4 (4 - 5)	5 (4 - 6)	7 (6 - 9)	n/a
Row 2	5 (2 - 7)	6 (4 - 7)	7 (6 - 8)	
Row 3	5 (3 - 6)	6 (5 - 7)	7 (5 - 8)	
Row 4	4 (0 - 5)	5 (4 - 7)	6 (4 - 8)	
Row 5	2 *	3 (2 - 4)	6 (3 - 7)	
Row 6		2 *	4 (3 - 6)	
Row 7			2 (2 - 3)	
No. yellow chromatophores associated with each transverse row				
Row 1	6 (4 - 8)	6 (4 - 8)	4 *	n/a
Row 2	0 *	0 *	0 *	
Row 3	5 (0 - 7)	8 (6 - 8)	0 *	
Row 4	2 (0 - 3)	0 *	5 (0 - 6)	
Row 5	2 (0 - 2)	2 (0 - 2)	0 (1 - 7)	
Row 6	0 *	2 (0 - 2)	2 (1 - 2)	
Row 7	0 *	0 *	0 (1 - 2)	
Total no. chromatophores (entire hatchling)	82 (77 - 88)	97 (88 - 103)	93 (91 - 99)	100 (94 - 113)
Mantle length (mm)	1.5 (1.3 - 1.7)	1.6 (1.4 - 1.7)	1.8 (1.7 - 2.0)	2.7 (2.5 - 3.2)

n/a = Not applicable
* = No variation

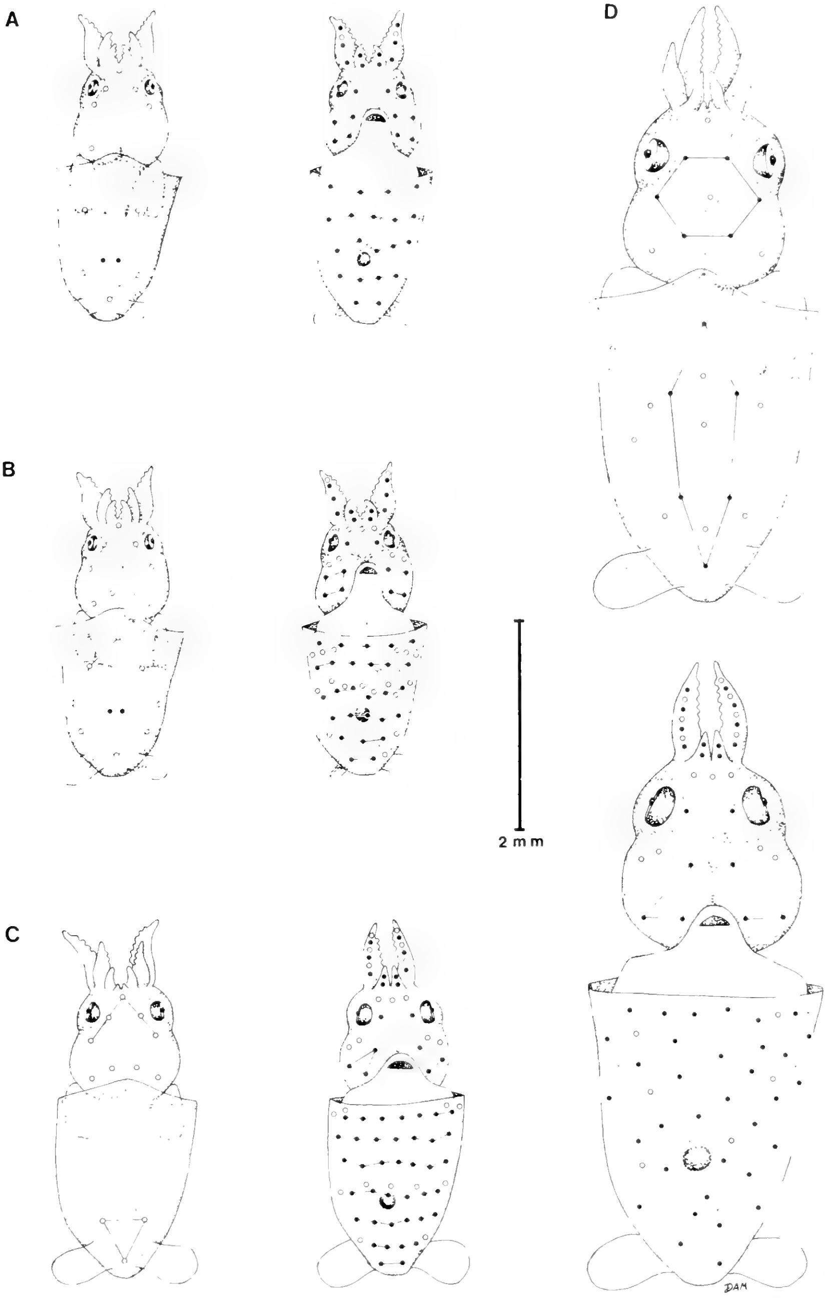

FIG. 1. Diagrammatic drawings of the model arrangements of chromatophores of four species of loliginid squid hatchlings. A) *Loligo plei*, B) *Loligo pealei*, C) *Lolliguncula brevis* and D) *Loligo opalescens*. Dorsal view on left, ventral view on right for A, B, C; dorsal view on top and ventral view on bottom for D. All drawn to same scale. Retracted red chromatophores represented by ●, retracted yellow chromatophores by ○. Solid lines connecting individual chromatophores are explained in the text.

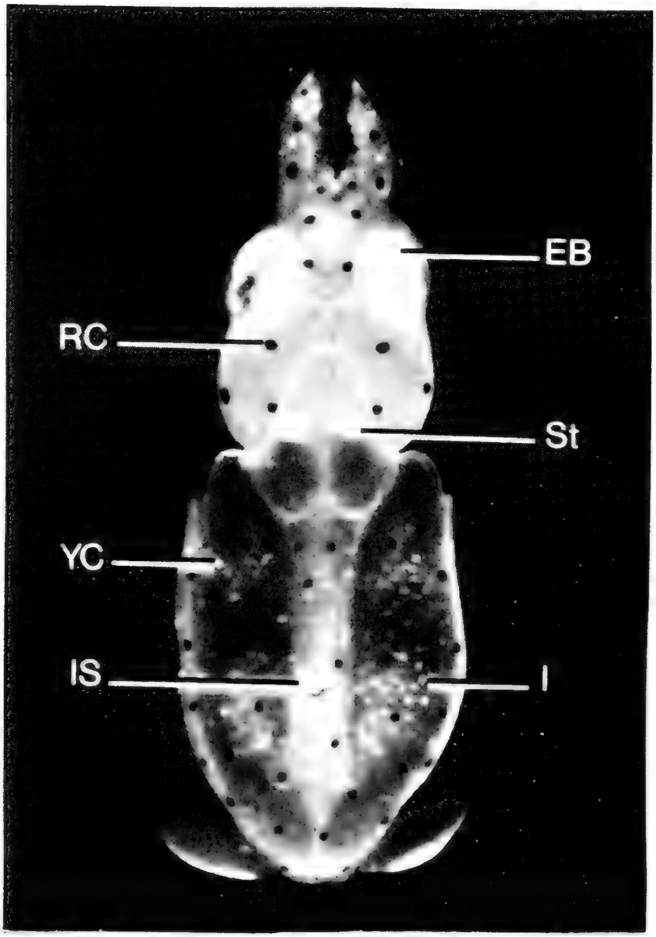

FIG. 2. Ventral view of a live *Lolliguncula brevis* hatchling. EB—eye ball, RC—red chromatophore, St—statolith, YC—yellow chromatophore, IS—ink sac, I—iridophore.

& Paul, 1950: pl. 8, no. L-8) and yellows appear Burnt-orange (ibid.: pl. 3, no. E-12). *Lolliguncula brevis* has a mean mantle length of 1.8 mm at hatching.

No red chromatophores occur dorsally, but nine yellow chromatophores are on the head and three on the mantle. The dorsal chromatophores on the head occur in an inverted "V" and a transverse row as described for *L plei* and *L. pealei.* The three yellow chromatophores at the posterior end of the mantle describe a triangle when connected by lines.

The 31 chromatophores on the ventral head are positioned as follows: on the tentacles in alternating rows of red (3) and yellow (3), a pair of reds on each fourth arm, a row of three yellows posterior to the fourth pair of arms, a pair of reds between the eyes and a pair of yellows posterior to each eye. Three red chromatophores on each side of the posterior end of the head form a triangle. The 39 red chromatophores on the ventral mantle are arranged in seven transverse rows. Yellow chromatophores are located in three areas: in pairs laterally at each end of row 1, just anterior to and intermixed with row 4 and individually at each end of row 6.

Loligo opalescens: This species has a standard number of 100 chromatophores (26 dorsal and 74 ventral) (Fig. 1D). The red (Brazil brown) and yellow (Burnt-orange) chromatophores are similar in color to those of *Lolliguncula brevis.* Mean mantle length at hatching is 2.7 mm.

The arrangement of the ten chromatophores on the dorsal head is best described by six prominent red chromatophores that form a hexagon, within which a single yellow chromatophore is centered. There is a single yellow chromatophore at the base of the first pair of arms and two others positioned laterally at the posterior base of the head. Of the 16 chromatophores on the dorsal mantle, six are red and ten are yellow. The six red chromatophores form a longitudinally oriented elongate hexagon. The ten yellow chromatophores are variable in their positions but closely resemble the arrangement diagrammed.

Ventrally there are 34 chromatophores on the head and 40 on the mantle. The ventral surface of each tentacle usually has seven or eight chromatophores alternating red and yellow. Many chromatophores are located in positions similar to those described for the other three species: two red chromatophores on each fourth arm, the transverse row of three yellow chromatophores posterior to the fourth pair of arms, the pair of reds between the eyes and the pair of yellows posterior to each eye. Three red chromatohores at the posterior end of the head form a triangle similar to *Lolliguncula brevis.* The 34 red chromatophores on the ventral mantle are irregular in arrangement. Both red and yellow chromatophores on the ventral mantle are variable in their positions but most commonly resemble the arrangement in Fig. 1.

Comparison of the four species. *Dorsal arrangement of chromatophores:* The arrangement and color of chromatophores on the head are identical for *L. plei, L. pealei* and *Lolliguncula brevis. L. opalescens* is differentiated by a hexagon of red chromatophores surrounding a yellow chromatophore. These comparisons are particularly consistent because the dorsal surface of the head of each species is the area of least variability.

L. opalescens can be separated from the other three species by the greater number of both yellow and red chromatophores on its dorsal mantle. It has six reds, as opposed to two in *L. plei* and *L. pealei* and none in *Lolliguncula brevis. L. plei* and *L. pealei* are not readily distinguishable because they have a similar arrangement and number of chromatophores that overlap somewhat due to the variability of occurrence of individual chromatophores. *Lolliguncula brevis* may be separated from the rest since it has no red chromatophores on its dorsal mantle and only three yellow chromatophores. Twenty percent of the *L. plei* hatchlings had only three yellows in the same arrangement as *Lolliguncula brevis,* but *L. plei* always had two red chromatophores on the dorsal mantle.

Ventral arrangement of chromatophores: The ventral head is relatively stable in arrangement for all four species except at the tip of the tentacles and the posterior base of the head.The occasional addition of a single red chromatophore at the base of the head will change the triangular shape described for *Lolliguncula brevis* and *L. opalescens* to the trapeziform shape described for *L. plei* and *L. pealei.* Conversely the rare deletion of a red chromatophore from the trapezium described for *L. plei* and *L. pealei* creates the triangle shape associated with *Lolliguncula brevis* and *L. opalescens.* Therefore this area alone is not reliable as an indicator of species identity.

The ventral mantle has the greatest number of chromatophores in all four species and their arrangement is complex. Distinctions can be made by comparing the arrangement of chromatophores, number of transverse rows created by red chromatophores and the total number of red chromatophores. *Lolliguncula brevis* has the largest total number of reds. They are arranged in seven transverse rows that easily differentiates this species from the other three. *L. plei* and *L. pealei* are the most similar in arrangement but usually differ in the number of transverse rows (5 versus 6, respectively) and the sum of red chromatophores (20 versus 27, respectively). *L. opalescens* is best identified by an irregular arrangement of red chromatophores on the ventral mantle. Statistical comparisons of the total number of red chromatophores on the ventral mantle indicate that the four species are different at a .01 significance level. However, the ranges for numbers of red chromatophores on the ventral mantle given in Table 1 show the possibility of overlap between *L. plei* and *L. pealei,* and between *Lolliguncula brevis* and *L. opalescens.* Yellow chromatophores on the ventral mantle are similar in location and number in *L. plei, L. pealei* and *Lolliguncula brevis; L. opalescens* is different, having only six yellows that occur in relatively random locations.

Total number of chromatophores: L. plei has the fewest chromatophores and can be separated from the others at the .01 significance level; however, a rare possibility of overlap between the upper limit of *L. plei* (88) and the lower limit of *L. pealei* (88) does exist. Although *Lolliguncula brevis* and *L.*

opalescens have a statistically different total number of chromatophores, sufficient overlap occurs to reduce the usefulness of this character. Comparisons of *L. pealei* with *Lolliguncula brevis* and *L. opalescens* show no statistical differences; the total number of chromatophores of *L. pealei* is within the range of either of those species.

Mantle length: L. opalescens has a substantially greater mantle length (mean ML 2.7 mm) at hatching that distinguishes it from *Lolliguncula brevis* (1.8 mm), *L. pealei* (1.6 mm) and *L. plei* (1.5 mm); these differences are statistically significant at the .01 level. Although there is a statistically significant difference between *Lolliguncula brevis* and *L. pealei* or *L. plei,* overlap does occur. Mantle length is a distinguishing character only at hatching because at present growth rates and methods of determining age (e.g. from growth rings of statoliths) are not known for these species.

Summary: All four species are distinguishable by their characteristic arrangement of chromatophores. *L. opalescens* and *Lolliguncula brevis* are the most easily identifiable species while *L. plei* and *L. pealei* are the most similar.

L. opalescens is immediately recognized at hatching by its greater mantle length. This species differs from the other three by its greater total number of dorsal chromatophores, in particular the twelve dorsal red chromatophores. The irregular arrangement of the red chromatophores on the ventral mantle is peculiar to this species.

Lolliguncula brevis contrasts with the other three species by having no red chromatophores on the dorsal mantle and only three yellows. Both the greater number of transverse rows (7) and larger total number of red chromatophores on the ventral mantle distinguish this species. The mantle length of *Lolliguncula brevis,* less than *L. opalescens* but greater than *L. pealei* and *L. plei,* is also a good indicator.

L. pealei can be differentiated from *L. plei* on the basis of three additional yellow chromatophores on its dorsal mantle. *L. pealei* has six transverse rows in the ventral arrangment of the mantle chromatophores while five rows occur in *L. plei. L. plei* also may be singled out by its lower total numbers of chromatophores.

DISCUSSION

When Fioroni (1965) explored the use of chromatophores as a taxonomic character for the hatchlings of several Mediterranean cephalopods, he described the chromatophores of Naef's (1921–1928) late embryonic stages. Fioroni's (1965) descriptions of hatchlings at Stage XX and older were based on color, location and number of chromatophores and indicated substantial variability among the three characters. But while he observed that "individual variations occur so that only practically two or three completely identical embryos can be found" (our translation), he also stressed that the more constant elements may provide a characteristic arrangement. Our study provides such a model for four New World loliginid species, as well as the methodology for determining characteristic arrangements for related species.

Application of this technique may ultimately lead to a key for live squid hatchlings. Already comparisons can be made. Fioroni's (1965) assumption, based on descriptions by Brooks (1880), Verrill (1881) and Berry (1912), that *L. opalescens* and *L. pealei* had significantly fewer chromatophores than *L. vulgaris,* is verified by our findings that *L. opalescens* and *L. pealei* hatchlings have 100 and 97 chromatophores, respectively, while *L. vulgaris* has 200. Such a key used in conjunction with morphometric indices would be most instructive in the field of cephalopod taxonomy, which suffers from a lack of study of comparative anatomy and development on the vast majority of species (Voss, 1977). It may also help to establish phylogenetic affinities within the family Loliginidae. For instance, our findings suggest that *L. plei* and *L. pealei* may be more closely related to each other than to the other two species examined.

The eventual taxonomic differentiation of young squids would also benefit squid fisheries research. Most adult loliginids are schooling animals, and this contagious or clumped spatial distribution (Cassie, 1971) makes estimates of actual abundance difficult. Estimates based on the more randomly distributed young stages soon after hatching could be more accurate.

In general the significance of patterning in hatchling cephalopods is poorly understood. The relationships of body patterning and behavior in cephalopods have only recently been investigated, and these studies cover only a few genera such as *Octopus* (Packard & Sanders, 1971; Wolterding, 1971; Warren et al., 1974; Packard & Hochberg, 1977), *Sepia* (Holmes, 1940), *Loligo* (Hanlon, 1978) and *Sepioteuthis* (LaRoe, 1971; Moynihan, 1975). The only true body patterns that young *Loligo* or *Lolliguncula* are known to be capable of are *"Clear"* and *"All Dark"* (Hanlon, 1978). In *"Clear"* the chromatophores are retracted and the animal is translucent. The iridophores, which are located beneath the chromatophores and reflect blue and green wavelengths of light, are also elements of patterning. The scattered iridophores on the mantle of hatchlings may or may not be conspicuous depending on the angle and amount of light reflected; but the iridophores that densely cover the eye balls and ink sac are always prominent and render these organs opaque or iridescent. Therefore, the eye balls and ink sac act as patterning components in the *"clear"* pattern, as suggested by Fioroni (1965) and Packard & Sanders (1969). In the *"all dark"* pattern all chromatophores are expanded, and since there are more chromatophores ventrally, a ventro-dorsal gradient of color is present. This is a curious phenomenon since most pelagic marine animals are darker on the dorsal surface and lighter underneath for countershading. The significance of the ventro-dorsal shading gradient is unknown. Field observations of hatchlings and information on their habitat and mode of life during the first few weeks may clarify the significance of the higher number of chromatophores present ventrally. However, it is known that the hatchlings do not swim upside down as was stated by Fioroni (1965). In the course of growth and the subsequent addition of chromatophores the gradient becomes dorso-ventral. In small *L. plei* (30 mm ML) the squid is already capable of several chromatic components. Thus, knowledge of the exact placement of chromatophores at hatching may provide baseline information to study the growth of chromatophores and the ontogeny of patterning.

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LOCOMOTION RATES AND SHELL FORM IN THE GASTROPODA: A RE-EVALUATION

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ABSTRACT

A reconsideration of data from Linsley (1978a) indicates that the association between crawling speed and shell form is not likely to be a causal one. The correlation between speed and form is due largely to multiple adaptations to different habitats (particulate versus rocky substrates). In addition, a conservative estimate of the energy saved by reducing drag experienced at crawling speeds is shown to be more than three orders of magnitude less than the energy expended during normal activity. One may be able to distinguish surface dwelling from burrowing gastropods in the fossil record based on shell form, but not "fast" from "slow" moving species.

INTRODUCTION

Linsley (1978a,b) has recently advanced the proposition that shell form in marine gastropods may be related to rates of locomotion, finding that more rapidly moving animals have subjectively lower drag shells than slower moving ones in general. The purpose of this paper is to examine some alternative hypotheses accompanied by additional data which suggest this correlated association is not a causal one, but is very likely a consequence of other covarying biological and environmental factors.

The additional information I have compiled (Table 1) falls into three categories: 1) type of locomotion (muscular waves of various types versus cilia); 2) habitat type (predominantly sand versus rock); and 3) some estimates of the actual drag forces experienced by snails at crawling speeds in relation to their tenacity. I present this information only for the species that Linsley (1978a) has considered, and while much more extensive data exist on the rates of locomotion for many prosobranch species (Miller, 1972, 1974a) the general conclusions adequately obtain from his smaller sample.

PROCEDURES AND RESULTS

In Table 1, I have arrayed species in the five 'form rank' categories of Linsley (1978a) where increasing rank relates to presumed increases in drag experienced by the shells. This is a compound subjective ranking based on some measure of bilateral symmetry (presumably symmetry with respect to the direction of motion rather than with respect to the axis of coiling, though this is not clear in his description of methods) and on the amount of shell ornamentation, where both greater asymmetry and more extensive sculpture are believed to increase drag. Species followed by an 'M' carry their shell at least partially covered either by the mantle or foot during locomotion.

Locomotor types have all been identified from the appendix of Miller (1974b). For species not listed in this appendix, I have assigned the mode of locomotion determined either for other members of the same genus or the same family. Such inferences are indicated by the subperscripts G and F respectively in column 2 of Table 1. The details of the different locomotor types are illustrated and discussed in Miller (1974b).

The habitat information is unfortunately crude but I think sufficient for the distinctions I would like to make. It has been collected from several sources identified by the footnotes at the top of each column (columns 3–7, Table 1). The column headed 'summary' (column 8) indicates what is considered to be the "average" or "typical" habitat of the species based on these varied sources and it is this habitat assignment to which I refer in subsequent discussion. As with locomotory modes, a G or F superscript indicates an inference from

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TABLE 1. Habitat, estimated drag at crawling speed and tenacity of the species from Linsley (1978a) and from various other sources. Species followed by an 'M' in column 1 carry their shell at least partially covered by the mantle or foot during locomotion. Locomotor type abbreviations: Arhyth.—Arhythmic muscular waves (discontinuous, indistinct and terminating); Lat. mon.—Lateral monotaxic muscular waves; Dir. dit.—Direct ditaxic muscular waves; Ret. dit.—retrograde ditaxic muscular waves (including diagonal retrograde ditaxic waves); Ret. mon.—Retrograde monotaxic muscular waves. Habitat abbreviations: AC—associated with coral or coral reefs; AS—associated with sand or mud (i.e. sometimes found on rocks or in rubble); Go—on gorgonians; Gr—in or on seagrasses; Ma—on mangrove roots, pilings or driftwood; Rl—rocky intertidal; Ro—rocky habitat (not restricted to the intertidal); Ru—in rubble, either coral or rock; S—sand or mud; UR—under rocks; X—species not listed in that reference;-- —species listed but no habitat information provided. Under 'drag calculations' L refers to approximate adult shell length; D to approximate adult shell diameter; Re to Reynolds number; and C_d to the drag coefficient. G or F superscripts to locomotor type, habitat or tenacity indicate the information has been inferred from other members of the same genus or family respectively. See text for a more detailed discussion.

		Habitat						Drag calculations						
		References							Approx. shell size[6]					
Species	Locomotor type[2]	3	4	5	6	7	Summary	Speed[1] (mm/s)	L (mm)	D (mm)	Re	C_d	Drag (dyn)	Tenacity (dyn × 10^5)[8]
Form Rank 2[1]														
Busycon contrarium	Arhyth.^{F}	S	X	S	--	X	S	4.0	255	114	1020	0.5	408.3	--
Cyphoma gibbosum (M)	Ciliary	Go	Go	Go	Go	Go	Go	1.3	30	12	39	1.6	1.5	--
Cypraea cervus (M)	Lat. mon.^{G}	Gr	--	--	--	X	Gr	2.8	130	71	364	0.6	99.3	--
C. cinerea (M)	Lat. mon.^{G}	X	UR	AC	UR,AC	UR,AC	Ru	4.3	30	19	129	0.9	23.1	--
C. spurca acicularis (M)	Lat. mon.^{G}	X	UR	Ru	UR	Ru	Ru	3.4	25	14	85	1.1	9.6	--
Cypraecassis testiculus	Ciliary^F	Ru	--	AC	UR	S,Ru	AS	5.6	50	36	280	0.7	114.9	4.0^F
Fasciolaria lilium hunteria	Ret. dit.^{G}	X	X	X	--	X	S^G	4.6	70	31	322	0.7	54.3	--
F. tulipa	Ret. dit.	X	Gr	S,Gr	--	S,Gr	S	6.5	140	58	910	0.5	284.6	--
Hyalina avena	Ciliary^F	X	UR	--	--	UR,AC	Ru	3.5	12	4	42	1.5	1.2	--
Marginella guttata (M)	Ciliary^F	X	X	S^F	UR	S^F	AS	3.0	15	8	45	1.5	3.5	--
M. lactea (M)	Ciliary^F	X	--	S^F	--	S^F	AS	1.8	6	3	11	3.0	0.4	--
M. pruniosum (M)	Ciliary^F	X	X	S^F	S,Gr	S^F	S	3.4	10	6	34	1.7	2.4	--
Mitrella ocellata	Ret. dit.^{G}	X	X	X	UR	UR,S	AS	1.9	12	5	23	2.1	0.8	5.2^F
Nitidella nitida	Ret. dit.^{F}	X	Ru	AC	Ru	UR	Ru	2.0	12	5	24	2.0	0.7	5.2^F
Oliva sayana (M)	Ciliary^G	X	X	S	S	S	S	8.4	55	21	462	0.6	70.9	0.5^G
Polinices duplicatus (M)	Ciliary	S	X	S	S	X	S	5.6	45	40	252	0.8	151.7	--
P. lacteus (M)	Ciliary^G	X	S	S	S	S	S	3.4	30	22	102	1.0	21.7	--
Tonna maculosa	Ciliary	S	--	AC	--	S,AC	S	3.6	90	58	324	0.7	1.2	--

Form Rank 3													
Columbella mercatoria	Ret. dit.	X	--	S,Gr	UR	UR,AC	AS	0.9	15	8	13	2.8	0.6	5.2^{F}
Melongena corona	Arhyth.^{G}	S	X	S	--	X	S	3.6	75	41	270	0.8	64.2	--
M. melongena	Arhyth.	X	X	X	--	X	S^{G}	2.4	115	69	276	0.7	78.6	--
Nassarius vibex	Ciliary^{G}	X	S	S	S	S	S	5.0	12	6	60	1.3	4.6	1.2^{G}
Trivia maltbiana (M)	Ciliary ?^{G}	X	--	Ro	Ro	X	Ro	0.8	10	6	8	3.5	0.3	--
Turbinella angulata	?	X	X	X	--	X	?	0.5	265	115	132	0.9	11.3	--
Form Rank 4														
Cassis flammea	Ciliary	Ru	--	--	--	X	Ru	1.8	100	74	180	0.8	54.3	4.0^{G}
Cittarium pica	Ret. dit.	Rl	Ro	Rl	Rl	X	Rl	0.9	60[9]	60	54	1.4	15.6	--
Crassispira cubana	Arhyth.^{F}	X	X	X	UR	X	Ru	0.4	20	8	8	5.0	0.2	--
Littorina angulifera	Ret. dit.	Ma	Ma	Ma	Ma	Ma	Ma	2.4	25	13	60	1.3	4.9	1.9^{G}
L. ziczac	Ret. dit.^{G}	Rl	Rl	Rl	Rl	Rl	Rl	0.6	15	8	9	4.5	0.4	1.9^{G}
Murex pomum	Ret. dit.	X	--	--	Ru	Ro	Ru	1.6	85	39	136	0.9	13.1	1.7^{F}
Nerita fulgurans	Ret. mon.^{G}	Rl	--	--	--	Rl	Rl	2.4	20	18	48	1.4	10.5	16.5^{G}
N. versicolor	Ret. mon.^{G}	Rl	Rl	Rl	Rl	X	Rl	2.6	20	18	52	1.4	12.0	16.5^{G}
Pisania auritula	Ret. mon^{G}	Ru	--	X	--	Ru,Ac	Ru	2.3	30	18	69	1.2	8.1	--
Planaxis nucleus	Ret. dit.	X	Rl	Rl	--	X	Rl	1.7	12	8	20	2.2	1.6	--
Tegula fasciata	Ret. dit.^{G}	X	UR	UR	UR	X	Ru	1.8	20[9]	20	36	1.7	8.5	5.2^{G}
T. lividomaculata	Ret. dit.^{G}	X	UR	UR	UR	X	Ru	0.9	20[9]	20	18	2.4	3.0	5.2^{G}
Thais rustica	Dir. dit.	Rl	Rl	--	--	Rl	Rl	2.4	40	23	96	1.0	12.2	4.6^{G}
Turbo canaliculatus	Ret. dit.^{G}	X	--	--	--	Ru	Ru	1.5	75[9]	75	113	0.9	46.7	6.8^{G}
Vasum muricatum	Arhyth.	Ru	--	--	--	X	Ru	0.3	83	51	26	2.0	1.8	--
Form Rank 5														
Leucozonia ocellata	Ret. dit.^{G}	X	--	UR	UR	Ro,AC	Ru	0.5	20	11	10	4.0	0.5	--
Nodilittorina tuberculata	Ret. dit.^{F}.	Rl	Rl	Rl	Rl	Rl	Rl	0.6	15	12	9	3.3	0.7	1.9^{F}
Ocenebra minirosea	Ret. dit.^{G}	X	--	X	--	X	Ro^{G}	0.3	6	3	2	16.0	0.04	0.7^{G}
Thais deltoidea	Dir. dit.	Ro	Rl	Rl	Rl	Rl	Rl	0.6	40	27	24	2.0	2.1	4.6^{G}
Vexillum dermestinum	Ciliary^{G}	X	X	X	--	Ro,S^{G}	AS	0.5	20	8	10	3.2	0.2	--
Form Rank 6														
Astraea phoebia	Ret. dit.	X	--	Gr	Gr	Ro,Gr	Gr	0.4	60[9]	60	24	2.0	4.6	31.8^{G}
A. tecta americana	Ret. dit.	X	--	UR,Gr	UR,Gr	X	Gr	0.3	25[9]	25	7	5.0	1.1	31.8^{G}
A. t. tecta	Ret. dit.	X	--	--	--	X	Gr^{G}	0.4	25[9]	25	10	4.0	1.6	31.8^{G}

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[1] Linsley (1978a); [2] Miller (1974b); [3] personal observation; [4] Warmke & Abbott (1961); [5] Abbott (1968); [6] Abbott (1974); [7] Rios (1970); [8] Miller (1974a); [9] for turbinate shells diameter is used instead of length.

species in the same genus or family respectively.

Drag has been estimated using the following equation (Alexander, 1968, eq. 28):

$$\text{Drag} = \tfrac{1}{2}\, rv^2AC_d$$

where r refers to the fluid density (essentially 1 gm/cm³ for seawater); v is the velocity of the object relative to the fluid (for these computations, crawling speeds from Linsley, 1978a); A is the measure of the area of the object [I have used frontal area, the projected area in the direction of motion, which for this analysis may be approximated as a circle whose diameter corresponds to the diameter of the body whorl (column D under shell size)]; and C_d is a drag coefficient whose numerical value has been determined from the empirical relation between C_d and Reynolds number (Tietjens, 1934, fig. 54) assuming the object to be a sphere of diameter L (the approximate length of the adult shell). This obviously unrealistic assumption of spherical snails introduces some error, but comparison of the C_d/ Reynolds number relationship for spheres and cephalopod shells (Chamberlain & Westermann, 1976, fig. 4) indicates that this error is probably slight. The crawling speeds are those measured by Linsley (1978a). Approximate adult shell sizes, both lengths (L) and diameters (D) were compiled from Abbott (1974) using the mean of the range of sizes given in the species' description. R_e values are Reynolds numbers, assuming a kinematic viscosity of 0.010 cm²/s for seawater, which were computed for shells using adult length and crawling speed. The drag values thus provide a rough approximation of the force required to push a shell of a given size through the water at crawling speeds and do not include any frictional resistance between the sole of the foot and the substrate.

Finally, tenacities (force required to dislodge an attached animal) as measured normal to the substrate have been compiled from Miller (1972) for comparison with the drag forces. Her tenacity values in gm/cm² of foot area have been converted to dyns through multiplication by the foot area and gravitational constant and are expressed as dyn × 10^5.

Table 2 summarizes the information in Table 1 for locomotor types and habitat. In addition to the correlation between shell form and speed noted by Linsley (1978a) there are also strong associations between shell form and 1) the manner in which the mantle and/or foot covers the shell; 2) whether the species use ciliary locomotion or muscular waves and 3) whether species live in a sand environment or in the rocky intertidal. Nearly two-thirds of the species of form rank 2 (presumed low drag shells) envelop their shell with either the mantle or the foot while moving so that the shell itself is not responsible for drag, yet no species in the higher drag categories (4–6) exhibit this behavior. Approximately half of the species of form ranks 2 and 3 utilize ciliary locomotion whereas nearly all the species of ranks 4 through 6 (presumed high drag shells) use muscular waves. Finally, two-thirds to three-quarters of the species with presumed low drag shells (ranks 2 and 3) are sand dwellers and none live in the rocky intertidal. Rocky intertidal dwellers are restricted to categories 4 and 5. Category 6 contains species from only one genus associated with rocky substrates and seagrasses.

Table 1 also tabulates the estimated drag forces experienced by the various species while moving through the water and it is clear by comparing these with what information is available on tenacities (Miller, 1974b) that the estimated drag forces at the speeds gastropods move is three to six orders of magnitude less than the force required to dislodge an

TABLE 2. Proportions of species of different locomotor types and from different habitats as a function of form ranking.

			Locomotion type		Habitat		
Form Rank	N	Enveloping mantle	Ciliary	Muscular waves	Sand	Rocky intertidal	Other
2	18	0.61	0.56	0.44	0.67	0.0	0.33
3[1]	5	0.20	0.40	0.60	0.80	0.0	0.20
4	15	0.0	0.07	0.93	0.0	0.47[2]	0.54
5	5	0.0	0.25	0.75	0.20	0.40	0.40
6	3	0.0	0.0	1.0	0.0	0.0	1.0

[1] Not including *Turbinella angulata* for which information is not available.

[2] Includes *Littorina angulifera,* living intertidally on mangrove roots.

animal while moving. Note that this is assuming no movement of water relative to the shell except that due to locomotion, i.e. no wave action or tidal current.

DISCUSSION AND RE-EVALUATION

Linsley's proposition (1978a) that drag reducing morphologies in marine gastropods may have evolved in response to higher locomotion rates derives from a correlation between average crawling speeds and a ranking of shell form based on presumed drag resistance. Considering the above results, it would appear that this correlation is due largely to a more complicated association of several other biologically or ecologically important factors. First, ciliary locomotion is on the order of two to three times faster than either retrograde monotaxic or retrograde ditaxic and nearly three times faster than arhythmic muscular waves on the average (Miller, 1974a, table 1). This is particularly true for smaller gastropods (less than 15 mm). If one only compares crawling speeds of *Conus* species, the mean speed of species using ciliary locomotion (1.56 mm/s, $N = 5$) is more than three times that of species using some form of muscular waves (0.43 mm/s, $N = 13$; Miller, 1972) and this difference is highly significant ($P < 0.001$, Mann-Whitney U test). Hence, the faster average speeds observed among species in form categories 2 and 3 are due at least in part to differences in locomotion modes. This does not affect the interpretation of the correlation between speed and form, it only provides a partial explanation for the differences in mean speed observed among the different form categories.

Second, species using ciliary locomotion are mostly sand dwellers (10 of 14, Table 1; 30 of 34 species identified in Miller, 1974a in her table 2). In fact, Miller (1974a: 146) states that "Ciliary and discontinuous locomotion in prosobranchs appear to be primarily adaptations to soft substrata." In addition, gastropod crawling speeds for ciliary locomotion are 1.5 to 2 times faster on Plexiglas than on sand (Miller 1974a: table 3). Thus crawling speeds of ciliary movers measured on Plexiglas will most likely be faster than those the animals experience in their natural environment, and this artifact may also contribute to the mean speed differences among form categories.

Third, species living in sandy environments spend at least some time burrowing in the sediment. This is true for *Busycon* (Paine, 1963), *Cassis* (Hughes & Hughes, 1971), *Fasciolaria* (Snyder & Snyder, 1971), *Melongena* (Hathaway & Woodburn, 1961), *Polinices* (Edwards & Huebner, 1977), and *Oliva* (Marcus & Marcus, 1959). The energy expended while burrowing has been measured at nearly 10 times that while crawling on the surface in a sand dwelling nassariid, *Bullia* (Trueman & Brown, 1976) presumably largely as a result of the increased resistance experienced while moving through sand. Consequently one would expect species that burrow to possess less sculpture and present a smaller cross-sectional area in the direction of movement than those species that do not burrow. This should be particularly true for shell sculpture since the markedly higher viscosity and lower crawling speeds in a sand/water "solution" will result in a lower Reynolds number and thus a relatively greater contribution of surface friction to overall drag. Given that two-thirds to three-quarters of the species in rank categories 2 and 3 are sand dwellers (Table 2) it is not surprising that they exhibit such lower drag shells. Much of the variation in drag reducing morphology between the form rank categories can thus be attributed to habitat constraints rather than crawling speed. Hence, because drag reducing morphologies and ciliary locomotion are both associated with a sandy environment where burrowing efficiency may be an important selective force, the association between surface crawling speed and shell form appears due in large part to the coevolution of multiple adaptations for inhabiting particulate substrates and not because of a direct response of shell form to open surface crawling speed per se.

Another habitat dependent factor is shell sculpture. Open surface (e.g. rocky intertidal) dwelling gastropods may be more exposed to shell crushing predation particularly by fishes than sand dwelling species. This is supported to some extent by Vermeij's observation (1978: 131) that while "the most profound interoceanic variations in architecture occur on open rocky surfaces," changes in sand dwelling species are considerably less pronounced. Consequently, sculptural defenses against crushing (Vermeij, 1978; Palmer, 1979) may be of greater importance to open-surface dwelling gastropods. Such a relative advantage of shell sculpture in open surface dwelling species compared to sand dwellers would be further augmented by its tendency to increase the drag experienced while burrowing among sand dwellers. The restriction of rocky intertidal species to rank categories 4 and 5 (Table 2) is due largely to a greater development of shell sculpture.

Further complicating the interpretation of hydrodynamic drag with respect to shell sculpture are conflicting observations of intraspecific variation related to wave action. The degree of sculptural development has been found both to increase (James, 1968; Sakai, 1972) and decrease (Struhsaker, 1968) intraspecifically in different species of *Littorina* in response to increasing wave action. At certain water velocities, sculpture may actually decrease drag (Chamberlain & Westermann, 1976). Thus, sculpture per se cannot always be assumed to increase the hydrodynamic drag experienced by surface dwelling gastropods.

Finally, and perhaps most importantly for a streamlining argument, is the consideraton of water velocities experienced by gastropods independent of their movement. Koehl (1977) has measured water velocities of up to 160 mm/s in tidal currents and 1300 mm/s in wave surge. These are 2 to 3 orders of magnitude greater than gastraopod crawling speeds. Given that environmental water velocities are so much greater than crawling speeds, the marginal increase in water velocity relative to the shell due to locomotion would seem to be insignificant. Further, if water velocity is such an important factor influencing shell form, one would predict that open surface dwelling species should exhibit low drag shells, and the data in Table 2 do not support this prediction. Rocky intertidal species are restricted to form categories 4 and 5 (presumed high drag shells) while species living in rubble or under rocks generally occur in all categories.

To place the drag experienced by snails at crawling speeds in perspective, it is informative to estimate the energy expended to overcome this drag and compare it to values for locomotory metabolism. A single example illustrates the point. From Table 1, the estimated drag on *Thais rustica* at crawling speed is 12.2 dyn (measured values for drag on an unsculptured morph of *Thais* (=*Nucella*) *lamellosa* of comparable size at a water velocity of 2 mm/s are less than one tenth of this; Palmer, unpublished). The power, or energy per unit time to overcome this force, equals the force times the crawling velocity, yielding a value of 2.4 ergs/s (12.2 dyn × 0.2 cm/s). Oxygen consumption in a comparable sized *Thais* (=*Nucella*) *lapillus* during "intermittent low activity" has been measured at approximately 70 μl/hr (Bayne & Scullard, 1978) which converts to 3.9×10^3 ergs/s [$(1.9 \times 10^{-2}\ \mu lO_2/s) \times (4.8 \times 10^{-3}$ cals/$\mu lO_2) \times (4.2 \times 10^7$ ergs/cal)]. The total energy expended to overcome drag is thus more than three orders of magnitude less than that expended during low levels of activity. Since one is really interested in energy saved due to *relative* differences in drag attributable to shell orientation or sculpture rather than *total* drag, the energy saved will be even a smaller fraction of the energy expended moving. Hence, even though one might argue that reducing drag at crawling speeds still represents an energy savings, this savings will be vanishingly small.

The preceding discussion has analyzed the relation between crawling speed and drag reducing morphologies without examining how various shell features contribute to drag. As already mentioned, certain kinds of shell sculpture can reduce drag in rapidly moving water though they may tend to increase drag due to surface friction at lower water velocities (Chamberlain & Westermann, 1976). However, shell shape will also affect drag, particularly pressure drag (that drag due to the momentum transferred by the moving body to the fluid in the form of eddies and turbulence in the wake). Species with low apical half-angles [i.e. more elongate spires like *Fasciolaria tulipa* (Linné)] should experience less pressure drag than those with high apical half-angles [shorter spires like *Busycon contrarium* (Conrad)] because more gradually tapering trailing edges will tend to reduce wake size (Alexander, 1968: 218). Note that both of these species are considered presumed low drag shells (rank category 2). Caution should be exercised when trying to assign complex forms such as marine gastropod shells to categories based on presumed differences in an equally complex physical stress such as hydrodynamic drag. In the absence of any empirical evidence, such assignments must be considered highly tentative.

CONCLUSIONS

Interpreting the adaptive value of gastropod shell form based on single factor correlations is risky for a variety of reasons, not the least of which is that alternative causal factors may account for the observed association. In such correlative studies, the safest procedure is to identify as many plausible causal hypotheses as possible and examine the degree to which different hypotheses present different predictions. Linsley (1978a,b) has examined the hypothesis that locomotory rates may have exerted an important influence on shell form. His prediction that faster moving snails should have lower drag shells is supported by a correlation between shell characteristics believed to reduce drag, and increased crawling speed. However, this association can just as readily be explained as a compound adaptive response to differences in habitat as I have discussed above. If one compares non-sand dwelling species whose shell is exposed to the water during movement (i.e. whose shells are not enveloped by the mantle or foot since in these situations it is the mantle or foot that is responsible for the drag, not the shell itself), there are no significant differences in crawling speeds between species with presumed low drag shells (rank categories 2 and 3 pooled) and high drag shells (rank categories 4 through 6 pooled, $P > 0.10$, Mann-Whitney U test). The inference that drag reducing morphologies are an adaptive response to increased surface crawling speed and the subsequent interpretation of life modes in Paleozoic gastropods based on this inference (Linsley, 1978a,b) do not appear justified in light of the preceding analysis.

The strong association between shell form and habitat (Vermeij, 1978 and above) suggests that a safer interpretation of life modes from shell form may be based on the differences between surface dwelling and burrowing species. Species exhibiting strong external sculpture will most likely have been restricted to an open surface existence while those whose shells are very smooth and streamlined are likely to have been associated with some degree of burrowing.

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SYSTEMATICS OF THE SUBFAMILY CLINOCARDIINAE KAFANOV, 1975 (BIVALVIA, CARDIIDAE)

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ABSTRACT

Revising the Cenozoic Cardioidea, the author has established the new subfamily Clinocardiinae. The history of studies of clinocardiines, the size and composition of the subfamily and its systematic position within the Cardiidae are considered. The paper presents keys to tribes, genera, species and subspecies, and detailed diagnoses for subfamily, tribes, genera and subgenera. The catalogue raisonné contains all the taxa of species rank (88) described until now with special notes on the original descriptions, type-localities and the depositories of the type materials. Necessary taxonomic remarks are given. For *Cardium pauperculum* Yokoyama, 1923 non Meek, 1871 a new name is suggested: *Serripes nodai* nom. nov.

Cardiidae are widely represented in Cenozoic marine deposits of the North Pacific and European Subarctic. For many stratigraphical subdivisions the representatives of this group are either zonal forms or the most characteristic species. They are also important in the identification of the Paleogene-Neogene boundary in the northwestern part of the Pacific mobile belt, and in the North Atlantic they are one of the most striking participants of the Neogene trans-Arctic migrations of the North Pacific molluscs.

Until recently almost all the diversity of North Pacific cardiids were assigned to only three genera: *Clinocardium* s.l., *Serripes* s.l. and *Papyridea* s.l. The revision made by the author (Kafanov, 1974a, b, 1975, 1976) has shown that some new taxa of generic rank and the new subfamily Clinocardiinae should be established for North Pacific Cardiidae.

The purpose of this paper is to review Recent and fossil Clinocardiinae. The taxonomic position of this subfamily within the Cenozoic Cardioidea Lamarck, 1809, is dealt with in detail in Kafanov & Popov (1977).

On the status of the subfamily Laevicardiinae Keen, 1936

When discussing the necessity for establishing a new genus for the North Pacific "*Cerastoderma,*" Keen (1936a) proposed the new subfamily Laevicardiinae. This subfamily includes forms which may be characterized by the following diagnosis (Keen, 1969: N589): "Elliptic-oblique; rib ornamentation of looped threads or small nodes, not spines; ribs of posterior slope weaker than those of central and anterior slopes or obsolescent; posterior margin wavy rather than notched; hinge long and arched (line joining laterals and cardinals bends more than 25 degrees); cardinal teeth somewhat unequal in size, anterior left lateral bladelike."

In this subfamily Keen (1951) originally included: *Laevicardium* Swainson, 1840 (with the subgenera *Laevicardium* s.s., *Fulvia* Gray, 1853 and *Dinocardium* Dall, 1900), *Serripes* Gould, 1841, *Cerastoderma* Poli, 1795 (with the subgenera *Cerastoderma* s.s., *Parvicardium* Monterosato, 1884), *Clinocardium* Keen, 1936, *Loxocardium* Cossmann, 1886 and *Plagiocardium* Cossmann, 1886 (with the subgenera *Plagiocardium* s.s., Maoricardium Marwick, 1944 and *Papillicardium* Sacco, 1899). In Keen's latest (1969) classification of the Cardioidea only the genera and subgenera *Laevicardium* s.s., *Laevicardium (Fulvia), Laevicardium (Dinocardium), Cerastoderma, Clinocardium* and *Serripes* are referred to the Laevicardiinae. More recently *Fulvia* has been raised to generic rank (Keen, 1973; Kafanov, 1974a).

Following Keen (1969), the author earlier adopted an identical interpretation of the Laevicardiinae (Kafanov, 1974a) but subdivided *Clinocardium* into *Clinocardium* s.s. and two new taxa, *Clinocardium (Keenocardium)* and *Ciliatocardium.* A year before, *Clinocardium (Fuscocardium)* was proposed by Oyama (1973). Glibert & van de Poel

(1970), however, consider the Laevicardiinae to include *Cerastoderma* together with the genus *Laevicardium* broadly understood by them and its four subgenera: *Laevicardium* s.s., *Dinocardium* s.s., *Clinocardium* and *Habecardium* Glibert & van de Poel, 1970. Popov (1977), taking into consideration Keen's (1950) remarks, considers the latter a subgenus of *Nemocardium* Meek, 1876.

More recently it has been found that the Laevicardiinae sensu Keen are polyphyletic (Kafanov, 1975; Popov, 1977; Kafanov & Popov, 1977). According to shell microstructure (Popov, 1977) and conchological features, its genera are subdivided into three different groups: 1) *Cerastoderma* closely related to *Acanthocardia* Gray, 1851 and *Parvicardium* on the one hand, and, on the other hand, to the Ponto-Caspian brackish-water Lymnocardiinae Stoliczka, 1870; 2) *Laevicardium* and *Fulvia* are similar to *Cardium* Linné, 1758, *Bucardium* Gray, 1853, *Vepricardium* Iredale, 1929 and *Trachycardium* Mörch, 1853 and other closely related genera; 3) *Clinocardium* s.l. and *Serripes* s.l. differed in their characteristic shell morphology and microstructure not observed in representatives of other cardiid genera, while *Dinocardium* has a microstructure rather similar to both genera above. *Clinocardium* s.l. and *Serripes* s.l. were assigned by the author (Kafanov, 1975) to the new subfamily Clinocardiinae. Together with the numerous features of morphological similarity, phylogenetic unity of the genera involved is also confirmed by the abundant paleontological data.

According to Keen (1936b), *Clinocardium* is most closely related to *Cerastoderma,* from which it differs by its prosogyrate beaks, its long, narrow and low ligament, its arched hinge margin and by its greater number of radial ribs. *Cerastoderma* and *Clinocardium* s.l., however, have different centres of origin (Kafanov, 1974a, 1975). *Cerastoderma* appeared in the Oligocene basins of the Eastern Paratethys, as is well documented by paleontological data (Merklin, 1974), but the early stages of the evolution of the Clinocardiinae occurred in the Northern Japan-Sakhalin Paleogene province. Therefore, some similar morphological peculiarities of these two groups really resulted from convergent development and do not indicate common origin.

The Lymnocardiinae in Keen's (1969) classification also is not a natural (monophyletic) taxon. Comparison of shell morphology in the numerous genera of the Ponto-Caspian brackish-water cardiids and the use of data on shell microstructure (Popov, 1973, 1977) convincingly confirm the view that the overwhelming majority of taxa of neolimnitic (sensu Martinson, 1958) genesis arose from *Cerastoderma,* namely from some lagoonal forms like the Recent extremely euryhaline *C. glaucum* (Poiret, 1789) (Eberzin, 1965, 1967; Starobogatov, 1970). The similarity of the general scheme of the stomach morphology (Starobogatov in Kafanov & Popov, 1977) and spermatozoids (Karpevich, 1961, 1964) in *Cerastoderma, Didacna* Eichwald, 1838 and *Hypanis* Menetries, 1832 affirm this origin unequivocally. However, the brackish-water cardiids and *Cerastoderma* are considered separate by Keen (1969): the former—to belong to the independent family Lymnocardiidae, the latter to the Laevicardiinae (Cardiidae s.s.).

Autochthony of the brackish-water faunas of the geological past almost unconnected genetically one with another and their relative short span of existence as compared with marine and fresh-water faunas have resulted in isolation from *Cerastoderma* of the brackish-water cardiids which occurred independently at different geological times. Similar structures, developed in parallel and asynchronously in different branches, recurred in new evolutionary lines (about eleven). This process determined the specific features of "supralimital specialization" (Myers, 1960) of the Ponto-Caspian groups of neolimnitic genesis. To the extent that the principle of the successive monophyly is the basis of construction for each natural system, *Cerastoderma* and the overwhelming majority of Ponto-Caspian brackish-water genera must be incorporated into one taxon of high rank (Kafanov, 1975; Popov, 1977; Kafanov & Popov, 1977). Only such a taxonomic interpretation shows the phylogenetic unity of all brackish-water cardiids. Hence, there is no place for *Cerastoderma* within the Laevicardiinae.

The taxonomic position of *Dinocardium* is the most mysterious. Shell configuration, costal ornamentation (transverse toruli or tubercula on the ridges) and the presence of the rudimentary external layer of the simple prismatic structure (Popov, 1977) resemble analogous characters in *Clinocardium.* However, it differs from the latter as follows (Fig. 1): 1) proximal end of the anterior part of hinge margin covers the anterior beak slope, frequently observed in *Laevicardium* and *Trachycardium*; 2) lunula formed by "lapel" of proximal end of the anterior part of hinge margin, and from anterior preapical valve surface restricted by deep vallicula; 3) scars of the dorso-umbonal muscles were not found, and 4) ligament is considerably higher and shorter than in *Clinocardium* and *Serripes*. According to the author (Kafanov & Popov, 1977), it would be better to consider *Dinocardium* a member of the Cardiinae until additional data are obtained.

Only *Laevicardium* and *Fulvia,* therefore, remain in the Laevicardiinae. *Cerastoderma, Clinocardium* s.l., *Serripes* s.l. and *Dinocardium* are considered to be separate.

Clinocardiinae Kafanov, 1975

The subfamily Clinocardiinae represents a discrete natural group. *Clinocardium* s.l. and *Serripes* s.l. assigned to this subfamily are distinguished by a rare type of shell microstructure and in this character they are very different from the other genera of Cardiidae (Oberling, 1964; Popov, 1973, 1977).

Stewart (1930) and Keen (1936a) were the first to establish a new genus for a fairly numerous group of the North Pacific Recent and fossil species, previously referred by most authors to either *Cerastoderma* or *Laevicardium.* Stewart (1930) discusses in some detail the relationship of *Cardium nuttallii* Conrad, 1837 (= *Cardium corbis* auct. plur.) to *Dinocardium,* and he includes *Cerastoderma* s.s. and *Cerastoderma (Dinocardium)* in the subfamily Trachycardiinae established by him, taking note, however, of their considerable similarity with the Cardiinae. Keen (1936b) proposed a new genus *Clinocardium* (type-species *Cardium nuttallii* Conrad, 1837) and referred it to the Laevicardiinae which initially incorporated eleven species.

The name *Clinocardium* has been used in most hydrobiological and paleontological papers and has been commonly accepted. However, *Clinocardium* sensu Keen is a highly nonhomogeneous group from the morphological point of view. As long ago as 1934, Makiyama, in classifying the North Pacific Tertiary *"Cerastoderma,"* suggested the distinction of three groups of species including *Cardium decoratum* Grewingk, 1850 (nomen dubium, most probably included in *Clinocardium* s.s.), *Cardium californiense* Deshayes, 1839 and *Cardium ciliatum* Fabricius, 1780, according to the sculptural peculiarities of the external shell surface. Thus, the problem of the homogeneity of *Clinocardium* was discussed before a formal determination of the genus. Chinzei (1959) especially distinguished a group with ribs tri-

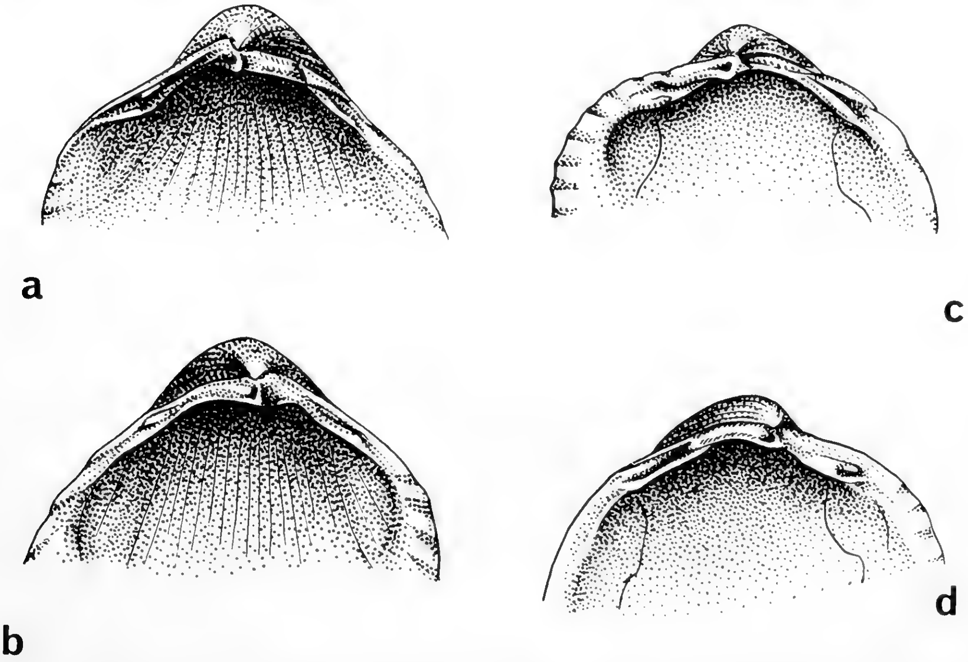

FIG. 1. Hinge structure in *Dinocardium robustum* (Lightfoot, 1768) (a–b) (Dinocardiini) and *Clinocardium nuttallii* (Conrad, 1837) (c–d) (Clinocardiini).

angular in cross section from Neogene Japanese *Clinocardium,* but Shuto (1960) emphasized that the majority of the *Clinocardium* representatives differed from type-species in the character of the radial ribs. The same author foresaw the possibility of separating some subgenera from the genus.

Analysis of the Recent and fossil forms assigned by Keen (1936b, 1954, 1973) to *Clinocardium* has shown that according to their morphological peculiarities and above all to the type of structure in transverse section of the radial ribs (Fig. 2) they form three taxa, separated by discontinuities, well differentiated from each other and representing the single phylogenetic lines which agree with the criteria for generic groups of Mayr (1971). These groups include the Recent *Cardium nuttallii, C. californiense* and *C. ciliatum,* respectively, which were designated the type-species for *Clinocardium* s.s., *Clinocardium (Keenocardium)* Kafanov, 1974 and *Ciliatocardium* Kafanov, 1974. In the present paper *Keenocardium* is raised to generic rank. The considerable morphological differences between *Clinocardium* s.s. and *Keenocardium,* various trends in their historical development and major changes of the adaptive zones of these two groups (Kafanov, unpublished) suggest the change in rank, as does the necessity of the taxonomic separation of *Clinocardium (Fuscocardium)* which is much

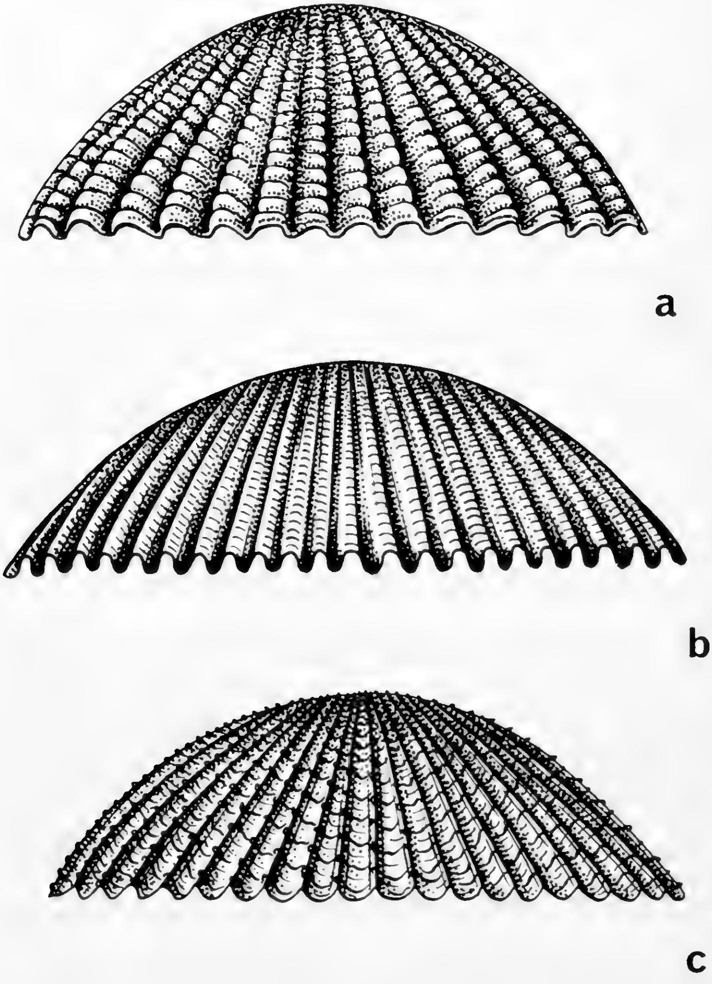

FIG. 2. Rib structure in *Clinocardium* (a), *Keenocardium* (b) and *Ciliatocardium* (c).

closer to *Clinocardium* s.s. than to *Keenocardium.* It should be emphasized that both conchological and anatomical differences (see key to the genera and diagnoses of the corresponding taxa) are the basis for subdivision of *Clinocardium* sensu Keen into three genera.

Similarly, the genus *Serripes* proves to be nonhomogeneous. At present among all the known species and subspecies five forms grouped around the Recent *Cardium (Serripes) notabile* Sowerby, 1915 perfectly form the isolated morphological and evolutionary lineages. The representatives of this group are distinguished by the carinate and markedly convex shells with narrow anterior margins, by strongly prosogyrate beaks, by more completely developed hinges, by the position and details of structure of anterior lower lateral teeth and also by topography of the rudimentary radial sculpture different from that of the typical *Serripes* (Fig. 3). For this group the author (Kafanov, 1975) erected a new genus *Yagudinella.*

Despite the definite morphological similarity of *Serripes, Yagudinella, Clinocardium* s.s., *Clinocardium (Fuscocardium), Keenocardium* and *Ciliatocardium,* the first two genera are more closely related to each other than to the other four, from which they differ in their strong reduction of the sculpture on the external valve surfaces and the less developed hinge. These differences enabled us to subdivide the Clinocardiinae into two tribes as follows: Clinocardiini and Serripedini (Kafanov, 1975), in perfect agreement with some internal shell structure as well (Popov, 1977).

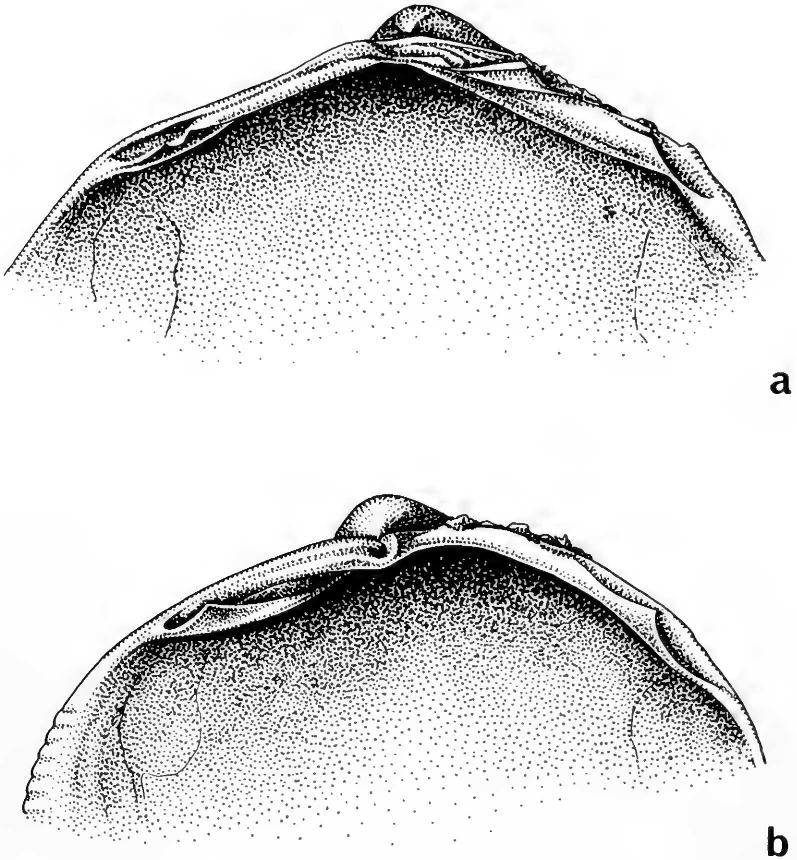

FIG. 3. Hinge structure in *Serripes groenlandicus* (Bruguière, 1789) (a) and *Yagudinella notabilis* (Sowerby, 1915) (b).

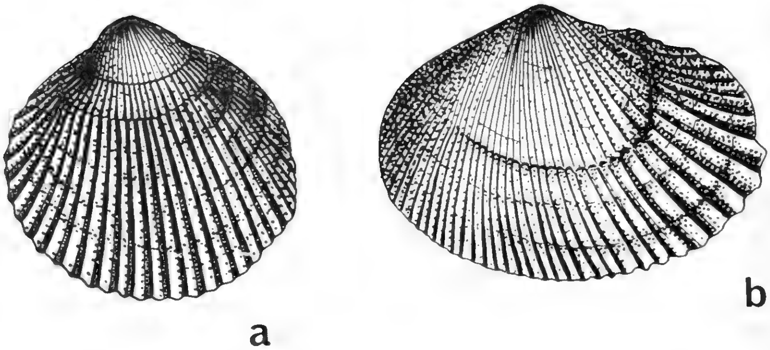

FIG. 4. Rib arrangement in Clinocardiini (a) and Profulviini (b).

The Far Eastern Tertiary *"Papyridea"* being extremely unusual and referred by the author (Kafanov, 1976) to the new genus *Profulvia* (type-species: *Papyridea harrimani* Dall, 1904), form the third tribus. The representatives of this tribus differ from the other Clinocardiinae by their carinate shells, anterior and posterior gapes, with nearly orthogyrate or slightly opisthogyrate apex and by the nature of the costae on the posterior valve surface: arched ribs with convexity anteriad while in the other Clinocardiinae the convexity is posteriad (Fig. 4).

The classification of the Clinocardiinae adopted in the present paper is the following one:

Family Cardiidae Lamarck, 1809

Subfamily Clinocardiinae Kafanov, 1975

- Tribus *Clinocardiini* Kafanov, 1975
  - Genus *Clinocardium* Keen, 1936
    - Subgenus *Clinocardium* Keen, 1936
    - Subgenus *Fuscocardium* Oyama, 1973
  - Genus *Keenocardium* Kafanov, 1974 grad. nov.
    - Genus *Ciliatocardium* Kafanov, 1974
- Tribus Profulviini Kafanov in Kafanov & Popov, 1977[1]
  - Genus *Profulvia* Kafanov, 1976
- Tribus Serripedini Kafanov, 1975
  - Genus *Serripes* Gould, 1841 (ex Beck, MS)
  - Genus *Yagudinella* Kafanov, 1975

Key to the tribes, genera and subgenera of Clinocardiinae:

1. Radial ribs not reduced 2
Radial ribs strongly or completely reduced 6
(Serripedini Kafanov, 1975)

2. Carina nearly obsolete; shell without gapes; ribs on the posterior valve surfaces convex back (Fig. 4a) 3
(Clinocardiini Kafanov, 1975)
Shell carinate, gaping at the back or from both sides; ribs on posterior valve surfaces curved with convexity forward (Fig. 4b) . . . . Profulviini Kafanov in Kafanov et Popov, 1977 (the monotypic tribus)

3. Ribs rounded, flattened or nearly rectangular in cross section, not placed on anterior valve surfaces; ridges of ribs with frequent transverse nodular tubercula or nearly smooth 4
Ribs triangular or roof-like in cross section (Fig. 2c) and often widely extended on the anterior valve surfaces; ridges of ribs with longitudinal rows of thin ciliated periostracum fringes (in poorly preserved fossil shells ribs may be differently smoothed) . . . . *Ciliatocardium* Kafanov, 1974

4. Beaks high; ribs about 20–40 in number; ridges of ribs with transverse nodular tubercula (Fig. 2a); labial palps short, about one-fourth length of the inner demibranch 5
(*Clinocardium* Keen, 1936)

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[1] "Profulviini Kafanov et Popov" as published with the original description is a typographical error.

Beaks low; ribs about 28–65 in number; nodular tubercula absent on ridges of ribs (Fig. 2b); labial palps relatively long but less than half the length of the inner demibranch .... *Keenocardium* Kafanov, 1974

5. Intercostal interspaces appreciably narrower than ribs; ribs about 30–40 in number, flattened and rounded in cross section .... *Clinocardium* s.s.
   Width of intercostal interspaces nearly equal to width of ribs; ribs about 20–30 in number, rectangular in cross section .... *Clinocardium (Fuscocardium)* Oyama, 1973
6. Beaks moderately prosogyrate or nearly orthogyrate; rudiments of radial ribs mainly observed on the posterior valve surfaces; hinge strongly reduced, frequently teeth completely absent; bases of the anterior lower lateral teeth lie on outer side of the internal branches of hinge margin (Fig. 3a) .... *Serripes* Gould, 1841 (ex Beck, MS)
   Bases obviously prosogyrate; rudiments of radial ribs largely presented on the anterior valve surfaces; hinge normal for Clinocardiinae; bases of the anterior lower lateral teeth tend to be on ventral side of the anterior branches of hinge margin, but their proximal parts elongated within the beaks (Fig. 3b) .... *Yagudinella* Kafanov, 1975.

Composition of the Clinocardiinae Kafanov, 1975

At present about 73 valid taxa of specific and subspecific rank are referred to the Clinocardiinae; 5 taxa are provisionally referred to this subfamily. A complete list of them was lacking. Slodkewitsch (1938) gives the detailed review of the North Pacific Tertiary "*Papyridea.*" Keen (1954) lists about 18 nominal species of *Clinocardium* s.l. and describes three new species from Neogene formations of northwestern America. Noda (1962) gives a systematic review of the Japanese *Serripes* s.l. Keen (1973) lists Far Eastern *Clinocardium* s.l., *Serripes* s.l. and *Fulvia* (including *Profulvia*). A list of Clinocardiini has previously been given by the author (Kafanov, 1974a). The known representatives of *Yagudinella* are also listed by Kafanov (1975). Finally, there is a very incomplete list of *Clinocardium* s.l. and *Serripes* s.l. in Popov's (1977) monograph.

The author excludes from the Clinocardiinae the following forms assigned by Keen (1973) to *Clinocardium* and *Serripes: Cardium annae* Pilsbry, 1904: 557, pl. 40, fig. 20; *Vasticardium arenicoloides* Akutsu, 1964: 284, pl. 59, figs. 6, 7; *Laevicardium (Cerastoderma) etheringtoni* Slodkewitsch, 1938 (ex Kogan, MS): 388, pl. 74, figs. 11, 11a, 12; *Cardium (Trachycardium) hanpeizanense* Nomura, 1933: 77, pl. 1, figs. 7, 8, pl. 2, figs. 8, 9; *Cardium (Cerastoderma) hanzawai* Nomura, 1933: 79, pl. 3, figs. 18, 19; *Cardium (Cerastoderma) hizenense* Nagao, 1928: 61(51), pl. 10, figs. 15–17; *Cardium coosense rhomboideum* Khomenko, 1934: 52, pl. 12, figs. 5, 6; *Vasticardium shimotokuraense* Akutsu, 1964: 283, pl. 59, figs. 9, 10. *Laevicardium (Cerastoderma) esutoruense* Krishtofovich, [1957]: 93, pl. 16, figs. 4, 5, 6, 6a, 8,13, mentioned by the author as *Keenocardium* (Kafanov, 1974: 1469) is *Laevicardium.*

Cardium (Laevicardium) jobanicum Yokoyama, 1924: 15, pl. 2, figs. 12–18 from the Oligocene Iwaki formation of the northeastern part of the Central Honshu included by Keen (1973) in *Clinocardium,* must be considered a member of the Veneridae, either *Protothaca* (Hatai & Nisiyama, 1952) or *Cyclina* Deshayes, 1849 non Gray, 1857 (Kamada, 1962).

Popov (1977) refers *Cardium gallicum* Mayer, 1866: 72, pl. 2, fig. 3 and *Cardium (Laevicardium) pantecolpatum* Cossmann & Peyrot, 1911: 517, pl. 23, figs. 32–35 from the Miocene of France, as well as *Cardium (Cerastoderma) scapoosense* Clark, 1925: 91, pl. 22, fig. 5 and *Cardium sookense* Clark & Arnold, 1923: 145, pl. 22, figs. 1a–b, 2 from the Oligocene of the Pacific coast of the North America to *Clinocardium.* The first two species have nothing in common with *Clinocardium* or with the Clinocardiinae in general. Generic relationship of the latter two forms is uncertain. The considerably shortened and strongly curved hinge margin, nearly orthogyrate beaks, cardinal teeth (with hypertrophied anterior tooth of the left valve in *C. sookense*) which are strong, straight and misplaced with respect to each other—all prevent us from assigning these two species to the Clinocardiini. It is noteworthy that Keen (1936b, 1954) does not mention either *C. scapoosense* and *C. sookense* as belonging to *Clinocardium.* One therefore should examine all the related groups to see whether one might be found with characters that would overlap.

Cardium (Trachycardium) kinsimarae Makiyama, 1934: 141, pl. 6, fig. 35 and *Cardium puchlense* Ilyina in Zhizhchenko, Korobkov, Krishtofovich & Eberzin, 1949: 144, pl.

28, figs. 6–8, mentioned as *Clinocardium* in Zhidkova et al. (1974) are also excluded from the subfamily. *Cardium taracaicum* Yokoyama, 1930: 414, pl. 77, figs. 1, 2, called *Clinocardium* in some papers (Makiyama, 1959; Zhidkova et al., 1974; Sinelnikova et al., 1976), the author, following Keen (1973), belongs in *Laevicardium* s.l.

Cardium hudsoniense Deshayes, 1855: 331, a possible holotype of which is figured by Fischer-Piette (1977: pl. 12, fig. 1), should be considered a *Parvicardium,* not as a *Corculum (Keenocardium).*

Diagnoses of the subfamily, tribes and taxa of the generic group, as well as annotated catalogue and keys of all known species and subspecies with indications of type-localities and depositories, are given below. Valid taxa of the specific group are emphasized with boldface in the text. Nomina nuda are not examined.

Subfamily Clinocardiinae Kafanov, 1975

Kafanov, 1975: 146.

Shell medium-sized or fairly large (to 120 mm and more), from truncate-trigonal to oblong-elliptical or neary ovate. Valve height usually less than length ($H = 0{,}926 \cdot L^{0{,}995 \pm 0.013}$ for the whole subfamily). Beaks prosogyrate, nearly orthogyrate or slightly opisthogyrate. Radial ribs about 20–65 in number. Ribs flattened and rounded, tectate or triangular in cross-section; combinations of these types are possible. Ribs smooth or with transverse nodular tubercula (but never with scales) or decorated with longitudinal rows of thin ciliated periostracal fringes (Fig. 2a–c). When sculpture of the external shell surface is obsolete, traces of the radial ribs will be found on posterior or rarely anterior valve surfaces. Hinge often strongly reduced. Typically there are (Fig. 1c–d): paired anterior lateral, paired cardinal and single posterior lateral teeth in right valve; paired cardinal and single lateral teeth in left valve. Reduction of the hinge elements is more often provided by that of the anterior upper lateral tooth of the right valve and of cardinal teeth. Posterior lateral tooth of the left valve may be split into two branches in distal part. Lunula and area are weak or absent. Ligament is long, narrow and low. Shell three-layered; mesostracum with cross-lamellar structure, ectostracum isolated and formed by spinose prisms or thin vertical plates oriented perpendicular to valve surfaces.

Paleocene(?)-Eocene-Recent; cold and temperate waters of the Northern Hemisphere, Paleogene and Neogene deposits of the North Pacific, North Atlantic and Arctic (Figs. 5–10).

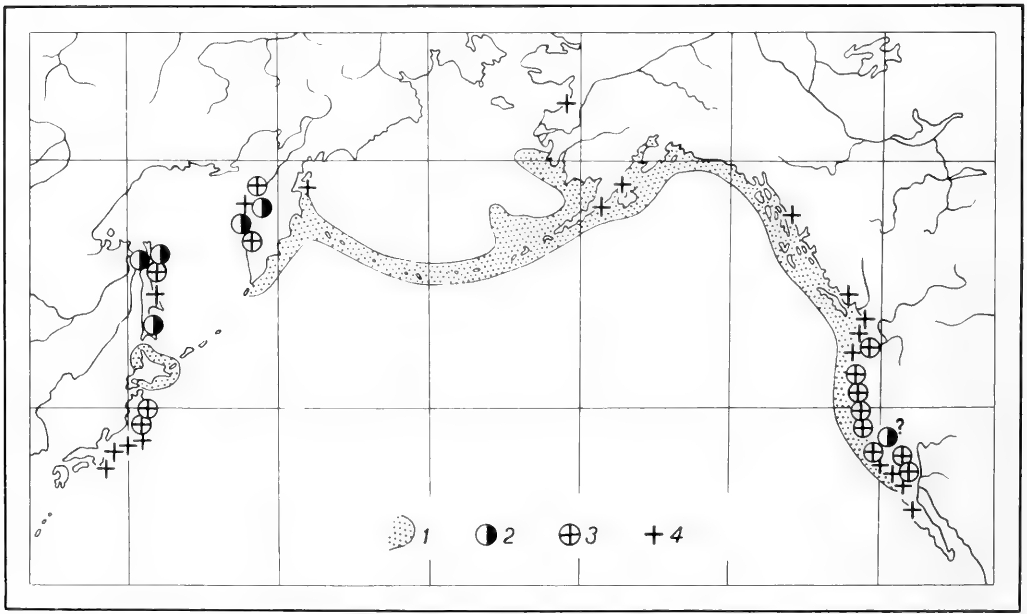

FIG. 5. Geographical and geological distribution of *Clinocardium.* 1—Recent; 2—Miocene; 3—Pliocene; 4—Pleistocene.

Tribus Clinocardiini Kafanov, 1975

Kafanov, 1975: 147.

Carina obsolete. Shell without gapes. Ribs well developed. Ribs on posterior part of valve posteriorly convex (Fig. 4a).

Geographical and geological distribution as in the subfamily.

Genus *Clinocardium* Keen, 1936

Clinocardium Keen, 1936b: 119; *Clinocardium (Clinocardium)* Keen: Kafanov, 1974a: 1468.

Type-species: *Cardium nuttallii* Conrad, 1837; Recent, off estuary of the Columbia River, Oregon, U.S.A. (original designation).

Shell medium-sized or large (to 100 mm and more), from flattened to fairly convex, oblong-elliptical or truncate-trigonal, inequilateral. Beaks high and prosogyrate. Ribs about 20–40 in number; ridges with transverse nodular tubercula sometimes slightly smoothed (Fig. 2b). Ribs flattened and rounded or rectangular in cross-section. Anterior lower lateral tooth of right valve with a small longitudinal ridge on dorsal surface. Lunula often well developed, lanceolate. Distal part of foot with narrow ventral sulculus surrounded on both sides by longitudinal rows of low papillae. Labial palps short, about one-fourth length of the internal demibranch.

Two subgenera—*Clinocardium* s.s. and *Clinocardium (Fuscocardium)* Oyama, 1973.

Middle Miocene-Recent; North Pacific (north to 60°N, south to Central Honshu and southern California, U.S.A.) (Fig. 5).

Subgenus *Clinocardium* Keen, 1936

Intercostal interspaces appreciably narrower than ribs. Ribs about 30–40 in number. Ribs flattened and rounded in cross-section; ridges with transverse nodular or tabular-shaped tubercula.

Geographical and geological distribution as in genus.

Key to the species and subspecies[2]

1. Average rib number about 34–35 . . . . *nuttallii* (Conrad, 1837).
   Average rib number about 28–30 . . . . 2.
2. Anterior margin of shell moderately narrower than their posterior margin . . . . *meekianum meekianum* (Gabb, 1866).
   Anterior margin of shell much more narrower than their posterior margin . . . . *meekianum myrae* Adegoke, 1969

Described taxa

californianum Conrad, 1837: 229, pl. 17, fig. 4 [*Cardium*]. Recent; vicinity of Santa Barbara, Califonia. Depository: unknown. Synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837).

corbis auct. plur., non *Corbis* Martyn, 1784, Taf. 80; non-binom. (Official Index . . . , 1958: 11, Opinion 456). Synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837).

? *decoratum* Grewingk, 1850: 347, pl. 4, figs. 3a–g [*Cardium*]. Unga Island, Alaska (type-locality here designated); "jüngsten Tertiärzeit" [Middle or Upper Miocene]. Depository: unknown. Due to the loss of the type material and inferiority of the original description and illustration *decoratum* must be considered a nomen dubium. Possible synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837). Its taxonomic position will be considered in detail elsewhere (Kafanov, in press).

meekianum Gabb, 1866: 27, pl. 7, fig. 46 [*Cardium*]. Eagle Prairie, Humboldt County, California: Pliocene [Wildcat formation according to Keen & Bentson, 1944]. Depository (holotype): Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A., reg.no. 4497.

meekianum myrae Adegoke, 1969: 117, pl. 3, figs. 7, 9, pl. 7, fig. 6 (paratypes) [*Clinocardium*]. Kettleman Hills area, San Joaquin Valley, California; Etchegoin Formation, Lower Pliocene. For figure of holotype see Woodring et al., 1941: pl. 29, fig. 14. Depository (holotype): U.S. National Museum, Washington, U.S.A., reg. no. 495769.

? nanum Khomenko, 1931: 74, pl. 10, fig. 19 [*Cardium*]. Ekhabi, Okhinskij District, Eastern Sakhalin; Ekhabinskaya suite, Middle Miocene. Depository (holotype): Central Research geological prospecting Museum, Leningrad, USSR, reg. no. 28/3456. A juvenile specimen.

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[2] Taxa conditionally included in the genus are not considered.

nuttallii Conrad, 1837: 229, pl. 17, fig. 3 [*Cardium*]. Recent; "muddy salt marshes, a few miles from the estuary of the Columbia River," Oregon. Depository (lectotype): Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A., reg. no. 54036. Recent records: along the Pacific coast of North America from San Diego, California, to Nunivak Island; Aleutian, Pribiloff and Commander Islands; Eastern Kamchatka (north to Sivuchij Cape); northern Kurile Islands (Paramushir); Hokkaido (along the Pacific side to Hakodate). Fossil records: Ilyinskaya suite of Western Kamchatka (Middle Miocene), San Pablo Formation of California (Upper Miocene), Enemtenskaya suite of Western Kamchatka (Lower Pliocene), Pliocene Montesano, Empire and Quillayute formations of Oregon and Washington, Pliocene Purisima, Etchegoin and Falor formations of California, Pleistocene of Alaska, Aleutian Islands, Kamchatka, Sakhalin, Washington, Oregon and California.

Subgenus *Fuscocardium* Oyama, 1973

Clinocardium (Fuscocardium) Oyama, 1973: 100.

Type-species: *Cardium braunsi* Tokunaga, 1906; Pleistocene, environs of Tokyo, Japan (original designation).

Width of intercostal interspaces nearly equal to width of ribs. Ribs about 20–30 in number, rectangular in cross-section. Transverse tabular-shaped tubercula on crests or ribs smooth.

Middle Miocene-Pleistocene; Honshu, Sakhalin and Kamchatka.

Key to the species

Average number of ribs about 20–22 .... *braunsi* (Tokunaga, 1906)
Average number of ribs about 27–30 .... *pseudofastosum* (Nomura, 1937)

Described taxa

braunsi Tokunaga, 1906: 51, pl. 3, fig. 11 [*Cardium*]. Oji, near Tokyo; "Upper Musashino," Pleistocene. Possible depository: College of Sciences, University of Tokyo, Tokyo, Japan. Characteristic species in Pleistocene deposits of the Kanto region, Central Honshu (Katori, Sakishima, Atsumi, Uemachi, Takinokawa and Toshima formations) and Eastern Sakhalin ("Nadnutovskaya" suite). Unknown in the Recent.

? nomurai Hayasaka, 1956: 18, pl. 2, figs. 4a–b [*"Clinocardium."*] Path side cutting at Onoda, Futaba District, Fukushima Prefecture, Honshu; Ishiguma formation, Pliocene, Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 77376. Assignment of a given species to this subgenus is very difficult because of poor preservation. Hayasaka (l.c.) compares it to *Clinocardium nuttallii* (Conrad, 1837). According to the author, however, the form described here is more closely related to *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

ovata Yokoyama, 1922: 157, pl. 12, fig. 4 [*Cardium tokunagai* var.]. Shisui, Chiba Prefecture, Honshu; "Upper Musashino," Pleistocene. Depository: Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Synonym of *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

pseudofastosum Nomura, 1937: 171, pl. 23, figs. 1 (holotype), 2 [*Cardium (Clinocardium)*]. Kitamata-gawa, along the upper course of Koromogawa, Isawa District, Iwate Prefecture, Honshu;[3] Yushima formation (Hatai & Nisiyama, 1952), Pliocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 2388. Very similar forms were reported from Ilyinskaya suite of western Kamchatka (Kafanov & Savitzky, in press).

tokunagai Yokoyama, 1922: 156, pl. 12, figs. 6 (lectotype; designated as holotype by Taki & Oyama, 1954: pl. 32), 5 [*Cardium*]. Otake, Chiba Prefecture, Honshu; "Upper Musashino," Pleistocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Synonym of *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906). Following Taki & Oyama (Taki & Omaya, 1954; Oyama, 1973) who saw Yokoyama's materials, the author con-

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[3] For detailed type-localities of Japanese species (Paleogene and Neogene) described prior to 1952 see Hatai & Nisiyama, 1952.

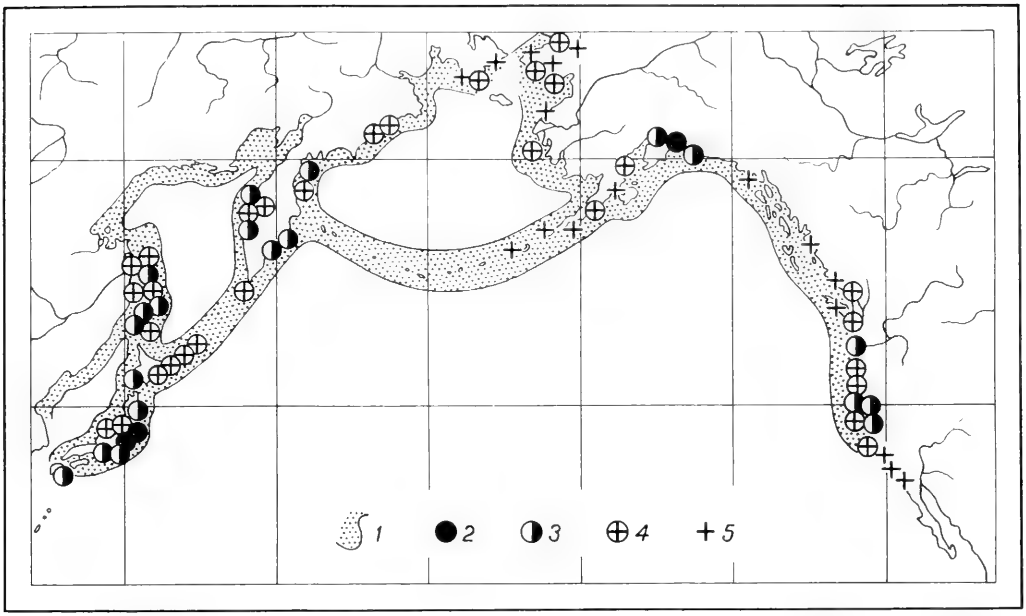

FIG. 6. Geographical and geological distribution of *Keenocardium*. 1—Recent; 2—Oligocene; 3—Miocene; 4—Pliocene; 5—Pleistocene.

siders *C. tokunagai* and *C. tokunagai* var. *ovata* to be *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

Genus *Keenocardium* Kafanov, 1974

Clinocardium (Keenocardium) Kafanov, 1974a: 1468.

Type-species: *Cardium californiense* Deshayes, 1839; Recent, [Eastern] Kamchatka (original designation).

Shell medium-sized (to 80 mm and more), elongated and rounded or oval-trigonal, inequilateral, slightly convex. Beaks only weakly prosogyrate, displaced somewhat forward, narrow, slightly elevated. Ribs about 28–65 in number, rounded or flattened and rounded in cross-section, separated by narrower intercostal spaces; ribs, as a rule, closely set on anterior part of valve. Costal surfaces smooth, interrupted by narrow concentric wrinkles only. Anterior lower lateral tooth of right valve frequently with a small longitudinal ridge on dorsal surface. No lunula and escutcheon. Distal part of foot with narrower ventral sulculus surrounded on both sides by smoothed magins. Labial palps long but less than a half the length of the inner demibranch.

Early Oligocene—Recent; North Pacific (southern to Korea, Northwestern Kyushu and southern California), Bering Strait and Northwestern Alaska (Fig. 6).

Key to the species and subspecies

1. Ribs of posterior area crowded and crumpled into an irregular channel .... 2.
   Ribs of posterior area not forming an irregular channel .... 3.
2. Average rib number about 44–46 .... *californiense californiense* (Deshayes, 1839).
   Average rib number about 49–51 .... *californiense uchidai* (Habe, 1955).
3. Shell ovate, rounded, orbicular, suborbicular or semi-quadrate in outline; posterior dorsal margin not sloping obliquely downward .... 4.
   Shell trigonal in outline; posterior dorsal margin sloping obliquely downward .... 13.
4. Maximum size of adult shell more than 40 mm .... 5.
   Maximum size of adult shell fewer than 40 mm .... 7.

5. Shell strongly inequilateral (beaks near the anterior 0,35–0,37); ribs 30–33 .... *iwasiroense* (Nomura, 1935).
   Shell subequilateral (beaks near the anterior 0,42–0,45); ribs 44–60 .... 6.
6. Height of shell less than length (average height/length ratio about 0,94–0,95); ribs 50–60 separated by much narrower interspaces .... *fastosum* (Yokoyama, 1927).
   Height of shell nearly equal to length (average height/length ratio about 1,00); ribs 44–49 sepated by somewhat narrower interspaces .... *coosense* (Dall, 1909).
7. Ribs 45 or more .... 8.
   Ribs fewer than 45 .... 10.
8. Shell semi-quadrate in outline; interspaces about equal to the width of the ribs .... *okushirense* (Uozumi & Fujie, 1966).
   Shell ovate or suborbicular in outline; interspaces somewhat narrower than the width of the ribs .... 9.
9. Shell subequilateral (beaks near the anterior 0,43); average height/length ratio about 0,86–0,87 .... *fucanum* (Dall, 1907).
   Shell inequilateral (beaks near the anterior 0,38); average height/length ratio about 0,95–0,96 .... *subdecussatum* (Shuto, 1960).
10. Ribs 38 or fewer .... 11.
    Ribs 39–44 .... 12.
11. Average height/length ratio about 0,96; interspaces narrower than the width of the ribs .... *andoi* (Itoigawa & Shibata, 1975).
    Average height/length ratio about 0,86; interspaces about equal to the width of the ribs or even somewhat broader .... *kljutschiense* (Krishtofovich, 1969).
12. Shell equilateral (beaks near the anterior 0,49) .... *blandum* (Gould, 1850).
    Shell subequilateral (beaks near the anterior 0,44) .... *arakawae* (Kamada, 1962).
13. Maximum size of adult shell more than 45 mm .... 14.
    Maximum size of adult shell less than 45 mm .... 16.
14. Ribs fewer than 40; interspaces about equal to the width of the ribs . *buelowi* (Rolle, 1896).
    Ribs more than 40; interspaces much narrower than the width of the ribs .... 15.
15. Ribs 42–48 .... *pristinum* (Keen, 1954).
    Ribs 60–65 .... *lispum* (Roth & Talmadge, 1975).
16. Ribs about 55 in number .... *hopkinsi* (Kanno, 1971).
    Ribs 35–40 .... 17.
17. Average height/length ratio about 1,00 .... *hannibali* (Keen, 1954).
    Average height/length ratio about 0,96 .... *praeblandum* (Keen, 1954).

Described taxa

andoi Itoigawa & Shibata, 1975: 24, pl. 7, figs. 9a–b (holotype), pl. 8, figs.1–4 [*Clinocardium*]. Togari-ST, Akeyo-cho, Mizunami City, Gifu Prefecture, Honshu; Mizunami Group, Yamanouchi member, Miocene. Depository (holotype): Mizunami Fossil Museum, Mizunami City, Japan, reg. no. 10029.

arakawae Kamada, 1962: 105, pl. 10, figs. 15 (holotype), 16, 17 [*Clinocardium asagaiense arakawae*]. Mukaida, Yumotomachi, Joban City, Joban coal-field, Honshu; Asagai Formation, Oligocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 79383. For taxonomic notes see: Kafanov, 1974a: 1470.

blandum Gould, 1850: 276; 1852: 418; 1861: 14, pl. 36, figs. 534, 534a [*Cardium*]. Recent; Puget-Sound, Washington. Depository (lectotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 3899. For figure of lectotype see: Schenck & Keen, 1940: pl. 2, figs. 17–20; Schenck, 1945: pl. 67, figs. 18–21.

boreale Broderip & Sowerby, 1829: 368 non Reeve, 1845, sp. 131, pl. 22 [*Cardium*]. Recent (?); Ice-Cape, Arctic coast of Alaska. Depository: unknown. Nomen oblitum presented to International Commission on Zoological Nomenclature for inclusion in Official Index of rejected and invalid names in zoological nomenclature (Kafanov, 1974b; see also: Mayr & Melville, 1976). Synonym of *Keenocardium californiense* (Deshayes, 1839).

brooksi MacNeil in MacNeil, Mertie & Pilsbry, 1943: 91, pl. 15, fig. 14 [*Cardium (Cerastoderma) ciliatum brooksi*] non Clark, 1943: 812, pl. 18, fig. 5 [*Cardium (Papyridea)*]. Intermediate Beach, between Center and Bourbon Creeks, near Nome, Alaska; Anvillian Pleistocene. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 499085. Synonym of *Keenocardium californiense* (Deshayes, 1839).

buelowi Rolle, 1896: 114, pl. fig. C [*Cardium*]. Recent; Yokohama, Honshu. Depository (possible syntypes): Museum für Naturkunde, Humboldt-Universität, Berlin, G.D.R.

californiense Deshayes, 1839: 360; 1841a, pl. 47 (nom. conserv. propos., see: Kafanov, 1974b) [*Cardium*]. Recent; [Eastern] Kamchatka (here limited: in 1836 the region of investigations conducted by the French expedition on "Venus" near Kamchatka visited only the eastern coast and the lectotype is derived from those materials; Deshayes in the original description mentions this species form "Côtes de Californie" where it is absent). Depository (lectotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. Recent records: Korea, northern and central Honshu (along the Pacific coast to Boso Peninsula, along the Sea of Japan coast to Noto Peninsula, Hokkaido, South Primorje, Sakhalin, Kurile Islands, Sea of Okhotsk, Kamchatka, Commander and Aleutian Islands, Southern Chukotka; along the Pacific coast of North America southward to Sitka Island, Alaska, and Vancouver Island (?), British Columbia. Fossil records: Kakertskaya and Etolonskaya suites of Kamchatka (Middle Miocene), lower and middle parts of Maruyamakaya suite of Sakhalin (Middle and Upper Miocene), Miocene Utsutoge, Hitosao and Gobansoyama formations of Honshu, lower part of Limimtevayamskaya suite of Karaginskij Island (Upper Miocene or Lower Pliocene), Empire Formation of Oregon (Lower Pliocene), upper part of Limimtevayamskaya and Ustj-Limimtevayamaskaya suites of Karaginskij Island (Pliocene), Nutovskaya, Uranajskaya, Ekhabinskaya, Pomyrskaya and upper part of Maruyamskaya suites of Sakhalin (Pliocene), Pliocene Setana formation of Hokkaido and Kotari formation of Honshu, Beringian strata and their equivalents of Alaska (Upper Pliocene), Pleistocene of Pribiloff Islands, Chukotka, Koryak Plateau, Kamchatka, Kurile Islands, Sakkalin and North Japan.

coosense Dall, 1909: 118, pl. 13, figs. 3, 4 [*Cardium (Cerastoderma)*]. Coos Bay, Oregon; Empire formation, Lower Pliocene. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 153933.

fastosum Yokoyama, 1927a: 178, pl. 48, fig. 5 [*Cardium*]. Kanazawa, Nagaya, Kosakamura, Kahoku District, Ishikawa Prefecture, Honshu; Onma formation, Lower Pliocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Makiyama (1959) referring to the personal communication of T. Kuroda, considers this species a synonym of *Keenocardium californiense* (Deshayes, 1839). This assignment is incorrect.

fucanum Dall, 1907: 112 [*Cardium*]. Recent; Juan-de-Fuca Strait, Puget-Sound, Washington. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 427773. For figure of holotype see: Schenck & Keen, 1940: pl. 2, figs. 21–24; Schenck, 1945: pl. 67, figs. 22–25.

hannibali Keen, 1954: 18, pl. 1, fig. 16 (holotype), text-fig. 9 [*Clinocardium*]. Chehalis and Summit Sts., Aberdeen, Washington; Montesano formation, Lower Pliocene. Depository (holotype): Stanford University, Paleo. Type collection, Stanford, U.S.A., reg. no. 8302.

hopkinsi Kanno, 1971: 68, pl. 5, figs. 7 (holotype), 6a–b [*Clinocardium*]. Near the head of the Gulf of Alaska; upper part of the Poul Creek formation, Lower Miocene(?). Depository (holotype): Tokyo University of Education, Tokyo, Japan, reg. no. 8434.

interrogatorium Fischer-Piette, 1977: 21, pl. 2, fig. 2 [*Laevicardium*]. Recent; "Californie." Depository (holotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. A juvenile specimen. It is possible that the type-locality is given erroneously. Synonym of *Keenocardium californiense* (Deshayes, 1839).

iwasiroense Nomura, 1935: 113, pl. 6, figs. 1, 2 (holotype not designated) [*Cardium (Cerastoderma)*]. Hitosao, Ogino District along the Agano-gawa, Fukushima Prefecture, Honshu; Hitosao Formation, Upper Miocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 2146.

kljutschiense Krishtofovich, 1969: 191, pl. 4, figs. 1 (holotype), 2, 3 [*Clinocardium*]. Goryachie Kljuchi, Tjushevskaya River, Kronotskij District, Eastern Kamchatka; "Goryachikh Kljuchej" suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R. reg. no. 59/6780.

lispum Roth & Talmadge, 1975: 3, text-fig. 1a (holotype), 1b [*Clinocardium*]. Off the U.S. Highway 101 bridge over Eel River, Humboldt County, California; Rio Dell formation, Pliocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14152.

okushirense Uozumi & Fujie, 1966: 150, pl. 12, figs. 4 (holotype), 5, 6 [*Clinocardium*]. Cliff along the river, about 400 m upper stream from the Miyatsu-gawa, Miyatsu, Okushiri Island, Southwest Hokkaido; Tsurikake Formation, Miocene. Depository (holotype): University of Hokkaido, Sapporo, Japan, reg. no. 13732.

praeblandum Keen, 1954: 15, pl. 1, figs. 6 (holotype), 1, text-figs. 5–6 [*Clinocardium*]. West end of Las Trampas Ridge near Walnut Creek, Concord Quadrangle, Contra Costa County, California; Briones formation, Upper Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14836.

pristinum Keen, 1954: 16, pl. 1, figs. 15 (holotype), 9, text-figs. 7 (holotype), 8 [*Clinocardium*]. Southwest part of Shell Ridge, near Walnut Creek, Concord Quadrangle, Contra Costa County, California; San Pablo group, Neroly Formation (?), Upper Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14838.

pseudofossile Reeve, 1845, sp. 52, pl. 10 [*Cardium*]. Recent; [Kamchatka] (type-locality here designated). Depository (syntypes): British Museum (Natural History), London, Great Britain, reg. no. 1975617. Synonym of *Keenocardium californiense* (Deshayes, 1839).

subdecussatum Shuto, 1960: 216, pl. 25, figs. 12 (holotype), 9, 10, 20, text-fig. 1c [*Clinocardium*]. Yamaji, Mino-mura, Koyu District, Miyazaki Prefecture; Kyushu; Miyazaki group, the lowest part of the Tsuma member, Upper Miocene. Depository (holotype): Department of Geology, Faculty of Sciences, Kyushu University, Fukuoka, Japan, reg. no. 4777.

californiense uchidai Habe, 1955: 11, pl. 2, figs. 5, 6 *[Clinocardium uchidai]*. Recent; Akkeshi Bay, Hokkaido. Depository (holotype): National Science Museum, Tokyo, Japan, reg. no. 53378. This form name was first published by Kira (1954: 111, pl. 55, fig. 1), where *"Clinocardium uchidai* Habe, MS" was illustrated without a formal description; Kira's specific name is therefore a nomen nudum.

vulva Jousseaume, 1898: 81 [*Cardium*]. Recent; "Japon." Depository (holotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. Synonym of *Keenocardium californiense* (Deshayes, 1839) fide Fischer-Piette, 1977, pl. 11, fig. 4.

Genus *Ciliatocardium* Kafanov, 1974

Ciliatocardium Kafanov, 1974a: 1469.

Type-species: *Cardium ciliatum* Fabricius, 1780: Recent, Greenland (original designation).

Shell medium-sized (to 80 mm and more), oval-rounded or truncated-trigonal, inequilateral, moderately inflated. Beaks fairly high, prosogyrate, elevated and curved. Ribs about 20–50 in number, often widely arranged on the anterior valve surfaces. Ribs triangular or tectate in cross-section. Crests of ribs with longitudinal rows of thin ciliated periostracal fringes (in poorly preserved fossil shells ribs may be differently smoothed); small spiniform (lobes) observed sometimes in juveniles on crests of ribs. Anterior lower lateral tooth of the right valve without longitudinal ridge on dorsal surface. Lunula oblong and cordiform or absent. Area if present narrow and lanceolate. Distal part of foot with narrow ventral sulculus surrounded on both sides by longitudinal rows of delicate papillae. Labial palps long but less than a half the length of the inner demibranch.

Paleocene(?)-Eocene-Recent; northwestern (south to Kyushu) and northeastern Pacific (south to Washington). Arctic and North Atlantic (south to Cape Cod, Iceland and southern Norway; in Pliocene south to England) (Fig. 7).

Key to the species and subspecies

1. Height of shell equal to or greater than length .... 2.
   Height of shell less than length .... 5.
2. Average rib number 30 or more than 30 .... 3.
   Average rib number fewer than 30 .... 4.
3. Shell inequilateral (beaks near the anterior 0,40–0,41), somewhat oblique ....
   .... *ciliatum dawsoni* (Stimpson, 1863).
   Shell subequilateral (beaks near the anterior 0,44–0,45), not oblique ....
   .... *yakatagense* (Clark, 1932).
4. Maximum size of adult shell more than 25 mm; shell trigonally ovate; average rib number about 26 .... *hataii* (Hayasaka, 1956).

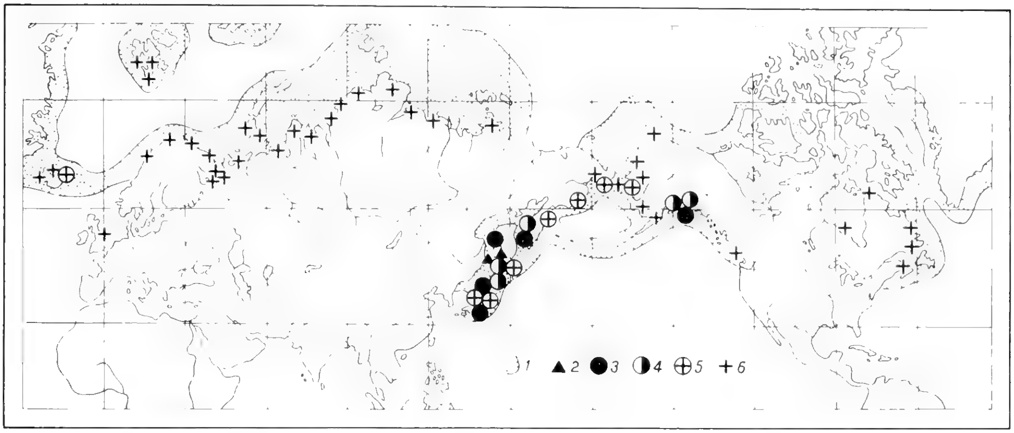

FIG. 7. Geographical and geological distribution of *Ciliatocardium*. 1—Recent; 2—Palaeocene and Eocene; 3—Oligocene; 4—Miocene; 5—Pliocene; 6—Pleistocene.

Maximum size of adult shell fewer than 25 mm; shell rounded; ....
average rib number about 28 .... *tigilense* (Slodkewitsch, 1938).
5. Average rib number 30 or more .... 6.
Average rib number fewer than 30 .... 14.
6. Average height/length ratio more than 0,86 .... 7.
Average height/length ratio less than 0,85 .... 12.
7. Maximum size of adult shell more than 45 mm .... 8.
Maximum size of adult shell less than 45 mm .... 10.
8. Average height/length ratio about 0,96; shell rather inequilateral ....
.... *ciliatum ciliatum* (Fabricius, 1780).
Average height/length ratio about 0,98; shell subequilateral or equilateral .... 9.
9. Shell subequilateral (beaks near the anterior 0,44–0,45) ....
.... *ciliatum chikagawaense* (Kotaka, 1950).
Shell equilateral (beaks near the anterior 0,48–0,49) ....
.... *ciliatum pubescens* (Couthouy, 1838).
10. Average height/length ratio about 0,91–0,92 .... *asagaiense* (Makiyama, 1934).
Average height/length ratio more than 0,94 .... 11.
11. Average rib number about 40 .... *ainuanum* (Yokoyama, 1927).
Average rib number about 35 .... *shinjiense* (Yokoyama, 1923).
12. Ribs 40 or more in number .... *ermanensis* (Sinelnikova, 1976).
Ribs 30–35 in number .... 13.
13. Maximum size of adult shell more than 50 mm; average height/length ratio about 0,84 ..
.... *iwatense* (Chinzei, 1959).
Maximum size of adult shell less than 50 mm; average height/length ratio about 0.81 ....
.... *schmidti* (Khramova, 1962).
14. Average height/length ratio 0,90 or more .... 15.
Average height/length ratio less than 0,90 .... 17.
15. Maximum size of adult shell less than 40 mm .... *yamasakii* (Makiyama, 1934).
Maximum size of adult shell more than 40 mm .... 16.
16. Ribs about 28 in number .... *makiyamae* (Kamada, 1962).
Ribs about 22–25 in number .... *matchgarense* (Makiyama, 1934).
17. Maximum size of adult shell more than 40 mm .... *uyemurai* (Kanehara, 1937).
Maximum size of adult shell less than 40 mm .... 18.
18. Average height/length ratio about 0,83–0,84; maximum size of adult shell about 36 mm .
.... *mutuense* (Nomura & Hatai, 1936).
Average height/length ratio about 0,86; maximum size of adult shell about 15 mm ......
.... *snatolense* (Krishtofovich, 1947).

Described taxa

ainuanum Yokoyama, 1927b: 202, pl. 51, figs. 7 (lectotype; designated by Hatai & Nisiyama, 1952: 35), 5, 6 [*Cardium*]. Sankebetsu, Haboromachi, Tomamae District, Teshio Province, Hokkaido; Haboro Formation, Lower or Middle Miocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?.

arcticum Sowerby, 1841a: 106; 1841b: 2, no. 27, fig. 26 [*Cardium*]. Recent; "Arctic Seas." Depository (possible syntypes): British Museum (Natural History), London, Great Britain, reg. no. 1975618. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

asagaiense Makiyama, 1934: 139, pl. 5, figs. 23 (holotype), 20, 22 [*Cardium (Cerastoderma)*]. Taira, Yotsukura, Iwaki District, Fukushima Prefecture, Honshu; Shiramizu group, Asagai Formation, Oligocene. Depository (holotype): Institute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 350011.

? brooksi Clark, 1932: 812, pl. 18, fig. 5 [*Cardium (Papyridea)*] non MacNeil in MacNeil, Mertie & Pilsbry, 1943: 91, pl. 15, fig. 14 [*Cardium (Cerastoderma)*]. Yakataga District (about 60°N), Gulf of Alaska; Poul Creek Formation, Upper Oligocene-Lower Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30402.

ciliatum chikagawaense Kotaka, 1950: 46, pl. 5, figs. 1, 2, 5 (holotype), 3, 4, 6 [*Clinocardium chikagawaense*]. The sea cliff at the outlet of Chikagawa River at Chikagawa, Tanabu-machi, Shimokita District, Aomori Prefecture, Honshu; Hamada Formation, Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 72999.

ciliatum Fabricius, 1790: 410 [*Cardium*]. Recent; Greenland [possibly southwestern coast]. Depository (lectotype: here designated): Universitetets Zoologiske Museum, København, Denmark, reg. no. ?. Recent records: North Pacific (south to Korea, Hokkaido, Boso Peninsula, Honshu, Aleutian and Commander Islands and Puget Sound, Washington), North Atlantic (south to southern Norway, south Iceland, south Greenland and Cape Cod, Massachusetts) and Arctic Seas. (Fig. 7). Fossil records: lower part of Maruyamskaya suite of Sakhalin (Middle Miocene), Komeutiyamskaya suite to Koryak Plateau (Upper Miocene), Utsutoge Formation of Honshu (Upper Miocene), Okobykajskaya suite of Northern Sakhalin (Upper Miocene), upper part of Limimtevayamskaya and Ustj-Limimtevayamskaya suites of Karaginskij Island (Pliocene), Alekhinskaya and Kamujskaya suites of Kurile Islands (Upper Miocene), Pliocene Golovinskaya suite of Kurile Islands, Setana Formation of Hokkaido, Kubo, Sawane and Shigarami formations of Honshu, Beringian Pliocene of Alaska and Pribiloff Islands, Upper Pliocene and Pleistocene of Iceland (Tjornes Crag, zone of *Serripes groenlandicus*), Chukotka (Pinakuljskaya suite), Iceland (Furuvik and Brejdavik), England (Icenian Crag) and Petchora Lowland (Kolvinskaya suite). One of the most widely distributed species in Quaternary deposits of Arctic and Subarctic.

comoxense Dall, 1900: 1093 [*Cardium*]. Vancouver Island, British Columbia; Pleistocene. Depository (lectotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 427772. For figure of lectotype see: Keen, 1954: pl. 1, figs. 5, 7, 8. Synonym of *Ciliatocardium* ciliatum (Fabricius, 1780).

ciliatum dawsoni Stimpson, 1863: 58, text-fig. [*Cardium dawsoni*]. Hope Cape, southeastern coast of Hudson Bay, Canada; Pleistocene (?). Depository: unknown.

ermanensis Sinelnikova in Sinelnikova, Fotjanova, Chelebaeva et al., 1976: 38, pl. 6, fig. 18, 1 [*Clinocardium*]. Near Enemten Rocks, Tigiljskij District, western Kamchatka; the lowest part of Ermanovskaya suite, Upper Miocene. Depository (holotype): Geological Institute of the U.S.S.R. Academy of Sciences, Moscow, U.S.S.R., reg. no. 366/388.

hataii Hayasaka, 1956: 18, pl. 2, figs. 3a–b [*Clinocardium*]. Cliff of the Takesegawa River west of Takakura, Futaba District, Fukushima. Prefecture, Honshu; Ishiguma Formation, Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 77375.

hayesii Stimpson, 1864: 142 [*Cardium*]. Recent; Disko Island, southwestern Greenland. Depository: unknown. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

icelandicum Reeve, 1845: sp. 54, pl. 11 [*Cardium*]. Recent; Iceland. Erroneously pro *islandicum* Bruguière, 1789. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

islandicum Bruguière, 1789: 222 [*Cardium*] ex Chemnitz, 1782: 200, pl. 19, figs. 195, 176, nonbinom. (Official index . . ., 1958: 5, Direction 1). Recent; Iceland. Depository (syntypes): Universitetets Zoologiske Museum, København, Denmark, reg. no. ?. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

iwatense Chinzei, 1959: 125, pl. 11, figs. 9 (holotype), 10 [*Clinocardium*]. Near Ochiai, Kintaichi-mura, Ninohe District, Iwate Prefecture, Honshu; Sannohe group, Kubo Formation, Pliocene. Depository (holotype): Institute of Geology, Faculty of Science, University of Tokyo, Tokyo, Japan, reg. no. 8572.

makiyamae Kamada, 1962: 104, pl. 10, figs. 18 (holotype), 19–21 [*Clinocardium asagaiense makiyamae*]. Nabezuka, Hironomachi, Joban coal-field, Honshu; Asaga Formation, Oligocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 15800. For taxonomic notes see: Kafanov, 1974a: 1470.

matchgarense Makiyama, 1934: 137, pl. 5, figs. 31 (holotype), 30 [*Cardium (Cerastoderma)*. Shore of Cape Marie, near Matchigar, Schmidt Peninsula, Northern Sakhalin; "Marie Formation" [Vengerijskaya suite], Upper Oligocene. Depository (holotype): Institute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 100007.

mutuense Nomura & Hatai, 1936: 279, pl. 33, fig. 11 [*Cardium (Clinocardium)*]. Komatazawa, Aiuti-mura, Mutu Province, Honshu; Isomatsu Formation, Oligocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 8799.

padimeicum Merklin & Zarkhidze in Merklin, Zarkhidze & Ilyina, 1979: 44, pl. 7, figs. 10 (holotype), 11 *[Clinocardium ciliatum]*. Nadejtyvis River, Padimejskaya suite, Pleistocene. Depository (holotype): Paleontological Institute of the U.S.S.R. Academy of Sciences, Moscow, U.S.S.R., reg. no. 2700/76. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

ciliatum pubescens Couthouy, 1838: 61, pl. 3, fig. 6 [*Cardium pubescens*]. Recent; Massachusetts Bay. Depository: unknown.

? sachalinense Khramova, 1962: 437, pl. 1, figs. 6 (holotype), 7 [*Clinocardium*]. Keton River, Poronajskij District, South Sakhalin; lower part of Kurasijskaya suite, Middle Miocene. Depository (holotype): All-Union Oil Research Geological Institute, Leningrad, U.S.S.R., reg. no. 659/46.

salvationemense Lautenschläger in Khramova, 1962: 438, pl. 1, figs. 8 (holotype), 9–12 [*Clinocardium*]. Cape Spassennyj, Tatar Strait coast, Alexandrovskij District, Western Sakhalin; Gennojshinskaya suite, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 84/6197. Synonym of *Ciliatocardium asagaiense* (Makiyama, 1934).

schmidti Khramova, 1962: 436, pl. 1, figs. 1 (holotype), 2, 3 [*Clinocardium*]. North coast of Schmidt Peninsula west of Matchigar Lake, Northern Sakhalin; middle part of Matchigarskaya suite, Upper Oligocene. Depository (holotype): All-Union Oil Research Geological Institute, Leningrad, U.S.S.R., reg. no. 659/24.

shinjiense Yokoyama, 1923: 7, pl. 2, figs. 6a–b [*Cardium*]. Fujina, Tamayu-mura, Yatsuka District, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

snatolense Krishtofovich, 1947: 74, pl. 8, fig. 7 [*Cardium (Acanthocardia) snatolensis*]. Sea cliff southwest of the mouth of the Ilinushka River, Western Kamchatka; upper part of Tigiljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 78/5610.

tigilense Slodkewitsch, 1938: 380, pl. 74, figs. 10, 10a [*Laevicardium(?)*]. Near the mouth of the Polovinnaya River, western Kamchatka; lower part of Kavranskaya suite, Upper Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 914/5060.

uyemurai Kanehara, 1937: 175, text-figs. 6–8 [*Cardium (Cerastoderma)*]. "Great Fuhdji, North Karafto" [Boljshaya Khudi River, Pogranichnyj District], southeastern part of North Sakhalin; "sandy shale of the Congi Series" [Pliocene]. Depository: "Geological Survey of Japan."[4]

yakatagense Clark, 1932: 813, pl. 18, fig. 8 [*Cardium (Cerastoderma)*], Yakataga District (about 60°N), Gulf of Alaska; upper part (?) of the Poul Creek Formation, Lower Miocene (?). Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30384.

yamasakii Makiyama, 1934: 138, pl. 5, figs. 23 (holotype), 24 [*Cardium (Cerastoderma)*]. Shore of Cape Marie, near Matchigar, Schmidt Peninsula, northern Sakhalin; "Marie Formation" [Vengerijskaya suite], Upper Oligocene. Depository (holotype): Insti-

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[4] According to Hatai & Nisiyama (1952), all collections from the Geological Survey of Japan were totally destroyed during the World War II.

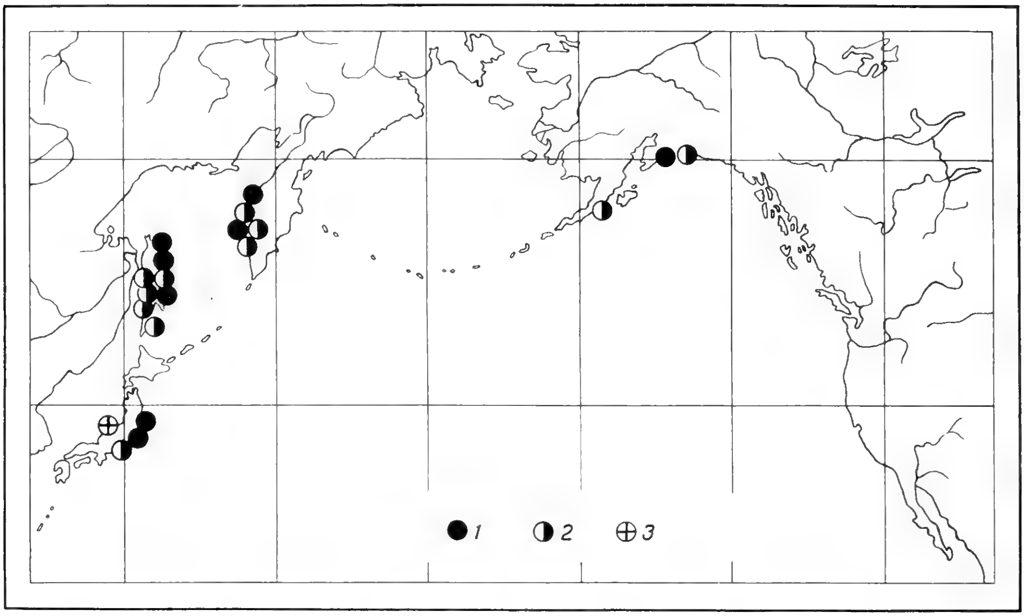

FIG. 8. Geographical and geological distribution of *Profulvia*. 1—Oligocene; 2—Miocene; 3—Pliocene.

tute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 100005.

Tribus Profulviini Kafanov in Kafanov & Popov, 1977

Kafanov & Popov, 1977: 62

Shell carinate, gaping posteriorly or at both ends. Radial ribs well developed, convex anteriorly, curved on posterior part of valve. Beaks nearly orthogyrate, weakly prosogyrate or opisthogyrate.

Oligocene-Pliocene; northwestern Pacific and Alaska (Fig. 8).

Genus *Profulvia* Kafanov, 1976

Profulvia Kafanov, 1976: 111.

Type-species: *Papyridea harrimani* Dall, 1904; Unga conglomerate, lower part of Middle Miocene, Popov Island, Alaska Peninsula (original designation).

Shell medium-sized or fairly large (about 100 mm and more), elongate-ovate, truncated, variably inequilateral, moderately convex, frequently carinate, with gape at posterior or both ends. Beaks relatively low, obtuse, weakly prosogyrate, nearly orthogyrate or opisthogyrate. Ribs about 30–65 in number. Ribs straight, narrow and low on the anterior valve surfaces, more curved posteriorly. Ribs convex anteriorly (Fig. 4b); their height and width increase and flattened intercostal spaces become deeper posteriad. Ribs frequently reduced on the posterior slope. Ribs rounded or triangular in cross-section, or combination of these two types observed: 1) ribs are low and rather rounded in cross-section on the anteror valve surface and 2) ribs are high, irregularly triangular with abrupt posterior wall and more sloped anterior wall on the posterior valve surfaces. Ridges of ribs with numerous commarginal lines, wrinkles and growth lines; weak nodes occur where growth lines cross costal crests. Dental margin weakly curved. Paired cardinal teeth small and straight in both valves; lateral teeth usually single. Lunula and escutcheon areas weak. Internal valve surfaces or at least their ventral part with distinct indentations and ventral margin serrated.

Geographical and geological distribution as in the tribus (Fig. 8).

Key to the species

1. Average height/length ratio about 0,83 or less .... 2.
   Average height/length ratio more than 0,84 .... 9.
2. Maximum size of adult shell less than 70 mm .... 3.
   Maximum size of adult shell more than 70 mm .... 8.
3. Shell inequilateral (beaks near the anterior 0,37–0,38) *sertunayana* (Slodkewitsch, 1938).
   Shell subequilaeral (beaks near the anterior 0,42–0,44) .... 4.
4. Ribs 38 or fewer .... 5.
   Ribs more than 38 .... 6.
5. Average height/length ratio about 0,81; ribs 36–37 ...... *angulata* (Slodkewitsch, 1938).
   Average height/length ratio about 0,75; ribs 32–33 .... *noyamiana* (Slodkewitsch, 1938).
6. Average height/length ratio about 0,82–0,83; ribs 40–45 ....
   .... *utcholokensis* (Slodkewitsch, 1938).
   Average height/length ratio about 0,70–0,77; ribs more than 45 .... 7.
7. Average height/length ratio about 0,70; maximum size of adult shell about 55 mm ......
   .... *kurodai* (Hatai & Nisiyama, 1952).
   Average height/length ratio about 0,75–0,77; maximum size of adult shell about 35 mm .
   .... *kovatschensis* (Ilyina, 1962).
8. Shell subequilateral (beaks near the anterior 0,41–0,42); ribs 50–60 ....
   .... *matschigarica* (Khomenko, 1938).
   Shell strongly inequilateral (beaks near the anterior 0,32); ribs 36–40 ....
   .... *securiformis* (Slodkewitsch, 1938).
9. Average height/length ratio about 0,90–0,92 .... 10.
   Average height/length ratio about 0,85–0,86 .... 11.
10. Ribs 40–45; maximum size of adult shell about 90 mm . *kipenensis* (Slodkewitsch,1938).
    Ribs 60 or more; maximum size of adult shell about 50 mm ....
    .... *hamiltonense* (Clark, 1932).
11. Ribs about 30 in number .... *sakhalinensis* (Slodkewitsch, 1938).
    Ribs about 40–45 in number .... *harrimani* (Dall, 1904).

angulata Slodkewitsch, 1938 (ex Kogan, MS): 404, pl. 81, figs. 8, 8a [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 180/5294.

hamiltonense Clark, 1932: 813, pl. 18, figs. 7 (holotype), 6,10 [*Cardium (Serripes)*]. Yakataga District (about 60°N), Gulf of Alaska; Poul Creek Formation (?), Upper Oligocene(?)-Lower Miocene (Addicott, 1971; Addicott et al., 1971). Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30405.

harrimani Dall, 1904: 114, pl. 10, fig. 5 [*Papyridea*]. North coast of Popov Island, Alaska Peninsula; Bear Lake Formation, Unga conglomerate, lower Middle Miocene, Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 164867.

kipenensis Slodkewitsch, 1938: 409, pl. 82, figs. 2 (holotype), 1, pl. 83, figs. 1–3 [*Papyridea*]. 18 km from the mouth of the Snatol River, western Kamchatka; upper part of the Kavranskaya series [Upper Miocene]. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 902/5060.

kovatschensis Ilyina, 1962: 343, pl. 2, figs. 8, 8a [*Papyridea*]. Utkholok Cape, western Kamchatka; "Tufogennyj horizon," lower part of Voyampoljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 121/6068.

kurodai Hatai & Nisiyama, 1952: 105 [*Papyridea (Fulvia)*] pro *Papyridea (Fulvia) nipponica* Yokoyama, 1926c: 294, pl. 34, fig. 16 non 1924: 17, pl. 3, figs. 3, 4. Sawane, Sado Island, Niigata Prefecture, Honshu; Sawane formation, Lower Pliocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?.

matschigarica Khomenko, 1938: 47, pl. 7, figs. 5 (lectotype), 6, 7, pl. 8, fig. 6, pl. 9, fig. 7 [*Papyridea*]. Between the Marie Cape and Matchigar Lake, Schmidt Peninsula, northern Sakhalin; lower part of the Machigarskaya suite, Oligocene. Depository (lectotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 81/5044. For figure of lectotype see: Slodkewitsch, 1938, pl. 84, fig. 2.

nipponica Yokoyama, 1924: 17, pl. 3, figs. 3, 4 [*Papyridea (Fulvia)*]. Tatsuta coal-field, Futaba District, Fukushima Prefecture, Honshu; Asagai Formation, Oligocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Following Hatai & Nisiyama (1952) and Makiyama (1957), the author considers this form a synonym of *Profulvia harrimani* (Dall, 1904).

noyamiana Slodkewitsch, 1938 (ex Kogan, MS): 413, pl. 86, figs. 3 (holotype), 2 [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geogical Prospecting Museum, Leningrad, U.S.S.R., reg. no. 181/5294.

sakhalinensis Slodkewitsch, 1938 (ex Kogan, MS): 412, pl. 86, fig.1 [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 182/5294.

securiformis Slodkewitsch, 1938: 411, pl. 85, fig. 1 [*Papyridea*]. Kovachina Bay, western Kamchatka; lower part of Kavranskaya series, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 899/5060.

sertunayana Slodkewitsch, 1938 (ex Kogan, MS): 405, pl. 82, figs. 3, 3a [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, Western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 185/5294.

utcholokensis Slodkewitsch, 1938: 403, pl. 82, figs. 6 (holotype), 4, 5 [*Papyridea*]. Utcholok Cape, western Kamchatka; lower part of Vayampoljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 911/5060.

Tribus Serripedini Kafanov, 1975

Kafanov, 1975: 147.

Radial ribs obsolete or absent but their traces can usually be observed on the posterior and rarely on the anterior valve surfaces. Hinge weak due to reduction of cardinal teeth.

Early Oligocene-Recent; northwestern Pacific south to south Honshu and northeastern Pacific south to Puget Sond, Arctic Seas and North Atlantic (south to Cape Cod, Iceland and south Norway; in later Pliocene and Early Pleistocene to England and to the Netherlands) (Figs. 9, 10).

Genus *Serripes* Gould, 1841 ex Beck, MS

Aphrodite Lea, [1837]: 111 non Leske, 1775, nec Link, 1807 (pro *Aphrodita* Linné, 1758), nec Hübner, [1819], nec Lendenfeld, 1886;

Aphrodita Leach in Sowerby, 1839: 70 (pro *Aphrodite* Lea, 1837 non Linné, 1758);

Acardo Swainson, 1840: 374 non Lamarck, 1799, nec Roissy, 1805, nec Mühlfeldt, 1811, nec Menke, 1828, nec Herrmannsen, [1846];

Serripes "Beck" Gould, 1841: 93.

Type-species: *Cardium groenlandicum* Bruguière, 1789; Recent, Greenland (by monotypy).

Shell medium-sized or fairly large (to 90 mm and more), flattened, oblong-elliptical or truncate-trigonal, variously inequilateral; as a rule, anterior and broader than posterior one. Posterodorsal margin smoothly joined with the posterior valve margin. Carina on the posterior valve surface obsolete. Beaks moderately prosogyrate or nearly orthogyrate. Radial ribs almost entirely reduced. Hinge strongly reduced, frequently teeth completely absent. Bases of the anterior lower lateral teeth lie on outer side of the internal branches of hinge margin (Fig. 3a). Distal part of foot with longitudinal row of crests or denticles, ventral sulculus absent. Labial palps long and nearly equal in length to inner demibranch.

Geographical and geological distribution as in the tribus (Fig. 9).

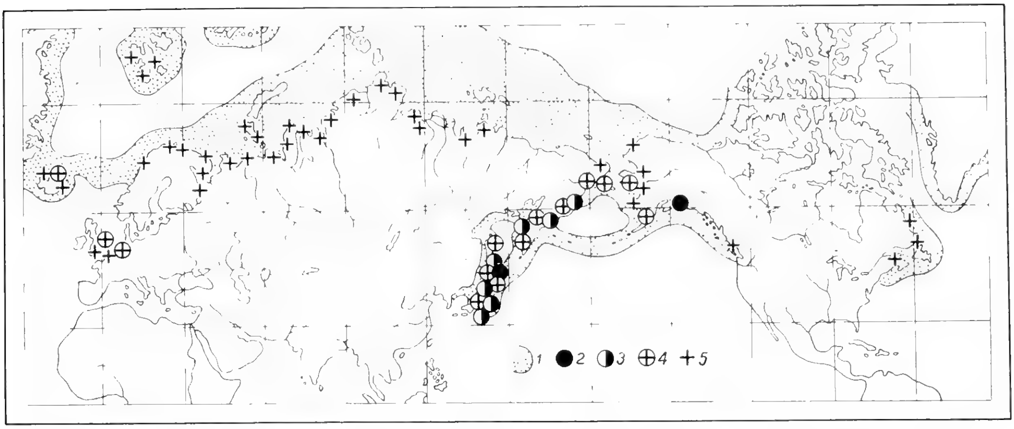

FIG. 9. Geographical and geological distribution of *Serripes*. 1—Recent. 2—Oligocene; 3—Miocene; 4—Pliocene; 5—Pleistocene.

Key to the species and subspecies

1. Traces of radial ribs well developed on the medial valve surfaces .... *shiobaraensis* Noda, 1962.
   Traces of radial ribs not developed on the medial valve surfaces .... 2.
2. Posterior valve margin almost straight; cardinal teeth not reduced .... *groenlandicus fabricii* (Deshayes, 1855).
   Posterior valve margin variously curved; cardinal teeth variously reduced .... 3.
3. Average length of adult shell more than 100 mm; shell much swollen; traces of radial ribs observed only on the anterior valve surfaces .... *expansus* Hirayama, 1954.
   Average length of adult shell less than 100 mm; shell variously inflated; traces of radial ribs present, as a rule, on the posterior valve surfaces .... 4.
4. Height/length ratio more than 0,96 .... 5.
   Height/length ratio less than 0,95 .... 9.
5. Average height/length ratio about 1,20 .... *muraii* Noda & Tada, 1968.
   Average height/length ratio about 0,99–1,10 .... 6.
6. Maximum size of adult shell about 95 mm; shell rather inequilateral (beaks near the anteror 0,41–0,42) .... *kamtschaticus* Ilyina, 1963.
   Maximum size of adult shell about 60 mm; shell subequilateral or nearly equilateral .. 7.
7. Shell nearly equilateral (beaks near the anterior 0,48); average height/length ratio about 1,00 .... *hataii* Noda, 1962.
   Shell subequilateral (beaks near the anterior 0,44–0,46); average height/length ratio about 1,10 .... 8.
8. Shell trigonal in outline .... *triangularis* Noda, 1962.
   Shell rounded .... *nodai* Kafanov nom. nov.
9. Average height/length ratio more than 0,90 .... 10.
   Average height/length ratio less than 0.90 .... 11.
10. Shell inequilateral (beaks near the anterior 0,39–0,40); average length of adult shell about 85 mm .... *ochotensis* Ilyina, 1963.
    Shell rather inequilateral (beaks near the anterior 0,42); average length of adult shell about 50 mm .... *squalidus* (Yokoyama, 1924).
11. Average height/length ratio about 0,75; maximum size of adult shell about 25 mm .... *uvutschensis* Ilyina, 1963.
    Average height/length ratio more than 0,78; maximum size of adult shell more than 40 mm .... 12.

12. Shell strongly inequilateral (beaks near the anterior 0,37–0,38) . . . *japonica* Noda, 1962.
Shell subequilateral or nearly equilateral (beaks near the anterior 0,44–0,48) . . . . 13.

13. Average height/length ratio about 0,87–0,88; shell subequilateral (beaks near the anterior 0,44–0,45) . . . . *groenlandicus* (Bruguière, 1789).
Average height/length ratio about 0,80–0,81; shell nearly equilateral (beaks near the anterior 0,48) . . . . *laperousii* (Deshayes, 1839).

Described taxa

album Verkrüzen, 1877: 53 [*Cardium (Aphrodite) groenlandicum* var.]. Recent; Newfoundland Bank. Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789) or *Serripes groenlandicus fabricii* (Deshayes, 1854).

boreale Reeve, 1845: sp. 131, pl. 22 [*Cardium*] non Broderip & Sowerby, 1829: 369. Recent; Greenland. Depository (holotype): British Museum (Natural History), reg. no. 1879.2.26.235. Synonym of *Serripes groenlandicus* (Bruguière, 1789).

columba Lea, 1834: 111, pl. 18, fig. 54 [*Aphrodite*]. Type-locality not given, nor was it given subsequently; Lea listed only "Hab . . ."; on p. 111–112 under Remarks he said: "Its habitat I am not acquainted with, having purchased my specimens at a dealer's in Europe, who could not inform me from what country they came." Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

edentulum Montagu, 1808: 29 [*Cardium edentula*] non Fleming, 1813: 92 nec Deshayes, 1838: 57, pl. 3, fig. 3–6 [*Cardium*]. Recent; "on the shore near Portsmouth, after a storm." Depository: Exeter Museum, Exeter, Great Britain (?). Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

expansus Hirayama, 1954: 66, pl. 4, figs. 1 (holotype), 2 [*Serripes*]. Nanatsuishi, Oyamada-shimogo, Oyamada-mura, Tochigi Prefecture, Honshu; Kobana Formation, Lower Miocene. Depository (holotype): Tokyo University of Education (Kyoiku Daigaku), Tokyo, Japan, reg. no. 10136.

groenlandicus fabricii Deshayes, 1855: 333 [*Cardium fabricii*]. Recent; Iceland. Depository (holotype): Zoological Institute of the U.S.S.R. Academy of Sciences, Leningrad, U.S.S.R., reg. no. 1/13460. For figure of holotype, see Middenforff, 1849: pl. 16, figs. 6, 7.

fujinensis Yokoyama, 1923: 5, pl. 2, figs. 2a–b [*Mactra*]. Matsue, Fujina, Tamayumura, Yatsuka District, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Unlike Noda (1962), the author considers this form a synonym of *Serripes groenlandicus* (Bruguière, 1789) rather than of *S. laperousii* (Deshayes, 1839) because of the general valve outlines, their considerable convexity and significantly elevated beaks.

groenlandicus Bruguière, 1789: 222 ex Chemnitz, 1782: 202, pl. 19, fig. 198, non-binom. (see: Official Index . . , 1958: 5, Direction 1) [*Cardium*]. Recent; [southeastern] Greenland (here limited; Chemnitz reports that the majority of representatives of this species was collected for him from Julianehob). Depository (possible syntypes): Universitetets Zoologiske Museum, København, Denmark, reg. nos. ? Recent records: North Pacific (south to central parts of Honshu, Korea?, Peter the Great Bay, Aleutian and Commander Islands and Puget Sound, Washington), North Atlantic (south to Iceland, southern Greenland and Cape Cod, Massachusetts) and epicontinental Arctic Seas. Fossil records: Miocene Echinskaya suite of Chukotka, Yakataga formation of Alaska, Undal-Umenskaya suite of Koryak Plateau, Pestrotsvetnaya and Yunjunjvayamskaya suites of Keraginskij Island, Ilyinskaya, Etolonskaya, Kuluvenskaya, Goryachikh Klyuchej and Nachikinskaya suites of Kamchatka, Alekhinskaya, Kamujskaya and Okruglovskaya suites of Kurile Islands, Uglegorskaya, Sertunajskaya, Uranajskaya, Borskaya, upper and middle parts of Maruyamskaya, Ausinskaya, Kurasijskaya and Okobykajskaya suites of Sakhalin, Okada, Chijubetsu, Magaribuchi, Sin-uryu, Wakkanai formations of Hokkaido, Kobana, Fujina, Kurosawa, Kanomatazawa, Ogino, Takahoko, Hongo and Utsutoge formations of Honshu; Pliocene Pinakuljskaya suite of Chukotka, upper part of Limimtevayamskaya and Ustj-Limimtevayamskaya suites of Karaginskij Island, Gavanskaya suite of Kamchatka, Golovinskaya, Parusnaya and Okeanskaya suites of Kurile Islands, upper part of Maruyamskaya, Mayamrafskaya, Matitukskaya and Pomyrskaya suites of Sakhalin, Gobansoyama, Ebishima, Rigashigawa, Sizun and Takinoe formations of Hokkaido and Northern Honshu; Pliocene and Plio-Pleistocene of Iceland (Tjornes Crag, zone of *Serripes groenlandicus*), England (Red Crag) and the Netherlands (Dutch Icenian); Pleistocene sediments of Arctic and Subarctic regions of the Northern Hemisphere.

? haboroensis Yokoyama, 1927b: 198, pl. 52, figs. 3 (lectotype; designated by Hatai & Nisiyama, 1952: 86), 4 [*Mactra*]. Sankebetsu, off Shinkukaku, Haboro-machi, Tomamae District, Teshio Province, Hokkaido; Chikubetsu Formation, Lower Miocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Shell form closely resembles that of *Serripes groenlandicus* (Bruguière, 1789). The author cannot refer this species with confidence to Serripedini for lack of data on hinge structure.

hataii Noda, 1962: 224, pl. 37, fig. 3 [*Serripes*]. Iwaigawa, Kamikurosawa, Hagihana-mura, Nishiiwai District, Iwate Prefecture, Honshu; lower part of the Nishikurosawa Formation, Lower Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 74593.

japonica Noda, 1962: 225, pl. 39, fig. 4 [*Serripes*]. Mukai, Sakekawa, Mogami District, Yamagata Prefecture, Honshu; Sakekawa Formation, Lower Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 78680.

kamtschaticus Ilyina, 1963: 102, pl. 43, figs. 2 (holotype), 3 [*Serripes*] sea cliff between the Moroshechnaya and Kovachina Rivers, western Kamchatka; Etolonskaya suite, upper Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 24/96338.

laperousii Deshayes, 1839: 360; 1841b: pl. 48 [*Cardium*]. Recent; Kadjak Island, Gulf of Alaska (type-locality here designated; in original description as type-locality are mentioned "Mers de Californie" but this species is absent from the coast of California). Depository: unknown. As fossil it was recorded from Middle and Upper Miocene and Pliocene of northeastern and north Honshu and Hokkaido (reviewed by Noda, 1962), from Upper Miocene and Pliocene of Sakhalin and Kurile Islands, but it should be noted that there is much evidence that the fossil representatives of this species in fact belong to *Serripes groenlandicus* (Bruguière, 1789) and to other species of the genus. It is unknown in Neogene deposits of the northeastern Pacific.

muraii Noda & Tada, 1968: 202, pl. 22, fig. 22 [*Serripes*]. Small tributary of the Kakkonda River, about 4 km NNW of the Takinoue Spa, Shizukuishi-machi, Iwate Prefecture, Honshu; Yamatsuda Formation, upper Middle Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 88058.

nodai Kafanov nom. nov. pro *Cardium pauperculum* Yokoyama, 1923: 6, pl. 1, figs. 2a–c non Meek, 1871: 306 [*Serripes*]. Kami-Ichiba, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? For taxonomic notes see: *pauperculum* Yokoyama, 1923.

ochotensis Ilyina, 1963: 102, pl. 42, figs. 2 (holotype), 1 [*Serripes*]. Sea cliff between the Etolona River and Nepropusk Cape; Etolonskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 248/6338.

pauperculum Yokoyama, 1923: 6, pl. 1, figs. 2–c non Meek, 1871: 306, nec Yokoyama, 1925c: 121, pl. 14, figs. 12, 13 nec 1926b, 243, pl. 30, fig. 3 [*Cardium*], Kami-Ichiba, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Following Noda (1962), Keen (1973) considers this species to be a synonym of *Serripes groenlandicus* (Bruguière, 1789). Yokoyama described and figured three different forms called *Cardium pauperculum*: 1) the holotype, a specimen which slightly resembles *Serripes hataii* Noda, 1962 and is much different in shell outlines from all Recent and fossil *Serripes groenlandicus* (Bruguière, 1789); 2) a specimen from the Oligocene Akahira Beds of Central Honshu described and figured by Yokoyama (1925c, 121: pl. 14, figs. 12, 13) for which Hatai & Nisiyama (1952: 39) suggest a new name, *Cardium arakawaense*; 3) a specimen from the Upper Miocene Wakkanai Formation of southwestern Honshu (Yokoyama, 1926b: 243, pl. 30, fig. 3) which really may be identified with *Serripes groenlandicus* (Bruguière, 1789). Noda (1962) in comparing *Cardium pauperculum* Yokoyama with *Serripes groenlandicus* (Bruguière, 1789) apparently took into account the third form mentioned above, because he cites the name in Yokoyama's paper of 1926 in synonymy with *Serripes groenlandicus* (Bruguière, 1789), but he does not mention the original description and figure of *Cardium pauperculum*

Yokoyama, 1923. Both Hatai and Nisiyama (1952) do not give it. According to the author the information does not justify the recognition of *Cardium pauperculum* Yokoyama, 1923 as a synonym of *Serripes groenlandicus* (Bruguière, 1789) and the species can retain its rank of an independent species. However owing to the presence of an older homonym, *Cardium pauperculum* Meek, 1871, *pauperculum* Yokoyama, 1923 is given the new name *Serripes nodai* in honour of the Japanese paleontologist Prof. Hiroshi Noda.

protractus Dall, 1900: 1112 [*Serripes groenlandicus* var.]. Recent; type-locality not given. Depository: unknown. Invalid name as nomen infrasubsp. s.s.

radiata Donovan, 1803: pl. 161 et text, non Spengler, 1802: 107 [*Mactra*]. Recent; "Langston Beach, near Portsmouth, after a severe storm . . ." Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

shiobaraensis Noda, 1962: 228, pl. 39, fig. 5 [*Serripes*]. Cliff facing the Hokigawa Electric Power Station along the Hoki River, Sekiya, Shiobara-machi, Shioya District, Tochigi Prefecture, Honshu; Kanomatazawa Formation, Middle Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 78587.

squalidus Yokoyama, 1924: 16, pl. 3, figs. 1, 1a [*Cardium (Laevicardium)*]. Dodaira, Misawa, Nakoso-shi, Fukushima Prefecture, Honshu; Iwaki Formation, Oligocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

titthus Krishtofovich, 1969: 192, pl. 4, figs. 4 (holotype), 5, 9, 12, 14 [*Serripes*]. Near the mouth of the Talovaya River, Kronotskij Reservation, East Kamchatka; Tyushevskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 62/6780. Synonym of *Serripes groenlandicus* (Bruguière, 1789).

triangularis Noda, 1962: 229, pl. 39, figs. 2 (holotype), 3 [*Serripes*]. Itanoki-sawa, Arakimura Mogami District, Yamagata Prefecture, Honshu; Mitsumori Formation, Upper Miocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 8410.

unciangulare Khomenko, 1931: 75, pl.10, fig. 21 [*Cardium groenlandicum unciangulare*]. Boljshoj Garomaj River, east Kamchatka; "Nadnutovskaya" suite, Pliocene. Synonym of *Serripes groenlandicus* (Bruguière, 1789) as shown by original description: "Form described here represents the extreme degree of inequilaterality of lower forms of *Cardium groenlandicum*. . . ." Moreover, according to the faunal lists in Khomenko's paper it frequently occurs together with the typical *Serripes groenlandicus* (Bruguière, 1789).

uvutschensis Ilyina, 1963: 76, pl. 25, fig. 5 [*Serripes (?)*]. Cliff of the Kovachina Bay near the mouth of Moroshechnaya River; Ilyinskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R. reg. no 103/6338.

Genus *Yagudinella* Kafanov, 1975

Yagudinella Kafanov, 1975: 147.

Type-species: *Cardium (Serripes) notabile* Sowerby, 1915; Recent, Wakasa Bay, Honshu (original designation).

Shell medium-sized or fairly large (to 100 mm and more), convex, truncated, obviously inequilateral. Anterior end much narrower than posterior one. Posterodorsal margin passes into posterior valve margin at an angle. Posterior valve surface, as a rule, with pronounced carina. Beaks strongly inclined forward and prosogyrate. Clear traces of the radial ribs on the anterior and posterior valve surfaces. Cardinal teeth somewhat reduced. Bases of the anterior lower lateral teeth lie on the ventral side of anterior part of hinge margin and their proximal parts extended posterodorsally toward beaks (Fig. 3b). Distal part of foot with longitudinal row of closely spaced combs but not denticles, which are high, inflated on the sides; ventral sulculus absent. Labial palps long and near equal in length to the inner demibranch.

Middle Miocene-Recent; northwestern Pacific (south to southwestern Honshu).

Key to the species and subspecies

1. Shell hatchet-shaped in outline . . . . *yokoyamai* (Otuka, 1935).
   Shell triangular in outline . . . . 2.
2. Shell strongly inequilateral (beaks near the anterior 0,38–0,39) . . . . 3.
   Shell subequilateral (beaks near the anterior 0,41–0,48) . . . . 4.

3. Average height/length ratio about 0,94 .... *makiyamai makiyamai* (Yokoyama, 1928).
Average height/length ratio about 0,83 .... *makiyamai nigamiensis* (Noda, 1962).
4. Average height/length ratio about 1,00; shell almost equilateral (beaks near the anterior 0,48) .... *notabilis notabilis* (Sowerby, 1915).
Average height/length ratio about 0,81–0,82; shell subequilateral (beaks near the anterior 0,41) .... *notabilis nomurai* (Otuka, 1943).

Described taxa

makiyamai Yokoyama, 1928: 360, pl. 69, fig. 3 [*Mactra*]. Nagaoka, River side at Hanzogane, Hanzogane-mura, Koshi District, Niigata Prefecture, Honshu; Ushigakubi Formation, Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

makiyamai nigamiensis Noda, 1962: 227, pl. 39, figs. 1a–c [*Serripes*]. Nigami, Ooshima-mura, Higashikubiki District, Niigata Prefecture, Honshu; Shiiya Formation, Upper Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Japan, reg. no. 78684.

notabilis nomurai Otuka, 1943; 56, pl. 3(2), fig. 10 [*Serripes*]. Nakanango, Saunai-mura, Hiraga District, Akita Prefecture, Honshu; Kurosawa Formation, Middle and Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Noda (1962) considers this form identical with *Serripes notabilis* (Sowerby, 1915). However, the numerous Recent and fossil specimens of the latter species are distinguished by their more angulate outlines and more truncated valves. The author there-

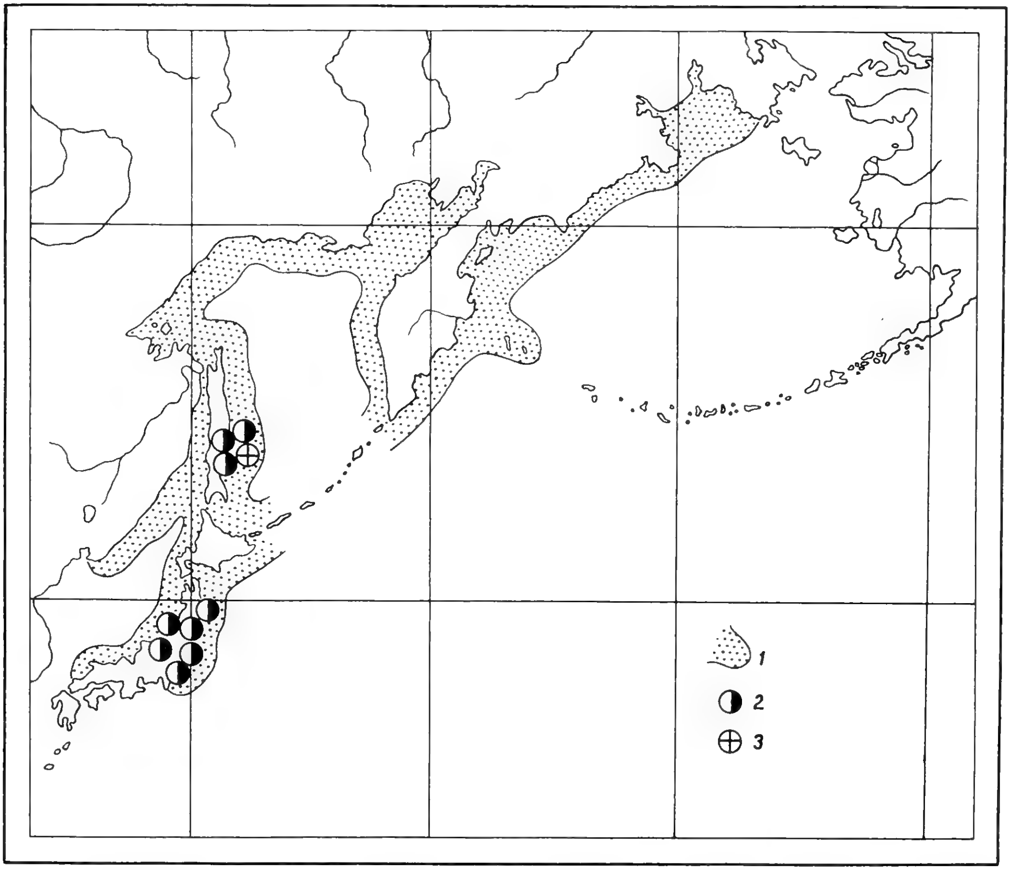

FIG. 10. Geographical and geological distribution of *Yagudinella*. 1—Recent; 2—Miocene; 3—Pliocene.

fore finds it quite possible that this form should retain its rank of a separate subspecies.

notabilis Sowerby, 1915: 169, pl. 10, fig. 9 [*Cardium (Serripes)*]. Wakasa Bay, Honshu; Recent. Depository (holotype): British Museum (Natural History), London, Great Britain, reg. no. 1919.12.31.38. Recent distribution: see Fig. 10. Fossil records reviewed by Noda (1962).

yokoyamai Otuka, 1935: 603, pl. 2, fig. 3, 4 (holotype), 5, 6 [*Serripes*]. Ogino, Yamanogomura, Yama District, Fukushima Prefecture, Honshu; Hitosao Formation, Middle and Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. 2531.

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Абстракт

Система и состав подсемейства **Clinocardiinae Kafanov,** 1975 **(Bivalvia, Cardiidae)**

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При ревизии кайнозойских **Cardioidea** автор установил новое подсемейство **Clinocardiinae.** В данной работе обсуждается история изучения клинокардиин, объем и состав подсемейства и его положение в системе **Carddiidae.** Даны определительные таблицы для триб,

родов, видов и подвидов, а также детальные диагнозы для подсемейства, триб, родов и подродов. Прилагаемый каталог содержит все описанные до сих пор таксоны видового ранга со ссылками на оригинальные описания, указаниями на типовые местонахождения и места депонирования типового материала. В необходимых случаях даны таксономические замечания. Для Cardium pauperculum Yokoyama, 1923 non Meek, 1871 предложено новое название: Serripes nodai nom.nov.

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DRILLING PREDATION OF BIVALVES IN GUAM: SOME PALEOECOLOGICAL IMPLICATIONS[1]

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ABSTRACT

All drill-holes in the valves of soft-bottom clams from Guam (Mariana Islands) are attributable to naticid gastropods; hard-bottom bivalves are drilled exclusively by muricaceans. Edge-drilling, which is reported in a naticid (*Polinices tumidus*) for the first time, is likely to have been a common cause of death of tropical bivalves for much of Tertiary time. Drilling frequencies are high in the Lucinidae and low in the Veneridae, Cardiidae, and Tellinidae. There is no straightforward relationship between bivalve shell traits and susceptibility to drilling. Underestimation of drilling intensity is likely in studies of fossils, since naticids kill many bivalves before drilling is initiated. Great variation in drilling frequencies at small and large geographical scales complicates the search for temporal patterns in predation.

INTRODUCTION

Drilling is one of the few modes of predation on mollusks that can be recognized postmortem on shells and treated quantitatively. There is a fairly extensive literature on the methods employed by muricacean and naticacean gastropods to detect and drill their prey (for reviews see Carriker & Yochelson, 1968; Sohl, 1969; Vermeij, 1978). The impact of drilling gastropods on populations of Recent bivalves is known primarily for temperate hard-bottom bivalves (Chapman, 1955; Seed, 1969; Fotheringham, 1974; Bayne & Scullard, 1978; Menge, 1978a, b; Suchaneck, 1978); comparatively few estimates of drilling intensity have been made for soft-bottom bivalves (Ansell, 1960; Reyment, 1967; Green, 1968; Jackson, 1972; Schäfer, 1972), and little is known about drilling in the tropics. Paradoxically, drilling on fossil bivalves has been relatively well studied; data on the frequency of drilled valves are available for the Eocene (Fischer, 1966; Taylor, 1970; Adegoke & Tevesz, 1974), Miocene (Hoffman et al., 1974; Kojumdjieva, 1974; Watkins, 1974; Dudley & Dudley, 1980), Pliocene (Boekschoten, 1967; Robba & Ostinelli, 1975), and Pleistocene (Stump, 1975). Several of these studies deal with warm-water bivalves.

In order to extend our knowledge of spatial and temporal variations in drilling predation, more data are needed on drilling of Recent bivalves, especially in the tropics. Information of this type will also be of practical value in culturing edible clams. In this paper I report drilling frequencies of the common bivalves on the reef-flats of Guam, the southernmost of the Mariana Islands in the tropical western Pacific; and I describe for the first time the occurrence of edge-drilling by naticid gastropods.

MATERIALS AND METHODS

Field estimates of drilling predation were obtained from large samples of empty valves from several reef-flats on Guam. Valves were collected by hand or with the aid of a hand-held dredge with 6 mm mesh in the period of January to May, 1979. All valves were sorted, identified, inspected for the presence of drill-holes, and measured with calipers to the nearest millimeter. Chi-square tests reveal that the number of right valves was never significantly different from the number of left valves in any of the samples listed in Table 1. Consequently, there is no evidence for differential sorting of right and left valves such as that documented in the Netherlands for *Donax vittatus* (da Costa) by Lever & Thijssen (1968). No more than one drill-hole was observed on any valve; therefore, in the case of holes drilled away from the valve margin, each drilled valve represents one drilled individual (two valves), and the intensity of drilling is expressed as twice the number of drilled valves divided by the total number of valves.

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Holes which are drilled at the valve margin usually affect both valves, though not necessarily to the same extent; marginal drills in a right and left valve of similar size are regarded as representing a single penetration only if the position of the hole in the two valves is the same. In all other cases, it is assumed that a valve which is drilled at the margin represents one drilled individual, so that the frequency of edge-drilling is twice the number of edge-drilled valves divided by the total number of valves in the sample.

In order to determine how bivalves are killed by naticids, seven *Polinices tumidus* (Swainson) (25.7 mm to 35.4 mm long) and one *Natica gualteriana* Récluz (20.8 mm in diameter) were maintained individually in running sea water with various prey species at the University of Guam Marine Laboratory. In addition, four *N. gualteriana* from Thursday Island (Torres Straits, Queensland) were kept in running sea water on board the R.V. Alpha Helix. The sediment on the bottom of the aquaria in which the snails were kept was a muddy sand 14 mm to 35 mm deep.

RESULTS AND DISCUSSION

Muricacean gastropods are responsible for all drill-holes observed on the valves of hard-bottom clams (Mytilidae and Arcidae) in Guam. At Gun Beach, on the west coast of the island, *Chicoreus brunneus* (Link) appears to be the principal predator of the semi-infaunal bench mussel *Modiolus auriculatus* (Krauss) (15 observations). At Pago Bay, on the windward east coast, where *C. brunneus* is absent, *M. auriculatus* is preyed upon by species of *Morula*. *Arca avellana* Lamarck, which in Guam is usually confined to crevices and the under surfaces of stones, is rarely drilled.

All drill-holes in the valves of soft-bottom clams (Lucinidae, Cardiidae, Veneridae, and Tellinidae) are attributable to naticid gastropods. Muricaceans, which commonly attack soft-bottom bivalves elsewhere in the tropics and subtropics (Wells, 1958; Paine, 1963; Vermeij, 1978) are absent from shallow-water sands and muds in Guam. Two types of drill-hole are present in the soft-bottom bivalves examined. The first is the typical circular naticid hole with tapering walls (Carriker & Yochelson, 1968), which penetrates through one of the two valves. The second type is a hole drilled at the commissure between the two valves. The hole is a beveled cone like that of the first type, but it is expressed on a valve as a semicircular nick in the margin. Edge-drills of this type can occur anywhere along the commissure.

Laboratory observations of the two common reef-flat naticids in Guam show that edge-drilling is commonly practiced by *Polinices (Polinices) tumidus* but never by *Natica (Naticarius) gualteriana* (Table 2). Of 49 clams eaten by *P. tumidus* in the laboratory, 30 (61%) were drilled at the margin, 4 (8.2%) were drilled through one valve, and 15 (31%) were killed without injury to the shell. Of 19 bivalves drilled by *N. gualteriana*, 17 (89%) were drilled through one valve, and 2 (11%), both *Arcopagia robusta*) were eaten without injury to the shell.

To my knowledge, edge-drilling has not previously been reported for naticid gastropods, even though it is widespread among Muricacea such as *Thais, Muricanthus,* and *Ceratostoma* (Chapman, 1955; Wells, 1958; Vermeij, 1978). Careful studies show that *Polinices (Neverita) duplicatus* Say, *P. (Euspira) catena* (da Costa), *P. (E.) nitida* (Donovan), and *Natica (Natica) millepunctata* Lamarck drill in the vicinity of the umbo or in other central regions of the valve, but not at the shell margin (Böttger, 1930; Carriker, 1951; Ziegelmeier, 1954; Paine, 1963; Negus, 1975; Edwards & Huebner, 1977). Many taxa in the Naticidae, including such widely distributed groups as *Polinices (Mammilla), P. (Glossaulax), P. (Stigmaulax), P. (Hypterita), Sinum,* and *Eunaticina,* have not yet been studied with respect to drilling behavior. *Polinices (Polinices),* the only subgenus in which edge-drilling is known thus far in the Naticidae, is nearly circumtropical in distribution and has a long history beginning in the Paleocene (Marincovich, 1977); *P. (P.) tumidus* has a broad geographical range extending from Hawaii to East Africa (Kilburn, 1976). Edge-drilling by naticids may have been important to bivalves throughout the tropics for most of Tertiary time.

Table 1 presents frequencies of drilling in the 12 bivalve species for which sample sizes were judged to be sufficient (20 valves or more). Among soft-bottom bivalves, the only species with consistently high frequencies of drilling are the lucinids *Codakia bella* and *Wallucina* sp. Members of the Veneridae and Tellinidae have significantly lower drilling frequencies than do the Lucinidae ($p < 0.001$ in each case, Mann-Whitney U-Test), but there is no significant difference between the Veneridae and Tellinidae. The cardiid *Fragum*

TABLE 1. Frequencies of edge-drilling (F_E) and of total drilling (F_{DR}) in bivalves from Guam.

Species	Site	N	F_E	F_{DR}	Mean size all valves ± SD (mm)	Mean size drilled valves ± SD (mm)
Arcidae						
Arca avellana Lamarck	PB	51	0	0	17.3 ± 4.1	—
Mytilidae						
Modiolus auriculatus Krauss	SH	44	.091	.091	23.3 ± 4.6	22.5
	GB	140	.057	.27	20.7 ± 6.8	21.9 ± 6.3
	PB	31	0	.58	14.1 ± 4.4	32.4 ± 2.9
Lucinidae						
Codakia bella (Conrad)	PR	59	0	.17	17.8 ± 3.4	20.3 ± 4.2
	CL	48	.17	.33	16.8 ± 4.5	15.3 ± 2.6
	BI	117	.31	.37	17.6 ± 3.8	17.8 ± 3.8
	PC	48	.21	.46	11.8 ± 2.7	12.0 ± 2.6
	TB	64	.53	.75	—	—
Wallucina sp.	AC	51	.20	.31	13.3 ± 3.8	12.0 ± 1.1
	PC	504	.24	.43	10.1 ± 1.4	10.1 ± 1.1
	TB	110	.33	.55	—	—
Veneridae						
Gafrarium pectinatum (L.)	PR	25	0	0	23.4 ± 5.5	—
	PB	21	.048	.048	23.9 ± 4.8	31
	BI	68	.088	.12	25.8 ± 5.7	31.5 ± 4.2
	AC	26	0	.15	22.6 ± 8.0	16.5
	CL	21	.19	.19	23.7 ± 4.6	17.5
G. tumidum Röding	SB	32	0	0	38.5 ± 11.5	—
Periglypta reticulata (L.)	PB	22	.091	.091	17.8 ± 6.8	20
Timoclea marica (L.)	CL	41	0	.049	17.7 ± 3.8	17
Cardiidae						
Fragum fragum (L.)	TB	76	0	0	25.9 ± 6.4	—
	BI	35	0	0	26.2 ± 8.3	—
	PC	54	0	0	11.3 ± 4.1	—
	AC	79	.023	.023	13.2 ± 5.4	23
	CL	39	.026	.226	18.6 ± 7.0	10
Tellinidae						
Arcopagia robusta (Hanley)	PC	318	0	.013	—	—
	AC	93	.022	.022	12.9 ± 2.0	13
	CL	40	.025	.025	14.8 ± 2.4	12
	TB	152	.013	.026	12.5 ± 1.9	—
Quidnipagus palatam Iredale	PR	57	0	.035	43.1 ± 6.4	45
	AC	213	.019	.056	32.7 ± 6.3	26.1 ± 9.0
	PC	27	0	.074	32.7 ± 7.4	12
	BI	86	.070	.12	36.3 ± 7.6	34.0 ± 9.0
	PB	45	.089	.18	37.5 ± 7.2	38.9 ± 6.9
Scissulina sp.	AC	42	0	.048	16.5 ± 2.7	14
	TB	76	.053	.079	—	—
	PC	91	.022	.13	14.2 ± 1.9	13.3 ± 2.0
	CL	22	.18	.27	25.3 ± 7.5	27.0 ± 6.6

Key:

N	Number of valves
F_E	Frequency of edge drilling
F_{DR}	Frequency of total drilling

Sites:

AC	Alupang Cove, west coast, north of Agana Bay
BI	Bangi Island, Agat, west coast
CL	Cocos Lagoon, southwest part, south end of Guam
GB	Gun Beach, west coast, north of Tumon Bay
PB	Pago Bay, east coast, at University of Guam Marine Laboratory
PC	Piti Channel, near Apra Harbor, west coast
PR	Pago River, east coast
SB	Sasa Bay, part of Apra Harbor, west coast
SH	Shark's Hole, west coast
TB	Tumon Bay, west coast

TABLE 2. Bivalves eaten by *Polinices tumidus* (n = 7) in the laboratory.

Prey species	Number of individuals killed by means of		
	Conventional drilling	Edge-drilling	Questionable means
Codakia bella	2	6	0
Gafrarium pectinatum	0	7	1
Timoclea marica	0	0	4
Arcopagia robusta	0	15	4
Quidnipagus palatam	2	2	6
Total	4	30	15

fragum is rarely drilled. The taxonomic distribution of edge-drilling is similar to that of total drilling frequency.

Within the size range of shells in the samples, drilled valves are not significantly different in size from undrilled valves in any sample (Table 1). ($p > 0.10$ in all cases, T-Test). In general, right valves are as likely to be drilled as left valves; however, there is a significant tendency for left valves to be drilled more often than right valves in *Codakia bella* from Bangi Island, *Wallucina* sp. from Piti Channel, and *Modiolus auriculatus* from Gun Beach ($p < 0.05$, chi-square test).

There is no straightforward relationship between shell traits and susceptibility to drilling in the bivalves from Guam. Previous authors have pointed to strong external sculpture, thick shells, and tight valve closure as traits that should prevent or prolong drilling (Reyment, 1967; Taylor, 1970; Vermeij & Veil, 1978). Robba & Ostinelli (1975), however, found that strongly sculptured bivalves from the Pliocene of Italy had higher frequencies of drilling (mean 0.17) than did smooth or weakly ornamented species (mean 0.055). Hoffman et al. (1974) found no correlation between sculpture and drilling intensity in bivalves from the Upper Miocene of Poland. In the Guam bivalves, low frequencies of drilling are characteristic of two contrasting groups of species: (1) those with tight valve closure (crenulated valve margins, well-developed heterodont hinge), thick shells, and strong sculpture (Cardiidae and Veneridae); and (2) species with relatively weak valve closure (smooth shell margins and less interlocking hinge), weak sculpture, and thin shells (Tellinidae).

Several factors may contribute to the lack of correspondence between shell characters and drilling frequency. Some bivalves (notably the jumping cockle *Fragum fragum*) can probably escape from naticid predators in the same way that they escape from other relatively slow predatory gastropods and asteroids (see Ansell, 1969; Nielsen, 1975; and Vermeij, 1978 for review and examples). Four *Fragum* kept for two weeks with *N. gualteriana* in the laboratory were not eaten. The impact of naticid predation may be seriously underestimated in species such as *Arcopagia robusta* and *Quidnipagus palatam* which can be eaten by naticids without drilling. It is likely that these clams suffocate while being enveloped by the predator's foot before drilling has proceeded very far. In this connection it is interesting that lucinids, which are generally tolerant of anaerobic conditions and can remain tightly closed for long periods (Jackson, 1973), were always drilled when eaten by naticids in the laboratory (11 observations).

Underestimation of predation by naticids may be a common problem in studies of fossils. Turner (1955), for example, noted that *Polinices duplicatus* occasionally consumes razor clams (*Ensis directus* Conrad) by attacking the soft parts through the gaping posterior end of the shell, and that *Ensis* is never drilled in nature. Edwards (1969) showed that the gastropod *Olivella biplicata* Sowerby is often suffocated in the foot of *Polinices* before drilling has ensued. Reliable comparative data on drilling intensity should therefore be obtained from taxa whose modern representatives are known to be tolerant of prolonged valve or opercular closure.

It is also important to point out that drilling may be overestimated from studies based on intact empty valves. Many crustaceans and fishes are known to consume bivalves by crushing the shell (for a review see Vermeij, 1978). Although it is difficult to estimate the importance of this cause of death, thin-shelled tellinids in tropical waters appear to be especially vulnerable to predation by fishes, whereas deeper-burrowing and thicker-shelled lucinids are less susceptible. Among mollusk-eating fishes of the West Indies, for example, 13 species ingest tellinids, 9 eat venerids, and only 5 consume lucinids (compilation from Warmke & Erdman, 1963; Randall, 1967; Randall & Warmke, 1967). Estimates of drilling intensity in fossils are thus most reliable for thicker-shelled species that live deeply buried in the sediment.

With the various sources of error firmly in mind, it is instructive to inquire how the drilling frequencies of bivalves in Guam accord with evidence for geographical and temporal variation in drilling intensity. The current consensus of opinion is that drilling gastropods first appeared during the Albian epoch of the Cretaceous period (Fischer, 1962; Carriker & Yochelson, 1968; Sohl, 1969). Present-day intensities of drilling were reached no later than the Eocene for turritellid gastropods (Dudley & Vermeij, 1978) and Early Miocene for glycymerid bivalves (Thomas, 1976). There is evidence from turritellids that the intensity of drilling is up to three times higher in Recent tropical and subtropical species than in cold-temperate forms (Dudley & Vermeij, 1978). Lucinids from Guam (median frequency 0.40, 8 samples) are significantly more prone to drilling than were warm-temperate lucinids from Upper Miocene deposits in Poland (median drilling frequency 0.21 for 4 samples of greater than 20 valves each; data from Hoffman et al., 1974). However, a sample of *Divaricella* spp. from the Upper Miocene of warm-temperate Bulgaria (frequency 0.75; Kojumdjieva, 1975) shows the same high intensity of drilling as the most perforated lucinid sample from Guam. No significant differences in drilling frequency exist between the venerids of Guam (median frequency 0.065, 8 samples) and those of tropical Eocene Europe and Nigeria (median frequency 0.11, 7 samples) or warm-temperate Late Miocene Poland and Bulgaria (median frequency 0.20, 13 samples; $p > 0.10$ in all cases by Mann-Whitney U-test) (fossil data from Fischer, 1966; Taylor, 1970; Adegoke & Tevesz, 1974; Hoffman et al., 1974; Kojumdjieva, 1974). With the geographical coverage of both Recent and fossil samples as patchy as it is, however, it would be rash to conclude from these comparisons that the intensity of drilling in Recent Indo-West-Pacific bivalves has remained unchanged since Eocene time. Data on bivalves from Panama and Venezuela (Vermeij, unpublished), in fact, reveal much higher frequencies of drilling in venerids than were observed in Guam.

From this comparison and from the data in Table 1, it is evident that the intensity of drilling varies greatly from place to place, on both a local and a larger geographical scale. For example, *Codakia bella* from Tumon Bay suffers more than 4 times as much drilling predation as does the same species in Pago Bay. Variation in predation intensity is likely to be the rule rather than the exception (see also Kojumdjieva, 1974; Dudley & Vermeij, 1978; Menge, 1978a, b), and must be taken into account in the search for geographical and temporal patterns of predation.

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