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International Journal of Malacology

Revista Internacional de Malacologia

Journal International de Malacologie

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### Special INQUA issue of MALACOLOGIA

The Institute of Malacology plans a special issue of MALACOLOGIA on the occasion of the VII International Congress of the International Association for Quaternary Research (INQUA), Boulder and Denver, Colorado, U. S. A., August 30-September 5, 1965. The issue is scheduled to appear in July 1965. Papers devoted primarily to Pleistocene mollusks must be submitted to an appropriate editor by January, 1965, and meet regular standards of the journal.

### INQUA-Heft von MALACOLOGIA

Anlässlich des VII. Internationalen Kongresses der Internationalen Vereinigung für Quaternärforschung (INQUA), der in Boulder und Denver, Colorado, V.S.A., vom 30. August bis 5. September 1965 tagen wird, plant das Malakologische Institut eine Sonderausgabe von MALACOLOGIA, die im Juli 1965 erscheinen soll. Beiträge über Pleistozänmollusken, die den sonstigen Anforderungen der Zeitschrift entsprechen, sind erwünscht, und vor Januar 1965 einem geeigneten Schriftleiter zuzusenden.

### Numéro spécial INQUA de MALACOLOGIA

L'Institut de Malacologie envisage un numéro spécial de MALACOLOGIA à l'occasion du VIIème Congrès International de l'Association Internationale pour les Recherches sur le Quaternaire (INQUA), qui aura lieu à Boulder et Denver, Colorado, É.U.A., du 30 août au 5 septembre 1965. MALACOLOGIA sollicite des contributions dévouées en premier lieu aux mollusques du Pleistocène et conformes au niveau du Journal, qui seront à adresser à un éditeur approprié avant le mois de janvier 1965.

### Número especial INQUA de MALACOLOGIA

El Instituto de Malacología planea para julio de 1965 un número especial de MALACOLOGIA, en conexión con el VII Congreso Internacional de la Asociación Internacional de Investigación del Cuaternario (INQUA), Boulder y Denver, Colorado, EE. UU., 30 agosto - 5 septiembre de 1965. Los artículos, dedicados primariamente a los moluscos del Pleistoceno y ajustados a los padrones de esta revista, deberán ser sometidos a un editor apropiado alrededor de enero de 1965.

### Специальный выпуск МАЛАКОЛОГИИ "ИНКВА"

Институт Малакологии подготавливает специальный выпуск МАЛАКОЛОГИИ к 7-му Международному Конгрессу Международной Ассоциации Четвертичных Исследований (ИНКВА), в городах Болдэр и Дэнвэр штата Колорадо, США, 30-го августа - 5-го сентября, 1965-го года. Этот выпуск предполагается выпустить в июле 1965-го года. Работы, посвященные главным образом моллюскам Плейстоцена и отвечающие требованиям журнала должны быть представлены соответствующему редактору до января 1965-го года.

SUPRASPECIFIC GROUPS IN THE SUBFAMILIES MURICINAE AND TRITONALIINAE  
(GASTROPODA: MURICIDAE)

Emily H. Vokes

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## ABSTRACT

At least 90 supraspecific names have been proposed for groups in the subfamilies Muricinae and Tritonaliinae.<sup>1</sup> This paper is an attempt to assess the validity of these names, and herein, 36 taxa are recognized as representing valid groupings, 56 are placed in synonymy, and many emendations and errors are disposed of. The names accepted as valid, either on the generic or subgeneric level, are: *Murex* s.s., *Haustellum*, *Bolinus*, *Harmatia*, *Chicoreus*, *Siratus*, *Phyllonotus*, *Hexaplex*, *Murexsul*, *Murexiella*, *Maxwellia*, *Pterynotus*, *Naquetia*, *Pterochelus*, *Nothotyphis*, *Poirieria*, *Paziella*, *Panamurex*, and *Muricopsis* in the Muricinae; and *Tritonalia*, *Hadriana*, *Miocenebra*, *Jaton*, *Pterorytis*, *Ceratostoma*, *Pteropurpura*, *Ocinebrellus*, *Calcitrapessa*, *Purpurellus*, *Poropleron*, *Homalocantha*, *Eupleura*, *Vitularia*, *Crassilabrum*, *Urosalpinx*, and *Ocinebrina* in the Tritonaliinae. In addition, 2 specific homonyms are renamed: *Tritonalia inermicosta* (*Murex fasciatus* Sowerby, not Gmelin) and *Tritonalia (Hadriana) craticuloidea* (*Murex craticulatus* Brocchi, not Linnaeus).

## INTRODUCTION

The Tenth Edition of Linnaeus' *Systema Naturae* (1758) listed 59 species of *Murex*, of which only the first 9 are today included in the Muricidae. In the 200 years since the appearance of that work the number of known species has grown to over 2500, although, as in the case of Linnaeus' species, many are no longer referable even to the Muricidae. Of these less than 1000 should be placed in either the Muricinae or the Tritonaliinae, and many of that number probably represent synonyms. At least 90 supraspecific names have been proposed for groups in these 2 subfamilies alone. In this paper, which is an attempt to assess the usefulness of these numerous supraspecific names, 36 groups are recognized as valid, and 56 are placed in synonymy. In addition a number of emendations and errors are disposed of. By no means are all of the known spelling errors included, for to do so would needlessly extend the synonymies. Only those errors are included which, in my subjective opinion, are con-

sidered "important."

Since the time of Linnaeus there has been a trend toward finer and finer division of his genera. Röding, in 1798, assigned the Linnaean species to his genera *Distorsio*, "*Strombus*", *Neptunea*, *Volema*, *Turris*, *Vasum*, *Tritonium*, *Drupa*, *Thais*, *Cymatium*, *Galeodes*, *Cabestana*, *Busycon*, *Cantharus*, *Tudicla*, "*Purpura*", and *Murex*. Unfortunately the work of Röding was largely overlooked until the 20th Century and Lamarck, continuing the work of Bruguière, was generally considered the first to attempt refinement although his subdivisions were essentially the same as those of Röding. Lamarck divided the Linnaean species among the genera *Cerithium*, *Pleurotoma*, *Turbinella*, *Fasciolaria*, *Fusus*, *Pyrula*, *Struthiolaria*, *Ranella*, *Triton*, *Ricinula*, *Purpura*, and *Murex*.

The next worker to propose an extensive classification of the Mollusca was Swainson in his *Treatise on Malacology* (1840). He seems to have been the first to make use of the concept of "subgenera" and, in spite of a preoccupation with what he called "the circle of affinity," his

<sup>1</sup>"Ocinebrinae" of authors.

divisions represent valid groupings. His classification of the Muricidae appeared as follows:

- Family: Muricidae
- Subfamily: Muricinae
- Genus: *Murex*
- Subgenera: *Murex* s.s., *Haustellaria*, *Phyllonotus*, *Muricanthus*, *Pteronotus*
- Genera: *Muricidea*, *Vitularia*, *Triton*, *Ranella*
- Subfamilies: Cassinae, Nassinae, Purpurinae, Buccinae

H. and A. Adams, in the *Genera of Recent Mollusca* (1853-1858), were the next to enlarge this classification. To Swainson's subgenera of *Murex* they added *Rhinocantha*, *Chicoreus*, *Homalocantha*, and *Ocenebra*. They also included in *Murex* Swainson's genera *Vitularia* and *Muricidea*.

In 1880, Jousseume proposed a *Division Méthodique de la Famille des Purpuridés*. In this classification he listed 47 genera which, he said, comprised "les genres *Murex* et *Typhis* des auteurs." Of these 47 genera 33 were new names proposed by Jousseume himself. Although the 1880 work was only a list of genera with their type species, it was actually an abstract of a longer work with generic descriptions which appeared subsequently in the *Revue et Magasin de Zoologie*. The exact date of publication of the longer memoir is not known, but it seems to be 1882. The date printed in the journal is 1879, but clearly it was issued after December, 1880, when the list appeared in *Le Naturaliste*. Jousseume has been condemned by many writers for his superfluity of genera, and it is true that he did propose some unnecessary names, but on the whole his concept of important morphological differences parallels that of the best of modern "splitters."

In the *Manuel de Conchyliologie* (1880-1887), P. Fischer proposed the most complete classification up until his time, a classification providing the pattern for all subsequent workers. Fischer did not use subfamilies but included in the genera *Murex* and "*Ocenebra*" all those groups now placed in the Muricinae and Tri-

tonaliinae respectively. His classification of these two genera appeared thus:

- Genus: *Murex*
- Subgenus: *Murex* s.s.
- Sections: *Murex* s.s., *Acupurpura*, *Haustellum*, *Tubicauda*
- Subgenus: *Bolinus*
- Subgenus: *Pteronotus*
- Sections: *Pteronotus* s.s., *Marchia*, *Triremisis*, *Poropteron*, *Alipurpura*, *Pteropurpura*
- Subgenus: *Chicoreus*
- Sections: *Chicoreus* s.s., *Siratus*, *Euphyllon*, *Inermicosta*, *Naquetia*
- Subgenus: *Muricantha*, emend.
- Sections: *Muricantha* s.s., *Hexaplex*, *Bassia*, *Favartia*, *Poirrieria* [sic], *Paziella*
- Subgenus: *Homalocantha*
- Subgenus: *Muricopsis*
- Genus: *Ocenebra*
- Subgenus: *Ocenebra* s.s.
- Sections: *Ocenebra* s.s., *Crassilabrum*, *Ocenebrina*, *Heteropurpura*
- Subgenus: *Ceratostoma* [including *Ocenebrellus*, *Pterohytis* (sic), and *Jaton* in synonymy]
- Subgenus: *Vitularia*
- Subgenus: *Hadriana*

Cossmann, in the *Essais de Paléoconchologie Comparée* (1903), was the first to recognize the need to separate a subfamily "Ocenebrinae" from the Muricinae, on the basis of the purpuroid operculum, characteristic of *Ocenebra*, as opposed to the muricoid operculum of *Murex*. At the same time he also proposed 3 other subfamilies, the Trophoninae, Typhinae, and Rapaninae, for the remainder of the family Muricidae.

Thiele in the *Handbuch der systematischen Weichtierkunde* (1929-1931) recognized *Tritonalia* as the correct name for *Ocenebra*, and placed *Cerastoma*, *Jatova*, *Ocenebrellus*, and *Poropteron* in that genus. *Favartia* he transferred to the genus *Aspella*. Thiele did not use the subfamilial designation, but treated the genera *Murex* and *Tritonalia* in the manner of Fischer.

The classification of the Muricidae in Wenz's *Handbuch der Paläozoologie* (1941) is essentially an amplification of that of Thiele. Some of the subfamilial groupings are difficult to accept, as the genera

here placed in the Tritonaliinae are located by him in the Drupinae, and the members of the Typhinae and the Trophoninae are included in the Muricinae.

Korobkov (1955) and Orlov *et al.* (1960) have most recently proposed classifications. In both of these a subfamily Tritonaliinae is recognized which is approximately that used by me. Otherwise there is little change from Thiele and Wenz.

I am a self-avowed "lumper" at the generic level. To my way of thinking one of the purposes of taxonomy is to demonstrate relationships, and this is not done by placing each species in a separate "pigeon-hole." Generic groupings should be broad enough to indicate the nearness or farness of related forms, not simply to indicate that one species is somewhat different from a similar species. The latter is achieved at the specific level. The following classification consists of generic and subgeneric names accepted as valid by me with an indication of relationships between groups.

## MURICINAE

- Genus: *Murex*  
*Murex* s.s., *Haustellum*, *Bolinus*,  
*Harmatia*
- Genus: *Chicoreus*  
*Chicoreus* s.s., *Siratus*, *Phyllonotus*
- Genus: *Hexaplex*  
*Hexaplex* s.s., *Murexsul*
- Genus: *Murexiella*  
*Murexiella* s.s., *Maxwellia*
- Genus: *Pterynotus*  
*Pterynotus* s.s., *Naquetia*, *Pterochelus*, *Nothotyphis*
- Genus: *Poirieria*  
*Poirieria* s.s., *Paziella*, *Panamurex*
- Genus: *Muricopsis*

## TRITONALIINAE

- Genus: *Tritonalia*  
*Tritonalia* s.s., *Hadriana*, *Miocenebra*
- Genus: *Jaton*  
*Jaton* s.s., *Pterorytis*, *Ceratostoma*
- Genus: *Pteropurpura*  
*Pteropurpura* s.s., *Ocinebrellus*,  
*Calcitrapessa*, *Purpurellus*, *Porop-  
 teron*
- Genus: *Homalocantha*
- Genus: *Vitularia*  
*Vitularia* s.s., *Crassilabrum*

- Genus: *Eupleura*  
 Genus: *Urosalpinx*  
*Urosalpinx* s.s., *Ocinebrina*

As was mentioned above, the operculum serves to distinguish the Muricinae from the Tritonaliinae. The Muricinae have a so-called "muricoid" operculum with a basal nucleus (Figs. 53-65). The Tritonaliinae have a "purpuroid" operculum with a lateral nucleus (Figs. 97-103). Other groups in the Muricidae have either muricoid or purpuroid opercula, and so the operculum is not an infallible guide to placement. Moreover the opercula of the various species within these subfamilies are slightly variable. In the Muricinae the nucleus, although essentially basal, may be on either the left or right side, or may even be almost central as in *Murex haustellum* (Fig. 55). In the Tritonaliinae the nucleus is always lateral but may vary from anterior to posterior (see Figs. 98 and 103). In general the shell form in the 2 subfamilies is remarkably parallel. A notable difference is the development in most groups of the Tritonaliinae of a completely closed siphonal canal, a trait confined to this subfamily and the Typhinae. In the Muricinae and the Tritonaliinae convergence has taken place to a considerable degree, and most of the species were originally described as "*Murex*." Throughout this paper in order to avoid confusion, all species will be cited by the genus to which they were originally referred. Thus under Tritonaliinae the reader will see the species called "*Murex*" although this is obviously a misnomer.

Of all the criteria for subfamilial differentiation the radula is the most consistent. The family Muricidae is grouped in the suborder Stenoglossa which is characterized by a radula consisting of a central tooth, one pair of cuspidate laterals, and no marginal teeth what so ever. The Muricinae have a central tooth which bears 5 unequal-sized cusps, the middle and outer ones being much larger than the 2 alternate ones (Figs. 39-52). The Tritonaliinae are distinguished by having a central tooth which has 2

or 3 larger cusps in the center, flanked by numerous smaller ones (Figs. 90-96). There may be, in addition, 2 large cusps at the outer extremities of the central tooth. The Trophoninae have a central tooth most like that of the Muricinae, differing in the development of 2 additional cusps at the outer extremity of the tooth. The Typhinae have a central tooth more akin to that of the Tritonaliinae, with 3 larger cusps and between each pair of these 3 smaller cusps. The Rapaninae are distinguished by having a central tooth with only the 3 larger cusps and the intermediate cusps reduced to small nodes, or completely lacking. In all groups the laterals are unicuspidate.

\* \* \* \* \*

#### Phylum MOLLUSCA

##### Class GASTROPODA

##### Subclass PROSOBRANCHIA (or STREPTONEURA)

##### Order NEOGASTROPODA

##### Suborder STENOGLOSSA

##### Superfamily MURICACEA

##### Family MURICIDAE

##### Subfamily MURICINAE

##### *MUREX* sensu stricto (Figs. 1-3, 39-41, 53, 54)

Linnaeus, 1758, *Systema Naturae*, ed. 10, p 746.

TYPE SPECIES: *Murex tribulus* Linn., (as *M. pecten* Montfort), by subs. design., Montfort, 1810.

*PURPURA* Martini, 1777, *Conchylien-Cabinet*, v. 3, p 287. (Martini did not apply the principles of binominal nomenclature and therefore this work was rejected for nomenclatorial purposes in I.C.Z.N. Direction 1, 1954).

Type species: *Purpura hystrix* Martini, by subs. design., Winckworth, 1945 (= *Murex tribulus* Linn.).

*ARANEA* Perry, 1810, *Arcana*, Pl. 47. Not *Aranea* Linn., 1758 (*Arachn.*).

Type species: *Aranea gracilis* Perry, by monotypy. (*Aranea gracilis* Perry, 1810, not *Murex gracilis* Montagu, 1803 = *Aranea trivremis* Perry, 1811 = *Murex pecten* Montfort.)

*TRIBULUS* Kobelt, 1877, *Jb. Dtsch. Malak. Ges.*, v. 4, p 144. Not *Tribulus* H. and A. Adams (ex Klein), 1853 (Moll.).  
Type species: *Murex tribulus* Linn., by tautonymy.

*ACUPURPURA* Jousseau, 1880, *Le Naturaliste*, Année 2 (42), p 335.

Type species: *Murex tenuispina* Lamarck, by orig. design. (= *M. pecten* Montfort).

*TUBICAUDA* Jousseau, 1880, *Le Naturaliste*, Année 2 (42), p 335.

Type species: *Murex brevispina* Lamarck, by orig. design.

"Shell unattached, univalve, with the spire elevated, varixed and armed; mouth rounded; columella smooth; outer lip bordered, sharp, armed with long spines; basal canal tubular, very long and very spinose." (Montfort, 1810, *translated*)

Discussion: "*Murex tribulus* Linnaeus" is usually cited as the type species of *Murex* s.s., by the subsequent designation of Montfort (1810: 619). However, the shell figured by Montfort is that known today as *Murex tenuispina* Lamarck and consequently question arises as to the true type of *Murex*. Linnaeus' *M. tribulus* included 3 different spinose shells, all considered one "species" by him. The first person to restrict the polyspecific *M. tribulus* was Röding (1798: 145) who referred the name to the species figured by Martini (1777), Vol. 3, Figs. 1052-1054 (his reference to Fig. 1051 is evidently a *lapsus*, as the shell figured is a *Distorsio*). Figure 1052 of Martini is the form later named *Murex scolopax* by Dillwyn (1817: 681) and Figs. 1053-1054 are the species later named *Murex tenuispina* by Lamarck, usually considered *M. tribulus* of authors. Perry (1811, Pl. 45, Fig. 2) gives an excellent figure of this species under the name *Aranea tribulus*. The third species included by Linnaeus in his *M. tribulus* was named *Murex histrix* by Röding, a name pre-occupied by *Murex hystrix* Linn. (vide I.C.Z.N. Code, Art. 58-2). This third species was subsequently given a variety of names by different authors, including: *Murex pecten* Montfort, 1810; *Aranea gracilis* Perry, 1810; *Aranea trivremis*

Perry, 1811; *Haustellum nobile* Schumacher, 1817; and *Murex tenuispina* Lamarck, 1822. It is this species which Montfort figured as the type of the genus *Murex*. His figure is of this shell and all of his references are to figures of this species. Montfort was probably unaware of the work of Röding, and he was no doubt restricting the *M. tribulus* of Linnaeus to the form he felt most characteristic of the genus. Unfortunately we are bound by the International Code of Zoological Nomenclature to recognize Montfort's designation of "*Murex tribulus* Linn." as the type of *Murex*, for this is the name included in Linnaeus' original list of species. Since the form named *M. pecten* was a part of the *Murex tribulus* of Linnaeus, although not of subsequent authors, the species today recognized as *M. tribulus* must stand as the type of the genus.

Certainly nothing is changed whether *M. tribulus* or *M. pecten* is considered the type, for they are so closely related that they must be grouped in the same subgenus. It should be noted that Fischer (1884) cited *Acupurpura* Jousseume as a subgenus of *Murex* s.s. This name had been used by Jousseume for the typical spinose murices because he did not wish to use the name "*Murex*" but preferred to adopt the pre-Linnaean name of *Purpura* for the genus *Murex* of Linnaeus. Therefore there is no "*Murex*" in Jousseume's list of genera. Subsequent workers up until the most recent (Orlov, *et al.*, 1960) have faithfully followed Fischer's example, although examination of the 2 species reveals no characteristics which can be said to be distinguishing. The point has been made by many authors that *M. pecten* is distinguishable by the "doubled" row of spines on the anterior canal, a trait which led to such early names as "*Murex tribulus duplicatus*", or "*Tribulus rostratus duplex*." However these same intercalary spines, although greatly reduced, also appear on *M. tribulus* and cannot be accepted as a basis for separation. If there is any basis for subgeneric differentiation it lies in the

nature of the operculum which in both *M. tribulus* and *M. pecten* has the nucleus located near the body wall, whereas in almost all the other Muricinae (including the other members of *Murex* s.s.) it is located toward the periphery. However the nucleus of the typical muricoid opercula varies slightly in position, and so its exact location probably is not of any great significance.

*Murex brevispina* Lamarck, type species of *Tubicauda*, differs from the *M. tribulus* group in the greatly reduced number of spines on the varices. However this characteristic is so exceedingly variable among the members of *Murex* s.s. that it does not seem to be a subgeneric criterion. *M. pecten* represents one extreme variation, *M. brevispina* the opposite one. *M. brevispina* bears a strong resemblance to *M. brandaris*, the type species of *Bolinus*, and presumably represents the intermediate form between *Bolinus* and *Murex* s.s. Because *M. brevispina* lacks the flaring inductura of *Bolinus*, and because it has 3 varices and the apertural tooth of *Murex* s.s., *Tubicauda* is placed in the synonymy of *Murex* s.s. rather than *Bolinus*.

#### HAUSTELLUM

(Figs. 4, 55)

Schumacher, 1817, *Essai Nouv. Syst. Vers. Test.*, p 213 (*ex Klein*).

TYPE SPECIES: *Murex haustellum* Linn., by tautonymy.

BRONTES Montfort, 1810, *Conchyl. Syst.*, v. 2, p 623. Not *Brontes* Fabricius, 1801 (Coleopt.).

Type species: *Murex haustellum* Linn., by orig. design.

BRONTESIA Reichenbach, 1828, *Zoologie*, v. 1, p 91. New name for *Brontes* Montfort (not seen; *fide* Neave).

HAUSTELLUM Deshayes, 1830 (*ex Klein*, "*Haustellum Bruguière*" of authors), *Encycl. Méth. (Vers)*, v. 2, p 188.

HAUSTELLARIA Swainson, 1833, *Zool. Illus.* (2) v. 3, expl. to Pl. 100.

Type species: *Murex erythrostoma* Swainson, by subs. design., Swainson, 1840. (*M. erythrostoma* Swainson, 1840, not *M. erythrostomus* Swainson, 1831 =

*M. haustellum*).

*BRONTIS* Griffith and Pidgeon, 1834, Anim. Kingdom, v. 12, p. 79. Error.

*BRONTA* Pusch, 1837, Polens Paläontologie, p. 130. Error.

"Shell more or less globose, the spire elevated, rarely depressed, with projecting apex. Aperture suborbicular; the beak long or very long, straight, rarely a little curved; the canal open the entire length by a slit; the outer lip crenulated, the inner lip formed of a lamella, almost a half-moon, the margin thickened and detached, but appressed and almost missing posteriorly." (Schumacher, 1817, translated)

Discussion: Although *Haustellum* has been placed by many recent writers in synonymy with *Murex* s.s., the unusual aperture and the operculum, with an almost central nucleus, distinguishes it from that group. MacNeil (1960: 62) has recently observed, "Probably most of the species that have been referred to *Haustellum* have been so referred on the more superficial characters. The sharp, often constricted, anal notch of *Haustellum* is so characteristic, however, it is doubtful that any species without it should be admitted to the genus." *Haustellum* is represented by only a few species other than the type, such as *Murex fallax* E. A. Smith and *M. hirasei* Hirase.

*BOLINUS*

(Figs. 6, 42, 43)

Pusch, 1837, Polens Paläontologie, p. 134.  
TYPE SPECIES: *Murex brandaris* Linn., by orig. design.

*HAUSTELLARIA* "Swainson" Mörch, 1852, Cat. Conchyl. Yoldi, v. 1, p. 98.  
Type species: *Murex brandaris* Linn., by subs. design., Kobelt, 1877.

*RHINOCANTHA* H. and A. Adams, 1853, Genera Recent Moll., v. 1, p. 72.  
Type species: *Murex brandaris* Linn., here designated.

*RHYNOANTHA* Bellardi, 1872, Moll. Terr. Terz., v. 1, p. 49. Error.

*PURPURA* Jousseaume, 1880 (ex Tournefort), Le Naturaliste, Année 2 (42), p. 335. Not *Purpura* Bruguière, 1789 (Moll.).

Type species: *Murex brandaris* Linn., by orig. design.

*MUREX* Bucquoy, Dautzenberg, and Dollfus, 1882, Moll. Mar. Roussillon, v. 1, p. 17. Not *Murex* s.s.

"Type species": "*M. cornutus* et *M. brandaris*" Linn.

*BRANDARIA* "Mörch" Monterosato, 1917, Boll. Soc. Zool. Ital., (3) v. 4, p. 20.  
Error for *Haustellaria* "Swainson" Mörch.  
"Type species": *Murex brandaris* Linn.

"Shell subturreted, whorls rounded, varices 4-10, and even more, all of equal rank, nodose or spinose, or foliate." (Pusch, 1837, translated)

Discussion: This group as originally set forth by Pusch was a motley lot as might be expected from the generic diagnosis given. Nevertheless *Murex brandaris*, the type species, is distinctive and is characterized by the presence of 5 to 7 spinose varices and a flaring inductura on the parietal wall which is unlike that of *Murex* s.s. It does, however, have the elongated siphonal canal of that group and is closely related.

*Rhinocantha* H. and A. Adams as originally proposed included 2 species: *Murex brandaris* and *Murex cornutus*, neither designated as type. In the "Additions and Corrections" which appeared in Vol. 2, the Adams' repudiated their name, stating "for '*Rhinocantha* H. and A. Adams', read '*Haustellaria* Mörch', the name *Haustellaria* of Swainson not being in use." *Haustellaria* Swainson has as type *M. haustellum* Linn., but when Mörch attempted to resurrect and "redefine" the term he included in it only *M. brandaris* and *M. cornutus*, neither being selected as type. Kobelt (1877: 143) subsequently designated *Murex brandaris* as type of *Haustellaria* Mörch, but I have been unable to find any formal designation for the type of *Rhinocantha*. Therefore, *Murex brandaris* is here designated, assuring that it will also be an absolute synonym of *Bolinus*.

*HARMA TIA*

(Fig. 5)

Noszky, 1940, Ann. Hist.-Nat. Mus. Natl.

Hungarici, Min., Geol., and Palaeont.,  
v. 33, p 28.

TYPE SPECIES: *Murex (Harmatia)*  
*stephani* Noszky, by orig. design.

"This new species is represented by a single specimen, but we must consider it as a new subgenus. Although it is of the *Murex* family it can be likened to *Fusus gothicus* Desh. (1-4, LXXIV, 9-10), as described from the French Auversian. However its siphonal canal is strongly prolonged, and bifurcated at the end, with one branch bending. This canal is not smooth as in *Fusus*, but is slightly wrinkled. The 16 mm wide shell which is preserved on the last two whorls (the tip of the spire is destroyed) is much smoother than the shell of *Murex* usually is. The portion above the suture is not steep and angular but bulbous as in *Fasciolaria*, and due to this it unites the characteristics of several forms. At the end of the 40 mm long canal there are wrinkled grooves. On the canal itself one can see several slight grooves, and the branch which is 8 mm long deviates from the main branch at an angle of 40 degrees. Although the branch which continues in a straight line was broken, one can see from the impression it made on the material beneath that it was barely half as long as the other. As regards this dual canal, to a certain extent it can be related to the subgenus *Alipurpura*, although in that case the canal is much shorter. Our specimen is somewhat broken, but in any case it is one of the most interesting representatives of the Kiscellian Clay molluscan fauna." (Noszky, 1940, translated)

**Discussion:** Due to the unusual nature of this subgenus based on a species from the Oligocene of Hungary, I have given a translation of the lengthy original description from the Hungarian. There is nothing that can be added to Noszky's statement, except perhaps to say that the canal represents 2/3 of the length of the shell, the total being 60 mm. The illustration shows no traces of varices, but appears to be completely smooth, a most un-muricoid trait. However the canal certainly looks muricine, and until I have opportunity to examine the type material, the assignment of Noszky will be followed.

CHICOREUS

(Figs. 7-9, 13, 17, 44, 45, 56)

Montfort, 1810, Conchyl. Syst., v. 2, p 611.

TYPE SPECIES: *Murex ramosus* Linn., by orig. design.

TRIPLEX Perry, 1810, Arcana, Pl. 23.

Type species: *Triples foliatus* Perry, by monotypy.

CICHORIUM Voigt, 1834, in Cuvier, Thierreich, v. 3, p 359. Error.

CHICORACEA Griffith and Pidgeon, 1834, Anim. Kingdom, v. 12, p 79. Error.

CHICORAX Pusch, 1837, Polens Paläontologie, p 130. Error.

FRONDOSARIA Schlüter, 1838, Kurz, syst. Verz. Conch., p 20.

Type species: *Frondosaria inflata* (Lamarck), here designated.

CICHOREUS Agassiz, 1846, Nomencl. Zool., p 85. Emendation.

CICHORACEUS Herrmannsen, 1847, Ind. Gen. Malakoz., v. 1, p 234. Emendation.

CICHOREUM Paetel, 1875, Fam. Gatt. Moll., p 43. Error for *Cichorium* Voigt.

EUPHYLLON Jousseau, 1880, Le Naturaliste, Année 2 (42), p 335.

Type species: *Murex monodon* Sowerby, by orig. design. (= "*Purpura*" *cornucervi* Roding.)

PIRTUS de Gregoria, 1885, Boll. Soc. Malac. Ital., v. 10, p 257.

Type species: *Murex (Pirtus) fiatus* de Gregorio, by monotypy (= *Murex dujardini* Tournouër).

TORVAMUREX Iredale, 1936, Rec. Australian Mus., Sydney, v. 19, p 323.

Type species: *Triples denudatus* Perry, by orig. design.

TORRAMUREX Salisbury, 1937, Zool. Rec. (Mollusca), v. 73 (1936), p 88. Error for *Torvamurex*.

FOVEOMUREX Wenz, 1941, Handb. Paläozool., v. 6(1), pt. 5, p 1091. Error for *Torvamurex* Iredale.

TORVOMUREX Vokes, 1963, Tulane Stud. Geol., v. 1(4), p 154. Error.

"Shell unattached, univalve, spire elevated and foliaceous; mouth rounded; columella smooth; outer lip armed, frilled and curly; basal canal broad and covered by a prolongation of the columella." (Montfort, 1810, translated)

**Discussion:** In *Chicoreus*, as in *Murex* s.s., we have the problem of the identity

of the type species. Montfort designated *Murex ramosus* Linn., but his illustration is of the shell now known as *Murex brevifrons* Lamarck. According to Dodge (1957: 88), *Murex ramosus* of Linnaeus included at least the following species: *Murex palmarosae*, *M. inflatus*, *M. axicornis*, *M. adustus*, and *M. brevifrons*, all of Lamarck. In addition there are various other figures in the Linnaean references which are specifically unidentifiable and, to quote Dodge, "the hodge-podge of figures. . . sufficiently establishes that Linnaeus was dealing with a composite species." Montfort clearly was using the name *M. ramosus* in the same composite sense, for although he gives an illustration of *M. brevifrons*, his synonymy includes references to figures of *M. palmarosae*, *inflatus*, *axicornis* and *adustus* of Lamarck, plus *M. monodon* and *M. torrefactus* of Sowerby, and many more, in addition to *M. brevifrons*, so he can scarcely be said to be restricting the name to his figured specimen. In 1798 Röding had used the name "*Purpura*" *ramosus*, but unfortunately gave no references. He did, however, cite another species, "*Purpura*" *incarnata*, with a reference to the Martini figures (1777, III, Figs. 980, 981) of the shell which is now known as *Murex inflatus* Lamarck, based on the same Martini figures. Dodge is of the opinion that Lamarck restricted the name *M. ramosus* to his *Murex inflatus* (which is today so considered) by including the name in his synonymy of that species, and giving other names to the remainder of Linnaeus' references. This was evidently Lamarck's intention for he said of *M. inflatus*, "Linné comprenait avec elle, sous le nom de *M. ramosus*, plusieurs des espèces qui suivent." (1822: 160). Therefore it would seem safe to say that the type of *Chicoreus* is *Murex ramosus* Linn., as restricted by Lamarck to the large Indo-Pacific species figured by Martini (III, Figs. 980, 981), which Lamarck named *Murex inflatus*.

The name *Triplex* was proposed by Perry for another shell of the *Chicoreus*

form. Both were named in 1810. The exact date of issue of the Montfort work is not generally known and for this reason some authors have employed the Perry name for the group. However, Iredale (1915: 457) states that the Montfort work was reviewed in the *Göttinger Anzeiger*, issued May 28, 1810, and thus it certainly precedes the Perry work which did not appear until June.

The monotype of *Triplex* is *Triplex foliatus* Perry, a species better known as *Murex palmarosae* Lamarck. If *Chicoreus* were to be retained in *Murex sensu lato*, then the name would be a junior homonym of *Murex foliatus* Gmelin. Unfortunately this still would not save the familiar *M. palmarosae*, for Perry renamed his species *Triplex rosaria* the following year. Röding used the name "*Purpura*" *rosarium* ("*Murex rosarium* Chemnitz" of authors) in 1798, but for a species referable to *Hexaplex*, so that it could not be said to preoccupy *Triplex rosaria*. Therefore it is unavoidable, unless one wishes to call all of these species "*Murex*," that the name *M. palmarosae* must be replaced by *T. foliatus* Perry.

The name *Chicoreus* has been subjected to considerable "emendation" or misspelling due to Montfort's choice of orthography. The French word for chicory, or endive, is *chicoree*, but the Latin is *cichorium*. Classically-minded emendators felt that Montfort's usage was of the vernacular and hence was to be "latinized." The confusion is heightened by the name *Murex cichoreus* Gmelin. This species, long known as *Murex endivia* Lamarck (truly "vernacular"), is the type of *Hexaplex*, and is not even a member of *Chicoreus*.

*Euphyllon*, *Pirtus*, and *Torvamurex* are placed in the synonymy of *Chicoreus* as it is felt that their type species do not exhibit any characteristics which permit their supraspecific distinction. If *Torvamurex* were to be accepted on the grounds that the varical ornamentation has a tendency toward coalescing into a solid flange, then the older name *Pirtus* should be used as it was based on a similar

species. I prefer to leave both in *Chicoreus* at this time.

*Frondosaria*, erected by Schlüter for all "frondose" species, included in addition to *Chicoreus* forms, *Murex erinaceus* and *Murex trunculus*. No type was indicated, only a list of species given - the first being "*inflata* (Lam.)." No subsequent type designation has been found and therefore *Murex inflatus* Lamarck is here selected as the type of *Frondosaria* Schlüter, assuring its synonymy with *Chicoreus*.

### SIRATUS (Figs. 10, 46)

Jousseume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: "*Purpura Sirat*" Adanson, by orig. design. (= *Murex senegalensis* Gmelin).

"Shell with more or less projecting conical spire, on each whorl three varices winged anteriorly and armed with simple spines or membranaceous extensions, between each [pair of] varices two or more nodes; canal shorter than the height of the spire, broad at the base, slender and bent anteriorly; aperture oval with a small posterior canal." (Jousseume, 1882, translated)

Discussion: This subgenus represents a "link" between *Murex*, *Chicoreus*, and *Pterynotus*. It has the spines of the first, the recurved canal of the second, and the winged varices of the last. Jousseume, in his list of species included in this group (1882: 324), cited several western Atlantic forms usually referred to *Murex* s.s. In a recent paper (1963: 95) I suggested that those species of *Murex* s.s. which have a deflected siphonal canal, and which correspond to Jousseume's species of *Siratus*, are perhaps to be segregated from the true *Murex* s.s. It is possible that these species, including *Murex antillarum* Hinds, *M. ciboney* Clench and Pérez Farfante, *M. motacillus* Gmelin, *M. cailleti* Petit, *M. finlayi* Clench, and others of this type, may more correctly be assigned to *Siratus* in spite of seeming affiliation with *Murex* s.s.

Certain of these species, especially *M. motacillus* and *M. finlayi*, possess characters which place them in an intermediate position between the 2 groups. The species which definitely belong to *Siratus* include *Murex beauii* Fischer and Bernardi, *Chicoreus pliciferoides* Kuroda, *Murex percoides* Löbbecke, and *Murex alabaster* Reeve.

### PHYLLONOTUS (Figs. 14, 47, 48, 57)

Swainson, 1833, Zool. Illustr. (2) v. 3, expl. to Pl. 100.

TYPE SPECIES: *Murex imperialis* var. *a* Swainson, by subs. design., *ibid*, Pl. 109. (*M. imperialis* var. *a* Swainson, 1833 = *M. imperialis* Swainson, 1831, not *M. imperialis* Fischer, 1807 = *M. margaritensis* Abbott)

PHYLLONOTA Conrad, 1847, Proc. Acad. Nat. Sci. Phila., v. 3, p 286. Error.

PHYCONOTUS Simroth, 1907, in Bronn, Klass. Ordn. Tierreichs, v. 3 (2), p 1039. Error.

"Canal moderate; varices foliated, lacinated, compressed, or resembling leaves." (Swainson, 1840)

Discussion: *Phyllonotus* has been synonymized with *Hexaplex* or *Muricanthus* by many writers; however Keen (1960) recently discussed the problem and concludes, as I, that it is truly distinct. The strongly flaring inductura on the parietal wall, the most obvious differentiating characteristic possessed by *Phyllonotus*, was not noted by Keen or apparently by any other person. This unique feature distinguishes the shell of *Phyllonotus* from that of any other group. (*Bolinus* has the same type of structure, but otherwise is almost completely different.) Keen (1959: 3) and Abbott (1958: 62) both observed that *Murex regius* Swainson from the west coast of Mexico closely resembles the type of *Phyllonotus* and suggested that *Phyllonotus* was therefore a synonym of *Hexaplex*. Neither apparently considered the possibility that *M. regius* was correctly to be referred to *Phyllonotus* instead of *Hexaplex*. The pink coloration of the aperture attributed by Keen to the *Hexaplex* groups is, instead,

more characteristic of *Phyllonotus* where it is almost invariably present, while occurring only sporadically in *Hexaplex*, even among specimens of *Murex cichoreus*, the type species.

*Murex brassica* Lamarck<sup>2</sup> and *Murex erythrostomus* Swainson, also from the west coast of Central America similarly belong in *Phyllonotus*. Miocene and Pliocene specimens of *Murex globosus* Emmons from the Atlantic Coastal Plain, usually incorrectly synonymized with *Murex pomum*, are almost indistinguishable from Recent specimens of *M. erythrostomus*. Likewise *Phyllonotus peratus*, Keen's Pacific analog of *M. pomum*, is remarkably close to Florida Pliocene specimens of *M. pomum*, and it is obvious that *Phyllonotus* cannot be restricted to the Atlantic Ocean. The group seems to be descended from species in the Oligocene and Miocene of the Gulf Coast of the United States (*Murex mississippiensis* Conrad, *M. trophoniiformis* Heilprin, etc.) and is restricted to the Western Hemisphere.

The type species of *Phyllonotus* has been the subject of controversy of late. In the past it has most often been dismissed as a synonym of *Murex pomum*. Abbott (1958: 61) suggested, however, that the 2 forms are not synonymous and proposed the new name *Murex margaritensis* for the preoccupied *M. imperialis*. He declared that the two differ in several important characters, such as the number of varices per whorl, the nature of the intervarical nodes, and the overall shape.

<sup>2</sup>The placement of *M. brassica* is somewhat difficult as it possesses characteristics of both *Phyllonotus* and *Hexaplex*. It has the brown and white stripes of *Hexaplex* combined with the pink aperture and flaring (but only slightly) inductura of *Phyllonotus*. In addition, it has an operculum unlike either of these, but more like that of *Murex haustellum*, and a type of closed spine which seems to be unique unto itself. The formation of the varices, with a projecting labrum in front of the spines, characteristic of *Phyllonotus*, but never present in *Hexaplex*, seems to throw the weight of evidence in favor of reference to *Phyllonotus*. It is these "misfits", such as *M. brassica*, which remind us that all supraspecific groups are artificial and have no absolute boundary lines.

Subsequently Clench (1959: 333) reduced *M. margaritensis* to the status of a subspecies of *M. pomum*, saying that the only consistent difference that he could observe was the pink coloration of the aperture. I have examined many specimens of *M. margaritensis* and agree with Abbott that the form is different from typical *M. pomum*. Whether this difference represents more than geographical variation cannot be established at this time. As is the case with many abundant species, *M. pomum* is highly variable. Perhaps *M. margaritensis* should be no more than a subspecies. Regardless of the final decision, the subgeneric characteristics will not change. In fact the possession of the varying number of varices to be found in *M. margaritensis* is more characteristic of the group than the consistent number of 3 which occurs in *M. pomum*.

#### HEXAPLEX

(Figs. 11, 12, 15, 16, 18, 19, 49, 58-60)

Perry, 1810, *Arcana*, expl. to Pl. 23 (genus without species); 1811, *Conchology*, Pl. 8.

TYPE SPECIES: *Hexaplex foliacea* Perry, by subs. design., Iredale, 1915 (= *Murex cichoreus* Gmelin).

PURPURA Röding, 1798, *Museum Bolenianum*, p 139. Not *Purpura Brugière*, 1789 (Moll.).

Type species: *Murex trunculus* Linn., by subs. design., Winckworth, 1945.

POLYPLEX Perry, 1810, *Arcana*, expl. to Pl. 23 (genus without species).

Type species: *Polyplex purpurascens* Perry, by subs. design., Baily, 1960 (= *Murex trunculus* Linn.).

EXAPLEX Férussac, 1820, *J. de Physique*, v. 90, p 284. Error.

CENTRONOTUS Swainson, 1833, *Zool. Illustr.*, (2) v. 3, Pl. 100. Not *Centronotus* Schneider, 1801 (Pisces).

Type species: *Murex (Centronotus) euryostomus* Swainson, by monotypy (= *Murex saxatilis* of authors).

MURICANTHUS Swainson, 1840, *Treatise on Malacology*, p 296. New name for *Centronotus* Swainson.

BASSIA Jousseume, 1880, *Le Naturaliste*, Anné 2 (42), p 335. Not *Bassia*

Quoy and Gaimard, 1830 (Coel.).

Type species: *Murex stainforthi* Reeve, by orig. design.

*MURICANTHA* Fischer, 1884, Man. de Conchyl., p 641. Emendation.

*TRUNCULARIA* Monterosato, 1917, Boll. Soc. Zool. Ital., (3) v. 4, p 20. Not *Truncularia* Wiegmann, 1832 (Bryozoa).

Type species: *Murex trunculus* Linn., by subs. design., Lamy, 1919.

*TRUNCULARIOPSIS* Cossman, 1921, Revue Crit. Paléozool., v. 25, p 79. New name for *Truncularia* Monterosato.

*MURITHAIS* Grant and Gale, 1931, San Diego Soc. Nat. Hist. Mem., v. 1, p 729.

Type species: *Murex trunculus* Linn., by orig. design.

*BASSIELLA* Wenz, 1941, Handb. Paläozool., v. 6 (1), pt. 5, p 1089. New name for *Bassia* Jousseume.

*AARONIA* Verrill, 1950, Minutes Conch. Club S. Calif., No. 103, p 4.

Type species: *Murex (Aaronia) strausi* Verrill, by orig. design.

*MURICANTUS* Korobkov, 1955, Spravochnik i methodicheskoe rukovodstvo, Pl. 70. Error.

"Shell univalve, spiral, divided longitudinally by six folds, from whence its name is derived; these folds are membranaceous and tuberculous, and sometimes spreading out into branched horns; the mouth is round; the beak long, and armed with several calcaria or spurs, in a similar manner to the genus *Triplex*." (Perry, 1811)

**Discussion:** Jousseume (1880: 335) was apparently the first to employ the name *Hexaplex* of Perry, designating the type as "*Murex cichoreus* Gmelin." However, in Perry's original publication of *Hexaplex* the name *cichoreus* does not appear, and thus is not "available" for selection as type, even though one of Perry's figures clearly is meant to represent that species. It was not until 1915 (:471) that Iredale correctly designated *Hexaplex foliacea* Perry as type species of this genus.

Unaware of (or ignoring) the Perry work, Swainson, in 1833, created the subgenus *Centronotus* for a species which he called *Murex eurystomus*, figuring the shell which is generally cited as *Murex*

*saxatilis*. This is however, the *M. saxatilis* of authors, not of Linnaeus, as the identity of Linnaeus' species is in doubt. Dodge (1957: 92) considers it a "*species dubia*", stating that "the *saxatilis* of Lamarck and authors, which is labeled *saxatilis* in most of our collections today, is certainly not the shell Linnaeus described." Most, if not all, of the figures cited by Linnaeus are referable to *Murex cichoreus*. Swainson was aware of this confusion when he named *Murex eurystomus*, saying "We feel some surprise that Lamarck should have viewed this large and imposing *Murex* as one of the varieties of *saxatilis*, from which it is unquestionably distinct." "*Purpura duplex* Röding, 1798, based on the excellent figure of this shell given by Martini (1777, III, Pl. 108, Fig. 1013) probably should be the correct name for the species.

Swainson, in 1840, noting that *Centronotus* was preoccupied, replaced that name with *Muricanthus*, to which he referred only 2 species, *Murex radix* and *Murex melanamathos*. *Murex eurystomus*, the type of *Centronotus*, he placed in *Phyllonotus*. Therefore both Gray (1847) and Herrmannsen (1847) designated *M. radix* Gmelin as the type of *Muricanthus*. Under modern rules of nomenclature *M. eurystomus* should still be considered the type of *Muricanthus*, although *M. radix* is usually cited following Gray and Herrmannsen. There are those who feel that the *M. radix* group represents a subgenus distinct from the typical *Hexaplex* form, and for this reason wish to see *Murex radix* established as the type species of *Muricanthus*. To me the 2 forms are inseparable above the specific rank and such an action is unnecessary. However, it is possible that because *Murex (Centronotus) radix* was also figured by Swainson in the *Zoological Illustrations* (Pl. 113) *Murex eurystomus* should not be considered type of monotypy, and the subsequent designation of Herrmannsen and Gray would then be valid. *Zoological Illustrations* was issued in parts and Plate 111 which first presents *Centronotus* appeared in number 22, while Plate 113

with *M. radix* did not appear until number 25. I have been unable to find any reference to the actual dates of issue of the parts and they may well have been issued simultaneously.

*Murex trunculus*, the type species of several nominal genera, is obviously also a close relative of *Murex cichoreus*, even having the brown and white color stripes which are so conspicuous in that species. A tendency toward this color pattern is very nearly a subgeneric characteristic, as it appears with great frequency among the species of *Hexaplex*, though not universally present. *Murex trunculus* is involved in another problem, created quite unnecessarily by Baily who, in 1960, resurrected the long ignored name *Polyplex* of Perry and designated *Polyplex purpurascens* (= *M. trunculus*) as type species. *Polyplex* was originally proposed in 1810 in the explanation to Plate 23 of Perry's *Arcana*, wherein he stated: "The *Monoplex* has one fold on its body; the *Biplex* two folds; the *Hexaplex* six folds, and so on with the following species, until we arrive at the greatest number, the *Polyplex*, in which the folds are very numerous, but the number not defined." He did not mention any species of *Polyplex* in this work. The following year, however, in the *Conchology*, he gave a plate (Pl. 9) with 5 figures which bore the name *Polyplex*. These 5 figures are poorly executed and portray 5 different genera. No doubt for this reason the name *Polyplex* has never been accepted, and has never appeared in any of the major zoological literature. By definition it would certainly be classified as a *nomen oblitum*, or "forgotten name", and as such should have been assigned to the limbo of the Official Index of Rejected Generic Names in Zoology. Baily chose to designate a type species for this genus in spite of his own admission that no matter which of the figures he selected a currently accepted name would be affected. He therefore designated *Polyplex purpurascens* (= *Murex trunculus* Linn.) because "established usage clearly will be least disturbed" by this selection.

Even though the official rules concerning treatment of *nomina oblita* did not appear in print until 1961 (I.C.Z.N. Code, Art. 23-b), long-forgotten names had been the subject of discussion for many years. At both the Copenhagen (1953) and the London (1958) International Zoological Congresses resolutions were passed which would conserve taxa threatened by the discovery of a previously overlooked older name. (See Copenhagen Decisions, 1953: 25-26, 119-122 and Bull. Zool. Nomencl., 1958, 15: 621-642.) At Copenhagen it was decided that there should be included in the revised *Règles* "a provision limiting the application of the Law of Priority in such a way as to preserve any well-known name which had been in use for a considerable period from being sunk as a junior synonym of some much older name which had not been used more than a small number of times in a specified recent period of considerable length." The Commission was then given the duty of preparing such a provision. It was further advised in the Copenhagen Decisions (:103) that taxonomists should guide themselves, during the period which must elapse before the revised *Règles* would come into force, by the decisions taken by the Congress. Baily's action in 1960 therefore was not only ill-advised but contrary to this advice, and, in my opinion, invalid. If such is technically not the case the matter will be appealed to the International Commission on Zoological Nomenclature with a request that *Polyplex* Perry be declared a *nomen oblitum*.

*Murex stainforthi*, type (and only) species of *Bassiella*, is much like certain color forms of *Murex cichoreus*, and is clearly derived from that line. There is no reason to distinguish this one species from the others of the group. It was separated originally because it has more than the "characteristic" 6 varices of *Hexaplex*. However *Murex cichoreus* may itself have more than 6 varices, the true range being between 5 and 8.

*Aaronia* was based on a single species from the Caribbean. From Verrill's figure and description it would seem to be closely

related to the *Murex radix* group of the west coast of Central America. Although it is of interest to find a species of this type in the Caribbean fauna, it does not warrant the erection of a new subgenus as there is at least one other representative of the group in these waters, *Murex fulvescens* Sowerby.

**MUREXSUL**  
(Figs. 20, 50, 61)

Iredale, 1915, Trans. Proc., New Zealand Institute, v. 47, p 471.

TYPE SPECIES: *Murex octogonus* Quoy and Gaimard, by orig. design.

*MUREXSUL* Habe, 1961, Coloured Illustrations of the Shells of Japan, v. 2, p 49. Error.

"*Murex octogonus* . . . does not match easily with any other species. . . In the British Museum collection it has been placed under *Ocinebra*, but it is obviously out of place, and the radula show the characters of *Hexaplex*. It may, therefore, be so classed, but a subgeneric name should be used to emphasize the peculiarities of this form. I therefore propose "*Murexsul* subgen. nov.," and name *Murex octogonus* Quoy and Gaimard as type." (Iredale, 1915).

Discussion: *Murexsul* least resembles other groups in the Muricinae, especially when the shell is somewhat worn and lacks the delicate fronds. The spire is higher than in other forms but the radula and the operculum indicate placement here rather than in the Tritonaliinae to which it bears a strong resemblance. *Murexsul* also closely resembles *Muricopsis*, but may be distinguished from that group by the strongly denticulated outer lip of the latter.

**MUREXIELLA**  
(Fig. 21, 22)

Clench and Pérez Farfante, 1945, *Johnsonia*, v. 1 (17), p 49.

TYPE SPECIES: *Murex hidalgoi* Crosse, by orig. design.

*MINNIMUREX* Woolacott, 1957, Proc. Roy. Zool. Soc. New South Wales (1955-1956), p 11.

Type species: *Minnimurex phantom*  
Woolacott, by orig. design.

"Shell possessing four to six varices with foliated spines. The spines are connected on each varix by a complex laminated webbing. This webbing is not formed of a single plate of material, but of several layers, the front margins separated and produced more or less horizontally to the vertical back. The forward side of this web appears as a series of layers between the foliated spines. Siphonal canal moderately broad and somewhat extended. Operculum unguiculate, with a subapical nucleus." (Clench and Pérez Farfante, 1945)

Discussion: Although this group superficially resembles *Hexaplex*, it may be distinguished by the regularly oval aperture, lacking any suggestion of an anal notch, as well as by the presence of the complex webbing between the varical spines. Some species of *Homalocantha* have a comparable type of webbing, but this represents convergence rather than close relationship.

*Murexiella* seems to have originated in North America, beginning in the Eocene with the species *Murex mantelli* Conrad. It continues through the Miocene with *Murex macgintyi facetus* Vokes, a subspecies of the Pliocene and Recent form *Murex macgintyi* M. Smith. In addition to the Caribbean representatives, at least one West coast species, *Murex humilis* Broderip, should be placed in this group. *Murexiella* also occurs in the Pliocene of Europe with the species *Murex absonus* Jan, and especially *Murex plioaspirata* Sacco, which is almost indistinguishable from *Murex macgintyi*.

In 1957 Woolacott proposed the genus *Minnimurex* for a new species of Australian Muricidae. The type species, *Minnimurex phantom*, closely resembles the species of *Murexiella*, especially *M. macgintyi* and *M. humilis*, and there seems to be little basis other than geographical separation for this new name. There is an unnamed species in the Pleistocene of Florida which is scarcely distinguishable from the illustration of Woolacott's

species.

*MAXWELLIA*  
(Figs. 23, 62)

Baily, 1950, *Nautilus*, v. 64, p 11.

TYPE SPECIES: *Murex gemma* Sowerby,  
by orig. design.

"Shell solidly built, with an elongated canal that is nearly closed, but at no point of which is the closure quite complete. Body whorl with approximately six varices, whose breadth exceeds that of the spaces alternating with them, as well as the elevation of the varices themselves. Varices extending across the suture to the periphery of the adjoining volution, resembling architectural buttresses. Suture rather deep, and divided by the varices into a series of pits which are the most distinctive feature of the shell. No sutural tubes as in *Typhis* and no expanded digitations of the outer lip as in *Homalocantha*. Operculum with marginal [i.e. basal] nucleus." (Baily, 1950)

Discussion: In addition to the type there is apparently only one other species referable to *Maxwellia*, which nevertheless seems to represent a valid subgroup. It is most closely related to *Murexiella*, as the type species seems to be an offshoot of the typical *Murexiella* in which the webbing of the varices has become fused into a solid, greatly thickened ridge of shell material. The second species of the group, *Murex santarosana* Dall, demonstrates this relationship more clearly than does *Murex gemma*.

*PTERYNOTUS*  
(Figs. 24-27, 51, 63)

Swainson, 1833, *Zool. Illus.*, (2) v. 3, expl. to Plate 100.

TYPE SPECIES: *Murex pinnatus* Swainson, by subs. design., *ibid.*, pl. 122.

*PTERONOTUS* Swainson, 1833, *Zool. Illus.*, (2) v. 3, Pl. 122. Not *Pteronotus* Rafinesque, 1815 (Mamm.).

*MARCHIA* Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.

Type species: *Murex clavus* Kiener,  
by orig. design. (*M. clavus* Kiener,

1843, not *M. clava* Gmelin, 1791, nor *M. clavus* Michelotti, 1841 = *M. elongatus* Lightfoot).

*TIMBELLUS* de Gregorio, 1885, *Boll. Soc. Malac. Ital.*, v. 10, p 275.

Type species: *Murex latifolius* Bellardi, here designated.

*MORCHIA* Baker, 1891, *Proc. Rochester Acad. Sci.*, v. 1, p 159. Error.

*TRIPLEX* "Humphrey" Newton, 1891, *Edwards Coll. Eocene and Oligocene Moll.*, p x, 297. To "replace" *Pteronotus* Swainson.

*PTERYMUREX* Rovereto, 1899, *Atti Soc. Ligustica*, v. 10, p 105. New name for *Pteronotus* Swainson.

*SUBPTERYNOTUS* Olsson and Harbison, 1953, *Acad. Nat. Sci. Phila.*, *Monogr.* 8, p 246.

Type species: *Murex textilis* Gabb, by orig. design.

*PTERYNOTIS* Emerson, 1960, *Amer. Mus. Novitates*, No. 2009, p 4. Error.

"Varices three, compressed, fin-shaped; canal moderate, generally closed by the union of the two lips at their base." (Swainson, 1840)

Discussion: *Pterynotus* has been variously misspelled and renamed because of the confusion in Swainson's original spellings. The name first appeared as *Pterynotus* in the text to plate 100 of his *Zoological Illustrations* (series 2) in a synopsis of the Muricidae, and later in the text to Plate 109. However, on Plate 122, when first used for a species, it was spelled *Pteronotus*, and as such was used by Swainson in the *Treatise on Malacology* (1840). As this latter spelling was preoccupied, various substitute names have been proposed by authors unaware of the valid original spelling.

In addition to the names intended to replace *Pteronotus*, there have been a number of names proposed which are based on species too closely related to *Murex pinnatus* to be supraspecifically differentiated. *Murex elongatus* Lightfoot<sup>3</sup> (*M. clavus* Kiener, not Gmelin, nor Michelotti) is certainly of the same group

<sup>3</sup>This species, named in the Portland Catalogue, has been attributed to Solander, however Dance (1962: 31) has recently shown that the correct author is Dr. John Lightfoot.

as *M. pinnatus*, as is *Murex latifolius* Bellardi. This latter species is very close to *M. tristichus* Dall, a delicate deep-water form from the Gulf of Mexico. (The name *Murex tristichus* of Dall, 1889, is preoccupied by *Murex tristichus* of Beyrich, 1854. However, I strongly suspect that the Dall species is synonymous with *Murex phaneus* Dall, also from the western Atlantic, and therefore it is deemed advisable not to rename this homonym pending further study.) De Gregorio did not designate a type species for the subgenus *Timbellus*, stating that he was proposing the name for that section of the Muricidae of the "tipo del *M. latifolius* Bell. e *latilabris* Bell. Mich-tti." Sacco (1904: 18) placed the name in synonymy with *Pteropurpura*, *Pteronotus* and *Pteryomurex* and did not designate a type. Therefore, *Murex latifolius* Bellardi is here designated as the type species of *Timbellus* de Gregorio.

*Subpterynotus* was based on a fossil species remarkable for the extreme length of the siphonal canal. The original description states that the new subgenus differs from *Pterynotus* "in having a perfectly straight anterior canal. . . . The former tip of the anterior canal is closely appressed to the main one and is not seen or noticed except on close scrutiny." This is the case in most specimens, but perfect specimens reveal that the distal end of the canal is recurved as in the species of *Pterynotus*, with the former canals in evidence on the side. These delicate appurtenances are usually broken off in the fossil state. This peculiar species persisted from the middle Miocene through the Pliocene in the Caribbean area and a similar species, *Murex graniferus* Michelotti, occurs in the Pliocene of Italy, but neither appears to have left any descendants.

The *Pterynotus* group is among the most ancient of the Muricinae, being first represented in the Paleocene of Alabama by the species *Murex matthewsensis* Aldrich. The only other known American Paleocene species of Muricinae is *Murex morulus* Conrad, exceedingly like *M.*

*matthewsensis* but bearing 6 varices. Presumably these oldest forms share a common ancestor, but it is not known whether that ancestral type possessed 3 or 6 varices.

The radula of *Murex pinnatus*, the type species of *Pterynotus*, is somewhat different from that of the normal Muricinae. It has lost the 2 smaller intermediate cusps of the central tooth (see Fig. 51). This appears to be a degenerate condition and may reflect feeding habits.

#### NAQUETIA (Figs. 28, 29, 64)

Jousseume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: *Murex triquetel* Born, by orig. design.

TRIPLEX "Humphrey" Harris, 1897, Moll. Brit. Mus., p 172.

"Type species": *Triples flexuosa* Perry, (= *M. triquetel* Born).

RHIZOPHORIMUREX Oyama, 1950, Geol. Surv. Japan, Rept. 132, p 10.

Type species: *Murex capuchinus* Lamarck (sic), by orig. design. (*M. capucinus* Lamarck 1822, not "*Purpura*" *capucina* Röding, 1798 = *M. permaestus* Hedley).

"Shell with elongated conical spire, whorls with three varices winged anteriorly, with two or three projecting nodes between the varices; canal in general short and broad at the base; aperture oval with a narrow posterior canal." (Jousseume, 1882. translated)

Discussion: This group differs from the typical winged *Pterynotus* in having flanges only on the anterior portion of the varices and in having a broad, short canal, as noted by Jousseume. *Murex capucinus* Lamarck, type of *Rhizophorimurex*, is a variable species and frequently displays no flanges whatsoever. However many specimens have well developed caudal flanges indicating their placement here. If "*Purpura*" *capucina* Röding (probably = *Murex adustus* Lamarck) is placed in *Murex* sensu lato, then it pre-occupies *M. capucinus* Lamarck, in which case *M. permaestus* Hedley is the next available name. Hedley (1914: 745) pro-

posed *M. permaestus* for "*M. capucinus*" of authors, because he had found upon examining the type of Lamarck's species in the Geneva Museum that it was a "large, massive, dark red shell, four and three-quarter inches long," and was probably related to *Murex torrefactus*. Lamarck, however, in his description cited Chemnitz figures (XI, Pl. 192, Figs. 1849, 1850) which represent "*Murex capucinus*" of authors, and we are faced with the problem of whether the subsequent discovery of a "type" specimen should take precedence over an author's original reference. Under these circumstances it is perhaps better to consider the name *M. capucinus* of Lamarck as being preoccupied and accept *M. permaestus* as the correct name for "*Murex capucinus*" of authors.

The name *Triplex* of Humphrey, as used by Perry in 1811, was revived by Harris for the *Pterynotus* group, to replace the preoccupied name *Pteronotus*. However he selected as "genotype" *Triplex flexuosa* (Perry's Pl. 7, Fig. 1), a figure which represents *Murex triqueter* Born, making his *Triplex* synonymous with *Naquetia*. Moreover his type designation was not valid for the name *Triplex* had been used by Perry in 1810, with *Triplex foliatus* type by monotypy, making it a synonym of *Chicoreus* Montfort.

### PTEROCHELUS

(Fig. 33)

Jousseume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: *Murex acanthopterus* Lamarck, by orig. design.

ALIPURPURA "Bayle MS" Fischer, 1884, Man. de Conchyl., p 641.

Type species: *Murex acanthopterus* Lamarck, by orig. design.

"Shell with very long conical spire, whorls depressed near the suture and armed with three lamellar varices; aperture irregularly triangular, lacking posterior canal, columellar margin appressed almost the entire length; canal wide and rather long." (Jousseume, 1882, translated)

Discussion: *Murex acanthopterus* dif-

fers from the typical *Pterynotus* in having an open spine at the shoulder, surrounded by the wing-like varix. This spine may be almost closed (approaching the closed tube of *Typhis*) but there always remains an open slit on the apertural side. The type species has this distinguishing feature much less developed than many others of the group. In fact if *M. acanthopterus* were the only included species there would be little reason to separate *Pterochelus* from *Pterynotus*. However such a separation is warranted by the existence of other species in the group such as *Murex angasi* (Crosse). A very extreme form in this line, in which the spine is completely closed, has been named *Nothotyphis* by Fleming.

The name *Pterochelus* was used by Oken in 1815 in a work which has been declared unavailable for nomenclatorial purposes (I.C.Z.N. Opinion 417, 1956) and therefore does not preoccupy *Pterochelus* Jousseume. It is possible that Oken validated the name subsequently, in which case *Alipurpura* is available.

### NOTHOTYPHIS

(Fig. 34)

Fleming, 1962, Trans. Roy. Soc. New Zealand Zool., v. 2 (14), p 116.

TYPE SPECIES: *Pterynotus (Nothotyphis) norfolkensis* Fleming, by orig. design.

"Small solid *Pterynotus* with closed siphonal and adapical canals, sculptured by broad rounded spiral cords on which are superposed fine intersecting spiral and radial threads, resulting in a trellised microtexture. Siphonal canal short. Protoconch paucispiral with bulbous nucleus." (Fleming, 1962)

Discussion: Fleming proposed this new subgenus of *Pterynotus* to distinguish those few species in which the adapical canal is completely closed in a manner resembling the genus *Typhis*. This resemblance is superficial for the tube formed is varical in origin in *Nothotyphis*, while in the Typhinae it is formed behind the varix. In *Tripterotyphis*, as noted by Fleming, the tube becomes enrolled in the varix and appear to be varical in origin,

thus simulating *Nothotyphis*.

According to Fleming the siphonal canal of *Pterynotus (Nothotyphis) norfolkensis* is completely closed in the adult, although open in the immature stage. If this is true then it is probable that *Nothotyphis* should be referred to the Typhinae, as the completely closed canal is typical of that group, but not of the Muricinae. It is not impossible, however, that this is also a case of convergence, paralleling the closed adapical canal.

### POIRIERIA

(Fig. 35)

Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.

TYPE SPECIES: *Murex zelandicus* Quoy and Gaimard, by orig. design.

POIRRIERIA Fischer, 1884, *Man. de Conchyl.*, p 641. Error.

"Swollen fusiform shell with elevated conical spire, whorls with five varices armed with long subulate and canaliculate spines; aperture rounded with wide and appressed columellar margins; canal rather long, narrow and curved." (Jousseume, 1882, *translated*)

Discussion: Although *Poirieria* and *Paziella* have been placed in synonymy by many authors it is felt that the 2 groups are distinguishable. There is considerable morphological similarity; however, the Caribbean *Paziella* species close the varical spines thereby forming a distinct labrum bearing conspicuous denticles within the aperture, but the neozelanic *Poirieria* forms never close the spines and lack this labrum. Specimens of *Murex pazi*, type of *Paziella*, may be seen with the spines still open, but this represents incomplete development.

Both *Paziella* and *Poirieria* have fossil records in their respective provinces dating back to the Miocene. Moreover, they bear a strong resemblance to certain Eocene species such as *Murex vanuxemi*. Conrad of the Gulf Coast of the United

States and *Murex calcitrapa* Lamarck<sup>4</sup> of the Paris Basin, so their geologic history may be even more ancient. Apparently they represent 2 successful and closely related stocks which have had little reason to change in spite of long separation.

### PAZIELLA

(Figs. 30, 31 36, 65)

Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.

TYPE SPECIES: *Murex pazi* Crosse, by orig. design.

BATHYMUREX Clench and Pérez Farfante, 1945, *Johnsonia*, v. 1 (17), p 41.

Type species: *Murex (Bathymurex) atlantis* Clench and Pérez Farfante, by orig. design.

DALLIMUREX Rehder, 1946, *Nautilus*, v. 59, p 142.

Type species: *Murex nuttingi* Dall, by orig. design.

"Fusiform shell with elevated conical spire, whorls slightly depressed at the suture, with seven spinose varices, the posterior spine very long and canaliculate; aperture nearly round with appressed columellar margin, and straight lip internally striated; canal recurved anteriorly and encircled with long spines near the base." (Jousseume, 1882, *translated*)

Discussion: The reasons for accepting *Paziella* as a group distinct from *Poirieria* have been discussed above. However, there are 2 other taxa, proposed for species from the Caribbean, which must be placed in the synonymy of *Paziella*. *Bathymurex* was established for a species which is undoubtedly of the *Paziella* group, even though it lacks the row of spines encircling the base. Kira (1962: 65) places *Bathymurex* in the genus *Trophonopsis* as the subgenus for the 2 Dall species *T. echinus* and *T. gorgon*. I am of the opinion that the 2 species in question

<sup>4</sup>*Murex calcitrapa* Lamarck, 1803, not *M. calcitrapa* Lamarck, 1822, a Recent species. In 1822 Lamarck invalidly renamed the Eocene species *M. calcitrapoides*, a name by which it is frequently cited.

are more correctly to be referred to *Poirieria* than to *Trophonopsis*. These 2 Japanese species, however, close the spines in a manner similar to *Paziella*, and perhaps should be referred to that group in spite of geography.

Study of a series of specimens reveals that *Murex nuttingi*, type of *Dallimurex*, cannot be distinguished other than specifically from *Murex pazi*. *Dallimurex* was erected by Rehder to include certain species from the lower Miocene Alum Bluff Group, subsequently described by Gardner (1947). However his selection of the dissimilar *M. nuttingi* as type species precluded their placement here, and Gardner's Miocene species were later placed in *Panamurex*, proposed by Woodring (1959) for a Panamanian Miocene species.

#### PANAMUREX

(Fig. 32)

Woodring, 1959, U. S. Geol. Surv. Prof. Paper 306-B, p 217.

TYPE SPECIES: *Murex gatenensis* Brown and Pilsbry, by orig. design.

"Of medium size, strongly shouldered. Axial sculpture consisting of sharp-edged varices, which bear a short, slender, erect spine on spiral cord at shoulder. Spiral sculpture strong, consisting of cords and threads. Interior of outer lip bearing strong elongate denticles or ridges. Siphonal canal moderately long, bent backward. Basal part of inner lip bearing three to five elongate denticles." (Woodring, 1959)

**Discussion:** This fossil group known from the Tertiary of the Gulf Coast of the United States and Panama may be distinguished from *Paziella* by the much stronger spiral sculpture and by the presence of the denticles on the basal part of the inner lip (both groups have a denticulated outer lip). In addition the type species bears a projecting tooth on the anterior portion of the outer lip, but this is not found in all members of the group. Although the type is from Panama, as the name implies, the form seems to be derived from Oligocene forms from

Mississippi: *Murex simplex* Aldrich, which occurs in the middle Oligocene, and *Murex simplex* var. *aspinosus* Meyer, from the lower Oligocene. The Florida Miocene species, for which Rehder originally intended the name *Dallimurex*, are: *Paziella lychnia* and *P. fusinoides* Gardner, and *Muricopsis laccapoia* Gardner, all of the Chipola Formation. In addition there are also "*Muricidea*" *alaquaensis* and "*M.*" *clarksvillensis* Mansfield from the upper Miocene Choctawhatchee Formation of Florida, and *Murex gilletteorum* Vokes from the lower Miocene Silverdale beds of North Carolina.

As I stated earlier, *Paziella* and *Poirieria* seem to be descended from certain Eocene species, and these may also be ancestral to the *Murex simplex* type. Since the Miocene fauna included *Paziella*-like species, *Panamurex* does not seem to be directly in the evolutionary sequence, but apparently represents a parallel development. The Miocene species of *Paziella* include: *Trophon dominicensis* Gabb from the Gurabo Formation, Dominican Republic (and its synonym *Murex werneri* Toula from Tehuantepec, Mexico), and *Murex collatus* Guppy from the Bowden Formation of Jamaica.

#### MURICOPSIS

(Figs. 37, 38, 52)

Bucquoy, Dautzenberg, and Dollfus, 1882, Moll. Mar. Roussillon, v. 1, p 19.

TYPE SPECIES: *Murex blainvillei* Payraudeau, by orig. design.

**MURICIDEA** "Swainson" of authors, not of Swainson.

"Type species": *Murex hexagonus* Lamarck (*M. hexagonus* Lamarck, 1822, not *M. hexagonus* Gmelin, 1791 = *M. oxytata* Maxwell Smith).

**JANIA** "Bellardi" Cossmann, 1882, Cat. Ill. Coq. Foss., Suppl., p 68. Not *Jania* Bellardi.

"Shell elongated, subfusiform, ornamented with longitudinal folds or varices and elevated decurrent cords, bearing subcanaliculate spines or nodose tubercles. Aperture oval, terminated at the base by an open canal of moderate length. Lip thickened and denticulated in the interior.

Coloration ordinarily fawn. Operculum horny, concentric, subapical." (Bucquoy, *et al.*, 1882, translated)

Discussion: In his *Treatise on Malacology* (1840) Swainson proposed a new genus, *Muricidea*, which he indicated as having the progressive growth of the shell marked by longitudinal ridges. He clearly stated, "The type of *Muricidea* is the harp-like *Murex magellanicus*" (:65), thus creating a synonym of *Trophon* Montfort, the type species of which is also *M. magellanicus*. In his list of species in *Muricidea*, Swainson cited *Murex hexagonus* Lamarck along with several non-muricid species. Mörch (1852:95) later used the name with an indication that he was "redefining" it, for *Murex hexagonus* and *Murex blainvillei* only. Jousseume, in the *Division Méthodique* (1880: 335), cited "*Muricidea* Swainson" giving as the type *Murex hexagonus* Lamarck, and the error became entrenched in the literature. Bucquoy, Dautzenberg, and Dollfus, recognizing the need for a subgenus to include shells of the *hexagonus-blainvillei* type, created *Muricopsis*, naming *Murex blainvillei* as the type species. In spite of the proposal of this valid genus for species of this type, use of the name "*Muricidea*" has persisted until recently. The shells of *Muricopsis* are not unlike those of the Australian *Murexsul* group. They may be distinguished by the extreme development of the denticles on the outer lip of *Muricopsis*.

Subfamily TRITONALINAE

TRITONALIA

(Figs. 66-68, 90, 97)

Fleming, 1828, *History British Animals*, p 564 (index) and corrigenda.  
 TYPE SPECIES: *Murex erinaceus* Linn., by subs. design., Gray, 1847.

OCENEBRA "Leach MS" Gray, 1847 (? Oct.), *Ann. Mag. Nat. Hist.*, v. 20, p 269; 1847 (Nov.), *Zool. Soc. London, Proc.*, p 133.

Type species: *Murex erinaceus* Linn., by

monotypy (? Oct.): or orig. design. (Nov.).

OCINEBRA "Leach MS" Gray, 1852, *Syn. Moll. Gt. Brit.*, p 117. Error.

INERMICOSTA Jousseume, 1880, *Le Naturaliste, Année 2* (42), p 335.

Type species: *Murex fasciatus* "Sowerby," by orig. design. (*M. fasciatus* Sowerby, 1841, not *M. fasciatus* Gmelin, 1791 = *Tritonalia inermicosta*, nom. nov.).

HETEROPURPURA Jousseume, 1880, *Le Naturaliste, Année 2* (42), p 335.

Type species: *Murex polymorphus* Brocchi, by orig. design.

OCENEBRA Hörnes and Auinger, 1885, *Die Gastropoden der Meeres-Ablagerung der Ersten und Zweiten Miocänen Mediterranstufe*, p 216. Error.

"Ovate, oblong, canal produced, sub-ascending, or bent to the left; ribs alternate or remote, not continuous on the whorls." (Fleming, 1828)

Discussion: The status of the name *Tritonalia* has been uncertain due to the peculiar nature of its proposal. Fleming, on p 356 of his *British Animals*, cited the genus *Triton* and listed below it *Murex erinaceus* and 8 "extinct species" referable to various genera. As he had already used the name *Triton* (presumably Laurenti, 1768, not Linnaeus, 1758) on p 157 for a group of salamanders, he changed the second *Triton* in the corrigenda to read *Tritonalia*. It has been suggested by many authors (e.g. Winckworth, 1934) that *Tritonalia* is therefore a new name for *Triton* Montfort, 1810, now known as *Charonia* Gistel, 1847. While species of *Charonia* could well be included in the group defined by Fleming's generalized description, nowhere does Fleming mention Montfort's name, and not one of the species which he places in this genus is actually referable to *Charonia*. Thus, whatever Fleming's intentions were, we can only conclude that *Tritonalia* was a new name for *Triton* Fleming and no one else. Gray (1847: 133) accepted it as such, placing it not in the synonymy of *Triton* Montfort, but of *Ocenebra* "Leach MS" with the type, *Murex erinaceus* Linn. Gray dated the Leach manuscript as 1818, and thus gave it priority over Fleming,

1828. The modern rules of nomenclature, however, would date *Ocenebra* from Gray's usage in 1847, so *Tritonalia* is the older name.<sup>5</sup> To add to the general confusion, Gray later published the name as "*Ocinebra*" and subsequent authors have vacillated between the 2 spellings.

*Inermicosta* was based on *Murex fasciatus* "Sowerby" by Jousseau, but Sowerby cited the species as "*Murex fasciatus* Risso?" Whether the specific name be attributed to Risso, 1826, or to Sowerby, 1841, it is nevertheless preoccupied by *Murex fasciatus* Gmelin, 1791, and consequently a new name is necessary. Therefore I here propose:

#### TRITONALIA INERMICOSTA nom. nov.

*Murex fasciatus* "Risso?" Sowerby, 1841, Conchol. Illustr., *Murex*, Pl. 192, Fig. 86.

Not *Murex fasciatus* Gmelin, 1791, Systema Naturae, ed. 13, v. 1, pt. 6, p 3528.

This species is exceedingly like *Murex erinaceus*, and clearly represents the same group. There is no valid basis for subgeneric separation. Likewise, *Murex polymorphus* Brocchi, type of *Heteropurpura*, cannot be subgenerically distinguished from typical *Tritonalia*. Cossmann (1903: 37) placed *Heteropurpura* in synonymy with *Ocenebra*, stating that *Murex polymorphus* differs from *Murex erinaceus* only by specific characteristics and that it is impossible to perceive any sectional differences.

<sup>5</sup>As both names appear almost equally in the literature this problem should be referred to the I. C. Z. N. for a final ruling. Bradley and Palmer (1963) have requested that the Commission place *Tritonalia* on the Official List of Generic Names in Zoology. However they did not submit a petition presenting the facts of the case, but only a letter to the Commission, basically on a completely different subject. By the time this paper appears in print a true petition by Myra Keen will be before the Commission. It is probable that the name *Ocenebra* will ultimately be given official sanction but until that time I shall use the nomenclatorially correct name *Tritonalia*.

#### HADRIANIA (Figs. 69, 91)

Bucquoy, Dautzenberg, and Dollfus, 1882, Moll. Mar. Roussillon, v. 1, p 33.

TYPE SPECIES: *Murex craticulatus* Brocchi, by orig. design. (*M. craticulatus* "L." Brocchi, not of Linnaeus, = *Tritonalia* (*Hadriania*) *craticuloides*, nom. nov.)

*HADRINA* Tryon, 1883, Struct. Syst. Conch., v. 2, p 127 (Error, *vide* Neave, not seen).

*ADRIANA* Cossmann, 1903, Essais Paléo. Comp., v. 5, p 45, "Suggested" emendation.

"Shell fusiform, with pointed conical spire. Whorls angular in the upper portion, ornamented by rather numerous, rounded, varicose longitudinal ribs, and rugose decurrent striae. Last whorl very convex. Aperture oval, terminated at the base by a rather long, stout canal, slightly twisted and closed anteriorly. Labium subsalient, angular at the apex. Color grayish or fawn, aperture whitish." (Bucquoy, *et al.*, 1882, translated)

Discussion: *Hadriania* was erected by Bucquoy, Dautzenberg and Dollfus for those shells which bear the characteristics of both *Murex* and "*Fusus*". The muricoid characters they cite are the closed canal and the varix-like longitudinal ribs; the fusoid characteristics are the general form and the salient labium. The closed canal, the purpuroid operculum, and the radula suggest close affiliation with the genus *Tritonalia* and the group is placed herein.

*Murex craticulatus* "L." of Brocchi is not the *Murex craticulatus* of Linnaeus; consequently it was renamed *Murex brocchii* by Monterosato in 1875. Unfortunately that name is preoccupied by *Murex "brocchii"* Cantraine, 1835, and another is still necessary. Therefore I here propose:

#### TRITONALIA (HADRIANIA) CRATICULOIDES nom. nov.

*Murex craticulatus* "L." Brocchi, 1814, Conch. Subap., v. 2, p 406, Pl. 7, Fig. 14.

Not *Murex craticulatus* Linnaeus, 1758,  
Systema Naturae, ed. 10, p 755.

### MIOCENEBRA

(Fig. 70)

E. H. Vokes, 1963, Tulane Stud. Geology,  
v. 1 (4), p 162.

TYPE SPECIES: *Tritonalia (Miocenebra)*  
*silverdalense* E. H. Vokes, by orig. design.

"Shell greatly elongated, spire much elevated, constricted above the shoulder with an appressed suture. Formation of the varices irregular, with one always present at the aperture, although the others may be reduced to strong nodes. Aperture oval, margin complete, outer lip slightly crenulated. Canal elongated and completely closed over to form a tubular structure." (Vokes, 1963)

Discussion: *Miocenebra* is based on a lower Miocene species from North Carolina. The closed siphonal canal and irregular formation of varices suggests that its closest relatives are the members of *Tritonalia* s.s. This subgenus is not unlike *Hadriania*, differing primarily in the presence of varices which are not found in that group. It may represent the intermediate form between *Tritonalia* s.s. and *Hadriania*. There is at least one living species, *Murex wakasanus* Nomura and Ninno (? = *Trophon fimbriatulus* A. Adams), off the coast of Japan.

### JATON

(Fig. 71)

Pusch, 1837, Polens Paläontologie, p 135.

TYPE SPECIES: *Murex decussatus*  
"Linn.," by orig. design.

JATON Gray, 1847, Proc. Zool. Soc.  
London, p 133. Emendation.

JATOVA Jousseume, 1880, Le  
Naturaliste, Année 2 (42), p 335.

Type species: "*Purpura jaton*" Adanson,  
by orig. design.

"Shell oblong, subturreted, five distinct whorls, deeply canaliculate above, three or four transverse plications, plicae (or costae) wide, smooth, rounded, separated by deep, slightly striated grooves; aperture oval, labrum with three or four plications, canal short, scarcely re-

curved." (Pusch, 1837, translated)

Discussion: The species figured by Adanson (1757, Pl. 9, Fig. 21) as "Le Jatou" has been burdened with more than the usual number of superfluous names. The oldest name seems to be that given by Gmelin, who in the references for his species *Murex decussatus* (1791: 3527) cited first the figure of "*Jaton*" (*sic*) Adanson, and then 3 figures from Martini which do not represent Le Jatou but *Murex erinaceus* Linn. For this reason many authors have placed *Murex decussatus* in synonymy with *M. erinaceus*, and consequently, *Jaton* and *Jatova* in synonymy with *Tritonalia*, of which *M. erinaceus* is the type. The 2 species are very different, and as Gmelin gives the habitat of *M. decussatus* as the West African seas, which would fit with Le Jatou but not with the Mediterranean *M. erinaceus*, I here restrict the name to the species figured by Adanson. Dillwyn (1817: 688), in effect, did this when he placed Le Jatou and *M. decussatus* in the synonymy of *M. lingua* "Chemnitz," stating that "Gmelin, under the name of *M. decussatus* appears, both in his description and references, to have strangely confounded this shell with some varieties of *M. erinaceus*." Pusch did essentially the same thing by naming his genus *Jaton*, with the type species *M. decussatus*, a form of "Linnaean tautonymy" (vide I.C.Z.N. Code, Art. 68-d-i). If the name *decussatus* should not prove satisfactory there are several later ones from which to choose. In chronological order they are: *Murex jatonus* Lamarck, 1816; *M. hemitripteris* Lamarck, 1816; *M. lingua* Dillwyn, 1817; *M. gibbosus* Lamarck, 1822; and *M. lingua-vervicina* Reeve (*ex* Chemnitz), 1845.

*Jaton* is the Recent member of an evolutionary sequence which goes back to the upper Miocene subgenus *Pterorytis*. This group has never been large at any time in its history. There are only 3 Miocene and 1 Pliocene species of *Pterorytis*. *Jaton* apparently has been reduced to the single type species, If *Murex hemitripteris* Lamarck is not just

a young individual of *M. decussatus*, as has been suggested by several authors, then it is the second species of the group.

*Murex festivus* Hinds, from the California coast, has been referred to *Jaton* by authors; however, it probably should be placed in *Pteropurpura*. The boundary lines between these groups is somewhat obscure. It is possible to consider a series of species grading imperceptibly from *Jaton* to *Pteropurpura* and to *Ceratostoma*. In this case one must resort to geography and phylogeny in order to make subgeneric assignments. The principal difference between *Jaton* and *Pteropurpura*, other than geographical separation, is the presence in *Jaton* of the monoceroid tooth on the outer margin of the aperture. This tooth is lacking in *M. festivus*, and consequently placement in *Pteropurpura* is suggested. But actually there is a faint trace on *M. festivus* of what may originally have been such a tooth. However, this controversial species bears a strong resemblance to *Murex trialatus* Sowerby, also from the California coast, which seems more definitely referable to the true *Pteropurpura*. I have recently described a species, *Tritonalia festivoidea*, from the lower Miocene of North Carolina which appears closely related to the Recent West American *M. festivus*. This species also possesses a faint apertural tooth, and so might justifiably be placed in *Jaton* if it were not for the fact that the phylogenetic history of *Jaton* with its upper Miocene pterorytid ancestry seems to preclude this affiliation. Undoubtedly the simplest solution would be to erect another subgenus for these intermediate species, but this solution seems, to me, to evade the issue. I believe it is better to accept the philosophical position that if we are to do more than pay lip service to the concept of evolution, we must admit that there necessarily have to be intermediate forms between supraspecific groups.

Maxwell Smith described a species from Key West, Florida, *Murex (Jaton) gaza*, which he compared with *Murex festivus*. Judging by his photograph it well may be

referable to *Jaton*, but as I have not seen a specimen I would prefer to withhold judgement.

### PTERORYTIS (Figs. 72, 74)

Conrad, 1863, Proc. Acad. Nat. Sci. Phila., v. 14, p 560.  
TYPE SPECIES: *Murex umbrifer* Conrad, by monotypy.

*PTERORHYTIS* Conrad, 1868, Amer. J. Conch., v. 4, p 64. Emendation?

Not *PTERORHYTIS* Conrad, 1875, North Carolina Geol. Surv., v. 1, Appendix A, p 21 (Pelecypod).

*PTEROHYTIS* Tryon, 1880, Man. of Conch., v. 2, p 136. Error.

*PTERORHYTHIS* Cossmann, 1903, Essais Paléo. Comp., v. 5, p 205 (index). Error, not emendation as often cited.

*PTEROPHYTIS* Simroth, 1907, in Bronn, Klass. Ordn. Tierreichs, v. 3 (2), p 1040. Error.

*PTEROHYTUS* Neave, 1940, Nomencl. Zool., v. 3, p 1026. Error for "*Pterohytis*" Tryon.

*NEURARHYTIS* Olsson and Harbison, 1953, Acad. Nat. Sci. Phila., Monogr. 8, p 252.

Type species: "*Purpura (Pterorhytis) fluviana*" Dall, by orig. design. (*Pterorhytis fluviana* of Dall).

"Fusiform; six prominent recurved foliated ribs; aperture ovate; channel closed." (Conrad, 1863)

Discussion: *Murex umbrifer*, the type species of *Pterorytis*, has 6 varices and the genus was therefore described as being characterized by 6 varices. However I have collected specimens from the Yorktown Formation at Hampton, Virginia, near the type locality of *Murex umbrifer* (Yorktown, Va.), which have only 4 varices in the adult but otherwise are identical with *M. umbrifer*. In the early stages the number of varices is irregular with as many as 9 in some specimens, gradually decreasing with each whorl. Whether these specimens represent a different species or only a subspecies of *M. umbrifer* is not yet determined, but their presence nevertheless necessitates a reevaluation of the generic diagnosis of

*Pterorytis*. *Neurarhytis* was distinguished from the typical form because it has only 4 varices, and consequently is not valid.

This group is known only from fossils with 3 Miocene species and 1 Pliocene species, all from the Atlantic Coastal Plain of the United States. The Miocene species are: *M. umbrifer*, from the upper Miocene of Virginia; "*Purpura*" *marshalli* Mansfield, from the upper Miocene of northern Florida; and *Murex conradiana* Dall (= *Murex conradi* Dall, 1890, not *Murex conradi* d'Orbigny, 1850) from the upper Miocene of South Carolina, Florida, and Maryland. The Pliocene species is *Pterorytis fluviana* Dall.

Emerson (1959) has recently monographed the group and proposed a new subgenus, *Microrhytis*, here placed in *Ceratostoma*.

#### CERATOSTOMA

(Figs. 73, 75, 76, 92, 98)

Herrmannsen, 1846, *Indicis Generum Malakoz.*, v. 1, p. 206. Emendation of *Cerostoma* Conrad.

TYPE SPECIES: *Murex (Cerostoma) nuttalli* Conrad, by monotypy.

"*PURPURA* Martyn, 1784" of authors (The Universal Conchologist is not consistently binominal, and has been declared unavailable for nomenclatorial purposes in I. C. Z. N. Opinion 456, 1957).

"Type species": *Purpura foliata* Martyn (= *Murex foliatus* Gmelin), by monotypy.

*CEROSTOMA* Conrad, 1837, *J. Acad. Nat. Sci. Phila.*, v. 8, p. 263. Not *Cerostoma* Latreille, 1802 (Lepidopt.).

Type species: *Murex (Cerostoma) nuttalli* Conrad, by monotypy.

*CERASTOMA* Herrmannsen, 1846, *Ind. Gen. Malakoz.*, v. 1, p. 206. Error. Not *Cerastoma* Koch, 1839 (Arachn.).

*SPINOSTOMA* Coen, 1943, *Acta Pont. Acad. Sci.*, v. 11, p. 90.

Type species: *Murex nuttalli* Conrad, here designated.

*MICRORHYTIS* Emerson, 1959, *Amer. Mus. Novitates*, No. 1974, p. 6.

Type species: *Pterorytis (Microrhytis) pecki* Emerson, by orig. design.

"Shell as in the genus *Murex*; labium with an erect tooth as in *Monoceros*."

(Conrad, 1837)

**Discussion:** This genus has been monographed recently by Hall (1959), who discusses other genera which have been confounded with it, but who neglects to consider *Jaton*, perhaps confusing it with *Tritonalia* for reasons discussed above. *Murex nuttalli*, type of *Ceratostoma*, is similar to *M. decussatus*, type of *Jaton*, differing only in the greater height of the spire and in having a denticulate outer lip. These forms seem to represent the end members of 2 lineages separated since Miocene time, but which nevertheless have maintained strong resemblances.

Coen, in 1943, reviewed the genus *Tritonalia* and proposed a new subgenus *Ternaria* for those forms having 3 varices at 120° angles, with one intervarical node between each pair. At the same time he proposed a new section for this subgenus, *Spinostoma*, for those shells with a labial tooth. In this new section he included only *Murex nuttalli* Conrad and *Purpura foliosa (sic)* Martyn; thus it is a synonym of *Ceratostoma*. As neither of these species was selected as type, *Murex nuttalli* is so designated here.

*Pterorytis (Microrhytis) pecki*, from the upper Miocene of Oaxaca, Mexico, is placed here with *Ceratostoma*, rather than with *Pterorytis*, because it also has a denticulate labrum. Although it has a somewhat lower spire than typical *Ceratostoma* it is not felt that this is sufficient basis for supraspecific separation. Perhaps *P. pecki* is the link between the *Pterorytis/Jaton* group in the Atlantic and the *Ceratostoma* group in the Pacific.

There is another Miocene species from the Atlantic Coast province of the United States which seems closely related to the *Ceratostoma* line. This is *Murex kellumi* Richards from the lower Miocene "Silverdale beds" of North Carolina, known from a single worn specimen. It seems more closely allied with the Pacific *Ceratostoma* line than with the subsequent Atlantic *Pterorytis* line. There are various strange

muricids in the Silverdale fauna which seem to bear no relation to the later Miocene faunas of the area.

Gray (1847: 134) listed "*Cerastoma* Conrad," but cited *Murex monodon* Sowerby as the type. One must assume that he confused it with *Murex monoceros* Sowerby, a shell similar to *M. nuttalli*. This citation is of course inconsequential since *M. nuttalli* had already been fixed as type by monotypy.

### PTEROPURPURA (Figs. 77, 78, 99, 100)

Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.

TYPE SPECIES: *Murex macropterus* Deshayes, by orig. design.

*CENTRIFUGA* Grant and Gale, 1931, *San Diego Soc. Nat. Hist. Mem.*, v. 1, p 706.

Type species: *Murex centrifuga* Hinds, by orig. design.

"Shell with spire elongated to triangular pyramid, whorls ornamented by three wide lamellar varices reaching almost the middle of the canal; aperture small, oval, margins continuous and detached; canal wide at the base, subulate anteriorly." (Jousseume, 1882, *translated*)

Discussion: The shells of this group bear a striking resemblance to those of *Pterynotus* but the radula and the purpuroid operculum indicate that this is due to convergence rather than close relationship. There is also a strong resemblance to the more alate members of the *Cerastoma* group such as *Murex foliatus*, but *Pteropurpura* may be distinguished by the lack of the monoceroid tooth and denticulate aperture characteristic of *Cerastoma*.

*Murex macropterus* Deshayes, the type of *Pteropurpura*, has been the subject of much debate, for the type locality was not known and the species had never been identified with certainty. Recently Emerson (1964) has located the type specimen at the École des Mines in Paris and identified Deshayes' species as that one known today as "*Pteronotus*" *carpenteri* Dall from the coast of California. The

reader is also referred to Emerson's earlier discussion of the problem (1960).

From the description and discussion given by Grant and Gale of their subgenus *Centrifuga* it is obvious that they were proposing a name for the form now known as *Calcitrapessa* Berry, type: *Murex leeanus* Dall. However their selection of *Murex centrifuga* as the type species negated this usage. Emerson (1960) has shown that *Murex centrifuga*, "a long-misunderstood and therefore neglected species," is a senior synonym of *Pterynotus swansoni* Hertlein and Strong, a not uncommon species referable to *Pteropurpura* from the west coast of tropical America (Gulf of California to Panama).

The vast majority of the shells of this group are found in the northern Pacific, both in Japan and on the coast of California. A few species range into tropical waters such as the above mentioned *Murex centrifuga*, *Murex erinaceoides* Valenciennes (synonym: *Murex californicus* Hinds), and *Murex rhyssus* Dall. *Pteropurpura* is also represented in the fauna of the western Atlantic by *Murex bequaerti* Clench and Pérez Farfante, the species reported by Dall in the "Blake Report" (1889: 201) as "*Murex macropterus* Deshayes."

### OCINEBRELLUS (Figs. 83, 93, 101)

Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.

TYPE SPECIES: *Murex eurypteron* Reeve, by orig. design. (= *Murex falcatus* Sowerby).

*OCINEBRELLUS* Cossmann, 1903, *Essais Paléo. Comp.*, v. 5, p 204 (Index). Error, not emendation as often cited.

*TERNARIA* Coen, 1943, *Acta Pont. Acad. Sci.*, v. 11, p 89.

Type species: *Murex eurypteron* Reeve, here designated.

"Shell with moderate spire, whorls very depressed at the suture, with four winged varices extending to the middle of the canal; aperture oval, the margins detached and continuous; closed canal rather long

and subulate in the anterior half." (Jousseau, 1882, *translated*)

**Discussion:** This group is exceedingly close to *Pteropurpura* and possibly should not be separated even in subgeneric rank. *Ocinebrellus* consists of a few Japanese species differing from *Pteropurpura* in the irregular arrangement of the varices. The number of varices is usually more than 3; however in the original description of *Murex eurypteron*, the type of *Ocinebrellus*, Reeve declared that the species had but 3 varices and was therefore distinct from *Murex falcatus* Sowerby. This species is variable in the number of varices, and there are specimens which have only 3 varices to a whorl. In such specimens the varical arrangement is not in the regular succession of *Pteropurpura*, but is irregular, and thus the 2 forms may be distinguished. Most authors place a great deal of supraspecific emphasis upon the number of varices possessed by different forms, but to me this seems a minor characteristic. There are far too many species such as *Murex eurypteron* having a variable number of varices for the number of 3, as opposed to 4, 5, 6, or a dozen, to be of any tremendous taxonomic value.

*Ternaria* was proposed by Coen as a subgenus of *Tritonalia* to include those species with 3 varices 120° apart and 3 intervarical "costole." He referred to this new subgenus *Murex eurypteron* Reeve plus various unfigured new or otherwise unrecognizable species. *M. eurypteron* was included even though it has more than the "characteristic" number of varices (see above comments) and in spite of Coen's admission that it properly belongs in *Ocinebrellus* Jousseau. This latter subgenus he dismissed with the statement that "non ritengo . . . abbia alcuna ragione di essere." As *M. eurypteron* is the only well-known species in his list it is here designated as the type of *Ternaria*. This will assure its synonymy and unregrettable demise.

### CALCITRAPESSA

(Fig. 82)

Berry, 1959, Leaflets in Malacology, v. 1 (18), p 113.

TYPE SPECIES: *Murex leeanus* Dall, by orig. design.

"Shell of moderate size, nearly smooth, bearing 3 low varices which usually are nearly obsolete except for the elevation from each of a very long erect spine which is strongly guttered along its face when first formed, but the gutter sometimes becomes largely closed by the folding over and fusion of the margins; an intervarical knob appears between each varix and its neighbor, with sometimes a hint of a rib leading down onto the body of the whorl; canal very long and nearly straight, slightly recurved, roofed over at the varical stage except near the tip." (Berry, 1959)

**Discussion:** The type species of this monotypic taxon has been placed with *Murex centrifuga* in the subgenus *Centrifuga*, but that group too closely resembles *Pteropurpura* to be separated from it. *Murex leeanus* seems to be a bizarre offshoot of the *Pteropurpura* lineage, but is sufficiently far removed from the main evolutionary line to warrant treatment as a separate subgenus. (It is necessary to keep in mind that every generic divergence started with one "bizarre offshoot.")

The appearance of this form is somewhat trophonoid but Dall's description of *Murex leeanus* (1890: 330) states, "The dentition is typically muricoid, the radula small and narrow, the central tooth very wide, very short, and with three inconspicuous denticles on its cusp. The soft parts hardly differ externally from those of *Murex brandaris*." What Dall did not say, although his illustration shows it, is that the operculum is purpuroid, and for this reason *Calcitrapessa* should be placed in the Tritonaliinae and not the Muricinae.

## PURPURELLUS

(Fig. 79)

Jousseaume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: *Murex gambiensis* Reeve, by orig. design.

TRIREMIS "Bayle MS" Fischer, 1884, Man. de Conchyl., p 641.

Type species: *Murex gambiensis* Reeve, by orig. design.

PURPURELLA Korobkov, 1955, Spravochnik i methodicheskoe rukovodstvo, p 283. Error.

TRIREMIA Korobkov, 1955, Spravochnik i methodicheskoe rukovodstvo, p 283. Error.

TRIMERIS Ovečkin, 1960, in Orlov *et al.*, Osnovy paleontologii, v. 4, p 205. Error.

"Shell with pointed spire in the form of a triangular pyramid, whorls ornamented by three winged varices, falcate and folded back superiorly; aperture small, oval, with margins continuous and detached; canal long and closed, bearing a wide lamella separated from the wing of the corresponding varix by a large indentation." (Jousseaume, 1882, *translated*)

Discussion: Although *Murex gambiensis* Reeve (? = *Murex osseus* Reeve) is closely related to *Pteropurpura*, the disruption of the foliaceous varices at the base of the body whorl, separating them into anterior and posterior portions, together with the greatly widened siphonal canal, permits *Purpurellus* to be distinguished from that subgenus. The distribution of this group is odd, with the type species occurring off West Africa, and the only other species of the group, *Murex pinniger* Broderip and *Centrifuga inezana* Durham, occurring off the west coast of tropical America. These latter 2 species are very similar and may prove to be synonymous; however they are geographically separated by about 3000 miles (*M. pinniger* comes from Ecuador, and *C. inezana* from the vicinity of Guaymas, Mexico.)

Thiele (1929: 289) has figured a radula said to be that of *Murex gambiensis* Reeve. If this is correct then *Pur-*

*purellus* should be placed in the subfamily Muricinae, for the radula depicted is of the typical muricine form. However, the shell morphology seems so more nearly akin to the *Pteropurpura* group that an error is suspected.

## POROPTERON

(Fig. 80)

Jousseaume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: *Murex uncinarius* Lamarck, by orig. design.

"Subtrigonal shell with rather elevated pyramidal spire, whorls ornamented by three lamellar varices, thick and crenulated by projecting canaliculate rays, terminated posteriorly by a rather long and recurved hook-like spine; aperture oval with margins continuous and detached; canal short and closed." (Jousseaume, 1882, *translated*)

Discussion: In the original citation of *Poropteron* the type species was given as "*Murex tubifer* Bruguière," but in the following number (Année 3, no. 43, Jan., 1881), it was corrected to *Murex uncinarius*. There is no doubt that this was a genuine error, for the name "*Murex tubifer* Bruguière" also appeared as the type of the genus *Typhis* immediately following *Poropteron*.

*Murex uncinarius*, the type species and apparently only representative of *Poropteron*, is most closely related to *Purpurellus*, but is sufficiently different with its digitate varices to be ranked in a monotypic subgenus. The canaliculate, recurved posterior spine of *M. uncinarius* has caused writers to associate the species now referred to *Nothotyphis* with *Poropteron*. According to Fleming, who described *Nothotyphis*, the 2 groups are strikingly different in sculpture. The shell of *Poropteron* is porcellanous, with the axial sculpture limited to a single intervarical node. The surface of *Nothotyphis* is ornamented with spiral cords and fine intersecting spiral and radial threads.

*Murex uncinarius* is confined to the African coast between the Cape of Good

Hope and Natal. This species, incidentally, has at least 2 synonyms, *Murex capensis* and *Murex mitraeformis*, both of Sowerby.

*HOMALOCANTHA*

(Figs. 81, 102)

Mörch, 1852, Cat. Conchyl. Yoldi, v. 1, p 95.

TYPE SPECIES: *Murex scorpio* Linn., by monotypy.

*HOMALACANTHA* Kobelt, 1877, Jb. Dtsch. Malak. Ges., v. 4, p 143. Error.

*HOMOLOCANTHA* Ludbrook, 1958, Trans. Roy. Soc. S. Australia, v. 81, p 58. Error.

Discussion: The characteristics of this group are so unmistakable that even though there was no "original description", merely a name in a catalogue, the association with *Murex scorpio*, the type by monotypy, was sufficient to diagnose the group. Because it has 5 to 6 foliaceous varices it might be considered as most closely related to *Hexaplex*, but the differences of the operculum and other features indicates that this resemblance is superficial.

In 1955 Burch (:12) made the following observations on *Hexaplex* Perry: "Before an intelligent use of *Hexaplex* can be made, one of Perry's species must be designated as type. Inasmuch as the first three species mentioned and figured by Perry are obviously those now assigned to the genus *Homalocantha*, it would seem logical to designate Perry's *Murex anatomica* [Perry's *Hexaplex anatomica*] as type in which case *Hexaplex* should certainly replace *Homalocantha*. This designation is clearly valid and should at least take the name *Hexaplex* out of consideration in connection with the species listed under *Muricanthus*. . ." If *M. anatomica* were to be taken as type of *Hexaplex*, the chaos wrought would be unbelievable, for the name *Homalocantha* is firmly entrenched in the literature, and conversely *Hexaplex* has never (except for Perry) been applied to the shells of that genus. Fortunately in 1915 Iredale had designated the type of *Hexaplex* as *Hexaplex foliacea* (= *Murex cichoreus* Gmelin), a shell which had long

been so considered on the basis of Joussemaume's invalid citation of *Murex cichoreus* as the type.

*VITULARIA*

(Figs. 84, 85, 103)

Swainson, 1840, Treatise on Malacology, p 297.

TYPE SPECIES: *Vitularia tuberculata* Swainson, by orig. design. (= *Murex vitulinus* Lamarck, *vide* Swainson).

*VITULINA* Swainson, 1840, Treatise on Malacology, p 64.

Type species: *Murex vitulinus* "of authors", by orig. design.

*TRANSTRAFER* Iredale, 1929, Mem. Queensland Mus., v. 9, p 290.

Type species: *Transtrifer longmani* Iredale, by orig. design.

"General habit of Muricidea, but the inner lip is depressed and flattened as in the Purpurinae; varices simple, nearly obsolete." (Swainson, 1840)

Discussion: The type species of this genus is generally considered to be *Murex miliaris* Gmelin, of which *Murex vitulinus* Lamarck is a synonym. Swainson, to avoid tautonymy, changed the name of the type species to *V. tuberculata*. The name *Vitulina* actually has "page priority" but usage has sanctioned the later *Vitularia*, evidently a *lapsus* on the part of Swainson. Lest there be any question of legality, *Vitularia* is here selected as the correct name by right of the "first reviser."

The genus *Transtrifer* was proposed by Iredale for a species that is exceedingly like *Murex vitulinus*. Iredale separated the Australian shell because, as he stated, "the lamellae are more developed, and therefore the window-like depressions are more pronounced." This difference in degree does not seem to be of supra-specific importance.

*CRASSILABRUM*

(Fig. 86)

Joussemaume, 1880, Le Naturaliste, Année 2 (42), p 335.

TYPE SPECIES: *Murex crassilabrum* "Gray", by orig. design. (*M. crassilabrum* Gray in Sowerby, 1834 = *M. labiosus*

Gray, 1828, not *M. labiosus* Wood, 1828).

*ANTIMUREX* Cossmann, 1903, *Essais Paléo. Comp.*, v. 5, p 12. New name for *Crassilabrum* Jousseume, not Megerle. (Neave cites only "*Crassilabrum* (Megerle MS) Scudder, *Nomen. Zool. Syst.*, p 88, nom. nud.," therefore this is probably an unnecessary name.)

"Shell with conical spire, the whorls grooved by longitudinal lamellae and circled by rather projecting ribs; aperture oval with columellar margin appressed, with the inner curve less rounded than that of the outer lip, the latter, very wide and thick, is internally denticulate; canal very wide and short." (Jousseume, 1882, *translated*)

Discussion: The shells of this group most closely resemble those of *Vitularia*, but they lack the peculiar shagreened surface so characteristic of that genus. However the surface texture of the only representative of the *Vitularia* line found on the west coast of Central America, *Murex salebrosus* King and Broderip, varies from rough to almost smooth so that the smooth shell of *Crassilabrum* may be the logical derivative of the form. The type and apparently only species of this group occurs along the west coast of South America from Peru to Chile.

#### *EUPLEURA* (Figs. 87, 95)

Adams, H. and A., 1853, *Genera Recent Mollusca*, v. 1, p 107.  
TYPE SPECIES: *Ranella caudata* Say, by sub. design., F. C. Baker, 1895.

"Spire moderate; front canal long, nearly closed; no posterior canal; inner lip smooth; varices spiny, fimbriated between the spines." (Adams, 1853)

Discussion: Although originally described as a subgenus of *Bursa* by H. and A. Adams, the radula of the type species shows clearly that this group is allied with the Tritonaliinae. *Eupleura* is a small group, including only some half-dozen species, found on both sides of the American continent.

#### *UROSALPINX* (Figs. 88, 96)

Stimpson, 1865, *Amer. J. Conch.*, v. 1, p 58.  
TYPE SPECIES: *Fusus cinereus* Say, by orig. design.

"Shell elongated oval, or short fusiform, longitudinally ribbed or undulated and spirally striated; aperture with a short canal. Operculum somewhat like that of *Purpura*, semi-cordate, with the nucleus at the outer edge a little below the middle. Lingual dentition nearly like that of *Trophon*, the lateral teeth having an elongate base of attachment; but the rhachidian tooth has numerous minute denticles between the principal ones, corresponding to ridges on the surface of the tooth, as in the Murices. . . It differs from *Trophon* in its operculum, and from *Ocenebra* in its smoother shell, want of varices, and open canal." (Stimpson, 1865)

Discussion: This genus appears most closely related to *Ocenebrina* and both lack the typical varices usually associated with the family Muricidae. They are placed in the Tritonaliinae because of the resemblance of their radulae to that of *Murex erinaceus*, rather than because of any strong conchological resemblances.

The genus *Scalaspira* Conrad, based on a species from the Miocene of Virginia, *Fusus strumosus* Conrad, has been placed in the synonymy of *Urosalpinx* by Tryon (1880: 152) and Cossmann (1903: 48) but it is not felt that this synonymy is justified. Until I have seen type material of Conrad's genus, no disposition will be made of the taxon.

#### *OCINEBRINA* (Figs. 89, 94)

Jousseume, 1880, *Le Naturaliste*, Année 2 (42), p 335.  
TYPE SPECIES: "*Fusus corallinus*" Scacchi, by orig. design. (*Murex corallinus* of Scacchi = *Murex aciculatus* Lam-arck).

*CORALLINIA* Bucquoy, Dautzenberg, and Dollfus, 1882, Moll. Mar. Roussillon, v. 1, p 24.

Type species: *Murex aciculatus* Lamarck, by orig. design.

*OCENEBRINA* Cossmann, 1903, Essais Paléo. Comp., v. 5, p 38. Emendation.

*DENTOCENEBRA* Monterosato, 1917, Boll. Soc. Zool. Ital., (3) v. 4, p 21.

Type species: *Murex edwardsii* (Payraudéau), by sub. design., Lamy, 1919.

"Shell with rather elevated conical spire, whorls ornamented by numerous longitudinal ribs, cut by circular striae, aperture oval with columellar margin appressed and much less curved than the outer margin, the latter internally denticulate; canal very short and closed anteriorly." (Jousseau, 1882, translated)

Discussion: Although this group was placed in *Murex* by Bucquoy *et al.*, it bears little resemblance to that genus. The radula of the type species is almost identical with that of *Urosalpinx cinerea* indicating its true position. *Ocenebrina* has, however, a closed anterior canal which is unlike that of *Urosalpinx*, and is presumably even more closely related to the *Tritonalia* line.

\* \* \* \*

The following taxa have been referred to the Muricinae or Tritonaliinae either by the original author, or by subsequent author(s). In my opinion they do not belong to either group.

*DERMOMUREX* Monterosato, 1890, Natural. Sicil., v. 9, p 181. New name for

*Poweria* Monterosato not Bonaparte.

Type species: *Murex scalarina* Bivona, by orig. design.

*POWERIA* Monterosato, 1884, Nom. gen. spec. Conch. Medit., p 113. Not *Poweria* Bonaparte, 1840 (Pisces).

= Subgenus of *ASPELLA* (The genus *Aspella* seems to be intermediate between the Muricinae and Tritonaliinae with the operculum of the first and a radula which is closer to the second. It is a small group which has been largely ignored by authors, who place it variously in the Trophoninae, Muricinae, or any other likely place.)

*FAVARTIA* Jousseau, 1880, Le Naturaliste, Année 2 (42), p 335.

Type species: *Murex breviculus* Sowerby, by orig. design.

= Subgenus of *ASPELLA*

*FORRERIA* Jousseau, 1880, Le Naturaliste, Année 2 (42), p 335.

Type species: *Murex belcheri* Hinds, by orig. design.

= *RAPANINAE*

*GRACILIMUREX* Thiele, 1929, Handb. syst. Weichtierkunde, v. 1, p 289.

Type species: *Murex bicolor* Thiele, by orig. design. (Not *Murex bicolor* Risso, 1826; nor Valenciennes, 1832; nor Cantraine, 1835).

= *ASPELLA*

*GRACILIPURPURA* Jousseau, 1880, Le Naturaliste, Année 2(42), p 335.

Type species: *Fusus strigosus* Lamarck, by orig. design.

*GRACILLIPURPURA* Jousseau, 1882, Rev. Mag. Zool., (3) v. 7 (1879), p 331. Error.

= *FUSINUS*

*HANETIA* Jousseau, 1880, Le Naturaliste, Année 2 (42) p 335.

Type species: *Murex haneti* Petit, by orig. design.

= *CANTHARUS*

*HERTLEINELLA* Berry, 1958, Leaflets in Malacology, v. 1 (16), p 95.

Type species: *Hertleinella leucostephes* Berry, by orig. design. (*H. leucostephes* Berry, 1958 = *Tritonalia turrita* Dall, 1919)

= *CANTHARUS*

*HEXACHORDA* Cossmann, 1903, Essais Paléo. Comp., v. 5, p 47.

Type species: *Murex tenellus* Mayer-Eymar, by orig. design.

*EXACHORDA* Sacco, 1904, Moll. Terr. Terz., v. 30, p 20. Error.

= Subgenus of *ASPELLA*

*LANGFORDIA* Dall, 1924, Proc. Biol. Soc. Washington, v. 37, p 89.

Type species: *Murex cuspidifera* Dall, by orig. design.

*Incertae sedis* (In the summer of 1963 a search of the collections of the United States National Museum failed to disclose the type specimen or any other specimens of *Murex cuspidifera* Dall.)

*ORANIA* Pallary, 1900, J. de Conchyl., v. 48, p 285.

Type species: *Murex spadae* Libassi, by orig. design.

= CORALLIOPHILIDAE

*PSEUDOMUREX* Monterosato, 1872, Not. conch. foss. Pellegrino and Ficarazzi, p 15, 33.

Type species: Not yet correctly designated, *teste* Myra Keen

= CORALLIOPHILIDAE

\* \* \* \* \*

The following genera are based on fossil species. Their subfamilial placement has not been determined.

*LYROPURA* Jousseau, 1880, Le Naturaliste, Année 2 (42), p 335.

Type species: *Murex crassicosatus* Deshayes. Eocene of Paris Basin.

*MUROTRITON* De Gregorio, 1890, An. Géol. Paléont., v. 7, p 97.

Type species: *Murotriton grassator* de Gregorio. Eocene of Alabama.

*ODONTOPOLYS* Gabb, 1860, J. Acad. Nat. Sci. Phila., (N.S.) v. 4, p 377.

Type species: *Murex compsorhytis* Gabb. Eocene of Texas, Louisiana, Alabama. (This genus is characterized by having 2 plaits on the columella, and probably does not belong in the Muricidae.)

*YASILA* Olsson, 1930, Bulls. Amer. Paleont., v. 17 (62), p 59.

Type species: *Yasila paytensis* Olsson. Eocene of Peru.

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The illustrations of shells, unless otherwise noted, are from the pen of George B. Sowerby, Jr. They are taken from the following works:

*Conchologia Iconica*, by L. A. Reeve, Vol. III. *Murex*, 1845.

*Thesaurus Conchyliorum*, by G. B. Sowerby, Jr., Pts. 33 and 34, *Murex*, 1879.

The illustrations of radulae, unless otherwise noted, are from:

*Das Gebiss der Schnecken*, by F. H. Troschel, Vol. II, pt. 3, 1869.

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PLATE I - MURICINAE  
(all figures approximately X 1/2)

## Figure

- |    |   |    |   |
|----|---|----|---|
| 1  | <b>MUREX</b> S. S.<br><i>Murex pecten</i> Montfort ( <i>M. tenuispina</i><br>Lamarck, Icon., Fig. 85)                     | 11 | <b>HEXAPLEX</b><br><i>Murex cichoreus</i> Gmelin (Icon., Fig.<br>27b)   |
| 2  | <b>MUREX</b> S. S.<br><i>Murex tribulus</i> Linn. (Icon., Fig. 82)  | 12 | <b>HEXAPLEX</b><br><i>Murex eurystomus</i> Swainson ( <i>Murex</i><br><i>saxatilis</i> "Linn.," Thesaurus, Fig. 177)                              |
| 3  | <b>MUREX</b> S. S.<br><i>Murex brevispina</i> Lamarck (Icon., Fig.<br>77)   | 13 | <b>CHICOREUS</b><br><i>Triplex denudatus</i> Perry (from speci-<br>men)   |
| 4  | <b>HAUSTELLUM</b><br><i>Murex haustellum</i> Linn. (Kiener, 1843,<br>Pl. 13, Fig. 1)                                      | 14 | <b>PHYLLONOTUS</b><br><i>Murex imperialis</i> Swainson (Icon., Fig. 35)   |
| 5  | <b>HARMATIA</b><br><i>Murex stephani</i> Noszky (Ann. Hist.-<br>Nat. Mus. Natl. Hungarici, 1940, v. 33,<br>Pl. 2, Fig. 4) | 15 | <b>HEXAPLEX</b><br><i>Murex trunculus</i> Linn. (Icon., Fig. 22a)   |
| 6  | <b>BOLINUS</b><br><i>Murex brandaris</i> Linn. (Kiener, 1843,<br>Pl. 3, Fig. 1)   | 16 | <b>HEXAPLEX</b><br><i>Murex radix</i> Gmelin (Kiener, 1843,<br>Pl. 38, Fig. 1)  |
| 7  | <b>CHICOREUS</b><br><i>Murex ramosus</i> Linn. (Icon., Fig. 3)  | 17 | <b>CHICOREUS</b><br><i>Murex fiatus</i> de Gregorio ( <i>Murex</i><br><i>dujardini</i> Tournouër, J. de Conchyl.,<br>1875, v. 23, Pl. 5, Fig. 4a) |
| 8  | <b>CHICOREUS</b><br><i>Triplex foliatus</i> Perry ( <i>Murex</i><br><i>palmarosae</i> Lamarck, Icon., Fig. 30)            | 18 | <b>HEXAPLEX</b><br><i>Murex strausi</i> Verrill (Minutes Conch.<br>Club S. Calif., 1950, No. 103, text<br>figure p 5)                             |
| 9  | <b>CHICOREUS</b><br><i>Murex monodon</i> Sowerby (= " <i>Purpura</i> "<br><i>cornucervi</i> Röding) (Icon., Fig. 21a)     | 19 | <b>HEXAPLEX</b><br><i>Murex stainforthi</i> Reeve (Icon., Fig. 68)  |
| 10 | <b>SIRATUS</b><br><i>Murex senegalensis</i> Gmelin (Kiener,<br>1843, Pl. 11, Fig. 2)                                      | 20 | <b>MUREXSUL</b><br><i>Murex octogonus</i> Quoy and Gaimard<br>(Voy. "Astrolabe," 1833, Pl. 36, Fig. 8),<br>X 3/4                                  |

# MURICINAE

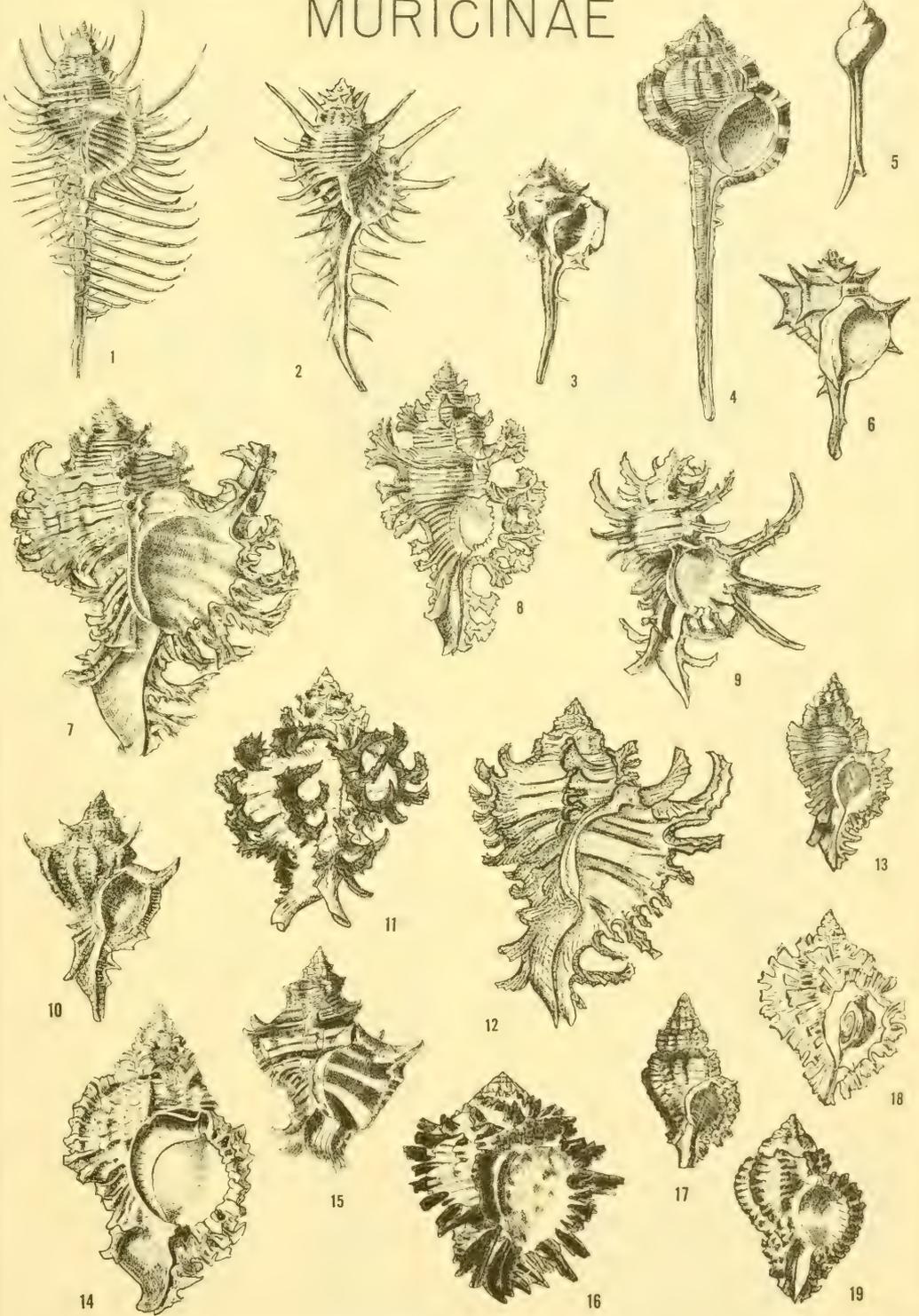


PLATE II - MURICINAE  
(all magnifications approximate)

## Figure

- 21 **MUREXIELLA**  
*Murex hidalgoi* Crosse (J. de Conchyl., 1871, v. 19, Pl. 1, Fig. 4), X 3/4
- 22 **MUREXIELLA**  
*Minnimurex phantom* Woolacott (Proc. Roy. Zool. Soc. N. S. W., 1957 Pl. 3, Fig. 8), X 2
- 23 **MAXWELLIA**  
*Murex gemma* Sowerby (Thesaurus, Fig. 214), X 3/4
- 24 **PTERYNOTUS**  
*Murex pinnatus* Swainson (Icon., Fig. 57), X 1/2
- 25 **PTERYNOTUS**  
*Murex clavus* Kiener (= *M. elongatus* Lightfoot) (Icon., Fig. 9), X 1/2
- 26 **PTERYNOTUS**  
*Murex latifolius* Bellardi (Moll. Terr. Terz., 1872, v. 1, Pl. 4, Fig. 5a), X 1/2
- 27 **PTERYNOTUS**  
*Murex textilis* Gabb (Wagner Free Inst. Sci., Trans., 1890, v. 3, pt. 1, Pl. 9, Fig. 4), X 1/2
- 28 **NAQUETIA**  
*Murex triquetter* Born (Icon., Fig. 4), X 1/2
- 29 **NAQUETIA**  
*Murex capucinus* Lamarck (= *M. permaestus* Hedley) (Icon., Fig. 10), X 1/2
- 30 **PAZIELLA**  
*Murex nuttingi* Dall (Bull. Iowa Nat. Hist. Lab., 1896, v. 4, Pl. 1, Fig. 1), X 3/4
- 31 **PAZIELLA**  
*Murex atlantis* Clench and Pérez Farfante (from specimen), X 1
- 32 **PANAMUREX**  
*Murex gahmensis* Brown and Pilsbry (from specimen), X 1
- 33 **PTEROCHELUS**  
*Murex acanthoplerus* Lamarck (Icon., Fig. 64), X 1/2
- 34 **NOTHOTYPHIS**  
*Pterynotus norfolkensis* Fleming (Trans. Roy. Soc. New Zealand, Zool., 1962, v. 2, Pl. 1, Fig. 18), X 2
- 35 **POIRIERIA**  
*Murex zelandicus* Quoy and Gaimard (Thesaurus, Fig. 150), X 1/2
- 36 **PAZIELLA**  
*Murex pazi* Crosse (J. de Conchyl., 1870, v. 18, Pl. 1, Fig. 4), X 1/2
- 37 **MURICOPSIS**  
*Murex hexagonus* Lamarck (= *M. oxytata* Smith) (Icon., Fig. 120b), X 1
- 38 **MURICOPSIS**  
*Murex blainvillei* Payraudeau (Icon., Fig. 110), X 1

## RADULAE

(approximately X 30)

## Figure

- 39 **MUREX S. S.**  
*Murex tenuispina* Lamarck (Troschel, Pl. 10, Fig. 19)
- 40 **MUREX S. S.**  
*Murex tribulus* Linn. (Troschel, Pl. 10, Fig. 21)
- 41 **MUREX S. S.**  
*Murex brevispina* Lamarck (Troschel, Pl. 10, Fig. 20)
- 42 **BOLINUS**  
*Murex brandaris* Linn. (Troschel, Pl. 11, Fig. 1)
- 43 **BOLINUS**  
*Murex cornutus* Linn. (Troschel, Pl. 11, Fig. 2)
- 44 **CHICOREUS**  
*Murex ramosus* Linn. (Troschel, Pl. 11, Fig. 3)
- 45 **CHICOREUS**  
*Murex brevifrons* Lamarck (Troschel, Pl. 11, Fig. 4)
- 46 **SIRATUS**  
*Murex senegalensis* Gmelin (Troschel, Pl. 11, Fig. 5)
- 47 **PHYLLONOTUS**  
*Murex pomum* Gmelin (Troschel, Pl. 11, Fig. 7)
- 48 **PHYLLONOTUS**  
*Murex regius* Swainson (Cooke, 1895, Fig. 119)
- 49 **HEXAPLEX**  
*Murex trunculus* Linn. (Troschel, Pl. 11, Fig. 8)
- 50 **MUREXSUL**  
*Murex octogonus* Quoy and Gaimard (Hutton, Trans Proc. New Zealand Inst., 1882, v. 15, Pl. 13, Fig. 3)
- 51 **PTERYNOTUS**  
*Murex pinnatus* Swainson (Habe, in litt.)
- 52 **MURICOPSIS**  
*Murex blainvillei* Payraudeau (Troschel, Pl. 11, Fig. 9)

## OPERCULA

## Figure

- 53 **MUREX S. S.**  
*Murex tribulus* Linn., X 1
- 54 **MUREX S. S.**  
*Murex antillarum* Hinds, X 1
- 55 **HAUSTELLUM**  
*Murex haustellum* Linn., X 1
- 56 **CHICOREUS**  
*Murex brevifrons* Lamarck, X 1
- 57 **PHYLLONOTUS**  
*Murex pomum* Gmelin, X 3/4
- 58 **HEXAPLEX**  
*Murex chichoreus* Gmelin, X 3/4
- 59 **HEXAPLEX**  
*Murex fulvescens* Sowerby, interior view, X 1/2
- 60 **HEXAPLEX**  
*Murex radix* Gmelin, X 1/3
- 61 **MUREXSUL**  
*Murex octogonus* Quoy and Gaimard, X 1
- 62 **MAXWELLIA**  
*Murex gemma* Sowerby, X 2
- 63 **PTERYNOTUS**  
*Murex pinnatus* Swainson, X 1
- 64 **NAQUETIA**  
*Murex permaestus* Hedley, X 1
- 65 **PAZIELLA**  
*Murex pazi* Crosse, X 1 1/2

# MURICINAE

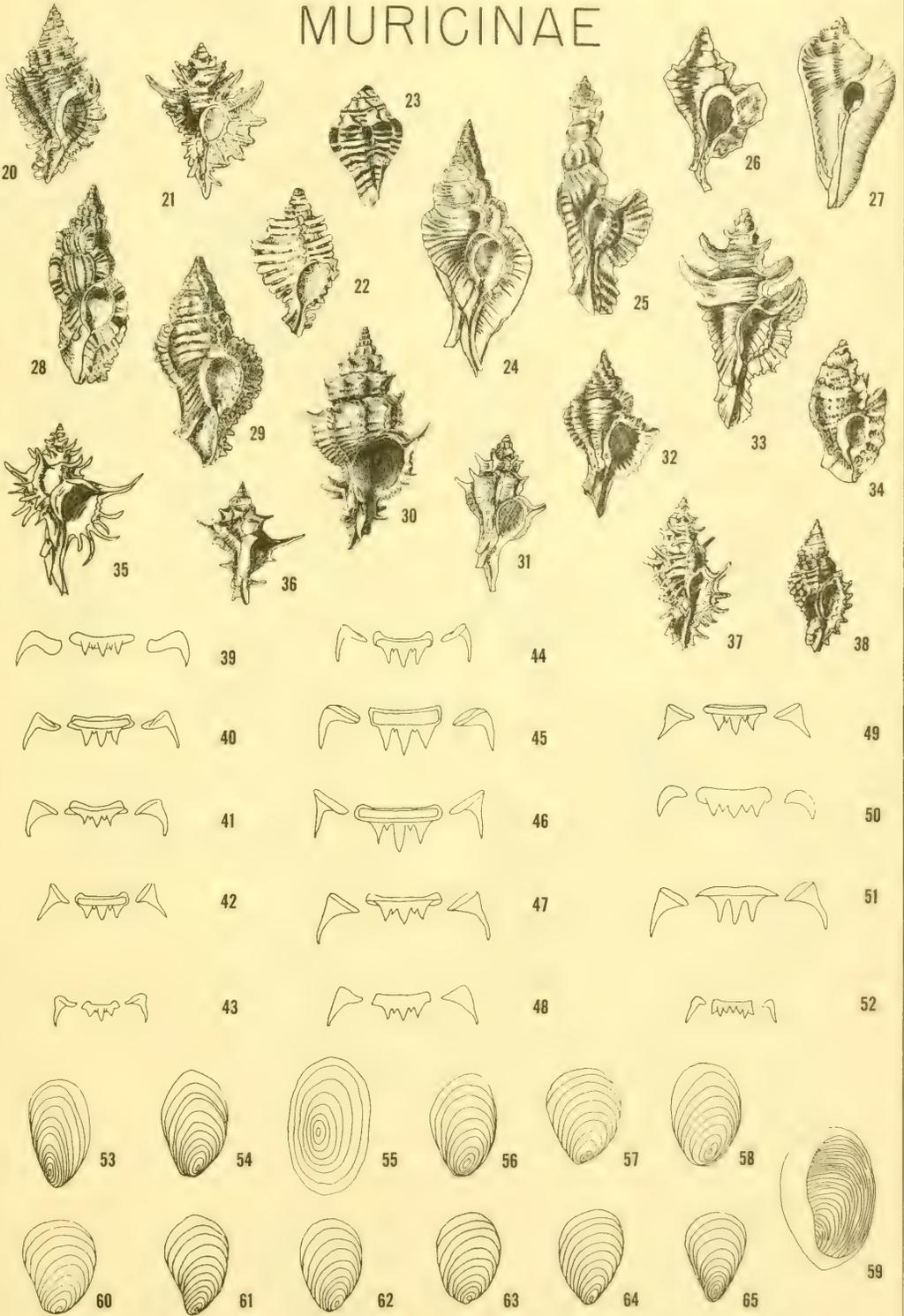


PLATE III - TRITONALIINAE  
(all magnifications approximate)

## Figure

- 66 *TRITONALLA*  
*Murex erinaceus* Linn. (Icon., Fig. 11), X 1/2
- 67 *TRITONALLA*  
*Murex fasciatus* Sowerby (= *Tritonalia inermicosta* nom. nov.) (Nicklès, 1950, Fig. 156), X 1
- 68 *TRITONALLA*  
*Murex polymorphus* Brocchi (Brocchi, 1814, Pl. 8, Fig. 4), X 1
- 69 *HADRIANLA*  
*Murex craticulatus* Brocchi (= *Tritonalia craticuloides* nom. nov.) (Brocchi, 1814, Pl. 7, Fig. 14), X 1
- 70 *MIOCENEBRA*  
*Tritonalia silverdalense* Vokes (from specimen), X 1
- 71 *JATON*  
*Murex decussatus* Gmelin (Nicklès, 1950, Fig. 155), X 1
- 72 *PTERORYTIS*  
*Murex umbrifer* Conrad (Am. J. Conch., 1868, v. 4, Pl. 5, Fig. 7), X 2/3
- 73 *CERATOSTOMA*  
*Murex nuttalli* Conrad (Tryon, 1880, Pl. 35, Fig. 381), X 2/3
- 74 *PTERORYTIS*  
*Murex fluviana* Dall (Trans. Wagner Free Inst. Sci., 1903, v. 3, pt. 6, Pl. 60, Fig. 21), X 2/3
- 75 *CERATOSTOMA*  
*Murex foliatus* Gmelin (Martyn, 1784, Universal Conchologist, Pl. 66), X 1/2
- 76 *CERATOSTOMA*  
*Pterorytis pecki* Emerson (from specimen), X 1
- 77 *PTEROPURPURA*  
*Murex macropterus* Deshayes (Icon., Fig. 123), X 1
- 78 *PTEROPURPURA*  
*Murex centrifuga* Hinds (Icon., Fig. 130), X 1/2
- 79 *PURPURELLUS*  
*Murex gambiensis* Reeve (Icon., Fig. 65), X 1/2
- 80 *POROPTERON*  
*Murex uncinarius* Lamarck (Icon., Fig. 156), X 1
- 81 *HOMALOCANTHA*  
*Murex scorpio* Linn. (Kiener, 1843, Pl. 9, Fig. 3), X 1/2
- 82 *CALCITRAPESSA*  
*Murex leeanus* Dall (Proc. U.S. Natl. Mus., 1890, v. 12, Pl. 7, Fig. 1), X 1/2
- 83 *OCINEBRELLUS*  
*Murex eurypteron* Reeve (= *M. falcatus* Sowerby) (Icon., Fig. 176b), X 1/2
- 84 *VITULARIA*  
*Murex vitulinus* Lamarck (Kiener, 1843, Pl. 47, Fig. 2), X 1/2
- 85 *VITULARIA*  
*Transtrefer longmani* Iredale (Mem. Queensland Mus., 1929, v. 9, pt. 3 Pl. 31, Fig. 10), X 1/2
- 86 *CRASSILABRUM*  
*Murex crassilabrum* "Gray" Sowerby (Icon., Fig. 146), X 1
- 87 *EUPLEURA*  
*Ranella caudata* Say (Icon., *Triton*, Fig. 57), X 1
- 88 *UROSALPINX*  
*Fusus cinereus* Say (Say, 1830, American Conchology, Pl. 29), X 1
- 89 *OCINEBRINA*  
*Murex aciculatus* Lamarck (Tryon, 1880, Pl. 36, Fig. 409), X 1

RADULAE  
(approximately X 30)

## Figure

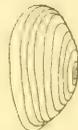
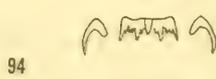
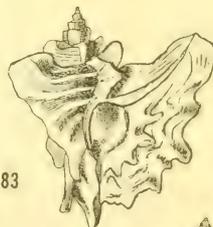
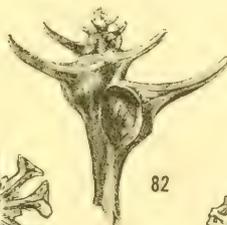
- 90 *TRITONALLA*  
*Murex erinaceus* Linn. (Troschel, Pl. 11, Fig. 11)
- 91 *HADRIANLA*  
*Murex brocchii* Monterosato (Thiele, 1929, Fig. 327)
- 92 *CERATOSTOMA*  
*Murexournieri* Crosse (Habe, in litt.)
- 93 *OCINEBRELLUS*  
*Murex aduncus* Sowerby (Habe, in litt.)
- 94 *OCINEBRINA*  
*Murex aciculatus* Lamarck (Troschel, Pl. 11, Fig. 13)
- 95 *EUPLEURA*  
*Ranella caudata* Say (Stimpson, Amer. J. Conch., 1865, v. 1, Pl. 8, Fig. 5)
- 96 *UROSALPINX*  
*Fusus cinereus* Say (Stimpson, Amer. J. Conch., 1865, v. 1, Pl. 8 Fig. 6)

## OPERCULA

## Figure

- 97 *TRITONALLA*  
*Murex erinaceus* Linn., X 2
- 98 *CERATOSTOMA*  
*Murex foliatus* Gmelin, X 1
- 99 *PTEROPURPURA*  
"*Pteronotus*" *carpenteri* Dall, X 1
- 100 *PTEROPURPURA*  
*Ocenebra modesta* Fulton, X 1 1/2
- 101 *OCINEBRELLUS*  
*Murex eurypteron* Reeve, X 1
- 102 *HOMALOCANTHA*  
*Hexaplex anatomica* Perry, X 1 1/2
- 103 *VITULARIA*  
*Murex salebrosus* King and Broderip, X 2

# TRITONALIINAE



## ZUSAMMENFASSUNG

## SUPRASPEZIFISCHE GRUPPEN IN DEN UNTERFAMILIEN MURICINAE UND TRITONALIINAE (GASTROPODA: MURICIDAE)

Mindestens 90 supraspezifische Namen sind für die verschiedenen Gruppen innerhalb der Muricinae und Tritonaliinae ("Ocenebrinae" der Autoren) vorgeschlagen worden. Hier wird der Versuch gemacht, die Berechtigung dieser Namen zu bewerten: 36 taxonomische Einheiten werden als gültige Gruppierungen anerkannt, 56 fallen in Synonymie und zahlreiche Irrtümer und "Berichtigungen" wurden beiseite gelassen. Die auf generischer oder subgenerischer Stufe als gültig anerkannten Namen sind, in den Muricinae: *Murex* s.s., *Haustellum*, *Bolinus*, *Harmatia*, *Chicoreus*, *Siratus*, *Phyllonotus*, *Hexaplex*, *Murexsul*, *Murexiella*, *Maxwellia*, *Pterynotus*, *Naquetia*, *Pterochelus*, *Nothotyphis*, *Poirieria*, *Paziella*, *Panamurex*, und *Muricopsis*; in den Tritonaliinae: *Tritonalia*, *Hadriana*, *Miocenebra*, *Jaton*, *Pterorytis*, *Ceratostoma*, *Pteropurpura*, *Ocinebrellus*, *Calcitrapessa*, *Purpurellus*, *Poropteron*, *Homalocantha*, *Eupleura*, *Vitularia*, *Crassilabrum*, *Urosalpinx*, und *Ocinebrina*. Ausserdem sind 2 spezifische Homonyme neu benannt: *Tritonalia inermicosta* (*Murex fasciatus* Sowerby, nicht Gmelin) und *Tritonalia (Hadriana) craticuloides* (*Murex craticulatus* Brocchi, nicht Linnaeus).

## RÉSUMÉ

## GROUPES SUPRASPECIFIQUES DANS LES SOUS-FAMILLES MURICINAE ET TRITONALIINAE (GASTROPODA: MURICIDAE)

Au moins 90 noms supraspécifiques ont été proposés pour divers groupes dans les sous-familles des Muricinae et Tritonaliinae ("Ocenebrinae" des auteurs). Cet article essaie d'évaluer la validité de ces noms: 36 entités taxonomiques sont reconnues valables comme groupements, 56 sont placées en synonymie et nombre d'erreurs et "d'amendements" sont éliminés. Les noms acceptés comme valides au niveau générique et subgénérique sont, dans les Muricinae: *Murex* s.s., *Haustellum*, *Bolinus*, *Harmatia*, *Chicoreus*, *Siratus*, *Phyllonotus*, *Hexaplex*, *Murexsul*, *Murexiella*, *Maxwellia*, *Pterynotus*, *Naquetia*, *Pterochelus*, *Nothotyphis*, *Poirieria*, *Paziella*, *Panamurex*, et *Muricopsis*; dans les Tritonaliinae: *Tritonalia*, *Hadriana*, *Miocenebra*, *Jaton*, *Pterorytis*, *Ceratostoma*, *Pteropurpura*, *Ocinebrellus*, *Calcitrapessa*, *Purpurellus*, *Poropteron*, *Homalocantha*, *Eupleura*, *Vitularia*, *Crassilabrum*, *Urosalpinx*, et *Ocinebrina*. En outre, 2 homonymes spécifiques sont renommés: *Tritonalia inermicosta* (*Murex fasciatus* Sowerby, non Gmelin) et *Tritonalia (Hadriana) craticuloides* (*Murex craticulatus* Brocchi, non Linné).

## RESUMEN

## GRUPOS SUPRAESPECIFICOS EN LAS SUBFAMILIAS MURICINAE Y TRITONALIINAE (GASTROPODA: MURICIDAE)

No menos de 90 nombres supraespecíficos han sido propuestos para las subfamilias Muricinae y Tritonaliinae ("Ocenebrinae" de los autores). Este trabajo intenta determinar la validez de esos nombres, de los cuales 36 se reconocen como representando grupos válidos, 56 son colocados en sinonimia, y muchas enmiendas y errores son eliminados. Los nombres aceptados como válidos, ya sea en el nivel genérico o subgenérico, son: *Murex* s.s., *Haustellum*, *Bolinus*, *Harmatia*, *Chicoreus*, *Siratus*, *Phyllonotus*, *Hexaplex*, *Murexsul*, *Murexiella*, *Maxwellia*, *Pterynotus*, *Naquetia*, *Pterochelus*, *Nothotyphis*, *Poirieria*, *Paziella*, *Panamurex* y *Muricopsis* en los Muricinae; y *Tritonalia*, *Hadriana*, *Miocenebra*, *Jaton*, *Pterorytis*, *Ceratostoma*, *Pteropurpura*, *Ocinebrellus*, *Calcitrapessa*, *Purpurellus*, *Poropteron*, *Homalocantha*, *Eupleura*, *Vitularia*, *Crassilabrum*, *Urosalpinx* y *Ocinebrina* en los Tritonaliinae. Adicionalmente, se dan nuevos nombres para dos homónimos específicos: *Tritonalia inermicosta* (*Murex fasciatus* Sowerby, no Gmelin), y *Tritonalia (Hadriana) craticuloides* (*Murex craticulatus* Brocchi, no Linnaeus).

СВЕРХВИДОВЫЕ ГРУППЫ В ПОДСЕМЕЙСТВАХ  
MURICINAE TRITONALIINAE (GASTROPODA: MURICIDAE)

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## А Б С Т Р А К Т

Классификация подсемейств *Muricinae* и *Tritonaliinae* содержит не менее 90 сверхвидовых названий. В настоящей статье сделана попытка оценить обоснованность этих наименований, причем 36 названий признаны действительными, 6 отнесены к синонимам, и устранены многие найденные неточности и ошибки. Следующие родовые или подродовые названия признаны действительными: *Murex* S.S., *Haustellum*, *Bolinus*, *Harmatia*, *Chicoreus*, *Siratus*, *Phyllonotus*, *Hexaplex*, *Murexsul*, *Murexiella*, *Maxwellia*, *Pterynotus*, *Naquetia*, *Pterochelus*, *Nothotyphis*, *Poirieria*, *Paziella*, *Panamurex*, и *Muricopsis* *Muricinae*; *Tritonalia*, *Hadriana*, *Miocenebra*, *Jaton*, *Pterorythis*, *Ceratostoma*, *Pteropurpura*, *Ocienbrellus*, *Calcitrapessa*, *Purpurellus*, *Poropteron*, *Homalocantha*, *Eupleura*, *Vitularia*, *Crassilabrum*, *Urosalpinx*, *Ocinebrina* *Tritonaliinae*.

Кроме того, два видовых омонима переименованы: *Tritonalia inermicosta* (*Murex fasciatus* Sby., non Gmelin) *Tritonalia (Hadriana) craticulocidus* (*Murex craticuloides* Brocchi, non Linnaeus).



THE DISTRIBUTION AND ABUNDANCE OF SUBTIDAL BENTHIC MOLLUSCA  
ON THE MAINLAND SHELF OF SOUTHERN CALIFORNIA<sup>1</sup>

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University of Southern California  
Los Angeles, California, U. S. A.

ABSTRACT

Sampling on the mainland shelf of southern California has shown that in this area mollusks do not play the impressive role of faunal dominance, that is reported from other parts of the world, and that they are conspicuous only in a limited number of biota. These are described in the following.

Three major animal communities occur on the northern portion of the mainland shelf of southern California: The *Amphiodia-Cardita*, the *Listriolobus*, and the *Nothria-Tellina* communities all involving pelecypod mollusks.

The *Amphiodia-Cardita* community is a local modification of the more extensive community dominated by the smooth red brittle star *Amphiodia urtica* (Lyman). Specimens of the pelecypod *Cardita ventricosa* Gould comprise about half of the total standing crop. Polychaete worms rank second. The gastropod *Bittium rugatum subplanatum* Bartsch is prominently associated with *Cardita*. Intra-community variation, population density, and the population size structure of *Cardita ventricosa* are analyzed; these analyses are based on 36 samples collected seasonally from a 9-station grid.

In water depths of 30 to 60 m, in a large silt deposit off Santa Barbara, the bottom fauna is dominated by the echiuroid worm *Listriolobus pelodes* Fisher. Among various pelecypod mollusks that commonly occur in this community, *Saxicavella pacifica* Dall may be considered to be the most characteristic because of its specially close (97%) association with *Listriolobus*. In spite of its close association with the community dominant and a frequency of 30 specimens/m<sup>2</sup>, a low mean standing crop value of 4 g/m<sup>2</sup> for *Saxicavella* precludes it from consideration as a co-dominant with an organism that averages 944 g/m<sup>2</sup>. Investigation of the *Saxicavella* population parallels that already described for the *Amphiodia-Cardita* community.

Inshore of the *Listriolobus* community the bottom sediments become progressively coarser, grading from sandy silts to silty sands and finally to sand. These sand bottoms contain a complex of animal associations dominated by a variety of organisms, including the polychaetes *Nothria elegans* (Johnson), *N. irridescentes* (Johnson), *Prionospio malmgreni* Claparede and *Diopatra ornata* Moore and the pelecypod mollusk *Tellina buttoni* Dall. The gastropod *Olivella baetica* Carpenter is prominently associated with *Tellina*. Areas of kelp and rock complicate the faunal pattern in this shallow zone.

In the southern portion of the southern Californian shelf, south of Hueneme submarine canyon, only a single faunal association is extensively distributed: The *Amphiodia urtica* community, which occurs generally on the outer portion, over the entire length of the southern shelf. Here the most abundant mollusks in the community are the pelecypods *Axinopsida serricata* (Carpenter) and *Mysella* spp. Inshore from the *Amphiodia* community, in most regions, sand bottoms are dominated mainly by polychaete communities: The *Nothria-Tellina*, *Diopatra* and *Prionospio* communities. The molluscan fauna of these areas includes a number of small gastropod and pelecypod species. Shallow bottoms may undergo extensive local modification as a result of high population densities of the echinoid *Dendraster excentricus* (Eschscholtz). Rock and kelp modify other areas. The molluscan fauna of the central shelf projection of Santa Monica Bay, the Palos Verdes shelf, the San Pedro Bay shelf, and the southern portion of the San Diego shelf is highly diversified and reflects the complex character of the sediments. The only faunal association involving a pelecypod mollusk on the southern portion of the shelf, that has received adequate study, is the association of

<sup>1</sup>Contribution No. 260 from the Allan Hancock Foundation, University of Southern California.

the pelecypod *Lima dehiscens* Conrad with the parchment worm *Chaetopterus vario-pedatus* (Renier).

A number of southern California pelecypod species, considered economically important, were absent or collected infrequently as juvenile specimens in this investigation. These may dominate small unsampled portions of the shelf.

With the exception of the few associations in which they are prominent, mollusks do not comprise the bulk of the bottom fauna. Mollusks averaged 16.5% of the total number of species, and 12.0% of the total number of specimens in 335 0.25 m<sup>2</sup> Hayward orange-peel bucket (=OPB) samples. They made up only 13.2% of the total macrofaunal standing crop (based on 495 OPB samples).

## INTRODUCTION

Mollusks play a dominant role in many benthic communities described from various parts of the world. Thorson (1957) has listed 23 communities with molluscan dominants and 21 in which other organisms dominate. A description of the distribution and abundance of the subtidal benthic molluscan fauna of the southern California mainland shelf is presented in this paper, and the significance of this faunal component in the structure of the shelf communities is assessed.

No previous study has attempted to cover the entire southern California shelf area. An extensive quantitative survey of the San Pedro Basin was made by Hartman (1955) in which she recorded the biological components of samples from 267 locations. Wilson (1957) catalogued the living molluscan species from the samples collected by Hartman. Based on the systematic work of Wilson, an analysis was made of the dominant trends in the San Pedro molluscan fauna by Bandy (1958). Clark contributed to the knowledge of mollusks in the San Pedro area in a paper by Natland (1957). Hartman (1956) extended her analysis of the southern California benthos with a study of the fauna of Santa Monica Bay, but the results are incomplete in respect to the molluscan elements of these samples.

Beginning in 1956 the sampling program of the Allan Hancock Foundation was extended to cover the mainland shelf of southern California from Point Conception to the Mexican border under a contract with the State Water Pollution Control Board. Some of the results concerning benthic biology have been reported by

Barnard and Hartman (1959), Barnard, Hartman and Jones (1959), Barnard and Zieshenne (1961), Hartman (1960), Hartman and Barnard (1960) and Hartman, Barnard and Jones (1960).

## METHODS

Deep-water samples were collected aboard the research vessel *Velero IV* by a modified Hayward Standard orange-peel bucket (=OPB) with an areal coverage of about 0.25 m<sup>2</sup> (actual rated areal coverage = 2-3/5 square feet). The nearshore portion of the shelf, in water depths of 2.4 to 10.1 m, was sampled from the motor launch of the R/V *Velero IV* using a 1/10 m<sup>2</sup> Van Veen grab. The animals collected were limited by the size of the mesh, 1 mm, through which the sediment was screened aboard ship before preservation and sorting (Durham, 1955; Barnard and Jones, 1960).

## ANALYSIS

For the purpose of this analysis the shelf was divided into eight geographic divisions selected, as much as possible, on the basis of natural differences in such factors as orientation, general shape, sediment character, topography and relative depth. Submarine canyons or prominent headlands were used to delimit the boundaries of these areas. The geographic features selected as boundaries do not necessarily form biological barriers, but do represent convenient markers by which the shelf may be logically divided (Fig. 1). The divisions of the mainland shelf thus determined are:

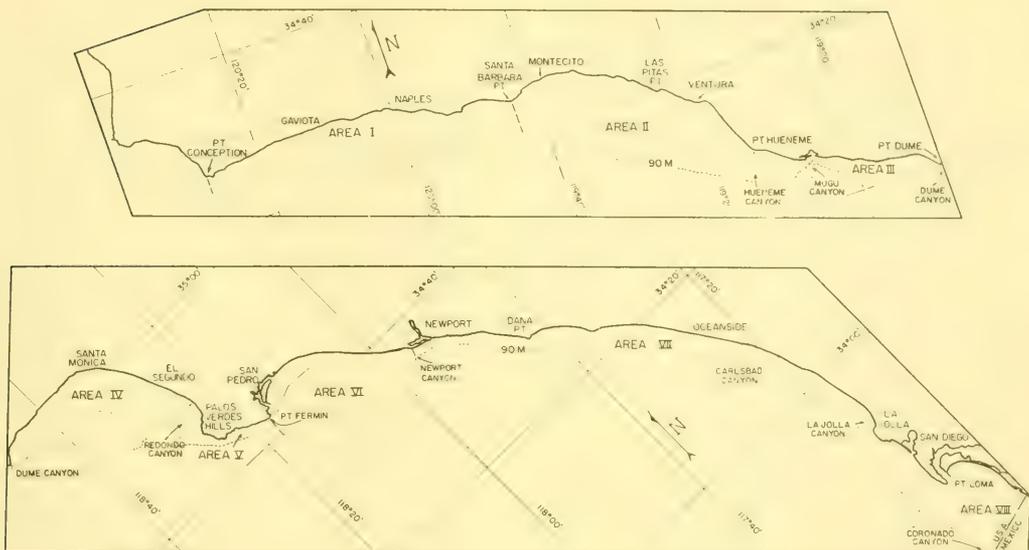


FIG. 1. A map of the mainland shelf of southern California showing the 8 geographic divisions and the place names mentioned in the text.

#### THE NORTHERN SHELF:

Area I, the Point Conception shelf, Point Conception to Santa Barbara Point;

Area II, the Santa Barbara shelf, Santa Barbara Point to Hueneme submarine canyon (subdivided at Las Pitas Point into sub-area IIa, western, and sub-area IIb, eastern);

#### THE SOUTHERN SHELF:

Area III, the Mugu shelf, Hueneme submarine canyon to Point Dume;

Area IV, the Santa Monica Bay shelf, Point Dume to Redondo submarine canyon;

Area V, the Palos Verdes shelf, Redondo submarine canyon to Point Fermin;

Area VI, the San Pedro Bay shelf, Point Fermin to Newport submarine canyon;

Area VII, the Newport-La Jolla shelf, Newport submarine canyon to La Jolla submarine canyon;

Area VIII, the San Diego shelf, La Jolla submarine canyon to Coronado submarine canyon, (off the Mexican border) (subdivided at Point Loma into sub-area VIIIa, northern, and sub-area VIIIb, southern).

A simple planimetric method (Barnard and Jones, 1960) was employed to determine the areal extent of the bottom included within each shelf segment and

within each depth class, and the shelf area covered by each sediment type. These determinations were based on U. S. Coast and Geodetic Charts 5101 and 5202 and, for sediments, on Figures 12, 17 and 20; in Stevenson, Uchupi and Gorsline (1959). The biological description of the faunal associations of the shelf is based in part on the following: Barnard and Hartman (1959), Barnard and Ziesenhenné (1961), Barnard, Hartman and Jones (1959) and Hartman, Barnard and Jones (1960).

Standing crop determinations (wet weight with shells on; method of Thorson, 1957: 492) were made on 495 Hayward orange-peel bucket (=OPB) samples and these were apportioned to the shelf areas as indicated in Table 1. Quantitative determinations were based on 335 OPB samples completely analyzed for all molluscan specimens larger than 1 mm; these were distributed by shelf areas as indicated in Table 1. Van Veen grab samples were collected at 121 nearshore locations, in depths of 2.4 to 10.1 m (mean = 6.7 m); these were arranged in 8 groups of 33 transects. The transects within any given geographic group were separated by a distance of 3.7 km. The

TABLE 1. Distribution of sampling locations by geographic areas

Area	Standing Crop Determinations		Quantitative Determinations		Nearshore Sampling Locations		
	Number Samples	Mean Volume (liters)	Number Samples	Mean Volume (liters)	Transect group Name, Number	Number of Transects per Group	Number of Stations per Group
I	53	33.1	44	32.9	Goleta, 1	4	11
II	124	46.7	74	48.8	Santa Barbara, 2	5	18
					Ventura, 3	4	17
III	35	16.4	19	15.3	-	-	-
IV	46	22.8	43	22.9	Santa Monica, 4	5	16
V	15	51.0	9	49.7	-	-	-
IV	60	18.1	44	19.3	Huntington, 5	4	16
VII	98	36.5	53	32.6	San Onofre, 6	3	17
					Oceanside, 7	3	12
VIII	64	24.6	49	24.9	San Diego, 8	4	14
Total Shelf	495	46.2	335	37.3		33	121

number of sampling locations per transect varied, but the majority had 3 or 4 stations.

Intra-community variation was investigated in 2 benthic communities of the Santa Barbara shelf. Two grids of 9 sampling locations were established. One was located in the *Listriolobus* community (center station, 34°23'08" N. Lat., 119°38'05" W. long., mean depth, 40.6m); the other was in the *Amphiodia-Cardita* community (center station, 34°19'29" N. Lat., 119°40'47" W. long., mean depth, 81.9 m). Each grid consisted of 3 lines of 3 stations about 300 meters apart; the sampling stations within each line were separated by a similar distance. Both grids were sampled 4 times - September, December, 1958; March, June, 1959. Mean values, ranges, standard deviations and coefficients of variation ( $SD/x \cdot 100 = \%$ ) have been calculated for each grid on a seasonal and yearly basis.

#### AREA

The offshore area of southern California is highly complex; it is noted for its islands, bands, ridges, basins, and troughs; hence Shepard and Emery (1941) have designated it by the term "continental borderland".

The mainland shelf of southern California is that portion of the ocean bottom lying immediately adjacent to the land area between Point Conception on the north and the Mexican border on the south. The depth of the outer edge of the shelf varies between 73 and 192 m, but 91 m (the 50 fathom contour of C and GS Charts 5101, 5202) may be taken as an approximate average depth.

#### Geographic Orientation, Size and Shape

The coastline of this part of California is in the form of a shallow concave indentation. Over its 486 km length the trend changes from east-west (Area I) to north-south (Area VIII).

The width of the mainland shelf varies between 22.0 km and about 0.9 km. The broader portions are the Santa Barbara shelf (maximum width, 17.6 km), the Santa Monica Bay shelf (18.0 km), the San Pedro Bay shelf (22.0 km) and the San Diego shelf (16.3 km). The shelf is narrowest at the heads of submarine canyons, as at the heads of Hueneme, Mugu, Dume, Redondo and La Jolla canyons.

#### Depth Distribution of Bottom Area

The area of the bottom included within the depth classes of 0-18, 18-37, 37-55, 55-73 and 73-91 m (based on the 10, 20, 30, 40 and 50 fathom contours of C and

GS Charts 5101, 5202) was determined for the mainland shelf and each of the areas used in the analysis. The distribution of bottom area by depth classes is essentially the same as that for the entire mainland shelf in all regions except Area I, the deepest shelf subdivision, Area IIa, the next deepest, Area IIb, the shallowest subdivision, and Area VI, the next shallowest. More than 50% of the Point Conception shelf lies deeper than 55m, whereas only 30% of the area of the total mainland shelf is below this depth. In the case of the Santa Barbara shelf, if the 37 m contour is selected, the following comparison may be made: in Area IIa 66.5% of the shelf lies below this depth, while in Area IIb only 22.4% is deeper than 37 m. The area of the mainland shelf below 37 m is 49%. The distribution of bottom area by depth classes for the San Pedro shelf is similar to that in Area IIb; here 59% of the bottom lies in water depths of less than 37 m.

#### Sediments of the Mainland Shelf

An analysis of the shoreline facing the open ocean has been made by Emery (1960). Based on his data, 16.5% is rocky, 26.4% is sandy and backed by lowlands, and 57.1% is sandy and backed by cliffs. It should not be surprising then that exposed rock forms the substrate of only 5.1% of the sublittoral area of the mainland shelf while sands, silty sands and sandy silts cover 80% of its area.

The sediment pattern is fairly simple along much of the shelf. Seaward of beaches and littoral and sublittoral rocky areas sediments become progressively finer, grading from sands to silty sands and then to sandy silts and silts toward the edge of the shelf. This generalized pattern of somewhat regular sediment distribution is characteristic of the central portion of the Point Conception shelf, the Mugu shelf, the long narrow Newport-La Jolla shelf, and the northern portion of the San Diego shelf.

The areas of major variation from this generalized pattern that should be noted are the following: (1) the extensive area of "green mud" (silt or sandy silt) which

covers 45-50% of the Santa Barbara shelf and a smaller area of similar sediment at the east end of the Point Conception shelf, (2) the areas of complex bottom sediments surrounding offshore rocky out-crops on the central shelf projection in Santa Monica Bay, on the San Pedro Bay shelf, and the southern portion of the San Diego shelf, (3) areas of coarse sand (particularly relic red sand) on the Santa Monica Bay shelf, the Palos Verdes shelf, the San Pedro Bay shelf, and the southern portion of the San Diego shelf, and (4) areas of blackened sediments affected by hydrogen sulfide from waste discharge operations as on the Santa Monica Bay shelf (Los Angeles City Outfalls), on the Palos Verdes shelf, about 5% of the area (Los Angeles County Outfall), and on the San Pedro Bay shelf (Los Angeles Harbor) (Reish, 1959; Stevenson, Uchupi and Gorsline, 1959).

#### NORTHERN SHELF MOLLUSK FAUNA

Three major animal associations occur on the northern portion of the mainland shelf: the *Amphiodia-Cardita*, the *Lis-triolobus*, and the *Nothria-Tellina* communities (Barnard and Hartman, 1959; Barnard and Ziesenhenné, 1961).

#### *Amphiodia-Cardita* Community

This association with the pelecypod mollusk *Cardita ventricosa* Gould is a modification of the more extensive community dominated by the smooth red ophiuroid *Amphiodia urtica* (Lyman) that occurs generally along the deeper outer portion (60 to 90 m) of the mainland shelf. The *Amphiodia-Cardita* community is the prominent feature of the biota of the Point Conception shelf between the shallow-shelf benthos and the deep-water benthos, thus forming a roughly banded pattern of animal aggregations.

A reflection of this banding is demonstrated in a map of standing crop (Fig. 2). This distribution of molluscan wet weight (method of Thorson, 1957: 492) in g/m<sup>2</sup> is illustrated by contour intervals of 20, 40 and 400 g. There is a ridge of high values along the length of the eastern 3/4 of the shelf. This is the result of the heavy

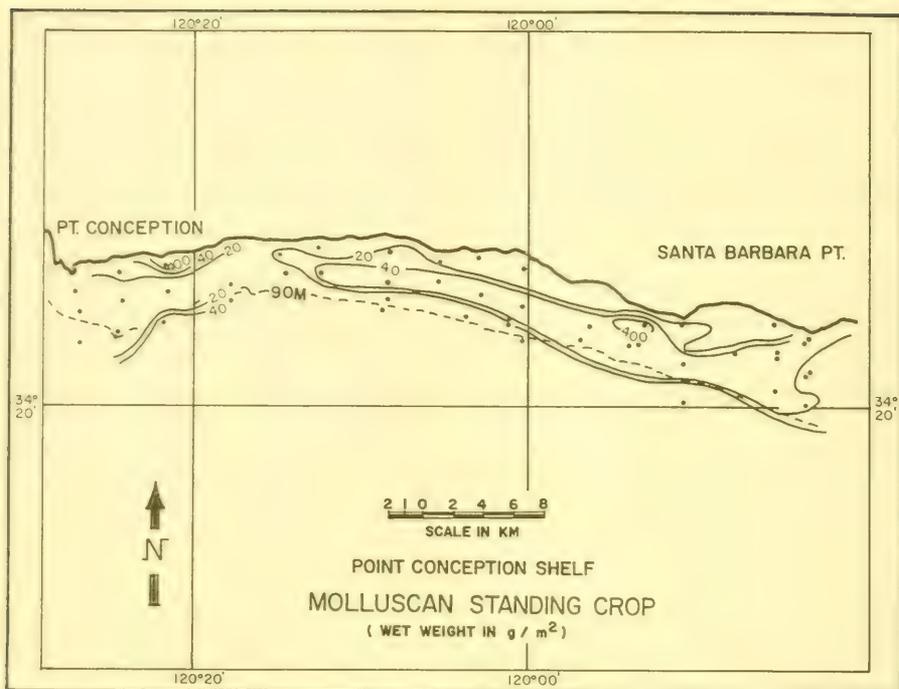


FIG. 2. A map showing the distribution of molluscan standing crop (wet weight in  $g/m^2$ ) on the Point Conception shelf. Contour intervals are 20, 40 and  $400 g/m^2$ .

weights of *Cardita*.

The *Amphiodia-Cardita* fauna also extends across the Santa Barbara shelf. Unlike that on the Point Conception shelf, the community here is not clearly marked by a ridge of high standing crop values. In fact, values diminish to less than  $40 g/m^2$  over most of the community. South of Hueneme submarine canyon the *Amphiodia-Cardita* community is no longer a part of the shelf biota. In fact, the dominant mollusk *Cardita ventricosa* inhabits the slope of San Pedro Basin where it has its center of distribution between 220 and 366 m (see "Dominant Pelecypod Fauna 6" in Bandy, 1958).

Prominently associated with *Cardita* is the gastropod *Bittium rugatum subplanatum* Bartsch. The peak number of this species (264 individuals) on the northern shelf (Point Conception area) was from an OPB sample collected off Orella in 65.2 m. Pelecypods commonly occurring with *Cardita ventricosa* are the following:

*Adontorhina cyclia* Berry, *Aligena redondoensis* Burch, *Axinopsida serricata* (Carpenter), *Mysella* spp., *Nucula tenuis* Montagu, *Nuculana hamata* (Carpenter), *Nuculana oxia* (Dall), *Psephidia lordi* Baird, *Saxicavella pacifica* Dall and *Solamen columbianum* (Dall).

Data from the analysis of 36 OPB samples collected from the 9-station grid off Santa Barbara provide information on intra-community variation, population density of dominants, and the population structure of *Cardita ventricosa* in the *Amphiodia-Cardita* community. Sample volume varied from 12.4-76.5 liters. An analysis of the variation in sample size was made and the results are shown in Table 2. In order to test the relationship of sample volume to each of the biological parameters investigated, coefficients of correlation ( $r$ ) were calculated for each variable. The calculated  $r$  values for the 8 parameters under consideration ranged from -0.002 to +0.251 (Table 2) and all

TABLE 2. *Amphiodia-Cardita* intra-community variation in standing crop (wet weight, g/m<sup>2</sup>) and population density (number/m<sup>2</sup>) for selected organisms and groups based on 36 samples from a 9-station grid<sup>3</sup>

		September	December	March	June	All Seasons	$\bar{r}$ value
Total Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	89.2	113.6	116.8	94.4	103.2	+.251
	S. D.	32.8	33.6	46.0	29.6	35.6	
	$\underline{C}$	37	30	40	31	34	
<i>Cardita ventricosa</i> Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	57.2	50.8	61.6	51.2	52.4	+.208
	S. D.	34.0	31.2	22.4	20.8	30.0	
	$\underline{C}$	61	52	43	40	58	
Polychaete Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	16.8	29.6	23.6	30.0	25.2	+.085
	S. D.	7.2	9.6	20.8	10.8	16.0	
	$\underline{C}$	45	34	37	34	67	
Ophiuroid Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	6.0	11.6	6.4	5.2	7.2	+.084
	S. D.	2.4	2.8	3.2	2.4	3.6	
	$\underline{C}$	27	24	42	63	44	
<i>Cardita ventricosa</i> (number/m <sup>2</sup> )	$\bar{X}$	148	140	156	124	144	+.058
	S. D.	76	72	56	76	68	
	$\underline{C}$	52	54	37	63	50	
<i>Amphiodia urtica</i> (number/m <sup>2</sup> )	$\bar{X}$	144	172	160	96	144	+.215
	S. D.	36	32	56	48	52	
	$\underline{C}$	29	19	37	51	38	
<i>Bittium r. subplanatum</i> (number/m <sup>2</sup> )	$\bar{X}$	4	120	140	132	100	-.002
	S. D.	4	48	40	104	80	
	$\underline{C}$	100	42	31	79	82	
Sample Variation (1/sample)	$\bar{X}$	36.2	39.1	55.5	40.2	42.5	-
	S. D.	16.1	9.6	11.6	20.1	16.1	
	$\underline{C}$	44	24	21	50	38	

<sup>3</sup>See ANALYSIS section; $\bar{X}$  = mean

S. D. = standard deviation

 $\underline{C}$  = coefficient of variation $\bar{r}$  = coefficient of correlationnumber/m<sup>2</sup> values rounded-off to whole numbers.

are below the 5% ( $\bar{r} = 0.325$ ) level of significance. Because of this, direct use of the grid data, without weighting it to account for sample volume, is justified.

A total of 1,286 specimens of *Cardita* were collected in these samples. The mean number per m<sup>2</sup> was 144 specimens (range: 0 to 268). The means for each of the 4 seasonal groups of 9 samples are fairly consistent: 124 to 156/m<sup>2</sup>. However, variation within each group of samples is substantial, as indicated by the ranges, standard deviations and co-

efficients of variation ( $\underline{C}$ ) (Table 2).

*Cardita* comprises half of the total standing crop (based on the grid sample annual means, 52.4/103.2 g/m<sup>2</sup>) of the community. The mean standing crop values for this species are nearly the same for each of the 4 seasonal groups of samples, 50.8 to 61.6 g/m<sup>2</sup>, or 45-64% of the total standing crop. Standing crop  $\underline{C}$  values ranged from 40-61% and thus approximate the observed variation based on the number of specimens per m<sup>2</sup>. Polychaetes comprise the second largest

fraction of the standing crop with a mean value of 25.2 g/m<sup>2</sup> (range: 8.8-77.6).

*Amphiodia urtica*, the other community dominant, averaged 144 specimens per m<sup>2</sup> (range: 12-232). The December mean is highest (172) and the June mean lowest (96). The value of C is lowest in December (19%) and highest in June (51%). These values parallel those for standing crop. Ophiuroid standing crop (principally *A. urtica*) varied from 0.8-16.8 g/m<sup>2</sup> with an annual mean of 7.2 g/m<sup>2</sup>.

The population density of *Bittium r. subplanatum* in the grid samples ranges from 0-344, with a mean of 100/m<sup>2</sup>. It was collected in low numbers in September (mean of 4/m<sup>2</sup>) when it was absent from 4 of 9 samples; the means for the other 3 seasonal groups are 120, 140 and 132/m<sup>2</sup> respectively.

Length measurements were made on all of the *Cardita* specimens from the grid samples. The distribution of the population with respect to size is illustrated in Fig. 3. *Cardita ventricosa* lacks a pelagic larval stage and instead broods its young in pouches in the ctenidia (Jones, in press). The minimum size of females with brooded young was observed to be 10 mm. If the males of this species are sexually mature at a similar size, then the reproducing population would be equal to nearly half (47%) of the total population.

#### *Listriolobus* Community

Inshore from the *Amphiodia-Cardita*

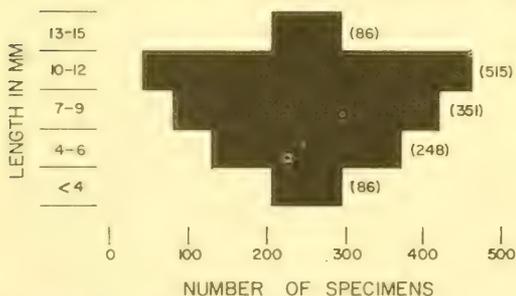


FIG. 3. A pyramid graph showing the size distribution of the *Cardita ventricosa* Gould population in the *Amphiodia-Cardita* community of the Santa Barbara shelf (based on length measurements of 1,286 specimens from 36 OPB grid samples.)

community, in the large silt deposit of the Santa Barbara shelf and in the similar deposit on the Point Conception shelf, is a unique association dominated by the echiuroid *Listriolobus pelodes* Fisher (Barnard and Hartman, 1959). This association occurs in depths of 30 m to 60 m. The greatest development of this association is along the 37 m contour, where the average number of *Listriolobus* is 100/m<sup>2</sup>, representing a standing crop of about 1,000 g/m<sup>2</sup> (wet weight). The maximum standing crop observed in this community was in excess of 1,600 g/m<sup>2</sup>. The eastward extension of this fauna narrows off the Ventura River and merges with the *Nothria-Tellina* community. Beyond this point the *Listriolobus* community does not appear as a distinct faunal unit.

Pelecypods predominate in the molluscan fraction of the *Listriolobus* community. Particularly prominent are the following: *Axinopsida serricata*, *Compsomyx subdiaphana* (Carpenter), *Mysella* spp., *Nucula tenuis*, *Nuculana taphria* Dall and *Saxicavella pacifica*.

*Saxicavella* may be considered to be the characteristic mollusk of this fauna because of its close association, 97% (in grid samples), with *Listriolobus*. Its depth distribution on Santa Barbara shelf is shown in Fig. 4. The greatest abundance occurs between 30 and 40 meters, but there is a lesser peak at 72 meters coincident with high numbers of *Cardita ventricosa*. The depth distribution of *Saxicavella* on the Point Conception shelf is similar. Two regions of high population density were observed: the greater at intermediate depths and the lesser at depths coincident with high numbers of *Cardita*. However, both peaks were located in slightly deeper water (45-58 and 70 m respectively) than on the Santa Barbara shelf. The highest number of *Saxicavella* (102 specimens) in a single OPB grab haul was collected off Naples in 48.2 m of water.

Intra-community variation, population density, and size structure of the *Saxicavella* population were investigated in

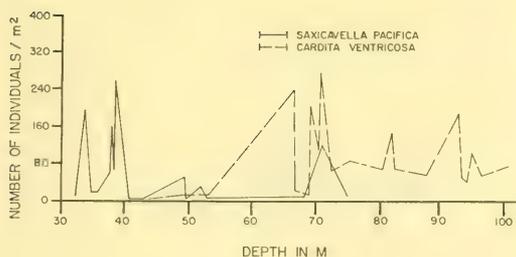


FIG. 4. The depth distribution of *Saxicavella pacifica* Dall and *Cardita ventricosa* Gould on the Santa Barbara shelf.

the *Listriolobus* community by means of a 9-station grid similar to that utilized in the *Amphiodia-Cardita* community. Sample volumes were less variable in this grid, 64.0-87.3 liters. An analysis of the variation in sample size is presented in Table 3. The relationship of sample size to each of the biological variables was again tested by calculating  $r$  values. These values ranged from  $-0.376$  to  $+0.375$ . Three of these, the values for phoronid standing crop ( $-0.376$ ), polychaete standing crop ( $-0.346$ ) and *Saxicavella* number of specimens ( $+0.375$ ), were above (or below in the case of the negative values) the 5% level of significance. Nevertheless, there is good reason to discount their correlation with sample volume and to make direct comparison without weighting the data: (1) the distribution of  $r$  values about the 0.000 correlation level suggests that there is little relationship between sample volume and the magnitude of the standing crop or the abundance of specimens for the parameters considered in the samples from this grid; (2) the coefficients of variation for sample volume determined for the 4 seasonal groups are exceedingly small (5-9%), being 3 times smaller than the smallest  $C$  value for any biological parameter; and (3) all of the grab hauls in the *Listriolobus* grid exceed 42.1 liters, the volume at which the OPB achieves the maximum areal coverage (Barnard and Jones, 1960).

*Listriolobus* comprises 81.5% of the total standing crop of the grid samples. Values range between 397.6 and 1629.2

$m^2$  (mean, 944.4  $g/m^2$ ). The magnitude and pattern of variation in the *Listriolobus* standing crop is very similar to that for total standing crop. Values decrease progressively from the first (September) to the last (June) sampling period. The  $C$  values include the lowest observed in either of the communities studied. The coefficient of variation for *Listriolobus* specimens per  $m^2$  is also low (27%) and equals that for standing crop. The mean number of specimens per  $m^2$  is 92 and ranges from 28-128.

In contrast to the *Amphiodia-Cardita* community, polychaetes comprise a much smaller fraction of the total standing crop. Values range from 13.6-279.2  $g/m^2$  (mean 67.2). Phoronids form a standing crop fraction similar in magnitude to polychaetes in the *Listriolobus* community. Values for these organisms range from 5.2-80.0  $g/m^2$  (mean 39.2) and the number of specimens range from 24-304/ $m^2$  (mean 140).

Mollusk standing crop is much lower in the *Listriolobus* community than in the *Amphiodia-Cardita* association. Mean values are nearly the same (ca. 8  $g/m^2$ ) for all seasonal groups but individual samples range from 2.4-20.0  $g/m^2$ . Variation ( $C$ ) ranges from 35 to 70%.

A total of 980 specimens of *Saxicavella pacifica* were collected in 36 grid samples. The mean number of specimens per  $m^2$  was 120 (range 4-412). The mean standing crop (wet weight) of this species was 4  $g/m^2$ . The mean number of specimens per  $m^2$  based on the 4 seasonal groups decreases during the year from a high of 164 to a low of 64. Values of  $C$  for this species are high, 54-89%. The mean weight of the "average individual" *Saxicavella* (annual mean standing crop per  $m^2$ /annual mean number of specimens per  $m^2$ ) is 0.037  $g/specimen$ . This is small in comparison with the dominant organism of the community, *Listriolobus*, which averages about 10 $g/specimen$ .

The distribution of the *Saxicavella* population with respect to size (length measurement) is illustrated in Fig. 5. The shape of this population pyramid is in

TABLE 3. *Listriolobus* intra-community variation in standing crop (wet weight, g/m<sup>2</sup>) and population density (number/m<sup>2</sup>) for selected organisms and groups based on 35 samples collected from a 9-station grid<sup>4</sup>

		September	December	March	June	All Seasons	$\bar{r}$ value
Total Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	1152.8	1150.8	1180.4	1016.8	1124.4	+.125
	S. D.	367.6	372.6	202.0	165.6	270.8	
	$\underline{C}$	32	28	17	16	24	
<i>Listriolobus pelodes</i> Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	905.2	976.0	914.0	898.8	944.4	+.177
	S. D.	318.4	276.8	174.8	168.0	279.6	
	$\underline{C}$	28	28	19	19	27	
Polychaete Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	34.4	61.2	115.2	54.8	67.2	-.346
	S. D.	20.8	30.4	97.6	23.2	59.6	
	$\underline{C}$	65	51	87	49	88	
Mollusk Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	8.4	7.6	7.6	9.2	8.0	+.242
	S. D.	2.8	5.6	4.0	3.6	4.0	
	$\underline{C}$	35	70	50	40	50	
Phoronid Standing Crop (g/m <sup>2</sup> )	$\bar{X}$	39.2	44.8	47.2	25.2	39.2	-.376
	S. D.	18.8	18.4	22.8	16.8	20.4	
	$\underline{C}$	47	42	48	70	51	
<i>Listriolobus pelodes</i> (number/m <sup>2</sup> )	$\bar{X}$	88	100	96	88	92	+.146
	S. D.	28	24	24	40	24	
	$\underline{C}$	31	24	26	44	27	
<i>Saxicavella pacifica</i> (number/m <sup>2</sup> )	$\bar{X}$	164	172	84	64	120	+.375
	S. D.	88	116	76	44	96	
	$\underline{C}$	54	67	89	71	79	
Phoronids (number/m <sup>2</sup> )	$\bar{X}$	172	148	160	80	140	-.282
	S. D.	68	76	68	64	76	
	$\underline{C}$	40	50	41	81	53	
Sample Variation (1/sample)	$\bar{X}$	76.2	76.7	73.9	77.3	76.2	-
	S. D.	3.8	5.1	7.0	4.0	5.1	
	$\underline{C}$	5	7	9	5	7	

<sup>4</sup>See ANALYSIS section;

$\bar{X}$  = mean,

S. D. = standard deviation,

$\underline{C}$  = coefficient of variation

$\bar{r}$  = coefficient of correlation;

number/m<sup>2</sup> values rounded-off to whole numbers.

marked contrast to the inverted pyramid illustrated for *Cardita ventricosa* (Fig. 4). The minimum length at sexual maturity was not determined for *Saxicavella*.

#### Fauna of Sand Bottoms

Inshore of the *Listriolobus* community the bottom sediments become progressively coarser, grading from sandy silt to silty sand and finally to sand. These bottoms contain a complex of animal

associations dominated by a variety of organisms including the polychaetes *Nothria elegans* (Johnson), *Nothria irridesceus* (Johnson), *Diopatra ornata* Moore, *Prionospio malmgreni* Claparede, and the pelecypod mollusk *Tellina buttoni* Dall. Areas of kelp and rock further complicate the faunal pattern in this shallow zone.

Along most parts of the mainland shelf

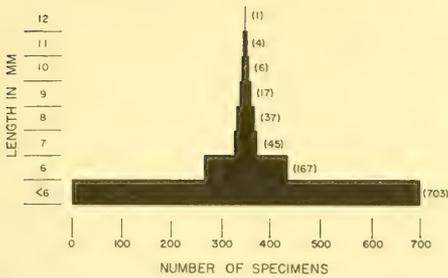


FIG. 5. A pyramid graph showing the size distribution of the *Saxicavella pacifica* Dall population in the *Listriolobus* community of the Santa Barbara shelf (Based on length measurements of 980 specimens from 35 OPB grid samples).

the shallow-water sand fauna is restricted to bottoms near shore and occurs only as a narrow belt inshore from the *Listriolobus* community in the western portion of the Santa Barbara shelf. However, sediments on the eastern portion of the Santa Barbara shelf, off Ventura, are much coarser than those to the west. Here extensive sand bottoms present an acceptable biotope whereby this fauna can extend far from shore (Barnard and Hartman, 1959; Barnard, 1963).

The stations occupied during the "near-shore survey" (Hartman, Barnard and Jones, 1960) furnish excellent examples of the shallow-water molluscan fauna of sand bottoms. On the Santa Barbara shelf 8 transects of 33 locations were sampled with a 1/10 m<sup>2</sup> Van Veen grab in depths of 2.2-10.1 meters (Table 1).

The richness and diversity of the molluscan fauna from the 8-station transect off Santa Barbara is in contrast to that of the remaining 7 lines (Montecito to Ventura). The average values of number of species, 97.0 (30-130) per m<sup>2</sup> and specimens, 1011.0 (400-1910), observed in samples from the Santa Barbara transect are considerably higher than the mean values for the other transects. The values for the eastern lines are 30.0 species per m<sup>2</sup> (range 0-50) and 87.0 specimens/m<sup>2</sup> (range 0-340). Thirty molluscan forms were recorded from the Santa Barbara transect and only 19 from

the remaining 7 nearshore transects. A summary of these results is presented in Table 4.

*Tellina buttoni* and *Olivella baetica* Carpenter are the most abundant species. In the Santa Barbara transect, *Tellina* was nearly 5 times more numerous than *Olivella* with a mean value of 566.0 specimens/m<sup>2</sup> for *Tellina* as compared with 122.0/m<sup>2</sup> for *Olivella*. The situation is somewhat different in the remaining samples from the Santa Barbara shelf. From these remaining stations, *Olivella* was present in 14 out of 15 samples with a mean value of 49.0/m<sup>2</sup> specimens, while *Tellina* was present in only 7 of the 15 samples with a mean of 33.0 specimens/m<sup>2</sup>.

Off Ventura, the shallow-water fauna extends about 3.7 km offshore, to depths of about 25 m. Off Port Hueneme, at the western edge of the submarine canyon, this fauna extends in depths of over 30 m nearly 7 km offshore. More extensive sampling of this sand area revealed faunal gradations not evident elsewhere. A summary of the changes in the conspicuous molluscan faunal elements with depth is shown in Table 5. On this eastern portion of the Santa Barbara shelf, *Tellina* is a prominent faunal element extending nearly 7 km from shore and in depths of 40 m.

#### Fauna of Sand Bottoms in Kelp Beds

The fauna on bottoms associated with kelp beds is one of the richest anywhere along the southern California coast. From Station 4822, in 11.3 m and west of Gaviota, animals were collected that exemplify this type of fauna. The sample contained much plant detritus and had a slight odor of hydrogen sulfide. Here, occurred the highest number of species (321) and specimens (13,280/m<sup>2</sup>) in all animal groups that were collected during this study.

Of mollusks, the pelecypod *Solemya panamensis* Dall was the most abundant (144 individuals/m<sup>2</sup>, or 35.5% of the mollusk specimens). Species of this genus have an interesting distribution in southern California. They have been collected from the shelf, the submarine canyons that cross the mainland shelf, and from

TABLE 4. The results of the analysis of the "Nearshore" samples from the Santa Barbara Shelf (Area II); Transects 5 through 13.

Name of Mollusk	Transect								
	5	6	7	8	9	10	11	12	13
<b>GASTROPODS:</b>									
<i>Acteocina culcitella</i> Gould	X								
<i>Acteon punctocoelata</i> Carpenter						X			
<i>Aglaja</i> sp.	X				X				
<i>Balcis</i> spp.						X	X		
<i>Cerithiopsis</i> sp.	X								
<i>Crepidula</i> sp.	X					X			
<i>Elaeocyma</i> sp.					X	X			
<i>Epitonium</i> sp.		X							
<i>Lacuna</i> sp.	X								
<i>Mangelia</i> spp.	X	X							
<i>Mitrella carinata</i> (Hinds)	X	X			X				
<i>Nassarius perpunguis</i> (Hinds)	X								
<i>Olivella baetica</i> Carpenter	X	X	X		X		X		X
<i>Olivella pedroana</i> (Conrad)					X				
<i>Phasianella</i> sp.	X								
<i>Terebra pedroana</i> (Conrad)	X						X		
<i>Turbonilla</i> spp.	X				X	X			
<i>Volvulella</i> spp.	X								
unidentified species	X								
<b>PELECYPODS:</b>									
<i>Aligena</i> sp.	X								
<i>Amiantis callosa</i> (Conrad)						X			
<i>Chione undatella</i> (Sowerby)	X								
<i>Chlamys</i> sp.	X								
<i>Ensis myrae</i> Berry	X								X
<i>Macoma</i> spp.	X								
<i>Macoma yoldiformis</i> Carpenter	X								
<i>Modiolus</i> spp.	X								
<i>Mysella</i> spp.	X								
<i>Nuculana</i> spp.	X								
<i>Poromya</i> sp.	X				X				
<i>Psephidia brunnea</i> Dall	X								
<i>Siliqua lucida</i> Conrad	X								
<i>Solen</i> sp.	X								
<i>Tellina buttoni</i> Dall	X		X		X	X	X		X
unidentified species	X		X			X			
Number of samples/transect	8	3	1	1	4	3	5	1	2

X indicates organism present in at least one sample/transect.

San Nicolas and Tanner Basins (*Solemya ? johnsoni* Dall; Hartman and Barnard, 1960). Emery (1960) reports high nitrogen percentages of 8.1% and 11.7% respectively from the sediments of these outer deep basins. On the shelf, *Solemya panamensis* is associated with areas of organic debris

such as regions of kelp, oil seeps, and other areas of natural organic material.

Other species often associated with such areas and occurring at this station near Gaviota are the gastropod *Nassarius cooperi* (Forbes) and the pelecypod *Lima dehiscens* Conrad. *Nassarius* is a

TABLE 5. A summary of the changes in the prominent molluscan faunal elements with depth in eastern portion of the Santa Barbara shelf (Area IIa)

Name of Mollusk	Depth (m)				
	0-8	8-15	15-22	22-30	30-46
<i>Olivella baetica</i> Carpenter	X	X	X		
<i>Tellina buttoni</i> Dall	X	X	X	X	X
<i>Siliqua lucida</i> Conrad		X	X	X	
<i>Macoma nasuta</i> (Conrad)			X		
<i>Solen sicarius</i> Gould			X	X	
<i>Ensis myrae</i> Berry				X	X
<i>Compsomyx sudiaphana</i> (Carpenter)				X	X
<i>Macoma yoldiformis</i> Carpenter				X	X
<i>Periploma discus</i> Stearns				X	X
<i>Nuculana taphria</i> Dall				X	X

X indicates organism is present in depth class.

scavenger and has been collected in great numbers from the area near the terminus of the Los Angeles City Outfall<sup>2</sup> in Santa Monica Bay. *Lima dehiscens* occurs at highest concentrations in association with the polychaete *Chaetopterus variopedatus* (Renier) in the area off Inspiration Point on the Palos Verdes shelf. Here the tubes of *C. variopedatus* form large mats on bottoms of blackened sediments high in organic debris. A gastropod species *Mitrella carinata* (Hinds), generally living on kelp, was also conspicuous in the bottom sample from the Gaviota area. Other species from the sample commonly living on shallow-water sand bottoms were the gastropods *Cylichnella attonsa* (Carpenter), *Olivella baetica*, and the pelecypods *Macoma yoldiformis*, *Nuculana taphria* and *Tellina buttoni*.

*Solemya panamensis* and *Nassarius cooperi* were collected in 2 other samples from the rich, shallow water, kelp bottoms off Gaviota. One of these, Station 4938 in 19.5 m, had a rich and diversified molluscan fauna with the highest number of mollusk species (43) and specimens (2796/m<sup>2</sup>) collected from the shallow-water zone

on the northern portion of the mainland shelf. The following forms were conspicuously abundant: the gastropods *Diala ? marmorea* Carpenter (964/m<sup>2</sup>), *Alvania acutilirata rosana* Bartsch (272/m<sup>2</sup>), *Phasianella* sp. (204/m<sup>2</sup>), *Cypraeolina pyriformis* (Carpenter) (116/m<sup>2</sup>), and the pelecypods *Mysella* spp. (280/m<sup>2</sup>), *Tellina buttoni* (212/m<sup>2</sup>), *Solemya panamensis* (104/m<sup>2</sup>), and *Nuculana penderi* (Dall) (76/m<sup>2</sup>).

#### Fauna of Subtidal Rocky Bottoms

Subtidal rocky bottoms were infrequently sampled in this study, but in the few OPB samples collected the most prominent mollusks were chitons. Station 5557 in 19.5 m, a few kilometers east of Point Conception, may be examined as a representative of the subtidal, shallow-water, molluscan epifauna. The sample consisted of 17.8 liters of broken shale. Here, the chiton *Lepidozona* sp. formed 86.5% (896/m<sup>2</sup>) of the mollusk specimens. Other forms present were the gastropods *Lamellaria* sp. (64/m<sup>2</sup>), *Balcis rutila* (Carpenter) (16/m<sup>2</sup>), *Crepipatella linguata* (Gould) (12/m<sup>2</sup>), *Acmaea insessa* (Hinds) (4/m<sup>2</sup>), *Calyptreaea contorta* (Carpenter) (4/m<sup>2</sup>), nudibranch (4/m<sup>2</sup>), *Phasianella* sp. (4/m<sup>2</sup>), *Olivella baetica* (4/m<sup>2</sup>); the pelecypods *Modiolus* sp. (8/m<sup>2</sup>), *Asthenothaerus villosior* Carpenter (4/m<sup>2</sup>), *Kellia laperousii* Deshayes (4/m<sup>2</sup>), *Solamen columbianum* (Dall) (4/m<sup>2</sup>),

<sup>2</sup>Collected by the Hyperion Engineers, 1.8 km seaward of the One-Mile Outfall in Santa Monica Bay (Collector, C. Imel), December, 1958; about 10,000 specimens collected clinging to a 0.6 meter diameter baited crab net.

and unidentified pelecypods ( $8/m^2$ ).

#### Fauna of the Outer Shelf and Slope

Seaward of the *Amphiodia-Cardita* community of the northern portion of the mainland shelf and of the *Amphiodia* community along the southern portions of the shelf, bottoms of the deeper shelf and slope are populated by associations in which the polychaetes *Omuphis nebulosa* Moore, *Pectinaria californiensis* Hartman, *Chloeia pinnata* Moore, *Travisia pupa* Moore, and *Pista disjuncta* Moore, the ophiuroids *Amphiacantha amphacantha* (McClendon), and *Amphiodia digitata* Nielsen, the echinoids *Brisaster townsendi* (A. Agassiz) and *Brissopsis pacifica* (A. Agassiz), and the pelecypod mollusks *Acila castrensis* (Hinds) and *Amygdalum pallidulum* (Dall) are prominent. This deeper shelf fauna is common to all of the areas of the mainland shelf.

Stations below 110 m on the Point Conception shelf are characterized by the following pelecypod species: *Adontorhina cyclia*, *Amygdalum pallidulum*, *Axinopsida serricata*, *Nuculana hamata*, *Tellina carpenteri* Dall, *Nemocardium centrifilum* (Carpenter) and *Acila castrensis*. The deep-water fauna was sampled more extensively covering a much greater area and to a slightly deeper depth on the Santa Barbara shelf than on the Point Conception shelf. Two additions to the molluscan fauna, not encountered on the Point Conception shelf, are the gastropods *Solariella peramabilis* Carpenter and *Nassarius insculptus* (Carpenter). Both are characteristic of deeper water.

#### SOUTHERN SHELF MOLLUSK FAUNA

South of Hueneme submarine canyon only one faunal association is extensively distributed. The *Amphiodia urtica* community occurs generally on the outer portion over the entire length of the southern shelf. The degree of its development is variable, and its distribution is discontinuous. It is reduced or missing in areas of great substrate complexity such as the central shelf projection in Santa Monica Bay, the Palos Verdes shelf,

the San Pedro shelf and the southern portion of the San Diego shelf (Barnard and Ziesennehenne, 1961).

Inshore from the *Amphiodia* community, in most regions, sand bottoms are dominated by associations similar to those described on the eastern portion of the Santa Barbara shelf. The most important of these are the *Nothria-Tellina*, *Diopatra* and *Prionospio* communities. Shallow bottoms may undergo extensive local modification as the result of high population densities of the echinoid *Dendraster excentricus* (Eschscholtz). Rock and kelp modify other areas. Southern shelf regions generally conforming to this pattern of faunal associations are (1) the short, narrow Mugu shelf, (2) the northern portion of the Santa Monica Bay shelf, (3) the long (104 km) but narrow Newport-La Jolla shelf, (4) and to a lesser extent the northern portion of the San Diego shelf. In the last named region subtidal rock and coarse sand cover much of the shallow-water region.

In these 4 regions the shallow-water molluscan fauna is somewhat similar to that on the eastern portion of the Santa Barbara shelf. In water depths of less than 15 meters, on sand bottoms the gastropods *Olivella baetica*, *Nassarius perpinguis* Hinds and *Cylichnella attonsa*, and the pelecypods *Tellina buttoni*, *Macoma nasuta* (Conrad) and *Siliqua lucida* (Conrad), are prominent. In somewhat deeper water the pelecypods *Solen.sicarius* Gould, *Ensis myrae* Berry, *Chione undatella* (Sowerby), *Periploma discus* Stearns and *Macoma yoldiformis* become more conspicuous.

Many mollusks associated with the *Lis-triobolus* community on the Santa Barbara shelf occur at intermediate depths (30-60 m) in these regions. Noteworthy are the pelecypods *Compsomyx subdiaphana*, *Nuculana taphria*, *Mysella* spp., *Axinopsida serricata*, *Nucula tenuis* and *Saxicavella pacifica*. Several of these, *Nuculana taphria*, *Mysella* and *Axinopsida*, have wide bathymetric ranges and may be expected in samples collected at almost any depth on the shelf. Although *Saxi-*

*cavella* was collected in bottom samples in some of these areas, it did not occur in the high numbers observed on the Santa Barbara shelf.

*Mysella* spp. and *Axinopsida serricata* are particularly abundant on bottoms between 60 and 90 m, the depth range of the *Amphiodia-Cardita* community of the northern shelf. Occurring with them are the pelecypods *Nemocardium centifilosum*, *Aligena redondoensis*, *Adontorhina cyclia* and *Nucula tenuis*. *Adontorhina* is most numerous in samples from the northern portion of the San Diego shelf.

The deep-water shelf and slope fauna is similar to that encountered on the northern portion of the mainland shelf. Additions include the pelecypods *Cardita ventricosa* and *Huxleyia (=Cyrilla) munita* (Dall) and the gastropods *Bittium eschrichtii* Middendorff and *Amphissa bicolor* Dall.

The remaining regions of the southern portion of the mainland shelf are characterized by complex patterns of substrate and faunal associations. Hartman (1956) employed the term "patchiness" to describe the arrangement of the various animal aggregations of Santa Monica Bay; her term might be applied with equal accuracy to the Palos Verdes shelf, the San Pedro Bay shelf or the San Diego shelf. Nearly a dozen communities exist in these areas. These include, in addition to the widely distributed *Amphiodia urtica*, *Nothria-Tellina*, *Diopatra* and *Prionospio* communities, a number of rather specialized faunal associations most of which occupy only a small fraction of the bottom area. These communities were infrequently sampled, and hence are poorly known.

Three communities merit attention; these are the *Amphioplus hexacanthus* community of the San Pedro shelf (13-55 m), the *Nothria stigmatus* (Treadwell)-*Spiophanes bombyx* (Claparede) or "red sand" community of all 4 regions, and the *Chaetopterus* community of the Palos Verdes shelf (10-28 m).

The *Amphioplus hexacanthus* community

is a modification of the *Amphiodia urtica* association. The latter species is considered a subdominant (Barnard and Ziesenhenné, 1961). The inarticulate brachiopod *Glottidia albida* (Hinds) reaches its maximum abundance in this community (Jones and Barnard, in press). The following polychaetes are abundant: *Aricidea* spp., *Chloeia pinnata*, *Pectinaria californiensis*, *Prionospio malmgreni* and *P. pinnata* Ehlers. The molluscan fauna of this association is rich (maximum, 30 species and 150 specimens/m<sup>2</sup>) but highly variable from sample to sample. Common elements are few and include the following: the gastropods *Turbonilla* spp., *Eulima* spp., *Bittium* spp. and *Olivella baetica*; the pelecypods *Mysella* spp., *Tellina buttoni* and *Nuculana taphria* and the scaphopod *Cadulus* spp.

Deposits of coarse red (iron oxide-stained) sands occur on the Santa Monica (10-30 m), San Pedro (5-90 m), Palos Verdes (10-90 m) and San Diego (18-40 m) shelves. These relic deposits are the most distinctive coarse-fraction type on the southern California mainland shelf. The macrofauna of this biotope is equally interesting. The polychaetes *Nothria stigmatus* and *Spiophanes bombyx* dominate. Other conspicuous species include the cephalochordate *Branchiostoma californiensis* Andrew, the sand crab *Blepharipoda occidentalis* Randall, the sipunculid *Sipunculus nudus* Linnaeus and the echinoderm *Lovenia cordiformis* A. Agassiz. Molluscan elements of this association include the pelecypods *Cardita bailyi* Burch, *Glycymeris corteziana* Dall and *Tellina buttoni*, and the gastropods *Micranellum crebricinctum* (Carpenter), *Halistylus subpupoideus* Tryon, *Phasianella* sp., *Alabina* sp., *Margarites* sp. and *Olivella baetica*.

The most prominent feature of the biota of the Palos Verdes shelf is the *Chaetopterus* community. Here on black sand and mixed bottoms, in relatively shallow depths close to shore, the parchment worm *Chaetopterus variopedatus* forms masses of its tubes. Prominently associated with it is the pelecypod *Lima*

TABLE 6. A summary by geographic areas of the mollusks collected in 40% or more of the 335 OPB samples from the mainland shelf of southern California (no data from Area V).

Name of Mollusk	Areas							
	I	IIa	IIb	III	IV	VI	VII	VIII
<i>Psephidia lordi</i>	X							
<i>Nucula tenuis</i>	X	X						
<i>Nemocardium centifilosum</i>	X	X						
<i>Cardita ventricosa</i>	X	X						
<i>Compsomyx subdiaphana</i>	X	X	X					
<i>Saxicavella pacifica</i>		X						
<i>Macoma yoldiformis</i>			X					
<i>Odostomia</i> spp.			X					
<i>Periploma discus</i>			X					
<i>Tellina buttoni</i>			X	X				
<i>Mangelia</i> spp.				X	X			
<i>Chaetodermantia</i>					X			
<i>Balcis</i> spp.					X			
<i>Tellina carpenteri</i>	X			X	X	X		
<i>Axinopsida serricata</i>	X	X	X	X	X	X	X	
<i>Volvulella</i> spp.	X		X	X			X	
<i>Mysella</i> spp.	X	X	X	X	X	X	X	X
<i>Cylichnella attonsa</i>	X		X	X	X		X	X
<i>Nuculana taphria</i>		X	X		X		X	
<i>Turbonilla</i> spp.			X	X	X	X	X	
<i>Cadulus</i> spp.			X			X	X	X
Number of samples	44	44	43	19	43	44	53	49

*dehiscens* (maximum, 404/m<sup>2</sup>). Other mollusks associated with this community are the gastropods *Nassarius cooperi*, *Nassarius perpinguis*, *Conus californicus* Hinds and *Mitrella carinata*, and the pelecypods *Solemya panamensis* and *Parvilucina tenuisculpta*. Other conspicuous species of this association are the polychaetes *Diopatra ornata* and *Phyllochaetopterus prolifica* Potts and the elbow crab *Heterocrypta occidentalis* (Dana).

Standing crop values measured in this community are higher than any on the shelf except for the *Listriolobus* association. In *Chaetopterus-Lima* association samples standing crop values in excess of 1,300 g/m<sup>2</sup> have been recorded. This association has been described previously by Hartman (1955) and Barnard, Hartman and Jones (1959).

#### QUANTITATIVE ANALYSIS

Quantitative observations on the frequency of mollusks on the mainland shelf are based on 335 completely analyzed OPB samples. A summary of the mollusks which occurred in 40% or more of these samples is presented by shelf regions in Table 6. Using these same samples as a basis, a summary was made to determine the most abundant benthic mollusks on the mainland shelf. Species included comprise at least 10% of the specimens in at least 20% of the samples from any given geographic region. The results of this analysis are contained in Table 7.

The mean number of species per 0.25 m<sup>2</sup> OPB sample is 15.2 (range 0-43), representing 16.5% (range 0-34.0) of the mean total number of species of all groups

TABLE 7. The most abundant mollusks from 335 OPB samples from the mainland shelf of southern California. Values are the per cent of stations at which these species exceed the 10% level of abundance

Name of Mollusk	Areas								Entire Shelf
	I	IIa	IIb	III	IV	VI	VII	VIII	
<i>Axinopsida serricata</i>	48	45		27	51	25	32		32
<i>Cardita ventricosa</i>	30	34							
<i>Bittium r. subplanatum</i>	30	23							
<i>Mysella</i> spp.		30		27	39		28	20	25
<i>Nucula</i> spp.		27							
<i>Saxicavella pacifica</i>		23							
<i>Tellina buttoni</i>			47	27	33	30	30	29	25
<i>Nuculana taphria</i>			20						
<i>Adontorhina cyclia</i>								20	
Number of Samples	44	44	30	19	43	44	53	49	335

per sample. The average number of specimens per  $m^2$  is 368.4 (range 0-4,112). This represents 12.0% (range 0-50.5%) of the average total number of individuals per  $m^2$ . The mean values for the 8 geographic shelf regions are summarized in Table 8.

The average number of species per OPB sample does not vary greatly from one area to the next, and the mean calculated for the Santa Monica Bay shelf was highest (18.9). The mean for the Point Conception shelf, 18.3, ranked second, but this area had the sample with the highest number of species in a single grab haul (43). The lowest values were for the Palos Verdes shelf, 12.7, and the San Diego shelf, 12.3. The mean number

of specimens per  $m^2$  was highest in samples from the Point Conception shelf, 712.0. The Santa Monica Bay shelf ranked second with 536.8. The lowest means for the number of specimens per  $m^2$  were on the Palos Verdes shelf, 205.2, and the San Diego shelf, 224.8.

The abundance of mollusks in the shallow water of the shelf near shore (2.4-10.1 m in depth) was determined on the basis of 100 completely analyzed 1/10  $m^2$  Van Veen grab samples. Only a few species were present in a high percentage of the samples examined and only one, *Tellina buttoni*, was present in more than 50% of the samples. *Olivella baetica* was encountered in 45% of the samples. Table 9 lists the forms present in more than

TABLE 8. The mean number of species per sample and specimens per  $m^2$  in the 8 geographic regions of the southern California mainland shelf.

Area	Mean Sample Volume (liters)	Mean (Range) (Species/Sample)	Mean (Range) Specimens/ $m^2$
I	32.9	18.3 (4-43)	712.0 (24-4112)
II	49.7	15.7 (3-35)	365.2 (28-1500)
III	15.3	16.4 (3-33)	433.6 (24-1472)
IV	22.9	18.9 (5-30)	536.8 (36-1568)
V	49.7	12.7 (1-23)	205.2 (16-724)
VI	19.3	14.3 (1-30)	282.0 (4-940)
VII	32.6	14.7 (1-31)	370.0 (4-1912)
VIII	24.9	12.3 (0-30)	224.8 (0-732)

TABLE 9. The most frequently occurring mollusks in 100 Van Veen grab samples from the nearshore portion of the mainland shelf of southern California, in depths from 2.4-10.1 m.

Name of Mollusk	% of Samples
<i>Tellina buttoni</i>	58
<i>Olivella baetica</i>	45
<i>Mangelia</i> spp.	23
<i>Mysella</i> spp.	17
<i>Crepidula</i> spp.	15
<i>Turbonilla</i> spp.	11

10% of these samples.

Seven of the 100 samples failed to contain living mollusks. The remaining 93 had an average of 3.9 species per sample (range 1-17). The mean number of specimens per m<sup>2</sup> was 178.0 (range 10-1630). On the deeper portions of the shelf (10-90+ m) the mean number of mollusk specimens per m<sup>2</sup> is 368.4 (based on 335 OPB samples).

Standing crop values for the mainland shelf are based on wet weight determinations made on 495 OPB samples. The mean standing crop is 24.4 g/m (range from 0.4-546.0), which represents an average of 13.2% (range 0.1-97.5%) of the mean total standing crop. Mean values of standing crop for the 8 shelf regions are summarized in Table 10.

Using the mean value for the number of specimens per m<sup>2</sup> and the molluscan

standing crop mean per m<sup>2</sup>, it is possible to calculate the weight of the "average subtidal benthic mollusk specimen". The result yielded is 0.066 g wet weight. This figure would be reduced further if the individuals (mostly immature forms) of less than 1 mm diameter were included in the calculation.

## DISCUSSION

According to Thorson (1957: 504) "the same types of bottoms are everywhere inhabited by species of 'parallel' animal communities, in which different species, of the same genera, replace one another as 'characterizing species.'" His extensive review illustrates the concept of "uniformity of the level sea bottom and its fauna" throughout the world. Mollusks and ophiuroids comprise the majority of all community dominants and these are restricted to a few genera: *Macoma*, *Tellina* and *Mercenaria* (= *Venus*) in the case of mollusks and *Amphiura* and *Amphiodia* among the ophiuroids are particularly important. Thorson summarizes 4 ophiuroid communities from the Pacific. Three are dominated by species of *Amphiodia* alone or in conjunction with co-dominants (*Turritella* in Japan and *Schizaster* in Chile) and one by *Amphioplus*.

Ophiuroid communities populate 26% of the southern California mainland shelf between 0 and 91 m (Barnard and Ziesenhenné, 1961). The major community of

TABLE 10. The mean standing crop values (wet weight, g/m<sup>2</sup>) for the 9 geographic areas of the mainland shelf of southern California based on 495 OPB samples.

Area	Mean Sample Volume (liters)	Mean Standing Crop (Range) in g/m <sup>2</sup>	% Mean Total Standing Crop (Range)
I	33.1	58.8 (0.4-546.0)	20.6 (0.1-69.4)
II	48.3	31.6 (0.4-258.0)	15.7 (0.1-97.5)
III	16.4	23.6 (0.4-161.6)	8.7 (0.1-51.6)
IV	22.8	14.4 (0.4-210.0)	11.7 (0.1-65.6)
V	51.0	88.8 (0.4-340.0)	11.8 (0.1-51.7)
VI	18.1	10.8 (0.4-101.2)	11.6 (0.1-40.9)
VII	36.5	14.8 (0.4-323.2)	8.6 (0.1-95.0)
VIII	24.6	18.0 (0.4-364.0)	14.1 (0.1-90.7)

the shelf is dominated by an ophiuroid, *Amphiodia urtica*. The *Amphiodia occidentale* community described by Weese and MacNab (1930) in Puget Sound has certain elements in common with the southern California fauna such as the mollusks *Parvilucina* (= *Phacoides*) *temisculpta*, *Pandora filosa*, *Macoma yoldiformis*, *Tellina* spp., *Psephidia* spp., *Dentalium* sp., *Lima* sp. and *Calyptraea* (the northern species, however), the polychaete *Sternaspis fossor* and the dominant organism *Amphiodia occidentale*. However, with the exception of *Sternaspis*, none of these are quantitatively important in the *Amphiodia urtica* community, which does not appear to parallel closely any of the Pacific ophiuroid communities outside the southern California area.

On the northern portion of the mainland shelf *Amphiodia urtica* co-dominates with the pelecypod *Cardita ventricosa* in the most important modification of the more extensive ophiuroid community. Lee (1944) has described a community from the east coast of the United States (off Martha's Vineyard, 10-14 m, mud with stones) that is dominated by the polychaete *Flabelligera* (= *Trophonia*) *affinis* and another member of the genus *Cardita*, *Cardita* (= *Venericardia*) *borealis*. Except for this similarity in molluscan co-dominants there is no parallelism between these 2 communities. The *Amphiodia-Cardita* community appears to be closely related only to the other ophiuroid communities of southern California.

The most important molluscan dominant on the southern California mainland shelf is the pelecypod *Tellina buttoni*. It is associated with the polychaete *Nothria elegans* in 3 sand dwelling assemblages, facies of the *Nothria-Tellina* community. These have been described in detail by Barnard (1963), who also discusses the relationship of the southern California *Nothria-Tellina* community to the *Tellina* communities of other areas. He cites the presence of a polychaete as a co-dominant, the occurrence of *Olivella baetica* rather than of terebrid snails as the important gastropods, and the importance of poly-

chaetes as a major element in the standing crop as the principal differences between this and the other *Tellina*-dominated communities.

Mollusks occur in important association with the dominant organisms of 2 other communities of the southern California shelf. *Saxicavella pacifica* forms an important element of the *Listriolobus pelodes* community where it averages 120/m<sup>2</sup> and forms a 97% association with the dominant. Its small size and low standing crop (4 g/m<sup>2</sup>) preclude its being considered a co-dominant in an association where the principal organism comprises 81.5% of the standing crop, averaging 944 g/m<sup>2</sup> and 92 specimens/m<sup>2</sup>. *Lima dehiscens* plays a somewhat analogous role in the *Chaetopterus variopedatus* community. Standing crop values of the dominant organism far exceed those of any other organism in the association including *Lima*, which attains a maximum value of only 6% of the total standing crop. Communities parallel to these 2 southern California faunal associations apparently are yet to be described from other parts of the world.

Molluscan community dominants and characterizing species are drawn from a relatively few genera. The most important of these are listed in systematic order by families (Thorson, 1957; Sanders, 1956, 1958; Keen, 1963): *Nucula* (Nuculidae); *Nuculana* and *Yoldia* (Nuculanidae); *Arca* (Arcidae); *Pecten* (Pectinidae); *Astarte* (Astartidae); *Cardita* (Carditidae); *Lucinoma* (Lucinidae); *Cardium* (Cardiidae); *Mercenaria* (= *Venus*), *Protothaca* (= *Tapes*; *Paphia*) and *Dosinia* (Veneridae); *Spisula* (Mactridae); *Tellina* and *Macoma* (Tellinidae); *Donax* (Donacidae); *Syndesmya* (Semelidae); *Mya* (Myidae); *Pandora* (Pandoridae); *Turritella* (Turritellidae); *Cerithium* (Cerithiidae); *Nassarius* (= *Nassa*) (Nassaridae) and *Philine* (Philinidae).

A number of representatives of these groups collected in this study are important components of the subtidal molluscan fauna of the southern California shelf: *Acila castrensis* and *Nucula temis*

(Nuculidae); *Nuculana taphria* and *Nuculana hamata* (Nuculanidae); *Cardita ventricosa* (Carditidae); *Nemocardium centifilum* (Cardiidae); *Compsomyx subdiaphana* and *Psephidia lordi* (Veneridae); *Macoma yoldiformis*, *Macoma nasuta*, *Tellina buttoni* and *Tellina carpenteri* (Tellinidae); *Bittium rugatum subplanatum* (Cerithiidae); and *Nassarius perpinguis* and *Nassarius cooperi* (Nassaridae).

However, a second group of important species, including many of the most frequently occurring and abundant forms on the southern California shelf, are not included in these taxa (see Tables 6 and 7). These are the pelecypods *Solemya panamensis* (Solemyacidae); *Glycymeris corteziana* (Glycymerididae); *Amygdalum pallidulum* and *Solamen columbianum* (Mytilidae); *Lima dehiscens* (Limidae); *Aligena redondoensis* (Kelliidae); *Mysella* spp. (Montacutidae); *Adontorhina cyclica* and *Axinopsida serricata* (Thyasiridae); *Solen sicarius*, *Ensis myrae* and *Siliqua lucida* (Solenidae); *Saxicavella pacifica* (Hiatellidae); *Periploma discus* (Periplomatidae); and the gastropods *Balcis rutila* and *Eulima* spp. (Eulimidae); *Crepidula* spp. (Calyptraeidae); *Mitrella carinata* (Columbellidae); *Olivella baetica* (Olividae); *Mangelia* spp. (Turridae); *Volvulella* spp. (Retusidae); *Turbonilla* spp. (Pyramidellidae); *Acteocina culcitella* and *Cylichnella attonsa* (Scaphandridae); and the scaphopod *Cadulus* spp. (Siphonodentaliidae); and aplacophorans of the order Chaetodermatina.

A number of southern California pelecypod species, considered economically important, were absent or collected infrequently as juvenile specimens in the samples gathered in this investigation. Many of these species attain considerable size, form "beds" and thus may dominate small unsampled portions of the shelf. For the most part, however, they are limited to lagoons, harbors and other embayments where a number of species form prominent elements of the fauna of the intertidal mud flats (Fitch, 1953).

With the exception of the few associations in which they are prominent, mol-

lusks do not comprise the bulk of the subtidal macrofauna of the southern California mainland shelf. Mollusks averaged 16.5% of the total number of species, and 12.0% of the total number of specimens in 335 0.25 m<sup>2</sup> Hayward orange-peel bucket (=OPB) samples. They made up only 13.2% of the total macrofaunal standing crop (based on 495 OPB samples). Certainly mollusks do not play the impressive role of faunal dominance in the southern California area that is reported for other parts of the world.

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#### ZUSAMMENFASSUNG

##### VERBREITUNG UND HÄUFIGKEIT DER MOLLUSKEN AM MEERESBODEN DER KONTINENTALLEISTE SÜDKALIFORNIENS

Probeentnahmen aus dem Benthos der südkalifornischen Küstenbank unterhalb der Gezeitenzone haben gezeigt, dass Weichtieren, in dieser Gegend, nicht die beeindruckende Rolle faunaler Dominanz zukommt, wie sie aus anderen Teilen der Welt bekannt ist, und, dass Mollusken nur in einer beschränkten Anzahl von Biozönosen hervortreten, wie folgt.

Am Boden des nördlichen Teiles der Kontinentalleiste Südkaliforniens kommen 3 wichtige Lebensgemeinschaften vor, die Muscheln einschliessen: die *Amphiodia-Cardita*, die *Listriolobus* und die *Nothria-Tellina* Gemeinschaften.

Die Erstere ist eine örtliche Abänderung einer Biozönose grösseren Ausmasses, in welcher der glatte rote Seestern *Amphiodia urtica* (Lyman) dominiert. Individuen der Muschel *Cardita ventricosa* Gould machen ungefähr die Hälfte der Gewichtsausbeute aus. Polychaete Würmer stehen an zweiter Stelle. Auffallend tritt der Gastropode *Bittium rugatum subplanatum* Bartsch zusammen mit *Cardita* auf. Variationen innerhalb der Biozönose, die Dichte der *Cardita* Population und deren Grössenstruktur wurden mittels 36 Proben untersucht, die zu verschiedenen Jahreszeiten aus einem Netz von 9 Standorten entnommen wurden.

In Wassertiefen von 30 - 60 m, auf einer bedeutenden Schlammablagerung vor Santa Barbara, dominiert in der Bodenfauna der echiuroide Wurm *Listriolobus pelodes* Fischer. Unter den verschiedenen hier vorkommenden Muscheln ist, wegen ihrer besonderen innigen Assoziation (97%) mit *Listriolobus*, *Saxicavella pacifica* Dall die Wichtigste. Trotz dieser engen Verbundenheit und einer Dichte von 30 Individuen/m<sup>2</sup>, macht der niedrige mittlere Gewichtsertrag (4 g/m<sup>2</sup>) von *Saxicavella* es unmöglich sie als Kodominante eines Organismus anzusehen dessen mittlere Gewichtsausbeute 944 g/m<sup>2</sup> beträgt. Die Untersuchungen über die *Saxicavella* Population entsprachen in jeder Hinsicht denen über *Cardita*.

Von dieser *Listriolobus* Biozönose gegen die Küste hin werden die Ablagerungen progressiv gröber, mit einem allmählichen Wandel von sandigem Schlamm, über schlammigen Sand bis zu reinem Sand. Diese Sandböden beherbergen einen verwickelten Biozönosen-Komplex, worin verschiedene Organismen dominieren, darunter auch die

Polychaeten *Nothria elegans* (Johnson), *N. irridescens* (Johnson), *Prionospio malmgreni* Clarapède und *Diopatra ornata* Moore, sowie die Muschel *Tellina buttoni* Dall. Mit dieser Letzteren ist hauptsächlich die Schnecke *Olivella baetica* Carpenter assoziiert. In dieser seichten Zone komplizieren ferner Seetang und Felsenpartien das Verbreitungsbild.

Im südlichen Teil der südkalifornischen Kontinentalleiste, südlich der Huene-Unterwasserschucht, ist nur eine Biozönose weitgehend verbreitet, nämlich die *Amphiodia* Gemeinschaft, die allgemein über die gesamte Länge des Aussenrandes der Kontinentalleiste anzutreffen ist. Hier sind die am häufigsten auftretenden Weichtiere die Muscheln *Axinopsida serricata* (Carpenter) und *Mysella* spp. Zur Küste hin dominieren auf sandigen Böden an den meisten Stellen die folgenden Polychaeten-biozönosen: die *Nothria-Tellina*, *Diopatra* und *Prionospio* Gemeinschaften. Die Molluskenfauna dieses Gebietes umfasst eine Anzahl kleiner Muscheln und Schnecken. An seichten Stellen wird die Fauna des öfteren durch gehäuftes Vorkommen des Seeigels *Dendraster excentricus* weitgehend örtlich verändert und zuweilen auch durch das Vorkommen von Felsen und Seetang. Die Molluskenfauna der vorspringenden Mittelpartie der Kontinentalleiste vor der Santa Monica Bucht, der Leiste vor Palos Verdes, vor der San Pedro Bucht und des südlichen Teiles der San Diego Leiste ist mannigfaltig und spiegelt die komplizierte Natur der Sedimente wieder. Die einzige Biozönose des südlichen Teiles der Kontinentalleiste, die eine Muschel umfasst und auch genügend erforscht ist, ist die Association der Muschel *Lima dehiscens* Conrad mit dem Wurm *Chaetopterus variopedatus* (Renier).

Eine Anzahl südkalifornischer Muscheln, die als ökonomisch wichtig gelten, wurden im Verlaufe dieser Untersuchung nicht, oder nur selten und in jungen Exemplaren angetroffen. Möglicherweise dominieren sie auf kleinen, nicht untersuchten Teilen der Kontinentalleiste.

Mit Ausnahme der wenigen Assoziationen wo sie stark hervortreten, bilden Weichtiere nicht einen Hauptanteil den Bodenfauna. Im Durchschnitt betrug der Molluskenanteil, in 335 Proben von je 0.25 m<sup>2</sup>, 16.5% der Arten und 12.0% der Individuen. Er betrug auch nur 13.2% des Gesamtgewichts der Makrofauna in 495 solcher Proben.

## RÉSUMÉ

### DISTRIBUTION ET FRÉQUENCE DES MOLLUSQUES BENTHIQUES DU PLATEAU CONTINENTAL DE LA CALIFORNIE MÉRIDIONALE

Un prélèvement d'échantillons sur le fond marin au-dessous du niveau des marées sur le plateau continental de la Californie méridionale a montré que, dans cette région, les mollusques ne jouent pas le rôle impressionnant de dominance faunale rapporté pour d'autres régions du monde, et qu'ils ne sont importants que dans un nombre restreint de communautés animales, comme suit.

Dans la partie septentrionale de ce plateau continental il y a 3 communautés principales comprenant des mollusques pélicypodes: la communauté de *Amphiodia-Cardita*, celle de *Listriolobus* et celle de *Nothria-Tellina*.

La première est une modification locale d'une communauté plus vaste, dominée par l'astérie rouge *Amphiodia urtica* (Lyman). Ici, le pélicypode *Cardita ventricosa* Gould constitue à peu près la moitié du poids des récoltes. Des vers polychètes viennent en second lieu. Le gastéropode *Bittium rugatum subplanatum* Bartsch est associé avec *Cardita* de manière prépondérante. La variation intercommunale, la densité de population de *Cardita* et sa structure selon la taille des individus ont été étudiées sur base de 36 échantillons récoltés saisonnièrement pour un réseau de 9 stations.

A une profondeur de 30 à 60 m, sur un grand dépôt de vase au large de Santa Barbara, la faune benthique est dominée par le ver échiuroïde *Listriolobus pelodes* Fischer. Des nombreux mollusques pélicypodes qui s'y trouvent communément, *Saxicavella pacifica* Dall est le plus caractéristique en raison de son étroite association (97%) avec *Listriolobus*. En dépit de cette association étroite et d'une densité de 30 individus/m<sup>2</sup>, la moyenne peu élevée de 4 g/m<sup>2</sup> ne permet pas de considérer *Saxicavella* comme une codominante d'un organisme dont la récolte moyenne s'élève à 944 g/m<sup>2</sup>. L'étude sur la population de *Saxicavella* a été conduite en tous points parallèlement à celle faite sur *Cardita*.

Vers la côte, les sédiments deviennent progressivement plus gros, se transformant de vase sablonneuse en sable vaseux et, finalement, en sable. Ces fonds sablonneux

hébergent divers complexes d'associations animales, dominés par des organismes divers, y compris les vers polychètes *Nothria elegans* (Johnson), *N. irridescens* (Johnson), *Prionospio malmgreni* Carpenter et *Diopatra ornata* Moore, et le mollusque pélecypode *Tellina buttoni* Dall. L'aspect faunal de cette zone peu profonde est compliqué par des aires de varech et des parties rocheuses.

Dans la partie méridionale du plateau continental Californien, au sud de la gorge sous marine de Hueneme, il n'existe qu'une seule association faunale à distribution étendue: celle dominée par *Amphiodia urtica*, qui s'étend généralement le long de la partie extérieure du plateau tout entier. Les mollusques les plus abondants ici sont les pélecypodes *Axinopsida serricata* (Carpenter) et *Mysella* spp. En général, dans la zone plus proche de la côte, les fonds sablonneux sont dominés par des communautés à polychètes, notamment celles de *Nothria-Tellina*, *Diopatra* et *Prionospio*. La faune de mollusques de ces parties comprend beaucoup de petites espèces de pélecypodes et de gastéropodes. Dans les parties peu profondes, des populations denses de l'échinoïde *Dendraster excentricus* (Eschscholtz) peuvent, par endroits profondément modifier la faune locale, et la présence de varech et de roches la modifient ailleurs.

La faune de mollusques de la saillie du plateau central dans la baie de Santa Monica, des portions au large de Palos Verdes, de la baie de San Pedro, et de San Diego, est très diverse et reflète le caractère complexe des sédiments. La seule association faunale de cette partie méridionale du plateau continental comprenant un mollusque et suffisamment étudiée est l'association du pélecypode *Lima dehiscens* Conrad avec le ver *Chaetopterus variopedatus* (Renier).

Au cours des présentes recherches, certaines espèces de pélecypodes de la Californie méridionale, qui sont considérées comme ayant une importance économique, étaient soit absentes soit ne furent trouvées que rarement et comme spécimens juvéniles. Ces espèces sont dominantes peut-être dans certaines portions limitées et non examinées du plateau continental.

À l'exception des associations peu nombreuses où les mollusques sont prédominants, ces derniers ne forment pas le gros de la faune du fond marin. Ils comprennent 16.5% du nombre total d'espèces et 12.0% du nombre des individus récoltés en 335 prélèvements de 0.25m chacune. Aussi ils ne forment que 13.2% du poids total de la macrofaune récoltée dans un total de 495 prélèvements.

#### RESUMEN

#### DISTRIBUCION Y ABUNDANCIA DE MOLUSCOS BENTICOS BAJO LA ZONA DE LAS MAREAS EN LA PLATAFORMA CONTINENTAL DEL SUR DE CALIFORNIA

Muestras tomadas de la plataforma continental en el sur de California indican que los moluscos no presentan allí la notable dominancia referida en otras partes del mundo, y que sólo son conspicuos en un número limitado de biotas.

Existen tres comunidades animales principales en la porción norte de la plataforma: las de *Amphiodia-Cardita*, de *Listriolobus* y de *Nothria-Tellina*, todas conteniendo pelecípodos.

La comunidad de *Amphiodia-Cardita* es una modificación local de otra más extensa dominada por la ofiura lisa *Amphiodia urtica* (Lyman). El pelecípodo *Cardita ventricosa* Gould constituye cerca de la mitad del contingente actual total, seguido en abundancia por gusanos poliquetos. El gastrópodo *Bittium rugatum subplanatum* Bartsch se asocia conspicuamente con *Cardita*. Las poblaciones de *Cardita ventricosa* son analizadas en cuanto a su variación dentro de la comunidad, su densidad y su estructura, sobre la base de 36 muestras colectadas a intervalos aproximadamente regulares por una red de nueve estaciones.

A profundidades de 30 a 60 m, en un grande depósito fangoso frente a Santa Bárbara, la fauna de fondo es dominada por el equiúrdo *Listriolobus pelodes* Fisher. Entre los pelecípodos frecuentes en esta comunidad, *Saxicavella pacifica* Dall se puede considerar como la más característica por su asociación especialmente estrecha (97%) con *Listriolobus*; a pesar de esto y de su frecuencia de 30 ejemplares/m<sup>2</sup>, el bajo valor promedio del contingente actual para *Saxicavella* no permite considerarla codominante con un organismo cuyo promedio es 944g/m<sup>2</sup>. La variación dentro de la comunidad, la densidad y la estructura de las poblaciones de *Saxicavella* fueron investigadas en esta comunidad por una red de nueve estaciones similar a aquella utilizada para la comunidad de *Amphiodia-Cardita*.

De la comunidad de *Listriolobus* hacia la playa los sedimentos se vuelven pro-

gresivamente más groseros, desde fangos arenosos a arenas limosas y finalmente arena. Estos fondos de arena contienen un complejo de asociaciones animales dominadas por una variedad de organismos, incluyendo los poliquetos *Nothria elegans* (Johnson), *N. irridescens* (Johnson), *Prionospio malmgreni* Claparède, *Diopatra ornata* Moore y el pelecípodo *Tellina buttoni* Dall al cual está conspicuamente asociado el gastrópodo *Olivella baetica* Carpenter. Areas de cachiyuyo y roca complican el aspecto faunístico de esta zona poco profunda.

En la porción meridional de la plataforma del sur de California, al sur del cañón submarino de Hueneme, sólo una única asociación faunística está extensivamente distribuída: la comunidad de *Amphiodia urtica*, la cual aparece generalmente en la parte externa, sobre la entera longitud de la plataforma. Aquí los moluscos más abundantes son los pelecípodos *Axinopsida serricata* (Carpenter) y *Mysella* spp. En la mayoría de las regiones, de esta comunidad de *Amphiodia* hacia la playa, los fondos arenosos están dominados principalmente por comunidades de poliquetos: de *Nothria-Tellina*, de *Diopatra* y de *Prionospio*. La fauna de moluscos de estas areas incluye muchas especies de pequeños gastrópodos y pelecípodos.

Los fondos someros pueden experimentar extensa modificación local como resultado de altas densidades de poblaciones del equinoideo *Dendraster excentricus* (Eschscholtz). La roca y el cachiyuyo modifican otras areas. La malacofauna de la proyección central de la plataforma de la Bahía Santa Mónica, de las plataformas de Palos Verdes y de la Bahía de San Pedro, y la porción meridional de la plataforma de San Diego, es altamente diversificada y refleja el carácter complejo de los sedimentos. La única asociación faunística que incluye un molusco pelecípodo, adecuadamente estudiada en la porción meridional de la plataforma, es la de *Lima dehiscens* Conrad con el gusano *Chaetopterus variopedatus* (Renier).

Muchos pelecípodos del sur de California, considerados importantes económicamente, estaban ausentes durante esta investigación o sólo aparecieron escasamente como formas juveniles. Quizá sean dominantes en pequeñas porciones no examinadas de la plataforma.

Con excepción de las pocas asociaciones en las cuales son conspicuos, los moluscos no constituyen el grueso de la fauna del fondo. Forman un promedio de 16,5% del número total de especies y 12,0% del total de ejemplares en 335 muestras de 0,25m<sup>2</sup> tomadas con baldes Hayward "cáscara de naranja" (OPB). Constituyen sólo 13,2% del contingente actual total de la macrofauna, como indican los datos de 495 muestras OPB.

#### А Б С Т Р А К Т

#### РАСПРЕДЕЛЕНИЕ И НАХОЖДЕНИЕ СУБЛИТОРАЛЬНЫХ МОЛЛЮСКОВ В БЕНТОСЕ МАТЕРИКОВОГО ПЛАТО ЮЖНОЙ КАЛИФОРНИИ.

Гилберт Ф. Джонс

Материал собранный на материковом плато южной Калифорнии показывает, что в этом районе моллюски не играют такой доминирующей роли, какая была описана для других частей света, и что они встречаются здесь в заметном числе только в некоторых сообществах, описание которых следует ниже.

В северной части материкового плато южной Калифорнии встречаются три главных сообщества в которых представлены двухстворчатые моллюски. Это - *Amphiodia-Cardita*, *Listriolobus* и *Nothria-Tellina*.

Сообщество *Amphiodia-Cardita* является местным видоизменением более обширного сообщества, в котором преобладает гладкая красная офиура *Amphiodia urtica* (Lyman). Особи двухстворки *Cardita ventricosa* Gould составляют около половины биомассы. Многощетинковые черви занимают второе место. Брюхоногий моллюск *Bittium rugatum subplanatum* Bartsch встречается преимущественно вместе с *Cardita*.

На основании 36 образцов собранных в разное время года на 9 станциях, на которых материал собирался с помощью решетки, автор дает анализ вариаций в пределах сообщества, плотности популяции, и структуру популяции *Cardita ventricosa*.

В обширных отложениях ила у берегов Санта Барбара, на глубине от 30 до 60 м, в донной фауне преобладает эхиуровый червь *Listriolobus pelodes* Fisher. Среди различных двухстворчатых моллюсков встречающихся в этом сообществе, наиболее характерным видом можно считать *Saxicavella pacifica* Dall по причине его близкой ассоциации (97%) с *Listriolobus*. Несмотря на

близкую ассоциацию с доминирующим видом и невзирая на факт, что на каждом кв. метре встречается 30 особей *Saxicavella*, эту форму нельзя рассматривать как совместно-доминирующую, так как биомасса этого вида составляет только 4 гр. на кв. метр, тогда как средняя биомасса доминирующего вида равна 944 гр. на кв. метр. Применяв метод сбора по решеткам на 9 станциях (подобный методу, примененному при изучении сообщества *Amphiodia-Cardita*), автор обследовал вариации в пределах сообщества *Saxicavella*, плотность популяции и ее структурный размер.

Донные отложения между сообществом *Listriolobus* и берегом становятся постепенно более грубыми, начиная от ила с песком, песка с илом, и кончая песком. На этих песчаных грунтах находятся различные ассоциации животных с различными доминирующими организмами, включая многощетинковых червей *Nothria elegans* (Johnson), *N. irridescens* (Johnson), *Prionospio malmgreni* Claparede и *Diopatra ornata* Moore и двухстворчатого моллюска *Tellina buttoni* Dall. Брюхоногий моллюск *Olivella baetica* Carpenter преимущественно встречается с *Tellina*. Площади покрытые бурными водорослями и скалы усложняют характер фауны этой мелководной зоны.

В южной части калифорнийского плато, к югу от подводного каньона Хвайнеме, широко распространена только одна фаунистическая ассоциация, это - сообщество *Amphiodia urtica*. Оно встречается главным образом во внешней части района вдоль всей длины южного плато. Наиболее многочисленными моллюсками здесь являются двухстворчатые *Axinopsida serricata* (Carpenter) и *Mysella* spp. В большинстве районов к берегу от сообщества *Amphiodia*, на песчаном дне, преобладают сообщества многощетинковых червей: *Nothria-Tellina*,

*Diopatra* и *Prionospio*. Фауна моллюсков этих районов состоит из нескольких мелких видов брюхоногих и двухстворчатых. Мелководье подвержено местным изменениям, которые происходят из за высокой плотности популяции морского ежа *Dendroaster excentricus* (Eschscholtz). Скалы и бурные водоросли видоизменяют другие районы. Фауна моллюсков центрального выступа плато в бухте Санта Моника, плато Палос Вердес и бухты Сан Педро и южной части плато Сан Диего очень разнообразна и отражает сложный характер морских осадков. Ассоциация двухстворки *Lima dehiscens* Conrad с трубчатым червем *Chaetopterus variopedatus* (Renier) является единственной достаточно изученной фаунистической ассоциацией в которой представлен двухстворчатый моллюск.

Многие калифорнийские виды двухстворчатых моллюсков имеющих экономическое значение, отсутствовали в сборах, или лишь изредка были представлены молодыми особями. Возможно, что эти виды преобладают в тех небольших районах плато где сборы не производились.

За исключением нескольких ассоциаций в которых моллюски занимают видное положение, они не составляют главную массу донной фауны. В среднем, моллюски образуют 16.5% общего числа всех видов и 12.0% из общего числа экземпляров, равного 335 на 0.25 кв. метра, собранных измерительным черпаком Хейварда (ОРВ). Моллюски составляли всего 13.2% всей биомассы макрофауны (на основании 495 проб взятых ОРВ).

Ясно, что в районе южной Калифорнии моллюски не играют той видной фаунистической роли, которая описана для других частей света.

MICROTEXTURAL VARIATION IN PELECYPOD SHELLS<sup>1</sup>

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## ABSTRACT

From a microscopic study of the structural composition of the shells of 4 marine pelecypods (3 Eulamellibranchs and 1 Taxodont) it is inferred that dendritic crystallization of the calcium carbonate plays an essential role in producing great textural variation.

A hierarchy of 5 cyclic groupings of growth layers occurs in the shells studied: one 1st-order layer consists of two 2nd-order layers, 24 3rd-order layers, approximately 365 4th-order layers, and about 1,460 5th-order layers. These growth layers are built of 3 types of ultra-fine ( $\approx 8\mu$ ) elemental layers (1) cryptocrystalline calcium carbonate, (2) opaque or semi-opaque material called conchiolin, and (3) conchiolin dispersed in a microcrystalline aggregate of aragonite.

A 5th-order layer is a simple alternation of conchiolin with either of the carbonate elements. The more complex 4th-order layer (average thickness ca.  $30\mu$ ) consists of exactly 8 elemental layers arranged as follows: 1, 2, 3, 2, 3, 2, 3, 2; 1, . . . etc. The thickness of the 4th-order layer varies cyclically with a period of 15 layers, resulting in a 3rd-order layer (average thickness about 0.5 mm). This layer is further characterized by a dark phase of relatively thick composite and conchiolin layers that alternates with a light phase in which the cryptocrystalline layers are almost as thick as the other layers. The 2nd-order layer has 2 phases: (a) normal phase, in which the quantity to conchiolin and composite elements exceeds that of the cryptocrystalline calcium carbonate, and (b) carbonate phase, in which the latter either equals or exceeds the 2 former elements. The thickness of this layer averages 6.5 mm, with the normal phase accounting for about 6.0 mm. The 1st-order layer (average thickness 13 mm) is characterized by a thickening and thinning of its 2 component layers.

Assuming that these growth layers reflect environmental periodicities, the 1st-order layer may be correlated with annual change of temperature and salinity, the 2nd-order layer with equinoctial tides and storms, the 3rd-order layer with the fortnightly tidal cycle, the 4th-order layer with day and night, and the 5th-order layer with the daily tidal rhythm.

The growth layers are superimposed upon 2 main layers which are parallel to the shell surfaces: (1) outer main layer in which the crystals are small and the growth layers are thick, and (2) inner or middle main layer in which the crystals are large and the growth layers are thin. The shell of the taxodont species *Anadara ovalis* has a third internal main layer with irregularly oriented acicular crystals and without growth layering.

Typically, each crystal is complexly shaped and foliated, and is surrounded by an aggregate of tiny crystallographically discrete units and conchiolin. Optical evidence indicates that this latter aggregate is an intergrowth of countless crystal branches. These structures are formed by dendritic crystallization, a process that is favored by rapid growth and abundant impurities. This interpretation is supported by the fact that intergrowths are best developed in the outer main layers where shell growth is most rapid and conchiolin is most abundant.

Occasionally, the outer main layer of *Mactra solidissima* has a few pinnate structures composed of several aragonite crystals associated with distorted growth layering. These anomalies point to recrystallization or to some unknown biological phenomenon.

Microscopic measurements of specimens from different environments indicate that crystal size is inversely related to increase of salinity, whereas the thicknesses of growth layers are directly related to temperature.

<sup>1</sup>This article is based on a part of a master's thesis which was completed by the writer in September, 1962, at the Pennsylvania State University.

Mathematical evaluation by more rigorous and extensive analyses of shell microtexture and ecological factors is desirable. Laboratory growth experiments and ecologic work should provide direct tests for the hypothesis that tidal periodicity is reflected by shell growth layering.

## INTRODUCTION

For at least a century, malacologists have known that the typical pelecypod shell is essentially composed of calcium carbonate in the mineral forms aragonite and calcite mixed with a complex aggregate of organic compounds called conchiolin. As early workers were quick to observe, upon taking a complete clam apart, the shell consists of several main layers of calcium carbonate and a surficial horny coating (periostracum) deposited by certain secretive parts of the mantle both within and outside the pallial line. Superimposed upon these main layers they found growth layers which result from irregularities of growth. Within the pallial line, the growth layers are parallel to the general shell surfaces whereas outside the pallial line, the growth layers are steeply inclined or reclined to the shell surfaces and crop out at the exterior surface forming surficial growth rings. Microscopists attributed the complexity of microtextural patterns to the influences of intra- and extra-pallial organic impurities: "... a condition well known to every chemist as interfering with proper crystalline angles and planes by altering the regular arrangement of the calcareous particles." (Stoddart, in Higgins, 1868). Despite this view, Carpenter (1847-1849) opined that clam shells are built of protoplasmal cells which secrete internal calcareous fillings, that shell growth involved the direct transformation of tissue (ossification). Huxley (1859) and Williamson (1860) successfully refuted this idea, asserting that cellular (prismatic) shell structures result from concretionary aggregation of crystals. Sometime later, another hypothesis was proposed by Moynier de Villepoix (1892): that the formation of a shell involves replacement depending upon the concentration of ions by calcium phosphate

granules.

Later workers have shown that there are probably several processes of shell formation. Firstly, both of the early hypotheses have been supported by microscopic observations and chemical analyses of ossification in snails (Abolinš-Krogis, 1958) and of carbonation of calcium phosphate granules in pelecypods (Bevelander and Benzer, 1948). Secondly, several additional observations have been made:

According to Robertson (1941) DeWaele claimed evidence of extra-pallial precipitation of clam shell from a calcium proteinate fluid caused by loss of carbon dioxide.

Crofts (1930) described crystallization of amorphous granules pre-formed in the epithelial cells of the mantle of the snail *Helix pomatia*. Bevelander (1953) has observed this process in other mollusks.

Electronmicroscopic studies (see workers cited by Wilbur, 1960) of several oysters grown under controlled conditions have inferred several principles of shell growth: (1) the rate of shell growth increases with increase of temperature and salinity; (2) the rate of shell growth is inversely related to the size and degree of idiomorphism of shell-making crystals; (3) the mode and place of nucleation of the calcium carbonate crystals vary with the species; and (4) crystal growth is dendritic.

However, it should be mentioned here that these studies have introduced some artifices such as maintaining pieces of mantle epithelium on thin glass plates or inserting coverslips between the mantle and the shell. The interested reader should investigate further the diversities of materials, methods, and phenomena described in the references cited.

Perhaps the most classic study of shell structure was made by Bøggild (1930) who described 8 types of structure:

- (1) The homogeneous structure: apparently structureless aggregate of crystals with mutually parallel orientation and with their c axes perpendicular to the shell surface.
- (2) The prismatic structure: "prisms" with regular or irregular outlines
  - (a) Normal: single crystal of variable size delimited either by straight distinct lines or by irregular lines.
  - (b) Complex: prism composed of many fine crystals.
  - (c) Composite: prism composed of smaller prisms arranged in a feathery manner, oriented horizontally in the radial shell direction with the smaller prisms diverging toward the margin.
- (3) The foliated structure: calcite aggregate characterized by parallel leaves oriented horizontally or irregularly and, also, by the irregular orientation of optic axes.
- (4) The nacreous structure: aggregate of small (less than  $1\mu$ ) leaves of aragonite interbedded with conchiolin.
- (5) The grained structure: irregular grains with irregular orientation of optic axes.
- (6) The larger crystal structures: entire shell consists of one crystal.
- (7) The crossed-lamellar structure: usually aragonite, sometimes calcite, composed of single crystals termed "first order lamellae" intersected by "second order lamellae" (intracrystal layers of an unknown substance that are less than  $1\mu$  in size).
- (d) The complex crossed-lamellar structure: coarse undulose prism made up of first order lamellae oriented with their crystallographic axes mutually parallel in the center of the prism, and at various angles to each other near the prism periphery.

Oberling (1955) referred to some of the above structures in a systematic study of 230 pelecypod species. He claimed that there are 3 main structural groups of pelecypods:

- (1) Nacro-prismatic: characterized by a prismatic main layer formed outside the pallial line, a nacreous main layer formed within the pallial line, and a nacreous main layer sandwiched between the preceding and formed outside the pallial line.
- (2) Foliated group: entire shell formed by nacreous or foliated structure.
- (3) Complex-lamellar group: characterized by a complex crossed-lamellar main layer formed within the pallial line and a crossed-lamellar main layer formed outside the pallial line.

More recently, MacClintock (1963) has successfully applied the Bøggild classi-

fication in a taxonomic study of some archaeogastropods.

Although Bøggild (1930) claimed that the chemical and mineralogical properties of marine invertebrate exoskeletons are inherently determined, Lowenstam (1954), Chave (1954), and other workers have shown that they are modified by water temperature and salinity.

The growth layering of molluscan shells, studied megascopically, has been correlated with annual changes of temperature, food, and salinity (Belding, 1910; Crozier, 1918; Weymouth, 1923; and Orton, 1928). Orton demonstrated that the dark-colored growth rings seen on the exterior surfaces of *Cardium edule* valves are produced whenever the organism is exposed to the atmosphere, indicating the existence of "disturbance rings" having less than annual significance. Massy (1914) and Weymouth (1923) suggested that the finer growth layers occurring within the annual growth layers of their specimens represent daily or tidal variations of growth. Oberling (1955) considered the thicker and more darkly colored growth layers of his specimens as "fast-growth layers." But none of these conjectures were specific and the growth layers involved were not analyzed microscopically.

Some descriptions of skeletal growth layering have been given by students of corals. Faul (1943) observed that a Devonian tetracoral (*Prismatophyllum*) shows a periodic thinning of dissepiments associated with thickening of the skeleton, increased carination, and a bunching of tabulae. He suggested that this cyclic layer resulted from annual change of temperature and associated phenomena. More recently, Wells (1963) has reported that several fossil and Recent corals show a cyclic increase and decrease of the spacing of epithecal ridges and that the number of ridges per cycle increases with increase of geological age. He has conjectured that the ridges are daily layers, that their cyclic grouping is of annual significance, and that the number of "daily" layers per "annual" layer is an index of the earth's rate of rotation relative to its speed of

revolution around the sun.

Despite the preceding studies, an interpretative classification of shell microtextures formed in nature has not been given. This paper is intended to provide a detailed description of the crystalline structural constituents and a test for the effect of environmental influences on shell growth, with emphasis on the microscopic appearance of growth layering. As I endeavor to show, the main layers in the shells of this study are intergradational and 5 of Bøggild's structures seem to be differing sections of branched, foliated crystals that have varying sizes, shapes, and orientations. The taxonomic and ecological aspects of shell microtexture study are discussed briefly.

#### PROCEDURE

To compare shells with their environments, it was necessary to select species that are widely available. Specimens of 2 such species were procured from places ranging from Prince Edward Island (Canada) to Florida: 15 *Mercenaria mercenaria* (Linnaeus) and 7 *Mactra solidissima* Dillwyn. Five specimens of *Chione cancellata* (Linnaeus) and 3 of *Anadara ovalis* (Bruguière) were also collected for comparison<sup>2</sup> (see Table 1). All of the 30 specimens were collected alive from littoral areas near United States Coast and Geodetic Survey Stations, where temperature and salinity data are available for periods exceeding the life spans of the sampled organisms. Each specimen was cleaned under a jet of tap water in order to remove soft parts without damaging the shell.

The thin sections upon which this study is based were either perpendicular to the shell surface along the maximum radius connecting the umbo and ventral margin (*radial*), parallel to the convex shell surface at a given point (*tangential*), or normal to the shell surface along the

the postero-anterior axis (*longitudinal*). Thirty radial thin sections of shells from different localities (see Table I) plus 2 longitudinal and 2 tangential thin shell sections of each species were studied with a light polarizing microscope at magnifications ranging up to X450.

Mineral composition was determined semi-quantitatively by x-ray diffraction (smear method), stain tests, and heavy liquid separations.

Variations of organic matter, or conchiolin, content were assumed to be expressed by density anomalies in samples of pulverized shell, when related to an ideal aggregate having a calcite-aragonite percentage equal to that of the sample.

#### COMPOSITION AND OPTICAL ORIENTATION

The calcium carbonate of the shells was predominantly or entirely aragonite (anomalies less than 5% calcite).

Estimates of the conchiolin content were based on the specific gravities and mineral compositions of the shells (see above) and on the assumption that the specific gravity of conchiolin lies within the range known for animal tissues (Lange et al., 1956). The resulting values range from 4-12 weight percent conchiolin. Approximately the same percentages were obtained for different parts of individual shells.

Moderately well-centered Bxa (acute bisectrix) figures were conoscopically observed in tangential sections. In the central parts of these sections, the Bxo (obtuse bisectrix) direction coincided with the maximum shell growth radius. Away from the center, the Bxa figure became off-center while a preference for Bxo orientation decreased until there was no preferred orientation of the Bxo. Since aragonite is optically negative, the Bxa is the vibration direction of the fast ray (nx) and the Bxo is the vibration direction of the slow ray (nz). The c crystallographic axis of aragonite corresponds to the nx direction, the a and b axis to ny

<sup>2</sup>Following the classification of Thiele (1935) the genera *Mercenaria*, *Mactra*, and *Chione* are referred to the order Eulamellibranchia, the genus *Anadara* to the order Taxodonta.

and  $n_z$  respectively. Therefore, the plane of a radial thin shell section is approximately: (1) normal to the  $\underline{a}$  axis in the endostracum but becomes more randomly oriented to it in the ectostracum, (2) in the same plane as the  $\underline{c}$  axis in both the ectostracum and endostracum, and (3) in the same plane as the  $\underline{b}$  axis in the endostracum, though it becomes more randomly oriented to it in the ectostracum.

### GENERAL DESCRIPTION

All shells used in this study have a pigmented ectostracum and a white endostracum. Superimposed upon these main layers are growth layers that are parallel to the main layers near the concave surfaces of the shells and inclined or reclined at various angles near the convex surfaces. Partial dissolution of the specimens in dilute HCl leaves organic residues that are most abundant on the thicker and darker layers, indicating that these are richer in organic matter (conchiolin); hence, pigmentation is considered to be an index of conchiolin content.

The concave surfaces of the specimens are white with some marginal coloration, whereas the convex surfaces display white rings in alternation with purple, red-brown or yellow-brown ones. Two general types of texture are visible at low magnifications (25-50X) on both surfaces: viz., *granular* and *smooth but pitted*. The granular texture is apparently due to the natural removal of organic shell matrix. Some of the pits are geometrically shaped and are characteristically oriented in relation to the growth layers: (a) pyramidal with one side tangent to a growth layer plane and apex pointing to a raised area, (b) dipyramidal with long axis perpendicular to a growth layer, (c) plano-curved or oval pits with their long axes mutually parallel to the growth layers, and (d) linear depressions oriented parallel to the growth layers. Other pits occur as irregularly shaped depressions with gradually sloping surfaces and complementary hillocks. The geometrically shaped pits are more abundant on the

concave surfaces than the irregular ones.

### MICROTEXTURE

Two types of microtexture, dominant in all of the specimens, and here termed Type A and Type B, are shown in Figure 1. Type A is an aggregate of optically

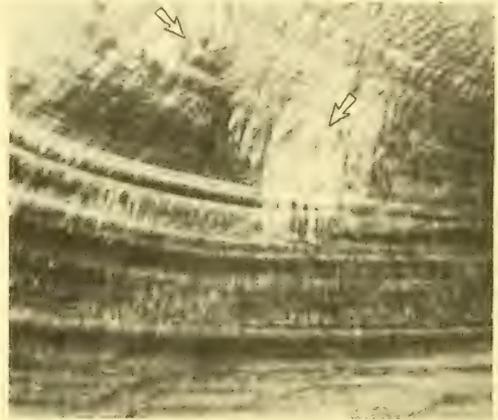


FIG. 1. *Mactra solidissima*, radial section (X20, crossed nicols). The homogeneous and heterogeneous microtextures are shown in the lower and upper halves of this figure; also shown are pinnate structures consisting of several larger crystals located near the convex surface (arrows).



FIG. 2. *Anadara ovalis*, radial section (X200, plane polarized light). The type C aggregate of complexly arranged fibrous aragonite crystals and organic matter (dark).

homogeneous foliated crystals oriented with a high degree of crystallographic parallelism, their *c* axes perpendicular to the growth layers. Type B is characterized by optically heterogeneous crystalline columns or blocks, oriented with their longest directions parallel to one another and perpendicular to the growth layers. The endostracum of the taxodont species *Anadara ovalis* shows a third type of microtexture (Fig. 2) termed here Type C. Type C is an aggregate of fibrous aragonite crystals that are usually without a preferred orientation but are sometimes arranged radially around an axis.

All of the specimens have microtextures that are intergradational between types A and B. Variation occurs in 2 mutually perpendicular directions: (1) along a growth layer from the outer convex surface to the inner concave surface, resulting in the formation of main layers, and (2) along a given radius of growth, producing growth layers.

#### Main Layers

The ectostraca of the eulamellibranch species *Mastra solidissima*, *Mercenaria mercenaria*, and *Chione cancellata* show an extreme development of Type B and an abundance of pigmented conchiolin. The endostraca of these species show an extreme development of Type A and a relatively small amount of pigmented conchiolin. In the shell of each of these species, the endostracum and ectostracum are separated by a relatively thin (50-200 $\mu$ ) non-pigmented myostracum which consists of cryptocrystalline calcium carbonate.

The ectostracum of *Anadara ovalis* shows an extreme development of Type B and an abundance of pigmented conchiolin in its outer half, and an extreme development of Type A in its inner half. The endostracum, which is also separated from the ectostracum by a cryptocrystalline myostracum, shows the Type C texture and is almost devoid of pigmented conchiolin except at the inner concave shell surface where dark brown optically amorphous fibers have been included.

The amount of change (or range between Types A and B) was greatest for the eulamellibranch specimens. These are also characterized by their higher degree of development of optical homogeneity (in Type A).

#### Growth Layering

A growth layer may be defined as a uniquely organized unit of shell constituents formed under a certain set of physicochemical conditions prevalent for a certain period of time between the mantle and the shell surface. Observation has shown that crystallization during shell growth varies between the 2 extreme modes associated with textures A and B, with Type A progressively predominating over Type B in the direction of shell growth. This variation produces a hierarchy of 5 orders of cyclic growth layers based ultimately upon 3 types of ultrafine ( $<8\mu$  thick) elemental layers: (1) cryptocrystalline calcium carbonate, (2) conchiolin, and (3) conchiolin dispersed in a microcrystalline aggregate of aragonite (composite layer). These cyclic growth layers are described below (see also Fig. 3), in ascending order of size, the 5th-order layers being the smallest cyclic growth layers, and each higher order comprising a number of growth layers of the preceding rank.

*5th-order layer.* A simple alternation of conchiolin with either cryptocrystalline calcium carbonate or the composite element defines the 5th-order layer.

*4th-order layer.* A more complex layer consisting of exactly 8 elemental layers arranged in the following way: 1, 2, 3, 2, 3, 2, 3, 2; 1 . . . etc. The thickness of the 4th-order layer varies from 5-60 $\mu$ .

*3rd-order layer.* The 4th-order layers thicken and thin cyclically with a period of 12-15 layers (15 common), thus forming the 3rd-order layers. The 3rd-order layers are also characterized by a cyclic variation of pigmented conchiolin; viz., a dark phase of relatively thick composite and conchiolin layers alternates with a light phase in which the cryptocrystalline calcium carbonate layers are almost as thick as the composite and the conchiolin

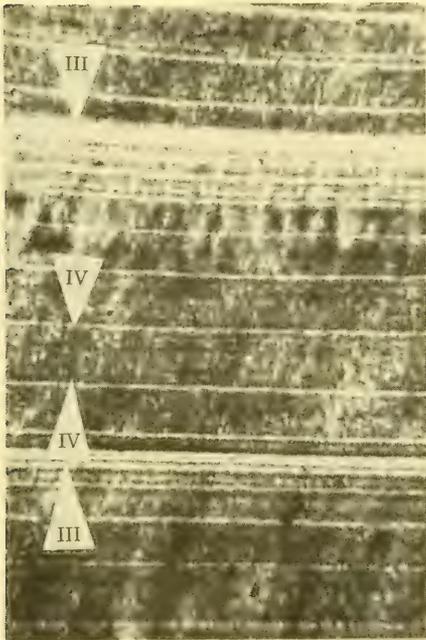


FIG. 3. *Mactra solidissima* radial section (X70, plane polarized light). In this figure, a 3rd-order layer composed of 15 4th-order layers is delimited by arrows marked III and a 4th-order layer composed of 8 5th-order layers is indicated by arrows marked IV.

layers. The 3rd-order layer varies from 0.1-0.9 mm in thickness.

**2nd-order layer.** This layer consists of 2 phases: (a) normal phase in which the quantity of conchiolin and composite elements exceeds that of the cryptocrystalline calcium carbonate, and (b) carbonate phase in which the cryptocrystalline calcium carbonate either equals or exceeds the conchiolin and composite elements. The thickness of this layer ranges from 0.9-11 mm, with the normal phase accounting for 0.8-10 mm and the carbonate phase 0.1-1 mm.

**1st-order layer.** This layer is also characterized by thickening and thinning of its 2 component layers; it consists of a relatively thick and a relatively thin 2nd-order layer. It is so large (1.8-22 mm) that it cannot be observed entirely within the field of most microscopes.

### Crystalline Constituents

Three size grades of crystalline constituents have been observed: (a) sub-microscopic structures barely visible, in the elemental layers; (b) microscopic layers; and (c) larger structures. These 3 groups tend to occur with their longer dimensions and Bxa directions oriented perpendicularly to the growth layers.

The blocks are seen in radial and longitudinal sections as columns that are perpendicular to the growth layers. Occasionally, this orientation is disrupted by branching (Fig. 4). In tangential sections the blocks are lath-like, their size seemingly dependent on the orientation of the section relative both to the main and to the growth layering. When the tangential section is perpendicular to the columns, small structures ( $\leq 5\mu$ ) are visible that are pyramidal or dipyramidal in shape.

With regard to polarization, there are



FIG. 4. *Anadara ovalis*, radial section (X450, crossed nicols). The crystalline constituents characteristic of all specimens: the blocks with normal extinction (dark) and blocks with an apparently undulose or patchy extinction (light).

2 kinds of blocks that alternate with each other in the shell: N, a block which has normal, i.e. complete parallel extinction, and U, an adjacent block which upon  $360^{\circ}$  rotation with crossed nicols remains illuminated or has an apparently undulose extinction. These patterns of extinction show that the U blocks are not crystallographically continuous whereas the N blocks are single crystals. Without the analyzing nicol it can be seen in radial section (parallel to optic axial plane) that the N and U blocks are of approximately equal relief when their longer dimensions are parallel to the direction of polarization and that upon  $90^{\circ}$  rotation N is higher in relief. Textural details (tiny layers and leaflike protrusions shown in Fig. 4) also change upon rotation, varying systematically in the N blocks and randomly in the U blocks. When the focal plane is raised, the Becke and interference-color lines may move either away from or toward the block with the higher relief. These latter observations indicate clearly that textural detail is not solely dependent upon the optical orientation of the blocks, but is rather a function of their shape. (Evidently, the surfaces of contact between the blocks are inclined to the plane of section so that the relative thicknesses vary, causing a change of light retardation when the focal plane is moved.)

When a growth layer is followed from the outermost part of the ectostracum to the innermost part of the endostracum, it is seen that the widths of the N blocks increase in relation to the widths of the U blocks. For this reason the N and U blocks may be regarded as the elements of textural Types A and B respectively.

Contrasting with the above blocks are pinnate structures that occur in the ventral  $2/3$  of the ectostraca of the *Maetra solidissima* specimens (Fig. 1). Three morphological changes involving these structures take place in the ventral direction:

- (1) Their size increases to a maximum of one millimeter at the margin.
- (2) Their perpendicularity to the growth

layers is lost.

(3) Their abundance decreases with an increase of pigmented conchiolin. Many of these structures differ further from the blocks, in that they consist of 2 or 3 optical units joined along a plane which intersects the  $\underline{a}$  and  $\underline{b}$  crystallographic axes and coincides with the plane of the  $\underline{c}$  axis (oriented h, k, O), but there are some that have an uncountable number of components of uncertain orientation. Notable are fine ( $\leq 5\mu$ ) crystal layers that intersect the h, k, O plane at variable angles. Within the pinnate structures, growth layering is either faint and contorted or absent.

#### An Interpretative Model for the Essential Structural Constituents

Bøggild (1930) observed that the "second-order lamellae" (layers inside crystals) of mollusk shells appear to be oriented accidentally and that they are not subject to crystallographic control. Although I agree that these crystal layers have a variable orientation relative to both optical directions and crystal morphology, I suggest in addition, that they are impurity layers engulfed during crystal growth, most likely by the dipyramidal faces of aragonite and that their deviation from ideal orientation is likely to be due to irregularities of crystal growth, e.g., alternate inequalities of facial development. Hence, it is thought that textural Types A and B have the following genetic<sup>3</sup> characters in common:

- (1) Growing crystals incorporate organic impurities as layers.
- (2) The presence of impurities during crystal growth results in the development of branches and protrusions.
- (3) The amounts of organic impurity are approximately the same in each of the processes that form the 2 textures.

Genetic differences between Types A and B must explain the following characteristic properties:

- (1) The Type A blocks are foliated crystals that have at least 2 orders of branches (block

<sup>3</sup>"genetic" here relates to genesis, or mode of production.

branches and protrusions).

(2) The Type B blocks are aggregates of 2 or more coalescent crystals.

(3) Their indices of refraction are different.

(4) Their crystallization rates are different. That the rate of shell growth is greatest near the convex surface is indicated by 2 observations:

(a) A simple geometric measurement shows that the convex surface is greater than the concave surface and that therefore the rate of shell growth along any radius must be greater at the convex surface than at the concave one.

(b) If any temporal significance is assigned to the growth layers, then their greater thickness within the outer main layers presupposes a relatively fast growth near the convex surface.

Since the conchiolin contents of the main layers are apparently equal, this difference between shell growth rates is, at least superficially, synonymous with difference between crystallization rates.

A model which fits all of the above requirements is a branched foliated crystal, the center of which is optically homogeneous with normal extinction. It has a relatively high index of refraction for rays vibrating parallel to its short axis ( $n_z$ ). This crystal is surrounded by an intergrowth of its branches and those of one or more adjacent crystals, so oriented that their transmitted rays vibrate in directions of lower refractive index (resultant of  $n_z$  and  $n_y$ ).

Such a model implies a dendritic growth process upon which may be superimposed the effects of crystal deformation and orientation of seed crystals as a result of various physicochemical conditions.

#### Origin of the Varietal Constituents

The larger pinnate structures of the *Maetra solidissima* shells seem to be anomalous in relation to the essential constituents. The fact that they are confined to the convex surface where mechanical and thermal stresses should

be greatest, together with an observed antipathetic relationship between these pinnate structures and conchiolin, supports a hypothesis of recrystallization during or shortly after the life of the clam. An alternative hypothesis is that some biological phenomenon excluded conchiolin from the regions in which the pinnate structures were formed.

Texture Type C has very little in common with Types A and B. Its extreme complexity might represent mechanical action (such as movement of the mantle) during crystallization. The tendency of some of the acicular crystals to aggregate about an axis could result from inclusion of a foreign body, but if such inclusions exist, they were not visible in the thin sections examined and must be soluble also in dilute HCl.

#### MICROTEXTURAL VARIATIONS AND ENVIRONMENT

Assuming a positive relationship between the rate of shell growth and the rate of crystallization, it is postulated that the thicknesses of the growth layers and the widths of the crystalline blocks should be affected by water temperature and salinity. In order to test this hypothesis empirically, the layers and blocks from 1 slide each of 15 *Mercenaria mercenaria* and 7 *Maetra solidissima* shells from environments of different mean temperature and different mean salinity were measured and compared with temperature-salinity data recorded at the nearest coast and geodetic stations. A few specimens of *Chione cancellata* and *Anadara ovalis* from southern latitudes were similarly measured for comparison. These data are presented in Table I. The correlation coefficients calculated for these data are summarized in Table II. Since all of these specimens are of littoral origin it was possible to infer a plausible relationship between tides and layering (see below, Origin of Growth Layering and Table III).

#### Technique

In an attempt to minimize the effects

TABLE I. Average thicknesses of 4th-order layers and average widths of crystalline blocks, at center of outer main layers of the shell of 4 species of marine clams from environments of different mean temperatures and salinities.

Species and sample	Location <sup>5</sup>	$\bar{X}_1$	$\bar{X}_c$	$\bar{X}_t$	$\bar{X}_s$
		in microns		°F	o/oo
<i>Mercenaria mercenaria</i>					
1	Boothbay, Maine	22.0	15.0	46.0	29.8
2	" "	25.2	14.0	46.0	29.8
3	" "	27.2	15.8	46.0	29.8
4	Stone Harbor, N. J.	28.5	14.1	53.9	31.5
5	" "	31.7	14.0	53.9	31.5
6	" "	31.7	14.7	53.9	31.5
7	Bogue Sound, N. C.	37.0	14.6	68.5	31.0
8	" "	34.6	14.6	68.5	31.0
9	" "	40.0	12.8	68.5	31.0
10	Charleston, S. C.	34.5	14.6	68.0	30.2
11	" "	34.8	14.8	68.0	30.2
12	" "	34.5	15.2	68.0	30.2
13	Bradenton, Fla.	47.3	16.2	75.3	26.9
14	" "	42.6	15.7	75.3	26.9
15	" "	47.9	14.7	75.3	26.9
<i>Maetra solidissima</i>					
16	Prince Edward Island, Canada	27.5	31.1	46.0	31.7
17	Boothbay, Maine	27.2	24.4	46.0	31.7
18	" "	30.7	24.7	46.0	31.7
19	Stone Harbor, N. J.	32.7	22.4	53.9	31.5
20	" "	35.4	24.6	53.9	31.5
21	" "	33.2	19.5	53.9	31.5
22	Nagshead, N. C.	35.1	20.1	69.3	35.1
<i>Chione cancellata</i>					
23	Nagshead, N. C.	20.3	13.2	69.3	35.1
24	Myrtle Beach, S. C.	20.2	15.6	66.4	33.6
25	Bradenton, Fla.	28.3	16.0	75.3	26.9
26	" "	22.1	18.0	75.3	26.9
27	Aransas Bay, Texas	23.0	15.1	70.9	31.5
<i>Anadara ovalis</i>					
28	Stone Harbor, N. J.	14.8	9.1	53.9	31.5
29	Charleston, S. C.	20.0	10.1	68.0	30.2
30	Daytona Beach, Fla.	22.0	8.6	72.0	35.2

<sup>5</sup>From north to south.

N. J. = New Jersey

N. C. = North Carolina

S. C. = South Carolina

Fla. = Florida

$\bar{X}$  = arithmetic mean.

$\bar{X}_1$  = mean thickness of 4th-order layer in 2nd-formed 1st-order layer (from 24 measurements).

$\bar{X}_c$  = mean width of crystalline columnar constituents.

$\bar{X}_t$  = mean of annual temperature means.

$\bar{X}_s$  = mean of annual salinity means.

TABLE II. Sample correlation coefficients, calculated from data given in Table I.

Species	Variables					
	$\bar{X}_1/\bar{X}_c$	$\bar{X}_1/\bar{X}_t$	$\bar{X}_1-\bar{X}_s$	$\bar{X}_1/\bar{X}_s$	$\bar{X}_c/\bar{X}_s$	$\bar{X}_t/\bar{X}_s$
<i>Mercenaria mercenaria</i> N = 15	0.192	0.913	-0.626	0.168	-0.607	-0.491
<i>Mactra solidissima</i> N = 7	-0.667	0.804	0.388	-0.678	-0.381	-0.800
<i>Chione cancellata</i> N = 5	0.281	0.719	-0.731	0.606	-0.826	-0.917
<i>Anadara ovalis</i> N = 3	-0.082	0.998	0.517	-0.022	-0.896	0.464

N = number of radial thin shell sections measured.

of intrashell variation, sampling was confined to equivalent parts of each of the 3rd-order layers; these layers occur within the second-formed 1st-order layer, in the center of the outer main layer (see Table I). The thicknesses of 4th-order layers, as seen in radial section, were measured with a graduated ocular. The widths of the columns composing the crystalline blocks were averaged by dividing their linear density into the ocular traverse length.

#### Correlations

As summarized in Table II, the mean widths of the columns ( $\bar{X}_c$ )<sup>4</sup> vary inversely with the means of annual salinity means ( $\bar{X}_s$ ) and the thicknesses of the 4th-order layers ( $\bar{X}_1$ ) vary directly with the means of annual temperatures ( $\bar{X}_t$ ). Some interdependence of these variables is suggested by the relatively low positive correlations for  $\bar{X}_c$  vs.  $\bar{X}_t$  and the relatively low negative correlations for  $\bar{X}_1$  vs.  $\bar{X}_s$ . These particular correlations are of dubious significance because:

If  $\bar{X}_c = F(\bar{X}_t)$  and  $\bar{X}_1 = F(\bar{X}_s)$  where F is an unknown function, it follows by substitution that  $\bar{X}_c = F(\bar{X}_1)$ . This is not true, since the sample correlation coefficients for  $\bar{X}_c$  vs.  $\bar{X}_1$  are relatively low and erratic in sign (or negative). If  $\bar{X}_s = F(\bar{X}_t)$ , the corresponding coefficient of correlation should be high and consistent in sign. Although 2 are

relatively high, 2 are low and the signs vary extremely with the species represented.

Therefore a causative interaction of these variables has not been shown. It is most likely that the correlations for  $\bar{X}_t$  vs.  $\bar{X}_s$  are the results of sampling bias. Such a conclusion should be expected at the outset, since the shell samples were collected from areas where surface runoff may be an important factor of salinity.

The preceding relationships agree with those established by studies of shell growth under controlled conditions (see Wilbur, 1960). Specifically, increase of salinity causes an increase in the rate of crystallization which lowers the widths of the crystalline constituents by producing a greater number of crystals. Conceivably, an increase in temperature should do the same; however, the sample correlation coefficients obtained in this study indicate that its contribution to the decrease of crystal size is relatively negligible.

Variations in the thickness of growth layers are best accounted for by temperature changes, salinity being a subordinated factor. It is suggested that water temperature controls the metabolism of the organism and influences the amount of food available, while salinity influences the composition of the secretory fluids by osmotic processes (some osmotic effects of growing oysters, such as puckering of the mantle, death, etc., are described by Worsnop and Orton, 1923,

<sup>4</sup> $\bar{X}$  being the arithmetic mean.

and Robertson, 1941).

### Origin of the Growth Layering

The main environmental factors influencing shell growth are considered to be water temperature and salinity, because the metabolism of an organism is an organized system of chemical reactions that are accelerated by an increase in temperature; and because the availability of the necessary constituents in sufficient quantity within a littoral area is influenced both by salinity and temperature. The water temperatures and salinities of the sample localities vary cyclically in response to tidal and climatic changes that have periods ranging from 12 hours to one year. Assuming that these variations affect shell growth, the following scheme is proposed as the most likely interpretation of the shell growth layering which has been seen and measured in several specimens of 2 orders of Pelecypoda:

- I. The 1st-order layer is an expression of the annual temperature cycle.
- II. It is probable that equinoctial storms inhibit shell growth, causing the formation of very fine carbonate-rich layers that differ markedly from the

thick conchiolin-rich layers produced during calmer periods.

- III. The tidal amplitudes of the sample localities vary cyclically with a of 15 days. Thus, there are 2 phases of the 3rd-order cycle viz., a spring tide condition of maximum circulation of food associated with rapid shell growth and a neap tide condition of minimum circulation of food.
- IV. Since the water temperatures in a shallow area are highest during the day and lowest during the night, the 5th-order day layers are thicker than those formed at night; also, the day layers are richer in conchiolin than are the night layers. This suggests a 24 hour periodicity for the formation of 4th-order layers.
- V. The 5th-order layer reflects the diurnal tidal rhythm and thus has a 6 hour periodicity; whereas the calcium carbonate layers are formed when the shell is either closed or open, the conchiolin is deposited during the process of closing or opening.

The above hypothesis and some mor-

TABLE III. Explanation of the origin of cyclic shell-growth layering in clams from shallow marine environments.

Growth layers	Thickness range	Sublayers	Phases of cycle	Probable period
5th-order	1-16 $\mu$	Calcium carbonate Conchiolin	Shell open or closed at high or low tide Shell in process of opening during tidal change	6 hours
4th-order	5-60 $\mu$	Thick 5th-order Thin 5th-order	Day (fast growth) Night (slow growth)	24 hours
3rd-order	0.1-0.9 mm	Thick 4th-order Thin 4th-order	Maximum tidal amplitude Minimum tidal amplitude	15 days
2nd-order	0.9-11 mm	Conchiolin-rich Conchiolin-poor	Normal conditions Equinoctial conditions	1/2 year
1st-order	2-22 mm	Thick 2nd-order Conchiolin-rich Thin 2nd-order Conchiolin-poor	Summer Winter	1 year

phological measurements are summed-up in Table III, to enable the reader to visualize the correlation of the hypothesis and data. The more than 1000 4th-order layers of an average pelecypod shell seem to be reasonably correlated with the daily cycle and expected life spans of marine pelecypods.

### DISCUSSION

The shells examined show microtextures that are intergradational between the fast-growth Type B and the slow-growth Type A, depending upon dendritic intergrowth of foliated crystals, orientation of seed crystals, and deformation of crystal lattices. The physicochemical factors that govern these processes are discussed below.

A real crystal differs from an ideal one in that it is modified by changes of the external medium and by individual properties of the faces. Corresponding structures are, respectively, layered or zonal growths and sector growths. Specific mechanisms for modification of an ideal crystal involve impurity concentration in the solution and crystal deformation during growth. It is well-known to students of crystallization that the tendency of a crystal to grow is greatest along a direction in which its atoms are most densely packed and least along a direction in which its atoms are the least densely packed. Thus, crystal faces result, the ones of greatest area being oriented perpendicular to directions of minimal growth and those of minimal area oriented normal to directions of maximal growth. However, the shape of a crystal shows the influence of forces that are not determined by the symmetry of the unit cell. There are conditions for maximal development of faces, i.e., equal growth in all directions resulting in a spheroid, and there are conditions for minimal development of faces and consequently, maximal elongation, i.e., a needle- or platy-shaped euhedron.

Studies of the environmental factors of crystal morphology have been reviewed

by Buckley (1952), Krynine (1957), and Saratovkin (1959). It is known that dendritic growth results from rapid crystallization in a highly saturated solution and is enhanced by increase of impurity concentration. In such a viscous fluid, surface tension can pull apart crystal layers, causing dislocations in the crystal lattice. Seed crystals tend to become oriented with their long axes perpendicular to a solid-liquid interface and the orientation of the earliest formed crystals influences later growth. Therefore, the development of textural Type B (heterogeneous aggregate of coalescent crystals) depends primarily upon the rapidity of crystallization and the impurity concentration. Possibly, the mechanical deformation and anomalous orientation of small crystals augments the heterogeneity of crystal intergrowths (elements of the Type B texture).

In addition to the above quantitative factors, the kind of organic impurities may also influence shell microtexture. Krynine (1957) has reviewed intensive studies of the crystallization effects of various organic compounds which show that for a given concentration of organic impurities, the effectiveness of an organic barrier to ionic movement depends upon the molecular natures of the crystal faces and the impurities involved. For example, scores of replicate experiments have shown that equal quantities of blood from well and sick persons have characteristically different effects on the growth of copper chloride crystals. Possibly, the association between texture Type B and pigmented conchiolin is due to a similar phenomenon.

The taxonomic aspects of this model for crystallization during shell growth are inviting. The metabolism of a pelecypod species is characteristically unique and therefore the chemical composition of its body fluids and its process of shell formation must be associated with a characteristic shell microtexture. However, microtexture is influenced by environmental phenomena which affect shell growth both directly and through the

intermediation of metabolism. An understanding of shell microtexture in terms of crystallographic properties and physicochemical factors is a prerequisite to taxonomic shell structure study. Future development of both optical and electron microscopic techniques should aid in the exploration of the nature and distribution of intra-crystal layers and diverse crystal shapes. Such study should be disciplined by crystallographic orientation, an achievement which has been roughly approximated in reconnaissance work done so far.

Here, shell microtexture is shown to vary between 2 textural extremes resulting in 5 distinct orders of growth layers. The relative sizes of these layers and their coordination in the shells suggest a periodicity of formation induced by the environment, i.e. a system of temperature-salinity-tide cycles. At the smaller level of organization, this system involves daily fluctuations of sea level, at the larger level, annual changes of derived conditions of temperature and salinity of the water, chemical potentials, the kind and abundance of food available, and perhaps other interacting phenomena. Although the layers hypothetically formed during the summer are as much as 10 times thicker than the winter layers, there is no microscopic evidence of a complete cessation of shell growth in the species examined. Seemingly these shells are natural calendars which record tidal and climatic events. Hence, we might speculate on the expression of environmental rhythms in molluscan shells.

Forbes (1854) observed that neritic and deeper water bivalves are not as complexly "sculptured" as littoral and inner neritic bivalves. Does the growth layering hierarchy of pelecypod shells become less complex with increase of depth?

Emery et al. (1957) have discussed some estuarine environmental rhythms that are different from the rhythms of an open shoreline. Are these differences detectable in the growth layering of molluscan shells?

It is well-known that seasonality

generally increases with increase of latitude. Might mathematical analyses of growth layering graphs facilitate correlations of growth layering patterns and climatic zones?

The paleontologist, ranging farther into the dimension of time, should encounter the sunspot cycles detected by dendrologists (see Douglass, 1936), a changing rate of the earth's rotation (Wells, 1963), precession of the equinoxes, obliquity of the ecliptic, and, perhaps, hitherto undetected celestial aberrations that influence the rhythms of the biosphere.

I suggest that the first steps are to conduct laboratory growth experiments and ecological investigations in order to test the hypothesis that growth layering reflects environmental periodicities.

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## RESUMEN

## VARIACION MICROTTEXTURAL EN CONCHAS DE PELECIPODOS

Del estudio microscópico de la composición estructural de la concha de cuatro peleciopodos marinos (tres Eulamelibranquios y un Taxodonte), se infiere que la cristalización dendrítica del carbonato de calcio representa un papel esencial en la variabilidad de la textura.

En las conchas estudiadas aparecen, jerarquizados, cinco grupos cíclicos de capas de crecimiento: una capa de 1<sup>er</sup> orden consta de dos capas de 2<sup>o</sup> orden, 24 de 3<sup>er</sup> orden, aproximadamente 365 de 4<sup>o</sup> orden y alrededor de 1460 de 5<sup>o</sup> orden. Estas capas de crecimiento están formadas por tres tipos de capas elementales ultrafinas ( $\approx 8\mu$ ): (1) carbonata de calcio criptocristalino, (2) material opaco, o semiopaco, llamado conquiolina, y (3) conquiolina dispersa en un agregado microcristalino de aragonita.

Una capa de 5<sup>o</sup> orden es simplemente una alternancia de conquiolina con cualquiera de los carbonatos. La capa de 4<sup>o</sup> orden, más compleja (espesor promedio cerca de 30  $\mu$ ), consiste exactamente de 8 capas elementales dispuestas como sigue: 1, 2, 3, 2, 3, 2, 3, 2; 1, . . . etc. El espesor de la capa de 4<sup>o</sup> orden tiene una variación cíclica con periodo de 15 capas, resultando en una capa de 3<sup>er</sup> orden (grosor promedio cerca de 0,5 mm). Esta capa está además caracterizada por una fase oscura de capas compuestas y de conquiolina relativamente espesas que alterna con una fase clara en la cual las capas criptocristalinas son casi tan gruesas como las otras. La capa de 2<sup>o</sup> orden tiene dos fases: (a) normal, en la cual la cantidad de conquiolina y elementos compuestos excede aquella del carbonato de calcio criptocristalino, y (b) fase de carbonato, en que el último elemento iguala o excede a los dos primeros. El grosor de esta capa es de un promedio de 6,5 mm, con la fase normal alrededor de 6,0 mm. La capa de 1<sup>er</sup> orden (grosor promedio 13 mm) se caracteriza por el engrosamiento y el adelgazamiento de sus dos capas componentes.

Suponiendo que estas capas de crecimiento reflejan periodicidades ambientales, la de 1<sup>er</sup> orden puede estar correlacionada con el cambio anual de temperatura y salinidad, la de 2<sup>o</sup> orden con mareas y tormentas equinocciales, la de 3<sup>er</sup> orden con el ciclo quincenal de mareas, la de 4<sup>o</sup> con el día y la noche, y la de 5<sup>o</sup> con el ritmo diario de la marea.

Las capas de crecimiento se superponen a dos capas principales que son paralelas a la superficie de la concha: (1) capa principal externa, en la cual los cristales son pequeños y las capas de crecimiento son gruesas, y (2) capa principal interna o media, en la cual los cristales son grandes y las capas de crecimiento son delgadas. En la especie taxodonte *Anadara ovalis* la concha tiene una tercera capa principal, interna, con cristales aciculares irregularmente orientados y sin estratificación de crecimiento.

Típicamente cada cristal presenta configuración y foliación complejas, y está rodeado de un agregado de unidades cristalográficas minúsculas y distintas y conquiolina. Ópticamente estos agregados constituyen una interpenetración de innumerables ramificaciones cristalinas. Estas estructuras están formadas por cristalización dendrítica, proceso que es favorecido por el crecimiento rápido y abundancia de impurezas. Esta interpretación tiene a su favor el hecho de que tales interpenetraciones están más desarrolladas en las capas principales externas, donde el crecimiento de la concha es más rápido y la conquiolina es más abundante.

La capa principal externa de *Mactra solidissima* tiene ocasionalmente unas pocas estructuras pinadas compuestas de varios cristales de aragonita asociados a una distorsión de las capas de crecimiento. Tales anomalías indican recristalización o algún fenómeno biológico desconocido.

Las medidas microscópicas de ejemplares de ambientes diferentes indican que el tamaño de los cristales está inversamente relacionado al aumento de la salinidad, mientras que el espesor de las capas de crecimiento está directamente relacionado con la temperatura.

Sería de mucho interés una valuación matemática, por análisis más extensos y rigurosos, de la microtextura de la concha y de los factores ecológicos. Experimentos de crecimiento en el laboratorio y trabajos ecológicos proveerán pruebas directas para la hipótesis de que la periodicidad de las mareas se refleja en la disposición de las capas de crecimiento.

## ВАРИАЦИИ В МИКРОСТРУКТУРЕ РАКОВИН ДВУХСТВОРЧАТЫХ МОЛЛЮСКОВ

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## А Б С Т Р А К Т

Изучение микроскопической структуры раковин 4 морских двухстворчатых моллюсков ( 3 *Eulamellibranchiata* и 1 *Taxodonta* ) привело к заключению, что дендритная форма отложений углекислого кальция играет важную роль в образовании разнообразных структурных вариаций.

В изучаемых раковинах наблюдалась последовательность в группировке пяти циклических слоев роста: один слой 1-го порядка состоит из двух слоев 2-го порядка, 24 слоев 3-го порядка, приблизительно 365-ти слоев 4-го порядка и около 1460-ти слоев 5-го порядка. Эти слои роста построены из трех типов ультрамикроскопических элементарных слоев ( 8 ): (1) слой криптокристаллического углекислого кальция, (2) непрозрачного или полупрозрачного материала называемого конхиолином, и (3) конхиолина, рассеянного в микрокристаллическом агрегате арагонита.

Слой 5-го порядка является простым чередованием конхиолина с тем или другим элементом углекислого кальция. Более сложный слой 4-го порядка (средняя толщина около 30 ) состоит точно из 8-ми элементарных слоев, расположенных следующим образом: 1,2,3,2,3,2,3... и т.д. Толщина слоя 4-го порядка варьирует циклически с периодом в 15 слоев, в результате чего образуется слой 3-го порядка (средняя толщина около 0.5 мм). Этот слой характеризуется также темной фазой сравнительно толстого отложения смешанного состава и конхиолиновыми слоями, которые чередуются со светлой фазой состоящей из криптокристаллических слоев почти такой же толщины как и другие слои. Слой 2-го порядка имеет 2 фазы: а) нормальную фазу, в которой количество конхиолина и составных элементов больше чем количество криптокристаллического углекислого кальция, и б) углекислую фазу, в которой количество углекислого кальция равно или превосходит количество двух других элементов. Средняя толщина этого слоя - 6.5 мм, причем нормальная фаза занимает около 6.0 мм. Слой первого порядка (средняя толщина 13 мм) характеризуется увеличением и уменьшением толщины двух его составляющих слоев. Предполагая, что эти слои роста зависят от периодических изменений в окружающей среде, можно думать что слой первого порядка зависит от годовых изменений в температуре и солености; слой второго порядка - от равноденственных приливов и штормов; слой 3-го порядка - от двухнедельного приливного цикла; слой 4-го порядка - от дня и ночи, и слой 5-го порядка - от ежедневного приливного ритма.

Слои роста наложены на два главных слоя параллельных поверхностям раковины: (1) в наружном главном слое кристаллы мелкие, а слои роста толстые и (2) во внутреннем или среднем главном слое кристаллы крупные, а слои роста тонкие. В раковине таксонотного вида *Anadara ovalis* имеется третий внутренний главный слой с неправильно ориентированными игловидными кристаллами, и без прослоек роста.

Характерно то, что форма каждого кристаллика сложная; кристаллы слоистые и окружены скоплениями маленьких кристаллографически отдельных элементов, и конхиолином. Оптические наблюдения указывают, что этот агрегат кристалликов является в результате прорастания бесчисленных кристаллических веточек. Такие структуры образуются благодаря дендритной кристаллизации, - процессу, которому благоприятствует быстрый рост и обильное засорение. Это объяснение подтверждается тем фактом, что прорастание лучше всего развито в наружных главных слоях, где рост раковины происходит наиболее быстро и количество конхиолина наиболее обильно.

Иногда главный наружный слой раковины *Mactra solidissima* содержит небольшое количество перистых образований, состоящих из нескольких кристалликов арагонита, встречающихся в случаях неправильного образования прослоек роста. Эти аномалии указывают на перекристаллизацию, или же на какое-то неизвестное биологическое явление.

Микроскопические измерения особей собранных в разных экологических условиях показывают, что размер кристалла обратно пропорционален увеличению солености воды, в то время как толщина слоев роста прямо пропорциональна температуре.

Желательно произвести математическую оценку этих данных на основании более строгого и более широкого анализа микроскопического строения раковины и ее связи с экологическими факторами. Лабораторные опыты над ростом и экологические наблюдения должны дать материал для прямой проверки гипотезы о влиянии периодичности приливов на рост слоев раковины.

SURFACE INSPIRATION AND CILIARY FEEDING IN *POMACEA PALUDOSA*  
(PROSOBRANCHIA: MESOGASTROPODA: AMPULLARIIDAE)<sup>1</sup>

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ABSTRACT

*Pomacea paludosa* uses both a gill and a lung in respiration. The gill obtains oxygen from a water current drawn through the mantle cavity. The lung obtains oxygen by a process termed "surface inspiration." Although food is normally obtained from the substrate with the radula, *P. paludosa* also gathers food from the surface film in a behavior termed "ciliary feeding." A series of observations and experiments were made of these 2 processes.

A "surface inspiration" was anticipated by formation of the mantle's left inhalent aperture into a siphon. Snails then crawled to the surface of the water and typically contacted the surface film first with the left tentacle. The siphon then extended to the surface film and air was drawn to the lung in the mantle cavity by a series of body contractions. A single inspiration consisted of approximately 16 contractions, each lasting 1 second. Snails then usually turned down to their right and crawled down or fell from the vessel wall. The stimulus for surface inspiration was associated with decreased lung volume. Tentacles oriented a snail to air. However, inspiration took place if the siphon alone contacted air. Increase in temperature, irritant (NH<sub>4</sub>OH) in the water, decrease of oxygen level in the water, and starvation of snails all significantly increased inspiration rate. Decrease in temperature and dissolved food in the water significantly decreased inspiration rate. Food placed in the surface film, sediment in the water, and substitution of nitrogen for the air over the water had no significant effect on inspiration rate. The inspiration rate decreased with time in each experiment. This was largely due to a concomitant decrease in the number of active snails. The frequency distribution of inspirations among snails was similar in all experiments. Decrease in water temperature and presence of dissolved food significantly decreased rate of movement. Dissolved food also caused snails to continually rasp with their radulae at the floor of the vessel. Snails inspiring nitrogen repeated the normal series of contractions up to 10 times, and tended to remain at the surface of the water. Snails denied access to the surface aggregated on the underside of the barrier, although the water was oxygen saturated.

In ciliary feeding, snails formed the anterior part of the foot into a funnel, the mid-part into a tube. Pedal cilia then drew food from the surface film into the funnel and down through the tube. The food, which was bound together with mucus, collected at the base of the tube. At intervals, a snail thrust its head into the tube and ingested the gathered food. Prior feeding did not lower the frequency of ciliary feeding among active snails. The stimulus for ingestion of gathered food was not correlated with either weight of gathered food, or degree of starvation. There was no evidence that depletion of pedal mucus caused ingestion. Submergence of the foot stimulated snails to ingest, regardless of the amount of the food gathered. Ciliary feeding occurred infrequently unless food was placed in the surface film.

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## INTRODUCTION

Members of the family Ampullariidae use both a gill and a lung in respiration. The gill is located in the right portion of the mantle cavity, the lung in the left. The gill receives oxygen from a respiratory current which is drawn through the mantle cavity. At intervals, at least in captivity, ampullariids travel to the surface of the water, extend a siphon to the air water interface, and draw air down the siphon to the lung by a series of body contractions. In the present paper, each trip to the surface to obtain air will be termed a "surface inspiration." A summary of the literature on ampullariid respiration is given by Prashad (1925).

Although ampullariids normally feed by rasping at the substrate with their radulae, *Pomacea paludosa* and *P. canaliculata* also feed by gathering food from the surface film with pedal cilia. Johnson (1952) and Cheesman (1956) have described this "ciliary feeding" behavior.

In connection with a study of the effect of removing statocysts from *P. paludosa*, I investigated those behavior patterns which might be under statocysts control. As it was suspected that surface inspiration and ciliary feeding might fall within this category, a series of studies, reported in this paper, were made of these 2 behavior patterns. A subsequent paper will deal with the behavioral alterations which result from statocyst removal.

Preliminary observations showed that *P. paludosa* tended to become inactive in standing water. Therefore, an initial study was made to determine whether snails placed in standing water would be active enough to allow profitable observation. A study was next made of *P. paludosa*'s rate of movement under various conditions, as this was considered of probable importance to an understanding of the 2 behavior patterns. After completion of these initial studies, a series of observations and experiments were undertaken to determine the factors which govern surface inspiration and ciliary feeding.

## MAINTENANCE AND GENERAL METHODS

*Pomacea paludosa*, a common tropical aquarium snail, was raised in the laboratory from stock purchased in Milwaukee, Wisconsin, U. S. A. Colonies were maintained in 20-gallon glass aquaria filled with charcoal filtered tap water and covered with plexiglass. Meta Frame Hi-volume filters, manufactured by the Metal Frame Aquarium Company, Pine Brook, N. J., U. S. A., were installed to provide continuous circulation of water in each aquarium. Water temperature was maintained at  $26 \pm 2^{\circ}\text{C}$ . Aquaria were in a room with a northern exposure. Additional light was provided by overhead cool white fluorescent lights. No attempt was made to control light intensity or photo-period. Snails were fed Wardley's fine grade Supremix (Wardley Products Company, Inc., Long Island City, N. Y., U. S. A.). This food was chosen because its fine texture was suitable for ciliary feeding experiments. Daily feeding consisted of approximately 0.1 gm of food per adult snail. Aquaria were cleaned every 4 to 6 weeks. Although oviposition was most common in spring, it occurred during all seasons. Egg capsules were laid on the underside of the plexiglass or on the upper aquarium walls. The number of snails maintained in each aquarium varied with snails size. Thus, up to 200 newly hatched snails, but not over 30 adults were maintained in any one aquarium. Snails over 6 gm in weight were considered adults. Snails lived at least a year under favorable laboratory conditions.

When an experiment required the identification of individual snails, numbers were painted on shells with deco-write, an enamel paint manufactured by the Craftint Manufacturing Co., Cleveland 10, Ohio, U. S. A. Peeling was avoided by first roughing shells with a dental burr. In the majority of experiments, the following regimen was followed: snails to be used were placed in a 20-gallon aquarium in a darkened room on the evening preceding an experiment. The aquarium was il-

luminated with incandescent light at 07:30 the following morning. The experiments themselves were then begun at 09:30. Vessels used in experiments contained filtered water maintained at approximately 26°C by water baths. Overhead incandescent bulbs provided 32 foot-candle illumination at the water's surface. The above regimen was not followed when general observations were made of surface inspiration and ciliary feeding, or in those experiments described under "relation between lung volume and inspiration," "stimulus responsible for ciliary feeding" and "stimulus responsible for ingestion."

## EXPERIMENTS ON ACTIVITY

### 1. Effect of standing water on activity.

Observations were made on 3 successive days; 20 snails were observed each day. Tests were made in 2 plastic dishes. Each contained 3.5 liters of water. Ten snails were placed in each dish, and observed for 4 hours. The number and location of all inactive snails were recorded at 5-minute intervals.

Figure A gives the number of inactive snails during the 4-hour period. Inactivity was negligible for the first 50 minutes;

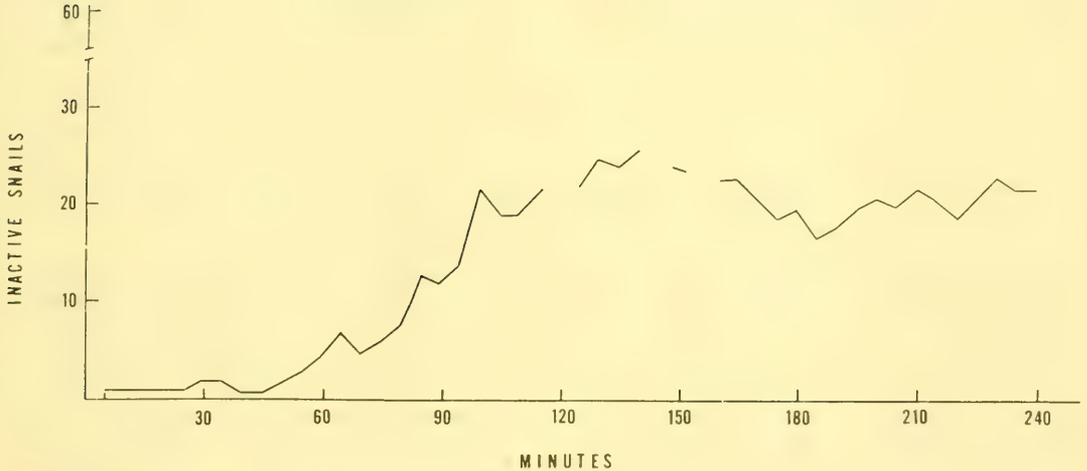


FIG. A. Inactivity level among 60 snails observed during a 4-hour period. Breaks indicate intervals during which data were not taken.

Instead, snails were tested or observed either when in maintenance aquaria, or directly upon removal.

To evaluate the significance of responses under various conditions, either chi square or Student's *t*-test was applied in several experimental series.

then it steadily increased until 100 minutes, when over 1/3 of all snails were inactive. The duration of inactivity for individual snails varied from 5 to 170 minutes. Inactive snails were normally located on dish floors, and either retracted completely into their shells or remained

attached with their foot. A few inactive snails were attached to dish walls, or floated. As a result of this study, remaining experiments were designed to last no more than 80 minutes.

## 2. Rate of movement.

Four experiments were conducted on 4 successive days. The snails were tested in a plastic dish containing 700 ml of water. The underside of the transparent dish was marked with a grid so that movements of snails in the dish could be recorded on paper marked with a similar grid. Snails were placed singly in the dish. The movement of each snail was recorded for 5 minutes, the snail removed, the dish cleaned and a new snail introduced. Experimental snails were subjected to the following variations: 1st experiment: 36°C water; 2nd experiment: 16°C water;

dish floor. This behavior presumably represented a search for the point of origin of the stimulus, which under natural conditions would commonly be the substrate. Under temperature increase, snails behaved abnormally, raising their feet from the substrate and frequently twisting their shells.

## STUDIES OF SURFACE INSPIRATION

### 1. General observations.

Data on performance of surface inspiration were obtained by observing snails in maintenance aquaria. Surface inspiration was anticipated by the formation of the inhalent aperture at the left side of the mantle into a short tube or siphon. The siphon then commonly elongated for short periods of time before a snail

TABLE 1. Rate of movement under various conditions

Experiment	Snails			Average distance traveled in 5 min. (in cm)	T-Test
	Nature	Numbers observed	Average wt. in gms		
Dissolved food in water	Exptl.	16	1.3	17	2.21*
	Control	16	1.3	39	
Increased water temperature	Exptl.	19	1.9	51	0.03
	Control	16	1.9	51	
Decreased water temperature	Exptl.	17	1.5	23	8.5*
	Control	17	1.6	50	
Decrease in light	Exptl.	7	2.0	44	0.76
	Control	8	2.1	49	

\* Indicates significant at .05 level of rejection.

3rd experiment: water containing 2 gm peptone and 0.2 gm dextrose; 4th experiment: light intensity reduced to 1 foot candle. Controls were run for each of these experiments.

Decrease in temperature and introduction of dissolved food significantly lowered rate of movement. Increase in temperature and reduction of light intensity caused no significant change in rate (Table 1). When subjected to dissolved food, snails rasped continually at the

reached the surface of the water: elongation occurred in 55 of 80 snails (68.8%) observed prior to inspiration. When fully elongated, the siphon of an adult snail measured over 3 cm in length, and approximately 2 mm in diameter at its aperture.

Snails crawling upwards on an aquarium wall to inspire followed an irregular path. First contact with the surface film however, was usually made with the left tentacle. The siphon then reached upwards

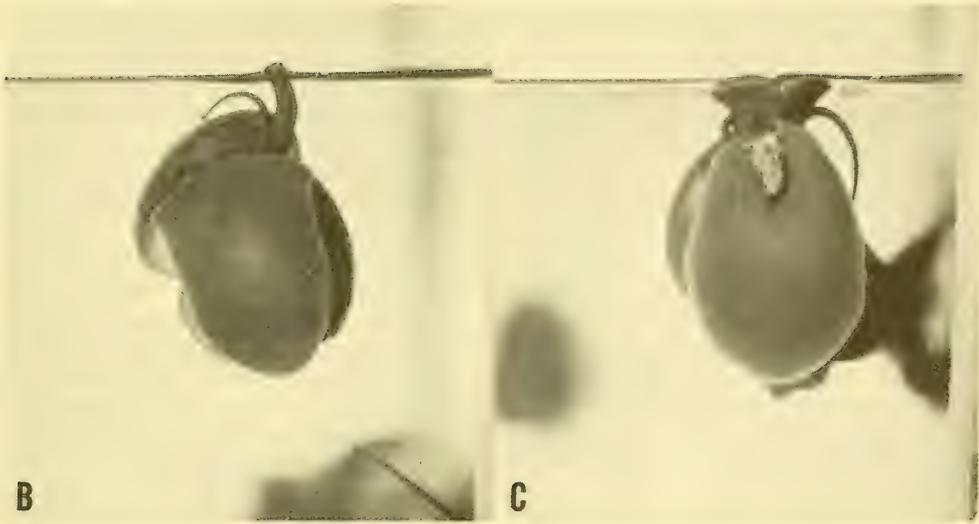


FIG. B. *Pomacea paludosa* undergoing surface inspiration. Foot, which is approximately 4 cm in length, is against aquarium wall.

FIG. C. *Pomacea paludosa* engaged in ciliary feeding. Anterior portion of foot is formed into funnel at surface film. Mid foot is formed into tube. Note food accumulating just below tube.

to the surface film, made contact, withdrew, and reextended to the film again. The exhalent aperture at the right side of the mantle cavity now closed, and the snail drew its head under the shell (Fig. B). A series of body contractions then drew air down through the siphon into the lung. As indicated in Table 2,

TABLE 2. Surface inspiration\* in 2 size groups of snails.

Snails		Inspirations	
Size and average weight	Number	Average number of contractions	Average duration in seconds
Small 4.8 gm	15	15	17.1
Large 9.1 gm	10	18.7	20.5

\*One inspiration observed for each snail.

contraction occurred at intervals of approximately 1 second. Of 55 snails observed, 49 (89%) inspired with a single sequence of contractions. In 6 snails, inspiration consisted of 2 such sequences, interrupted by a pause of 10-60 seconds.

After inspiring, snails crawled down an aquarium wall or dropped to the aquarium floor. Of 51 snails observed, 43 (84.3%) turned down to their right, 8 (15.7%) to their left. If food was present in the surface film, snails remained and began ciliary feeding.

2. Relation between lung volume and inspiration.

It was suspected that snails rising to inspire would have a reduced volume of gas in their lungs. The relation between lung volume and inspiration was therefore explored in 2 experiments, both using snails in maintenance aquaria. In the first experiment a closed plastic tube was lowered over the siphon of snails

and notes were made of water level changes within the tube during contractions. The water level at first rose within the tube, then moved up and down. This suggests that the first few contractions drew air into the lung, while the remaining ones drew air both in and out.

The second experiment concerned the effect of inspiration on buoyancy: 24 snails, averaging 8.4 gm in weight, were dislodged from aquarium walls just before inspiring and their rate of fall measured; 24 others averaging 8.1 gm in weight were tested just after inspiration. To fall 40 cm, the first group required an average of 5.8 seconds, the second group, 15.5 seconds. Thus, the buoyancy of snails was significantly less before surface inspiration than after.

These data indicate that the stimulus which causes surface inspiration is associated with a reduced lung volume. It is probable that the stimulus itself results from O<sub>2</sub> depletion, for this has been shown to be so for pulmonates (Precht, 1939).

### 3. Sensitivity of siphon and tentacles to stimuli.

Four experiments were conducted in a 20-gallon aquarium. Snails were placed in the aquarium, allowed to acclimatize for 30 minutes and then tested. At time of testing, subjects were crawling upward on the aquarium wall, but were at least 20 cm from the surface of the water. Experiments consisted of the stimulation of siphon or tentacles with a plastic tube which contained either air or water. The tube was carefully lowered by hand over the organ to be stimulated. When air was used a bubble was protruded from the tube by means of a plunger at the other end. The tube was rinsed with tap water between each use.

The 1st experiment tested the ability of tentacles to orient a snail to air. The right or left tentacle of 101 snails was stimulated with an air bubble extended from the plastic tube; tentacle contact with the tube itself was held to a minimum. Of these snails, 69 responded to the stimulus by turning to face the bubble, suggesting that during inspiration snails

use their tentacles in orienting to the air above the surface film.

The 2nd experiment tested the reaction of snails to a tactile stimulation of the tentacles with the tube itself. The right or left tentacles of 21 snails were stimulated with the water-filled tube, the tentacle being allowed to touch the tube wall. Sixteen snails (76%) turned toward the tube, suggesting that tentacles probably serve to orient a snail to a variety of substances in addition to air.

The 3rd experiment tested the response of the siphon to tentacle stimulation. The right tentacles of 37 snails were each stimulated with an air bubble and the reaction of the shortened siphon noted. Ten snails (27%) elongated their siphon during or immediately after stimulation, 27 (or 73%) showed no siphon reaction. Thus, there was no evidence that tentacle stimulation caused a siphon to elongate.

The 4th experiment tested the sensitivity of the siphon to a direct stimulation with air. The shortened siphons of 24 snails were each stimulated with an air bubble. In 16 cases (66.6%) the siphon elongated. In 2 of these, prolonged contact caused the snail to attempt inspiration. This attempt ceased after a few contractions, as water rose in the tube and broke air-siphon contact. Thus, stimulation of the siphon alone can cause elongation and inspiration to occur. The siphon, however, is relatively insensitive to air. This was indicated by the fact that when an air bubble was placed beside the tip of an elongating siphon, the latter would extend up past the air rather than bend to it, although siphons are capable of such bending movements.

### 4. Effect of environmental conditions on surface inspiration.

A series of 10 experiments was conducted. A single population of 120 snails, 7 months old, was used for the first 8 experiments. The last 2 experiments (starvation of snails, and food in surface film) used a different population of 120 snails, 9 months old. For each set of experimental conditions, a total

of 60 snails from the population pool were tested, in 2 batches of 30 snails, on 2 different days, with several days of rest between experiments. Parallel control series were run with an equal number of snails from the same population. During experimentation, each population had a mortality of less than 5%.

Experiments were carried out in 2 glass cylinders, 46 cm in height by 21 cm in diameter. One of these held the experimental snails, the other, the controls. Cylinders were oil-cloth covered and each contained 8 liters of water. At 09:30, 15 snails were placed in each cylinder, and allowed to acclimatize for 20 minutes. Alternations necessary for the experiment in question were then made and snails were observed for 1 hour.

Records were made of a) the activity of all snails at the surface at 2-minute intervals, b) the number of inactive snails at 0, 25, 50 and 60 minutes, and c) all surface inspirations. If a snail carried out 2 surface inspirations separated by less than 10 minutes, these were considered as 1.

During the last 10 minutes of the hour, overhead lights were extinguished and dim lateral lights substituted. At the hour's end snails were removed, cylinders washed and a second group of 30 snails similarly tested.

The 10 experiments were designed as follows:

1) *Dissolved food in water:* 16 gm of dextrose dissolved in 100 ml of water were added to the experimental cylinder. Control cylinder received 100 ml of water.

2) *Decreased water temperature:* Overhead tanks supplied 12°C water to experimental cylinder, 26°C water to control cylinder. Siphons kept water level in cylinders unchanged. Siphons and inflow tubes entered water at mid-cylinder to avoid contacting snails. After 5 minutes, inflow was stopped, siphons and inflow tubes removed. Water in the experimental cylinder was now 20°C. This temperature was maintained by water bath adjustment.

3) *Increased water temperature:*

Design was similar to 2), except in that experimental cylinder received 36°C water, thereby raising its temperature to 30°C.

4) *Suspended particles in water:* 1/10 gm of powdered charcoal was added to the experimental cylinder and kept in suspension by running a plunger through the cylinder every 10 minutes. A similar plunger was operated in the control cylinder.

5) *Irritant in water:* 100 ml of 0.001 M  $\text{NH}_4\text{OH}$  were added to the experimental cylinder. Control cylinder received 100 ml of water.

6) *Starvation of snails:* The snails used as experimental animals were starved for 2 days prior to testing.

7) *Food in surface film:* 0.05 gm of Wardley's Supremix was placed on the water in the experimental cylinder. Food was replenished as snails rose and collected it.

8) *Lack of access to surface of water:* Air saturated water was circulated between each cylinder and a companion tank. Tubing used for circulation entered the water at mid cylinder to avoid contacting snails. Circulation continued throughout the experiment. Oxygen level in cylinders was thus raised from 7.4 ppm to 9 ppm. Determinations were by the Winkler method (Welch, 1948). Temperature and water level in cylinders remained unchanged. At the start of circulation, a perforated plexiglass disc 20 cm in diameter was fixed 4 cm below the surface of the water in the experimental cylinder.

9) *Reduction of  $\text{O}_2$  level in water:* Circulation was established as in 8), except that the companion tank to the experimental cylinder contained nitrogen saturated water, driving the oxygen content in the experimental cylinder down to 3.9 ppm.

10) *Nitrogen atmosphere over water:* Circulation was established as in 8). In addition, the top of each cylinder was covered with Saran Wrap (Dow Chemical Co., Midland, Mich., U. S. A.). The experimental cylinder received nitrogen

in the space below the Saran Wrap cover, the control cylinder received air. In both cases, introduced gas expanded the Saran Wrap, then escaped through small holes.

Surface inspiration, or attempts to inspire occurred in all experiments. This was true even in oxygen saturated water. When a barrier to the surface was present, snails collected on its underside and attempted to crawl around the barrier or through the holes in it. If allowed to inspire nitrogen, a snail would make the usual contractions, pause for several seconds to a minute, then repeat the process. In some cases there were as many as 10 repetitions. This suggested that mere expansion of the lung did not remove the stimulus to inspire.

Oxygen consumption rates of snails are typically independent of changes in the

work, as expected, an increase in temperature also raised *P. paludosa's* inspiration rate while a decrease lowered it. In the latter case, the lower inspiration rate also resulted from the fact that snails moved more slowly at a lower temperature (see p 82), and so took longer to reach the surface of the water to inspire. Starvation increased the rate of surface inspiration. This was unexpected, as Von Brand et al. (1948) found that starvation lowered a snail's oxygen consumption rate.

Presence of an irritant increased the rate of surface inspiration. Many snails reacted to the irritant by elongating their siphons. Suspended particles in water and food in the surface film had no significant effect on surface inspiration rate. Dissolved food caused snails to

TABLE 3. Number of surface inspirations under various conditions during a 1-hour period in 60 snails and their controls.

Nature of Experiment	Total Inspirations		Chi-square
	Experimental snails (60)	Control snails (60)	
Irritant in water	105	42	94.5*
Reduction of O <sub>2</sub> level in water	110	61	39.4*
Increased water temperature	71	50	8.8*
Starvation of snails	34	21	8.0*
Lack of access to surface of water	--	62	-
Nitrogen atmosphere over water	58	50	1.3
Suspended particles in water	43	45	0.1
Food in surface film	28	37	2.2
Dissolved food in water	24	51	14.3*
Decreased water temperature	18	49	19.6*

\*Indicates significant at .05 level of rejection

oxygen supply (Von Brand et al., 1948; Berg and Ockelmann, 1959). In the present work, decreasing the water's oxygen level therefore accelerated use of lung oxygen, which in turn increased the rate of *P. paludosa's* surface inspiration. Both Von Brand et al. (1948) and Berg and Ockelmann (1959) have shown that the oxygen consumption rate of snails varies directly with temperature. In the present

work, as expected, an increase in temperature also raised *P. paludosa's* inspiration rate while a decrease lowered it. In the latter case, the lower inspiration rate also resulted from the fact that snails moved more slowly at a lower temperature (see p 82), and so took longer to reach the surface of the water to inspire. Starvation increased the rate of surface inspiration. This was unexpected, as Von Brand et al. (1948) found that starvation lowered a snail's oxygen consumption rate.

Presence of an irritant increased the rate of surface inspiration. Many snails reacted to the irritant by elongating their siphons. Suspended particles in water and food in the surface film had no significant effect on surface inspiration rate. Dissolved food caused snails to rasp at the cylinder floor and to move more slowly (see p 82). This behavior caused a decrease in the rate of surface inspiration. The above results are summarized in Table 3.

In several experiments of this series, there was a significant difference in the time spent at the surface by experimental and control snails (Table 4). In the food in surface film experiment, this was due

TABLE 4. Average time spent at surface by inspiring snails<sup>+</sup> under various experimental conditions.

Nature of Experiment	Snails (60 each)	Number of observations	Average time at surface (in minutes)	T-Test
1) Dissolved food in water	Exptl.	24	4.3	1.88
	Control	48	2.9	
2) Decreased water temperature	Exptl.	18	4.4	2.01*
	Control	47	2.9	
3) Increased water temperature	Exptl.	67	7.5	3.09*
	Control	49	3.1	
4) Suspended particles in water	Exptl.	41	2.4	2.34*
	Control	44	4.2	
5) Irritant in water	Exptl.	101	2.8	2.09*
	Control	41	3.5	
6) Starvation of snails	Exptl.	34	3.5	1.71
	Control	21	2.1	
7) Food in surface film	Exptl.	23	11.4	4.11*
	Control	37	3.2	
8) Lack of access to surface of water	Exptl.	-	-	-
	Control	61	2.5	
9) Reduction of O <sub>2</sub> in water	Exptl.	104	2.64	0.048
	Control	60	2.63	
10) Nitrogen atmosphere over water	Exptl.	57	12.8	7.49*
	Control	49	2.4	

<sup>+</sup> Number of observations is typically slightly smaller than in Tables 3, 5 and 7 as data on time at surface were not available in all cases.

\*Indicates significant at .05 level of rejection.

to the fact that snails in the experimental cylinder followed inspiration by ciliary feeding. In the nitrogen atmosphere experiment, it was due to the repeated inspirations characteristic of snails under such conditions. There is no obvious explanation for the difference in the other experiments. The rate of surface inspiration decreased with time (Table 5). This was in part due to a corresponding decrease in the number of active snails (Table 6). The frequency distribution of surface inspiration was similar in all experiments (Table 7). Decrease in light intensity during the last 10 minutes of each experiment had no effect on surface inspiration behavior.

## STUDIES OF CILIARY FEEDING

### 1. General observations.

Data on performance of ciliary feeding were obtained by observing snails in maintenance aquaria. Cheesman (1956) has stressed the importance of ciliary feeding as a way of collecting the monolayer of protein which is present at the surface of quiet bodies of water. It is probable that under natural conditions ampullariids frequently collect this monolayer. In the present study, however, this occurred only infrequently, and it was necessary to add small amounts of food to the surface film before snails would

TABLE 5. Number of surface inspirations during first, middle and last third of each experiment, in 60 snails and their controls.

Nature of Experiment	Snails (60 each)	Number of inspirations in 1 hour			
		first 1/3	middle 1/3	last 1/3	Total
1) Dissolved food in water	Exptl.	16	2	6	24
	Control	25	15	11	51
2) Decreased water temperature	Exptl.	6	6	6	18
	Control	27	13	9	49
3) Increased water temperature	Exptl.	34	25	12	71
	Control	27	13	10	50
4) Suspended particles in water	Exptl.	28	10	5	43
	Control	17	14	14	45
5) Irritant in water	Exptl.	45	37	23	105
	Control	19	15	8	42
6) Starvation of snails	Exptl.	16	12	6	34
	Control	6	8	7	21
7) Food in surface film	Exptl.	15	9	4	28
	Control	19	10	8	37
8) Lack of access to surface of water	Exptl.	-	-	-	-
	Control	31	21	10	62
9) Reduction of O <sub>2</sub> in water	Exptl.	32	44	34	110
	Control	26	22	13	61
10) Nitrogen atmosphere over water	Exptl.	27	18	13	58
	Control	24	13	13	50

feed with any regularity.

Observations indicated that snails were able to sense the presence of this food in the surface film from a distance of several centimeters. As snails neared a surface film containing food, they often waved their tentacles more actively than was usual and stretched their proboscides upwards to the food. After reaching the surface film a snail drew the margins of its forefoot together to form a funnel. The rim of the funnel was normally in the plane of the surface film, but it occasionally projected several millimeters above. The margins of the mid-part of the foot then curved together to form a tube. The rear part of the foot usually adhered to the aquarium wall or to some other solid surface, although on occasion a snail fed while suspended from the surface film. When snails fed while

suspended from an aquarium wall, the tube was often only partially formed. It was always fully formed, however, when a snail was suspended from a smaller surface such as a floating thermometer or the back of another snail, or when suspended from the surface film. Figure C shows the typical posture assumed in ciliary feeding. Cilia drew the surface film with its food particles over the rim of the funnel and down into the tube. The food, mixed with mucus, was collected at the base of the tube. While gathering, a snail commonly rasped food from the surface film with its radula. At intervals a snail ceased gathering, thrust its head forward into the tube and ingested the food collected there. Macroscopic examination of the funnel revealed no specialized tracts for food collection. Instead, food streamed centripetally from all points on the margin.

TABLE 6. Number of inactive snails, among 60 snails and their controls; under various experimental conditions.

Nature of Experiment	Snails (60 each)	Number of inactives			
		0 minutes	25 minutes	50 minutes	60 minutes
1) Dissolved food in water	Exptl.	0	0	0	2
	Control	2	6	15	22
2) Decreased water temperature	Exptl.	1	0	8	19
	Control	0	6	12	16
3) Increased water temperature	Exptl.	1	14	27	29
	Control	1	9	23	29
4) Suspended particles in water	Exptl.	0	2	13	18
	Control	0	4	9	20
5) Irritant in water	Exptl.	5	5	18	27
	Control	2	15	33	36
6) Starvation of snails	Exptl.	14	18	35	40
	Control	18	37	40	46
7) Food in surface film	Exptl.	11	13	11	8
	Control	11	19	32	38
8) Lack of access to surface of water	Exptl.	1	1	3	3
	Control	2	1	2	8
9) Reduction of O <sub>2</sub> level in water	Exptl.	7	2	7	12
	Control	4	4	2	4
10) Nitrogen atmosphere over water	Exptl.	4	8	12	16
	Control	9	12	18	19

When small (1 mm square) bits of aluminum foil or paper were added to the surface film these were taken into the funnel, passed down into the tube and became aggregated with food particles at the base of the tube. Thus, there were no observable tracts for rejection of inedible materials.

### 2. Stimulus responsible for ciliary feeding.

It seemed possible that food satiation might inhibit ciliary feeding. This was tested as follows: 24 snails were placed in a plastic dish and allowed to feed on substrate food for 1 hour; 22 others were placed in a similar dish but not fed. Snails were then placed singly in 2 liter beakers filled to 1 cm of the rim with filtered water at 26 C. In each beaker 0.1 gm of food was placed in the surface film of the water and a record was made of those snails which engaged in ciliary feeding.

Of the 24 snails allowed to feed from substrate food for an hour, 18 (75%) became inactive when placed in beakers. However, all of the 6 which remained active, engaged in ciliary feeding. Of the 22 snails not allowed to feed from substrate food, 5 (22.8%) became inactive when placed in beakers, 17 (77.2%) remained active and engaged in ciliary feeding. Thus, presence of food in the surface film will induce ciliary feeding in all active snails, regardless of whether they have recently fed or not. Snails which have recently fed, however, tend to be inactive.

### 3. Stimulus responsible for ingestion.

It seemed possible that snails might ingest after gathering a food aggregate of a fixed size. To test this possibility, 18 snails, averaging 7.5 gm in weight, were placed singly in beakers and allowed

TABLE 7. Frequency distribution of surface inspirations among 60 snails and their controls, under various experimental conditions.

Nature of Experiment	Snails (60 each)	Number of snails					Total inspirations
		0 insp.	1 insp.	2 insp.	3 insp.	+3 insp.	
1) Dissolved food in water	Exptl.	38	21	0	1	0	24
	Control	18	34	7	1	0	51
2) Decreased water temperature	Exptl.	44	14	2	0	0	18
	Control	20	31	9	0	0	49
3) Increased water temperature	Exptl.	9	31	20	0	0	71
	Control	17	36	7	0	0	50
4) Suspended particles in water	Exptl.	24	31	3	2	0	43
	Control	24	28	7	1	0	45
5) Irritant in water	Exptl.	0	28	20	11	1	105
	Control	26	27	6	1	0	42
6) Starvation of snails	Exptl.	32	22	6	0	0	34
	Control	45	9	6	0	0	21
7) Food in surface film	Exptl.	37	19	3	1	0	28
	Control	28	28	3	1	0	37
8) Lack of access to surface of water	Exptl.	-	-	-	-	-	-
	Control	14	31	14	1	0	62
9) Reduction of O <sub>2</sub> in water	Exptl.	5	17	25	11	2	110
	Control	11	38	10	1	0	61
10) Nitrogen atmosphere over water	Exptl.	18	27	14	1	0	58
	Control	23	25	11	1	0	50

to gather food from the surface film. Nine gathered from a heavy concentration of food, 9 others from a sparse concentration. As snails ceased gathering and prepared to ingest, their food aggregates were removed with the aid of a blunt probe. Each food aggregate was then dried and weighed. The aggregates which were gathered from a heavy food concentration averaged 12 mg in weight; the aggregates gathered from a sparse concentration averaged 4 mg. These results indicate that ingestion is not dependent on the gathering of a certain amount of food.

A second possibility was that an internal stimulus resulting from need for food may cause a snail to ingest. If this were so, hungry snails would presumably cease gathering to ingest more often than would

satiated snails. To test this, the food aggregates collected by the snails utilized in the experiment entitled "stimulus for ciliary feeding" were examined. Aggregates of 5 starved and 5 satiated snails were compared. In each group of snails, weights averaged approximately 10.5 gm. Food aggregates of the 5 recently fed snails averaged 22.5 mg; aggregates of the 5 starved snails, 24.7 mg. This indicates that starvation does not act as a stimulus for ingestion.

A third possibility was that pedal mucus might be exhausted during the gathering process and that this would cause ingestion to occur. If this were so, it seemed probable that mucus would be only partially replenished during ingestion. Thus, the amount of mucus available to a snail would decrease over successive gather-

TABLE 8. Number of ciliary feedings during 1 hour period, among 60 snails used in each experiment and their controls.

Experiment	Experimental snails (60)	Control snails (60)
Food in surface film	45	0
Increased water temperature	8	4
Starvation of snails	7	1
Dissolved food in water	6	5
Suspended particles in water	5	5
Decreased water temperature	4	1
Irritant in water	3	3
Lack of access to surface of water	-	0
Nitrogen atmosphere over water	0	0
Reduction of O <sub>2</sub> level in water	0	0

ings, and the latter would decrease in size. To test this possibility, 20 snails were placed singly in beakers and allowed to gather food from the surface film. Each snail was allowed to make 3 gatherings. These were each removed, dried, weighed and ranked in order of weight. In 14 cases (70%), the third aggregate of a snail weighed more than the first. In 6 cases (30%), the third aggregate weighed less. These results do not eliminate the possibility that depletion of pedal mucus causes ingestion. They do, however, indicate that, in that case, pedal mucus must be completely replenished in the interval between successive gatherings.

Finally, submergence of the foot below the water's surface was considered a possible stimulus for ingestion. In this test, 64 snails were placed singly in beakers and allowed to gather surface food. During gathering, the snails were submerged by either tipping beakers or adding water. 56 snails (87.5%) responded to submergence by ingesting. Approxi-

mately 1/3 of these had large aggregates, 1/3 moderate aggregates, and 1/3 little or no aggregates in their feet. Submergence does, therefore, act as a stimulus for ingestion.

#### 4. Effect of environmental conditions on ciliary feeding.

The 10 experiments designed to study environmental influence on surface inspiration also provided information with respect to ciliary feeding. Table 8 gives the rate of ciliary feeding. When successive feedings were separated by less than 10 minutes, they were counted as one. When food was placed in the surface film, a significant increase in ciliary feeding rate took place. Occasional ciliary feedings occurred in other experiments. These were ephemeral in nature and were presumably stimulated by traces of edible material in the surface film.

#### DISCUSSION

Surface inspiration behavior of *P. paludosa* resembles that of the Pulmonata. Inspiration in pulmonates is associated with a decrease in lung volume (Dawson, 1911). The tentacles and siphon of pulmonates have been implicated as sensory organs of importance to surface inspiration. Thus, if *Physa* is stimulated on either the head or the siphon with an air bubble, the siphon will react (Dawson, 1911). *Lymnaea pereger* will inspire only after its tentacles have been bent to a critical angle by the surface film (Hunter, 1953). The rate of pulmonate surface inspiration varies with water temperature and oxygen content, and pulmonates will aggregate at the top of their container if denied access to air (Cheatum, 1934).

Among the Ampullariidae, studies have been made of surface inspiration in *Ampullaria effusa* (Bavay, 1873, 1875), *A. insularum* (Semper, 1883; Fischer and Bouvier, 1890; Bouvier, 1891), *A. vermiformis* (Robson, 1922), *Pila globosa* (Ramanan, 1903; Prashad, 1925), and *Lanistes boltieniana* (Bouvier, 1891). In

most of these studies, descriptions of surface inspiration agree with that given here for *Pomacea paludosa*. In 2 species, however, there appear to exist significant differences. According to Prasad (1925), *Pila globosa* swims to the surface with lashing motions of its tentacles, and is able to suspend from the surface film by its siphon. Ramanan (1903) describes the siphon of that species as expanding to an aperture width of 15 mm at the air water interface, and states that surface inspiration is marked by an absence of any contractions. According to Bouvier (1891), *L. bolteniana* protrudes its siphon above the surface film, and inspires with almost no visible bodily motion. These data suggest that a detailed comparative study of surface inspiration among ampullariids might be of value. Such a study should be undertaken in the field if possible, for evidence from studies on pulmonates shows that laboratory conditions may profoundly alter the rate of surface inspiration. Pulmonates can exist in nature without access to the water's surface (Cheatum, 1934; Noland and Reichel, 1943) and under natural conditions the pulmonate lung may either be water filled or act as a physical gill (Hunter, 1953).

Among prosobranchs, a type of ciliary feeding which involves collection of particulate matter from water currents passing through the mantle cavity is not uncommon, and has been well documented (Graham, 1938; Yonge, 1938; Cook, 1949; Fretter and Graham, 1962). Ciliary feeding of the type found in ampullariids, however, does not appear to be common. Patterns of behavior which may anticipate this type of ciliary feeding occur in some snails. The pulmonate *Lymnaea stagnalis* for example, collects mucus from the surface film, and gathers it into a mass at the middle part of the foot (Dawson, 1911). The prosobranch *Peringia ulvae* forms a mucus sheet on the surface of the water and gathers this, with its accumulated food, by means of its radula (Newell, 1962).

Among ampullariids, ciliary feeding has

been described for *Pomacea paludosa* (Johnson, 1952), and *P. canaliculata* (Cheesman, 1956). The observations of these workers agree with those given here. No other descriptions of ampullariid ciliary feeding are known to the writer, although it is probable that this behavior is common within the family.

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## ZUSAMMENFASSUNG

EINATMUNG UND ZILIARE NAHRUNGS-AUFNAHME AN DER WASSEROBLERFLÄCHE  
BEI *POMACEA PALUDOSA*  
(PROSOBRANCHIA: MESOGASTROPODA: AMPULLARIIDAE)

*Pomacea paludosa*, eine häufig im Aquarium gehaltene tropische Schnecke, gebraucht zur Atmung sowohl eine Kieme als auch eine Lunge. Eine durch die Mantelhöhle geleitete Wasserströmung versorgt die Erstere mit Sauerstoff, und ein Vorgang, der hier als "Wasserspiegel-Inspiration" bezeichnet wird, die Letztere. Obwohl Nahrung normalerweise mittels der Radula aus dem Substratum gewonnen wird, versorgt sich *P. paludosa* auch aus dem Oberflächenhäutchen des Wassers mittels einer Methode die "ziliare Futteraufnahme" genannt werden mag. Über diese beiden Vorgänge wurden eine Reihe von Versuchen und Beobachtungen angestellt.

Die Schnecke bereitet eine "Wasserspiegel-Inspiration" vor, indem sie die linke Einatmungsöffnung des Mantels zu einem Atemrohr formt. Sie kriecht dann an die Oberfläche des Wassers, die sie typischerweise zuerst mit ihrem linken Fühler ermittelt; dann streckt sie das Atemrohr bis an die Luft vor und saugt diese durch eine Reihe von Körperkontraktionen, die je eine Sekunde dauern, in die Lunge der Mantelhöhle. Danach wenden sich die Schnecken gewöhnlich zu ihrer Rechten und kriechen entweder die Gefäßwand hinunter oder lassen sich fallen. Der Anreiz zur "Inspiration" ist durch vermindertes Lungenvolumen gegeben. Die Fühler orientieren die Schnecke zur Luft, aber Einatmung erfolgt auch wenn bloss das Atemrohr mit der Luft in Berührung kommt. Erhöhte Temperatur, Anwesenheit von Reizstoffen ( $\text{NH}_4\text{OH}$ ) im Wasser, verminderter  $\text{O}_2$  Gehalt des Wassers und Aushungern der Schnecken, erhöhten alle die Häufigkeit der Inspiration in bedeutsamer Weise, und Herabsetzen der Temperatur und im Wasser gelöste Nährstoffe setzten sie bedeutungsvoll herab, während Anwesenheit in der Oberflächenschicht des Wassers, Partikelsuspensionen im Wasser oder eine Stickstoffatmosphärr darüber keinen bedeutsamen Einfluss hatten. Im Verlaufe eines jeden Versuchs senkte sich die Häufigkeit der Inspirationen, was weitgehend einer gleichzeitigen Verringerung in der Zahl der aktiven Schnecken entsprach. Die Häufigkeitsverteilung dieser Inspirationen war bei allen Versuchen eine Ähnliche. Herabsetzung der Temperatur und Anwesenheit gelöster Nährstoffe bewirkten ausserdem auch ein bedeutungsvolles Nachlassen der Bewegungsfreudigkeit. Gelöste Nährstoffe

hatten ferner zur Folge, dass die Schnecken fortwährend den Boden des Gefässes mit ihrer Radula abraspelten. Beim Einatmen von Stickstoff wiederholten die Schnecken die normalen Kontraktionen bis zu 10 mal und neigten dazu am Wasserspiegel zu verweilen. Schnecken, die durch ein Hindernis am Erreichen des Wasserspiegels verhindert worden waren, sammelten sich unterhalb desselben an, auch wenn das Wasser sauerstoffgesättigt war.

Bei der ziliaren Nahrungsaufnahme bilden die Schnecken mit dem vorderen Teil des Fusses einen Trichter und mit dem mittleren eine Röhre. Durch die Wirkung der pedalen Zilien wurden in der Oberflächenschicht befindliche Nahrungspartikelchen in den Trichter gezogen und, mit Schleim verkittet, im unteren Teil der Röhre angesammelt. Von Zeit zu Zeit streckt die Schnecke ihren Kopf in die Röhre und verzehrt das dort angesammelte Futter. Bei aktiven Schnecken setzt eine vorhergegangene Fütterung die Häufigkeit des ziliaren Futterns nicht herab. Der Anreiz zum Verschlingen der angesammelten Nahrung war weder in deren Gewicht zu finden noch stand sie mit dem Aushungern der Schnecken in Zusammenhang oder mit einem denkbaren Schleimentzug; Untertauchen des Fusses jedoch veranlasste die Schnecken immer zum Verschlingen der angesammelten Nahrung ohne Bezug auf deren Menge. Ziliares Futtern erfolgte nur selten, ausser wenn man Nahrung in Pulverform auf den Wasserspiegel streute.

### RÉSUMÉ

#### INSPIRATION EN SURFACE ET ALIMENTATION CILIAIRE CHEZ *POMACEA PALUDOSA* (PROSOBRANCHIA: MESOGASTROPODA: AMPULLARIIDAE)

Pour respirer, *Pomacea paludosa*, un mollusque tropical d'aquarium commun utilise une branchie et un poumon. La branchie capte de l'oxygène au moyen d'un courant d'eau circulant à travers la cavité palléale, et le poumon par un procédé appelé ici "Inspiration en surface." Quoique la nourriture soit d'habitude détachée du substrat par la radule, *P. paludosa* en prélève également sur le film de surface de l'eau par un procédé ici nommé "alimentation ciliaire." Une série d'observations et d'expériences furent faites, comme suit.

Une "inspiration en surface" s'annonçait par la disposition de l'ouverture palléale inhalante gauche en siphon. Ensuite les mollusques rampaient à la surface de l'eau et ils prenaient typiquement contact d'abord par le tentacule gauche. Puis le siphon s'allongeait sur le film de surface et l'air était conduit au poumon par une série de contractions du corps, durant chacune 1 seconde. L'inspiration terminée, les mollusques tournaient d'habitude vers leur droite et rampaient vers le bas, ou bien se laissaient tomber depuis la paroi du récipient. Le stimulus pour une inspiration en surface était lié à la réduction de volume du poumon. Les tentacules orientaient l'animal vers l'air. Ainsi l'inspiration, avait lieu même quand le siphon seul prenait contact avec l'air. Le taux d'inspiration en surface se trouvait augmenté par: l'élévation de la température, la présence d'un irritant ( $\text{NH}_4\text{OH}$ ) dans l'eau, la diminution du taux d'oxygène dans l'eau et le jeûne des mollusques; il se trouvait réduit par: l'abaissement de la température et la présence de matières nutritives dissoutes dans l'eau, tandis qu'il n'était pas altéré de façon significative par la présence de nourriture pulvérisée dans la pellicule de surface, de particules fines en suspension dans l'eau, ou d'une atmosphère d'azote au dessus de l'eau. Le taux d'inspiration diminuait progressivement au cours de chaque essai, ce qui était en rapport avec une réduction parallèle du nombre des mollusques actifs. La distribution des fréquences d'inspiration parmi les mollusques était semblable dans tous les essais. La mobilité se trouvait diminuée de manière significative par une baisse de température et par la présence de nourriture dissoute. Celle-ci incita en outre les mollusques à râper continuellement le fond du récipient avec leur radule. Les mollusques respirant de l'azote exécutaient une série normale de contractions, jusqu'à 10 fois, et avaient tendance à rester à la surface. Ceux dont l'accès à la surface fut empêché par une barrière, se rassemblaient à sa face inférieure, même quand l'eau était saturée d'oxygène.

Dans l'alimentation ciliaire, les mollusques disposaient la partie antérieure du pied en entonnoir et la partie médiale en tube. Par l'action des cils pédieux les particules alimentaires se trouvant dans la pellicule de surface de l'eau étaient attirées dans l'entonnoir et puis dans le tube, à la base duquel, enduites de mucus, elles s'accumulaient. A certains intervalles le mollusque mettait sa tête dans le tube et avalait

la nourriture amassée. Le fait de les avoir nourris au préalable n'a pas diminué la fréquence de la méthode ciliaire d'alimentation parmi les mollusques actifs. L'ingestion n'était stimulée ni par le poids de la nourriture recueillie ni par le degré du jeûne des mollusques et ne semblait pas liée à un épuisement possible de mucus, mais elle l'était toujours par la submersion du pied, sans considération de la quantité de nourriture accumulée. A moins d'avoir dispersé de la nourriture en poudre sur la surface de l'eau l'alimentation ciliaire n'avait lieu que rarement.

## RESUMEN

INSPIRACION SUPERFICIAL Y ALIMENTACION CILIAR EN *POMACEA PALUDOSA*  
(PROSOBRANCHIA: MESOGASTROPODA: AMPULLARIIDAE)

En el caracol anfíbio *Pomacea paludosa* el pulmón recibe oxígeno por un proceso de "inspiración superficial" y los cilios del pie pueden ejecutar la función de "alimentación ciliar" conduciendo a la boca las partículas suspendidas en la película superficial. Se presenta a continuación un resumen de observaciones y experimentos acerca de estos dos procesos.

La inspiración superficial es precedida por la transformación de la abertura inhalante izquierda del manto en un sifón. En seguida el caracol se dirige a la superficie del agua y toma contacto típicamente con la película superficial, primero con el tentáculo izquierdo. El sifón se extiende entonces a la película y conduce el aire que es atraído a la cámara pulmonar por una serie de contracciones del cuerpo. Cada inspiración consiste aproximadamente de 16 contracciones, durando 1 segundo cada una. Después el caracol se vuelve hacia abajo por la derecha y reptó o cae al fondo. El estímulo para la inspiración superficial está asociado a la reducción del volumen pulmonar. Los tentáculos orientan el caracol hacia el aire. Sin embargo, para haber inspiración es necesario que sólo el sifón entre en contacto con el aire. La frecuencia de la inspiración es significativamente aumentada por la elevación de la temperatura, la presencia de  $\text{NH}_4\text{OH}$  como irritante en el agua, la reducción del nivel de oxígeno y la inanición, y disminuida por el descenso de la temperatura y la presencia de alimento disuelto en el agua. No es alterada por la presencia de alimento en la película superficial y de sedimento en el agua, ni por la sustitución del aire por nitrógeno sobre el agua. La frecuencia de la inspiración decrece en función del tiempo en cada experimento, debido principalmente a una reducción concomitante en el número de caracoles activos. La distribución de las frecuencias de inspiraciones es similar en todos los experimentos. El descenso de la temperatura del agua y la presencia de alimento disuelto disminuyen la frecuencia del movimiento. El alimento disuelto también estimula los caracoles a raspar con su rádula el fondo de la vasija. Aquellos que inspiran nitrógeno repiten hasta 10 veces la serie normal de contracciones, tendiendo a permanecer en la superficie del agua. Cuando se les impide el acceso a la superficie, se aglomeran bajo la barrera, aunque el agua esté saturada de oxígeno.

En la alimentación ciliar, los caracoles convierten la parte anterior del pie en un embudo y la parte media en un tubo. Los cilios del pie arrastran las partículas desde la película superficial al embudo y luego al tubo; ellas son aglutinadas por moco y se acumulan en la base del tubo. De tiempo en tiempo el animal introduce la cabeza en el tubo y deglute el alimento acumulado. Una comida previa no disminuye la frecuencia de la alimentación ciliar en caracoles activos. El estímulo para la ingestión no está correlacionado con la cantidad de alimento acumulado ni con el grado de inanición, ni tampoco, al parecer, con el agotamiento del moco del pie. La ingestión es estimulada por la sumersión del pie, cualquier que sea la cantidad de alimento acumulado. La alimentación ciliar ocurre infrecuentemente, a menos que se ponga alimento en la película superficial.

Дыхание на поверхности воды и ресничное питание у  
*POMACEA PALUDOSA* (PROSOBRANCHIA: MESOGASTROPODA: AMPULLARIIDAE)

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Обыкновенная аквариумная тропическая улитка *Pomacea paludosa*, дышит жабрами и легкими. Жабры получают кислород из воды поступающей в полость мантии. Легкое получает кислород путем так называемого "вдыхания на поверхности воды". Хотя нормально улитка добывает пищу из субстрата пользуясь радулой, *P. paludosa* собирает свою пищу также с поверхностной пленки с помощью "ресничного питания". Оба эти процесса изучались автором в ряде наблюдений и опытов.

Начало "вдыхания с поверхности воды" можно было предвидеть заметив превращение левого приемного отверстия мантии в сифон. После этого улитки выползали на поверхность воды и типичным образом прикасались к поверхностной пленке своим левым щупальцем. После этого, несколько раз сокращая свое тело, они вытягивали сифон до поверхностной пленки и вытягивали воздух в легкое находящееся в полости мантии. Одно дыхание требовало приблизительно 16 сокращений тела; каждое сокращение продолжалось одну минуту. После этого улитки обычно поворачивались на правую сторону и сползали вниз, или падали вдоль стенки сосуда. Уменьшение объема легкого было связано со стимуляцией вдыхания с поверхности. Благодаря щупальцам улитки ориентировались по направлению к воздуху. Однако, вдыхание наступало и в том случае, когда только сифон касался воздуха. Повышение температуры, присутствие в воде раздражающего вещества ( $\text{NH}_4\text{OH}$ ), уменьшение кислородного уровня и голодание значительно увеличивали темп вдыхания. Понижение температуры и присутствие в воде растворенной пищи значительно уменьшали темп вдыхания. Пища положенная на поверхностную пленку, седименты и замена воздуха над водой азотом, не оказывали значительного влияния на темп вдыхания. В каждом опыте темп вдыхания уменьшался с продолжительностью наблюдения. Это происходило, главным образом, из за сопутствующего опыту уменьшению числа активных улиток. Кривая распределения частоты вдыханий среди улиток была одинакова во всех опытах. Понижение температуры воды и присутствие растворенной пищи значительно уменьшали темп движения. В присутствии растворенной пищи улитки без перерыва соскребали радулой дно сосуда. У вдыхавших азот улиток число сокращений повторялось до 10 раз, и была заметна тенденция оставаться на поверхности воды. Улитки, которым был прегражден доступ к поверхности, скоплялись на нижней стороне барьера, хотя вода была насыщена кислородом.

При ресничном питании улитки свертывали переднюю часть ноги в воронку, а её среднюю часть - в трубку. Пища втягивалась из поверхностной пленки в воронку действием ножных ресничек. Пища, окруженная слизью, собиралась у основания трубки. Время от времени улитка всовывала голову в трубку и заглатывала собранную пищу. Среди активных улиток предшествующая еда не понижала частоту ресничного питания. Стимул к заглатыванию собранной пищи не имел отношения ни к весу пищи ни к степени голодания. Нет оснований думать, что истощение слизи на ноге вызывало заглатывание. Погружение ноги стимулировало улиток заглатывать пищу независимо от её количества. Ресничное питание наблюдалось не часто, за исключением случаев когда пища помешалась на поверхностную пленку.

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PUERTO RICAN SPECIES OF *TROPICORBIS* AND *DREPANOTREMA*;  
COMPARISON WITH *AUSTRALORBIS GLABRATUS* AND OTHER PLANORBIDS<sup>1</sup>

Charles S. Richards<sup>2</sup>

ABSTRACT

Descriptions and diagnostic characteristics are given of 3 species of *Tropicorbis* (*T. albicans*, *T. obstructus*, and *T. riisei*) and 5 species of *Drepanotrema* (*D. anatinum*, *D. hoffmani*, *D. cimex*, *D. harryi*, and *D. simmonsii*) from Puerto Rico and the Virgin Islands. Emphasis is placed on morphologic and histologic features as studied in living material. These species are compared with living material of 7 other planorbid species (*Australorbis glabratus*, *A. tenagophilus*, *Tropicorbis stramineus*, *T. janeirensis*, *T. peregrinus*, *T. pallidus*, and *T. havanensis*) from the Caribbean Islands, South America, and the United States as well as with descriptions of related forms reported in the literature.

Life history data, including egg-to-egg cycle and number of eggs per clutch, are presented. These are based on laboratory culture through several generations of isolated individuals that originate from field collections representing ecologic and geographic diversity. Cultures of 43 different strains of the variable Puerto Rican *T. riisei* were compared. In this and other species cultured, intraspecific variations in both shells and internal morphology were observed: between different field strains, from generation to generation in the same strain, and with age variation in individual snails.

Histologic observations concerned particularly the male reproductive system. Occurrence and variations in proximal verge sac tubules are discussed. An oblique third verge muscle layer is described for several planorbid species, with a distinctive and characteristic pattern in each species. The "diaphragm" between verge sac and preputium is compared in different species and sarcobelar "setae", velar folds, and related structures are discussed.

The systematic status of 3 *Drepanotrema* species (*D. hoffmani*, *D. harryi*, and *D. simmonsii*) is discussed. *D. simmonsii*, which has been confused with the genus *Tropicorbis* because of shell resemblance, is retained in the genus *Drepanotrema* on the basis of the punctate shell pattern, verge sac flagella, and jaw of numerous small plates. *D. simmonsii* is related to the South American *D. nordestense* and *D. aeruginosus*.

INTRODUCTION

Widespread interest has been shown for certain planorbid genera of the Caribbean and South American Region: *Australorbis*, the intermediate host of *Schistosoma mansoni*, *Tropicorbis*, an experimental and natural host, as well as for *Drepanotrema*, a non-vector. Morphologic studies on *Tropicorbis* and *Drepanotrema* were reported by Baker (1945), Hubendick (1955, 1961), Ferguson and Gerhardt

(1956), and Paraense and Deslandes (1955-1960, 1962). Puerto Rican species of these genera from recent collections are listed by Ferguson and Richards (1963) and distribution data will be shortly given by Richards and Ferguson (in manuscript). Morphologic, histologic, and biologic data are here presented on 8 planorbid species from Puerto Rico and the Virgin Islands: 3 species of *Tropicorbis* (*T. riisei*, *T. obstructus* and *T. albicans*) and 5 species of *Drepanotrema* (*D. anatinum*, *D.*

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*hoffmani*, *D. cimex*, *D. harryi* and *D. simmonsii*), that supplement the information given in earlier papers. Observations on these species are compared with those made on live Puerto Rican *Australorbis glabratus* (Say), on 6 species of *Tropicorbis* obtained alive from other areas, and with the literature.

Provision of living specimens for comparative studies is gratefully acknowledged: *Australorbis tenagophilus*, *Tropicorbis stramineus* (= *centimetralsis*), and *T. janeirensis* from Brazil and *T. peregrinus* from Uruguay by Dr. Lobato Paraense; *T. pallidus* from Jamaica by Dr. Harold Harry; and *T. havanensis* from Louisiana, U. S. A. by Dr. Elmer Berry.

#### METHODS

Availability of living specimens from widely distributed and discontinuous localities in Puerto Rico and the Virgin Islands enabled extensive histologic studies of fresh material and laboratory culture for biologic information and comparative morphology at known developmental stages. Janus green was employed as a vital stain in examination of fresh material and "MIF" (Sapero and Lawless, 1953) stain-preservative for permanent slides.

#### RESULTS

##### *Tropicorbis riisei* (Dunker)

This species was described in part by Baker (1945) and Van der Schalie (1948). The shell varies greatly in form (Fig. 1). The maximum size observed was 13.5 mm in diameter with 6 whorls. Apertural ribs, but no apertural lamellae, occur in *T. riisei* (Richards, 1963a). The mantle is mottled with round to elongate-transverse black patches, well defined against an unpigmented background. Head and foot are gray with white granules, the latter forming paired spots on the head.

The tentacles have black pigment granules except for a clear region at the base. In a specimen with a clear shell, the ovoid testis appears pink to cream colored, lacking black pigment in its covering. A continuous dorsal-rectal fold is present in the mantle cavity; renal fold absent. Salivary glands are yellow (rarely white), wide, strongly lobed, and fused. The seminal vesicle consists of short tubular diverticula, white speckled with golden brown. The long prostate has about 10 branched diverticula (Fig. 10). The seminal receptacle is typically ovate with a narrow duct approximately the same length as the body. The distal part of the uterus is short and includes a glandular pouch. The vas deferens may be even in width or wider in the middle. Verge sac and preputium are about equal in length, with variation in age and individuals (Figs. 11, 12). The proximal end of the verge sac is not appreciably enlarged, has proximal tubules (Fig. 13), and is asymmetrical. The verge is usually shorter than the verge sac, has longitudinal and circular muscle layers, is not enlarged proximally, and has the sperm canal central and not convoluted. The distal lining of the verge sac has thickened and glandular longitudinal folds (Figs. 14, 15). The crater-like sarcobelum has a ring of "setae" around its rim, is lined with glandular epithelium, and has circular muscles internally. The glandular velum has about 10 well-developed folds. The preputium is lined by cilia beginning distal to the velar folds. Retractor muscles are attached at the junction of verge sac and preputium.

Forty-three field strains of *T. riisei* were cultured in isolation in the laboratory through several generations. Considerable intraspecific variation was observed, both in morphology and in growth and maturation rates. Laboratory culture of 2 strains is illustrated in Figs. 1 and 2. The numerous variations among the strains cultured, were demonstrated. In a few strains (Fig. 2) there occurred fusion of some of the radular teeth, and passage of this abnormality through

successive generations suggested it was a hereditary character. Although the aperture of *T. riisei* was not commonly deflected, examples of marked deflection to the right and to the left, as well as reflection of the whole aperture, occurred in culture even within a single strain (Fig. 1). Curvature of the whorls on both right and left sides ranged from evenly rounded to almost flat, with some showing a definite shoulder. In addition to variation between strains or between succeeding generations of the same strain, internal morphology showed appreciable changes from early maturity to old age in individual specimens. Morphology of such diagnostic features as the prostate, verge sac, and preputium showed developmental changes with age (Figs. 14, 15). This could lead to confusion in preserved field specimens of unknown age but similar size, where some individuals maturing early (e.g., at a size of 3.0 mm) would reach old age at a diameter at which others were just reaching maturity (e.g., 7.5 mm). Size at onset of egg laying (puberty) ranged from 3.0-7.7 mm in diameter (Fig. 5); shortest observed egg-to-egg cycle was 27 days. Average number of eggs per clutch was 8; average egg diameter 0.7 mm. Range in diameter and number of whorls at puberty is shown in Fig. 5 for 315 individuals observed and measured; the range for a total of 366 young mature and old mature *T. riisei* in Fig. 6. Relations of maximum shell height to maximum diameter (289 individuals measured) and diameter of right umbilicus to maximum diameter (173 measured) are shown in Fig. 7.

This species was experimentally infected with *S. mansoni* (Richards, 1961).

#### *Tropicorbis albicans* (Pfeiffer)

The shell of *T. albicans* was illustrated by Baker (1945) and van der Schalie (1948); shell and morphology by Paraense and Deslandes (1962). In Puerto Rico it has been collected up to a maximum diameter of 7.0 mm with 4 1/2 whorls. About 25% of mature *T. albicans* had apertural lamellae associated with puberty (Richards, 1963a). Mature specimens typically have the aper-

ture deflected to the left. Mantle pigment varies but is commonly restricted to a black band around the mantle collar with sometimes a few scattered black patches. The pericardium and membrane covering the ovotestis are usually black pigmented. Head and foot are gray with white granules that form paired markings on tentacle bases and head. The tentacles usually lack black pigment. A continuous dorsal-rectal fold is present in the mantle cavity; a renal fold is absent. Salivary glands are white, fused, only slightly lobed. The seminal vesicle consists of a series of yellow-orange, poorly developed bud-like diverticula. The prostate has about 10 widely spaced and poorly developed diverticula, some usually branched (Fig. 16). The seminal receptacle is small and club-shaped, tapering gradually to a short duct leading to the vagina. The distal part of the uterus is short and includes a small glandular pouch. The vas deferens is usually of even width throughout. Verge sac and preputium are both short and the short verge constricts abruptly near the distal end. Proximal tubules are few and small (Fig. 17). The verge has longitudinal and circular muscle layers. The lining of the verge sac is glandular and thickened distally. A crater-like glandular sarco-belum with "setae" and circular muscles and glandular velar folds are present but poorly developed (Fig. 18). Retractor muscles are attached at junction of verge sac and preputium.

Specimens of *T. albicans* from several different field localities were cultured in isolation (e.g., Fig. 3). Shells at puberty ranged from 3.4-6.0 mm in diameter (Fig. 5); shortest observed egg-to-egg cycle 29 days. Average number of eggs per clutch was 7, average egg diameter 0.55 mm. In culture glasses, eggs were most often laid in the angle formed by side and bottom of glass. Range in diameter and number of whorls at puberty is shown in Fig. 5 for 51 individuals measured; the range for a total of 58 young mature and old mature *T. albicans* in Fig. 6. Relations of maximum shell height to

maximum diameter (56 measured) and diameter of right umbilicus to maximum diameter (40 measured) are shown in Fig. 8.

This species was experimentally infected with *S. mansoni* (Richards, 1963b).

*Tropicorbis obstructus* (Morelet)

Baker (1945) illustrated the shell and described some of the morphology of this species. Apertural lamellae were formed, in association with puberty, in about 10% of the specimens observed (Richards, 1963a). The shell is usually more flattened than that of *T. riisei*, but varies greatly. The maximum size observed was 11.0 mm with 5 1/2 whorls. The mantle is mottled with black pigment, the spots usually smaller and more nearly round than in *T. riisei*. Head and foot are grayish green with white granules, the latter forming a patch on the head. The tentacles usually lack black pigment. The ovotestis has a black-pigmented membrane. A continuous dorsal-rectal fold is present in the mantle cavity; a renal fold absent. Salivary glands are white, fused, and not lobed. The seminal vesicle has well developed, tubular diverticula; orange proximally (pigment granules) and white distally (no pigment). The prostate has about 15 branched, fingerlike diverticula (Fig. 19). The seminal receptacle is a broadly oval body, narrowing abruptly to a duct of about the same length as the body. The distal part of the uterus has a small glandular pouch. The vas deferens is usually of equal width throughout. The preputium is longer than the verge sac (Figs. 20, 21). The verge sac is usually not enlarged proximally and proximal tubules are poorly developed (Fig. 22). The verge is swollen proximally and the sperm canal is convoluted. The verge has longitudinal and circular muscle layers. The lining of the verge sac is thickened and glandular distally (Fig. 23). The sarco-belum (Fig. 24) has a circle of "setae" and epithelial glandular lobes, and internally a ring of circular muscles; the velum 10-12 glandular folds. Retractor muscles are attached at the junction of verge sac and preputium.

Specimens of *T. obstructus* from 5 field localities were cultured in isolation (e.g.,

Fig. 4). Shells at puberty ranged from 4.3-7.4 mm in diameter (Fig. 5); shortest egg-to-egg cycle was 26 days. Average number of eggs per clutch was 5.5; average egg diameter 0.65 mm. Range in diameter and number of whorls at puberty is shown in Fig. 5 for 53 individuals measured; range for a total of 65 young mature and old mature *T. obstructus* in Fig. 6. Relations of maximum shell height to maximum diameter (66 measured) and diameter of right umbilicus to maximum diameter (55 measured) are shown in Fig. 9.

*Drepanotrema anatinum* (d'Orbigny)

Shell and internal morphology of this species were described by Baker (1945), Hubendick (1955, 1961), and Paraense and Deslandes (1956, 1958c). Specimens of *D. anatinum*, the smallest planorbid known in Puerto Rico, have been collected with a maximum diameter of 3.0 mm. The body has black markings as shown by Paraense and Deslandes (1956). Mantle cavity lacks renal and dorsal-rectal folds. The prostate has few and poorly developed diverticula. Seminal receptacle and lower uterus are shown in Fig. 25. There are 2 long glandular flagella; verge usually longer than verge sac, evenly tapered to the terminal opening, and curved at the end (Fig. 26). Fig. 27 shows the junction of verge sac and preputium, with simple sarcobelum, ciliated preputial wall, and with thickened, glandular, inner epithelium of the distal part of the verge sac. The proximal part of the preputium has large cells filled with secretion droplets. In laboratory culture, isolated *D. anatinum* laid eggs at 2.5 mm diameter. The shortest egg-to-egg cycle observed was about 30 days. The number of eggs per clutch averaged 4.

*Drepanotrema hoffmani* Baker

This species was described from Puerto Rican specimens by Baker (1945) and was further characterized and illustrated by Ferguson and Gerhardt (1956) who called it *D. anatinum*. Specimens have been collected in Puerto Rico with a maximum diameter of 7.0 mm. The body has black markings as illustrated by Baker (1945).

Mantle cavity lacks renal and dorsal-rectal folds. Seminal receptacle and lower uterus are shown in Fig. 28. The proximal end of the verge sac, showing the communication of the verge sac cavity with the ducts of the 2 short flagella is shown in Fig. 29. The verge sac is long, but the sinuous verge is usually longer, extending into the preputium. The junction of verge sac and preputium is shown in Fig. 30. There is a simple sarcobelum, and the inner surface of the proximal part of the preputium is ciliated. The inner epithelium of the distal part of the verge sac is thickened and glandular. The proximal portion of the preputium consists mainly of large cells filled with secretory droplets or granules, that are lacking in the distal part of the preputium. In laboratory culture, isolated *D. hoffmani* laid viable eggs, and were successfully reared through several generations.

*Drepanotrema cimex* (Moricand)

This species, reported from Puerto Rico by Aguayo (1961), was described by Paraense and Deslandes (1958a). Some specimens have been collected in Puerto Rico with a maximum diameter of 9.0 mm. The body has black markings as illustrated by Paraense and Deslandes (1958a). Mantle cavity lacks renal and dorsal-rectal folds. Seminal receptacle and lower uterus are shown in Fig. 31. The verge sac is short; preputium longer (Fig. 32), the long verge usually extends into the preputium, and there appears to be a single short flagellum. As shown in Fig. 33, however, in addition to the flagellum there is a second pouch communicating with the proximal end of the verge sac cavity which probably represents a second rudimentary flagellum. Junction of verge sac and preputium is shown in Fig. 34. The inner wall of the distal end of the verge sac is glandular and moderately enlarged. There is a simple sarcobelum and the inner surface of the proximal part of the preputium is ciliated. The wall of the proximal part of the preputium contains large cells filled with secretion droplets. In laboratory culture, isolated *D. cimex*

laid viable eggs and were successfully reared through several generations.

*Drepanotrema harryi* Ferguson and Gerhardt

This species was described from St. Croix, Virgin Islands, by Ferguson and Gerhardt (1956) and is not known to occur in Puerto Rico. They illustrated the shell and Y-shaped flagellum. The maximum-sized specimen collected had a diameter of 8.5 mm. Characteristic body markings, striking in this species as in the above 3 species, were described by Ferguson and Gerhardt (1956). The mantle cavity lacks renal and dorsal-rectal folds. Seminal receptacle and lower uterus are shown in Fig. 35. The prostate with a row of about 45 tubular unbranched diverticula, many bent at the ends, is shown in Fig. 36. The verge sac is shorter than the preputium (Fig. 37). Under low magnification it is apparent that the Y-shaped flagellum is composed of 2 elements, fused halfway and free for the terminal half. Under higher magnification (Fig. 38) a thin partition is seen, revealing that the ducts of the 2 flagella are separate and that each communicates with the verge sac cavity. The glandular enlargement of the lining of the flagella extends for a short distance into the verge sac cavity. The junction of verge sac and preputium with the sarcobelum is shown in Fig. 39. There are sarcobelum, irregular velar folds, and what appear to be distal verge sac glands. The inner epithelium of the distal part of the verge sac is thickened and glandular. The proximal part of the preputium consists mainly of large cells filled with secretion droplets. The verge is longer than the verge sac and the end is bent at a right angle. The characteristic pattern of the verge muscles is shown in Fig. 46a-c. For a short distance at the terminal end the outer muscle layer is circular. Starting at the bend in the verge on one side the muscle fibers appear circular, but as they extend around they become oblique, meeting at an angle on the other side. An inner muscle layer has a different oblique angle. In laboratory culture,

isolated *D. harryi* laid viable eggs and were successfully reared through several generations.

*Drepanotrema simmonsii* Ferguson and Gerhardt

This species was described by Ferguson and Gerhardt (1956), who illustrated the shell and part of the male reproductive system. It is one of the most common planorbids in Puerto Rico and St. Croix, occurring in temporary as well as permanent habitats. It survives long periods of aestivation in damp or dry soil and may be found in highly polluted water. Superficially the shell resembles some of the *Tropicorbis* species, but close examination reveals spiral markings typical of *Drepanotrema*. Head and foot are gray, lacking the black markings of the 4 preceding species, but with scattered green vacuoles throughout foot and tentacles. Red vacuoles occur in the mantle near the pseudobranch. The mantle cavity has a dorsal-rectal fold, but no renal fold. The jaw consists of a series of many plates (Fig. 40). Radular teeth, with a formula 22-1-22, are shown in Fig. 41.

The prostate gland has a double row of tubular diverticula, many of which have reflexed ends (Fig. 42). The subspherical seminal receptacle has a short duct, and is filled with flagellate protozoa in a high percentage of individuals. The 2 flagella are short, usually of equal length, and attached together except where they join the verge sac cavity on opposite sides of the verge sac. The histology of the glandular flagella was described by Ferguson and Gerhardt (1956). Verge sac and preputium are both short and of about equal length. In all the dissected specimens from many localities in Puerto Rico and St. Croix, the main retractor muscle was attached to the middle of the verge sac (Figs. 42, 43). Concretions occur in the tissues at the proximal end of the verge sac and the junction of verge sac and preputium. Both sarcobelum and velum are present, consisting mainly of glandular tissues (Figs. 44, 45). Sarcobelar "setae" were observed. The prepu-

tium is lined with cilia distal to the velum. The inner lining of the verge sac is thickened and glandular at its distal end. Also at the distal end of the verge sac are groups of elongate glandular cells appearing to communicate with the verge sac cavity by a series of ducts. The verge of *D. simmonsii* has a characteristic musculature and a foot-shaped end (Fig. 47a-c). At the end of the verge an outer circular muscle layer is evident. A short distance from the end of the verge this outer layer becomes longitudinal on the concavity of the verge and oblique around the convex side and an inner circular muscle layer becomes apparent. Proximal to the curve of the verge the outer muscle layer is again circular, the muscle fibers joining at an angle along one side of the verge.

*D. simmonsii* was successfully cultured in the laboratory through several generations, and isolated individuals produced viable eggs. Minimum shell diameter at puberty was 2.7 mm, and shortest observed egg-to-egg cycle was 24 days. Number of eggs per clutch ranged from 1-6 with an average of 4. In nature and when reared together in the laboratory, shells of *D. simmonsii* were typically covered with egg masses.

## DISCUSSION

The Puerto Rican and Virgin Islands species of *Tropicorbis* and *Drepanotrema* described have been compared with living material of 6 other available species of *Tropicorbis* and with Puerto Rican *Australorbis glabratus*.

### Tentacle pigmentation

Tentacle pigmentation is illustrated in Fig. 54a-e. In *A. glabratus*, the tentacles have fine black pigment granules throughout their length and continuous to the body. In *Tropicorbis* the tentacles may lack black pigment as in *T. albicans* and *T. obstructus*; or if black pigment is present as in *T. riisei*, *T. havanensis*, and *T. pallidus*, there is a clear region at the tentacle base. In *T. pallidus*, white pigment granules are fewer but coarser than in the other species. In *D. anatum*, *D.*

*hoffmani*, *D. cimex*, and *D. harryi* there is a prominent black stripe down the center of each tentacle. In *D. simmonsii*, this stripe is lacking and most specimens have characteristic green vacuoles.

#### Pallial folds

Dorsal and rectal ciliated folds in the mantle cavity are typical of *Tropicorbis*, while they are absent in *Drepanotrema*, with the exception of *D. simmonsii* and related species (*D. nordestense* and *D. aeruginosus*). These folds and an additional renal fold are present in *A. glabratus* (Paraense and Deslandes, 1959). Since the dorsal and rectal folds are continuous proximally they are here referred to as the "dorsal-rectal" fold.

#### Reproductive tract

The membrane covering the ovotestis is transparent in *T. riisei*, *T. havanensis*, *T. pallidus*, and *T. peregrinus*; while it is black pigmented in *T. albicans*, *T. obstructus*, *T. janeirensis*, and in *A. glabratus* and *D. simmonsii*. It is interesting to note that those *Tropicorbis* which have an unpigmented ovotestis membrane lack apertural lamellae; the 3 species with pigment and *A. glabratus* all show lamellae in some individuals. In living material, the pigmentation, as well as the shape of the seminal vesicles, is a prominent and characteristic feature. In *Australorbis* and *Tropicorbis* the seminal vesicles consist of lateral tubules or bulbs on the convoluted hermaphroditic duct, while in *Drepanotrema* they are enlargements of the convolutions of the duct. In some the seminal vesicles are speckled with golden brown (*T. riisei*, *A. tenagophilus*, *T. peregrinus*), in some they are densely pigmented by orange or yellow granules (*T. albicans*, *T. obstructus*), and in some they lack pigment, appearing white with sperms (*T. stramineus*, *T. janeirensis*, *T. havanensis*, *T. pallidus*).

In all the species discussed here, the branches of the prostate gland empty into the vas deferens. No evidence of a separate prostate gland duct was observed in any species of *Tropicorbis* nor in any of the other species studied.

Enlargement of the middle portion of the

vas deferens was described as characteristic of *T. pallidus* (Pilsbry, 1934). This appears to be a variable feature, enlargement also occurring to a lesser degree in some *A. glabratus*, *T. riisei*, *T. obstructus*, *T. havanensis*, *A. tenagophilus*, *T. stramineus*, and *T. peregrinus*. In all species studied the proximal section of the vas deferens has a wide sperm canal and thin layers of circular and longitudinal muscles. In the distal section of the vas deferens, beginning where it is embedded in muscle tissues at the base of the preputium, the sperm canal becomes narrow and the inner circular and outer longitudinal muscles become thickened. That part of the distal vas deferens that parallels the preputium and verge sac usually is the widest part, particularly in *T. pallidus*. Approaching its junction with the proximal end of the verge sac, the vas deferens becomes narrower but still has strong muscle layers. This histologic differentiation of proximal and distal portions of the vas deferens was described and illustrated by Paraense and Deslandes (1955a) and by Pan (1958).

In *Australorbis* and *Tropicorbis*, the main retractor muscles are attached to the proximal end of the preputium; in *Drepanotrema*, usually to the proximal end of the verge sac; in *D. simmonsii*, to the middle of the verge sac.

The shapes and relative lengths of preputium, verge sac, and verge were used by Mandahl-Barth (1954) in characterizing the species of *Biomphalaria*. These characters varied somewhat within the species in the forms here studied. Within the verge the sperm canal is convoluted in *A. glabratus*, *A. tenagophilus*, *T. peregrinus*, and *T. obstructus*; the tissues between the sperm canal and the verge wall were more compact and the sperm canal was relatively straight in the other species of *Tropicorbis* studied. The sperm canal is typically eccentric in the verge of *A. glabratus* and of those species of *Tropicorbis* and *Drepanotrema* with an oblique muscle layer; it is essentially central in other species.

As described previously, *D. simmonsii*

and *D. harryi* have characteristic muscle patterns in the distal region of the verge. Paraense and Deslandes (1955b) described a third muscle layer (longitudinal) in *T. stramineus* (= *centimetralis*) outside the circular muscle layer, as seen in cross sections of the verge. Examinations of fresh preparations and fixed whole mounts of the verge of *T. stramineus* show that there is an outer muscle layer that has a characteristic pattern, the muscle fibers curving around the verge obliquely to join at an angle (Fig. 48a-e). This oblique muscle layer, which would appear to be longitudinal in cross section, was not evident in the proximal third of the verge nor at the terminal end. An oblique muscle layer over part of the verge was also observed in *T. havanensis* (Figs. 49-51) and *T. pallidus* (Figs. 52-53). This verge muscle pattern was typical of every specimen of *T. stramineus*, *T. havanensis*, *T. pallidus*, *D. simmonsii*, and *D. harryi* examined; it was different and characteristic for each species, and was not seen in any other species studied (specimens of *Tropicorbis* from Colombia with oblique verge muscles may be *T. havanensis*). The morphology of the verge was different and characteristic in each species also. In specimens of *T. pallidus* and *T. havanensis* with the preputium everted for copulation the verge was observed to be strongly twisted.

Flagella attached to the verge sac of the 5 species of *Drepanotrema* have been described and illustrated (Figs. 26, 29, 33, 37, 38, 43). The occurrence of 2 flagella is apparent in *D. anatinum*, *D. hoffmani*, and *D. simmonsii*. Detailed examination showed that the Y-shaped flagellum of *D. harryi* is made of 2 flagella that are partially fused, the ducts separated by a partition, and that *D. cimex* has a second rudimentary flagellum in addition to the single short one apparent under low magnification. In each case the flagella have ducts communicating with the verge sac cavity, and are lined by a glandular epithelium which extends into the verge sac cavity for a short distance.

In commenting on the paired multiple

flagella of *Plesiophysa*, Hubendick (1955) made reference to the "proximal tubules" of *Lymnaea*. Multiple "proximal tubules" were observed in every species of *Australorbis* and *Tropicorbis* studied (Figs. 55-59). These tubules vary in size, shape, and number with the different species and with age, but all have a glandular epithelium and communicate with the verge sac cavity.

Baker (1945) referred to the junction of verge sac and preputium as having a "muscular diaphragm". Pan (1958) described the diaphragm of *A. glabratus* as "a muscular ring with papilla-like protrusions of epithelial folds into the lumen". Abdel-Malek (1954) discussed the relation of structure to function of the male organs of *Helisoma* as compared to genera lacking the preputial organ. In *Helisoma*, fluids necessary for eversion of the verge in copulation are provided in part by glandular cells in the verge sac (these cells increasing in number near the "diaphragm") and in part by glandular cells in the preputial organ. In genera lacking the preputial organ, glandular cells occur in the preputial wall as well as in the verge sac. In all the species of *Australorbis*, *Tropicorbis*, and *Drepanotrema* here studied, the distal lining of the verge sac consisted of thickened and glandular folds. The "diaphragm" in *Australorbis* and *Tropicorbis* consists of 2 rings of inward-folded tissues; proximal sarcobelum and distal velum. Examinations of these structures in fresh preparations at magnifications up to 950x indicated that the sarcobelum is crater-like; with the rim being formed of a series of glandular lobes with a circle of "setae" embedded in the tissues just outside the rim and extending distally; and internally it has large glandular cells and a ring of circular muscle fibers. The "setae" (Figs. 24, 61, 62) form a ring around the sarcobelum, which is deeply embedded in the tissues, and extending singly or in branching groups out into the space between the sarcobelum and the velar folds; they appear bristle-like and rigid, with the end modified, possibly barbed

or adhesive. Referring to *Lymnaea stagnalis*, Holm (1946) described the sarcobelum as having "a few scattered bundles of longitudinal fibers and a poor development of the circular muscle". This appeared to be the situation in all the planorbids I examined. Ciliation of the preputial lining epithelium begins at the distal bases of the velar folds (Fig. 63). In most species of *Australorbis* and *Tropicorbis* (except *T. albicans*) the velum predominates. In the species of *Drepanotrema* studied in which both structures were evident (*D. simmonsii*, *D. harryi*), the sarcobelum was more prominent; and in those with only one circular structure apparent, the histology and orientation suggested it was homologous with the sarcobelum. The proximal region of the preputial wall of *D. anatinum*, *D. hoffmani*, *D. cimex*, and *D. harryi* outside the epithelial lining consisted of large cells filled with secretion droplets, these inclusions being absent from the cells of the distal portion of the preputium. In many specimens of the various species studied there appeared to be groups of glandular cells in the fold of the sarcobelum that were connected by ducts to the distal verge sac cavity. Study of serial cross sections is needed to determine if these are homologous with the distal verge sac glands of *Plesiophysa* (Hubendick, 1955; Richards and Ferguson, 1962).

The position of the velar folds, when the preputium is everted in copulation is shown in Fig. 63 for *A. glabratus*. The velar folds and the thickened folds of the distal end of the verge sac probably secrete lubricating fluids to facilitate eversion of the preputium and protrusion of the verge. The sarcobelum with its ring of "setae" may serve to anchor the preputium in place during copulation, to stimulate the genital opening of the other snail and aid in entry of the unarmed verge, or both.

Systematic status of certain *Drepanotrema* species

Paraense and Deslandes (1960) synonymized *D. hoffmani* with *D. surinamense*. Until it is determined whether the few differences that appear to occur represent

intraspecific variation or valid specific distinctions, the name *D. hoffmani* is here retained for the Puerto Rican form. The prostatic diverticula of *D. hoffmani* are long finger-like, unlike the egg-shaped diverticula illustrated for *D. surinamense*; although finger-like diverticula are described as sometimes occurring in *D. surinamense*. The pouch of the oviduct of *D. hoffmani* (Fig. 28) differs from the illustration of *D. surinamense*. The verge of *D. hoffmani* is typically longer than the verge sac with a central sperm canal, rather than shorter than the verge sac with an eccentric canal, as in *D. surinamense*. The spermatheca of *D. hoffmani* typically is wide throughout, frequently lacking a duct (Fig. 28), while in *D. surinamense* it has a narrow duct as long as or longer than the body.

The shell of *D. harryi* resembles descriptions for *D. cultratum*, *D. kermatoides*, and *D. depressissimum*. As indicated by Paraense and Deslandes (1957, 1958d) and Hubendick (1961), the morphology of *D. cultratum* (which may be the same as *D. kermatoides*) has not been satisfactorily described. The flagella of *D. kermatoides* are reduced to small diverticula. The two flagella of *D. depressissimum* were described by Paraense and Deslandes (1957) as usually unequal and about twice as long as the verge sac; the verge with histologic structure similar to *D. anatinum*. In *D. harryi* the 2 flagella are well developed but shorter than the verge sac and joined about halfway to resemble a "Y". The verge has a characteristic 90° bend near the end and the oblique muscle layer (Fig. 46) differs histologically from that in *D. anatinum*.

*D. simmonsii* closely resembles *D. nordestense* and *D. aeruginosus* as described by Paraense and Deslandes (1958b) and Hubendick (1961) respectively. Both *D. simmonsii* and *D. nordestense* have been placed under *Tropicorbis* because of resemblances of their shells to those of the members of that genus, but these species and *D. aeruginosus* all have the spiral rows of minute dots on the shell

typical of *Drepanotrema*. The characters as described for *D. simmonsii*, including a jaw of numerous small plates and verge sac flagella, place it in *Drepanotrema*. Both *D. simmonsii* and *D. aeruginosus* have red vacuoles in the mantle lobe and pseudobranch. The 3 species under discussion have the dorsal-rectal ridge in the mantle cavity present in *Tropicorbis* but lacking in most *Drepanotrema*. The prostate of *D. simmonsii* has numerous well-developed diverticula as in *D. aeruginosus*, while *D. nordestense* has only about 4-9 small diverticula. The spermatheca is large and almost spherical with a short duct in all 3 species. The paired flagella of *D. aeruginosus* are long; those of the other 2 species short. The verge of *D. simmonsii* with its foot-shaped end and muscle pattern is distinctive. The retractor muscle of *D. nordestense* and *D. aeruginosus* is typical of *Drepanotrema*, i.e. attached to the proximal end of the verge sac, while in *D. simmonsii* it is attached to the middle of the verge sac. The radulae of *D. nordestense* and *D. aeruginosus* are typical of *Drepanotrema*. The radular teeth of *D. simmonsii* (Fig. 41) are larger and comparable in size to those of *Tropicorbis*. Small lateral cusps were not observed on the central tooth.

#### Shell characteristics and measurements

Comparison of diameter and number of whorls at puberty for 6 planorbid species is shown in Fig. 5. While extremes in diameter ranged from 2.5-11.5 mm (averages for species 2.5-9.5 mm), number of whorls ranged only from 3-5 (averages for species 3 3/4-4 3/4).

The ranges in size of measured mature specimens of the 3 Puerto Rican species of *Tropicorbis* are compared in Fig. 6. The size range for *T. riisei* (3.0-13.5 mm) extended to both extremes beyond the combined variation of mature *T. albicans* and *T. obstructus*. Relations of height and right umbilicus to diameter for these species are shown in Figs. 7-9. The shell of *T. obstructus* tends to become flattened in older specimens. Each whorl embraces the preceding one in *T. albicans* to a lesser degree than in the other 2

species, the umbilicus being relatively wider.

#### Presence of ciliate protozoa

The occurrence in the pulmonary cavity of many of the planorbids, particularly in the genus *Drepanotrema*, of species of the genus *Trichodina* is of interest (Richards, in manuscript). Characteristic species, host limited, were found in *Australorbis glabratus*, *Tropicorbis obstructus*, and in each of the 5 species of *Drepanotrema* here described.

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FIG 1. *Tropicorbis riisei*; graph depicting laboratory culture of strain 132b (irrigation pond near Patillas, Puerto Rico).

FIG. 2. *T. riisei*; graph depicting laboratory culture of strain 173c (limesink pond near Guajataca, Puerto Rico).

FIG. 3. *T. albicans*; graph depicting laboratory culture of strain 86 (farm pond near Caguas, Puerto Rico).

FIG. 4. *T. obstructus*; graph depicting laboratory culture of strain 115a (stream pool on Vieques Island).

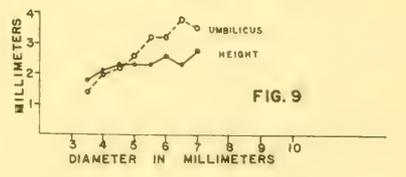
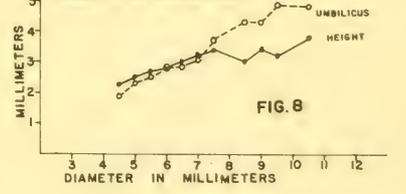
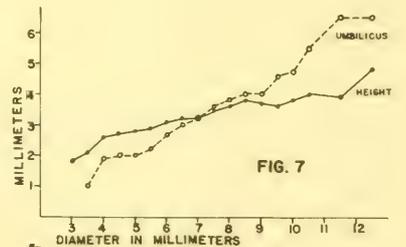
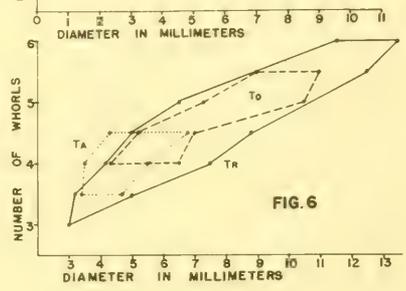
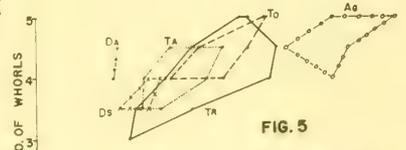
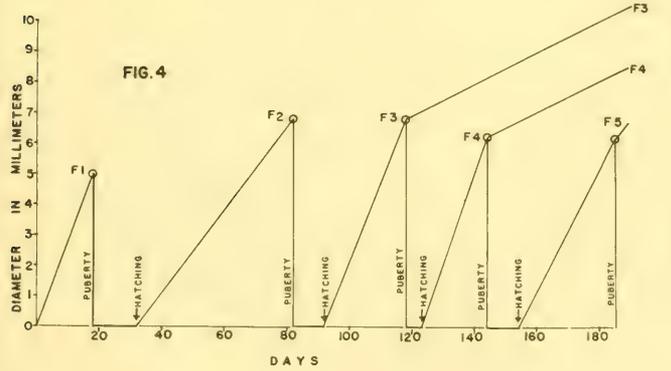
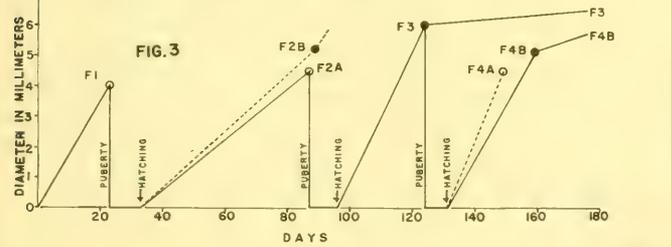
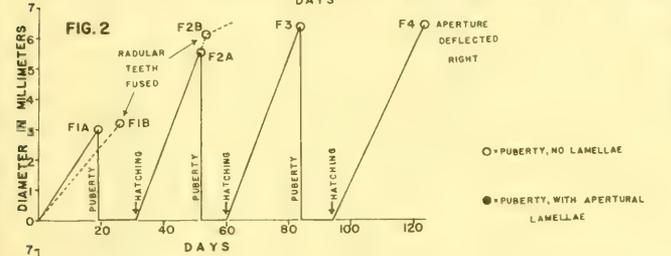
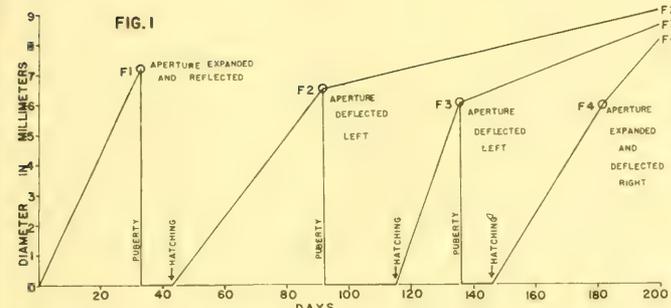
FIG. 5. Graph showing ranges in number of whorls and diameter at puberty for 6 Puerto Rican Planorbis species; (Ag) *Australorbis glabratus*, (Da) *Drepanotrema anatinum*, (Ds) *D. simmonsii*, (Ta) *Tropicorbis albicans*, (To) *T. obstructus*, and (Tr) *T. riisei*.

FIG. 6. Graph showing ranges in number of whorls and diameter from puberty to old age for *T. riisei*, *T. albicans*, and *T. obstructus*.

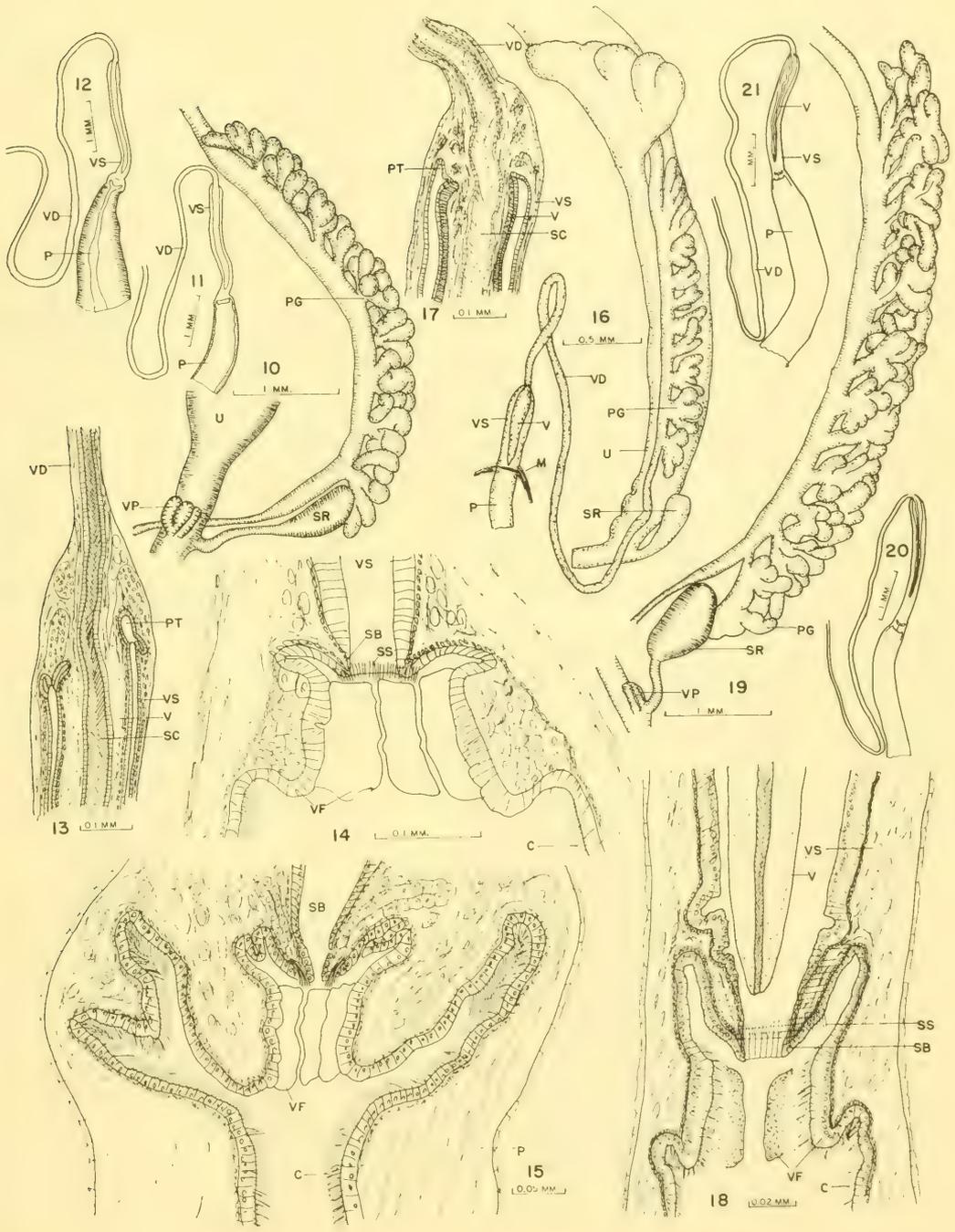
FIG. 7. *T. riisei*; graph showing relations of maximum shell height and diameter of right umbilicus to maximum diameter.

FIG. 8. *T. albicans*; graph showing relations of maximum shell height and diameter of right umbilicus to maximum diameter.

FIG. 9. *T. obstructus*; graph showing relations of maximum shell height and diameter of right umbilicus to maximum diameter.



- FIG. 10. *Tropicorbis riisei*; prostate, seminal receptacle, uterine pouch.
- FIG. 11. *T. riisei*, at puberty; verge sac and preputium.
- FIG. 12. *T. riisei*, old adult; verge sac and preputium.
- FIG. 13. *T. riisei*; proximal end of verge sac showing proximal tubules.
- FIG. 14. *T. riisei*, at puberty; junction of verge sac and preputium.
- FIG. 15. *T. riisei*, old adult; junction of verge sac and preputium.
- FIG. 16. *T. albicans*; prostate, uterus, seminal receptacle, vas deferens, verge sac, and preputium.
- FIG. 17. *T. albicans*; proximal end of verge sac and verge.
- FIG. 18. *T. albicans*; junction of verge sac and preputium.
- FIG. 19. *T. obstructus*; prostate, seminal receptacle, and uterine pouch.
- FIG. 20. *T. obstructus*; verge sac and preputium at puberty.
- FIG. 21. *T. obstructus*; verge sac and preputium, old adult.



- FIG. 22. *Tropicorbis obstructus*; proximal end of verge sac showing proximal tubules.
- FIG. 23. *T. obstructus*; junction of verge sac and preputium.
- FIG. 24. *T. obstructus*; enlargement of sarcobelum.
- FIG. 25. *Drepanotrema anatinum*; seminal receptacle and lower uterus.
- FIG. 26. *D. anatinum*; preputium, and verge sac with verge and flagella.
- FIG. 27. *D. anatinum*; junction of verge sac and preputium.
- FIG. 28. *D. hoffmani*; seminal receptacle and lower uterus.
- FIG. 29. *D. hoffmani*; proximal end of verge sac, showing flagella, vas deferens and muscle.
- FIG. 30. *D. hoffmani*; junction of verge sac and preputium.
- FIG. 31. *D. cimex*; seminal receptacle and lower uterus.
- FIG. 32. *D. cimex*; preputium, and verge sac with flagellum, muscle, vas deferens, and verge.
- FIG. 33. *D. cimex*; proximal end of verge sac showing developed and rudimentary flagella, vas deferens, and muscle.

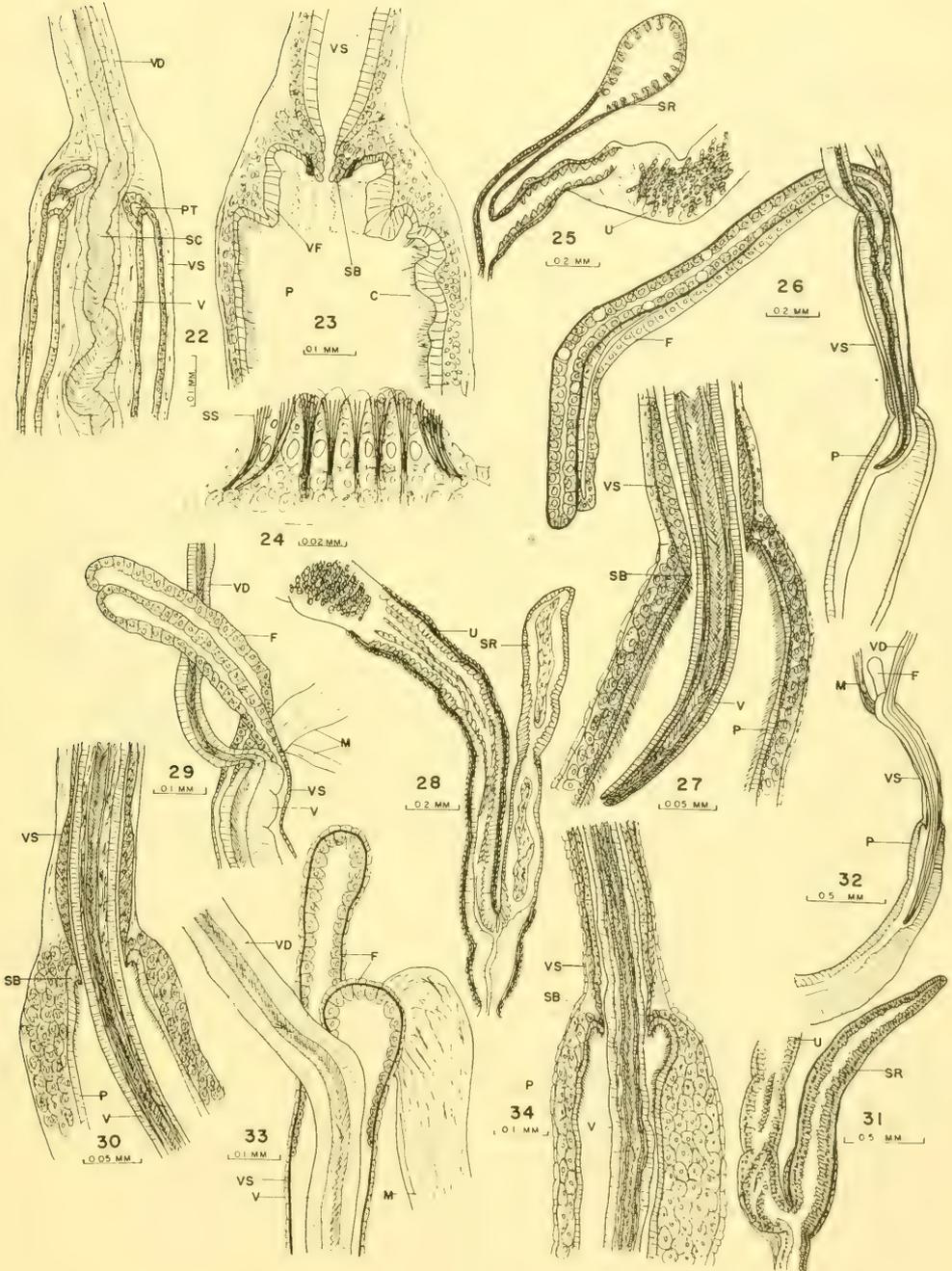


FIG. 34. *Drepanotrema cimex*; junction of verge sac and preputium.

FIG. 35. *D. harryi*; seminal receptacle and lower uterus.

FIG. 36. *D. harryi*; uterus and prostate.

FIG. 37. *D. harryi*; preputium, and verge sac with flagella, muscle, vas deferens, and verge.

FIG. 38. *D. harryi*; proximal end of verge sac with flagella, muscle, vas deferens.

FIG. 39. *D. harryi*; junction of verge sac and preputium.

FIG. 40. *D. simmonsi*; jaw.

FIG. 41. *D. simmonsi*; radular teeth; (a) central, (b) 1st lateral, (c) 4th lateral, (d) 8th lateral, (e) 13th marginal.

FIG. 42. *D. simmonsi*; (a) prostate, uterus, seminal receptacle, vas deferens, verge sac (with muscle and flagella), and preputium; (b) reverse side of prostate.

FIG. 43. *D. simmonsi*; verge sac with verge, flagella and muscle; preputium.

FIG. 44. *D. simmonsi*; junction of verge sac and preputium.

FIG. 45. *D. simmonsi*; junction of verge sac and preputium.

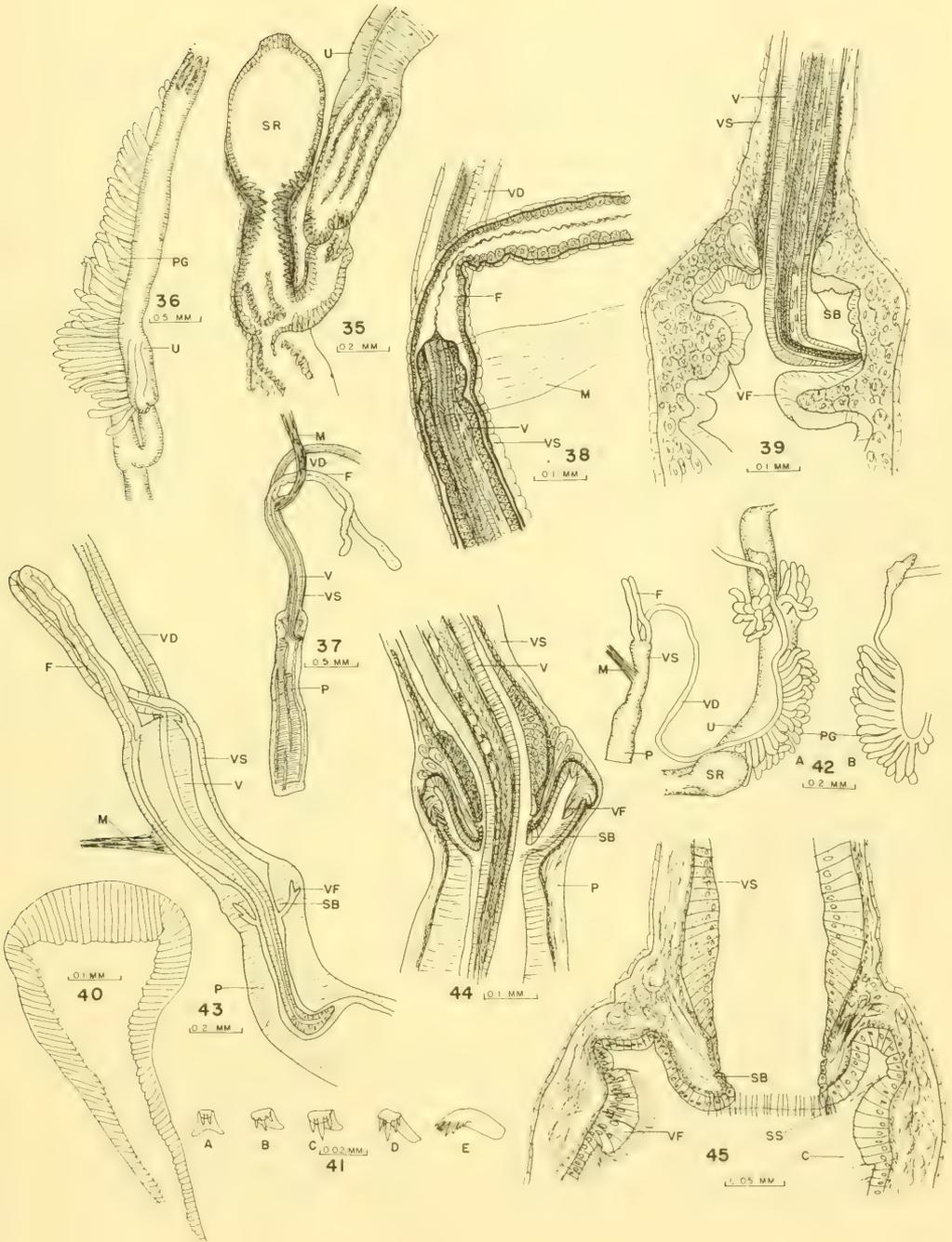


FIG. 46. *Drepanotrema harryi*; end of verge; (a) focus above middle, (b) optical mid-section, (c) focus below middle.

FIG. 47. *D. simmonsii*; end of verge; (a) focus above middle, (b) optical mid-section, (c) focus below middle.

FIG. 48. *Tropicorbis stramineus*; verge showing oblique muscle pattern; (a) verge sac with entire verge, (b) optical mid-section, proximal region, (c) optical mid-section, middle region, (d) optical mid-section, distal end of verge, (e) focus above middle, distal end of verge.

FIG. 49. *T. havanensis*; verge.

FIG. 50. *T. havanensis*; distal end of verge; (a) focus above middle, (b) optical mid-section, (c) focus below middle.

FIG. 51. *T. havanensis*; middle region of verge; (a) focus above middle, (b) optical mid-section, (c) focus below middle.

FIG. 52. *T. pallidus*; verge sac and verge.

FIG. 53. *T. pallidus*; (a) distal region of verge showing muscle pattern; (b) optical mid-section, proximal region of verge; (c) optical mid-section, middle region of verge, (d) optical mid-section, distal end of verge.

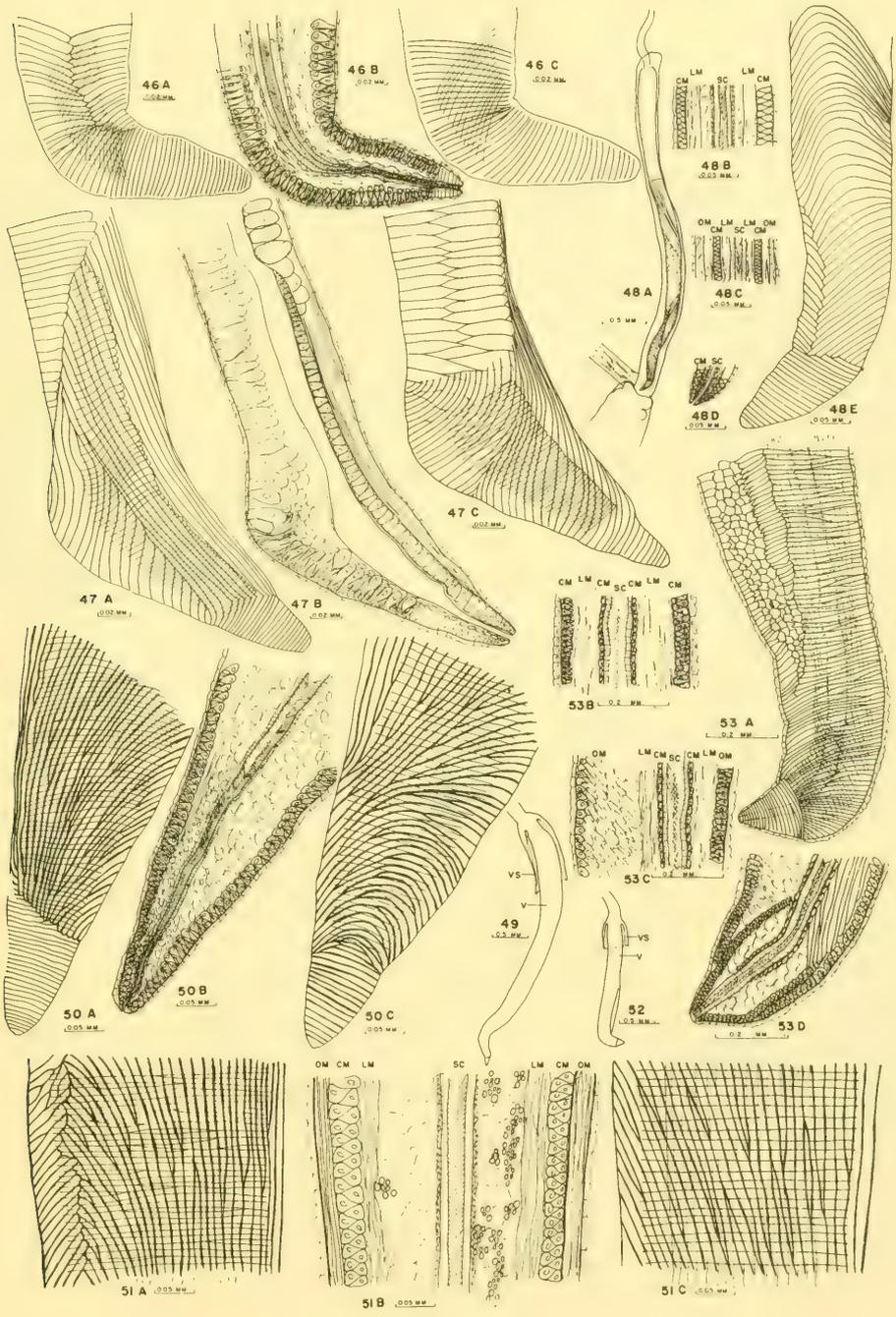


FIG. 54. Comparison of 5 types of tentacle pigmentation in planorbids: (a) *Australorbis glabratus*, (b) *Tropicorbis riisei*, (c) *T. albicans*, (d) *Drepanotrema simmonsii*, (e) *D. anatinum*.

FIG. 55. *A. glabratus*; optical cross section through proximal end of verge sac showing verge and proximal tubules.

FIG. 56. *A. tenagophilus*; proximal end of verge sac, proximal tubules, convoluted sperm canal.

FIG. 57. *T. janeirensis*; proximal end of verge sac; proximal tubules, sperm canal not convoluted.

FIG. 58. *T. stramineus*; proximal end of verge sac; proximal tubules, sperm canal not convoluted.

FIG. 59. *T. peregrinus* (from Uruguay); proximal end of verge sac; proximal tubules, convoluted sperm canal.

FIG. 60. *T. stramineus*; junction of verge sac and preputium.

FIG. 61. *A. glabratus*; sarcobelum with "setae", and parts of 2 velar folds.

FIG. 62. *T. pallidus*; sarcobelum with "setae", and velar folds.

FIG. 63. *A. glabratus*; preputium everted showing ciliation and velar folds as the organ probes the surface of another snail for the vaginal opening.

C = cilia

CM = circular muscle

LM = longitudinal muscle

M = muscle

OM = oblique muscle

P = preputium

PG = prostate

PT = proximal tubule

SB = sarcobelum

SC = sperm canal

SR = seminal receptacle

SS = sarcobelar setae

U = uterus

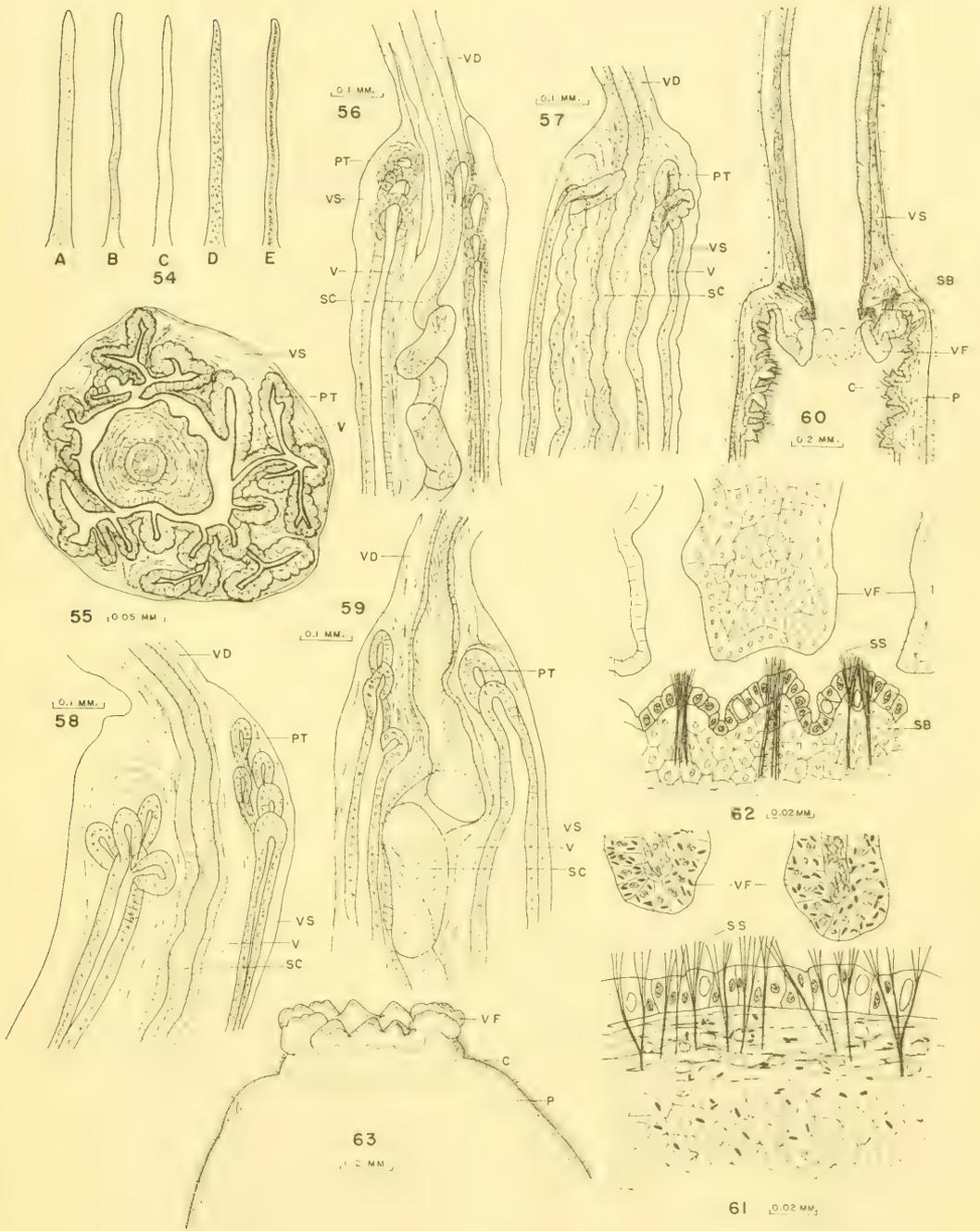
V = verge

VD = vas deferens

VF = velar folds

VP = vaginal pouch

VS = verge sac



## RESUMEN

ESPECIES PORTORRIQUENAS DE *TROPICORBIS* Y *DREPANOTREMA*  
COMPARACION CON *AUSTRALORBIS* Y OTROS PLANORBIDOS

Se dan descripciones y características diagnósticas de tres especies de *Tropicorbis* (*T. albicans*, *obstructus* y *riisei*) y cinco especies de *Drepanotrema* (*D. anatinum*, *hoffmani*, *cimex*, *harryi* y *simmonsii*) de Puerto Rico y las Islas Vírgenes. Se realza la importancia de los aspectos morfológicos e histológicos estudiados en ejemplares vivos. Estas especies son comparadas con material vivo de siete otras especies de planorbidos (*Australorbis glabratus*, *tenagophilus*, *Tropicorbis stramineus*, *janeirensis*, *peregrinus*, *pallidus* y *havanensis*) de la América del Sur, de los Estados Unidos y de las islas del Caribe, así como con descripciones de formas relacionadas registradas en la literatura.

Se presentan datos sobre el ciclo vital, incluyendo el ciclo de huevo a huevo y el número de huevos por masa ovífera. Estos datos corresponden a individuos cultivados aisladamente a través de varias generaciones a partir de ejemplares colectados en el campo y representativos de diversas condiciones ecológicas y geográficas. Se estudiaron comparativamente cultivos de 43 cepas de *T. riisei* de Puerto Rico, especie particularmente variable. En esta y otras especies cultivadas se observaron variaciones intraespecíficas, tanto en la conchilla como en la morfología interna, no solos entre cepas diferentes, sino también entre generaciones de la misma cepa, y entre las diversas fases del desarrollo individual.

Las observaciones histológicas conciernen particularmente al sistema reproductor. Se discute la presencia y variación de los túbulos proximales en el saco de la verga. Se describe una tercera capa, oblicua, de músculo en la verga de varias especies de planorbidos, con una disposición distintiva y característica en cada especie. El "diafragma" entre el saco de la verga y el prepucio se compara en diferentes especies y se discuten las "setas" sarcobelares, los pliegues velares y estructuras relacionadas.

La discusión incluye el estado sistemático de tres especies de *Drepanotrema* (*D. hoffmani*, *harryi* y *simmonsii*). *D. simmonsii*, que ha sido confundida con el género *Tropicorbis* por la semejanza de la conchilla, se retiene en el género *Drepanotrema* debido al punteado de la conchilla, a los flagelos en el saco de la verga y a la mandíbula constituida de placas numerosas y pequeñas; también se relaciona con las especies sudamericanas *D. nordestense* y *aeruginosum*.

## А Б С Т Р А К Т

ВИДЫ РОДОВ *TROPICORBIS* И *DREPANOTREMA* ИЗ ПУЭРТО-РИКО ПО СРАВНЕНИЮ  
С *AUSTRALORBIS GLABRATUS* И ДРУГИМИ ВИДАМИ СЕМЕЙСТВА КАТУШЕК.

Карл С. Ричардс

Описания и диагностические признаки даны для трех видов рода *Tropicorbis* (*T. albicans*, *T. obstructus* и *T. riisei*) и для пяти видов рода *Drepanotrema* (*D. anatinum*, *D. hoffmani*, *D. cimex*, *D. harryi* и *D. simmonsii*) из Пуэрто-Рико и Виргинских островов. Особое внимание уделено морфологическим и гистологическим признакам, которые можно было изучить на живом материале. Данные, полученные при изучении этих видов, сравниваются с наблюдениями над живым материалом 7 других видов катушек (*Australorbis glabratus*, *A. tenagophilus*, *Tropicorbis stramineus*, *T. janeirensis*, *T. peregrinus*, *T. pallidus* и *T. havanensis*), собранных на островах Карибского моря, в Южной Америке и в США, а также с имеющимися в литературе описаниями близких форм.

История жизни изучаемых видов описана начиная с развития яйца и кончая нерестом. Эти данные основаны на изучении нескольких поколений изолированных особей, которые были первоначально собраны из мест отличавшихся по своим экологическим и географическим условиям, и содержались в лабораторных культурах. Сделано сравнительное описание культур 43-х различных рас варьирующего пуэрто-риканского вида *T. riisei*. В культурах этого и других видов наблюдались внутривидовые вариации в раковинах и во внутренней морфологии: а именно, вариации между различными расами, живущими в естес-

твенной обстановке, вариации в разных поколениях одной расы, и возрастные вариации индивидуальных улиток.

Гистологические наблюдения касались, главным образом, органов размножения. Описаны случаи нахождения и вариации трубочек мешка совокупительного органа. Для нескольких видов катушек описан третий косой слой мускулов совокупительного органа; расположение этого слоя характерно для каждого вида. Дано сравнительное описание диафрагмы между мешком совокупительного органа и препуцием, и обсуждается значение мантийных "щетинок", складок мантии, и относящихся к ним структур.

Рассматривается таксономическое положение трех видов *Drepanotrema* (*D. hoffmani*, *D. harryi* и *D. simmonsii*). *D. simmonsii*, ошибочно относимая к роду *Tropicorbis* из за сходства раковины, оставлена в роде *Drepanotrema* на основании следующих признаков: раковина с окрашенными точками, жгутики в мешке совокупительного органа и челюсть с многочисленными маленькими пластинками. *D. simmonsii* близка к южноамериканским видам *D. nordestense* и *D. aeruginosus*.



SYSTEMATIC STUDIES ON MEXICAN LAND SNAILS OF THE  
GENUS *HOLOSPIRA*, SUBGENUS *BOSTRICHOCENTRUM*  
(STYLOMMATOPHORA: UROCOPTIDAE)

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ABSTRACT

Three species of *Holospira* (*Bostrichocentrum*) are described as new, and anatomical notes are given for another closely related species, *H. (B.) goldmani* Bartsch. The 3 new species are diagnosed as follows: *H. centricostata* sp. n.: shell cylindrical-conic, cone attenuate, curved, numerous fine axial riblets, 12 1/2 - 13 3/4 whorls, 12.2-14.5 mm long, 4.9-5.4 mm wide; *H. perplexa* sp. n.: shell cylindrical-conic, cone short, obtuse, cylindrical portion of shell striate, nearly smooth, 11 1/2 - 13 3/4 whorls, 10.5-15.2 mm long, 4.4-5.4 mm wide; *H. pupa* sp. n.: shell obovate or club shaped, cone abbreviate, cylindrical portion of shell striate, nearly smooth, 9 3/4-13 1/8 whorls, 9.5-13.8 mm long, 4.7-5.8 mm wide.

The species of the subgenus *Bostrichocentrum* are difficult to distinguish because of the similarity and variability of the shells. However, the retractor muscles possess gross, discrete features which permit consistent separation of the species. In *H. centricostata* the free retractor muscles are relatively small, the right pedal retractor is broad and stout, and the pharyngeal retractor gives off a single band that inserts at the base of the radular sac. *H. goldmani* has much larger retractor muscles, the right pedal retractor is slender, and there is also a single band of muscle extending from the pharyngeal retractor to the base of the radular sac. In *H. perplexa* this latter muscle is bifurcate. *H. pupa* has very large muscles compared to the other 3 species, and has 2 muscle bands extending from the pharyngeal retractor to the base of the radular sac.

The subgenera *Holospira* s.s. and *Bostrichocentrum* are very similar anatomically, being distinguished only by the radula. *Holospira* s.s. has 53-55 teeth per row; *Bostrichocentrum* has 39-45 teeth per row. Both of these subgenera are distinguished from the subgenus *Metastoma* and the genus *Coelostemma* by the presence of a long appendix on the spermathecal duct.

The urocoptid genus *Holospira* consists of a multitude of species that inhabit Texas, New Mexico, Arizona and Mexico. Most of the described species are known only from the shell. Subgenera, species and subspecies have all been defined by conchological characters, which form the basis for speculations on the relationships of the various taxa. The following results presented in this study indicate that such systematic relationships are best determined by the soft anatomy, and that the shell is unreliable for this purpose.

This paper includes the descriptions of 3 new species (*Holospira centricostata* n. sp., *H. perplexa* n. sp., and *H. pupa* n. sp.) and anatomical notes on another, *H. goldmani* Bartsch. All belong to the subgenus *Bostrichocentrum*.

The Mexican *Bostrichocentrum* belong

to a series of 13 species, which are more closely interrelated than they are to species referred to this subgenus from the United States. They are distinguished by shell characters as follows:

*H. anomala* Pilsbry, 1953: parietal lamella present in penultimate whorl; shell cylindrical-conic; cone attenuate, slightly curved; whorls of cylindrical portion striate, nearly smooth; 13 1/2 - 14 whorls; 2 1/2 embryonic whorls; 12.0-13.2 mm long; 3.5-3.6 mm wide.

*H. veracruziana* Dall, 1895: shell cylindrical-conic; cone short, rounded; cylindrical portion striate, nearly smooth; 17 whorls; 1 1/2 embryonic whorls; 17.5 mm long; 5 mm wide.

*H. veracruzicola* (Bartsch), 1943: shell cylindrical-conic; cone moderately long, slightly curved; cylindrical portion

striate, nearly smooth; 12.8 whorls; 2.7 embryonic whorls; 12 mm long; 2.9 mm wide.

*H. pilsbryi* Dall, 1895: shell cylindrical-conic; cone moderately long, nearly straight sided; cylindrical portion striate, nearly smooth; 12-14 whorls; 2 embryonic whorls; 10.3-13.0 mm long; 3.5-4.0 mm wide.

*H. tryoni* (Pfeiffer), 1867: shell cylindrical-conic; cone short, obtuse; cylindrical portion with numerous coarse striations or fine, nearly obsolete riblets; 11 3/8-15 whorls; 1 1/2 embryonic whorls; 9.7-13.5 mm long; 3.8-4.5 mm wide.

*H. perplexa* new species: shell cylindrical-conic; cone short, obtuse; cylindrical portion striate, nearly smooth; 11 1/2-13 3/4 whorls; 1 3/4 embryonic whorls; 10.5-15.2 mm long; 4.4-5.4 mm wide.

*H. goldmani* Bartsch, 1906: shell cylindrical-conic; cone short, rounded, with protruding embryonic whorls; cylindrical portion striate, nearly smooth; 12-14 whorls; 1 3/4 embryonic whorls; 13.0-16.4 mm long; 5.3-6.3 mm wide.

*H. pupa* new species: shell obovate or club shaped; cone abbreviate, with protruding embryonic whorls; whorls below cone striate, nearly smooth; 9 3/4-13 1/8 whorls; 1 3/4 embryonic whorls; 9.5-13.8 mm long; 4.7-5.8 mm wide.

*H. eurybia* Bartsch, 1926: shell pupoid; cone short, straight sided; all whorls with numerous axial riblets; 12.2 whorls; 2.2 embryonic whorls; 11.5 mm long; 4.5 mm wide.

*H. centicostata* new species: shell cylindrical-conic; cone attenuate, curved; whorls with numerous fine, closely spaced axial riblets; 12 1/2-13 3/4 whorls; 2 embryonic whorls; 12.2-14.5 mm long, 4.9-5.4 mm wide.

*H. tamaulipensis* Bartsch, 1906: shell elongate-conic; cone attenuate, straight sided; whorls with strong, regularly spaced ribs; 11-13 1/2 whorls; 2 embryonic whorls; 9.9-13.4 mm long; 3.7-4.4 mm wide.

*H. ronzonei* (Bartsch), 1943: shell pupiform; cone short, curved, obtuse;

whorls with widely spaced axial ribs; 12 1/4 whorls; 2 embryonic whorls; 10.1 mm long; 3.9 mm wide.

*H. hidalgoana* Bartsch, 1906: shell cylindrical-conic; cone attenuate, slightly curved; whorls with thick, wide spaced ribs; 16-17 whorls; 3 embryonic whorls; 20.3-20.5 mm long; 4.2-4.3 mm wide.

Species from geographically remote areas occasionally possess very similar shells even though anatomical affinities may be with species that have shells of very different aspect, but are from geographically proximal areas. In this respect *H. centicostata* resembles *H. tamaulipensis* although it is anatomically very similar to *H. goldmani*.

The Mexican species all appear to be constant in lamellar structure and, with the exception of *B. anomala* Pilsbry, all have a single axial lamella. The United States species from Arizona and New Mexico are highly variable in lamellar structure, and in addition to the axial lamella, members of a given colony may have a superior or a basal lamella or both (Pilsbry, 1946: 122-123). Excluding the species from the United States, *Bostrichocentrum* is readily defined and separated from *Holospira* s.s. by its lamellae and short whorls. The United States species have probably evolved independently from holospiroid ancestors, and pending anatomical examination, may be removed from *Bostrichocentrum*.

In addition to the species listed above 2 other Mexican species have been placed in the subgenus *Bostrichocentrum*, *H. galathea* Bartsch, 1926 and *H. gealei* (H. Adams), 1872. Both species are of uncertain status. *H. galathea* was described from a single shell recovered from drift material along the Rio Balsas, and its characters do not distinguish it from *H. pilsbryi*. Because it is from drift material the identity of its parent population can never be determined, and therefore it can never be known whether it is or is not distinct from *H. pilsbryi*. The internal structure of the shell of *H. gealei* is unknown, preventing proper subgeneric allocation. Also, the description does not

distinguish it from *H. tryoni*, *goldmani*, *perplexa* or *pupa*.

Even though some of the species of the subgenus *Bostrichocentrum* are distinguished by slight differences only, I recognize them as distinct entities for the following reasons. (1) The species occur in geographically limited and small populations, which apparently do not overlap or intergrade (although characters of the populations may tend to overlap). (2) Members of a given population are rather uniform in their characters, regardless of the habitat occupied within the colony. (3) Adjacent populations occurring in what appear to be biotically and physically similar environments are often very different, which argues against the probability that they are ecological variants. (4) Species of similar appearance from geographically proximal areas may be very different anatomically (a prime example being *H. goldmani* and *H. pupa*). (5) Until the anatomy of the remaining forms has been investigated we will not know how similar or different they actually are, and nothing would be gained by lumping similar forms or relegating them to sub-specific status.

*Holospira (Bostrichocentrum)*  
*centicostata*, new species

(Pl. I, Figs. 12-15; Pl. II, Fig. 1;  
Pl. III, Figs. 4, 8-10)

Shell cylindric-conic, with a tapering spire, thin but solid, opaque, white. Umbilicus perforate, rimate or imperforate (rimate in type). Whorls tightly coiled, flat sided or slightly rounded, 12 1/2-13 3/4; 5-6 whorls comprising cylindric portion of shell; remaining whorls forming attenuate convex spire; 2 embryonic whorls, protruding, nipple shaped, dull flesh-colored, smooth; remaining whorls crossed by numerous oblique riblets, which become heavier and more widely spaced on later whorls; 93-131 riblets on 7th whorl (131 in type), 64-85 riblets on penultimate whorl (75 in type). Aperture subcircular, vertical or slightly oblique, angular at parietal

margins. Peristome usually adnate to the preceding whorl, reflected. Axis about 1/6 diameter of shell, increasing slightly in diameter in later whorls, and then becoming slightly thinner in last whorl. A single low rounded axial lamella begins at base of cone, and continues into last whorl, born on lower portion of axis in each whorl, not visible from aperture.

Measurements of type: height, 13.9 mm; width, 5.2 mm; 13 3/8 whorls.

Measurements of paratypes: height, 12.2-14.5 mm (av. 13.4); width, 4.9-5.4 mm (av. 5.1).

Type: UMMZ<sup>1</sup> 213218; 14.4 miles northwest of Acatlan, Puebla; 4300 feet altitude; collected July 21, 1955 by Fred G. Thompson.

Paratypes: UMMZ 213219 (15), USNM 634573 (2): same data as the type.

Radula (Pl. III, Fig. 10): 1.65 mm long by 0.6 mm wide; formula 12-7-1-7-12. Central 25  $\mu$  wide by 20  $\mu$  high with a single long mesocone. Laterals unicuspid, with a single long mesocone. First 3 marginals bicuspid, with a large mesocone and a small ectocone; next 6 marginals tricuspid because of the presence of an additional small ectocone; 10th and 11th marginals of variable size and shape, usually with 2 large jagged cusps; last marginal much reduced, or variable shape and acuspid.

Retractor muscles (Pl. III, Figs. 4, 8): Free retractors extending about 5 whorls into shell, about 7 mm long, split near origin producing 2 stout broad bands about 5.7 mm long. The outer band divides to form a heavy pharyngeal retractor (PR) and a thinner branch, which in turn divides to form the left pedal retractor (LP) and the left ocular retractor (LO). The pharyngeal retractor is about 3.5 mm long and divides near its insertion to form short narrow heads that attach to the base of the buccal mass (BM) above the esophagus. An additional

<sup>1</sup>Catalog numbers, UMMZ = Museum of Zoology, University of Michigan, Ann Arbor, Michigan. USNM = U. S. National Museum, Washington, D. C.

narrow band originates on the right dorsal surface of the pharyngeal retractor, and inserts at the base of the radular sac. The inner band of the columellar retractor divides to form a broad right pedal retractor (RP), and a narrow band which gives rise to the right ocular retractor (RO). The right ocular retractor passes between the body wall and the vagina, and between the spermathecal duct and the penis. Near the base of the vagina it gives off a series of fine fibers, which attach to the base of the vagina and spermathecal duct. The origin of the ocular retractors are so delicate that they are easily torn, and it is difficult to determine their lengths.

Foot: sole short and broad, unipartite, holopod. Dorsal surface of foot depressed, rounded; dorsum and sides pebbled; lines of pebbles forming a reticulate network. No dorsal mucus pore or medial groove.

Genital organs (Pl. II, Fig. 1): genital opening below and behind right ocular tentacle. Genital atrium small, sacular, without a conspicuous neck attaching it to body wall. Vagina long, slender, tapering, increasing in diameter toward the uterus, 2.9-4.2 mm long, with 4 longitudinal internal folds. Uterus long and simple, 6.0-9.6 mm long. Albumen gland long and sickle shaped, 4.2-6.4 mm long. Hermaphroditic duct long, strongly convoluted near albumen gland. Ototestis consisting of 6-9 lobes, each containing 4-6 club shaped glands (not illustrated for this species). Spermatheca reniform, 1.4-1.7 mm long, on a long duct which is normally appressed to the vagina and the uterus. Spermathecal duct beginning as a large tubular pedicel about 1 mm long, and then becoming reduced in diameter and convoluted for a short distance. The convoluted portion is surrounded by a thin muscular sheath. Remainder of duct long and slender, and bearing a long terminal appendix which is appressed to the albumen gland when in its natural position; it may extend along the digestive gland for a short distance. Appendix 4.4-14.4 mm long. Length of spermathecal duct to origin of appendix 9.2-14.2 mm.

Penis small, simple, with 2 internal folds, both of which are crossed by 2 narrow grooves. Penis with a small terminal knob to which the penial retractor muscle is attached. Penial retractor muscle slender, originating on inner wall of lung, about 2.6-4.6 mm long. Epiphallus long and continuous with vas deferens, enlarged near penis, with 4 longitudinal papillose internal folds. Prostate imbedded in the uterus.

*Holospira centicostata* may be recognized by its single low axial lamella, size, shape, flat sided whorls and costulate sculpture. It most closely resembles *H. (B.) tamaulipensis* but is distinguished by its larger diameter and more numerous whorls. Anatomically, this species is close to *H. (B.) goldmani*.

*Holospira (Bostrichocentrum) goldmani*

Bartsch, 1906

(Pl. II, Fig. 4; Pl. III, Figs. 3, 7)

Specimens were collected at 5.7 miles northwest of Huajapan de Leon, Oaxaca (6500 feet altitude), and 2.2 miles south-east of Chila, Puebla (6100 feet altitude).

Anatomy as in *H. (B.) centicostata* except: radular formula, (13-14) -7-1-7- (13 or 14). Columellar retractor larger, about 10 mm long. Genital organs generally larger; genital atrium with a short tubular neck attaching to body wall; vagina 5.0-10.0 mm long; uterus 14.0-18.7 mm long; albumen gland more elongate, 6.4-10.0 mm long; hermaphroditic duct not as strongly convoluted, entering near base of albumen gland; spermatheca more saccular, 1.4-2.8 mm long; appendix 7.8-17.6 mm long; spermathecal duct to origin of appendix 13.5-17.0 mm long; penial retractor muscle 1.3-2.4 mm long.

*Holospira (Bostrichocentrum) perplexa*  
new species

(Pl. I, Figs. 7-11; Pl. II, Fig. 3;

Pl. III, Figs. 2, 6)

Shell cylindrical-conic, occasionally slightly club shaped and widest at about

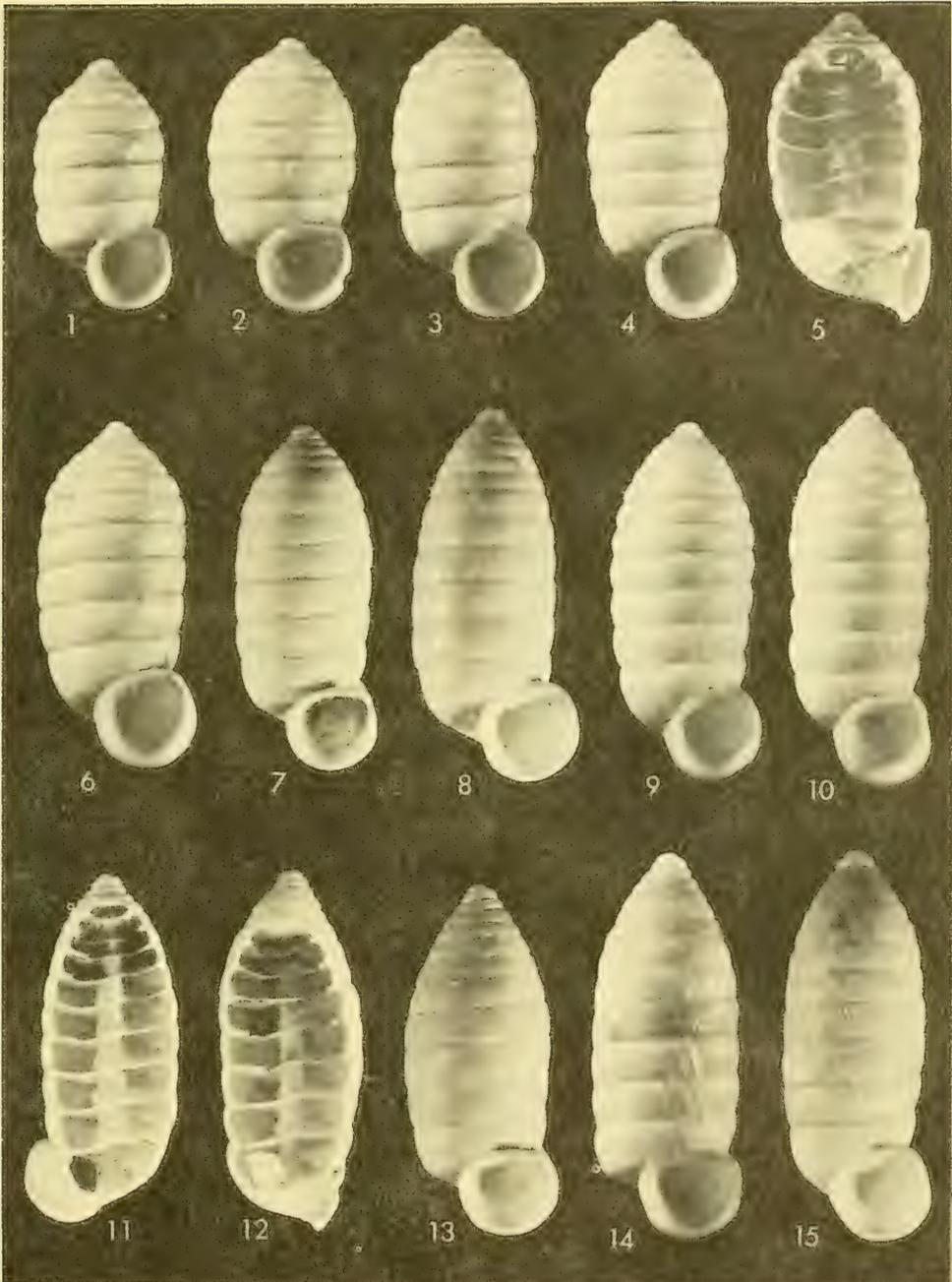


PLATE I

FIGS. 1-6. *Holospira pupa*, n. sp. FIGS. 1, 2, 4, 5, 6, Paratypes; FIG. 3, Type.

FIGS. 7-11. *Holospira perplexa*, n. sp. FIGS. 7, 9, 10, 11, Paratypes; FIG. 8, Type.

FIGS. 12-15. *Holospira centicostata* n. sp. FIGS. 12, 13, 15, Paratypes; FIG. 14, Type.

the 8th whorl. Umbilicus rimate. Whorls 11 1/2-14 3/4, average 12 5/8, nearly flat sided; 1 3/4 embryonic whorls, large, protruding, smooth, dull yellow white; cylindrical portion of shell consisting of about 4-5 whorls; remaining whorls forming a relatively long, slightly convex spire. Early whorls of spire crossed by numerous fine oblique riblets, which become obsolete on about the 7th whorl; remaining whorls nearly smooth, except last quarter of body whorl which bears heavier, regular riblets that are continuous from the suture into the umbilicus where they become sharp crests. Aperture vertical, usually free from preceding whorl, subcircular, angular at the upper outer margin and obtusely angulate at the upper inner margin. Peristome strongly reflected along its lower and umbilical margin, less strongly reflected along its parietal margin, only slightly reflected along its outer margin. Axis about 1/5 the diameter of the shell, with a single lamella which extends the length of the cylindrical portion of the shell, and is usually located on the lower half of the axis in each whorl. Lamella regularly increasing in size and usually largest and calloused in the penultimate whorl; lamella not visible from the aperture. Axis smooth, with fine irregular longitudinal white streaks.

Measurements of type: height, 14.6 mm; diameter, 5.4 mm; 14 1/8 whorls.

Measurements of paratypes: height, 10.5-15.2 mm (av. 12.6); diameter, 4.4-5.4 mm (av. 4.9).

Type: UMMZ 213220; 10.3 miles northwest of Huajapan de Leon, Oaxaca; 6200 feet altitude. Collected July 21, 1955 by Fred G. Thompson.

Paratypes: UMMZ 213221 (52), USNM 634575 (10); same data as the type.

Anatomy as in *H. (B.) centicostata* except: radular formula, (12-15) -7-1-7- (12-15). Free retractor muscle about 6 mm long; accessory band originating on right side of pharyngeal retractor and dividing into 2 heads which insert at base of radular sac. Genital organs larger; genital atrium with a short tubular neck

attaching to body wall; vagina 5.0-6.3 mm long; uterus 9.3-13.5 mm long; albumen gland 6.2-7.8 mm long; hermaphroditic duct not convoluted near base; ovotestes with 6-8 lobes; spermatheca 2.0-2.4 mm long; appendix 7.5-14.0 mm long; length of spermathecal duct to origin of appendix 13.0-16.5 mm; penial retractor muscle 1.5-5.0 mm long.

*Holospira (B.) perplexa* is most similar to *H. (B.) tryoni*. It is distinguished from that species by its larger diameter, the shape of its spire, and its sculpture. *H. perplexa* is 4.4-5.4 mm in diameter, has a lanceolate spire and is irregularly striate on the cylindrical portion of the shell. *H. tryoni* is 3.8-4.5 mm in diameter; the conic portion of the spire is abbreviate and rounded and has numerous nearly obsolete riblets on the cylindrical portion of the shell.

*Holospira (Bostrichocentrum) pupa*  
new species

(Pl. I, Figs. 1-6; Pl. II, Fig. 2;  
Pl. III, Figs. 1, 5)

Shell obovate or club-shaped, usually widest at base of cone. Color dull white. Umbilicus rimate or perforate. Whorls 9 3/4-13 1/8, average 11 3/8, nearly straight sided and occasionally slightly scalariform; 1 3/4 embryonic whorls, large, protruding, smooth, dull yellow-white; cylindrical portion of shell consisting of about 5 whorls, remaining whorls forming a short rounded conic spire, terminated by the nipple-like embryonic whorls. Whorls of spire crossed by numerous fine oblique riblets, which become decreasingly distinct on the 6th whorl, and are subobsolete or obsolete on the remaining portion of the shell; last half of body whorl crossed by heavier, irregular, varix-like ribs, which become rugose in the umbilical region. Aperture circular, angulate at the upper, outer margin, slightly oblique, usually free and extending beyond the margin of the preceding whorl. Peristome completely reflected around the aperture. Axis about 1/5 diameter of the shell, bearing a single

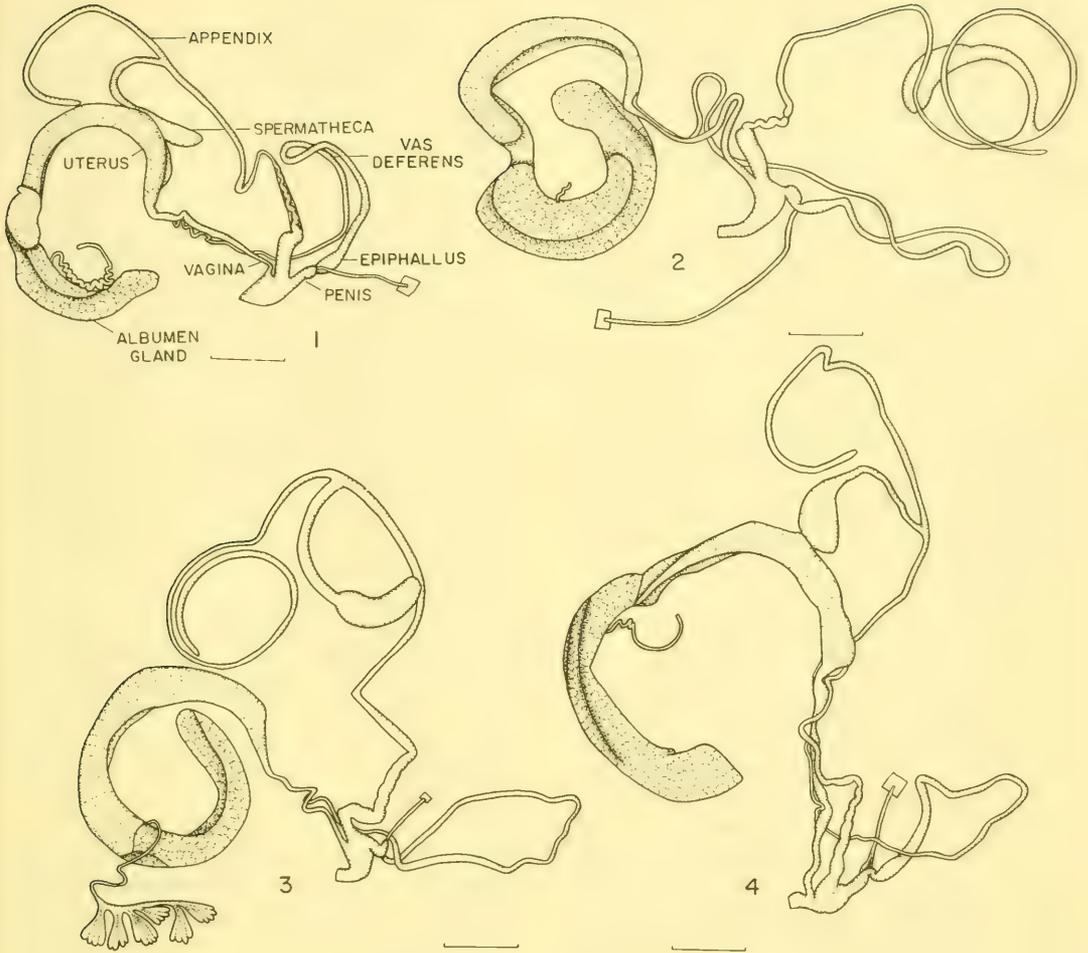


PLATE II

FIGS. 1-4. Reproductive systems of 4 species of *Holospira*: 1. *H. centicostata*, n. sp. 2. *H. pupa*, n. sp. 3. *H. perplexa*, n. sp. 4. *H. goldmani* (Bartsch).

lamella which begins at the base of the cone and extends into the last whorl. The lamella occurs only as a slight swelling in the middle of the earlier whorls, but becomes heavier and cristate in the penultimate whorl, where it occurs on the basal half of the axis; lamella not visible from the aperture. Axis with occasional fine longitudinal white streaks.

Measurements of type: height, 11.6 mm; diameter, 5.4 mm; 11 1/4 whorls.

Measurements of paratypes: height, 9.5-13.8 mm (av. 11.7); diameter, 4.7-5.8 mm (av. 5.2).

Type: UMMZ 213216; 15 miles southeast of Acatlan, Puebla; 4900 feet altitude; collected July 21, 1955 by Fred G. Thompson.

Paratypes: UMMZ 213217 (61), USNM 634574 (10); same data as the type.

Anatomy as in *H. centicostata* except: radular formula, (12 or 13) -7-1-7- (12 or 13). Free retractor muscles very stout, extending about 6 whorls into shell, about 14 mm long; pharyngeal retractor about 8 mm long, with 2 narrow accessory bands which attach at the base of the radular sac. Genital organs generally larger; genital atrium with a long tubular neck attaching to the body wall; vagina 4.5-6.7 mm long; uterus 9 mm long; albumen gland large, stocky, 8.0-8.4 mm long; ovotestis with 6-10 lobes; spermatheca 1.4-1.9 mm long; appendix 13.0-16.5 mm long; penial retractor muscle 4.2-7.0 mm long.

This species may be recognized by its obovate shape, size, number of whorls, sculpture and axial structure. It is similar in shell features to *H. (B.) goldmani*, but differs from that species in being shorter, having fewer whorls, and in having an obovate shape as opposed to a cylindrical-conic shape. *H. (B.) pupa* is similar in shape to *H. (B.) eurybia* but differs in having nearly smooth body whorls as opposed to being distinctly ribbed.

#### ANATOMICAL DIFFERENTIATION WITHIN THE GENUS *HOLOSPIRA*

Seven subgenera are currently recog-

nized within *Holospira* s.l. Four of these, *Haplocion*, *Megaxis*, *Allocoryphe* and *Prionolopax*, remain anatomically unknown, leaving *Holospira* s.s., *Metastoma* and *Bostrichocentrum* as the only subgenera in which the anatomy has been investigated.

Pilsbry (1903: 68-71) described the anatomy of *H. (H.) nelsoni*, *H. (Metastoma) roemeri* and the closely related *Coelostemma dalli*, and the radula of *H. (H.) nelsoni*, *H. (H.) goldfussi*, *H. (M.) roemeri*, *H. (Bostrichocentrum) pilsbryi*, *H. (B.) tryoni*, *Coelostemma dalli* and *C. elizabethae*. Strebel and Pfeffer (1880: 82) reported on the anatomy of *H. (H.) goldfussi*, but as Pilsbry (1903) contended, it is probable that they had confused species, for their description and illustrations in no way resemble the anatomy of any known species of the genus *Holospira*. In most important features the anatomy of *Holospira* s.s., *Bostrichocentrum*, *Metastoma* and *Coelostemma* are alike. *Holospira* s.s. and *Bostrichocentrum* are closely related by the presence of an appendix on the spermathecal duct. *Metastoma* and *Coelostemma* lack such an appendix.

The number of radular teeth is the only anatomical feature that separates the subgenus *Holospira* s.s. from *Bostrichocentrum*. The number of teeth in species of *Holospira* s.s. is: *H. nelsoni* (55), *H. goldfussi* (53); species of *Bostrichocentrum*: *H. pilsbryi* (39), *H. tryoni* (41), *H. centicostata* (39), *H. pupa* (39-41), *H. perplexa* (39-45), *H. goldmani* (41-43). A distinction between the 2 groups by means of the radula is of limited use because of the large number of species in which the radula is not known.

Anatomical differentiation within the subgenus *Bostrichocentrum* involves differences of proportion and size in the reproductive system, and differences of size and structure of the retractor muscles. The reproductive systems of the 3 new species described in this paper, and *Holospira goldmani*, possess aspects that tend to characterize each species (Table 1).

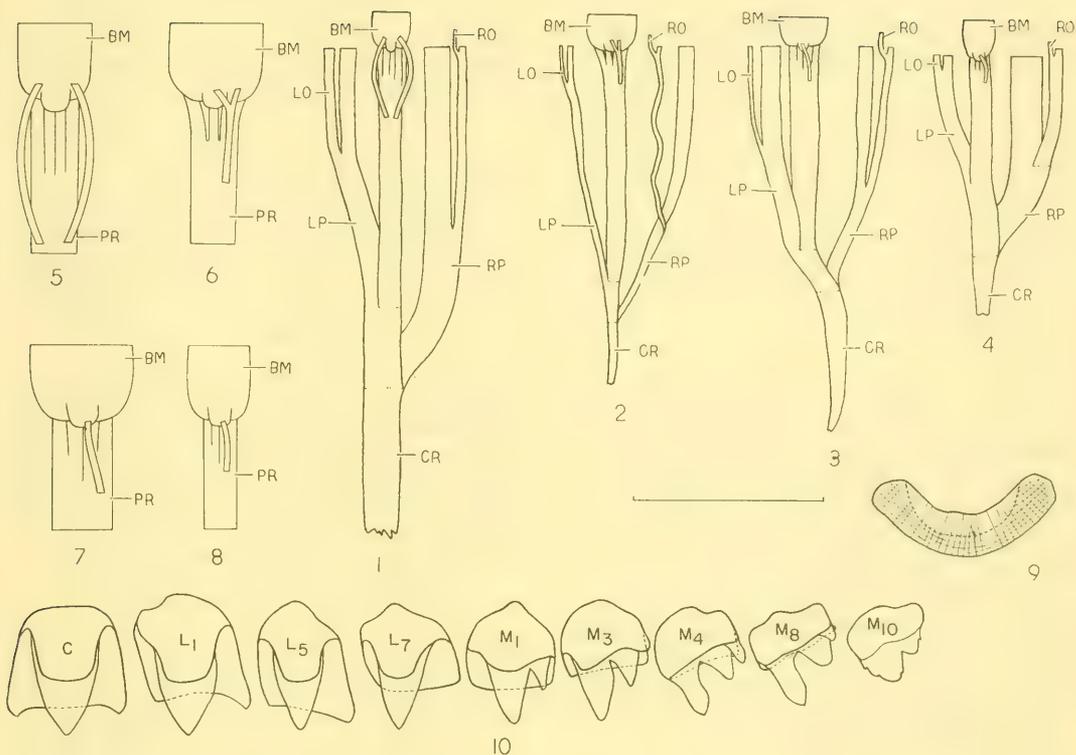


PLATE III

FIGS. 1-4. Free retractor muscles in 4 species of *Holospira*: 1. *H. pupa*, n. sp. 2. *H. perplexa*, n. sp. 3. *H. goldmani* (Bartsch). 4. *H. centicostata* n. sp.

FIGS. 5-8. Muscles attached to buccal mass in 4 species of *Holospira*: 5. *H. pupa*, n. sp. 6. *H. perplexa*, n. sp. 7. *H. goldmani* (Bartsch). 8. *H. centicostata*, n. sp.

FIG. 9. Jaw of *Holospira centicostata* n. sp.

FIG. 10. Radula of *Holospira centicostata* n. sp., showing the central, laterals 1, 5, 7 and marginals 1, 3, 4, 8, 10.

Legend for symbols.

- |                             |                              |
|-----------------------------|------------------------------|
| BM - buccal mass.           | LP - left pedal retractor.   |
| CR - columellar retractor.  | RO - right ocular retractor. |
| LO - left ocular retractor. | RP - right pedal retractor   |
| PR - pharyngeal retractor.  |                              |

Scale refers to retractor muscles.

TABLE 1. Differences in size of reproductive structures of 4 species of *Bostrichocentrum*. Measurements are in millimeters.

Organ	<i>centicostata</i>	<i>goldmani</i>	<i>perplexa</i>	<i>pupa</i>
Vagina	2.9-4.2	5.0 - 10.0	5.0 - 6.3	4.5 - 6.7
Uterus	6.0-9.6	14.0 - 18.7	9.3 - 13.5	9.0
Albumen gland	4.2-6.4	6.4 - 10.0	6.2 - 7.8	8.0 - 8.4
Spermatheca	1.4-1.7	1.4 - 2.8	2.0 - 2.4	1.4 - 1.9
Appendix	4.4-13.4	7.8 - 17.6	7.5 - 14.0	6.0 - 14.2
Spermathecal duct	9.2-14.2	13.5 - 17.0	13.0 - 16.5	13.0 - 16.5
Penial retractor muscle	2.6-4.6	1.3 - 5.0	1.5 - 5.0	4.2 - 7.0

As is shown, *H. centicostata* tends to have a smaller vagina, uterus and albumen gland than do the other 3 species. *H. goldmani* differs from *H. perplexa* and *H. pupa* by its much larger uterus. It differs further from *H. pupa* by the smaller size of its penial retractor muscle. *H. pupa* tends to differ from *H. perplexa* by the smaller size of its uterus and the larger size of its albumen gland. These characters are of limited use because of the variability that occurs.

One other character that appears to be meaningful is the attachment of the genital atrium to the body wall. While *H. centicostata* is distinct in having almost no neck between the atrium and the body wall, *H. pupa* is equally distinct in having a very long neck (Pl. II, Figs. 1, 2).

Features of the retractor muscles readily allow distinction of the 4 species (Pl. III). These muscles are relatively independent of the size and number of whorls of the shell, they show little variation in size, and no significant variation in structure within a species. The retractor muscles of *H. pupa* are much larger than those in the other 3 species, despite the fact that it has a smaller shell. *H. pupa* differs further in having 2 accessory slips of muscle inserting at the base of the radular sac (Pl. III, Figs. 1, 5). *H. perplexa* has relatively slender retractor muscles and a single accessory muscle inserts on the radular sac. This muscle slip is bifurcate near its insertion (Pl. III, Figs. 2, 6). *H. goldmani* and *H. centicostata*

are alike in the structure of the retractor muscles (Pl. III, Figs. 3, 7, 4, 8), except that the muscles of *H. goldmani* are longer, and the right pedal retractor is much more slender than the corresponding muscles of *H. centicostata*.

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## ZUSAMMENFASSUNG

SYSTEMATISCHE STUDIEN UBER MEXIKANISCHE LANDSCHNECKEN DER  
GATTUNG *HOLOSPIRA*, UNTERGATTUNG *BOSTRICHOCENTRUM*  
(STYLOMMATOPHORA: UROCOPTIDAE)

Drei Arten von *Holospira* (*Bostrichocentrum*) sind hier als neu beschrieben und anatomische Angaben werden über eine weitere, nah verwandte Art, *H. (B.) goldmani* (Bartsch) gegeben. Die Diagnose für die 3 neuen Arten lautet wie folgt. *H. centicostata* sp. n.: Schale zylindrisch, kegelförmig verjüngt, konischer Teil gebogen, mit feinen axialen Rippchen, 12 1/2 - 13 3/4 Umgänge, 12.2 - 14.5 mm lang, 4.9 - 5.4 mm breit; *H. perplexa*, sp. n.: Schale zylindrisch-konisch Konus kurz, stumpfwinkelig, zylindrischer Teil gerieft, beinahe glatt, 11 1/2 - 13 3/4 Umgänge, 10.2 - 15.2 mm lang, 4.4 - 5.4 mm breit; *H. pupa*, sp. n.: Schale weiteiförmig oder keulenförmig, konischer Teil verkürzt, zylindrischer Teil der Schale gerieft, beinahe glatt, 9 3/4 - 13 1/8 Umgänge, 9.5 - 13.8 mm lang, 4.7 - 5.8 mm breit.

Wegen der Ähnlichkeit und Veränderlichkeit ihrer Schalen sind die Arten der Untergattung *Bostrichocentrum* schwer zu unterscheiden. Jedoch zeigen die Retraktormuskeln grobe und deutliche Züge, die eine konsequente Trennung der Arten ermöglicht. In *H. centicostata* sind die freien Retraktoren relativ klein; der rechte m. retractor pedalis ist breit und kräftig; vom Pharynxretractor geht eine einzelne Muskelstrang zur Basis des Radulasackes. *H. goldmani* hat viel grössere Retraktoren; der rechte m. retractor pedalis ist dünn; auch hier führt nur ein einziger Strang vom Pharynxretractor zum Radulasack. Dieser letztere Muskel ist bei *H. perplexa* gegabelt. *H. pupa* hat im Vergleich zu den 3 anderen Arten sehr grosse Muskeln und 2 Muskelstränge führen vom Pharynxretractor zum Radulasack.

Die anatomisch sehr ähnlichen Untergattungen *Holospira* s.s. und *Bostrichocentrum* lassen sich durch ihre Radula unterscheiden. *Holospira* s.s. hat 53-55 Zähne pro Reihe, *Bostrichocentrum* hat deren 39-45. Diese beiden Untergattungen unterscheiden sich von den Untergattungen *Metastoma* und *Coelostemma* durch die Anwesenheit eines langen Fortsatzes am Spermathecalduct.

## RÉSUMÉ

ÉTUDES SYSTÉMATIQUES SUR LES MOLLUSQUES TERRESTRES MEXICAINS DU  
GENRE *HOLOSPIRA* SOUS-GENRE *BOSTRICHOCENTRUM*  
(STYLOMMATOPHORA: UROCOPTIDAE)

Trois espèces d'*Holospira* (*Bostrichocentrum*) sont ici décrites et des détails anatomiques sont donnés pour une autre espèce parente, *H. (B.) goldmani* (Bartsch). La diagnose des 3 espèces est donnée comme suit: *H. centicostata*, sp. n.: coquille cylindrique, spire atténué, arquée, ayant de nombreuses et fines costulations axiales; tours de spire 12 1/2 à 13 3/4, longueur 12.2 - 14.5 mm, largeur 4.9 - 5.4 mm. *H. perplexa* sp. n.: coquille cylindrique-conique, cône court, obtus, portion cylindrique striée, presque lisse, tours de spire 11 1/2 à 13 3/4, longueur 10.5 - 15.2 mm, largeur 4.4 - 5.4 mm; *H. pupa*, sp. n.: coquille subovale ou claviforme, cône abrégé, portion

cylindrique striée, presque lisse, tours de spire  $9\frac{3}{4}$  à  $13\frac{1}{8}$ , longueur 9.5 - 13.8, largeur 4.7 - 5.8 mm.

Les espèces du sous-genre *Bostrichocentrum* sont difficiles à distinguer à cause de leurs coquilles semblables et variables. Une séparation nette des espèces est pourtant possible car les muscles rétracteurs montrent des caractères grossiers bien définis. Dans *H. centicostata* les muscles rétracteurs libres sont relativement petits; le rétracteur pédieux droit est large et gros et le rétracteur pharyngien émet une seule bande qui s'insère à la base du sac radulaire. *H. goldmani* a des muscles rétracteurs beaucoup plus grands; le rétracteur pédieux droit est plus mince; il y a aussi une seule bande musculaire reliant le rétracteur pharyngien au sac radulaire. Dans *H. perplexa* ce muscle est bifurqué. Comparé aux espèces précédentes, *H. pupa* a des muscles très grands; et de plus, 2 bandes musculaires relient le rétracteur pharyngien au sac radulaire.

Les sous-genres *Holospira* s.s. et *Bostrichocentrum* sont anatomiquement très semblables et ne peuvent être distingués que par leur radula. *Holospira* s.s. a de 53 à 55 dents par rangée, *Bostrichocentrum* en a de 39 à 45. Ces 2 sous-genres se distinguent des sous-genres *Metastoma* et *Coelostemma* par la présence d'un appendice long sur le conduit spermathecal.

#### RESUMEN

#### ESTUDIOS SISTEMATICOS SOBRE CARACOLES TERRESTRES MEXICANOS DEL GENERO *HOLOSPIRA*, SUBGENEROS *BOSTRICHOCENTRUM* (STYLOMMATOPHORA: UROCOPTIDAE)

Se describen tres nuevas especies de *Holospira* (*Bostrichocentrum*), con notas anatómicas sobre otra especie estrechamente relacionada, *H. (B.) goldmani* Bartsch.

Las nuevas especies se diagnostican como sigue: *H. centicostata* - concha cilindro-cónica, cono atenuado, curvado, costillas axiales finas y numerosas, 12  $1/2$ -13  $3/4$  vueltas, 12,2-14,5 mm de largo, 4,9-5,4 mm de ancho; *H. perplexa* - concha cilindro-cónica, cono corto, obtuso, porción cilíndrica estriada, casi lisa, 11  $1/2$ -13  $3/4$  vueltas, 10,5-15,2 mm de largo, 4,4-5,4 mm de ancho; *H. pupa* - concha ovoide o claviforme, cono acortado, porción cilíndrica estriada, casi lisa, 9  $3/4$ -13  $1/8$  vueltas, 9,5-13,8 mm de largo, 4,7-5,8 mm de ancho.

Las especies de *Bostrichocentrum* son difíciles de distinguir debido a la similitud y variabilidad de las conchas. Sin embargo, los músculos retractores poseen caracteres macroscópicos que aseguran el reconocimiento de las especies. En *H. centicostata* los músculos retractores libres son relativamente pequeños y el retractor pedal derecho es ancho y robusto. *H. goldmani* tiene retractores más grandes y el pedal derecho es delgado. *H. pupa* tiene músculos mucho más grandes que en las otras especies. En todas ellas hay una banda muscular, que se origina en el retractor faríngeo y corre a insertarse en la base del saco radular, y que es simple en *centicostata* y *goldmani*, bifurcada en *perplexa* y doble in *pupa*.

Los subgéneros *Holospira* s.s. y *Bostrichocentrum* son muy similares anatómicamente, distinguiéndose sólo por la radula. *Holospira* s.s. tiene 53-55 dientes por hilera, mientras que *Bostrichocentrum* tiene 39-45. Estos dos subgéneros se distinguen del subgénero *Metastoma* y del género *Coelostemma* por la presencia de un largo apéndice en el ducto de la spermateca.

#### А Б С Т Р А К Т

#### ИЗСЛЕДОВАНИЯ ПО СИСТЕМАТИКЕ МЕКСИКАНСКОЙ НАЗЕМНОЙ УЛИТКИ РОДА *HOLOSPIRA*, ПОДРОДА *BOSTRICHOCENTRUM* (STYLOMMATOPHORA: UROCOPTIDAE)

Фред Г. Томпсон

Автор дает описание трех новых видов *Holospira* (*Bostrichocentrum*) и приводит анатомические данные для другого близкого рода *H. (B.) goldmani* Bartsch. Диагноз трех новых видов следующий: *H. centicostata* - раковина цилиндро-коническая, конус удлинённый, изогнутый, многочисленны тонкие продольные ребра от  $12\frac{1}{2}$  до  $13\frac{3}{4}$  оборотов длина 12.2 до 14.5

мм, ширина от 4.9 до 5.4 мм. *H. perplexa* - раковина цилиндрико-коническая, конус короткий и тупой, цилиндрическая часть раковины бороздчатая, почти гладкая, от  $11\frac{1}{2}$  до  $13\frac{3}{4}$  оборотов, длина от 10.5 до 15.2 мм, ширина от 4.4 до 5.4 мм. *H. pupa* - раковина яйцевидная или утолщенная на одном конце, конус укороченный, цилиндрическая часть раковины в бороздках, почти гладкая, от  $9\frac{3}{4}$  до  $13\frac{1}{8}$  оборотов, длина от 9.5 до 13.8 мм, ширина от 4.7 до 5.8 мм.

Различные виды подрода *Bostrichocentrum* трудно различимы из за сходства и изменчивости их раковин. Однако, надежными признаками по которым можно с уверенностью определить разные виды, являются мускулы ретракторы. У *H. centicostata* свободные мускулы ретракторы сравнительно малы; правый ретрактор ноги широкий и толстый, а от ретрактора глотки отходит единственный пучок мускульных волокон и прикрепляется к основанию мешка радулы. У *H. goldmani* мускулы ретракторы значительно больше; правый ретрактор ноги тонкий, и также имеется один пучок мускульных волокон, который отходит от ретрактора глотки и прикрепляется к основанию мешка радулы. У *H. perplexa* раздвоенный мускул начинается от ретрактора глотки и прикрепляется к основанию мешка радулы. По сравнению с тремя другими видами, мускулы *H. pupa* очень большие, и два пучка мускульных волокон отходят от ретрактора глотки и прикрепляются к основанию мешка радулы.

С анатомической точки зрения, подроды *Holospira* s.s. *Bostrichocentrum* очень похожи друг на друга, и могут быть отличимы только по радуле. У *Holospira* s.s. имеется 53 - 55 зубов в каждом ряду; у *Bostrichocentrum* 39 - 45 зубов в каждом ряду. Эти оба подрода отличаются от подрода *Metastoma* и рода *Coelostemma* присутствием длинного отростка в канале сперматеки.



SHELL REGENERATION IN *ONCOMELANIA FORMOSANA*  
(GASTROPODA: HYDROBIIDAE)<sup>1</sup>

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ABSTRACT

In connection with microsurgery performed on *Oncomelania formosana* (Pilsbry and Hirase), an amphibious prosobranch snail native to Taiwan (Formosa), the regeneration of shell was studied in mature specimens of that species. The shell was drilled open in the third whorl from the aperture. Drilled snails of laboratory raised stock were maintained singly in Petri dish culture chambers and observed over a period of a month. The culture chamber was lined with filter paper which served as food and was flooded to a depth of 7 mm with Lymnaeid Ringer's Solution (physiological saline). The temperature was  $23^{\circ}\text{C} \pm 1^{\circ}\text{C}$ . The second day after drilling, a membrane started to form at the inside edge of the hole. The membrane "grew" across the hole becoming completed in 50% of the snails in 4 days, in 90% in 6 days, and 100% in 13 days. The membrane appeared proteinaceous, acellular, and structureless.

When the membrane was nearly completed granules were seen to form on the exterior surface of the membrane. These granules "grew" into 2 types of crystals: 1) scale-like crystals which "grew" and coalesced to produce a smooth shell of polygonal units, and 2) tear-shaped crystals which branched and formed spherulites, which fused into a roughened shell of polygonal units. Both types of crystals were frequently found on the same membrane.

The membrane became completely calcified in 10% of the snails 5 days after drilling, in 50% of the snails 28 days after drilling. At that time an additional 15% of the snails were 90% calcified or more, while the remaining 35% were 50% calcified or less.

Upon near completion of the primary membrane-shell complex further membranes were deposited beneath the first. These became calcified by: 1) supporting crystalline growth above the membrane, 2) calcification within the membrane.

*Pomatiopsis lapidaria*, a related American snail, used for the same type experiments, showed a high rate of mortality and did not regenerate a shell. Further experiments need to be conducted with this species.

INTRODUCTION

I became interested in the regeneration of shell in the amphibious prosobranch *Oncomelania formosana* (Pilsbry and Hirase) when experimenting with intra-specific gonadal transplantation in that snail. It was noted that the shell regenerated in the areas where the shell had been damaged in order to perform the micro-surgery connected with the transplantation. It was realized that this process was associated with rapid tissue repair and survival of the snail after transplantation. As transplantations were

carried out under non sterile conditions, rapid shell regeneration served to create a barrier sealing off the snail's internal environment from microbial accumulation in the snail culture environment. Regenerated shell serves to halt osmotic disturbances and leakage of blood from the host's tissues.

Shell regeneration has been studied by many workers for over 50 years. This subject has been approached from many points of view and at a variety of levels; general morphological, histological, physiological, and biochemical. The general status of knowledge concerning

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shell regeneration is reviewed extensively by several authors: Haas (1935), Graham (1957), Manigault (1960), Fretter and Graham (1962). Wilbur (1960), presents an excellent review on molluscan shell structure and the mechanisms, both empirical and theoretical, operative in shell formation. Abolins-Krogis (1958) discusses in detail the chemical composition and formation of crystals in the regenerating shell of the gastropod *Helix pomatia*. These authors have brought together an extensive coverage of the literature pertaining to shell structure and formation.

Other investigators have been primarily concerned with the origin of those substances which unite to form the natural or regenerating shell, with the chemical nature of their crystals, or with the physiological mechanisms which control the process of shell formation. I am primarily interested in:

1. the capacity of a species to regenerate shell;
2. the time necessary for a species to regenerate shell as a characteristic which can be compared with other species;
3. the morphological types of crystals found in regenerating shell;
4. the comparison of the crystal types of one species with those of other species.

The capacity of a species to regenerate shell and the time involved in regeneration pertain directly to experiments such as gonadal transplantation. The comparative aspects are of interest as they may have value in systematics, e.g., species comparisons within a genus or comparison of species of genera within the same family.

The purpose of this paper is to present the following:

1. The orderly stages which occur in the regeneration of shell in *Oncomelania formosana*.
2. The description of the morphology of the crystals which unite to form the regenerated shell in *O. formosana*.
3. The results of an attempt to duplicate the experiments performed on *O. formo-*

*sana* with *Pomatiopsis lapidaria* (Say), a North American species reported to be closely related to *Oncomelania*, a genus occurring in the Far East.

#### MATERIALS AND METHODS

Three month old mature laboratory reared snails measuring 4.0-7.0 mm were used for experiments involving *Oncomelania formosana*. The snails were an F<sub>1</sub> generation of parental stock sent to our laboratories from Taiwan (Formosa).

Culture chambers for maintaining the snails were devised to fit the basic needs of the organism as well as to provide a maximum control on the snail's environment. Petri dishes 9 cm wide and 1.5 cm deep were used. Angel filter paper number 202 was fitted to the bottom of each dish. The filter paper served as a substrate for the snail to feed on. It has been known for some time that species of the genus *Oncomelania* could feed on and digest filter paper (McMullen, 1949). The physiological basis for such digestion in these snails was revealed by Winkler and Wagner (1959).

The filter paper was flooded with about 7 mm of Carriker's Lymnaeid Ringer's Solution (physiological saline) (Carriker, 1946). The solution consisted of the following:

Salt	gm per liter
NaCl	2.0
NaHCO <sub>3</sub>	2.0
KH <sub>2</sub> PO <sub>4</sub>	0.1
MgCl <sub>2</sub>	0.3
CaCl <sub>2</sub>	0.3

This salt solution had a pH of about 7.8. Once the snails were placed in culture the saline was replaced every second or third day. The saline was not sterilized.

The dishes were covered with the normal Petri dish top as these fitted loosely enough to permit adequate gaseous exchange. *O. formosana*, as an amphibious snail, can derive oxygen from the atmosphere or from water. The cultures were maintained at a temperature of 23° C + 1° C.

In the present study the shell was opened in the same manner and placed as in the

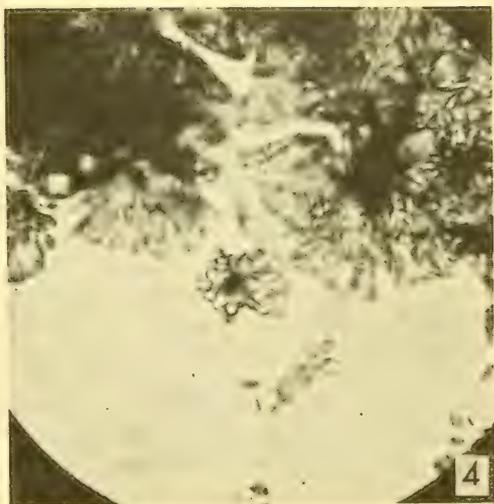
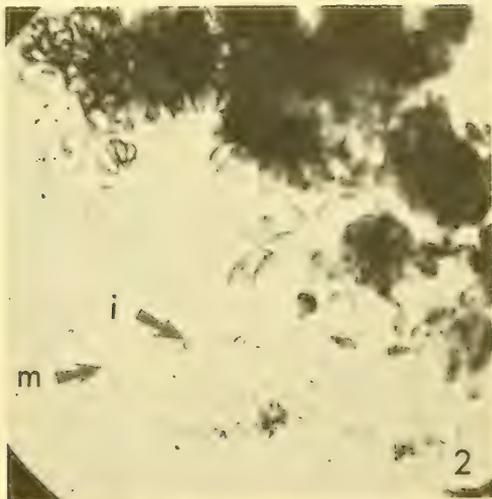
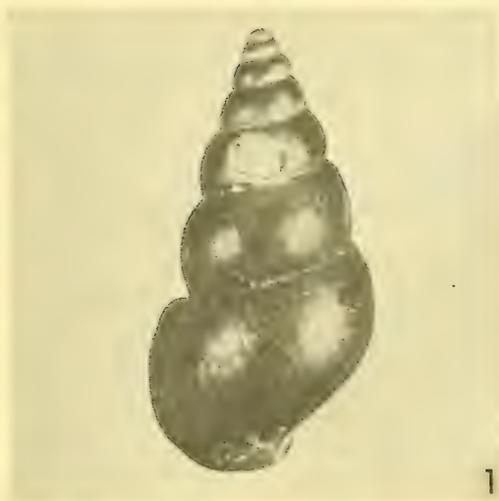


FIG. 1. Shell of *O. formosana* (6 mm long) showing the position of the drilled hole and the calcified membrane filling it.

FIG. 2. Primary membrane (m) supporting initial granular deposits (i), radial configuration of tear-shaped crystals (center), and spherulites (background). Each tear-shaped crystal is about 14-15  $\mu$  long.

FIG. 3. Membrane-supported granules, tear-shaped crystals (about 12  $\mu$  long), and granules having elongated in opposite directions. In the lower left, a scale-like crystal.

FIG. 4. The development of a radial arrangement of tear-shaped crystals often produces an erect, radially symmetrical spherulite, such as shown in center (diameter 39  $\mu$ ). In the background are several interlocking spherulites.

earlier gonadal transplantations. It was drilled in the third whorl from the aperture, a position corresponding to an area over the digestive gland, near the stomach, and close to the snail's gonad (Figs. 1 and 5). This area was above those influenced directly by the glandular mantle edge. The perforation was made with a small electric hand drill, with a minute number 700 dental burr. The shell was opened while being observed with a dissecting microscope and while the snail was pressed down firmly on a molded wax surface with a finger nail. The disturbed area averaged 0.4 mm<sup>2</sup>. Immediately after drilling, the snail was submerged in physiological saline and the drilled area was washed with a stream of water from a mouth pipette until the area was cleared of shell debris.

Usually some shell material slipped inside the hole into the space between the snail's body and the shell. When gently tapping the soft part of the body with a minute, fire-polished, glass tamp, the shell chips could be washed out of the hole.

Frequently the snail's epithelium would be scraped or broken in one of the procedures but the data showed no correlation between such damage and mortality.

The specimens of *Pomatiopsis lapidaria* used were mature adults collected from the banks of Fleming Creek, Ann Arbor, Michigan. The population was heavily infected with *Cercaria marilli*. Drilling the snail clearly exposed the infected condition as this parasite develops under the epithelium in the area drilled. Only non-parasitized drilled snails were used. Controls were chosen without regard to the parasitized condition as attempts at shedding the parasite did not adequately reveal the true percentage of infected snails.

#### EXPERIMENTS

In initial experiments it was noted that soon after the shell of *O. formosana* was drilled a membrane formed across the inside of the hole and that this membrane soon became calcified. Systematic observations were then begun so as to follow the sequence of events more closely, i.e. to determine the times needed for completion of membrane and of calcifi-

cation, and to study the process of crystal formation. Experiments were also conducted to determine whether, and to what extent, the shell of this species would regenerate in an ion free environment, and also whether, under similar conditions, *Pomatiopsis* would similarly regenerate its shell.

1. Observations on membrane formation and calcification in *O. formosana* under maintenance conditions.

A total of over 170 snails (in 3 groups) were drilled and placed in culture. Observations on duration and completion of the regeneration processes were carried on for 30 days on 1 group of 100 snails and another of 20 snails. From the third group of over 50 snails, membranes with their developing crystal systems were removed from time to time, mounted on glass slides under glycerine jelly, and studied under the light and phase (dark field) contrast microscopes.

The second day after drilling, a fine membrane was noted forming on the inside edge of the hole. In the majority of cases this membrane developed equally from the circumference inwards; in a few, it started developing from a given arc of the hole and "grew" across it as a sheet. In either case the speed of membrane formation was about the same, the membrane becoming completed in 60% of the snails after 4 days, in 80% after 6 days, and in 90% after 22 days. In the smaller group of 20 snails, the process was analogous, but a little faster, the membrane becoming completed in 50% of the snails after 4 days, in 90% after 6 days, and in 100% after 13 days.

The membrane attached to the inside shell surface. When the body of the snail pressed continuously against the hole, the membrane formed across the hole or up inside the hole (Fig. 6A) thereby sealing off the internal environment. If the hole was drilled in a position where the body did not normally press against the hole, the membrane attached at the point where the body did make contact with the shell, often at a distance of 1/2 mm from the edge of the hole. In this latter case the membrane was not limited to the area of shell immediately around the hole but

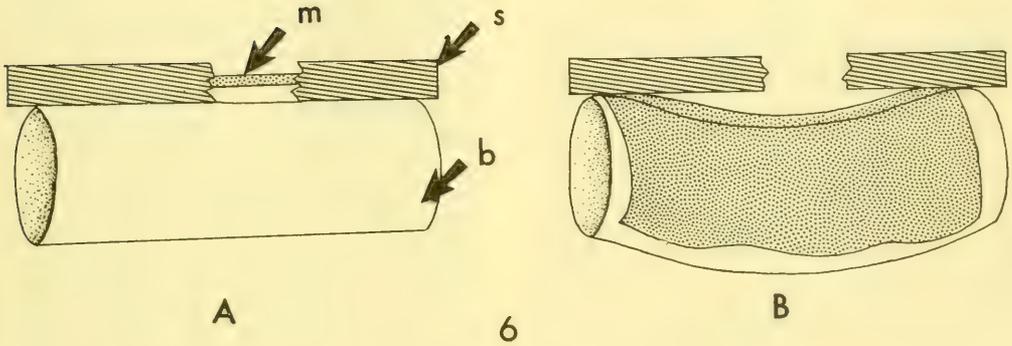
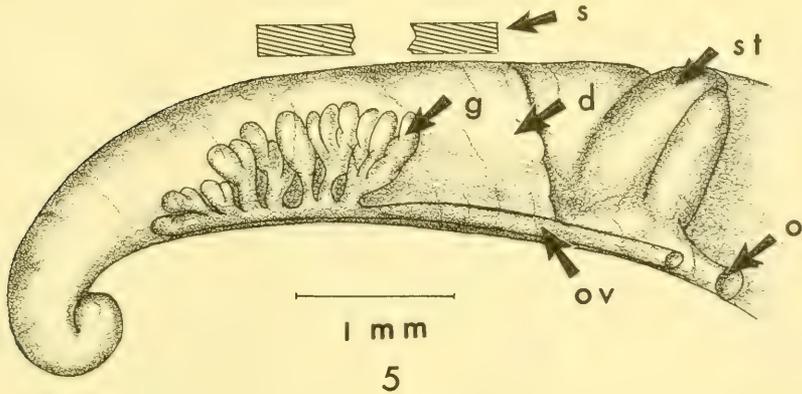


FIG. 5. Uncoiled apical whorls of *O. formosana* showing columellar side of body. The damaged shell is shown in relationship to the underlying anatomical areas; d, digestive gland; g, female gonad; o, oesophagus; ov, oviduct; s, shell; st, stomach.

FIG. 6. Schematic drawing representing the relationship of the body tube (b) to the drilled shell (s) and regenerating membrane (m). A. When body tube presses rather continuously against hole, the membrane forms up inside the hole or across the hole at the inside shell surface. B. When position of hole is such that body tube does not press against hole, the membrane attaches at contact points between shell and body tube. It does not close the hole but encircles the body tube, laying the foundation for a new tubular section of shell inside the old shell.

encircled the body, leaving uncovered only that part where the inside coil of the body pressed against the columella (Fig. 6B); and, as shell formed along the exterior contours of the membrane, a new tubular section of shell was formed inside the old shell.

Under a magnification of X1500 the membrane appeared proteinaceous, acel-

lular, and structureless. It was about 5-6  $\mu$  thick, as determined by focusing first on one membrane surface, then on the other. The membrane appeared to be covered by regularly positioned minute spots. When the membranes were studied under phase contrast, certain areas of spots appeared to be milky white, with the same light diffractive characteristics

as were found in crystalline deposits on the outer surface of the membrane. The spots measured, as closely as could be approximated with a standard ocular micrometer, about 0.25-0.30  $\mu$  in diameter.

The rate at which the membranes became calcified varied greatly from individual to individual. In one case, one day after drilling, the membrane was 75% completed and covered with minute calcareous granules. In another case granules were noted after 2 days, when the membrane was almost 1/2 completed.

Granular deposits were most frequently noted to appear when the membrane was 90% completed or more. Granules were usually scattered over the membrane. They increased in number, "grew" larger in size, formed crystalline patterns, merged with other crystals, and finally formed a calcareous sheet of interlocking polygonal units on the membrane. The primary membrane-shell complex was 100% completed in 10% of the snails 5 days after drilling, but in no more than 50% of the snails 28 days after drilling. At that time, an additional 15% of the snails were 90% calcified or more, while 35% were 50% calcified or less.

In *O. formosana* 2 morphological types of crystals were observed developing on the membranes.

Type 1. The minute granular deposits on the exterior surface of the membrane (Fig. 2) often elongated along one axis into a tear-shaped structure which "grew" into a unit 16-20  $\mu$  long (Figs. 2, 3). Several of these units commonly developed on a radial pattern around a central space or central point (Figs. 2, 3). The initial deposits also commonly elongated in opposite directions forming 2 tear-shaped or club-like units from one "growing" granule (Figs. 3, 8). When these units developed beyond 15-16  $\mu$  they branched (Figs. 3, 7, 9). As material was added to the branches, the initial rather smooth crystal acquired a rough texture (Figs. 3, 9). Each major branch developed numerous, rough, needle-like

projections and the individual branches lost their identity (Figs. 3, 9). The crystal of 20-25  $\mu$  diameter developed a circular construction forming a spherulite (Fig. 10). Many "growing" spherulites began to interlock with each other, thus forming the primary membrane-shell complex (Figs. 2, 4, 10).

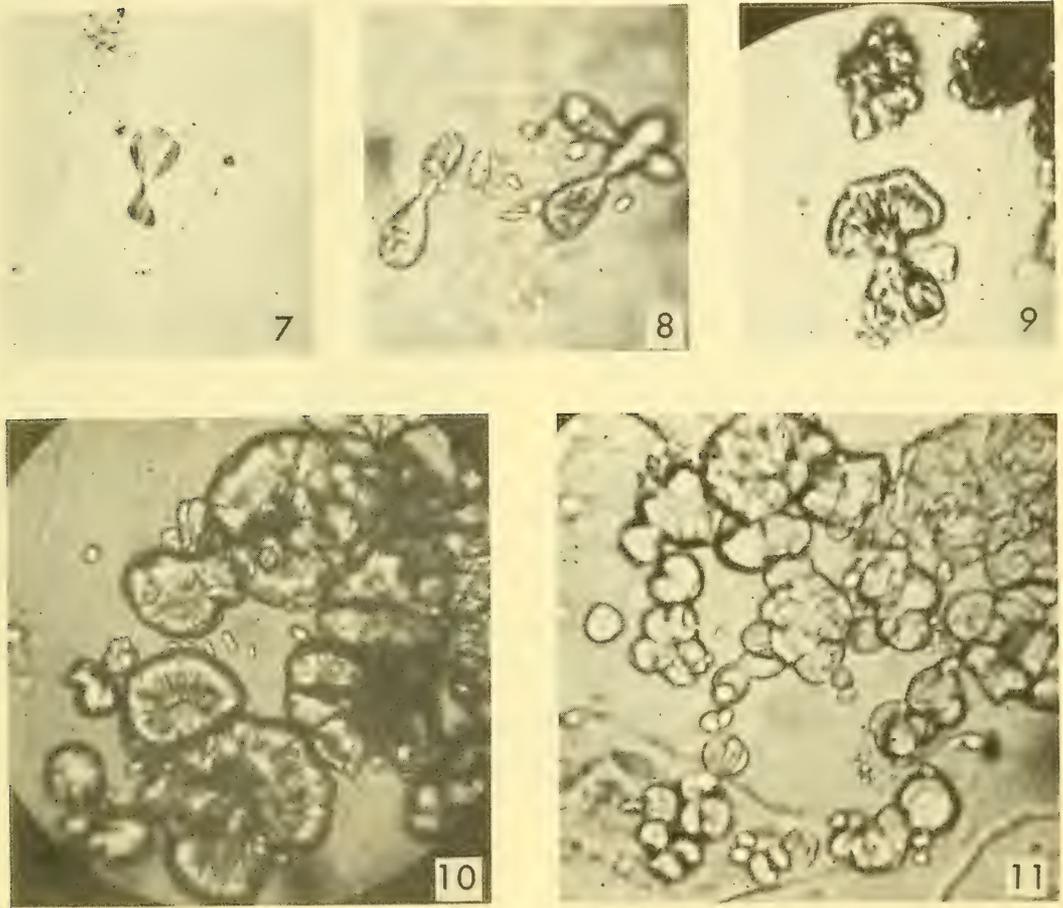
Generally, when the tear-shaped crystals developed in opposite directions from the initial granular deposit, the spherulite developed in a plane parallel to the membrane (Figs. 3, 8). Where the tear-shaped crystal developed with a radial configuration, quite often the spherulite would develop vertically giving rise to an erect spherulite with radially symmetrical branching (Fig. 4).

The fusion of spherulites which developed from tear-shaped structures gave rise to a shell of polygonal units, each unit being rather rough and coarse. The general effect was a rough, pebbly-textured shell.

Type 2. The second type of crystal also developed from minute granular deposits but here the developing crystals were thin, flattened, and scale-like (Fig. 11). Quite often these crystals developed lobes (Fig. 12). Additional growth to the crystals occurred by regular concentric addition of material (Figs. 12, 14). Many scale-like crystals "grew" and coalesced, forming a shell made up of smooth polygonal units (Fig. 11).

The 2 crystalline systems were often concentrated on the same membrane, in which case the primary membrane-shell complex would possess both smooth and rough areas.

Upon completion, or near completion, of the primary membrane-shell complex, other membranes were deposited below it. These secondary membranes seemed to become calcified in 2 ways: 1) by supporting the growth of scale-like crystals above the membrane surface, i.e. towards the exterior and 2) by actual calcification within the membrane. In several cases examined, the secondary system had formed a shell as thick as the original within about 14 days after



- FIG. 7. Initial branching of a tear-shaped crystal (total length- $40\ \mu$ ). Note membrane to the left.
- FIG. 8. Several initial granules, elongated in opposite directions, forming tear-shaped crystals developing parallel to the plane of the membrane (length of longest about  $40\ \mu$ ).
- FIG. 9. Upper crystal (greatest width  $40\ \mu$ ) shows multiple branches. Lower crystal (total length  $66\ \mu$ ) shows branches occluded by the concentric addition of salts and beginning development of a radial configuration.
- FIG. 10. Many spherulites interlock to form the primary regenerated shell of rough polygonal units (diameter of largest spherulites  $50-60\ \mu$ ).
- FIG. 11. Scale-like crystals interlock, forming a primary regenerated shell of smooth polygonal units (smaller crystals  $13-16\ \mu$  diameter).

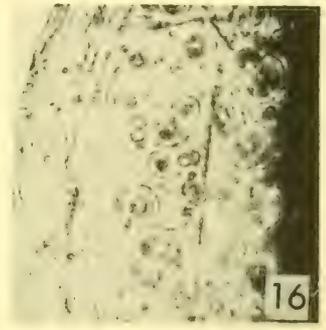
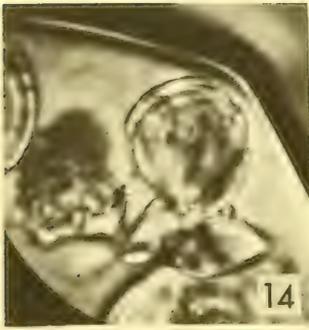
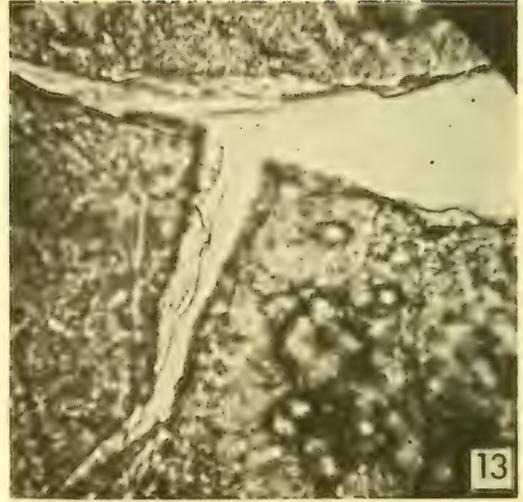
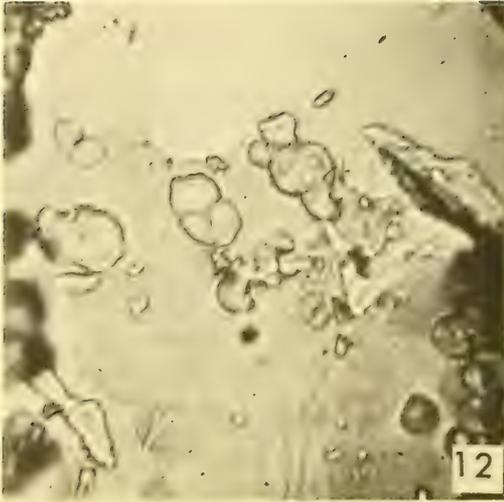


FIG. 12. The scale-like crystals often appear lobed.

FIG. 13. Oblique break in a regenerated shell, revealing some calcified secondary membranes.

FIG. 14. Scale-like crystal showing new concentric "growth".

FIG. 15. Section through the digestive gland showing some of its lobules (ld), connective tissue strands, and the cuboidal nature of the mantle cells (mc).

FIG. 16. Scale-like crystals of the regenerating shell of *Pedalion* where the calcium content of the culture medium was reduced to 50% (Bevelander and Benzer, 1948).

completion of the primary complex.

In Fig. 13 is shown a regenerating shell which was removed from the snail 14 days after the shell was drilled. This regenerated shell was cracked under a coverslip and one oblique break revealed several of the leaf-like calcified layers of the secondary membrane system. This

system would often develop when the primary system was only 90% or more calcified.

## 2. Study on shell regeneration of *O. formosana* in an ion free environment.

Forty snails were selected at random from 100 mature adults. Each was drilled

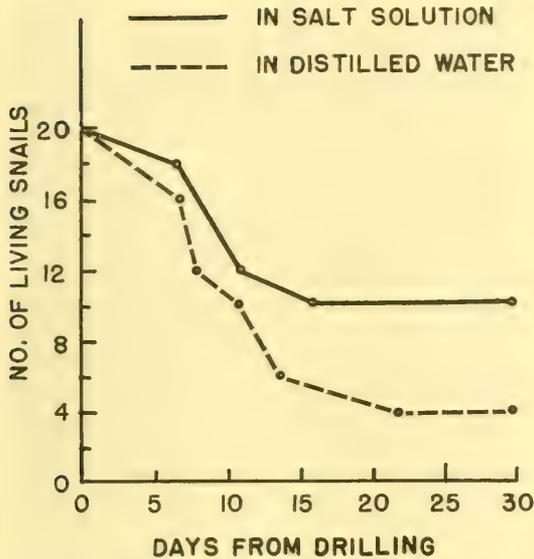


FIG. 17. Mortality rates of undrilled (control) *Oncomelania formosana* maintained in physiological saline and distilled water (Experiment 2).

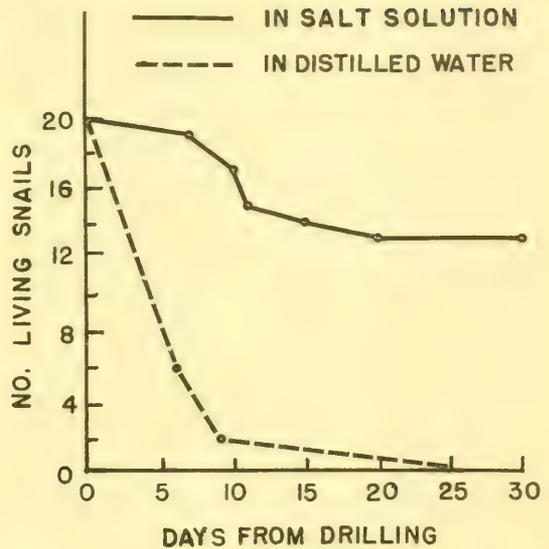


FIG. 18. Mortality rates of drilled *Oncomelania formosana* maintained in physiological saline and distilled water (Experiment 2).

and placed in a separate container: 20 were provided with distilled water and 20 with physiological saline. Another 40 undrilled controls were distributed in a like manner. These snails were observed for 30 days.

As was expected, the distilled water had an adverse effect on the snails with as much as 80% of the control snails dying in a period of a month, while 100% of the drilled snails had died in 25 days (compare Figs. 17, 18). Of the drilled snails, about 5% succeeded in regenerating shells only to subsequently die in the ion free environment. The overall process of regenerating shell in an ion free environment paralleled the processes described above.

Consideration of the data plotted for this experiment (Figs. 17 and 18) reveals that there is little difference in the survival rates of snails maintained in physiological saline, whether drilled or undrilled. The same trend is apparent in Fig. 19, showing the mortality of another series of *O. formosana* (20 drilled, 20 controls) in physiological saline. The level of mortality, however, was not the same in

the 2 experimental groups, which may possibly be due to physiological differences, such as their state of fitness.

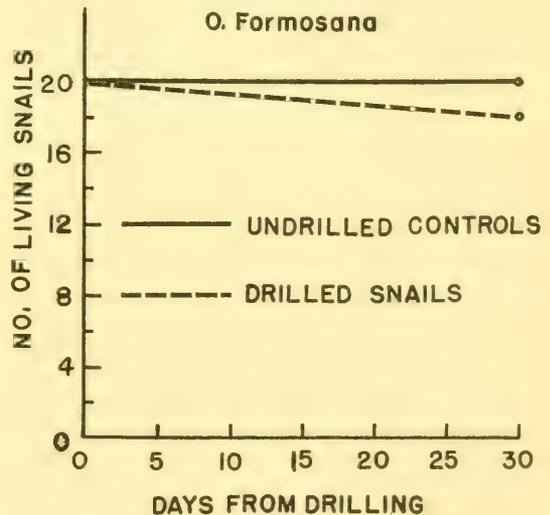


FIG. 19. Mortality rates of drilled and undrilled *Oncomelania formosana* maintained in physiological saline concurrently with the experiment using *Pomatiopsis lapidaria* (Experiment 3).

TABLE 1. Mortality among drilled *Pomatiopsis lapidaria* and their controls (20 each)

Days after drilling	Number of snails dead	
	drilled	controls
1	0	0
2	0	0
3	6	0
4	8	1
5	3	0
6	2	0
7	1	2
8		1
9		4
10		0
11		4
20		0
22		4
30		0
total	20	13

### 3. Study on shell regeneration in *Pomatiopsis lapidaria*.

Forty snails, 20 drilled and 20 controls, were placed in culture under conditions corresponding entirely to those in which 40 *O. formosana* were maintained (see Fig. 19) and observed for one month.

As shown in Table I, all drilled snails died within the first week while in that period only 3 controls had died. At the end of a month's observation period 7 controls remained alive. None of the drilled snails deposited a primary membrane. In 80% of the drilled snails a mucoïd mass appeared at the edge of the drilled hole 1 to 2 days after drilling, before the snail had died. Upon microscopic inspection this mass proved to be composed of swarms of rod-shaped bacteria.

### DISCUSSION

In discussing the results presented in this paper, 2 statements made by Fretter and Graham (1962) are well kept in mind:

- 1) As yet "no clear account can be given of the way in which the whole shell is produced in the case of any mollusc",
- 2) "the secretion of the calcareous layers of the molluscan shell is still, frankly, improperly understood. . .".

Though a great deal of work has been done in studying the formation of shell, the vast majority of it has been done with species of the terrestrial gastropod genus *Helix* and with various pelecypods, notably the oyster. Moreover, most of the work has concentrated on the growth and deposition of shell where it naturally occurs, at the edge of the mantle.

The regenerative process studied here took place in the apical areas of the shell. In this area the mantle is reduced to a single layer of cuboidal cells (Fig. 15). The core of the body in this area is made up of tubules of the digestive gland and between these and the mantle is a fair amount of blood space traversed by connective tissue strands. The tissues in this area appear devoid of secretory cells or glands which could secrete the elements of the membrane or calcium.

The source and nature of the membrane, the source of calcium, and the manner of deposition of calcium in other molluscs are topics reviewed at length by the authors previously cited. Their view on these subjects are here shortly summarized and discussed, to permit a better understanding of the relationships between the morphological entities described here and the means by which they might possibly have arisen.

#### 1. The membrane

It is generally agreed that a membrane is necessary for supplying a substratum which will support crystalline growth (Fretter and Graham, 1962; Abolins-Krogis, 1958; Wilbur, 1960). Bevelander and Benzer (1948) state "there are two distinct processes which occur: (1) the elaboration of a fibrous organic membrane, and (2) the concentration and deposition of mineral salts." When it is a matter of repairing a break in the shell in apical areas where the mantle's edge

cannot make contact, the first membrane which seals the shell, the organic matrix previous to calcification, is made of a substance called calcaffine. Fretter and Graham (1962) state that calcaffine cannot be considered homologous to conchiolin, the organic substance of the matrix formed from mantle-edge secretions, which is the precursor to the addition of new shell in a growing mollusc. In their view there is little evidence that areas over the visceral mass have the potential for secreting conchiolin. Biederman (1902) thought that, in *Helix pomatia*, only the epithelium of the mantle edge could produce normal shell and that the epithelium of the mantle in other areas could only produce thinner shell in irregular layers. Abolins-Krogis (1958) refutes this notion, stating that the mantle secretion is liberated in the space between the shell and mantle as pallial fluid, which can be transported to all inner areas of the shell including damaged areas.

Fretter and Graham (1962) state that the calcaffine may be derived from a film of protein on the surface of the extra-pallial fluid. Wagge (1951) found that in *Helix aspersa* the calcaffine or substance of the membrane was transported by waves of amoebocytes to the area of damage. In general, the question as to the origin of the membrane in *O. formosana* and other gastropods is open to a great deal of further investigation.

Grégoire et al. (1955) present electron micrographs which depict the microstructure of the conchiolin sheet of *Astrea olivacea* (Gastropoda) and show a series of regularly arranged pores. The nature of the minute spots on the membrane in *O. formosana* and the apparent secretion of calcareous material through the membrane equally suggest that the membrane in *O. formosana* is porous.

## 2. The source of calcium

Had the liquid medium in the experiment or shell regeneration in an ion-free environment been an isotonic, calcium deficient, salt solution instead of distilled water, the mortality of the snails would

probably have been considerably less. Some of the snails did regenerate shell in such an ion-free environment, showing that the calcium for regeneration of shell is provided from within that mollusk either from stored calcium granules, from re-absorbed shell, or from food (the calcium content of the filter paper is unknown). Bevelander and Benzer (1948) modified the calcium content of the medium in which young specimens of *Pedalion* (Pelecypoda) were maintained. They demonstrated that, in an external environment of only 1/8 the normal calcium content, the organic matrix (membrane) did not become calcified. Apparently the calcium content of the external environment is an important factor in the formation of shell in some, if not all, marine pelecypods.

Wilbur's excellent review on the mineralization in mollusks should be consulted for a detailed survey on the findings to date, dealing with the calcification of the organic matrix. Fretter and Graham (1962) conclude after a survey of the literature, that calcium is brought into the extra-pallial fluid in solution or by amoebocytes from stores of calcium in the connective tissue or other areas of storage. Wagge (1951) reported that calcium from stores in the digestive gland of *Helix aspersa* is transferred to the extra-pallial fluid by amoebocytes. Wilbur (1960) stated that in marine pelecypods the major process involves the "movement of calcium in the dissolved form from the mantle cells"; the calcium subsequently crystallizes on the matrix from solution. The final deposition of the salts is thought to be an extra-cellular, physico-chemical process.

## 3. The growth of crystals

Wilbur (1960) stated that the "mineralization of shell occurs by the growth of individual crystals of calcium carbonate on or in the conchiolin matrix . . .". Abolins-Krogis (1958) showed that in *Helix pomatia* organic crystals are first formed on the matrix and that these enlarge to form the framework supporting the orderly deposition of calcium salts. Bevelander

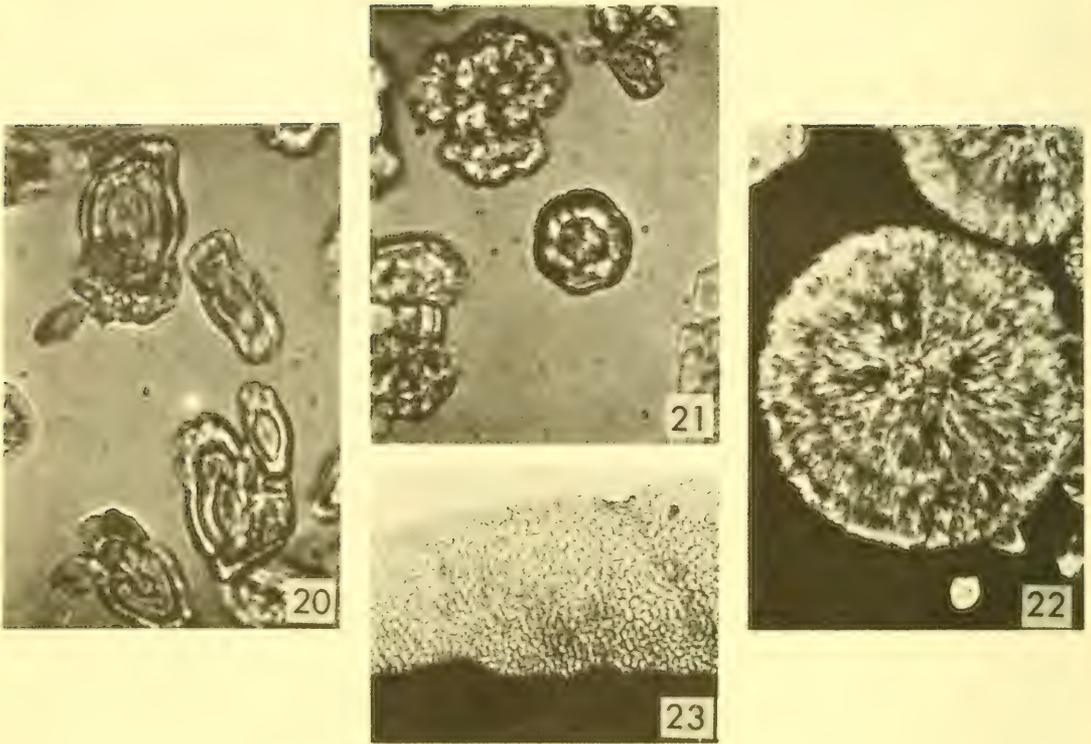


FIG. 20. Boat-shaped crystals (the largest 25-27  $\mu$  long) of the regenerating shell of *Helix pomatia* (Abolins-Krogis, 1958).

FIG. 21. Round-shaped disc (about 17.5  $\mu$  diameter) from the regenerating shell of *Helix pomatia* (Abolins-Krogis, 1958).

FIG. 22. Typical spherulite from the regenerating shell of *Helix pomatia* (diameter about 55  $\mu$ ) (Abolins-Krogis, 1948).

FIG. 23. Normal regenerated shell of *Pedalion* maintained in artificial sea water (Bevelander and Benzer, 1948).

and Benzer (1948) as did Biedermann (1902) state the the initial phases of crystal formation are formed by calcium phosphate which is later replaced by calcium carbonate.

The crystals shown by Bevelander and Benzer (1948) for some marine bivalves are not as complex as those forming the spherulites in this paper. The crystals regenerated by *Pedalion* in sea water containing 50% normal calcium appeared very similar to the scale-like crystals of this investigation (Fig. 16).

Abolins-Krogis (1958) described in

detail 3 types of developing crystal systems in *H. pomatia*: 1) elongate boat-like discs (Fig. 20). 2) discs with concentric rings (Fig. 21). 3) spherulites (Fig. 22).

1. The boat-like crystals probably originated from 2 initial granules which secondarily became enclosed in "a common elliptical sheet of calcifying substance".

2. The discs became multilobular and finally transformed into "regular clusters of radially outgrowing needles."

3. The spherulite developed from

broad elongate corpuscles to the sides of which additional material was deposited and from this developed a regular spherulite with its concentrically disposed cluster of needle-like crystals.

All crystalline types described by Abolins-Krogis (1958) finally produced "more or less regular needle clusters which in turn" yielded "the definitive polygonal crystals of calcium carbonate".

The crystals described in this paper were not of the same morphological type as those described by Abolins-Krogis (1958) for *H. pomatia*, though the description of the initial granules seemed to apply to the initial granules described here. The scale-like crystals in this paper did not form spherulites, but coalesced to form a smoothish shell somewhat of the type depicted by Bevelander and Benzer (1948) for *Pedalion* (Fig. 23).

The tear-shaped crystals did form spherulites and developed "needle-clusters" at the periphery of the concentrically growing crystals. These spherulites differed from those described from *H. pomatia* by: 1) their mode of development; 2) the dendritic pattern and "needles", which were more irregular and coarse.

4. The time required for regeneration of the shell

Biedermann (1902) stated that, upon removal of a piece of shell from *Helix pomatia*, the wound closed within 1-2 hours with a membrane supporting calcareous corpuscles. Abolins-Krogis (1958) reported that 1-2 hours after damaging the shell in *H. pomatia* the area was covered with a thin organic sheet. Within 24 hours the membrane was so far calcified that the crystals often lay 2 or 3 layers deep.

The rate of regeneration in *H. pomatia* is quite rapid compared with that in *Oncomelania formosana*. Perhaps the rapid response of *H. pomatia* reflects an adaptation to the terrestrial environment where the problem of desiccation is a pressing one, especially when a shell is broken. *O. formosana* is amphibious and lives in very moist areas and often stays

in the water for prolonged periods of time.

It would be interesting to know the relationships between rates of regeneration and types of crystals formed in different species of the same genus or species of different genera of gastropod within the same family. A point in case is the attempted comparison between *O. formosana* and *Pomatiopsis lapidaria*. While *O. formosana* produced a shell, *P. lapidaria* rapidly died without a sign of shell regeneration. This is particularly interesting because *P. lapidaria* has been considered very closely related to the genus *Oncomelania* (Abbott, 1948; van der Schalie, et al., 1962) or even perhaps congeneric (Burch, 1960).

The response of these 2 species to the parallel experiments discussed may reflect only species specific responses to the induced trauma. An adjustment of the culture medium might be sufficient to enable *P. lapidaria* to survive and regenerate a shell. Even if this were the case the experiment has pointed out a marked difference in physiology between 2 supposedly "closely" related species. More experiments with *P. lapidaria* are needed before further comment can be made.

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## ZUSAMMENFASSUNG

REGENERIERUNG DER SCHALE BEI *ONCOMELANIA FORMOSANA*  
(GASTROPODA: HYDROBIIDAE)

Im Anschluss an Gonadentransplantationen bei *Oncomelania formosana* (Pilsbry und Hirase), einer aus Taiwan (Formosa) stammenden amphibischen prosobranchen Schnecke, wurden Untersuchungen über die Regenerierung der Schale bei dieser Art angestellt. Die Schale wurde im dritten, von der Mündung gerechneten Umgang angebohrt. Im Labor gezüchtete, angebohrte Schnecken wurden einzeln in zugedeckten Petri Schälchen gehalten und einen Monat lang beobachtet. Der Boden der Schälchen war mit Filterpapier ausgelegt, das als Nahrung diente, und stand 7 mm tief unter lymnaeider Ringer Lösung. Die Temperatur lag bei  $23^{\circ}\text{C} \pm 1^{\circ}$ . Am zweiten Tag nach dem Anbohren begann die Bildung einer Membran am Innenrand des Loches, die sodann darüber "wachs". Sie war bei 50% der Schnecken nach 4 Tagen, bei 90% der Schnecken nach 6 Tagen und bei 100% der Schnecken nach 13 Tagen vollständig zugewachsen. Diese Membran war proteinös und ohne erkennbare Struktur.

Noch vor völliger Vollendung der Membran erschienen an ihrer äusseren Oberfläche Körnchen, die sich dann zu 2 Kristalltypen ausbildeten: 1) zu schuppenförmigen Kristallen die sich vergrösserten und zu einer glatten Schale aus polygonalen Elementen verschmolzen und 2) zu tropfenförmigen Kristallen, die sich verzweigten und Sphaerulite bildeten, die ihrerseits zu einer rauhen, ebenfalls aus polygonalen Elementen zusammengesetzten Schale verwachsen. Häufig befanden sich beide Kristallformen an derselben Membran.

Die Membran war vollständig verkalkt: bei 10% der Schnecken 5 Tage nach Anbohrung; bei 50% der Schnecken 28 Tage nachher. Zu diesem Zeitpunkt waren weitere 15% der Schnecken zu 90% oder mehr verkalkt und die übrigen 35% zu 50% oder weniger.

Noch vor Vollendung des primären Membran-Schale Komplexes werden weitere

Membranen unterhalb der Ersten angelegt. Diese verkalken auf doppelte Weise: 1) indem sie als Träger für auflagernde Kristallisation dienen und 2) indem sie selbst verkalken.

Unter den gleichen Bedingungen zeigte *Pomatiopsis lapidaria*, eine verwandte amerikanische Art, eine hohe Sterblichkeit ohne Regenerierung der Schale. Weitere Versuche mit dieser Art sind wünschenswert.

#### RÉSUMÉ

#### RÉGÉNÉRATION DE LA COQUILLE CHEZ *ONCOMELANIA FORMOSANA* (GASTROPODA: HYDROBIIDAE)

À la suite d'une série de transplantations microchirurgicales chez *Oncomelania formosana* (Pilsbry et Hirase), Gastéropode Prosobranchie amphibien provenant de Taiwan (Formose), une étude a été faite de la régénération de la coquille chez cette espèce. Utilisant des spécimens de culture, la coquille fut perforée au troisième tour de spire partant de l'ouverture. Les individus perforés furent maintenus séparément dans des boîtes de Petri couvertes et furent observés pendant un mois. Le fond des cuvettes était recouvert de papier-filtre, qui servait de nourriture, et se trouvait sous 7 mm de solution de Ringer pour lymnéides. La température était maintenue à 23° C ± 1°. Le second jour après perforation, une membrane commença à se former au bord intérieur du trou et à "croître" au travers de celui-ci, se complétant chez 50% des mollusques en 4 jours, chez 90% en 6 jours et chez 100% en 13 jours. Cette membrane était protéinique, acellulaire et sans structure.

Avant la clôture parfaite du trou, des granules se montrèrent sur la face extérieure de la membrane. Ceux-ci évoluèrent en cristaux de 2 types: 1°) cristaux en écaille, dont la croissance et la coalescence formèrent une coquille lisse à éléments polygonaux et 2°) cristaux en forme de goutte, qui se ramifiaient et formaient des sphérulites qui, à leur tour, par fusion, formèrent une coquille rugueuse, à éléments polygonaux. Fréquemment les 2 types de cristaux se trouvaient sur la même membrane.

La membrane se trouvait calcifiée, chez 10% des mollusques 5 jours après perforation et chez 50% des mollusques après 28 jours. A ce moment, 15% des mollusques étaient déjà calcifiées à 90% ou plus, et les 35% restants à 50% ou moins.

Un peu avant l'achèvement du complexe primaire membrane-coquille, des membranes supplémentaires firent apparition au dessous de la première. Celles-ci se calcifièrent par 2 moyens; 1°) en réalisant une croissance cristalline au dessus de leur surface et 2°) en se calcifiant elles-mêmes.

Dans les mêmes conditions, *Pomatiopsis lapidaria*, un mollusque américain apparenté montra une haute mortalité, sans régénération de la coquille. Des essais complémentaires avec cette espèce seraient désirables.



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KEPPEL HARCOURT BARNARD

It is with deep regret that we announce the death of one of MALACOLOGIA'S editors, Dr. Keppel Harcourt Barnard. He worked at the South African Museum since 1911 and was the Director from 1946 until his retirement in 1956. He was actively engaged in malacological activities up to the time of his death on September 22, 1964.

## ABSTRACTS

Providing abstracts in 5 languages has proved onerous and has caused considerable delays. To speed up publication, MALACOLOGIA will, for the time being, restrict preparation of abstracts to 3 languages: one Germanic (English), one Romance (Spanish) and one Slavic (Russian). Abstracts in German and French will be discontinued unless supplied by the authors, except for those already at hand. Moreover, the Russian abstracts will be published after completion of the volume, together with the Index.

## ZUSAMMENFASSUNGEN

Die Vorbereitung von Zusammenfassungen in 5 Sprachen hat bisher beträchtliche Verzögerungen verursacht. Um diese weitgehend zu vermeiden wird MALACOLOGIA die Abfassung der Auszüge vorderhand auf 3 Sprachen beschränken: eine germanische (englisch), eine romanische (spanisch) und eine slawische (russisch), dagegen deutsche und französische Zusammenfassungen, so weit sie nicht bereits vorliegen, in Hinkunft nur dann einschliessen, wenn sie vom Autor selbst geliefert werden. Auch sollen die russischen Zusammenfassungen erst nach Fertigstellung des Bandes, mit dem Index zusammen, herauskommen.

## AVIS AU SUJET DES RÉSUMÉS

La préparation des résumés en 5 langues s'est avérée onéreuse et a causé des retards considérables. Pour éviter ces délais, MALACOLOGIA restreindra ces abstraits à 3 langues: une germanique (l'anglais), une romane (l'espagnol) et une slave (le russe), et ne publiera dorénavant des abstraits en langue française et allemande que lorsque les auteurs eux-mêmes les fournissent, à l'exception de ceux qui son déjà préparés. En outre, les résumés russes ne seront publiés qu'après l'achèvement du volume ensemble avec l'index.

## RESUMEN

La inclusión de reseñas en 5 idiomas ha resultado muy onerosa y causa de considerables atrasos. Para acelerar la publicación, MALACOLOGIA restringirá la preparación de reseñas a 3 idiomas: uno germánico (Inglés), uno neolatino o románico (Español), y uno eslávico (Ruso). Las reseñas en alemán o francés serán interrumpidas a menos que las provean los mismos autores, (con excepción de aquellos últimos trabajos para los cuales ya han sido preparadas). Asimismo, las reseñas en ruso se publicarán después de haberse completado el volumen, junto con el Índice.

## А Б С Т Р А К Т Ы

Перевод и печатание абстрактов на 5 языках оказалось затруднительным делом, сильно задерживавшим издание. Чтобы ускорить выпуск текущих номеров, Малакология решила ограничить перевод абстрактов тремя языками: одним германским (английским), одним романским (французским) и одним славянским (русским). Абстракты на немецком и французском языках будут печататься только в тех случаях, когда текст их составлен автором. Это не относится, однако, к абстрактам уже полученным редакцией. Кроме того, абстракты на русском языке будут помещаться в конце каждого тома вместе с индексом.

THE SCALLOP SUPERSPECIES *AEQUIPECTEN IRRADIANS* (LAMARCK) 2000

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## ABSTRACT

HARVARD  
UNIVERSITY

Statistical analysis of intra-population morphological variation in the economically important "species" *Aequipecten (Plagioctenium) irradians* has led to the definition of 3 subspecies and one closely related but distinct species within that group. Primary characters used are rib count, width to length ratios, relative inflation, and frequency of white right valves. The 4 taxa recognized are: *A. amplicostatus* (Dall) found from central Texas to Mexico with apparently disjunct populations at Miami, Florida and Cartagena, Colombia; *A. i. concentricus* (Say) occurring from New Jersey to South Carolina and western Florida to eastern Texas; *A. i. irradians* (Lamarck), intergrading with *A. i. concentricus* in the zone of contact and occurring from Massachusetts to New Jersey; and *A. i. sablensis*, ssp. n., an apparently extinct, post-Pleistocene form from Sable Island, Nova Scotia. In the interests of stability the generic name *Aequipecten* is maintained for this group, a neotype of *A. i. concentricus* is designated, and the type locality of *A. i. irradians* is restricted to Falmouth, Massachusetts. Conclusions are presented regarding the phylogeny of the subgenus *Plagioctenium* in North America, the relationship between increased valve compression and increased north latitude in this and other groups, and the adaptive value of white right valves and morphological diversity in terms of apostatic selection.

## INTRODUCTION

Among Western Atlantic marine mollusks, the bay scallop *Aequipecten irradians* (Lamarck) combines the qualities of aesthetic beauty, commercial importance, and biological interest to a degree probably unmatched by any other species. Pectens are famous for their classic design and pleasing colors and *A. irradians*, with its pastel reds, browns, grays and yellows, is no exception. In 1961, 13,479,000 pounds of bay scallops valued at \$1,347,000 were harvested in the United States (Power, 1963). The present paper, however, is concerned with some aspects of the biology of these interesting animals, specifically their intraspecific variation, systematics, and evolution. For other aspects of their biology, *i.e.* anatomy, reproduction, growth and ecology, see Marshall (1960), Sastry (1962, 1963), Turner (1954) and especially Gutsell (1931). The interested reader is also referred to Fleming (1957), Grant and Gale (1931), and Grau (1959) for much additional information on the Family Pectinidae.

The study here reported began in 1962

when, in response to a request for specimens, Mrs. Fred Andrewsckuk of Sable Island, Nova Scotia, kindly sent to the writer a random collection of 91 valves of *A. irradians* from that locality.<sup>1</sup> The anomalous occurrence of this isolated population some 500 miles northeast of all other populations of *A. irradians* was first made known by Willis (1857) and accounts for the northern limit "Nova Scotia" given for this species in the literature. Willis also noted that Sable Island specimens appeared to have a few more ribs than specimens from Massachusetts, but no detailed examination of Sable Island material has been reported by him or by any subsequent author.

Since a large quantity of comparative material is available, the present author has been able to make such an examination. Not surprisingly, it was found that

<sup>1</sup> Sable Island is a low sandy island approximately 20 miles long and one-half mile wide, located in the Atlantic about 100 miles southeast of Canso, Nova Scotia. It is famous as the graveyard of the Atlantic because more than 300 ships have been wrecked on its surrounding shoals. For further information see Erskine (1954) and Patterson (1894).

TABLE 1. Characters differentiating the subspecies of *Aequipecten irradians* according to Abbott, 1954.

Feature	<i>irradians</i> s. s.	<i>concentricus</i>	<i>amplicostatus</i>
number of ribs	17-18	19-21	12-17
shape of ribs	low, roundish	squarish	high squarish to slightly roundish
color of lower valve	slightly lighter than upper	lightest, commonly all white	commonly all white
color of upper valve	drab gray-brown with indistinct, darker-brown markings	dull bluish gray to brown	similar to <i>concentricus</i>
relative inflation	most compressed of the 3 subspecies	—	more gibbose than <i>concentricus</i>

in order to place the population in its proper systematic position a rather extensive reappraisal of the intraspecific variation and systematics of the whole *irradians* complex was necessary. The results of that reappraisal, previously reported only in abstract (Clarke, 1964), are given in detail below.

#### TAXONOMIC CHARACTERS

The *Aequipecten irradians* superspecies is here considered as including all populations identified by recent authors as *Aequipecten irradians* (*sensu lato*). The basis for regarding the group as a superspecies is discussed in subsequent sections of this paper. As a preliminary to a discussion of the subdivisions within this complex and their systematic relationships, it is necessary to review briefly the previously accepted divisions and the criteria by which they were determined. It is also useful to discuss the taxonomic characters used in the present study and aspects of their variation.

According to Abbott (1954) who has differentiated taxa within the *irradians* group more clearly than any previous author (for instance Dall, 1925), *Aequipecten irradians* may be divided into 3 subspecies: *A. irradians*

s. s., *A. i. concentricus* (Say), and *A. i. amplicostatus* (Dall). The nominate subspecies is recorded as ranging from Nova Scotia to Long Island, New York; *A. concentricus* from New Jersey to Georgia and from Tampa, Florida to Louisiana; and *A. amplicostatus* from Central Texas to Mexico and Colombia. The differences between these forms which he observed are given in Table 1.

The large population sample from Sable Island which was available appeared to be different in several respects from other populations samples of *A. irradians*. Accordingly, a large number of samples from the collections of the National Museum of Canada (NMC), the Academy of Natural Sciences of Philadelphia (ANSP), the Museum of Comparative Zoology at Harvard College (MCZ), and the United States National Museum (USNM), were brought together for statistical analysis. An effort was made to secure as many large, unbiased collections from the entire range of the *irradians* complex as possible. As is often the case with larger species, population samples of 15-30 or more specimens are not common in collections and some populations were represented only by samples containing less than 5 specimens.

No specimens were available from the

TABLE 2. *Aequipecten* population samples analyzed statistically

Population	Locality*	No. of valves		Source
		L.	R.	
A	Sable I., Nova Scotia	17	74	NMC
B	Brewster, Massachusetts	3	5	ANSP
C	Hyannis, Massachusetts	18	22	NMC, ANSP
D	Falmouth, Massachusetts	26	27	NMC
E	Greenwich Bay, Rhode Island	16	16	ANSP
F	"New Jersey Coast"	6	7	USNM
G	Atlantic City, New Jersey	4	4	ANSP
H	Sinepuxent Bay, Maryland	3	3	MCZ
I	Hog I., Virginia	27	30	USNM
J	Beaufort, N. Carolina	8	12	ANSP
K	Swansboro, N. Carolina	4	2	MCZ
L	Off Bear's Cut, Miami, Florida	0	2	USNM
M	Sanibel I., Florida	11	11	ANSP
N	Boca Grande, Florida	14	17	ANSP
O	Cedar Keys, Florida	9	9	ANSP
P	Crooked I., Florida	25	22	ANSP
Q	Fort Morgan, Alabama	0	5	USNM
R	Chandeleur Is., Louisiana	4	1	USNM
S	Matagorda, Texas	1	3	USNM
T	Port Aransas, Texas	18	9	ANSP
U	Port Isabel, Texas	10	12	ANSP, USNM
V	Tampico, Mexico	1	5	MCZ
W	Cartagena, Colombia	0	1	USNM

\*Compare with Fig. 5.

L. = left  
R. = right

NMC = National Museum of Canada  
ANSP = Academy of Natural Sciences,  
Philadelphia  
USNM = U. S. National Museum, Wash., D. C.  
MCZ = Museum of Comparative Zoology,  
Harvard

region between Cape Rojo, Mexico and Cartagena, Colombia or, except for one small lot labelled "South Carolina", from between Swansboro, North Carolina and Miami, Florida. The former apparent gap in distribution may be real or may represent lack of collecting, but the latter gap probably represents a real absence or at least an extreme scarcity of *A. irradians* in that region. This is substantiated by Power (1963) who, in a complete summary of United States fisheries statistics for 1961, reports substantial landings of bay scallops for all coastal states from Massachusetts to Texas

with the exception of South Carolina, Georgia, and eastern Florida, where no landings are reported. The calico scallop, *Aequipecten gibbus* (Linnaeus), is the only commercial scallop reported from that area. In addition, a good collection of all available scallops accumulated over a period of several months at Sapelo Island, Georgia, by Dr. Dirk Frankenberg, failed to contain any *A. irradians*. Some of the Georgia sounds, for example, appear to be hydrographically suitable for *A. irradians*, (Marshall 1960), and its absence from this extensive region remains enigmatic.

The 23 population samples which were treated statistically are listed in Table 2 (compare with Fig. 5). In this and in subsequent tables and charts the samples are arranged in sequence beginning with Sable Island in the north and continuing south to eastern Florida, then north and west along the Gulf of Mexico coast, and south to Colombia. Many other lots of small size from intermediate localities were also studied but not analyzed statistically.

At this point a note on valve orientation is necessary. The byssus in Pectinidae is homologous with the foot in non-anisomyarian bivalves; the byssal gape is therefore antero-ventral and the umbones are antero-dorsal. If paired valves are held in this position it will be seen that the byssal notch is in the right valve. This, in life, is also the lower valve. In the *irradians* group the right or lower valve is usually lighter in color and more convex than the left or upper valve.

Characters which were found useful and amenable to quantification were number of ribs, relative inflation of valves, relative width of valves, and percent of total right valves which are predominantly or wholly white. Attempts to use other characters were also made, *i.e.* shape and height of ribs, color of valves (other than white), relative width of ribs with respect to width of grooves, relative weight of valves with respect to area, shape and number of hinge teeth, number of teeth in the byssal notch, and relative width of auricles, but these characters were found to be either not revealing or not useful with slightly beach-worn specimens. (The Sable Island specimens were all single valves whose teeth and auricles were somewhat worn and some of the available population samples [L, Q, R, S, V, W] were also composed of slightly beachworn specimens.) No attempt was made to treat statistically characters which, on careful inspection, did not appear to vary geographically.

Total ribs were counted from the convex side of the shell and, in the marginal

areas below the auricles where the ribs give way to striations, doubtful ribs were considered as true ribs only if the edge of the shell showed a distinct undulation at the termination of the questionable rib. This method gave similar results to that used by Davenport (1900), which consisted in counting internal grooves, but was found more precise in doubtful cases. Length (L) was measured from the umbo to the opposite end of the shell. Width (W) was measured as the maximum dimension at right angles to the length. Height (H) was measured as the greatest vertical height of a valve when placed on a flat, horizontal surface with its convex side uppermost. All measurements are in mm.

Since scallops continue to grow during suitable periods throughout life (approximate limit 24-30 months [Gutsell, 1931]) and also since the population samples measured were collected on different dates and were often composed of more than one year class, standard error of the mean (S. E.) and standard deviation (S. D.) of length measurements were considered not meaningful and were omitted. For other characters S. E. and S. D. calculations were also omitted when N (the number) was less than 6; (N-1) was used for S. D. calculations when N was less than 15. Occasionally individuals occurred which had interpolated an additional rib or had lost a rib during growth but these aberrations were seen in less than 1% of the specimens studied.

Merrill (1961) has shown that W/L ("H/L") indices in *Placopecten magellanicus* (Gmelin) increase gradually from about .91 to 1.06 as length increases from 58 to 178 mm. The *Aequipecten* specimens from Sable Island here discussed exhibited a minor shift in both W/L and H/L indices of right valves with growth (.99 and .258 respectively in the 20.0 to 29.9 mm length class, increasing to 1.02 and .278 in the 50.0 to 59.9 mm class) but no such trends were discernable in other population samples. Occasionally, in fact, slight reverse trends in both indices of similar magnitude were observed, *e.g.*, in population J. Heterogonic growth with

TABLE 3. Statistics of 23 populations samples of the *Aequipecten irradians* group.

Feature	N	Range	Mean	S. E.	S. D.
<b>Sample A</b>		(white right valves:	10/59 = 17.0%)		
L. valve:					
ribs	17	19.0-22.0	20.47	.20	.85
length	17	15.8-54.3	34.71	-	-
W/L	17	.918-1.04	.981	.007	.029
H/L	17	.230-.257	.243	.002	.008
R. valve:					
ribs	74	19.0-22.0	20.42	.10	.87
length	74	19.6-59.0	38.31	-	-
W/L	74	.959-1.07	1.001	.003	.026
H/L	74	.229-.301	.271	.002	.016
<b>Sample B</b>		(white right valves:	6/26 = 23.1%)		
L. valve:					
ribs	24	16.0-20.0	17.29	.17	.82
length	22	22.6-49.3	31.38	-	-
W/L	22	1.01-1.11	1.065	.006	.030
H/L	22	.185-.234	.211	.003	.016
R. valve:					
ribs	26	16.0-19.0	17.08	.19	.91
length	24	22.9-49.2	30.42	-	-
W/L	24	1.02-1.14	1.072	.005	.031
H/L	24	.192-.256	.223	.003	.015
<b>Sample C</b>		(white right valves:	7/28 = 25.0%)		
L. valve:					
ribs	18	16.0-19.0	17.06	.24	1.03
length	18	14.6-72.5	41.52	-	-
W/L	18	.983-1.08	1.041	.006	.026
H/L	18	.197-.267	.224	.004	.018
R. valve:					
ribs	22	16.0-19.0	17.09	.18	.82
length	22	17.7-73.0	39.69	-	-
W/L	22	.963-1.08	1.041	.006	.026
H/L	22	.219-.280	.252	.004	.019
<b>Sample D</b>		(white right valves:	10/29 = 34.5%)		
L. valve:					
ribs	26	16.0-19.0	17.21	.14	.70
length	26	30.2-73.5	60.72	-	-
W/L	26	1.02-1.12	1.057	.004	.022
H/L	26	.177-.254	.215	.003	.017
R. valve:					
ribs	27	16.0-19.0	16.96	.15	.79
length	27	30.0-73.8	61.40	-	-
W/L	26	1.02-1.11	1.060	.004	.020
H/L	27	.200-.268	.243	.003	.016

TABLE 3 (continued)

Feature	N	Range	Mean	S. E.	S. D.
<u>Sample E</u>		(white right valves: 8/16 = 50%)			
L. valve:					
ribs	16	16.0-19.0	17.38	.22	.86
length	16	33.5-81.2	51.03	-	-
W/L	16	.985-1.08	1.054	.008	.031
H/L	16	.172-.244	.204	.005	.021
R. valve:					
ribs	16	16.0-19.0	17.44	.22	.87
length	16	33.6-80.6	50.99	-	-
W/L	16	1.01-1.09	1.063	.005	.021
H/L	16	.212-.269	.237	.005	.019
<u>Sample F</u>		(white right valves: 2/7 = 29%)			
L. valve:					
ribs	6	16.0-19.0	17.50	.56	1.28
length	6	48.4-71.0	59.18	-	-
W/L	6	1.07-1.10	1.086	.005	.012
H/L	6	.176-.223	.206	.007	.018
R. valve:					
ribs	7	16.0-19.0	17.14	.41	1.14
length	7	48.1-72.8	61.17	-	-
W/L	7	1.08-1.11	1.093	.004	.010
H/L	7	.221-.288	.250	.009	.023
<u>Sample G</u>		(white right valves: 3/4 = 75%)			
L. valve:					
ribs	4	18.0-19.0	18.50	-	-
length	4	53.9-63.6	58.55	-	-
W/L	4	1.01-1.06	1.042	-	-
H/L	4	.231-.245	.237	-	-
R. valve:					
ribs	4	18.0-19.0	18.25	-	-
length	4	54.0-64.3	58.90	-	-
W/L	4	1.04-1.06	1.050	-	-
H/L	4	.269-.305	.281	-	-
<u>Sample H</u>		(white right valves: 3/3 = 100%)			
L. valve:					
ribs	3	18.0	18.0	-	-
length	3	48.0-68.8	55.20	-	-
W/L	3	1.02-1.06	1.044	-	-
H/L	3	.250-.275	.262	-	-
R. valve:					
ribs	3	18.0-19.0	18.67	-	-
length	3	48.0-64.2	55.66	-	-
W/L	3	1.04-1.06	1.053	-	-
H/L	3	.327-.332	.329	-	-

TABLE 3 (continued)

Feature	N	Range	Mean	S. E.	S. D.
<u>Sample I</u>		(white right valves: 30/30 = 100%)			
L. valve:					
ribs	27	18.0-21.0	19.22	.13	.68
Length	27	36.2-64.2	57.23	-	-
W/L	27	.979-1.08	1.026	.005	.024
H/L	27	.252-.323	.278	.003	.017
R. valve:					
ribs	30	17.0-20.0	18.73	.16	.85
length	30	37.0-72.5	59.76	-	-
W/L	30	.971-1.06	1.010	.004	.023
H/L	30	.305-.372	.334	.003	.015
<u>Sample J</u>		(white right valves: 10/12 = 83%)			
L. valve:					
ribs	8	18.0-20.0	18.86	.30	.84
length	8	51.9-75.4	63.01	-	-
W/L	8	1.00-1.05	1.017	.006	.017
H/L	8	.225-.264	.244	.004	.012
R. valve:					
ribs	12	18.0-21.0	19.25	.28	.96
length	12	45.0-76.0	64.23	-	-
W/L	12	.995-1.07	1.021	.006	.022
H/L	12	.279-.339	.309	.004	.015
<u>Sample K</u>		(white right valves: 2/2 = 100%)			
L. valve:					
ribs	4	20.0-22.0	20.50	-	-
length	4	62.0-70.1	65.60	-	-
W/L	4	1.05-1.10	1.074	-	-
H/L	4	.268-.274	.271	-	-
R. valve:					
ribs	2	18.0-19.0	18.50	-	-
length	2	72.2-73.6	72.90	-	-
W/L	2	1.01-1.03	1.021	-	-
H/L	2	.310-.333	.322	-	-
<u>Sample L</u>		(white right valves: 2/2 = 100%)			
No left valves					
R. valve:					
ribs	2	14.0-15.0	14.50	-	-
length	2	42.7-49.5	47.10	-	-
W/L	2	1.00-1.01	1.007	-	-
H/L	2	.334-.358	.346	-	-

TABLE 3 (continued)

Feature	N	Range	Mean	S. E.	S. D.
<u>Sample M</u>		(white right valves: 9/11 = 82%)			
L. valve:					
ribs	11	21.0-24.0	21.64	.31	1.03
length	11	41.5-65.1	51.84	-	-
W/L	11	.992-1.06	1.028	.007	.022
H/L	11	.244-.280	.261	.004	.011
R. valve:					
ribs	11	21.0-23.0	21.91	.25	.83
length	11	42.4-65.8	52.47	-	-
W/L	11	.995-1.06	1.027	.006	.020
H/L	11	.289-.340	.324	.005	.016
<u>Sample N</u>		(white right valves: 6/7 = 86%)			
L. valve:					
ribs	14	19.0-24.0	21.21	.38	1.42
length	14	35.2-71.6	58.27	-	-
W/L	14	.959-1.05	1.010	.007	.026
H/L	14	.233-.274	.253	.003	.013
R. valve:					
ribs	7	19.0-22.0	20.86	.40	1.07
length	7	29.1-70.0	53.93	-	-
W/L	7	.976-1.05	1.008	.009	.024
H/L	7	.313-.354	.327	.006	.015
<u>Sample O</u>		(white right valves: 7/7 = 100%)			
L. valve:					
ribs	7	18.0-22.0	20.14	.55	1.46
length	7	25.4-65.8	45.26	-	-
W/L	7	.972-1.05	1.003	.010	.025
H/L	7	.247-.292	.265	.006	.017
R. valve:					
ribs	7	18.0-21.0	19.57	.37	.98
length	7	25.7-55.6	42.60	-	-
W/L	7	.957-1.02	.992	.008	.021
H/L	7	.300-.351	.326	.007	.017
<u>Sample P</u>		(white right valves: 22/22 = 100%)			
L. valve:					
ribs	25	18.0-23.0	20.64	.23	1.13
length	25	24.5-70.7	52.44	-	-
W/L	25	.902-1.07	1.014	.007	.035
H/L	25	.228-.292	.263	.004	.018
R. valve:					
ribs	22	19.0-22.0	20.50	.17	.78
length	22	36.3-69.1	58.54	-	-
W/L	22	.955-1.06	1.020	.005	.022
H/L	22	.286-.379	.332	.005	.025

TABLE 3 (continued)

Feature	N	Range	Mean	S. E.	S. D.
<u>Sample Q</u>					
(white right valves: 5/5 = 100%)					
No left valves					
R. valve:					
ribs	5	20.0-22.0	20.60	-	-
length	5	41.4-55.0	41.4	-	-
W/L	5	.993-1.04	1.010	-	-
H/L	5	.298-.337	.315	-	-
<u>Sample R</u>					
(white right valves: 1/1 = 100%)					
L. valve:					
ribs	4	18.0-21.0	19.00	-	-
length	4	23.5-62.7	50.40	-	-
W/L	4	.989-1.06	1.033	-	-
H/L	4	.213-.280	.257	-	-
R. valve:					
ribs	1	20	-	-	-
length	1	64.5	-	-	-
W/L	1	1.05	-	-	-
H/L	1	.333	-	-	-
<u>Sample S</u>					
(white right valves: 3/3 = 100%)					
L. valve:					
ribs	1	15.0	-	-	-
length	1	40.0	-	-	-
W/L	1	.988	-	-	-
H/L	1	.285	-	-	-
R. valve:					
ribs	3	16.0-17.0	16.33	-	-
length	3	45.0-64.8	55.00	-	-
W/L	3	.993-1.08	1.027	-	-
H/L	3	.311-.353	.334	-	-
<u>Sample T</u>					
(white right valves: 8/9 = 89%)					
L. valve:					
ribs	22	14.0-18.0	15.59	.25	1.33
length	22	24.4-68.6	38.39	-	-
W/L	22	.955-1.04	.996	.005	.025
H/L	22	.280-.349	.299	.004	.018
R. valve:					
ribs	9	13.0-17.0	15.22	.49	1.48
length	9	27.7-50.7	38.10	-	-
W/L	7	.957-1.03	1.000	.012	.031
H/L	9	.325-.364	.345	.004	.012

TABLE 3 (continued)

Feature	N	Range	Mean	S. E.	S. D.
<u>Sample U</u>		(white right valves: 12/12 = 100%)			
L. valve:					
ribs	10	15.0-17.0	15.40	.22	.70
length	10	30.0-51.5	38.64	-	-
W/L	10	.968-1.09	1.029	.014	.043
H/L	10	.247-.361	.298	.007	.021
R. valve:					
ribs	12	13.0-16.0	15.08	.29	1.00
length	12	27.1-54.0	41.08	-	-
W/L	12	.952-1.06	1.016	.008	.029
H/L	12	.313-.412	.352	.007	.026
<u>Sample V</u>		(white right valves: 4/5 = 80%)			
L. valve:					
ribs	1	15.0	-	-	-
length	1	43.8	-	-	-
W/L	1	.970	-	-	-
H/L	1	.288	-	-	-
R. valve:					
ribs	5	16.0-18.0	17.00	-	-
length	5	36.8-52.5	45.46	-	-
W/L	5	.943-1.05	.970	-	-
H/L	5	.286-.372	.330	-	-
<u>Sample W</u>		(white right valves: 1/1 = 100%)			
No left valves					
R. valve:					
ribs	1	15.0	-	-	-
length	1	59.3	-	-	-
W/L	1	1.03	-	-	-
H/L	1	.346	-	-	-

N = number

S. E. = standard deviation

S. D. = standard error of the mean

respect to overall shell shape therefore appears not to be a significant factor in *Aequipecten* and W/L and H/L indices are considered valid even though derived from mixed year classes. Very small specimens were avoided, however. Also, no specimens were used which were beach-worn to a degree which could affect the measurements or which were stained after death by chemicals in the substrate.

Except for Sable Island material, most specimens were apparently collected alive.

The population statistics determined are given in Table 3. Compilations of measurements of all individual specimens are on file at the National Museum of Canada.

Inspection of Table 3 shows that rib count, relative width (W/L) and relative inflation (H/L), especially of right valves,



FIG. 1. Rib count values of 23 population samples (A-W) treated statistically. Total variation observed (right valves only) is represented by a vertical line, the mean by a horizontal line, one standard deviation on either side of the mean by a vertical bar, and one standard error of the mean on either side of the mean by an open rectangle. There is no variation for samples R and W (one valve only).

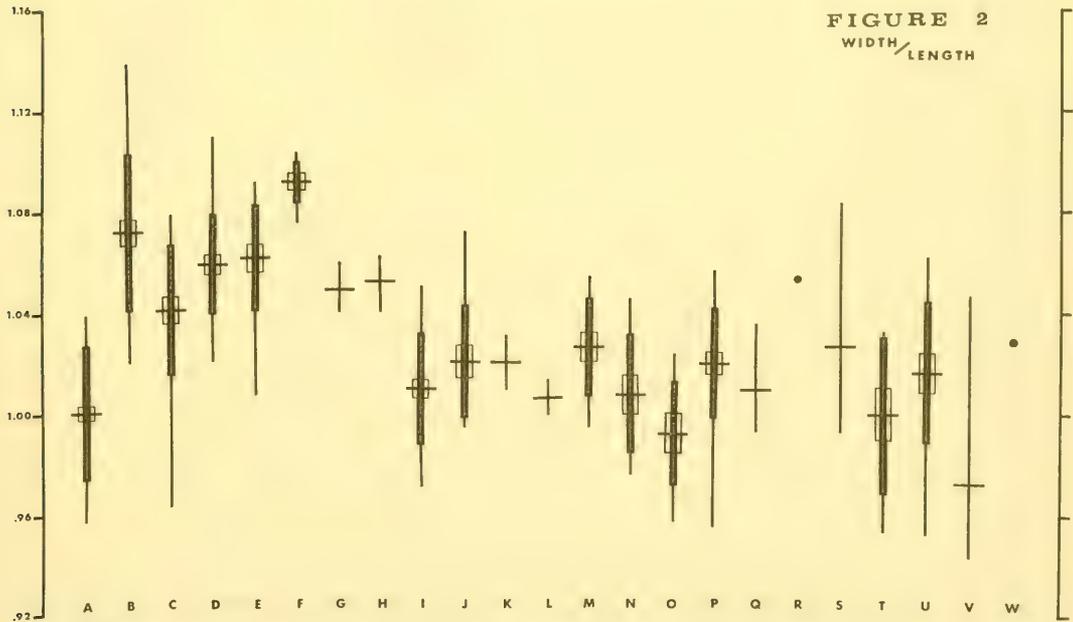


FIG. 2. Indices of relative width for the 23 population samples (A-W) treated statistically. Symbols are as in Fig. 1.

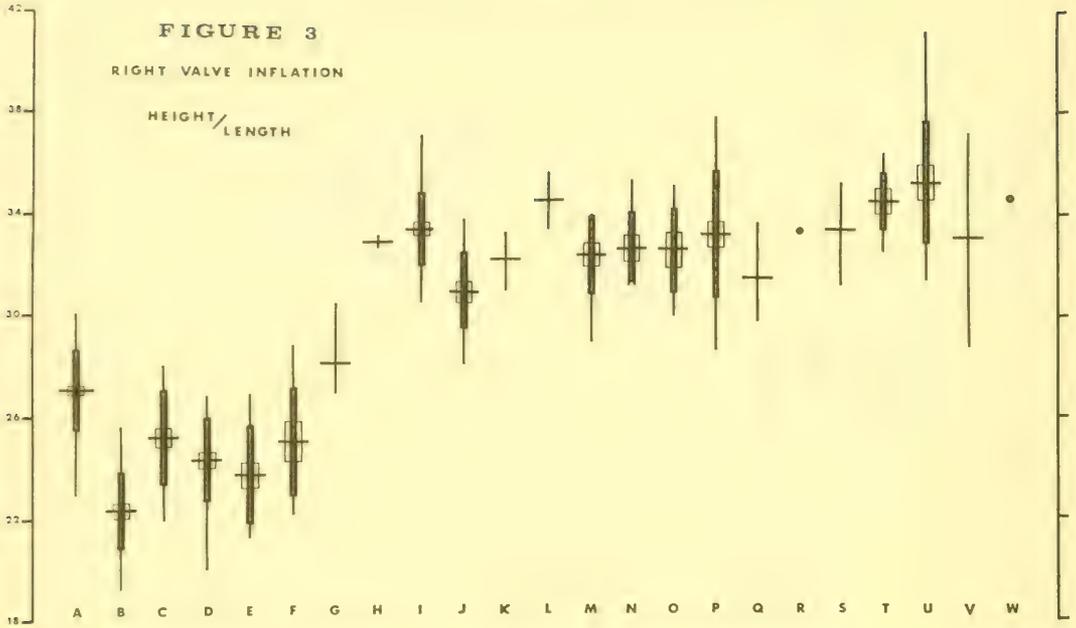


FIG. 3. Indices of right valve inflation for the 23 population samples (A-W) treated statistically. Symbols are as in Fig. 1.

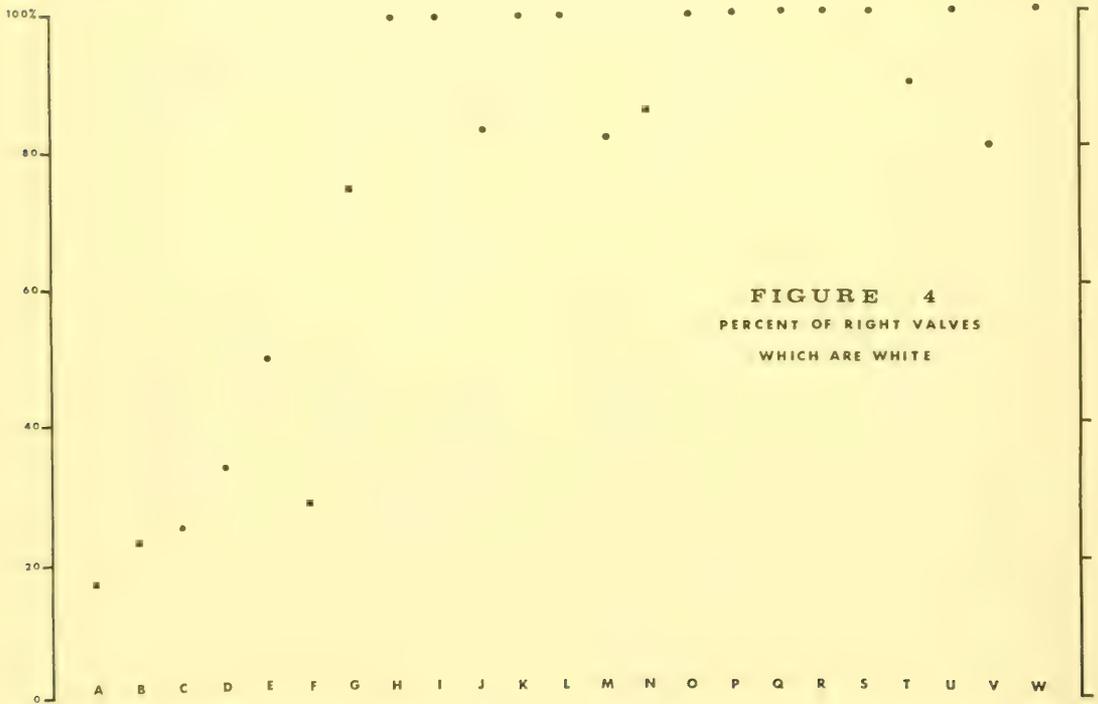


FIG. 4. Percent of white right valves in the 23 population samples (A-W) treated statistically.

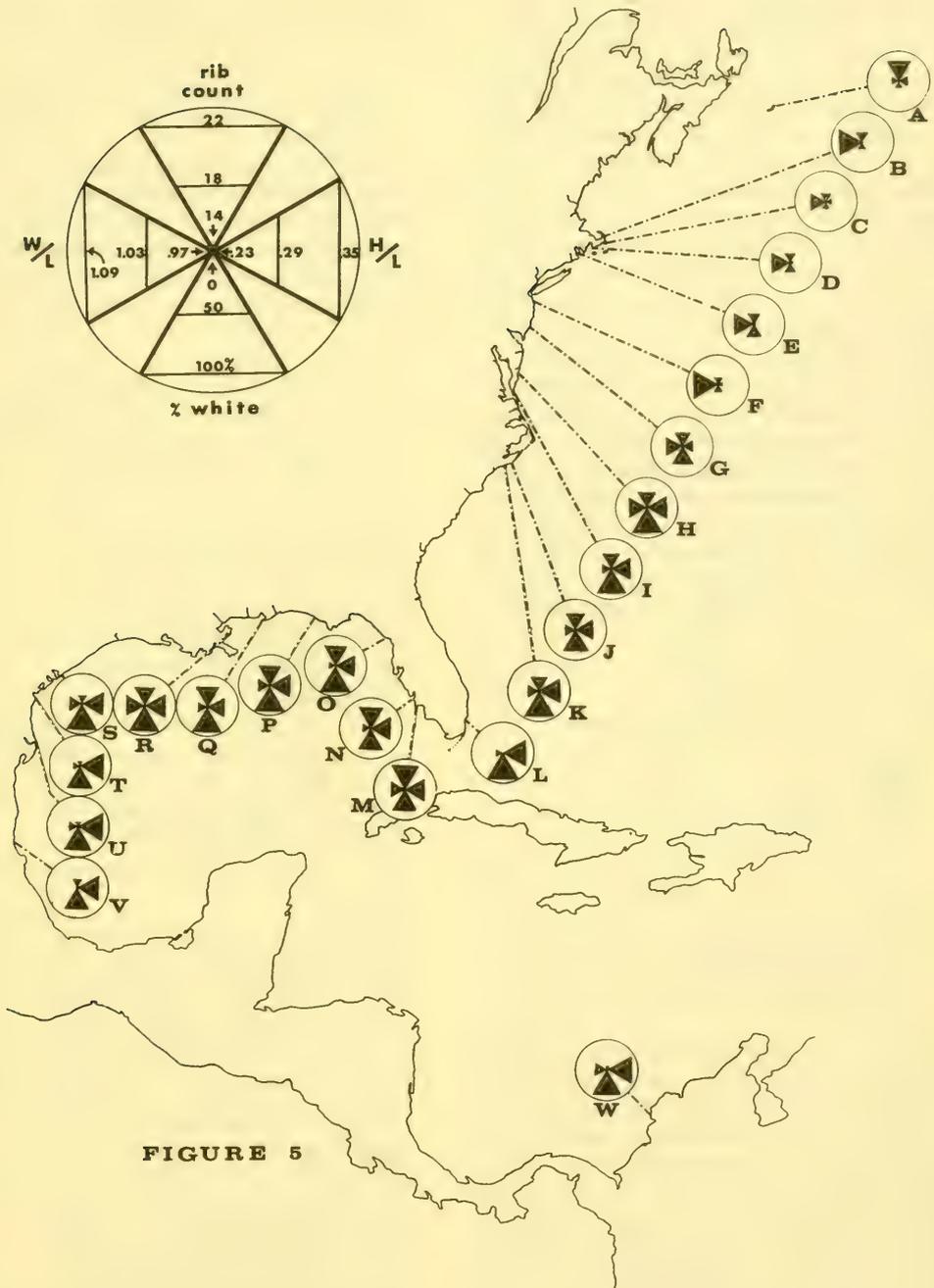


FIGURE 5

FIG. 5. Geographical location of 23 statistically analyzed population samples and relationships with respect to the means of 4 primary characters (of right valves): rib count, relative width, relative inflation, and percent of white right valves. Similarities and differences among populations may be perceived by comparing the shapes of the composite diagrams obtained: 4 groups can be discerned: (I) A; (II) B-F; (III) G-K, M-R; (IV) L, S-W.

varies significantly between populations. The variation of these characters and of the frequency of white valves, all with respect to right (lower) valves, are charted in Fig. 1 to 4. The charts indicate that the inter-population variation which exists with respect to these characters is substantially geographic in nature.

Figure 5 represents an attempt to combine the means of all 4 characters in a manner which will indicate overall similarities and differences among the population samples studied. The results indicate the presence of 4 groups: (I) population A, (II) populations B through F, (III) populations G through K and M through R, and (IV) populations L and S through W. Within group III, populations G. through K are also somewhat different from populations M through R. The taxonomy and relationships of all of these groups and further analyses of the charts will be discussed in detail in the following section.

SYSTEMATICS

Genus *Aequipecten* Fischer

*Aequipecten* Fischer, 1886, Man. de Conchyl., p 844.

Type species (by monotypy): *Ostrea opercularis* L.

Subgenus *Plagioctenium* Dall

*Plagioctenium* Dall, 1898, Trans. Wagner Free Inst. Sci. 3(4): 696.

Type species (by original designation): *Pecten circularis* Sby.

The type species of *Aequipecten* exhibits noticeable differences from the type species of *Plagioctenium* and from the members of the *irradians* and *gibbus* groups of that subgenus (upper valve more convex than lower in *A. opercularis*; shape and texture of shell different, etc.); but their relationships appear close enough to allow retention of *Plagioctenium* as a subgenus of *Aequipecten*. The writer feels that the name *Aequipecten* is too well established for this economically important group to be discarded without more compelling reasons than appear to exist.

I also agree with Keen (1960) that *Argopecten* Monterosato (1889), as used by Grau (1959), is not applicable because the species which must be regarded as its type (*Pecten solidulus* Reeve, 1853) is not identifiable.

The following key is designed to assist in the taxonomic identification of representative population samples, and therefore populations, of the *A. (P.) irradians* group. Single specimens will sometimes key out incorrectly.

KEY TO THE TAXONOMIC IDENTIFICATION OF POPULATIONS OF THE SUPERSPECIES *AEQUIPECTEN IRRADIANS*

1. Mean rib count, 19 or more . . . . . 2  
    Mean rib count less than 19 . . . . . 3
  
2. Less than 50% of the right valves are white. Mean H/L index of right valves .25-.29. Known range: Sable Island, Nova Scotia (shells only, subspecies now extinct) . . . . . *Aequipecten irradians sablensis* Clarke  
    More than 50% of the right valves are white. Mean H/L index of right valves .28-.35. Known range: New Jersey to South Carolina and Florida West Coast to eastern Texas . . . . . *Aequipecten irradians concentricus* Say
  
3. Less than 50% of the right valves are white. Mean H/L index of right valves .19-.29. Width greater than length (mean W/L index usually 1.02-1.10). Known range: Massachusetts to New Jersey . . . . . *Aequipecten irradians irradians* Lamarck  
    More than 50% of the right valves are white. Mean H/L index of right valves .28-.41. Width and length approximately equal (mean W/L index usually .96-1.04). Known range: New Jersey and south . . . . . 4
  
4. Mean rib count 18-19. Known range: New Jersey to South Carolina and Florida West Coast to Eastern Texas . . . . . *Aequipecten irradians concentricus* Say  
    Mean rib count 17 or less (usually 15-16). Known range: Southeast Florida: Cartagena, Colombia; and Texas to Mexico . . . . . *Aequipecten ampicostatus* Dall

*Aequipecten irradians sablensis* ssp. n.  
Plate 1, Fig. 1-6.

**Description.** Shell up to 59 mm long in specimens examined, width approximately equal to length, valves somewhat compressed and sculptured with 19 to 22 radiating ribs and numerous fine, concentric lines. External color of left (upper) valves gray or brown and variable, often with purple or orange tints; color of right (lower) valves gray, brown, purple, orange, white or a combination of these. Right valves white or nearly white in 17% of specimens seen. Ribs rounded in cross section. Radial threads and cords present on auricles and on disc near auricles. Byssal notch in right valve apparently with 2 to 4 minute teeth. Teeth worn away in many specimens, however. Interior of valves sub-nacreous to chalky and whitish or exhibiting the external coloration in a reduced degree. Muscle scars and pallial line faint or not discernible. Ratios of W/L and H/L approximately .98 and .24 respectively for left valves and 1.00 and .27 for right valves. See Table 4.

TABLE 4. Measurements of type material of *Aequipecten irradians sablensis*

Specimen	valve	length	width	height	ribs
Paratype	left	59.0	62.8	16.5	19
Holotype	left	44.4	43.6	11.8	21
Paratype	right	48.2	47.8	11.1	21
Paratype	right	36.6	36.4	9.4	20

See Table 3, population A, for more extensive measurements.

**Types.** The holotype, a left valve, is in the National Museum of Canada and bears catalogue number 14153A. Paratypes are in the National Museum of Canada, the United States National Museum, the Academy of Natural Science, and the Museum of Comparative Zoology.

**Remarks.** *Aequipecten irradians sablensis* differs significantly from *A. i.*

*irradians* in total rib count. If coefficients of difference, as defined by Mayr, Linsley, and Usinger (1953), are calculated for rib count in sample A (*sablensis*) as compared with each sample in the B through F series (*irradians*), values of 1.71 to 2.10 result. These are allequivalent to non-overlap values greater than 95%, well above the conventional level of distinctness. Substantial differences are also apparent with respect to W/L indices.

The new subspecies differs from both *A. i. concentricus* and *A. amplicostatus* in regard to frequency of white right valves and with respect to index of inflation (H/L). The probability of white right valves occurring in a frequency as low as that observed in sample A (*sablensis*) if it belonged to the same population as any sample in the H to W series, is much less than 1%. Calculations of coefficient of difference with respect to H/L values for sample A compared with samples I, J, M, N, O, P, T, or U, indicates a non-overlap value of 89% for sample I and non-overlap values exceeding 93% for each of the other samples. (Samples G, H, K, L, Q, R, S, V, and W, are too small to allow this kind of comparison). In addition, *A. i. sablensis* differs strikingly from *A. amplicostatus* with respect to total rib count.

All of these contrasts may be observed by comparing the values shown in Figures 1 to 4 and the composite diagrams shown in Figure 5. On morphological and geographical grounds, *A. sablensis* clearly qualifies as a distinct subspecies.

Although Willis (in Patterson, 1894) included "*Pecten concentricus*" (now *A. i. sablensis*) in his list of species presumably occurring alive at Sable Island, it is not clear whether that species really lived there at that time. The specimens collected in 1962 were all somewhat worn, lacked all remnants of soft parts and ligament, and exhibited a high (4.4:1) ratio of right to left valves indicating that much natural sorting had occurred (see Lever, 1958). Specimens were submitted to Geochron Laboratories, Inc., Cambridge,

Massachusetts for radiocarbon analysis and an age of 1432 + 125 years was determined. Neither Mrs. Andrewschenk nor Dr. Mansfield, the collectors who obtained the material, have ever seen living or recently dead specimens of *A. i. sablensis* at Sable Island. In addition, no specimens which were collected alive or in a freshly dead condition have been seen in North American museums. The subspecies is therefore considered extinct. In all probability it was a survivor from some period in the post-Pleistocene when a warm-water fauna extended continuously from Cape Cod to the Gulf of St. Lawrence. Since the 1432 + 125 year age does not correspond to any known period of climatic deterioration, and since the physiography of Sable Island has undergone major changes even in the past 75 years, it appears probable that the extermination of *A. i. sablensis* may have been linked with destruction of its proper habitat.

Range and Records. *Aequipecten irradians sablensis* is apparently restricted to Sable Island, Nova Scotia. No specimens from other localities have been seen.

*Aequipecten irradians irradians*  
(Lamarck)

Plate 1, Figs. 7-9; Plate 2, Figs. 1-7;  
Plate 3, Figs. 1-4

*Pecten irradians* Lamarck, 1819, Anim. sans Vert. 6: 173 (no figure or type locality). Types figured by Benj. Delessert, 1841, Plate 15, Figs. 4a, b and by J. C. Chenu, 1843, 3: Plate 30, Figs. 10-11 (la Méditerranée).

*Pecten borealis* Say, 1822, J. Acad. Nat. Sci. Phila. (1) 2: 259 (no figure; type locality "coast of New England").

Description. Shell up to 92 mm long in specimens examined, width slightly greater than length, valves rather thin, compressed and sculptured with 16-20 radiating ridges and numerous fine, concentric lines. External color of left (upper) valves gray, white, or muted shades of brown, yellowish or orange; usually streaked or banded, and often with purplish suffusions. Right (lower) valves similar

or lighter in color and commonly nearly, or entirely white. Ribs usually 16 to 18 in number and rounded in cross section. Radial threads and cords present on auricles and on disc near auricles. Byssal notch in right valve usually with 3 or 4 minute, erect teeth. Interior of valves somewhat nacreous and white to bluish white or exhibiting the external coloration to some degree, especially near the margin. Muscle scar and pallial line faint or not discernible. Ratios of W/L and H/L approximately 1.06 and .21 respectively for left valves and 1.06 and .24 for right valves. Representative measurements for 4 specimens are given in Table 5.

TABLE 5. Representative measurements of *Aequipecten irradians irradians*

Origin	valve	length	width	height	ribs
Falmouth, Mass.	left	73.5	77.4	14.8	16
	right	73.5	77.6	18.0	17
	left	62.0	64.8	13.8	18
	right	62.3	64.9	15.8	17
Green- wich Bay, R. I.	left	81.2	84.0	14.0	16
	right	80.6	85.0	17.1	17
	left	63.5	66.7	15.2	19
	right	63.2	67.2	17.0	18

See Table 3, populations B through F, for more extensive measurements.

Types. According to Dr. Eugène Binder, 2 of Lamarck's original specimens of *P. irradians* are in the Muséum d'Histoire Naturelle, Geneva, Switzerland, along with the bulk of Lamarck's collection. Photographs of these specimens are reproduced in Plate 1 and Plate 2. One of these, an obese and apparently somewhat malformed individual, was figured by Delessert and Chenu (Fig. 11) and the other, an apparently normal specimen, was also figured by Chenu (Fig. 10) but not by Delessert. The latter specimen is here designated as lectotype.

TABLE 6. Measurements of 2 of Lamarck's specimens (A and B) of *Pecten irradians* from the Muséum d'Histoire Naturelle, Geneva

Feature	A		B	
	left	right	left	right
ribs	19	18 (19?)	18 (19?)	19
annual growth rests	2	2	3	3
length	74.5	74.5	73.0	73.0
width	78.3	78.7	81.6	82.4
height	19.8	19.8	14.7	14.7
W/L	1.05	1.06	1.12	1.13
H/L	0.266	0.266	0.201	0.201

Although both specimens are accompanied by a label bearing the locality "Méditerranée", this is clearly erroneous. See "Remarks" below.

**Remarks.** Lamarck's brief description (*loc. cit.*) of this species is as follows: "Peigne rayonnant. *Pecten irradians*. *P. testa rotundata, subaequali, albida, fulvo fuscoque variegata; radiis 18 ad 20 convexis: striis transversis exilissimis*. Habite . . . mon cabinet. Coquille rare, éxotique, ayant l'aspect d'un p. operculaire très-rembruni. Largeur, 74 millimètres."

Measurements of Lamarck's specimens, partly supplied by Dr. Binder and partly deduced from examining the photographs, are given in Table 6.

Much information regarding the original locality of these specimens can be deduced from the specimens themselves. Their prominent growth rests indicate an origin north of North Carolina. Growth rests in specimens from south of that region are either not well marked or are entirely absent. With respect to rib count and W/L and H/L indices, Lamarck's specimens do not fall entirely within the observed range of any single population sample seen. They do, however, fall within the overall range of Group II (see p 15), i.e. population samples B to F, and they are outside the overall range for

either Group I (*sablensis*), Group III (*concentricus*) or Group IV (*ampliocostatus*). The rich brown color illustrated by Chenu is much like that of specimens from the United States National Museum labelled "New Jersey", but in this species group color, other than white, and within broad limits, appears to be a non-conservative character and the appearance of similarly colored individuals elsewhere would not be surprising. In addition, New Jersey is within the zone of intergradation of groups II and III. Since no characters preclude a more northern origin, and since the designation *irradians* is widely accepted as applying to the taxon represented by Group II, in the interests of precision and stability it is advisable to restrict the type locality to a region inhabited by specimens which belong unequivocally to Group II. Such a locality is Waquoit Bay, 7 mi. NE of Falmouth, Massachusetts, and the type locality of *A. irradians* s.s. is hereby restricted thereto. See Table 3, Sample D, for a description of the variation of *A. irradians* from the new type locality.

**Range.** North Shore of Cape Cod at Barnstable and Provincetown, Massachusetts to New Jersey. Disjunct populations also exist at Cohasset and at Scituate, Massachusetts. The precise southern limit of *A. i. irradians* is unknown but evidence (populations G and H) indicates that it intergrades with *A. i. concentricus* in the region of New Jersey and Maryland. Geologic range: Pleistocene to Recent (Dall, 1898).

**Specimens Examined.** Massachusetts: Scituate, Duxbury, Barnstable, Yarmouth, Brewster, Wellfleet, Provincetown, Eastham, East Orleans, South Orleans, Chatham, Harwich, Dennisport, South Dennis, West Dennis, West Yarmouth, Hyannis, Hyannisport, Cotuit, Waquoit, Falmouth, Woods Hole, North Falmouth, Monument Beach, Marion, New Bedford, South Dartmouth, Acoaxet, Lagoon Pond and Edgartown (both Martha's Vineyard Island), Brant Point and Wauwinet (both Nantucket Island). Rhode Island: 6 mi. south of Tiverton (2-3 fathoms), Tiverton, Newport,

Pawtucket, Warwick, Buttonwoods, Greenwich Bay, Wakefield, Westerly. Connecticut: Stonington, New Haven. New York: Orient, Amagansett, Little Peconic Bay, Conkling Point, Cold Spring Harbor, Pine Neck, Oak Beach, Long Beach Bay. New Jersey: "New Jersey".

*Aequipecten irradians concentricus*  
(Say)

Plate 3, Figs. 5-12; Plate 4, Figs. 1-8

*Pecten concentricus* Say, 1822, J. Acad.  
Nat. Sci. Phila. 2: 257 (no figure: type  
locality "coast of New Jersey").

Description. Shell up to 95 mm long in specimens examined, width equal to or slightly greater than length, valves not as thin as in *A. irradians* s.s., somewhat inflated, and sculptured with 17 to 23 radiating ribs and numerous fine, concentric lines. External color of left (upper) valves gray, brown, purple, orange, yellowish or white, often streaked, banded or somewhat variegated; color of right (lower) valves white or nearly so (in 75-100% of the specimens observed in each population) or similar to the left valve

but usually lighter in color. Ribs evenly rounded or with flattened tops. Radial threads and cords present on auricles and on disc near auricles. Byssal notch in right valve with about 4 minute, erect teeth. Interior of valves nacreous or white and exhibiting the exterior color near the margin (but not as prominently as in *A. irradians* s.s.) and sometimes, to a slight degree, over the whole inner surface. Muscle scars and pallial line faint or not discernible. Ratios of W/L and H/L approximately 1.03 and .26 respectively for left valves and 1.02 and .32 for right valves. In Table 7 representative measurements are given for 6 specimens.

Types. Virtually all of Say's types which are still in existence are at the Academy of Natural Sciences, in Philadelphia. None of his original specimens of *Pecten concentricus* are in that institution, the Museum of Comparative Zoology, or the United States National Museum and it must be presumed that they are lost. In the interests of stability a neotype, corresponding as closely as possible to Say's original description and locality, is here selected (Plate 3, Figs. 5-8). It bears catalogue number 56295 and is in the collection of the Academy of Natural Sciences, Philadelphia. It was collected alive at Atlantic City, New Jersey by S. R. Morse, and is one of a lot of 4 specimens. This lot is described more fully as Sample G in Table 3.

Remarks. Inspection of the charts in Figures 1 to 5 indicates that Group II (*irradians*) and Group III (*concentricus*) are quite dissimilar throughout most of their ranges but that they intergrade in the region from New Jersey to Maryland. Gutsell (1931) and Sastry (1963) have shown that significant differences in spawning behavior between the 2 forms also exist. The name *A. concentricus* is in wide use for Group III and it is desirable to maintain that name for this economically important subspecies if possible. By selection of a neotype from Atlantic City the name is fixed to an intermediate population which is morphologically closer to Group III than to Group II, and although this is not

TABLE 7. Representative measurements of *Aequipecten irradians concentricus*

Specimen	valve	length	width	height	ribs
Neotype	left	53.9	56.4	12.6	19
	right	54.0	57.0	14.5	18
Atlantic City, N.J.	left	63.6	67.4	15.0	18
	right	64.3	68.2	17.7	18
Beaufort, N. C.	left	75.4	77.3	17.0	18
	right	76.0	78.4	22.0	18
Sanibel I., Fla.	left	71.0	71.3	16.6	19
	right	72.0	73.0	20.1	20
	left	65.1	64.6	16.3	20
	right	65.8	65.5	19.0	22
	left	44.3	44.4	11.5	22
	right	44.8	45.0	14.5	23

See Table 3, populations G through K and M through R for more extensive measurements.

an ideal solution to the problem, it is the best that can be done.

In terms of total rib count, the Atlantic Coast populations of *A. i. concentricus* differ somewhat from the Gulf Coast populations of that subspecies. Average rib counts for the 2 subgroups are 18.7 and 20.6 respectively, but since the range of variation of both subgroups overlap extensively (see Fig. 1) and no other differential characters have been found, it is considered unwise to attempt to differentiate them taxonomically.

Range. New Jersey to South Carolina and Florida West Coast to eastern Texas. More precise limits are at present unknown. Geologic range: Pleistocene to Recent (Dall, 1898).

Records. New Jersey: Great Egg Harbor, Atlantic City, Cape May. Maryland: Sinepuxent Bay. Virginia: Hog Island, Smith Island, Cape Charles, Issac Island, mouth of Chesapeake Bay, Lynnhaven Inlet, 10 mi. south of Virginia Beach. North Carolina: Hatteras Village, Beaufort, Morehead City, Piver's Island, Swansboro. South Carolina: "South Carolina". Florida: 7 mi. south of Marco I., Naples, Sanibel I., Boca Grande, Sarasota Bay, Long Key, Longboat Key, St. Petersburg, Port Tampa, Tampa, Gulfport, Treasure I., Ozoma, Cedar Key, North Key, James I., St. Joseph Bay, Crooked Island, Panama City. Alabama: Fort Morgan. Louisiana: Chandeleur I., Texas: Galveston.

*Aequipecten amplicostatus* (Dall)

Plate 4, Figs. 9-14

*Pecten gibbus* var. *amplicostatus* Dall, 1898, Trans. Wagner Free Inst. Sci. 3(4): 747 (no figure; type locality: "occurs chiefly west of the Mississippi, on the Texas coast, and south to Cartagena").

Description. Shell up to 65 mm long in specimens examined, width about the same as length, lower valve more inflated than upper valve, and both valves sculptured with 12-18 radiating ribs and numerous fine, concentric lines. External color of left (upper) valves gray, brown,

purplish or reddish and mottled or streaked with white. Right (lower) valves usually white, occasionally tinged with the same color as the left valve. Ribs usually 14 to 16 in number, rounded to slightly flattened and, in the left valve about the same width as, or slightly wider than, the grooves; in the right valve the ribs are heavier, broader, and much wider than the grooves between. Radial cords on auricles and on disc near auricles. Byssal notch in right valve with about 4 minute, erect teeth. Interior of valves nacreous to porcelaneous and usually white or bluish white. Muscle scars and pallial line faint to not discernible. Ratios of W/L and H/L approximately 1.00 and .29 respectively for left valves and 1.01 and .34 for right valves. Representative measurements for several specimens are given in Table 8.

Types. The holotype of this species is number 106990 in the United States National Museum. Its locality is "Texas". Since there is no ambiguity concerning the identity of *A. amplicostatus*, no restriction of the type locality will be made here.

Remarks. Several kinds of evidence exist which appear to indicate that *A. amplicostatus* is specifically distinct. Rib number and general appearance are obvious differences between *A. ampli-*

TABLE 8. Representative measurements of *Aequipecten amplicostatus*

Specimen	value	length	width	height	ribs
Holotype	left	48.0	50.8	14.1	13
	right	49.1	50.9	17.4	12
Off Bear's Cut, Miami Fla.	right	49.5	50.2	17.7	14
Matagorda, Texas	left	40.0	39.5	11.4	15
	right	64.8	65.1	21.9	16
Tampico, Mexico	left	43.8	42.5	12.6	15
	right	52.5	50.0	19.3	16
Cartagena, Colombia	right	59.3	61.0	20.5	15

See Table 3, population L and populations S through W, for more extensive measurements.

*costatus* and *A. i. concentricus* and there is no difficulty in distinguishing them. In areas of proximity no intergradation occurs between them (or between *A. amplicostatus* and *A. gibbus*); in fact there is even a suggestion of character displacement in such areas. Although no collections of the 2 forms from closely adjacent localities are available, the populations of *A. i. concentricus* (M and R) which are geographically nearest to populations of *A. amplicostatus* are morphologically more divergent from *A. amplicostatus* than are the other Gulf of Mexico populations of *A. i. concentricus* (see Fig. 5). Furthermore, the presence of *A. amplicostatus* in the Pliocene and *A. i. concentricus* in the Pleistocene of Florida (Dall 1898, 1925), together with the disjunct distribution of both *A. amplicostatus* and *A. i. concentricus* at the present time, indicates that over the past million years both *A. amplicostatus* and *A. irradians* (*sensu lato*) have undergone substantial range expansions and contractions and presumably have had repeated opportunities for interbreeding and for the achievement of morphological unity. This has not occurred. The evidence, therefore, indicates that *A. amplicostatus* is a distinct species and it is so considered here.

**Range.** The Gulf of Mexico extending at least from Matagorda, Texas to Cape Rojo, Mexico. Disjunct populations also occur off Miami, Florida and at Cartagena, Colombia. Geologic range; Pliocene to Recent (Dall, 1898).

**Specimens Examined.** Florida: Miami (off Bear's Cut, at 30 fathoms, Eolis sta. 122). Texas: Matagorda, Matagorda Bay, Espirito Santo Bay, Port Aransas, 5 mi. north of Rockport, Aransas Pass, Corpus Christi, Corpus Christi Bay, Port Isabel, Laguna Madre Bay, 3 mi. north of Rio Grande, Brownsville. Mexico: Bahia Jesus Maria, Tampico, Tamiahua. Colombia: Cartagena ("Schott").

#### EVOLUTION AND ADAPTATION

The superspecies *Aequipecten irradians* is composed of 4 taxonomic units: *A. i.*

*irradians*, *A. i. sablensis*, *A. i. concentricus*, and *A. amplicostatus*. These taxa, with *A. gibbus* (L.), *A. g. nucleus* (Born), and *A. g. portusregii* Grau constitute the subgenus *Plagioctenium* (Dall, 1898) in the western North Atlantic. (See Abbott, 1954, and Sastry, 1962, for differences between the *irradians* and *gibbus* groups.) The ancestral species within the North American segment of *Plagioctenium* is probably *A. gibbus* (L.), an abundant, Recent, warm-water species known from deposits as old as the late Miocene (Dall, 1898). *A. amplicostatus* has been reported associated with *A. gibbus* in Pliocene deposits (the Caloosahatchee marl) but *A. i. irradians* and *A. i. concentricus* have not been found in deposits older than Pleistocene (Dall, 1898). *A. i. sablensis*, *A. g. nucleus* and *A. g. portusregii* are known only from the Recent. Dall's observation that Pleistocene specimens of *A. i. concentricus* exhibit fewer ribs than Recent specimens is probably also significant since it implies that *concentricus* and *irradians* s.s. were less divergent at that time than at present.

The available paleontological and morphological data appear to be sufficient to permit a tentative reconstruction (Fig. 6) of the evolutionary pathways within the North American component of the subgenus *Plagioctenium*. The existence of only *A. (P.) gibbus* in the Miocene is supported by the fact that it alone has a close relative in the eastern Pacific, *A. (P.) circularis* (Sowerby). The former marine connection across the Isthmus of Panama closed in the late Miocene or early Pliocene.

*A. i. sablensis* is apparently of post-glacial origin. Its ancestors may have migrated to Sable Island during the hypsithermal warm period about 4000 to 6000 years ago (Deevey and Flint, 1957; Terasmae, 1961) and probably survived during the worsening of climate at least until about 500 A. D. when, one may speculate, the protected environments still populated were exposed or obliterated by shifting sands. The survival of numerous other

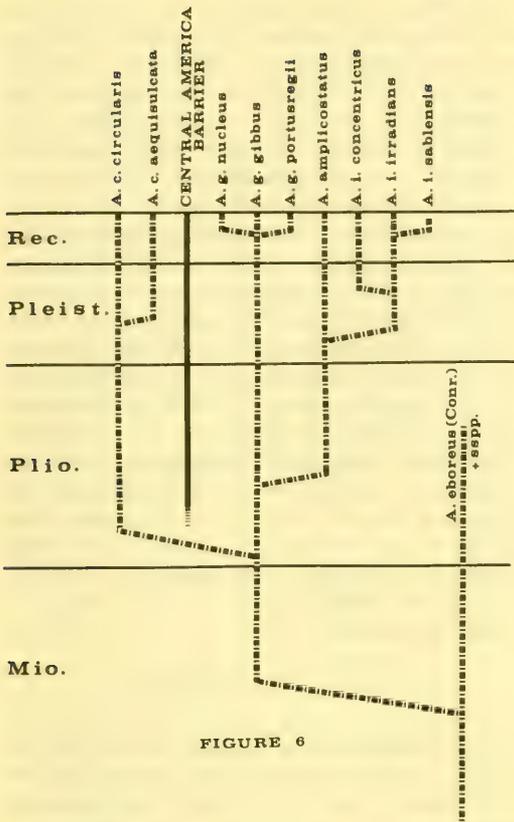


FIGURE 6

FIG. 6. Hypothetical phylogeny of the subgenus *Plagioctenium* in North America. Postulated relationships are indicated by broken lines. Data are from Dall, 1898 and 1925, Grau, 1959, and the present study.

warm-water species in protected areas of eastern Canada is well-known (Ganong, 1887; Whiteaves, 1901; Bousfield, 1960). Presumably, the range extensions of the other elements of this warm-water fauna to northern New Brunswick were also associated with the hypsithermal warm period.

Examples of every stage of divergence up to recently completed speciation are therefore evident within the *irradians* group. *A. irradians* has now reached the specific level of divergence from *A. amplicostatus*. Neither *A. i. concentricus*, a Pleistocene derivative of *A. i. irradians*, nor *A. i. sablensis*, a Recent derivative, seem to have attained specific distinctness. The Atlantic Coast populations

of *A. i. concentricus* have differentiated to a more limited extent from the Gulf of Mexico populations of the subspecies. Finally, minor differences between most of the populations within the superspecies are also evident as indicated in Figures 1 through 5. Several other species groups which, when analyzed, were found to contain populations exhibiting diverse levels of differentiation, have been incisively discussed by Mayr (1963).

Finally, it is of interest here to speculate briefly on the adaptive value of the characters which have been found useful in differentiating the taxa within this species group. Without experimental evidence, speculations of this nature are most profitable in the case of genetically controlled characters which appear to vary in correlation with geographically varying features of the environment (Brown, 1958). In the *A. irradians* superspecies, changes in the percent of right valves which are white and, to a lesser extent, changes in index of inflation (H/L), appear to be correlated with changes in latitude and climate.

Several groups of bivalves exhibit a tendency to be more compressed in the north and more inflated in the south. In North American species of the subgenus *Plagioctenium* this trend appears to be general. According to the literature it is exhibited in the northern subspecies of both *A. (P.) gibbus (portusregii* [Grau]) and *A. (P.) circularis (aequisulcata* [Carpenter]) as well as in the *irradians* group. The marine bivalve *Mulinia lateralis* also appears to exhibit this condition and a similar relationship exists between the members of several closely related species pairs in the Veneridae. Such a tendency has recently been described in some species of the freshwater mussel genus *Lampsilis* (Cvancara, 1963). The writer's own research (unpublished) has confirmed this trend in *Lampsilis* and has indicated it in some other unionid genera as well. A direct or indirect relation to temperature is suggested but no adequate explanation for this phenomenon can be offered at the present time.

Further investigations to determine the frequency of this relationship among other pelecypod groups and its causes would be of great interest.

Percent of white right valves appears to be related to the generalization that selection in the north is strongly climatic while in the south it is strongly biological<sup>2</sup>. The possession of a white lower valve in conjunction with a pigmented upper valve may have selective biological advantage. During escape from a predator a disruptive pattern would be exhibited and, in addition, the scallop would then present a strikingly different appearance than when at rest. A phenomenon similar to apostatic selection (Owen, 1963) might occur but on an individual basis and to a predator with functional vision the escaping scallop would not look like the same desirable prey which had been at rest. Examples of species which appear to have derived selective advantage by exhibiting vivid, contrasting coloration only during flight or in the process of escaping from predators (individual chromatic apostasis) occur among other animal groups, e.g. in squids, in locusts, and in tree frogs.

Apostatic selection in its original sense, however, appears to hold promise as a productive new approach in our attempt to understand the selective value of chromatic polyphasy at the species level, especially within certain brightly colored tropical genera of marine and terrestrial mollusks, and perhaps even at the community level, e.g. within coral reef communities composed of brilliant hued fishes, mollusks, etc. If Klopfer (1962) and others are correct in stating that behavior in tropical animals tends to be more stereotyped than in temperate animals, tropical

predators would also be expected to be more selective in their diets. Since tropical communities characteristically contain large numbers of species, the probability is high that the prey first captured by any single predator will be other than, say, species A. If the subsequent feeding of the predator is stereotyped and controlled to a significant degree by image fixation or some other mechanism, it will be advantageous for species A to look very different from as many other prey species as possible. If other factors do not offset the tendency, strong selection for morphological diversity between species will occur in such a community. Individual chromatic apostasis will be similarly favoured. In more temperate habitats where predation is less selective this effect would be reduced and both intraspecific and interspecific diversity would be expected to be less. This, in fact, is the case.

#### ACKNOWLEDGMENTS

Grateful thanks are extended to Mrs. Fred Andrewsckuk, Sable Island, and to Dr. Arthur Mansfield, Fisheries Research Board of Canada, Arctic Unit, Montreal, for supplying specimens of *A. irradians* from Sable Island. Thanks are also due to Mr. Arthur S. Merrill, U. S. Fish and Wildlife Service, Oxford, Maryland; Dr. Dirk Frankenberg, University of Georgia Marine Institute, Sapelo Island; Dr. W. W. Sutow, Houston, Texas; Messrs. Lawrence Potter, Bellport, New York and Richard Welsh, New York, New York and Mrs. Dorothy Raeihle, Elmhurst, New York, for contributing valuable series of pectens for this study. Appreciation is also expressed to Drs. R. Tucker Abbott and Robert Robertson, Academy of Natural Sciences of Philadelphia; to Dr. William J. Clench, Museum of Comparative Zoology, at Harvard; and to Dr. Harald A. Rehder, United States National Museum, Washington, D. C. for the generous loan of specimens of *Aequipecten* and for freely making available the research facilities of their respective institutions to the

<sup>2</sup>Detailed knowledge of predators on bay scallops is lacking. According to Marshall (1960) the most destructive predator of post-larval *Aequipecten* in Connecticut is probably the green crab *Carcinides maenas* (L.) although depredations of the oyster drill *Urosalpinx cinereus* (Say) and the starfish *Asterias vulgaris* Verrill are also important. Gutsell (1931) lists the herring gull as a conspicuous predator in North Carolina. Undoubtedly other predators, especially of larval scallops, also exist.

writer. Dr. Eugène Binder, Muséum d' Histoire Naturelle, Geneva, has been most generous in providing photographs of Lamarck's types of *Pecten irradians* and information about them, and Dr. Rehder has helped further by providing photographs of Dall's type specimen of *Pecten gibbus* var. *amplicostatus*. Finally, I wish to thank numerous friends and colleagues, especially Prof. Ernst Mayr, Drs. E. L. Bousfield, W. J. Clench, W. A. Newman, and R. D. Turner, and Messrs A. S. Merrill and R. I. Johnson, for discussing some of the problems which arose during this study. Mrs. A. M. Rick's assistance in mechanical aspects of the statistics is also appreciated. The author, however, is responsible for all statements, errors, and omissions.

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*Postscript:* While this paper was in press, through the kindness of Messrs. A. S. Merrill and R. E. Petit, the writer was able to examine a fine specimen of *Aequipecten irradians concentricus* collected alive at Cherry Hill Inlet in northern South Carolina. The specimen is similar  
 logical and ecological differences in two closely related species of scallops, *Aequipecten irradians* Lamarck and *Aequipecten gibbus* Dall from the Gulf of Mexico. Quart. J. Fla. Acad. Sci. 25(1): 89-95.  
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- to North Carolinian specimens in appearance and constitutes the only unequivocal record of the species from South Carolina. In 1957 Mr. Petit collected six living specimens at that locality but he has been unable to find any additional specimens there since then.

## RESUMEN

LA SUPERESPECIE DE VIEIRA *AEQUIPECTEN IRRADIANS* (LAMARCK)

Análisis estadísticos de las variaciones morfológicas en las intrapoblaciones de la económicamente importante especie *Aequipecten (Plagiocentrum) irradians*, permitieron la definición de tres subespecies y otra estrechamente relacionada pero distinta especie dentro del grupo. Los caracteres primarios usados son, número de costulas, relación ancho-largo, relativa inflación y frecuencia de valvas blancas derechas. Los 4 taxa reconocidos son: *A. ampliocostatus* (Dall) que se encuentra desde la costa central de Texas hasta México; *A. i concentricus* (Say) desde N. Jersey a Carolina del Sur y desde el oeste de Florida a Texas; *A. i. irradians* (Lam.) intergradando con *A. concentricus* en la zona de contacto desde Massachusetts a N. Jersey; *A. i. sablensis* subsp. n., aparentemente extinta, del post-Pleistoceno de la Isla Sable, Nueva Escocia. Por razones de estabilidad se mantiene el nombre genérico *Aequipecten* para el grupo, un neotipo de *A. i. concentricus* se designa, y la localidad típica de *A. irradians* se restringe a Falmouth, Massachusetts. Se presentan conclusiones acerca de la filogenia del subgénero *Plagiocentrum* en Norte América, la relación entre el aumento de compresión de las valvas y el aumento de latitud N. en éste como en otros grupos, el valor adaptivo de las valvas blancas derechas y la diversidad morfológica en términos de selección apostática.

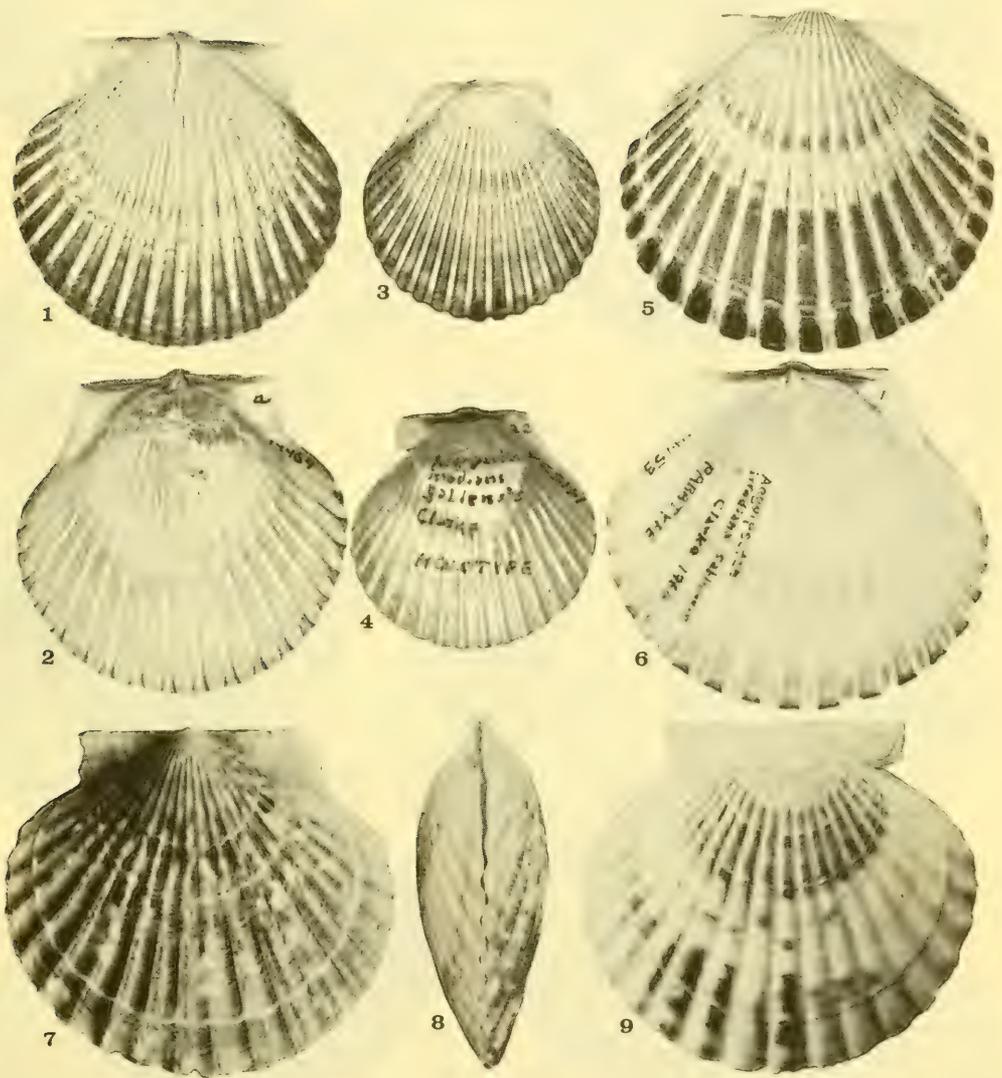
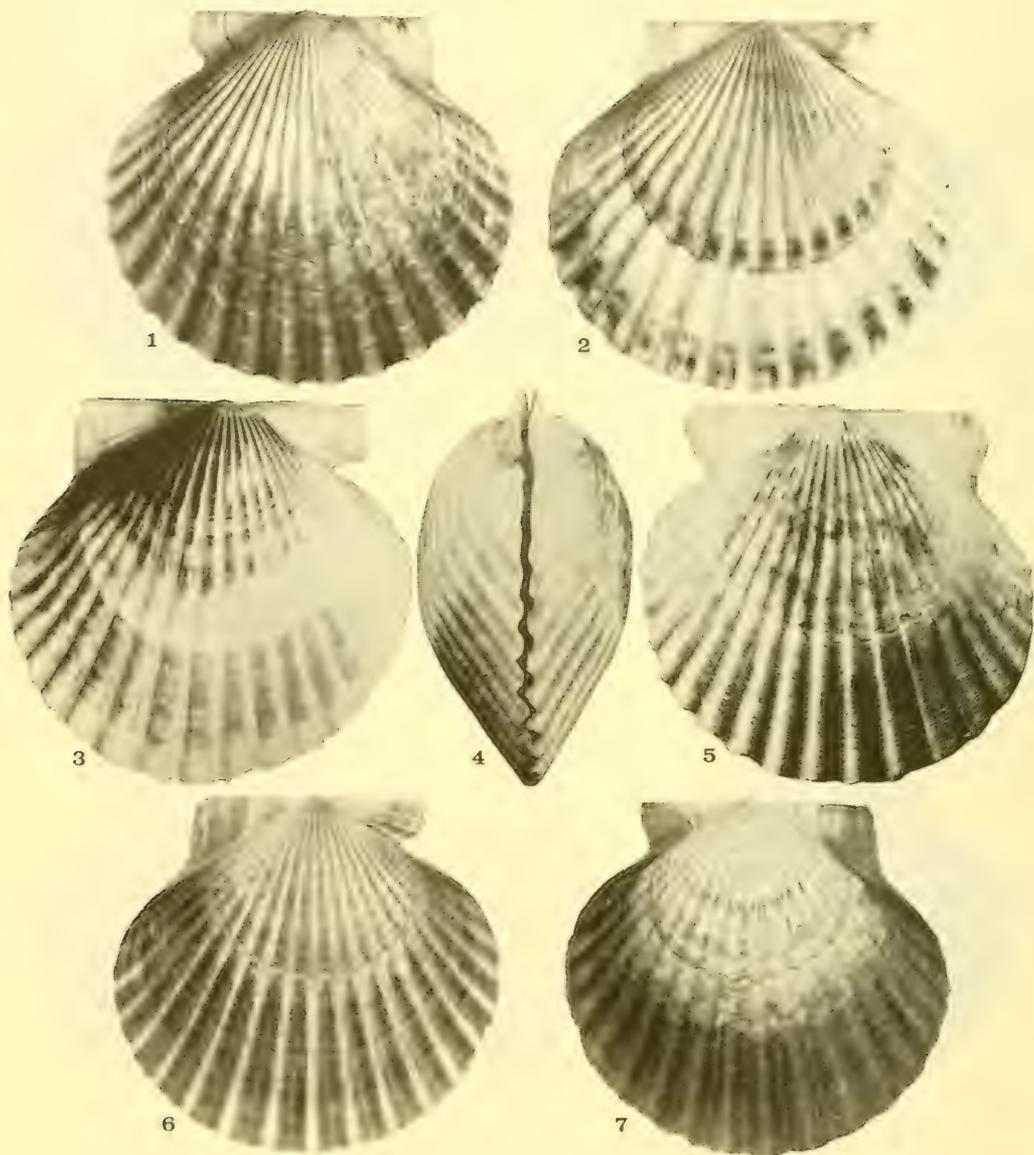


PLATE 1.

Figs. 1-6, *Aequipecten irradians sablensis*, ssp. n. (1, 2, 5, 6, paratypes; 3, 4, holotype). Figs. 7-9, *Aequipecten irradians irradians* (Lamarck), lectotype. All figures X .8.



## PLATE 2.

Figs. 1, 2, 6, 7, *Aequipecten irradians irradians* (Lamarck), topotypes from restricted type locality. Figs. 3-5, *A. i. irradians*, lectoparatype figured by Delessert and by Chenu (see text). All figures X .8.

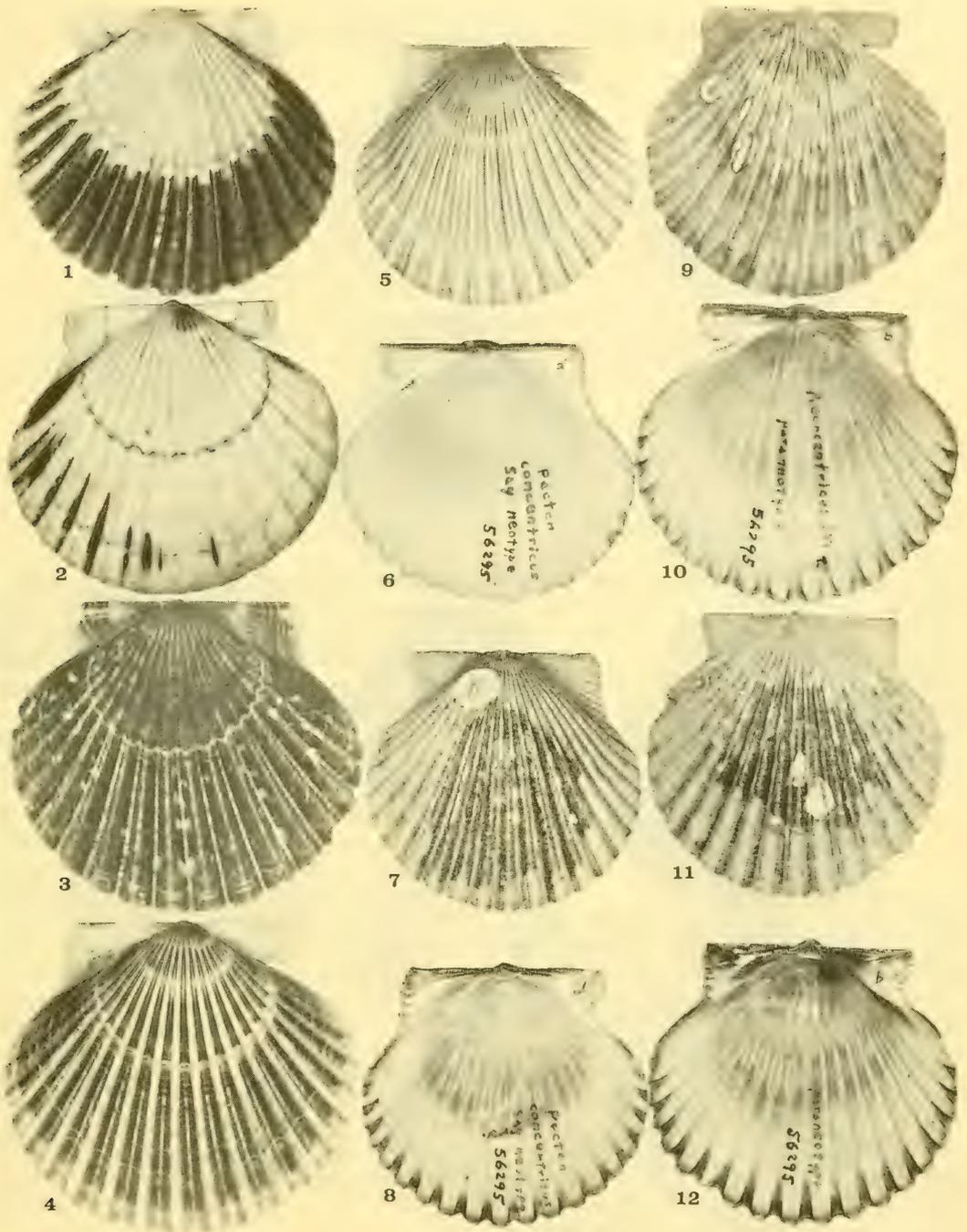


PLATE 3.

Figs. 1-4, *Aequipecten irradians irradians* (Lamarck), "New Jersey Coast" (see text).  
 Figs. 5-12, *A. i. concentricus* (Say) (5-8, neotype; 9-12 neoparatype). All figures X .8.

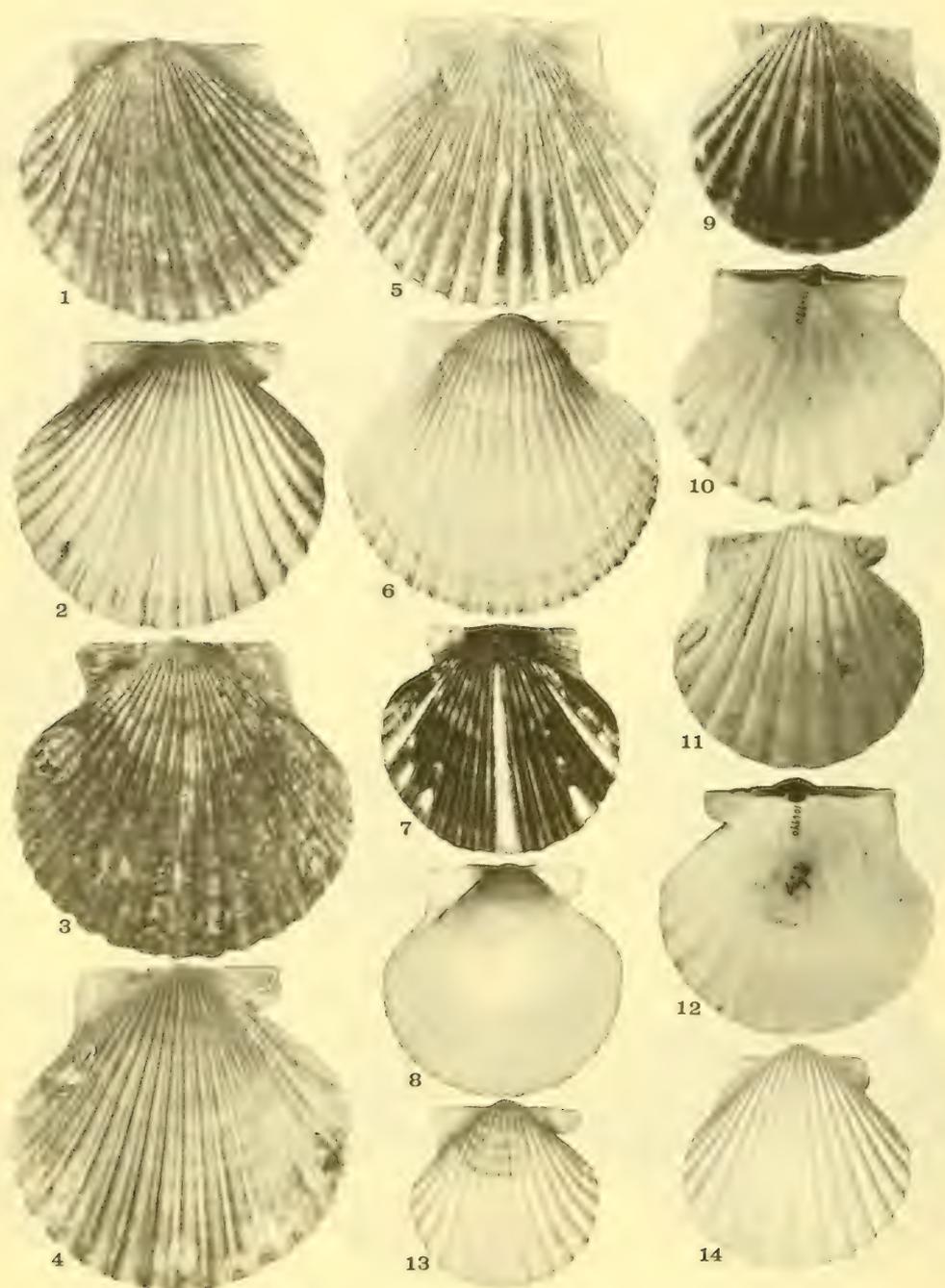


PLATE 4.

Figs. 1-8, *Aequipecten irradians concentricus* (Say) (1-4, Beaufort, N. C.: 5-8, Sanibel I., Fla.). Figs. 9-14, *Aequipecten amplicostatus* (Dall) (9-12, holotype: 13-14, off Bear's Cut, Miami, Fla., at 30 fathoms). All figures X .8. Figs. 9-12, courtesy of the United States National Museum.

TERTIARY FRESH-WATER MOLLUSKS FROM PACIFIC ISLANDS<sup>1</sup>

Harry S. Ladd

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## ABSTRACT

Two fresh- or brackish-water gastropods, a planorbid (*Gyraulus bikiniensis* Ladd, sp. n.) and a neritid (*Neritilia traceyi* Ladd, sp. n.) are described from the lower Miocene (Tertiary *e*) limestone of Bikini, Marshall Islands. Both were obtained from beds that may be related to the solution unconformity at the top of the Tertiary *e* section. The unconformity was developed at a time when Bikini stood above the sea as a high limestone island that supported a more varied fauna and flora than is found there today.

A river snail (*Clithon corona* Linnaeus) was collected from a marine tidal flat deposit in the lower Miocene (Tertiary *f*) of Fiji. Also in Fiji, a fresh- or brackish-water thiarid (*Melanoides cf. tuberculatus* Müller) occurs in abundance in a dark shaly material that probably represents an upper Tertiary mangrove swamp or bog.

## INTRODUCTION

Deep drilling and detailed field mapping have shown that Tertiary marine deposits are widespread on the islands of the open Pacific. Terrestrial fossils are rare; they include land shells and spores and pollen of a number of land plants but, to date, the only fossil freshwater mollusk has been a single river snail, *Clithon corona*, described from the upper Tertiary of Fiji. A second upper Tertiary snail, *Melanoides* has now been found in Fiji along with fragmentary remains of clams that probably record a fresh- or brackish-water environment. From a deep drill hole on Bikini in the Marshall Islands have come two other non-marine snails, a fresh-water planorbid (*Gyraulus bikiniensis* sp. n.) and a fresh- or brackish-water neritid (*Neritilia traceyi* sp. n.), both from lower Miocene (Tertiary *e*) sediments. These mollusks, the only Tertiary examples known from the open Pacific, are described in the present paper and paleoecological aspects are briefly considered.

## LOCALITIES

The Marshall Island shells (*Neritilia*

and *Gyraulus*) were recovered from lower Miocene (Tertiary *e*) beds in drill hole 2B on Bikini Island (Figs. 1, 2). The Fijian occurrences are from surface exposures of the upper Tertiary Suva Formation on the high island of Viti Levu: the *Clithon* from the type section near sea level on Walu Bay, (Sta. 160, Fig. 3); the *Melanoides* and pelecypod fragments from higher ground in the north central part of the island (Sta. C 136, Fig. 3).

## NATURE OF OCCURRENCES

The Bikini shells were picked from drill cuttings. Shells as small as these can, of course, circulate in the drilling fluid, particularly if the fluid be a heavy mud. Under these conditions there is, admittedly, some doubt as to the exact depth from which the shells were derived. It is possible that they may have come from a somewhat shallower horizon. Their preservation indicates clearly, however, that they are fossils, not shells of living forms that fell into the open hole or were pumped in from the mud pits.

The *Clithon* from Fiji was collected from a richly fossiliferous outcrop of conglomerate on Walu Bay at Suva (Sta.

<sup>1</sup>Publication authorized by the Director, U. S. Geological Survey.

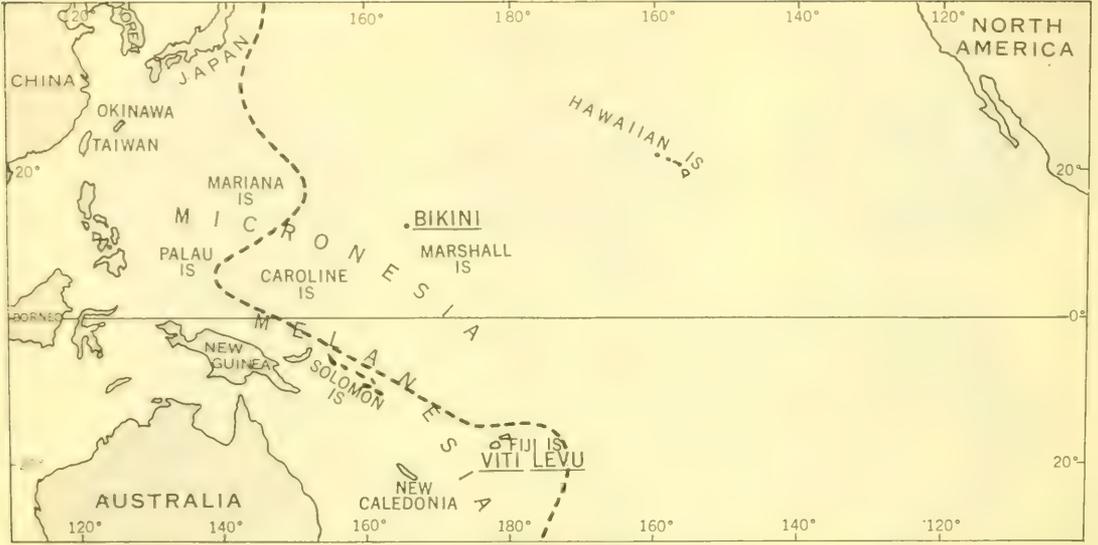


FIG. 1. Index map. Dashed line (Andesite line) marks structural boundary of the Pacific Basin.

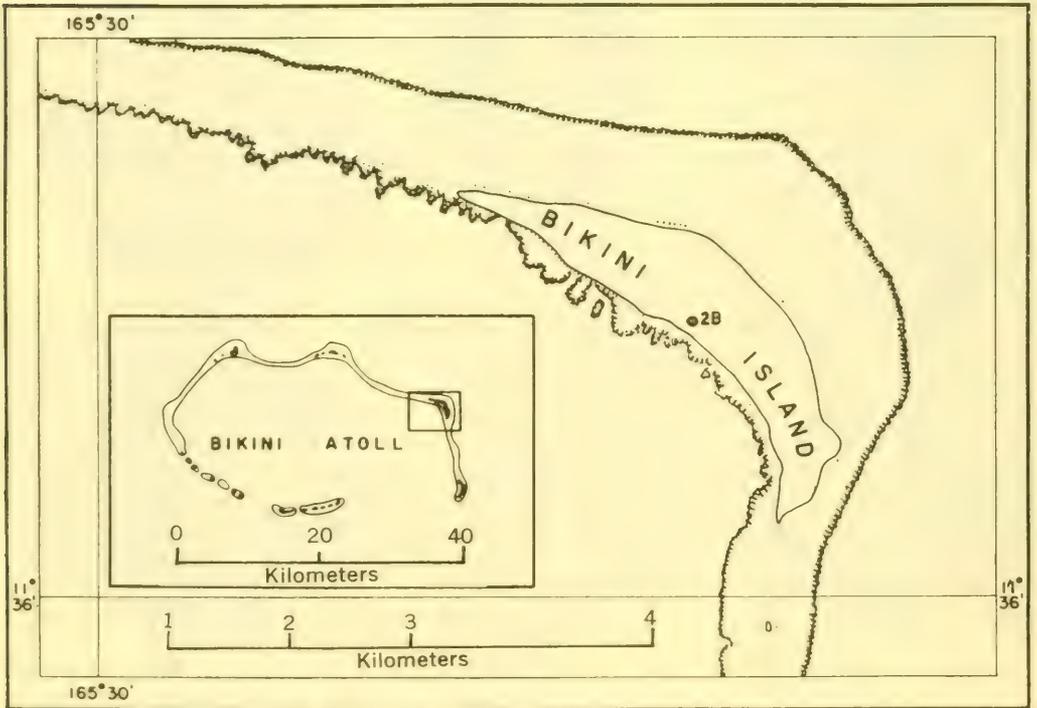


FIG. 2. Sketch map of Bikini, Marshall islands.

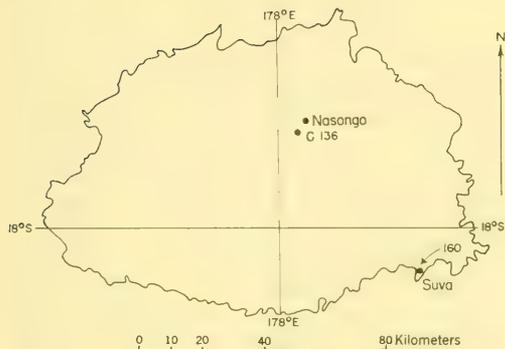


FIG. 3. Sketch map of Viti Levu, Fiji, showing locations of fossil-bearing rocks.

160, Fig. 3). The fauna is shallow-water marine and many of the mollusks and corals are worn, as is the transported river snail.

The numerous specimens of *Melanoides* were obtained from a large boulder of soft shaly material in the bed of Nasaranga Creek near the village of Nasongo in the northern interior of Viti Levu. A friable rock of this type cannot have traveled far from its outcrop in this heavily forested area.

## SYSTEMATIC DESCRIPTIONS

### Family Neritidae

Genus *Clithon* Montfort (1810, *Conchyl. Syst.*, 2, p 327).

Type (by original designation): *Nerita corona* Linnaeus. Recent, rivers of Asia and Indonesia to Melanesia.

Subgenus *Clithon* sensu stricto  
*Clithon (Clithon) corona* (Linnaeus)  
Pl. 1, Figs. 1-2

*Nerita corona* Linnaeus, 1758, *Syst. Nat.* 10th ed., p 777.

*Neritina brevispina* Lamarck, 1822, *Animaux sans vertèbres*, 6, pt. 2, p 185.

*Theodoxus corona* Baker, 1923, *Acad. Nat. Sci. Phila. Proc.* 75, p 155.

*Theodoxus (Clithon) corona* Ladd, 1934, *Bishop Mus. Bull.* 119, p 208, Pl. 35, Fig. 16; Pl. 36, Fig. 1.

*Clithon corona* Benthem Jutting, 1959, *Treubia*, 23, pt. 2, p 275, Figs. 1 and 6 (see additional citations).

A single fossil example of this widely distributed Recent Indo-Pacific fluviatile species was described from the lower Miocene (Tertiary *f*) Suva Formation of Viti Levu Ladd, 1934: 208). The species lives in Fiji today and Recent shells exhibit considerable variation in the development of the spiral ridge and its spines. The Fiji fossil clearly falls within the range exhibited by Recent shells. The species has also been recorded from the upper Pliocene and Pleistocene of Java (Benthem Jutting, 1937: 102, Table 4; 1956: 276).

Genus *Neritilia* Martens (in Martini and Chemnitz, 1879, *Systematisches Conchylien-Cabinet*, Bd. 2, Abt. 10, p 18).

Type (by original designation): *Neritilia rubida* Pease. Recent freshwater, Tahiti.

*Neritilia traceyi* Ladd, sp. n.  
Pl. 1, Figs. 3, 4

Minute, obliquely elliptical, smooth, thick; aperture lunate; inner lip convex, its margin edentulous; columellar deck convex, heavily callused, posterior margin of callus broadly convex.

Measurements of the holotype, USNM<sup>2</sup> 648336: height 1.9 mm, diameter 2.5 mm.

Occurrence: Holotype (only specimen) from drill hole 2B, Bikini Atoll at depth of 2154-2165 feet; age, lower Miocene (Tertiary *e*). The genus has not previously been reported as fossil.

*N. traceyi* has the edentulous inner lip that is characteristic of *Neritilia* but the lip margin is convex, whereas in typical *Neritilia* it is straight. The inner lip of the fossil is more heavily callused than that of the type-species, *N. rubida* (Pease), but a callused lip comparable to that of

<sup>2</sup>U. S. National Museum Catalog number.

the fossil is present on a small brackish-water *Neritilia* found in abundance, by J. P. E. Morrison, near the mouths of coastal rivers in New Caledonia. The outer lip of the fossil is worn and this accounts, in part, for the apparent great thickness of the shell and the shortness of its elliptical outline.

#### Family Thiaridae

Genus *Melanoides* Olivier (1804, Voyage dans l'Empire Othoman, l'Egypte et la Perse, 3, p 69).

Type (by monotypy): *Melanoides fasciolata* Olivier = *Nerita tuberculata* O. F. Müller.  
Recent Coromandel, India.

#### *Melanoides (Melanoides) cf tuberculatus* (Müller)

Pl. 1, Fig. 5

Small, slender; whorls moderately convex, somewhat flattened immediately below impressed suture; aperture elongate-oval, angular above, rounded below; imperforate; peristome incomplete. Sculpture consisting of spiral cords, 4-7 on penultimate whorl; on some shells the spirals are crossed by weak or moderately developed axials that give the shell a clathrate appearance, with the intersections beaded in some instances; in a few shells the axials are developed into strong curved ridges (Fig. 5).

Measurements of the figured specimen, USNM 648447: height (incomplete) 3.9 mm; diameter (body whorl incomplete) 1.4 mm.

Occurrence: Abundant at Station C 136; boulder in Nasaranga Creek about 5 kilometers southwest of Nasongo, Viti Levu, Fiji; age, probably upper Tertiary. *M. tuberculatus* was originally described as a Recent shell from Coromandel, India. The species has been widely reported from Asia Minor, Africa, India, Malaya through southern China, Indonesia, north Australia, and from a number of Pacific islands, including Fiji (Germain, 1932: 55). Fossil shells have been reported from the upper Miocene (Martin, 1905: 238),

and the Pliocene and Pleistocene of Java (Bentham Jutting, 1956: 416).

According to Mrs. van Bentham Jutting, who described Recent shells from Java and other Indonesian islands (1956: 415; 1958: 325), *M. tuberculatus* generally is found in fresh water but occasionally in brackish waters. It seems to prefer slowly running water but has been found living in stagnant, even polluted, waters; it also occurs in swamps.

The Fijian fossils almost certainly represent the exceedingly variable and widely distributed *M. tuberculatus*, but on none of the numerous fossils is the apex or the aperture complete or well preserved. The fossils have been compared with Recent shells from many areas. The fossils are smaller than most Recent shells and most of the fossils show a well developed flattened area immediately below the suture. An area of this sort is found on some Recent shells.

#### Family Planorbidae

Genus *Gyraulus* Charpentier (1837, Catalogue des mollusques terrestres et fluviatiles de la Suisse, Neue Denkschr. Allg. Schweiz. Gesell., 1(2): 21).

#### Subgenus *Gyraulus* sensu stricto

Type (by subsequent designation, Dall, 1870, Ann. Lyceum Nat. Hist. 9, p 351): *Planorbis albus* Müller. Recent, rivers of Europe.

#### *Gyraulus (Gyraulus) bikiniensis*

Ladd, sp. n.

Pl. 1, Figs. 6-8

Shell minute, thick; 2 1/2 visible rounded whorls coiled in a discoid spiral that is flattened below; suture deep, apex sharply sunken, aperture semi-oval, oblique, its lower margin projecting forward; peristome incomplete, slightly callused both above and below at its junction with the penultimate whorl. Sculpture consisting of fine curved growth lines that are more conspicuous near the aperture than elsewhere.

Measurements of the holotype, USNM 648448: height 1.0 mm, diameter 2.0 mm.

**Occurrence:** Holotype (only specimen) from drill hole 2B, Bikini Atoll, at depth of 1723-1734 feet; age, lower Miocene (Tertiary e).

*G. bikiniensis* is characterized particularly by its height, which is equal to one-half the diameter, and by the absence of spiral sculpture and any trace of a peripheral keel. The single specimen may be immature.

It is proportionately much higher than *G. albus*, the type species. It more nearly resembles *G. brongersmai*, a Recent species described from West New Guinea (Bentham Jutting, 1963: 495, Figs. 50a, 50b) but the Recent shell has more numerous whorls, a peripheral keel and a less deeply sunken apex.

In the Pacific area, a number of species of *Gyraulus* have been reported from the western islands (Japan, Philippines, New Guinea). Three species have been reported from the islands of the open Pacific: *G. singularis* (Mousson) from Fiji (Germain 1923: 146); *G. montrouzieri* (Gassies) from the New Hebrides (Solem 1959: 164) and New Caledonia (Germain, 1923: 147); and *G. rossiteri* (Crosse) from the Loyalty Islands (Crosse 1880: 142) and New Caledonia (Solem, 1961: 440). None of these species closely resembles the Miocene *G. bikiniensis* from the Marshall Islands.

#### Pelecypods

Associated with the numerous crushed shells of *Melanoides* are a number of small fragments of pelecypod shells. Most of these show growth lines, but these are not diagnostic. A few retain parts of a dark-brown periostracum. One fragment is a badly eroded hinge area that may represent the left valve of a small *Batissa*, a genus common in the fresh and brackish waters of Viti Levu today. Another fragment with close-set rounded ribs and an internal pearly luster probably represents a mytilid, possibly a species of *Arcuatula*, an intertidal and brackish-water group.

#### PALEOECOLOGY

Three distinct environments seem to be represented by the shells described above: (1) a lower Miocene elevated reef island in the Marshalls, (2) a Miocene tidal flat deposit in Fiji, and (3) an upper Tertiary mangrove swamp or bog, also in Fiji.

(1) The planorbid, *Gyraulus*, and the *Neritilia* from drill hole 2B on Bikini were recovered from cuttings below the solution unconformity that marks the top of Tertiary e beneath both Bikini and Eniwetok. These relations are clearly portrayed by Schlanger (1963: 995; Fig. 308). The unconformity is a leached interval in which original aragonite has been replaced by calcite (Ladd and Tracey, 1957: 218). The zone is thought to record a time when the atoll stood some hundreds of feet above the sea and underwent prolonged subaerial erosion. The drill hole that furnished the fresh-water shells also yielded a high-land land snail, *Ptychodon subpacificus* (Ladd, 1958: 189) at a depth of 1807-1818 feet, an interval lying between the *Gyraulus* occurrence (1723-1734 feet) and the *Neritilia* bed (2154-2165 feet).

The solution zone in drill hole 2B extends from about 1100 feet to about 1600 feet (Schlanger, 1963: 995, Fig. 308). I think that the 3 non-marine shells, all small and showing some evidence of wear, occurring 100 to 500 feet below the solution zone, lived at the time the beds were being leached. Bikini at this time is thought to have stood above the sea with high island vegetation and with pools of fresh or brackish water near sea level that could have furnished a suitable environment for the planorbid and the *Neritilia*. One brackish pool (probably artificial, at least in part) exists on Bikini Island today. The surface of the pool lies just above sea level; it is fed by the thin Ghyben-Herzberg lens of fresh water that underlies the island (Emery et al., 1954: 50, 204). No species of *Gyraulus* or *Neritilia* were found living on Bikini and nearby atolls during extensive field work by the Geological Survey nor were any land shells of the *Ptychodon* type discovered. How-

ever, in early Miocene times, when the island was larger and stood higher, natural pools of fresh and brackish water apparently existed, as they do on many elevated limestone islands today.<sup>3</sup>

Living planorbids of the *Gyraulus* type have been reported from all continents. They are abundant in Indonesia and the Philippines and, as noted above (p 9), have been reported from the New Hebrides, New Caledonia, Fiji, and other Pacific islands. None, however, have been reported living in the Marshall Islands. They live in fresh, mostly stagnant, water and also occur in sluggish streams (Bentham Jutting 1956: 463). Small and fragile shells of *Gyraulus* were dredged from depths of about 300 to 700 fathoms in Indonesian waters by the U. S. Fish Commission steamer *Albatross* (Specimens in USNM collection). Many of the living animals are remarkably hardy. They inhabit small pools that may become nearly or completely dry during periods of dry weather (Baker, 1945: 17). According to Kew, planorbids have survived even after being frozen in solid ice for a period of a month. This suggested a new means of dispersal across arms of the sea (Kew, 1893: 42), but tropical species can hardly take advantage of this uncertain means of dispersal. They manage, however, to get around. Living in the shallow waters of ponds favored by wading birds, they do, on occasion, attach themselves to the feathers of such a bird and are transported. Roscoe has reported finding representatives of 3 fresh-water snail families (one a planorbid, *Helisoma*) on a White-faced Glossy Ibis (Roscoe, 1955).

*Neritilia* has not been found living in the

Marshall Islands in spite of intensive collecting there. It has been collected from many other island groups in the southwest Pacific, the nearest to the Marshall Islands being Samoa and Fiji. The Miocene shell from Bikini appears to be the first fossil occurrence.

(2) In Fiji the single specimen of the river snail, *Clithon corona* was collected from the conglomerate layer that underlies reef limestone in the type section of the Miocene (Tertiary *f*) Suva Formation on Walu Bay, Viti Levu. The conglomerate ranges in thickness from a few inches to more than 10 feet. It contains well rounded pebbles and boulders of several types of igneous rocks as much as 6 inches in diameter, along with coral heads. The corals are water worn, as are many of the shells of about 50 species of marine mollusks that occur with them. The mollusks are reef and reef-flat species and the worn coral heads also suggest a reef flat or shore platform. The well rounded igneous boulders and the worn river snail were probably brought to the flat by a stream descending from a steeply rising coast. Several such streams enter Suva Harbor in this area today and river snails of several sorts are found in abundance on boulders in their beds.<sup>4</sup>

(3) The Fijian sample that yielded the numerous crushed specimens of the fresh-water snail, *Melanoides*, and fragments of at least 2 pelecypods is a soft, nearly black shaly material whose dark color distinguishes it from the buff to green tuffs that blanket much of the large island of Viti Livu. The sample contains abundant coaly black material that, on ignition, leaves a well-bedded residue of the shape and size of the original particle. The black organic matter seems to impregnate a fine-grained sediment. The rock also contains microscopic gypsum which may represent pyrite that has reacted with shell remains under oxidizing conditions (Milton, Charles, written

<sup>3</sup>Numerous specimens of an undescribed *Iravadia* that may have lived in brackish water were recovered from Miocene beds in all 3 deep holes on Eniwetok at depths of 670-937 feet. Most of them are in beds referred to Tertiary *g* but a few are from the underlying Tertiary *f*. All are in the unleached zone between 2 solution unconformities (Schlanger, 1963: 995). The type-species of *Iravadia* lives in the brackish waters of the Irrawaddy delta but other species apparently are near-shore marine.

<sup>4</sup>A review of the molluscan fauna of Fiji, including land and fresh-water types, has been published by Germain (1932).

communication, 1963). The dark sediments also contains a good deal of pollen and the spores of land plants. Prevalent forms are true mangrove (*Rhizophora*) and a mangrove habitat genus, *Sonneratia*. Also present are a strand plant (*Terminalia* or *Cambretum*), ferns (including *Pteridium*) and upland forest plants (Leopold, Estella, written communication, 1964). All in all, the dark rock seems to represent a fine clay sediment laid down in the fresh or slightly brackish waters of a coastal swamp or bog.

#### FRESH-WATER FOSSIL MOLLUSKS FROM THE ISLANDS OF THE OPEN PACIFIC

The oldest identified fresh-water mollusk in the Pacific Island area is a gastropod from the Upper Cretaceous of New Caledonia, described by Avias and Rey (1958) as *Pyrgulifera glypta* (Rey, 1961: 7-10, Pl. 1, Figs. 1, 2). In 1958, Freneix (p 195) noted fragments of pelecypods from an argillaceous schist of Late Cretaceous age from New Caledonia. The 2 incomplete specimens were questionably referred to the Unionidae but it was stated that they occurred with gastropods and other pelecypods that appeared to be marine.

In the Tertiary, the oldest fresh-water mollusks from the islands are the *Neritilia* and the *Gyraulus* from Bikini, here described. The *Clithon* and the *Melanoides* from Fiji are somewhat younger.

Though fresh-water pelecypods are found living in several island groups in the open Pacific today, their fossil record in these places is meager. It consists of the questionable fragments from New Caledonia and the incomplete shells from C136 in Fiji, already mentioned. The Fijian fossils occur with fresh-water snails, but the pelecypods are too incomplete for certain generic determination.

Fossil pelecypods from Fiji supposed to be of fresh-water origin were described by A. Morley Davies who, with some

reservations, gave the name of *Nodularia vitiensis* to rather poorly preserved internal molds of a pelecypod collected from an outcrop near Nasongo in Viti Levu (Fig. 3). With these fossils he recognized fragmentary molds of a small holostome gastropod, thought possibly to be a *Vivipara* (Matley and Davies, 1927: 72-75). Later, having examined photographs and descriptions of better material collected in the same area by Ladd, Davies agreed that the species thought to be a *Nodularia* was definitely mactroid and marine (Davies, 1930).

In Indonesia with its large continental islands the earliest records of fresh-water mollusks are from the Eocene and Miocene (Van der Vlerk 1931: 254, 262; Van Es, 1931: 52, 136). As Mrs. van Benthem Jutting points out, however, in Java the bulk of the non-marine mollusks does not appear prior to the middle Pliocene (1937: 86).

#### CONCLUSIONS

The fossil occurrences here described indicate that fresh and brackish-water environments existed on widely separated island areas in the southwest Pacific at least as early as the lower Miocene. This is not surprising in the case of Fiji whose large, mountainous, and geologically complicated islands are known to date back at least to the Eocene (Cole, 1960). The 2 mollusks described from the Marshall Islands, an area where no fresh-water shells live today, are of particular interest because they occur in a Miocene section which has also yielded a species of high-island land shell (Ladd, 1958) and an assemblage of pollen and spores pointing to a richer and more varied flora than is found in the area today (Leopold, in press). These paleontologic data all support a conclusion based on a petrographic study of the limestones, namely that during the Miocene, Bikini and nearby Eniwetok stood higher above the sea than they do today (Schlanger, 1963).

## ACKNOWLEDGMENTS

The sample from northern Viti Levu that yielded the *Melanoides* and associated fossils was collected by Peter Rodda of the Geological Survey Department in Fiji. This sample was examined petrographically by Charles Milton and palynologically by Estella Leopold, both of the U. S. Geological Survey.

I am indebted to J. P. E. Morrison and Harald A. Rehder of the U. S. National Museum and Dwight W. Taylor of the U. S. Geological Survey for assistance in checking identifications of some of the species and for their review of the completed manuscript. The drawings were made by Miss Roberta C. Wigder of the U. S. Geological Survey.

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## RESUMEN

## MOLUSCOS TERCIARIOS DE AGUA DULCE DE LAS ISLAS DEL PACIFICO

Dos gastrópodos de agua dulce o salobre, un planórbido (*Gyraulus bikiniensis* sp. n.) y un nerítido (*Neritilia traceyi* sp. n.) se describen, procedentes del calcareo del Mioceno inferior (Terciario *e*) de Bikini en las Islas Marshall. Ambos fueron obtenidos en estratos que pueden estar relacionados con la discordancia erosiva en el techo de la sección *e* del Terciario. La discordancia se desarrolló en una época cuando Bikini emergía sobre el océano como una alta isla de caliza que mantenía una fauna y flora más variada que la de hoy.

Un caracol fluvial (*Cliton corona* L.) se colectó en un depósito de baja marea del Mioceno inferior (Terciario *f*) de Fiji. También en Fiji, un tiárido dulceacuícola o salobre (*Melanoides* cfr. *tuberculatus* Mull.) aparece en abundancia en materiales pizarrosos oscuros que probablemente representa un pantano de mangrove del Terciario superior.

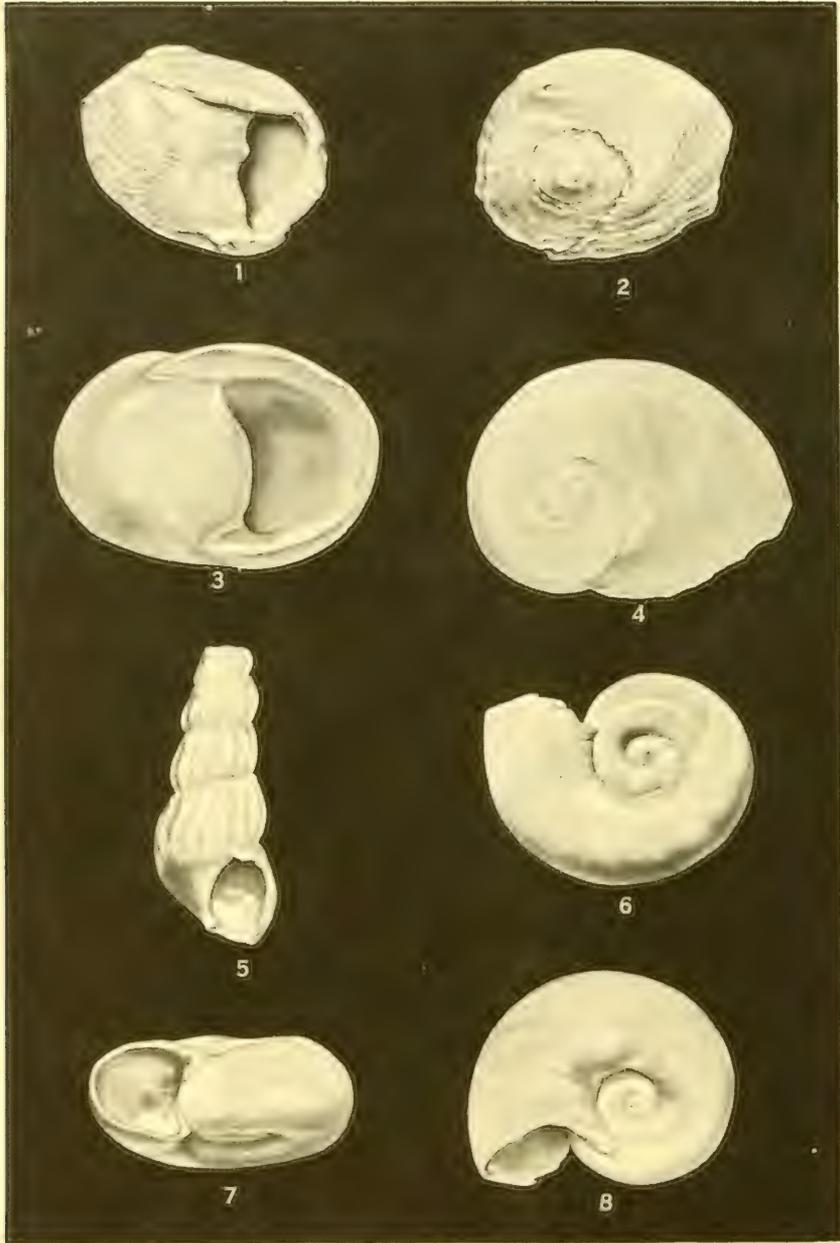


PLATE I

FIGS. 1, 2. *Clithon (Clithon) corona* (Linnaeus). Height 14.5 mm, Sta. 160, Viti Levu, Fiji; lower Miocene (Tertiary *f*). Bishop Mus., Geol. No. 1194. FIGS. 3, 4. *Neritilia traceyi* Ladd, sp. n. Holotype, height 1.9 mm, drill hole 2B, Bikini Atoll, depth 2154-2165 feet; lower Miocene (Tertiary *e*). USNM 648336. FIG. 5. *Melanoides (Melanoides) cf. tuberculatus* (Müller). Height (incomplete) 3.9 mm, Sta. C136, Viti Levu, Fiji; upper Tertiary. USNM 648447. FIGS. 6-8. *Gyraulus (Gyraulus) bikiniensis* Ladd, sp. n. Holotype, height 1.0 mm, drill hole 2B, Bikini Atoll, depth 1723-1734 feet; lower Miocene (Tertiary *e*). USNM 648448.

FEEDING AND DISPERSAL IN THE SNAIL  
*STAGNICOLA REFLEXA* (BASOMMATOPHORA: LYMNAEIDAE)

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ABSTRACT

In ponds typical of *S. reflexa*, there is a tendency for this snail to aggregate on patches of the alga *Spirogyra*. Laboratory experiments were done to confirm the food preferences, to test the capacity for distant chemoreception, and to study the behavioral response of locomotion to the presence and absence of food. Neutral water was used; light and temperatures were closely regulated.

Food preference experiments confirmed the preference noted in the field. In a long, narrow tank (300 x 15 cm) with alternating patches of various vascular plants and *Spirogyra*, snails aggregated after 12 hours on the alga rather than on the vascular plants, in the ratio of 3:1, from 1620 position recordings.

Chemoreception experiments: in a smaller tank (70 x 7 cm), a clump of *Spirogyra* was placed at one end. Snails placed in the center of the tank moved equally to both ends, as they did in the control situation with no food present. However, those that did move onto the alga remained to feed and ultimately created aggregations. In a Y tank with a leg of 60 cm, snails did not enter the arm containing algal homogenate to a greater degree than the control arm. Those which did enter the algal arm remained to feed. No distant chemoreception was noted, but, when in contact with either intact or homogenized alga, locomotion ceased and feeding began. While distant chemoreception is well documented for carnivorous snails, it is not for herbivores, perhaps for want of sufficient study. It is proposed that herbivores such as *S. reflexa*, with their food more widely available than carnivores, may not need distant perception to locate food precisely.

Dispersal experiments: in a long, narrow tank (300 x 15 cm), the rate of locomotion is much less when the tank is filled with algae than when the tank is barren. Movement in algae is less than in a tank filled with pond debris and vegetation. Starvation increases the rate of locomotion in any situation. It is concluded that *S. reflexa* moves randomly without any direction towards algal food. As more individuals come into contact with the preferred food and their locomotion is slowed, the result finally is aggregation. This is a type of kinesis to an optimum site; the laboratory situation reflects that found in the field.

In shallow ponds of northwestern Iowa, large numbers of the snail *Stagnicola reflexa* Say, are concentrated in algal beds rather than on the more prominent vascular plants or on the non-living substratum. Such stagnant ponds, often dry in summer, are the characteristic habitat of this species of snail, though they are also present in the shallow waters of the embayments of Lake West Okoboji (Bovbjerg and Ulmer, 1960). The range is extensive, from Nebraska to eastern Quebec and from the Ohio River north to Manitoba (Baker, 1928; Goodrich and van der Schalie, 1939; Dawley, 1947). The specific, contagious, dispersion

pattern suggested investigations of feeding responses and movement.

Preliminary observations in the field and at the Iowa Lakeside Laboratory indicated a wide food range. The snails fed on natural vegetation such as water cress, buttercup, *Elodea* and various algae. They also fed on the algal growth on stones, woody debris, or submerged vegetation. In the laboratory they ate lettuce and liver. When food was wrapped in cloth, however, there was no attraction, suggesting a lack of distant chemoreception.

Other lymnaeid snails have been cultured on many diets. *Lymnaea stagnalis*

and *Stagnicola palustris* have been reared on lettuce, spinach, bacteria, and algae (Carriker, 1946; Noland and Carriker, 1946; Rodina, 1948; Kopsch, 1949). Baker (1928) mentions food habits for only 2 of 30 species of lymnaeids. He designates *S. elodes* as a plant eater, scavenger and carnivore; he found *L. stagnalis* on pond weeds, both living and dead, and in blanket algae. But Macan (1950) denies any correlation between specific plant foods and any particular snail species. The precise physiological mechanisms of chemoreception in pulmonate snails have not been extensively investigated. Kohn (1961) has reviewed the general problem with respect to gastropods; studies on lymnaeid snails indicated that the anterior edge of the foot is the primary site of contact chemoreception. No study was made of the chemoreceptive mechanisms of *S. reflexa* during the investigations reported here.

No unique features distinguish the locomotion of *S. reflexa* from that of other pulmonates. Movement is similar to that of *S. palustris* described by Walter (1906) as gliding, hunching, ascent or descent. The animal is large and moves rapidly, over 1 meter within 1/2 hour. The water surface film is utilized as well as the substratum of gravel, sand, mud, or living and dead vegetation. No specific responses to light were seen. Walter found no significant difference in the clockwise or counterclockwise turns for *S. palustris*. The movement does not appear to be directed; it is periodically interrupted by surfacing for gaseous exchange. In *S. palustris* this surfacing has been found to vary with temperature and oxygen levels, from very frequent to once in 2 hours (Cheatum, 1934).

*S. reflexa* is then a species with good powers of locomotion which is frequently found in algal beds. If the movement is not directed by distant chemoreception, how is feeding related to dispersal or to the aggregation in algae? A hypothesis is: Random movements carry the individuals to the many areas including those with the most appropriate food; the snails engaged in feeding remain, while those in

less favorable regions are eventually stimulated by hunger to increased but still random locomotion. There would eventually be a population shift to optimal feeding areas, fitting the concept of "kinesis to optimum". While the preliminary observations suggested this behavior pattern, questions on chemoreception, food preference, and the relationships of feeding to movement, prompted experimentation.

#### FEEDING EXPERIMENTS

Three approaches were used in the study of feeding responses. First, choice of algal or vascular plant foods was tested in the laboratory. Second, reactions to algal homogenates were noted, and third, response to clumps of intact alga were observed to determine the level of chemoreception. Natural pond water was used; overhead fluorescent lighting was approximately 100 foot candles and water temperatures were  $22 \pm 2^{\circ}$  C.

1) To experimentally test the field observations that *S. reflexa* has a feeding preference of algae over vascular plants, a tank 3 m long by 15 cm wide was filled with 10 alternating patches of algal and vascular plant materials. Three snails were placed in each of these sectors and 12 hours later the position of each animal was recorded, on the vascular plant or on the alga. The alga was a species of *Spirogyra* and the vascular plants were, in successive experiments, *Ceratophyllum demersum*, *Myriophyllum exalbescens* and *Ranunculus longirostris*; 18 trials were made with each of these 3 combinations. To duplicate the dispersion seen in ponds, the snails should hypothetically move from the vascular plants to the alga but not the reverse.

Such a shift did indeed occur. Of the 1620 position recordings, it was 80% alga over *C. demersum*; 70% alga over *M. exalbescens*; 77% alga over *R. longirostris*. Apparently the alga is a preferred food, and the experiments seem to reflect the situation in nature where these snails tend to aggregate on *Spirogyra* beds. But the nature of the movement, whether

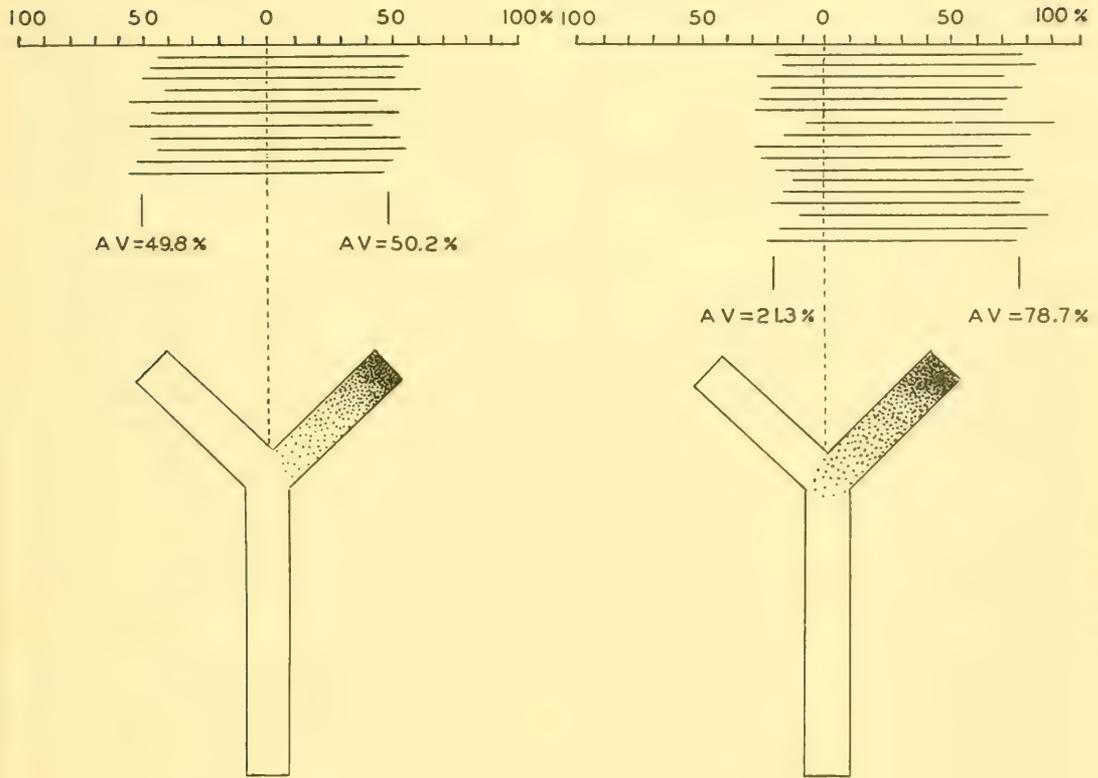


FIG. 1. Response of *S. reflexa* to algal homogenate in "Y" chamber. Left: algal material entirely within one arm. Right: algal material extending into leg of "Y". Each line above represents the dispersal of one trial of 50 snails, expressed as percent found in each arm.

directed or random, is not indicated by this experiment, nor whether the food is recognized by distant or contact chemoreception.

2) Experiments to test chemoreception were done in a plastic "Y" chamber with a single leg of 60 cm and 2 arms 30 cm long. It was 6 cm wide and the water depth was 4 cm. *Spirogyra* sp. was homogenized in a blender and introduced slowly through a funnel into one of the arms of the "Y" chamber; the other arm then acted as a control. As the algal

materials diffused slowly down the arm of the chamber in decreasing density, the leading pale edge of green could be followed visually. After a few minutes, it slowed to imperceptible movement.

Two sets of experiments were done. In the first, algal material filled one arm and penetrated the upper end of the leg of the "Y" chamber. In the second, the algal homogenate was kept entirely within the arm but extended to the junction with the leg of the chamber (See Fig. 1). In each experiment, light was of equal

intensity from all sides; water temperature was uniform. After each trial, the control and experimental arms were reversed to preclude learning as a factor. Fifty snails were released at the base of the leg 5 minutes after the algal material had stabilized in position. Movement appeared to be random, though any sustained motion had to be up the leg of the chamber. The bottom, sides and water surface film were used as avenues of locomotion. When a snail had progressed 10 cm into one of the 2 arms, it was removed and its choice recorded. An average of 35 snails of the initial 50 moved into one or the other of the arms in the 1/2 hour observation period. Twenty-nine trials were made: 1018 choices were recorded.

The results of these 2 sets of experiments are graphically illustrated in Fig. 1. In the 12 trials in which the algal materials were confined within one arm, choice between it and the control was evenly divided; 49.8% went to the control and 50.2% went to the arm with the algal homogenate. A different response occurred in the 17 trials in which the homogenate extended down into the leg of the Y chamber. Here the snails turned to the side with the algal materials at a 4 to 1 ratio (78.7% to 21.3%). Once they had come into the dense green material movement stopped.

These data indicate contact but not distant chemoreception. In the presence of algal particles, snails directed their locomotion up a chemocline into the arm containing the dense homogenate. At a distance of 1-2 cm there was apparently no detection of the algal substance or at least no directional response toward it.

3) To examine a situation approximating that which occurs in nature, a set of experiments was designed to test distant and contact response to intact alga. An elongate tank measuring 70 by 7 cm was filled with lake water to a depth of 2 cm. A clump of *Spirogyra* sp. was placed at one end. After a 5 minute stabilization period, 10 snails were carefully placed in the center of the tank; the position of

each snail was recorded at 15 minute intervals over a 90 minute period to the nearest cm. Twenty-five different groups of snails were tested as well as an equal number of control groups with no algae present. If these snails lacked distant chemoreception, then it could be predicted that snails of both experimental and control groups would move randomly toward both ends of the tank rather than directly toward the algal food.

Figure 2 presents the data graphically. Within 15 minutes, the experimental as well as control groups had distributed themselves uniformly throughout the tank. Movement appeared to be without direction, not directed toward the food. However, once in contact with the algal clump, snails stopped movement; this resulted in aggregation on the algal material. Comparison with the control is striking; here random activity of the animals continued throughout the 90 minute period.

#### Discussion of feeding experiments

*Stagnicola reflexa* does not direct its movement toward food; it does not orient toward homogenates of that food even when 1-2 cm away. But when these snails come into contact with the green homogenate, they respond by active movement up into the dense algal material. When in contact with large algal patches, the response is a reduced locomotion and intensified feeding.

Therefore, *S. reflexa* does not seem to display a distant chemoreception but does exhibit contact or taste chemoreception.

Kohn (1961), in a general review of gastropod chemoreception, concludes that chemoreception is the most important means of detecting distant foods among carnivores as well as scavengers and herbivores. His data support this view for carnivores and scavengers but are not impressive for the herbivores. Work on littorine snails (Barkman, 1955; van Dongen, 1956) does indicate some distant perception of their preferred food, *Fucus*. With *Australorbis glabratus* no distant perception of plant foods, on which they were maintained, was found. This species

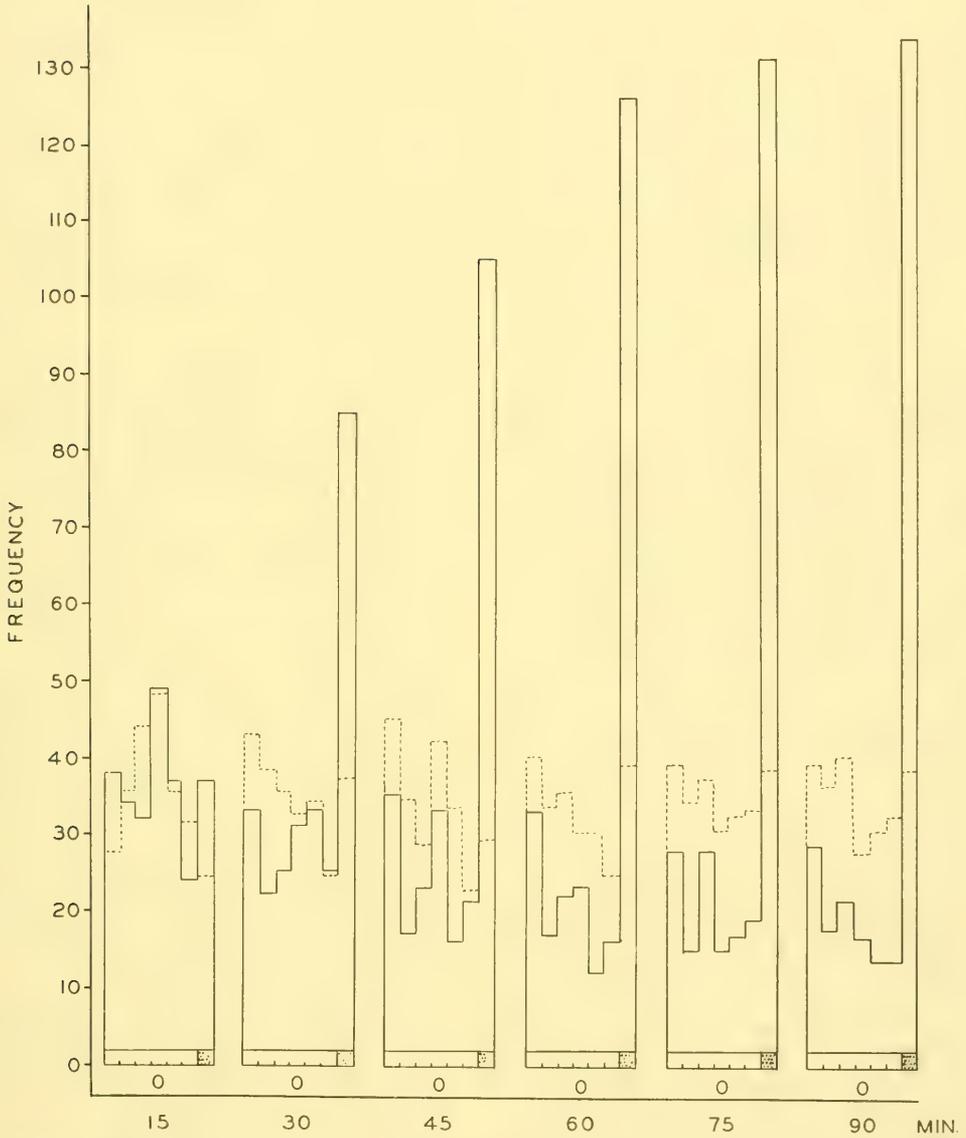


FIG. 2. Distribution of snails (500) on both sides of release point (0) during 6 successive 15 minute periods in a linear channel (70 x 7 cm) with a clump of algal food at one end as indicated by shading at the base of each histogram. Broken line indicates control groups with no alga present. Twenty-five experimental and 25 control groups of 10 snails each were tested.

did evidence distant chemoreception to such substances as wheatgerm (Michelson, 1960). While the foods of scavengers and predators are local and specific, the food of herbivores is more diffuse and tends to be more general; therefore distant chemoreception would seem of less survival value to the herbivore, though like all gastropods they display contact chemoreception. The data for *S. reflexa* support this concept; extensive study of many herbivorous species would be necessary to confirm this hypothesis.

#### DISPERSAL EXPERIMENTS

In the feeding experiments, presence of food appeared to slow locomotion. Further experiments were done to record the rates of movement for snails in the presence and in the absence of algal food. These snails came either from a large, vegetation-filled, culture tank or from barren aquaria after a week of starvation. Four experimental situations were thus established with well-fed snails in barren and nutritive environments, and starved snails in the same 2 environments. Measurement of linear distance from the release point was recorded after a 2-hour period.

Duplicate experimental channels were constructed of aluminum walls in a large indoor concrete tank. The substratum was washed gravel; lake water was maintained at a depth of 5 cm. Illumination was uniform from above. Temperature, though not regulated, varied little from 20.0° C. The channel was 3 m long and 15 cm wide; the sides were calibrated in 10 cm units.

One of these adjacent channels was loosely filled with filamentous algae: *Spirogyra* sp.; the other was filled to a comparable degree with shredded wood (such as is used in packaging). Movement of animals was possible on the bottom gravel, sides, surface film, and over the alga or shredded wood. The essential difference in the 2 environments was presence and absence of food.

The animals used in the experiments

were locally collected, adult *S. reflexa* which were maintained in large tanks filled with pond vegetation. About 200 animals were stocked; these displayed vigorous movement, feeding, copulation and egg laying; very few deaths occurred. For experiments with starved snails, groups of 30 were kept in clean glass aquaria with no food; water was changed daily. After 5 days fecal strands were almost absent; Carriker (1946) working with *L. stagnalis* noted that 5 days of starvation cleared the alimentary tract. One week was adjudged adequate time for evacuation of all nutrient from the gut.

In the experimental channels, both barren and alga-filled, 30 snails were placed in a release area at mid-point. Two hours later all snails were recovered and the position recorded to the nearest decimeter. The 2 groups were then reversed, tested in the alternate situation and returned to the stock tank. In experiments following starvation, snails were tested first in the barren tank, and on the following day in the algal tank.

Approximately 5,000 snail trials were made: 1,450 fed snails in the algal channel, 1,600 fed snails in the barren channel, 1,050 starved snails in the barren channel, and 900 starved snails in the algal channel. Distances moved and frequency for each decimeter of movement in the 2-hour period was compiled for each experimental series and means were computed from these. The data for all 4 experiments are presented in Figs. 3 and 4.

Well-fed snails from the culture tank moved, on the average, 3 times farther in the barren than in the algal channel (Fig. 3, C and A; means: 29.5 cm to 10.3 cm). Snails starved for one week moved 2 1/2 times farther in the barren than in the algal channel (Fig. 3, D and B; means: 53.4 cm to 20.4 cm). These data support the contention that locomotion slows when snails are in the midst of food, whether they are well fed or starved. On the other hand, starved snails moved approximately twice as far as well-fed animals in both experimental situations.

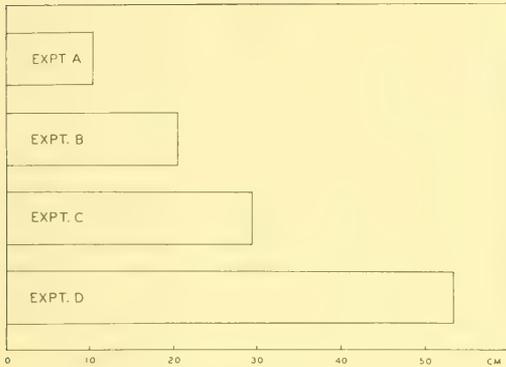


FIG. 3. Mean distance moved in 2 hours by snails (in channel), under 4 experimental conditions, from about 5000 trials. In experiments A and B the channels were filled with algae: snails in A well-fed and in B starved; in experiments C and D the channels were barren: snails in C well-fed and in D starved.

These data also support the contention that a hunger drive or its converse, satiety, have effects on locomotion.

While the mean distance moved in a 2-hour period is a general measure of the rate of movement, it is perhaps more profitable to examine the motion of the snails in terms of their actual position in the channel to the nearest decimeter. Fig. 4 is a series of histograms of such frequencies in order of increasing movement. In the experiments following prolonged feeding the bulk of the snails in the algal channel (Fig. 4, A) remained at or near the release point; less than 1% reached the half-way point of the channel. Animals in the barren channel (Fig. 4, C) were sparse at the release point and some had moved the entire distance of the channel in the 2-hour period.

A more striking difference is seen when comparing the starved snails in the 2 situations; here the locomotion of those in the barren channel (Fig. 4, D) has

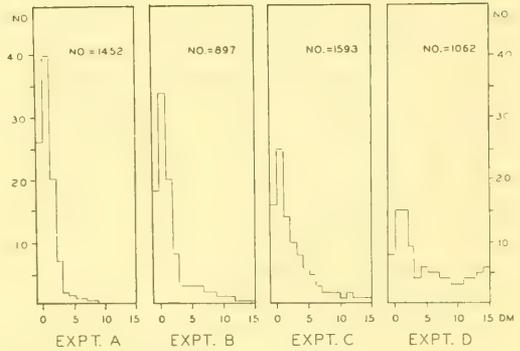


FIG. 4. Distribution of snails in channel to the nearest decimeter, after 2-hour periods, under 4 experimental conditions, from about 5000 trials. In experiments A and B the channels were filled with algae: snails in A well-fed and in B starved; in experiments C and D the channels were barren: snails in C well-fed and in D starved.

carried a large proportion to the end of the channel, many of which turned about and returned to the central stretches during a 2-hour period. In the algal channel (Fig. 4, B), starved animals tended to remain relatively nearer the release point with less than 1% reaching the end.

#### Discussion of dispersal experiments

One must conclude that *S. reflexa*, whether well-fed or starved, reduce locomotion in the presence of algal food, or that movement is increased in absence of food. It also appears that starvation is a stimulus to movement, as evidenced by the greater movement of starved animals in both environments. The nature of these 2 stimuli is opposite in action because the stimulus from starvation is positive for locomotion and the stimulus of available food is negative for movement.

The laboratory artificiality is an objection to the experiments; the pond is a complex of living and dead food and not

patches of alga or shredded wood. To more nearly parallel food choice in the field, an additional 1,700 trials were made using non-algal pond vegetation. Both green and dead cat-tail leaves, bladderwort, buttercup, liverworts, duckweed, sticks and unsorted debris were placed in the chute. Well-fed snails in this relatively natural environment moved a mean distance of 35.1 cm in the 2-hour period. This is a movement of over 3 times that of snails on algae (10.3 cm) and only a very little more than the mean distance moved in shredded wood (29.5 cm).

These experiments may have physiological, behavioral, or ecological implications with respect to *S. reflexa*. That the general concept of activity, in this case locomotion, is influenced by internal physiological states, is not new. Jennings (1906) said: "The sea anemone that is well fed remains quiet; while the individual that has exhausted the material for metabolism toils painfully away on a tour of exploration." Such colorful description might well apply to *S. reflexa* and indeed, phrased more generally, seems a truism.

Behaviorally, the orientation is a classical kinesis in the sense of Fraenkel and Gunn (1940). Movement appears random but is affected by environmental differences; as the snail encounters its optimal feeding environment, it slows to feed. In its more unfavorable feeding environment, it continues movement. Hunter (1953), working with *Radix peregrina* noted absence of snails in newly flooded lake areas until after algal growth; the snail then populated these areas. A similar response of *S. palustris* to light is described by Walter (1906); snails in bright sunlight were far more active than those in weak light, which resulted in a gathering of snails in the darker areas. Moon (1940) interprets movements of most fresh-water invertebrates as "wandering in search of food". The mussel, *Lampsilis siliquoidea* slows its movement in the presence of dense plankton (Bovbjerg, 1957). Elton (1927) stresses the "rather vague and erratic shifting of the animals from one place to another" as a result

of their normal daily activities. Such movements are often random kinesis rather than a directed movement or taxis, such as has been described for another snail, *Campeloma decisum* (Bovbjerg, 1952), or the distant chemotaxis of the carnivorous snails (Kohn, 1961).

Ecologically, the results of such kinesis are contagious distribution, "the rule in nature" (Allee *et al.*, 1949). The local pattern of dispersion and species density are in this way related to the behavioral and physiological attributes; the survival value to the species is implicit since the most suitable areas of the habitat are occupied by the *S. reflexa* population.

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## RESUMEN

ALIMENTACION Y DISPERSION DE *STAGNICOLA REFLEXA*

En charcos típicos por su contenido de *S. reflexa*, este caracol muestra tendencia gregaria sobre aglomeraciones de *Spirogyra*. Para confirmar sus preferencias alimenticias se experimentó en el laboratorio probando la capacidad químico-receptora distante y el comportamiento locomotivo en presencia o ausencia de alimento. Se usó agua de ambiente natural, luz y temperatura reguladas.

En tanques largos y angostos (300 x 15 cm) con aglomeraciones, alternadas, de varias plantas vasculares y *Spirogyra*, los caracoles se agruparon, después de 12 horas, sobre el alga antes que sobre las plantas vasculares, confirmando la preferencia notada en el ambiente natural, en la proporción de 3 a 1 en 1600 posiciones registradas. En otro tanque más pequeño (70 x 7 cm) se colocó, en un extremo, una masa de *Spirogyra*; caracoles colocados en el centro se trasladaron a ambos extremos, como ocurrió en la situación controlada cuando el tanque no contenía alimento. Sin embargo, aquellos que se movieron hacia el alga, últimamente formaron agregados. En un tanque en forma de Y con un pie de 60 cm, los caracoles no entraron en la rama que contenía algas homogeneizadas en mayor grado que el brazo controlado: pero aquellos que entraron quedaron allí a alimentarse. No se notó recepción química a la distancia, pero al entrar en contacto con algas, homogeneizadas o intactas, la locomoción cesó y los caracoles empezaron a comer. Recepción química distante se conoce bien en caracoles carnívoros pero no en herbívoros, quizá por falta de estudio suficiente. Se propone que los herbívoros como *L. reflexa*, cuyo alimento es más ampliamente obtenible que los carnívoros, pueden no necesitar la recepción distante para localizarlo.

En el tanque largo y angosto la locomoción de los caracoles se acentuaba cuando contenía algas en abundancia. Inanición aumenta la velocidad de locomoción.

En conclusión *L. reflexa* se mueve al azar hacia el alimento (algas). Cuanto mayor número de individuos entran en contacto con el alimento preferido y la locomoción disminuye, el resultado final es agregación. Este un tipo de kinesis hacia un sitio óptimo: la situación en el laboratorio refleja aquella del ambiente natural.



ABNORMAL DEVELOPMENT IN A HYBRID *ONCOMELANIA*  
(GASTROPODA: HYDROBIIDAE)<sup>1,2</sup>

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ABSTRACT

A male hybrid resulting from crossing a female *Oncomelania quadrasi* with a male *O. formosana* was found to be abnormal in several ways. Externally, there were multiple abnormal tentacles with 7 eye masses. The histology of these eye masses revealed 7 lenses, with one eye lacking a lens, and 3 without a cornea. One "eye" contained 2 lenses; 3 lenses were badly distorted. Only 5 of the eyes were considered functional.

The tentacular mass on the right side of the head was devoid of pigment and without glandular units comprising the "eyebrow" discussed in the literature.

Internally, the salivary glands were malformed; the tentacular nerves were greatly thickened; the left dorsal labial nerve entered the left tentacular area instead of travelling in the normal manner to the dorso-lateral tip of the rostrum; the pleuro-subesophageal ganglion was elongated.

The gonad was shriveled and histological examination revealed that the relatively few germ cells were primarily in early prophase. Very few sperm were evident. Abnormal large brown sphaeroids were present in the gonad. These could not be positively identified as parasites. The vas deferens was greatly shriveled in diameter.

After almost 2 years in culture with female snails no young were produced, although copulation was frequently observed.

Since thousands of normal and fertile hybrids have been observed, this case of abnormality cannot be definitely attributed to general genetic incompatibility.

Results of crossing experiments involving 2 or more of the 4 nominal species of *Oncomelania* have been reported by Wagner *et al.*, 1957; Komiya and Kojima, 1958; Wagner and Chi, 1959. Research at the 406 Medical Laboratory confirms that these "species" interbreed with almost equal facility and without reduced viability of the F<sub>1</sub> or F<sub>2</sub> generations.

In all of these studies no abnormalities have been reported. Of the thousands of

hybrids observed in the 406 laboratory only one instance of abnormal development was noted. This isolated case involved an F<sub>1</sub> male resulting from crossing a female *O. quadrasi* with a male *O. formosana*. The male used in the cross was from the Pu Yen village snail population in Taiwan. The abnormal individual was noted because of its irregular tentacular branching and the presence of multiple "eyes."

The purpose of this paper is to discuss:

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1) the survival and behavior of this individual in laboratory culture; 2) the abnormal features of this snail compared with the normal morphology of hybrids of similar parental origin; and 3) to indicate that the rarity of abnormal development in snails resulting from crossing 4 species which are widely separated geographically coupled with the success in producing F<sub>1</sub> and F<sub>2</sub> generations of hybrids, are evidence for genetic similarity of a conspecific nature.

#### LABORATORY CULTURE AND LIFE HISTORY

At 2 months of age the malformed hybrid was placed in a small aquaterrarium with several females. The females were hybrids from a cross of a female *O. nosophora* with a male *O. lupensis*. The snails were reared according to procedures outlined by Moose *et al.*, 1962. Under normal circumstances young would have been produced. Copulation was noted several times over a period of 21 months but no young resulted. The behavior of the malformed snail in culture was normal with respect to mode of progression, feeding, mating behavior, and negative geotropism. At the end of 21 months the snail was removed from culture for anatomical studies.

#### EXTERNAL MORPHOLOGICAL OBSERVATIONS

The above mentioned abnormalities are shown in Figs. 1-3. Only tentacle A (Fig. 2) and the eye at its base (no. 6) appeared comparable with the normal condition. When a normal snail is placed under direct illumination one can observe a glint of light which is reflected from the lens through the cornea. This glint of light was noted for eye 6 but not for any of the other "eyes." Below tentacle A, tentacle B arose as a strong trunk which subsequently forked. The "eye" at its base (no. 7) was only half in evidence as observed from the dorsal aspect, the remainder being buried deep in the

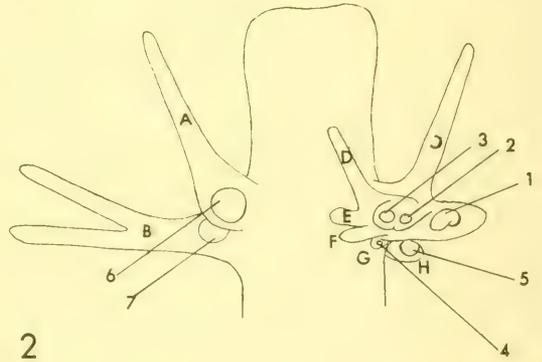
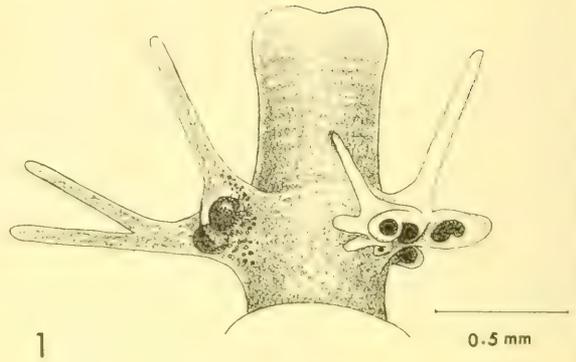


FIG. 1. Dorsal view of the head of the living hybrid showing the abnormal tentacles, eye masses, lack of pigment in the right eye mass, and absence of glandular units on the right which are evident bordering the eye masses on the left.

FIG. 2. Tentacles and eyes labeled for simplification in reference throughout the text.

flesh below tentacle A.

On the right side of the head an extremely abnormal fleshy mass had developed. The mass projected laterally as a blunt, rounded "tentacle" the dorsal curvature of which supported 3 eye-like masses (Fig. 2, 1-3). Three weak lobes (E-G) projected medially with the smallest of them, G, bearing a small pigmented mass ("eye" 4). Two tentacular structures projected anteriorly from the mass (C-D) with only C appearing normal and somewhat comparable with A.

Separated from the dorsal fleshy mass and postero-ventral to it a tubercle grew

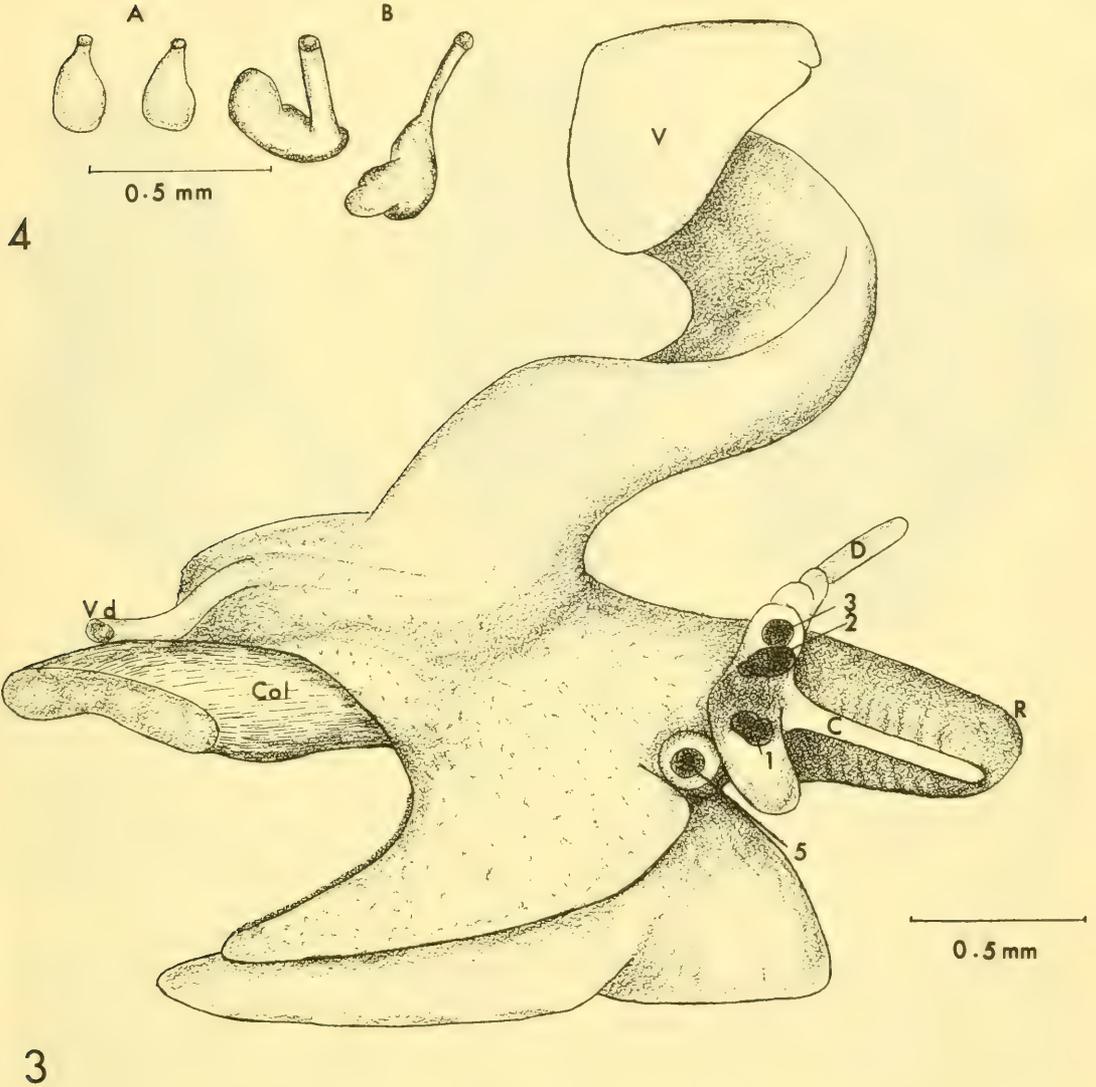


FIG. 3. Lateral view of the head of the living hybrid showing the position of eyes 1, 2, 3, 5 and tentacles C and D, the verge, V, vas deferens leading from the prostate to the tip of the penis, Vd, Columellar muscle, Col., and the rostrum, R.

FIG. 4. A comparison of the size and shape of the abnormal salivary glands, A, with normal salivary glands, B.

from the side of the head (Figs. 1-3; tentacle H, "eye" 5). This tubercle contained an eye-like mass. Only eye 6 appeared normal in size and position

compared to control individuals. The functional nature of these "eyes" is discussed below.

The head was normally pigmented with



FIG. 5. Three views of a shell quite similar to the shell of the abnormal hybrid in height, width, erosion of the apical whorls, and age.

the exception of the right tentacular mass which was devoid of any pigment. Even tentacle C which appeared normal in size compared with A was devoid of the pigment which is usually found along the tentacles.

The crescent shaped band of glandular units comprising the so called "eyebrow" described in the literature was absent on the right side while it encircled eye 6, appearing bright yellow and quite normal.

The shell was 4.2 mm high and 2.6 mm wide. The apex was badly eroded and only 3 whorls were evident. Control snails of the same age were studied and many were found with the same dimensions and eroded shells. One of these controls was chosen as a representative of several which appeared similar to the shell of the abnormal snail (Fig. 5).

#### INTERNAL ANATOMY

Upon opening the animal, further ab-

normalities were found in the nervous, digestive and reproductive systems.

Nervous system. In Fig. 6 is shown a portion of the nervous system of the abnormal snail (A) compared with that of a normal snail (B). Only those ganglia and nerves are shown which are abnormal or provide a frame of reference for the reader. The reader is referred to Itagaki (1955) for a more complete set of drawings depicting all the ganglia and nerves. Although Itagaki's paper concerns the anatomy of *O. nosophora*, the nerves and ganglia involved are homologous to those described here. Three abnormal features were observed in the hybrid in question: 1) the tentacular nerves (T) were greatly thickened as compared with those of the control; 2) the left dorsal labial nerve (Ld) (labeled ventral nerve of the proboscis by Itagaki, Plate 1, Fig. 3) forked into 2 branches which entered the left rostral wall at a point corresponding to an area opposite the left tentacles. Usually

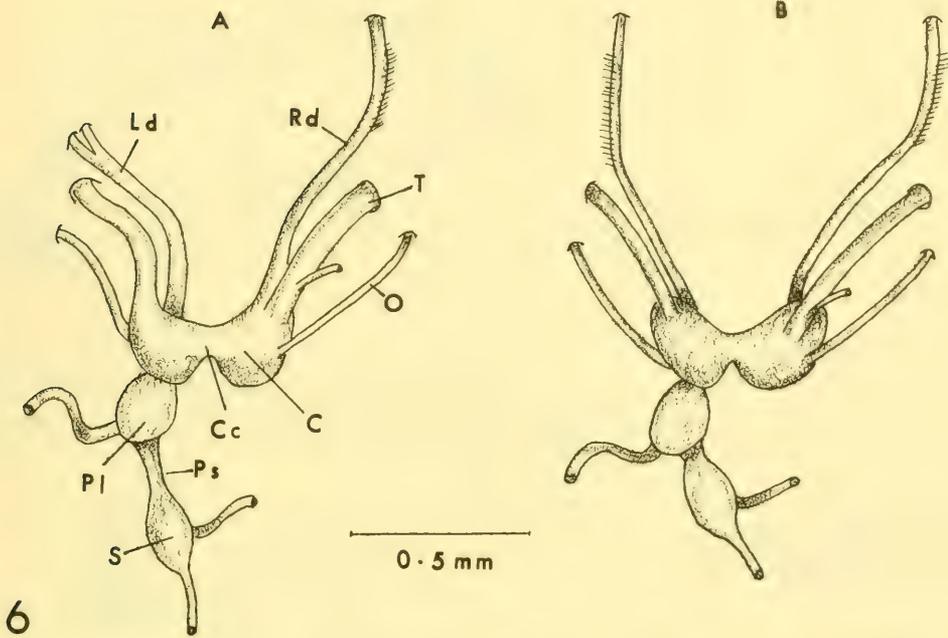


FIG. 6. A comparison of an abnormal portion of the nervous system, A, compared with the normal condition, B. Many of the normal nerves and ganglia have been left out (as they would only occlude the comparison intended). Note the thickened tentacular nerves, T, in the abnormal snail, the lengthened pleuro-subesophageal connective, Ps, and the left dorsal labial nerve, Ld, which forks and enters the left rostral wall instead of traveling anterior as that nerve does in the normal condition. Rd, right dorsal labial nerve; O, optic nerve; C, cerebral ganglion; Cc, cerebral commissure; S, subesophageal ganglion; Pl, Pleural ganglion.

this nerve fuses with the inside surface of the rostral wall and runs anteriorly to the dorso-lateral tip of the rostrum; 3) the left pleural ganglion is usually connected to the subesophageal ganglion by an extremely short connective. In the abnormal snail this connective (Ps) was elongated in a pronounced manner. The optic nerves appeared quite normal.

**Digestive system.** The salivary glands were the only malformed organs of the digestive system. The abnormal glands (Fig. 4 A) were mere flaps of tissue appressed to the buccal mass. The collecting duct of each gland was extremely short and barely noticeable. In the control (Fig. 4 B), as is the normal condition, the salivary glands are quite pronounced and swollen, projecting beyond

the buccal mass and usually overlaying the cerebral commissure. The collecting duct of each gland leading into the buccal mass was elongated and cylindrical.

The stomach, crystalline style, and pellet compressor were normal in function and morphology.

**Reproductive system.** The verge (v) was normal in position and size (Fig. 3). The coiling and uncoiling of the verge as observed in the living animal indicated normal functional potential. The vas deferens from the prostate to the tip of the verge was normal. The vas deferens (Fig. 7, Vd<sub>1</sub>) from the gonad to the prostate was abnormal in that it was extremely shrunken in diameter although the length was normal. This shrunken condition suggested that the vas deferens could

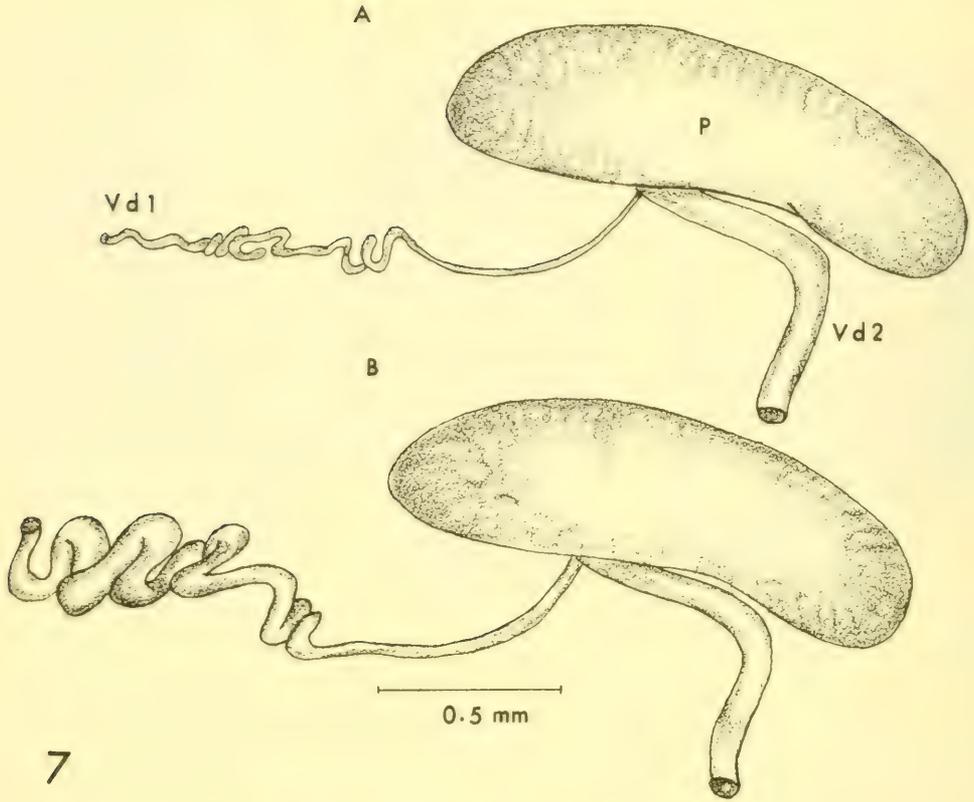


FIG. 7. A comparison of the vas deferens, Vd1, leading from the gonad to the prostate, P, in the abnormal snail, A, with that found in the normal condition, B. Vd2, the vas deferens leading from the prostate to the tip of the verge.

function but was not receiving gonadal products.

The gonad appeared abnormal in that it was a pale orange color, was reduced in size to being only 1.4 mm long, and the lobules were shriveled and appeared empty. The control gonad was bright yellow as is usual for a functional gonad, 2.0 mm long, and the lobules were swollen with gonadal products.

The abnormal gonad was removed for histological analysis, which showed that there were relatively few germ cells compared with the control gonad. The cells of the former were primarily in early prophase while in the latter, cells were detected in all stages of division with a preponderance in later stages of

spermatogenesis. Only a small peripheral area of the abnormal gonad seemed to be producing sperm and these were extremely few, about 4-5 per section with a total of about 50 sections. In the control gonad spermatid and sperm were abundant and packed throughout.

The gonad of the abnormal snail contained many large sphaeroidal brownish bodies which did not have a distinct internal structure. These were highly abnormal and have not been observed in the gonad of any of the numerous specimens studied in other investigations of this species complex. Due to the lack of distinctive structure it could not be discerned if these sphaeroids were parasites or not.

TABLE 1. An analysis of the eye masses in the abnormal hybrid

Eye No. (Fig. 2)	Cornea present or absent	Lens present or absent	Diameter of lens $\mu$	Eye considered functional
1				
lens a	-	+	35	-
lens b	-	+	63	-
2	+	+	56 x 87 <sup>3</sup>	+
3	+	+	45 x 35 <sup>3</sup>	+
4	-	-		-
5	+	+	63 x 49 <sup>3</sup>	+
6	+	+	70	+
7	? <sup>4</sup>	+	56	+

<sup>3</sup>The double dimensions indicate the lens was elongated in one axis.

<sup>4</sup>In eye no. 7 the tissue was too torn to determine the presence or absence of a cornea.

#### HISTOLOGICAL ANALYSIS OF THE "EYE"

The partially dissected rostrum was fixed in Bouins, sectioned, and stained in standard hematoxylin/eosin. Due to the dissected nature of the tissue, it did not section well, with the result that the tissue was often torn and only an incomplete analysis of the nerve tracts was possible. The tentacles and "eyes" on the left side of the rostrum were fully innervated. It was impossible to follow the course of the left dorsal labial nerve after it entered the tentacular area. Little could be determined about the innervation of the tentacular mass on the right.

The normal eye in *Oncomelania* has an anterior cornea. The cornea and the pigmented retina form a fluid-filled sac enclosing a large, discoidal, highly eosinophilic lens. A study of the sectioned material yielded data concerning the presence or absence of cornea and lens, the size of the lens, and whether or not an "eye" was considered functional (Table 1).

The "eyes" were considered functional if they possessed cornea, lens, and retina. The nerve supply to the left side was demonstrated and that to those right eye masses was considered functional because of the strong nerve roots seen to enter

the tentacular area.

Eye mass 1, studied histologically, actually enclosed 2 lenses side by side separated by a pigmented layer but with a common external pigment layer. The presence of these 2 lenses accounts for the odd shape of the mass described above (Fig. 1). In "eye" 2 the lens was extremely distorted, bulging anteriorly with a diameter of 45  $\mu$  (Table 1) and extending postero-ventrally 87  $\mu$  while becoming more slender. The postero-ventral tip was only 35  $\mu$  wide. This accounts for the elongated pigment mass shown in Fig. 3. The lens of "eye" 5 was not circular but oblong.

#### DISCUSSION

It is known that the tentacles of *Oncomelania* are prone to abnormal branching. Wong and Wagner (1956) state that of their stock *Oncomelania* 4 specimens in several thousand had simple tentacular branching, i.e., one additional tentacle on each side. A similar rate of tentacular branching has been observed for *O. quadrasi*, *O. nosophora*, and *O. formosana* reared in the laboratory at Michigan (van der Schalie and Davis, unpublished) and in the 406 laboratory. Wong and Wagner (1956) demonstrated the sensitive and plastic nature of the tissue forming the tentacles

in experiments where they induced tentacular branching with ultraviolet light. They found that, in snails whose tentacles had branched and which had survived radiation, the abnormal branches tended to become lost when radiation treatments were stopped, and that stunted, and in some cases normal tentacles regenerated. In 2 cases the eyes were damaged by the radiation, leaving only whitish masses. The damaged eyes, upon cessation of radiation, regenerated along with the tentacles into the normal condition.

In the snail under discussion no traumatic treatment such as radiation was involved. The abnormal branching and irregular eye masses were structurally integrated and stable, having developed as the snail grew and matured in the 21 months it was observed.

Experience has shown that, by the time the gonad becomes differentiated, the head and tentacles are well developed and the snail is in its 6th - 7th week of growth under the culture condition described above.

The abnormal condition of the gonad may well have been correlated with the other abnormal conditions, but not necessarily so. The presence of the large sphaeroids suggest parasitism which could have caused parasitic castration. This phenomenon has been observed in developing *Pomatiopsis lapidaria*, a species closely related to species of *Oncomelania*, where *Cercaria marilli* was present in such abundance that the gonad was reduced to an epithelial shell and functional cells were absent altogether. However, the possibility remains that the abnormalities described in the gonad were directly or indirectly associated with the cephalic abnormalities.

From the number and magnitude of the malformations it seems most likely they did not arise from an extrinsic shock but from an abnormal mode of development directed by the genetic constitution of the hybrid. As this example is the only one of its type described for hybrid *Oncomelania*, one cannot definitely attribute this case of abnormality to genetic incompatibility arising from

crossing 2 species of different genetic composition. In fact, the overwhelming success in crossing these "species" without reduced viability of F<sub>1</sub> and F<sub>2</sub> generations is evidence for genetic compatibility of a subspecific or conspecific nature.

#### ACKNOWLEDGEMENTS

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## RESUMEN

DESARROLLO ANORMAL EN UNA *ONCOMELANIA* HIBRIDA

Un híbrido macho, resultante de la cruce de una hembra de *Oncomelania quadrasi* con un macho de *O. formosana*, se desarrolló anormalmente en varios aspectos. Externamente aparecieron múltiples tentáculos con siete masas oculares; la histología de estas masas revelaron siete lentes, faltando un lente en un ojo, y tres sin córnea. Un ojo contenía dos lentes y otros tres lentes estaban muy distorsionados. Sólo cinco de los ojos se consideraron funcionales.

La masa tentacular del lado derecho de la cabeza estaba desprovista de pigmento y sin unidades glandulares. Internamente, las glándulas salivares malformadas; los nervios tentaculares muy engrosados; el nervio labial dorsal izquierdo entraba en el área tentacular izquierda en lugar de dirigirse de la manera normal al extremo dorso-lateral del rostro. El ganglio pleuro-subesofágico era alargado.

La gonada estaba fruncida y el examen histológico reveló que las, relativamente pocas, células germinativas estaban en profase primaria. Muy poco esperma evidente. Cuerpos esféricos marrones, anormalmente grandes, estaban presentes en la gonada; estos no se pudieron identificar como parásitos. El vas deferens estaba muy reducido en diámetro.

Después de conservarse en cultivo con caracoles hembras, aunque copulación fué frecuente, no se produjeron crías. Habiéndose observado millares de híbridos normales y fértiles, este caso de anomalía no se puede atribuir definitivamente a incompatibilidad genética general.



ON THE ANATOMY OF THE CENTRAL NERVOUS SYSTEM  
AND THE LOCATION OF NEUROSECRETORY CELLS IN  
*AUSTRALORBIS GLABRATUS*

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ABSTRACT

In the literature only casual attention has been paid to the central nervous system of *Australorbis glabratus*, the important American intermediate host of *Schistosoma mansoni*. The present study consists of 2 parts.

First, a detailed micro-anatomical study was undertaken of the complex of central ganglia of this species, which, as in most other pulmonates, consists of paired buccal, cerebral, pleural, parietal and pedal ganglia, and a single visceral ganglion.

Projection drawings were made of the entire central ganglia complex of a specimen with a maximum shell diameter of 19.5 mm, using photographs of each 4th section of a complete series of the central nervous system. In this way it was possible to determine not only the exact form and dimensions of the ganglia, but also to give a detailed description of the points of attachment of all commissures, connectives and peripheral nerves.

Second, particular attention was paid to the phenomenon of neurosecretion. It appeared that neurosecretory cells are present in both cerebral and parietal ganglia and in the visceral ganglion. In each cerebral ganglion a large group of these cells is found near the so-called medio-dorsal body, which lies partly upon the intercerebral commissure. Furthermore, some special cells of this type are located in the lateral lobe of this ganglion, which, as in all basommatophoran snails, protrudes near the origin of the optic and tentacular nerves. The product of the medio-dorsal neurosecretory cells is transported to the median lip nerves. In the left parietal ganglion one dorsal cell and a group of rostral cells show neurosecretory characteristics. The right parietal ganglion has only 1 neurosecretory cell, while the visceral ganglion contains a long band of such cells curving around the left parieto-visceral connective.

The numbers and location of the neurosecretory cells were determined in sections of the central nervous system of 10 specimens of different sizes, ranging from 5.5-23 mm shell-diameter. It appeared that the medio-dorsal group of the cerebral ganglia and the large group in the visceral ganglion already show neurosecretory cells in the smallest specimens studied. However, most of the other cells mentioned above have a neurosecretory character only when the snails have reached a size of 10-15 mm shell-diameter.

A comparison with *Lymnaea stagnalis* shows that *Australorbis glabratus* is less abundant in neurosecretory manifestations. In *L. stagnalis* the cerebral ganglia do not only have a medio-dorsal but also a latero-dorsal group of neurosecretory cells: the cells are more numerous in these and in the parietal ganglia, and the pleural ganglia contain 3 distinct groups of such cells, completely lacking in *A. glabratus*.

There is one exception to this rule: in *Australorbis glabratus* the number of neurosecretory cells in the visceral ganglion is higher than in *Lymnaea stagnalis*.

INTRODUCTION

Descriptions of the gross anatomy of the planorbid snail *Australorbis glabratus*, the American intermediate host of *Schistosoma mansoni*, have been published by Baker (1945) and by Paraense and Deslandes (1955), while the general histology and topographic microanatomy have been

investigated by Pan (1958). In these studies the anatomy of the central nervous system (CNS) has hardly been considered. But not for this reason alone was a detailed study of the ganglia-complex undertaken. Neurosecretory products are known to have important endocrine functions in many groups of animals (*e.g.* arthropods and vertebrates), and further-

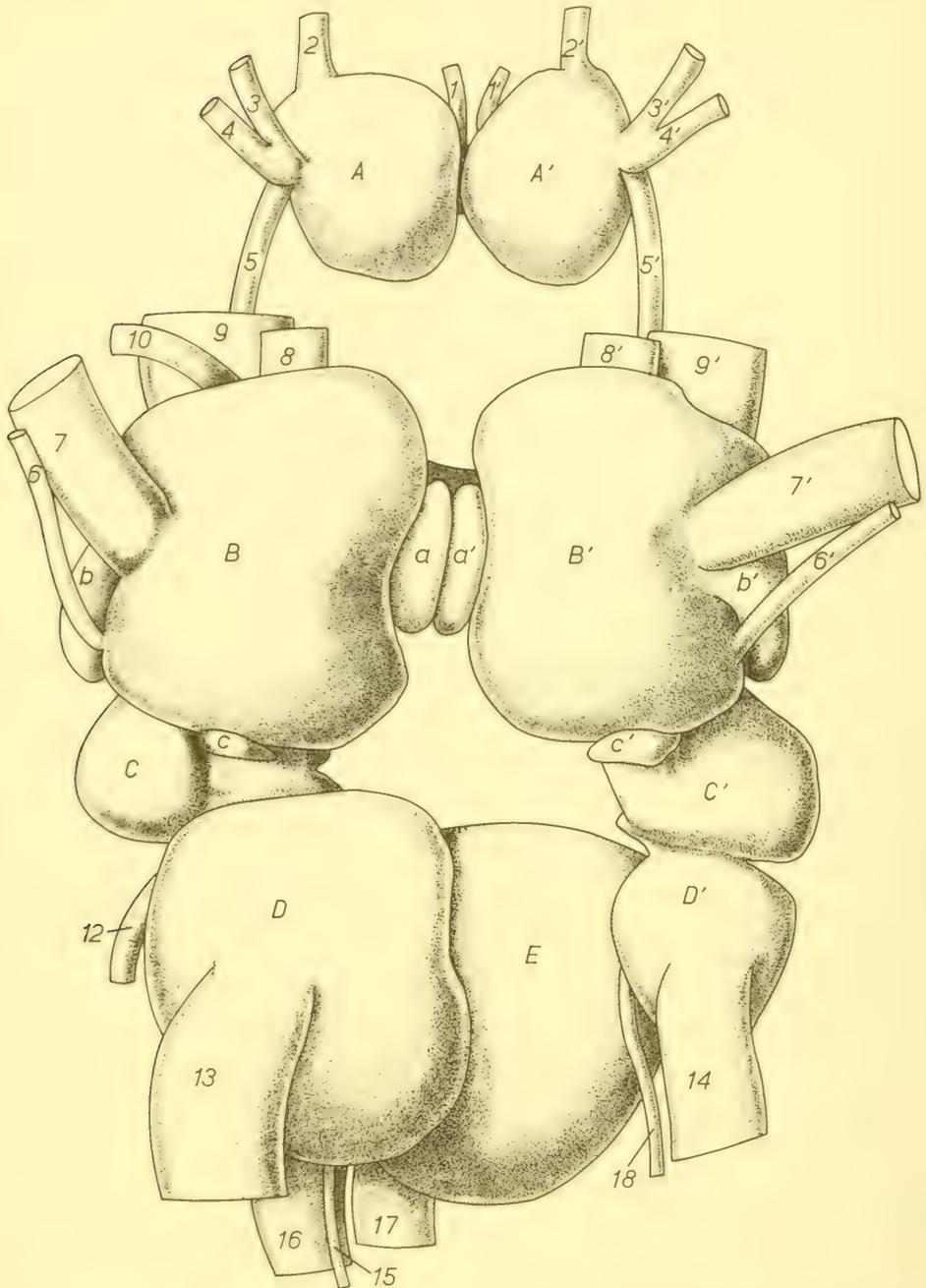


FIG. 1. Dorsal view of the central nervous system of *Australorbis glabratus*.

A, A': buccal ganglia; B, B': cerebral ganglia; C, C': pleural ganglia; D, D': parietal ganglia; E: visceral ganglion; a, a': medio-dorsal bodies; b, b': lateral lobes; c, c': latero-dorsal bodies; 1, 1': n. receptaculus radulae; 2, 2': n. gastricus; 3, 3', 4, 4': n. pharyngeales; 5, 5': cerebro-buccal connective; 6, 6': n. opticus; 7, 7': n. tentacularis; 8, 8': n. frontolabialis superior; 9, 9': n. labialis medius; 10: n. penis; 12: n. pallialis sinister externus; 13: n. pallialis sinister internus; 14: n. pallialis dexter; 15: n. genitalis; 16: n. analis; 17: n. intestinalis; 18: n. cutaneus pallialis.

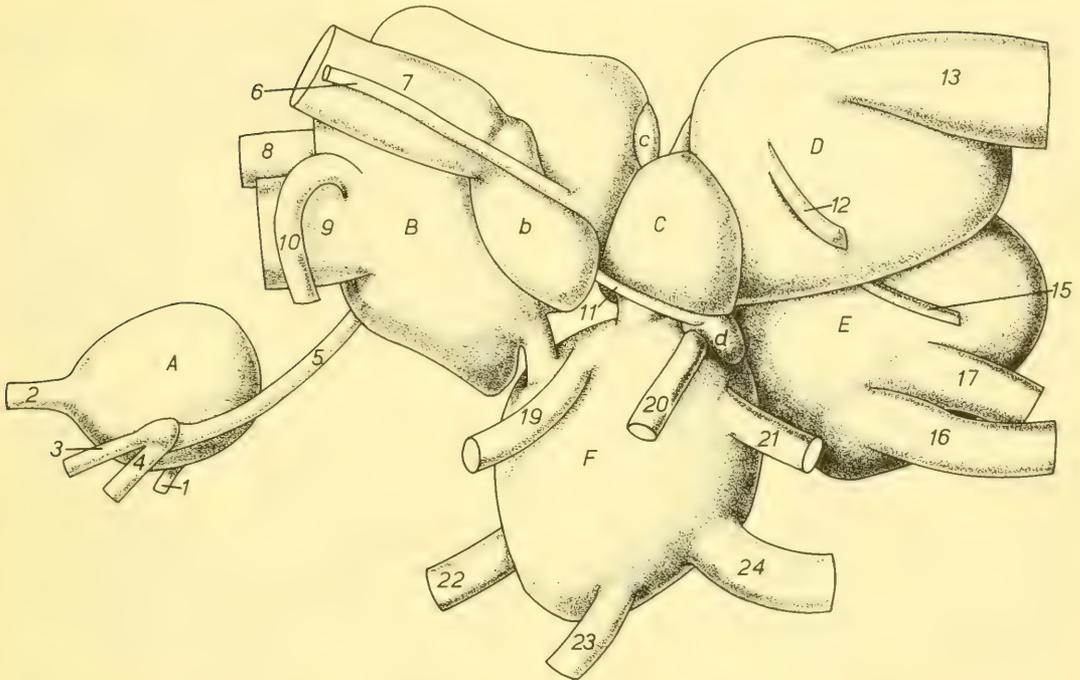


FIG. 2. The central nervous system of *Australorbis glabratus* seen from the left. See legend of Fig. 1.

F: left pedal ganglion; d: statocyst; 11: n. staticus; 19: n. cervicalis superior; 20: n. cervicalis inferior; 21: n. columellaris; 22: n. pedalis superior; 23: n. pedalis medius; 24: n. pedalis inferior.

more peculiar neurosecretory phenomena have been found in various other basommatophoran snails (Lever, 1957, 1958; Lever *et al.*, 1959; Wautier *et al.*, 1961; Joosse, 1964). It therefore seemed worthwhile to pay special attention to these cytological phenomena in this important vector snail.

#### MATERIALS AND METHODS

For the anatomical part of this study, apart from animals used for dissection, the CNS of 1 specimen, an animal with a maximum shell-diameter of 19.5 mm, was fixed in Suza and embedded in paraffin (m. p. 54°C). Serial sections were cut (thickness 5  $\mu$ ) and these were stained with Gomori's chrome-hematoxylin-phloxin method. From each 4th section a photograph was made (magnification 210x) and these were used for making projection drawings in 2 perpendicular planes (nearly vertical and horizontal).

All animals were dissected after narcotization, using the method described by Joosse and Lever (1959).

For cytological purposes the central nervous systems of 10 specimens divided over 4 size-classes (see below), were used. These snails were decapitated and the ganglia-complexes were fixed in Stieve-sublimate, and embedded, cut, and stained in the same way as that of the first-mentioned snail.

#### ANATOMY OF THE CENTRAL NERVOUS SYSTEM

As reported by Pan (1958) *Australorbis glabratus*, in conformity with most other pulmonates, has 11 central ganglia: paired buccal, cerebral, pleural, and pedal ganglia, a large left and a small right parietal, and a single visceral ganglion.

Fig. 1 gives a dorsal view of the central ganglion complex, in exact proportions (based upon the projection drawings),

TABLE 1. Maximum length (L), width (W) and height (H) in  $\mu$  of the central ganglia of a specimen with a maximum shell-diameter of 19.5 mm.

Ganglion		L	W	H
Buccal	Left	225	210	220
	Right	240	200	205
Cerebral	Left	420	385	485
	Right	425	360	430
Pleural	Left	180	285	205
	Right	185	240	255
Parietal	Left	420	370	355
	Right	200	210	305
Visceral		440	350	385
Pedal	Left	340	425	380
	Right	320	420	390

while in Fig. 2 it is seen from the left.

The maximum dimensions of the CNS of the specimen of 19.5 mm shell-diameter, excluding the buccal ganglia, were: length 965  $\mu$ , width 870  $\mu$ , and height 840  $\mu$ . The data for the individual ganglia are given in Table I.

The ganglia will be described successively. For the nomenclature of the nerves the publications of De Lacaze-Duthiers (1872) and Elo (1938-1939) were consulted. All figures refer to the specimen of 19.5 mm shell-diameter.

*a.* The small *buccal ganglia* (A and A') in Figs. 1 and 2) have approximately identical dimensions (Table I). They are interconnected by the inter-buccal commissure which originates at the ventral part of the ganglia. This commissure has a length of 100  $\mu$  and a thickness of 75  $\mu$ .

At the ventral side of the commissure near its points of attachment a n. receptaculus radulae (1, 1') arises (thickness 18  $\mu$ ). This nerve is unpaired in *Lymnaea stagnalis* (Elo 1938-1939). Both nerves enter the dorso-caudal side of the pharynx wall and innervate part of the pharyngeal musculature and the radula sac.

At the latero-anterior part of these ganglia a n. gastricus (2, 2') can be found

(thickness 28  $\mu$ ), showing successively the following branches: 1. a n. gastricus posterior which divides into a branch innervating the part of the esophagus adjacent to the buccal ganglion and a branch running caudally along the latero-ventral side of the esophagus; 2. a n. glandulae salivaris innervating the salivary gland; 3. a n. gastricus anterior running forward and bifurcating into a branch going to the anterior part of the esophagus and another to the pharynx wall.

At the ventro-lateral side of each buccal ganglion a pair of nervi pharyngeales (3, 3', 4, 4') with a thickness of 25  $\mu$  arise in common with the cerebro-buccal connective (5, 5'). Both n. pharyngeales run along the buccal mass and innervate the pharyngeal musculature. In the fixed specimen the cerebro-buccal connectives had a length of 375  $\mu$  and a thickness of 25  $\mu$ . In life, however, they are elastic and thus their length and thickness vary.

*b.* The *cerebral ganglia* (B, B') are the largest ganglia of the CNS. They are connected by the intercerebral commissure (length 70  $\mu$  and thickness 100  $\mu$ ). As can be seen in Table I the left cerebral ganglion is larger than the right one. This, in all probability, is due to the sinistrality of *Australorbis*, as in dextral species (e.g. *Lymnaea*) the reverse is found. In addition, each cerebral ganglion shows a number of peculiar structures.

First of all 4 so-called *dorsal bodies* (De Lacaze-Duthiers, 1872; Pelseneer, 1901; Lever, 1958) are present. Because in *A. glabratus* the colour of these bodies and that of the dorsal part of the cerebral ganglia are nearly alike, they can not easily be distinguished under the dissection microscope. The dimensions of these bodies are given in Table II.

Both medio-dorsal bodies (Fig. 1 a and a') partly embrace the proximal parts of the intercerebral commissure and extend over the medio-dorsal side of the ganglia. Although the medio-dorsal bodies lie close together they are always separate.

The much smaller latero-dorsal bodies (c, c') are found at the origin of the short

TABLE 2. Maximum length (L), width (W) and height (H) in  $\mu$  of the dorsal bodies and the lateral lobes of the cerebral ganglia of the specimen mentioned in Table 1.

Part of cerebral ganglion		L	W	H
Medio-dorsal body	Left	225	48	113
	Right	225	48	113
Latero-dorsal body	Left	118	98	43
	Right	143	108	48
Lateral lobe	Left	225	62	130
	Right	225	62	130

cerebro-pleural connectives. They are situated partly upon these connectives, partly upon the cerebral ganglia.

Against the capsule of the lateral side of the dorsal part of each cerebral ganglion can be found a small (Table II) oblong protrusion (b, b'), the *lateral lobe* (see Lever, 1957; Lever and Joosse, 1961). Each lobe has 2 very short connections with the cerebral ganglion, the anterior and posterior lobe connections. As in all other basommatophoran snails studied so far, each lateral lobe of *Australorbis glabratus* also contains a follicle, which, in this species, is situated near its ventral periphery (see Lever, 1958; Lever *et al.*, 1959).

From the latero-dorsal part of the cerebral ganglia a group of nerves arise innervating the main sense organs. The n. opticus (6, 6') originates at the latero-dorsal side just above the lateral lobe. This nerve has a thickness of 20  $\mu$ . In the same area the much thicker (105  $\mu$ ) n. tentacularis (7, 7') arises near the anterior part of the lateral lobe. Finally, the thin (20  $\mu$ ) n. staticus (11) originates near the caudal part of the lateral lobe (Fig. 2). We therefore disagree with Pan (1958), who thought the static nerves of *Australorbis glabratus* to originate from the pleural ganglia.

From the ventro-anterior part of each cerebral ganglion a pair of lip nerves arise: the n. fronto-labialis superior,

85  $\mu$  thick, (8, 8') originating at the anterior side, and, more ventro-laterally, the extremely thick (170  $\mu$ ) n. labialis medius (9, 9'). From the proximal part of the left n. labialis medius, close to the ganglion, the much thinner (40  $\mu$ ) unpaired n. penis (10) arises.

It must be emphasized that no nervi nuchales, as described by Elo (1938-1939) in *Lymnaea stagnalis*, could be found in *Australorbis glabratus*.

The cerebro-buccal connectives, described above, are attached to the ventro-median sides of the ganglia. Near their origin the commissura subcerebralis can also be found. This long (700  $\mu$ ) and thin (25  $\mu$ ) nerve connects both cerebral ganglia. From each proximal part of this commissure an extremely thin branch runs along a blood vessel.

The left and right cerebro-pleural connectives are very short (50 and 60  $\mu$  respectively) and thick (100 and 80  $\mu$ ). They arise at the ventro-caudal side of the dorsal part of the cerebral ganglia. The much thinner (40  $\mu$ ) cerebro-pedal connectives (length 65  $\mu$ ) are attached to the caudal side of the ventral part of the cerebral ganglia.

c. The *pleural ganglia* (C, C') are rather small (Table I). They are connected with the neighbouring ganglia by the short cerebro-pleural and pleuro-parietal connectives, which are attached to the anterior and posterior dorso-median sides of the pleural ganglia respectively, and by the short pleuro-pedal connectives which originate at the ventro-lateral side. The left and right pleuro-parietal connectives have a length of 40 and 65  $\mu$ , and a thickness of 120 and 150  $\mu$ , respectively. Both pleuro-pedal connectives are 60  $\mu$  thick and have a length of 50  $\mu$ .

The pleural ganglia have no peripheral nerves.

d. The *left parietal ganglion* (D) is very large (see Table I), especially when compared to the right one.<sup>1</sup> This ganglion has 2 peripheral nerves. The n. pallialis

<sup>1</sup>In dextral species, e.g. in *Lymnaea*, the left parietal ganglion is small and the right one is large.

sinister externus (12) originates at the lateral side of the ganglion. This slender nerve (thickness  $30 \mu$ ) runs backwards along the visceral ganglion and, at some distance from this ganglion, fuses with the n. analis (16). Shortly before this fusion the n. pallialis sinister externus has 2 branches. These run to the left and innervate the body wall area near the female sex opening.

The second nerve is the extremely thick ( $150 \mu$ ) n. pallialis sinister internus (13), which is attached to the dorsal part of the ganglion. This nerve bends to the left and enters the body wall not far from the mantle edge. Here it branches behind the female sex opening, innervating also the osphradium, the pneumostome, and part of the wall of the mantle cavity.

With regard to the connectives the following remarks are sufficient. The left pleuro-parietal connective (see above) enters the ganglion at the anterior side, whereas the extremely short ( $15 \mu$ ) left parieto-visceral connective (thickness  $75 \mu$ ) originates at its medio-ventral side.

e. The *right parietal ganglion* (D') is a comparatively small ganglion (Table I), with only 1 thick ( $115 \mu$ ) peripheral nerve, the n. pallialis dexter (14), originating at the dorso-caudal side. This nerve innervates the mantle edge. The right pleuro-parietal and parieto-visceral connectives ( $10 \mu$  in length,  $60 \mu$  thick) are attached to the same areas as the connectives of the left side.

f. The *visceral ganglion* (E) is one of the largest ganglia of *Australorbis glabratus*. It has 4 peripheral nerves. At the left dorso-lateral side of the ganglion, shortly behind the left parieto-visceral connective, arises the very thin ( $15 \mu$ ) n. genitalis (15). This nerve runs backwards along the aorta. Whether it innervates the sex organs could not be ascertained. Elo (1938-1939) introduced the name n. genitalis. We follow Elo with some reserve.

At the left ventro-lateral side 2 rather stout nerves originate, the n. analis (16) and the n. intestinalis (17), which have a thickness of 105 and  $95 \mu$  respectively.

The n. analis runs backwards through the body cavity. It enters the body wall and branches near the anal opening, innervating among other organs the pneumostome and the mantle edge.

The so-called n. intestinalis (Elo) runs also in a posterior direction. One of its branches innervates the prostate gland, another one terminates in the wall of the mantle cavity near the intestine.

Finally, immediately behind the right parieto-visceral connective, the thin ( $20 \mu$ ) n. cutaneus pallialis (18) arises from the right latero-dorsal side of the visceral ganglion. This nerve runs along the n. pallialis dexter and enters the body wall near the mantle edge.

The left and the right parieto-visceral connectives originate from the dorso-lateral sides of the visceral ganglion.

g. The *pedal ganglia* (the left one, F, is visible in Fig. 2) lie below the ring formed by the cerebral, pleural and parietal ganglia, and the visceral ganglion. They are connected with the cerebral and the pleural ganglia. The cerebro-pedal and pleuro-pedal connectives (see above) are attached anteriorly to the latero-dorsal side of the pedal ganglia (see Fig. 2). The pedal ganglia are interconnected by 2 commissures: a dorso-medial so-called anterior interpedal commissure (thickness  $35 \mu$ ) and a more caudally attached ventro-medial posterior interpedal commissure (thickness near its origin  $24 \mu$ , see below).

In an indentation at the caudo-dorsal side of each pedal ganglion a statocyst (Fig. 2: d) is present (length  $80 \mu$ , width  $110 \mu$ , and height  $80 \mu$ ), innervated by the n. staticus.

Each pedal ganglion bears 6 peripheral nerves. Three of them, all with a thickness of approximately  $50 \mu$ , arise at the dorsal side. The n. cervicalis superior (19) originates at the latero-dorsal side near the cerebro-pedal connective (see Fig. 2). This nerve runs forwards and innervates the body wall area behind the tentacle. The n. cervicalis inferior (20) is attached near the statocyst and runs in a lateral direction to innervate the body

wall of the side of the head-foot.

The third dorsal nerve, the n. columellaris (21), arises from the caudo-lateral side of the pedal ganglia, and runs to the columellar musculature in the neck area.

The ventral part of each pedal ganglion has 3 motor nerves: the n. pedalis superior (22), the n. pedalis medius (23), and the n. pedalis inferior (24), originating from the anterior, lateral and posterior sides of the ganglion, respectively, and innervating the musculature of the corresponding areas of the foot. In the same sequence the thickness of these nerves is 65, 55, and 85  $\mu$ .

Finally, at the ventral side of the posterior interpedal commissure a thin (20  $\mu$ ) unpaired nerve arises, the n. columellaris commissurae interpedalis posterioris. Near the point of origin of this nerve the commissure is thickened (70  $\mu$ ).

#### LOCATION OF NEUROSECRETORY CELLS

In all specimens studied neurosecretory cells have been observed. With the Gomori-method used the cytoplasm of such cells stains more or less dark violet, and they contain blue or black granules, droplets, or still larger inclusions. The nucleus stains slightly red. Often dark granules could also be observed in the axons. In general it was not possible to trace the entire route of the granules. In one case, however, the end-area was found. No clear indications of phloxinophilic neurosecretory cells, containing red-stained inclusions, such as have been described in *Lymnaea stagnalis* (Joose, 1964), were observed in *Australorbis glabratus*.<sup>2</sup>

The exact numbers and location of the neurosecretory cells were determined in the central nervous systems of 10 specimens, chosen out of 4 size-classes: 4 from class I (shell-length 20-23 mm),

2 from class II (15-18 mm), 2 from class III (10-11 mm), and 2 from class IV (5.5-6.5 mm).

a. In the cerebral ganglia 2 centres of neurosecretory activity were found. The first is present at the dorsal side of the ganglia, partly under the medio-dorsal bodies. Here a group of neurosecretory cells could always be found. The cytoplasm of these cells stains dark. The neurosecretory material consists of evenly distributed small granules or of larger inclusions which are located mainly at the periphery of the cells. Occasionally the entire cell is filled with a very dark-staining product. Sometimes cells show peripheral vacuoles, which frequently contain small black granules. The size of the cells of these medio-dorsal groups varies considerably, from 11-45  $\mu$ . Generally, the smallest cells are found in the centre of the groups. The size of the nuclei varies from 5-25  $\mu$ . In the largest specimens the nuclei of these cells frequently show the lobed shape often observed in neurosecretory cells (see Lever, 1957).

The total number of cells in these medio-dorsal groups is variable, as can be seen in Table III. It is clear that the groups of medio-dorsal neurosecretory cells are only fully differentiated when the snails have reached a size of 10-15 mm shell-diameter. The number of cells then varies between 27 and 47. The product of these cells is transported via the axons to the n. labialis medius (9, 9' in Figs. 1 and 2). Here it is stored in the periphery of the nerve, and, most probably, from there it can enter the blood. This observation confirms the results obtained by Joosse (1964) in *Lymnaea stagnalis*.

A second neurosecretory centre of the cerebral ganglia is found in the lateral lobes. As in *Lymnaea stagnalis*, in the larger animals 2 so-called "droplet cells" are always present (Lever and Joosse, 1961). These cells, which have a rather clear cytoplasm, contain characteristic globular dark-violet or black granules. One droplet cell lies dorsally in the lobe, and the other one is found in the ventral

<sup>2</sup>In 3 of the 4 largest specimens the dorsal periphery of the intercerebral commissure contained many phloxinophilic particles. Most probably this is identical with the neurosecretion of this type, described in *L. stagnalis* by Joosse (1964).

TABLE 3. Total numbers of neurosecretory cells present in the cerebral ganglia of 10 *Australorbis glabratus*.

Shell size: Class	Medio-dorsal groups		Lateral lobes			
	left	right	left		right	
			droplet cells	other cells	droplet cells	other cells
I (20-23 mm)	42	37	2	1	2	-
	27	33	2	1	2	+
	29	31	2	1	2	1
	47	46	2	1+	2	1
II (15-18 mm)	42	46	2	-	2	1
	40	29	2	+	2	-
III (10-11 mm)	36	28	1+	1+	2	2
	+	+	+	-	-	+
IV (5.5-6.5 mm)	12+	13+	-	-	-	-
	11+	17	-	-	-	-

+indicates that, apart from the number of cells showing clear neurosecretory phenomena, one or more dubious cells were observed.

part. Quite often vacuoles occur in the droplet cells of *Australorbis glabratus*. Table III shows that the differentiation of these cells takes place when the snails grow from size-class III to II.

Near the lateral periphery of the lobe of the large individuals (class I) 1 other neurosecretory cell is generally present. The quantity of small granules it contains can vary. Its stainability and also its shape resembles those of the cells of the medio-dorsal groups described above. Most probably this cell is homologous with the giant "canopy cell", previously found in ancyliids (Lever, 1958) and in *L. stagnalis* (Lever and Joosse, 1961).

b. In the left parietal ganglion 2 areas show neurosecretory activity. Firstly, a group of cells is found rostrally at the right side near the parieto-visceral connective. Generally this group consists exclusively of small cells (approximately 20  $\mu$  in diameter), containing large very dark staining inclusions. In 1 of the snails of class I also some larger cells were present, but these had the same characteristic large amount of dark product. The numbers of cells in this

rostral group vary considerably, as can be seen in Table IV. This table also shows that there are no clear differences between the classes.

Secondly, with the exception of the smallest animals, 1 other neurosecretory cell is always present in the left parietal ganglion. This cell, which is of the vacuolized type, may be found in various places within a small area of the dorso-anterior part of the ganglion.

Apart from the rostral group and the single dorsal cell, some other neurosecretory cells were found, in a few cases, in the left parietal ganglion. In 2 snails, belonging to size-classes I and II respectively, 2 or 3 such cells were present in the left ventral part of the ganglion.

More puzzling was the observation of a group of 21 rather dark staining cells in only 1 specimen of class I. These cells were situated latero-dorsally of the pleuro-parietal connective. Indications of the presence of this group were found in none of the other specimens.

c. In the small *right parietal ganglion* only 1 neurosecretory cell is present (see Table IV). This cell, which was

TABLE 4. Total numbers of neurosecretory cells present in some special areas of the parietal ganglia and the visceral ganglion of 10 *Australorbis glabratus*.

Shell size: Class	left parietal ganglion		right parietal ganglion	visceral ganglion
	rostral group	dorsal cell		
I (20-23 mm)	14	1	1	35+
	5	1	1	42
	6	1	1	41
	1	1	1	40+
II (15-18 mm)	5	1	1	44
	5+	1	1	19+
III (10-11 mm)	10	1	1	25
	4	-	-	38
IV (5.5-6.5 mm)	4	-	-	19+
	-	-	-	23+

+: see Table 3.

always found to contain vacuoles, lies in the ventral part of the ganglion near the parieto-visceral connective. It has a considerable size (49-72  $\mu$ ) and contains a large nucleus (largest diameter 30-52  $\mu$ ). Like the single dorsal cell in the left parietal ganglion, this cell was not seen in small specimens.

d. In the *visceral ganglion* only 1 group of neurosecretory cells was found. These cells are characterized by their intensely staining cytoplasm and by the presence of large violet-black droplets or clots in the peripheral parts. At high magnifications the clots appear to consist of smaller granules. These cells are comparatively large, ranging between 50 and 70  $\mu$ , with a nucleus of 13-48  $\mu$ . They are scattered in a long band at the left dorso-lateral side of the ganglion, curving around the origin of the left parieto-visceral connective. Table IV shows that the number of these cells varies considerably. Moreover, it appears that these cells can be found in rather high numbers even in snails of size-class IV.

e. The *buccal*, *pleural* and *pedal ganglia* lack neurosecretory phenomena. Only once has a neurosecretory cell been found in the dorsal area of the right pedal ganglion of a specimen of class I.

This cell was located latero-dorsally of the origin of the pleuro-pedal connective.

#### DISCUSSION

Surveying the results the following points are of interest.

1. It is clear that the phenomenon of neurosecretion is restricted to special parts of the CNS: the largest accumulations of cells with this type of inclusions are present in the cerebral ganglia and the visceral ganglion, while the left parietal ganglion contains only few neurosecretory cells, and the right parietal ganglion has only one. The buccal, pleural and pedal ganglia lack this phenomenon.

2. A comparison between the size-classes demonstrates that only the medio-dorsal groups of the cerebral ganglia and the group of the visceral ganglion already show a rather intensive activity in small specimens, although an increase during growth is evident. The same is possibly true for the rostral group of the left parietal ganglion, but here the number of active cells varies considerably. On the other hand, the smallest specimens studied show an absence of activity in the lateral lobes, and, also, the dorsal

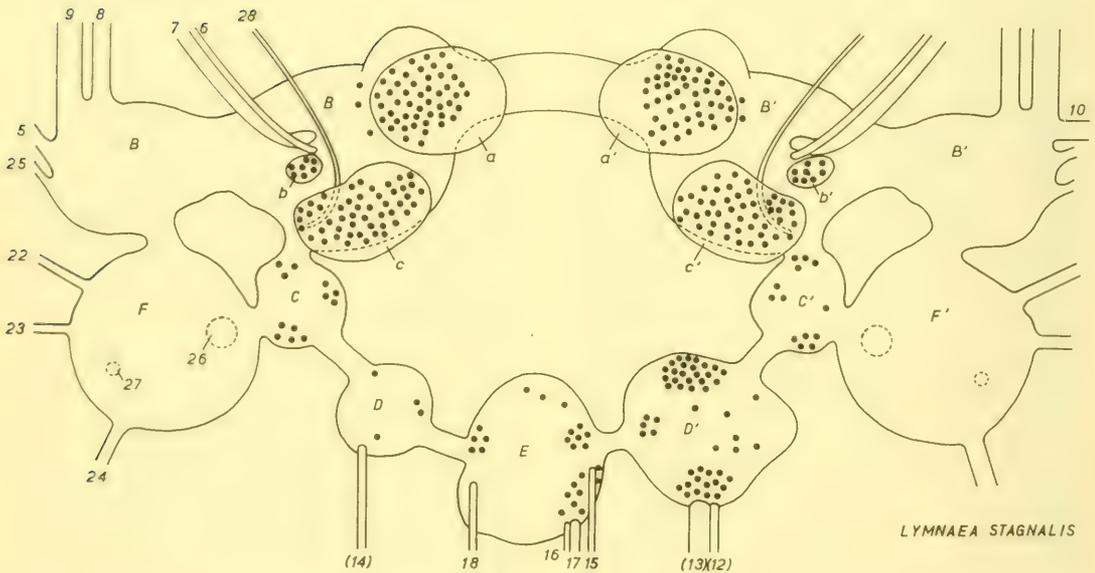
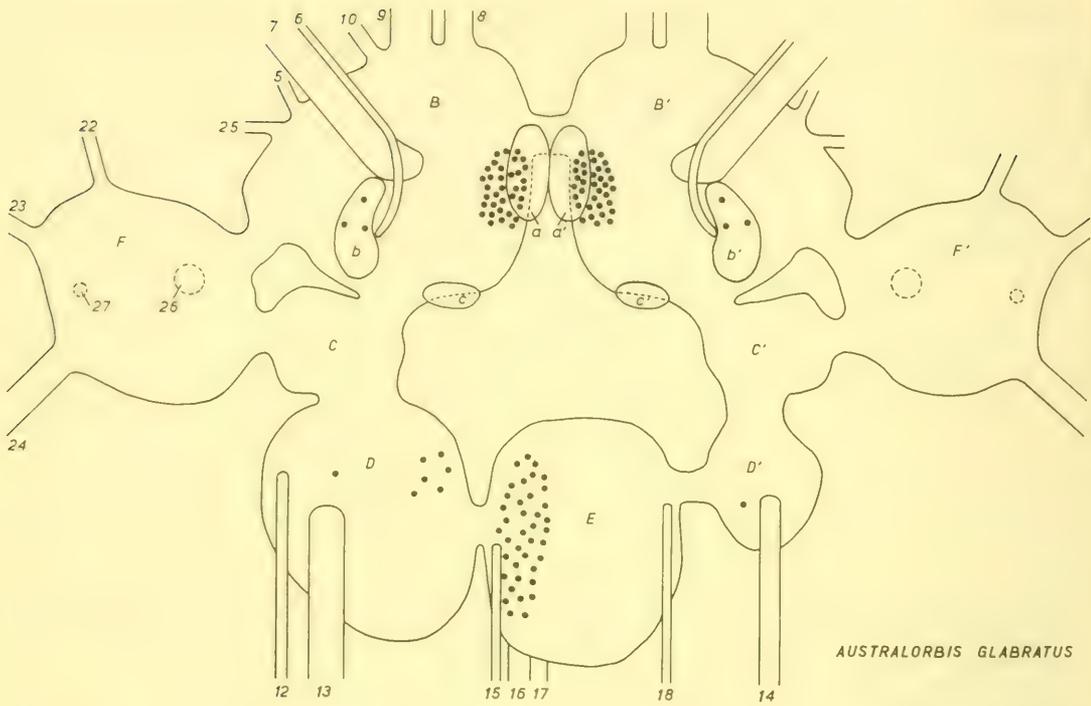


FIG. 3. The location of neurosecretory cells in the central ganglia of *Australorbis glabratus* and of *Lymnaea stagnalis*. See legend of Fig. 1.

25: commissura subcerebralis; 26: commissura interpedalis anterior; 27: commissura interpedalis posterior; 28: n. nuchalis.

cells of the left parietal ganglion and the single cell of the right parietal ganglion could not be distinguished. These cells show their neurosecretory character only in snails which have reached a size of 10-15 mm shell-diameter.

3. In Fig. 3 the number and location of neurosecretory cells in full-grown specimens of *A. glabratus* (class I) and of *L. stagnalis* (Lever *et al.*, 1961) are compared. There are some rather striking differences, generally indicating that neurosecretory phenomena in *A. glabratus* are much less abundant than in *L. stagnalis*.

It appears that, whereas the main part of each cerebral ganglion of *L. stagnalis* contains 2 nearly equally large groups of neurosecretory cells, *A. glabratus* lacks the group adjacent to the latero-dorsal body. Furthermore, although in the pleural ganglia of *L. stagnalis* 3 groups of active cells can be found, those of *A. glabratus* are entirely devoid of such cells. In the parietal ganglia the differences are less radical, but the number of secretory cells in *A. glabratus* is always lower than in *L. stagnalis*.

The only ganglion where the reverse can be observed is the visceral ganglion. In 6 specimens of *L. stagnalis* with a shell-length of 30-40.5 mm the number of neurosecretory cells in this ganglion varied between 15 and 32, whereas in the class I *A. glabratus* specimens 35-42 of such cells were found.

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#### RESUMEN

##### SISTEMA NERVIOSO CENTRAL DE AUSTRALORBIS

La atención prestada en la literatura al sistema nervioso central de *Australorbis glabratus*, el importante huésped americano de *Schistosoma mansoni*, ha sido sólo casual. El presente estudio consiste de dos partes.

Primero, se procedió a un detallado estudio macro-anatómico del complejo ganglionar central en esta especie la cual, como en la mayoría de los pulmonados, consiste en pares de ganglios bucales, cerebrales, pleurales, parietales, pedales, y un sólo ganglio visceral.

El complejo central completo de un ejemplar con diámetro máximo de 19.5 mm, se dibujó mediante una proyección fotográfica del sistema en cuatro secciones. De esta manera fué posible determinar la forma y dimensiones exactas de los ganglios y ofrecer una descripción detallada de los puntos de fijación de todas las comisuras y nervios conectivos y viscerales.

Segundo, se prestó particular atención al fenómeno de neurosecreción, y es aparente que células neurosecretoras están presentes en los ganglios cerebrales y parietales, y en el visceral. En cada ganglio cerebral un grupo grande de estas células se encuentra cerca del llamado cuerpo medio-dorsal, el cual descansa en parte sobre la comisura cerebral. Además algunas células especiales de este tipo están localizadas en el lobulo lateral del ganglio el cual, como en todos los basomatóforos emerge cerca del origen de los nervios ópticos y tentaculares. El producto de la neurosecreción medio-dorsal es acarreado a los nervios labiales medianos. En el ganglio parietal izquierdo, una célula dorsal y un grupo de células rostrales muestran características neurosecretoras. El ganglio parietal derecho tiene sólo una de estas células, mientras que el visceral contiene una larga banda de células neurosecretoras alrededor del conectivo visceroparietal izquierdo.

El número y ubicación de las células neurosecretoras fué determinado en secciones del sistema nervioso central de 10 ejemplares de tamaño diferente, desde 5.5 mm a 23 mm de diámetro (conchilla). El grupo medio dorsal de los ganglios cerebrales y el grupo grande en el ganglio visceral muestran células neurosecretoras en los ejemplares más pequeños. Sin embargo muchas de las otras células de este tipo tienen carácter neurosecretor sólo cuando han alcanzado un tamaño de 10 a 15 mm en el diámetro de la conchilla.

Comparaciones con *Lymnaea stagnalis* muestran que *Australorbis glabratus* es menos abundante en manifestaciones neurosecretoras. *E. L. stagnalis* los ganglios cerebrales tienen no sólo un grupo medio-dorsal pero también otro latero-dorsal de células neurosecretoras: las células son más numerosas en estos ganglios y en los parietales, y los ganglios pleurales contienen tres distintos grupos de tales células, faltando completamente en *A. glabratus*. Excepción a la regla: en *A. glabratus* el número de células neurosecretoras en el ganglio visceral es mayor que en *L. stagnalis*.

METHODS FOR NARCOTIZING AND ANAESTHETIZING GASTROPODS

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ABSTRACT

Of the narcotization techniques investigated the use of freezing and Stovaine are not recommended. Formalin is recommended for nudibranchs and Nembutal/propylene phenoxetol for slugs. Menthol, Nembutal, Sevin/CO<sub>2</sub>, propylene phenoxetol, and magnesium salts are recommended for general use.

Urethane, ether, and, in marine organisms, diluted sea water were found to be anaesthetics suitable only for superficial operations and injections. Magnesium chloride, propylene phenoxetol and Nembutal/MS 222 can be recommended for internal operations.

INTRODUCTION

During investigations into some aspects of the physiology of gastropods it was necessary to kill and fix animals in as life-like a position as possible for dissection and also to perform internal operations on live snails. A search of the literature revealed a number of methods for narcotizing and anaesthetizing snails, but, from other workers' criticisms, these obviously vary considerably in their effectiveness. We therefore attempted an investigation of the usefulness of these methods and, in the process, worked out some additional techniques. The present paper outlines our experience in this field. While it covers the majority of published techniques it is not intended to be exhaustive.

For the purpose of this paper the term 'narcotization' is restricted to the relaxation of animals in as life-like a position as possible, and to such an extent that they do not contract when fixed; 'anaesthesia' denotes relaxation of the muscles and extension of the animal so that various experimental procedures can be carried out and the animal then be allowed to recover.

MATERIAL AND METHODS

The animals were all obtained locally and the chemicals used were of the highest

purity available.

NARCOTIZATION METHODS

*Freezing*

Gohar (1937) reports that if certain marine invertebrates are allowed to expand in plenty of clean water, which is then cooled until it is frozen solid, these frozen animals can be fixed without contraction. He claims that this method works very well for some nudibranchs. We have not investigated nudibranchs with this technique, but, in the case of fresh water gastropods (*Lymnaea stagnalis*, *Potamopyrgus jenkinsi*, *Planorbis complanatus*) it gave very poor results. The frozen animals were fully expanded but retracted when treated with formol calcium.

*Formalin*

The use of formalin is mentioned by Gohar (1937) as being very successful with some nudibranchs and is the standard method used by Lemche (1963) in his studies on this group of gastropods. Gohar's method is as follows: the animals are placed in 50-500 times their volume of sea water and allowed to expand; 3 drops of 1% formalin/100 ml sea water are added every 15 minutes for one hour and the amount of formalin added is doubled every hour; when the animals become insensitive to stimuli, they can be killed and fixed. We confirmed the effectiveness

of this method on the nudibranch *Dendro-notus frondosus*. Relaxation took almost 4 hours and the final result was excellent, the animal contracting only slightly. When this method was used on the fresh-water snails *Lymnaea stagnalis*, *Potamopyrgus jenkinsi*, *Planorbis complanatus* and *Ancylastrum fluvialis*, they retracted into their shells after only one hour in the case of the small species and after 4 hours with *L. stagnalis*, and produced large amounts of mucus.

#### Stovaine

A 1% solution of this drug (Amylocaine hydrochloride; May & Baker) has been used by E. H. Smith (1960) for the narcotization of opisthobranchs. We attempted this method on the saccoglossan *Limapontia capitata* and the marine prosobranch *Nucella lapillus*. On first contact with the narcotic, *N. lapillus* retracted into its shell violently. *L. capitata* on the other hand could be fixed with formol calcium without contracting when left in the solution for 3 hours. This method, however, had the disadvantage of causing rapid maceration of the animal. Very soon after immersion the darkly pigmented surface epithelium began to flake off, and after 3 hours it had nearly all gone, leaving only a thin remnant of the body wall.

#### Menthol

Menthol has been in use for a long time as a narcotic for invertebrates and its use for molluscs has been recommended by Berry (1943) and Abdel-Malek (1951). Van der Schalie (1953) found its use unpredictable and Gohar (1937) reported that maceration sometimes occurred before full relaxation. We have found that in the case of *L. stagnalis* and *N. lapillus* relaxation is good when used overnight but that, when placed in the cold fixative, retraction occurs. Even if the fixative is injected contraction results, and the only satisfactory technique seems either to transfer the animal very gently to 4% formalin at 60° C (Gohar, 1937), or to remove most of the water and pour on boiling concentrated formalin (Van

Eeden, 1958). Both methods of using hot formalin produce excellent results; however, to prevent undue hardening the animals were transferred to formol calcium as soon as possible. Van Eeden has used menthol in combination with chloral hydrate but this method was not investigated because the time of relaxation reported is as long as when using menthol alone. We have tried using menthol both sprinkled on the surface of the water and as a saturated solution in 95% alcohol, and, contrary to the results of Abdel-Malek (1951), we found that the latter method did not result in appreciably quicker relaxation times.

#### Nembutal

The use of Nembutal (sodium pentobarbitone) for the relaxation of molluscs was first suggested by Van der Schalie (1953) and we have found that for pulmonates other than slugs, it is by far the most effective method we have investigated. The snails are placed in a 0.08% solution of pure Nembutal and left there until relaxed completely. Perfect relaxation was obtained with every species used in 12-55 hours (Table I). The only drawback is a slight swelling of the animal which is perhaps an advantage as far as dissection is concerned. The swelling is reduced if the animals are fixed with hot formalin before complete relaxation has occurred.

The only marine gastropod on which this technique has been attempted is *Limapontia*; with 0.08% Nembutal in sea water, relaxation is excellent. Since this method was very successful, we did not attempt the use of Nembutal and menthol together (McGraw 1958), as the reported relaxation time is approximately the same as with Nembutal alone.

#### Nembutal and propylene phenoxetol

While the above technique will also work for slugs within the time limits valid for snails, a much quicker method was discovered. A solution containing 0.08% Nembutal and 1% propylene phenoxetol relaxes slugs efficiently in a few minutes

TABLE 1. Narcotization of various gastropods by submersion in 0.08% Nembutal solution.

Species	Shell Ht. cm	Relaxation time hrs.
Prosobranchia		
<i>Potamopyrgus jenkinsi</i>	0.4-0.5	45-48
Basommatophora		
<i>Ancylastrum fluviatilis</i>	0.15-0.2	45-50
<i>Carychium minimum</i>	0.15-0.2	24-30
<i>Lymnaea pereger</i>	1.2-1.6	50-55
<i>Lymnaea stagnalis</i>	3.3-3.7	75-80
Stylommatophora		
<i>Achatina fulica</i>	1.0-1.5	15-20
	3.5-5.0	25-30
<i>Ashfordia granulata</i>	0.4-0.6	24-30
<i>Cepaea nemoralis</i>	1.2-1.6	35-40
<i>Clausilia rugosa</i>	0.7-1.1	48-50
<i>Cochliopa lubrica</i>	0.4-0.6	30-35
<i>Goniodiscus rotundatus</i>	0.15-0.3	24-30
<i>Helicella caperata</i>	0.3-0.5	30-35
<i>Helix aspersa</i>	0.3	12-15
	0.4-0.5	15-20
	0.7-0.8	20-25
	1.5	30-35
	2.5-3.0	35-40
<i>Oxychilus cellarius</i>	0.3-0.4	24-30
<i>Pupilla muscorum</i>	0.25-0.3	24-30
<i>Succinea putris</i>	0.8-1.0	48-50
<i>Trichia striolata</i>	0.5-0.7	40-48

(Table 2). The percentage of perfectly fixed animals was often rather low, largely because the tentacles were retracted. These, however, can usually be expressed

if the head is gently squeezed and almost 100% of the animals are then obtained in perfect shape. Cold formalin can be used for fixation but the hot solution is more

TABLE 2. Relaxation of slugs with Nembutal/propylene phenoxetol in 0.08% and 1% solution respectively.

Species	Length cm	Relaxation time min.	% well relaxed
<i>Agriolimax caruanae</i>	2.0-2.5	1-2	77.7
<i>Agriolimax reticulatus</i>	2.0-2.5	2-4	12.5
<i>Arion ater</i>	3.0-7.5	4-10	44.4
<i>Arion circumscriptus</i>	1.5-2.0	2-3	18.7
<i>Arion hortensis</i>	2.0-3.5	3-4	25
<i>Arion subfuscus</i>	3.0-4.5	2-3	100
<i>Limax arborum</i>	2.5-4.0	2-5	71
<i>Limax flavus</i>	3.5-5.5	9-10	50
<i>Limax maximus</i>	3.0-5.5	5-7	75
<i>Milax sowerbyi</i>	3.5-4.0	4-7	60

efficient in preventing contraction. One curious exception to the efficiency of this technique was found: in the case of the dark grey variety (var. *plumbea*?) of the slug *Arion ater*, very strong contraction occurred as soon as they were placed in the narcotic; this did not occur with other colour varieties.

This method relaxes snails rapidly but not in an extended condition.

#### *Sevin and Carbon Dioxide*

Carriker and Blake (1959) found with muricids that, of a number of relaxing agents, the most efficient were carbon dioxide and Sevin (1-naphthyl N-methyl-carbamate; Union Carbide) and that together they were even more effective. After a relaxation for 1 hour in 10 ppm of Sevin in sea water and then for 3 hours in fresh Sevin solution of the same concentration saturated with carbon dioxide, the snails would still retract when placed in formalin. They could be killed rapidly before contraction by placing on dry ice. We attempted this technique on *N. lapillus* and obtained good relaxation. In the absence of dry ice we fixed the animals successfully with hot formalin.

#### *Propylene phenoxetol*

Owen and Steedman (1958) report that propylene phenoxetol can be used for the relaxation of gastropods. We repeated their technique; a globule of propylene phenoxetol was placed on the bottom of a container and water added so that the narcotic constituted less than 1% of the total volume. Snails were placed in this solution, were kept clear of the globule, and left overnight. Relaxation of snails (terrestrial and marine), slugs, and nudibranchs was very variable. The technique was most efficient with the terrestrial pulmonates.

### ANAESTHETIC METHODS

#### *Urethane*

This drug has been used by Michelson (1958) for the relaxation of the planorbid *Australorbis* prior to injection. As

the animals were still reactive and slightly contracted after this treatment, he found it necessary to stretch the animals on a form of rack. We repeated this technique on *L. stagnalis* and found that, after 48 hours in 0.5% and 1% urethane, the animals were relaxed but that a strong stimulus caused a violent contraction. Since we regarded the procedure as unsuitable for internal operations we did not persevere. The technique, though, could have advantages for simple injections. The animals recovered from the 0.5% but not from the 1% solution.

#### *Ether*

Ripplinger and Joly (1960) have used ether anaesthesia for operation on the nervous system of *Helix pomatia*. We have repeated this method on *H. aspersa* and have found that the injection of 1 ml of a Ringer solution saturated with ether causes the snails to produce enormous quantities of mucus and to retract. After about 1/4 hour they could be pulled out of the aperture of the shell. In order to perform operations on the head, a mechanical method for maintaining extension of the animal would have been necessary. Recovery from the anaesthetic was 100%.

#### *Dilute Sea Water*

In operating on the osphradial nerve of the marine gastropod *Bullia* Krijgsman and Brown (1960) anaesthetised the animals by diluting the sea water in which they were crawling and inducing a state they called "water rigour". They reported that salinities of 18-23.5‰ were effective and that a gradual dilution over about 1 hour was needed. In our experiments with *Nucella* this technique caused retraction but, if the sea water was gradually diluted to 50‰ over 24 hours, rigour was obtained. The animals swell very considerably (rigour) but they still react slightly to stimulation. While this technique might be useful in external operations, in our opinion it is of little use for internal operations because of the enormous swelling of the tissues.

Recovery from the anaesthetic was only 30%.

#### *Nembutal and MS 222*

Joosse and Lever (1959) have developed a technique using Nembutal and MS 222 (Sandoz; meta-amino-benzoic acid ethyl ester methansulphonate) which they successfully used with *L. stagnalis*. In their experiments survival was almost 100%. In this laboratory only 11 out of 93 snails anaesthetized by this method survived after operation. The most probable explanations for this difference may lie in the length and thoroughness of the washing procedure after operation, or in the severity of the operation.

Lever *et al.* (1964) have recently modified the above technique, shortening the time required for anaesthesia and reducing after effects: snails are placed for 5 minutes in 0.1% Nembutal which has previously had nitrogen bubbled through it for 3 minutes, carbon dioxide is then bubbled through the solution for another 5 minutes. The animals are then transferred for 5 minutes to a 0.1% Nembutal solution containing 0.3% MS 222. At the above dosage all procedures are carried out at 20° C. After the operation the animals are kept in tap water, preferably aerated. Preliminary experiments in this laboratory on *L. stagnalis* have shown that relaxation is excellent and recovery (without operation) is 100%.

#### *Nembutal*

Vicente (1963) applied Joosse and Lever's 1959 technique to Opisthobranchs but found that he was able to dispense with the MS 222. The animals were treated at 18° C with 0.1 mg Nembutal/ml sea water and were relaxed after 20-30 minutes. We have not yet experimented with this method.

#### *Propylene phenoxetol*

In his description of the use of propylene phenoxetol as a relaxing agent Owen (1955) noted that lamellibranchs would recover from the anaesthetic if washed thoroughly. We have managed to adapt this method

for the anaesthesia of *Arion ater*. The slugs are put into a 0.5-1% propylene phenoxetol solution in water, which must be stirred until there is no undissolved phenoxetol. Anaesthesia occurs after 10-15 minutes and the slug is then lifted out, stripped of mucus and washed in clean tap water. After operation the animal is washed in fast running tap water for 20 minutes; it is then put into a bowl with damp sphagnum moss and left to recover. Survival rates for anaesthesia alone were 70% and after various operations ranged from 8-50% (Table 3).

TABLE 3. Anaesthesia of the slug *Arion ater* using propylene phenoxetol in 0.5-1% aqueous solution for 10-15 minutes.

Organs removed:	Number of animals	Recovery %
(Control)	10	70
Optic tentacles	14	50
Cerebral ganglia	4	25
Hermaphrodite gland	26	7.68

#### *Magnesium chloride*

This is probably the most widely used narcotizing agent for molluscs and other invertebrates and we were able to confirm its effectiveness. Its use as an anaesthetic, however, has not previously been reported. Specimens of the terrestrial pulmonates *H. aspersa*, *Achatina fulica*, and *A. ater* were injected with a 10% solution of magnesium chloride. Animals were first allowed to crawl freely until they were completely extended. Injection was facilitated by prior gentle downward pressure on the shell (for snails), or gentle pinching of the anterior part of the body (for slugs). The hypodermic needle (Record No. 18) was then inserted into the right side of the body so that the needle point was close to the 'brain' and the magnesium chloride was injected. In the majority of cases complete relaxation occurred very rapidly and lasted for 5-15 minutes; operations were then carried

TABLE 4. Injection of magnesium chloride as an anaesthetic for gastropods

Species	Size cm	Volume of 10% MgCl <sub>2</sub> solution injected ml	Duration of relaxation min.	Number of animals	Survival after one week %
<i>Achatina fulica</i> anaesthesia only	1.5-3.0	0.1-0.2	10	48	22.91
<i>Arion ater</i> anaesthesia only	5.0-7.0	0.2-0.3	10	8	37.5
	2.5-3.0	0.1-0.2	50	12	0.0
operated	-	-	-	71	32.39
<i>Helix aspersa</i> anaesthesia only	1.5-2.0	0.1-0.2	10	35	77.0
	2.0-2.5	0.2-0.3	15	24	91.66
	2.5-3.0	0.3-0.4	15	36	91.0
operated	-	-	-	227	85.0
<i>Littorina littorea</i> <sup>1</sup> operated	2.5-3.0	0.2	3-5	149	80.53
<i>Nucella lapillus</i> <sup>1</sup> anaesthesia only	3.0-4.0	0.2	3-5	10	20.0

<sup>1</sup>Pretreatment overnight in MgCl<sub>2</sub> solution (see text).

out on the left side of the animal. Recovery from the anaesthetic was highly variable: the animals first became sensitive to stimuli and later contracted or moved without stimulation; they appeared normal 4-12 hours after injection. Survival rates after one week ranged from 23-92%, except for one series of very young *A. ater* which recovered after anaesthesia, but all died within 24 hours (Table 4).

The marine operculates *Littorina littorea* and *Nucella lapillus* were found to contract very rapidly into their shells when the above technique was attempted. The following modified technique was found to work quite well however. The snails were first put into clean sea water and a 20% magnesium chloride solution was added slowly from a burette which was dipped below the surface of the water and was situated as far away from the animal as possible. Sufficient solution was added to attain a volume ratio of 1:10 of MgCl<sub>2</sub> solution and sea water. The animals were left overnight in this solution. They can be prevented from crawling out by coating the wall of the vessel above the liquid with the 20% magnesium chloride solution. The

next morning the snails will be found to be hanging out of their shells but are still slightly sensitive. The animal is then held out of its shell by its operculum while a 10% solution of magnesium chloride is injected. Relaxation is immediate but only lasts for about 3-5 minutes. Survival rates for *Littorina* (almost 81%) after operation were higher than for *Nucella* (20%) without operation (Table 4).

#### DISCUSSION

During this investigation it became evident that there was considerable variation between species in their susceptibility towards narcotic and anaesthetic chemicals. The methods therefore need to be tested for effectiveness on any given species before they are put into use.

The range of available narcotization techniques is much wider if they are used in conjunction with the hot formalin method (Van Eeden, 1958 and Gohar, 1937). As long as the animals are extended they can be killed so rapidly with this method that slight reactivity is not important. In our

laboratory these specimens are fixed in formol-calcium, washed well in running tap water, and preserved in propylene phenoxetol/glycerine (Owen & Steedman, 1958), with excellent results.

The number of anaesthetic methods available is very small and these have been attempted only on a small range of animals. As so little is known of the effect on molluscs of the chemicals used, there is no theoretical foundation for this work. If such knowledge were available, the development of more effective techniques might be possible.

In our operations on gastropods we have found the difficulties of wound healing to be a limiting factor. The problem was very important with *Arion* but was occasionally observed with other species also. Silk suture thread was broken down within 4 or 5 days, and unless the wound had already nearly healed by that time the internal organs were extruded through the wound on contraction of the body. Thus *Arion* was found to recover very well from propylene phenoxetol and magnesium chloride anaesthesia but, due to this factor, survival was very poor. Experiments are now under way to discover if other suture materials are more effective.

Our work indicates that molluscs are quite good experimental animals even though the body cavity is a haemocoel. They appear to be able to lose a lot of blood and tissue and to survive well. The main need in this work however is for a more efficient anaesthetic of wide application.

#### ACKNOWLEDGEMENTS

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#### RESUMEN

##### METODOS PARA ANESTISIAR Y NARCOTIZAR GASTROPODOS

De las técnicas de narcotización investigadas, el uso de la Estovaina y el de congelación no son recomendables. Formalina se recomienda para nudibranchios y Nembutal/propileno-fenoxetol para babosas. Mentol, Nembutal, Sevin/CO<sub>2</sub>, propileno-fenoxetol y sales de magnesio para uso general.

Urethane, Ether y, en organismos marinos, agua de mar diluida probaron ser anestésicos usables sólo para operaciones superficiales e inyecciones. Cloruro de Magnesio, propyl/fenox. y Nembutal/MS 222 pueden recomendarse para operaciones internas.

CYTOLOGICAL STUDIES OF PLANORBIDAE (GASTROPODA: BASOMMATOPHORA)  
II. SOME AFRICAN PLANORBINAE, PLANORBININAE AND BULININAE<sup>1,2</sup>

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ABSTRACT

The chromosome numbers are reported for 20 species and subspecies of African planorbid snails. A haploid number of 18 was found in *Anisus crassilabrum* and *Gyraulus costulatus* of the Planorbinae; in *Planorbina alexandrina alexandrina*, *P. pfeifferi pfeifferi*, *P. pfeifferi gaudi*, *P. pfeifferi madagascariensis* and *P. sudanica tanganyicensis* of the Planorbininae; and in *Bulinus (Bulinus) tropicus tropicus*, *B. (B.) guernei*, *B. (Physopsis) globosus*, *B. (P.) jousseaumei*, *B. (Pyrgophysa) beccarii*, *B. (Py.) forskalii* (from Ghana, Tanganyika and South Africa), *B. (Py.) reticulatus* and *B. (Py.) senegalensis* of the Bulininae; while *B. truncatus truncatus*, *B. truncatus rohlfssii*, *B. coulboisi* and *B. "sericinus"* had 36 pairs of chromosomes and previously one population of *B. "sericinus"* from W. Aden had 72 pairs.

*Bulinus forskalii* from Angola had 19 elements (presumably bivalents) at Prophase I and Metaphase I, and *B. natalensis* from Southern Rhodesia had 19, 20 and 21 elements (some of which may have been univalents) present at Metaphase I.

The above results and previous data show that in the Bulininae, polyploidy seems to occur only in the subgenus *Bulinus* s.s., where its presence has been found only in those species, all of the "truncatus" group, implicated in the transmission of human and bovine schistosomiasis. Chromosome number *per se* seems to have no correlation with infectability by schistosomes in the bulinine subgenera *Physopsis* and *Pyrgophysa*, or in the planorbinine genus *Planorbina*.

INTRODUCTION

Chromosomes of various planorbid snails have been previously studied by Le Calvez and Certain (1950), Inaba and Tanaka (1953), Bonham (1955), Azevedo and Gonçalves (1956), Natarajan (1960), Burch (1960a, b, c, d, 1961, 1963, 1964) and Burch, et al. (1964). These earlier studies include 9 species from North America, 2 from Europe, 5 from Asia and 9 from Africa and the Near East and, in addition, 3 subspecies, all belonging to the African genus *Bulinus*. Of these 28 species and subspecies investigated,

21 are characterized by having 18 pairs of chromosomes, 2 by having 19 pairs, 4 by having 36 pairs and 1 by having 72 pairs. The basic number of chromosomes for the family is undoubtedly 18 and species with 36 and 72 pairs of chromosomes have had polyploid origins. Those species with 19 pairs of chromosomes have arisen by aneuploidy (or perhaps the specimens studied were from populations exhibiting supernumerary chromosomes).

The largest previous study of planorbid chromosomes is that of Burch (1964) on the African bulinine subgenus *Bulinus* s.s. In that study the difference in

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chromosome numbers of the "tropicus" and "truncatus groups" (18 and 36 pairs resp.) was pointed out, and the occurrence of polyploidy as a character of the latter group was clearly established. The significance of these cytological findings in regard to the susceptibility of the snails of the subgenus *Bulinus* s.s. to infection with larval trematodes causing human and herbivore schistosomiasis was revealed: only the northern "truncatus" group, alone receptive to schistosomes of the haematobium group, is polyploid, whereas the more southern "tropicus" group of *Bulinus* s.s., which is refractory to the same schistosomes, is diploid. This led us to investigate the chromosomes of members of the 2 other bulinine subgenera, and of *Planorbina* (= *Biomphalaria*) as well, since they are also implicated in the transmission of human schistosomiasis. The present preprint has included a restudy of several of the species previously investigated and extends the cytological information to include 13 additional African species and subspecies.

#### SYSTEMATICS

The African and Near Eastern Planorbidae comprise 4 subfamilies, the Planorbinae, Planorbininae, Segmentininae and Bulininae. The most prominent of these subfamilies in number of species and geographical distribution are the Planorbininae and the Bulininae. Also, these 2 subfamilies are the most important economically because they both transmit human schistosomiasis and the Bulininae also bovine schistosomiasis. Mandahl-Barth (1958, 1960) has monographed these latter 2 groups and a brief review of his systematics in regard to the Bulininae was given by Burch (1964) in his cytological study of *Bulinus* s.s. In that paper, Burch has already suggested that a reconsideration was needed in regard to "*Bulinus truncatus sericinus*" since the octaploid chromosome complement of specimens from Western Aden Protectorate would most likely make that group reproductively isolated from the tetraploid

*B. truncatus*. In addition, a third *Bulinus* s.s. species, also tentatively identified as "*sericinus*", a normal diploid, was found to occur in Ethiopia. This population, although perhaps morphologically similar to both *B. truncatus* and *B. sericinus*, is undoubtedly isolated reproductively from both because of the great differences in chromosome numbers.

The subfamily Planorbininae is represented in Africa and Madagascar by the Genus *Planorbina* Haldeman, 1843 (= *Biomphalaria* Preston, 1910)<sup>4</sup>. The classification of this genus is still far from clear in spite of recent studies by Mandahl-Barth (1958, 1960), but in our study we have largely followed his nomenclature and classification because none better is available. According to Mandahl-Barth's (1960) latest work on the genus, his 1958 classification is modified as follows:

#### *Pfeifferi* group

- B. pfeifferi* (Krauss)
- B. germaini* (Ranson)
- B. rhodesiensis* Mandahl-Barth

#### *Choanomphala* group

- B. choanomphala choanomphala* (Martens)

<sup>4</sup>A petition has been submitted (Wright, 1963) to the International Commission on Zoological Nomenclature to suppress the generic names *Planorbina* Haldeman, 1843, *Taphius* Adams and Adams, 1854, and *Armigerus* Clessin, 1884, in favor of *Biomphalaria* Preston, 1910; but Walter (1963) has expressed the opinion, which we believe has not been adequately refuted, that at least one of these genera (i.e., *Taphius*) is not congeneric with what is commonly accepted as *Planorbina* (or its synonyms *Biomphalaria* and *Australorbis*), thereby reducing the validity of the proposal as it now stands. In addition, Baker (1960) contends that *Australorbis* Pilsbry, 1934, has been used more than *Biomphalaria*. Therefore, until there is a decision by the International Commission on Zoological Nomenclature, we are using the oldest valid name, *Planorbina*.

- B. choanomphala elegans* (Mandahl-Barth)  
*B. smithi* Preston  
*B. stanleyi* (Smith)

*Alexandrina* group

- B. alexandrina alexandrina* (Ehrenberg)  
*B. alexandrina watsoni* Mandahl-Barth  
*B. angulosa* Mandahl-Barth  
*B. tchadiensis* (Germain)?

*Sudanica* group

- B. camerunensis camerunensis* (Boettger)  
*B. camerunensis manzadica* Mandahl-Barth  
*B. sudanica sudanica* (Martens)  
*B. sudanica tanganyicensis* (Smith)

Mandahl-Barth (1960) has suggested dropping all subspecific names in *Planorbina pfeifferi*, but in the face of the many uncertainties in planorbinine systematics we are retaining 2 trinomials for the time being because their populations are geographically remote from the main *P. pfeifferi* distribution. These names are *P. pfeifferi gaudi* from West Africa and *P. pfeifferi madagascariensis* from Madagascar.

MATERIALS AND METHODS

The species used in this investigation are listed below:

Subfamily Planorbininae

*Anisus crassilabrum* Ranson. Gardens of the Institut Pasteur, Tananarive, Madagascar. E. R. Brygoo, April 19, 1961.

*Gyraulus costulatus* (Krauss). Kaapmuiden irrigation canal, Kaapmuiden, Transvaal, Republic of South Africa. C. H. J. Schutte, July 7, 1961. Identified to species by G. Mandahl-Barth.

Subfamily Planorbininae

*Planorbina alexandrina alexandrina* (Ehrenberg). Mena area, Giza Province, Egypt. Collected by Fikry el Tawil, March 9, 1961.

Khurshid Lateral, Khurshid Village, Beheira Province, Egypt. Col-

lected by B. C. Dazo, March 24, 1963. *Planorbina pfeifferi pfeifferi* (Krauss). Mwanza, Tanganyika. From live stocks maintained at the East African Institute for Medical Research: their original stock came from a local river. John McClelland, May 13, 1961.

Salisbury, Southern Rhodesia. V. de V. Clarke and C. J. Shiff, April 13, 1961.

Three localities in Transvaal, Republic of South Africa: Buffelspruit, Malelane; Kaapmuiden irrigation canal, Kaapmuiden; Millar and Simmons irrigation dam, Karino. C. H. J. Schutte, July 7, 1961.

*Planorbina pfeifferi gaudi* (Ranson). From live stocks maintained at the Liberian Institute for Tropical Medicine, Harbel, Liberia; their original stock came from a creek at Cuttington Station, on Central Highway, Suakoko, Central Province, Liberia. H. J. Walter, May, 1961. A second lot was collected at that locality by J. B. Burch, November, 1961.

Gbanga Mission, Central Province, Liberia. J. B. Burch and H. J. Walter, November, 1961.

Vicinity of Kumasi, Ashanti, Ghana. F. Wickremasinghe, May, 1961.

*Planorbina pfeifferi madagascariensis* (Smith). Gardens of the Institut Pasteur, Tananarive, Madagascar. E. R. Brygoo, April 19, 1961.

*Planorbina sudanica tanganyicensis* (Smith). From live stocks kept at the East African Institute for Medical Research, Mwanza, Tanganyika; sent on May 9, 1961 by John McClelland. Originally collected in a local river near Mwanza. Identified by G. Mandahl-Barth.

Subfamily Bulininae

*Bulinus (Bulinus) coulboisi* (Bourguignat). From live stocks maintained at the Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U. S. A.; originally collected by John McClelland at Mwanza, Tanganyika, May, 1961.

*Bulinus (Bulinus) "sericinus (Jickeli)".* Belas, Western Aden Protectorate. From live stocks at the British Museum (Natural History). Courtesy of C. A. Wright.

*Bulinus (Bulinus) truncatus truncatus* (Audouin). Three lots of laboratory reared specimens from stocks originally coming from Egypt. These lots were from laboratory stocks maintained in the following institutions: Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U. S. A.; the Laboratory of Parasitic Diseases, National Institutes of Health, Bethesda, Maryland, U. S. A.; and The Liberian Institute of the American Foundation for Tropical Medicine, Harbel, Liberia, W. Africa.

*Bulinus (Bulinus) truncatus rohlfsi* (Clessin). From live stocks maintained at the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U. S. A.; originally collected by F. Wickremasinghe, May, 1961, in the vicinity of Kumasi (Ashanti), Ghana, West Africa.

*Bulinus (Bulinus) natalensis* (Küster). Lake McIlwaine, Southern Rhodesia. Collected by A. D. Harrison, January 27, 1963.

*Bulinus (Bulinus) tropicus tropicus* (Krauss). From stocks maintained at the Laboratory of Parasitic Diseases, National Institutes of Health, Bethesda, Maryland, U. S. A. Sent by E. G. Berry, May, 1963; original specimens from Kenya.

Small tributary of Gwebi River on New England Farm, near Salisbury, Southern Rhodesia. Collected by A. D. Harrison, January 25, 1963. Two animals studied.

From stocks maintained at the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U. S. A. Originally from Salisbury, Southern Rhodesia. V. de V. Clarke and C. J. Shiff, April 13, 1961.

*Bulinus (Bulinus) guernei* (Dautzenberg). Maka Sarakole, near Kortia (Tamba Counda), Senegal, October 17,

1963. Courtesy of E. G. Berry. *Bulinus (Physopsis) globosus* (Morelet). From live stocks maintained at the Liberian Institute for Tropical Medicine, Harbel, Liberia; originally from 1st Creek, Toendee, about 6 miles east of Ganta, Central Province, Liberia. Courtesy of H. J. Walter.

Gbanga Mission, Central Province, Liberia. J. B. Burch and H. J. Walter, November, 1961.

Rice field near Gbanga Mission, Central Province, Liberia. J. B. Burch and H. J. Walter, November, 1961.

Cuttington, Central Province, Liberia. J. B. Burch and H. J. Walter, November, 1961.

Vicinity of Kumasi (Ashanti), Ghana. Collected by F. Wickremasinghe, May, 1961.

Mazabuka, Northern Rhodesia. P. L. LeRoux. From live stocks maintained at the London School of Hygiene and Tropical Medicine.

Salisbury, Southern Rhodesia. V. de V. Clarke and C. J. Shiff, April 13, 1961.

Salisbury, Southern Rhodesia. A. D. Harrison, January, 1963.

Two lots from Eastern Transvaal, Republic of South Africa; sent by R. J. Pitchford and C.H.J. Schutte, July, 1961: Buffelspruit (Malelane) and Millar and Simmons irrigation dam (Karino), Transvaal, Republic of South Africa.

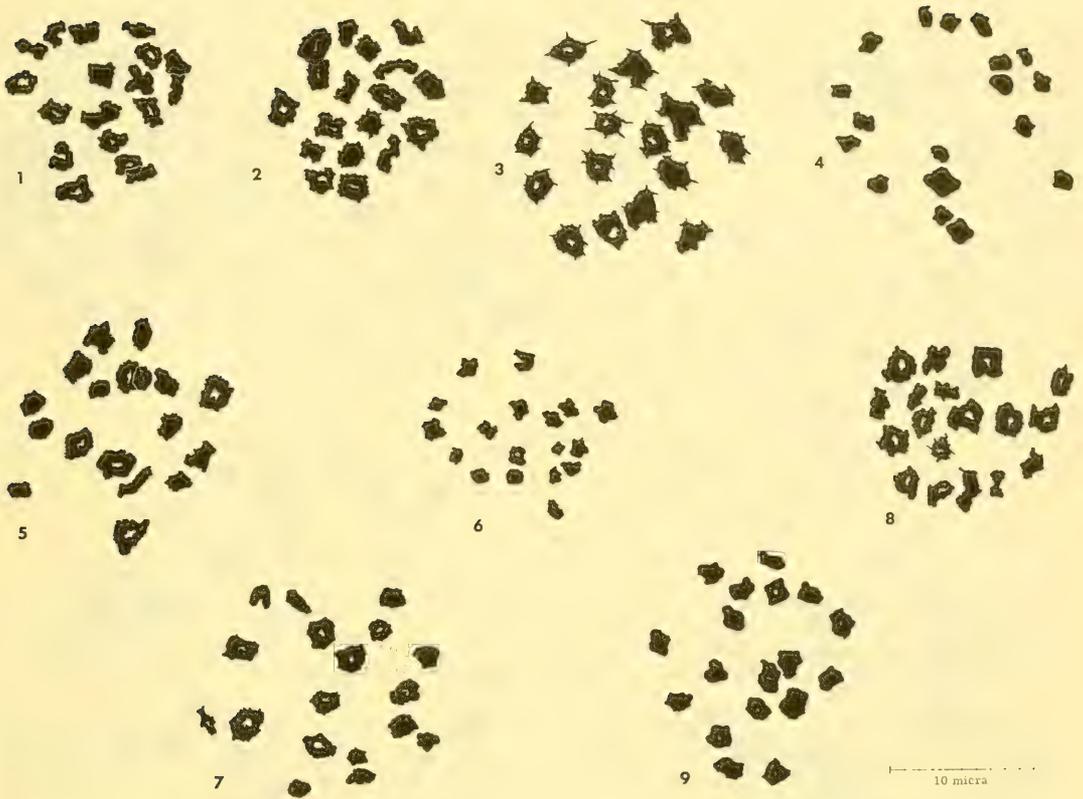
*Bulinus (Physopsis) jousseaumei* (Dautzenberg). Casamance River at Kolda, High Casamance, Senegal, October 20, 1963. Courtesy of E. G. Berry.

*Bulinus (Pyrgophysa) forskalii* (Ehrenberg). Vicinity of Kumasi (Ashanti), Ghana. Collected by F. Wickremasinghe, May, 1961.

Lagoa Tanguila, Angola. Courtesy of C. A. Wright.

Mwanza, Tanganyika. Collected by John McClelland, May, 1961.

The Rest farm dam, Nelspruit, Transvaal, Republic of South Africa.



FIGS. 1-9. Camera lucida drawings of diakinesis (spermatogenesis) chromosomes of Planorbinae and Planorbininae. FIG. 1. *Anisus crassilabrum*. FIG. 2. *Gyraulus costulatus*. FIG. 3. *Planorbina alexandrina alexandrina*, Beheira Province, Egypt. FIG. 4. *P. pfeifferi pfeifferi*, S. Rhodesia. FIG. 5. *P. p. pfeifferi*, Transvaal. FIG. 6. *P. p. gaudi*, Gbanga Mission, Liberia. FIG. 7. *P. p. gaudi*, Ghana. FIG. 8. *P. p. madagascariensis*. FIG. 9. *P. sudanica tanganyicensis*.

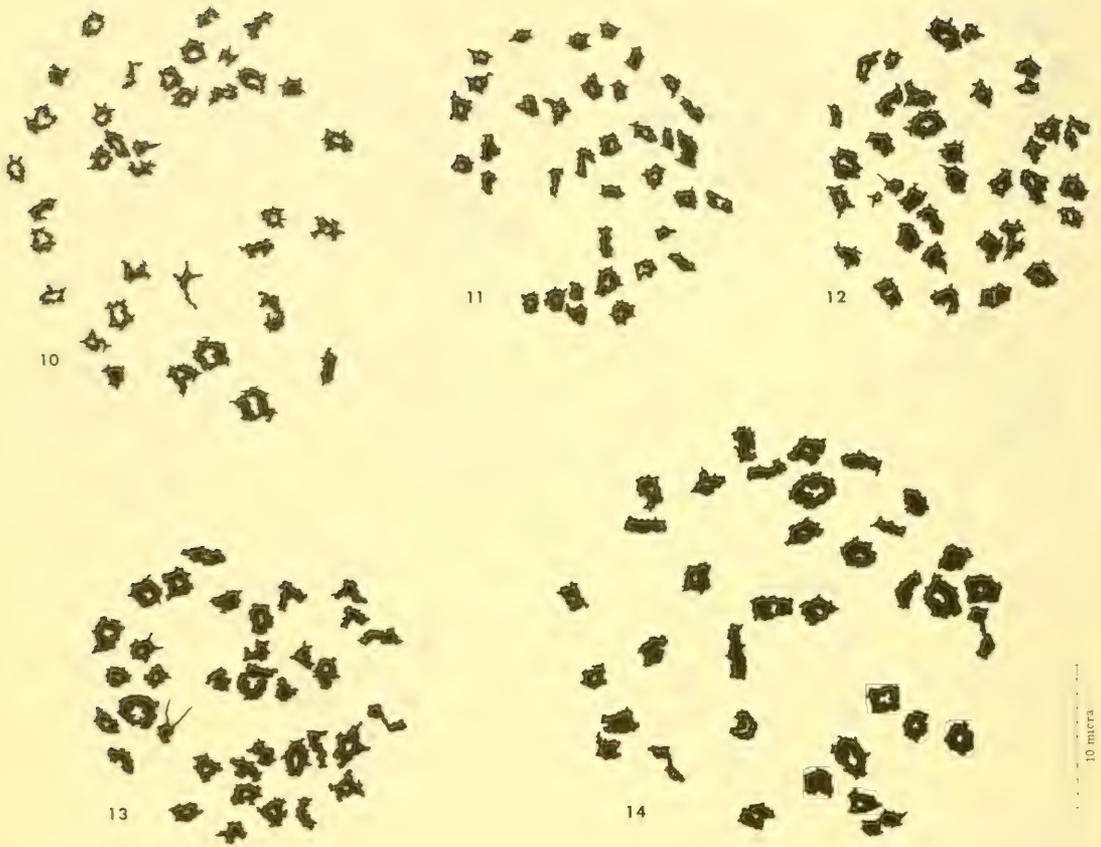
R. J. Pitchford and C. H. J. Schutte,  
July, 1961.

*Bulinus* (*Pyrgophysa*) *senegalensis*  
Müller. Birkelane (30 km east of  
Koalack), Senegal, October 21, 1963.  
Courtesy of E. G. Berry. Identified  
by G. Mandahl-Barth.

*Bulinus* (*Pyrgophysa*) *reticulatus*  
Mandahl-Barth. Western Aden Pro-  
tectorate. From live stocks at the  
British Museum (Natural History).  
Courtesy of C. A. Wright.

*Bulinus* (*Pyrgophysa*) *beccarii*  
Paladilhe. Dirgag, Western Aden

Protectorate. From live stocks at  
the British Museum (Natural History).  
Courtesy of C. A. Wright. This  
species was listed as a possible  
synonym of *Bulinus cernicus* (More-  
let) by Mandahl-Barth (1958),  
although he states that *B. cernicus*  
is "known with certainty only from  
Mauritius". Since our specimens  
are not from Mauritius, and the  
type locality of *B. beccarii* is  
Aden, we prefer for the time being  
to retain the latter name for our  
specimens.



FIGS. 10-14. Camera lucida drawings of diakinesis (spermatogenesis) chromosomes of Bulininae. (*Bulinus* s. s., "truncatus group"). FIG. 10. *Bulinus truncatus truncatus*, Egypt (N. I. H. aquaria stock). FIG. 11. *B. t. truncatus*, Egypt (L. I. T. M. aquaria stock). FIG. 12. *B. t. truncatus*, Egypt (U. M. M. Z. aquaria stock). FIG. 13. *B. coulboisi*. FIG. 14. *B. "sericinus"*.

The material examined consisted of ovotestes in active stages of gametogenesis. The tissues were fixed and preserved in either Carnoy's (1887) (acetic-ethanol-chloroform, 1:6:3) or Newcomer's (1953) fixatives and stained by the acetic orcein squash technique (La Cour, 1941). Observations were made with Nikon (Nippon Kogaku) microscopes using 100X (n.a. 1.25) oil immersion objectives and 10, 20 and 30X oculars. The chromosomes were drawn with the aid of a camera lucida and reproduced at a table-top magnification of 5400X. Photographs

were taken using a 20X ocular, an oil immersion objective, a Kodak Wratten 57A (green) filter, and Kodak High Contrast Copy film.

#### OBSERVATIONS AND DISCUSSION

Chromosome numbers of the species studied in this investigation and in previous studies are shown in Table 1. *Anisus crassilabrum* of the Planorbinae had 18 pairs of chromosomes (Fig. 1), as did *Gyraulus costulatus* (Fig. 2). These numbers are the same as found in other



FIGS. 15-19. Camera lucida drawings of meiotic (spermatogenesis) chromosomes of *Bulinus* s.s., "tropicus group". FIG. 15. *Bulinus guernei*. FIG. 16. *B. t. tropicus*, Kenya. FIG. 17. *B. t. tropicus*, S. Rhodesia (Clarke and Shift). FIG. 18. *B. t. tropicus*, S. Rhodesia (Harrison). FIG. 19. *B. natalensis*. Figs. 15-17, 19 are of diakinesis chromosomes: Fig. 18 shows Metaphase I chromosomes.

members of this subfamily from other geographical regions (Le Calvez and Certain, 1950; Burch, 1960b; Burch, et al., 1964) except for the North American *Gyraulus circumstriatus* which has 36 pairs of chromosomes (Burch, 1960c).

The 5 species and subspecies of *Planorbina* (*Planorbinae*) studied from Africa also had 18 pairs of chromosomes (Figs. 3-9), the same number reported for *Planorbina glabrata* from Puerto Rico by Burch (1960d). *Planorbina sudanica* from the Sudan also was reported previously to have 18 pairs of chromosomes (Burch, 1960d), but the species identification of the laboratory stock used was based on information supplied by Emile A. Malek, who later determined the specimens to be *P. glabrata*.

In the bulinine genus *Bulinus*, 12 species and 1 subspecies were inspected in the present study.

Four of these species and 1 subspecies, all belonging to the subgenus *Bulinus* s.s., were studied previously: *B. truncatus*

*truncatus* (Figs. 10-12), *B. truncatus rohlfsii* and *B. coulboisi* (Fig. 13) with 36 pairs of chromosomes, *B. natalensis* with 19+ elements at meiosis, and *B. tropicus tropicus* with 18 pairs of chromosomes (Burch, 1964). The  $n=36$  species belong to the "truncatus group" and the  $n=18$  species belong to the "tropicus group". Two other species of the "tropicus group" examined in the earlier study, *B. tropicus angolensis* and *B. tropicus zanzebaricus* also had 18 pairs of chromosomes. One of the new *Bulinus* s.s. species studied, *B. guernei*, had 18 pairs of chromosomes (Fig. 15), which would seem to confirm Mandahl-Barth's (1958) placement of it in the "tropicus group".

The 2 specimens of "*Bulinus sericinus*" from Belas, Western Aden Protectorate studied had 36 pairs of chromosomes (Fig. 14), indicating that this population belongs to the "truncatus group". Previously, *Bulinus "sericinus"* from Tarbak, Western Aden Protectorate, was found to have 72 pairs of chromosomes, and *Bulinus*

"? *sericinus*" from Awasa, Ethiopia to have 18 pairs (Burch, 1964). The latter species was therefore considered to belong to the "tropicus group" and the former species to the polyploid "truncatus group".

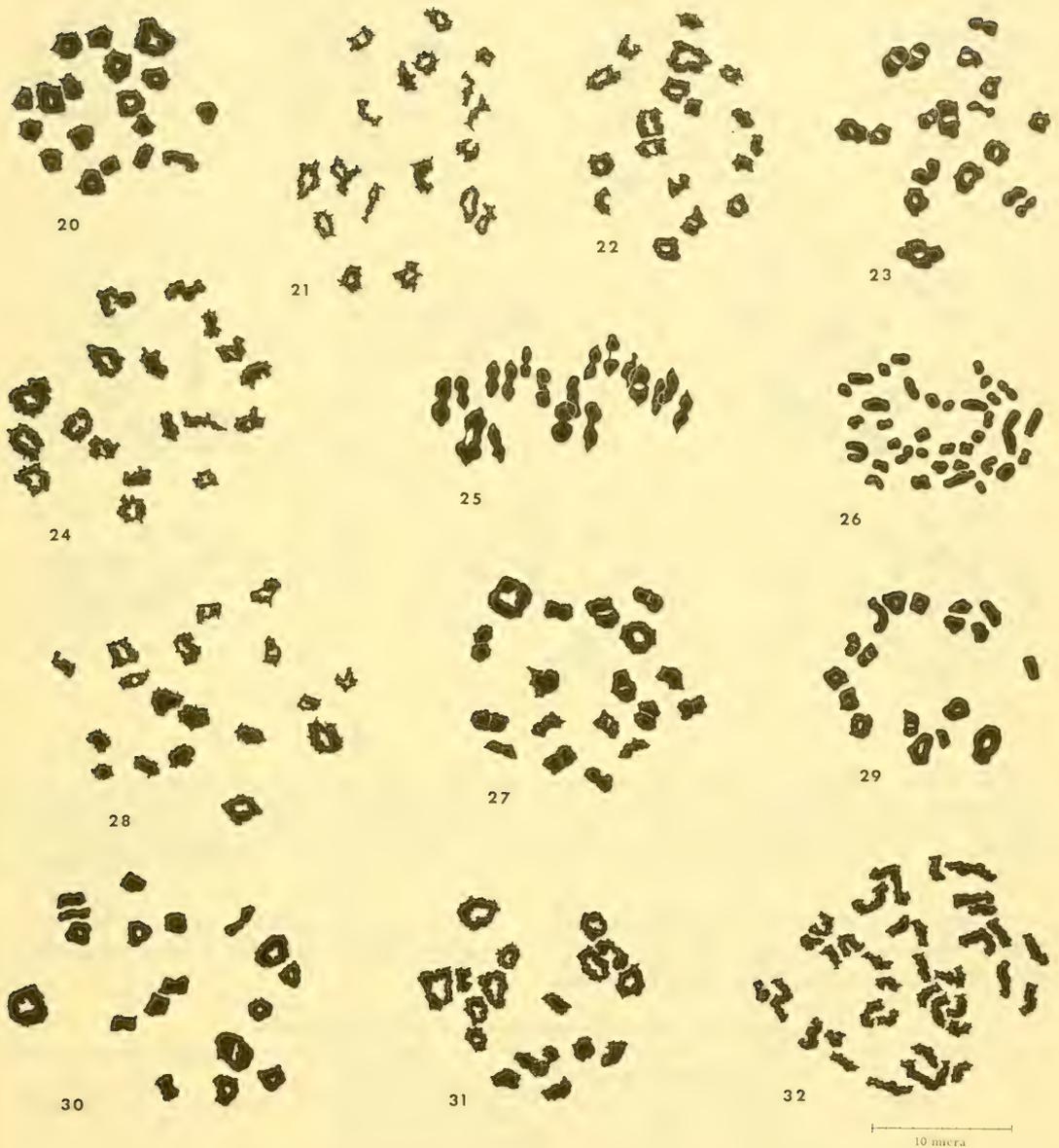
These chromosomal differences in snails diagnosed as *Bulinus sericinus* on morphological and geographical grounds raise some interesting questions as to the proper placement of Jickeli's original species and its relationship to the other species of *Bulinus* s.s. in the Ethiopia-Eritrea-Sudan area as well as in Southern Arabia. The type, Jickeli's *Isidora sericina*, came from Mekerka on the Toqor River, Ethiopia. If the population from which he collected had 18 pairs of chromosomes, as did our Ethiopian specimens from Awasa, then *B. sericinus* is no doubt a member of the "tropicus group" as contended earlier by Mandahl-Barth (1958). If, however, Jickeli's species has 36 pairs of chromosomes, as did our Belas, Western Aden specimens, then *B. sericinus* is a member of the "truncatus group" as contended later by Mandahl-Barth (1960), and our Awasa specimens belong to an unidentified *Bulinus* species. In the unlikely event that Jickeli's species should have 72 pairs of chromosomes, as did our Tarbak, Western Aden specimens, *B. sericinus* would still belong to the polyploid "truncatus group", and our specimens from both Awasa and Belas would then belong to 2 different *Bulinus* species. Until specimens from the type locality can be examined cytologically, the true identity not only of *Bulinus sericinus*, but of the other nominal species of the area as well, will remain in doubt.

With the exception of the 1 specimen that we studied of *Bulinus (Pyrgophysa) forskalii* (n=19) from Angola (Fig. 37), all members of the subgenera *Physopsis* and *Pyrgophysa* available to us were found to have 18 pairs of chromosomes, the number common to most other planorbid snails (Burch, 1960b; Burch, et al., 1964) (Figs. 20-36, 38-41). A chromosome number of n=36 was reported earlier (Burch, 1960d) for specimens of *Bulinus (Physopsis) ugandae* brought from the

White Nile, south of Khartum, Sudan, by Emile A. Malek. However, offspring from this same lot at both the Laboratory of Parasitic Diseases, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, Maryland, U. S. A., and the Department of Zoology, British Museum (Natural History), London, England, are now all *B. truncatus* (fide E. G. Berry and C. A. Wright). On the other hand, the several shells saved from the original lot at the Museum of Zoology, The University of Michigan appear to be *B. ugandae*. C. A. Wright (personal communication) is of the opinion that the original lot was probably a mixture of both species, and that only the *B. truncatus* survived to breed in the laboratory. If it is true that Dr. Malek's original material was a mixture of the 2 species, then it is quite likely that, because of its chromosome number, the single specimen of "*B. ugandae*" studied previously was in reality *B. truncatus*. It is desirable to study further the chromosomes of *B. ugandae* from the type locality and either confirm or correct the original report. If it can be shown that *B. ugandae* does not have 36 pairs of chromosomes, then it will be interesting to note that polyploidy in the Bulininae seems to be restricted to the "truncatus group" of the subgenus *Bulinus* s.s.

The 12 specimens of *Bulinus forskalii* from Ghana, Tanganyika and South Africa all had 18 pairs of chromosomes (Figs. 34-36, 38), but the single specimen from Angola had 19 elements present at diakinesis and Metaphase I (Fig. 37). These elements all appeared to be normal bivalents; but accurate counts could not be made on mitotic cells. This specimen may have come from an aneuploid race, have been an aneuploid individual of a normal n=18 race, or have been a specimen with supernumerary or B chromosomes (for similar anomalies in the Planorbidae, see Burch, 1960b, 1964; Burch, et al., 1964).

Polyploidy, found to occur in the more northern members of the subgenus *Bulinus* s.s. and apparently correlated with only



FIGS. 20-32. Camera lucida drawings of chromosomes (spermatogenesis) of Bulininae (*Bulinus*, subgenus *Physopsis*). FIG. 20. *Bulinus globosus*, Toendee, Liberia. FIG. 21. *B. globosus*, Cuttington, Liberia. FIG. 22. *P. globosus*, Gbanga Mission, Liberia. FIG. 23. *P. globosus*, Rice field near Gbanga Mission, Liberia. FIG. 24. *P. globosus*, N. Rhodesia. FIGS. 25-27. *P. globosus*, S. Rhodesia (A. D. Harrison). FIG. 28. *P. globosus*, S. Rhodesia (Clarke and Schiff). FIG. 29. *P. globosus*, Malelane, S. Africa. FIG. 30. *P. globosus*, Karino, S. Africa. FIGS. 31, 32. *B. jousseaumei*. Figs. 20-22, 24, 27-31 are of diakinesis chromosomes; Figs. 23 and 25 are of Metaphase I chromosomes; Fig. 26 is of spermatogonial metaphase chromosomes; and Fig. 32 is of spermatogonial prophase chromosomes.



FIGS. 33-41. Camera lucida drawings of chromosomes (spermatogenesis) of Buliniinae (*Bulinus*, subgenus *Pyrgophysa*). FIG. 33. *Bulinus beccarii*. FIGS. 34, 35. *B. forskalii*, Ghana. FIG. 36. *B. forskalii*, Tanganyika. FIG. 37. *B. forskalii*, Angola. FIG. 38. *B. forskalii*, S. Africa. FIGS. 39-40. *B. senegalensis*. FIG. 41. *B. reticulatus*. Figs. 33-38, 40, 41 are of diakinesis chromosomes: Fig. 39 is of spermatogonial metaphase chromosomes.

those species susceptible to infection with *Schistosoma haematobium* (Burch, 1964), has not been found in any species of the

subgenera *Physopsis* and *Pyrgophysa* (except for the doubtful *B. ugandae* above).

TABLE 1. Chromosome numbers of African Planorbidae

Species	Chromosome Number		Meiotic Cells Studied <sup>5</sup>	Number of Individuals Successfully Examined	Source	Reference <sup>6</sup>
	n	2n				
PLANORBINAE						
<i>Anisus</i>						
<i>A. crassilabrum</i>	18	-	I♂	4	Madagascar	I
<i>Gyraulus</i>						
<i>G. costulatus</i>	18	-	I♂	3	S. Africa	I

<sup>5</sup>I♂ = cells studied from 1st meiotic division of spermatogenesis; II♂ = 2nd ♂ division; I♀ = 1st meiotic division of oögenesis.

<sup>6</sup>I. This present study. II. Burch (1960 d). III. Burch (1963, 1964).

TABLE 1. (cont.)

Species	Chromosome Number		Meiotic Cells Studied	Number of Individuals Successfully Examined	Source	Reference
	n	2n				
<b>PLANORBININAE</b>						
<i>Planorbina</i>						
<i>P. alexandrina alexandrina</i>	18	-	I♂	2	Egypt	I
<i>P. pfeifferi pfeifferi</i>	18	-	I♂	2	Tanganyika	I
	18	-	I♂	2	S. Rhodesia	I
	18	-	I♂	4	S. Africa	I
<i>P. pfeifferi gaudi</i>	18	-	I♂	4	Liberia	I
	18	36	I♂	2	Ghana	I
<i>P. pfeifferi</i>						
<i>  madagascariensis</i>	18	-	I♂	2	Madagascar	I
<i>P. sudanica tanganyicensis</i>	18	-	I♂	4	Tanganyika	I
<b>BULININAE</b>						
<i>Bulinus</i>						
<i>B. (B.) truncatus truncatus</i>	36	-	I♂	4	Sardinia	III
	36	-	I♂	2	Iran	III
	36	72	I♂	5	Iraq	III
	36	-	I♂	10, 13	Egypt	I, III
	36	72	I♂	9, 4	Sudan	II, III
<i>B. (B.) truncatus rohlfsii</i>	36	ca. 72	I♂	2, 4	Ghana	I, III
<i>B. (B.) truncatus coulboisi</i>	36	-	I♂	2, 5	Tanganyika	I, III
<i>B. (B.) "sericinus"</i>	36	-	I♂	2	W. Aden	I
<i>B. (B.) "sericinus"</i>	72	ca. 144	I♂	3	W. Aden	III
<i>B. (B.) tropicus tropicus</i>	18	-	I♂	5	Kenya	I
	18	-	I♂	10, 13	S. Rhodesia	I, III
	18	-	I♂	2	S. Rhodesia	I, III
	18	36	I♂♀	10	S. Africa	III
<i>B. (B.) tropicus angolensis</i>	18	-	I♂	6	N. Rhodesia	III
<i>B. (B.) tropicus zanzebaricus</i>	18	-	I♂♀	6	Tanganyika	III
<i>B. (B.) guernei</i>	18	-	I♂	6	Senegal	I
<i>B. (B.) natalensis</i>	19, 20, 21	-	I♂	4, 3	S. Rhodesia	I, III
<i>B. (B.) ("natalensis")</i>	18, 19	-	I♂♀	2	S. Rhodesia	III
<i>B. (B.) ("sericinus")</i>	18	-	I♂	2	Ethiopia	III
<i>B. (B.) sp.</i>	18	-	I, II♂	8	Kenya	III
<i>B. (P.) globosus</i>	18	-	I♂	16	Liberia	I
	18	-	I♂	1	Ghana	I
	18	36	I♂	3	N. Rhodesia	I
	18	36	I♂	6	S. Rhodesia	I
	18	-	I♂	2	S. Rhodesia	I
	18	-	I♂	10	S. Africa	I
<i>B. (P.) jousseaumei</i>	18	36	I♂	10	Senegal	I
<i>B. (P.) ugandae</i>	?36	-	I♂	8	Sudan	II
<i>B. (Py.) beccarii</i>	18	-	I♂	1	W. Aden	I
<i>B. (Py.) forskalii</i>	18	-	I♂	1	W. Aden	I
	18	-	I♂	6	Ghana	I
	18	-	I♂	3	Tanganyika	I
	19	-	I♂	1	Angola	I
	18	-	I♂	3	S. Africa	I
<i>B. (Py.) reticulatus</i>	18	-	I♂	4	W. Aden	I
<i>B. (Py.) senegalensis</i>	18	36	I♂	5	Senegal	I

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#### ADDENDUM

The polyploid chromosome number report ( $n=36$ ) of *Gyraulus circumstriatus* mentioned on p 245 of this paper, needs correcting. In a recent study of this species from Montana, U. S. A., it was found to have only 18 pairs of chromosomes, which prompted a reexamination of shell specimens from the lot on which the previous study was made. Drs. Burch and Taylor now conclude that the material on which the original chromosome report was based is the closely related (and often nearly indistinguishable) *G. (T.) parvus*. Specimens of *G. parvus* from 3 additional localities in Michigan have been examined recently by J. B. Burch (unpublished) and they were found also to have 36 pairs of chromosomes, the same number that occurred in the original lot. Magnifications of the chromosomes

figured in the previous paper in this series (Burch, 1964, Malacologia, 1(3): 387-400) are as follows: Figs. 4-10, approximately 2660X; Figs. 11, 12, 15 and 17, approximately 1210X; Figs. 13, 14, 16 and 18-22, approximately 1900X; and Figs. 23-32, approximately 1970X.

Parts of two of the bivalents of the cell shown in Figs. 4 and 13 of Burch (1964) were nearly separated due to the pressure of the squash when the slide was prepared, the parts being held together only by a thin strand. When Fig. 13 was reproduced by the printer the connecting strand of the bivalent on the right margin of the drawing was lost, making the single bivalent actually appear as 2 chromosomal complements (compare this bivalent in Figs. 4 and 13 of that publication).

#### RESUMEN

##### ESTUDIOS CITOLÓGICOS DE PLANORBIDAE

##### II. ALGUNOS PLANORBIDOS AFRICANOS, PLANORBININAE Y BULIMINAE

Se registran los números cromosómicos para 20 especies y subespecies de planorbidos africanos. El número haploide 18 se encontró, entre los Planorbinae, *Anisus crassilabrum* y *Gyraulus costulatus*; el mismo número en *Planorbina alexandrina alexandrina*, *P. pfeifferi pfeifferi*, *P. pfeifferi gaudi*, *P. pfeifferi madagascariensis* y *P. sudanica tanganyicensis* entre los Planorbininae; y en *Bulinus (Bulinus) tropicus tropicus*, *B. (B.) guernei*, *B. (Physopsis) globosus*, *B. (P.) jousseaumei*, *B. (Pyrgophysa) beccarii*, *B. (Py.) forskalii* (from Ghana, Tanganyika and South Africa), *B. (Py.) reticulatus* y *B. (Py.) senegalensis*; mientras *B. truncatus truncatus*, *B. truncatus rohlfsii*, *B. coulboisi* y *B. "sericinus"* tienen 36 pares de cromosomas, y previamente en una población de *B. "sericinus"* del oeste de Aden se contaron 72 pares.

*B. forskalii* de Angola tenía 19 elementos (presumibles bivalentes) en la profase I y metafase I, y *B. natalensis* de la Rhodesia del Sur, tenía 19, 20 y 21 elementos presentes en metafase I (algunos quizá univalentes). Estos resultados, así como previas informaciones, muestran que en los Bulimulinae, la poliploidía parece ocurrir sólo en el subgénero *Bulinus* s.s. donde tal presencia fué encontrada en aquellas especies, todas del grupo "truncatus", implicadas en la transmisión de esquistosomiasis humana y bovina. El número cromosómico, *per se*, parece no tener correlación con la susceptibilidad de infección por esquistosomas en los subgéneros de Bulininae, *Physopsis* y *Pyrgophysa*, o en los planorbininos del género *Planorbina*.



CYTOTAXONOMIC STUDIES OF FRESHWATER LIMPETS  
(GASTROPODA: BASOMMATOPHORA)

III. JAPANESE *FERRISSIA* AND *GUNDLACHIA*<sup>1,2</sup>

J. B. Burch<sup>3</sup>

ABSTRACT

Three species of freshwater limpets are presently known from Japan. The haploid chromosome number of both *Ferrissia japonica* and *Gundlachia japonica* is 18. This is the first time this chromosome number has been reported in the Ancyliidae, although it is the number most commonly found in other Basommatophora. *F. nipponica* apparently has the haploid number 17 (fide Inaba).

The great differences in chromosome numbers between the North American *Ferrissia* (n=30) and the Japanese species (n=17, 18) indicate that the species of these 2 continents are probably not congeneric, regardless of similarities in the sculpturing of their shell apices. The similar chromosome numbers of *F. japonica* and *G. japonica* (n=18) may point to a systematic relationship, but *F. nipponica* probably has little in common with the American *Laevapex* and the African *Burnupia*, although all 3 have 17 pairs of chromosomes.

INTRODUCTION

The chromosomes of nearly all Japanese freshwater basommatophoran snails have been studied previously (Burch et al., 1964). However, there are no reports which include the Japanese freshwater limpets (family Ancyliidae). Because of the prominence of ancyliids in freshwater pulmonate zoogeography, their wide range of reported chromosome numbers, and their perplexing systematics and phylogenetic relationships (due largely to our lack of knowledge), I am presenting my studies of the chromosomes of 2 species of Japanese freshwater limpets, along with information on a third species studied by my colleague, Dr. Akihiko Inaba (personal communication), and published with his

permission.

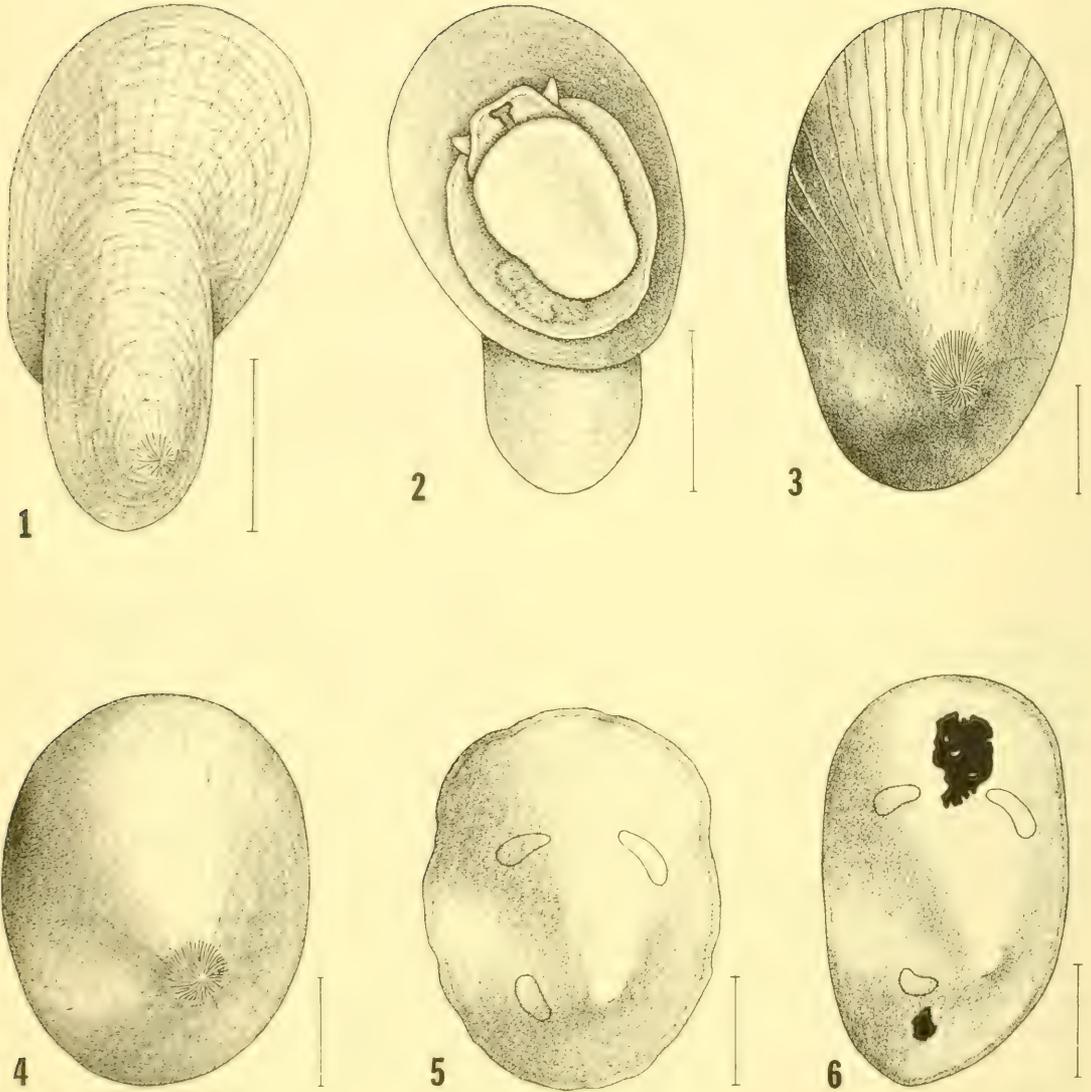
Three species of freshwater limpets (Euthyneura: Ancyliidae) are known to occur in Japan, *Ferrissia nipponica* (Kuroda, 1949) (Figs. 4, 5), *F. japonica* Habe and Burch, 1965 (Figs. 3, 6) and *Gundlachia (Kincaidilla) japonica* Burch, 1964 (Figs. 1, 2). The generic placement of all 3 species was based originally on characters of the shell, because it is on such characters that our prevailing system of ancyliid systematics rests. All 3 species have radially striate apices, and the *Gundlachia* species has, in addition, a septate shell. The inadequacy of such a system of classification that is based only on shell characters is brought out in the present paper.

Grateful acknowledgement is made to

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<sup>3</sup>Museum and Department of Zoology, University of Michigan, Ann Arbor, Michigan, U. S. A., in cooperation with the 406 Medical Laboratory, U. S. Army Medical Command, Japan.



FIGS. 1-6. Japanese freshwater limpets. FIGS. 1, 2. Dorsal and ventral aspects of *Gundlachia japonica*. FIG. 3. Dorsal view of the shell of *Ferrissia japonica*. FIGS. 4, 5. Dorsal views of the shell and mantle of *F. nipponica*. FIG. 6. Dorsum of the mantle of *F. japonica*. Length of line 1 mm.



FIGS. 7-10. Camera lucida drawings of meiotic chromosomes of *Gundlachia* and *Ferrissia*. FIG. 7. Diakinesis chromosomes of *G. japonica*. FIG. 8. Diakinesis chromosomes of *F. japonica*. FIG. 9. Metaphase I chromosomes of *G. japonica*. FIG. 10. Metaphase I chromosomes of *F. japonica*. All figures 2170X.

Mr. James E. Williams, 406 Medical Laboratory, U. S. Army Medical Command, Japan, for help in securing *Ferrissia japonica*, and to Dr. Hiroshi Itagaki, Azabu Veterinary College, Fuchinobe, for the specimens of *Gundlachia japonica*. I am also indebted to Major John W. Moose of the 406 Medical Laboratory and to Prof. Henry van der Schalie, Museum of Zoology, The University of Michigan, for facilities and many kindnesses.

#### MATERIALS AND METHODS

The 16 specimens of *Ferrissia japonica* used in this study were collected from the backwaters of the Shio River, Nirasaki, Yamanashi Prefecture in August, 1963. Only 3 specimens were satisfactory for cytological studies. The 14 non-septate paratype specimens<sup>4</sup> of *Gundlachia japonica* were taken from a pool at the residence of Dr. Hiroshi Itagaki in Tokyo,

October, 1963. Only 4 specimens of *G. japonica* gave satisfactory results.

The material examined consisted of ovotestes killed, fixed and preserved in Newcomer's (1953) fluid. Cells of the ovotestes were stained by the acetic-orcein squash technique (La Cour, 1941). All observations were on cells of spermatogenesis and were made with Nikon microscopes using 100X (n.a. 1.25) oil immersion objectives and 10, 20 and 25X oculars. All drawings of chromosomes were made with the aid of a camera lucida and reproduced at a table top magnification of 5100X.

#### OBSERVATIONS AND DISCUSSION

The haploid chromosome number of both *Ferrissia japonica* and *Gundlachia japonica* is 18. The 18 bivalents can easily be seen at diakinesis and metaphase of the first meiotic division (Figs. 7-10). The size and shape of these chromosomes are much like those seen in other ancyliid snails (Burch, 1960a, b; Burch, Basch and Bush, 1960). Exact counts of the chromosomes of spermatogonial cells could not be made, but the diploid number of some almost favorable cells was clearly about 36. Mitotic metaphase

<sup>4</sup>Thirty-five specimens of living *G. japonica* were in the original lot: 1 holotype (mounted in balsam in a depression slide), 20 paratypes preserved in 70% ethanol and 14 paratypes fixed in Newcomer's fluid.

TABLE 1. Chromosome Numbers in Freshwater Limpets

Species	Chromosome Number		Locality	Reference
	n	2n		
1. Superfamily ?				
Latiidae				
<i>Latia neritoides</i>	18	-	New Zealand	Burch and Patterson, 1963
2. Acroloxacea				
Acroloxidae				
<i>Acroloxus lacustris</i>	18	36	England	Burch, 1962
3. Ancyloacea				
Ancyliidae				
a. Ancylinae				
<i>Rhodacmea cahawbensis</i>	15	30	U. S. A.	Burch et al., 1960
<i>Ancylys fluviatilis</i>	60	ca. 120	England	Burch et al., 1960
b. Ferrissiinae				
<i>Ferrissia parallela</i>	30	60	U. S. A.	Burch et al., 1960
<i>Ferrissia tarda</i>	30	-	U. S. A.	Burch et al., 1960; Burch 1962
<i>Ferrissia nipponica</i>	17	-	Japan	Inaba (personal communication)
<i>Ferrissia japonica</i>	18	-	Japan	This report
<i>Gundlachia japonica</i>	18	-	Japan	This report
c. Laevapecinae				
<i>Laevapex fuscus</i>	17	34	U. S. A.	Burch, 1960b
<i>Burnupia</i> sp.	17	-	S. Africa	Burch, 1962

chromosomes are monocentric and are either metacentric, submetacentric or nearly acrocentric. The sizes of spermatogonial metaphase chromosomes correspond to those reported from similar squash preparations for other Basomatophora (Burch, 1960a).

Previous publications of significance on chromosomes of freshwater limpets are those of Burch (1960a, b; 1962), Burch, Basch and Bush (1960) and Burch and Patterson (1963). The chromosome numbers reported in those publications, shown in Table I, represent 3 very diverse groups, the Latiidae, Acroloxacea and Ancyloacea.

It is interesting to note that the greatest diversity in chromosome numbers is found in the latter group, ranging from  $n=15$  to  $n=60$ . It is also perhaps quite significant that the chromosome numbers of 4 of the species studied in the Ancyloacea are either 15 or multiples of 15, indicating that polyploidy probably occurs here. In both the Latiidae and Acroloxacea, only the single haploid number 18 has been found.

The chromosome numbers in euthyneuran gastropods tend to be very conservative (Burch, 1961). This is especially true at the generic level, where there is usually little or no variation in chromo-

some number between the various species of any given genus. In those rare instances where there is variation, the number does not seem to vary more than  $\pm 1$  (haploid), except in obvious cases of polyploidy.

In the genus *Ferrissia*, the chromosome numbers of only 2 other species have been determined previously: *F. parallela* and *F. tarda*, from Michigan, U. S. A. (Burch, Basch and Bush, 1960), both with the haploid chromosome number 30. This number is in great contrast to that reported for *F. nipponica* and *F. japonica* from Japan ( $n=17, 18$  resp.), and in light of these highly divergent chromosome numbers, it seems very unlikely that the North American and Japanese species could belong to the same genus. Although the shells of both groups have striate apices, the soft anatomy might prove different enough to warrant their systematic placement in different genera. It is therefore readily apparent that a critical morphological study of the Ancyliidae on a world-wide basis is needed.

The fact that both *Ferrissia japonica* and *Gundlachia japonica* have the same chromosome number ( $n=18$ ) brings to mind the unsettled controversy as to whether the genus *Gundlachia* is a real genetically determined biological (taxonomic) entity, or merely a growth form initiated under certain unfavorable environmental conditions. Although most recently reviewed and discussed by Basch (1959, 1963) the subject has not been finally settled by definite proof on one side or the other, and the problem still awaits a critical morphological study. At any rate, it is interesting to note that Dr. Itagaki did not notice *Gundlachia*-like shells in his pool before they were discovered by me and that he has not been able to find any since. However, as mentioned in the original description (Burch, 1964), young non-septate *G. japonica* shells differ from *F. japonica* (referred to as "*Ferrissia* sp.") shells of similar size, and, in addition, the pigment patterns on the mantle of the 2 species differ. Should *G. japonica* Burch, 1964, turn out to be only an environmentally produced form of *F.*

*japonica* Habe and Burch, 1965, then it will simply bear the name *F. japonica* (Burch, 1964). However, it will retain the generic designation "*Ferrissia*" only if it is shown to be congeneric with *Ancylus rivularis* Say 1817, the type species of *Ferrissia* Walker, 1903.

The haploid chromosome number 17 found by Inaba (personal communication) in *Ferrissia nipponica* is the same as that found in *Laevapex fuscus* from the U. S. A. and *Burnupia* sp. from Africa (Burch, 1960a, 1962). However, a close relationship with these 2 species seems unlikely; their shells differ in apical sculpturing and *F. nipponica* lacks the pigment and adductor muscle pattern characteristic of *Laevapex* and *Burnupia*.

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## RESUMEN

ESTUDIOS CITOTAXONOMICOS DE LAS LAPITAS DE AGUA DULCE  
III. LAS *FERRISSIA* Y *GUNDLACHIA* JAPONESAS

Tres especies de lapas fluviales se conocen en el Japón. El número cromosómico haploide de *Ferrissia japonica* y *Gundlachia japonica* es 8 en ambas. Esta es la primera vez que este número se registra en los Ancyliidae, aunque es el más común en otros Basommatoforos. *F. nipponica* aparentemente tiene el número haploide 17 (según Inaba).

La gran diferencia en el número de cromosomas entre las *Ferrissia* norteamericanas (n=30) y las japonesas (n=17-18) indica que las especies de los dos continentes probablemente no son congénicas, a pesar de las similitudes en la escultura de sus ápices. El número cromosómico similar de *F. japonica* y *G. japonica* (n=18) puede señalar una relación sistemática, pero *F. nipponica* es probable que tenga poco de común con los *Laevapex* norteamericanos y los *Burnupia* africanos, aunque los tres tienen 17 pares de cromosomas.

THE CHROMOSOMES OF *TULOTOMA ANGULATA*  
(STREPTONEURA: VIVIPARIDAE)<sup>1,2</sup>

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ABSTRACT

*Tulotoma* is a rare genus endemic to the Alabama and Coosa rivers of the southeastern United States. Some authors have recognized 3 distinct species, others only 1. The chromosome number of *T. angulata* is  $n=13$  ( $2n=26$ ). Pollister and Pollister (1940, 1943) reported the chromosome number of *T. magnifica* as  $n=12$ . This apparent difference in chromosome numbers favors the concept that the genus contains more than 1 species. If the hypothesis that phylogenetic advancement is accompanied by a gradual increase in chromosome number is applied to the Streptoneura, then the family Viviparidae ( $n=7-14$ ) is considerably more primitive than currently contended.

*Tulotoma angulata* has 3 pairs of metacentric chromosomes, 7 pairs submetacentric, 2 pairs nearly acrocentric and a pair of dimorphic sex chromosomes. The sex-determining mechanism of this species, previously unknown in Viviparidae, is XX in the female and XY in the male.

INTRODUCTION

There are only a few reliable cytological studies on viviparid snails, and there is only 1 previously published paper in which the chromosome squash technique has been used. Consequently, most of the older reports lack the necessary clarity to enable comparative karyotype analyses or to determine presence and type of chromosomal sex determining mechanisms. The purpose of this paper is not only to present and demonstrate the usefulness of such cytological details, but also to give information on a rare endemic freshwater mollusk of North America.

The genus *Tulotoma* Haldeman, 1840, is restricted to the Alabama and Coosa river systems of the southeastern United States. It has been considered by some authors (e.g., Haldeman, 1843; Clench, 1962) to be monotypic, containing only the

species *T. magnifica* (Conrad, 1834) with several variants. Other authors (e.g., Wetherby, 1876; Walker, 1918; Goodrich, 1944) consider the genus to include as many as 3 distinct species, *T. magnifica*, *T. angulata* (Lea, 1841) and *T. coosaensis* (Lea, 1841)<sup>3</sup>.

Grateful acknowledgement is made to Drs. William H. Heard, Florida State University and Henry van der Schalie, University of Michigan, for the opportunity to study the specimens on which this report is based, and to Drs. J. B. Burch and Dwight W. Taylor, University of Michigan, for their stimulating interest and helpful suggestions concerning the manuscript.

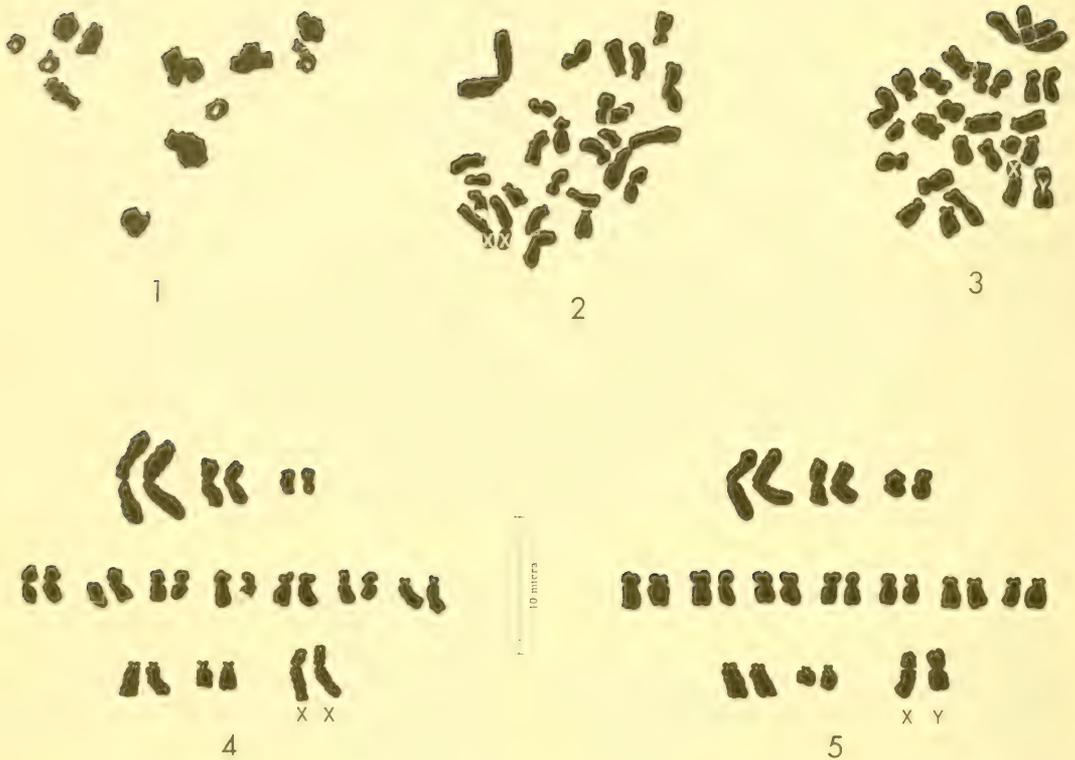
MATERIALS AND METHODS

The specimens used in this study were collected by William H. Heard from the

<sup>1</sup>Contribution No. 1, Southeast American Mollusks Program, Institute of Malacology.

<sup>2</sup>This investigation was supported (in part) by research grant 5 T1 AI 41-07 from the National Institute of Allergy and Infectious Diseases, U. S. Public Health Service.

<sup>3</sup>No one seems to consider *T. bimonilifera* (Lea, 1834) a valid species, but only a form of *T. magnifica*.



FIGS. 1-5. Camera lucida drawings of chromosomes of *Tulotoma angulata*. FIG. 1. Late meiotic prophase (diakinesis) chromosomes. FIG. 2. Oögonial metaphase chromosomes. FIG. 3. Spermatogonial metaphase chromosomes. FIG. 4. Chromosomes of Fig. 2 paired and arranged according to decreasing length with the X chromosomes labelled. FIG. 5. Chromosomes of Fig. 3 paired and arranged according to decreasing length with the X and Y chromosomes labelled.

Coosa River at Wetumpka, Elmore Co., Alabama on August 1, 1964.

The reproductive gland (ovary or testis) was dissected from 6 living specimens (3 males and 3 females) and immediately fixed and preserved in Newcomer's (1953) fluid for cytological examination. The preserved tissue was then prepared and stained by the acetic-orcein squash technique (La Cour, 1941). The chromosomes in Figs. 1-5 were drawn with the aid of a camera lucida, using a 30X ocular and reproduced at a table-top magnification of 5340X.

#### OBSERVATIONS

The haploid chromosome number of *Tulotoma angulata* is  $n=13$ . Fig. 1 shows the diakinesis chromosomes of a female. Pairing appears to be normal in the formation of the 13 bivalents.

Gonial metaphase plates provided excellent material for chromosome counts as well as a thorough karyotype analysis. Figs. 2-5 show the 26 chromosomes of the diploid complement. The chromosomes are clearly monocentric; their chromatid margins are irregularly out-

lined because contraction was not yet complete. The chromosomes range in length from 3.5 micra for the largest pair to 1.9 micra for the smallest pair.

The somatic karyotype of *Tulotoma angulata* (Figs. 4 and 5) consists of 3 pairs of metacentric (medianly constricted) chromosomes, 7 pairs of submetacentrics (submedianly constricted) and 2 pairs of almost acrocentric (subterminally constricted) chromosomes. One pair of the metacentric chromosomes is conspicuously large, the largest pair of the chromosome complement. One metacentric pair is intermediate in size, the other pair is relatively small. All of the submetacentric chromosomes and 1 pair of the subterminally constricted chromosomes are in the intermediate size range. One pair of subterminally constricted chromosomes is relatively smaller.

Two relatively large chromosomes in spermatogonial metaphase cells cannot be matched with morphologically similar homologues. One is medianly constricted, the other is distinctly submedianly constricted (Figs. 3 and 5). These are presumably the sex chromosomes, one being an "X", the other a "Y". In oögonial metaphase cells the corresponding submedianly constricted chromosome is duplicated and the metacentric chromosome is lacking (Figs. 2 and 4). This indicates that the submetacentric chromosomes are the Xs, and that the metacentric is a Y chromosome. Thus, in *Tulotoma angulata* the sex-determining mechanism is XX in the female and XY in the male. The sex chromosomes show no apparent heterotypic behavior during the chromosome cycle.

#### DISCUSSION

Previous chromosome studies of viviparid snails are those of Franz (1932), Pollister and Pollister (1940, 1943), Inaba and Tanaka (1953), Ramamoorthy (1958) and Rainer (1963). The chromosome numbers reported by those authors are

shown in Table I.<sup>3</sup> The haploid chromosome numbers range from 7 to 14; species of the subfamily Lioplacinae have only higher chromosome numbers, while some members of the subfamilies Viviparinae and Bellamyinae have low chromosome numbers.

Karyotypes for viviparid snails have been presented by 3 authors: Inaba and Tanaka (1953) for *Cipangopaludina malleata*, Ramamoorthy (1958) for *Bellamyia dissimilis* and *B. bengalensis* and Rainer for *Viviparus cunctus* and *V. ater*. However, these analyses provide only fragmentary information since in Inaba's report the sectioning method was used and therefore the chromosomes are poorly characterized; Ramamoorthy's report lacks karyograms and measurements to show detailed chromosome size and morphology necessary for comparative analysis of karyotypes; and Rainer presents an analysis based only upon the length of mitotic metaphase chromosomes without regard to position of centromeres. None of these authors observed dimorphic sex chromosomes.

Since my studies show that *Tulotoma angulata* has 13 pairs of chromosomes and Pollister and Pollister (1940 and 1943) found only 12 pairs for *T. magnifica*, these differences seem to strengthen the older precedent of recognizing more than a single species in the genus. It is desirable to make a comparative karyotype investigation of the chromosomes of *T. magnifica* and *T. coosaensis* should living specimens of these rare endemic species be found again.

Chromosome numbers in the gastropod subclass Streptoneura range from 7 to 36 haploid (Franz, 1932; Rainer, 1963; Makino, 1956; Nishikawa, 1962). In the

<sup>3</sup>Species names used in the table are in accordance with Wenz, 1938-44. Two reports of chromosome numbers are not included in the table:  $n=7$  ( $2n=14$ ) for *Viviparus viviparus* (Ankel, 1924) is considered invalid;  $2n=12$  for *Campeloma rufum* (Mattox, 1937) needs to be confirmed.

TABLE 1. Chromosome numbers reported in the Viviparidae.

Species	Haploid No.	Diploid No.	Source	Reference
Bellamyinae				
<i>Cipangopaludina malleata</i>	9	18	Japan	Inaba and Tanaka, 1953
" "	9	18	U. S. A.	Pollister and Pollister, 1940, 1943
<i>Bellamyia dissimilis</i>	-	22	India	Ramamoorthy, 1958
<i>B. bengalensis</i>	-	22	India	Ramamoorthy, 1958
Viviparinae				
<i>Viviparus contectus</i>	7	-	Europe	Franz, 1932
" "	7	14	Europe	Rainer, 1963
<i>V. ater</i>	9	-	Europe	Franz, 1932
" "	9	18	Europe	Rainer, 1963
<i>V. viviparus</i>	10	-	Europe	Franz, 1932
<i>V. georgianus</i>	12	24	U. S. A.	Pollister and Pollister, 1940
<i>V. contectoides</i>	13	26	U. S. A.	Pollister and Pollister, 1940, 1943
" "	-	26	U. S. A.	Patterson (unpubl.)
<i>V. intertextus</i>	13	26	U. S. A.	Pollister and Pollister, 1940
<i>Tulotoma magnifica</i>	12	24	U. S. A.	Pollister and Pollister, 1940, 1943
<i>T. angulata</i>	13	26	U. S. A.	Patterson, this paper
Lioplacinae				
<i>Campeloma decisum</i>	-	26-28	U. S. A.	Pollister and Pollister, 1940
<i>C. ponderosum</i>	14	28	U. S. A.	Pollister and Pollister, 1940, 1943
<i>C. p. coarctatum</i>	-	28	U. S. A.	Patterson (unpubl.)
<i>C. subsolidum</i>	-	26-28	U. S. A.	Pollister and Pollister, 1940

Archeogastropoda, the range in chromosome numbers is  $n=9-21$ , with the Acmaeidae, Patellidae and Neritidae having chromosome numbers of  $n=9$  or  $11$  and the remaining families with  $n=18$  or a closely related number (Nishikawa, 1962). Members of the Mesogastropoda have haploid chromosome numbers ranging from  $n=7$  for the lowest to the more common  $n=17-18$ . The Neogastropoda are characterized by higher haploid chromosome numbers (with the exception of one member of the Muricidae) ( $n=ca. 30$ ) with the base number probably about

$n=35$  or  $36$  according to Nishikawa (1962).

Among the 365 species of gastropods that have been examined cytologically, only 96 (26.5%) have been reported to have chromosome numbers less than 18. Even fewer species (44 or 12%) have haploid numbers of 14 or less ( $n=14$  is the highest number reported in the Viviparidae) (see Table II.). Such low numbers may be significant in the phylogenetic placement of these various species, since Burch (1961) suggests that in the subclass Euthyneura low chromosome numbers may indicate primitiveness and high numbers

TABLE 2. Number of species of Gastropoda with 14 or less pairs of chromosomes

Systematic Group	Number of Species Investigated	Number of Species $n \leq 14$	Haploid Chromosome Numbers
<b>EUTHYNEURA<sup>4</sup></b>			
<u>Notaspidea</u>			
Pleurobranchidae	1	1	12
<u>Nudibranchia</u>			
Dorididae	6	6	13
Polyceridae	2	2	13
Goniodorididae	1	1	13
Fimbriidae	1	1	13
Arminidae	1	1	13
Cuthonidae	2	2	13
<u>Stylommatophora</u>			
Succineidae	8	2	5-22
<b>STREPTONEURA<sup>5</sup></b>			
<u>Archaeogastropoda</u>			
Patellidae	3	3	9
Acmaeidae	6	6	9
Neritidae	1	1	11
<u>Mesogastropoda</u>			
Viviparidae	14	14	7-14
Pleuroceridae	1	1	8
Valvatidae	2	2	9-10
<u>Neogastropoda</u>			
Muricidae	9	1	13

<sup>4</sup>From Burch, 1964a, 1964b, 1965.

<sup>5</sup>From Makino, 1956; Nishikawa, 1962; Table 1, this paper.

greater advancement. If such a hypothesis is applied to the Streptoneura, then the family Viviparidae ( $n=7-14$ ) is considerably more primitive than has been contended (Wenz, 1938-44; Fretter and Graham, 1962).

Sex chromosomes have been reported in 9 species of marine gastropods (Nishikawa, 1962), 1 freshwater snail, *Paludomus tanschawrica* (Thiaridae) (Jacob, 1959) and 2 amphibious species, *Pomatiopsis lapidaria* and *P. cincinnatensis* (Hydrobiidae) (Burch, 1960c;

Patterson, 1963). All reports, except those of Jacob, Burch and Patterson, were published before 1931 and were based upon material prepared by the paraffin section technique. Concerning sex chromosomes in mollusks, Nishikawa (1962) states: "So far as the findings by the present author are concerned, there is no evidence showing the presence of [a] particular chromosome which is heterotypic in behavior and morphology characteristic to the sex-chromosome observed in other animals. According to the author's view,

the X-element designated by some authors is no other than the chromosome which is mechanically displaced unusually by the influence of technical procedures." The inability of Nishikawa and others to identify sex chromosomes may be due partly to inadequacies of the paraffin section technique. This paraffin method compresses the chromosomes to as much as 1/3 to 1/2 of their size as seen in squash preparations, and their morphological characteristics cannot be easily discerned (Burch, 1960a, b). A heteromorphic pair of chromosomes is clearly demonstrated in the karyotype of *Tulotoma angulata* males from squash preparations, and the corresponding X chromosome is seen in duplicate in females, which lack the Y. This indicates that at least some streptoneuran snails do indeed have sex chromosomes.

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## RESUMEN

LOS CROMOSOMAS DE *TULOTOMA ANGULATA*

*Tulotoma* es un género raro y endémico de los ríos Coosa y Alabama en el sudeste de los Estados Unidos. Algunos autores reconocieron tres distintas especies, otros sólo una. El número cromosómico de *T. angulata* es  $n=13$  ( $2n=26$ ). Pollister y Pollister (1940, 1944) informaron el número de *T. magnifica* como  $n=12$ . Esta aparente diferencia favorece el concepto de que el género contiene más de una especie. Si la hipótesis de que el avance filogenético es acompañado por un aumento gradual del número cromosómico se aplica a los Estreptoneuros, entonces la familia Viviparidae ( $n=7-14$ ) es considerablemente más primitiva de lo que se admite corrientemente. *T. angulata* tiene tres pares de cromosomas metacéntricos, siete pares submetacéntricos, dos pares casi acrocéntricos y un par de cromosomas sexuales dimórficos. El mecanismo determinante del sexo en esta especie, previamente desconocido en Viviparidae es XX en las hembras y XY en los machos.



ON THE MODES OF INFECTION OF *ACHATINA FULICA*  
BY THE LARVAE OF *ANGIOSTRONGYLUS CANTONENSIS*<sup>1</sup>

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ABSTRACT

The members of 2 groups of *Achatina fulica* were infected experimentally with known numbers of first-stage larvae of *Angiostrongylus cantonensis*. The first group was infected orally while the second was infected by placing larvae onto the extended foot of each snail. By comparing the percentages of third-stage larvae recovered from the foot musculature of the members of both groups, it was ascertained that both methods of infection were possible and equally as efficient. Under natural conditions, both methods of infection are believed to occur.

INTRODUCTION

*Achatina fulica* Bowdich, the giant African snail, originating in East Africa, has become widely distributed in Asia and in the Pacific Basin (see Mead, 1961). It was first introduced to the Hawaiian Islands in 1936 when 2 specimens were brought to the island of Oahu from Formosa and additional specimens were imported through the mails from Japan to the island of Maui (Pemberton, 1938). Since that time, this terrestrial gastropod has become well established in Hawaii. Alicata (1962) was the first to point out that *A. fulica* is a compatible intermediate host for the metastrongylid nematode *Angiostrongylus cantonensis* (Chen). This parasite has been identified as the etiological agent of one type of eosinophilic meningoencephalitis in humans in Hawaii (Horio and Alicata, 1961; Rosen *et al.*, 1962) and Formosa (Nomura and Lin, in Hsieh, 1959), and is most probably the etiological agent for this disease on various islands in the Pacific. This

disease has been referred to as "parasitic meningoencephalitis" by Alicata (in Horio and Alicata, 1961).

The adults of *A. cantonensis* are normally parasites in the pulmonary arteries and lungs of rats. The life history of this nematode has been elucidated by Mackerras and Sandars (1955) and expanded upon by Weinstein *et al.* (1963). During its life cycle, first-stage larvae, passing out in the feces of infected rats, enter the molluscan host and undergo 2 molts. Third-stage larvae, which are the infective form to mammals, are introduced into the rat when infected molluscs are ingested. A variety of molluscs serve as suitable hosts for this nematode of which *A. fulica* is a common one in Hawaii. Other known molluscan hosts, along with the locations where infected molluscs have been found, are presented in Table I.

The mechanism(s) by which the molluscan host becomes infected with the first-stage larvae of *A. cantonensis* is rather indefinite. Mackerras and Sandars (1955) reported that, in the case of the

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TABLE 1. Known molluscan intermediate hosts of *Angiostrongylus cantonensis* and locations where infected molluscs have been found.

Molluscan intermediate host	Australia	Hawaii (USA)	Tahiti	New Caledonia	Rarotonga (Cook Islands)	Fiji	Lifou (Loyalty)
<i>Agriolimax laevis</i>	+1	+2	+2	+2	+2		
<i>Limax arborum</i>	+1						
<i>Onchidium</i> sp.	+1						
<i>Bradybaena similaris</i>		+1, 2	+2	+2	+2		+2
<i>Subulina octona</i>		+1, 2		+2	+2		+2
<i>Achatina fulica</i>		+1, 2					
<i>Veronicella alta</i>		+1, 2		+2			
<i>Vaginulus plebeius</i> <sup>3</sup>			+2	+2	+2	+2	+2
<i>Limax maximus</i>							
<i>Deroceras reticulatum</i>							
<i>Australorbis glabratus</i> <sup>1,4</sup>							
<i>Lymnaea ollula</i>		+1					
<i>Helix aspersa</i>				+?5			
<i>Girasia peguensis</i>							
<i>Pila polita</i>							
<i>Macrochlamys resplendens</i>							
<i>Microparmarion malayanum</i>							
<i>Parmarion</i> sp.							
<i>Semperula</i> sp.							
<i>Pupina complanata</i>							
<i>Opeas javanicum</i>							

1. Experimentally infected. 2. Naturally infected. 3. The presence of *A. cantonensis* larvae in Fiji (Alicata, 1962) is now in doubt (Alicata and McCarthy, 1964). 4. Richards (1963) reported in an abstract that he successfully infected 16 of 17 species of freshwater molluscs; however, only *A. glabratus* was mentioned by name. 5. There is a serious doubt whether *H. aspersa* is a suitable intermediate host (see Loison *et al.*, 1962).

slugs *Limax arborum* Bouchard-Chantreaux and *Agriolimax laevis* (Müller) and the terrestrial snail *Onchidium* sp.: "they were infected by allowing a suspension of larvae to trickle around them from a pipette." These workers did note, however, that: "The slugs which we used . . . appear to be attracted to rat feces, and have been observed eating

them. Thus there is the possibility that they may become infected orally, as well as by the penetration of larvae through the body-wall or foot." Weinstein *et al.* (1963) reported that they succeeded in infecting the slugs *Limax maximus* Linn. and *Deroceras reticulatum* (Müller) "by placing them for about an hour on lettuce leaves or moist paper toweling smeared

TABLE 1. (continued)

Espiritu Santo (New Hebrides)	Maryland (USA)	Malaya	Thailand	Micronesia	References
					Mackerras and Sandars (1955); Alicata and Brown (1962a,b); Alicata (1963); Alicata and McCarthy (1964).
					Mackerras and Sandars (1955).
+2					Mackerras and Sandars (1955).
+2					Ash (1962); Alicata and Brown (1962a,b); Alicata (1963); Alicata and McCarthy (1964).
					Ash (1962); Alicata (1963); Alicata and McCarthy (1964).
					Alicata (1962).
+2					Horio and Alicata (1961); Ash (1962); Alicata (1962, 1963).
	+1				Alicata and Brown (1962a,b); Alicata, Loison, and Cavallo (1963); Alicata (1963); Alicata and McCarthy (1964).
	+1				Weinstein, Rosen, Laqueur and Sawyer (1963).
					Weinstein, Rosen, Laqueur and Sawyer (1963).
					Richards (1963).
					Alicata and Brown (1962b).
					Loison, Cavallo and Vervent (1962).
		+2			Joe (per. comm.).
			+2		Punyagupta (per. comm.).
		+2			Joe (per. comm.).
		+2			Lait, Kong, and Joe (1962).
		+2			Lait, Kong, and Joe (1962).
		+2			Lait, Kong, and Joe (1962).
				+2	New host.
				+2	New host.

with fresh feces containing first-stage larvae of *A. cantonensis*." Finally, Richards (1963) reported that: "Observations on *Australorbis glabratus* indicated that infection occurred via the digestive tract following ingestion of first-stage larvae in rat feces." In this laboratory, various snails have been successfully infected by dropping larvae suspended in water onto the body surface of the molluscs. It thus appeared to be of some interest to determine experimentally whether the molluscan host, in this case *A. fulica*, becomes infected when first-

stage larvae penetrate the integument, or when they are ingested, or both.

#### MATERIALS AND METHODS

Surveys conducted to determine the incidence and distribution of infection in *Achatina fulica* by *Angiostrongylus cantonensis* on the island of Oahu, Hawaii, revealed that at one site, in a grove adjacent to a residential area on the leeward side, the snails were for all purposes free of helminth parasites. Examination of over 90 snails from this location

revealed only 3 specimens which were infected with *A. cantonensis* and in each of these, only 1-3 larvae were present. For this reason, snails collected from this site were used as the experimental animals. A total of 31 snails ranging from 5.2 cm to 11 cm in length (apex to distal edge of aperture) were used during this study. These were divided into 2 groups. The members of one group, consisting of 15 snails, were fed first-stage larvae of *A. cantonensis*, while the members of the other groups, also consisting of 15 snails, were exposed individually to larvae by placing the larvae onto the foot of each snail.

The nematode larvae used during this study were collected from the fresh feces of experimentally infected white rats by use of the Bearmann apparatus and concentrated by centrifugation. The number of larvae employed to infect each snail was determined by the dilution method. After the number of larvae was determined in 0.2 - 0.4 ml samples of aqueous suspensions, each of the snails of the first group was fed such a suspension. The snails had been starved previously for 48 hours and although they withdrew into their shells when agitated, each one was induced to extend its foot and head quite readily by dropping cold tap-water onto its retracted foot. Furthermore, as the result of dropping cold water on their head region after they became partially extended, they readily protruded their heads and opened their mouths. When this occurred, the suspended larvae were introduced into their mouths by using a Pasteur pipette. In most instances, the snails held onto the tip of the pipette. After introducing the suspension of larvae, some water was fed to each snail in the same manner.

In the case of the members of the second group of snails, samples of water containing known numbers of larvae were carefully pipetted onto the ventral (crawling) surface of the foot. After each snail was thus exposed to the larvae, it was held in an upside down position for 30 minutes, thus preventing the loss of any

larvae during this period. The surface of the foot was rinsed before each snail was returned to its container.

All of the snails were maintained in large glass dishes (10 inches in diameter), on moist soil, which had been previously autoclaved and to which 40 ml of a 1% aqueous suspension of  $\text{CaCO}_3$  had been added. Dried leaves, which had been autoclaved also, were used to cover the surface. The snails were fed every other day on lettuce leaves and the soil was maintained moist.

#### Recovery and Counting Procedures

The number of third-stage larvae embedded in the foot musculature of each snail was determined between 30 and 46 days after infection (Tables 2, 3). This was accomplished in the following manner. Each snail was carefully washed in cold tap-water before its shell was crushed and its foot was severed at the foot-viscera junction. The foot was then placed and left in a 1% NaCl solution for 15 minutes to stimulate the secretion of mucus. After most of the mucus had been removed, the surface of each foot was wiped with paper to remove the adhering mucus after which the entire foot was coarsely minced in a small meat grinder and digested in 100 ml of 1% pepsin solution, to which 1 ml HCl had been added. The digestion was carried out at 37°C for 2 hours after which the suspension was strained through a fine metal mesh into an Imhoff sedimentation cone and allowed to stand for 2 hours. The supernatant was then carefully siphoned off and the sediment was centrifuged to concentrate the larvae in 5 ml of fluid.

The larvae were suspended homogeneously in the 5 ml of fluid by repeatedly drawing the suspension into a pipette and blowing it out. Ten 0.1 ml samples were then pipetted from the 5 ml suspension and the number of larvae present in each sample was determined under a stereomicroscope. The mean number of larvae per 0.1 ml of sample was then multiplied by 50 to give an estimation of the total number of larvae

TABLE 2. Oral infection of 15 *Achatina fulica* with larvae of *Angiostrongylus cantonensis*

Snail No.	Length of snail (cm)	No. of 1st stage larvae used	Date infected 1963	Duration of infection (Days)	Estimated No. of 3rd stage larvae recovered (1/5 sample x 5)	Per cent recovered
OR-1	6.8	2,004	Oct. 16	30	55	2.7
OR-2	7.5	2,004	Oct. 16	30	220	10.9
OR-3	7.2	2,004	Oct. 16	30	100	4.9
OR-4	7.2	2,004	Oct. 16	30	25	1.2
OR-5	7.3	2,004	Oct. 16	33	65	3.2
OR-6	7.2	2,000	Oct. 18	31	280	14.0
OR-12	9.4	3,500	Oct. 18	31	0	0
OR-13	6.1	3,500	Oct. 18	31	5	0.1
OR-21	5.8	1,638	Nov. 29	45	80	4.8
OR-22	6.3	1,638	Nov. 29	45	680	41.5
OR-24	7.3	1,638	Nov. 29	35	180	10.9
OR-25	6.0	1,638	Nov. 29	46	520	31.7
OR-26	6.5	3,511	Nov. 29	35	70	1.9
OR-27	6.8	3,511	Nov. 29	35	800	22.7
OR-28	6.2	3,511	Nov. 29	45	1,410	40.1
$\bar{X}$		2,407				12.7

TABLE 3. Infection through the foot of 15 *Achatina fulica* with larvae of *Angiostrongylus cantonensis*

Snail No.	Length of snail (cm)	No. of 1st stage larvae used	Date infected 1963	Duration of infection (Days)	Estimated No. of 3rd stage larvae recovered (1/5 sample x 5)	Per cent recovered
E-7	6.1	2,000	Oct. 16	34	34	1.7
E-8	6.9	2,000	Oct. 16	34	45	2.2
E-9	7.9	2,000	Oct. 16	34	80	4.0
E-10	7.0	2,000	Oct. 16	34	1,410	70.5
E-11	7.8	2,000	Oct. 16	35	20	1.0
E-14	11.0	3,500	Oct. 18	33	85	2.4
D-21	7.3	1,638	Nov. 29	38	40	2.4
D-22	5.2	1,638	Nov. 29	46	20	1.2
D-24	7.3	1,638	Nov. 29	41	40	2.4
D-15	8.0	3,511	Nov. 29	38	1,360	38.7
D-26	5.5	3,511	Nov. 29	39	1,780	50.6
D-27	6.4	3,511	Nov. 29	39	1,730	49.2
D-28	7.0	1,755	Nov. 29	39	830	47.3
D-29	6.7	2,900	Nov. 29	39	950	32.7
D-30	5.2	2,900	Nov. 29	41	150	5.1
$\bar{X}$		2,433				20.7

in each snail.

## RESULTS

The estimated number of third-stage larvae recovered from each snail of both groups is tabulated in Tables 1 and 2.

By applying the statistical test:

$$z = \frac{P_1 - P_2}{\sqrt{\frac{pqN}{N_1 N_2}}}$$

$$z \left( z = \frac{X - \mu}{\sigma} \text{ or } \frac{\text{value tested-theoretical mean}}{\text{standard error of mean}} \right)$$

was found to be 0.35. Therefore, the 20.7% worm recovery from snails which were infected through the foot is statistically not significantly different from the 12.7% worm recovery from snails which were infected orally at the 5% level.

## DISCUSSION

It is apparent from these data that *Achatina fulica* can be infected with the first-stage larvae of *Angiostrongylus cantonensis* by both ingestion and penetration through the integument. These modes of infection probably occur in most if not all species of suitable molluscan hosts. From our studies, it has also been demonstrated statistically that one method of infection is as efficient as the other as determined by the percentages of third-stage larvae recovered.

In nature, snails foraging on vegetation or garbage on which the feces of infected rats are deposited can thus be infected with *A. cantonensis*. Observations in the field have also revealed that *A. fulica* favors damp places and in Hawaii, is often found at the base of banana trees after a heavy rain where small shallow puddles of rain water have accumulated. In areas where infected rats frequent similar sites, larvae-containing feces can be deposited in such puddles and the escaping larvae can thus infect snails crawling through the water.

It is also evident that there does not appear to be any correlation between the size of the snail and the percentage of

worm recovery among the molluscs studied although preliminary studies suggest that very young snails, 1-2 weeks old, are markedly refractile to infection by this nematode.

Naturally infected *A. fulica* collected on the island of Oahu commonly include 1,000 or more larvae of *A. cantonensis*. This suggests that either the snails are exposed to large numbers of first-stage larvae at one time, or are repeatedly infected by smaller numbers of larvae. Since second-stage larvae are fairly commonly found in naturally infected snails together with third-stage larvae, the latter probably occurs more frequently.

Not all species of gastropods are equally "susceptible" to *A. cantonensis*. Mackerras and Sanders (1955) have reported that *Limax arborum* and *Onchidium* sp. are rather poor hosts when compared to *Agriolimax laevis*, and Alicata and Brown (1962) have reported that *Lymnaea (Fossaria) ollula* Gould is a compatible host while *Melania mauianensis* Lea, *Physa compacta* Pease, and *Melania newcombi* Lea are not. Little is known yet about the mechanism(s) by which incompatible or less susceptible molluscs either prevent the invasion by *A. cantonensis* or absorb it after it enters their tissues. Mackerras and Sanders, however, did point out that in the case of *Onchidium* sp.: "larvae invaded the foot normally, and began to develop in large numbers, but relatively few reached the infective stage, the majority becoming surrounded by fibrous tissue and absorbed by the slug." This type of defense mechanism, termed encapsulation (see review by Cheng and Sanders, 1962), may also be responsible for the small number of third-stage larvae recovered in the majority of snails used in this study. However, this is not the only explanation, since first-stage larvae of *A. cantonensis* were observed in fecal smears from snails from 1-5 hours after they had been infected orally; thus a number of the first-stage larvae are lost in this way. It is possible that first-stage larvae eliminated in the feces of one snail may serve to infect another. This

is quite possible since *A. fulica* will readily ingest one another's fecal material.

A third method of infection, although not yet subjected to experimental verification, has been suggested by observations in the field and in the laboratory. It is well known that *A. fulica* will readily and even avidly consume the flesh of individuals of the same species which are injured, moribund, or dead (see Mead, 1961). This sporadic cannibalistic behavior may be responsible for the transfer of *A. cantonensis* larvae from one snail to another.

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## RESUMEN

SOBRE LOS MEDIOS DE INFECCION DE *ACHATINA FULICA* POR LA LARVA DE *ANGIOSTRONGYLUS CANTONENSIS*

Los miembros de dos grupos de *Achatina fulica* fueron infectados experimentalmente con cantidad conocida de larvas de *Angiostrongylus cantonensis* en su primer estado. El primer grupo fué infectado oralmente, mientras que el segundo lo fué por colocación de la larva encima del pié extendido de cada caracol. Por comparación del porcentaje de larvas en el 3<sup>er</sup> estado, recogidas de la musculatura pedal de los miembros de ambos grupos, pudo verificarse que los dos medios de infección eran igualmente eficientes. Puede creerse que bajo condiciones naturales la infección también se produce por estos métodos.

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SOME EFFECTS OF STATOCYST EXTIRPATIONS IN *LYMNAEA STAGNALIS*

J. Lever and J. J. Geuze

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ABSTRACT

In the literature there are only indirect indications about the function of statocysts in pulmonates. These are derived exclusively from experiments with stylommatophoran snails and no extirpations of these sense-organs were ever made.

In the present investigation, one or both statocysts were removed from specimens of *Lymnaea stagnalis* (Linnaeus) and the effects upon the positive geotactic movements shown by these snails upon a slope in air (angle of inclination 15° or 30°) were studied.

It was found that bilateral statocyst extirpation caused a complete loss of the geotactic ability. Therefore the downward directed movement of *Lymnaea stagnalis* upon a slope in air is induced by the statocysts and not by asymmetrical body wall tensions, as was supposed for stylommatophorans by several authors.

The mean downward track on the slope of normal unoperated snails deviated to the left of the perpendicular. There are indications that this is caused by a domination of the effect of the left statocyst, but the possibility that the asymmetrical position of the shell may be involved cannot be excluded.

The mean track of snails from which the left statocyst had been extirpated deviated to the right and that of snails lacking the right statocyst, to the left, when compared with the mean track of the unoperated control snails. This shows that in normal pond snails the direction of the downward movement upon a slope in air is the resultant of the effects of the 2 statocysts.

INTRODUCTION

Conclusions about the function of the statocysts in pulmonates have been drawn exclusively from observations on the behaviour of intact stylommatophorans and by comparing these with the results obtained with other groups of animals. The most convincing phenomena pointing to geotactic functions in these snails are: 1. The compensatory head orientation reflexes, *i.e.* the turning of the head toward the normal horizontal position when the foot loses contact with the substrate; 2. the negative geotaxis shown by land snails when kept under water; and 3. the compensatory movements of the eye-bearing tentacles after changes of the spatial orientation of the body (Baunacke, 1913; Piéron, 1928; Jäger, 1932; von

Buddenbrock, 1935, 1952).

Moreover, several authors studied the creeping of stylommatophorans upon inclined surfaces in air, and found the angle of orientation on the plane to be proportional to the angle of inclination of the surface to the horizontal (Wolf, 1927; Cole, 1928; Crozier, 1935). According to most authors, not the stimulation of the statocysts but the distribution of tensions exerted asymmetrically upon the body wall musculature is the primary excitation leading to orientation, under these conditions.

It was clear that for a further evaluation of the role of the statocysts in snails, studies on the behaviour of animals from which these organs had been removed would be valuable. As far as molluscs are concerned such experiments have only

been done with heteropods (Tsachotin, 1908) and cephalopods (*e.g.* Boycott, 1960; Dijkgraaf, 1961), whereas, with lamelli-branchs, von Buddenbrock (1915) studied the comparable effects of cutting the static nerves. In pulmonates such operations have never been carried out. Von Buddenbrock (1935) even thought that extirpation of statocysts in pulmonates would never succeed, because of the small size of these organs and their hidden position.

In the present investigations we studied the effects of extirpation of one or both statocysts upon positive geotactic movements shown by the basommatophoran *Lymnaea stagnalis* (Linnaeus), when kept outside the water upon a slope.

#### MATERIAL AND METHODS

Using a modification of techniques described earlier (Joosse and Lever, 1958) we anaesthetized the snails at 27°C by immersion in a 0.08% nembutal solution for 15-20 minutes and a subsequent immersion in a 0.3% MS 222 solution for 5-10 minutes. After rinsing the animals with tap-water we operated under a dissection microscope. The shell of an anaesthetized snail was placed tip downwards in a corresponding hole in a rubber disc, so that the completely extended body rested upon the surface of the disc with its rostral side facing away from the operator. Since, in this position, the neck area is curved, the oesophagus and the central nervous system lie immediately under the body wall. A transverse cut about 4 mm long was made in this area. By pulling the transparent membrane which extends from the central nervous system and surrounds the buccal mass we could raise the ganglia to the body surface. By manipulating the oesophagus we could expose the pedal ganglia. Then the statocysts were visible as small whitish spheres located latero-dorsally upon the pedal ganglia, medio-caudally from the cerebro-pedal connective. They are embedded in the periganglionic connective tissue sheath. As this layer becomes increasingly opaque during life, the stato-

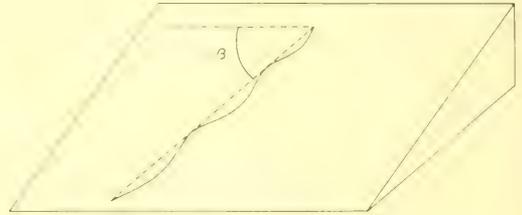


FIG. 1. The angle,  $\beta$ , between the horizontal and the line connecting start and end of the track of the snail is used to measure its deviation on the slope.

cysts are difficult to distinguish in full-grown snails. Therefore specimens with a shell-height of about 20 mm were used. With the aid of a stainless steel hook with a very small and thin bent tip we were able to remove the statocysts. Due to the elasticity of the inner tissues and of the skin the wound closed immediately after the operation. Kept in aerated tapwater most snails came out of the anaesthesia in approximately 1 hour. In general, over 80% of the animals survive the operation.

The positive geotaxis shown by pond-snails when kept in air was tested by studying the downward movements of the animals upon an inclined glass plate (see Fig. 1). Before each experiment the surface of the glass plate was covered with a thin layer of wet quartz powder. This layer prevents the snails from slipping down and the tracks made by the creeping snails remain clearly visible. Afterwards the paths were copied on paper and then the angle between the line connecting start and end of the track and the horizontal (angle  $\beta$  in Fig. 1) could be determined.

TABLE 1. The mean values of  $\beta$ , the angle of the track with the horizontal, of the controls and of snails with the unilateral extirpation of the statocyst at inclinations of the slope of 30° and 15°

Experiment	Inclination of slope	Number of animals per group	-Left statocyst	Controls	-Right statocyst
I	30°	20	73.25°	92.55°	112.00°
	15°	20	67.00°	92.25°	123.05°
II	15°	20	59.20°	90.65°	131.45°
	15°	20	69.75°	96.50°	126.16°
III	15°	100	-	96.16°	-

## EXPERIMENTS

*Experiment I.* Four groups of 20 snails were used: in the first, the right statocyst had been removed; in the second, the left; in the third, both; and in the fourth, which served as control, none.

All animals were tested once upon a slope inclined 15° to the horizontal, and once on a slope of 30°.

*Experiment II.* To study the reproducibility of the effects and the individual variation, each snail used in experiment I was tested twice upon a slope with an inclination of 15°.

*Experiment III.* In order to determine the mean value of  $\beta$  (the angle of the track with the horizontal) of control snails more exactly, 100 unoperated snails were tested upon a slope with an inclination of 15°.

## RESULTS

*Experiment I.* The values of  $\beta$  obtained with the control snails and with the snails from which only one statocyst had been extirpated are shown in Fig. 2, the mean values are given in Table 1.

The following points are of interest.

1. Examination of the results of this experiment shows that the mean values of  $\beta$  for the snails which lack their left statocyst are definitely smaller and those for the snails lacking their right statocyst are definitely larger than those of the controls, *i.e.* that the average track

constantly deviates to the right of the control track in the former case and to its left in the latter. The symmetry test of Wilcoxon revealed that the mean values of  $\beta$  for the operated groups differed significantly ( $P < 0.01$ ) from those of the controls, at both inclinations of the slope (30° and 15°).

2. These deviations of the means seemed to be larger at an inclination of 15° than at 30°. The two-sample test of Wilcoxon showed, however, that the means of  $\beta$  of the groups of operated snails tested at 15° did not differ significantly from those at 30°.

3. While, from the above it is clear that the unilaterally operated animals did still show a positive geotactic reaction, it was found that animals from which both statocysts had been extirpated, had lost the ability of geotactic orientation upon the slope. Fig. 3 illustrates the differences between the groups.

*Experiment II.* The repetition of the former experiment, at an inclination of 15°, showed the same statistically significant differences between the mean deviations of the 2 experimental groups and the controls (Table 1; Fig. 2). On the other hand, the correlation test of Spearman showed that no statistically significant correlation existed between the 2 tracks made by the individual snails ( $P > 0.10$ ). It appeared also that the magnitude of the mean deviation to the right of the animals possessing only the right statocyst and that to the left of the

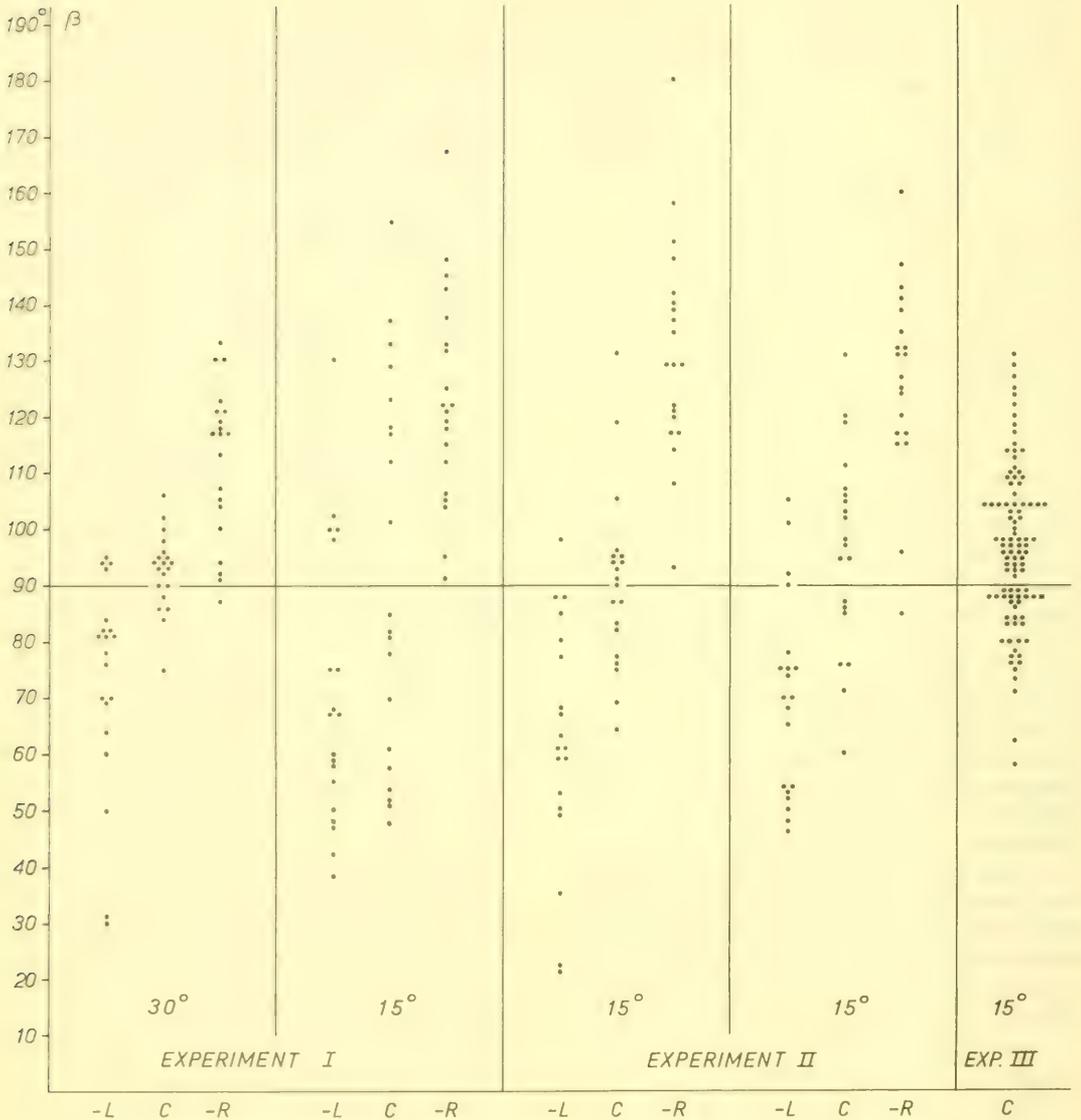


FIG. 2. The values of  $\beta$  obtained in the 3 experiments. -L: minus left statocyst; -R: minus right statocyst; C: controls.

animals having only the left statocyst, when compared with the mean of the controls, did not differ significantly (two-sample test of Wilcoxon).

*Experiment III.* All mean values for  $\beta$  in the control groups of experiments I and II exceeded  $90^\circ$ . This difference did not appear to be statistically significant (according to the symmetry-test of Wilcoxon). A repetition, however, with

100 specimens (Fig. 2) had a positive result ( $P < 0.01$ ).

#### CONCLUSIONS

From the results the following conclusions can be drawn.

1. The present investigation showed that *Lymnaea stagnalis* displays a positive geotaxis in air, inversely to the negative

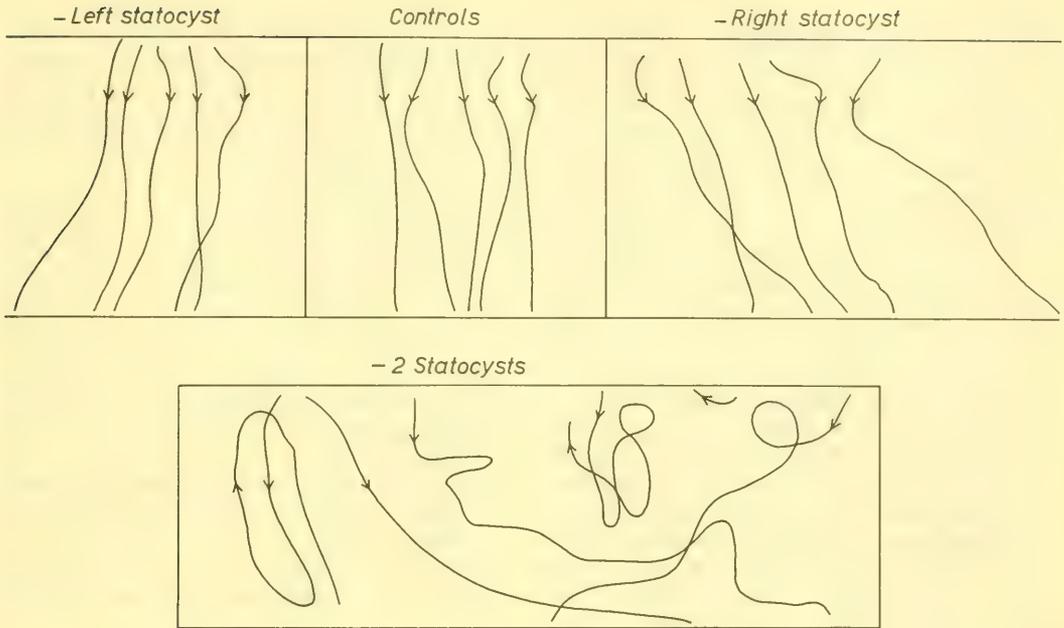


FIG. 3. Some representative examples of tracks of operated and intact *Lymnaea stagnalis* demonstrating the deviation of the tracks to the side of the remaining statocyst (note greater deviation to the left) and complete disorientation when both statocysts are lacking. Inclination of the slope  $30^\circ$ .

geotaxis observed in stylommatophoran land snails kept in water.

2. The fact that the snails from which both statocysts had been extirpated were disorientated upon a slope, demonstrates that the downward directed movements of normal pond snails upon a slope in air are not primarily controlled by asymmetrical body wall tensions, which are identical for snails operated upon and for normal snails, but by the statocysts.

3. Since it was observed that specimens having the use of only the right statocyst deviated to the right and those with only the left statocyst to the left, when compared with the intact controls, it can be concluded that each statocyst controls its corresponding body side. Thus, in normal snails the direction of the downward movement upon a slope in air is the resultant of the effects of the 2 statocysts.

4. Experiment III showed that the mean value of  $\beta$  of intact snails was slightly

larger than  $90^\circ$ . This means that the track of normal snails deviates to the left from the perpendicular on the slope. Similarly, the average deviation to the left of the average control track, by snails lacking the right statocyst, was found to be greater than the corresponding deviation to the right of that track, by snails lacking the left statocyst (see differences in the values of  $\beta$ , Table 1). This greater deviation to the left in both cases might perhaps be due to a dominant effect of the left statocyst, but as no sufficient statistical support for this supposition was obtained the possibility is not excluded that another factor may play a role, e.g. the asymmetrical position of the shell.

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## RESUMEN

ALGUNOS EFECTOS DE LA EXTIRPACION DE ESTATOCISTOS EN *LYMNAEA*

La literatura sobre pulmonados contiene sólo indicaciones indirectas acerca del funcionamiento de los estatocistos: estas se derivan casi exclusivamente de experimentos con caracoles estilomatóforos y no se ha practicado extirpación de esos organos sensoriales. En la presente investigación, uno o ambos estatocistos fueron extraídos de ejemplares de *Limnaea stagnalis* (L.) para mostrar el efecto sobre los movimientos geotácticos positivos de estos caracoles, sobre un plano inclinado fuera del agua (con ángulo de 15° o 30°). Se descubrió que la extirpación bilateral produce pérdida completa de habilidad geotáctica: en consecuencia, el movimiento cuesta abajo de las *Limnaea*, es inducido por los estatocistos y no por la tensión asimétrica de las paredes del cuerpo como algunos autores ha supuesto para los estilomatóforos.

En caracoles normales, no operados en esta forma, el descenso sobre el plano inclinado se desvía hacia la izquierda. La causa de esto parece estar indicada por un efecto dominante del estatocisto izquierdo, aunque no se excluye la posibilidad de que la posición asimétrica de la conchilla intervenga en este efecto.

La mayoría a los cuales se les extirpó el estatocisto izquierdo desviaron hacia la derecha, y viceversa, en oposición, comparada, con los caracoles no operados. Esto demuestra que en caracoles lacustres normales la dirección del movimiento cuesta abajo fuera del agua, es el resultante del efecto de los dos estatocistos.

STUDIES ON THE STRUCTURE AND FUNCTION OF THE FEEDING APPARATUS  
OF *PHILINE APERTA* WITH A COMPARATIVE CONSIDERATION OF SOME  
OTHER OPISTHOBRANCHS

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ABSTRACT

A study has been made of the fine anatomy of the buccal region of *Philine aperta* (Linn.) and of the vascular and nervous supply of the anterior region of the body. An explanation of the functioning of the apparatus is given, based on observations of feeding, the varying relation of constituent parts of the buccal apparatus and the results of experimental stimulation and injection.

The walls of the buccal region are well provided with intrinsic muscles and are capable of great change in shape. They enclose a compact buccal mass in which the radula is supported by large muscles and a malleable tissue of vacuolated cells with cell inclusions and interspersed muscle fibres. This supporting tissue also serves as a base for muscle attachment, whilst one large pair of muscles also acts in closing the radula. The last is opened by 2 sets of oblique muscle fibres running in the buccal mass walls. Four pairs of small buccal tensors bind the buccal mass together. The intrinsic musculature maintains the shape and relationship of component parts of the buccal mass, causes its rising and sinking movements when releasing food to the oesophagus and is involved in movements of the teeth.

The buccal region is attached to the body wall by 6 pairs of extrinsic muscles which determine its topographical position. In feeding, 4 pairs of these pull the buccal region forward and the buccal mass is protruded so that the radula is well in advance of the mouth and can be used as a grab. Protrusion may be accompanied by extrusion and expansion of the anterior oesophagus to form a blood-filled extrovert, depending on specialization of the blood system and the degree of relaxation of separate bundles of the columellar muscle. These muscles open and close the mouth and control blood-flow to the anterior regions by their ability to constrict the anterior aorta. This vessel may also be constricted posteriorly where it passes through the diaphragm. It is confluent with many small haemal sacs and some large anterior sinuses involved in control of the protrusion and retraction of the proboscis. Withdrawal depends largely on strong contraction of the 6 pairs of proboscis retractors, which can also cause side-to-side and rotatory movements of the proboscis. The radula is short and each row of teeth comprises only a single pair of laterals. These pairs may be widely opened or closed so that adjacent ones interdigitate or can grasp food firmly. Opening depends on lateral pull of muscles with increased blood pressure below the radular membrane to flatten it, whilst in closing it is folded longitudinally by muscular pull from below.

Whilst many gastropods can protrude the buccal mass to a certain extent it has been shown that in *Philine* it can protrude further, forming part of a large gut extrovert. Use of the teeth does not depend on a bending plane nor is to and fro movement of the radular membrane involved. Some other opisthobranchs have been compared with *Philine* and their diet is given. Of these, *Scaphander lignar-*

*ius* (Linn.) is very similar, although the blood system does not exhibit so many adaptive changes. *Acteon tornatilis* (Linn.), *Cylichna cylindracea* (Pennant) and *Retusa* spp. do not use a proboscis; the probable method of feeding in *Acteon* and *Cylichna* is suggested. *Retusa* spp. have lost the buccal mass and feed by suction. Evolutionary trends are not readily traceable due to extreme adaptation of the buccal region for the mode of feeding.

## INTRODUCTION

Feeding in gastropod molluscs normally depends on a radula and a buccal mass as the means of manipulating it. In most prosobranchs, the ability of the radular teeth to obtain food depends on the presence of a bending plane, first described by Ankel (1937). When the buccal mass is brought forward and sometimes slightly protruded the radular membrane is pulled out over it and flattened, so that the teeth are erected or spread out, thus achieving a suitable position for feeding. The buccal mass is so constructed as to produce a bending plane and cause the teeth to move over it. To this end the musculature is adapted and cartilaginous supports are a necessary adjunct.

Apart from Lemche's work on *Cylichna* (1956) no full account of the feeding apparatus in an opisthobranch has yet been given, and the method of obtaining food differs markedly from that outlined above. In *Philine aperta* (Linn.) the whole buccal mass may be protruded along with the anterior oesophagus so that the radula can grasp prey. There is considerable manoeuvrability of the protruded part and the use of the radular teeth does not depend on the existence of a bending plane. The teeth are erected by flattening of the radular membrane, which is achieved by lateral or oblique pulling of muscles inserted on its under surface. Further movement of the teeth depends on changing tensions in these muscles and closure is effected by downward pull on the radular membrane causing it to become deeply grooved in the median longitudinal plane. No cartilaginous support is present in the buccal mass but in other respects *Philine* is structurally similar to prosobranchs.

## SECTION I

### THE FEEDING APPARATUS OF *PHILINE APERTA*

#### 1. GENERAL DESCRIPTION

*Philine aperta* is a tectibranch mollusc which lives in sublittoral sand, burrowing into the surface layers. It is a carnivore and has been described as feeding on small molluscs (Guiart, 1901; Förster, 1933; Fretter, 1939; Pruvot-Fol, 1954), young bivalves (Vayssière, 1880), Foraminifera (Brown, 1934; Fretter, 1939), naviculate diatoms, unicellular algae, planktonic remains (Fretter, 1939) and worms (Pruvot-Fol, 1954), whilst Vayssière (1880) also found remains of urchins and zooantharian spicules in the gut.

Small specimens collected off Plymouth and Helsingør had taken Foraminifera such as *Polystomella*, small rissoids and *Turbonilla elegantissima*, together with sand grains and miscellaneous small bottom debris. Brown (1934) suggested that *Philine* is a selective feeder since he found that the proportion of Foraminifera to sand grains was higher in the gut than in the bottom deposits. Some evidence in support of this has been found at Red Wharf Bay in Anglesey where larger specimens of *Philine* had been feeding almost exclusively on *Pectinaria*. A few had pieces of bivalve shells in their gizzards but there has been little other evidence of *Philine* feeding on bivalves.

*Philine* is able to take its prey in whole by means of a proboscis. This organ is not described by any of the above authors. Cuvier (1802, 1815) and Fretter (1939) mentioned that the odontophore is protracted with teeth opened to grab food, whilst Brown (1934) suggested that *Philine*

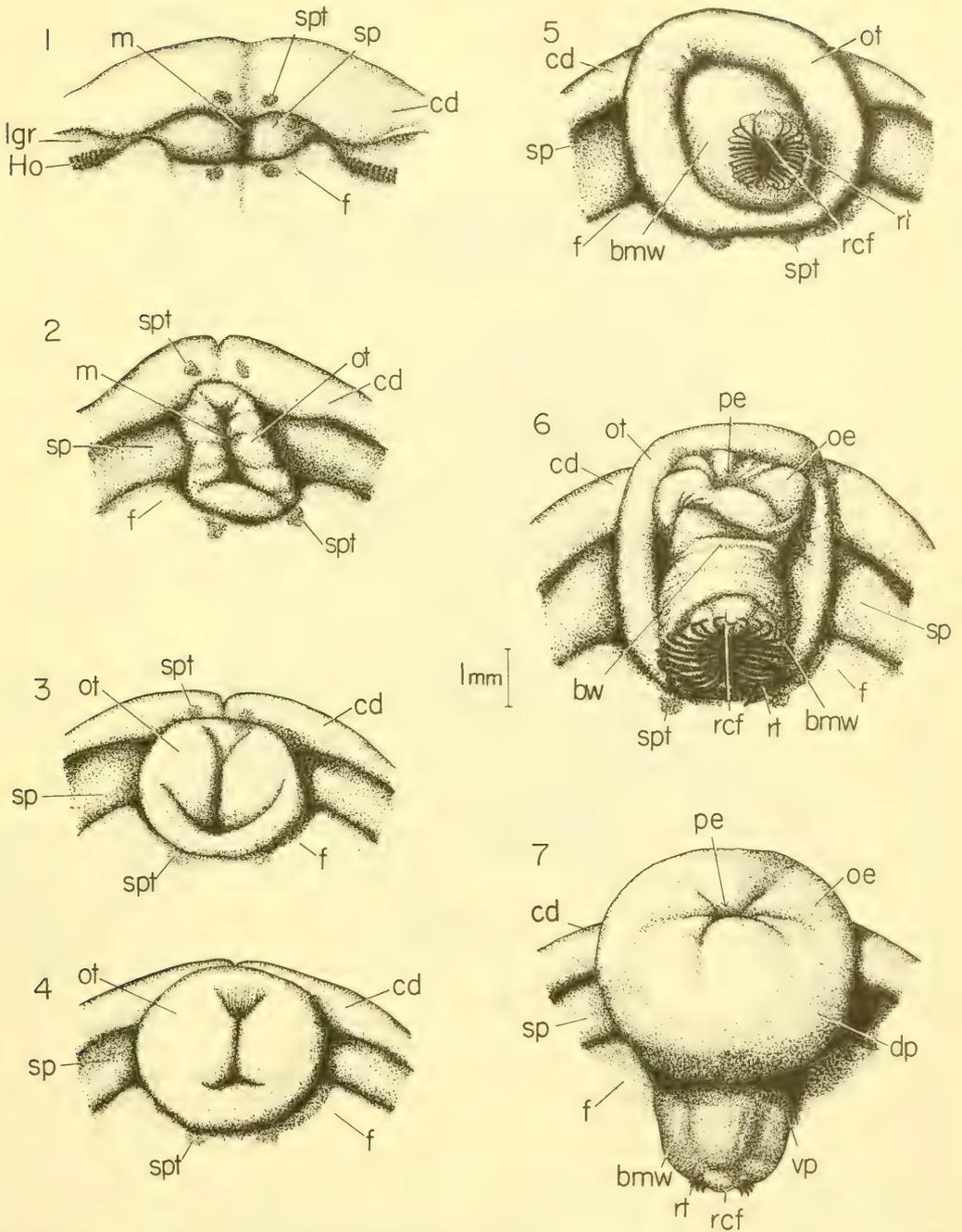


FIG. 1. *Philine*: anterior view showing stages (1-7) of protrusion of the proboscis. bmw, buccal mass wall; bw, buccal wall; cd, cephalic disc; dp, dorsal part of proboscis; f, foot; Ho, Hancock's organ; lgr, lateral groove; oe, oesophagus; ot, oral tube; pe, proboscis entrance; rcf, radular caecal fold; rt, functional radular tooth; sp, sensory palp; spt, sensory patch; vp, ventral part of proboscis.

uses its teeth in the manner of a grab to take up sand and Foraminifera. Both methods may be involved in conjunction with the use of the proboscis.

When *Philine* is crawling, its body is usually fully extended with the mouth and sensory areas surrounding it exposed (Fig. 1, stage 1). The former is a vertical slit capable of great widening to allow the passage of the proboscis. On each side is Hancock's organ (Ho), the largest of the sensory areas, and anterior to it a sensory palp (sp) which may be pushed out considerably when the animal is questing for food. Two sensory patches (spt) lie on the leading edge of the cephalic disc (cd) and two in a corresponding position on the foot (f). These are the dorsal and ventral sensory pits of Brown (1934), who also described the sensory palps, as did Fretter (1939). All the sensory areas are yellowish. When *Philine* is not extended the dorsal and ventral sensory patches and the lateral palps may be drawn in to such an extent that the mouth becomes subterminal.

The proboscis emerges as shown in the sequence of diagrams (Fig. 1, stages 2-7). As the animal searches for food, its proboscis may be partially protruded (stage 2) and be withdrawn again. Food may be effectively captured at stage 5 when the radular teeth are able to close on the prey and drag it in. This is presumably the action which Fretter described (1939). When the proboscis is further protruded (stages 6-7) a considerable variety of movements is possible. These will be described and discussed later (p 320-321).

The sensory areas probably help in locating food. *Philine* approaches prey such as *Pectinaria* with the sensory palps and Hancock's organs well exposed. On touching the worm, these organs widen and the palps are extended forward. The first part of the proboscis (Fig. 1, stage 2) is shot out, swiftly reaching stage 5, with the radular teeth opening as they appear. The widely spread teeth then close on the worm, pulling it in whole, often with at least part of its tube of

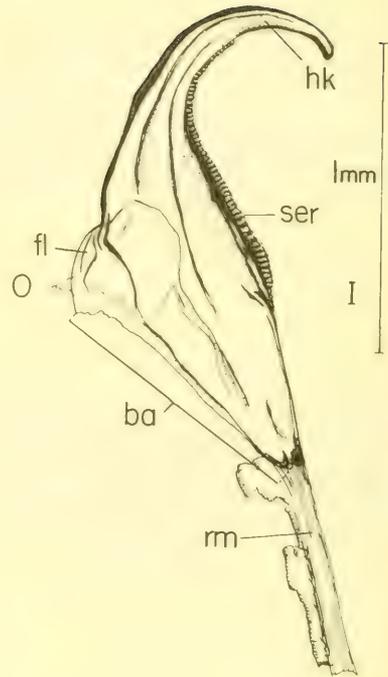


FIG. 2. *Philine*. Posteromedian view of left functional radular tooth. ba, base of tooth; fl, flange (of Brown, 1934); hk, hooked tip; I, inner aspect of tooth; O, outer aspect of tooth; ser, serrated edge.

sand grains. If the prey is imperfectly grasped at the first attempt *Philine* will immediately make a second grab without further investigation by the sensory palps. In this case full protrusion of the proboscis is not necessary for an effective capture.

The radula is short, generally with 12-13 rows of functional teeth (small specimens may have only 9 rows) or in Year II specimens, up to 26 rows. Each row comprises a single pair of laterals. The radula formula 1.0.1 agrees with the findings of Pruvot-Fol (1954) and Tchang-Si (1934) who gave it as 22 x 1.0.1. Each tooth is large and hook-shaped, with a serrated inner edge (Fig. 2). In grasping, the pairs of teeth interdigitate and allow a firm grip to be maintained on the prey.

Specimens of *Philine* collected varied in total length from 1.5-4.5 cm. An animal useful for experiments was 3 cm

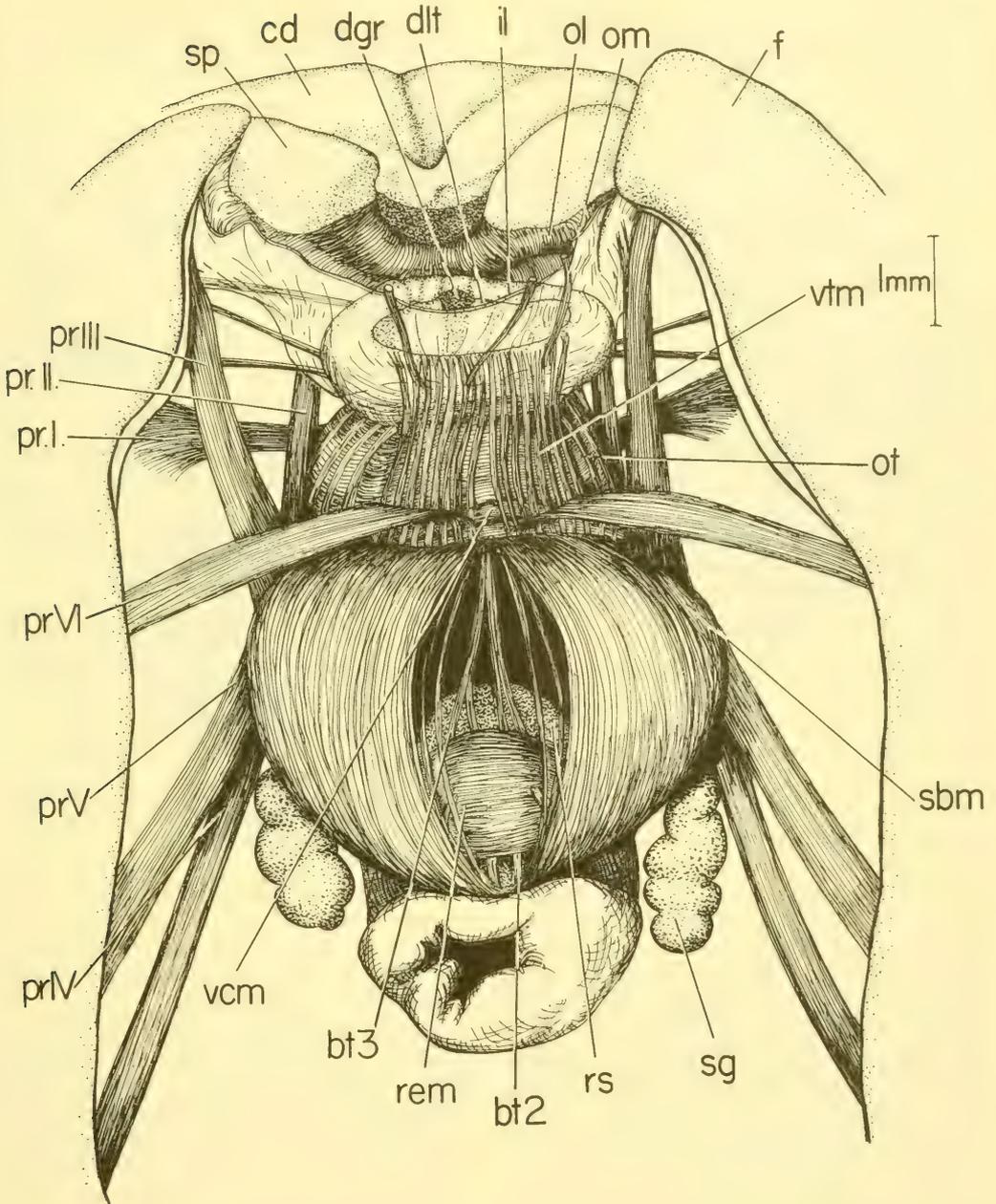


FIG. 3. *Philine*. Ventral view of buccal region displayed by making a median longitudinal cut in the foot and pinning it out. Muscles pr VI are thus stretched. The oesophagus has been cut off near its anterior end. The connective tissue sheet between the inner and outer lips has been freed ventrally and the ventral oral muscles have been cut from their origins. bt 2, 3, buccal tensors 2, 3; cd, cephalic disc; dgr, dorsal groove; dlt, dorsolateral thickening; f, foot; il, inner lip; ol, outer lip; om, oral muscle; ot, oral tube; pr I-VI, proboscis retractors I-VI; rem, radular elevator muscle; rs, radular sac; sbm, superficial buccal musculature; sg, salivary gland; sp, sensory palp; vcm, ventral circular muscle; vtm, ventral tensor muscle.

long. In such an animal, the total length of the buccal region of the gut is about 0.5 cm and its depth through the widest part 0.3 cm.

## 2. THE BUCCAL REGION AND ITS MUSCULATURE

A longitudinal cut into the anterior body cavity of *Philine* exposes the gut as far as the posterior part of the oesophagus. The buccal region is marked anteriorly by the mouth, leading to the oral tube and buccal cavity, and ends posteriorly at the oesophagus. This part of the gut, muscular and compact, is concerned with food intake. The fairly small, yellowish salivary glands (Fig. 3, 7a, sg) open dorsolaterally into the buccal cavity by short ducts. They are not otherwise attached to the walls of the gut. The topographical position of the buccal region is largely determined by the state of contraction of 6 pairs of extrinsic muscles (Fig. 3, pr I-VI) attaching it to the body wall. These have been incompletely described by several authors including Cuvier (1802), Guiart (1900), Förster (1933), Tchang-Si (1934), Brown (1934). The shape of the buccal region depends also on the inter-relationships of its intrinsic muscles.

The anterior end of the oral tube has a very definite rim (Figs. 3, 4, 5, 9, 11) which is the inner lip. It is attached to the outer lip (ol) by a thin sheet of connective tissue containing muscle fibres and also by small circumoral muscles (om). The lumen is triangular in transverse section, with the apex dorsal. This is due to localized thickening of the walls, which forms a ventral pad and a large dorso-lateral cushion on each side (Figs. 3, 4, 9, dlt). The thickness is due to big connective tissue cells with interspersed radial muscle fibres. In the contracted and shortened oral tube, these cushions may meet and close the lumen. The epithelium of the oral tube is columnar and is ciliated along the apex of the lumen, which thus constitutes a dorsal groove (Figs. 3, 4, 9, dgr) continuing back into the oesophagus. The shape of the lumen

and restriction of the ciliated areas of the epithelium agree with the account of Fretter (1939) whilst Brown's diagram (1934) is inaccurate.

The lumen becomes more circular where the oral tube joins the buccal cavity. The upper part of the buccal mass projects ventrally within it (Figs. 4, 7b, 9) almost filling the lower part of the cavity. It is covered here by its own wall which will be referred to as the buccal mass wall (Figs. 4, 7b, 8, 9, bmw). Laterally and posteriorly this is confluent with the buccal wall and anteriorly with the floor of the oral tube. The narrow spaces between the vertical buccal mass wall and the lateral buccal walls represent the lateral pouches. Between the lateral and posterior part of the buccal wall is a very marked vertical area of thickening, also mentioned by Brown (1934). It is in this region that fibres from 4 pairs of extrinsic muscles (Fig. 5, pr II, III, IV, V) enter the gut wall. The openings of the salivary ducts (Fig. 4, esd) are at the upper end of each lateral pouch just posterior to the vertical thickening and may be obscured by the folds of the oesophagus (as in Fig. 9). This position agrees with the figures of Guiart (1901) and Fretter (1939) but Brown (1934) incorrectly placed the openings more anteriorly. Between the lateral and dorsal parts of the buccal wall is a longitudinal furrow continuing back into the oesophagus (Figs. 4, 9). The posterior buccal wall is muscular but unthickened.

The oral tube has an outer muscle coat (Fig. 5). Dorsally and dorsolaterally, this consists of fibres running longitudinally and in a transverse direction and these continue back without interruption to join the outer intrinsic musculature of the oesophagus. Laterally and ventrally the transverse fibres of the oral tube become much more numerous and form a sphincter-like group, the ventral circular muscles (Figs. 3, 5, vcm). Overlying these are 2 tracts of longitudinal fibres, the ventral tensor muscles (Figs. 3, 5, vtm) each divided into several groups, extending from the

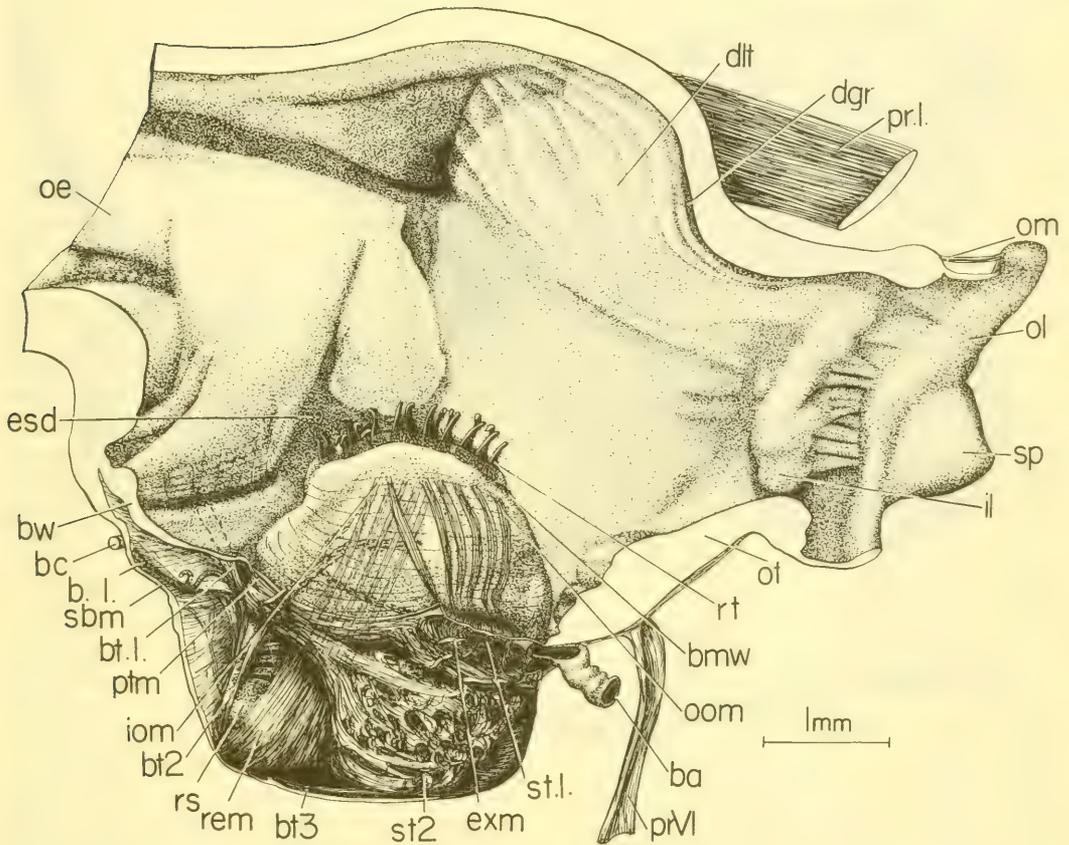


FIG. 4. *Philine*. Lateral view of the buccal region of the gut with the right half of the oral tube, buccal wall, superficial buccal musculature and oesophagus removed. ba, buccal artery; bc, buccal commissure; bmw, buccal mass wall; b 1, buccal nerve 1; bt 1-3, buccal tensors 1-3; bw, buccal wall; dgr, dorsal groove; dlt, dorsolateral thickening; esd, entry of salivary duct; exm, extrinsic muscle fibres; il, inner lip; iom, inner oblique muscles; om, oral muscle; oom, outer oblique muscles; ot, oral tube; pr I, VI, proboscis retractors I, VI; ptm, posterior transverse muscle; rem, radular elevator muscle; rs, radular sac; rt, functional radular tooth; sbm, superficial buccal musculature; sp, sensory palp; st 1, 2, supporting tissues 1, 2.

oral rim to the anterior limit of the buccal mass.

The buccal mass contains the radular apparatus and intrinsic muscles concerned with its functioning. Its lower part projects ventrally posterior to the oral tube. It is covered with a loose

sling-like muscle coat, the superficial buccal musculature (Figs. 3, 4, 5, 8, 9, sbm), briefly described by Brown (1934). It extends from just posterior to the insertions of retractor muscles II, III, IV and V and beneath the ventral edge of the oesophagus to cover the posterior and

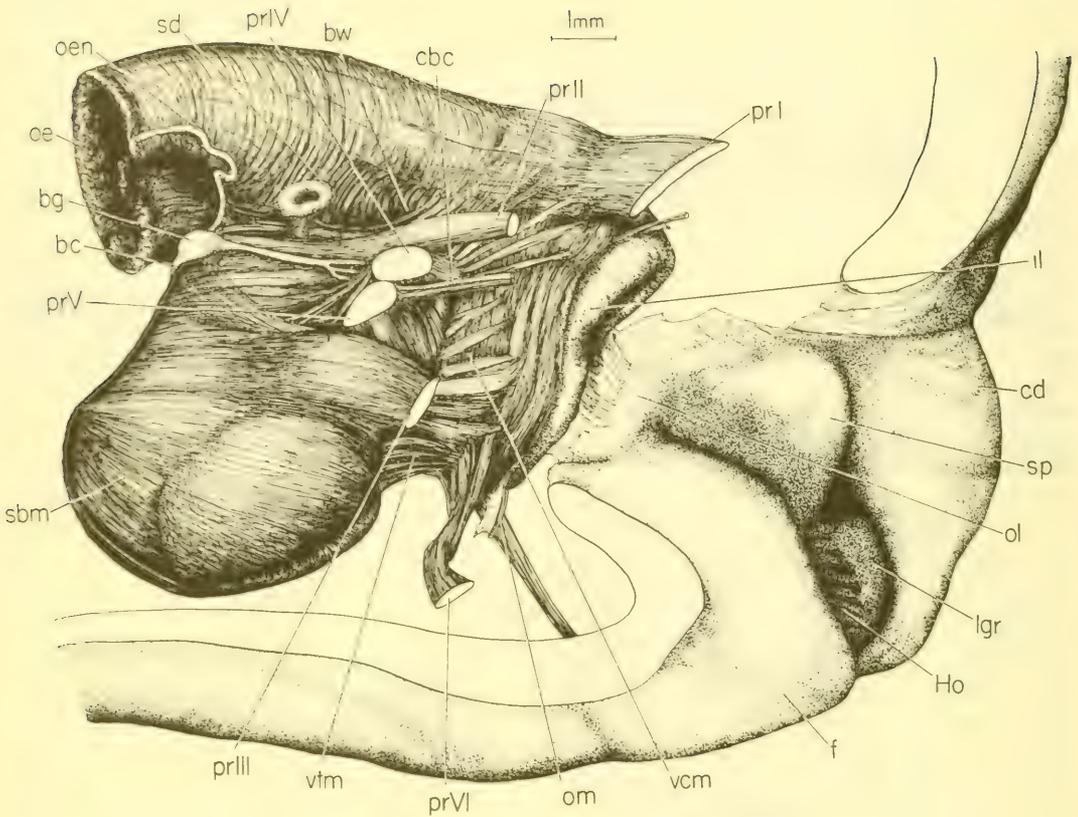


FIG. 5. *Philine*. Lateral view of buccal region of gut. Extrinsic muscles cut short, but pr VI of left side is in situ. Right side of body wall removed from centre foot to right of the median line of the cephalic disc. The latter has been pulled forward. bc, buccal commissure; bg, buccal ganglion; bw, buccal wall; cbc, cerebrobuccal connective; cd, cephalic disc; f, foot; Ho, Hancock's organ; il, inner lip; lgr, lateral groove; oe, oesophagus; oen, oesophageal nerve; ol, outer lip; om, oral muscles; pr I-VI, proboscis retractors I-VI; sbm, superficial buccal musculature; sd, salivary duct; sp, sensory palp; vcm, ventral circular muscles; vtm, ventral tensor muscles.

lateral parts of the buccal wall and surround the lower part of the buccal mass. It is attached to the last anteriorly. Ventrally, it is partially open and partially attached to the intrinsic muscles; the extent of attachment is variable. The superficial buccal musculature receives a large number of contributory fibres from the extrinsic retractor muscle pair II (Fig. 5). These enter the lateral buccal walls at the upper ends of the

vertical thickenings a short distance anterior to the salivary glands. They are linked across the midline by a band of fibres running below the oesophagus, and marking the upper posterior limit of the superficial buccal musculature. A few fibres pass dorsal to the salivary ducts, most below them. This band, linking right and left retractor muscles II, is partly hidden by the buccal ganglia and their commissure (Figs. 5, 6, 7a, 9,

bg, bc) which lie on the junction between buccal wall and oesophagus. A second group of fibres passes ventrally from each retractor II and fans out in the superficial buccal musculature. The cerebrobuccal connective passes under these (Figs. 5, 7a, cbc).

Entering the vertical thickening of the buccal wall immediately ventral to retractor muscle II on each side are the extrinsic muscles IV, V and III, one below the other in that order (Fig. 5, pr II, IV, V, III; Figs. 7a, 7b, pr IV, V, III). From the bases of IV and V some groups of fibres fan out obliquely. Some pass anteriorly to insert superficially on the oral tube, some posteriorly either into the superficial buccal musculature or onto the buccal wall (Fig. 5, pr IV, V). A few fibres also pass anteriorly from each retractor muscle V alongside the cerebrobuccal connective as it emerges from between retractor muscles IV and V (pr V, cbc).

Fibres pass back from each muscle III into the superficial buccal musculature (pr III) and some pass from one side to the other, anterior to the buccal mass. The latter form a narrow strip attached to the anterior transverse muscle (described later), which is rather conspicuous and has been called the transverse strand by Brown (1934). The anterior edge of the superficial buccal musculature attaches to this strand and so do the posterior ends of the ventral tensor muscles (Figs. 3, 5, sbm, vtm).

Fibres from the 4 pairs of extrinsic muscles also enter the buccal mass more deeply, passing through the vertical thickening of the buccal wall and many, mostly from retractor muscle III and to a less extent from muscles IV and V, enter the anterior transverse muscle (Fig. 8, exm, atm) of the buccal mass. This muscle runs across joining the bases of the vertical thickenings on each side (Figs. 4, 8, st 1). Its position has been described by Brown (1934) and will be discussed further (p 294).

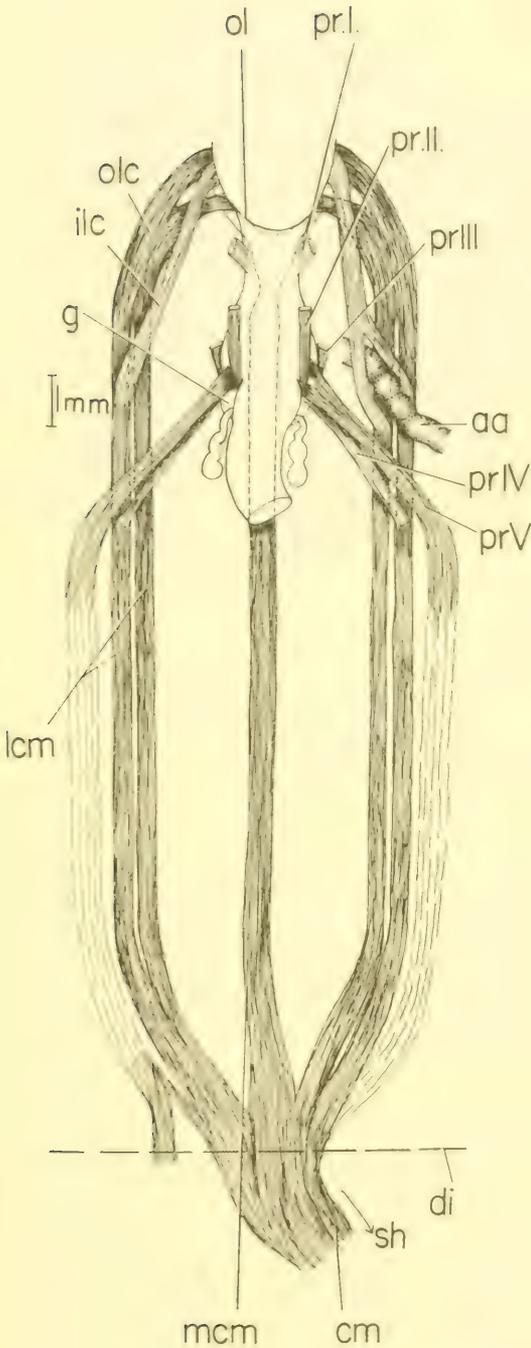
Another 2 pairs of extrinsic muscles (Figs. 3, 4, 5, 9, pr I, pr VI) insert on the

oral tube - pr I dorsolaterally, pr VI ventrally. The origins of pairs I, II and III lie near the mouth (Fig. 14, pr I, II, III) so that they run towards their insertions in a posterior direction. Pair VI originates from the foot (Fig. 14, pr VI) whilst retractor muscles IV and V are branches of the columellar muscle. Their origins lie posterior to the buccal region of the gut. Previous authors have not mentioned their columellar nature and have not agreed as to whether they represent 1 or 2 muscles (Cuvier, 1802; Förster, 1933). In fact, they are sometimes connected near their insertions, as suggested by Förster (1933), and are innervated by a common nerve (Fig. 14, p 9). The visceral loop passes between the 2 muscles where they are separate and not through either as Cuvier (1802) indicated. Förster (1933) also gave an incomplete account of the columellar muscle.

All 6 pairs of buccal extrinsic muscles act as proboscis retractors and are thus numbered I-VI. This numbering corresponds with I-VI of Förster (1933).

Interweaving with retractor muscles I, II and III around the mouth are fibres from the columellar muscles, which insert here in several groups. All the muscle fibres around the mouth and anterior body wall are discussed in greater detail below.

Within the anterior part of the body cavity the columellar muscle is restricted to discrete longitudinal bands (VII, VIII, IX, of Förster, 1933). These include a median columellar muscle (Fig. 6, mcm) and a lateral columellar muscle (lcm) on each side. The lateral muscles are variable and each may run as a single or double tract (shown double in Fig. 6) superficially embedded in the muscles of the body wall. At the anterior end they branch to produce an inner and an outer branch (Fig. 6, ilc, olc). The inner branch of the right lateral columellar has a double origin and the anterior aorta (aa) passes between the 2 parts. Proboscis retractors V leave the lateral tracts midway between diaphragm and insertion. Proboscis retractors IV leave columellar



fibres running in the foot at a slightly posterior and more dorsal level.

The median columellar muscle is not embedded in the foot except superficially near the diaphragm. Here all the longitudinal tracts of the columellar muscle unite, with the addition of some muscle fibres from the body wall. The unified muscle then enters the visceral haemocoel and finally reaches its origin on the shell. Cuvier (1802, 1815) described the shell as completely unattached to muscles.

The mouth is a narrow vertical aperture. Its outer lip is formed by the leading edges of cephalic disc and foot and the sensory palps (Fig. 1, m, cd, f, sp). These areas may be pulled in, becoming folded longitudinally (as in Figs. 5, 14) and forming a closed funnel at the posterior end of which is the mouth. The anterior end of the foot is drawn into the funnel mid-ventrally by the median columellar muscle. The sensory palps and cephalic disc are pulled in by the lateral columellar muscle.

The median columellar muscle gives small branches to the reproductive system and to the foot (Fig. 16, fcm) a little posterior to the origins of the proboscis retractors. The remainder of its fibres insert on each side of the tip of the foot, and the longest ones reach the insertion of the lateral columellar muscle. The inner and outer anterior branches of each lateral columellar muscle run parallel to each other. The inner inserts adjacent to the sensory palp, the outer slightly more laterally (Figs. 6, 16, ilc, olc). Both branches give groups of fibres passing to insertions on the cephalic disc

FIG. 6. *Philine*. Diagrammatic representation of columellar muscle with the buccal region of the gut in situ. aa, anterior aorta; cm, undivided columellar muscle; di, region of diaphragm; g, gut; ilc, inner branch of lateral columellar muscle; lcm, lateral columellar muscle; mcm, median columellar muscle; ol, outer lip; olc, outer branch of lateral columellar muscle; pr I-V, proboscis retractors I-V; sh, shell.

and foot (Figs. 14, 16).

Median and slightly dorsal to the insertion of the inner branch of each lateral columellar muscle is the origin of one of the pair of proboscis retractors II (Figs. 14, 16, pr II). This origin is quite narrow, with fibres emerging from the cephalic disc and joining to form a fairly small flat band going back towards the buccal mass. The origin of each pair III (Figs. 14, 16, pr III) is similar but wider since the muscle is a larger one, also flat and strap-like. These origins are situated in the foot lateral to the median columellar muscle and fibres from this go both over and under pair III to insert widely on the anterior tip of the foot.

A much wider origin altogether is that of each proboscis retractor I (Figs 3, 14, pr I). On each side it includes fibres arising from a position ventral and lateral to the origin of retractor muscle II but median to the insertion of the lateral columellar muscle. These fibres are joined by others from a wide origin on the anterior part of the cephalic disc. The 2 groups join on each side to form a flat muscle shortly inserting on the oral tube. The more dorsal side of the muscle, composed of fibres from the cephalic disc, inserts more posteriorly on the oral tube and these fibres are thus those of the greatest length within the muscle.

The proboscis retractors VI are another pair of muscles each with a wide origin on the anterior part of the body wall (Figs. 14, 16, pr VI). These leave the foot a short distance posterior to the mouth. Each origin is oblique, the more median end being more posterior. The fibres constituting each of pair VI quickly approach one another to form a strap-like muscle going towards its insertion on the oral tube, where the fibres again become slightly splayed (Figs. 3, 5, 9, 14, 16, pr VI).

Posterior to the origin of each retractor muscle VI a few strands travel together to insert in the foot. They are from the median columellar muscle (Fig. 14, fcm). These strands together with retractor muscles VI and I are closely associated

with the walls of certain blood sinuses and with nerves to be described below (Fig. 14). Several fine muscle strands travel within the sinus walls in seemingly random directions.

Dissection allows the buccal mass to be investigated and the relations of its constituent parts clarified. The superficial buccal musculature is readily removed and immediately the underlying pigmented buccal wall is exposed (Fig. 7a, bw) together with some intrinsic muscles concerned with the buccal mass (Fig. 7, bt 1-3, ptm, rem), large areas of supporting tissue (Fig. 4, st 1, st 2, Fig. 7, st 2) and part of the radular sac (Figs. 4, 7, rs).

The buccal wall receives fibres running obliquely from muscles IV, V and III (Fig. 7a, bw). Attached to its ventral edge is a prominent muscle - the posterior transverse muscle (ptm). This muscle receives contributory fibres from III at each side (pr III). Its fibres fan out on either side to insert on the supporting tissues (Figs. 4, 7, 8, ptm, st 1, st 2). From its centre muscle fibres emerge and join in groups to form 2 pairs of small muscles (Figs. 7, 8, bt 1, bt 2). One pair (bt 1) travels dorsalwards to insert on the ventral wall of the oesophagus. (In Fig. 7a, the upper edge of the superficial buccal musculature is not removed, and bt 1 may be seen passing under it.) The second pair (bt 2) goes to the ventral tip of the radular sac (Figs. 4, 7, 8, bt 2, rs). Obscuring its insertion here is the large U-shaped radular elevator muscle (Figs. 3, 4, 7, 8, 9, rem) running transversely below the radular sac and turning on each side to disappear beside it under the buccal wall. This is the muscle P of Brown (1934). He also shows a muscle W which represents rom and st 2 in the present account.

If a cut is now made along the upper dorsal edge of the posterior transverse muscle, continued vertically immediately posterior to the bases of retractor muscles III, IV, V and II and across the ventral edge of the oesophagus, this will result in complete removal of the posterior buccal wall, leaving a window through

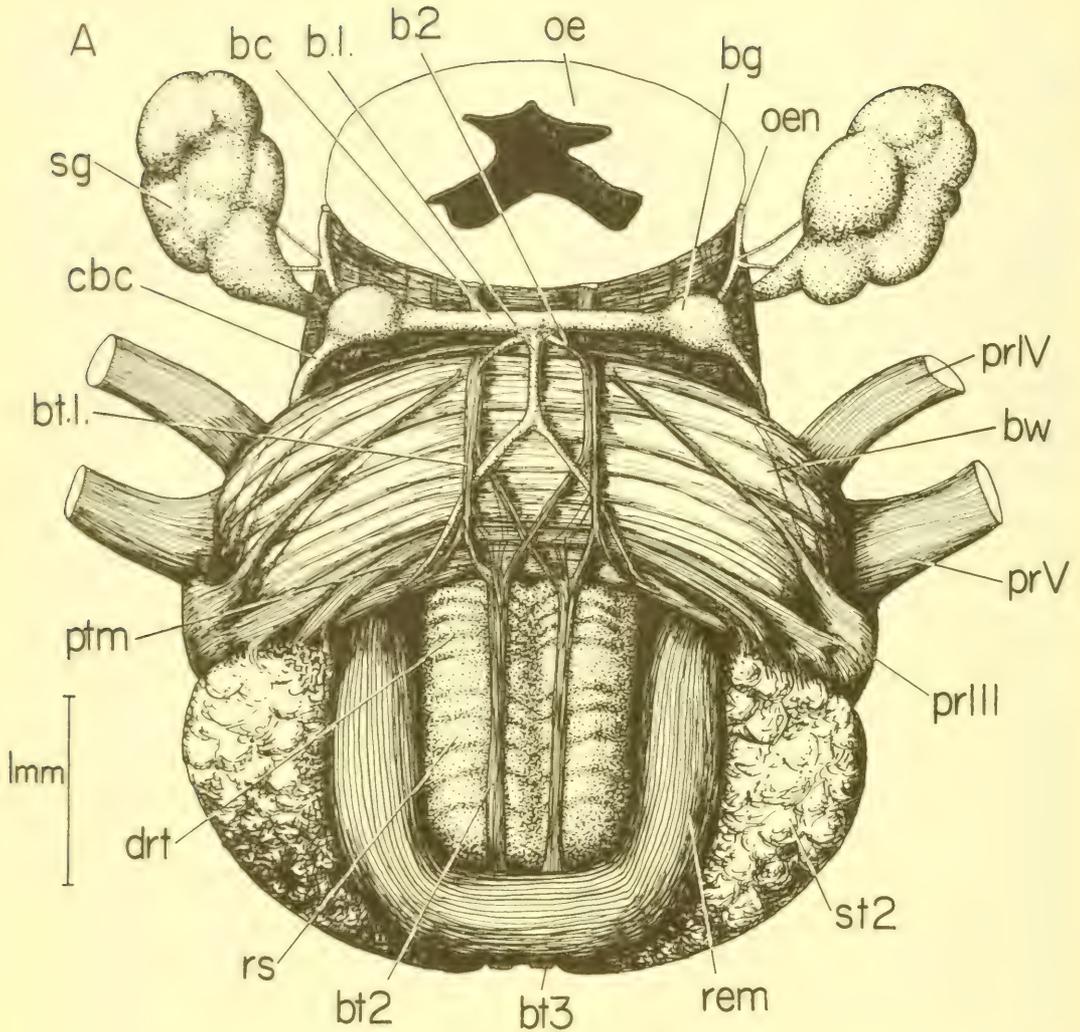


FIG. 7. *Philine*. Successive dissections of the buccal region of the gut in ventroposterior view. a: the superficial buccal musculature has been removed and the proboscis retractors IV and V cut short.

which the cylindrical upper half of the buccal mass can be seen, entirely surrounded by the buccal mass wall (Fig. 7b). This wall is bounded at the lower edge by the posterior transverse muscle (bmw, ptm). Dorsally it turns in around the radula and passes beneath the radular membrane (Figs. 4, 7b, 8, 9, rm).

When at rest, the short radular membrane has a median longitudinal fold

forming a V-shape in transverse section and bringing the tooth-bearing surfaces together. Hence the teeth stand up almost vertically (Figs. 4, 7b, 8, 9, rt) with the hooked tips from each side interdigitating. The short row of crossed hooks can be seen by looking on to the top of the cylindrical mass. If the central posterior part of the buccal mass wall and posterior transverse muscle is also removed (Fig.

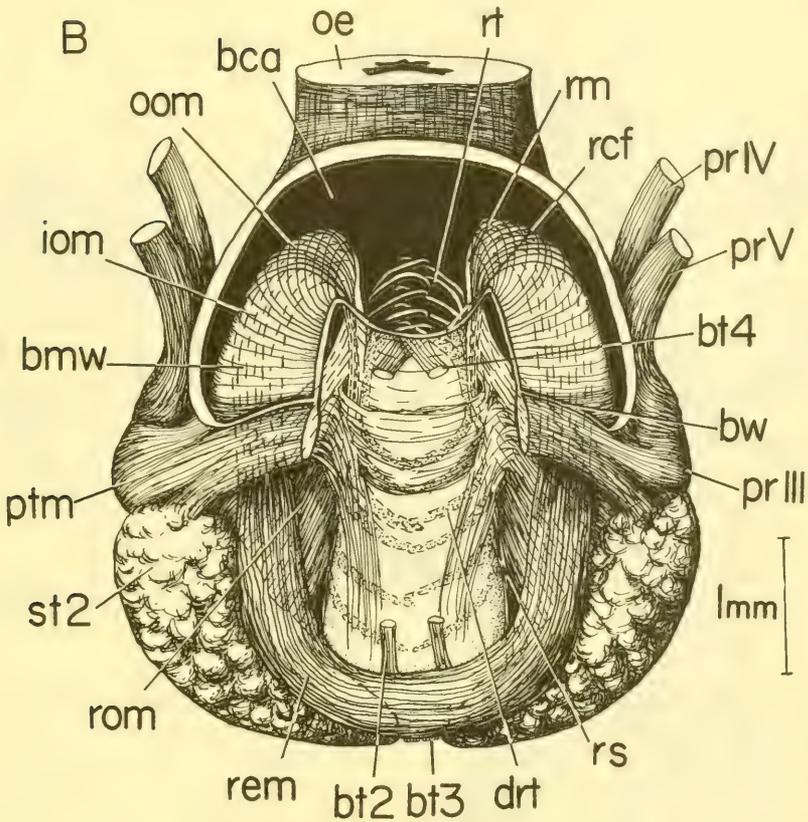


FIG. 7. *Philine*. Successive dissections of the buccal region of the gut in ventroposterior view.

b: after removal of the buccal ganglia, their nerves, the salivary glands and the posterior part of the buccal wall, a window has been cut in the posterior buccal mass wall, and the central part of the posterior transverse muscle cut away. b 1, 2, buccal nerves 1, 2; bc, buccal commissure; bca, buccal cavity; bg, buccal ganglion; bmw, buccal mass wall; bt, 1-4, buccal tensors 1-4; bw, buccal wall; bca, cerebrobuccal connective; drt, developing radular tooth; iom, inner oblique muscles; oe, oesophagus; oen, oesophageal nerve; oom, outer oblique muscles; pr III-V, proboscis retractors III-V; ptm, posterior transverse muscle; rcf, radular caecal fold; rem; radular elevator muscle; rm, radular membrane; rom, radular occlusor muscle; rs, radular sac; rt, functional radular tooth; sg, salivary gland; st2, supporting tissue 2.

7b) the upper end of the short vertical radular sac is exposed (rs). Its posterior wall bends forward partially closing the radular sac before bending outwards again to join the buccal mass wall. This transverse fold, the radular caecal fold (Figs. 7b, 8, 9, rcf) is referred to by Brown (1934) as the posterior lobe, and lies between the developing radular teeth (Figs. 7, 9, drt) and the functional ones (Figs.

4, 7b, 8, 9, rt). The insertions of the pair of buccal tensors (bt 4) are on the central part of the radular caecal fold (Figs. 7b, 8, 9, bt 4). Each travels obliquely outwards to the posterior transverse muscle (Figs. 8, 9, bt 4, ptm).

The buccal mass wall is thickened with connective tissue, especially laterally (Figs. 8, 9, bmw). Some muscle fibres enter it from the posterior transverse

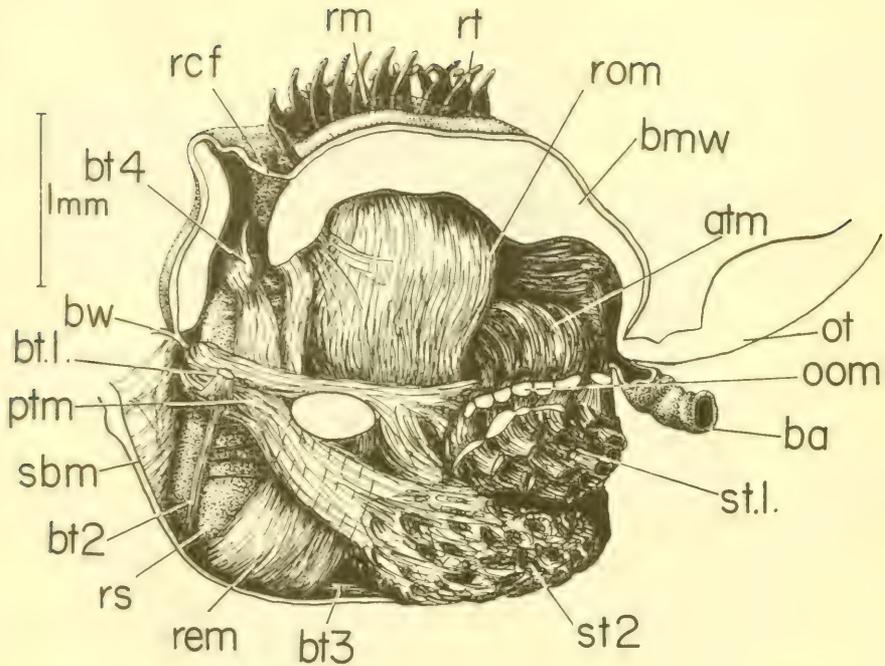


FIG. 8. *Philine*. Right lateral view of the buccal mass with the right half of the buccal mass wall and superficial buccal musculature removed, in dissection subsequent to Fig. 4. atm, anterior transverse muscle; ba, buccal artery; bmw, buccal mass wall; bt 1-4, buccal tensors 1-4; bw, buccal wall; oom, outer oblique muscles; ot, oral tube; ptm, posterior transverse muscle; rcf, radular caecal fold; rem, radular elevator muscle; rm, radular membrane; rom, radular supporting tissues; rs, radular sac; rt, radular tooth; sbm, superficial buccal musculature; st 1, 2, supporting tissues 1, 2.

muscle, including the buccal tensors 2 (Fig. 4, bt 2). They interweave with circular fibres running in the wall. Also obvious are 2 sets of oblique muscle fibres each arranged in several almost parallel groups (Figs. 4, 7b). The inner set (iom) originates from the radular elevator muscle (rem) which enters the buccal mass wall on each side, lateral to the radular sac and between the fibres of the posterior transverse muscle (Fig. 8, rem, ptm). These inner oblique muscle fibres run through the wall and over its dorsal edge to insert on the under surface of the radular membrane. The outer oblique muscles (Figs. 4, 7b, oom) also insert here but travel at right angles to the inner set. They originate from the supporting tissue (st 1) lateral to the

anterior transverse muscle (Fig. 8, st 1, atm, oom). The oblique muscles of the buccal mass wall were inadequately described by Brown (1934), who referred to the outer set as X1 and X2.

The anterior transverse muscle is extremely large (Figs. 8, 9, atm). It receives contributory fibres from retractors III, IV and V and is embedded in connective tissue at either end. The latter forms an important support (Figs. 4, 8, st 1) for the buccal mass and is a region for muscle attachment (p 289). In fresh animals, it often contains white granules described as calcium salts and glycogen by Gabe & Prenant (1952). It consists of elongated cells with large vacuoles and fibrous walls. Muscle fibres run between the cells. Closely attached

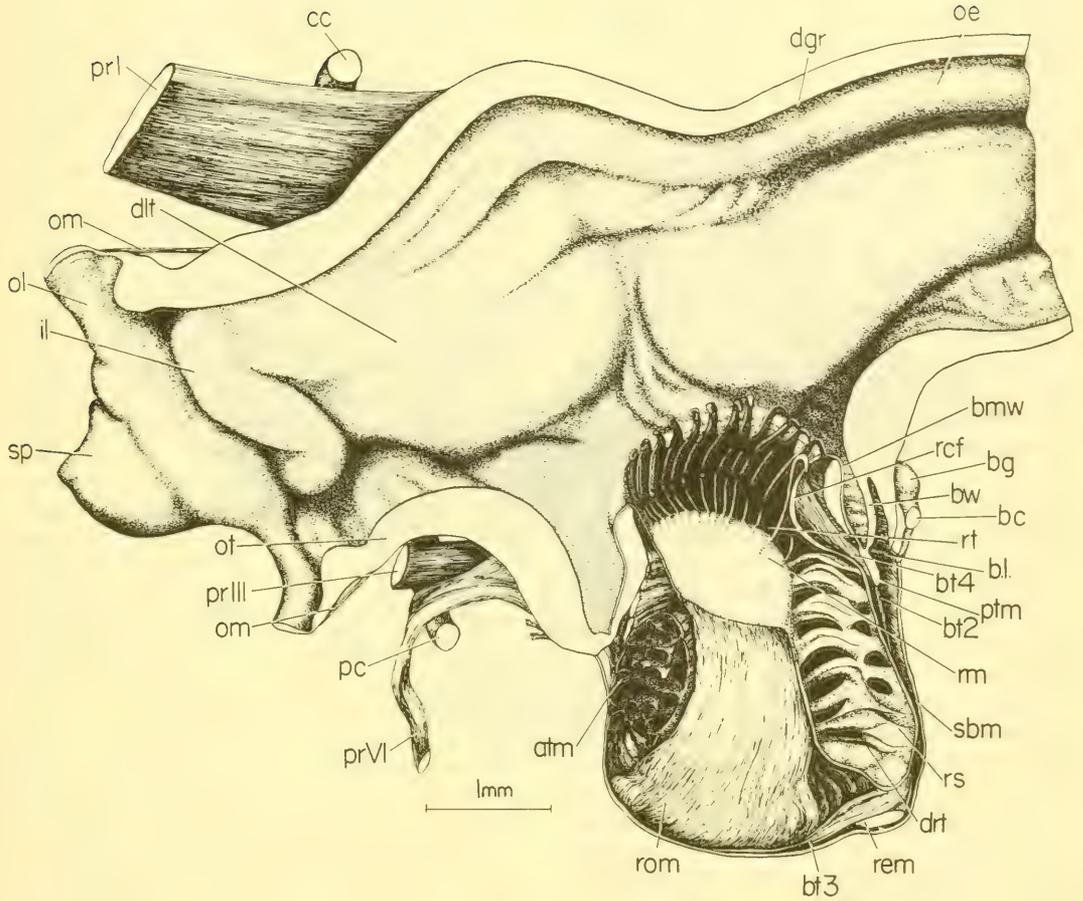


FIG. 9. *Philine*. Right sagittal half of the buccal region when withdrawn. atm, anterior transverse muscle; bc, buccal commissure; bg, buccal ganglion; bmw, buccal mass wall; b 1, buccal nerve 1; bt 2-4, buccal tensors 2-4; bw, buccal wall; cc, cerebral commissure; dgr, dorsal groove; dlt, dorsolateral thickening; drt, developing radular tooth; il, inner lip; oe, oesophagus; ol, outer lip; om, circumoral muscles; ot, oral tube; pc, pedal commissure; pr I, III, VI, proboscis retractors I, III, VI; rem, radular elevator muscle; rcf, radular caecal fold; rm, radular membrane; rom, radular ocluser muscle; rt, functional radular tooth; rs, radular sac; sp, sensory palp; sbm, superficial buccal musculature.

to the posterior aspect of the anterior transverse muscles and the supporting tissue (st 1) are blocks of a similar support (Figs. 4, 7, 8, st 2), forming the base for attachment of the large radular ocluser muscles (Figs. 7b, 8, 9, rom).

These are paired, although their fibres intermingle at the anterior end. They form a support for the radular sac and insert widely on the outer side of the radular membrane (Figs. 7b, 9, rom, rm), each also sending a branch to insert on

the radular sac. Running centrally between the radular occlusor muscles in an antero-posterior direction are the buccal tensors 3 (Figs. 3, 4, 5, 7, 8, 9, bt 3). These originate from the centre of the anterior transverse muscle and are not always entirely separable from the radular occlusor muscles until reaching their insertion on the tip of the radular sac. Near the origin of the buccal tensors 3, the superficial buccal musculature is often attached to them, causing it to be tucked up ventrally. It usually also sends a variable number of muscle fibres to attach to the radular elevator muscle (Figs. 3, 4, 9, sbm, rem).

The structure of the buccal region of the gut is adapted for the method of feeding. The walls are well provided with muscle fibres and extrinsic musculature and are capable of much change in shape. The buccal mass itself is a firm egg-shaped mass, bound together by some of its intrinsic muscles, whilst others act as supports or movers of the radular sac and radular teeth. Support is also provided by thickened areas placed ventrolaterally and anterolaterally. Four of the 6 large pairs of extrinsic muscles insert on the more anterior supporting tissues and form the main anchorage of the buccal mass.

The positions of the intrinsic muscles of the buccal mass depend upon the form and functioning of the radular apparatus. Thus the paired radular occlusor muscles (Figs. 7b, 8, 9, rom) form substantial pillar-like supports for the short radular sac (rs) which stands upright between and slightly posterior to them. They are in turn firmly anchored to the ventrolateral supporting tissue blocks (Figs. 4, 7, 8, st 2). Forming a large strong bar across the anterior end of the buccal mass is the anterior transverse muscle (Figs. 8, 9, atm). It presses into the concave anterior faces of the radular occlusor muscles along its length, and at its ends enters the anterolateral supporting tissue blocks (Figs. 4, 8, st 1). Since the anterolateral and ventrolateral supporting tissues are bound together both ventrally

and posteriorly via the posterior transverse muscle (Figs. 4, 7, 8, 9, ptm), whilst the radular occlusor muscles insert on the radular sac and membrane, the whole radular apparatus, supporting tissues and largest intrinsic muscles form a basic block. A further system of muscles holds the buccal mass as a functional entity. This includes the 4 pairs of buccal tensors (Figs. 3, 4, 7, 8, 9, bt 1-4). These act in a median plane and together bind the buccal mass from its junction with the oesophagus to the centre of its anterior face.

By pulling on the radular membrane, the remaining intrinsic muscles are responsible for opening and moving the teeth. In this function they oppose the radular occlusor muscles, but in their secondary function of supporting the radular sac and holding the upper and lower halves of the buccal mass together they work with the radular occlusors. One of these muscles is the radular elevator muscle (Figs. 3, 6, 7, 8, 9, rem), which forms a sling-like band supporting the radular sac from below, and at its upper ends provides the radular teeth with the inner oblique muscle fibres (Figs. 4, 7b, 9, iom). The inner oblique muscles open the teeth, but tend to pull them in a posterior direction whereas the outer oblique muscles pull them anteriorly.

The upper part of the buccal mass is hidden within the walls of the buccal cavity (Figs. 4, 7, 8, 9, bw) which are continuous with the buccal mass wall (Figs. 4, 7b, 8, 9, bmw). The lower half projects into the haemocoel and is covered by the superficial buccal musculature (Figs. 3, 4, 5, 8, 9, sbm) which is held in place by fibres from some of the extrinsic muscles (Fig. 5, pr II, pr III).

When the proboscis is protruded, the buccal mass appears outside the body as a firm cylinder forming the ventral part of the proboscis (Fig. 1, stage 7, vp). The proboscis is produced by the rolling inside-out of the oral tube, buccal wall and the extreme anterior end of the oesophagus (Fig. 1, stages 2-7, ot, bw, oe). It is thus technically not a true

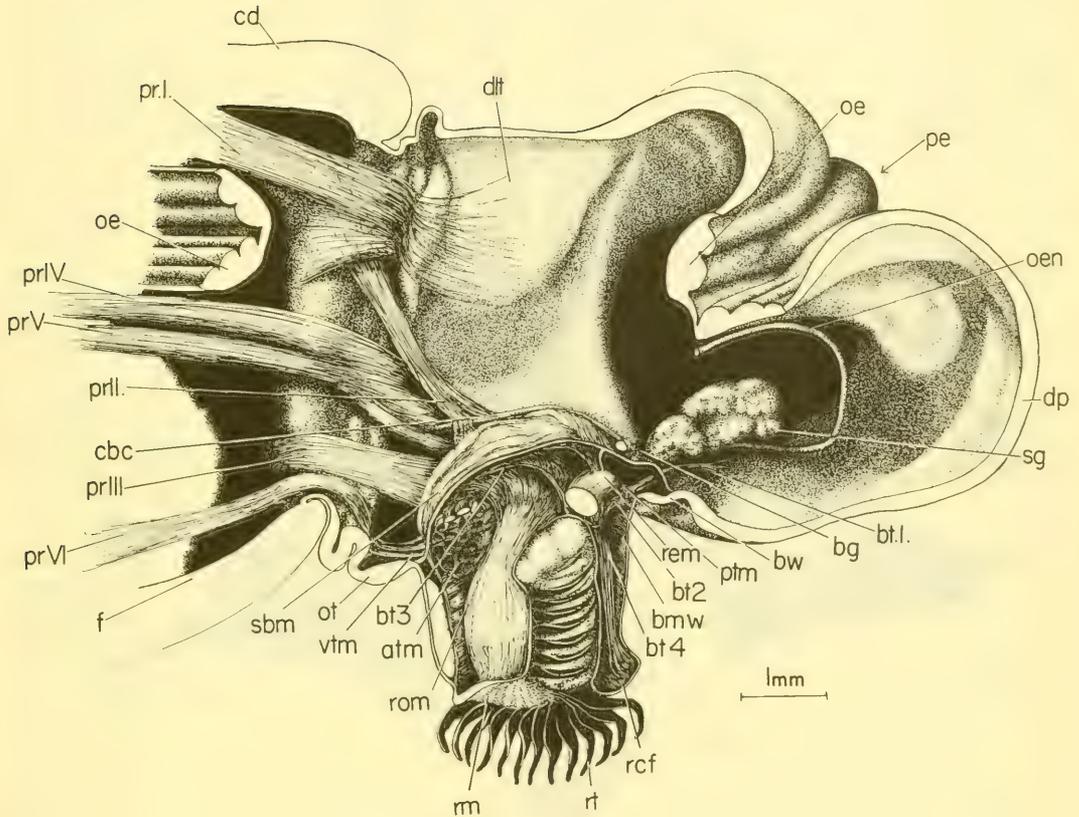


FIG. 10. *Philine*. Left sagittal half of the proboscis and anterior part of the body. The nerve ring is not shown. atm, anterior transverse muscle; bg, buccal ganglion; bmw, buccal mass wall; bt 1-4, buccal tensors 1-4; bw, buccal wall; cbc, cerebrobuccal connective; cd, cephalic disc; dlt, dorsolateral thickening; dp, dorsal part of proboscis; f, foot; oe, oesophagus; oen, oesophageal nerve; ot, oral tube; pe, proboscis entrance; pr I-VI, proboscis retractors I-VI; ptm, posterior transverse muscle; rcf, radular caecal fold; rem, radular elevator muscle; rm, radular membrane; rom, radular ocluser muscle; rt, functional radular tooth; sbm, superficial buccal musculature; sg, salivary gland; vtm, ventral tensor muscle.

proboscis, but an extrovert. Its dorsal part (Fig. 1, stage 7; Fig. 10; dp) is large and swollen, of variable shape. It has an anterior entrance (Figs. 1, 10, 11, pe) leading to the oesophagus at a point normally (i.e. when the proboscis is with-

drawn) posterior to the buccal cavity. At the proboscis entrance the oesophageal walls turn inside out to help form the wall of its dorsal part. Posterior to the turning point, the oesophagus remains as a tube enclosed within the proboscis (Figs.

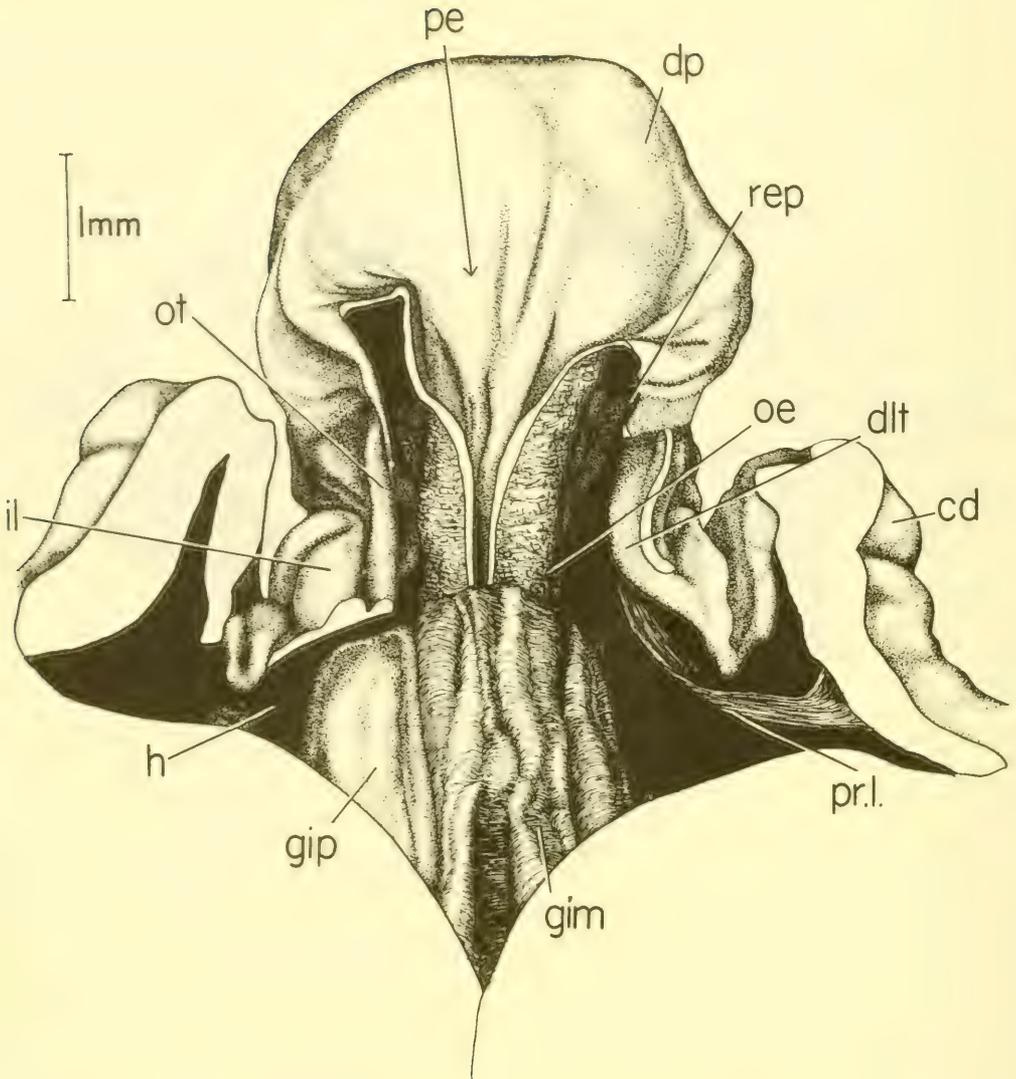


FIG. 11. *Philine*. Dorsal view of proboscis opened dorsally with a median longitudinal cut. The cephalic disc has also been opened mid-dorsally. cd, cephalic disc; dlt, dorsolateral thickening; dp, dorsal part of proboscis; gim, gizzard muscle; gip, gizzard plate; h, haemocoel; il, inner lip; oe, oesophagus; ot, oral tube; pe, proboscis entrance; pr I, proboscis retractor I; rep, reproductive system.

10, 11, oe). The turning point has no exact position but depends on the degree of protrusion. A few animals have been found in which the gizzard had partially or completely entered the dorsal part of the proboscis. In these cases, which were

unusual, the turning point and proboscis entrance were as far back as the oesophagus would permit. Quite often some of the anterior coils of the reproductive system had entered the proboscis (Fig. 11, rep). The gizzard does not

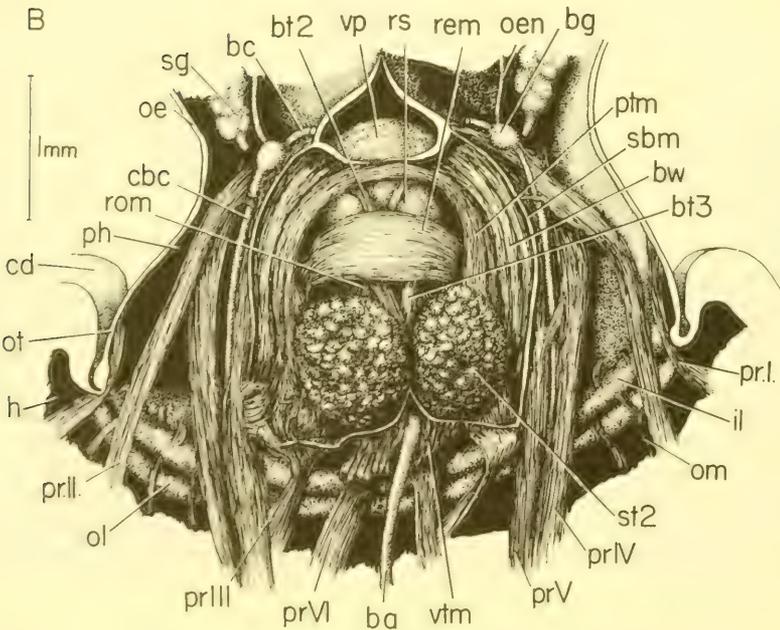
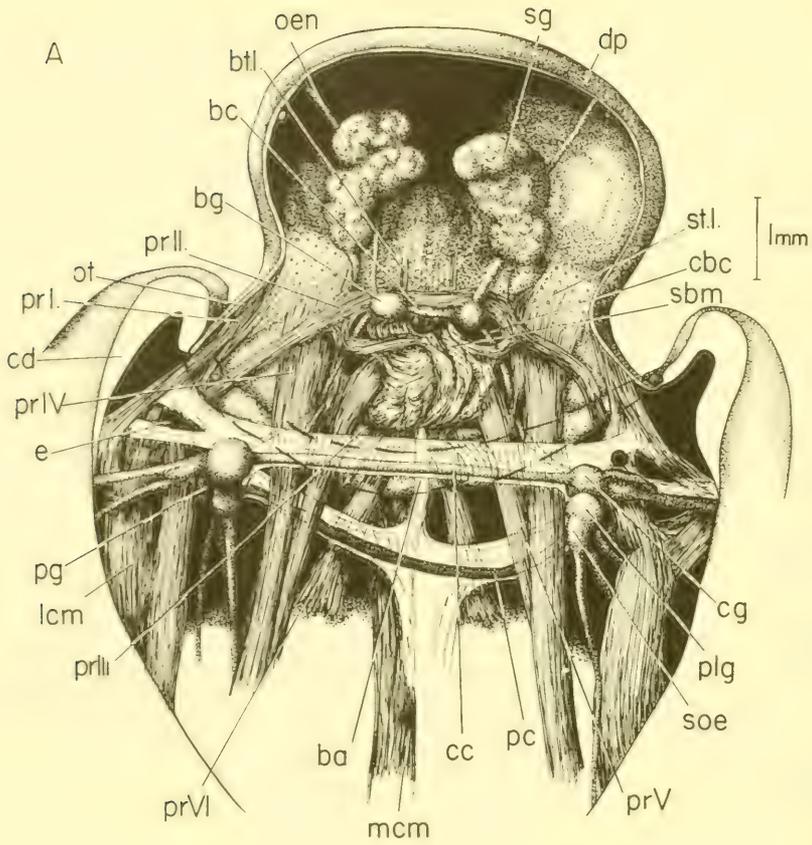
usually pass through the mouth.

The inner and outer parts of the oesophagus may be displayed together (as in Fig. 11) by opening the proboscis with a dorsal longitudinal cut. If the inner part is removed by cutting round the perimeter of the anterior entrance, it becomes possible to look down on the base of the ventral cylindrical portion of the proboscis. This part is covered by the superficial buccal musculature (Figs. 10, 12, sbm) which is no longer stretched around the basal half of the buccal mass, but lies in folds hiding the latter from dorsal view within the proboscis (Fig. 12a). The buccal ganglia can be seen on the now anterior edge of the superficial buccal musculature (bg, sbm). Approximately lateral to them on each side are the salivary glands (sg) trailing in an anterior direction from their ducts. Running anteriorly from each buccal ganglion is a large nerve supplying the oesophagus (oen), now much more taut than when the oesophagus was not protruded. They run forward parallel to the stretched anterior wall of the proboscis before turning back to go along the inner oesophageal tube. Passing posteriorly are the cerebrobuccal connectives (cbc), travelling towards the cerebral ganglia in the nerve ring. This ring does not change its position in the body cavity when the proboscis is everted. All the above-mentioned structures may also be seen in lateral view in sagittal section (Fig. 10).

With the exception of retractors IV and V the branches of the columellar muscle still lie within the main body cavity (Fig. 12a, lcm, mcm). The paired proboscis retractors IV and V (Figs. 10, 12a, pr IV, pr V), however, are now much elongated, and pass through the nerve ring to reach their insertions in the proboscis lateral to the folded superficial buccal musculature (sbm). Proboscis retractors IV terminate in the more anterior position. The insertions of all the extrinsic muscles are now anterior to their origins and are within the cavity of the proboscis. This enables them to act efficiently as proboscis retractors

when necessary. Pair I inserts widely on the proximal dorsolateral walls of the proboscis (pr I, dlt), pair II immediately anterior to the insertion of IV and hence posterior and lateral to the buccal ganglion (bg) near the exit of the salivary duct (sg). The insertions of pairs III and VI are more ventral and usually partially obscured by the folds of the superficial buccal musculature (pr III, pr VI, sbm). Pair III inserts slightly median and posterior to the insertions of pair V; VI joins the proximal ventral wall of the proboscis on either side of the midline. Thus, whereas when the buccal region of the gut was withdrawn, the extrinsic muscles II, IV, V and III entered the buccal wall in lateral vertical areas of thickening, they now lie on each side in an oblique line with pair II most anterior. The vertical areas of thickening have thus become tipped forward as the buccal walls turned inside out in the proboscis. The distance between the most ventral part of the areas has remained little changed since these paired supports are connected by the anterior transverse muscle (Fig. 10, atm). Thus, the anterior transverse muscle may be considered as a horizontal pivot over which the buccal mass turns during protrusion. This important muscle is firmly attached to the inner lip (which now appears as the proximal rim of the proboscis) by the ventral tensor muscles (Fig. 10, vtm). These have an extremely important tensor function as the main anchor for the cumbersome ventral part of the proboscis. Proboscis retractors VI help in this function (Fig. 10).

The intrinsic musculature of this ventral part cannot be seen dorsally from within the cavity of the proboscis until the barrier of the superficial buccal musculature is removed, as in Fig. 12b. The interior of the buccal mass is thus revealed in a morphologically ventral view. Most obvious are the large areas of supporting tissue (Fig. 12b, st 2) to right and left. Between them are the buccal tensors 3 (bt 3) joining the radular sac (rs) anteriorly and disappearing posteriorly



amongst the fibres of the anterior transverse muscle. The last is now posterior to the rest of the buccal mass, and all the intrinsic musculature is similarly inverted due to the 180° turn which the buccal mass has undergone in protrusion. It has changed from an upright position, crowned with the functional radular teeth, within the buccal cavity, to lie upside down outside the buccal and main body cavities with the teeth projecting ventrally. This change can best be explained by reference to the sagittal sections (Figs. 9, 10).

Whilst within the buccal cavity, the upper half of the buccal mass was covered by the buccal mass wall, but its lower part was covered by the superficial buccal musculature. When it is protruded as the ventral part of the proboscis, the buccal mass wall covers the major part of the buccal mass. Basally and proximally, however, it is now covered by the buccal wall (Fig. 13, a-b, c-d). This has become possible since in protrusion the fold between buccal and buccal mass walls (which had enclosed a narrow space around the buccal mass [p 286]) is straightened out as the buccal wall turns inside out. Since the superficial buccal musculature is attached dorsal to this fold, it is not only relieved of its former function of enclosing the lower half of the buccal mass, but its edges are not pulled down

into the ventral part of the proboscis. Since the buccal mass wall (together with the inner and outer oblique muscles) is stretched downwards in the fully protruded proboscis, the radular membrane is opened to form a very wide V (Fig. 13d, rm). The teeth thus fan out around the distal edge of the buccal mass (Fig. 1, 10, rt). They can be closed only when partial retraction of the buccal mass occurs - for instance, by contraction of the centrally placed radular occlusor muscles.

### 3. INNERVATION OF THE BUCCAL REGION AND OF THE ANTERIOR REGIONS OF THE BODY

The nerve supply of the buccal region and neighbouring parts has been studied by dissection of unstained preserved animals and by intravital staining with oxidized methylene blue and leucobase methylene blue as prepared by Smith (1946). The silver staining method of Alexandrowicz (1960) was not as successful for tracing fine nerves as methylene blue reduced with Rongalit white. For studying the innervation of the intrinsic musculature of the gut walls and buccal mass, the buccal region of the gut was observed after the method of Alexandrowicz (1932).

In a specimen of *Philine* with the proboscis in, the nerve ring surrounds the

FIG. 12. *Philine*. 12a: dorsal view of proboscis and anterior part of body cut open mid-dorsally as in Fig. 11. Here a larger part of the dorsal wall of the proboscis has been removed and also the inner part of the oesophagus.

12b: a subsequent dissection with only the ventral part of the proboscis shown. The intrinsic muscles of the buccal mass are revealed by removal of the superficial buccal musculature. A longitudinal cut has been made in the mid-ventral part of the oesophagus and buccal wall. Through this cut the most ventral, undissected region of the proboscis may be seen.

ba, buccal artery; bc, buccal commissure; bg, buccal ganglion; bt 1-3, buccal tensors 1-3; bw, buccal wall; cbc, cerebrobuccal connective; cc, cerebral commissure; cd, cephalic disc; cg, cerebral ganglion; dp, dorsal part of proboscis; e, eye; h, haemocoel; il, inner lip; lcm, lateral columellar muscle; mcm, median columellar muscle; oe, oesophagus; oen, oesophageal nerve; ol, outer lip; om, circumoral muscles; ot, oral tube; pc, pedal commissure; pg, pedal ganglion; ph, proboscis haemocoel; plg, pleural ganglion; pr I-VI, proboscis retractors I-VI; ptm, posterior transverse muscle; rem, radular elevator muscle; rom, radular occlusor muscle; rs, radular sac; sbm, superficial buccal musculature; sg, salivary gland; soe, supra-oesophageal ganglion; st 1, 2, supporting tissues 1, 2; vp, ventral part of proboscis; vtm, ventral tensor muscle.

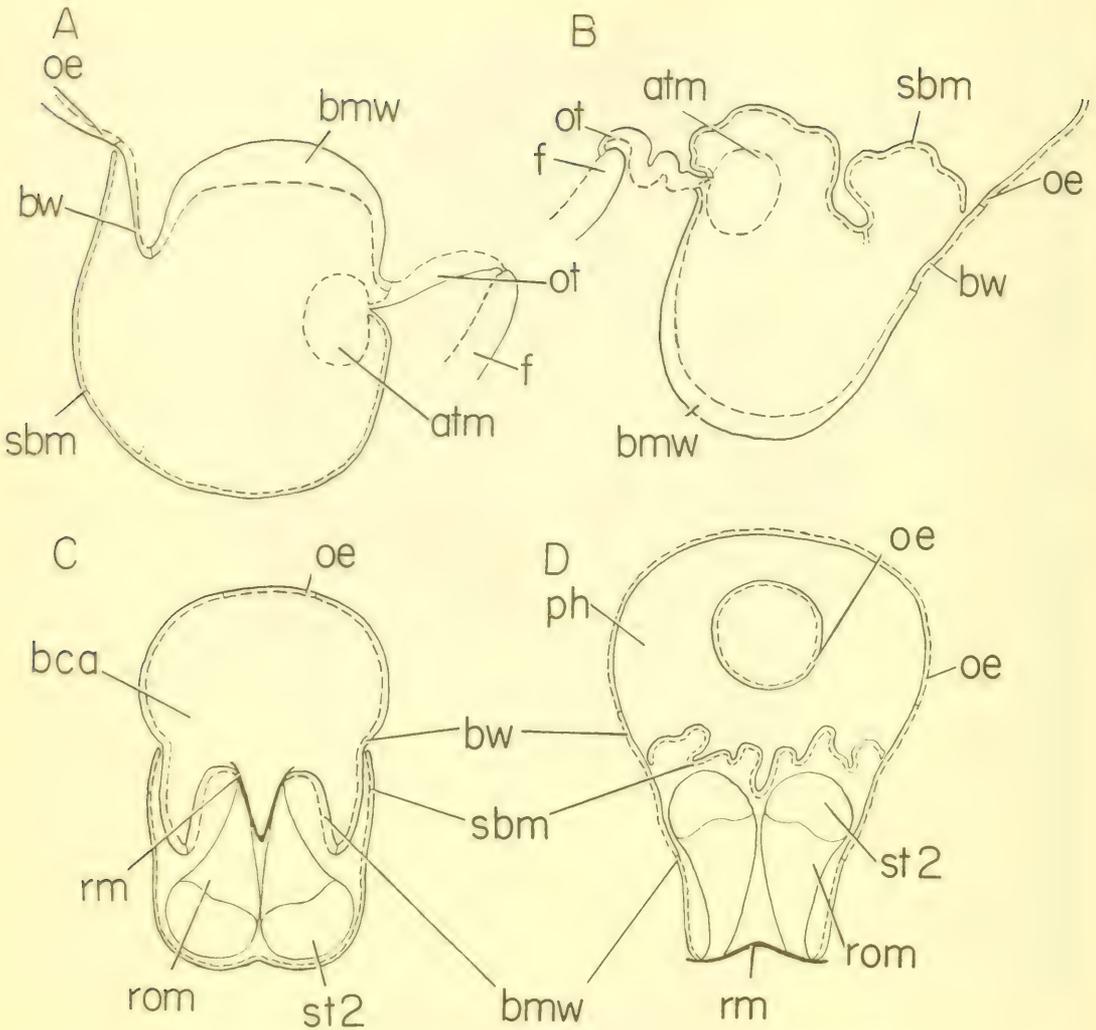


FIG. 13. *Philine*. Diagrams to show the changes in position of the walls of the buccal region when the proboscis is protruded. In all, the morphological inner side of the gut wall is shown with a dashed line. The first two (a, b) are longitudinal sections through the buccal mass, with only the anterior transverse muscle and walls in situ. The second two (c, d) are transverse sections of the buccal region through the supporting tissues st 2. Only the radular membrane and radular ocluser muscles are shown in the buccal mass. In each pair the left diagram shows the proboscis withdrawn, the right, the proboscis protruded. atm, anterior transverse muscle; bca, buccal cavity; bmw, buccal mass wall; bw, buccal wall; f, foot; oe, oesophagus; ot, oral tube; ph, proboscis haemocoel; rm, radular membrane; rom, radular ocluser muscle; sbm, superficial buccal musculature; st 2, supporting tissue 2.

oral tube and the extrinsic muscles joining it, whereas when the proboscis is protruded, the nerve ring encircles the oesophagus.

The cerebral ganglia innervate the anterior sensory areas, the oral tube, part of the anterior body wall and muscle fibres in the walls of the anterior blood

sinuses. Nerves leave the pedal ganglia for the ventral sensory patches, the foot, branches of the columellar muscle and the muscular walls of the anterior blood sinuses. The buccal ganglia innervate extrinsic muscles I, II, III and IV, the walls of the buccal region of the gut, together with the oesophagus and the intrinsic musculature of the buccal mass.

#### *The cerebral ganglia and nerves*

Thirteen nerves leave each cerebral ganglion. Of these, 7 nerve roots supply organs direct, whilst 6 lead to commissures and connectives. Besides being joined by the large cerebral commissure (Figs. 5, 9, 12a, 14, 15, cc) dorsal to the gut, the cerebral ganglia are linked by a very small commissure (Fig. 15, cc2) travelling ventral to the oral tube adjacent to the pedal commissure.

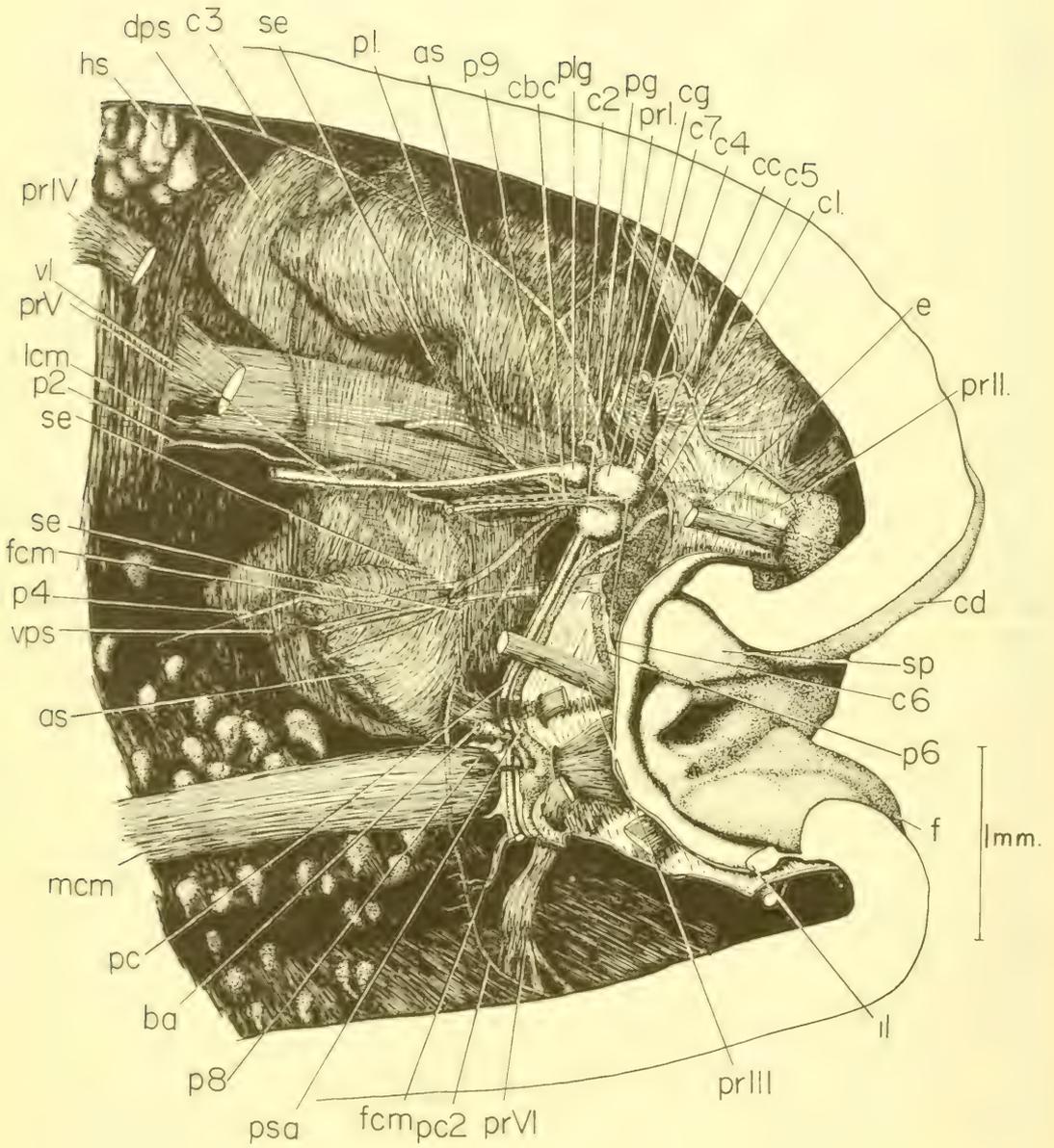
The large cerebral commissure (Figs. 14, 15, cc) leaves from an anterodorsal position whilst the smaller (cc2) has an anteroventral root. Both leave from the inner side of the ganglion. From near the base of cc2 leaves cerebral nerve 6 (Figs. 14, 15a, 16, 17a, c6), a tiny nerve which soon divides to 2 parts, one supplying the oral tube ventrally, whilst the other branches to supply fibres of retractor III and the median columellar muscle (mcm) where they interweave at their insertions.

Also leaving the inner anteroventral face of the ganglion from a point slightly anterior and dorsal to cc2 is the cerebro-buccal connective (Figs. 14, 17a, cbc). This runs to the corresponding buccal ganglion enclosed in a thin sheath with pedal nerve 9 (p 9) which accompanies it as far as the insertions of retractor muscles IV and V together with the few fine strands of muscle described earlier (p 289; Fig. 5) linking the latter to the lateral columellar muscle.

The main cerebropleural connective leaves the posterior face of the cerebral ganglion, (Figs. 14, 15, cg, plg) whilst the larger cerebropedal connective (Figs. 14, 15, cpc) leaves mid-ventrally. The second cerebropedal connective (Fig. 15, cpc2)

has a double root from the bases of c5 and c7. The 2 fine branches join shortly and travel close to the outer surface of the cerebral ganglion as one small connective, together with some muscle fibres, eventually reaching the postero-dorsal face of the pedal ganglion. This connective is described by Vayssière (1880) in *Gastropteron* and *Philine* and as typical of tectibranchs in general. The statocyst on the dorsal surface of the pedal ganglion is innervated from the cerebral ganglion as described by Lacaze-Duthiers (1872). The nerve responsible for this is the small c9 (Fig. 15).

The remaining cerebral nerves leave the outer face of each ganglion to travel either above or below the inner branch of the lateral columellar muscle (Figs. 14, 15, 16, c1, c2, c3, c4, c5, c7, c8, lcm, ilc). On each side this branch is large and runs very close to the ganglion. The eye rests on a few of its fibres (Fig. 12a, 3) and is supplied by a fine nerve (Figs. 14, 15, 16, c4) which takes a very meandering course in contracted specimens. Nerve c4 leaves from a point dorsal to the lateral columellar muscle. The roots of c3 and c7, sometimes united, are very near to its base (Figs. 14, 15, 16, c3, c7). Nerve c3 is the more dorsal and divides to 2 parts both of which supply the cephalic disc. This nerve runs very close to the anterior sinus sac wall (Fig. 14, c3, as). Its larger branch enters the muscle layers of the body wall just posterior to this sinus and eventually runs back to the posterior tip of the cephalic disc. The smaller branch enters more anteriorly and runs deeper. Nerve c7 leaves the cerebral ganglion parallel to nerve c2 below it (Figs. 14, 15, c7, c2). Both travel towards Hancock's organ, the most anterior part of which is supplied by c1, a huge nerve which leaves the outer ventral face of the cerebral ganglion and dives down median and ventral to the inner branch of the lateral columellar muscle (Figs. 14, 15, 16, c1, lcm, ilc). The innervation of Hancock's organ is thus similar to the figure given by Guiart (1901). Nerves c5 and c8 are more dorsal.



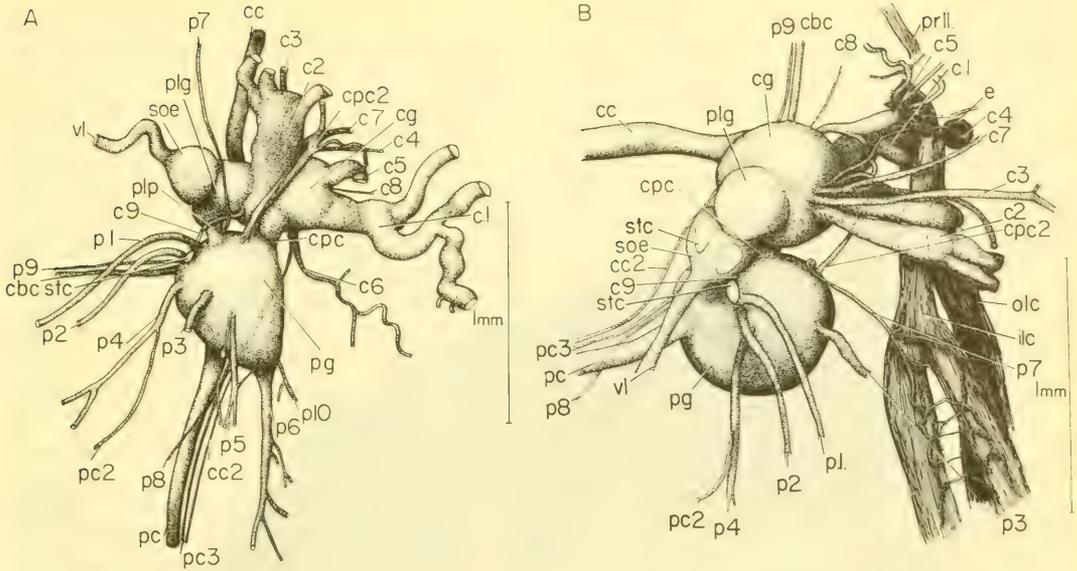


FIG. 15. *Philine*. The ganglia on the right side of the nerve ring: a, in ventrolateral view with the proboscis withdrawn; b, in posterior view with the proboscis out. c 1-9, cerebral nerves 1-9; cbc, cerebrobuccal connective; cc, cc2, cerebral commissures 1, 2; cg, cerebral ganglion; cpc, cpc2, cerebropleurial connectives 1, 2; e, eye; ilc, inner branch of lateral columellar muscle; olc, outer branch of lateral columellar muscle; p 1-10, pedal nerves 1-10; pc, pc2, pc3, pedal commissures 1, 2, 3; pg, pedal ganglion; plg, pleural ganglion; plp, pleuropedal connective; prII, proboscis retractor II; soe, supra oesophageal ganglion; stc, statocyst; vl, visceral loop.

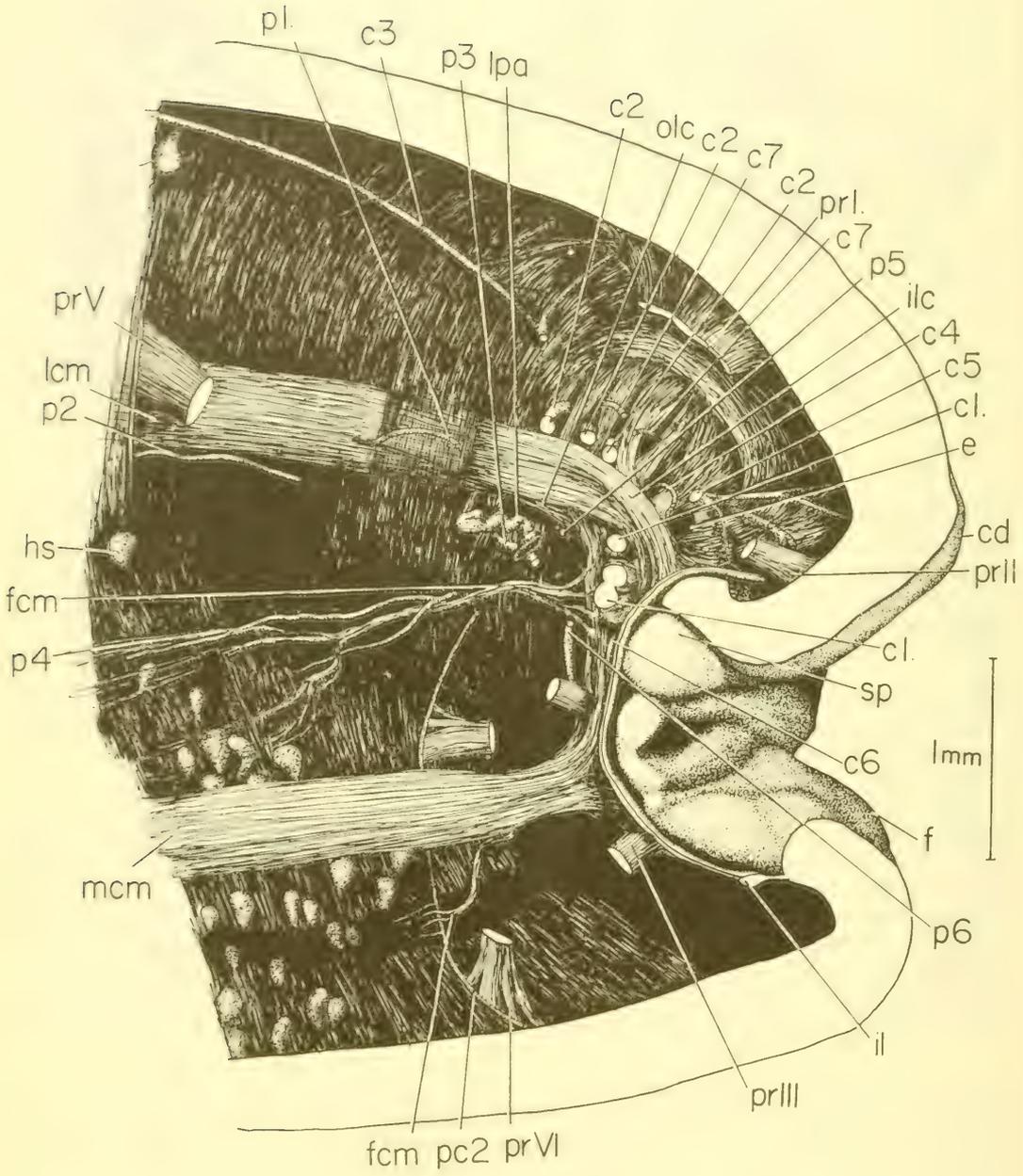
Nerve c8 is very fine and divides amongst the fibres of retractor muscle pr I where they insert in the cephalic disc. Nerve c5 has a stout basal part from which part of the second cerebropedal connective leaves proximally, whilst distally 3 nerves depart for anterior destinations. The first divides finely in the anterior part of the cephalic disc; the second travels more deeply and eventually branches many times to supply the dorsal sensory patch and the surrounding area; the third gives one branch passing amongst the inserting

fibres of the lateral columellar muscle, and another to the rim of the oral tube.

*The pedal ganglia and nerves*

Fourteen nerves leave each pedal ganglion including 3 pedal commissures and 3 connectives (Fig. 15). Four of the pedal nerves leave the posterior face (Figs. 14, 15, p1, p2, p3 and p4). Nerves p1 and p2 are sometimes joined at their bases, which lie immediately adjacent to the statocyst on the posterodorsal surface of the ganglion. They run back, at first

FIG. 14. *Philine*. Left sagittal half of the body with gut removed posterior to the inner lip. as, anterior sinus; ba, buccal artery; c 1-7, cerebral nerves 1-7; cbc, cerebrobuccal connective; cc, cerebral commissure; cd, cephalic disc; cg, cerebral ganglion; dps, dorsal posterior sinus; e, eye; f, foot; fcm, factor of columellar muscle; hs, haemal sac; il, inner lip; lcm, lateral columellar muscle; mcm, median columellar muscle; p 1, 2, 4, 6, 8, 9, pedal nerves 1, 2, 4, 6, 8, 9; pc, pc2, pedal commissures 1, 2; pg, pedal ganglion; plg, pleural ganglion; pr I-VI, proboscis retractors I-VI; psa, pedal sinus artery; se, septum; sp, sensory palp; vl, visceral loop; vps, ventral posterior sinus.



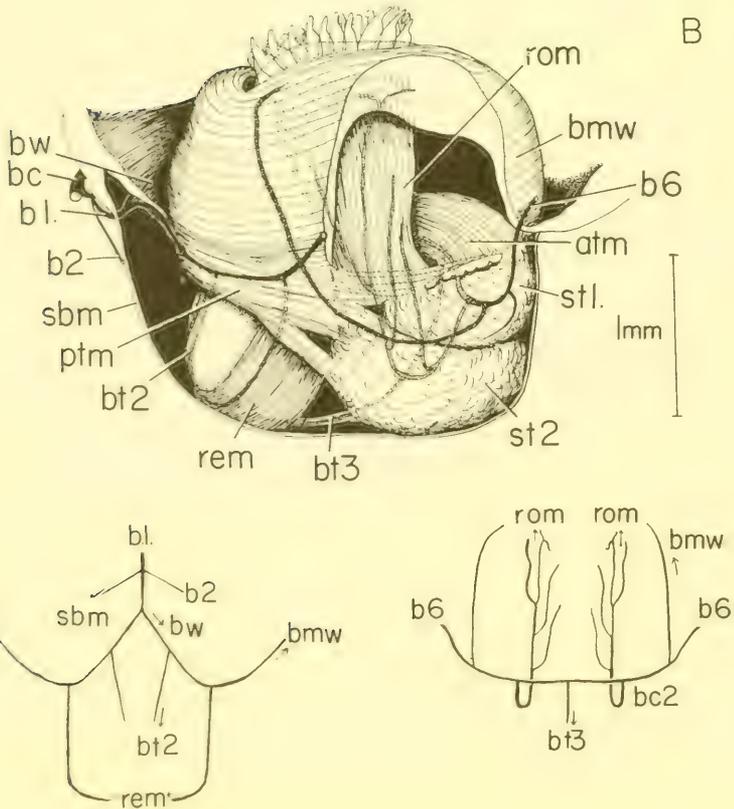
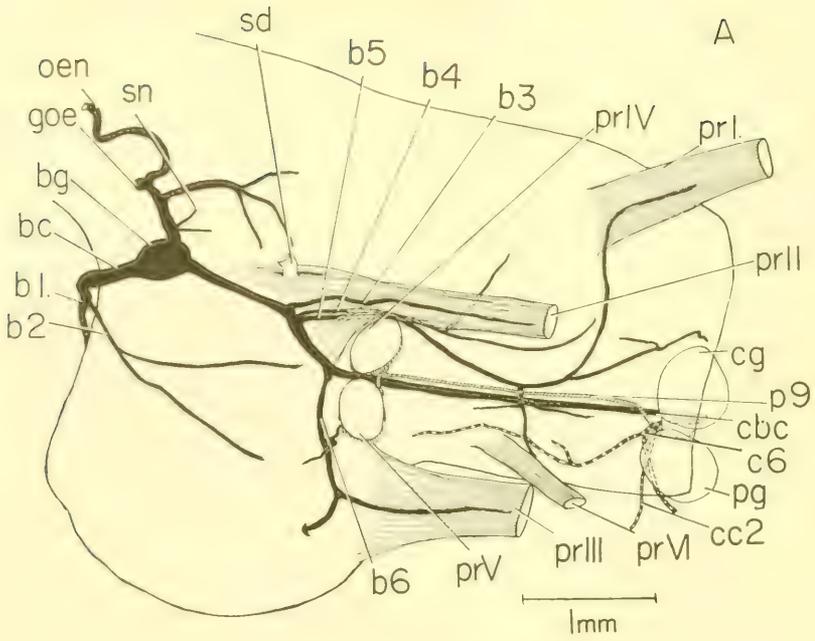
closely parallel, and enter the foot just below the lateral columellar muscle (Figs. 14, 16, lcm, p1, p2). Nerve p1 dives under transverse fibres of the body wall with the lateral columellar muscle, slightly posterior to the origins of its inner and outer branches. Nerve p2 enters further back. Nerve p3 leaves the pedal ganglion nearer its outer face and shortly enters the foot anterior to p1 and p2, and median to both inner and outer branches of the lateral columellar muscle (Figs. 15, 16, p3). The root of p4 (Fig. 15, p4) departs between and below those of p1 and p2 and that of p3. Like c3, it is closely associated with the wall of a blood sinus (Fig. 14, as, p4). After giving a small branch to the anterior coils of the reproductive system its main branch enters the foot posterior to the sinus. Where it enters, it divides around the inserting fibres of a small factor of the columellar muscle (Figs. 14, 16, p4, fcm). A thin inner branch of p4 travels across the foot in the surface layers to meet its opposite number and form an elongated parapedal commissure (Figs. 14, 15, 16, pc2). This commissure runs posterior to the origins of the proboscis retractors VI. From its centre 2 small branches enter the foot on either side of another factor of the columellar muscle (Figs. 14, 16, pc2, pr VI, fcm).

The commissure pc3 is even smaller (Fig. 15, pc3). It leaves the inner antero-dorsal surface of the pedal ganglion and runs with cc2 adjacent to the large pedal commissure (pc) which has an antero-ventral root. From near the base of pc3 on each side a tiny nerve p8 leaves for the median columellar muscle (Figs. 14, 15, p8). Similar small nerves p7 and p9 supplying the lateral columellar muscle and the proboscis retractors with

columellar origins (pr IV and pr V) also leave the dorsal surface of the pedal ganglion (Fig. 15, p7; Figs. 14, 15, p9). Nerve p9 leaves just posterior to pc3 and bends dorsalwards median to the cerebral ganglion, subsequently crossing outside the cerebrobuccal connective (cbc) and running alongside it until reaching proboscis retractors IV and V. Here p9 branches to form a network across and between the 2 muscles near their origins. Nerve p7 forms a similar network across the anterior branches of the lateral columellar muscle (Fig. 15b, ilc, p7). Its root is between those of the 2 cerebro-pedal connectives (Fig. 15, cpc, cpc2). It passes towards the lateral columellar muscle median to cpc2. Between its root and the roots of p1 and p2 leaves the short pleuropedal connective (plp).

The remaining pedal nerves leave the outer surface of the pedal ganglion. The most anterior is the tiny p10 (Fig. 15a) which branches widely in the ventral suspension sheet of the sinus surrounding the main pedal commissure (pc1). It supplies the above-mentioned fibres of the columellar muscle (Figs. 17, 22, fcm) which insert lateral to muscle VI with the main branch of p4. Posterior to the root of p10 is the much larger one of p6 (Figs. 14, 15a, 16, p6). This nerve has several parts, the largest of which supplies the ventral sensory patch, the smaller ones innervating the anterior parts of the reproductive system, and the margin of the foot. From the base of p6 is a small connective running to p5. This nerve leaves the pedal ganglion posterior to p6 near to p3 (Fig. 15a, p5). It has several branches to the foot below Hancock's organ (Fig. 16, p5). There is usually a ganglionic swelling near the base of one of its smaller factors (Fig.

FIG. 16. *Philine*. Left sagittal half of the body with gut removed posterior to the lip. In dissection subsequent to Fig. 14, the sinuses and ganglia have been removed and the extrinsic muscles trimmed back. c 1-7; cerebral nerves 1-7; cd, cephalic disc; e, eye; f, foot; fcm, factor of columellar muscle; hs, haemal sac; il, inner lip; ilc, inner branch of lateral columellar muscle; lcm, lateral columellar muscle; lpa, left pedal artery; mcm, median columellar muscle; olc, outer branch of lateral columellar muscle; p 1-6, pedal nerves 1-6; pc2, pedal commissure 2; pr I-VI, proboscis retractors I-VI; sp, sensory palp.



15a, p 5).

*The buccal ganglia and nerves*

The buccal ganglion of each side has 3 main nerves leaving it. The first leaves laterodorsally (Figs. 5, 7, 10, 12a, 17a, oen) and goes to the oesophagus, giving branches to the salivary gland (Fig. 17a, sn) and dorsolateral wall of the buccal region. It has been called the gastro-oesophageal nerve by Lacaze-Duthiers (1872). After these branches leave there is a small ganglionic swelling and the nerve then follows a meandering lateral course along the oesophagus. It is thus capable of spanning a greater distance when the proboscis is out and the oesophageal wall stretched. Such ganglionic swellings have been noticed in other opisthobranch molluscs. This one may be comparable to the gastro-oesophageal ganglion described by Russel (1929) as mainly confined to nudibranchs. However, Guiart (1901) has described gastro-oesophageal ganglia in the tectibranch *Gastropteron*.

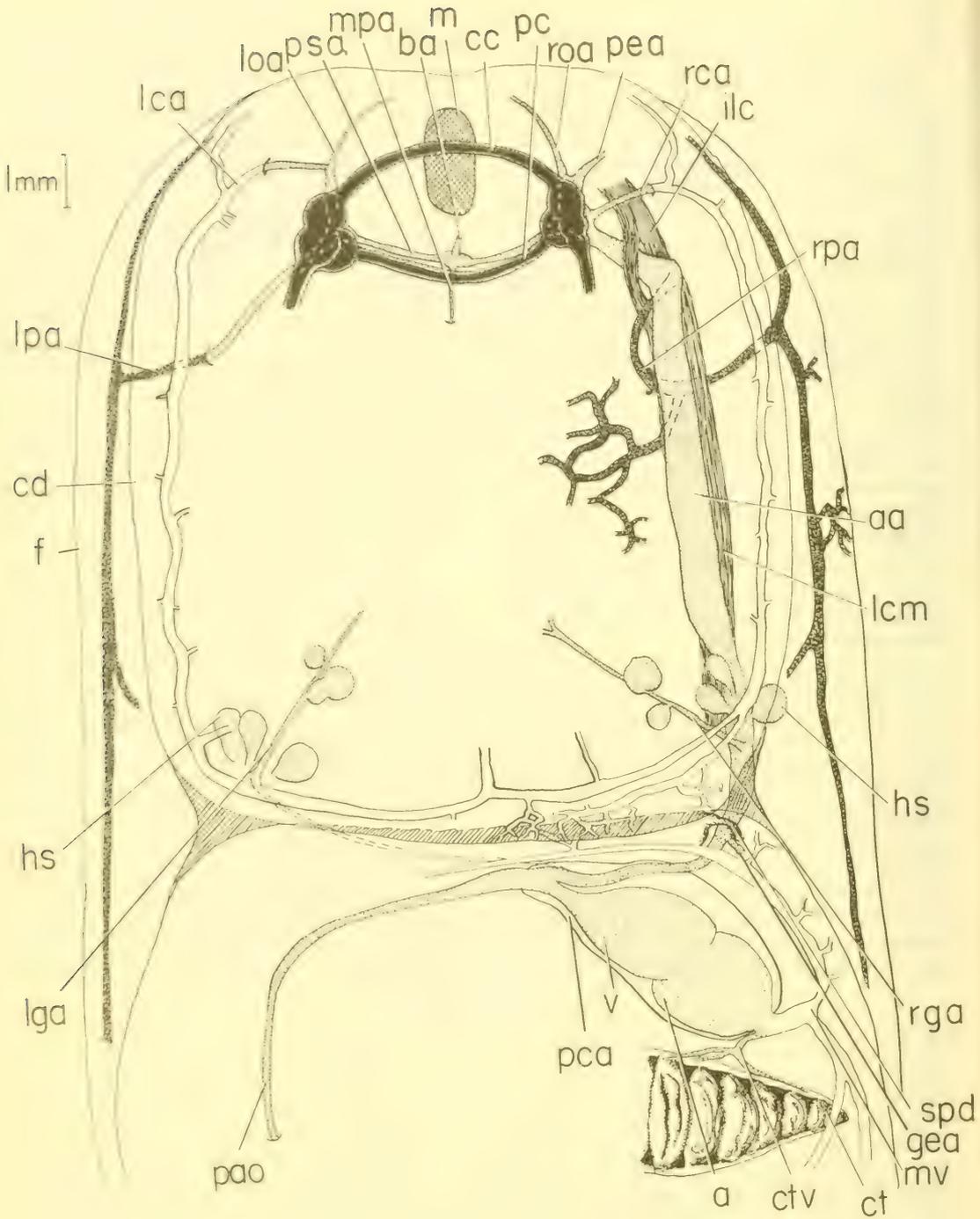
The second nerve trunk leaves the buccal ganglion laterally. It is the common trunk of the cerebrobuccal connective and other nerves which branch off before the extrinsic muscles IV and V are reached (Fig. 17a, cbc, b3, b4, b5, b6). The latter nerves have been collectively called the pharyngeal nerve by Lacaze-Duthiers (1898). Nerves b3, b4 and b5 leave the nerve trunk almost together, going slightly dorsalwards, whilst b6 departs a little further along, immediately posterior to the insertions of muscles IV and V.

Nerve b3 supplies muscle II which it enters almost immediately (b3, pr II), b4 bifurcates and innervates the dorso-lateral wall of the oral tube (b4, ot), whilst b5, the largest of the 3, runs laterally giving branches to the oral tube and finally supplying muscle I and the oral rim (b5, ot, pr I). Nerve b6 goes ventrally away from the cerebrobuccal connective giving a branch to retractor III (Fig. 17, b6, cbc, pr III). It subsequently enters the buccal mass in the region of the supporting tissue (Fig. 17b, st 1) and, passing along the anterior transverse muscle (atm), unites with its partner from the other side. Thus a small buccal commissure is established (bc2). This commissure gives on each side a small branch to the buccal wall and a larger one dividing several times within the radular occlusor muscle (rom). A median nerve leaves to supply buccal tensor 3 (bt3).

The third nerve trunk leaving each buccal ganglion is the large buccal commissure (Figs. 5, 7a, 9, 10, 12b, 17, bc). From its centre leaves the important nerve b1 (Figs. 7a, 17, b1) supplying the remainder of the intrinsic muscles of the buccal mass. This is the radular nerve of Lacaze-Duthiers (1898) and the buccal nerve of Brown (1934). A pair of small nerves (Figs. 7a, 17, b2) leaves from near the base to supply the superficial buccal musculature. Shortly after their exit, b1 divides into 2 parts. Each runs diagonally outwards entering the pigmented buccal wall (bw) superficially, and near the posterior transverse muscle (ptm) gives a branch going ventrally to

FIG. 17. *Philine*. The innervation of the buccal region:

- a, the nerves of the walls and extrinsic muscles shown in right lateral view;  
 b, the buccal mass dissected from the right side to a stage mid-way between Figs. 4 and 8, to show its nerve supply. The diagrams inset below show the branches of buccal nerve 1 in posterior view and those of buccal nerve 6 in anterior view. atm, anterior transverse muscle; b 1-6, buccal nerves 1-6; bc, bc2, buccal commissures 1, 2; bg, buccal ganglion; bmw, buccal mass wall; bt, 2, 3, buccal tensors 2, 3; bw, buccal wall; c 6, cerebral nerve 6; cbc, cerebrobuccal connective; cc2, cerebral commissure 2; cg, cerebral ganglion; goe, gastro-oesophageal ganglion; oen, oesophageal nerve; p 9, pedal nerve 9; pg, pedal ganglion; pr I-VI, proboscis retractors I-VI; ptm, posterior transverse muscle; rem, radular elevator muscle; rom, radular occlusor muscle; sbm, superficial buccal musculature; sd, salivary duct; sn, salivary nerve; st 1, 2, supporting tissues 1, 2.



the buccal tensor 2 (bt 2) and another to the radular elevator muscle (rem), continuing towards the supporting tissue (st 1) where the extrinsic retractor muscles II, III, IV and V insert.

#### 4. THE BLOOD SYSTEM OF THE ANTERIOR REGIONS

The blood system has been studied by injecting it with dilute Nile blue. This method has met with some success in both *Philine* and its larger relative *Scaphander lignarius* (Linn.). The blood system of *Philine*, however, has some interesting features which do not appear in *Scaphander*.

The heart of *Philine* lies to the right of the body, posterior to the diaphragm. The ventricle is anterior to the auricle (Fig. 18, v, a). The latter collects blood from the gill (ctv) and also from a network of vessels on the mantle roof. The mantle vessels (mv) enter in 2 main directions: from the anterior edge and from the lateral and posterior surfaces. Blood then passes into the ventricles, which it leaves by 2 large blood vessels, the anterior and posterior aortae (aa, pao). Brown (1934) described the course of these briefly. Pelseneer (1893) referred to a "glande sanguine" as an expansion of the aortic wall within the pericardium. It has not been investigated in the present study.

The posterior aorta (Fig. 18, pao) curves around the visceral mass, entering it deeply to supply the digestive gland, stomach, intestine and gonad. The anterior aorta (aa) goes across the floor of the pericardial cavity (pca) then gives a small blood vessel, the genital artery (gea),

which shortly branches twice to supply the female genital duct and parts of the reproductive system within the visceral mass. The aorta then passes under the spermathecal duct (spd) at the right side of the body and below the visceral ganglion before turning towards the head. Still wide in diameter, it pursues a meandering course closely applied to the body wall adjacent to the lateral columellar muscle (lcm). Its course so far agrees with the account of Brown (1934). As the anterior aorta turns forward, it gives a small vessel to the gut immediately posterior to the gizzard (rga). A similar vessel also approaches the gut from the left side of the body (lga); this probably originates from the base of the anterior aorta as in *Scaphander*. Continuing its lateral course, the anterior aorta passes between the origins of retractors IV and V and then through the double origin of the inner branch of the lateral columellar muscle (Figs. 6, 18, ilc, aa). Just before reaching the origin of this inner branch, a vessel leaves for the foot (Fig. 18, rpa). The anterior aorta then bends towards the mouth and divides to 2 parts. The dorsal one supplies the ganglia at the right side of the nerve ring and also gives a penial artery (pea) and one to the cephalic disc (rca). Around the nerve ring is a system of confluent sinuses enclosing the main commissures and connectives. These appear in dissection as a sheath around the nerves concerned (Figs. 14, 18, 19). Immediately anterior to the pedal commissure a large blood vessel, the pedal sinus artery (Figs. 14, 18, psa), runs in the thin sheath. Dorsal to the median columellar muscle (mcm) this vessel enlarges in diameter and gives

FIG. 18. *Philine*. Plan of the blood vessels of the anterior part of the animal with the gut removed. a, auricle; aa, anterior aorta; ba, buccal artery; cc, cerebral commissure; cd, cephalic disc; ct, ctenidium; ctv, ctenidial vessel; f, foot; gea, genital artery; hs, haemal sac; ilc, inner branch of lateral columellar muscle; lca, left cephalic artery; lcm, lateral columellar muscle; lga, left gizzard artery; loa, left oral artery; lpa, left pedal artery; m, mouth; mpa, median pedal artery; mv, mantle vessel; pao, posterior aorta; pc, pedal commissure; pea, pericardial cavity; pea, penial artery; psa, pedal sinus artery; rca, right cephalic artery; rga, right gizzard artery; roa, right oral artery; rpa, right pedal artery; spd, spermathecal duct; v, ventricle.

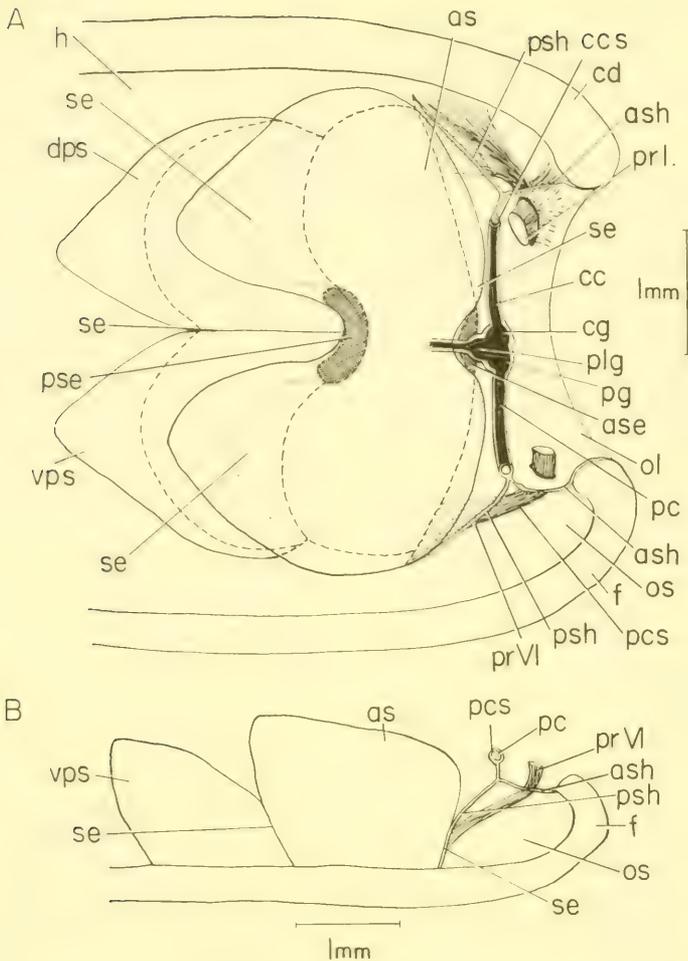


FIG. 19. *Philine*. a) Diagram of left anterior sagittal half with gut removed as in Fig. 14, to show relationship between blood sinuses and commissural sheaths. b) A longitudinal section through the ventral part shown in diagram a. The broken line indicates where sinus walls join the body wall. The finely dotted line shows the limits of septa between anterior and posterior sinuses and between anterior and oral sinuses. as, anterior sinus; ase, anterior sinus entrance; ash, anterior suspensory sheet; cc, cerebral commissure; ccs, cerebral commissure sinus; cd, cephalic disc; cg, cerebral ganglion; dps, dorsal posterior sinus; f, foot, h, haemocoel; ol, outer lip; os, oral sinus; pc, pedal commissure; pcs, pedal commissure sinus; pg, pedal ganglion; plg, pleural ganglion; pr I, VI, proboscis retractors I, VI; pse, posterior sinus entrance; psh, posterior suspensory sheet; se, septum; vps, ventral posterior sinus.

a fairly large buccal artery entering the buccal mass medially at its anterior limit (Figs. 4, 8, 14, 18, ba). A tiny vessel goes down to the foot, running between the muscle fibres associated with the parapedal commissure (Fig. 14,

fcm, pc2; Fig. 18, mpa). The main vessel continues in the pedal sinus to the left side of the nerve ring. There blood leaves it to enter the nerve sinus system, to go to the foot in the left pedal artery (Fig. 18, lpa) and to the cephalic

disc in another vessel (lca). Both branches of the anterior aorta continue forward as the oral arteries (roa, loa). In *Scaphander* these supply the lips and the anterior end of the oral tube. Vayssière (1880) mentioned the penial artery, 2 pedal and 2 cerebral arteries and the buccal supply. Brown (1934) described the anterior aorta as "connected with a system of sinuses".

The largest sinuses of the anterior region are very sizeable (Figs. 14, 19). They extend from the region of the nerve ring back nearly to the origins of proboscis retractors IV and V. In a sagittal section of the body with gut removed (Fig. 14) they may be seen as thin-walled bags joining the body wall at their edges. Four peaked bags are present on each side (Figs. 14, 19, as, dps, vps). The 2 anterior sacs (as) are confluent but are divided from the posterior ones by a dorsoventral septum (se) perforated only in the centre. The 2 posterior sacs represent dorsal and ventral sinuses separated by a horizontal septum. Blood can, however, pass from one to the other via the perforated septum between anterior and posterior sinuses. The limits of these sinuses have been checked by the introduction of an air bubble. This bubble, on manipulation, proved them to be confluent by only a small gap, the posterior sinus entrance (Figs. 14, 19, pse), in the septum between anterior and posterior sinuses.

The large anterior sinus (Fig. 14, 19, as) is delimited anteriorly by another septum (Fig. 19a, 19b, se) formed by fusion of its wall with the posterior suspensory sheets (psh) of the cerebral commissure sinus (ccs) and the pedal commissure sinus (pcs). This septum is supported by fibres from the proboscis retractors I and VI (pr I, pr VI). The arrangement of anterior and posterior suspensory sheets (ash, psh) from the cerebral and pedal commissure sinuses (ccs, pcs) encloses a further cavity anterior to them, limited on the third side by the body wall and continuous around the extreme anterior end of the body, forming an oral sinus (os). The middle parts of proboscis retractors I and VI

are free within the oral sinus but they are closely associated with the suspensory sheets (its walls) near their origins. Here fibres from both pairs of muscles run in the posterior suspensory sheet and each muscle passes through the anterior suspensory sheet to reach the oral tube. Some of the most anterior fibres of proboscis retractors I, originating from the outer lip rather than the cephalic disc, run within the anterior suspensory sheet. Because of the anterior suspensory sheet attaching to the outer lip from cerebral and pedal commissure sinuses blood escaping from the open anterior sinus entrance (ase) of the large lateral sinuses tends to pass to the haemocoel (h) median to the nerve ring.

There is extensive association between sinus walls and suspensory sheets with both muscles and nerves. Nerve c3 runs in the dorsal walls of the anterior sinus (Fig. 14, c3, as), its posterior branch following the posterior wall and its anterior branch the anterior wall. Similarly p4 (Fig. 14) runs with the posterior wall of the ventral posterior sinus (vps) and its anterior branch, pc2, runs in the anteroventral wall of the anterior sinus. The columellar muscle factors (fcm) associated with p4 and pc2 are even more close to the respective sinus walls. The suspensory sheets of the cerebral and pedal commissure sinuses also contain muscle fibres and fine nerves. Nerve c6 lies in the anterior suspensory sheet of the pedal commissure sinus and p 10 in its posterior suspensory sheet. Nerves cc2, pc3 and p8 run within the walls of the pedal commissure sinus itself during part of their course.

This account of the system of sinuses is necessarily incomplete due to a shortage of large specimens of *Philine*. The buccal artery was particularly difficult to fill successfully after it entered the buccal mass. Blood appeared to pass in front of the anterior transverse muscle and between the radular occlusor muscles, then on to either side of the radular sac. In *Scaphander*, which has a buccal mass similar in most respects, the course of

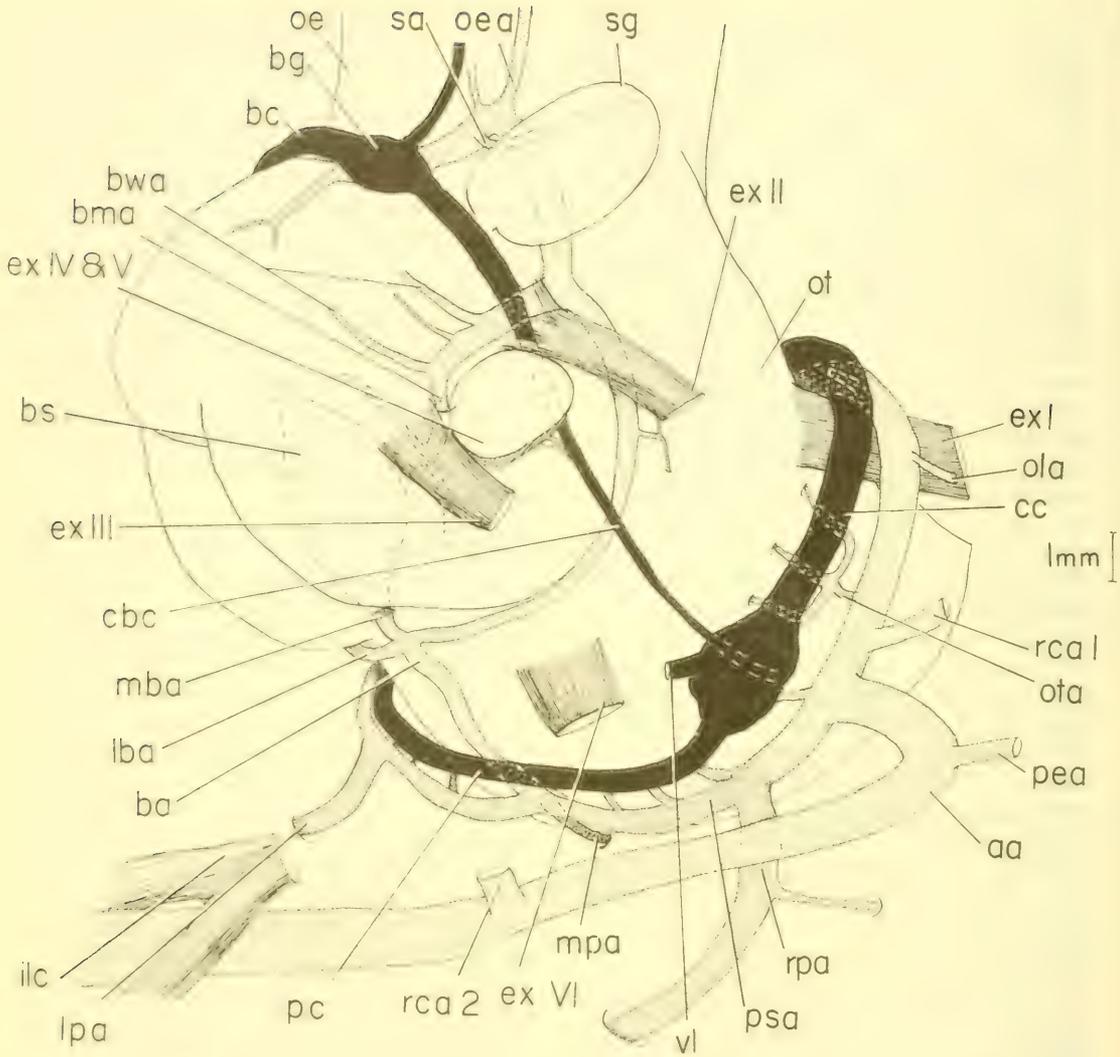


FIG. 20. *Scaphandor*. Right posterolateral view of buccal region, in the form of a diagram, to show the blood supply. The extrinsic muscles have been cut short and only those of the right side shown. aa, anterior aorta; ba, buccal artery; bc, buccal commissure; bg, buccal ganglion; bma, buccal mass artery; bs, buccal sinus; bwa, buccal wall artery; cbc, cerebrobuccal connective; cc, cerebral commissure; ex I-VI, extrinsic muscles I-VI; ilc, inner branch of lateral columellar muscle; lba, lateral buccal artery; lpa, left pedal artery; mba, median buccal artery; mpa, median pedal artery; oe, oesophagus; oea, oesophageal artery; ola, outer lip artery; ot, oral tube; ota, oral tube artery; pc, pedal commissure; pea, penial artery; psa, pedal sinus artery; rca 1, 2, right cephalic arteries 1, 2; rpa, right pedal artery; sa, salivary artery; sg, salivary gland; vl, visceral loop.

blood was easier to trace (Fig. 20). In this animal the buccal artery (ba) also

enters the buccal mass medially at its anterior ventral limit. A large outer

branch, the lateral buccal artery (lba), departs to each side at the point of entry, and the median buccal artery (mba) continues to form a small sinus (bs) below the radula. Each outer branch passes up the lateral buccal wall and dorsally above the insertions of the buccal extrinsic muscles. It then divides to 2 parts. One continues dorsal to the salivary gland, to which it sends a small vessel (sa) and also supplies the buccal ganglion before reaching the oesophagus where it again branches (oea). The other part of the lateral buccal artery passes ventrally immediately posterior to the insertions of the extrinsic muscles. It supplies the intrinsic muscles of the buccal mass (bma) and the buccal wall (bwa). The large lateral buccal arteries of *Scaphander* are very obvious, but have not been seen in *Philine*. However, stain has sometimes reached the anterior part of the oesophagus and Vayssière (1880) mentioned 2 vessels going laterally around the buccal mass and up the oesophagus.

An important feature of the blood system in *Philine* (not in *Scaphander*) is the presence of haemal sacs (Figs. 14, 18, hs). These are thin-walled sacs which may be filled with blood, projecting from all sides into the posterior end of the main anterior body cavity, their long necks disappearing between the muscle fibres of the body wall. They can be easily filled with Nile blue by an injection made in the heart or anterior aorta. The stain does not then appear in the general haemocoel. The sacs are thus confluent with blood vessels and a few have been seen leaving the gizzard arteries and the anterior aorta (Fig. 18). The connections of the majority have not been traced. They are not filled by direct injection into the foot or cephalic disc.

In both foot and cephalic disc, there is a very extensive network of blood vessels (Fig. 18). The structure of the body wall consists of a thick layer of muscle fibres running in all directions. Amongst this spongework weave many interconnected vessels which can be filled by injecting respectively pedal or cephalic arteries.

In *Scaphander* this network is not represented although the arteries branch several times. The area around the sensory patches can also be filled with blood via the pedal and cephalic arteries.

##### 5. THE FUNCTIONING OF THE BUCCAL MASS INVESTIGATED BY STIMULATION

Three groups of movements have been observed in living *Philine* with the common effect of transporting food from the outside world to the oesophagus. The first concerns capture of prey. The walls of the buccal region of the gut are rolled inside out to a varying degree and the buccal mass is brought forward and through the mouth. The teeth open, seize prey (previously located by the sensory areas) by closing on it, and then drag it in. The second group of movements brings about release of prey to the oesophagus. The buccal mass, with teeth closed on the food, rises in the buccal cavity whilst the buccal region shortens, so that the dorsolateral thickenings of the oral tube meet. As they rise the rows of teeth open, releasing their burden to the oesophagus. The buccal mass then sinks, with teeth closing on the way. These 2 groups of movements alone constitute an efficient feeding process. The third group concerns searching for food with the proboscis fully protruded and often very active and mobile.

Stimulation experiments have been carried out with the aim of artificially reproducing some of the feeding movements and gaining evidence about the function of the muscles involved. Since protrusion of the proboscis is due to a complex interplay of muscular movements and changes in haemocoelic pressure, it has not been possible to produce it by electrical stimulation. Placing of the electrodes inevitably necessitates opening of the body cavity, which immediately removes all possibility of normal blood pressure changes, and pinning of the body wall means that muscular movements are no longer strictly normal. In spite of

these difficulties it has been possible to simulate the rising and sinking movements involved in release of prey to the oesophagus in animals with proboscis in. In specimens with proboscis out a number of food-search and tooth movements have been evoked.

The stimulator used was built at the Royal Veterinary College, London, to the specification of Dr. R. H. Nisbet. Tapered silver electrodes, insulated at their tip with either Araldite (a commercial resin glue) or nail varnish, were set up in holders so that they could be moved in a horizontal or vertical direction. In later experiments the electrodes were modified: the silver wire emerging from the end of the glass holder was long and coiled in a spring; this gave it an ability to swing so that the electrode moved with the animal as it contracted.

The buccal ganglia are important as primary governors of the feeding process and as such have been the points of stimulation that yielded most information. It was attempted to analyse the general response resulting from stimulation of the buccal ganglia by stimulating individual muscles and nerves, but this method is subject to certain limitations: the size of the electrodes makes exact placing difficult; the nerves are often buried deeply amongst muscle fibres and the stimulus is therefore not precise; to reach certain of the intrinsic muscles it is necessary to cut others, and since muscles often work in functional groups the results may be unlike those seen in an intact animal. Particular difficulties in confining stimulation to one or a single pair of muscles are presented by the fact that one nerve trunk may branch to supply several muscles and unless the nerve is cut the stimulus may easily be transmitted to an area not in contact with the electrodes. Conclusions have been based on those results which seemed relatively normal.

#### *Animals with proboscis in*

Stimulation of the buccal ganglia was most easily done from the ventral side.

The foot was cut open by 3 longitudinal cuts, 1 median, 2 just below the lateral tracts of the columellar muscle, from the posterior margin of the foot nearly to the mouth. A cut was made across the posterior edge of the foot joining the longitudinal cuts so that the foot could be turned forward in 2 triangular pieces and pinned out. This slightly stretched the buccal region by way of extrinsic muscles VI, the origins of which were now displaced and pinned anterior to the buccal region with the triangular pieces of foot. The stretching caused the angle between buccal mass and oesophagus to enlarge and thus made the buccal ganglia more accessible.

In a typical experiment a pair of electrodes was placed on each buccal ganglion giving stimuli of dial voltage 9 at a frequency of 1 stimulus every  $2/3$  sec. This produced a regular rising and sinking movement of the buccal mass within the surrounding superficial buccal musculature.

As the buccal mass rose, the whole buccal region became shorter and wider due to contraction of the extrinsic muscles I, II, III and VI. Extreme shortening of the oral tube caused its dorsolateral walls to meet and its floor to become very convex within the lumen. The postero-ventral bulge usually occupied by the buccal mass flattened, with the radular elevator muscle and radular sac almost disappearing under the buccal wall. The superficial buccal musculature contracted slightly but remained slack around the buccal mass. Since the lower half of the buccal mass moved upwards (by contraction of buccal tensors 2 and the radular elevator muscle) the buccal mass wall became stretched. This, combined with the contraction of the radular elevator muscle and outer oblique muscles, caused the radular membrane to be pulled laterally and flattened, thus opening the teeth. All the intrinsic muscles of the buccal mass wall contracted together.

In sinking the reverse happened. The buccal region elongated whilst its walls contracted, and were pulled in laterally

due to contraction of the anterior transverse muscle. The superficial buccal musculature stretched around the sinking buccal mass and the posteroventral bulge became deep and prominent. The radula moved down and as a result the tip of the radular sac became pressed forward (helped by the pull of buccal tensors 3 which contracted) and could be seen protruding mid-ventrally. The teeth closed, partly due to lateral and posterior pressure from the buccal walls caused by the contracted anterior and posterior transverse muscles, but mainly due to contraction of the radular occlusor muscles. This was accompanied by relaxation of the radular elevator muscle, the outer oblique muscles and buccal tensors 2. Much of the radular sac and elevator muscle now projected below the posterior transverse muscle. Buccal tensors 4 contracted and helped to pull the radular sac down. The radular caecal fold was thus most prominent at this stage, and pressed down firmly over the radular sac. It was not widened by lateral stretch when the buccal tensors 4 contracted since their origins overlap, obviating the outward pull they would otherwise have given.

Direct stimulations of some of the muscles involved in the rising and sinking movements were carried out to see if the functions were what they would seem. The results may not be particularly reliable for the reasons already enumerated.

#### Intrinsic muscles contracting in the rising phase

*The radular elevator muscle:* A large number of experiments were carried out with 1 or 2 pairs of electrodes placed on the radular elevator muscle. With varying voltage and frequency it was possible to obtain several effects. These included a twitching of the muscle in unison with a stimulus of low voltage (9-15V) and frequency 1.5-3/sec. At 9V and 10-15/sec. a general contraction ensued and the radular sac moved up into the buccal cavity whilst the anterior end of the buccal mass wall moved slightly

downwards. Stimulation of the radular elevator muscle also caused the teeth to open, sometimes rather jerkily, starting with the most anterior pair. In many animals the teeth remained closed at dial voltages up to 9V, but at 9V they opened and above this closed again. Ten per second seemed to be the frequency at which rapid twitches were absorbed into a single contraction.

*Buccal tensors 2:* It was sometimes possible to cause contraction of buccal tensors 2 by direct stimulation, but this was difficult due to the small size of the muscles and consequent difficulty in placing electrodes. When contraction occurred the tip of the radular sac moved up and towards the posterior transverse muscle.

*Outer oblique muscles:* Due to their size and situation, these muscles also proved difficult to stimulate directly when the buccal mass was not protruded. Results of stimuli applied when the proboscis was out proved that the outer oblique muscles are able to move the teeth closer together and towards the anterior transverse muscle. Stimulation of the corresponding muscles in *Scaphander* on one side only, with the buccal mass within the buccal cavity, caused the teeth of that side to open slightly.

*Superficial buccal musculature:* Rhythmic contractions can be induced by a stimulus of 9V at the rate of 1 every 2/3 sec. These are similar to those observed in the rising phase caused by stimulation of the buccal ganglia.

*Oesophagus:* Stimulation of the oesophageal nerve caused the buccal region to become dorsoventrally flattened as in the rising phase. After cutting the oesophagus from the buccal region and stimulating the cut edge above the buccal ganglia the buccal cavity and its oesophageal exit widened. Simultaneously the ventral floor of the oral tube moved up. If this is a genuine effect it would be useful when the radular teeth open in the rising phase, encouraging the released food to pass into the oesophagus.

### Intrinsic muscles contracting in the sinking phase

*The radular occlusor muscles:* Stimulation of these has usually been with electrodes placed on the supporting tissue (st2) at the base of the muscles. Since the nerve supply is buried deeply here, it seems doubtful whether the stimulus would be very effective. In fact, in only one animal was contraction caused. On this occasion the whole buccal mass was pulled down promptly. The functional teeth were firmly closed with the radular membrane folded into a deep V-shape within the buccal mass wall. The radular occlusors are extremely large and are the most important muscles involved in closing and withdrawing the radula.

*Buccal tensors 3 and 4:* No reliable results were obtained in stimulating pair 3 because of the close association of these with the superficial buccal musculature and the radular occlusors. Pair 4 was not stimulated to give any decipherable result.

*Posterior transverse muscle and buccal wall:* These were stimulated through their nerve supply (b1, b2). This caused slight contraction and consequent squeezing of the buccal mass.

*Anterior transverse muscle:* It proved difficult to stimulate this muscle without transmitting the stimulus to extrinsic muscles II, III, IV and V. Contraction of the anterior transverse muscle with consequent approaching of the supporting tissues (st 1) was sometimes obtained. The radular occlusor muscles, anterior transverse muscle and buccal tensors 3 are all supplied by branches of a single nerve trunk - further circumstantial evidence for these all contracting together as a functional unit as they seem to do in the sinking phase.

### Extrinsic muscles

Contraction of the proboscis retractors I, II, III and VI occurred during the rising phase. Their action was to protract the buccal mass whilst shortening the oral tube. They were stimulated in pairs directly. In contraction both

their insertions and origins moved due to lack of haemocoelic pressure, which in an intact animal would prevent great retraction of the anterior region where these muscles originate.

*Pairs I and VI:* These on contraction pulled the oral tube forward, widening it at the same time; both thus tended to help in protracting the buccal mass. However, in very relaxed animals the origin of pair VI is sometimes posterior to its insertion when it will not cause protraction.

*Pair II:* These reacted readily to direct stimulus. When both were stimulated they shortened considerably and pulled the buccal mass forward. The posterior tract of fibres joining pair II below the oesophagus (see p 288-289) shortened and thus caused the posterior face of the buccal mass to become more vertical. As this occurred the teeth closed further, probably due to pressure from the surrounding walls. With stimuli repeated every 2/3 of a second, a nodding movement can be evoked in the buccal mass due to small regular contractions and relaxations of pair II.

*Pair III:* Contraction of these was easily induced by a stimulus of dial voltage 9 and frequency of 10/sec. It caused the buccal mass to move forward and down, advancing particularly at the basal end. When pair III contracts alone, it also causes some squeezing of the ventrolateral walls of the buccal cavity and consequent bulging dorsolaterally.

All contractions of proboscis retractors I, II, III and VI caused some protraction of the buccal mass. Their most effective contractions occurred when the large retractors IV and V, from the columellar muscle, were relaxed.

*Pairs IV and V:* Stimulation of these 2 at their bases caused the buccal mass to take up the sinking phase position. Similar effects could be obtained by stimulating the buccal nerve trunk before it divided near the entries of II, IV, V and III. More satisfactory stimulation of IV and V was given by placing the electrodes along their length not far from the side of the buccal mass. This caused contraction and consequent retraction of the

buccal mass. Sometimes stimulation with electrodes on the cerebrobuccal connective caused contraction of IV and V. This is due to the fact that the nerve p9 which innervates them runs closely parallel to the connective and within the same sinus sheath.

When muscles IV and V are stimulated with the proboscis out, it is slightly retracted and, if the stimulus is on one side only, the buccal mass often twists towards the contracted muscles. These movements are caused by stimulus of any one of the proboscis retractors. All the proboscis retractors act as such whilst the proboscis is out, although their action may be so weak as to cause only slight movement in the direction in which they pull. The function of IV and V, however, is retraction of the buccal mass even when it is not protruded as part of the proboscis. The other proboscis retractors are in fact buccal mass protractors whilst the whole buccal region is within the main body cavity. If all 6 pairs of proboscis retractors contract together, their effects will thus oppose one another whilst the buccal mass is within the buccal cavity. When it is out, forming the ventral part of the proboscis, their effects will summate and retract it. In view of this it is obvious that contraction of the proboscis retractors must be in a definite sequence for protraction of the proboscis to occur. This sequence will be discussed later.

*Other parts of the columellar muscle:* Stimulation of these caused shortening of the body laterally or medially according to the position of the electrodes. Contraction of the lateral columellar muscle may close the lateral groove of the body. The role of the columellar muscle in protrusion of the proboscis is discussed below.

The regular rising and sinking movements of the buccal mass normally used in release of food from the radular teeth to the oesophagus may thus be experimentally induced. The muscles involved work together in groups. In rising, the radular elevator muscles, buccal tensors 2 and the outer oblique muscles cause

the radula to be slightly projected from the buccal mass and opened by stretching the radular membrane laterally. Simultaneously muscles I and VI contract, shortening the oral tube, whilst II and III pull the buccal mass forward, tipping its free upper end slightly back towards the oesophagus. The dorsolateral walls of the oral tube meet due to its extremely shortened state, aided by contraction of its longitudinal muscles. Thus food is released by the opened teeth and, following the nearest available route, is able to go into the oesophagus. In the sinking phase, all these muscles relax whilst others come into action. The radular occlusors close the radular teeth and pull the radula down within the relaxed buccal mass walls, with the help of buccal tensors 3 and 4. The anterior and posterior transverse muscles contract and force the buccal mass down into the superficial buccal musculature. Proboscis retractors IV and V may contract and pull the buccal mass still further down and back. The accompanying squeezing of the buccal walls helps to send food into the oesophagus in a peristaltic manner.

Another feature occurring with regularity on appropriate stimulation is an indentation and relaxation of the region around the entry of the buccal artery. Indentation may be induced by stimulation of any one of pair III, buccal tensor 3, the superficial buccal musculature, the ventral tensor muscles of the oral tube, or the supporting tissues. All these have in common the fact that they are in contact with the transverse strand of Brown (1934) which has been described (p 289) as a strip of muscle fibres linking the two muscles III to which the superficial buccal musculature and ventral tensor muscles attach. The anterior transverse muscle, supporting tissues and buccal tensors 3 are in close contact with it. Indentation appears to be due to contraction of this transverse strand, possibly together with the ventral circular muscles of the oral tube. It would appear to have the function of closing the buccal artery at its buccal entry and allowing it to open when in-

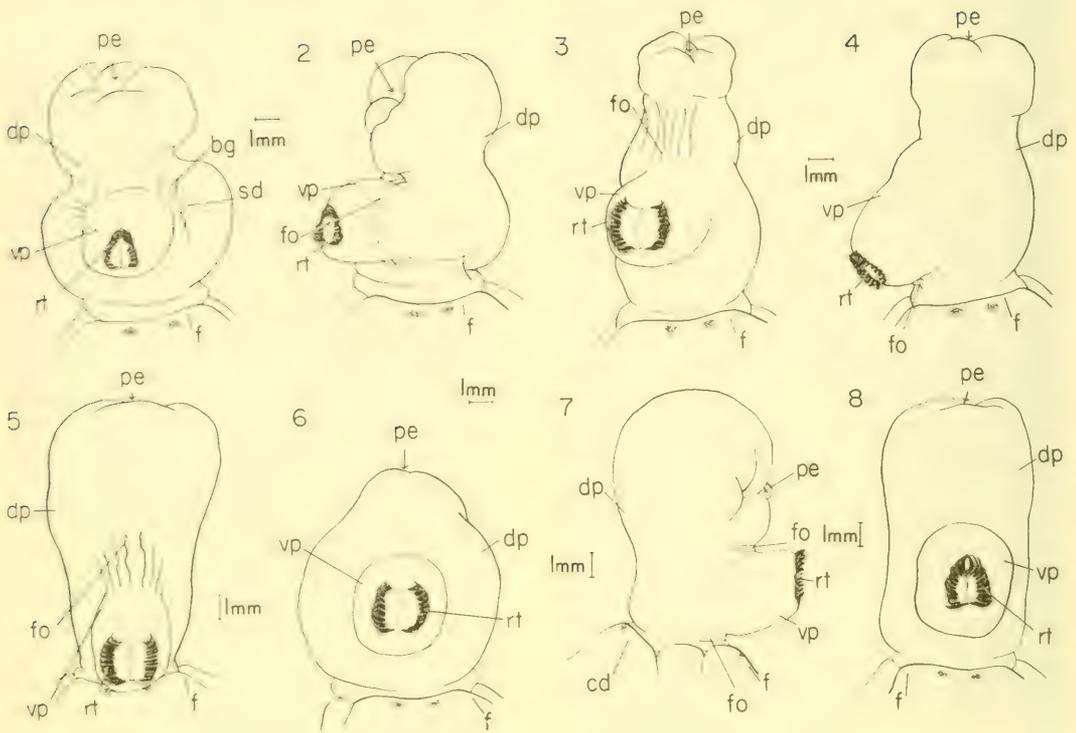


FIG. 21. *Philine*. Diagram to illustrate the changeable shape of the proboscis. bg, buccal ganglion; cd, cephalic disc; dp, dorsal part of proboscis; f, foot; fo, fold; pe, proboscis entrance; rt, radular tooth; sd, salivary duct; vp, ventral part of proboscis.

dentation ceases. This may have a circulatory function, allied to those described for *Haliotis* (Crofts, 1929) and *Monodonta* (Nisbet, 1953). Indentation may also help in opening the radular membrane by holding blood in the buccal sinus (Fig. 20, bs) and thus increasing turgidity. Its function in this respect cannot be fully elucidated since its timing has not been correlated with the sequence of the rising and sinking phases.

#### *Animals with proboscis out*

The everted proboscis is basically a dorsal fluid-filled bag and a ventral muscle-filled cylinder (Fig. 10). Between the 2 is the area covered by the pigmented buccal wall (Fig. 22a, bw) which

undergoes great changes in its degree of contraction, particularly anteriorly and laterally. Leaving it laterally from within the proboscis are extrinsic muscles II, IV, V and III (Fig. 12). If the buccal wall contracts, the free parts of the salivary glands (sg) float towards the anterior end, in which position they are nearly always found on dissecting the proboscis. A more obvious feature of this contraction is that it causes the tip of the ventral cylinder to move anteriorly. Thus the angle between the base of the cylinder and the anterodorsal part of the proboscis becomes very small (Fig. 21, positions 2, 7). This effect is helped by contraction of buccal tensors 1. Great contraction has been observed in this area causing it to

lie in transverse folds (Fig. 21, position 7). On relaxation the buccal wall usually bulges out (position 4) and the ventral cylinder moves to point posteriorly (vp), sometimes helped by contraction of the oral tube immediately posterior to it (fo). Lateral bending is induced by contraction and inpulling of the wall on one side of the cylinder base (position 2, vp, fo). These bending movements are helped by contraction of the proboscis retractors inserting in this area (see p 299) in different combinations. Bending in the cylinder itself was not very marked but was due to contraction of muscles running in its walls. It could be induced by stimuli applied to the buccal mass wall around the ventral part of the proboscis.

As may be seen in Fig. 21, the dorsal part of the proboscis is capable of considerable change in shape, pressure being provided by the intrinsic musculature of its walls; the changes are instigated and controlled by the nerve supply. They are sometimes accompanied by peristaltic movements of the inner part of the oesophagus, also innervated by the oesophageal nerve. The shape of the dorsal part of the proboscis varies from that of an elongated oval balloon (position 8, dp) to an hour-glass shape (positions 1, 2, dp). In the former case the diameter may be greater proximally (6, dp) or distally (5, dp). Some changes in shape may be due to inpulling of the oesophagus at its anterior entrance (pe). A change such as that from position 5 to 6 may be caused by stimulation of the tip of the proboscis. The proboscis entrance may be dorsal (Fig. 11, pe), anterior (Fig. 10; Fig. 21, positions 1, 3, 4, 5, 6, 8, pe), or ventral (Fig. 21, positions 2, 7, pe). Movement of the entrance from position 4 to 7 occurs on stimulation of the ventral part of the outer oesophageal wall. Proximal contraction due to intrinsic muscles often causes longitudinal wrinkling of the ventral wall and is accompanied by opening of the radular teeth to their widest (Fig. 21, positions 3, 5, dp, fo, rt); this can sometimes be produced by direct stimulation of the buccal wall. The rosette-

like folds around the proboscis entrance may disappear due to a movement of fluid to this region from the squeezed area (f, pe, dp, fo). Carmine particles placed on the dorsal part of the proboscis will move into the entrance by ciliary action, but this is the only observed evidence of objects going in here.

When the radular membrane is flattened out as in the final stage of the rising movement previously described, the teeth open. They may remain wide open for long periods, but in general the most anterior rows are closed and the posterior ones partially open (Figs. 21 (1, 2, 4, 7, 8), 22a, rt). They can be fully closed, which is usually preparatory to complete or partial retraction of the buccal mass through the mouth. Sometimes they remain open until the buccal mass is almost withdrawn (Fig. 22b, rt). The width of the spaces between the rows of functional teeth may be altered. This has been caused experimentally by stimulation of the outer oblique muscles. The origin of these is posterior to their insertion in the proboscis, and when they contract the teeth move back and the posterior rows approximate more closely. Mechanical pressure on the base of the ventral part of the proboscis caused it to protrude and the teeth to open, whilst pressure on the posterior end of the radular membrane caused the teeth to close and be pulled well down into the cylinder whilst it moved back further into the proboscis.

## 6. PROTRUSION OF THE PROBOSCIS

By integration of the information already presented, it is possible to suggest the probable method of protrusion of the proboscis. Firstly, the functions of the muscles concerned have been deduced from their positions in animals at all stages between full withdrawal with strong contraction and full protrusion with a marked degree of relaxation. Secondly, observations on living animals have suggested the way in which the proboscis comes out. Thirdly, some experiments with mechanical pressure have afforded

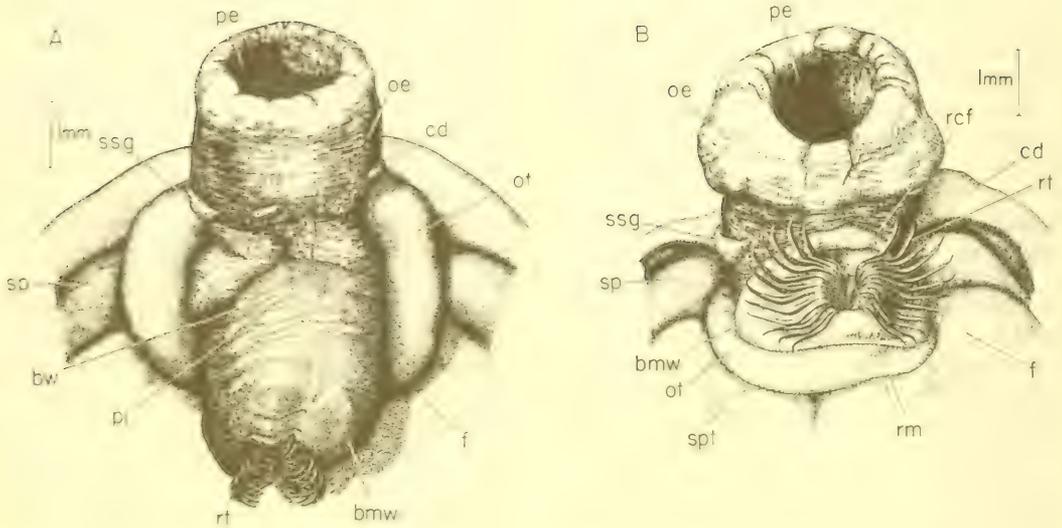


FIG. 22. *Philine*. Two anterior views of the proboscis partially collapsed prior to withdrawal, to illustrate the variable positions of the teeth, which may remain wide open until almost completely withdrawn. bmw, buccal mass wall; bw, buccal wall; cd, cephalic disc; f, foot; oe, oesophagus; ot, oral tube; pe, proboscis entrance; pi, pigment; rcf, radular caecal fold; rm, radular membrane; rt, radular tooth; sp, sensory palp; spt, sensory patch; ssg, secretion of salivary gland.

circumstantial evidence for the importance of blood pressure. Moreover, injections of the blood system have indicated that blood may be concentrated in certain areas and cause considerable local changes in pressure. Fourthly, the nerve supply of the anterior region has been found to be strongly concentrated around the sensory areas and the mouth, while the buccal mass and anterior gut walls are also well supplied with nerves. This indicates that the animal is capable of locating and identifying food easily and by virtue of very adequate musculature is able to perform diverse movements to capture it.

These sources provide a reasonable basis of support for the method of protrusion suggested. It is unfortunate that the major part of the information obtained

from stimulation experiments concerned movements of the buccal region whilst within the body walls or after protrusion, and not during the process of moving from the one position to the other. The reasons for this have already been mentioned.

Before protrusion can occur it is necessary for the anterior region of the body to be suitably stretched. The process may thus be divided into 2 parts: the preparatory and the final phase. In the preparatory phase, this part of the body elongates, with the sensory palps exposed and the mouth open (Fig. 1, stage 1, sp, m). The dorsolateral thickenings of the oral tube are at first touching in the midline, closing the lumen, but then draw apart as the final phase begins. During this phase the inner lip (or rim

of the oral tube) begins to bulge out (Fig. 1, stage 2, ot). The tip of the buccal mass appears and is pushed right out, followed by the anterior end of the oesophagus (stages 5-6). The latter then begins to expand above it, bringing about an appearance as in Fig. 1, stage 7.

*Philine* may stay in the preparatory stage for long periods. During this time the proboscis may be pushed out by mechanical means, either by pressure applied externally just behind the buccal region (the more successful method) or (occasionally) by a quick injection of sea water into the main anterior body cavity. For either method to be successful the pressure rise must be speedy or the animal is apt to contract violently so that protrusion is no longer possible. This suggests that, provided the muscles are in suitable positions, the final stages of protrusion of the proboscis are brought about by blood pressure alone.

The first prerequisite for attaining the preparatory position is relaxation of the columellar muscle. This allows the foot to lengthen and the outer lips to be stretched forward, exposing the sensory palps. Fibres of the median and lateral columellar muscles enter the outer lips and overlap in a complete semicircle around the ventral part of the mouth (Fig. 16). These may represent the oral sphincter of Brown (1934) and Fretter (1939). Their relaxation enables the mouth to open widely. A further effect of columellar muscle relaxation is that its components proboscis retractors IV and V can lengthen so that they no longer pull the buccal mass firmly back within the anterior body cavity.

Extension of the body is partly due to flow of blood into the anterior region of the haemocoel. The anterior aorta may allow greater passage of blood when the columellar muscle has relaxed since it passes under part of the inner branch of the right lateral muscle (Fig. 6, aa, ilc) and is therefore probably constricted when the muscle is contracted. The factors of the columellar muscle (Figs. 14, 16, fcm) running in the walls of the large anterior

sinuses may lengthen allowing them to expand fully. Another physiological valve affecting blood flow to the anterior body cavity occurs where the anterior aorta passes through the diaphragm or cephalic septum.

At this stage in the preparatory phase any pressure applied posteriorly to the buccal region of the gut could push it out as a proboscis, since the main anchors (retractors IV and V) no longer act as such, and the lips and regions adjacent to them are not pulled in to prevent passage of the proboscis.

Under natural conditions protrusion by increase in blood pressure is helped by contraction of 4 pairs of proboscis retractors, I, VI, II and III. The net effect of these draws the buccal region forward (Fig. 23). Since pairs I and VI are closely associated (p 313) with the anterodorsal and anteroventral walls of the anterior sinus (Fig. 19) they may tend to reduce its size, thus encouraging blood to flow out of the anterior entrance (ase). This blood would probably be unable to flow posteriorly since the widest part of the buccal region would fill the space in the body cavity median to the sinuses. Pressure by the buccal mass on their walls might even encourage blood to flow forward out of the sinuses helped by contraction of the inner muscular layer of the body wall, which reduces the diameter of the body cavity. Blood will thus tend to flow forward through the nerve ring, funnelled on by the anterior suspensory sheets from the cerebral and pedal commissures attached to the outer lip. It will thus cause the oral tube to bulge forward as in Fig. 1, stages 1 to 4 (ot) and Fig. 23 (stages 2-4).

The exact effects of proboscis retractors I, VI, II and III are as follows. Pairs I and VI act as dilators and protractors of the oral tube. After the mouth has opened in the preparatory phase of protrusion the inner lip stretches due to contraction of the circumoral muscles. Then, whilst the circular intrinsic muscles of the oral tube relax, pair I contracts more, separating the dorsolateral thicken-

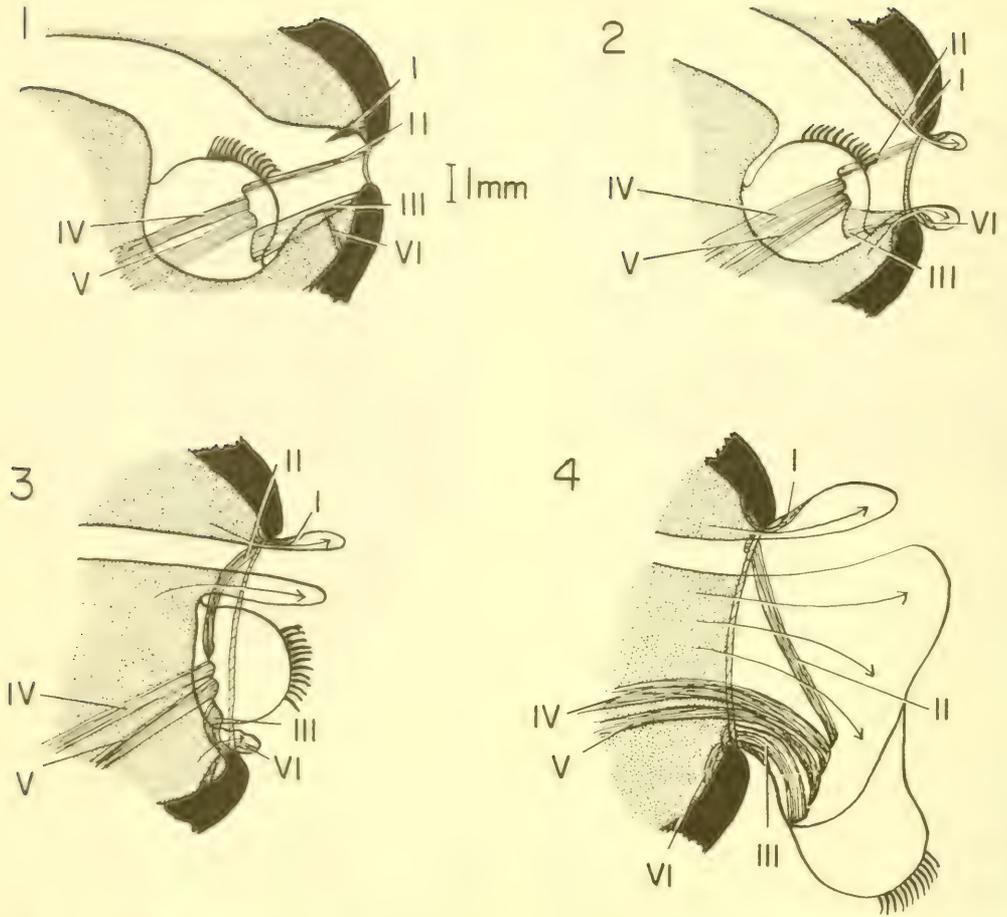


FIG. 23. *Philine*. Diagrammatic representation of 4 stages in the protrusion of the proboscis seen from the side by transparency. I-VI, proboscis retractors I-VI.

ings, and contraction of pair VI pulls down the floor of the oral tube. This results in enormous widening of the lumen. The oral tube simultaneously shortens due to contraction of its longitudinal intrinsic muscles and the ventral tensor muscles. Synchronously proboscis retractors II and III contract, pulling the buccal mass forward so that the radular teeth appear at the mouth (Fig. 23, stages 1-3). In these circumstances they act as protractors but cannot pull the buccal mass further than the region of their origins.

Anterior haemocoelic pressure builds up and besides flowing into the bulging oral tube, protruded inside out through

the mouth, blood begins to press on the superficial buccal musculature surrounding the posterior part of the buccal mass. The buccal mass is pushed out through the mouth dragging after it the buccal wall and the oesophagus. The value of the 3 pairs of buccal tensors, 1, 2 and 4, in holding the walls of the buccal region firmly together and close to the buccal mass, is now of great account. Meanwhile, blood still enters the proboscis, forced in this direction by the approach of the large gizzard to the anterior part of the body (Fig. 11, gi). The dorsal wall of the buccal cavity and the oesophagus are also forced inside out

to accommodate the fluid, and join the oral tube in forming the dorsal part of the proboscis (Figs. 10, 21, dp, Fig. 23, stages 3-4).

Thus during the final phase of protrusion the proboscis appears in 3 stages. Firstly, the oral tube widens and is brought forward, beginning to bulge inside out and to project through the mouth, surrounded by the greatly stretched outer lips (Fig. 23, stage 2). Secondly, the buccal mass is pulled forward and its tip appears encircled by the bulging oral tube (stage 3). The third and last stage involves the appearance of the oesophagus above the buccal mass, also surrounded by the oral tube. Eventually the oral tube and extreme anterior part of the oesophagus together form the blood-filled dorsal part of the proboscis, whilst the buccal mass is fully protruded as the ventral part (stage 4). The proboscis entrance is closed when the proboscis is turgid. All 3 stages depend on correlated changes in the degree of contraction of the intrinsic musculature of the gut walls, proboscis retractors and on the continued relaxation of the columellar muscle. The process of protrusion is helped and completed by increased blood pressure, itself due firstly to increase in the amount of blood in the anterolateral sinuses, secondly to reduction in their size by contraction of the extrinsic muscles I, VI, II and III, of the inner muscle layer of the body wall and by pressure from the forward-moving gut. As completion occurs all the proboscis retractors are relaxed, the buccal mass turns over the anterior transverse muscle and is held firmly by the ventral tensor muscles (see p 299).

As the buccal region passes out, the buccal ganglia and nerves go with it. This manoeuvre is facilitated since the cerebrobuccal connective and its accompanying nerve p9 are rooted in the adjacent anterior inner faces of their respective ganglia. No nerve roots obstruct the passage of the proboscis, whilst cerebral and pedal commissures are long and allow a maximum of space. The

oesophageal nerves can follow the stretched contours of the oesophageal wall due to their initial meandering course.

The proboscis is withdrawn in an order not the reverse of the stages of protrusion. The buccal mass goes in first, followed by the oral tube and lastly the oesophagus. Withdrawal is preceded by a fall in blood pressure within the proboscis. The dorsal part collapses (Fig. 22, oe) and the buccal mass begins to be pulled in. The 6 pairs of proboscis retractors are responsible (directly or indirectly according to the position of their insertions) for drawing the buccal mass back through the mouth. The oral tube is pulled by the circumoral muscles and by contraction of its longitudinal intrinsic musculature, the ventral tensor muscles and proboscis retractors I and VI. The oesophagus does not appear to be easily withdrawn and this is eventually accomplished by the dragging effect of the retreating buccal mass and oral tube coupled with contraction of its own intrinsic musculature.

It is of interest to note that the haemal sacs of *Philine* lie between the 2 points of possible constriction of the anterior aorta. Their function is a matter for speculation. They probably do not help in the blood movements causing proboscis protrusion but may help to prevent re-protrusion as follows. Blood is likely to re-enter the anterior sinuses as well as the general haemocoel, when the proboscis is withdrawn. This could result in back-flow along the anterior aorta. When the animal is fully contracted - a state usually accompanying full retraction of the proboscis - both physiological valves controlling the anterior aorta are closed. This will prevent blood passing back into the heart or going forward again into the anterior sinuses. To accommodate large quantities of blood here the anterior aorta is large and moreover, haemal sacs are attached to it and will hold a further volume of fluid. This condition may continue until the buccal region is completely retracted and extreme contraction of the body ceases.

SECTION II  
OTHER OPISTHOBRANCHS

The feeding apparatus has been briefly investigated in some other opisthobranchs, chosen for possible similarity to *Philine* in the method of obtaining food, and all burrowing forms of carnivorous habit. They include *Scaphander lignarius* (Linn.), *Acteon tornatilis* (Linn.), *Cylichna cylindracea* (Pennant), *Retusa obtusa* (Montagu), *R. umbilicata* (Montagu) and *R. truncatula* (Bruguière).

1. COLLECTION AND FOOD

*Scaphander lignarius* has been frequently dredged in small numbers with *Philine*, especially from deeper waters. Specimens were examined from the south and west coast of Great Britain: Plymouth, Millport and Anglesey. The food included bivalves (Plymouth, Millport), young sea urchins, Foraminifera, small tectibranchs (Plymouth) and *Pectinaria* (Anglesey). Debris in the crop and gizzard contained sand grains, diatoms and the hard parts of prey, such as radular teeth, pieces of shell. Previous authors described *Scaphander* as taking *Turritella* shells containing the gephyrean *Phascolosoma* (Vayssière, 1880; Guiart, 1901), gephyreans, molluscs and worms (Pruvot-Fol, 1954), whilst Fretter (1939) found *Turritella* in the gizzard, but did not indicate whether or not the shells contained *Phascolosoma*. This range of food is not unlike that described for *Philine*. *Scaphander* was not observed in the process of feeding, but is able to take relatively large prey. A specimen from Plymouth, 5 cm long, had taken a young bivalve (*Venus* sp.) which measured 1.1 cm length x 0.9 cm depth. Crop and gizzard measured 1.6 cm length x 1.8 cm depth, and the buccal region was 1 cm length x 0.6 cm depth. A similar specimen from Millport contained two *Corbula gibba*, each 1.2 x 1.0 cm, packed into the crop. Animals from Anglesey had taken enough *Pectinaria* to fill both crop and gizzard.

Spawning specimens of *Acteon tornatilis* were dug from Rhossili beach in the Gower peninsula, Bristol canal, South Wales. Many were dissected in order to determine their food, of which no previous account has been given. A number had taken *Owenia fusiformis*, but none was observed in the process of feeding.

*Cylichna cylindracea* and the 3 species of *Retusa* mentioned were dredged in the Øresund from Helsingør, Denmark. Preserved specimens of *Cylichna cylindracea* were obtained from Cullercoats, Northumberland. In one *Cylichna*, from the Øresund, a foraminiferan was found in the crop, but in other cases the food was not identifiable. Lemche (1956) suggested that *Cylichna* feeds on rhizopods. All dredge samples with large numbers of *Retusa* spp. came from stations in the Øresund where the bottom deposits were of fine sand at 14-20 m depth. Other specimens of *R. obtusa* were sent from Barry Island harbour, near Cardiff (Bristol Canal). These were collected from fine silty mud and their general diet has not been determined, although one had a foraminiferan in the crop. In the Øresund specimens the crop and gizzard were frequently filled with Foraminifera and sand grains, whilst in *R. obtusa* and *R. truncatula* rissoids had also been taken. In the crop of *R. truncatula*, the largest of the 3 species, an occasional small bivalve was also found. All survived well in a small aquarium with a good supply of Foraminifera. Bacescu and Caraion (1956) described 2 species of *Retusa* from the Black Sea as feeding almost exclusively on foraminiferans, whilst Jeffreys (1865) suggested that *R. alba* feeds on *Hydrobia ulvae*.

*R. truncatula* was observed feeding, during which process the mouth was widely open. This caused expansion of the lateral groove between the cephalic region and the foot (Fig. 24). The animal sucked in Foraminifera and sand grains from a small pile of debris in front of it. Feeding did not appear to be selective, but the numbers of foraminiferans present in the aquarium was very high so that

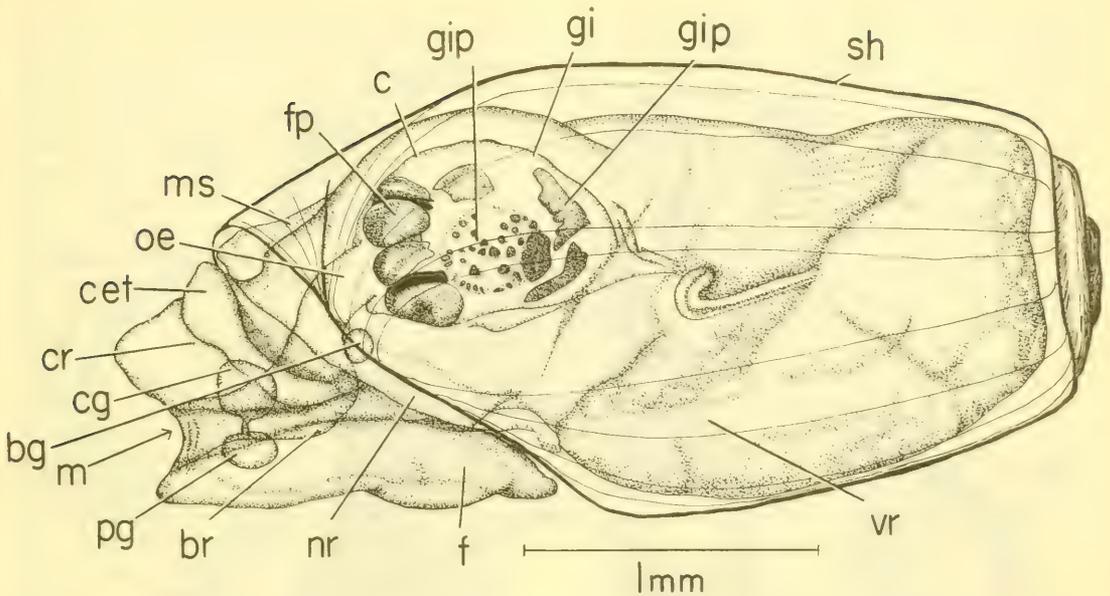


FIG. 24. *Retusa*. Left side view of whole animal seen by transparency through the shell. The mouth is stretched widely open to suck in food, whilst the entrance to the crop is constricted. The anterior part of the gut is shown by transparency. The crop is distended, containing part of a foraminiferan; the 3 gizzard plates can be seen, one in inner surface view, the other 2 (to the right of the diagram) are up-ended towards the left side. The cerebral, pedal and buccal ganglia of the left side are shown. bg, buccal ganglion; br, buccal region; c, crop; cet, cephalic tentacle; cg, cerebral ganglion; cr, cephalic region; f, foot; fp, food particle; gi, gizzard; gip, gizzard plate; m, mouth; ms, mantle skirt; nr, neck region; oe, oesophagus; pg, pedal ganglion; sh, shell; vr, visceral region.

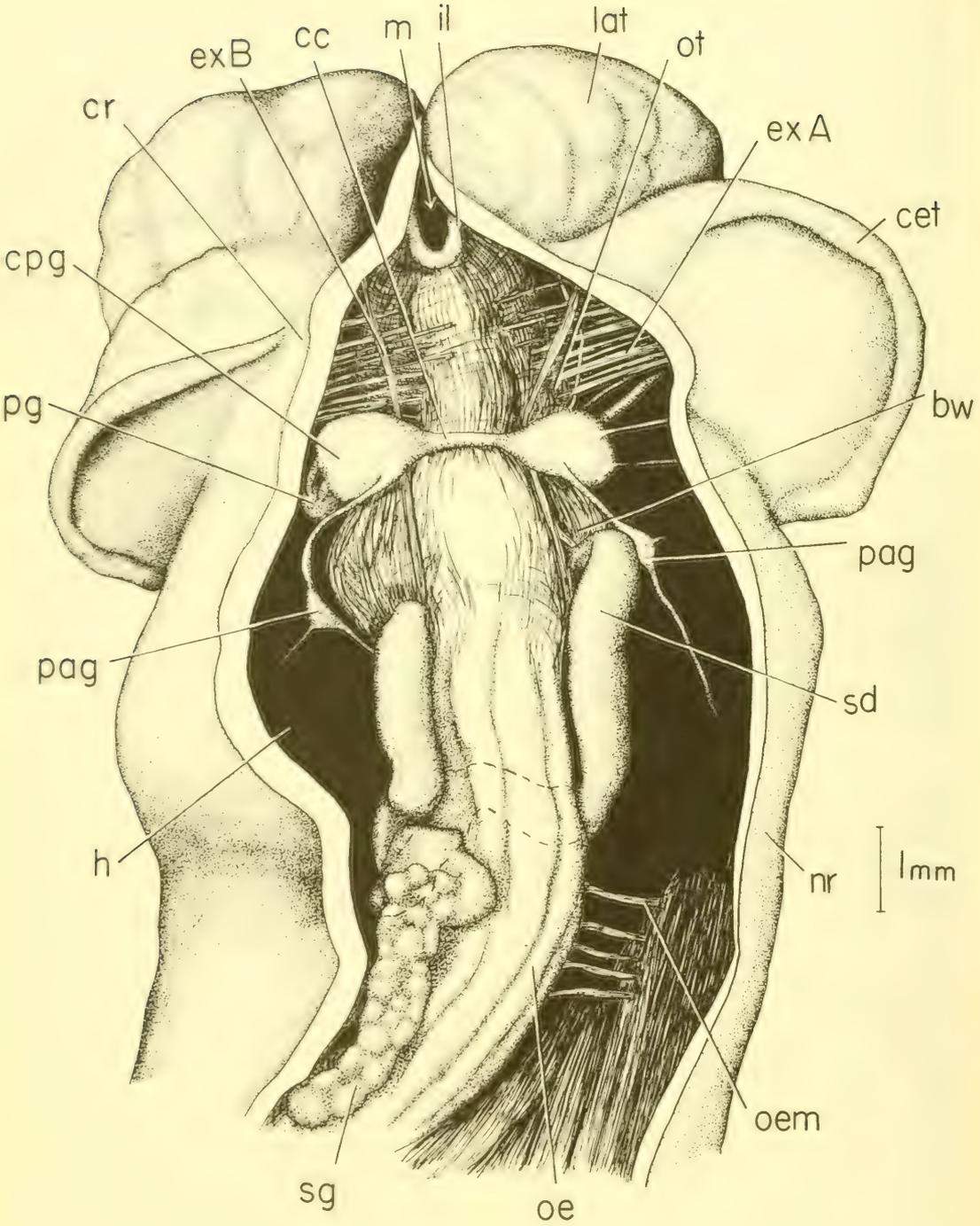
any area presented an adequate proportion of food to sand grains. During feeding, the cilia on the cephalic region stopped moving; they normally beat in an antero-posterior direction sending small particles up over the dorsal side. Such ciliary currents have been observed in *Philine*, *Scaphander* and *Acteon*, and *Cylichna* (Lemche, 1956). Their action helps in burrowing, but would be disadvantageous to *Retusa* whilst feeding, since its food particles are small enough to be removed in a dorsal direction were the cephalic cilia in action.

## 2. FORM OF THE BUCCAL REGION AND OESOPHAGUS

In *Philine*, the anterior region of the gut comprises the buccal region leading to a much modified oesophagus, able to

dilate into a large crop, behind which is an elaborate crushing gizzard with 3 large plates (Fig. 11, gip) bound together with muscle (gim). The whole lies within the spacious anterior part of the haemocoel. In *Scaphander*, *Cylichna* (Fig. 30) and *Retusa* (Fig. 31) this general pattern is repeated, whereas in *Acteon* (Fig. 25) the oesophagus is a simple tube conducting food to the stomach (Fretter & Graham, 1954). Another difference in *Acteon* is that the surrounding haemocoel is not spacious and the gut is closely attached to the body wall by small muscles.

In *Scaphander* the form of the buccal region and its associated musculature is essentially similar to that of *Philine*. The 5 pairs of extrinsic muscles correspond in position and relative length to proboscis retractors I-VI of *Philine*, with IV and V (p 289) represented on each



side by a single large muscle bundle with a columellar origin (Fig. 20). The visceral loop passes dorsal to this bundle, whereas in *Philine* it runs between IV and V. The muscles corresponding to pair I are less wide but similarly run closely associated with a connective tissue sheet from the cerebral commissure to the outer lip. The buccal mass is compact and slightly different from that of *Philine* since it projects anteriorly above the floor of the oral tube so that a sublingual pocket is present; the radular sac is shorter. The keel-shaped anterior bulge of the buccal mass accommodates a larger sinus below the radular membrane (Fig. 20, bs) than is possible in *Philine*. The radular teeth are like those of *Philine* but are stronger and more heavily chitinised. There are about 25 rows of functional teeth, each with only a single pair of laterals. Each side of the radular membrane seems to be capable of great movement along the longitudinal axis of the buccal mass; thus, for instance, the left side may be placed in advance of the right, so that several teeth become anterior to their right counterparts. Opening into the buccal cavity above the buccal mass are the short, cylindrical salivary glands (Fig. 20, sg); they are otherwise unattached to the gut (a condition described by Vayssière (1880) as confined to *Philine* and *Scaphander*). The large gizzard of *Scaphander* (p 326) has already been adequately described by Vayssière (1880), Lacaze-Duthiers (1898), Guiart (1901) and Fretter (1939).

In *Acteon* the buccal region is tightly enclosed in the haemocoel, and its musculature differs from that of *Philine* (Figs. 25, 26). The extrinsic muscles include none which could retract it, but 2 small pairs (Fig. 26, ex B, ex C) in a

position corresponding to retractors II and III of *Philine* may act as protractors. A large number of muscles (Figs. 25, 26, 27, ex A) fan out laterally and a few dorsally from the oral tube to origins on the adjacent body wall: these would be capable of expanding the lumen considerably. From the ventral wall of the oral tube a pair of muscles (Figs. 26, 27, ex D) runs down almost vertically to adjacent origins in the anterior part of the foot; they may correspond to pair VI of *Philine*.

The outer intrinsic muscle coat surrounding the buccal region (Fig. 26) is relatively weaker than that in *Philine*. There is a muscle running transversely below the buccal commissure. This muscle is continuous with the protractors (extrinsic muscles B) and corresponds with the transverse band linking pair II in *Philine*. A conspicuous median band of longitudinal fibres runs from below the transverse muscle to join the ventral longitudinal fibres of the oral tube. A similar tract in *Cylichma* is shown in Fig. 28. The oral tube is relatively long and wide, and its intrinsic musculature recalls that of *Philine*. Lying below the above-mentioned longitudinal fibres (= ventral tensors of *Philine*) a large number of well marked muscles run transversely, corresponding to the ventral circular muscles of *Philine*. They continue up below the weak lateral longitudinal muscles, disappearing below the dorsal longitudinal ones. Posterior to the oral tube the buccal walls are laterally thickened (lt). A second protractor (extrinsic muscle C) leaves from the anterior limit of the thickening.

In the sagittal section (Fig. 27) the jaws (j) are shown. These lie approximately level with the extrinsic muscles

FIG. 25. *Acteon*. Anterior region opened by a mid-dorsal longitudinal cut to show the buccal region of the gut. The visceral loop on the right side, which normally crosses above the gut, has been displaced. bw, buccal wall; cc, cerebral commissure; cet, cephalic tentacle; cpg, cerebropleural ganglion; cr, cephalic region; ex A, B, extrinsic muscles A, B; h, haemocoel; il, inner lip; lat, labial tentacle; m, mouth; nr, neck region; oe, oesophagus; oem, oesophageal muscles; ot, oral tube; pag, pallial ganglion; pg, pedal ganglion; sd, salivary duct; sg, salivary gland.

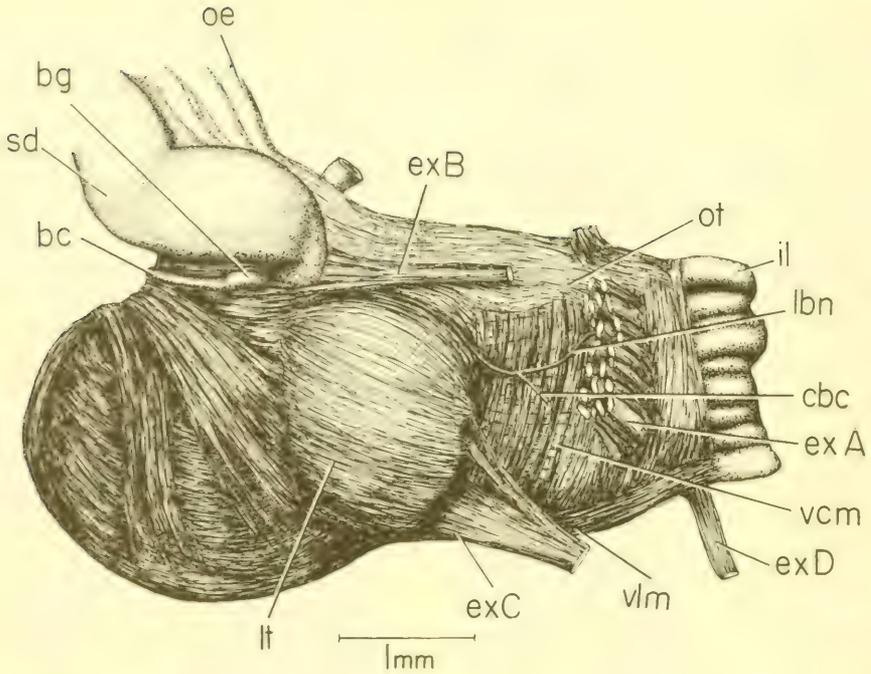


FIG. 26. *Acteon*. Lateral view of the buccal region removed from the body cavity. The extrinsic muscles are cut short. bc, buccal commissure; bg, buccal ganglion; cbc, cerebrobuccal connective; ex A-D, extrinsic muscles A-D; il, inner lip; lbn, lateral buccal nerve; lt, lateral thickening; oe, oesophagus; ot, oral tube; sd, salivary duct; vcm, ventral circular muscle; vlm, ventral longitudinal muscle.

A. Their structure has been described by Gabe and Prenant (1953) and by Fretter and Graham (1954) who have also discussed the radula. The buccal mass has a form quite unlike the firm cylindrical structure of *Philine* and *Scaphander*. In *Acteon* the radular membrane (rm) is similarly longitudinally grooved in the midline, but is much more extensive, spreading on each side up and over the edge of the flattened lateral cushion representing the remainder of the buccal mass. Each cushion is semicircular in sagittal section and is attached to the buccal wall (bw) ventrally and laterally. Posteriorly it bears 2 vertical transverse grooves into which the radular membrane fits. They may represent the radular sac, but there is no caecum containing the developing teeth as in other opisthobranchs. The inner

surfaces of the radular membrane on the lateral cushions are closely apposed and covered with many rows of minute teeth (rt). In each row the teeth are similar and very numerous. The lateral cushions are composed of connective tissue with deposits of calcium salts and glycogen (Gabe and Prenant, 1953). The salivary ducts (esd) open dorsal to the cushions in a posterolateral position. They and the salivary glands (sd, sg) are long and bulky, lying folded adjacent to the oesophagus (oe), to which they are superficially attached. Many fine muscle strands attach the oesophagus to the body wall (Fig. 25, oem).

The buccal region of *Cylichna* has been extensively investigated by Lemche (1956) and his account has been checked in several respects, although the full details of the intrinsic musculature have

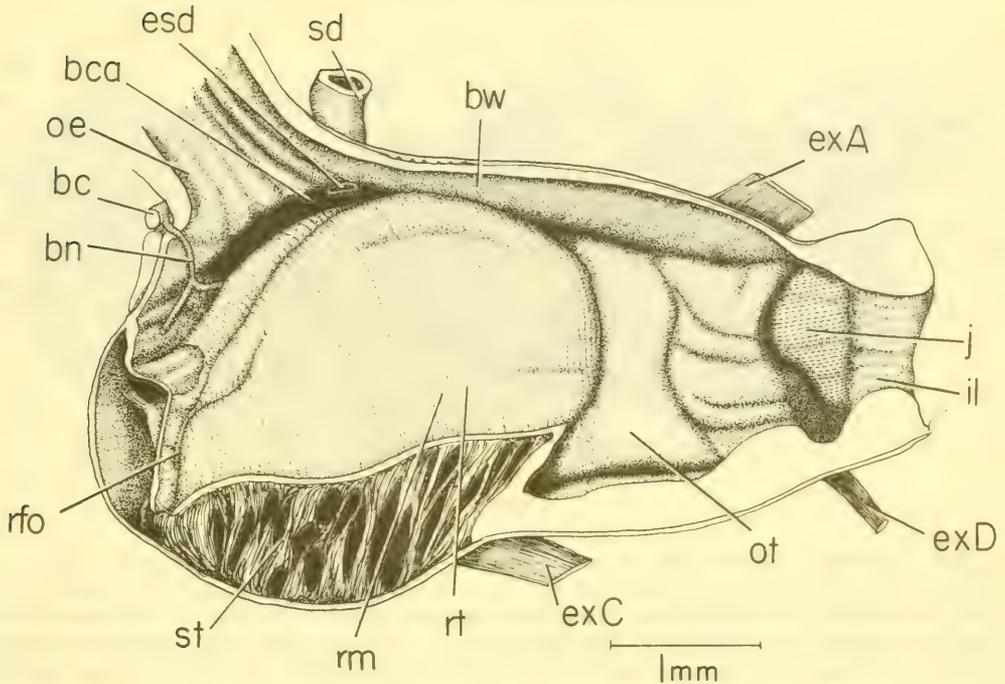


FIG. 27. *Acteon*. Left sagittal half of the buccal region. bc, buccal commissure; bca, buccal cavity; bn, buccal nerve; bw, buccal wall; esd, entry of salivary duct; ex A,C,D, extrinsic muscles A, C, D; il, inner lip; j, jaw; oe, oesophagus; ot, oral tube; rfo, radular fold; rm, radular membrane; rt, radular tooth; sd, salivary duct; st, supporting tissue.

not been studied. This region is the most elongated amongst the opisthobranchs surveyed here. It is divided into 2 parts visibly separable by the differing amount of intrinsic musculature thickening their walls (Figs. 28, 30). Between the 2 is the anterior constriction (ac) described by Lemche (1956). Posterior to this constriction the walls are muscular and are comparable with those of the buccal region of *Philine* (Fig. 5) or *Acteon* (Fig. 26). Anterior to the constriction the walls of the oral tube are much folded longitudinally and are glandular. It is this part which gives added length to the buccal region. Around the anterior constriction lies the nerve ring (Fig. 30).

Several pairs of extrinsic muscles attach the buccal part of the gut to the body wall. Two small pairs (Figs. 28,

30, om), undescribed by Lemche (1956), leave its extreme anterior end and run to the outer lip; these are comparable with the circumoral muscles of *Philine*. Two larger pairs insert on the muscular wall of the gut just posterior to the anterior constriction. One pair is laterodorsal (Figs. 28, 30, adp) with a fairly wide insertion. The muscles are long, flattened and run forward under the cerebral commissure (Fig. 30, cc) afterwards turning dorsally and outwards to origins in the cephalic region of the body wall. The second pair inserts on the ventral longitudinal intrinsic muscles (Fig. 28, avp, vlm) and runs forward through the nerve ring to pedal origins. These 2 pairs may protract the muscular part of the buccal region and might represent either pairs I and VI (from the position of the insertions) or pairs II and III (functionally) of *Philine*. They

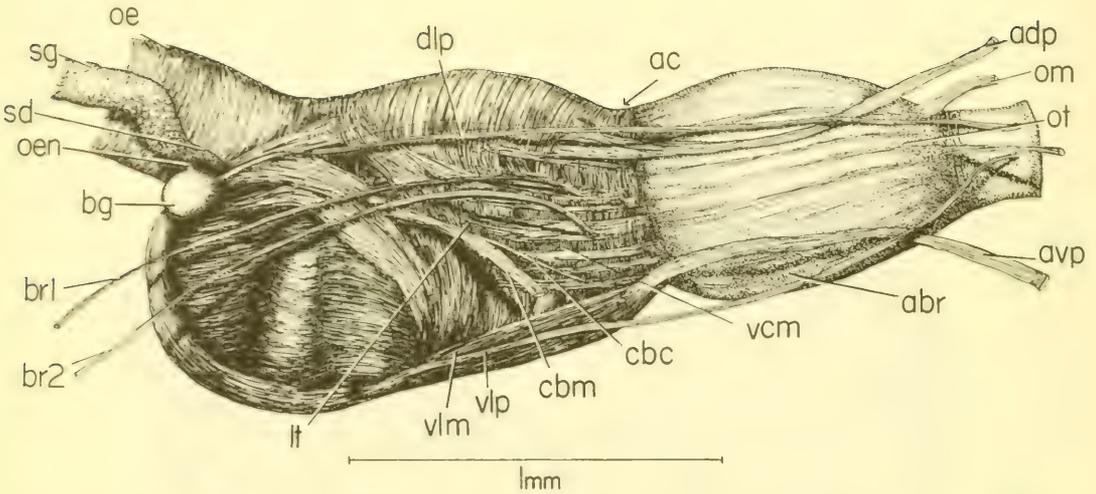


FIG. 28. *Cylichna*. Lateral view of the buccal region removed from the body cavity. abr, anterior buccal region; ac, anterior constriction; adp, anterior dorsal protractor; avp, anterior ventral protractor; bg, buccal ganglion; br, 1, 2, buccal retractors 1, 2; cbc, cerebrobuccal connective; cbm, cerebrobuccal muscle; dlp, dorsolateral protractor; lt, lateral thickening; oe, oesophagus; oen, oesophageal nerve; om, oral muscle; ot, oral tube; sd, salivary duct; sg, salivary gland; vcm, ventral circular muscle; vlm, ventral longitudinal muscle; vlp, ventrolateral protractor.

are called dorsal and ventral protractors of the pharynx by Lemche. As he described, their insertions are level with the jaws. A further 2 pairs of dorsal and ventral protractor muscles are present: Lemche's protractor pharyngis dorsolateralis and protractor pharyngis ventrolateralis. Their insertions correspond to those of pairs II and III in *Philina*, but they originate in the extreme anterior end of the oral tube (Fig. 28, dlp, vlp, ot), not from the outer lip. Each pair is elongated and passes through the nerve ring outside the protractors mentioned above (Fig. 30). These muscles could protract the buccal mass by shortening the buccal region. Lemche mentioned the possible presence of a retractor muscle leaving from near the place where the cerebrobuccal connective leaves the buccal wall. His statement may refer to one of two undescribed pairs of extremely minute retractor muscles (Figs. 28, 30, br 1, br 2) which leave from a point approx-

imately between the insertions of the more anterior dorsal and ventral protractors (level with the jaws). Each pair is very long and runs back to the foot (Fig. 30) probably with a columellar origin. These retractors may correspond to pairs IV and V of *Philina*. However, they are so small that they would hardly be adequate to pull the buccal region back within the body cavity. A further pair of extrinsic buccal muscles (cbm) is that leaving the lateral columellar muscle on each side to run to the buccal wall adjacent to the cerebrobuccal connective (cbc), which, in fact, runs within the muscle for at least part of its length. This muscle was represented by a few fibres only from the base of retractor V in *Philina* (p 289), but is well marked in *Cylichna*. Lemche described it as the musculus cerebrobuccalis.

The positions of the muscle fibres in the outer muscle coat of the posterior half of the buccal region (Fig. 28) have not been particularly studied in relation

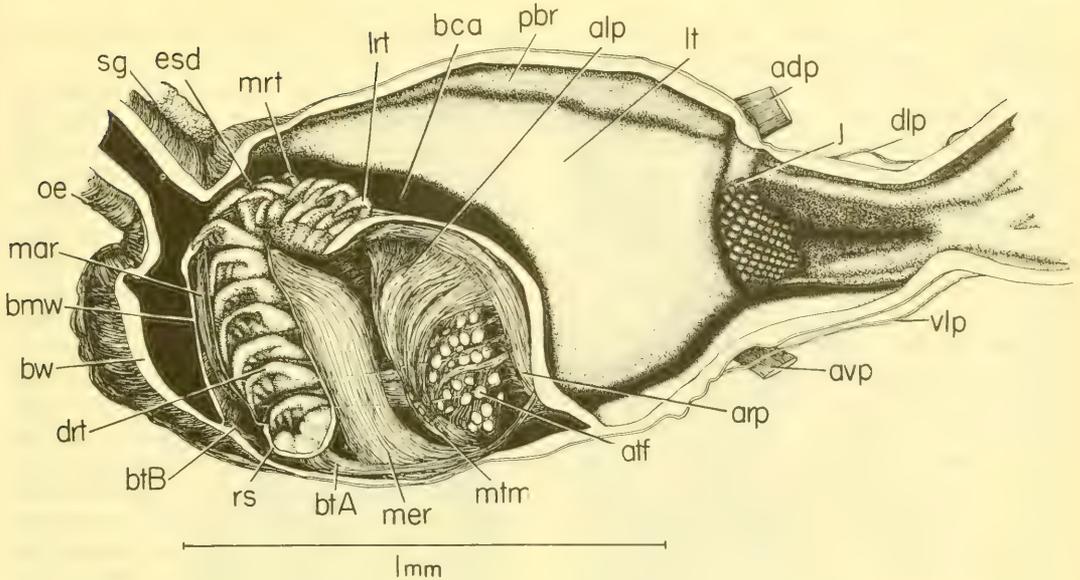


FIG. 29. *Cylichna*. Left sagittal half of the buccal region, with the oral tube cut short. (In parentheses are Lemche's (1956) abbreviations for the musculature.) adp, anterior dorsal protractor (= pr. ph. d.); alp, anterolateral radular protractor (=pro. ra.); arp, anterior radular protractor (=m. ro. d-v.); atf, anterior transverse fibres; avp, anterior ventral protractor (=pr. ph. v.); bca, buccal cavity; bmw, buccal mass wall; bt A, B, buccal tensors A (=m. pp. lo.), B; bw, buccal wall; dlp, dorsolateral protractor (=pr. ph. d-l.); drt, developing radular tooth; esd, entry of salivary duct; j, jaw; lrt, lateral radular tooth; lt, lateral thickening; mar, marginal retractor (=re. r. ma.); mer, median retractor (=re. r. me.); mrt, marginal radular tooth; mtr, median transverse muscle (=m. ro. tr.); oe, oesophagus; pbr, posterior part of buccal region; rs, radular sac; sg, salivary gland; vlp, ventrolateral protractor (=pr. ph. v-l.).

to Lemche's account (1956), but of those mentioned by him, the following are certainly present: the longitudinal ventral muscle (vlm, corresponding to the ventral tensors of *Philine*), the circular muscles concentrated around the anterior constriction, the U-shaped strong dorsoventral muscles (vcm, as in *Philine*), the transverse dorsal muscles (which are very obvious on dissection), the longitudinal dorsal muscles (consisting of very few fibres indeed). The 'buccal muscle' of Lemche is well marked and corresponds to the posterior band linking retractor pair II in *Philine*. The relationship in *Cylichna* of the buccal muscle to the dorsolateral protractors is also very similar. Very obvious were the radial and 'internal dorsoventral' muscles, which cause thickening of the lateral

buccal walls immediately anterior to the buccal mass. These are also represented in *Philine* but are more scattered and irregular, with much spongy connective tissue between them. Some strongly marked intrinsic muscle tracts shown in Fig. 28 do not seem to agree entirely with Lemche's account but probably represent his musculus masticatorius and m. pharyngis posterior.

The form of the buccal mass and its more immediately obvious intrinsic muscles are shown in sagittal section (Fig. 29). Its shape is similar to that of *Scaphander* in that it bulges forward anterior to the rows of functional radular teeth. Each row in *Cylichna* consists of several teeth (rt). The laterals are strong and hook-shaped with wide bases, as in *Philine* and *Scaphander* but

marginals and median tooth are also present. The radular formula is 3-1-1-1-3 or, occasionally (Lemche, 1956), 4 marginals may be present. The radular sac (rs) is short and vertical, lying posteriorly in the buccal mass and supported anteriorly by a large bundle of muscle fibres (mer). These insert on the radular sac and membrane and represent the large radular occlusor muscles of *Philine*. Lemche called the muscle the medial radular retractor. He correctly mentioned that the nuclei of the fibres are all placed together, near the base of the muscle. This is also true of the radular occlusors of *Philine*. The origin of the medial retractors is described as being in the posterior constriction. This lies immediately posterior to the thickened lateral buccal walls mentioned above, is by no means as obvious as the anterior constriction and hardly deserves emphasis.

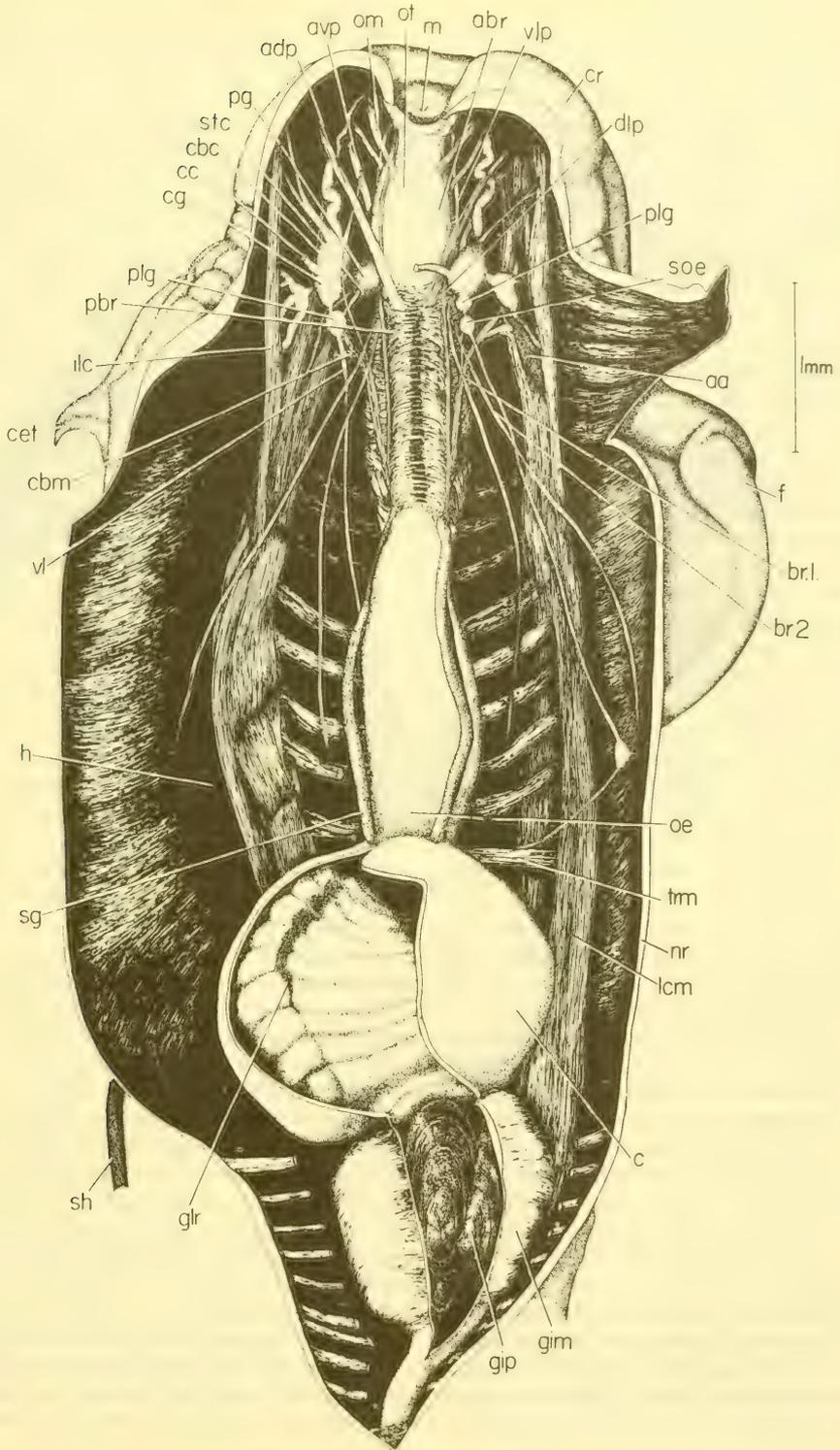
Two other muscles are described by Lemche (1956) as inserting on the radular sac. Of these, one is the marginal radular retractor originating outside and above the medial retractors and inserting on the posterior surface of the radular sac (Fig. 29, mar). It probably also inserts on the part of the radular membrane bearing functional teeth. It is difficult to compare this muscle with any found in *Philine*. The other muscle described by Lemche is comparable to buccal tensors 3 of *Philine* (bt A). Another small muscle (bt B), not mentioned by him, inserts in the tip of the radular sac and passes back to the posterior junction between buccal wall and

buccal mass wall; it corresponds to buccal tensors 2 in *Philine*.

Anterior to the radular occlusors or medial radular retractors of *Cylichna* is the large radular protractor muscle (Fig. 29, rpr) described by Lemche (1956). It originates between the medial retractors and bends forward to a wide insertion on the anterior walls of the buccal mass. As Lemche mentioned, the most anterior fibres with the most ventral insertions are strongly curved. He did not, however, discuss the large number of transverse fibres (atf) which cross the buccal mass from side to side below and between the most ventral fibres of the radular protractor. They correspond in approximate position to the anterior transverse muscle of *Philine*. The concentrated supporting tissues 1 and 2, present in the buccal mass of *Philine* are not represented in *Cylichna*. The only transverse fibres described by Lemche are those close to the most posterior part of the radular protractor which he calls m. rotellae transversus. The fibres appear in Fig. 29 (mtm). The remaining large dorsoventral muscle (arp) described by Lemche corresponds in general position and function to the outer oblique muscles of *Philine*. The circular intrinsic muscles of the buccal mass wall are present as in *Philine*.

The large jaws (j) are another feature of the buccal region obvious in a sagittal section (Fig. 29). Their anterior edges are slightly serrated while their posterior edges curve out into the buccal wall. The inner surfaces are covered with even rows of pointed tubercles, each with a square

FIG. 30. *Cylichna*. Anterior region opened by a mid-dorsal longitudinal cut. The crop and gizzard have been cut open with a laterodorsal longitudinal incision on the left side. The cerebral commissure has been cut and the ganglia of the left side pulled outwards by means of the left cut end of this commissure. aa, anterior aorta; abr, anterior part of buccal region; adp, anterior dorsal protractor; avp, anterior ventral protractor; br, 1, 2, buccal retractors 1, 2; c, crop; cbc, cerebrobuccal connective; cbm, cerebrobuccal muscle; cc, cerebral commissure; cet, cephalic tentacle; cg, cerebral ganglion; cr, cephalic region; dlp, dorsolateral protractor; f, foot; gim, gizzard muscle; gip, gizzard plate; glr, glandular ridge; h, haemocoel; ilc, inner branch of lateral columellar muscle; lcm, lateral columellar muscle; m, mouth; nr, neck region; oe, oesophagus; om, oral muscle; ot, oral tube; pbr, posterior part of buccal region; pg, pedal ganglion; plg, pleural ganglion; sg, salivary gland; sh, shell; soe, supra-oesophageal ganglion; stc, statocyst; trm, transverse muscle; vl, visceral loop; vlp, ventrolateral protractor.



base.

In Fig. 30 the oesophagus is shown with crop and gizzard cut open laterodorsally on the left side. The long salivary glands (sg) can be seen with their posterior tips superficially attached to the extreme anterior end of the crop (c). The interior of the walls of the crop is specialized and its histology was given by Lemche (1956). Dorsally it is smooth and thin-walled, whilst the inner surface of the ventral walls is thrown into transverse folds ending on the left side in a ridge of pigmented glandular cells. This ridge ends between two of the gizzard plates (gip) at the entrance to the gizzard. The gizzard muscle (gim) is well marked and forms a continuous encircling sheet of fibres, unlike the condition in *Philine* (Fig. 11) where the muscles lie in blocks between the plates, as described by Förster (1934).

Lemche (1948) described the genus *Retusa* as being without a radula. In all species examined this has been so, there being a complete absence of jaws, radula and associated musculature. The walls of the buccal region are unthickened and not strongly muscular, unlike the other genera studied. There is no obvious division between oral tube and buccal cavity. The walls are longitudinally folded, and the nerve ring, with its large ganglia (Fig. 31) surrounds the oral region. The oesophagus leaves posterodorsally and on its junction with the posterior buccal wall lie the buccal ganglia linked by a short commissure, as in *Cylichna*. The cerebro-buccal connective leaves the cerebral ganglion on its inner anteroventral surface, as in *Cylichna* and *Philine*. A nerve runs from this connective to the lateral walls of the buccal region as in these animals. The extrinsic muscles of the region are usually twisted in such a way that the pairs appear asymmetrical. Many small circumoral muscles are present amongst which 2 small pairs of muscles (1 dorsal, 1 ventral) pass forward to their origins. The insertions of these 2 pairs lie just posterior to the nerve ring, through which they pass. These correspond in position to pairs I and VI of

*Philine* and to the dorsal and ventral protractors (Fig. 28, adp, avp) running forward from the region of the anterior constriction in *Cylichna*. A large group of muscle fibres (Fig. 31, lbd) leaves the anterolateral walls to reach insertions amongst the fibres of the lateral part of the columellar muscle. These lateral groups could, on contraction, considerably dilate the anterior part of the buccal region in feeding (p 326). In a position to retract the buccal region are a pair of long flat muscles (brm) inserting posterolaterally so that fibres enter both above and below the cerebrobuccal connective, most being below it. These originate from the columellar muscle and may be traced back to its more posterior lateral fibres. A pair of minute salivary glands is present, discharging just anterior to the buccal ganglia.

The long oesophagus dilates into a large crop (Figs. 24, 31, c) the entrance to which is surrounded by a sphincter muscle. The crop is thin-walled and becomes considerably folded when empty. It may also push back between the gizzard plates (gip). These are 3 in number as in *Philine*, *Scaphander* and *Cylichna*. The gizzard is more open anteriorly and the plates are not smooth as in the other genera. Posteriorly each plate has a solid pyramidal projection into the lumen with several rounded tubercles anteriorly. The position of the gizzard in the body varies according to the degree of contraction of the specimen. Externally *Retusa* (Fig. 24), like *Acteon* and *Cylichna*, is divided into an obvious head (cr), neck region (nr) and visceral part (vr). The neck and part of the head are often drawn back under the mantle skirt (Fig. 24) or even further, when the whole animal disappears into its shell. The foot is relatively small. The gizzard may be seen by transparency, and in a relaxed animal lies just posterior to the neck region. It may, however, be brought forward to the anterior part of the neck, especially if the animal is slightly contracted, in which case the crop lies within the head. *R. obtusa* has been seen extruding a rissoid through the mouth

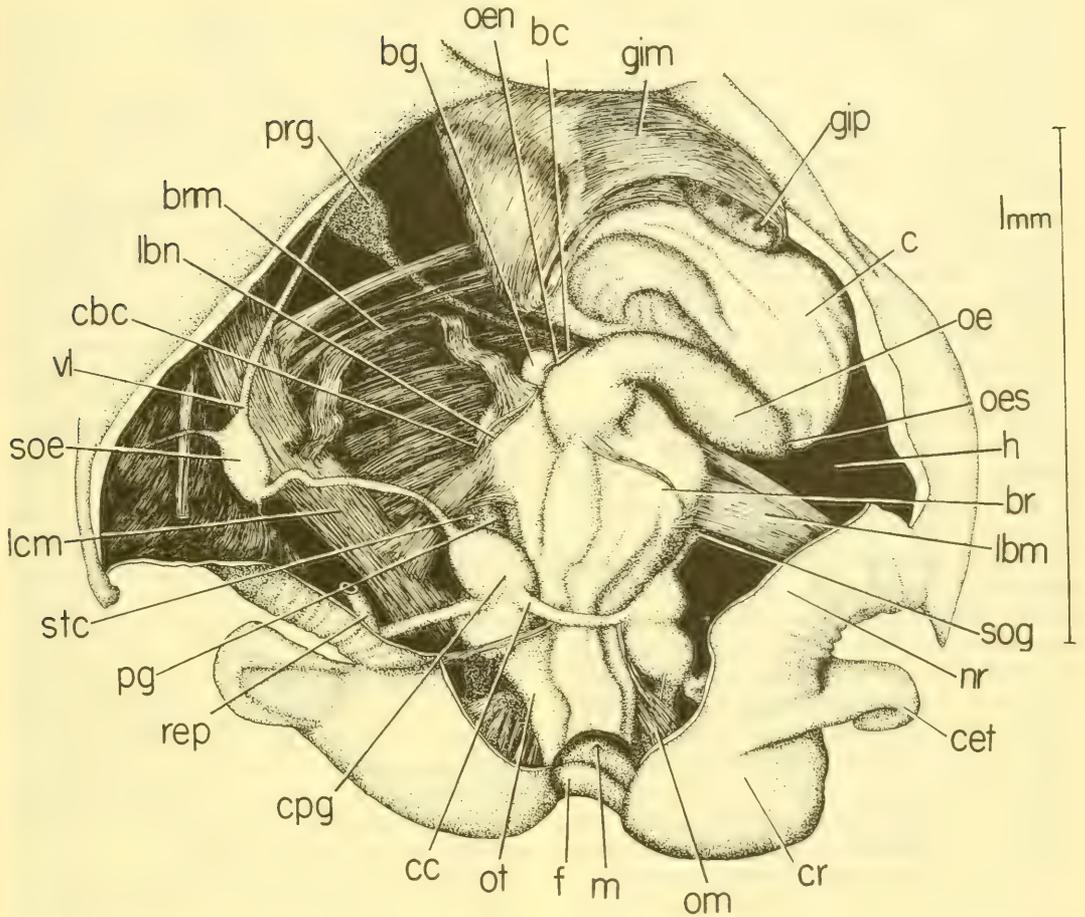


FIG. 31. *Retusa*. Anterior region opened by a mid-dorsal longitudinal cut. The major part of the reproductive system has been removed. bc, buccal commissure; bg, buccal ganglion; br, buccal region; brm, buccal retractor muscle; c, crop; cbc, cerebrobuccal connective; cc, cerebral commissure; cet, cephalic tentacle; cpg, cerebropleurial ganglion; cr, cephalic region; f, foot; gim, gizzard muscle; gip, gizzard plate; h, haemocoel; lbn, lateral buccal nerve; lcm, lateral part of columellar muscle; m, mouth; nr, neck region; oe, oesophagus; oen, oesophageal nerve; oes, oesophageal sphincter; om, oral muscle; ot, oral tube; prg, parietal ganglion; pg, pedal ganglion; rep, reproductive system; soe, supra-oesophageal ganglion; sog, sub-oesophageal ganglion; stc, statocyst; vl, visceral loop.

after bringing the crop well forward. It is possible that the crop may roll inside out to extrude material. Lemche (1956) described *Retusa* as expelling food from its crop when it withdraws into its shell, but this does not always occur even when the crop is fairly full.

#### DISCUSSION

An unspecialized body plan is regarded as primitive, and its evolutionary possibilities are wide. More advanced animals may elaborate and emphasize one or another of these, and it is of interest to

study the varied exploitation of a particular system. Although opisthobranchs are generally believed to have originated from a prosobranch stock, no agreement has been reached concerning the probable evolutionary route by which they arose. A study of the gut in both groups may throw light on the problem. However, deductions from such a comparison should be judged with caution, not only because such a study covers only a few of the relevant factors, but also because the gut is a system particularly susceptible to morphological modification due to changes in diet.

The feeding apparatus and mechanism have been investigated in *Philine*, and it is proposed to discuss these in relation to some other gastropods. *Monodonta* is generally agreed to possess the most primitive gastropodan feeding apparatus which has been studied (Nisbet, 1953). Nisbet described the buccal mass as "a complex and massive system of slings and guy-ropes"; its complexity arises from its ability to work in several different ways. The shape and functioning of the apparatus depend on the skeletal support offered by 2 pairs of cartilages, to which more than half the muscles attach. All the methods of feeding depend on to and fro movements of the cartilages and the pulling of the radular membrane over them. Variation in the topographical position of the buccal mass is decided by the balance of opposing actions in certain muscles, whilst others maintain the relative positions of component parts.

In *Philine*, the buccal apparatus is less complex, because specialized for a narrower range of feeding methods. The movements required are brought about by a less elaborate interplay of muscles and the shape is maintained by supporting tissues, which also provide a base for muscle attachment. The functioning of the radula does not depend on to and fro movements of the radular membrane relative to the supporting tissue. The degree of protraction and retraction of the buccal mass is much greater, and in the process blood pressure is of more

importance than in *Monodonta*. In both animals feeding takes place in 3 stages: (a) protraction, (b) use of the radula, (c) retraction. These involve movements of the anterior body wall, buccal mass, oesophagus and blood. In *Monodonta*, jaws also play a part.

Feeding occurs in both animals by interaction of muscles working in functional groups. In *Monodonta* the following stages are evident. The mouth opens and the buccal mass is protracted so that its tip protrudes. The radula is pulled ventrally past the angular tip of the buccal mass, which is pressed forward by the horns (anterior tips) of the anterior cartilages to form the bending plane. Here the membrane is tensed by lateral pull of muscles and by the pressure of blood below it. Tension promotes the opening of the teeth as they pass the bending plane. Subsequently the horns of the anterior cartilages rotate ventrally behind the membrane and the teeth close as they become dorsal to the bending plane. Closure and retreat by muscular pull continue and finally movement of the cartilage horns is reversed, just before the radula is withdrawn completely and the mouth closed. The jaws act as guides during closing of the radula.

In *Monodonta* only the extreme tip of the feeding apparatus protrudes from the mouth; thus many of the muscles causing the necessary movements are able to insert on the body wall. In *Philine*, where the buccal mass operates outside both buccal and body cavities, the possible areas for muscle attachment are less extensive. Only those muscles determining the position of the buccal mass relative to the body cavity attach it to the body wall. All musculature involved in moving the radula and maintaining the relative positions of components of the buccal mass is enclosed within the latter.

The radular sac and radular membrane of *Monodonta* are much longer than those of *Philine* and many muscles are attached to both. These arrangements are necessary for the mode of action of the radula.

In *Monodonta* the following 4 factors are essential for successful flattening of the membrane and use of the teeth: the bending plane, produced and moved by the cartilages; muscles able to protract and retract the radula; muscles pulling the membrane laterally; control of blood pressure below it. In *Philine*, unlike the majority of prosobranchs, only the last 2 are used. The method of using the radula by changing its position relative to the cartilages was regarded by Geddes (1879) as the only possible one. This view is disproved by *Philine* and a number of its relatives.

Although, in *Philine*, the use of cartilages as pivoting structures associated with a bending plane is superfluous, their other functions - as preservers of shape and bases for muscle attachment - are carried out by the supporting tissues. These are comparable with the cartilages of *Monodonta*. Nowikoff (1912) and Nisbet (1953) have described the histological structure of molluscan cartilages. Briefly, they consist of cells separated by an exiguous matrix and flattened in the peripheral regions to form a limiting sheath. The structure of the supporting tissues of *Philine* has been given (p 294). They are extensive and have no limiting sheath. All thickenings in the buccal region are similar, but those designated st 1 and st 2 (Fig. 8) are the most marked. The means by which the structure achieves its firmness has not been fully investigated. It appears to be partly due to cell inclusions (Gabe & Prenant, 1952) and to a turgidity which may arise from osmotic uptake. The possibility of inflow of blood is unlikely for several reasons: the tissue has not been found in a collapsed condition and does not alter in size or consistency when cut open; intercellular spaces are not extensive, nor has colour entered the supporting tissues on injecting the blood system, although it has sometimes penetrated the thickened buccal mass wall. The connective tissue cells are large and vacuolated, whilst firmness is also promoted by the fibres present. Inserting muscle fibres form a meshwork

between the cells and their interweaving helps to prevent them from pulling out when they contract. Other fibres are associated with the connective tissue cells. These may be an integral part of the cell walls, or extracellular and collagenous. Gabe & Prenant (1952) described the tissue as chondroid and like the radular cartilage of prosobranch gastropods. It seems also to resemble the 'vesiculo-muscular odontophoral cartilage' of the pulmonate *Lymnaea* described by Carriker (1946) and the paired cartilages of *Aplysia* described as 'spongy' by Eales (1921).

The supporting tissues of *Philine* are thus not so discrete as in *Monodonta*. The largest areas (st 1, st 2) are bound together by muscles as are the cartilages of *Monodonta*. The extensiveness of support in *Philine* is due to the extremely exposed position the buccal region reaches when the proboscis is protruded. The thickening of the buccal mass wall, forming a cushion around the radula, is particularly important in this respect. It provides a firm area through the outer layers of which the oblique muscles may act in unfolding the radular membrane, and on which the latter may rest. The flexible nature of the support in *Philine* may be an advantage when the buccal region passes through the mouth to the feeding position.

Increased blood pressure below the radular membrane is important in both *Monodonta* and *Philine* (p 319-320), but in the latter a further function of such pressure changes is to help in protrusion of the proboscis. Inflow of blood to this has been described (p 323-325) and is due to redistribution of the available fluid. This is brought about by muscular constriction of the anterior sinuses and use of the buccal region of the gut as a plunger whilst it is being protracted.

The histological structure of the oesophagus is such that it may change shape considerably and be readily swollen to form the dorsal part of the proboscis. Changes in distribution of blood within this part are due to muscular movement of its walls (p 321). A further

adaptation of the blood system is associated with completing withdrawal of the proboscis and involves the haemal sacs (p 315, 325).

The grabbing motion of the radula of *Philine* is superficially like the plucking action which may occur in *Monodonta* (Nisbet, 1953) when the snout is not firmly pressed to the substratum. This action involves a quick closing of the teeth when the radula is pulled back over the bending plane, which itself moves ventrally. Closing in *Philine* is not brought about in this way. Plucking, as in *Monodonta*, has been adopted by many gastropods, for instance *Physa* (Eigenbrodt, 1941; Nisbet, 1953), and has superseded other ways of using the radula. It is an emphasis of the rotatory phase of feeding. Some prosobranchs have adopted the forward pushing of the radula over the substratum: *Patella* (Ankel, 1938; Eigenbrodt, 1941; Nisbet, 1953), *Haliotis* (Crofts, 1929), whilst others use only the brushing motion also seen in *Monodonta*, e.g. *Littorina* (Ankel, 1937; Nisbet, 1953). With reference to *Philine*, the most interesting prosobranch group to have adopted a plucking or carding use of the radula is that of the carnivorous stenoglossans. These show further superficial resemblances in that they feed with a proboscis and have a relatively shorter buccal mass than *Monodonta*. The radula is like that of *Philine*, having a formula 0.1.1.1.0, with lateral teeth which are large and hook-shaped.

The most complete account of the stenoglossan feeding apparatus has been given by Carriker (1943) for *Urosalpinx*. The radular teeth are erected by passing out over the bending plane as in *Monodonta*, but on closing, during the reverse movement, the arc through which the teeth move is greatly accentuated by longitudinal folding of the radular membrane into a deep groove. This results in a strong gripping action. The last part of the process appears very similar to the method used by *Philine*, which seems to have emphasized it as the sole means of achieving an inward swing of the teeth to

grasp prey. The radular membrane, after being flattened by lateral muscular pull, together with increased subradular blood pressure, is infolded deeply into a longitudinal groove to close it, just as in the stenoglossans.

The proboscis of *Urosalpinx* and other stenoglossans is a structure derived from an extension of the anterior region of the body wall and is not a gut extrovert as is that of *Philine*. Carriker (1943) described its protrusion by means of 'hydrostatic pressure and circular muscles in its walls' and stated that it is 'retracted by longitudinal proboscis retractors'. Thus in stenoglossans also, blood pressure is of greater initial importance in obtaining food than in (for instance) *Monodonta*, since the feeding position cannot be achieved without it. Long retractor muscles are present in both *Urosalpinx* and *Philine* and are necessary for withdrawal of the large protruded structure.

The proboscides of stenoglossans and *Philine* are analogous in that each is a means of placing the buccal mass in such a position that it may be more easily manoeuvred around the food. The distance through which the buccal mass of the stenoglossan may be advanced is much greater than in *Philine*, although it remains passive in the process and does not move forward relative to the buccal cavity, owing to its situation at the tip of the elongated inturned anterior end of the body. When the latter is extended it forms a very mobile structure, slender and well suited for a specialized carnivorous feeding method. Thus, Ankel (1938) quoted the insertion of the proboscis of *Sycotypus* into the shell of its prey, and *Urosalpinx* (Carriker, 1943) feeds in a similar way on oysters. By use of the proboscis in this way, stenoglossans are able to reach otherwise inaccessible parts of their prey. In *Philine*, unlike the stenoglossans, the method of bringing the buccal mass forward represents an emphasis of the protraction which occurs in all gastropods. *Philine* may either protract the buccal mass alone (p 315) or, by augmenting changes in blood pressure, protrude it as

part of the proboscis. This faculty allows wider possibilities in ways of feeding. The method used is suited to the nature and distribution of the food. Firstly, when readily accessible prey is available, the buccal mass is protruded, grabbing it with great accuracy as described on p 284. Secondly, when prey is less accessible, perhaps buried in sand, the proboscis is used. The buccal mass then projects downwards (Fig. 10), so that it is able to grope in the sand, and with the aid of the bending and rotatory movements described (p 321) to disinter the food. With the dorsal part of the proboscis used as a basis for muscular and blood movements the ventral part may be placed with great nicety and remain exposed for long periods. This arrangement enables *Philine* to wait for the emergence of such an animal as *Pectinaria* from shelter after sensing the inhalant respiratory or exhalant rejection currents of the worm (Watson, 1928). Thirdly, the exposed condition of the oesophagus, when the proboscis is protruded, may enable *Philine* to use suction, which probably plays a part in food intake in most gastropods. It is usually oesophageal and peristaltic in origin, and implies the presence of dilator muscles. In general, the buccal cavity or oral opening is quickly enlarged when required. In the proboscis of *Philine*, the oesophageal entrance has replaced the oral opening and must itself widen. Changes in the degree of relaxation of its intrinsic musculature may allow widening and peristalsis of the part of the oesophagus within the proboscis has been observed. This activity may draw food particles entering by ciliary action (p 321) into the more posterior regions of the gut and suck in large quantities of small food, such as Foraminifera. The 2 actions of the proboscis - to disentangle food and to suck it in - may be used together. Thus the proboscis need not necessarily be completely withdrawn in order to take in food. Its entrance can function as a secondary mouth whilst the true mouth is lost as the site of direct communication between buccal cavity and

outside world. This mode of feeding occurs in situations where food is relatively small and plentiful and allows slow and accurate intake. Where larger prey has been manipulated by the radular teeth and buccal mass on the ventral part of the proboscis, it may be necessary for the food to be dragged in as an accompaniment of complete retraction of the anterior part of the gut. In this case, and in feeding by simple protraction of the buccal mass alone, the true mouth acts in the normal way as the place where food first enters the gut.

The evolutionary trends which have been observed in the gastropods considered have been these: firstly, the feeding method of a primitive prosobranch (the trochacean, *Monodonta*) is versatile and includes various movements. The second stage of evolution has concerned amplification of a particular movement resulting in more specialized feeding with more restricted usage of the buccal apparatus and consequent simplification; at this stage are the docoglossans which have emphasized forward rasping, the taenioglossans, brush-feeders, and a pulmonate, *Physa*, which uses plucking action. The stenoglossans are at a third stage, since not only have they elaborated and emphasized a particular basic action - plucking - but have added further modifications of their own which lead to greater efficiency. *Philine* represents a fourth stage, probably reached by an entirely different evolutionary route, in which the original action, dependent on a bending plane, has been completely replaced. Thus, it grasps by folding the radular membrane longitudinally, using this procedure alone as the means of closing the teeth. Part of the basic bending plane or strap and pulley process, however, (lateral pull and subradular blood pressure) is still used in conjunction with this to allow reopening of the teeth. *Philine* also augments another process, that of suction, which is present as an integral though often minor part of feeding in other gastropods. Although the tendency to specialize in particular methods and lose

others is readily seen as it occurs in living gastropods, these animals may all represent separate lines of evolution. Similarities have arisen by convergence due to common problems such as similar food, or the necessity for accurate placing of the feeding apparatus.

Information on such trends in opisthobranchs is much more scanty than in prosobranchs. As regards those briefly discussed in section II, in common with *Philine* they do not possess the strap and pulley arrangement of cartilages and radula, but have vesiculo-muscular supporting tissue for muscle attachment. All feed on slow moving food often with a hard protective covering.

It is likely that *Scaphander* feeds in a similar manner to *Philine* since its feeding apparatus is almost exactly the same and it lives in a similar habitat, taking the same food: indeed, it may be considered an outsize *Philine*. Both have the following anatomical adaptations:

### 1. Buccal mass

- (a) The muscles concerned in its movements, as distinct from those causing changes in topographical position, lie within it, and so are efficient whatever its position.
- (b) The radular sac is short. This is a general feature amongst carnivorous gastropods that may occur either because the wearing out of teeth is not particularly swift, or may reflect greater efficiency in speed of tooth production.
- (c) The radular membrane is short, with the minimal number of functional teeth compatible with efficient gasping of prey. Correlated with reduction in length is the elaboration of a new method of opening the teeth.
- (d) The supporting tissues of the buccal mass are not rigid. This is advantageous for movement of the buccal mass through the mouth and is compatible with the new method of tooth function.

- (e) Jaws have been lost for similar reasons.

### 2. Buccal region

- (a) The mouth and oral tube are very distensible and allow the buccal mass and large hard prey to pass through them.
- (b) The oesophagus is capable of great extension and expansion, correlated with its functions as a sucking organ and support for the ventral part of proboscis.
- (c) The retractor muscles are capable of great change in length.
- (d) Small muscles attaching the buccal region to the body wall have been lost.
- (e) The salivary glands are small and unattached except by their ducts.

### 3. Nervous system

- (a) The ganglia are placed in a compact group at each side of the nerve ring. Few nerves leave their medial surfaces, and these only at the anterior edge (cbc, c6, cc2, pc3), thus minimizing possible damage as the buccal region and its musculature pass through.
- (b) The cerebral and pedal commissures are long, the nerve ring wide, allowing a maximum of space for the passage of the buccal region
- (c) The long cerebrobuccal connectives are accompanied by muscle fibres which ensure that the buccal ganglia maintain their position relative to the buccal part of the gut. Lemche (1956) suggested, in discussing *Cylichna*, that such fibres 'prevent entangling of the buccal connective when the pharynx is protracted'.
- (d) Nerves which supply regions of the gut liable to stretching in the formation of the proboscis, follow a meandering course (e.g. b4, bt, c6 oen) and are often enclosed in muscular sheaths (oen). Such sheaths were first described in *Archachatina* by Nisbet (1961).

4. *Blood system*

- (a) The anterior part of the haemocoel is large so that the anterior region of the gut is not restricted by other systems and fluid is available for eversion of the proboscis.
- (b) The anterior aorta allows a large flow of blood; it can be constricted in two places allowing fluid to be restricted to a particular area.
- (c) In *Philine* there are haemal sacs which are used as a reservoir for fluid returning down the anterior aorta.
- (d) In *Philine* anterior sinuses act as reservoirs from which blood may be forced forward and made available for pushing out the proboscis.
- (e) In *Scaphander* a horizontal septum below the gut divides the anterior part of the haemocoel into upper and lower parts; this arrangement may be functionally equivalent to the reservoirs of *Philine*.
- (f) The buccal artery leads to a sinus below the radular membrane, which can be shut off from the rest of the vascular system.

These characteristics adapt the anterior part of the gut as an extrovert for use in feeding. Some (for instance 1: a; 2: c, d; 3: a, b, d; 4: a, b, f) appear essential, others advantageous. The extrovert allows feeding by both grabbing and sucking or by a combination of the two.

The remaining opisthobranchs considered will be discussed with reference to the method by which they feed. *Acteon* lacks adaptations considered essential for a proboscis. It is, however, able to eat sedentary worms, as *Philine* and *Scaphander* do. Since it has no crushing gizzard it is unable to make use of prey with hard parts, such as bivalves. *Owenia*, on which it feeds at Rhossili, South Wales, has a tube composed of sandgrains, which is flexible, unlike that of *Pectinaria* (an important prey of *Philine* and *Scaphander*). *Acteon* is probably able to suck the worm out of its tube and take it in as follows:

dilatation of the oral tube by the extrinsic muscles (ex A, ex D, Fig. 25) and expansion of the oesophagus by contraction of the oesophageal muscles (oem) provide an area of low pressure sufficient to draw prey in. Contraction of extrinsic muscles B and C tends to protract the buccal mass and to draw the lateral cushions of the buccal mass apart. This separates the 2 halves of the radular membrane so that the worm, sucked in and held by the jaws, is placed between them, prevented from escaping by the back-pointing radular teeth. Subsequent passage of the worm into the oesophagus is aided by peristaltic movements of the oesophageal walls which are prevented from moving forward by dilator muscles (oem) attaching them to the body wall. Saliva probably coats hard particles entering the gut, so that its walls are not damaged. This method of feeding may well be possible without any alteration in the angle of the teeth. The use of recurved teeth is not uncommon in gastropods and occurs in such widely separated animals as the ptenoglossans (Fretter & Graham, 1962), the slug *Testacella* (Ankel, 1938; Quick, 1960), and the Naticidae (Ankel, 1938) in which a dorsal palatine tooth prevents escape of prey. No observations have been made on *Acteon* in the process of feeding, but it is unlikely to protract the buccal mass far, since it has no retractor muscles and suction is probably of great importance. Erection of teeth is dispensed with but they may be used to drag in prey as in ptenoglossans and *Testacella*.

Although *Cylichna* possesses adaptations which might be compatible with eversion of the anterior end of the gut, accompanying features which would not easily permit such eversion include the great elongation of the oral region, the comparative weakness of the retractor muscles (br 1, 2) and the possession of jaws. It is probably able to feed successfully without the aid of a proboscis. The function of the greatly emphasized anterior glandular region is not known. Sterner (1912) described the glands of the anterior regions of some tectibranchs, including

*Philine* and *Acteon*: these are not of great extent. *Cylichna* appears to have specialized inglandular development since it also possesses a glandular ridge (Fig. 30, glr) within the crop, which has been described by Lemche (1956) and which does not appear to be homologous to any prosobranch structure described by Graham (1932) or Fretter & Graham (1962).

The muscular posterior part of the buccal region of *Cylichna*, containing the buccal mass and jaws, is probably pulled forward through the nerve ring and up to the mouth in order to feed, and this is likely to occur as Lemche (1956) suggested.

Opening and closing of the teeth probably occur by a means similar to that of *Philine* since the intrinsic musculature of the buccal mass is essentially similar, as has been described (p.333-334). Thus *Cylichna* uses the grabbing motion of *Philine* without protrusion of the buccal mass or particular emphasis on sucking. It has retained jaws.

Since *Retusa* is devoid of buccal mass and jaws it can employ only suction as a means of obtaining food. It is brought about by great dilatation of the buccal cavity, using the lateral buccal dilators (Fig. 31, lbm), whilst the entrance to the crop is constricted to prevent regurgitation and the posterior end of the buccal cavity held back by a pair of retractors (brm). *Retusa* has emphasized suction to such a degree that it has lost the buccal equipment of other gastropods, which would present an impediment to the passage of food. The large size of the crop and gizzard (Figs. 24, 31, c, gi) allows ingestion of much material.

There are few accounts of the buccal apparatus of opisthobranchs and they include little information on feeding methods. In none has the degree of protrusion of the buccal region described been so great as in *Philine*. The herbivorous tectibranchs *Haminea* and *Bulla* may protrude the buccal mass to a certain extent (Guiart, 1901), but the oesophagus does not also emerge to form a large

extrovert. Berrill (1931) described a temporary feeding mechanism in the veliger of *Bulla hydatis*, in which the buccal mass is extruded so that setae on its tip project divergently: on retraction they close together and are withdrawn. *Gastropteron*, in which the buccal anatomy, nervous and vascular systems are like those of *Philine* (Vayssière, 1880), is also able to protract the buccal mass to some extent. This carnivore may feed as *Cylichna* does, or be capable of protruding the gut to a greater degree, despite the presence of jaws, since it has more adequate retractor muscles. In all these animals protraction of the buccal mass is probably more marked than in many prosobranchs, but there is no proboscis comparable to that of *Philine*. Thompson & Slinn (1959) however have described *Pleurobranchus*, which has a gut extrovert used in feeding. This eversion seems to involve extrusion of the elongated oral tube only, and is thus again unlike that of *Philine*.

Eales (1921) and Howells (1942) both described the process of feeding in aplysians: no extrovert is formed and jaws are used in conjunction with the radula. *Aplysia* holds seaweed within the lips and jaws, closes the radular teeth around them and then tightens the grip by contraction of a sphincter round oral tube and mouth (I3 of Howells, corresponding apparently to vcm of *Philine*), simultaneously pulling the buccal mass back so that a piece of weed is torn off. The radular teeth then release the weed to the oesophagus. The movements of the buccal mass within the buccal cavity are similar to the rising and sinking movements described in *Philine* (p.315, 319). This is to be expected since the musculature used appears similar to that of *Philine*. The following muscles apparently correspond (Howell's names are given first): E1 = proboscis retractor II of *Philine*; E2 = retractor III; I1 - longitudinal intrinsic musculature of the oral tube of *Philine*; I2 = superficial buccal musculature; I3 = ventral circular muscle; I4 = radular occlusor; I5 = buccal

tensor 3; I6 = anterior transverse muscle. Since *Aplysia*, like *Acteon*, has no retractor muscles, it is unlikely to protrude the buccal mass in the manner suggested by Guiart (1901). The tectibranch *Akera bullata* described by Morton and Holmes (1955), also feeds without a proboscis and its buccal mass and activities are exactly like those of *Aplysia*.

Boettger (1954) gave a detailed classification of opisthobranchs, but the results of the present work do not allow much comment on this: the gut of these animals has undergone such a high degree of adaptation for efficient feeding, that it cannot be used as a reliable guide to evolutionary trends. The Philinidae and Scaphandridae are certainly close, as Boettger suggested; *Retusa*, on the characteristics of its buccal region, cannot be placed with any accuracy, due to the loss of buccal apparatus, but is likely to be advanced. *Acteon* is not very like the other genera studied, and its buccal region does not seem unspecialized. Although *Acteon* shows a mixture of prosobranch and opisthobranch characters and is therefore probably primitive in some respects, its buccal region is unlike that of any ancestral form likely to have given rise to *Philine*, *Scaphander* or *Cylichna*.

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## RESUMEN

ESTUDIOS SOBRE LA ESTRUCTURA Y FUNCION DEL APARATO ALIMENTADOR DE *PHILINE APERTA*, Y COMPARACION CON OTROS OPISTOBRANQUIOS

Se estudia la anatomía bucal, y el suministro vascular y nervioso en la parte anterior del cuerpo de *Philine aperta* (L.). El funcionamiento es explicado en base a observaciones sobre la alimentación, la relación variable de las partes constituyentes del aparato bucal, y el resultado de estimulación experimental e inyecciones.

La paredes de la región bucal estan provistas de músculos intrínsecos, capaces de grandes cambios en forma: encierra una masa bucal compacta en la cual la rádula se soporta por grandes músculos y un tejido maleable de células vacuoladas, con inclusiones celulares y fibras musculares repartidas. Este tejido de soporte sirve también de base para la adherencia muscular, mientras un par de grandes músculos actua en el cierre de la rádula, la cual al abrirse lo hace por medio de dos juegos de fibras musculares que corren en la pared de la masa bucal. Cuatro pequeños pares de tensores bucales mantienen junta la masa bucal. La musculatura intrínseca conserva las formas y relaciones de las partes componentes de la masa bucal, causa sus movimientos de arriba a abajo al pasar los alimentos al esófago e interviene en el movimiento de los dientes.

La región bucal está adherida a la pared del cuerpo por seis pares de músculos extrínsecos los cuales determinan su posición topográfica. Al comer, cuatro de estos pares tiran la región bucal hacia adelante y la entera masa bucal es proyectada hacia afuera de modo que la rádula queda en posición anterior a la boca y puede usarse como un garfio. La protrusión puede estar acompañada de extrusión y expansión del esófago anterior para formar una extroversión con inclusión sanguínea, dependiendo de la especialización del sistema sanguíneo y el grado de flojedad de los paquetes del músculo columelar. Estos músculos abren, cierran la boca, y controlan el suministro sanguíneo de las regiones anteriores por su habilidad constrictora sobre la aorta anterior. Esta vaso también puede contraerse posteriormente donde pasa a través del diafragma. Es confluyente con muchos sacos hemáticos pequeños y algunos senos anteriores grandes que controlan la protrusión y retracción de la proboscis. El recogimiento depende, en gran parte, de seis pares de retractores proboscidales, los cuales también causan los movimientos rotatorios de la proboscis. La rádula es corta y cada fila de dientes comprende sólo un par único de laterales, que se abren y cierran ampliamente, de modo que otros adyacentes se intercalan, o pueden asir el alimento firmemente. La abertura depende del tiraje de los músculos laterales con presión sanguínea aumentada debajo de la membrana radular, mientras en el cierre se pliega longitudinalmente por tiraje muscular desde abajo.

Mientras que muchos gastrópodos pueden producir protrusión de la masa bucal hasta cierto límite, se demuestra que en *Philine* se extiende más afuera, formando parte de un gran saco extrovertido. Algunos otros opistobranquios se han comparado con *Philine* y se dan sus dietas: de estos, *Scaphander lignarium* (L.) es muy similar aunque el sistema sanguíneo no exhiba tantos cambios adaptivos. *Actaeon tornatilis* (L.), *Cylichna cylindracea* (Pennant) y *Retusa* sp. no usan proboscis: se sugiere el probable metodo alimenticio de estos últimos. *Retusa* has perdido su masa bucal y se alimenta por succión. Tendencias evolucionarias no son facilmente trazables debido a la adaptación extrema de la región bucal y el modo de alimentarse.



FEEDING AND PARTICLE-SORTING IN *YOLDIA ENSIFERA*  
(BIVALVIA: PROTOBRANCHIA),  
WITH NOTES ON OTHER NUCULANIDS

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ABSTRACT

Detailed observations of several species of the protobranch family Nuculanidae demonstrate that they, like the Nuculidae, collect food not only from the substratum by means of extensible palp appendages, as hitherto believed, but also from suspension by means of a ctenidium-palp association. The ciliated, unridged surfaces of the palp lamellae are partly or wholly acceptory, according to species, and direct potential food towards the sorting areas between the apposed palp lamellae. As in the Nuculidae, the relative significance of these food-gathering devices is unknown.

Particle-sorting occurs on complicated ctenidia and, when compared with conditions in the Nuculidae, on relatively simple ciliary tracts on the folds of the labial palp lamellae.

Relative spacial relationships of the pallial organs are as significant as their structure in collection and transference of potential food particles by the ctenidia to the labial palps.

The usual belief that the nuculoid Protobranchia, especially the Nuculanidae, do not employ the ctenidia as food-collecting structures is erroneous and is based upon unsatisfactory anatomical and experimental evidence.

Purchon's view that the Septibranchia and the Nuculanidae shared a protobranchiate common-ancestor is supported by functional as well as behavioral continuity of ctenidial activity.

INTRODUCTION

Traditionally, the protobranch families Nuculidae and Nuculanidae have been thought to feed exclusively by gathering material directly from the substratum with extensible palp appendages that reach out from between the shell valves. That some inconsequential amount of potential food might be passed from the ctenidium to the palp appendages was believed possible in the Nuculidae alone. An association of ctenidium and labial palp, such as that employed by lamellibranchiate bivalves in the feeding process, was considered to be totally lacking (Yonge, 1939).

Research undertaken during the summer of 1959, at the Friday Harbor Laboratories, Washington, revealed the existence of a feeding association of ctenidium

and palp lamellae in the Nuculidae (Stasek, 1961). Extraordinarily complex ciliary devices for the sorting of potential food particles were also observed. These findings led to comparative studies of the association of gill and palp in the entire class of Bivalvia and to the publication of a synopsis of general anatomical conditions (Stasek, 1963a). The Nuculidae are now known to have an association of gill and palp quite like that present in many lamellibranchiate forms.

Among bivalves examined since 1959 have been members of the Nuculanidae, a more specialized and diversified group than the Nuculidae. The present paper describes new aspects of food collection from suspension, as well as details of the sorting of particles as these processes were observed in some of the nuculanids

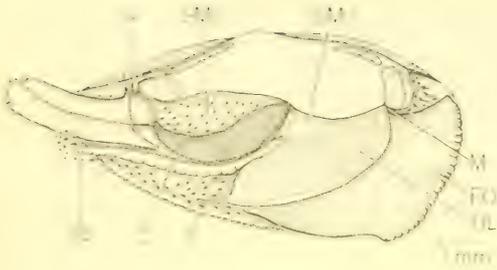


FIG. 1. *Yoldia ensifera*. Disposition of the organs in pallial cavity as seen from the right side. Dotted lines of outer palp lamella (OL) suggest faintly visible palp folds on medial surface of the translucent lamella. Arrows indicate direction of ciliary beat on suspensory membrane of ctenidium (SMC) and on mantle (unlabelled). (See below for List of Abbreviations.)

#### LIST OF ABBREVIATIONS

A -- Anus  
 AM -- Accumulated mass on inner demibranch  
 C -- Ctenidium  
 CA -- Ctenidial axis  
 CJ -- Ciliary junction between leaflets  
 D -- Demarcation between rejectory border of lamella and that of filament

DG -- Distal oral groove  
 F -- Filament of outer palp lamella  
 Fe -- Coarse frontal cilia (Location)  
 fc -- Fine frontal cilia (Location)  
 FO -- Foot  
 G -- Gonad  
 ID -- Inner demibranch  
 IL -- Inner palp lamella  
 lc -- Lateral cilia (Location)  
 LG -- Lateral oral groove  
 M -- Mouth  
 MA -- Acceptory margin of palp lamella  
 MC -- Membrane (cut)  
 MM -- Division of muscle from palp appendage attaching to mantle  
 MP -- Proximal margin of palp lamella  
 MR -- Rejectory margin of palp lamella  
 OD -- Outer demibranch  
 OL -- Outer palp lamella  
 PA -- Palp appendage  
 PM -- Pedal muscle inserting on shell  
 RC -- Rejection channel of inner demibranch  
 RP -- Point of rejection from palp lamella  
 RT -- Rejection tract on mantle  
 SM -- Suspensory membrane of palp  
 SMC -- Suspensory membrane of ctenidium  
 TA -- Accessory tract on acceptory margin of palp lamella  
 TE -- Unpaired tentacle  
 VB -- Blood vessel  
 X -- Tract directing material received from ctenidia into enlarged tract 4

available in the Friday Harbor region. Historical and phylogenetic perspectives are also presented.

Because the species was most abundant, *Yoldia ensifera* Dall, 1897, is described in most detail, information on other species having been relegated to the section on comparative notes.

Sorting behavior on the palps was observed in relaxed specimens, from which one valve and mantle lobe had been removed, and in entire excised palps pinned out over black wax. Ciliary sorting on the palp folds appeared to be the same in either case, the latter being the simpler to observe and from which more detailed information could be obtained. Admittedly, neither condition is normal. Young individuals have transparent shells,

and in undamaged specimens of these one could observe gross aspects of sorting on the palps, the results being comparable to those observed in dissected organs. Details of the association of ctenidium and palp were especially clear in these young specimens. Graphite ("Aquadag"), powdered carborundum ("Crystolon") of various grades, and natural detritus were used to trace ciliary tracts.

#### THE LABIAL PALPS

Gross anatomy and terminology. The labial palps of the Protobranchia, with the exception of the Solemyidae, resemble one another in gross anatomy (see esp. Yonge, 1939). There is a pair of large labial palp lamellae on either side of

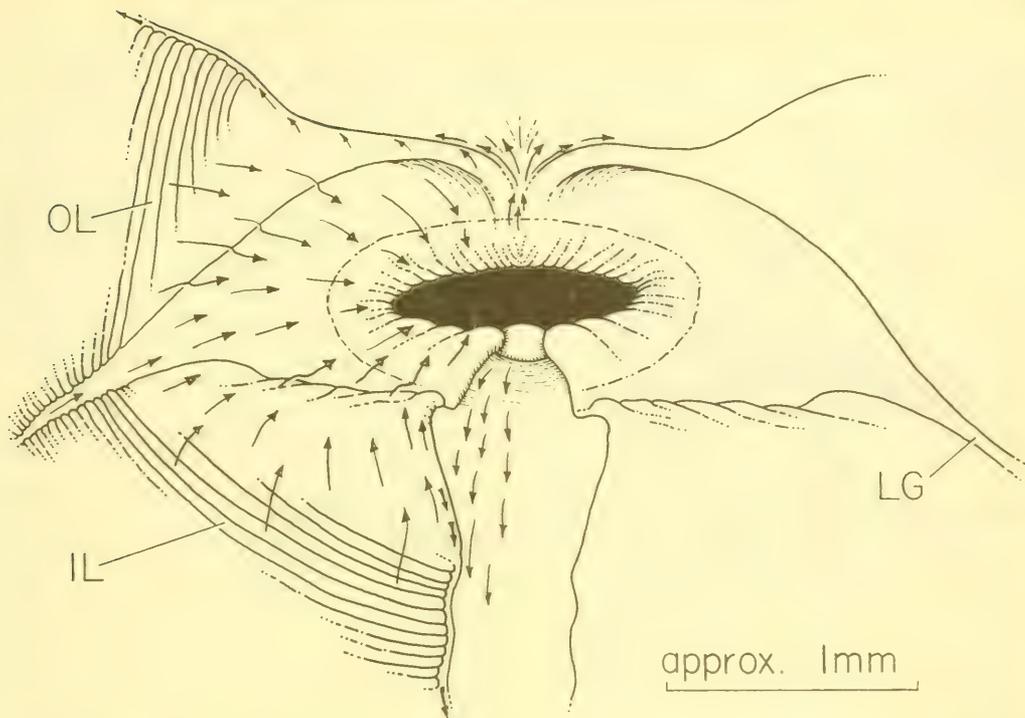


FIG. 2. *Yoldia ensifera*. Frontal view of mouth (in solid black) showing relationships to labial palps and lateral oral groove (LG). The normally apposed faces of the inner (IL) and outer (OL) palp lamellae have been spread apart like leaves of a book to expose their folded surfaces, folds and ciliary tracts being indicated on one side only. The large tract below the mouth and between the inner lamellae is that of the foot.

the foot. The more lateral of each pair is the "outer" (Fig. 1, OL), while the more medial, hidden in Fig. 1, is the "inner" lamella. The lamellae of either palp are in antero-posterior juxtaposition and bear upon their apposed faces a series of ciliated ridges termed lamellar or palp folds.

The outer and inner lamellae of either palp are mutually joined along their proximal borders and are suspended by a single thin membrane (SM) from the roof of the mantle cavity. Intact lamellae are easily removed from the body by cutting this membrane.

The mouth lies at the anterior extremities of the lamellae, which are said to form upper and lower lips, although in *Yoldia* there are distinct clefts in the median plane above and below the mouth (Fig. 2; Kellogg, 1915: Fig. 72).

Posteriorly, on the outer lamella of each pair is a modified portion, the extensible palp proboscis or appendage (Fig. 1, PA). This appendage bears a deep trough along its entire length, and, in the Nuculidae at least, is equivalent to a single pair of hypertrophied palp folds of the outer lamella (Drew, 1901: 354). The appendage is the terminal portion of the outer lamella in the Nuculanidae. In the Nuculidae the appendage is penultimate in position, for there exists in this family an additional, non-extensible appendage, the palp pouch, likewise representing a pair of hypertrophied palp folds.

The term "proboscis" referring to the extensible appendage is not used in this paper. This has been done, firstly, to emphasize the derived nature of that structure; the appendage as it appears in the Protobranchia seems best regarded

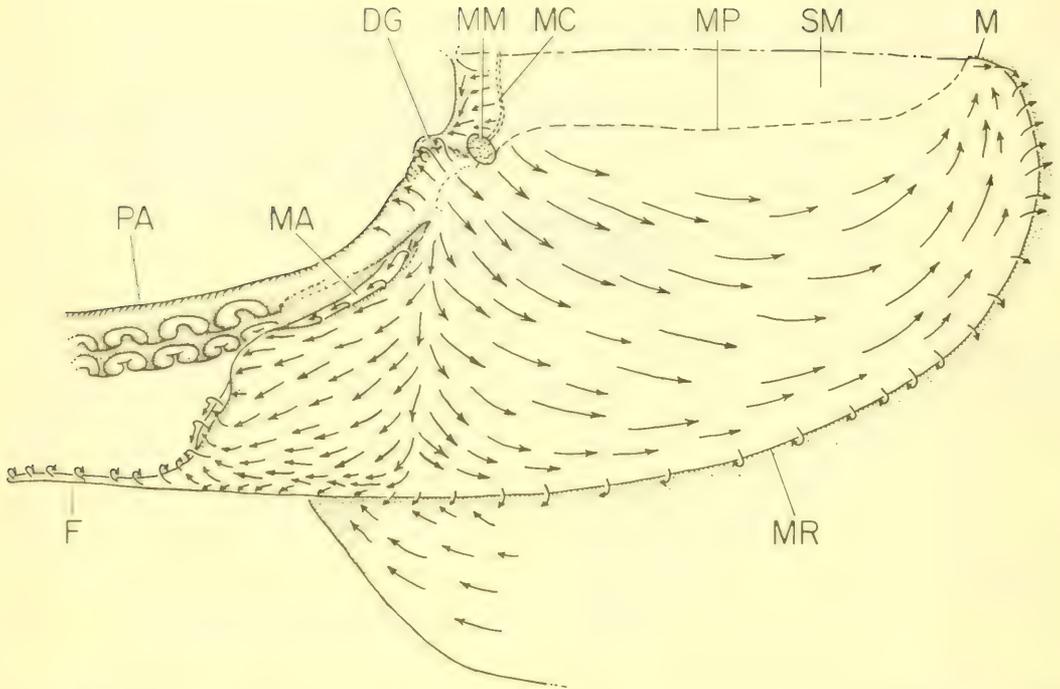


FIG. 3. *Yoldia ensifera*. Direction of ciliary beat on unridged surface of right outer palp lamella. Note that the major portion of this surface is occupied by rejectory tracts directing material onto the mantle in the region of the mouth (M). The acceptory portion of this surface directs material towards and over the acceptory border of the lamella (MA). The suspensory membrane (SM) has one border at the line of fusion of the palp lamellae (MP) and another, shown as an irregularly broken line, where the membrane is fused to the body wall. (See p 350 for List of Abbreviations.)

as a secondary ontogenetic and phylogenetic development from the outer palp lamella.

On the other hand, by definition, a proboscis is rightly a prolongation of the head. Whether this condition applies to the Protobranchia is a matter of opinion based upon the probable embryological origin of the palp lamellae (and hence eventually the appendages) from the velum, or "head" of the larva (see Stafford, 1913: 61; Allen, 1961: 263; Ansell, 1962: 430). But since adult Bivalvia are said to be characterized by headlessness, the existence of a prolongation from the head becomes semantically incongruous.

The homologies of the labial palps of the Solemyidae are not well known. At present they are thought to represent the

unpaired palp appendages of other proto-branchs, the lamellae being reduced to mere ridges (Yonge, 1939: 115).

Comparatively, each labial palp of a lamellibranchiate bivalve consists only of 2 lamellae; the specialized appendages of the Protobranchia have no known counterparts outside that subclass.

Most authors have regarded each lamella as a palp. That is, they write of 4 rather than of 2 palps. Some authors have considered the 2 outer palp lamellae as one palp, the 2 inner lamellae being the other member of the pair. This problem of nomenclature resembles that in which each demibranch of a ctenidium was formerly looked upon as a separate structure, a definitely inhibitory view described by Pelsener (1888: 37) and by

Stafford (1913: 70). With the palp as with the ctenidium, the structure on either side of the body seems best regarded as a single entity comprised of a pair of functionally related lamellae and their modifications.

The following terminology, applicable to all bivalves, is suggested for the borders of a palp lamella, which is essentially triangular: The border receiving material from the collecting organs, either appendages or ctenidia, is the aboral or acceptory margin or shelf (Fig. 3, MA); the generally unridged border leading rejected particles away from the mouth is the distal or rejectory margin (Fig. 3, MR); the border adjacent to the lateral oral groove, which lies along the line of fusion of inner and outer lamellae, is the proximal margin (Fig. 3, MP). The reason for avoiding directional terms such as anterior, posterior, etc., is that differences in relative orientation of the lamellae within the mantle cavities of divergent bivalve taxa may lead to confusion when the borders are so designated.

Where used with reference to the entire organism, directional terms follow the recommendations outlined elsewhere (Stasek, 1963b: 212).

The superior end of any palp fold terminates at the lateral oral groove or, depending upon the group, at the acceptory shelf of the lamella. The inferior end of a palp fold is adjacent to the rejectory margin of the lamella. A fold has oral and aboral slopes, which define the walls of the groove or sulcus between 2 folds.

Ciliation and function. Feeding by means of the palp appendages has been described for *Yoldia limatula* by Drew (1899: 11). He did not give an account of the sorting behavior of the palp lamellae, and the description of this process as reported by Kellogg (1915: 697) is cursory. Atkins (1936: 202), in describing sorting on the palps of *Nuculana minuta*, mentioned only that particles on the lamellae may be moved in 3 directions: away from the lateral oral groove,

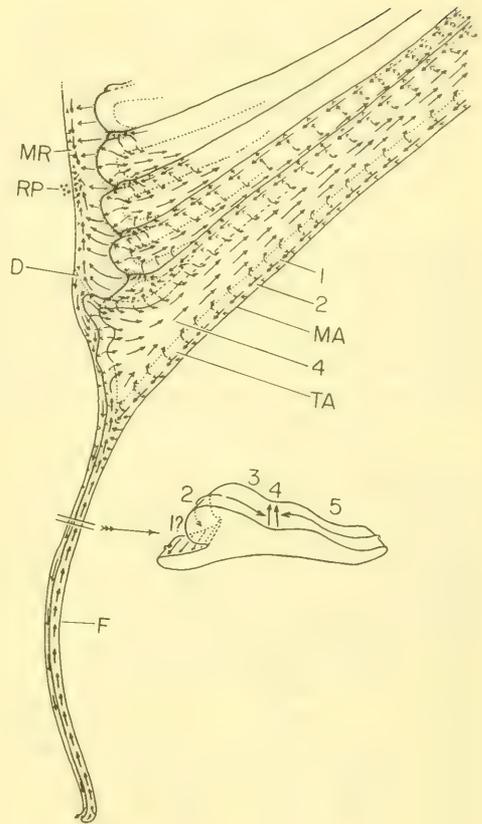


FIG. 4. *Yoldia ensifera*. Distal portion of right outer palp lamella and enlarged 3-dimensional cross-section of the filament (F), the latter with ciliary tracts numbered to suggest probable equivalence to normal palp fold (Fig. 5). (See p 350 for List of Abbreviations.)

towards the lateral oral groove, and transversely towards the mouth. The account given by Yonge (1939: 116) adds little more. The following observations of ciliary sorting apply to *Yoldia ensifera* Dall, 1897.

Particles, upon being led in the trough of the appendage to the palp lamellae, are transferred to the acceptory border of the outer lamella, which is folded over in such a way that its modified inner, ridged surface lies inserted within

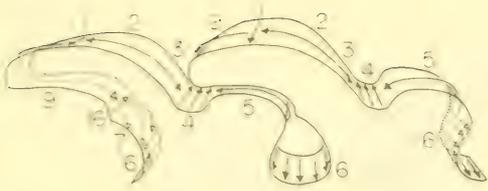


FIG. 5. *Yoldia ensifera*. Diagrammatic, 3-dimensional cross-section of 2 palp folds slightly spread apart to show ciliary tracts. Arrows indicate direction of beat of numbered ciliary tracts. For orientation, tracts 2 are orally directed, and tracts 4 are directed towards the lateral oral groove.

the trough (Fig. 3, MA). The folding has been occasionally observed to be reversed, and the outer, unridged surface contacts the trough. The appendage is relatively thin, its trough shallow at this, its proximal end.

The entire acceptory border of the outer lamella may be interpreted to represent 2 modified and enlarged palp folds (Fig. 4, MA). Understanding these folds may be easier if the conformities of more anterior folds are described first. A diagrammatic cross-section of 2 typical folds is shown in Figure 5. Except for those of the acceptory margins, folds of inner and outer lamellae are the same.

The ciliary tracts have been numbered to conform to similarly numbered tracts of *Acila castrensis* (Nuculidae; Stasek, 1961: 532). Not all the tracts of *Acila* have counterparts in *Yoldia*, hence the numbers given to tracts in the latter genus (Fig. 5) are not consecutive, and their actual equivalence in these genera is moot.

Acceptation tracts are of 2 types: 4 and 16 tend to lead particles towards the lateral oral groove (Fig. 2, LG), which is situated along the proximal line of fusion of the 2 palp lamellae; tracts 2 and 9 tend to lead particles transversely across the folds and towards the mouth.

Rejection tracts 1 and 6 tend towards the unfolded, rejectory margins (Fig. 4, MR).

Accessory tracts, such as 5 and 7, move particles into or out of acceptation or rejection tracts.

These categories are not intended to be mutually exclusive, for the functions may be combined in various tracts, or the functions of a tract may differ according to its location on the lamella. As examples, tract 5 not only moves particles anteriorly, but also shifts them into, and aids in holding them in tract 4. Tracts 2 and 9 move particles anteriorly, but, since the lamellae become dorso-ventrally shorter as the mouth is approached (Fig. 3), and since the more posterior folds are oblique to the rejectory palp margins, particles shifted along tracts 2 and 9 tend towards these margins.

On the modified, acceptory folds of the outer lamella, rejection tract 6 is not represented, and it is tract 4 of the penultimate fold that is enlarged and that receives particles from the palp appendages. The last fold is represented only by narrow tracts 1 and 2 with an additional accessory tract (Fig. 4, TA) not observed on any other fold.

These last folds of the outer lamella are prolonged into a filament (Figs. 1 & 4, F), reported in some other but not in all nuculanids (Yonge, 1939: 117). Unlike previous reports on other species, this filament in *Yoldia ensifera* is not concerned solely with rejection. Particles have been observed to pass from rejection tracts on the mantle onto the filament, being led once more between the palp lamellae. The rejection tract directed towards the tip of the filament does not seem to represent a simple extension of the rejectory shelf of the lamella, for there is a distinct line of demarcation between the ciliation of this and of the margin of the filament (Fig. 4, D).

Anterior to these receptory areas, the palp folds become successively narrower. Also, where the palp lamellae are fused

together proximally, the folds are much narrower than at their opposite ends (Fig. 1). These regional differences in relative size of the lamellae and of the folds upon them are as vital to particle-sorting as are the ciliary tracts themselves.

Actual sorting appears to be a relatively simple process, although in the presence of several concomitant conditions it is difficult to describe. Rapid sorting of particles into graded size categories was strikingly apparent when mixed grades of powdered carborundum were placed on the lamellae.

Particles are moved proximally in tract 4 until this tract, as well as the entire fold, becomes relatively too small for them, and they contact tracts 2 and 9. The particles are then shifted crest-to-crest in these tracts obliquely towards the rejectory margins. The sporadic influence of tracts 1 and the angle at which the folds lie with respect to the rejectory border account for the direction of movement. Particles that reach the rejectory margins are directed towards a concentration point opposite about the 4th or 6th fold from the distal margin (Fig. 4, RP) and then, as pseudofeces, are led onto rejection tracts on the unridged surface of the *inner* palp lamella adjacent to the foot. Their route from this region will be described in the section dealing with rejection.

Alternatively, because inferior regions of succeeding folds become relatively larger than more superior regions of folds crossed earlier, the particles may be shifted into a suitably sized sulcus and into acceptance tracts 4. Particles acceptable on more anterior folds are the smaller ones of the total mass passed from the primary acceptory folds.

In essence, the smaller the particles the more proximally they can go in any one tract 4, which progressively narrows as the lateral oral groove is approached. The smallest particles are passed nearest the lateral oral groove out of which they continue to be shifted, only to re-enter again a bit more anteriorly. This re-

entry is abetted by an absence of tracts 1 on the superior portions of all but the 2 posterior-most folds.

Besides the region adjacent to the lateral oral groove, there is an orally directed pathway parallel to the rejectory margins of the lamellae and just above the inferior tips of the palp folds. Whether actual transport occurs here in the intact animal is not known, but of the particles and dissociated masses often moving in this pathway in opened individuals, larger particles tend to be transferred to the rejectory shelf. Smaller particles tend to be kept in line by the opposing activity of tracts 4, into which they may pass, and of tracts 1. Tracts 1 in this inferior region, together with tracts 2 and the conformities of the folds, form a series of anteriorly directed currents (Fig. 11, A) that jointly seem to comprise a major acceptory pathway. Even relatively large masses 3 or more folds wide move in this pathway towards the mouth if such masses are loosely composed.

An important rejectory action consists of a strong and sustained contraction of the palp lamellae. The result of the contraction is a covering of all tracts 4 and a "crinkling" of the palp folds in such a manner that each is bent longitudinally into an extremely sinuous form. Curves of all folds follow closely upon one another in an antero-ventral direction, and any masses on the folds are all led obliquely to the rejectory shelf.

## THE CTENIDIA

Ciliation and particle-sorting. The ctenidia of diverse nuculanids have been described by Yonge (1939), who also summarized the literature. Conditions in the species I have examined differ in important functional respects from those reported for other members of the family.

General relationships of the ctenidia to other organs in the mantle cavity are shown in Fig. 1.

Each ctenidium is composed of a series

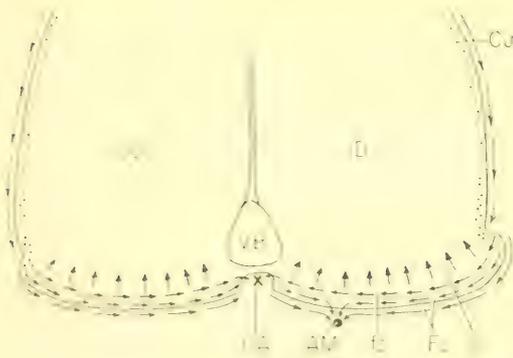


FIG. 6. *Yoldia ensifera*. Cross-section of ctenidium showing ciliation of demibranchs. "X", anteriorly directed ciliary tract in ctenidial axis. (See p 350 for List of Abbreviations.)

of juxtaposed platelets forming inner and outer demibranchs, which are separated by the ctenidial axis (Figs. 6 & 7, ID, OD, CA). The inner demibranch is slightly wider than the outer. A water current created by the lashing of lateral cilia (Fig. 6, lc) is passed between the ctenidial platelets. Particles in this current are strained out by frontal cilia of 2 kinds, coarse (Fc) and fine (fc), as described for *Nuculana minuta* by Atkins (1936). Cilia of the coarse type are located on ridges raised above the rounded shelves upon which the tracts of fine cilia are found (Fig. 7, C).

While on the anterior 8 or so platelets the tracts of coarse cilia on both inner and outer demibranchs pass material to the ctenidial axis, larger particles trapped by the coarse cilia on more posterior platelets of the outer demibranch are led towards and across the ctenidial axis to the inner demibranch. There, tracts of coarse cilia beat away from the axis (Figs. 6; 7, A, B). These tracts meet similar tracts of coarse cilia, also on the inner demibranch, but beating in the opposite direction. Where these opposing tracts meet on the frontal edge of a platelet, particles are accumulated in small masses

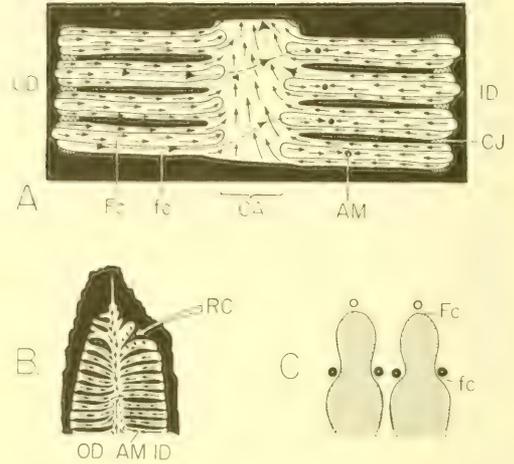


FIG. 7. *Yoldia ensifera*. A, Frontal view of 4 ctenidial leaflets showing direction of ciliary beat (smaller arrows), pathways commonly taken by particles (long, dashed arrows), and oblique row of accumulation points on the inner demibranch (large dots). B, Frontal view of anterior portion of right ctenidium showing direction of ciliary beat and rejection channel (RC) of inner demibranch. C, Diagrammatic cross-section through edges of 2 ctenidial leaflets indicating raised ridge bearing coarse frontal cilia (Fc) and low shelves bearing fine frontal cilia (fc); separation of finer from coarser material is suggested by large dots and circles respectively. (See p 350 for List of Abbreviations.)

(Figs. 6, 7, AM).

The most anterior accumulation point is on about the 8th platelet and is very near the ctenidial axis (Fig. 7, B). Succeeding accumulation points are positioned relatively farther from the ctenidial axis (Fig. 7, A), but none were observed on the medial margin of the inner demibranch.

Posterior to the first point of accumulation the cilia of the ctenidial axis beat anteriorly to meet an opposing tract at the level of the first point of accumulation (Fig. 7, B).

Particles anywhere in the ctenidial axis are delivered there from the tracts

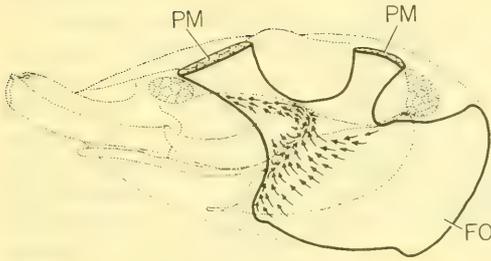


FIG. 8. *Yoldia ensifera*. Rejactory ciliation of foot. Remainder of body stippled (See p 350 for List of Abbreviations.)

of fine frontal cilia on the ctenidial platelets (Fig. 6, fc). Such particles, all of which are smaller than those transported by the coarse tracts of cilia, are led to the first accumulation point on the inner demibranch.

Larger particles passed into the ctenidial axis are almost immediately transferred out of it, apparently by contacting the swollen ends of the ridges as they overhang the ctenidial axis (Fig. 6).

Thus the ctenidia not only gather particles, but sort them by size, finer particles being led to the anterior part of the ctenidia, where they accumulate in a mass, coarser particles being massed at several, successively more posterior points.

Rejection of particles from the mantle cavity. Material rejected by the palp folds and led to the rejactory margins of the palp lamellae is passed onto the unridged surface of the inner palp lamella. Except for the posterior rim, this surface bears tracts leading towards the anterior end of the ctenidium.

The heel and posterior surfaces of the foot likewise bear ciliary tracts converging at the anterior end of the ctenidium (Fig. 8). All particles in this region are quickly passed between 2 swollen and heavily ciliated ctenidial platelets forming a rejection channel on the inner demibranch (Fig. 7, B, RC). This spe-

cialized channel, first described by Kellogg (1915), leads into the suprabranchial chamber between the suspensory membranes of the 2 ctenidia. The lateral surfaces of the suspensory membranes also bear rejactory ciliation (Fig. 1, SMC). All material in the suprabranchial chamber is ejected through the excurrent siphon in large quantities (Rhoads, 1963).

Whereas the posterior quarter of the unridged surface of the outer palplamella is acceptory, directing particles to and over the posterior border of the outer lamella, the remaining three-quarters is rejactory (Fig. 3). Particles placed there are led to the anterior extremities of the palp and onto the mantle, which possesses posteriorly directed tracts (Fig. 1). These particles are then extruded through the opening from which the palp appendages are extended from the mantle cavity.

There exists an alternative or subsidiary function for the rejactory ciliation of the mantle surfaces. The posterior region of the mantle surface in the infrabranchial chamber bears a short longitudinal ridge, apparently forming with its mate on the mantle surface opposite, a wall dorsal to which the palp appendages find their way to the exterior. Hence, the extended appendages are surrounded on all sides: on the right and left by the smooth mantle surfaces; ventrally, by the apposed ridges of the mantle just described; and dorsally, by the high and narrow ridges confluent with the inner margins of the inhalant siphon (see Fig. 10 for a comparable ridge in *Yoldia thraciaeformis*). All these regions bear cilia beating posteriorly and ostensibly cleansing the infrabranchial chamber, but at the same time, as observed on several occasions, actually moving the tips of the palp appendages to their proper point of exit.

#### THE ASSOCIATION OF CTENIDIUM AND PALP

Although no direct fusion of the

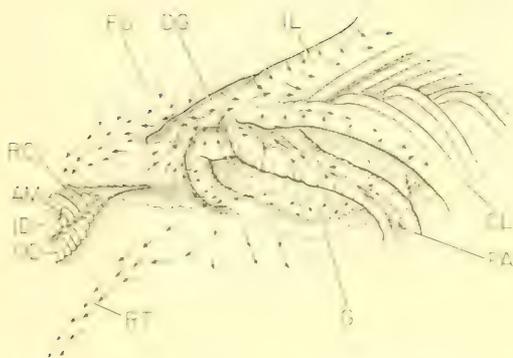


FIG. 9. *Yoldia ensifera*. Distal oral groove of left labial palp. View from right side with foot (FO) folded back. Normally the groove would contact the anterior end of the ctenidium. (See p 350 for List of Abbreviations.)

ctenidium and palp exists, these organs are intimately associated in the living organism. The relationships reported below were observed in opened specimens relaxed in magnesium chloride and in young specimens with transparent shells.

The distal oral groove. As in many bivalves, there are 2 aspects to the association of ctenidium and palp. There is a distal oral groove (Figs. 3, 9, DG), the walls of which extend dorsally from the acceptory margins of the palp lamellae. This groove was first noted in *Yoldia* by Kellogg (1915), although he apparently did not recognize it as equivalent to the distal oral groove of other bivalves.

Yonge (1939: 116) mistakenly considered the medial wall of the distal oral groove of certain nuculanids, including *Nuculana minuta*, individuals of which I have inspected, to be a reduced palp pouch. The derivation of the palp pouch from 2 palp folds of the outer palp lamella, while the medial wall of the distal oral groove is an extension of the inner, demonstrates the lack of affinity of these structures.

As in all other bivalves in which a distal oral groove is found, that of *Yol-*

*dia ensifera* contacts the anterior end of the ctenidium. Contact is intermittent, as described below, and the region of the ctenidium so involved lies anterior to the first accumulation point on the inner demibranch. While particles on the lateral surfaces of the outer wall of the distal oral groove pass into the groove, particles on the medial surface of the inner wall pass through the rejection channel of the inner demibranch and into the suprabranchial chamber.

The inner palp lamella. A second aspect of the association concerns the inner palp lamella. It will be recalled that the acceptory border of the outer lamella is folded over and contacts the trough of the palp appendage. The acceptory border of the inner lamella is likewise folded over, in this instance the ridged surface faces the ctenidium. The folding is firm, apparently having been "built into" the tissues.

The ciliation, like that of the acceptory margin of the outer lamella, seems to represent a modification of a palp fold. As here interpreted, it is a greatly enlarged tract 2 that covers the acceptory margin of the inner lamella, the comparable tract on the outer lamella being much smaller (Fig. 4).

The ctenidium, having sorted its gathered particles, transfers the finest of them from the first accumulation point to the palp at a point near the juncture of the 2 palp lamellae (Fig. 9, IL, OL). From this position these particles pass anteriorly along the superior ends of the palp folds where re-sorting is minimal (see p 355). Larger particles, in contrast, are transferred to the inner lamella from more posterior accumulation points. That is, coarser particles from the ctenidium "automatically" commence their passage across the palp folds at more inferior regions where sorting is rigorous. Thus the relative disposition of the ctenidium, with its series of accumulation points, and of the labial palp is indicative of close functional interdependence.

In this regard the statements of Atkins

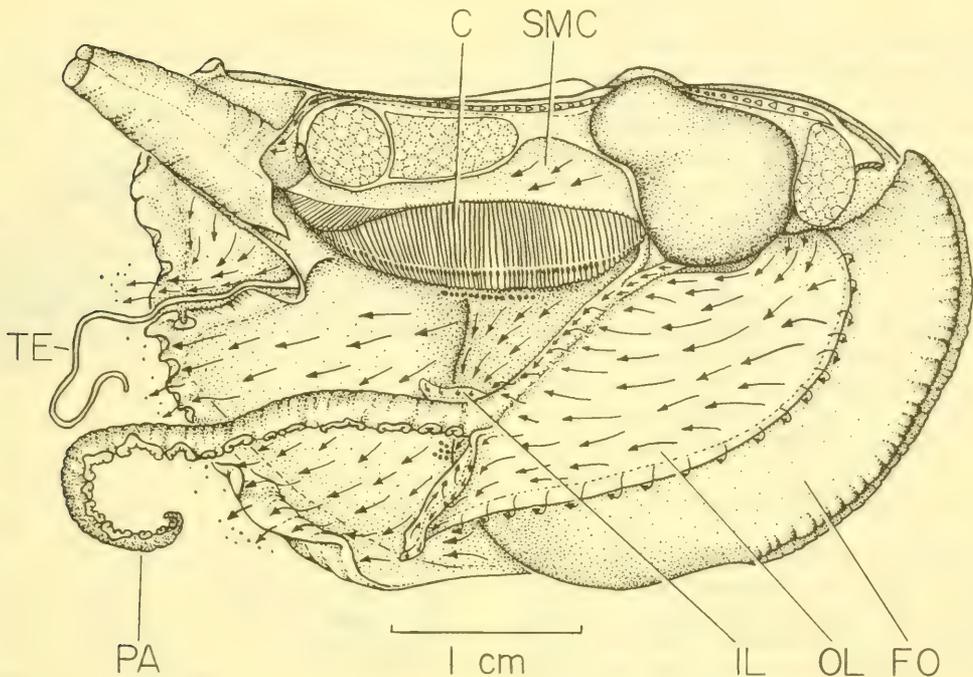


FIG. 10. *Yoldia thraciaeformis*, relaxed specimen. Disposition of organs in pallial cavity as seen from the right side. (See p 350 for List of Abbreviations.)

(1936: 200) are of interest. She stated that "In *Nuculana* accumulations of material along the inner edges of the gills either drop on the mantle and are conveyed posteriorly to be ejected..., or are removed by the palp appendages and the smooth posterior or upper margins of the inner palps and transported to the palp surface."

**Pumping by the ctenidia.** Drew (1899: 15) and Yonge (1939: 102) described the ways in which the ctenidia of the *Nuculanidae* are modified as pumping organs. The following observations are representative of activities often seen in *Yoldia ensifera*. Using light transmitted through the shell, it was possible to see the disposition of the organs in a specimen measuring 7mm in greatest dimension. Suspended particles and agglutinated masses of Aquadag, a commercial graphite lubricant, were drawn into the inhalant chamber by a strong but temporary flow created by a sharp, upward

movement of the ctenidia.

All these particles and masses, probably more concentrated than normally encountered by *Yoldia*, were pulled into contact with the ctenidia, and, when the ctenidia moved ventrally prior to another pumping movement, the accumulated material was transferred from the ctenidia to the palp lamellae where they were gathered at the posterior-most palp folds in a rather large mass. From this mass smaller masses were torn by ciliary activity and moved antero-ventrally to the rejectory margins, often near the mouth. As these rejected masses were transported posteriorly they were sometimes picked up by the inferior ends of more posterior palp folds and directed anteriorly once again. Often these already once-rejected masses moved directly to the mouth.

Commonly, in the ventral position, the posterior ends of the ctenidia were so deeply bowed as to completely cover the

inner opening of the inhalant siphon. As determined by lack of movement of particles suspended in the surrounding water, there was no observable inward flow of water when the ctenidia were in this position, although a weak current could sometimes be detected emerging from the exhalant siphon. This might be explained by a slow and undetected closure of the shell valves.

Particles often moved into the supra-branchial chamber via the exhalant siphon as the ctenidia were lowered. Thus, during downward movement of the ctenidia, the water in the infrabranchial chamber is not the only water displaced.

#### COMPARATIVE NOTES

Figure 10 illustrates the pallial organization of *Yoldia thraciaeformis* Storer, 1838, 2 specimens of which were studied. Whereas in *Y. ensifera* the ciliation of the unridged surfaces of the outer palp lamella is mainly rejectory (Fig. 3), that of *Y. thraciaeformis* is acceptory, as it is in *Acila* (Stasek, 1961). Particles on these surfaces are led either over the acceptory border of the outer lamella or to the surface of the palp appendage and into the extremely short distal oral groove.

General ciliation of the mantle surface is rejectory and leads particles to the posterior mantle edge where they are removed from the mantle cavity. These posterior margins are wrinkled in such a way that small masses of rejecta are concentrated or rolled up as they are moved into the troughs between folds. The area of rejection is large, but is comparable to the much more limited region of extrusion in *Y. ensifera* (compare Figs. 1 & 10).

The ctenidia undergo regular pumping activity with rest periods of about 20 seconds between pumping movements, each of which lasts about 3 or 4 seconds.

There is no rejection channel as found on the inner demibranch of *Y. ensifera*, and rejectory tracts on the foot con-

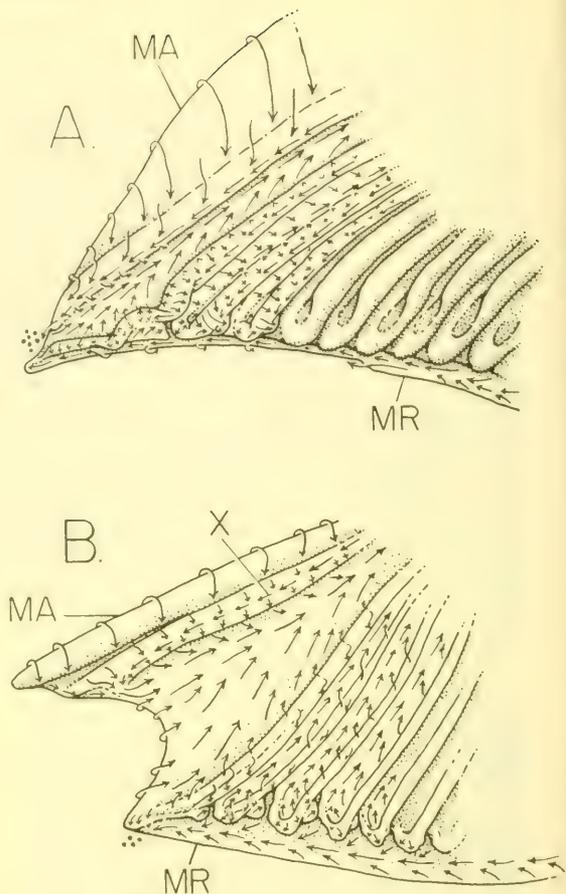


FIG. 11. Distal portions of right inner palp lamellae of *Yoldia ensifera* (A) *Yoldia thraciaeformis* (B). The acceptory margin (MA) in the former would normally be bent out of sight. (See p 350 for List of Abbreviations.)

verge at its heel.

On one ctenidium there were 125 platelets. Ciliation on the anterior 25 of these passed material backwards while the posterior 70 passed material anteriorly. All such material was collected in a mass extending over the 30 central platelets of the inner demibranch (Fig. 10, large dots under ctenidium). The anterior 17 of the 30 central platelets possessed, on the inner demibranch, coarse frontal cilia covering one-quarter of the frontal surfaces nearest the ctenidial axis and beating away from the axis, an arrangement resembling the

situation found in *Y. ensifera*.

Accumulated material on the inner demibranch has been observed to pass onto the acceptory border of the inner palp lamella, an action also occurring in *Y. ensifera*. All material so transferred appears to be moved in the tract marked 'X' in Figure 11, B, and then into the enlarged acceptory sulcus (tract 4) that receives particles in the following additional way.

The unridged surface of the inner palp lamella bears a posteriorly directed rejectory tract along the ventral margin, which is covered by the over-folded margin of the outer lamella. The remaining broad surface of the inner lamella bears tracts that lead all particles postero-ventrally, over the edge of the lamella, and into the ridged sorting areas. The passage over the edge of the lamella occurs at a distinct notch (Fig. 11, B). In *Y. ensifera* ciliation of the unridged surface of the inner lamella is rejectory, leading towards the rejection channel of the inner demibranch. What appears to be the homologue of the notch in *Y. thraciaeformis* is very small in *Y. ensifera* (Fig. 11, A) and has never been observed to function in the way described for *Y. thraciaeformis*.

Ciliation of the ctenidia of *Nuculana minuta* (Fabricius, 1776) was like that observed in *Yoldia ensifera*, tracts of coarse cilia converging on the frontal edges of the inner demibranch and not passing particles to the midline between ctenidia as described for this species by Atkins (1936, Fig. 3).

While the ctenidia of one specimen of *Yoldia scissurata* Dall, 1898, sorted particles as described for *Y. ensifera*, another did not. In the latter instance all particles contacting the ctenidia were passed to the ctenidial axis and then anteriorly to about the 15th platelet, which, with 5 or 6 other adjacent ones, were the only platelets bearing cilia beating away from the axis. The posterior half of the inner demibranchs of this individual had coarse frontal cilia beating obliquely across the frontal edges

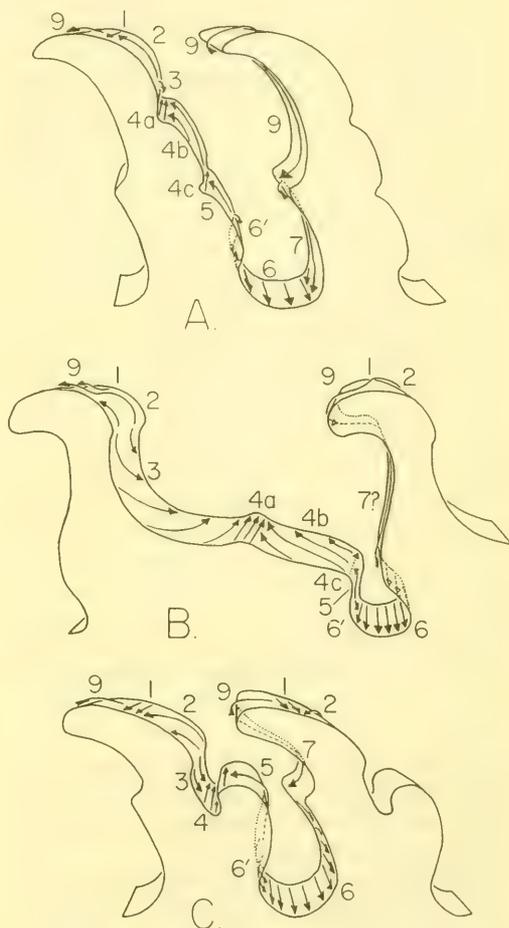


FIG. 12. Diagrammatic, 3-dimensional cross-sections of palp folds in (A) anterior and (B) posterior palp lamellar regions of *Yoldia thraciaeformis* and in (C) *Y. myalis*. Arrows suggest direction of beat of numbered tracts. For orientation, tracts 9 are orally directed, and tracts 4 beat towards lateral oral groove. The folds have been spread apart, thus exposing all ciliary tracts.

of the platelets in an anterior direction, particles being eventually led into the ctenidial axis. These differences between 2 individuals of the same species point out that several specimens of any species

TABLE 1. Direction of beat of ciliary tracts on single palp folds in some Protobranchia. (←, oral; →, aboral; ↑, superior; ↓, inferior; --, absent; dashed arrows indicate weak tracts; brackets suggest tract probably best considered as one.)

Tract n.	<i>Acila castrensis</i> *	<i>Yoldia ensifera</i>	<i>Y. myalis</i>	<i>Y. thraciaeformis</i>
1	↓	↓	↓	↓
2	←	←	↙	←
3	→	→	→	→
4	↑	↑	↑	↗ ↖
5	←	←	←	←
6'	--	--	→	→
6	↓	↓	↓	↓
7	←	↙	[ ↙ ↘ ]	↙
9	←	←		←
16	↑	↑	--	--

\*Cross-section below lamellar division ridge (Stasek, 1961).

should be observed so that anomalous, but no less functional conditions, if such exist, should not be mistaken as characteristic of the group.

Configurations and ciliation of the palp folds of *Yoldia thraciaeformis* and *Y. myalis* Couthouy, 1838, are shown in Figure 12. Palp folds of *Y. scissurata* are not figured but seem to be like those of *Y. ensifera* (Fig. 5). Table 1 summarizes the kinds of ciliary tracts present on single palp folds of those protobranchs studied. By and large, they are similar, but especially noteworthy is the subdivision of tract 4 in *Y. thraciaeformis*. The functional significance of this subdivision is unknown.

The cross-sectional view of inferior portions of 2 posterior folds of *Y. thraciaeformis* (Fig. 12, B) reveals that the region comparable to the aboral wall of more anterior folds is here flattened out into a broad shelf; tract 4a is raised

on a low ridge and tract 3 sweeps obliquely into tract 4a. More superior portions of these same folds resemble those of more anterior palp folds (Fig. 12, A). The divisions between tracts 2, 1, and 9 were not distinct in this postero-inferior region.

#### CONCLUSIONS AND DISCUSSION

On the basis of conditions reported above, I conclude that a filter-feeding mechanism, in which pumping by the ctenidia probably plays an integral part, exists in *Yoldia ensifera* as suspected for *Y. limatula* by Kellogg (1915: 695). As in the Nuculidae, the relative food-gathering importance of the palp appendages and of the ctenidia is unknown. One may assert that the former means is more significant than the latter, but until actual measurements are made, no firm conclusions can be reached.

Respiratory and circulatory functions of pumping activity, if such exist, may be secondary or correlative.

Probably most of the Nuculanidae collect some amount of potential food material by means of ctenidial ciliation. Particle-sorting, which in itself suggests the presence of a feeding mechanism, occurs on the ctenidia of the species of *Yoldia* and *Nuculana* described in this paper (except *Y. thraciaeformis*, which requires further study). A similar process probably occurs in most of the species discussed by Yonge (1939). Although Yonge did not attribute ctenidial food-collection to these species, this function is indicated by the division of frontal ciliation into adjacent tracts with opposed direction of beat similar to conditions described in the present paper.

The ctenidia of *Yoldia* actively sort collected material to a greater degree than do those of known members of any other family of the Bivalvia. Rather than simply collecting or rejecting constituents of the total incoming mass, ctenidial-sorting in *Yoldia* results in an accumulation of small masses representing, in general, an antero-posterior gradient of smaller to larger particles. Thus, when shifted to the palp lamellae, smaller particles begin their orally directed transference near the lateral oral groove, from which position further sorting tends to be minimal. Larger particles, in contrast, are transferred to the palp lamellae in regions farther from the lateral oral groove and are therefore more rigorously sorted on the palp folds. As in the majority of bivalves, it is the inner demibranch that is associated with transference of gill collections to the palp lamellae. Because there is no fusion of ctenidial filaments to the distal oral groove, the association of ctenidium and labial palp falls into Category I, which also includes the Nuculidae, Mytilacea, Unionacea, and Astartidae (Stasek, 1963a).

Historically, the view that significant ctenidial food collections are not made in the Protobranchia stems primarily from

the following erroneous conclusions: (1) that there is no connection between the ctenidia and palps; (2) that all material collected by the ctenidia is rejected by means other than the palps; (3) that the primitive ctenidia are too small to serve as food collectors; (4) that, in *Nucula*, the following features speak against the ctenidia acting as food collectors: the ciliary connections of the gills are not permanent, and the smallest particles entering the mantle cavity pass between ctenidial platelets into the suprabranchial chamber. Principal investigators fostering these ideas include Mitsukuri (1881), Pelseneer (1888: 11), Drew (1899), Hirasaka (1927), Atkins (1936) and Yonge (1939). It was conceded, at best, that collections made by the ctenidia, such as Orton (1912: 463) had observed, might incidentally be passed to a point where the palp appendages could remove them. It was to this minor function of the gills in food collection that Yonge (1939: 117) was referring. In a more recent paper that author (1959: 210) stated that "Food collection by the ctenidia is slight [in the Nuculidae] and possibly almost incidental; indeed in the more specialized Nuculanidae the similar palp proboscides are certainly the sole agents for feeding". Presumably Yonge was again referring to Orton's observations, but precisely why the implication was most recently altered (Morton & Yonge, 1964: 37) to suggest that material on the ctenidia of *Nucula* is passed "...toward the palplamellae..." was not made clear.

Because of the usually accepted view that the ctenidia of the Nuculanidae do not collect potential food material, the presence of the ciliated extension of the lateral oral groove (i. e. the distal oral groove) was given little attention (Yonge 1939: 117), although the organization of the palps convinced Kellogg (1915) that in *Yoldia limatula* they were constructed to receive gill collections. Also ignored was Atkins' observation (1936: 200) of the transfer of gill collections to the acceptory margins of the inner palp lamellae in *Nuculana minuta*.

Experiments to determine possible suspension-feeding in the Protobranchia include those of Drew (1899), who placed specimens of *Yoldia limatula* in shallow dishes supplied with water in which living organisms were abundant. "Under these conditions many specimens died with all the symptoms of starvation, and those that still survived after several weeks of this treatment were very weak and without the usual color. These weak specimens, when placed in their native mud, where the palp-appendages could be used, regained their strength and color very rapidly" (Drew, 1899: 16).

The length of time that *Yoldia* can survive total starvation is, to my knowledge, unknown. That the specimens observed by Drew barely survived "several weeks" might suggest not that they were unable to collect particles in suspension, but that the organisms supplied by Drew were not present in proper kind, condition, or quantity. Drew apparently did not observe ciliary sorting on the ctenidia.

Caspers (1940) demonstrated that *Nucula*, suspended in water, had the capacity for ingesting particles and concluded that *Nucula* was a suspension feeder.

Owen (1956: 553) stated that "...*Nucula* is certainly able to ingest particles present in suspension in the water but, as demonstrated by Hirasaka (1927) and Yonge (1939), the Nuculidae normally lie beneath the surface of the substrate and use the extensile palp proboscides to collect bottom deposits. Caspers's experiments are therefore of little value in determining the method of feeding of *Nucula* under natural conditions".

One must accept Owen's criticism that natural conditions were not duplicated, but it should not have been ignored that there exists an anatomical mechanism by which *Nucula* is able to ingest particles drawn into the mantle cavity. That such a strong possibility was not investigated is indicative of the strength of the generally accepted theory underlying Owen's statement.

As reported by Yonge (1959), unpub-

lished observations by Mortimer have revealed that the young of *Nucula* are suspension feeders. This led Yonge to conclude that support for the view that feeding by structures similar to palp appendages is primitive must depend largely upon "inherent probability".

Most recently it was found that the nuculid *Acila castrensis* possesses an association of gill and palp and that specimens from which the palp appendages had been excised were able to collect and ingest particles drawn into the mantle cavity (Stasek, 1961).

I should like to draw special attention to and express my admiration of Atkins who wrote (1936: 209), "It seems probable that it [the gill of *Nuculana*] has been derived from a form in which the gills were much more important as food collectors. . . . It is perhaps possible, however, that the gills are specialized to catch some particular planktonic food". Although the ciliation of the ctenidia of *Nuculana* and of *Yoldia* probably does not represent the derivation from more complicated types, but the culmination of trends toward specialization of sorting mechanisms, Atkins' method of presentation is to be emulated, for hers is the kind of statement that will open the door to further investigation.

In the absence of evidence other than strong, but unfounded assertions to the effect that a filter feeding mechanism is lacking in the adult Protobranchia, I conclude from observations related above and previously (Stasek, 1961) that all 3 families of the Protobranchia, that is the Nuculidae, the Nuculanidae, and the Solemyidae (Yonge, 1939), do employ ctenidial ciliation in the collection of potential food from particles temporarily suspended within the mantle chamber. Admittedly, the relative degree of importance of the collections remains unknown, for in the former 2 families palp appendages are present, and in the Solemyidae much material enters the mantle cavity through muscular activity of the foot and mantle (Owen, 1961).

Purchon (1963) presented convincing

evidence that the Septibranchia evolved from a protobranchiate ancestor. Although no actual phylogenetic relationship was conceived to exist between the Nuculanidae and the Septibranchia, the pumping activity of the septa, by which the latter obtain their food, was regarded as having evolved by specialization of respiratory pumping movements retained in the Nuculanidae.

Anatomical and functional studies of post-larval stages of the Septibranchia will aid in further clarifying phylogenetic relationships, but one may agree that Purchon's views are reasonable on present evidence. The discovery that the pumping ctenidia of the Nuculanidae are food collectors to some unknown degree further contributes to the validity of Purchon's conclusions, for functional as well as behavioral continuity is thus established between ancestors of the Nuculanidae and those of the Septibranchia. Indeed, that all existing Bivalvia had suspension-feeding ancestors now seems a relative certainty (Stasek, 1963a).

#### ACKNOWLEDGEMENTS

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## RESUMEN

ALIMENTACION DE *YOLDIA ENSIFERA*

Observaciones en varias especies de protobranquios de la familia Nuculanidae han demostrado que, igualmente que Nuculidae, recogen alimentos no sólo del substrato por medio de palpos extensibles como hasta ahora se ha supuesto, sino también partículas en suspensión mediante la actividad asociada de palpos y ctenidios. Las superficies lisas pero ciliadas de las lamelas palpales son en parte, o enteramente, aceptoras, de acuerdo a las especies, y conducen el potencial alimento hacia áreas de selección entre las lamelas palpales. La significación relativa de estas estructuras colectoras de alimentos es desconocida en estos como en los Nuculidae. La selección o distribución de partículas ocurre sobre ctenidios muy complicados, si se comparan con las condiciones en Nuculidae en tractos ciliares relativamente simples sobre los pliegues labiales de las lamelas palpales.

La opinión de Purchon de que los Septibranchios y Nuculanidae tienen un antecesor común, se sostiene en base a este conocimiento de la actividad funcional así como la continuidad de comportamiento de los ctenidios.

GENERIC DIAGNOSES FOR SOME BURROWING BIVALVES  
OF THE AUSTRALIAN PERMIAN

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ABSTRACT

The differing classifications of some burrowing bivalves of the Australian Permian by Newell (1956) and Dickins (1963) are reviewed. Morphological details not considered by these authors, such as dentition and musculature, support Dickins in his recognition of a number of genera, rather than Newell, who regarded only a few as valid. Generic diagnoses are given for *Megadesmus* Sowerby, *Astartila* Dana, *Pyramus* Dana, *Myonia* Dana, *Notomya* M'Coy, and *Pachymyonia* Dun. Two new genera are erected, *Globicarina*, with type species *Globicarina grossula* sp. n. and *Vacunella*, with type species *Allorisma curvatum* Morris. The latter species has been referred to *Chaenomya* by authors, but detailed comparison with topotypes of *C. leavenworthensis* show important differences in shape, posterior gape and musculature. The interrelationships between the genera are outlined.

INTRODUCTION

The Permian bivalve genera *Megadesmus*, *Myonia* and their allies were large sediment-burrowing shells especially characteristic of the marine faunas that lived in cold waters close to the ice-sheets of Gondwana. They are most abundant in eastern Australia, but occur widely, especially in the Sakmarian (basal Permian) of India, Pakistan (Waagen, 1891; Reed, 1932, 1936) and perhaps Brazil (Reed, 1930) and Argentine (Harrington, 1955; Dickins, 1963) when the ice-sheets of Gondwana were at their maximum extent. They have also been reported from the middle Permian of New Zealand (Waterhouse, 1963, 1964; Waterhouse and Vella, 1965) and from the Kazanian of Siberia (Popov, 1958). Much attention was focused on these shells in the early days of geological and palaeontological exploration in Australia, and the following taxa have been erected:

*Megadesmus* Sowerby 1838  
*Pachydomus* Morris 1845  
*Pyramus* Dana 1847  
*Cleobis* Dana 1847  
*Astartila* Dana 1847

*Myonia* Dana 1847  
*Notomya* M'Coy 1847  
*Maeonia* Dana 1849  
*Pyramia* Dana 1849  
*Clarkia* de Koninck 1877  
*Pachymyonia* Dun 1932

Of these names *Pachydomus* was erected by Morris as a substitute for *Megadesmus* Sowerby (1838) not *Megadesma* Bowdich (1822). *Pyramia* and *Maeonia* are variant spellings of *Pyramus* and *Myonia*, introduced without cause. The type species of *Clarkia* de Koninck is *Pyramus myiformis* Dana, which is also the type species of *Pyramus*, so that *Clarkia* is an objective synonym of *Pyramus*.

Other allied shells have been referred to *Edmondia* de Koninck (1844) and to *Chaenomya* Meek (1865). With the exception of these latter forms the entire group has been revised recently by Newell (1956) after examining specimens in museums in Great Britain, Australia and the United States, where most of the types are kept. Newell considered that the early workers had subdivided the group excessively and recognised only 4 genera as valid:

1. *Pachydomus* Morris (= *Megadesmus* Sowerby, *Astartila* Dana)
2. *Myonia* Dana (= *Maeonia* Dana, *Pachymyonia* Dun)
3. *Pyramus* Dana (= *Notomya* M'Coy, *Pyramia* Dana, *Clarkia* de Koninck)
4. *Cleobis* Dana

All 4 were stated to have an identical hinge, with a tooth in each valve. *Pachydomus cuneatus*, the supposed type of *Pachydomus*, was characterised by its lack of an umbonal carina or posterior gape, *Myonia elongata* by its umbonal carina, *Pyramus myiformis* by its pallial sinus and *Cleobis* by its slight posterior gape and thin shell, although Newell (1956: 11, 13) noted that this genus might in fact be a large *Pachydomus*.

The other worker who has recently expressed views on the group is Dickins, working more especially on forms from Western Australia, but also on collections from eastern Australia. Dickins (1956, 1957, 1961, 1963) subdivided the group much more closely than Newell, and also used subgenera to indicate affinities between different taxa. His conclusions may be summarised as follows:

Following the decisions of the 1953 International Commission of the Zoological Nomenclature *Megadesmus* Sowerby (1838) is recognised as a valid genus, and not a homonym of *Megadesma* Bowdich, or senior synonym of *Pachydomus* (see also Vokes, 1956). The type species of *Megadesmus*, *M. globosus* Sowerby, cited by Woodward (1856) as the type of *Pachydomus* Morris (= *Megadesmus* J. Sowerby), is considered by Dickins (1963) to be congeneric with *Cleobis grandis*, the type of *Cleobis*. *Astartila* is recognised as a genus or subgenus of *Megadesmus*; *Pachymyonia* is distinguished from *Myonia* by its strongly carinate posterior umbonal ridge, and treated as a genus or subgenus. *Notomya* is considered to be distinct from *Pyramus*. The bivalve genera *Edmondia* and *Chaenomya* were also recognised in the Australian Permian.

In summary Dickins recognised the

following genera:

*Megadesmus* Sowerby (= *Cleobis* Dana, *Pachydomus* Morris)  
*Myonia* Dana (= *Maeonia* Dana)  
*Pyramus* Dana (= *Pyramia* Dana, *Clarkia* de Koninck)  
*Astartila* Dana (or subgenus of *Megadesmus*)  
*Notomya* M'Coy  
*Pachymyonia* Dun (or subgenus of *Myonia*)  
*Edmondia* de Koninck  
*Chaenomya* Meek

Hill and Woods (1964: 20), presumably following Dickins for they acknowledged his help in their introduction, used the taxa *Chaenomya*, *Astartila*, *Myonia* and *Pyramus*, and treated *Cleobis* as a subgenus of *Megadesmus*.

In assessing the validity of these genera (apart from *Edmondia* and *Chaenomya*) Dickins used virtually the same criteria as Newell - that is, mainly shell shape, gape, and pallial sinus, though he did place more stress on shell size, and shell thickness, and definition of muscle scars. He also qualified Newell's report of a tooth in each valve, considering that only the right valve has a tooth. Allowing for these minor differences it would thus seem that Newell and Dickins differ considerably over the significance of what are almost the same criteria, and that the decision as to the validity of the various genera must be an arbitrary one, that will possibly vary according to each worker in the field, or one that requires considerable statistical analysis to reveal subtle differences over which agreement can be reached.

It has been found however that in most of these genera objective criteria are readily available which support an initial grouping according to shape, such as outlined by Dickins. These criteria lie in the hinge and musculature, which appear to differ consistently from genus to genus (as recognised herein). A compound illustration (Fig. 1) shows various generalized morphological features of use in

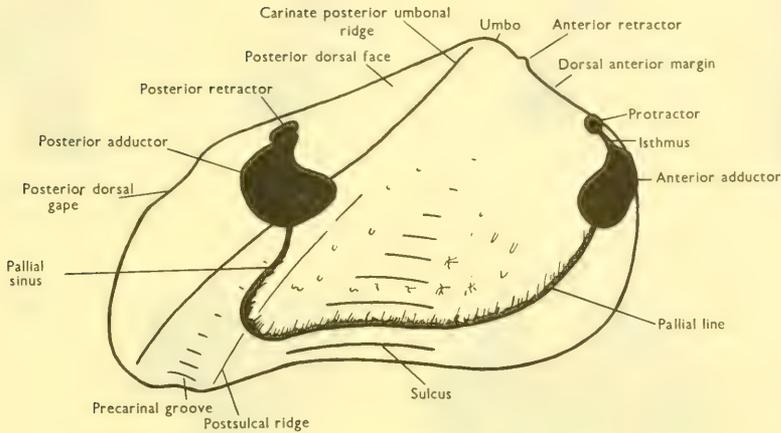


FIG. 1. Internal mould of right valve, generalised to show various morphological features of *Myonia*, *Megadesmus* and their allies. The shell outline and ctenidial markings are taken from the lectotype of *Myonia valida*, the other features are compounded from various genera.

characterising these bivalves, and Figs. 2 and 3 show how the muscle scars differ in each genus. The criteria were gathered partly from plaster duplicates made of all available types at the British Museum (Natural History), London; Sedgwick Museum, Cambridge; Smithsonian Institution, Washington; and the Australian Museum, Sydney, as well as by examination of large suites of Australian and New Zealand fossils at the Bureau of Mineral Resources, Canberra; the Australian Museum, Sydney; and New Zealand Geological Survey, Lower Hutt, with further specimens contributed by other institutions as recorded in the acknowledgements. The following account outlines generic diagnoses, based chiefly on the type species, and supplemented where necessary from allied species.

Genus MEGADESMUS Sowerby 1838

Type Species. *M. globosus* Sowerby

(1838), designated by Woodward (1856). Stoliczka (1871) later selected *Megadesmus cuneatus* as type, but this is invalid. The sole specimen figured by Sowerby (1838, Pl. 3, Fig. 1, 2) is designated lectotype (L 61043, British Museum, Natural History).

Synonymy. *Pachydomus* Morris (1845). *Cleobis* Dana (1847) with type species *C. grandis* Dana is externally identical.

Diagnosis. Moderately large, oval, thin to thick shelled inflated species with faintly prosogyrous umbones, and shallow anterior depression or sulcus on the lower flanks of the shell, concave forward in outline throughout its height (or extent). Dorsal posterior margin concave in outline, and no posterior umbonal ridge or posterior gape. Ligament opisthodontic, parinvicular, supported by nymphs, set in moderately defined posterior depression. Internal details poorly known in type species.

In externally similar species *Edmondia*

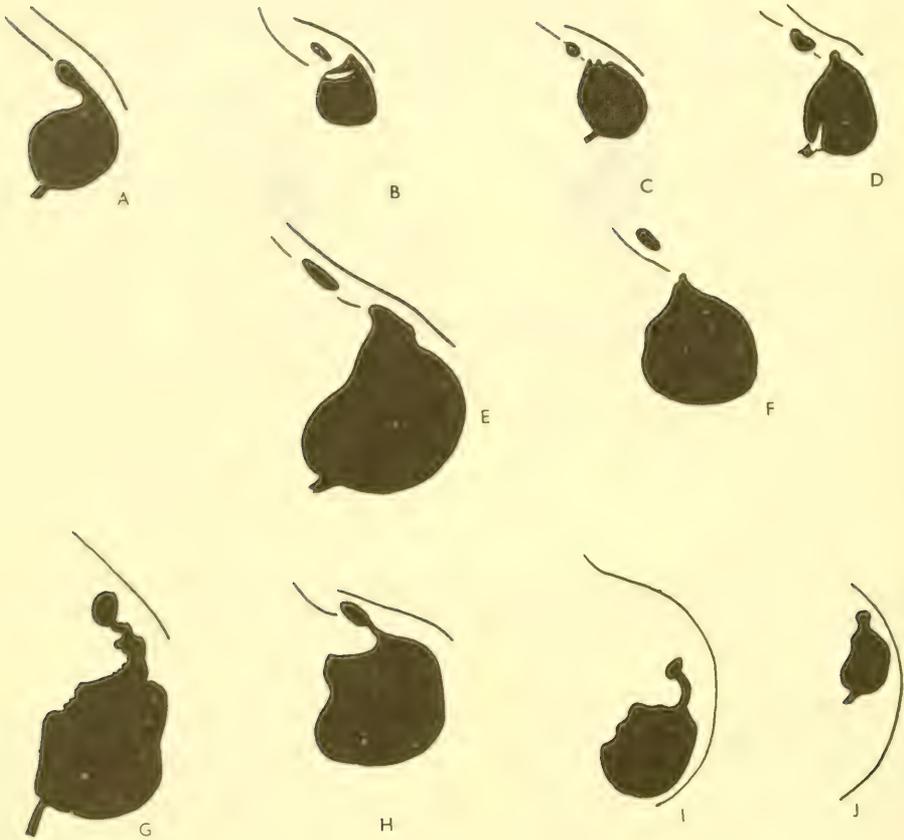


FIG. 2. Sketches of anterior adductor and protractor impressions on internal moulds of the right valve, slightly below natural size. A. *Megadesmus nobilissimus* (de Koninck). B. *Astartila intrepida* Dana (from the specimen figured as *Pachydomus ovalis* M'Coy). The large adductor has a sharp bend in its surface. C. *Pyramus myiformis* Dana, from a paratype. D. *Notomya securiformis* M'Coy, from lectotype - the adductor is raised near the posterior ventral margin. E. *Globicarina grossula* n. sp. from holotype, F 21750, Australian Museum. F. *Globicarina* n. sp. (Farley beds) from F 53, Australian Museum. G. *Myonia elongata* Dana, from *M. valida* Dana, lectotype. H. *Pachymyonia* sp. n., TM 3806, New Zealand Geological Survey. I. *Vacunella curvata* (Morris) from F 197, Australian Museum. J. *Chaenomya leavenworthensis* (Meek and Hayden) from photographs of type, and USNM 32985, Smithsonian Institution.

The line to the right indicates the anterior margin of the shell, and the line to the left the umbo-  
 nal ridge. Angles of observation differ slightly, to show the position of the muscle scars most  
 clearly in each instance. Where necessary, details observed on well preserved left valves have  
 been transposed into details of right valves.

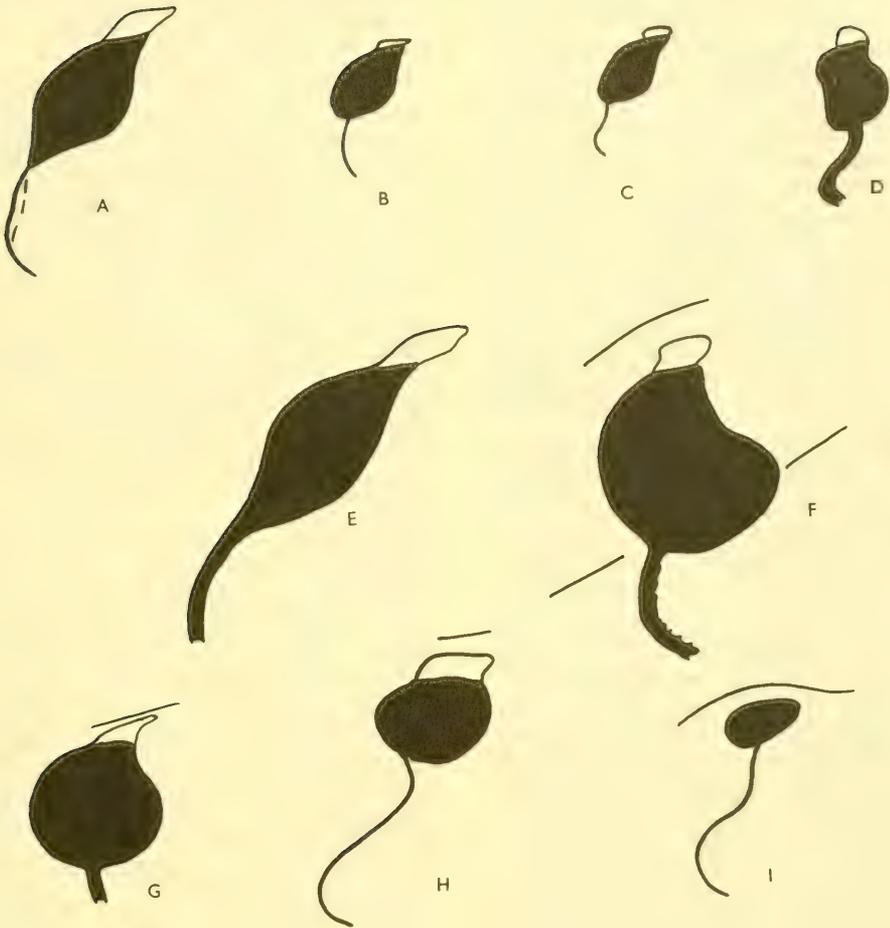


FIG. 3. Sketches of posterior adductor and retractor impressions with posterior part of pallial line, on internal moulds of right valve, slightly below natural size. A. *Megadesmus nobilissimus* (de Koninck), from specimens at Geology Department, Australian National University, Canberra, with the outlines of 2 pallial lines from different specimens, one with a shallow sinus, one without. Retractor slightly uncertain. B. *Astartila intrepida* Dana from *A. cytherea* Dana. C. *Pyramus myiformis* Dana, from lectotype. Retractor not seen. D. *Notomya securiformis* M'Coy, from lectotype. E. *Globicarina grossula* n. sp. from holotype, F 21750, Australian Museum, outline of scars and pallial line speculative. F. *Myonia elongata* Dana, from lectotype of *M. valida* Dana. G. *Pachymyonia morrisii* (Etheridge), from F 26275, Australian Museum, H. *Vacunella curvata* (Morris) from F 197 and F 30077, Australian Museum, highly speculative, and possibly quite inaccurate. I. *Chaenomya leavenworthensis* (Meek and Hayden) sketched from figure of type.

The line above the muscle scars indicates the dorsal margin, the line below indicates the position of the posterior carina. Angles of observation differ slightly, to show the musculature clearly. Where necessary, the details observed on well preserved left valves have been transposed to right valves.

*nobilissima* de Koninck (1877) and *Cleobis robusta* Laseron (1910), the anterior adductor is extended dorsally to meet an oval deeply impressed protractor (Fig. 2A). Anterior retractor small, placed on anterior umbonal ridge, in front of umbo. Posterior adductor large (Fig. 3A), posterior retractor small, attached to anterior dorsal margin of posterior adductor. Pallial line with very shallow sinus in some forms, none in others. Right valve with large right tooth, adjoining anterior commissure, socket in left valve shallow, formed by excavation of commissure. Behind the tooth and socket lies a narrow ridge, on the lower inner side of the nymphs.

**Discussion.** *M. globosus* from Allandale beds (Sakmarian) at Harper's Hill, Hunter Valley, New South Wales, Australia, is poorly known, for the shell is preserved, obscuring internal details. Most of the internal details described are observed in a large collection at the New Zealand Geological Survey of *Edmondia nobilissima* de Koninck from the Farley beds of the Hunter Valley, New South Wales. This species is closely allied to *M. globosus* - indeed it appears to be a late Sakmarian descendent. *Cleobis robusta* Laseron is a Baigendzinian (i.e. upper Artinskian - Kungurian) species of *Megadesmus* from the South Coast, New South Wales, with anterior musculature and pallial line well preserved. Queensland *Megadesmus* also show the hinge and musculature well.

#### Genus *ASTARTILA* Dana 1847

**Type species.** *A. intrepida* Dana (1847), designated by Stoliczka (1871). The lectotype is figured by Dana (1849, Pl. 3, Fig. 5, 5a), USNM 3594, Smithsonian Institution, as indicated by Fletcher (1929, caption to Pl. 26, Fig. 6).

**Diagnosis.** Small thin to thick shelled inflated species of suboval shape, with strongly prosogyrous umbones and the posterior dorsal margin convex in outline. No posterior umbonal ridge is differentiated. No lunule. Ligament opistho-

detic, parinvicular, not set in any defined depression, supported by sturdy nymphs. A shallow depression, usually concave forward in outline, lies on the anterior flanks of the shell. No posterior gape. Anterior adductor large (Fig. 2B), subquadrate, not prolonged posteriorly. Protractor placed within the umbonal ridge near the commissure, discrete from adductor. Anterior retractor probably on anterior umbonal ridge. Posterior adductor large (Fig. 3B), posterior retractor elongated, narrow, attached to dorsal edge of adductor. Pallial line entire. Right tooth small, adjoining commissure, left socket shallow, enclosed anteriorly by prominent buttress, which was called a tooth by Newell (1956) and which fits into a condyle in the right valve.

**Discussion.** Externally this genus is like *Megadesmus* in that it lacks a posterior umbonal ridge, but it differs from even juvenile *Megadesmus* by the convex rather than concave outline of its posterior dorsal margin, and by the poorly defined posterior ligament depression. Muscle scars as noted in the diagnosis differ considerably between the 2 genera. In *Astartila* the anterior adductor is subquadrate and not prolonged dorsally, and the protractor is completely discrete, unlike that of *Megadesmus*. The posterior retractor is longer and narrower in *Astartila* and a pallial sinus is never developed. Furthermore the dentition differs, for the anterior buttress of the left socket is not found in *Megadesmus*.

The diagnosis is based on plaster duplicates of the type and of the other *Astartila* species described by Dana from the same locality at Wollongong, New South Wales, Australia, all of which are probably conspecific, as noted by Newell (1956).

#### Genus *PYRAMUS* Dana 1847

**Type species.** *Pyramus myiformis* Dana (1847), designated by Newell (1956). Woodward (1856) noted only the species *ellipticus* Dana (1847) after the name *Pyramus*, but did not specify that it was

to be considered the type. The lectotype is USNM 3587, figured by Dana (1849, Pl. 6, Fig. 4a-c), and designated by Newell (1956, p 9).

Synonymy. *Pyramia* Dana (1849); *Clārkiā* de Koninck (1877).

**Diagnosis.** Moderately inflated usually thin-shelled species with shallow submedian sulcus below, and not anterior to the umbo, straight or concave backwards in outline. There is no carinate posterior umbonal ridge and the posterior dorsal face of the shell is convex. Ligament opisthodic, parinvicular, set in moderately well defined depression, supported by nymphs. Ornament of fine narrow concentric costae. Slight posterior gape. Anterior adductor large (Fig. 2C), with 2 or 3 lobes along the dorsal margin, of which the posterior is presumably a protractor. A large oval discrete protractor lies closer to the umbo. Anterior retractor not known. Posterior adductor large (Fig. 3C), posterior retractor faintly defined, long, narrow, not extending beyond adductor, almost merging with adductor. Shallow pallial sinus. Tooth in right valve well formed, not joining the commissure. Socket in left valve also well formed, with low anterior buttress, not as high as that of *Astartila*. Behind the tooth and socket lies a well defined depression on the inner side of the nymphs, bordered ventrally by a slender inner ridge. The ridge is possibly homologous to the inner ridge of *Edmondia*, but is much lower.

**Discussion.** The diagnosis is based on plaster moulds, rubber moulds, and photographs of the lectotype and paratypes collected and described by Dana (1847, 1849). In spite of the good preservation, the posterior retractor is scarcely to be distinguished from the posterior adductor. Neither Newell (1956) or Dickins (1961) questioned the validity of *Pyramus*: it is easily distinguished from *Astartila* and *Megadesmus* by its elongated outline, and its medianly placed sulcus. As is here shown, the tooth and socket are better formed than in these genera and are independent of the commissure, and the

musculature also differs.

#### Subgenus *NOTOMYA* M'Coy 1847

**Type species.** *Notomya securiformis* M'Coy (1847), which is probably a junior subjective synonym of *Pyramus ellipticus* Dana (1847) from the same area. The lectotype of *N. securiformis*, here designated, is specimen E 10776, Sedgwick Museum, figured by M'Coy (1847, Pl. 15, Fig. 5, 5a). The lectotype of *Pyramus ellipticus* Dana, here designated, is specimen USNM 3583, Smithsonian Institution, figured by Dana (1849, Pl. 6, Fig. 5a).

**Diagnosis.** Well inflated shells without a posterior umbonal ridge, and with a convex posterior dorsal face. Shallow to moderately deep submedian sulcus, straight or concave in outline posteriorly. Ligament opisthodic, parinvicular, supported by nymphs, placed in depression defined by distinct step from outer shell. Ornament of moderately fine costae with smooth to slightly ragged crests. Slight posterior gape, at least in larger specimens. Anterior adductor large (Fig. 2D), with small protractor attached to dorsal posterior margin; a second discrete oval larger protractor scar lies closer to the umbo. Small anterior retractor lies on umbonal ridge, just in front of the umbo. Posterior adductor large (Fig. 3D), posterior retractor large, subquadrate, attached to dorsal margin of adductor. Pallial sinus shallow. Tooth in right valve and socket in left valve comparatively well formed, not in contact with commissure. The depression on the inner side of the nymphs behind the tooth and socket, seen in *N. clavata* M'Coy, slightly shallower than in *Pyramus myiformis*, and the ventral ridge more massive.

**Discussion.** The diagnosis is based on plaster duplicates of the types of *Notomya securiformis* M'Coy and *N. clavata* M'Coy, here considered a synonym, and *Pyramus ellipticus* Dana, supplemented by observations on the types and other specimens of *Megadesmus cuneatus* Sowerby and *P. antiquatus* Sowerby, here held to belong to *Notomya*.

Newell (1956) considered *N. securiformis* to be not only congeneric, but conspecific with *Pyramus myiformis*. Dickins (1961) placed the 2 in different genera, and distinguished them by the greater inflation and thicker shell and deeper muscle scars of *Notomya*. I would not regard these differences as of generic significance in themselves, but there might be supporting evidence in the musculature and perhaps the definition of the inner ridge behind the tooth and socket. Unfortunately the musculature is not fully resolved for *Pyramus*, nor the variation in appearance of the inner side of the nymphs in *Pyramus* or *Notomya*. I therefore take the cautious viewpoint of considering *Notomya* to be a subgenus of *Pyramus*, rather than a full genus. They are obviously closely allied by shape and dentition, and the chief difference seems to lie only in the size and shape of the posterior retractor.

Genus **GLOBALICARINA** gen. nov.

Type species. *Globicarina grossula* n. sp., here designated.

Diagnosis. Very large inflated species, with strongly incurved weakly prosogyrous umbones, and a shallow depression on the flank of the shell, placed near the anterior margin and concave forward in outline. A weakly to well defined posterior umbonal ridge is present, and a concave posterior dorsal face. Ligament opisthodontic, parinvicular, supported by moderately sturdy nymphs, contained in a moderately well defined posterior depression. Slight or negligible posterior gape. Ornament of low costae, shell thin. Anterior musculature (Fig. 2E, F) much as in *Notomya*; anterior adductor large, with moderately large protractor attached to its dorsal posterior margin, a second large discrete protractor lies nearer the umbo, within the umbonal ridge, as in *Astartila*. Anterior retractor pit tiny, set on anterior umbonal ridge. Posterior adductor large (Fig. 3E), posterior retractor impression poorly known, possibly attached to dorsal margin of posterior adductor as a long

large scar. Posterior part of pallial line not known to me. Tooth in right valve well formed, discrete from commissure, to judge from a New Zealand specimen. Inner side of nymph with shallow depression and very low ridge.

Discussion. *Megadesmus cuneatus* Sowerby, here referred to *Notomya*, has anterior musculature almost identical with that of *Globicarina grossula*, the only difference being that the anterior protractor is larger in *Globicarina*, and the posterior protractor tends to lie within the umbonal ridge, and not on it. *Globicarina* also has a somewhat similar well formed tooth in the right valve. Differences from *Notomya* are found externally in its anterior, not median sulcus, and in its posterior umbonal ridge and concave posterior dorsal face. Internally the anterior musculature differs slightly, and the posterior retractor seems to be larger and longer.

In many respects *Globicarina grossula* resembles *Megadesmus globosus* - both are well inflated shells, with an anterior sulcus and strongly incurved umbones. But *Megadesmus* lacks a posterior umbonal ridge, and internal differences of musculature and probably of the hinge are considerable.

**GLOBALICARINA GROSSULA** sp. n.

Figs. 4, 5

Holotype. Specimen F 21750, Australian Museum, from middle Permian (Artinskian - Kungurian) beds of South Coast, New South Wales.

Diagnosis. Large elongated *Globicarina* with anterior umbones and deeply concave anterior margin. Distinguished from a species of the Lower Artinskian or upper Sakmarian Farley beds of New South Wales by its greater length and less carinate posterior umbonal ridge.

Discussion. The species will be fully described and illustrated in a forthcoming paleontological bulletin of the New Zealand Geological Survey. A number of specimens are present at the Australian Museum from Permian localities along

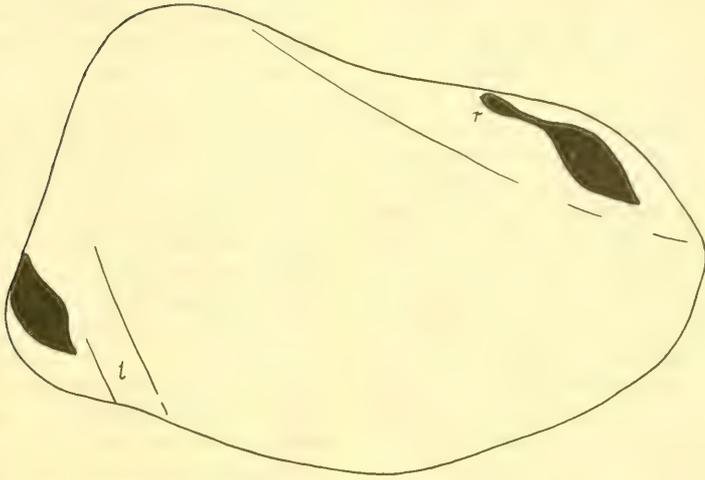


FIG. 4. Outline of left valve of *Globicarina grossula* n. sp. with muscle scars, holotype F 21750, Australian Museum, x 0.5 approx. Lateral view. i = depression or sulcus on shell surface; r = posterior retractor.

the South Coast. Previously some have been confused with *Cleobis grandis*, but *C. grandis* lacks a well developed posterior umbonal ridge, and has a less anterior umbo. It is probable that differences of musculature and hinge are also considerable - but internal details are not known for *C. grandis*.

Genus *MYONIA* Dana 1847

Type species. *Myonia elongata* Dana (1847) (= *Myonia valida* Dana, 1847), designated by Newell (1956). The lectotype of *M. elongata*, USNM 3584, Smithsonian Institution is figured by Dana (1849, Pl. 47, Fig. 2) and Fletcher (1932, Pl. 47,

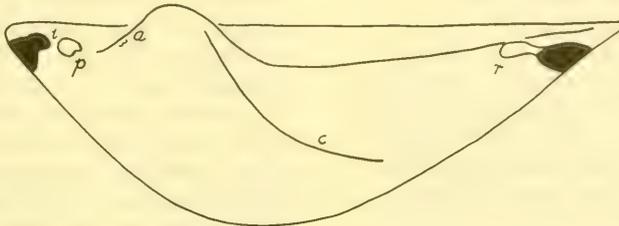


FIG. 5. Dorsal outline and muscle scars of left valve of *Globicarina grossula* n. sp. holotype 21750, Australian Museum, x 0.5 approx. a = anterior retractor scar; c = posterior umbonal ridge; i = anterior protractor scar attached to anterior adductor; p = posterior protractor scar; r = posterior retractor.

Fig. 2), and indicated by Fletcher (1932: 409). The lectotype of *M. valida*, USNM 3665, Smithsonian Institution, is figured by Dana (1849, Pl. 47, Fig. 4a, b) and Fletcher (1932, Pl. 48, Fig. 3) and indicated by Fletcher (1932: 410).

Synonymy. *Maeonia* Dana 1849.

Diagnosis. Large little inflated prosocline shells with anterior orthogyrous umbones, and a shallow sulcus on the median flank. The posterior umbonal ridge is prominent, and the posterior dorsal face usually concave. No posterior gape. Ligament opisthodic, parinvicular, supported by sturdy nymphs, set in moderately defined depression. Ornament of even-crested costae and wrinkles, shell thin. Anterior adductor large and subquadrate (Fig. 2G), with a protractor scar at its dorsal margin, adjoining a second protractor - in some shells the second protractor is almost discrete. Anterior retractor below umbonal ridge on outer flank of shell, at least in the lectotype of *M. valida*. Posterior adductor large (Fig. 3F), posterior retractor well formed, subquadrate, attached to dorsal margin of adductor, in some shells almost discrete. Pallial line entire. Hinge edentulous, with concave commissural face bordered ventrally by low ridge.

Discussion. The diagnosis is based on plaster duplicates of *M. elongata* and *M. valida* described by Dana (1849). Details of the hinge, not well shown in these specimens, are seen in various New Zealand specimens (e.g. TM 3815, 3816) of *M. elongata* and in specimens kept at the Australian Museum.

The validity of *Myonia* has not been questioned in recent years, but the nature of the hinge has been misunderstood. Newell (1956) reported that the hinge was identical to that of *Pachydomus* and *Astartila*, and this statement was accepted by Dickins (1963: 48). In fact, the hinge is edentulous. Etheridge (1892) reported that the hinge was edentulous in well exposed specimens of *Myonia carinata* and Fletcher (1932) also stated that the hinge was edentulous. The genus is thus readily

separated from the preceding genera, and is further distinguished by the position of the anterior retractor below the umbo, instead of in front of the umbo on the crest of the anterior umbonal ridge.

#### Genus *PACHYMYONIA* Dun 1932

Type species. *Myonia morrisii* Etheridge (1919), by original designation. The lectotype F 16978, Australia Museum, as designated by Dun (1932: 412), is figured by Etheridge (1919, Pl. 28, Fig. 7, 8).

Diagnosis. Well inflated shells with anterior prosogyrous or orthogyrous umbones, and a shallow to moderately deep median sulcus on the flanks of the shell. Posterior umbonal ridge sharply angular in cross-profile, and the posterior dorsal face flat or concave. Ornament of low costae and wrinkles. Shell thick in type species, but thin in related species. Ligament opisthodic, parinvicular, supported by sturdy nymphs, set in moderately defined depression. Anterior adductor large (Fig. 2H), its dorsal margin extended posteriorly towards well defined protractor; seemingly no second protractor. Anterior retractor set in umbonal ridge. Posterior adductor placed very close to hinge, well in from carina, posterior retractor narrow, elongated (Fig. 3G). Pallial line entire. Hinge edentulous.

Discussion. The diagnosis is based on the type species, with internal details of the hinge well shown in F 26275 at the Australian Museum. Muscle scars are moderately well exposed in this specimen, and in a New Zealand specimen of a younger species, registered as TM 3806 at the New Zealand Geological Survey. Some doubt is attached to the nature of the protractors, for the diagnosis is based on the New Zealand specimen, which does not belong to the type species. The protractors are a little more obscure on F 26275. It may be that the second anterior protractor is present, as in *Myonia*, but is almost fused to the adductor. F 26275 does have a pit on the umbonal

ridge, suggestive of an anterior retractor, whereas that of *Myonia* lies below the umbonal ridge. Also the posterior retractor is narrower and extends more anteriorly in *P. morrisii* than in *M. elongata*, and the posterior adductor lies much closer to the hinge in *Pachymyonia*. It thus seems that there are at least minor differences in musculature between the 2 taxa. Newell (1956) however synonymised *Pachymyonia* with *Myonia*. Dickins (1957) kept the 2 distinct, and in 1963, suggested that *Pachymyonia* could be treated as a subgenus of *Myonia*.

#### Genus *VACUNELLA* gen. n.

Type species. *Allorisma curvatum* Morris (1845). The lectotype, PL 3692, British Museum here designated, is figured by Morris (1845, Pl. 10, Fig. 1).

Diagnosis. Inflated shells with anterior orthogyrous umbones, and a shallow depression near the anterior margin in some forms and below the umbo in others. Posterior umbonal ridge well rounded in cross-profile, posterior dorsal face concave. Moderately wide posterior dorsal gape. Ornament of concentric wrinkles, costae and very fine pustules. Shell thin, of simple platy structure. Ligament opisthodontic, parinvicular, supported by sturdy nymphs, contained in moderately defined depression. Anterior adductor (Fig. 2I) placed close to anterior ventral extremity, attached by attenuated portion of isthmus to deeply impressed protractor. Anterior retractor lies closer to the umbo on the anterior umbonal ridge. Posterior adductor large (Fig. 3H), placed close to the hinge, posterior retractor elongate, attached to adductor, subrectangular posteriorly, extended well beyond adductor anteriorly. Pallial line probably with a large shallow sinus. Hinge edentulous, thickened under nymphs and in front of umbo.

Discussion. The diagnosis is based on Morris' type specimen, and on a large suite of specimens at the Australian Museum, of which F 197 and F 30077 are most useful.

*Allorisma curvatum* was referred to *Chaenomya*? by Etheridge (1892), together with its allies, which include *Homomya* (*Platymya*) *audax* Dana and *H. glendonensis* Dana, *Sanguinolites etheridgei* de Koninck, *Chaenomya* ? *bowenensis* Etheridge and other forms. Most of these species are closely allied to and perhaps conspecific with *Allorisma curvatum*. The reference of the species to *Chaenomya* has not been challenged for 70 years, but a comparison with topotypes of *Chaenomya leavenworthensis* (Meek and Hayden, 1858) suggests that *A. curvatum* belongs to a new genus. *Chaenomya leavenworthensis* differs considerably in shape, having subparallel dorsal and ventral margins, and a huge posterior gape that occupies the maximum width of the shell. By contrast *A. curvatum* is a more inflated shell, with a more rounded ventral margin, the maximum width near mid-length and a relatively small posterior dorsal gape. It is much less adapted for burrowing, looking like a *Pleuromya*, whereas *Chaenomya* looks like *Panopea*. Also the pustules are much finer (15-20 in 1 mm) in *A. curvatum*, compared with 2 or 3 in 1 mm in *Chaenomya*. The hinge and shell structure are much the same in both types, but the musculature differs. The anterior adductor lies much higher on the shell in *Chaenomya* (Fig. 2J), and is elongated vertically, and adjoins a deeply impressed rounded protractor, without being prolonged. The sinus is probably much the same in both forms but is poorly known in *Vacunella*, and the posterior musculature is not well shown in *Chaenomya* available to me (Fig. 3I), nor very clear in this new genus.

#### INTERRELATIONSHIPS BETWEEN GENERA

The genera described above fall into 2 or perhaps 3 natural groups. The largest group, with the genera *Megadesmus*, *Astartila*, *Pyramus*, *Notomya*, and *Globicarina* is characterised by the presence of a tooth in the right valve and socket in

the left. These genera are referred to the Edmondiidae King (1850) by Dickins (1961, 1963), and to a distinct family, the Pachydomidae, by Fischer (1887), Newell (1956), and Müller (1958). The ridge on the inner side of the nymphs of the Australian genera is reminiscent of the inner plate of *Edmondia*, but *Edmondia* lacks the tooth and socket of *Megadesmus*, *Astartila*, *Pyramus*, *Notomya* and *Globicarina*. Two subdivisions are seen in the Pachydomids, one with *Astartila* and *Megadesmus*, which differ from each other in many respects, and a second more closely knit group, with similar dentition and anterior musculature, *Pyramus*, *Notomya*, and *Globicarina*. Another group of genera is *Myonia* and *Pachymyonia*. These have edentulous hinges, and so are more closely similar to *Edmondia*. The relationship of the new genus *Vacunella* is more problematical. It may represent a rather unexpected loss of specialization by the Carboniferous-Permian genus *Chaenomya*, with gain of ventricosity, reduction in posterior gape, and change in method of valve rotation, as shown by the different muscle scars. Or it may represent a divergence from pre-*Myonia* stock, with the gain of a pallial sinus and posterior gape, in becoming adapted to a burrowing habit.

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## RESUMEN

DIAGNOSIS GENERICA DE ALGUNOS BIVALVOS EXCAVADORES  
DEL PERMICO DE AUSTRALIA

Se revisan las clasificaciones de Newell (1956) y de Dickins (1963), para algunos bivalvos permicos australianos. Detalles morfológicos no considerados por esos autores, tales como dentición y musculatura, apoyan el reconocimiento que hizo Dickins de cierto número de géneros, antes que la de Newell quien reconoce validez a unos pocos. Se dan las diagnosis genéricas para *Megadesmus* Sowerby, *Astartila* Dana, *Pyramus* Dana, *Myonia* Dana, *Notomya* McCoy, y *Pachynomya* Dun. Se crean dos nuevos géneros, *Globicarina* con la especie *Globicarina grossula* n. sp. como tipo, y *Vacunella* con *Allorisma curvatum* Morris. La última especie fué referida por los autores a *Chaenomya*, pero comparaciones detalladas con topotipos de *C. laevenworthensis* muestran importantes diferencias en forma, porción hiente anterior y musculatura. Se delinean las interrelaciones entre los géneros.

COMPARATIVE LIFE HISTORIES OF  
NORTH AMERICAN PILL CLAMS (SPHAERIIDAE: *PISIDIUM*)<sup>1,2</sup>

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ABSTRACT

Most information on sphaeriid clams is taxonomic in nature, although there have been embryological and life history studies on *Sphaerium* and *Musculium*. The present investigation is the first attempt to determine in detail the seasonal life histories in the genus *Pisidium* C. Pfeiffer.

Quantitative field collections were made throughout all seasons, largely in southern Michigan, U. S. A., in order to investigate (a) intraspecific variation, (b) interspecific variation within a single subgenus, and (c) interspecific variation between members of different subgenera in terms of general life history, gonad activity, and other aspects of reproduction.

Both intraspecific and interspecific variation in a single subgenus are reflected in differences in time of gonad activity and average litter size, although intraspecific variation is primarily ecological in nature and interspecific variation is essentially genetic in origin. Striking differences in the life histories of subgenera were found in regard to the number of litters produced in the lifetime, the duration of life, and the litter size. *Pisidium* s.s. produces 1 relatively large litter a year for several years, *Rivulina* lives only 1 year and reproduces just once (Palearctic representatives display contrasting behavior, appearing to live longer and reproduce more often), and *Neopisidium* produces 2 smaller litters a year and can potentially live several years.

The present study allows speculation on the possible evolutionary relationships of *Pisidium* s.s., *Rivulina*, and *Neopisidium*. Assuming an evolutionary change (1) in iteroparous species (a) either to an increase in the number of litters per year or (b) to a semelparous reproductive habit (regression?), and (2) in semelparous animals from a smaller to a larger litter size, one can conjecture that the anatomically more primitive *Pisidium* s.s. independently gave rise to *Rivulina* and *Neopisidium*. Their relationships to the Ethiopian subgenera *Afropisidium* and *Odhneripisidium* are unknown at the present time.

INTRODUCTION

The clams of the molluscan family Sphaeriidae (Dall, 1895) are considered to comprise 6 genera: *Sphaerium* Scopoli (1777), *Musculium* Link (1807), *Eupera* Bourguignat (1854), *Byssanodonta* d'Orbigny (1846), *Pseudocorbicula* Dautzen-

berg (1908), and *Pisidium* C. Pfeiffer (1821). The animals of this family are uniformly monoecious and ovoviviparous. Their fertilized eggs are retained and incubated within the body of the parent, and the subsequent development of the embryos into post-dissoconch fry takes place in the marsupia or brood sacs

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formed by the inner (anterior) gills. Although these tiny bivalves are without external sexual characteristics and lack copulatory organs, the brood chambers in the gills of these larviparous animals may be considered to function as accessory sexual organs (Coe, 1943).

Everyone who has attempted to identify sphaeriid clams has been impressed with the overabundance of specific and varietal names in this group. The existence of such a chaotic condition in the taxonomy of sphaeriids has led to a general hesitancy on the part of most biologists to study them. However, in the work that has been accomplished, several regional research trends are evident. In Europe Stepanoff (1865), Ziegler (1885), Stauffacher (1896), and Meisenheimer (1901) have investigated the development of *Sphaerium*. The origin, structure, and function of the marsupial sacs of this genus were considered by Jacobsen (1828), Schmidt (1854), Leidig (1855), Poyarkoff (1910), Schereschewsky (1911), Wasserloss (1911), and Groene-wegen (1926). More recently, Thiel (1924, 1928, 1930) contributed information on growth, reproduction, and life history of *Sphaerium*. Aside from several primarily taxonomic accounts (e.g., Woodward, 1913; Favre, 1943; Ellis, 1940, 1962; Boettger, 1961, 1962), much of the work on *Pisidium* has been morphological and was contributed by Odhner (1921, 1922, 1929a), although some general biological data have also been given by that author (Odhner, 1929a, 1951). Kuiper (1960a, 1960b, 1961, 1962a) has presented information on the *Pisidium* faunas of Europe and in addition he has been concerned with African sphaeriids (1952, 1953, 1954, 1956, 1957, 1960c). Okada (1935a, 1935b, 1936) has published on the reproduction and embryology of *Musculium heterodon* (= *Sphaerium japonicum*) in Japan. North American contributions have been overwhelmingly taxonomic (e.g., Prime, 1865; Sterki, 1916; Herrington, 1962), although Drew (1896) and Monk (1928) were concerned with the anatomy of *Sphaerium*. Gilmore (1917), Woods (1931), and Foster (1932) considered the reproduction and

life histories of *Sphaerium*, and Gilmore (1917), Herrington (1944, 1948), and Thomas (1954, 1959) contributed similar data on *Musculium*.

No biological studies of Nearctic *Pisidia* have ever been undertaken. Furthermore there are no studies which deal in seasonal detail with the reproduction and life history of any member of this genus. This situation needs to be remedied because it has become increasingly evident that there are many shortcomings in a strictly typological approach to systematics (see Mayr et al., 1953). The life history approach as a tool in systematics has in recent years become increasingly more significant in both invertebrate and vertebrate zoology.

I wish to express my sincere appreciation to Professor Henry van der Schalie for his unfailing encouragement and support during the course of this investigation. I am also greatly indebted to Drs. J. B. Burch and Claude W. Hibbard for their assistance and advice in the preparation of this report. A note of special gratitude is accorded Professor Frank E. Eggleton for introducing me to the Sphaeriidae and for his many stimulating discussions.

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#### CLASSIFICATION IN *PISIDIUM* C. PFEIFFER

Clessin (1873) and Sterki (1916) created subgroups of *Pisidium* which, because they were based on variable shell characters, have proven largely artificial and meaningless. Odhner's morphological investigations and Kuiper's (1962b) use of the position of the hinge ligament have, however, indicated the existence of natural groups which have been designated by them as subgenera. These groups, which

have undergone recent partial revision (see Boettger, 1961, 1962; Kuiper, 1962b), may be summarised in the following arrangement:

Subgenus 1. *Pisidium* s.s. Type: *Tellina amnica* Müller 1774 (= *P. amnicum* (Müller)). Branchial siphon rudimentary (*P. dubium*) or represented only by a slit in the fused mantle; large posterior (external) gills present in addition to large anterior (internal) gills; posterior gills with ascending (inner) lamellae as well as descending (outer) lamellae; dorsal loop or lobe of the nephridia cleft. Represented in this study by *P. dubium*.

Subgenus 2. *Rivulina* Clessin 1873 (= *Galileja* Costa as used by Boettger, 1961, and *Eupisidium* Odhner as used by Heard, 1962). Type: *Pisidium nitidum* Jenyns. Branchial siphon represented by a short slit in the fused mantle; small posterior gills usually present behind large anterior gills; posterior gills with ascending lamellae only; dorsal loop or lobe of the nephridia cleft. These characters were observed in the present study in *P. casertanum*, *P. compressum*, *P. fallax*, *P. nitidum*, *P. variabile*, and *P. walkeri*.

Subgenus 3. *Neopisidium*<sup>3</sup> Odhner 1921. Type: *Pisidium torquatum* Stelfox (= *P. moitessierianum* Paladilhe). Complete absence of branchial siphon; posterior gills entirely lacking; dorsal loop or lobe of the nephridia united; constant retention of juvenile characters. In this study these characters were found in *P. conventus* and *P. punctatum*.

Subgenus 4. *Odhneripisidium* Kuiper 1962b. Type: *Pisidium stewarti* Preston.

Subgenus 5. *Afropisidium* Kuiper 1962b. Type: *Pisidium lepus* Kuiper. *Odhneripisidium* and *Afropisidium* are reported to be anatomically closely related to *Neopisidium*, but each differs from the other 3 subgenera in the position of the ligament. In *Pisidium* s.s., *Rivulina*, and *Neopisidium* the ligament is enclosed, contained in the hollow of the hinges of the 2 valves. However, in *Odhneripisidium* the ligament lies below the hinges of the valves at a right angle to the symmetrical plane of the shell, while the ligament in *Afropisidium* is external (see Kuiper, 1962b; Fig. 1). So far as is known no members of *Odhneripisidium* and *Afropisidium* occur in North America, and the data in this paper therefore pertain only to *Pisidium* s.s., *Rivulina*, and *Neopisidium*.

The differentiation of these subgenera is not always definite since some intermediate types are known. For example, *Pisidium bulgaricum* (see Odhner, 1929b) combines the anatomical characteristics of *Neopisidium* and *Rivulina* in that it has cleft nephridia but lacks posterior gills and the branchial siphon, respectively. However, most species of *Pisidium* can be readily placed into one of these subgenera which can be considered to represent natural groups. Any intergrading forms may then be considered as links or as side branches in the evolution within this genus.

Shell size, in addition to anatomical characters, can also be used in grouping Nearctic *Pisidia* into subgenera. *Pisidium* s.s. (up to about 10 mm long) is slightly greater than twice as large as *Cycladina* which only rarely exceeds 5 mm, and approximately three times as large as *Neopisidium* whose length lies under 3 mm.

The objectives of the present investigation were: (1) to study reproductive processes and life histories of several species of pill clams, placing special emphasis on certain aspects of variation between (a) different population of a single

<sup>3</sup>The taxon *Neopisidium* has been considered by some workers to represent a composite of several genera or subgenera. However, until further information is available, a conservative course will be followed here.

species, (b) different species in the same subgenus, and (c) representative species of different subgenera; and (2) to assess the value of this information in regard to present concepts of relationships and taxonomy in the genus.

#### MATERIALS AND METHODS

Many periodic collections (every month) of *Pisidia* were made in southern Michigan, U. S. A., during 1959-1961. Five habitats were visited at intervals of approximately 4 weeks throughout 1-2 calendar years. These collections were made so as to provide a life history sample as well as animals which were preserved for subsequent anatomical-histological studies. The size of the life history collection was determined by the population size of each species, and it ranged from about 20 animals per collection of *Pisidium* (*P.*) *dubium* to nearly 150 animals per collection of *P.* (*Rivulina*) *fallax*. In addition other sites (viz., Lake Superior, uppermost of the North American Great Lakes, and Tennessee, U. S. A.) were collected at irregular intervals when animals were preserved but no quantitative life history samples were taken.

All of the life history samples were prepared in the field by the method developed by Dr. F. E. Eggleton: each animal of the sample was isolated in a 1/2 ounce screw-cap glass bottle filled with water. This isolation technique yielded a measure of the reproductive performance of each animal of each species (see Heard, 1964). After the tissues decayed, the intact shell of the adult ( $P_1$ ) as well as the shells of any post-dissoconch embryos ( $F_1$ ) were recovered. These shells were counted and measured to provide quantitative data on aspects of the life history of each species in the time sequence represented. However, it was necessary to dissect the adults to recover the embryos of *Pisidium conventus* (Lake Superior) and *P. punctatum* (Tennessee), since these animals were all preserved prior to their study.

The live animals not used in the life history samples were relaxed, fixed, and preserved in preparation for histological study of seasonal gonad activity. After the animals were relaxed in a 10% solution of sodium nembutal (see van der Schalie, 1953), they were fixed in Bouins fluid or Lavdovsky's fixative (=acetic acid - formalin - ethyl alcohol) (see Guyer, 1953), and finally preserved in 70% ethyl alcohol. Specimens used for histological study were embedded in paraffin and sectioned (in transverse, frontal, and sagittal planes) at a thickness of 10 micra. Sections were stained in Harris' hematoxylin and counterstained in 0.5% alcoholic eosin solution.

#### LIST OF COLLECTION SITES

The first 2 sites in this list, situated in the northern and south-central United States respectively, were visited in an irregular manner. The remaining 5 localities, all in southern Michigan (42°-42° 30' north latitude), were visited every 4 weeks over a period of at least one calendar year.

- (1) Lake Superior of the North American Great Lakes, off the northern shore of the Upper Peninsula of Michigan (46° - 47° N lat.). *Pisidium conventus* was collected from this habitat by A. M. Beeton of the U. S. Bureau of Commercial Fisheries at intervals of approximately 1 month over a period of six months (see Heard, 1963).
- (2) Tributary to White Oak Creek at Bethel Valley Road, Roane County, Tennessee (35° 45' N lat.). Collections of *Pisidium punctatum* were made in May and November, 1960.
- (3) Fleming Creek at Cherry Hill Road, Washtenaw County, Michigan (T2S-R7E-S13<sup>4</sup>). Studied from this locality were *Pisidium casertanum*, *P. com-*

<sup>4</sup>Use of Township Tier, Range, and Section allows one to locate a site in a county immediately within one square mile.

- pressum illinoisense*, and *P. variabile*.
- (4) Tributary to Mill Creek at Michigan Highway 92, Washtenaw County, Michigan (T3S-R3E-S13). A nearly monospecific population of *Pisidium casertanum* occurred here.
- (5) Ore Creek at Townley Road, Livingston County, Michigan (T3N-R6E-S8). Present here were *Pisidium casertanum*, *P. compressum*, *P. dubium*, and *P. walkeri*.
- (6) Oxbow Lake at Elizabeth Lake Road and Avonlea Street, Oakland County, Michigan (T3N-R8E-S26). *Pisidium compressum pellucidum* and *P. nitidum* were sampled from this site.
- (7) River Raisin at Sharon Hollow, Washtenaw County, Michigan (T3S-R3E-S29). Extensive collections of *Pisidium fallax* were made here.

LIST OF SPECIES

For the convenience of the reader, the species of *Pisidium* examined in the course of this investigation are recorded below with an additional listing of the localities from which each was collected. Samples of the shells of each species are deposited in the collections of the University of Michigan Museum of Zoology (UMMZ), and the relevant catalog numbers are given.

Subgenus *Pisidium* s.s.

*Pisidium dubium* (Say).

Ore Creek, Michigan. UMMZ 209831.

Subgenus *Rivulina* Clessin

*Pisidium casertanum* (Poli).

Fleming Creek, Michigan. UMMZ 209824.

Tributary to Mill Creek, Michigan. UMMZ 209825.

Ore Creek, Michigan. UMMZ 209826.

*Pisidium compressum* (s.l.)

Fleming Creek, Michigan. UMMZ 209827. The shell shape, degree of striation, size of beaks, and shape and position of the appendiculae compare closely with *P.*

*compressum illinoisense* Sterki. Ore Creek, Michigan. UMMZ 209828. The shape of these shells resembles *P. altile* Prime (= *P. compressum* Prime, *teste* Prime). The striae resemble those of *P. compressum illinoisense*, but are more evenly spaced. The beaks are narrower than in *P. c. illinoisense* and in the typical *P. compressum*, and while this Ore Creek form varies from the typical form and its nominal (?) varieties it does not appear to warrant subspecific designation.

Oxbow Lake, Michigan. UMMZ 209829. Although the beaks are less prominent than in *P. compressum pellucidum* Sterki, the shape, striae and slight gloss are identical to that variety.

*Pisidium fallax* Sterki.

River Raisin, Michigan. UMMZ 209832.

*Pisidium nitidum* Jenyns.

Oxbow Lake, Michigan. UMMZ 209833. A few of the shells approach *P. pauperculum* Sterki (= *P. nitidum* Jenyns, *teste* Herrington, 1962) in being shorter, heavier, and having more prominent beaks than typical *P. nitidum*.

*Pisidium variabile* Prime.

Fleming Creek, Michigan. UMMZ 209835.

*Pisidium walkeri* Sterki.

Ore Creek, Michigan. UMMZ 209836.

Subgenus *Neopisidium* Odhner.

*Pisidium conventus* Clessin.

Lake Superior. UMMZ 209830.

*Pisidium punctatum*. Sterki.

Tributary to White Oak Creek, Tennessee. UMMZ 209834. Herrington (1962) considered *P. punctatum* a synonym of *P. punctiferum* (Guppy), although Kuiper (1962c) treats both as valid, distinct species. Kuiper's taxonomic treatment will be followed here (also see Heard, 1963).

LIFE HISTORIES IN THE SUBGENUS  
*PISIDIUM* S. S.

*Pisidium dubium* (Say)

Shell . . . "very pale horn colour or whitish, with sometimes a darker, but not raised band, marking the preceding years growth of the shell" (from Say's original description, 1816). Shells from the Ore Creek habitat either lack any such growth annulus, or they may exhibit 1 or even 2 annuli. The number of annuli reflects the age of the individual animal. Each life history collection contained an assemblage of animals of different age classes. Shells lacking any annuli are less than 1 year of age. Those with 1 annulus are older than 1 year but less than 2 years of age. Specimens with 2 annuli are more than 2 years of age; these animals die after releasing their litter upon attaining their third year of life (see Plate I).

The paired gonads produce ova in the medial region and spermatozoa in the lateral areas. The pattern of seasonal gonad activity is identical in all 3 age classes. Oögenesis occurs in all seasons but is most active during early summer. Spermatogenesis, however, occurs only in the summer. Mature ova are also found throughout the year but are most abundant in mid-summer. Spermatozoa appear only briefly at this same time (Plate II, Fig. 4). The shells of each age class (Plate III) increase in size from birth until early summer when (a) the third-year class dies, (b) members of the second-year class continues to increase in size as the new third-year class, (c) members of the first-year class continue to increase in size as the new second-year class, and (d) the fry released in late spring by all 3 age classes appear as the new first-year class.

Post-dissoconch embryos first appear in all 3 age classes in the fall, develop in the marsupial sacs of their parents during the winter, and are released (born) in late spring. The litter size of *P. (P.) dubium* is observed to be large when com-

pared to those in *Neopisidium* and in several species of *Rivulina*. The average number of embryos per parent varies with the age class of the parent (Table 1). There is a marked increase in the average number of fry produced as the age of the parent increases.

The sizes of the embryos (Table 1) reveal several interesting relationships. In any single collection, embryos in the third-year-class animals tend to be larger than embryos in second-year-class animals, which in turn tend to be larger than embryos in first-year-class animals. Furthermore, as the parturition period proceeds, the embryos continue to increase in size. While the average number of embryos per parent decreased from April through May, the remaining embryos increased in size more than two-fold during this same period. Evidently the embryos are released in a wide range of sizes, but they cannot be grouped into size classes or categorized with regard to the age class of the parent.

LIFE HISTORIES IN THE SUBGENUS  
*RIVULINA* CLESSIN

All 6 species of *Rivulina* examined in the present study exhibited nearly identical behavior. Therefore, only one species, *Pisidium fallax* Sterki, is discussed in detail as a representative of the group, and only those collecting containing gravid animals of *Pisidium casertanum*, *P. compressum* s.l., and *P. nitidum* are analyzed here. *Pisidium variabile* and *P. walkeri* occurred in such small populations that consistently large life history series were unavailable, and only the seasonal gonad activity of these 2 species is reviewed.

*Pisidium fallax* Sterki

Thirteen consecutive monthly collections of *P. fallax* were made in an attempt to investigate seasonal phenomena in the life history of this species. The ovotestes produce spermatozoa in lateral areas and ova in medial regions. Spermatogenesis and oögenesis are most active

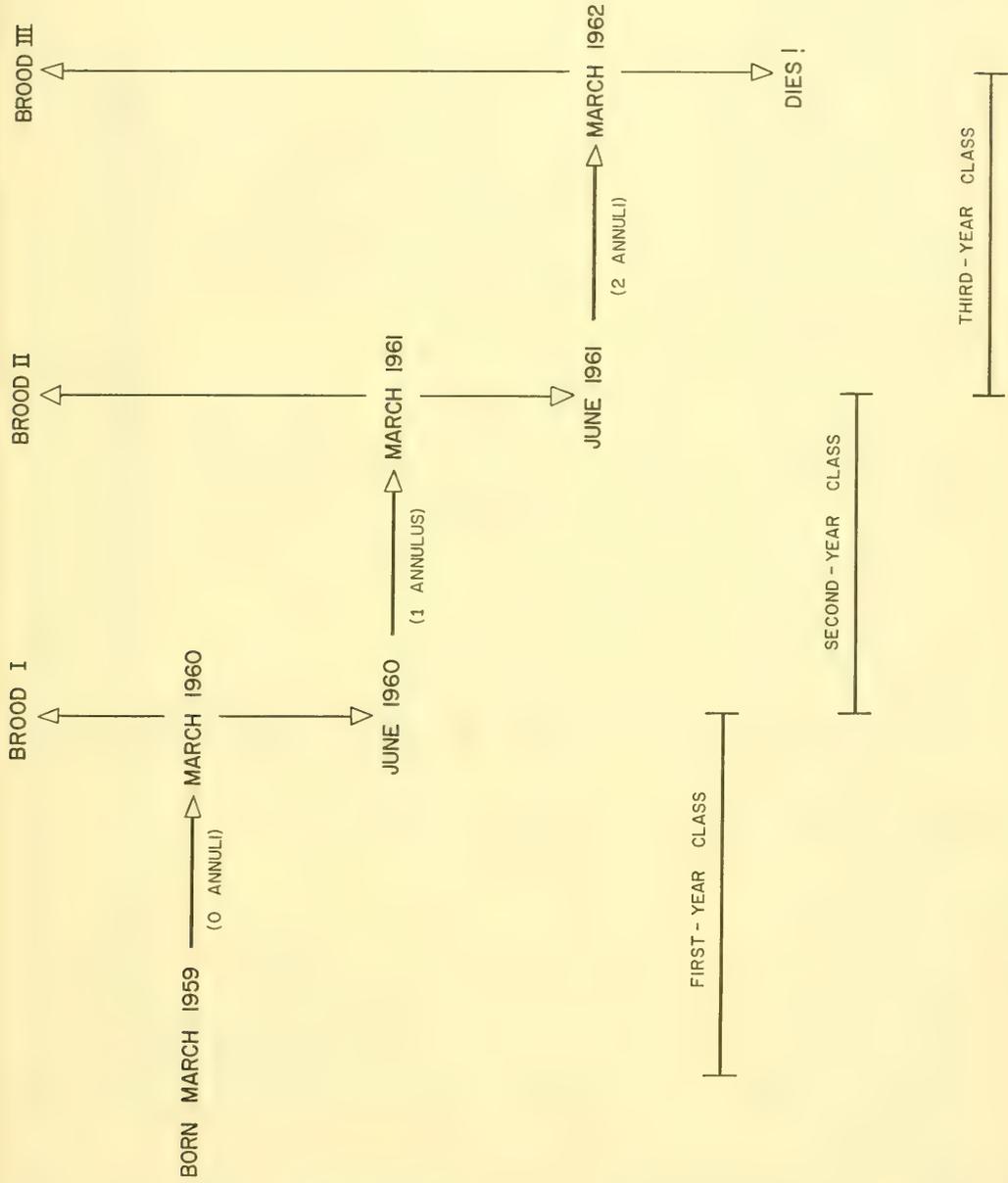


PLATE I. Iteroparous litter production in *Pisidium (Pisidium) dubium* (Say).

TABLE 1. Numbers and sizes of post-dissocoonch embryos in different age classes of *Pisidium (Pisidium) dubium* (Say) from Ore Creek, Michigan, in April and May, 1961.

Age in years	No. P <sub>1</sub> examined		No. F <sub>1</sub> examined		Range of litter size		Average litter size		Range in length of embryos (mm)		Ave. length of embryos (mm)	
	April	May	April	May	April	May	April	May	April	May	April	May
1 (0 annuli)	11	6	71	19	4-19	3-8	10.14	4.75	0.192-0.744	1.008-1.701	0.493	1.437
2 (1 annulus)	5	10	57	95	11-18	7-16	14.25	10.55	0.192-0.912	1.197-2.394	0.469	1.842
3 (2 annuli)	5	6	80	61	15-26	9-18	19.20	12.20	0.168-0.960	1.386-2.520	0.658	1.936

TABLE 2. Gonad activity in *Rivulina* in Michigan<sup>5</sup>

Species	Locality	Peak periods of gametogenesis	Mature gametes most abundant
<i>P. casertanum</i>	trib. of Mill Creek	May-July	October-March
<i>P. casertanum</i>	Fleming Creek	July-October	December-March
<i>P. casertanum</i>	Ore Creek	May-October	December-April
<i>P. compressum</i>	Ore Creek	June-October	December-March
<i>P. c. illinoisense</i>	Fleming Creek	June-September	December-March
<i>P. c. pellucidum</i>	Oxbow Lake <sup>6</sup>	Sept. - Nov. - ?	?-March-May
<i>P. fallax</i>	River Raisin	Aug. - October	Dec. - February
<i>P. nitidum</i>	Oxbow Lake <sup>6</sup>	Sept. - October	?-March
<i>P. variabile</i>	Fleming Creek	Aug. - October	December-March
<i>P. walkei</i>	Ore Creek	Aug. - October	December-April

<sup>5</sup>Based upon histological examination of 5 animals per monthly collection sorted in a graded size series from the smallest to the largest (in length). All 5 animals displayed the same behavior regardless of size.

<sup>6</sup>Heavy ice cover made winter collections impossible.

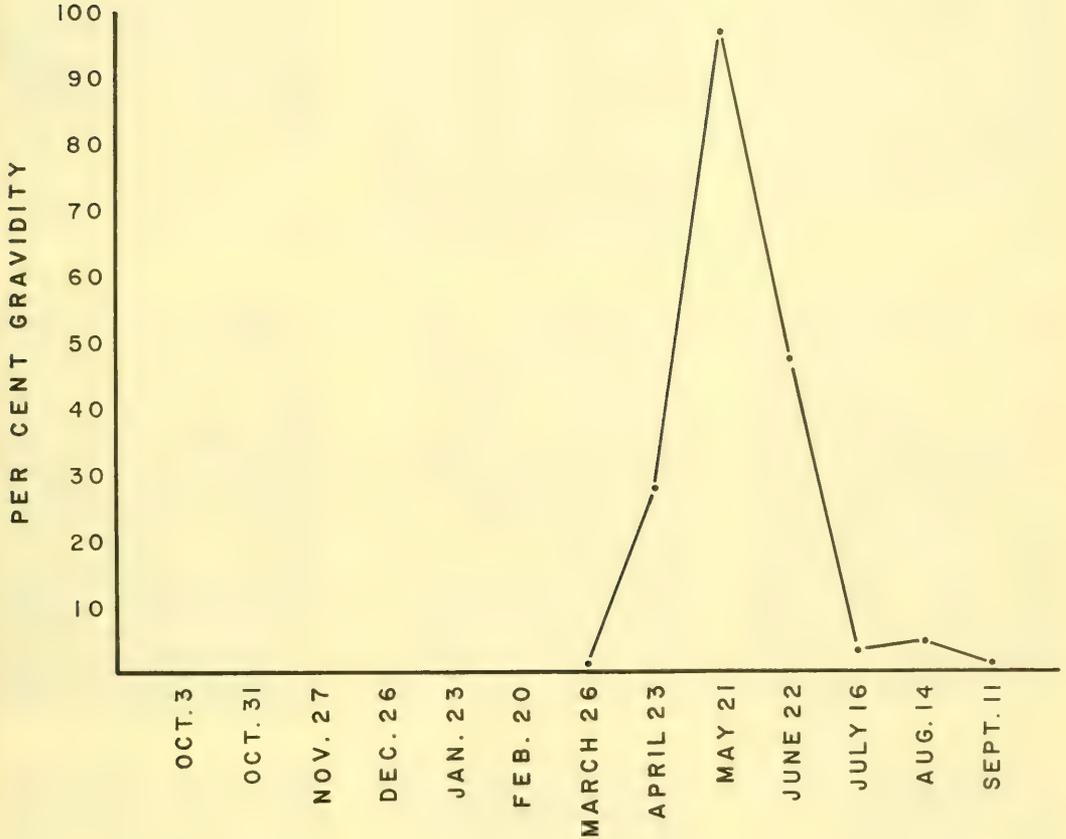


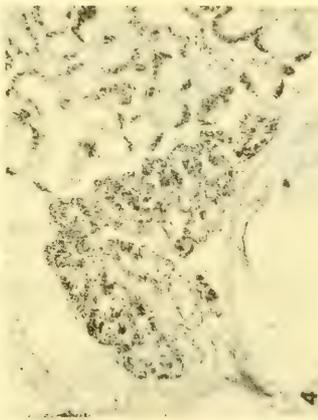
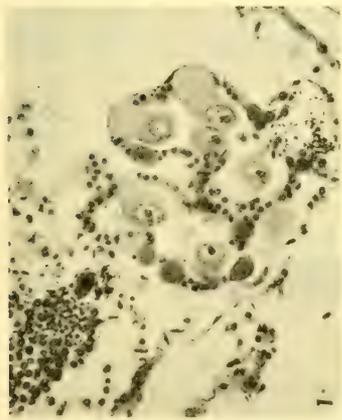
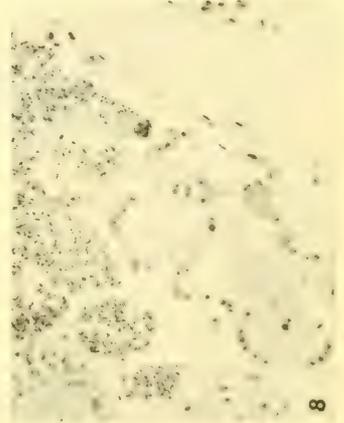
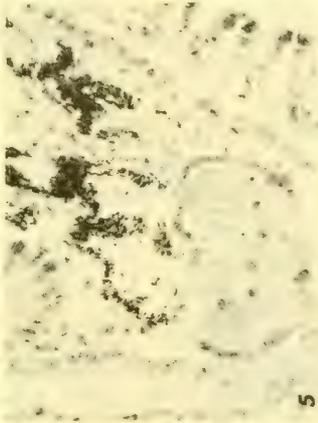
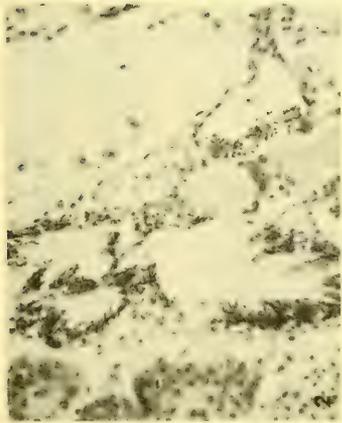
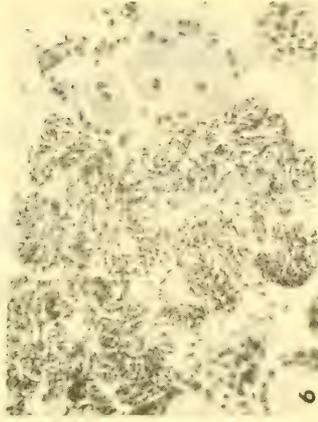
FIG. 1. Seasonal gravidity in *Pisidium (Rivulina) fallax* Sterki.

in the late summer and early fall. A few mature eggs and sperm may be found simultaneously at all times, although both types of germ cells occur in greatest abundance during the winter months (demonstrated in Plate II, Fig. 5). Analysis of the life history collections shows

that the shells increase in size from late summer through the early part of the following summer when, in August, there is a sudden disappearance of larger animals (Plate IV). Annual growth rest marks (annuli) are absent from the shells in all collections except for the largest

## PLATE II.

Gonad sections in pill clams, demonstrating simultaneous occurrence of mature ova and sperm at peak abundance. Mature gametes were present together at all seasons in 6 species (*Rivulina*); in *P. dubium* only in mid-summer and in *P. conventus* and *P. punctatum* for the period investigated. FIG. 1. *Pisidium (Rivulina) casertanum* (Poli). November 5, 1960. 200X. FIG. 2. *Pisidium (Rivulina) compressum illinoisense* Sterki. Jan. 7, 1961. 400X. FIG. 3. *Pisidium (Neopisidium) conventus* Clessin. July 21, 1960. 400X. FIG. 4. *Pisidium (Pisidium) dubium* (Say). July 16, 1960. 100X. FIG. 5. *Pisidium (Rivulina) fallax* Sterki. February 20, 1960. 400X. FIG. 6. *Pisidium (Rivulina) nitidum* (Jenyns. November 27, 1961. 400X. FIG. 7. *Pisidium (Neopisidium) punctatum* Sterki. November 4, 1960. 700X. FIG. 8. *Pisidium (Rivulina) variabile* Prime. December 10, 1960. 400X. FIG. 9. *Pisidium (Rivulina) walkeri* Sterki. November 5, 1960. 400X. (The above are not the actual printed magnifications, but refer to the microscope lens combinations used when taking the photographs.)



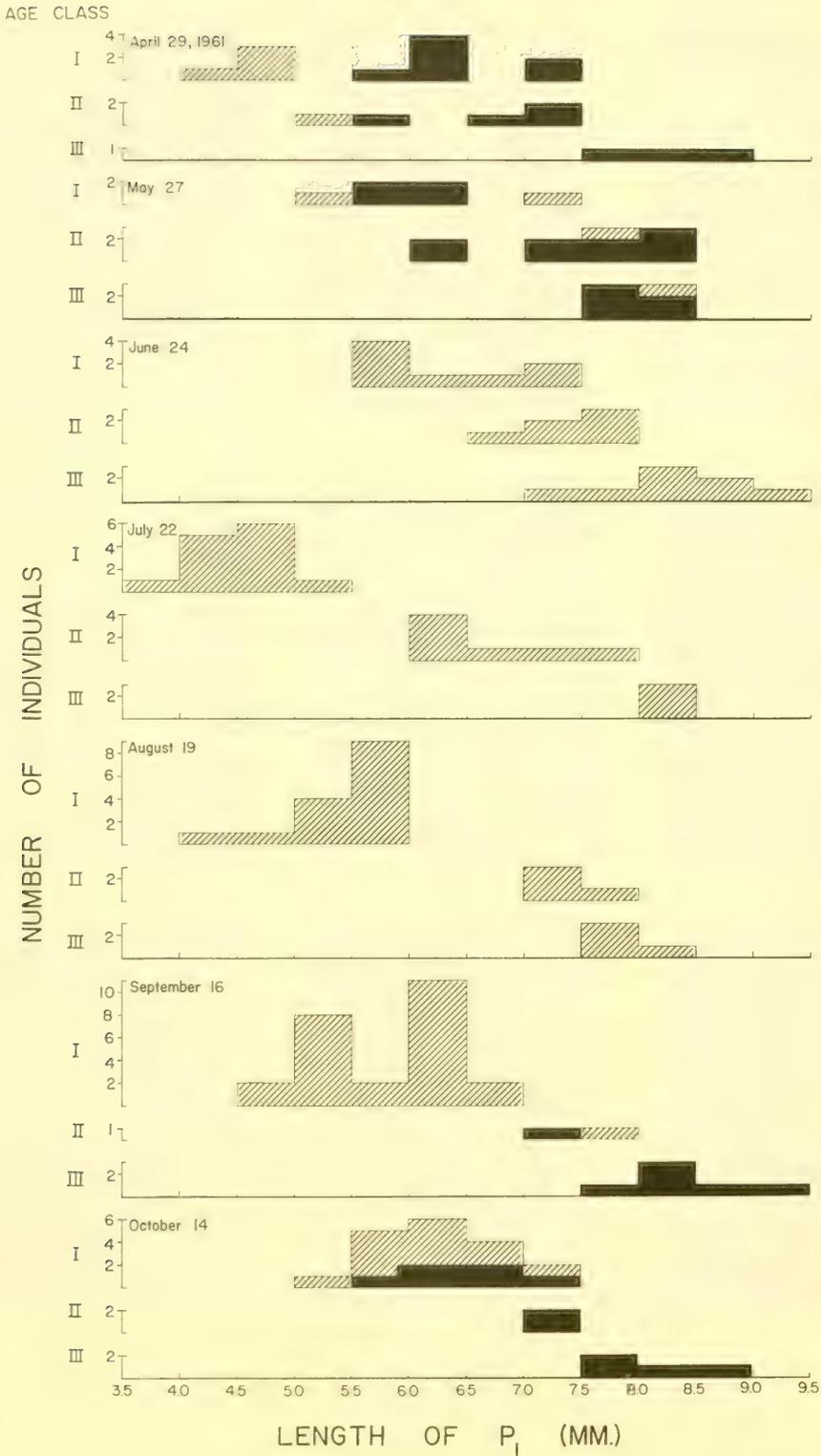


PLATE III. Seasonal size-frequency distribution of *Pisidium (Pisidium) dubium* (Say).

$P_1$  represents the adult generation. Black areas represent gravid animals. Age is classified by the number of growth annuli; I = 1st year; II = 2nd year; III = 3rd year.

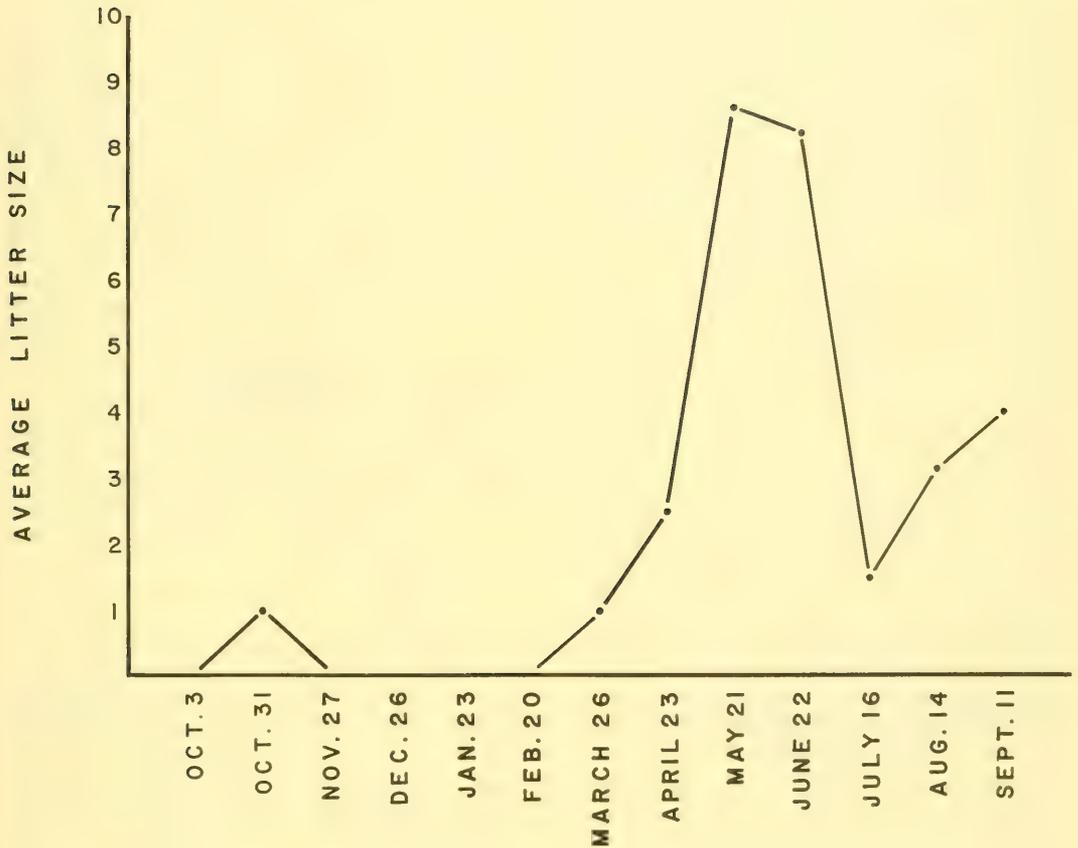


FIG. 2. Seasonal distribution of litter size in *Pisidium (Rivulina) fallax* Sterki.

specimens in the summer months, which have a single annulus. Embryos are present only in the spring and summer. The proportion of the population which is gravid rises to a maximum in late May after which it declines (Fig. 1). The average number of post-dissoconch embryos per

parent (=litter size) parallels the gravid percentage of the population in that it also displays a normal distribution (Fig. 2). The average number of embryos per parent was greatest (8.6) when the "per cent gravidity (i.e., that proportion of the population which is gravid)" was highest

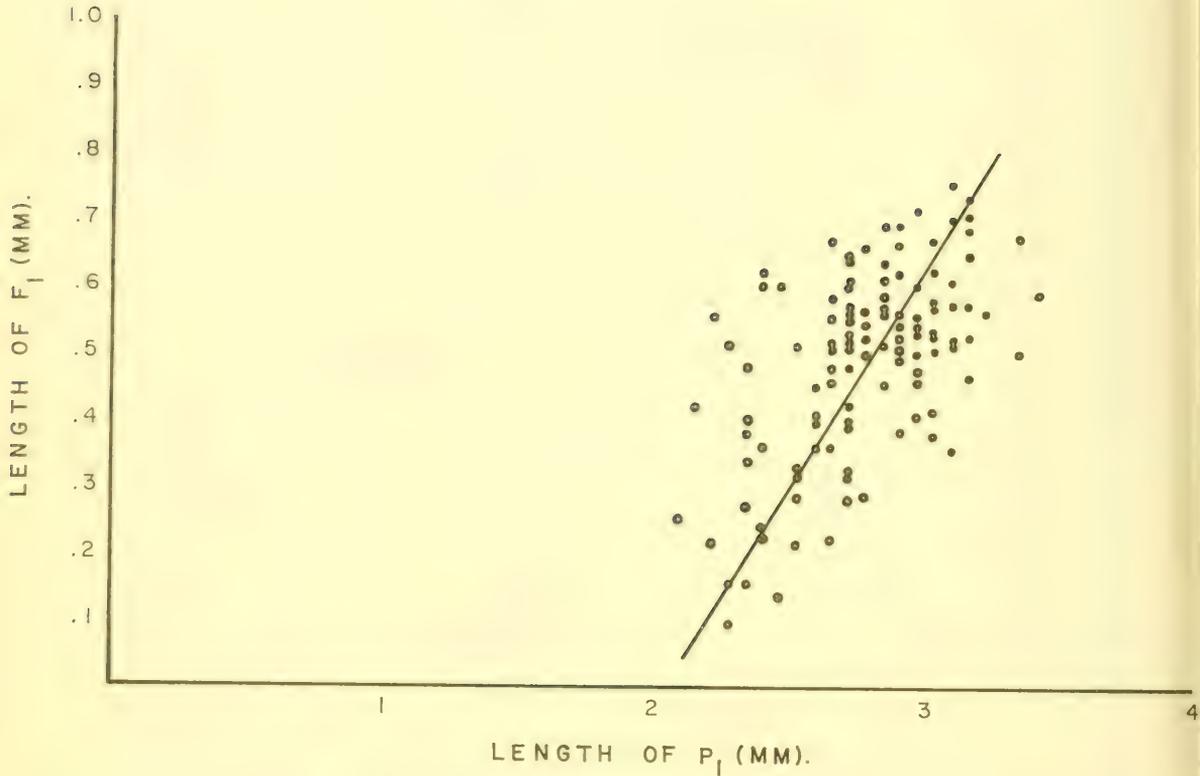


FIG. 3. Relationship of size of embryos to size of parent animals of *Pisidium (Rivulina) fallax* Sterki. Based on measurements of 123 adults which contained 1055 post-dissoconch embryos. P<sub>1</sub> represents the adult generation, and F<sub>1</sub> represents the embryonic generation produced by the P<sub>1</sub>.

(96% in May). All embryos in the same parent were nearly equal in size. The sizes of the embryos increase as the size of the parent increases (Fig. 3) supporting Odhner's (1929a) findings. All

of these data indicate that *Pisidium fallax* lives only 1 year, and that the release of the single litter provides a new generation that replaces the parental generation which dies shortly after the appearance of

the last young of the litter.

*Pisidium casertanum* (Poli)

Gametogenesis was at peak activity from late spring through early summer in the Mill Creek tributary population. A few mature ova and spermatozoa occurred simultaneously throughout all seasons but were most abundant in the fall and winter (Plate II, Fig. 1). The life history collections showed embryos to be present only during late spring and in the summer months (Plate V, Figs. A-D). The average number of embryos per parent was 8.5 when the % gravidity was 30% in May (Table III). All embryos in the same parent were nearly of equal size.

Consecutive monthly samples of *P. casertanum* from Fleming Creek and Ore Creek were also examined histologically. These animals likewise produced at least a few mature gametes throughout the year with greatest abundance during the winter.

*Pisidium compressum* sensu lato

The Fleming Creek population of *Pisidium compressum illinoense* was sampled at monthly intervals for 2 consecutive years. There was no substantial variation between the 2 years in the production of gametes. Ova and spermatozoa were present in all seasons but were far more abundant in winter (Plate II, Fig. 2). The animals increased in size until summer when, in July, there was a significant decrease in the number of individuals in the parental generation. A single growth annulus was present on only the largest shells at that time. Embryos were present only during late spring and early summer. The average litter size in samples from the 2 different years varied significantly. On May 28, 1960, it was 15.7, and on June 3, 1961, it was 20.3 (Table III). This striking variation was probably due in large part to the rather small sample size in each case, and also to the significantly greater % gravidity in the June, 1961, collection.

All embryos in the same litter were of the same approximate size.

Heavy ice cover on Oxbow Lake made winter collections of *Pisidium compressum pellucidum* impossible. Animals from the samples taken in all other months were found to bear some mature eggs and sperm at all times but with markedly greater abundance in the spring. Embryos were present only in the middle and late summer (Plate V, Figs. E-G). The maximum observed average number of embryos per parent was 2.6 when the gravid percentage of the population was 21.2 in June (Table III).

The greatest abundance of mature gametes in *P. compressum* from Ore Creek also occurred during the winter, although both spermatozoa and ova were present at all times.

*Pisidium nitidum* Jenyns

Winter collections were not made from Oxbow Lake. From examination of the samples taken at all other months, however, it was deduced that *P. nitidum* continually produces mature gametes simultaneously with maximum abundance during the winter (Plate II, Fig. 6). Life history studies (Plate V, Figs. H-J) reveal that embryos are present only during the summer. The maximum observed average litter size was 5.4 when the % gravidity was 70.9 in June (Table III). All embryos in the same litter were of the same size.

*Pisidium variabile* Prime

Analysis of gonad activity of animals from the Fleming Creek station revealed that the peak activity of gametogenesis was from late summer through early fall (Table II). Mature gametes were most abundant during the winter (Plate II, Fig. 8), although a few were simultaneously present during all seasons.

*Pisidium walkeri* Sterki

Ore Creek animals of this species exhibited maximum gametogenesis in late

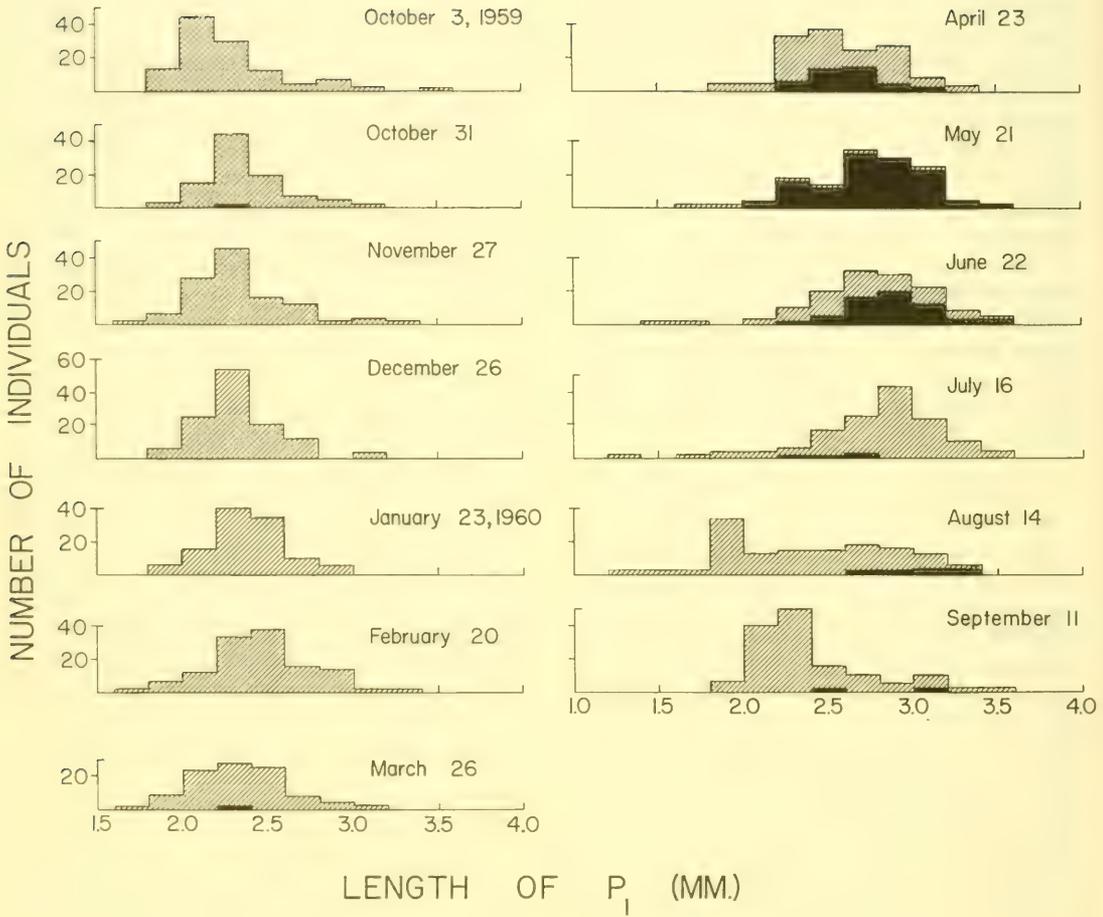
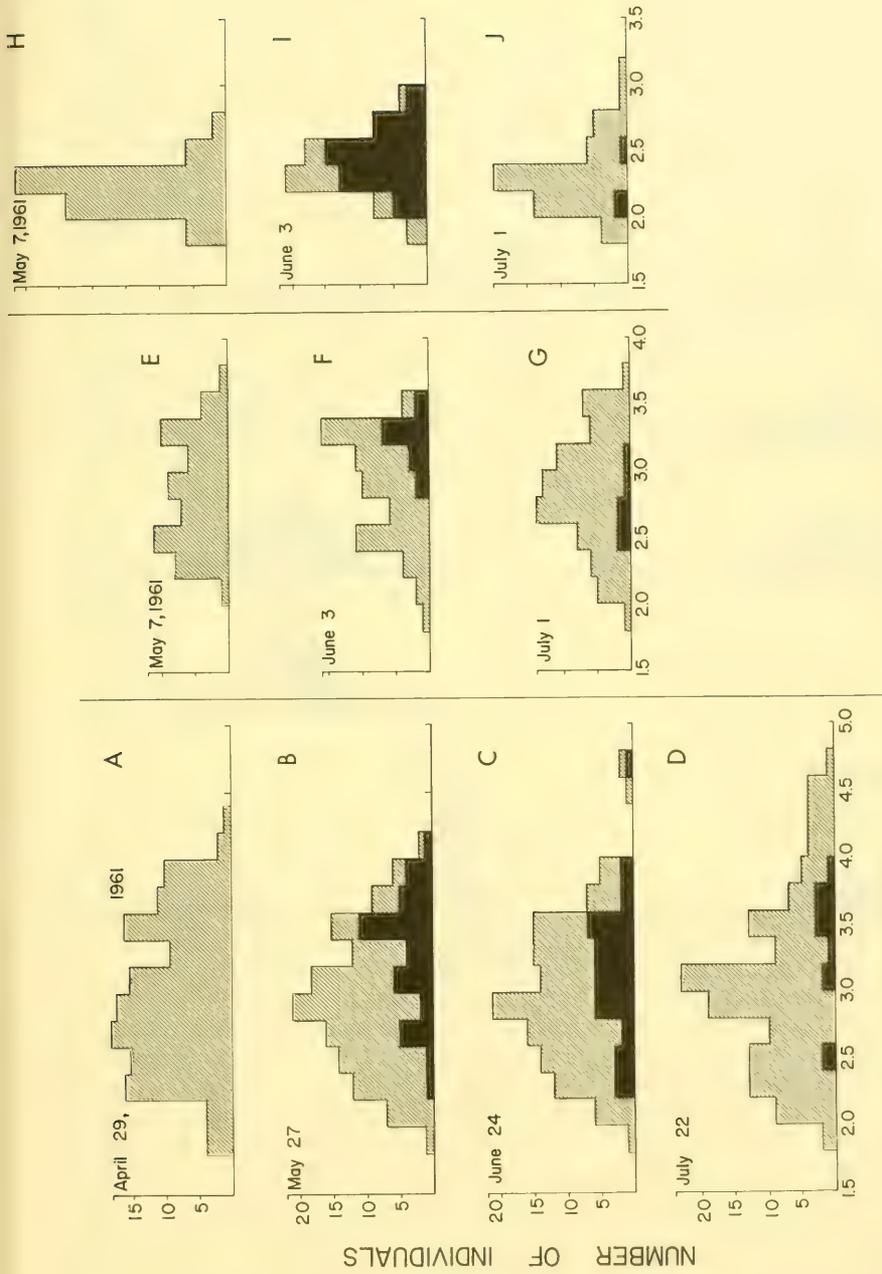


PLATE IV. Seasonal size-frequency distribution of *Pisidium (Rivulina) fallax* Sterki.

$P_1$  represents the adult generation. Black areas represent gravid animals.



LENGTH OF  $P_1$  (MM.)

PLATE V. Seasonal size-frequency distribution of representative rivulinas.

FIGS. A-D. *Pisidium casertanum* (Poli). Tributary Mill Creek, Washtenaw Co., Michigan.  
 FIGS. E-G. *Pisidium compressum pellucidum* Sterki. Oxbow Lake, Oakland Co., Michigan.  
 FIGS. H-J. *Pisidium nitidum* Jenyns. Oxbow Lake, Oakland Co., Michigan.  $P_1$  represents the adult generation. Black areas represent gravid animals.

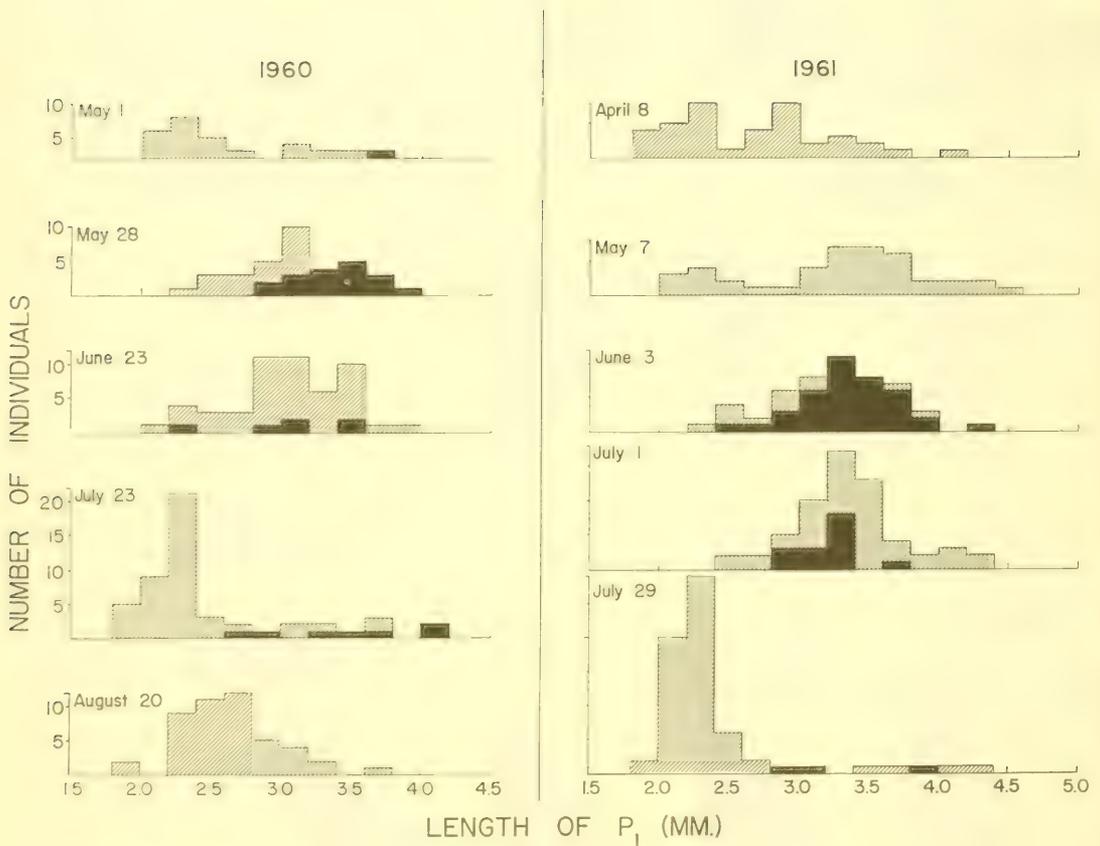


PLATE VI. Seasonal size-frequency distribution of *Pisidium (Rivulina) compressum illinoense* Sterki. P<sub>1</sub> represents the adult generation. Black areas represent gravid animals.

summer and early fall. Ripe ova and spermatozoa occurred most abundantly during the winter (Plate II, Fig. 9) and early spring, but were always present together during all seasons.

This investigation indicates that in American rivulinas the embryos develop in the spring and early summer. The rare instances of embryos found beyond this time is explained on the basis of individual variation and differential development within the population. There exists no fall "bloom" of fry in the form of a second litter. In only four of nearly 5000 shells examined during the course of this investigation were there as many as two annuli. These annual species bear one litter, approximately one year after their own birth, and die shortly thereafter.

Differences between Nearctic rivulinas (see also under Discussion) appear to lie primarily in numbers of embryos which in some instances reach those observed for *Pisidium* s.s. and in others are lower. These variations are listed in Table III.

#### LIFE HISTORIES IN THE SUBGENUS NEOPISIDIUM ODHNER

##### *Pisidium conventus* Clessin

The ovotestes produce ova in the lateral (distal) areas and spermatozoa in the medial (proximal) regions. In animals from Lake Superior mature eggs and sperm occurred simultaneously (Plate II, Fig. 3) from May through October. Samples from other months were unavailable for examination, although there seemed to be a general decrease in gonad activity toward October. Embryos were also present from May through October (see Plate VII, Figs. A and B). Gametogenesis provided the foundation for a future brood (litter II) while the embryos (litter I) in the gills were developing and approaching the time of their release. The periods of appearance of the different litters are not accurately known, but the large sizes of the embryos in the May and

October collections suggest that the new generations are born in summer and winter. Because of the seasonal lag in heat absorption in the Great Lakes, these periods are actually equivalent, ecologically, to the fall and spring seasons in the surrounding inland lakes and streams. The number of post-dissoconch embryos ranged from 1 to 10 and averaged 6 per parent in the 15 animals examined from the October collection. This figure agrees well with Odhner's (1923) report of 8 embryos in animals from Novaya Zemlya and 6 from the Oxfjord region in Norway. All individuals in the same litter were nearly identical in size.

Odhner (1951) reported that in the laboratory animals of *P. conventus* from Sweden may live several years before reproducing, then producing several litters about a half-year apart. Those litters were produced by self-fertilization; it is unknown whether self- or cross-fertilization (or both) is (are) employed in nature. In addition, while the life-span of laboratory-bred *P. conventus* is potentially several years, the life-span of this species in nature is unknown. It should be noted, however, that in both the Lake Superior animals and Odhner's specimens the gestation period was about 6 months.

##### *Pisidium punctatum* Sterki

Mature ova and spermatozoa were found together in the same ovotestes and were abundant in animals of this species collected in May and November (Plate II, Fig. 7). These animals also contained embryos. Two samples of 25 specimens each were taken at random from both collections and were dissected; the post-dissoconch embryos were measured and counted (Plate VII, Figs. C and D). In the May sample only 3 of the 25 animals were gravid. The litter size ranged from 4-18, and the embryos varied in length from 0.1-0.7 mm. In the November sample 12 of the 25 animals were gravid. The post-dissoconch embryos ranged from 2-12 in number, averaging about 6, and

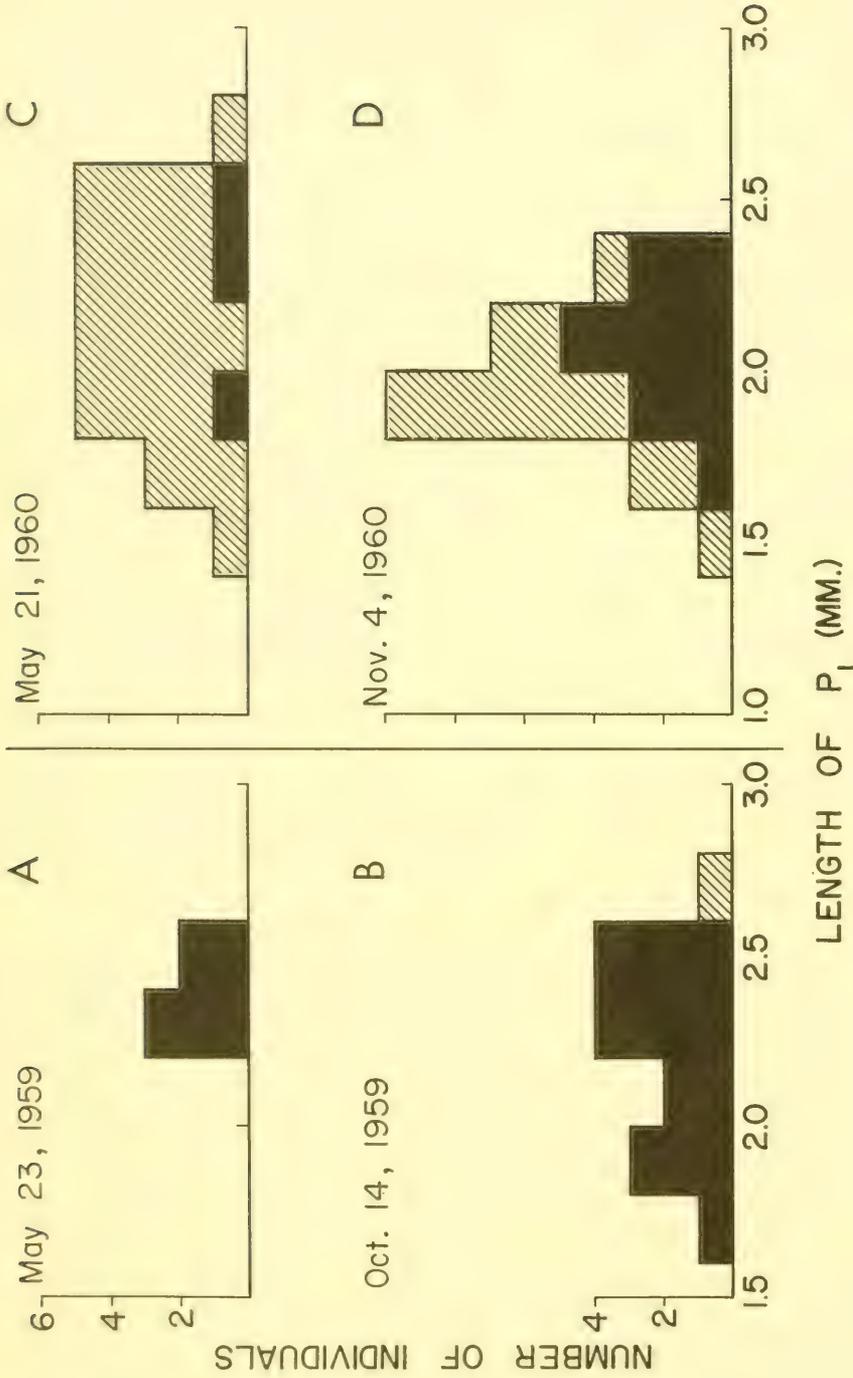
PLATE VII. Size-frequency distribution in *Neopisidium*.

FIG. A. *Pisidium conuentus* Clessin. Lake Superior. May 23, 1959. FIG. B. *Pisidium conuentus* Clessin. Lake Superior. October 14, 1959. FIG. C. *Pisidium punctatum* Sterki. Tributary White Oak Creek, Tennessee, May 21, 1960. FIG. D. *Pisidium punctatum* Sterki. Tributary White Oak Creek, Tennessee, Nov. 4, 1960. P<sub>1</sub> represents the adult generation. Black areas represent gravid animals.

from 0.1-0.8 mm in length. In the gravid specimens of both collections all embryos in the same litter were approximately the same size.

In comparison with developmental stages of *Pisidium conventus* it appears that the May collection of *P. punctatum* was made after the release of litter I and barely after the initial development of litter II. The November collection was made late in the development of litter II and at a time when gametogenesis was providing the basis for a potential third litter. With these observations in mind, the gestation period for *P. punctatum*, as well as for *P. conventus*, appears to be about 6 months. Annuli were either absent or obscured in both *P. conventus* and *P. punctatum*, and consequently the natural life-span of *Neopisidium* is unknown.

#### DISCUSSION

Pill clams exhibit a remarkable gonad performance which is somewhat intermediate between proterogyny and functional ambisexuality (see Coe, 1943). In proterogyny the female gametes mature in advance of the male gametes, while in functional ambisexuality both types of sex cells are continuously produced simultaneously. Despite the seasonal differences in gonad activity observed between members of different subgenera, the patterns are essentially identical: a few mature eggs and sperm are found throughout the year but are simultaneously most abundant for only a relatively short time. In *Pisidium (Pisidium) dubium* spermatozoa appear only briefly, although some ova are always present.

Laboratory observations have clearly demonstrated that *Pisidium (Neopisidium) conventus* (see Odhner, 1951), *P. (Rivulina) milium* (see Odhner, 1929a), and *Musculium partumeium* (see Thomas, 1959) have the capacity for production of fry through self-fertilization. That all sphaeriids possess this characteristic has been widely reported and has probably gained widespread acceptance because it has long been known that the eggs and

sperm are produced simultaneously. However, this is not positive evidence that self-fertilization either can or does occur in all species of the family. Hermaphrodites in many animal groups typically cross-fertilize even though they possess a potential for self-fertilization. Sphaeriids probably also reproduce by facultative autogamy, normally breeding in nature by cross-fertilization and only occasionally breeding by self-fertilization, i.e., in the laboratory or in nature under unusual environmental conditions.

Although universal in the freshwater clams of the Unionacea (families Margaritiferidae, Mycetopodidae, Mutellidae, Unionidae) and the Sphaeriidae (Sphaeriacea), ovoviviparous reproduction also occurs in a diverse assemblage of terrestrial, marine, and other freshwater mollusks (see van der Schalie, 1936). The freshwater snail family Viviparidae, for example, is uniformly ovoviviparous. Not only are there differences between its genera with respect to the functional organization of the reproductive system, but there is evidently considerable variation with the genera (see Van Cleave and Lederer, 1932; Van Cleave and Chambers, 1935; Van Cleave and Altringer, 1937). *Campeloma rufum* is parthenogenetic, while *Lioplax subcarinata occidentalis* has separate sexes. *Viviparus bengalensis* and *V. contectoides* are dioecious, but *V. angularis* is monoecious. Despite these variations, the Nearctic *Campeloma*, *Lioplax*, and *Viviparus* all carry the embryonic snails during the winter and release them in the late spring and early summer.

The genera of sphaeriid clams in the northern Temperate Zone also present several striking differences in their life histories. *Sphaerium* (see Foster, 1932; Monk, 1928) carries the embryos over the winter and releases them in late spring and early summer as does *Pisidium* s.s. Gametogenesis in the fall provides for the next (spring) generation. In *Musculium* (Herrington, 1944, 1948; Okada, 1935a, 1935b; Thomas, 1954) gametogenesis occurs throughout the year

with certain peak activities (spring and autumn) when the eggs are presumably fertilized. Although embryos may be found at all times, maximum numbers appear in the fall and spring, corresponding to the spring and autumn fertilization, respectively. The reproductive habits in *Pisidium* differ depending on the species. *Pisidium* s.s. in Michigan lives several years and produces litters of larger sizes each year in the spring. Fertilization occurs in the late summer, and the embryos overwinter in the parents. Michigan members of *Rivulina* are annual species which carry embryos in the early spring, releasing them in late spring and early summer. Fertilization takes place in fall and winter. *Neopisidium* in North America produces more than one litter per year and may live several years. There is no available information concerning the life histories of the species of *Eupera* Bourguignat (Africa, Central and South America), *Byssanodonta* d'Orbigny (South America), and *Pseudocorbicula* Dautzenberg (Africa).

There is also considerable variation in the life histories of pill clams at the population, specific, and subgeneric levels. These differences are discussed in the sections to follow.

#### Intraspecific Variation in *Rivulina* Life Histories

Examination of gonad activity of populations of *Pisidium casertanum* from the Mill Creek tributary, Fleming Creek, and Ore Creek (Table 2) shows that although there may be considerable differences in time of maximum gametogenesis, mature gametes are most abundant within the same relatively restricted time range, i.e., fall or winter to spring.

In *Pisidium compressum* s.l. periods of maximum gametogenesis also differed more than periods of greatest abundance of mature gametes (Table 2). The Fleming Creek and Ore Creek populations exhibited nearly identical performance, but the Oxbow Lake population appeared to lag in gonad activity by several months. This

should not seem unusual in view of temperature relations in lentic and lotic waters. Lakes tend to warm up slower in the spring than streams, and frequently there is a corresponding lag in biological activities.

Life history collections of *Pisidium compressum* also revealed a significant variation in numbers of embryos between *P. c. illinoisense* in Fleming Creek (up to 42) and *P. c. pellucidum* in Oxbow Lake (up to 6) (Table 3). This large difference was probably due to a lower % gravity and to the effects of parasitism in the latter case. Two populations of pill clams studied in this investigation (see Table 3) were heavily infected with trematodes. While the effects of parasitism on the reproductive biology of mollusks are still incompletely known, it is believed that the parasites may inhibit the functional development and activity of the gonad(s). In the pond snail *Physa occidentalis* the gonad appears to suffer no harm in light infections, but in severely diseased animals this organ entirely vanishes (Hurst, 1927). Whether the parasitism of *P. c. pellucidum* caused the marked variation in numbers of embryos observed in comparison with uninfected animals of *P. c. illinoisense*, or whether these differences are genetic in nature and represent subspecific variation is not known. It seems probable that the former explanation has more merit as there is a corresponding difference in the numbers of embryos between infected animals of *Pisidium casertanum* from the Mill Creek tributary and uninfected animals of *P. casertanum* from Fleming Creek (see Table 3).

#### Interspecific Variation in Life Histories

Data bearing on the seasonal gonad activity and life history of 6 rivulinas are presented in Tables 2 and 3. The range of most gametogenesis occurs over a longer period of time in *Pisidium casertanum* and *P. compressum* than in *P. nitidum*, *P. variabile*, and *P. walkeri*, ranging from late spring through late fall

TABLE 3. Comparisons of differences in numbers of embryos (litter size) in *Rivulina* in Michigan. The data shown were selected to present litter sizes at maximum gravidity.

Species	Locality	Date	No. clams examined	Per Cent gravidity	Range of litter size	Average litter size
<i>P. casertanum</i> <sup>7</sup>	trib. to Mill Creek	May 21, 1960	133	30	1-32	8.5
<i>P. casertanum</i>	Fleming Creek	May 28, 1960	32	63.7	1-42	16.3
<i>P. compressum illinoisense</i>	Fleming Creek	May 28, 1960	35	51.4	1-42	15.7
		June 3, 1961	51	78.4	1-42	20.3
<i>P. c. pellucidum</i> <sup>7</sup>	Oxbow Lake	June 3, 1961	66	21.2	1-6	2.6
<i>P. fallax</i>	River Raisin	May 21, 1960	129	96.1	1-24	8.6
<i>P. nitidum</i>	Oxbow Lake	June 3, 1961	62	70.9	1-13	5.4

<sup>7</sup>Heavily infected with trematodes.

in the former 2 species, but from late summer through late fall in the latter 3 species (Table 2). Overlap of (a) periods of maximum abundance of mature gametes in the fall and winter, and (b) periods when the species are gravid in late spring and early summer may, however, mask any relevant differences that might exist between the species.

More significant differences between species of *Rivulina* are found with respect to numbers of embryos (Table 3). Each species appears to have its own relatively characteristic number of fry produced. Because these values also overlap, the average litter size is more meaningful. Perhaps, as more quantitative information of this kind becomes available for other species, these average numbers will also overlap. Some species may then be found to constitute natural groupings, although parallel evolution, if present, might confuse the situation.

The previous discussion is based primarily on genetic variation between species, but abiotic and biotic ecological forces also bear upon the reproductive biology of animals. Examination of data on several species of *Rivulina* (*Pisidium casertanum*, *P. compressum*, and *P. variabile*) collected from the same habitat (Fleming Creek) at the same times reveals that the periods of most active gametogenesis, most abundant mature gametes, and gravidity coincide exactly. Only the

numbers of embryos differ. As mentioned previously, parasitism influences the reproductive biology of mollusks, not only in gonad activity but presumably also in the numbers of young produced. Abiotic environmental forces (e.g., temperature of the water) would seem to affect seasonal gonad activity rather than numbers of young, while certain biotic forces such as parasitism could influence both.

The findings on the life histories in North American *Rivulina*, which in Michigan indicate a normal life span of one year and a single litter in spring or early summer, are not in agreement with Odhner's (1929a) data on Swedish species of this group which (a) contain embryos twice yearly, in late spring and in the fall, (b) reach the age of 3 to 4 years according to the number of annuli on the valves, and (c) attain sexual maturity during the second year of life with reproduction also proceeding into the third year. These great differences between Swedish and Michigan species of *Rivulina* may be due either to genetic variation between animals of 2 presently isolated continents, or to a clinal reproductive behavior which is influenced ecologically by different latitudinal climates which serve to determine, at least in part, the lengths of the developmental, dormant, and/or reproductive periods in the life of each species.

Odhner's (1929a) observations on

Swedish sphaeriids were not quantitative, and just how indicative his data on litter size in *Rivulina* (see Table 4) are cannot be stated because (a) the % gravity is unknown, (b) the average litter size varies with the % gravity, and (c) the presence or absence of parasitism is unknown. Odhner reported animals with embryos in early spring and in late fall, but it is not known whether these embryos truly constitute two distinct litters or whether they actually belong to the same litter, the individuals being released over a very long period of time. The greater northern latitudes of Sweden<sup>8</sup> suggest a longer cold (= dormant or stimulating?) period characterized by animals displaying slow growth, slow maturity, and small size. More southern latitudes (e.g., Michigan) suggest larger animals with more rapid development and maturity. The role of climate as a stimulating or retarding influence in the life history of sphaeriids is not adequately known at the present time, however, and the warming effect of the Gulf Stream upon Europe is a further complicating factor since locations in Europe are warmer than at places of corresponding latitudes in North America. In addition certain animals (most species of *Pisidium* s.s. and *Rivulina* appear to be better adapted to more northerly climates than others (most species of *Neopisidium*).

While one cannot presently compare life histories of *Pisidium* in Europe and North America, it is possible to speculate upon a possible latitudinal clinal reproductive behavior within the Nearctic Region.

The original data concerning Michigan populations of *Pisidium* presented here

clearly indicate a series (or sequence) of time-limited reproductive phases (i.e., periods of gametogenesis, times of greater abundance of mature gametes, and release of fry), but Herrington (1950) found no evidence of a time-restricted breeding season<sup>9</sup> in Great Slave Lake, Northwest Territories, Canada, for *Pisidium* (*Pisidium*) *idahoense*, *P. (Rivulina) lilljeborgi*, and *P. (R.) subtruncatum*.

Although Herrington (1950) found no specific breeding season in *Pisidium* (*Pisidium*) *idahoense* Roper, additional data (Heard, unpublished) suggest that this species from Great Bear Lake, Northwest Territories, Canada, attains a smaller size but produces a larger litter than in the more southern Prince Edward Island (Province), Canada. The shorter (warm) growing season in the northernmost locality is presumably responsible, at least in part, for the stunted form.

The natural reproductive patterns of sphaeriids in areas further south than Michigan are not currently known. However, the life history of *Pisidium* (*Pisidium*) *dubium* in northern Florida, U.S.A., is now under investigation by the author, and when completed these data will be compared to similar data presented here for the same species in Michigan.

It is premature to speculate upon the direction of the possible clinal reproductive behavior in sphaeriids, but if such a phenomenon exists it may be reflected in (a) the length of the embryonic incubation period and (b) the length of time or precise season of parturition, or less likely, (3) the number of litters per year and (4) the litter size.

#### Life History Variation at the Subgeneric Level

The life histories of certain Nearctic representatives of *Pisidium* s.s., *Rivulina*, and *Neopisidium* have already

<sup>8</sup>Latitudes are: Sweden, 55°-69° north; Great Bear Lake, Northwest Territories, Canada, 65°-67° 30' north; Great Slave Lake, Northwest Territories, Canada, 61°-63° north; Prince Edward Island (Province), Canada, 46°-47° north; Michigan, U.S.A., 42°-47° north (area of this study 42°-42° 30'); northern Florida, U.S.A., 30° 30' north.

<sup>9</sup>"...with the possible exception of *P. conventus*..." although the evidence was not quantitative.

TABLE 4. Qualitative life history data on Swedish rivulinas (from Odhner, 1929a)

Identification	Date	Size of adult (length in mm)	Number of embryos
<i>P. cinereum</i> (= <i>P. casertanum</i> <sup>10</sup> )	Aug. 5, 1914	4.0	17
<i>P. henslowanum</i> <sup>11</sup>	June 27, 1908	4.4	7
<i>P. hibernicum</i> (= <i>P. ferrugineum</i> ?)	?	2.6	20
<i>P. liljeborgi</i> <sup>10</sup>	?	3.7	13
<i>P. milium</i> <sup>10</sup>	July 7, 1908	?	11
<i>P. nitidum</i> <sup>10</sup>	July 9, 1919	2.3	7
<i>P. obtusalastrum</i> (= <i>P. obtusale</i> <sup>10</sup> )	?	?	16
<i>P. pulchellum</i>	Sept., 1919	3.0	5
<i>P. subtruncatum</i> <sup>10</sup>	July 29, 1914	3.8	5

<sup>10</sup>Circumpolar species

<sup>11</sup>Introduced into North America.

been discussed individually and are briefly summarized in Table 5.

The breeding habits of pill clams may be classified as iteroparous or semelparous (see Cole, 1954). Iteroparous animals exhibit more than one reproduction in their lifetime and have overlapping generations (i.e., different age classes). Semelparous animals, however, have just one reproduction in their lifetime and may or may not be annual

species, although they are generally considered to have non-overlapping generations. *Pisidium* s.s. and *Neopisidium* are clearly iteroparous. *Rivulina* was found to exhibit a semelparous habit in central North America, but other findings suggest that this group is iteroparous in northern Europe. Since certain species of *Rivulina* apparently reproduce several times, the life histories of the 3 subgenera might also serve to evaluate their probable

TABLE 5. Comparison of the life histories of *Pisidium* s.s., *Rivulina*, and *Neopisidium* in central North America.

Taxon	Peak periods of gametogenesis	Mature gametes most abundant	Life span (years)	No. broods per year	Period of gravidity	Parturition period	Litter size
sg. <i>Pisidium</i> s.s.	early summer	early summer	3	1	fall through spring	spring	increases with each year of life
sg. <i>Rivulina</i> <sup>12</sup>	summer through fall	fall through winter	1	1	spring	spring	variable (TABLE I)
sg. <i>Neopisidium</i>	summer? and winter?	fall? and spring?	? <sup>13</sup>	2	winter and summer	spring and fall	small

<sup>12</sup>North America: 1-year life span, 1 annual brood; Sweden: life span of several years, 2 broods yearly.

<sup>13</sup>Potentially several in laboratory animals (see Odhner, 1951).

TABLE 6. Known reproductive patterns in *Pisidium* C. Pfeiffer

Identification	Length of pre-reproductive life		Life span (years)		No. litters per year		Litter size	
	short	long	1	>1	1	2	small	large
<i>Pisidium</i> s. s.								
Michigan, U. S. A.								
<i>P. dubium</i>		X		X	X			X
Sweden <sup>14</sup>								
<i>P. amnicum</i>	?	?	?	?	?	?	?	?
<i>Rivulina</i>								
Michigan								
<i>P. adamsi</i> <sup>15</sup>	?	?	?	?	?	?		X
<i>P. casertanum</i>	X		X		X			X
<i>P. compressum</i> s.l.	X		X		X			X
<i>P. fallax</i>	X		X		X		X	
<i>P. nitidum</i>	X		X		X		X	
<i>P. variabile</i> <sup>15</sup>	X		X		X			X
<i>P. walkeri</i>	X		X		X		?	
Sweden <sup>14</sup>								
<i>P. casertanum</i>	?	?		X		X		X
<i>P. henslowanum</i>	?	?		X		X	X	
<i>P. hibernicum</i>	?	?		X		X		X
<i>P. lilljeborgi</i>	?	?		X		X		X
<i>P. milium</i>	?	?		X		X		X
<i>P. nitidum</i>	?	?		X		X	X	
<i>P. obtusale</i>	?	?		X		X		X
<i>P. pulchellum</i>	?	?		X		X	X	
<i>P. subtruncatum</i>	?	?		X		X	X	
<i>Neopisidium</i>								
Lake Superior (Mich.)								
<i>P. conventus</i>	?	?	?	?		X	X	
Tennessee, U. S. A.								
<i>P. punctatum</i>	?	?	?	?		X	X	
Sweden <sup>16</sup>								
<i>P. conventus</i>		X		X		X	X	

<sup>14</sup>See Odhner, 1929a.<sup>15</sup>See Heard, 1964.<sup>16</sup>Laboratory observations; see Odhner, 1951.

evolutionary connection. Unfortunately, their phylogenetic relationships to *Odhneripisidium* and *Afropisidium* remain unknown.

Animals can increase their biotic potential by increasing (a) the litter size in a single reproduction or (b) the number of litters by repeated reproduction (see Cole, 1954). Iteroparous reproduction

has value in greater potential ability to produce more young than does semelparous reproduction. The significance of changes in litter size and changes in the number of litters produced purportedly depends on the rate of maturation, i.e., how soon reproduction first appears. The selective value of iteroparity is presumably greatly increased with delayed

maturation, i.e., longer pre-reproductive life, and there would seem to be added value in increased litter size in iteroparous species with delayed maturity.

Anatomically, the relatively large *Pisidium* s.s. is more primitive, while *Rivulina* and *Neopisidium* show structural reduction in the posterior gill and the branchial siphon as well as smaller size. Utilizing the biological concepts of semelparity and iteroparity, it can be postulated that the changes in reproductive patterns that have apparently accompanied these morphological changes have evolved from the long pre-reproductive life and large size of the single annual litter in *Pisidium* s.s. to (1) a shorter pre-reproductive life and variable size in multiple litters (?) in *Rivulina* and (2) shorter pre-reproductive life and smaller size of multiple litters in *Neopisidium* (see Table 6).

The seemingly semelparous life cycles of the Michigan rivulinas require critical evaluation. There would be little value in a change from iteroparity in the more primitive *Pisidium* s.s. to semelparity in *Rivulina*. It seems more likely that iteroparity, despite a shorter pre-reproductive life, was retained, only to be retarded (disguised?) by varying latitudinal climates. This would perhaps explain the occurrence of mature gametes in Michigan rivulinas while the annual (spring) nears the parturition period; the adults die, following the release of the fry, before these sex cells can provide for a second (fall) brood. If large litter size were also retained in *Rivulina* (e.g., in *P. compressum*), the advantage of multiple litters per year would be obvious. If the litter size were reduced (e.g., in *P. fallax*), the total number of young produced each year might still be approximated by multiple litters. The behavior of *P. (R.) fallax* is somewhat like that of *Neopisidium* which is characterized by reduced litter size, multiple litters per year, and shorter pre-reproductive life. These observations suggest that in this genus delayed maturity does not necessarily hold significant selective advantage

over a short pre-reproductive life.

Since information bearing on the life histories of the subgenera *Odhneripisidium* and *Afropisidium* are entirely wanting, attempts to plot extensive phylogenetic relationships within the entire genus *Pisidium* C. Pfeiffer are premature. However, it has been possible to speculate on the possible affinities of the subgenera *Pisidium* s.s., *Rivulina*, and *Neopisidium*.

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## RESUMEN

BIOLOGIA COMPARADA EN ALMEJITAS NORTEAMERICANAS DEL GENERO *PISIDIUM* (SPHAERIIDAE)

Aunque existen algunos estudios embriológicos sobre *Sphaerium* y *Musculium*, la mayoría de la información que tenemos sobre estos pequeños bivalvos esféricos, son de naturaleza taxonómica. La presente investigación es el primer intento para determinar, en detalle, la biología estacional en el género *Pisidium* Pfeiffer.

Se hicieron colecciones cuantitativas en todas las estaciones del año, principalmente en el sur de Michigan, con el objeto de investigar, a) variación intraespecífica, b) variación interespecífica dentro de un mismo género, y c) variación interespecífica entre miembros de diferentes subgéneros en términos de biología general, actividad gonadial y otros aspectos de la reproducción.

Ambas variaciones intraespecíficas e interespecíficas en un mismo subgénero se reflejan en diferencias de tiempo en la actividad gonadial y tamaño promedio de las crías, aunque variación intraespecífica es primariamente ecológica y la interespecífica esencialmente genética en origen. Sorprendentes diferencias en la historia natural de los subgéneros se encontraron con relación al número de crías producidas en la vida del

individuo, la duración de esta vida y el tamaño de las crías. *Pisidium* s.s. produce cada año crías relativamente grandes, y durante varios años. *Rivulina* vive sólo un año y reproduce una sola vez (representantes paleárticos muestran opuesto comportamiento, pareciendo vivir más tiempo y reproduciéndose con más frecuencia), y *Neopisidium* produce dos crías anuales y potencialmente puede vivir dos años.

El presente estudio permite especular sobre las posibles relaciones evolutivas de *Pisidium* s.s., *Rivulina* y *Neopisidium*. Asumiendo un cambio evolucionario (1) en especies iteróparas (a) ya sea por un aumento en el número de crías o (b) por un hábito reproductivo semélparo (regresión ?), y (2) en animales semélparos de un menor a un mayor tamaño en las crías, se puede conjeturar que *Pisidium* s.s., anatómicamente más primitivo, dió lugar a la aparición de *Rivulina* y *Neopisidium*. Sus relaciones con los géneros etiípicos *Afropisidium* y *Odhneripisidium* son hasta ahora desconocidas.



РОДОВЫЕ ДИАГНОЗЫ ДЛЯ НЕКОТОРЫХ ЗАКАПЫВАЮЩИХСЯ ДВУХСТВОРЧАТЫХ  
МОЛЛЮСКОВ АВСТРАЛИЙСКОЙ ПЕРМИ

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АБСТРАКТ

Тут рассматриваются различные классификации некоторых закапывающихся двухстворчатых моллюсков австралийской перми, сделанные Ньюэллом (1956) и Диккинсом (1963). Морфологические детали, как например формулы замков и мускулатуры, не рассмотренные этими авторами, тем не менее согласуются с признанием Диккинсом числа генов, в противоположность Ньюэллу, считавшему активными лишь несколько генов. Родовой диагноз предложен для *Megadesums Sowerby*, *Astartila Dana*, *Pyramus Dana*, *Myonia Dana*, *Notomya M'Coу*, и *Pachymyonia Dun*. Добавлены два новых рода: *Globicarina*, с генотипом *Globicarina grossula sp. n.* и *Vacunella*, с генотипом *Allorisma curvatum Morris*. Последний вид был отнесен авторами к роду *Chaenomya* но детальное сравнение с топотипом *C. leavenworthensis* указывает на важное различие в форме, заднем зиянии и мускулатуре. Выявлена родственная связь между родами.

РЕГЕНЕРАЦИЯ РАКОВИНЫ У *ONCOMELANIA FORMOSANA*

Г. М. Дэйвис

В связи с микрохирургическими операциями совершенными над *Oncomelania formosana* (Pilsbry и Hirase), земноводными преднежаберными моллюсками с острова Тайван (Формоза), регенерация раковины изучалась у взрослых экземпляров этого вида. Раковина просверливалась на третьем обороте от устья. Просверленные улитки из числа выращенных в лаборатории содержались по одному экземпляру в блюдечках Петри и наблюдались в течение одного месяца. Каждая камера была выложена бумажным фильтром, который служил ей пищей, и наполнена лимнадным раствором Рингера (физиологически солевой) на 7 мм в глубину. Температура поддерживалась на 23° С, плюс-минус 1° С. На второй день после сверления на внутреннем крае отверстия стала образовываться мембрана. Эта мембрана "вырастала" на отверстии, и оно заполнилось у 50% улиток через 4 дня, у 90% через 6 дней и у 100% через 13 дней. Новая мембрана выглядела протеинообразной, бесклеточной и аморфной.

Когда мембрана была почти закончена, на ее поверхности появились зернышки. Эти зернышки "выросли" в два типа кристаллов: 1) чешуйки-кристаллы, "вырастающие" в сростную многоугольную массу, образуя гладкую поверхность, и 2) слезообразные кристаллы, разветвляющиеся и образовывавшие сферулиты, которые срастаясь составляли грубую поверхность из многоугольных единиц. Оба типа кристаллов часто можно было найти на одной и той же мембране.

Мембраны полностью кальцифицировались у 10% улиток через 5 дней после сверления, и у 50% через 28 дней после сверления. За это время еще 15% улиток кальцифицировалось на 90% или более, в то время как остальные 35% были кальцифицированы на 50% или меньше.

По заполнении первичного комплекса "мембрана-раковина", другие мембраны откладывались под первой. Эти кальцифицировались следующим образом:

1. Путем поддерживающего кристаллического образования над мембраной, и
2. Кальцификацией внутри самой мембраны.

*Pomatiopsis lapidaria*, родственная американская улитка которой пользовались для подобных же опытов, показала высокую степень смертности и не регенерировала раковину. Необходимы дальнейшие эксперименты над этим видом.

#### АНОМАЛЬНОЕ РАЗВИТИЕ ГИБРИДА *ONCOMELANIA* (GASTROPODA: HYDROBIDAE)

Г.М. Дейвис, Д. В. Муз и Д. Е. Вильямс

#### АБСТРАКТ

В результате скрещивания самки *Oncomelania quadrasi* с самцом *O. formosana* получается гибрид, в нескольких отношениях ненормальный. Снаружи у него имеются многочисленные ненормальные щупальца с 7-ю глазными массами. Гистология этих глазных масс обнаруживает присутствие 7 хрусталиков; один глаз без линзы и 3 глаза без роговой оболочки. Один "глаз" с двумя линзами, и 3 линзы сильно деформированы. Только 5 глаз можно рассматривать как функционирующие.

Щупальцевидная масса на правой стороне головы не покрыта пигментом, и не имеет железистых образований составляющих "бровь", описанную в литературе.

Внутри, слюнные железы уродливы; нервы щупальцев сильно утолщены; левый дорсо-лабиальный нерв входит в левое щупальце вместо своего нормального направления к дорсо-латеральному концу рострума; плевро-подпищеводный ганглий удлинен.

Половая железа сморщена; гистологическое исследование показывает сравнительно небольшое число зародышевых клеток, главным образом в стадии ранней профазы. Спермы очень мало. В половой железе были найдены ненормальные большие коричневые сфероиды. Их нельзя было признать за паразитов. Семеновод сильно сужен в диаметре.

Хотя в течение почти двухлетних наблюдений над культурой самок совокупление часто имело место, молодые улитки не было обнаружены.

Поскольку были найдены тысячи нормальных и плодовитых гибридов, описанная ненормальность не может быть отнесена к общей генетической несовместимости.

#### ГРЕБЕШОК-НАДВИД *AEQUIPECTEN IRRADIANS* (LAMARCK)

Артур Кларк

#### АБСТРАКТ

Статистический анализ морфологических вариаций в пределах популяции экономически ценного вида *Aequipecten (Plagiecten) irradians* при-

вел к определению 3 подвигов и одного близкого, но отличимого от других видов входящих в эту группу. Автор пользовался следующими главными признаками "число ребер, отношение ширины к длине, относительная инфляция и частота нахождения белых правых створок. Автор различает 4 таксономические группировки: *A. amplicostatus* (Dall) из центрального Техаса и Мексики и повидимому образующий отдельные популяции около Майами, штат Флорида, и Картагены, штат Колумбия; *A. i. concentricus* (Say) встречающийся в районах от Нью Джерси до Южной Каролины и от западной Флориды до восточного Техаса; *A. i. irradians* (Lamarck), в зоне контакта с *A. i. concentricus* встречающийся от Массачусетса до Нью Джерси; и *A. i. sablensis*, ssp. n., новый подвид - очевидно вымершая постплеоценовая форма острова Сабль в Новой Шотландии. В целях стабильности родовое название *Aequipecten* удерживается для этой группы; *A. i. concentricus* считается неотипом; типичное местонахождение *A. i. irradians* ограничивается фалмусом в штате Массачусетс. Автор приводит выводы касательно филогении подрода *Plagiocentium* в Северной Америке; отношения между увеличением сжатия створки и прогрессивным распространением к северу этой и других групп; значение белых правых створок для приспособления и морфологическое разнообразие в пределах "апостатического" отбора.

#### ТРЕТИЧНЫЕ ПРЭСНОВОДНЫЕ МОЛЛЮСКИ С ОСТРОВОВ ТИХОГО ОКЕАНА.

Гарри С. Ладд

#### АБСТРАКТ

Автор дает описание двух брюхоногих моллюсков пресной или солоноватой воды: катушка (*Gyraulus bikiniensis* Ladd, sp. n.) и неретиды (*Neritilia traceyi* Ladd, sp. n.) из известняка нижнего третичного *e* миоцена из Бикини (Маршалские острова). Оба моллюска были найдены в слоях, которые можно отнести к слою прерванному растворением наверху третичной скции *e*. Эти условия создались в то время, когда Бикини находился выше уровня моря и имел вид известкового острова с флорой и фауной более разнообразными чем современные.

Речная улитка (*Clithon corona* Linnaeus) была найдена в осадках морской приливной зоны в нижнем миоцене (третичный период *f*) на острове Фиджи. Также на Фиджи была найдена в изобилии пресноводная или солоноватая тиарида (*Melanoides* cf *tuberculatus* Müller) в темном сланцевом материале вероятно из верхнего третичного болота или топи.

#### К АНАТОМИИ ЦЕНТРАЛЬНОЙ НЕРВНОЙ СИСТЕМЫ И ЛОКАЛИЗАЦИИ НЕЙРОСЕКРЕТОРНЫХ КЛЕТОК *AUSTRALORBIS GLABRATUS*

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#### АБСТРАКТ

В литературе только иногда уделяется внимание центральной системе *Australorbis glabratus*, важного американского промежуточного хозяина

*Schistosoma mansoni*. Настоящее исследование состоит из двух частей: первая содержит детальное микроанатомическое изучение комплекса центральных ганглий этого вида; этот комплекс у большинства других легочных состоит из парных буккальных, церебральных, плевральных, париетальных и ножных ганглий, и одного висцерального ганглия. Проекционные зарисовки всего центрального комплекса ганглий у особи с максимальным диаметром раковины в 19.5 мм были сделаны с каждого четвертого среза, взятого из полной серии центральной нервной системы. Точная форма и размеры ганглий не могли быть определены этим способом, и не было возможности дать детальное описание мест прикрепления всех комиссур, коннектив и периферических нервов.

Во второй части особое внимание было обращено на явление нейросекреции. Повидимому нейросекреторные клетки находятся как в церебральных и париетальных ганглиях, так и в висцеральном ганглии. В каждом церебральном ганглии большая группа этих клеток находилась в так называемом медиодорсальном теле, частично лежащим на междуцеребральной комиссуре. Кроме того, некоторые специальные клетки этого типа находятся в латеральной доле этого ганглия, которая, как и у всех сидячеглазых улиток, выступает недалеко от места выхода оптических и щупальцевых нервов. Продукт выделения медиодорсальных нейросекреторных клеток передвигается к нервам средней губы.

В левом париетальном ганглии, в одной дорсальной клетке и в группе ростральных клеток имеются нейросекреторные признаки. В правом париетальном ганглии имеется только одна нейросекреторная клетка, в то время как висцеральный ганглий содержит длинный тяж таких клеток расположенных вокруг левой париетовисцеральной коннективы.

Число и положение занимаемое нейросекреторными клетками было установлено на срезах центральной нервной системы десяти особей, размеры которых варьировали от 5.5 до 23 мм в диаметре раковины.

Повидимому, даже в самых маленьких особях нейросекреторные клетки находятся в медиодорсальной группе церебральных ганглий, и в большой группе висцерального ганглия. Однако, в большинстве других клеток упомянутых выше, признак нейросекреции обнаруживается только в улитках достигших размера от 10 до 15 мм диаметра раковины.

По сравнению с *Lymnaea stagnalis* нейросекреция у *Australorbis glabratus* менее обильна. В церебральных ганглиях *L. stagnalis* нейросекреторные клетки имеются не только в медиодорсальных, но и в латеродорсальных группах; клетки эти более многочисленны как в этих так и в париетальных ганглиях; плевральные ганглии содержат 3 различных группы этих клеток, совершенно отсутствующих у *A. glabratus*.

Имеется единственное исключение из этого правила: число нейросекреторных клеток в висцеральном ганглии *Australorbis glabratus* больше чем у *Lymnaea stagnalis*.

#### ЭКСТИРПАЦИЯ У СТАТОЦИСТОВ ОЗЕРНИКА *LYMNAEA STAGNALIS*

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#### АБСТРАКТ

В литературе имеются только косвенные указания относительно функций статоцистов у легочных моллюсков. Эти сведения получены исключительно

путем экспериментов с стебельчатоглазыми улитками и экстирпация этих органов чувств никогда не была произведена.

В настоящем исследовании, у озерника *Lymnaea stagnalis* были удалены один или обастатоциста и наблюдались результаты их геотактических движений на покатой плоскости и на воздухе (от 15 и до 30 градусов).

Было установлено, что экстирпация билатеральныхстатоцистов вызвала полную потерю геотактической способности. Поэтому движение озерника вниз по наклонной плоскости на воздухе происходило благодаря действиюстатоцистов, а не из-за напряжения асимметричного тела, как это предполагалось у стебельчатоглазых некоторыми авторами.

Нормальные, не оперированные улитки, при движении по наклону вниз в среднем числе уклонялись от прямой линии влево. Есть указания, что это отклонение влево происходит в результате доминирующего влияния левогостатоциста, хотя возможность влияния напряжения асимметричного тела не может быть исключена.

Улитки, у которых была произведена экстирпация левогостатоциста, в среднем числе уклонялись вправо, а улитки без правогостатоциста - влево, по сравнению с путем нормальных, не оперированных улиток. Это является показателем того, что в нормальных озерниках путь вниз по наклонной поверхности на воздухе является результатом действия двухстатоцистов.

#### ЦИТОЛОГИЧЕСКИЕ ИССЛЕДОВАНИЯ СЕМЕЙСТВА (GASTROPODA: BASOMMATOPHORA)

#### НЕКОТОРЫЕ АФРИКАНСКИЕ PLANORBINAE, PLANORBININAE И BULININAE

Р. Натарьян, Дж. Б. Берч и Анна Гизман.

#### АБСТРАКТ

Описано число хромосом для 20 видов и подвидов африканских катушек. Гаплоидное число в 18 было найдено у *Anisus crassilabrum* и *Gyraulus costulatus* в подсемействе Planorbininae; у *Planorbina alexandrina alexandrina*, *P. pfeifferi pfeifferi*, *P. pfeifferi gaudi*, *P. pfeifferi madagascariensis* и у *P. sudanica tanganyicensis* в подсемействе Planorbininae; и у *Bulinus (Bulinus) tropicus tropicus*, *B. (B.) guernei*, *B. (Physopsis) globosus*, *B. (P.) jousseaumei*, *B. (Pyrgophysa) beccarii*, *B. (Py.) forskalii* из Ганы, Танганики и Южной Африки, *B. (Py.) reticulatus* и *B. (Py.) senegalensis* в подсемействе Bulininae; тогда как *B. truncatus truncatus*, *B. truncatus rohlfsii*, *B. coulboisi* и *B. "sericinus"* имели по 36 пар хромосом и ранее одна популяция *B. "sericinus"* из Западного Адена имела 72 пары. *Bulinus forskalii* из Анголы имел 19 элементов (вероятно бивалентов) в профазе 1 и в метафазе 1, и *B. natalensis* из Южной Родезии имел 19, 20 и 21 элемент (из которых некоторые были унивалентами) находившиеся в метафазе 1.

Вышеуказанные результаты, как и прежние данные указывают на то, что у Bulininae; полиплоиды находятся только в подроде *Bulinus* s.s., где их присутствие обнаружено только в тех видах - всех из группы "truncatus" которые подозреваются в передаче шистосомиазиса человека и

животного. Число хромосом само по себе по всей вероятности не связано с восприимчивостью к заражению шистосомиазисом в подродах *Physopsis* и *Pyrgophysa* подсемейства *planorbinine* или в роде катушковных *Planorbina*.

ХРОМОСОМЫ *TULOTOMA ANGULATA*  
(*STREPTONEURA: VIVIPARIDAE*)

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АБСТРАКТ

Редкий род *Tulotoma* эндемичен для рек Алабама и Куза в юго-восточной части С.Ш.А. Некоторые авторы различают 3 отдельных вида, другие только один. Число хромосом у *T. angulata*  $n=13$  ( $2n=26$ ). Поллистер и Поллистер (1940, 1943) нашли 12 хромосом  $n=12$  у *T. magnifica*. Разница в числе хромосом повм повидимому подтверждает представление о том, что род состоит из более чем одного вида. Если распространить на *Streptoneura* гипотезу о том, что филогенетический прогресс сопровождается постепенным увеличением числа хромосом, то надо рассматривать семейство *Viviparidae* ( $n=7-14$ ) как более примитивное, чем это обычно делается.

У *Tulotoma angulata* имеются 3 пары метацентрических хромосом, 7 пар субметацентрических, 2 пары почти акроцентрических и одна пара диморфных половых хромосом. Механизм определяющий пол, до сего времени неизвестный у *Viviparidae*, следующий: XX у самки и XY у самца.

МЕТОДЫ НАРКОТИЗАЦИИ И АНЕСТЕЗИРОВАНИЯ  
БРЮХОНОГИХ

Н.В. Ронхам, К. Исаранкура и Б. Дж. Смит.

Среди исследованных методов наркотизации пользование замораживанием и стоваином не рекомендуется. Формалин рекомендуется для голых моллюсков и нембутал (пропилен феноксетол) для слизняков. Ментол, нумбутал, севин  $CO_2$ , пропилен феноксетол и соли магnezия рекомендуются для общего употребления.

Уретан, эфир и, для морских организмов разбавленная морская вода, были признаны анестезирующими годными только для поверхностных операций, и вспрыскиваний. Хлористый магний, пропилен фенокситол и нембутал MC 222 могут быть рекомендованы для внутренних операций.

ПИТАНИЕ И СОРТИРОВКА ЧАСТИЦ У *YOLDIA ENSIFERA*  
(BIVALVIA: PROTOBRANCHIA)

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АБСТРАКТ

Подробные наблюдения над несколькими видами семейства протобранхов *Nuculanidae* указывает на то, что они подобно семейству *Nuculidae*, собирают пищу не только среди субстрата, при помощи вытягиваемых щупальцев, как думали до сих пор, но также и среди суспензии с помощью ассоциации щупальцев-ктенидия. Реснитчатые неотграниченные поверхности слоя щупальцев являются вполне или частично приемниками в разных видах, и направляют питательный материал к сортировочному месту между противостоящими ламеллярными щупальцами. Также как и у *Nuculidae*, относительное значение аппарата для собирания пищи неизвестно.

Сортировка частиц происходит на складках лабиальных пластинчатых щупальцев. Родство органов осязания так же значительно как и их структура, при собирании и отправке питательных частиц с помощью ктенидия к лабиальным щупальцам.

Распространенное мнение, что нжулоидные протобранхи, в частности *Nuculanidae* не пользуются ктенидиями для собирания пищи - неправильно, и основывается на недостаточно удовлетворительных анатомических и экспериментальных данных.

Мнение Пурчона, что септибранхи и *Nuculanidae* имеют общего предка из протобранхов, подкрепляется как функциональной, так и последовательной деятельностью ктенидия.

О МЕТОДАХ ЗАРАЖЕНИЯ *ACHATINA FULICA* ЛИЧИНКАМИ *ANGIOSTRONGYLUS*

Фома С. Чент и Иосиф Е. Аликата

АБСТРАКТ

Две группы особей *Achatina fulica* были экспериментально заражены известным числом личинок первой стадии *Angiostrongylus cantonensis*. Первая группа была заражена через рот, а вторая была заражена личинками, положенными на вытянутую ногу каждой улитки. Сравнивая проценты личинок 3-ей стадии, найденных в мускулатуре улиток в каждой группе, было установлено, что оба метода инфекции возможны и в равной мере эффективны. Оба метода вероятно встречаются в естественных условиях.

СРАВНИТЕЛЬНЫЕ ИСТОРИИ ЖИЗНИ СЕВЕРО-АМЕРИКАНСКОЙ ГОРОШИНКИ.  
(SPHAERIIDAE: *PISIDIUM*)

Вильям Х. Херд.

АБСТРАКТ.

Большая часть информации о шаровках и горошинках касается их классификации, хотя существуют работы, исследующие эмбриологию и историю жизни родов *Sphaerium* и *Musculium*. Настоящее исследование является первой попыткой подробно определить историю жизни по сезонам рода *Pisidium* C. Pfeiffer.

Количественные сборы производились во все времена года, главным образом в южной части штата Мичиган, США, чтобы исследовать а) внутривидовые вариации, б) варианты между видами одного и того же подрода и в) варианты между видами разных подродов в смысле общей истории жизни, деятельности гонад и прочих аспектов репродукции.

Как интраспецифические так и интерспецифические вариации одного подрода отражаются на разнице во времени деятельности гонад и на величине среднего приплода, хотя интраспецифические вариации по существу являются генетическими по своему происхождению. Была замечена крупная разница в истории жизни подродов в отношении количества приплодов в течение их жизни, в продолжительности жизни и в величине приплодов. *Pisidium* дает лишь один сравнительно крупный приплод в год в продолжение нескольких лет; *Rivulina* живет всего только один год и дает приплод только один раз (палеарктические представители проявляют контрастное поведение, живут, как будто, дольше и размножаются чаще), а *Neopisidium* дает два меньших приплода в год и потенциально может жить несколько лет.

Данное исследование позволяет предположить о возможном эволюционном средстве родов *Pisidium*, *Rivulina*, и *Neopisidium*.

Допускаются эволюционные изменения:

1. У интерпаровых видов

- а) в увеличении числа приплодов в год, или
- б) семейпаровые методы репродукции (регрессия?), и

2. У семейпаровых особей от приплодов малых размеров к приплодам больших размеров, можно предположить, что более примитивный анатомически *Pisidium* помог независимо развиваться родам *Rivulina* и *Neopisidium*.

Об их родстве с абиссинскими подродами *Afropisidium* и *Odhneripisidium* в настоящее время неизвестно.

ИССЛЕДОВАНИЯ ПО СТРУКТУРЕ И ФУНКЦИИ ПИТАТЕЛЬНЫХ ОРГАНОВ *PHILINE APERTA*  
С СРАВНИТЕЛЬНЫМ РАССМОТРЕНИЕМ НЕКОТОРЫХ ДРУГИХ ЕДНЕЖАБЕРНЫХ

Анна Хэрст

АБСТРАКТ

Тонкая анатомия ротовой полости у *Philine aperta* (Linn.) была исследована, так же как и васкулярное и нервное снабжение передней части тела.

Дается объяснение функции аппарата, основанное на наблюдениях над питанием, на различном соотношении составных частей буккального аппарата и на результатах экспериментального стимула и впрыскиваний.

Стены буккального района хорошо снабжены мускулами и могут сильно видоизменять свою форму. Они охватывают компактную буккальную массу, в которой радула поддерживается широкими мускулами и упругими тканями вакуольных клеток со включением разбросанных клеток с мускульными волокнами. Эта поддерживающая ткань также служит для прикрепления мускулов, в то время как пара больших мускулов также действует и при закрывании радулы. Радула открывается двумя группами мускульных волокон тянущихся вдоль стенок буккальной массы. Буккальная масса связывается четырьмя парами маленьких буккальных щупальцев. Внутренняя мускулатура поддерживает форму и связь с остальными частями буккальной массы, являясь причиной ее движения вверх и вниз при выделении пищи в эзофагус, и также принимает участие в движении зубов.

Ротовая полость соединена со стенками тела 6 парами наружных мускулов, определяющих его топографическое расположение. При питании 4 пары этих мускулов вытягивают ротовую полость вперед и буккальная масса выдвигается настолько, что радула выпячивается далеко впереди рта и может служить хватющим органом. Это выпячивание может сопровождаться втягиванием и растягиванием передней части эзофагуса, образуя наполненные кровью экстраверты, зависящие от специализации кровеносной системы и степени ослабления отдельных связок мускулов столбика. Они открывают и закрывают рот и контролируют приток крови к передней части тела, путем сжатия передней аорты. Этот сосуд может быть также сокращен в задней части, где он проходит через диафрагму. Он имеет направление общее с многочисленными буккальными мешечками и некоторыми большими передними синусами, участвующими в контроле выпячивания и втягивания хобота. Втягивание зависит главным образом от сильных сокращений 6 пар хоботных ретракторов, которые могут также двигать хобот в стороны и по кругу. Радула короткая, а каждый ряд зубов составляет всего одну пару латеральных. Эти пары могут быть широко открыты или закрыты так, что смыкаясь, они могут прочно захватывать пищу. Открывание зависит от латеральной тяги мускулов с увеличением давления крови ниже радульной мембраны, которое ее сплющивает, в то время как при закрывании она складывается по длине мускульной тягой снизу.

Хотя многие брюхоногие могут выпячивать буккальную массу до известного предела, было найдено, что у *Philine* она может выпячиваться еще дальше, образуя часть внешнего кишечника. Пользование зубами не зависит от плоскости сгибания или от движения взад и вперед радульной мембраны. Некоторые другие заднежаберные виды сравниваются с *Philine* и даются сведения об их питании. Среди них очень сходным является *Scaphander lignarius* (Linn.) хотя его кровеносная система не выявляет такого количества адаптивных изменений. *Acteon tornatilis* (Linn.), *Cylichna cylindracea* (Pennant) и *Retusa* spp. не пользуются хоботом; высказываются предположения о наиболее вероятном способе их питания. *Retusa* spp. потеряли буккальную массу и питаются всасыванием. Эволюционные стремления не так легко проследить благодаря исключительной способности ротовой полости применяться к способу питания.

ЦИТОТАКСОНОМИЧЕСКИЕ ИССЛЕДОВАНИЯ ПРЕСНОВОДНЫХ БЛЮДЕЧЕК  
(GASTROPODA: BASOMMATOPHORA)  
ЯПОНСКИЕ РОДЫ *FERRISSIA* И *GUNDLACHIA*

Дж. Б. Берч

АБСТРАКТ

В Японии известны 3 вида пресноводных блюдечек. Как у *Ferrissia japonica* так и у *Gundlachia japonica* гаплоидное число хромосом равно 18. Это число впервые найдено у *Ancylidae*, хотя оно обычно встречается у других *Basommatophora*. Гаплоидное число хромосом у *F. nipponica* равно 17 (fide Inaba).

Большая разница в числе хромосом у северно-американских *Ferrissia* ( $n=30$ ) и у японских видов ( $n=17, 18$ ) указывает на то, что виды, встречающиеся на двух континентах вероятно не принадлежат к одному роду, несмотря на сходство в скульптуре верхушек их раковин. Сходное число хромосом у *F. japonica* и у *G. japonica* ( $n=18$ ) возможно указывает на их систематическое родство, но *F. nipponica* вероятно имеет мало общего с американским родом *Laevapex* и африканским родом *Burnupia*, хотя у всех трех видов имеется по 17 пар хромосом.

ПИТАНИЕ И ПЕРЕДВИЖЕНИЕ УЛИТКИ *STAGNICOLA REFLEXA*  
(BASOMMATOPHORA: LYMNÆIDAE)

Р. В. Бовбьерг

АБСТРАКТ

Типичная *S. reflexa*, обычно собирается в прудах на скоплениях водоросли *Spirogyra*. Чтобы подтвердить наличие предпочтения в пище, установить способность улитки реагировать на расстоянии на присутствие химических веществ и изучить ее передвижения при присутствии и отсутствии пищи, были проделаны лабораторные опыты, в которых употреблялась естественная вода, а свет и температура строго регулировались.

Предпочтение пищи, наблюдаемое в природных условиях, подтверждается лабораторными опытами. Улитки помещенные в длинный и узкий сосуд (300 x 15 см.) с чередующимися группами высших растений и *Spirogyra*, за 12 час. концентрировались в большем количестве на водорослях, чем на высших растениях. Из 1620 зарегистрированных в природе положений занимаемых улитками, это предпочтение выразилось в пропорции 3 : 1.

Если пучок *Spirogyra* был положен у одного конца небольшого сосуда (70 x 7 см.), то улитки помещенные в центре сосуда двигались одинаково к обоим концам таким образом, как они делали это в контрольных условиях при отсутствии пищи. Однако те которые достигали водорослей, оставались на них для питания, и таким образом образовывали скопления. В сосуде имеющем форму английской буквы каждый рукав которого равнялся 60 см. в длину, улитки проникали в рукав содержащий гомогенат водоросли не в большем числе, чем в контрольный рукав. Те, которые проникли в рукав содер-

жащий водоросли, оставались там для питания. Химической восприимчивости на расстоянии не наблюдалось, но в контакте с целой или размельченной водорослью улитки переставали двигаться и начинали кормиться. Хотя для хищных улиток химическая восприимчивость на расстоянии хорошо установлена, у травоядных она не наблюдалась, возможно, из-за недостатка наблюдений. Поскольку пища травоядных, таких как *S. reflexa*, доступна им легче чем хищным улиткам, то можно предположить, что травоядным не нужна способность к точному распознаванию пищи на расстоянии.

В длинном узком сосуде (300 x 15 см.) темп движения значительно медленнее когда сосуд заполнен водорослью, чем когда он пуст. Среди водорослей улитки менее подвижны, чем в сосуде наполненном прудовым мусором и растительностью.

Во всех случаях голодание ускоряет темп движения. В заключение, движения *S. reflexa* случайны, без определенного направления к водорослям. По мере того как большее число особей приходит в соприкосновение с желательной для них пищей, их движения замедляются и в результате образуется скопление.

Это - тип движения к наилучшему месту; лабораторные условия отражают то что наблюдается в природе.



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