

MAL
WH7

HARVARD UNIVERSITY



Library of the
Museum of
Comparative Zoology

MALACOLOGIA

International Journal of Malacology

Revista Internacional de Malacologia

Journal International de Malacologie

Международный Журнал Малакологии

Internationale Malakologische Zeitschrift

Publication date
Vol. 20, No. 2—17 June 1981

MALACOLOGIA, VOL. 21

CONTENTS

SECOND INTERNATIONAL SYMPOSIUM ON EVOLUTION
AND ADAPTIVE RADIATION OF MOLLUSCA
SPONSORED BY
UNITAS MALACOLOGICA
SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS
PERPIGNAN, FRANCE. 31 August-7 September 1980

P. BOUCHET	Evolution of larval development in eastern Atlantic Terebridae (Gastropoda), Neogene to Recent	363
A. J. CAIN	Variation in shell shape and size of helcid snails in relation to other pulmonates in faunas of the Palaearctic region	149
P. CALOW	Adaptational aspects of growth and reproduction in <i>Lymnaea peregra</i> (Gastropoda: Pulmonata) from exposed and sheltered aquatic habitats	5
G. M. DAVIS	Introduction to Symposium	1
G. M. DAVIS	Different modes of evolution and adaptive radiation in the Pomatiopsidae (Prosobranchia: Mesogastropoda)	209
V. FRETTER, A. GRAHAM and J. H. McLEAN	The anatomy of the Galapagos rift limpet, <i>Neomphalus fretterae</i>	337
W. HAAS	Evolution of calcareous hardparts in primitive molluscs	403
K. E. HOAGLAND and R. D. TURNER	Evolution and adaptive radiation of shipworms (Bivalvia, Teredinidae)	111
R. S. HOUBRICK	Anatomy, biology and systematics of <i>Campanile symbolicum</i> with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia)	263
J. H. McLEAN	The Galapagos rift limpet <i>Neomphalus</i> : relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation	291
B. MORTON	The Anomalodesmata	35
W. NARCHI	Aspects of the adaptive morphology of <i>Mesodesma mactroides</i> (Bivalvia: Mesodesmatidae)	95
P. G. OLIVER	The functional morphology and evolution of Recent Limopsidae (Bivalvia, Arcoidea)	61
L. v. SALVINI-PLAWEN	The molluscan digestive system in evolution	371

MALACOLOGIA
CONTENTS (cont.)

S. TILLIER	
Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs)	177
E. R. TRUEMAN and H. B. AKBERALI	
Responses of an estuarine bivalve, <i>Scrobicularia plana</i> (Tellinacea) to stress	15
C. M. YONGE	
On adaptive radiation in the Pectinacea with a description of <i>Hemi- pecten forbesianus</i>	23

AWARDS FOR STUDY AT
The Academy of Natural Sciences of Philadelphia

The Academy of Natural Sciences of Philadelphia, through its Jessup and McHenry funds, makes available each year a limited number of awards to support students pursuing natural history studies at the Academy. These awards are primarily intended to assist predoctoral and immediate postdoctoral students. Awards usually include a stipend to help defray living expenses, and support for travel to and from the Academy. Application deadlines are 1 April and 1 October each year. Further information may be obtained by writing to: Chairman, Jessup-McHenry Award Committee, Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

WHY NOT SUBSCRIBE TO MALACOLOGIA?

ORDER FORM

Your name and address _____

Send U.S. \$17.00 for a personal subscription (one volume) or U.S. \$27.00 for an institutional subscription. Make checks payable to "MALACOLOGIA."

Address: Malacologia, Academy of Natural Sciences
Nineteenth and the Parkway, Philadelphia
PA 19103, U.S.A.

Mollusca

VOL. 21 NO. 1-2

NOV 1981

1981

HARVARD
LIBRARY

MALACOLOGIA

SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS
SYMPOSIUM PROCEEDINGS

Second International Symposium on Evolution
and Adaptive Radiation of Mollusca
5-6 September 1980, Perpignan, France

International Journal of Malacology

Revista Internacional de Malacologia

Journal International de Malacologie

Международный Журнал Малакологии

Internationale Malakologische Zeitschrift

MALACOLOGIA

Editors-in-Chief:

GEORGE M. DAVIS

ROBERT ROBERTSON

Editorial and Subscription Offices:

Department of Malacology
The Academy of Natural Sciences of Philadelphia
Nineteenth Street and the Parkway
Philadelphia, Pennsylvania 19103, U.S.A.

Associate Editors:

JOHN B. BURCH
University of Michigan, Ann Arbor

ANNE GISMANN
Maadi, A. R. Egypt

Editorial Assistants:

MARY DUNN
GRETCHEN R. EICHHOLTZ
CHAMBERLIN

MALACOLOGIA is published by the INSTITUTE OF MALACOLOGY (2415 South Circle Drive, Ann Arbor, Michigan 48103, U.S.A.), the Sponsor Members of which (also serving as editors) are:

J FRANCES ALLEN, *Emerita*
Environmental Protection Agency
Washington, D.C.

CHRISTOPHER J. BAYNE, *President*
Oregon State University, Corvallis

ELMER G. BERRY, *Emeritus*
Germantown, Maryland

KENNETH J. BOSS
Museum of Comparative Zoölogy
Cambridge, Massachusetts

JOHN B. BURCH

MELBOURNE R. CARRIKER
University of Delaware, Lewes

GEORGE M. DAVIS, *Executive*
Secretary-Treasurer

PETER JUNG
Naturhistorisches Museum, Basel, Switzerland

OLIVER E. PAGET
Naturhistorisches Museum, Wien, Austria

ROBERT ROBERTSON

CLYDE F. E. ROPER
Smithsonian Institution
Washington, D.C.

W. D. RUSSELL-HUNTER, *Vice-President*
Syracuse University, New York

NORMAN F. SOHL
United States Geological Survey
Washington, D.C.

RUTH D. TURNER, *Alternate*
Museum of Comparative Zoölogy
Cambridge, Massachusetts

SHI-KUEI WU, *President-Elect*
University of Colorado Museum, Boulder

Institute meetings are held the first Friday in December each year at a convenient place. For information, address the President.

EDITORIAL BOARD

- J. A. ALLEN
*Marine Biological Station,
Millport, United Kingdom*
- E. E. BINDER
*Muséum d'Histoire Naturelle
Genève, Switzerland*
- A. J. CAIN
*University of Liverpool
United Kingdom*
- P. CALOW
*University of Glasgow
United Kingdom*
- A. H. CLARKE, Jr.
Mattapoisett, Mass., U.S.A.
- B. C. CLARKE
*University of Nottingham
United Kingdom*
- E. S. DEMIAN
*Ain Shams University
Cairo, A. R. Egypt*
- C. J. DUNCAN
*University of Liverpool
United Kingdom*
- Z. A. FILATOVA
*Institute of Oceanology
Moscow, U.S.S.R.*
- E. FISCHER-PIETTE
*Muséum National d'Histoire Naturelle
Paris, France*
- V. FRETTER
*University of Reading
United Kingdom*
- E. GITTENBERGER
*Rijksmuseum van Natuurlijke Historie
Leiden, Netherlands*
- A. N. GOLIKOV
*Zoological Institute
Leningrad, U.S.S.R.*
- S. J. GOULD
*Harvard University
Cambridge, Mass., U.S.A.*
- A. V. GROSSU
*Universitatea Bucuresti
Romania*
- T. HABE
*Tokai University
Shimizu, Japan*
- A. D. HARRISON
*University of Waterloo
Ontario, Canada*
- K. HATAI
*Tohoku University
Sendai, Japan*
- B. HUBENDICK
*Naturhistoriska Museet
Göteborg, Sweden*
- S. HUNT
*University of Lancaster
United Kingdom*
- A. M. KEEN
*Stanford University
California, U.S.A.*
- R. N. KILBURN
*Natal Museum
Pietermaritzburg, South Africa*
- M. A. KLAPPENBACH
*Museo Nacional de Historia Natural
Montevideo, Uruguay*
- J. KNUDSEN
*Zoologisk Institut & Museum
København, Denmark*
- A. J. KOHN
*University of Washington
Seattle, U.S.A.*
- Y. KONDO
*Bernice P. Bishop Museum
Honolulu, Hawaii, U.S.A.*
- J. LEVER
Amsterdam, Netherlands
- A. LUCAS
*Faculté des Sciences
Brest, France*
- N. MACAROVICI
*Universitatea "Al. I. Cuza"
Iasi, Romania*
- C. MEIER-BROOK
*Tropenmedizinisches Institut
Tübingen, Germany (Federal Republic)*
- H. K. MIENIS
*Hebrew University of Jerusalem
Israel*
- J. E. MORTON
*The University
Auckland, New Zealand*

R. NATARAJAN
*Marine Biological Station
Porto Novo, India*

J. ØKLAND
*University of Oslo
Norway*

T. OKUTANI
*National Science Museum
Tokyo, Japan*

W. L. PARAENSE
*Universidade de Brasília
Brazil*

J. J. PARODIZ
*Carnegie Museum
Pittsburgh, U.S.A.*

W. F. PONDER
*Australian Museum
Sydney*

A. W. B. POWELL
*Auckland Institute & Museum
New Zealand*

R. D. PURCHON
*Chelsea College of Science & Technology
London, United Kingdom*

O. RAVERA
*Euratom
Ispra, Italy*

N. W. RUNHAM
*University College of North Wales
Bangor, United Kingdom*

S. G. SEGERSTRÅLE
*Institute of Marine Research
Helsinki, Finland*

G. A. SOLEM
*Field Museum of Natural History
Chicago, U.S.A.*

F. STARMÜHLNER
*Zoologisches Institut der Universität
Wien, Austria*

Y. I. STAROBOGATOV
*Zoological Institute
Leningrad, U.S.S.R.*

W. STREIFF
*Université de Caen
France*

J. STUARDO
*Universidad de Chile,
Valparaiso*

T. E. THOMPSON
*University of Bristol
United Kingdom*

F. TOFFOLETTO
*Società Malacologica Italiana
Milano*

W. S. S. VAN BENTHEM JUTTING
Domburg, Netherlands

J. A. VAN EEDEN
*Potchefstroom University
South Africa*

J.-J. VAN MOL
*Université Libre de Bruxelles
Belgium*

N.H. VERDONK
*Rijksuniversiteit
Utrecht, Netherlands*

B. R. WILSON
*National Museum of Victoria
Melbourne, Australia*

C. M. YONGE
Edinburgh, United Kingdom

H. ZEISSLER
Leipzig, Germany (Democratic Republic)

A. ZILCH
*Natur-Museum und Forschungs-Institut
Senckenberg
Frankfurt-am-Main, Germany (Federal
Republic)*

SECOND INTERNATIONAL SYMPOSIUM ON EVOLUTION
AND ADAPTIVE RADIATION OF MOLLUSCA

SPONSORED BY

UNITAS MALACOLOGICA

Seventh International Malacological Congress
Perpignan, France
31 August–7 September 1980

JEAN-M. GAILLARD, PRESIDENT
Museum National d'Histoire Naturelle
Laboratoire de Biologie des Invertébrés Marins et Malacologie
55, rue de Buffon
75005 Paris, France

ORGANIZED BY

GEORGE M. DAVIS
Academy of Natural Sciences of Philadelphia
Nineteenth and the Parkway
Philadelphia, Pennsylvania, U.S.A.

CO-CHAIRMEN

Professeur MAXIME LAMOTTE
Laboratoire de Zoologie
Ecole Normale Supérieure
46 Rue d'Ulm
75005 Paris, France

Dr. CLAUD MEIER-BROOK
Tropenmedizinisches Institut der Universität
D74 Tübingen
Wilhelmstrasse 27
Federal Republic of Germany

INTRODUCTION TO THE SECOND INTERNATIONAL SYMPOSIUM ON EVOLUTION AND ADAPTIVE RADIATION OF MOLLUSCA

George M. Davis¹

*Academy of Natural Sciences, Nineteenth and the Parkway,
Philadelphia, Pennsylvania, U.S.A.*

The Second International Symposium on Evolution and Adaptive Radiation of Mollusca was held in Perpignan, France, on the fifth and sixth of September, 1980. This Symposium was part of the Seventh International Malacological Congress sponsored by Unitas Malacologica.

As with the first symposium, the organizers of the second symposium felt that a better understanding of the relationships among organisms could be obtained by studies based on modern evolutionary biological principles rather than solely by standard systematic practices. By standard practices, I mean the systematic study of organisms in order to assess relationships (or affinities, Cain & Harrison, 1958) solely on the basis of shared or different character states and to erect, by whatever methods, an hierarchical classification on the basis of the assessment.

Much more is to be gained if one considers the evolutionary relationships among organisms with particular emphasis on the adaptation of organisms to their environments. Still more is gained if one considers both historical and ecological impacts on populations in addition to the characters that allow one to score similarities or differences among taxa. I emphasize these aspects because one finds very few papers that give us an objective account of the evolution and adaptive radiation of any group of Mollusca.

What is meant by adaptive radiation? Osborn (1918) created the term and discussed the concept at length. The concepts involved in adaptive radiation and adaptive zones were used and considerably expanded by Simpson (1944, 1953, 1960), Wright (1940), Huxley (1954), and many others to explain the radiation of taxa they observed where species were variously adapted to different niche dimensions but all had certain morphological features in common. They de-

veloped the concept that a new radiation might occur when a novel, genetically controlled innovation is selected for by a shift in environmental pressures. With selection for this innovation, there is entrance into a new adaptive zone and with it, the possibility for speciation. With the invasion of new ecological space such as terrestrial environments following the first vertebrate incursions, it was argued that innovations would be selected in small, peripherally isolated populations. Each species in the new radiation has the morphological or physiological innovation but differs from other species in character states reflecting adaptations to different niche variables. The historical element seen in the radiation is the commonality of the innovative feature marking entrance to the new adaptive zone. As argued by Cain (1964) this historical element is seen as a common feature because it is adaptive, not because it is historical and thus passively carried along.

One sees in the literature a broad, generalized concept of adaptive radiation (Simpson, 1953; Stanley, 1979). One speaks of the mammalian radiation or the reptilian radiation. There are, however, two different levels of adaptive radiation that should be considered in the study of macroevolution. One level I have called macroradiation (Davis, this symposium), which encompasses higher taxa, such as the Mammalia, in which there are several clades, which are genera, subfamilies, or yet higher taxa. The other level is a subset of macroradiation and consists of a single genus. This subset I call a first order radiation. We see from an evolutionary biological viewpoint and from the discussion above that a genus is not an arbitrary grouping of species. While it may be difficult, if not impossible to delineate the whole phylogeny of a macroradiation, it may be more possible to work out the details of many first order radi-

¹Supported, in part, by National Institutes of Health Grant TMP #11373.

ations. In this regard, it is not surprising to see the intensive work now being done with what have been considered species-rich genera such as the land snail genera *Partula* (Murray & Clarke, 1966, 1968), *Cerion* (reviewed by Woodruff, 1978) and the marine snail genus *Patella* (Branch, 1971, 1974a,b, 1975a,b, 1976), to mention only three.

Establishing a credible account of the evolution of any group is not an easy task, and may be impossible in many, if not most cases. Cain & Harrison (1960) have clearly and elegantly discussed the problem. Summarizing their points, in discussing the evolution and adaptive radiation of a group, one must establish that the group is monophyletic. To establish monophyly one must eliminate cases of convergence. However, convergence is surely the most underestimated problem in systematic studies (Davis, 1979) and, in imperfectly known groups, one may be unable to detect it. The problem of convergence becomes acute when one studies adaptive radiation. As Cain (1964) pointed out, the phenotypic expressions we see are the result of adaptations of an organism to its environment. Two snail species of different phylogenies may have similar looking shells because they live on rocks in rapidly flowing water; they may, because of this environment, have similar reproductive strategies and thus the penis of both species may be similar, gonadal morphology may be the same, and other character states may be held in common as well.

If one can eliminate convergent taxa and establish monophyly for a group, the problem of establishing clades arises. By clade, I mean, the term as first used by Huxley (1959), discussed in detail by Cain & Harrison (1960), and demonstrated (with production of a cladogram) using set theory analysis by Wilson (1965). I do not refer to a neo-cladism cherished with religious fervor by some practicing systematists, for whom a clade can only be recognized by assessing relationships among taxa on the basis of certain dogmatic rules selecting primitive character states and derived character states, grouping taxa on the basis of shared derived character states, establishing sister groups, ignoring the fossil record, and ignoring ecological factors as they relate to adaptation.

The problem of recognizing and selecting primitive character states has been thoroughly discussed (Cain, 1964; Cain and Harrison, 1960). I am distrustful of stating that a given

character state is primitive. If a character state is widespread among species in a radiation, some will call this character state primitive; I think it unwise to do so for the following reasons. A widespread character state may reflect the successful adaptation of organisms to their environment because of that state. The character state could have been derived from a character state seen in only one species where other species with the "primitive" state are extinct because that character state is now selected against in most microhabitats. Some would consider the character state seen in only one species to be unique and thus derived. In essence, what is the direction of evolution of certain character states in question? The problem is compounded when one realizes that in any systematic study some of the useful characters are unordered multistate characters. In the absence of a fossil record, each choice for the primitive character state from among the unordered states increases the probability of error. The seasoned neo-cladist will respond that one should do an outgroup comparison. If a character state is widespread in a group A and also in outgroup B then surely this is the primitive character state. However, if the first operation is to eliminate cases of convergence, and if outgroup B converges on A and has been eliminated from our assessment of the course of evolution of A, then it would be circular reasoning to state that a character state widespread in A is primitive because it is widespread in B. The distribution of this character state may simply result from the same successful solution of adjusting to the same environmental pressures in both groups (Cain, 1964).

What can be done towards eliminating convergence and establishing clades depends on the data base available. If sufficient data are available from the fossil record and/or from geological events that give evidence for the rates and direction of change, then one may be able to say a great deal about clades and phylogeny. On the other hand, if there are too few data to allow for elimination of cases of convergence and therefore for determining cladistic affinities, all that may be possible is a phenetic analysis (Cain & Harrison, 1960; Hoagland & Davis, 1979). Unlike mammalogists and ichthyologists, malacologists have no fossil data for those suites of characters that are essential for establishing the phylogeny of any group of mollusks. There are no fossilized reproductive systems, digestive

systems (exclusive of radulae), nervous systems, etc. As shell convergence is a major problem in assessing cladistic relationships among molluscan groups (Davis, 1979), it is a most difficult task to discuss the phylogeny of any group of mollusks objectively. The burden of proof rests upon the data base.

In this symposium there are two papers dealing with populations. One is on populations of the same species of lymnaeid gastropod (Calow), the other on a population of a single species of marine bivalve (Trueman). These papers show ranges of adaptability of populations to different types of environmental pressure. Genetically controlled population variability indicates adaptation under varying conditions of environmental stress and is essential for adaptive radiation. At the other extreme, two papers involve evolutionary trends in the phylum Mollusca, i.e. those of Salvini-Plawen on the evolution of the molluscan digestive system and of Haas on the evolution of molluscan calcareous hard parts.

Of the 16 papers in this symposium, five involve marine bivalve radiations with emphasis on macroradiations. Four of these reflect the comparative anatomical school of thought established by C. M. Yonge while one (Hoagland & Turner) combines ecological and molecular genetical data with morphometric analyses to discern patterns of adaptive radiation.

Seven papers involve gastropod radiations and/or deployment; four are about marine groups, two on land snails, and one on a freshwater-amphibious group. Three of these papers (McLean, Fretter et al., Houbrick) present detailed anatomical data on a single species. The species they describe are enigmatic species, relicts important for understanding the possible relationships among largely extinct marine radiations. These papers and that given by Bouchet on the Terebridae clearly show the relevance of combining fossil data with neontological data to assess modes and tempos of evolution and adaptive radiation.

The land snail papers (Cain, Tillier) clearly demonstrate the need for detailed ecological studies in order to understand how phenotypes reflect adaptations to different environmental pressure. What have been described as numerous species on the basis of the usual standard systematic analysis often reduce to one or a few species once one discovers that subtle differences of rainfall, altitude, and sympatry greatly affect shell

shape and size parameters within a single species. Shell shape and size have been widely used to describe species of land snails.

One paper (Davis) demonstrates that with the ability to establish monophyly by eliminating convergent groups, and with paleontological and geological time markers, one may indeed establish a phylogeny and assess the direction, tempos, and modes of evolution and adaptive radiation within a nearly world-wide family. Two different modes and tempos of evolution are discussed, one fitting a punctuational model, the other a gradualistic model.

In summary, in many of these papers the reader will see the essential role of fundamental systematic studies for understanding relationships among organisms. It is clear, however, that an awareness and practice of modern principles involved in ecology, evolution, macroevolution, and adaptive radiation are essential if one aspires to understand the origin, evolution, and adaptive radiation of any group.

LITERATURE CITED

- BRANCH, G. M., 1971, The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 1. Zonation, movements and feeding. *Zoologica Africana*, 6: 1-38, 5 pl.
- BRANCH, G. M., 1974a, The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 2. Reproductive cycles. *Transactions of the Royal Society of South Africa*, 41: 111-160, 3 pl.
- BRANCH, G. M., 1974b, The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth rates. *Transactions of the Royal Society of South Africa*, 41: 161-193.
- BRANCH, G. M., 1975a, The ecology of *Patella* species from the Cape Peninsula, South Africa. 4. Desiccation. *Marine Biology*, 32: 179-188.
- BRANCH, G. M., 1975b, The ecology of *Patella* species from the Cape Peninsula, South Africa. Commensalism. *Zoologica Africana*, 10: 133-162.
- BRANCH, G. M., 1976, Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology*, 45: 507-530, 1 pl.
- CAIN, A. J., 1964, The perfection of animals, p. 36-63. In: CARTHY, J. D. & DUDDINGTON, C. L. (eds.), *Viewpoints in Biology*, 3. Butterworths, London.
- CAIN, A. J. & HARRISON, G. A., 1958, An analysis of the taxonomist's judgement of affinity. *Proceedings of the Zoological Society of London*, 131: 85-98.
- CAIN, A. J. & HARRISON, G. A., 1960, Phyletic weighting. *Proceedings of the Zoological Society of London*, 135: 1-31.

- DAVIS, G. M., 1979, The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Monograph of the Academy of Natural Sciences of Philadelphia*, 20: ix, 1–120.
- HOAGLAND, K. E. & DAVIS, G. M., 1979, The Stenothyrid radiation of the Mekong River. 1. The *Stenothyra mcmulleni* complex (Gastropoda: Prosobranchia). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 131: 191–230.
- HUXLEY, J. S., 1954, The evolutionary process, p. 1–23. In: HUXLEY, J., HARDY, A. C. & FORD, E. B. (eds.). *Evolution as a Process*. Allen and Unwin, London.
- HUXLEY, J. S., 1959, Clades and grades, p. 21–22. In: CAIN, A. J. (ed.), *Function and Taxonomic Importance*. Systematics Association Publication 3, London.
- MURRAY, J. & CLARKE, B., 1966, The inheritance of polymorphic shell characters in *Partula* (Gastropoda). *Genetics*, 54(5): 1261–1277.
- MURRAY, J. & CLARKE, B., 1968, Partial reproductive isolation in the genus *Partula* (Gastropoda) on Moorea. *Evolution*, 22: 684–698.
- OSBORN, H. F., 1918, *The Origin and Evolution of Life*. Scribners' Sons, New York, 322 p.
- SIMPSON, G. G., 1944, *Tempo and mode in evolution*. Columbia University, New York, 237 p.
- SIMPSON, G. G., 1953, *Major features of Evolution*. Columbia University, New York, 434 p.
- SIMPSON, G. G., 1960, The history of life, p. 117–180. In: TAX, S. (ed.), *The evolution of life*. The University of Chicago Press, Chicago.
- STANLEY, S., 1979, *Macroevolution*. Freeman, San Francisco, xi, 332 p.
- WILSON, E. O., 1965, A consistency test for phylogenies based on contemporaneous species. *Systematic Zoology*, 14: 214–220.
- WOODRUFF, D. S., 1978, Evolution and adaptive radiation of *Cerion*: a remarkably diverse group of West Indian land snails. *Malacologia*, 17: 223–239.
- WRIGHT, S., 1940, The statistical consequences of Mendelian heredity in relation to speciation, p. 161–183. In: HUXLEY, J. (ed.), *The New Systematics*. Clarendon Press, Oxford.

ADAPTATIONAL ASPECTS OF GROWTH AND REPRODUCTION IN *LYMNAEA PEREGR*A (GASTROPODA: PULMONATA) FROM EXPOSED AND SHELTERED AQUATIC HABITATS

P. Calow

Department of Zoology, University of Glasgow, Glasgow G12 8QQ, United Kingdom

ABSTRACT

Lymnaea peregra from wave-swept shores and fast-flowing streams were smaller than contemporaries from ponds and slow-flowing canals. Laboratory observations made on snails from both types of habitat, under the same constant conditions, suggest that they did not differ significantly in growth rate but that the snails from the sheltered habitats grew longer than the others. This difference in growth pattern was associated with differences in reproductive pattern. The snails from the exposed habitats, for example, initiated reproduction earlier and put more effort into it than the snails from the sheltered habitats. These differences in growth and reproduction could be explained in terms of differences in selection pressure between habitats of varying exposure. Conditions in exposed sites approximated to *r*-selection and conditions in sheltered sites to *K*-selection.

INTRODUCTION

An adaptive radiation begins when populations become isolated in differing ecological circumstances. Spatially limited bodies of freshwater represent a uniquely available series of natural experiments for investigating this process. In these systems there are a few species occupying a wide range of habitats and showing a considerable degree of within-species variation. It has been suggested that such partial speciation, or radiation at the species level, is due on the one hand to the habitat isolation noted above and, on the other, to the transitory (in terms of geological time) nature of freshwater bodies which prevents the process of radiation going far enough to result in good species (Russell-Hunter, 1970). In studying such within-species variation, however, it is necessary to distinguish genetically determined differences from those due to more immediate environmental effects. It is also important to distinguish between "random" variation and that which can meaningfully be ascribed to the process of adaptation.

Lymnaea peregra (Müller) is a widespread freshwater animal which shows considerable variation between populations, some of which is correlated with the habitat type in which it is found. Thus, individuals from exposed habitats (shores of lakes and streams) are usually smaller than individuals from sheltered habi-

tats (ponds, lakes and slow-flowing canals). However, the extent to which these differences are genetically determined has been the subject of some controversy. Bondesen (1950), for example, refers to the small individuals from exposed sites as "hunger forms" implying an environmental rather than genetic cause whereas Boycott (1936) was convinced that some of the differences in size could be ascribed to genetic differences.

Using a technique in which snails from different populations were cultured under the same, carefully controlled conditions I attempt, in this paper, to distinguish between these two hypotheses. I also attempt to explain the differences in growth pattern in terms of the possible selection pressure experienced in each kind of habitat and to relate the results to more general life-cycle theory. In this way it may be possible to clarify the general principles involved in radiation at the species level as they influence life-cycle traits.

MATERIALS AND METHODS

a) Habitats and initial collection

Snails were collected, initially, from four habitats: 1) an exposed shore on the banks of Loch Lomond (Grid ref. NS 365965); 2) a fast-flowing stream (flow $> 50 \text{ cm sec}^{-1}$) entering Loch Lomond (Grid ref. NS 445905);

3) a weedy portion of the Forth and Clyde Canal (Grid ref. NS 635735); 4) the weeds of a small, closed pond (Grid ref. NS 745605). Sites 1 and 2 will be referred to as the "exposed" habitats and sites 3 and 4 as the "sheltered" habitats. Water movements in the body of the canal were very slow ($< 5 \text{ cm sec}^{-1}$) and were negligible in the weed beds of this habitat.

All samples were taken in November. Large, random collections (200–300 snails) were obtained from each site. Since *L. peregra* is semelparous all individuals were assumed to be approximately the same age. Most snails were killed on collection and stored in 4% formalin and these were used for the analysis of the initial size-frequency distribution. Here, shell length (SL as defined in Russell-Hunter, 1961a & b) was taken as the index of snail size and was determined to the nearest 0.1 mm using vernier callipers.

b) Culture techniques

Observations in culture were restricted to the stream and canal snails. Sixty (i.e. thirty pairs) of the snails, from the initial sample from each site, were kept alive and cultured in pairs in perforated, perspex pots (150 ml) in a water bath (total volume = 50 l) through which water was recycled (100 ml per min.) over activated charcoal and glasswool. The water was prepared synthetically and was equivalent to the "SSW medium" of Thomas (1973). The pH of the medium stabilised at around 8 and the conductivity was approximately $422 \mu\text{mhos cm}^{-2}$. The medium from the whole tank was replenished fortnightly.

Snails were fed weekly on cooked lettuce (all prepared at the same time and stored frozen until use) and at this time pots were cleared of old food and faeces. Food was always in excess.

A constant temperature of $18(\pm 2)^{\circ}\text{C}$ (measured in the perspex pots) was used throughout. This is because preliminary experiments on the growth and fecundity of snails from the canal population had suggested that the best performance would be obtained at between 16 and 22°C . As temperature increased and fell about this range, growth rates and egg production rates reduced sharply. Similar results have been obtained for other temperate lymnaeids (Van der Schalie & Berry, 1972).

Using the above regime, the following pa-

rameters were measured: size of adults when they began to spawn (they lay egg capsules containing up to 100 eggs); capsule production per adult per day; adult mortality. Fifty capsules were collected in one week (approximately one month after capsule production had begun) from each group and were used to determine the number of eggs per capsule, hatching time and percentage hatchability. Upon hatching a sub-sample of 100 hatchlings was used to determine initial size and a further sub-sample of 50 snails (canal and stream only) was set collectively in a 500 l tank with circulation and feeding regimes as before. The large tank was divided into two equal sections to accommodate sub-samples from each of the populations. At first it was also necessary to confine (using perforated baffles) the small snails in a smaller portion of the larger sections. As snails increased in size the confinement was relaxed until at about fifty percent of their full size, they were allowed full access to the total volume of the relevant section of the tank. Under these conditions I measured SL, size when capsules were first produced (SL_{rep}), capsule production per snail and adult mortality. Unlike the first series of observations, snails could not be identified individually, so size and fecundity were measured as population averages.

At the end of the second laboratory generation, egg capsules were again collected from each population and treated as before. A third generation of hatchlings was cultured through to adulthood, and measurements repeated as above. Snails collected from the field were referred to as generation 1, their progeny as generation 2, and the progeny of these as generation 3. In all generations, observations on capsule production and adult mortality were restricted to a five week period.

c) Energy budgets

Energy budgets were carried out on reproductive adults in generation 2. Known weights of lettuce were fed to ten individuals from each habitat type and after a 24 hr period snails were removed to clean water with no food and the remaining lettuce was reweighed. Faecal pellets were collected from the snails until no more "green" ones were produced (usually 48 hr). Wet weight to dry weight ratios of food and energy values of food and faeces were estimated using standard techniques (Phillipson, 1964). Reproductive losses were determined from the energy

values of hatchlings, again using bomb calorimetry. All energy values were expressed in Joules (approx. 4.2 J/cal.).

RESULTS

a) Size of snails in field populations

The mean sizes of snails on collection were: 11.97 mm (SE = 1.94)—canal; 9.77 mm (SE = 1.50)—pond; 6.37 mm (SE = 1.01)—stream; 6.29 mm (SE = 1.08)—loch. Analysis of variance, based on a completely randomised design, indicated that there were significant differences in the data ($F = 5.2$, $P < 0.01$ for 3/167 df). Specific differences between individual means were identified approximately using the "least significant range test" of Sokal & Rohlf (1969) which defines the least significant difference (LSR) allowed at a given level of probability. LSR ($P = 0.05$) for the data was approximately equal to 3. Hence differences existed within but not between the "exposed" and "sheltered" habitat-groups.

Because of differences in the physical form of the four habitats it proved impossible to obtain comparative density estimates for each of the four snail populations. Subjectively, though, it was clear that the density of the pond and canal populations was much greater than the density of the stream and littoral populations.

b) Growth

Typical of most freshwater snails, growth under laboratory conditions was sigmoid (Calow, 1973). Hence when the data were plotted on semi-logarithmic co-ordinates (Fig. 1) there was an initial linear, exponential phase after which size decelerated on to a steady-state. The equations for the linear part of the curve (first 10 weeks), based on all the individual measurements, were:

Canal

$$\text{Gen. 2: } \text{Log}_e \text{ SL} = 0.169t - 0.151$$

$$\text{Gen. 3: } \text{Log}_e \text{ SL} = 0.174t - 0.181$$

Stream

$$\text{Gen. 2: } \text{Log}_e \text{ SL} = 0.174t - 0.184$$

$$\text{Gen. 3: } \text{Log}_e \text{ SL} = 0.168t - 0.167$$

where: e = base of natural logarithms (=2.718), SL = shell length (mm), t = time

(weeks). In these equations the regression coefficients differed significantly from zero ($t > 10$, $P < 0.001$) but not from each other ($t < 1$, $P > 0.05$). Similarly the other constants, representing SL at time zero, did not differ significantly from each other ($t < 1$, $P > 0.005$). Hence the snails from each population had the same rates of growth over the exponential phase (mean slope of regression lines = coefficient of exponential growth = 0.171) and the same initial size.

However, mean steady-state SLs (SL_∞) for each group (estimated by eye and by extrapolation) were approximately 14–18 mm for the canal snails (all generations) and 9–12 mm for the stream snails (all generations). These differences are clearly seen in Fig. 1 for generations 2 and 3. Snails from the canal reached a larger final size than snails from the stream.

c) Size at reproduction

Table 1 gives the mean sizes of snails in the laboratory populations at the start of capsule production for each of the three generations. Analysis of variance demonstrated that significant differences occurred between the mean sizes of snails from all four populations in generation 1. The LSR ($P = 0.05$) for these data was 3.6 so that significant differences occurred between but not within the "exposed" and "sheltered" habitat groups. Snails from the "exposed" habitats began to produce egg capsules at a smaller, adult size than snails from the "sheltered" habitats. This difference was maintained between the canal and stream populations over a further two laboratory generations (Table 1).

The average size at maturity in the different populations is marked in Fig. 1, and this shows that reproduction began before growth ceased in both groups.

d) Fecundity and viability of eggs

For the most part, information on fecundity is restricted to the canal and stream populations.

Table 2 shows: (a) mean capsule production per individual; (b) mean eggs per capsule; (c) the average, total number of eggs produced per individual per week ($c = a \times b$). There was no significant difference between

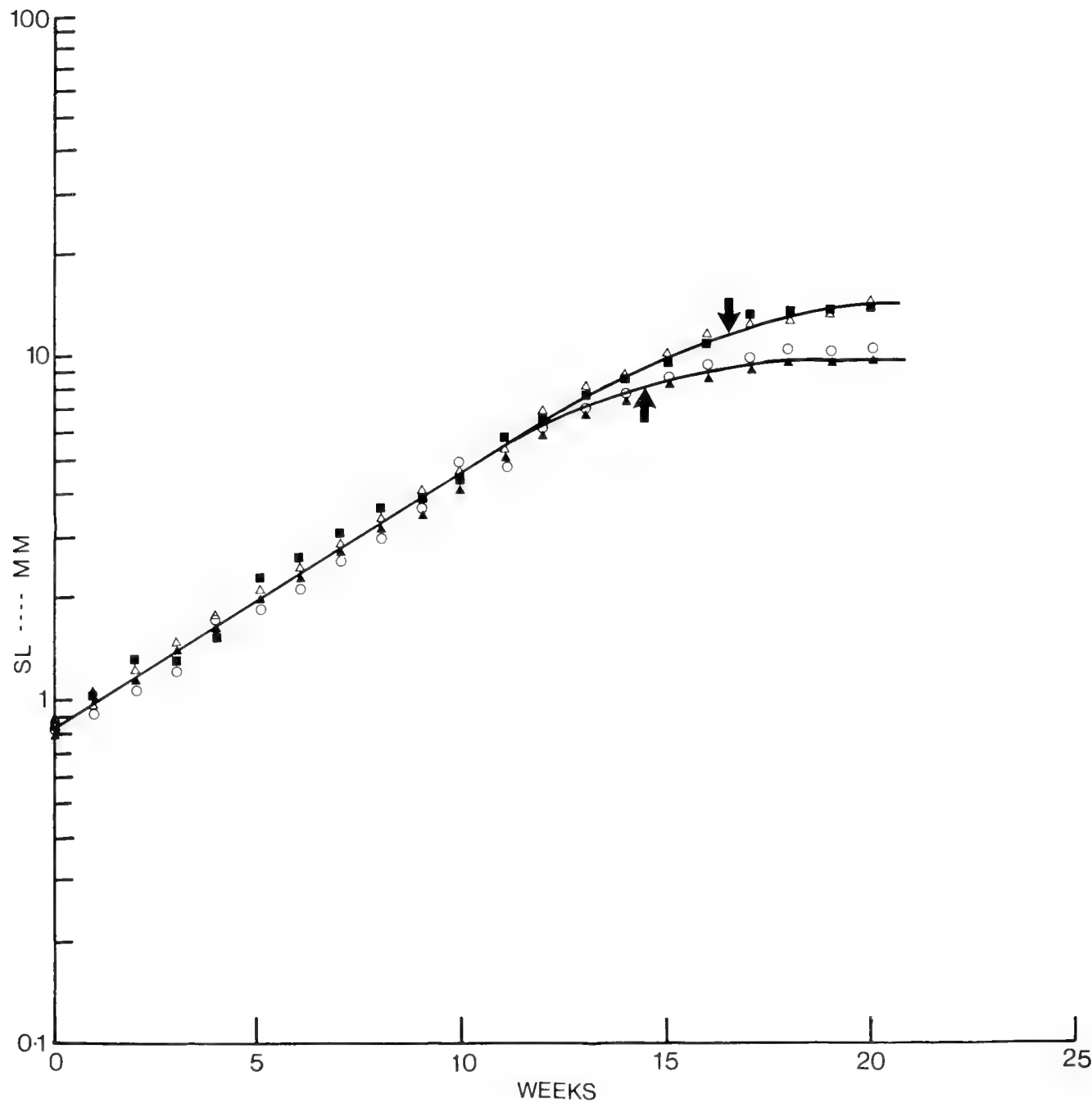


FIG. 1. Graph of log SL against time for canal snails (Gen. 2—△; Gen. 3—■) and stream snails (Gen. 2—○; Gen. 3—▲). Points are averages but the regression equations given in the text are based on individual measurements. Arrows indicate times at which capsules were first discovered in the cultures.

the mean capsules produced per individual between populations for any generation ($t = 0.2$ to 0.4 , for > 9 df; $P > 0.05$) but the number of eggs per capsule was consistently greater in the canal population (for gen. 1 and 2, $t > 2$, $P < 0.05$; for gen. 3, $t = 1.8$, $P < 0.1$). Canal snails therefore produced the same number of capsules over the experimental period but a greater number of eggs than stream snails. It should be noted, however, that capsule production and eggs per capsule reduced with each successive generation in both groups of snails; possibly a laboratory effect. Correlated with the larger egg-load, the

capsules of the canal snails were significantly longer (L) and wider (B) than the capsules of the stream snails ($d = 2 - 4$; $P < 0.05$; grand means: $L = 15.98 (\pm 1.08)$ mm for canal snails and $10.35 (\pm 1.4)$ mm for stream snails; $B = 3.41 (\pm 0.4)$ mm for canal snails and $3.02 (\pm 0.3)$ mm for stream snails). I have no quantitative laboratory data on capsule production from the littoral and pond snails but a field survey over three years has shown the mean eggs per capsule to be $17.1 (\pm 4.3)$ and $29.8 (\pm 2.1)$ in the littoral and pond snails respectively. These were significantly different ($d = 4.1$; $P < 0.001$) as were the

TABLE 1. Shell length (mm) at the onset of reproduction.

Population	Gen. 1			Gen. 2			Gen. 3		
	SL ⁺	SE*	N ⁺⁺	SL	SE	N	SL	SE	N
Canal	14.4	1.2	31	13.4	1.1	32	12.9	1.3	31
Pond	12.8	1.0	30						
Stream	8.1	1.1	35	7.6	1.0	28	7.2	1.1	25
Littoral	8.4	1.0	37						
F/d**		5.9			2.3			2.0	
df		3/129							
P		0.01			0.02			0.05	

+SL = shell length.
*SE = standard error.
++N = number of replicates.
**F for analysis of variance on four habitats; d for test of significance between two habitats.

TABLE 2. Reproductive output in snails from different habitats.

Population	(a) Caps./ind./week	(b) Eggs/caps.	(c) Eggs/ind./week
Canal			
Gen. 1	1.67(±0.51)	31.2(±2.3)	52.10
Gen. 2	1.37(±0.43)	28.6(±3.3)	39.18
Gen. 3	1.09(±0.27)	23.3(±1.9)	25.39
		average	38.89
Stream			
Gen. 1	1.59(±0.33)	26.1(±2.2)	41.49
Gen. 2	1.29(±0.11)	22.3(±1.8)	28.76
Gen. 3	1.01(±0.10)	19.5(±2.3)	19.70
		average	29.98

Confidence limits = 2 standard errors.

sizes of capsules from each habitat; L = 13.2 (±0.28) for pond snails and 5.8 (±0.48) for the littoral snails (d = 19.5, P < 0.001), B = 3.55 (±0.32) for pond snails and 2.33 (±0.12) for littoral snails (d = 2.8, P < 0.01). Clearly, the capsules of the pond snails approximated in egg content and physical dimensions to those of the canal snails whereas the capsules of the littoral snails were even smaller in content and physical dimensions than the stream snails.

Data on the hatchability and subsequent size-at-hatching of snails from the stream and canal populations are summarized in Table 3. There was no significant difference in either the time taken for eggs to hatch (ca. 12–13 days) or in the percentage hatchability of capsules (ca. 60–70%) or in the size of the snails on hatching (ca. 0.86 mm SL; see also Fig. 1).

The percentage of adults surviving for the five-week observational period in each consecutive year were ca. 65, 56, 58 for the canal population and 43, 50, 48 for the stream population. Hence, on average, adult survivorship during the breeding period was greater for the canal snails than for the stream snails. In both groups, survivors continued to lay eggs for some time after the five-week observational period.

e) Energy budgets

The dry weight to wet weight ratio of lettuce (from 30 determinations) was 0.17 (±0.03) and the Joule equivalent was 15.3 (±2.8) J mg⁻¹ dry weight. The mean amounts eaten by the canal and stream snails were respectively 54.83 (±6.43) and 35.69 (±4.98) J indi-

TABLE 3. Hatchability, hatching time and size at hatching.

	% Capsules hatching	Time to hatch (days)	Size at hatching (mm)
Canal			
Gen. 1	65.02	13.92(±1.74)	0.84(±0.016)
Gen. 2	73.31	12.11(±1.00)	0.85(±0.017)
Stream			
Gen. 1	61.94	13.09(±1.20)	0.84(±0.013)
Gen. 2	71.44	11.67(±0.89)	0.89(±0.054)
F		1.91	0.0256
df		3/85	3/397
P		>0.05	>0.05

Confidence limits = 2 standard errors.

vidual⁻¹ day⁻¹ and these are significantly different ($t = 5.22$, $P < 0.001$ for 19 df).

The partitioning of the input energy by the snails is illustrated in Fig. 2. Absorption efficiencies for both types of snail approximated to 60%. The respiratory losses were derived from the equation of Berg & Ockelman (1959) relating the fresh weight of *L. peregra* to oxygen consumption at 18°C for snails taken from the field in June. The mean fresh weights for each experimental group of ten snails were 115.4 mg and 225.3 mg for the stream and canal groups respectively. An oxy-joule equivalent of 21 J/ml oxygen uptake was employed.

Reproductive losses were estimated from:

$$\frac{\alpha \text{ (ash-free dry weight of hatchlings) joules mg}^{-1} \text{ dry weight}}{\beta}$$

where the mean ash-free dry weight for all hatchlings was 0.0012 mg and the joule equivalent was 23.1 J mg⁻¹ ash free dry weight (there being no differences between groups; $P > 0.05$). α was the mean number of eggs produced per individual per day and was derived from Table 2 and β was the efficiency of conversion of freshly laid gametes to hatchlings and was taken to be 0.6 (Calow, 1979a).

That part of the budget unaccounted for (= Rest) represents energy lost in egg capsules, excreta and secreta (e.g. mucus; Calow, 1977) and that available for somatic growth. Of the absorbed energy most was used in respiratory metabolism and of the non-respired fraction of the absorbed energy (N-RA) 30.73% was invested in reproduction by the canal and 40.91% by the stream snails. However, it is to be noted that these figures will underestimate the investment in repro-

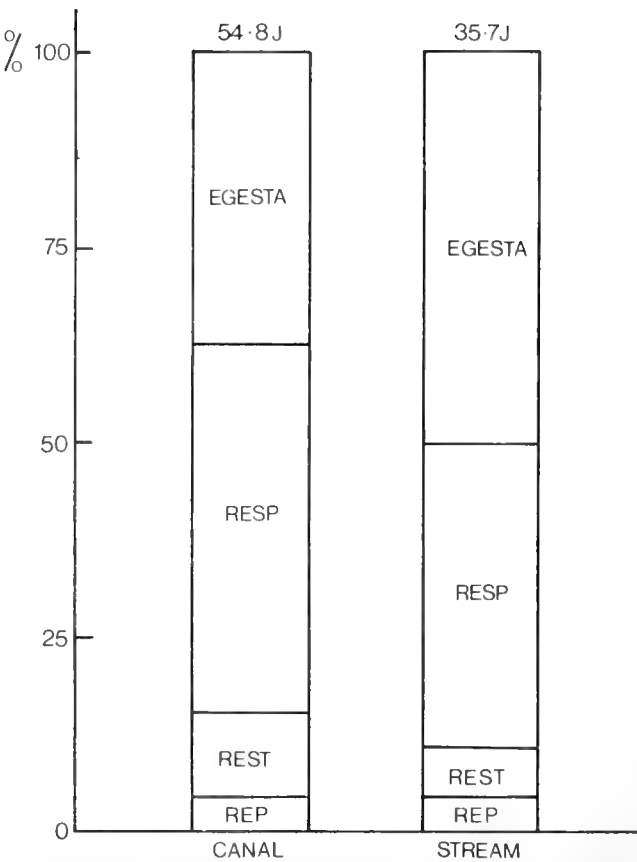


FIG. 2. Percentage allocation of ingested energy between egesta (faeces), respiration (Resp), reproduction (Rep) and other aspects of metabolism (Rest—see text for further specification). Figures over columns = energy ingested individual⁻¹ day⁻¹. Resp + Rest + Rep = absorbed energy. Rest + Rep = non-respired fraction of absorbed energy (N-RA).

duction since they do not include estimates for the wall material of the capsule. Since more of the latter is produced per egg of stream than canal snails (see above) the difference between the proportionate investments in reproduction of these two groups is likely to be more than suggested above.

DISCUSSION

Over the period of exponential growth, SL doubled approximately once every four weeks irrespective of whether the snails were derived from the canal or stream populations. A similar growth rate was recorded by Turner (1926) who made observations in the laboratory (under approximately the same temperature conditions as those used here) on more than 30,000 snails (mainly of pond origin) over five generations as part of the Boycott-Diver project on the inheritance of sinistrality in *L. peregra* (Boycott et al., 1930). The growth rate of this species, when measured in the exponential phase and under constant conditions, therefore seems to vary little from one population to another.

Despite these similarities, between-population differences did begin to occur in growth after the inflexion of the growth curve. Stream snails became reproductive at a smaller size (SL_{rep}) and hence earlier in time than the canal snails and ultimately reached a smaller steady-state size (SL_{∞}). The snails in the experiments of Turner (1926) started producing capsules at 10 mm SL but grew to a SL_{∞} of 15 to 19 mm and these results are similar to my data on snails from the canal. SL_{rep} of the Glasgow pond snails was also similar to the results of Turner whereas the SL_{rep} of the littoral snails conformed more closely to that of the stream snails. It is possible, therefore, that the growth strategies of the stream and canal snails apply more generally to *L. peregra* in "exposed" and "sheltered" habitats respectively. That is, in exposed conditions *L. peregra* starts laying eggs earlier and reaches a smaller final size than snails in sheltered conditions.

As well as differences in the pattern of growth and the timing of reproduction there were differences between the stream and canal snails in the amounts of eggs produced. Canal snails had a higher fecundity (as measured by egg output per parent) than the stream snails and circumstantial evidence suggests that similar differences occurred between the pond and littoral snails; the former corresponding more closely to the canal snails and the latter to the stream snails. However, since there were differences in the sizes of the parents at reproduction these apparent differences in absolute fecundity may not give a true indication of the cost of reproduction to the parents and energy budgets offer a better measure (Hirshfield & Tinkle, 1975; Calow,

1978, 1979b). These, as summarised in Fig. 2, suggest that stream snails invest more of their N-RA in reproduction than the canal snails, particularly if capsule walls are taken into account, and that in both groups there is little residual energy for somatic growth once reproduction has been initiated. Hence the stream snails trade-off growth for reproduction more completely and at an earlier stage than the canal snails. Furthermore they may also trade-off adult survivorship for high reproductive effort (Calow, 1979b) since, in culture, the stream snails are more mortality-prone than the canal snails once reproduction has begun.

The major differences in phenological properties between the "exposed" and "sheltered" populations, then, were size at reproduction and probably reproductive effort. These differences were maintained under constant laboratory conditions over at least two generations and so were likely to have been determined genetically, not by proximate environmental factors. Can they, therefore, be explained on the basis of environmental variations that bring about differences in selection pressure between the populations? Under "exposed" conditions mortality is likely to be of an unpredictable and age-independent kind due to spates and wave action. Food supply may also be unpredictable due to the scouring action of water movement on encrusting algae (Calow, 1974), the major food of *L. peregra* (Calow, 1970). Hence it is likely that here selection will have favoured early reproduction in terms of both the size of snails and their age. This is because restrictions in food supply might limit the growth of the snails and necessitate reproduction at an earlier adult size and because early reproduction is of clear advantage when there is unpredictable, age-independent mortality. For the same reasons, once begun, as much effort as possible should be invested in reproduction. Alternatively, under the more predictable "sheltered" conditions it may be advantageous to put breeding off in order to "cash-in" on a larger absolute fecundity made possible by a larger adult size. This is important since selection operates on the basis of eggs per parent not energy involvement in reproduction or any other index of reproductive output.

Snails from "exposed" and "sheltered" habitats also differed in the way they packaged eggs into capsules in that the stream snails put fewer eggs into smaller capsules than the canal snails. The relative merits of these two kinds of strategy are probably related to egg

survivorship and the efficiency of using the energy made available for reproduction. Under "exposed" conditions, for example, small capsules are probably less susceptible to scouring and, since the loss of a capsule in spate will be all-or-nothing the chances of the loss of a complete batch of all eggs produced by an individual will be lessened by spreading eggs between a larger number of capsules. This trend, to produce physically small capsules containing few eggs, was also observed in the littoral snails. Alternatively the amount of capsule membrane/egg will increase as capsule size becomes reduced and since the energy value of the membrane may not be insignificant (Calow, unpublished) then the number of eggs produced per unit energy made available for reproduction will not be as great for the small capsule-producers. For *L. peregra* which occur in Loch Lomond, Russell-Hunter (1961a & b) has suggested that there may be polymorphism in capsule size (there being large and small capsule morphs). Such a genetic trait might reflect the occurrence of semi-isolated populations living under different conditions of exposure and wave action in this large lake.

Finally, it is worth noting that the difference in selection between "exposed" and "sheltered" conditions correspond approximately to the differences envisaged in 'r' and 'K' selection (Pianka, 1970). The "exposed" conditions approximate to 'r' conditions of selection in that unpredictable mortality is likely to predominate whereas "sheltered" conditions approximate more closely to 'K' conditions of selection since here density-dependent regulation is more likely to dominate. Similar differences in the nature and intensity of selection may also occur within habitats where there is a cline in exposure. For example, in the marine littoral region, the upper shore is more exposed than the lower and, interestingly, Spight & Emlen (1976) have discovered exactly the same differences in growth and reproduction in certain marine gastropods occupying different parts of the shore as those noted above for *L. peregra* in different habitats. *Thais lamellosa*, a low shore snail, grows for longer and produces a larger clutch than *Thais emarginata*, an upper shore snail. Of course, not all organisms in exposed conditions will be subjected to the same forces of selection. For example, some species, like the freshwater river limpet *Ancylus fluviatilis*, which lives in both fast-flowing streams and on wave-swept shores, escapes the scouring action of water movements

by virtue of its streamlined shell and muscular foot, and may be limited in population size more by density-dependent constraints imposed by a poor food supply (Calow, 1974). Similarly, littoral, freshwater triclads are limited by density-dependent competition for a restricted food supply (e.g. Reynoldson, 1966). Hence, the sort of selection pressure experienced by a population will depend not only on the character of the environment but also on the adaptive characters of the organisms themselves (see also Calow & Woollhead, 1977).

REFERENCES CITED

- BERG, K. & OCKELMAN, K. W., 1959, The respiration of freshwater snails. *Journal of Experimental Biology*, 36: 690–708.
- BONDESEN, P., 1950, A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. *Natura Jutlandica*, 3: 1–208.
- BOYCOTT, A. E., 1936, The habitats of freshwater Mollusca in Britain. *Journal of Animal Ecology*, 5: 116–186.
- BOYCOTT, A. E., 1938, Experiments on the artificial breeding of *Limnaea involuta*, *Limnaea burnetti* and other forms of *Limnaea peregra*. *Proceedings of the Malacological Society of London*, 23, 101–108.
- BOYCOTT, A. E., DIVER, C., GARSTANG, S. & TURNER, F. M., 1930, The inheritance of sinistrality in *Limnaea peregra* (Mollusca, Pulmonata). *Philosophical Transactions of the Royal Society of London*, Ser. B, 219: 51–131.
- CALOW, P., 1970, Studies on the natural diet of *Limnaea peregra obtusa* (Kobelt) and its possible ecological implications. *Proceedings of the Malacological Society of London*, 39: 203–215.
- CALOW, P., 1973, On the regulatory nature of individual growth: some observations from freshwater snails. *Journal of Zoology*, 170: 415–428.
- CALOW, P., 1974, Some observations on the dispersion patterns of two species-populations of littoral, stone-dwelling gastropods (Pulmonata). *Freshwater Biology*, 4: 557–576.
- CALOW, P., 1977, Ecology, evolution and energetics; a study in metabolic adaptation. *Advances in Ecological Research*, 10: 1–62.
- CALOW, P., 1978, The evolution of life-cycle strategies in freshwater gastropods. *Malacologia*, 17: 351–364.
- CALOW, P., 1979a, Conversion efficiencies in heterotrophic organisms. *Biological Reviews*, 52: 385–409.
- CALOW, P., 1979b, The cost of reproduction—a physiological approach. *Biological Reviews*, 54: 23–40.
- CALOW, P. & WOOLLHEAD, A. S., 1977, The relationship between reproductive effort and evolu-

- tion of life-history strategies—some observations on freshwater triclads. *Journal of Animal Ecology*, 46: 765–781.
- HIRSHFIELD, M. F. & TINKLE, D. W., 1975, Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences, U.S.A.*, 72: 2227–2231.
- PHILLIPSON, J., 1964, A miniature bomb calorimeter for small biological samples. *Oikos*, 15: 130–139.
- PIANKA, E. R., 1970, on 'r' and 'K' selection. *American Naturalist*, 104: 592–597.
- REYNOLDSON, T. B., 1966, The distribution and abundance of lake-dwelling triclads—towards a hypothesis. *Advances in Ecological Research*, 3: 1–71.
- RUSSELL-HUNTER, W. D., 1961a, Annual variations in growth and density in natural populations of freshwater snails in the West of Scotland. *Proceedings of the Zoological Society of London*, 135: 219–253.
- RUSSELL-HUNTER, W. D., 1961b, Life cycles of four freshwater snails in limited populations in Loch Lomond, with a discussion of intraspecific variation. *Proceedings of the Zoological Society of London*, 137: 135–171.
- RUSSELL-HUNTER, W. D., 1970, *Aquatic Productivity*. Macmillan, London.
- SCHALIE, VAN DER H. & BERRY, E. G., 1972, The effects of temperature on growth and reproduction of aquatic snails. *Sterkiana*, 50: 1–92.
- SOKAL, R. R. & ROHLF, F. J., 1969, *Biometry*. Freeman, San Francisco.
- SPIGHT, T. M. & EMLEN, J., 1976, Clutch sizes of two marine snails with a changing food supply. *Ecology*, 57: 1162–1178.
- THOMAS, J. D., 1973, Schistosomiasis and the control of molluscan hosts of human schistosomes with particular reference to self-regulatory mechanisms. *Advances in Parasitology*, 11: 307–394.
- TURNER, F. M., 1926, The rate of growth of *Limnaea peregra*. *Naturalist (Leeds)* Aug. 1: 231–235.

RESPONSES OF AN ESTUARINE BIVALVE, *SCROBICULARIA PLANA*
(TELLINACEA) TO STRESS

E. R. Trueman and H. B. Akberali

Zoology Department, University of Manchester, Manchester, M13 9PL, England

ABSTRACT

The activity of *Scrobicularia plana* (da Costa)—an estuarine bivalve—has been monitored in the laboratory, under simulated field conditions, by continuously recording valve movements, heart rate and water flow. Rapid changes in environmental salinity ($30-6^{\circ}/\infty$) induce the response of valve closure and inactivity which apparently effectively isolate the tissues from the environment. Prolonged closure (<1 hr) results in anaerobiosis and an accumulation of acid metabolites in the absence of ventilation of the mantle cavity. Whereas in low salinities the ionic concentration of most ions in the body fluids decreases that of calcium ions increases. Experiments with ^{45}Ca using autoradiographic and counting techniques have demonstrated that the calcium ions are derived from the interior of the valves. Similar behaviour has been observed in respect to copper pollution. The ability to close the valves and to remain isolated from the environment for up to 7 days suggests that *Scrobicularia* is particularly well adapted to withstand the stresses of estuarine life whether these are changing salinity or pollutants.

INTRODUCTION

Scrobicularia plana (da Costa) is an estuarine bivalve found abundantly in intertidal muds. Its behaviour in respect of heart rate, pumping, valve movements and oxygen consumption have been monitored in the laboratory under conditions simulating the natural habitat and in the field in respect to heart rate (Earll, 1975; Akberali, 1978; Akberali & Trueman, 1979). In many bivalves studied, e.g. *Mya*, *Mytilus*, *Ostrea* (Thompson & Bayne, 1972; Walne, 1972), changes in pumping activity elicit little variation in the heart rate, but in *Scrobicularia* the heart rate and amplitude fall markedly with reduction of pumping. During activity, periods of pumping (30-60 min.) alternate with ventilatory pauses and the reduction of heart rate, e.g. 20-5 beats min^{-1} , is observed to correspond with the cessation of pumping (Fig. 1). During longer periods of apparently spontaneous quiescence (4-12 hr duration) pumping ceases, the valves close, bradycardia occurs and in some instances the heart beat completely ceases (Fig. 1C).

The purpose of this article is to consider recent work on the behaviour and physiology of *Scrobicularia* as they are affected by the stress of changing salinity or by the presence

of pollutants. The ability of this species to detect and to respond to adverse environmental changes, such as may be found in estuaries, will be reviewed. The response to stress conditions is commonly valve closure and isolation of the tissues from the external habitat. This may, in *Scrobicularia*, be sustained for at least seven days and the effectiveness of this mechanism, as an adaptation to estuarine life, is assessed.

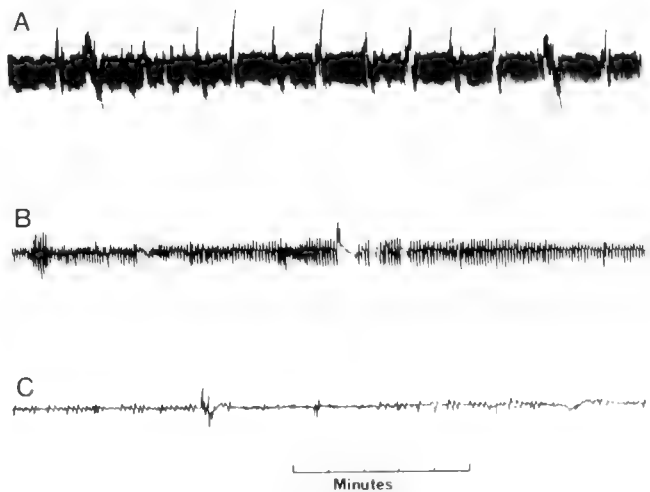


FIG. 1. Examples of recordings of the heart beat of *Scrobicularia plana* during A, activity; B, ventilatory pause; and C, quiescence.

METHODS

The details of the methods used in these investigations have been presented fully in previous articles and it is only intended to refer briefly to these. Activity of the clam was recorded on a pen recorder in respect of valve movements and heart rate by use of the impedance technique (Trueman et al., 1973) and gill pumping by a thermistor flow meter in the exhalant water current (Foster-Smith, 1976). The flow meter was used simply as an 'on/off' detector, no attempt being made to calibrate the instrument for the amount of flow. Estimation of oxygen and carbon dioxide in mantle cavity water was carried out on samples withdrawn by hypodermic needle from between the valve margins by use of a Radiometer PHM 73 Blood gas analyser. Each animal was discarded after the sample was withdrawn (Akberali & Trueman, 1979). The pH of the mantle cavity water was monitored on a pen recorder using a microelectrode (Pye, Ingold) inserted in the mantle cavity through a fine hole drilled in the shell. Calcium ions present in the various body fluids were measured using an Atomic Absorption Spectrophotometer with EDTA added to the extracts to a final concentration of 0.78% to prevent phosphate interferences. The fate of calcium previously incorporated into the shell during stress situations was investigated by placing *Scrobicularia*, with the outer surface of the valves protected by varnish, in sea water to which ^{45}Ca had been added. After 48 hours in unlabelled sea water to flush out ^{45}Ca from the mantle cavity and extrapallial fluids the clams were subjected to a standard salinity stress by immersion in 20% sea water ($S = 6\text{‰}$) whilst controls were left in normal sea water. Valves from animals of both groups were thoroughly scrubbed, dissolved in dilute hydrochloric acid, prior to the ^{45}Ca content being measured (Akberali, 1980).

Animals were collected fortnightly from Morecambe Bay, transported to Manchester University and kept in an aquarium at 10°C during all experiments. A standard salinity stress was applied by a sudden reduction of salinity from normal to 20% sea water (30‰ – 6‰). Studies on the effect of copper pollution were carried out in normal sea water to which copper was added from a stock $\text{Cu}(\text{NO}_3)_2$ solution to give predetermined final concentrations (Akberali & Black, 1980).

EXPERIMENTAL OBSERVATIONS

Application of rapid changes of salinity of the medium in the form of a standard salinity stress to *Scrobicularia* results in valve closure and inactivity whilst the tissues are effectively isolated from the surrounding water (Fig. 2). During this stress, *Scrobicularia*, in common with other bivalves, respire anaerobically and produces succinic acid, alanine and other volatile fatty acids (De Zwaan & Wijsman, 1976). Adverse environmental conditions, such as aerial exposure, salinity or pollutant stress, can cause *Scrobicularia* to close its valves for periods up to 7 days with only short and occasional pumping activity (Fig. 2). After this period of salinity stress, pumping activity

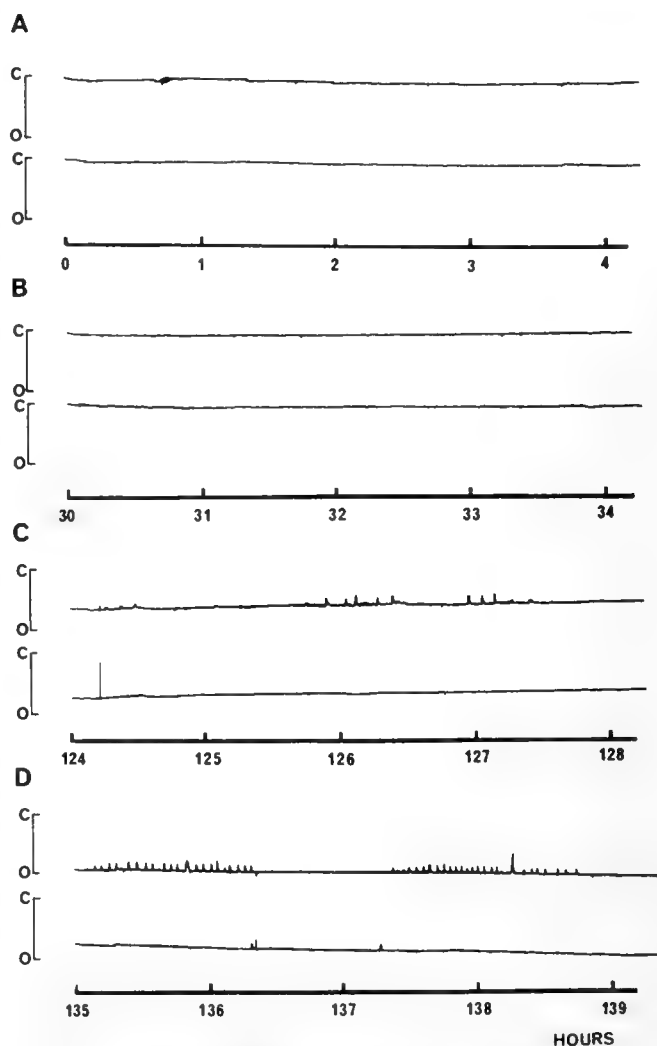


FIG. 2. Recordings of the valve movements of *Scrobicularia plana* immediately following transfer directly from 100% sea water at 0 hr to 20% sea water: records A to D are 4 hr sections of a continuous 168 hr recording which have been selected to show events described in the text; traces are of two individual *Scrobicularia* recorded simultaneously.

gradually increases in duration to more than 50% of the time as the clams come into equilibrium with the external medium (Akberali, 1978).

It should not, however, be assumed that during periods of stress the valves are always tightly closed, completely sealing the animal off from the habitat. The pO_2 in the mantle cavity of *Scrobicularia* falls from 140 to about 50 mm Hg in 2 hr after valve closure but at about 3 hr a temporary increase of 20 mm Hg occurs (Fig. 3). This is probably due to a slight opening of valve and mantle margins allowing diffusion, for it does not occur when the valves are forcibly sealed. Over the same period the pCO_2 increases from 2 to 10 mm Hg, when the valves are forcibly sealed, but only to about 5 mm Hg when the clam is being affected by salinity stress alone. This suggests that lower levels may be stabilised by outward diffusion. During aerial exposure *Scrobicu-*

laria shows a comparable increase in the oxygen content after 3 hr except when the valves are forcibly closed (Fig. 4).

To effect these changes in oxygen tension when the valves are apparently closed the mantle must be in contact with the media along a narrow margin between the valves. When the valves are closed, *Scrobicularia* gives a rapid response to the change of salinity or pollutants of the surrounding water (Akberali & Black, 1980). This is presumably because of the mantle being in contact with the medium, so allowing the clam to exploit conditions of minimum stress fully as they occur. This is advantageous in an estuarine environment where conditions are continuously changing.

When *Scrobicularia* is transferred from 30‰ to 6‰ aerated seawater the concentration of ions, except Ca^{++} , in the mantle cavity fluid and blood falls to the level of the

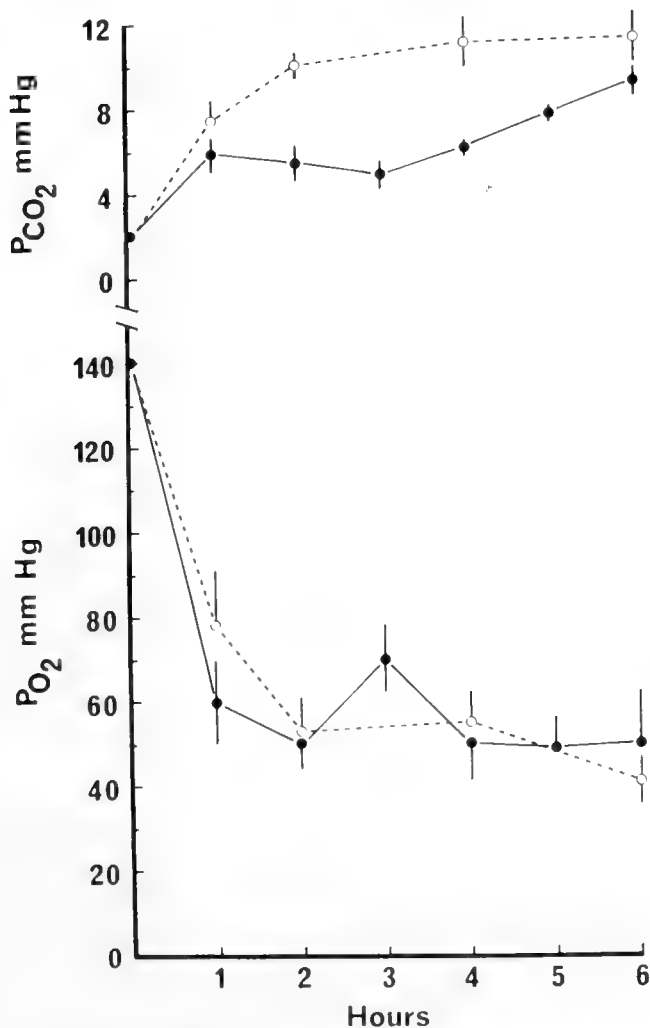


FIG. 3. PO_2 and PCO_2 levels in the mantle cavity of normal (●—●) and forcibly closed (O---O) *Scrobicularia* when transferred directly from sea water to 20‰ sea water at 0 hr. Each point is a mean for 6 animals, which were then discarded. Bars represent S.E.

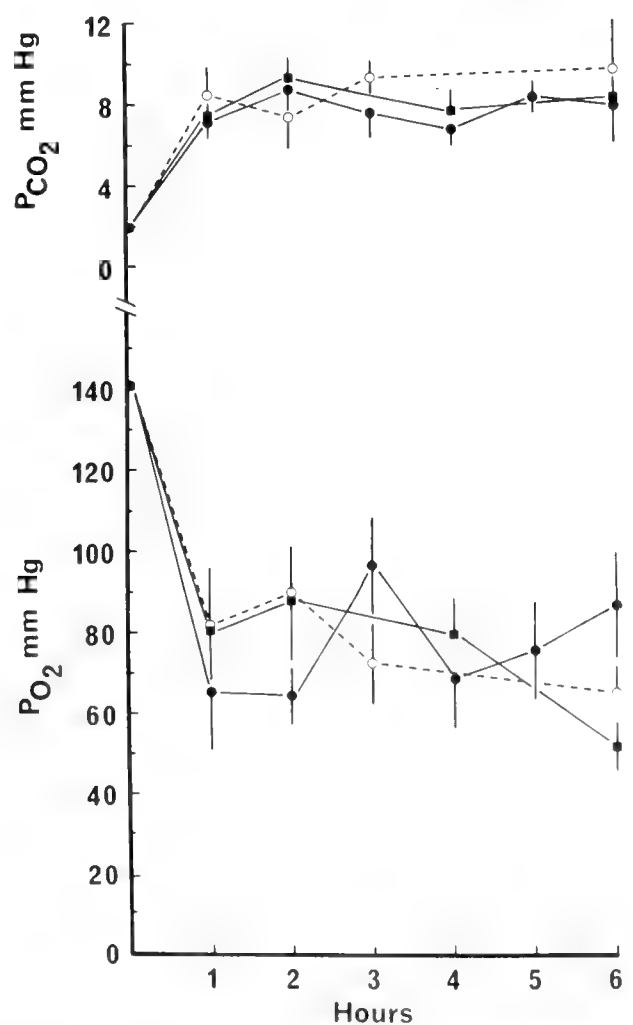


FIG. 4. PO_2 and PCO_2 levels of mantle cavity water of *Scrobicularia* when placed at 0 hr in air (●—●), in atmosphere of nitrogen (■—■) or in air with valves forcibly closed (O---O). Each point a mean of 7 animals, which were then discarded. Bars represent S.E.

external medium within 14 days (Akberali et al., 1977). The blood calcium rises (Fig. 5) in concentration to a maximum of 30 mM (about $\times 3$ that in normal sea water) within 5–7 days when it drops towards that of the external medium, stabilising at a new low level at about 18 days (Akberali et al., 1977). Similar changes are observed in extra-pallial and mantle cavity fluid. To determine whether the increase of calcium over the first 7 days is related to anaerobic metabolism, clams were placed in oxygen-free sea water where they exhibit only a slight rise in calcium levels (Fig.

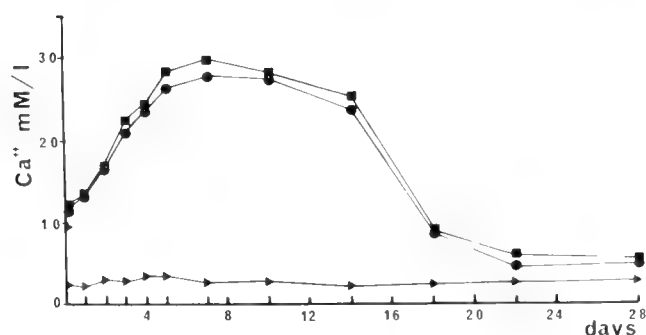


FIG. 5. Calcium concentrations of *Scrobicularia* transferred directly from 100% sea water at day 0 to 20% sea water, mantle cavity water, (■—■); blood from the ventricle, (●—●); medium (▲—▲). Each point is the mean of four determinations made on samples pooled from 12–14 individual *Scrobicularia* selected randomly.

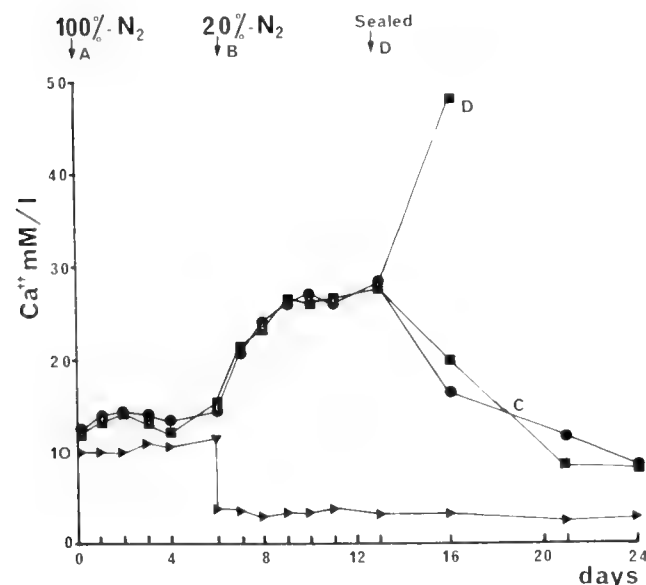


FIG. 6. Calcium concentrations of *Scrobicularia* placed in oxygen-free 100% sea water (A). After 6 days, the clams were additionally subjected to salinity stress, by immersion in oxygen-free 20% sea water (B and C). After 7 days the valves of 20 animals were forcibly closed (D). Mantle cavity water, (■—■); blood from the ventricle, (●—●); medium, (▲—▲).

6). Only when the valves are closed by immersion in 20% sea water and the mantle cavity not ventilated do calcium levels increase markedly. Forcible closure of the valves results in a rapid increase of calcium over 2 days to about the same level as that reached by animals in 20% aerated sea water in 7 days. Continuous flow of oxygen-free 100% sea water through the mantle cavity, may explain the absence of a significant rise in calcium ions (Fig. 6, A-B) for in this condition no anaerobic metabolites would accumulate and no buffering would be required. The calcium ions have been shown to be derived from the interior of the valves of the shell by dissolution during stress using ^{45}Ca and autoradiographic and counting techniques (Akberali, 1980). The deposition of ^{45}Ca by unfed *Scrobicularia*, in which the outer surfaces of the valves are painted with varnish to reduce absorption of calcium, was estimated to be 0.228 ng ^{45}Ca per valve for a 72 hr experimental period. When these clams are subjected to the standard salinity stress about 50% of the incorporated ^{45}Ca is lost within the first 24 hours (Fig. 7). This suggests that the freshly deposited calcium is more labile than the remainder of the valve and is lost initially in stress conditions. With longer term stress (21 days) a greater demand for calcium may

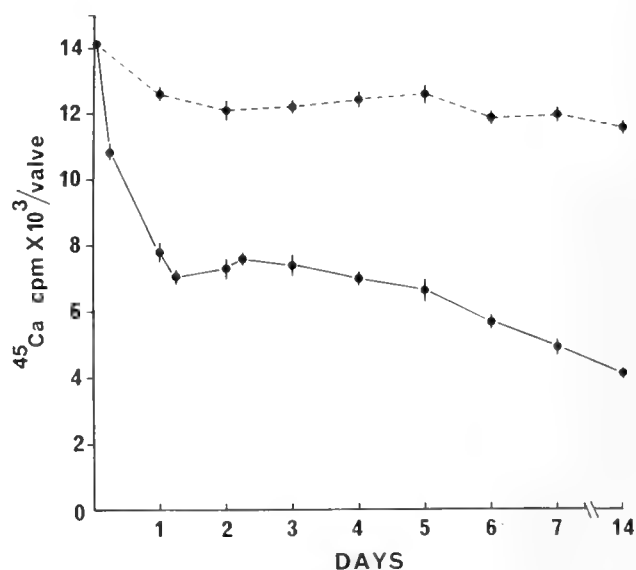


FIG. 7. *Scrobicularia* with their valves covered with amyl acetate varnish left for 72 hours in ^{45}Ca -labelled sea water ($5 \mu\text{Ci/L}$) for incorporation of labelled calcium in the valves, followed by placing those clams in unlabelled sea water for 48 hours, the clams were then either subjected to a salinity stress at day 0 for 14 days (●—●) or placed in normal sea water as a control (■—■); values are presented as means of total ^{45}Ca counts per minute (cpm) per valve ($n = 8$); bars represent S.E.

TABLE 1. Animals were transferred directly from 100% to 20% sea water at 0 hr. At various intervals the animals were removed and the calcium content of the mantle cavity fluid measured. The shell valves were weighed and the area recorded. The shell valve was broken (shell crushing force) in compression between the plates of an Instron 1122 standard mechanical testing machine with the kind cooperation of Prof. Currey, University of York. Standard deviation in brackets. N.S. not significant.

Period	Mantle cavity fluid Ca ⁺⁺ Con. mM/L n = 7	Shell weight gms/sq cm. n = 14	Shell crushing force Newtons/sq cm. n = 14
0 hr.	10.32 (0.31)	0.1791 (0.015)	3.4641 (0.92)
24 hr.	11.64 (1.26) P < 0.02	0.1764 (0.028) N.S.	3.8284 (1.02) N.S.
72 hr.	18.44 (4.40) P < 0.001	0.1671 (0.013) P < 0.02	2.7753 (0.97) N.S.
7th day	23.79 (6.57) P < 0.001	0.1627 (0.011) P < 0.002	3.0256 (0.80) N.S.
14th day	9.20 (10.13) N.S.	0.1563 (0.028) P < 0.01	3.0290 (0.84) N.S.
21st day	5.45 (2.16) P < 0.002	0.1535 (0.013) P < 0.001	3.0148 (0.82) N.S.

lead to the mobilisation of more tightly bound calcium and gives rise to a significant decrease in shell weight but no apparent reduction in strength (Table 1).

Other behavioural features may be related to the removal of metabolites derived from periods of valve closure. During short term stress periods (4–7 hr) and natural periods of quiescence the pH of the mantle cavity water falls from 7.8 to 7. This is probably due to the accumulation of acid metabolites. A common feature of recovery in *Scrobicularia* and other species is the repeated sharp adduction of the valves and overshoot of the heart rate. A brief interval (ca 30 s) after each adduction the pH of the mantle cavity of *Scrobicularia* falls markedly to be followed by a slow rise as ciliary ventilation continues (Fig. 8). Similar stepwise changes of pCO₂ and pO₂ occur during recovery from longer periods of anaerobiosis (circa 7 days) and imply intermittent recovery compatible with hyperventilation caused by valve adduction (Akberali & Trueman, 1979). Simultaneous pressure pulses are generated

in both mantle cavity and tissues at adduction resulting in outflow of water from the mantle cavity (Trueman, 1966). However, the pressure lasts longer in the tissues (1–2 s) than in the mantle and could well bring about rapid flushing out of metabolites from the tissues whilst between adductions normal ciliary pumping would remove these from the mantle cavity.

Scrobicularia responds to copper in solution in sea water at concentrations of 0.01 ppm in a manner similar to *Mytilus* (Davenport, 1977) and other bivalve molluscs (Manley & Davenport, 1979). Siphonal retraction and valve closure are the initial response followed by a rapid drop in heart rate (Akberali & Black, 1980). In concentrations in sea water of 0.05–0.01 ppm copper in sea water the clams begin to interact with the medium after two to three hours. In 0.5 ppm the valves remain closed and the heart rate is maintained at a low level over a 6 hr exposure period (Fig. 9). Replacement of the polluted water by normal sea water even with the highest con-

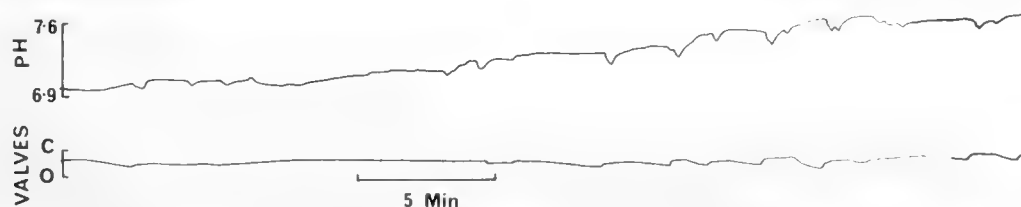


FIG. 8. Rapid valve movements (sharp rise representing adductions) observed shortly after transference to sea water after exposure to a salinity stress for 24 hours. These valve movements correspond to a stepwise increase in the pH of the mantle cavity water. With commencement and continuation of activity, pH returns to normal.

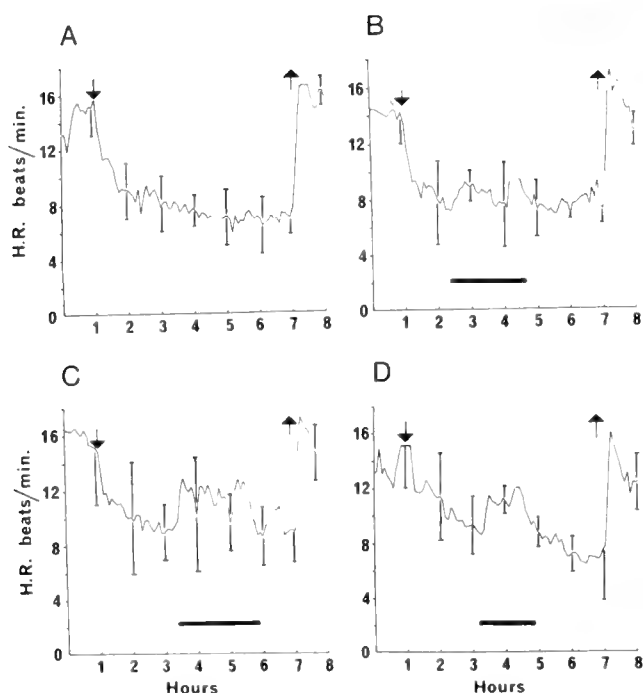


FIG. 9. Heart rate (H.R.) of *Scrobicularia* subjected to various copper concentrations over the 6 hr exposure period. A, 0.5 ppm; B, 0.1 ppm; C, 0.05 ppm and D, 0.01 ppm copper concentrations in sea water (S, 31‰). Addition of copper solution indicated by arrow (\downarrow), replacement with normal sea water. Horizontal bars (—) refer to increased activity in heart-rate and valve movements during the 6 hour exposure period. Vertical bars represent the range of individual variation (\updownarrow).

centration of copper used (0.5 ppm), leads to recovery within 10–15 min, the valves opening with an overshoot in the heart rate.

DISCUSSION

Mobilisation of calcium from the shell in order to buffer the end products of anaerobic respiration is a relevant physiological adaptation to salinity stress or pollution since the animals can protect the tissues by valve closure for short periods, while sustaining basal metabolism by anaerobiosis (Akberali, et al., 1977; Akberali, 1980). However, with longer exposure to copper (8 days), the clams apparently have to interact with the medium to flush out excretory and respiratory end-products and when they open in 0.5 ppm copper, poisoning takes place and as a result mortality occurs (Akberali & Black, 1980). *Scrobicularia*, when subjected to low salinity stress, begins to interact more freely with the medium after 5–7 days (Akberali, 1978). It is possible that this is a critical period since depletion of energy resources or accumulation

of metabolites may then necessitate valve opening and interaction with the medium.

The ability of *Scrobicularia* to close the valves and to remain effectively isolated from the environment and yet to continue to respond to external changes suggests that this clam is particularly well adapted to withstand the stresses of estuarine life whether these are of changing salinity or pollutants. Such adaptations in behaviour and their physiological consequences are necessary for success in an estuarine environment and the adaptations required to avoid salinity stress appear to be equally effective against pollutants provided the application is of similar relatively short duration.

Rapid detection of pollutants in solution is clearly of prime importance to the species. The siphon of *Scrobicularia* reacts to copper ions in the same manner whether isolated or in preparations of the whole clam and it appears that this may be due to copper affecting the neuromuscular junctions (Akberali & Trueman, unpublished). In contrast to the direct action of copper on the tissues, the sense organ in the cruciform muscle complex, recognised by Odiete (1978) to respond to polluted water, has recently been shown in our laboratory to be the site of detection of zinc ions in solution (Akberali, Wong & Trueman, in prep.). The cruciform muscle complex is located at the base of the siphons near the mantle margins, where it may readily function as a chemoreceptor organ in respect of water drawn into the mantle cavity.

ACKNOWLEDGEMENTS

We are grateful to Drs. Iles and Jones of the Department of Zoology, Manchester University, for critically reading the manuscript. These investigations have been supported by N.E.R.C. Research Grant GR3/3436.

REFERENCES CITED

- AKBERALI, H. B., 1978, Behaviour of *Scrobicularia plana* (da Costa) in water of various salinities. *Journal of Experimental Marine Biology and Ecology*, 33: 237–249.
- AKBERALI, H. B., 1980, 45 Calcium uptake and dissolution in the shell of *Scrobicularia plana* (da Costa). *Journal of Experimental Marine Biology and Ecology*, 43: 1–9.
- AKBERALI, H. B. & BLACK, J. E., 1980, Behavioural responses of the bivalve *Scrobicularia plana* (da

- Costa) subjected to short term copper (Cu II) concentrations. *Marine Environmental Research*, 4: 97–107.
- AKBERALI, H. B., MARRIOTT, K. R. M. & TRUEMAN, E. R., 1977, Calcium utilization during anaerobiosis induced by osmotic shock in a bivalve mollusc. *Nature*, 256: 852–853.
- AKBERALI, H. B. & TRUEMAN, E. R., 1979, PO_2 and PCO_2 changes in the mantle cavity of *Scrobicularia* (Bivalvia) under normal and stress conditions. *Estuarine, Coastal and Marine Science*, 9: 499–507.
- DAVENPORT, J., 1977, A study of the effects of copper applied continuously and discontinuously to specimens of *Mytilus edulis* (L.) exposed to steady and fluctuating salinity levels. *Journal of the Marine Biological Association of the United Kingdom*, 57: 63–74.
- EARLL, R., 1975, Temporal variation in the heart activity of *Scrobicularia plana* (da Costa) in constant and tidal conditions. *Journal of Experimental Marine Biology and Ecology*, 19: 257–274.
- FOSTER-SMITH, R. L., 1976, Some mechanisms for the control of pumping activity in bivalves. *Marine Behaviour and Physiology*, 4: 41–60.
- MANLEY, A. R. & DAVENPORT, J., 1979, Behavioural responses of some marine bivalves to heightened sea water copper concentrations. *Bulletin of Environmental Contamination and Toxicology*, 22: 739–744.
- ODIETE, W. O., 1978, The cruciform muscle and its associated sense organ in *Scrobicularia plana* (da Costa). *Journal of Molluscan Studies*, 44: 180–189.
- THOMPSON, R. J. & BAYNE, B. L., 1972, Active metabolism associated with feeding in the mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, 9: 111–124.
- TRUEMAN, E. R., 1966, Fluid dynamics of the bivalve molluscs *Mya* and *Margaritifera*. *Journal of Experimental Biology*, 45: 369–382.
- TRUEMAN, E. R., BLATCHFORD, J. G., JONES, H. D. & LOWE, G., 1973, Recordings of heart rate and activity of molluscs in their natural habitat. *Malacologia*, 14: 377–383.
- WALNE, P. R., 1972, The influence of current speed, body size, and water temperature on the filtration rate of five species of bivalves. *Journal of the Marine Biological Association of the United Kingdom*, 52: 345–374.
- ZWAAN, A. DE & WIJSMAN, T. C. M., 1976, Review. Anaerobic metabolism in Bivalvia (Mollusca). Characteristics of Anaerobic metabolism. *Comparative Biochemistry and Physiology*, ser. B, 54: 313–324.

ON ADAPTIVE RADIATION IN THE PECTINACEA WITH A
DESCRIPTION OF *HEMIPecten FORBESIANUS*

C. M. Yonge

Department of Zoology, University of Edinburgh,
West Mains Road, Edinburgh EH9 3JT, United Kingdom

ABSTRACT

Evolution of the highly efficient monomyarian condition in the Pectinacea is followed through stages represented now by the heteromyarian (and so byssally attached) Mytilacea and the similarly attached but less specialized monomyarian Pteriacea (e.g. *Pinctada*).

The Pectinacea are pleurothetic, posture being controlled by the left (upper) statocyst. The inner ligament layer forms a spherical elastic pad responsible for the very wide gape; the inner mantle margin ("velum") is correspondingly enlarged. Increase in the ratio of striated ("quick") to smooth ("catch") muscle in the adductor is considered to be initially connected with expulsion of pseudofaeces. Pallial eyes are possessed regardless of habit and are regarded as initially associated with the wide gape and so danger from predators. Anterior as well as posterior expulsion of pseudofaeces accounts for the complex lip apparatus and provides the means of jet propulsion.

In habits the early separated Propeamussiidae, attached or free, without eyes or lip apparatus, and some carnivorous, exploit abyssal depths. The Pectinidae are initially attached by byssus, this further developed in *Pedum* and in *Hemipecten* (here first fully described and compared with the Anomiacea), each associated with scleractinian corals; this habit replaced by freedom as in *Pecten* and *Amusium* and by cementation in *Hinnites*. The same habit is attained earlier in life in the Spondylidae, this family differing in hinge and ligament, the outer ligament layers moved inward and replaced by fused periostracum with accompanying acquisition of ball-and-socket hinge teeth.

INTRODUCTION

This paper represents the association of information and deductions on the Pectinacea contained in a series of papers extending over many years (Yonge, 1936, 1951, 1953, 1967, 1973, 1975). More recent work, primarily on the ligament, has shown that the Plicatulidae, despite superficial resemblance by way of secondary ball-and-socket teeth to the Spondylidae, should be removed from the Pectinacea and associated with the Dimyidae (Yonge, 1978a) in a new superfamily Plicatulacea¹ (Yonge, 1975, 1977a). But the extent of radiation with the family Pectinidae has been increased by new observations herein recorded, on structure and mode of life in *Hemipecten forbesianus* Adams & Reeve, 1850.

KEY FOR ABBREVIATIONS ON FIGURES

a	anus
adc	adductor, smooth muscle
adq	adductor, striated muscle
aol	anterior outer ligament layer
aur	auricle (of right side)
by	byssal strands
byn	byssal notch
ct	ctenidium
dd	digestive diverticula
e	eyes (on middle marginal fold)
f	foot
fif	fused inner marginal folds
fl	fused lips
if	inner marginal fold
il	inner ligament layer
lp	labial palp
pc	pericardium

¹Waller (1978) does not accept this separation of *Plicatula* from the Pectinacea nor the differences between ligamental structure in the Pectinidae and in the Spondylidae. But criteria differ profoundly, those of palaeontology rest on the nature of the secreted shell while those of comparative anatomy must be based on the nature of the secreting epithelia.

pol	posterior outer ligament layer
pr	pedal retractor (of left side)
r	rectum
so	sense organ
v	ventricle
vm	visceral mass

EVOLUTION OF THE PECTINACEA

The Bivalvia, it is postulated, are primarily infaunal molluscs with anterior and posterior adductors formed by cross fusion of pallial muscles at each end of a laterally compressed body (Yonge, 1953, 1978b). Attachment of the mantle lobes near the margin of the shell (found in no other Mollusca) results from muscular development in the innermost of the three marginal folds which is concerned with control of the increased water flow produced by the hypertrophied bivalve ctenidia. Calcification, it is further maintained, followed compression with an uncalcified mid-dorsal region forming the ligament—thus the means of opening the valves appeared *pari passu* with the means of closing them.

Subsequent evolution in a diversity of bivalves and by a variety of routes led to loss of the anterior adductor, and reorganization of the organs around the remaining enlarged and centrally placed muscle. This change to a monomyarian condition has been achieved with outstanding success in the order Pterioidea of the subclass Pteriomorpha (classification of Newell, 1965). Evolved in the Ordovician this process culminated in the appearance of the Pectinacea which, including the ubiquitous and outstandingly successful scallops, represent one of the peaks of success within the Bivalvia. The course of evolution must have proceeded by way of a heteromyarian condition which, wherever it appears, involves byssal attachment and change from infaunal to epifaunal life (Yonge & Campbell, 1968). At this stage the evolving monomyarian could have resembled the modern Mytilacea. This is presumed to have been followed by a preliminary, also byssally attached, monomyarian condition, the organs now reorganized around the central adductor and with limited bilateral asymmetry. This condition may have resembled that now present in the least modified of the modern Pteriacea, genera of the family Pteriidae such as *Pinctada*.

The ultimate monomyarian condition involving greater reorganization around the central

adductor with assumption of a pleurothetic habit—the sagittal plane now horizontal—and with great modification of hinge and ligament appears in the Pectinacea, also byssally attached initially. Far from representing finality, this highly specialized body form and habit was the starting point for a striking range of diverging adaptations which it is the purpose of this paper to describe. Later, at the end of the Palaeozoic, the similarly monomyarian, but byssally cemented Anomiacea were to display equally impressive adaptive radiation involving the appearance of the limpet-like *Enigmonia* and the completely free although immobile *Placuna* (Yonge, 1977b).

The major alterations involved in change from the heteromyarian to the initial monomyarian (pteriacean) condition are shown in Fig. 1. The heteromyarian is equivalve but inequilateral, the anterior pedal retractors reduced. In the monomyarian, apart from loss of the reduced anterior adductor, there is change in shell shape from the inevitable triangular form of the heteromyarian to the laterally flattened and circular form of the monomyarian. The reduced foot being morphologically mid-ventral, almost the entire widely open mantle cavity is posterior. In the adductor the striated muscle component is much the larger due to need for frequent expulsion of pseudofaeces which collect opposite the posterior end of the ctenidia (Herdman & Hornell, 1904). The foot retains its locomotory function in young stages but in the adult is exclusively concerned with secreting and planting the byssal threads that emerge through a notch in the right valve, the animal inclining towards that side. Both right pedal retractors are reduced. Immobilized by the presence of the large byssus, the foot can have no cleansing function, only in the elongated *Malleus* is a long, very active accessory foot available for this purpose (Yonge, 1968). The nervous system is that of a typical bivalve (Herdman & Hornell, 1904).

It is easy to see how modification of shell form with a central adductor influences the disposition of both pallial and visceral organs but not how the ligament could alter. That of the heteromyarian is extremely opisthodontic with a greatly enlarged posterior outer layer extending over the full length of the inner layer, the anterior outer layer reduced to a vestige (Yonge & Campbell, 1968). The Pteriacea have a long hinge line but it is secondarily amphidetic with anterior outer, middle and posterior outer layers all about the

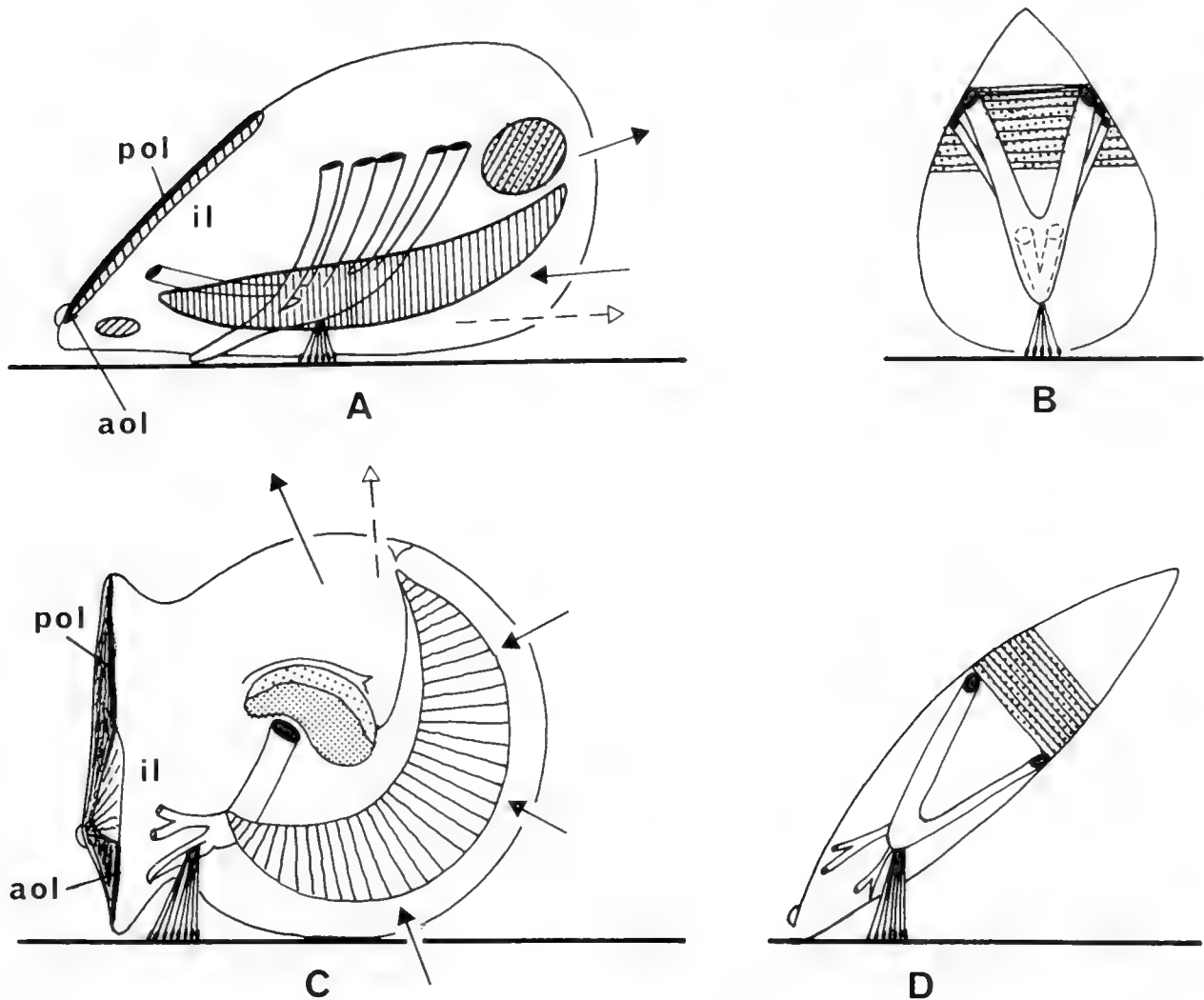


FIG. 1. Comparison between inequilateral heteromyarian (mytilacean) condition and the inequivalve monomyarian (pteriacean) condition, viewed from left side (A, C) and in transverse section from posterior end (B, D), showing adductors, foot with retractors and byssus, ligament layers and ctenidium. Striated and smooth muscle in adductor (C) denoted respectively by fine and coarse stipple. Solid arrows indicate sites of inhalant and exhalant currents, broken arrows those of pseudofaecal extrusion. For key to abbreviations see p. 23–24.

same length (Fig. 1C). This could not have evolved from the extreme opisthodontic condition of the Mytilacea but, of course, within that superfamily the heteromyarian condition represents the end point of an evolutionary trend. The necessarily heteromyarian ancestors of monomyarians must be envisaged as less committed and the original, largely amphidetic condition as being more easily regained.

STRUCTURE IN THE PECTINACEA

In this highly modified monomyarian superfamily the animal becomes bilaterally asymmetrical, always resting on the right side. Even although the valves may be very similar, the pleurothetic habit involves a functional asymmetry. This was originally demonstrated

by Buddenbrock (1911, 1915) who showed that in "*Pecten*" (actually largely species of *Chlamys*) although both statocysts persist the nerves from *both* mantle lobes are associated exclusively with the better developed *left* statocyst. Attached individuals always settle on the right side, unattached ones turn over on to that side if displaced. The highly specialized ligament is another basic feature. The inner ligament layer is condensed into a characteristic spherical rubber-like pad. This, as pointed out by Trueman (1953a,b) is less calcified than in the majority of bivalves which accounts for its high modulus of elasticity. Alexander (1966) further described it as an "elastic block of amorphous cross-linked protein, plasticized with water" and acting as "a very efficient compression spring working in antagonism to the adductor." These and other observations on this structure have

been made on species of *Chlamys* and *Pecten* particularly in relation to their swimming habits. Certainly it is one of the structures that have made swimming possible but this ligament is no less developed in species that are byssally attached or cemented. It permits an unusually wide gaping of the valves. The remainder of the straight edentulous hinge line is occupied by long stretches of anterior and posterior outer ligament layer (this with the exception of the Spondylidae as noted later).

Wide separation of the valves involves changes in the mantle margins. The inner muscular mantle fold with fringing tentacles hypertrophies so that the entire gape can be covered and appropriate openings locally created for the inflowing current and the extrusion of both exhalant current and of pseudofaeces. The latter are of major significance in pleurothetic species owing to the special need to remove waste from the depth of the mantle cavity on the under side. In the Pectinacea, unlike the Pteriacea, pseudofaeces collect at *both* ends of the mantle cavity at the base of auricles where their expulsion, with mantle margins locally separating, provides the backward "jet" responsible for swimming—as distinct from escape—movements in free living scallops. These expulsions are due to sudden contractions by the striated (quick) component in the adductor. This is especially large in pectinaceans, particularly in those that swim. Its oblique orientation in relation to the valves appears as an adaptation which assists the closure of the valves and so more efficient ejection (Thayer, 1972).

The reduced foot, initially solely concerned with byssal formation (as in the Pteriacea) retains the left posterior retractor needed for pulling the animal down on the byssal attachment. Where the byssus is lost (both in freedom and where cemented) the terminal pedal cone may be enlarged to act as a cleansing organ (as it is also in the Anomiacea) while the pedal retractor atrophies. The foot is never lost.

More complete reorganization of the visceral organs around the central adductor has been accompanied by enlargement of the visceral ganglia and reduction and posterior migration of the cerebro-pleural ganglia. These come close to the pedals in *Pecten* but unite with the viscerals in *Spondylus* (Dakin, 1928a; Watson, 1930). This is in marked contrast to the unmodified condition noted in the Pteriacea.

There remain for discussion two structures, completely characteristic of the Pectinacea yet both absent in the one family Propeamussidae, namely the lip apparatus and the pallial eyes. The former consists of arborescent growths, two from the upper, and three from the lower, lip which intimately interlock without fusing to form a finely perforated tube covering the mouth and proximal oral grooves between these and the labial palps (Pelseneer, 1931). The apparatus in *Pecten maximus* is described in great detail by Gilmour (1964) while Bernard (1972) has reviewed the occurrence of such lip hypertrophy throughout the Bivalvia. It is confined to the Pectinidae, Spondylidae and the unrelated Limidae. Clearly important because of its high elaboration, there are varying views as to its function, the lip apparatus appears to be associated with the presence of an anterior rejection area. This is so near the mouth that food streams would tend to be carried away within it if these were not confined within tubes that allow only water to escape (Yonge, 1967). Gilmour (1964) suggests a possible correlation with the "anisomyarian" monomyarian condition, but there is no lip apparatus in the equally monomyarian Anomiacea (Yonge, 1977b).

The highly organized pallial eyes (Dakin, 1910) are situated usually among long sensory tentacles on the middle fold of the mantle margin, conspicuous glistening spots against the often deeply pigmented inner mantle folds. They occur in more or less equal numbers on both mantle lobes and are just as numerous and well developed in the attached *Pedum*, *Hemipecten* and *Hinnites* and in the Spondylidae (Dakin, 1928b) as they are in the swimming scallops. The contention is not that they evolved in direct connexion with swimming as is often assumed but at a far earlier stage when the animals were byssally attached and in association with the wide gape and extensively exposed pallial tissues. This still applies to all attached species. Capable of being stimulated by a passing or approaching shadow, these eyes would detect the presence of a predator and initiate a reflex response involving sudden closure of the valves. Where the animals are free this involves an "escape" reaction, water being expelled forward, and the animal making a sudden movement hinge foremost.

Consideration of adaptive radiation in the Pectinacea must, therefore, start at a stage before the Pectinidae evolved with the early separation of the now abyssal Propeamus-

siidae. There the shell (Waller, 1971, 1972, 1978) differs from that of the other Pectinacea, the right valve dominated by prismatic calcite with crossed-lamellar aragonite present in both valves and so resembling the Palaeozoic Pernopectinidae of which they may be the modern survivors. Adaptations in this family will therefore be initially discussed followed by those in byssally attached, free and then cemented pectinids with the Spondylidae, resembling the last considered pectinid in habit, dealt with last of all.²

ADAPTIVE RADIATION

Propeamussiidae Abbott, 1954 (Fig. 2b)

This family consists of deep-sea species the habits of which can only be deduced. Species of *Propeamussium* are free, but species of *Cyclopecten* are byssally attached. Personal examination has been made of the four species of "*Amussium*" described by Knudsen (1967) from the *John Murray* Expedition and obtained from the British Museum

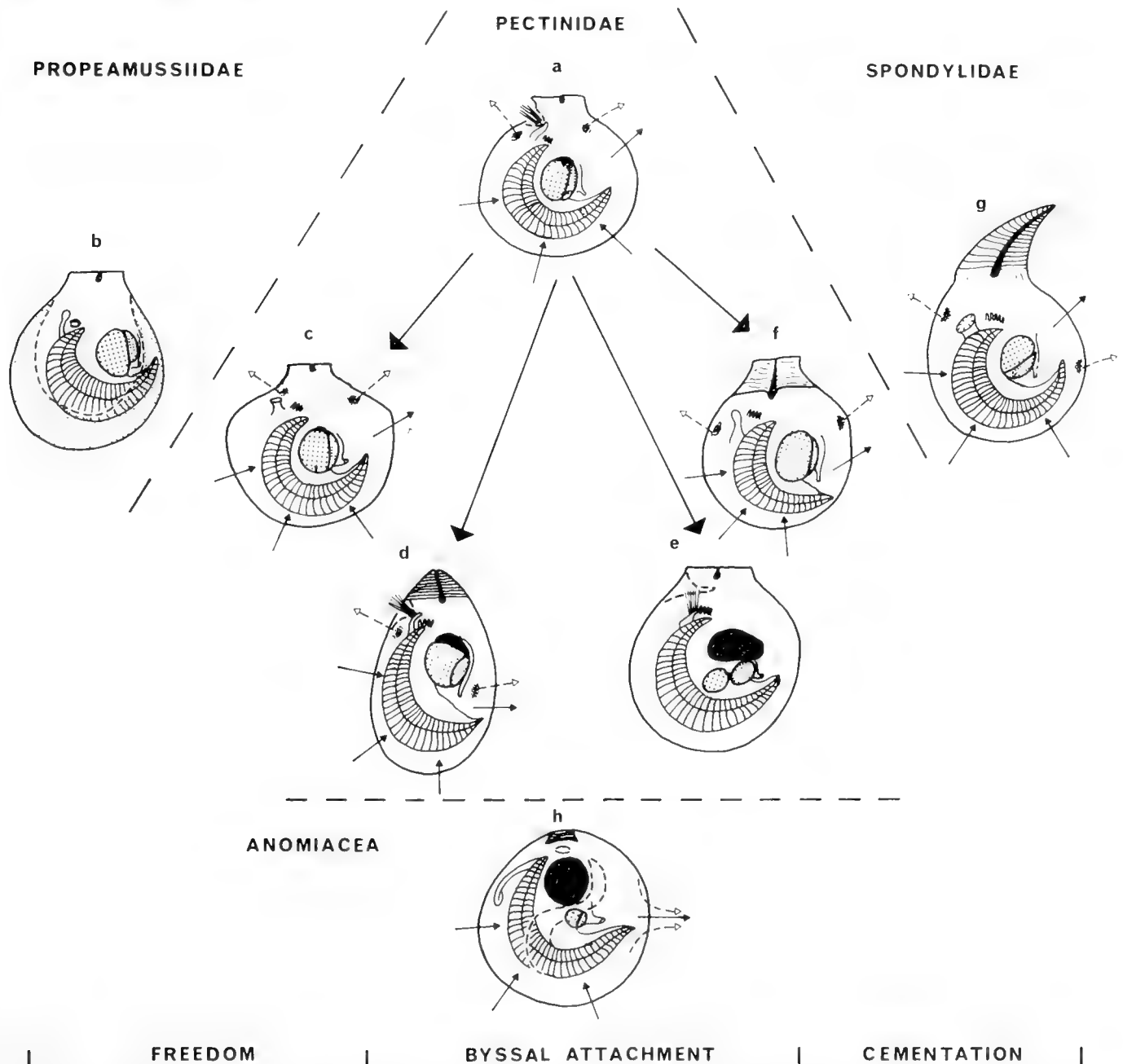


FIG. 2. Adaptive radiation within the Pectinacea; drawings from above (left side) showing two regions of adductor, foot with byssus and retractor (black), ctenidium and frilled lips (or open mouth); arrows as before. a, *Chlamys varia*; b, *Propeamussium* sp.; c, *Amusium*, etc.; d, *Pedum spondyloideum*; e, *Hemipecten forbesianus*; f, *Hinnites multirugosus*; g, *Spondylus americanus*; also (for comparison) h, *Pododesmus* sp. (Anomiacea) (byssus obscured by retractor).

²The recently established family Syncyclonemidae Waller, containing both byssally attached and free Recent species, is known only from the shell (Waller, 1978).

(Nat. Hist.). All are small with the maximum dimension (height) between 15 and 50 mm, the very delicate shell strengthened by internal radiating ribs. There is no byssal notch and the valves are of similar external convexity. Ligament and general body form are typically pectinacean but the ctenidia are simpler being non-plicate and without interlamellar junctions. There is a unique 6:1 ratio of striated to smooth muscle in the adductor and the former is more obliquely disposed than in other pectinaceans (Thayer, 1972). The foot is without obvious terminal dilation but it may distend with blood pressure and so could assist in cleansing; it can have no other function. Knudsen (1967) notes the presence of tentacles and absence of eyes on the middle marginal fold and hypertrophy of the inner fold (velum), and this is very pronounced in the specimens personally examined (shown stippled in Fig. 2b). Some species of *Cyclopecten* (Knudsen, 1970; Bernard, 1978) have a byssal notch, the small foot possessing a byssal apparatus, the solitary left retractor being divided. The ratio of striated to smooth muscle is here some 3:1. There is the unique presence of a strand of muscle overlying the rectum and connected with a large abdominal sense organ (Bernard, 1978).

There is every indication that *Propeamusium* spp. are most highly efficient swimmers; the habits of *Cyclopecten* with some spp. attached are more difficult to deduce. From identification of crustacean and other animal remains in the stomach of species of *Propeamusium* Knudsen deduces a carnivorous habit. This is supported by the extreme depth of the inner mantle folds which indicates an exceptionally wide gape, prey being possibly entrapped during the swimming movements and then held within the mantle cavity. Absence of a lip apparatus would enable small animals to enter the mouth. The presence of an anterior ejection current (necessary for the forward and possibly "feeding" movements) would not divert food of this size. There is no corresponding evidence that *Cyclopecten* species are carnivorous.

Pectinidae Rafinesque, 1815

Chlamys varia (Fig. 2a)

This species, fully pleurothetic but usually byssally attached throughout life, a habit that persists in a variety of pectinids, is taken as representing the original mode of life in the

Pectinidae. The general characters have already been outlined, the shell rounded and the valves with large auricles and, apart from the byssal notch on the right, very similar in form and convexity. A small left posterior pedal retractor persists in functional association with the attaching byssus. The ratio of quick to catch muscle in the adductor is some 2.5:1, a presumed adequate provision for the needs of pseudofaecal extrusion.

Amusium, *Pecten* and *Chlamys* spp. (Fig. 2c)

After brief initial attachment, all species of the two first genera become free and many, such as *C. opercularis* in the last genus (although *C. septemradiatus* remains attached for two years (Allen, 1953)). Movement is by jet-propulsion, its relation to muscular mechanics fully discussed for many pectinids by Gould (1971), Moore & Trueman (1971) and Thayer (1972). Conclusions that, apart from possibly *Propeamusium* spp., the most efficient swimmers are species of the highly streamlined *Amusium* with internally ribbed very equivalve shell has now been demonstrated in life by Morton (1980) for *A. pleuronectes* which attains a speed of between 37 and 45 cm/sec. Necessary turning over of these free pectinids if coming to lie on the left is accomplished by localized overlapping of the inner mantle folds and a "downward" expulsion of water. *Pecten maximus* and related species are very inequivalve, with the right valve deeply concave internally and the left valve almost flat. They create cavities in a usually sandy substrate and may seldom swim although making efficient escape movements if a predator, usually an echinoderm, approaches. All these swimmers retain a very small left posterior pedal retractor. The ratio of striated to smooth muscle is some 3:1 in *C. opercularis* and *P. maximus* but increases to 5:1 in *Amusium*. The ubiquity and great abundance of unattached scallops indicates the success of this epifaunal and mobile mode of life.

Pedum spondyloideum (Fig. 2d)

Here adaptation involves retention of byssal attachment but to a specific substrate, namely the living surface of a scleractinian coral that reacts by its growth to the presence of the bivalve (Yonge, 1967). This solitary species of the genus which occurs usually (perhaps always) on species of *Porites* was

originally described and figured *in situ* by Quoy & Gaimard (1830–35) in their account of the zoology of the voyage of the *Astrolabe*. Living individuals were personally studied at Rabaul, New Britain, during the cruise of the Stanford University Research Vessel *Te Vega* in February 1965.

The veliger larva must metamorphose exclusively on the living coral surface to make permanent byssal attachment with the free margins of the valves pointed upward. It so influences the growth of the coral that the elongate pectinid comes to live in deep clefts in which the heavily pigmented inner mantle lobes with the glistening eyes are highly conspicuous when the valves open. There is a large byssal notch, only exceeded by that in *Hemipecten*. The foot is exclusively concerned with secretion and planting of the large byssus which involves hypertrophy of the left posterior pedal retractor, the contraction of which draws the animal downward in the cleft when the adductor also contracts. Owing to the necessary upward growth which prevents overgrowth by the coral, there is a considerable ventral (upward) migration of the hinge line, a condition otherwise only present in the cemented species. There is some movement (near to the opening above) of the posterior pseudofaecal accumulation but the anterior accumulation continues to be situated near the mouth which is protected by the lip apparatus. For better food collection within the enclosing cleft, the posterior tips of the ctenidia extend beyond the confines of the shell to be withdrawn by enlarged branchial muscles. The ratio of striated to smooth muscle in the adductor is much as in *Chlamys varia* indicating a corresponding need for pseudofaecal extrusion.

This is a very specific instance of adaptation with the living substrate reacting to provide a very secure habitat to the elongate pectinid.

Hemipecten forbesianus (Figs. 2e, 3–5)

The most intimate development of byssal attachment occurs in this widely distributed species. With the type-locality in the Sulu Archipelago, living specimens were personally examined in January 1978 after they had been collected off Dunsborough, some 200 miles S of Perth, Western Australia, by Dr. Barry Wilson then of the Western Australian Museum. Later preserved specimens with drawings and photographs were received

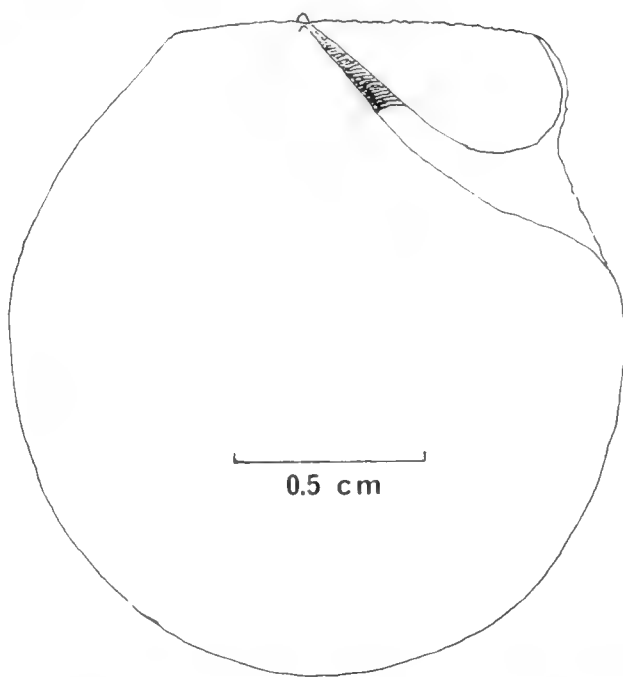


FIG. 3. *Hemipecten forbesianus*, right (under) valve showing circular form and depth of byssal notch.

from Mrs. S. M. Slack-Smith, Curator of the Mollusc Department in that Museum, who will be producing a general description of this species including ecology and distribution.

The specimens originally collected were attached to the smooth under surface of colonies of the scleractinian coral, *Turbinaria mesenterina* (Dana) which grow in the form of stalked cake baskets with the large polyps rising exclusively from the upper surfaces. The extremely compressed and almost completely circular pectinids were up to 2 cm in diameter, the upper valves reddish brown and rough, usually with epiphytic growths, the lower valves extremely thin and completely smooth. They conform perfectly to the coral surface against which they are adpressed. The byssal notch is extremely deep, curving inward towards the umbo (Fig. 3). The massive byssus extends through it in an obliquely upward (dorsal) direction (Figs. 4, 5). The stout threads appear to be calcified terminally but this may be due to adherence of fragments of coral skeleton.

As noted by Adams & Reeve (1850) in their original description of this species, "this interesting shell is intermediate in its characters between *Pecten* and *Anomia*" with "a sinus so deeply cut in the direction of the hinge-margin as to remind one of *Pedum*." Actually, as already noted, the notch is much less deep in that pectinid. In the one previous description of the animal of *H. forbesianus*—a solitary specimen obtained during the Siboga

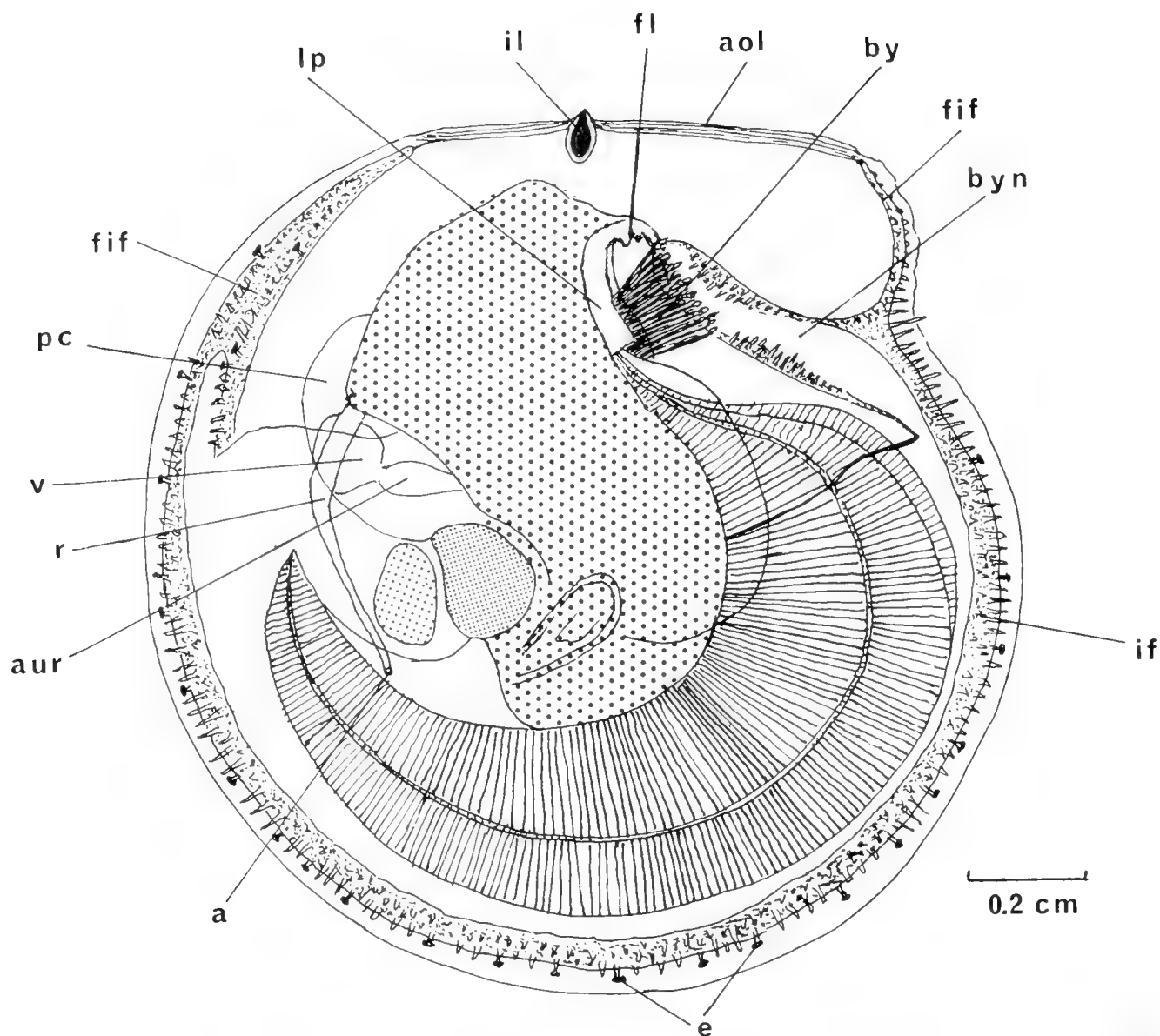


FIG. 4. *H. forbesianus*, animal viewed from right side after removal of right valve and greater part of right mantle lobe.

Expedition—Pelseneer (1911) refers to various earlier views stressing these intermediate characters but concludes that this is an undoubted pectinid. Interest resides in the extreme intimacy of byssal attachment. This involves the deep byssal notch with the hypertrophied byssal apparatus (Figs. 3, 4) which has been pushed far forward on the right side. This produces asymmetry at the anterior end, the left palps lying above the right palps and the small pedal tip (f) displaced to the left side (Fig. 5). There is some asymmetry also in the heart and pericardium. The mantle margins are richly supplied with eyes but the inner marginal fold with fringing tentacles is of only moderate size: both sides of the pallial notch in the region where the byssus extends bear numerous tentacles. Probably the valves do not gape widely when adductor and pedal re-

tractor relax. The homorhabdic ctenidia have 12 rows of ciliary junctions in the descending lamellae but only six on the much shorter ascending limb. There is no evidence that the ctenidia extend beyond the shell margins as they do in *Pedum*. The small mouth is guarded by frilled lips. This was noted by Pelseneer (1911) who also observed the absence of a right anterior pedal retractor and the immense hypertrophy of the left retractor where conditions do approach those in the Anomiacea (cf. Figs. 2e & h). The two portions of the smaller adductor are separate with the smooth part only a little the smaller. Owing to the posture of the animal, prolonged adduction must be as important as cleansing contractions.

H. forbesianus resembles *P. spondylioid-eum* in being the sole species in the genus, being permanently attached by byssus

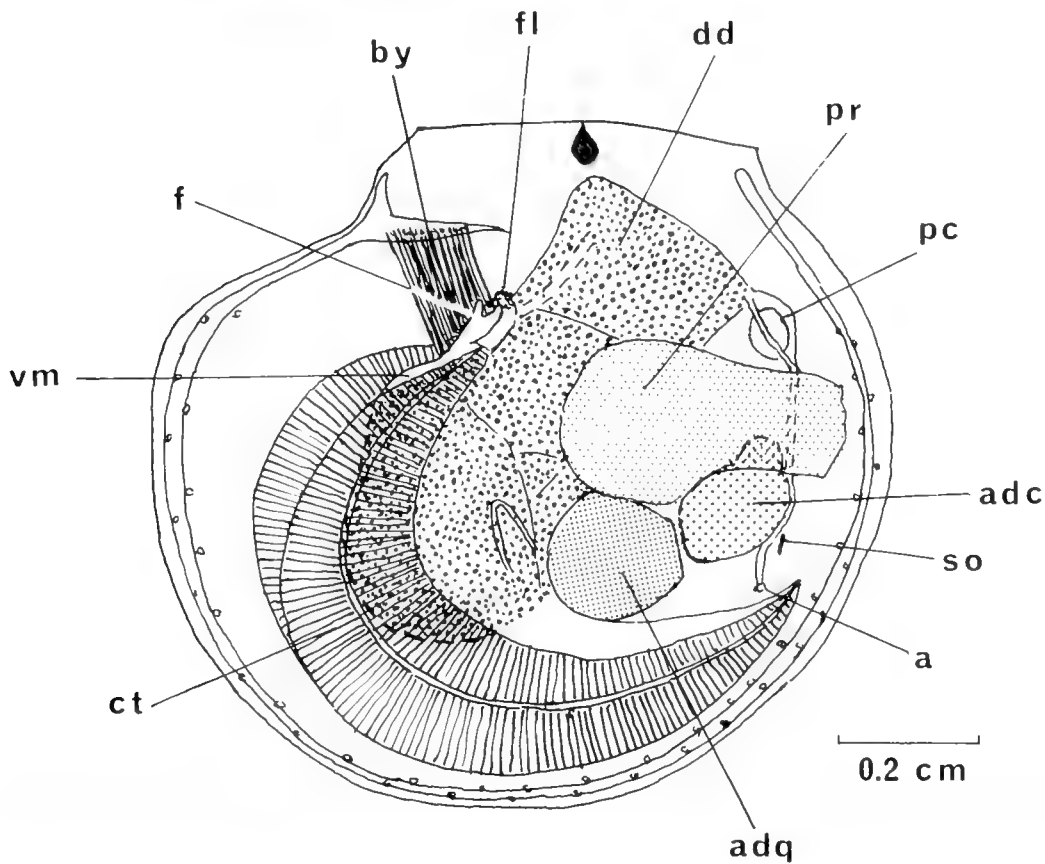


FIG. 5. *H. forbesianus*, animal viewed from left side after removal of valve; only eyes indicated on mantle margins.

threads and apparently always to scleractinian corals although without affecting their growth. In both, the larvae must settle by preference on the living surface of appropriate corals. The mode of attachment is more specialized in *Hemipecten*, resembling the Anomiacea with the byssus emerging more or less centrally but in the former directed dorsally instead of laterally (i.e. topographically downward) and so without the same separation of the anterior region of the ctenidia (Fig. 2h) with the palps. In *Hemipecten* hypertrophy of the byssal apparatus is associated with atrophy of the terminal regions of the foot unlike the Anomiacea where this extends as a potent cleansing organ and is so retained in *Placuna* where the byssus apparatus is lost (Yonge, 1977b).

Hinnites multirugosus (Fig. 2f)

Here settlement and metamorphosis are followed by a period of freedom, the animals behaving like other scallops, swimming by jet propulsion with periods of temporary byssal attachment. In the Californian *H. multirugosus*, common on rocks to depths of 60 m, to which knowledge of the living animal is

largely confined (Yonge, 1951) cementation occurs at diameters of between 2.2 and 4.2 cm. This is easily determined by examination of the under valve, the surface being regular prior to attachment and then conforming to an irregular rocky substrate, the upper valve becoming correspondingly irregular. As described elsewhere (Yonge, 1979), cementation involves a change in the physical properties of the periostracum which comes from the groove on the inner side of the outer marginal fold on the right mantle lobe. At this stage in growth this must alter physically so as to adhere to the substrate, the prismatic layer secreted by the outer surface of the outer fold attaching to this and so also the inner calcareous layer formed by the outer mantle surface.

The rounded pectinid form is initially little affected, the most striking difference, due to attachment (as in *Pedum*), being the hinge line which is displaced ventrally with accompanying loss of the auricles. Large specimens reach lengths, hinge to free margin, of 20 cm. The ligament is normal, its previous stages apparent on the exposed dorsal area of the right valve. The sites of pseudofaecal extrusion move somewhat ventrally but the lip ap-

paratus is retained. After attachment the byssal apparatus atrophies and the foot persists as a cleansing organ although it is less modified for that purpose than in *Pecten*. The inner mantle folds are deep, some 1.5 cm in an animal 8 cm in diameter, fringed with small tentacles and deep orange in colour with black pigment internally. The middle fold bears long tentacles and conspicuous eyes. The ratio of striated to smooth muscle in the adductor is an unexpected 4:1 but the shell is much thicker and so heavier than in byssally attached or free pectinids and so may require great force for sudden ejection but owing to the weight of the free valve have less need for the means of continued closure.

Spondylidae Gray, 1820

Spondylus americanus (Fig. 2g)

This family comprises large and conspicuous members of the associated fauna of coral reefs, this species alone in the Caribbean, but many species in the Indo-Pacific. The thick left valve is often richly coloured and bears characteristic spines. Internally both valves are concave, the right one deeper. The shell is even more inequivalve than in *Hinnites*, the dorsal hinge region of the right valve elongate and curved representing change in the hinge line during growth. Cementation occurs very early, apparently immediately after prior byssal attachment which is indicated by the presence of a byssal notch in the postlarval shell.

Knowledge of anatomy is based primarily on the work of Dakin (1928a) on the Mediterranean *S. gaederopus* and Yonge (1973) on *S. americanus* which involved study in life. The general form of the visceropedal mass is very similar to that of the Pectinidae, unlike the Propeamussidae; both lip apparatus and pallial eyes are present. There are the same anterior and posterior accumulations of pseudofaeces, the ratio of striated to smooth muscle in the adductor about 2:1, a difference from conditions in *Hinnites* to be explained by differences in the hinge. The foot becomes a highly efficient cleansing organ (Yonge, 1973). There is a very interesting difference in the nervous system with a much greater concentration of nerve ganglia in the visceral region than in the Pectinidae (Dakin, 1928a; Watson, 1930; Pelseneer, 1931).

The major differences between the families reside in the mantle/shell with major effects on the hinge and ligament. Taylor, Kennedy & Hall (1969) note significant differences in shell structure. Although the hinge superficially resembles that in the Pectinidae, the long lateral regions are occupied by fused periostracum *not* by outer ligament layer. The epithelia secreting this have been displaced centrally where their secretion is added to both sides (i.e. topographically above and below) the inner ligament layer. Formation of the secondary ball-and-socket hinge teeth is also associated with this downward invasion of the fused mantle margins from both ends. There are resemblances here to the Plicatulacea but the visceropedal affinities with the Pectinacea are undoubtedly of greater significance.

ACKNOWLEDGEMENTS

Thanks are initially due to Dr. Barry Wilson and Mrs. Shirley Slack-Smith both then of the Western Australian Museum, Perth, for introduction to *Hemipecten forbesianus* in Western Australian waters, then to Dr. J. E. N. Veron of the Australian Institute of Marine Science, near Townsville for his identification of the coral to which this pectinid attaches itself, to the British Museum (Nat. Hist.) by way of Dr. John Taylor for the supply of various species, notably of the Propeamussidae. Mr. J. J. Holmes, Departmental Superintendent gave great assistance in the preparation of figures. I have finally to thank Prof. J. M. Mitchison, F.R.S., for facilities in his Department, my wife for technical and typing help and the Natural Environment Research Council for the assistance provided by Grant GR3/1380.

LITERATURE CITED

- ADAMS, A. & REEVE, L., 1850, *Zoology of the voyage of H.M.S. Samarang—Mollusca*. London, Reeve, Benham & Reeve.
- ALEXANDER, R. M., 1966, Rubber-like properties of the inner hinge ligament of Pectinidae. *Journal of Experimental Biology*, 44: 119–130.
- ALLEN, J. A., 1953, Observations on the epifauna of the deep-sea muds of the Clyde Sea area with special reference to *Chlamys septemradiata* (Müller). *Journal of Animal Ecology*, 22: 240–260.
- BERNARD, F. R., 1972, Occurrence and function of lip hypertrophy in the Anisomyaria (Mollusca,

- Bivalvia). *Canadian Journal of Zoology*, 50: 53–57.
- BERNARD, F. R., 1978, New bivalve molluscs, subclass Pteriomorpha, from the Northeastern Pacific. *Venus*, 37: 61–75.
- BUDDENBROCK, W. VON, 1911, Untersuchungen über die Schwimmbewegungen und die Statocysten der Gattung *Pecten*. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse*, 28: 24 p.
- BUDDENBROCK, W. VON, 1915, Die Statocysten von *Pecten*, ihre Histologie und Physiologie. *Zoologische Jahrbüchern Abteilung für allgemeine Zoologie und Physiologie der Tiere*, 35: 301–356.
- DAKIN, W. J., 1910, The eye of *Pecten*. *Quarterly Journal of Microscopical Sciences*, 55: 49–112.
- DAKIN, W. J., 1928a, The anatomy and phylogeny of *Spondylus*, with a particular reference to the lamellibranch nervous system. *Proceedings of the Royal Society of London, Ser. B*, 103: 337–354.
- DAKIN, W. J., 1928b, The eyes of *Pecten*, *Spondylus*, *Amusium* and allied lamellibranchs, with a short discussion on their evolution. *Proceedings of the Royal Society of London, Ser. B*, 103: 355–369.
- GILMOUR, T. H. J., 1964, The structure, ciliation and function of the lip-apparatus of *Lima* and *Pecten* (Lamellibranchia). *Journal of the Marine Biological Association of the United Kingdom*, 44: 458–498.
- GOULD, S. J., 1971, Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology*, 14: 61–94.
- HERDMAN, W. A. & HORNEILL, J., 1904, Anatomy of the pearl oyster. (*Margaritifera vulgaris* Schum.) *Report on the Pearl Oyster Fisheries of the Gulf of Manaar, Royal Society, Part II*: 37–76.
- KNUDSEN, J., 1967, The deep-sea Bivalvia. *Scientific Reports of the John Murray Expedition 1933–34*, 11: 237–343.
- KNUDSEN, J., 1970, The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report*, 11: 1–241.
- MOORE, J. D. & TRUEMAN, E. R., 1971, Swimming of the scallop, *Chlamys opercularis* (L.). *Journal of Experimental Marine Biology and Ecology*, 6: 179–185.
- MORTON, B., 1980, Swimming in *Amusium pleuronectes* (Bivalvia: Pectinidae). *Journal of Zoology*, 190: 375–404.
- NEWELL, N. D., 1965, Classification of the Bivalvia. *American Museum Novitates*, 2206: 1–25.
- PELSENEER, P., 1911, Lamellibranches de l'expédition du Siboga. Partie anatomique. *Siboga-Expeditie*, 53a: 1–125.
- PELSENEER, P., 1931, Quelques particularités d'organisation chez des Pectinacea. *Annales de la Société royale Zoologique de Belgique*, 61: 12–17.
- QUOY, J. R. & GAIMARD, J., 1830–35, *Voyage de . . . l'Astrolabe . . . pendant 1826–29, sous le commandement de M. J. Dumont d'Urville, etc. Zoologie*: 4 vols. and Atlas, Paris.
- TAYLOR, J. D., KENNEDY, W. J. & HALL, A., 1969, The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea—Trigoniacea. *Bulletin of the British Museum (Natural History) Zoology*, supplement 3: 1–125.
- THAYER, C. W., 1972, Adaptive features of swimming monomyarian bivalves (Mollusca). *Forma et Functio*, 5: 1–32.
- TRUEMAN, E. R., 1953a, The ligament of *Pecten*. *Quarterly Journal of Microscopical Science*, 94: 193–202.
- TRUEMAN, E. R., 1953b, Observations on certain mechanical properties of the ligament of *Pecten*. *Journal of Experimental Biology*, 30: 453–467.
- WALLER, T. R., 1971, The glass scallop *Propeamussium*, a living relict of the past. *American Malacological Union Annual Report*, 1970, p. 5–7.
- WALLER, T. R., 1972, The functional significance of some shell microstructures in the Pectinacea (Mollusca: Bivalvia). 24th International Geological Congress, Section 7, p. 48–65.
- WALLER, T. R., 1978, Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London, Ser. B*, 284: 345–365.
- WATSON, H., 1930, On the central nervous system of *Spondylus* and what happens to a headless mollusc's brain. *Proceedings of the Malacological Society of London*, 19: 31–36.
- YONGE, C. M., 1936, The evolution of the swimming habit in the Lamellibranchia. *Mémoires du Musée royal d'Histoire naturelle de Belgique*, (2) 3: 77–100.
- YONGE, C. M., 1951, Studies on Pacific coast mollusks. III. Observations on *Hinnites multirugosus* (Gale). *University of California Publications in Zoology*, 55: 409–420.
- YONGE, C. M., 1953, The monomyarian condition in the Lamellibranchia. *Transactions of the Royal Society of Edinburgh*, 62: 443–478.
- YONGE, C. M., 1967, Observations on *Pedum spondyloideum* (Chemnitz) Gmelin, a scallop associated with reef-building corals. *Proceedings of the Malacological Society of London*, 37: 311–323.
- YONGE, C. M., 1968, Form and habit in species of *Malleus* (including the "hammer oysters") with comparative observations on *Isognomon isognomon*. *Biological Bulletin*, 135: 378–405.
- YONGE, C. M., 1973, Functional morphology with particular reference to hinge and ligament in *Spondylus* and *Plicatula* and a discussion on relations within the superfamily Pectinacea (Mollusca: Bivalvia). *Philosophical Transactions of*

the Royal Society of London, Ser. B, 267: 173–208.

YONGE, C. M., 1975, The status of the Plicatulidae and the Dimyidae in relation to the superfamily Pectinacea (Mollusca: Bivalvia). *Journal of Zoology*, 176: 545–553.

YONGE, C. M., 1977a, The ligament in certain "Anisomyarians." *Malacologia*, 16: 311–315.

YONGE, C. M., 1977b, Form and evolution in the Anomiacea-Pododesmus (*Monia*), *Anomia*, *Patro*, *Enigmonia* (Anomiidae); *Placunanomia*, *Placuna* (Placunidae Fam. Nov.). *Philosophical Transactions of the Royal Society of London, Ser. B*, 276: 453–523.

YONGE, C. M., 1978a, On the Dimyidae with special reference to *Dimya corrugata* Hedley and

Basiliomya goreau Bayer. *Journal of Molluscan Studies*, 44: 357–375.

YONGE, C. M., 1978b, Significance of the ligament in the classification of the Bivalvia. *Proceedings of the Royal Society of London, Ser. B*, 202: 231–248.

YONGE, C. M., 1979, Cementation in bivalves. In VAN DER SPOEL, S., VAN BRUGGEN, A. C. & LEVER, J. (eds.), *Pathways in Malacology*, Bohn, Scheltema & Holkema, Utrecht, and Junk, The Hague, p. 83–106.

YONGE, C. M. & CAMPBELL, J. I., 1968, On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Transactions of the Royal Society of Edinburgh*, 68: 21–43.

THE ANOMALODESMATA

Brian Morton

Department of Zoology, University of Hong Kong, Pokfulam Road, Hong Kong

ABSTRACT

The bivalve subclass Anomalodesmata Dall, 1889 is globally distributed and characterized by widely diverse species, both in form and habits, occupying extremely specialized, narrow, almost exclusively marine niches.

The subclass possesses a single order—the Pholadomyoida Newell, 1965—and is generally considered to comprise a number of extant superfamilies, though their definition is not universally agreed upon. More agreement has been reached with regard to the number of families—higher taxa for which clearer definitions are available. Each family comprises but a few extant genera and species.

The possession by most of a number of common characters, i.e. no hinge teeth, a ligamental lithodesma, gill structure of type E, the presence of a fourth pallial aperture, extensive mantle fusion and simultaneous hermaphroditism, indicates that the subclass arose from a pholadomyacean stock in the early Palaeozoic. A few representatives of the Pholadomyacea survive today and it is from a study of these that present views on the phylogeny of the Anomalodesmata have been derived. In the Palaeozoic, the Pterioida were the dominant colonizers of hard intertidal and shallow sublittoral surfaces and generally exploiting the epi- and endobyssate modes of life. They are still widely dominant in this habitat today.

The Anomalodesmata, with the Trigoniacea, were thus largely infaunal and enjoyed a brief expansion, widely diversifying and adopting shallow and deep burrowing modes of life. Thereafter, in the Mesozoic, the Anomalodesmata reveal a pattern of declining importance (in relation to the period of expansion that will occur in the Caenozoic) but one superfamily—the Thraciacea (herein defined) survived in specialized habitats. The decline in importance of the Anomalodesmata at this time possibly reflects the increasing importance of the evolving heterodont Veneroida which then and now have come to dominate most 'generalist' infaunal, marine and estuarine habitats—even coming to colonize fresh waters. The Anomalodesmata, it is here argued, produced two further lineages, leading ultimately to the modern Poromyacea, Verticordiacea and Cuspidariacea, which have thrived in deep waters and convergently came to adopt macrophagous feeding habits. By modern standards these are the most successful anomalodesmatans, accounting for a significant component of abyssal faunas.

In the Caenozoic, the Anomalodesmata have enjoyed a further expansion to produce the Pandoracea and the Clavagellacea, both of which are primitively infaunal but have subsequently radiated onto hard environments by the adoption of byssally attached and cemented modes of life.

Anomalodesmatan attempts at diversification have largely failed in competition with more 'generalist' bivalves (especially with regard to their simpler reproductive strategies) and the living remnants of this, at times, numerous subclass remain today like the widely spaced outermost twigs of a tree, the roots of which have long since perished and the trunk, represented today by a few representatives of the Pholadomyacea, reduced to some of the rarest molluscs. Conversely, however, they are wonderfully equipped to survive in specialized niches.

This paper reviews the main branches of anomalodesmatan evolution and attempts to show how apparently irreconcilable morphological differences are but widely diverse expressions of a unifying theme. Recent studies of extant pholadomyaceans have provided clues to an understanding of the Anomalodesmata in general but more importantly to the origin of the Clavagellacea and the Poromyacea, Verticordiacea and Cuspidariacea—groups for which there were hitherto no recognized phylogenetic backgrounds.

INTRODUCTION

The subclass Anomalodesmata Dall, 1889 with only one order—the Pholadomyoida Newell, 1965—is represented today by a diverse assemblage of marine, littoral, sub-lit-

toral and deep water bivalves, occupying extremely narrow niches and exploiting a wide variety of life styles. Only a single species of the Lyonsiidae—*Guianadesma sinuosum*—is fresh water (Morrison, 1943).

Although a few, e.g. members of the

Lyonsiidae, i.e. *Lyonsia* and *Entodesma* (Yonge, 1952; Narchi, 1968; Morgan & Allen, 1976), are byssally attached and others are cemented, e.g. members of the Clavagellidae, Cleidothaeridae and Myochamidae, i.e. *Clavagella*, *Cleidothaerus* and *Myochama* (Soliman, 1971; Morton, 1974; Yonge & Morton, 1980), the vast majority are infaunal. The burrowing species can be divided into two major categories. Members of the Poromyacea (i.e. including the three families Verticordiidae, Cuspidariidae and Poromyidae) (as defined by Newell, 1969) are abyssal whereas members of the Clavagellacea, Pandoracea and "Thraciacea"¹ live in shallow waters. Two extant members of the otherwise extinct and ancient superfamily Pholadomyacea are equally divided, *Pholadomya candida* occupying shallow waters (Morton, 1980a), species of *Parilimya* living in deep waters (Morton, in prep.).

Within the deep water anomalodesmatans there is a general trend towards a scavenging and carnivorous mode of life (Yonge, 1928; Reid & Reid, 1974; Allen & Turner, 1974; Allen & Morgan, in press). The Poromyacea has variously been considered to be mono- and polyphyletic. Pelseneer (1888a,b, 1891, 1911) and Allen & Morgan (in press) believe the sequence Verticordiidae-Cuspidariidae-Poromyidae to constitute a natural progression of increasing specialization. Bernard (1974), however, and, earlier, Dall (1890) and Plate (1897) argued a diphyletic origin for the Poromyacea, indicating that the Verticordiidae and the Cuspidariidae are more properly derived from a lyonsiid-like ancestor, while the Poromyidae, with an external ligament, have a separate, older origin. The adoption of the carnivorous habit in the Cuspidariidae and Poromyidae would thus represent convergent evolution (Yonge & Morton, 1980). Bernard (1979) subsequently modified his views somewhat and located only the Verticordiidae (and resurrected family Lyonsiellidae G. Sars, 1871) in the Pholadomyoidea, placing the Poromyacea and the Cuspidariacea in a separate order, the Septibranchioidea.

The Pandoracea are a recent, Caenozoic, assemblage and much easier to understand because of a generally similar life style. They can be derived from a lyonsiid ancestor (Yonge & Morton, 1980), with a sunken primary ligament, invariably a ventral lithodesma

and tending towards distinct valve inequality.

As noted earlier, the families Thraciidae, Periplomatidae and Laternulidae have traditionally been located in the Pandoracea (Newell, 1965, 1969) but, it will later be asserted, they should be relocated in a separate superfamily—the Thraciacea Stoliczka, 1870. In these bivalves the primary ligament is located between deep chondrophores, the shell is thin and the lithodesma, where present, is V-shaped, located on the anterior face of the ligament, and constitutes an additional means of valve alignment which is clearly not always essential in some representatives of these families.

The Clavagellacea are possibly the strangest of all anomalodesmatans with a tiny bivalve shell and an enormous tube-like adventitious shell and with an exchange of water via the expanded "watering pot" plate around the pedal gape, at least in *Brechites* (Purchon, 1956a, 1960).

The ancient superfamily Pholadomyacea is represented today by a number of exceptionally rare genera, including *Pholadomya* and *Parilimya* (Morton, 1980a, in prep.). Though specialized, these bivalves foreshadow conditions in the more recent, extant, anomalodesmatans and it has been from a study of these bivalves that a better understanding of the Anomalodesmata has been obtained—the adaptive radiation of which is the subject of this paper.

PANDORACEA Rafinesque, 1815 (comprising the Lyonsiidae Fischer, 1887, Pandoridae Rafinesque, 1815, Myochamidae Bronn, 1862 and Cleidothaeridae Hedley, 1918)

Most studies of the Anomalodesmata have concerned themselves with the Pandoracea. The constituent families arose in the Caenozoic. The oldest extant pandoraceans are the Lyonsiidae and Yonge & Morton (1980) consider this family to be the most primitive especially in terms of ligament structure. By and large also, the Lyonsiidae (Fig. 1) exhibit a relatively simple plan, being only slightly inequivalve, with a typical ctenidium of type E ciliation, protruding siphons with sensory tentacles, extensive mantle fusions and a fourth pallial aperture. *Lyonsia norvegica* is infaunally buried (Ansell, 1967) but pos-

¹For a variety of reasons, Yonge & Morton (1980) have suggested that members of the Thraciidae, Periplomatidae and Laternulidae should be separated from the other families of the Pandoracea as defined by Newell (1965, 1969).

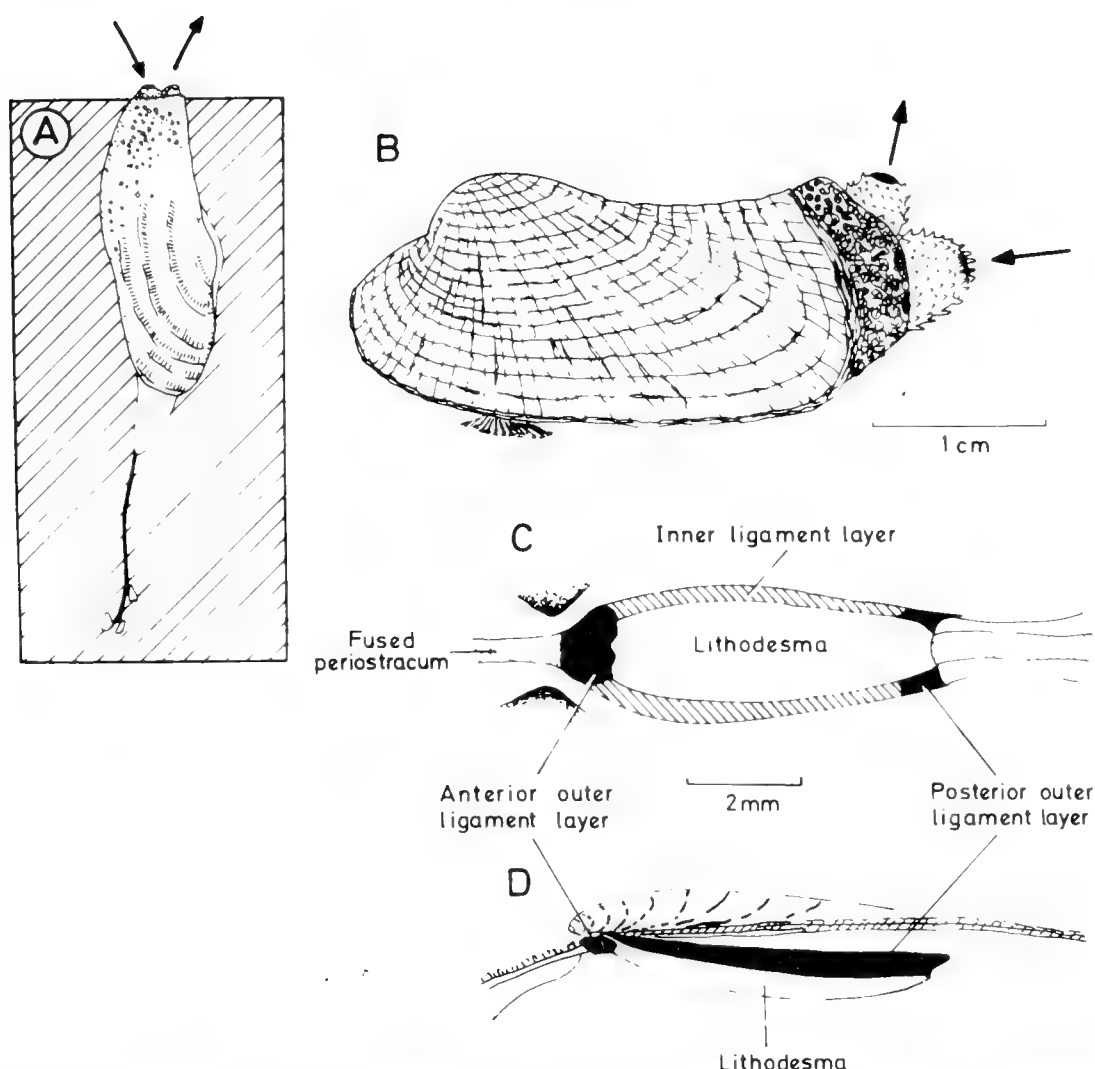


FIG. 1. The Lyonsiidae. (A), *Lyonsia norvegica* in its natural position in sand (redrawn after Ansell, 1967); (B), *Entodesma saxicola* (redrawn after Yonge, 1952); (C), (D), the ligament of *E. saxicola*, as seen from the ventral and lateral aspects respectively (redrawn after Yonge, 1976).

sesses a tiny byssus. Most other lyonsiids are strongly epibyssate e.g. *Entodesma* (Yonge, 1952), and are thus typically weakly heteromyarian in form and occupy crevices on rocky shores. *Mytilimeria* inhabits the tunics of tunicates (Yonge, 1952).

The Pandoridae (Fig. 2) have been studied by Allen (1954, 1961a), Allen & Allen (1955) and Boss & Merrill (1965). In this family there is a marked valve inequality, the right flat, the left convex. The shell is rounded ventrally and peaked dorsally, the primary ligament, with a long lithodesma, being sunken and located between shallow resilifers. The shell possesses 'secondary' hinge teeth (Yonge & Morton, 1980). *Pandora inaequalis* lies on the convex left valve, buried in sheltered sands at an angle of 40° to the surface (Allen & Allen, 1955).

The Myochamidae (Fig. 3) comprise two genera. Of these *Myadora* is the mirror image of *Pandora*, the left valve flat, the right con-

vex. It occupies a similar ecological niche in the Indo-Pacific as *Pandora* does in the Atlantic, and also lies buried in the sand on the left, but flattened, valve. *Myadora striata* inhabits high energy beaches in New Zealand (Morton, 1977). In the second genus of the Myochamidae—*Myochama*—the potential advantages of valve inequality are first realised and the animal is cemented by the right valve to the protruding posterior borders of the shell of shallow sublittoral bivalves (Yonge & Morton, 1980). The ornament of *Myochama* mimics that of the host. Unlike members of the Chamidae (Yonge, 1967) and Cleidothaeridae (Morton, 1974), however, there is no tangential growth component and in many respects *Myochama* is but a cemented *Myadora*. The dorsal region of the right valve is not cemented to the substratum so that there is no inequality to the ligament or the ventral lithodesma. Similarly left and right organs of the mantle cavity are of equal size.

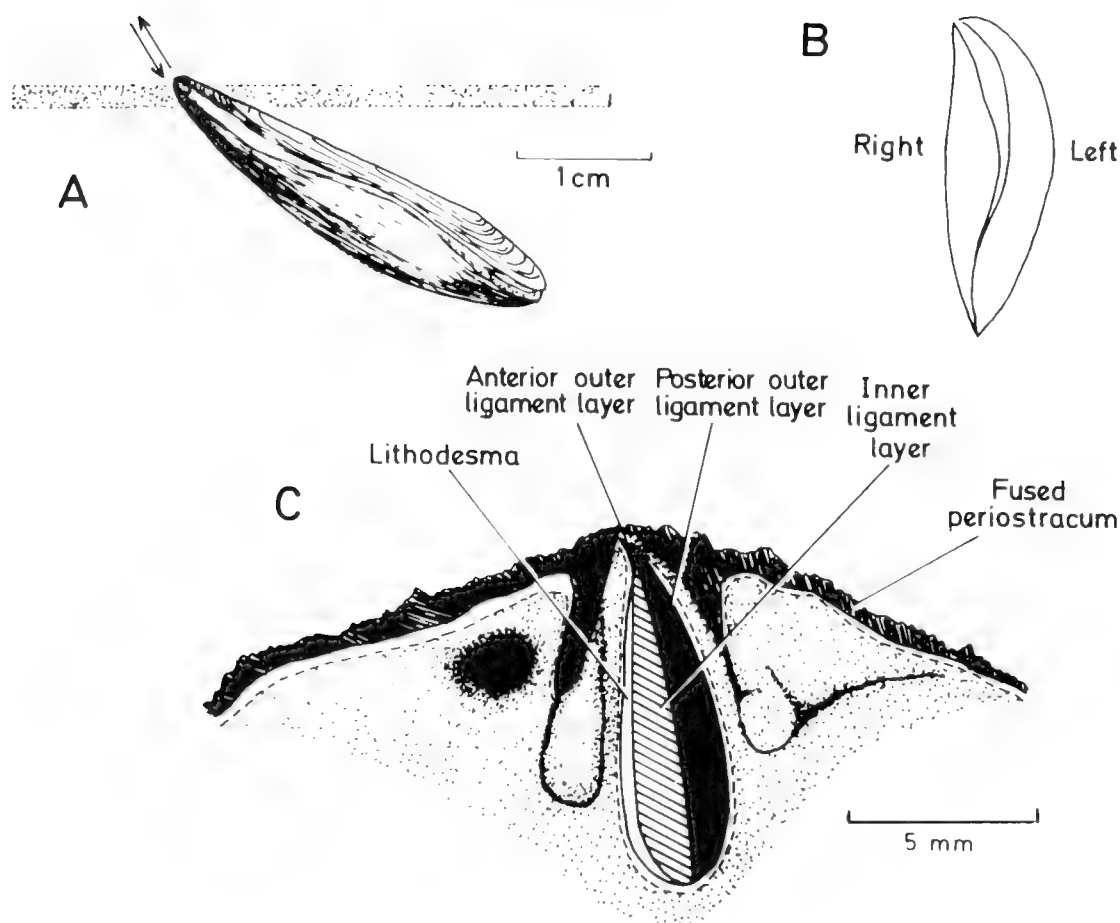


FIG. 2. The Pandoridae. (A), *Pandora inaequalis* in its natural position in the sand (redrawn from Allen, 1954 and Allen & Allen, 1955); (B), (C), the shell of *P. inaequalis* as seen from the anterior and the structure of the ligament as seen from the left (redrawn after Yonge & Morton, 1980).

The siphons are separate and there is a fourth pallial aperture.

The full effects of this general trend within the superfamily towards increasing valve inequality are seen in the single genus—*Cleidothaerus*—of the Cleidothaeridae (Fig. 4). The animal is attached by the right valve which forms a deep cup, the left valve being a flat disc. This marked valve inequality results from the adoption of a cemented habit and is accompanied by a tangential component to growth not seen in other pandoraceans. Because of this component, the secondary ligament of fused periostracum is split anteriorly and the umbones separated, while the primary, sunken ligament largely comprises inner ligament layer, is inequilateral and the lithodesma appears to coil around it (Yonge & Morton, 1980). The valve inequality is also reflected in the organs of the mantle cavity, those of the left being smaller than those of the right (Morton, 1974). As noted by Yonge (1967) for the Chamidae, inequality only affects the organs of the mantle cavity and not the visceral mass (Morton, 1974).

The Pandoracea are best seen as relatively modern descendants of a pholadomyacean stock, that through valve inequality have evolved a wide range of morphological specialisations and have successfully colonized restricted niches in the lower intertidal and the sublittoral, characteristically either lying on one or other valve, rarely vertically, or cemented by one valve. The Lyonsiidae are the only known, extant anomalodesmatans with a well developed byssus. In all cases these adaptations allow occupation of high (wave) energy environments. Other modifications appropriate to such niches include rapid reburial in some (e.g. *Myadora*), but not others (*Pandora*); large labial palps and efficient rejectory currents in the mantle cavity for the removal of sediment and extremely sensitive siphons quickly withdrawn between slightly gaping valve margins.

Runnegar (1974) has accepted the views of Pelseneer (1888a, b) of a continuous morphological transition from a lyonsiid to a septibranch (i.e. the Poromyidae and Cuspidariidae) via a verticordiid and thus places the

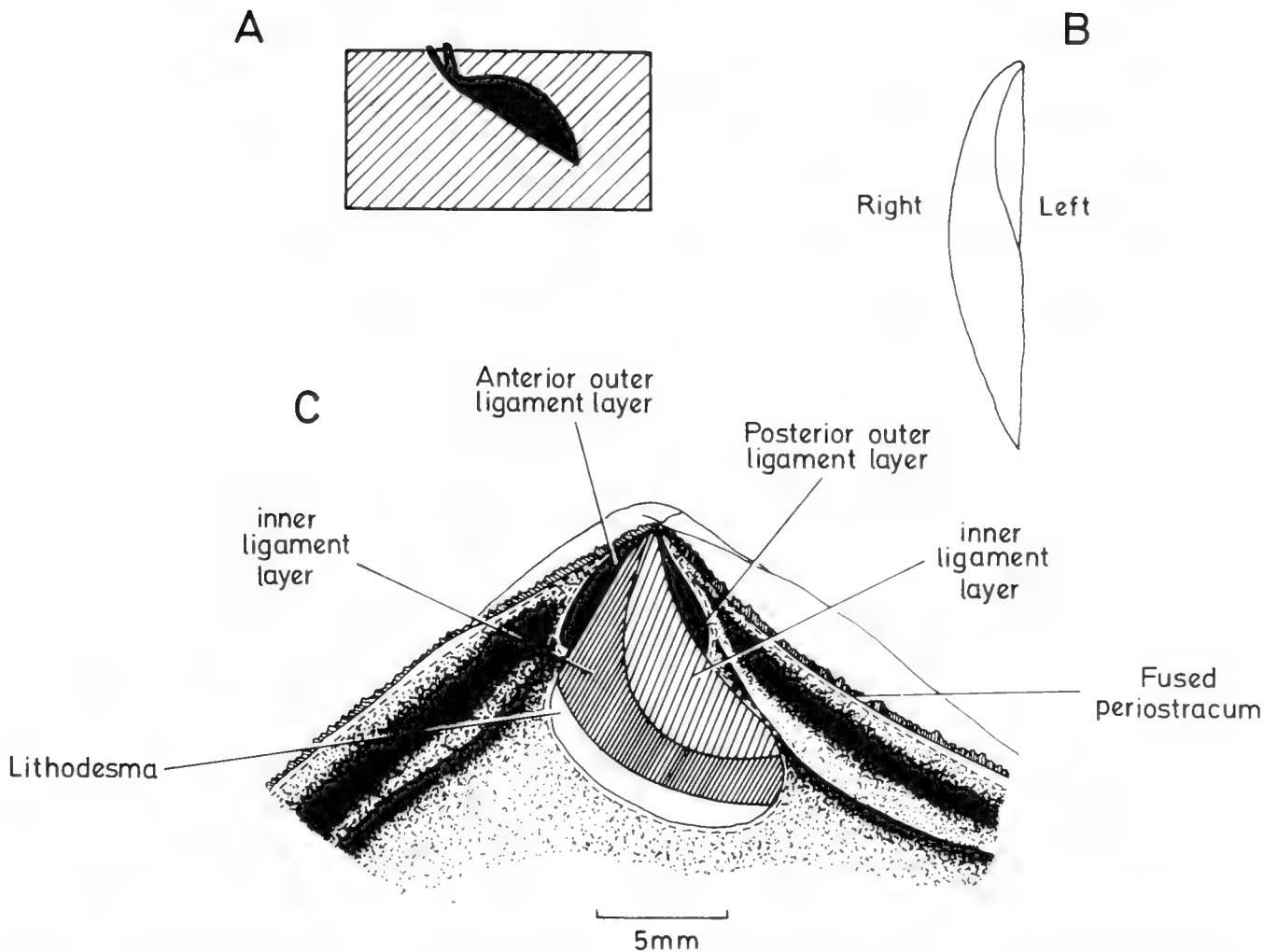


FIG. 3. The Myochamidae. (A), *Myadora striata* in its natural position in the sand (redrawn after Morton, 1977); (B), (C), the shell of *M. striata* as seen from the anterior and the structure of the ligament as seen from the left (redrawn after Yonge & Morton, 1980).

Verticordiidae, typically located within the Poromyacea (Newell, 1965, 1969) in the Pandoracea. Certain morphological features are possessed in common but the most recent study of the Verticordiidae by Allen & Turner (1974) indicates that they are well placed within the Poromyacea (as defined by Newell, 1969). This will be further discussed.

THRACIACEA Stoliczka, 1870 (comprising the Thraciidae Stoliczka, 1870, Periplomatidae Dall, 1895 and Laternulidae Hedley, 1918)

The Thraciacea form a natural assemblage of three families—the Thraciidae, Periplomatidae and the Laternulidae and it is here formally proposed following earlier statements (Yonge & Morton, 1980), that this be recognised in the classification of the Anomalodesmata. As pointed out by Boss (1978), the members of this superfamily arose in the Jurassic, whereas the other families of the

Pandoracea (previously described) and to which they were earlier linked (Newell, 1965, 1969; Runnegar, 1974) arose in the Caenozoic. This division of the superfamily Pandoracea is strongly supported, indeed was originally given substance by the researches of Boss (1978) and Yonge & Morton (1980) the latter investigating the structure of the primary ligament, a feature of high taxonomic value (Yonge, 1978).

The Thraciidae (Fig. 5) are insufficiently studied though Allen (1961b) has described the shell morphology of the British species and attempted an understanding of the ligament of *Thracia villosiuscula*, this, apparently, being essentially similar to that of *Cochloidesma* (Periplomatidae) with an anterior lithodesma linking two chondrophores and a primary ligament composed largely of inner ligament layer (Allen, 1961b, fig. 2C). However, I have examined *Thracia phaseolina* and *T. villosiuscula* and found them to possess an external primary ligament with a very

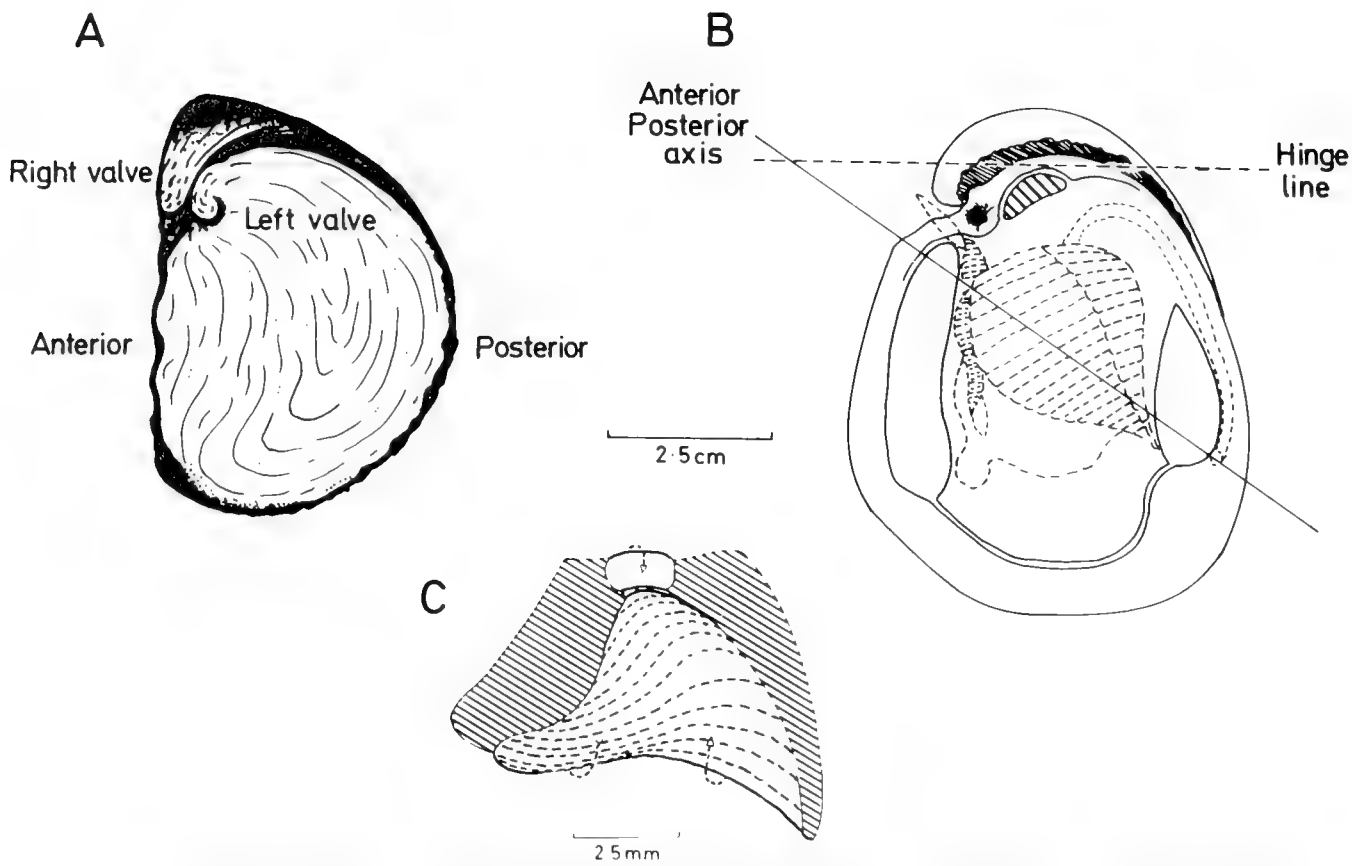


FIG. 4. The Cleidothaeridae. (A), *Cleidothaerus maorianus* as seen from the left anterior aspect and (B) an internal view of the right shell valve showing the effect of the tangential component of growth upon the orientation of the body (redrawn after Morton, 1974); (C), a dorsal view of the primary ligament almost exclusively comprising inner ligament layer with the lithodesma coiled around it (redrawn after Yonge & Morton, 1980).

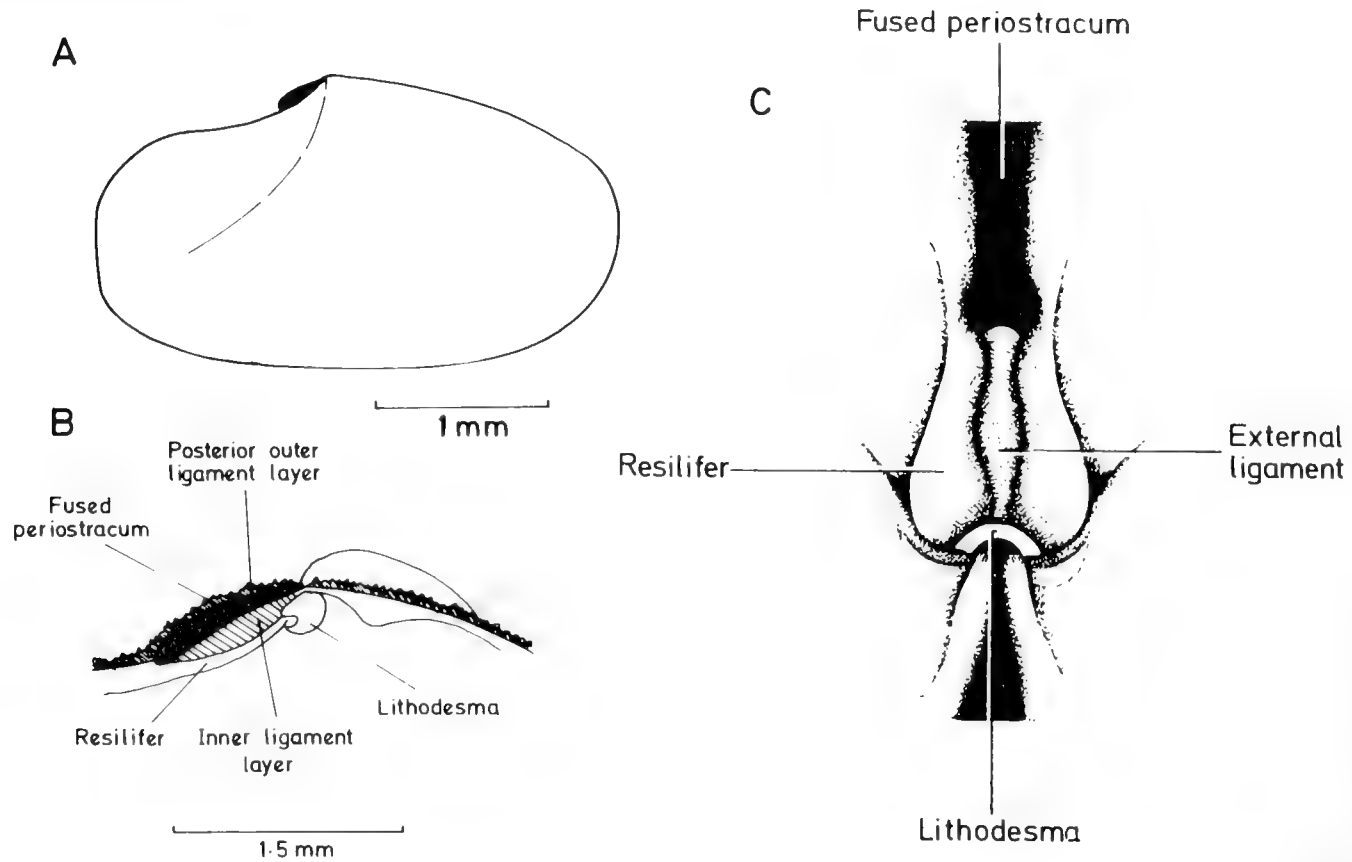


FIG. 5. The Thraciidae. *Thracia villosiuscula*. (A), The shell as seen from the right and (B), the ligament as also seen from the right; (C), the ventral view of the ligament of *T. phaseolina*.

weakly defined amorphous lithodesma. Clearly Allen was actually examining *Cochlodesma praetenu* and not *Thracia villosiuscula*.

Members of the Thraciidae are approximately equivalve, with exceptionally thin shell valves; there is no obvious transverse crack in the shell as there is in members of the Periplomatidae and Laternulidae. The animal typically lies vertically disposed in sandy deposits. The foot is large and the pedal gape extensive. There are separate siphons (with long siphonal retractors) which are pushed upwards and form mucus-lined tubes with separate siphonal holes in the sand (Yonge, 1937) as also occurs in *Offadesma angasi* (Periplomatidae) (Morton, 1981).

Members of the Periplomatidae (Fig. 6) have been investigated by Pelseneer (1911) (*Asthenothaerus*), Allen (1958, 1960) (*Cochlodesma*) and more recently by Morton (1981) (*Periploma* (*Offadesma*) *angasi*). In these bivalves there is an inequivalve shell, this being of less significance in *Cochlodesma* but of greater importance in *Offadesma*. The primary ligament, largely comprising inner ligament layer, is internal and located between spoon-shaped chondrophores. *Cochlodesma praetenu* does (Allen, 1958, 1960) but *Offadesma angasi* does not (Morton, 1981) possess an anterior lithodesma. The dorsal margin of the shell valves are strongly united by periostracum forming a secondary ligament. Of much greater impor-

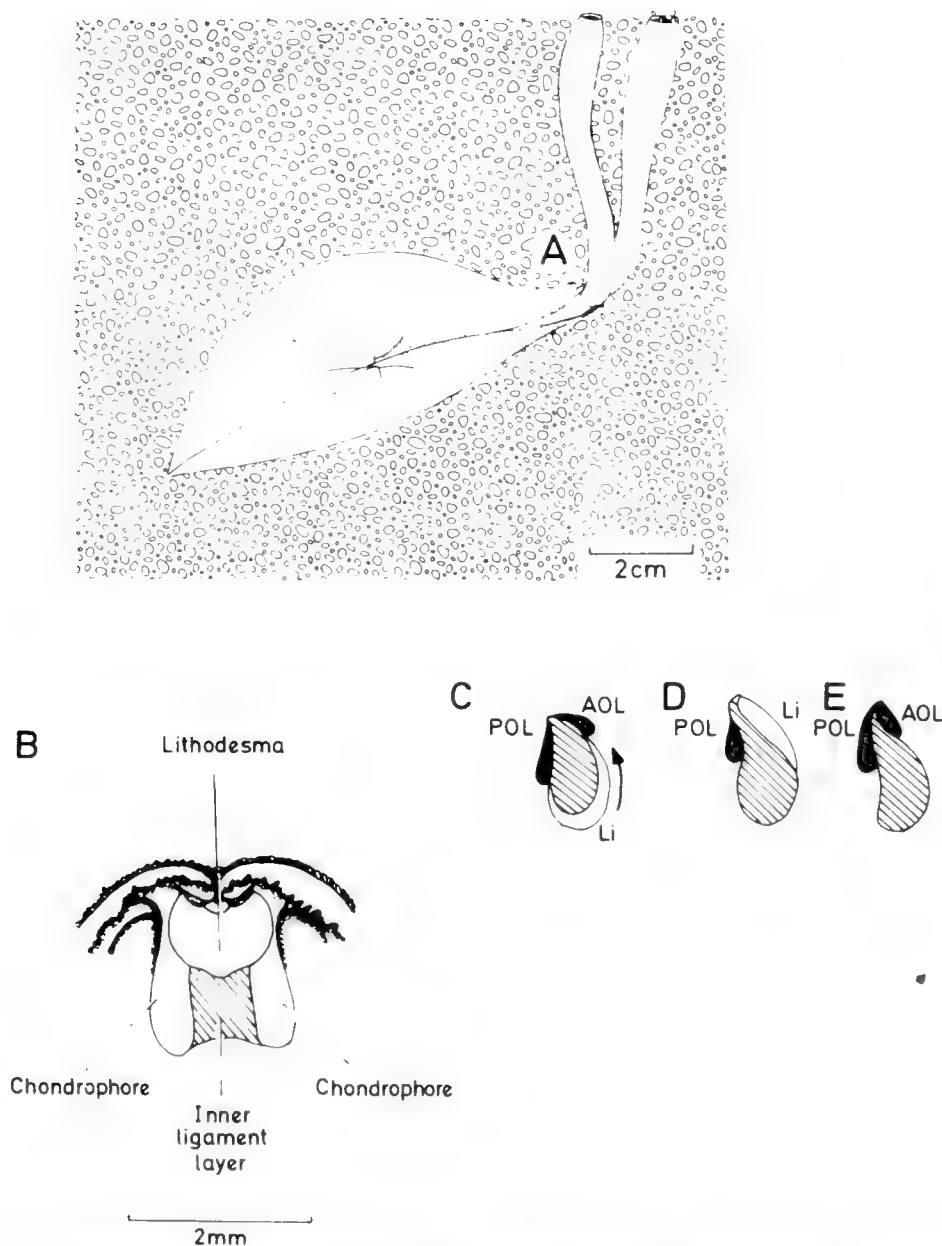


FIG. 6. The Periplomatidae. (A), *Offadesma angasi* in its natural position in the sand (redrawn after Morton, 1981); (B), anterior view of the ligament of *Cochlodesma praetenu*; medial section through the ligament of (C), a hypothetical ancestor; (D), *Cochlodesma praetenu*; (E), *Offadesma angasi*. (B, C, and D redrawn after Yonge & Morton, 1980).

tance in the Laternulidae, the Periplomatidae (but not obviously the Thraciidae) possess a transverse umbonal crack in each valve. This is formed as the result of a trend in the superfamily for the antero-dorsal region of the shell to overarch the postero-dorsal border, resulting also in the ligament swinging downwards (for different reasons a similar ligament is seen in the Cuspidariidae (Yonge & Morton, 1980)). Typically the thin valves gape both anteriorly and posteriorly and *Offadesma angasi* lies buried on its left valve some 6 cm below the surface in sub-littoral fringe sands of high (wave) energy beaches. Separate siphons, very similar to those of *Thracia* (Yonge, 1937), project up to the water above. *Offadesma* cannot rebury itself, the foot and pedal gape being small unlike those of *Thracia* which are large. The ctenidia are large, the palps long and there are extensive pallial glands to aid the discharge of the large amounts of material that must enter the mantle cavity.

The Laternulidae (Fig. 7) are the most unusual and the most advanced family of the Thraciacea. Indo-Pacific in distribution (Morton, 1976a), they possess a thin, approximately equivalve shell and lie more or less vertically disposed in soft sediments ranging from tropical mangrove muds (*Laternula truncata*) (Morton, 1973), to the Antarctic benthos (*L. elliptica*) (Burne, 1920). There are always wide anterior and posterior gapes and the exchange of mantle fluids is by anterior and posterior adduction and thus flexion of the valves at the transverse umbonal crack against the fulcrum provided by the primary ligament and the ventral shell margin (Morton, 1976a). A buttress, only weakly developed in the Thraciidae but somewhat more robust in the Periplomatidae, is strongly developed in these bivalves and prevents breaking of the valves under the forces generated by the adductor muscles. A boomerang-shaped lithodesma occurs on the anterior face of the primary ligament of some (e.g. *L. truncata* and *L. boschasina*) but not other (*L. elliptica*, *L. anatina*, *L. anserifera*) species (Morton, 1976a) and aids, in the absence of hinge teeth, the secondary ligament of periostracum in valve alignment.

The siphons of *L. truncata* are fused to the tips and, unlike any of the families earlier described, all of which possess simple sensory papillae, the siphonal orifices are surrounded by a complex array of sensory tentacles and by nine pallial eyes with a complexity of struc-

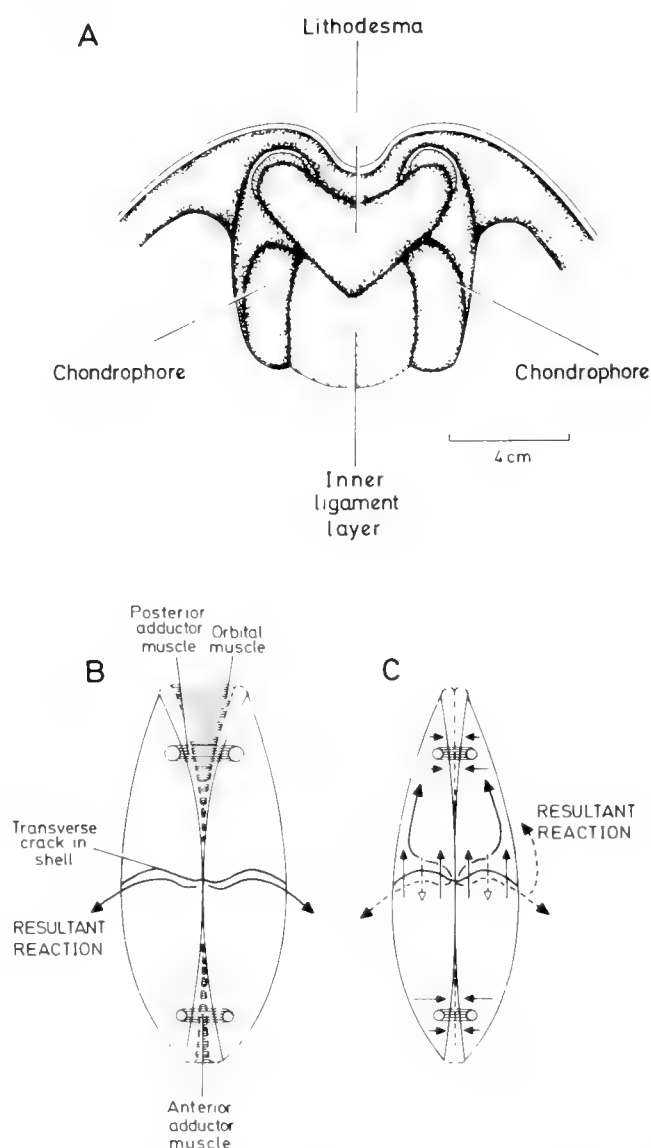


FIG. 7. The Laternulidae. *Laternula truncata*. (A), anterior view of the ligament (redrawn after Morton, 1973); (B) and (C) the mode of operation of the shell (redrawn after Morton, 1976a).

ture similar to that seen in the Pectinidae (Adal & Morton, 1973) and more reminiscent of vertebrate optical structures. In most respects the organs of the mantle cavity and visceral mass are, however, similar to those of other families of the Thraciacea. Indeed this generalization can be broadened to include members of all families of the Pandoracea and the relatively uniform nature of the organs of the mantle cavity does not approach the complexity seen in other members of the remaining anomalodesmatan lineages.

CLAVAGELLACEA d'Orbigny, 1844 (comprising only the Clavagellidae d'Orbigny, 1843)

The Clavagellacea (Fig. 8) are an enigma with no recognized ancestor. They have

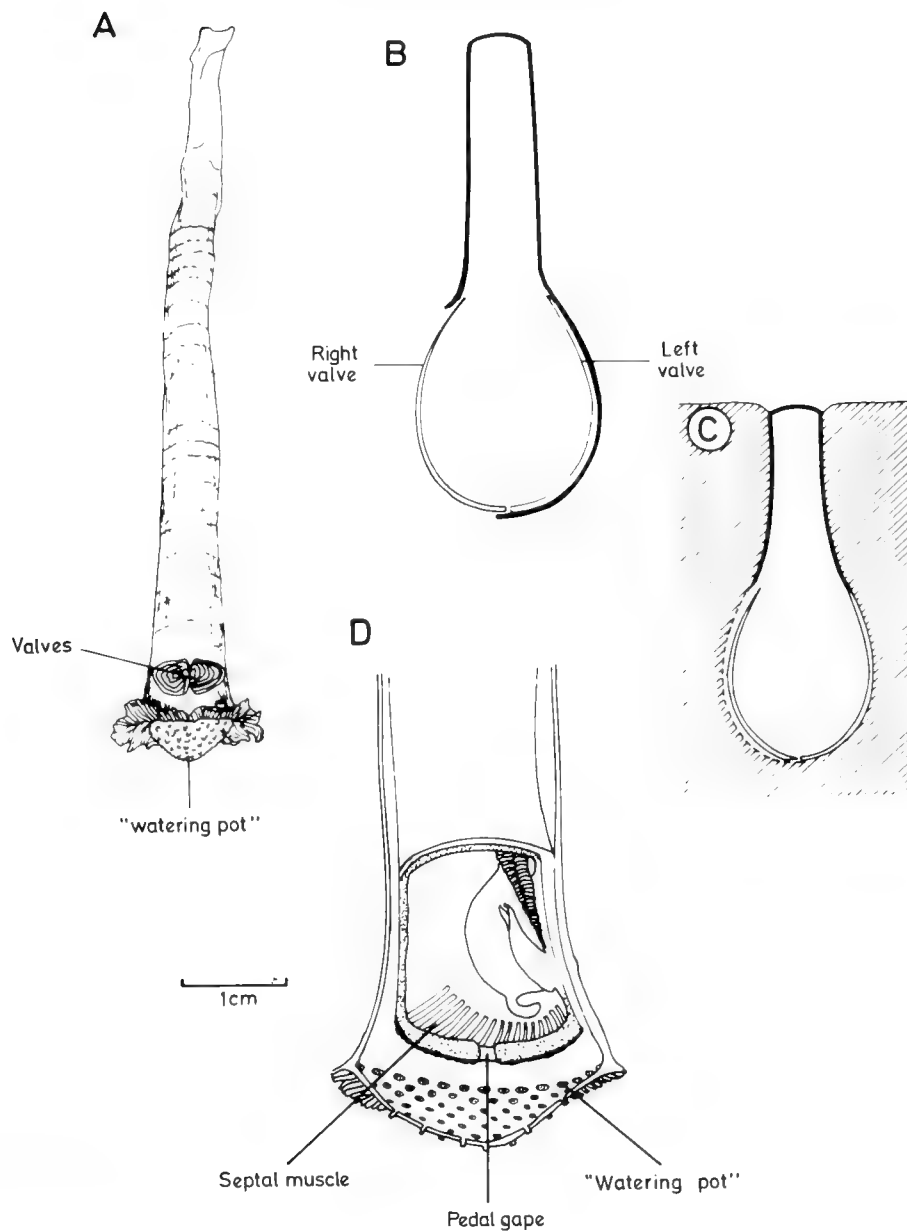


FIG. 8. The Clavagellidae. The shell and adventitious shell of *Penicillus* sp. (redrawn after Taylor, Kennedy & Hall, 1973); (B), (C), the shell and adventitious shell of two species of *Clavagella* (redrawn after Soliman, 1971); (D), *Brechites penis*. A dissection of the anterior end as seen from the right side (redrawn after Purchon, 1960).

arisen relatively recently, the oldest fossils (of *Clavagella*) being recorded from the Upper Cretaceous. *Brechites penis* has been studied alive by Purchon (1956a, 1960) and *Clavagella* by Soliman (1971) though there are earlier studies of, presumably, preserved specimens by Owen (1835) and Lacaze-Duthiers (1870). Smith (1971) has revised the taxonomy of the group, dividing the living representatives into the two genera noted above, though Keen & Smith (1969) recognise three genera, *Clavagella*, *Humphreyia* and *Penicillus*. In *Clavagella*, one valve only is fused to an adventitious shell while in *Brechites* both valves are so fused. In both genera the true shell valves are reduced to small proportions in relation to the adventi-

tious shell which may be exceedingly large and in *Brechites* (Purchon, 1956a, 1960) forms a very long tube. Smith (1978) has presented a few ideas on how the adventitious shell is secreted. The anterior end of the adventitious shell of *Brechites* is formed into a "watering pot," or expanded plate perforated by many small pores. This end lies buried in the sand and water is pumped in and out of it by complex "septal" muscles around the pedal gape (Purchon, 1956a, 1960).

Members of the Clavagellacea possess an external ligament. Because of their immobile way of life and reduced shell valves relative to the adventitious shell the adductor muscles are either very reduced or absent. Again, however, typical ctenidia and labial palps are

present and the organs of the visceral mass seem unspecialized. Individual species, however, await detailed examination.

POROMYACEA Dall, 1886 (comprising the Verticordiidae Stoliczka, 1871, Cuspidariidae Dall, 1886 and Poromyidae Dall, 1886)

Altogether three families of deep water bivalves—the Verticordiidae, Cuspidariidae and Poromyidae—are usually linked in a single superfamily, the Poromyacea (Newell, 1965) 1969). Thus Pelseneer (1888a) and Ridewood (1903) and, most recently, Allen & Turner (1974) and Allen & Morgan (in press) recognise a continuous morphological sequence—Verticordiidae – Cuspidariidae–Poromyidae—culminating, in the latter two families, in the adoption of a carnivorous mode of life (Yonge, 1928; Reid & Reid, 1974). There are, however, strong arguments against such a simplistic view and the opinions of other authors (reviewed by Morton, in prep.) conflict with this.

It seems therefore appropriate to describe each family in turn and later to discuss their relationships one with the other and with the other members of the Anomalodesmata.

The Verticordiidae (Figs. 9, 10) possess a thin shell with a sunken primary ligament and a ventral lithodesma. Ligament structure is exactly as described for *Lyonsia* (Pandoracea) (Yonge, 1976; Yonge & Morton, 1980). The shell is also three layered as in members of the Pandoracea and Thraciacea (Taylor, Kennedy & Hall, 1973). Members of the Verticordiidae have been extensively described by Allen & Turner (1974). They are hermaphrodite and possess a reduced ctenidium, of typical anomalodesmatan structure and labial palps formed into a trumpet for the reception of large food particles. They also possess—as in members of the Pandoracea, e.g. *Lyonsia* (Prezant, 1979), and Thraciacea, e.g. *Offadesma* (Morton, 1981)—well defined radial mantle glands that serve to adhere sand grains to the

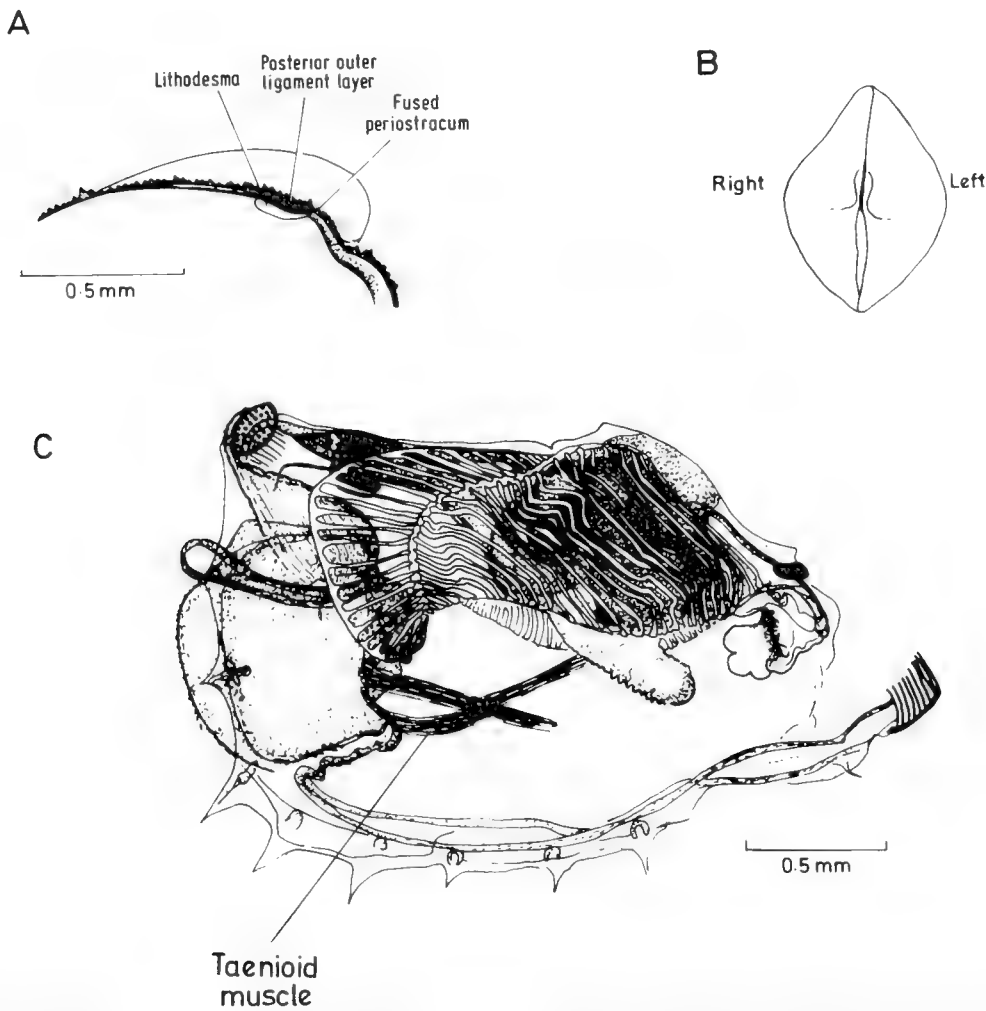


FIG. 9. The Verticordiidae. *Lyonsiella abyssicola*. (A), (B), The ligament as seen from the right side and the shell as seen from the dorsal aspect (redrawn after Yonge & Morton, 1980); (C), the tissues of *Lyonsiella fragilis* (redrawn after Allen & Turner, 1974).

periostracum. The siphonal tentacles are complex, large and sticky and it is thought that they form a fan of spreading papillate adhesive structures which capture either dead but possibly living organisms. In some verticordiids the siphons are withdrawn by siphonal retractors (taenioid muscles), some of which are longer and have separate points of insertion upon the shell. In this feature *Lyonsiella fragilis* (Allen and Turner, 1974) most strongly resembles the pholadomyacean *Parilimya* (Morton, in prep.).

The Cuspidariidae (Fig. 11) also possess a thin shell and a sunken, opisthodetic primary ligament with a lithodesma. The posterior margin of the shell is typically rostrate. The siphons, particularly the inhalant, are extremely long and raptorial, to be rapidly distended to catch living, mobile prey. Correspondingly there are also numerous, large sensory tentacles and accessory siphonal ganglia (Reid & Reid, 1974; Reid & Crosby, 1980). The ctenidia are reduced to a horizontally oriented septum perforated by pores or ostia. The septum is used for prey capture, the process involving the complex interaction of a number of muscle blocks and hydrostatic forces all designed to rapidly evert the inhalant siphon. The structure of the septum and the mode of operation of the organs of the mantle cavity have been described by Yonge (1928), Reid & Reid (1974), Reid & Crosby (1970) and Allen & Morgan (in press).

The Poromyidae (Fig. 12) differ from the two previous families in one important characteristic, the primary ligament is external and does *not* possess a lithodesma (Yonge & Morton, 1980). In many other respects the Poromyidae closely recall conditions in the Cuspidariidae, owing to the common presence of a septum, again for the capture of living prey. The shell of the Poromyidae is not, however, rostrate and clearly prey capture must be by some other means, different from that employed in the Cuspidariidae. *Poromya* has siphonal appendages similar to those of verticordiids (Yonge, 1928).

In both the Cuspidariidae and the Poromyidae the stomach is modified for the digestion of large organisms (Yonge, 1928; Bernard, 1974); in *Cardiomya* a digestive pro-tease has been found (Reid, 1978).

PHOLADOMYACEA Gray, 1847 (Pholadomyidae Gray, 1847)

Modern representatives of this ancient, oldest lineage of the Anomalodesmata are among the rarest bivalves. Hitherto the Pholadomyacea have been considered to comprise a single extant family—the Pholadomyidae Gray, 1847, the type-genus and species being *Pholadomya candida* Sowerby, 1823 (Morton, 1980a). Morton (in prep.), however, is erecting a second family—the Parilimyidae Morton, 1981—following a detailed ex-

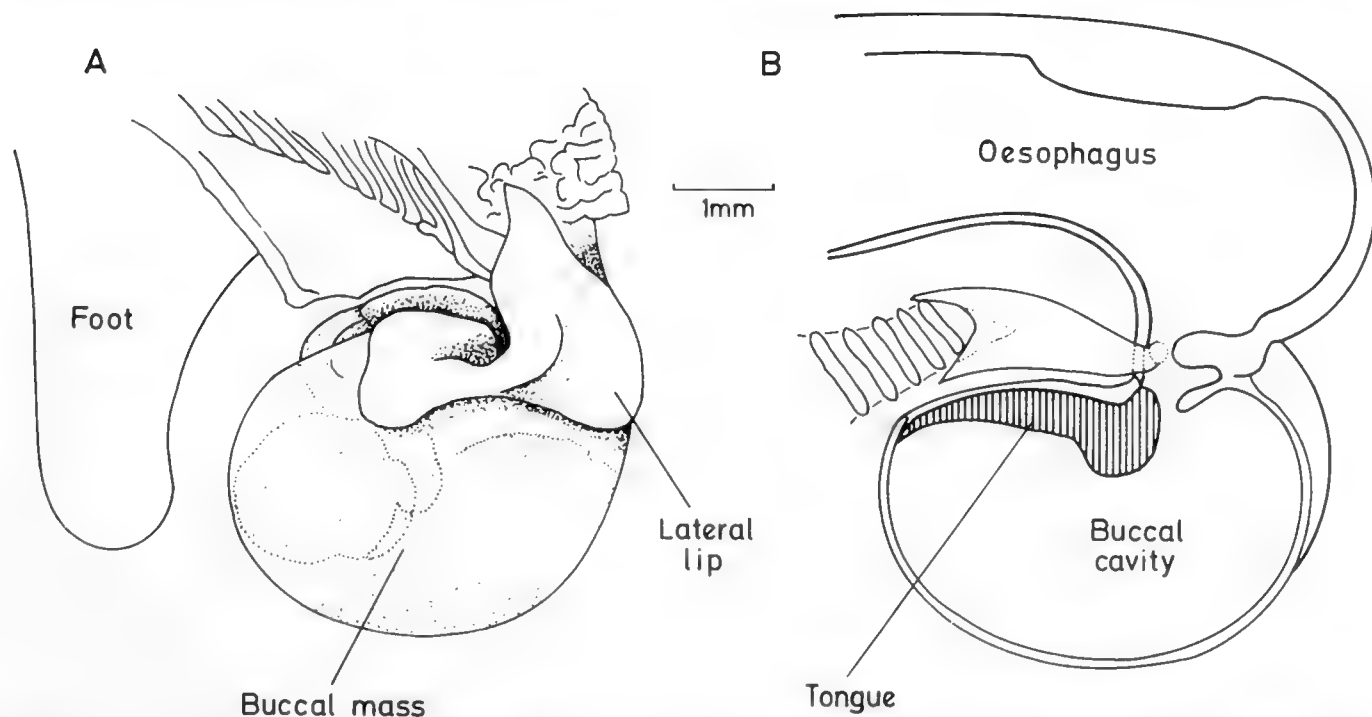


FIG. 10. The Verticordiidae. *Lyonsiella formosa*. (A), (B), Lateral views of the mouth region and the same in longitudinal sagittal section (redrawn after Allen & Turner, 1974).

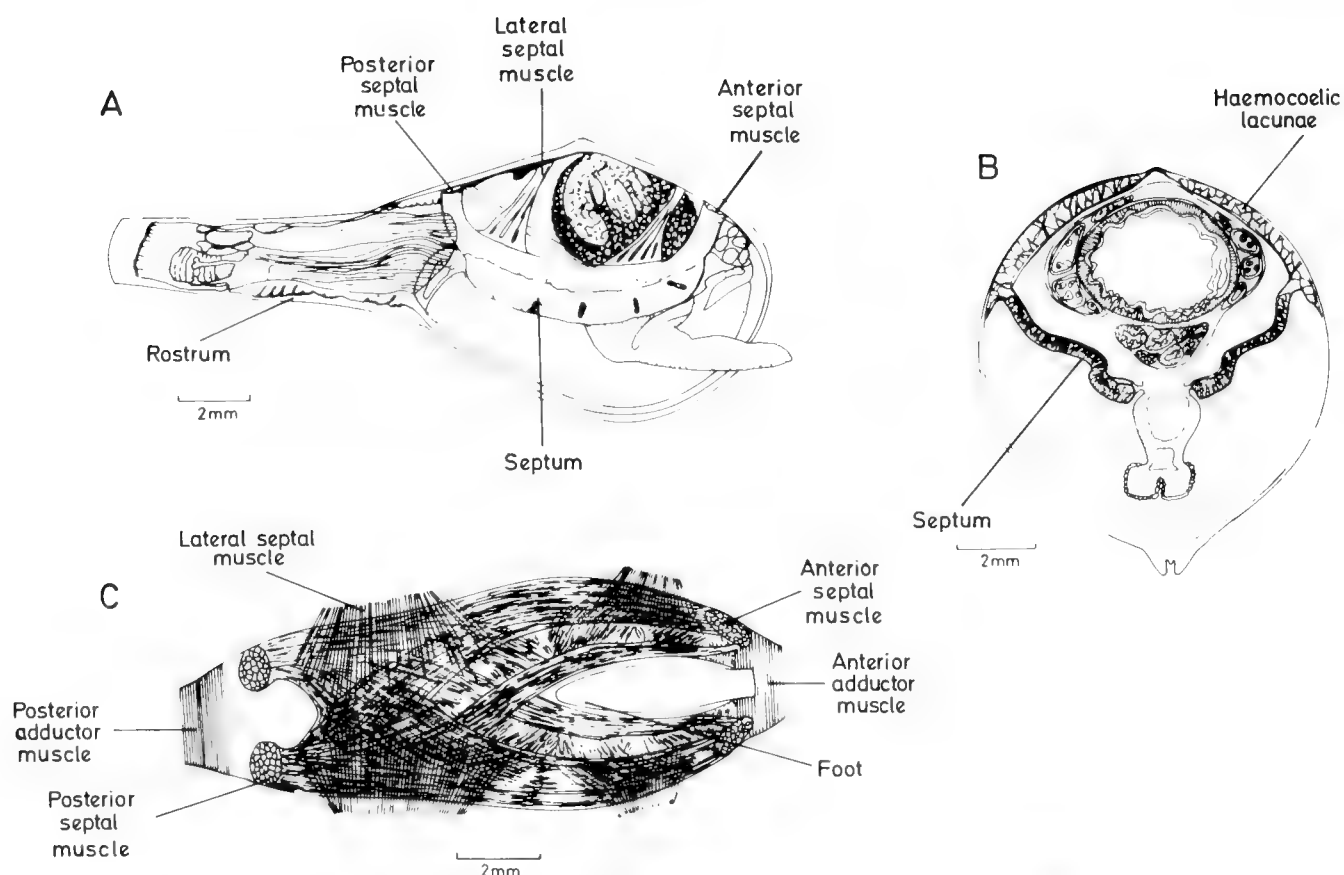


FIG. 11. The Cuspidariidae. (A), *Cuspidaria rostrata*, a decalcified specimen seen from the right. (B), Transverse section through *Cuspidaria* sp.; (C), the septum, as seen from the ventral aspect, of *Cuspidaria cuspidata*. (A, B, redrawn after Reid & Reid, 1974; C, redrawn after Yonge, 1928).

amination of *Parilimya fragilis* Grieg, 1920. Other constituent genera of the new family include *Panacca* and *Nipponopanacca*. All are deep water bivalves.

In *Pholadomya candida* (Figs. 13, 14)—probably the only living representative of the genus—the ligament is external, there is no lithodesma and the shell gapes widely both anteriorly and especially posteriorly. The thick siphons are fused almost to their tips with no terminal sensory tentacles. Instead, a sensory appendage—the opisthopodium—is located on the posterior region of the visceral mass and monitors water flow, supplying information directly, and unusually, to the pedal ganglia. In most anatomical respects *Pholadomya* is similar to other anomalodesmatans but with one or two further notable exceptions. The lips of the mouth (Fig. 14) are fused into two, round, laterally positioned spheres which probably serve, as in other bivalves in which this occurs, e.g. members of the Pectinidae, Spondylidae and Limidae (Morton, 1979), to prevent food material from being flushed out of the oral grooves by strong water currents in the anterior region of the mantle cavity. The second, major, modification involves the

pedal gape. From a point of attachment to each shell valve outside the anterior adductor muscle arises a thin muscle which crosses over, anterior to the pedal gape, and has its other insertion at the pallial line on the opposite valve (Runnegar, 1979; Morton, 1980a). These taenioid muscles have a structure reminiscent of the cruciform muscles of the Tellinacea (Yonge, 1949). The foot is glandular, possesses two extravagantly complex statocysts and is plug-like. It has been suggested (Morton, 1980a), on the evidence of the above adaptations, that *P. candida* lies diagonally on its back in the sand and pumps deposits into the mantle cavity via the pedal gape, the foot acting as a piston with the (mechanical) “valve” of the pedal gape and its musculature. The gut is variously adapted for dealing with large amounts of sediments.

Parilimya fragilis (Figs. 15, 16) is clearly very different from *Pholadomya*; indeed, Runnegar (1974) considered that it might belong to a different family, but linked to the superfamily by the possession of an external ligament, a distinctly radially ridged shell which, however, does not gape or if so only slightly and the common presence of taenioid

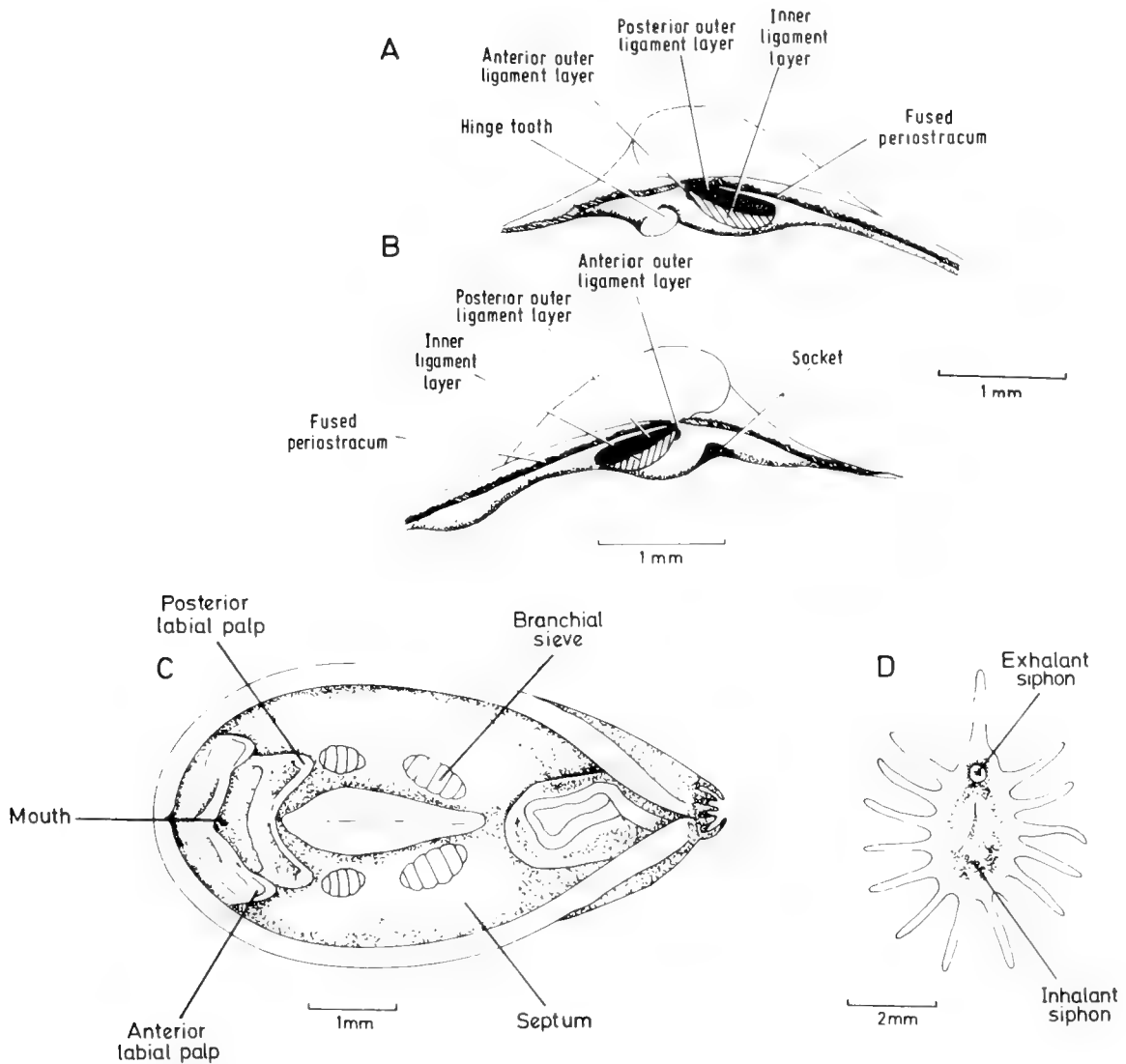


FIG. 12. The Poromyidae. Right (A) and left (B) views of the hinge plate of *Poromya tornata*; (C), ventral view of *P. granulata* with septum exposed and (D), the siphons of *P. granulata* (C and D redrawn after Yonge, 1928).

muscles. Members of this genus are more numerous, there being a number of extant species, all recorded from deep waters. In a major revision of these bivalves, Morton (in prep.) has placed *Parilimya*, *Panacca* and *Nipponopanacca* in a new family—the Parilimyidae—so different is the type-genus *Parilimya* from *Pholadomya*—but nevertheless still included in the Pholadomyacea.

The organs of the mantle cavity of *Parilimya fragilis* are typical of other anomalodesmatans except with regard to the labial palps and the siphons. In the latter case the inhalant siphon is greatly elongate and muscularized and can be withdrawn into the mantle cavity, possibly rapidly, by two extraordinarily long siphonal retractor muscles (one on each side) and which find insertion on the shell towards the anterior end of the mantle cavity. Similar “taenoid” muscles, as noted earlier, occur, albeit greatly reduced, in *Pholadomya* and in

Lyonsiella fragilis and possibly also *Laevicordia horrida* in the Verticordiidae (Allen & Turner, 1974). The ctenidia are relatively large. The labial palps (Fig. 16) are small, muscular, with few sorting grooves. Structure and interpreted function appear reminiscent of the palps of the Poromyidae (Yonge, 1928) and Verticordiidae (e.g. *Lyonsiella formosa*) (Allen & Turner, 1974) i.e. for holding large food items and certainly not for sorting fine particles. Final evidence for a scavenging or carnivorous mode of life in *Parilimya* comes from an examination of the stomach and intestine which is modified, as in the Cuspidariidae, Poromyidae and some members of the Verticordiidae, i.e. stomach type II (Purchon, 1956b) for the digestion of large pieces of food (Morton, in prep.).

The structure and interpreted modes of life of *Pholadomya* and *Parilimya* gives valuable insights into the evolution of two

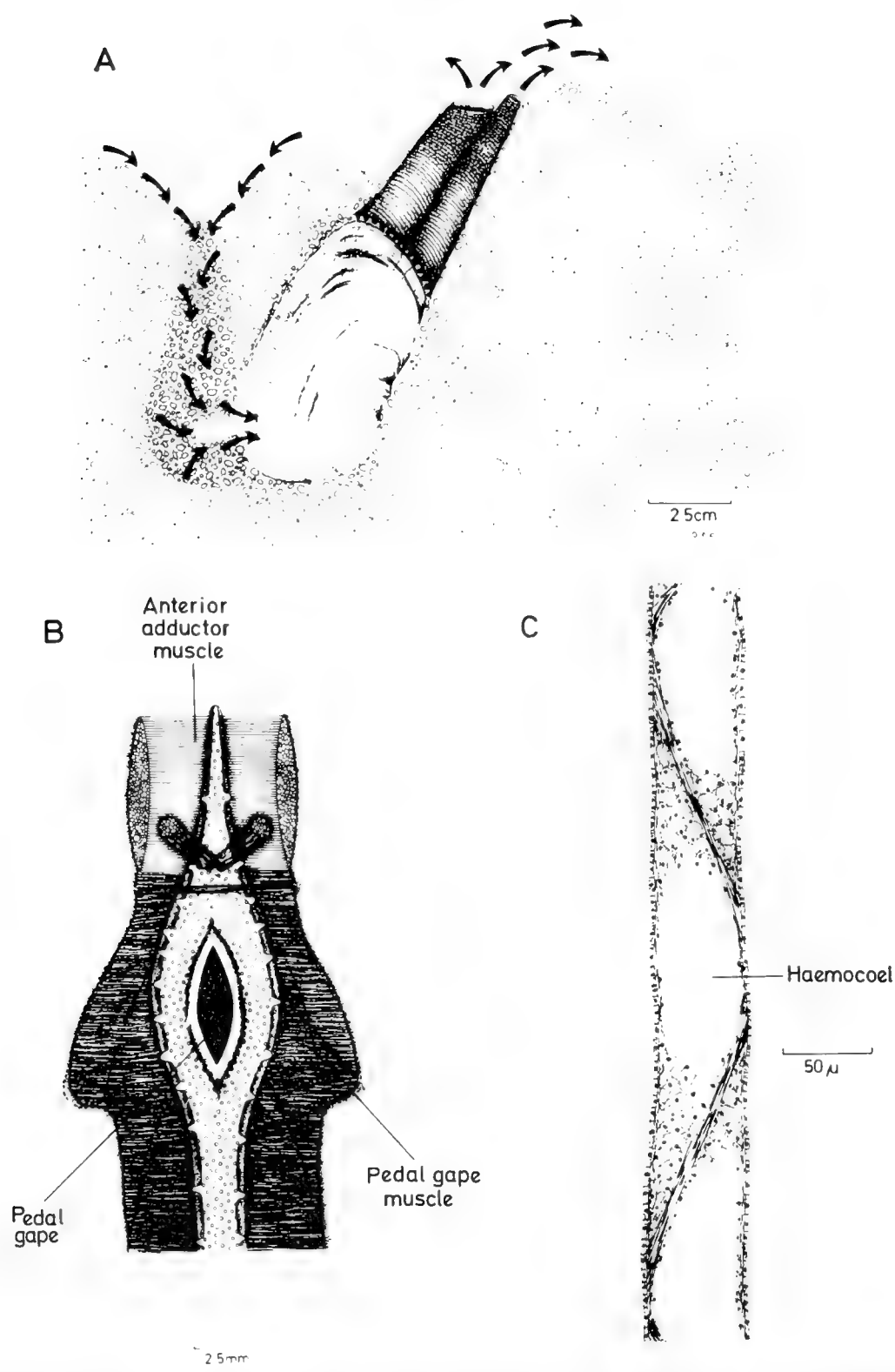


FIG. 13. The Pholadomyidae. *Pholadomya candida*. (A), the animal in its interpreted position in the sand; (B), exterior view of the pedal gape and musculature; (C), transverse section through the mantle (all redrawn after Morton, 1980a).

other anomalodesmatan superfamilies—the Clavagellacea and the Poromyacea (as defined by Newell, 1969)—though again, study of the Pholadomyacea casts further light on the evolution of the subclass as a whole.

PHYLOGENETIC LINEAGES

It is clear that the Pholadomyacea is the stem superfamily of the Anomalodesmata—adaptive radiation proceeding in a number

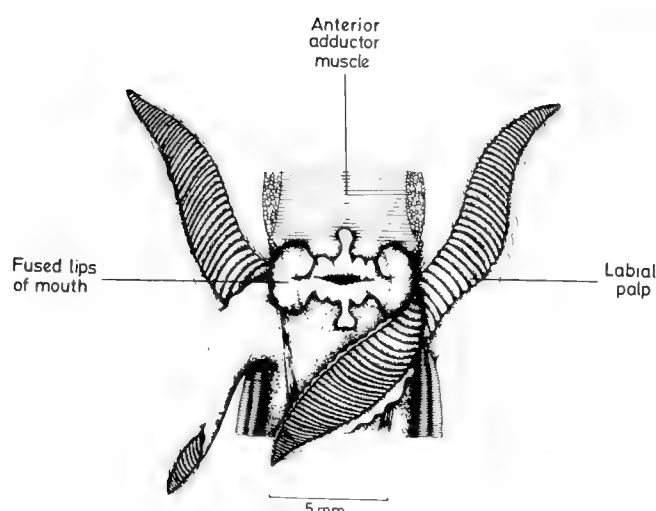


FIG. 14. The Pholadomyidae. Ventral view of the fused lips and labial palps of *Pholadomya candida* (redrawn after Morton, 1980a).

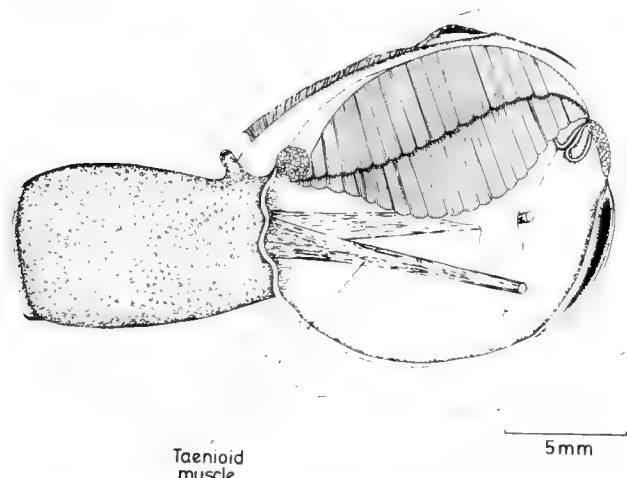


FIG. 15. The Parilimyidae. *Parilimya fragilis* as seen from the right side after removal of the right shell valve and mantle lobe (redrawn after Morton, in prep.).

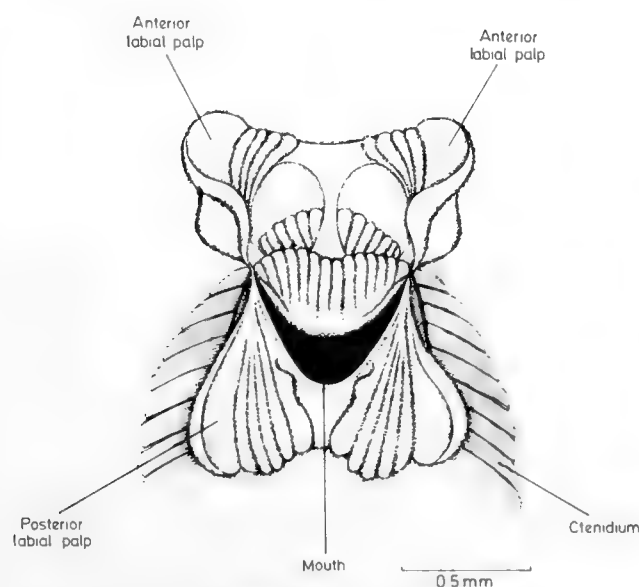


FIG. 16. The Parilimyidae. *Parilimya fragilis*. A ventral view of the mouth, lips and labial palps (redrawn after Morton, in prep.).

of lines, and at different times from this group (Fig. 17).

Runnegar (1974) especially has given an excellent broad account of the fossil history of the Anomalodesmata and their extinct representatives. This paper concerns itself with the extant anomalodesmatans with regard to which much more detailed information is now available.

All agree that the ligament is of prime taxonomic importance in the Anomalodesmata (Yonge, 1978; Runnegar, 1979; Yonge & Morton, 1980) and it is this structure which affords valuable clues as to the origins of the various anomalodesmatan lineages.

Origin of the Thraciacea

The Thraciacea arose in the Mesozoic with the Thraciidae constituting the oldest fossils. Species of *Thracia* possess an external, primary ligament but with a characteristic, anteriorly located, lithodesma attached by resilifers direct to the valves. A relatively simple body plan, long separate siphons, wide pedal gape and an axe-like digging foot are features that clearly prewise the Periplomatidae and Laternulidae.

In the Periplomatidae and Laternulidae, however, the antero-dorsal region of the shell arches over the postero-dorsal resulting in the primary ligament swinging downwards to be located between chondrophores. The over-arching process is hinted at in the Thraciidae and indeed so superficially similar are shells of *Thracia* and *Cochlodesma* that Allen (1961b) has mistaken them.

The superfamily remains infaunal but occupies extremely specialized niches, most being deep "passive" burrowers relying upon siphon withdrawal only (except *Thracia*) for defense (Morton, 1973; 1981).

Origin of the Poromyacea (Poromyidae, Verticordiidae and Cuspidariidae) (Newell, 1965, 1969) (the septibranchs)

The Anomalodesmata possess among the most interesting of all bivalves, namely the scavenging and carnivorous septibranchs. The septibranchs comprise three generally regarded discrete families—the Verticordiidae, Cuspidariidae and Poromyidae. Higher taxonomic categories are, however, disputed. Thus, Ridewood (1903) placed all three families in the Poromyacea. Others, as described earlier, link the Mesozoic Cuspi-

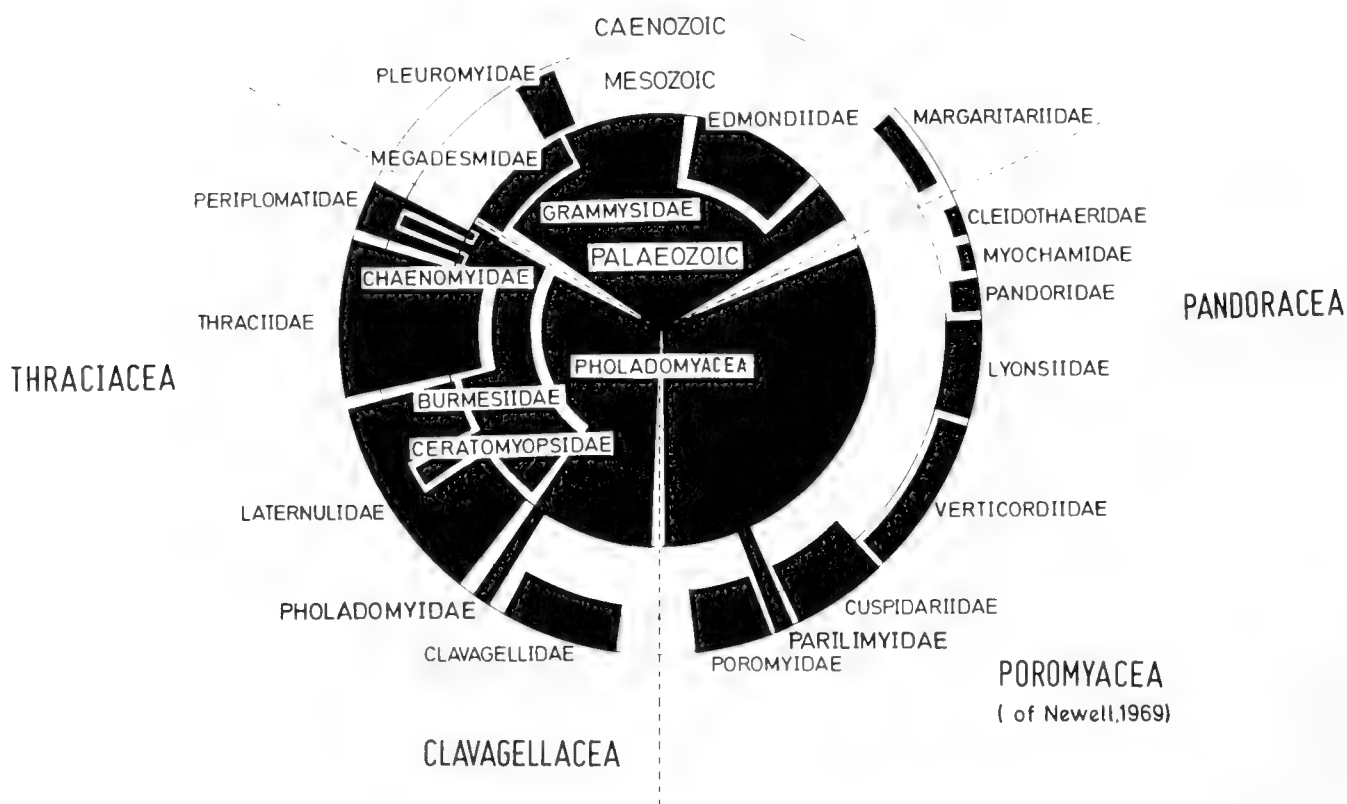


FIG. 17. The adaptive radiation in the Anomalodesmata.

dariidae and Poromyidae in the Poromyacea while the Caenozoic Verticordiidae are placed in the Verticordiacea. Runnegar (1974) placed the Verticordiidae in the Pandoracea, the Cuspidariidae in the subclass Palaeotaxodonta (a now wholly discredited notion (Yonge & Morton, 1980) originally formulated by Purchon (1956b)) leaving only the Poromyidae in the Poromyacea. Bernard (1974) concluded that the septibranchs were a diphyletic terminal order within the subclass Anomalodesmata dividing the families into two superfamilies the Verticordiacea and the Poromyacea (the Poromyidae and Cuspidariidae). Subsequently, however, Bernard (1979) has altered his views somewhat and now considers all three families to have superfamily status (the Verticordiacea belonging to the order Pholadomyoidea and the Poromyacea and Cuspidariacea belonging to the order Septibranchioidea). Almost conversely, Allen and Morgan (in press) place the Verticordiidae and Poromyidae in the Poromyacea and the Cuspidariidae in its own superfamily. Morton (in prep.) elevates all three families to superfamily status, deriving all from a pholadomyacean ancestor possibly similar to *Parilimya* and thus abandons the order Septibranchioidea.

A recent study of *Pholadomya candida* (Pholadomyacea) (Morton, 1980a) showed

that this species possessed a number of characters possibly also possessed by some "septibranchs." Thus the sense organ (opisthopodium) on the posterior region of the visceral mass of *Pholadomya* is also apparently possessed by *Halicardia flexuosa* (Dall, 1895), *H. nipponense* (Nakazima, 1967) and *Poromya eximia* (Pelseneer, 1911). Possibly significantly, *Euciroa pacifica* possesses fused lips laterally and a medial lappet on the posterior lip (Dall, 1895) also as in *Pholadomya candida*.

An examination of *Parilimya fragilis* (Morton, in prep.) has revealed even more striking similarities between this pholadomyacean and some of the septibranchs, notably members of the less specialized Verticordiidae, but also the much more specialized Cuspidariidae and Poromyidae.

In particular, *P. fragilis* and members of the Verticordiidae, e.g. *Lyonsiella fragilis* (Allen & Turner, 1974), possess taenioid muscles which are elongate components of the siphonal retractors having separate insertions on each valve. These, in both, may aid rapid siphon withdrawal. Morton (in prep.) also suggests that the posterior longitudinal septal muscles of *Cuspidaria* can be derived from the taenioid muscles of *Parilimya*. Similarly the labial palps of *P. fragilis* have reduced ridges and the lips are thickened, the anterior

arching over the posterior as in many members of the Poromyidae and Verticordiidae. The lips of *Lyonsiella formosa* are fused (Allen & Turner, 1974) like those of *Pholadomya candida* (Morton, 1980a). Possibly equally significant, however, is that the inhalant siphon of *Parilimya fragilis* has the same raptorial nature as that of members of the Cuspidariidae and though lacking the complex, apical sensory nerve endings of *Cuspidaria cuspidata* (Reid & Reid, 1974) and *Cardiomya planetica* (Reid & Crosby, 1980) the fundamental structure of the siphonal apparatus is the same. Most significantly the intestine and stomach of *P. fragilis* are adapted for dealing with large pieces of food, as in all "septibranchs." There is thus some evidence in *Parilimya* to indicate that a verticordiid-cuspidariid line of evolution has arisen from a pholadomyacean stock, and not, as suggested by Allen & Turner (1974) and Runnegar (1974), from a pandoracean (lyonsiid) ancestor.

Species of *Parilimya* may also have more to reveal with regard to the origin of the Poromyidae. Very significantly, the ligament of *P. fragilis*, indeed of all pholadomyaceans, is external as in members of the Poromyidae and it seems at least possible that from a wider, possibly as yet unstudied group of pholadomyacean ancestors has arisen either two or three major deep water, scavenging anomalodesmatan lineages, the most advanced members of which have convergently evolved to be highly specialized carnivores. Such an interpretation finds general agreement with that of Bernard (1974). At one time or other, however (see Morton in prep. for a review), the three constituent families of the Poromyacea (as defined by Newell, 1965, 1969) have been variously linked one with the other by numerous authors. Pending publication of the review of the Cuspidariidae and Poromyidae by Allen & Morgan (in press), I prefer to regard each family as a superfamily, but all having a pholadomyacean ancestry. It seems at least possible that each superfamily will eventually be shown to comprise a number of families: Bernard (1979) has already for example divided the Verticordiacea into the Verticordiidae and Lyonsiellidae.

The origin of the septum in the Poromyidae, Cuspidariidae and some members of the Verticordiidae is problematic. Dall (1890) considered the septum to be formed from the forward extension of the siphonal retractor muscles and the intersiphonal septum. This view

was supported by Plate (1897). Other authors (Pelseneer, 1888a, b, 1891, 1911; Grobben, 1892; Ridewood, 1903; Yonge, 1928) consider it to be derived from the ctenidia by a reduction in the number of branchial apertures and an increase in the degree of muscularization. Bernard (1974, 1979) has reasserted that the septum has a pallial origin. The origin of the septum seems to have been resolved by Allen & Morgan (in press) who have recognised progressive degrees of gill reduction and septal development from the Verticordiidae to the Poromyidae via the Cuspidariidae. In *Poromya* and *Cetoconcha*, however, the anterior pedal retractor muscles pass into the septum anteriorly to form the inner longitudinal septal muscle. Similarly, Allen & Morgan (in press) note that the outer longitudinal septal muscle may have a pallial origin. I find it very difficult to understand how the pedal retractor muscles can become involved in the muscularization of a septum in which, undoubtedly, the major component is ctenidial with pallial involvement. However, *Pholadomya candida* is characterized by a pair of pedal gape muscles that cross from valve to valve, in front of the pedal gape and serve as a mechanical "valve" with the foot being used as a piston (Morton, 1980a). Incorporation of these muscles into the septum would seem a much more plausible suggestion particularly with regard to the anterior longitudinal septal muscles. Similarly the taenioid muscles of *Parilimya* (Morton, in prep.) (and *Lyonsiella fragilis*) (Allen & Turner, 1974) would seem to be a logical progenitor of the posterior longitudinal septal muscles as originally postulated by Dall (1890). In *Pholadomya* there can be seen the first signs of the muscularization of the posterior end of the ctenidium, and which is ultimately fulfilled in the Cuspidariidae and Poromyidae.

Clearly both *Pholadomya candida* and *Parilimya fragilis* are highly specialized bivalves but collectively they have many features reminiscent of the more modern Poromyidae, Cuspidariidae and Verticordiidae. A more detailed investigation of other extant but nevertheless rare pholadomyaceans may provide more clues with regard to the origin of the septibranchs.

In the Cuspidariidae rapid eversion and withdrawal of the siphon is largely by the translocation of blood from pallial lacunae to the siphon and back. A similar mechanism is required for *Pholadomya candida* extending

and retracting the foot so that the pallial haemocoel is also large. It would seem that the origin of the Cuspidariidae at least among the septibranchs and the Clavagellacea can best be explained by the exploitation of a primitive means of rapidly changing fluids in the mantle cavity, the former via the siphons (and similar adaptations do also occur in *Parilimya*), the latter via the pedal gape (as in *Pholadomya*).

Origin of the Clavagellacea

The Clavagellacea have no known ancestors of more typically "bivalve" plan and the origin of this group has never been adequately explained. The most important feature of the infaunal clavagellids is that there is, as described by Purchon (1956a, 1960) for *Brechites*, a change of fluids between the mantle cavity and the subterranean muds mediated via the pedal gape. Extensive muscles surround the pedal gape and form a septum, which, by its movement up and down forces water out of and into the infra-branchial chamber through a wide, perforated plate—"the watering pot"—of the adventitious shell. The exact function of this action is unknown, though it would hardly seem likely, as proposed by Purchon (1960), that it functions as a means of burrowing, except perhaps incidentally, since the animal cannot be mobile—the foot being imprisoned within the sealed adventitious shell. Possibly the watering pot acts as a coarse sieve retaining material that might enter the mantle cavity during pumping of the septum. Fine particles penetrating the sieve might constitute a source of food. In the extinct Hippuritidae it seems that water was drawn through the pores on the outer surface of the left valve to be eventually trapped on the broad and radially crenulate right mantle margin (Skelton, 1976).

If this attributed function is correct then *Brechites* can be compared with *Pholadomya candida* which is also postulated (Morton, 1980a) to feed on deep deposits, via the pedal gape. In this, albeit highly specialized, member of the primitive Pholadomyacea a pair of muscles arise from outside the anterior adductor muscle and cross over anterior to the pedal gape and attach to the opposite valve at the pallial line. Contraction of these muscles will close the pedal gape around, it has been suggested, the foot which by repeated rapid expansion and contraction acts as a suctorial piston with the pedal gape form-

ing a (mechanical) "valve." Although the Clavagellacea are clearly highly specialized, modern bivalves with an adventitious shell, they do share with *Pholadomya candida* the distinction of being the only (known) anomalodesmatans in which the movement of fluids via the pedal gape (for whatever reason) has been hypothesized. Pedal feeding is not unique to these bivalves. The Indo-Pacific mangrove bivalve *Polymesoda (Geloina) erosa* has been shown to feed this way, using less sophisticated methods (Morton, 1976b).

Also significantly, clavagellids, like the pholadomyaceans, possess an external ligament and as in *Pholadomya candida* the rectum passes beneath the heart.

It is thus suggested that the origin of the infaunal Clavagellacea, i.e. *Brechites*, should be sought amongst the Pholadomyacea and that *Pholadomya candida* gives some insight into how this superfamily arose. Clearly the cemented members of the Clavagellacea (Soliman, 1971; Smith, 1971), represented by *Clavagella*, are a specialization from this primitive infaunal stock with an appropriate decrease in the pedal gape and greater reliance upon the siphons for the exchange of mantle fluids and the collection of potential food. The genus *Clavagella* is, according to Keen & Smith (1969), older than *Brechites*, the former arising in the Upper Cretaceous, the latter in the Upper Oligocene. However, the thin shells of the latter may not fossilize easily.

The cemented habit has arisen independently in other anomalodesmatan families, notably the Cleidothaeridae and Myochamidae (Morton, 1974, 1977) and in the case of the latter (*Myochama*) it is also assumed that this has been from an infaunal ancestor (*Myadora*) (Yonge & Morton, 1980). In all cases, the evolution of the cemented habit in the Anomalodesmata is a relatively recent (Caenozoic) phenomenon.

Origin of the Pandoracea

The Pandoracea (as here redefined) arose in the Caenozoic and though none possess an external ligament, species of *Lyonsia* possess an opisthodetic ligament, with a ventral lithodesma, that Yonge & Morton (1980) regard as primitive (to the Pandoracea).

In these bivalves there is a strong trend towards valve inequality and the colonisation of hard intertidal surfaces by means of byssal

attachment in the Lyonsiidae and cementation in the Myochamidae and Cleidothaeridae.

Clearly, in the Pandoracea, there has been adaptive radiation from a wide, relatively modern stock to colonize widely diverse and extremely narrow niches in coastal and in-shore waters almost globally.

DISCUSSION

The extant Anomalodesmata are unusual bivalves. They are diverse in both form and habitat but a critical examination of them reveals first, basic, common underlying morphological characteristics and second that they occupy narrow, marginal niches. Nowhere, except possibly in the deep sea, the fauna of which is relatively sparse anyway (compared with the littoral zone), are they numerous. Each species is difficult to find. Clearly they are a group the representatives of which are highly specialized for life in highly specific niches. Thus the Lyonsiid *Guianadesma sinuosum* (Morrison, 1943) is only known from the Essequibo drainage of British Guiana; species of *Cleidothaerus* are only known from Australia and New Zealand (Morton, 1974); *Offadesma angasi* is similarly only recorded from these waters (Morton, 1981), though Rosewater (1968) has shown that the family Periplomatidae has an almost global distribution, whereas the Laternulidae is Indo-Pacific (Morton, 1976a).

There are relatively few extant anomalodesmatans each family often comprising but a few genera and each genus only a few species. There are, for example, probably only six species of the single genus *Laternula* (Laternulidae) (Morton, 1976a), but two species (probably one) of *Cleidothaerus* (the sole genus of the Cleidothaeridae) (Morton, 1974), and only some 30 species of the Periplomatidae comprising the genera *Periploma* and *Cochlodesma* (Rosewater, 1968) and one species of the Pholadomyidae (Morton, 1980a). Because of their extremely specialized habitats some probably await discovery but nevertheless they are by any standards rare. *Pholadomya candida* is probably one of the rarest molluscs, only two specimens ever having been found alive and then from surf beaches after storms (Morton, 1980a). For many species, the habitats are unknown.

Far, however, from being the remnants of a primitive stock, in many cases, e.g. the

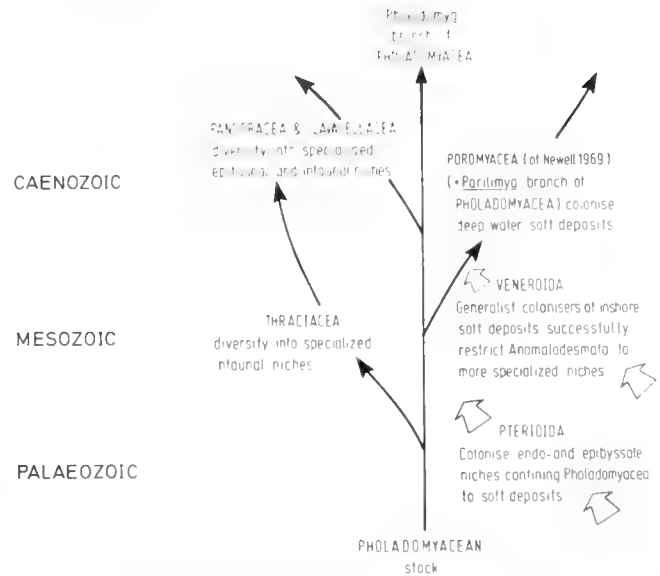


FIG. 18. The origin of the various extant superfamilies of the Anomalodesmata.

Clavagellacea, Poromyacea and Pandoracea, they are relatively modern bivalves. Some constant features of their anatomy, however, clearly link these modern bivalves to the ancient, stem superfamily Pholadomyacea, with its origins in the Palaeozoic. Thus, living representatives of the Anomalodesmata are like solitary pieces of a jigsaw which though having a character of their own, individually tell us little of their common ancestry. It is only when the jigsaw is constructed that a fuller picture can be obtained. Unfortunately, however, the great majority of the pieces are missing, because the Anomalodesmata have undergone phases of expansion and then massive retreat that makes the construction of a lineage or an adaptive strategy very difficult. An alternative analogy is with a tree, the outermost twigs representing extant species of anomalodesmatans. Many branches are missing, the pholadomyacean trunk is represented by only a few extant species and the root system is virtually absent. What is attempted here therefore, is, it is admitted, speculative.

The Pholadomyacea arose in the early Palaeozoic (Fig. 18) and radiated into soft sediments, becoming numerous and with the Trigoniacea constituting the dominant component of the late Paleozoic bivalve infauna (Stanley, 1972; Yonge & Morton, 1980). Such an assemblage, with these two groups dominant, survived until at least the Cretaceous (Hatai, Kotaka & Noda, 1969). At the same time, the Pterioida were coming to dominate the epifaunal niche, the neotenous retention

and subsequent wide use of a byssal apparatus by most representatives of this order having far reaching consequences. Even today, this ancient group has not been displaced from its dominant position on hard, marine surfaces. From the period of the late Palaeozoic, we can obtain links in an anomalodesmatan lineage that will take us to the present day, notably with regard to a fairly united group of families, the Thraciidae, Laternulidae and Periplomatidae that Yonge & Morton (1980) and Morton (1980b) have suggested (and which is now here formally proposed) should constitute a separate superfamily—the Thraciacea Stoliczka, 1870.

In many respects the extant species of *Thracia* are a link with a pholadomyacean stock, the external opisthodontic ligament being a primitive feature (Runnegar, 1974; Yonge & Morton, 1980). Also in *Thracia* we see the first signs of an arching of the antero-dorsal region of the shell over the postero-dorsal, though a transverse umbonal slit is not here developed. With a simple body plan, large separate siphons, large ctenidia, simple labial palps and a digging foot *Thracia* adequately prefigures the more specialized Periplomatidae and Laternulidae. In this line of evolution should also be included the extinct Burmesiidae (Morton, 1980a).

For most of the Anomalodesmata, however, the advent of the Mesozoic was a period of declining importance (though they are numerous in Jurassic and Cretaceous rocks), probably because of competition with the now expanding, generalist, order Veneroida. These relatively unspecialized bivalves came in the Mesozoic to dominate shallow water, soft substrates—and still do. Effectively the Pterioida and Veneroida have partitioned the shallow water domain. From the Cretaceous of India, Chiplonkar & Tapaswi (1976, 1977) have described fossil communities of veneroids, pterioids and pholadomyoids. Thus by the late Mesozoic, the Anomalodesmata were surviving in narrow, restricted habitats, but had also radiated into the deeper waters of the sea where during this period a lineage or more probably a number of lineages of bivalves arose all adapted to feeding either on the rain of invertebrate carcasses falling from the surface waters above or, ultimately, upon living invertebrates, typically crustaceans that were captured with a raptorial inhalant siphon. These bivalves constitute the Poromyacea, in the widest definition of the term, but here now divided into the Poromyacea (Poromyidae), Verticordiacea (Verticordiidae) and Cuspi-

dariacea (Cuspidariidae). In this environment these bivalves have become relatively numerous. Knudsen (1979) has shown that in bathyal and abyssal depths, the Anomalodesmata, together with another ancient group, the Palaeotaxodonta, similarly largely excluded from the littoral zone and fringe, have become dominant. In inshore waters, however, the other members of the Anomalodesmata, excluding the septibranch superfamilies, occur as scattered descendants of a once populous group.

In the Caenozoic, however, the Anomalodesmata, represented mainly by the Clavagellacea and the Pandoracea have undergone a further, narrower, phase of expansion. In this period they have diversified from their ancestral mode of life and produced families which are for example byssally attached (e.g. the Lyonsiidae) and even families which are cemented, e.g. the Clavagellidae, Cleidothaeridae and Myochamidae. Conveniently some representatives of the Clavagellidae and the Myochamidae are uncemented, infaunal species, that permit comparison with their cemented colleagues, allowing us to understand more easily this phase of adaptive radiation. In highly specialized niches these bivalves too enjoy a measure of success.

The Anomalodesmata are characterized by a number of very important features. Possibly the most significant of these is concerned with reproduction. With the possible exception of the Cuspidariidae, which are dioecious (Bernard, 1979), all anomalodesmatans are simultaneous hermaphrodites. It has also been shown for the Pandoridae (Allen, 1961a), Periplomatidae (Morton, 1980b), and for *Pholadomya candida* and the deep water members of the Poromyacea (Morton, 1980a; Knudsen, 1979) that large, telolecithal eggs are produced which are often encapsulated. The precise reason for this is unknown but can be interpreted in two ways (Morton, 1980a). Possibly the large amounts of yolk provide nourishment for the developing embryo over a long period of time while it is also protected and possibly made buoyant by the capsule. Spermatozoa may be embedded in the capsule, to fertilize the egg later, possibly after a period of dormancy in the plankton. These would be adaptations for a long pelagic larval stage. Alternatively, fertilization may occur within the common urinogenital cloaca typical of many of these bivalves or the supra-branchial chamber and development of a large larva, requiring large amounts of yolk may be rapid but also taking place within the

protective confines of the capsule. Allen (1961a) has shown that development is extremely rapid in *Pandora inaequalis* and is completed within four days, the veliger spending less than one day in the plankton. Allen considers this an adaptation to *limiting* the spread of juveniles so that the species rapidly recolonizes the parental habitat before the larvae can be washed away. This of course is opposite to the vast majority of the Pterioidea and Veneroidea where oligolecithal eggs are released for colonization of new habitats further afield. A notable exception to this role in the Veneroidea are members of the Leptonacea which produce large eggs—but they too occupy extremely specialized niches and as with the Anomalodesmata are monoecious, though typically protandrous consecutive hermaphrodites (Morton, 1980b). Large eggs are also characteristic of bathyal bivalves (Knudsen, 1979) and most anomalodesmatans from this habitat have either a very short, non-feeding larval stage or no pelagic stage at all. Thus, hermaphroditism and rapid development, in all species, is an essential requisite for their successful occupation of their narrow niches. To the contrary, however, such characteristics are completely the opposite of those possessed by the generalist Pterioidea and Veneroidea and it is easy to see how the Anomalodesmata have consistently failed in competition for broader habitats.

The shell of anomalodesmatans is relatively uniform, generally comprising a prismatic aragonite or being of a homogeneous nature (Taylor, Kennedy & Hall, 1973). Only with regard to the ligament, however, are there significant differences between the superfamilies.

The primitive condition is represented by the Pholadomyacea, with an external primary ligament. This is retained in *Thracia* (Thraciacea), with the addition of an anterior lithodesma, and members of the Clavagellacea and Poromyacea of the more modern lineages and provides compelling evidence of the manner in which the Anomalodesmata have diversified from a pholadomyoid stock. Thus, the presence of an external ligament in the Clavagellacea lends support to the notion that this group arose from a pholadomyid stock which have evolved (like *P. candida*) pedal feeding. Similarly it is possible to suggest a link between the pholadomyacean *Parilimya* and the Poromyacea because of similar features and the common presence of an external ligament. Finally, *Thracia* may

well be a link between the Pholadomyacea and the more specialized Periplomatidae and Laternulidae and, again, the presence of an external ligament supports this. In the other superfamilies the ligament sinks to become internal (a possibly intermediate condition is seen in the Ceratomyacea with a bilaterally asymmetrical ligament (Runnegar, 1974)). Thus in the Lyonsiidae, probably representing a more primitive condition (Yonge & Morton, 1980), the ligament is opisthodontic, with the development ventrally of a lithodesma, by calcification of a central strip of the inner ligament layer. The lithodesma serves to make an otherwise inefficient ligament more effective as explained by Yonge & Morton (1980). Variations on this theme characterize the remainder of the Pandoracea, Verticordiacea and the Cuspidariacea—the most modern anomalodesmatan lineages.

In the Thraciacea the ligament is located in a dorso-ventral plane and the lithodesma, where present, is anterior and the antero-dorsal edge of the shell arches over the postero-dorsal. The transverse crack in the shell, characteristic of the Periplomatidae and Laternulidae, but not obvious in the Thraciidae, facilitates an unusual method of valve adduction, at least in the Laternulidae (Morton, 1976a), to effect an exchange of water between the mantle cavity and the sea.

A lithodesma is not present in all representatives of families which characteristically possess one, being absent in, for example, *Guianadesma* in the Lyonsiidae (Morrison, 1943), in *Offadesma* in the Periplomatidae (Morton, 1981) and in different species of the single genus *Laternula* comprising the Laternulidae (Morton, 1976a). It is thus not a prerequisite for any functional mode of operation of the shell but probably rather improves upon an established design. A lithodesma is also not absolutely characteristic of the Anomalodesmata; one is found in *Montacutona compacta* (Leptonacea) (Morton, 1980b). Nevertheless a ligamental lithodesma is a recurring, though inconsistent, feature of the living Anomalodesmata.

In most species, mantle fusion is of folds additional to the inner, so that the margins and the siphons tend to be thick and often covered in periostracum. Radial mantle glands are found in representatives of the Lyonsiidae (Prezant, 1979), Verticordiidae (Allen & Turner, 1974), Periplomatidae (Morton, 1981) and in *Parilimya fragilis* (Morton, in prep.). They produce a glue which sticks sand grains to the periostracum though

the significance of this is not understood. Often the mantle margin possesses a fourth pallial aperture. Such an aperture also occurs in members of the Solenidae and Mactridae where it acts as a pressure release "valve" in these fast burrowing bivalves (Yonge, 1948). In *Pholadomya candida* a similar function was envisaged but here as a mechanical "valve" to prevent damage either to the thin shell or to the various organ systems of the body (Morton, 1980a) during pedal feeding, when powerful pressures are built up in the mantle cavity. Where it occurs in other anomalodesmatans, e.g. the Thraciidae (Allen, 1954), Lyonsiidae (Yonge, 1952; Narchi, 1968), Myochamidae and Cleidothaeridae (Morton, 1974, 1977), its function, because of so contrasting life styles, is less obvious. In yet other anomalodesmatans, e.g. the Pandoridae, Periplomatidae (Allen, 1954, 1958) and Laternulidae (Morton, 1973) it is absent.

With the exception of the Cuspidariidae and Poromyidae, gill structure and ciliation in the Anomalodesmata are remarkably constant. The ctenidia comprise a complete inner and a reduced outer demibranch composed of the descending lamella only. The labial palps and lips of the mouth are typically of the normal bivalve type though in the Pholadomyacea and the Poromyacea and Verticordiacea they are modified. In *Pholadomya candida*, the lips form two fused lateral pouches which prevent food being flushed out of them whereas in the latter two superfamilies and in *Parilimya* (Pholadomyacea) they are reduced, muscularized and have fewer sorting grooves—all adaptations to a macrophagous feeding style (Allen & Turner, 1974).

Another, unusually variable feature is the degree of association between the heart and the rectum. The rectum may pass beneath it, e.g. *Pholadomya* (Morton, 1980a), penetrate

it as in members of the Periplomatidae and Laternulidae (Allen, 1958; Morton, 1973) or pass above it, e.g. *Cleidothaerus* (Morton, 1974).

The stomach and the style sac seem uniform in structure and of Type IV (Purchon, 1958) except in *Cuspidaria*, *Poromya* (Purchon, 1956b) and *Parilimya* (Morton, in prep.) where there is a simplification of form associated with a macrophagous life style and the development of an extensive chitinous lining and a reduction in sorting areas. This is the stomach type II of Purchon (1956b). Bernard (1974) has investigated, in detail, features of the stomach of members of the Verticordiidae, Cuspidariidae and Poromyidae and shown them to be clearly differentiated into two groups. The Poromyidae and Cuspidariidae are very similar, possibly because of very similar feeding styles, whereas that of the Verticordiidae is much more like that of other eulamellibranchs with a small gastric shield and a well-developed food sorting caecum. Almost certainly *Parilimya* (Pholadomyacea) is a link in the evolution of the carnivorous habit in the Cuspidariidae, Poromyidae and some members of the Verticordiidae (Morton, in prep.)

The apparently random assignment of many of these characters to the various representatives of the Anomalodesmata makes it a difficult group to understand and clearly the picture of them and their ancestry is only going to clarify when each is studied individually.

SUMMARY

The subclass Anomalodesmata Dall, 1889 is judged to comprise one order Pholadomyoida Newell, 1965, seven extant superfamilies and 13 families as follows:

Pholadomyacea Gray, 1847

Thraciacea Stoliczka, 1870

Clavagellacea d'Orbigny, 1844

Pandoracea Rafinesque, 1815

Poromyacea Dall, 1886

Verticordiacea Stoliczka, 1871

Cuspidariacea Dall, 1886

Pholadomyidae Gray, 1847

Parilimyidae Morton, 1981

Thraciidae Stoliczka, 1870

Periplomatidae Dall, 1895

Laternulidae Hedley, 1918

Clavagellidae d'Orbigny, 1843

Lyonsiidae Fischer, 1887

Pandoridae Rafinesque, 1815

Myochamidae Bronn, 1862

Cleidothaeridae Hedley, 1918

Poromyidae Dall, 1886

Verticordiidae Stoliczka, 1871

Cuspidariidae Dall, 1886

The stem superfamily Pholadomyacea arose in the Palaeozoic and was largely confined to soft inshore sediments because the endo- and epibyssate modes of life were principally occupied by the Pterioidea. In this habitat they widely radiated producing a large number of taxa (Runnegar, 1974). One of these adaptive assemblages—the Thraciacea—still survive with the Thraciidae as the link with the Pholadomyacea. In the Mesozoic, however, the Pholadomyacea appear to have been largely displaced by the evolving heterodont Veneroidea, but they were ideally preadapted to survive in deep water, where they are now a major component composed of up to three lineages, the Verticordiacea, Cuspidariacea and Poromyacea, all of which have evolved from the Pholadomyacea possibly independently but from similar stocks that may find common origin in the pholadomycean *Parilimya* and its ancestors. Comparatively recently, in the Caenozoic, two further superfamilies have evolved—the Clavagellacea and Pandoracea—which have widely radiated into various shallow water niches, both groups producing cemented genera and the latter byssally attached genera for exploitation of specialized hard niches.

In general terms the representatives of the Anomalodesmata are characterized by a number of features, but probably the most significant of these is the occurrence in all (except the Cuspidariidae) of simultaneous hermaphroditism and a short, pelagic larval life. These are adaptations to colonization of narrow niches and adequately explain how the group has been unable to survive competition with the more generalist Pterioidea and Veneroidea which are typically dioecious producing large numbers of oligolecithal eggs and long-lived larvae that may be widely dispersed.

The evolution of the Thraciacea and Pandoracea from a primitive pholadomycean is fairly easily understood especially in the former superfamily where the Thraciidae form a clear link.

In the case of the hitherto unexplained Clavagellacea, however, a study of the rare pholadomycean *Pholadomya candida* has indicated that *Brechites* can be derived from a pholadomycean ancestor in which occurs an exchange of mantle fluids via the pedal gape. In the case of *Pholadomya* this is thought to be a feeding current; possibly this is also true of the Clavagellidae, but is uncertain.

Similarly, the evolution of the Poromyacea, Cuspidariacea and Verticordiacea can proceed from pholadomycean ancestors similar to the extant genus *Parilimya*, a study of one species of which has shown it to possess all the prerequisites essential for such a transition including features that will lead all lineages, convergently, into the scavenging and ultimately the carnivorous mode of life.

The Pholadomyacea were predisposed to the rapid movement of water into and out of the mantle cavity, by rapidly channelling blood into the haemocoel between the mantle epithelia. This is also seen in the Clavagellacea and the Poromyacea, Cuspidariacea and Verticordiacea; possibly enabling the unusual feeding methods thought typical of these groups.

The adaptive radiation in the Anomalodesmata must be seen as the evolution of a group, once widely successful, but surviving now in narrow, specialized niches and demonstrating a wide diversity of adaptations, reflecting a long and varied history, and the extant superfamilies of which have arisen at various times.

ACKNOWLEDGEMENTS

I am grateful to Sir Maurice Yonge (University of Edinburgh) and Dr. Bruce Runnegar (University of New England, Armidale, Australia) for their critical reading of the first draft of the manuscript of this paper.

REFERENCES CITED

- ADAL, M. N. & MORTON, B. S., 1973, The fine structure of the pallial eyes of *Laternula truncata* (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Zoology*, 171: 533–556.
- ALLEN, J. A., 1954, On the structure and adaptations of *Pandora inaequalvis* and *P. pinna*. *Quarterly Journal of Microscopical Science*, 95: 473–482.
- ALLEN, J. A., 1958, Observations on *Cochlodesma praetenu* (Pulteney) (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom*, 37: 97–102.
- ALLEN, J. A., 1960, The ligament of *Cochlodesma praetenu* (Pulteney). *Journal of the Marine Biological Association of the United Kingdom*, 39: 445–447.
- ALLEN, J. A., 1961a, The development of *Pandora inaequalvis* (Linné). *Journal of Embryology and Experimental Morphology*, 9: 252–268.
- ALLEN, J. A., 1961b, The British species of *Thracia*

- (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom*, 41: 723–735.
- ALLEN, J. A. & MORGAN, R., in press, The functional morphology of the families Cuspidariidae and Poromyidae (Mollusca: Bivalvia) and an analysis of the evolution of the septibranch condition. *Philosophical Transactions of the Royal Society of London*, ser. B.
- ALLEN, J. A. & TURNER, J. F., 1974, On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. *Philosophical Transactions of the Royal Society of London*, ser. B, 268: 401–536.
- ALLEN, M. F. & ALLEN, J. A., 1955, On the habits of *Pandora inaequalis* (Linné). *Proceedings of the Malacological Society of London*, 31: 175–185.
- ANSELL, A. D., 1967, Burrowing in *Lyonsia norvegica* Gmelin (Bivalvia: Lyonsiidae). *Proceedings of the Malacological Society of London*, 37: 387–393.
- BERNARD, F. R., 1974, Septibranchs of the Eastern Pacific (Bivalvia: Anomalodesmata). *Allan Hancock Monographs in Marine Biology*, 8: 1–279.
- BERNARD, F. R., 1979, New species of *Cuspidaria* from the Northeastern Pacific (Bivalvia: Anomalodesmata) with a proposed classification of Septibranchs. *Venus*, 38: 14–24.
- BOSS, K. J., 1978, Taxonomic concepts and superfluity in bivalve nomenclature. *Philosophical Transactions of the Royal Society of London*, ser. B, 284: 417–424.
- BOSS, K. J. & MERRILL, A. S., 1965, The family Pandoridae in the Western Atlantic. *Johnsonia*, 4: 181–215.
- BURNE, R. H., 1920, Mollusca. IV. Anatomy of Pelecypoda. *British Antarctic ("Terra Nova") Expedition 1910. Natural History Report, Zoology*, 2: 233–256.
- CHIPLONKAR, G. W. & TAPASWI, P. M., 1976, On some Veneroids and Pholadomyoids from the upper Cretaceous of Trichinopoly District, South India. *Biovigyanam*, 2: 151–160.
- CHIPLONKAR, G. W. & TAPASWI, P. M., 1977, Comments on some pteroids (excluding Inoceramids and Ostreids), Veneroids and Pholadomyids from the upper Cretaceous of Trichinopoly District, South India. *Journal of the University of Poona, Science and Technology*, 50: 199–208.
- DALL, W. H., 1890, Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Scientific results of explorations by the U.S. Fish Commission Steamer *Albatross*. No. VII. *Proceedings of the United States National Museum*, 12: 219–326.
- DALL, W. H., 1895, Scientific results of explorations by the U.S. Fish Commission steamer *Albatross*. No. 34. Report on Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian islands with illustrations of hitherto unfigured species from northwest America. *Proceedings of the United States National Museum*, 17: 675–733 pl. 23–32.
- GROBBEN, C., 1892, Beiträge zur Kenntniss des Baues von *Cuspidaria (Neaera) cuspidata* Olivi. *Zoologisches Institut Wien Arbeiten*, 10: 101–146.
- HATAI, K., KOTAKA, T. & NODA, H., 1969, Some marine Mollusca from Shimanokoshi harbor in Tanohata-cho, Shimohei-gun, Iwata prefecture, Northeast Honshu, Japan. *Saito Ho-On Kai Museum Research Bulletin*, 38: 29–36.
- KEEN, M. & SMITH, L. A., 1969, Superfamily Clavagellacea d'Orbigny, 1844. p. N857–859. In MOORE, R. C. (ed.) *Treatise on Invertebrate Paleontology*, Part N, Vol. 2 (of 3) Mollusca 6, Bivalvia. Geological Society of America, and University of Kansas Press.
- KNUDSEN, J., 1979, Deep-sea bivalves. In SPOEL, S.v.d., BRUGGEN, A.c.v. & LEVER, J. (eds.) *Pathways in Malacology*, Utrecht, 295 p.
- LACAZE-DUTHIERS, H. DE, 1870, Sur l'organisation de l'Arrosoir, *Aspergillum javanicum*. *Comptes Rendus . . . Académie des Sciences, Paris*, 70: 268–271.
- MORGAN, R. E. & ALLEN, J. E., 1976, On the functional morphology and adaptations of *Entodesma saxicola* (Bivalvia: Anomalodesmata). *Malacologia*, 15: 233–240.
- MORRISON, J. P. E., 1943, A new type of freshwater clam from British Guiana. *Nautilus*, 57: 46–52.
- MORTON, B. S., 1973, The biology and functional morphology of *Laternula truncata* (Lamarck 1818) (Bivalvia: Anomalodesmata: Pandoracea). *Biological Bulletin*, 145: 509–531.
- MORTON, B. S., 1974, Some aspects of the biology and functional morphology of *Cleidotherus maorianus* Finlay (Bivalvia: Anomalodesmata: Pandoracea). *Proceedings of the Malacological Society of London*, 41: 201–222.
- MORTON, B. S., 1976a, The structure, mode of operation and variation in form of the shell of the Laternulidae (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies*, 42: 261–278.
- MORTON, B. S., 1976b, The biology and functional morphology of the S.E. Asian mangrove bivalve *Polymosoda (Geloina) erosa* (Solander 1786) (Bivalvia: Corbiculidae). *Canadian Journal of Zoology*, 54: 482–500.
- MORTON, B. S., 1977, The biology and functional morphology of *Myadora striata* Quoy and Gaimard (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies*, 43: 141–154.
- MORTON, B. S., 1979, A comparison of lip structure and function correlated with other aspects of the functional morphology of *Lima lima*, *Limaria (Platylimaria) fragilis*, and *Limaria (Platylimaria) hongkongensis* sp. nov. (Bivalvia: Limacea). *Canadian Journal of Zoology*, 57: 728–742.
- MORTON, B. S., 1980a, The anatomy of the "living fossil" *Pholadomya candida* Sowerby 1823

- (Bivalvia: Anomalodesmata: Pholadomyacea). *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening*, 142: 7–102.
- MORTON, B. S., 1980b, Some aspects of the biology and functional morphology (including the presence of a ligamental lithodesma) of *Montacutona compacta* and *M. olivacea* (Bivalvia: Leptonacea) associated with coelenterates in Hong Kong. *Journal of Zoology*, 192: 431–455.
- MORTON, B. S., 1981, The biology and functional morphology of *Periploma (Offadesma) angasai* [Sic]. (Bivalvia: Anomalodesmata: Periplomatidae). *Journal of Zoology*, 193: 39–70.
- MORTON, B. S., in prep. The functional morphology of *Parilimyia fragilis* (Grieg 1920) (Bivalvia: Parilimyidae nov. fam.) with a discussion on the origin and evolution of the carnivorous septibranchs and a reclassification of the Anomalodesmata.
- NAKAZIMA, M., 1967, Some observations on the soft parts of *Halicardia nipponensis* Okutani. *Venus*, 25: 147–158.
- NARCHI, W., 1968, The functional morphology of *Lyonsia californica* Conrad, 1837. *Veliger*, 10: 305–313.
- NEWELL, N. D., 1965, Classification of the Bivalvia. *American Museum Novitates*, 2206: 1–25.
- NEWELL, N. D., 1969, Classification of Bivalvia, p. N205–N224. In MOORE, R. C. (ed.) *Treatise on Invertebrate Paleontology*, Part N, Vol. 1, Mollusca 6, Bivalvia. Geological Society of America and University of Kansas Press.
- OWEN, R., 1835, On the anatomy of *Clavagella*, Lam. *Transactions of the Zoological Society of London*, 1: 269–274.
- PELSENEER, P., 1888a, Report on the anatomy of the deep-sea Mollusca collected by H.M.S. Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger . . .*, Zoology, 27: 8–40.
- PELSENEER, P., 1888b, Les pélecypodes (ou lamellibranches) sans branchies. *Comptes Rendus . . . Académie des Sciences*, Paris, 106: 1029–1031.
- PELSENEER, P., 1891, Contribution à l'étude des lamellibranches. *Archives de Biologie*, 11: 147–312.
- PELSENEER, P., 1911, Les lamellibranches de l'expédition du Siboga. Partie Anatomique. *Siboga Expeditie Monogr.* 53a, 125 p., 26 pl.
- PLATE, L., 1897, Giebt es septibranchiate Muscheln? *Gesellschaft naturforschender Freunde, Berlin, Sitzungsberichte*, 1897: 24–28.
- PREZANT, R. S., 1979, The structure and function of the radial mantle glands of *Lyonsia hyalina* (Bivalvia: Anomalodesmata). *Journal of Zoology*, 187: 505–516.
- PURCHON, R. D., 1956a, A note on the biology of *Brechites penis* (L.). Lamellibranchia. *Journal of the Linnean Society of London, Zoology*, 43: 43–54.
- PURCHON, R. D., 1956b, The stomach in the Protobranchia and Septibranchia (Lamellibranchia). *Proceedings of the Zoological Society of London*, 127: 511–525.
- PURCHON, R. D., 1958, The stomach in the Eulamellibranchia; Stomach Type IV. *Proceedings of the Zoological Society of London*, 131: 487–523.
- PURCHON, R. D., 1960, A further note on the biology of *Brechites penis* (L.). Lamellibranchia. *Proceedings of the Malacological Society of London*, 34: 19–23.
- REID, R. G. B., 1978, Gastric protein digestion in the carnivorous septibranch *Cardiomya planetica* Dall; with comparative notes on deposit and suspension feeding bivalves. *Comparative Biochemistry and Physiology*, 56A: 47–58.
- REID, R. G. B. & CROSBY, S. P., 1980, The raptorial siphonal apparatus of the carnivorous septibranch *Cardiomya planetica* Dall (Mollusca: Bivalvia), with notes on feeding and digestion. *Canadian Journal of Zoology*, 58: 670–679.
- REID, R. G. B. & REID, A. M., 1974, The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). *Sarsia*, 56: 47–56.
- RIDEWOOD, W. G., 1903, On the structure of the gills of the Lamellibranchia. *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 147–284.
- ROSEWATER, J., 1968, Notes on Periplomatidae (Pelecypoda: Anomalodesmata), with a geographical checklist. *American Malacological Union Annual Reports*, 1968: 37–39.
- RUNNEGAR, B., 1974, Evolutionary history of the bivalve subclass Anomalodesmata. *Journal of Paleontology*, 48: 904–939.
- RUNNEGAR, B., 1979, *Pholadomya candida* Sowerby: the last cadaver unearthed. *Veliger*, 22: 171–172.
- SKELTON, P. W., 1976, Functional morphology of the Hippuritidae. *Lethaia*, 9: 83–100.
- SMITH, B. J., 1971, A revision of the family Clavagellidae (Pelecypoda, Mollusca) from Australia with descriptions of two new species. *Journal of the Malacological Society of Australia*, 2: 135–161.
- SMITH, B. J., 1978, Further notes on the Clavagellidae, with speculation on the process of tube growth. *Journal of the Malacological Society of Australia*, 4: 77–79.
- SOLIMAN, G. N., 1971, On a new clavagellid bivalve from the Red Sea. *Proceedings of the Malacological Society of London*, 39: 389–397.
- STANLEY, S. M., 1972, Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology*, 46: 165–212.
- TAYLOR, J. D., KENNEDY, W. J. & HALL, A., 1973, The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, Conclusions. *British Museum (Natural History) Bulletin, Zoology*, 22: 255–294. pl. 1–15.
- YONGE, C. M., 1928, Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Philosophi-*

- cal Transactions of the Royal Society of London*, ser. B, 216: 221–263.
- YONGE, C. M., 1937, The formation of siphonal openings by *Thracia pubescens*. *Proceedings of the Malacological Society of London*, 22: 337–338.
- YONGE, C. M., 1948, Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (da Costa) and *Lutraria lutraria* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 27: 585–596.
- YONGE, C. M., 1949, On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Philosophical Transactions of the Royal Society of London*, ser. B, 234: 29–76.
- YONGE, C. M., 1952, Studies of Pacific coast mollusks. 5. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttalli* Conrad, with a discussion on evolution within the Family Lyonsiidae (Eulamellibranchia). *University of California Publications in Zoology*, 55: 439–450.
- YONGE, C. M., 1967, Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the Rudists (Hippuritacea). *Philosophical Transactions of the Royal Society of London*, ser. B, 252: 49–105.
- YONGE, C. M., 1976, Primary and secondary ligaments with the lithodesma in the Lyonsiidae (Bivalvia: Pandoracea). *Journal of Molluscan Studies*, 42: 395–408.
- YONGE, C. M., 1978, Significance of the ligament in the classification of the Bivalvia. *Proceedings of the Royal Society of London*, ser. B, 202: 231–248.
- YONGE, C. M. & MORTON, B. S., 1980, Ligament and lithodesma in the Pandoracea and Poromyacea with a discussion on evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *Journal of Zoology*, 191: 263–292.

THE FUNCTIONAL MORPHOLOGY AND EVOLUTION OF RECENT LIMOPSIDAE (BIVALVIA, ARCOIDEA)

P. Graham Oliver

*Department of Zoology, National Museum of Wales, Cathays Park,
Cardiff CF1 3NP, United Kingdom*

ABSTRACT

The bivalve family Limopsidae is divided into thirteen morphological classes which have not previously been recognized. These classes are defined from both shell and anatomical features. Of the former the most relevant are the degree of anterior reduction, tumidity, periostracal bristles, hinge and ligament, and of the latter the pedal, byssal and gill axis musculature. One of the most significant morphological observations is the recognition of four ligament types within the family. The morphological classes are sorted into three major functional groups—Limopsiform, Glycymeriform and Abyssate Burrowing.

The Limopsiform group contains eight of the morphological classes; in general these are semi-infaunal with degrees of endobyssate and epibyssate attachments. There are three components: 1. Ploughing. Mobile crawlers through soft substrates or over hard substrates rarely employing a byssus. 2. Endobyssate. Less mobile, generally infaunal employing a multiple-stranded byssus. 3. Epibyssate. Epifaunal with a well-adapted byssus of multiple strap-like threads.

The Glycymeriform group contains two classes which show a marked convergence with the Glycymerididae and are poor shallow burrowers: 1. A ribbed sculptured class with a wide Recent distribution. 2. A finely decussate sculptured class with a restricted range in southeast Australia.

The Abyssate Burrowing group contains three classes which may not be closely related, yet do have an antipodean bias in their distribution. Two classes are limited to southeast Australia and contain small species with some affinities with the Glycymeriform group. These are argued to be poor burrowers in sands and gravels. The third class is endemic to Antarctica and is hypothesized to contain shallow burrowers living in muddy substrates.

The evolutionary history of the Limopsidae indicates an early Cretaceous semi-infaunal origin with rapid radiation into the Limopsiform classes by the late Cretaceous. There was little functional radiation within the Limopsiform group after the Cretaceous, but there must have been a subsequent parallel morphological radiation giving rise to those species with the more advanced ligament structure. An early offshoot of this semi-infaunal group was the Glycymeriform line which appeared in the middle Cretaceous. The Glycymeriform and the Abyssate Burrowing groups, excluding the Antarctic one, had a Mid-Cenozoic radiation in the antipodean provinces, but declined in the northern hemisphere. The Antarctic class is apparently recent in origin and, significantly, possess the most advanced ligament form.

The extent of the radiation is compared with that of other byssate and burrowing arcoids and, although it is considered to be relatively wide functionally, it is not so morphologically, nor are the species diversity and distribution comparable.

A preliminary analysis suggests that the growth and morphological features of the limopsid ligament prevented radiation into the anteriorly reduced byssate forms in all except the most minute species, and that the same ligament could also not be adapted to achieve enough strength to allow radiation into the burrowing habit. The family as a whole, therefore, remained semi-infaunal. However, semi-infaunal bivalves had already been largely excluded by advanced burrowing heterodonts and consequently the limopsids were restricted to environments where competition was less extreme, e.g. the deep sea.

INTRODUCTION

The Limopsidae are a small family of arcoid bivalves which because of their generally deep water distribution have received little attention. The affinities of the family are with the

Glycymerididae and Philobryidae, although the exact nature of the relationship is not agreed upon (Tevesz, 1977; Nicol, 1950).

The Limopsidae and Philobryidae are of considerable interest with regard to the adaptive radiation of the Arcoidea. They represent

the only extant forms which lack the typical chevron (duplivincular) ligament. They also possess compressed, rounded or oval shells which contrast markedly with the quadrate shells of the Arcacea. Thomas (1976) outlined the adaptive limitations of the duplivincular ligament, but it is apparent that in terms of species diversity, habitat range and geographical range the Limopsidae and Philobryidae are even more restricted.

By examining both the functional morphology and evolution of the oldest family, the Limopsidae, this paper aims to develop an hypothesis to explain at least in part why there are such restrictions.

MATERIALS AND METHODS

Previous studies on limopsids have on the whole not taken into account the variability of shell form which arises through ontogeny or ecological factors (Dell, 1964; Knudsen, 1967, 1970; Oliver & Allen, 1980b). This has led to the erection of an unnecessary number of species and genera. For this reason it is not possible to discuss morphology or radiation using current systematic groupings. Ninety percent of the known Recent species have been examined in this study. Of the fifty species, eighteen were obtained with intact soft parts. Observations based on them have been used to construct a revised classification. Due to nomenclatural problems, all species have been placed in *Limopsis sensu lato*. The diagnoses of these morphological classes are presented in the Appendix which provides notes on habitat, depth range, geographical range and species included in each class. Throughout the text the morphological classes are referred to numerically: M.C. I to M.C. XIII. Note that the figures are in two series: Figs. 1 to 12, and App.[endix] Figs. 1 to 27.

KEY TO ABBREVIATIONS OF INSTITUTIONS FROM WHICH FIGURED SPECIMENS WERE OBTAINED

AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University

MNHNP	Muséum National d'Histoire Naturelle, Paris
NM	Natal Museum, Pietermaritzburg
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
RSM	Royal Scottish Museum, Edinburgh
SAM	South Australian Museum, Adelaide
USNM	United States National Museum, Washington, D.C.

FUNCTIONAL MORPHOLOGY

Studies on the morphology of limopsids are very few. Pelseneer (1888) described the morphology of *Limopsis cancellata* (Reeve, 1843) and Burne (1920) did likewise with *L. marionensis* Smith (1885). Purchon (1957) and Dinamani (1967) described the anatomy of the stomach of *L. vaginata* Dall (1891) and *L. belcheri* (Adams & Reeve, 1850) respectively. Little functional interpretation, if any, was made in these studies. Jeffreys (1864) observed living *L. aurita* (Brocchi, 1814) and noted its ability to crawl on a smooth surface and to produce a byssus consisting of a single fine thread. Atkins (1951) noted that the ciliary currents are like those of *Glycymeris glycymeris* and *Arca tetragona* (Atkins, 1936).

Tevesz (1977) studied both the Philobryidae and Limopsidae, basing his conclusions primarily on observations made on two live Australian species, *Limopsis loringi* Angas (1873) and *L. soboles* (Iredale, 1931). Tevesz concluded that in general limopsids are convergent with the Glycymerididae, being poor shallow burrowers with an endobysate attachment. Tevesz, however, also noted that *L. antillensis* Dall (1881) is convergent with the philobryid genus *Cratis* and that philobryids are generally epibysate.

Oliver (1978) and Oliver & Allen (1980b) examined the functional morphology of the deep water Atlantic species with special reference to adaptations for this habitat. They noted a larger variety of habits than was suggested by Tevesz's study. Examination of live *L. aurita* showed that this species typically ploughs through the surface of soft sediments, remaining in a vertical position in muds but falling onto one valve in sands. It was also observed to crawl over gravels and was able to suspend itself by its byssus from larger stones or the sides of the aquarium. The large abyssal species *Limopsis tenella* Jeffreys (1876) (= *pelagica* Smith, 1885) was also suspected to be a ploughing form, but from the distribution

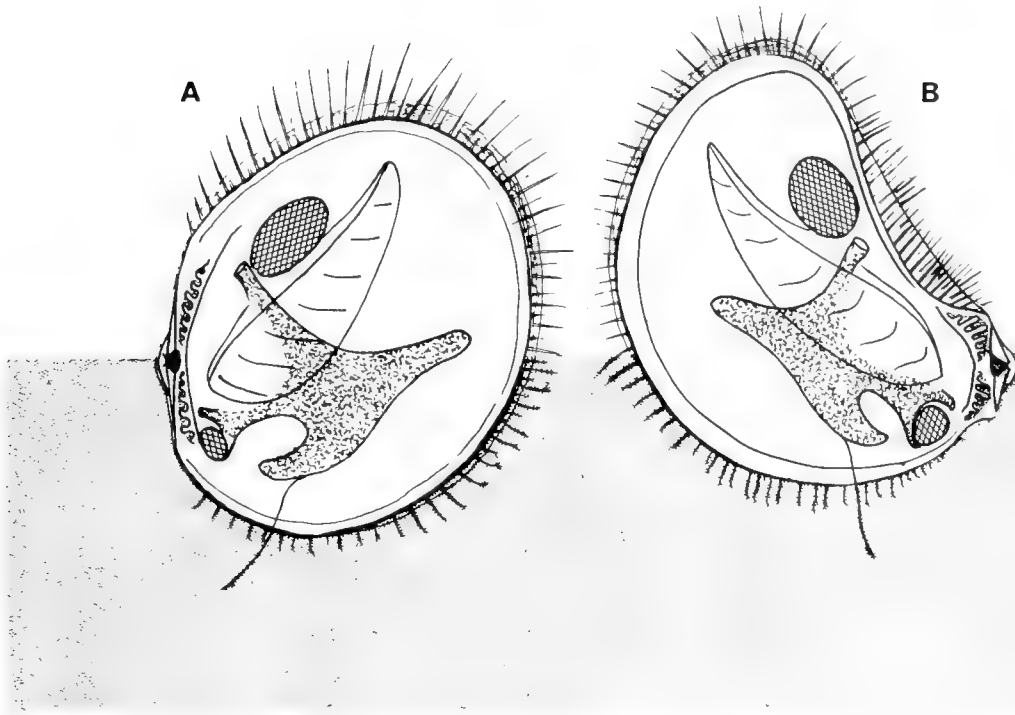


FIG. 1. Reconstructions of life positions. A. *Limopsis marionensis* (M.C. I). B. *L. vaginata* (M.C. III).

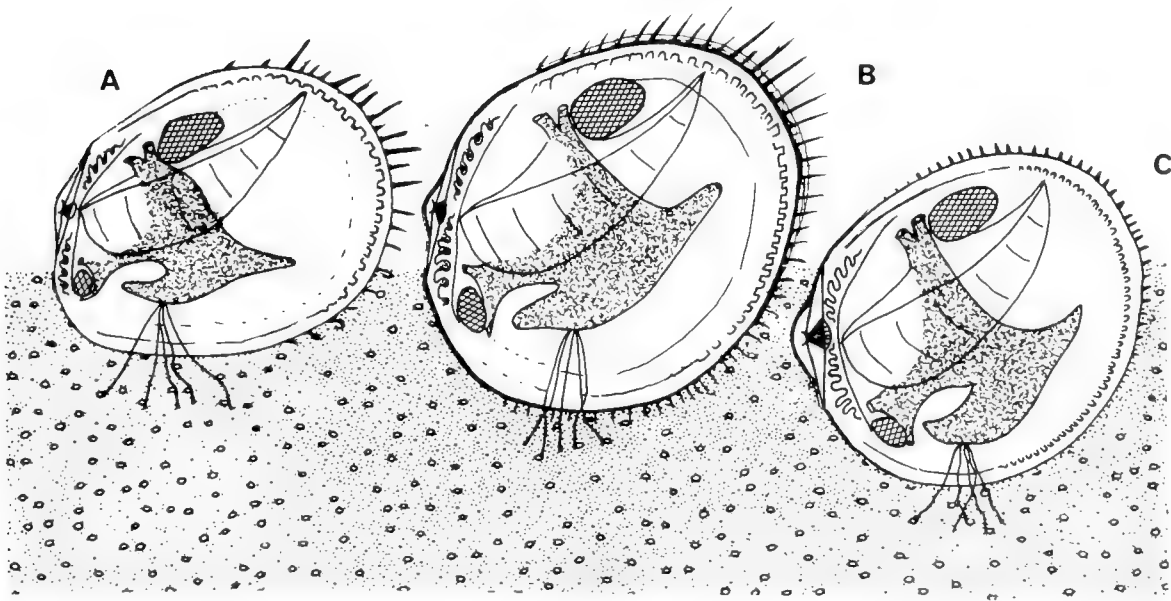


FIG. 2. Reconstructions of life positions of species in M.C. V. A. *Limopsis affinis*. B. *L. diegensis*. C. *L. oblonga*.

and size of some of the shell epifauna it was further concluded that much of its life must be spent lying on one valve. The byssus was rarely observed in *L. tenella*. A much smaller species, *L. cristata* Jeffreys (1876) (including *L. affinis* Verrill, 1885), was shown to be more infaunal, with a multiple, but finely threaded byssus. *L. minuta* (Philippi, 1836) was suspected to be, to a great extent, epibyssate.

The morphological variety exhibited in the thirteen classes is greater than any suggested

by previous studies. This variety is, however, expressed in relatively minor differences of shell and anatomical detail. Functionally significant shell characters are the outline, tumidity, anterior reduction, marginal crenulations and hinge strength. Anatomical characters of importance are the foot, byssus apparatus, gill axis musculature and mantle margin musculature. Using these characters it is possible to recognize three major groups containing morphological classes with a high degree of

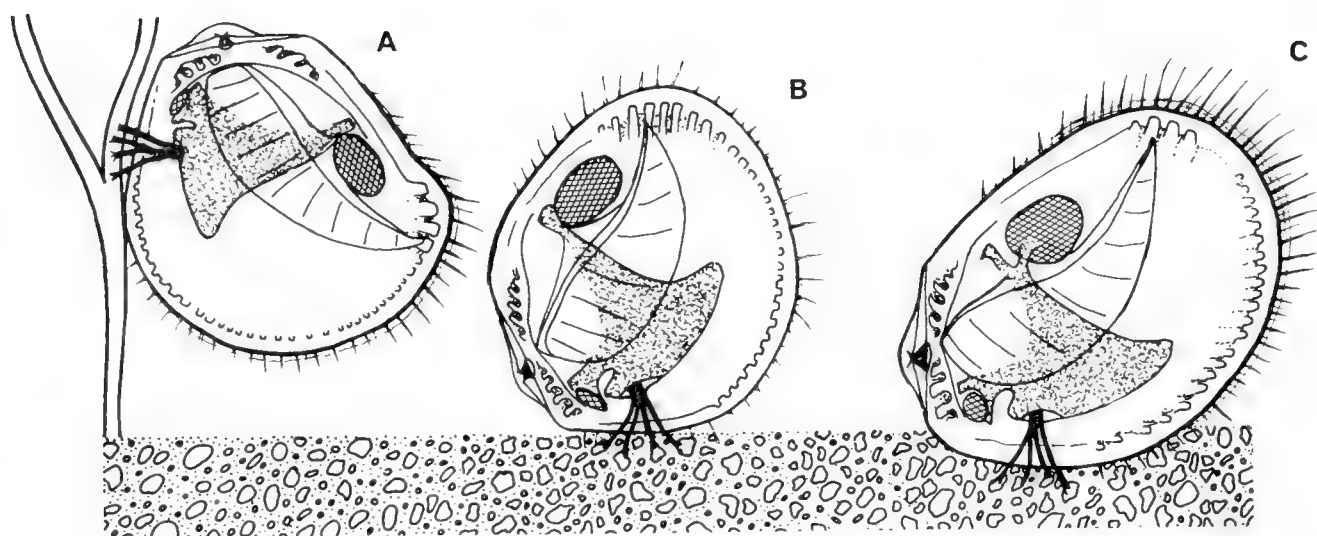


FIG. 3. Reconstructions of life positions. A. *Limopsis natalis* (M.C. VIII). B. *L. elachista* (M.C. VIII). C. *L. minuta* (M.C. VII).

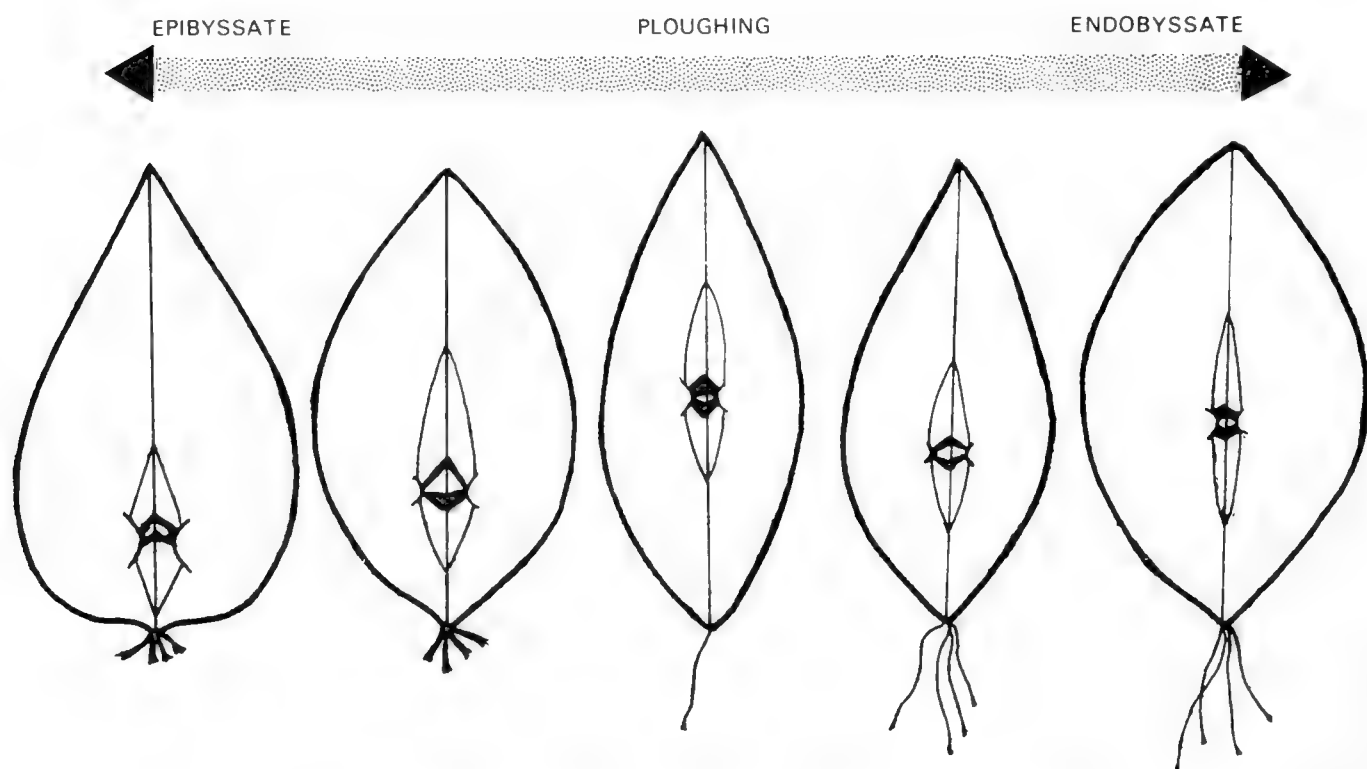


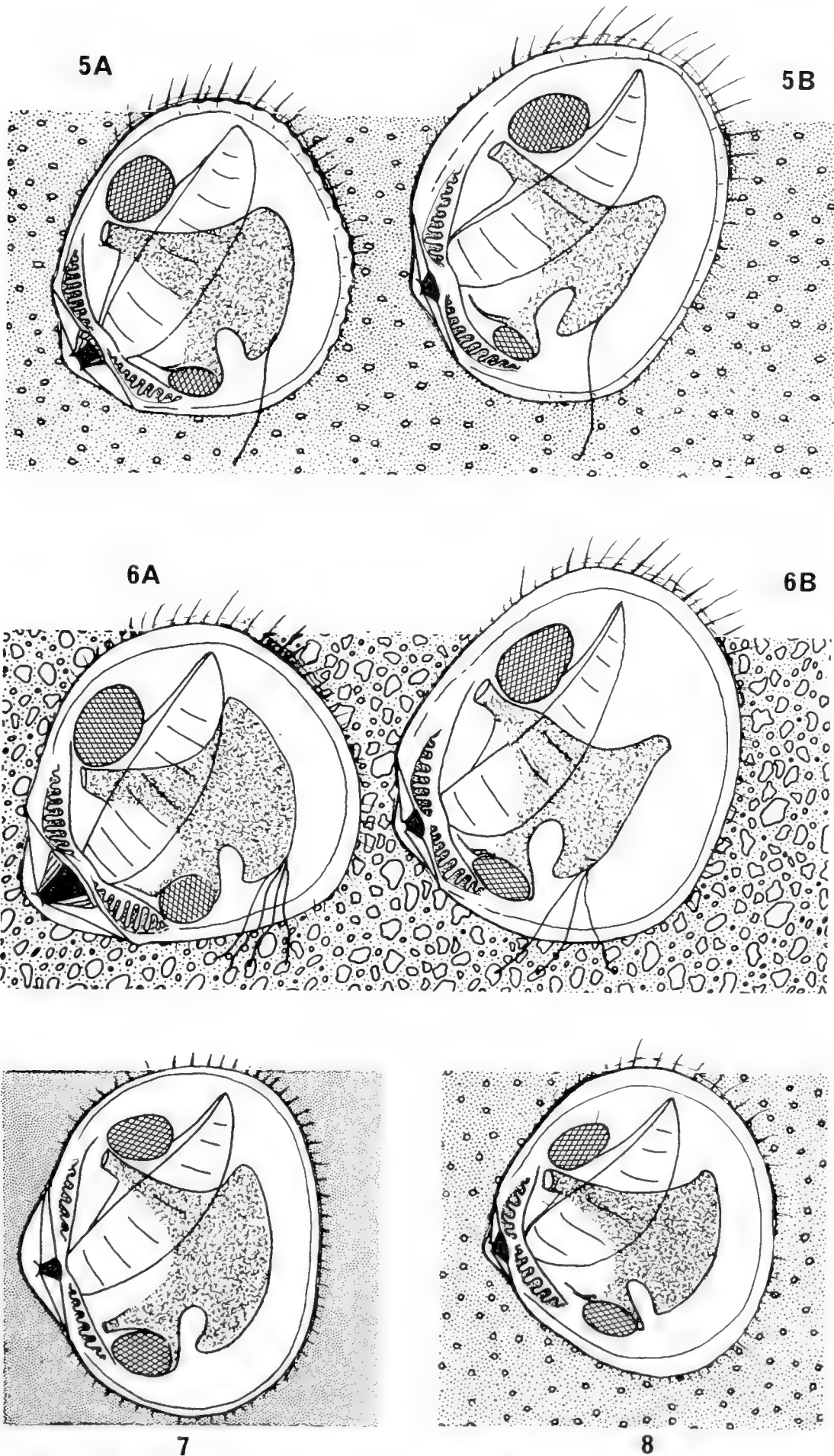
FIG. 4. Tumidity and anterior reduction in relation to limopoid habits.

functional similarity: 1. **Limopsiform.** (M.C. I–M.C. VII). Shell thin, strongly oblique, hinge weak, heteromyarian condition advanced. Foot with a long toe, byssus functional, gill axis muscular. 2. **Glycymeriform.** (M.C. IX–M.C. X). Shell thick, oblique, hinge strong, heteromyarian condition moderate. Foot blade-like, byssus functional, gill axis weakly muscular. 3. **Abyssate.** (M.C. XI–M.C. XIII). Subequilateral, almost elliptical, hinge moderate, almost isomyarian. Foot blade-like, byssus not functional in adult, gill axis feebly muscular.

Limopsiform group

Within the limopsiform classes there is a series of linked progressive character changes which indicate a range of life modes from 'ploughing' through endobyssate to epibyssate. This progression is linked to the strength and use of the byssus, involving related changes in pedal morphology and shell characters.

The ligaments found within the limopsiform group are of Types A, B and C (App. Fig. 1).



FIGS. 5–8. Reconstructions of life positions. Fig. 5. Glycymeriform. A. *Limopsis multistriata* (M.C. IX). B. *L. bassi* (M.C. IX). Fig. 6. Glycymeriform. A. *L. loringi* (M.C. X). B. *L. eucosmus* (M.C. IX). Fig. 7. Abyssate Burrowing *L. lilliei* (M.C. XIII). Fig. 8. Abyssate Burrowing *L. vixornata* (M.C. XI).

However, there is apparently no relation between the ligament type and habits. In ligament Types A and B there are both ploughing and epibyssate species and a similar range occurs in species with the Type C ligament. The detailed function of these ligaments requires evaluation, but for the present, without suitable material, little can be done.

Ploughing (M.C. I-M.C. IV): The behaviour of *Limopsis aurita* (M.C. IV) in soft sediments is typical of the ploughing mode (App. Fig. 12). Effectively, the behaviour is crawling, with depth of penetration depending on the resistance of the substrate. The long toe is capable of considerable extension and the animal is progressively pulled across or into the substrate, there being no stationary burrowing motions. The long sole created by the extension of the foot into the toe and heel gives a stable crawling base. Conversely, this foot form is not adapted for efficient burrowing. The heteromyarian condition, weak hinge and weak ligament, are also indicative of a non-burrowing habit. The compressed shell acts as

a blade and aids substrate penetration, but if this is not achieved the animal is unstable in an upright position. The byssus, although weak, is frequently employed in *L. aurita* and gives some anchoring effect. The byssus activity is reflected in the presence of a small byssus

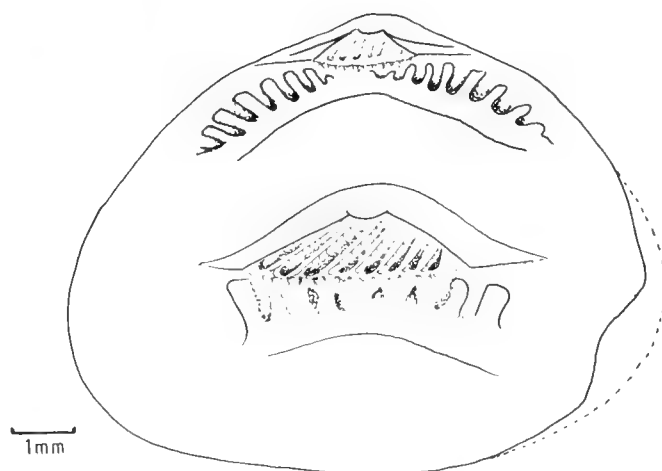


FIG. 9. *Limopsis minima* Sow. (= *oolithica* Buvignier) with ligament area enlarged to show remains of obliquely grooved ligament.

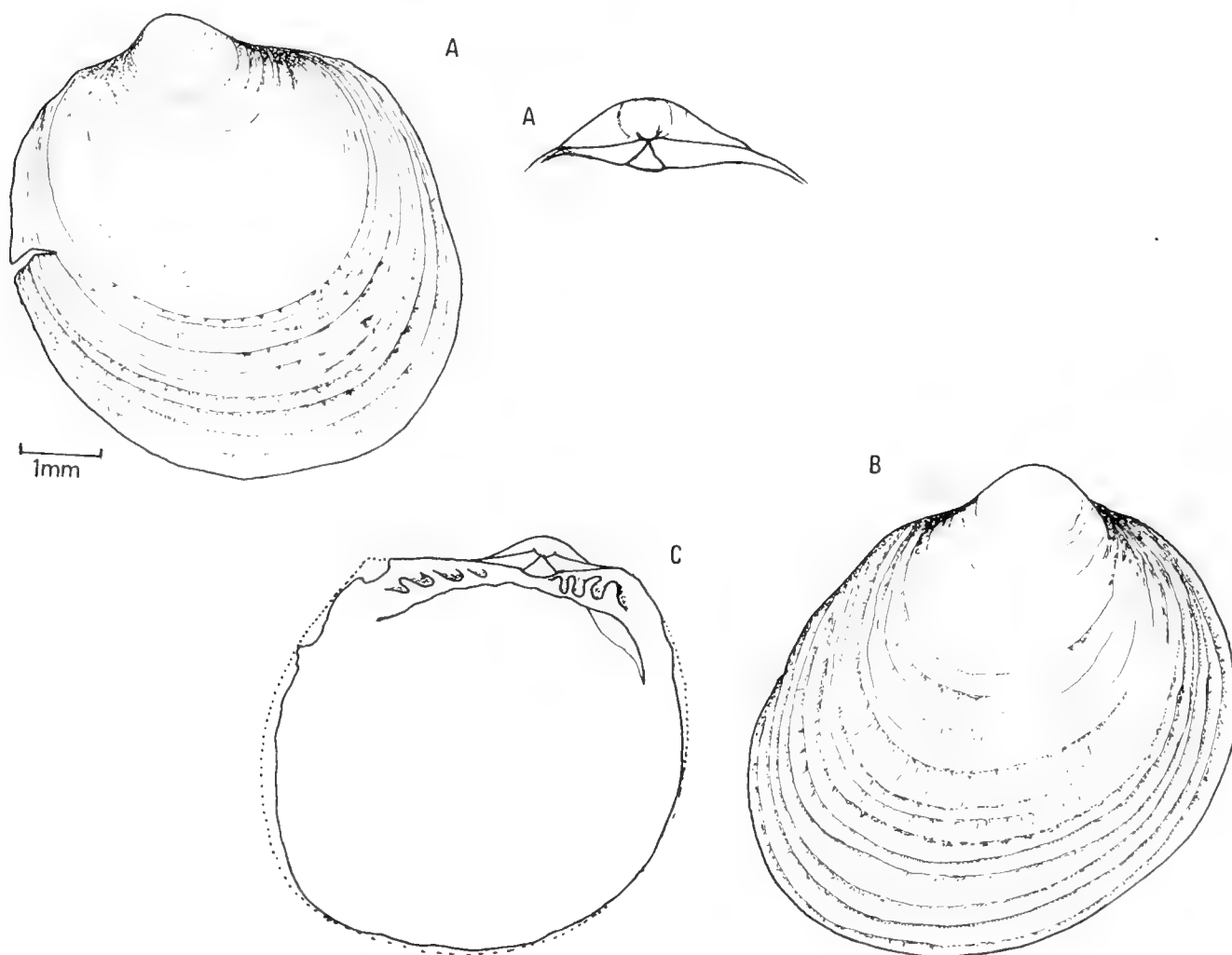
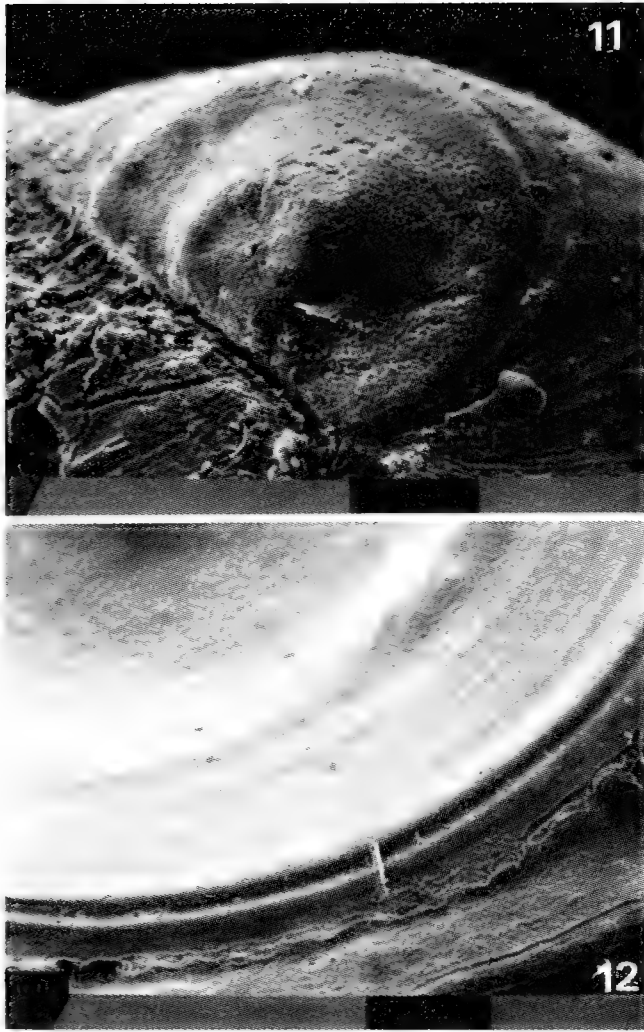


FIG. 10. Some early Cretaceous limopsids. A. *Limopsis albiensis* Woods. B. *L. coemansi* Briart & Cornet. C. *L. hoeninghausii* Müller.



FIGS. 11–12. *Nipponolimopsis decussata* (A. Adams). Capped prodissoconch (Fig. 11) and marginal locking groove (Fig. 12).

retractor element in the posterior pedal retractor (App. Fig. 11). A consequence of this variability in substrate penetration is the inconsistent positioning and size of the inhalant aperture. Oliver & Allen (1980b) observed that frequently the whole limit of the shell gape was open. This led to considerable amounts of unwanted matter entering the mantle cavity and this was frequently expelled by gill contraction and valve clapping. This behaviour explains the large amounts of axis muscle in *L. aurita* (App. Fig. 11). In soft sediments the gape was reduced and the mantle cavity was protected by interlocking edges of the periostracal interlocking edges of the periostracal bristles.

This apparently generalised form provides a good interpretive base. *Limopsis marionensis* (App. Fig. 2 and 5; M.C. I) is a considerably larger species, is more compressed and the anterior margin is more rounded. The two latter features further aid substrate penetration and stabilisation respectively. The posterior pedal retractor has no separate byssus element and

the rare occurrence of the byssus thread suggests that the ploughing habit is employed and is probably more efficient than in *L. aurita* (M.C. IV). Observations on another species (*L. tenella*) showed that the umbonal and posterior portions were most heavily infested, again adding to the premise that M.C. I species are semi-infaunal (Oliver & Allen, 1980b). M.C. I species are almost exclusively found in soft sediments where endobysate anchoring is least necessary. *L. marionensis* has been recorded from coarser substrates and here this species must be surface-living. In all substrates it is expected that frequent dislodgment will occur and that surface positions will not be uncommon.

In all characteristics other than the inner serrated margin and ligament, the species of M.C. II (App. Fig. 3) are identical morphologically to M.C. I and are also presumed to be ploughers. The serrated margin is a weak form of marginal crenulation which more commonly occurs in the endobysate and epibysate species.

The presence of the cleft in *Limopsis vaginata* and *L. cumingi* A. Adams (1862) (App. Fig. 4; M.C. III) is no doubt of some functional significance, but without direct observations it remains obscure. The ontogenetic development of the cleft (App. Fig. 7) clearly shows that it is analogous to the small indentations seen at either end of the dorsal area in many typical species. It is, therefore, tempting to associate the cleft with the hinge mechanics. In *L. vaginata* the hinge plate, because of its restriction to a shorter area, is more arched and probably stronger. The advantage of this in an otherwise ploughing form is obscure. Another consequence of the cleft is the spouting or projecting of the postero-ventral margin. Fig. 1 shows *L. vaginata* and a typical M.C. I form orientated along the same axis. In *L. vaginata* the major inhalant area is raised higher in the water column. This spouting effect may help to cut down the amount of substrate derived matter entering the mantle cavity.

Endobysate forms (M.C. V–M.C. VI): A more sedentary infaunal habit is evidenced in some of the smaller limopsiform species by the presence of a multiple, long, fine-stranded byssus and a separate byssus element (App. Fig. 13) in the posterior pedal retractor. The byssus threads have no terminal disc and have small sediment particles attached along their length. This strong evidence of endobysate attachment is substantiated by other features. The periostracal bristles are gener-

ally spicate (App. Fig. 9) and act in a manner similar to shell spines, i.e. as a stabilising mechanism. This type of periostracum no longer acts as a protective grid and the mantle margins in some species are more muscular, indicating their ability to form discrete inhalant and exhalant apertures.

The outline and relative tumidity are somewhat variable and this gives a variety of orientations to the endobyssate species (Fig. 2). The majority are relatively compressed and have a tendency towards a straight anterior margin, e.g. *Limopsis cristata* and *L. affinis*. In *L. affinis* this development reaches its extreme, giving a pseudo-modioliform appearance. The orientation of this form is probably sub-surface with the greater part of the shell not buried. Shell epifauna data from Oliver & Allen (1980b) support this conjecture.

In the more rounded forms which in some, e.g. *L. oblonga* A. Adams, 1860 (App. Fig. 14), are relatively tumid, a deeper position is hypothesized. The rounded, less oblique outline is consistent with the burrowing species and the true ploughing forms. In muds, which are the most common habitat for these species, penetration would not be difficult. In fact, the tumidity may be a stabilising influence preventing the animal from becoming buried beyond the postero-ventral margin. *L. galathea* Knudsen, 1970 (M.C. VI) represents the extreme of this fixed infaunal habit (Oliver & Allen 1980b), the reduced heteromyarian condition, stubby periostracum and relative tumidity are indicators of this. *L. galathea* lives in soft abyssal oozes where overpenetration is very likely.

The larger compressed species *Limopsis diegensis* Dall, 1908 (App. Fig. 10) with its thatched periostracum outwardly resembles a ploughing form; anatomically it is endobyssate. This intermediate character probably reflects a more active habit as a plougher. Ploughing activity by the endobyssate forms is probably common as all species possess a long-soled foot. Physical and biological disturbance is probably a frequent occurrence and the ability to crawl away and re-establish itself would be advantageous.

In all the endobyssate forms the inner margin is evenly crenulated by raised ridges or nodules. In these small species this character is regarded as a counteracting mechanism to the weak hinge and ligament. It is presumed to prevent shearing of the valves which may be caused by physical or biological disturbance.

Epibyssate forms (M.C. VII–M.C. VIII; Fig. 3): The epibyssate mode is evidenced in the limopsiform group through the strength of the byssus and the classically associated shell characteristics of tumidity and anterior reduction (Stanley, 1972) (Fig. 4). The byssus consists of three to six short strap-like strands attached to a basal sheath. They have divided ends with no terminal discs, but have been observed firmly attached to particles of gravel. In M.C. VIII (App. Fig. 16), the outline of the shell is quadrate with a marked antero-dorsal straight margin. This straight edge gives a stable area on which the shell can rest. The tumidity of these forms is relatively great and this prevents toppling. The quadrate outline of M.C. VII (App. Fig. 15; *Limopsis minuta*) is less and it is presumed that this group is not so highly adapted to the epibyssate mode.

In both M.C. VII and M.C. VIII the anterior reduction is advanced, but the anterior adductor and anterior hinge teeth are never lost.

The byssus retractor systems in the two classes are different. The minute forms of M.C. VIII have no separate byssus retractor element. No specimens have been available to carry out detailed anatomical studies; it is presumed that the posterior pedal retractor is large enough to assume this role. The condition may be even more extreme where the posterior retractor has its main muscle attachments to the byssus gland rather than to the base of the foot. In the larger M.C. VII class a highly specialized byssus retractor is present (App. Fig. 17) and this may be a function of the larger size, but may also be related to the less adapted shell outline. The less quadrate form of *Limopsis minuta* is less stable and to counteract this, the byssus retractor is stronger.

Marginal crenulations reach the peak of development in the epibyssate forms and their restriction to the postero-ventral margin is undoubtedly linked to the high degree of anterior reduction. In these forms the hinge no longer acts as a major valve-locking mechanism, this being taken over by the posterior adductor. To prevent shearing around the adductor, a new pseudo-hinge is formed across the adductor utilising the now small true hinge at one end and the postero-ventral crenulations at the other.

Intermediate forms may be represented by *Limopsis elachista* Sturany (1899) which, while possessing a 'strap' byssus, does not become quadrate until late in its development. This species may be partially endobyssate.

Unfortunately, no observations on live animals are available for this group and although Fig. 3C shows the minute quadrate form in a true epifaunal habit, this may not be correct. The comparable byssus strength of similarly-sized epibyssate arcaceans is much greater, e.g. *Bathyarca pectunculoides* (Oliver & Allen, 1980a), and consists of a single thick stalk. The epibyssate limopsids may, therefore, require some degree of support and could live in crevices or nestle at the base of larger sedentary epifauna. *Limopsis minuta* although normally taken from shell and coral gravels, has also been recorded from muds. These mud-dwelling species must be partially infaunal and Oliver & Allen (1980b) noted that some specimens did not develop the anterior straight margin and remained in outline very similar to *L. aurita*.

Glycymeriform group

The morphological features of classes M.C. IX (App. Figs. 18 and 20) and M.C. X (App. Fig. 21) are strongly convergent with those of the Glycymerididae. From the morphological features alone one could deduce the poor shallow burrowing ability of these forms and this is confirmed by the observations of Taylor (personal communication) and Tevesz (1977) (Figs. 5 and 6).

The anatomy of the foot is quite different from those of the Limopsiform classes and has only a very small toe and heel, being altogether blade-like and very muscular. The burrowing ability of this foot is aided by the large posterior retractor. The dominance of the posterior retractor is probably the cause of the reduced condition of the anterior retractor which has no or very little shell attachment. This is identical in *Glycymeris*. Since valve movements are important in burrowing, the adductor and hinge are both stronger. The former is evidenced in the reduced heteromyarian condition and the latter in the stronger hinge teeth which are set on a high arch. In general, both classes tend towards an equilateral outline; this too is a feature of the glycymeridids. In both classes the shell is thick, and this is necessary in arcoids not only to develop strong hinge and muscle attachments, but it is also needed to protect the animal when dislodged. Furthermore the thick shell gives protection from crushing predators (Vermeij, 1978).

Dislodgement is probably very common in this group, as noted by Taylor (personal com-

munication) and may be one of the stronger adaptive forces as it is for glycymeridids (Thomas, 1975). Unlike glycymeridids, the byssus remains functional, especially in M.C. X. This suggests that this class is subject to dislodgment and their occurrence on shell hash supports the theory that the habitat is subject to strong currents and consequent disturbance. M.C. IX species possess a very weak byssus by comparison, but they apparently prefer sandy or muddy sand substrates which are probably more stable. The prominent ribbing on the M.C. IX species such as *Limopsis multistriata* (Forskål, 1775) and *L. forteradiata* (Cotton, 1931) may act to stabilize the shell in these finer sediments.

The fixed sedentary burrowing mode confines the inhalant and exhalant apertures to a small area along the postero-ventral edge. The strongly muscular mantle margin in this region is capable of forming discrete apertures and regulating the currents. The intake of unwanted matter is, therefore, reduced and the cleansing actions are required to a lesser extent. This is reflected in the small amount of gill axis muscle in these forms (App. Fig. 6B). The periostracum, due to abrasion, is normally largely removed, but, if persistent, is only so around the postero-ventral margin where it still protects the current apertures.

Limopsis bassi Smith, 1885 (App. Fig. 19) and *L. eucosmus* Verco, 1907 (App. Fig. 22) represent intermediate forms between the limopsiform and glycymeriform groups, *L. bassi* being a M.C. IX associate and *L. eucosmus* to M.C. X. Both tend towards a more oblique form with a more advanced heteromyarian condition and the foot has a more strongly developed toe. The retractors, hinge and other shell characters remain glycymeriform. It is assumed that these intermediates are less capable burrowers and subsequently the extent of penetration is less. Tevesz (1977), however, reports that *L. soboles* (Iredale, 1931) behaves like *L. loringi* and from examination of figures only there is a similarity between the former species and *L. eucosmus*. In Figs 5B and 6B the intermediates are shown as only semi-infaunal, but may be able to completely burrow to the posterior shell margin.

Abyssate group

The third group contains three classes which are apparently not closely related morphologically. They share an almost equi-

lateral outline, an almost isomyarian condition and an apparent lack of byssus function. These characters alone are sufficient to suggest a shallow burrowing mode. Classes M.C. XI (*Limopsis vixornata* Verco, 1907; App. Figs. 23 and 25) and M.C. XII (*L. brazieri* Angas, 1871; App. Fig. 26) share the slight prosogyrate condition. The hinge, dorsally attenuate shape, buttressed adductor and internally striate shell of *L. vixornata* cause it to resemble the *L. loringi* (M.C. X) class. Anatomically the foot and pedal retractors are similar also. The greater equilateral form and abyssate condition is, however, quite different, but it is not unreasonable to assume that *L. vixornata* represents an extension of the glycymeriform burrowing type to a more efficient free burrowing type (Fig. 8). *L. brazieri* with its elliptical outline probably represents one extreme development of the burrowing trend in the Limopsidae, but confirmation from anatomical data is required. No habitat details are available for either class but their sublittoral/shelf range and normal lack of perios-tracum suggests that they inhabit sands or coarser sediments.

Limopsis lilliei Smith (1885) (M.C. XIII; App. Figs. 24 and 27), although sharing the major characters of this group, differs in possessing a thin shell, covered by a pilose perios-tracum, in the relatively weak hinge and the complex ligament. The former differences can be related to the soft muddy sediments preferred by this class in which dislodgment and abrasion are likely to be less. The perios-tracum is invariably clogged by sediment and the fine erect hairs aid stabilization, through preventing either sinking or dislodgment. The weak hinge is unusual in burrowing limopsids, but the well-developed secondary ligament placed at the ends of the dorsal area are presumed to help in holding the valves together. The intact lamellar layer is much larger than in the ligament Types A-C. Combining the more efficient ligament and the large equal adductors suggests that this class is made up of relatively more efficient burrowers. It is expected that these forms would burrow up to their postero-ventral margins (Fig. 7). The mantle edge is especially thickened here and could form precise inhalant and exhalant openings. The gill axis musculature is almost negligible and shows a further progression of the condition seen in the glycymeriform group.

EVOLUTION

The current extent of knowledge of the evolution of the Limopsidae is poor due to the limitations of the fossil record and lack of investigation. To examine all the available material is beyond the scope of this paper and reliance is placed mainly upon the published data. The collection of Mesozoic limopsids in the British Museum (Natural History) was examined.

Tevesz (1977) studied the problem of limopsid origins, proposing a neotenous derivation from the Grammatodontinae. Heinberg (1976, 1978) extensively examined an assemblage of late Cretaceous (Maastrichtian) limopsids; his study provides very significant data on form and radiation. The functional interpretations made by Heinberg (1979) do not entirely agree with those in this paper and consequently there are some revisions here. Heinberg (1979) underestimates the extent of endobyssate attachment and ploughing, postulating either epifaunal or infaunal habits. This study clearly shows that ploughing and endobyssate habits in soft substrates are the dominant limopsid life habits. Consequently, the homeomorphs of the Recent compressed, anteriorly reduced, heteromyarian forms are not always epibyssate as suggested by Heinberg but many are semi-infaunal endobyssate or ploughing species.

Cenozoic limopsids are more numerous but there are apparently no studies concerned with them alone.

Origins

Tevesz (1977) placed the origin of the Limopsidae in the middle Jurassic (Bathonian) citing *Limopsis minima* (Sowerby, 1825) [= *oolithica* (Buvignier, 1852)] as the oldest known species. Tevesz places great emphasis on the ligament pit as a limopsid character and his interpretation rests strongly on its presence. *L. minima* and *L. oblonga* (Sowerby, 1825) are both well represented in the BMNH collection. Contrary to the specific name and small dimension of the type of *L. minima*, it reaches a maximum size of 20 mm. It is sub-quadrate with slight posterior extension, isomyarian and possesses a thick shell with an impressed ligament area. In the small species this ligament area resembles that of a limopsid, but in some of the larger,

better preserved specimens the area is marked by oblique grooves and ridges (Fig. 9). This ridged ligament area is consistent with the reduced duplivincular form seen in grammatodonts. Oblique grooves are not found in multivincular limopsid ligaments, any ridging found being vertical. The form of the juvenile ligaments in *L. minima* is typical of most juvenile arcaceans and in itself is not evolutionarily significant. There are no grounds, therefore, for assigning *L. minima* to the Limopsidae or for regarding this form as a more probable limopsid ancestor than any other grammatodont. A similar argument is applicable to *L. corallensis* (Buvignier, 1852) a late Jurassic species which has a distinct duplivincular ligament.

Arkell (1929–1936) describes an unnamed species from the late Jurassic (Oxfordian) strata near Pickering, Yorkshire, England. This species reaches 22 mm, is obliquely circular, but the hinge is not preserved.

It is not until the lower Cretaceous (Albian) that the first truly recognizable limopsid is found. *Limopsis albiensis* (Woods, 1899) is small—6 mm (Fig. 10A), obliquely circular, heteromyarian with a smooth sculpture and a small ligament pit. Overall it is an exact homeomorph of juvenile Recent ploughing species, e.g. *L. aurita*.

Although the exact origins of the Limopsidae have not been elucidated, it is important to note that whether *L. sp.* Pickering or *Limopsis albiensis* represents the ancestral form; both are obliquely circular. This indicates that the ancestral life habit was semi-infaunal and probably byssate.

Radiation

The initial trend is seen in two species which occur in the Upper Albian, *Limopsis coemansi* Briart & Cornet, 1868 (Fig. 10B) and *L. hoeninghausii* (Müller, 1846) (Fig. 10C). *L. coemansi* is roundly oblique, oval and rather tumid whereas *L. hoeninghausii* is quadrate and tumid. These species show an initial radiation into the endobyssate and epibyssate modes.

Interpreting the shell character of Heinberg's (1979) species on the basis of the anatomical data in this paper it is possible to recognise the extent of the Late Cretaceous (Maastrichtian) radiation. The Limopsiform radiation is extensive: ploughing habits are

represented in *Limopsis misjae* Heinberg, 1976, endobyssate habits in *L. ravni* (Heinberg, 1976) and *L. augustae* (Heinberg, 1976). The respective Recent conchological homeomorphs of these would be *L. aurita*, *L. oblonga* and *L. cristata* and for both epibyssate species *L. elachista*. It is of note that there are no large ploughing species in the white chalk assemblage. The quadrate epibyssate species differ from Recent forms in lacking any marginal crenulation.

Limopsis amandae (Heinberg, 1976) is relatively tumid, but otherwise is typical of the ploughing form. This tumidity, as Heinberg notes, is indicative of an infaunal habit. However, given the strong heteromyarian condition of that species it seems doubtful whether the adductor strength would be sufficient to facilitate burrowing. A semi-infaunal habit is, therefore, proposed for *L. amandae*.

Limopsis nanae (Heinberg, 1976) is a minute species (2.6 mm) which possesses peculiar sub-concentric ridges on the inner shell margin. Heinberg postulates that the size negates any requirement for anterior reduction to facilitate epibyssate attachment. However, *L. nanae* represents the juvenile form of numerous limopsids which are not necessarily epibyssate. Probably all limopsiform species are able to crawl and the small size would aid this function (Tevesz, 1977) giving *L. nanae* a broad niche. Heinberg attaches no significance to the marginal concentric ridges but they appear to be analogous to the marginal ridge present in *Nippono-limopsis decussata* (Adams, 1862) (= *nipponica* Yokoyama, 1920) (Fig. 12). *N. decussata* has not been included in this paper because, due to the presence of a prodissococonch cap (Fig. 11), it is considered to be a philobryid. It was intended to make this observation the subject of a small paper, but it is now useful to mention it here. This form of margin is considered to be a valve locking mechanism and is apparently unique to the Limopsacea. The temptation to link *Limopsis nanae* to *N. decussata* is strong and would give added credence to Tevesz's (1977) theory that the Philobryidae arose neotenuously from the Limopsidae. The temporal and spatial separation of the two species is so large that such a link is doubtful, *N. decussata* being known only from the Pleistocene of Japan.

Limopsis helenae (Heinberg, 1976) has no

Recent homeomorphs and the epibyssate habit is accepted.

The Glycymeriform radiation is also apparent in the late Cretaceous (Newell, 1969) in the form with radial ribbing. Heinberg's glycymeriform species *Limopsis maggae* (Heinberg, 1978) is in contrast a smooth-shelled form. In the northern hemisphere the smooth-shelled forms are not apparent in the Cenozoic, whereas the ribbed variety is frequent, e.g. *L. scalaris* (Sowerby, 1825) (Eocene). In the southern hemisphere there are numerous smooth-shelled homeomorphs of *L. loringi* and *L. eucosmus* occurring from the Eocene onwards in the New Zealand and Magellanic provinces (Fleming, 1966). From the Cretaceous onwards there is an increase in maximum size of both groups of glycymeriform limopsids.

The limopsiform groups display little further radiation in the Cenozoic, the appearance of large ploughing forms in Recent times being the only event of significance. The epibyssate species and fixed endobyssate species remained small but did develop marginal crenulations.

The isomyarian groups have poor fossil records. M.C. XI (*Limopsis vixornata*) has a probable homeomorph in the Palaeocene of New Zealand, *L. microps* Finlay & Marwick, 1937 (Fleming, 1966). *L. brazieri* (M.C. XII) has a very short fossil record, *L. adamsiana* (Yokoyama, 1920) from the Pleistocene of Japan is probably a homeomorph. M.C. XIII (*L. lilliei*) has no fossil record and is presumably of relatively recent origin.

The fossil record of the limopsids is so scant that the formulation of phylogenies can only be hypothetical.

The origins of the family are not apparent but if for the sake of discussion one follows Stanley (1972), Tevesz (1977) and Morton (1978) and invokes a neotenous derivation of the Limopsacea, one must retain the Jurassic arcacean ancestry. This ancestor, whether a grammatodont or a cucullaeid, would presumably be isomyarian and retain the juvenile arcoid ligament in a small triangular resilifer. However, in the Limopsidae this ligament when large becomes multivincular and lacks chevrons. Furthermore the additions of new ligament material are in lateral positions unlike the central growth of the duplivincular ligament. Therefore one must not simply assign the limopsid's origin to a neotenic event but must also consider that the developmental characteristics of the ligament have changed.

This change must now be interpreted in view of Waller's (1978) classification of ligaments in which he considers all Limopsacean ligaments to be duplivincular. Waller (1978) does not indicate either ligament types B, C or D and clearly there is much more work to be done in this area before one can define the significance of limopsid ligaments. In addition, the initial radiation was towards the obliquely oval heteromyarian condition which is unlike all other arcoid tendencies as defined by Stanley (1972). Stanley's repetitive neotenic events consistently gave rise to trapezoidal epibyssate forms or orbicular sub-trapezoidal, shallow burrowing forms. The limopsid condition therefore represents a radical radiation away from the arcoid plan and is only paralleled in the Arcacea by a few members of the Striarcinae (*Ovalarca*) and Trinacriinae (*Stenzelia*). Although the neotenous derivation of the Limopsids is not discounted here it is felt that an oversimplification may be perpetuated and it is urged that the Jurassic arcoid radiation be reconsidered, especially with regard to the almost simultaneous appearance of the Arcidae, Noetiidae and Limopsidae.

The initial radiation of the Limopsiform groups into epibyssate, endobyssate and ploughing modes is well documented and has followed the classic patterns defined by Stanley (1972). The evolution of the ligament types A, B and C within the limopsiform groups is unclear. From the Recent forms there appears to be little difference in the radiation of those with Type A or C ligaments. This suggests that the selective value may be neutral and that these variations may have existed for a long time. The presence of the Type C ligament does, however, consistently occur in those Recent species which also possess crenulated margins. Such margins are not observed in the early fossils and therefore if the characters are linked there may be a case for the Type C ligament being secondary and forming a phyletic group. Conversely if the selective value of the Type C ligament is neutral it may well have arisen almost at random throughout the evolution of the limopsiform group.

The radiation into the glycymeriform and abyssate burrowing modes is apparently secondary. This is quite certain in the glycymeriform group where their appearance in the late Cretaceous and early Cenozoic is documented. The retention of a heteromyarian condition testifies to this but it must be noted that in

Limopsis loringi this condition is now slight. This reversal can be equated with the "Case II" evolution outlined by Stanley (1972) for the endobyssate to free-burrowing sequences seen in some of the Carditacea.

The radiation within the Glycymeriform species has resulted in two distinct groups: M.C. IX and M.C. X. Despite their similar habits and morphologies there is no fossil evidence to assume that they are part of a single lineage. These groups could well represent convergence within the Limopsidae. If so, this would indicate that such radiation occurred at least once in the now antipodean region and also in the now Mediterranean, Caribbean Indo-Pacific region. This has resulted in the distinct Recent distribution patterns of the two classes.

The complete isomyarian conditions noted in classes M.C. XI–M.C. XIII also appear to be secondary. There appears to be reason to accept this for M.C. XI and M.C. XII as a continuance of the glycymeriform radiation pattern. The fossil record is so scant that lineages are not considered. M.C. XIII (*Limopsis lilliei*), however, represents the appearance of ligament type D, associated with rather non-glycymeriform shell characters. In this class there are no fossil homeomorphs known and a gradual evolution of the Stanley Case II form seems untenable. This radiation may well be attributable to yet another neotenous event of the Case I type but associated with ligament changes.

In conclusion, the limopsids rapidly reached a peak in radiation by the early Cenozoic. This was achieved from a semi-infaunal stock radiating into the byssate modes to give rise to the Limopsiform classes with reversals into burrowing modes. These reversals may well have been numerous and thus one sees no evidence of a single lineage in the glycymeriform and abyssate burrowing groups. Coinciding with the early Cenozoic peak there appears to be a high diversity of species with a widespread shallow water distribution. This situation declined gradually so that one now sees the restrictive distributions and low species diversity of recent Limopsidae.

LIMITING FACTORS IN THE MORPHOLOGICAL RADIATION, DIVERSITY AND DISTRIBUTION OF LIMOPSIDS

Despite the functional radiation into ploughing, endobyssate, epibyssate, glycymeriform and burrowing habits, the morphology of the

limopsids has remained remarkably conservative. The functional diversity has been achieved through relatively small changes in shell form and anatomy. The relatively high functional diversity has, however, not been paralleled by a high Recent species diversity, there being at the most sixty valid species. Of these, at least seventy percent are semi-infaunal, either ploughing or endobyssate. Only eleven percent are epibyssate, twelve percent glycymeriform and eleven percent non-glycymeriform burrowers. In comparison with other Limopsacea there are at least eight times as many glycymeridids as glycymeriform limopsids.

Distributionally, the limopsids are limited—in the case of the limopsiform group, bathymetrically and the burrowing groups, geographically.

In the Atlantic Ocean the limopsiform species are found almost exclusively from the continental margin zone to the abyss, and never occur in shallow shelf waters. Exceptions to this are few; some polar emergence occurs in Norwegian fjords and the epibyssate quadrate *Limopsis antillensis* occurs in relatively shallow waters in the Caribbean. The Japanese zonation (Okutani, 1968) is similar, although the outer shelf is inhabited by some species. Only in the Antarctic do limopsiform species occur widely on the shelf (Dell, 1964). In general, the Limopsiform species are restricted to cold water and normally do not occur on the shelf.

The ribbed glycymeriform class is not deep water and occurs from the littoral to 400 m. This class is, however, geographically restricted to the Indo-Pacific and Mediterranean (Coen, 1931). The smooth-shelled glycymeriform class is restricted to the shelf and continental margin zone and is endemic to southeast Australia. The non-glycymeriform burrowing classes are similarly restricted geographically, two classes being endemic to southeast Australia and the third to Antarctica.

The Limopsidae with their restricted morphological diversity and distributional limitations could be considered a relatively unsuccessful family especially in their degree of attainment of the epibyssate and burrowing habits. The semi-infaunal forms are more numerous but in a life mode which has been abandoned by the majority of the Recent bivalves. The mechanism and extent of these limitations warrant further analysis for each major functional group.

The glycymeriform limopsids represent the initial radiation into the burrowing habit. This occurred very soon after the appearance of the Glycymerididae (Aptian/Albian). However, despite this almost equal time scale, there is a marked contrast in the relative success of the two groups.

Thomas (1976) showed the glycymeridid duplivincular ligament to be too weak to enable efficient burrowing and with the result that the animals were subject to repeated dislodgment. They are therefore not only adapted to survive the subsequent physical and predation pressures, but also to rapidly re-establish themselves in the substrate. The shells are consequently large, thick and orbicular with a strong hinge. As there is considerable convergence between the two groups, one can expect similar limitations to operate. The weakness of the glycymeridid ligament involves a combination of an inherent structural frailty with allometric growth. The strength of the limopsid alivincular ligament could not be measured as no live specimens were available. The glycymeriform limopsid ligament (Type A) is always formed in a very shallow resilifer and one never observes the deep resilia seen in *Ostrea* or *Vulsella*. This shallow ligament area is reminiscent of the typical arcoid structures and may well not possess the qualities of non-arcoid types. It is assumed here that the limopsid ligament is no more efficient than the duplivincular, especially with regard to their similarities in length of attachment, thickness of non-split layers and degree of umbonal growth. Allometric relationships between the ligament and shell of limopsids can be shown. In two ploughing species, *Limopsis aurita* and *L. marionensis*, results for mean log-log reduced major axis regressions indicated allometric relationships of ligament height, length and area with shell height. Results for *L. aurita* ligament areas were a correlation coefficient of 0.94 and a slope of 3.09 where a slope of 2 would be considered isometric for a linear-area relationship. Results for ligament heights and lengths separately were for *L. aurita*: ligament height $r = 0.93$, slope 1.54; ligament length $r = 0.94$, slope 1.58 and for *L. marionensis*: ligament height $r = 0.95$, slope = 1.35; ligament length $r = 0.96$, slope = 1.57. In these results the parameters are both linear and have an expected slope of 1.0 for an isometric relationship. The consequences of allometric growth are rapid dorsal splitting of the ligament (Trueman, 1969) and the re-

sulting ventral growth which interferes with the hinge. In glycymeridids the replacement is central but in large limopsids where the ligament becomes multivincular, replacement is also in lateral sites. Consequently, ventral encroachment is more widespread in the limopsids, so much so that in some large specimens (60 mm) of *L. marionensis*, no well-formed hinge teeth remain. Glycymeridids, however, may attain a much greater size (120 mm) without such severe tooth loss. It is noted that in glycymeriform limopsids multivincular structures are never developed and this may reflect the need to maintain a strong hinge. Furthermore, the multivincular ligament involves considerable elongation of the dorsal area with consequent changes in shell outline. This has been classically shown in *Perna* (Trueman, 1954) but is also true to a lesser extent here as evidenced in the ontogenetic changes seen in *L. tenella* (Oliver & Allen, 1980b) and *L. marionensis*. Such changes in outline would severely impair the burrowing ability of glycymeriform limopsids.

In these limopsids most growth is ventral and thus one observes deeply cleft dorsal areas and dorsally attenuated forms. This developmental restriction may therefore account for the small size of glycymeriform limopsids. This in itself may be disadvantageous as the smaller shells may be more prone to attack by crushing predators, a situation which (Vermeij, 1978) may contribute to the limited success of the limopsids in shallow water.

An additional disadvantage inherent in the glycymeriform limopsids is their derivation from a heteromyarian stock. Although this condition is reduced in recent forms there must be restrictions to burrowing caused by the weakness of the anterior adductor and the unequal forces created by this condition. The glycymeridids arose as an isomyarian group and have thus not been influenced in this manner.

The few isomyarian burrowing limopsids that exist are small forms. *Limopsis brazieri* and *L. vixornata* have a structural affinity with the glycymeriform group and are therefore believed to be subject to the same adaptive restrictions. Despite the isomyarian condition of these groups, their diversity and distribution is more limited than that of the glycymeriform group. This adds more credence to the hypothesis that the ligament structure is the major adaptive restriction. The Antarctic isomyarian group is, in contrast, widespread in its endemic province and also occurs in large

numbers to the extent that they may be the dominant bivalve in many samples. These species, e.g. *L. lilliei*, contrast morphologically in possessing a weak, thin shell with a weak hinge. Considerable ventral encroachment occurs in these forms and an edentulous space is rapidly developed, restricting the number of teeth to 3–5 on either side. The alivincular ligament is proportionately large and may be aided by the secondary ligament areas on the dorsal areas. These secondary areas may also strengthen the hinge as they lie immediately above the remaining hinge teeth. It has already been argued that such a thin-shelled, weak-hinged form is not viable and that the limopsid ligament is incapable of providing the mechanism for efficient burrowing. But here is an apparently successful burrowing limopsid. Mechanics alone cannot explain this anomaly. An examination of the Antarctic fauna highlights some contrasting competitive pressures experienced by non-siphonate, shallow burrowers. The Antarctic bivalve fauna has a unique make-up and has few siphonate suspension feeders (Powell, 1960; Dell, 1964). Furthermore, the diversity of non-siphonate burrowers is not as high as in temperate or tropical regions. It is probable, therefore, that the inefficient burrowing limopsids are subject to less competitive pressure in the Antarctic province. The Antarctic is unusual in that the fauna as a whole is impoverished and in particular lacks any benthic decapod Crustacea (Vermeij, 1978). Following Vermeij (1978) it can be argued that the lack of crushing predators has not necessitated the evolution of heavy, strong-hinged shells. Consequently ligament encroachment on the hinge in *L. lilliei* would not be too disadvantageous in relation to predation. Allometric ligament growth could then proceed, creating a stronger ligament for more efficient burrowing.

In comparison with other bivalve groups, the limopsiform classes are poorly adapted. The endobysate class has not paralleled the Modiolidae, Pinnacea or Pteriacea and a similar condition occurs between the epibyssate class and the Mytilidae and Arcidae. The semi-infaunal classes do have analogues in the Palaeozoic, represented by some members of the Cyrtodontidae, Inoceramidae, Modiomorphacea and Carditacea, but few in the Recent. Stanley (1972) discusses the Palaeozoic and Mesozoic decline of the semi-infaunal bivalve and its replacement by highly adapted infaunal burrowing forms. A

consequence of this decline was the emergence of the epibyssate bivalves during the late Palaeozoic and Mesozoic.

In the Mesozoic there must have been considerable adaptive pressure to radiate into the two highly adapted life modes of burrowing and epibyssate attachment. The Limopsidae, arising as semi-infaunal species, rapidly responded to this pressure, reaching their peak as represented by the monomyarian *Limopsis augustae* in the late Cretaceous. From this point the epibyssate and endobysate limopsid radiation remained static and the highly adapted byssate forms were never paralleled. Apparently unable to adapt further, the limopsids were at a considerable disadvantage and could not compete with the now dominant advanced byssate forms. Consequently the limopsiform classes were restricted to zones of higher stability and less competition—thus their deep water bathymetric range and occurrence in the low diversity, highly endemic Antarctic fauna. This limitation is very close to that experienced by the Brachiopoda and, at least in the Atlantic and Antarctic, the co-occurrence of limopsids and brachiopods is high (personal observations).

The mechanism preventing further limopsid radiation into the epibyssate and endobysate habits is probably a function of the degree of anterior reduction. The extent of anterior reduction in the Arcacea is limited by the functional and growth constraints of the duplivincular ligament (Thomas, 1978a, 1978b). As limopsids possess an alivincular ligament this mechanism may at first not appear to be relevant, a view which was supported by Heinberg (1979).

Anterior reduction in limopsids necessitates reduction of the hinge teeth and dorsal area. In mytiliform bivalves this is of little consequence as the ligament is strong enough to hold the valves together and to articulate them. The limopsid alivincular ligament is restricted to a very shallow triangular resilifer displaced on the dorsal area and is, therefore, not suited to maintain valve adhesion without hinge teeth. However, the Philobryidae, which accepting Tevesz (1977) and Morton (1978) are derived from Limopsidae, have succeeded in radiating into edentulous mytilid homeomorphs via a progression from the limopsid-like genus *Cratis* to *Cosa* to *Philobrya*. The significant feature of epibyssate radiation in both the Limopsidae and Philobryidae is the universal small size of the shells. This suggests that the edentulous, anteriorly re-

duced form is attainable only through miniaturization and this leads one to consider again the growth characteristics of limopsids. Combining the effects of the anterior reduction on the size of the dorsal area and number of hinge teeth with the allometric ligament, it is observed that the two are mutually exclusive. As anterior reduction diminishes the size of the dorsal area, it reduces the potential size of the ligament. In very small species this effect is negligible. However, as the linear dimension of the shell increases, the limitation of the ligament size is rapidly increased, the counteracting forces soon preventing further growth.

The limitations of the limopsid radiation, their recent diversity and distribution therefore appear to be a function of inherent morphological constraints. These constraints are primarily the inefficient alivincular ligament and the lack of any siphonal development. Some minor evolutionary events such as the initial heteromyarian condition may have contributed to the limitation of the family. However, competitive and predation pressures have also played a modifying role. These in general have been restrictive, resulting in the absence of semi-infaunal species from shelf waters and the further restriction of burrowing species. In the case of the Antarctic, such pressures are reduced and one observes a more diverse and prominent limopsid element in the fauna.

ACKNOWLEDGEMENTS

I thank Roger D. K. Thomas for his very helpful comments on the manuscript of this paper. Among many others who aided with advice and specimens were S. Whybrow, N. J. Morris, D. Heppell, K. Boss, H. Coomans, B. Metivier, R. Kilburn, W. Ponder and T. Habe.

REFERENCES CITED

- ADAMS, A., 1860, On some new genera and species of Mollusca from Japan. *Annals and Magazine of Natural History*, ser. 3, 5: 405–413.
- ADAMS, A., 1862, Descriptions of some new species of *Limopsis* from the Cumingian collection. *Proceedings of the Zoological Society of London*, 1862: 229–231.
- ADAMS, A. & REEVE, L., 1850, Mollusca. *The Zoology of the Voyage of H.M.S. Samarang 1843–1846*, 87 p.
- ANGAS, G. F., 1871, Descriptions of 34 new species of shells from Australia. *Proceedings of the*

- Zoological Society of London*, 1871: 13–21.
- ANGAS, G. F., 1873, Descriptions of eight new species of land and marine shells from various localities. *Proceedings of the Zoological Society of London*, 1873: 182–184.
- ARKELL, W. J., 1929–1936, A monograph of British corallian Lamellibranchia. *Palaeontological Society of London*, 392 p.
- ATKINS, D., 1936, On the ciliary mechanisms and inter-relationships of lamellibranchs. *Quarterly Journal of Microscopical Science*, 79: 181–308.
- ATKINS, D., 1951, On the ciliary mechanisms of *Limopsis aurita* (Brocchi). Unpublished manuscript, Library, British Museum (Natural History), London.
- BARNARD, K. H., 1964, The work of S. S. Pieter Faure in Natal waters with special reference to the Crustacea and Mollusca: with descriptions of new species of Mollusca of Natal. *Annals of the Natal Museum*, 16: 9–29.
- BRIART, A. & CORNET, F. L., 1868, Descriptions minéralogique géologique et paléontologique de la Meule de Bracquégries. *Mémoires Couronnés et Mémoires des Savants Etrangers. Académie Royale des Sciences et Belle-Lettres de Bruxelles*, 34: 1–92, pl. 1–8.
- BROCCHI, G., 1814, *Conchiologia Fossile Subapennina*. Milan, 2 vols., 712 p.
- BURNE, R. H., 1920, Mollusca. Part IV. Anatomy of the Pelecypoda. *British Antarctic ("Terra Nova") Expedition 1910. Zoology*, 2: 233–256.
- BUVIGNIER, A., 1852, *Statistique géologique, minéralogique, métallurgique et paléontologique du Département de la Meuse*. Paris, New York. Baillières, 694 p.
- COEN, G., 1931, Un nuovo Lamellibranco (*Limopsis stalioti* n. sp.). *Atti del 'Accademia Veneto-Trentino-Istriana*, 21: 117–120.
- COTTON, B. C., 1931, Pelecypoda of the "Flindersian" Region, South Australia. *Records of the South Australian Museum*, 4: 223–240.
- DALL, W. H., 1881, Preliminary report on the Mollusca. Results of the dredgings from the U.S.S.S. "Blake." *Bulletin of the Museum of Comparative Zoology, Harvard*, 9: 33–144.
- DALL, W. H., 1891, On some new or interesting West American shells obtained from the dredgings of the U.S. Fish Commission "Albatross" in 1888. *Proceedings of the United States National Museum*, 14: 171–191.
- DALL, W. H., 1908, The Mollusca and the Brachiopoda. *Bulletin of the Museum of Comparative Zoology*, 43: 205–487.
- DELL, R. K., 1956, Some new off-shore Mollusca from New Zealand. *Records of the Dominion Museum, Wellington*, 3: 27–59.
- DELL, R. K., 1964, Antarctic and Sub-Antarctic Mollusca, Amphineura, Scaphopoda and Bivalvia. *Discovery Reports*, 33: 93–250.
- DINAMANI, P., 1967, Variation in the stomach structure of the Bivalvia. *Malacologia*, 5: 225–268.
- FINLAY, H. J. & MARWICK, J., 1937, The Wanganaloan and associated molluscan faunas of

- Kaitangata-Green Island subdivision. *New Zealand Geological Survey, Palaeontological Bulletin*, 15: 1–140.
- FISCHER, P., 1870, in FOLIN, A. G. DE & PÉRIER, L., *Les Fonds de la Mer*. Livr. 15: 225–240.
- FLEMING, C. A., 1966, Marwick's Illustrations of New Zealand Shells. *New Zealand Department of Scientific and Industrial Research, Bulletin* 173: 456 p. Wellington.
- FORSKÅL, P., 1775, *Descriptiones animalium . . . quae in itinere orientali . . .* Hauniae, Heineck & Faber, 164 p.
- HABE, T., 1953, Descriptions of twelve new Japanese shells. *Venus*, 17: 130–144.
- HEDLEY, C. & PETTERD, F. W., 1906, Mollusca from three hundred fathoms off Sydney. *Records of the Australian Museum*, 6: 211–225.
- HEINBERG, C., 1976, Bivalves from the white chalk (Maastrichtian) of Denmark. *Limopsidae. Bulletin of the Geological Society of Denmark*, 25: 57–70.
- HEINBERG, C., 1978, Bivalves from the white chalk (Maastrichtian) of Denmark. II, Arcoida. *Bulletin of the Geological Survey of Denmark*, 27: 105–116.
- HEINBERG, C., 1979, Evolutionary ecology of nine sympatric species of pelecypod *Limopsis* in Cretaceous chalk. *Lethaia*, 12: 325–340.
- IREDALE, T., 1931, Australian molluscan notes I. *Records of the Australian Museum*, 18: 201–235.
- JEFFREYS, J. G., 1864, *British Conchology*. Vol. 2. *Marine Shells*. London.
- JEFFREYS, J. G., 1876, New and peculiar Mollusca of the *Pecten*, *Mytilus* and *Arca* families. *Valorous Expedition. Annals and Magazine of Natural History*, ser. 4, 18: 424–436.
- KNUDSEN, J., 1967, The deep-sea Bivalvia. *Scientific Reports of the John Murray Expedition*, 11: 235–343.
- KNUDSEN, J., 1970, The systematics and biology of abyssal and hadal Bivalvia. *Galathea Reports*, 11: 7–241.
- MABILLE, J. & ROCHEBRUNE, A. T. DE, 1889, Mollusques. *Mission Scientifique du Cape Horn 1882–1883*. 6, *Zoologie*, 129 p.
- MORTON, B., 1978, The biology and functional morphology of *Philobrya munita* (Bivalvia: Philobryidae). *Journal of Zoology*, 185: 173–196.
- MULLER, J. M., 1946, *Monographie der Petrefakten der aachener Kreideformation*, Part I: 48 p., Bonn.
- NEVILL, G. & NEVILL, H. H., 1874, Descriptions of new marine Mollusca from the Indian Ocean. *Journal Asiatic Society of Bengal*, 43: 1–30.
- NEWELL, N.D., 1969, Limopsacea. Part N, Mollusca 6, Bivalvia Vol. I. In MOORE, R. C. & TEICHERT, E. (eds.), *Treatise on Invertebrate Paleontology*. Geological Society of America and University of Kansas Press, Lawrence.
- NICOL, D., 1950, Origin of the pelecypod family Glycymeridae. *Journal of Paleontology*, 24: 89–98.
- OKUTANI, T., 1968, Systematics, ecological distribution and palaeoecological implications of archibenthal and abyssal Mollusca from Sagami Bay and adjacent areas. *Journal of the Faculty of Science of the University of Tokyo*, 17: 1–98.
- OLIVER, P. G., 1978, *The functional morphology of the deep sea representatives of the superfamilies Limopsacea and Arcacea (Bivalvia)*. Unpublished Ph.D. thesis, University of Newcastle-upon-Tyne, England.
- OLIVER, P. G. & ALLEN, J. A., 1980a, The functional and adaptive morphology of the deep sea species of the family Arcacea (Bivalvia: Arcoida) from the Atlantic. *Philosophical Transactions of the Royal Society of London*, ser. B, 291: 45–76.
- OLIVER, P. G. & ALLEN, J. A., 1980b, The functional and adaptive morphology of the deep sea species of the family Limopsidae (Bivalvia: Arcoida) from the Atlantic. *Philosophical Transactions of the Royal Society of London*, ser. B, 291: 77–125.
- PELSENEER, P., 1888, Report on the anatomy of the deep sea Mollusca collected by H. M. S. Challenger in the years 1873–1876. *Zoological Reports of the Scientific Results of the Voyage of H.M.S. Challenger*, 74: 1–42.
- PELSENEER, P., 1903, Mollusques. *Résultats du Voyage du SY "Belgica."* 1897–1899. *Zoologie*, 85 p.
- PHILIPPI, R. A., 1836, *Enumeratio Molluscorum Siciliae*, vol. 1: 267 p.
- POWELL, A. W. B., 1958, Mollusca from the Victoria-Ross Quadrants of Antarctica. *Banzare Reports*, ser. B, 6: 165–215.
- POWELL, A. W. B., 1960, Antarctic and sub-Antarctic Mollusca. *Records of the Auckland Institute and Museum*, 5: 117–193.
- PURCHON, R. D., 1957, The stomach in the Filibranchia and Pseudolamellibranchia. *Proceedings of the Zoological Society of London*, 129: 27–60.
- REEVE, L., 1843, On new species of *Conus*, *Pleurotoma*, *Pectunculus* and *Cardita*. *Proceedings of the Zoological Society of London*, 1843: 188–191.
- REHDER, H. A., 1971, A molluscan faunule from 200 m off Valparaíso, Chile with descriptions of four new species. *Proceedings of the Biological Society of Washington*, 83: 585–596.
- SMITH, E. A., 1885, Report on the Lamellibranchiata collected by H.M.S. Challenger during the years 1873–76. *Reports of the Scientific Results of the Voyage of H.M.S. Challenger*, *Zoology*, 13: 241 p.
- SMITH, E. A., 1915, Mollusca. *British Antarctic ("Terra Nova") Expedition, 1910. Natural History Reports. Zoology*, 2: 61–112.
- SOWERBY, G. B., 1914, New Mollusca of the genera *Pleurotoma* (*Surcula*), *Oliva*, and *Limopsis* from Japan. *Annals and Magazine of Natural History*, ser. 8, 13: 445, pl. 18.
- SOWERBY, J. DE C., 1825, *The Mineral Conchology of Great Britain*, 5: 504–545.

STANLEY, S. M., 1972, Functional morphology and evolution of byssally attached bivalve molluscs. *Journal of Paleontology*, 46: 165–212.

STURANY, R., 1899, Lamellibranchiaten des Rothen Meeres. *Expedition S. M. Schiff "Pola" in das Rothe Meer. Zoologische Ergebnisse*, 14: 41 p.

TEVESZ, M. J. S., 1977, Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). *Postilla*, 171: 64 p.

THIELE, J., 1912, Schnecken und Muscheln. *Deutsche Sudpolar Expedition 1901–3*, 13, *Zoologie*, 5: 185–285.

THIELE, J. & JAECKEL, S., 1931, Muscheln der Deutschen Tiefsee Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem dampfer "Valdivia" 1898–9*, 21: 162–268.

THOMAS, R. D. K., 1975, Functional morphology, ecology and evolutionary conservatism in the Glycymeridae (Bivalvia). *Palaeontology*, 18: 217–245.

THOMAS, R. D. K., 1976, Constraints of ligament growth form and function on evolution of the Arcoida (Mollusca: Bivalvia). *Paleobiology*, 2: 64–83.

THOMAS, R. D. K., 1978a, Shell form and the ecological range of living and extinct Arcoida. *Paleobiology*, 4: 181–194.

THOMAS, R. D. K., 1978b, Limits to opportunism in the evolution of the Arcoida (Bivalvia). *Philosophical Transactions of the Royal Society of London*, ser. B, 284: 335–344.

TRUEMAN, E. R., 1954, The structure of the ligament of *Pedalion* (Perna). *Proceedings of the Malacological Society of London*, 30: 160–166.

TRUEMAN, E. R., 1969, Ligament. Part N, Mollusca 6, Bivalvia vol. I: 58–64. In MOORE, R. C. & TEICHERT, C. (eds.). *Treatise on Invertebrate Paleontology*. Geological Society of America and University of Kansas Press, Lawrence.

VERCO, J. C., 1907, Notes on South Australian marine Mollusca with descriptions of new species. Part VI. *Transactions of the Royal Society of South Australia*, 31: 213–230.

VERMEIJ, G. J., 1978, *Biogeography and Adaptation, Patterns of Marine Life*. Harvard University Press, 332 p.

VERRILL, A. E., 1885, Third catalogue of Mollusca recently added to the fauna of the New England coast, consisting mostly of deep sea species with notes on other species previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6: 395–452.

VERRILL, A. E. & BUSH, K.J., 1898, Revision of the deep water Mollusca of the Atlantic coast of North America with descriptions of new genera and species. *Proceedings of the United States National Museum*, 20: 777–901.

WALLER, T. R., 1978, Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London*, ser. B, 284: 345–365.

WOODS, H., 1899, A monograph of the Cretaceous Lamellibranchia of England, vol. 1. *Palaeontographical Society*, 232 p.

WOODS, J. E. T., 1877, Census; with brief description of the marine shells of Tasmania and the adjacent islands. *Proceedings of the Royal Society of Tasmania*, 1877: 3–34.

YOKOYAMA, M., 1920, Fossils from the Miura Peninsula and its immediate north. *Journal of the College of Science of the Imperial University of Tokyo*, 39: 1–193.

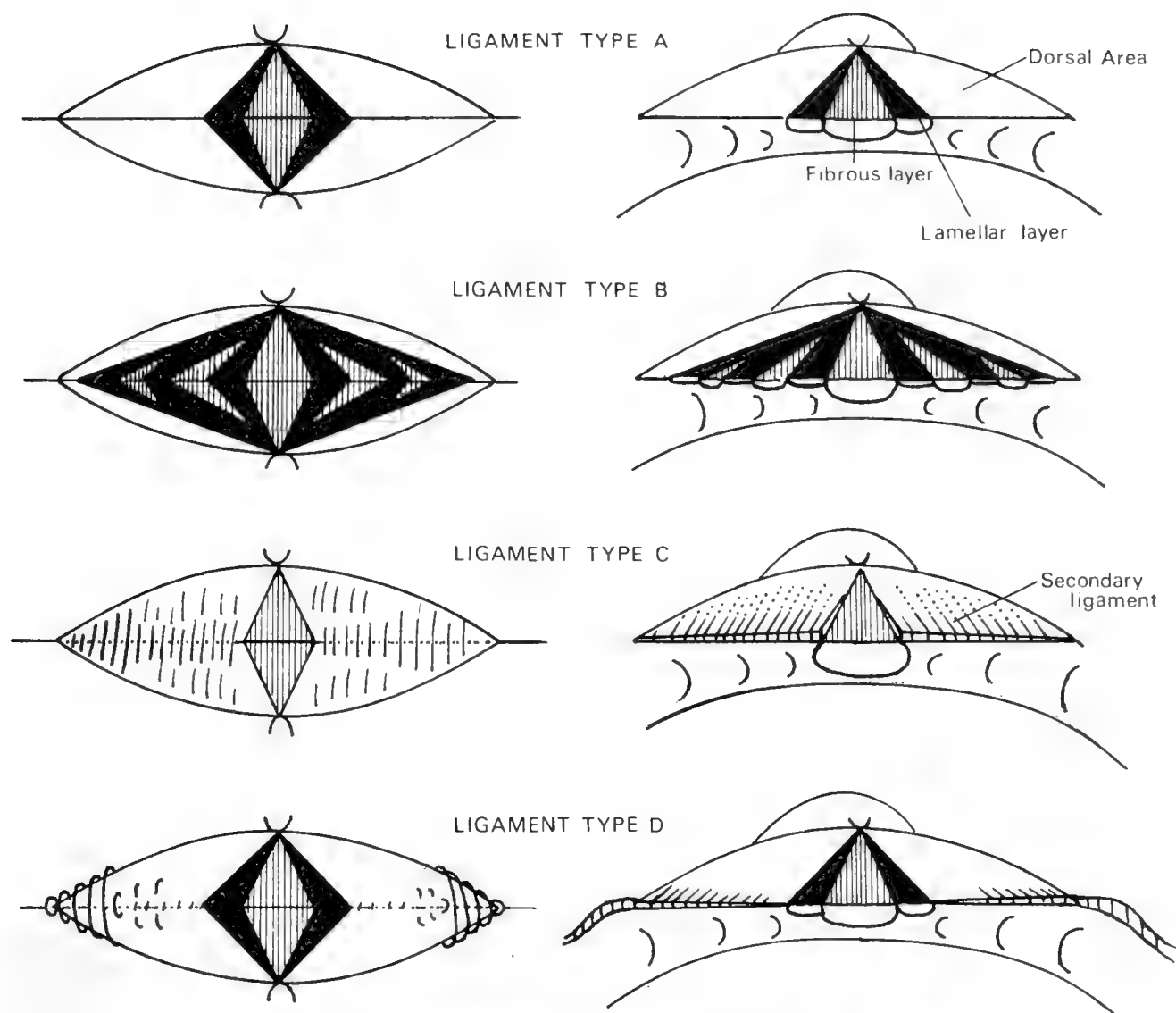
KEY TO ABBREVIATIONS USED IN
APPENDIX ANATOMICAL FIGURES

A	Anus
AA	Anterior adductor muscle
ARM	Anterior retractor muscle
B	Byssus
BRE	Byssus retractor element
BRM	Byssus retractor muscle
CT	Connective tissue
DG	Digestive gland
F	Foot
G	Gill
GD	Gonad
GA	Gill axis
GAM	Gill axis muscle
H	Heart
HG	Hind gut
K	Kidney
KD	Kidney duct
ME	Mantle edge
MN	Mantle nerve
P	Palps
PA	Posterior adductor muscle
PPM	Pedal protractor muscle
PRM	Posterior retractor muscle

APPENDIX: MORPHOLOGICAL CLASSES
OF RECENT LIMOPSIDS

To present all the morphological data on fifty species would be confusing and consequently the species have been divided into classes of similar morphology. These classes cannot be rigidly defined and therefore there are some intermediate species. These are described separately only if they provide significant additional data. There are thirteen distinct classes which require definitions. The descriptions have been confined to concise diagnoses, using only characters of functional significance.

Some of the shell characters of the Limopsidae have not been adequately defined before. This has not only given rise to the con-



APP. FIG. 1. Ligament structures within the Limopsidae.

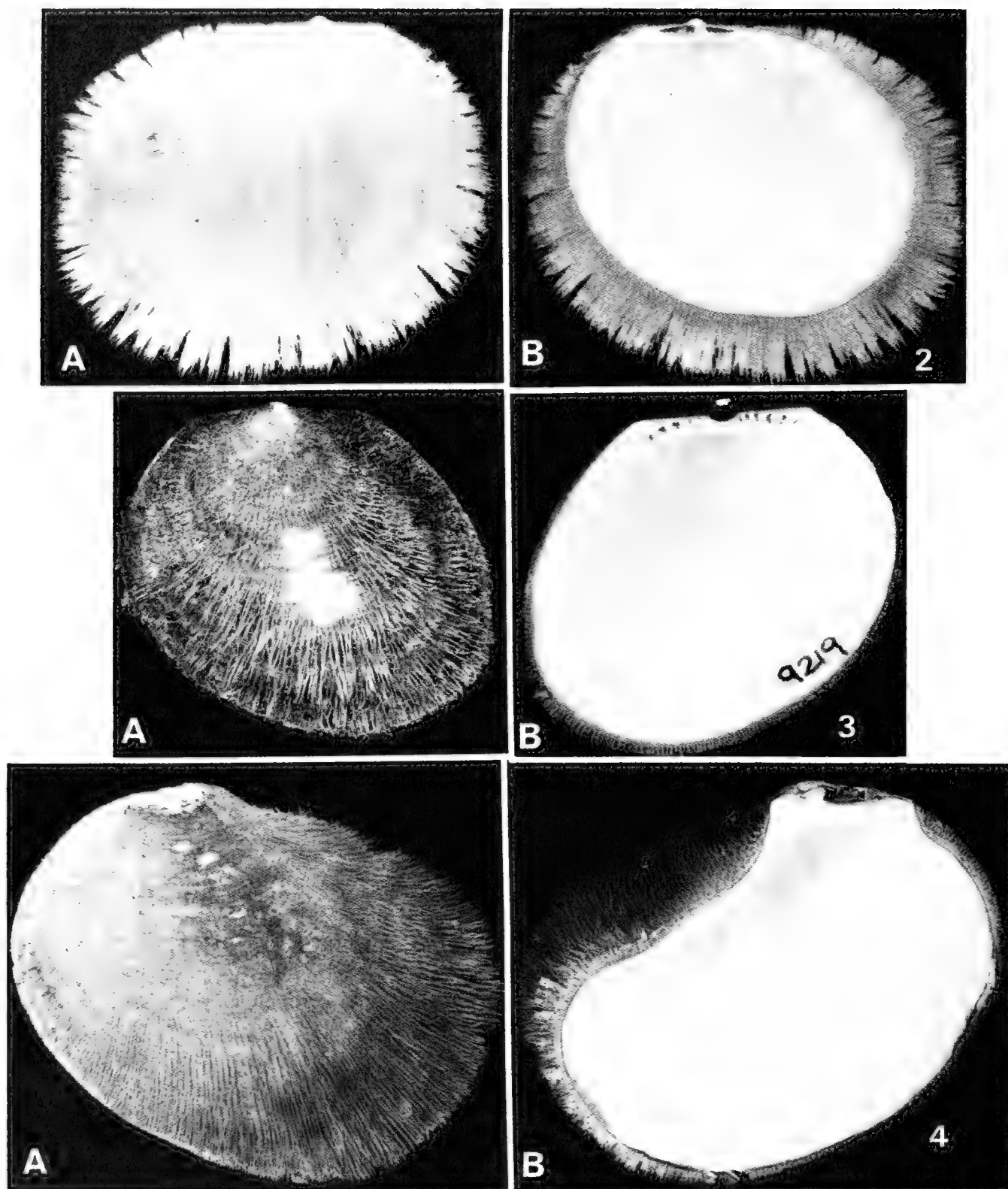
fused state of limopsid systematics, but has also obscured functional interpretation.

Ligament: The ligament in the limopsids, although typically alivincular (Trueman, 1969), is not always of the simple amphidetic type. There are four distinct forms (Oliver, in prep.) in which the disposition of the fibrous and lamellar layers differ; there is also a secondary ligament in some. The nature of the secondary ligament is uncertain and at this moment it is not known whether it is periostracal or a fusion layer. **Type A.**—Amphidetic alivincular: Primary ligament in a shallow resilifer, remainder of dorsal area covered by undifferentiated periostracum (App. Fig. 1). **Type B.**—Amphidetic multivincular: Primary ligament of multiple lamellar and fibrous segments all in shallow resilifer, remainder of dorsal area covered by undifferentiated periostracum (App. Fig. 1). **TYPE C.**—Primary ligament of fibrous layer only in a relatively deep and narrow resilifer. Dorsal area

covered by a thick layer of presumed secondary ligament joining the whole length of the dorsal area. The dorsal area may, however, be covered by the lamellar layer (App. Fig. 1).

Type D.—Primary ligament of the amphidetic alivincular form (Type A). Dorsal area covered with a secondary ligament which is especially thickened at the ends of the hinge plate (App. Fig. 1).

Marginal crenulations: **Type A.**—Nodular, margin marked by alternating nodules and pits or ridges and troughs. Distinguishing ridges and nodules are impractical due to ontogenetic changes from one to the other. **Type B.**—Serrated, margin smooth except for fine serrations on its inner edge. This type is probably formed from Type A by overgrowth as the shell increases in size. **Type C.**—Fluted, the inner margin is more or less smooth except for weak undulations or corrugation which coincide with the radial ribs of the external sculpture.



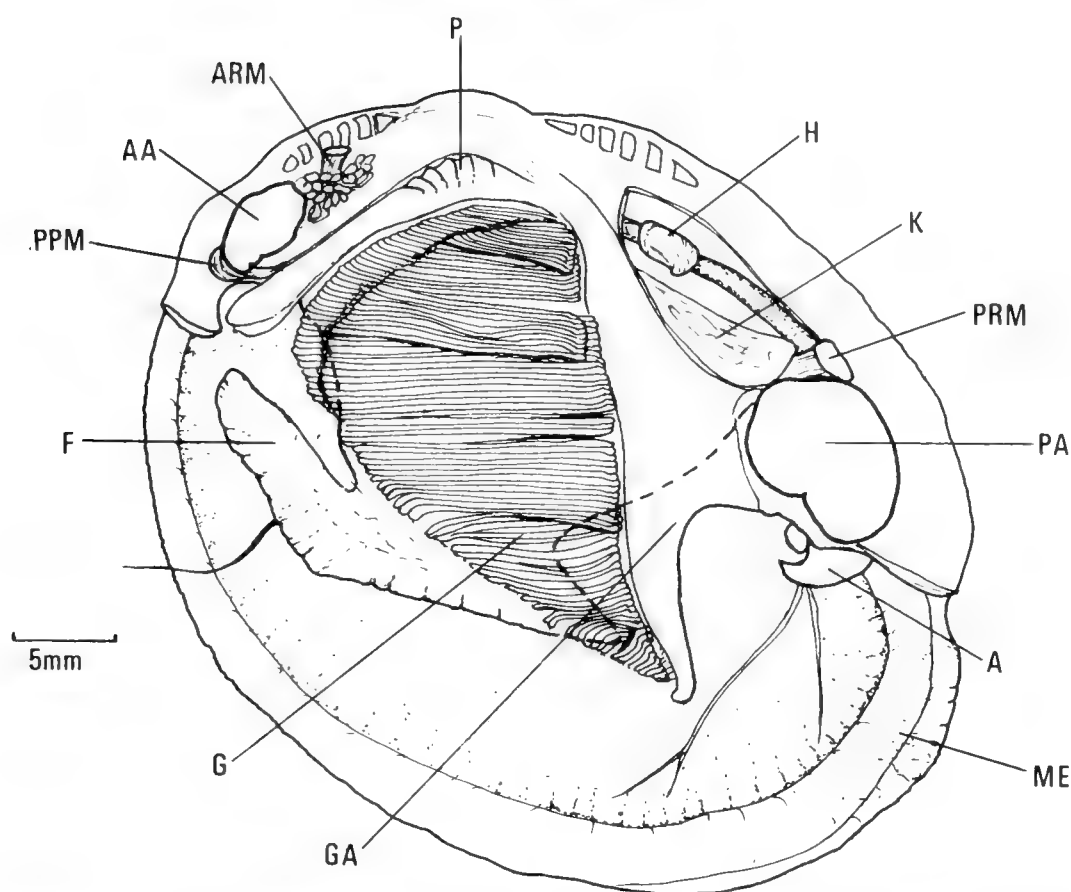
APP. FIG. 2. *Limopsis marionensis* Smith. Baie de Penguins, Antarctica. IRSNB. Diam. 65 mm. APP. FIG. 3. *Limopsis chuni* Thiele & Jaeckel. Natal, South Africa. NM. Diam. 30 mm. APP. FIG. 4. *Limopsis vaginata* Dall. Bering Sea. IRSNB. Diam. 35 mm.

Periostracal bristles: Thatched.—Long fine bristles lying flat against the shell and forming a wide fringe. **Spicate.**—Short blade-like bristles standing more or less erect and not forming a wide fringe. **Lanceolate.**—Long needle-like bristles standing more or less erect and not forming a wide fringe. **Stubby.**—Short blunt coarse bristles standing

erect from shell. **Pilose.**—Moderately long very fine bristles, dense, standing erect.

Morphological Class I

Diagnosis: Larger species 20–60 mm max. diam. Equivalve, compressed, inequilateral, becoming obliquely oval or obliquely circular,



APP. FIG. 5. Gross anatomy of *Limopsis marionensis* Smith (left mantle removed).

i.e. strongly extended posteriorly. Shell thin. Sculpture weak, of concentric lines cut by radially arranged markings corresponding to periostracal bristle insertions. Periostracum thatched. Ligament (Type A) variable, becoming large or multivincular (Type B) in big specimens of large species. Dorsal area typically long, narrow and not deeply cleft, but may widen disproportionately. Hinge weak with numerous small teeth set in two series on a low arch, an edentulous space of variable size is present. Heteromyarian condition advanced, the anterior adductor is reduced and possesses a weak scar-umbonal ridge (myophore). Internal margin smooth (App. Fig. 2).

Foot with prominent toe and heel. Pedal retractors not large. Byssus gland active, producing a single long fine thread without any terminal disc. The byssus is rarely observed and is usual only in juveniles. Gill axis orientated obliquely to the hinge plate, highly muscular. Palps small with few weak sorting ridges. Mantle margin thickened postero-ventrally but not greatly (App. Figs. 5 and 6).

Habitat: Typically from sands, muds and oozes, but also from gravels.

Bathymetric range: 50–5500 m.

Distribution: cosmopolitan, but absent from the Arctic Ocean.

Species complement: *Limopsis marionensis* Smith, 1885; *L. tajimae* Sowerby, 1914; *L. dalli* Knudsen, 1970; *L. tenella* Jeffreys, 1876 (= *pelagica* Smith, 1885); *L. ruizana* Rehder, 1971; *L. surinamensis* Oliver & Allen, 1980b; *L. zonalis* Dall, 1908.

Tentatively included are *Limopsis janeiroensis* Smith, 1915; *L. indica* Smith, 1885; *L. siberutensis* Thiele & Jaeckel, 1931 and *L. paradoxa* (Iredale, 1931).

Morphological Class II

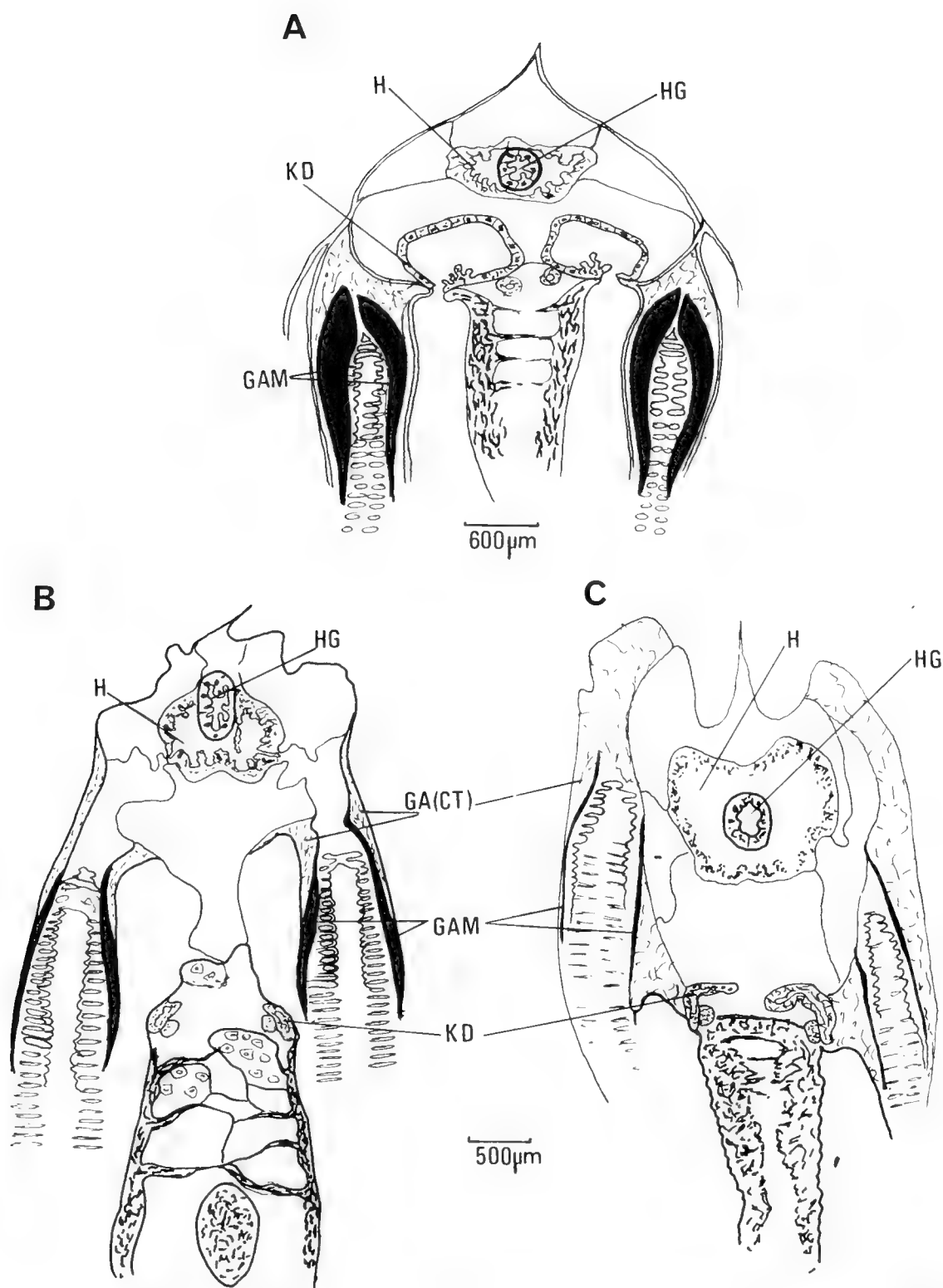
Diagnosis: Like M.C. I except that the sculpture is stronger and the periostracum a little coarser. Inner margin serrated. Ligament Type C. Anatomy essentially as in M.C. I (App. Fig. 3).

Habitat: Sands and muds.

Bathymetric range: 70–500 m.

Distribution: Indian Ocean (East and South Africa) and Korean Sea.

Species complement: *Limopsis chuni* Thiele & Jaeckel, 1931; *L. sansibarica* Thiele & Jaeckel, 1931; *L. belcheri* (Adams & Reeve, 1850).



APP. FIG. 6. Transverse sections through the region of the heart to show comparative extent of the gill axis musculature. (A) *Limopsis tenella* (Limopsiform). (B) *L. multistriata* (Glycymeriform). (C) *L. lillei* (Burrowing).

Morphological Class III

Diagnosis: Like M.C. I except for the presence of a cleft formed by an indentation of the postero-dorsal shell margin. The cleft appears in juveniles as a small notch below the end of the dorsal area and increases in size with growth. There is a much smaller anterior cleft

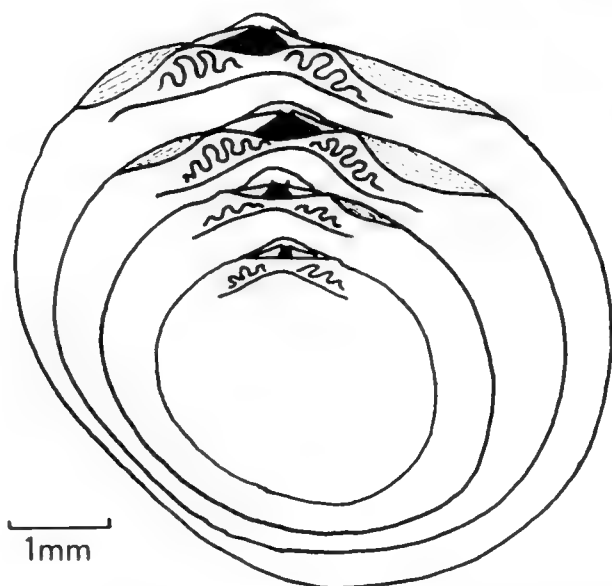
in *Limopsis cumingi*. Ligament Type A. Anatomically similar to M.C. I (App. Figs. 4 and 7).

Habitat: Fine sands and muds.

Bathymetric range: 80–650 m.

Distribution: North Pacific (Alaska-Japan).

Species complement: *Limopsis vaginata* Dall, 1891; *L. cumingi* A. Adams, 1862.



APP. FIG. 7. Growth series of *Limopsis cumingi* A. Adams to show development of the clefts.

Morphological Class IV

Diagnosis: Medium-sized species: diam. 12–20 mm. Compressed, becoming strongly and obliquely oval. Periostracum thatched. Shell moderately thick. Ligament Type A. Hinge moderately strong, teeth larger than those in M.C. I. Heteromyarian condition advanced, greatly reduced anterior scar with well developed myophore. Anatomy as in M.C. I except that the posterior pedal retractor is slightly divided into byssus and pedal elements, the former being far the weaker. Byssus of a single long fine thread which is frequently observed (App. Figs. 8 and 11).

Habitat: Muddy gravels, shell gravels, sands and muds.

Bathymetric range: 100–1300 m.

Distribution: Atlantic Ocean and Japan.

Species complement: *Limopsis aurita* (Brocchi, 1814); *L. sulcata* Verrill & Bush, 1898; *L. obliqua* A. Adams, 1862.

Some of the smaller species included in M.C. I may belong here but the anatomical characters are not known, e.g. *Limopsis indica*, *L. janeiroensis*.

Habits: The following behaviours of *Limopsis aurita* were observed by Oliver & Allen (1980b):

In mud: *L. aurita* ploughs through the sediment surface penetrating only to a depth marked by a line through the umbos and postero-ventral margin. No burrowing movements were observed. When ploughing

ceased, most specimens remained in an upright position and produced the fine byssus (App. Fig. 12).

In sand: A similar behaviour occurs, but penetration is much less and the byssus is not able to prevent the animals from falling onto one valve (App. Fig. 12).

On gravel: The crawling persists, but no penetration is effected and the byssus is cemented to stones. In many cases the animals suspended themselves from larger stones hanging freely in the water (App. Fig. 12).

Morphological Class V

Diagnosis: Small species: diam. 5–12 mm. Compressed, inequilateral, becoming obliquely oval, occasionally obliquely circular, some developing a straight anterior margin. Shell thin, sculpture weakly decussate. Periostracal bristles stout, lanceolate or spicate, arranged in distinct radial or concentric patterns, persistent especially postero-ventrally. Ligament Type C. Hinge weak, teeth small on a low arch. Heteromyarian condition advanced, small anterior scar with weak myophore. Internal margin evenly crenulated, nodular. Anatomically similar to M.C. IV but the divided posterior pedal retractor has a stronger byssus element. The byssus consists of 3–6 long fine threads. Mantle margin thickened postero-ventrally (App. Figs. 9 and 13).

Habitat: Sands, muds and oozes.

Bathymetric range: 50–2500 m.

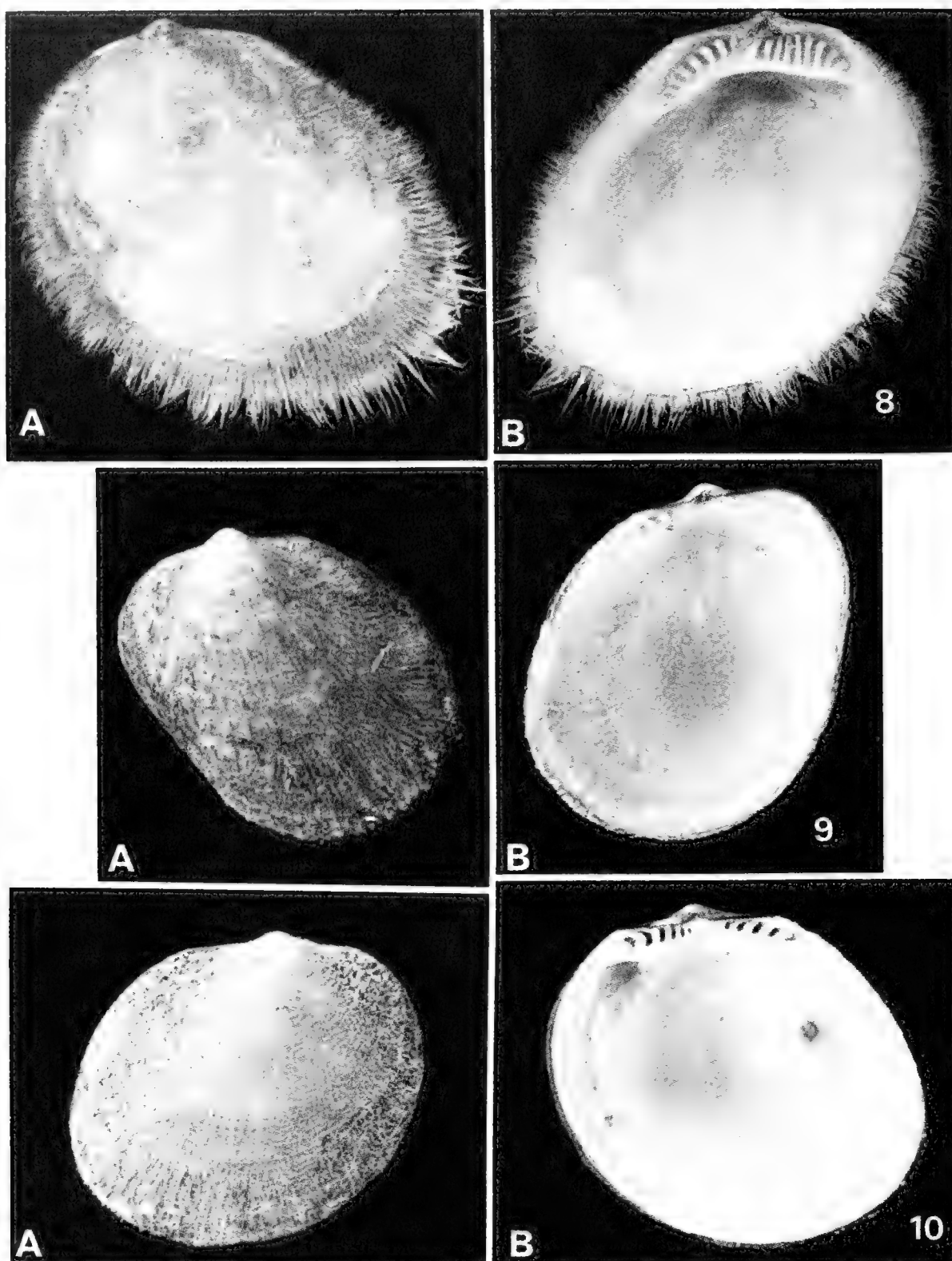
Distribution: Cosmopolitan except for the Arctic Ocean.

Species complement: *Limopsis affinis*, Verrill, 1885; *L. cristata* Jeffreys, 1876; *L. erecta* Hedley & Petterd, 1906; *L. idonea* (Iredale, 1931); *L. intermedia* Oliver & Allen, 1980b; *L. longipilosa* Pelseneer, 1903; *L. perieri* Fischer, 1870; *L. scabra* Thiele, 1912; *L. spicata* Oliver & Allen, 1980b; *L. lanceolata* Oliver & Allen, 1980b; *L. tasmani* (Dell, 1956).

The following species are tentatively included: *L. diazi* Dall, 1908; *L. mabillana* Dall, 1908 and *L. stimpsoni* Dall, 1908.

Limopsis diegensis Dall, 1908 (App. Figs. 10 and 13)

This species closely resembles M.C. V species both in shell and anatomy. It is larger, reaching 15 mm in diam. and possesses a 'thatched' periostracum. It is obliquely circular rather than obliquely oval.



APP. FIG. 8. *Limopsis aurita* Brocchi. Bay of Biscay. MNHNP. Diam. 15 mm. APP. FIG. 9. *Limopsis affinis* Verrill. Off New England, U.S.A. USNM. Diam. 10 mm. APP. FIG. 10. *Limopsis diegensis* Dall. Off California. USNM. Diam. 12.5 mm.

Limopsis oblonga A. Adams, 1860 (App. Fig. 14)

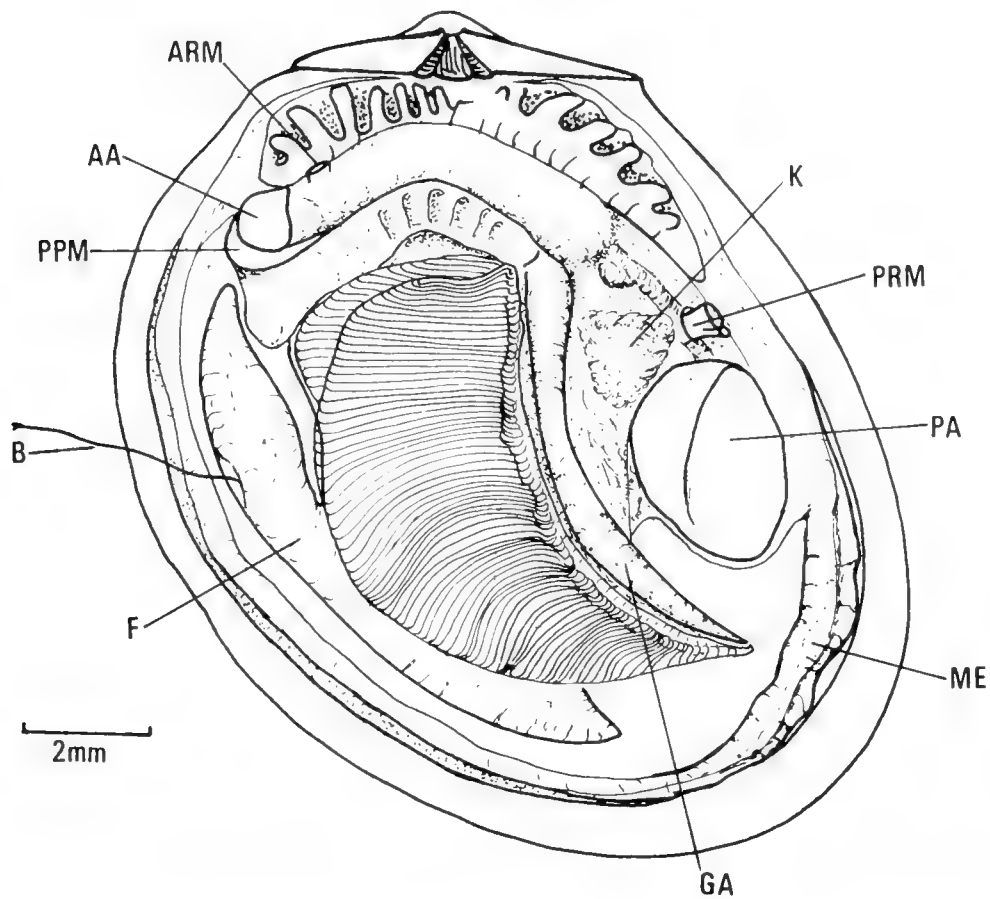
This is another species with an evenly crenulate margin and a somewhat spicate periostracum. It is, however, larger, reaching 15 mm in diam. and is relatively a little tumid.

Juveniles have a concentric spicate periostracum, but the adults are more of the 'thatched' type.

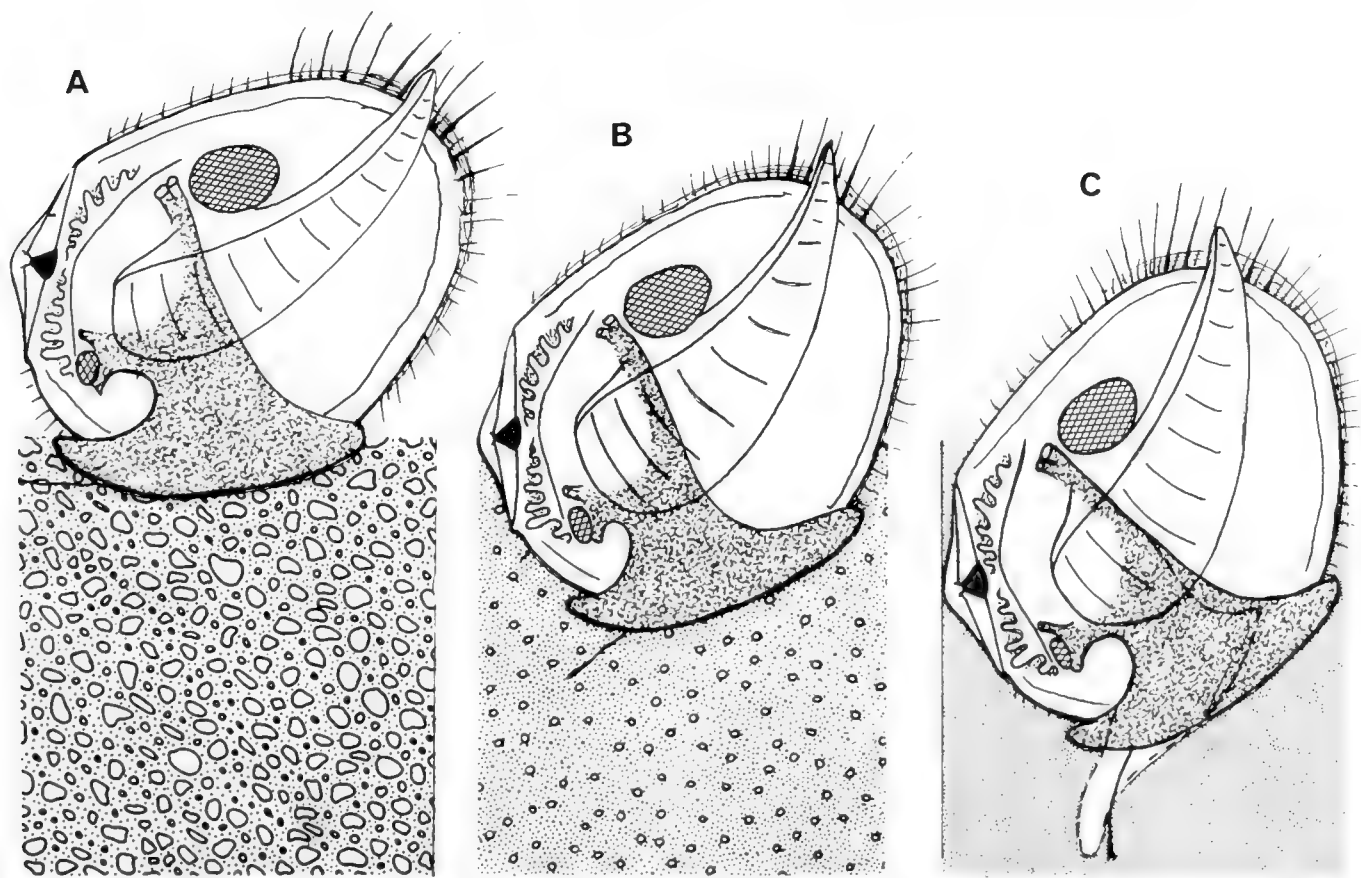
Habitat: Sands and muds.

Bathymetric range: 100–2020 m.

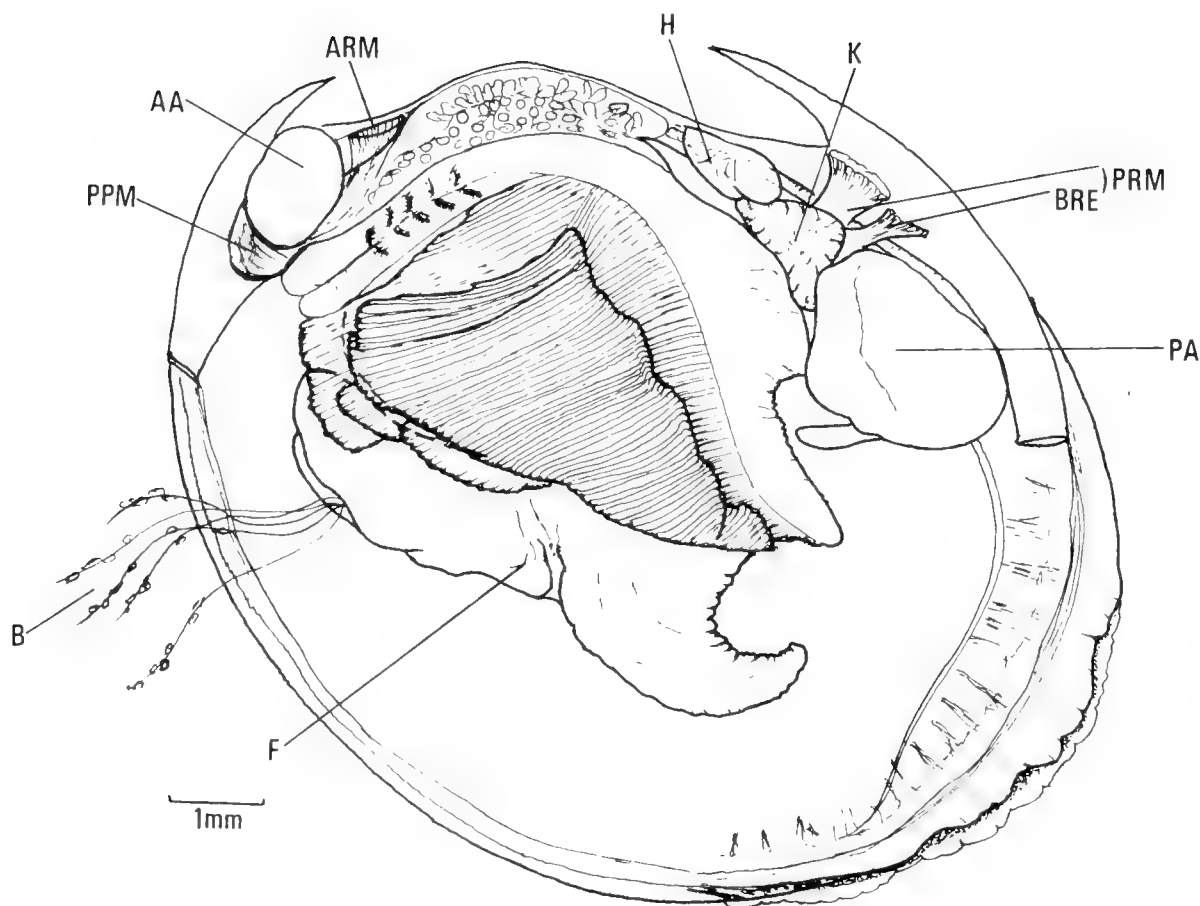
Distribution: Japan.



APP. FIG. 11. Gross anatomy of *Limopsis aurita* Brocchi (left mantle lobe removed).



APP. FIG. 12. Life positions of *Limopsis aurita* in A gravel, B sand and C mud.



APP. FIG. 13. Gross anatomy of *Limopsis diegensis* Dall (left mantle lobe removed). This anatomy is typical of all M.C. V forms.

Morphological Class VI

Diagnosis: Small species: diam. 6 mm. Relatively slightly tumid, inequilateral, becoming slightly obliquely oval. Sculpture weak. Periostracum pilose, of dense short stubby bristles, not fringing. Heteromyarian condition slight. Hinge moderately strong but consisting of few teeth. Ligament small, Type C. Inner margin crenulate and nodular. Anatomically similar to M.C. V, but showing a suite of abyssal adaptations (Oliver & Allen, 1980b). Byssus of 3–5 slender, long, fine threads.

Habitat: Ooze.

Bathymetric range: 3500–5500 m

Distribution: Atlantic Ocean.

Species complement: *Limopsis galathea* Knudsen, 1970.

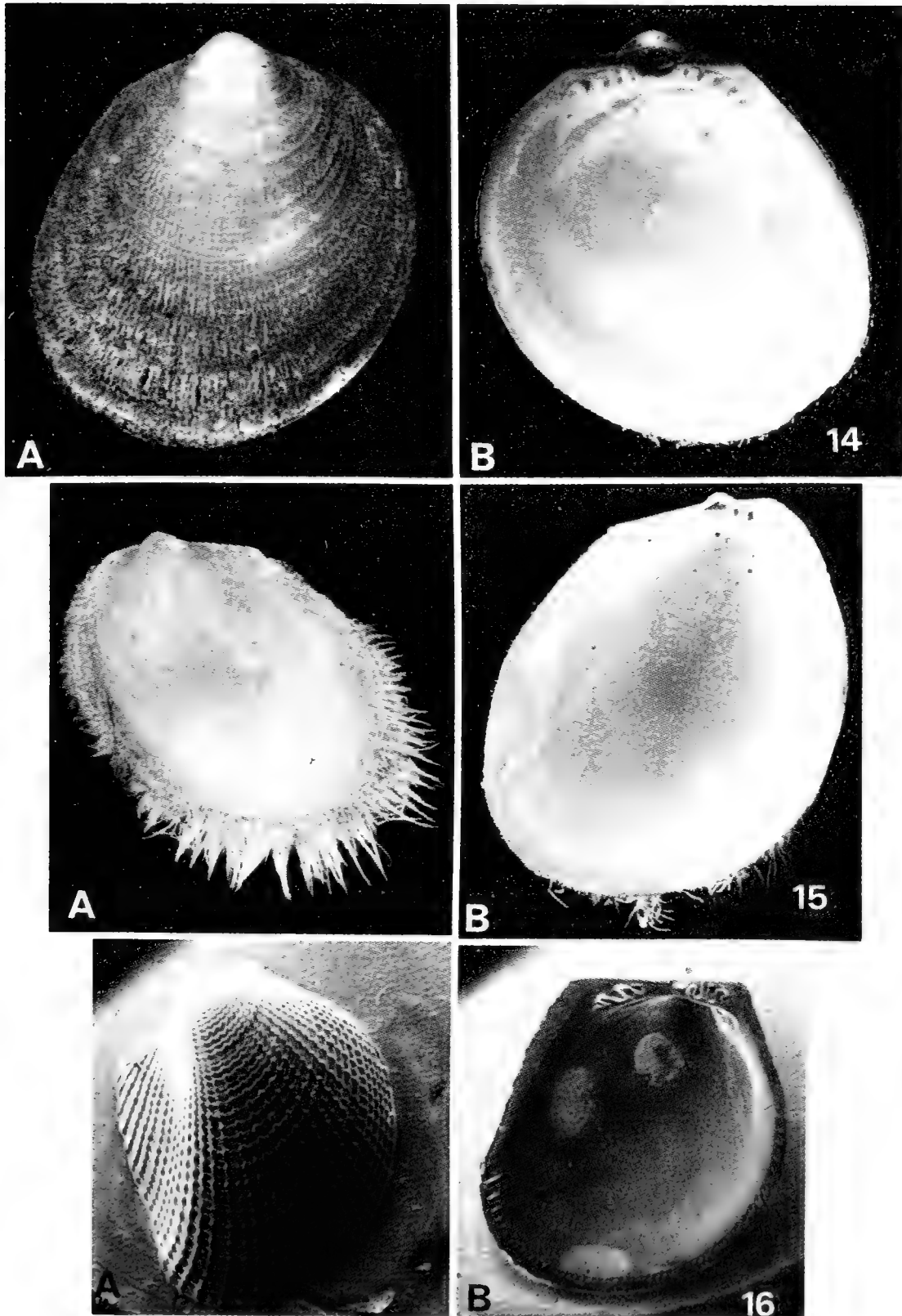
Two abyssal Pacific species have shell similarities to *Limopsis galathea* but anatomical data are not available to substantiate this overall similarity. The species are *L. panamensis* Dall, 1908 and *L. juarezi* Dall, 1908.

Morphological Class VII

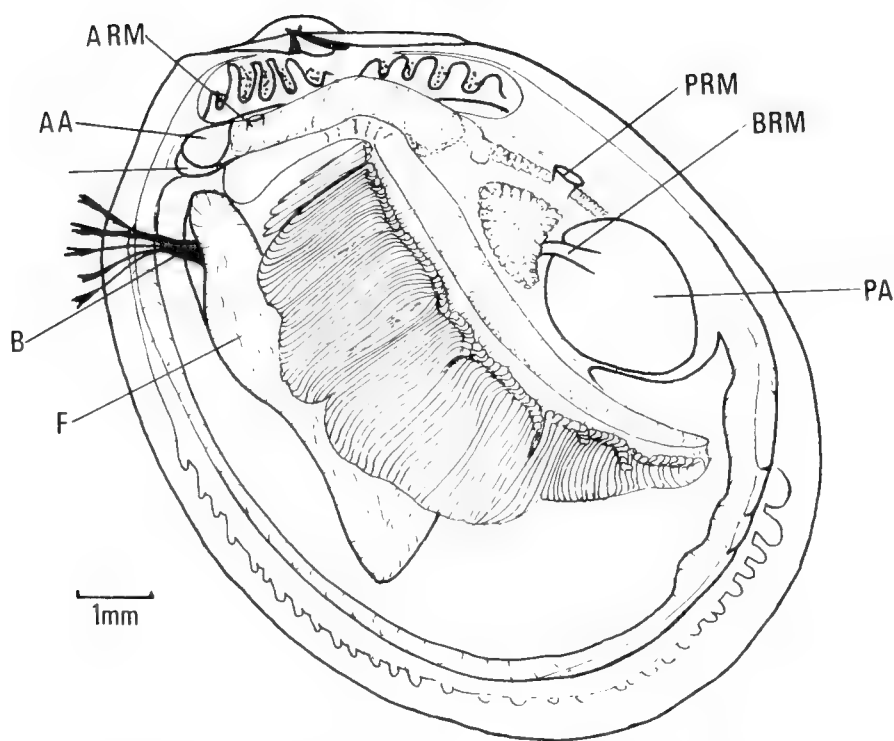
Diagnosis: Small species reaching 15 mm diam. Relatively tumid, inequilateral, becoming markedly obliquely oval with a tendency to develop a short straight antero-dorsal margin. This development may not always occur. Shell relatively thick. Hinge reduced anteriorly, but teeth relatively large. Ligament Type A. Heteromyarian condition extreme, the minute anterior adductor with a prominent myophore. Inner margin crenulate, evenly nodular in juveniles, in adults reduced to 3–5 strong postero-ventral ridges. Anatomically similar to M.C. IV, but the byssus element of the posterior retractor is large and not attached to the shell but inserted into the posterior adductor. The toe of the foot is bulbous and the byssus gland is large. The byssus consists of a sheath with 4–6 short strap-like threads (App. Figs. 15 and 17).

Habitat: Gravels, shell and coral hash, occasionally on finer sediments.

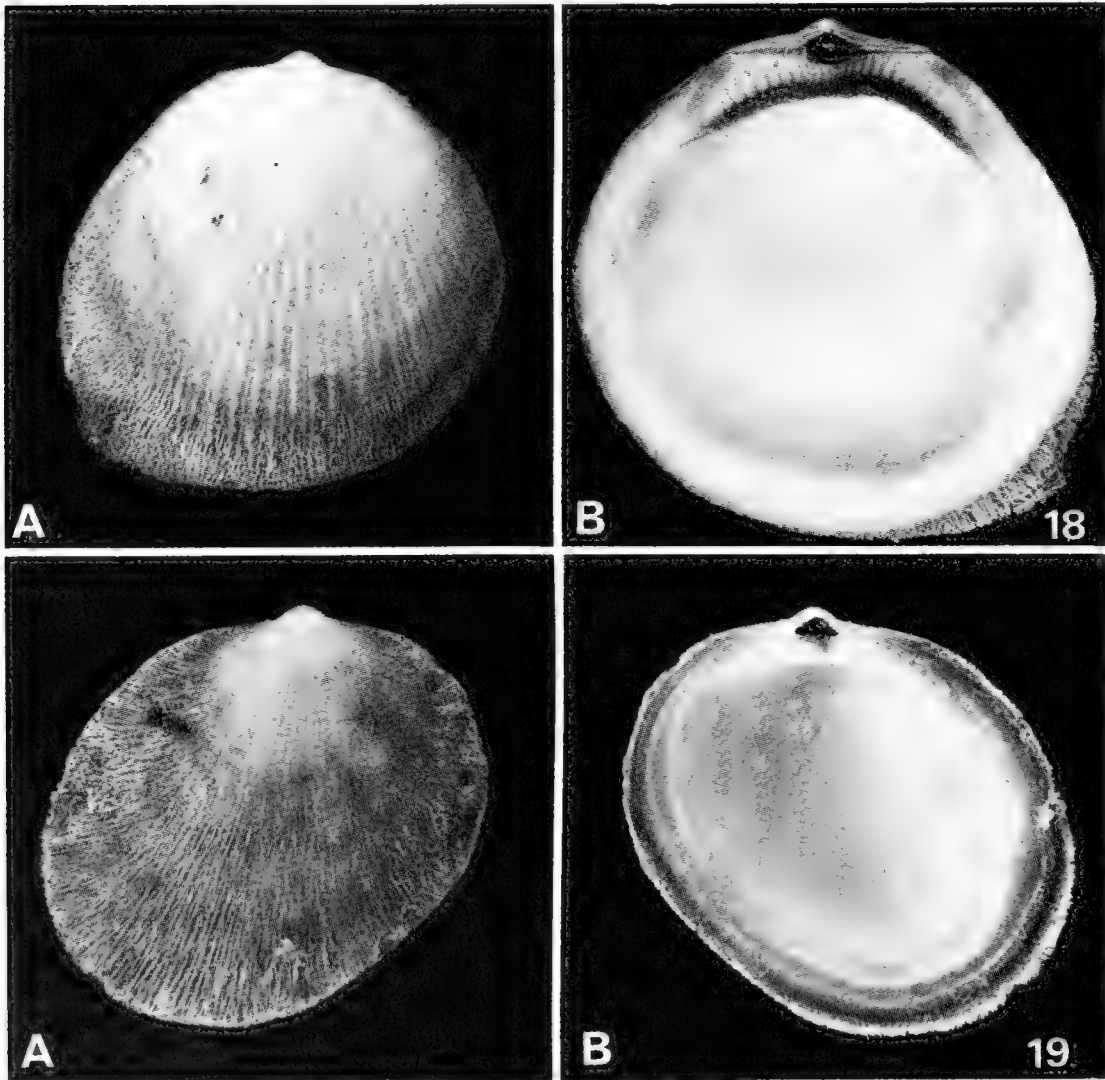
Bathymetric range: 50–2500 m.



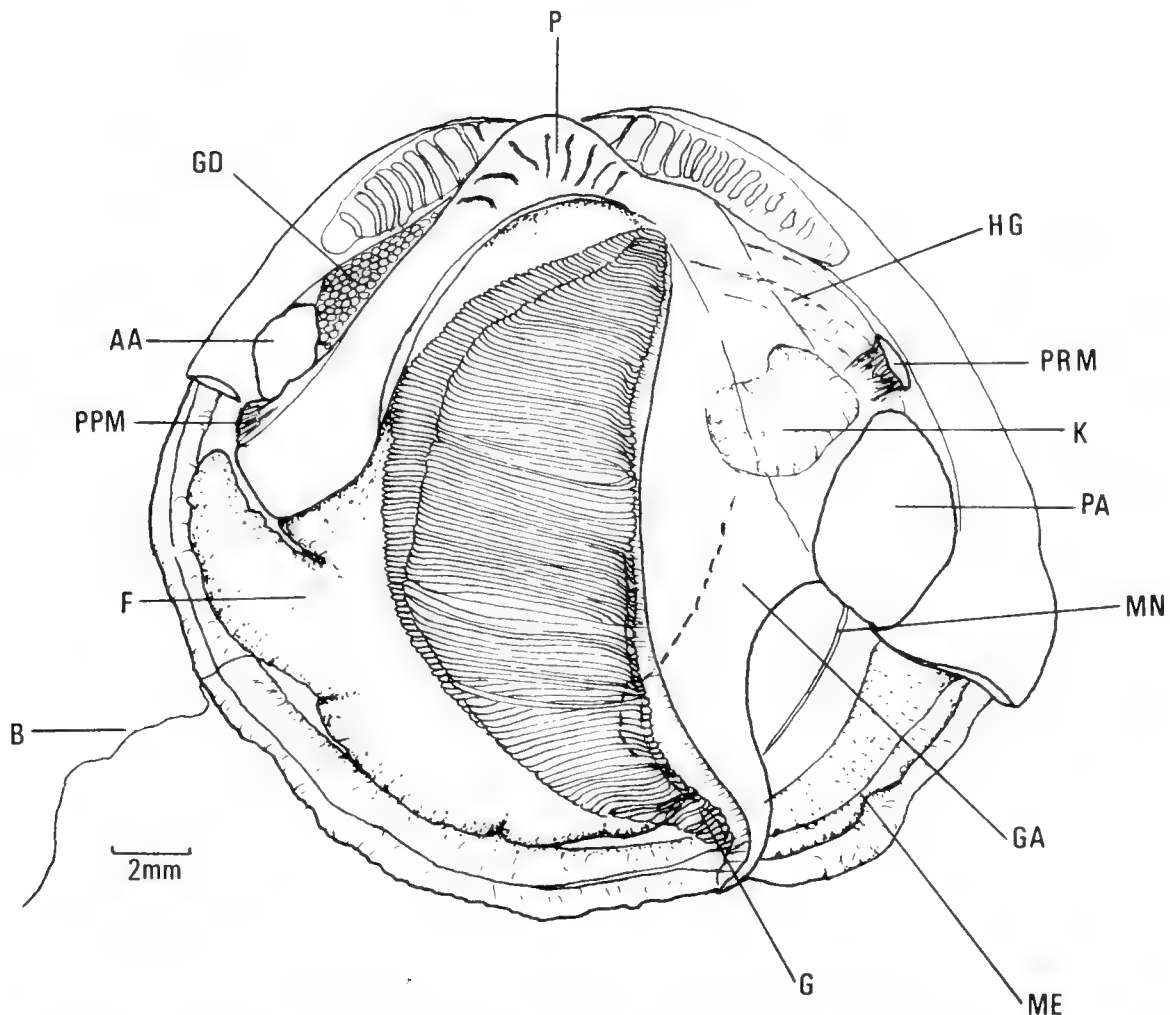
APP. FIG. 14. *Limopsis oblonga* A. Adams. Sagami Bay, Japan. RSM. Diam. 14 mm. APP. FIG. 15. *Limopsis minuta* Philippi. Bay of Biscay. MNHNP. Diam. 12 mm. APP. FIG. 16. *Limopsis natalis* Barnard. Off Natal. NM. Diam. 4 mm.



APP. FIG. 17. Gross anatomy of *Limopsis minuta* Philippi (left mantle lobe removed).



APP. FIG. 18. *Limopsis multistriata* (Forskål). Off Kenya. MCZ. Diam. 25 mm. APP. FIG. 19. *Limopsis bassi* Smith. South Australia. SAM. Diam. 25 mm.



APP. FIG. 20. Gross anatomy of *Limopsis multistriata* (left mantle lobe removed).

Distribution: Atlantic Ocean.

Species complement: *Limopsis minuta* (Philippi, 1836) and *L. abyssicola* A. Adams, 1862.

The New Zealand species *Limopsis lata* Smith, 1885 has a similar shell morphology but no confirmatory anatomical details are available.

Morphological Class VIII

Diagnosis: Minute species rarely exceeding diam. of 5 mm, relatively tumid, becoming obliquely quadrate with a long straight antero-dorsal margin. Sculpture weakly decussate. Periostracum 'thatched.' Ligament small, Type C. Dorsal area small. Hinge reduced anteriorly with few but relatively large teeth. Heteromyarian condition extremely advanced. Anterior myophore small. Margin crenulated as in M.C. VII except that the postero-ventral emphasis is present in all but the smallest specimens. Anatomically similar to M.C. VII but there is no specialized byssus

retractor. Byssus consists of 3–5 short strap-like strands (App. Fig. 16).

Habitat: Sands and shell gravels.

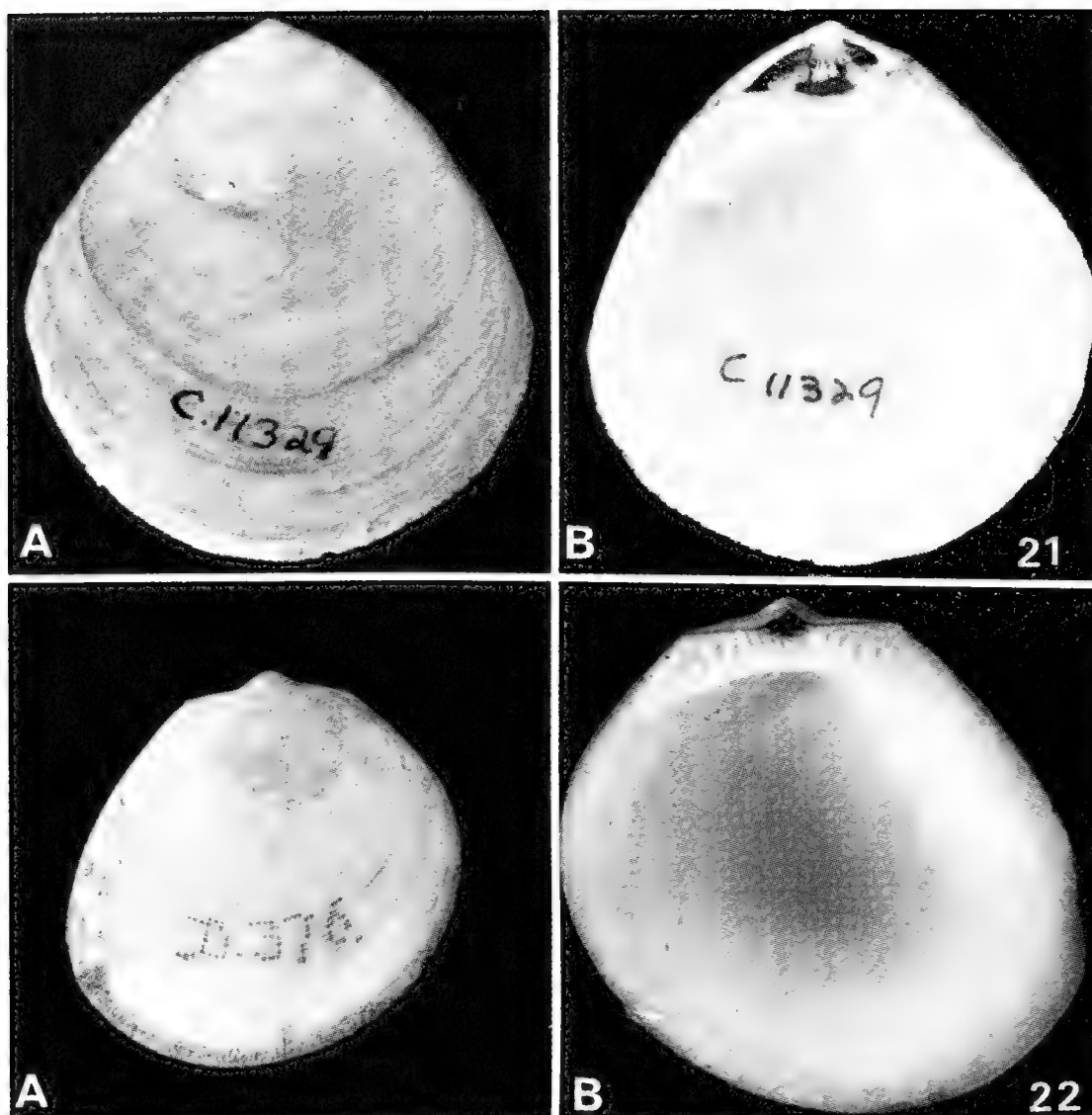
Bathymetric range: 100–600 m.

Distribution: Caribbean and Southeast Africa.

Species complement: *Limopsis antillensis* Dall, 1881; *L. natalis* Barnard, 1964 and *L. elachista* Sturany, 1899.

Morphological Class IX

Diagnosis: Moderately large species: diam. 25–45 mm. Equivalve, compressed, becoming obliquely circular, some large specimens dorsally attenuate. Shell thick. Sculpture of both concentric and radial ridges, more or less decussate in juveniles but radially ribbed in adults. Periostracum 'thatched,' but not persistent except at the postero-ventral margin. Dorsal area variable, usually small and narrow, but in dorsally attenuate species this area is expanded, remaining deeply cleft. Ligament Type A, variable and may be large.



APP. FIG. 21. *Limopsis loringi* Angas. Port Stephen, New South Wales. AMS. Diam. 33 mm. APP. FIG. 22. *Limopsis eucosmus* Verco. Gt. Australian Bight. SAM. Diam. 21 mm.

Hinge strong, teeth numerous, in two distinct series set on a high arch, central teeth of each set are the largest. Heteromyarian condition slight, both scars with fine buttresses. Shell between scars evenly radially striate. Inner margin crenulated, fluted. Foot with reduced toe and heel, blade-like, highly muscular. Posterior pedal retractors simple, large. Anterior dorsal retractors spread over the visceral mass with little or no shell attachment. Byssus gland small but capable of producing a single long fine thread which is, however, rarely observed. Gill axis orientated vertically relative to the hinge plate; axis musculature very small. Palps with numerous well-developed sorting ridges. Mantle edge greatly thickened postero-ventrally (App. Figs. 6B, 18 and 20).

Habitat: Sands, silts and muds.

Bathymetric range: 0–400 m.

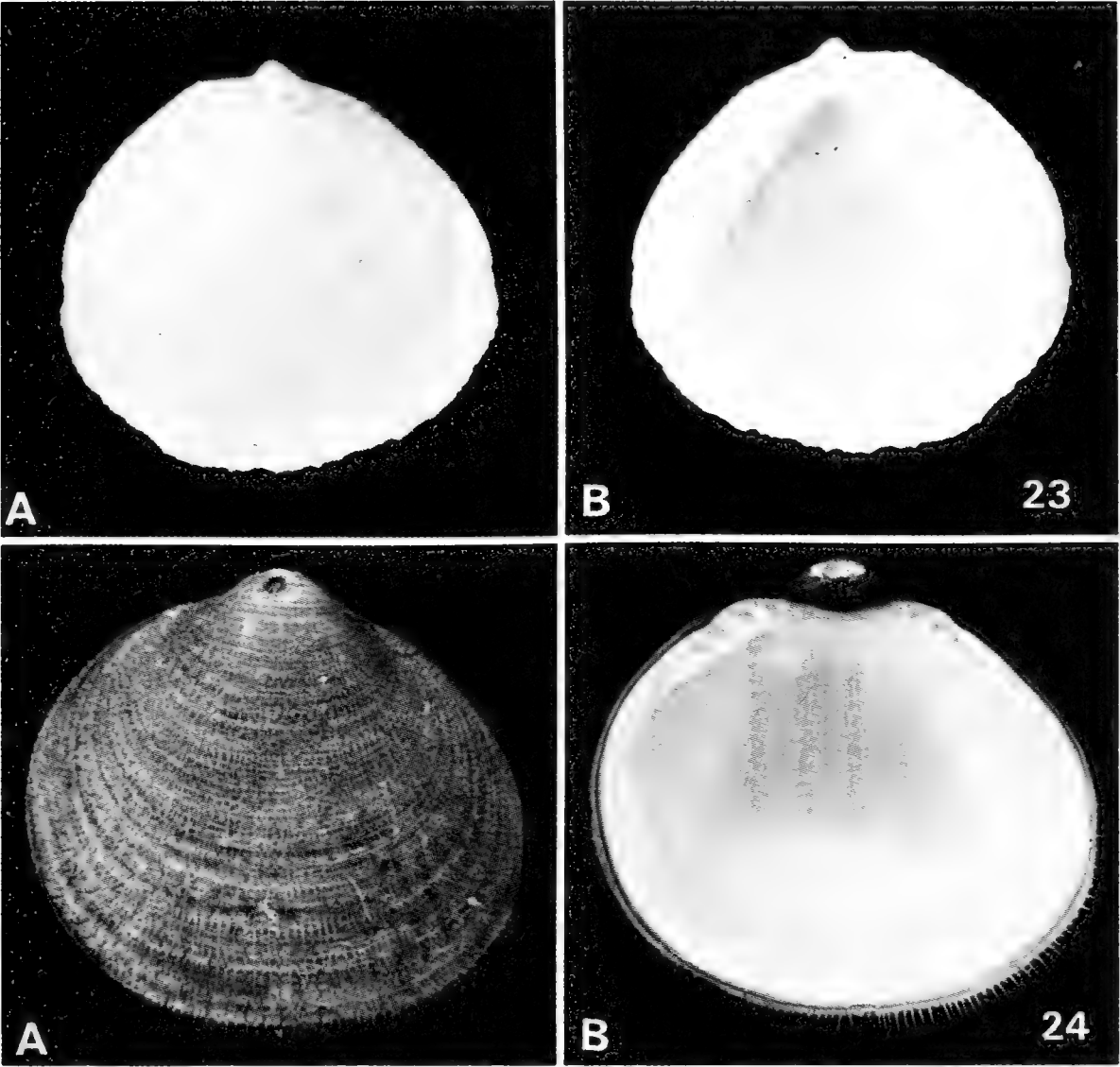
Distribution: Indo-Pacific and South Australia.

Species complement: *Limopsis multistriata* (Forskål, 1775); *L. compressa* G. & H. Nevill, 1874; *L. cancellata* (Reeve, 1843); *L. woodwardi* A. Adams, 1862; *L. macgillivrayi* A. Adams, 1862; *L. torresi* Smith, 1885; *L. japonica* A. Adams, 1862; *L. forskali* A. Adams, 1862; *L. soyoae* (Habe, 1953); *L. tenisoni* T. Woods, 1877; *L. tenuiradiata* Cotton, 1931; *L. forteradiata* Cotton, 1931.

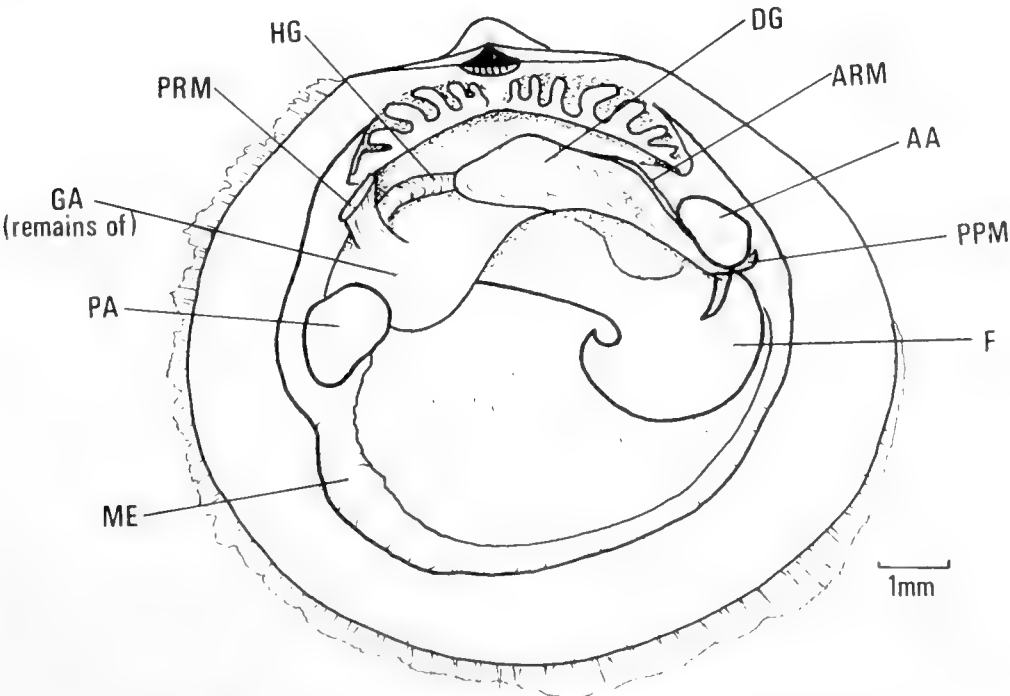
Habits: J. D. Taylor (personal communication) has observed *Limopsis multistriata* living in sub-littoral sands off Shimoni, Kenya. They were observed to burrow completely in the sand although a number were lying free on the surface.

Limopsis bassi Smith, 1885

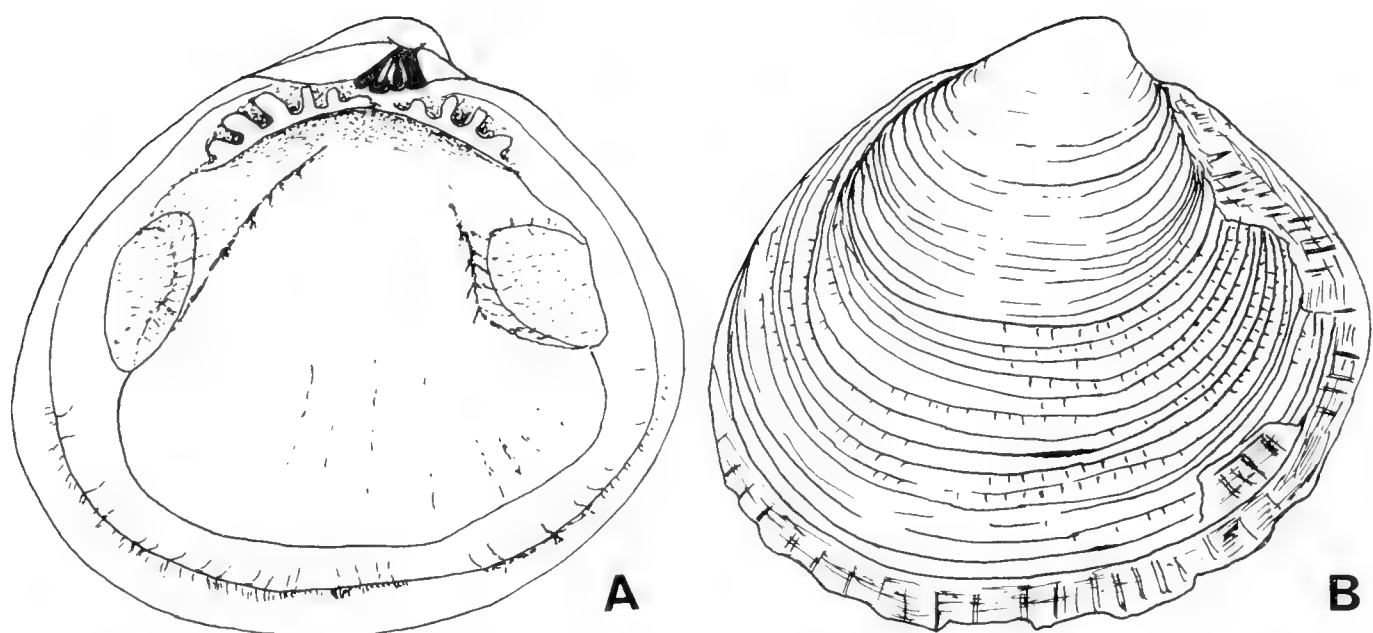
This species is similar to M.C. IX species, but is obliquely oval with a less rounded anterior margin. The sculpture is weaker, as is



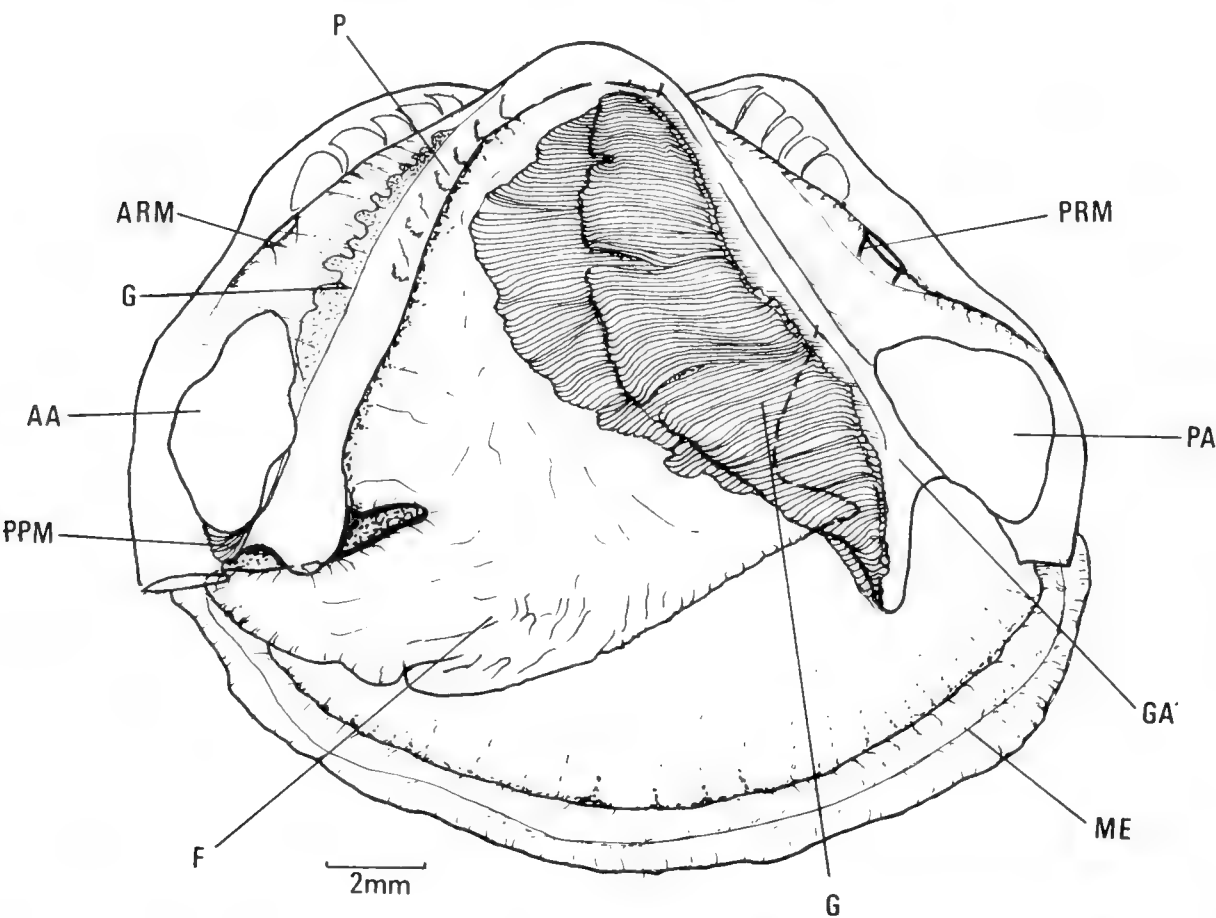
APP. FIG. 23. *Limopsis vixornata* Verco. Neptune Island. South Australia. SAM. Diam. 10 mm. APP. FIG. 24. *Limopsis lilliei* Smith. South Orkney Islands, Antarctica. NMW. Diam. 14 mm.



APP. FIG. 25. Gross anatomy of *Limopsis vixornata* Verco.



APP. FIG. 26. *Limopsis brazieri* Angas. Port Jackson, New South Wales. BMNH. Diam. 5 mm.



APP. FIG. 27. Gross anatomy of *Limopsis lilliei* Smith (left mantle lobe removed).

the hinge. The heteromyarian condition is greater, similar to that of M.C. I. The foot has a well-developed toe. The antero-dorsal retractors have shell attachments. The gill axis is orientated obliquely (App. Fig. 19).
Habitat: Sands.
Bathymetric range: Shelf zone.
Distribution: South Australia.

Morphological Class X
Diagnosis: Very similar to M.C. IX, but the sculpture is very finely decussate and the inner margin is smooth. Tevesz (1977) shows the anatomy to be similar to that of M.C. IX in the form of the foot and orientation of the gill axis. The byssus differs in being active, pro-

ducing up to five long fine threads (App. Fig. 21).

Habitat: Shell hash.

Bathymetric range: 40–70 m.

Distribution: Southeast Australia.

Species complement: *Limopsis loringi* Angas, 1873; *L. soboles* (Iredale, 1931) and *L. dannevigii* (Iredale, 1931).

Habits: Tevesz (1977) described the burrowing actions of *Limopsis loringi* and *L. soboles*. Burrowing action is slow, taking up to 45 mins to burrow completely up to the postero-ventral margin. No indication of ploughing activity was given by Tevesz.

Limopsis eucosmus Verco, 1907 (App. Fig. 22)

This is a South Australian species which is similar in outline and anatomy to *L. bassi*, i.e. it is a heteromyarian oblique form with a toed foot. Its other shell characters are, however, of the M.C. X form. The variety *penelevis* Verco, 1907 is even more extreme in its thinner shelled compressed form. The character of the byssus is not known; the byssus slit is well developed.

Morphological Class XI

Diagnosis: Small species reaching 12 mm in diam. Equivalve, compressed, almost inequilateral, sub-circular with a slight posterior extension, large specimens dorsally attenuate. Umbos very slightly prosogyre. Shell moderately thick. Sculpture concentric with very weak radial markings. Periostracum 'thatched' but not persistent. Dorsal area small, narrow. Ligament small, Type A. Hinge moderate, teeth in two series on a moderate arch, central teeth in each set dominant. Adductor scars sub-equal, heteromyarian condition slight, both scars weakly buttressed. Margin smooth. Examination of dried soft parts showed some critical features. Foot bladeliike with small heel and toe. Posterior pedal retractors large. Anterior retractor with little or no shell attachment. The dried translucent foot showed no trace of the dark staining typical of the byssus gland. No byssus slit was observed. Mantle edge greatly thickened (App. Figs. 23 and 25).

Habitat: Unknown.

Bathymetric range: 70–200 m.

Distribution: South Australia.

Species complement: *Limopsis vixornata* Verco, 1907 and *L. occidentalis* Verco, 1907.

Morphological Class XII

Diagnosis: Small shells reaching 7 mm in diam. Equivalve, relatively slightly tumid, sub-equilateral with slight posterior extension, longer than high; sub-elliptical. Umbos prosogyre. Shell thick. Sculpture concentric with very weak radial markings. Dorsal area short, ligament relatively large Type A. Hinge moderately strong but with few teeth. Heteromyarian condition slight, adductor scars sub-equal, both buttressed. Margin smooth. No anatomical details available (App. Fig. 26).

Habitat: Unknown.

Bathymetric range: Shallow shelf zone.

Distribution: New South Wales, Australia.

Species complement: *Limopsis brazieri* Angas, 1871.

Morphological Class XIII

Diagnosis: Medium-sized species: diam. 20–25 mm. Equivalve, relatively slightly tumid, sub-equilateral, very slightly posteriorly extended, sub-elliptical. Shell thin. Sculpture finely decussate. Periostracum pilose, persistent. Hinge weak, teeth in two series on a low arch, ligament Type D. Adductor scars large, sub-equal, with very fine buttress lines. Internally striate. Margin smooth. Foot large, toe and heel not elongate, pedal retractors simple, posterior pair large. Byssus gland present but very small, no byssus observed. Gill axis orientated vertically with very little musculature. Mantle edge thickened, especially postero-ventrally (App. Figs. 6C, 24, and 27).

Habitat: Muds, muddy sand and muddy gravel mixtures.

Bathymetric range: 80–500 m.

Distribution: Antarctic Ocean.

Species complement: *Limopsis lilliei* Smith, 1885; *L. hirtella* Mabile & Rochebrune, 1889; *L. enderbyensis* Powell, 1958 and *L. scotiana* Dell, 1964.

ASPECTS OF THE ADAPTIVE MORPHOLOGY OF *MESODESMA MACTROIDES* (BIVALVIA: MESODESMATIDAE)

Walter Narchi

*Departamento de Zoologia, Universidade de São Paulo, Caixa Postal 20.520, 01000
São Paulo, Brasil*

ABSTRACT

Mesodesma mactroides Deshayes, 1854 lives in southern Brazil, occurring in shallow water on clean sand beaches where there is much wave action. *M. mactroides* is infaunal and possesses a number of morphological adaptations that suit it for a life in sandy beaches and for feeding in water with suspended particles. The most significant of these adaptations concern the organs of the mantle cavity. A comparison is made between *M. mactroides* and other infaunal mesodesmatids.

Interest in this species also centres around its habit of living infaunally, possessing a well-developed foot, an elevator pedal muscle and a wedge-shaped shell well designed for high speed burrowing, particularly by young animals. Adult clams are found 15-20 cm deep. They have a thin shell and two well developed and separate siphons. Siphonal hearts in *M. mactroides* are described for the first time; they are rounded structures located between the internal openings of the exhalant and inhalant siphons and contract spontaneously or under slight stimulation. The principal function of the siphonal hearts seems to be the pumping of blood into the long siphons, which possibly act as respiratory organs similar to the mantle and gills, or the long siphons may require an accessory pump in order to circulate blood within them. No other bivalves with long siphons are known to have similar structures. The major structural features and ciliary currents of *M. mactroides* are described; its functional morphology is similar to that of related genera such as *Mactra*, *Spisula*, *Lutraria* and *Caecella*.

INTRODUCTION

The wide post-Paleozoic radiation of infaunal bivalves led to a preponderance of new Mesozoic and Cenozoic groups which were burrowers feeding by means of siphons (Stanley, 1968). Infaunal bivalves are thus of primary importance in most of the benthic communities of modern seas (Thorson, 1957). The bivalves which burrow in soft substrata may be active or more or less sedentary, and often live well below the sediment-water interface. According to Stanley (1968), life habit data suggest that bivalve adaptive radiation is related to mantle fusion and the development of siphons. There is a general agreement among bivalve taxonomists that most of the commonly recognized bivalve superfamilies, essentially similar to the "Stirps" of Thiele (1934), represent natural groups of related taxa.

The superfamily Mactracea appeared in the late Mesozoic (Cretaceous) and existed throughout the Cenozoic. As with most heterodont bivalve superfamilies, the

Mactracea are restricted to suspension-feeding with eulamelibranch ctenidia.

The paleontological records show that the mesodesmatid ancestral stock originated in Australasia, whence it gradually invaded South Africa, New Zealand, the Antarctic and, in successive migrations, South America. From the Tertiary deposits of Patagonia there are no fossil records. Ihering (1907) believed that *Mesodesma* appeared in South America in the late Pliocene or possibly in the early Pleistocene during a great migration of molluscs from the Antarctic, following two cold currents: the Malvinas on the east coast and the Humboldt on the west coast. This migration was probably caused by decreasing temperatures towards the end of the Tertiary and early Quaternary periods. According to Ihering, the dispersion of *Mesodesma* on the Patagonian coast occurred during the Pleistocene and has only recently encompassed the Brazilian littoral, delayed by a zoogeographic barrier, the mouth of La Plata River.

Recent studies on the genus *Mesodesma*

are mainly concerned with taxonomy, shell morphology, anatomy and ecology (Ihering, 1897; Lamy, 1914; Carcelles, 1939; Castellanos, 1948; Coscaron, 1959; Davis, 1964, 1965, 1967; Stanley, 1970; Olivier et al., 1971; Beu, 1972; Habe, 1973). Purchon (1960) has described the stomach of *Atactodea*, regarded by Thiele (1934) as a section of the genus *Mesodesma*, and Allen (1975) described the functional anatomy of *Mesodesma arctatum*, restricted to the northwest Atlantic.

Except for the thin shells which are not disproportionately heavy as Allen (1975) described for *Mesodesma arctatum*, *M. mactroides* Deshayes, 1854 agrees with the general characters of the family Mesodesmatidae cited by Cox et al. (1969). The only difference is that the hinge of the specimens found in São Paulo is not strong and the teeth are very poorly developed.

Mesodesma mactroides occurs from the southern part of Brazil to Patagonia (Carcelles, 1944). It is a moderately frequent shallow water species and is common in Brazilian waters where it has been recorded along the coasts of Rio de Janeiro (Rios, 1970, 1975), São Paulo (Lange de Morretes, 1949) and Paraná (Gofferré, 1950). It was first recorded from Brazilian waters by Ihering (1897) and is called "sernambi," "marisco" or "marisco branco" by the local fishermen. The animals are eaten by the coastal population steamed or with rice, and it is an important food supply mainly in Rio Grande do Sul, Uruguay and Argentina. Deshayes (1854) described *M. mactroides* without giving a type-locality. Carcelles (1939) gives a good systematic account of the species. Ihering (1897) refers to *M. arechavalettoi* known as "almeja amarilla" from the mouth of La Plata River, which is bigger, robust and with a yellow periostracum. Lamy (1914) and Carcelles (1939) considered *M. arechavalettoi* to be *M. mactroides*. The animals from São Paulo have a transparent periostracum, and a much thinner shell than the specimens from Argentina.

Isolated references to *Mesodesma mactroides* are found mainly in systematic accounts; Castellanos (1948) studied its anatomy and Olivier et al. (1971) described the life-history, ecology and observed a population of *M. mactroides* during a period of two years at Mar Azul, a resort 115 km N of the city of Mar del Plata, Argentina. Until now, no studies of the functional morphology of *M. mactroides* have been undertaken.

MATERIALS AND METHODS

Living specimens were obtained from beaches at Santos and Bertioga on the coast of São Paulo, Brazil. They were collected during low tide from clean sand in disturbed waters with wave movement. The water contained a large amount of suspended material. The species is a rapid burrower; the pointed foot emerges from the elongate antero-ventral region of the shell and probes the sand quickly to gain a foothold. Erection of the shell is normally accomplished by a single burrowing sequence which pulls the animal directly downward without the rocking movement described for *Mesodesma arctatum* by Stanley (1970).

Small specimens of *Mesodesma mactroides* measuring less than 2 cm long co-occur with *Donax hanleyanus* at the Santos beaches, in the lower eulittoral. *M. mactroides* is flushed from the sand by the advancing surf and transported up the beach. The clams would be carried down in the backwash, but by extending their siphons and foot to act as brakes, they prevent being washed away.

Adult *Mesodesma mactroides* clams, unlike *M. arctatum* (Allen, 1975), are found 15–20 cm deep (Fig. 1) in firm sand, with the large foot extended as an anchor, their long siphons lying flush with the surface of the sand. *M. mactroides* lives buried at depths about four times greater than that of *M. arctatum* (Stanley, 1970), i.e. about twice the length of the shell of the latter. The beaches of São Paulo, where the animals were found, are flat, and when the tide recedes, the bivalves are stranded above the water line. The sand becomes more compact during the ebb tide. The mean particle diameter is less than 0.5 mm.

The clams could usually be found by locating the small siphon holes on the surface of the sand. Only adult clams, in their deep burrow, can hold their position on the beach using their enlarged foot. Because the smaller clams are anchored less firmly, they are flushed out more frequently and washed farther up the beach than the large clams.

The animals were collected during low tide by digging into the sand with a small mattock.

I will describe the structure, ciliary currents of feeding and digestion and other functional adaptations of *Mesodesma mactroides* in relation to their environment. Drawings are of relaxed and preserved specimens. Magnesi-

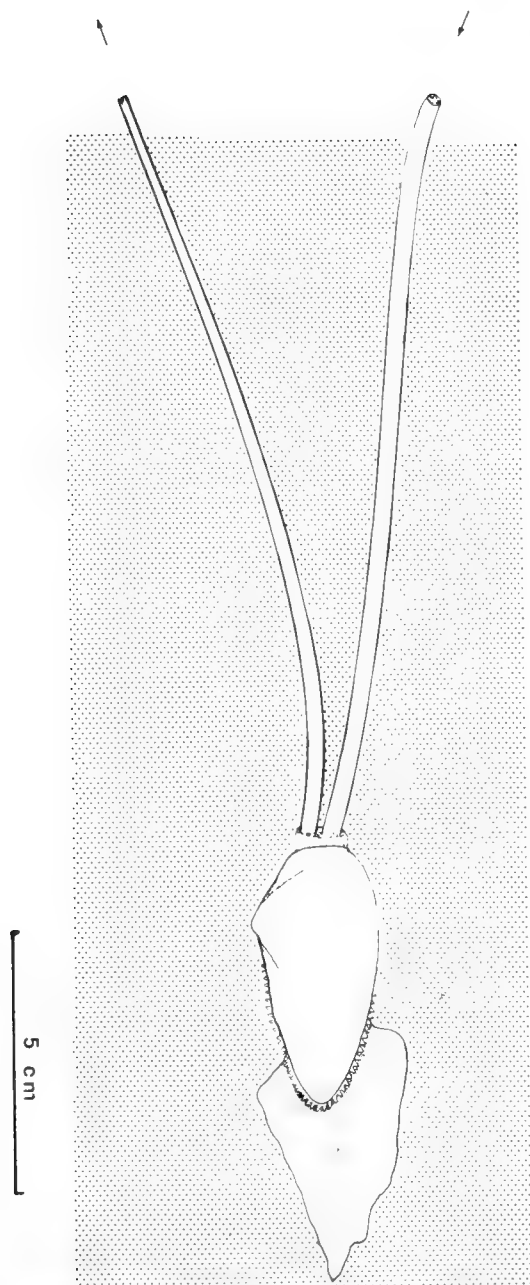


FIG. 1. *Mesodesma mactroides*. External view of the left side. Living specimen digging in firm sand with its large foot extended.

um sulphate was used as a relaxing agent, ciliary currents were studied using carborundum, carmine and Aquadag suspensions. Sections (6 to 8 μ m thick) were made of tissues fixed in Bouin's fluid, stained with Ehrlich's haematoxylin and eosin, and Mallory's Triple Stain.

Living specimens were observed at the Departamento de Zoologia, Universidade de São Paulo.

FUNCTIONAL MORPHOLOGY

The shell

Contrary to the other species of *Mesodesma*, *M. mactroides* does not have a ro-

bust shell. It is thin, a little inflated, elongate-oval, inequilateral, tapering slightly toward the rear, rostrate behind, the rostration prolonged to a moderately acute tip. The anterior margin is acute, the ventral margin almost straight, the posterior margin rounded below and obliquely subtruncate above. Beaks low, situated at the posterior third. The shell surface is slightly marked by delicate concentric lines, covered by a transparent periostracum.

The anterior muscle scar is relatively long and lenticular, with a ragged inner and a smooth outer margin; the posterior scar is broadly oval. The pallial sinus is asymmetrically arcuate. It rises from the inner and lower surface of the posterior adductor scar, is obtusely subangular at the forward end, and joins the faint pallial line near the posterior third.

The hinge plate (Fig. 2) is not strong and broad as in *Mesodesma arctatum* (Allen, 1975). There are two lateral teeth and two cardinal teeth with an accessory lamina in the left valve. In the right valve there are two cardinal and three lateral teeth, which are smooth without serration as in *M. arctatum* (Allen, 1975).

The external ligament is not prominent but a subtriangular chondrophore is well developed in both valves.

The lunule is rudimentary and the escutcheon vestigial. The surface of the shell is marked by delicate concentric growth lines. The shell is generally white but in some specimens the shell margin is darkly colored.

The periostracum is translucent but in a few specimens it is yellowish.

The shell of the largest animal studied measured 5.8 cm in length, 3.2 cm in height, and 1.6 cm in width.

The siphons

The siphons are separate and well developed. In a specimen 5 cm long, the siphons were both almost 15 cm long. The detailed structure is shown in Fig. 3. The external surface of both siphons bears two longitudinal rows of small, colourless, sensitive papillae without surrounding pigmentation, as found in *Ensis ensis* (Deshayes, cited in Haas, 1934). Franc (1960) described two rows of small papillae on the exhalant siphon and only one on the inhalant siphon of *Ensis ensis* (not *Corbula mediterranea* as he states: compare fig. 312 of Haas, 1934, with fig. 1633 of Franc,

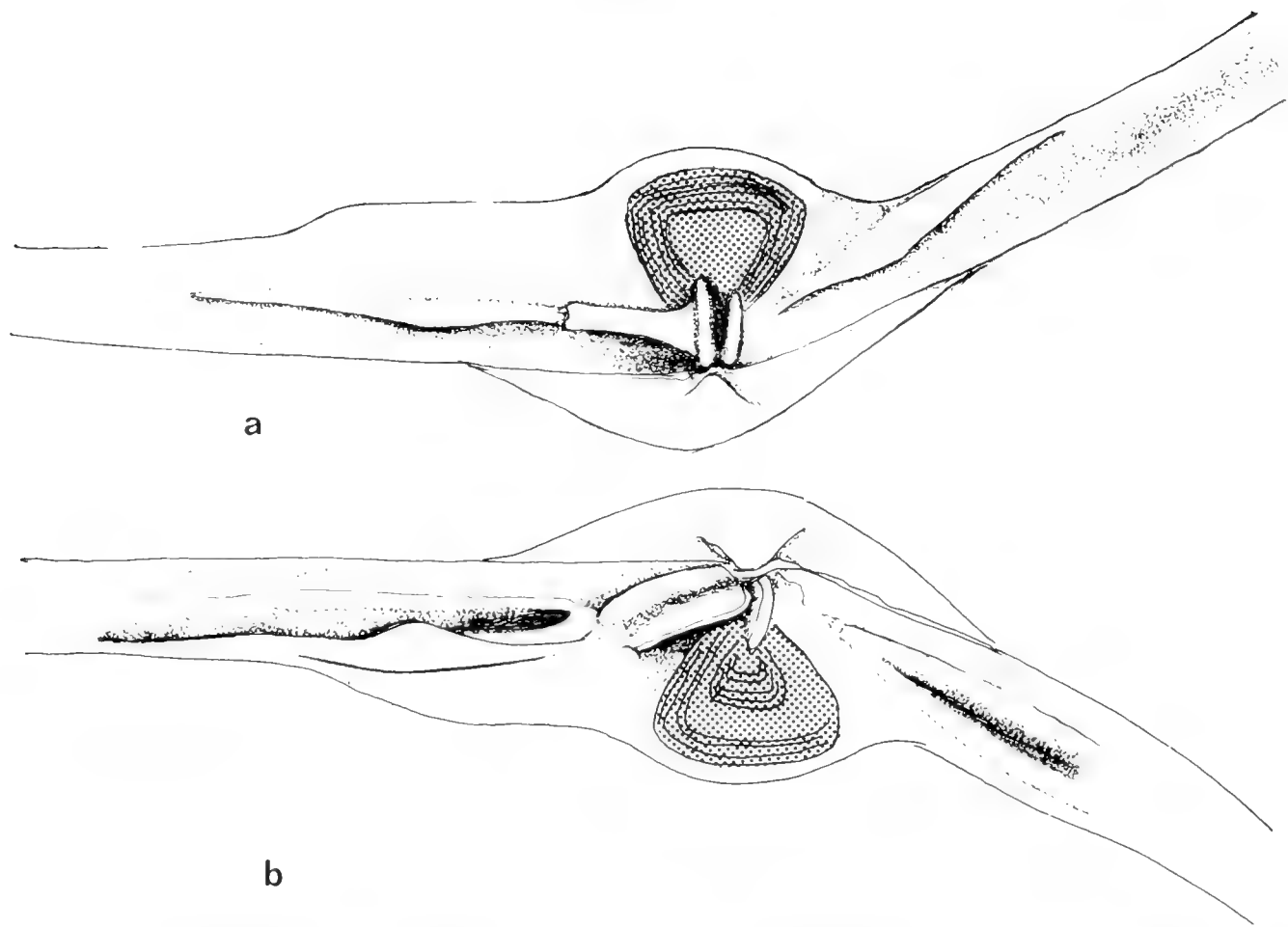


FIG. 2. *Mesodesma mactroides*. Internal view of the hinge plate. a, right valve; b, left valve.

1960). The inhalant aperture is fringed with three cycles of tentacles surrounding the aperture, and is similar to that of *Mesodesma cornea* (Fischer, 1887). The innermost series, the largest and the most ramified, is formed by eight tentacles. They are directed inwards when the animal is pumping water. These tentacles are interspersed by small accessory papillae. The two series of smaller foliose tentacles surround the inner. They too are directed inwards so that the inhalant aperture is, in effect, covered by a coarse sieve. The 48 tentacles are unpigmented, unlike those of *Tivela mactroides* (Narchi, 1972). The aperture of the exhalant siphon is a little smaller than that of the inhalant. Twenty simple tentacles surround the exhalant opening as in *T. mactroides* (Narchi, 1972). In specimens 2 cm in length, six tentacles sometimes are better developed and have a divided tip. An extensive siphonal flap is developed across the inner opening of the inhalant siphon. This is a vertical extension of the posterior margin of the septum dividing inhalant from exhalant channels.

The positions of the siphons in life are shown in Fig. 1.

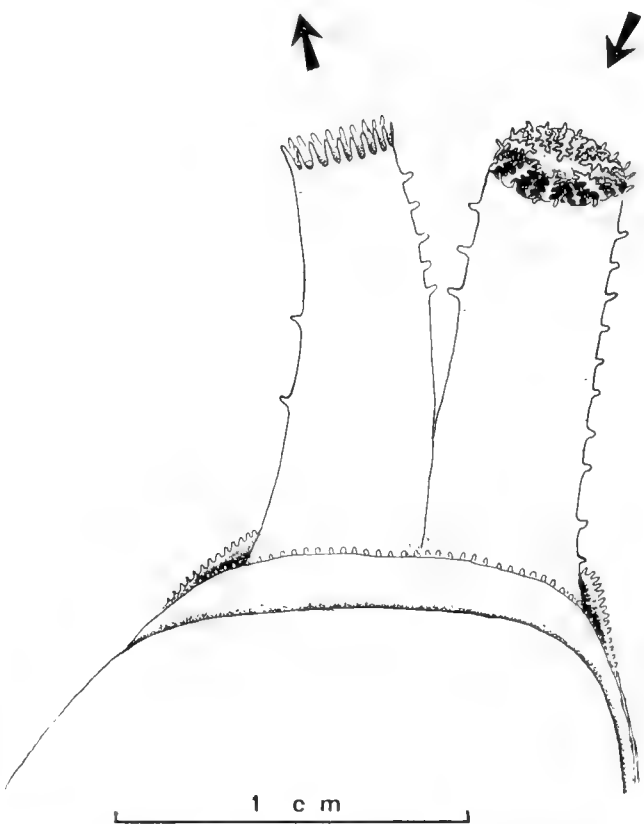


FIG. 3. *Mesodesma mactroides*. The siphons of the live animal. The arrows show the direction of the inhalant and exhalant currents.

The circulatory system and the siphonal hearts

Some invertebrates possess certain peripheral blood vessels specialized to pump blood into organs that would otherwise have little circulation. Among molluscs the best known are the "gill hearts" of cephalopods and the "accessory hearts" in oysters (Hopkins 1934a, 1934b, 1936).

Removal of one mantle lobe of *M. mactroides* exposes a pair of well-defined, rounded structures within the supra-axial chamber just below the inner opening to the exhalant siphon (Fig. 4). These structures, recorded here for the first time in the Bivalvia, contract spontaneously or under mechanical stimulation. They are not the peripheral blood vessels that Galtsoff (1964) observed in *Crasostrea virginica*, and I term them siphonal hearts.

The well-developed muscular fibres of the walls of the siphonal hearts resemble those of the ventricle (Fig. 5).

The connection of the siphonal hearts to other blood vessels has been studied using the modified injection method of Galtsoff

(1964). When the ventricle is injected, fluid enters the anterior and posterior aortas. From the posterior aorta the fluid passes to the aortic bulbs and from here it enters the siphonal hearts. Injecting the siphonal hearts fills the arteries of the siphons.

The mantle and its ciliary currents

The two mantle lobes are unfused anteriorly, forming a large pedal gape. The two mantle lobes fuse mid-ventrally, this fusion extending up to the inhalant siphonal aperture. Fusions also occur between inhalant and exhalant siphons and dorsal to the exhalant siphon. Only the inner folds are fused. The middle mantle fold is moderately well developed and bears two regular rows of small papillae, those external with two or four digitate projections.

The inner surface of the mantle is ciliated and its ciliary currents are shown in Fig. 6. On each lobe they converge mid-ventrally, posterior to the foot, and enter a ventral tract formed by erectile mantle folds that may be elevated and bent toward each other until they almost or quite meet, forming the "waste

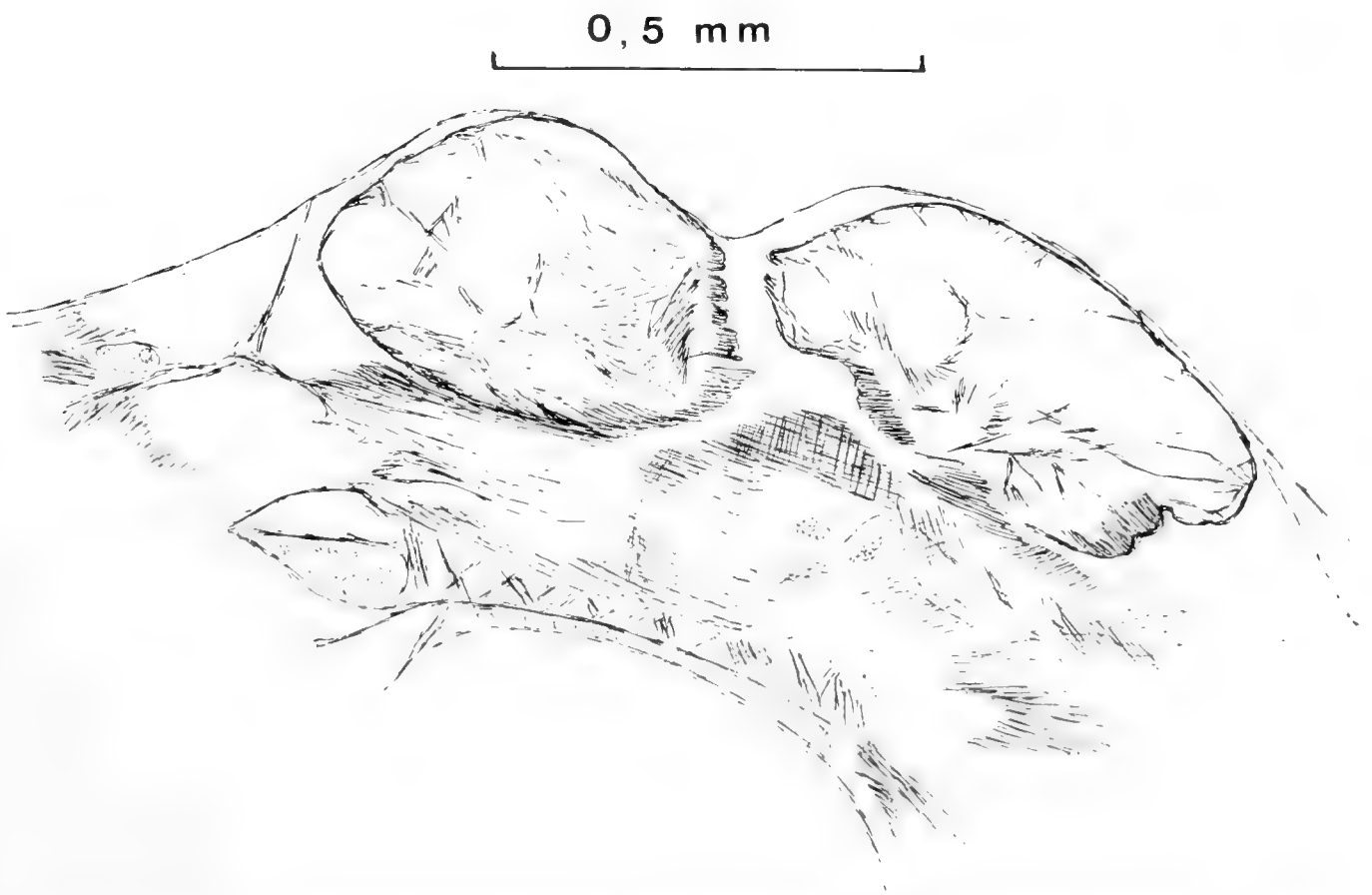


FIG. 4. *Mesodesma mactroides*. A transverse section through the siphonal hearts showing the arrangement of muscle fibres.

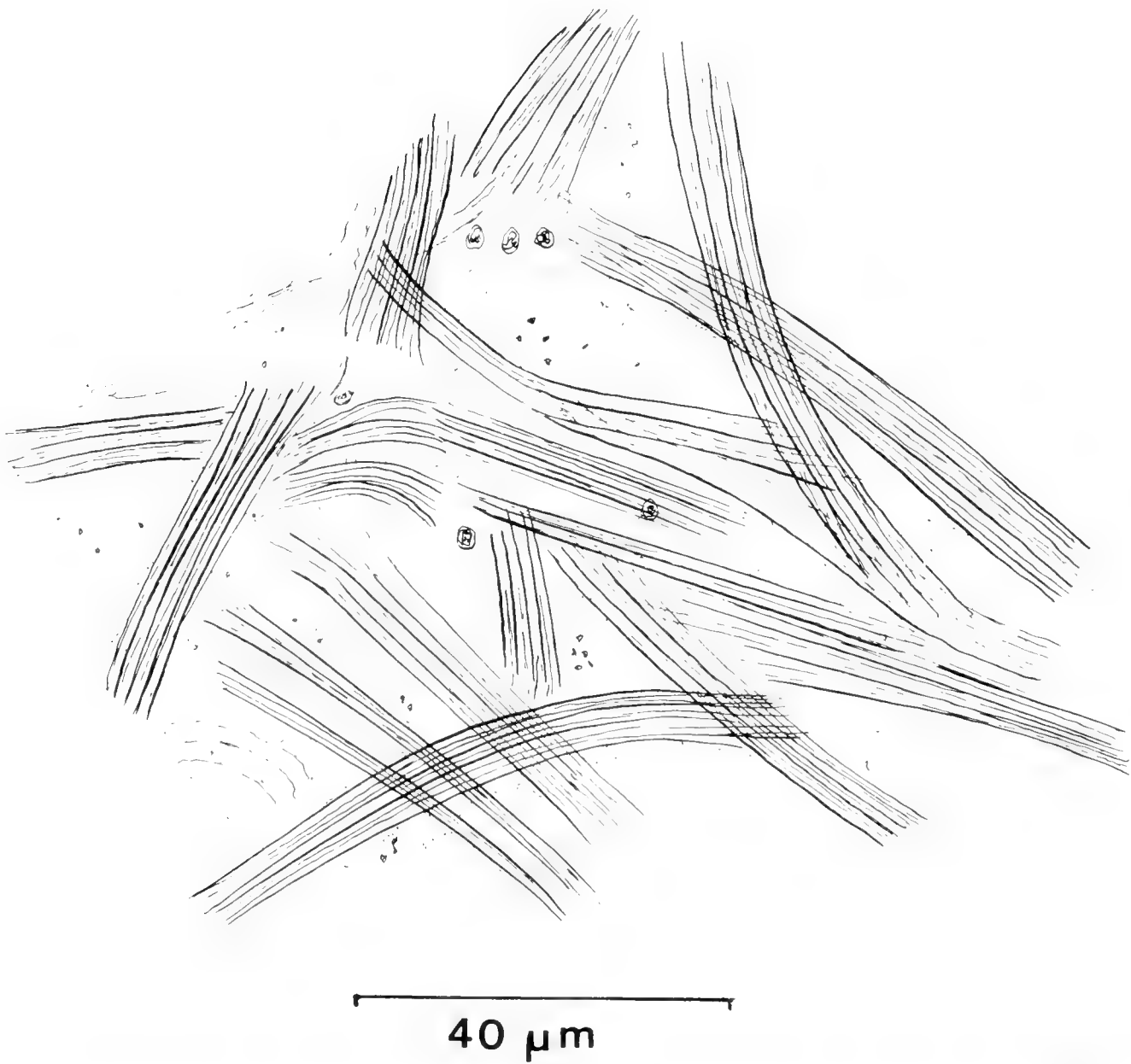


FIG. 5. *Mesodesma mactroides*. A transverse section of the siphonal heart wall showing the muscle fibres.

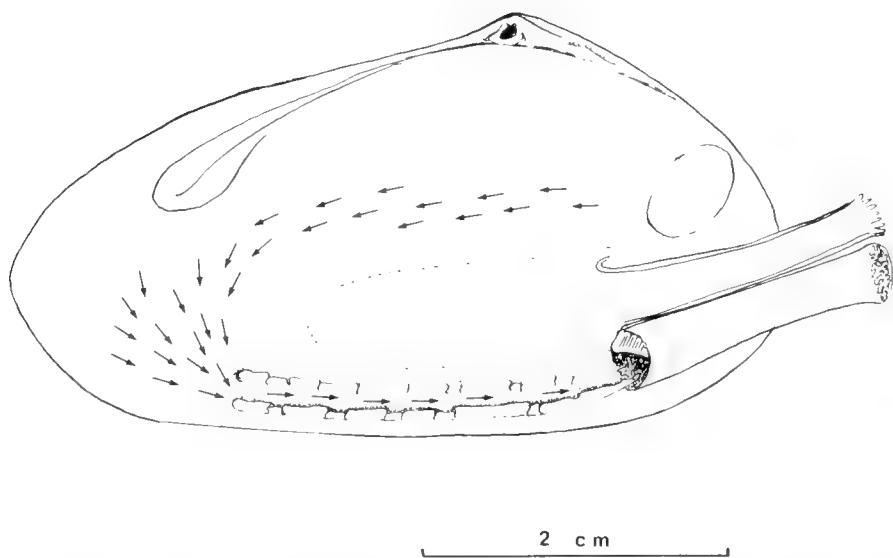


FIG. 6. *Mesodesma mactroides*. The inner surface of the right mantle lobe to show the ciliary cleansing currents.

canal" (Kellogg, 1915). The accumulated waste from the visceral mass and palps usually passes into this canal, in which all particles are carried backwards as recorded for *Spisula*, *Lutraria* (Yonge, 1948), *Mesodesma arctatum* (Allen, 1975), and *Caecella chinensis* (Narchi, 1980). On the mantle surface of *M. mactroides*, the direction of the ciliary currents is different from that of *M. arctatum* (Allen, 1975) and *Macra solidissima* (Kellogg, 1915), and is very similar to that of *Lutraria lutraria* and *C. chinensis*. On the posterior two-thirds, particles are carried forwards, and from there, ventrally directed currents convey them to the entrance of the waste canal. Currents around the margin of the pedal gape carry material inwards to the same point. The fusion of the mantle edges makes ventral ejection of waste material impossible, this taking place via the inhalant siphon. As in *M. arctatum* (Allen, 1975) and *M. solidissima* (Kellogg, 1915), a well-developed siphonal membrane rejects large particles downward, and acts, like the waste canal, in preventing undesirable material from being carried back into the mantle chamber. As in *M. arctatum*, *M. mactroides* does not possess a fourth pallial aperture.

Musculature, foot and pedal gape

The adductor muscles lie ventral to the hinge line and differ considerably (Fig. 7). The anterior adductor (aam) is a relatively long,

narrow and elongate muscle, slightly tapering at the posterior end, transverse and curved upward. Its posterior surface is indented by a deep groove. Into the posterior region of the groove pass a few fibres of the protractor pedal muscle (pa). The anterior adductor muscle lies in front of the mouth and has a different form from that of *Mesodesma arctatum* (Allen, 1975). The posterior adductor (pam) is oval in section. The disposition of the muscles is similar to that of *Donax vittatus* (Graham, 1934) and *D. hanleyanus* (Narchi, 1978).

The foot (f) is axe-shaped without a flattened sole. There is no byssus gland.

The outermost muscular layer of the foot comprises the protractor muscles (pa). These pass to the anterior adductor and are inserted either on the ventral surface of that muscle or on the parts bordering the transverse groove.

The anterior pedal retractor (arm) comprises two layers separated by a component of the posterior pedal retractor muscle. One layer of the former muscle intermingles with the layers of the pedal protractor and comprises a thin sheet of more or less circular fibres. The second layer of the anterior pedal retractor lies deeper in the foot.

The posterior pedal retractor (prm) is also divided into two in the ventral region of the foot.

The two pedal elevator muscles (e) form the innermost pedal muscles. Like the posterior retractor muscles, they fuse in the foot

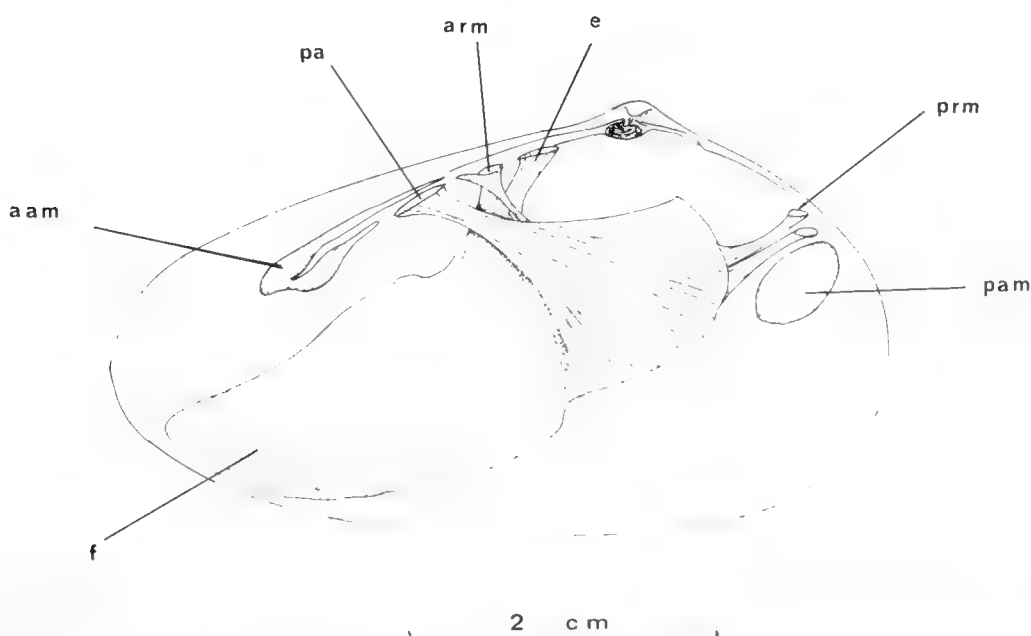


FIG. 7. *Mesodesma mactroides*. The arrangement of the musculature; aam, anterior adductor muscle; arm, anterior retractor muscle; e, elevator pedal muscle; f, foot; pa, protractor pedal muscle; pam, posterior adductor muscle; prm, posterior retractor muscle.

only to separate subsequently. In *Caecella chinensis* (Narchi, 1980) these muscles are poorly developed, but in *Donax hanleyanus* (Narchi, 1978) and *D. vittatus* (Yonge, 1949) they are well developed. Castellanos (1948) did not recognize the elevator muscles in the specimens of *M. mactroides* she studied. The mantle edge is fused to form the inhalant and exhalant siphons. Fusion ventral to the inhalant siphon extends for about half the length of the ventral margin of the mantle, thus limiting the pedal gape.

The ctenidia

The arrangement of organs in the mantle cavity after removal of the left valve and mantle lobe is shown in Fig. 8. The siphons, foot and posterior mantle lobe are somewhat contracted.

The form of the ctenidia and the general

course of the ciliary currents are shown diagrammatically in Fig. 9. The inner demibranch (id) is somewhat longer than the outer (od). Gill ciliation is of Type C (1a) (Atkins, 1937), due to the presence of two oralward currents: one in the ventral food groove of the inner demibranch, the other in the ventral, un-grooved, margin of the outer demibranch. Allen (1975) described particles in *Mesodesma arctatum* moving anteriorly along the margin of the outer demibranchs being transferred to the inner demibranchs. The ctenidia of *M. mactroides* are similar to those of *Donax hanleyanus* (Narchi, 1978) and *Caecella chinensis* (Narchi, 1980) in the possession of an incipient oralward current in the posterior region of the ventral margin of the outer demibranch only.

On the ascending and descending lamellae of both demibranchs, there are downward ciliary currents on the crests of all filaments

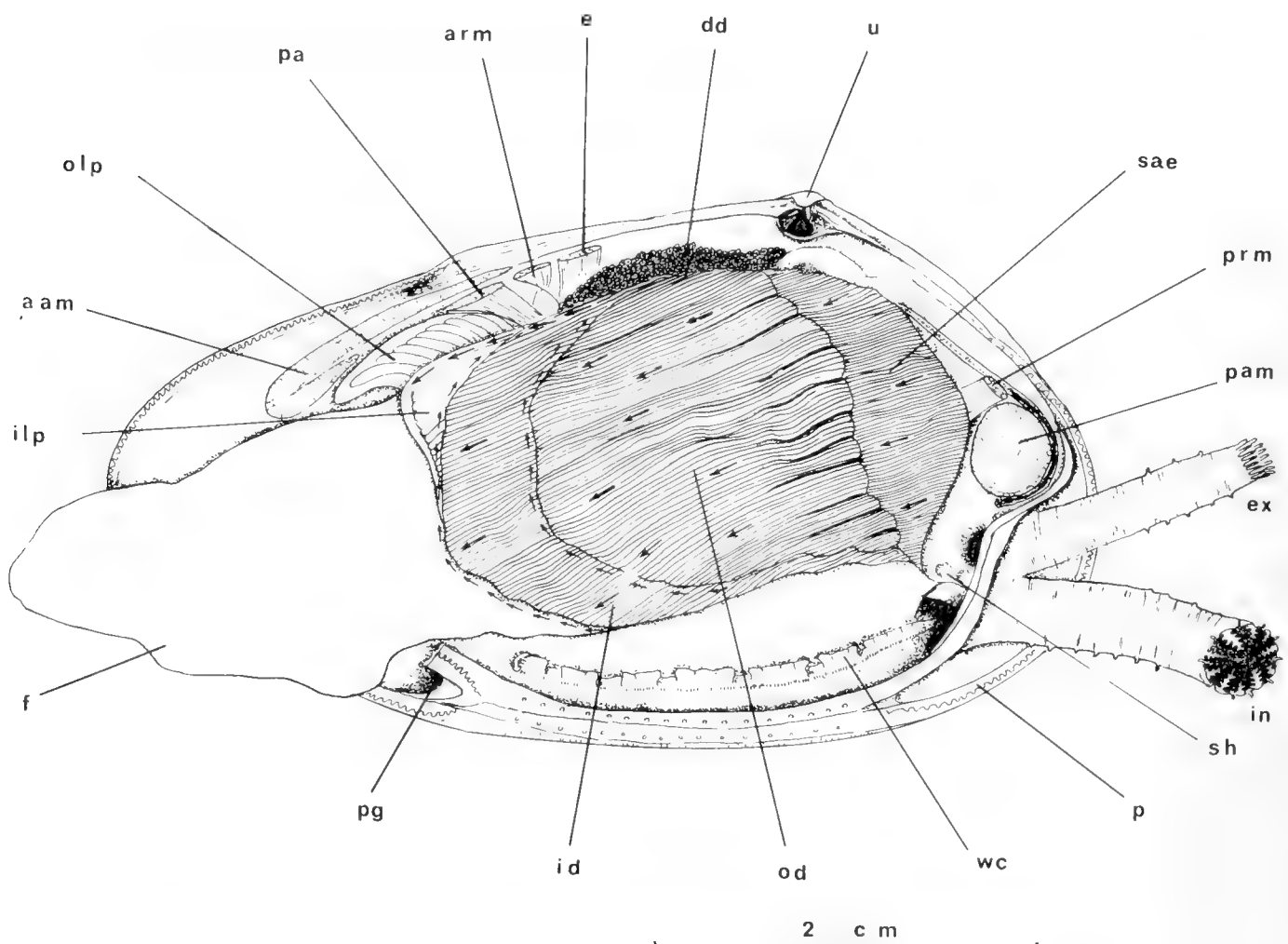


FIG. 8. *Mesodesma mactroides*. The organs of the mantle cavity viewed from the left side after removal of the left shell valve and mantle lobe; aam, anterior adductor muscle; arm, anterior retractor muscle; dd, digestive diverticula; e, elevator pedal muscle; ex, exhalant siphon; f, foot; id, inner demibranch; ilp, inner labial palp; in, inhalant siphon; od, outer demibranch; olp, outer labial palp; p, periostracum; pa, protractor pedal muscle; pam, posterior adductor muscle; pg, pedal gape; prm, posterior retractor muscle; sae, supra-axial extension of outer demibranch; sh, siphonal heart; u, umbo; wc, waste canal.

and in the plical troughs. In the proximal region of the ctenidial axis is an additional oralward current fed by upwardly beating cilia on both descending lamellae. On each side of the body, there are thus three oralward currents as in *Tivela mactroides* (Narchi, 1972). A supra-axial extension (sae) of the outer demibranch is also present.

Mesodesma mactroides has moderately plicate lamellae as in *Donax hanleyanus*. The plicae are shallow and occur over the greater part of both lamellae with an average number

of 12 filaments per plica, ranging from a minimum of ten to a maximum of fifteen in the outer and inner demibranchs. Ridewood (1903) observed fewer in *M. novae-zelandiae*. Also as in this species and species of *Donax*, *M. mactroides* has no differentiated principal filaments. Pelseneer (1911) showed that *M. complanata* has unplicate lamellae, while *M. mactroides* has slightly plicate ctenidia. Pelseneer (1911) found in *Donax* species with either flat, slightly plicate, or strongly plicate lamellae. Narchi (1978) found the ctenidium of *Donax hanleyanus* to be variably plicate.

The filaments (Fig. 10) are separated by laterofrontal cilia (lfc), 5 μm long. The frontal cilia (fc), 4 μm in length give way to longer terminal cilia in the distal region and which are 28 μm in length.

The ventral tips of the anterior filaments of the inner demibranch only are inserted and fused to a distal oral groove (Fig. 11A) and the ctenidial-labial palp junction is thus of Category II (Stasek, 1963).

The labial palps

The palps are triangular and relatively long. The inner faces are deeply plicate and the outer faces smooth (Fig. 11A). The dorsal margin of each palp is relatively wide and

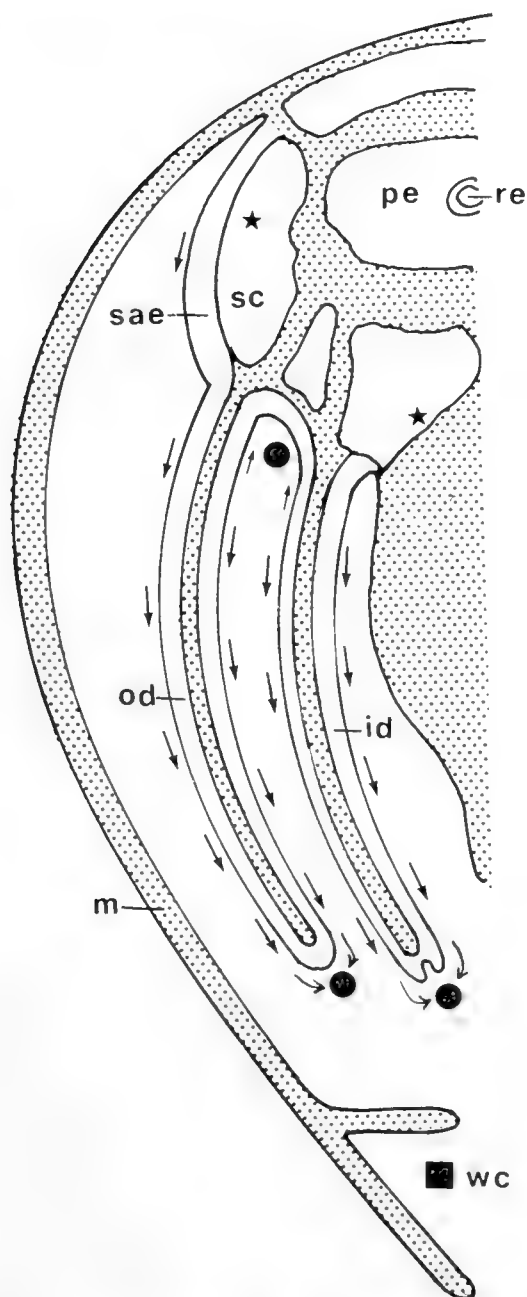


FIG. 9. *Mesodesma mactroides*. Diagrammatic vertical section through one half of the body to show the ciliary currents of the ctenidium and mantle; id, inner demibranch; m, mantle lobe; od, outer demibranch; pe, pericardium; re, rectum; sae, supra-axial extension of outer demibranch; sc, supra-branchial chamber; wc, waste canal.

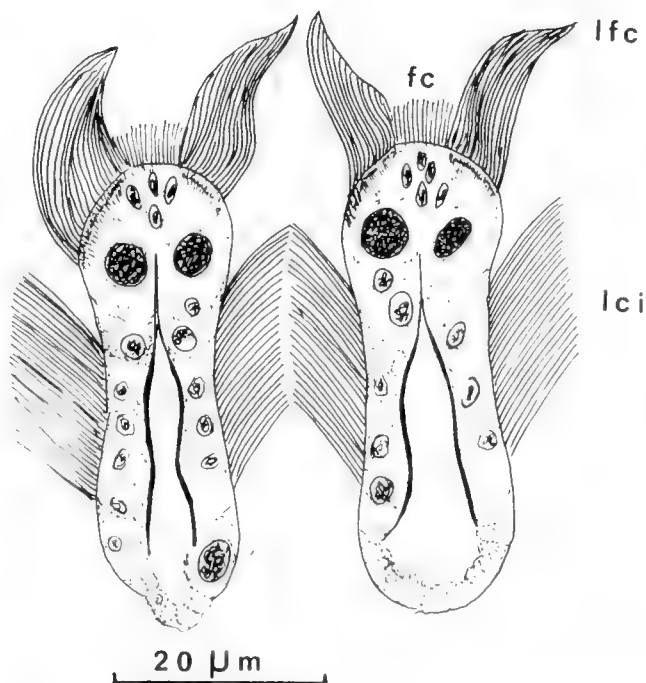


FIG. 10. *Mesodesma mactroides*. A transverse section of two filaments of the inner demibranch showing the arrangement of the various ciliary groups; fc, frontal cilia; lci, lateral cilia; lfc, laterofrontal cilia.

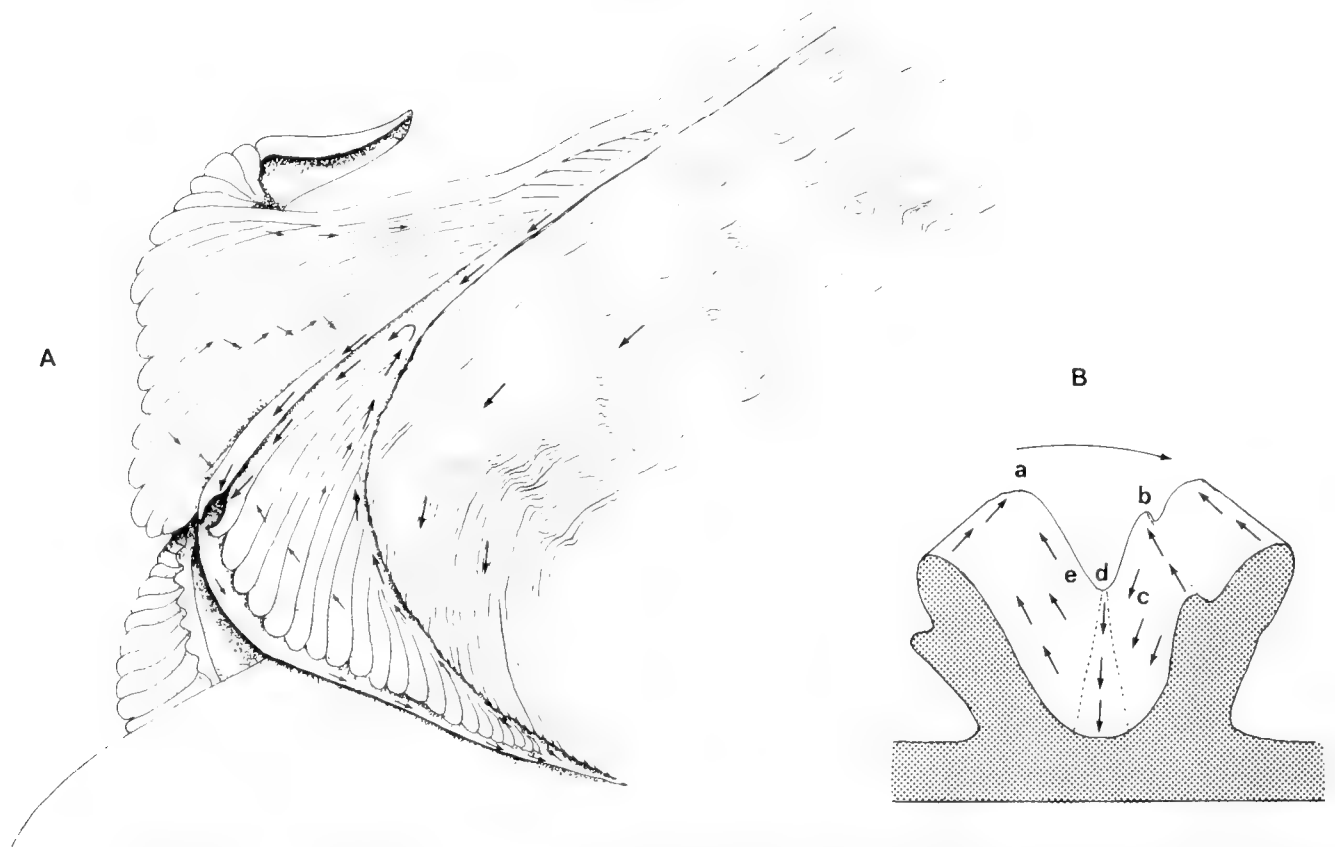


FIG. 11. *Mesodesma mactroides*. A, The relationship between inner demibranch and labial palps showing ciliary currents and acceptance tracts; B, diagrammatic representation of the ciliary currents of two folds of the inner surface of the labial palp. (For explanation see text.)

smooth. The narrow ventral margin carries particles backwards to the tip, whence they are passed into the mantle cavity. Particles collected on the outer faces of the palps are carried over onto the dorsal margin of the inner faces. Particles carried along the dorsal margin are usually caught up by cilia on the inner palp surface and carried forwards.

Small particles that have passed along the ventral marginal food grooves of the ctenidia tend to pass directly into the groove between the palps. Larger particles travelling along the ventral marginal food groove usually drop onto the visceral mass or mantle before reaching the palps.

Particles arriving at the palps from the ctenidial axis usually pass into the distal oral groove and then into the groove between the palps. In addition, the palps have sorting currents on their inner faces. In Fig. 11B, the following symbols are used to differentiate the ciliary tracts of adjacent palp folds: a) an acceptance tract which passes small particles oralward over the crests of the folds; c) a rejection tract passing large particles into the troughs, from which d) removes unwanted particles; b) and e) are currents which sort particles of intermediate size to be selected or

rejected. The latter particles are either rejected via the dorsal or ventral edges of the palps or reach the proximal oral groove. The ciliary tracts of the palps in *Mesodesma mactroides* are similar to those of *Asaphis dichotoma* (Narchi, 1980).

The alimentary canal

The mouth (Fig. 12) opens into a fairly long oesophagus which enters the antero-dorsal part of the stomach. As in *Mesodesma arctatum* (Allen, 1975) the oesophagus is ciliated with narrow longitudinal ridges along its entire length. According to Castellanos (1948), the oesophagus of *M. mactroides* is short. There is no appendix in the postero-dorsal region of the stomach.

Mesodesma mactroides is similar to species of the Mactridae in possessing a separate style sac and mid-gut.

The mid-gut and style sac are similar to those of *Donax hanleyanus* (Narchi, 1978) and *Caecella chinensis* (Narchi, 1980). Both open near to each other on the anteroventral wall of the stomach. The long and curved style sac extends antero-ventrally from the stomach to a point level with and anterior to

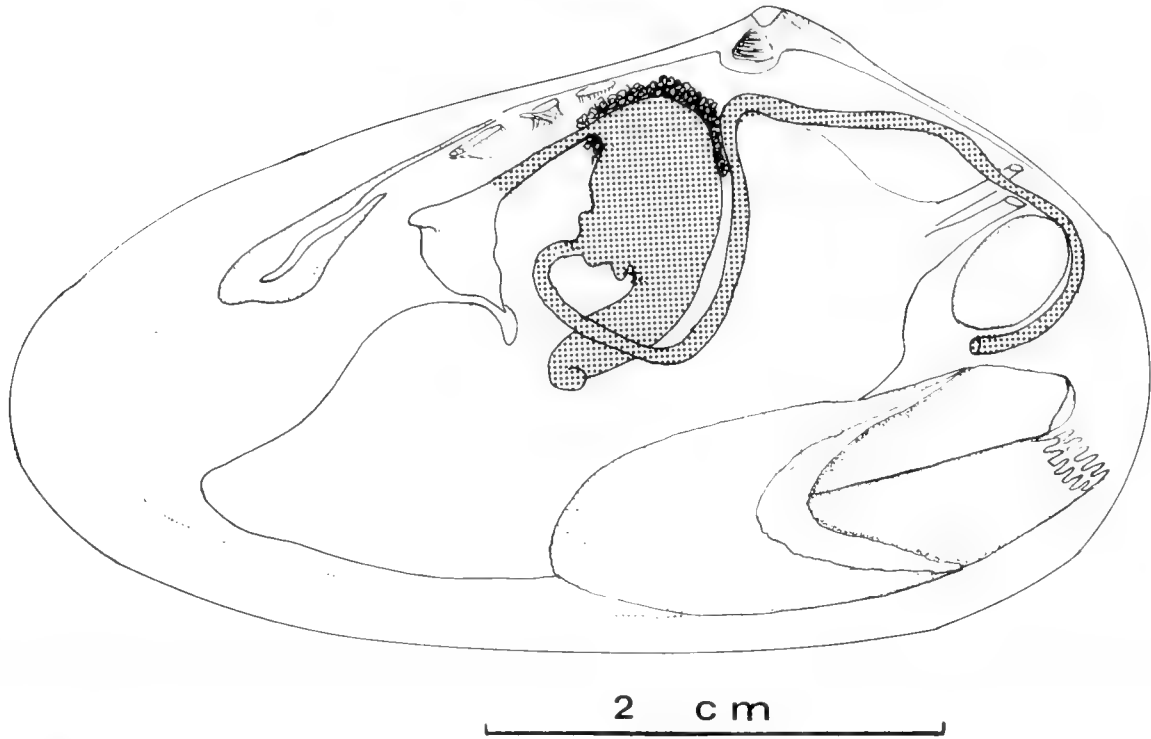


FIG. 12. *Mesodesma mactroides*. A diagram of the dissected alimentary canal, as seen from the left side.

the mouth. The mid-gut leaves the ventral right wall of the stomach. It passes forwards and curves ventrally into the foot. Unlike *D. vittatus* (Graham, 1934), it does not coil. Castellanos (1948) described two coils in the intestine of *M. mactroides*, but these were not observed in my specimens. On reaching the point where the style-sac bends anteriorly, the mid-gut passes to the left posterior side of the style sac and then ascends to the heart. It enters the pericardial cavity on its anterior wall again without coiling. The hind-gut passes through the pericardial cavity and the ventricle and opens via the anus on the posterior face of the posterior adductor muscle.

The stomach

In a series of studies on the structure of the bivalve stomach, Purchon (1960) recognized five types. *Mesodesma mactroides* has a stomach of type V and is typical of the Mesodesmatidae.

The large and irregular stomach (Fig. 13) is similar to that of *Atactodea glabrata* Lamarck (Purchon, 1960). The slender oesophagus (o), opens into the anterior face of the stomach. There is a large globular swelling at the left anterior border of the opening of the style-sac (ss) into the stomach, and this swelling extends forward as a ridge, which runs anteriorly over the floor of the stomach.

As in *Atactodea glabrata* (Purchon, 1960),

Mesodesma mactroides does not possess a minor typhlosole.

The greatly swollen major typhlosole (ty) is accompanied throughout its course by the intestinal groove; it passes forwards and onto the right side of the stomach, entering a broad and shallow right caecum (rc) within which it forms a half circle before emerging. Eight ducts from the digestive diverticula opens into the right caecum.

From the right caecum the typhlosole extends transversely across the anterior wall of the stomach to enter the extensive left caecum (lc) which receives fourteen ducts from the digestive diverticula. The major typhlosole forms a loose spiral of about two and a half turns on the median and posterior walls and terminates on its posterior wall near the opening.

The dorsal hood (dh) is relatively small and lies on the postero-lateral wall of the stomach. On its anterior wall there is an extensive sorting area (sa_g) of ridges and grooves, which extends over the roof of the stomach to the right side of the oesophageal opening. Cilia beat downward in the grooves while an acceptance tract passes from right to left, along its anterior border conveying particles into the dorsal hood. This tract is delimited anteriorly by a ridge which passes from the left border of the oesophagus to the opening of the dorsal hood. The oesophageal aperture has a series of papillae (pr) which lie on its

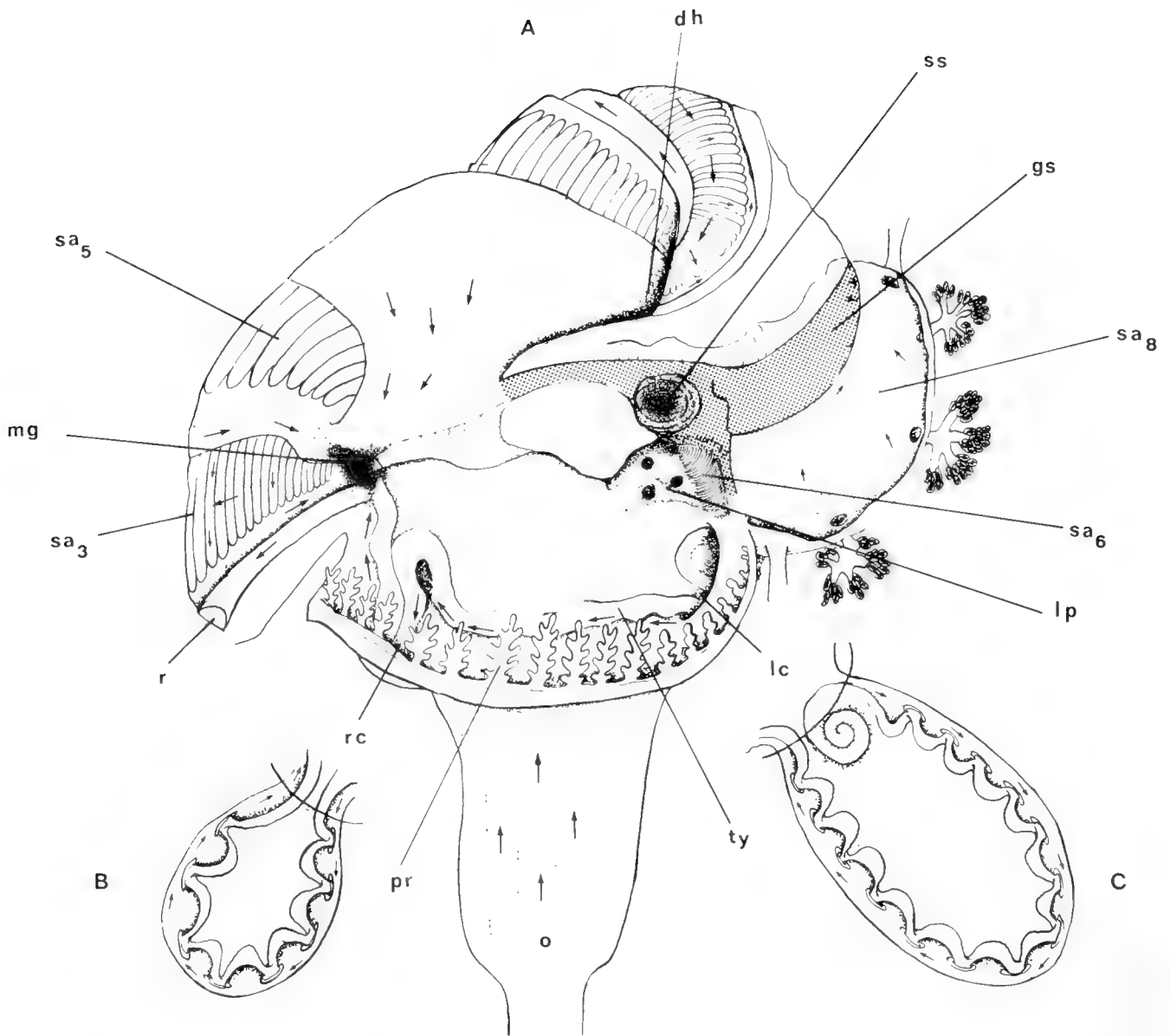


FIG. 13. *Mesodesma mactroides*. A, the interior of the stomach seen after being opened by an incision along the right wall; B, right caecum; C, left caecum; dh, dorsal hood; gs, gastric shield; lc, left caecum; lp, left pouch; mg, mid-gut; o, oesophagus; pr, processes ornamenting the oesophageal orifice; r, ridge; rc, right caecum; sa₃, principal sorting area of the dorsal hood; sa₅, sorting area on the posterior wall of the dorsal hood; sa₆, sorting area of the left pouch; sa₈ sorting area on the anterior roof of the stomach; ss, style sac; ty, major typhlosole.

right side and ventrally between it and the intestinal groove. Small papillae occur on the right side of the sorting area (sa₈) and gradually increase in size and complexity along a series of about twenty such papillae. Each one bears a double series of lobes on its upper border. A similar series of papillae has been found in *Pholadidea loscombiana* (Purchon, 1955), *Mactra mera*, *Caecella cumingiana* (Purchon, 1960) and *C. chinensis* (Narchi, 1980).

Dorsalward, ciliary currents occur on the smooth posterior sides of these papillae and, along the anterior side of the bases of the papillae, a ciliary current passes from left to

the right. These papillae exhibit considerable muscular activity.

On the roof of the dorsal hood there is a sorting area (sa₃). Cilia on this convey particles over the crests of the folds towards the apex of the dorsal hood. In the grooves between the folds cilia beat forward into a rejection tract. The sorting area extends to the right side of the stomach. The rejection tract which discharges material into the intestinal groove is separated from the posterior border of the right caecum by a well-defined ridge (r). On the posterior wall of the dorsal hood there is a sorting area (sa₅) of relatively large folds, on which cilia beat ventrally and out of the dorsal

hood where the area joins a longitudinal ridge. As in *Macra mera*, this sorting area terminates on the right side of the stomach where there is a conspicuous, ventrally projecting swelling which normally arches over the intestinal groove to touch the major typhlosole.

The left pouch (lp) lies on the left anterior wall of the stomach, between the left caecum and the dorsal hood. There is no special line of demarcation between these apertures. Four digestive ducts enter the left pouch in *Mesodesma mactroides*; *Atactodea glabrata* (Purchon, 1960) has eight ducts. A narrow band of fine transverse ridges and grooves (sa₆) is present on the floor of the left pouch, penetrates the apex and then passes on its dorsal side.

About eight ducts from the digestive diverticula open along the posterior border of a sorting area on the roof of the stomach (sa₈).

The gastric shield is firm and sends a deep flare into the mouth of the dorsal hood; it also envelops the posterior border of the left pouch.

I did not observe a small sorting area of fine radiating ridges and grooves on the posterior border of the aperture of the mid-gut that is present in *Atactodea glabrata* (Purchon, 1960).

DISCUSSION

Mesodesma mactroides is an intertidal suspension feeder, well adapted to its mode of life. The siphons are similar to those species of similar habits (*Tivela mactroides*: Narchi, 1972), having numerous branched tentacles, which curve over the aperture to form a grate when the animal is pumping water.

Mesodesma mactroides lives on open sandy beaches, where large numbers of particles are constantly lifted into suspension by wave movement.

Mesodesma mactroides occurs in a firm substratum and has a well-developed foot, an elevator pedal muscle and a wedge-shaped shell, well designed for high speed burrowing, particularly in young animals. Small specimens (with *Donax hanleyanus*) in the Santos beaches were flushed from the sand by the advancing surf and carried up the beach in the uprush. Instead of being carried down with the backwash they extended the foot to act as a braking device.

The clams are highly specific with regard to their choice of sand and are absent from some beaches of our littoral. Few other animals can survive in the places that have the right requirements. As a result, populations of *Mesodesma mactroides* develop without much competition. The same type of habitat is shared only with *Donax hanleyanus*. The populations of these two species compete when *M. mactroides* is of small size. Thus, in places where adult *M. mactroides* occur, it is usually the most abundant in terms of biomass and may be regarded as dominant in its habitat. *M. mactroides* is a good indicator of beach type and condition.

The ctenidia of *Mesodesma mactroides* are of type C (la) (Atkins, 1937), the same type as in *Donax hanleyanus* (Narchi, 1978). This similarity probably results from convergent adaptation to the same habitat.

As stated by Allen (1975) for *Mesodesma arctatum*, "the cilia of the posterior half of the mantle, dorsal to the mantle fold, direct particles ventrally and anteriorly where they either join the main current from the palp to the fold or are directed onto the dorsal surface of the fold. At the dorsal junction of the fold and general mantle surface there is an anteriorly directed ciliated tract to the anterior end of the fold." In *M. mactroides*, all currents from the posterior half of the mantle convey particles anteriorly where they join the main currents from the palp, entering the rejection canal between the fold and inner muscular lobe. This difference probably is related to the great development of the pallial sinus in *M. mactroides*.

Mesodesma mactroides possesses a waste canal, in which pseudofaeces can accumulate without interfering with the inflow of water through the inhalant canal. The waste canal is roofed by the mantle folds which terminate posterior to the siphonal membrane in the same manner as in *M. arctatum* (Allen, 1975). Similar longitudinal folds are also present in the Mactridae.

A siphonal membrane is present in *Mesodesma mactroides*, in *M. arctatum* (Allen, 1975) and in the Mactridae (Yonge, 1948). Yonge (1948) concluded that such a structure evolved in shallow-burrowing animals as an adaptation to life in silty waters.

Unlike *Schizothaerus nuttalli*, the mantle edges of *Mesodesma mactroides* are not fused as far forward as the anterior end of the mantle folds. The mantle folds and the waste canal end behind the siphonal membrane and

accumulated waste is ejected through the long inhalant siphon in the usual manner. Kellogg (1915) suggested that the function of the siphonal membrane was to pass large particles downwards onto the mantle edges, and away from the gills, especially when much sediment is present in the inflowing water. Yonge (1948) concluded that the membrane is an adaptation for life in silty water and that for this reason *Schizothaerus* has retained the siphonal membrane. *M. mactroides* also has a siphonal membrane, probably because wave action in its habitat lifts up large amounts of sediment.

Siphonal hearts in *Mesodesma mactroides* are described for the first time. They are rounded structures located between the internal openings of the exhalant and inhalant siphons and they contract spontaneously or under slight stimulation. They differ from the accessory hearts of *Crassostrea virginica* (Galtsoff, 1964) and the pulsating vessels of *Ostrea gigas* (Hopkins, 1934a, 1934b, 1936). The principal function of the siphonal hearts seems to be the pumping of blood into the long siphons, which possibly act as respiratory organs similar to the mantle and gills or the long siphons may require an accessory pump in order to circulate blood within them. Counts of the rates of pulsation of the heart and siphonal hearts show that they act independently. The rate of pulsation, as in the accessory hearts of oysters, is probably determined by the rate at which they fill with blood, and is thus regulated by the heart. No other bivalves with long siphons have similar structures.

The alimentary canal of *Mesodesma mactroides* is similar to that of *Donax vittatus* (Graham, 1934) but with some differences: the intestine of adult *M. mactroides* is not coiled and the style sac is smaller.

The mid-gut and style sac of *Mesodesma mactroides* are separated. The stomach has much the same structure and functions as that of a typical suspension-feeding eulamellibranch. It is essentially similar to other mesodesmatids studied earlier. The oesophageal orifice possesses a series of pinnate lobes on the ventral and right borders. A similar series of papillae have been recorded for *Pholadidea loscombiana* (Purchon, 1955), *Mactra mera*, *Caecella cumingiana* (Purchon, 1960), *Mesodesma arctatum* (Allen, 1975) and *Caecella chinensis* (Narchi, 1980). These lobes are muscular and pos-

sibly prevent large particles entering the stomach.

SUMMARY

Mesodesma mactroides Deshayes, 1854 is an inhabitant of clean sand in waters disturbed by wave movement. The species occurs from southern Brazil to Patagonia. It lives infaunally and possesses many features adapting it for life in sandy beaches: (1) lack of a robust shell; (2) anterior muscle scar long and lenticular, posterior one broadly oval; (3) long separate siphons; (4) a pair of rounded structures in the supra-axial chamber just below the inner opening to the exhalant siphon, recorded here for the first time and called siphonal hearts; (5) moderately plicate lamellae without differentiated principal filaments; (6) waste canal conveying particles and accumulated waste from the visceral mass and palps backwards; (7) no appendix in the postero-dorsal region of the stomach; (8) separate style sac and mid-gut; (9) many openings from stomach into digestive diverticula.

REFERENCES CITED

- ALLEN, J. A., 1975, The functional morphology of *Mesodesma arctatum* (Conrad) (Bivalvia: Mesodesmatidae). *Proceedings of the Malacological Society of London*, 41: 601-609.
- ATKINS, D., 1937, On the ciliary mechanisms and interrelationships of lamellibranchs. Part III. Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science*, 79: 375-421.
- BEU, A. G., 1972, Genera of the bivalve family Mesodesmatidae, with comments on some Australasian species. *Journal of the Malacological Society of Australia*, 2(2): 113-131.
- CARCELLES, A., 1939, "*Pectunculus longior*" y "*Mesodesma mactroides*" de la Argentina y Uruguay. *Physis*, 17: 735-743.
- CARCELLES, A., 1944, Catálogo de los moluscos marinos de Puerto Quequén. *Revista del Museo de la Plata*, new ser., 3: 233-309, 15 pl.
- CASTELLANOS, Z. A., 1948, Estudio anatómico sobre *Mesodesma mactroides* Desh. (Almeja amarilla). *Dagi-publicaciones técnicas*, 5(1): 1-49.
- COSCARON, S., 1959, La "almeja amarilla" (*Mesodesma* (T.) *mactroides* Deshayes) de la costa de la provincia de Buenos Aires. *Agro-Publicacion Técnica*, 3: 1-65.
- COX, L. R. et al., 1969, Bivalvia. In MOORE, R. C.

- (ed.), *Treatise on Invertebrate Paleontology*. Geological Society of America and University of Kansas, Part N, vol. 2, Mollusca 6, Bivalvia, p. ii + 491–952.
- DAVIS, J. D., 1964, Lectotype designation for *Mesodesma arctatum*. *Nautilus*, 78: 3–6.
- DAVIS, J. D., 1965, *Mesodesma deauratum*: synonymy, holotype and type locality. *Nautilus*, 78: 96–100.
- DAVIS, J. D., 1967, *Ervilia concentrica* and *Mesodesma concentrica*: clarification of synonymy. *Malacologia*, 6: 231–241.
- DESHAYES, G. P., 1854, Description of the new shells from the Collection of Hugh Cuming. *Proceedings of the Zoological Society of London*, 22: 317–371.
- FISCHER, P., 1887, *Manuel de Conchyliologie et de Paléontologie Conchyliologique*. Paris, p. 1009–1369.
- FRANC, A., 1960, Classe des Bivalves. In GRASSÉ, P.-P., *Traité de Zoologie*. Masson, Paris, 5(2): 1845–2164.
- GALTSOFF, P., 1964, The American oyster *Crassostrea virginica* Gmelin. *Fishery Bulletin of the [United States] Fish and Wildlife Service*, 64: 1–480.
- GOFFERJÉ, C. N., 1950, Contribuição à zoogeografia da malacofauna do litoral do Estado do Paraná. *Arquivos do Museu paranaense*, 8: 221–282, pl. 31–35.
- GRAHAM, A., 1934, The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proceedings of the Royal Society of Edinburgh*, 54: 158–187.
- HAAS, F., 1934, Bivalvia. In BRONNS, *Klassen und Ordnungen des Tierreichs*. Akademische Verlagsgesellschaft, Leipzig, Band 3, Mollusca, Abteil. 3, Bivalvia, Teil 1, Lief. 5, p. 545–704.
- HABE, T., 1973, Family Mesodesmatidae of Japan and adjacent area with the description of a new species. *Venus*, 32: 4–8.
- HOPKINS, A. E., 1934a, Accessory hearts in the oyster. *Science*, 80: 411–412.
- HOPKINS, A. E., 1934b, Accessory hearts in the oyster, *Ostrea gigas*. *Biological Bulletin*, 67: 346–355.
- HOPKINS, A. E., 1936, Pulsation of blood vessels in oysters, *Ostrea lurida* and *O. gigas*. *Biological Bulletin*, 70: 413–425.
- IHERING, H. VON, 1897, A Ilha de São Sebastião. *Revista do Museu Paulista*, 2: 129–216, 2 pl.
- IHERING, H. VON, 1907, Les mollusques fossiles du tertiaire et du crétacé supérieur de l'Argentine. *Anales del Museo Nacional de Buenos Aires*, ser. 3, 7: 1–611.
- KELLOGG, J. L., 1915, Ciliary mechanisms of lamellibranchs with descriptions of anatomy. *Journal of Morphology*, 26: 625–701.
- LAMY, E., 1914, Révision des Mesodesmatidae vivants du Muséum d'Histoire Naturelle de Paris. *Journal de Conchyliologie*, 62: 1–74.
- LANGE DE MORRETES, F., 1949, Ensaio de catálogo dos moluscos do Brasil. *Arquivos do Museu paranaense*, 7(1): 5–216.
- NARCHI, W., 1972, Comparative study of the functional morphology of *Anomalocardia brasiliensis* (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae). *Bulletin of Marine Science*, 22: 644–670.
- NARCHI, W., 1978, Functional anatomy of *Donax hanleyanus* Philippi, 1847 (Donacidae-Bivalvia). *Boletim de Zoologia, São Paulo*, 3: 121–142.
- NARCHI, W., 1980, A comparative study of the functional morphology of *Caecella chinensis* Deshayes 1855 and *Asaphis dichotoma* (Anton 1839) from Ma Shi Chau, Hong Kong. *Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China*. MORTON, B. S. (ed.). Hong Kong University Press, p. 253–276.
- OLIVIER, S. R., CAPEZZANI, D. A. A., CARRETO, J. I., CHRISTIANSEN, H. E., MORENO, V. J., AIZPUN DE MORENO, J. E., PENCHASZADEH, P. E., 1971, Estructura de la comunidad, dinamica de la poblacion y biologia de la almeja amarilla (*Mesodesma mactroides* Desh. 1854) en Mar Azul (Pdo. de Gral. Madariaga, Bs. As. Argentina). *Contribución del Instituto de Biología Marina*, 122: 1–90.
- PELSENEER, P., 1911, Les lamellibranches de l'expédition du Siboga. Partie Anatomique. *Siboga-Expeditie*, 53a: 1–125, 26 pl.
- PURCHON, R. D., 1955, The structure and function of the British Pholadidae (rock-boring Lamelli-branchia). *Proceedings of the Zoological Society of London*, 124: 859–911.
- PURCHON, R. D., 1960, The stomach in the Eulamelli-branchia, stomach types IV and V. *Proceedings of the Zoological Society of London*, 135: 431–489.
- RIDEWOOD, W. G., 1903, On the structure of the gills of the Lamelli-branchia. *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 147–284.
- RIOS, E. C., 1970, *Coastal Brazilian Seashells*. Fundação Cidade do Rio Grande, Museu Oceanográfico de Rio Grande, 255 p., 4 maps, 60 pl.
- RIOS, E. C., 1975, *Brazilian marine mollusks iconography*. Fundação Universidade do Rio Grande, Centro de Ciências do Mar, Museu Oceanográfico, 331 p., 91 pl.
- STANLEY, S. M., 1968, Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. *Journal of Paleontology*, 42: 214–229.
- STANLEY, S. M., 1970, Relation of Shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir* 125: 1–296.
- STASEK, C. R., 1963, Synopsis and discussion of association of ctenidia and labial palps in the bivalved Mollusca. *Veliger*, 6: 91–97.

THIELE, J., 1934, *Handbuch der systematischen Weichtierkunde*, Jena, 2(3): 779–1022.

THORSON, G., 1957, Bottom communities (sublittoral or shallow shelf). *Geological Society of America Memoir* 67(1): 461–534.

YONGE, C. M., 1948, Cleansing mechanisms and the function of the fourth pallial aperture in

Spisula subtruncata (Da Costa) and *Lutraria lutraria* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 27: 585–596.

YONGE, C. M., 1949, On the structure and adaptation of the Tellinacea, deposit-feeding Eulamellibranchia. *Philosophical Transactions of the Royal Society of London*, ser. B, 234: 29–76.

EVOLUTION AND ADAPTIVE RADIATION OF WOOD-BORING BIVALVES (PHOLADACEA)

K. Elaine Hoagland¹ and Ruth D. Turner²

ABSTRACT

Wood-boring bivalves represent a major worldwide adaptive radiation in the marine environment. This paper reviews that radiation and the morphological adaptations central to it. The fossil record, population genetics, and some ecological features of some Teredinidae are discussed as they bear upon the adaptive radiation. The wood-borer radiation began with the evolution of woody plants, which provide substrate in the form of driftwood and salt-tolerant living plants. Key adaptations were, first, the ability to bore into wood, and second, the ability to use wood for food. There were actually radiations in two related families of the superfamily Pholadacea: the Pholadidae (27 fossil and living genera, 5 of which are wood-borers) and the Teredinidae (15 living genera, all obligate wood-borers).

The Pholadidae and the Teredinidae share some anatomical features such as the reduced hinge, projections inside the shell, large pedal gape, and discoid foot, although these may be convergent. The relative success of the teredinid wood-borer radiation, compared with the pholads, is probably due to the development of a calcareous tube and attachment of the siphonal retractor muscles to it, elongation of the body, reduction of the shell, and the evolution of pallets to close the tube. The pholads have not undergone shell reduction and they lack pallets. They do have accessory plates on the shell.

The wood-borer radiation, based on a patchy and temporary substrate, has led to variable-sized, patchily-distributed, inbred populations of most species. This population structure provides mechanisms for both the complex speciation pattern and the wide ranges of single species that characterize the Pholadacea.

Features such as pallet shape are variable among teredinid species, illustrating multiple solutions to a common problem. Other features such as siphon morphology have clear functional significance and hence can be assigned a role in the adaptive radiation of the Pholadacea. Finally, there are examples of multiple selective pressures dictating the structure of one organ, such as the adaptation of the gill for brooding young as well as for respiration and feeding.

Most Teredinidae are protandrous, but a few can function as simultaneous hermaphrodites, and one has separate sexes with dwarf males. These modes of sexuality are related to life in temporary habitats. Ways of coping with crowding are plasticity in size at maturity and cessation of wood-boring in favor of filter feeding. Broad physiological tolerances help to insure dispersal to new sources of wood and survival in estuaries. Species with planktonic development are not more broadly distributed worldwide than those that brood the young and disperse as adults in driftwood or boats.

Population genetical data involving 32 enzyme loci show striking species differences related to dispersal. *Bankia gouldi* and *B. fimbriatula* with planktonic larvae are more diverse genetically than two species with brooded larvae. A species with partial brooded development is intermediate.

The constraints of life in wood have made wood-borers unrivalled as opportunistic species, hence the success of many species when introduced to new localities. A review of life histories shows that teredinids have characteristics of both r- and K-selected species. The most important traits are short generation time, a high rate of increase, and tolerance of crowding leading to good competitive ability. Sympatric teredinids coexist because of the patchy temporal and spatial availability of wood, allowing the presence of numerous species that reproduce at different times. One species can monopolize a piece of wood if availability of the wood and competent teredinid pediveligers coincide. The spread of adult shipworms by man's use of wood in the marine environment could be responsible for slowing the speciation process by enhancing the spread of species with genotypes adapted for colonization, and/or by increasing outbreeding of all species.

Numerical taxonomic methods are applied to the character states of Pholadacean species in order to develop hypotheses on the relationship of morphology to ecology and to develop

¹Lehigh University, Bethlehem, PA 18015, U.S.A.

²Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A.

possible evolutionary sequences. A simple cladistic method using unique and unreversed characters can elucidate relationships at the generic level. Both that method and phenetic analyses reveal convergences of character states in the Pholadacea. Phenetic analyses emphasize similarities among the taxa based on wood-boring habits, while the analysis of unique characters provides a possible sequence of taxa that developed from a rock-boring ancestor. Both methods reveal problems in determining homologous characters.

Both numerical taxonomy and electrophoretic data support the current taxonomic structure of the Pholadacea, except that the data suggest polyphyly of the Bankiinae. Also, the genus *Lyrodus* may not be a natural, monophyletic group. Limited data available for *Kuphus* indicate that its unique combination of primitive and specialized character states place it apart from the other Teredinidae. In fact, the Kuphinae does not appear to be of equal taxonomic rank with the Bankiinae and the Teredininae. Wood-boring may have evolved in two lineages of the Pholadidae, one continuing into the teredinid lineage.

INTRODUCTION

Wood-boring bivalves are members of the superfamily Pholadacea. They occur in marine, estuarine, and in a few places, virtually freshwater (upper estuarine) environments. Besides these bivalves, there are only a few crustaceans (e.g., *Sphaeroma* and *Limnoria*) capable of a marine wood-boring existence. The adaptive radiation of the wood-boring bivalves, based as it is on the occupation of wood is a narrow one, with severe limitations on ecological deployment. Yet the wood-borers include two related families in the Pholadacea, 20 living genera, and approximately 175 living species found in all oceans. The radiation can be interpreted as two parallel radiations, perhaps in competition, represented by the two families.

We first review what is known of the evolution of those Pholadacea that are wood-borers, based on the meager fossil record. We then review the morphological features characteristic of wood-boring clams in general, and those characteristic of the two major families. We present new data on the population genetics and ecology of six species, three living sympatrically in Barnegat Bay, New Jersey, and three living sympatrically in southern Florida. We analyse some aspects of the morphology, physiological tolerances, population structure, life history characteristics, zoogeography, and population genetics of teredinids as they bear on the evolution of wood-borers. The six species examined in detail were chosen because they represent several of the divergent patterns of life history and ecology comprising the adaptive radiation of the Pholadacea.

We analyse the characters of the Pholadacea using numerical taxonomic procedures, in order to understand how the characters are correlated, how they might be related to selective pressures of the environment of wood-

borers, and how the taxa might be related (or, at least, how similar they are). Finally, we summarize the modes of evolution of the wood-boring bivalves, with emphasis on limitations to the adaptive radiation and on the role of man in the present course of the radiation.

METHODS

Morphology and Evolutionary History

The evolutionary history, functional morphology, and zoogeographic data presented here are based on the literature, especially earlier works by one of us (Turner). The data used to compile taxonomic characters for the Pholadacea came primarily from Turner (1954, 1955, 1956, 1962, 1965, 1966, 1971, 1972a & b, 1973), Purchon (1941), and Knudsen (1961). Some details of shell shape and umbonal reflection of the pholads were omitted from the data matrix because it was not possible to quantify them.

Population Dynamics

Data were obtained on the population dynamics of teredinids from Barnegat Bay, New Jersey, U.S.A. White-pine panels of equal size were placed on racks at 20 stations between Manahawkin and Holly Park, New Jersey, from 1971 to 1980 (Hoagland & Turner, 1980). One panel was added each month and removed one month later to determine the timing and rates of larval settlement. One panel was added each month and removed 12 months later to analyze species composition, timing of reproduction, lifespan, sex ratio, population age structure, and the effects of crowding. Also, 12 panels were placed at each station in May of each year and removed, one each month, until none

were left. From these cumulative panels, growth rates, age at maturity, and generation time could be estimated. In the laboratory, all teredinids were removed from the wood, identified, measured, and examined for larvae in the gills. Further details of the methodology are in Hoagland et al., 1977, and Hoagland & Crocket, 1979.

Population Genetics

Horizontal starch-gel electrophoresis followed by staining for specific enzymes was performed, using the general methods of Ayala et al. (1973) as applied to mollusks by Dillon & Davis (1980) and Davis et al. (1981). Specimens of *Teredo bartschi*, *T. navalis*, and *Bankia gouldi* were obtained live from wood panels deployed in the inner coast of Barnegat Bay, New Jersey, between Waretown (39° 47.7' N; 74° 10.9' W) and Holly Park (39° 54' N; 74° 8' W). Specimens of *Bankia fimbriatula*, *Lyrodus floridanus*, and *Martesia striata* were obtained from panels deployed at the University of Miami (*L. floridanus*) and Hobe Sound, Florida, U.S.A. (*B. fimbriatula*, *M. striata*). Approximately 50 specimens of each species were analysed. Voucher specimens number A8680 a-c and 353444 are on deposit at the Academy of Natural Sciences of Philadelphia. The animals were dissected live from the wood and frozen in tris tissue buffer (pH 7.4) until used. Preliminary experiments showed that tissues from various organs (mantle, siphons, gill, viscera) yielded similar results though of different intensity, as long as eggs and larvae were excluded. Therefore, entire animals were homogenized unless they were carrying larvae in the gill pouches; in those cases the gills were excised and discarded before homogenization.

Five wicks of No. 3 Whatman filter paper were saturated with the homogenate, blotted,

and applied, one wick from each individual, to each gel. Five gels were run concurrently; each was then sliced into three slabs. Therefore one individual could be analysed for 15 enzyme systems. Each population was run on two days, so that a total of 30 enzyme systems could be evaluated. As 31 wicks fit on one gel, 25 experimental individuals from the population being tested, plus six individuals from a reference population, could be run on a single gel.

Starch gels (13%) were prepared using 33.5 g of Electrostarch and 250 ml of one of four gel buffers. The buffers were tris citrate (TC), pH 6.0, tris NaOH borate (Poulik), pH 7.6 (tray buffer)/8.9 (gel), and tris-EDTA-borate (TEB) at both pH 8.0 and 9.1 (Table 1). Four systems were run on TEB gels of pH 9 but with tray buffers of pH 8 (TEB 9/8). The gels were run at 35 MA or 350 volts, but not exceeding either. Table 2 details the enzyme systems, their buffer systems, current/voltage levels, and durations of the runs. No results were obtained for octopine dehydrogenase, fumerase, octanol dehydrogenase, succinate dehydrogenase, or aldolase.

The stain buffers and other components of the stains are as described by Dillon & Davis (1980) and Davis et al. (1981). Agar overlays (10 ml of a 2% solution) were employed for all enzyme assays except those for AAT, G3PDH, and LAP, for which solutions were used. Standard recipes for all systems are in Shaw & Prasad (1970), Brewer (1970), and Poulik (1957).

Gels were scored as in Ayala et al. (1973). The alleles of each locus were identified by the distance, in \pm mm, that they migrated with respect to the most common allele of a reference population, which was given the arbitrary number 100. *Teredo bartschi* from Oyster Creek was used as the reference population because it was nearly monomor-

TABLE 1. Buffers used in gels and electrode trays. Concentration of ingredients (Molarity).

Buffers		pH	Tris	Citric acid (monohydrate)	Boric acid	Na ₂ EDTA	NaOH
TC	Tray	6.0	.237	.085	0	0	0
	Gel	6.0	.0083	.0030	0	0	0
TEB	Tray	8.0	.500	0	.645	.0179	0
	Gel	8.0	.050	0	.097	.0018	0
TEB	Tray & Gel	9.1	.087	0	.0087	.0011	0
Poulik	Tray	7.6	0	0	.3	0	.05
	Gel	8.9	.076	.005	0	0	0

TABLE 2. Enzymes studied, buffers, current, voltage, and duration of electrophoresis.

Enzyme		Gel & Tray Buffer	Current/Voltage		Run time (Hr)
Acid phosphatase	(AcPh)	TC 6	35 MA		3.5
Adenolate kinase	(Adkin)	Poulik	35 MA		3.0
Aldehyde oxidase	(AO)	TEB 9		350V	4.5
Aspartate amino transferase	(AAT)	TEB 9		350V	4.5
Esterase NA	(EST NA)	TEB 9/8		35 MA	2.0
Esterase NP	(EST NP)	TEB 9/8		35 MA	2.0
Glucose-6-phosphate dehydrogenase	(G6PD)	TC 6	35 MA		2.0
Glucose-6-phosphate isomerase	(GPI)	TC 6	35 MA		2.0
Glutamate dehydrogenase	(GDH)	Poulik	35 MA		3.0
Glyceraldehyde-3-phosphate dehydrogenase	(G3PD)	TEB 8	35 MA		3.5
α -Glycerophosphate dehydrogenase	(α GPDH)	Poulik	35 MA		3.0
Hexokinase	(HEX)	Poulik	35 MA		3.0
Isocitrate dehydrogenase	(IsDH)	TEB 8	35 MA		3.5
Lactate dehydrogenase	(LDH)	TEB 8	35 MA		3.5
Leucine amino peptidase	(LAP)	TC 6	35 MA		2.0
Mannose-6-phosphate isomerase	(MPI)	TEB 9/8	35 MA		2.0
NAD-dependent malate dehydrogenate	(NAD-MDH)	TC 6	35 MA		3.5
Peptidase G	(PepG)	TEB 8	35 MA		3.5
Peptidase T	(PepT)	TEB 8	35 MA		3.5
Phosphoglucomutase	(PGM)	TC 6	35 MA		2.0
		TEB 9		350V	4.5
6-phosphogluconate dehydrogenase	(6-PGD)	Poulik	35 MA		3.0
Sorbitol dehydrogenase	(SoDH)	Poulik	35 MA		3.0
Superoxide dismutase	(SOD)	TEB 9/8	35 MA		2.0
Triose phosphate isomerase	(TPI)	TEB 8	35 MA		3.5
Xanthine dehydrogenase	(XDH)	Poulik	35 MA		3.0

phic and was abundant. Assignment of electrophoretic patterns to loci was done with the aid of data collected on the same enzyme systems for other mollusks (Dillon & Davis, 1980; Davis et al., 1981). An electromorph was not scored if it was found only once.

Calculations were made of: 1) allele frequencies at each locus; 2) A, the average number of alleles per locus for each population; 3) P, the percent polymorphic loci per population; 4) H, the average individual heterozygosity; 5) I, Nei's normalized genetic identity of genes over all loci; and 6) D, Nei's genetic distance, or accumulated number of codon substitutions per locus, between population pairs (Nei, 1972; Ayala et al., 1973). The first value is basic to calculation of the others. A, P and H estimate genetic variability within populations, and are used to compare populations in terms of degree of genetic variability. Genetic identity (I) and D allow comparisons of genetic relationships among populations and species. We record fixation of alternative alleles as well as the allele frequencies in order to note significant genotypic differences among populations.

Numerical Taxonomy

The morphological data were analysed at the genus level using Wilson's consistency test for phylogenies (Wilson, 1965), a simple cladistic method. Subsets of taxa were organized according to shared versus unique and unreversed character states. In addition, a phenetic analysis using the NT-SYS numerical taxonomy program package (Rohlf et al., 1972) was used, focussing on similarities among the taxa that may or may not be related to phylogeny. A data matrix of 146 taxa (appendix A) and 90 binary or ordered multi-state characters (Appendix C) was compiled. Taxa for which insufficient information was available are listed in Appendix B.

The matrix was standardized by rows (characters), such that each character had a mean of 0 and standard deviation of 1. Both correlation and taxonomic distance matrices were generated, and cluster analysis was performed on each, using the unweighted pair-group method with arithmetic averaging. The minimum spanning tree (MST) and subsets subprograms of NT-SYS were used to find

phenetic relationships among the taxa. The minimum spanning tree configuration is superior to the phenogram because it does not average all the relationships between a taxon entering a cluster and those already clustered.

The standardized data matrix was used to generate character correlations, which were subjected to Principal Components Analysis, with components extracted until the eigenvalues were less than 1.0. A transposed matrix of the first three principal components with their character load was post-multiplied by the standardized matrix to yield a matrix of operational taxonomic unit (OTU) projections in principal component space (Rohlf et al., 1972).

The 146 taxa \times 90 character matrix was used to find correlations among all the characters for the two related families of wood-borers. Smaller matrices containing first, only the Pholadidae, and second, only some of the Teredinidae (Appendix A, numbers in parentheses), were used to obtain more detailed relationships among the taxa, because anatomical characters unique to the family could be added to the matrix (Appendix C).

RESULTS

Classification and Evolutionary History

An examination of the adaptive radiation of wood-boring bivalves requires that we cross

family lines to consider evolution of all wood-boring lineages, including those portions of the lineages that have not adopted the wood-boring habit. Table 3 shows that obligate wood- and mud or rock-boring species exist together in the Pholadidae, while the Teredinidae are almost exclusively wood-borers. From this family structure, we might guess that wood-boring evolved from mud-boring in the family Pholadidae. Nonetheless, the fossil record is insufficient to validate or reject this hypothesis. Rock-borers are much more likely to be preserved, because fossilization of marine wood is relatively rare. For the moment, we are assuming that the lineages as expressed by the family structure of the Pholadacea (Table 3) are correct.

The fossil burrows of wood-boring Martesiinae, Xylophaginae*, and Teredinidae can often be distinguished (Turner, 1969). The first fossil Martesiinae are suspected from the Carboniferous, and definitely occur in the Jurassic (Turner, 1969). Pholadinae also are suspected from the Carboniferous. The other pholad subfamilies first appear in the Cretaceous; all recognized subfamilies have survived to the Recent. Most pholad genera are not recognizable in the fossil record until the Tertiary, although *Martesia*, *Barnea*, and *Xylophaga*, representing three subfamilies, are found in the lower Cretaceous. *Xylophoma* is known only from the Cretaceous. In North America, fossil Pholadidae are common only since the beginning of the Pliocene (Kennedy, 1974). The fossil genus *Teredina*,

TABLE 3. Taxonomic position of wood-boring bivalves.

Subclass Heterodonta
Order Myoida
Suborder Pholadina
Superfamily Pholadacea
Family Pholadidae
Subfamily Xylophaginae ^{1*}
Genus <i>Xylophaga</i> (Cretaceous–Recent)
<i>Xylopholas</i> (?–Recent)
<i>Xyloredo</i> (?–Recent)
Subfamily Martesiinae ²
Genus <i>Martesia</i> ¹ (?Carboniferous–Recent)
<i>Lignopholas</i> ¹ (?–Recent)
<i>Xylophoma</i> ¹ (Cretaceous–?; not Recent)
Family Teredinidae
Subfamily Kuphinae ³ (?Eocene–Recent)
Teredininae ¹ (Eocene–Recent)
Bankiinae ¹ (Paleocene–Recent)

¹All members of these groups are obligate wood-borers.

²3 of 9 genera are wood-borers.

³Only one genus and species; may be a facultative wood-borer.

*This spelling follows Turner (1969: N721). Xylophaginae is the correctly formed name (I.C.Z.N. Code Article 29(a)) but is a homonym which should be brought before the I.C.Z.N. for a ruling (Article 55(a)). ED.

assigned to the Martesiinae, occurs in fossilized wood in the lower Eocene of Europe (Wrigley, 1929). It is notable because its elongate growth form is similar to that of the Teredinidae.

There are records of tubes associated with wood in the Jurassic and Cretaceous that have been assumed to be Teredinidae of undetermined genus and species (Durham & Zullo, 1961). However, these tubes could be *Xyloredo*. "*Teredo*" *pulchella* was named from material from the Jurassic (Moll, 1942). Cretaceous teredinids were broadly distributed; they have been found in Japan (Hatai, 1951), India (Stoliczka, 1871), and North America (Stephenson, 1952). However, Teredinidae with pallets preserved and hence identifiable to genus are known only from the Paleocene onward.

Pallets of *Bankia* and *Nototeredo* have been dated from the Paleocene (Elliott, 1963; Cvanara, 1966). The two major branches of the Teredinidae, the Teredininae and the Bankiinae, with their distinguishing pallet types, had diversified by the Eocene (Wrigley, 1929). In fact, pallets attributable to *Nausitora*, *Bankia*, *Neobankia*, *Teredo*, *Psiloteredo*, and *Teredina* (a pholad) are all found in either the London Clay or other English Eocene deposits (Elliott, 1963), revealing a rich, sympatric fauna of wood-borers. In addition, *Nototeredo* and *Teredora* are known from the Eocene of France and Belgium (Vincent, 1925). The Kuphinae may also have been present in the Eocene, although fossil remains are questionable until the Oligocene (Moll, 1942), and even then cannot be positively identified by the tubes alone.

It appears that both the Pholadidae and the Teredinidae were world-wide by the Jurassic, and that most Recent subfamilies and genera existed by the Eocene. The adaptive radiation of the Teredinidae was probably very rapid, as is characteristic of radiation events (Stanley, 1979).

The modern extent of the wood-borer radiation can be seen in Figs. 1 and 2. In addition, five fossil genera of Teredinidae have been described. The greatest diversification has taken place in *Bankia*, *Teredo*, and *Xylophaga*. Within each subfamily, there are many genera with low diversity and one with very high diversity, a few being intermediate. When the subfamilies are collected into families, the pattern is more evident. It is further strengthened if all the wood-boring members

of the Pholadacea are combined and the rock-borers are removed (Fig. 2). Ecologically, the radiation is split into the deep-sea forms (the Xylophaginae) and forms occupying water less than 250 m deep (Teredinidae and Martesiinae).

While taxonomic characters and their states are listed (Appendix C), the assignment of scores for each taxon is too lengthy to include here, but forms a separate publication (Hoagland & Turner, 1981). The Pholadacea share many characters that clearly are related to boring in hard substrates. These include insertion of the anterior adductor muscle on the umbonal reflection in an exterior position, so that it works in opposition to the large posterior adductor muscle. Others are a closed mantle, reduced beak and hinge, a rounded anterior portion of the shell, a large pedal gape, denticulate shell sculpture, a discoid foot, and presence of well-developed internal shell projections (apophyses, dorsal and ventral condyles, and chondrophore). There is also a tendency for shell elongation or reduction and the development of an umbonal-ventral ridge and sulcus in both families. A ventral adductor muscle is often present.

Population Genetics

The allele frequencies for 32 loci and the six species analysed are summarized in Table 4. Although results were obtained also for peptidase T and esterase NP, these were not as clear as those obtained for peptidase G and esterase NA, respectively. Because esterases and peptidases are nonspecific enzymes, redundancy would occur if all the data were scored. Therefore, we do not include results for peptidase T and esterase NP.

Tables 5 and 6 present the genetic relationships among the taxa based on those 26 enzyme loci for which scorable results were obtained for all six species. Fig. 3 plots a dendrogram based on the genetic distances of Table 6. Clearly, *Martesia striata* is separate, while *Bankia* forms one group and *Teredo* and *Lyrodus* another within one large grouping. On the basis of these data, *Lyrodus* does not appear to be a separate genus.

Genetic variability for the six species is shown in Table 7. All 32 loci were used to calculate these values. The most interesting result is the correlation between larval type and level of genetic variability. Over all three indices, the long-term brooder *Teredo bartschi* has low variability, while the spawn-

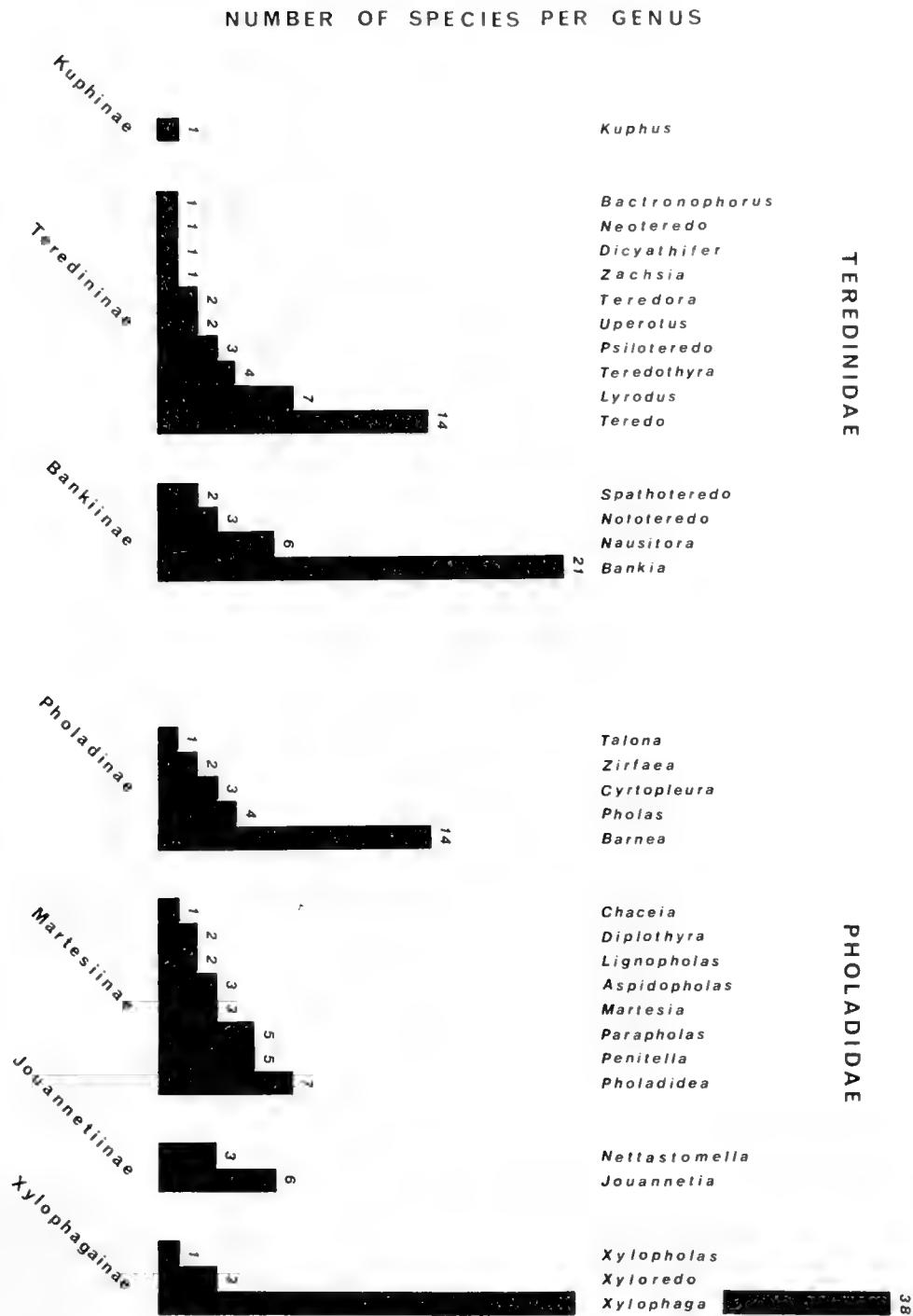


FIG. 1. Patterns of numbers of species per genus in subfamilies of Teredinidae and Pholadidae.

ers *Bankia gouldi*, *B. fimbriatula*, and *Martesia striata* have high variability. *Teredo navalis* and *L. floridanus*, which are short-term brooders, are intermediate.

Ecology and Zoogeography

Our population studies of three species from Barnegat Bay, New Jersey (Hoagland et al., 1977, 1980; Hoagland & Crocket, 1979) have shown that the species vary not only in type of larvae, but in many other population parameters (Table 8). *Teredo bartschi* is a tropical/subtropical species that was intro-

duced to Barnegat Bay (Hoagland & Turner, 1980), so its population parameters may in part represent its recent past geography. The evidence from year-long exposure panels is that *Bankia gouldi* survives winter temperatures far better than either *Teredo navalis* or *T. bartschi*. Physiological experiments (Hoagland, 1981) show that *T. bartschi* has a higher temperature tolerance than either of the native New Jersey species but has poorer cold tolerance than *B. gouldi*. The temperature tolerances of the three teredinids thus appear to be in harmony with the natural ranges of the species.

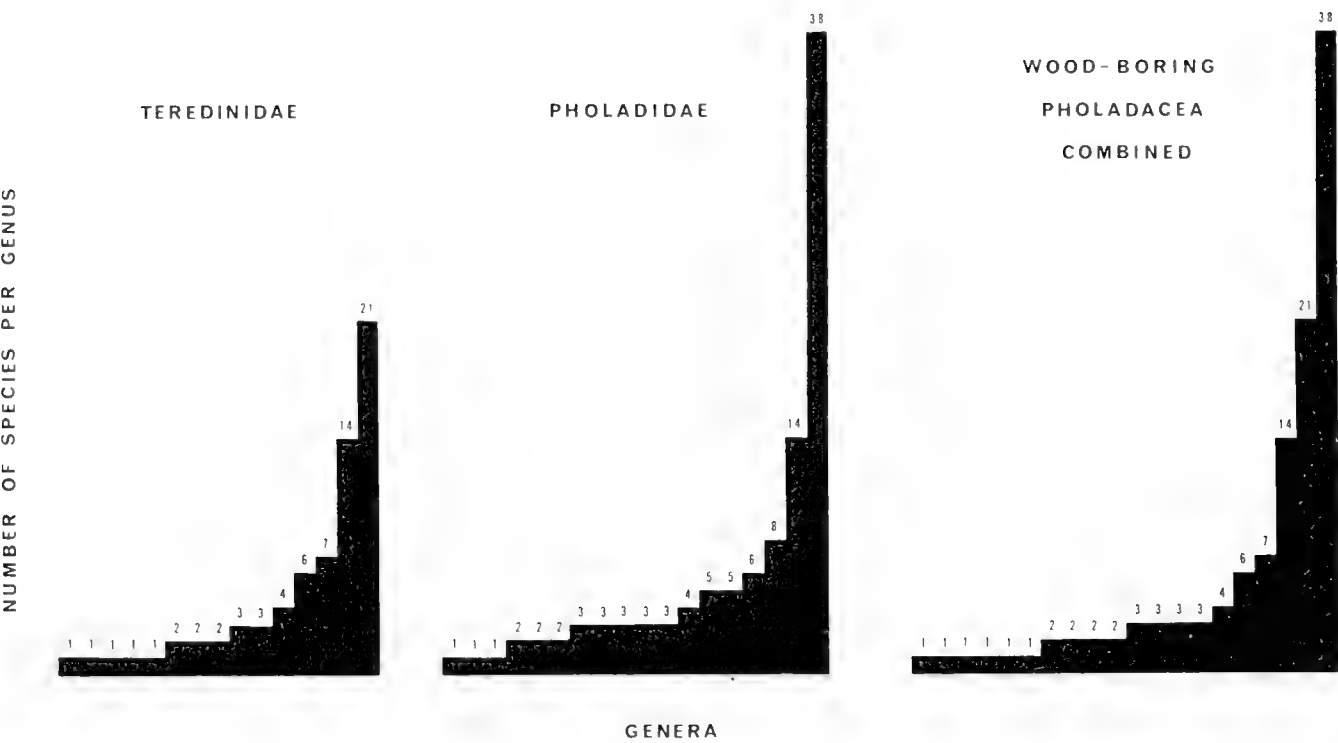


FIG. 2. Patterns of numbers of species per genus in families of Pholadacea, and in wood-boring Pholadacea.

TABLE 4. Allele Frequencies.

Locus and Allele	<i>Teredo bartschi</i>	<i>Teredo navalis</i>	<i>Lyrodus floridana</i>	<i>Bankia gouldi</i>	<i>Bankia fimbriatula</i>	<i>Martesia striata</i>
AcPh 98		1.00				
100	1.00			1.00		1.00
103			1.00		1.00	
Adkin 95		1.00				
97				.43	.97	
100	1.00		.95	.57	.03	
103			.05			1.00
AO I 85						1.00
97			.43	.29		
100	1.00	1.00	.57	.71	.85	
102					.15	
AO II ¹ 98					.40	—
100	1.00	1.00	1.00	1.00	.60	—
AAT 78						.08
80						.22
82						.70
93			1.00	.86	.05	
95				.14	.69	
97					.26	
100	1.00	1.00				
EST NA I 93						.98
95						.02
100	1.00	.96	.96	.16		
103		.04	.04	.84	1.00	
EST NA II 98						.68
100	.97			.74	1.00	.32
102	.03	.84	.04	.26		
103		.08	.96			
105		.08				

TABLE 4. (Continued)

Locus and Allele	<i>Teredo bartschi</i>	<i>Teredo navalis</i>	<i>Lyrodus floridana</i>	<i>Bankia gouldi</i>	<i>Bankia fimbriatula</i>	<i>Martesia striata</i>
EST NA III 100	1.00		.04	.97	.80	
101		.93	.04			
103		.07			.20	.40
105			.92	.03		
106						.60
G6PD 91						1.00
100	1.00	.06		.09		
103		.94				
105			1.00	.91		
108					1.00	
GPI I 100	1.00					
102					.30	.05
105		.51	.20	.57	.70	.50
107		.34	.76	.02		.35
109			.04			.07
111		.06		.36		.03
115		.09		.05		
GPI II ¹ 95	.23		—	.06	—	—
100	.77	1.00	—	.85	—	—
105			—	.09	—	—
GDH ¹ 99		.07			.05	—
100	1.00	.86	1.00	1.00	.89	
101		.07			.05	—
G3PD 97						1.00
100	1.00	1.00		.14		
103			1.00	.86	1.00	
α -GPDH ¹ 98			—	.90	—	
100	1.00	.91	—	.10	—	
106		.09	—		—	1.00
HEX 91						.90
94						.10
97		.73	.04	.68	.35	
100	1.00	.27	.96	.25	.65	
102				.07		
IsDH I 100	1.00	1.00	1.00	1.00	1.00	1.00
IsDH II ¹ 95				1.00		—
97			.03			—
100	1.00	.92	.97		.54	—
102		.08				—
103					.46	—
LDH 97						1.00
100	1.00	1.00	1.00		.25	
101				1.00	.75	
LAP 96		.07		.07		
99		.03				
100	1.00	.64		.51	.56	
102		.10	.02	.26	.44	.13
104		.12	.98	.16		
105		.04				.28
106						.09
108						.50

TABLE 4. (Continued)

Locus and Allele		<i>Teredo bartschi</i>	<i>Teredo navalis</i>	<i>Lyrodus floridana</i>	<i>Bankia gouldi</i>	<i>Bankia fimbriatula</i>	<i>Martesia striata</i>
MPI	92				.09	.15	
	94		.19	.70	.66	.65	
	96		.25		.14		
	98		.45	.23	.11	.20	.11
	100	1.00	.11	.07			.16
	102						.74
MDH I (NAD)	95				.99		
	100	1.00	1.00	1.00	.01	1.00	
	101						
	104						.98
	109						.02
MDH II ¹ (NAD)	95			—		—	1.00
	100	.57	1.00	—	.94	—	
	102	.43		—		—	
	105			—	.06	—	
PepG I	100	1.00	1.00	1.00	.17	1.00	1.00
	103				.66		
	105				.17		
PepG II	100	1.00	.25		.03	.21	
	103				.50	.69	.54
	105		.75	1.00	.16	.06	.28
	107				.31	.04	.12
	109						.06
PepG III	90				.09		
	93				.11		
	95				.14		.10
	98		.24		.66		.45
	100	1.00	.76	1.00			.37
	103					.88	
	104						.08
	105					.12	
PGM	95						.02
	97		.05	1.00	.09	.08	.11
	100	1.00	.11		.09	.50	.09
	102		.69		.75	.08	.78
	104		.15		.07	.30	
	106					.04	
6-PGD	100	1.00	1.00	1.00			.92
	101				1.00	1.00	
	105						.08
SoDH	94		.86	.06	.03	1.00	
	98		.14	.94	.83		.80
	100	1.00			.14		.20
SOD I	95		1.00				
	100	1.00		1.00	.96	1.00	1.00
	102				.04		
	106						
SOD II	100	1.00		1.00	.44	.92	.91
	102		1.00		.56	.08	.09
TPI	97			1.00			
	100	1.00			.32	.08	.06
	104		1.00		.68	.92	.94
XDH	100	1.00	1.00	1.00	1.00	1.00	1.00

¹Enzyme systems with missing data; not used in calculation of genetic distance.

Dendrogram of Genetic Distances

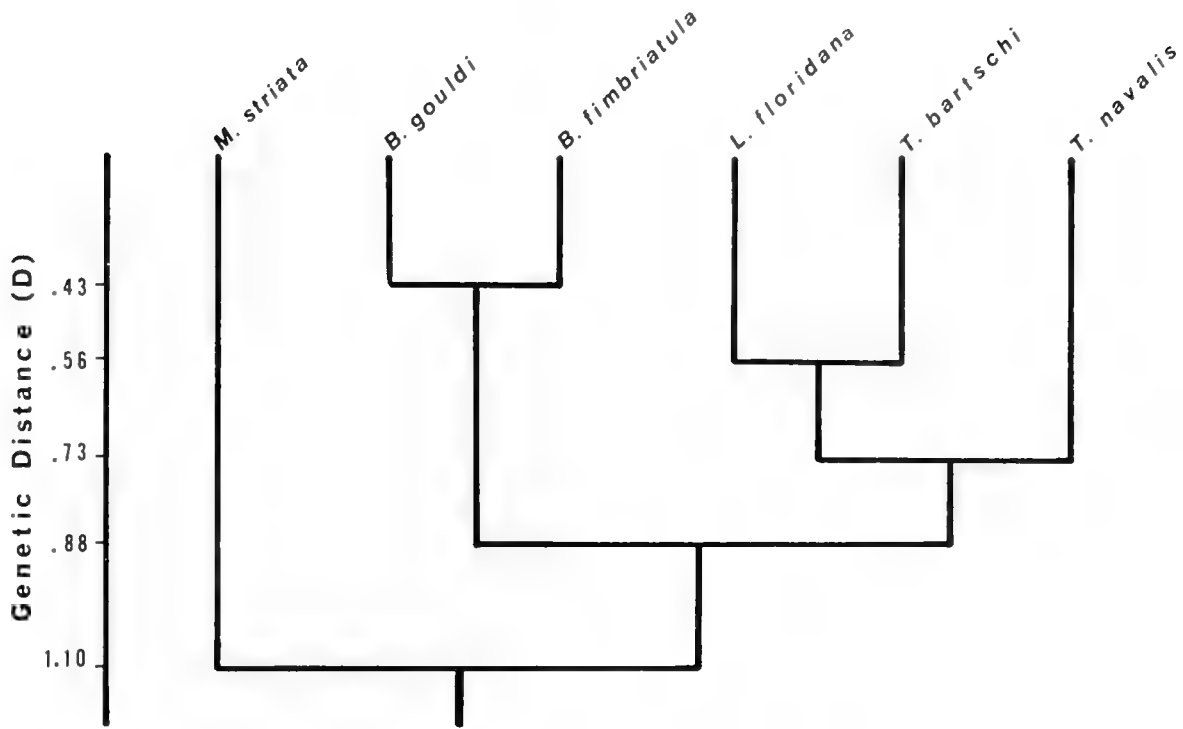


FIG. 3. Dendrogram of genetic distances.

TABLE 5. Genetic Identity Values (I).

	<i>T. navalis</i>	<i>L. floridana</i>	<i>B. gouldi</i>	<i>B. fimbriatula</i>	<i>M. striata</i>
<i>T. bartschi</i>	.506	.568	.429	.443	.321
<i>T. navalis</i>		.456	.341	.375	.290
<i>T. floridanus</i>			.460	.441	.327
<i>B. gouldi</i>				.649	.384
<i>B. fimbriatula</i>					.341

TABLE 6. Nei Genetic Distances (D)

	<i>T. navalis</i>	<i>L. floridana</i>	<i>B. gouldi</i>	<i>B. fimbriatula</i>	<i>M. striata</i>
<i>T. bartschi</i>	0.682	0.565	0.847	0.814	1.135
<i>T. navalis</i>		0.785	1.077	0.980	1.237
<i>L. floridanus</i>			0.776	0.818	1.118
<i>B. gouldi</i>				0.433	0.956
<i>B. fimbriatula</i>					1.077

TABLE 7. Genetic variability.

	Percent polymorphic loci (P)	Average number alleles per locus (A)	Average individual heterozygosity (H)
<i>Bankia gouldi</i>	.78 ¹	2.36	.124
<i>Bankia fimbriatula</i>	.61	1.94	.135
<i>Martesia striata</i>	.56	2.03	.125
<i>Teredo navalis</i>	.50	1.86	.073
<i>Lyrodus floridanus</i>	.39	1.55	.042
<i>Teredo bartschi</i>	.08	1.08	.003

¹.78 = 78%.

TABLE 8. Relative values of population parameters for three teredinids with different modes of larval development, in Barnegat Bay, New Jersey.

Parameter	<i>B. gouldi</i>	<i>T. navalis</i>	<i>T. bartschi</i>
Brooding	Absent	Short	Long
No. eggs per reproductive event	Numerous (~10 ⁶)	Intermediate (~10 ⁴)	Few (~10 ³)
Size and stage of offspring at release	Small, eggs & sperm	Medium, straight hinge	Large, pediveliger
Adult body size, uncrowded	Large (~300 mm)	Medium (~250 mm)	Small (~100 mm)
Lifespan	Several years	Several years	Usually 1–2 years
Age at first reproduction	3–4 months	3–4 months	6–8 weeks
Tolerance to crowding	Moderate	Moderate	High
Sex ratio	Skewed to ♀	Skewed to ♀	Highly skewed to ♀
Breeding season	Summer	Late summer & fall	Late spring to late fall
% females with larvae during breeding season	—	20–30%	Usually 80%
Stability of population size	Moderate	Moderate	Low
Adult phoresis	Common	Common	Common
Females retain larvae in winter	—	No	Yes
Adult winter mortality	Moderate	High	High
Juvenile mortality	Very high	High	Low
Turnover rate	Moderate	Moderate	High
Stability of substrate	Low	Low	Low
Genetic polymorphism	High	Medium	Low

The major zoogeographical distinction between the Pholadidae and the Teredinidae is that most species of wood-boring pholads occur in the deep sea, while teredinids breed in water less than 250 m deep. The major exceptions are the wood-boring members of the subfamily Martesiinae, and a few species of *Xylophaga* that occur in shallow water. Our records are not yet sufficient to analyse species deployment in the deep sea, but there is evidence of allopatry among species from the same group of *Xylophaga* based on morphological similarity (Table 9). Those *Xylophaga* that do extend into shallow water are found in high latitudes, e.g. *X. globosa* (Chile), *X. dorsalis*, *X. praestans*, and *X. atlantica* (N. Atlantic) and *X. washingtona* (N. Pacific). In the deep sea, two to five species of *Xylophaginae* have been found in a wood panel at any one station (Turner, unpublished). In shallow water, rarely is more than one species of wood-boring pholad found in a piece of wood. Yet it is possible to find eight sympatric species of tropical, shallow-water teredinids living together, often with a representative of *Martesia*.

Data on zoogeography of the Teredinidae were compiled from Turner (1966, 1971) and were augmented by more recent investigations. The division of species according to type of larvae and geographic range are shown in Table 10. Long-term larviparous species tend to occur in only one latitudinal

TABLE 9. Species subsets within the genus *Xylophaga*.¹

I. <i>X. concava</i> <i>X. sp. 1</i> ² <i>X. erecta</i> <i>X. grevei</i> <i>X. wolffi</i> <i>X. lobata</i>	IV. <i>X. foliata</i> <i>X. sp. 5</i> ² <i>X. atlantica</i> <i>X. abyssorum</i> <i>X. duplicata</i>
II. <i>X. galathea</i> <i>X. hadalis</i> <i>X. sp. 2</i> ² <i>X. murrayi</i> <i>X. panamensis</i> <i>X. africana</i>	V. <i>X. washingtona</i> <i>X. rikuensis</i> <i>X. aurita</i> <i>X. turnerae</i>
III. <i>X. bruuni</i> <i>X. obtusata</i> <i>X. suppicata</i> <i>X. sp. 3</i> ² <i>X. sp. 4</i> ²	VI. <i>X. globosa</i> <i>X. mexicana</i> <i>X. indica</i> <i>X. dorsalis</i>
	VII. <i>X. praestans</i>

¹Data used to separate the groups are from Turner, in prep., and Knudsen, 1961. The major characters that separate the groups are shell and siphon characters (Hoagland & Turner, 1981).

²Turner, in prep.; undescribed *Xylophaga*.

zone, but in more than one ocean. Planktonic species tend to be in one ocean, but at wide-spread latitudes; however, the trend is not statistically significant.

Of the approximately 70 teredinid species, over 2/3 are tropical; at least six of the tropical

TABLE 10. The division of species according to type of larvae and geographical range. The first number is the observed number of species; the second is the expected number based on the assumption that larval type and distribution are independent.

	Endemic or 1 Ocean		Two or more Oceans	
	O	E	O	E
Planktonic	25	21.3	7	10.7
Short term Larviparous	5	6.0	4	3.0
Long term Larviparous	4	6.7	6	3.3
$\chi^2 = 5.70, p < .10$ (close to .05)				
	One latitudinal Zone		Two or more Zones*	
	O	E	O	E
Planktonic	28	28.5	5	4.5
Short term Larviparous	6	6.9	2	1.1
Long term Larviparous	10	8.6	0	1.4
$\chi^2 = 2.55, p < .50$ (not significant)				

A latitudinal zone is defined here as 30° of latitude, starting at the equator.

species are circumtropical. Most of the temperate-zone species are broadly distributed. The small teredinid genera (those containing fewer than 6 species) are almost entirely tropical, and these species tend to be narrowly distributed.

Taxonomic Characters and Taxonomic Relationships

The raw morphological data were analysed by the method of Wilson (1965) to produce cladograms based on derived, and in particular, unique and unreversed character states (Figures 4 and 5). *Zachsia* is omitted because anatomical data at the genus level are being revised.

Major morphological characters cannot be traced through the Pholadacea without involving loss or repeated evolution of certain structures (Tables 11–13). For example, accessory shell plates must be highly convergent (Table 14). The wood-boring habit causes correlation of such genetically independent and probably convergent traits as long burrow, the presence of burrow lining, and often, but not necessarily, separate siphons. *Teredora* does not have separate siphons. The most troublesome aspect of Fig. 5 is that it requires the Jouannetiinae and the Xylophaginae independently to lose the apophyses, a structure which appears functionally advantageous. Alternatively, the two subfamilies could have

shared a common ancestor (dotted line, Fig. 5). But then, the Jouannetiinae and the Martesiinae would have to have developed both the callum and siphonoplax independently. There is no objective way to choose between these two alternatives as likely evolutionary sequences without the inclusion of more characters, including some unique and unreversed characters. Data on the embryological development of callum, siphonoplax, caecum and apophyses in the various subfamilies would also aid in the choice by showing whether they are really homologous in all subfamilies.

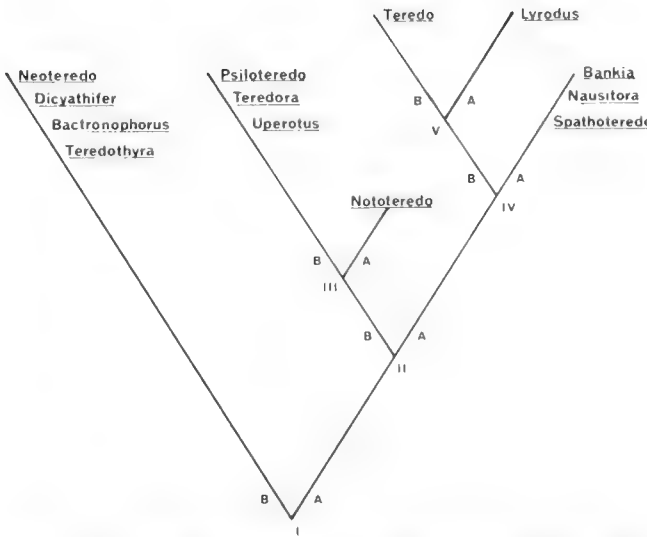


FIG. 4. Analysis of the Bankiinae and Tereidinae using derived character states.

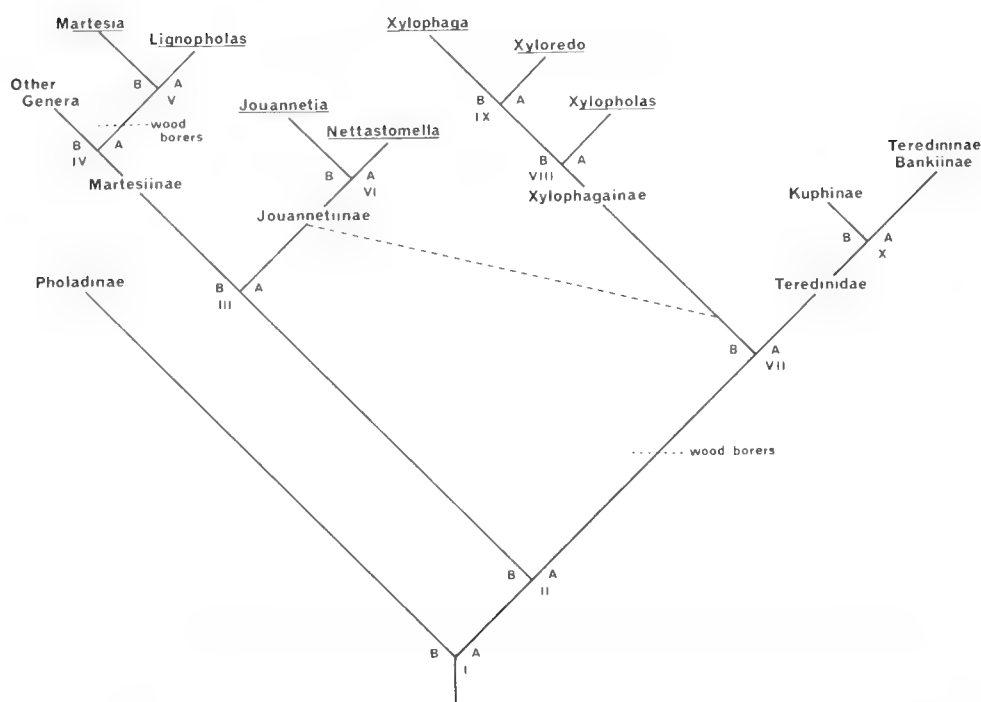


FIG. 5. Analysis of the Pholadacea using derived character states.

The major discontinuity in morphology within the Teredinidae occurs between *Kuphus* and the other genera (Fig. 5). *Kuphus* is composed of a single species that lacks the wood-storing caecum. It shares some characteristics with pholads, but it does have pallets. It has so many unique features that it must be considered specialized, yet it is basal within the Teredinidae because its intestine passes through the heart. The differences between it and the other adult Teredinidae emphasize those characters that are correlated with adult wood-boring. Adult *Kuphus* is thought to live within its thick tube, reaching a length of several feet, in decaying wood or in mud. Neither of the authors have observed live animals *in situ*.

A phenetic analysis of the Pholadacean data set emphasizes overall similarity of the various taxa, without regard for actual evolutionary relationships. It allows us to see if there are interesting correlations among character states. Our Principal Components analysis of 52 characters and 72 taxa took 13 components to explain 90% of the variation in the data. Only the first two components each explained more than 10% of the variation. The factor loadings on the first component (43% of the variation) are in Table 15. Table 16 is a list of the 24 characters out of 52 that were associated with the first Principal Component. Many of the characters, such as the denticular ridges on the shell, the very large posterior

adductor muscle, the presence of a calcified burrow, the gill with single demibranch, the small labial palps, and the wood-storing caecum, are associated with wood-boring. In fact, the first two characters are associated with wood-boring in all of the major groups of wood-boring clams: the Teredinidae, the Xylophaginae, and the Martesiinae. However, some of the characters with high loadings on the first axis are functionally related to length of the burrow, and not to wood-boring itself. Examples are on length of the body, the position of the visceral mass relative to the shell, and the position of the siphonal retractor muscle on the burrow lining.

Confounding the wood-boring and burrow length characters of the first component are characters separating the Pholadidae from the Teredinidae that are not necessarily related to wood-boring. These characters can be separated from the others according to the degree that they load onto the first factor axis (Table 15), because wood-boring pholads join rock-borers in one set of characters but join the teredinids in the other set. Characters related to wood-boring that are unique to the teredinids have the highest values in Table 15, column 1. Table 17 shows the relationship between each taxon and the first Principal Component. Wood-boring species project negatively because of the particular assignment of numerical values to the traits (Appendix C). The rock-boring pholads and the

TABLE 11. Presumed Ancestral and Derived Character States in the Pholadacea.

Pholadacean character states present in all pholadaceans and therefore presumed to have been present in the ancestral group.

1. Fused mantle
2. Discoid foot
3. Pedal gape
4. Shell with reduced umbo and hinge
5. Elongate gills (except in *Xylophaginae*, *Jouannetiinae*)
6. Anterior adductor muscle attached at the umbonal reflection of the shell, an exterior attachment site.

Pholadacean character states retained in all the Pholadinae, altered in at least one of the other subfamilies. These are presumed to be either ancestral or unique by virtue of their evolution after the lineage split.

1. Gill with 2 demibranchs
2. Caecum lacking
3. Short burrow
4. Shell covers viscera
5. Posterior adductor muscle about the same size as anterior adductor muscle.
6. Siphons united
7. Callum not present
8. Apophyses
9. Non wood-boring
10. Periostracal lamellae absent
11. Mesoplax present (accessory shell plates)
12. Burrow not lined with calcium
13. Siphonal retractor muscles attach on the shell
14. Umbonal-ventral sulcus not well developed
15. Weakly denticulated shell sculpture
16. Intestine goes through pericardium
17. Large ventricular bulb of heart

Derived character states of the Pholadacea (illustrated in Figs. 4 and 5). Traits that were not unique and unreversed are in brackets.

- I. Branch A: Development of umbonal-ventral sulcus, loss of protoplax
- II. Branch A: Development of wood-storing caecum, long burrow and wormlike body, posterior adductor muscle enlarged compared with anterior adductor muscle, siphons not completely united, development of strong denticulated ridges on anterior portion of shell; one demibranch
Branch B: Development of a callum, siphonoplax
- III. Branch A: Shell is inequivalve, [apophyses lost]
Branch B: Hypoplax, metaplax
- IV. Branch A: Evolution of wood-boring habit: [truncated beak of shell], [denticulated shell sculpture]
- V. Branch A: Fringed periostracal lamellae on shell
- VI. Branch A: Callum incompletely calcified, [mesoplax lost]
- VII. Branch A: Siphonal retractor muscles attached to tube, pallets close the tube, viscera extend in loop beyond posterior adductor muscle, highly developed dorsal condyles, [loss of mesoplax]
Branch B: [apophyses lost]
- VIII. Branch A: Siphonal plates with siphonal retractor muscles attached
- IX. Branch A: [Periostracal/calcareous burrow lining]
- X. Branch A: Intestine does not go through heart, small ventricular bulb of heart
Branch B: Highly reduced shell, very thick calcareous tube, [caecum lost]

Derived character states in the Bankiinae and Teredininae (Fig. 5).

- I. Branch A: Open anal canal
- II. Branch A: Elongate stomach, short intestine
- III. Branch A: Fragmented pallets, approaching a segmented condition
- IV. Branch A: Segmented pallets
Branch B: Gills adapted for brooding
- V. Branch A: Periostracal-capped pallets

TABLE 12. Evidence of a nonlinear Evolutionary Sequence: Character States of Several Important Characters.

Pholadinae	Martesiinae	Jouannetiinae	Xylophaginae	Kuphinae	Other Teredinidae
Two demibranchs	Two demibranchs	Two demibranchs	One demibranch	One demibranch	One demibranch
No caecum	No caecum	No caecum	Caecum	No caecum ¹	Caecum
Apophyses	Apophyses	No apophyses ¹	No apophyses ¹	Apophyses	Apophyses
Intestine through heart	Intestine through heart	Intestine through heart	Intestine through heart	Intestine through heart	Intestine not through heart
Siphonal retractors inserted on shell	Siphonal retractors inserted on shell	Siphonal retractors inserted on shell	Siphonal retractors inserted on shell	Siphonal retractors inserted on tube	Siphonal retractors inserted on tube
No callum	Callum ¹	Callum variable	No callum	No callum	No callum
Body short	Body short	Body short	Body wormlike	Body wormlike	Body wormlike

¹Evidence that evolution of the Pholadacea was not in a linear sequence, or that character-state reversion took place.

TABLE 13. Convergent and Non-linearly evolving Features in the Pholadacea.

1. Brooding	Arose independently in <i>Xylophaga</i> and <i>Teredininae</i> ; structures are different.
2. Accessory shell plates	Anastomosing pattern of presence-absence in the <i>Pholadidae</i> (Table 14).
3. Callum and Apophyses	One or both of these characters must have evolved more than once in the <i>Pholadidae</i> . <i>Martesiinae</i> and <i>Jouannetiinae</i> have callum; <i>Jouannetiinae</i> and <i>Xylophaginae</i> lack apophyses (Table 12).
4. Labial palps	Large in rockborers; small in most woodborers. But large in <i>Nototeredo norvagica</i> ; small in <i>Psiloteredo megotara</i> , <i>Bankia gouldi</i> , <i>Teredo navalis</i> .
5. Posterior adductor muscle	Large in all woodborers; reverts (?) to small size in <i>Kuphus</i> .
6. Stomach shape	Globular in most teredinids; elongate in <i>Bankiinae</i> , except for <i>Nototeredo</i> , which has a globular stomach. Either <i>Nototeredo</i> 's pallet type is convergent with <i>Bankiinae</i> , or its stomach type is convergent with the <i>Teredininae</i> .
7. Heart size and position	Variable in the <i>Teredinidae</i> subfamilies, but usually posterior in the <i>Bankiinae</i> .
8. Caecum	Variable in the <i>Teredininae</i> but large in the <i>Bankiinae</i> . Lacking in the <i>Kuphinae</i> but present in the <i>Xylophaginae</i> .
9. Gill shape	In both the <i>Teredininae</i> and <i>Bankiinae</i> , some species have broad gills while others have narrow gills.
10. Degree of siphon separation	Siphons are separate in <i>Kuphus</i> , but variable within the other subfamilies.
11. Filter-feeding apparatus	Gill-length and degree of siphon papillation are variable in both the <i>Teredininae</i> and <i>Bankiinae</i> .

TABLE 14. Variability in Accessory Shell Plates in the Pholadidae.

	Pholadinae	Martesiinae	Jouannetiinae	Xylophaginae
Siphonoplax	no	variable	yes	no
Hypoplax	no	variable	no	no
Metaplax	no	variable	no	no
Protoplax	usually	no	no	no
Mesoplax	usually	yes	variable	yes
Callum	no	yes	variable	no

wood-boring teredinids have the highest factor scores; the pholads project positively and the teredinids negatively. The wood-boring pholads with long burrows and the teredinid *Kuphus* project weakly negatively while the wood-boring pholads (e.g., *Xylophaga*) project slightly positively.

The second Principal Component (13% of the variation) consists mainly of characters that separate the bulk of the Pholadacea from *Xylophaga*, such as lack of faecal pellets in the burrow, presence of apophyses, long ctenidia, and a longer incurrent than excurrent siphon. No new insights are produced by this information.

A Principal Components analysis of the *Pholadidae* alone (78 taxa and 73 characters; Table 18) allowed entrance into the analysis of many shell characters lacking in the *Teredinidae*, such as shape of the accessory shell plates. The wood-boring *Pholadidae* could be compared with the rock- and mud-borers. Many of the characters with high factor loadings on the first axis are related to wood-boring, but also many are characters peculiar to the large genus *Xylophaga*. Wood-boring *Xylophaginae* are characterized by a small crystalline style, stomach, and labial palps, but large wood-storing caecum. The shell beak is truncated. Ctenidia tend to be

TABLE 15. Factor loadings on the first 3 Principal Components explaining 63% of the variance, Pholadacean morphological data.

	Principal Components		
	1	2	3
Percent of Trace:	42.92%	12.96%	7.03%
Characters			
1 Shell size (large) ¹	0.802	-0.405	0.301
2 Anterior sculpture (ridges)	-0.869	-0.294	-0.079
3 Radial ribs	0.888	0.286	0.115
4 Beak shape (truncated)	-0.881	-0.304	0.023
5 Valves (asymmetrical)	0.218	-0.016	0.364
6 Umbonal-ventral ridge	-0.531	-0.255	0.729
7 Mesoplax present	0.701	-0.421	0.102
8 Posterior muscle scar (sculptured)	0.016	-0.756	-0.152
9 Siphonoplax present	0.416	-0.004	0.490
10 Hypoplax present	0.248	-0.028	0.396
11 Metaplax present	0.379	0.051	0.075
12 Protoplax present	0.476	0.232	-0.688
13 Callum present	0.581	0.083	0.738
14 Apophyses present	-0.149	0.821	-0.083
15 Ventral condyle present	-0.824	0.185	0.381
16 Dorsal condyle present	-0.813	0.434	0.268
17 Posterior concentric sculpture	0.509	0.198	-0.244
18 Posterior ribs	0.220	0.155	-0.416
19 Pedal gape	-0.523	-0.223	0.364
20 Adductor muscle attachment (to lamina)	0.129	-0.022	0.246
21 Shell auricle present	-0.921	0.326	0.005
22 Pallets present	-0.931	0.334	-0.031
23 Calcareous burrow lining	-0.886	0.269	-0.078
24 Periostracal burrow lining	-0.138	-0.085	-0.029
25 Consolidated faecal pellets	0.117	-0.770	0.008
26 Incur./Excur. siphon width >1	0.469	0.207	0.008
27 Incur./Excur. siphon length >1	-0.118	-0.703	-0.141
28 Incurrent siphon long	0.642	0.026	-0.494
29 Papillae on incurrent siphon	0.208	0.130	0.197
30 Papillae on excurrent siphon	-0.230	-0.014	0.267
31 Siphons united	0.703	-0.155	0.102
32 Siphons partially calcareous	0.181	0.058	0.082
33 Visceral ganglion (posterior)	-0.931	0.334	-0.031
34 Post. adductor muscle large	-0.875	0.025	0.264
35 Post. add. musc. shape (irregular)	-0.293	0.119	0.095
36 Adductors close together	-0.931	0.334	-0.031
37 Siphonal retractors (on burrow lining)	-0.939	0.307	-0.039
38 Ctenidia (long)	0.005	0.962	0.159
39 Number of demibranchs (2)	0.942	0.277	0.123
40 Stomach large	0.909	0.018	0.121
41 Labial palps (large)	0.722	0.382	0.144
42 Wood in gut	-0.942	-0.277	-0.123
43 Caecum present	-0.847	-0.329	-0.098
44 Intestine traverses heart	0.921	-0.326	-0.005
45 Gill position (posterior)	-0.942	-0.277	-0.123
46 Sperm transfer (direct)	-0.553	-0.386	-0.037
47 Substrate: rock	0.793	0.231	0.235
48 Substrate: mud	0.639	0.275	-0.349
49 Substrate: nuts	-0.016	-0.810	-0.005
50 Substrate: wood	-0.827	-0.329	-0.002
51 Substrate: live roots	-0.139	0.031	-0.009
52 Burrow long	-0.861	0.247	0.028

¹Parentheses indicate the trait with the highest character state.

TABLE 16. Characters associated with the Principal Component of Table 15 explaining 43% of the variation in the Pholadacea data matrix. Characters are associated at a level of .60 or higher. Characters associated at a lower level were more highly associated with another principal component.

Shell highly reduced ^{1,2,3}
Denticular ridges of shell ¹
Absence of continuous, prominent radial ribs on shell ¹
Shell beak truncated ¹
Absence of accessory shell plates ³
Strong ventral and dorsal condyles ¹
Shell flange present ¹
Pellets present ³
Calcified burrow ^{1,2}
Siphons not united for entire length ^{1,2}
Posterior position of visceral ganglia ²
Posterior position of gills ²
Large posterior adductor muscle ¹
Close positioning of adductor muscles; visceral mass loops posterior to shell ^{2,3}
Siphonal retractor muscle inserts on burrow lining ^{2,3}
Gills possess 1 demibranch ¹
Presence of anal canal ¹
Stomach small ¹
Labial palps small ¹
Products of boring enter gut ¹
Wood-storing caecum ¹
Intestine does not pass through heart ³
Body elongate and worm-like ²
Long incurrent siphon ²

¹Characters related to wood-boring.

²Characters related to long burrow.

³Characters unique to the Teredinidae, not necessarily related to wood-boring.

short; the gill is posterior and has only one demibranch. The wood-boring Martesiinae, however, have two demibranchs, and lack a caecum. The Xylophaginae do not have the gill extending beyond the posterior adductor muscle; the Martesiinae do. Despite these important differences, the two subfamilies of borers have a few similarities. The anterior shell sculpture of most woodborers is denticulate without posterior ribs. The absence of apophyses and the presence of a pedal gape tend to be traits of adult wood-borers.

The second Principal Component explained 11% of the variation, and expressed a relationship between shell shape and the accessory shell plates. Correlated characters at a level above 0.7 were small shell, poorly developed umbonal-ventral ridge, absence of a hypoplax, one-piece metaplast (if it is present at all), presence of a protoplax, absence of a callum, solid apophyses in the adult, and small condyles. One problem in interpreting this axis is the uncertainty of homology of the accessory plates given the same name.

The last set of character correlations was done with a reduced species set of 34 Teredinidae for which detailed anatomical data were available. There were a total of 61 characters. Eight Principal Components were required to explain 90% of the variation (Table 19). Component one separated *Kuphus*, thought to be mud-dwelling as an adult, from the other Teredinidae. Its factor score was -2.984 on the first component (Table 20). The characters associated with the first Principal Component (Table 21) could be related to the lack of dependence on wood in older adults. Specifically, the shell of *Kuphus* is poorly developed for boring, the burrow lining is thick enough to withstand breakage outside of wood, and there is no wood-storing caecum, at least in the few specimens that have been dissected.

Component two (15% of the variation) showed an association of thumbnail-shaped and sculptured, inflexible pallets with united siphons and calcareous deposits, especially rings, in the burrow lining. Other characteris-

TABLE 17. Factor Scores of Pholadacean Species on the First Two Principal Components.

Species	Components	
	1	2
1. <i>Barnea candida</i>	0.812	0.288
2. <i>Barnea parva</i>	0.748	0.215
3. <i>Barnea lamellosa</i>	0.732	0.215
4. <i>Barnea subtruncata</i>	0.701	0.201
5. <i>Cyrtopleura costata</i>	0.862	0.352
6. <i>Cyrtopleura lanceolata</i>	0.747	0.143
7. <i>Cyrtopleura cruciger</i>	0.794	0.137
8. <i>Pholas dactylus</i>	0.798	0.138
9. <i>Pholas campechiensis</i>	0.903	0.204
10. <i>Pholas chiloensis</i>	0.828	0.188
11. <i>Zirfaea pilsbryi</i>	0.633	0.154
12. <i>Talona explanata</i>	0.839	0.168
13. <i>Chaceia ovoidea</i>	0.653	0.170
14. <i>Penitella fitchi</i>	0.627	0.102
15. <i>Penitella conradi</i>	0.627	0.102
16. <i>Penitella penita</i>	0.683	0.151
17. <i>Penitella gabbi</i>	0.612	0.118
18. <i>Pholadidea loscombiana</i>	0.790	0.167
19. <i>Pholadidea melanura</i>	0.647	0.133
20. <i>Pholadidea quadra</i>	0.730	0.133
21. <i>Pholadidea tubifera</i>	0.692	0.097
22. <i>Lignopholas rivicola</i>	0.379	-0.032
23. <i>Martesia striata</i>	0.376	-0.165
24. <i>Martesia fragilis</i>	0.483	-0.104
25. <i>Diplothyra smithi</i>	0.588	0.041
26. <i>Parapholas californica</i>	0.748	0.010
27. <i>Parapholas acuminata</i>	0.712	0.010
28. <i>Jouannetia duchassaingi</i>	0.707	-0.066
29. <i>Jouannetia globosa</i>	0.715	-0.096
30. <i>Nettastomella japonica</i>	0.607	0.086
31. <i>Nettastomella rostrata</i>	0.651	0.017
32. <i>Xylophaga dorsalis</i>	0.076	-0.977
33. <i>Xylophaga convexa</i>	0.059	-0.938
34. <i>Xylophaga atlantica</i>	0.041	-1.047
35. <i>Xylophaga washingtona</i>	0.058	-1.174
36. <i>Xylophaga turnerae</i>	0.043	-1.195

Table 17 (Continued)

Species	Components	
	1	2
37. <i>Xylophaga africana</i>	0.003	-0.898
38. <i>Xylopholas altenai</i>	-0.117	-0.747
39. <i>Xyloredo ingolfia</i>	-0.189	-0.752
40. <i>Kuphus polythalamia</i>	-0.284	0.128
41. <i>Bactronophorus thoracites</i>	-0.673	0.114
42. <i>Neoterodo reynei</i>	-0.613	0.182
43. <i>Dicyathifer manni</i>	-0.726	0.181
44. <i>Teredothyra dominicensis</i>	-0.657	0.136
45. <i>Teredothyra matocotana</i>	-0.635	0.159
46. <i>Teredora malleolus</i>	-0.564	0.187
47. <i>Teredora princesae</i>	-0.564	0.187
48. <i>Psiloteredo healdi</i>	-0.660	0.117
49. <i>Psiloteredo megotara</i>	-0.629	0.148
50. <i>Psiloteredo senegalensis</i>	-0.660	0.117
51. <i>Zachsia zenkewitschi</i>	-0.756	0.097
52. <i>Uperotus clavus</i>	-0.539	0.131
53. <i>Uperotus panamensis</i>	-0.539	0.131
54. <i>Lyrodus massa</i>	-0.690	0.118
55. <i>Lyrodus medilobata</i>	-0.690	0.118
56. <i>Lyrodus floridana</i>	-0.728	0.117
57. <i>Teredo clappi</i>	-0.690	0.118
58. <i>Teredo furcifera</i>	-0.690	0.118
59. <i>Teredo navalis</i>	-0.728	0.117
60. <i>Teredo poculifer</i>	-0.690	0.118
61. <i>Nototerodo edax</i>	-0.577	0.160
62. <i>Nototerodo knoxi</i>	-0.625	0.138
63. <i>Nototerodo norvagica</i>	-0.613	0.204
64. <i>Spathoterodo obtusa</i>	-0.622	0.141
65. <i>Spathoterodo spatha</i>	-0.648	0.151
66. <i>Nausitora dunlopei</i>	-0.661	0.148
67. <i>Nausitora fusticula</i>	-0.727	0.084
68. <i>Nausitora hedleyi</i>	-0.706	0.110
69. <i>Bankia australis</i>	-0.677	0.128
70. <i>Bankia campanellata</i>	-0.703	0.139
71. <i>Bankia gouldi</i>	-0.758	0.069
72. <i>Bankia setacea</i>	-0.677	0.128

TABLE 18. Factor loadings on the first 3 Principal Components explaining 55% of the variance, Pholadidae morphological data.

	Principal Components		
	1	2	3
Percent of Trace:	35.52%	10.56%	9.21%
Characters			
1 Shell size (large)	0.421	-0.661	0.414
2 Anterior sculpture (ridges)	0.916	-0.001	-0.155
3 Radial ribs	-0.916	0.001	0.155
4 Beak shape (truncated)	0.896	-0.173	-0.187
5 Valves (asymmetrical)	-0.197	0.256	0.131
6 Umbonal-ventral ridge	0.431	-0.560	-0.166
7 Mesoplax present	0.445	-0.466	-0.091
8 Mesoplax divided	0.678	-0.037	-0.029
9 Mesoplax wrinkled	-0.537	-0.794	-0.027
10 Mesoplax sculptured	0.829	0.058	-0.089
11 Mesoplax with tube	0.317	0.058	0.179
12 Mesoplax shape (complex)	0.533	-0.399	0.291
13 Posterior muscle scar (sculptured)	0.686	0.037	0.242

Table 18 (Continued)

	Principal Components		
	1	2	3
Percent Trace:	35.52%	10.56%	9.21%
14 Siphonoplax present	-0.349	-0.291	0.049
15 Siphonoplax calcareous	0.234	0.473	0.076
16 Siphonoplax tube-like	-0.220	-0.300	-0.127
17 Siphonoplax sculptured	-0.028	0.457	0.079
18 Hypoplax present	-0.262	-0.575	-0.032
19 Hypoplax divided	-0.054	-0.111	0.053
20 Metaplax present	-0.350	-0.320	0.028
21 Metaplax divided	0.040	-0.674	-0.046
22 Protoplax present	-0.395	0.530	0.135
23 Protoplax divided	-0.006	-0.003	0.010
24 Callum present	0.574	-0.639	0.000
25 Callum sculptured	-0.112	-0.511	0.109
26 Callum size (large)	0.008	0.002	0.051
27 Siphonal plate present	0.073	0.089	-0.315
28 Periostracal lamellae present	-0.196	-0.397	-0.065
29 Periostracal lamellae divided	0.115	0.107	-0.207
30 Apophyses present	-0.854	-0.249	0.014
31 Apophyses solid	-0.076	0.698	0.145
32 Ventral condyle present	0.051	-0.793	-0.604
33 Dorsal condyle present	-0.584	-0.735	-0.118
34 Posterior concentric sculpture	-0.412	0.104	0.006
35 Posterior ribs	-0.189	0.295	0.104
36 Pedal gape	0.470	-0.208	-0.148
37 Post. adductor muscle attachment (to lamina)	-0.109	0.086	0.088
38 Calcareous burrow-lining	0.106	0.115	-0.875
39 Periostracal burrow lining	0.106	0.115	-0.875
42 Consolidated faecal pellets	0.823	-0.238	0.349
43 Incur./Excur. siphon width >1	-0.407	-0.419	0.143
44 Incur./Excur. siphon length >1	0.499	-0.019	-0.155
45 Excur. siphon long	-0.526	0.201	-0.045
46 Incur. siphon long	-0.302	0.395	0.139
47 Papillae on incur. siphon	-0.236	-0.201	0.664
48 Papillae on excur. siphon	0.569	-0.002	0.414
49 Siphons united	-0.127	-0.140	0.931
50 Siphons calcareous	-0.023	0.038	-0.118
51 Post. add. musc. large	0.471	-0.582	-0.057
52 Post. add. musc. shape (irregular)	-0.036	-0.277	-0.203
53 Siphonal retractors (on burrow lining)	0.073	0.089	-0.315
54 Ctenidia (long)	-0.982	-0.056	0.097
55 Number of demibranchs (2)	-0.982	-0.056	0.097
56 Stomach large	-0.947	-0.012	-0.246
57 Labial palps (large)	-0.982	-0.056	0.097
58 Wood in gut	0.982	0.056	-0.097
59 Caecum present	0.952	0.072	-0.250
60 Extended excur. canal	0.106	0.115	-0.875
61 Crystalline style (large)	-0.955	0.015	-0.289
62 Gill position (posterior)	0.982	0.056	-0.097
63 Accessory genital organ	0.933	-0.008	0.320
64 <i>Vesicula seminalis</i>	0.933	-0.008	0.320
65 Sperm transfer (direct)	0.030	0.071	0.148
66 Larviparity	0.688	0.067	0.270
67 Long-term brooding	0.964	-0.205	0.139
68 Brooding place (gills)	-0.805	0.238	-0.110
69 Substrate: rock	-0.822	-0.077	0.145
70 Substrate: mud	-0.640	0.194	0.082
71 Substrate: nuts	0.948	-0.021	-0.137
72 Substrate: wood	0.929	-0.068	-0.178
73 Burrow long	-0.019	0.053	-0.779

TABLE 19. Factor loadings on the first 3 Principal Components explaining 57% of the variance, Teredinidae morphological data

	Principal Components		
	1	2	3
Percent Trace:	29.57%	14.67%	12.58%
Characters			
1 Shell size (large)	0.765	-0.244	0.297
2 Anterior sculpture (ridges)	0.987	0.062	0.026
3 Ventral condyle present	0.987	0.062	0.026
4 Dorsal condyle present	0.987	0.062	0.026
5 Shell auricle present	0.987	0.062	0.026
6 Pallets in cones	0.133	-0.322	0.101
7 Pallet cones unfused	-0.010	-0.409	-0.020
8 Pallet with cups	0.219	0.471	0.046
9 Pallet cups: shape (thumbnail)	0.010	0.628	-0.421
10 Pallet sculpture (ribbed)	-0.012	0.516	-0.500
11 Pallet with periostracal cap	0.139	-0.471	-0.169
12 Pallet with calcareous cap	0.080	-0.213	0.081
13 Periostracal awns	-0.014	-0.294	-0.084
14 Calcareous burrow lining	-0.725	0.068	0.240
15 Periostracal burrow lining	0.042	-0.015	-0.016
16 Rings on burrow lining	-0.266	0.810	-0.090
17 Ridges on burrow lining	-0.299	-0.380	0.747
18 Incurrent < excurrent siphon width	0.070	0.096	0.486
19 Incurrent < excurrent siphon length	-0.987	-0.062	-0.026
20 Excurrent siphon (long)	-0.987	-0.062	-0.026
21 Incurrent siphon (long)	-0.987	-0.062	-0.026
22 Papillae on incur. siphon	0.361	0.398	-0.292
23 Papillae on excur. siphon	0.214	0.279	-0.543
24 Siphons united	0.146	0.645	-0.214
25 Dorsal lappets present	0.013	0.260	0.567
26 Muscular collar present	-0.987	-0.062	-0.026
27 Large post. add. muscle	0.987	0.062	0.026
28 Stomach (large)	0.074	0.596	-0.357
29 Labial palps (large)	-0.345	0.607	-0.425
30 Caecum (large)	0.606	-0.303	-0.212
31 Extended excurrent canals	0.987	0.062	0.026
32 Intestine traverses heart	-0.987	-0.062	-0.026
33 Sperm transfer direct	0.040	-0.445	-0.079
34 Larviparity	0.040	-0.442	-0.021
35 Long-term brooding	0.021	-0.380	-0.454
36 2 sexes (dwarf ♂)	0.014	-0.017	-0.019
37 Substrate: mud	-0.987	-0.062	-0.026
38 Substrate: nuts	-0.055	0.388	-0.369
39 Substrate: wood	0.765	-0.244	0.297
40 Substrate: roots	0.042	-0.015	-0.016
41 Heart large	-0.282	0.308	0.671
42 Ventricular bulb (long)	-0.987	-0.062	-0.026
43 Heart posterior	-0.117	-0.388	0.061
44 Auricles pigmented	-0.329	0.249	0.637
45 Mantle thick	-0.639	-0.123	0.306
46 Gill (long)	-0.351	0.119	-0.659
47 Stomach elongate	0.279	-0.757	-0.355
48 Stomach anterior	0.298	0.502	-0.071
49 Esophagus long	-0.078	-0.073	-0.036
50 Visceral mass/body ratio high	0.279	0.447	0.150
51 Kidney surrounds intestine	-0.004	0.219	0.498
52 Anal canal (closed)	0.434	0.338	0.745
53 Anal papillae present	-0.060	0.349	0.843
54 Intestine traverses anal canal	-0.027	0.714	-0.561

Table 19 (Continued)

	Principal Components		
	1	2	3
Percent Trace:	29.57%	14.67%	12.58%
55 Intestine long	0.185	0.496	0.116
56 Intestine over style sac	0.099	0.923	0.159
57 Faecal pellets produced	0.060	-0.349	-0.843
58 Anterior gill section	0.498	-0.560	0.186
59 Gill broad	-0.272	0.386	0.624
60 Branchial food groove	-0.047	0.028	-0.387
61 Pellets flexible	0.146	-0.622	-0.061

TABLE 20. Factor scores of Teredinidae Species on the First Three Principal Components.

Species	Components		
	1	2	3
1. <i>Kuphus polythalamia</i>	-2.984	-0.113	-0.077
2. <i>Bactronophorus thoracites</i>	0.100	0.291	0.502
3. <i>Neoteredo reynei</i>	-0.006	0.474	0.987
4. <i>Dicyathiifer manni</i>	-0.061	0.311	0.606
5. <i>Teredothyra dominicensis</i>	0.069	0.234	0.447
6. <i>Teredothyra matocotana</i>	0.060	0.273	0.522
7. <i>Teredora malleolus</i>	0.095	0.533	-0.399
8. <i>Teredora princesae</i>	0.080	0.548	-0.460
9. <i>Psiloteredo healdi</i>	0.087	0.369	-0.003
10. <i>Psiloteredo megotara</i>	0.121	0.364	-0.266
11. <i>Psiloteredo senegalensis</i>	0.125	0.288	-0.115
12. <i>Zachsia zenkewitschi</i>	0.130	-0.037	-0.047
13. <i>Uperotus clavus</i>	-0.173	0.790	-0.680
14. <i>Lyrodus massa</i>	0.131	-0.187	-0.093
15. <i>Lyrodus medilobata</i>	0.158	-0.352	-0.164
16. <i>Lyrodus floridana</i>	0.145	-0.359	-0.191
17. <i>Lyrodus takanoshimensis</i>	0.156	-0.334	-0.116
18. <i>Teredo clappi</i>	0.119	-0.256	-0.167
19. <i>Teredo fulleri</i>	0.138	-0.206	-0.155
20. <i>Teredo furcifera</i>	0.105	-0.288	-0.179
21. <i>Teredo navalis</i>	0.117	-0.238	-0.119
22. <i>Teredo poculifer</i>	0.105	-0.288	-0.179
23. <i>Nototeredo edax</i>	0.086	0.157	-0.032
24. <i>Nototeredo knoxi</i>	0.068	0.219	-0.014
25. <i>Nototeredo norvagica</i>	0.098	0.286	0.061
26. <i>Spathoteredo obtusa</i>	0.101	-0.189	0.062
27. <i>Spathoteredo spatha</i>	0.107	-0.236	0.038
28. <i>Nausitora dunlopei</i>	0.134	-0.277	0.208
29. <i>Nausitora fusticula</i>	0.121	-0.223	-0.018
30. <i>Nausitora hedleyi</i>	0.126	-0.314	0.063
31. <i>Bankia australis</i>	0.099	-0.315	-0.085
32. <i>Bankia campanellata</i>	0.086	-0.250	0.097
33. <i>Bankia gouldi</i>	0.059	-0.397	-0.049
34. <i>Bankia setacea</i>	0.096	-0.277	0.015

TABLE 21. Characters associated with the first Principal Component, explaining 30% of the variation in the Teredinidae data matrix. Characters are associated at a level of .6 or more.

Shell highly reduced, reduced ear (auricle) on posterior slope ¹
Shell sculpture reduced ¹
Ventral and dorsal condyles poorly developed ¹
Thick burrow lining and mantle ¹
Long siphons
Muscular collar near siphons ¹
Small posterior adductor muscle ¹
No wood-storing caecum ¹
Extended excurrent canals
Large ventricular bulb of the heart

¹Characters possibly associated with reduced ability to bore into wood in the adult in *Kuphus*.

tics with high factor loadings on the second component were a large anterior stomach, large palps, and long intestine. Genera projecting positively on the second component were *Uperotus*, *Teredora*, *Neoterodo*, *Psiloteredo*, *Dicyathifer*, *Bactronophorus*, and *Teredothyra* (Table 20). The Bankiinae plus *Teredo* and *Lyrodus* projected negatively. Component three (12% of the variation) revealed a relationship among characters of the heart, gill, and siphon. These were elaborate papillae on the excurrent siphon, long gills, short heart, unpigmented auricles, smooth burrow lining, and an open anal canal. Taxa projecting positively and strongly on this axis were *Uperotus*, *Teredora*, and *Psiloteredo megotara*.

Similarity of the Pholadidae was assessed by constructing a minimum-spanning tree diagram of genera (Fig. 6) and one of species (Fig. 7). Both figures are based on correlation coefficients, although distance coefficients gave the same pattern. The correlation of cophenetic values and the correlation coefficients was 0.96. The most interesting results are that the traditional subfamily structure remained intact, while *Lignopholas* appeared intermediate between the *Xylophagainae* and the *Martesiinae*.

The species-level analysis (Fig. 7) shows most genera as tight clusters, although divergence has occurred in *Cyrtopleura*, *Nettastomella*, and *Xylophaga*. There are several subsets within *Xylophaga*. The subsets determined by multivariate analysis of data from Knudsen (1961) and Turner (in prep.) are very similar to those determined on the basis of a few key characters by Turner (in prep.).

The minimum-spanning tree (MST) of the Teredinidae was dependent upon whether correlation coefficients or distance coefficients were used. This technique is not very reliable because there are no criteria to use or choose between the two solutions. The features of the minimum-spanning trees that were conserved in the two methods were a close relationship between or among: 1) *Dicyathifer*, *Teredothyra*, *Bactronophorus*, and *Neoterodo*; 2) *Psiloteredo* and *Teredora*; 3) *Teredora* and *Uperotus*; 4) *Teredo* and *Lyrodus*; 5) *Bankia*, *Nausitora*, and *Spathoteredo*; 6) *Bactronophorus* and *Psiloteredo*; 7) *Psiloteredo* and *Nototerodo*; and 8) *Lyrodus* and *Bankia*. In both MST diagrams, *Kuphus* was widely separated from the other teredinid taxa. The link in the MST using coefficients of distance was at 3.38 units, whereas the next largest distance was 1.45 units. *Lyrodus massa* was separated from the other *Lyrodus* species because of differences in its pallets (Turner, 1966). *Uperotus clavus* and *Teredora princessae* were so similar that one could hypothesize that they belong in the same genus. Comparing these relationships with those in Turner (1966, fig. 25), we find that relationships 1–5 are the same, but 6–8 are different. The phenetic assessment could be due to either convergences or real phylogeny; at least it raises the possibility that *Nototerodo* is not closely linked with the other Bankiinae and that the Bankiinae could be polyphyletic.

Results of the teredinid data suggested one other manipulation of the data. All characters concerning the pallets, except whether or not they had multiple segments and whether or not there was a periostracal cap, were removed, in order to see if anatomical data gave a different phenetic arrangement. The result was a MST diagram virtually the same as that with all the pallet data. In both cases, anatomical data such as large intestine, large gill, position of the heart, and size of the stomach determined the position of *Nototerodo*, removed from the other Bankiinae. Therefore the pallet characters did not alter the phenetic classification.

DISCUSSION

Taxonomic Characters and Functional Morphology

A possible sequence in the adaptation of bivalves for wood-boring is: 1) ability to bore

Relationships Among Genera of Pholadidae

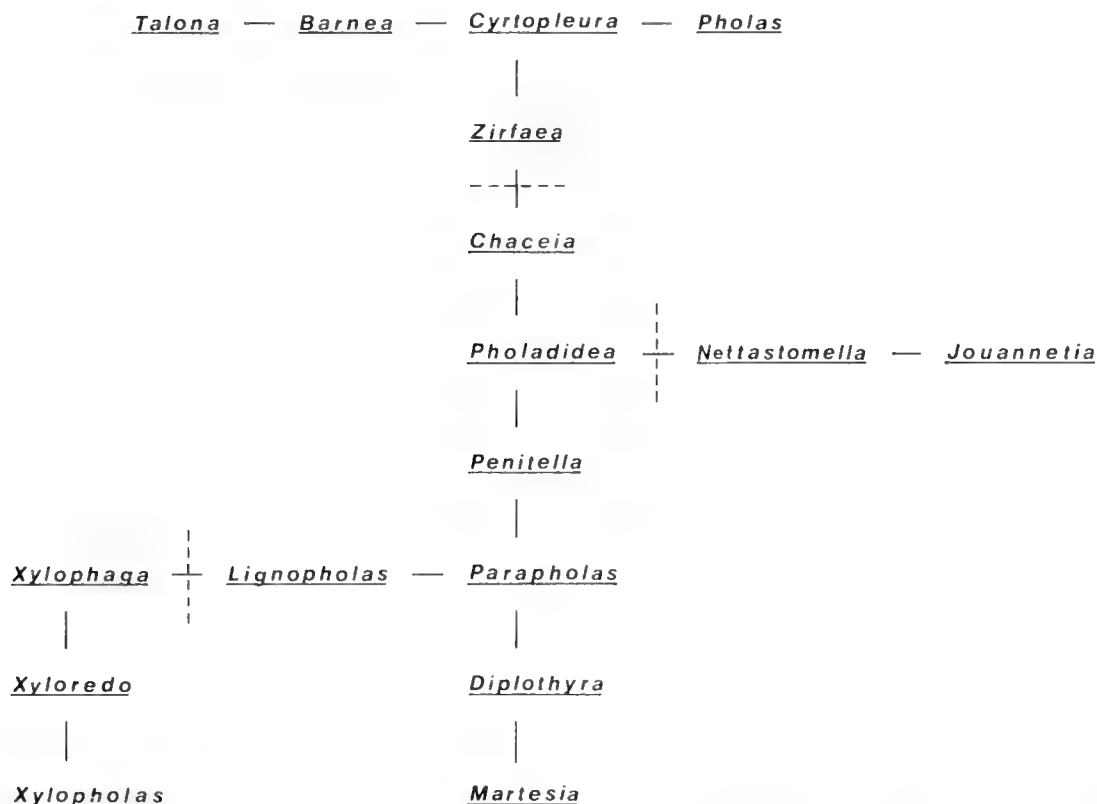


FIG. 6. Phenetic relationships among the genera of Pholadidae: Minimum Spanning Tree using Correlation coefficients.

into hard mud and rock for protection; 2) ability to bore into wood, which was not available until woody plants evolved, giving a time dimension to the radiation, and 3) ability to use wood for food. This sequence allows for a period of adaptation for boring into hard substrate before there was wood. It is logical that use of wood for food could come only after the animals could actually inhabit it. The fossil record is consistent with, but does not prove, this sequence. The species of Pholadidae that occasionally occupy wood but do not derive nutrition from it (e.g., species of *Barnea*) provide a model for the evolution of wood-borers within the Pholadacean lineage.

Superfamily-level innovations that allowed entrance into wood (Table 16) include hinge reduction, development of inner shell projections that altered muscle attachment and hence muscle action, shell elongation, shell reduction, denticulated shell ridges, a pedal gape, and the development of a discoid foot. Some of these characters do not appear in our numerical taxonomic analysis because all species in both families have them.

Groups in both families developed the ability to use wood for food, as shown by the

presence of a wood-storing caecum in both *Xylophaga* and the teredinids. Use of wood for nutrition and filter-feeding are not mutually exclusive. Many of the taxonomically useful characters of the teredinids are related to the degree of filter-feeding: a large gill or elaborate siphonal tentacles, a small caecum, long intestine, and elaboration of sorting mechanisms such as those of the labial palps are characteristics of filter-feeding. Genera with the gill extending to the mouth (*Uperotus* and *Teredora*) could represent the ancestral filter-feeding condition. *Nausitora fusticula* could represent a secondary elaboration of filter-feeding tentacles on the incurrent siphon after reduction of the gills has occurred in the lineage.

Probably all species obtain nutrition from both wood and plankton at some time in the life of an individual. When the gonad of a teredinid enlarges prior to reproduction, the wood-storing caecum may be reduced. Perhaps then the animals rely on plankton. The flexibility of feeding is also of critical importance when crowding occurs and further growth is impossible. Active wood boring may cease in favor of filter-feeding under such cir-

cumstances. Data are required to test these suggestions.

It is clear from the extent of the wood-borer radiation (Figs. 1, 2) that the Teredinidae have radiated successfully in shallow water, and the Xylophaginae have done so in the deep sea. Not enough is known of the deep sea and the living Xylophaginae to explain the differential radiation in terms of water depth, but there are some morphological explanations for the radiation of the Teredinidae.

The relative success of the teredinids is most probably related to the development of a calcareous tube and attachment of the siphonal retractor muscle to it, together with elongation of the body and reduction of the shell. Elongation of the body so that the viscera extend in a loop beyond the closely-set adductor muscles has had enormous impact on the anatomical organization of the Teredinidae, compared with the Pholadidae, which still resemble the basic bivalve anatomy (Turner, 1966, figs. 5–11). The result is a very flexible, wormlike animal that can take advantage of woody material by twisting and turning as it grows within it, in a way unavailable to any of the pholads but most closely approached in *Xyloredo*.

Pholads receive protection from added shelly plates, e.g. the siphonoplax, which are rather inflexible in closing the burrow when compared with the tubes and pallets of the teredinids with their associated musculature. Have the Xylophaginae been relegated to the deep sea by competitively superior teredinids, successful only there because of some physiological character lacking in the teredinids? This speculation has been made for other groups of deep sea organisms such as *Neopilina*, but there are no data on which to base it.

Many features of the Teredinidae are variable among species, illustrating multiple solutions to a common problem. For example, the four basic types of pallets are all designed to close the burrow: simple plugs (*Teredo*), a plug plus tube thickenings (*Psiloteredo*) pallets with flexible periostracal caps (*Lyrodus*), and pallets that grow by adding segments of increasing size at the proximal end (*Bankia*). These differences seem representative of phylogeny, but have no obvious relationship to ecological differences between the genera.

Other features are highly convergent, being correlated with similar ecological deployment of distantly-related species. For example, mantle and tube thickness are greater in

mangrove and brackish-water species, such as *Kuphus polythalamia*, *Neoterodo reynei*, *Bactronophorus thoracites*, and brackish-water *Bankia* species (Turner, 1966). These characters are probably partly under environmental control.

The siphon anatomy of the Pholadidae is variable at the genus and species levels. Separate siphons occur more often in wood-borers. Likewise, the anal canal in teredinids seems to have a functional relationship with other characters. It can be closed by a sphincter in *Bactronophorus*, *Neoterodo*, *Dicyathifer*, and *Teredothyra*, allowing retention of loose faecal matter. One might expect a correlation between a closed anal canal and fertilization in the epibranchial cavity, but this combination did not appear in the numerical analysis, possibly because of lack of data for some species. There is a correlation between well-formed faecal pellets and brooding of young.

Possible Evolutionary Pathways

Evolutionary pathways for the Pholadacea have been proposed by several authors (Turner, 1962, 1966; Purchon, 1941; Knudsen, 1961). All were based primarily on analysis of shell and a few anatomical characters. The computer-generated MST diagrams of relationships (Figs. 6–7) are not phylogenetic trees. They show only degrees of similarity among modern groups, without reference to ancestors. As alternative hypotheses of an evolutionary sequence they might be useful, except that there are several problems with the technique illustrated by the lack of congruence of MST diagrams of the Teredinidae. One problem lies in the coding of the data. There are problems in interpreting covariation when the linearity of multiple character states is in doubt. The best use of the phenetic methods will come when detailed ecological and life historical data are available for each species, so that anatomical similarities and differences among taxa can be correlated with ecological factors and interpreted functionally. Then, in comparison with cladistic analyses, convergences can be identified.

Further application of cladistic methods, on the other hand, are warranted by the results of our simple analysis of unique and unreversed characters (Figs. 4, 5). Our assumption that wood-borers of the Pholadidae evolved from a common ancestor in the non-wood-boring lineage of Pholadidae allowed us to "root" the

tree at I on Fig. 4. The wood-boring mode of existence is so specialized that one would expect strong convergences (or a lack of divergence) between wood-boring lineages. We still cannot be certain that the Teredinidae diverged from the Pholadidae after some pholads became wood-borers, but it is likely because of the pattern of shared unique and unreversed characters in the Xylophaginae and Teredinidae (Table 11). On the other hand, teredinids could have arisen from neotenous pholads. For example, *Barnea* spp. are well into the substrate before the protoplax develops, and adult *Barnea* spp. are often found in wood. The neoteny theory is as yet untested by embryological data and is not the simplest explanation, however.

The evolutionary sequence suggested in Figs. 4 & 5 is harmonious with those based on our phenetic analysis (Fig. 6) but not with the belief of Purchon (1941) that the Xylophaginae are derived from the Martesiinae. Fig. 5 agrees with the phenetic analysis in that the Pholadinae are most divergent from the wood-boring lineages.

Our genetic and morphological analyses of species groups within the Teredinidae (Figs. 3–5) independently suggest that *Teredo* and *Lyrodus* are not more distinct than are many species within the genus *Teredo*. However, unpublished work on embryology by one of us (Turner) reveals some differences between some species of *Lyrodus* and *Teredo*. Cladistic treatment (Figs. 4, 5; Table 11) and phenetic treatment of the morphological data both suggest that the Kuphinae are not of equal taxonomic rank with the Bankiinae and the Teredininae. The method of unique and unreversed characters placed *Nototeredo* far from the other Bankiinae, despite its segmented pallets (Fig. 5), supporting the hypothesis derived from the phenetic analysis (Figs. 6–7) that the Bankiinae may be polyphyletic. The Bankiinae, the Teredininae, and the genus *Lyrodus* are traditionally defined on the basis of a single character—pallet shape—and hence could be convergent. These findings should be used to form hypotheses to be tested by molecular genetic techniques.

Population Genetics

The phenogram constructed on the basis of genetic distance (Fig. 3) correlates well with the currently used taxonomic structure of the Pholadacea. Although no rule exists to de-

lineate taxonomic levels on the basis of genetic distance, our genetic identity and distance values compare well with the values cited by Avise (1976) for other organisms, including mammals and insects, at the same presumed taxonomic levels.

One difficulty with the current taxonomic structure concerns the genus *Lyrodus*. We find that *L. floridana* is very similar to the two species of *Teredo*, especially *T. bartschi*. As mentioned above, more data are needed for other species of *Lyrodus* to test the validity of the genus.

The genetic distance values (Table 6) suggest that *Martesia striata* is distantly related to all the Teredinidae that we have tested, but is slightly closer to *Bankia* than to *Teredo*. However, the D values are all so large that the subtle difference between the distances to the *Bankia* and those to the species of *Teredo* should not be given any importance. In fact, if one compares the most common allele for each locus in *Martesia striata* versus *Bankia* and *Teredo* (Table 4), *M. striata* is more similar to *Teredo* than to *Bankia* at five loci, while it is more similar to *Bankia* at only one locus (peptidase G). If one makes the same comparisons but includes only the monomorphic loci (those with at least 0.95 frequency of one allele for every species), *M. striata* is unique at five loci, is similar to both *Bankia* and *Teredo* at five loci, is similar to *Teredo* at two loci, and is similar to *Bankia* alone at no loci.

The values for genetic variability obtained in this study (Table 7) are within the range expected on the basis of earlier work. Selander (1976) reviewed the literature, and reported mean P values of 0.587 for marine invertebrates (0.469 for all invertebrates). The mean value for our six Pholadacea is 0.487, 0.568 without the unusually monomorphic *Teredo bartschi*. Because the *T. bartschi* population used in this analysis is introduced, it probably has lost genetic diversity due to founder effects. Recent experiments with other populations of *T. bartschi* show twice as high a heterozygosity value in a Florida population compared with the New Jersey population and one introduced into Connecticut (Hoagland, 1981).

Average H values are 0.147 for marine invertebrates, 0.083 for marine snails (Selander, 1976), 0.084 for the six Pholadacea, and 0.100 for the five pholadacean species omitting *T. bartschi*.

The genetic data were analysed for fixation of alternate alleles within a single population,

evidence of self-fertilization (Selander & Hudson, 1976). Such evidence was not found, suggesting that none of the species examined is exclusively self-fertilizing. However, many enzyme systems have heterozygote deficiency (Hoagland, in prep.) and self-fertilization is known to occur in *Lyrodus pedicellatus* (Eckelbarger & Reish, 1972).

Teredo bartschi and *Lyrodus floridana* are successful colonizers despite their low genetic variability. They fit the "general purpose genotype" mode of evolution described by Selander & Hudson (1976) and McCracken & Selander (1980). These authors state that the optimal genotype for colonizing individuals should have great phenotypic plasticity, but not necessarily great heterozygosity, as others had previously argued. The importance of these ideas for evolution is that some species apparently maintain potential for broad ecological deployment via heterozygosity and polymorphism, but another avenue to the same end is a uniform, nearly monomorphic genotype that is broadly adaptive. This avenue has been documented for *Corbicula fluminea*, the Asian clam introduced to the United States (Smith et al., 1979). We would predict low levels of speciation in such monomorphic taxa.

Ecology and Extent of the Radiation

The pattern of the number of species per genus (Figs. 1, 2) is reminiscent of the curves of number of individuals per species in ecological community studies. It has a probabilistic basis. It appears that, in a given radiation, only a few innovations lead to numerous similar species, whereas numerous lineages stabilize at low diversity. The pattern is based on different rates of evolution, not on different ages of the genera, for several of the smaller genera were fossilized as early as *Bankia* and *Teredo*. Also, it is not based on larval type, for the three largest genera possess all three major larval types. The largest genera occupy all latitudes short of the extreme north and south where there is no wood.

The ecological extent of the adaptive radiation of the wood-borers can be seen by summarizing the habitats where they are found: deep sea, open ocean in floating wood, mangroves, shoreline where wood collects and where man has added wooden structures, driftwood in estuaries all the way to essentially fresh water, and even rhizomes of sea grass (*Zachsisia zenkewitschi*, recently studied

by Turner & Yakovlev (1981). Most species live in dead wood, but *Z. zenkewitschi* inhabits living plant material. It is highly specialized, with reduced shell (it bores into very soft material), a tough, rapidly-secreted membrane that lines the burrow, and a heavy calcareous tube. It has separate sexes with dwarf males living in the mantle pouches of the female. Dwarf males insure a sperm supply to the females in their precarious existence in the rhizomes, which may be torn from the substrate during storms and which decay when the plant dies.

No other wood-borers have developed dwarf males, although this mode of sexuality would appear to be of advantage. It was once believed that all Teredinidae and *Xylophaga* were protandrous, but true hermaphroditism has been found in *Lyrodus pedicellatus* (Eckelbarger & Reish, 1972). *Xylophaga* can probably store sperm (Purchon, 1941), and may self-fertilize as may some teredinids, but more research is needed to confirm self-fertilization. All three modes of sexuality in the Pholadacea are related to life in temporary habitats, where isolation of a few individuals often occurs.

All Bankiinae so far studied have a pattern of oviparity and planktonic development. All the Teredininae are larviparous and retain fertilized eggs, but the length of larval brooding is not even a genus-level character. Many life history traits tend to be intercorrelated, as shown in Table 8. All the Teredinidae are good colonizers and must be opportunistic because they destroy their own substrate. Species of the *Bankia gouldi* type are good long-distance colonizers, but their populations are rarely as dense as those with the *Teredo bartschi* reproductive pattern. Both species types have high intrinsic rates of increase and high competitive ability, *B. gouldi* by its rapid growth and large number of offspring, *T. bartschi* by its short generation time and the high survival rate of its offspring. *B. gouldi* has greater gene flow than *T. bartschi*, but the patchy nature of the substrate is still great enough for reproductive isolation. These circumstances could explain the high level of speciation achieved by the genus *Bankia*, compared with other teredinid genera (Fig. 1).

The planktonic versus larviparous reproductive pattern does have an effect on distribution (Table 10), but not as strong an effect as might be supposed. Many long-term larviparous species are constrained to one latitudinal zone, but appear relatively more capa-

ble of movement across oceans than are planktonic species. This pattern suggests some physiological limitation in the larviparous species relative to the other species, but none is known. Larviparous species disperse in wooden boats and are often transported to areas unsuitable for their survival. This must have been the case with *Teredo bartschi*, for it was only after two nuclear power plants established warm-water effluents in the northwestern Atlantic that populations spread from the tropics to those areas. There is no indication that the pattern of dispersal of adults and larvae changed; only that the environments became more hospitable.

The success of wood-borers in terms of numbers of individuals, species, and genera seems related to the physiological flexibility of individuals and species, and the phenotypic plasticity in general, as well as to the opportunistic life history patterns. Many teredinids are tolerant of salinities as low as 5‰ (Blum, 1922). Adults of *Teredo bartschi* withstand temperatures from 11° to 35°C. and salinities from 5 to 45 ‰ in the adult stage (Hoagland et al., 1980; Hoagland, 1981). Tereidinids in our laboratory have withdrawn the siphons and remained alive for at least 4 weeks with little oxygen, and without producing any frass, indicating that wood-boring has ceased. Some shipworms have even withstood day-long freezing, according to observations by one of us (Turner).

The fact that the virtually freshwater wood-borers belong to at least four genera (*Teredo poculifer*, *Nausitora* species, *Psiloteredo healdi*, and *Lignopholas* species) in two families is indicative of the ecological potential of the superfamily. Broad physiological tolerances help to insure dispersal of individuals to new sources of wood, because dispersal of both larvae and adults is in large part passive. Physiological differences do exist between species, however, and they help to delineate species ranges. For example, the introduced *Teredo bartschi* has a higher temperature range (11–35°) than does the native *Bankia gouldi* (0–30°C) in New Jersey.

Other examples of teredinid flexibility are the plasticity of the body size and shape at maturity and the ability of some species to filter-feed facultatively. Most species can delay metamorphosis and settlement if no substrate is available. Phenotypic plasticity is a key feature in the evolution of organisms confined to a substrate; the same pattern is seen in barnacles and in plants.

One might ask if competition among species is important in the evolution and ecology of wood-borers. Competition is important in a given piece of wood. Fast-growing *Bankia gouldi* occlude smaller *Teredo bartschi*. However, staggered settlement periods and different modes of larval dispersal may lead to dominance by one species in one piece of wood and another in an adjacent piece. Wood becomes available at irregular intervals, favoring maintenance of several species in each locality. This temporal instability of the substrate, plus transport of adults in moving wooden objects and planktonic dispersal of some species, allow for the maintenance of a rich marine borer community.

CONCLUSION

Marine wood-boring bivalves form a classical adaptive radiation based on innovations of morphology that allowed entrance into a new substrate. Fossil evidence indicates that the radiation was rapid once the innovations occurred. It was a radiation probably spinning off from that of the rock-boring Pholadidae, and itself was split quite early into two parts with different but overlapping sets of adaptations for wood-boring. In turn, the rock- and wood-borer radiations created new substrate complexity that has been exploited by other organisms. The major causes of the divergence between wood- and rock-borers are derived from the nature of wood: it is more limited and temporary than rock and hard mud, although these, too, fall apart. It is a food source, and wood newly introduced to water floats, thereby transporting adult animals.

Morphologically, wood-borers are limited by their sedentary nature as adults and by the confinement of their wood-boring habit. Selection pressures for the mechanical aspects of wood-boring are strong. We expect and find very conservative shell shape, sculpture, and adaptations for dispersal that are as strongly developed as those in parasites, which also destroy their own substrates.

The radiation of wood-boring bivalves, based on a patchy, limited, and temporary resource, has led to patchily-distributed populations of variable size and stability. The species vary in the amount of inbreeding they have undergone, but potential for inbreeding is high in most. Isolation, yet the ability of the Tereidinidae and *Martesia* to disperse as adults in floating wood as well as in the swimming or crawling larval stage, creates an ad-

vantage for either high polymorphism or high phenotypic plasticity. Isolation plus dispersal provides a mechanism for a complex world-wide pattern of speciation.

Natural dispersal plus transport due to man's extensive use of wood in the marine environment has led to the world wide ranges of single species. In fact, man's activities may have reduced the future potential for speciation in the Teredinidae and Martesiinae by increasing genetic exchange among populations of some species and by spreading species that have genetic uniformity such as *Teredo bartschi*.

The study of the adaptive radiation of the wood-boring Pholadacea will profit from greater knowledge of homologies that will come from more embryological study. Greater knowledge of life histories of particular species and greater ability to correlate ecology and natural selection pressures with convergences of morphology are also needed. New methods of numerical taxonomy show promise in allowing us to exploit these expanding data bases.

ACKNOWLEDGMENTS

Biochemical and computing facilities were made available through G. M. Davis (NSF grant #DEB 78-01550) at the Academy of Natural Sciences of Philadelphia. L. Crocket, C. Hesterman, M. Rochester, J. McKinley, and J. Harms provided technical assistance. Numerous residents of Barnegat Bay, New Jersey, allowed use of their property for field sites. We were funded by U.S. Nuclear Regulatory Commission contract #NRC-04-76-347 to Lehigh University, a Fleischmann Foundation grant to the Wetlands Institute (Lehigh University), and Office of Naval Research contracts Nonr-1866 (45), NR104-687, and N00014-67A-0298-0027 to R. D. Turner, Harvard University. G. M. Davis, T. Waller, S. J. Gould, B. Calloway, and P. Williamson read and commented upon the manuscript. Collections at the Museum of Comparative Zoology (Harvard University) and the Academy of Natural Sciences of Philadelphia were used in the course of the study.

LITERATURE CITED

- AYALA, F. J., HEDGECOCK, D., ZUMWALT, G. S. & VALENTINE, J. W., 1973, Genetic variation in *Tridacna maxima*, an ecological analog of some unsuccessful evolutionary lineages. *Evolution*, 27: 177-191.
- BLUM, H. F., 1922, On the effect of low salinity on *Teredo navalis*. *University of California Publications in Zoology*, 22: 349-368.
- BREWER, G. J., 1970, *An introduction to isozyme techniques*. Academic Press, New York, 186 p.
- CVANCARA, A. M., 1966, Revision of the fauna of the Cannonball Formation (Paleocene) of North and South Dakota. *University of Michigan Museum of Paleontology Contribution*, 20: 277-370.
- DAVIS, G. M., HEARD, W. H., FULLER, S. L. H. & HESTERMAN, C., 1981, Molecular genetics and speciation in *Elliptio* and its relationships to other taxa of North American Unionidae (Bivalvia). *Biological Journal of the Linnean Society*, 15: 131-150.
- DILLON, R. T. & DAVIS, G. M., 1980, The *Goniobasis* of Southern Virginia and northwestern North Carolina: genetic and shell morphometric relationships. *Malacologia*, 20: 83-98.
- DURHAM, J. W. & ZULLO, V. A., 1961, The genus *Bankia* Gray (Pelecypoda) in the Oligocene of Washington. *Veliger*, 4: 1-3.
- ECKELBARGER, K. J. & REISH, D. J., 1972, A first report of self-fertilization in the wood-boring family Teredinidae (Mollusca: Bivalvia). *Bulletin of the Southern California Academy of Sciences*, 71: 48-50.
- ELLIOTT, G. F., 1963, A Palaeocene teredinid (Mollusca) from Iraq. *Palaeontology*, 6: 315-317. pl. 51-52.
- HATAI, K. M., 1951, A lower Cretaceous *Teredo*. *Short papers from the Institute of Geology and Paleontology, Tôhoku University, Sendai* (3): 29-32.
- HOAGLAND, K. E., 1981, Life history characteristics and physiological tolerances of *Teredo bartschi*, a shipworm introduced into two temperate zone nuclear power plant effluents. In LEE, S. S. & SENGUPTA, S. (ed.), *Final Proceedings, Third International Conference on Waste Heat Management and Utilization*. In press.
- HOAGLAND, K. E. & CROCKET, L., 1979, Analysis of populations of boring and fouling organisms in the vicinity of the Oyster Creek Nuclear Generating Station. *Annual Progress Report*, Sept. 1, 1977-Aug. 31, 1978. NTIS #NUREG/CR-0634, 113 p.
- HOAGLAND, K. E., CROCKET, L. & TURNER, R. D., 1980, Ecological studies of woodboring bivalves in the vicinity of the Oyster Creek Nuclear Generating Station, Sept. 1, 1979-Feb. 28, 1980. Report to the U.S. Nuclear Regulatory Commission. NTIS #NUREG/CR-1517, 65 p.
- HOAGLAND, K. E. & TURNER, R. D., 1980, Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Marine Biology*, 58: 55-64.
- AVISE, J. C., 1976, Genetic differentiation during speciation. In AYALA, F. J. (ed.), *Molecular Evolution*, p. 106-122. Sinauer Associates, Sunderland, Massachusetts.

- HOAGLAND, K. E. & TURNER, R. D., 1981, Taxonomic characters of the Pholadacea. *Tryonia*, in press.
- HOAGLAND, K. E., TURNER, R. D. & ROCHES-TER, M., 1977, Analysis of boring and fouling organisms in the vicinity of the Oyster Creek Nuclear Generating Station with discussion of relevant physical parameters over the period: April 30–November 30, 1976. Report to the U.S. Nuclear Regulatory Commission. Jan. 1, 1977, 61 p.
- KENNEDY, G., 1974, West American Cenozoic Pholadidae (Mollusca: Bivalvia). *San Diego Society of Natural History Memoir*, 8: 9–25.
- KNUDSEN, J., 1961, The bathyal and abyssal *Xylophaga* (Pholadidae, Bivalvia). *Galathea Report*, 5: 163–209.
- MCCRACKEN, G. F. & SELANDER, R. K., 1980, Self-fertilization and monogenic strains in natural populations of terrestrial slugs. *Proceedings of the National Academy of Sciences, U.S.A.*, 77: 684–688.
- MOLL, F., 1942, Die fossilen Terediniden und ihre Beziehung zu den rezenten Arten. *Palaeontographica*, Bd. 94, Abteilung A, Lief. 3–6: 134–153, pl. 24–26.
- NEI, M., 1972, Genetic distance between populations. *American Naturalist*, 106: 283–292.
- POULIK, M. D., 1957, Starch gel electrophoresis in a discontinuous system of buffers. *Nature*, 180: 1477–1479.
- PURCHON, R. D., 1941, On the biology and relationship of the lamellibranch *Xylophaga dorsalis* (Turton). *Journal of the Marine Biological Association of the United Kingdom*, 25: 1–39.
- ROHLF, F. J., KISHPAUGH, J. & KIRK, D., 1972, NT-SYS; Numerical Taxonomy System of Multivariate Statistical Programs. SUNY, Stony Brook, New York (computer printout, available from the senior author).
- SELANDER, R. K., 1976, Genic variation in natural populations. In AYALA, F. J. (ed.), *Molecular Evolution*, p. 21–45. Sinauer Associates, Sunderland, Massachusetts.
- SELANDER, R. K. & HUDSON, R. O., 1976, Animal population structure under close inbreeding: the land snail *Rumina* in southern France. *American Naturalist*, 110: 695–718.
- SHAW, R. S. & PRASAD, R., 1970, Starch gel electrophoresis of enzymes—a compilation of recipes. *Biochemical Genetics*, 4: 297–320.
- SMITH, M. H., BRITTON, J., BURKE, P., CHESSEN, R. K., SMITH, M. W. & HAGEN, J., 1979, Genetic variability in *Corbicula*, an invading species. In BRITTON, J. (ed.), *Proceedings, First International Corbicula Symposium*, p. 243–248. Texas Christian University, Fort Worth, Texas.
- STANLEY, S. M., 1979, *Macroevolution: pattern and process*. Freeman, San Francisco, 332 p.
- STEPHENSON, L. W., 1952, Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. [United States] Geological Survey Professional Paper, 242: 138–142, pl. 34.
- STOLICZKA, F., 1871, Cretaceous fauna of southern India; Pelecypoda. *Palaeontologia Indica*, 3: 9–25, 2 pl.
- TURNER, R. D., 1954, The family Pholadidae in the Western Atlantic and the Eastern Pacific. Part I—Pholadinae. *Johnsonia*, 3: 1–63.
- TURNER, R. D., 1955, The family Pholadidae in the Western Atlantic and the Eastern Pacific. Part II—Martesiinae, Jouannetiinae and Xylophaginae. *Johnsonia*, 3: 65–160.
- TURNER, R. D., 1956, Notes on *Xylophaga washingtona* Bartsch and on the genus. *Nautilus*, 70: 10–12.
- TURNER, R. D., 1962, *Nettastomella japonica* Yokoyama in North America and notes on the Pholadidae. *Occasional Papers on Mollusks*, Museum of Comparative Zoology, Cambridge, Massachusetts, 2: 289–308, pl. 47–53.
- TURNER, R. D., 1965, Anatomical relationships in the Teredinidae. *American Malacological Union Annual Reports*, 1964: 16–17.
- TURNER, R. D., 1966, A survey and illustrated catalogue of the Teredinidae. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 265 p.
- TURNER, R. D., 1969, Superfamily Pholadacea. In MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part N, vol. 2, Mollusca 6, Bivalvia, p. N702–N741. Geological Society of America & University of Kansas, Lawrence, Kansas.
- TURNER, R. D., 1971, Australian Shipworms. *Australian Natural History*, 17: 139–145.
- TURNER, R. D., 1972a, A new genus and species of deep water wood-boring bivalve (Mollusca, Pholadidae, Xylophaginae). *Basteria*, 36: 97–104.
- TURNER, R. D., 1972b, *Xyloredo*, a new teredinid-like abyssal wood-borer (Mollusca, Pholadidae, Xylophaginae). *Breviora*, 397: 1–19.
- TURNER, R. D., 1973, Deep water wood-boring mollusks. *Proceedings of the Third International Congress on Marine Corrosion and Fouling*, National Bureau of Standards, Gaithersburg, Maryland, U.S.A., p. 836–841.
- TURNER, R. D., in prep. Monograph of the Xylophaginae.
- TURNER, R. D. & YAKOVLEV, Y. M., 1981, The ecology and reproduction of *Zachsia zenkevitschi*, a teredinid with dwarf males. In KASYANOV, L. V. (ed.), Proc. Symposium "Reproduction and growth of marine invertebrates," XIV Pacific Science Congress, Khabarovsk, U.S.S.R. (in press).
- VINCENT, E., 1925, Le taret des sables de Wemmel. *Annales de la Société Royale Zoologique de Belgique*, 55: 21–23.
- WILSON, E. O., 1965, A consistency test for phylogenies based on contemporaneous species. *Systematic Zoology*, 14: 214–220.
- WRIGLEY, A., 1929, Notes on English boring Mollusca, with descriptions of a new species. *Proceedings of the Geologists' Association*, London, 40: 376–383.

APPENDIX A:

Table of Operational Taxonomic Units (OTU's)

Numbers to the left of the species names are OTU numbers for the comparison of pholads and teredinids using shell and anatomical data. Numbers to the right of the species names, in parenthesis, are OTU numbers for detailed anatomical comparison of the teredinids alone. Among the pholads, an asterisk indicates that the species is an obligate wood-borer. All teredinids except *Kuphus polythalamia* are obligate wood-borers. Not all known species of Pholadacea were used in the multivariate analysis because of lack of detailed information on morphology of some species. Appendix B lists the species omitted from the analysis.

Pholadidae

Pholadinae

1. *Barnea candida*
2. *B. parva*
3. *B. lamellosa*
4. *B. truncata*
5. *B. subtruncata*
6. *Cyrtopleura costata*
7. *C. lanceolata*
8. *C. cruciger*
9. *Pholas dactylus*
10. *P. campechiensis*
11. *P. chiloensis*
12. *Zirfaea crispata*
13. *Z. pilsbryi*
14. *Talona explanata*

Martesiinae

15. *Chaceia ovoidea*
16. *Penitella fitchi*
17. *P. conradi*
18. *P. penita*
19. *P. gabbi*
20. *Pholadidea loscombiana*
21. *P. melanura*
22. *P. quadra*
23. *P. tubifera*
- *24. *Lignopholas clappi*
- *25. *L. rivicola*
- *26. *Martesia striata*
- *27. *M. fragilis*
- *28. *M. cuneiformis*
29. *Diplothyra smithi*
30. *D. curta*
31. *Parapholas californica*
32. *P. acuminata*
33. *P. branchiata*
34. *P. calva*

Jouannetiinae

35. *Jouannetia duchassaingi*
36. *J. pectinata*
37. *J. quillingi*
38. *J. globosa*
39. *J. cumingii*
40. *Nettastomella darwinii*
41. *N. japonica*
42. *N. rostrata*

Xylophaginae

- *43. *Xylophaga dorsalis*
- *44. *X. concava*
- *45. *X. globosa*
- *46. *X. erecta*
- *47. *X. mexicana*
- *48. *X. lobata*
- *49. *X. atlantica*
- *50. *X. galathea*
- *51. *X. washingtona*
- *52. *X. aurita*
- *53. *X. abyssorum*
- *54. *X. turnerae*
- *55. *X. praestans*
- *56. *X. panamensis*
- *57. *X. hadalis*
- *58. *X. duplicata*
- *59. *X. grevei*
- *60. *X. foliata*
- *61. *X. africana*
- *62. *X. wolffi*
- *63. *X. bruuni*
- *64. *X. tubulata*
- *65. *X. obtusata*
- *66. *X. indica*
- *67. *Xylopholas altenai*
- *68. *Xyloredo nooi*
- *69. *X. naceli*
- *70. *X. ingolfia*
- *71. *Xylophaga rikuzenica*
- *72. *X. supplicata*
- *73. *X. sp. 1¹*
- *74. *X. sp. 2¹*
- *75. *X. murrayi*
- *76. *X. sp. 3¹*
- *77. *X. sp. 4¹*
- *78. *X. sp. 5¹*

Teredinidae

Kuphinae

79. *Kuphus polythalamia* (1)

Teredininae

80. *Bactronophorus thoracites* (2)
81. *Neoteredo reynei* (3)
82. *Dicyathifer manni* (4)
83. *Teredothyra dominicensis* (5)
84. *T. excavata*

¹Turner, in prep.; undescribed *Xylophaga*.

85. *T. matocotana* (6)
86. *T. smithi*
87. *Teredora malleolus* (7)
88. *T. princesae* (8)
89. *Psiloteredo healdi* (9)
90. *P. megotara* (10)
91. *P. senegalensis* (11)
92. *Zachisia zenkewitschi* (12)
93. *Uperotus clavus* (13)
94. *U. panamensis*
95. *Lyrodus affinis*
96. *L. bipartita*
97. *L. massa* (14)
98. *L. medilobata* (15)
99. *L. pedicellatus* (16)
100. *L. floridana*
101. *L. takanoshimensis* (17)
102. *Teredo aegypos*
103. *T. bartschi*
104. *T. clappi* (18)
105. *T. fulleri* (19)
106. *T. furcifera* (20)
107. *T. johnsoni*
108. *T. mindanensis*
109. *T. navalis* (21)
110. *T. poculifer* (22)
111. *T. portoricensis*
112. *T. renschi* (may be synonym)
113. *T. somersi*
114. *T. triangularis*

Bankiinae

115. *Nototerredo edax* (23)
116. *N. knoxi* (24)
117. *N. norvagica* (25)
118. *Spathoterredo obtusa* (26)
119. *S. spatha* (27)
120. *Nausitora dryas*
121. *N. dunlopei* (28)
122. *N. fusticula* (29)
123. *N. hedleyi* (30)
124. *N. schneideri*
125. *N. saulii*
126. *Bankia anechoensis*
127. *B. australis* (31)
128. *B. barthelowi*
129. *B. bipalmulata*
130. *B. bipennata*
131. *B. brevis*
132. *B. campanellata* (32)
133. *B. carinata*
134. *B. cieba*
135. *B. destructa*
136. *B. fimbriatula*
137. *B. fosteri*
138. *B. gouldi* (33)
139. *B. gracilis*
140. *B. martensi*

141. *B. orcutti*
142. *B. philippi*
143. *B. rochi*
144. *B. setacea* (34)
145. *B. zeteki*
146. *B. nezatalia*

APPENDIX B:

List of Valid Species Omitted from
Multivariate Analysis*Barnea*

alfredensis
australasiae
birmanica
dilatata
fragilis
inornata
manilensis
obturamentum
similis

Pholas

orientalis

Aspidopholas

cheveyi
obtecta
yoshimurai

Teredo

parksii

Penitella

turnerae

Pholadidea

fauroti
kamokuensis
suteri

Parapholas

quadrizonata

Xylophaga

guineensis
japonica
knudseni
tomlini
teramachii

There are approximately 20 taxa of Pholadacea which may be valid species in addition to those discussed in this paper. Many are *Xylophaga* spp. (Turner, in prep.).

APPENDIX C:

List of Characters and Character States
used in Multivariate Analysis*Shell Characters*

1. Shell size
 - Highly reduced (0)
 - Reduced, valves cannot cover visceral mass (1)
 - Valves cover visceral mass only (2)
 - Valves cover whole body (3)
2. Shell sculpture, anterior portion; presence of denticulated ridges (0, 1)
3. Presence of radial ribs and concentric ridges (imbrications) (0, 1)
4. Beak truncated (0, 1)
5. Valves asymmetrical (0, 1)
6. Presence of a well-developed umbonal-ventral ridge and sulcus (0, 1)
7. Mesoplax
 - Absent (0)
 - Rudimentary (1)
 - Present (2)
8. Mesoplax division
 - Not divided (0)
 - Two pieces (1)
 - A ventral portion (third piece) present (2)
9. Mesoplax wrinkled (0, 1)
10. Mesoplax sculpture
 - Smooth (0)
 - Concentric ridges (1)
 - Cuneiform ridges (2)
11. Tube extending from mesoplax (0, 1)
12. Mesoplax shape
 - Narrow, long (0)
 - Triangular, transverse (1)
 - Round or rectangular (2)
 - Lobed (3)
 - Semicircular, vertical (4)
 - Ear-shaped (5)
 - Longitudinally folded (6)
13. Posterior muscle scar
 - Smooth (0)
 - Irregular, basically transverse ridges (1)
 - Transverse ridges (2)
 - Transverse to radiating depressions (3)
 - Radiating depressions (4)
 - Herring-bone marks (5)
14. Siphonoplax
 - Absent (0)
 - One (1)
 - Two (2)
15. Siphonoplax calcareous (0, 1)
16. Tube-like siphonoplax (0, 1)
17. Siphonoplax sculpture
 - Smooth (0)
 - Pectinate (1)
 - Spiny (2)
18. Hypoplax present (0, 1)
19. Hypoplax divided posteriorly (0, 1)
20. Metaplax present (0, 1)
21. Metaplax divided posteriorly (0, 1)
22. Protoplax
 - Absent (0)
 - Periostracal (1)
 - Calcareous (2)
23. Protoplax divided (0, 1)
24. Pedal gape closed by callum in animals that have ceased boring
 - Callum absent (0)
 - Callum mostly periostracal (1)
 - Callum calcareous (2)
25. Callum sculpture
 - Mottled (0)
 - Growth lines (1)
 - Flutes (2)
 - Longitudinal ridges (3)
26. Callum size
 - Narrow band (0)
 - Incomplete (1)
 - Complete (2)
 - Overlapping (3)
27. Presence of siphonal plate (0, 1)
28. Presence of periostracal lamellae
 - Absent (0)
 - Posterior slope only (1)
 - Covers more than posterior slope (2)
29. Posterior periostracal lamellae divided (0, 1)
30. Apophyses present (0, 1)
31. Shape of apophyses
 - Short, flattened distally, hollow proximally (0)
 - Long, thin, solid (1)
32. Ventral condyle
 - Absent (0)
 - Weak (1)
 - Moderately well-developed; is reduced in adult (2)
 - Highly developed (3)
33. Dorsal condyle
 - Absent (0)
 - Modified umbo, weakly developed (1)
 - Well-developed (2)
34. Posterior shell sculpture, concentric
 - Smooth, growth line only (0)
 - Foliated concentric ridges (1)
35. Posterior shell sculpture, other than concentric
 - None (0)
 - Ribs (1)
 - Ribs extended to form spines (2)

36. Pedal gape in species without a callum
Absent (0)
Slit (1)
Oval (2)
37. Posterior adductor muscle attached to special lamina (0, 1)
38. Posterior slope of shell enlarged as a flange (or auricle) (0, 1)
39. Presence of pallets (0, 1)
40. Pallet constructed as a series of cones; growth by adding cone elements (0, 1)
41. If cone-type pallet, construction
Short, fused, friable material (0)
Elongate, fused cones (1)
Fused in juvenile stage (2)
Nonfused cones (3)
42. If solid pallet, construction
Unsegmented, solid (0)
Sheath and dagger (1)
Weak ridge partially dividing the pallet (2)
Cups within a cup at some stage in development (3)
43. If pallet has cups within a cup,
One (0)
Two (1)
Two as juvenile; thumbnail shape as adult (2)
44. Pallet sculpture, if pallet is solid type
None (0)
Weakly developed radiating ribs (1)
Well-developed radiating ribs (2)
45. Pallet with periostracal cap in adult (0,1)
46. Pallet with calcareous cap in adult (0, 1)
47. Periostracum on cone-type pallets
Awns absent or poorly developed (0)
Awns smooth (1)
Awns fringed (2)

Burrow Characters

48. Burrow lined with calcium
Absent (0)
Thin (1)
Very thick (2)
49. Burrow lined with heavy periostracum
None (0)
Regular periostracum (1)
Membranous periostracum (2)
50. Calcareous burrow lining: inside deposits
None (0)
Material at posterior (1)
Regular rings (2)
51. Calcareous burrow, material at posterior
Concamerations (0)
Posterior division (1)
Posterior longitudinal ridges (2)

52. Burrow filled with consolidated faecal pellets (0, 1)

Siphon Characters

53. Ratio of siphon widths
Incurrent/Excurrent less than 1 (0)
Incurrent/Excurrent about equal to 1 (1)
Incurrent/Excurrent greater than 1 (2)
54. Ratio of siphon lengths
Incurrent/Excurrent less than 1 (0)
Incurrent/Excurrent about = 1 (1)
Incurrent/Excurrent greater than 1 (2)
55. Excurrent siphon morphology
Absent (0)
Partial groove (1)
Complete groove, smooth lappets (2)
Groove with fringed lappets (3)
Siphon complete, short (4)
Siphon complete, long (5)
56. Incurrent siphon length
Short (0)
Long (1)
57. Papillae on incurrent siphon
Absent (0)
Short, simple (1)
Elaborate (2)
58. Papillae on excurrent siphon
Absent (0)
Short, simple (1)
Elaborate (2)
Clump to one side (3)
59. Siphons united
Siphons separate (0)
Siphons $\frac{1}{2}$ to $\frac{3}{4}$ united (1)
Siphons united except at tip (2)
60. Material imbedded in siphon tissue
None (0)
Chitinous (1)
Calcareous (2)

General Anatomical Characters

61. Dorsal lappets just anterior to siphons
Absent (0)
Tubercles (1)
Present, large (2)
62. Visceral ganglion
Normal bivalve position, surface of posterior adductor muscle (0)
Posterior, end of pericardium (1)
63. Muscular collar posterior to shell (0, 1)
64. Size of posterior adductor muscle
Small, about equal to anterior adductor muscle (0)
Larger than anterior adductor muscle (1)
Very large shell modified in area of attachment (2)

65. Shape of posterior adductor muscle
 - Round (0)
 - Oval, elongate (1)
 - Irregular (2)
66. Relative position of posterior and anterior adductor muscle
 - Far apart (0)
 - Close together, visceral mass extends in a loop beyond posterior adductor muscle (1)
67. Insertion of siphonal retractors
 - On shell valves (0)
 - On siphonal plates (1)
 - On burrow lining (2)
68. Ctenidia length
 - Short (0)
 - Long (1)
69. Number of demibranchs, gill (1, 2)
70. Stomach size (relative to body size)
 - Small (0)
 - Medium (1)
 - Large (2)
71. Size of labial palps
 - Small, attached (0)
 - Large, free at ends (1)
72. Products of boring enter gut (0,1)
73. Wood-storing caecum
 - Absent (0)
 - Small (1)
 - Medium (2)
 - Large, gonads dorsal to it (3)
74. Extended excurrent and/or incurrent canals (0, 1)
75. Intestine traverses heart (0, 1)
76. Large crystalline style (0, 1)
77. Gill position
 - Before posterior adductor muscle (0)
 - Beyond posterior adductor muscle (1)
78. Presence of accessory genital organ (0, 1)
79. Presence of *Vesicula seminalis* (0, 1)
80. Type of sperm transfer
 - Free-spawning; fertilization external (0)
 - Female sucks in sperm (1)
 - Pseudocopulation (2)
81. Larval type
 - Oviparity (0)
 - Larviparity (1)
82. If larviparous,
 - Short-term brooding (0)
 - Long-term brooding (1)
83. If larviparous, brooding method
 - In burrow, on back of shell (0)
 - At base of siphons (1)
 - In mantle cavity (2)
 - In gills (3)

84. Sex
 - Protandrous (0)
 - Dwarf male (1)

Ecological Characters

85. Burrows in rock (0, 1)
86. Burrows in mud, clay, peat (0, 1)
87. Burrows in nuts, seeds, husks, jute (0, 1)
88. Burrows in wood (0, 1)
89. Burrows in living roots (0, 1)
90. Burrow length
 - Short (0)
 - Long (1)
91. Lives in full ocean salinity ($>25\text{‰}$) (0,1)
92. Lives in brackish water (0, 1)
93. Lives in fresh water ($<4\text{‰}$) (0, 1)

Detailed Anatomical Characters, Reduced Species Set (Teredinids)

94. Heart size/body size (ratio)
 - $\leq .2$ (0)
 - .3 – .5 (1)
 - .6 – .9 (2)
95. Size of ventricular bulb
 - Short (0)
 - Long (1)
96. Heart position
 - Anterior (0)
 - Median (1)
 - Posterior (2)
97. Pigmentation of auricles
 - Not pigmented (0)
 - Lightly pigmented (1)
 - Heavily pigmented (2)
98. Mantle thickness
 - Thin (0)
 - Thick (1)
 - Very thick (2)
99. Ratio of gill length/body length
 - Short, to .2 (0)
 - Medium, .3 – .5 (1)
 - Long, .6 – .7 (2)
 - Almost the length of the animal, .8 – .9 (3)
100. Shape of stomach
 - Globular (0)
 - Intermediate (1)
 - Elongate (2)
101. Position of stomach
 - Posterior (0)
 - Anterior (1)
102. Esophagus long (0, 1)

103. Ratio of visceral mass to body length

≤.2 (0)

.3 – .5 (1)

.6 – .9 (2)
104. Kidney surrounds intestine (0, 1)
105. Anal canal

Absent (0)

Open (2)

Closed (2)
106. Anal papillae (0, 1)
107. Intestine travels down anal canal (0, 1)
108. Length of intestine

Short (0)

Moderately long (1)
- Very long (2)

Many extra coils (3)
109. Intestine loops over style sac (0, 1)
110. Production of faecal pellets (0, 1)
111. Gill with anterior portion (0, 1)
112. Gill width

Blade-like, narrow (0)

Broad and flat (1)
113. Branchial food groove well-developed, (0, 1)
- Ecological Characters, Reduced Species Set (Teredinids)*
114. Pallets flexible (0, 1)

VARIATION IN SHELL SHAPE AND SIZE OF HELICID SNAILS IN RELATION TO OTHER PULMONATES IN FAUNAS OF THE PALAEARCTIC REGION

A. J. Cain

Department of Zoology, Liverpool University, Liverpool L69 3BX, England

ABSTRACT

A study is made of the distribution of values of shell height h and maximum breadth d in the family Helicidae, which is the most variable in these characters in the Palaearctic fauna. In most terrestrial gastropod faunas, plotting h against d gives two separate scatters, the upper one corresponding to high-spined shells, the lower to equidimensional to discoidal ones. The vast majority of the Helicidae are in the lower scatter, with a few in the upper. Scatters for the separate subfamilies and other major subgroups show that when such groups coexist, they either differ markedly in average shell size or, if their size-ranges coincide, they differ in local habitat.

A survey of separate faunas from the Atlantic islands through Europe and the U.S.S.R. to the Pacific shows that, except in some islands and in the Far East, the Helicidae are accompanied throughout by much the same suite of other families which complete the two scatters, each occupying a characteristic area within them. Where in the Atlantic islands there is a poor representation of small-shelled species of other families, the Helicidae produce a number of small species. In the Central Asian mountains, the larger shells of the lower scatter are a mixture of helicids and bradybaenids, and in the Maritime Territory of the U.S.S.R. all the larger shells are of bradybaenids, the few helicids being medium-sized. In this region the Palaearctic and Oriental faunas meet, and the ecological and historical interpretation of replacement of Helicidae by Bradybaenidae is discussed. Within the continental faunas generally, variation in major subgroups seems to correspond to overall ecological differences in different regions with the possible exception of hygromiines and helicellines; the restriction of the scatters in steppe, tundra, and regions with highly continental climates is discussed. The sporadic production of high-spined forms occurs in coastal districts of the Mediterranean (several helicellines), on Porto Santo, on Santa Maria (Azores), and in the Austrian Alps. The coastal forms seem to be in a habitat without other tall shells. The others are presumably also filling vacant niches.

Comparison of the family Helicidae with families in other faunas suggests strongly that its comparative constancy in shell proportions is caused by competition from the rather uniform suite of other families that accompany it, not by any evolutionary or physiological constraints.

INTRODUCTION

It has been shown elsewhere (Cain, 1977a) that the distribution of shell height and breadth in free-crawling, fully terrestrial gastropods which can retract completely into their shells—i.e. excluding slugs and semi-slugs—is not random but shows a consistent pattern. In the Stylommatophora (and indeed in land prosobranchs in most faunas: Cain, 1978b) a scatter diagram of maximum shell height, h , against maximum shell breadth, d , gives two main scatters corresponding to high-spined shells and to equidimensional to discoidal shells, with a gap between them at all shell sizes. These two scatters are found in faunas as taxonomically different as those of western Europe, eastern North America, Puerto Rico,

New Caledonia, the former Belgian Congo (Cain, 1978b), and, with only partial exceptions, the Philippines and the New Guinea region (Cain, 1978a). Some pulmonate families are found only in the upper scatter (of tall shells), some only in the lower, but several have a few or many representatives in both. There are strong indications that within a fauna families tend to be mutually exclusive within a scatter, each occupying a definite area and combining with the others to fill up the scatter area (Cain, 1977a). This suggests some form of interaction between groups, probably competition. Some taxonomic groups may overlap within a fauna. However, at least in the western European fauna, they tend to occupy different habitats, or perhaps, as in the case of the partly carnivorous zo-

nitids, they may be taking different food. Few or none are food specialists to the same extent that so many insects are found to be.

The suggestion that such food generalists may avoid competition by feeding preferentially on surfaces of different inclination, and that shell shape is at least partly adapted for locomotion at different angles (Cain, 1977a) is supported by studies on the British fauna (Cain & Cowie, 1978; Cameron, 1978). On a larger scale, families or other groups should show replacement by each other in the scatter diagrams of different faunas. The purpose of this paper is to determine the variation in *h* and *d* of the family Helicidae, in both continental and insular faunas.

MATERIALS AND METHODS

Measurements of helicid shells for this paper were taken from representative specimens in the collections of the Academy of Natural Sciences of Philadelphia, and are those specified by Cain (1977a). They were supplemented by those of the British Museum (Natural History) and checked against the literature. Considering the variation in *h* and *d* within most species, slight differences in the modes of taking measurements are highly unlikely to introduce any perceptible bias in such a survey as this. The Academy collections contain many lots from the Lowe-Wollaston collection of Macaronesian shells, and from P. Hesse's European collection which were themselves originally collected by Pallary, Bourguignat and others. The vexed question of the validity of specific limits (especially with Bourguignat's material, see Dance, 1970) remains unsettled for want of a biological approach made on well-localised live material, and has prevented an adequate examination of North African faunas. Since it is at any rate likely that species which are the types of genera, subgenera and sections are valid species, these are marked specially in Figs. 1-9 which show variation in *h* and *d* in major groups within the helicids. The other species can be seen to cluster around them, few being aberrant. It is probable, therefore, that particular scatters do show an adequate representation. But while emphasis is put on the area occupied by a scatter, little is put on the exact number of points within the scatter. While in a few faunas the points shown may represent a nearly complete enumeration of the species present, in most they are only a sample.

For helicid species not available to me, and those of other families, mean measurements have been taken from the data given by Likharev & Rammelmeier (1962), brought up to date by the monograph of Shileyko (1978a) on the Helicoidea. Wollaston (1878) and Nobre (1931) were used for the Madeiran archipelago, Mandahl-Barth (1943) being followed for the Madeiran helicids. Backhuys's excellent monograph (1975) was used for the Azores, and various scattered papers for the Canaries.

The classification of higher groups used is that of Taylor & Sohl (1962), but more subgroups of the Helicidae are used than are recognised by them or Thiele (1931). The purpose of this is simply to ensure that groups that might have ecologically distinctive characters are recognised, and that heterogeneous groups are not lumped together; there is no intention of expressing any taxonomic judgment on their rank.

The classification of the Helicidae is, at present, in a state of change. Watson (1943) remarked in passing that there was a curious correspondence between the genera of the helicellines and the hygromiines, but he left them as coordinate groups. Shileyko (1978a, b) brings forward convincing evidence that the helicellines are derived polyphyletically from the hygromiines. He separates the helicodontinae as a distinct family, with the Helicodontinae and the new Lindholmiolinae as subfamilies, removes to the hygromiines a number of species from the Bradybaenidae, and elevates the hygromiines to a family, with subfamilies Trichiinae, Hygromiinae, Archaicinae (new), Euomphaliinae (new), Paedhoplitinae (new) and Metafruticicolinae. The helicelline genera *Helicopsis*, *Xeropicta* and *Helicella* are in the Trichiinae, *Cernuella* and *Xerosecta* in the Hygromiinae; *Monacha* is in the Euomphaliinae. Perhaps more surprising is the transfer to the Polygyridae of *Isognomostoma subpersonatum* (Midd.), which occurs near the sea of Okhotsk.

In the present paper, I have retained the Helicodontidae and Hygromiidae as subfamilies of the Helicidae in its more usual sense, and left the helicellines separate since their ecological habits are distinct. The following subgroups of the Helicidae are therefore used: Hygromiinae, Helicodontinae, Lep-taxinae, Helicigoninae (Ariantinae in Shileyko), Monachines (for *Monacha* and its subgenera or allied genera), Sphincterochilinae, Geomitrinae, Helicellinae and Helicinae.

Murella and *Tacheocampylaea*, considered as subfamilies by Germain (1930), are included in the Helicinae.

VARIATION WITHIN SUBFAMILIES AND OTHER GROUPS OF THE HELICIDAE

The family Helicidae is distributed naturally in the Palaearctic region including Africa north of the Sahara, with one genus, *Lejeania*, isolated in the Abyssinian highlands. Eastwards it ranges into Mesopotamia and Persia and the Central Asian mountains, from the Kopet Dag to the Tien Shan, with a few stragglers into Siberia and across to the Pacific (Hygromiinae: *Zenobiella rubiginosa* and *Z. nordenskioldii* to the Maritime Territory of the U.S.S.R., *Perforatella bicallosa* to the Altai, *P. gerstfeldti* to the Lake Baikal district and Maritime Territory). To the west, one species only (Helicinae: *Cepaea hortensis*) may perhaps be a native of the north-eastern coast of the U.S.A. The family is well represented in the Macaronesian Islands (Azores, Madeira group, Canaries and Cape Verdes) in which there are two endemic subfamilies, the Leptaxinae and Geomitrinae, and various endemic genera in other subfamilies. A series of oceanic faunas is therefore available to compare with the continental ones.

Figs. 1–9 show the *h*, *d* scatters for all the subgroups of the Helicidae. All are wholly or predominantly within the lower scatter, but in the Leptaxinae (Fig. 3), Helicigoninae (Fig. 4) and Geomitrinae (Fig. 7) a single species is high-spined. In the Helicellinae (Fig. 8) seven are well across the bisector (the line on which $h = d$), and another five cross it but could be considered part of the principal cluster. In the Leptaxinae, the high-spined species is *Helixena sanctaemariae* in the Azores; in the Helicigoninae it is *Cylindrus obtusus* in the Austrian Alps; in the Geomitrinae it is *Discula (Hystricella) turricula* in Porto Santo (Madeira group). The principal high-spined helicellines are the three species of the genus *Cochlicella*, on Mediterranean and Atlantic shores of Europe and North Africa. The remainder are a scattering of species in *Candidula*, *Cernuella* and (mainly) *Trochoidea* in the Mediterranean region. Apart from the various helicellines, therefore, the clearly high-spined helicids are geographically and taxonomically isolated—there is no one region in which helicids tend to be high-spined.

The vast majority of the helicids, then, be-

long to the lower scatter. The Helicinae (Fig. 9) are unique in that they appear to be heterogeneous in *h*, *d* with one subscatter well into the lower scatter area and somewhat below the bisector (i.e. it is of slightly to markedly depressed shells). A second subscatter which runs along and slightly above the bisector and on average is composed of larger shells. These are in fact the species of the genus *Helix* itself, with its numerous subgenera. (The type-genus, as is not unknown elsewhere, is therefore somewhat abnormal in the family.) The Helicinae are generally large for the family, with values of *d* from about 15 to about 50 mm. In most other subgroups (except for a few comparatively giant species) *d* ranges from 5 to 25 mm, but the Helicigoninae (Fig. 4) range from 10 to 35 mm and the Sphincterochilinae (Fig. 6) from 13 to 30 mm.

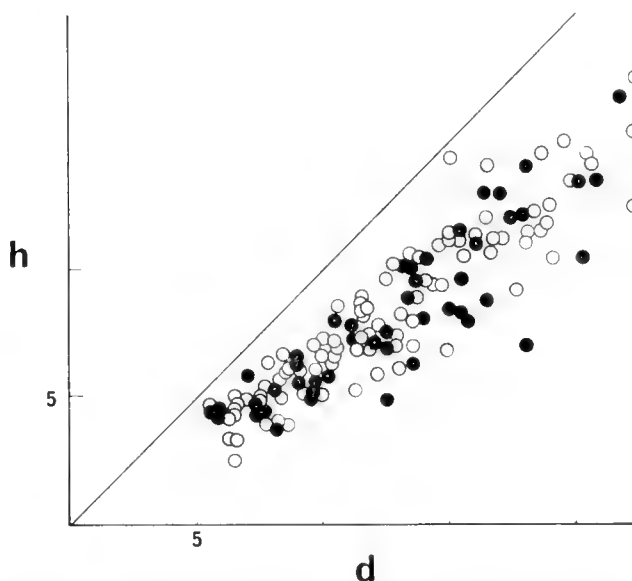


FIG. 1. Scatter-diagram for *h* (shell height) and *d* (maximum breadth) for the Hygromiinae. Each symbol gives *h* and *d* for adult shells of a single species. Black circles, type-species of genera, subgenera or sections. Both axes marked at 5 mm intervals.

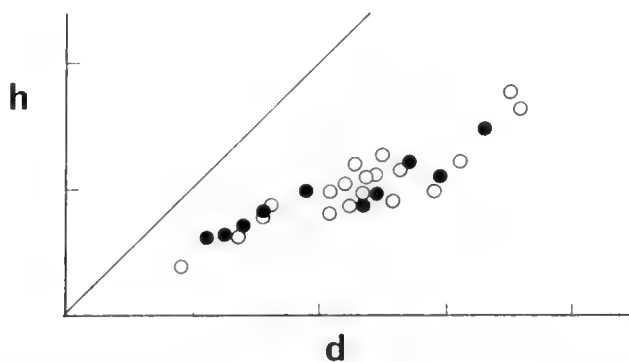


FIG. 2. Helicodontinae; *h*, *d* scatter diagram. Symbols as in Fig. 1.

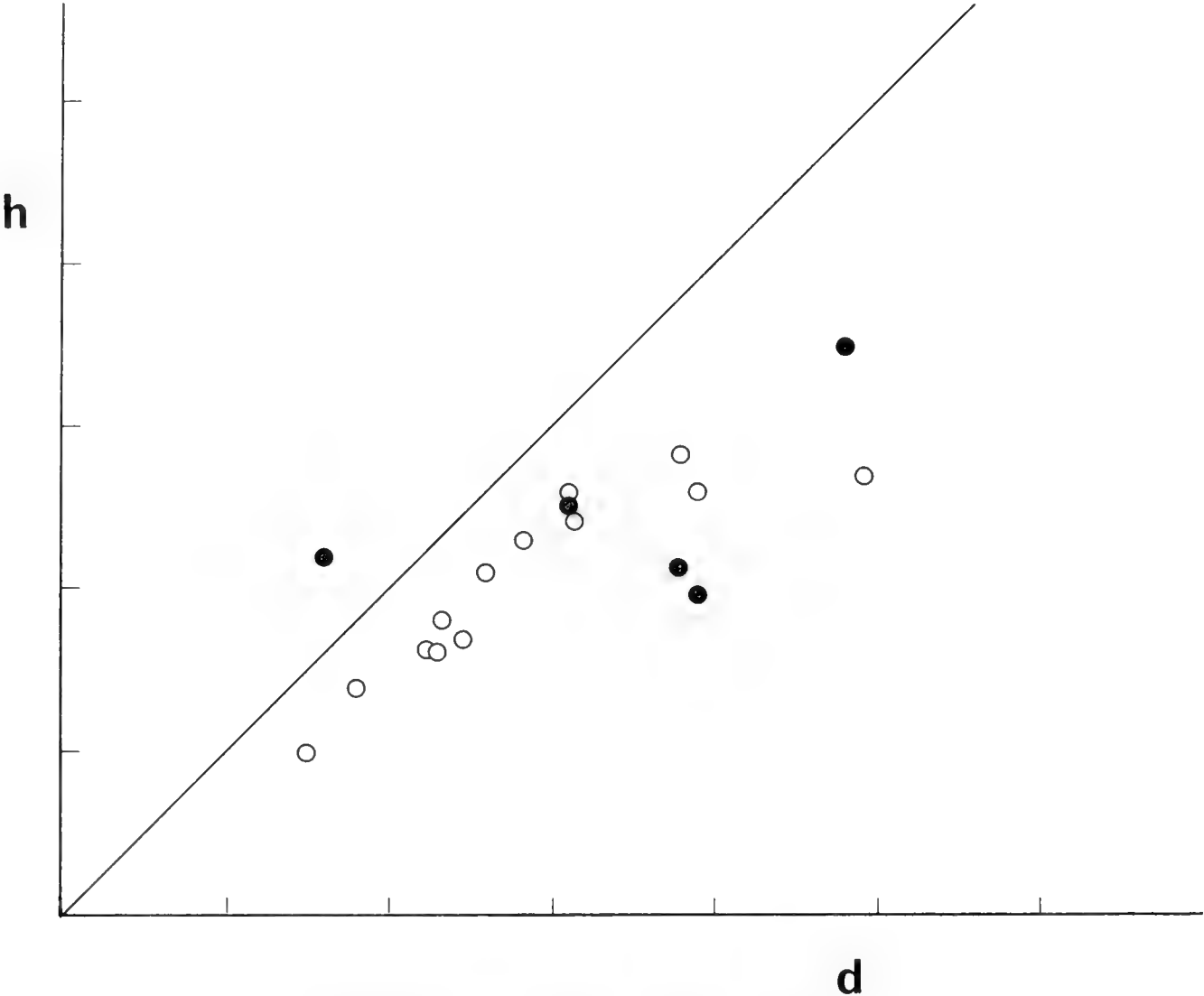


FIG. 3. Leptaxinae; h, d scatter diagram. Symbols as in Fig. 1.

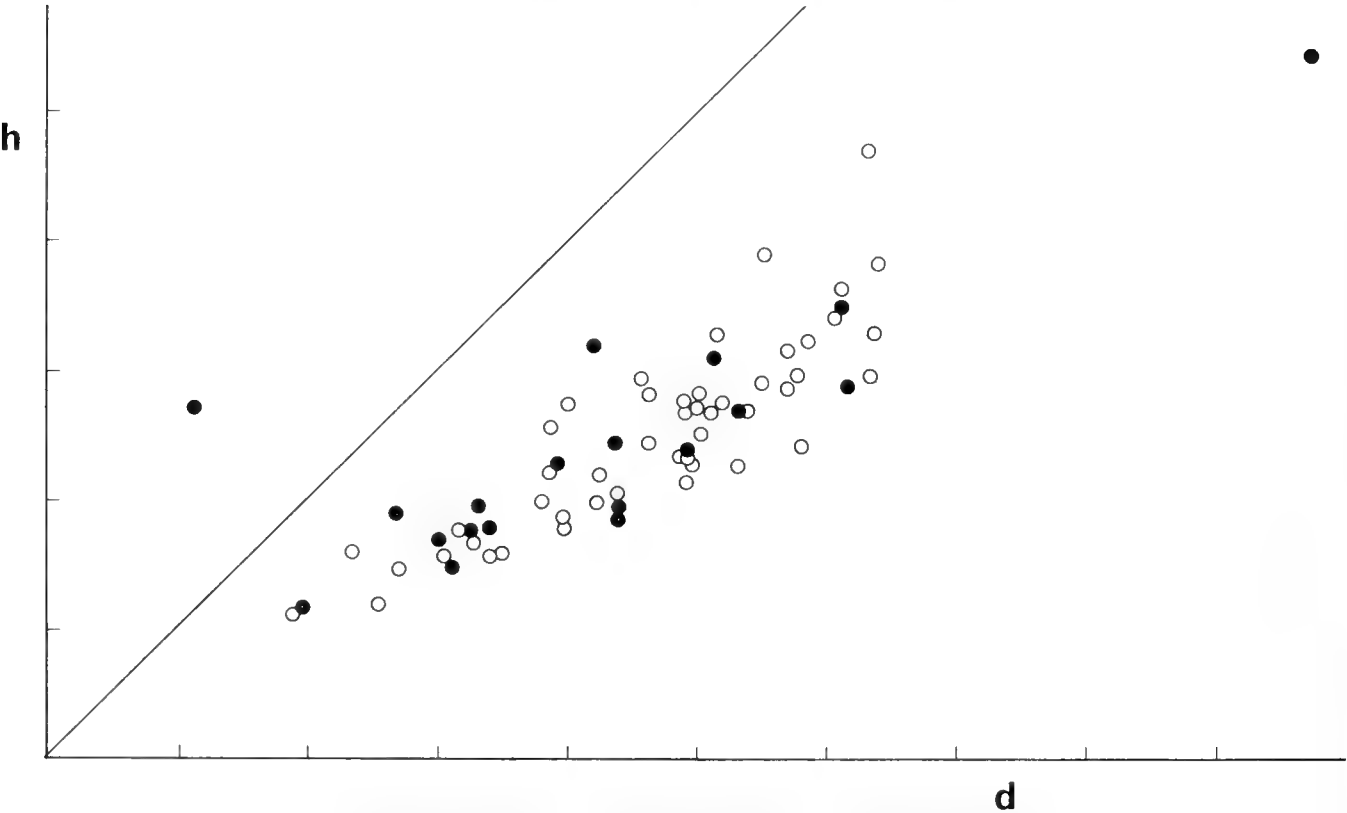


FIG. 4. Helicigoninae; h, d scatter diagram. Symbols as in Fig. 1.

The abundance of rather small shells in the family is clear in Fig. 10. This gives the scatter for the whole of the Helicidae, and emphasizes again the peculiarity of the large shells along the bisector (*Helix* s. l.). The bulk of the symbols lie clearly below it except for the helicelline small shells that trespass across.

Overlap between the subgroups of the helicids is therefore extensive. The major parts of the scatter areas occupied by the hygromiines, helicellines, leptaxines and helicigonines are coincident, and the helicodontines, geomitrines, monachas and sphincterochilines coincide with this principal area. Of these groups, the leptaxines and geomitrines are Macaronesian, occurring together in abundance in the Madeira group and showing less overlap in their scatters than each does with other subgroups. The sphincterochilines inhabit hot arid country where they coincide with some helicines, usually of larger size, and with some heli-

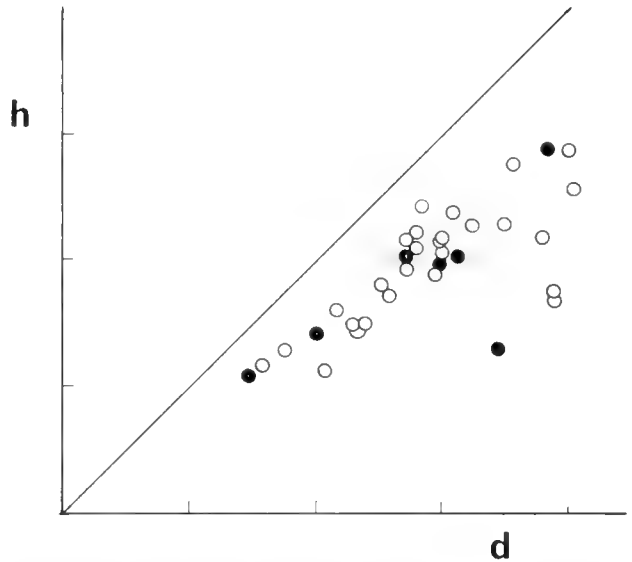


FIG. 5. *Monacha* and related genera; h, d scatter diagram. Symbols as in Fig. 1.

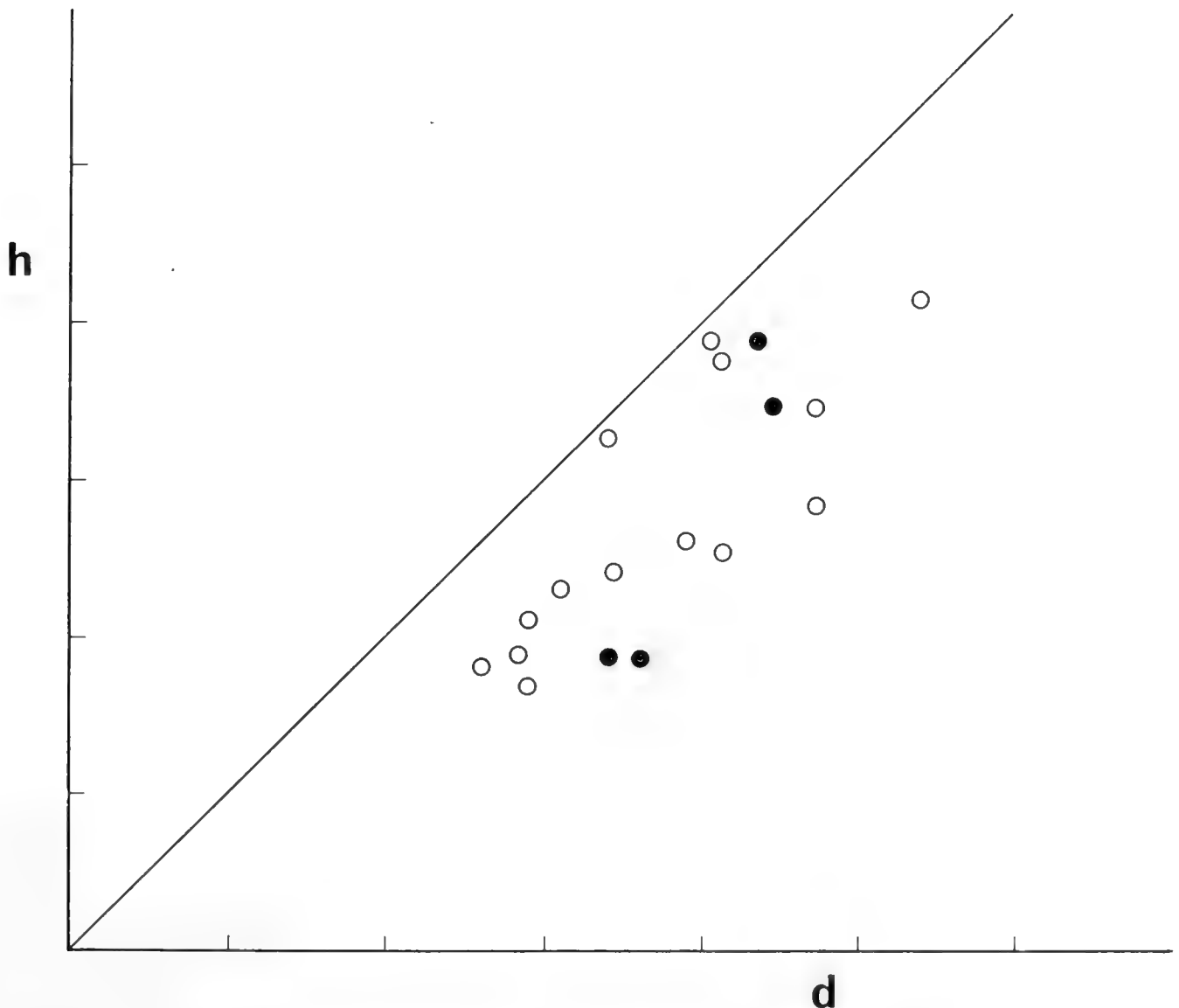


FIG. 6. *Sphincterochilinae*; h, d scatter diagram. Symbols as in Fig. 1.

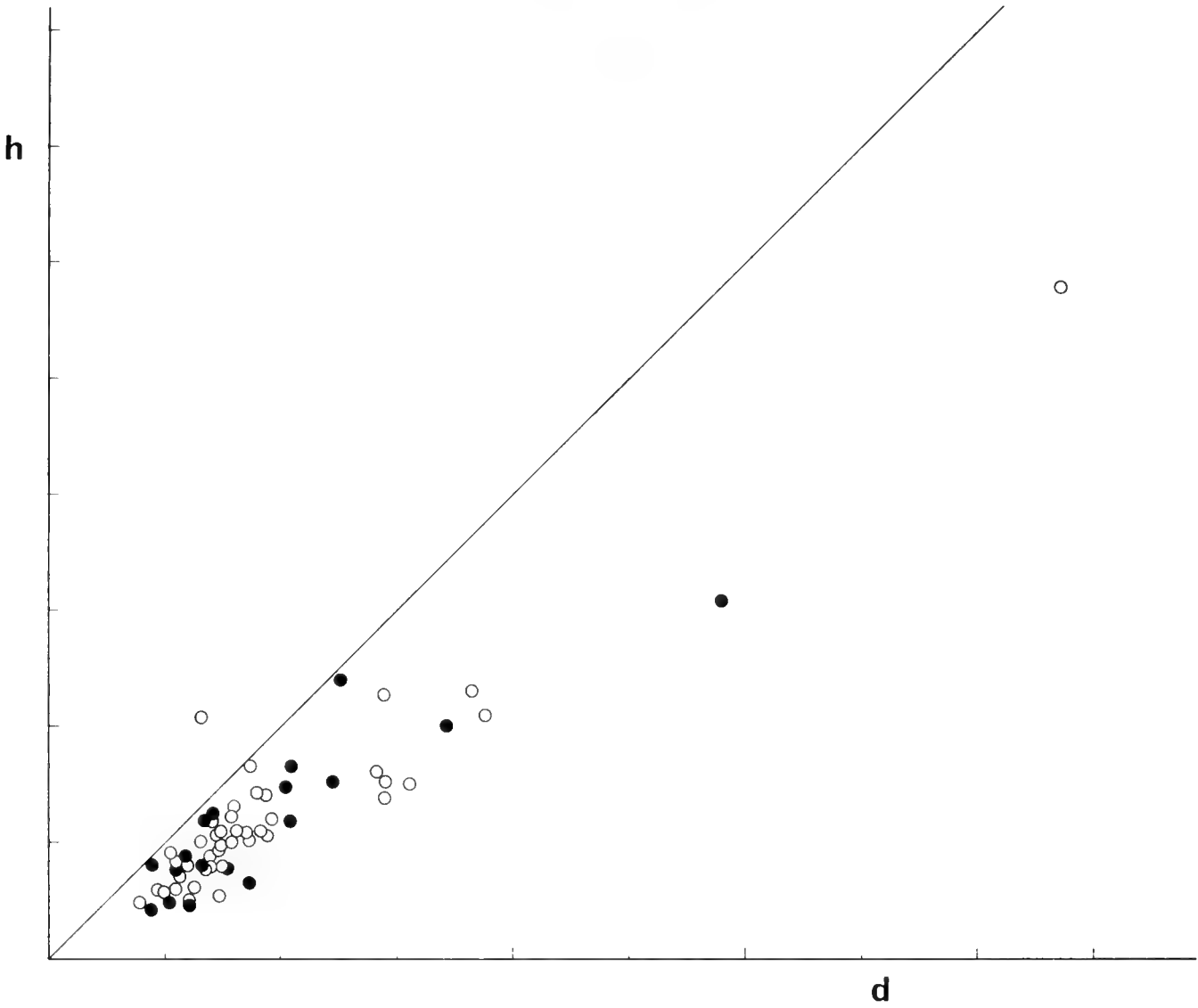


FIG. 7. Geomitrinae; h, d scatter diagram. Symbols as in Fig. 1.

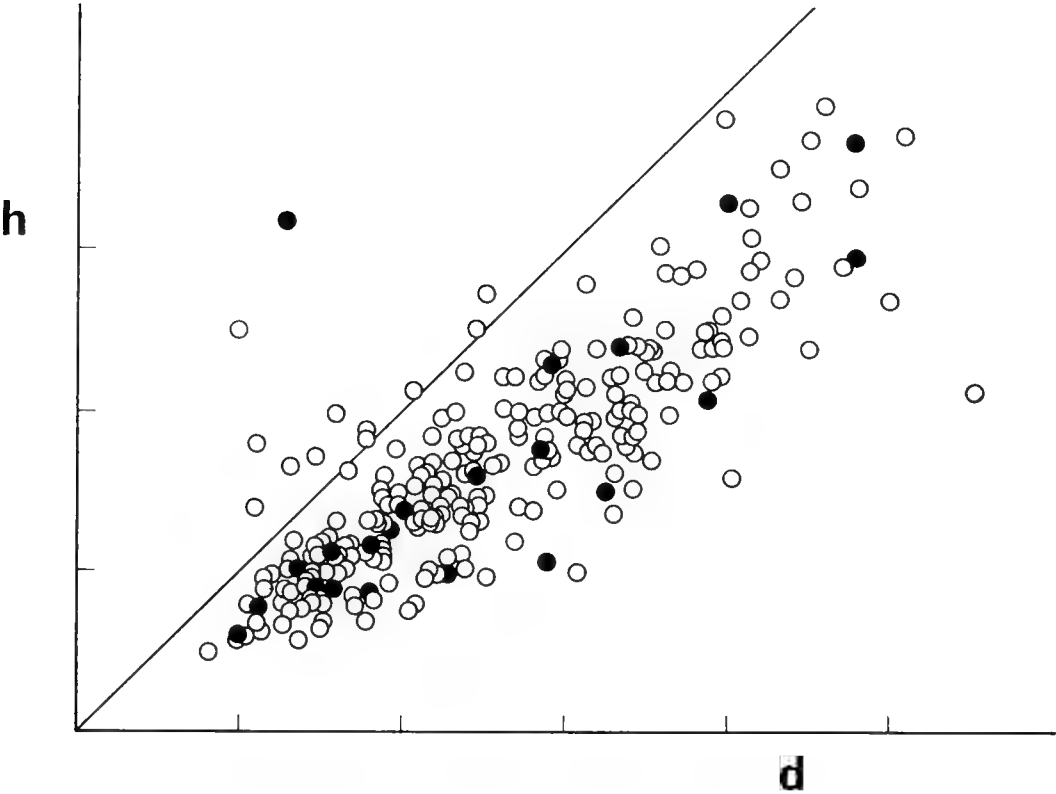


FIG. 8. Helicellinae; h, d scatter diagram. Symbols as in Fig. 1.

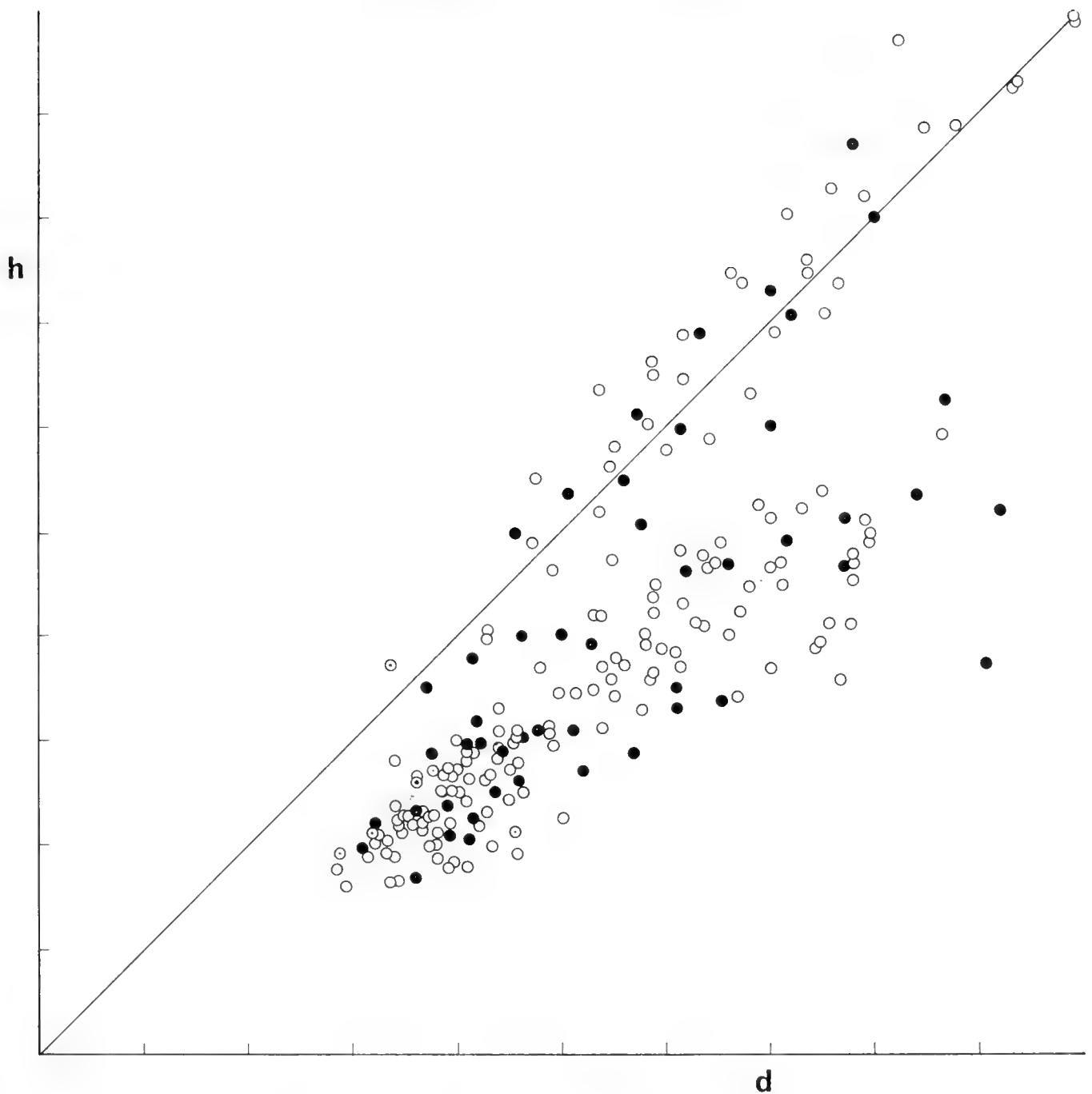


FIG. 9. Helicinae; h, d scatter diagram. Symbols as in Fig. 1.

cellines which are usually smaller. Of the rest, helicodontines and most helicigonines are montane or alpine; helicodontines are, on average, notably the smaller. In western and central Europe, the hygromiines, the *Monacha* group (which taxonomically is placed with them), and the helicellines occur together and are of much the same size range; the helicines with which they coincide are markedly larger. The similar forms, however, differ in habits (and colour pattern correspondingly: Cain, 1977b). The helicellines sit out during the day in very open habitats exposed to sun. Monachas are perhaps intermediate. Hygromiines prefer more densely vegetated, shadier and damper places and do not sit out.

Some hygromiines, however, in the south of Europe and apparently in regions further east stand as much exposure as monachas and probably as helicellines. The greatest abundance of helicelline species is in the Mediterranean region, and elsewhere hygromiines probably take on their habits and colour-patterns. This is suggested strongly by some of the pictures in Shileyko (1978a) and made explicit by Shileyko (1978b), and it is hoped that Russian workers will give some further account of the ecology and habits of the abundant hygromiine species of the Caucasus and further east.

Unfortunately, not too much has been recorded of habits and habitats of many Euro-

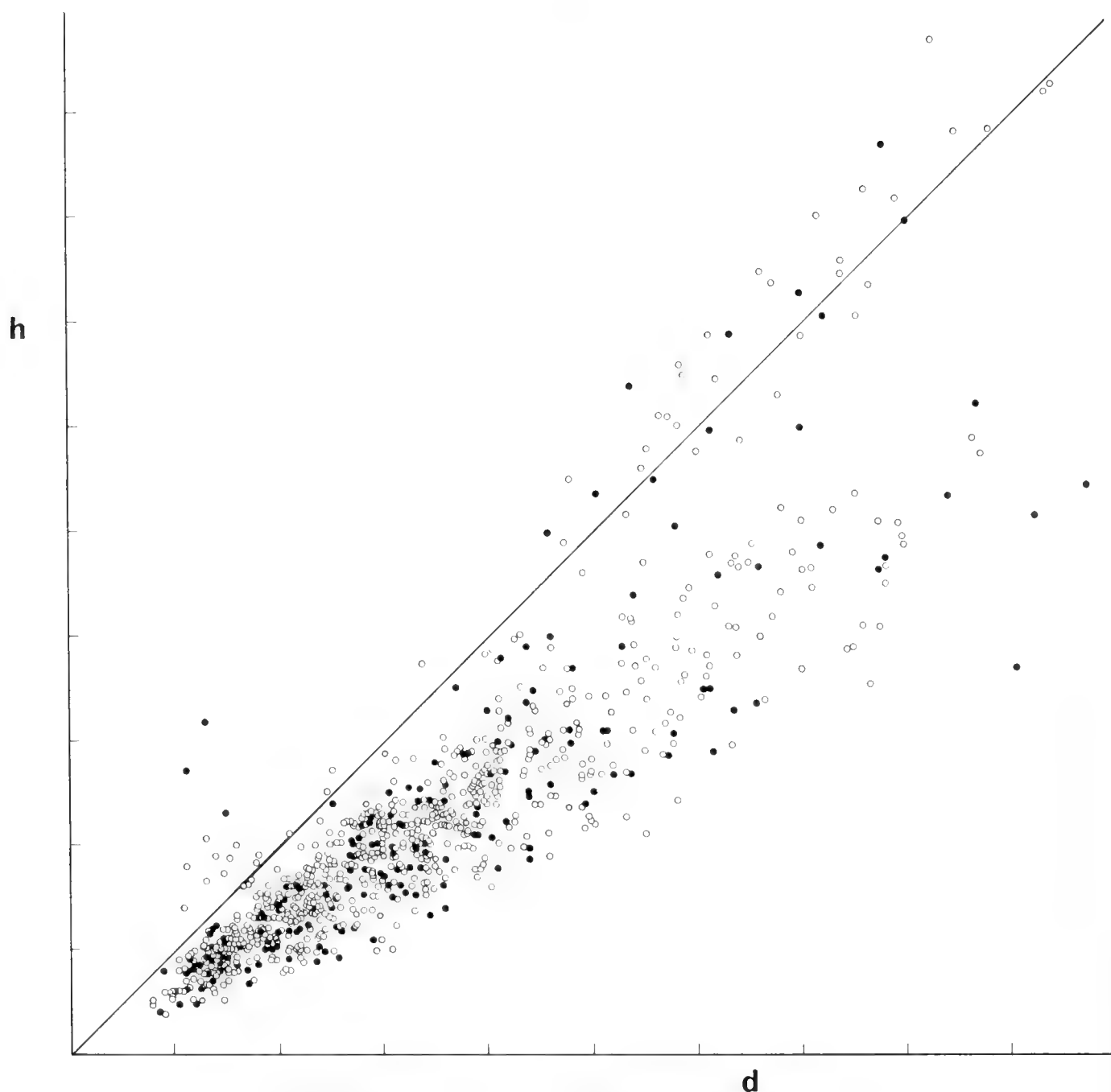


FIG. 10. Scatter diagram (h, d) for all the Helicidae. Symbols as in Fig. 1.

pean snails, either. The necessarily very general remarks just made do suggest, however, that subgroups coinciding geographically *either* differ in average shell size *or* take up different habitats.

The general distribution of h and d within the family as a whole now needs examination in relation to those of the other families with which the Helicidae coincide. Cain (1977a: 338–390 and figs. 6–8) has shown that in western Europe, although the subgroups of the Helicidae overlap widely with each other, they overlap very little with the accompanying families which are themselves mostly mutual-

ly exclusive in h, d. The question now is whether this is true over the rest of the heli-cids' range.

VARIATION WITHIN OTHER FAMILIES

An inspection of the figures in Germain's volume (1930) on the terrestrial malacofauna of France, and similar monographs, is enough to show that the other families of pulmonates in the regions of the Palaearctic considered here are much less variable in h, d than are the Helicidae. They are listed below with their variation in shell shape.

Suborder ORTHURETHRA

Superfamily **Cionellacea**

Cionellidae (= Cochlicopidae)

tall shells only

Pupillacea

Pyramidulidae

moderately depressed

Vertiginidae

rather tall to tall

Orculidae

tall only

Chondrinidae

tall only

Pupillidae

tall to very tall

Valloniidae

subglobular to depressed

Valloniinae

very depressed

Acanthinulinae

subglobular to depressed

Strobilopsinae

depressed

Enidae

tall only

Chondrulinae

Jaminiinae

Eninae

Napaeinae

Suborder MESURETHRA

Superfamily **Clausiliacea**

Clausiliidae

very tall only

Clausiliinae

Phaedusinae

Cochlodininae

Suborder HETERURETHRA

Superfamily **Succineacea**

Succineidae

omitted (semiaquatic)

Suborder SIGMURETHRA

Infraorder Holopodopes

Superfamily **Achatinacea**

Ferussaciidae

tall

Subulinidae

very tall, but decollated

Infraorder Aulacopoda

Superfamily **Endodontacea**

Endodontidae

depressed only

Punctinae

Discinae

Arionidae

omitted (slugs)

Superfamily **Zonitacea**

Vitrinidae

somewhat depressed

Zonitidae

depressed

Vitreinae

Zonitinae

Gastrodontinae

Daudebardiinae

omitted (slugs)

Parmacellidae, Milacidae, Limacidae,

Trigonochlamydidae

omitted (all slugs)

Superfamily **Ariophantacea**

Euconulidae

somewhat depressed

Ariophantidae

depressed

Superfamily **Testacellacea**

Testacellidae

omitted (slugs)

Infraorder Holopoda

Superfamily **Polygyracea**

Polygyridae

here, depressed

Superfamily **Oleacinacea**

Oleacinidae

tall here

Superfamily **Helicacea**

Bradybaenidae

subglobular to depressed here

(Helicidae)

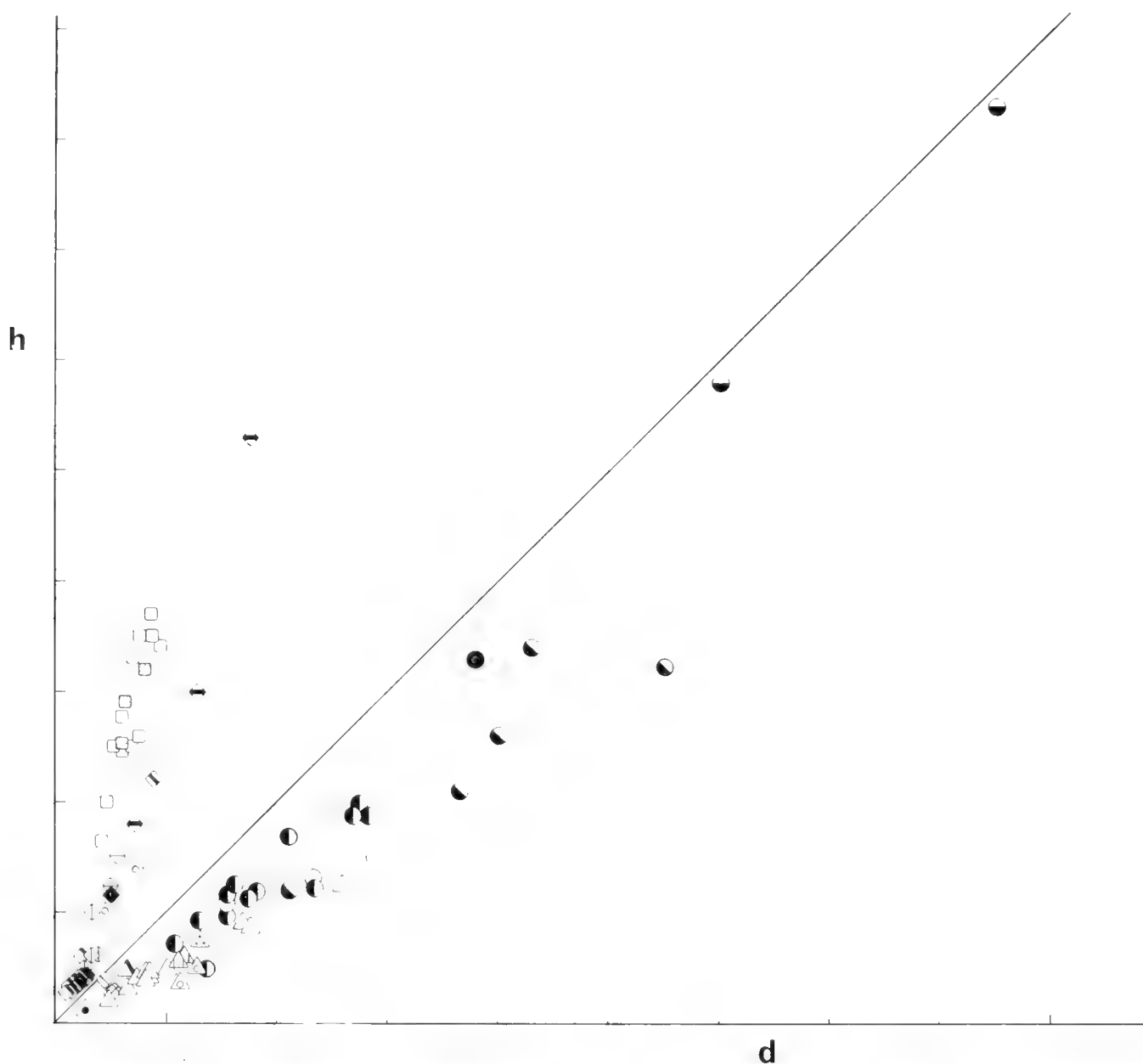


FIG. 11. Russian Carpathians; h, d scatter diagram for the pulmonate fauna. Axes marked at 5 mm intervals. Symbols for Figs. 11–24:—

Suborder ORTHURETHRA, *diamonds*.

Cionellidae, all black. Pyramidulidae, black bar left upper side. Vertiginidae, black bar right upper side. Orculidae, circle in centre. Chondrinidae, horizontal line. Pupillidae, vertical line. Valloniidae: Valloniinae, oblique line sloping down to left; Acanthinulinae, oblique line down to right; Strobilopsinae, black cross. Enidae: Chondrulinae, black oblique bar down to right; Jaminiinae, black vertical bar; Napaeinae, black oblique bar down to left.

Suborder MESURETHRA, *squares*.

Clausiliidae: Clausiliinae, all white; Phaesusinae, all black; Cochlopininae, speckled.

Suborder HETERURETHRA omitted (Succineidae, semi-aquatic).

Suborder SIGMURETHRA

Infraorder Holopodopes, *crosses*

Ferussaciidae, oblique cross. Subulinidae, vertical cross.

Infraorder Aulacopoda, *triangles*.

Endodontidae: Punctinae, central black dot; Discinae, central circle. (Arionidae omitted, slugs). Vitrinidae, two vertical lines. Zonitidae: Vitreinae, speckled; Zonitinae, all white; Gastrodontae, 3 black dots. (Daudebardiinae, Parmacellidae, Milacidae, Limacidae, Trigonochlamyidae all omitted, slugs). Euconulidae, black bar, right side. Ariophantidae, black bar, left side. (Testacellidae omitted, slugs).

Infraorder Holopoda, *circles*.

Oleacinidae, with circle inscribed. Bradybaenidae, all black. Helicidae: Helicellinae, all white; Geomitrinae, central black dot; Hygromiinae, left half black; *Monacha* group, right half black; Helicodontinae, right lower half black (oblique); Helicigoninae, left lower half black (oblique); Leptaxinae, upper half black; Helicinae, lower half black; Sphincterochilinae, 4 black dots.

VARIATION WITHIN THE PALAEARCTIC REGION

(i) Continental regions

(a) Europe

The deployment with respect to *h* and *d* of the Helicidae and other families in the Russian Carpathians is shown in Fig. 11, which agrees well with that given by Cain (1977a) for western Europe. Both are or were forested regions, with montane habitats, and, in the southern part of western Europe, both experience a Mediterranean climate, hot and dry throughout the summer. In Fig. 11, by comparison with western Europe, large helicines

are rather few, and zonitids, clausiliids, enids about the same. Hygromiines are rather well represented, as would be expected from a forested region, and helicellines proportionately few. There is little variation, therefore, in distribution of *h* and *d* and taxonomy from oceanic western to continental eastern Europe at the family and major sub-group level, except that which might be expected from differences in habitat. (There is considerable difference, of course at the generic and specific levels.)

(b) Crimea and Caucasus

The warm maritime climate of the Crimea (Krim) gives an oasis of Mediterranean cli-

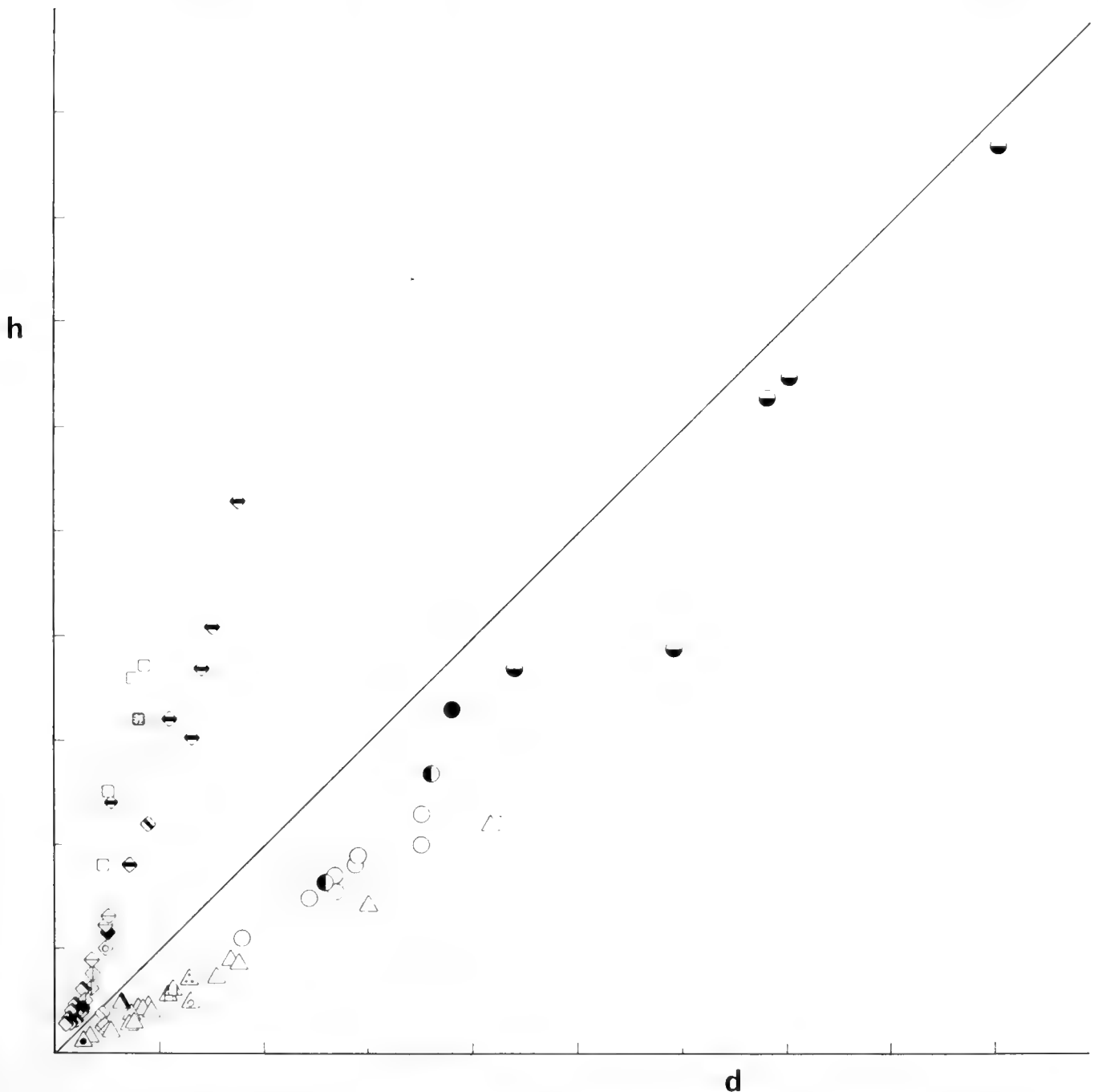


FIG. 12. Crimea (Krim); *h*, *d* scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

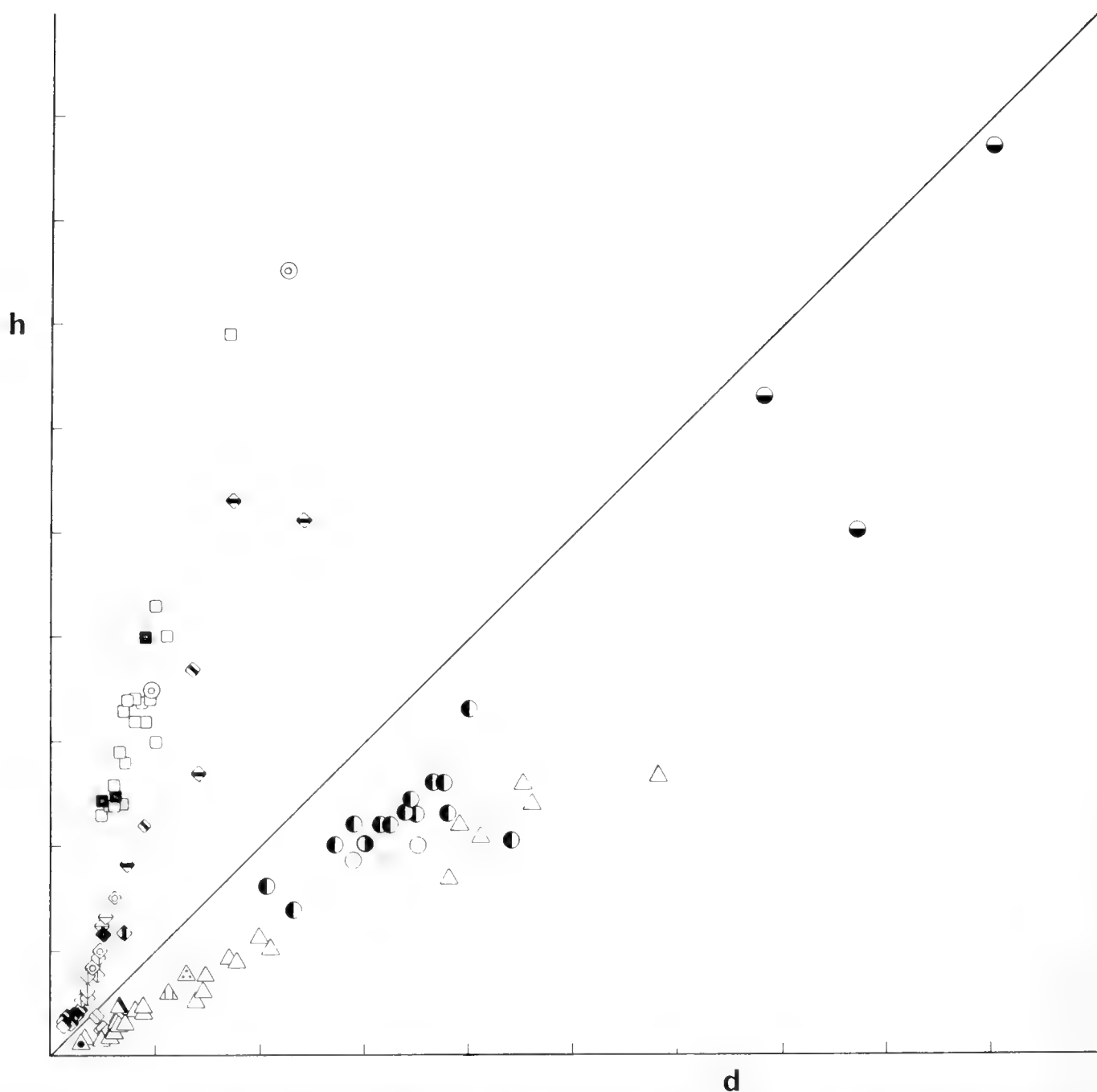


FIG. 13. Kuban-Abkhasia; h , d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11. If *Poiretia* is considered to be a spiraxid, the symbols at $h = 37.5$, $d = 11.25$ and $h = 17.5$, $d = 4.7$ should be altered to a maltese cross.

mate in a highly continental area, with forests on the hills grading rapidly into dry steppe country. It has long been known as an outpost for the Mediterranean fauna, with numerous endemics.

Fig. 12 gives the h , d distribution for the Crimea, in which the same bimodality is shown as before, but the proportion of heli-cellines has increased greatly to correspond with drier conditions and the hygromiines have nearly gone. Large zonitines now appear. Clausiliids are reduced (compare Fig. 11) but enines are more frequent, and may well include forms like *Zebrina*, more accustomed to exposure to the sun.

The vastly more extensive and more ecologically diversified region of the Caucasus and Transcaucasia has a rich fauna (and flora) with numerous endemic species, and preserves genera and species which have vanished from Europe, including some snails now relict in the Caucasus and widespread in eastern Asia (Likharev & Rammel'meier, 1962). Nevertheless, the snail fauna as a whole is almost entirely palaeartic in affinity. The complexity of climate and vegetation in the Caucasian region requires more than one diagram. Fig. 13 is for Kuban-Abkhasia, in Likharev & Rammel'meier's (1962) West Caucasian district, which has a climate heav-

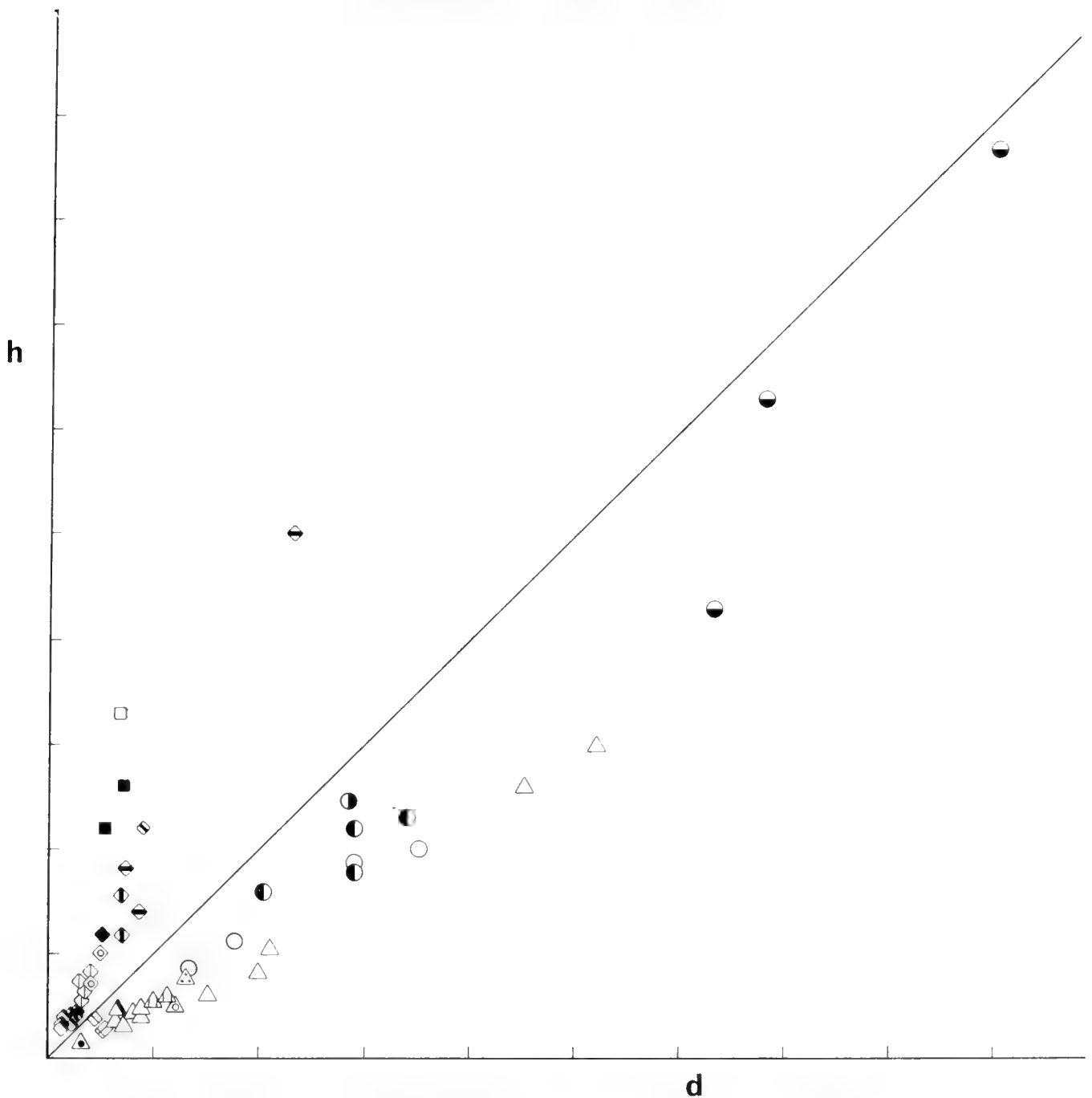


FIG. 14. Talysch; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

ily influenced by the Black Sea and rich, mixed, deciduous forests. Fig. 14 gives the same information for Talysch, bordering the Caspian Sea, with a humid subtropical climate which extends eastwards along the north Persian coast. Fig. 15 is for Likharev and Rammel'meier's Armenian district, which has a highly continental climate with cold winters and hot dry summers, and consists mainly of mountainous desert and steppe. The fauna has affinities with that of Mesopotamia, and the district is classed by them as part of a Sumerian province. Their detailed descriptions of the districts and analyses of their faunas should be consulted. The three

sub-districts illustrated here (out of their eight) give an epitome of the faunal variation.

Again, the same bimodal distribution is found as in the previous diagrams. In Kuban-Abkhazia the upper scatter reaches considerably higher values of h than have been seen so far, with one large clausiline and the carnivorous oleacinid *Poiretia*. Large zonitines, which just appeared in the Crimea, are now a feature of the lower scatter. Clausiliids are abundant, including members of the Phaedusinae, otherwise eastern Oriental; they do not, however, take over from clausiliines and are as scattered as were cochlodinines in the Carpathians. Large dry-country enines are

reduced as compared with those in the Crimea. Hygromiines are again abundant and form most of the middle part of the lower scatter, rather as in the Carpathians but with larger values of d. Almost the same large helicines appear as in the Crimea, with the addition of two endemic species of *Caucasotachea*. In Talysch (Fig. 14), a reduced version of the same picture is seen, with phaedusines now a greater part of the upper scatter. Apparently they are specialized for a rather peculiar climate or vegetation. In the Armenian district (Fig. 15) the fauna is again somewhat reduced. Some characteristic hygromiines appear that seem to be adapted to dry country, and correspondingly the heli-cellines do not increase. Large zonitines

seem to be absent. The place of *Caucasotachea* is now taken by two species of *Levan-tina*, also helicine, which are strongly hot dry-country forms. In the upper distribution, there is a much greater prevalence of enids, and the clausiliids are reduced to two species of *Armenica* (Clausiliinae), a genus confined to Transcaucasia, Asia Minor and Syria.

Clearly, then, in Figs. 10–15 we have the same general faunal type, with variations largely related to variations in climate and vegetation. The upper limit of the upper scatter varies, as does the extent of filling in of the upper part (d more than 25 mm) of the lower scatter. Otherwise the same two scatters appear, differently filled in, in different districts. In more forested areas, clausiliids are fre-

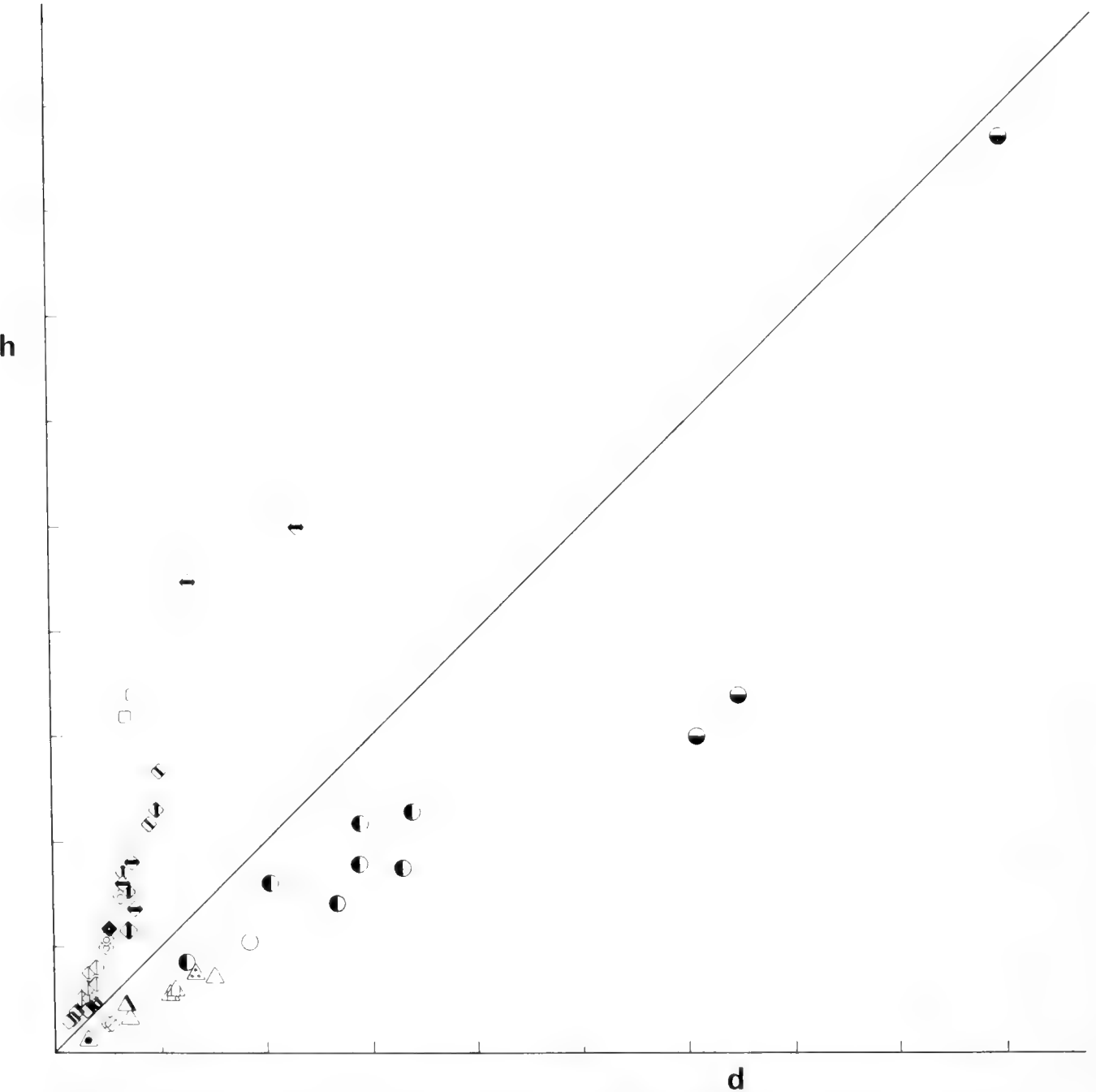


FIG. 15. Armenian district; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

quent in the upper scatter, hygromiines in the lower, and, in more open, dryer country, enids and helicellines take over, except where dry-country hygromiines take over in the Armenian district. A closer analysis of climate and habitats would probably suggest a reason for this. Throughout the various changes in the upper parts of each scatter, the faunas of the lower parts (h or d below 10 mm) remain remarkably constant, with only a slight increase of pupillines and orculids, and disappearance of the few gastrocoptines, to the east. Many of these small species are widespread and can find a suitable niche where large ones might be in difficulty.

(c) *Transition to the Oriental Region*

The boundary between the Palaearctic and Oriental regions is notoriously difficult to draw in the north. In the mountains of Central Asia, there are a number of endemic hygromiines, plus others that extend right across to the mountains or southern coast of Europe (Likharev & Rammel'meier, 1962, as corrected by Shileyko, 1978a). These mountains have a harshly continental climatic regime. It is not surprising, therefore, that the family Bradybaenidae, with many members accustomed to the rigors of the north Chinese climate spread into them (Fig. 16, central and

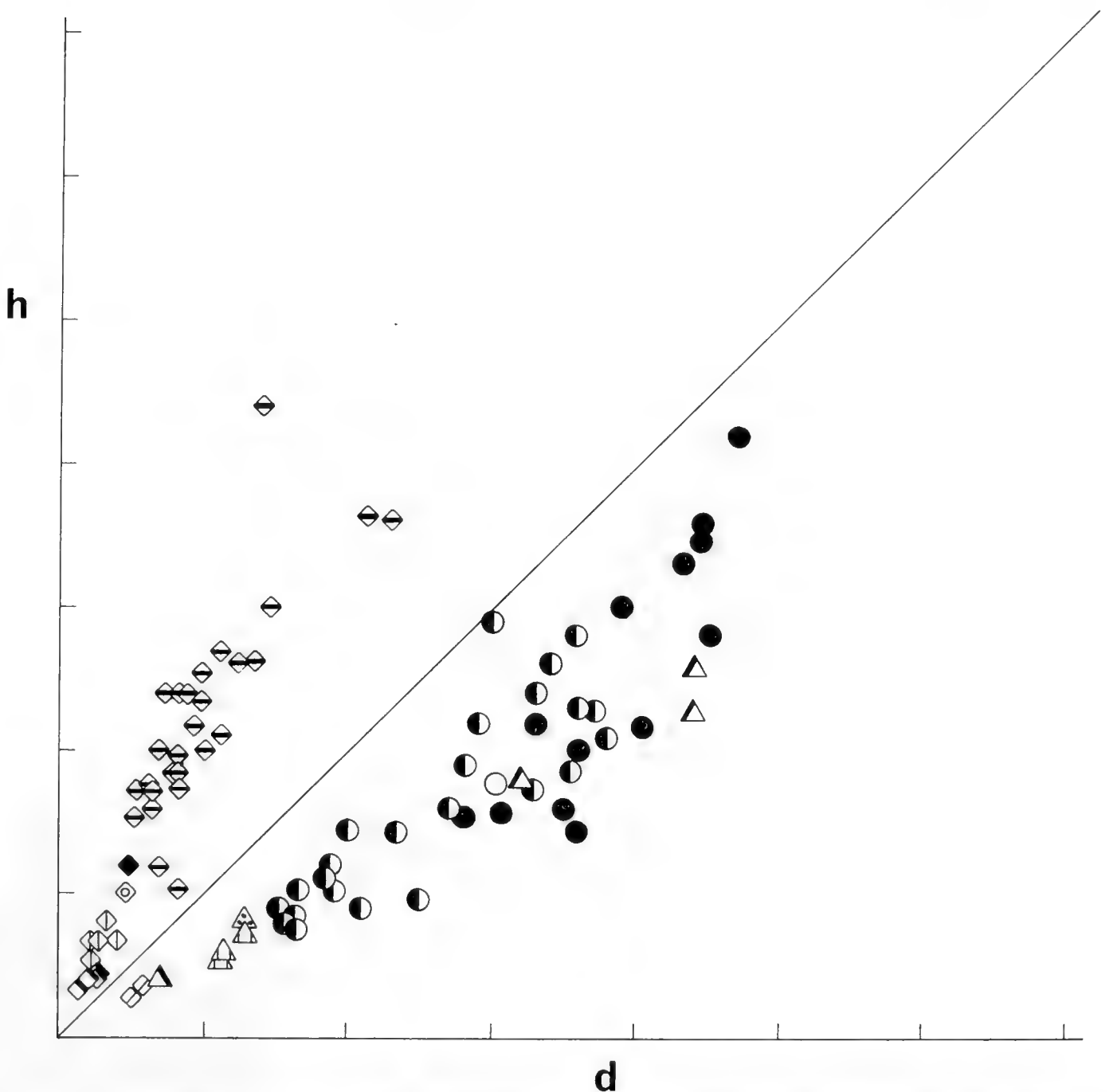


FIG. 16. Central Asian mountains (Alai, Transalaiskii; Fergana and Chatkal; Trans-Ili range and Semirech'e; Kirgizian and Talasskii ranges); h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

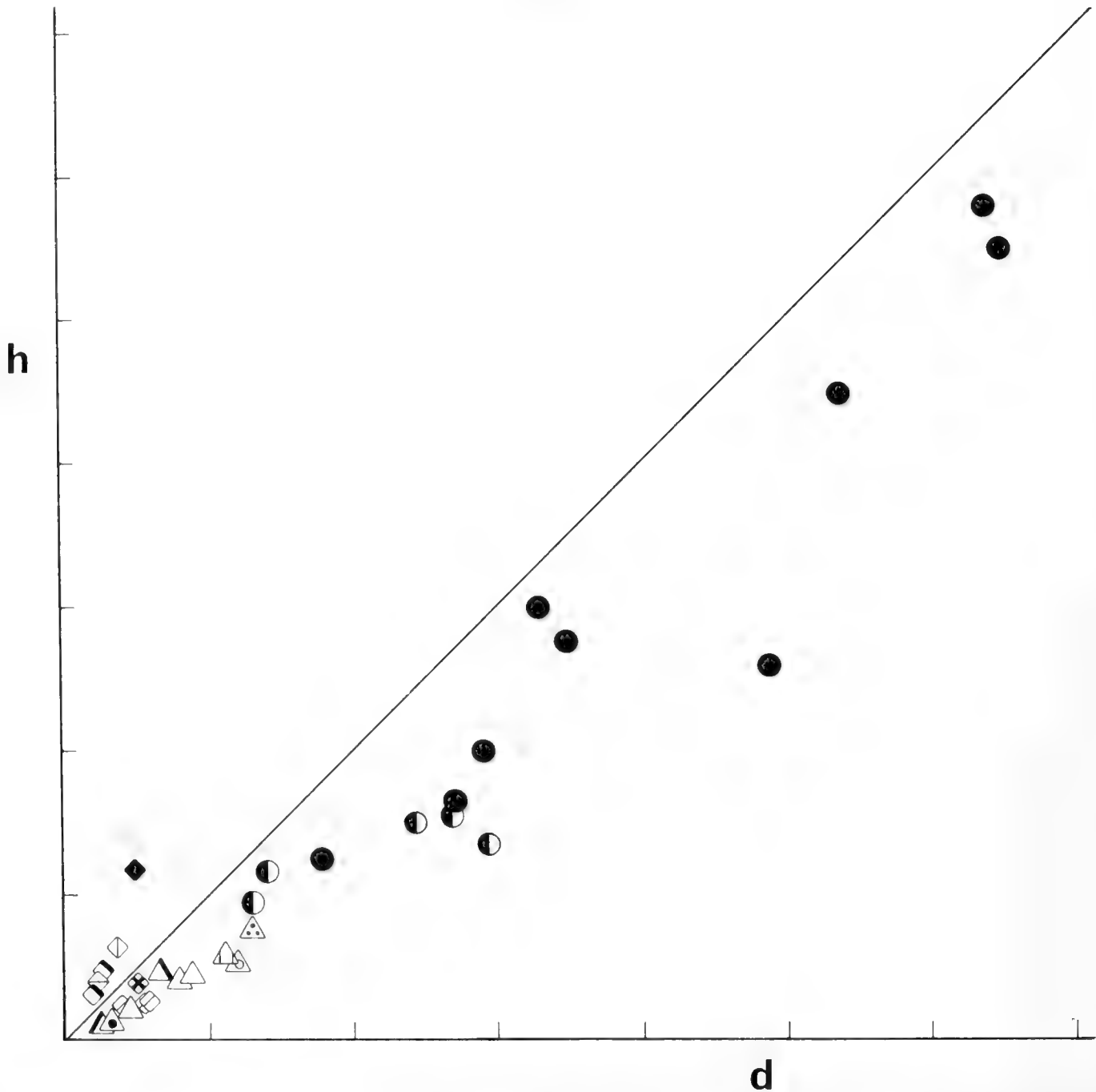


FIG. 17. Maritime Territory; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11. If *Isognomostoma subpersonatum* is a triodopsine polygyrid, the symbol at h = 4.2, d = 6.9 should be altered accordingly from hygromiine.

eastern ranges). There is an apparent overlap, in the lower scatter, of bradybaenids and hygromiines which may well be reduced if the central and eastern ranges are considered separately, or if the species' detailed habitats were known. The same might be true of the few ariophantids. The Eninae now make up most of the upper scatter (except for those small and hardy species that extend across Asia to the Pacific), and clausiliids are missing.

Near the Pacific Ocean (Fig. 17), the Maritime Territory, although with considerable mixed and deciduous forest, has apparently a poorer representation than in the Central

Asian mountains. This is especially pronounced in the upper scatter, which is very poor. Almost the same is true, however, in the case of the fauna of the cold north-eastern districts of the U.S.A., which also have an eastern continental climate with mixed coniferous and deciduous woodland.

In these last two diagrams, then, the scatters are maintained (the upper one greatly reduced in the Maritime Territory), but by means of bradybaenids, not helicids (with a few exceptions) in the lower scatter; bradybaenids (with a single exception, see Fig. 10) do not occur in Europe where the helicids are widespread, and take their place in the lower scat-

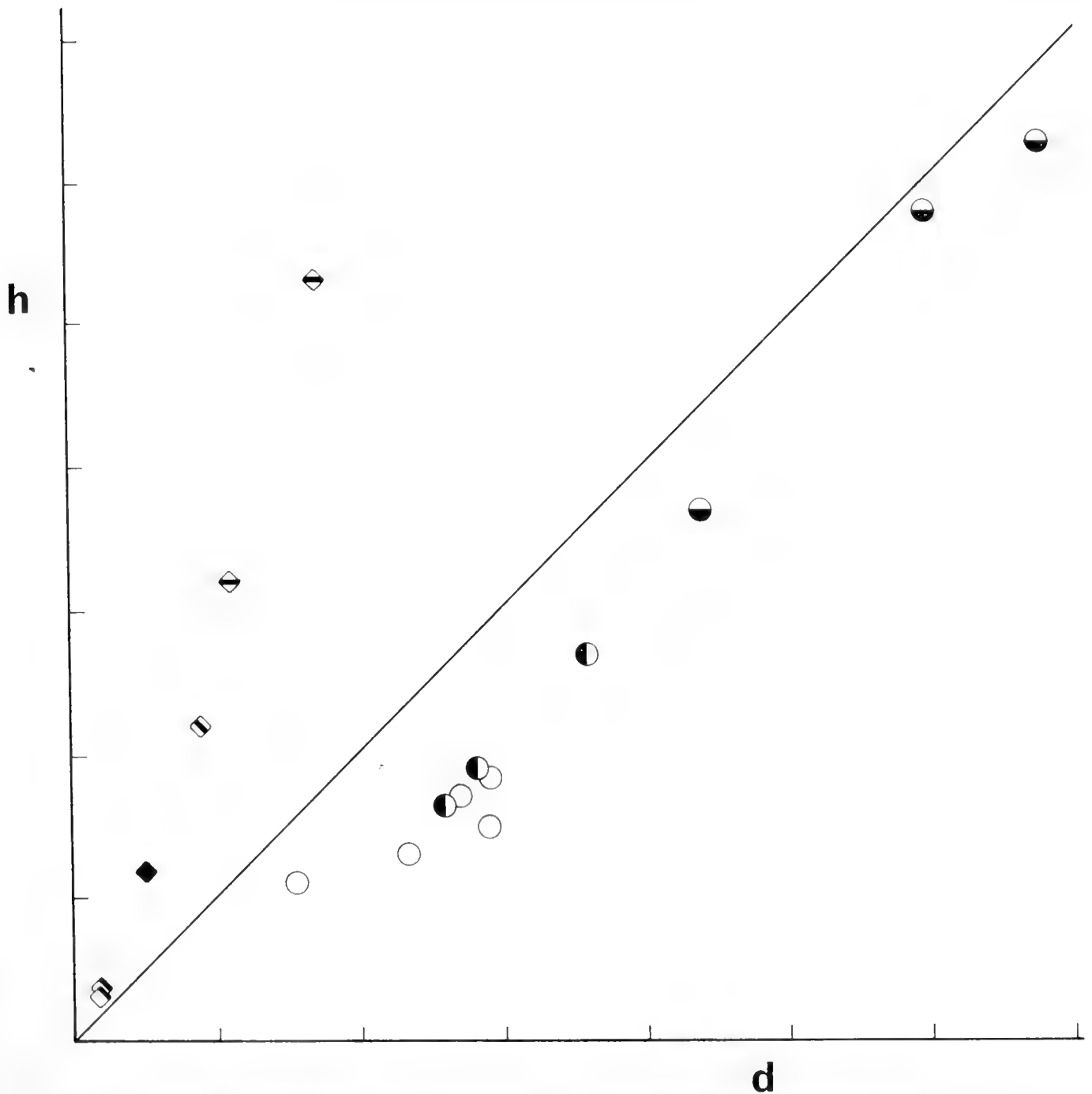


FIG. 18. European steppe; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

ter in the northern Oriental region. Here we have a replacement of one group by another, as already shown for very different groups within the North American fauna, and between the North American and European (Cain, 1977a). In the upper scatter, however, we have only the enhancement of one group at the expense of another with which it co-exists over an enormous region; it gives no grounds for distinguishing the Palaearctic from the Oriental fauna.

(d) *Tundra, steppe and forest*

In the diagrams so far, the fauna shown has contained, from the point of view of snails, a considerable forest or woodland element,

even in the Armenian and Central Asian regions along water courses. On high mountains in Europe, some woodland forms can persist in the alpine zones, or sheltered in crevices and scree, so that montane regions devoid of woodland can carry woodland species. Much of the faunal variation can be understood as a variation between woodland in a broad sense, or better, sheltered forms and open-habitat forms. The change from helicids to bradybaenids, however, appears to be due to separate development of faunas with subsequent meeting, and it is possible that the replacement of the largely European helicellines by hygromiines in the Caucasus and eastwards is so too. Likharev &

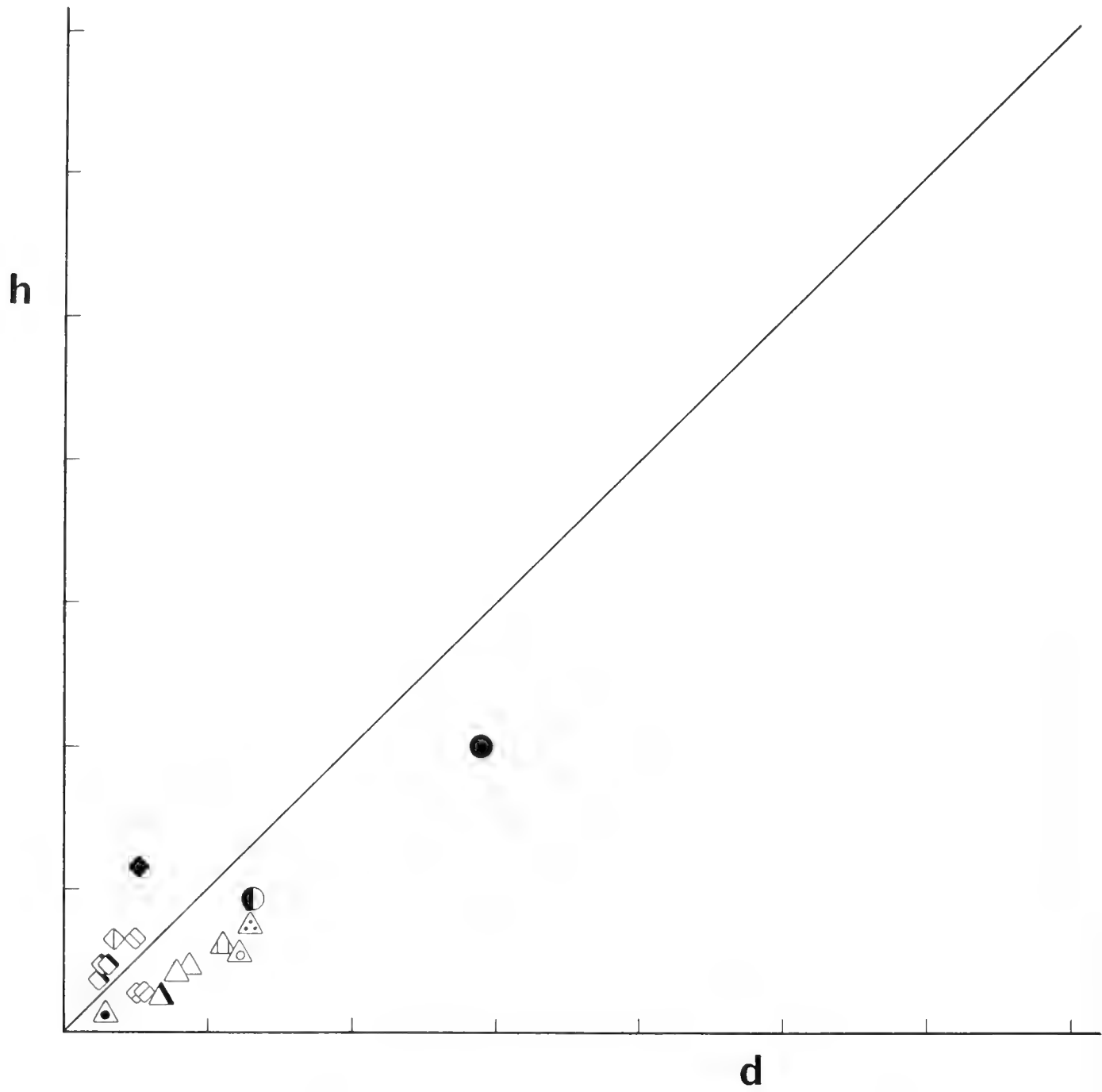


FIG. 19. Tundra; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

Rammel'meier's data (1962: 30–32, 36–37), however, allow one to go further and contrast such regions with European steppe (Fig. 18) and with tundra (Fig. 19). In both, as might be expected, the number of species is reduced as compared with more forested regions, most so in the tundra. In the steppe, the few large molluscs in the lower scatter are almost all associated with the occurrence of occasional bushes. (Many more species, as Likharev & Rammel'meier point out, penetrate along water-courses, but do not belong to the steppe as such). It is not clear whether their group of widely ranging species should occur here as well, but it is unlikely that it should not,

and it has been included in the diagram. The tundra fauna indeed, apart from the addition of a few arctic forms, is largely composed of widely-spread species, of small shell size but still showing the two scatters. Many of them appear in the diagrams given here for Europe, the Crimea and the Caucasus; a few are absent from Central Asia, and from the Far East. No species, as Likharev & Rammel'meier remark, is endemic to the tundra, nor to the steppe, and only a very few cold-adapted forms to the tundra plus taiga. (A few in the taiga belt are Siberian endemics, but with close relatives in the west.)
Generally speaking, then, at the family and

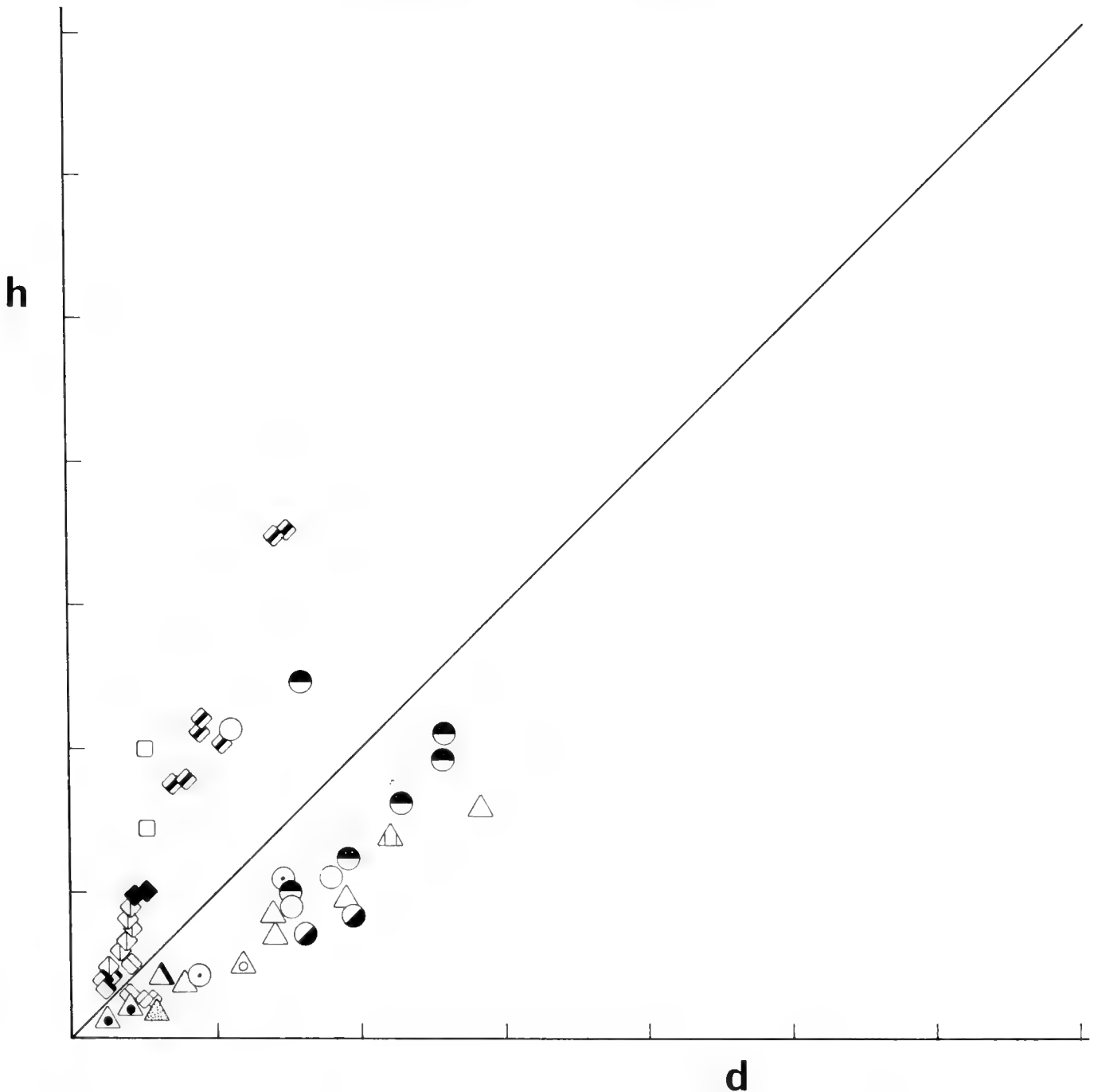


FIG. 20. Azores; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

subfamily levels, we do not find specialized faunas, each in a major climatic belt or vegetation type. We find instead a single fauna with a few very tolerant and widespread species nearly everywhere, less tolerant ones coexisting with the widespread ones in more favourable habitats, and many coming in only in woodland, or only in open habitats. The distinction between a woodland faunule and an open-country faunule is the best to be found in these regions and, as already indicated, probably accounts for a good deal of faunal variation from place to place in the diagrams.

(ii) *Macaronesia*

The Cape Verdes, Canaries, Madeira group and Azores, like other oceanic islands, are characterized by much endemism and a puzzling variation in faunal composition from one group (or even island) to the next. It is tempting to ascribe this variation simply to chance colonization. However, the island groups, although oceanic, differ considerably in climate and vegetation (now mostly destroyed), and, until a careful survey has been made of their different characteristics, it would be rash to assume that the variation is due to

nothing but chance. One cannot expect the Azores, formerly covered at lower altitudes by dense laurel forests and with lower temperatures generally (see Backhuys, 1975, for a description of their vegetation), to allow the same species arriving from Europe to survive as would the hot dry Desertas to the south-east of Madeira (Cook, Jack & Pettitt, 1972).

Very little seems to have been done on the Cape Verde fauna. That of Madeira is probably the richest, and that of the Canaries next in richness. Backhuys's excellent volume gives us an up-to-date picture of the Azores.

The land-snail fauna of Macaronesia, excluding obviously introduced forms, has only a single species of *Punctum* (Endodontidae)

that is nearctic (Backhuys, 1975: 275), the rest being all palaearctic. The degree of endemism is high. Two subfamilies of Helicidae, the Leptaxinae (about 22 species) and Geomitriinae (about 65 species) are confined to Macaronesia, the former in the Madeira group, Canaries, Cape Verdes, and Azores, the latter especially well developed in the drier areas of the Madeira group, except for a very few which occur in the Azores and one in the Canaries. In the Helicinae, one genus, *Hemicycla*, is confined to the Canaries, with about 45 nominal species. In the Helicellinae, the genus *Monilearia* with about ten species is also Canarian. The genus *Canariella* with a few nominal species (subfamily Helicodonti-

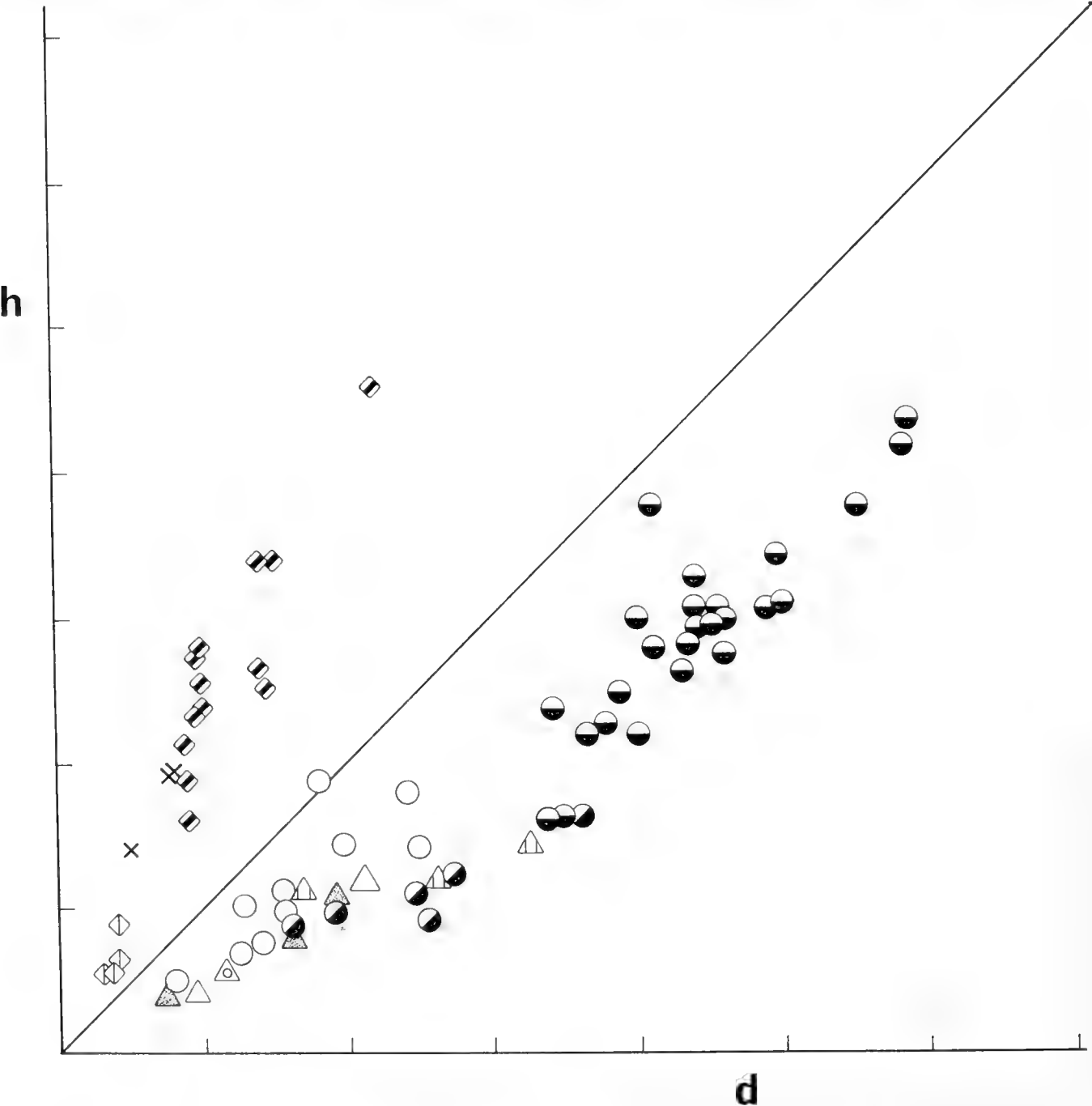


FIG. 21. Canaries; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

nae) is confined to the Canaries. One sub-genus of *Helix* consists of a single endemic species, perhaps still surviving, on Porto Santo (Madeira). A thin sprinkling of other helicids, a few of them endemic but most of them probably introduced, completes the helicid component, which is therefore very largely endemic. Even when not restricted to a single island group, the Macaronesian helicid genera very rarely have species common to more than one. Such a high degree of endemism is characteristic of oceanic islands.

No other family except the Enidae has an endemic subfamily in Macaronesia, but several genera or subgenera are confined to it or

nearly so, and the distribution of several groups that are also found elsewhere is often restricted. In the Pupillidae, the genus *Leio-styla*, also known from Europe, is widespread with numerous endemic species (Azores, Canaries, Madeira). *Janulus* (Endodontidae) is remarkable for being known fossil from Europe, and living in Madeira. There are local developments of Vitrinidae, Zonitidae (especially *Oxychilus*, Azores and Canaries; *Retinella* (*Tyrodiscus*), Canaries), Ferussaciidae (Canaries and Madeira group), Endodontidae (*Discus* in Madeira), Clausiliidae (*Boettgeria* in Madeira, *Balea* in the Azores). Perhaps most conspicuous is the development of the

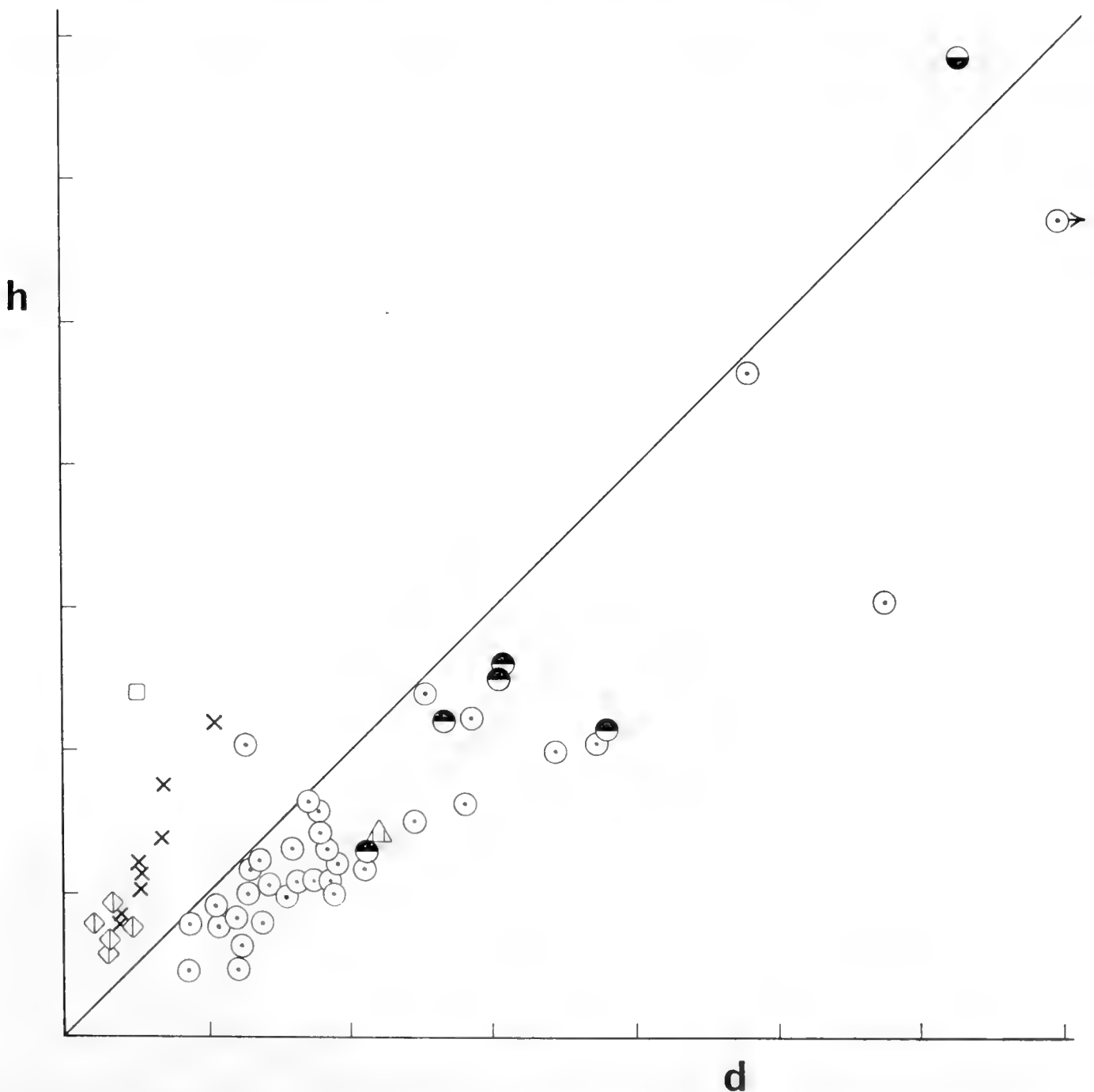


FIG. 22. Porto Santo, Madeiran Archipelago; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

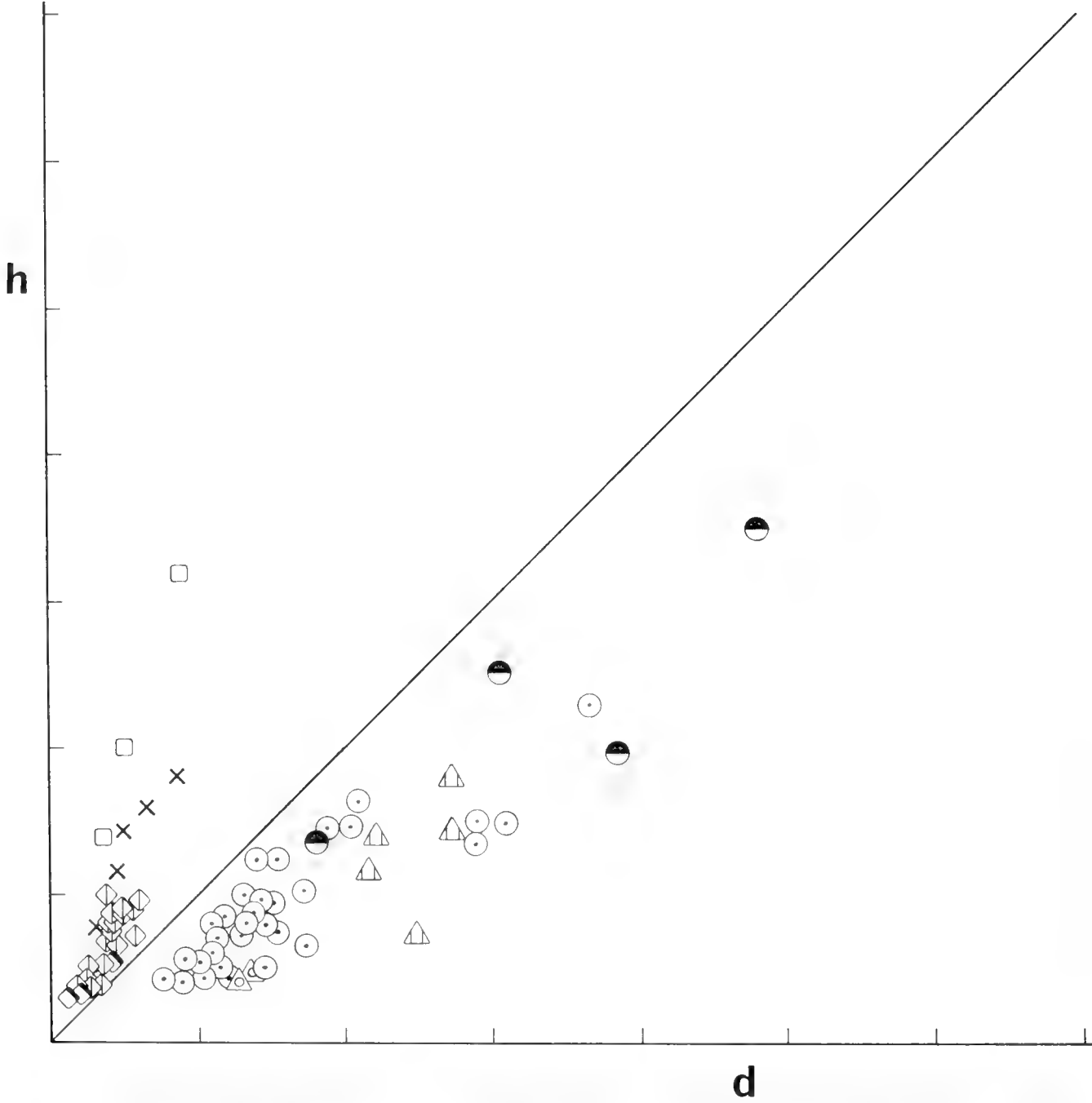


FIG. 23. Madeira and the Desertas; h, d scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

endemic genus *Napaeus* (Enidae, Napaeinae), which may or may not merit subfamily rank, in the Canaries (about 40 nominal species) and Azores (7 species) and perhaps Cape Verdes (one species) but totally absent from the Madeira group (Wollaston, 1878; Backhuys, 1975). This genus is known fossil from Europe; other European fossils have been ascribed to the Leptaxinae and Geomitrinae, perhaps not very securely. Certainly, Macaronesia may well preserve a number of forms that have become extinct in Europe, more intolerant members of an ecological group still represented in extreme western Europe by the lusitanian element of the pulmonate fauna.

For completeness it should be mentioned also that the land operculates include one archaeogastropod (*Hydrocena gutta*, Azores and Canaries, nearest relative in Dalmatia), an endemic subfamily of mesogastropods (Craspedopomatinae, with about five species in the Canaries, Madeira group, and Azores, and nearest relatives in the tropics), and a few species of the European mesogastropod *Pomatias* in the Canaries).

The diagrams (Figs. 20–24) show clearly the very different composition of the faunas of each island group, even of the Cape Verdes, which are poorly known and not recently revised. In the upper scatter, the napaeines of the Azores and Canaries contrast with the

clausiliids of the Madeira group. In the lower scatter, the leptaxines of the Azores, Cape Verdes, and Madeira group are replaced by the helicine *Hemicycla* in the Canaries, in which scatter the lower part is formed by *Monilearia* (helicelline), not as in the Madeira group by geometritines. In short, we still have the same two scatters but made up in very different ways. While the differences in the lower scatter are not as great as those between Europe and the Maritime Territory, they are greater than between many of the other regions or districts investigated, and those in the upper scatter are largely the same as between the clausiliid-rich regions of Europe and the Caucasus, and the enid-rich Central

Asian mountains, although using a different subfamily of the Enidae. Nevertheless, throughout we still get a good approximation to the same two scatters as are seen in western Europe and other parts of the world.

DISCUSSION

This investigation shows the maintenance of a bimodal distribution of *h* and *d* among land stylommatophorans fully retractable into their shells, from the Macaronesian islands through Europe and Central Asia to the Maritime Territory. Yet, as already indicated for western Europe as against North America

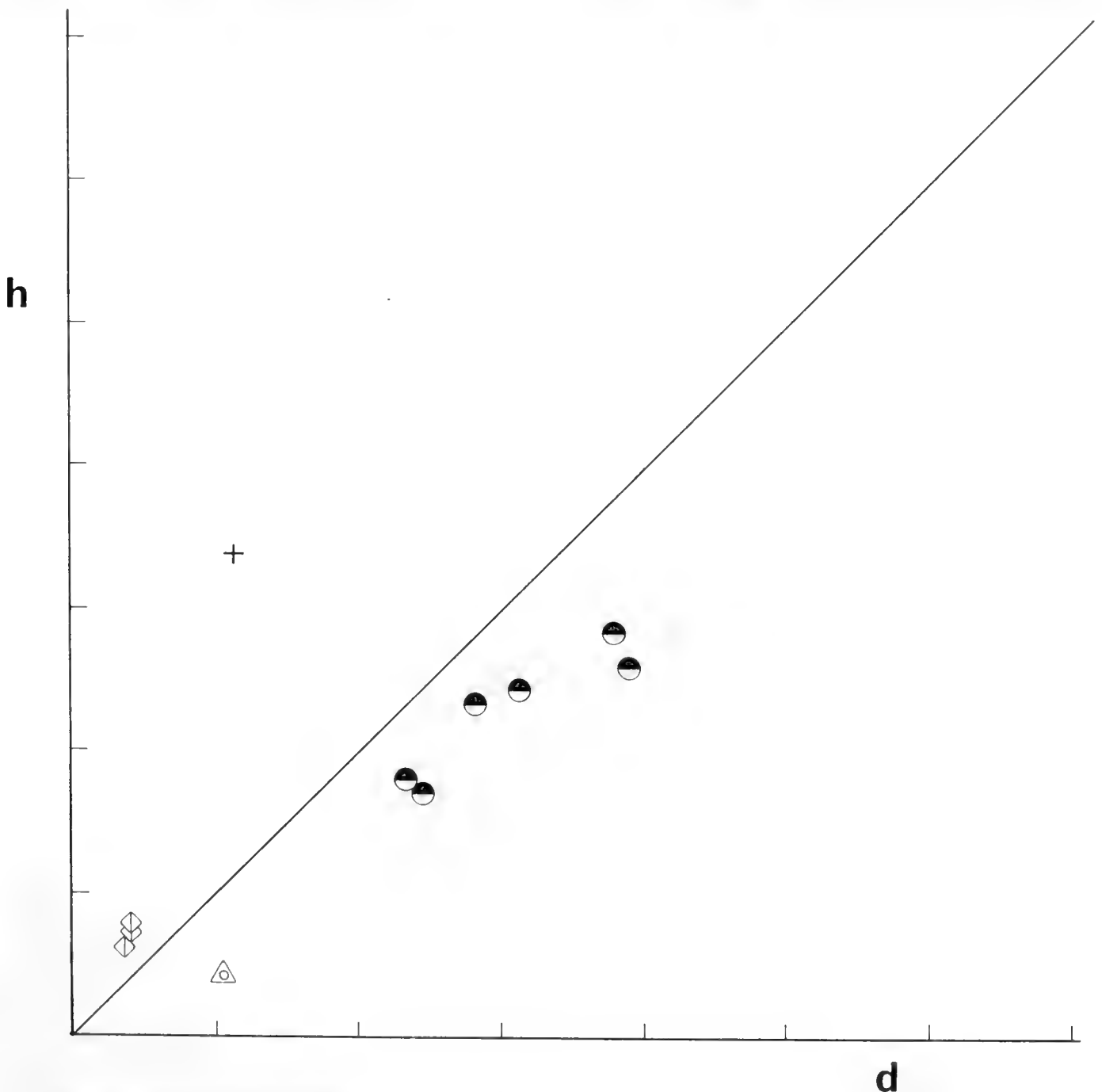


FIG. 24. Cape Verde Islands; *h*, *d* scatter diagram for the pulmonate fauna. Symbols as in Fig. 11.

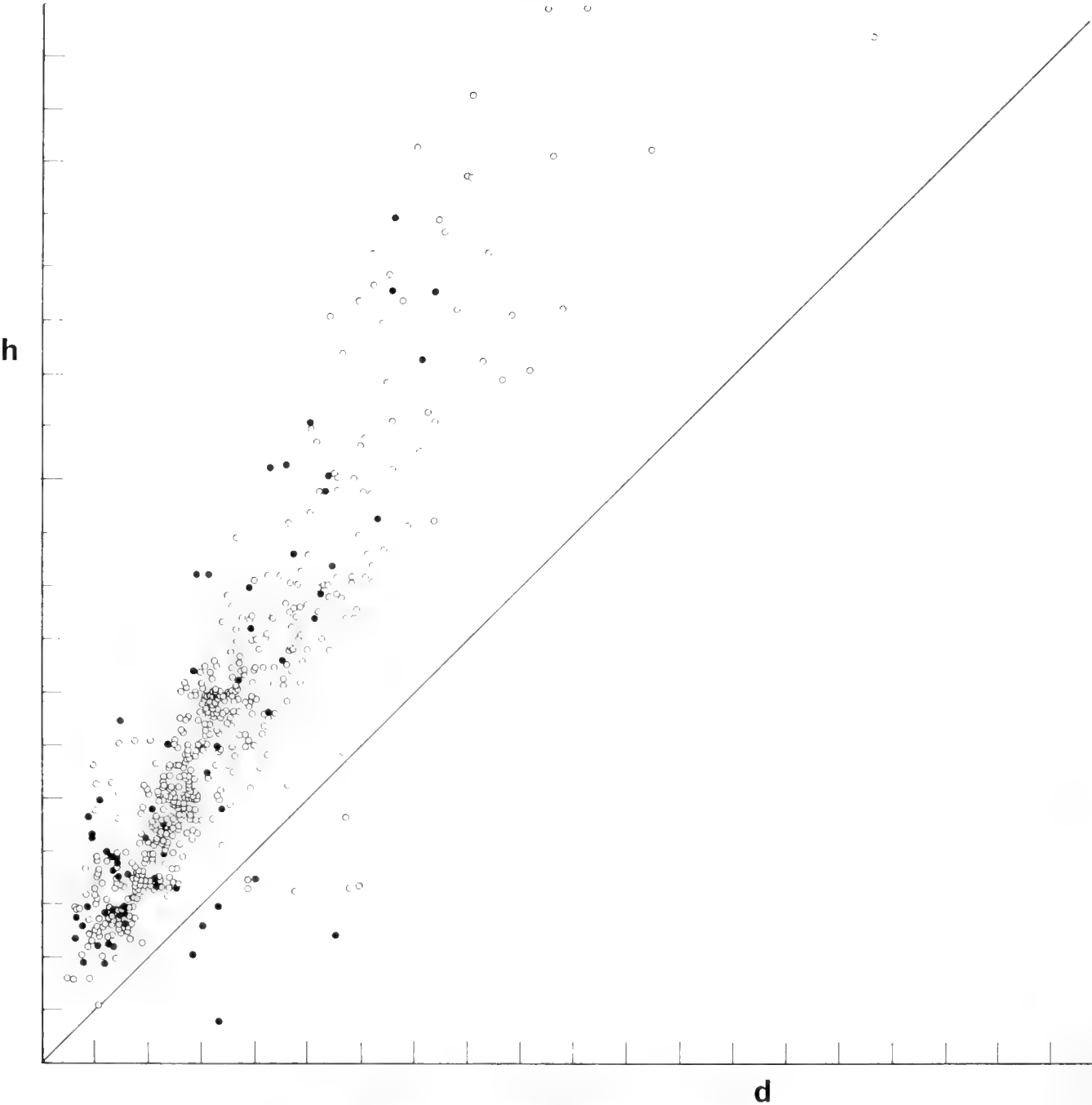


FIG. 25. Bulimulidae; h, d scatter diagram. Symbols as in Fig. 1.

(Cain, 1977a), the compositions of the two scatters can vary remarkably from region to region. In the present examples, an extreme case is the replacement of the Helicidae in the lower scatter by Bradybaenidae in the Central Asian mountains and the Maritime Territory; lesser examples are given in the different ways the lower scatter is made up in different island groups of Macaronesia. Variation in the upper scatter in continental regions seems largely related to difference in available habitats in different regions; it cannot be said yet that this is not so in Macaronesia. Even in the apparently straight-forward case of the helicids and bradybaenids the interpretation is

far from simple. At first sight, what has happened is obvious; during the extremer periods of the glaciations much of Central Asia must have been a dry desert with very little life, and an enormous stretch of country must have separated the Helicidae in the western Palae-arctic and the Bradybaenidae in the Far East. Each family adapted to local conditions (very successfully, considering the numbers of species in each) including the same range of habitats in both. When conditions ameliorated, each spread out from its refuge areas, together with the advancing vegetation. There is now a confrontation of ecologically similar forms in the central Asian region, but a few

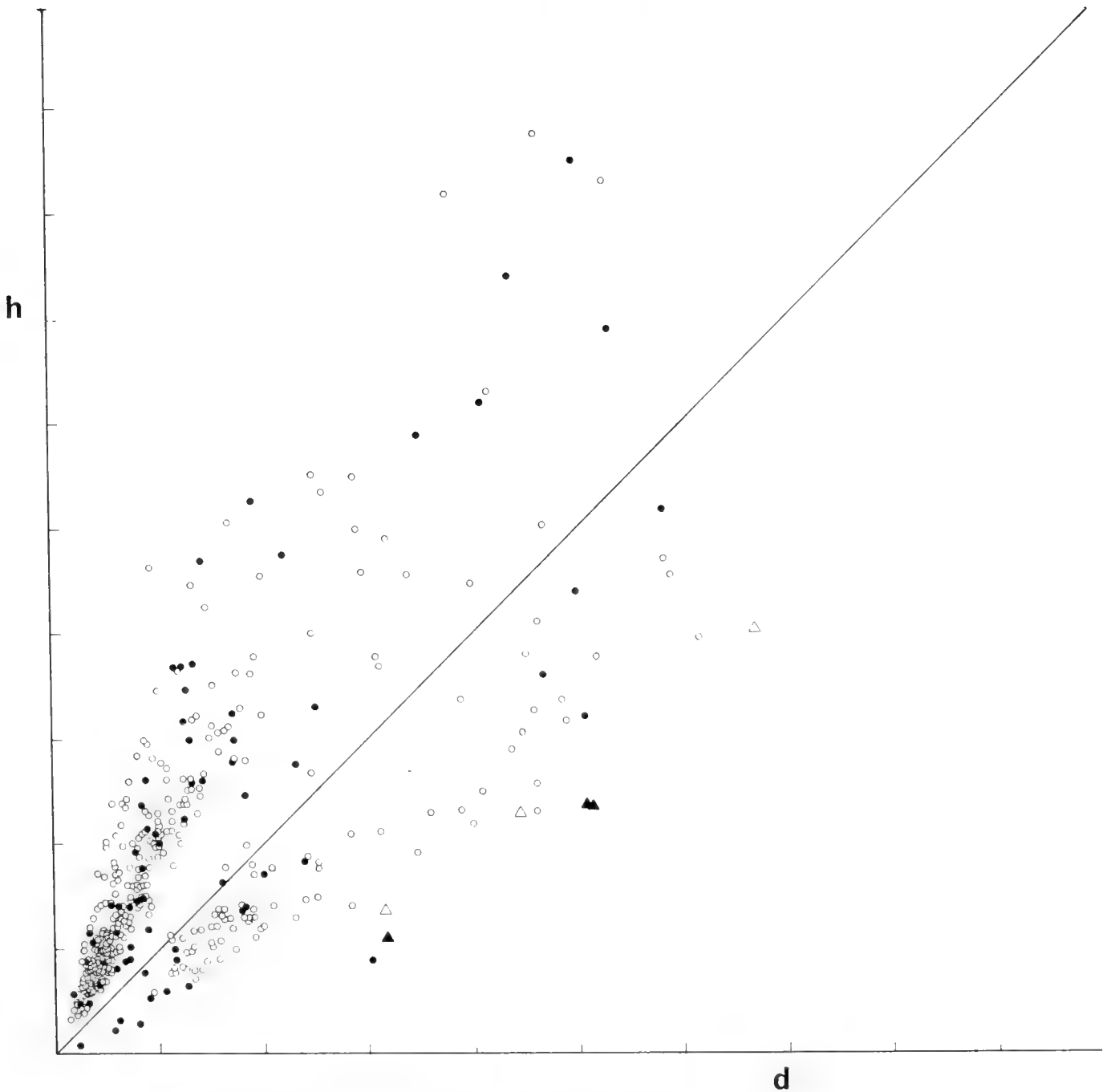


FIG. 26. Streptaxidae; h, d scatter diagram. Symbols as in Fig. 1.

species on either side, no doubt being specialized in particular ways, are able to invade new territory, the helicid *Zenobiella* reaching the Pacific and *Bradybaena fruticum* coming as far west as eastern France. In course of time there will be further spreading, with elimination of unfit forms; as most malacologists refer to the Helicidae as the 'highest' evolutionarily of the stylommatophoran snails, no doubt in the end they will win.

This explanation is plausible but doubtful. In the first place, the Maritime Territory, although maritime, has a continental climate, as does the corresponding area in the New World, the north-eastern United States and Nova Scotia.

The climate of western Europe is far more oceanic, and resembles in the northern hemisphere that of coastal British Columbia, with the difference that the oceanic influence spreads inland all over Europe, whereas the great barrier ranges running north and south in the western United States and Canada cut it off abruptly closer to the west coast. There is a gradient in increasing continentality from western Europe right across to the Stanovoi Range, reversing only slightly from there to the Pacific coast. It is at least as arguable that the helicid/bradybaenid border is stationary precisely where *each* type becomes inferior to the other. In that case, the present distribution

is a consequence of present ecological conditions, not of past history, and the replacement in the lower scatter may be as direct a consequence of present-day ecology as is, with high probability, the replacement in the upper one.

In the second place, the argument really assumes that any group, while retaining its characteristic features, can adapt to any local ecology possible at all for that general type of animal and therefore that since helicid snails occur from the deserts of northern Africa to the alpine meadows of Scandinavia, and from the steppes of southern Russia to the extreme Atlantic climate of Ireland or the Azores, they could equally well occur in China, if history had allowed. The helicids are distinguishable from the bradybaenids chiefly on the genitalia. In the Bradybaenidae the mucus glands are not long and branched as in most helicids, and they open directly or indirectly into the dart-sac, not independently into the uterus. The physiological significance of these differences is wholly unknown.

Many secondary sexual characters—the shape of the dart in helicids, the shape and number of the genital chaetae in oligochaetes, the various chitinous processes, claspers, plates, combs and bristle patches in the genitalia of many insects, the courtship dances of different species of sticklebacks, and the courtship songs of many birds, to cite a few examples—seem to be wholly arbitrary signals, closely similar in closely related forms but with one or two different and specific features. If they really are signals, not subject to selection in relation to differences in the species' mode of life, then they may be the best indicators of phyletic relationship we have (Cain, in prep.). In that case, they may indeed be purely historical records in the present example; as a matter of history, Europe and the Far East were separated for a long period by dry cold desert, and helicids with their peculiar genitalia developed into their present adaptive radiation in the west, bradybaenids in the east. Had the course of ecological history been different, we might now have the middle of the lower scatter made up by helicids and the outer part of it by bradybaenids (or vice versa) from the Atlantic to the Sea of Okhotsk. If the characters of the genitalia are not arbitrary, however, and do have some functional significance other than as signals, the possibility remains that the helicid pattern is adapted to the milder conditions of the west, the

bradybaenid to the harsher ones of the east. Remote though this possibility may seem, it cannot be ignored.

These considerations may apply to the hygromiine radiation in the Caucasus and eastward and to the helicelline radiation in southern Europe, but with the complication that the helicellines are a polyphyletic group derived from the hygromiines. Shileyko (1978b) remarks that the dull-coloured, rather fragile and often hirsute hygromiines of Europe are largely forest forms, while the more solid, less often hirsute, and sometimes more brightly patterned forms are in dryer habitats. He points out a characteristic rock-living facies with more or less flattened and ribbed shells occurring in Caucasian forms and probably independently in a European species. Correspondingly, in coastal regions of the Mediterranean, with its hot rainless summers, helicid snails that sit out exposed to the hot sun (helicellines, sphincterochilines, and the taxonomically difficult helicine *Theba pisana*) have rather solid shells, often very white and frequently strikingly patterned with black or yellow bands. Such a facies is clearly associated with particular habits and may very well have evolved several times over. Some helicellines penetrate far into northern Europe, and one or two have even become hirsute and hygromiine-like in habits, for example *Xerotricha conspurcata* (Germain, 1930), a reversal of the evolutionary trend. If the special characters of the genitalia are again phylogenetically rather conservative, then assemblages of species defined on the genitalia will be monophyletic, those on other characters will not, and the sort of analysis given by Shileyko (1978b) enables us to trace out minor or local adaptive radiations.

In our present state of ignorance of the detailed habits of most land-snails, little can be said of one of the most interesting features of the family Helicidae, which is its several independent excursions into the upper scatter. As remarked above, several of the helicellines involved, especially the genus *Cochlicella*, live in coastal sand dunes and other maritime habitats. Here, they do not coincide with clausiliids and enids, and it is possible that they are the substitutes in these habitats for the usual Palaearctic tall-shelled families.

A suggestion for future investigation may perhaps be made for the high-spined leptaxine in the Azores, *Helixena sanctaemariae* of Santa Maria. This species was formerly placed in *Napaeus* (Enidae) but

Backhuys (1975) showed by dissection that it is a leptaxine (Helicidae). Of the four species of *Leptaxis* in the Azores of which living specimens are known, excluding one certainly introduced, *L. azorica azorica* occurs on São Miguel, Faial and Flores, *L. azorica minor* on Santa Maria, *L. caldeirarum* on São Miguel (and perhaps Faial), *L. drouetiana* on Faial, and *L. terceirana* on Terceira. (One recently extinct species, *L. vetusta* is known from Santa Maria and one species, *L. niphas*, only from the type collection from São Miguel). The present distribution is therefore with a subspecies of *azorica* or a related species (*terceirana*) on all the large islands except São Jorge, and with a second species on São Miguel (*caldeirarum*) and Faial (*drouetiana*). Backhuys (1975: 234, 246) reports *L. azorica minor* "In more or less primary woods on the slopes of the mountains (Pico Alto)," and *H. sanctaemariae* "in woods along dead leaves, under logs, under stones, etc." For *Napaesus*, he refers to a forthcoming paper which will provide ecological data, but his distribution records show that there are three on Santa Maria (one of them also in the Canaries, a rare example of inter-island-group distribution of a species), four on São Miguel and Terceira, and three on Faial and Flores. It is just possible, therefore, that *H. sanctaemariae* on Santa Maria is replacing a napaene rather than a leptaxine ecologically. Available studies on *Cylindrus obtusus* (Fuchs, 1926; Adensamer, 1937; Klemm, 1961; Backhuys, 1969) give no indication of its mode of life relative to other forms. It is just possible that it is a high-altitude form complementing the enids; the data given in Adensamer's paper (1937) do not rule this out. Nothing seems to be known of the habits of *Discula turricula*.

Although the family Helicidae is the most variable in h, d in the Palaearctic region, it is much less variable than others elsewhere. The total scatter for the Bulimulidae is shown in Fig. 25. This family is most variable in Central and South America, its outliers in Melanesia and Western Australia being all tall-shelled. It crosses the bisector much further than do the helicids. The ecological circumstances under which it does so are not known; but it certainly coincides with the Camaenidae which occupy much of the lower scatter, and probably restrict its variation below the bisector. The Bradybaenidae, mainly lower-scatter, have a number of very tall-shelled

species in China, Korea and Taiwan, and in the Philippines (Cain, 1978a) occurs a subfamily of large shells, the Helicostylinae which ranges from discoidal to tall with no interruption. Fig. 26 gives the scatter for the carnivorous Streptaxidae, which are equally distributed in both scatters but do, in general, preserve the gap between the scatters. No analysis of them by faunas has yet been made. The Camaenidae are of special interest in having a disjunct distribution. In Central and South America they coincide with the Bulimulidae (Fig. 25) and there they occupy entirely the medium-sized to large-sized shells' area of the lower scatter—effectively acting like medium to large helicids. In south-east Asia and northern Australasia, however, they coincide with a few very tall slender species (Clausiliidae, Megaspiridae, Subulinidae) but with no tall stout ones of other families; they themselves fill in the vacant area with the genus *Amphidromus* in south-east Asia (Cain, in prep.) and with various tall shells belonging to the subfamily Papuininae in the New Guinea region (Cain, 1978a).

If, then, variation in h, d can itself vary from family to family, and, within a family, from region to region according to the others that are present, it seems likely that the comparative constancy of the family Helicidae to the middle and outer areas of the lower scatter is because it is usually accompanied by a sufficient suite of outer families to fill up the rest of the two scatters. That there is nothing inherent in being a helicid which restricts it is shown by the occurrence of the various tall-shelled helicid species. If they had not been there, presumably helicids could have filled the whole range, as the streptaxids do. But if this is so, presumably the enids, or clausiliids could equally have done so, given the ecological opportunity. How, then, did these families come together in the first place and share out the ecological opportunities in the way we see now?

ACKNOWLEDGMENTS

I am grateful to Dr. G. M. Davis and Dr. R. Robertson for criticism of this paper. I thank most especially H. Wallace and Carol Roberts of Philadelphia, without whose delightful and discriminating hospitality I could not have done much of the work for it.

LITERATURE CITED

- ADENSAMER, W., 1937, *Cylindrus obtusus* (Draparnaud, 1805), seine reliktische Verbreitung und geringe Variabilität, sowie zoogeographische-phylogenetische Betrachtungen über alpine Mollusken überhaupt. *Archiv für Molluskenkunde*, 69: 66–114, pl. 4.
- BACKHUYS, W., 1969, The elevation effect in *Cylindrus obtusus* (Draparnaud 1805). [Abstract.] *Malacologia*, 9: 251–252.
- BACKHUYS, W., 1975, *Zoogeography and taxonomy of the land and freshwater molluscs of the Azores*. Backhuys & Meesters, Amsterdam, xii + 350 p., 97 fig., 32 pl.
- CAIN, A. J., 1977a, Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Philosophical Transactions of the Royal Society of London, Ser. B, Biological Sciences*, 277: 377–428.
- CAIN, A. J., 1977b, The uniqueness of the polymorphism of *Cepaea* (Pulmonata: Helicidae) in western Europe. *Journal of Conchology*, 29: 129–136.
- CAIN, A. J., 1978a, Variation of terrestrial gastropods in the Philippines in relation to shell shape and size. *Journal of Conchology*, 29: 239–245.
- CAIN, A. J., 1978b, The deployment of operculate land snails in relation to shape and size of shell. *Malacologia*, 17: 207–221.
- CAIN, A. J. & COWIE, R. H., 1978, Activity of different species of land-snail on surfaces of different inclinations. *Journal of Conchology*, 29: 267–272.
- CAMERON, R. A. D., 1978, Differences in the sites of activity of coexisting species of land molluscs. *Journal of Conchology*, 29: 273–278.
- COOK, L. M., JACK, T. & PETTITT, C. W. A., 1972, The distribution of land molluscs in the Madeiran Archipelago. *Boletim do Museu Municipal do Funchal*, 26(112): 5–30.
- DANCE, S. P., 1970, "Le fanatisme du nobis": a study of J.-R. Bourguignat and the "Nouvelle école." *Journal of Conchology*, 27: 65–86.
- FUCHS, A., 1926, Über die Verbreitung von *Cylindrus obtusus* Drap. *Archiv für Molluskenkunde*, 58: 83–86.
- GERMAIN, L., 1930, *Faune de France 21. Mollusques terrestres et fluviatiles (première partie)*. Lechevallier, Paris, p. 1–477.
- KLEMM, W., 1961, Fortführung der Numerierung der Fundorte von *Cylindrus obtusus* (Draparnaud). *Archiv für Molluskenkunde*, 90: 43–49.
- LIKHAREV, I. M., & RAMMEL'MEIER, E. S., 1962, *Terrestrial mollusks of the fauna of the USSR*. Israel program for scientific translations, Jerusalem, p. [iv+] 574. (English translation of LIKHAREV, I. M. & RAMMEL'MEIER, E. S., 1952, *Nazemnye mollyuski fauny SSSR*. Izdatel'stvo Akademii Nauk SSSR, Moscow and Leningrad).
- MANDAHL-BARTH, G., 1943, Systematische Untersuchungen über die Heliciden-Fauna von Madeira. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Abhandlung* 469: 1–93, 17 pl.
- NOBRE, A., 1931, *Moluscos terrestres, fluviais e das águas salobras do Arquipélago de Madeira*, Instituto de Zoologia da Universidade do Pôrto, Pôrto, p. [1]–208, 4 pl.
- SHILEYKO, A. A., 1978a, *Nazemnye mollyuski nadsemeistva Helicoidea*. Fauna SSSR novaya seriya no. 117, Mollyuski vol. 3 part 6. Akademiya Nauk SSSR Zoologicheskii Institut. 'Nauka' Leninradskoye Otdelenie, Leningrad. (In Russian).
- SHILEYKO, A. A., 1978b, On the systematics of *Trichia* s. lat. (Pulmonata: Helicoidea: Hygromiidae). *Malacologia*, 17: 1–56.
- TAYLOR, D. W. & SOHL, N. F., 1962, An outline of gastropod classification. *Malacologia*, 1: 7–32.
- THIELE, J., 1931, *Handbuch der systematischen Weichtierkunde* 1, Gustav Fischer, Stuttgart; reprinted 1963, Asher, Amsterdam. p. [viii+] 778.
- WATSON, H., 1943, Notes on a list of the British non-marine Mollusca. *Journal of Conchology*, 22: 13–22, 25–47, 58–72.
- WOLLASTON, T. V., 1878, *Testacea atlantica, or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. Reeve, London, 588 p.

CLINES, CONVERGENCE AND CHARACTER DISPLACEMENT IN NEW CALEDONIAN DIPLOMMATINIDS (LAND PROSOBRANCHS)

Simon Tillier

Laboratoire de Biologie des Invertébrés marins et de Malacologie, Muséum national d'Histoire naturelle, 55, rue Buffon, F-75005 Paris, France

ABSTRACT

Eleven diplommatinid species, seven of them previously undescribed, are found in New Caledonia and adjacent islands. Two species are endemic to the adjacent islands, and the nine New Caledonian mainland species show varying degrees of endemism. Up to three species were found to be sympatric. These diplommatinids occur from 0 to 1000 m in elevation, in very dry to very wet environments. All the species live in more or less decomposed leaf litter.

Species vary considerably in both shell size and shape, and form a continuum of shell characters. In many cases the species can be distinguished only by their anatomy. Except in cases of species interaction, shell shape is correlated with moisture. Species exhibit clinal variation in shell characters that are related to environmental conditions. Shell characters overlap when species are allopatric, and diverge when sympatric. This type of character displacement is so common that the clinal variation could be interpreted to be the result of species interaction on a large scale.

The female genital apparatus exhibits four evolutionary steps in a process which may be either the acquisition or the loss of a seminal receptacle. This process probably occurred many times in the diplommatinid stock. Added to this the probable convergence of shell characters makes the value of supraspecific names dubious.

INTRODUCTION

The original purpose of this study was to discriminate among and accurately describe the New Caledonian species of the family Diplommatinidae, which were poorly known from only a few samples of shells collected at the end of the last century. Sorting out the species of these very small land prosobranchs, one to four millimeters high, was in fact very difficult. It is always easy to distinguish several species when they occur together and in a small number of samples. However, the more than one thousand shells collected in fifty-six New Caledonian localities form nearly a continuum in shell characters. It became obvious that the shell characters used for discriminating species since Kobelt's revision (1902) are inadequate to describe species and supraspecific groups. This study attempts only to address the problems at the specific level. The problems at the generic and suprageneric level, in particular the definition of genera and the history of the group from a biogeographical point of view, cannot be solved without much more data. Accordingly, supraspecific levels will be treated only superficially.

This study is based on two main ideas: 1)

the female genital anatomy is less variable than other characters, and allows one to recognize to which species an animal belongs; all other characters can be convergent; 2) Peake's observation (1973) that sympatric species do not overlap morphologically proved particularly useful and stimulated my search for character displacement and analyses of clines.

Diplommatinid distribution and nomenclature

Since Tiecke (1940) established his classification of the superfamily Cyclophoracea, the family Diplommatinidae (= Tiecke's Cochlostomatidae: Solem, 1959) is divided into two subfamilies: the Cochlostomatinae of Europe and the Diplommatininae, which are mainly east Asian and possibly include the doubtfully attributed South American *Adelopoma*. In the western Pacific region, the Diplommatininae occur in Japan, the Marianas, Caroline, Palau, Bismarck, Solomon, Fiji, Samoa and Tonga islands, and reach Norfolk and Lord Howe islands and eastern Australia (Solem, 1959: fig. 17). Most genera are relatively well defined on the basis of their shell characters, but this is not the case in the *Diplommatina-Palaina* group to which all the

southern species belong, including the New Caledonian ones. Rensch (1929) and Van Benthem Jutting (1948) considered that the presence of an apertural tooth characterizes *Diplommatina*, but the study of some Solomon Island species (Solem, 1960b; Tillier, unpublished) and of New Caledonian species (this study) shows the insignificance of this character in taxonomy, even at the specific level. Although Peake (1973) relegated Solomon islands species to *Diplommatina*, *Palaina* is used here for New Caledonian species (as was done by Solem (1959) for New Hebridean ones) for the sole reason that the type-species of *Palaina* is found to be geographically much closer to New Caledonia than the type-species of *Diplommatina*. This choice is arbitrary and does not allow any conclusions about relationships within the group. At least *Palaina macgillivrayi*, which is the type-species from Lord Howe Island, does not seem incompatible in any character with New Caledonian species with reference to the generic level (Figs. 1, 2).

Kobelt & Moellendorff (1898) and Iredale (1937, 1944, 1945) used shell shape as a supraspecific character within *Palaina* (names listed by Solem, 1959). This study shows that this character cannot be considered diagnostic before all data concerning the variability of the species have been compiled. As comprehensive data are not available for most species, no subgeneric groupings are used here.

Habitat and dispersal

All New Caledonian species are in the leaf mould during the day. They are almost always found at ground level. In only one of the fifty-six collecting localities were they found in humus accumulated at the bases of *Pandanus* leaves. The wetter the environment is, the more they are dispersed in the litter. When the environment dries they tend to concentrate where humus retains moisture, i.e., in decaying wood interstices or in a very small wetter surface of the litter. This pattern probably explains why the most important samples here studied were collected in relatively dry conditions. This need for wet humus may explain why the snails are mostly found in forest, but occasionally they are found in maquis, particularly in the northernmost part of New Caledonia, where the latter provides sufficient plant cover. When several species are found together, field observations do not show any

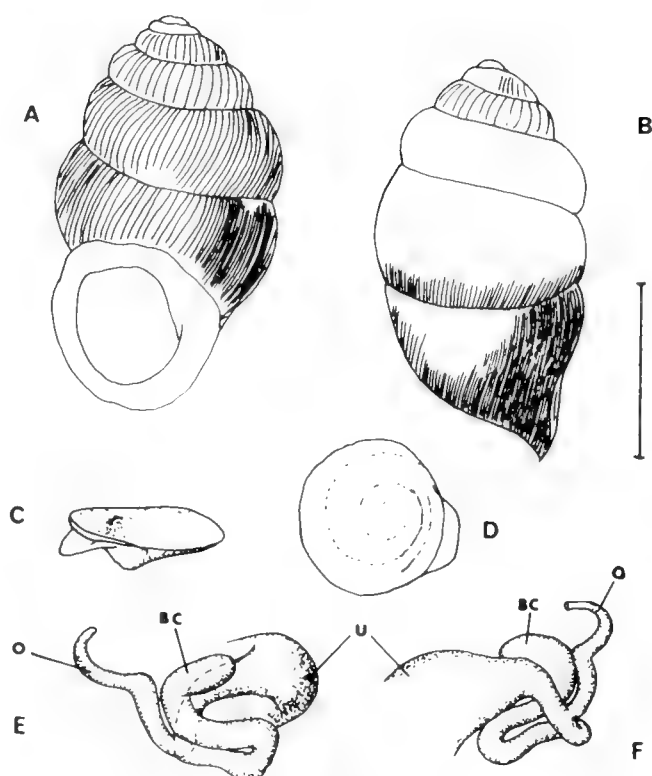


FIG. 1. *Palaina macgillivrayi*, Mt. Gower, Lord Howe Island, 820 m, AMS-C 191369. A and B, shell; C and D, operculum; E and F, female genitalia. Scale line, A and B, 2.5 mm, C, D, E and F, 1.25 mm. BC, bursa copulatrix; O, oviduct; U, uterus.



FIG. 2. Radula of *Palaina macgillivrayi*, same animal as Fig. 1. Scale line 0.025 mm.

kind of specialization. Although no accurate test was made, it seems that sampling in a very small surface ($\pm 400 \text{ cm}^2$) in a wet environment gives the same proportions of species as sampling in a larger surface (i.e., a few square meters). In fact, ecological differences among species have been detected only by statistical analyses of environmental variables at each station.

Data concerning the collecting stations are given in Table 1 and Fig. 7. One sees that *Palaina* was not collected in Ouvéa and Lifou. It is possible that we failed to collect them, but it is also possible that *Palaina* has not yet col-

onized them; these two islands are the most recent in the New Caledonian archipelago. On the mainland no *Palaina* was collected higher than 1000 m, and we have collected enough at such altitudes to interpret the absence of *Palaina* as significant. The high altitude stations are wetter and colder than those supporting *Palaina*, but it may also be remarked that in New Caledonian high altitude rainforest, vegetation decays much more slowly than elsewhere. As a result there is an absence of real humus which could be a limiting factor for *Palaina*.

Peake (1968, 1969, 1973) postulated that passive transport was the most important factor in the dispersal of small land snails such as diplommatinids, even within terrestrial areas. If it is true that no other type of transport can be postulated for the colonization of isolated islands such as the Loyalty Islands, this is not the case for colonization inside the mainland of New Caledonia and possibly for the closest islands (Belep Islands, Isle of Pines) which were probably not permanently isolated by the sea. As a matter of fact, the occurrence of clines over small distances is an argument for the predominance of active dispersal. For example, in cases where we observe a cline along a steep slope over a short distance (e.g., *Palaina boucheti* in the Paéoua), the predominance of passive transport down the slope would imply that the variability observed at the summit influences the variability at the bottom. This is not the case in any such cline that we have observed; on the contrary, the few aberrations observed (e.g., *Palaina mariei* on the Paéoua) consist in the presence of the low altitude form also at the summit. This suggests that the dispersal is active, and we have no reason to presume that *Palaina* spreads inside each island by other major means (small mammals are absent and birds scarce).

Radula and feeding

I have not found any specific differences between New Caledonian *Palaina* radulae. All are taenioglossate with similar teeth (Fig. 3). The central tooth has generally five cusps, the first lateral four, the second lateral three or four, and the marginal teeth have two or three; the minor variations in number of cusps are caused by their partial or total fusion. As indicated by Peake (1973), the *Palaina* species are probably grazers. It is quite surprising to observe that the size of the teeth and their

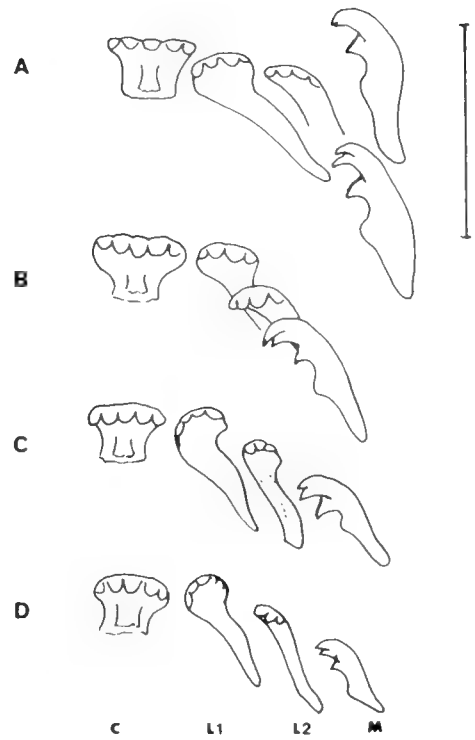


FIG. 3. Radulae of New Caledonian *Palaina*. A, *P. montrouzieri*, Lindéralique (sta. 11). B, *P. perroquini*, Mt. Guemba (sta. 47). C, *P. mariei*, Mé Maoya (sta. 28). D, *P. nanodes*, Touaourou (sta. 48). Scale line 0.025 mm.

cusps vary much less than the size of the animals (Fig. 3). The central tooth is always about the same size in all species and the greatest differences in size are found in the marginal teeth. However, the size of the latter varies only in the ratio 1:2 as the shell height varies in the ratio 1:4. When compared with the very large differences in the size of the animals, this radula similarity suggests that animal size is not related with food as suggested by Peake (1973). The niches of the sympatric species are therefore probably not differentiated by the particle size of the food, for which competition possibly occurs.

Shell and operculum

All New Caledonian, Australian and some of the Solomon Islands species of *Palaina* have similar opercula. They are thin, corneous, slightly concave and oligogyrous (Fig. 4; Tillier, unpublished). The opercula of these species have an arcuate, narrow thickening, parallel to the columellar border; they are attached to the foot by their central area, which is granulous. In some Solomon Islands and Lord Howe Island species, the operculum is more developed and is fixed to the foot by a lamellar process, protruding internally, and

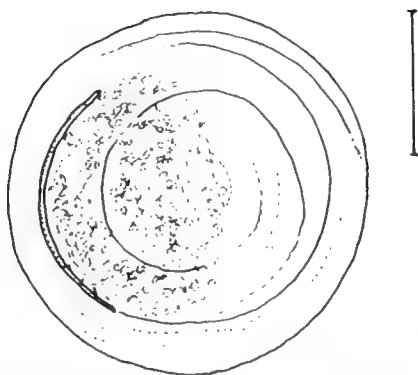


FIG. 4. Operculum of *P. mariei*, Mé Maoya (sta. 28). Scale line 0.125 mm.

parallel to the columellar side of the aperture (Fig. 1c, d). The thickening of New Caledonian opercula is probably homologous to this process.

Shell shape varies from a high and conical morphotype, called *Macropalaina* as a genus by Moellendorff (1897), to a short and stout one which may be called *Palaina*, or even *Cylindropalaina* when the shell approaches a perfect cylinder in shape. All intermediates occur and could be called the *Velepaina* morphotype. Each species has a definite range of morphotype variability, either from *Macropalaina* to *Velepaina* and *Palaina* or from *Velepaina* to *Palaina* and *Cylindropalaina*. None of these names can have taxonomic value until each type-species has proved to represent a distinct group of species within the *Diplommatina-Palaina* complex. It will be demonstrated further that the variations of the morphotypes are correlated with environmental conditions, and in particular with moisture. Comparisons with morphotypes found in other Melanesian regions may be interesting. The *Velepaina* morphotype is found in eastern Australia and in the New Hebrides (Iredale, 1937; Solem, 1959). In Australia, *Eclogarinia* represents a morphotype characterized by a high conical shell with the penultimate whorl narrower in diameter than the preceding one. "*Eclogarinia*" *gowl-landi* does not exhibit any other peculiar anatomical or morphological feature (Tillier, unpublished). This morphotype is quite common farther north and is found also in New Guinea. In the Solomon Islands shell shapes vary between this type and typical *Palaina*, with intermediates quite similar to the stoutest shells of the New Caledonian *Palaina perroquini* (Fig. 29A; Peake, 1973, Fig. 1). Lord Howe Island species vary around the typical *Palaina* morphotype (the type-species among them!),

whereas the two Norfolk Island species have a loose last whorl but otherwise approach the *Velepaina* morphotype (Iredale, 1945). Sinistral species are dominant in Australia and the Solomon Islands, and no dextral species is found in New Caledonia, New Hebrides, Norfolk and Lord Howe Islands.

All New Caledonian species have thin shells, with an ornamentation consisting of very thin spiral threads crossed by radial lamellae, which may project as wings in well-preserved juvenile specimens of some species. The distances between ornamental elements on each whorl vary but tend to be different in each species. In well-preserved specimens it can be observed that the spiral threads are continuous over the radial lamellae. Just before the adult aperture is formed there is no significant change in the interval between successive radial ribs. A first peristome is formed by the expansion of one rib, and then the ribs are very close and not expanded on a very short distance before the definitive expanded peristome is formed (Fig. 26). In all species but one, the peristome is approximately parallel to the shell axis.

This type of ornamentation and aperture is the commonest in Melanesia, but all Solomon Islands species and some Lord Howe Island species have a thicker shell and a different type of aperture. In these species, the radial ribs become closer about one quarter of a whorl before the peristome is formed; the latter is very thick and formed by crowded, slightly expanded radial ribs (see Rensch, 1929, fig. 6 and *Palaina macgillivrayi*, Fig. 1b).

The embryonic shell is irregularly pitted in the same way in all New Caledonian species, and is similar in other Melanesian species examined.

Animal and general anatomy

A preserved animal is shown in Fig. 5. The most striking feature is the well-defined propodium, mesopodium and metapodium, which are separated by distinct and constant grooves. This feature, which is exceptional in marine mesogastropods (Fretter & Graham, 1962), may also be seen in the Cochlostomatinae. According to Girardi's figures (1978), such grooves are absent in poteriids. This character could serve to define families, but unfortunately I could not check it in other Cyclophoracea and cannot reach any definitive conclusion. Among other land proso-

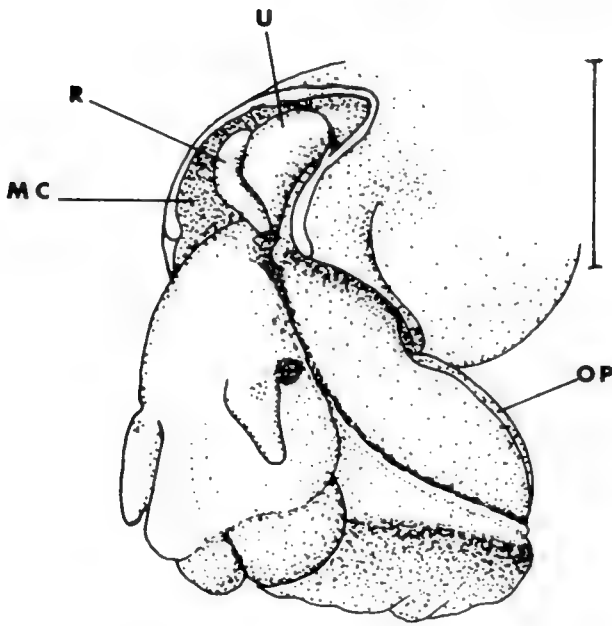


FIG. 5. Animal of *P. montrouzieri*, Pombei (sta. 13). Scale line 0.5 mm. MC, mantle cavity; OP, operculum; R, rectum; U, uterus.

branches, pedal grooves are found also in truncatellids (Fretter & Graham, 1978).

The mouth opens into a slit between two well-defined, rounded lobes. Above these lobes the head forms a sort of apron, posteriorly limited by the anterior pedal groove which separates the propodium from the mesopodium. The animals are completely white, except the tentacles that are sometimes grey. There is always a grey spot at the base of the tentacles, in front of the eyes. This spot may be either rounded (Fig. 5) or form a transverse bar joining the eye; its shape is neither specific nor sex-determined, although each individual shows one or the other of the two spot shapes.

The mantle cavity occupies about the last one and a half whorls of the visceral mass (Fig. 6). The uterus or prostate runs along the columellar side of the mantle cavity, without protruding into the upper visceral cavity, and is bordered externally by the rectum. The kidney occupies about one quarter of a whorl above the upper part of the mantle cavity and hides the small heart that lies just under its proximate extremity. The oesophagus runs up along the columella before bending back outwards into a large cylindrical stomach, about one third of a whorl long. The stomach has no distal caecum but a distal inflated ring, which is probably the equivalent, whereas the Cochlostomatinae have a true caecum. Fecal pellets are formed in the proximal intestine which is parallel to the spire, less than half a

whorl long and often regularly inflated by fecal matter. In the distal intestine the pellets are always well formed and distinct. Just proximally to the mantle cavity, the intestine forms one loop before running into the latter between the pallial gonoduct and the kidney. The same disposition is found in the Cochlostomatinae. Among Cyclophoracea poteriids have the same type of stomach but without any trace of a caecum (Girardi, *in litt.*; data lacking for other families).

Genital anatomy, reproduction and growth

Males have no penis, and thus males and females have the same disposition of their genital apparatus. The gonad lies along the columellar side of the visceral mass for about one whorl, starting from the beginning of the third whorl from the apex. The genital duct then coils along the columella, together with the oesophagus, to the upper parietal corner of the mantle cavity aperture where it opens just beside the anus (Figs. 5, 6). At the proximal end of the mantle cavity it enlarges

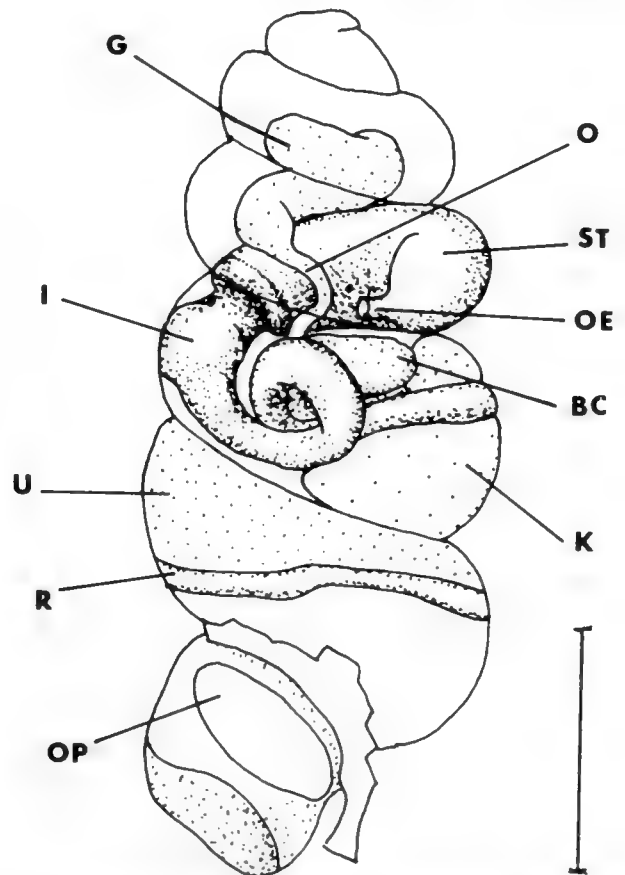


FIG. 6. General anatomy of *P. mariei*, Mé Maoya (sta. 28). Scale line 0.5 mm. The upper intestine is inflated by a pellet. BC, bursa copulatrix; G, gonad; I, intestine; K, kidney; O, oviduct; OE, oesophagus (sectioned); OP, operculum; R, rectum; ST, stomach; U, uterus.

abruptly into a prostate or a uterus. In males there is no other morphological differentiation, but in females the differentiation of the distal oviduct, just proximally to the upper extremity of the uterus, into a bursa copulatrix and a seminal receptacle provides the only specific anatomical characters that I could find in *Palaina*. These female organs are located behind the intestinal loop (Fig. 6).

The bursa copulatrix is relatively constant in shape and disposition within each species. Its inflated head is generally appressed against the proximal end of the uterus, but its stalk may point either upwards or downwards from the distal oviduct; in the latter case its head may occasionally, but constantly within a population, point within the intestinal loop instead of above it.

The seminal receptacle may be absent or present, as in the Cochlostomatinae (Giusti, 1971). Four steps in its position and development are found: 1) The seminal receptacle is well developed and opens into the oviduct close to the base of the stalk of the bursa copulatrix: found in New Caledonian *Palaina montrouzieri* (Fig. 20); 2) The seminal receptacle is well developed, but opens into the basis of the bursa stalk: found in some Solomon Islands species (Tillier, unpublished); 3) The seminal receptacle is reduced to a swelling located approximately in the middle of the bursa stalk, on the outside of the bend of the latter: found in New Caledonian *Palaina mariei* (Fig. 22), *P. obesa* (Fig. 23), and in some Solomon Island species (Tillier, unpublished); 4) The seminal receptacle is absent in New Caledonian *Palaina mareana* (Fig. 34), *P. perroquini*, *P. boucheti* (Fig. 25), *P. opaoana* (Fig. 32) and *P. nanodes* (Fig. 27), and in some Australian, Solomon Islands (Tillier, unpublished) and Lord Howe species (Fig. 1).

Only the two extreme arrangements are known in the Cochlostomatinae (Giusti, 1971), and an arrangement somewhat equivalent to the intermediate ones is found in the Pupinidae (Tielecke, 1940) where it is therefore not a familial character.

We have no data on reproductive behaviour, and do not know how individuals recognize each other, the males having no penis. The populations collected are formed of sets of specimens of the same apparent age, and it therefore seems that all individuals of one population reproduce at the same time.

Berry (1963a, b) observed that the space between two radial ribs represents one day's

growth in Malayan *Opisthostoma*. As far as this result can be generalized for any Diplomatinae, this means that species with distant varices grow faster than species with close varices. If this hypothesis is true, the time necessary before New Caledonian species begin to build their peristome varies from about 80 days in *Palaina mareana* to about 160 days in *P. nissidiophila*. The genital apparatus is formed at about the same time as the first expansion of the peristome, but reaches its full development only when the second expansion is built.

SPECIES VARIATIONS AND INTERACTIONS

Schindel & Gould (1977) reviewed and discussed character displacement, with particular reference to land snails. The methodology herein adopted for demonstrating character displacement is very simple, and consists of: 1) An analysis of the relationships between the variations of the species and the variations of their environment; 2) An analysis of the variations found in populations of sympatric species, with reference to the first analysis. I cannot but hope that these analyses provide a rebuttal to Schindel & Gould's statement according to which the fossil record is superior to the living one for assessing such evolutionary processes.

Materials and methods

More than 1000 specimens, collected at 56 stations all over New Caledonia and adjacent islands, were used for this study. Shells are much more numerous than animals taken alive, but living animals were found at 33 stations. Two samples were borrowed from the National Museum of New Zealand (NMNZ), Wellington; all the other specimens are housed in the Muséum national d'Histoire naturelle, Paris (MNHN), and consist of: 1) A few old samples, collected mainly by Marie around Nouméa and the Baie de Prony (= Baie du Sud), which are important because they contain most of the previously described type-specimens; 2) About nine-tenths of all the material was collected by Philippe Bouchet between April 1978 and July 1979, and by Bouchet and Tillier in June–July 1979.

A complete list of the stations is given in Table 1, and their localities are shown in Fig.

7. For each station we know the altitude, the type of vegetation and the rainfall. The latter was estimated from Moniod's data (1966) published by ORSTOM. In some cases the value given by the ORSTOM map is aberrant. For example, the northwestern mountains, the summits of which are covered with high altitude rainforest, are in a very dry zone of the map. In such cases I estimated the rainfall as being the same as in another place with the same vegetation where it has been measured.

The number of specimens at each station will be found in brackets within the list of material of each species in the systematic part of this work. Shell height, H , and shell diameter, D , were measured on 937 shells (in one sample of more than 200 shells, only 128 were measured to avoid a disproportionate influence on the results of the analyses). For measurements, shells were placed under the microscope with the aperture upward and dimensions measured on mm paper placed under the camera lucida; precision was $\pm 10 \mu\text{m}$. H is the largest dimension parallel to the shell axis, D is the diameter of the body whorl, perpendicular to the shell axis, from the outer border of the aperture to the most external opposite point of the body whorl. The number of radial ribs should be useful for cline analyses. It was not used because of the impossibility of obtaining reliable counts without counting all the ribs of one shell, which is impractical with such a large number of small shells.

After shells were measured, most of the preserved specimens were dissected. This was useful for establishing anatomical variability of each species and absolutely necessary for naming the specimens representative of the morphological overlap of two species.

Statistical methods

The statistical analysis was made to try to understand the relations, within different sets of specimens, between the dimensions and shape of the shells, and the environmental variables. The IRIS 80 computer of the Université Pierre et Marie Curie, Paris, was used to perform: 1) The analysis of the distribution of the variables with the HISTO program; 2) The factor analysis of several sets of specimens for several sets of variables with the ANACOR program. Both programs come from the statistical library of the computer and

were published by Jambu & Lebeaux, 1979 (HISTO) and Benzécri, 1980 (ANACOR).

All data were first computed in a single matrix with one row for each specimen, numbered from 1 to 937. In each row the characteristics of each specimen are written in nine columns. These variables are the species, coded by a number between 1 and 11, shell height H , shell diameter D , number of the station between 1 and 56, longitude, latitude and rainfall. Two additional morphometric data, which in fact were more significant than height and diameter, were calculated for each specimen and introduced as columns. These are shell size, approximated by the product $H \times D$, and shell shape, approximated by the ratio H/D . The sets of specimens (all specimens from one locality, or all specimens belonging to one species, etc.) and different sets of variables for these specimens were extracted from this general table for the analyses.

The HISTO program then permitted establishing histograms for each quantitative variable, partitioned into twenty classes of equal amplitude. These histograms do not show any classic distribution (normal, γ , etc.) for any variable, even after simple transformations and even when established species by species and population by population. For this reason I turned to factor analysis (correspondence analysis), which may be used without any preliminary hypothesis about the distribution of the variables. As correspondence analysis requires nearly equal frequencies of the classes, the basic histograms were used previous to each analysis to establish class limits allowing subequal effectives of classes. As a result the same symbols do not represent the same absolute values in the different analyses.

Once the variables have been grouped into modalities of equal effectives, the ANACOR program analyses the matrix coded 0 or 1. It locates each individual in the space of the variables (or each modality in the space of the individuals) and extracts the principal component axes, classified in function of the percentage of variance loading on them. The final result is a projection of the individuals and of the variables on the planes determined by the axes of the principal components. Only the projections of the variables are reproduced here. The projections of the individuals were used to check the verisimilitude of proposed interpretations, but are unreproducible in a printed paper (937 numbered points on each).

TABLE 1. List of collecting stations.

1. Pott (Belep Islands), bay of Panane, thalweg with Gaiacs. Rainfall 1190 mm. Bouchet and Chérel coll. 27.8.1978. 2. Art (Belep Islands), bay of Pairomé, littoral dry forest with <i>Cycas</i> on sand and pumice. Rainfall 1190 mm. Bouchet and Chérel coll. 25.8.1978. 3. Niénane (Daos du Nord Islands), northeastern bay, littoral dry forest on sand and pumice. Rainfall 1190 mm. Bouchet and Chérel coll. 23.8.1978. 4. Mt. Tiébaghi, 500 m, low maquis on peridotite. Rainfall 1200 mm. Tillier coll. 6.1979. 5. Le Cresson, 100 m, dry forest on calcareous outcrop. Rainfall 1200 mm. Tillier coll. 30.6.1979. 6. Koum, 80 m, dry forest on calcareous outcrop. Rainfall 1200 mm. Tillier coll. 30.6.1979. 7. Mandjélia, 400 m, 5 km from the sawmill, rainforest. Rainfall 1900 mm. Tillier coll. 2.7.1979. 8. Oubatche, 500 m, rainforest. Rainfall 2500 mm. Hedley coll. (AMS). 9. Ruisseau de l'Etoile du Nord (Oué Paoulou), 150 m, dry forest probably on a calcareous outcrop. Rainfall 1100 mm. Tillier coll. 30.6.1979. 10. Kavatche, 50 m, river drift in slightly disturbed rainforest. Rainfall 2200 mm. Bouchet coll. 25.11.1979. 11. Lindéralique, 20 m, decaying plant accumulation in holes in a massive calcareous outcrop. Rainfall 2267 mm. Bouchet coll. 26.11.1978. 12. Taom Mt., 900 m, altitude rainforest in a thalweg, on peridotite. Rainfall 2500 mm. Tillier coll. 3.7.1979. 13. Pombei, 100 m, rainforest. Rainfall 2781 mm. Bouchet and Tillier coll. 7.1979. 14. Momies de la Faténaoué, 150 m, dry forest, Rainfall 1250 mm. Tillier coll. 4.7.1979. 15. Poindimié, 20–50 m, rainforest 300 m from the shore. Rainfall 3200 mm. Bouchet coll. 29.9.1978. 16. Plateau de Tango, track to Bobeitio, 300–350 m, rainforest. Rainfall 1800 mm. Bouchet coll. 24.12.1978. 17. Aoupinié, 350 m, track to the saw-mill above Goa tribe, rainforest. Rainfall 2500 mm. Bouchet coll. 18. Goipin, 50 m, southwestern lower slopes of the Mt. Aoupinié, rainforest. Rainfall 1525 mm. Bouchet coll. 6.5.1979. 19. Forêt Plate, 540 m, slope of Mt. Paéoua, rainforest. Rainfall 1841 mm. Bouchet and Tillier coll. 15.7.1979. 20. Mt. Paéoua, 950–1000 m altitude rainforest. Rainfall 3000 mm. Tillier coll. 5.7.1979. 21. between Nékliai and Nétéa, 100 m, lower slopes of Mt. Boulinda, rainforest. Rainfall 1500 mm. Tillier coll. 7.7.1979. 22. Nindiah, 50 m, near the mission, small calcareous outcrop. Rainfall 1842 mm. Bouchet coll. 30.12.1978. 23. Plaine aux Gaiacs, probably sublittoral dry forest. Rainfall 1000 mm. Dell coll. (NMNZ). 24. Népoui, Presqu'île de Muéo, littoral dry forest. Rainfall 1000 mm. Tillier coll. 5.7.1979. 25. Adio caves, 180 m, decaying plant accumulation in holes in calcareous outcrop. Bouchet coll. 6.5.1979. 26. Col des Roussettes-Bogui, 150 m, rainforest. Rainfall 1600 mm. Bouchet coll. 15.5.1978. 27. Col des Roussettes, 550 m, rainforest. Rainfall 1658 mm. Kuschler coll. 31.10.1978 (NMNZ). 28. Junction of the two rivers running down the Mt. Mé Maoya and the Dent de Poya, 50 m, rainforest. Rainfall 2000 mm. Bouchet and Tillier coll. 15.6.1979. 29. Mt. Mé Ori, 530 m, southeastern slope, rainforest. Rainfall 2000 mm. Bouchet coll. 30.4.1979. 30. Col de Pétchékara-Dothio, 250 m, rainforest. Rainfall 2000 mm. Bouchet coll. 8.7.1978. 31. Oua Oué, 50 m, decaying plant accumulation in holes in calcareous outcrop. Rainfall 1364 mm. Bouchet coll. 31.12.1978. 32. Poé beach, secondary dry forest on sand. Rainfall 1000 mm. Bouchet coll. 19.8.1978. 33. Roche Percée, Bourail, littoral maquis on sand. Rainfall 1000 mm. Bouchet coll. 10.12.1978. 34. Col. des Arabes, 100 m, maquis. Rainfall 1000 mm. Bouchet, Tillier and Warén coll. 9.6.1979. 35. Nassirah, 100 m, on the right slope of the Fonwhary valley, rainforest. Rainfall 1300 mm. Bouchet coll. 8.7.1978. 36. Mine Galliéni, 700–750 m, gallery forest in a thalweg on peridotite. Rainfall 1600 mm. Bouchet coll. 19.5.1979. 37. Mt. Dzumac, 1000 m, altitude rainforest. Rainfall 3000 mm. Bouchet and Tillier coll. 6.1979. 38. Plaine aux Cailloux, 100 m, rainforest. Rainfall 1267 mm. Bouchet coll. 3.2.1979. 39. Ndé, 60 m, hill near the tribe, secondary forest. Rainfall 1267 mm. Bouchet coll. 2.7.1978. 40. Yahoué, 200 m, slopes of the Mt. Koghi, rainforest. Rainfall 1400 mm. Bouchet coll. 24.11.1978. 41. Nouméa, old collections, probably dry forest. Rainfall 1100 mm. 42. Baie Tina, Nouméa, littoral dry forest. Rainfall 1200 mm. Bouchet coll. 16.12.1978. 43. Rivière Bleue, 150 m, rainforest on peridotite. Rainfall 3000 mm. Bouchet coll. 6.1.1979. 44. Mamié, 50 m, high maquis with boulders on peridotite. Rainfall 2800 mm. Bouchet coll. 14.1.1979. 45. Waho, 20 m, rainforest on uplifted coral reef. Rainfall 2800 mm. 46. Mt. Guemba, 200 m, rainforest on peridotite. Rainfall 2938 mm. Bouchet coll. 13.1.1979. 47. Mt. Guemba, 450 m, rainforest on peridotite. Rainfall 3200 mm. Bouchet coll. 16.2.1979. 48. Touaourou, 10 m, rainforest on uplifted coral reef. Rainfall 3000 mm. Bouchet coll. 8.12.1978. 49. Kuébéni, 50–80 m, rainforest on slope on peridotite, left bank of the Kuébéni river. Rainfall 2500 mm. Bouchet coll. 15.2.1979. 50. Goro, 15 m, rainforest on peridotite. Rainfall 1900 mm. Bouchet and Chérel coll. 8.4.1979. 51. Baie de Prony, on peridotite, old collections. Rainfall 2800 mm. 52. Mt. Oungoné, 450 m, rainforest on steep slope. Rainfall 3500 mm. Bouchet coll. 1.10.1978. 53. Ouro, Isle of Pines, 15 m, littoral dry forest on uplifted coral reef. Rainfall 1800 mm. Bouchet coll. 21.10.1978. 54. Enéné, Maré Island, 60 m, wet bottom of a large dolina. Rainfall 1500 mm. Bouchet coll. 7.4.1979. 55. Medu, Maré Island, dry forest on uplifted coral reef. Rainfall 1500 mm. Bouchet coll. 4.1979. 56. Nécé, Maré Island, 15–20 m, dry forest on uplifted coral reef. Rainfall 1500 mm. Bouchet coll. 5.4.1979.	
---	--

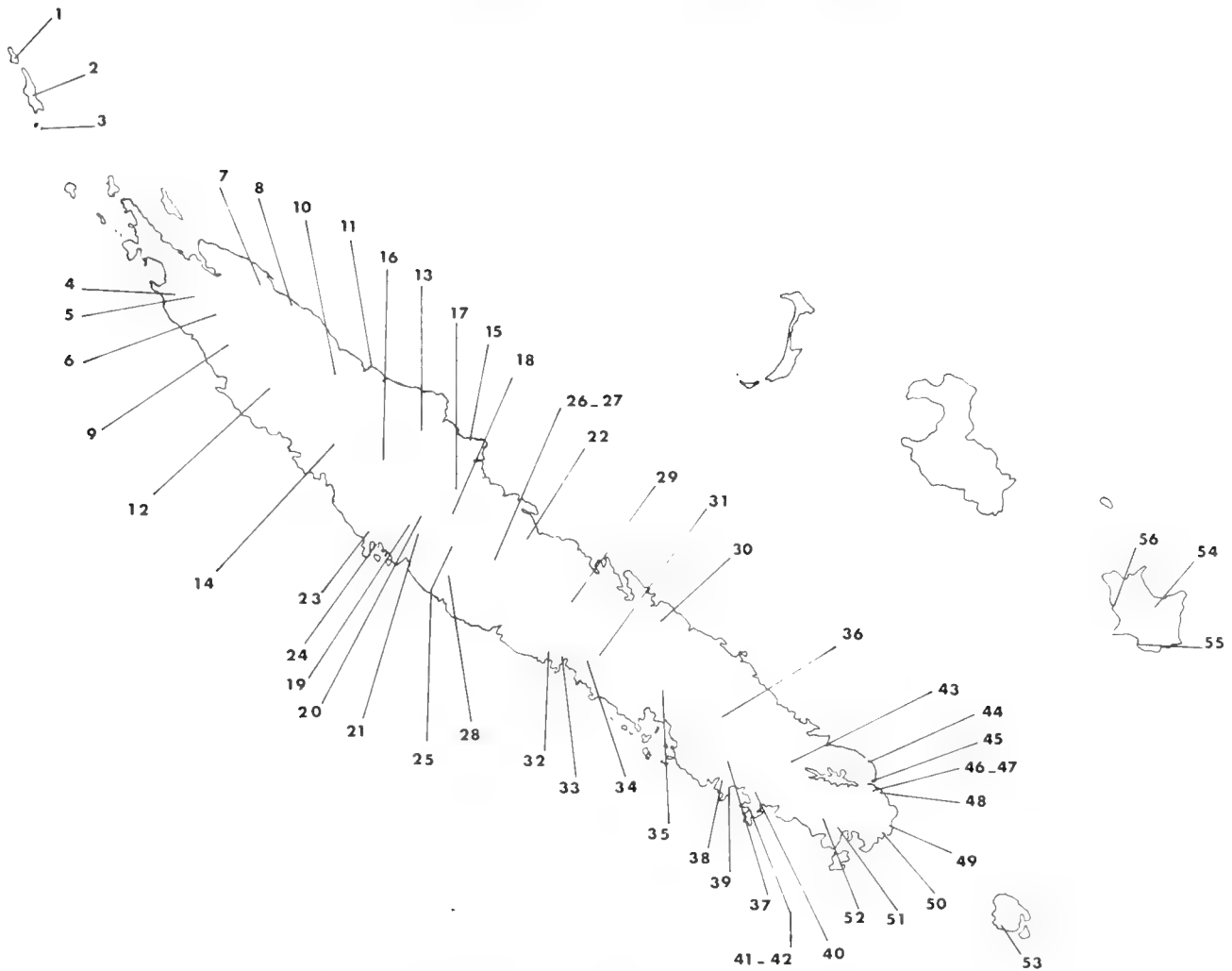


FIG. 7. Map of the collecting localities (listed in Table 1).

Geography, ecology and morphometric variability

Each species exhibits a well defined range for each geographical, ecological and morphometric variable. The specific ranges for height, diameter, size, shape and rainfall are given in Figs. 8 to 11. The geographic data are summarized in Table 2. Altitude was eliminated from this step onwards because its significance, if it has any, is masked by the influence of rainfall; nearly all the eastern coast is very wet from sea level to high altitudes and the rainfall is approximately proportional to the altitude along the western coast. All the intermediate situations are found when crossing New Caledonia.

Palaina mariei is the only species that may be expected anywhere on the mainland, except in the extreme north. It is also the only species that exists in the whole rainfall range

of New Caledonian *Palaina*, from 1000 to 3500 mm a year. It is a rather small species of variable shape, but occupies the mid-range of all shapes. It has been found sympatric with *Palaina montrouzieri*, *P. opaoana* and *P. boucheti*.

Palaina montrouzieri and *P. opaoana* have about the same mid-size, but the former may attain larger sizes than the latter. They are found in the same rainfall range of 1000 to 3125 mm rain a year but occupy adjacent geographic ranges, *P. montrouzieri* being found in northern, central, eastern and possibly southern New Caledonia, and *P. opaoana* being found only in central New Caledonia but very commonly along the western coast. *Palaina montrouzieri* generally has a more elongate shape than *P. opaoana*.

Palaina boucheti is a small species, generally less elongated than *P. mariei*, occurring throughout southern, central, eastern and

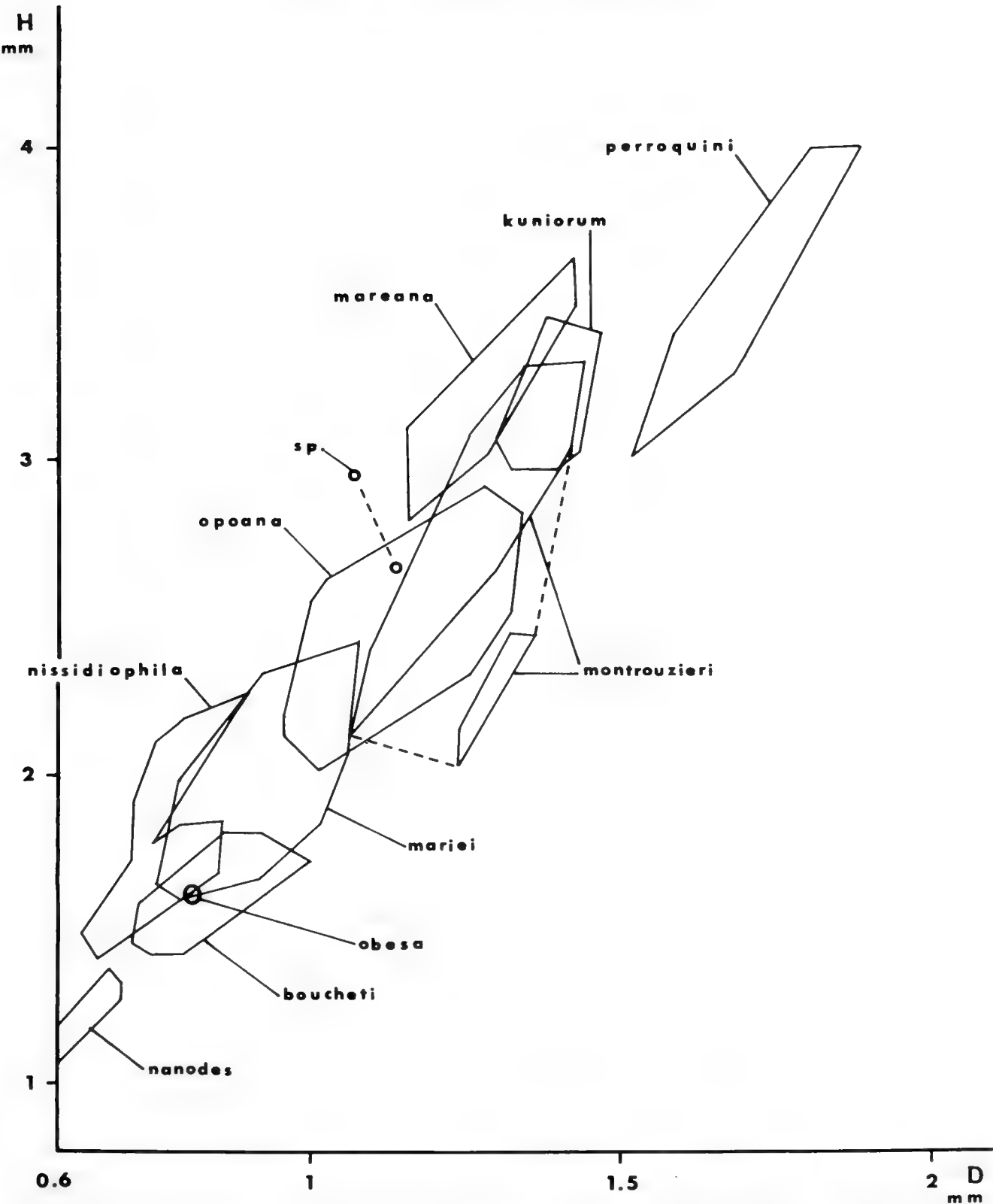


FIG. 8. Scatter diagram of New Caledonian species of *Palaina* for shell height (H) and diameter (D).

northeastern New Caledonia. It was found in areas with rainfall ranging from 1500 to 3500 mm a year.

Palaina nissidiophila occurs only in the Belep Islands and along the northwestern coast of New Caledonia. It attains the smallest sizes found. It is restricted to areas with low rainfall (1125 to 1275 mm rain a year). The species varies enormously in shape.

Palaina perroquini is the largest New Caledonian species. It is restricted to the region south of the great southern mountain mass, with high rainfall (from 2750 to 3125 mm rain a year).

Palaina obesa and *P. nanodes* are both very small and very stout species showing a very restricted endemism in regions with high rainfall, the former in the northeastern moun-

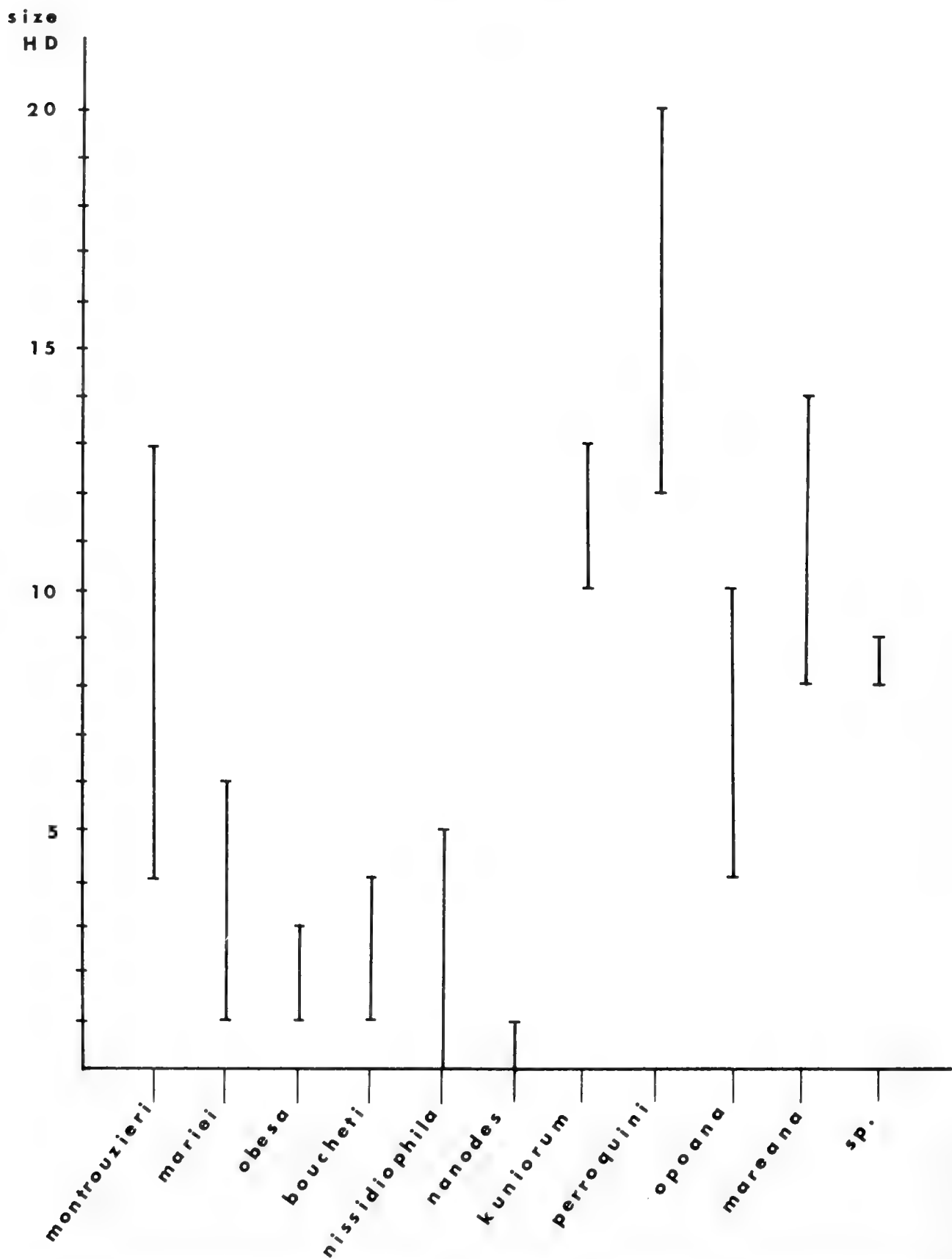


FIG. 9. Size range of New Caledonian species of *Palaina*. Units = total range/20 (= limits of size classes).

tain range and the latter in the southeastern border of the mainland.
Palaina kuniorum and *P. mareana* are both insular endemics, the former in the Isle of Pines (for which Kunié is the Melanesian

name), and the latter in Maré, Loyalty Islands. *Palaina* sp., seemingly endemic in Adio but known from only two specimens, will be discussed in the systematic section.
Note that species that are most restricted in

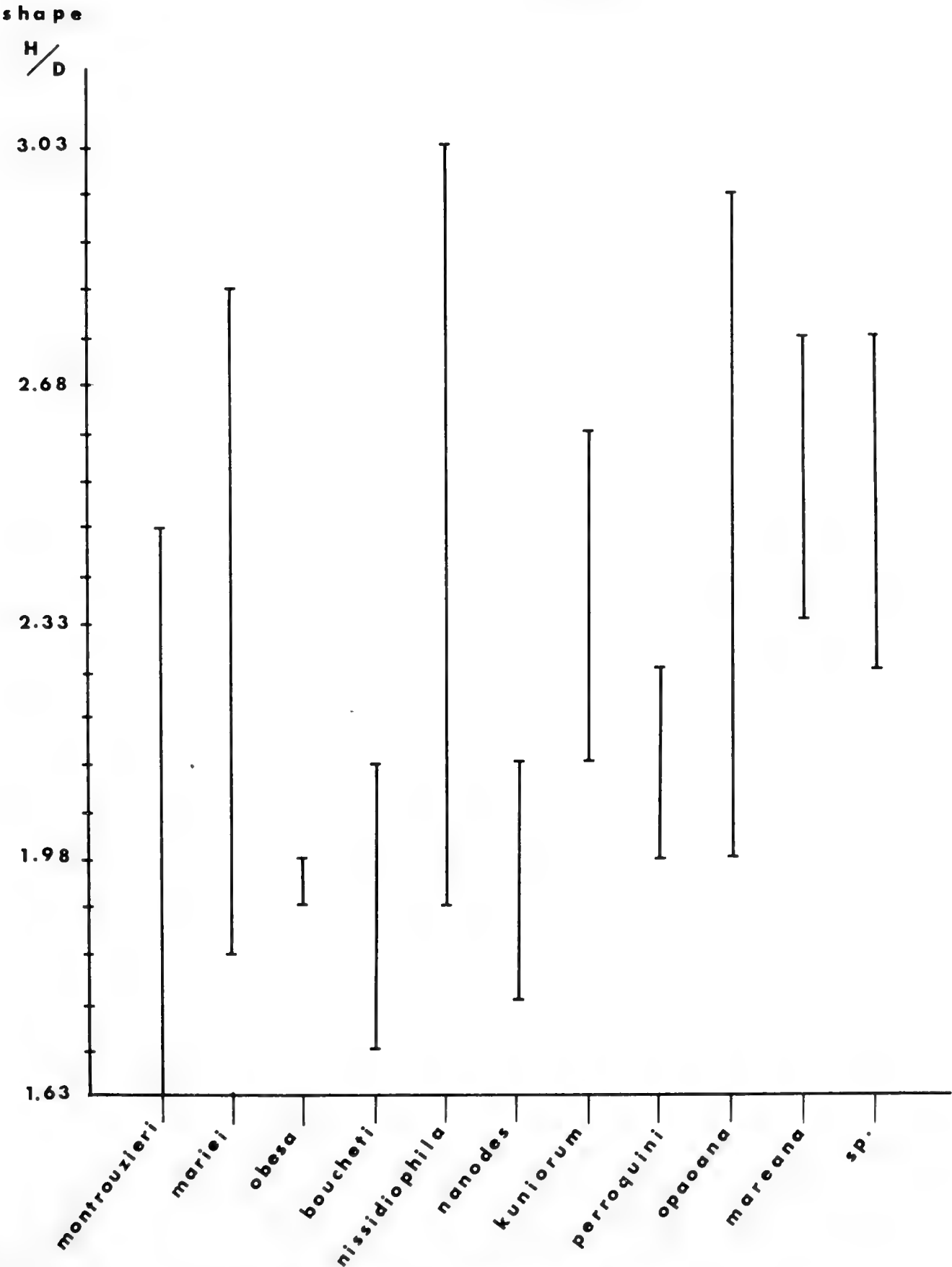


FIG. 10. Shape range of New Caledonian species of *Palaina*.

geographic distribution have a very narrow rainfall range, which was not immediately obvious because of the enormous variation of rainfall over very short distances. Conversely,

Palaina mariei, which is the most widely distributed species, tolerates the widest rainfall range. *Palaina nissidiophila* occupies a relatively wide geographic range although re-

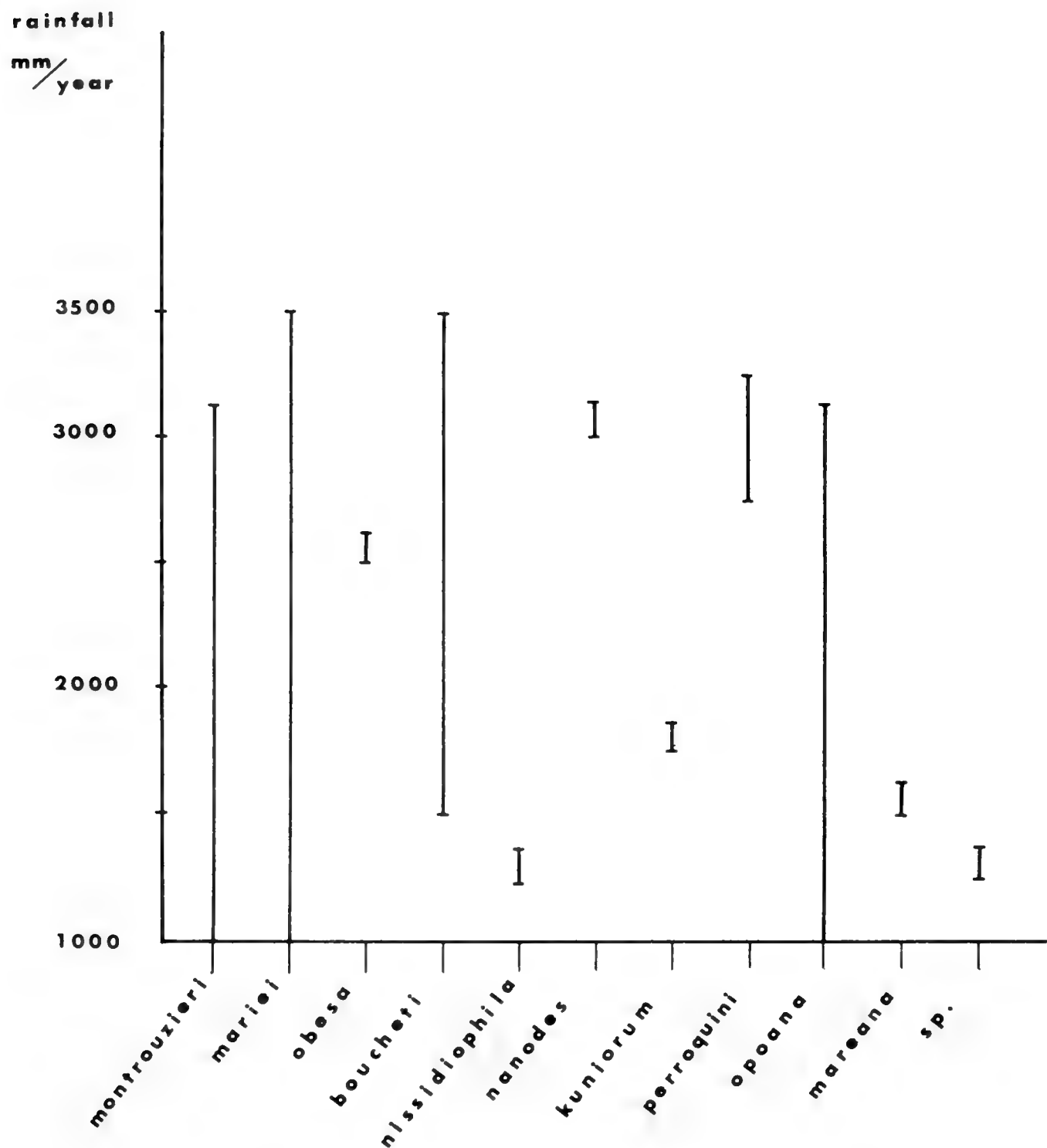


FIG. 11. Rainfall range of New Caledonian species of *Palaina*.

stricted to low rainfall, but is found over the largest homogeneously dry region of New Caledonia.

Rainfall and shell shape

By tracing on Fig. 8 the scatter of each population for H versus D, instead of the scatter of each species, it seems that the lower scatters represent populations collected in high rainfall areas, and that the upper scatters

represent populations collected in low rainfall areas. In other words, it seems that stout shells are found in wetter areas than slender shells (the diagram is not reproduced here because it would be unreadable at a size compatible with printing). To check this, a factor analysis of the contingency table of the variables of shape ($HS = H/D$) and rainfall (PL) was made using the ANACOR program. This table was established with the modalities HS as lines and the modalities PL as col-

umns, and by counting the specimens at each intersection. The class limits corresponding to each modality are given in Tables 3 and 4.

The result of the analysis is shown in Fig. 12. This projection represents 92% of the inertia of the scatter, and the other axes do not change the relative position of the variables. On this projection the axis 2 quite clearly separates low levels of rainfall and elongated shells, on the right side, from very high levels of rainfall and very stout shells well grouped at the extreme left. The complementary projection of the individuals does not show the predominance of any particular species on this result, and thus it may be said that in New Caledonian *Palaina*, the occurrence of very stout shells is linked to very high rainfall, whereas the occurrence of slender shells is linked to low rainfall. Rainfall probably represents the degree of moisture of the environment.

A similar analysis was made for size (HD) and rainfall. It showed a linkage between very high rainfall and extreme sizes, but no general conclusion can be deduced about the selective action of rainfall on size because very large and very small species are not scattered

and appear weighted as species more than as individuals.

Clines

If the scatter of each population is traced on a H versus D diagram, two species exhibit obvious clines for size. The size of *Palaina nissidiophila* increases regularly from the extreme north to the south, between the Belep Islands (sta. 1) and the Faténaoué valley (sta. 14); the shape of the shells is also gradually transformed. The size of *Palaina montrouzieri* also increases from the north-western Tiébaghi mountain (sta. 4) to the southeastern Lindéralique (sta. 11) through stations 9 and 10.

To understand these clines and to try eventually to discriminate less obvious ones, a factor analysis of the species represented by a large number of specimens over a large area was done. These species are *Palaina montrouzieri* (n = 129 specimens), *P. nissidiophila* (n = 156), *P. mariei* (n = 282), *P. boucheti* (n = 108), and *P. opaoana* (n = 193). The variables analysed were shell shape (HS), shell size (HD), and rainfall (PL).

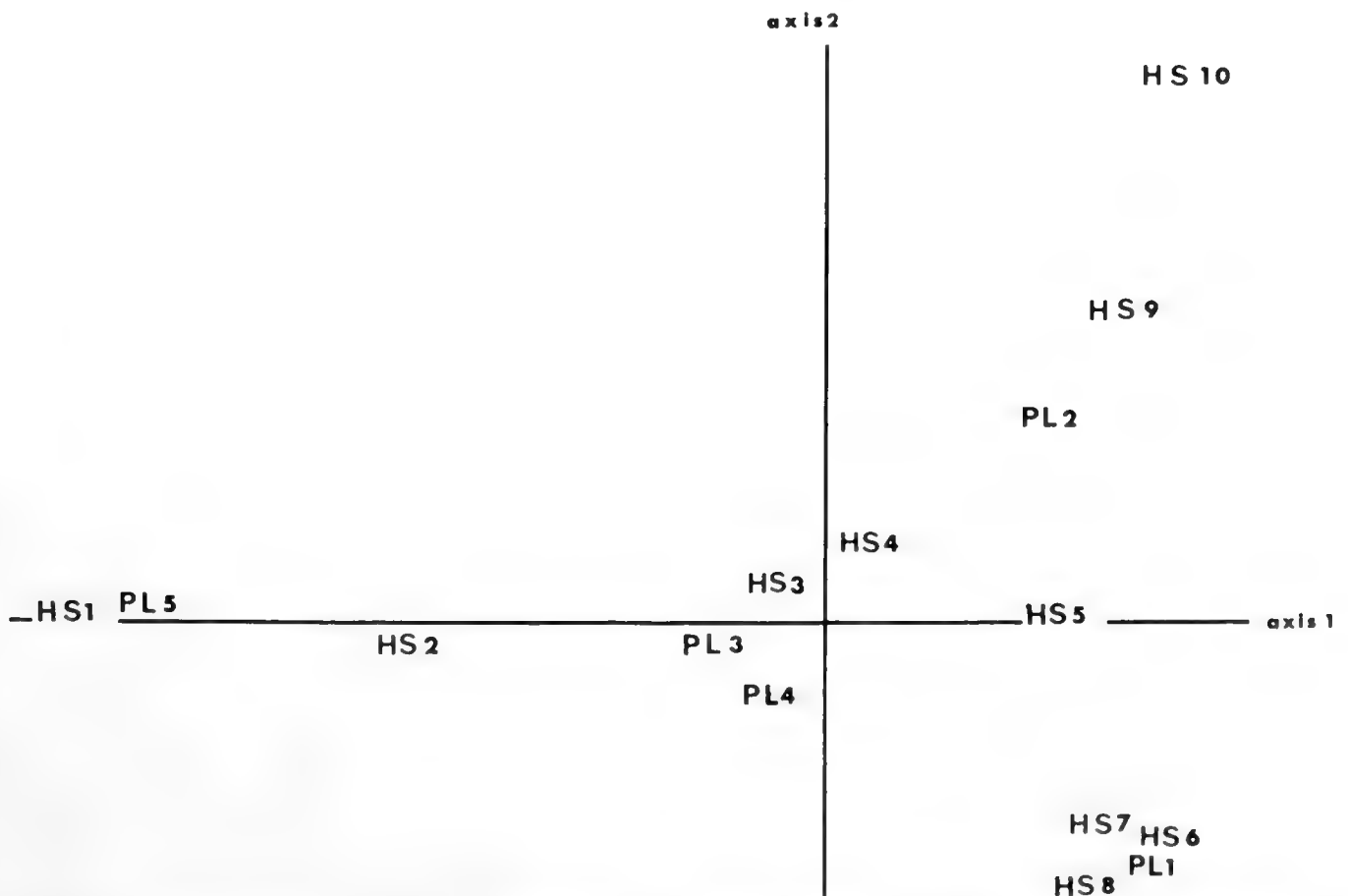


FIG. 12. Factor analysis of the contingency table of the variables rainfall (PL) and shape (HS). Projection of the variables. Axis 1: proper value 0.38, inertia 66%; axis 2: proper value 0.15, inertia 26%.

TABLE 3. Limit values for the modality PL used in Fig. 12 (in mm rainfall/year).

PL1	PL2	PL3	PL4	PL5
950, 1150	1150, 1500	1500, 2125	2125, 2750	2750, 3500

TABLE 4. Limit values for the modality HS (ratio H/D) used in Fig. 9.

HS1	HS2	HS3	HS4	HS5	HS6	HS7	HS8	HS9	HS10
1, 63; 1, 91	1, 91; 2, 05	2, 05; 2, 12	2, 12; 2, 17	2, 17; 2, 21	2, 21; 2, 26	2, 26; 2, 3	2, 3; 2, 4	2, 4; 2, 54	2, 54; 3, 03

TABLE 5. Limit values for each modality in Figs. 13–16. HS = H/D ratio; HD in square units of 20 μm each; PL = rainfall in mm/year.

	PL1	PL2	PL3	PL4	PL5	HD1	HD2	HD3	HD4	HD5	HS1	HS2	HS3	HS4	HS5
<i>mariei</i>	950	1000	1200	1900	2100	3078	3588	3928	4439	4949	1.804	2.071	2.14	2.204	2.293
	1000	1200	1900	2100	3500	3588	3928	4439	4949	6480	2.071	2.14	2.204	2.293	2.694
<i>boucheti</i>	1500	1900	2500	3000		2590	3005	3254	3669		1.73	1.831	1.895	1.939	1.983
	1900	2500	3000	3500		3005	3254	3669	4250		1.831	1.895	1.939	1.983	2.135
<i>nissidiophila</i>	1125	1190	1200			2240	2653	3066	3480	3893	1.93	2.1	2.184	2.336	2.54
	1190	1200	1250			2653	3066	3480	3893	4995	2.1	2.184	2.336	2.54	2.946
<i>opaoana</i>	950	1000	1658	1900		5040	5700	6000	6580	7460	1.81	2.106	2.179	2.24	2.29
	1000	1658	1900	3000		5700	6000	6580	7460	9440	2.106	2.179	2.24	2.29	2.549
<i>montrouzieri</i>		950	1200	2200	2300	5565	8407	9038	9670	10500	1.629	2.039	2.121	2.202	2.284
		1200	2200	2300	3500	8407	9038	9670	10500	11880	2.039	2.121	2.202	2.284	2.448

The station numbers (used because they make an analysis much easier than coordinates) were introduced as supplementary columns, which means that they do not influence the analysis but are projected on the diagrams. The class limits for each modality in each species are given in Table 5.

The projection of the variables for *Palaina nissidiophila* is shown in Fig. 13. The cline for size from north (sta. 1) to south (sta. 14) is clearly shown, and appears to be linked to increase of rainfall. In the northern part of the range (stas. 1–6) stouter shells are found in higher rainfall, but in the southern part of the range (sta. 14) the shells become more slender whereas rainfall increases. This apparent aberration will be analysed further.

I can analyze the variations of *Palaina montrouzieri* only over the northern half of New Caledonia (it is known from the southern half only from the type-specimen). The projection in Fig. 14 shows a correlative variation of shell size and shell shape from stout small shells to large slender shells. Along axis 1, relatively small shells are associated with lower rainfall whereas the relatively large

shells are associated with relatively high rainfall. The very high rainfall PL5 is opposed to all the lower rainfalls along axis 2. The interpretation, with stations, is a very clear cline for size and shape from the Tiébaghi to Lindéralique (stas. 4, 9, 10, 11) related with the increase of rainfall. Inside this cline several clines for shape are induced by very high rainfall at stations 8, 17 and 20, which are all on mountains where rainfall is much higher than in surrounding lowland area. The Pompei specimens (sta. 13) have a stout shape linked to high rainfall, but are abnormally large; that is why station 13 is farther left on the diagram than the other equivalent stations. A tentative explanation will be given later.

Palaina mariei is, at first sight, a different case compared with the two preceding species. When examining the scatter of the different populations on a H/D diagram, variations look geographically random and no clines are obvious except over a very short distance, which raises doubt about interpretation. However, the projection of the variables on the (1, 2) plane as shown in Fig. 15 is

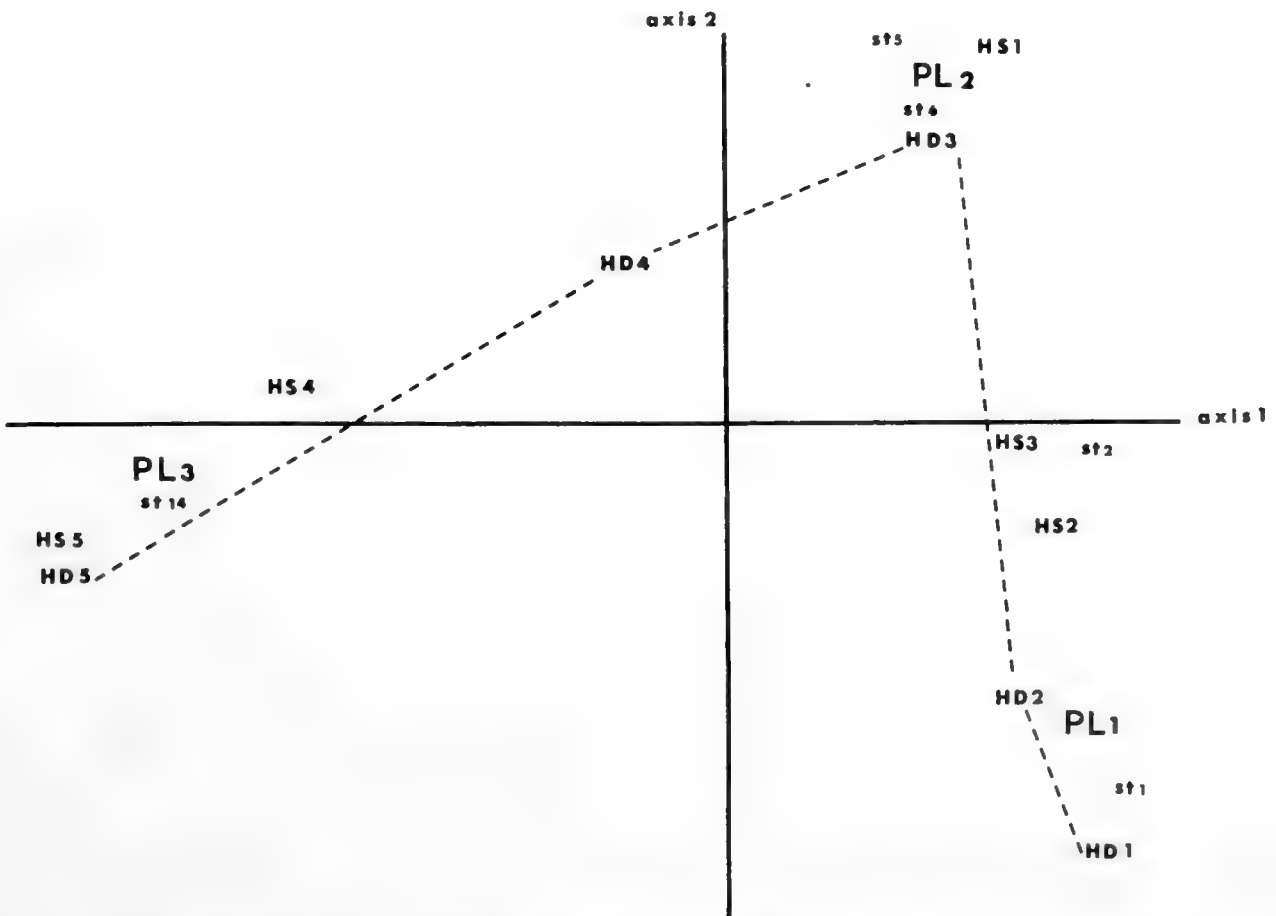


FIG. 13. Factor analysis of *P. nissidiophila* for rainfall (PL), size (HD) and shape (HS); projection of the variables and of the stations. Axes 1 and 2 have respectively 0.88 and 0.57 as proper values and represent 26% and 17% of the variance.

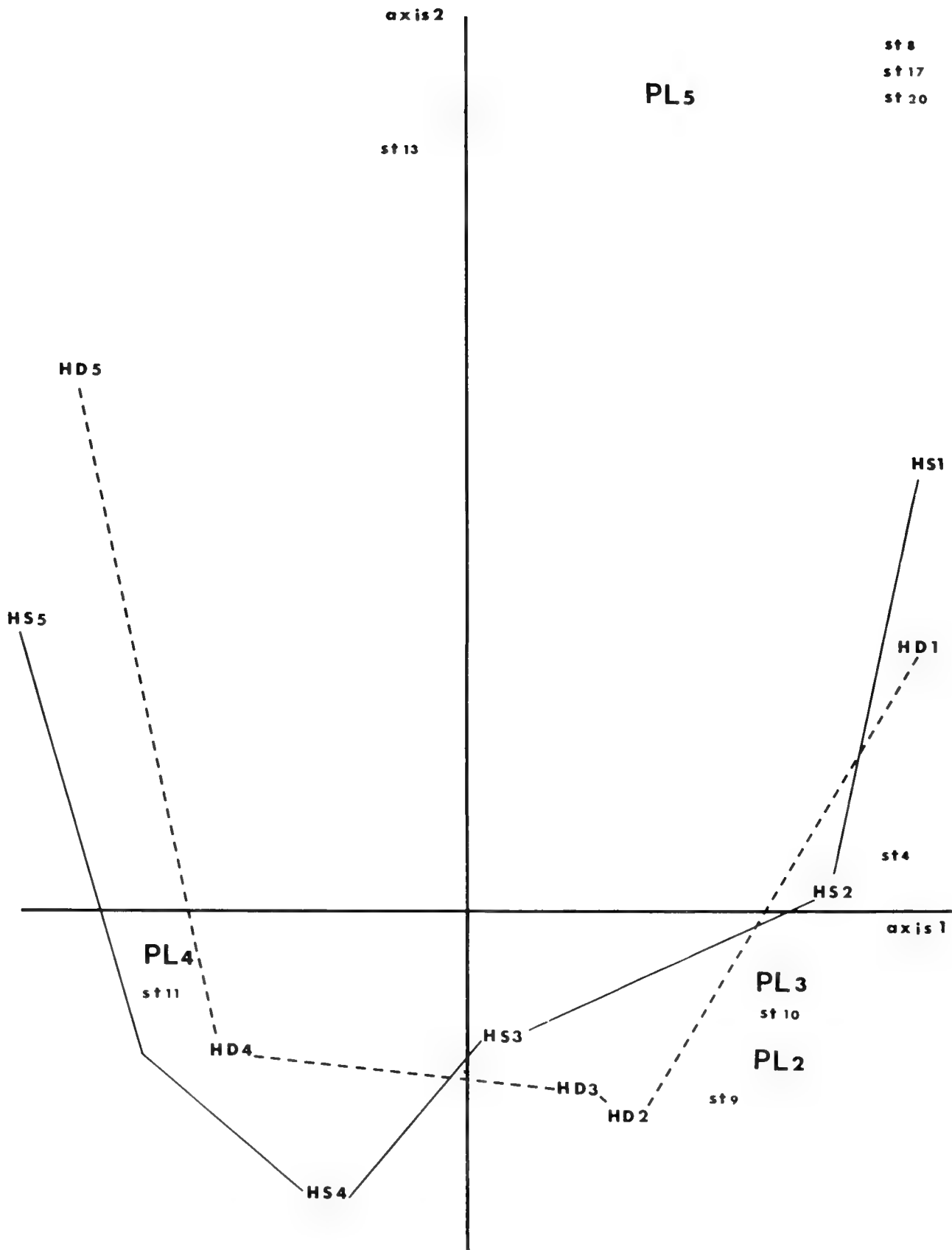


FIG. 14. Factor analysis of *P. montrouzieri* for rainfall (PL) size (HD) and shape (HS); projection of the variables and of the stations. The axes 1 and 2 have each 0.72 and 0.53 as proper values and represent 20 and 15% of the variance.

clear. Large and slender shells are associated with very low rainfall, small and stout shells with high rainfall and very stout shells with very high rainfall. As the species occupies a geographic range exhibiting a climatic patch-

work, the clines caused by the same mechanism as the preceding ones cannot be observed over a distance exceeding a few tenths of a kilometer and, as a result, geographic variations look random.

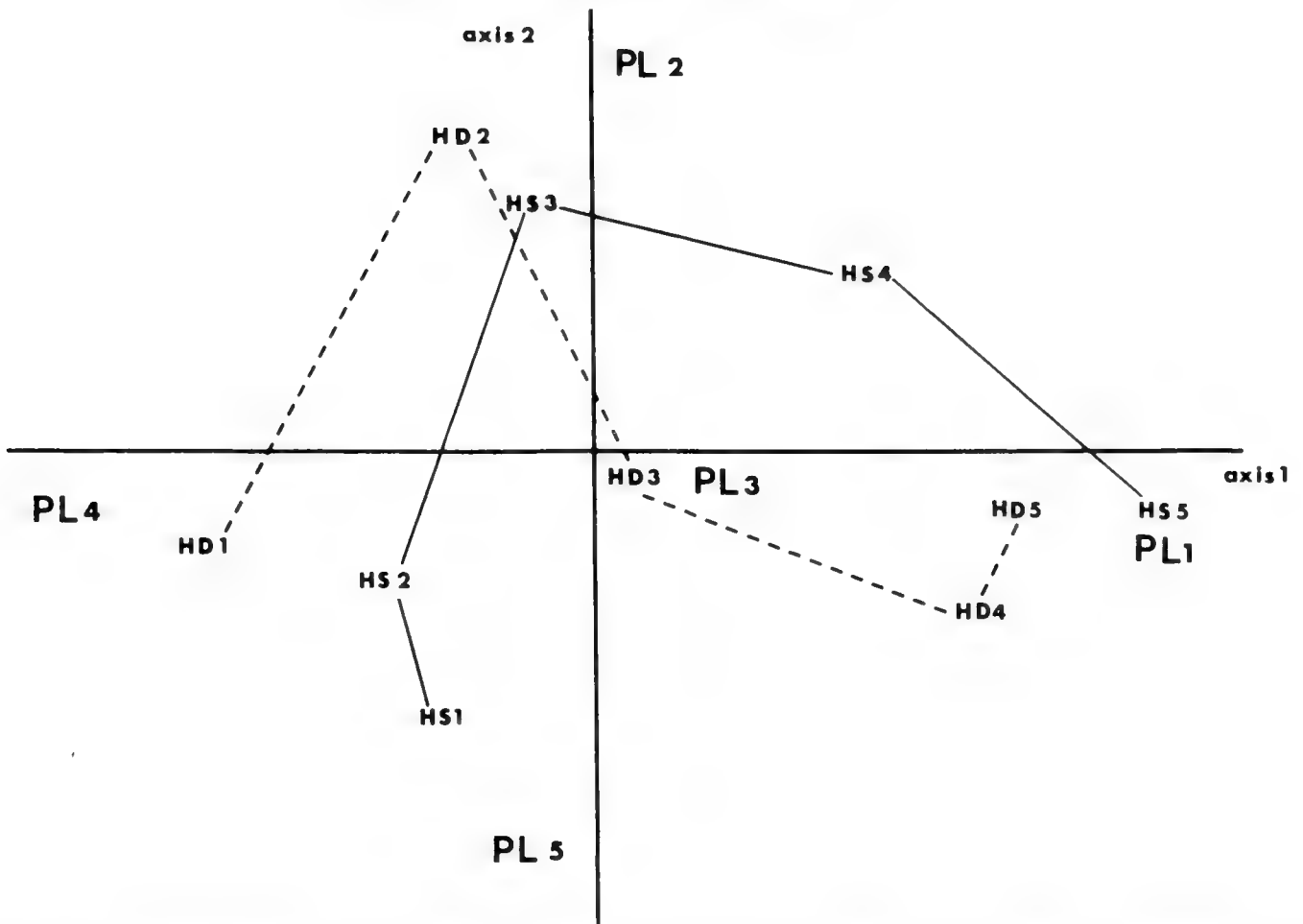


FIG. 15. Factor analysis of *P. mariei* for rainfall (PL), size (HD) and shape (HS); projection of the variables. The axes 1 and 2 have each 0.64 and 0.49 as proper values and represent 16% and 12% of the variance.

Palaina boucheti (Fig. 16) shows the same trends as *P. mariei*. A cline of increasing sizes from high to low rainfall is seen, together with a cline for shape associating the two stoutest classes with the two highest rainfalls and the three most slender classes with the two lowest rainfalls.

A similar diagram for *Palaina opaoana* is impossible to interpret, except for the association of large sizes and high rainfall. This may be due not only to large differences in sample sizes (50% of the specimens in a single station), but also to interaction with *Palaina montrouzieri*.

In conclusion it may be said that rainfall (and thus moisture) influences both size and shape. Its effect on shape is constant, but size increases with rainfall in some species and decreases in some others. Rainfall possibly does not directly influence shell size. This action of rainfall may explain the large clines in the northern mainland where climatic change is continuous over large distances, as the apparent random variation which is found further south and east; the latter being in fact clines

over small distances. However, influence of rainfall does not explain all the observed variation. The hypothesis involving species interaction will now be explored.

Interaction of species and character displacement

Peake (1973) remarked that sympatric species of Solomon Islands diplommatinids do not overlap morphologically. Fig. 8 shows that, in New Caledonia, there are large zones of overlap of the morphological scatter of the species when all populations are considered. However, there is not one case where there is morphological overlap where species were collected together. The data on allopatry and sympatry are summarized in Table 2. The species which converge when allopatric and diverge when sympatric are: 1) *Palaina nissidiophila* and *P. mariei* in station 14; 2) *P. mariei* and *P. boucheti* in stas. 20, 50, 51, 52; 3) *P. opaoana* and *P. mariei* in stas. 21, 22, 27, 28; 4) *P. montrouzieri* and *P. opaoana* were found only to be allopatric, but in the

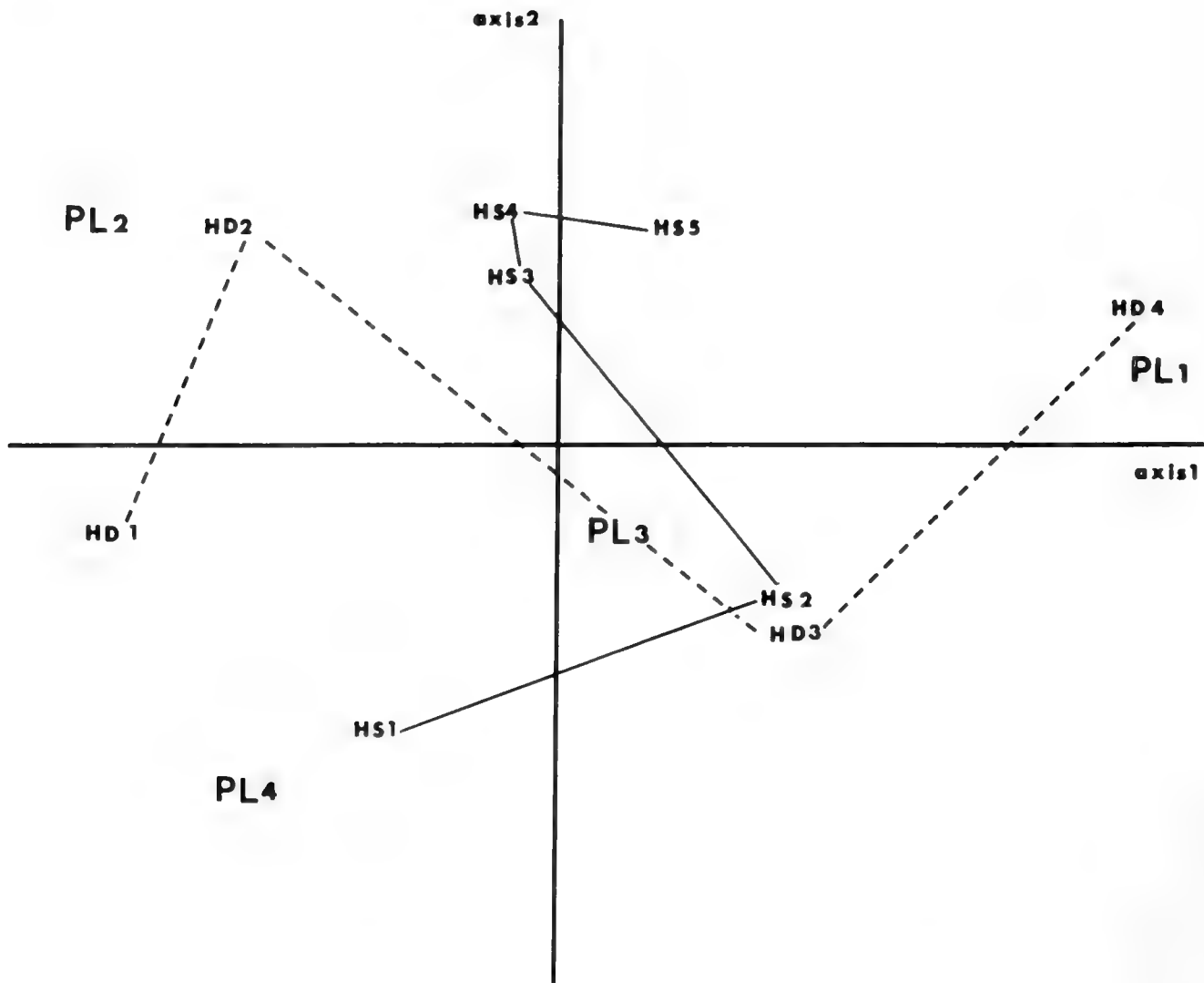


FIG. 16. Factor analysis of *P. boucheti* for rainfall (PL), size (HD) and shape (HS); projection of the variables. The axes 1 and 2 have respectively 0.62 and 0.45 as proper values and represent 19% and 14% of the variance.

same geographic range. *Palaina obesa* and *P. nanodes* were found sympatric with only much larger species.

In most cases it is the size scatter of the populations which appear reduced to avoid the overlap. An example is given for *Palaina opaoana* and *P. mariei* in Nindiah (sta. 22) as illustrated in Fig. 14. The displacement of size caused by sympatry may also be the origin of the aberrant position of station 13 (Pombeï) in Fig. 11. In the cline of *Palaina montrouzieri*, this station appears to be a good intermediate between dry and wet stations of the northeastern coast, but shell size is larger than expected there. This may be related with the fact that the largest *Palaina boucheti* were found in this station, fitting in their cline for size and rainfall.

In only one case do we have evidence for character displacement in shape. As seen in Fig. 10, *Palaina nissidiophila* has a clinal variation from northern small sizes to south-

ern larger sizes, correlated with a normal variation of the shell shape in the northern part of the range which abnormally reverses in the southern part. Between the region of Koumac (stas. 5, 6) and the Faténaoué valley (sta. 14), shells were expected to become stouter as rainfall increases but become more slender. In fact, as shown in Fig. 18, the place where the cline for shape reverses is the northern limit of the area of *Palaina mariei*, the scatter of which on a H/D diagram is the one which would have been expected for *P. nissidiophila* in this region.

Two solutions may be proposed here to explain these character displacements. If we admit that competition for food occurs, which is quite possible as far as all species have the same radula, differences in shell shape and/or size could allow sympatric species to exploit different sizes of interstices in the same leaf litter; or the presence of several species in the same leaf litter could cause

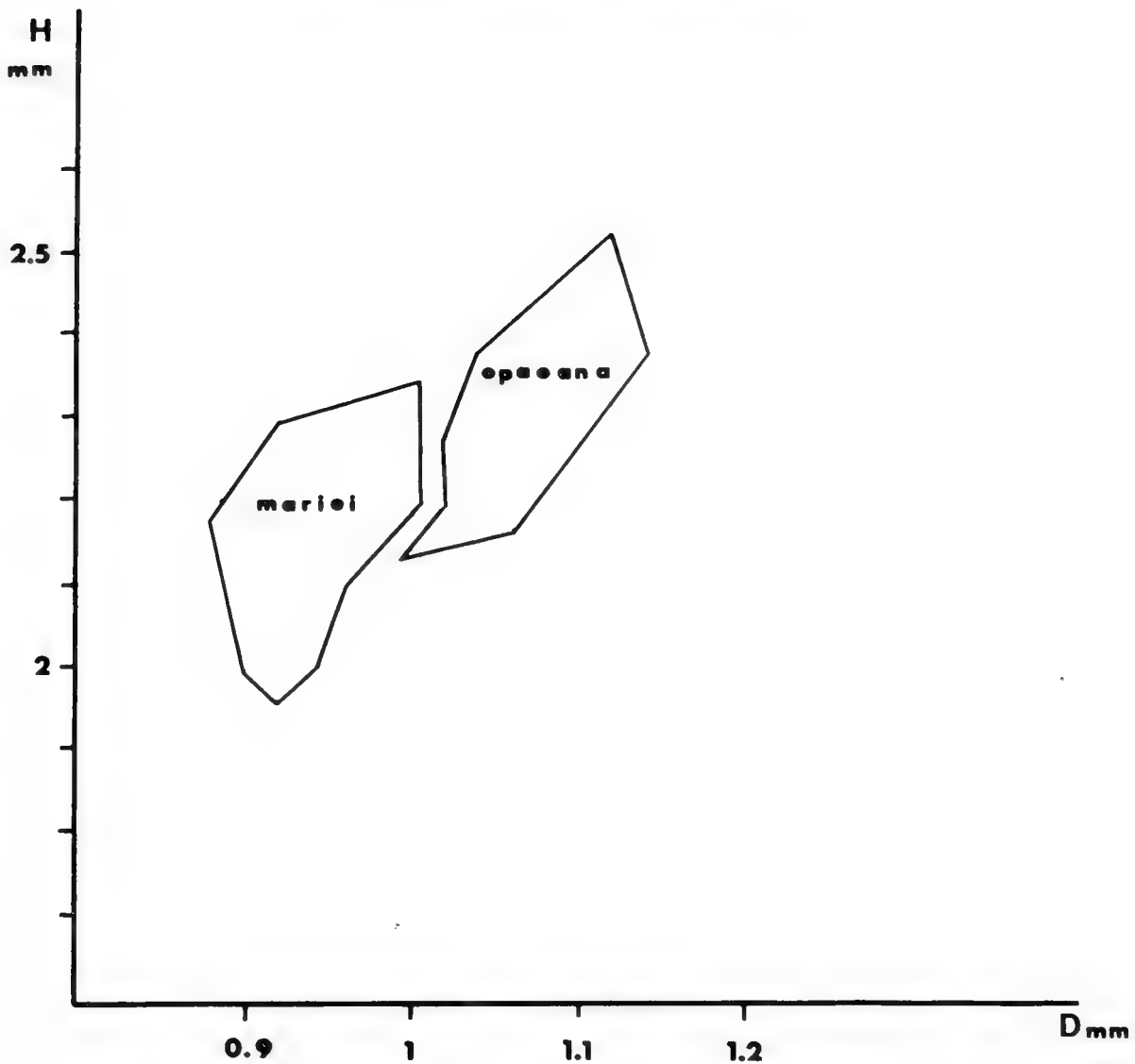


FIG. 17. Reduced scatter of H and D in sympatric *P. opaoana* and *P. mariei* from Nindiah (sta. 22). Compare with the scatter of the whole species, Fig. 8.

them to live outside of their optimal range of moisture, so that different shell shapes or sizes would be selected. On the other hand, males have no penis and if individuals do not recognize each other chemically for mating (which we do not know), we can postulate that they recognize each other by shell shape and size. Thus the animals having the same shape and size, but belonging to different species, would be less successful in reproduction, often mating with the wrong partners, and would be eliminated generation after generation, provoking the morphological divergence of sympatric populations. Of course the observed character displacements can also be the result of the combination of factors proposed here as well as some others that we do not suspect.

As character displacement seems so common, the observed clinal variations in New Caledonian diplommatinids could be the re-

sult of coevolution of species having adjacent scatters for H and D. The final and purely theoretical stage of such a coevolution, which can never be attained because environment is not constant through time, would be the establishment of parallel clines of all species over all of mainland New Caledonia. Several tests have been made to try to demonstrate the interdependency of the clines of the various species, this interdependency being interpretable as the result of such an evolutionary process. Unfortunately, and as only factor analysis could be accepted for methodological reasons explained earlier, the results were not more conclusive than the simple H/D diagrams. However two remarks can be made: First, the clines of *Palaina mariei* and *P. boucheti*, which both occur over nearly all the mainland, are roughly parallel (Figs. 15, 16), so that identical shells are found in both species, but in different environmental conditions:

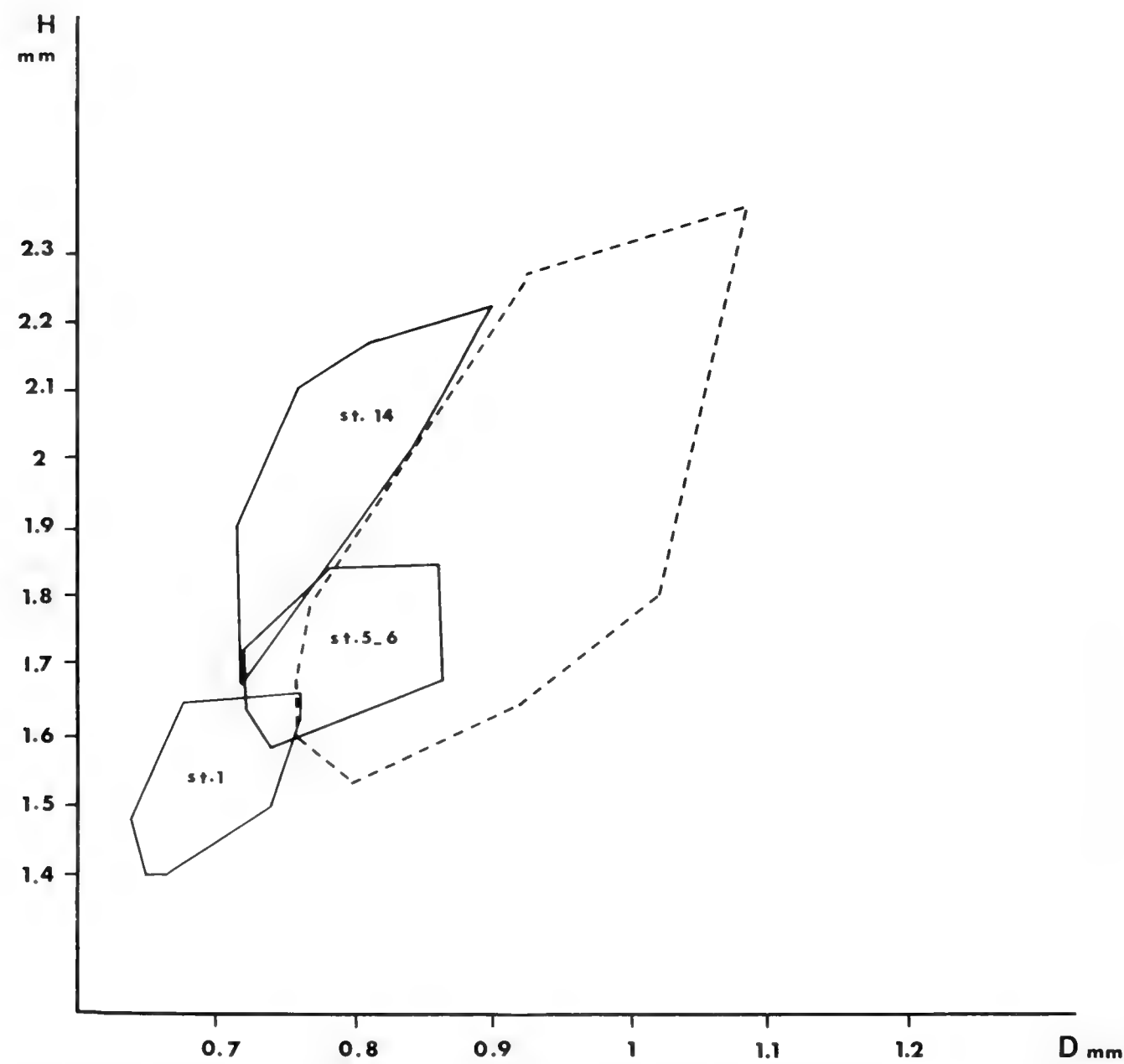


FIG. 18. Character displacement in shell shape of *P. nissidiophila*. Clinal scatter from sta. 1 to sta. 14 in full lines; scatter of *P. mariei*, sympatric with *P. nissidiophila* in sta. 14, in dotted line.

that is shown by the shells of the Figures 21I and 24B–24D, but the *P. mariei* shell comes from the extreme south whereas the *P. boucheti* shells come from the extreme north. Secondly, *Palaina montrouzieri* and *P. opaoana* seem to exclude each other over the entire geographic range of the latter. In central western New Caledonia, only *Palaina opaoana* was found at low altitudes and only *P. montrouzieri* was found at high altitudes. Shapes correlated with the rainfall found in this region are missing in the H/D diagram of *P. montrouzieri* (Fig. 8), and we have seen that no interpretable cline is found in the known material of *P. opaoana*. This could indicate species interaction on a large scale.

Implications for diplommatinine systematics

As the shells vary so enormously, no one considering only a few samples representative of the extreme forms would hesitate to consider them as belonging to different species. As nearly all diplommatinine species have been described from single samples, it is probable that a large proportion of the specific names are synonyms. It has already been demonstrated that four states are found in female genital apparatus. These four states probably represent four steps of the same evolutionary process but, although I believe that this process is the loss of the seminal receptacle, I have no argument

which proves that it is not the acquisition of the receptacle. The steps of this process are found in all parts of Melanesia, and probably over the entire range of the Diplommatinidae. On the other hand, the species found in one region look more similar to each other than to the species found elsewhere. For example, nine Solomon Islands species have a mean H/D ratio of about 1.94, whereas New Caledonian species have a mean H/D ratio of about 2.16. Because we know that this ratio depends on rainfall in New Caledonia and because the Solomon Islands are wetter than New Caledonia, it is not possible to use this apparent general dissimilarity as a supraspecific character. Thus, in the *Diplommatina-Palaina* group, we have no argument, either anatomical or conchological, to determine what is convergence and what is monophyletism and as a result cannot at the moment discriminate any supraspecific group.

DESCRIPTION OF SPECIES

In the lists of materials, each sample is defined by the number of the station (locality indicated in Table 1 and Fig. 7) and the number of specimens in brackets. The abbreviations used are: AMS, Australian Museum, Sydney; MNHN, Muséum national d'Histoire naturelle, Paris; NMNZ, National Museum of New Zealand, Wellington.

Palaina montrouzieri (Crosse, 1874)

Figs. 19, 20

Diplommatina montrouzieri Crosse, 1874a: 110; Crosse, 1874b: 394, pl. 12, fig. 8 (Baie du Sud).

Palaina montrouzieri (Crosse), Franc, 1957: 41, pl. 4, fig. 48; Solem, 1961: 427; Kobelt, 1902: 401.

Diplommatina sp., Hedley, 1898: 103, fig. 11 (Oubatche).

Holotype: Baie du Sud, MNHN; Fig. 19B.

Other material: sta. 4 (12), sta. 8 (1), sta. 9 (> 50), sta. 10 (27), sta. 11 (> 50), sta. 13 (4), sta. 20 (4), sta. 17 (2).

Preserved material: sta. 4, sta. 10, sta. 11, sta. 13, sta. 20.

Geographic range: probably nearly all of New Caledonia, except the northern point and the western coastal border; possibly absent from the Mt. Guemba southeastern coastal

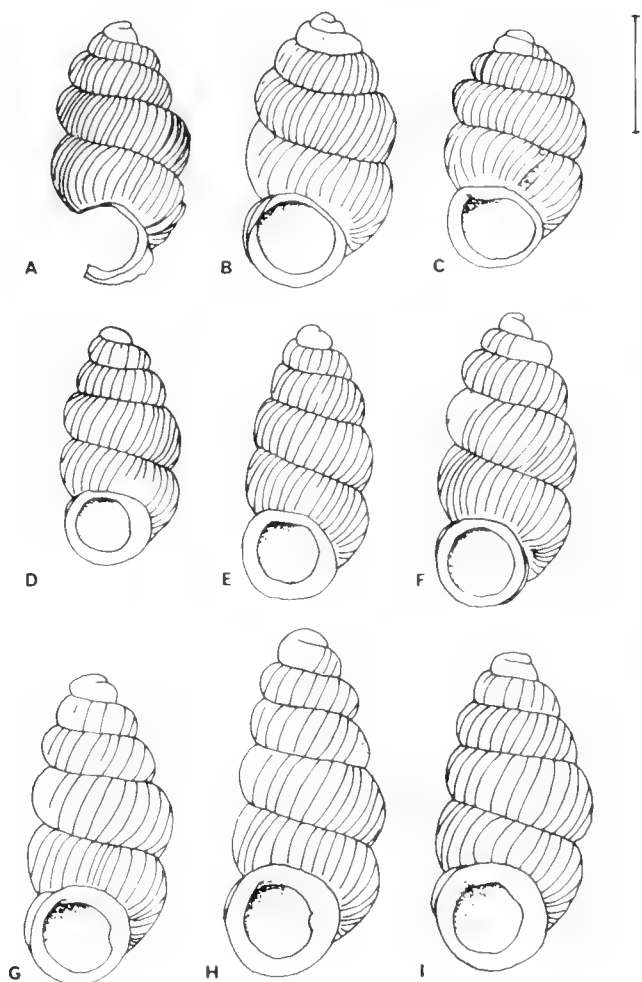


FIG. 19. Shells of *Palaina montrouzieri*. Scale line 1 mm. A, Aoupinié (sta. 17); B, holotype, Baie de Prony (sta. 51); C, Paéoua (sta. 20); D and E, Tiébaghi (sta. 4); F, Kaala (sta. 9); G and H, Lindéralique (sta. 11); I, Kavatche (sta. 10).

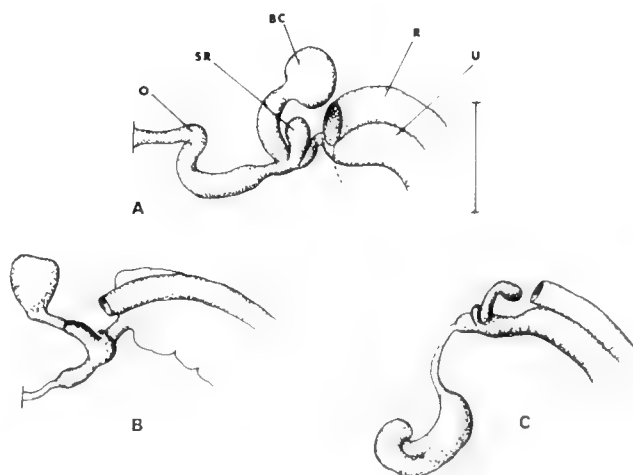


FIG. 20. Female genital anatomy of *P. montrouzieri*. Scale line 0.5 mm. A, Pombei (sta. 13); B, Lindéralique (sta. 11); C, Tiébaghi (sta. 4). BC, bursa copulatrix; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

range. Although we did not collect it farther south than the Aoupinié (sta. 17), we have no reason to doubt the accuracy of the type locality.

Shell (Fig. 19): from 1.45×3.3 mm in Lindéralique (sta. 11) to 1.05×2.1 mm in the Tiébaghi (sta. 5) through a geographic cline. Stouter in the central range (Aoupinié), at high altitude in the western mountain masses (Paéoua) and in the southernmost region (Baie de Prony): from 1.4×2.4 mm to 1.24×2 mm. A small columellar tooth present in the northeastern coast samples, absent elsewhere. Radial ribs always *slightly oblique*, crowded at the middle, only slightly more crowded in the body whorl; more spaced in Lindéralique (sta. 11), closer when going farther from this locality in any direction.

Female genitalia (Fig. 20): bursa copulatrix rising upwards from the oviduct, with a nearly spherical head. Seminal receptacle a small elongated pouch, appressed along the bursa stalk but opening independently into the oviduct.

Recognition: the only New Caledonian species with the seminal receptacle opening into the oviduct. Shell dimensions overlapping with those of *Palaina mareana*, *P. kuniorum*, *P. opaoana* and probably *P. mariei*. The latter is only smaller, and without anatomical data the distinction between the largest *P. mariei* and the smallest *P. montrouzieri* is delicate in the regions where they are potentially sympatric (see the case of the Nindiah population here attributed to *P. mariei*). *P. mareana* and *P. kuniorum* are always allopatric with *P. montrouzieri*; the former is more regularly conical, with more impressed sutures, more convex whorls and radial ribs much more spaced. *P. kuniorum* has the body whorl more constricted and has also radial ribs more spaced, particularly on the upper whorls, although less than in *P. mareana*. *P. opaoana* is potentially sympatric with *P. montrouzieri* and have about the same size. Apart from the anatomical differences, it is in most cases easily recognized by its radial ribs largely spaced on the first whorls and crowded on the last ones.

Remark: Franc's (1957) drawing of the holotype, "voluntarily" (*sic*) drawn without a camera lucida, is very different from the specimen, here depicted in Fig. 19B.

***Palaina mariei* (Crosse, 1867)**

Figs. 21, 22

Diplommatina mariei Crosse, 1867: 179, pl. 7, fig. 6 (Nouméa).

Palaina (*Cylindropalaina*) *mariei* (Crosse), Kobelt, 1902: 408; Franc, 1957: 41, pl. 4, fig. 49; Solem, 1961: 428.

Palaina montrouzieri var. *humilior* Cockerell, 1930: 20, fig. 2; Solem, 1960a: 5; Solem, 1961: 428 (near Bourail).

Lectotype (here designated): Nouméa (sta. 41), MNHN; fig. 21G.

Paralectotypes: 2 specimens labelled "var. type" by Crosse + 1 shell from H. Fischer ex Crosse ex Marie, 1966—all in MNHN.

Other material: sta. 9 (50), sta. 10 (12), sta. 14 (5), sta. 15 (3), sta. 18 (2), sta. 19 (2), sta. 20 (2), sta. 21 (36), sta. 22 (39), sta. 23 (>50), sta. 24 (3), sta. 28 (40), sta. 26 (1), sta. 27 (2), sta. 31 (6), sta. 32 (1), sta. 33 (6), sta. 38 (1), sta. 39 (numerous juv.), sta. 40 (2), sta. 42 (2), sta. 44 (2), sta. 49 (3), sta. 50 (1), sta. 51 (13).

Preserved material: sta. 9, sta. 15, sta. 18, sta. 19, sta. 21, sta. 24, sta. 27, sta. 28, sta. 31, sta. 39, sta. 42, sta. 44, sta. 49.

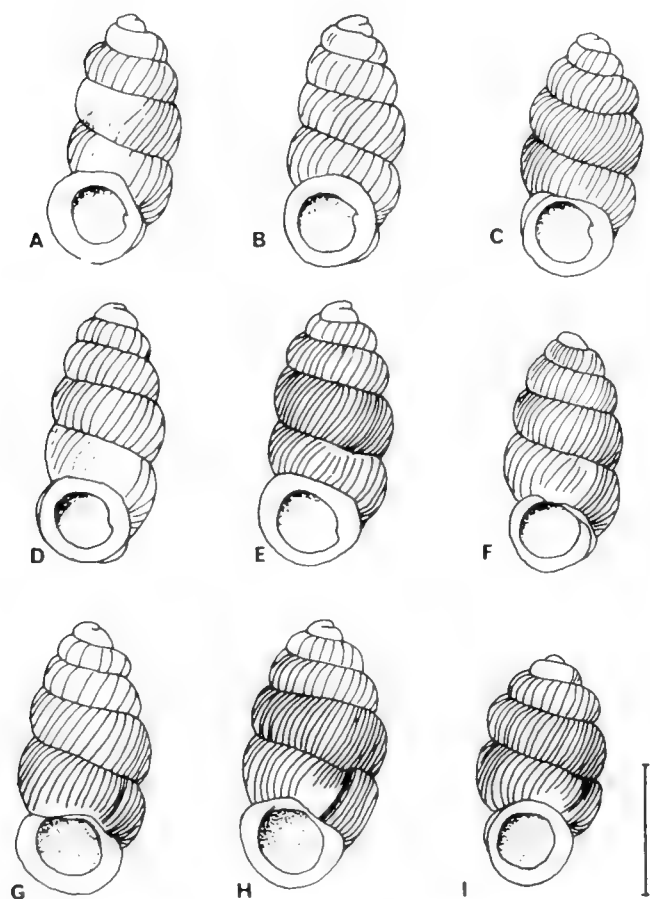


FIG. 21. Shells of *Palaina mariei*. Scale line 1 mm. A, Kaala (sta. 9); B, Nékliai (sta. 21); C, Poindimié (sta. 15); D, Plaine aux Gaiacs (sta. 23); E, Goipin (sta. 18); F, Mamié (sta. 44); G, lectotype, Nouméa (sta. 41); H, Baie de Prony (sta. 51); I, Mt. Oungoné (sta. 52).

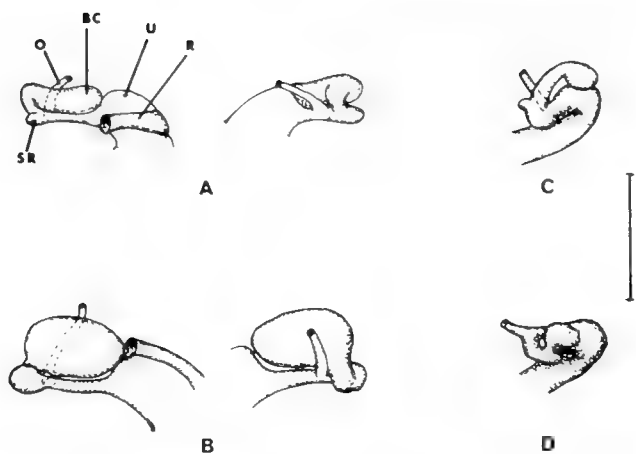


FIG. 22. Female genital anatomy of *P. mariei*. Scale line 0.5 mm. A and B, Mé Maoya (sta. 28); C, Baie Tina (sta. 42); D, Col des Roussettes (sta. 26). BC, bursa copulatrix; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

Geographic range: nearly all the mainland, except possibly the northern point and the northeastern mountain range. Frequent along the coastlines, rather uncommon in the central and southern ranges.

Shell (Fig. 21): dimensions varying from 1.1×2.4 mm to 0.8×1.6 mm probably through numerous clines. Stouter in the southernmost mainland, with dimensions reaching 1×1.8 mm to 0.86×1.7 mm on the Mt. Oungoné (sta. 52). A columellar tooth generally present farther north than Bourail, absent farther south. Radial ribs as in *P. montrouzieri*; more spaced along the western coast, closer when going eastwards, or southwards from Nouméa.

Female genitalia (Fig. 22): the basal part of the stalk of the bursa copulatrix prolongs the distal oviduct from which the proximal oviduct diverges inwards and upwards. The upper part of the stalk, which is longer than the basal one, bends back along the distal oviduct in such a way as the more or less inflated bursa head is appressed against the proximal end of the uterus. The seminal receptacle is a swelling which prolongs the basal part of the bursa stalk outside of the bend of the latter. Two dispositions are found: farther north than the Col des Roussettes (sta. 27), the basal part of the bursa stalk is parallel to the spire; farther south, it is bent downwards.

Recognition: only *Palaina obesa* has a similar female genital anatomy in New Caledonia. It is found only in the northeastern range, is smaller and has more spaced radial ribs on the upper whorls. The dimensions of the shells of *P. mariei* overlap with those ob-

served in *P. opaoana*, *P. boucheti* and *P. nissidiophila*, but it was found sympatric with all three. The former is generally larger, never has a columellar tooth, and has more widely spaced ribs on the upper whorls. *P. boucheti* is generally smaller, more cylindric and has closer radial ribs on the upper whorls. *P. nissidiophila* has a shape varying from cylindrical to conical, but its sutures are less impressed and its whorls less convex than those of *P. mariei*; it also has much closer radial ribs, and a more oblique aperture.

Remarks: the specimen labelled by Crosse "var. B" is here selected as the lectotype because the two shells labelled "var. type" are very badly preserved.

No preserved specimen was obtained from Nindiah (sta. 22), and this sample could have been attributed to *P. montrouzieri*. It is here identified as *P. mariei* because shell dimensions are closer to those of the *P. mariei* found in the same region. If it proves to belong to *P. montrouzieri*, the character displacement shown in Fig. 14 would be much greater than proposed here.

***Palaina obesa* (Hedley, 1898)**

Fig. 23

Diplommatina obesa Hedley, 1898: 102, fig. 10 (Oubatche).

Palaina (Macropalaina) obesa (Hedley), Kobelt, 1902: 410; Franc, 1957: 41–42, pl. 4, fig. 50.

Palaina obesa (Hedley), Solem, 1961: 428.

Type material (not seen): Oubatche, AMS (sta. 8).

Other material (preserved): sta. 7 (3).

Geographic range: northeastern range (= Chaîne du Panié).

Shell (Fig. 23A, C): from 1.4×0.75 mm to 1.6×0.8 mm, very stout. Columellar tooth present or absent. Radial ribs distinctly more widely spaced on the upper whorls than on the following ones.

Female genitalia (Fig. 23B): bursa stalk straight and rather short, perpendicular from the oviduct upwards. The seminal receptacle is a very short pouch, prolonging the distal oviduct through the basis of the bursa copulatrix. It opens into the stalk, and not directly into the oviduct.

Recognition: *Palaina obesa* is distinct from both *P. mariei* and *P. boucheti* by its female genital anatomy. A similar disposition is found in *P. mariei* but the portion of the bursa stalk between the oviduct and the seminal recepta-

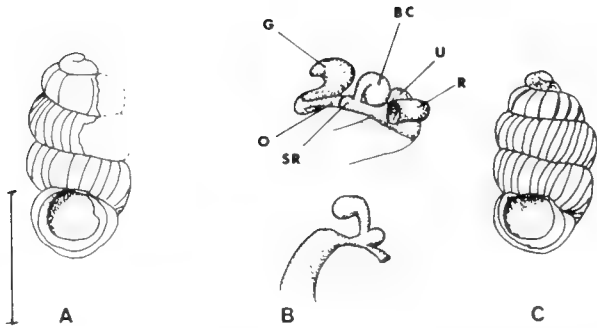


FIG. 23. *Palaina obesa*, Mandjéla, sta. 7. Scale line 1 mm. A and C, shells; B, female genital anatomy. BC, bursa copulatrix; G, gonad; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

cle is much shorter in *P. obesa*. The shell differs from the shell of *P. mariei* by its smaller size and by the more widely spaced radial ribs of the upper whorls. *P. obesa* is convergent with the smallest *P. boucheti*, except for the anatomy and the spacing of the ribs; but the latter reaches its maximum size in the north-eastern region where it is potentially sympatric with the much smaller *P. obesa*.

***Palaina boucheti* Tillier, n.sp.**

Figs. 24, 25

Holotype: Mé Ori, 530 m, P. Bouchet coll. 30.4.1979 (sta. 29), MNHN.

Paratypes: 11, same locality.

Other material: sta. 12 (14), sta. 13 (10), sta. 16 (1), sta. 20 (4), sta. 36 (1), sta. 45 (1), sta. 46 (3), sta. 47 (8), sta. 48 (12), sta. 50 (34), sta. 52 (4), sta. 51 (4).

Preserved material: type locality, sta. 12, sta. 13, sta. 20, sta. 46, sta. 47, sta. 48.

Geographic range: central New Caledonia farther south than Kaala-Gomen; absent from the western coastal plains and probably from the eastern coastline; probably replaced by *P.obesa* to the northeast of its range. Littoral only around the southernmost range, from the Ouinné river to the Baie de Prony.

Shell (Fig. 24): from 0.86 × 1.7 mm to 0.75 × 1.4 mm in the type series, reaching 1 × 1.7 mm to 0.86 × 1.8 mm elsewhere. Generally smaller and more cylindric than *P. mariei*. A columellar tooth present or absent in northern New Caledonia (Taom sta. 12, Pombei sta. 13, Paéoua sta. 20), always absent farther south.

Female genitalia (Fig. 25): no seminal receptacle. The bursa stalk goes downwards from the oviduct. Two dispositions are found: in western samples (sta. 20, sta. 12, sta. 29),

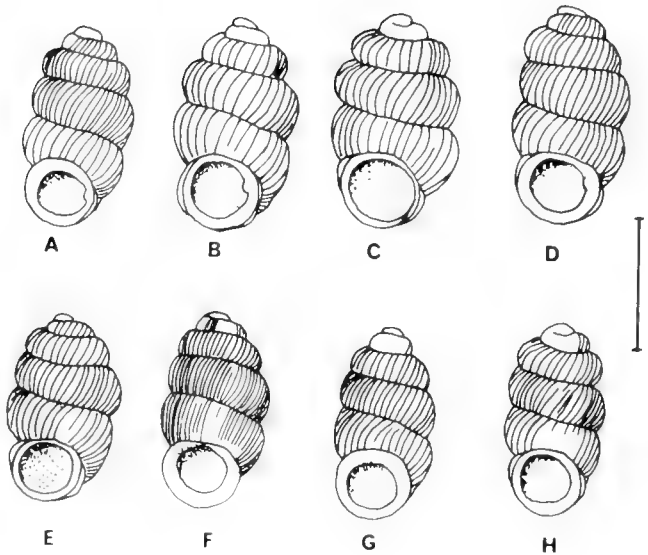


FIG. 24. Shells of *Palaina boucheti*. Scale line 1 mm. A, Taom (sta. 12); B and C, Paéoua (sta. 20); D, Pombei (sta. 13); E, Mt. Guemba (sta. 47); F, Touaourou (sta. 48); G and H, Mé Ori (sta. 29, paratypes).

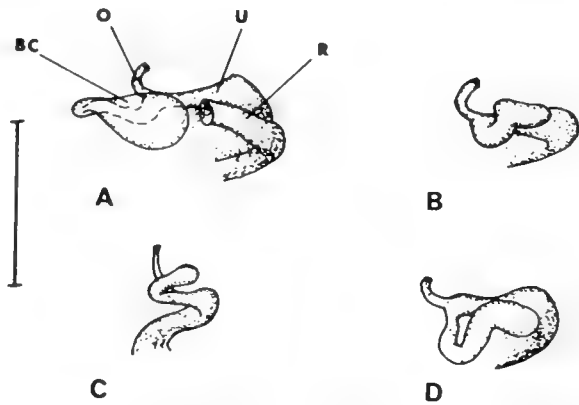


FIG. 25. Female genital anatomy of *P. boucheti*. Scale line 0.5 mm. A, Paéoua (sta. 20); B, Touaourou (sta. 48); C, Taom (sta. 12); D, Pombei (sta. 13). BC, bursa copulatrix; O, oviduct; R, rectum; U, uterus.

the basal part of the stalk runs parallel to the spire before bending upwards back to the proximal uterus, whereas in the eastern samples (sta. 13 to Touaourou sta. 48), the basal part of the stalk goes downwards parallel to the shell axis before bending back.

Discussion: the largest *Palaina boucheti* have shells completely convergent with the smallest *P. mariei* (Figs. 21I, 24D) but in different environmental conditions and in different parts of the common range of the two species. In such cases, dissection is necessary to check the presence or absence of a seminal receptacle. The dimensions of *P. boucheti* also overlap with those of *P. nissidiophila* which was never found sympatric with it, be-

ing a species found in dry environments in northwestern New Caledonia. *P. boucheti* has much more impressed sutures and rounded whorls, and much less crowded radial ribs.

***Palaina nissidiophila* Tillier, n.sp.**

Fig. 26

Holotype: Niénane (Iles Daos du Nord), Bouchet and Chérel coll., 23.8.78 (sta. 3), MNHN; Fig. 26B.

Paratypes (all dry): 9, same locality.

Other material (all dry): sta. 1 (50), sta. 2 (1), sta. 5 (21), sta. 6 (25), sta. 14 (50).

Geographic range: from Pott (Belep Islands) to the Koniambo mountain through Art, the Daos du Nord Islands, the northern point (probably) and the northwestern coastal plains.

Shell (Fig. 26): from 0.65×1.4 mm in Pott (sta. 1) to 0.85×1.8 mm in Koum (sta. 6) through a geographic cline, reaching 0.9×2.2 mm farther south. Suture not impressed and whorls generally only slightly convex; shape nearly cylindrical from Pott to Koum, becoming an elongated cone farther south. A small columellar tooth present in Le Cresson (sta. 5), present or absent in Koum (sta. 6), absent elsewhere. Peristome thicker than in other New Caledonian species, always oblique. Radial ribs always very crowded.

Discussion: the non-impressed sutures and the crowded ribs make *P. nissidiophila* easy to recognize. It is sympatric with *P. mariei* south of Koum (sta. 6) to the Koniambo (sta. 14) and thus there is no doubt about their specific distinction. Without anatomical data, there are less arguments for considering it as specifically distinct from *P. boucheti* which is always allopatric with it. The reason which makes me consider *P. nissidiophila* a distinct species is the large gap between it and *P. boucheti* in ornamentation and whorl contour. Geographically, they are found near one another.

***Palaina nanodes* Tillier, n.sp.**

Fig. 27

Holotype: Touaourou, 10 m, Bouchet coll. 8.12.1978 (sta. 48), MNHN.

Paratypes (8 preserved): 17 specimens, same sample.

Geographic range: *P. nanodes* was found only in Touaourou, but probably occurs along

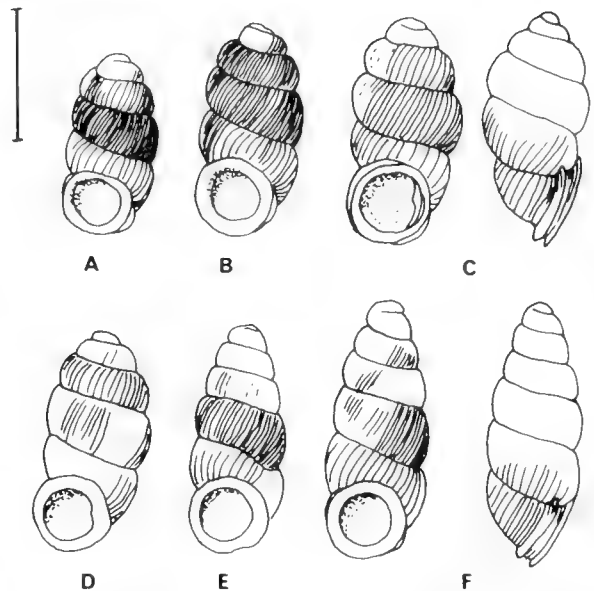


FIG. 26. Shells of *Palaina nissidiophila*. Scale line 1 mm. A, Pott (sta. 1); B, Holotype, Niénane (sta. 3); C, Le Cresson (sta. 5); D and E, Koum (sta. 6); F, Faténaoué (sta. 14).

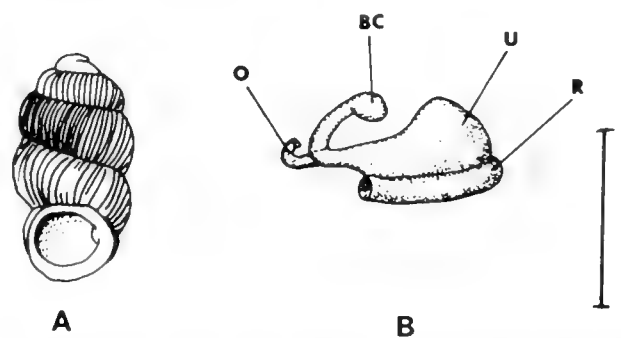


Fig. 27. *Palaina nanodes* Tillier, n. sp. Scale line A, 1 mm; B, 0.5 mm. A, shell; B, Female genital anatomy; both paratypes from Touaourou (sta. 48).

the coast, on the upraised reef between Yaté and Goro. At least one much bigger *Pararhytida* has the same odd range.

Shell (Fig. 27A): probably the smallest of all described *Palaina-Diplommatina* species, from 0.6×1.05 mm to 0.7×1.38 mm. Otherwise looks like a very small *P. boucheti*, but has closer radial ribs. Columellar tooth present or absent.

Female genitalia (Fig. 27B): no seminal receptacle. A very short portion of the bursa copulatrix stalk prolonging the distal oviduct, a much longer portion bent back upward to the proximal end of the uterus. A small rounded bursa head.

Discussion: there is no overlap for dimensions with any other New Caledonian species. The smallest *P. nissidiophila* are more slender (but found in drier conditions), with less impressed sutures, and *P. nanodes* was found sympatric with *P. boucheti*.

***Palaina kuniorum* Tillier, n.sp.**

Fig. 28

Holotype: Ouro, Ile des Pins, Bouchet coll. 21.10.1978. (sta. 53), MNHN; Fig. 28B.

Paratypes (all dry): 13, same sample.

Geographic range: Ile des Pins (called Kunié by Melanesians).

Shell (Fig. 28): in the only population collected, dimensions from 3.5×1.45 mm to 3×1.3 mm. Holotype 3.35×1.4 mm. No columellar tooth. Radial ribs rather widely spaced, closer on the body whorl. Body whorl distinctly constricted.

Discussion: the dimensions of *P. kuniorum* overlap those of *P. mareana*, which is easy to recognize by its more convex whorls and regularly conical shape. It seems closer to *P. montrouzieri*, from which it differs only by its more widely spaced radial ribs and more distinctly constricted body whorl. On the other hand the constriction of the body whorl is a variable character, but the form of *P. montrouzieri* from Lindéralique (sta. 11; Fig. 19G, H), which is the closest to *P. kuniorum* by its loose radial ribbing, has a more regularly conical shape (both are found on calcareous soils: does this allow a faster growth?). All the specimens of *P. montrouzieri* approaching *P. kuniorum* by their shell characters come from northern New Caledonia, but we know only the holotype as coming from the southern regions and may suspect that it is not very representative of the southern populations of *P. montrouzieri*. Lastly, there is a low probability for *P. montrouzieri* to occur along the coast of the mainland between Yaté and the Baie de Prony, that is the closest to the Ile des Pins and where P. Bouchet already collected four species. All these arguments

are contradictory, and the status of *P. kuniorum*, species or subspecies, will remain dubious as long as its female genital anatomy is not known. I have considered it a species because it could as well be related to *P. opaoana*, *P. mareana*, *Palaina* sp. or even to *P. perroquini* as conchological characters prove to be so variable.

***Palaina perroquini* (Crosse, 1871)**

Fig. 29

Diplommatina perroquini Crosse, 1871: 204; 1873: 44, pl. 12, fig. 8 (New Caledonia).

Palaina (Macropalaina) perroquini (Crosse), Kobelt, 1902: 410; Franc, 1957: 42, pl. 4, fig. 51.

Palaina perroquini (Crosse), Solem, 1961: 428.

Type material: the specimen depicted by Franc as the holotype, here redrawn in Fig. 29A, is probably not even type material: judging from the label it was given by Marie to Crosse in 1873, and we do not know whether

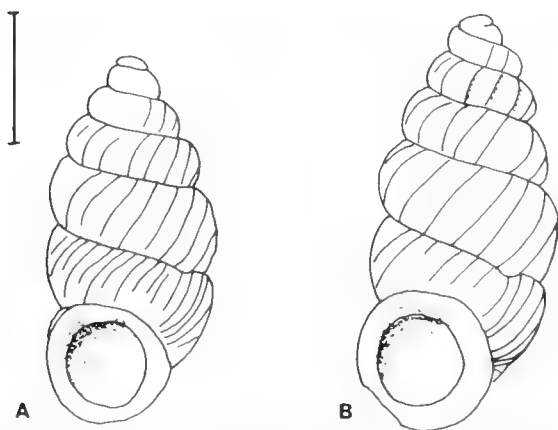


FIG. 28. *Palaina kuniorum* n. sp. Scale line 1 mm. Ouro, Isle of Pines (sta. 53). A, paratype; B, Holotype.

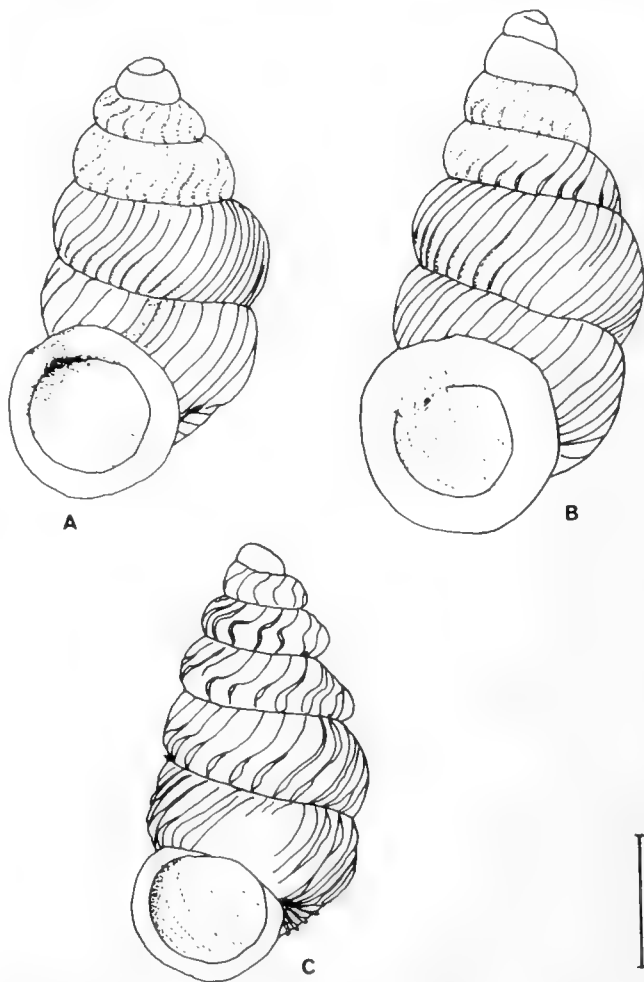


FIG. 29. *Palaina perroquini*. Scale line 1 mm. A and B, Baie de Prony (sta. 51) (A = specimen depicted as the holotype by Franc); C, Mt. Guemba (sta. 47).

Crosse had seen it previous to his first description in 1871. Two other samples, containing fifteen shells, are housed in the MNHN as acquired by Crosse from Petit in 1874. They are possibly syntypes, collected by Perroquin and given to Petit before 1871, and then acquired by Crosse, but we have no evidence to confirm that Crosse had seen them before his first description of the species. If necessary, Franc's "holotype" should be selected as a neotype, but *P. perroquini* is so easy to recognize that a neotype is not needed.

Other material: sta. 43 (1 + juv.), sta. 47 (4 + juv.), sta. 48 (3 + juv.), sta. 51 (14), plus about ten shells without accurate locality.

Preserved material: sta. 43, sta. 47, sta. 48.

Geographic range: southeasternmost part of the mainland, from the Yaté river to the Baie de Prony through the Plaine des Lacs, and further east to the coastline.

Shell (Fig. 29): from 1.5×3 mm to 1.85×4 mm. Regularly conical when tall, with penultimate whorl slightly inflated when short. Body whorl slightly constricted. No columellar tooth. Radial ribs *sigmoid on the upper whorls*, forming wing-like expansions in juveniles but more or less eroded in adults; more crowded on the last and often on the penultimate whorl.

Female genitalia: full adult not seen. In sub-adult females, the developing bursa copulatrix seems to be similar to the bursa found in *P. mareana* (Fig. 32), but I cannot be sure that there is no seminal receptacle at all outside of the bend of the bursa stalk, as is found in some Solomon Islands species and in the Australian *Palaina strangei* (Tillier, unpublished).

Recognition: the size, shape and sigmoid radial ribs of *P. perroquini* are not found in any other New Caledonian diplommatinid.

***Palaina opaoana* Tillier, n.sp.**

Figs. 30, 31, 32

Holotype: junction of the rivers running down the Mé Maoya and the Pic Poya, alt. 50 m, Tillier and Bouchet coll. 15.6.1979 (sta. 28), MNHN.

Paratypes (preserved): 10, same sample.

Other material: sta. 21 (2), sta. 22 (39), sta. 27 (4), sta. 30 (5), sta. 34 (>200), sta. 35 (5), sta. 37 (3).

Preserved material: sta. 21, sta. 27, sta. 28 (type locality), sta. 30, sta. 35, sta. 37.

Geographic range: central western New Caledonia between the latitude of Houaïlou and the Dzumac range (the latter is the last

mountain before the southern lowland). Probably never littoral.

Shell (Figs. 30, 31): from 1.3×2.9 mm to 1.1×2 mm; may be stouter, reaching 1.25×2 mm on the Dzumac (alt. 1000 m; sta. 37), or much more slender, reaching 1.1×2.6 mm in the dry Col des Arabes (Figs. 31D, E; sta. 34). Close to *P. montrouzieri* by its size and shape, but the upper whorls more convex. Radial ribs widely spaced and *parallel to the shell axis on the upper whorls* (closer and oblique in *P. montrouzieri*), close and slightly oblique on the following ones.

Female genitalia (Fig. 32): no seminal receptacle. Bursa stalk going outwards and downwards from the oviduct before bending back parallel to the oviduct in the westernmost samples (sta. 37, sta. 28, sta. 21). In central and eastern samples, the bursa stalk goes downwards almost perpendicular from the oviduct and bursa head is in the centre of the intestinal loop instead of being appressed against the proximal end of the uterus. The intermediate position is found in the Col des Roussettes (sta. 27).

Recognition: differs from *P. montrouzieri* and from the largest *P. mariei*, which may

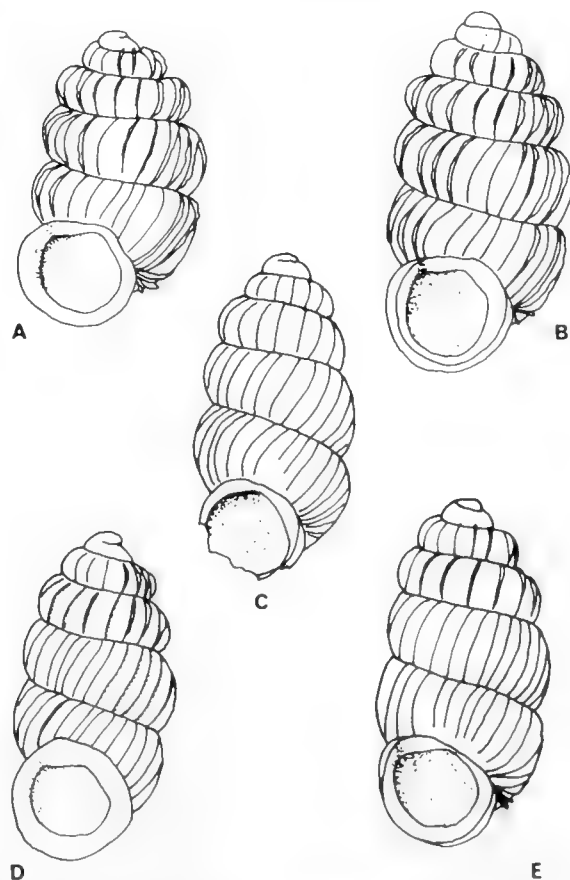


FIG. 30. Shells of *Palaina opaoana* Tillier, n. sp. Scale line 1 mm. A and B, Mt. Dzumac (sta. 37); C, Col des Roussettes (sta. 27); D and E, Mé Maoya (sta. 28); D, paratype; E, Holotype.

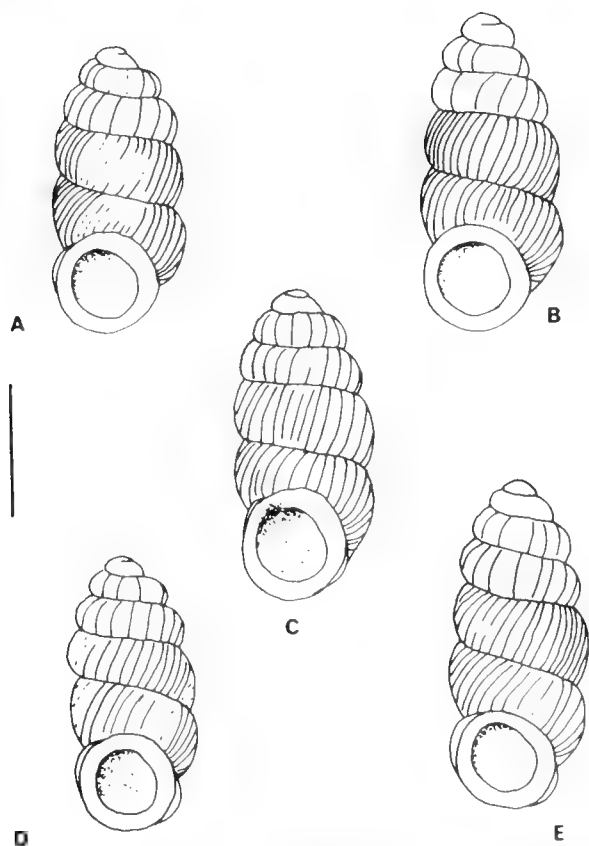


FIG. 31. *P. opaoana*. Scale line 1 mm. A and B, Dothio (sta. 30); C, Nassirah (sta. 35); D and E, Col des Arabes (sta. 34).

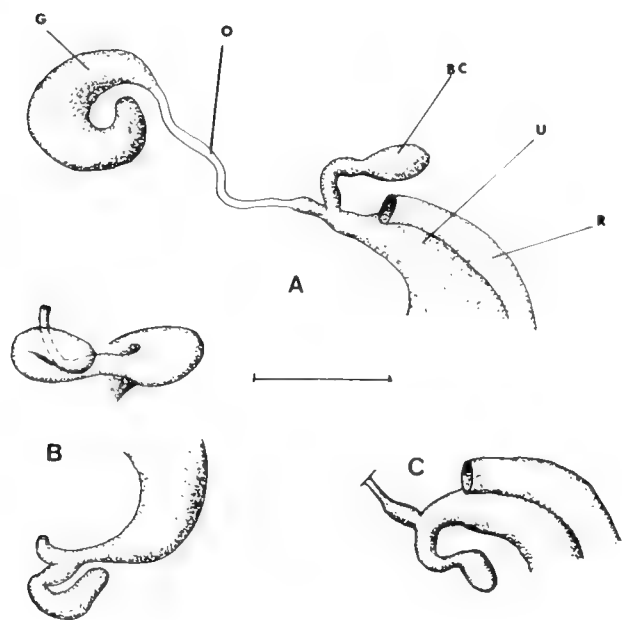


FIG. 32. Female genital anatomy of *P. opaoana*. Scale line 0.5 mm. A, Mé Maoya (sta. 21); B, Nassirah (sta. 35); C, Mt. Dzumac (sta. 37); BC, bursa copulatrix; G, Gonad; O, oviduct; R, rectum; U, uterus.

converge with it by their dimensions, by the female genitalia and by the radial ribs of the upper whorls. By shell size and genital anatomy, two geographic sets of population can be distinguished: one western, with larger shells (Fig. 30), and with the disposition of the bursa copulatrix shown in Fig. 32A, C; the second eastern, with smaller shells (Fig. 31) and the genital disposition shown in Fig. 32B; the transition is probably found nearby (intermediate found in the Col des Roussettes, sta. 27).

Palaina opaoana resembles the four (?) New Hebridean species, which have the same type of shell shape and sculpture, but whose anatomy is unknown.

***Palaina mareana* Tillier, n.sp.**

Figs. 33, 34

Holotype: Enéné, Maré Island, Bouchet coll. 7.4.1979 (sta. 54), MNHN.

Paratypes (preserved): 6, same sample.

Other material: sta. 55 (1), sta. 56 (5).

Preserved material: sta. 54 (type locality), sta. 56.

Geographic range: Maré Island, Loyalty Islands.

Shell (Fig. 33): from 1.4×3.7 mm to 1.2×2.8 mm, the largest shells being more regu-

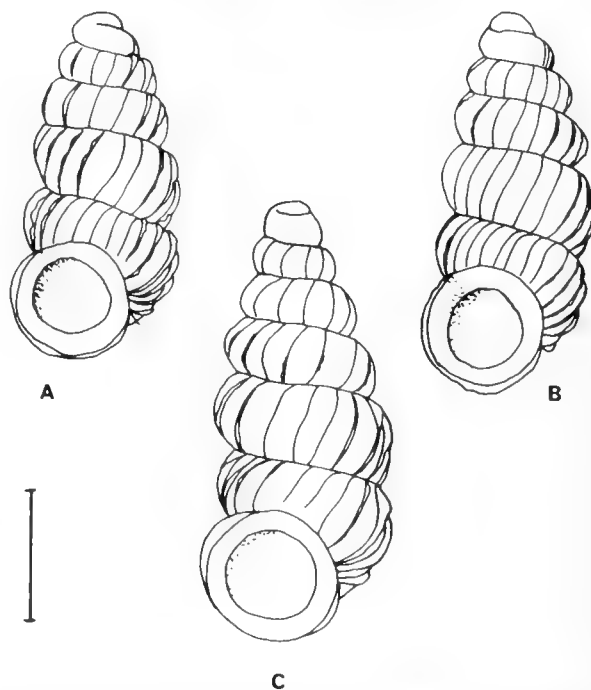


FIG. 33. *Palaina mareana* Tillier, n. sp. Scale line 1 mm. A and B, Nécé (sta. 56); C, Enéné (sta. 54), paratype.

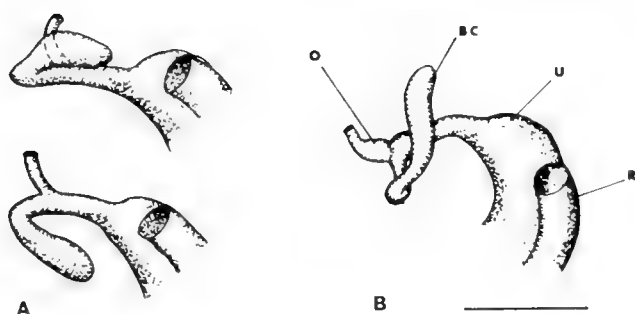


FIG. 34. Female genital anatomy of *P. mareana*. Scale line 0.5 mm. Paratypes, Enéné (sta. 54); BC, bursa copulatrix; O, oviduct; R, rectum; U, uterus.

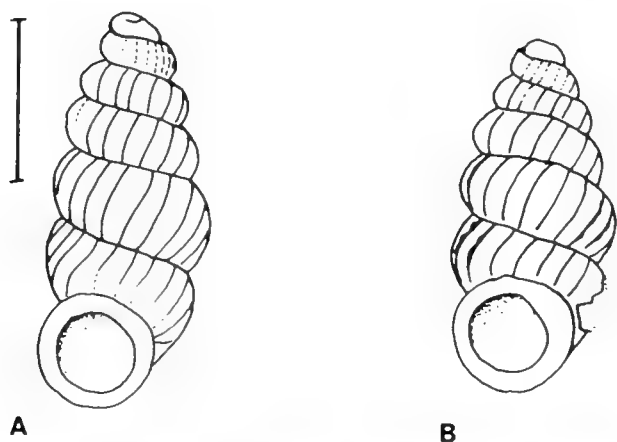


FIG. 35. Shells of *Palaina* sp., Adio (sta. 25). Scale line 1 mm.

larly conical than the smallest ones. Sutures impressed, whorls convex. Radial ribs always lamellar, widely spaced, often becoming slightly more crowded on the body whorl.

Female genitalia (Fig. 34): no seminal receptacle. Bursa copulatrix long and slender. Bursa stalk first running parallel to and under the oviduct and then bent back forwards to the proximal end of the uterus.

Discussion: distinct from any other New Caledonian species, the smaller *Palaina* sp. excepted, by its conical elongated shape, convex whorls and loose radial sculpture. Close to the Australian *P. strangei* in its shell characters, but the latter has a stouter shell and a seminal receptacle outside of the bend of the bursa stalk (Tillier, unpublished).

Palaina sp.

Fig. 35

Material (dry): three shells, the best preserved broken, sta. 25.

Geographic range: seems restricted to the calcareous outcrop of Adio (sta. 25).

Shell (Fig. 35): similar to *P. mareana* but smaller, the two preserved shells measuring 2.6×1.2 mm and 2.9×1.1 mm.

Discussion: although I do not believe it, these shells could be elongated *Palaina mariei* with a loose radial sculpture possibly due to the occurrence of calcareous rocks; but *P. mariei* is found unmodified on such rocks in Nindiah (sta. 22) and on the south-eastern upraised coral reef (sta. 45, sta. 49). I prefer to consider it a species which spread when calcareous rocks were not eroded and which is now restricted to the outcrop in Adio. If the elongated conical shape, convex whorls and loose sculpture are not correlated with calcareous rocks, *Palaina* sp. could be related with the Australian *P. strangei* and with *P. mareana*.

ACKNOWLEDGEMENTS

I am most grateful to Frédérique Vallée and Hughes Demongeot, who worked out the statistical treatment of the data in the Laboratoire de Statistiques, Université Pierre et Marie Curie, Paris. I am also indebted to Professor A. J. Cain for criticism and advice and to Dr. G. M. Davis, who reviewed the manuscript. For the loan of specimens I thank Drs. F. Climo of the National Museum of New Zealand, Wellington, P. Mordan and J. Peake of the British Museum (Natural History), and W. Ponder of the Australian Museum, Sydney.

LITERATURE CITED

- BENTHEM-JUTTING, W. S. S. VAN, 1948, Systematic studies on the non-marine Mollusca of the Indo-Australian archipelago—I—Critical revision of the Javanese operculate land-shells of the families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Cochlostomatidae. *Treubia*, 19: 539–604.
- BENZECRI, J. P., 1980, L'analyse des données, II, L'analyse des correspondances. Dunod, Paris, 632 p.
- BERRY, A. J., 1963a, The growth of *Opisthostoma* (*Plectostoma*) *retrovertens* Tomlin, a minute Cyclophorid from a Malayan limestone hill. *Proceedings of the Malacological Society of London*, 35: 46–49.
- BERRY, A. J., 1963b, Growth and variation of the shell in certain Malayan limestone hill snails. *Proceedings of the Malacological Society of London*, 35: 203–206.

- COCKERELL, T. D. A., 1930, A new operculate land snail from New Caledonia. *Journal of Conchology*, 19: 20.
- CROSSE, H., 1867, Description d'un genre nouveau et de plusieurs espèces inédites provenant de la Nouvelle-Calédonie. *Journal de Conchyliologie*, 15: 177–194, pl. 5, 7.
- CROSSE, H., 1871, Diagnoses Molluscorum Novae Caledoniae incolarum. *Journal de Conchyliologie*, 19: 201–206.
- CROSSE, H., 1873, Description d'un *Diplommatina* inédit, provenant de la Nouvelle-Calédonie. *Journal de Conchyliologie*, 21: 44–45, pl. 1, fig. 6.
- CROSSE, H., 1874a, Diagnoses Molluscorum, Novae Caledoniae. *Journal de Conchyliologie*, 22: 104–112.
- CROSSE, H., 1874b, Description d'espèces de Mollusques inédites, provenant de la Nouvelle-Calédonie. *Journal de Conchyliologie*, 22: 387–396, pl. 12.
- FRANC, A., 1957 (1956), Mollusques terrestres et fluviatiles de l'archipel néo-calédonien. *Mémoires du Muséum national d'Histoire naturelle*, sér. A, 13: 200 p., 24 pl.
- FRETTER, V. & GRAHAM, A., 1962, *British Prosobranch Molluscs; their functional anatomy and ecology*. Ray Society, London, xvi + 755 p.
- FRETTER, V. & GRAHAM, A., 1978, The prosobranch molluscs of Britain and Denmark; part 2—Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea. *Journal of Molluscan Studies Supplement* 5: 101–152.
- GIRARDI, E. L., 1978, The Samoan land snail genus *Ostodes* (Mollusca: Prosobranchia: PoterIIDae). *Veliger*, 20: 191–250.
- GIUSTI, F., 1971, Primo contributo alla revisione del genere *Cochlostoma* Jan e descrizione di *Toffoletia* n. gen. Notulae malacologicae XIII. *Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano*, 112: 353–380, pl. 67–71.
- HEDLEY, C., 1898, Descriptions of new Mollusca, chiefly from New Caledonia. *Proceedings of the Linnean Society of New South Wales*, 23: 97–105.
- IREDALE, T., 1937, A basic list of the land Mollusca of Australia. *Australian Zoologist*, 8: 287–333.
- IREDALE, T., 1944, The land Mollusca of Lord Howe Island. *Australian Zoologist*, 10: 299–334, pl. 17–20.
- IREDALE, T., 1945, The land Mollusca of Norfolk Island. *Australian Zoologist*, 11: 46–71, pl. 2–5.
- JAMBU, M. & LEBEAUX, M. O., 1979, *Classification automatique pour l'analyse des données, II, Logiciels*. Dunod, Paris, 400 p.
- KOBELT, W., 1902, Cyclophoridae. *Das Tierreich*, 16: 662 p., 1 map.
- KOBELT, W. & MÖLLENDORFF, O. VON, 1898, Katalog der gegenwärtig lebend bekannten Pneumonopomen (2). *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft*, 30: 129–160.
- MÖLLENDORFF, O. VON, 1897, Diagnosen neuer und kritischer Landdeckelschnecken. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft*, 29: 31–45.
- MONIOD, F., 1966, *Notice explicative—Nouvelle Calédonie—Carte des Précipitations annuelles*. ORSTOM, Centre de Nouméa, 11 p., 1 map.
- PEAKE, J. F., 1968, Habitat distribution of Solomon Islands land Mollusca. *Symposium of the Zoological Society of London*, 22: 319–346.
- PEAKE, J. F., 1969, Patterns in the distribution of Melanesian land Mollusca. *Philosophical Transactions of the Royal Society of London*, ser. B, 255: 285–306.
- PEAKE, J. F., 1973, Species isolation in sympatric populations of the genus *Diplommatina* (Gastropoda, Prosobranchia, Cyclophoridae, Diplommatininae). *Malacologia*, 14: 303–312.
- RENSCH, I. & RENSCH, B., 1929, Neue landmollusken aus dem Bismarck-Archipel. *Zoologische Anzeiger*, 80: 75–86.
- SCHINDEL, D. E. & GOULD, S. J. 1977, Biological interaction between fossil species: character displacement in Bermudian land snails. *Paleobiology*, 3: 259–269.
- SOLEM, A., 1959, Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana; Zoology*, 43: 359 p., 34 pl.
- SOLEM, A., 1960a, New Caledonian non-marine snails collected by T. D. A. Cockerell in 1928. *Notulae Naturae of the Academy of Natural Sciences of Philadelphia*, 338: 9 p.
- SOLEM, A., 1960b, Non-marine Mollusca from Florida Island, Solomon Islands. *Journal of the Malacological Society of Australia*, 4: 39–56, pl. 4–6.
- SOLEM, A., 1961, New Caledonian land and freshwater snails: an annotated checklist. *Fieldiana; Zoology*, 41: 413–501.
- TIELECKE, H., 1940, Anatomie, Phylogenie und Tiergeographie der Cyclophoriden. *Archiv für Naturgeschichte*, n.f., 9: 317–371.

DIFFERENT MODES OF EVOLUTION AND ADAPTIVE RADIATION IN THE POMATIOPSIDAE (PROSOBRANCHIA: MESOGASTROPODA)

George M. Davis¹

Academy of Natural Sciences, Nineteenth and the Parkway, Philadelphia, PA 19103, U.S.A.

ABSTRACT

Two subfamilies of the Pomatiopsidae are shown to have different tempos and modes of evolution. Data for the Triculinae are not new but represent a synthesis of several data sets (Davis, 1979, 1980; Davis & Greer, 1980). Data for the Pomatiopsinae with emphasis on the *Tomichia* radiation of South Africa are new. The distribution of modern pomatiopsid taxa is vicariant, a relict distribution with a secondary elaboration in Southeast Asia and the Far East extending to North America. There are eight pomatiopsine genera, one each in South Africa, South America, and Australia; one genus is found in an arc from western China to the Philippines and Sulawesi with taxa reaching Japan; two are endemic in Japan; one is found in Manchuria, Japan, and western U.S.A.; one is endemic in the U.S.A. There are 16 triculine genera, all but one of which are located entirely in Southeast Asia or western China. *Tricula* extends in an arc from India through China to the Philippines and in an arc through Burma to Malaysia.

The Triculinae have undergone an extraordinary endemic radiation in the Mekong River, yielding three tribes, 11 genera and over 90 species in a period of about 12 million years. This burst of cladogenesis was apparently driven by extrinsic processes correlated with the massive tectonics caused by the Himalayan orogeny that led to the formation of the major river systems of Southeast Asia, and western China. The morphological changes in the entirely aquatic group of snails that marked the entrance into various new adaptive zones involved a series of innovations in the female reproductive system, the male reproductive system posterior to the penis, and the central tooth of the radula. Bursts of speciation following each morphological innovation or series of correlated innovations yielded clusters of species that are considered discrete genera. The genera are separated by distinct gaps defined by morphological distances that are measures of morphological changes indicative of entrances into new adaptive zones.

Pomatiopsine taxa are aquatic, amphibious, or terrestrial. Modes of evolution in the Pomatiopsinae of the southern continents are in marked contrast to those in the Triculinae. In South Africa there are, at most, eight species of *Tomichia* with an evolutionary history of at least 80 million years. In Australia there are, at most, nine species of *Coxiella*. *Tomichia* and *Coxiella* are very similar anatomically. No burst of cladogenesis or considerable speciation is seen. Species of *Tomichia* do not differ very much in anatomy. The apparent low rate of speciation and lack of cladogenesis correlate with the lack of tectonic upheaval and gradual climatic changes since proto-*Tomichia* and proto-*Coxiella* were separated by the breakup of Gondwanaland. The limited *Tomichia* radiation is apparently in response to increasing aridity spreading from west to east in South Africa since the breakup of Gondwanaland. Speciation has not involved morphological modification but rather, adaptation to different ecological settings: freshwater streams, freshwater lakes, amphibious ecotones, temporary brackish water pools. Preadapted morphological features for an amphibious existence were probably the large, powerful foot and the elongate spermathecal duct.

The tempo of the Mekong River triculine evolution is rapid ($R = \text{about } 0.40$ contrasted with a slower rate ($R = \text{about } 0.139$) for the *Tomichia* radiation. The mode of triculine evolution is rapid, episodic speciation involving considerable morphological innovation and cladogenesis, all associated with extreme tectonism. The mode of *Tomichia* evolution involves a physiological radiation with low morphological diversity associated with gradual climatic change and general absence of tectonism.

INTRODUCTION

Modes and tempos of evolution above the species level are highly relevant topics for contemporary students of biological evolution.

In considering tempos I am concerned with rates of cladogenesis, the number and extent of adaptive radiations in phyletically allied clades (per unit time), and the rate of extinction of species and lineages. By extent of

¹Supported by U.S. National Institutes of Health grant No. A1-11373.

adaptive radiation, I mean the number of species of a single radiation and the different niche dimensions these species occupy.

In considering modes of evolution, I am concerned with how organisms respond to the selective pressures of different types of changing environments, and with how organisms respond to different rates of environmental change. The presumption is made that speciation and evolution above the species level will not occur in environmental stasis.

The purpose of this paper is to demonstrate two vastly different modes and tempos of evolution in the rissoacean family Pomatiopsidae. One mode involves a radiation of considerable morphological uniformity but physiological divergence in a setting of gradual environmental change. The other mode involves a radiation exhibiting numerous morphological innovations associated with rapid tectonic environmental changes. The most important comparisons made here involve the extraordinary triculine radiation in the Mekong River and the more modest *Tomichia* radiation in South Africa. Data pertinent for discussing the triculine radiation have been published (Davis, 1979, 1980; Davis & Greer, 1980). Data for the *Tomichia* radiation are new. Two different clades are involved, because the Mekong River radiation belongs to the Triculinae and *Tomichia* is a member of the Pomatiopsinae. Together these two subfamilies comprise the Pomatiopsidae as recently defined (Davis, 1979).

The family Pomatiopsidae

The origin and evolution of the family have been discussed with emphasis on the adaptive radiation of the Triculinae in the Mekong River (Davis, 1979). The evolutionary topology of the family is shown in Fig. 1 based on the hypothesis that the Pomatiopsidae evolved and diverged into two Gondwanian subfamilies prior to the breakup of Pangaea.

Published zoogeographical, morphological, and paleontological data (Davis, 1979) are consistent with the following concepts: 1) the distribution of modern pomatiopsid taxa is vicariant. There is a relictual distribution in the southern continents with a secondary elaboration in the Far East extending to North America (Table 1). 2) Triculinae and Pomatiopsinae were introduced into the Asian mainland via the Indian Plate. 3) The patterns

of distribution of Pomatiopsidae throughout Asia and North America and the direction of evolution of derived morphological character states indicate a direction of evolution from Gondwanaland to Asia (Davis, 1979).

The subfamily Triculinae

The subtending of the Asian continent by India initiated the Himalayan orogeny beginning in the Oligocene some 38 million years ago (Molnar & Tapponier, 1975). The orogeny began at the western end of the mountain chain and spread eastward as the Indian Plate rotated, bringing the northeast corner into contact with the Asian mainland in the Miocene. As the Tibetan region was lifted from the sea, drainage patterns were initiated that became the major rivers of Southeast Asia and much of China. These are the Irrawaddy, Salween, Mekong, and Yangtze rivers. Estuarine and finally fluvial deposits were laid down in northern Burma at the end of the Miocene; in the Pliocene the sediments of the Irrawaddy River became entirely freshwater (Pascoe, 1950).

It is apparent that proto-Triculinae were introduced from the Indian Plate into the newly forming drainages of the Asian mainland (Davis, 1979, 1980; Davis & Greer, 1980). All Triculinae thus far studied are entirely freshwater in streams, lakes, and rivers. They extend in three arcs. One arc extends from northwestern India through China to the Philippines. The second arc extends from India through northern Burma and western Yunnan, China and throughout the Mekong River drainage but ending in northern Cambodia. The third arc extends through northern Burma, northwestern Thailand into Malaysia.

Tricula, the genus with the most generalized morphology and least derived character states (Davis & Greer, 1980) is found along each of these arcs. Taxa with the most derived character states are found endemic in the Mekong and Yangtze River drainages and in lakes in Yunnan, China between the rivers (Davis, 1980; Davis & Greer, 1980). These derived taxa are *Halewisia* and *Pachydrobia* of the Triculini and all members of the Lacunopsini and Jullieniini. As shown in Table 1, of 16 genera and 120 species of Triculinae, 10 genera and 92 species (76.7%) are endemic to the Mekong River drainage.

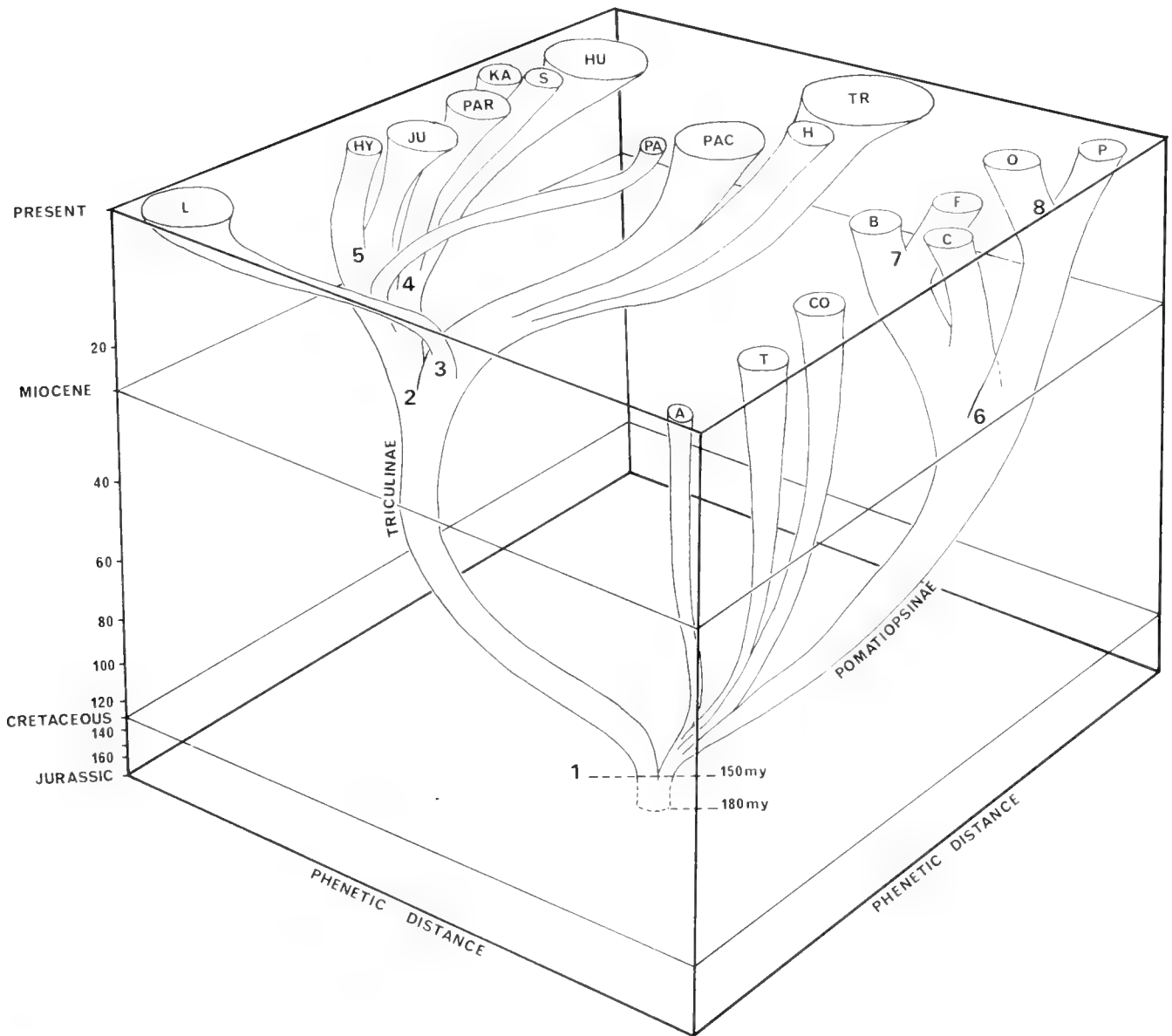


FIG. 1. Phyletic topology of the Pomatiopsidae with time given in millions of years (on a log scale) from the Jurassic to the present. Branching points: 1. Triculine and pomatiopsine lineages established in Gondwanaland prior to the breakup of the southern continent. 2. Divergence to form the Jullieniini (left grouping) in the Miocene. 3. Radiation of specialized *Lacunopsis* (Lacunopsini), which diverges from the Triculini. *Lacunopsis*, on shell characters, resembles marine and freshwater Neritidae. Some species converge on *Anculosa* (Pleuroceridae), *Littorina* (Littorinidae), or *Calyptreaea* (Calyptraeidae). 4. Seven genera evolved in the Miocene, probably much at the same time. *Pachydrobiella* (PA) converges on *Pachydrobia* (PAC) of the Triculini in shell shape and structure. 5. Anatomical and shell data clearly indicate that *Hydrorissoia* (HY) and *Jullienia* (JU) diverged from a common ancestor. 6. A late Miocene radiation took place in Japan, giving rise to the endemic genera *Blanfordia* (B) and *Fukuia* (F), and *Cecina* (C). *Cecina* spread to western North America, while *Pomatiopsis* (P) occurs only in the U.S.A. 7. *Blanfordia* and *Fukuia* have either diverged from a common ancestor or are the same genus. Data thus far available support the former interpretation.

A. *Aquidauania*, South America. B. *Blanfordia*, Japan. C. *Cecina*, Japan, Manchuria, U.S.A. CO. *Coxiella*, Australia. F. *Fukuia*, Japan. H. *Halewisia*, Mekong River. HU. *Hubendickia*, Mekong River. HY. *Hydrorissoia*, Mekong River. JU. *Jullienia*, Mekong River. KA. *Karelainia*, Mekong River. L. *Lacunopsis*, Mekong River. O. *Oncomelania*, China, Japan, Philippines, Sulawesi. P. *Pomatiopsis*, U.S.A. PA. *Pachydrobiella*, Mekong River. PAC. *Pachydrobia*, Mekong River, PAR. *Paraprosiothenia*, China. Mekong River (Thailand, Lao). S. *Saduniella*, Mekong River. T. *Tomichia*, South Africa. TR. *Tricula*, India, Burma, China, Philippines, Mekong River (from Davis, 1979).

TABLE 1. Classification, numbers of taxa, and zoogeography of the Pomatiopsidae. (), number of species; M, endemic in Mekong River drainage; +, placement of *Delavaya* (1), *Fenouillia* (1), and *Parapyrgula* (1) uncertain; they are probably Jullieniini.

Pomatiopsinae			Triculinae	
<i>Aquidauania</i> Davis, 1979	(1)	South America	Tribe Triculini+	
<i>Blanfordia</i> A. Adams, 1863	(2)	Japan	<i>Halewisia</i> Davis, 1979	(2)
<i>Cecina</i> A. Adams, 1861	(1)	Japan, Manchuria, northwest United States	<i>Pachydrobia</i> Crosse & Fischer, 1876	(17)
<i>Coxiella</i> E. A. Smith, 1894	(10)	Australia, Tasmania	<i>Robertsella</i> Davis and Greer, 1980	(2)
<i>Fukuia</i> Abbott & Hunter, 1949	(2)	Japan	<i>Tricula</i> Benson, 1843	(20)
<i>Oncomelania</i> Gredler, 1881	(2)*	China, Japan, Taiwan, Phil., Sulawesi		
<i>Pomatiopsis</i> Tryon, 1862	(4)	United States	Tribe Lacunopsini	
<i>Tomichia</i> Benson, 1851	(7)	South Africa	<i>Lacunopsis</i> Deshayes, 1876	(15)
			Tribe Jullieniini	
			<i>Hubendickia</i> Brandt, 1968	(16)
			<i>Hydrorissioia</i> Bavay, 1895	(9)
			<i>Jullienia</i> Crosse & Fischer, 1876	(16)
			<i>Karelainia</i> Davis, 1979	(4)
			<i>Lithoglyphopsis</i> Thiele, 1928	(4)
			<i>Pachydrobiella</i> Thiele, 1918	(1)
			<i>Paraprososthenia</i> Annandale, 1919	(10)
			<i>Saduniella</i> Brandt, 1970	(1)
TOTAL: 8 genera	29 species		16 genera	120 species (92 endemic in the Mekong River)

**O. hupensis* has 6 subspecies.

The tribes and genera of the Triculinae are separated by discrete qualitative morphological gaps (Davis, 1979, 1980; Davis & Greer, 1980). Some 28 characters are of use in recognizing these taxa because the taxa have shared derived states of these characters and/or uniqueness of certain derived states (Table 2). Of these characters, 14 are from the female reproductive system (50%), seven

are from the male reproductive system (25%) (only one is from the penis), four are shell characters (14%), two are radular characters (7%), and one is osphradial (4%).

The Triculinae provide an excellent opportunity for studying how higher taxa evolve. The monophyletic assemblage (Davis, 1979) is large enough to explore how species of various adaptive zones have radiated, and to un-

TABLE 2. A list of 28 characters that are used to recognize tribes and genera of the Triculinae. References to illustrations or discussions of character-states are given; these are one or more of Davis, 1979, 1980 (= 1980a below); Davis & Greer, 1980 (= 1980b below); Davis et al., 1976.

Shell	
1. shape	1979, figs. 28–30; 1980a, fig. 7
2. sculpture	1979, figs. 28–30; Table 12; 1980a, fig. 7
3. size	1979, figs. 28–30; Table 11; 1980a, fig. 7; Table 6
4. thickness	1979, figs. 28–30; 1980a, fig. 7
Central tooth	
5. anterior cusp morphology	1979, fig. 4; 1980a, fig. 6
6. size of blade supports	1979, fig. 4; 1980a, fig. 6
Osphradium	
7. length	1976, fig. 7
Female reproductive system	
8. gonad morphology	1979, figs. 11–15; 1980a, fig. 11
9. coiling of the oviduct posterior to the bursa copulatrix	1980a, figs. 4, 8, 13
10. position of the opening of the seminal receptacle	1979, figs. 3, 11–18; 1980b, fig. 10
11. length of seminal receptacle	1979, fig. 12
12. oviduct configuration at the bursa copulatrix region	1979, fig. 3
13. length of the bursa copulatrix relative to length of pallial oviduct	1979, figs. 12, 13
14. length of duct of the bursa copulatrix	1979, figs. 11–16; 1980a, fig. 13
15. position of the pallial oviduct relative to the columellar muscle.	1979: 107
16. Coiling of the spermathecal duct	1979, fig. 12
17. encapsulation of the spermathecal duct	1980b, fig. 7
18. vestibule of the spermathecal duct	1980b, fig. 7
19. extension of the spermathecal duct into the mantle cavity (= sperm uptake organ)	1979, fig. 14C; 1980b, fig. 10
20. position of opening of the spermathecal duct into the bursa copulatrix complex of organs	1979, fig. 3; 1980a, figs. 8, 13; 1980b, fig. 10
21. method by which sperm enter female reproductive system at the posterior end of the mantle cavity	1979, fig. 3; 1980a, figs. 5, 8; 1980b, fig. 10
Male reproductive system	
22. gonad morphology	1979, fig. 19; 1980a, fig. 11; 1980b, fig. 9
23. position of coiling of the seminal vesicle	1979, figs. 11–15; 1980a, fig. 12
24. relative length of the vas deferens (Vd ^a) between the gonad and seminal vesicle	1980a, fig. 12
25. coiling of the vas deferens posterior to the penis	1979, fig. 12A
26. position where vas deferens leaves the prostate	1979, figs. 14, 15
27. penis has stylet or papilla	1976, fig. 10; 1979, fig. 10; 1980b, fig. 9
28. status of vas efferens	1979, figs. 11–15; 1980a, fig. 11; 1980b, fig. 9

derstand the directions of morphological change that permitted the crossing of thresholds of various adaptive zones to new adaptive zones.

In the Triculinae, as in other higher taxa, we see four aspects of adaptive radiation: first order adaptive radiations, null radiation, second order adaptive radiations, and macro-adaptive radiation.

The term adaptive radiation was first used by Osborn (1918) and fully exploited by Simpson (1949) who stated: "Adaptive radiation is, descriptively, this often extreme diversification of a group [e.g. mammalian or reptilian radiation] as it evolves in all the different directions permitted by its own potentialities and by the environments it encounters." Stanley (1979) stated: "Adaptive radiation is the rapid proliferation of new taxa from a single ancestral group." These authors are discussing what I call here macro-adaptive radiation, a higher taxon or a higher taxon clade that is, in fact, recognized as such because of its component clades. The Triculinae are a macro-adaptive radiation.

A first order radiation is equated with a genus, which is a composite of at least two, but usually more than two species. The entrance into a new adaptive zone made possi-

ble by a new morphological or physiological innovation is associated with the rapid proliferation of new species that fill various niche dimensions. A null radiation is a monotypic genus, a taxon recognized by the discrete morphological gap from other genera to which it is phylogenetically allied. Such a genus may be the basis for a first order radiation of the future, or represent a dead-end due to the very nature of the morphological innovation(s) that distinguishes it. Planispiral *Saduniella* of the Triculinae is such a genus. A second order radiation involves two or more phylogenetically allied first order radiations and can be equated to named taxa between generic and high taxon clades under discussion. Within the Triculinae, the tribes Triculini and Jullieniini are second order radiations.

Detailed discussions of the evolution of derived character-states and taxa with those states have been given (Davis, 1979, 1980; Davis & Greer, 1980). In review, the most profound changes involved the reproductive systems as the progenitors of the modern Triculinae adapted to the evolving Mekong and Yangtze River systems. Changes were essentially in two directions involving two clades, the Lacunopsini and Jullieniini. These changes show divergence from *Tricula*, which

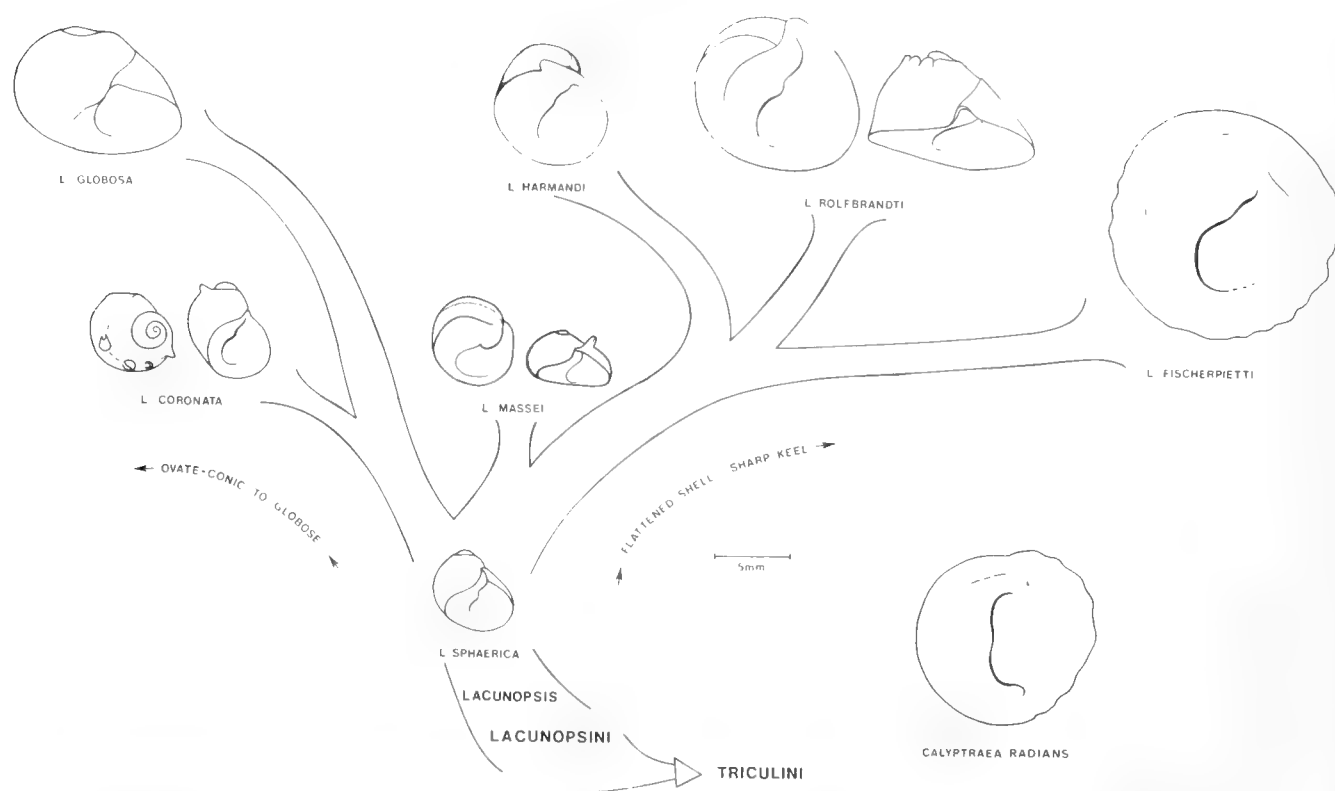


FIG. 2. Shells of representative species of the Lacunopsini showing diversity in shell shape and showing a closer relationship of the Lacunopsini to the Triculini than to the Jullieniini (also see Fig. 1). The marine mesogastropod *Calyptraea radians* is illustrated to show how similar the species is to *L. fischerpietti*. These two species are highly convergent in shape, growth patterns, and sculpture (from Davis, 1979).

has the most generalized character-states. Many of these derived innovations are correlated with swift-water habitats as has been shown statistically (Davis, 1979). There is a lack of species with generalized character-states adapted to swift-water habitats.

The Lacunopsini (Fig. 2) most likely evolved from an ancestor that also gave rise to *Tricula bollingi* (Davis & Greer, 1980). A single first order radiation is involved, all in the Mekong River. The niche dimensions filled are swift-water habitats on rocks where species differences are seen in shell shape and sculpture, and positional relationships in the water column involving rock slope, depth, rock surface, degree of current. Shell shapes are astonishing for freshwater hydrobioids as shapes con-

verge on those of marine Neritidae, Littorinidae, and Fossaridae. The most remarkable changes in the reproductive system are the loss of the seminal receptacle as seen in *Tricula* and the development of several accessory seminal receptacles, and the degree to which the pericardium is modified and used to accommodate sperm during reproduction. All species are similar in that the central tooth is a derived type (Fig. 5) modified for scraping food from rock.

The Jullieniini (Fig. 4) comprise one of the most spectacular second order molluscan radiations ever seen in freshwater. This radiation in the Mekong River has five first order radiations and two null radiations. We know too little about the Chinese genera *Litho-*

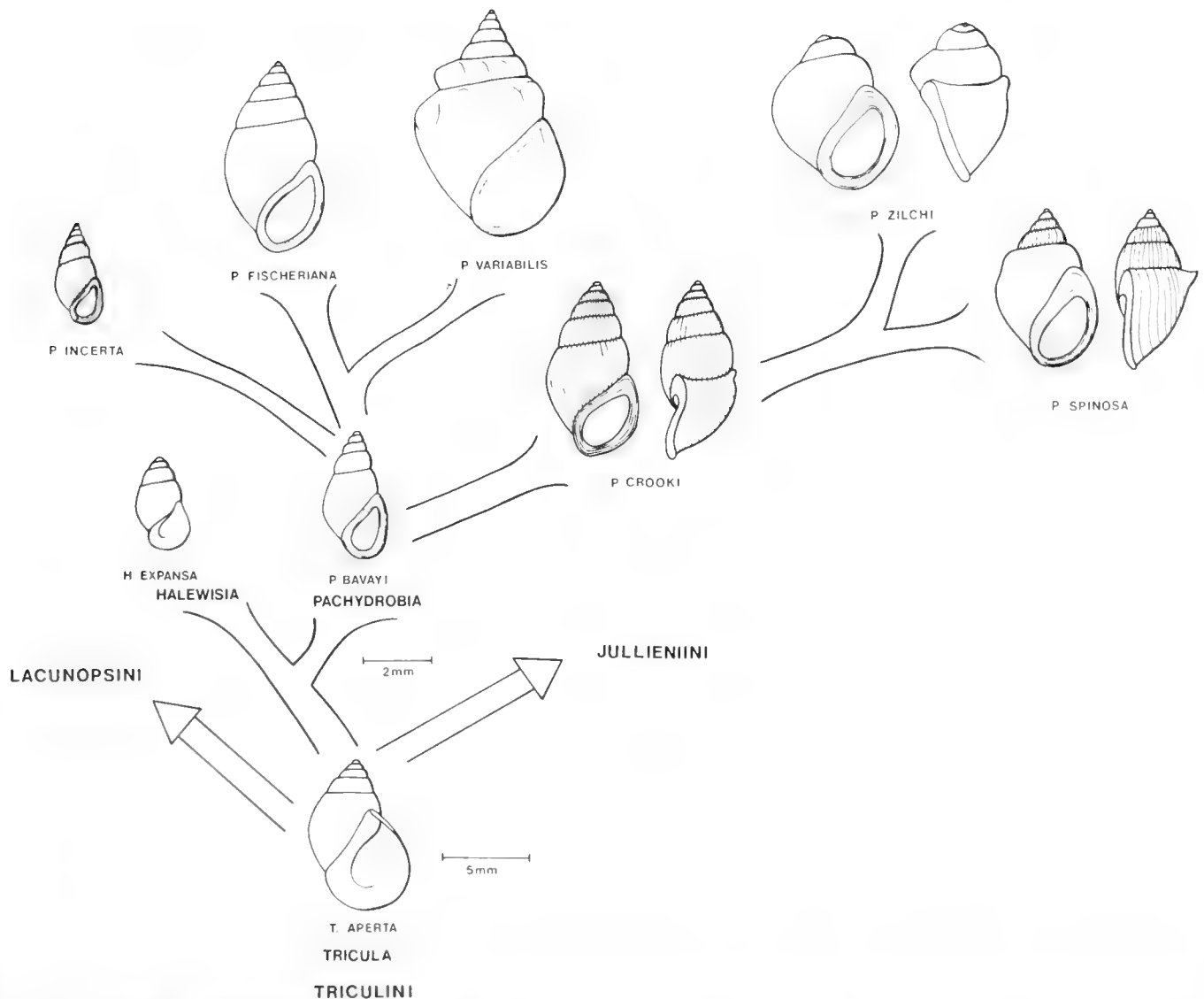


FIG. 3. Shells of representative species of the three genera of the Triculini. The implication of this tree-like configuration is that *Pachydröbia* has more derived character states than does *Tricula*, reflected in certain shell features, e.g. ribs, bosses (odd lump[s] on the shell), and solitary spines. Also implied is the basal status of *Tricula* relative to the divergent tribes Lacunopsini and Jullieniini, which have more derived character states (also see Fig. 1). Note also the increase in size (only *L. aperta* is drawn at a larger scale, as indicated by the 5 mm scale bar) in *P. variabilis*, *P. fischeriana*, etc., compared with *Halewisia* and *Tricula* (from Davis, 1979).

glyphopsis, *Delavaya*, *Fenouilia*, and *Parapyrgula* (Table 1) to say anything about them. Incremental derived changes in the female reproductive system are in the direction of increasing volume and complexity of the reproductive organs (Davis, 1979, 1980). The generalized hydrobioid oviduct is thrown into a 360° complex with the seminal receptacle and spermathecal duct (Fig. 6). This 360° loop is small in diameter in the least derived genus (*Karelainia*) and increases markedly in diameter in the more derived genera. The gonad is the generalized pomatiopsisid type in *Karelainia* and is considerably modified in morphology in the more derived genera. Elongation of the seminal receptacle is seen in only a few species of *Hubendickia* while extreme elongation is seen in more derived genera such as *Paraprososthenia*, *Jullienia*, *Hydrorissoia*, and *Pachydrobiella*. Extreme elongation and recurving or coiling of various sections of the vas deferens are seen in the more derived genera and especially pronounced in the most derived genera, *Jullienia* and *Hydrorissoia*.

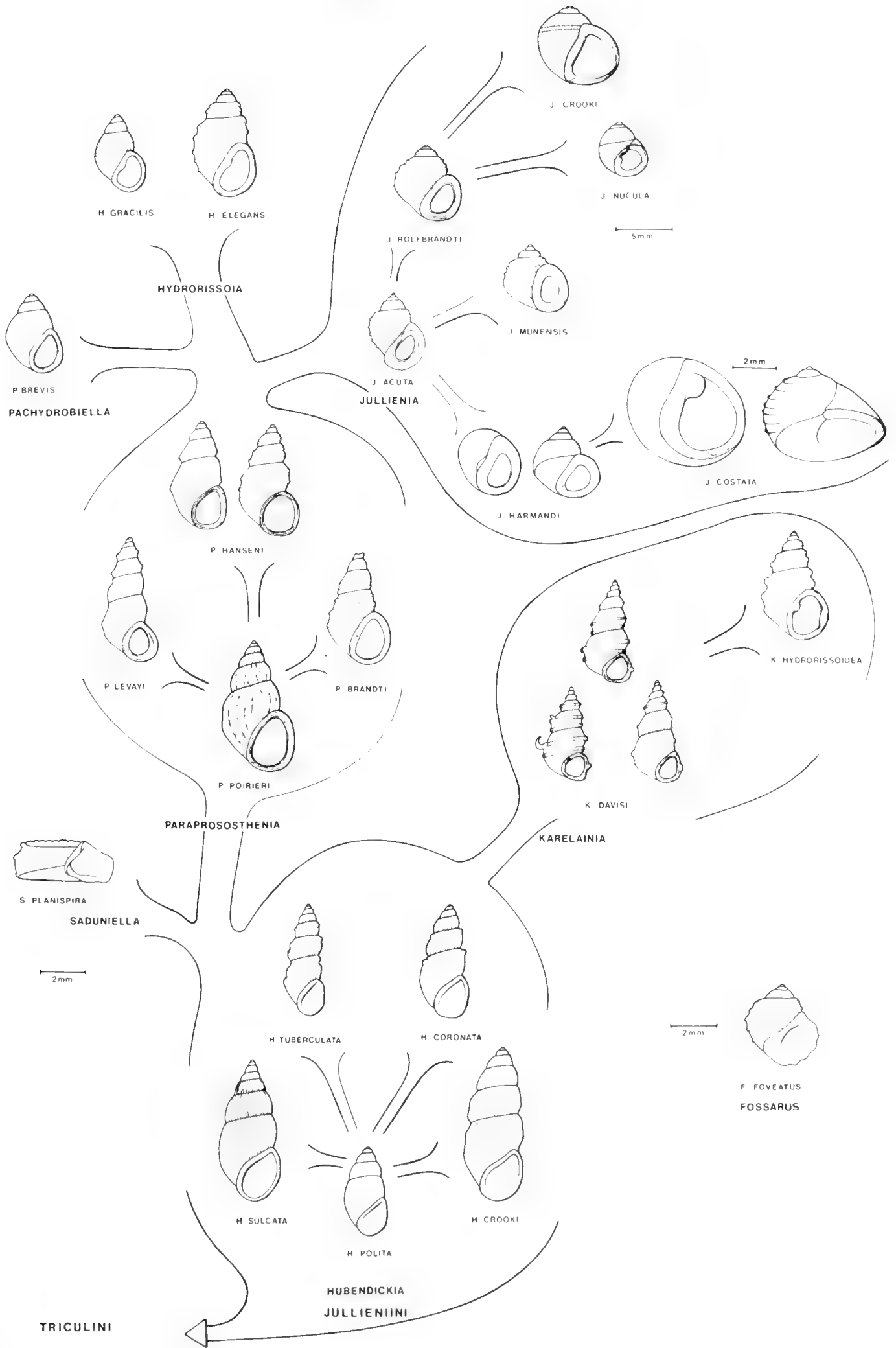
Increasing complexity in the reproductive system is associated with exploitation of differing (even if slight) reproductive strategies. Increasing bulk and complexity of the reproductive system are associated with the Mekong River triculine fauna (Davis, 1979). These species are colonizers and opportunistic species in a river that goes through an annual cycle of rampaging floods during the monsoon season (June through November) to relative quiet and shallow flow during the dry season (December through May). The floods bring high density-independent mortality because of the distribution of habitats and the sweeping away of snails from low-water depositional areas. There are high reproductive rates in the single short low-water

breeding season available to these annual species. The relative volume of reproductive organs discussed above coupled with the tremendous biomass of young produced (see Davis, 1979) attest to comparatively great amount of energy put toward reproduction (contrast Pomatiopsinae, Davis, 1979: 69).

Growth and reproductive activities of Mekong River species are remarkably in phase with the annual river cycles. Different groups of species mature, reproduce, and die at different times once the dry season begins and water levels begin to drop. All Triculinae are semelparous as far as is known. Once *Pachydrobia* reproduces, the reproductive system slowly disintegrates. This is first seen in the male where the penis begins to disintegrate; it is later seen in the female where the ovary and pallial oviduct disintegrate. The snails live on for a month or more after the onset of this disintegration process. Once *Tricula aperta* has laid its eggs, it dies and there is a period of about one month when no adults are seen and no hatched young can be found.

Additionally, there is a temporal division of river habitat as regards maturation and reproduction. A given habitat may have one group of species at one period of low water that reproduce and die, to be replaced by different species that hatch, grow to maturity, etc. (Davis, 1979). The temporal division keeps pace with the annual cycle of habitat emergence. As water levels begin to decrease in October, habitats begin to emerge and form. First island masses and the larger waterfalls appear, followed by smaller islands, embayments between islands, lakes and pools on islands, smaller rapids, sandbars, and finally shallow quiet areas allowing for considerable mud deposition. From mid-October or November through June most habitats are free

FIG. 4. Shells of representative species of the seven genera of the Jullieniini grouped to reflect relationships and a radiation of shell types within each genus. The trend from bottom to top is one of generalized to specialized both in shell features and anatomy. Spiral and nodulate sculpture is derived. *Jullienia* is most specialized in terms of sculptural patterns, large size, and odd shapes (e.g. flattening of the base of the shell in some species) as well as anatomy. In *Hubendickia*, the shells, depending on the species, are smooth or ribbed. Nodes are seen on the adapical ends of the ribs in two species. In *Paraprososthenia*, shells range from smoothly ribbed, with solid spiral cords, or with spiral rows of nodes. *P. hanseni* has morphs ranging from smooth, one spiral row of nodes to several spiral rows of nodes on the body whorl. *Hydrorissoia* and *Jullienia* are, on the basis of anatomy, phenetically very similar. Together with *Paraprososthenia* they form the *Jullienia* complex. *Karelainia* parallels *Paraprososthenia* in shape and sculpture but diverges considerably in anatomy. Note that *K. davisii* has several morphs. *Fossarus foveatus* is shown as an example of convergence between unrelated taxa. *F. foveatus* is similar to species of *Jullienia* in shell shape and sculpture. *F. foveatus* is in the marine family Fossaridae. All shells are drawn to the same scale except the six *Jullienia* with the 5 mm scale bar (from Davis, 1979).



from flooding and destruction caused by the monsoons. Because of the floods, the configurations of sandbars, islands, and rapids change yearly. A population that flourished in a muddy depositional area one year may be buried under stones and cobbles the next year. Species with the most derived reproductive systems appear to grow and mature rapidly and to reproduce during lowest water. Taxa with the most generalized systems reproduce during higher water periods before and after the four-month lowest-water months (Davis, 1979).

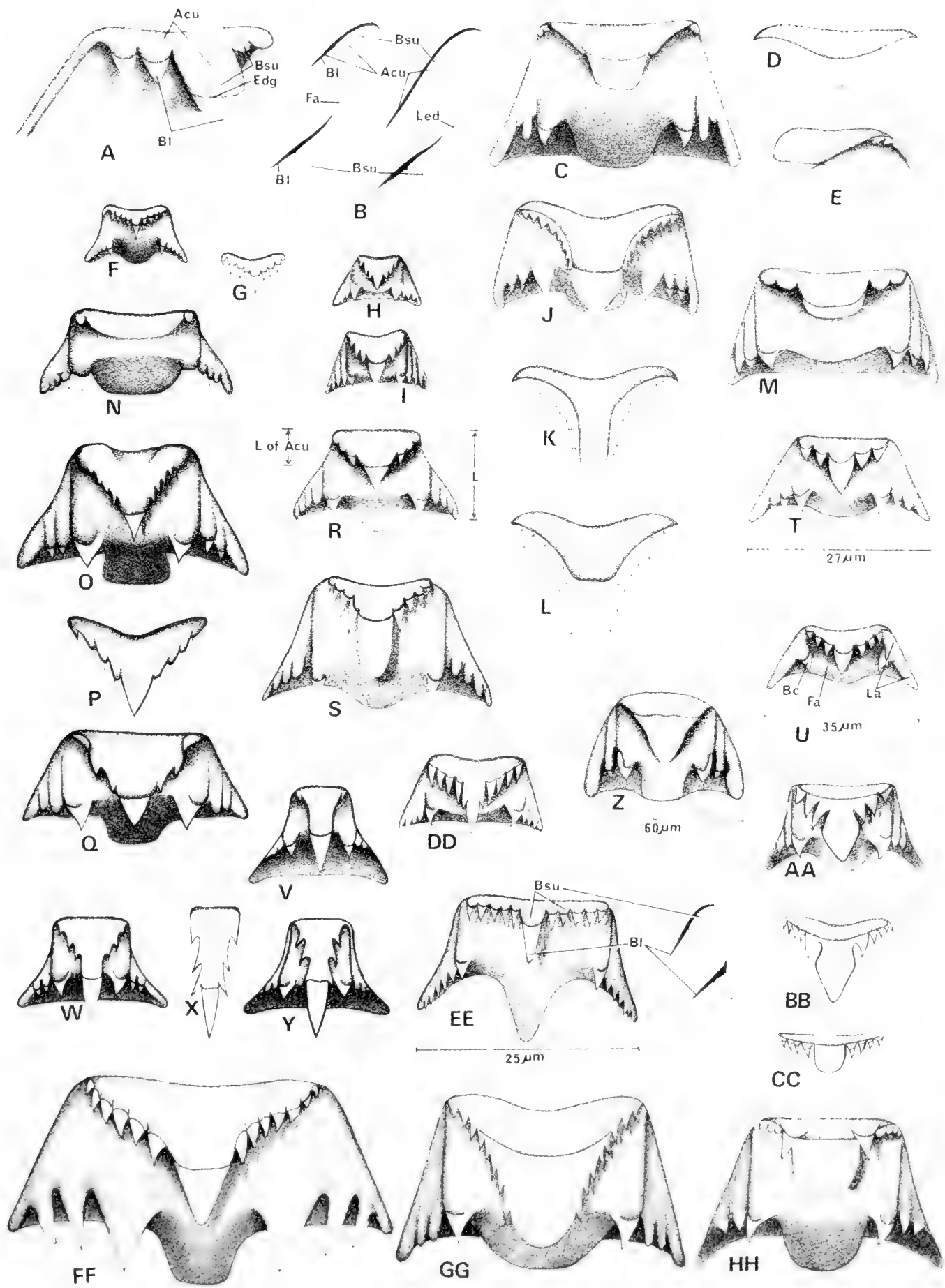
The foregoing discussion has involved 75% of the derived characters. Different feeding habits involve yet another niche dimension especially exploited in the second order Jullieniini radiation. This is reflected by the morphology of the central tooth of the radula (Fig. 5). The generalized central tooth seen in the Triculini and all Pomatiopsinae is found only in a few species of *Hubendickia* of the Jullieniini. Species of all other genera have derived types of teeth. Finally, shell characters reflect adaptations to different microhabitats and perhaps to living in sympatry with different species (Figs. 2–4). Only two or three species of *Hubendickia* have the smooth, ovate-conic, small shell that is the generalized hydrobioid type (Davis, 1980). Modification of shell characters from generalized to most derived follows a parallel course in each of the two second order and Lacunopsini first order adaptive radiations of the Triculinae. There is a net increase in size, and there appears to be a progression from smooth to ribbed, nodulate ribs, reticulate sculpture, spiral noded cords, and finally odd spines and nodes.

There is another progression from ovate-conic to diverse symmetric shapes including planispiral, and finally to asymmetry. In the Jullieniini the trends in increasing complexity of the reproductive systems generally parallel the three trends in shell characters and the trends in central tooth morphology.

It is in *Hubendickia* that we have an indication that certain sculptural character-states are related to species living in sympatry. We see a possible case of character displacement. At Khemarat, Thailand five species of *Hubendickia* live sympatrically. It is common to find four species in great numbers (hundreds) in a handful of algae. Each of these species has a distinctive shell sculpture involving ribs. One of these species was called *H. spiralis* Brandt because of pronounced spiral micro-sculpture. These species crawl over each other continuously. It seems probable, although it is untested, that sculpture serves for species recognition for mating purposes. It was determined on the basis of overall morphological similarity that *H. siamensis spiralis* was a synonym of *H. sulcata* (Bavay) of the lower Mekong River (near Cambodia) as was also *H. siamensis* Brandt of the Mun River that flows into the Mekong River at the isles of Ban Dan (Davis, 1979). No other species of *Hubendickia* lives in the Mun River where one finds the population of *H. sulcata* referred to by Brandt as *H. siamensis*. Snails of this population entirely lack spiral micro-sculpture. Over 100 miles south of Khemarat at Khong Island there are more than 50 species of Triculinae but few species of *Hubendickia*. Populations of *Hubendickia* are rarely sympatric in the sense that they are found

FIG. 5. Central teeth of representative species of Triculinae and Pomatiopsinae compared with the central tooth of *Hydrobia totteni*. A, B. Stylized drawings showing structures of the central tooth. Note that the blade (Bl, blackened layer) is a layer fused on the dorsal aspect of the blade support (Bsu). The lateral view of the tooth is shown in B and EE. C-E. *Hydrorissoia hospitalis* (Triculinae: Jullieniini). F, G. *Hubendickia cylindrica* (Triculinae: Jullieniini). H. *Saduniella planispira* (Triculinae: Jullieniini). I. *Paraprososthenia levayi* (Triculinae: Jullieniini). J-L. *Jullienia harmandi* (Triculinae: Jullieniini). M. *Pachydrobia variabilis* (Triculinae: Triculini). N. *Hubendickia coronata* (Triculinae: Jullieniini). O-Q. *H. gochenouri* (Triculinae: Jullieniini). R. *H. polita* (Triculinae: Jullieniini). S. *H. pellucida* (Triculinae: Jullieniini). T. *Oncomelania hupensis* (Pomatiopsidae: Pomatiopsinae). U. *Hydrobia totteni* (Hydrobiidae: Hydrobiinae). V-Y. *Hydrorissoia elegans* (Triculinae: Jullieniini). Z. *Lacunopsis conica* (Triculinae: Lacunopsini). AA-CC. *Halewisia expansa* male (Triculinae: Triculini). DD. *Karelainia davis* (Triculinae: Jullieniini). EE. *Tricula aperta* (Triculinae: Triculini). FF. *Jullienia acuta* (Triculinae: Jullieniini). GG. *Pachydrobiella brevis* (Triculinae: Jullieniini). HH. *Halewisia expansa* female (Triculinae: Triculini). All teeth without μm bars are drawn to the same scale as EE. Z was drawn at $\frac{1}{3}$ the magnification of EE. Note the multiserrated blade of J-L and GG and the pauciserrated blade of AA (from Davis, 1979).

Acu, anterior cusp; Bc, basal cusp; Bl, blade; Bsu, blade support; Edg, edge of the blade support; Fa, face of the tooth; L, length of tooth; La, lateral angle; L of Acu, length of anterior cusp (to the Edg); Led, lateral edge of tooth face.



living intermixed on the same substrate in the same area. Spiral microsculpture is weakly developed in a few populations of *H. sulcata*, found on only some individuals of other populations, and is entirely lacking from individuals of yet other populations. It is evident that in the absence of high incidence of congeneric sympatry, spiral microsculpture breaks down.

Many shell shapes are clearly interpretable when one observes how the species live. The shells of one species converge on the shells of phyletically totally unrelated groups because the animals of these different groups position themselves on various substrates in the same way. The resemblance of various *Lacunopsis* species to marine *Littorina* has been discussed in detail elsewhere (Davis, 1979, 1980).

Tricula of the Triculini radiation (Fig. 3) has the most generalized morphology and is represented in the Mekong River by only one species, *T. aperta* (Temcharoen). The one successful Triculini radiation in the Mekong River involves *Pachydrobia*. Again, this species-rich radiation involves innovations in the female reproductive system and establishment in a range of habitat types as reflected in a range of shell morphologies that fit the trends discussed above.

It is evident that entrance into an adaptive zone, which permitted a new first order radiation of Triculinae, enabled some species of that radiation to overlap many niche dimensions of species of other first order radiations. A single scoop of a hand sieve (500 ml capacity) through a muddy substrate often yields several thousand snails of eight to ten species of three to six genera (Davis, 1979). Numerous species in sympatry on a rock or patch of mud or small area of sandy-mud is the rule, not the exception. The snails do not seem to be resource limited unless it is for space for egg deposition.

A number of species do occupy unique space. An example is *Lacunopsis fischerpietti* Brandt, the largest triculine in the Mekong River (shell diameter of 15 to 18 mm), which closely resembles the marine species *Calyptraea radians*. *L. fischerpietti* lives one or two per boulder on the vertical faces of huge boulders, facing the swiftest current. Other examples are: *Lacunopsis harmandi*, which lives at the interface of swiftly flowing water and air. *Jullienia costata* lives crowded by the thousands, packed shell to shell, on vertical cliff walls in rushing waterfalls, splashed continuously by the spray. Some populations of *Hubendickia polita* are nearly

amphibious, living on damp rock just above the water line. *Lacunopsis massei* lives with no other species, each individual is separated by at least 15 mm from other individuals on a polished smooth horizontal rock surface over which a strong current runs and the water is at least one meter deep. Several species of *Pachydrobia* live allopatrically in sandbars where few or no other species live.

Tempo and mode of triculine evolution

Given the time period for the Himalayan orogeny, initiation of the river drainage systems involved, and the presence of freshwater sediments in the critical region of northern Burma, it is reasonable to estimate the age of the modern triculine radiation as starting about 10 to 12 million years ago at the longest (Davis, 1979, 1980). Following the arguments of Stanley (1975, 1979) I calculate R , the fractional increase of species per unit time using the equation $N_t = N_0 e^{Rt}$, which is equivalent to $R = (1 \ln N)/t$. N_0 is the original number of species (= 1 considering that the Triculinae are monophyletic and a single successful introduction from the Indian Plate is all that was needed to produce the macro-radiation fanning out along the three aforementioned arcs); N is the number of species now living, t is the time, e is the base of the natural logarithm. For the Asian Triculinae as a whole $R = 0.40$ to 0.48 (My^{-1}) depending on t of 12 or 10 million years ago. This rate is extremely great and exceeds that of the mammalian Muridae that have evolved over 19 millions years ($R = 0.35$). R for the Triculinae is several times greater than for any other molluscan group known ($R = \text{about } 0.067 \text{ My}^{-1}$ for several families of marine gastropods; $R = 0.046 - 0.087 \text{ My}^{-1}$ for several families of marine bivalves; see Stanley, 1979). If we calculate R for two second order radiations and major primary radiation we see the following result: Triculini, $R = 0.31 \text{ My}^{-1}$; *Lacunopsini*, $R = 0.23 \text{ My}^{-1}$; *Jullieniini*, $R = 0.35 \text{ My}^{-1}$.

This explosive monophyletic macro-radiation is coincident with the massive, abrupt, and recent tectonics of the Himalayan orogeny. The strong positive association between tectonic events, bursts of speciation and cladogenesis, endemism have been reviewed (Taylor, 1966; Davis, 1979, 1980). Rapidly shifting selective pressures and new pressures are in evidence as seen in the geological and geographically distributed aftermath of the processes forming the modern river drainage patterns of the Irrawaddy,

Salween, Mekong and Yangtze rivers. One sees in the now empty ancient river beds and dead or drying lake basins of northwestern Thailand, Laos, and northern Burma how tectonic changes created new aquatic systems only to surrender these to new stream captures, new lake formations leaving behind isolated lakes or empty basins. We see in the transient aquatic world at the eastern end of the Himalayan orogeny, over the past 12 million years, the elements needed for rapid evolutionary change, the subdivision of population into small, isolated, peripheral units (Wright, 1940). Eldredge & Gould (1972) and Gould & Eldredge (1977) argue that evolution proceeded more by rapid and episodic events of speciation in such peripheral populations than by gradual change, a theme elaborated on by Stanley (1979). We see the rapid appearance of two secondary radiations and a number of primary radiations that are separated from each other by discrete morphological gaps. Given the abundance of species that exist and the recentness of the radiation we do not see continuous series of morphological change in transition from one primary radiation to another. We do not see any semblance of gradual change. The macro-adaptive radiation of the Triculinae represents an excellent case of the punctuational model as defined by the above authors.

The problem with involving punctuated equilibrium is one of scale. How much can be resolved in the fossil record over slices of time involving one million years when new species can arise in thousands of years? Paleontologists do not have the relevant data (Smith, 1981). However, data from *Drosophila* research reviewed by Jones (1981) clearly indicate that some populations have sufficient hidden genetic variation to enable instant speciation under certain conditions, which can involve morphological and behavioral characteristics as well as reductive isolation. These conditions apparently involve organisms that disperse easily, have relatively short generation times, and live under conditions where new ecological space opens. These conditions apply to the triculine radiation and are persuasive in considering the triculines as fitting a punctuational model.

The Pomatiopsinae and the *Tomichia* radiation: Introduction

The general features of the pomatiopsine macro-adaptive radiation have been presented (Davis, 1979). There are eight genera:

Aquidauania, Brazil, South America; *Tomichia*, South Africa; *Coxiella*, Australia; *Oncomelania*, Asia; *Blanfordia* and *Fukuia*, Japan; *Cecina*, Japan, Manchuria, western U.S.A.; *Pomatiopsis*, U.S.A. Unlike the Triculinae, various pomatiopsine taxa are amphibious, saltwater tolerant, terrestrial and arboreal in addition to being freshwater aquatic. The relictual vicariant distributions of *Tomichia*, *Coxiella*, and *Aquidauania* are consistent with a Gondwanaland origin, especially as these genera are more closely related to each other (in terms of overall morphological similarity) than any one of them is to the more derived *Oncomelania*. *Oncomelania* has a distribution from northern Burma (Pliocene-Pleistocene fossil) to Japan with an arc following the Yangtze River, through Taiwan, to the Philippines and Sulawesi (Davis, 1979, 1980).

I knew from preliminary dissections of *Tomichia ventricosa* sent to me at the University of Michigan, Ann Arbor, Michigan, U.S.A., in 1964 that this species was a member of the Pomatiopsinae. Connolly (1939) listed 10 species of *Tomichia* from South Africa but said nothing about their soft parts, morphology or ecology. On the basis of shell and radula data presented by Connolly (1939), I saw a resemblance between *Tomichia differens*, *T. natalensis*, and *T. cawstoni* and various species of *Tricula*. I thought that these species might, in fact, be species of *Tricula*. Accordingly, I initiated studies in South Africa in 1977 to 1) see if one or all of the three species in question were *Tricula*, thus strengthening the hypothesis of South Central Gondwanian origin of the Triculinae; 2) assess the extent of morphological divergence among species of *Tomichia* and *Tricula* that I might find there; 3) assess the extent of the *Tomichia* radiation; 4) learn about the ecology of the relevant species and, if possible, about the origin and radiation of *Tomichia*.

Methods of collection and dissection were those of Davis & Carney (1973) and Davis (1979). Collections were made from the Orange River, Namaqualand in the west beneath the escarpment along the entire coast of South Africa eastward to Richard's Bay near Mozambique (Appendix 1). All localities where snails were found are shown in Figs. 7, 8. Anatomical data and systematic analyses are given in Appendix 2. Types examined are discussed in Appendix 3. As a result of these data I have reduced the number of species of *Tomichia* in South Africa to seven (Table 3). The shells and distribution of these species

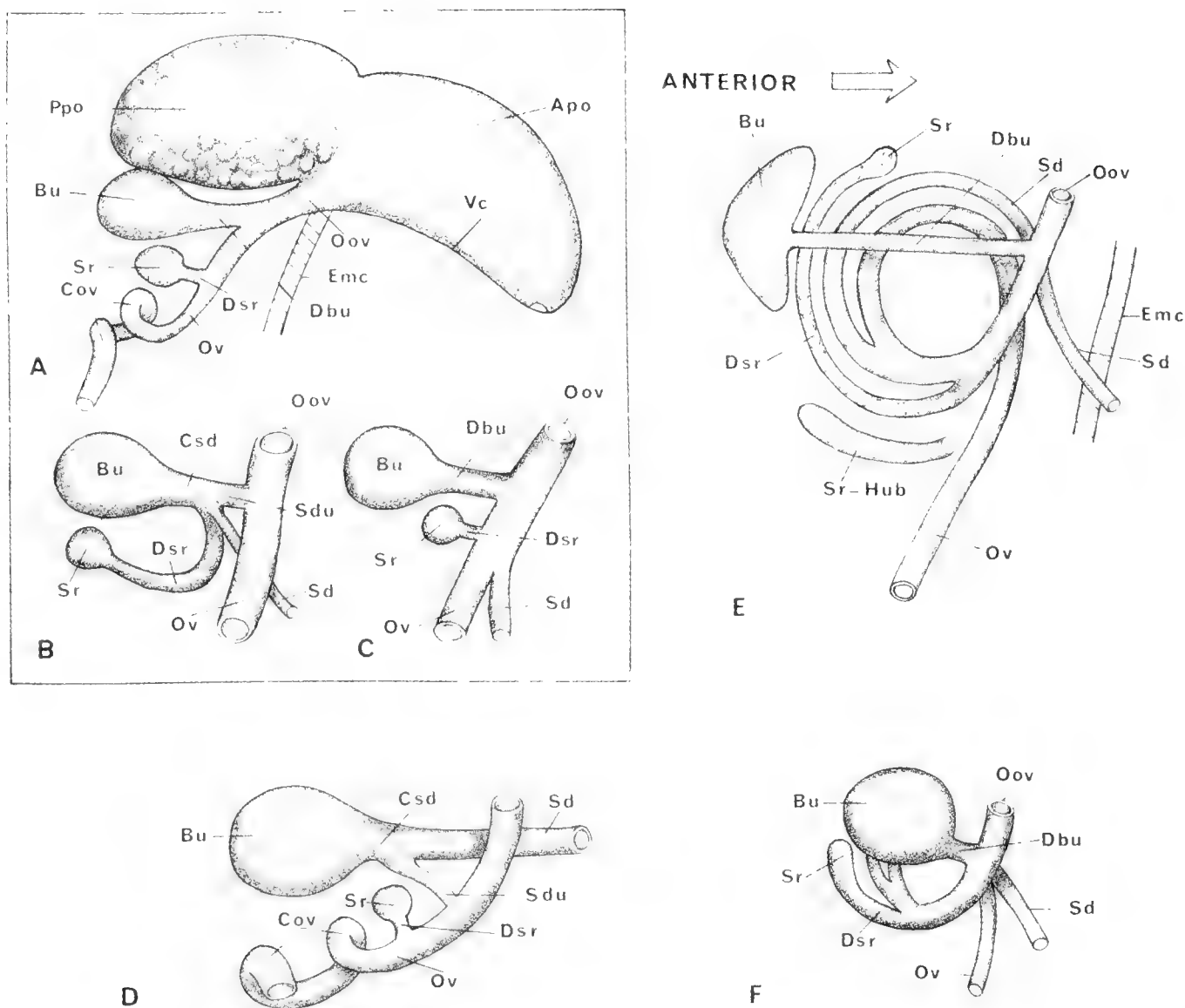


FIG. 6. Female reproductive system. The generalized character states are seen in the box: A, Hydrobiidae; B, *Tricula burchi*, *Tricula aperta*; C, *Tricula bollingi*. D, Pomatiopsinae. E, Derived oviduct circle complex of the Jullieniini. The short seminal receptacle of *Hubendickia* (Sr-Hub) is considered generalized; the elongate one (Sr), derived. F, *Karelainia*; a very condensed oviduct circle complex with short Sr.

Abbreviations: Apo, anterior pallial oviduct; Bu, bursa copulatrix; Cov, Coiled section of oviduct; Csd, common sperm duct; Dbu, duct of the bursa; Dsr, duct of the seminal receptacle; Emc, posterior end of the mantle cavity; Oov, opening of oviduct to Ppo; Ov, oviduct; Ppo, posterior pallial oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle; Sr-Hub, seminal receptacle of *Hubendickia*; Vc, ciliated ventral channel (from Davis, 1980).

are shown in Figs. 7 and 8. *T. cawstoni* is possibly extinct (see Appendix 3). *T. alabastrina* (Morelet) listed by Connolly (1939) is not a species of *Tomichia* but of *Hydrobia* s.s. (Davis, in prep.).

Morphological species concepts

Few morphological differences serve to separate the species (Appendix 2, Tables 4–6). *T. natalensis* and *T. differens* are unques-

tionably species of *Tomichia*. Those differences that do occur among species are primarily quantitative. The only morphological differences seen among species involve shell shape, size, tendency for shell micro-sculpture, position of the tip of the radular sac, very slight differences of point of entry of the spermathecal duct into the bursa copulatrix and slightly different positional relationship between the openings of the sperm duct and spermathecal duct into the bursa copulatrix.

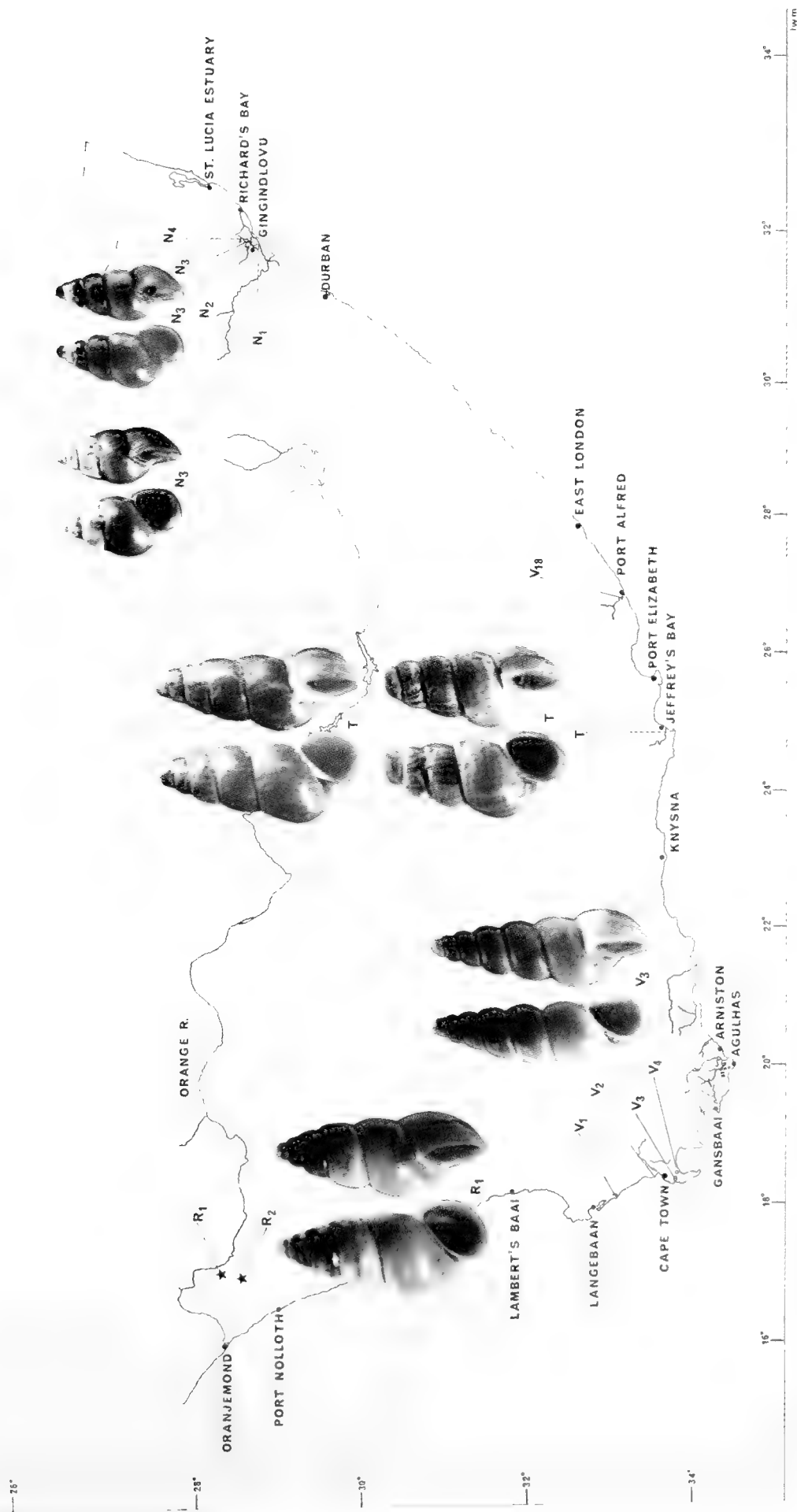


FIG. 7. Shells and distribution of *Tomichia rogersi* (R), *T. ventricosa* (V), *T. tristis* (T), and *T. natalensis* (N). Further distributions of *T. ventricosa* are given in Fig. 8 with emphasis on the Agulhas area. The coastal stretch from East London to Durban is devoid of *Tomichia* because cliffs fall abruptly to the sea and deep eroded stream channels provide no suitable habitat. Also, this stretch has little or no calcium deposits (see Fig. 11). Shell sizes are given in Table 12. Numbers, e.g. V₁ refer to collection sites listed in Appendix 1. All shells are printed at the same scale.

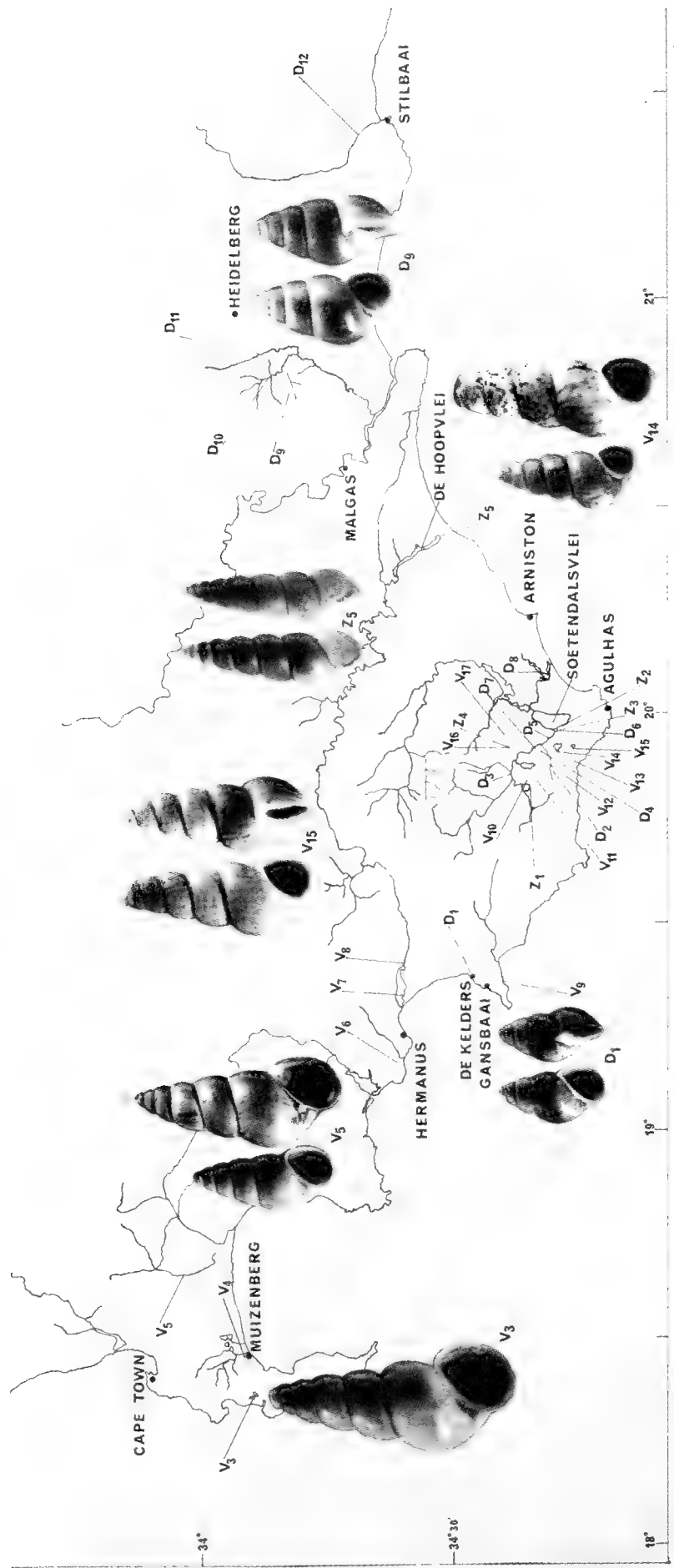


FIG. 8. Shells and distribution of *Tomichia ventricosa* (V), *T. differens* (D), and *T. zwelldamensis* (Z). Shell sizes are given in Table 12. Numbers, e.g. D1 refer to collection sites listed in Appendix 1. All shells are printed at the same scale.

TABLE 3. South African species of *Tomichia* Benson, 1851.

Type-species: *Truncatella ventricosa* Reeve, 1842: 94, pl. 182, fig. 2, by monotypy.
Type-locality: South Africa, marshes of the Cape Flats.
Distribution of type-species: South Africa, coastal regions below the escarpment from Ysterfontein to Agulhas, Cape Province.

Species of *Tomichia* (+ = synonyms)

1. *T. cawstoni* Connolly, 1939. Kokstad, Cape Province
2. *T. differens* Connolly, 1939. Die Kelders, on coast of Walker Bay, about 10 mi. S of Stanford, Cape Province
3. *T. natalensis* Connolly, 1939. Lower Umkomaas, Natal Province
4. *T. rogersi* (Connolly, 1929). Stinkfontein, Namaqualand
Hydrobia rogersi Connolly, 1929
5. *T. tristis* (Morelet, 1889). Port Elizabeth, Cape Province
Hydrobia tristis Morelet, 1889
+ *T. lirata* (Turton, 1932). Port Alfred, Cape Province
Assimineia lirata Turton, 1932
6. *T. ventricosa* (Reeve, 1942)
+ *T. producta* Connolly, 1929. Eerster River, Cape Flats, Cape Province
7. *T. zwellendamensis* (Küster, 1852). Lakes and streams in Zoetendol Valley, Bredarsdorp District, Cape Province
Paludina zwellendamensis Küster, 1952: 53, pl. 10, figs. 19–20.

TABLE 4. Comparison of *Tomichia* species using 25 characters and their states. There is at least one difference among the species involving each character. Characters 18 to 24 involve scaling (see Table 6). In a two state character 0 = no; 1 = yes. NC, no data.

Characters and character states	<i>T.d.</i>	<i>T.n.</i>	<i>T.r.</i>	<i>T.t.</i>	<i>T.v.</i>	<i>T.z.</i>
1. Shell length based on length of last three whorls (see Fig. 12). a. small (0) b. medium (1) c. large (2)	0	0	2	1	1	0
2. Shell aperture shape a. ovate (0) b. ovate-pyriform (1) c. subquadrate (2)	1	2	0	0	0	0
3. Shell shape a. ovate (bullet-shaped) (0) b. ovate-conic (1) c. turreted (2)	0	1	2	2	2	2
4. Shell peristome brown-rimmed (0, 1)	0	1	0	0	0	0
5. Shell peristome complete and well-developed (0, 1)	1	1	1	1	1	0
6. Shell columellar twist evident (0, 1)	0	0	0	0	0	1
7. Shell outer lip thin (0, 1)	0	0	0	0	1	1
8. Shell spiral microsculpture a. none (0) b. on some shells (1) c. commonly seen (2) d. strong and producing malleations (3)	2	0	1	3	1, 2	0
9. Shell inner lip reflected a. not so (0) b. slightly (1) c. pronounced (2)	0	0	0	1	2	1

TABLE 4 (Continued)

Characters and character states	<i>T.d.</i>	<i>T.n.</i>	<i>T.r.</i>	<i>T.t.</i>	<i>T.v.</i>	<i>T.z.</i>
10. Radula central tooth formula 3 – 1 – 3 (0) 2 – 2 2 – 1 – 2 (1) 2(3) – (3) 2	1	1	0	1	1	0
11. Radula cusps on outer marginal may be > 11 (0, 1)	0	0	0	0	0	1
12. Radula cusps on inner marginal may be > 13 (0, 1)	0	0	0	0	1	1
13. Tip of radular sac ventral to buccal mass (0, 1)	0	1	1	1	1	1
14. Sexual dimorphism in shell length (0, 1)	0	1	0	NC	NC	0
15. Shells of males and females a. have same no. whorls (0) b. males have more (1) c. females have more (2)	0	1	2	NC	NC	0
16. Spermathecal duct opens into the bursa: a. posterior end, <.35 mm from end (0) b. >.40, <.60 mm (1) c. >.70 (2)	1	0	2	1	1	1
17. Spermathecal duct opens into left ventrolateral edge of bursa (0, 1)	0	1	0	0	0	0
18. Pleuro-subesophageal connective longer than expected for body size (0, 1)	0	1	0	0	0	0
19. Body length relative to shell length a. longer than expected (0) b. shorter than expected (1) c. as expected (2)	2	2	2	0	1	2
20. Length radula/length of buccal mass a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	0	2	1	2	2
21. Length of bursa/length of pallial oviduct a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	0	2	2	2	2
22. female gonad a. longer than expected (0) b. shorter than expected (1) c. as expected (2)	1	2	2	2	2	2
23. Length of pleurosupraesophageal connective a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	2	2	2	2	1
24. Gill filaments (male and female) a. more than expected (0) b. fewer than expected (1) c. as expected (2)	2	2	2	2	2	0
25. Gill filament no. sexual dimorphism (0,1)	0	1	0	0	1	0

There are differences in the number of gill filaments. A number of quantitative differences are seen once data are arranged to permit scaling (Table 6). We do not see the kind of shell shape and sculptural diversity that is common among species of various triculine genera. We do not see any cladogenesis.

Discussion of relationships

On the basis of the morphological data (Tables, Appendix 2), 25 characters and their character states serve to discriminate among species (Table 4). As seen in Table 5, species

differ by as few as seven (28%) and as many as 20 character states (80%). Of these characters, 9 (36%) involve shell characters, 4 (16%) involve radular characters, 3 (12%) relate to sexual dimorphism (shell, gill filament number), 2 (8%) are internal anatomical features involving the bursa copulatrix and 7 (28%) involve scaling (Table 6)—comparisons of all species to assess whether or not the number and/or size of organs/structures correlate with overall size.

Aside from shell size and shape, the species do not differ much from each other. There are only two qualitative differences of internal morphology, i.e. clearly seen changes in structure or position of organs or structures. These are the position on the bursa where the spermathecal duct joins the bursa; the position on the bursa where the sperm duct joins the bursa. All other differences are quantitative and the seven character-state differences involving scaling necessitated a careful comparison of all species for all measurements to uncover subtle differences.

In analyzing data for scaling (Table 6) trends are looked for that clearly deviate from the expected. Expected trends are: 1) a de-

TABLE 5. Number of differences among species of *Tomichia* based on data in Table 4.

	<i>T.d.</i>	<i>T.n</i>	<i>T.r.</i>	<i>T.t.</i>	<i>T.v.</i>	<i>T.z.</i>
<i>T. differens</i>	—	14	9	9	10.5	14
<i>T. natalensis</i>		—	14	13	14	20
<i>T. rogersi</i>			—	7	8.5	12
<i>T. tristis</i>				—	7	12
<i>T. ventricosa</i>					—	11
<i>T. zwellendamensis</i>						—

TABLE 6. Species ranked in decreasing shell size based on length of the last three whorls in order to assess if size or numbers of structures correspond to overall size based on shell size.

Species	Length of last three whorls	Length of body (♀)	Length of buccal mass	Length of radula ÷ length of buccal mass	Length of bursa copulatrix ÷ length of pallial oviduct	Length of bursa copulatrix
<i>T. rogersi</i>	6.8 ± 0.18	12.3 ± 1.1	1.3 ± 0.1	1.07	.36 ± 0.04	1.70 ± 0.11
<i>T. tristis</i>	5.7 ± 0.29	12.6 ± 1.8*	1.3 ± 0.1	0.95*	.32 ± 0.02	1.41
<i>T. ventricosa</i>	5.3 ± 0.48	8.7 ± 0.6*	1.0 ± 0.2	1.06	.31 ± 0.07	1.18 ± 0.15
<i>T. differens</i>	4.3 ± 0.14	8.3 ± 0.4	1.0 ± 0.2	1.26*	.31 ± 0.04	1.11 ± 0.11
				1.19		
<i>T. zwellendamensis</i>	4.1 ± 0.19	8.4 ± 0.8	0.9 ± 0.2	1.08	.29 ± 0.04	1.09 ± 0.23
<i>T. natalensis</i>	4.1 ± 0.22	8.2 ± 0.6	0.9 ± 0.02	0.98	.40 ± 0.02*	1.26 ± 0.06*
	Length of ♀ gonad	RPG ratio	Length of pleuro-supraesophageal connective	No. of gill filaments		Length of pleuro-subesophageal connective
				♂	♀	
<i>T. rogersi</i>	2.26 ± 0.3	.61 ± .06	.62 ± .15	51 ± 4	52 ± 3	.08 ± .11
<i>T. tristis</i>	2.0 ± 0.2	.61 ± .09	.50 ± .09	58	56 ± 3	.13 ± .15
<i>T. ventricosa</i>	1.23 ± 0.3	.54 ± .04	.42 ± .09	40 ± 3	55 ± 2**	.04 ± .05
<i>T. differens</i>	1.05 ± 0.3*	.49 ± .06	.30 ± .07	28 ± 3	29 ± 3	.03 ± .03
<i>T. zwellendamensis</i>	1.3 ± 0.1	.51 ± .07	.23 ± .07*	66*	51 ± 8	.02 ± .02
<i>T. natalensis</i>	1.20 ± 0.2	.57 ± .04	.36 ± .03	30	38 ± 2**	.14 ± .07*

*Pronounced departure from the expected trend.

**Sexual dimorphism noted.

crease in body length as shell length decreased, 2) a correlation of decrease in organ length with body length decrease, 3) an optimal size of organ length over a range of body lengths, 4) the decrease of organ length with body length until a constraint is reached where the organ could not function properly at a smaller size. With regard to the expected trends we see in Table 6 that buccal mass length fits the class 3 expectation above and there is no significant difference among the four smallest species. On the other hand one notes, examining columns 3 and 4, that the

fourth smallest species has a ratio of length of radula divided by length of buccal mass that is significantly greater than that seen in any other species, larger or smaller; also, the smallest species has a much larger ratio of length of bursa copulatrix divided by length of pallial oviduct (column 5) than all but the largest species. Other departures from the expected are marked in Table 6.

There are no pronounced radular differences (Figs. 9, 10). There is variability in central tooth center cusp width but very little in cusp number. There are none of the profound

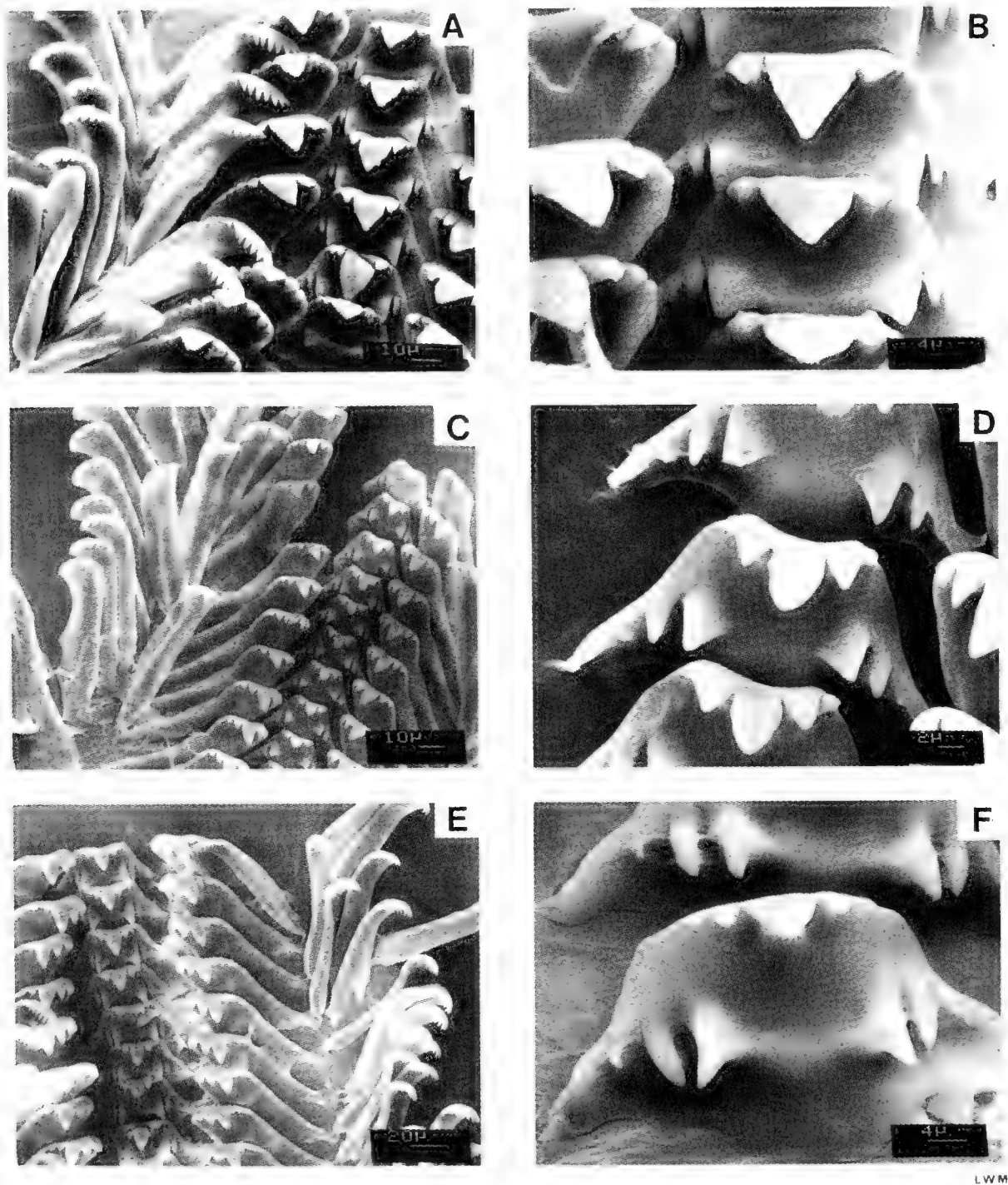


FIG. 9. Scanning electron micrographs of radulae A, B. *Tomichia differens* (D77-13); C, D. *T. natalensis* (D78-212); E, F. *T. rogersi* (D77-20).

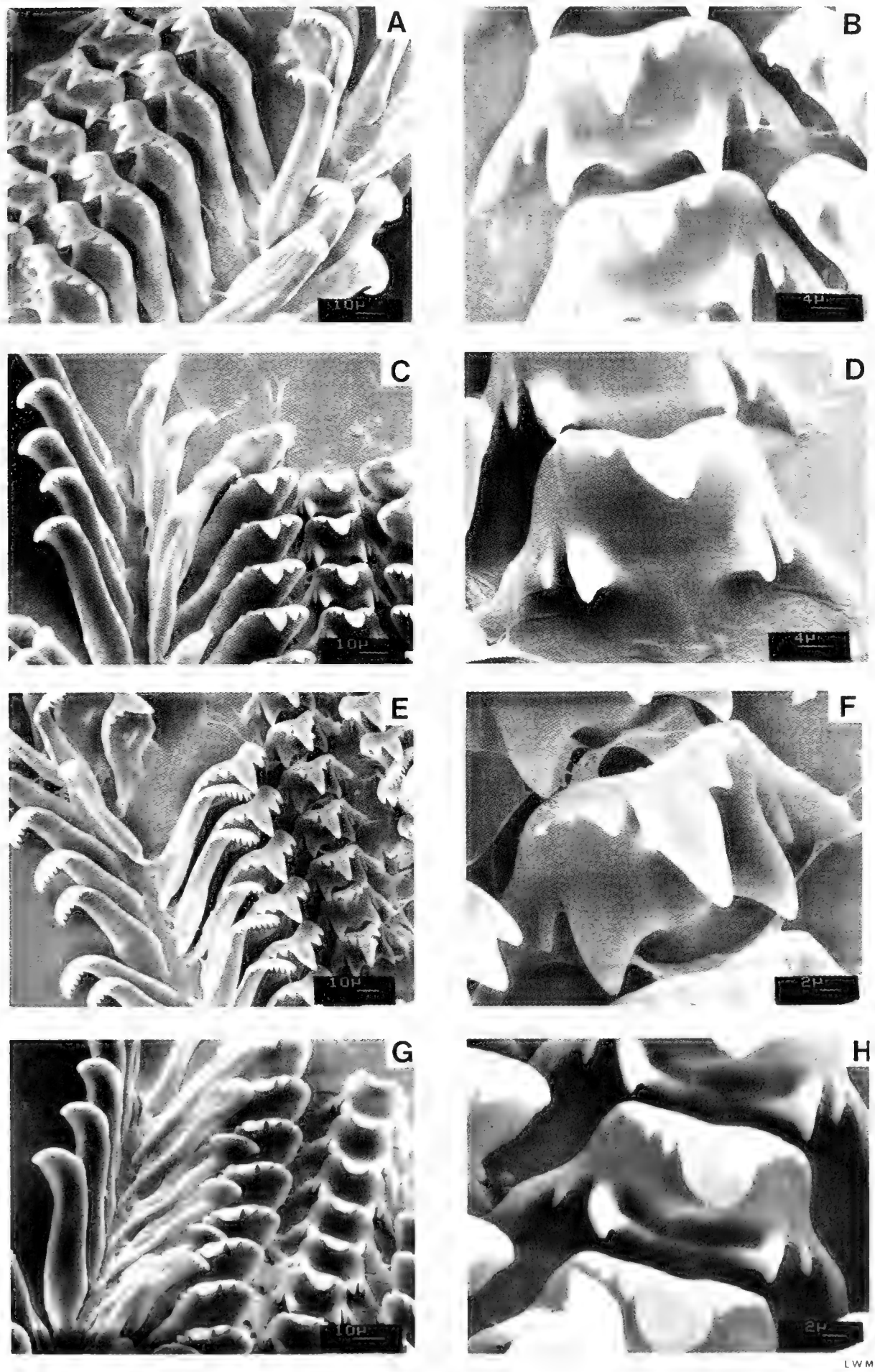


FIG. 10. Scanning electron micrographs of radulae. A, B. *Tomichia tristis* (D78-53); C, D. *T. ventricosa* (D77-16); E, F. (D78-80); G, H. *T. zwellendamensis* (D78-74).

differences in structure marking different modes of feeding as seen in the *Hubendickia* or *Hydrorissoia* radiations (Pomatiopsidae: Triculinae) in the Mekong River (Davis, 1979: fig. 4). The variation in cusp number is not impressive considering the notorious variability recorded for pomatiopsine populations or subspecies of *Oncomelania hupensis* and *Pomatiopsis lapidaria* (Davis & Carney, 1973; Davis, 1967).

The anterior central cusp of the central tooth may be narrow and elongate in some individuals of some populations of *T. ventricosa* (Figs. 10E, F). Only one in nine individuals of the V_1 populations had this morphology while 90% of the individuals from V_{15} had the narrow cusp. Refer to Connolly (1939: fig. 48) for figures of radulae of taxa considered species by him. He considered that there were distinct radular types. I conclude from this study that variation within one or two populations of *T. ventricosa* encompasses most of the types considered distinct by Connolly.

One of Connolly's taxa requires special comment. *T. producta* Connolly was named with the Eerste River, Cape Flats, Cape Province, as type locality. The species differed from *T. ventricosa* by more rounded whorls, deeper sutures, and tall turreted spires of up to 10 whorls. The anterior central cusp of the central tooth was very broad contrasting the narrower cusp seen in *T. ventricosa*. Variability in cusp diameter has been discussed. Shells matching Connolly's figure (1939: fig. 47D) are seen most frequently in pans as defined earlier in this paper. The form is especi-

ally seen in the pans near Zoetendalsvlei. No data support consideration of this form as a distinct species; it represents part of the variability of *T. ventricosa*.

Considering the minor differences that do occur among species it is clear (Table 5) that *T. ventricosa*, *T. tristis*, and *T. rogersi* have the greatest similarity, with *T. differens* clustering close to these three species. *T. natalensis* and *T. zwellendamensis* are distinctly divergent from each other and from the cluster containing the other four species. *T. zwellendamensis* shares more character states in common with *T. ventricosa*; *T. natalensis* is closest to *T. tristis*.

Ecology

The greatest differences seen among species of *Tomichia* are physiological differences not morphological ones. These differences, summarized in Table 7, are discussed below.

Tomichia ventricosa—This species lives in the broadest range of environments seen for any species of *Tomichia*. The species is found in shallow rivers (H_2O , 0‰), coastal wetlands and estuarine settings with low salinity (4–8‰). *T. ventricosa* is also found in vleis and pans where the basin fills with water during the rainy season and dries out slowly during the dry season, often becoming totally dry for varying periods of time, i.e. weeks to months. With the onset of rain, water in the newly filled basins has a salinity (8–10‰); as they dry out the water becomes increasingly saline (to >160‰).

The river populations apparently live con-

TABLE 7. Habitat types and salinity measurements from habitats where species of *Tomichia* were found.

Species of <i>Tomichia</i>		Habitat	Salinity (American Optical Refractometer)
<i>T. cawstoni</i>	species extinct?		—
<i>T. differens</i>	aquatic		\bar{X} , 2.3‰ (0–4‰; 1 locality, 9.5‰), N = 11
<i>T. natalensis</i>	amphibious, stream banks		stream 0‰, N = 4
<i>T. rogersi</i>	aquatic, amphibious		(4–5‰), N = 2
<i>T. tristis</i>	terrestrial, amphibious; high above shoreline of aborted estuary		lagoon 20‰, N = 1
<i>T. ventricosa</i>	aquatic, amphibious, rivers vleis		(4–8‰), N = 2 \bar{X} , 34‰, (8–83‰), N = 9
	pans		(25–32‰), N = 2
<i>T. zwellendamensis</i>	aquatic in vleis, lakes		\bar{X} , 2.6‰ (0–8‰), N = 5

tinuously submerged in perennially flowing water. It is probable that the rivers of Sandvlei, Muizenberg (D77-50) and Kleinrivier near Hermanus (D7) occasionally do dry up during periods of severe drought but I saw no evidence for this. I have collected living specimens of this species in only two rivers.

The situation in temporary standing water vleis and pans is in stark contrast to that in perennial rivers. Pans are circular and rain-filled shallow pools most frequently seen near the shore behind the foredunes of the Cape Province, especially near Agulhas and Hermanus. Vleis are irregularly shaped catchment basins or playa lakes often associated with streams and small rivers that go dry annually or, in some cases, irregularly. Because of their proximity to the sea and the evaporative cycle, pans and vleis are saline as evidenced by the *Salicornia*-rich fringing vegetation. The cycle involving *Tomichia ventricosa* is shown by a study of this species at Ysterfontein Vlei in the Cape Province (refer to Tables 8, 9). I first visited the vlei on 15 November 1977 and it was nearly full of water

with 12‰ salinity. Snails were found under rocks near the edge of the water. Blooms of coarse-stranded green algae were starting. I marked the high water point and returned on 30 December 1977 during which time the water had receded horizontally 26 m and the salinity had more than doubled. Snails were found in hundreds per m² in the shallows, on the substrate and in algal masses that had accumulated. The snails did not appear in the least affected by the salinity approximately equal to that of the offshore ocean water. I also took soil-substrate samples (400 cm²) at intervals between the water and the high-water mark and found that over 92% of the snails found in the samples were living (Table 9).

On the 4th of February, 1978, the water had receded another 15 m and the salinity was approximately double that of sea water. Snails were found concentrated as before. Out in the Vlei, salt crystals were encrusting the algal mats exposed to the sun (83‰) but the snails were moving about normally. On shore where the water had retreated, algal

TABLE 8. Record of the drying up of Ysterfontein Vlei (V₁, D77-11) and the associated increase in salinity.

Date	Meters from first highwater marker to edge of water	Salinity (‰)
15 November 1977	0	12
30 December 1977	26	28
4 February 1978	41 (edge H ₂ O)	58
	91 (out in shallow H ₂ O)	83
March 1978	>.8 km	>160
April 1978	>.8 km	>160

TABLE 9. Snails, living and dead, sorted from small substrate samples (soil to 2", grass, *Salicornia* spp., rocks) taken from three localities along a transect from the 15 November 1977 high water mark to the edge of the water, 26 m away at Ysterfontein Vlei; see Table 8; 30 December 1977.

Size class (mm)*	7.3 m (from high water mark)		16.5 m		21 m	
	Living	Dead	L.	D.	L.	D.
<1.84	4	0	20	0	26	0
1.84-1.96	14	1	16	0	15	1
2.00-2.20	25	1	13	1	33	0
2.24-2.44	30	1	18	2	25	0
2.48-2.68	15	0	16	0	21	0
2.72-2.92	12	2	12	0	12	1
2.96-3.16**	1	0	3	0	2	0
>3.20	1	3	2	0	2	0
	102	8	100	3	124	2
% living	92.7		97.1		98.4	

*length of body whorl

**size class for \bar{X} of mature males and females used for anatomical studies: Appendix 2, Table 12.

masses had settled on the *Salicornia* and *Arthrocnemum* plants forming a continuous thick, tough, dry roof separated from the substrate by 3 to 8 cm. Upon cutting open a hole in the algal-mat roof one could see active snails on the moist substrate below. The snails were amphibious in this humid, moist environment.

I also watched the drying up of the Vermont Pan near Hermanus. As long as there was water in the pan, snails were seen crawling about on the compressed sandy substrate; there were hundreds per m². There was little fringing *Salicornia* and/or *Arthrocnemum* and no masses of algae in the water. When the pan was dry and sunbaked, the edge of the pan was ringed with windrows of dead *Tomichia ventricosa* shells. Upon pulling up rocks and digging down along fissure-like cracks I collected snails that, upon being placed in water, were found to be living. It was thus evident that snails could survive by burrowing below the surface to areas harboring some moisture, and survive there in estivation until the next rain.

In yet another pan near Agulhas, the substrate was packed sand and the water level was nowhere greater than 15 to 20 cm deep. The salinity was 25‰ and snails were of approximately the same density on the substrate as in the Vermont Pan. The banks of the pan were packed sand and at the high water mark were windrows of dead snails with some piles 20 to 30 cm deep with thousands of *T. ventricosa* shells.

No other snails are capable of living in the vleis and pans inhabited by *T. ventricosa*. *T. ventricosa* that survive the period of desiccation emerge during the rainy period into an environment filling with freshwater where salinity levels probably reach 9 to 10‰. It is most likely that at this time they reproduce with exceptionally high intrinsic rate of natural increase (*r*). With the dry season the snails adjust to dwindling water and increasing salinity until they are forced into an amphibious mode of existence or into estivation. Snails not reaching safety within the moist chambers provided by *Salicornia* plants and algal-mat roofs or beneath rock piles or other subterranean refuges die due to stranding and desiccation or by osmotic death when the remaining pools of water reach a salinity of 130 to 160‰ (as in Ysterfontein Vlei, March and April, 1978; see Table 8).

Tomichia ventricosa has adapted to the greatest range of environmental conditions

and stresses of any species of snail I know: freshwater, brackish to hyper-saline, amphibious, dry substrate estivation.

T. differens—This species is found living in streams and small rivers with perennial water. At the type-locality this species lives on rocks, feeding on algae and algal-associated material under a thin sheet of continuously flowing water (5 mm to 3 cm depth). The stream is an outflow from a limestone cave, some 5 to 6 m above sea level; the distance from the cave opening to the sea is some 20 to 25 m. The species is common along the base of aquatic sedges in the Nuwejaarsrivier (River) flowing into Soetendalsvlei, a large lake near Agulhas. In other areas (Appendix 1, D11) this species is common in and on algal mats in a small stream. At one locality (Appendix 1, D4) near Soetendalsvlei, the species was common in a small stream on 1 January 1978, the stream had dried up but the snails were alive under stones and rocks. This stream flows into the Nuwejaarsrivier and on 19 January 1978, this species was still common in this river and water levels in the river were only slightly lowered from levels seen on 1 January 1978.

The salinity of the water was 0 to 4‰ in 10 of 11 habitats tested; 9.5‰ in only one habitat (Table 7; Appendix 1). I consider *T. differens* to be a freshwater aquatic species living in perennially flowing waters. It probably has some capability for withstanding desiccation for a limited period of time.

T. natalensis—This species is only found in Natal; it is primarily amphibious on stream banks with mud slopes of 45° or less and in considerably shady and humid environments provided by grassy vegetation. The habitat is a cross between that seen for *Pomatiopsis lapidaria* and *P. cincinnatiensis* of the eastern United States (Van der Schalie & Dundee, 1955, 1956; Van der Schalie & Getz, 1962, 1963). In one location (Appendix 1, N3) snails were exceedingly numerous among and under stacks of soggy reeds; many of the snails were obviously living submerged while others were out of water. The water always had 0‰ salinity.

This species was only found in the Zululand region of Natal. Widespread sugar cane farming in upland and coastal Natal has had a profound negative impact on streams there. The few remaining habitats of *T. natalensis* are, in fact, bounded by cane fields and their future is insecure.

T. rogersi—This, the largest species of

Tomichia, is found in only two localities, isolated from each other in the high desert of Namaqualand. The species is freshwater-aquatic with some tendency towards being amphibious. In Lekkersing, a tiny community of human desert dwellers, this species is located in a blind canyon with only a single small spring for water. The spring was capped with a stone base and windmill. From the base of the windmill, a tiny trickle of water has resulted in a seepage channel some 23 m long that ends in sand. The seepage supports a narrow grassy strip about 0.6 m on each side. The soil is only damp as there is insufficient water to maintain any visible surface flow. Snails are numerous among and under rocks and among the basal grass stems along the seepage channel.

The habitat at Eksteenfontein, the second locality, is rather similar except that the spring is larger and the flow of water produces a visible stream. Where the water flows through coarse grass, snails are abundant at the stems of the grass at the mud-emergent grass interface just at water level, not submerged in water.

A search of remaining isolated springs in Namaqualand, e.g. Khubus (28° 28' S.; 17° 00' E.) or Annisfontein (28° 25' S.; 16° 53' E.) either yielded no snails or only the pulmonate *Bulinus*.

T. tristis—I consider this species to be terrestrial-amphibious. I found the species in only one locality (Appendix 1, T), along the west bank of the large lagoon at Aston Beach, Cape Province. The bank was near the junction of Seekoeirivier (River) and the lagoon, and close to human habitation. The snails were not in a marshy area, but high up on the shore, in a well drained area next to the mowed lawn of the residence. The snails were on black loam beneath branches, logs and piles of similar debris along with a species of *Assimineia*. The habitat was moist and humid but not wet. It was evident on the basis of a healthy terrestrial environment that this locality was only rarely flooded. The snails were numerous, reaching hundreds per m² but patchy, being found only under trash, brush or logs. Water of the lagoon some meters away was 20‰. There were no snails of any kind among the *Salicornia* plants at waters edge or in the lagoon.

T. zwellendamensis—This species is freshwater-aquatic living on stems of sedges or on the bottom of lakes and ponds, not in fast flowing water, of the Agulhas area. The species is particularly abundant near the opening

into Soetendalsvlei and in De Hoopvlei, a large lake along the road from Aguihas to Potbergsvier (Appendix 1, Z5). In the Hoopvlei, snails were hundreds per m² on the marl-sandy bottom and algal patches. They live in permanent lakes or ponds of water with 0 to 8‰ salinity (Table 7).

Sympatric Species

I have found sympatry in only two localities involving three species: *T. differens*, *T. zwellendamensis*, and *T. ventricosa*. *T. differens* and *T. zwellendamensis* were found in a pan next to the Nuwejaarsrivier just before the river emptied into Soetendalsvlei (Appendix 1, D6, Z3). The depth of water in the pan was 5 cm, the bottom was of marl and the water rather muddy (not due to any recent rain). The edge of the pan was some 3 m from the river. *T. zwellendamensis* was common in grass on the bottom. There was an occasional *T. differens* among them. *T. differens* was common in the river on the stems of rushes and sedges while there were very few *T. zwellendamensis* in that habitat.

The other locality showing sympatry was a few miles from Soetendalsvlei, i.e. Longepan (Appendix 1, V17; Z4). *T. ventricosa* was common in the main part of the vlei, both on sedges and the sandy bottom. *T. zwellendamensis* was located where the vlei exited, flowing to the east, on the stems of reeds in quiet water. The salinity of the water in the vlei was 8‰.

DISCUSSION

In this section I discuss 1) the proposition that no concrete evidence supports the origin of *Tricula* on the African plate, 2) the age and distribution of *Tomichia* in South Africa, 3) the effects of changing environment on *Tomichia*, 4) preadaptive features in Pomatiopsinae for an amphibious or terrestrial existence, and 5) the tempos and mode of pomatiopsine evolution.

African *Tomichia* and the *Tricula* question

There are three species considered to be *Tomichia* that occur in central Africa (Brown, 1980). Verdcourt (1951) placed his *Hydrobia hendrickxi* from Kakonde, E. Zaire, in the genus *Tomichia* because of the morphology of the central tooth of the radula. *Tomichia*

was characterized by a peculiar raised basal projection of the central tooth giving the impression of a transverse line across the face of the tooth (Connolly, 1939; Verdcourt, 1951). The natural affinities of these central African taxa, removed some 2000 miles from the South African radiation, cannot be clarified without a thorough anatomical study. In attempts to learn more about the evolution of *Tomichia* it will be essential to study these taxa in detail to learn if they are, in fact, *Tomichia*, and to determine the degree of morphological relationships to South African *Tomichia*.

The transverse bar across the face of the central tooth is clearly illustrated in Connolly (1939) and by Davis (1968) in describing new species of *Tricula* from northwestern Thailand. On the basis of this basal bar and shell morphology it seemed certain that at least *Tomichia cawstoni*, *T. natalensis*, or *T. differens* would be, in fact, members of the tribe Triculini (Davis, 1979). On the basis of the anatomical data this is clearly not the case. The shells and radulae of certain *Tricula* and the above named species of *Tomichia* are extremely similar yet they belong in different subfamilies given their overall morphology. Accordingly, the relationship of *Hydrobia hendrickxi* to various pomatiopsid taxa is quite uncertain. Shell and radula alone are not sufficient for assessing relationships.

The so-called basal bar on the central tooth is a weak and uncertain character. The SEM pictures of the central tooth (Figs. 9, 10) do not reveal such a structure. Reexamining these radulae with transmitted light microscopy reveals the line but at a focal plane beneath the surface of the face of the tooth. Thus there is no pronounced ridge on the face of the tooth; the line is a subsurface structure. What is characteristic of the *Tomichia* central tooth is the extreme development of the inner pair of basal cusps that swell out far above the face of the tooth (well illustrated in Fig. 10B). So great is the outgrowth of these basal cusps that they often appear connected by a ridge (Fig. 10H), but this ridge is not in the same place as the illustrated basal line (Connolly, 1939). Another prominent feature of the *Tomichia* central tooth is the deep cavity beneath the basal cusps bounded by the lateral angle (see Fig. 10D or H).

There is no evidence substantiating the hypothesis (Davis, 1979) that there are Triculini in Africa. The amazing similarity in shell and radula discussed above among cer-

tain species of *Tomichia* and *Tricula* may reflect a common ancestry in the Cretaceous but no morphologically defined Triculini have been found in Africa to substantiate this contention. The similarity could just as well reflect ecology. This weakens the hypothesis that the Triculinae and Pomatiopsinae diverged from a common ancestor but does not, in light of other morphological characters and their history as hosts of parasites compel one to reject a common ancestor.

Age, modern distribution, man and the *Tomichia* radiation

The present coastal configuration of southern Africa was established by the end of the Cretaceous (Tankard et al., 1981). The fossil record of the Upper Cretaceous of South Africa and northern India reveals the presence of freshwater hydrobioid snails that were, with high probability, precursors of modern Pomatiopsidae (Davis, 1979). At that time when we first can track early Pomatiopsidae, they are freshwater-aquatic. The earliest record we have of the modern *Tomichia* radiation is from the Pliocene, in particular from Varswater Formation of Langebaanweg (west of Ysterfontein Vlei, Cape Province) (Kensley, 1977). Of particular interest are the freshwater species among the 20 gastropod, 2 bivalve and 1 chiton species found. *Tomichia ventricosa* was found with the freshwater limpet *Burnupia capensis* (Walker), the discoidal planorbid *Ceratophallus natalensis* (Krauss), and the spired planorbid *Bulinus* cf. *tropicus* (Krauss). The shells of *T. ventricosa* were fragmented (possibly implying transport) while the fragile planorbids and limpet shells were beautifully preserved.

There was a marine transgression in the Pliocene. There is evidence for freshwater and estuarine environments behind dunes (Tankard, 1975; Tankard et al., 1981). The juxtaposition of marine, estuarine, and freshwater species indicates an environment similar to that seen today along the Cape Province coast, e.g., the Hermanus estuary. Evidently, a river flowed into a lagoon, which opened to the sea. Quiet freshwater pond-like areas adjacent to and connected with the river would provide a habitat suitable for the planorbids. There are also numerous remains of the aquatic plant *Chara* that suggest such a habitat. *Tomichia* would perhaps have lived as seen today in the river flowing into the Hermanus lagoon (Appendix 1, 7, D77-29).

These data strengthen the hypothesis that the modern *Tomichia* radiation began with freshwater snails in a perennial freshwater environment.

There are to my knowledge no fossils of other Miocene to post Miocene species of *Tomichia* of South Africa. The modern physiological radiation probably evolved starting in the Pliocene with the full establishment of aridity in western South Africa and the effects of aridity spreading eastward.

Two major factors besides aridity apparently affect the distribution of *Tomichia* in South Africa: calcium availability and man. The distribution of calcretes in South Africa are shown in Fig. 11 as adapted from Netterberg (1971). A calcrete is a material formed by calcium carbonate deposited from soil water. Areas that show absence of calcification are marked on the map. *Tomichia* is limited to the narrow coastal strip associated with the short drainage systems beneath the escarpments above which are desert or semi-desert conditions. *Tomichia* is not found in areas that are calcium deficient (compare Figs. 7, 8, and 11).

Of particular interest is the area between the Hoopvlei and Jeffrey's Bay ($21^{\circ} 30'$ to $24^{\circ} 30'$ E. longitude). This strip of coast includes the Knysna-Wilderness lakes. Initially, I expected to find *Tomichia* here because there

was an abundance of perennial freshwater involving lakes and streams connecting lakes. These lakes and rivers are, from west to east, Touwsrivier (= Touws River) emptying at Wilderness (salinity 4‰), Island Lake (= Eilandvlei) (7‰), Longvlei (10‰), Rondevlei (16‰); then draining to the east Swartsvlei (13‰), Groenvlei (3‰). The Karatararivier (River) flowing into Ruigtevlei that in turn flows into Swartsvlei had a salinity of 1‰ . No *Tomichia* were found; a limpet was found in Groenvlei and numerous *Hydrobia* were found in Swartsvlei. No gastropods were found in any of the lakes or rivers except those mentioned.

The history of these lakes relates to fluctuations of land and sea level from the upper Pleistocene with a major marine transgression within the past 7,000 years. During periods of low sea level, the lakes were probably dry; the Recent lakes were probably formed by reflooding (Martin, 1962). In summary, calcium deficiency and the Recent history involving marine transgression in a series of basins originating in the upper Pleistocene are sufficient to explain the absence of *Tomichia*. *Tomichia* sp. recorded from the Pleistocene fossil deposits on terraces above the present lakes (Martin, 1962) are undoubtedly *Hydrobia*.

Man has had a profound influence on the

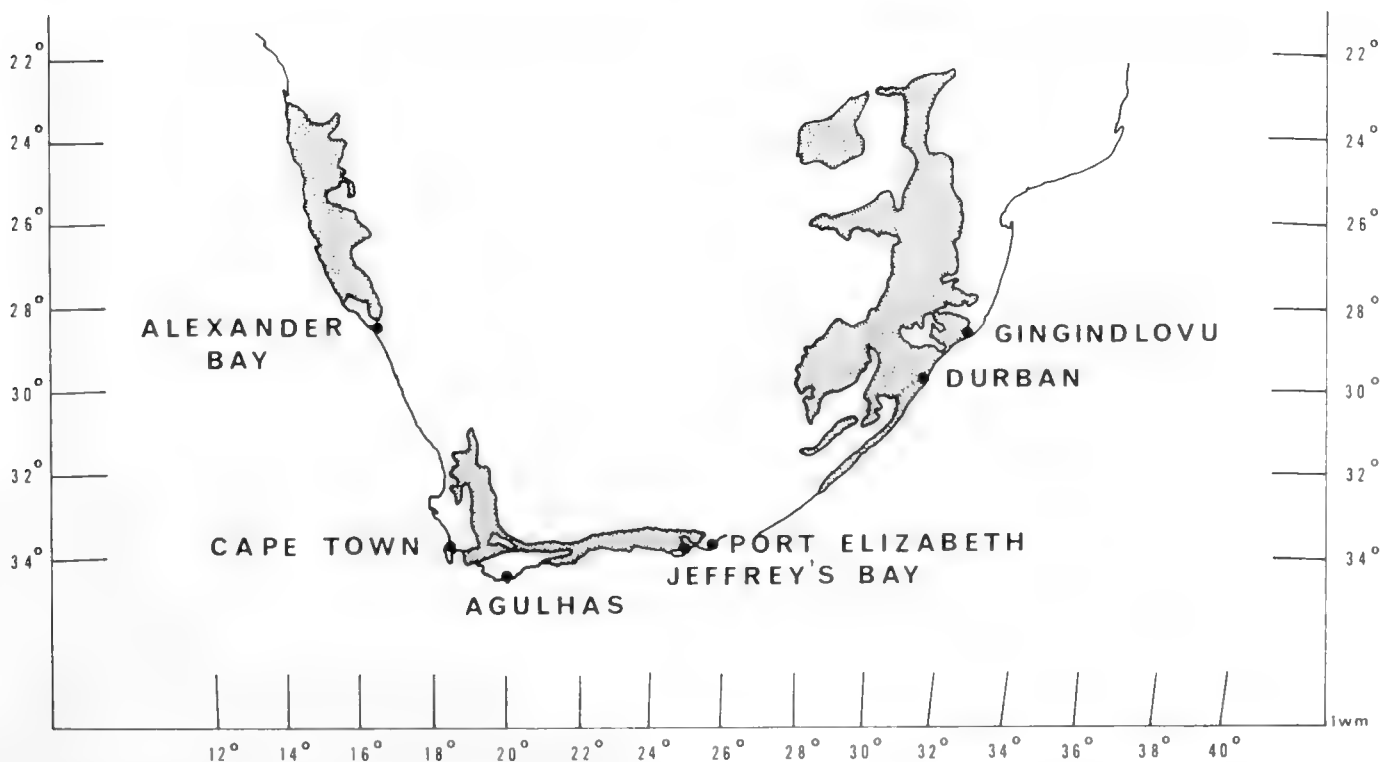


FIG. 11. Distribution of calcium deposits in South Africa. The shaded areas lack calcium deposits or calcretes (adapted from Netterberg, 1971).

distribution of *Tomichia*. Species of this genus are extremely sensitive to changes in their ecosystems relative to pollution of all types as well as interferences in the natural dry-wet seasonal cycles.

Only dead shells of *Tomichia* are now to be found in classic sites of Kuils River (34° 01' S.; 18° 39' E., near Cape Town Airport), Wild Bird Vlei, Cape Peninsula (34° 08' S.; 18° 21' E.), Kommetjie Vlei (34° 09' S.; 18° 20' E.), Reitvlei (33° 30' S.; 18° 30' E.). We found extensive evidence for organic pollution in Kuils River. In Wild Bird Vlei, a sewage plant now makes use of the limited available freshwater. Where there once was a healthy ecosystem, one now finds a series of hypersaline ponds of about 1/3 normal volume (judged on the basis of the obvious basin that was filled a few years ago) with salinity $>150\text{‰}$, stinking black mud, numerous dead fish. Kommetjie Vlei has been drained off; Reitvlei was dredged out some years ago to supply fill to make the docks at Cape Town. Instead of a shallow vlei there is a large, deep artificial pit. Numerous subfossil shells are found on the northern shore above the high water line.

Environment and the modern *Tomichia* radiation

We see today in the Agulhas region of Cape Province, South Africa, what was common throughout South Africa in the Eocene into the Miocene, i.e. an abundance of perennial freshwater. I assume, on the available evidence, that proto-*Tomichia* of the Eocene was aquatic, abundant, and widespread. In the one area of South Africa where there is still an abundance of freshwater, i.e. the Agulhas area, there are numerous lakes, streams, and ponds and rivers of low salinity, but of suitable alkalinity for hydrobioid snail life. It is here that one finds the greatest concentration of snail-rich habitats and species, two of which are freshwater-aquatic in perennial systems with salinity $<9\text{‰}$; mostly 0–5‰.

It is evident that the *Tomichia* radiation is species poor compared with the South-east Asian Triculinae radiations involving *Hubendickia*, *Pachydrobia*, etc. The *Tomichia* radiation is a physiological-ecological radiation, not one characterized by morphological changes. What accounts for this radiation?

The most plausible explanation is the progressive desertification in South Africa since

the late Eocene, some 39 million years ago when temperate rain forests in Namaqualand became depleted and replaced by mixed sclerophyllic vegetation (Axelrod & Raven, 1978). There has been progressive climatic change. There has not been a history of tectonic change in the Cenozoic that is associated with morphological changes and explosive speciation events seen elsewhere.

The Mesozoic break-up of Gondwanaland caused changing patterns of ocean currents and climatic processes causing progressive aridity in South Africa. These changes are related to the history of glaciation at high latitudes, especially Antarctic glaciation (Tankard et al., 1981). While glaciation in Antarctica persisted throughout the Oligocene, its present thickness developed about mid-Miocene and has existed in present condition from the late Miocene (Shackelton & Kenneth, 1975; Tankard et al., 1981). The aridity of western South Africa relates to upwelling of cold water of the Benguela Current and the origin of a cold Southern Ocean and thus could not have pre-dated the late Oligocene (Tankard et al., 1981).

In the Miocene, there was a pan-African vertebrate fauna in Namaqualand, there was a mosaic of sclerophyllus woodland, grassland, and scrub vegetation and summer rainfall that persisted throughout the late Tertiary. The earliest evidence of a modern semi-arid environment and winter rainfall in the southwestern Cape Province dates to the Pliocene (5 million years ago) (Tankard, 1978). Full semi-arid conditions with winter rainfall were achieved in western South Africa by the end of the Pliocene or early Pleistocene.

Progressive aridity stretched eastward. The short coastal rivers from the Orange River to Agulhas dry up for the most part during the dry season, or are reduced to very low flow. The effect on the estuarine section of the rivers is that currents and wind-driven waves heap sand across the openings of the rivers with the result that lagoon-like aborted estuaries are formed that range in salinity from freshwater ($<5\text{‰}$) to 22 to 32‰ with some becoming hypersaline due to evaporation. How fresh the aborted estuary is depends on how impermeable the bar is to salt water. *Tomichia* is never found in the lagoon section of aborted estuaries while *Hydrobia* (Hydrobiidae) is common there.

In this century, the Agulhas region has been affected by eastward reaching aridity. In the summers of 1969 and 1970 certain large

lakes in the Agulhas region dried up for the first time in 50 years. Farmers stated that the winter rains filled the lakes which usually had water all year long. Zoetendalsvlei was dry throughout a six to seven year drought that ended about 1973–1974. During the period of drought there were pools of water in the river beds, but the vleis were dry, especially during summer.

It is evident that populations of *Tomichia* responded to increasing aridity in different ways depending on longitudinal gradients of aridity and general ecological setting. The changes were from freshwater-aquatic towards greater physiological tolerance to increased salinity, amphibious, and finally terrestrial modes of existence. The climatic changes were generally gradual with pulses of severe drought increasing from west to east. Changes in selective pressures would likewise be gradual with erratic events of extreme desiccation increasing from west to east.

What we see in Namaqualand today are two relict populations where water availability is so limited that the snails are virtually amphibious. Namaqualand at one time had innumerable streams with perennial water. These streams probably had *Tomichia*. Today, two springs represent the last vestige of these once widespread populations, and their continued existence is tenuous.

The coastal vleis and pans so common from Ysterfontein across the Cape Flats to Agulhas have probably had annual cycles of drying from the Pliocene onward, a period of about 5 million years during which *T. ventricosa* and *T. tristis* became adjusted to their current ecological situations.

As one passes from Cape Province through the Transkei to Natal Province one passes into a wetter and tropical zone. It is here that one finds amphibious *T. natalensis*. Presumably there was perennial water in Natal throughout the Cenozoic; it is not known what caused *T. natalensis* to become amphibious. It is probable that pulses of drought in this area caused this adaptation.

Pre-adaptation for an amphibious existence

No modern Triculinae are amphibious or terrestrial while some Pomatiopsinae have become amphibious or terrestrial in various places and at different times. Are there morphological character-states that pomatiopsine taxa have that are not shared by triculine taxa

and that predate pomatiopsine taxa of amphibious life? The answer is yes. The broad foot that all pomatiopsines have is essential for the amphibious mode of existence. Another feature is the elongated spermathecal duct extending to the anterior end of the mantle cavity that surely would facilitate successful copulation and sperm transfer out of water.

There is evidence that genetically and physiologically at least some pomatiopsines are pre-adapted to survive under increased salinities and desiccation. This was evident during experiments comparing the perennially aquatic topotype population of *T. differens* with the Ysterfontein Vlei population of *T. ventricosa* for survival under different conditions of salinity and desiccation.

In all desiccation experiments 25 adult snails from each population were placed in 9 cm Petri dishes. There was a dry and humid set for each species. Filter paper was fitted inside the lid and kept moist to produce a humid chamber. Dry chambers had no filter paper. The filter paper was moistened only to the extent that snails would not move about in the chamber. One dry and one humid chamber were removed from each of the sets and flooded with water from that species' environment on days 7, 14, 30, 60, 120, 150. The percentage of snails living and dead was determined by observing them for movement over a 24 hour period following flooding. There were no replicates to permit an analysis of variance. The results shown in Table 10 clearly indicate the profound differences between species as one would predict. Humidity is an essential feature for prolonged survival out of water for both species. Although not as

TABLE 10. Percentage of each species of *Tomichia* surviving after different lengths of time in dry and humid chambers.

Days	Species			
	<i>T. ventricosa</i>		<i>T. differens</i>	
	humid	dry	humid	dry
7	96	100	96	28
14	96	100	92	4
30	96	92	76	0
60	92	60	60	0
90	96	28	40	0
120	88	16	0	0
150	96	8	0	0

TABLE 11. Percentage of each species surviving one month in water of different salinities (‰).

Salinities	Species		
	(Not oxygenated)		(Oxygenated)
	<i>T. ventricosa</i>	<i>T. differens</i>	<i>T. differens</i>
0	84	100	96
5	96	100	100
10	96	68	100
15	92	68	100
20	80	0	96
25	100	0	100
33	100	0	0
42	84	0	0
50	52	0	0

tolerant of desiccation as *T. ventricosa*, a significant percentage of *T. differens* can survive at least three months without water in humid areas. No Mekong River triculine can exist more than a week out of water.

In the salinity experiments a range of salinities was established using water from Ysterfontein Vlei (50‰) and DieKelders (0‰). Chambers with 5, 10, 15, 20, 25, 33, 42, and 50‰ were established. A number of snails were gradually acclimated to each salinity by slowly increasing or decreasing salinities every day. Finally 25 snails were placed in each of the eight containers. There were three sets; two sets were not aerated (one with *T. ventricosa*, one with *T. differens*), and one set aerated (with *T. differens*). *T. differens* normally lives in highly oxygenated environments. Algae were grown in the water for food and oxygen (under standing water conditions). The water was changed every 4 to 5 days and dead snails were removed daily to prevent fouling of the water. After 30 days the percentage of snails living was determined by noting activity over 24 hours. Results are shown in Table 11. Again, there is a profound difference between species as expected. Oxygenated water clearly improves survival of *T. differens* under high salinity stress but only up to 25‰. Snails could be acclimated to 33‰ salinity and be active for two weeks before withdrawing into their shells and dying within one month. With oxygenation *T. differens* can probably live for months at 15 to 20‰. The point to be made here is that *T. differens* shows considerable salinity and desiccation tolerances as a freshwater species and could probably be selected to live

under conditions somewhat similar to those where one finds *T. ventricosa*.

Tempo and mode of pomatiopsine evolution

There has been no cladogenesis that one can detect in the southern continental pomatiopsines. The *Coxiella* radiation of Australia is small and parallels the ecological adjustments seen in *Tomichia ventricosa*. The seven modern species of *Tomichia* of South Africa seem to have evolved starting in the mid-Miocene to early Pliocene in response to progressive aridity spreading from west to east. There was no pronounced tectonism associated with opening of new ecological space and considerable morphological diversity as seen in Southeast Asia. What is seen is more of a gradual adjustment to changing climate over a period extending some 25 million years. This gradual adjustment has resulted in a few physiologically defined species that have few morphological differences among them.

There are insufficient data to know when, precisely, the modern *Tomichia* radiation began, i.e. the date of origin of that species from which the seven modern taxa evolved. *T. ventricosa* is found in the Pliocene and presumably this precursor was present in the mid-Miocene about 14 million years ago. If this date is used as a rough estimate for the origin of the modern *Tomichia* radiation, then $R = 0.139$. Even if an individual speciation event was rapid, the overall picture over a period of 2 to 14 million years indicates a gradual change contrasted with the Triculinae radiation. It is clear, in contrasting the Mekong River Triculinae with the South African Pomatiopsinae, that there are two distinctly different tempos of evolution.

The mode of speciation of South African Pomatiopsinae clearly differs from that of the Mekong River Triculinae. The difference is one of a physiological radiation with low morphological diversity versus a radiation involving pronounced morphological diversity and comparatively narrow range of physiological adjustment. While this is the major aspect of mode that I wish to stress, more should be said of that aspect of mode involving the paradigms of punctuated equilibrium and phyletic gradualism. As discussed above, the Mekong River Triculinae generally fit the conditions expected in the punctuated equilibrium mode of Gould & Eldredge (1977) and Stanley (1979). South African *Tomichia* fit the

gradualistic model only in so far that there is slight, gradual morphological change and if the species are defined in traditional terms of morphology and presumed reproductive isolation. However, the physiological radiation opens a new dimension for consideration in comparing paradigms. We do not know the extent to which the physiological changes may be punctuational in the sense discussed by Jones (1981) for *Drosophila*. Given the scenario of gradual climatic change and the absence of an adequate fossil record in South Africa documenting the presence of species of *Tomichia* other than that of *T. ventricosa*, one can only assume a gradual change in genetically controlled physiological tolerances.

The mode and tempo of pomatiopsine radiation in Asia is more similar to that of the Triculinae. The introduction of proto-*Oncomelania* from the Indian Plate to mainland Asia was followed by dispersal to Japan and North America. At the end of the Miocene, there was a modest adaptive radiation in Japan involving cladogenesis and speciation (Table 1) associated with Japanese tectonism at that time (Davis, 1979). There is considerable morphological divergence as well as ecological divergence (Davis, 1979, table 2). *Cecina* is marine intertidal; *Oncomelania minima* and *Pomatiopsis binneyi* are freshwater-aquatic, *Blanfordia* is terrestrial. Considering introduction into Asia at 12 or 10 million years ago, and the 16 modern species that have evolved (including the subspecies of *Oncomelania hupensis*), $R = 0.23$ or 0.28 My^{-1} for the Asian pomatiopsine radiation. This is a comparatively rapid rate considering any group of animals, one associated with tectonics and a series of morphological changes. Therefore, it is the tempo and mode of environmental change and the extent of ecological space and complexity that determines the tempos and modes of evolution; it is not a matter of genetic background.

ACKNOWLEDGEMENTS

I acknowledge the immense help and support of the South African Museum and its staff, especially Drs. A. Hully and V. Whitehead; Drs. A. C. Brown and G. Branch and Ms. Jean Smits of the Department of Zoology, Capetown University; Dr. R. Kilburn of the Natal Museum. Assistance and helpful discussions were provided by Dr. D. Brown and

staff of the British Museum (Natural History) and D. A. Tankard, Department of Geosciences, University of Tennessee, Knoxville. I acknowledge the help and cooperation of the Zoological Museum of Oxford. I am indebted to Drs. K. E. Hoagland, J. B. C. Jackson, W. D. Russell-Hunter, A. Tankard, and D. Woodruff for reading and commenting on this manuscript. Jean Smits, an honors student of Capetown University, conducted the physiological experiments. Ms. Lynn Weidensaul Monarch prepared and analyzed the radulae, and prepared the figures of shells and maps. I made the drawings of anatomy but the final rendering was done by Ms. Mary Fuges.

LITERATURE CITED

- AXELROD, D. I. & RAVEN, P. H., 1978, Late Cretaceous and Tertiary vegetation history of Africa. *Monographiae Biologicae*, 31: 77–130.
- BENSON, W. H., 1851, Characters of *Tomichia*, a new palustrine testaceous mollusc from southern Africa, heretofore referred to the genus *Truncatella*. *Annals and Magazine of Natural History*, ser. 2, 7: 377–380.
- BROWN, D. S., 1980, *Freshwater snails of Africa and their Medical Importance*. Taylor & Francis, London, 487 p.
- CONNOLLY, M., 1929, New non-marine Mollusca from South Africa. *Annals of the Natal Museum*, 6: 219–244, pl. 14.
- CONNOLLY, M., 1939, A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum*, 33: 1–660, 19 pl.
- DAVIS, G. M., 1967, The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). *Malacologia*, 6: 1–143.
- DAVIS, G. M., 1968, New *Tricula* from Thailand. *Archiv für Molluskenkunde*, 98: 291–317.
- DAVIS, G. M., 1979, The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Academy of Natural Sciences of Philadelphia Monograph* 20, 120 p.
- DAVIS, G. M., 1980, Snail hosts of Asian *Schistosoma* infecting man: Evolution and coevolution. In: *The Mekong Schistosoma*, Malacological Review Supplement 2, BRUCE, J. I. & SORNMANI, S., eds., p. 195–238.
- DAVIS, G. M. & CARNEY, W. P., 1973, Description of *Oncomelania hupensis lindoensis*, first intermediate host of *Schistosoma japonicum* in Sulawesi (Celebes). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125: 1–34.
- DAVIS, G. M. & GREER, G. J., 1980, A new genus and two new species of Triculinae (Gastropoda: Prosobranchia) and the transmission of a

- Malaysian mammalian *Schistosoma* sp. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 132: 245–276.
- DAVIS, G. M., KITIKOON, V. & TEMCHAROEN, P., 1976, Monograph on "*Lithoglyphopsis*" *aperta*, the snail host of Mekong River schistosomiasis. *Malacologia*, 15: 241–287.
- ELDREDGE, N. & GOULD, S. J., 1972, Punctuated equilibria: an alternative to phyletic gradualism. In: SCHOPF, T., ed., *Models in Paleobiology*, Freeman Cooper, San Francisco, p. 82–115.
- GOULD, S. J. & ELDREDGE, N., 1977, Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology*, 3: 115–151.
- JONES, J. S., 1981, Models of speciation—the evidence from *Drosophila*. *Nature*, 289: 743–744.
- KENSLEY, B., 1977, A second assemblage of Pliocene invertebrate fossils from Langebaanweg, Cape. *Annals of the South African Museum*, 72: 189–210.
- KÜSTER, H. C., 1852, Die Gattungen *Paludina*, *Hydrocaena* und *Valvata*. In: MARTINI & CHEMNITZ, *Systematisches Conchylien-Cabinet*. Nürnberg, Vol. 1, No. 21, 96 p., 14 pl.
- MARTIN, A. R. H., 1962, Evidence relating to the Quaternary history of the wilderness lakes. *Transactions of the Geological Society of South Africa*, 65: 19–42, 2 pl.
- MOLNAR, P. & TAPPONNIER, R., 1975, Cenozoic tectonics of Asia: effects of a continental collision. *Science*, 189: 419–426.
- MORELET, A., 1889, Coquilles nouvelles de l'Afrique méridionale. *Journal de Conchyliologie*, 29: 1–20.
- NETTERBERG, F., 1971, Calcrete in road construction. *National Institute for Road Research Bulletin* 10: viii, 1–73; Council for Scientific and Industrial Research, *Research Report* 286. Pretoria, South Africa.
- OSBORN, H. F., 1918, *The Origin and Evolution of Life*. Scribner's Sons, New York. 322 p.
- PASCOE, E. H., 1950, *A manual of the geology of India and Burma*. Ed. 3, Government of India Press, Calcutta. p. 1–483.
- REEVE, L., 1842, *Conchologia Systematica*, Vol. 2, 337 p., 300 pls.
- SCHALIE, H. VAN DER & DUNDEE, D., 1955, The distribution, ecology and life history of *Pomatiopsis cincinnatiensis* (Lea), an amphibious operculate snail. *Transactions of the American Microscopical Society*, 74: 119–133.
- SCHALIE, H. VAN DER & DUNDEE, D., 1956, The morphology of *Pomatiopsis cincinnatiensis* (Lea), an amphibious prosobranch snail. *Occasional Papers of the Museum of Zoology, University of Michigan*, no. 579: 1–17, 7 pl.
- SCHALIE, H. VAN DER & GETZ, L., 1962, Distribution and natural history of the snail *Pomatiopsis cincinnatiensis* (Lea). *American Midland Naturalist*, 68: 203–231.
- SCHALIE, H. VAN DER, GETZ, L. L. & DAZO, B. C., 1963, Hybrids between American *Pomatiopsis* and Oriental *Oncomelania* snails. *American Journal of Tropical Medicine and Hygiene*, 2: 418–420.
- SHACKLETON, N. J. & KENNETT, P. J., 1975, Late Cenozoic and carbon isotope changes at D.S.D.P. site 284: implication for glacial history of the northern hemisphere and Antarctica. *Initial Reports of the Deep Sea Drilling Project*, 29: 801–807. U.S. Government Printer, Washington, D.C.
- SIMPSON, G. G., 1949, *The meaning of evolution*. Yale University Press, New Haven, Conn., 364 p.
- SMITH, J. M., 1981, Macroevolution. *Nature*, 289: 13–14.
- SOWERBY, G. B., 1892, *Marine shells of South Africa*. London, 89 p., 5 pl.
- STANLEY, S. M., 1975, A theory of evolution above the species level. *Proceedings of the National Academy of Science of the U.S.A.*, 72: 646–650.
- STANLEY, S. M., 1979, *Macroevolution*. Freeman, San Francisco, 322 p.
- TANKARD, A. J., 1975, Varswater Formation of the Langebaanweg-Saldanha area, Cape Province. *Transactions of the Geological Society of South Africa*, 77: 265–283.
- TANKARD, A. J. & ROGERS, J., 1978, Late Cenozoic palaeoenvironments on the west coast of South Africa. *Journal of Biogeography*, 5: 319–337.
- TANKARD, A. J., JACKSON, M. P., ERIKSSON, K. A., HOBDAI, D. K., HUNTER, D. R. & MINTER, W. E., 1981, *Crustal evolution of South Africa: 3.8 billion years of earth history*. Springer-Verlag, New York.
- TAYLOR, D. W., 1966, Summary of North American Blancan nonmarine mollusks. *Malacologia*, 4: 1–172.
- TURTON, W. H., 1932, *The marine shells of Port Alfred*. Oxford University, 331 p., 70 pl., 1843 figs.
- VERDCOURT, B., 1951, The distribution of the genus *Tomichia* Bens. in Africa. *Revue de Zoologie et de botanique Africaines*. 44: 173–174.
- WRIGHT, S., 1940, The statistical consequences of Mendelian heredity in relation to speciation. In: HUXLEY, J., ed., *The New Systematics*. Clarendon Press, Oxford, p. 163–183.

APPENDIX 1. Field data for species of *Tomichia* collected for this study. The numbers (e.g. D₁) correspond to sites marked in Figs. 7 and 8. Coded sequences such as D77-13 refer to field numbers (D = Davis; 77 = 1977; 13 = 13th collection in 1977).

T. differens

- D₁ D77-13; type-locality; from rocks in stream flowing from cave at the base of the cliff in front of the hotel, Die

- Kelders; Cape Prov.; 34° 33' S.; 19° 22' E. Davis, G. M. and Smits, J.; 19 Nov. 1977; salinity 2‰.
- D₂ D78-83; headwaters of stream flowing into Soetendalsvlei via Southbos' farm, crosses track between Jacobsdam and Bergplass about 6.5 to 7.0 mi. west of Soetendalsvlei; Cape Prov.; 34° 43' S.; 19° 51' E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 2‰.
- D₃ D78-70; small stream with sedges, Nuwejaarsrivier, 5 km. NW of Elands—drift, opposite Vogelvlei; Agulhas region, Cape Prov.; 34° 38' S.; 19° 52' E. Davis, G. M.; 17 Jan. 1978; salinity ?
- D₄ D78-2; bridge crossing stream flowing into Soetendalsvlei, road from Agulhas to Elim, 2.5 km. NW of Soutbos' farm; Agulhas region, Cape Prov.; 34° 42' S.; 19° 56' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 1 Jan. 1978; salinity 2‰.
- D78-78; same as D78-2; stream dried up, snails alive under stones, rocks. Davis, G. M. and Dichmont, T.; 19 Jan. 1978.
- D₅ D78-71; on sedges in Nuwejaarsrivier, before entering Soetendalsvlei, opposite Soutbos' farm; Agulhas region, Cape Prov.; 34° 43' S.; 19° 57' E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.
- D₆ D78-73; in Nuwejaarsrivier and vlei next to the river at opening of river into Soetendalsvlei; Agulhas region, Cape Prov.; 34° 44' S.; 19° 58' E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.
- D₇ D78-79; on rocks and water plants in Nuwejaarsrivier below the vlei, where road from Agulhas forks to Elim and Bredarsdorp. In sympatry with *Gyraulus* sp.; Agulhas region, Cape Prov.; 34° 41' S.; 19° 55' E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 0‰.
- D₈ D78-62; on grass, sticks, mud at stream margins of Karsrivier, about 2 mi. SW of Bredarsdorp-Arniston road; Cape Prov.; 34° 35' S.; 20° 00' E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 0‰.
- D₉ D78-6; on grass in roadside pool, pool about 70' long × 20' wide, ankle deep, road from Malgas to Heidelberg, 20 km. from Heidelberg; Cape Prov.; 34° 11' S.; 20° 46' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 3‰.
- D₁₀ D78-7; small streams alongside road from Malgas to Heidelberg, 18 km. from Heidelberg, Karringmelksrivier drainage; Cape Prov.; 34° 09' S.; 20° 48' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 3‰.
- D₁₁ D78-8; large stream, Slangrivier, where road from Malgas to Heidelberg crosses, about 8 km. from Heidelberg. Snails common on algal mats; Cape Prov.; 34° 08' S.; 20° 52' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 9.5‰.
- D₁₂ D78-55A; stream to E of road from Riversdale to Stillbaai, Riversdale area, 4 km. N of Stillbaai, stream flows into Kafferkuilsrivier. Snails numerous on the algae; Cape Prov.; 34° 19' S.; 21° 24' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 8 Jan. 1978; salinity 4‰.
- T. natalensis*
- N₁ D78-208; snails amphibious on mud stream banks, Inyezane River, 2 km. from Gingindlovu where back road from Gingindlovu to the shrimp farm crosses the river; Zululand, Natal Prov.; 29° 03' S.; 31° 37' E. Davis, G. M.; 4 Sept. 1978; salinity 0‰.
- N₂ D78-207; snails amphibious, distributed on damp mud slopes of Inyezane River, under old reed stems in shaded areas. Where highway N₂ from Gingindlovu to Empangani crosses the stream, some 6 km. NE of Gingindlovu; Zululand, Natal Prov.; 28° 59' S.; 31° 39' E. Davis, G. M.; 4 Sept. 1978; salinity 0‰.
- N₃ D78-212; snails numerous on mud, stacks of reeds, amphibious. Imbati River where highway N₂ crosses between Emoyeni and Mtunzini; Zululand, Natal Prov.; 28° 57' S.; 31° 42' E. Davis, G. M.; 5 Sept. 1978; salinity 0‰.

- N₄ D78-213; snails amphibious on banks of Ubati River at N₂ road crossing between D78-212 and Mtunzini turn-off; Zululand, Natal Prov.; 28° 57' S.; 31° 43' E. Davis, G. M.; 5 Sept. 1978; salinity 0‰.

T. rogersi

- R₁ D77-20; type-locality; stream opposite schoolhouse, Eksteenfontein. Eksteenfontein = Stinkfontein (name changed from meaning stinking spring to no longer stinking spring). Beginning of Stinkfontein River flowing to the Orange River; Namaqualand; 28° 50' S.; 17° 14' E. Davis, G. M. and Smits, J.; 29 Nov. 1978; salinity 5‰.
- R₂ D77-19; seepage from small capped (windmill) spring, Lekkersing; Namaqualand; 29° 01' S.; 17° 6' E. Davis, G. M., Whitehead, V. and Smits, J.; 29 Nov. 1977; salinity 4‰.

T. tristis

- T D78-53; snails amphibious, high shoreline under branches, logs, with *Assimineia* sp., soil dark black loam. W side of Seekoeirivier, lagoon at upper end of the lagoon near Aston, Bay Beach; Cape Prov.; 34° 05' S.; 24° 53' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 6 Jan. 1978; salinity in lagoon 20‰.

T. ventricosa

- V₁ D77-11; snails clustered on rocks in vlei, Ysterfontein; Cape Prov.; 33° 20' S.; 18° 10' E. Davis, G. M.; 15 Nov. 1977; salinity 12‰.
- D77-51; 30 Dec. 1977; salinity 28‰.
- D78-88; 4 Feb. 1978; salinity 58‰ at center of vlei; 83‰ in shallows.
- V₂ D78-86; dead shells collected on northern shore, Rietvlei, Milnerton; Cape Prov.; 33° 50' S.; 18° 32' E. Davis, G. M.; 28 Jan. 1978; salinity 8‰.
- V₃ D77-44A; all dead shells in vlei, vlei three quarters of the way from sewage plant to Chapmans Bay, Wild Bird Vlei; Cape Peninsula, Cape Prov.; 34° 08' S.; 18° 21' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 29 Dec. 1977; salinity 158‰.

D77-44B; all dead shells in vlei, vlei at point where water goes subterranean near Chapmans Bay; salinity 40‰.

D77-44C; vlei half way between sewage plant and Chapmans Bay; salinity 160‰.

- V₄ D77-27; Quaternary fossils collected in central area, Sandvlei, Ladeside near Muizenberg; Cape Prov.; 34° 05' S.; 18° 28' E. Davis, G. M. and Smits, J.; 6 Dec. 1977; salinity 2‰.

D77-28; same as D77-27, collected from main lake, no live snails; salinity 4‰.

D77-29; in masses of green algae in small pool to west of small dirt road that runs between vlei and railroad tracks, above Marina Dagama, Muizenberg; Cape Prov.; 34° 06' S.; 18° 28' E. Davis, G. M. and Smits, J.; 6 Dec. 1977; salinity 10‰.

D77-50; snails on underside of floating algal masses, Sandvlei, Muizenberg; Cape Prov.; 34° 06' S.; 18° 28' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 29 Dec. 1977; salinity 8‰.

- V₅ D77-39; turn off N₂ at first Kuilsrivier exit from Cape Town, bridge over Kuilsrivier, up stream ½ mile. No live snails; Cape Prov.; 34° 01' S.; 18° 39' E. Davis, G. M. and Hoagland, K. E.; 28 Dec. 1977; salinity 3‰.

- V₆ D78-87A,B; Bermont, Vermont vlei next to road between Hawston and Onrus. Vlei had dried up completely; Cape Prov.; 34° 25' S.; 19° 10' E. Davis, G. M. and Whitehead, V.; 29 Jan. 1978; salinity 60‰.

- V₇ D77-16; just before Kleinriviersvlei widens into Hermanus Lagoon, W of Stanford between Stanford and Wortelgat; Cape Prov.; 34° 27' S.; 19° 25' E. Davis, G. M. and Smits, J.; 20 Nov. 1977; salinity 4‰.

- V₈ D77-17; Kleinriviers; dead snails under masses of algae; Cape Prov.; 34° 25' S.; 19° 19' E. Davis, G. M. and Smits, J.; 20 Nov. 1977; salinity 22‰.

- V₉ D77-14; dead shells ¾ mile up Boemans River from bridge at shore, Franskraal; Cape Prov.; 34° 35' S.;

- 19° 24' E. Davis, G. M. and Smits, J.; 19 Nov. 1977; salinity 19‰.
- V₁₀ D78-67; vlei 4 km. NW of Wiedrift; Agulhas Region, Cape Prov.; 34° 40' S.; 19° 54' E. Davis, G. M.; 17 Jan. 1978; salinity 10‰.
- V₁₁ D78-69; small, shallow vlei between Waskraals vlei and Voëlvlei; Agulhas region, Cape Prov.; 34° 39' S.; 19° 51' E. Davis, G. M.; 17 Jan. 1978; salinity ?
- V₁₂ D78-82; small vlei between Vitkyk and Bergplaas farms, just N of Soetanysberg, 6 mi W of middle of Soetendalsvlei; Cape Prov.; 34° 42' S.; 19° 53' E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity ?
- V₁₃ D78-81; small vlei in nature reserve on N side of road from Rhenosterkop to Asfontein, on S side of Soetendalsvlei; Cape Prov.; 34° 46' S.; 19° 54' E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity ?
- V₁₄ D78-75A; W side of road from Soetendalsvlei to Springfield, crosses stream flowing to salt pan; Cape Prov.; 34° 44' S.; 19° 55' E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 25‰.
- D78-75B; dried, twisting channel to salt pan on E side of road, snails under dried algae mats and rocks; salinity ?
- V₁₅ D78-80; pan at Rhenosterkop, 4 mi W of S end of Soetendalsvlei. Snails numerous on sand and clustered on stones; Cape Prov.; 34° 46' S.; 19° 56' E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 32‰.
- V₁₆ D78-64; Rondepan, large vlei on S side of road from Bredarsdorp to Elim, 14 km. from Bredarsdorp. Snails under stones; Cape Prov.; 34° 37' S.; 19° 56' E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 20‰.
- V₁₇ D78-65A; Langepan, main part of vlei. On road from Bredarsdorp to Elim, 16 km. from Bredarsdorp. Snails on sedges and sandy bottom; Cape. Prov.; 34° 37' S.; 19° 54' E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 8‰.
- V₁₈ D78-38; Kowie River, Port Alfred; Cape Prov.; 33° 36' S.; 26° 53' E. Davis, G. M. and Hoagland, K. E.; 5 Jan. 1978; salinity 32‰.
- T. zwellendamensis*
- Z₁ D78-68; Waskraalsvlei, snails on stems of sedges; Agulhas region, Cape Prov.; 34° 40' S.; 19° 50' E. Davis, G. M.; 17 Jan. 1978; salinity 0‰.
- Z₂ D78-74; large circular vlei in the Nuwejaarsrivier, about 1 km. W of Soetendalsvlei. Snails numerous on marl bottom and on sedges; Cape Prov.; 34° 43' S.; 19° 58' E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity ?
- Z₃ D78-73A; vlei next to the Nuwejaarsrivier at opening of river into Soetendalsvlei; Agulhas region, Cape Prov.; 34° 44' S.; 19° 58' E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.
- D78-73B; in Nuwejaarsrivier opposite vlei; salinity 0‰.
- Z₄ D78-65B; Langepan, where vlei exits along road flowing to the east. On road from Bredarsdorp to Elim, 16 km. from Bredarsdorp. Snails in reeds; Cape Prov.; 34° 37' S.; 19° 54' E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 8‰.
- Z₅ D78-4; De Hoopvlei on road from Skipskop to Potbergsvier. Snails on sand, rocks, stems of grass and algae; Cape Prov.; 34° 29' S.; 20° 26' E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 5‰.

APPENDIX 2. Systematics.

Tomichia ventricosa: type-species

Introduction—Anatomical data presented for *T. ventricosa* serve to define the genus as well as the species. The only data discussed for other species are those demonstrating differences among species. The anatomy of *Tomichia ventricosa* clearly indicates that this genus belongs to the Pomatiopsidae: Pomatiopsinae as defined by Davis (1967,

TABLE 12. Shell measurements (mm) of species of *Tomichia* from specimens used for anatomical studies yielding data in Tables 13–28. Mean \pm standard deviation; (range). N = 5 unless otherwise indicated.

Species	Length	Length of body whorl	Width	Length of aperture	Width of aperture
<i>T. differens</i>					
Females; 6.0–6.5 whorls	4.66 \pm 0.14 (4.44 – 4.80)	3.12 \pm 0.14 (2.92 – 3.28)	2.48 \pm 0.13 (2.36 – 2.69) N = 4	2.14 \pm 0.12 (2.0 – 2.28) N = 4	1.38 \pm 0.12 (1.32 – 1.55) N = 4
Males; 6.0–6.5 whorls	4.92 \pm 0.36 (4.32 – 5.28)	3.06 \pm 0.16 (2.8 – 3.2)	2.48 \pm 0.12 (2.4 – 2.6)	2.10 \pm 0.12 (1.92 – 2.28)	1.34 \pm 0.06 (1.28 – 1.40)
<i>T. natalensis</i>					
Females; 6.0–6.5 whorls	4.99 \pm 0.12 (4.88 – 5.12)	2.98 \pm 0.04 (2.92 – 3.0)	2.48 \pm 0.06 (2.40 – 2.50)	1.99 \pm 0.06 (1.92 – 2.08)	1.49 \pm 0.05 (1.4 – 1.52)
Males; 6 whorls	4.50 \pm 0.19 (4.4 – 4.8)	2.74 \pm 0.10 (2.68 – 2.88)	2.24 \pm 0.07 (2.16 – 2.32)	1.86 \pm 0.10 (1.72 – 2.0)	1.30 \pm 0.04 (1.28 – 1.36)
<i>T. rogersi</i>					
Females; 6.5–7.0 whorls	7.74 \pm 0.23 (7.44 – 7.92) N = 4	4.47 \pm 0.15 (4.64 – 4.92)	3.54 \pm 0.17 (3.28 – 3.76)	2.92 \pm 0.13 (2.76 – 3.04) N = 4	2.08 \pm 0.06 (2.04 – 2.16) N = 4
Males; 7.0–7.5 whorls	8.6 \pm 0.26 (8.2 – 8.84)	5.02 \pm 0.09 (4.88 – 5.12)	3.85 \pm 0.14 (3.72 – 4.00)	2.99 \pm 0.14 (2.83 – 3.20)	2.22 \pm 0.07 (1.08 – 2.32)
<i>T. tristis</i>					
Mixed males and females; eroded apices N = 7	7.15 \pm 0.67 (6.08 – 8.08)	4.0 \pm 0.10 (3.84 – 4.12)	3.30 \pm 0.11 (3.2 – 3.48)	2.52 \pm 0.14 (2.32 – 2.71)	1.76 \pm 0.07 (1.72 – 1.88)
<i>T. ventricosa</i>					
Females; 3 whorls (eroded)	5.43 \pm 0.43 (5.08 – 6.08)	3.46 \pm 0.37 (2.88 – 3.76)	2.63 \pm 0.14 (2.48 – 2.84)	2.18 \pm 0.23 (2.00 – 2.52)	1.44 \pm 0.16 (1.32 – 1.72)
Males	4.4 \pm 0.38 (3.88 – 4.92)	2.90 \pm 0.29 (2.52 – 3.32)	2.09 \pm 0.21 (1.92 – 2.36) N = 4	1.76 \pm 0.18 (1.52 – 2.00)	1.16 \pm 0.10 (1.04 – 1.28)
<i>T. zwellendamensis</i>					
Females; 7.5–8 whorls N = 4	5.41 \pm 0.32 (5.0 – 5.68)	2.71 \pm 0.18 (2.52 – 2.88)	2.14 \pm 0.19 (1.88 – 2.32)	1.78 \pm 0.12 (1.60 – 1.84)	1.18 \pm 0.16 (0.96 – 1.36)
Males; 7.5–8 whorls	5.47 \pm 0.20 (5.20 – 5.72)	2.60 \pm 0.12 (2.40 – 2.68)	2.08 \pm 0.13 (1.96 – 2.24)	1.70 \pm 0.07 (1.60 – 1.76)	1.18 \pm 0.08 (1.08 – 1.36)

1968, 1979). Characters and character states serving to define family and subfamily categories are not discussed here.

Shells (Figs. 7, 8)—Shells of mature adults of the Ysterfontein population (Appendix 1, V₁) are invariably eroded, three to five whorls but mostly three whorls. Statistics of shell measurements are given in Table 12. The length of the last three whorls is 5.46 \pm 0.34 mm (Fig. 12). Shape is turreted (Figs. 7, 8). Whorls moderately convex, sutures correspondingly moderately impressed. Color light brown to brown-yellow; shell glistening. Aperture ovate (Fig. 13) lips moderately thick; peristome complete with well-developed parietal callus. Inner lip reflected from parietal

callus to abapical end of aperture; reflection over umbilical and basal region of body whorl. Reflection of lip at abapical end creates nearly spout-like appearance. Due to reflection of inner lip, broad arc of columella exposed inside aperture.

Umbilicus varies from chink to widely open. Shells mostly smooth (12 \times); some with pronounced irregular growth lines. Spiral micro-lines on some whorls of a few shells. Outer lip with little or no sinuation (side view).

Shell of adults from Kleinrivier (Appendix 1, V₈) differ from those discussed above as follows: all shells with eroded apices, two or three whorls remaining. Color, dull brown due to thick periostracum; thus shell not glistening.

TABLE 13. Length dimensions (mm) or number of non-neural organs of *Tomichia ventricosa*.

	No.	\bar{X}	Sd	Range
Organ (♀)				
Body	5	8.70	0.64	7.6–9.2
Buccal mass	5	1.03	0.17	1.40–3.40
Anterior pallial oviduct	4	2.30	0.82	1.40–3.40
Posterior pallial oviduct	4	1.80	0.49	1.20–2.40
Total pallial oviduct (Po)	4	4.10	0.75	3.80–5.20
Bursa copulatrix (Bc)	5	1.18	0.15	1.00–1.40
Bc/Po	4	0.31	0.07	0.23–0.40
Seminal receptacle	5	0.16	0.03	0.14–0.20
Digestive gland	5	2.98	0.60	2.20–3.60
Gonad	4	1.23	0.33	0.90–1.60
Mantle cavity	4	2.87	0.43	2.60–3.50
Ctenidium	4	2.43	0.40	2.10–3.00
Gill filaments (no.)	5	55.4	1.67	54–58
Organ (♂)				
Body	5	7.02	1.31	5.8–8.6
Prostate	5	1.07	0.20	0.76–1.30
Digestive gland	5	3.18	0.55	2.60–3.90
Gonad	5	3.06	0.50	2.60–3.90
Seminal vesicle	4	1.60	0.49	1.0–2.20
Penis	5	1.63	0.39	1.20–2.10
Mantle cavity	5	2.34	0.24	2.00–2.60
Ctenidium	5	2.10	0.15	1.94–2.30
Gill filaments (no.)	5	39.8	2.28	36–42

Aperture an elongate oval (Fig. 13), lips thin, outer lip very fragile. Parietal callus dips slightly into and filling umbilicus of most shells. Inner lip slightly reflected; columellar arc inside aperture not pronounced and narrows to thin strip about mid-parietal callus.

Umbilicus lacking; <5% have chink. Shells with regular discernable growth lines (12×). Length of last three whorls 5.30 ± 0.48 mm (Fig. 12).

Organ measurements—See Table 13 for measurements, counts, or ratios involving non-neural organs or structures; Table 14 for statistics on neural structures.

External features—The head (Fig. 14) is densely pigmented except for the tip of the snout (Sn). Scattered white glandular units (Gl) are concentrated around the eyes (Ey) and extend a short distance out along the

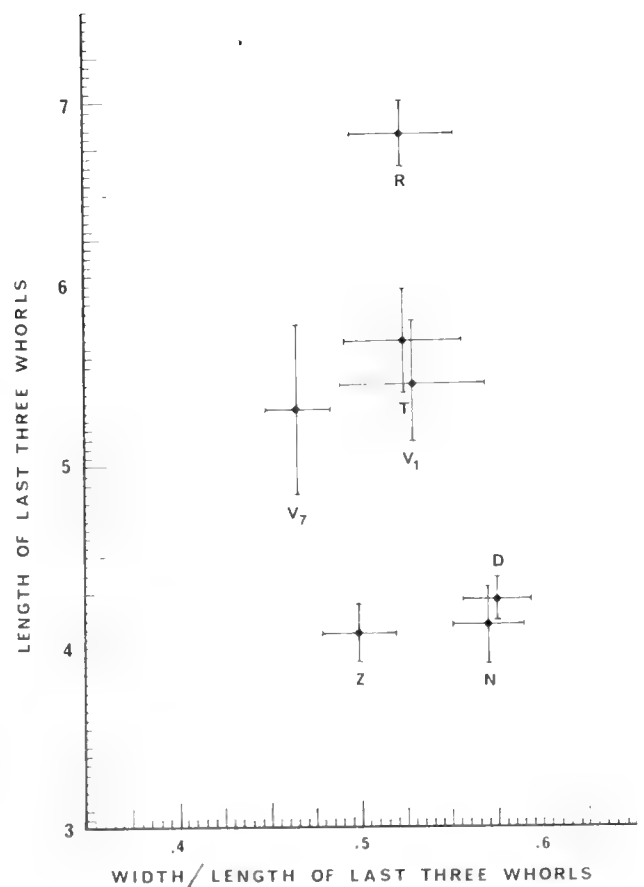


FIG. 12. Mean and standard deviation for length of last three whorls (mm) plotted against the ratio width: length of last three whorls. D, *Tomichia differens* (topotypes); N, *T. natalensis*; R, *T. rogersi* (topotypes); T, *T. tristis*; V, *T. ventricosa*; Z, *T. zwellendamensis*.

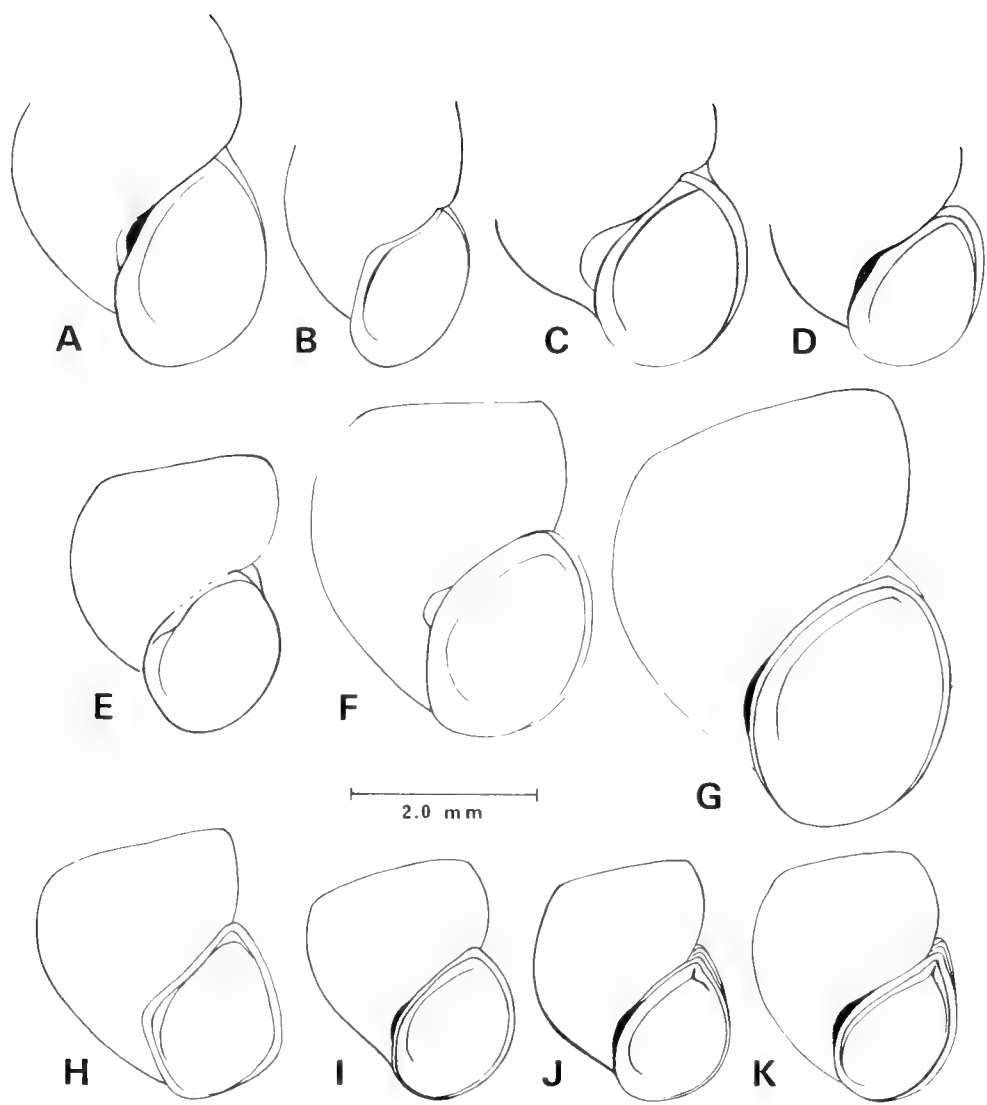


FIG. 13. A demonstration of differences among taxa in aperture shape. A, B, *Tomichia ventricosa* (D77-16); C, D, *T. ventricosa* (D77-51); E, *T. zwellendamensis* (Note fold on columella); F, *T. tristis*; G, *T. rogersi* (topotypes); H, I, *T. natalensis*; J, K, *T. differens* (topotype).

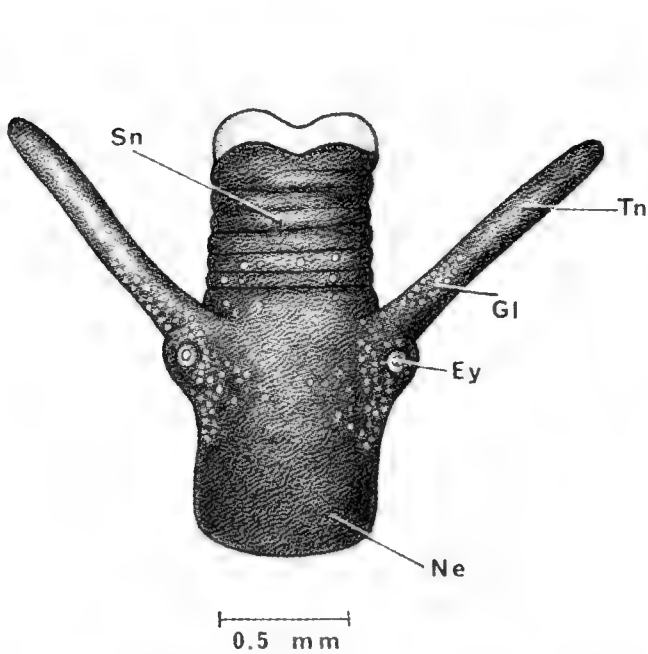


FIG. 14. The head of *Tomichia ventricosa*. Ey, eye; Gl, white glandular units; Ne, neck; Sn, snout; Tn, tentacle.

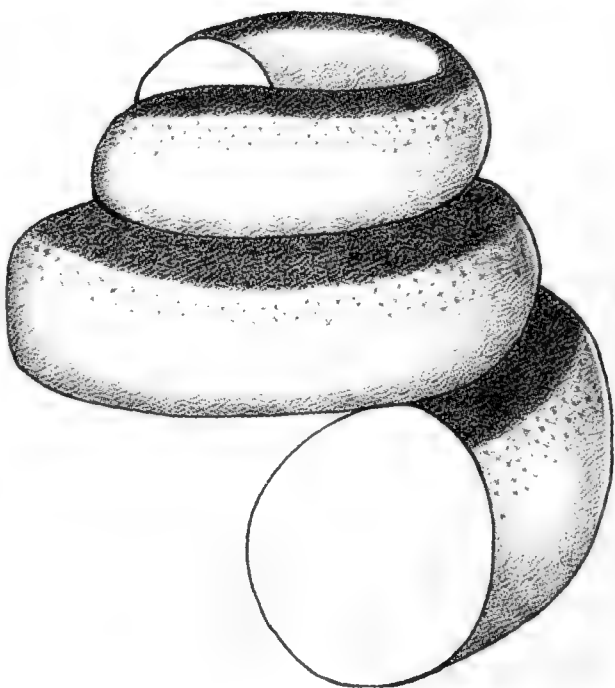


FIG. 15. Body whorls of *T. ventricosa* demonstrating dorsal strip of dense melanin pigment.

TABLE 14. Measurements (mm) of lengths of neural structures from female *Tomichia ventricosa*.

Structure	No.	\bar{X}	Sd	Range
Cerebral ganglion	5	0.32	0.03	0.28–0.36
Cerebral commissure	5	0.25	0.03	0.20–0.28
Pleural ganglion—right (1)	5	0.18	0.03	0.16–0.22
—left	5	0.15	0.04	0.10–0.20
Pleuro-supraesophageal connective (2)	5	0.42	0.09	0.30–0.50
Supraesophageal ganglion (3)	5	0.17	0.02	0.16–0.20
Osphradiomantle nerve	2	0.12	—	0.10–0.14
Pleuro-subesophageal connective	5	0.04	0.05	0.02–0.14
Subesophageal ganglion	5	0.14	0.02	0.12–0.16
Pedal ganglion	4	0.26	0.04	0.20–0.30
Pedal commissure	5	0.07	0.03	0.04–0.10
Statocyst (diameter)	5	0.11	0.01	0.10–0.12
Osphradial ganglion	4	0.48	0.07	0.40–0.56
Visceral ganglion	5	0.21	0.02	0.18–0.24
RPG ratio	5	0.54	0.04	0.48–0.59

tentacles (Tn). The dorsal aspect of the whorls of the body have a dense pigment band (Fig. 15).

Digestive system—Radular data are given in Tables 15–17. SEM pictures of the radula are given (Fig. 10). The radula is typically pomatiopsid. The tip of the radular sac (Fig. 16, Trs) is directly beneath the central posterior aspect of the buccal mass.

Female reproductive system (Figs. 17–20)—The uncoiled female is shown without head and kidney tissue revealing the standard pomatiopsine ground plan (Fig. 17). Cutting across the mantle cavity and removing connective tissues from the bursa copulatrix reveals organs as shown in Fig. 18. One clearly sees the opening of the kidney (Oki) projecting into the rear of the mantle cavity. The bursa copulatrix (Bu) is shown in the same relationship to the pallial oviduct (Ppo) as in Fig. 17. The bursa is extremely long, 31% the length of the pallial oviduct (Table 13). The anterior tip of the bursa (Tbu) extends into the cavity of the kidney anterior to that point where the oviduct passes into the posterior pallial oviduct (= albumen gland) (Opo). The tip of the bursa is within the narrowing funnel of the kidney just before the kidney opens into the mantle cavity.

The bursa copulatrix complex shown in Figs. 19, 20 is in the same position as shown in Figs. 17, 18. The interrelationships of the

FIG. 16. Dorsal buccal mass of A, *T. ventricosa* and B, *T. differens*. Cg, cerebral ganglion; Dsg, duct of salivary gland; Opt, optic nerve; Pig, pigmented region on dorsal buccal mass; Sg, salivary gland; Sl, supralabial nerve; Tn, tentacular nerve; Trs, tip of radular sac.

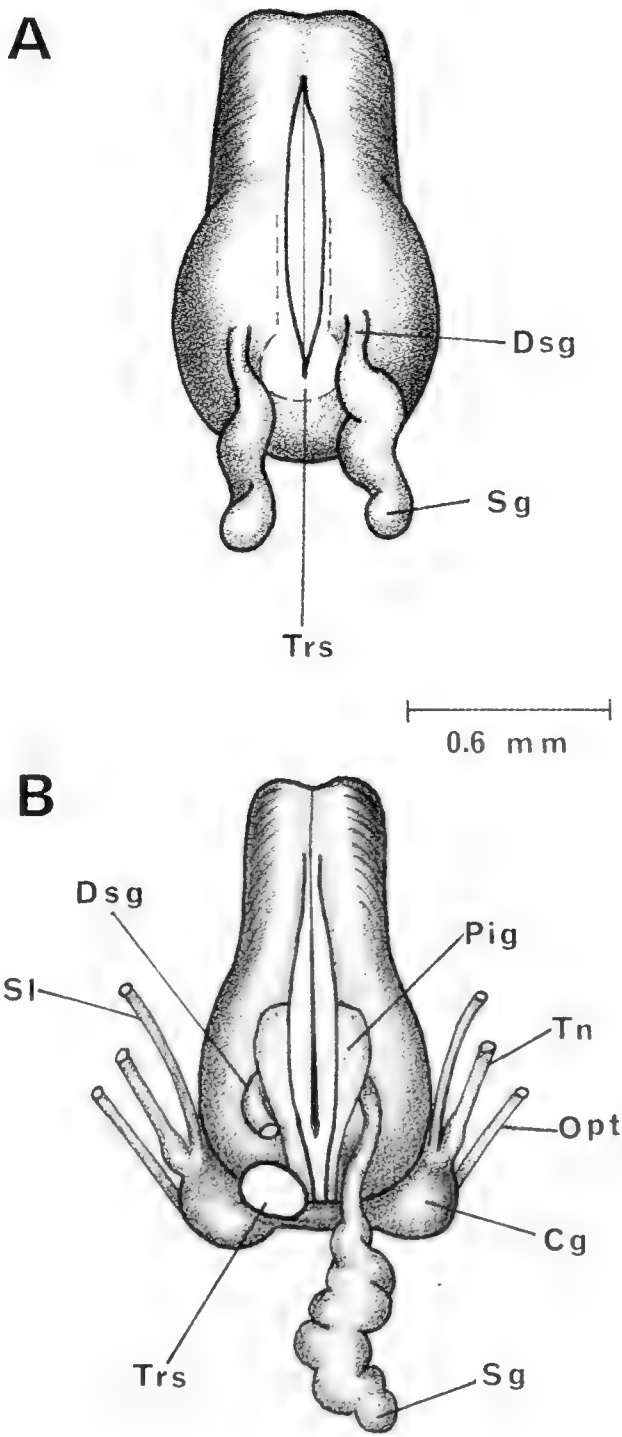


TABLE 15. Radular statistics. Mean \pm standard deviation; (range). Measurements in mm. No. = number of radulae studied unless otherwise stated as N =.

Taxon	Population: see Appendix 1	No.	Radula length	Radula width	No. rows teeth	No. rows forming	Central tooth width	Length of radula \div length of buccal mass
<i>T. differens</i>	D ₁	17	1.28 \pm 0.07 (1.16 – 1.38)	0.17 \pm 0.01 (0.16 – 0.18)	70.5 \pm 3.8 (65 – 76)	10.5 \pm 1.1 (5 – 26) N = 16	0.042 \pm 0.001 (0.04 – 0.043) N = 5	1.26
	D ₁₁	3	0.87 \pm 0.09 (0.79 – 0.97)	0.13 \pm 0 (0.13)	64.7 \pm 6.5 (58 – 71)	6.7 \pm 0.6 (6 – 7)	0.030 \pm 0 (0.03)	—
	D ₁₂	9	1.21 \pm 0.11 (1.12 – 1.34)	—	93.3 \pm 4.7 (86 – 100)	12.7 \pm 3.2 (7–17)	0.031 \pm 0.002 (0.028 – 0.033)	1.19
	D ₄	3	1.16 \pm 0.08 (1.09 – 1.23)	0.15 \pm 0 (0.15)	83.0 \pm 2.0 (81 – 85)	7 \pm 0 (7)	0.032 \pm 0.001 (0.03 – 0.033)	—
<i>T. natalensis</i>	N ₃	9	0.91 \pm 0.05 (0.85 – 0.97)	0.12 \pm 0.01 (0.11 – 0.13)	71.2 \pm 5.0 (63 – 78)	6.1 \pm 0.8 (5 – 7)	0.027 \pm 0.003 (0.023 – 0.031)	0.98
	R ₁	4	1.39 \pm 0.04 (1.36 – 1.43)	0.18 \pm 0.01 (0.17 – 0.19)	72.0 \pm 3.2 (68 – 75)	5.8 \pm 0.5 (5 – 6)	0.043 \pm 0.002 (0.041 – 0.045)	1.07
<i>T. rogersi</i>	R ₂	9	—	—	—	—	0.041 \pm 0.002 (0.037 – 0.043)	—
<i>T. tristis</i>	T	8	1.23 \pm 0.09 (1.12 – 1.40)	0.15 (0.14 – 0.16) N = 2	77.6 \pm 6.5 (69 – 87)	5.3 \pm 1.5 (4 – 8)	0.035 \pm 0.001 (0.034 – 0.036)	0.95
	V ₁	2	—	—	—	—	0.040 \pm 0.001 (0.039 – 0.041)	—
<i>T. ventricosa</i>	V ₇	14	1.10 \pm 0.09 (0.96 – 1.21)	0.15 \pm 0.01 (0.13 – 0.16)	72.1 \pm 3.6 (67 – 79)	6.8 \pm 0.98 (6 – 9)	0.038 \pm 0.002 (0.035 – 0.041)	1.06
	V ₄	5	1.14 \pm 0.07 (1.06 – 1.22)	—	69.6 \pm 3.2 (65 – 74)	11.0 \pm 1.0 (10 – 12)	0.035 \pm 0.001 (0.034 – 0.036)	—
	V ₁₈	3	0.78 \pm 0.07 (0.70 – 0.82)	0.12 \pm 0 (0.12)	60.6 \pm 3.0 (57 – 63)	4.7 \pm 0.6 (4 – 5)	0.028 \pm 0.003 (0.025 – .030)	—
	V ₁₅	8	1.20 \pm 0.11 (1.07 – 1.36)	0.16 \pm 0.01 (0.15 – 0.17)	59.0 \pm 7.3 (51 – 66)	5.1 \pm 0.4 (5 – 6)	0.041 \pm 0.003 (0.038 – 0.045)	—
(+ <i>producta</i>)	Z	8	0.93 \pm 0.07 (0.89 – 1.04)	0.13 \pm 0.004 (0.13 – 0.14)	65.3 \pm 5.1 (59 – 73)	5.9 \pm 0.6 (5 – 7)	0.039 \pm 0.004 (0.035 – 0.045)	1.08

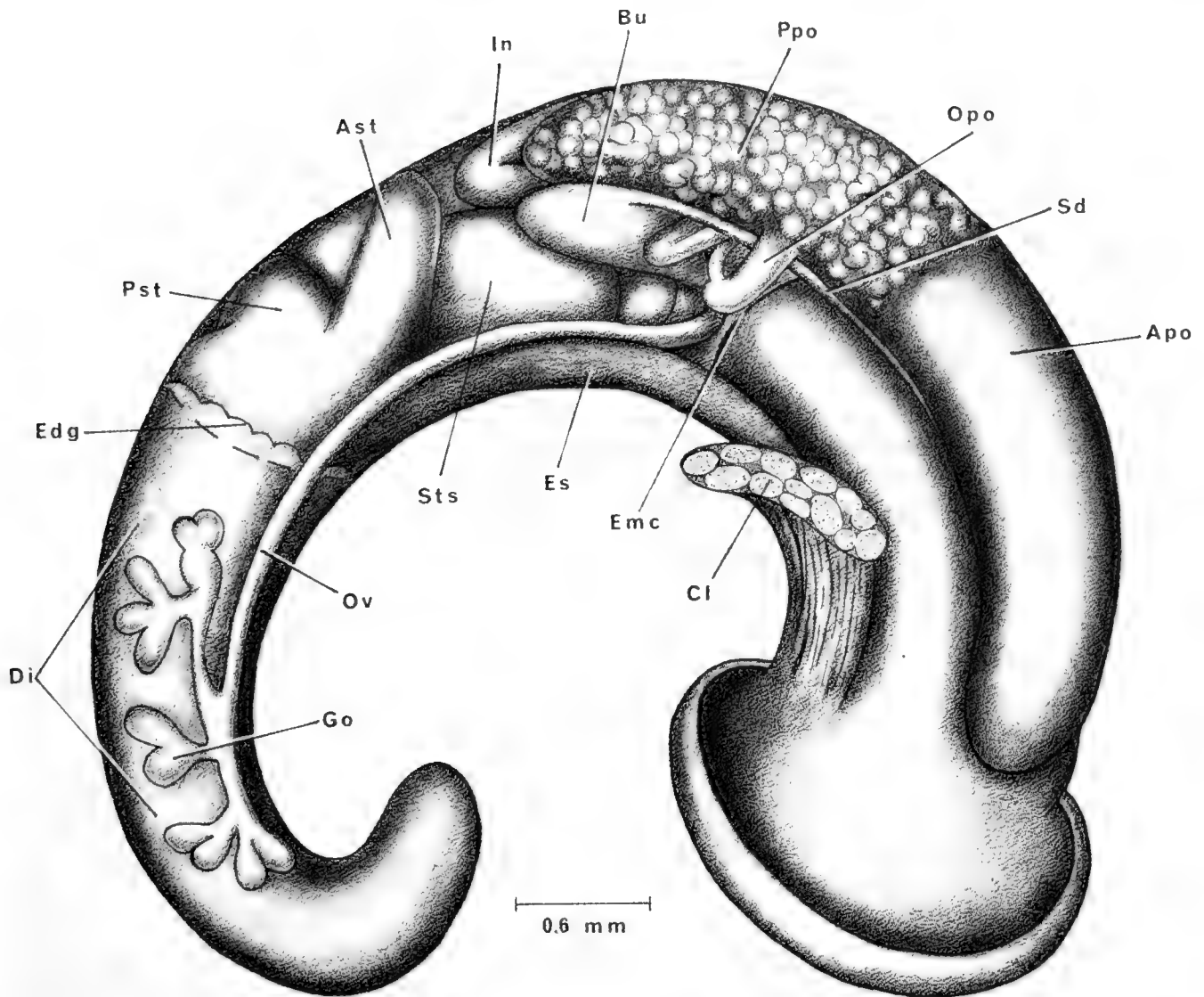


FIG. 17. Female *T. ventricosa*, uncoiled, with head and kidney tissue removed. Apo, anterior pallial oviduct (= capsule gland); Ast, anterior chamber of stomach; Bu, bursa copulatrix; Cl, columellar muscle; Di, digestive gland; Edg, anterior end of digestive gland; Emc, posterior end of mantle cavity; Es, esophagus; Go, gonad; In, intestine; Opo, opening to oviduct into posterior pallial oviduct (albumen gland); Ov, oviduct; Ppo, posterior pallial oviduct (= albumen gland); Pst, posterior chamber of stomach; Sd, spermathecal duct; Sts, style sac.

spermathecal duct (Sd), sperm duct (Sdu), seminal receptacle (Sr), oviduct (Ov), and bursa are shown. In Fig. 19A, from a different individual, the bursa was rotated slightly and the oviduct at the opening to the pallial oviduct (Opo) pulled through an arc of 90° toward the observer from its position shown in Figs. 18, 19B to clearly show the position of the seminal receptacle, the nature of the coils of the sperm duct and oviduct. Note that the oviduct is densely pigmented between the point where the sperm duct connects and the opening into the pallial oviduct (Fig. 19A, Fig).

My figure of the bursa complex (Davis 1979, fig. 9) is in error as it shows the sperm duct (Sdu) connecting the oviduct to the

spermathecal duct as in *Pomatiopsis*, and as it shows the seminal receptacle dorsal to the bursa as in *Pomatiopsis*. This figure was from dissections of two individuals in 1964 when I was dissecting *Pomatiopsis lapidaria*. In fact the sperm duct arises from the bursa copulatrix close to, and anterior to the point where the spermathecal duct enters the bursa. The seminal receptacle tucks between the coils of the sperm duct and the bursa on the ventral surface of the bursa.

The opening (Op) of the pallial oviduct (Apo) is shown together with the opening of the spermathecal duct (Osp) (Fig. 19C). These openings are at the anterior end of the mantle cavity. The pallial oviduct produces a

TABLE 16. Cusp formula for populations of South African *Tomichia*. () * = % radulae with the formula if other than 100%.

Taxon	Populations: See Appendix 1	No.	Central tooth	Lateral tooth	Inner marginal	Outer marginal
<i>T. differens</i>	D ₁	5	2 - 1 - 2 (80)*	3 - 1 - 3 (90)*	9 - 10	9 - 10
			2 - 2			
	D ₄	3	1 - 1 - 1 (20)*	3 - 1 - 4 (10)*		
			2 - 2			
			2 - 1 - 2	3 - 1 - 3	10 - 11	9 - 10
<i>T. natalensis</i>	D ₁₂	9	2 - 1 - 2 (78)*	3 - 1 - 3(4) (44)*	12 - 13	11
			3 - 3			
	D ₁₄	3	2 - 1 - 2 (22)*	3 - 1 - 3 (56)*		
			2 - 2			
			2 - 1 - 2	3 - 1 - 3	10	8 - 9
<i>T. rogersi</i>	N ₃	5	2 - 1 - 2	2(3) - 1 - 3	8 - 9	8 - 10
			3 - 3			
	R ₁	9	2 - 1 - 2 (89)*	2 - 1 - 3(4) (89)*	10 - 12	8 - 10
			3 - 3			
			2 - 1 - 2 (11)*	2 - 1 - 3 (11)*		
			2 - 2			

<i>T. tristis</i>	R ₂	9	$\frac{2-1-2}{2-2}$ (43)*	2-1-(4)3 (89)*	11-12 (71)*	9-10
			$\frac{3-1-3}{2-2}$ (57)*	2-1-3 (11)*	12-13 (29)*	
	T	6	$\frac{2-1-2}{2-2}$	3-1-(4)3 (33)* 3-1-(2)3 (33)* 3-1-3 (33)*	11-12	9-10
	V ₁	2	$\frac{2-1-2}{3-3}$	3-1-3	14-15	9-10
<i>T. ventricosa</i>	V ₇	9	$\frac{2-1-2}{2-2}$ (33.3)*	3-1-3(4)	10 (3.3)* 11 (9.0)* 14 (13.3)* 12-13 (74.4)*	8-11 (on one radula 11 on left side 9 on right side)
			$\frac{2-1-2}{3(2)-3}$ (22.2)*			
			$\frac{2-1-2}{3-3}$ (44.4)*			
	V ₄	5	$\frac{2-1-2}{3-3}$	3-1-3 (80)* 3-1-(4)3 (20)*	13-14	10-11
<i>T. zwellendamensis</i>	V ₁₈	3	$\frac{2-1-2}{3-3}$	3-1-3	14-15	10-11
	V ₁₅	5	$\frac{2-1-2}{2(3)-(3)2}$	3-1-(4)3 (80)* 2-1-3 (20)*	10-12	9-11
	Z ₅	5	$\frac{3(4)-1-3}{2-2}$	3-1-3	12-14	11-13

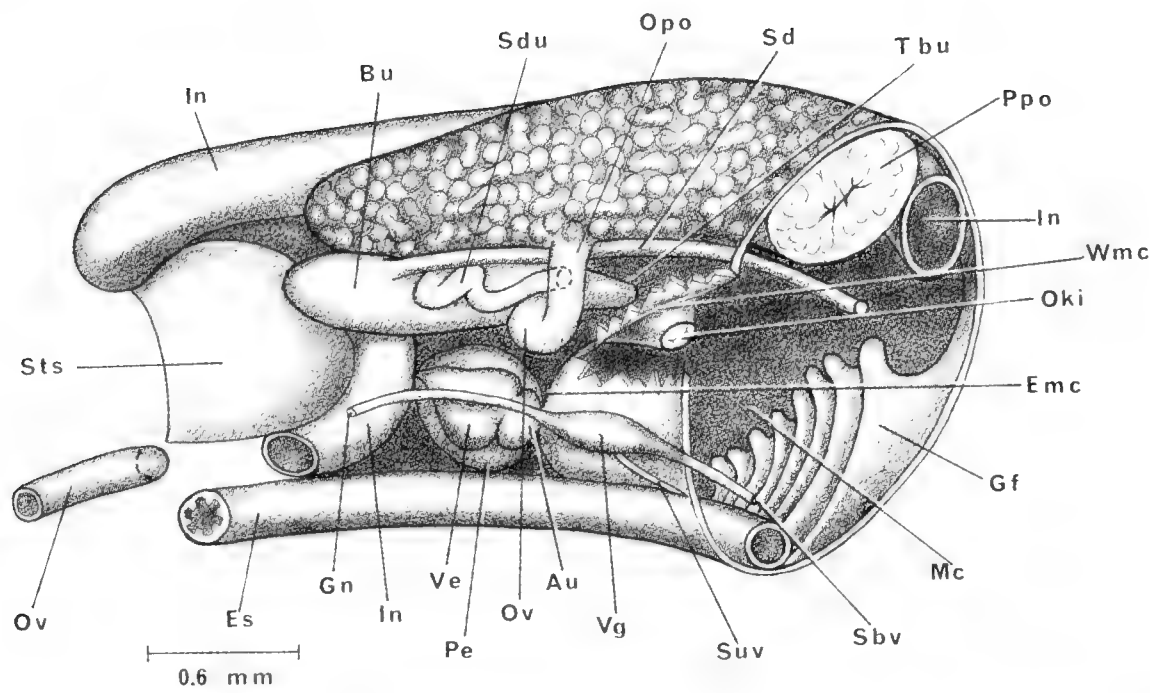


FIG. 18. Female *T. ventricosa* positioned exactly as in Fig. 17, but with the posterior stomach and digestive gland removed posteriorly (to the left) and a cut across the body through the mantle cavity, pallial oviduct and intestine (to the right) exposing the mantle cavity (Mc) and the structures within the cavity, e.g. opening of kidney through posterior wall of the mantle cavity (Oki), cross sections of the esophagus (Es), posterior pallial oviduct (Ppo), intestine (In), and spermathecal duct (Sd). The remaining gill filaments (Gf) of the ctenidium are seen.

The purpose of the illustration is to show the relationship of the elongate bursa copulatrix (Bu) to the posterior pallial oviduct (Pop), opening of the oviduct into the posterior pallial oviduct (Opo), and the anterior tip of the bursa (Tbu) within the cavity of the kidney in the funnel of the kidney leading to the opening of the kidney (Oki).

Au, auricle; Bu, bursa copulatrix; Emc, posterior end of the mantle cavity; Es, esophagus; Gf, gill filament; Gn, gonadal nerve; In, intestine; Mc, mantle cavity; Oki, opening of kidney into the posterior mantle cavity; Opo, opening of oviduct into posterior pallial oviduct; Ov, oviduct; Pe, pericardium; Ppo, posterior pallial oviduct; Sbv, subvisceral connective; Sd, spermathecal duct; Sdu, sperm duct; Sts, style sac; Suv, supra-visceral connective; Tbu, anterior tip of bursa copulatrix; Ve, ventricle; Vg, visceral ganglion; Wmc, reflected cut wall of mantle cavity.

TABLE 17. General cusp formula for each species of South African *Tomichia*. ()^{*} = % of cusps.

Taxon	Central tooth	Lateral tooth	Inner marginal	Outer marginal
<i>T. differens</i>	2(1) – 1 – (1)2 2(3) – (3)2	3 – 1 – 3(4)	9 – 13	9 – 11
<i>T. natalensis</i>	2 – 1 – 2 3 – 3	2(3) – 1 – 3	8 – 9	8 – 10
<i>T. rogersi</i>	2(3) – 1 – (3)2 2(3) – (3)2	2 – 1 – 3(4)	10 – 13	8 – 10
<i>T. tristis</i>	2 – 1 – 2 2 – 2	3 – 1 – (4)3 (66) [*] 3 – 1 – (2)3 (33) [*]	11 – 12	9 – 10
<i>T. ventricosa</i>	2 – 1 – 2 2(3) – (3)2	3(2) – 1 – 3(4)	10 – 15	8 – 11
<i>T. zwellendamensis</i>	3 – 1 – 3 2 – 2	3 – 1 – 3	12 – 14	11 – 13

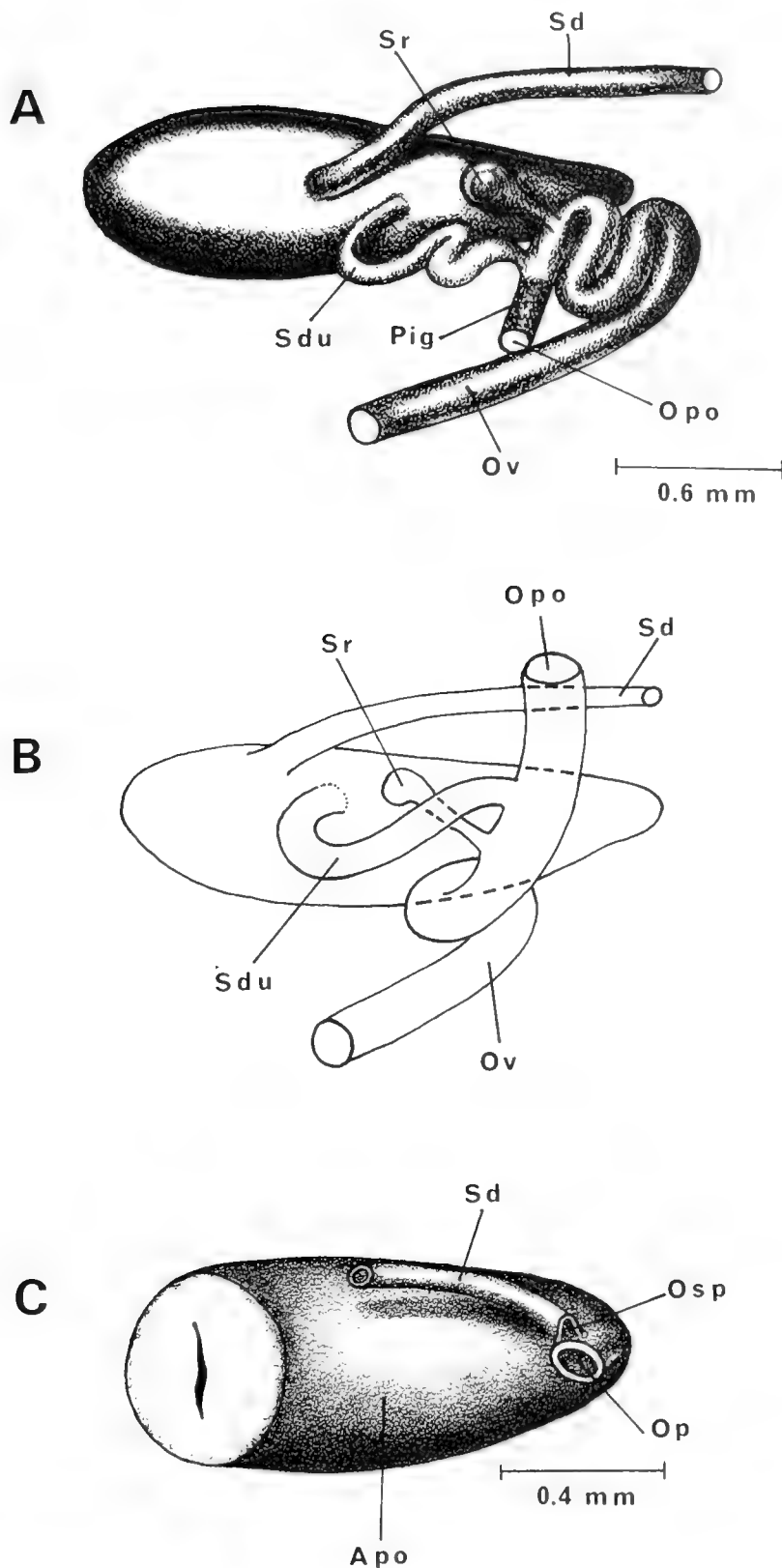


FIG. 19. Female reproductive system of *T. ventricosa*. A, B, bursa copulatrix complex with bursa positioned as in Figs. 17, 18. C, anterior end of pallial oviduct (Apo) showing the opening of the pallial oviduct (Op) at the end of a nipple-like extension of the pallial oviduct. The opening (Osp) of the spermathecal duct (Sd) is shown in relationship to the opening of the pallial oviduct.

In B, the positions of the ducts and organs are shown in usual configuration as in Fig. 18. In A, the oviduct at the pallial oviduct (Opo) has been shown pulled 90° towards the reader to show the seminal receptacle (Sr) in its usual position. Note the densely pigmented (Pig) section of the oviduct where it opens into the pallial oviduct.

Apo, anterior pallial oviduct; Op, anterior opening of pallial oviduct; Opo, opening of oviduct into the posterior pallial oviduct; Osp, anterior opening of spermathecal duct; Ov, oviduct; Pig, pigmented section of oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle.

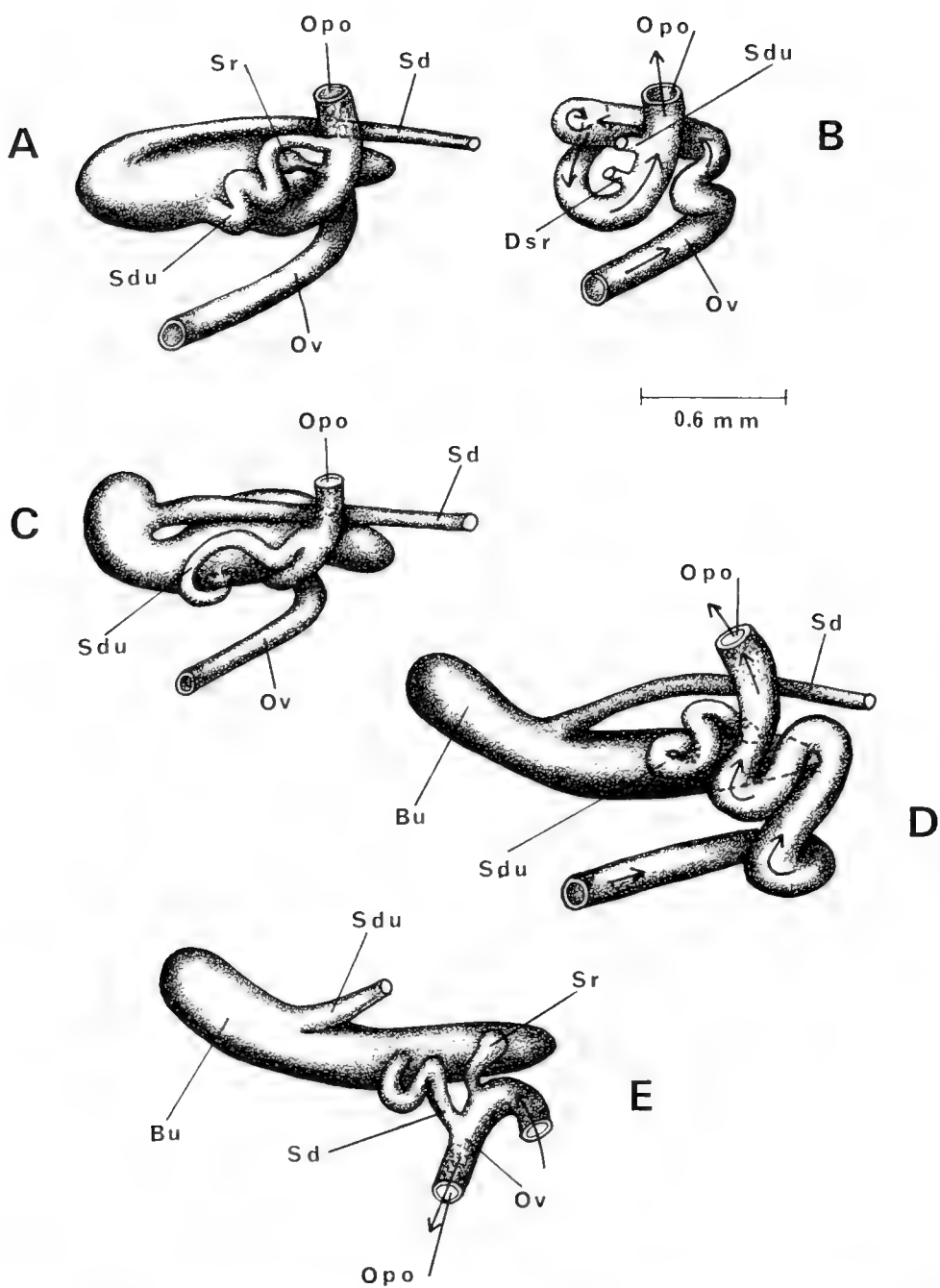


FIG. 20. Bursa copulatrix complex as in Fig. 19. A–C, *T. natalensis*; D, E, *T. rogersi*. The spermathecal duct enters the posterior bursa in *T. natalensis*. The posterior bursa is particularly elongate in *T. rogersi*. B, the coils of the oviduct and path of sperm are shown.
Bu, bursa copulatrix; Dsr, duct of seminal receptacle; Opo, opening of oviduct into posterior pallial oviduct; Ov, oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle.

nozzle-like extension at the anterior end of the pallial oviduct at the tip of which is the opening.

Male reproductive system (Figs. 21, 22)—The system is standard pomatiopsine. Penis with eversible papilla, ciliated anterior epithelium and glandular edge on proximal concave curvature (Fig. 22) The vas deferens does not have a thickened ejaculatory section either in the base of the penis or proximal to the base of the penis.

Nervous system—The nervous system is standard pomatiopsid. Measurements of neural structures are given in Table 14. The RPG ratio (Table 14) is 0.54, significantly larger than that in *Oncomelania* and *Pomatiopsis* and similar to that recorded for *Hydrobia* (Davis et al., 1976). This larger ratio is due to a comparatively long pleuro-supraesophageal connective and indicates a more open (as opposed to condensed) central nervous system.

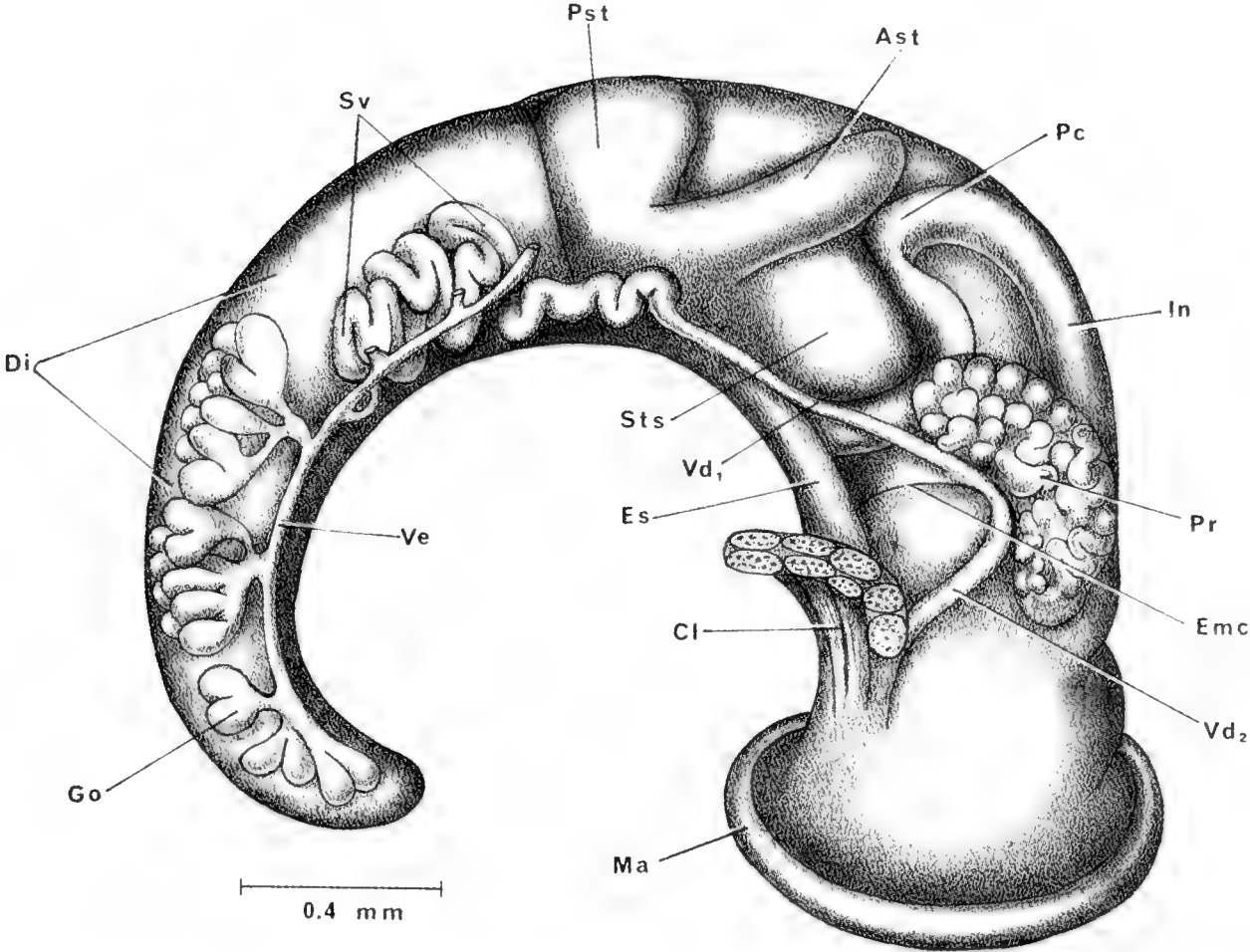


FIG. 21. Male reproductive system of *T. ventricosa*. Head and kidney tissue were removed. Part of the gonad (Go) was removed to reveal the coiled seminal vesicle (Sv).

Ast, anterior chamber of stomach; Cl, columellar muscle; Di, digestive gland; Emc, posterior end of the mantle cavity; Es, esophagus; Go, gonad; In, intestine; Ma, mantle edge = collar; Pc, pellet compressor; Pr, prostate; Pst, posterior chamber of stomach; Sts, style sac; Sv, seminal vesicle; Vd₁, vas deferens posterior to prostate; Vd₂, vas deferens anterior to prostate; Ve, vas efferens.

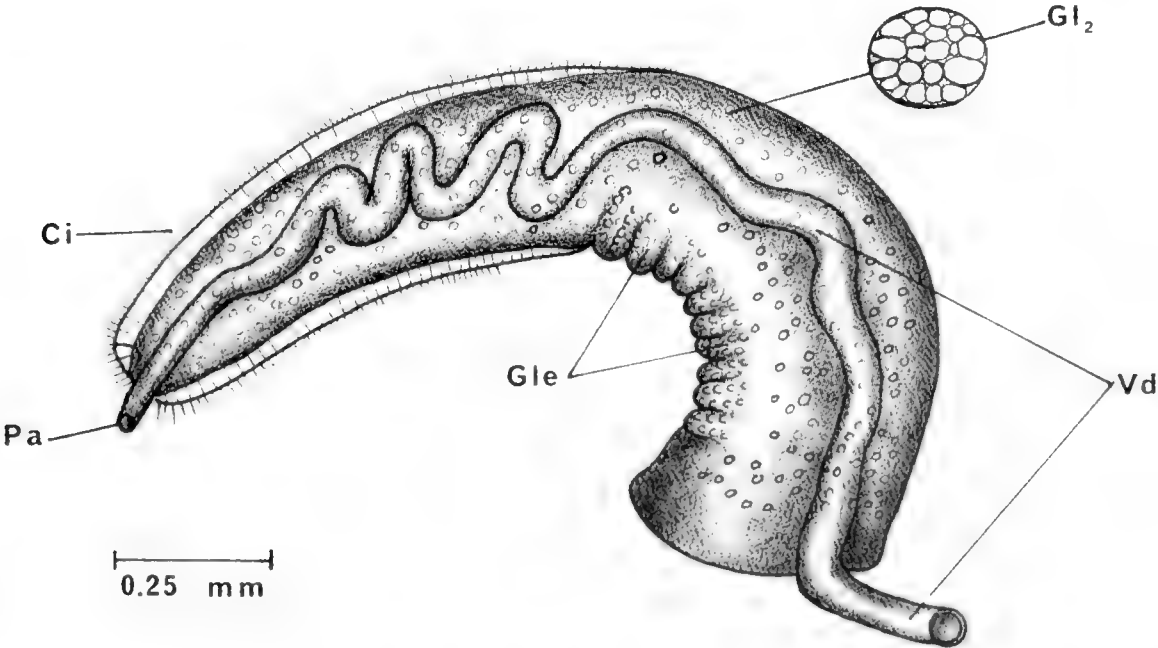


FIG. 22. Penis of *T. ventricosa*. Ci, cilia; Gle, glandular edge of the penis; Gl₂ subepithelial gland types; Pa, papilla; Vd, vas deferens.

T. differens

Shell (Fig. 8)—Type-locality (Appendix 1, D₁) not much eroded, males and females 6.0 to 6.5 whorls. Statistics in Table 12. Length of last three whorls 4.25 ± 0.14 mm (Fig. 12). Shape ovate (bullet-shaped). Whorls flat-sided to slightly convex, sutures shallow. Color light brown, glistening. Aperture ovate-pyriform with produced adapical end (Fig. 13), lips thick, peristome complete with thick parietal callus. Inner lip not reflected; abapical end of aperture projecting slightly below base of body whorl. Slight arc of columella seen inside aperture.

No umbilicus or only a chink (<5%). Smooth body and penultimate whorl (about 40%). Outer lip straight or with slight sinuation (side view).

Organ measurements—See Table 18 for measurements or ratios of non-neural organs; Table 19 for measurements of neural structures.

Unique features—The tip of the radular sac extends beyond the end of the buccal mass and curls dorsally between the cerebral nervous system and the buccal mass (Fig. 16B, Trs). Other aspects as in *T. ventricosa*.

Radula—See Fig. 9, Tables 15–17.

T. natalensis

Shell (Fig. 7)—Locality (N₃, Appendix 1), invariably entire with males 6.0 whorls and females 6.0 to 6.5 whorls. Statistics, Table 12. Length of last three whorls 4.10 ± 0.22 (Fig. 12). Shape ovate-conic. Whorls moderately convex, sutures correspondingly impressed. Color dark brown due to heavy periostracum. Peristome entire, with dark brown edge, thick. Aperture shape variable, widely ovate to sub-quadrate, slightly produced at adapical end in some specimens. Parietal callus well formed, straight to slightly sinuate. Inner lip not reflected over umbilical or basal areas of the body whorl. Inside aperture only very narrow strip of columella seen (Fig. 13).

No umbilicus; a few with chink. Shells smooth, dull, without pronounced growth lines, no spiral micro-lines. Outer lip of most shells with marked sinuation.

Organ measurements—See Table 20 for non-neural organs; Table 21 for neural structures.

Radula—See Fig. 9, Tables 15–17.

Unique features—The spermathecal duct enters the bursa at, or close to the posterior end of the latter (1) (Figs. 20A, C) and is separated from the opening of the sperm duct into

TABLE 18. Dimensions (mm) or number of non-neural organs of topotype *Tomichia differens*, D 77-13.

		No.	\bar{X}	Sd	Range
Organ (♀)					
Body	L.	5	8.32	0.36	8.0–8.8
Buccal mass	L.	5	1.01	0.16	0.9–1.3
Anterior pallial oviduct	L.	6	1.55	0.12	1.4–1.7
Posterior pallial oviduct	L.	6	1.95	0.10	1.8–2.1
Total pallial oviduct (Po)	L.	6	3.50	0.17	3.3–3.8
Bursa copulatrix (Bc)	L.	6	1.11	0.11	1.0–1.28
Bc/Po		6	0.31	0.04	0.26–0.37
Seminal receptacle	L.	3	0.14	0.03	0.10–0.16
Digestive gland	L.	5	3.32	0.22	3.0–3.6
Gonad	L.	4	1.05	0.28	0.9–1.1
Mantle cavity	L.	5	2.32	0.13	2.1–2.4
Ctenidium	L.	4	1.82	0.27	1.6–2.2
Gill filaments	No.	5	28.8	2.86	25–32
Organ (♂)					
Body	L.	5	8.92	0.76	8.0–9.6
Prostate	L.	5	0.88	0.25	0.5–1.20
Digestive gland	L.	4	4.88	0.83	4.0–6.0
Gonad	L.	6	4.72	0.62	4.0–5.4
Seminal vesicle	L.	4	1.40	0.28	1.0–1.6
Penis	L.	5	1.94	0.38	1.5–2.5
Mantle cavity	L.	5	2.22	0.15	2.0–2.4
Ctenidium	L.	5	1.72	0.08	1.6–1.8
Gill filaments	No.	5	27.6	2.60	26–32

the bursa by 0.26 mm or more, usually 0.30 mm. (2) In *T. ventricosa* this distance is usually 0.20 mm or less. (3) The opening of the sperm duct into the bursa is at the left ventro-lateral edge of the bursa or on the left dorso-lateral edge instead of mid-ventral bursa (Figs. 20A, C).

T. rogersi

Shell (Fig. 7)—Type-locality (Appendix 1, R₁). Mostly entire, males 7.0–7.5 whorls, females 6.5–7.0 whorls. Statistics in Table 12. Length of last three whorls 6.84 ± 0.18 mm (Fig. 12). Shape turreted. Whorls moderately

TABLE 19. Measurements (mm) of lengths of neural structures from female *Tomichia differens*.

Structure	No.	\bar{X}	Sd	Range
Cerebral ganglion	5	0.35	0.04	0.30–0.40
Cerebral commissure	5	0.22	0.06	0.16–0.30
Pleural ganglion—right (1)	5	0.16	0.01	0.14–0.16
—left	5	0.15	0.01	0.14–0.16
Pleuro-supraesophageal connective (2)	5	0.30	0.07	0.20–0.38
Supraesophageal ganglion (3)	5	0.15	0.02	0.14–0.18
Osphradimantle nerve	5	0.16	0.06	0.10–0.20
Pleuro-subesophageal connective	5	0.03	0.03	0 –0.06
Subesophageal ganglion	5	0.14	0.03	0.10–0.16
Pedal ganglion	5	0.26	0.11	0.20–0.32
Pedal commissure	5	0.08	0.02	0.04–0.10
Statocyst (diameter)	3	0.11	0.01	0.10–0.12
Osphradial ganglion	7	0.42	0.06	0.32–0.48
Visceral ganglion	4	0.15	0.01	0.14–0.16
RPG ratio: 2/1 + 2 + 3	5	0.49	0.06	0.40–0.56

TABLE 20. Length dimensions (mm) or number of non-neural organs of *Tomichia natalensis*.

	No.	\bar{X}	Sd	Range
Organ (♀)				
Body	4	8.2	0.58	7.6 –8.7
Buccal mass	5	0.92	0.02	0.9 –0.94
Anterior pallial oviduct	3	1.53	0.15	1.4 –1.7
Posterior pallial oviduct	3	1.75	0.05	1.7 –1.8
Total pallial oviduct (Po)	4	3.18	0.10	3.1 –3.3
Bursa copulatrix (Bc)	5	1.26	0.06	1.2 –1.3
Bc/Po	4	0.40	0.02	0.38–0.42
Seminal receptacle	1	0.20	—	—
Digestive gland	4	3.45	0.24	3.2 –3.7
Gonad	3	1.20	0.17	1.0 –1.3
Mantle cavity	4	2.63	0.29	2.3 –3.0
Ctenidium	4	2.03	0.29	1.7 –2.4
Gill filaments	4	37.8	2.29	35–40
Organ (♂)				
Body	2	8.0	—	7.8 –8.2
Prostate	2	1.35	—	1.3 –1.4
Digestive gland	2	3.7	—	3.6 –3.8
Gonad	2	3.0	—	0
Seminal vesicle	2	1.1	—	0
Penis	3	2.77	0.55	2.4 –3.4
Mantle cavity	2	2.85	—	2.7 –3.0
Ctenidium	2	2.40	—	0
Gill filaments	2	30	—	0

convex, sutures correspondingly impressed. Color yellow brown, without heavy periostracum and surface thus glistening. Peristome complete, lips thickened but without dark brown edge. Aperture ovate, not produced at adapical end (Fig. 13); inner lip not reflected over umbilical or basal areas of the body whorl. Parietal callus well formed, straight or arcuate. Inside aperture columella not seen or only very narrow strip seen.

Umbilicus lacking, a chink, or moderately open. Shells smooth, without pronounced

growth lines. Some shells have spiral micro-lines while others (<5%) have oddly spaced raised micro-cords that give area of the shell a malleated appearance. Outer lip of most shells straight or with very slight sinuation (side view).

Organ measurements—See Table 22 for non-neural organs; Table 23 for neural structures.

Radula—See Fig. 9, Tables 15–17.

Unique features—1) large size, 2) the bursa posterior to the opening of the spermathecal

TABLE 21. Measurements (mm) of lengths of neural structures from male *Tomichia natalensis*. N = 4.

Structure	\bar{X}	Sd	Range
Cerebral ganglion	0.22	0.02	0.30–0.24
Cerebral commissure	0.09	0.01	0.08–0.10
Pleural ganglion—right (1)	0.12	0.03	0.10–0.16
—left	0.22	0.08	0.16–0.34
Pleuro-supraesophageal connective (2)	0.36	0.03	0.34–0.40
Supraesophageal ganglion (3)	0.15	0.03	0.12–0.18
Osphradiomantle nerve	0.11	0.03	0.08–0.16
Pleuro-subesophageal connective	0.14	0.07	0.08–0.20
Pedal ganglion	0.21	0.01	0.02–0.22
Pedal commissure	0.09	0.01	0.08–0.10
Statocyst (diameter)	0.10	0.01	0.08–0.10
Osphradial ganglion (N = 3)	0.58	0.06	0.52–0.64
RPG ratio	0.57	0.04	0.52–0.61

TABLE 22. Length dimensions (mm) or number of non-neural organs of topotype *Tomichia rogersi*.

	No.	\bar{X}	Sd	Range
Organ (♀)				
Body	5	12.28	1.07	10.6 –13.4
Buccal mass	5	1.30	0.14	1.1 – 1.40
Anterior pallial oviduct	5	2.56	0.71	2.0 – 3.80
Posterior pallial oviduct	5	2.26	0.09	2.2 – 2.4
Total pallial oviduct (Po)	5	4.82	0.79	4.2 – 6.2
Bursa copulatrix (Bc)	5	1.70	0.11	1.6 – 1.8
Bc/Po	5	0.36	0.04	0.29– 0.40
Seminal receptacle	5	0.27	0.03	0.24– 0.30
Digestive gland	5	5.02	0.23	4.8 – 5.3
Gonad	5	2.26	0.33	2.0 – 2.8
Mantle cavity	5	4.16	0.09	4.0 – 4.2
Ctenidium	5	3.70	0.14	3.5 – 3.8
Gill filaments	5	51.6	2.70	50–55
Organ (♂)				
Body	5	12.58	0.78	11.9 –13.8
Prostate	5	1.28	0.11	1.20– 1.40
Digestive gland	5	6.84	0.32	6.34– 7.0
Gonad	5	7.24	0.43	7.0 – 8.0
Seminal vesicle	5	3.04	0.52	2.4 – 3.8
Penis	5	2.36	0.40	1.8 – 2.9
Mantle cavity	5	4.04	0.26	3.8 – 4.4
Ctenidium	5	3.46	0.26	3.2 – 3.8
Gill filaments	5	50.6	4.44	45–56

TABLE 23. Measurements (mm) of lengths of neural structures from female *Tomichia rogersi*.

Structure	No.	\bar{X}	Sd	Range
Cerebral ganglion	5	0.36	0.03	0.32–0.40
Cerebral commissure	5	0.27	0.03	0.24–0.30
Pleural ganglion—right (1)	5	0.18	0.02	0.16–0.20
—left	5	0.21	0.02	0.20–0.24
Pleuro-supraesophageal connective (2)	5	0.62	0.15	0.50–0.88
Supraesophageal ganglion (3)	5	0.20	0.02	0.18–0.22
Osphradiomantle nerve	3	0.18	0.03	0.14–0.20
Pleuro-subesophageal connective	5	0.08	0.11	0.02–0.28
Subesophageal ganglion	5	0.18	0.03	0.12–0.20
Pedal ganglion	5	0.30	0.03	0.26–0.34
Pedal commissure	5	0.08	0.04	0.02–0.10
Statocyst (diameter)	5	0.14	0.02	0.12–0.16
Osphradial ganglion	5	0.71	0.08	0.60–0.80
Visceral ganglion	4	0.25	0.02	0.22–0.26
RPG ratio: 2/1 + 2 + 3	5	0.61	0.06	0.57–0.71

TABLE 24. Measurements of individual shells of *Tomichia tristis* with entire whorls.

Whorl no.	Length	Width	Length of body whorl	Length of aperture	Width of aperture	Length of last three whorls
7.5	6.52	3.0	3.6	2.32	1.64	5.4
7.5	6.00	2.6	3.16	1.92	1.48	4.72
7.5	6.80	2.96	3.84	2.40	1.72	5.52
7.5	7.08	3.04	3.88	2.52	1.68	5.68
8.0	7.28	3.08	3.8	2.44	1.72	5.68

TABLE 25. Length dimensions (mm) or number of non-neural organs of *Tomichia tristis*.

	No.	\bar{X}	Sd	Range
Organ (♀)				
Body	4	12.63	1.82	11.3–15.2
Buccal mass	3	1.3	0.10	1.2–1.4
Anterior pallial oviduct	4	2.0	0.33	1.6–2.4
Posterior pallial oviduct	4	2.53	0.49	1.8–2.8
Total pallial oviduct (Po)	4	4.53	0.28	4.2–4.8
Bursa copulatrix (Bc)	4	1.42	0.06	1.36–1.50
Bc/Po	4	0.32	0.02	0.29–0.35
Seminal receptacle	3	0.29	0.12	0.20–0.42
Digestive gland	4	4.75	0.81	3.6–5.4
Gonad	3	1.97	0.21	1.8–2.2
Mantle cavity	4	3.95	0.41	3.4–4.4
Ctenidium	4	3.61	0.29	3.4–4.4
Gill filaments (no.)	4	56	2.94	52–59
Organ (♂)				
Body	2	11.1	—	10.6–11.6
Prostate	1	1.2	—	—
Digestive gland	2	5.7	—	4.6–6.8
Gonad	1	4.8	—	—
Seminal vesicle	—	—	—	—
Penis	2	2.35	—	1.6–3.1
Mantle cavity	2	3.4	—	3.0–3.8
Ctenidium	2	3.0	—	2.6–3.4
Gill filaments (no.)	2	57.5	—	56–59

duct is frequently elongate, >0.70 mm (Figs. 20D, E); it is about 0.40 mm (and rarely attains 0.60) in *T. ventricosa*.

T. tristis

Shells (Fig. 7)—Various degrees of erosion of apical whorls. Mixed mature males and females with eroded apices measured 8.15 ± 0.67 mm length. Statistics, Tables 12, 24. Length of last three whorls 5.68 ± 0.29 mm (Fig. 12). Shape turreted. Whorls slightly con-

vex to straight-sided. Sutures moderately shouldered. Color brown or dull yellow brown; periostracum moderate but sufficient to make shells dull. Peristome complete, lips moderately thickened, without dark brown edge. Aperture narrowly ovate, not produced adapically (Fig. 13). Inner lip slightly reflected over umbilical and basal areas of the body whorl. Parietal callus well formed, arcuate or straight, but sunk below the curvature of the body whorl. Inside aperture columellar strip prominent because of inner lip reflection.

TABLE 26. Measurements (mm) of lengths of neural structures from male and female *Tomichia tristis*. N = 4.

Structure	\bar{X}	Sd	Range
Cerebral ganglion	0.35	0.02	0.32–0.36
Cerebral commissure	0.26	0.04	0.20–0.30
Pleural ganglion—right (1)	0.19	0.02	0.16–0.20
—left	0.18	0.03	0.14–0.20
Pleuro-supraesophageal connective (2)	0.50	0.09	0.40–0.60
Supraesophageal ganglion (3)	0.18	0.03	0.14–0.20
Osphradiomantle nerve	0.13	0.03	0.10–0.16
Pleuro-subesophageal connective	0.13	0.15	0.02–0.34
Pedal ganglion (N = 2)	0.29	—	0.28–0.30
Statocyst (diameter) (N = 1)	0.10	—	—
Osphradial ganglion (N = 3)	0.77	0.18	0.60–0.96
Visceral ganglion	—	—	—
RPG ratio 2/1 + 2 + 3	0.61	0.09	0.50–0.72

TABLE 27. Length dimensions(mm) or number of non-neural organs of *Tomichia zwellendamensis*.

	No.	\bar{X}	Sd	Range
Organ (♀)				
Body	5	8.4	0.75	7.6 – 9.6
Buccal mass	3	0.88	0.19	0.74– 1.1
Anterior pallial oviduct	5	2.16	0.42	1.7 – 2.8
Posterior pallial oviduct	5	1.63	0.34	1.4 – 2.2
Total pallial oviduct (Po)	5	3.83	0.42	3.36– 4.20
Bursa copulatrix (Bc)	6	1.09	±0.23	0.80– 1.4
Bc/Po		0.29	0.04	0.23– 0.33
Seminal receptacle	3	0.19	0.02	0.16– 0.20
Digestive gland	6	3.07	0.30	2.6 – 3.4
Gonad	5	1.3	0.10	1.2 – 1.4
Mantle cavity	6	2.85	0.40	2.2 – 3.2
Ctenidium	6	2.57	0.41	1.96– 2.80
No. filaments	6	51.2	8.1	40–62
Organ (♂)				
Body	1	9.0	—	—
Prostate	2	1.07	—	1.01– 1.14
Digestive gland	1	4.8	—	—
Gonad	1	4.8	—	—
Seminal vesicle	2	1.0	—	—
Penis	2	1.5	—	1.3 – 1.7
Mantle cavity	1	2.8	—	—
Ctenidium	1	2.2	—	—
No. filaments	1	66	—	—

TABLE 28. Measurements (mm) of lengths of neural structures from male and female *Tomichia zwellendamensis*. N = 3.

Structure	\bar{X}	Sd	Range
Cerebral ganglion	0.26	0.02	0.24–0.28
Cerebral commissure	0.13	0.04	0.10–0.18
Pleural ganglion—right (1)	0.1	0	0
—left	0.11	0.02	0.09–1.2
Pleural-supraesophageal connective (2)	0.23	0.07	0.16–0.30
Supraesophageal ganglion (3)	0.11	0.01	0.08–0.10
Pleural-subesophageal connective	0.02	0.02	0 –0.02
Subesophageal ganglion (N = 2)	0.11	—	0.09–1.2
Pedal ganglion	0.20	0.02	0.18–0.22
Pedal commissure	0.03	0.03	0 –0.06
Statocyst (diameter)	0.09	0.01	0.08–0.10
Osphradial ganglion (N = 5)	0.47	0.09	0.34–0.56
Visceral ganglion	—	—	—
RPG ratio: 2/1 + 2 + 3	0.51	0.07	0.44–0.58

Shells with umbilical chink to wide open umbilicus. Shell surface rough, some shells with pronounced growth lines, many (60%) with malleation on the body whorl. Spiral micro-striations common. Outer lip sinuate (side view).

Organ measurements—See Table 25 for non-neural organs; Table 26 for neural structures.

Radula—See Fig. 10, Tables 15–17.
Unique features—none.

T. zwellendamensis

Shells (Fig. 8)—Locality (Appendix 1, Z₅), varying degress of erosion of apical whorls. Mature males and females 7.5 to 8.0 whorls. Statistics on shell measurements, Table 12. Length of last three whorls 4.06 ± 0.19 mm (Fig. 12). Shape, slender-turreted. Whorls moderately to quite convex; sutures deep. Color straw yellow. Periostracum slight, shells very fragile and translucent. Peristome not complete in >90%; if complete, only a hint of a parietal callus. Lips thin, without dark brown edge. Aperture ovate, not produced adapically (Fig. 13). Inner lip slightly reflected over umbilical and basal areas of the body whorl; slight arc of columella seen inside aperture because of this slight reflection.

Shells not umbilicate. Shell surface smooth, rarely with growth lines. Twist in columella evident in many shells where outer lip starts reflection. Outer lip straight (side view).

Organ measurements—See Table 27 for non-neural organs; Table 28 for neural structures.

Radula—See Fig. 10, Tables 15–17.
Unique features—only some shell character-states.

APPENDIX 3. Types examined and the status of *Tomichia cawstoni*

Types examined:

Hydrobia alabastrina Morelet, 1889: 19, pl. 2, fig. 5. British Museum (Nat. Hist.); examined 9 February 1978. Mixed lot; small specimen is *Rissoa capensis* Sowerby, 1892. Holotype as figured by Connolly, 1939.

Tomichia cawstoni Connolly, 1939: 585, text fig. 48L, British Museum (Nat. Hist.); examined 9 February 1978. The shell is yellow, straight and flat-sided, not umbilicate, very *Tricula*-like.

Tomichia differens Connolly, 1939: 583, text fig. 47M, South African Museum; examined circa 14 November 1977. Material indistinguishable from my collections at the type locality, D77-13, 19 November 1977.

Assiminea lirata Turton, 1932: pl. 35, fig. 1097. Zoological Museum, Oxford University; examined 10 February 1978. Holotype figured. This shell phenotype is the same seen in some individuals of a single population where other shells clearly resemble *Tomichia tristis*, described and figured by Morelet, 1889: 18, pl. 2, fig. 4, and Connolly, 1939.

Tomichia natalensis Connolly, 1939: 586, text fig. 470. British Museum (Nat. Hist.), examined 9 February 1978.

Tomichia producta Connolly, 1929: 242, pl. 14, fig. 40. British Museum (Nat. Hist.); examined 9 February 1978. Specimen clearly referable to *T. ventricosa*.

Hyrobia rogersi Connolly, 1929: 242, pl. 14, fig. 41. South African Museum; examined circa 14 November 1977.

Tomichia cawstoni was described from Kokstad, Cape Province. Kokstad is a small highland community situated N of national road R₂, to the east of the Transkei, close to

the border of Natal Province. Dr. David Brown (now of the British Museum (Natural History)) and I have both searched for this species and have not located it. I examined stream banks, streams, and marshes around the area of Kokstad to no avail. There are very few streams in this region and Kokstad is situated in an isolated pocket in the hills.

A stream-marsh area along the main highway (R₂) opposite the turnoff to Kokstad appeared to provide a suitable habitat. This area, upon inspection, was polluted with oil. The fields surrounding were extensively used for grazing cattle. I presume this species to be extinct.

ANATOMY, BIOLOGY AND SYSTEMATICS OF *CAMPANILE SYMBOLICUM*
WITH REFERENCE TO ADAPTIVE RADIATION OF THE
CERITHIACEA (GASTROPODA: PROSOBRANCHIA)

Richard S. Houbbrick

*Department of Invertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.*

ABSTRACT

Campanile symbolicum Iredale is the sole survivor of a long lineage of large mesogastropods in the family Campanilidae. The family was well represented in the Tethys Sea and underwent a widespread adaptive radiation in the early Tertiary. Several of the fossil species are among the largest known gastropods. The living relict is confined to southwestern Australia where it is common in shallow, subtidal, sandy habitats. It is a herbivore with a generalized taenioglossate radula and thick jaws. The large, elongate conical shell has a chalky periostracum and the aperture, which has a central anterior canal, is at a 45 degree angle to the shell axis. The open pallial gonoducts in both sexes and aphyllous males are conservative characters found in all cerithiaceans. These, and the characters derived from the shell, operculum and radula unequivocally refer *Campanile* to the superfamily Cerithiacea. Anatomical features of the sensory, reproductive, alimentary and nervous systems of *Campanile* are unique among the Cerithiacea and indicate that it should be allocated to a separate family, the Campanilidae.

Among the external anatomical features peculiar to *Campanile* are a short thick snout, tiny eyes, and a deep ciliated pedal gland around the entire margin of the sole of the foot. Small papillae surround the entire mantle edge. The columellar muscle is long and has a large prominence. A short oval bipectinate osphradium is located at the anterior end of the mantle cavity adjacent to the long ctenidium. It closely resembles the osphradia of neogastropods and several families of higher mesogastropods. The hypobranchial gland is modified into tiny leaflets where it is adjacent to the anus. Two simple laminae comprise the pallial oviduct and are longitudinally folded. The internal folds of the proximal end of the left lamina of the pallial oviduct are elaborated into broadly ovate transverse ridges forming a large albumen gland. A sac-like seminal receptacle projected into the pericardial sac opens into the left proximal end of the pallial oviduct. It occurs in both sexes but is more highly developed in females. Although sexes are separate, this suggests that *Campanile* is a protandric hermaphrodite. The head and foot of a mature animal become bright pink. It appears that *Campanile* forms spermatophores. Sperm taken from the vas efferens are all eupyrene. Spawn masses are large gelatinous tubes deposited on the substratum and contain spirally arranged capsules, each of which contains one to several moderately sized eggs. Development is either direct or with a short demersal larval stage. Veliger stages are attained within the spawn mass and the embryonic shell is smooth, bulbous and lacks a sinusigera notch. The radula of *Campanile* is wide and robust but unusually short in comparison to the size of the snail. Paired salivary glands and their ducts and paired buccal pouches lie anterior to the nerve ring. The mid-esophagus encloses the dorsal and ventral food channels. It has shallow lateral folds but no esophageal gland and is surrounded by a large mass of connective tissue in the middle of which is a thin muscular sheet. The stomach has a style sac but lacks a gastric shield and a style. In the sorting area is a series of leaflets spirally arranged in a deep pit. In the posterior of the stomach is the vestige of a spiral caecum. The nervous system comprises a mixture of loosely connected and condensed ganglia and is dialyneurous and zygoneurous.

The Campanilidae appeared in the late Cretaceous to early Tertiary as did most other substantial cerithiacean families. Each family radiated into a specific adaptive niche and has remained essentially the same in ecology and general physiognomy of its members. Although the Campanilidae were abundant in the Paleocene and Eocene, it is the only cerithiacean family to have undergone serious diminution in species to the point of virtual extinction. Campanilid snails were the largest animals in the superfamily and were undoubtedly grazers of microalgae in the shallow waters of the Tethys. A hypothesis for the demise of the Campanilidae is trophic competition with another group of large grazing gastropods, the Strombidae, which became established in the late Eocene to early Miocene and flourished in a similar ecological niche.

INTRODUCTION

During the early Tertiary, genera of the family Campanilidae Douvillé, 1904, were a group of many species that were common in the Tethys Sea. There is an extensive literature about these spectacular gastropod fossils. Some species, such as *Campanile giganteum* (Lamarck, 1804), attained a length of 1 m and are among the largest gastropods on record. The family is represented today by a single living species: *Campanile symbolicum* Iredale, 1917, from southwestern Australia.

This living species is a subtidal, shallow-water dweller that is common within its limited range. Although it is unusually large for a cerithiid, and a relict species of an extinct group, it is not well known to malacologists and is poorly represented in museum collections outside Australia. Virtually nothing has been published about its ecology or life history and no recent comprehensive account of the anatomy of this interesting animal exists; consequently, its relationship to other cerithiacean groups and to the numerous fossil species within the family Campanilidae is conjectural and is based solely on shell characters. Indeed, some authors have questioned whether *Campanile symbolicum* is of the same lineage as the larger Tethyan fossils.

Much of the literature on this group has dealt with the selection of a proper type-species for the genus and with nomenclatural problems. The nomenclature of the generic and specific names has a complex history.

In May, 1979, I observed a population of *Campanile symbolicum* at Pt. Peron, near Perth, Western Australia. I studied the living animals and dissected narcotized specimens in order to make anatomical comparisons with other cerithiaceans. Egg masses and embryos were also studied.

This paper presents my findings and includes an historical review of the genus *Campanile*. My description of *Campanile symbolicum* includes anatomical, embryological, opercular and radular characters as well as shell features. I also include some aspects of the reproductive biology and brief notes on the ecology of the species. These findings indicate that *Campanile* should be assigned to a separate family, Campanilidae. The relationship of this relict family to other families within the Cerithiacea reflects the adaptive radiation of the superfamily.

MATERIALS AND METHODS

Specimens were collected by hand while snorkeling from Pt. Peron, Western Australia and living animals were examined in the field to determine their exact habitat. Individual snails were maintained in seawater aquaria at the Western Australian Museum, Perth, for behavioral observations. For anatomical studies, animals were extracted from their shells that had been cracked with a large vise and were relaxed in 7.5% MgCl₂. Dissections were made with the aid of a binocular dissecting microscope. Material for histological sections was prepared in Bouin's Fixative, embedded in paraffin and sectioned on the microtome at 5 μ m. Sections were stained with Harris' hematoxylin and counterstained with Eosin Y. The radula, jaws, periostracum and shell ultrastructure were studied with a scanning electron microscope. The geographic range of the species was determined by examination of specimens in major museums in the United States and Australia, and statistics of shell measurements computed from a large series of adult shells. Preserved spawn masses and embryos were studied with a Wild stereo dissection scope and a scanning electron microscope was used to study embryonic shells.

KEY TO ABBREVIATIONS ON FIGURES

a	—anus
aa	—anterior aorta
ag	—albumen gland
as	—attachment surface
au	—auricle
b	—baffle
bg	—buccal ganglion
bm	—buccal mass
bp	—buccal pouch
bv	—blood vessel
cem	—cut edge of mantle
cf	—ciliated furrow
cm	—columellar muscle
cnt	—connective tissue
ct	—ctenidium
ctb	—ciliated tube
ctr	—ciliated tract
dg	—digestive gland
dol	—division of outer lamina
dpg	—distal part of pallial oviduct
dsr	—duct of seminal receptacle

ebv	—efferent branchial vessel	sl	—sorting leaflets
es	—esophagus	sn	—snout
eso	—esophagus opening	sp	—sperm in smooth chamber
ev	—esophageal valve	sr	—seminal receptacle
exs	—exhalant siphon	ss	—style sac
f	—foot	st	—stomach
ff	—fold emerging from spiral caecum	t ₁	—major typhlosole
fg	—food groove	t ₂	—minor typhlosole
FL	—sperm flagellae	tn	—tentacle nerve
gil	—glandular part of inner lamina	ve	—ventricle
gs	—"gastric shield"	wps	—wall of pericardial sac
gsa	—grooved channel	z	—zygoneury between right pleural ganglion and subesophageal ganglion.
H	—head of sperm		
hg	—hypobranchial gland		
il	—inner lamina		
ins	—inhalant siphon		
int	—opening to intestine		
j	—jaw		
k	—kidney		
ko	—kidney opening		
lcg	—left cerebral ganglion		
ld	—lower duct		
les	—lumen of esophagus		
lhg	—leaflets of hypobranchial gland		
lpg	—left pleural ganglion		
lpn	—left pallial nerve		
mc	—mantle cavity		
me	—mid-esophagus		
ml	—thin muscular layer		
mp	—mantle papillae		
od	—odontophore		
odg	—oviducal groove		
odu	—oviduct		
OES	—opening to esophagus		
ol	—outer lamina		
op	—operculum		
opn	—optic nerve		
os	—osphradium		
osr	—opening of seminal receptacle		
ov	—ovary		
pp	—propodium		
ppg	—proximal part of pallial oviduct		
ps	—pericardial sac		
r	—rectum		
ra	—radula		
rcg	—right cerebral ganglion		
rl	—renal lamellae as seen by transparency		
rpd	—renopericardial duct		
rpg	—right pleural ganglion		
RW	—receptacle wall		
sa	—sorting area		
sc	—spiral caecum		
sec	—supraesophageal connective		
seg	—supraesophageal ganglion		
sg	—salivary gland		

DESCRIPTION

This section deals with the descriptions of the shell, operculum, radula, anatomy, spawn and larvae of *Campanile symbolicum*, and will bring together my own observations and those of previous authors. The anatomical description includes external and internal features and is supplemented with histological studies. The functional interpretations of various systems are proposed and most of the significant anatomical features are figured. Brief discussions on ecology and the fossil history of *Campanile* are included.

Specimens examined—Great Australian Bight (NMV); Recherche Archipelago, 23°15'S, 122°50'E, including Mondrain Id., Salisbury Id., Middle Id., Boxer Id. (all NMV); Nares Id., Duke of Orleans Bay (WAM); Lucky Bay (WAM); Two Mile, Hopetoun (AMS, WAM); Bremer Bay (WAM); Princess Royal Harbour (AMS); Pallinup River Estuary (WAM); Point Irwin (DMNH); South Point, S side of Two People Bay, Albany (AMS); Irwin River Inlet, W of Albany (AMS); Middletown Beach, Albany (WAM); Frenchman's Bay, Albany (WAM); Albany (ANMH); Cowaramup Bay (AMNH); Augusta (WAM); Sarge Bay; Cape Leeuwin (WAM); Hamelin Bay (WAM); Bunker Bay, Cape Naturaliste (WAM, USNM, ANSP, MCZ); N side of Cape Naturaliste Light (AMS, USNM); Busselton (WAM); Dunsborough (WAM, AMNH); Yallingup Brook (WAM, NMV); Yallingup (WAM, NMV, AMS); Canal Rocks, S of Yallingup (AMS); Geographe Bay (AMS); Cape Mentelle, Kilcarneys (AMS); Bunbury, reef at Capel (AMS); W side of Carnac Id. (WAM); Rockingham (AMS); Fremantle (ANSP, DMNH, WAM); near Garden Id., Fremantle (MCZ);

SW of Garden Id., Fremantle (AMS); Kwinana (AMS); Dunn Bay (USNM); Swan River (NMV); Cottesloe (WAM); Carnac Id. (WAM); Point Peron, Perth (AMNH, WAM, USNM); Trigg Id. (WAM); Yanchep Reef (WAM); Pal-linup Estuary (WAM); Port Denison (WAM); Jurien Bay (WAM); Dongara (AMS); Beach Colony Shore, Geraldton (MCZ, AMS).

Shell description (Figs. 1–2)—Shell large, ranging from 60 to 244 mm in length (See Table 1 for measurements), turreted, elongate, having apical angle of 25° and teleoconch of about 25–30 flat-sided whorls that become weakly inflated or angular on penultimate and body whorls. Outline of entire spire concave and early whorls usually missing. Each whorl

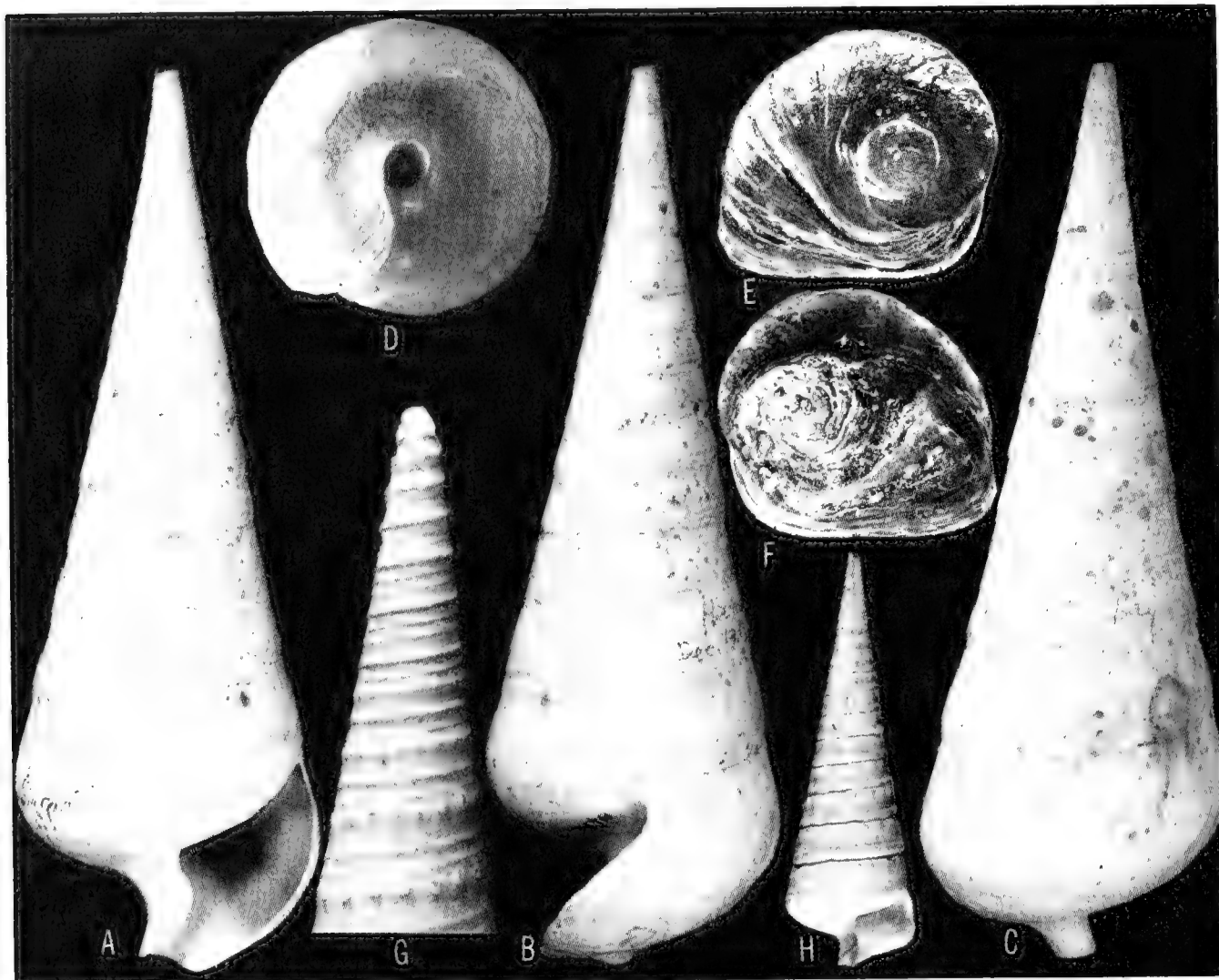


FIG. 1. A–F, Shell and operculum of *Campanile symbolicum* from Hamelin Bay, Western Australia (Western Australian Museum N4514), 120 mm long, 68 mm wide; operculum 17 mm diameter. A, Apertural view; B, Side view showing sinuous outer lip; C, dorsal view; D, Anterior view of centrally placed siphonal canal; E, Free surface of operculum showing subcentral nucleus; F, Attachment surface showing large oval muscle scar on lower two thirds of operculum; G, Detail of sculpture of early whorls on specimen from Salisbury Id., Recherche Archipelago, Western Australia (National Museum, Victoria); H, Holotype of *Cerithium leve* Quoy & Gaimard (National Museum of Natural History, Paris, photograph courtesy of Mr. Foubert).

FIG. 2. *Campanile symbolicum*. a–c, Advanced embryonic shells from egg mass found at Rottnest Id., Western Australia (diameter, 0.05 mm); d, SEM of single jaw showing attachment surface (5 mm long); e, SEM of jaw showing cutting edge (5 mm long); f, Longitudinally cut shell showing apex with calcareous septa in interior whorls; g, Whole shell cut longitudinally from apex to anterior canal showing whorl configuration and columella; h, SEM of cross section of jaw, showing four layers, about .055 mm wide. The bottom layer is the attached portion; i, SEM enlargement of attachment surface of jaw showing microscopic polygonal pits, each about $7\ \mu\text{m}$ long; j, SEM detail of surface periostracum showing cancellate, pitted appearance, $28\times$; k, SEM detail of cross section of shell showing, from top to bottom, calcified periostracum with subsurface tubules, and cross lamellar aragonite, $86\times$.

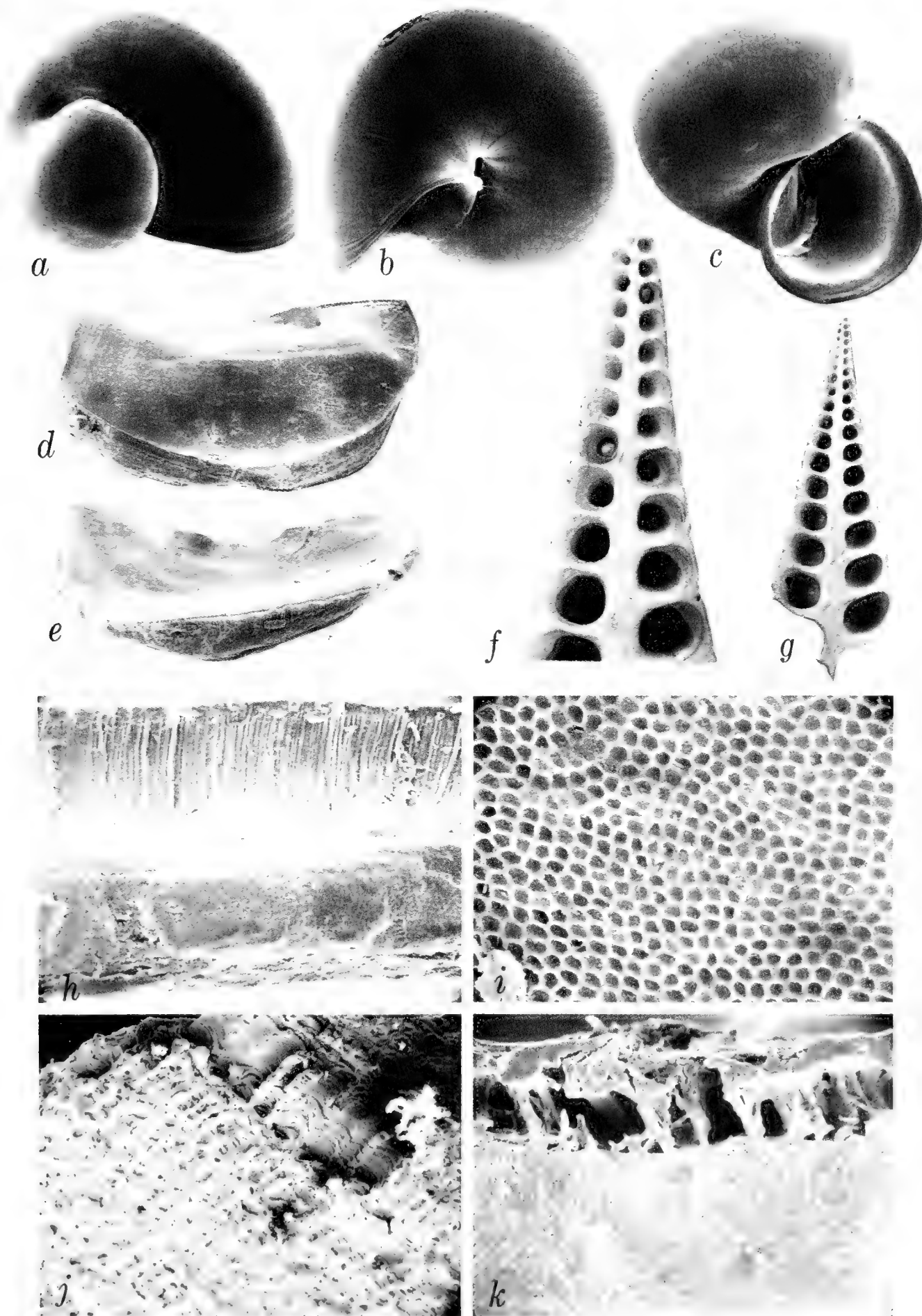


TABLE 1. Statistical summary of shell measurements of *Campanile symbolicum* (in mm).

Character	Number	Range	Mean	SD
Length	29	60 –244	142.8	50.84
Width	29	21.5–74	44.1	15.81

sculptured with a presutural spiral cord that produces a weak keel at the base. This spiral cord is more medianly placed on very early whorls and may be divided into two spiral cords on some shells. Early whorls and mid whorls have a subsutural spiral that tends to disappear on later whorls (Fig. 1G). Nodules frequently elongated axially, sometimes entirely absent. Penultimate and body whorls usually smooth. Below nodules each whorl sculptured with many microscopic spirally incised lines that are crossed over by numerous axial, sinuous, growth lines. Suture distinct and straight. Protoconch (Fig. 2a–c) smooth, bulbous, about 1½ whorls. Protoconch lip slightly flared at base. Body whorl is round with the anterior siphonal canal in the center. Aperture triangular-fusiform and at a 45° angle to axis of shell. Aperture one-fourth to one-fifth the length of shell. Interior of aperture glossy white. Anterior siphonal canal distinct, deep and moderately short, almost straight but slightly twisted to left of shell axis. Columella short, concave and twisted slightly to left at anterior canal. A slight plait appears at the columella base but does not continue into the aperture and up the axis of the shell. Older, larger specimens have an inner columellar lip, slightly detached from parietal area. Outer lip thin, sinuous, smooth and with a deep sinus where attached to body whorl. Lower portion of outer lip crosses over anterior canal when shell is viewed anteriorly.

A shell cut in half longitudinally, from apex to anterior canal, exposing the whorl interiors reveals that the columella is concave throughout the shell axis and that each whorl is round in cross section (Fig. 2f,g). Scanning electron micrographs of cross section of the shell wall show that it is composed of cross lamellar aragonite which appears in a wide bottom layer overlain with looser disordered aragonite (Fig. 2k).

The periostracum of *Campanile* is unusual and closely resembles that of some muricid gastropods such as those in the genus *Aspella* Mörch. It is thick and comprises a cancellate, calcified outer layer and an under-

lying scabrous layer (Fig. 2i,j). Radwin & D’Attilio (1976: 245) considered this to be a chalky white surface layer of the shell and called it the “intritacalx” but it is simply the calcified outer portion of the periostracum (Waller, personal communication), as can be seen in scanning electron micrographs of the fractured shell edge (Fig. 2k). In *Campanile*, the outer calcified layer of the periostracum has a cancellate appearance at the surface that is most clearly seen in young specimens. Beneath the surface are numerous fine hollow tubes that run spirally around each whorl. This layer is fragile and flakes off easily in dried specimens. In older shells the surface appears to be pitted and chalky. The pits are merely depressions formed by the cancellate pattern in the outer layer. Wrigley (1940: 99) noted tiny pitted lines on the surface of all fossil species of *Campanile* he examined and I have also seen this pattern on fossils of *Campanile giganteum*. This calcified thick periostracum thus appears to be a characteristic of the family Campanilidae.

The brown-colored operculum (Fig. 1E–F) is corneous, moderately thick and paucispiral with a subcentral nucleus. The operculum has a straight growing edge and the edge nearest the nucleus is partially covered with the foot when the animal is extended. The ovoid attachment scar is on the obverse, bottom two-thirds of the operculum (Fig. 1F). The operculum diameter is much smaller than that of the aperture, allowing the animal to retract deeply into the mid whorls of the shell. In this retracted state, the operculum fits snugly into the shell aperture.

Animal (Figs. 3–7)—A brief but accurate description of the animal was given by Quoy & Gaimard (1834: 107–108) in the original description. A more detailed account of the gross anatomy that centered on the nervous system but included observations of other systems was presented by Bouvier (1887a,b), who compared *Campanile* with other cerithiids. Although Bouvier’s (1887b) work is accurate and thorough, he failed to describe the reproductive tract which is essential for an analysis of comparative relationships among cerithiaceans. Bouvier’s papers were published in French journals that were apparently missed by subsequent authors.

The only figure of a living animal of *Campanile* is the one originally given by Quoy & Gaimard (1833: pl. 54, fig. 2), and it only shows the head-foot. Part of the foot covers the edge of the operculum nearest the oper-

cular nucleus. If the shell is cracked, the snail may withdraw as far as one-half the length of the shell, causing the edges of the operculum to fold.

When animals are extracted from their shells it is apparent that the upper portion of the visceral mass, comprising the digestive gland and gonad, does not fill the upper whorls of the shell apex. These are walled off by a series of concave, calcareous partitions or septa and the earliest whorls are totally

filled. The concavity of each septum is adapical (Fig. 2f-g). Just anterior to the last septum the shell whorls are lined with a thin brown membrane. Attached to this membrane is another thin, transparent, membrane that is invested with tiny brown spherules of unknown function. Both of these membranes are of obvious organic origin and are probably laid down by the mantle.

The head-foot and mantle edge of live snails from Point Peron are white to flesh

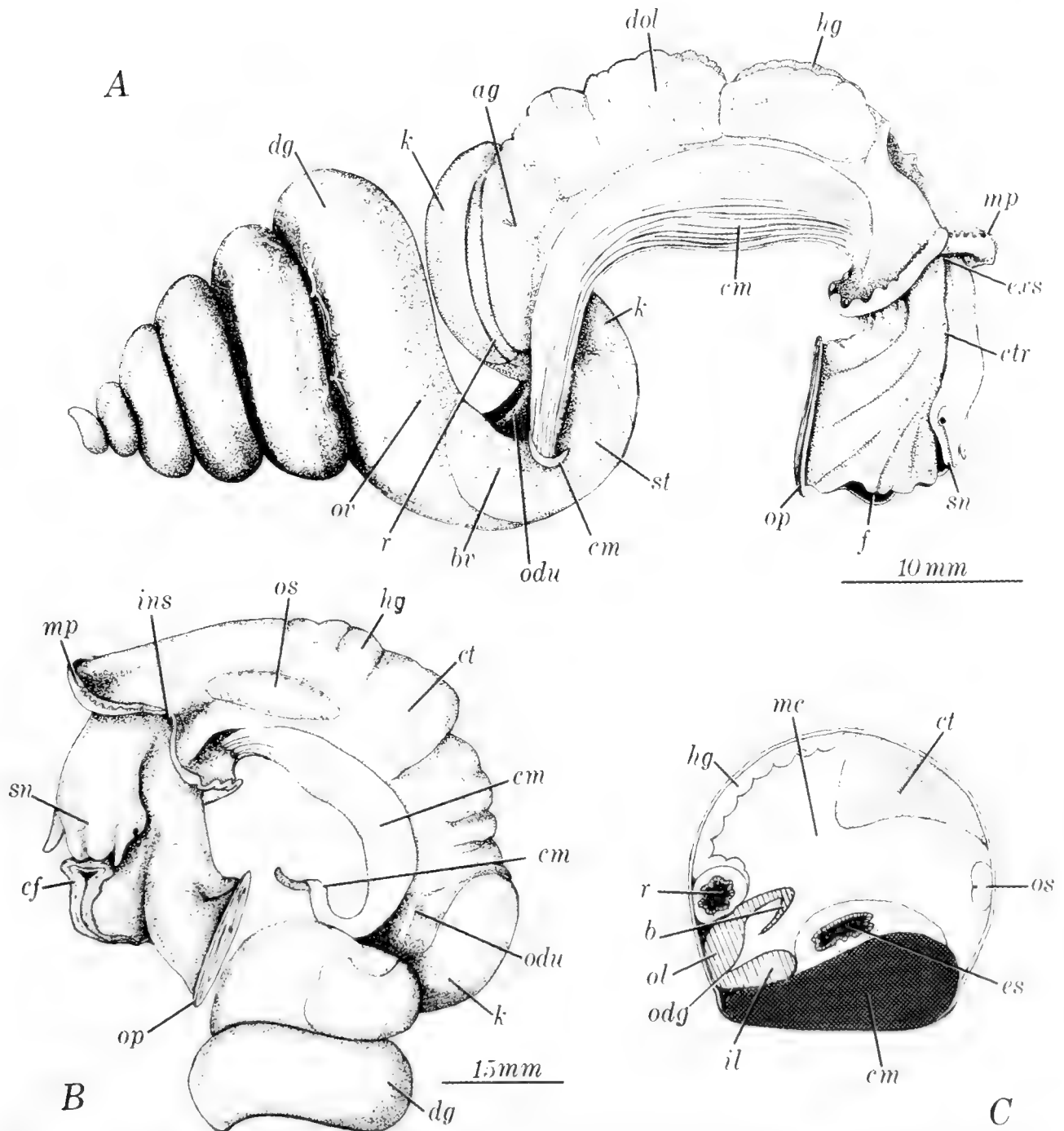


FIG. 3. *Campanile symbolicum*, removed from shell. A, View of right side of female showing major external structures and free part of columellar muscle; B, Left side of animal; C, Cross section of female through mid mantle cavity showing relationship of major pallial organs. (See Key to Abbreviations, p. 264, for explanation of lettering.)

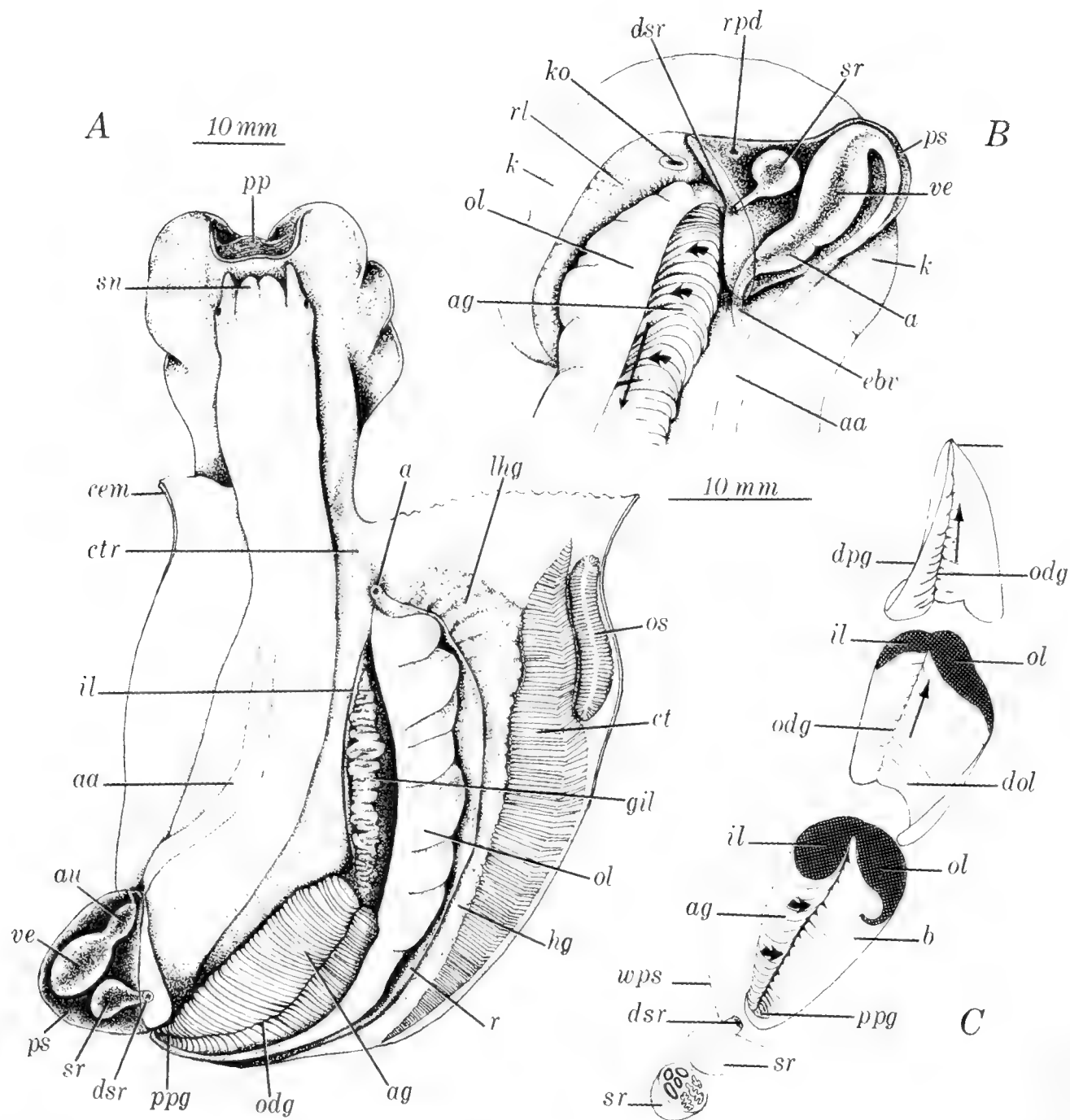


FIG. 4. Internal anatomy of *Campanile symbolicum*. A, Female removed from shell with mantle cavity opened with a lateral-dorsal cut; B, Detail of proximal portion of pallial oviduct showing relationship of kidney, pericardial sac and seminal receptacle to oviduct. The kidney has been pulled back to expose the proximal part of the pallial oviduct; C, Diagrammatic representation of sections of pallial oviduct and seminal receptacle showing major anatomical features. Compare with pallial oviduct depicted in drawing A, this figure. (See Key to Abbreviations, p. 264, for explanation of lettering.)

colored and slightly mottled with light brown and pink. Extracted snails are small in relation to their shells. The snout is short, broad and thick and is conspicuously bilobed at the tip (Fig. 3B, *sn*). Tentacles are short and bright pink, each with a tiny black eye at its broad base.

Emerging from the exhalant pallial siphon (Fig. 3A, *exs*) and running down the right side

of the head-foot, beneath the right eye and tentacle and down the outer surface of the foot is a deep ciliated groove (Figs. 3A, 4A, *ctr*) in which fecal pellets and other debris are expelled from the mantle cavity in a string of mucus. This is probably also used by females during oviposition. Although I found no evidence of a structure that could be interpreted as an ovipositor, one associated with this cili-

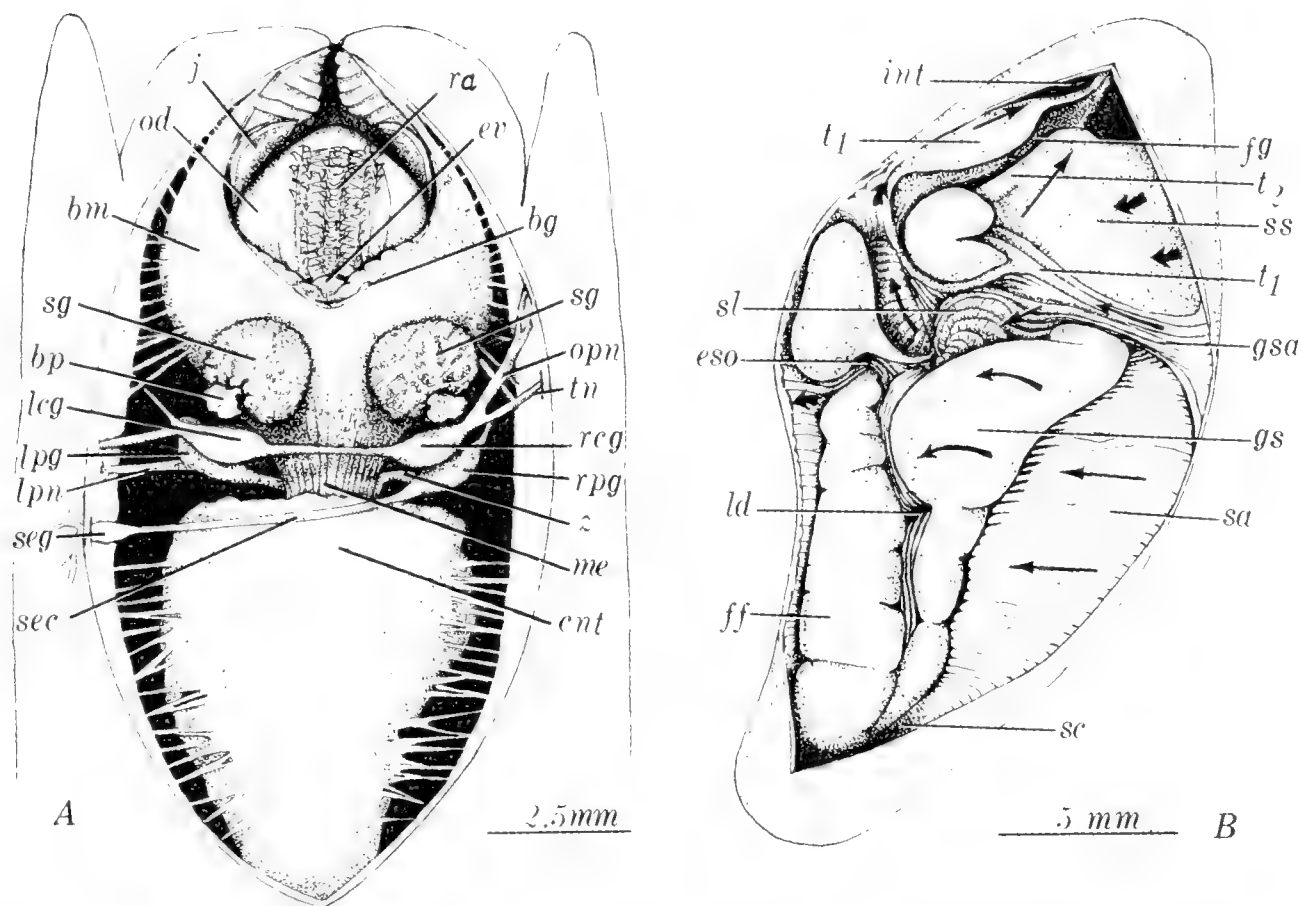


FIG. 5. A, Dissection of head opened by a dorsal longitudinal cut to expose anterior alimentary tract. Connective tissue surrounding nerve ring has been removed. Subesophageal ganglion hidden beneath mid-esophagus. B, Stomach opened by a dorsal longitudinal cut. Arrows indicate direction of ciliary currents. (See Key to Abbreviations, p. 264, for explanation of lettering.)

ated groove may develop during the spawning season.

The foot is moderately small in relation to the shell and has a whitish sole with slight traces of yellow. Quoy & Gaimard's (1834: 107) observations on the color of animals from King George Sound agree with mine. They noted that the underside of the foot was yellowish and striated. I did not see striations in the Point Peron specimens. The entire edge of the sole has a deep ciliated glandular furrow (Fig. 3B, *cf*) that appears to be a pedal gland. It produces mucus, but it was not determined if the gland cells were epithelial or subepithelial. The foot is capable of contraction into numerous, compact transverse folds that appear to secrete mucus in living animals. It is powerful enough to pull the heavy shell enabling animals to partially burrow and even crawl up rocky surfaces.

The large columellar muscle (Fig. 3A-C, *cm*) is very long, comprising 2-3 whorls in a retracted animal. This muscle is white and thick anteriorly but flattens and tapers rapidly

near its proximal origin on the columella of the shell.

Posterior to the mantle cavity is the visceral mass of 6-7 whorls that consists of a large two-lobed kidney (Fig. 3A, *k*), a long stomach (Fig. 3A, *st*) of $1\frac{1}{2}$ whorls and a digestive gland-gonad complex (Fig. 3A, *dg*). The latter has a distinctive banded appearance, clearly seen in both living and preserved snails: at the periphery of each whorl it is light gray while the inner surfaces of the whorls are darker brown, spotted with gray and overlain by a ramose network of white calcium.

The digestive gland is dark brown and is slightly overlain by the gonad in mature animals. Ovaries are externally yellow and consist of tiny spherules located along the periphery of the whorls. The testis is not as easily differentiated from the digestive gland except for a change of external texture along the periphery of the whorl. I did not observe animals during their peak reproductive season; consequently ripe snails may have more conspicuous, characteristic gonads. Gonads

are discussed in more detail in the section on the reproductive tract.

Mantle cavity and associated organs (Figs. 3–4). The mantle cavity is wide and deep. At the base of the left side is a large brown, oval-shaped, bipectinate osphradium (Fig. 3B–C, os; Fig. 4A, os) directly adjacent to the ctenidium. It begins behind the distal end of the ctenidium and closely resembles it in overall morphology, except that the leaflets are wider and more oval. It is referred to by Bouvier (1887b) as the “fausse branchie.” It runs parallel to the ctenidium but does not extend the length of the mantle cavity as in other cerithiaceans. The osphradium is slightly elevated from the mantle skirt on a central axial ridge that bears a series of numerous, flat, bipectinate leaflets. Each of these is attached to the stem of the axis and also fused basally to the mantle skirt. Histological sections show that each leaflet has an external morphology

of numerous parallel ridges that run dorso-ventrally or vertically to the osphradium axis. Cross sections reveal a surface structure covered with ciliated cells and more numerous darkly-stained cells.

The typically monotocardian ctenidium (Fig. 3B, ct; Fig. 4A, ct) is pink and extends most of the length of the mantle cavity to end a short distance from the inhalant pallial siphon. A large, white efferent branchial vessel (Fig. 4B, ebv) lies along the basal length of the left side of the ctenidium.

The thick mantle edge is weakly bilobed, flared and has a slightly scalloped appearance. It consists of an inner row of tiny papillae found only on the upper two thirds of the mantle edge and an outer, continuous, scalloped border (Fig. 3A–B, mp). The scallops are larger on the ventral part of the mantle edge. The deep groove between the two mantle lobes secretes the shell but also traps

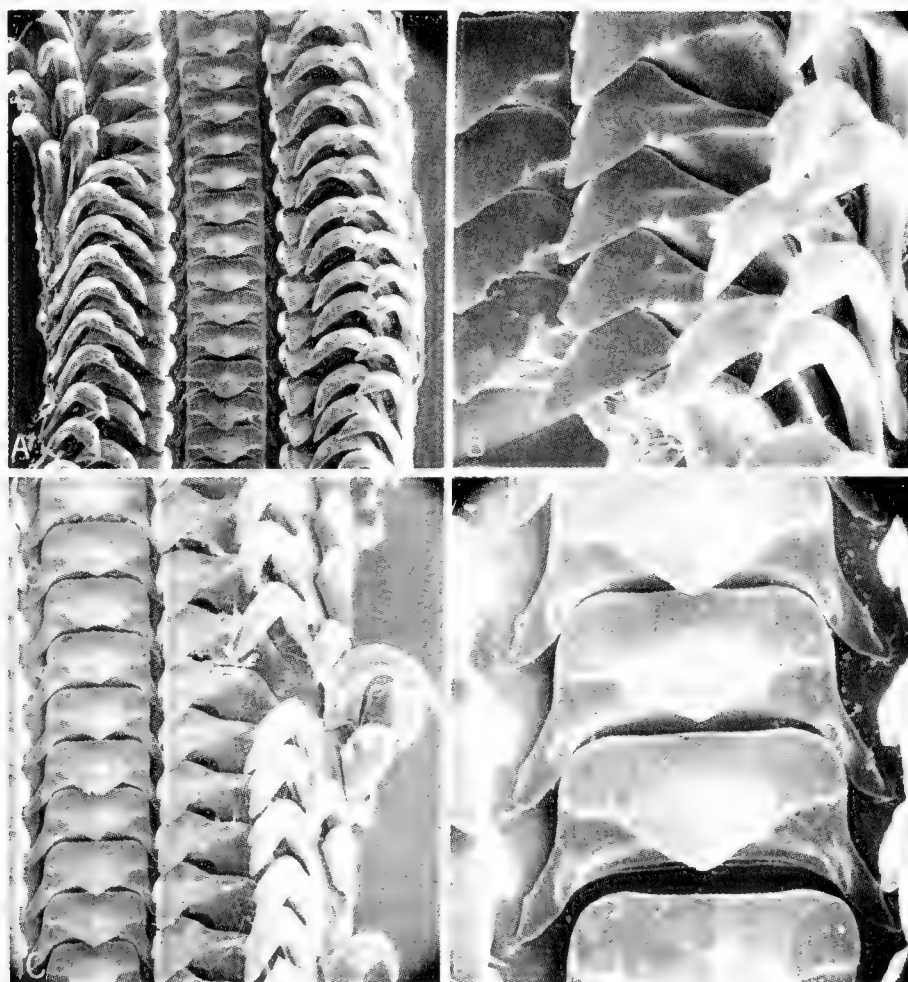


FIG. 6. SEM micrographs of radular ribbon of *Campanile symbolicum*. A, View of central portion of radula showing relationship of various taenioglossate teeth. Radular ribbon is 8.2 mm long and 2.15 mm wide; B, Detail of lateral and marginal teeth, showing tiny cusps adjacent to large cusp of lateral tooth and smooth outer surfaces of inner and outer marginal teeth; C, Enlargement of half row of radular ribbon with marginal teeth folded back showing their insertion on underlying radula membrane; D, Detail of rachidian teeth showing basolateral projections.

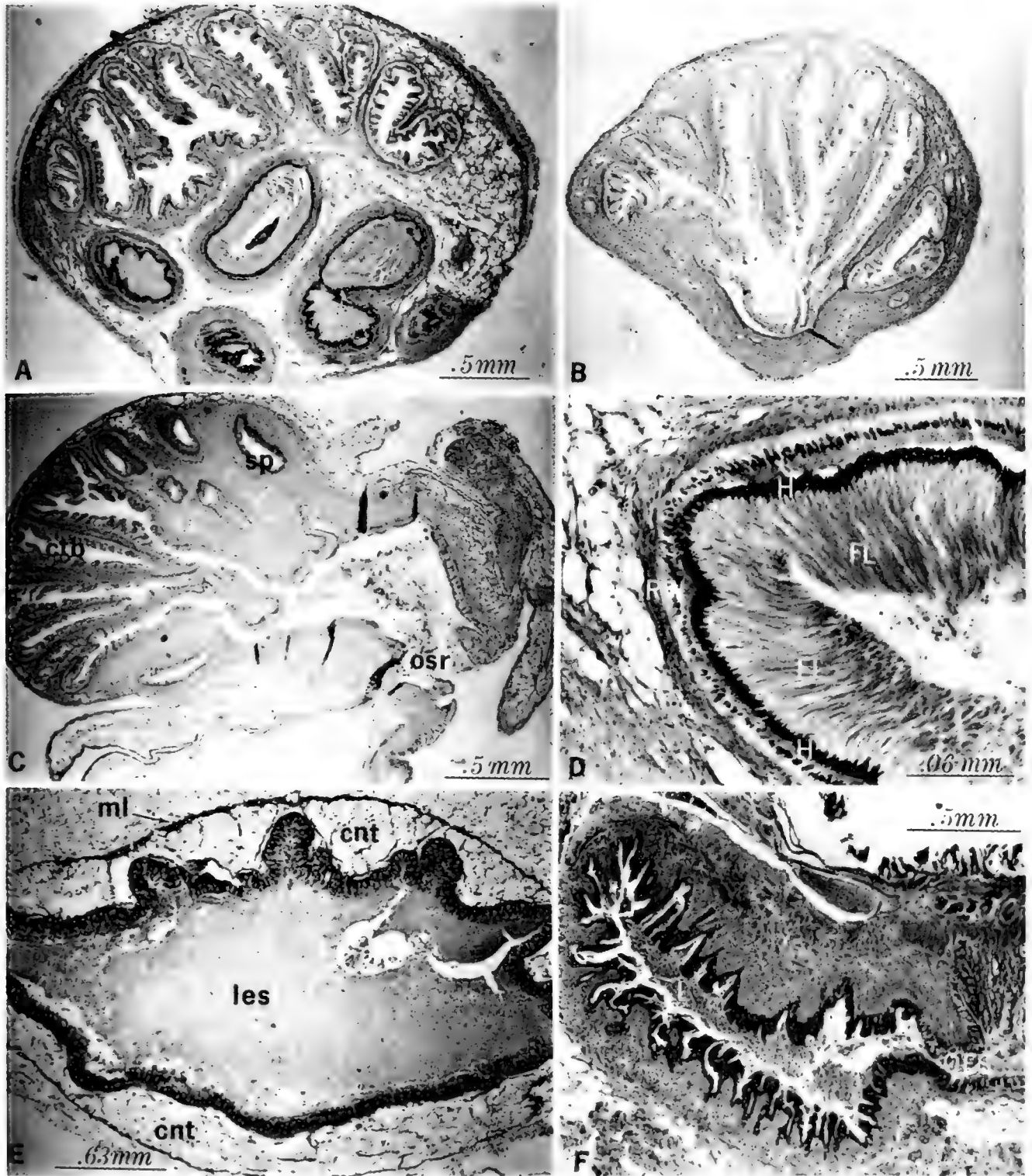


FIG. 7. Histology of reproductive and alimentary tracts. A, Transverse cross section of seminal receptacle, showing network of tubules. Note villous walls of empty tubules at top and smooth walled chambers containing sperm at bottom; B, Longitudinal cross section of seminal receptacle showing connection of tubules; C, Oblique section of seminal receptacle showing opening of duct (osr) leading from seminal receptacle to pallial oviduct; D, Detail of sperm filled chamber in seminal receptacle showing spermatozoans with dark heads (H) oriented along wall of chamber (RW) and flagella (F) projecting into chamber lumen; E, cross section of mid esophagus showing shallow folds in esophagus wall. The lumen (les) is filled with detritus. Note mass of connective tissue (cnt) and thin muscular layer (ml) surrounding esophagus; F, Cross section of esophageal pouch showing deeply folded walls and opening into esophagus (OES).

debris and moves particles by ciliary action from between the mantle and shell. The inhalant siphon (Fig. 3H, *ins*) is thick and comprises a slight fold in the mantle wall, but is not well marked in contrast to the thicker exhalant siphon (Fig. 3A, *exs*).

The hypobranchial gland (Fig. 3A–C, *hg*; Fig. 4A, *hg*) is a large organ, about 6 mm wide, pinkish-tan in color that extends the length of the mantle cavity where it lies between the ctenidium and intestine. It partially covers one half of the intestine, longitudinally, in a thick sheet. The hypobranchial gland begins immediately behind the exhalant pallial siphon and is thus the most anterior of all pallial organs. Its surface is composed of numerous transverse ridges or folds which are papillate along their edges, and most numerous and thin at the rear of the mantle cavity. They become progressively thicker toward the anterior of the snail. The ridges are flocculent in texture and easily fall apart when touched with a probe. The papillate ridges of the hypobranchial gland adjacent and anterior to the anus are thicker and extended into numerous, tiny, flat leaflets (Fig. 4A, *lhg*). The gland in this region is thicker and appears to be slightly different in texture. In cross section, it is separated from the posterior part by a band of tissue that is part of the siphonal musculature. Sections show that it consists mainly of elongate goblet cells and it may produce additional mucus used in conjunction with the exhalant siphon. Its exact function is uncertain. Sections of the hypobranchial gland show that it is composed of elongate, multivacuolated goblet cells that are attached to a basal membrane adjacent to the circular muscular tissue of the mantle wall. Most of the vacuoles appear empty in fixed tissue but some are filled with tiny, darkly stained granules.

The rectum (Figs. 3A, 4A, *r*) is a long, dark brown tube, about 3–4 mm thick that lies between the hypobranchial gland and pallial gonoduct ending near the exhalant siphon. The anal opening (Fig. 4A, *a*) is surrounded by tiny papillae.

The pallial gonoducts lie to the right of the intestine, are open and comprise two laminae which are highly glandular, especially in the female.

Alimentary tract.—The alimentary system of *Campanile* is slightly different from that of most cerithiaceans. One of the notable features is a short, wide, bilobed snout (Fig. 4A, *sn*) that was noted by Bouvier (1877a, b) as a

distinguishing character. The mouth lies at the tip of the snout, recessed between the two lobes that comprise the snout apex. The snout area and head are thick and very muscular.

A pair of large, thick, semilunar-shaped jaws (Fig. 5A, *j*) that are yellowish brown in color and about 5 mm long are inserted in the upper lateral walls of the anterior end of the buccal cavity. The jaws are superficially smooth except for their irregular cutting edges that appear to be formed of numerous transverse rods (Fig. 2d–e). Scanning electron micrographs of the jaws reveal a complex ultrastructure. The free surface of each jaw, exclusive of the cutting edge, is generally smooth but shows concentric lines of growth radiating from the base where the jaw is inserted in the wall of the buccal cavity. The attached surface of each jaw is made up of many microscopic polygonal pits (Fig. 2i). Each pit is about 7 μm in length and its polygonal walls probably conform to individual cell boundaries. Each pit is perforated with numerous tiny holes. The cutting edge of a jaw comprises a matrix of many thin, transverse rod-like structures. In cross section, a jaw is composed of four consecutive layers (Fig. 2h). At the smooth surface is a wide layer of transverse rods and beneath this is another thin layer of transverse rods. Another thin, nondescript layer follows and beneath this a final thick layer of smooth material. It is this final layer that is attached to the wall of the buccal cavity and has the pitted surface. The growing surface of the jaw appears to be the concave portion opposite the cutting edges. The functional significance of the complex ultrastructure of the jaws was not determined.

The buccal mass (Fig. 5A, *bm*) is spherical and attached to the walls of the buccal cavity by numerous tensor muscles that insert onto its entire surface. These are more numerous laterally and ventrally. The odontophoral cartilages (Fig. 5A, *od*) are very large and thick.

The radula (Fig. 6A–D) is stout, moderately short and wide, and about one-tenth the length of the shell. Two radular ribbons from animals with shells about 100 mm in length averaged 8 mm long, 2.25 mm wide and comprised 43 rows of teeth. The rachidian tooth is straight and has a large, plate-like cutting edge comprising a large, broad, triangular cusp flanked on each side by a single, tiny, blunt denticle. The lateral tooth (Fig. 6B–C) is

trapezoid in shape, and has a basal plate with a slight median bulge and a long lateral extension that attaches to the basal membrane. The top is slightly concave and has a cutting edge comprising one small, sharp denticle, a large, platelike triangular, sharp cusp and one to two tiny blunt denticles, consecutively from the inner side. The marginal teeth (Fig. 6B–C) are stout, curved and hook-like with sharp tips and a single denticle on the upper, inner side of each tooth. The bases of the marginal teeth are spatulate where they attach to the basal membrane.

Two yellowish, spherical, loosely-compacted salivary glands (Fig. 5A, *sg*) lie anterior to the nerve ring and lateral and dorsal to the origin of the esophagus. The glands lie close against the nerve ring but do not pass through it. Externally, each of these glands appears to be composed of a matrix of fine tubules. No salivary ducts leading to the oral cavity are visible in gross dissections. Sections of the salivary glands stained blue with Harris' hematoxylin reveal numerous fine tubules comprised of dark-staining secretory cells and lighter, more numerous, highly vacuolated mucoid cells. A salivary duct is embedded in the lateral portion of each gland, adjacent to the buccal mass. The exact point of entry of the salivary ducts into the oral cavity was not determined, but is probably in front of the nerve ring.

Anterior and adjacent to the nerve ring and emerging laterally at the base of the salivary glands is a pair of small, darkly-colored, lobate buccal pouches (Fig. 5A, *bp*). They are connected to the buccal cavity and lie dorso-laterally to it. The buccal pouches are composed of muscular tissue and internally each cavity is highly folded and lined with non-ciliated tissue that comprises a large surface area of tightly packed, dark-staining cells filled with many dark granules (Fig. 7F). Beneath this layer of cells is another layer of more loosely packed cells with simple nuclei that stain pink with Eosin Y indicating an abundance of cytoplasm. The histology (Fig. 7F) of the buccal pouches differs markedly from that of the buccal cavity and anterior esophagus.

Cross sections of the anterior esophagus reveal a deep dorsal food channel and two deep, ventrolateral channels which are all highly folded longitudinally and lined with long cilia. Most of the cells lining the remainder of the anterior esophagus are not ciliated but elongate and goblet-shaped.

At the point where the anterior esophagus

becomes the mid-esophagus (Fig. 5A, *me*) the body cavity is divided by a thin transverse septum lying directly behind the nerve ring. This septum is closely associated with the many muscular elements of the posterior buccal mass and walls of the buccal cavity. It was not clear if this septum completely divides the cephalic hemocoel as does the transverse septum of trochaceans. Its function and exact relationship to the cephalic hemocoel remain uncertain. As the anterior esophagus passes through the nerve ring the food channel and grooves become highly folded and the dorsal food channel seems to disappear directly behind the nerve ring at the point of torsion.

The mid-esophagus is a wide, dorso-ventrally flattened tube that, in comparison with the anterior esophagus, has few longitudinal folds or grooves. The ventral portion of the mid-esophagus is smooth while the dorsal and lateral parts have 4–6 shallow depressions (Fig. 7E). The histology of the mid-esophagus is identical to that of the anterior esophagus only there are more ciliated columnar epithelial cells. The mid-esophagus is buried in a large mass of loosely compacted connective tissue (Fig. 5A, *cnt*) which begins immediately behind the nerve ring where it is thickest. It gradually tapers posteriorly and becomes concentrated to the left of the esophagus. Cross sections of the mid-esophagus show that a thin layer of loose connective tissue (Fig. 7E, *cnt*) surrounds the mid-esophagus for its whole length and it is surrounded by a very thin muscular layer (Fig. 7E, *ml*) which, in turn, is enveloped in more loose connective tissue. The esophagus is thus surrounded by a double layer of connective tissue which histological sections show has no connection or relationship to the interior esophagus. The function of this thin muscular membrane and its relationship to the esophagus and surrounding connective tissue is unknown.

The posterior esophagus is oval to round in cross section, and the wall is folded longitudinally. The interior surface is ciliated, and made up of elongate columnar epithelial cells and few mucus cells.

The stomach (Fig. 5B) occupies 1½ coils of the lower visceral mass and differs markedly from those of other cerithiaceans I have examined in several features. It is a complex structure and difficult to interpret, functionally. Although a style sac (Fig. 5B, *ss*) is present at the intestinal end of the stomach, there is no crystalline style. Freshly collected specimens

I dissected had no trace of a style in their stomachs, but a normal fecal rod or protostyle was present and led into the intestine. *Campanile* lacks a cuticular gastric shield that one sees in other cerithiaceans. Instead there is an elongate raised, non-cuticular muscular area (Fig. 5B, *gs*) and a very complex grooved sorting area (Fig. 5B, *gsa*) lying adjacent to the esophageal opening at the middle of the stomach. The largest portion of the raised muscular area is probably homologous to the area supporting the gastric shield.

If the stomach is opened by a dorsal longitudinal cut, the posterior esophagus (Fig. 5B, *eso*) is seen to open into the stomach at its left mid-section through a circular sphincter muscle. Food passing into the stomach is immediately directed to a large sorting area marked by many latitudinal folds (Fig. 5B, *sa*). From here it moves to a deep grooved channel (Fig. 5B, *gsa*) and into a deep pit lined with glandular tissue that is folded into spirally arranged leaflets (Fig. 5B, *s/l*). There are about five major leaflets at the top of the sorting area and many smaller ones leading to the base of the pit. Each leaflet is further folded into longitudinal ridges on each of its sides. The bases of the leaflets are smoother and have fine longitudinal grooves. Ciliary currents move down the longitudinal folds and grooves to the base of each leaflet and thence deeper into the muscular pit of the sorting area. The base of the pit is blind. In the pit of the sorting area are found larger particles and sand grains up to 1.5 mm in diameter.

After sorting, food is probably transferred to the posterior portion of the stomach. This large, white, tapering sac-like area (Fig. 5B, *sc*) lies at the rear of the stomach and is lined with fine transverse folds within which food particles are rotated. The area is probably a vestige of the spiral caecum. Emerging from the caecum is a large flat fold (Fig. 5B, *ff*). At the base of the "gastric shield" is a deep groove leading to the digestive gland (Fig. 5B, *ld*). The muscular walls of the caecal area are thick and internally consist of loose connective tissue interlaced with thousands of fine fibrous muscle strands. Anterior to the large muscular area or gastric shield is a deep ridged groove that leads into the style sac and is bordered at its left by the major typhlosole (Fig. 5B, *t₁*) and on its right by the minor typhlosole (Fig. 5B, *t₂*). The style sac is essentially a smooth area bisected by the major typhlosole and food groove (Fig. 5B, *fg*) leading into the intestine (Fig. 5B, *int*). Tiny, ovoid,

fecal pellets found in the intestine and rectum are held in a fine mucous strand.

Excretory system. The kidney (Fig. 3A–B, *k*) is a large dark brown organ, about 1.5 coils in length. It overlays the end of the mantle cavity and covers part of the albumen gland and much of the pericardium. As it nears the stomach it tapers rapidly and is less thick. The under surface of the kidney is covered by the thin mantle through which may be seen the renal lamellae (Fig. 4B, *rl*). The kidney opening (Fig. 4B, *ko*) is a small slit located at the anterior end near the pericardium and faces the mantle cavity. Another small opening, the renopericardial duct (Fig. 4B, *rpd*), leads from the kidney into the pericardial sac. The part of the kidney bordering the pericardium is lighter in color and looks like a nephridial gland, but sections of this part of the kidney do not show any cellular differences.

An area of distinctive tissue lies adjacent to the rear of the main part of the kidney and extends over the anterior portion of the stomach. It is of a different structure and texture from the kidney and is deeply embedded around the style sac of the stomach. The internal structure is a tubular matrix of fine tiny sacs that are filled with yellowish concretions that are probably waste.

Nervous system. Bouvier (1887b: 149) has described this in great detail and presented accurate figures of it (Bouvier, 1887b: pl. 8, fig. 33). His drawings are difficult to interpret at first glance because he shows the nerve ring with the cerebral commissure cut and the cerebral ganglia reflected back to expose the pleural and subesophageal ganglia.

The cerebral ganglia (Fig. 5A, *lcg*, *rcg*) are above the esophagus posterior to the buccal mass. They are large, elongate and joined by a long cerebral commissure. Four primary nerves emerge anteriorly from each cerebral ganglion and three others run into the walls of the buccal cavity. These innervate the lips, tentacles and eyes and the fourth is the connective to the buccal ganglion (Fig. 5A, *bg*). Each of the pleural ganglia (Fig. 5A, *lpg*, *rpg*) are joined to the cerebral ganglia by very distinct, different connectives. The right pleural ganglion (Fig. 5A, *rpg*) lies close to the right cerebral ganglion and is joined to it by a short, thick connective. The left pleural ganglion differs in lying farther away from the left cerebral ganglion and is joined to it by a long slender connective. A large left pallial nerve (Fig. 5A, *lpn*) emerges from the left pleural ganglion

and runs into the body wall. A long supraesophageal connective (Fig. 5A, *sec*) emerges from the right pleural ganglion, passes over the esophagus and runs into the left body wall where it enlarges to form the supraesophageal ganglion (Fig. 5A, *seg*). This is connected to the left pallial nerve by a moderately long dialyneury. The two pedal ganglia are joined to the cerebral and pleural ganglia by long slender connectives. The pedal commissure is slender and of moderate length. Although I did not see any statocysts, Bouvier (1887b: 149) described them as lying at the posterior base of the pedal ganglia and noted that each statocyst contained numerous statoliths.

At the base of the left pleural ganglion lies the subesophageal ganglion. The connection between these two ganglia is very short and thick and it is difficult to separate the two. The subesophageal ganglion is joined to the right pleural ganglion by a thick zygoneury. There is a long visceral nerve that runs to the visceral ganglia and a typical visceral loop is present.

In summary, the cerebral, pedal and left cerebral-pleural connectives are long, slender and contribute to a "loose" state of the nerve ring. In contrast, condensation of the nerve ring is achieved by the close connection between the left pleural and the subesophageal ganglia, the short, thick connective between the right cerebral and pleural ganglia, and the dialyneury between the pleuro-supraesophageal ganglion and left pallial nerve.

Reproductive system. Males and females have open pallial gonoducts and males are aphyallic. The pallial gonoducts of both sexes are relatively simple and their open condition is best visualized as a slit tube running the length of the mantle cavity, forming dorsal and ventral lobes with the slit facing the mantle cavity. Each lobe comprises an inner and outer lamina (Fig. 3C, *il*, *ol*; Fig. 4C, *il*, *ol*) fused together along their axes to the mantle wall. The inner lamina is also fused on its right side to the mantle while the outer lamina is mostly free except for its fused axis. Both laminae are lined internally with numerous transverse glandular folds.

Campanile may be a protandric hermaphrodite because both sexes have a seminal receptacle. This is discussed in more detail later in this paper.

The female pallial duct is larger and more glandular than that of the male. At its proximal left end is an opening that leads to a sac-like

seminal receptacle (Fig. 4B, *sr*) which is unusually placed in that it bulges into the pericardial sac (Fig. 4B, *ps*) although it is histologically distinct from it. The seminal receptacle (Fig. 4A-C, *sr*) is usually a single compact sac but may have several lobes. The interior is a branching series of villous tubes converging at the base of the receptacle (Fig. 7B) to form a single duct that opens to the distal pallial oviduct near the beginning of the albumen gland (Fig. 7C, *osr*). Sections of the seminal receptacle show that the columnar epithelium (Fig. 7B) is ciliated. Sperm are stored in the tubes (Fig. 7A) with the heads (Fig. 7D, *H*) oriented in the walls (Fig. 7D, *RW*) and their flagella (Fig. 7D, *FL*) projecting into the lumen of the tubes. Some tubes did not contain sperm and are more villous than others, as may be seen in a cross section of the receptacle (Fig. 7A, top portion; C, *ctb*). These may function as a bursa.

The pallial oviduct (Fig. 4C) has no sperm collecting gutter, no bursa or spermatophore receptacle and no tubes in the walls of the laminae. The inner surface of each lamina is thrown into transverse folds along its entire length. These folds become yellow, thin, broadly laminate at the proximal end of the oviduct and constitute the albumen gland (Fig. 4A, C, *ag*). Bouvier (1887b: 147), unaware that this was part of the pallial gonoduct, remarked that this area resembled gill leaflets. These leaflets secrete copious amounts of albumen when stimulated. Sections of the albumen gland show large cells with little nuclear material and large vacuoles. The mid (Fig. 4A, *gil*) and distal parts of the pallial gonoduct differ from the albumen gland in having a thick outer lamina of white glandular tissue and probably give rise to the gelatinous portion of the spawn mass. The base of the open oviduct (Fig. 4A, C, *odg*) is lined with fine transverse folds and is densely ciliated. The entire wall of the outer lamina has a median longitudinal furrow (Fig. 4C, *dol*), where the thickness of the wall is reduced so that the free half can be folded over the inner lamina like a baffle to form a physiologically closed tube as in other prosobranchs with an open duct (Fig. 3C, 4C, *b*). The inner lamina is fused on its right side to the body wall and appears comprised of thick, irregular glandular folds on its inner functional surface (Fig. 4A, *gil*).

The male pallial gonoduct is a thinner, more simple open duct and is highly glandular only at its proximal end where it probably functions

as a prostate. The inner lamina is fused on its left side to the body wall as in the female. An opening to a small seminal receptacle occurs in the proximal left end of the pallial gonoduct and leads to a sac-like receptacle that lies within the pericardial sac. It appears to be morphologically identical to the female seminal receptacle. Remains of what appeared to be a disintegrating spermatophore were found in the female oviducal groove; thus, the male pallial gonoduct may also secrete spermatophores, but this needs confirmation. Sections through the testis show typical seminiferous tubules filled with various stages of developing spermatozoans. Sperm extracted from the vas efferens were all eupyrene but my specimens were taken in early winter; thus, spermic dimorphism should be looked for more closely in spring during the height of the reproductive season when animals are seen pairing.

REPRODUCTIVE BIOLOGY

The head-foot region of sexually mature snails becomes pink when they are ripe. This is especially marked in females whose ovaries and eggs are also the same color. The significance of this color in the head-foot is unknown. Pairing was not observed but deposition of spawn begins in September and lasts throughout November (Dr. Robert Black, personal communication). Spawn masses are attached to marine angiosperm grass blades, macroalgae, rocks or other objects on the substratum and are frequently cast up on the beach. Spawn masses seem to be neutrally buoyant.

Eggs are deposited in large jelly-like, crescent-shaped spawn masses (Fig. 8A–B), and closely resemble the spawn of opisthobranchs. An average spawn mass is 175 mm in length, 21 mm wide and 5 mm thick, and contains about 4,000 pink eggs (Table 2). A spawn mass is transparent, free of debris on its surface and viscous throughout. The attachment surface is opaque (Fig. 8A, as) and is located at the base of the mass, usually at one end. The outer covering is very thin, parchment-like and has tiny longitudinal striations. Within the jelly mass the egg capsules, joined by chalazae, appear as a continuous spirally coiled strand (Fig. 8B). There is an average of three eggs per capsule (range 1–5), each about 0.5 mm in diameter. It was not determined if any of the eggs functioned as nurse eggs.

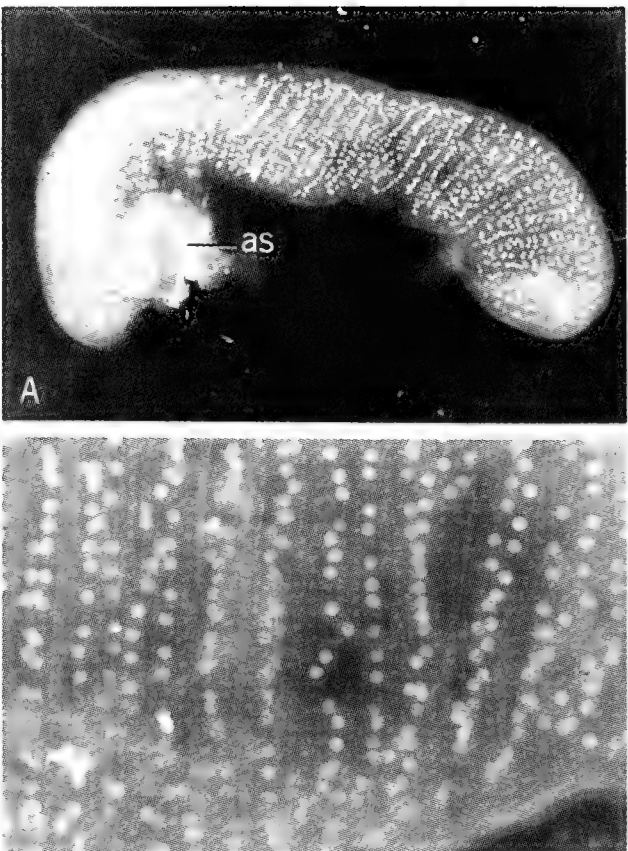


FIG. 8. Spawn of *Campanile symbolicum*. A, Individual spawn mass showing attachment surface (as), 117 mm long; B, Detail of jelly strands and eggs composing spawn mass.

TABLE 2. Statistical summary of spawn measurements of *Campanile symbolicum* (in mm).

Statistic n = 5	Mean	Range	SD
Length	120.2	78–240	66.77
Width	22.4	18–75	2.96
Thickness	4.7	3.8–6.5	1.13
Number of Embryos	4025	3000–6624	1484.2

Embryonic stages ranging from early cleavage to advanced veligers are present within a single spawn mass. Advanced veliger stages have black eyes, small velar lobes, and the embryonic shells (Fig. 2a–c) are smooth, comprise 1½ whorls and lack a sinusigera notch, so typical of mainly planktonic larval shells. A free veliger is unknown, but the advanced state of the late veliger stages and the embryonic shell suggest direct or a short demersal development. Growth of newly hatched snails is rapid (Robert Black, personal communication), but nothing is known of the age of adult snails.

ECOLOGY

Campanile symbolicum normally occurs subtidally in large populations on sandy patches between rocks on limestone reefs. The substratum may have seagrass, macroalgae or may be predominantly sandy. The species is sometimes found in the intertidal zone but the bulk of the population is subtidal. At Pt. Peron, Western Australia, I observed a large population at a depth of 3 m. Animals lie on the sand, sometimes slightly buried, or adjacent to rocky shelves where they are frequently found jammed together. They appear to be inactive during the day with only a few traces in the sand to indicate movement. The species is probably nocturnal because ani-

mals kept in an aquarium were active mostly at night. *Campanile* shells have numerous *Hipponix conicus* (Schumacher) attached to their last two whorls. These are usually on the base of the body whorl adjacent to the siphon or on the outer lip.

The outer lip of adult *Campanile* shells is thin and frequently broken. Crustacean predators can peel back the lip only a short way because it becomes very thick on the penultimate whorl and resists breakage. Moreover, the animals can retract deeply into their shells and thus appear to be safe from predators. No drilled shells were seen.

Fossil records.—*Campanile symbolicum* occurs as a fossil in the Pliocene (George Kendrick, personal communication) and in the

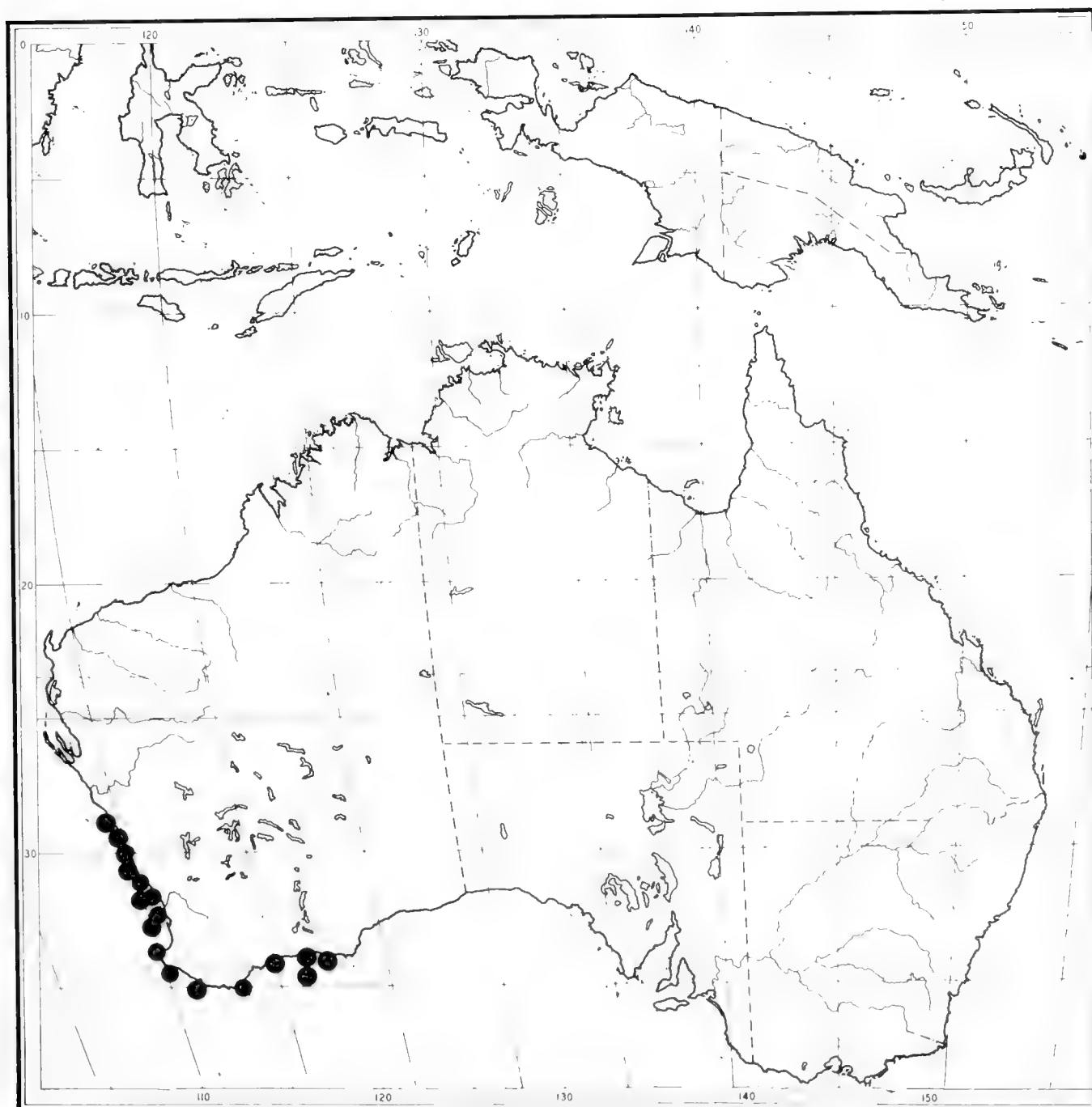


FIG. 9. Geographic distribution of *Campanile symbolicum*.

early Pleistocene (Ludbrook, 1971) of the Eucla Basin of South Australia, although most workers now consider the Eucla Basin to be late Pliocene (Ponder, personal communication). The Pliocene fossil, *Telescopium gigas* Martin, 1881 from Java is very similar to *Campanile symbolicum* and is either conspecific with it or a close relative.

Geographic distribution.—Confined to southwestern Australia.

SYSTEMATICS

Superfamily Cerithiacea Fleming

Family Campanilidae Douvillé, 1904

Diagnosis.—Shell large with chalky surface, elongate, turreted, with straight-sided or slightly convex whorls and moderately incised suture. Body whorl wide and truncate. Growth lines sinuous. Sculpture of suture cords and nodes frequently absent or weak. Aperture narrow and fusiform, anterior canal of moderate length, columella smooth or plaited, periostracum chalky. Operculum ovate, corneous, paucispiral and with eccentric nucleus. Radula taenioglossate, sexes separate, males aphyallic, pallial gonoducts open.

Remarks.—Shell characters, the radula, operculum and open pallial gonoducts of both sexes point to the superfamily Cerithiacea as a proper assignment for this group.

The family Campanilidae was proposed by Douvillé (1904: 311) who later, without explanation, transferred the genus *Campanile* back to the family Cerithiidae Fleming (Douvillé, 1928: 9) and finally regarded it as a subgenus of *Cerithium* Bruguière (Douvillé & O'Gorman, 1929: 362). Most subsequent accounts have ignored the family name and have generally placed *Campanile* in the Cerithiidae. Thiele (1931: 215), Wenz (1940: 771) and Franc (1968: 281) recognized the group as a subfamily, Campanilinae, in the Cerithiidae. Anatomically, *Campanile symbolicum* cannot be referred to the family Cerithiidae and does not fit the limits of any other cerithiacean family. I believe familial status is justified for this group on the basis of a coherent lineage seen in an extensive fossil record, a unique shell structure and physiognomy, and the distinctive anatomical characters described in detail in this paper.

Genus *Campanile* Fischer, 1884

Type-species: *Cerithium giganteum* Lamarck, 1804 [Eocene] (by subsequent designation, Sacco, 1895: 37).

Synonymy

Campanile "Bayle" in Fischer, 1884: 680; Sacco, 1895: 37; Douvillé, 1904: 311; Cossmann, 1906: 71; 1908: 19–27; Boussac, 1912: 19; Iredale, 1917: 325 (in part); Delpey, 1941: 3–5; Cox, 1930: 148–150; Wenz, 1940: 771; Andrusov, 1953: 452; Franc, 1968: 282.

Ceratoptilus Bouvier, 1887a: 36 (type-species, by monotypy, *Cerithium leve* Quoy & Gaimard, 1834); 1887b: 146, pl. 8, fig. 33; pl. 9, fig. 38 (in part).

Campanilopa Iredale, 1917: 325–326 (replacement name for *Campanile*, to be applied to fossil species only) (in part); Delpey, 1941: 20.

Diagnosis.—Shell large, turreted, elongate and with straight-sided whorls or slightly convex whorls and moderately incised suture. Body whorl sharply truncate. Shell with chalky, cancellate outer periostracum that forms a microscopic, pitted surface. Growth lines sinuous. Aperture narrow, fusiform, and at a 45° angle to shell axis. Anterior siphonal canal moderately long, twisted slightly to left. Outer lip thin, smooth and sinuous with an anal notch. Base of outer lip extends over anterior siphonal canal. Columella smooth, concave. Shell sculpture of early whorls comprised of spiral cords and spiral rows of nodules; later whorls usually smooth. Protoconch smooth, 2½ whorls. Operculum ovate, corneous, paucispiral with eccentric nucleus. Radula taenioglossate (2+1+1+1+2). Sexes separate, males aphyallic, pallial gonoducts open, albumen gland large, seminal receptacle projected into pericardium. Spawn comprised of jelly-like strings with large eggs. Ctenidium monopectinate, osphradium short, bipectinate. Pair of salivary glands in front of nerve ring. Stomach complex, without style. Nervous system zygoneurous. Commissures of nerve ring long.

Remarks.—The type-species of this taxon has been the subject of debate. *Campanile* was originally proposed to accommodate a mixed group of large cerithiid-like snails. The name *Campanile* was proposed as a sub-

genus of *Cerithium* by Fischer (1884: 680), who credited the name to Bayle. Fischer's diagnosis was based mainly on conchological characters derived from both the fossil species and from the Recent one, because the operculum is mentioned. Although this diagnosis mentioned the living species first (cited as *Cerithium laeve*) and then cited *Cerithium giganteum* Lamarck, 1804 as a fossil example, a type-species was not designated.

Douvillé (1904: 311) regarded the genus *Campanile* as sufficiently distinct from other cerithiaceans to comprise a separate family and cited *Cerithium laeve* Quoy & Gaimard (= *Campanile symbolicum* Iredale) as representative of the family.

Cossmann (1906: 72), who considered *Campanile* to be a subgenus of *Cerithium* Bruguière, apparently unaware of Sacco's (1895) prior designation of a type-species, selected *Cerithium giganteum* Lamarck. Cox (1930: 148) cited Cossmann's (1906) designation and most other authors have erroneously attributed the selection of the type-species to Cossmann.

Most of the large Tethyan species are characterized by shells with columellar plaits that extend along the entire axis of the shell and have a more nodulose sculpture. In contrast, the living species and a Pliocene fossil, *Cerithium gigas* (Martin, 1881), lack these characters. Cossmann (1906), noting this difference as well as other sculptural and apertural ones, doubted that the living species and its Pliocene fossil homologue from Java should be included together in the same group. He pointed out that there were no fossil representatives of *Campanile* known from the Miocene, implying a broken lineage. He did not, however, propose a new generic name for the group without plaits.

The living species, *Campanile symbolicum* was subsequently referred to the genus *Telescopium* Schumacher by Sowerby (1865; cited as *Cerithium laeve*), who noted that there were essential differences between it and the fossil, *Cerithium giganteum* Lamarck (cited as *Cerithium gigas*, probably in error for *giganteum* because the name *gigas* was proposed in 1881 for a different fossil species).

The soft parts of *Campanile symbolicum* were described by Bouvier (1887a: 36; cited as *Cerithium laeve* Quoy & Gaimard), who realized that this species is anatomically very different from animals in the genera *Cerithium* and *Telescopium*; consequently he proposed

the genus *Ceratoptilus* to accommodate it. Bouvier (1887a, b) was obviously unaware that the name *Campanile* Fischer, 1884, was available. He included the Tertiary fossils in his new genus.

Iredale (1917: 325), also unaware of Sacco's (1895) designation of *Cerithium giganteum* Lamarck as the type-species of *Campanile*, did not accept Cossmann's (1906) designation of this taxon as type-species. Iredale (1917) believed that the name *Campanile* should be restricted to the living species because the original diagnosis of Fischer (1884) employed opercular characters. He stated that *Cerithium giganteum* Lamarck could not be regarded as congeneric because it was, in his opinion, much more like *Terebralia* Swainson, 1840 "in every essential shell character." Iredale (1917) thus excluded the fossil species from *Campanile* and proposed the genus *Campanilopa* for them. It should be noted that Iredale's opinion regarding the type-species is incorrect: had Sacco (1895) not already designated a type-species, Cossmann's (1906) designation of *Cerithium giganteum* Lamarck would be correct, Iredale's (1917: 325; 1949: 20) opinions notwithstanding. The name *Campanilopa* Iredale, 1917, which Iredale applied to the large Tethyan fossils, thus becomes a junior synonym of *Campanile*. *Campanilopa* was regarded as a subgenus of *Campanile* by Delpy (1941: 21) for those fossil species that have columellar plaits. Iredale (1917) was unaware that some of the Tertiary species had smooth columellas and were very much like the Recent *Campanile symbolicum*.

Boussac (1912: 22–23), noting Cossmann's (1906) suggestion that *Cerithium laeve* was probably essentially different from the large fossil *Campanile* species, carefully examined the shells of both groups. He found no essential differences between the Recent species and the fossils and concluded that they were congeneric and should both be assigned to *Campanile*. He did not consider *Campanile* to constitute a family.

Wrigley (1940: 111) concurred with Boussac (1912) and regarded the English Eocene fossil *Campanile* species to be congeneric with the Recent species, *Campanile symbolicum*, from Australia. He was convinced that the sculptural differences did not warrant a generic separation.

Iredale (1949: 20), in a short note, disagreed with Wrigley (1940) and stated that

examination of a series of specimens from Australia convinced him that the Recent species had "nothing whatever to do with the British Eocene fossils." He suggested that the fossils were probably distantly related to the genus *Terebralia* Swainson, 1840.

Delpey (1941) wrote the most comprehensive paper on *Campanile* and presented a thorough history of the nomenclature, tracing the fossil lineage of the group. She delineated the generic characters of *Campanile* and showed that there is considerable interspecific variation in the presence, placement and number of columellar and parietal plaits as well as in shell sculpture. Delpey (1941: 20–21) recognized three subgenera within *Campanile*: *Diozoptyxis* Cossmann, 1896, *Campanilopa* Iredale, 1917 and *Campanile* Fischer, 1884, s.s. She noted that *Campanile gomphoceras* Bayan, 1870, of the Eocene, lacked a columellar plait and closely resembled *Campanile gigas* (Martin) of the Pliocene of Java which she considered to be the direct ancestor of the Recent *Campanile symbolicum*. Delpey (1941) suggested that the genus migrated from the Tethys Sea to Australia and that *Campanile symbolicum* (cited as *Cerithium laeve*) was the modern survivor of a long lineage within the family Campanilidae. She considered the earliest representatives of the group to have arisen from the Nerineidae, a fossil group characterized by elaborate parietal, palatal and columellar folds, and noted the resemblance of some species in the subgenus *Diozoptyxis* to the nerineids. *Diozoptyxis* is not regarded as a nerineid (Sohl, personal communication). Although I do not agree with her about relationships with the nerineids (see Discussion, this paper), her arguments regarding *Campanile* phylogeny appear to be both comprehensive and reasonable. While I do not consider it within my expertise to comment on these speculative relationships, I concur with her conservative classification of the family Campanilidae. In this paper I will deal only with *Campanile symbolicum*, and exclude taxonomic treatment of the fossil species and supraspecific taxa. The question of the generic allocations of the numerous fossil species in relation to the Recent one are beyond the scope of this paper.

Campanile symbolicum Iredale
(Figs. 1–9)

Cerithium leve Quoy & Gaimard, 1834: 106–108; 1833, Atlas, pl. 54, figs. 1–3, non-

binomial (holotype: MNHNP, not registered; type-locality: Port of King George, Australia (= King George Sound, Western Australia) [non *C. laevis* Perry, 1810].

Cerithium truncatum Gray [in] Griffith & Pidgeon, 1834: pl. 13, fig. 1 (error, corrected in Index to *C. laeve* Gray; see Iredale, 1917: 326).

Cerith. leve Quoy [sic], Kiener, 1841: 14–15, pl. 17, fig. 4.

Cerithium laeve Quoy [sic] Deshayes, 1843: 306–307; Sowerby, 1855: 855, pl. 85, fig. 270; Tryon, 1887: 149, pl. 29, fig. 71; Cossmann, 1906: 72–73; Thiele, 1931: 215.

Telescopium laeve (Quoy & Gaimard). Reeve, 1865: pl. 1, figs. 2a, b.

Cerithium (Pyrazus) laeve Quoy [sic]. Kobelt, 1898: 46–47, pl. 10, fig. 1.

Campanile symbolicum Iredale, 1917: 326 (new name); Iredale, 1949: 20; Allan, 1950: 88, pl. 17, fig. 24; Wilson & Gillett, 1971: 32, pl. 12, fig. 1; 1979: 58, pl. 10, fig. 1.

Ceratoptilus laevis (Quoy & Gaimard). Bouvier, 1887a: 37–38; 1887b: 146, pl. 8, fig. 33, pl. 9, fig. 38.

Remarks.—The original species name proposed by Quoy & Gaimard (1834) was spelled "leve" but most subsequent authors have used "laeve." This name is preoccupied by *Cerithium laevis* Perry, 1810, which although slightly different in spelling, does not vary enough to constitute a significant difference (see Code, Article 58), Quoy & Gaimard's name thus becomes a junior primary homonym. In the original description, Quoy & Gaimard (1834: 108) remarked that several hundred individuals were collected in shallow water and that their shells were somewhat similar to those of *Telescopium*, but were longer and had sharper spires. They described the external anatomy of the animals and briefly discussed the internal organs of the mantle cavity. Some notes on the habitat and sexual state of the specimens were presented and the shell, animal and operculum are accurately depicted on pl. 54, figs. 1–3, of the Atlas (Quoy & Gaimard, 1833). Although the Atlas appeared a year earlier than the description, no Latin name was given; consequently the Atlas is non-bionomial.

Iredale (1917: 326) noted that the name *Cerithium leve* was preoccupied and proposed a new name *Campanile symbolicum*, to replace it. Iredale (1917: 326) also pointed out that the name *Cerithium truncatum* Gray, 1834, was an error. Griffith & Pidgeon (1834)

figured the shell under the name *truncatum*, but this was a careless slip and was corrected in the index of the same work.

DISCUSSION

Campanile symbolicum is a relict species representing the end of a long lineage of large mesogastropods in the family Campanilidae. The anatomical evidence derived from the living species places this group within the superfamily Cerithiacea. I agree with Delpy (1941) that this large family probably comprised several genera that underwent a widespread adaptive radiation in the Tertiary. The family is well represented by many fossil species that were abundant in the Tethys Sea and is represented in New World deposits by the endemic genus *Dirocerithium* Woodring & Stenzel, 1959. Woodring (1959) pointed out the Tethyan affinities and also noted the close resemblance of *Campanile gomphoceras* Bayan, 1870, of the European Eocene, to *Dirocerithium*. He also regarded *Bellatara* Strand to be closely related to this lineage. In the Old World the family comprised numerous species in the genera *Diozoptyx* Cossmann, 1896, *Campanilopa* Iredale, 1917 and *Campanile* Fischer, 1884. It is apparent that the entire fossil assemblage is in need of further revision and study before the composition and lineages within the family can be understood, a task beyond the scope of this paper.

I do not believe that sculptural differences such as placement and number of columellar plaits, between the living species and the fossil taxa warrant a separation of the Recent species from the fossil groups. While the living species may not be congeneric with some of the fossils, it is surely in the same family. It is apparent that the family comprises several supra-specific categories that differ from the living species and future taxonomic studies of the family may show the need for a new genus to accommodate the Recent form. In this paper I prefer to be conservative and refer the living species to the genus *Campanile*.

The shell of the living species does not differ substantially from that of the fossils (see Delpy, 1941) and present understanding of plate tectonics provides sufficient explanation for the linkage between the Tethyan fossils and the living species in southwest Australia without having to invoke any farfetched migration theories.

The pitted surface of Eocene *Campanile*

fossils noted by Wrigley (1940: 111) resembles the pattern seen on the thick, calcified periostracum or "intritacalx" of the living species. I suggest that the pits on the fossils are periostracal in origin and that this is probably a family character.

Delpy (1941) noted that some of the fossil campanilids with elaborate parietal, palatal and columellar folds closely resembled members of the Nerineidae and suggested that the Campanilidae arose from the nerineid lineage. This is most unlikely because nerineids have heterostrophic protoconchs and deep anal sulci and are considered to be in the subclass Euthyneura (Taylor & Sohl, 1962: 11, 16–17). Thus, any resemblance between these two groups is due to convergence and does not imply relationship.

Both the living species and the fossil taxa have been referred to genera within the family Potamididae Fleming by Sowerby (1865) and Iredale (1917: 1949) but I do not concur. The ecology and anatomy of *Campanile* differ substantially from those of the amphibious potamidids which have multispiral, circular opercula, differently arranged open pallial gonoducts, thin, ridge-like osphradia and long snouts with radulae that frequently bear basal cusps.

The elongate, multi-whorled shell, the apertural physiognomy, corneous operculum, taenioglossate radula, aphyllous males and open pallial gonoducts in both sexes are conservative characters found in nearly all cerithiaceans; however, the combined anatomical features of sensory, reproductive, alimentary and nervous systems of *Campanile* are, as far as is known, unique among the Cerithiacea and support its allocation to a separate family, the Campanilidae. A discussion of these unique anatomical features and speculation about the phylogenetic relationship of *Campanile* to other higher cerithiacean taxa follows.

The external anatomy of *Campanile* differs from that of other cerithiaceans in several features: *Campanile* has a deep ciliated pedal gland around the edge of the entire sole of the foot (Fig. 4B, cf) whereas in cerithiids and some potamidids there is only a propodial furrow. In a few potamidids there is a centrally placed pedal gland. The entire mantle edge of *Campanile* has papillae on it, although these are reduced ventrally (Fig. 3A–B, mp), while in the cerithiids the ventral part of the mantle edge is always smooth. In vermetids and pleurocerids, the entire mantle edge is smooth and in the turritellids completely

papillate; while in the thiarids the condition is mixed, depending upon the genus or species. The short, thick snout of *Campanile*, noted by Bouvier (1887b), differs from that of most other cerithiids which have longer and more extensible snouts.

The columellar muscle of *Campanile* is unusual among cerithiaceans in that it is unusually long and forms a long prominence at its proximal end (Fig. 3A–B, *cm*). This may enable the animal to withdraw more deeply into its shell. A similar columellar muscle has been depicted by Morton (1965) and Hughes (1978) for the members of vermetid genera *Vermetus*, *Serpulorbis*, *Dendropoma* and *Petalconchus*, all capable of deep withdrawal into their shells.

The short, oval, bipectinate osphradium (Fig. 4A, *os*) differs from those of all other known cerithiaceans and most mesogastropods where the osphradium is normally a long slender structure that traverses the length of the mantle cavity adjacent to the ctenidium. Other mesogastropods with a short bipectinate osphradium include members of the Cypraeaacea, Calyptraeidae, and the genera *Velutina* and *Balcis*. In *Campanile*, the osphradium is unusual in that it is placed anteriorly in the mantle cavity, and both its placement and anatomy are identical to those seen in most neogastropods.

The extension of the hypobranchial gland and its modification by folding into tiny leaflets adjacent to the anus (Fig. 4A, *lhg*) are anatomical features unrecorded for other cerithiaceans. The presence of numerous elongate goblet cells in this tissue testifies to its secretory ability. It may produce additional mucus to bind fecal pellets as they pass out the exhalant siphon and down the ciliated groove on the right side of the foot.

The pallial oviduct of *Campanile* is simple in comparison to those of the cerithiids, modiolids, turritellids and vermetids in that the laminae comprising it lack the internal tubes and bursae associated with spermatophore retention and sperm transfer. Instead, the pallial oviduct is a simple slit tube (Fig. 4C), but one in which the transverse interior folds of the distal end of the laminae are elaborated into rounded filaments forming a large albumen gland (Fig. 4A, *ag*) unlike anything seen so far in other cerithiaceans. As seen earlier, the spawn mass produced by the animal is quite large and gelatinous (Fig. 8A–B) and it is possible that this gland and the mid-glandular part of the oviduct contribute to its formation.

One of the more unusual features of *Campanile* reproductive anatomy is the presence of a sac-like seminal receptacle that bulges into the pericardial sac (Fig. 4A–B, *sr*, *ps*). I know of nothing else like this in any cerithiacean, although several rissoacean species store sperm in the pericardium (Ponder, personal communication). The arrangement is rare among prosobranchs. There is convincing anatomical evidence to suggest that *Campanile* is a protandric hermaphrodite. A seminal receptacle is present at the proximal left side of the pallial gonoduct in both sexes but is more fully developed in females where it may consist of several lobes. It appears that larger individuals are females and smaller ones males. Sections of the gonads of larger snails revealed only developing ova while those of smaller animals clearly showed seminiferous tubules filled with varying stages of developing spermatozoans. Although I found no histological evidence of simultaneous hermaphroditism, transitional stages between sexes should be looked for by future workers.

Sections of the seminal receptacle (Fig. 7A, D) show that the branching chambers containing oriented sperm have relatively smooth walls (Fig. 7A, lower chambers; Fig. 7D, C, *sp*), while the empty chambers are villous and ciliated (Fig. 7A, upper chambers; C, *ctb*). The receptacle thus appears to be divided into two kinds of interconnected branching chambers. The empty tubes and chambers may assist in sperm transport, but their exact function remains undetermined.

Another unusual aspect of *Campanile* reproductive biology is the bright pink color of the head-foot in ripe animals, particularly females. I know of no other cerithiacean in which this phenomenon has been recorded and its significance is unknown.

The presence of what appeared to be a disintegrating spermatophore in the pallial oviduct needs reconfirmation; however, most cerithiaceans such as the cerithiids, modiolids and vermetids produce spermatophores. If *Campanile* has only eupyrene sperm, it is unusual because all cerithiaceans heretofore studied show spermic dimorphism.

The spawn of *Campanile* (Fig. 8A–B) are unusual because of their large size, high gelatinous content, the lack of individual hyaline capsules for each egg and the presence of a chalaza connecting the egg capsules. The spawn resemble those of opisthobranchs and polychaetes more than those of

prosobranch spawn. Robertson (1976: 231) pointed out that chalazae are characteristic of opisthobranchs and primitive pulmonates, but among the prosobranchs are known only in the genus *Valvata* and in members of the Architectonicidae, which are not typical of the group. The connections between egg chambers in *Campanile* may not be truly homologous with the chalazae of opisthobranch spawn. The presence of eggs within mucous capsules rather than hyaline capsules is also unusual and the fact that several eggs may be in an individual capsule points to the possibility of nurse eggs. While the high number of eggs per spawn mass and moderate size of individual eggs would seem to indicate indirect development, the developmental mode appears to be direct or demersal. Evidence for non-pelagic development is strong: advanced veliger stages with tiny velar lobes were observed in preserved spawn and the embryonic shell (Fig. 2a-c) is smooth, bulbous, lacks a sinusigera notch and has only one and a half whorls.

All of the above observations raise more questions and it is obvious that more careful work on the developmental biology of *Campanile* is needed.

While most cerithiid jaws are thin and consist of many tiny, flat plates, those of *Campanile* (Fig. 2d-e, h-i) are very thick and structurally complex, as outlined previously. The significance of this difference is unclear, but their structure is undoubtedly related to their ontogeny and needs further detailed study. The typically taenioglossate radula (Fig. 6A-D) is short in comparison to the size of the animal and has fewer rows of teeth than the radulae of other cerithiids which are much smaller animals than *Campanile*. This is peculiar because most snails that graze on coarse substrates, as does *Campanile*, have long radular ribbons. The radula of *Campanile*, however, is wide and robust and cusps of the anterior rows of teeth are only slightly worn.

The thin septum behind the nerve ring that divides the cephalic hemocoel of *Campanile* is more anterior than the transverse septum of trochids which lies where the mid-esophagus joins the posterior esophagus (Fretter, in litt.).

The paired salivary glands and their ducts lie anterior to the nerve ring (Fig. 5A), as in the cerithiids, modulids (Houbrick, 1980), vermetids (Morton, 1951: 29) and in nearly all rissoids (Davis et al., 1976: 276; Ponder, personal communication). This is further documentation that the location of salivary

glands and their ducts is a variable feature among the mesogastropods.

The presence of paired buccal pouches (Fig. 5A, bp) in *Campanile* is noteworthy, because they are unknown among other cerithiaceans. I previously thought that the salivary glands of *Cerithium* were buccal pouches and stated that their ducts passed through the nerve ring, but this was erroneous (Houbrick, 1974: 43). Although found in littorinids, it appears that the cerithiids, modulids, vermetids and turritellids all lack buccal pouches. It is interesting to note that buccal pouches and anterior salivary glands are required for neogastropod ancestors.

The mid-esophagus loses all traces of the dorsal and ventral food channels but is unusual in having shallow lateral folds (Fig. 7E). *Campanile* differs from anatomically known cerithiids and modulids in lacking an esophageal gland, but the vermetids and turritellids known also lack this gland. Although it is not uncommon for gastropods to have loose connective tissue surrounding the esophagus, the mass of loose connective tissue that surrounds the mid-esophagus of *Campanile* (Fig. 7E, cnt) is unusually large and noteworthy. Although this tissue superficially looks like an esophageal gland, sections show that it has no glandular elements or connections with the esophagus. A further distinction of this region is the thin muscular sheet in the middle of the connective tissue surrounding the mid-esophagus (Fig. 7E, ml). The function of this loose connective tissue and its thin muscular sheet was not determined.

The stomach of *Campanile* has a well-developed style sac (Fig. 5B, ss), but a cuticular gastric shield is lacking, and I was unable to find any trace of a style, even in freshly collected animals. It is possible that a style is present only at certain times, as in some bivalves. One of the most unusual features of the stomach is the series of leaflets spirally arranged in a deep pit located in the sorting area (Fig. 5B, sl). Although I have seen a similar structure in the stomach of *Gourmya gourmyi* (Crosse), which is a cerithiid snail, I know of no structure like this in any other prosobranchs with the exception of the volute *Alcithoe*, for which Ponder (1970: 19) described similar gastric leaflets. In *Alcithoe*, they are arranged in parallel rows rather than in a spiral pit, but the structure and ciliary currents of each leaflet are the same. Ponder noted that they are an efficient sorting device in a relatively uncomplicated stomach; this is

in direct contrast to the complex stomach of *Campanile*. The pit and leaflets probably deal with the larger particles and this is a modification from other cerithiaceans. The posterior of the stomach, which I interpret as the vestige of a spiral caecum, is another distinctive structure (Fig. 5B, sc). Reduced spiral caeca have been recorded in other mesogastropods, such as some turritellids, cerithiids and calyptraeids, by Fretter & Graham (1962: 224) but in *Campanile* this structure is much larger and more conspicuous.

A mixture of loose and condensed neural elements including dialyneury and zygoneury exists in *Campanile*. It is difficult to assess the significance of this arrangement of the nervous system because not enough is known of other cerithiacean nervous systems to make meaningful comparisons with *Campanile*.

As seen in the foregoing discussion, *Campanile* falls well within the cerithiacean anatomical groundplan but the relationship of the Campanilidae to other cerithiacean families is more difficult to assess. It appears to be closest to the Potamididae and Cerithiidae in general physiognomy and ecology, but is probably related to them only distantly. There are several anatomical features of *Campanile* that are reminiscent of neogastropods. Among these are the short, distally located bipectinate osphradium, anterior position of salivary glands and ducts relative to the nerve ring, and the complex spirally arranged leaflets in the sorting area of the stomach although the latter are not typical of neogastropods. The presence of a calcified periostracum or intritacalx is known in some rissoids and epitoniids but is not common in mesogastropods. Although I do not believe that these features indicate a relationship between *Campanile* and the neogastropods, they are unusual and set this group apart from other cerithiaceans and most mesogastropods.

The Campanilidae is an old family as are other cerithiacean marine families such as the Cerithiidae, Potamididae, Vermetidae, Turritellidae, Dialidae, Cerithiopsidae, and the Modulidae. All these families were present in the late Cretaceous and appear to have undergone little change in basic shell form since then. The cerithiaceans appear to constitute a large monophyletic assemblage. All share the basic primitive anatomical traits of open pallial gonoducts and aphyllous males and are algal-detrital feeders with taenioglossate radulae and complex stomachs.

Nearly all members of the group have a crystalline style.

In general, each cerithiacean family has radiated into a distinctive spatial, trophic niche. It is obvious that the success of many families is due to basic morphological innovations in shell and soft parts or to physiological modifications that led to new adaptations in feeding and exploitation of new habitats such as the estuarine and fresh-water biotopes. Other modifications have occurred in the reproductive systems (spermatophores, spermatzeugma, dimorphic sperm, complex ducts in open pallial gonoducts, brooding chambers), but the adaptive significance of these modifications is not always clear. A brief summary of the major cerithiacean families and their ecological niches follows.

The Turritellidae, characterized by long coiled shells, is an abundant subtidal group of animals that tend to live on soft substrata where they are detrital-filter feeders (Graham, 1938; Fretter & Graham, 1962). The Vermetidae is an intertidal to subtidal, sessile group of snails with uncoiled shells usually found on hard substrata feeding on detritus by ciliary mechanisms and mucous nets (Morton, 1965; Hadfield, 1970; Hadfield et al., 1971; Hughes, 1978). The Potamididae comprise a large group of intertidal estuarine amphibious snails with turreted shells that are grazers on algae and detritus. They are frequently large animals and are common in tropical mangrove habitats, salt marshes and muddy environments. The Cerithiidae are a large, complex family of intertidal to subtidal snails with turreted shells common in tropical areas. This group is primarily composed of algal-detritus feeders and has radiated into a variety of habitats including coral reefs, rocky beaches, sandy lagoons, mud flats and grass beds (Houbrick, 1974; 1978). The Pleuroceridae, regarded as the freshwater branch of the Cerithiidae, comprises a large family of turreted snails that live in well-oxygenated water in temperate and tropical regions (Morrison, 1954). The Dialidae, Litiopidae, and Diastomidae are little known families, the former comprising small snails common in tropical areas and the latter a largely extinct group of larger snails with turreted shells and with only one living species. The Modulidae is a small family of subtidal snails with trochoid shells that live in grass beds or on coral reefs (Houbrick, 1980). The Planaxidae is a small group of tropical snails that live in the rocky intertidal and brood their

young in special incubation chambers in the head (Ponder, 1979). The Thiaridae, a large family of freshwater snails, tend to be parthenogenetic and ovoviviparous and are thought to be derived from the marine Planaxidae (Morrison, 1954). The Cerithiopsidae are small multispired snails that have an acrembolic proboscis (Fretter, 1951) and feed on sponges. They are no longer considered cerithiaceans (Fretter, 1979).

The major adaptive radiations of cerithiacean marine families occurred at the end of the Cretaceous and it is not at all clear from the fossil record or from our knowledge of anatomy how these groups are related to each other. The Campanilidae stands apart from the other families in some aspects of anatomy and is also noteworthy because of the large size attained by many of its members. Although it is not uncommon for some species of other cerithiacean families such as the Turritellidae, Vermetidae, Potamididae and Cerithiidae, to be large animals, the Campanilidae developed this trait to an extraordinary degree.

These large snails were most common in the early Tertiary when they seem to have reached an evolutionary peak in number of species. Members of the Campanilidae probably played the same ecological role in Tethyan shallow water ecosystems as Recent Strombidae in similar contemporary habitats. They undoubtedly were feeders on epiphytic algae and occupied the same trophic niche as do large snails of the living strombid genera *Strombus*, *Lambis* and *Tibia*.

The Strombidae became established in the late Eocene to early Miocene and flourished during the Pliocene and early Pleistocene (Abbott, 1960: 33). Competition with this trophically similar group of large snails probably led to the diminution in species of the Campanilidae. The living survivor, *Campanile symbolicum*, is now confined to southwest Australia where only one small stromb species occurs, *Strombus mutabilis* Swainson (Abbott, 1960: 74). It is noteworthy that southern Australia harbors several other Tethyan relicts, the monotypic gastropod *Neodistoma melanooides* (Reeve), family Diastomidae, and the bivalve *Neotrigonia*, family Trigoniidae, although the latter lives all around Australia.

The actual reasons for the virtual extinction of the Campanilidae are unknown, but sea level changes and fluctuating temperatures

associated with the closure of the Tethys Sea undoubtedly placed additional stress on this group of remarkably large gastropods.

ACKNOWLEDGMENTS

I am indebted to Dr. Fred Wells of the Western Australian Museum, Perth, for his kind assistance and for the use of laboratory space and a vehicle for field work during my stay there. I also thank Ms. Miriam Rogers for her help in collecting specimens and for processing field material.

For examination of specimens in their charge I thank Dr. George Davis, Academy of Natural Sciences of Philadelphia, Dr. William K. Emerson, American Museum of Natural History, Dr. Brian Smith, National Museum of Victoria, and Dr. Winston Ponder, The Australian Museum, Sydney.

I thank Dr. Robert Black of the University of Western Australia for sending me preserved samples of spawn and for information about spawning.

Histology was done at the Smithsonian Institution's Fort Pierce Laboratory. I thank Dr. Mary Rice for her kind assistance in using this facility, and Mrs. June Jones for typing the original draft of this paper. The scanning electron micrographs were supplied by the Smithsonian Scanning Electron Microscope Lab. All other photography was done by Mr. Victor Krantz of the Smithsonian Photographic Services.

This research was accomplished with the aid of a Smithsonian Research Award.

I thank Dr. Winston Ponder and Dr. Vera Fretter for critically reading the first draft of this paper.

LITERATURE CITED

- ABBOTT, R. T., 1960, The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca*, 1: 33-146.
- ALLAN, J., 1950, *Australian Shells*. Melbourne, 487 p., 44 pl.
- ANDRUSOV, D., 1953, Nové Paleontologické Nálezy V Karpatskom Paleogéne. *Geologický Sborník Slovenskej Akadémie vied*, 4: 431-496, pl. 71-74.
- BAYAN, F., 1870, Sur les terrains tertiaires de la Vénétie. *Bulletin de la Société Géologique de France*, ser. 2, 27: 444-486.
- BOUSSAC, J., 1912, Essai sur l'évolution des Cérithidés dans le Mésonummulitique du Bas-

- sin de Paris. *Annales Hébert. Annales Stratigraphie et de Paléontologie du Laboratoire de Géologie de la Faculté des Sciences de l'Université de Paris*, 6: 1–93, 16 pl.
- BOUVIER, E. L., 1887a, Observations sur le genre *Ceratoptilus* créé dans la famille des Cérithidés. *Bulletin de la Société Philomathique de Paris*, ser. 7, 11: 36–38.
- BOUVIER, E. L., 1887b, Système nerveux, morphologie général et classification des Gastéropodes, prosobranches. *Annales des Sciences naturelles*, ser. 7, 3: 1–510.
- COSSMANN, M., 1896, Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris faisant suite aux travaux Paleontologiques de G. P. Deshayes. *Annales de la Société Royale Malacologique de Belgique*, 31: 1–94, 3 pl.
- COSSMANN, M., 1906, *Essais de Paléoconchologie Comparée*, 7: 248 p. Paris.
- COSSMANN, M., 1908, A propos de *Cerithium cornucopiae* Sow. *Mémoire de la Société Linnéenne de Normandie*, 23: 19–27, pl. 2.
- COX, L. R., 1930, Mollusca of the Hangu Shales. *Palaeontologica Indica*, new ser. 15: 129–121, pl. 17–22.
- DAVIS, G. M., KITIKOON, V. & TEMCHAROEN, P., 1976, Monograph of "*Lithoglyphopsis*" *aperta*, the snail host of Mekong River Schistosomiasis. *Malacologia*, 15: 241–287.
- DELPEY, G., 1941, Histoire du Genre *Campanile*. *Annales de Paléontologie*, 24: 3–25.
- DESHAYES, G. P., 1843, In: LAMARCK, *Histoire Naturelle des Animaux sans Vertèbres . . .*, ed. 2, 9: 728 p.
- DOUVILLE, H., 1904, Mollusques Fossiles, In: MORGAN, J. DE, *Mission Scientifique en Perse*, Vol. 3, *Études Géologiques*, part 4, *Paléontologie*: 191–380, pl. 25–50.
- DOUVILLÉ, H., 1928, Les couches à *Cardita beaumonti*. *Memoirs of the Geological Survey of India. Palaeontologia Indica*. new ser., 10: 1–25, 4 pl.
- DOUVILLÉ, H. & O'GORMAN, 1929, L'Éocène du Bearn. *Bulletin de la Société Géologique de France*, ser. 4, 29: 329–390, pl. 29–32.
- FISCHER, P., 1884, *Manuel de Conchyliologie et de Paléontologie Conchyliologique*. Paris, p. 609–688.
- FRANC, A., 1968, Classe des Gastéropodes (Gastropoda Cuvier, 1798). In: GRASSÉ, P. O. (ed.), *Traité de Zoologie, Anatomie, Systématique Biologie*, Vol. 5, *Mollusques Gastéropodes et Scaphopodes* (Fascicule III), Paris, 1083 p.
- FRETTER, V., 1951, Observation on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 29: 567–586.
- FRETTER, V., 1979, The evolution of some higher taxa in gastropods. In: *Symposium on the Biology and Evolution of Mollusca*, Sydney, Australia (unpublished mimeographed abstract).
- FRETTER, V. & GRAHAM, A., 1962, *British Prosobranch Molluscs, their Functional Anatomy and Ecology*. Ray Society, London, 755 p.
- GRAHAM, A., 1938, On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proceedings of the Zoological Society of London*, 108: 453–463.
- GRAY, J. E. See GRIFFITH & PIDGEON, 1834.
- GRIFFITH, E. & PIDGEON, E., 1834, *The Mollusca and Radiata*. In: CUVIER, *The Animal Kingdom*, 12: 601 p., 20 pl. London.
- HADFIELD, M., 1970, Observations on the anatomy and biology of two California vermetid gastropods. *Veliger*, 12: 301–309.
- HADFIELD, M., KAY, E. A., GILLETTE, M. U. & LLOYD, M. C., 1971, The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology*, 12: 81–98.
- HOUBRICK, R., 1974, The Genus *Cerithium* in the western Atlantic. *Johnsonia*, 5(50): 33–84.
- HOUBRICK, R., 1978, The Family Cerithiidae in the Indo-Pacific. Part 1: The Genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*. *Monographs of Marine Mollusca*, No. 1: 130 p.
- HOUBRICK, R., 1980, Observations on the anatomy and life history of *Modulus modulus* (Prosobranchia: Modulidae). *Malacologia*, 19: 117–142.
- HUGHES, R., 1978, The biology of *Dendropoma corallinaceum* and *Serpulorbis natalensis*, two South African vermetid gastropods. *Zoological Journal of the Linnean Society*, 64: 111–127.
- IREDALE, T., 1917, More molluscan name changes, generic and specific. *Proceedings of the Malacological Society of London*, 12: 322–330.
- IREDALE, T., 1949, Western Australian Mollusks. *Proceedings of the Royal Zoological Society of New South Wales*, 1947–1948, p. 18–20.
- KIENER, L. C., 1841(–1842), *Spécies général et iconographie des coquilles vivantes*. Genre Cérîte. Paris, 5: 104 p., 32 pl.
- KOBELT, W., (1888–)1898, Die Gattung *Cerithium*, 297 p., 47 pl. In: MARTINI, F. H. W. & CHEMNITZ, J. H., *Neues systematisches Conchylien-Cabinet . . .* 1(26). Nurenburg.
- LAMARCK, J., 1804, Suite des mémoires sur les fossiles des environs de Paris. *Annales du Muséum National d'Histoire Naturelle*, 3: 436–441.
- LADBROOK, N., 1971, Large gastropods of the families Diastomatidae and Cerithiidae (Mollusca: Gastropoda) in southern Australia. *Transactions of the Royal Society of South Australia*, 95: 29–42, 6 pl.
- MARTIN, K., 1881, Tertiaer-Versteinerungen von Östlichen Java. *Sammlungen des Geologischen Reichsmuseums in Leiden*, 1: 105–130, pl. 6–8.
- MORRISON, J. P. E., 1954, The relationships of old and new world Melanians. *Proceedings of the United States National Museum*, 103: 357–394.
- MORTON, J. E., 1951, The structure and adaptations of the New Zealand Vermetidae. *Transactions of the Royal Society of New Zealand*, 79: 1–51.
- MORTON, J. E., 1965, Form and function in the

- evolution of the Vermetidae. *Bulletin of the British Museum (Natural History)*, 11: 585–630.
- PERRY, G., 1810(–1811), *Conchology: or the Natural History of Shells . . .* London, 61 pl. + text.
- PONDER, W. F., 1970, The morphology of *Alcithoe arabica* (Gastropoda: Volutidae). *Malacological Review*, 3: 127–165.
- PONDER, W. F., 1979, Cephalic brood pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda). Unpublished abstract in program for *Symposium on the biology and evolution of Mollusca*, Sydney, Australia, May, 1979.
- QUOY, J. R. C. & GAIMARD, J. P., (1833–)1834, *Voyage de decouvert de l'Astrolabe executé par ordre du Roi pendant les années 1826–1827–1828–1829 sous le commandement de M. J. Dumont D'Urville*. *Zoologie*, 3: 1–366 + Atlas (1833), 93 pl.
- RADWIN, G. & D'ATTILIO, A., 1976, *Murex Shells of the World. An Illustrated Guide to the Muricidae*, 284 p., 32 pl., illustrated. Stanford.
- REEVE, L. A., 1865, *Conchologia Iconica: or illustrations of the shells of molluscos animals*. Vol. 15, *Cerithium*, 20 pl. + index. London.
- ROBERTSON, R., 1976, Marine Prosobranch Gastropods: Larval Studies and Systematics. *Thalassia Jugoslavica*, 10(1–2): 213–238.
- SACCO, R., 1895, In: BELLARDI, L., *I Molluschi dei Terreni Terziarii del Piemonte e della Liguria*. Parte XVII (Cerithiidae, Triforidae, Cerithiopsidae e Diastomidae), 83 p., 3 pl.
- SOWERBY, G. B., 1855, *Thesaurus Conchylorum, or monographs of genera of shells*, Vol. 2, *Cerithium*: 847–859, pl. 176–186. London.
- SOWERBY, G. B., 1865, In: REEVE, L. A., *Conchologia Iconica: or illustrations of the shells of molluscos animals*. Vol. 15. London.
- SWAINSON, W., 1840, *A Treatise on Malacology or the Natural History of Shells and Shellfish*, 419 p. London.
- TAYLOR, D. W. & SOHL, N., 1962, An outline of gastropod classification. *Malacologia*, 1: 7–32.
- THIELE, J., 1929, *Handbuch der systematischen Weichtierkunde*. Fischer, Jena. Vol. 1, part 1, 376 p.
- TRYON, G. W., 1887, *Manual of Conchology; structural and systematic; with illustrations of the species*. ser. 1, 9: *Cerithium*, p. 127–149, pl. 20–29. Philadelphia.
- WENZ, W., 1940, Gastropoda, Teil 1, Allgemeiner Teil/Prosobranchia, In: SCHINDEWOLF, O. H., *Handbuch der Paläozoologie*, 6, Lief. 4, p. 721–960. Borntraeger, Berlin.
- WILSON, B. & GILLET, K., 1971, *Australian Shells*, 168 p., 106 pl. Rutland, Vermont.
- WILSON, B. & GILLET, K., 1979, *A Field Guide to Australian Shells. Prosobranch Gastropods*, 287 p., 66 pl. Sydney.
- WOODRING, W. P., 1959, Geology and Paleontology of Canal Zone and Adjoining Parts of Panama. Descriptions of Tertiary Mollusks (Gastropods: Vermetidae to Thaididae). [United States] *Geological Survey Professional Paper* 306-B: iii + 239 p., pl. 24–38.
- WOODRING, W. & STENZEL, W., 1959, In: WOODRING, W. P., 1959 (as above).
- WRIGLEY, A., 1940, The English Eocene Campanile. *Proceedings of the Malacological Society of London*, 24: 97–112.

THE GALAPAGOS RIFT LIMPET *NEOMPHALUS*: RELEVANCE TO
UNDERSTANDING THE EVOLUTION OF A MAJOR
PALEOZOIC-MESOZOIC RADIATION¹

James H. McLean

Los Angeles County Museum of Natural History, Los Angeles, California 90007, U.S.A.

ABSTRACT

Neomphalus fretterae, new species, genus, family, and superfamily, was first collected in 1977 at the vents of thermal springs along the Galapagos deep-sea spreading center at depths of 2,478 to 2,518 m. Shells reach 30 mm in diameter and are cap-shaped with a horizontally lying initial coiled phase. The shell is protected by periostracum and is composed of lamellar aragonite. In form and function *Neomphalus* is convergent with the Calyptraeidae, having a flattened neck and a deep mantle cavity on the left with long gill filaments extending to the food groove on the right. *Neomphalus* is the first known gastropod with a bipectinate gill modified for filter feeding.

As further detailed in the adjoining paper on internal anatomy (Fretter, Graham & McLean, 1981), *Neomphalus* has such archaeogastropod characters as a rhipidoglossate radula, bipectinate ctenidium, epipodial tentacles, and anterior loop of the intestine. Features of the mesogastropod level of organization include loss of the right pallial complex, a monotocardian circulatory system, expanded left kidney, and glandular gonoducts. Unique features are: 1) a dorsal food groove, which leads to the mouth over the right cephalic tentacle rather than under it as in all other filter-feeding gastropods, 2) a mantle cavity not enveloped by the shell muscle on the left side, 3) posteriorly directed cephalic tentacles, 4) reproductive specializations: the male with the left tentacle enlarged to form a copulatory organ, and the female with a separate seminal receptacle.

The first postprotoconch whorl is coiled; growth stoppage in the second postprotoconch whorl on the columellar lip prevents the muscle from enveloping the mantle cavity on the left, but forces lip expansion on the right to produce the limpet shell form.

There are no living relatives, nor has any fossil record of *Neomphalus* been found, yet the ctenidium is so adaptive that a radiation on this theme must have taken place, and the highly specialized *Neomphalus* can only represent one ultimate expression of this basic plan. Paleontologists have recently hypothesized that the extinct Euomphalacea, which underwent a major radiation in the Paleozoic and declined in the Mesozoic, were filter feeders because their discoidal or open coiled shells with radial apertures differ from those of motile gastropods having tangential apertures and the capacity to balance the shell over the cephalopedal mass. The anatomy of *Neomphalus* could function in a coiled shell and would explain the euomphalacean anatomy, the differences between *Neomphalus* and euomphalaceans being about equivalent to differences between calyptraeids and turritellids. As in turritellids the operculum of euomphalaceans would loosely block the aperture in feeding position. The columellar muscle in the euomphalaceans would be at the right of the cephalopedal mass, instead of ventral to it as in those motile gastropods that balance the shell over the cephalopedal mass. The coiling axis in euomphalaceans has to shift relative to the substrate from horizontal to vertical during growth, as shell-balancing capacity is lost and filter feeding replaces grazing. Because the position of the columellar muscle in *Neomphalus* is to the right of the cephalopedal mass and because *Neomphalus* also shifts the coiling axis of its initial whorls, *Neomphalus* is the logical limpet derivative of an euomphalacean.

The discoidal euomphalaceans became extinct in the Cretaceous, having no defense against shell-crushing predators that arose in the Mesozoic, but the limpet derivative is protected against such predators and exploits the abundant chemosynthetic bacterial food source not accessible to soft-substrate-dwelling animals. During the Mesozoic, hydrothermal vents may have been accessible along rift zones in shallow water, providing stepping stones to deep-water rift systems. The rift-vents in deep water fortuitously lack such usual molluscan predators as drill snails

¹Contribution number 17 of the Galapagos Rift Biology Expedition, supported by the [United States] National Science Foundation.

and sea stars; thus, the rift-vent habitat has been a stable refugium for a relict family at least since the Cretaceous, the period of the last surviving euomphalaceans.

Only the Pleurotomariidae share with the Neomphalidae the absence of afferent support to the ctenidium. The Euomphalacea can be independently derived from the Pleurotomariacea, upon loss of the right pallial complex, probably from an early pleurotomariacean stock of flat-lying discoidal shells with a slit on the upper whorl surface, as the Ordovician *Lesueurilla*. The unique dorsal food groove of *Neomphalus* is here interpreted as a primitive character. The tips of filaments from paired ctenidia, modified for filter feeding, could have converged upon a dorsal food groove in this group of early pleurotomariaceans, the shells of which are no better designed for locomotion than those of euomphalaceans.

The new archaeogastropod suborder Euomphalina, to include the superfamilies Euomphalacea and Neomphalacea, is proposed, an independent line derived from early pleurotomariaceans. It has attained the mesogastropod level of advancement in its circulatory and reproductive systems but retains the primitive characters of the rhipidoglossate radula and the bipectinate ctenidium.

Possible affinities of other extinct archaeogastropods are discussed in Appendix 1, with the conclusion that Macluritacea and Clisospiracea are lineages apart from Euomphalacea and Trochacea. Pseudophoracea, Platyceratacea, Anomphalacea, Microdomatacea, and Palaeotrochacea may have had the pallial complex of the Trochacea.

In Appendix 2 the Liotiidae are recognized in the Paleozoic, making the Trochacea older than previously supposed, and the Craspedostomatacea and Amberleyacea are merged with the Trochacea.

INTRODUCTION

Strange new deep-sea communities associated with thermal springs along sea-floor spreading centers have recently been discovered both at the Galapagos Rift (Ballard, 1977; Lonsdale, 1977; Corliss & Ballard, 1977; Corliss et al., 1979; Crane & Ballard, 1980) and the East Pacific Rise (Corliss et al., 1979; Spiess et al., 1980). Chemosynthetic bacterial production deep within the springs provides a source of food (Rau & Hedges, 1979; Karl et al., 1980; Jannasch & Wirsén, 1979, 1981). Another source of food derived from photosynthetic sources may be made accessible by advection currents through the vents (Enright et al., 1981). The hydrothermal vent communities are richly provided with filter-feeding animals, predators, and a conspicuous gutless animal—the vestimentiferan pogonophoran *Riftia pachyptila* Jones, 1981. Questions in the fields of ecology, physiology, reproduction, dispersal, and taxonomic origins of the rift-vent species have engendered an extraordinary interest among marine biologists. Nearly all members of the rift-vent community are new species.

Mollusks are conspicuous members of these communities. In addition to two large bivalve species, a mytilid and the large white clam, *Calyptogena magnifica* Boss & Turner, 1980, there are several limpets. The largest of the limpets from the Galapagos Rift is described here as the new genus and species *Neomphalus fretterae*. Its anatomy is so un-

like that of any living gastropod that it can not be assigned to an existing superfamily or even to a suborder in the Gastropoda.

The external anatomy resembles that of the mesogastropod family Calyptraeidae, having a similar flattened neck, a deep mantle cavity on the left side, and long gill filaments converging upon a food groove. Unlike the calyptraeids, in which the gill is monopectinate, *Neomphalus* has a bipectinate gill, with filaments on both sides of the axis. Bipectinate gills are characteristic of the Archaeogastropoda, the oldest and most primitive order of prosobranchs. Additional archaeogastropod features include the epipodial tentacles surrounding the foot and the rhipidoglossate radula. Unlike such other single-gilled, rhipidoglossate archaeogastropods as the Trochacea and Neritacea, the neomphalid heart is monotocardian, having but a single auricle as in mesogastropods. Other mesogastropod-like features of *Neomphalus* include expansion of the left kidney to serve as a cavity in which some organs lie, and reproductive advancements that include glandular gonoducts, a copulatory organ in males and a seminal receptacle in females. The internal anatomy of *Neomphalus* and its affinity to other living gastropods is treated in a separate paper in this issue of MALACOLOGIA (Fretter, Graham & McLean, 1981).

One must assume that *Neomphalus* represents an evolutionary line that underwent an adaptive radiation, as have nearly all animal

groups in which a morphological innovation, in this case the unique filter-feeding ctenidium, has opened a new feeding zone to exploitation.

The absence of living relatives suggests that the radiation must have taken place in the past. Yet, no fossil record of this limpet has been found. However, because all limpets derive from coiled predecessors, the search for relatives may be directed to the extinct coiled groups. Archaeogastropods were the dominant gastropods in the Paleozoic, the period in which the origins of all other higher categories of living archaeogastropods took place.

Because the limpet shell form imposes few constraints upon anatomy, many features of limpet anatomy are likely common to the coiled predecessor. There are some groups of Paleozoic gastropods that seem so poorly designed for locomotion that they have recently been considered to have been sedentary and therefore likely to have been filter feeders. These groups, the Macluritacea and the Euomphalacea, are prime candidates as predecessors to *Neomphalus*. The discussion section of this paper presents the case for *Neomphalus* as a limpet derivative of the Euomphalacea. The neomphalid mantle cavity is suited to function within a coiled shell. Apart from the ease with which the neomphalid mantle cavity can account for filter feeding in euomphalaceans, there are clues in the shell ontogeny of *Neomphalus* that also suggest a derivation from the Euomphalacea.

The two superfamilies Macluritacea and Euomphalacea have been united in the suborder Macluritina (Cox & Knight, 1960), but this relationship has recently been questioned by paleontologists; the differences are sufficiently pronounced that subordinal separation can be justified. As this has not yet been done, the formal proposal of the suborder Euomphalina, to include the superfamilies Euomphalacea and the new superfamily Neomphalacea, is given at the conclusion to the discussion section in this paper.

Some other extinct superfamilies of archaeogastropods were considered as possible predecessors to *Neomphalus*. My opinions about feeding modes and affinities of these groups are given in Appendix 1. Because the Euomphalacea have shell characters that overlap those of the Trochacea, an effort has been necessary to define the shell characters that distinguish the two groups.

Few arguments could be found to preclude many of the extinct groups from having the pallial complex of the Trochacea. The evidence seems sufficient to merge the Craspedostomatacea and Amberleyacea with Trochacea, as discussed in Appendix 2.

MATERIALS AND METHODS

The thermal springs along the spreading axis of the Galapagos Rift were first observed from the deep submersible research vessel ALVIN in February 1977. Although biological collecting had not been anticipated, pieces of volcanic rock (Fig. 12A) were retrieved with the mechanical arm of ALVIN. Limpet specimens ranging in diameter from 7 to 30 mm were removed aboard the support ship and were transmitted to me in June 1977. These came from the vent-fields named Oyster Bed (dives 723 and 726) and Garden of Eden (dive 733).

Second and third expeditions were made to the Galapagos Rift site in February and December 1979 by biologists from Woods Hole Oceanographic Institution and Scripps Institution of Oceanography (Ballard & Grassle, 1979). Small specimens of *Neomphalus* were recovered from samples of the mytilid collected at the Garden of Eden vent-field (dive 884) and were transmitted to me.

All specimens were originally fixed in 4% buffered formalin and were subsequently transferred to 70% ethyl alcohol. Some specimens were dissected. Transverse and sagittal sections of males and females were made. Material for sectioning was embedded in paraffin; sections were cut at a thickness of 15 μ m and stained with Mayer's hematoxylin and eosin. Shells of two small specimens were examined with a scanning electron microscope (SEM), and the intact animals of two others were critical-point dried for SEM examination. The radula was also examined with the SEM.

The internal anatomy of *Neomphalus*, its bearing on feeding and reproduction and the relationship to other living gastropods is treated separately by Fretter, Graham & McLean in this issue of MALACOLOGIA. The discussion section in the present paper therefore follows the discussion in the joint paper.

A report on the shell structure by Roger L. Batten, American Museum of Natural History, is in preparation and will be published separately.

In this paper frequent references are made to extinct genera and families of archaeogastropods. All are diagnosed and illustrated in the archaeogastropod volume of the *Treatise on Invertebrate Paleontology* (1960), in which the Paleozoic groups were treated by J. B. Knight, R. L. Batten & E. L. Yochelson, those of the Mesozoic by L. R. Cox, and those of the Cenozoic by A. M. Keen and R. Robertson. Knight's (1941) "Paleozoic Gastropod Genotypes" provides photographic illustrations useful for comparison with the shell drawings in the *Treatise*. Authors, dates, and type-species of genera are not given here; citations are readily available in these works.

SYSTEMATICS AND DESCRIPTIONS

NEOMPHALACEA McLean, new superfamily

Diagnosis: Having the characters of the family as follows:

NEOMPHALIDAE McLean, new family

Diagnosis: Shell cap-shaped, composed of lamellar aragonite and having an adherent periostracum; protoconch and first postprotoconch whorl with coiling axis perpendicular to final aperture; first whorl rounded, suture deep; conversion to limpet form in second postprotoconch whorl by process of lip expansion on upper half of whorl and growth stoppage on columella; radula rhipidoglossate; foot with anterior mucous gland and epipodial tentacles bunched along posterior sides of foot; shell muscle crescent-shaped, enveloping the visceral cavity but not the mantle cavity or pericardial cavity; mantle cavity deep, extending entire length of animal on left side; heart monotocardian, ventricle not traversed by rectum; right ctenidium and auricle lacking but represented by prominent efferent pallial vein in mantle skirt; left ctenidium lacking afferent membrane, attached to floor of mantle cavity by thickened efferent membrane; elongate gill filaments arching over flattened neck to food groove, which cuts over top of head directly to mouth; left kidney enlarged to form body cavity; gonads discharging through glandular gonoducts; left cephalic tentacle of male enlarged to serve as copulatory organ; seminal receptacle in female unconnected to genital duct.

Neomphalus McLean, new genus

Diagnosis: With the characters of the family plus shell features that include a nearly central position of the apical whorls, sculpture of fine radial ribs, and an internal shell ridge within the area of the muscle scar that increases the area for muscle insertion.

Type-species: *Neomphalus fretterae*, new species. Other species are yet unknown but may be expected at other rift-vent sites.

Etymology: The generic name combines the Greek prefix *neo* (new), and the generic name *Euomphalus* J. Sowerby, 1814, in keeping with my theory that the Neomphalidae are limpet derivatives of the Euomphalacea. The specific name honors Dr. Vera Fretter, of the University of Reading, in recognition of her contributions to our understanding of the relationships among prosobranchs.

Neomphalus fretterae McLean, new species
Figs. 1–12

Material: 115 specimens in the initial series, 69 ♀ and 46 ♂ from 3 dives of the ALVIN at the Oyster Bed and Garden of Eden vent-fields on the Galapagos Rift: Dive 723, Oyster Bed, 27 February 1977, 0°47.5'N, 86°08.0'W, 2478–2490 m, 15 ♀, 5 ♂; Dive 726, Oyster Bed, 9 March 1977, same coordinates and depths, 17 ♀, 18 ♂; Dive 733, Garden of Eden, 16 March 1977, 0°47.69'N, 86°07.74'W, 2482–2518 m, 37 ♀, 23 ♂. Position of Oyster Bed from the 1977 expedition, that of Garden of Eden from the 1979 expeditions; depths from ranges recorded on the 1979 expeditions, courtesy Fred Grassle.

Type Material: The holotype (Figs. 3A, B), an intact ♀ attached to the shell, from dive 723, Oyster Bed, is deposited in the U.S. National Museum of Natural History, Washington (USNM), no. 784637. Designated paratypes from dives 723, 726, and 733, as follows: USNM no. 784638, 3 ♀, 2 ♂; Los Angeles County Museum of Natural History (LACM), no. 1966, 17 ♀, 8 ♂, including specimens illustrated in Figs. 1, 4–9, some specimens dissected, 5 specimens sectioned; Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), no. 280321, 5 ♀, 5 ♂. Additional paratype lots preserved with the body attached to the shell, have been sent to the mollusk departments of the following museums, the lot consisting of either two ♀ and one ♂ or one ♀ and one ♂, each specimen

individually labeled by sex and dive number: Academy of Natural Sciences, Philadelphia; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; California Academy of Sciences, San Francisco; Department of Paleontology, University of California, Berkeley; Scripps Institution of Oceanography, La Jolla; National Museum of Canada, Ottawa; Museo Nacional de Historia Natural, Santiago; British Museum (Natural History), London; National Museum of Wales, Cardiff; Royal Scottish Museum, Edinburgh; Museum National d'Histoire Naturelle, Paris; Zoological Museum, Copenhagen; Zoological Museum, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Forschungs-Institut Senckenberg, Frankfurt; Zoological Institute, Academy of Sciences, Leningrad; P. P. Shirshov Institute of Oceanology, Moscow; National Science Museum, Tokyo; Australian Museum, Sydney; National Museum of Victoria, Melbourne; Western Australian Museum, Perth; National Museum of New Zealand, Wellington; Auckland Institute and Museum, Auckland.

Additional Material: USNM 784639, dive 733, 23 specimens, 12 ♀ and 11 ♂, associated with the vestimentiferan *Riftia*, frozen and thawed in Bouin's fixative (which destroyed the shells) by M. Jones; MCZ 280323, 9 specimens, 1977 expedition, dive number not re-

corded; LACM 67728, Dive 884, Garden of Eden, 25 January 1979, 17 small specimens removed from shells and residue associated with the mytilid bivalve, including specimens illustrated in Fig. 10. Specimens from dives 723, 726, and 733 not designated as paratypes have been sent to Dr. Vera Fretter, Dr. Roger L. Batten, and Dr. Richard A. Lutz.

Geographic Range: Oyster Bed, Garden of Eden, Rose Garden, and Mussel Bed vent-fields at the Galapagos Rift. Although specimens from the latter two vent-fields have not been examined, *Neomphalus* has been identified by Dr. Fred Grassle and Ms. Linda Morse-Porteous in the collections from these vent fields that were made on the January-February, 1979, expedition.

Description

Shell (Figs. 1, 3, 9, 10): Maximum diameter of females 30.0 mm, of males 25.5 mm. The initial series had 30 females 22 mm in diameter or larger but only 3 males that size or larger. Shell height 0.23 to 0.33 times diameter. Dimensions of holotype: Maximum diameter 30.0, lesser diameter 26.7, height 7.8 mm.

The shell is white under a light-brown periostracum, moderately elevated and irregular in outline. The adult shell is composed

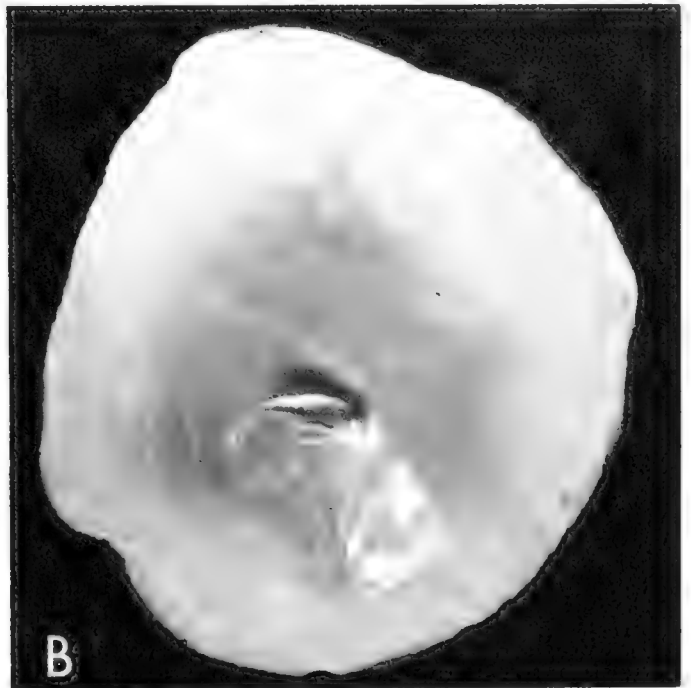
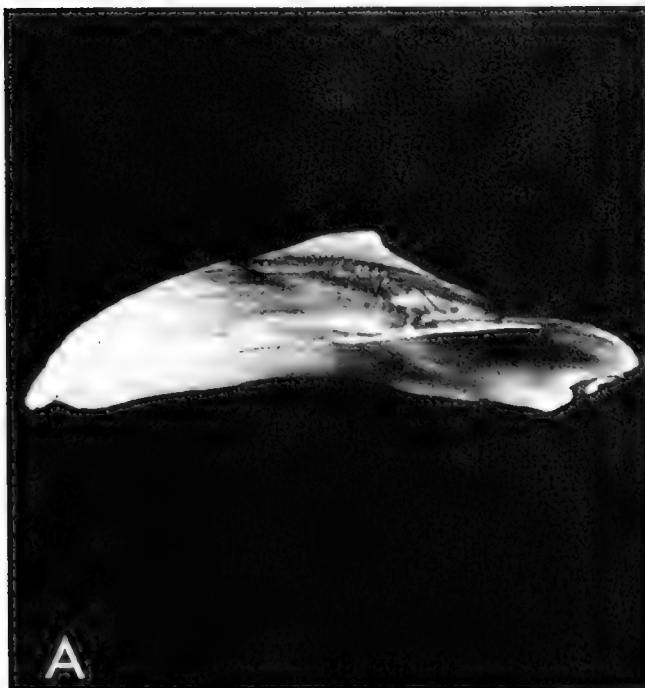


FIG. 1. *Neomphalus fretterae* McLean. Shell of mature female, dive 733, Garden of Eden, maximum diameter 26.6 mm, maximum height 6.5 mm. A) Lateral view from left side, showing the irregular shell margin. B) Interior view, anterior at top, showing the crescent-shaped muscle scar in the lower left quadrant and the shell ridge within the anterior arm of the muscle scar.

of two layers of lamellar aragonite, an outer complex crossed-lamellar layer and a thicker inner radial crossed-lamellar layer.² The lamellae of the inner layer are readily visible under low magnification, running parallel to lines of growth. The light-brown periostracum is thin but persistent. It projects beyond the margin of the shell and has prominent ridges corresponding to the radial sculpture.

The apex is posterior and slightly to the right of center, positioned at 0.6 the shell length from the anterior margin. The protoconch (Figs. 10A, B) has 1.2 rounded whorls and is sculptured with an irregular network of low ridges. The maximum protoconch diameter is 0.2 mm. The first post-protoconch whorl is rounded and the suture deeply incised; on the second whorl the area next to the suture has a flattened appearance, and faint spiral sculpture appears. The growth line trace on the second whorl continuously increases its extent with growth until it makes a full circle as the shell diameter reaches 1.8 mm. Further growth takes place along the entire margin.

The shell is sculptured with radial ribs that appear at a shell diameter of about 2 mm. Ribs are well defined, slightly curved until the shell diameter reaches about 7 mm, then more or less straight. Rib surfaces are rounded, with the interspaces about equal to the width of the ribs. Secondary ribs emerge in the rib interspaces after the shell attains a diameter of about 7 mm. Every 6th to 10th rib is stronger than the rest and has a correspondingly strong periostracal ridge. There are 23 to 25 strong ribs on mature shells. Most shells have irregular concentric interruptions representing resting stages or growth rings, the first interruption at a diameter of 6 to 7 mm, the second at a diameter of 9 to 13 mm. The periostracal ridges are stronger after crossing the first concentric interruption.

The growing edge of the shell is very thin and fragile and extends in short digitations corresponding to the rib pattern reflected in the overhanging periostracum.

The muscle scar (Figs. 1B, 9B) is crescent-shaped and located entirely within the lower left quadrant. The scar extends left from the apical pit and curves to the right, its closest approach to the shell margin about $\frac{1}{4}$ the radius. A shell ridge that is twice as high as wide originates at the deepest point on the apical depression. It extends along the inner

border of the muscle scar crescent for a distance of about $\frac{1}{4}$ the length of the inner margin of the crescent. The ridge may be 4 mm in length in large specimens. Its position is entirely within the area of the muscle scar; thus, it serves to increase the area available for muscle insertion.

Although thin, the shell of *Neomphalus* offers highly effective protection. None of the specimens showed any loss of periostracum or shell erosion. Specimens remain intact when dried, although the shell margin and periostracum may crack.

Similar overhanging periostracum is known in limpets of the families Capulidae and Hipponicidae. These limpets are immobile—the overhanging periostracum may function to provide a tighter seal along the margin.

Shell structure of lamellar aragonite is known in at least the innermost layer of the Fissurellidae, Scissurellidae, Skeneidae, Phasianellidae, Neritidae, Phenacolepidae, Cocculinidae and the extinct Bellerophonacea (Bøggild, 1930; MacClintock, 1963, 1967; Batten, 1975; Gainey & Wise, 1980). This is in contrast to the nacreous aragonitic internal layer of Pleurotomariidae, Haliotidae, Trochidae, Turbinidae, and Seguenziidae (Bøggild, 1930; Batten, 1972; Bandel, 1979; Gainey & Wise, 1980), and to the complex layering in the Patellacea (MacClintock, 1967).

The protoconch lacks the pointed tip illustrated for trochacean species by Bandel (1975), Rodriguez Babio & Thiriot-Quievreux (1975), and Fretter & Graham (1977). The diameter of the protoconch is well within the size limits for archaeogastropod protoconchs tabulated by Bandel (1979).

Radula (Figs. 2A, B, C, D, E): The radula is rhipidoglossate, with a monocuspitate rachidian, five monocuspitate laterals, and about 20 marginal teeth. The rachidian has a long main cusp that overhangs half its height, its tip sharp-pointed and its sides serrate and concave. The base is three times the width of the overhanging tip and has lateral and basal protrusions that fit in corresponding sockets on the adjacent lateral teeth. The first lateral has a basolateral extension and a longer overhanging tip than the rachidian. The second lateral has a longer overhanging tip than the first lateral and an even broader lateral extension. Bases of the lateral teeth are notched to provide space for the overhanging tips of

²Roger L. Batten, *in litt.*

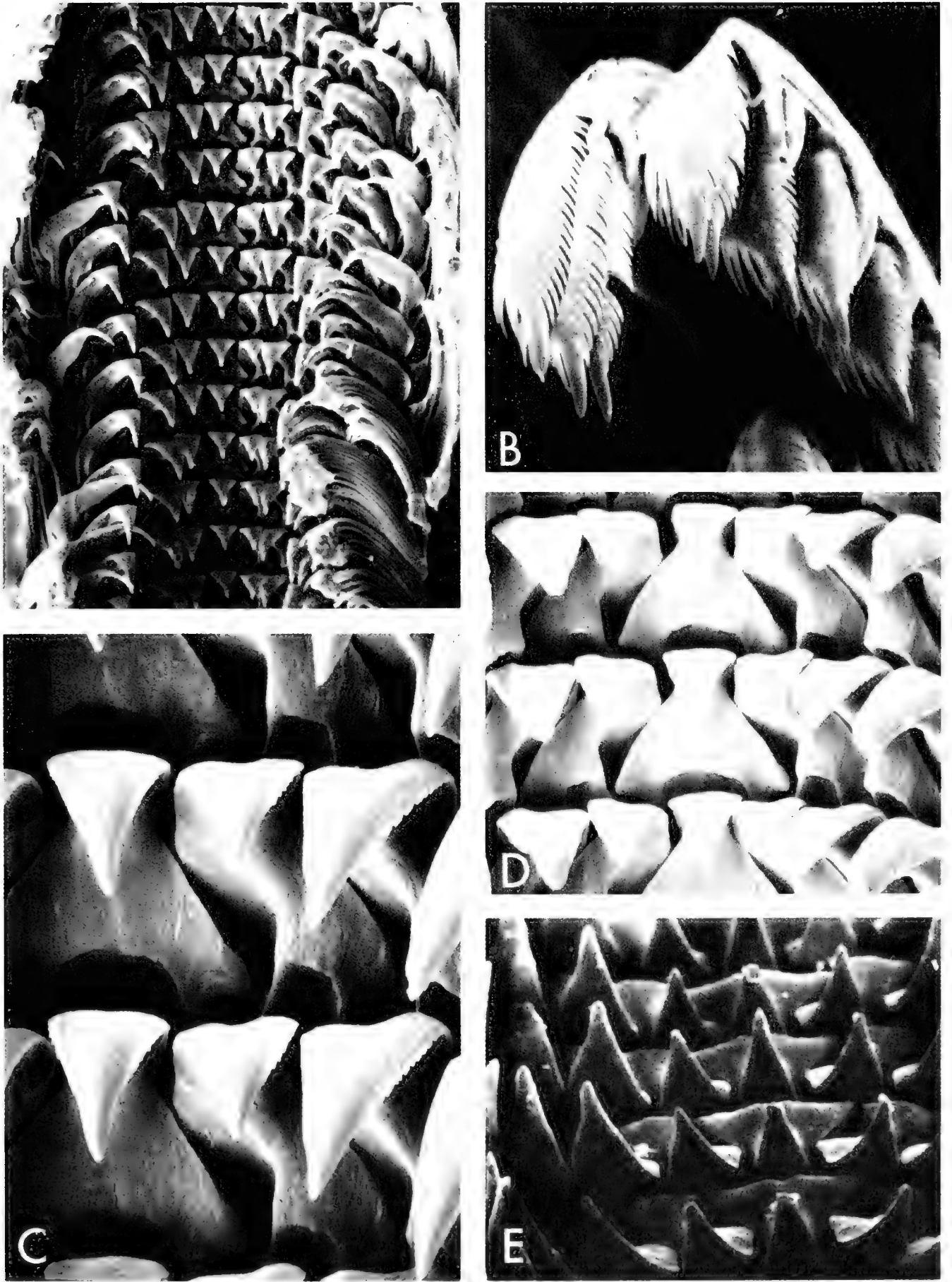


FIG. 2. *Neomphalus fretterae*. SEM views of radula. A) Full width of ribbon, showing rachidian, 5 laterals, and sheaths of incompletely separated marginal teeth. $\times 160$. B) Finely fringed tips of marginal teeth. $\times 1700$. C) Rachidian and first three laterals, showing fine denticulation on both sides of the main cusp of the rachidian but only on the outer sides of the main cusp of the laterals. $\times 950$. D) Rachidian and first three laterals showing tooth wear. $\times 575$. E) Intact radular ribbon projecting from mouth of preserved specimen.

the lateral teeth in the row below. The third lateral tooth has a narrow overhanging cusp about as long as that of the first lateral and a long, curved basal portion with a central strengthening ridge. The fourth lateral is similar to the third, and the fifth lateral is thin throughout and has only a sharp-pointed tip. The overhanging tips of the maginal teeth have a large, pointed denticle at the tip, with as many as 21 smaller comblike denticles on the sides.

The shafts of the marginal teeth have a tendency not to separate completely, producing an irregular arrangement, as has been noted by Hickman (1980b: 292, fig. 6C), who suggested that this may be due to a partial loss of function for these marginal teeth. The size of the radula is comparable to that of the Calyptraeidae and not to that of a grazing archaeogastropod, in which it is about ten times larger. The shortness of the radular ribbon indicates that the teeth are not rapidly used and replaced. The main function of the radula must be to rake in the food string, as in the Calyptraeidae.

The radula of *Neomphalus* is unlike any other rhipidoglossate radula. Elongation of the third, fourth and fifth laterals is unusual, recalling the elongate teeth in the Pleuro-

tomariidae (Woodward, 1901; Bouvier & Fischer, 1902; Fretter, 1964), but there is not the multiplicity of the lateral teeth in that family. There is no enlarged first marginal as in fissurellids and some trochaceans. The radular morphology of *Neomphalus* is so different from that of other archaeogastropods that it offers no useful phylogenetic clues.

External Anatomy in Ventral View (Figs. 3A, 4A, 5B, 6): Shrinkage resulting from preservation has retracted the mantle margin away from the growing edge of the shell, in most specimens decreasing the diameter of the animal by about a third (Fig. 3A). (In the following description of the ventral surface all references to left and right sides are from the normal dorsal aspect.)

Along the retracted mantle margin very fine mantle tentacles in nearly retracted condition are visible under high magnification on the outer edge; these tentacles correspond to grooves in the overhanging periostracum. Larger projections correspond to the major periostracal ridges on the shell.

The sole of the foot is oval except for its obtusely pointed posterior tip. It projects slightly on all sides, the anterior edge projecting to the greatest extent, where there is a straight edge and a prominent transverse fur-

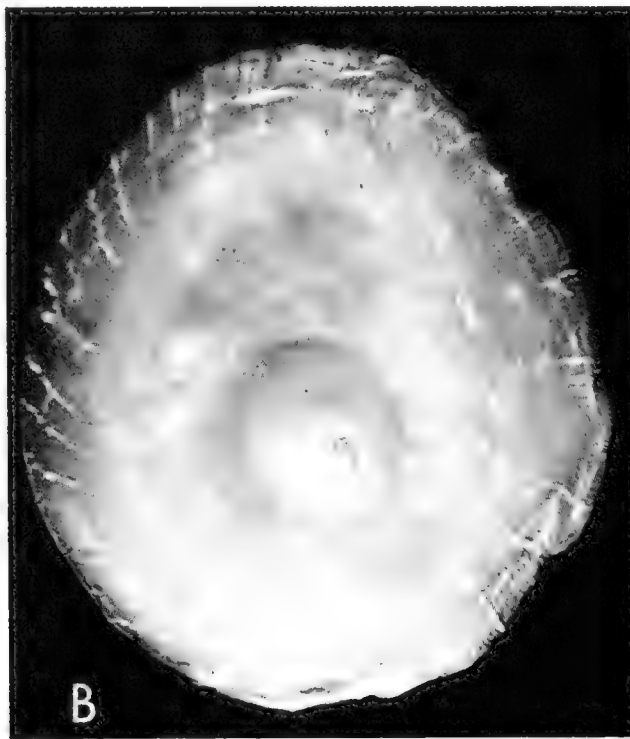


FIG. 3. *Neomphalus fretterae*. Holotype, USNM 784637, mature female attached to shell, dive 723, Oyster Bed, maximum diameter 30.0, maximum height 7.8 mm. A) Ventral view, showing the contraction of the body away from the shell margin and the projecting periostracum. The broad mid-ventral line on the neck is an artifact from shrinkage, marking the position of the esophagus. B) Exterior view, anterior at top, showing the periostracal ridges.

row, the opening of the anterior pedal mucous gland.

A thin epipodial ridge encircles the foot and extends forward on the ventral sides of the neck, where it fades and disappears. Tentacles are borne on this ridge only posteriorly. Those on the right side occur on the posterior third of the epipodium, the anteriormost concentrated on a projecting lobe bearing 4 to 9 short, stubby tentacles, with another two more broadly spaced tentacles between this group and the posterior tip of the foot. Tentacles on the left side (the mantle cavity side) are more limited, occurring only on the posterior fifth of the epipodium, the anteriormost being in a closely spaced group of 5 or 6, of which the first is the shortest; beyond this group are two longer and more broadly spaced tentacles.

The mantle cavity fills a space adjacent to the foot along the entire left side of the animal, extending posteriorly to a point opposite the foot tip. Adjacent to the foot the mantle cavity is closed and the gill axis shows through as a

supporting rod on the floor of the cavity. Adjacent to the neck the floor of the cavity is open and the gill filaments arch over the neck. The open portion of the mantle cavity extends over the head to a corresponding point on the right side.

Epipodial tentacles are prominent features in archaeogastropods other than Pleurotomariidae, Neritacea, and Patellacea. In no other family is there a similar elaboration in which they are entirely restricted to the posterior region and bunched together.

The pedal mucous gland is prominent in Pleurotomariidae, Scissurellidae and some trochaceans but is lacking in Haliotidae and Fissurellidae.

External Anatomy in Dorsal View (Figs. 4B, 5A): Upon removal of the shell the crescent-shaped columellar muscle is exposed. It surrounds the visceral mass except at the left side. No portion of the mantle cavity is enveloped by the shell muscle. A slit in the anterior portion of the muscle marks the position of

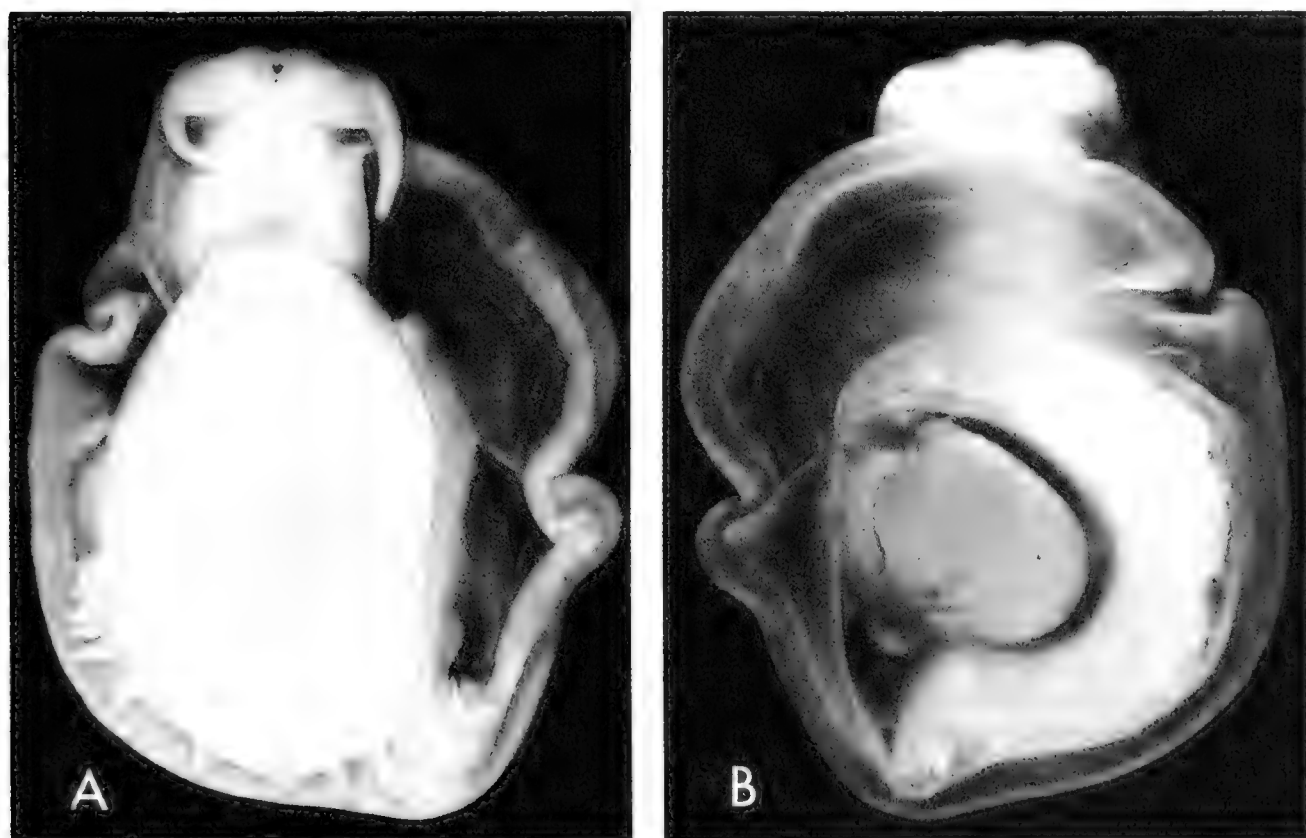


FIG. 4. *Neomphalus fretterae*. Mature female removed from shell, the ctenidium and its skeletal support on the floor of the mantle cavity excised. A) Ventral view, showing the epipodial tentacles bunched along the posterior sides of the foot, the obtusely pointed tip of the foot, and the opening of the anterior pedal mucous gland. Oral lappets extend on either side of the mouth, ventral to the posteriorly directed cephalic tentacles. B) Dorsal view, showing the efferent pallial vein in the mantle skirt, the food groove cutting diagonally toward the mouth, the crescent-shaped shell muscle surrounding the visceral mass except at the left side. The dorsal surface of the visceral mass is covered by the ovary on the right and the narrow, three-chambered glandular gonoduct on the left. The triangular pericardial cavity is left of the posterior arm of the shell muscle, containing the large, dark-appearing auricle on the left, and the smaller, lighter-appearing ventricle on the right.

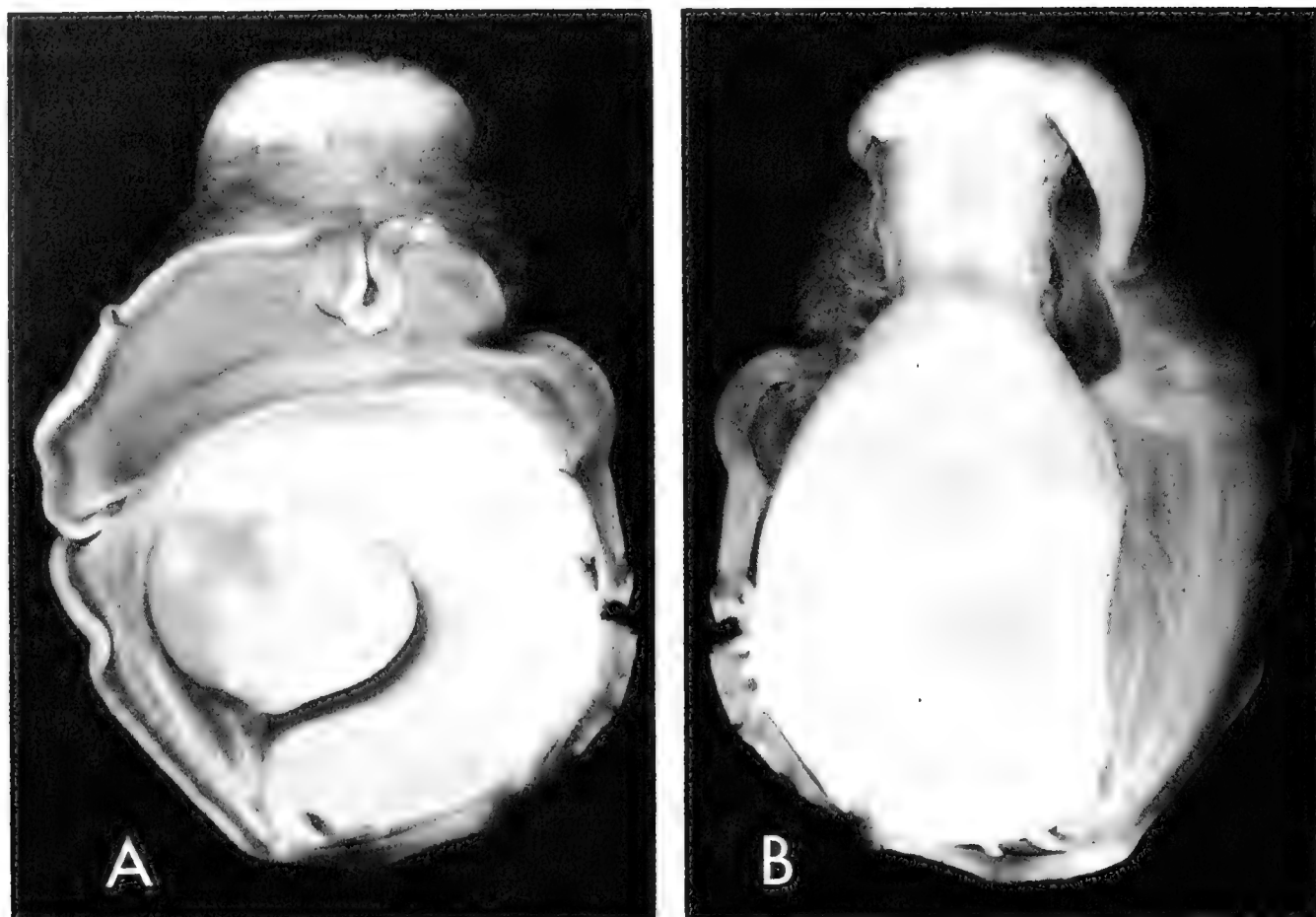


FIG. 5. *Neomphalus fretterae*. Mature male removed from shell. A) Dorsal view, showing the crescent-shaped shell muscle surrounding the visceral mass, which is covered by the testis on the right and prostate on the left. The mantle skirt is contracted and folded. The free tip of the ctenidium lies over the neck and the filaments extend to the right. B) Ventral view, showing the enlarged left cephalic tentacle adjacent to the left neck groove; other structures as in the female, Fig. 4A.

the interior shell ridge, which provides additional surface for muscle insertion.

The mantle skirt is relatively thin, apart from a thickened margin. It extends laterally in all directions; it is narrow to the right of the shell muscle and broad to the left where it roofs the mantle cavity, and broad anteriorly where it overlies the gill filaments that extend to the right above the neck.

The pallial vein is prominent in the mantle skirt, having its origin in the right anterior region of the mantle skirt and running midway along the roof of the mantle cavity on the left side of the animal. It extends to the posterior-most region of the mantle cavity, where it enters the auricle.

The triangular pericardial cavity is bordered on the right by the posterior arm of the shell muscle, on the left by the mantle cavity, and anteriorly by the visceral mass. The auricle is elongate, lying within the left side of the pericardial cavity; the shorter ventricle fills the right side.

The right-dorsal portion of the visceral mass is occupied by the gonad, entirely concealing the digestive gland and stomach beneath. Tubules within both the ovary and testis are visible externally, converging in both sexes at the left anterior region. Males (Fig. 5A) have a large bilobed prostate gland left of the testis; in females the glandular duct region is narrower than the prostate of the male, presenting a curved dorsal surface about three times longer than wide (Fig. 4B). The glandular duct of the female is comprised of three separate chambers, as detailed in the description of internal anatomy (Fretter, Graham & McLean, 1981).

Aside from the unique arrangement by which the shell muscle envelops only the visceral mass and not the mantle cavity, the dorsal position of the gonad is unusual; in other rhipidoglossate limpets the gonad shares the dorsal position with the digestive organs.

Head and Neck (Figs. 3A, 4, 5, 6, 7): The

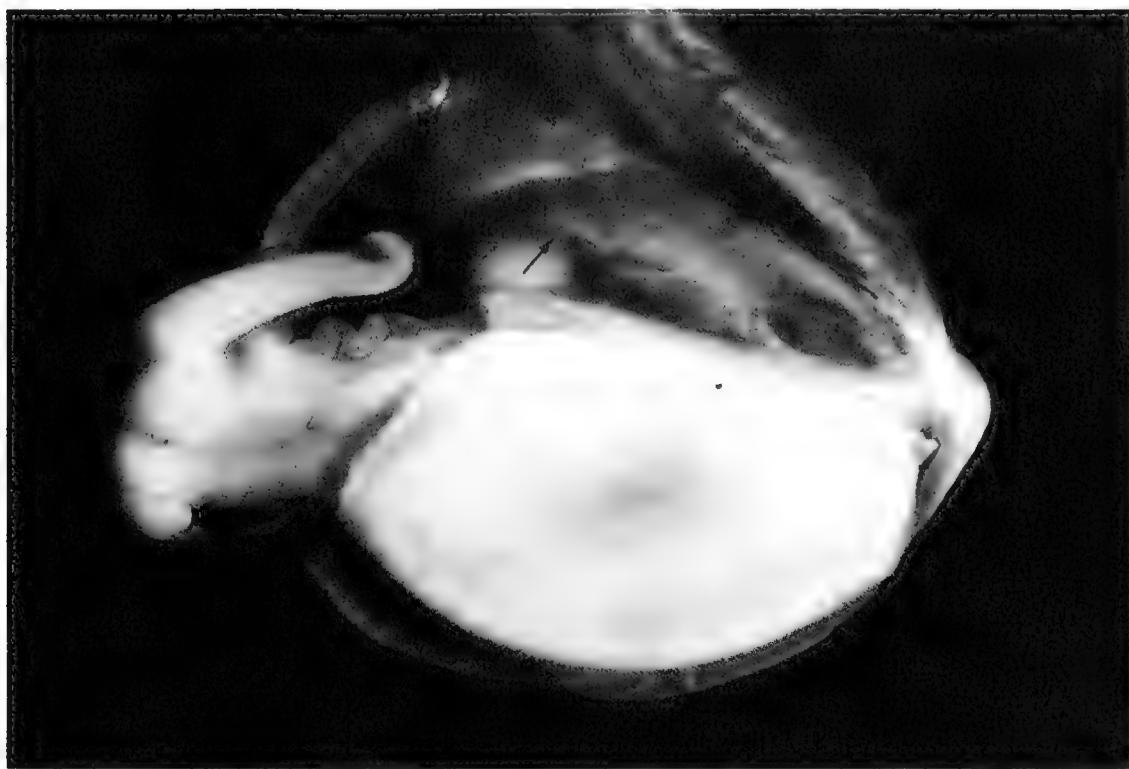


FIG. 6. *Neomphalus fretterae*. Left-ventral view of male specimen after cutting ventrally along the floor of the mantle cavity adjacent to the foot and folding up the ctenidium, showing the enlarged left cephalic tentacle adjacent to the left neck groove. The mouth is a vertical slit between the oral lappets. Arrow points to the male genital opening.

neck is long, wide, and flattened, so that its thickness is only about $\frac{1}{4}$ the height of the shell muscle. It lies at the level of the foot, the space above filled by the ctenidium. The anterior end of the head is blunt—nothing projects beyond the base of the cephalic tentacle—a snout is therefore absent.

The mouth is a recessed vertical slit at the ventral anterior edge of the head. Some specimens are preserved with the inner lips closed, the mouth appearing as a slit between the outer lips; in others the outer lips are parted and the buccal mass, jaw, and radula protrude.

The dorsal anterior region of the head is continuous with a pair of posteriorly directed cephalic tentacles. Eyes are lacking. In males of all sizes the left cephalic tentacle is larger than the right and may extend along the opening of the mantle cavity for $\frac{2}{3}$ the length of the neck. In most females the left tentacle is the same size or only slightly larger than the right tentacle. One specimen was observed in which the left tentacle was sufficiently large to suggest that it was male, but it proved on gonad inspection to be female; thus, tentacle dimorphism is not fully reliable for sex determination.

The neck has lateral extensions or lobes on both sides. The right neck lobe is simple and

flaplike, its connection to the neck defined along most of its length by the food groove. Anteriorly the food groove arcs across the dorsal surface of the cephalic lobe, cutting deeply toward a notch directly above the mouth. The right neck lobe merges with the base of the right cephalic tentacle anteriorly.

The left neck lobe borders the opening to the mantle cavity and is comprised of two ridges with a deep channel between. The ventral ridge is straight and smooth, and the dorsal ridge is somewhat more ruffled or contracted (at least in preserved material). Anteriorly the ridges rise above the base of the left tentacle and fade dorsally where the tentacle emerges from the head. No direct groove leads to the mouth. Posteriorly the channel margins terminate against the foot side, below the ventral opening to the mantle cavity.

The head and neck of *Neomphalus* are highly modified in relation to filter feeding and thus are not comparable to the head and neck in other archaeogastropod limpets. Neck lobes in trochaceans are considered to be forward extensions of the epipodium, but this seems not the case in *Neomphalus* because the neck lobes are not continuous with the epipodial ridge. The flattened head and neck is more like that of the Calyptraeidae but exhibits the following unique features: 1) the

posteriorly directed cephalic tentacles, 2) the enlarged left tentacle of the male (which certainly has a copulatory function), 3) the dorsal route taken by the food groove (in the Calyptraeidae and all other filter-feeding prosobranchs it passes beneath the right cephalic complex rather than over it), 4) and the depth of the left neck channel (the Calyptraeidae have a left neck groove, but it is shallow in comparison).

Mantle Cavity (Figs. 4, 6, 7, 9): The mantle cavity lies over the head, as in most prosobranchs, but differs from most in having its closed portion extending to the left of the cephalopodal mass, so that its total shape is that of an inverted "L." In most limpets there is a horseshoe-shaped shell muscle that is open anteriorly and fully envelops the posterior-most extent of the mantle cavity, but in *Neomphalus* the opening in the muscle envelops only the visceral mass, and the opening is shifted 90° to the left. The anterior portion of the shell muscle lies directly between the neck and all of the visceral cavity. Access to the right side of the animal is thereby unavailable to the mantle cavity organs normally associated with the right side.

Structures within the mantle cavity can be observed either by cutting into it ventrally be-

tween the base of the gill and the foot (the mantle skirt folded up with the gill attached), or by cutting dorsally to the right of the pallial vein and the gill folded down.

The ctenidium (Fig. 8) fills the entire mantle cavity. It is attached on the floor of the deep, enclosed portion of the cavity and its free tip extends beyond the ventral opening of the cavity to fill the entire space above the head. It is bipectinate throughout, with long narrow filaments of equal length on both sides of the axis. There is no dorsal (afferent) membrane—the attachment is entirely ventral (efferent). The thickened ventral axis continues along the free tip, providing support for the long filaments.

The gill axis within the closed portion of the mantle cavity is placed so that afferent and efferent vessels are aligned nearly vertically; where the cavity opens ventrally the axis makes a 120° bend to the right and turns to lie flat. Here the two vessels are horizontally aligned and the filaments from both sides of the axis are directed over the neck. Water currents thus may pass through filaments on both sides of the axis.

On a large specimen 190 separate leaflets were counted on each side of the gill axis. Those that emerge deep in the mantle cavity

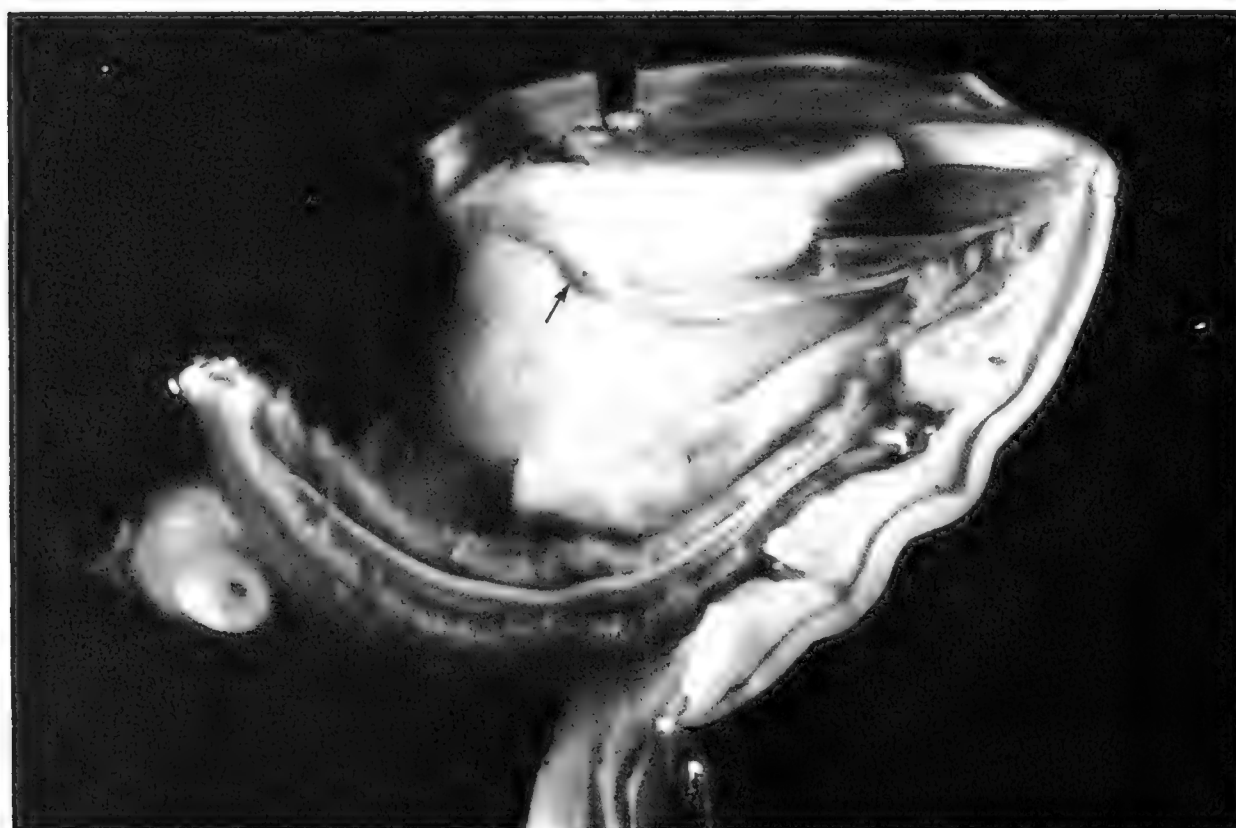


FIG. 7. *Neomphalus fretterae*. Female specimen from left side after cutting the mantle skirt between the visceral mass and the pallial vein; tips of ctenidial filaments excised to show the afferent side of the ctenidial axis. Arrow points to the female opening.



FIG. 8. *Neomphalus fretterae*. Ctenidium from specimen in Fig. 4, showing the close spacing and rounded tips to the filaments and the bend to the right midway along the axis. Filaments that arise beyond the bend terminate in a line corresponding to the position of the food groove where it traverses the neck.

are short and do not reach the opening. Filaments arising closer to the bend are longer, and those that emerge at the end are the longest. Tips of all the filaments impinge upon the food groove. On a large specimen the longest filament measured 9 mm in length and 0.4 mm in width throughout its length, which was therefore 22 times the width, comparable to the figure of 26:1 given by Yonge (1938) for *Crepidula*. Tips of the filaments are rounded. The filaments are not easily separated; a single filament cannot be removed without tearing the adjacent filaments. The cilia on the filaments and the skeletal rods within are treated in detail by Fretter, Graham & McLean (1981).

The food groove may be traced from the posterior end of the right neck lobe to near the innermost part of the mantle cavity, though sometimes appearing as a ridge rather than a groove. From the neck lobe it runs to the left over the dorsal surface of the head-foot and then backward, ventral to the anus, the genital opening, the ciliated area alongside that in females, and the kidney and pericardial cavity.

The osphradium consists of two elongated patches of dark-staining sensory epithelium at the base of the gill within the closed portion of

the mantle cavity behind the separation of the free tip to the ctenidium. This position is compatible with the normal position of the osphradium in aspidobranch gastropods, in which it is located at the leading edge of the efferent membrane that supports the free tip to the ctenidium. In *Neomphalus* the efferent membrane is thick and extends through the free tip, so that the osphradium has to be partitioned on both sides of the ctenidial axis to retain its usual position.

The left kidney opening is a tiny pore deep on the dorsolateral wall of the mantle cavity slightly posterior to the ventral inhalant opening and just within the anterior limb of the shell muscle. In females the genital opening has prominent rosette-shaped lips; from their base a series of fine, ciliated ridges and grooves runs posteriorly, dorsal to the food groove, to the opening of the receptaculum seminis. In males the opening is recessed, and the lips curve forwards to form a groove lying ventral to the rectum. The extreme leftward shift and considerable depth of the mantle cavity has the important consequence of keeping the genital openings on the left side of the body, unlike the condition in all other single-gilled prosobranchs, in which the reproductive functions are entirely performed at

the right side of the head. The displacement of the genital opening to the left side explains why it is the left rather than right cephalic tentacle of the male that is modified as a copulatory organ.

The rectum, upon emerging from the kidney cavity at about the position of the genital opening, is suspended dorsally in the mantle cavity, running adjacent to the shell muscle. The anus is positioned directly over the mid-point of the neck. A rod of fecal material continues in a groove in the mantle skirt adjacent to the shell muscle, which carries the fecal rod to the right, where it can be expelled when the shell edge is raised.

No distinct region in the mantle skirt can be regarded as hypobranchial gland, although scattered subepithelial gland cells are present. This is in striking contrast to the prominent ridged and convoluted development of discrete left and right hypobranchial glands in the pleurotomariids, haliotids and trochaceans. In these groups left and right hypobranchial glands are separated by the rectum in the mantle skirt. In *Neomphalus* the rectum does not traverse the mantle skirt. Hypobranchial gland development comparable to that of *Neomphalus* occurs in the Fissurellidae, in which gland cells are present in the

mantle skirt but do not form a discrete organ with a folded surface.

The ctenidium of *Neomphalus* is unique in the Gastropoda. It is the only ctenidium bipectinate throughout its entire length in which the filaments are elongate and the afferent membrane is lacking. Its length and mass is no doubt greater than that of any other living gastropod. Only in bivalves may the length of the gill be equal to that of the animal. The afferent membrane is lacking in one other family in the Archaeogastropoda—the Pleurotomariidae. Pleurotomariid ctenidia differ in being paired, the filaments not elongated, the efferent membranes not thickened. The pleurotomariid mantle cavity extends even deeper than that of *Neomphalus*, past the ctenidial origin.

Growth and Shell Ontogeny: Four small specimens, having shell diameters of 1.7, 3.2, 3.8, and 4.0 mm, were collected on the second expedition in February 1979. The shell of the 1.7 mm specimen was mounted for SEM examination of the aperture (Fig. 10C); the 3.2 mm specimen remains intact; the 3.8 mm specimen was critical-point dried for SEM examination of the animal (Fig. 10D); and the 4.0 mm specimen was used for SEM study of its exterior (Figs. 10A, B).

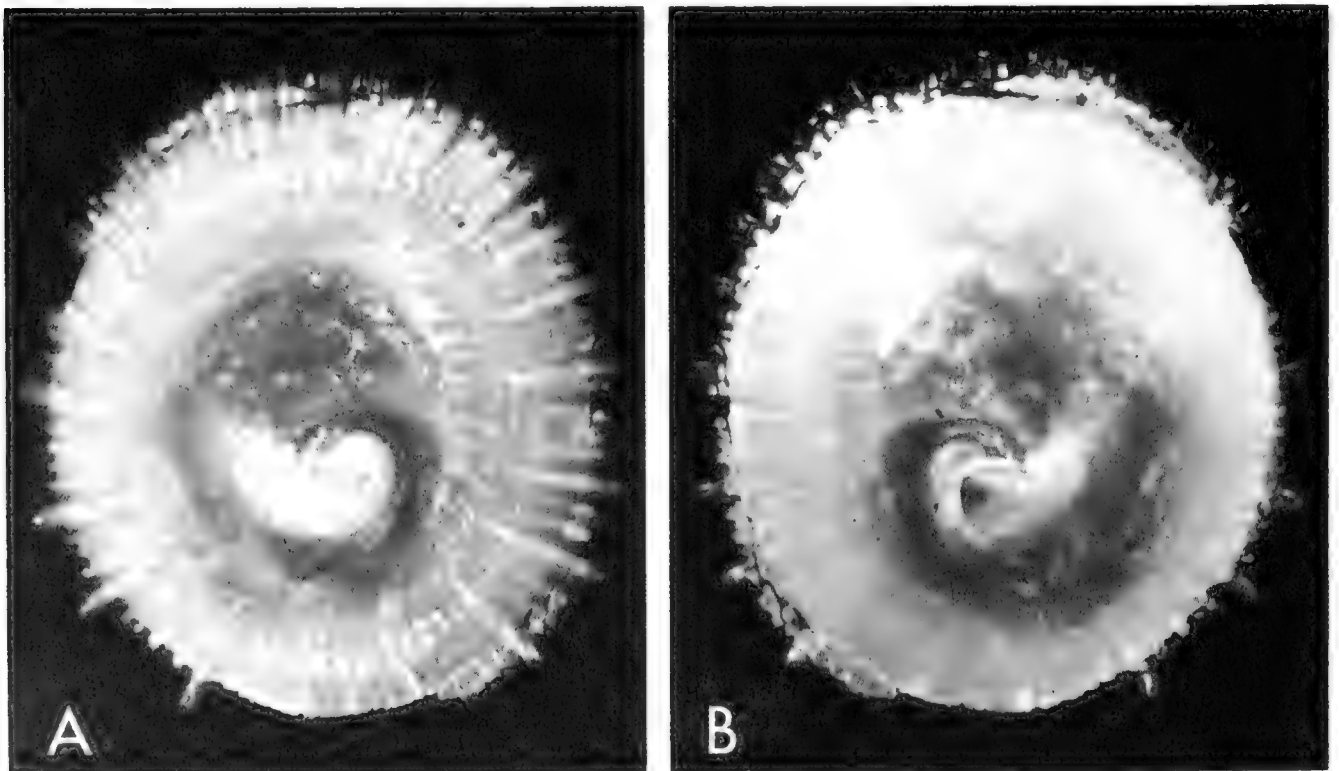


FIG. 9. *Neomphalus fretterae*. Juvenile shell of female, dive 733, Garden of Eden, diameter 7.0 mm. A) Exterior, anterior at top, showing flat-lying coil of early whorls. B) Interior, anterior at top, showing abandoned columella from the early coiled phase, the muscle scar and the shell ridge now positioned directly over the base of the early shell.

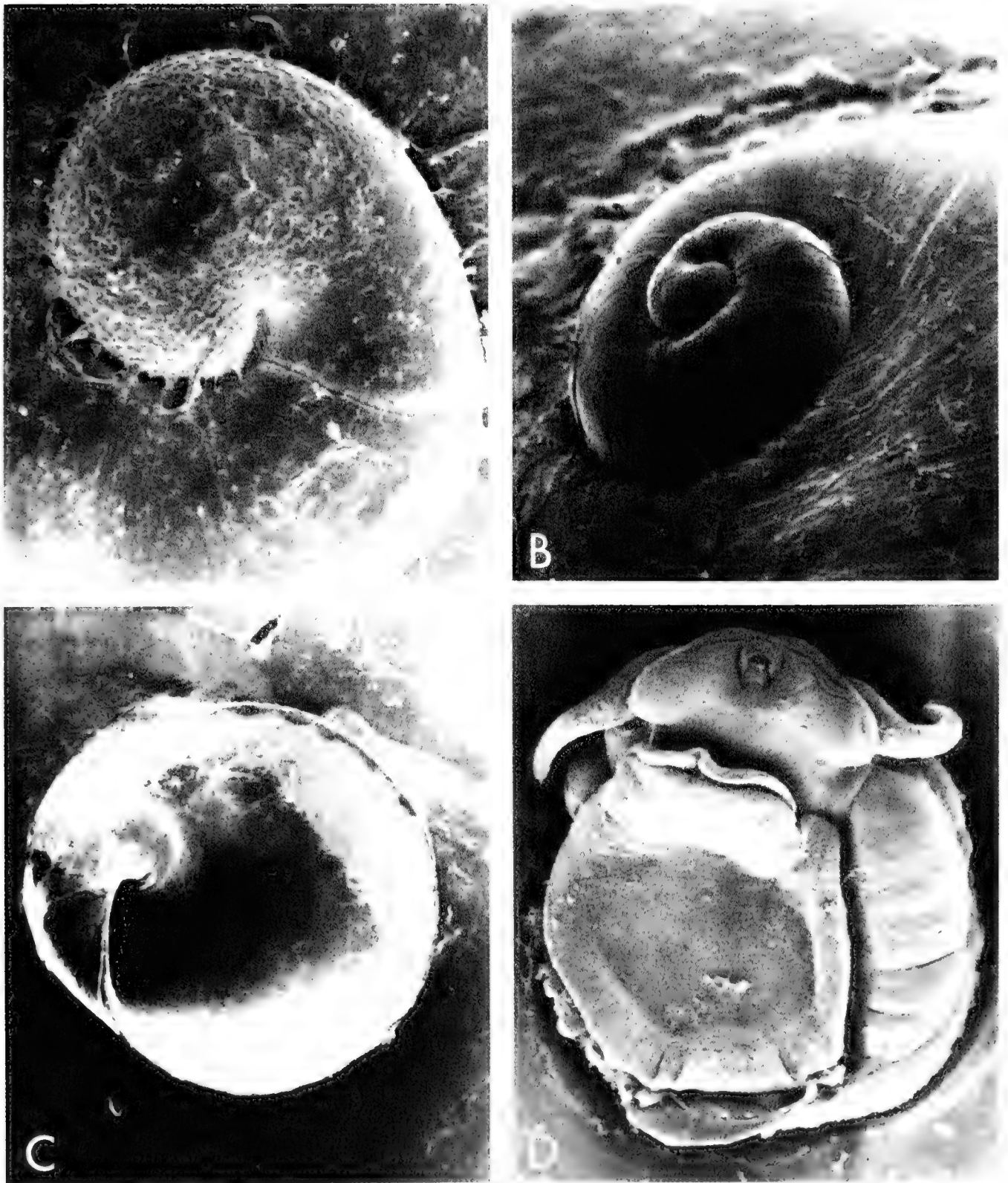


FIG. 10. *Neomphalus fretterae*. SEM views of early stages. A) Protoconch, maximum diameter 0.2 mm. B) Oblique view of protoconch and first two postprotoconch whorls, same specimen as Fig. 10A. C) Basal view of coiled juvenile shell 1.7 mm in diameter, showing the rudiment of the shell ridge, the rounded columellar lip along which growth has stopped, and the encirclement by lip growth on the right $\frac{3}{4}$ complete. D) Ventral view of critical-point-dried juvenile attached to shell, shell diameter 3.8 mm, showing larval operculum 0.8 mm in diameter, the prominent opening of the anterior pedal mucous gland, jaws and other adult features, except that the neck is short, the mantle cavity not open on the left and the gill filaments not in evidence.

The critical-point dried specimen Fig. 10D) shows the larval operculum attached vertically at the rear of the foot, its diameter 0.8 mm. It has a tight central coil of 5 whorls and a paucispiral final whorl. Epipodial tentacles, jaws, the oral lappets, and the anterior pedal gland are well developed. Major differences from the adult are that the neck is relatively short, the gill filaments are not visible, and the mantle cavity opening ventral and left of the neck is not apparent nor is the left neck groove. Cephalic tentacles are laterally directed. The larval operculum of *Neomphalus* reaches a larger size and persists through more advanced stages of development than in limpets of any other family.

Neomphalus is also unique among limpets in the manner in which it makes the transformation from a coiled juvenile to the adult shell form. The transformation takes place in the second postprotoconch whorl, and results from cessation of growth of the columellar lip and accelerated growth along the suture and upper margin of the lip. A new suture is laid upon the periphery of the *Lamellaria*-like shell until the lip extends a full 360°. The stage at which the process begins is not marked by a line of transition on the external surface. This transformation is nearly complete on the 1.7 mm diameter specimen (Fig. 10C), in which the columellar lip is rounded and the base of the shell exposed, as yet uncovered with callus deposits. The total cessation of growth on the columellar lip is clearly indicated in larger juvenile shells (Fig. 9B), in which the old columella remains visible in the apical position of the shell interior.

The transformation to the limpet form involves a 90° shift in the orientation of the animal relative to the initial axis of coiling. Such a change is inferred because the larval stage in the 0.2 mm long protoconch would have the orientation common to all veliger stages with the head balanced relative to the axis of coiling. Because the animals in all the small specimens are oriented perpendicular to the plane of the aperture, they must have completed this 90° shift during the growth of the second postprotoconch whorl, coinciding with cessation of growth on the columellar lip.

Cessation of coiling fixes the orientation of the head and columellar muscle at an early stage. The columellar muscle of the coiled juvenile would be just inside the columellar lip; the cessation of coiling forces the growing muscle to emerge and assume a position on the base of the shell, where it expands with

growth. The rudiments of the shell ridge are apparent on the 1.7 mm specimen (Fig. 10C).

The cessation of growth along the basal part of the columellar lip explains why the columellar muscle does not form the encompassing horseshoe-shaped shell muscle of most other limpets. In transitional forms between normally coiled trochids and auriform limpet-like stomatellid trochaceans, the columella is lengthened, as is the columellar muscle. This expansion of the columellar muscle along the left side (viewing the animal dorsally) envelops the mantle cavity on the left, producing, upon further reduction of coiling, the horseshoe-shaped muscle that entirely envelops the visceral mass posteriorly and the mantle cavity anteriorly. In *Neomphalus* the left arm of the muscle is not stretched along an expanding columella and thus does not envelop the mantle cavity on the left side.

Thus many of the unusual features of *Neomphalus* can be traced to growth stoppage on the juvenile columella, which halts coiling and generates the limpet form, at the same time preventing the mantle cavity from being enveloped on the left side. The orientation of the animal relative to the columella and axis of coiling is forced to change.

Shell ontogeny in the Calyptraeidae, recently described by Fretter (1972), follows a different course: the columellar lip of the protoconch expands, altering the axis of coiling, followed by the addition of a projecting peripheral rim on all sides, producing the limpet shell. Folds of the mantle produce the calyptraeid septum by adding a flange to the original columella. *Neomphalus* differs in that the limpet shell results from progressive rather than simultaneous encirclement and the old columella is completely abandoned. In the calyptraeid the columellar muscle is drawn out along the septum, retaining major attachment points at both ends; hence the calyptraeid has the horseshoe-shaped muscle with its extremities at both sides of the mantle cavity, as in most limpets. In the Patellacea, Fissurellacea, and the neritacean limpets, the horseshoe-shaped muscle results from fusion of the left and right muscles; only minor changes in the orientation of the animal relative to the axis of coiling are involved.

Life habits

Neomphalus limpets live clustered near and extending into the vents (Fig. 11), where

they are in close association with the vestimentiferan *Riftia pachyptila* Jones (1981). Vent effluent at the Garden of Eden vent-field has a maximum temperature of 17°C, in contrast to the ambient bottom temperature of approximately 2°C. Vent effluent contains hydrogen sulfide and is reported as anoxic above 10°C, but presumably mixes sufficiently with oxygenated ambient water to sustain the limpets. Current flows of 2 to 10 cm/sec have been measured (all data from Corliss et al., 1979, p. 1082). The limpets are often in contact and some are positioned on the shells of others, as shown on the large fragment of pillow basalt from the Garden of Eden (Fig. 12A). The broad anterior surfaces of the limpets on the boulder (Fig. 12A) are facing in different directions, indicating that there was no orientation with reference to currents. *Neomphalus* may attach to the tubes of *Riftia* (Fig. 12B), although there is no indication of this in Fig. 12A.

Neomphalus is primarily sedentary; the shell margin is irregular, evidently conforming to a particular site. Those attached to other shells leave no attachment scars nor cause

any damage to the periostracum of the lowermost shell. The periostracum should provide a seal along the shell edge that would protect it from the claws of the brachyuran crab *Bythograea thermydron* Williams (1980), a potential predator at the Galapagos Rift. The foot of *Neomphalus* is sufficiently muscular for locomotion. Some motility would be required for the mating we deduce from the anatomy (Fretter, Graham & McLean, 1981).

Suspended bacterial cells in the rift-vent effluent have been measured in the range of 5×10^5 to 10^6 per ml (Karl et al., 1980) during the January 1979 expedition; Corliss et al. (1979) reported a count of 10^8 to 10^9 bacterial cells per ml in preserved samples from the 1977 expedition. Thus there is a sufficient source of suspended food to sustain large populations of filter-feeding animals. Mats of microorganisms also develop on shell or rock surfaces in the vicinity of the vents (Jannasch & Wirsén, 1981), providing a source of food for limpets that feed by grazing.

Gut contents in *Neomphalus* suggest that feeding is a combination of grazing and filter feeding (Fretter, Graham & McLean, 1981).

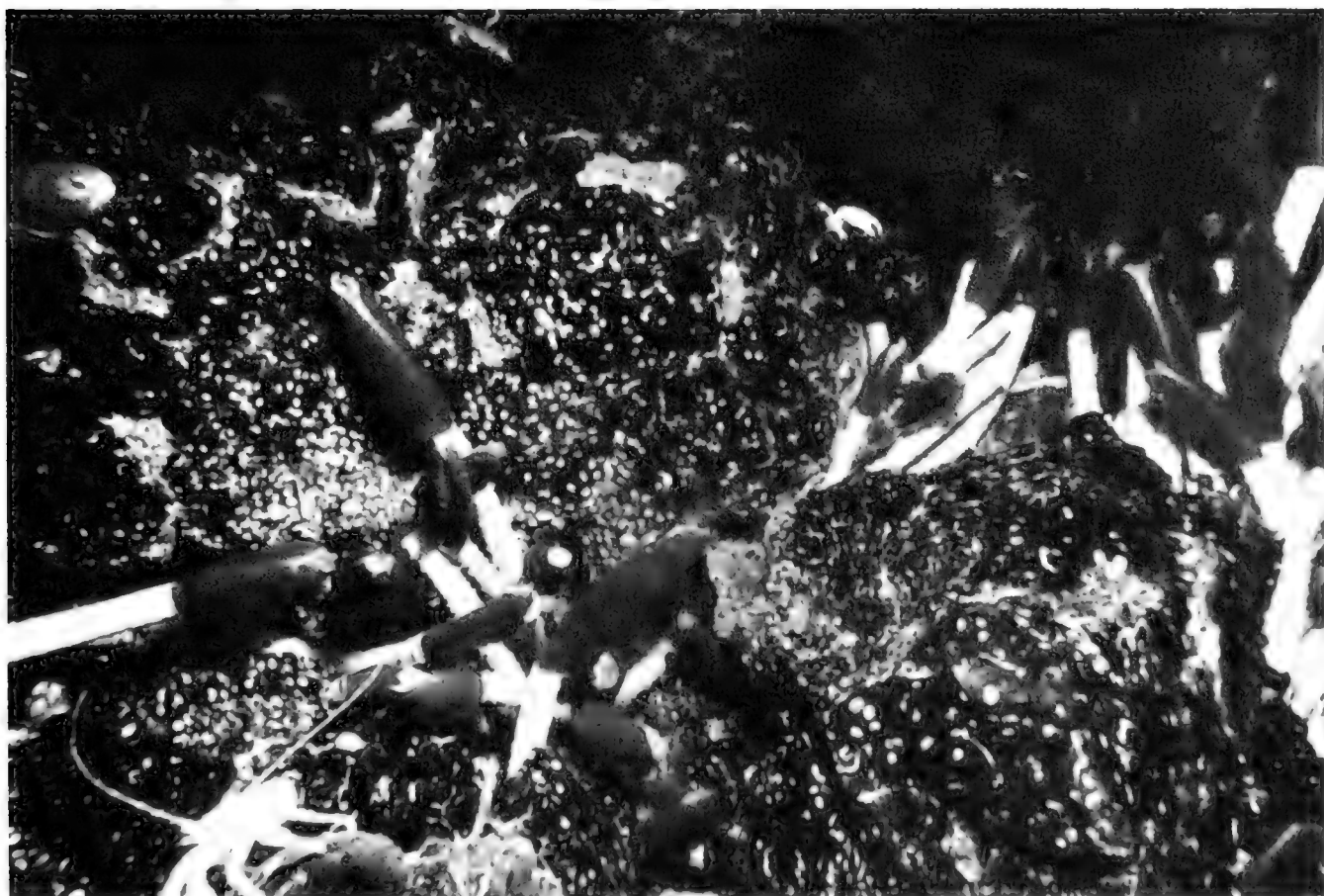


FIG. 11. Oyster Bed vent-field, dive 726, showing the vestimentiferan, *Riftia pachyptila*, the brachyuran crab *Bythograea thermydron* in upper center, the galatheid crab at lower left, and numerous *Neomphalus fretterae* on all exposed surfaces.

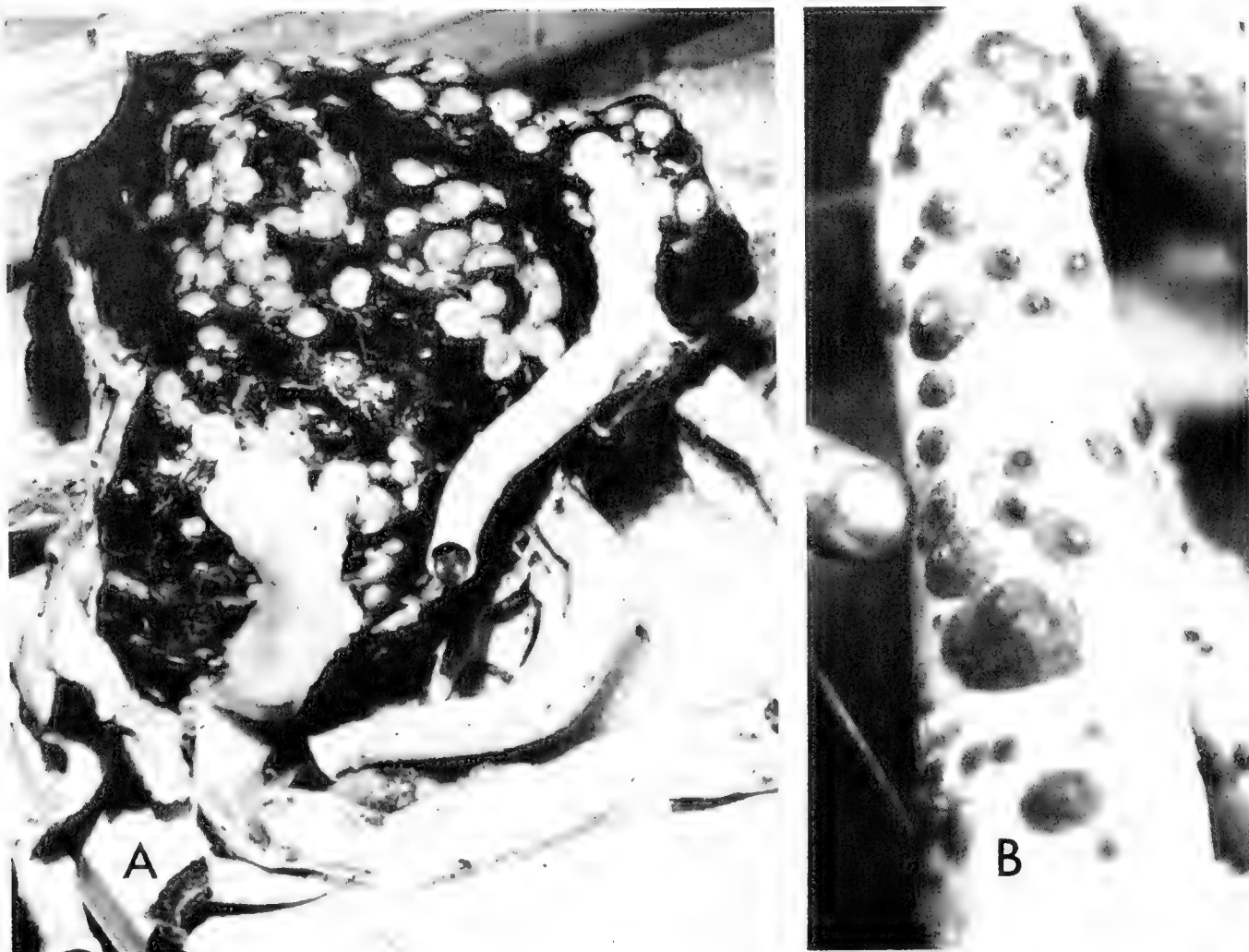


FIG. 12. A) 72 lb fragment of pillow basalt from dive 733, Garden of Eden, photographed on deck of support ship, showing *Neomphalus* in place and tubes of the vestimentiferan, *Riftia*. B) Tube of *Riftia* with attached *Neomphalus* in place, from 1979 expeditions, dive number unknown.

Wear on the rachidian and lateral teeth (Fig. 2D) provides additional evidence that the radula is used for grazing. The prominence of the jaw and buccal development and retardation of the gill development in juvenile specimens (Fig. 10D) suggests that grazing is the exclusive feeding mode of young stages. A retention of the grazing capacity and a combination of the two feeding modes in adults is therefore not surprising.

Sectioned specimens examined by Fretter, Graham & McLean (1981) showed ripe gonads with gametes in all stages of development, indicating that reproduction is a constant process throughout the year, in agreement with observations that in the absence of seasonal stimuli, most deep-sea invertebrates spawn throughout the year (Rokop, 1974; Rex et al., 1976).

The reproductive anatomy of *Neomphalus* indicates that copulation must take place, that sperm are stored in a receptaculum seminis, that fertilization probably takes place in the

proximal arm of the genital duct, and that fertilized eggs receive a coating of jelly-like material before extrusion from the distal arm of the genital duct (Fretter, Graham & McLean, 1981). Egg capsules have not been collected; thus, the next step is unknown and it is uncertain whether individually encapsulated eggs are released freely or attached to the substratum. A sufficient number of females have been collected to rule out the possibility that developing young are brooded under the shell. Egg masses have apparently not been found attached to the boulders from which the specimens were collected. The free release of coated eggs therefore seems most likely.

A coated egg, upon expulsion from the mantle cavity might settle in a crevice or perhaps become entangled by the byssal threads of the rift-vent mytilid. A postprotoconch larval shell with a sharp transition preceding the onset of adult sculpture is lacking, indicating that there is no planktotrophic veliger stage (Shuto, 1974; Robertson, 1976). Plankto-

trophic veligers are unknown in archaeogastropods (Fretter, 1969) and *Neomphalus* is no exception. Direct development through the trochophore and veliger stages probably takes place within the egg coating; crawling juveniles would emerge. During the growth of the first and second postprotoconch whorls, the juvenile *Neomphalus* would be active but would remain in crevices or among the byssal thread of the mytilids. When the transformation to the limpet is completed by the end of the second postprotoconch whorl, the limpets would take up a more sedentary, primarily filter-feeding existence where exposed to the strong flow of the rift-vent effluent. Those juvenile specimens recovered were recovered from residue samples associated with the mussels. The mature mussels live in a zone further away from the vents; thus there is some evidence that the early life of the juvenile takes place away from the vents.

The hypothesized course of development should enable the continuation of populations at each vent site, but it does not account for a mechanism of dispersal to more distant vent sites. Individual vent fields have been postulated to have a rather brief, ephemeral existence of several hundred years, necessitating the colonization of the new vent sites that emerge along the spreading sea floor.

Unlike *Neomphalus* the mytilid from the Galapagos Rift seems to have an effective dispersal mechanism. Because it has a well-defined larval shell, Lutz et al. (1979) inferred that there is a planktotrophic larval stage capable of long-range dispersal via bottom currents, its metamorphosis indefinitely delayed because of lower metabolic rates at ambient bottom temperatures. For *Neomphalus*, however, the colonization of new vents may be a matter of passive transport via larger, as yet unknown animals that may move between the springs.

DISCUSSION

As discussed by Fretter, Graham & McLean (1981), the neomphalid anatomy is an extra-

ordinary combination of archaeogastropod and mesogastropod characters combined with some unique features. That it is a highly modified and specialized archaeogastropod cannot be doubted, for it has such primitive archaeogastropod characters as a rhipidoglossate radula, a bipectinate ctenidium, epipodial tentacles, and the anterior loop of the intestine. Its features at the mesogastropod level of organization include the nearly complete reduction of the right pallial complex, a monotocardian circulatory system, expansion of the left kidney and formation of a nephridial gland, a copulatory organ in the male, and glandular gonoducts in both sexes. Unique features include the split osphradia, absence of a snout, dorsal position of the food groove, posteriorly directed cephalic tentacles, the enlargement of the left tentacle to form a copulatory organ, and an unusually positioned receptaculum seminis in the female.

Fretter, Graham & McLean (1981) discuss the leftward rotation on the anterior-posterior axis and the 90° of further torsion, so clearly shown in the placement of the internal organs, that accounts for many of the unusual aspects of the anatomy. These shifts and rotations can be understood as resulting from the early ontogeny, as described here, in which growth stops along the columella, forcing the columellar muscle to emerge to the base of the shell, and changing the orientation of the animal from its initial axis of coiling. Can it be shown that some of the features of this ontogeny occur in the evolutionary history of *Neomphalus*? Although *Neomphalus fretterae* is the only known member of a group that can be assigned to no family, superfamily, or suborder with living representatives, its evolutionary history can be sought in the fossil record, even though no fossil record of the genus itself has been found.³

Argument for an Archaic Origin

The neomphalid ctenidium is a departure from other gastropod ctenidia. It is a morphological innovation, an effective adaptation for filter feeding. The course of evolution is

³Four poorly known Devonian genera, *Procrucibulum*, *Paragalerus*, *Progalerus*, and *Protocalyptraea*, have names that imply some similarity to the shell form of calyptraeids. An affinity of these genera to the Calyptraeidae, which appeared in the Cretaceous (Hoagland, 1977) has to be ruled out. However, these genera are of interest as possible precursors to the Neomphalidae. Except for *Paragalerus*, drawings of reconstructed shells were illustrated in the Treatise (Knight et al., 1960). Each genus is known only from the type-species (Yochelson, personal communication), holotypes of which were described and illustrated by Knight (1941). The first three are represented by internal molds that lack information about protoconchs and muscle scars. *Protocalyptraea* is based on a small incomplete specimen (see also Linsley et al., 1978: 111), in which the peripheral frill would seem to preclude it as a precursor for *Neomphalus*. Affinity of these genera with the Neomphalidae cannot be completely dismissed, but it cannot be discussed further until better material is known.

marked by adaptive radiations, proliferations of new taxa following the introduction of successful morphological innovations (Simpson, 1953; Stanley, 1979). Thus, the neomphalid ctenidium should either have given rise to experimentation or be an end result of experimentation that has already taken place. Because *Neomphalus* has many unique and very specialized features and because it occurs in an environment with many limiting parameters, it surely must represent a single twig of a larger branch in a group having the same ctenidial structure. Its predecessors need not be limpets, for limpets are evolutionary dead ends, giving rise to adaptive radiation within a family or superfamily, but not serving as raw material for the further evolution of higher categories.

The limpet form has been derived from coiled predecessors with some frequency in gastropods. Among archaeogastropods, mesogastropods, opisthobranchs, and pulmonates there are many families of limpets. One example is known in a siphonostomate neogastropod—that of *Concholepas*. Except for the docoglossate patellaceans, for which a convincing derivation has never been offered, the limpet families are closely related to families or superfamilies having regular coiling, particularly those in which the shell aperture is holostomate rather than siphonostomate.

In some families or superfamilies—for example the trochacean Stomatellidae—there are limpet derivatives in which the entire progression from a trochiform to auriform and to a limpet shell form is represented. In others, like the Patellacea and the Calyptraeidae, there are no clues as to the shell form of the closest relatives. In these groups the derivation may have been sudden, in a process of paedomorphosis, a phylogenetic derivation in which reproductive maturity is attained in a stage before the development of adult characters (see Gould, 1968; Stanley, 1979). Normal adult coiling does not take place; rather, shell growth expands the aperture of the juvenile shell. In each case the limpet's anatomy, though modified by loss of coiling, retains a sufficient number of characters common to its ancestor (shared primitive characters) to permit its taxonomic placement. The external features of any limpet animal—for instance the modifications of the head for its generally constant retention under the protective shield of the shell—have some similarity from one family to another, but there are so many diverse anatomies represented in limpet fami-

lies that it is apparent that the form itself imposes few constraints upon the internal anatomy. Thus, the major features of a limpet's anatomy must be a reflection of primitive characters in its coiled predecessor.

In the absence of a living coiled group with anatomy comparable to that of a particular limpet, one may hypothesize the anatomy of the coiled predecessor, basing the reconstruction around the characters displayed by the limpet that are assumed to be primitive and not a consequence of the limpet mode.

Although the ctenidial filaments of *Neomphalus* are highly modified for filter feeding, the basic configuration of the neomphalid gill—aspidobranch with afferent attachment lacking—is a character that would be shared with the coiled predecessor. The only comparable condition in which an aspidobranch gill lacks an afferent membrane occurs in the Pleurotomariidae, in which the gills are paired. The Pleurotomariidae are regarded as the most primitive living gastropods. The superfamily Pleurotomariacea has a fossil record that is continuous from the Upper Cambrian. The possible affinity of *Neomphalus* to the extinct groups contemporary with the early pleurotomariaceans must be considered.

Although the subordinal classification of archaeogastropods proposed by Cox & Knight (1960) for use in the *Treatise* (Knight et al., 1960) is due for modification, all of the major divisions they recognized are traceable to the early Paleozoic, the only remaining doubt being that surrounding the appearance of the Patellina—whether early or late in the Paleozoic. Most of the living archaeogastropod families made their appearance by the early Mesozoic, well in advance of the burst of evolution in the Neogastropoda during the Cretaceous. If all other high-level, subordinal origins and initial radiation of archaeogastropod taxa took place in the Paleozoic, it is logical to assume that the subordinal distinction in *Neomphalus* also had a Paleozoic origin.

Excluding the living and fossil groups for which there is reasonable certainty that the gill condition was dibranchiate, and excluding the neritaceans, a completely divergent line (Fretter, 1965), for which the fossil record is well understood, those extinct, conispirally coiled archaeogastropods that may have had a unibranchiate mantle cavity were placed by Knight et al. (1960) in two of the suborders of Cox & Knight—the Macluritina and the Trochina. In that classification the extinct

superfamilies in the suborder Macluritina were the Macluritacea and Euomphalacea; in the suborder Trochina there were four extinct superfamilies: Platyceratacea, Microdomatacea, Anomphalacea, and Oriostomatacea. In addition there were five superfamilies of "doubtful subordinal position," for which single gills were likely: the Clisospiracea, Pseudophoracea, Craspedostomatacea, Palaeotrochacea, and Amberleyacea. These represent major evolutionary lines for which there is no direct information about their anatomies. Implicit in the ranking of these groups as families and superfamilies is the assumption that they had anatomical differences comparable to those that distinguish the living families for which the anatomy is known. Was there in fact as great a diversity in anatomies as is implied by the number of available supraspecific categories?

In the Trochacea, the only superfamily of the suborder Trochina recognized as living, many authors (Risbec, 1939, 1955; Yonge, 1947; Clark, 1958; Graham, 1965) have found the structure of the ctenidium to be virtually identical among species examined in all trochacean families, including the Trochidae, Stomatellidae, Turbinidae, and Phasianellidae.⁴ In its most familiar condition the trochacean ctenidium has a free tip with a strong ventral skeleton and gill leaflets of equal size on both sides of the axis. Posterior to the free tip about $\frac{2}{3}$ the length of the ctenidium is supported by both dorsal afferent and ventral efferent membranes (Fretter & Graham, 1962, figs. 53, 170). Here the leaflets on the right side of the axis, where there is more space, are larger than those of the left side, which are confined in a deep narrow chamber (see Yonge, 1947, fig. 25). The number of leaflets in the deepest reaches of this chamber may be reduced compared to those on the right. There are two modifications of this basic plan, that of *Umboonium* (Fretter, 1975) in which the entire gill is monopectinate and fused to the mantle wall throughout its length, and that noticed in *Margarites* (Fretter, 1955: 161) in which "the long aspidobranch gill lies freely in the mantle

cavity, and both afferent and efferent membranes are short. . . ." I have found that this latter condition is true of several other trochacean groups, as will be discussed further in a separate paper (McLean, in preparation).

All three of these different expressions of the trochacean gill have in common the transverse pallial vein, an additional conduit to the afferent ctenidial vessel, requiring at least a short afferent membrane for support (except in *Umboonium*). The left gill of the trochacean differs in this way from the left gill of the pleurotomariid, which lacks the transverse pallial vein and thereby has far less efficient circulation to the ctenidium. The trochacean pallial complex has evidently been highly effective from its inception, for the Trochacea are the most successful of living archaeogastropods in numbers of extant species and diversity of habitat. The extent of adaptive radiation possible for a group with the trochacean pallial complex has probably been attained.

The anatomical similarity of trochacean families is a remarkable fact, considering the diversity of shell shape, shell structure, and opercular structure. The close anatomical relationships between families with nacreous interiors and the Skeneidae and Phasianellidae, in which the primitive nacre is replaced by lamellar aragonite, would seem to belie the frequently emphasized principle that shell structure is a conservative character (for example, Batten, 1972, 1975). It is entirely possible that many of the extinct groups could have had anatomies that would place them in the Trochacea. The diversity of shell form in the Trochacea is broad enough to encompass the extremes of shell shape in some, though not all, of the extinct superfamilies. The problem can be approached by asking how the shell features in extinct groups would impose functional constraints upon their anatomies.

The Trochacea are dated from the Triassic by Knight et al. (1960: 247), but there is no clear argument in the literature to exclude many older extinct families or even super-

⁴The Skeneidae, doubtfully considered trochaceans a short time ago (Fretter & Graham, 1962: 618), are now shown to have trochacean anatomy (Fretter & Graham, 1977: 81). I have examined the pallial complex in Liotiidae and have found a gill condition like that described by Fretter (1955: 161) for *Margarites*. The Seguenziidae, however, despite the nacreous interior and modified rhipidoglossate radula (Bandel, 1979) have, in addition to the right subocular peduncle often occurring in trochids (see Crisp, 1981), a very large penis behind the right cephalic tentacle, as well as a fully monopectinate ctenidium (personal observation on a preserved specimen). This suggests, pending study of the internal anatomy, that mesogastropod-like specializations in the reproductive system have been attained and that a superfamily apart from Trochacea may be required.

families from the Trochacea. In Appendix 1, I show that a Permian group assigned to the Craspedostomatacea cannot be distinguished from extant trochacean Liotiidae, which suggests that the trochacean anatomy was well established in the Paleozoic.

The trochaceans share so many characters with the living Pleurotomariidae—nacreous interior, left kidney a large papillary sac, spiral caecum in the stomach, paired auricles, skeletal rods in the ctenidial filaments, large paired hypobranchial glands—that their derivation from a pleurotomariacean stock is readily understood (Fretter, 1964, 1966). However, the pallial condition of the Trochacea with the transverse pallial vein is not what would remain after a change amounting to little more than the loss of the right ctenidium.

Between the dibranchiate Pleurotomariacea and the unibranchiate Trochacea, *Neomphalus* is the only living form that is transitional in having a single bipectinate ctenidium with supporting skeletal rods in the filaments, no afferent support, and thereby no additional afferent conduits to the auricle.⁵ Except for its modification for filter feeding, the neomphalid ctenidium represents what remains after the loss of the right ctenidium of a pleurotomariacean. With or without the filament elongation, the pallial condition of *Neomphalus*, if it existed in a coiled shell, would be an alternative anatomy that could provide an explanation for the anatomies of some extinct Paleozoic groups. This pallial complex, like the trochacean pallial complex, would also impose constraints upon the diversity attained by adaptive radiation in some extinct groups.

As discussed in the section that follows, paleontologists have recently hypothesized that filter feeding was the likely feeding mode in the extinct Macluritacea and Euomphalacea. The neomphalid ctenidium provides a mechanism by which these archaic gastropods could have been filter feeders. Apart from the ease with which the neomphalid ctenidium may be invoked to account for filter feeding, there are clues about the coiled predecessor in the shell, for *Neomphalus* has a coiled phase in its first postprotoconch whorl. The ontogeny of *Neomphalus* provides clues to its phylogeny. My theory is that the Neomphalidae are limpet derivatives of the Euomphalacea.

The Euomphalacea, along with the Macluritacea, have been regarded as comprising the archaeogastropod suborder Macluritina (Knight et al., 1960). Yochelson (manuscript) provides arguments that a close affinity between the two groups is no longer tenable and that subordinal separation can be justified. A suborder Euomphalina is therefore necessary to include the superfamily Euomphalacea and the new superfamily Neomphalacea. Formal proposal of the new suborder is given in the concluding section of this paper. The Macluritacea are discussed further in Appendix 1.

In the section that follows, I summarize what is known of the Euomphalacea, with a particular effort to contrast the group with the Trochacea. This is followed by a review of the recent work that proposed a filter-feeding mode for the Euomphalacea.

Current Understanding of the Euomphalacea (Fig. 13)

Diagnosis: Shell low-spired to discoidal, broadly umbilicate, some genera open-coiled; coiling dextral, some discoidal genera with the coiling rising slightly above the apical whorl rather than descending below; peritreme complete, upper lip trace usually sinuous but not with slit or selenizone; aperture radial, its plane passing through the coiling axis; operculum (where known) calcified, external pattern multispiral, inner surface with adventitious layers.

Included Families: Euomphalidae de Koninck, 1881 (Middle Ordovician to Triassic); Euomphalopteridae Koken, 1896 (Silurian); Oriostomatidae Wenz, 1938 (Upper Silurian to Lower Devonian); Omphalocirridae Wenz, 1938 (Devonian); Omphalotrochidae Knight, 1945 (Devonian to Upper Triassic); Weeksiidae Sohl, 1960 (Triassic to Cretaceous).

The above diagnosis reflects an altered concept of the Euomphalacea, which is consistent with the paleontological literature that has appeared since the last attempt at full classification by Knight et al. (1960). They recognized three constituent families (Helicotomidae, Euomphalidae, and Omphalotrochidae) in contrast to six recognized earlier by Wenz in 1938 (Euomphalidae, Omphalo-

⁵A short afferent membrane is present in both neritaceans and the acmaeid patellaceans; both groups also differ from the Pleurotomariidae in lacking skeletal rods in the ctenidial leaflets (Yonge, 1947; Fretter, 1965). The cocculinid gill is not bipectinate and there are no skeletal rods (Thiele, 1903).

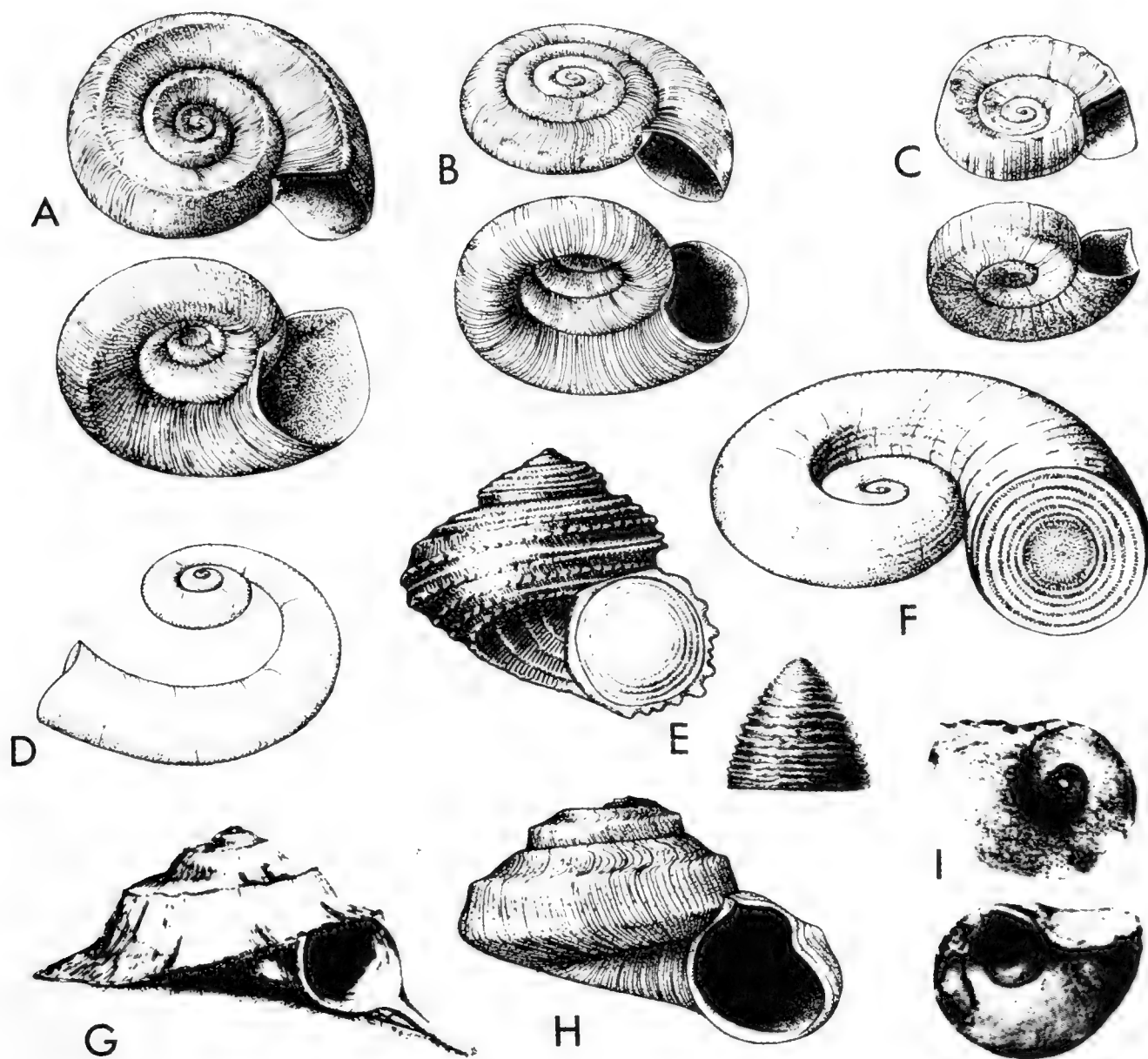


FIG. 13. Euomphalacean shells. A) *Euomphalus pentangulatus* J. Sowerby, 1814, Carboniferous (Euomphalidae), $\times 0.9$. B) *Straparollus laevis* (Archiac & Verneuil, 1842), Devonian, with attachment scars for shell fragments (Euomphalidae), $\times 1.5$. C) *Amphiscapha reedsi* (Knight, 1934), Pennsylvanian (Euomphalidae), $\times 1.1$. D) *Serpulospira centrifuga* (F. A. Roemer, 1843), Devonian (Euomphalidae), $\times 1.1$. E) *Oriostoma coronatum* Lindström, 1884, with operculum (identified by Lindström to genus) in lateral view, Silurian (Oriostomatidae), $\times 1.7$. F) *Beraunia docens* (Perner, 1903), Silurian (Oriostomatidae), $\times 1.1$. G) *Euomphalopterus alatus* (Wahlenberg, 1821), Silurian (Euomphalopteridae), $\times 0.6$. H) *Omphalotrochus whitneyi* (Meek, 1864), Permian (Omphalotrochidae), $\times 1.1$. I) *Weeksia lubbocki* Stephenson, 1941, Cretaceous (Weeksiidae), $\times 1.7$. After Knight et al. (1960), except operculum in E, after Lindström, 1884, and G, after Linsley et al., 1978.

cirridae, Platyacridae, Cirridae, Oriostomatidae, Poleumitidae, and Macluritidae). Two recognized by Wenz—the Omphalocirridae and Oriostomatidae—are now returned to the list. Of the other families recognized by Wenz, Platyacridae and Cirridae are here regarded as trochacean (see Appendix 2), Poleumitidae is synonymous with Euomphalidae (Knight et al., 1960) and Macluritidae is dis-

cussed in Appendix 1. In the absence of an overall revision of the Euomphalacea, the important changes since 1960 may be summarized as follows:

Omphalocirrus was regarded by Wenz (1938) as a sinistral euomphalacean, but by Knight et al. (1960) as macluritacean; Yochelson (1966) returned it to the Euomphalacea (Euomphalidae) as a dextral form with the

spinose projections on the under rather than the upper side; Linsley (1978a) independently proposed a family Omphalocirridae to include also the genus *Liomphalus* (Fig. 14), which lacks the spinose projections, neglecting to note that Wenz (1938) had previously proposed the family.

Euomphalopterus (Fig. 13G) had been treated as pleurotomariacean, until its peripheral frill was no longer regarded as the site of a selenizone by Linsley et al. (1978), who transferred its family to the Euomphalacea.

Oriostoma (Fig. 13E), with its multispiral operculum and nacreous interior, was given family and superfamily status in the Trochina by Knight et al. (1960); Linsley (1978a) suggested the transfer of Oriostomatidae to the Euomphalacea, in which it had been previously placed by Wenz (1938). Opercular characters support this assignment, as discussed in the section that follows.

Euomphalid genera of the Mesozoic included by Knight et al. (1960) require further attention: some may need to be reassigned to the Trochacea. Sohl (1960) proposed the euomphalacean family Weeksiidae for three biangulate, discoidal genera—*Weeksia* (Fig. 13I), *Discohelix*, and *Amphitomaria*—differing from euomphalids in having a prosocline upper whorl surface. He also noted that *Hippocampoides* is a magiliniid (i.e., coralliophilid). I assign *Anosostoma*, which had a greatly expanded final lip (Fig. 18B) to the trochacean Liotiidae in Appendix 2; no genera with expanded apertures remain in the Euomphalacea.

Yochelson (manuscript) removes *Lesueurilla* (Fig. 15A) and other genera with a slit or slit-like feature on the upper lip to the Pleurotomariacea, and suggests that all such genera should be reconsidered. Rohr & Smith (1978) have treated *Odontomaria* (Fig. 15C) as pleurotomariacean. I propose that *Helicotoma* (Fig. 15D) with its elevated slit be included in this transfer, thereby removing the Helicotomidae of Knight et al. (1960) from the Euomphalacea. Transfer of such genera to the Pleurotomariacea is in essence a return to the classification of Wenz, who associated them with the raphistomatid pleurotomariaceans.

The Euomphalidae have been reduced since 1960 by the removal of groups mentioned above. The content of the Omphalotrochidae (Fig. 13H) remains unchanged.

It is beyond the scope of this review even to

estimate the number of euomphalacean taxa. Additional genera have been proposed since 1960, and there are several entries per year in the *Zoological Record* pertaining to the group. In the monographic series on Permian gastropods of the southwestern United States (Yochelson, 1956, 1960; Batten, 1958), 45 bellerophontacean species, 32 pleurotomariacean species, and 31 euomphalacean species were treated. All the other archaeogastropods (Patellacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea) together totaled only 21 species. It is therefore clear that the Euomphalacea comprised a major share of the Paleozoic gastropod fauna.

Shell characters: Shell structure has heretofore been an important part of the diagnosis for the Euomphalacea, but it is omitted here because the admission of the nacreous Oriostomatidae (Lindström, 1884; Knight et al., 1960) changes the previous concept that the Euomphalacea were entirely non-nacreous. As discussed above, the inclusion of families with different shell structure is currently accepted in the Trochacea. Thus, the inclusion of nacreous and non-nacreous families in the Euomphalacea is not without precedent.

Bøggild (1930: 301), in his classic survey of the shell structure of mollusks, reported on the Euomphalidae as follows: "In the shells of this old family the aragonite is, of course, never preserved but it seems to have existed originally. In most members examined by me there is a prismatic layer which is sometimes rather regular and which indicates that the shell, in such instances, must have possessed an upper calcitic layer." Knight et al. (1960: 189) essentially repeated Bøggild's remarks in their superfamilial diagnosis.

The calcitic layer need not have great taxonomic significance, for Bøggild (1930: 298) noted that it "must be said to be a rather accidental element," for it occurs "in a great number of families," and may be lacking altogether in some genera within families where it is otherwise known.

Shell structure would be an extremely useful character in archaeogastropod classification if it were always possible to determine the original structure of fossil shells. Little can be said of most Paleozoic and Mesozoic genera and nothing can be established for those of the Cambrian and Ordovician. Presumably, as in the Trochacea, nacreous interiors would be primitive in the Euomphalacea, persisting

only in the family Oriostomatidae, a group unknown past the Devonian.⁶

Although the range of possible shell forms in the Trochacea overlaps that of the Euomphalacea (see Appendix 2), the euomphalaceans are generally lower spired. Some, like the genus *Serpulospira* (Fig. 13D), are open-coiled, defined by Yochelson (1971: 236) as "shell forms that fail to have some or all of the whorls in contact but that do not obviously deviate from logarithmic factors in rate of coiling." Open coiling occurs with some frequency in the Euomphalacea, but in a review of living forms that are open-coiled, Rex & Boss (1976) reported no trochaceans with this mode of coiling.

The diagnosis for Euomphalacea given here omits reference to the mode of coiling as either orthostrophic or hyperstrophic, as in Knight et al. (1960). Hyperstrophic coiling was defined by Cox in Knight et al. (1960: 131) as: "dextral anatomically, but shell falsely sinistral. . . ." This is a concept easily understood in conspirally coiled forms in which there is dextral anatomy within a sinistral shell, as diagrammed by Cox in Knight et al. (1960: 111) for the ampullariid genus *Lanistes*,⁷ but it is here (on the advice of Yochelson) considered as an inappropriate term to describe the coiling in such discoidal euomphalacean genera as *Beraunia* (Fig. 13F), *Amphiscapha* (Fig. 13C) and *Liomphalus* (Fig. 14), in which the coiling rises slightly above the apex instead of below it. Living gastropods that are anatomically dextral have an operculum with a counterclockwise spiral on the external surface (Pelseneer, 1893; Robertson & Merrill, 1963). Opercula with a counterclockwise spiral are known in such euomphalacean genera as *Liomphalus* (Fig. 14), providing the evidence generally accepted by paleontologists that

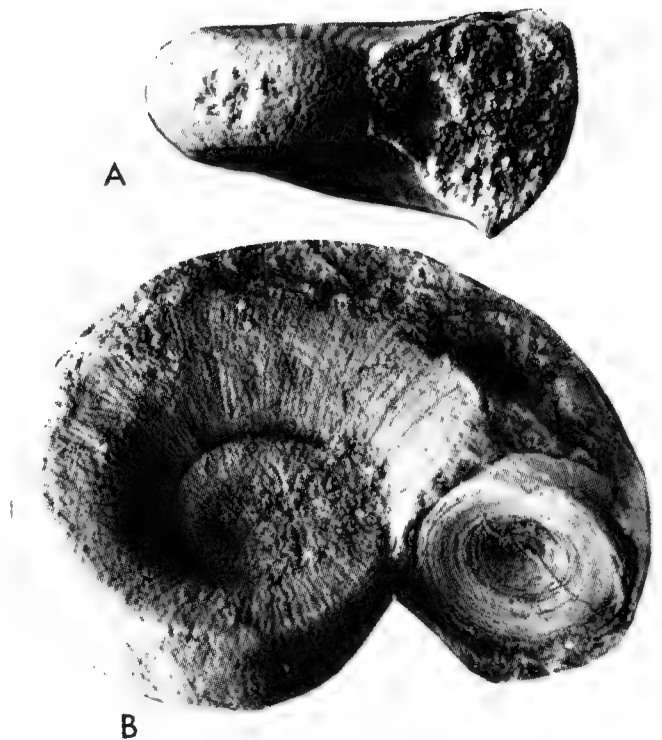


FIG. 14. *Liomphalus northi* (Etheridge, 1890), Devonian, Lilydale Limestone, Lilydale, Victoria, Australia. Showing the omphalocirrid operculum in place and coiling differences attributed to sexual dimorphism by Linsley (1978a). A) Apertural view of specimen thought to be an immature female, diameter 20 mm, coiling essentially orthostrophic. B) Oblique apical view of specimen considered a mature male, diameter 75 mm, operculum in place, coiling "hyperstrophic." Photos courtesy R. M. Linsley, specimens in the National Museum of Victoria.

this and similar "hyperstrophic" genera for which opercula are unknown were anatomically dextral.

"Hyperstrophic" coiling has been used as a generic-level character in some members of the families Euomphalidae, Omphalocirridae

⁶Quinn (1981) has suggested that the nacreous Seguenziidae (see also Bandel, 1979) could have been derived from the Omphalotrochidae, a family here included in the Euomphalacea. Because nacre is unknown in the Omphalotrochidae, such a derivation would require the unlikely reversion to nacre.

⁷Hyperstrophy is known in two living mesogastropod families—in the larval stages of architectonicids and in the African ampullariid genus *Lanistes* (see Wenz, 1938). In architectonicids it is normally limited to the planktotrophic veliger stage (Robertson, 1964), although rare abnormal specimens have been found in which hyperstrophy persists in the adult (Robertson & Merrill, 1963). Normally the coiling changes to orthostrophic in the first teleconch whorl. In *Lanistes* it is apparent that these moderately high-spired forms carry the shell directed to the left rear as in sinistral gastropods, but that water currents move in the mantle cavity from left to right as in dextral gastropods (Lang, 1891: 368, fig. 21, copied in part by Cox in Knight et al., 1960, fig. 67). Andrews (1965: 71) studied *Lanistes* and noted that its mantle cavity is deeper than that of orthostrophic members of the family, but she did not discuss the functional advantage of hyperstrophy in *Lanistes*. Hyperstrophy raises some questions, for, according to descriptions of torsion (Crofts, 1955), the normal course of development leads to dextral orthostrophic coiling. Crofts showed that in the archaeogastropods *Haliotis*, *Patella*, and *Calliostoma*, the first phase of torsion involves a delayed development of the left compared to the right post-torsional retractor muscle, which imposes an immediate asymmetry upon the protoconch, causing the direction of coiling to proceed in the usual dextral manner. In sinistral gastropods the anatomical sinistrality may be traced to the first stages of cleavage, as recently reviewed by Verdonk (1979). Discussions of torsion (Lever, 1979, and references therein) make no mention of hyperstrophy. How hyperstrophy in architectonicids and *Lanistes* can follow torsion is worthy of further investigation.

and Oriostomatidae. Linsley (1978a) considered that the four omphalocirrid species he studied showed sexual dimorphism—a reasonable conclusion based on the equal numbers of supposed male and female morphotypes in each species. Those he interpreted as females (Fig. 14A) tended to have isostrophic to orthostrophic coiling, in contrast to the decidedly “hyperstrophic” males (Fig. 14B). This intraspecific variability in coiling direction indicates that there was no anatomical difference between orthostrophic and “hyperstrophic” euomphalaceans.

There are no families or genera in the Euomphalacea in which there is a thickened final lip or abrupt change in coiling direction, as in the Trochacea (see Appendix 2).

The diagnosis for the Euomphalacea in Knight et al. (1960, p. 189) included the provision: “commonly with channel presumed to be exhalant occupying angulation on outer part of upper whorl surface.” Yochelson (manuscript) now notes that most euomphalaceans do not have a prominent shoulder and that in those that have an angulation the shell is thickened in that area and there is no interior channel to be regarded as an exhalant route. Thus, this provision of the diagnosis is no longer included. It is to be noted that the growth line on the upper lip of many euomphalaceans is often sinuous and opisthocline, as in *Omphalotrochus* (Fig. 13H), although *Weeksia* (Fig. 13I), with a prosocline lip, is an exception. The trochacean lip is usually prosocline.

Euomphalacean protoconchs were described by Yochelson (1956: 195) as “commonly discoidal,” but to my knowledge have not been illustrated. Dzik (1978) illustrated protoconchs of some Ordovician gastropods that resemble those of modern archaeogastropods. However, it is not certain whether any of those he figured are referable to the Euomphalacea.

The concept of the “radial aperture” was introduced by Linsley (1977: 196), defined as “an aperture whose plane passes through the axis of coiling and thus lies along a radius from the coiling axis to the shell periphery.”

Radial apertures are characteristic of all families in the Euomphalacea. Apertures in the Trochacea tend to be oblique, or—in Linsley’s terminology—tangential, defined as “an aperture whose plane is tangent to the body whorl,” so that it and the ventralmost part of the body whorl lie in one plane.

Multispiral calcareous opercula are known in the families Omphalocirridae (Fig. 14) and Oriostomatidae (Figs. 13E, F). Other euomphalacean families may have had multispiral opercula that were uncalcified, or their original aragonitic opercula may have preserved poorly compared to the calcitic shell. Such mineralogic differences between shell and operculum are known in some Recent turbinids and neritids (Adegoke, 1973). The omphalocirrid operculum is best known in *Liomphalus northi* (Fig. 14). It has recently been described by Yochelson & Linsley (1972) and Tassell (1976: 9). This type of operculum varies in thickness, is disc-shaped, slightly concave externally, beveled to fit tightly within a circular aperture, and has numerous externally visible volutions and internal laminar layers. It is quite similar to the *Cyclosporgia* operculum, an operculum first thought to be a sponge, but redetermined by Solem & Nitecki (1968) as a gastropod operculum from an unknown shell.⁸ External surfaces of opercula are known in two other omphalocirrids treated by Linsley (1978a). The oriostomatid operculum is known in *Beraunia* (Fig. 13F) (see also Knight, 1941, pl. 80) and in *Oriostoma* (Fig. 13E) (see also Lindström, 1884, pl. 17, and Kindle, 1904, pls. 11, 14). Externally, the oriostomatid operculum is conical, in some cases higher than broad, the central nucleus projecting, the succeeding whorls descending and having raised edges. The mode of formation of both the omphalocirrid and oriostomatid opercula would be similar, with accretions at the edge produced in the opercular groove on the animal’s foot, and adventitious layers added on the underside, as it rotates in a clockwise direction to produce the counterclockwise coil of the external surface. These opercula are unlike the turbinid operculum, in which a

⁸Yochelson & Linsley (1972) considered that the *Cyclosporgia* operculum matches the operculum described by Tyler (1965: 348, pl. 48, figs. 19–25) and assigned by Tyler to his species *Turbinilopsis anacarina*. That assignment violates the well-reasoned hypothesis of Solem & Nitecki that the shell of *Cyclosporgia* must have been a “planorbiform, depressed helicoidal, or helicoidal shell possessing a circular aperture, deep sutures. . . .” *Turbinilopsis* as applied by Tyler is assigned to the Anomphalacea. In my opinion, such a shell is wholly inappropriate for the *Cyclosporgia* operculum because it has a tangential aperture and lacks an umbilicus. I cannot agree with Yochelson & Linsley (1972) that an operculum as discrete as those of *Liomphalus* and *Cyclosporgia* can be convergent in widely different families. I am certain that a euomphalacean shell eventually will be found for the *Cyclosporgia* operculum.

paucispiral or multispiral pattern is preserved on the inner surface but is obliterated on the external surface where it is enveloped by the animal's foot. The omphalocirrid and orio-stomatid opercula differ from the trochid, turbinid and liotiid opercula in depositing adventitious layers on the internal surface. Thus, the euomphalacean and trochacean opercula, though both multispiral, are entirely different. There is convergence in shell form in the Trochacea and Euomphalacea, but the distinction may be clearly drawn between those members in which opercula are known.

Feeding and locomotion: During the preceding decade a number of papers have considered possible modes of locomotion and feeding in the Euomphalacea. The theme has been developed that these gastropods rested with the aperture perpendicular to the substratum, unlike the trochaceans in which the shell is balanced over the cephalopedal mass and the aperture maintained in a position parallel to the substratum.

Yochelson (1971) discussed open coiling and septation in the Devonian euomphalid *Nevadispira* (which is similar to *Serpulospira*, Fig. 13D). He suggested that it had a sedentary life mode because an animal with open coiling would have great difficulty balancing the shell for locomotion, the septation that shortened the body mass would further hamper locomotion, the open coiling would increase the area of contact with the substratum, and the "hyperstrophic" coiling would raise the aperture above the sediment. Thus, this "would appear to be a natural response in shape change for a coiled animal living a sedentary life on a mud bottom." He suggested that euomphalids may have been deposit feeders rather than herbivores and that the open-coiled members "may have further specialized toward ciliary feeding." This suggestion was in contrast to the traditional dictum that all archaeogastropods are herbivorous.

Linsley & Yochelson (1973) discussed Devonian members of *Straparollus* (Fig. 13B) and *Euomphalus* that had the habit of attaching foreign matter to the shell in a way comparable to that of the modern Xenophoridae. They concluded (1973: 16) that these euomphalids were unlikely to have balanced the shell like trochaceans, it being "most unlikely that *Straparollus laevis* could have held its shell motionless in the normal carrying position for the several hours required" for implantation of objects. This was further evidence

that euomphalaceans were sessile animals resting on the base of the shell.

Peel (1975a) also discussed the probability that open-coiled Paleozoic gastropods were sedentary. He contrasted open-coiling with the uncoiling of higher-spired forms, which also suggests a sedentary existence (see also Gould, 1969). He concluded that "Paleozoic gastropods were more diverse in their feeding habits than comparison with extant gastropods would suggest."

Linsley (1977, 1978b, 1978c, 1979) developed the concept of the radial aperture—in which the plane of the aperture would pass through the coiling axis. Gastropods with radial apertures would have difficulty balancing the shell over the cephalopedal mass. His "law of radial apertures" states (1977: 109): "Gastropods of more than one volution with radial apertures do not live with the plane of the aperture parallel to the substrate. Most typically it is perpendicular to the substrate." Few living gastropods have radial apertures. In one major example, the Architectonicidae, the animals are mostly sedentary and "usually lie with the shell on the substrate" (Linsley, 1977). For the Euomphalacea he stated (1977: 204): "I suggest that all had adopted a rather atypical gastropod posture of lying with the shell flat on the sediment, rarely if ever hoisting it above the cephalopedal mass in the stance associated with the majority of modern forms." The only possible means of locomotion would be what Linsley has called "shell dragging." In view of the sedentary habit, Linsley has considered suspension feeding to be the most likely feeding mode, "either by filtering with their gill(s) or by casting mucous nets" (1979: 251).

Schindel (1979) found encrusting epibionts on the exposed apical cavity surface of the "hyperstrophic" euomphalid *Amphiscapha* (Fig. 13C), whereas the basal surfaces were free of encrustations. This indicates that the basal surface was never exposed as would happen if the life mode involved shell balancing. This provides further confirmation for Linsley's principle.

I can here add the observation that the orio-stomatid operculum precludes locomotion by shell balancing in that group. Shell-balancing gastropods use the operculum as a protective pad placed between the shell and the foot. In the turbinids the dorsal surface of the foot envelops the external surface of the operculum, keeping it smooth, or in some species producing intricate sculpture. The

turbinid operculum is not so thick that it cannot be carried in the usual position between the foot and the shell. However, the conical orio stomatid operculum, which may be higher than broad (Fig. 13E), was not enveloped by the foot (which would have altered its sharp sculpture) and is too large and sharply pointed in the center to have been carried between the foot and the shell during locomotion.

Extinctions: Euomphalacean genera and species proliferated in the Paleozoic. Few stocks survived the mass extinctions at the close of the Permian. Vermeij (1975, 1977) correlated their further decline in the Mesozoic with the appearance of such shell-crushing predators as teleosts, stomatopods and decapod crustaceans. The broadly umbilicate or openly coiled euomphalacean shells are poorly constructed to resist crushing. There are few broadly umbilicate forms among modern marine gastropods. Shells tend to be sturdier, with narrower apertures, often having such modification as apertural dentition or spiny external surfaces to strengthen the shell.

More recently Thayer (1979) has discussed a trend in the evolution of marine benthic communities. Paleozoic communities on soft sediments were dominated by immobile suspension feeders such as articulate brachiopods, dendroid graptolites, tabulate and rugose corals, bryozoa, cystoids, and blastoids. In the Mesozoic and Cenozoic, the soft-bottom benthic communities are dominated by infaunal deposit feeders that include protobranch bivalves, irregular echinoids, certain crustaceans, holothurians, and annelids. The disruption or bioturbation of the sediments by the large infaunal deposit feeders would foul or bury the soft-substrate suspension feeders, particularly their juvenile stages. This, in addition to their vulnerability to shell-crushing predators, could also account for the demise of the soft-substrate living Euomphalacea, a group not mentioned by Thayer.

Previous interpretations of euomphalacean anatomy: The Euomphalacea have been variously interpreted as either dibranchiate or unibranchiate. Knight (1952: 40), in his classic paper on primitive gastropods concluded that in "hyperstrophic" forms there was "very little room for a right ctenidium" and assumed that it and the associated organs had been lost. Yochelson (1956: 195) considered that the Euomphalacea were dibranchiate: "The characteristic keel on the upper whorl surface

probably was the locus of an anus as in the Macluritacea, and the distance of this keel from the suture would have allowed ample space in the mantle cavity for paired ctenidia." Cox & Knight (1960: 262) took a position on middle ground: "Right ctenidium inferred to have been reduced and in some forms possibly absent." Golikov & Starobogatov (1975) included the "Order Macluritida" among the dibranchiate gastropods.

Linsley (1978c: 440) suggested that Macluritacea and Euomphalacea "had only one inhalant and one exhalant stream and probably only a single gill," and that the shape of the aperture "makes sense if these forms did not undergo torsion." Thus, they "therefore should not be considered gastropods." Linsley's theory has not as yet been fully detailed. It seems to me, however, that the euomphalacean operculum strongly suggests gastropod affinities.

Yochelson (manuscript) now advocates the removal of genera with a slit from the Euomphalacea and finds no indication of an exhalant canal in those that remain; he therefore finds no evidence of paired gills.

My theory for the anatomical reconstruction of the Euomphalacea includes torsion, allows both orthostrophy and "hyperstrophy," and reconstructs them as unibranchiate, as originally proposed by Knight (1952). Peel (1975a: 218) understood that bipectinate ctenidia modified for filter feeding would entail some essential differences from the ctenidia of modern filter feeders: "The effects of this difference in the structure or even number of ctenidia upon the form of a mantle cavity adapted to ciliary feeding are perhaps impossible to estimate. It is certainly possible that another arrangement of ctenidia and mantle cavity was required and that this was at variance with the elongate ctenidium and long narrow mantle cavity of the Recent species." The neomphalid mantle cavity now provides the best model for the reconstruction of the euomphalacean mantle cavity. There is little essential difference between the filter-feeding mantle cavities of calyptraeid limpets and the coiled turritellids. The placement of the neomphalid feeding mechanism within the euomphalacean shell is equally plausible. I therefore accept the filter-feeding mode of life for the euomphalaceans recently suggested by Yochelson, Peel, and Linsley.

Apart from the ease with which the neomphalid mantle cavity could be construed as having been possible within a coiled shell,

there is a strong correlation between the musculature and ontogenetic development of the shell in *Neomphalus* and that of the euomphalaceans, as discussed in the section that follows.

Neomphalus as a Euomphalacean Derivative

Evidence has been presented in the preceding section that their radial apertures precluded the euomphalaceans from balancing the shell over the cephalopedal mass. Thus they had to rest the shell on its base, which was concave for orthostrophic shells or flat for "hyperstrophic" shells. This is in complete contrast to the life mode of the trochaceans.

Trochaceans have tangential apertures—the tangential aperture exposes less body surface than the radial aperture when the animal is attached to a hard substratum. The shell is balanced over the cephalopedal mass and the columellar muscle is ventral to it during locomotion. Even when retracted within the shell, the cephalopedal mass remains dorsal to the columellar muscle, which means that the animal actually rests upon its left side when the shell is resting upon the base. Thus the head always maintains a position that is perpendicular to the axis of coiling. When the animal extends, a twist in the alignment of the head of approximately 45° is necessary to balance the shell, tilting the spire up and to the right rear.

What can be said about the position of the head relative to the axis of coiling in the extinct euomphalaceans? In the absence of shell balancing, there is no reason to assume that the cephalopedal mass of mature animals was aligned to the coiling axis. In normal feeding posture the head of any animal needs to be balanced relative to the substratum. If the head and body of a euomphalacean animal in retracted condition was aligned toward the coiling axis, a 90° twist would be required to place it in a feeding posture, an unnecessary requirement for an animal that never needs to balance its shell. Moreover, the feeding posture of a filter-feeding gastropod is one in which the head remains within the shell aperture, as in *Turritella*. Most likely the head would be permanently aligned relative to the substratum. The columellar muscle would therefore be lateral rather than ventral to the cephalopedal mass. Modern gastropods with irregular coiling have abandoned coiling and thereby dissociated the columellar muscle from the axis of coiling. For the Euom-

phalacea, my supposition is that regular coiling continues, but the alignment of the body relative to the coiling axis shifts by 90°. Mechanical considerations require that the major area for muscular insertion on any discoidal shell be on the inner, columellar wall. Muscle attachment on any other surface would be unnecessary. For an animal oriented to the substratum in a flat-lying shell, this will mean that the right side of the body assumes the entire muscle attachment function. There is no need for a left columellar muscle. The left side of the body is therefore available for a long, deep mantle cavity.

Neomphalus is the logical result of the conversion of the euomphalacean body plan to the limpet form. One of the most significant features of *Neomphalus* is the occlusion by columellar muscle of the entire right side of the body posterior to the neck. The columellar muscle is lateral to the body mass, just as it must have been in a euomphalacean.

Veliger stages of all gastropod larvae are similar in having the shell balanced over the cephalopedal mass. Post-veliger euomphalaceans would be motile, would balance the shell, and would feed by grazing. Growth of the columellar muscle would be programmed to shift the muscle to the right of the cephalopedal mass, causing the animal to lose the shell-balancing capacity and assume the filter-feeding mode.

In its protoconch and first postprotoconch whorl, the neomphalid animal must carry its shell with the coiling axis and plane of the aperture parallel to the substratum. Its transformation to the limpet form involves cessation of coiling and a 90° shift of the shell to place the coiling axis perpendicular to the substratum. The same 90° shift in the placement of the coiling axis is presumed to occur in the ontogeny of all the extinct euomphalaceans in which the regular coiling continues. The euomphalacean alters the orientation of the animal within the shell; the neomphalacean effects the change by growth stoppage along the columellar lip; in both cases the initial coiling axis becomes perpendicular to the substratum. This is the essential requirement in euomphalacean and neomphalacean ontogeny that distinguishes these superfamilies from all other living archaeogastropods, whether coiled or limpet derivatives of coiled forms.

The relatively large size of the neomphalid larval operculum and its vestigial retention in juvenile sizes far larger than that of other

limpets is additional evidence that a coiled ancestry is phylogenetically close. The presence of epipodial tentacles only near the site of the operculum is consistent with the idea that euomphalaceans were filter feeders in which the head and foot were kept within the shell in feeding position. There would be no use of epipodial structures away from the operculum in euomphalaceans.

The origin of *Neomphalus* may have been a rapid event brought about by a relatively simple alteration of the developmental process, one that inhibited growth along the basal portion of the columellar lip, forcing continued growth to produce lip expansion and the formation of a limpet in much the same process as revealed in the ontogeny of *Neomphalus*. If such an event in an euomphalacean stock took place near an active rift-vent site, the new limpet would be especially adapted to utilize the abundant sulphur bacteria in this rocky environment. *Neomphalus* represents a highly successful response to an abundant food supply, entailing no loss of body size, using less calcium than that required by a coiled shell, and affording some protection from shell-crushing predators. The limpet conversion represented by the Neomphalidae was perhaps the only as yet untested morphological theme in a stock already specialized for filter feeding.

The Mesozoic euomphalacean family Weeksiidae, proposed by Sohl (1960), has some features in common with *Neomphalus*. Characters shared by *Neomphalus* and the Cretaceous *Weeksia* (Fig. 13I) mentioned by Sohl (1960: 50) are: "ornament usually poorly developed . . . growth lines prosocline on upper surface . . . moderately large shell with raised naticoid protoconch." The discoidal shell of *Weeksia* has an orthostrophic protoconch whereas the later whorls are faintly "hyperstrophic." The early shell ontogeny of *Neomphalus* does not include a stage having the biangulate lateral profile of weeksiid genera. However, I have examined specimens of the similarly constructed biangulate euomphalacen *Amphiscapha* and note that the earliest whorls are unsculptured. Thus the postprotoconch whorls of *Weeksia* and *Neomphalus* can be considered far less different than the mature teleoconch whorls. If the juvenile shells are to provide the only characters in common, it is unlikely that the direct ancestor of *Neomphalus* will ever be known.

If *Neomphalus* was derived from weeksiid euomphalaceans, the minimal age for the family would be Cretaceous. Because the euomphalaceans were the dominant uni-branchiate gastropods in the Permian, it can be argued, however, that the Paleozoic, when numerous stocks were present, is the most likely time of origin of the Neomphalidae.

Entry of *Neomphalus* into the Rift-Vent Community

The rift-vent habitat has probably been available over long periods of geologic time, because it is likely that hydrothermal vents have accompanied tectonic movements throughout the entire history of the earth. The oceanic rift system is global in magnitude (Corliss et al., 1979: 108), although the full extent of hydrothermal activity along it is unknown. Vents have not yet been found along the mid-Atlantic Rift, but at least two widely separated sites in the Pacific are now known.

As stated by Spiess et al. (1980: 1424): "The similarity of the East Pacific Rise and Galapagos Rift fauna suggests that these vent communities are widespread and that their species are equipped with sophisticated dispersal mechanisms well suited for the detection of the discontinuous and ephemeral vent conditions." This similarity also suggests stability of the community. Invasions of species from other habitats must be of rather infrequent occurrence. Possible barriers to new colonizations of the community include the differing chemical conditions, cold water masses separating the warm environment of the habitat from other warm environments, and the scarcity of hard substrates to serve as stepping stones from shallow water into a deep-sea hard-substrate environment. Molluscan predators such as sea stars and drill snails are not known to be present. In the absence of these predators, the rift-vent community seems well suited to provide refuge for an archaic molluscan group specialized for filter feeding.

Modern filter-feeding gastropods, the turritellids and the calyptraeids, occur in shallow water from the intertidal zone to the continental shelf, with none known from continental slope or abyssal depths. This evidently reflects a scarcity of sufficient suspended food for these relatively large forms under normal conditions at abyssal depths. A filter-feeding gastropod the size of *Neomphalus* would

have to have a shallow-water origin, from which it would make the transition to the rift-vent community with no interruption in abundance of the food source, through rift-vent sites in progressively deeper water. A shallow-water origin for the Neomphalidae is also consistent with findings by Clarke (1962) that no molluscan families have originated in the deep sea. Shallow water occurrences at one time are known for all deep-sea mollusks with continuous Paleozoic to Recent fossil records.

There is precedence for the interpretation of a rift-vent community member as a relict species. Newman (1979) considered the stalked barnacle *Neolepas zeviniae*, which he named from hydrothermal vents on the East Pacific Rise at 21° N latitude (see Grassle et al., 1979; Spiess et al., 1980), to represent a stage of barnacle evolution attained in the Mesozoic.

Newman's hypothesis for the origin of *Neolepas* is as follows (Newman, 1979: 153): "Habitat also favors the interpretation that *Neolepas* is a relict form, having found refuge near deep, hydrothermal springs. Such a refuge may have been attained in the late Mesozoic when predation pressures on sessile organisms are inferred to have dramatically increased. Though immigration into the hydrothermal environment by deep-sea stocks is a distinct possibility, in the present case, the route appears more likely to have been from relatively shallow waters of warm and tropical seas where tectonically active rifts intersect continental crust, and perhaps where islands are forming along ridge crests."

This explanation provides for both the antiquity and the route into the rift-vent community for *Neolepas zeviniae*. It is also the best hypothesis to account for the presence of *Neomphalus* in the rift-vent community. If the origin of *Neomphalus* was quickly followed by submergence, as postulated by Newman for *Neolepas*, a fossil record of *Neomphalus* in shallow water would be elusory. Fossil records of deep-sea mollusks are all but unknown because of the solubility of calcium carbonate shells at abyssal depths (Berger, 1978; Killingley et al., 1980).

According to my supposition, the origin of the Neomphalidae took place at some point between Late Paleozoic to Late Mesozoic, giving it an age in the range of 70 to 250 million years. If a fossil record for the family could verify such an age, it could be called a

"living fossil," a term limited by Eldredge (1975) and Stanley (1979: 258) to "taxa that have persisted for long intervals of time with little evolutionary change and that are primitive or archaic in comparison with living taxa of the same class or phylum." It can be argued that the neomphalid gill can only be archaic, since it is not represented in any other family in normal marine habitats.

If there were a fossil record of the family, the Neomphalidae could be compared to the nautiloid cephalopods, the neopilinid monoplacophorans, the pleurotomariid archaeogastropods, and the abyssochrysid loxone-mataceans, recently added to the list of living fossils by Houbrick (1979). These families were once diverse in shallow seas of the Paleozoic and Mesozoic but survive now at the lower limits of the continental shelf to the abyss. Each family is still represented by several species. Speciation events have apparently kept pace with extinctions. The average duration—the Lyellian curve—for marine gastropod longevity is about 10 million years (Stanley, 1979: 237). Even if a neomphalid species could endure as long as 20 or 30 million years, numerous speciation events should have occurred, and other species (or genera) are likely to be living now at other rift-vent systems. An effective dispersal mechanism for *Neomphalus* is unknown. This is a factor that should increase its speciation potential, because new colonies would stay isolated the longer. The possibility that a single species has represented the family throughout its entire existence seems the least plausible alternative.

Reconstruction of Euomphalacean Anatomy

An attempt to reconstruct the anatomy of euomphalaceans can be based upon two models: *Neomphalus* and *Turritella*. Because *Turritella* is a mostly sedentary filter-feeding animal on soft bottoms (Graham, 1938; Yonge, 1946), there should be many parallels. Differences between the mesogastropod Calyptraeidae and the Turritellidae should be about equivalent to the differences between *Neomphalus* and the euomphalaceans.

Coiling differences are reflected in the orientation of the turritellid and euomphalacean mantle cavities. The mantle cavity of the extremely high-spired *Turritella* has to turn like a corkscrew through at least one full whorl; that of the euomphalacean maintains a

horizontal position but has to curve to the right. It may be a requirement that filament tips of a bipectinate ctenidium have to relate to a horizontally aligned food groove; the single rack of filaments of a pectinibranch filter-feeder should have no difficulty relating to the food groove, whatever the orientation.

Although the columellar muscle of *Turritella* is ventral to the cephalopodal mass as in motile gastropods, the extremely high-spined shell is too heavy to be balanced for locomotion. In *Turritella* the early whorls are made heavy and are partially filled by septation and deposition of callus (Andrews, 1974). A similar process of septation and deposition in the early whorls is also characteristic of euomphalacean shells (Yochelson, 1971). Stability on soft bottoms is thus enhanced in both groups.

There are remarkable parallels between *Turritella* and the euomphalaceans in aperture shape and structure of the operculum. In both groups the aperture is radial and the operculum multispiral. The sinuous whorl side of *Turritella* marks the position of a dorsal excurrent siphon; a similar opisthocline sinus in the upper lip of some euomphalaceans, particularly the omphalotrochids, can also be interpreted as the excurrent sinus.

In feeding posture *Turritella* lies partially buried on soft bottoms so that the operculum nearly blocks the aperture. The exceptionally small foot (Yonge, 1946) remains contracted, sole up, directly behind the operculum (Fretter & Graham, 1962, figs. 57, 64), except when used to clear an incurrent depression in the substratum (Yonge, 1946, fig. 1). Continuous inhalant and exhalant currents are maintained unless the foot and operculum are fully retracted.

Placement of the neomphalid anatomy in the euomphalacean shell would require the foot to curl forward so that it comes to lie, sole up, underneath the long neck, which would position the operculum so that it loosely blocks the aperture, as in turritellids. In most euomphalaceans the foot must have been contained entirely within the aperture, for there is no ventral gape in the shell. Like the turritellid foot, the euomphalacean foot would be relatively small. Because the aperture is so far to the side of the shell's center of gravity, the euomphalaceans were probably no better adapted for burrowing than for locomotion.

The euomphalacean would have its entire visceral mass deep within the coils of the shell. The columellar muscle would be at-

tached about $\frac{1}{3}$ of a whorl behind the aperture and the mantle cavity would extend at least another third of a whorl deeper. The neck and head would extend forward of the area of muscle attachment and would be broad and flattened as in *Neomphalus* because of compression from above and below. The space above is taken by the free tip to the ctenidium and the space below is taken by the foot. A deeply channeled left neck groove like that of *Neomphalus* would help to keep some open space at the left and to provide a rejection and cleansing channel for the mantle cavity.

In *Turritella* pallial tentacles provide a coarse filter for the incurrent stream. In euomphalaceans, tentacles of either pallial or epipodial origin would be used for that purpose. Other features of the mantle cavity should be like those of *Neomphalus*: a bipectinate ctenidium would extend the length of the mantle cavity, attached ventrally to the mantle skirt, the free tip emerging near the region of columellar attachment and extending over the neck; the split osphradium located at the separation of the free tip; the dorsal afferent membrane lacking, so that the filament tips from both sides of the gill axis can reach the food groove; the food groove extending the full length of the mantle cavity, running anteriorly over the dorsal surface of the long neck and cutting directly to the mouth.

Because both *Turritella* and the calyptraeids have eyes and anteriorly directed cephalic tentacles, it is likely that the euomphalacean head would have such features, having a need for greater sensory contact outside of the shell than that of *Neomphalus*. However, the dorsal food groove precludes the presence of a snout, so the most reasonable assumption is that the head and neck were structured much like that of *Neomphalus*.

In *Neomphalus* a fecal groove extends well beyond the mid-dorsal anus, the ctenidial filaments keeping the fecal groove in the mantle skirt well separated from the food groove on the neck. The same arrangement must have obtained in the euomphalacean, the general pattern of water currents in the mantle cavity being ventral to dorsal, rather than left to right.

The euomphalacean mantle cavity is completely asymmetrical, extending laterally and ventrally rather than dorsally over the cephalopodal mass. This asymmetry would also work to dislodge the primitive juxtaposition of the rectum and ventricle, so that the complete

monotocardian condition is a necessary consequence of the euomphalacean body plan. In the absence of a similar leftward displacement of the mantle cavity, the Trochacea and Neritacea have remained diotocardian, despite their loss of the right ctenidium.

Although the monotocardian condition is a likely consequence of the leftward shift of the mantle cavity, the mesogastropod level of reproductive advancement need not be. It is problematic whether these features were primitive to euomphalaceans or represent an adaptation of *Neomphalus* to the rift-vent environment. It is clear that the genital opening in euomphalaceans would have to be within the mantle cavity on the left side. If a copulatory appendage was present, it would have been on the left side because this is the side close to the genital opening and there would be more space for it on the left than the right. The likely immobility of euomphalaceans makes it improbable that they could have moved to copulate effectively. There is no reason to suggest that broadcast spawning through an unmodified left kidney would not be suitable for an immobile animal in concentrated shallow-water populations.

If my basic assumption—that the columellar muscle is positioned to the right rather than ventral to the body mass of the euomphalacean—is valid, then the variable expression of “hyperstrophy” or orthostrophy can be considered a result of the shift in position of the body relative to the columellar muscle. The direction of coiling then becomes entirely a matter of convenience to elevate or lower the aperture above the substratum as an adaptation to particular bottom conditions. Thus the hyperstrophy hypothesized for the Euomphalacea is unlike that of larval architectonicids or *Lanistes* in the Ampullariidae, in which the columellar muscle is always ventral to the cephalopedal mass. This justifies the rejection of the term hyperstrophy with reference to the Euomphalacea.

My theory predicts that ontogeny in a euomphalacean involves these changes: 1) the columellar muscle shifts, relative to the cephalopedal mass, from the ventral position in the postveliger to the right lateral position in the adult, 2) the feeding mode changes from grazing to filter-feeding, which involves lengthening of the gill filaments, and a corresponding decrease in the relative size of the radula. The extent to which these changes were effected could have varied in different lineages. An incomplete shift in the position of

the muscle would enable retention of shell-balancing mobility and could account for some of the more high-spined euomphalaceans with shell shapes that converge upon those of the Trochacea (some orioistomatids, some euomphalids, some omphalotrochids). If the radula retained its early prominence, the initial grazing capacity would be retained.

The relatively high-spined euomphalaceans could have behaved like the freshwater mesogastropod *Viviparus*. Though quite capable of normal shell-balancing, locomotion and rasping with the radula, *Viviparus* also employs a filter-feeding stance in which the shell lies half buried, aperture up, the operculum partially blocking the aperture (Cook, 1949; Fretter & Graham, 1978).

The fossil chronology indicates that the earliest euomphalaceans were low-spined and discoidal. This suggests that the monotocardian condition with a fully bipectinate ctenidium was primitive to all euomphalaceans. Given this premise, many different expressions of the basic body plan were possible.

Origin of the Euomphalacea

Although Knight (1952) did not mention the Euomphalacea in his classic paper on primitive gastropods, he discussed a derivation of Macluritacea from the Bellerophontacea. Two years later, Knight, Batten, and Yochelson (1954) diagrammed a phylogeny of Gastropoda in which the Macluritacea were derived from the Bellerophontacea and the Euomphalacea in turn derived from the Malcuritacea, a view also followed by Knight et al. (1960).

Yochelson (manuscript) has a new theory that seems more compatible with my reconstruction for the Euomphalacea. He speculates that they could have been derived in the Ordovician from a *Lecanospira*-like pleurotomariacean following the loss of the right ctenidium in a way comparable to the separate derivation of the Trochacea. *Lecanospira* (Fig. 15B) had previously been regarded by Knight et al. (1960) as a macluritid, but Yochelson presents convincing arguments that it and genera like *Lesueurilla* (Fig. 15A) with a deep V-shaped notch in the upper aperture are best interpreted as pleurotomariaceans. This group of genera was limited to the early Paleozoic, none being represented in the extensive euomphalacean fauna of the Permian (see Yochelson, 1956).

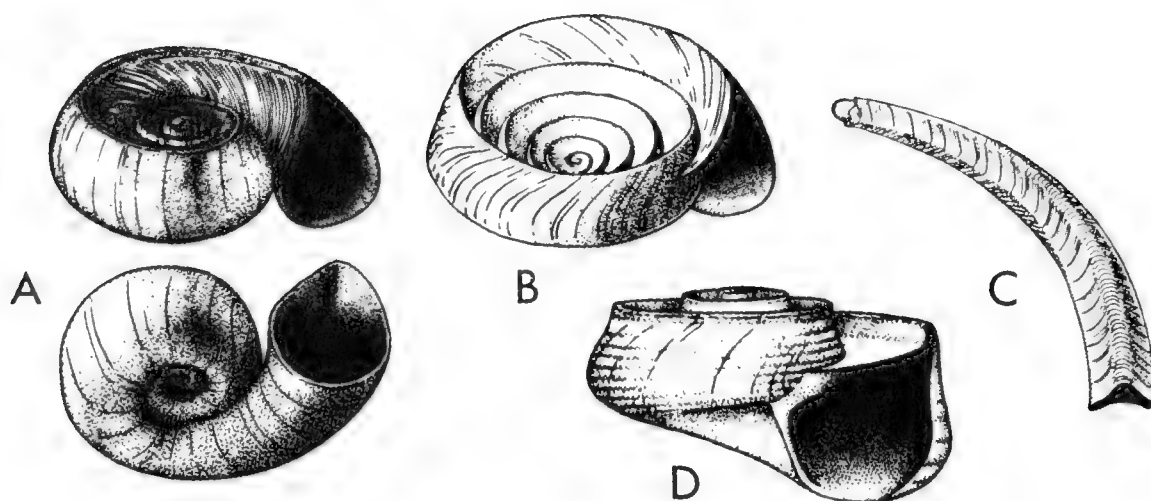


FIG. 15. Early Paleozoic genera now excluded from the Euomphalacea for having a prominent raised slit or selenizone. This group of genera is now regarded (Yochelson manuscript) as the low-spired pleurotomariacean group ancestral to the Euomphalacea. A) *Lesueurilla infundibulum* (Koken, 1896), Ordovician, $\times 1.1$. B) *Lecanospira compacta* (Salter, 1859), Ordovician, $\times 1.1$. C) *Odontomaria elephantina* C. F. Roemer, 1876, Devonian, $\times 0.8$. D) *Helicotoma planulata* Salter, 1859, Ordovician, $\times 1.6$. All after Knight et al. (1960).

Like euomphalaceans, such genera are low-spired and discoidal. Open coiling is represented in *Odontomaria* (Fig. 15C) (see also Rohr & Smith, 1978). *Lecanospira* and *Lesueurilla* are "hyperstrophic," like some euomphalaceans. This shell form, whether represented in a unibranchiate or a dibranchiate gastropod, presents the same constraints for locomotion already discussed. Thus these genera were probably sedentary forms resting for the most part on their flat bases. Assuming that they were dibranchiate pleurotomariaceans, the question arises: could these forms have been filter feeders?

The food groove of *Neomphalus* provides a relevant clue, for *Neomphalus* is the only known prosobranch in which the food groove takes a dorsal route to the mouth. In pectinibranch filter feeders and even in the trochid *Umbonium* the right lateral food groove has developed independently in several families by "conversion of the tract on the right of the mantle cavity, along which the food particles are led to the mouth, into a deep gutter . . . which runs across the whole of the floor of the mantle cavity to a point just under the right cephalic tentacle" (Fretter & Graham, 1962: 100). They noted that no living gastropods with paired gills are known to be ciliary feeders: "The reason for this in zeugobranchs is most likely to be found in the disposition of the currents within the mantle cavity—so long as there are two sets of these, right and left, converging upon the mid-line, it will prove impossible for the material which they carry in

suspension to be collected into a place where the gastropod may use it. It is only when the water current is the transverse stream of the mesogastropod that this happens" (Fretter & Graham, 1962: 98).

The possibility that the food groove in a dibranchiate filter-feeder could take a dorsal route over the head to the mouth has not heretofore been considered. Lengthened ctenidial filaments arising from both gills could converge upon a central food groove. The food groove of *Neomphalus* is deflected toward the right before arching toward the mouth, but this could be a vestige of its primitive mid-dorsal position. Many of the unusual features of the body plan of *Neomphalus* can be understood in terms of additional torsion and rotation on the anteroposterior axis, as discussed by Fretter, Graham & McLean (1981), but no such shifts could account for a migration of the food groove (or a corresponding ciliated tract) across the right cephalic complex to a dorsal position. One way to account for the dorsal position of the food groove is to consider it a primitive character shared by the dibranchiate ancestor. Thus there is good reason to suggest that filter feeding in a group of low-spired Ordovician pleurotomariaceans preceded the derivation of the Euomphalacea.

Diagnosis of the New Suborder Euomphalina

The preceding account of the relationships between the Euomphalacea and Neomphal-

acea is concluded with the proposal of a new suborder for the two superfamilies, coordinate in detail with the subordinal definitions of Cox & Knight (1960) and Knight et al. (1960).

EUOMPHALINA McLean, new suborder

Diagnosis: Shell low-spired to discoidal, or cap-shaped; coiled shells broadly umbilicate, aperture radial; operculum (where known) calcified, multispiral externally, with adventitious layers internally; radula rhipidoglossate; left ctenidium entirely bipectinate, afferent membrane lacking; right ctenidium and right auricle lacking; ventricle not traversed by rectum; columellar muscle lateral to cephalopodal mass.

The subordinal classification of archaeogastropods in the Treatise (Knight et al., 1960) has been both inflated (Golikov & Starobogatov, 1975) and deflated (Salvini-Plawen, 1980).⁹

I prefer to follow a middle ground, more or less equivalent to that of Cox & Knight, recognizing for now three suborders of living unibranchiate rhipidoglossates: Euomphalina, Trochina, and Neritina, each of which has undergone major radiations that exploited the evolutionary potential of their very different body plans.¹⁰

The addition of *Neomphalus* to the ranks of molluscan classification is a major milestone in malacology. New finds with as much to contribute to our knowledge of molluscan diversity and evolution are unusual events. Not since the discovery of *Neopilina* has there been an animal that could fuel so many lines of speculation. Few living malacologists have been as privileged as I in having free rein over

such an exciting find.¹¹ Now it is to be hoped that *Neomphalus*, like *Neopilina*, will inspire others to offer alternative or modified interpretations. One cannot approach the subject of phylogeny without some preconceived notions, and I could hardly expect that all of those expressed here will endure.

ACKNOWLEDGMENTS

I am grateful most of all for the opportunity to report upon this remarkable animal, and I thank those members of the committee who offered it to me.

Dr. J. B. Corliss of Oregon State University preserved the initial collection and forwarded the material to me. Additional specimens were sent by Dr. J. F. Grassle of Woods Hole Oceanographic Institution, Dr. M. L. Jones of the U.S. National Museum of Natural History, Dr. R. D. Turner of Harvard University, and Ms. L. Morse-Porteous of Woods Hole.

Serial sections were expertly prepared by my volunteer laboratory technician, Jo-Carol Ramsaran. Superb photography of whole and dissected specimens was done by museum volunteer Bertram C. Draper. Scanning electron micrographs of the radula were provided by Dr. Carole S. Hickman, University of California, Berkeley (NSF Grant DEB77-14519). SEM micrographs of the juvenile shells were made with the assistance of David R. Lindberg, University of California, Santa Cruz.

Drafts of the manuscript were read and helpful commentary offered by Drs. Eugene V. Coan and A. Myra Keen. Others who may have read early drafts or have helped in various ways through discussion and correspond-

⁹Salvini-Plawen's (1980: 261) suborder Vetigastropoda for superfamilies "Macluritoidea, Pleurotomarioidea, Cocculinoidea, Trochoidea, and Murchisonioidea," "defined by the dominant presence of the (posttorsional) right dorso-ventral retractor muscle as well as the right excretory organ and bilamellate ctenidia with skeletal rods," has these difficulties: *Neomphalus* with its skeletal rods in the ctenidium lacks the right kidney, and *Cocculina* has no right kidney, no skeletal rods, nor even a true ctenidium (Thiele, 1903).

¹⁰Too little is now known of the Cocculinacea, Lepetellacea and Seguenziacea to include them in this scheme.

¹¹Over the three years that I have had *Neomphalus* under consideration, my conclusions about it have undergone some major changes. Progress reports have been given at meetings, which occasioned the entry of abstracts in the literature, some of the statements in which are no longer supported. The first abstract (McLean, 1979) submitted in 1978, drew no firm conclusion, although I announced at the Geological Society of America meeting in San Jose, California, on 9 April 1979 that I assigned the limpet to the suborder Macluritina as then understood. On 21 May 1979 I discussed the limpet at the Symposium on the Biology and Evolution of Mollusca at the Australian Museum, Sydney. The abstract (1980a), which was completed in April 1979, did not mention the unfound left kidney (so large and thin-walled that it was mistaken for a body cavity), but it incorrectly stated that the gonads discharge through the right kidney. In 1980 I developed my current view that the musculature of *Neomphalus* is the necessary consequence of its ontogeny and phylogeny. On 5 September 1980, for the Seventh International Malacological Congress in Perpignan, France, my abstract (1980b) incorrectly stated that the left kidney was vestigial. Fortunately for this novice anatomist, Drs. Fretter and Graham examined the serial section in September, 1980, and agreed to add their expertise to the account of the internal anatomy, resulting in the adjoining paper. The excretory and reproductive systems proved to be more advanced than I had realized, leaving *Neomphalus* with fewer of the archaeogastropod characters than I had originally claimed for it.

ence (though not necessarily agreeing with all of my conclusions) include: R. L. Batten, K. J. Boss, G. M. Davis, J. F. Grassle, R. R. Hessler, C. S. Hickman, R. S. Houbrick, M. L. Jones, D. R. Lindberg, R. M. Linsley, R. A. Lutz, N. J. Morris, W. A. Newman, J. Pojeta, Jr., W. F. Ponder, R. Robertson, B. Runnegar, L. v. Salvini-Plawen, R. S. Scheltema, D. E. Schindel, and R. D. Turner.

I particularly want to thank my principal reviewers, Drs. Vera Fretter of the University of Reading, England, and Ellis Yochelson of the U.S. Geological Survey at the National Museum of Natural History, Washington, D.C. Vera Fretter has provided helpful review commentary throughout the entire course of this work. I was especially pleased that she and Dr. Alastair Graham were able to add their expertise to the account of the internal anatomy. My discussion on the Paleozoic relationships would not have been possible without the frequent assistance of Ellis Yochelson, who directed me to many references and generously allowed me to cite some conclusions from his manuscript on the classification of early gastropods.

LITERATURE CITED

- ADEGOKE, O. S., 1973, Mineralogy and biogeochemistry of calcareous operculi and shells of some gastropods. *Malacologia*, 14: 39–46.
- ANDREWS, E. B., 1965, The functional anatomy of the mantle cavity, kidney and blood system of some pilid gastropods (Prosobranchiata). *Journal of Zoology*, 146: 70–94.
- ANDREWS, H. E., 1974, Morphometrics and functional morphology of *Turritella mortoni*. *Journal of Paleontology*, 48: 1126–1140, 1 pl.
- BALLARD, R. D., 1977, Notes on a major oceanographic find. *Oceanus*, 20: 35–44.
- BALLARD, R. D. & GRASSLE, J. F., 1979, Return to oases of the deep. *National Geographic*, 156: 689–705.
- BANDEL, K., 1975, Das Embryonalgehäuse mariner Prosobranchier der Region von Banyuls-sur-mer. *Vie et Milieu*, ser. A, 25: 83–118.
- BANDEL, K., 1979, The nacreous layer in the shells of the gastropod-family Seguenziidae and its taxonomic significance. *Biomineralisation*, 10: 49–61.
- BANKS, M. R. & JOHNSON, J. H., 1957, *Maclurites* and *Girvanella* in the Gordon River Limestone (Ordovician) of Tasmania. *Journal of Paleontology*, 31: 632–640, pl. 73–74.
- BATTEN, R. L., 1958, Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae. *Bulletin of the American Museum of Natural History*, 114: 153–246, pl. 32–42.
- BATTEN, R. L., 1972, The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of eastern United States. *American Museum Novitates*, 2501: 1–34.
- BATTEN, R. L., 1975, The Scissurellidae—Are they neotenously derived fissurellids? *American Museum Novitates*, 2567: 1–29.
- BATTEN, R. L., 1979, Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685: 1–26.
- BERGER, W. H., 1978, Deep-sea carbonate: pteropod distribution and the aragonite compensation depth. *Deep-Sea Research*, 25: 447–452.
- BEU, A. G. & CLIMO, F. M., 1974, Mollusca from a Recent coral community in Palliser Bay, Cook Strait. *New Zealand Journal of Marine and Freshwater Research*, 8: 307–332.
- BØGGILD, O. B., 1930, The shell structure of the mollusks. *Det Kongelige Danske Videnskabskabernes Selskabs Skrifter, Niende Raekke, Naturvidenskabelig Og Mathematisk Afdeling* 9, Raekke 2: 231–326, 15 pl.
- BOSS, K. J. & TURNER, R. D., 1980, The giant white clam from the Galapagos Rift, *Calyptogena magnifica* species novum. *Malacologia*, 20: 161–194.
- BOUVIER, E.-L. & FISCHER, H., 1902, L'Organisation et les affinités des gastéropodes primitifs d'après l'étude anatomique du *Pleurotomaria beyrichi*. *Journal de Conchyliologie*, 50: 117–272, pl. 2–6.
- BOWSHER, A. L., 1955, Origin and adaptation of platyceratid gastropods. *University of Kansas Paleontological Contributions, Mollusca*, article 5: 1–11, 2 pl.
- CLARK, W. C., 1958, Notes on the mantle cavities of some trochid and turbinid Gastropoda. *Proceedings of the Malacological Society of London*, 33: 57–64.
- CLARKE, A. H., Jr., 1962, On the composition, zoogeography, origin and age of the deep-sea mollusk fauna. *Deep-Sea Research*, 9: 291–306.
- COOK, P. M., 1949, A ciliary feeding mechanism in *Viviparus viviparus* (L.). *Proceedings of the Malacological Society of London*, 27: 265–271.
- CORLISS, J. B. & BALLARD, R. D., 1977, Oases of life in the cold abyss. *National Geographic*, 152: 441–453.
- CORLISS, J. B., DYMOND, J., GORDON, L. I., EDMOND, J. M., HERZEN, R. P. VON, BALLARD, R. D., GREEN, K., WILLIAMS, D., BAINBRIDGE, A., CRANE, K. & ANDEL, T. H. VAN, 1979, Submarine thermal springs on the Galapagos Rift. *Science*, 203: 1073–1083.
- COSSMANN, M., 1915, *Essais de Paléoconchologie Comparée*, 10. Paris, 292 p., 12 pl.

- COSSMANN, M., 1918, *Essais de Paléoconchologie Comparée*, 11. Paris, 388 p., 11 pl.
- COX, L. R., 1960, Gastropoda—General Characteristics of Gastropoda. In MOORE, R. C., ed., *Treatise on Invertebrate Paleontology*, Part I, Mollusca 1: 84–169.
- COX, L. R. & KNIGHT, J. B., 1960, Suborders of Archaeogastropoda. *Proceedings of the Malacological Society of London*, 33: 262–264.
- CRANE, K. & BALLARD, R. D., 1980, The Galapagos Rift at 86°W: 4. Structure and morphology of hydrothermal fields and their relationship to the volcanic and tectonic processes of the rift valley. *Journal of Geophysical Research*, 85: 1443–1454.
- CRISP, M., 1981, Epithelial structures of trochids. *Journal of the Marine Biological Association, United Kingdom*, 61: 95–106.
- CROFTS, D. R., 1955, Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proceedings of the Zoological Society of London*, 125: 711–750.
- DZIK, J., 1978, Larval development of hyolithids. *Lethaia*, 11: 293–299.
- ELDREDGE, N., 1975, Survivors from the good old, old, old days. *Natural History*, 84: 60–69.
- ENRIGHT, J. T., NEWMAN, W. A., HESSLER, R. R. & MCGOWAN, J. A., 1981, Deep-ocean hydrothermal vent communities. *Nature*, 289: 219–221.
- FRETTER, V., 1955, Some observations on *Tricolia pullus* (L.) and *Margarites helycinus* (Fabricius). *Proceedings of the Malacological Society of London*, 31: 159–162.
- FRETTER, V., 1964, Observations on the anatomy of *Mikadotrochus amabilis* Bayer. *Bulletin of Marine Science*, 14: 172–184.
- FRETTER, V., 1965, Functional studies of the anatomy of some neritid prosobranchs. *Journal of Zoology*, 147: 46–74.
- FRETTER, V., 1966, Observations on the anatomy of *Perotrochus*. *Bulletin of Marine Science*, 16: 603–614.
- FRETTER, V., 1969, Aspects of metamorphosis in prosobranch gastropods. *Proceedings of the Malacological Society of London*, 38: 375–386.
- FRETTER, V., 1972, Metamorphic changes in the velar musculature, head and shell of some prosobranch veligers. *Journal of the Marine Biological Association, United Kingdom*, 52: 161–177.
- FRETTER, V., 1975, *Umbonium vestiarium*, a filter-feeding trochid. *Journal of Zoology*, 177: 541–552.
- FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs; their functional anatomy and ecology*. London, Ray Society, xiv + 755 p.
- FRETTER, V. & GRAHAM, A., 1977, The prosobranch molluscs of Britain and Denmark. Part 2—Trochacea. *Journal of Molluscan Studies, Supplement 3*: 39–100.
- FRETTER, V. & GRAHAM, A., 1978, The prosobranch molluscs of Britain and Denmark. Part 3—Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea. *Journal of Molluscan Studies, Supplement 5*: 101–152.
- FRETTER, V., GRAHAM, A. & MCLEAN, J. H., 1981, The anatomy of the Galapagos rift limpet, *Neomphalus fretterae*. *Malacologia*, 21: 337–361.
- GAINEY, L. F., Jr. & WISE, S. W., Jr., 1980, Convergent shell morphology in intertidal gastropods. *Journal of Molluscan Studies*, 46: 192–207.
- GOLIKOV, A. & STAROBOGATOV, Y. I., 1975, Systematics of prosobranch gastropods. *Malacologia*, 15: 185–232.
- GOULD, S. J., 1968, Ontogeny and the explanation of form: an allometric analysis. *Paleontological Society, Memoir 2*: 81–98, pl. 10.
- GOULD, S. J., 1969, Ecology and functional significance of uncoiling in *Vermicularia spirata*: an essay on gastropod form. *Bulletin of Marine Science*, 19: 432–445.
- GRAHAM, A., 1938, On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proceedings of the Zoological Society of London*, ser. A, 108: 453–463.
- GRAHAM, A., 1965, Observations on the anatomy of some trochacean gastropods. *Bulletin of Marine Science*, 15: 202–210.
- GRASSLE, J. F., BERG, C. J., CHILDRESS, J. J., GRASSLE, J. P., HESSLER, R. R., JANNASCH, H. J., KARL, D. M., LUTZ, R. A., MICKEL, T. J., RHOADS, D. C., SANDERS, H. L., SMITH, K. L., SOMERO, G. N., TURNER, R. D., TUTTLE, J. H., WALSH, P. J. & WILLIAMS, A. J., 1979, Galapagos '79: initial findings of a deep-sea biological quest. *Oceanus*, 22(2): 2–10.
- HICKMAN, C. S., 1980a, Paleogene marine gastropods of the Keasey formation in Oregon. *Bulletins of American Paleontology*, 78: 1–112, 10 pl.
- HICKMAN, C. S., 1980b, Gastropod radulae and the assessment of form in evolutionary paleontology. *Paleobiology*, 6: 276–294.
- HOAGLAND, K. E., 1977, Systematic review of fossil and Recent *Crepidula* and discussion of evolution of the Calyptraeidae. *Malacologia*, 16: 353–420.
- HORNÝ, R., 1964, New Lower Paleozoic gastropod genera of Bohemia (Mollusca). *Casopis Národního Musea*, 133: 211–216, 2 pl. [in Czech with English summary].
- HOUBRICK, R. S., 1979, Classification and systematic relationships of the Abysochrysidae, relict family of bathyal snails (Prosobranchia: Gastropoda). *Smithsonian Contributions to Zoology*, 290: 1–21.
- HUDDLESTON, W. H., 1887–1896, A monograph of the British Jurassic Gastropoda. Part 1. The Inferior Oolite Gasteropoda. *Palaeontographical Society, London*, 514 p., 44 pl.
- JANNASCH, H. W. & WIRSEN, C. O., 1979, Chemosynthetic primary production at East Pacific sea floor spreading centers. *BioScience*, 29: 592–598.

- JANNASCH, H. W. & WIRSEN, C. O., 1981, Morphological survey of microbial mats near deep-sea thermal vents. *Applied and Environmental Microbiology*, 41: 528–538.
- JONES, M. L., 1981, *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galapagos Rift geothermal vents (Pogonophora). *Proceedings of the Biological Society of Washington*, 93: 1295–1313.
- KARL, D. M., WIRSEN, C. O. & JANNASCH, H. W., 1980, Deep-sea primary production at the Galapagos hydrothermal vents. *Science*, 207: 1345–1347.
- KILLINGLEY, J. S., BERGER, W. H., MACDONALD, K. C. & NEWMAN, W. A., 1980, $^{18}\text{O}/^{16}\text{O}$ variations in deep-sea carbonate shells from the Rise hydrothermal field. *Nature*, 288: 218–221.
- KINDLE, E. M., 1904, The stratigraphy and paleontology of the Niagara of northern Indiana. *Indiana Department of Geology and Natural Resources, 28th Annual Report*: 397–498, 25 pl.
- KNIGHT, J. B., 1941, Paleozoic gastropod genotypes. *Geological Society of America Special Papers* 32, 510 p., 96 pl.
- KNIGHT, J. B., 1952, Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections*, 117(13): 1–56.
- KNIGHT, J. B., BATTEN, R. L. & YOCHELSON, E. L., 1954, Status of Invertebrate Paleontology, 1953. V. Mollusca: Gastropoda. *Bulletin of the Museum of Comparative Zoology*, 112: 172–179.
- KNIGHT, J. B., COX, L. R., KEEN, A. M., BATTEN, R. L., YOCHELSON, E. L. & ROBERTSON, R., 1960, Systematic descriptions (Archaeogastropoda), In MOORE, R. C., ed., *Treatise on Invertebrate Paleontology*, Part I, Mollusca 1: 169–310, Geological Society of America and University of Kansas Press.
- KOKEN, E., 1897, Die Gastropoden der Trias um Hallstadt. *Abhandlungen der K. K. Geologischen Reichsanstalt*, 17(4), 112 p., 23 pl.
- LANG, A., 1891, Versuch einer Erklärung der Asymmetrie der Gasteropoden. *Veierteljahrsschrift Naturforschende Gesellschaft, Zürich*, 36: 339–371.
- LEVER, J., 1979, On torsion in gastropods. In VAN DER SPOEL, S., VAN BRUGGEN, A. C. & LEVER, J., eds., *Pathways in Malacology*. Junk, The Hague: 5–23.
- LINDSTROM, G., 1884, On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 19(6): 1–250, 25 pl.
- LINSLEY, R. M., 1977, Some “laws” of gastropod shell form. *Paleobiology*, 3: 196–206.
- LINSLEY, R. M., 1978a, The Omphalocirridae: a new family of Palaeozoic Gastropoda which exhibits sexual dimorphism. *Memoirs of the National Museum of Victoria*, 39: 33–54, pl. 2–10.
- LINSLEY, R. M., 1978b, Locomotion rates and shell form in the Gastropoda. *Malacologia*, 17: 193–206.
- LINSLEY, R. M., 1978c, Shell form and the evolution of gastropods. *American Scientist*, 66: 432–441.
- LINSLEY, R. M., 1979, Gastropods of the Devonian. *The Devonian System, Special Papers in Paleontology* 23, The Paleontological Association, London: 249–254.
- LINSLEY, R. M. & YOCHELSON, E. L., 1973, Devonian carrier shells (Euomphalopteridae) from North America and Germany. [United States] *Geological Survey Professional Paper*, 824: 1–26, 6 pl.
- LINSLEY, R. M., YOCHELSON, E. L. & ROHR, D. M., 1978, A reinterpretation of the mode of life of some Paleozoic frilled gastropods. *Lethaia*, 11: 105–112.
- LONSDALE, P., 1977, Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research*, 24: 857–863.
- LUTZ, R. A., RHOADS, D. C., JABLONSKI, D. & TURNER, R. D., 1979, Deep-sea hydrothermal vent bivalves: ecological and paleoecological implications of shell structure, mineralogy, and micromorphology. *The Geological Society of America, Abstracts with Programs*, 1979: 470.
- MACCLINTOCK, C., 1963, Reclassification of gastropod *Proscutum* Fischer based on muscle scars and shell structure. *Journal of Paleontology*, 37: 141–156, pl. 20.
- MACCLINTOCK, C., 1967, Shell structure of pateloid and bellerophonoid gastropods (Mollusca). *Peabody Museum of Natural History, Yale University, Bulletin* 22: 1–140, 32 pl.
- MCLEAN, J. H., 1979, On a new archaeogastropod limpet convergent with the Calyptraeidae from the submarine thermal springs on the Galapagos Rift. *Geological Society of America, Abstracts with Programs*, 11: 92.
- MCLEAN, J. H., 1980a, Filter feeding aspidobranch limpets from submarine thermal springs of the Galapagos Rift—A new superfamily of archaic archaeogastropods. *Journal of the Malacological Society of Australia*, 4: 225–226.
- MCLEAN, J. H., 1980b, The Galapagos Rift Limpet: relevance to understanding the evolution of a significant Paleozoic-Mesozoic radiation. *Haliotis, Société Française de Malacologie*, 10: 170.
- NEWMAN, W. A., 1979, A new scalpellid (Cirripedia); a Mesozoic relic [sic] living near an abyssal hydrothermal spring. *Transactions of the San Diego Society of Natural History*, 19: 153–167.
- PEEL, J. S., 1975a, A new Silurian gastropod from Wisconsin and the ecology of uncoiling in Palaeozoic gastropods. *Bulletin of the Geological Society of Denmark*, 24: 211–221.
- PEEL, J. S., 1975b, New Silurian gastropods from Nova Scotia and Britain. *Canadian Journal of Earth Sciences*, 12: 1524–1533.
- PELSENEER, P., 1893, À propos de l'Asymétrie

- des Mollusques univalves." *Journal de Conchyliologie*, 40: 229–233.
- PILSBRY, H. A., 1934, Notes on the gastropod genus *Liotia* and its allies. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 85: 375–381, pl. 13.
- QUINN, J. F., Jr., 1981, A preliminary overview of the Seguenziidae Verrill, 1884. *Bulletin of the American Malacological Union, Inc.*, 1980: 74.
- RAU, G. H. & HEDGES, J. I., 1979, Carbon-13 depletion in a hydrothermal vent mussel: suggestion of a chemosynthetic food source. *Science*, 203: 648–649.
- REX, M. A. & BOSS, K. J., 1976, Open coiling in Recent gastropods. *Malacologia*, 15: 289–297.
- REX, M. A., VAN UMMERSEN, C. A. & TURNER, R. D., 1976, Reproductive pattern in an abyssal snail. *American Zoologist*, 16: 269.
- RISBEC, J., 1939, Recherches anatomiques sur les Prosobranches de Nouvelle-Calédonie. *Annales des Sciences Naturelles, Zoologie*, ser. 11, 2: 235–299.
- RISBEC, J., 1955, Considérations sur l'anatomie comparée et la classification des gastéropodes prosobranches. *Journal de Conchyliologie*, 95: 45–82.
- ROBERTSON, R., 1964, The hyperstrophic larval shells of the Architectonicidae. *Annual Reports for 1963 of the American Malacological Union*: 11–12.
- ROBERTSON, R., 1976, Marine prosobranch gastropods: larval studies and systematics. *Thalassia Jugoslavica*, 10: 213–238.
- ROBERTSON, R. & MERRILL, A. S., 1963, Abnormal dextral hyperstrophy of postlarval *Heliacus* (Gastropoda: Architectonicidae). *Veliger*, 6: 76–79, pl. 13, 14.
- RODRIGUEZ BABIO, C. & THIRIOT-QUIÉVREUX, C., 1975, Trochidae, Skeneidae et Skeneopsidae (Mollusca, Prosobranchia) de la Région de Roscoff. Observations au microscope électronique à balayage. *Cahiers de Biologie Marine*, 16: 521–530, 4 pl.
- ROHR, D. M. & SMITH, R. E., 1978, Lower Devonian Gastropoda from the Canadian Arctic Islands. *Canadian Journal of Earth Science*, 15: 1228–1241.
- ROKOP, F. J., 1974, Reproductive pattern in the deep-sea benthos. *Science*, 186: 743–745.
- SALVINI-PLAWEN, L. V., 1980, A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, 19: 249–278.
- SCHINDEL, D. E., 1979, Habits and habitats of some Pennsylvanian molluscs from North-Central Texas. *Ninth International Congress, Carboniferous Stratigraphy, Abstracts of Papers*: 196.
- SHUTO, T., 1974, Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia*, 7: 239–256.
- SIMPSON, G. G., 1953, *The Major Features of Evolution*, New York, 434 p.
- SOHL, N. F., 1960, Archaeogastropoda, Mesogastropoda and stratigraphy of the Ripley Owl Creek, and Prairie Bluff Formations, Late Cretaceous gastropods in Tennessee and Mississippi. [United States] Geological Survey Professional Paper 331-A: 1–151, 18 pl.
- SOLEM, A. & NITECKI, M. H., 1968, *Cyclosporgia discus* Miller, 1891: a gastropod operculum, not a sponge. *Journal of Paleontology*, 42: 1007–1013, pl. 124.
- SPIESS, F. N., MACDONALD, K. C., ATWATER, T., BALLARD, R., CARRANZA, A., CORDOBA, D., COX, C., DIAZ GARCIA, V. M., FRANCHETEAU, J., GUERRERO, J., HAWKINS, J., HAYMON, R., HESSLER, R., JUTEAU, T., KASTNER, M., LARSON, R., LUYENDYK, B., MACDOUGALL, J. D., MILLER, S., NORMARCK, W., ORCUTT, J. & RANGIN, C., 1980, East Pacific Rise: hot springs and geophysical experiments. *Science*, 207: 1421–1433.
- STANLEY, S. M., 1978, Aspects of the adaptive morphology and evolution of the Trigoniidae. *Philosophical Transactions of the Royal Society of London*, ser. B, 284: 247–258, 2 pl.
- STANLEY, S. M., 1979, *Macroevolution, Pattern and Process*. San Francisco, 332 p.
- TASSELL, C. B., 1976, A revision of the gastropod fauna of the Lilydale limestone (Early Devonian) of Victoria. *Memoirs of the National Museum of Victoria*, 37: 1–22, 3 pl.
- TASSELL, C. B., 1980, Further gastropods from the Early Devonian Lilydale Limestone, Victoria. *Records of the Queen Victoria Museum*, 69, 27 p.
- THAYER, C. W., 1979, Biological bulldozers and the evolution of marine benthic communities. *Science*, 203: 458–461.
- THIELE, J., 1903, Die Anatomie und systematische Stellung der Gattung *Cocculina* Dall. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 7: 149–156, pl. 6–7.
- TYLER, J. H., 1965, Gastropods from the Middle Devonian Four Mile Dam Limestone (Hamilton) of Michigan. *Journal of Paleontology*, 39: 341–349, pl. 47–48.
- VERDONK, N., 1979, Symmetry and asymmetry in the embryonic development of molluscs. In VAN DER SPOEL, S., VAN BRUGGEN, A. C. & LEVER, J., eds., *Pathways in Malacology*. Junk, The Hague: 25–45.
- VERMEIJ, G. J., 1975, Evolution and distribution of left-handed and planispiral coiling in snails. *Nature*, 254: 419–420.
- VERMEIJ, G. J., 1977, The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 3: 245–258.
- WANGBERG-ERIKSSON, K., 1979, Macluritacean gastropods from the Ordovician and Silurian of Sweden. *Sveriges Geologiska Undersökning*, ser. C, 758: 1–33.
- WENZ, W., 1938, Gastropoda. *Handbuch der Paläozoologie*, 6. Teil 1: Allgemeiner Teil und Prosobranchia, Berlin, 1639 p.
- WILLIAMS, A. B., 1980, A new crab family from the

vicinity of submarine thermal vents on the Galapagos rift (Crustacea: Decapoda: Brachyura). *Proceedings of the Biological Society of Washington*, 93: 443–472.

WOODWARD, M. F., 1901, The anatomy of *Pleurotomaria beyrichii* Hilg. *Quarterly Journal of Microscopical Science*, 44: 215–268, pl. 13–16.

YOCHELSON, E. L., 1956, Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea. *Bulletin of the American Museum of Natural History*, 110: 173–276, pl. 9–24.

YOCHELSON, E. L., 1960, Permian Gastropoda of the southwestern United States. 3. Bellerophonacea and Patellacea. *Bulletin of the American Museum of Natural History*, 119: 205–294, pl. 46–57.

YOCHELSON, E. L., 1966, A reinvestigation of the Middle Devonian gastropods *Arctomphalus* and *Omphalocirrus*. *Norsk Polarinstitut—Årbok* 1965: 37–48, 2 pl.

YOCHELSON, E. L., 1971, A new Late Devonian gastropod and its bearing on problems of open coiling and septation. *Smithsonian Contributions in Paleobiology*, 3: 231–241, 2 pl.

YOCHELSON, E. L., 1979a, Gastropod opercula as objects for paleobiogeographic study. In GRAY & BOUCOT, eds., *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Oregon State University Press: 37–43.

YOCHELSON, E. L., 1979b, Early radiation of Mollusca and mollusc-like groups. In HOUSE, M. R., ed., *The Origin of Major Invertebrate Groups*. Systematics Association Special Volume No. 12, Academic Press: 323–358, pl. 4–6.

YOCHELSON, E. L., (manuscript), New data for a revision of Paleozoic gastropod classification.

YOCHELSON, E. L. & JONES, C. R., 1968, *Teiichispira*, a new Early Ordovician gastropod genus. [United States] *Geological Survey Professional Paper*, 613-B 15 p., 2 pl.

YOCHELSON, E. L. & LINSLEY, R. M., 1972, Opercula of two gastropods from the Lilydale Limestone (Early Devonian) of Victoria, Australia. *Memoirs of the National Museum of Victoria*, 33: 1–14, 2 pl.

YOCHELSON, E. L. & WISE, O. A., 1972, A life association of shell and operculum in the Early Ordovician gastropod *Ceratopea unguis*. *Journal of Paleontology*, 46: 681–684.

YONGE, C. M., 1938, Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journal of the Marine Biological Association, United Kingdom*, 22: 458–468.

YONGE, C. M., 1946, On the habits of *Turritella communis* Risso. *Journal of the Marine Biological Association, United Kingdom*, 26: 377–380.

YONGE, C. M., 1947, The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London*, ser. B, 232: 443–517, 1 pl.

APPENDIX 1: Possible Affinity of Other Extinct Superfamilies

The search for fossil predecessors to *Neomphalus* has led me to consider the relationships and possible feeding modes of some other extinct groups. My conclusions are given in this section.

Shell characters in the Macluritacea and the Clisospiracea, as in the Euomphalacea, exceed the limits of diversity now expressed in the Trochacea. Reasons to dissociate these two superfamilies from the Euomphalacea are given here. The Oriostomatacea have been synonymized with the Euomphalacea in the body of this paper. Reasons to synonymize the Craspedostomatacea and Amberleyacea with the Trochacea are given in Appendix 2. The remaining extinct superfamilies recognized by Knight et al. (1960) and thought to be unibranchiate are the Pseudophoracea, Platyceratacea, Anomphalacea, Microdomatacea, and Palaeotrochacea. Commentary on these groups is directed to the question: Do the shell characters exceed the limits now expressed in the Trochacea?

MACLURITACEA: The Ordovician genus *Maclurites* (Fig. 16A) had an exceptionally large “hyperstrophic” shell that could only have rested on its flat base (see Banks & Johnson, 1957; Knight et al., 1960: 188). A heavy, protruding operculum fits the aperture. Internally the operculum has two roughened areas that have been interpreted as attachment scars for right and left retractor muscles; externally it is paucispiral with one counter-clockwise volution, which provides the evidence that led Knight (1952) to interpret its anatomy as dextral. The *Maclurites* operculum is analogous to that of the Neritacea, upon which left and right columellar muscles insert, preventing it from rotating to produce a multispiral pattern. Horn-shaped opercula of a somewhat different type are known in the macluritacean genus *Teiichispira* (Yochelson & Jones, 1968). The shell of *Teiichispira* is poorly known, but Yochelson (1979a: 40) has concluded that it had a flattened base like that of *Maclurites*. Yochelson (in preparation) will report on the recently discovered operculum of the macluritid genus *Palliseria*.

Linsley (1978b, fig. 10) has depicted *Maclurites* as a filter-feeding form with the operculum loosely blocking the aperture in feeding position. Shells are heavy and the center of gravity is offset from the aperture. Linsley has therefore concluded that any

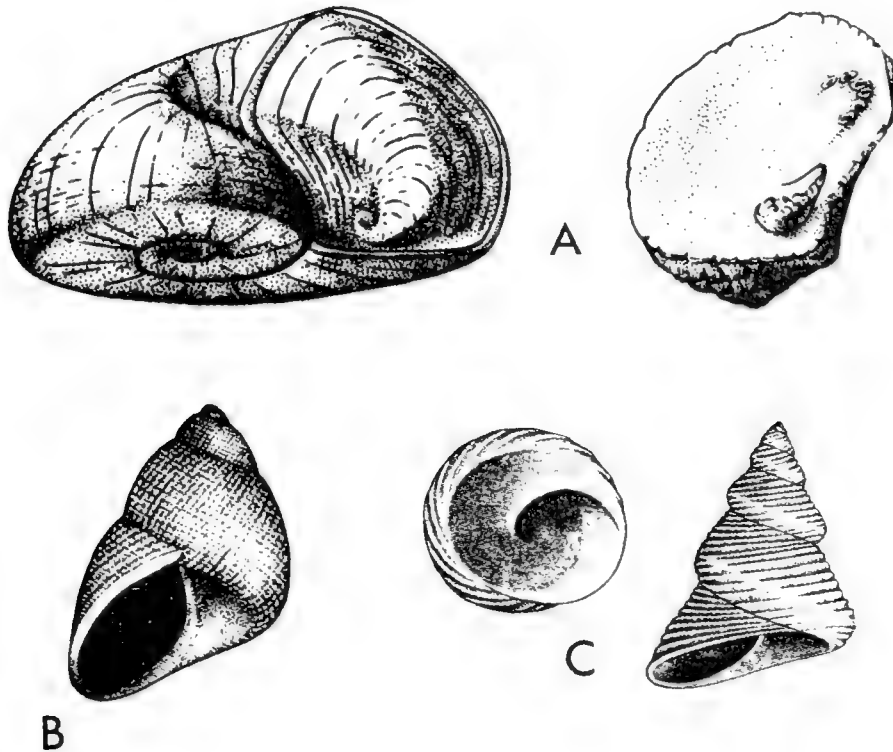


FIG. 16. Macluritacea and Clisospiracea. A) *Maclurites logani* (Salter, 1859), with internal view of operculum, Ordovician (Macluritacea: Macluritidae), $\times 0.6$. B) *Onychochilus physa* Lindström, 1884, Silurian (Clisospiracea: Onychochilidae), $\times 8.4$. C) *Mimospira cochleata* (Lindström, 1884), basal and apertural views, Silurian (Clisospiracea: Clisospiridae), $\times 3.4$. A & B after Knight et al. (1960), C after Wängberg-Eriksson (1979).

locomotion was by shell dragging. *Maclurites* may have had the pallial configuration of *Neomphalus*, but the paired musculature that has been assumed would entail some major differences from the Euomphalacea. As noted earlier, Linsley (1978c: 440) has a theory, not as yet fully detailed, that the Macluritacea (in addition to the Euomphalacea) were untorted and not gastropods. Yochelson (1979b: 347) has mentioned the possibility that the small Cambrian *Pelagiella* could be ancestral to the Macluritacea, though he now (manuscript) favors retention of Macluritacea as a gastropod lineage apart from Euomphalacea, rather than their predecessors, as implied by Knight et al. (1960).

The Macluritidae are now limited to genera with horn-shaped opercula; these genera are known only from the Ordovician. *Omphalocirrus* was transferred to the Euomphalacea by Yochelson (1966) and *Lecanospira* (Fig. 15B) to the Pleurotomariacea (Yochelson manuscript). The Ordovician *Ceratopea* is another genus with a horn-shaped operculum of yet another kind. Its poorly known shell was first associated with its well-known operculum by Yochelson & Wise (1972). The shell is orthostrophic, thereby differing from other macluritids, but I would be more inclined to

place it in a family within the Macluritacea because of its horn-shaped operculum, than to relate it (as suggested by Yochelson & Wise) to the suborder Pleurotomariina. In living pleurotomariaceans (families Pleurotomariidae and Scissurellidae), the operculum is multispiral. Wenz (1938: 211) placed *Ceratopea* in Macluritidae.

The family Onychochilidae, included by Knight et al. (1960) in the Macluritacea, is here transferred to the Clisospiracea, as discussed under the following heading.

CLISOSPIRACEA: The Clisospiridae (Fig. 16C) and Onychochilidae (Fig. 16B), both moderately to extremely high-spired and apparently sinistral, are here united in the superfamily Clisospiracea. Although Knight (1952) included *Clisospira* among the supposedly hyperstrophic genera related to *Maclurites*, this position was reversed by Knight et al. (1960), who interpreted *Clisospira* as sinistral. The Clisospiracea, then containing only Clisospiridae, were grouped among those superfamilies of "doubtful subordinal position." The Onychochilidae were regarded as dextral-hyperstrophic and were included in the Macluritacea, apparently in the belief that there were transitional forms leading to *Maclurites*. More recently, Horný (1964), Peel

(1975b), and Wängberg-Eriksson (1979) have found transitional forms between the Onychochilidae and the Clisospiridae. This led again to the assumption that clisospirids were hyperstrophic like the onychochilids and therefore to the assignment of both families to the Macluritacea. However, because opercula are unknown in both families, there is no direct evidence of hyperstrophy, and the entire assumption is open to question.

Whether the two families were sinistral or dextral-hyperstrophic, they differ from Macluritacea and Euomphalacea in having tangential rather than radial apertures. Onychochilids and clisospirids would have been able to clamp to the substratum and some should have been capable of more effective locomotion than that of a "shell dragger." The ontogenetic change in orientation, which would be required in euomphalacean and macluritacean development, was not a component in onychochilid and clisospirid development. The tangential rather than radial aperture plus the lack of the appropriate opercula is sufficient reason to exclude them from either the Macluritacea or Euomphalacea.

The Clisospiridae, exemplified by *Mimospira* (Fig. 16C), have moderately high-spired shells with smooth, concave bases. The only possible interpretation of the relation of such a shell to the substratum is that it attached, limpet-like, to hard surfaces. Hyperstrophy by definition means that the internal anatomy is dextral, with water currents flowing left to right, despite the sinistrality of the shell. Dextral anatomy is entirely possible within a high-spired sinistrally coiled shell like the ampullariid *Lanistes* (see Cox, 1960: 110, fig. 67), in which the plane of the aperture is nearly parallel to the axis of coiling, but it is not possible in a shell form in which the axis of coiling is perpendicular to the plane of the aperture (Fig. 16C). The left ctenidium under such an impossible condition would be forced to curve backwards around the columella. Thus the Clisospiridae could only have been sinistral in both shell and anatomy. If there is a transition between the Clisospiridae and the Onychochilidae, as has been proposed by Horny, Peel and Wängberg-Eriksson, then it follows that the Onychochilidae were also anatomically sinistral. The Devonian Progalierinae (see footnote 3) were regarded by Knight et al. (1960) as dextral clisospirids. It is possible that there were dextral as well as sinistral clisospiraceans, although there are

too few progalerine specimens known to enable any firm conclusions.

This analysis, however, is complicated by the fact that some *Mimospira* species have heterostrophic (not hyperstrophic) protoconchs (Peel, 1975b: 1528): "The protoconch is an open-coiled half whorl which, by way of a perpendicular change in direction of the axis of coiling from horizontal to vertical, assumes the hyperstrophic form of the teleconch." Because heterostrophic protoconchs are unknown in Recent archaeogastropods, I offer no further speculation. Linsley (1977: 204, fig. 7; 1978b: 201, fig. 9; 1978c, figs. 3, 12) has depicted *Onychochilus* (Fig. 16B) as carrying the shell with the spire directed anteriorly over the head of the animal. Such an unorthodox interpretation presumably is explained in his theory (1978c) that the entire group comprising the Macluritacea and Euomphalacea was untorted. The Onychochilidae appeared in the Upper Cambrian and thus are among the earliest known gastropods. A convincing explanation of their form and function would be of great importance to an understanding of gastropod phylogeny.

PSEUDOPHORACEA: Linsley et al. (1978) have discussed the life habits of pseudophorid genera (Fig. 17A) that have a peripheral frill, an extension of the base of the shell serving to raise the position of the aperture above the substratum. As in the Euomphalacea the coiling axis is perpendicular to the substratum, but the lip growth is prosocline and the aperture is tangential, so that the base of the shell is shielded on all sides. They concluded that the frill-bearing pseudophorids could have lived on a firm, but not hard, substratum, much as in the extant deposit-feeding Xenophoridae. Retention of spiral sculpture on the base of the Permian *Sallya* (Fig. 17A) precludes the limpet-like mode of the living calyptraeid *Trochita*, in which the entire base of the shell is smooth. The absence of inhalant access in the shell is no hindrance to filter-feeding limpets on hard substrates, but the example of *Turritella*, as well as that hypothesized for the Euomphalacea, suggests that filter feeders on soft substrates would not provide a tentlike shield over the head. I therefore think that the best hypothesis is that pseudophorids were deposit feeders. Although there are no living trochaceans with a peripheral frill, there are deposit-feeding trochaceans. I can think of no argument that would preclude the Pseudophoracea from having the trochacean pallial complex.

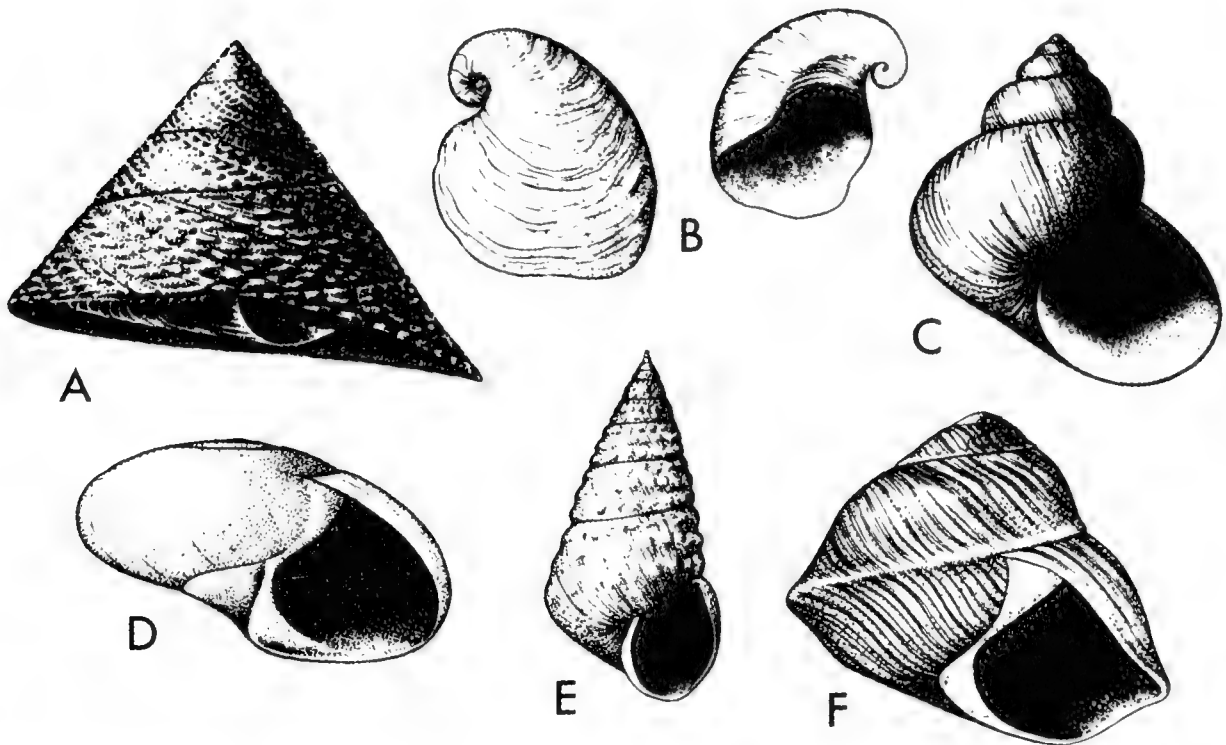


FIG. 17. Representative genera of extinct superfamilies discussed in Appendix 1, suborder Trochina. A) *Sallya linsa* Yochelson, 1956, Permian (Pseudophoracea: Pseudophoridae), $\times 3.4$. B) *Platyceras vetustum* J. C. Sowerby, 1829, Mississippian (Platyceratacea: Platyceratidae), $\times 0.6$. C) *Holopea symmetrica* Hall, 1847, Ordovician (Platyceratacea: Holopeidae), $\times 2.3$. D) *Anomphalus rotulus* Meek & Worthen, 1867, Carboniferous (Anomphalacea: Anomphalidae), $\times 8.4$. E) *Microdome conicum* Meek & Worthen, 1867, Carboniferous (Microdomatacea: Microdomatidae), $\times 5.7$. F) *Palaeotrochus kearneyi* (Hall, 1861), Devonian (Palaeotrochacea: Palaeotrochidae), $\times 0.6$. All after Knight et al. (1960).

PLATYCERATACEA: The Platyceratid limpets (Fig. 17B) have long been understood to have been coprophagous on crinoids and cystoids (Bowsher, 1955). Their presumed coiled predecessors, the Holopeidae (Fig. 17C), had an ordinary trochiform appearance.

Platyceratid limpets had a horseshoe-shaped muscle scar (see Yochelson, 1956, pl. 23, figs. 25, 30); the right columellar muscle of *Platyceras* was evidently large enough to envelop the mantle cavity as well as the visceral mass. This provides the argument that serves to eliminate the group as a possible predecessor for *Neomphalus*. The configuration of the platyoceratid muscle scar suggests that their derivation as limpets was parallel to that of the trochid family Stomatelidae, in which the single right columellar muscle is stretched along the columella as the whorl expands. There is no evidence to preclude the Platyceratacea from having a mantle cavity like that of the Trochacea.

Yochelson & Linsley (1972) described a calcareous operculum for the Devonian "*Cyclonema*" *lilydalensis* Etheridge, 1891. They noted that the platyoceratid genus

Cyclonema was inappropriate for this species, a problem treated recently by Tassell (1980), who proposed for it the genus *Australonema* in the Holopeidae. Of most interest here is the fact that the holopeid operculum is unlike any now known in the Trochacea. This provides the most useful argument to justify the retention of Platyceratacea as a superfamily separate from Trochacea.

ANOMPHALACEA: The smooth, mostly non-umbilicate shells of the Anomphalacea (Fig. 17D) are streamlined like those of the Naticidae and *Umbonium*. They could have been partially or completely enveloped by the mantle to enable burrowing in sand. There are no clues as to feeding habits; probably they were deposit feeders although the filter feeding of *Umbonium* cannot be ruled out. Nothing precludes their having the trochacean mantle cavity.

MICRODOMATACEA: I find no argument to preclude this small-shelled nacreous group with tangential apertures (Fig. 17E) from having a mantle complex like that of the Trochacea.

PALAEOTROCHACEA: Again there is no

argument to preclude a mantle complex like that of the Trochacea in this large-shelled group (Fig. 17F) with tangential apertures. A nacreous shell interior has not been demonstrated, but may prove to have been present.

Conclusion: It is entirely possible that the trochacean pallial complex, which is so uniform in the diverse living trochaceans (Risbec, 1939, 1955; Graham, 1965), could have accounted for all extinct single-gilled archaeogastropod superfamilies other than the Euomphalacea, Macluritacea, and Clissospiracea.

APPENDIX 2: Suppression of Superfamilies Craspedostomatacea and Amberleyacea

Two superfamilies proposed by the Treatise authors in 1960, the Craspedostomatacea and the Amberleyacea, were grouped by the authors with other superfamilies of "doubtful subordinal position." Evidence for the synonymization of these categories with the Trochacea is presented as follows:

CRASPEDOSTOMATACEA: This was proposed (Knight et al., 1960: 298) as a "probably polyphyletic and artificial group," mostly having in common the "expanded apertures in gerontic stages." Three families were included: the Craspedostomatidae, Upper Ordovician to Silurian; the Codonocheilidae, Upper Silurian to Middle Jurassic; and the Crossostomatidae, Middle Triassic to Middle Jurassic.

Expanded apertures are diagnostic for one living family in the Trochacea, the Liotiidae. In addition to the expanded aperture, which is more of a varix than a completely flared aperture, the family Liotiidae may be recognized by its flat spire in at least the early whorls, and predominating axial sculpture of spaced major ribs and sharp lamellar increments. The final lip is usually preceded by descent of the suture, making the aperture more oblique than that of early stages, in which the aperture is more nearly radial.¹² The Liotiidae can be traced to the Permian in the genera *Dichostasia* (Fig. 18A) and *Brochidium* (see

Yochelson, 1956: 207, 257, and Batten, 1979: 110). These genera have the characteristic sculpture of liotiids, and are hereby transferred to the Liotiidae, which places the origin of the Liotiidae as early as the Permian.

Craspedostoma (Fig. 18C) lacks the spaced axial ribs of the Liotiidae but has a similar kind of imbricate sculpture that suggests a sufficiently close relationship with the Liotiidae to warrant placement of the family Craspedostomatidae in the Trochacea.

In first proposing *Craspedostoma*, Lindström (1884: 182) remarked: "I have placed this genus with the Turbinidae in consequence of the congruence of its shell with several of the Liotidae [sic]." Cossmann (1918) continued the close association of Liotiidae and *Craspedostoma* in adjacent families. Wenz (1938) separated the two families, placing the Craspedostomatidae in the Trochonematacea and the Liotiinae as a subfamily of Turbinidae. This led to further separation in the raising of Craspedostomatidae to the superfamily Craspedostomatacea in Knight et al. (1960), leaving it to the students of this day to rediscover the affinity between *Craspedostoma* and the Liotiidae.

A thickened final lip is present also in the living trochid genus *Danilia* (Fig. 18D; see also Beu & Climo, 1974: 315), as well as in some small homalopomatine turbinids and some skeneids. Thus, a thickened final lip is a recurring theme in the Trochacea. The two Mesozoic genera in Cox's family Crossostomatidae may easily be encompassed within the Trochacea; so also at least for the Mesozoic genera included within the Codonocheilidae. Accordingly, I recommend that the Craspedostomatacea be synonymized with Trochacea, and that the trochacean pallial complex be considered to have been well established by the Silurian, the time of appearance of *Craspedostoma*.

AMBERLEYACEA: This was proposed by Cox in Knight et al. (1960: 303) for four families thought to have been limited to the Triassic through Oligocene. It was characterized as "a single new superfamily (that) serves to bring together a number of genera with obvi-

¹²The Triassic *Anisostoma* (Fig. 18B), thought by Koken (1897) and Knight et al. (1960) to be euomphalacean, has the final lip inflated to match the diameter of all previous whorls of the discoidal shell. Its quadrate shell profile resembles that of the architectonicid *Pseudomalaxis*. *Anisostoma* is so bizarre that its true affinity would remain unknown were it not for *Ilaira evoluta* (Reeve), a liotiid with a quadrangular whorl profile and a completely flat spire. In this species, according to Pilsbry (1934: 380), "the minute axial thread-lineolation usual in Liotiidae is well developed, but other axial sculpture is reduced to tuberculation of the four subequidistant carinae—at suture, base, and two at periphery." This description applies equally well to *Anisostoma*. In both *Anisostoma* and *Ilaira* the suture descends on the third whorl, though more abruptly in *Anisostoma*. In *Ilaira* there is no flaring of the lip, but it may be that mature examples with flared lips are yet unknown. The removal of *Anisostoma* from the Euomphalacea limits the euomphalaceans to genera that do not have a final varix.

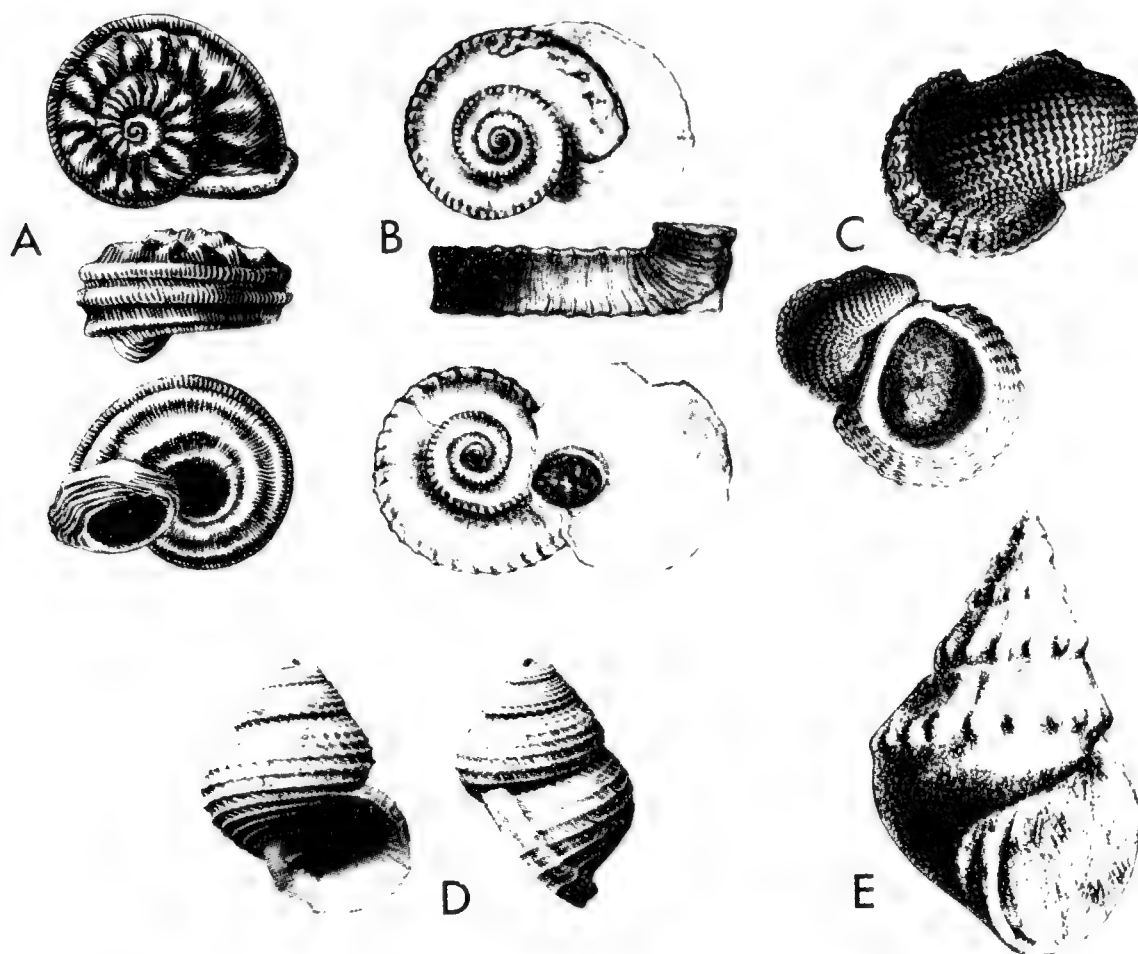


FIG. 18. Trochacean genera mentioned in Appendix 2. A) *Dichostasis complex* Yochelson, 1956, Permian (Liotiidae), $\times 5.1$. B) *Anisostoma suessi* (Hörnes, 1855), Triassic (Liotiidae), $\times 1.7$. C) *Crespedostoma spinulosum* Lindström, 1884, Silurian (Crespedostomatidae), $\times 1.7$. D) *Danilia insperata* Beu & Climo, 1974, Recent Trochidae, $\times 1.2$. E) *Amberleya bathonica* Cox & Arkel, 1948, Jurassic (Trochidae: Amberleyinae), $\times 0.8$. Fig. C after Lindström, 1884; Fig. D after Beu & Climo, 1974; others after Knight et al. (1960).

ous similarities." Unifying features were the nodose or cancellate sculpture and the resemblance to the Littorinacea, presumably because of the incomplete peritreme in Amberleyidae. Nacre was verified only in the Amberleyidae; the shell of the other groups may yet prove to have been nacreous.

Genera in the Amberleyidae have a striking resemblance to a group of modern genera that includes *Bathybembix*, *Cidarina*, and *Calliotropis*. *Bathybembix* species look like the Jurassic *Amberleya bathonica* Cox & Arkel (Fig. 18E) and many Jurassic species assigned to *Amberleya* by Huddleston (1887–1896) could readily be grouped in the Recent *Cidarina*. No reason can be advanced not to recognize the Recent taxa as a continuation of this Mesozoic lineage. This lineage has been in need of subfamilial recognition in the Trochidae (Hickman, 1980a: 16, and personal communication), based upon unifying radula and sculptural characters. The modern line-

age is hereby assigned to the trochid subfamily Amberleyinae (reduced from the Amberleyidae).

Removal of Amberleyidae from the Amberleyacea leaves three other originally included families for consideration—the Platyacridae, Cirridae, and Nododelphinulidae. The Platyacridae were characterized in having planispiral early whorls, which led Cossmann (1915) and Wenz (1938) to place them in the Euomphalacea. Mature shells are trochiform. Because planispiral early whorls occur in the Liotiidae, I have no hesitation in considering this group as trochacean. Because of its discoidal final whorl, the sinistral *Cirrus* was thought to be euomphalacean by Cossmann (1915) and Wenz (1938). However, it and other genera included in the Cirridae have the spinose sculpture of the Amberleyinae. I doubt that Cirridae is a natural group, for few prosobranch families are completely sinistral. Because of the close re-

semblance between *Amberleya* and *Cirrus*, the Cirridae are easily encompassed within the Trochacea. The five genera of Cox's Nododelphinulidae exhibit many sculptural features of both the Liotiidae and the genus *Angaria*; these genera are also easily placed within the Trochacea.

Conclusions: A comparison of treatments by Cossmann (1915, 1918), Wenz (1938) and the Treatise authors (1960), leads me to believe that taxonomic inflation of supraspecific categories has obscured some relationships. The Treatise authors introduced two new superfamilies with very weak justifications. They evidently followed Wenz's dogma that the Trochacea arose in the Triassic; therefore, everything occurring in the Paleozoic had to be placed elsewhere. If Wenz or the Treatise authors had pursued Lindström's or Cossmann's recognition of an affinity between *Craspedostoma* and *Liotia*, the accepted classification of today would have

been very different.

The suprageneric classification of the Trochacea is greatly in need of revision. I suggest that as a prelude to a new understanding of the Trochacea, the available families and subfamilies of the currently recognized Craspedostomatacea and Amberleyacea be reconsidered as possible familial or subfamilial lineages in the Trochacea. Many of the Mesozoic genera now uncomfortably left in the Euomphalacea also need to be reconsidered as possible trochaceans. The roots of the great radiation of the Trochacea are in the Paleozoic, as evidenced by the clear presence of the Liotiidae in the Permian and the likelihood that the Silurian *Craspedostoma* was also trochacean. Some members of other Paleozoic superfamilies also need to be considered as possible trochaceans, because few arguments can be advanced to disprove an affinity with the Trochacea (see Appendix 1).

THE ANATOMY OF THE GALAPAGOS RIFT LIMPET, *NEOMPHALUS FRETTERAE*¹

Vera Fretter,² Alastair Graham² and James H. McLean³

ABSTRACT

Neomphalus fretterae is limpet-shaped, the mantle cavity extending from the right side of the head anteriorly and along the whole left side of the animal. The ctenidial axis stretches from the inner end of the cavity to its mouth attached to the mantle skirt, and then freely for a distance equal to about a fourth of its total length. The filaments are supported by skeletal strips united at their base to strengthen the axis; they are elongated, lie across the cavity, their tips related to a ciliated food groove which runs from the posterior end of the cavity to its mouth and thence forward on the right side of the neck, dorsal to the right tentacle, to the mouth.

The buccal region contains jaws and an odontophore, the musculature of which is described. The mid-esophagus is elongated, dilated and glandular, but has no septa and shows no torsion. The posterior esophagus runs alongside the right side of the mantle cavity to a stomach with gastric shield and vestigial spiral caecum. The intestine has an anterior loop alongside the esophagus, does not enter the pericardial cavity, and opens by the anus, placed on the anterior border of the shell muscle.

The heart, consisting of one auricle and a ventricle, lies in a pericardial cavity placed posteriorly and sending prolongations into the visceral mass. Anterior and posterior aortae arise from a bulbus. The general plan of the circulation is as in monotocardians, with a renal portal system. All vessels have an endothelial lining. There is one kidney, the left, opening to the mantle cavity; it is greatly dilated, forms a body cavity round much of the gut and possesses a nephridial gland. No renopericardial canal was found. The nervous system is hypoathroid-dystenoid, with long cerebropleuropedal connectives and scalariform pedal cords. Many nerve cells lie in the nerves. The streptoneury of the visceral loop is very tight. There is a prominent branchial ganglion, small osphradia lie on the gill axis and a statocyst over each pedal ganglion. There are no eyes.

The sexes are separate, males normally distinguishable by the greater length of the left cephalic tentacle. The testis discharges to a large prostate gland opening to the mantle cavity near the anus; a seminal groove leads along the left side of the neck, whence a ciliated tract runs along the tentacle. In females the ovary opens to a U-shaped oviduct with two different glandular areas. A ciliated groove runs along the oviduct and originates at the mouth of a receptaculum seminis opening separately to the mantle cavity at a deeper level.

The anatomical peculiarities of *Neomphalus* are mainly brought about by (1) adoption of a patelliform facies; (2) enlargement of the mantle cavity; (3) an increased torsion (270°) of visceral mass on head-foot; (4) a leftwards roll of mantle cavity and visceral mass on an anteroposterior axis. The animal cannot be related to any living group of prosobranchs. It shows several features—gill, radula, anterior intestinal loop—characteristic of archaeogastropods, but in most respects the organization is monotocardian, in some ways convergent with that of other ciliary feeders. *Neomphalus* seems to represent a prosobranch stock passing from the archaeogastropod to the mesogastropod grade which has persisted by virtue of its unusual habitat.

INTRODUCTION

In the following pages an account is given of the internal anatomy of *Neomphalus fretterae*, its bearings on the functioning of the living animal and on its relationships. The external features of the Galapagos Rift limpet have already been described (McLean, 1981)

and are not dealt with here. The source of the animals and their mode of preservation have been given in the same paper. Much information was gained from study of serial sections, sagittal and transverse, cut 15 μ m thick and stained in Mayer's hematoxylin and eosin; animals were also dissected with the help of a stereomicroscope.

¹Contribution number 29 of the Galapagos Rift Biology Expedition supported by the [United States] National Science Foundation.

²University of Reading, Whiteknights, Reading RG6 2AJ, United Kingdom.

³Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. 90007.

ANATOMY

Ctenidium

The ctenidial axis (Fig. 1) consists of a tough skeleton of connective tissue with a bundle of longitudinal muscle fibers running dorsal to the afferent vessel. The efferent vessel, placed where the axis attaches to the mantle skirt, is surrounded by a thick wall of connective tissue strengthened on each side by the fibrous bases of the skeleton of the filaments.

The ctenidial filaments are attached obliquely to the axis, the afferent end anterior to the efferent. Each is flattened but bulges slightly along the afferent and efferent borders. The efferent edge is supported by two dense and fibrous skeletal rods which taper dorsally and do not extend far towards the afferent edge throughout the greater part of the length of the filament. Near its attachment to the axis, however, the skeletal rods become longer and thicker, extending over more

of the depth of the filament. Finally, near the axis, neighbouring filaments fuse and the skeletal rod on the side of one filament joins with that on the adjacent side of the next filament; still nearer the axis this unites with corresponding pieces in other filaments so that a zigzag skeletal structure is produced. This lies in the wall of the efferent vessel. Since there is a double row of filaments the result is that the efferent and the sides of the axis are braced by a complex and continuous skeletal support.

The narrow efferent edge of the filament carries some frontal cilia; its afferent edge carries abfrontals, as numerous as the frontals. The most conspicuous ciliation, however, is the set of strong lateral cilia placed on each flat side of the filament. The gill is therefore clearly equipped with the ciliation necessary to drive water from the lower, ventral side of the mantle cavity to the dorsal, and to move particles filtered from this stream to the tips of the filaments, where they are deposited in, or may be led to, the food groove.

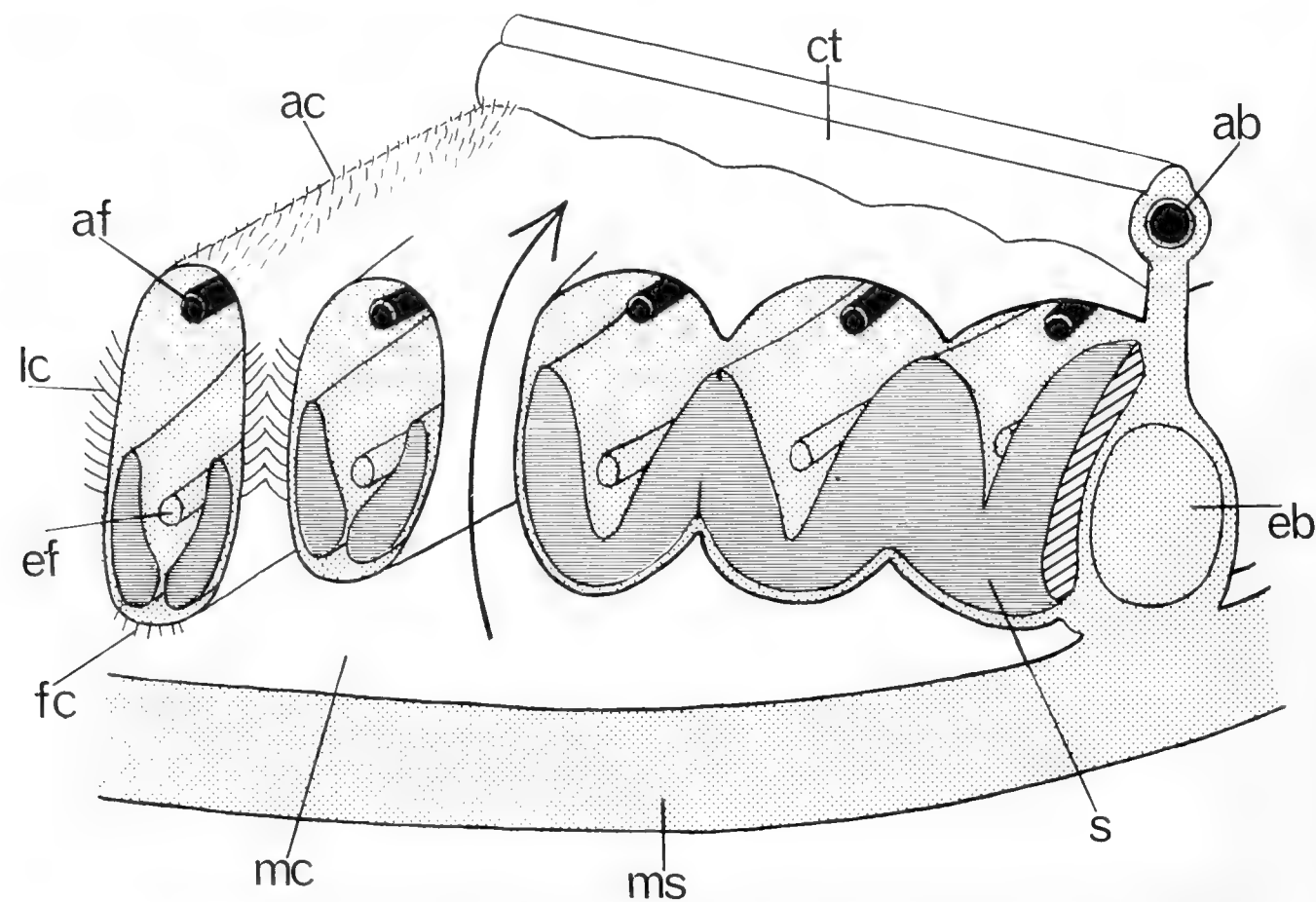


FIG. 1. Stereogram of part of mantle skirt, a short length of ctenidial axis, and the bases of five filaments on one side; those on the other side are not shown. The filaments are cut successively closer to the axis from left to right. Arrow shows direction of water current. ab, afferent branchial vessel in ctenidial axis; ac, abfrontal cilia; af, afferent vessel of filament; ct, ctenidial axis; eb, efferent branchial vessel in ctenidial axis; ef, efferent vessel of filament; fc, frontal cilia; lc, lateral cilia; mc, mantle cavity; ms, mantle skirt, s, gill skeleton.

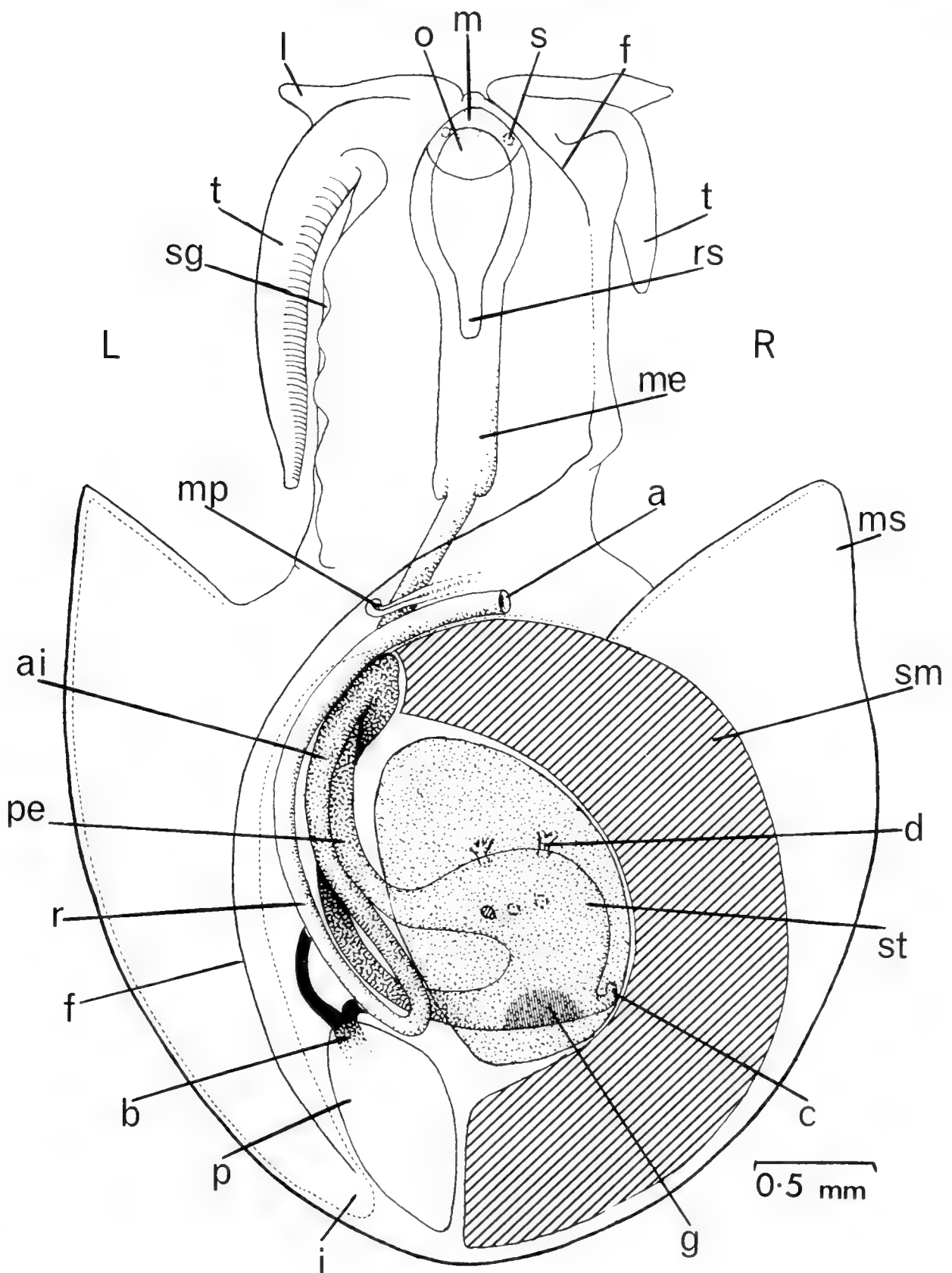


FIG. 2. Animal in dorsal view to show the general plan of the alimentary canal together with some features of the mantle cavity and head. a, anus; ai, anterior intestinal loop running above and below posterior esophagus; b, bulbus, dividing anteriorly into anterior and posterior aortae; c, spiral caecum; d, one of the ducts of the digestive gland (the position of others is indicated and the extent of the gland is stippled); f, food groove; g, gastric shield; i, innermost part of mantle cavity; L, left; l, oral lappet; m, position of mouth; me, mid-esophagus; mp, male pore, its lips extending right, ventral to the rectum; ms, mantle skirt, the pecked line indicating where it has been cut; o, odontophore; p, pericardial cavity; pe, posterior esophagus; R, right; r, rectum; rs, radular sac; s, salivary gland; sg, seminal groove running on to left tentacle; sm, shell muscle, hatched; st, stomach; t, tentacle.

Digestive system

The mouth (Figs. 2–5), a longitudinal slit when closed, is placed on the underside of the head practically at the extreme anterior end of the body. The short, vertically-directed oral tube to which it opens carries a jaw on each lateral wall. These are oval cuticular thickenings tapering ventrally to a thin edge. Their surface is smooth.

The buccal cavity is wide and has a well-developed odontophore on its floor with a rather shallow sublingual pouch beneath it. Between the point where the cerebral commissure crosses the roof of the cavity and the beginnings of the dorsal folds of the esophagus the roof is folded outwards to form a glandular pouch on each side of the mid-line: these may represent salivary glands; otherwise none are present. Dorsal to the odontophore is an opening leading to a broad but shallow space, the radular diverticulum; it rapidly narrows posteriorly and from its innermost part the radular sac runs back.

The esophageal opening lies dorsal to that of the diverticulum and is slit-like, narrow dorsoventrally and wide laterally. Behind the level of the cerebral ganglia, and about level with the mid-points of the odontophoral cartilages, the lateral parts of the esophagus expand ventrally so that the gut has a deep inverted U-shape in section. Dorsally its walls bear two longitudinal folds, low and well separated, and ventrally two similar ones. On each side one dorsal and one ventral fold separate a lateral pouch from a central area. Posterior to the tip of the radular sac the esophagus gradually becomes approximately circular in section, the ventral folds converge on the mid-ventral line and unite to form a single fold with a double free edge. All three folds run the whole length of this region of the esophagus, becoming taller posteriorly. They terminate when the esophagus is close to the level of the pleuropedal ganglia. Here the lateral pouches end, the diameter of the gut is abruptly reduced—it is tightly embraced by the visceral loop—and the wall becomes thrown into many low longitudinal folds, marking the beginning of the posterior esophagus. Although this is where one would expect to see the effects of torsion on the gut there is no sign of the twist visible in most prosobranchs, though it is clear in the vascular and nervous systems.

The posterior esophagus runs back, on the

left side of the body, to the visceral mass where it curves to the right and runs through the digestive gland to enter the stomach (Fig. 6). This is a U-shaped structure embedded in the gland, dorsoventrally flattened, the concavity facing left, with the esophagus entering the anterior limb and the intestine leaving the posterior one. Five ducts, all opening to the esophageal half, connect the stomach and digestive gland. At the apex of the stomach, on the right, a small, twisted tubular appendage, its walls bearing some ridges and grooves, seems to be a vestige of a spiral caecum, and on the wall of the intestinal limb lies an oval cuticular patch, raised marginally into crests, which must represent the gastric shield of other prosobranchs. Though much of the stomach wall is rather featureless, a ciliated intestinal groove can be recognized running along the intestinal limb and bordered by slightly elevated typhlosoles. This part therefore corresponds to the style sac of other prosobranchs.

The intestine passes from the stomach to the left and loops forward through the kidney, attached to its wall ventrally; emerging from this it enters the cephalopedal sinus and passes anteriorly, ventral to the posterior esophagus almost to the level of the supra-esophageal ganglion. There it turns through 180°, curves to the dorsal side of the esophagus and runs back nearly to the level of the anterior end of the pericardial cavity. Here it again projects into the kidney, and, skirting the pericardial cavity turns forward as the rectum, passing close to the efferent renal vein. Finally, it emerges from the kidney and, after a short course along the roof of the mantle cavity, opens by the anus which lies more or less in the mid-line of the head-foot and on the anterior edge of the shell muscle (Fig. 11A).

Except for that part which lies anterior to the posterior esophagus the alimentary tract is lined everywhere by a columnar ciliated epithelium with numerous goblet cells; additional gland cells of another type occur in the rectum, presumably concerned with the consolidation of fecal material. The initial part of the esophagus, however, may be divided into lateral unciliated, glandular areas, where the cells exhibit apocrine secretion, located between the ciliated dorsal and ventral folds on each side, and a ciliated channel between the two dorsal folds. Though the development of the lateral glandular areas is much less than in other archaeogastropods—particularly in

the absence of folding of the epithelium—it is distinct, and, despite the fact that it lies anterior to the region of torsion instead of coincident with it as in these animals, its organization allows this part of the gut to be identified as mid-esophagus.

In general the gastric epithelium is a simple ciliated columnar one. That underlying the gastric shield, however, stains more darkly and at intervals small protuberances project from it, away from the stomach lumen. These consist of bundles of cells, about twice as high as the ordinary gastric ones. Each bunch is bound by small muscle fibres. From their situation it may be presumed that they produce the cuticular material.

The digestive gland is markedly less volu-

minous than in most archaeogastropods. Its tubules are lined by cells which seem highly vacuolated and devoid of contents in the animals examined, staining very lightly. These correspond to the digestive cells of other prosobranchs. Other cells also appear, reminiscent of the glandular cells of these animals, darkly staining, with a swollen base lying against the surrounding blood space and connected to the lumen by a narrow neck. Sometimes these cells appear to be grouped. Some of the digestive cells bulge outwards into the blood spaces lying between tubules. Occasionally we have gained the impression that narrow, tubular spaces, lined by darkly-staining cells, project from the tubules into the blood spaces; there they turn to run briefly in

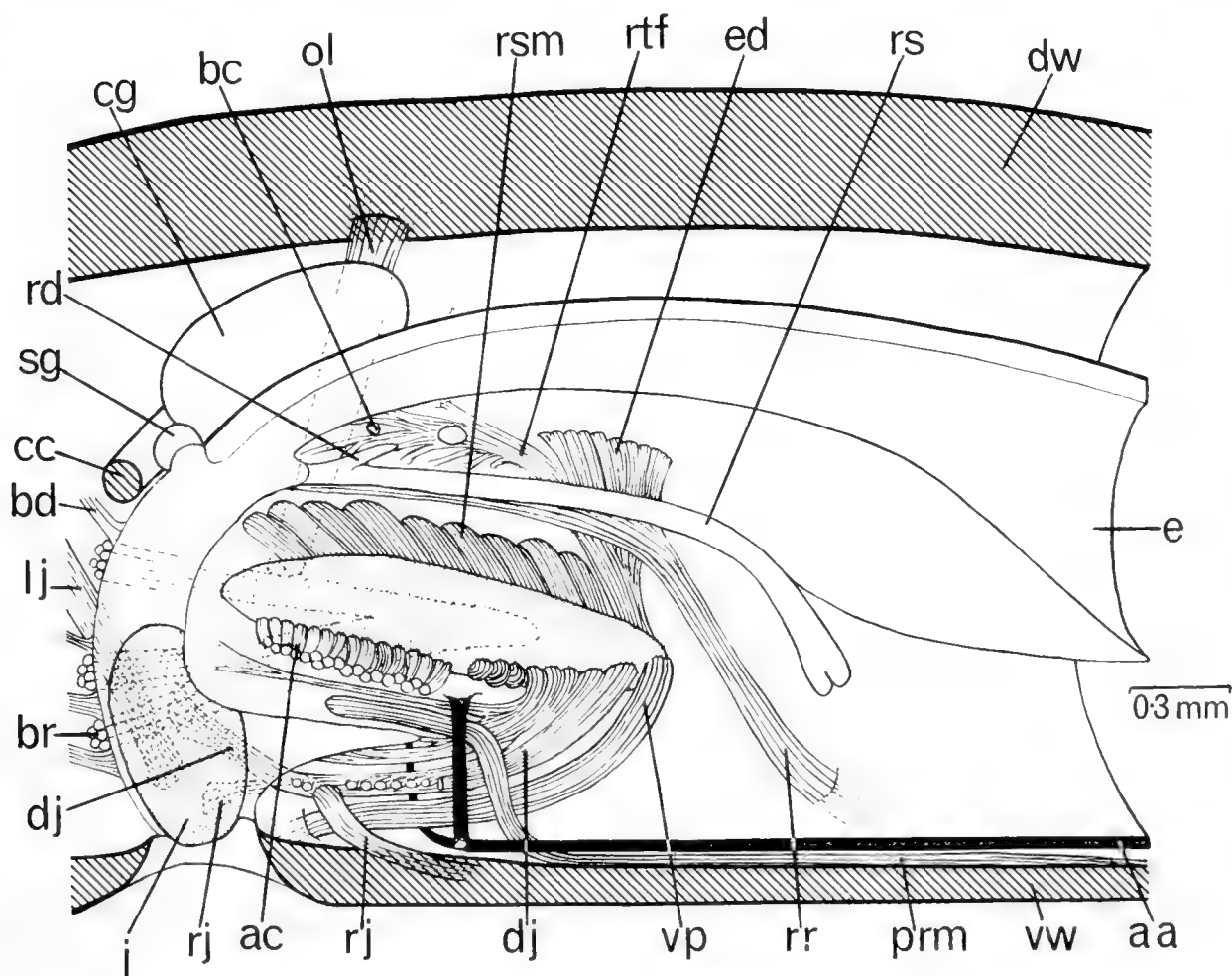


FIG. 3. Right sagittal half of the head and buccal mass. aa, anterior aorta (cephalic artery) which divides anteriorly into a dorsally-directed buccal artery and two lateral cerebral arteries; ac, approximator muscle of the cartilages; bc, buccal commissure running in the transverse fold; bd, buccal dilator muscle; br, buccal constrictor muscle; cc, cerebral commissure; cg, cerebral ganglion; dj, depressor muscle of the jaw which posteriorly fuses with muscles from the walls of the sublingual pouch and with the retractor of the radular membrane; dw, dorsal body wall; e, esophagus; ed, dilator muscles of the esophagus; j, jaw; lj, levator muscle of jaw; ol, levator muscle of the odontophore; prm, protractor of the radular membrane; rd, radular diverticulum; rj, retractor (remotor) muscle of the jaw; rr, radular retractor muscle; rs, radular sac; rsm, retractor muscle of the radular membrane; rtf, retractor muscle of the transverse fold; sg, salivary gland; vp, ventral protractor muscle of the odontophore; vw, ventral body wall.

the hemocoel, parallel to the base of the epithelium. They would thus seem comparable to short tubular glands. The fixation of the material, however, has not been good enough to let us resolve these structures clearly. Nu-

merous amebocytes, their cytoplasm containing yellow granules, occur in the blood spaces.

The intestine and rectum contain throughout most of their length a fecal rod, pieces of

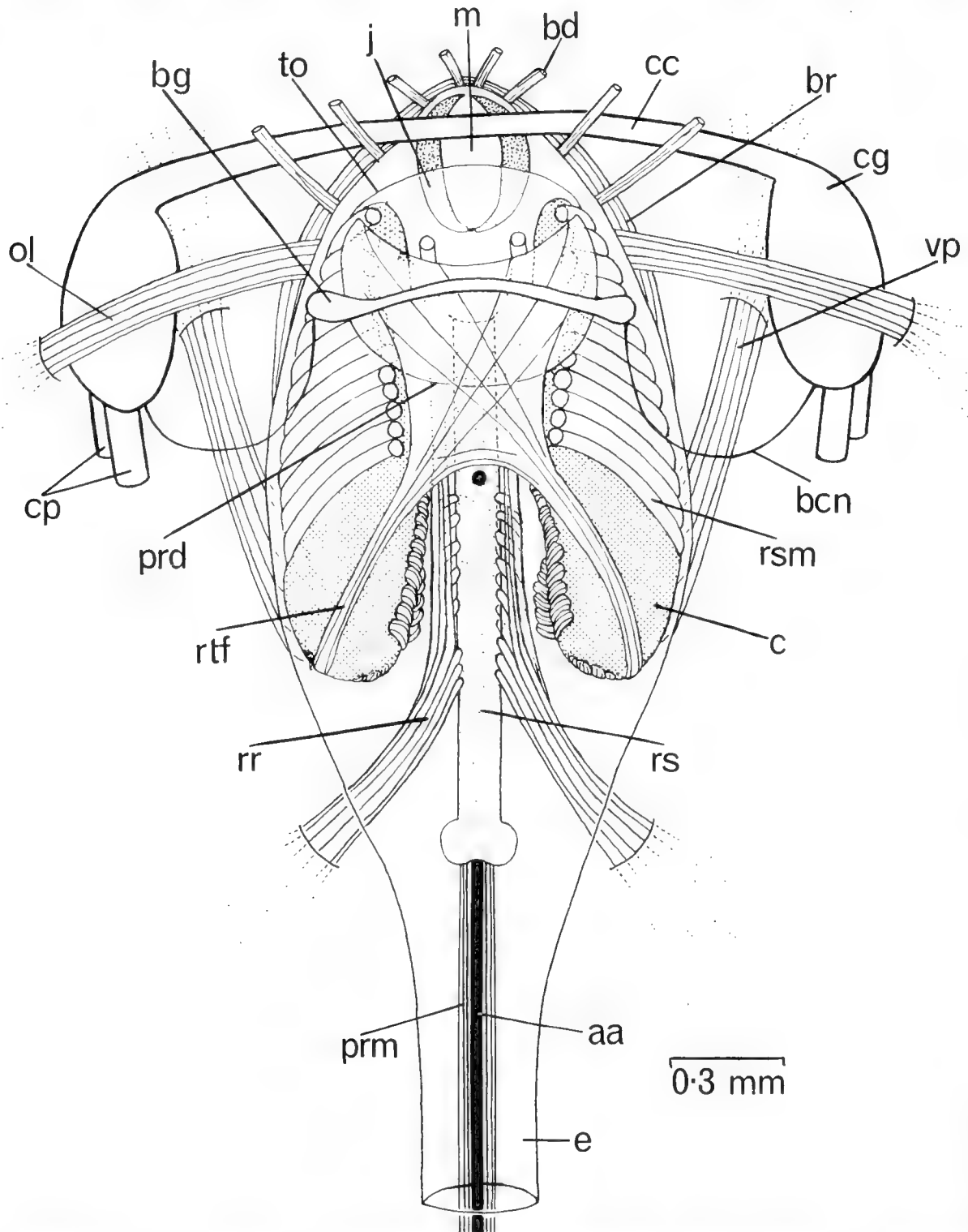


FIG. 4. Arrangement of muscles and related structures of the buccal mass; dorsal view. The central black spot indicates where the buccal artery opens from below into the buccal sinus. aa, anterior aorta (cephalic artery); bcn, buccal connective; bd, buccal dilator muscle; bg, buccal ganglion; br, buccal constrictor muscle; c, buccal cartilage; cc, cerebral commissure; cg, cerebral ganglion; cp, cerebropleural and cerebropedal connectives; e, esophagus; j, jaw; m, mouth; ol, odontophoral levator muscle; prd, posterior boundary of the radular diverticulum; prm, protractor of the radular membrane; rr, radular retractor muscle; rs, radular sac; rsm, retractor muscle of the radular membrane; rtf, retractor muscle of the transverse fold; to, anterior tip of odontophore; vp, ventral protractor of the odontophore.

which may also be seen within the mantle cavity. This contains much particulate matter of varied sorts, mainly minute, but pieces of grit, radiolarian, foraminiferan and crustacean skeleton are also numerous and often of con-

siderable size. The largest pieces of crustacean skeleton seen measured about $250 \times 90 \mu\text{m}$, and the largest piece of radiolarian skeleton about $200 \times 110 \mu\text{m}$. The rod is composed of mucus; in the rectal region and

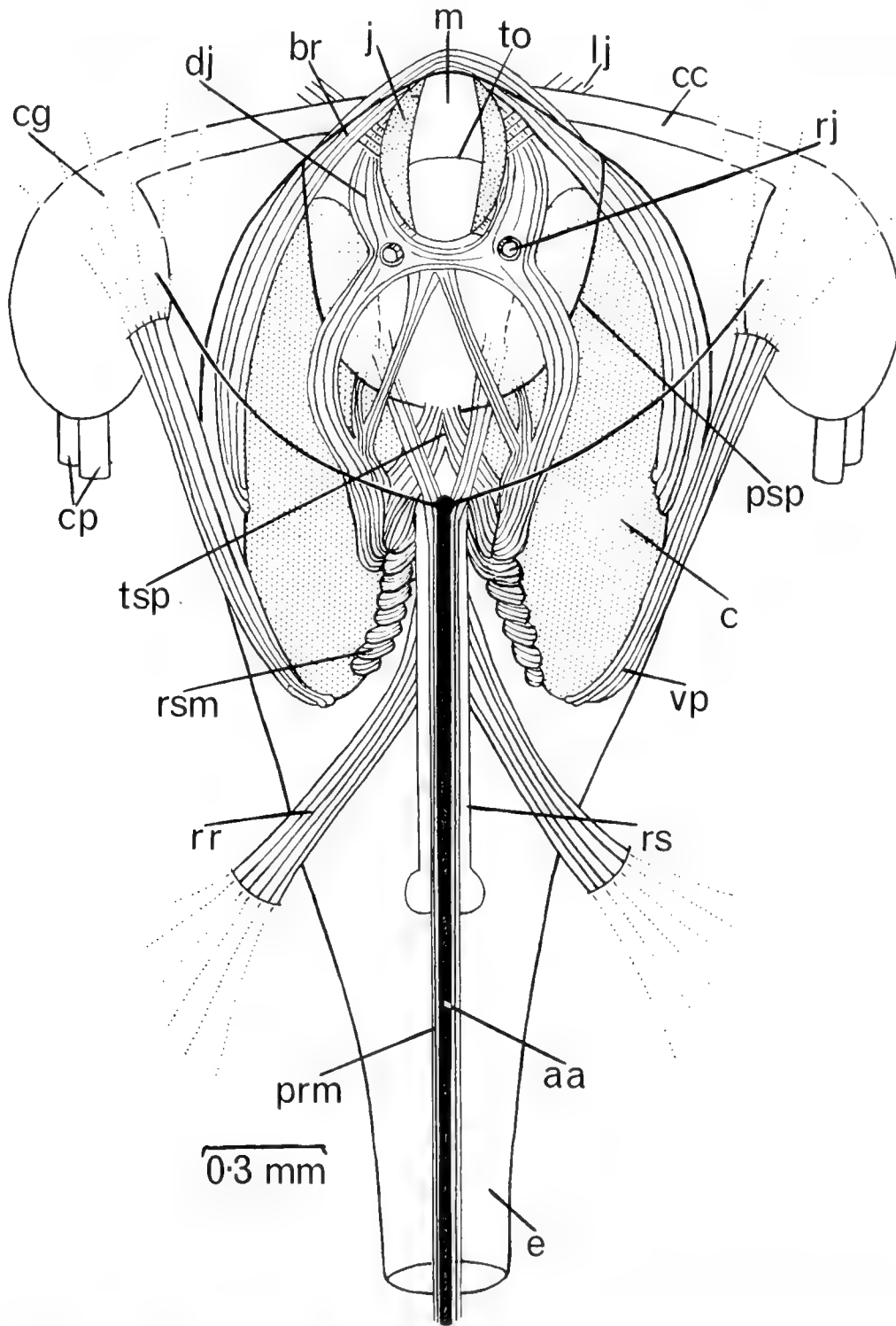


FIG. 5. Arrangement of muscles and related structures of the buccal mass; ventral view. aa, anterior aorta (cephalic artery) branching anteriorly into right and left cerebral arteries running to cerebral ganglia, and buccal artery passing dorsally to buccal sinuses; br, buccal constrictor muscle; c, buccal cartilage; cc, cerebral commissure; cg, cerebral ganglion; cp, cerebropleural and cerebropedal connectives; dj, depressor muscle of jaw; e, esophagus; j, jaw; lj, levator muscle of jaw; m, mouth; prm, protractor muscle of radular membrane; psp, posterior limit of sublingual pouch; rj, remotor muscle of jaw, cut where it penetrates the depressor of the jaw on its way to the ventral body wall; rr, radular retractor muscle; rs, radular sac; rsm, retractor muscle of the radular membrane; to, anterior tip of the odontophore; tsp, tensor muscles of the sublingual pouch; vp, ventral protractor muscle of the odontophore.

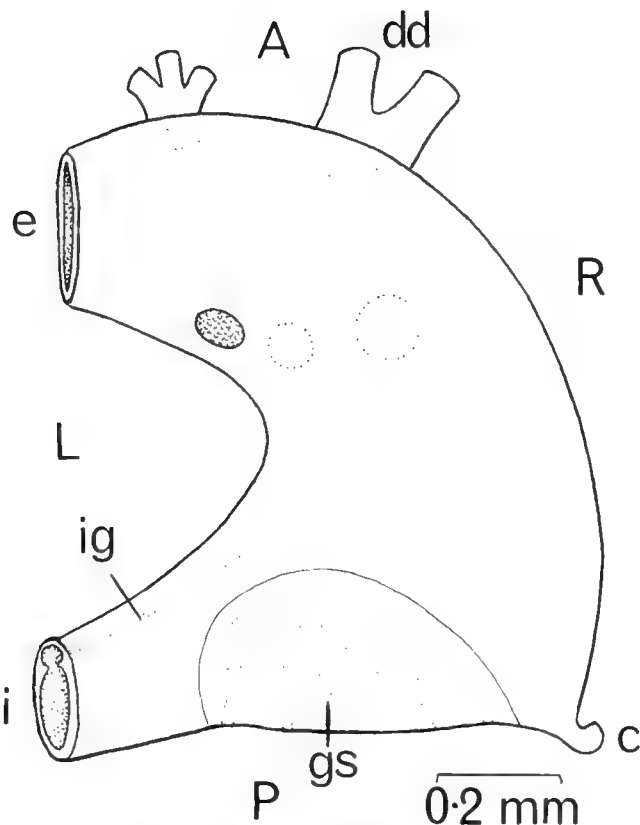


FIG. 6. The stomach in dorsal view. A, anterior; c, vestigial spiral caecum; dd, ducts of digestive gland (the position of others indicated); e, esophagus; gs, gastric shield; i, intestine; ig, intestinal groove; L, left; P, posterior; R, right.

mantle cavity it acquires a superficial layer with the same staining reaction as the rectal glands and probably derived from them, maintaining the integrity of the rod until it has passed out of the cavity.

The buccal region is organized as in other prosobranchs to allow the use of the odontophore and radula which are supported by a single pair of cartilages. The muscles associated with this apparatus are as follows (Figs. 3-5):

A. Muscles from the jaws and buccal roof.

1. Dilators of the buccal cavity (Figs. 3, 4, bd). Numerous small muscles run from the dorsal and dorsolateral walls of the oral tube and anterior part of the buccal cavity to origins in the body wall anteriorly and dorsally.

2. Levators (or retractors) of the jaws (Figs. 3, 5, lj). On each side a muscle runs from an origin in the anterodorsal body wall to an insertion centrally placed on the ventral half of the jaw.

3. Depressors and remoters of the jaws. On each side there are two muscles. The more powerful, the depressor (Figs. 3, 5, dj),

is inserted centrally on the dorsal region of the jaw and surrounding buccal wall, whence it passes ventrally to the mid-line where the muscles from right and left jaws unite and there is some decussation of the fibres. Under the sublingual pouch splits appear in the muscle allowing fibers of the remotor muscle of each side to pass medially. Thereafter the depressors run posteriorly as a single muscle but bifurcate into right and left portions again round the buccal artery. Each half then attaches to the ventral side of the ipsilateral cartilage.

The second muscle, the remotor (Figs. 3, 5, rj), is weaker. It is inserted on the jaw ventrally, close to the levator, passes back to lie ventral to the sublingual pouch, penetrates the depressor and then fuses with the ventral musculature of the head.

4. Constrictors of the mouth and buccal cavity (Figs. 3, 4, 5, br). A band of muscle originates on the lateral wall of each cartilage, more or less centrally. It runs forward ventral to the lateral expansion of the buccal cavity and terminates in the mid-line anteriorly (where it now lies morphologically dorsal to, but topographically anterior to the gut) partly by attaching to the buccal wall, partly by intermingling with its contralateral partner. In this way a sling muscle is formed which on contraction closes the mouth and constricts the anterior buccal region.

B. Muscles related to the radular membrane.

1. Protractors of the radular membrane (Figs. 3, 4, 5, prm). A pair of muscles inserts on the radular membrane where it forms the roof of the mouth of the sublingual pouch, one on either side of the mid-line. They run posteriorly to a point alongside the buccal artery then, one on either side of the vessel, pass ventrally with it to the inner side of the musculature of the neck. They travel posteriorly here, one on either side of the cephalic artery, almost as far as the pleuropedal ganglia, gradually attenuating as their fibers attach to body wall muscles. Contraction of these muscles brings the radular membrane and teeth outwards over the odontophoral tip.

2. Retractors of the radular membrane (Figs. 3, 4, 5, rsm). These are well developed and easily the most powerful components of the buccal musculature. They originate ventrally on each cartilage, some fibers on the medial side but most ventrolaterally and run thence dorsally and anteriorly to insertions on

the radular membrane. Their action retracts the membrane and teeth.

3. Radular retractors (Figs. 3, 4, 5, rr). On each side a muscle is inserted on the most medial parts of the radular membrane dorsally and on the side walls of the anterior half of the radular sac. Posterior to the cartilages these muscles diverge laterally, pass ventrally and enter canals in the lateroventral musculature of the body wall, where they gradually intermingle with the intrinsic muscles. Their action is synergic with that of the main retractors but also affects the radular sac.

C. Protractors and levators of the odontophore.

1. Ventral protractors (Figs. 3, 4, 5, vp). On each side a muscle runs forwards, laterally and ventrally from the posteroventral end of the cartilage. Posterior to the level of the mouth it passes into a channel penetrating the body wall musculature amongst the fibres of which it has its origin.

2. Levators (Figs. 3, 4, ol). A muscle inserts on the anterior part of each cartilage laterally. It passes dorsally, laterally and somewhat posteriorly, above the cerebral ganglion, to penetrate the dorsolateral body wall muscles where its fibers originate. Its action retracts and elevates the anterior part of the odontophore.

D. Other muscles. These are associated with the sublingual pouch, with the radular diverticulum, and run between the cartilages.

1. Retractors of the transverse fold (Figs. 3, 4, rtf). A small muscle originates on the posterior end of each cartilage dorsally. It runs forward and medially giving off a thin sheet laterally to the medial wall of the esophagus on the same side. More anteriorly it crosses the mid-line and ends in the tissue of the transverse fold (the sheet of tissue between radular sac, radular diverticulum and esophageal floor, in which the buccal ganglia lie). Some fibers of each muscle continue on the ipsilateral side and there is a marked cross-tie between the right and left muscles posterior to the point of decussation.

2. Tensors of the sublingual pouch (Fig. 5, tsp). Small muscles are inserted on each side on the roof, inner end and floor of the sublingual pouch. All pass posteriorly, lateral to the buccal artery and protractors of the radular membrane, intermingle with the de-

pressor muscle of the jaw and finally originate on the posterior medioventral region of the cartilage. Thus when the jaws and odontophore are protruded through the open mouth, the position of the walls of the sublingual pouch is adjusted to clear the passage and allow the radular teeth to move forward and downward.

3. Approximator of the cartilages (Fig. 3, ac). This is a prominent muscle which runs across the mid-line from the median ventral face of one cartilage to a corresponding situation on the other. On approximation of the cartilages ventrally their dorsal ends diverge, so spreading the radula.

Circulatory system

The part of the pericardial cavity which contains the heart (Fig. 7) lies left of the mid-line at the extreme posterior end of the visceral mass, bordered on the left by the innermost part of the mantle cavity and on the right by the posterior end of the shell muscle. It is somewhat triangular in outline, the longest side against the mantle cavity, narrow anteriorly and posteriorly. From the main cavity two extensions penetrate the visceral mass, one arising dorsally and passing forwards between gonad and digestive gland, lying directly under the mantle; the second starts ventrally, close to the bulb, and runs anteriorly, again between gonad (which lies dorsal to it) and digestive gland (which is ventral to it). The two extensions meet and fuse anteriorly. They are narrow clefts throughout their course.

In most places the pericardial cavity is lined by a squamous epithelium. In some areas, however, the epithelium is columnar, its cells loaded with spherules staining brightly with eosin and often giving evidence of apocrine secretion into the lumen. This type of cell is restricted to the pericardial wall in the neighborhood of the bulb and to the extensions into the visceral mass; in all situations, however, it occurs only where pericardial wall abuts against tubules of digestive gland.

There is only one auricle, the left, and there is no indication of a right one. It has a fusiform shape and lies partly posterior to and partly alongside the ventricle, on its left. Its wall is not markedly muscular and few muscular strands cross its lumen. Though the wall is generally smooth externally there are clear signs of filtration chambers as described in *Viviparus* (Andrews, 1979). The auricle com-

municates more or less at its mid-point with the ventricle by a small opening, the lip of which projects a little into the ventricular cavity, acting as a valve in the absence of true valves. The ventricle is a rather globular

chamber with much muscle in its wall and crossing its lumen, on the strands of which sit cells filled with brown granules. Anteriorly and ventrally the ventricle narrows to a short, muscular bulbus which passes out of the peri-

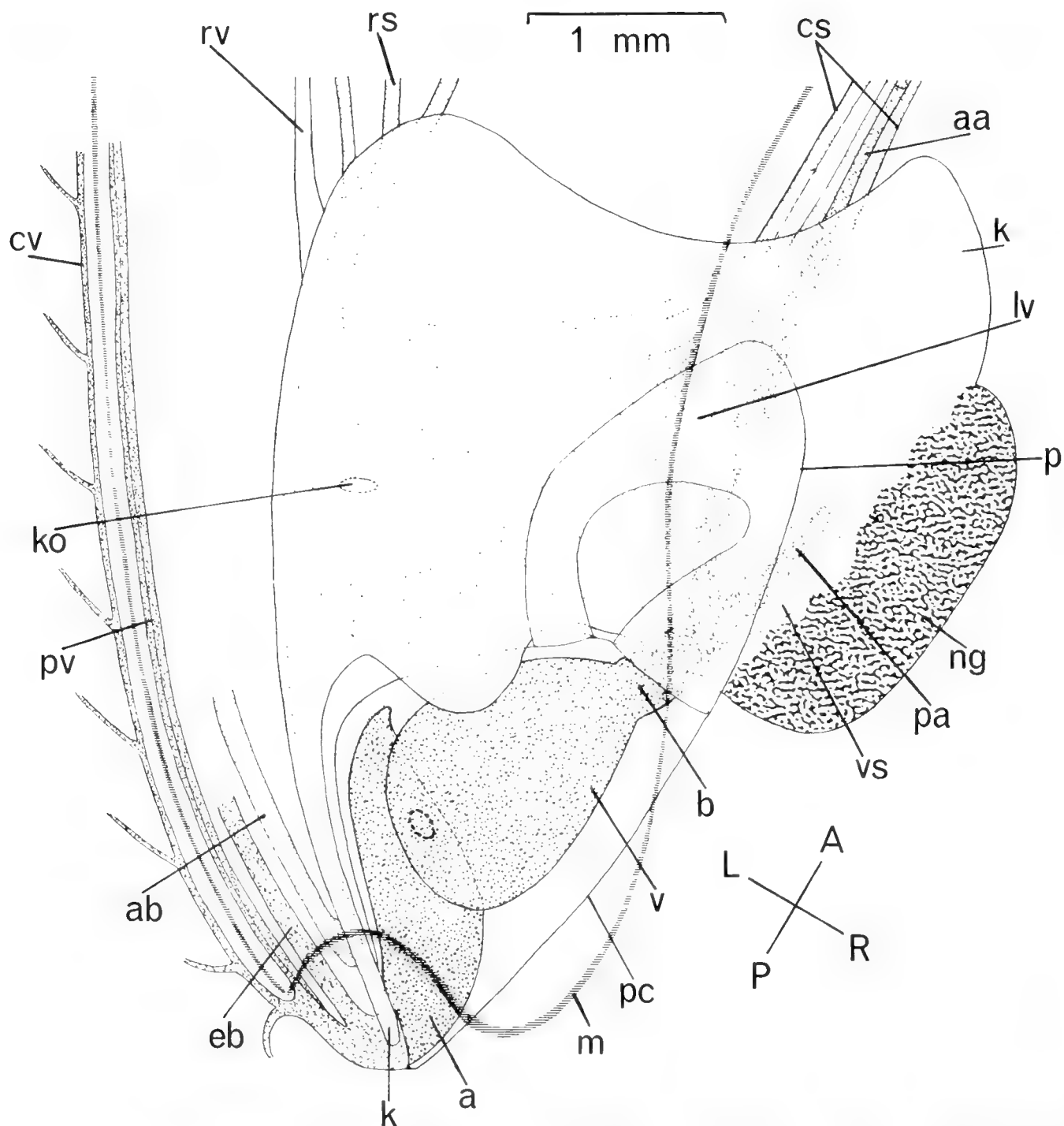


FIG. 7. Semi-diagrammatic representation of the relationships of the vascular, excretory and nervous systems at the posterior end of the mantle cavity and visceral mass. In life the right and left parts of the visceral loop (rv and lv) lie more or less vertically over one another: to make the anatomy clearer they have been spread apart by pushing the left structures over to the right of the figure. A, anterior; a, auricle; aa, anterior aorta within cephalopedal sinus; ab, afferent branchial vessel (in dorsal part of ctenidial axis); b, bulbus; cs, cephalopedal sinus; cv, circumpallial vessel; eb, efferent branchial vessel (in ventral part of ctenidial axis); k, kidney; ko, kidney opening; L, left; lv, left visceral ganglion in floor of kidney; m, limit of mantle cavity; ng, nephridial gland; P, posterior; p, extension of pericardial cavity into visceral mass; pa, posterior aorta within venous visceral sinus; pc, main pericardial cavity; pv, pallial vein; R, right; rs, vessel of rectal sinus connecting with plexus in kidney wall; rv, right half of visceral loop about to enter kidney; v, ventricle; vs, visceral sinus.

cardial cavity to lie on the ventral side of the visceral mass where that is connected to the head-foot. It rapidly divides into posterior and anterior aortae.

The posterior aorta passes to the right in a visceral venous sinus close to the ventral surface of the visceral mass. It sends branches to the nephridial gland, the kidney, digestive gland and reproductive organs.

The anterior aorta runs in the cephalopedal sinus (vein) and passes to the left side of the head-foot in close proximity to the anterior loop of the intestine and the posterior esophagus. It soon gives off a large pallial artery which passes to the floor of the mantle cavity and is traceable there to the anterior and posterior ends of the animal and is almost certainly circumpallial. The aorta runs forward to the level of the pleuropedal ganglia where it passes, parallel to the supra-esophageal connective, from a position dorsal to the esophagus to one ventral to it and gives rise to right and left lateral pedal arteries. These pass into the lateral parts of the foot, run backwards and forwards and give off numerous branches. The aorta (now properly the cephalic artery) continues forward in the floor of the cephalic hemocoel between the right and left protractor muscles of the radular membrane to a point about midway along the length of the odontophoral cartilages and just posterior to the sublingual pouch. Here it splits into three: (1) the buccal artery, which passes dorsally and opens to blood sinuses in the odontophore and round the radular sac; (2) and (3) lateral cerebral arteries, which pass one on each side to the cerebral ganglia and discharge to other cephalic blood spaces.

The venous spaces in the head all connect with a main cephalic hemocoel lying round the gut and cerebropleural and cerebropedal connectives. At the level of the pleuropedal ganglia a large pedal venous sinus passes dorsally from the foot in the central space of that group of four ganglia and joins the cephalic hemocoel to form the cephalopedal sinus or vein, in which lie the esophagus, the anterior aorta and the left half of the visceral loop. Posteriorly this sinus enters the base of the visceral mass just left of the roof of the mantle cavity and receives venous sinuses from the visceral mass. The combined vessel, the afferent renal vein, though continuing through the kidney as a conspicuous vein, breaks up into a large number of branches which form a plexus on the floor of the kidney.

Posteriorly the main vessel and the plexus connect with a prominent efferent renal vein running along the kidney wall on the left and more dorsally. All blood returning from the head-foot and visceral mass thus passes through the kidney and collects in the efferent renal. This vessel runs within the kidney almost to the most posterior level of the pericardial cavity where it turns abruptly into the ctenidial axis. Here it runs in a dorsal position along the whole length of the gill, giving rise to the vessels of the leaflets. These drain ventrally into the ctenidial efferent returning blood to the heart.

Anteriorly extensions of the efferent renal vein pass out of the kidney to form a plexus round the rectum. This seems to be much better developed in males than in females.

The pallial vein runs as a prominent vessel bulging into the mantle cavity from the more dorsal part of the mantle skirt, parallel to its edge, along its whole length. Anteriorly it relates to a small cluster of small lamellae that may represent a vestige of the right ctenidium. Near the point where it enters the auricle it receives blood from a pallial vein running parallel to it in the mantle edge which is fed from the circumpallial artery.

The blood spaces throughout the body are unusual in that all, down to the smallest, have an endothelial lining of squamous cells.

Excretory system

Neomphalus has only one kidney, the left. It is, however, more than just an excretory organ and forms a capacious body cavity, deep and wide. Indeed, it is more prominent as body cavity than as kidney since little of its surface seems to be involved in excretory activity, and only where the lining cells overlie the blood vessels in its walls (Fig. 7).

The kidney lies in the roof of the mantle cavity and extends widely under the visceral mass on the right, separating it from underlying shell muscle. Its anterior boundary is formed by shell muscle and its posterior boundary coincides approximately with the anterior wall of the pericardial cavity except for a lobe projecting dorsal to it and a long, narrow, horn-shaped canal which runs along its left side and does not terminate until level with the extreme posterior end of the auricle. The kidney opens to the mantle cavity by a pore with ciliated lips placed towards its left margin. We have found no pericardial connexion.

Near the point where the anterior and posterior aortae are formed by division of the bulbus, the right wall of the kidney gives rise to a series of tubules which extend ventral to part of the digestive gland and around the most posterior part of the cephalopedal sinus. The tubules open from the main chamber of the kidney by small apertures but then immediately dilate and become pressed against small arteries arising from the posterior aorta. The whole produces a spongy mass of spaces traversed by small blood vessels. This part of the organ drains to a vessel which runs on to the pericardial wall but which we have not been able to trace further. This area of the kidney corresponds to the nephridial gland of other prosobranchs.

The kidney is intimately related to a number of other organs. The afferent renal vein, formed from the fusion of cephalopedal and visceral venous sinuses, becomes associated with its ventral wall anteriorly and sends numerous branches over it. On the right this plexus drains to the efferent renal vein. This connects anteriorly with vessels lying around the rectum but runs mainly along the posterior horn of the kidney to become the afferent ctenidial vessel. The two visceral ganglia also lie in the kidney wall, the right in proximity to the efferent renal vessel, the left alongside the afferent renal.

Histologically most of the kidney is covered by a low cuboidal epithelium which may contain yellow granules but has no other distinct features. In some places—in the right extension under the visceral mass and in the nephridial gland—the epithelium is squamous. Wherever the cells overlie blood vessels, however, their appearance is different: they become columnar, have rounded apices very often clearly in the process of being budded off. There are few ciliated cells except in the immediate vicinity of the external opening.

Nervous system

The nervous system (Fig. 8) is in most respects a typical archaeogastropod one, though it also has some advanced features. It shows a primitive spread of nerve cells along nerve tracts rather than wholly concentrated into ganglia. Nerves, connectives and ganglia are all closely associated with the vascular system and almost without exception run in venous spaces.

The cerebral ganglia (Fig. 9) are ovoid bodies placed laterally and dorsally near the

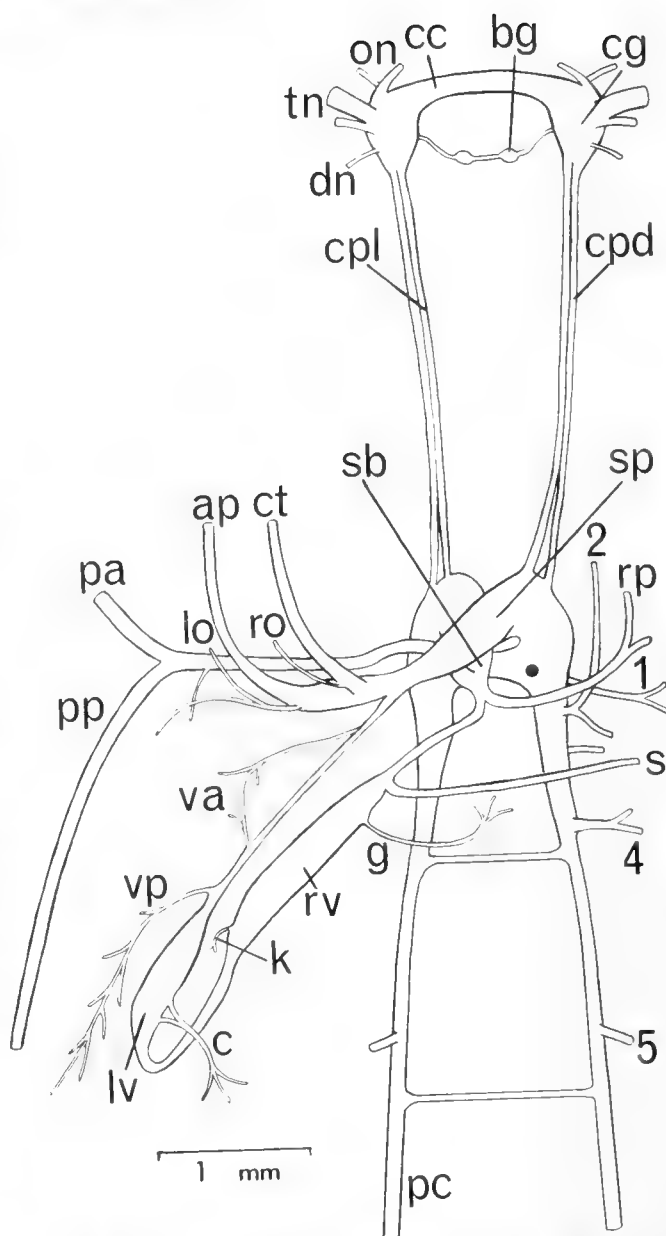


FIG. 8. Plan of nervous system; dorsal view. The black circle over the pedal ganglion marks the position of a statocyst. ap, anterior pallial nerve from branchial (osphradial) ganglion; bg, buccal ganglion; c, cardiac nerve; cc, cerebral commissure; cg, cerebral ganglion; cpd, cerebropedal connective; cpl, cerebropleural connective; ct, ctenidial nerve; dn, nerve to dorsal cephalic body wall; g, nerve to genital opening and anus; k, nerve to renal opening; lo, nerve to left half of osphradium; lv, left visceral ganglion; on, oral lappet nerves; pa, anterior branch of pallial nerve from subesophageal ganglion; pc, pedal cord; pp, posterior branch of pallial nerve; ro, right osphradial nerve; rp, right pallial nerve; rv, right visceral ganglion; s, nerve to shell muscle; sb, subesophageal ganglion; sp, supraesophageal ganglion; tn, nerves to tentacle; va, anterior nerve to floor of mantle cavity; vp, posterior nerve to same area; 1, 2, 4, 5, pedal nerves.

anterior end of the cephalic hemocoel and linked by a stout commissure which passes anterior (dorsal) to the buccal cavity at a level ventral to the salivary pouches and dorsal to

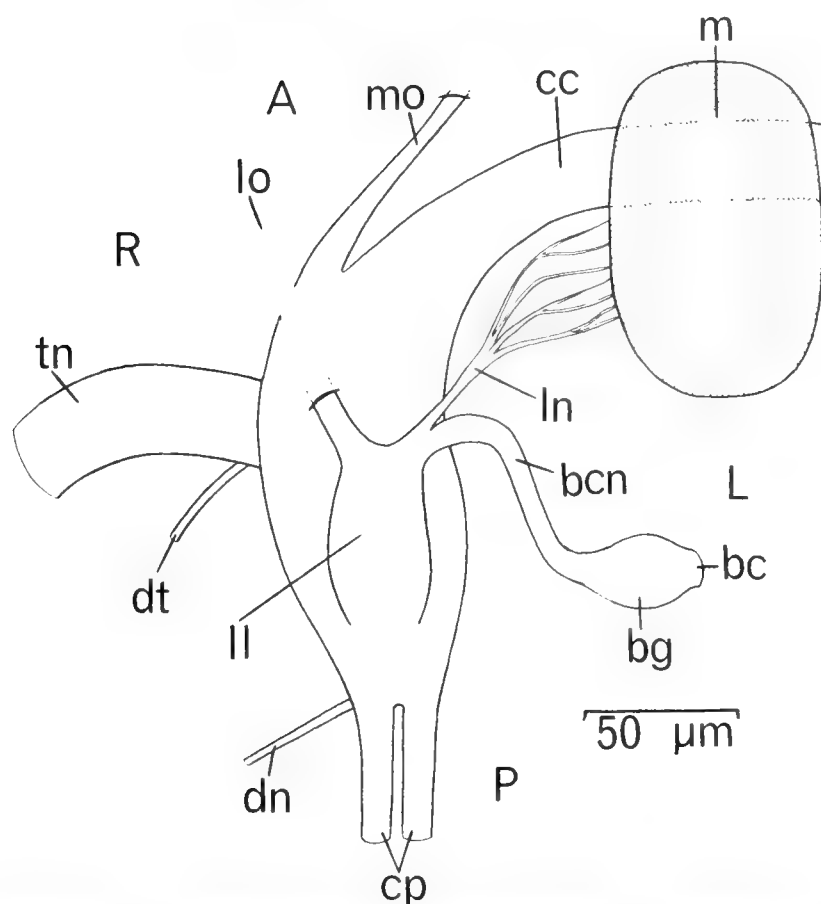


FIG. 9. Right cerebral ganglion, buccal ganglion and related nerves; ventral view. A, anterior; bc, buccal commissure; bcn, cerebrobuccal connective; bg, buccal ganglion; cc, cerebral commissure; cp, cerebropleural and cerebropedal connectives; dn, nerve to dorsal surface of head; dt, dorsal tentacular nerve; L, left; ll, labial lobe of cerebral ganglion; ln, labial nerve; lo, lateral nerve of oral lappet; m, mouth; mo, medial nerve of oral lappet; P, posterior; R, right; tn, tentacular nerve.

the inner ends of the jaws. On its ventral face each ganglion bears a labial lobe from which the buccal connective arises, and posteriorly it gives rise to a more dorsal cerebropleural connective and a more ventral cerebropedal one.

The following nerves originate from each ganglion in addition to the connectives and commissure.

From the main body of the ganglion:

1. Median nerve of the oral lappet, running to its anterior face.
2. A very stout tentacular nerve with a small dorsal branch.
3. A dorsal nerve from the base of the cerebropleural connective to the skin of the head.

From the labial lobe:

1. Lateral nerve of the oral lappet, running to its posterior face.

2. (As a branch from the base of the cerebrobuccal connective) a labial nerve which divides into anterior and posterior branches to the lips. Neither branch was seen to join with its contralateral partner to form a labial commissure.

The cerebropleural and cerebropedal connectives run posteriorly, one dorsal to the other, on the inner faces of the lateral walls of the neck, lying in subsections of the cephalic hemocoel. The pleuropedal ganglia are placed just posterior to the point where neck and foot join, alongside the beginning of the posterior esophagus. A constriction separates the more dorsal pleural from the more ventral pedal part.

The right pleural ganglion tapers backwards and to the left and soon connects with a prominent supra-esophageal ganglion. The left pleural narrows backwards and to the right and expands into a small subesophageal ganglion. No nerves seem to issue from the pleural ganglia (Fig. 10). The subesophageal,

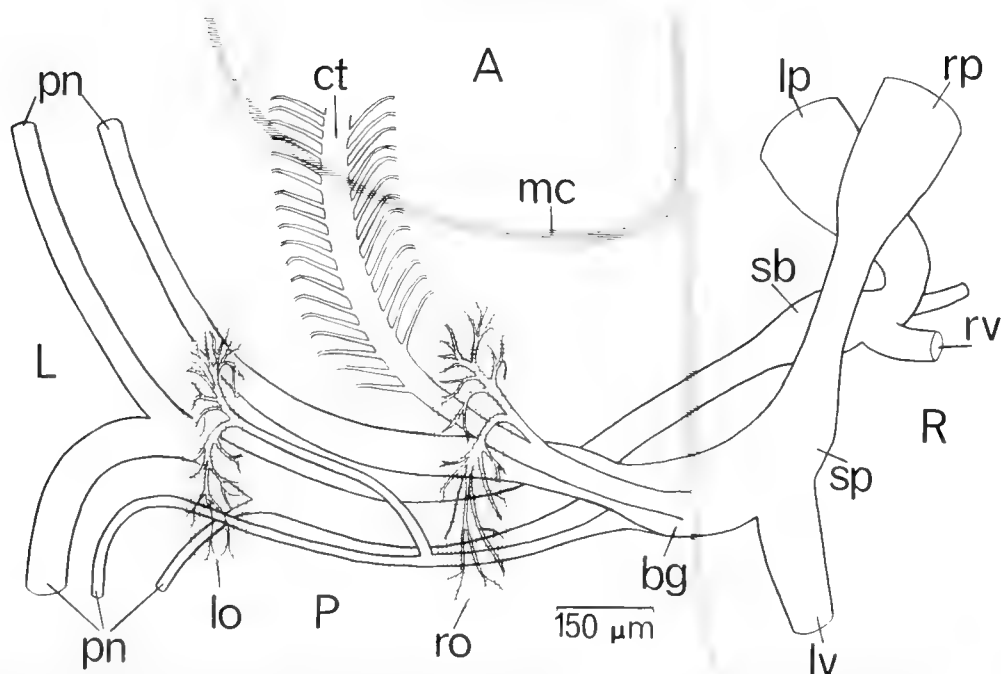


FIG. 10. Arrangement of nerves supplying gill, osphradium and mantle skirt; dorsal view. A, anterior; bg, branchial ganglion; ct, ctenidial nerve in gill axis; L, left; lo, left part of osphradium; lp, left pleural ganglion; lv, left half of visceral loop; mc, posterior limit of opening of mantle cavity; P, posterior; pn, pallial nerve; R, right; ro, right part of osphradium; rp, right pleural ganglion; rv, right half of visceral loop; sb, subesophageal ganglion; sp, supra-esophageal ganglion.

however, gives off a large nerve to the right, innervating part of the food groove and part of the shell muscle. An extremely large nerve originates from the left side of the ganglion and passes into the mantle skirt immediately anterior to the branchial extension of the supra-esophageal ganglion and very close but ventral to nerves coming from that ganglion. It divides into branches which run backwards and forwards near the pallial edge.

The supra-esophageal ganglion is confluent with a prominent branchial or osphradial ganglionic mass in the mantle skirt, from the dorsal surface of which arises a thick ctenidial nerve, containing many nerve cells. This runs to the point of attachment of the ctenidial axis; here it may be traced to the anterior tip of the gill. It becomes associated with an elaborate plexus of small nerves lying on its right and left sides; only this plexus extends along the posterior portion of the gill axis. From the base of the ctenidial nerve an osphradial nerve runs to an osphradial area lying right of the gill axis; another nerve, with a separate origin from the branchial ganglion, goes to a corresponding sensory area left of the axis and also sends a small branch to the posterior part of the mantle edge. A very large pallial nerve passes forward from the branchial ganglion to the pallial margin.

The left half of the visceral loop (Fig. 7) runs

posteriorly in the cephalopedal sinus to the floor of the kidney alongside the anterior loop of the intestine and the posterior esophagus, expanding, shortly before it enters the kidney, into an elongated visceral ganglion. The right half of the loop runs amongst muscle fibers on the left margin of the shell muscle close to the anus and genital pore. It lies nearly directly dorsal to the left half, especially posteriorly where it enters the ventral wall of the kidney and expands into an elongate right visceral ganglion linked by a short commissure to that on the left.

Some nerves originate from the visceral connectives. On the left a small plexus of nerves lies in the pallial floor with connexions anteriorly and posteriorly to the connective; another nerve, arising near the supra-esophageal ganglion, innervates the walls of the cephalopedal sinus. Just anterior to the left visceral ganglion a further nerve runs posteriorly into the pallial floor. On the right two nerves leave the visceral connective near the subesophageal ganglion and go to the food groove, whilst another, leaving the connective close to the point where it enters the kidney, goes to the region of the anus and genital pore. A large nerve to the shell muscle leaves the anterior part of the right visceral ganglion and a small one from its posterior end goes to the lips of the kidney opening. A cardiac nerve

originates from the left ganglion and runs in the wall between kidney and pericardial cavity.

The pedal ganglia form cords which run the length of the foot, gradually diverging and becoming more slender. A prominent commissure links them anteriorly and there are at least three further connexions more posteriorly, giving a generally scalariform pattern. Numerous nerves pass forward and laterally from the cords innervating the posterior part of the neck and the muscles and sense organs of the foot.

A statocyst containing a single statolith sits on the dorsal surface of each pedal ganglion. No trace of any eye or optic nerve can be found.

Reproductive system

In the male (Fig. 12) the testis lies on the dorsal side of the visceral mass, covering the right and posterior half. It is made of a series of blind tubules which converge towards the left anterior end of the organ on a short vas deferens. Spermatogenesis was in active progress in the animals examined and large numbers of ripe sperm filled the tubules and the duct. Only one type of sperm appeared to be present.

The vas deferens discharges to the lumen of an extremely large prostate gland which occupies the left dorsal part of the visceral mass; behind the vas deferens a narrow extension of the pericardial cavity lies between prostate and testis. The gland has an anterior and a larger posterior lobe, both formed of tubules discharging to the main ducts. The rather large central space of the gland leads to the male pore placed between the rectum dorsally and the right half of the visceral loop ventrally, just anterior to the anterior end of the kidney and more or less level with the anterior shoulder of the shell muscle. The lips of the pore spiral outwards and form the margins of a groove which runs for a short distance parallel and ventral to the rectum, gradually flattening (Fig. 11A).

Ventral to the bulbus of the heart the wall of the mantle cavity in males shows a small blind diverticulum. This corresponds in situation with the receptaculum seminis of the female of which it seems to be a rudimentary homologue. This would seem to indicate some hormonal control of its development.

In the female (Fig. 13) nearly the whole of the dorsal surface of the visceral mass is oc-

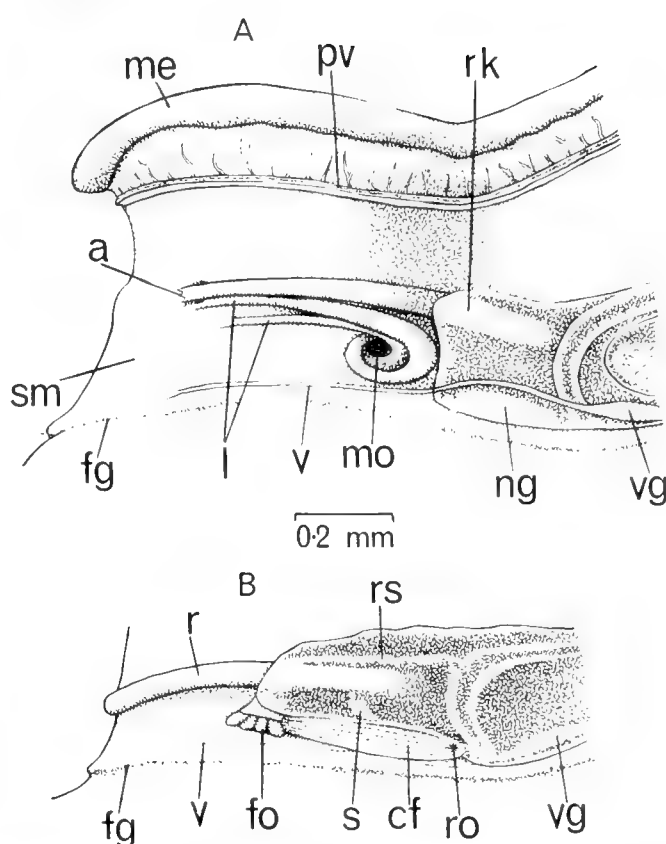


FIG. 11. A, dissection of male, showing area around male opening and anus; B, similar dissection of female. a, anus; cf, ciliated field linking openings of oviduct and receptaculum; fg, food groove, running from right side of neck (left in figure) to deep part of mantle cavity (right in figure); fo, female (oviducal) opening; l, lips of male pore extending to the right, ventral to the rectum; me, mantle edge; mo, male opening; ng, nephridial gland within kidney; pv, pallial vein with accompanying pallial nerve ventral to it; r, rectum; rk, rectum within kidney; ro, opening of receptaculum; rs, rectal sinus, communicating posteriorly with renal vessels; s, receptaculum seminis seen by transparency; sm, right shoulder of shell muscle; v, right half of visceral loop; vg, right visceral ganglion in floor of kidney.

cupied by the ovary. Like the testis it is formed of branching tubules and is bordered on its left by a pericardial extension. The tubules converge on a point on the left side of the ovary, nearly at its extreme anterior end. At this point the ovary opens, apparently without the intervention of any ovarian duct, into the first section of the female duct, the opening lying at the centre of a ring-shaped fold; some muscles run from its lips to the dorsal surface of the mantle and may regulate passage of eggs. A short and very narrow gonopericardial duct runs from the point where ovary and oviduct are linked to the innermost end of the pericardial extension.

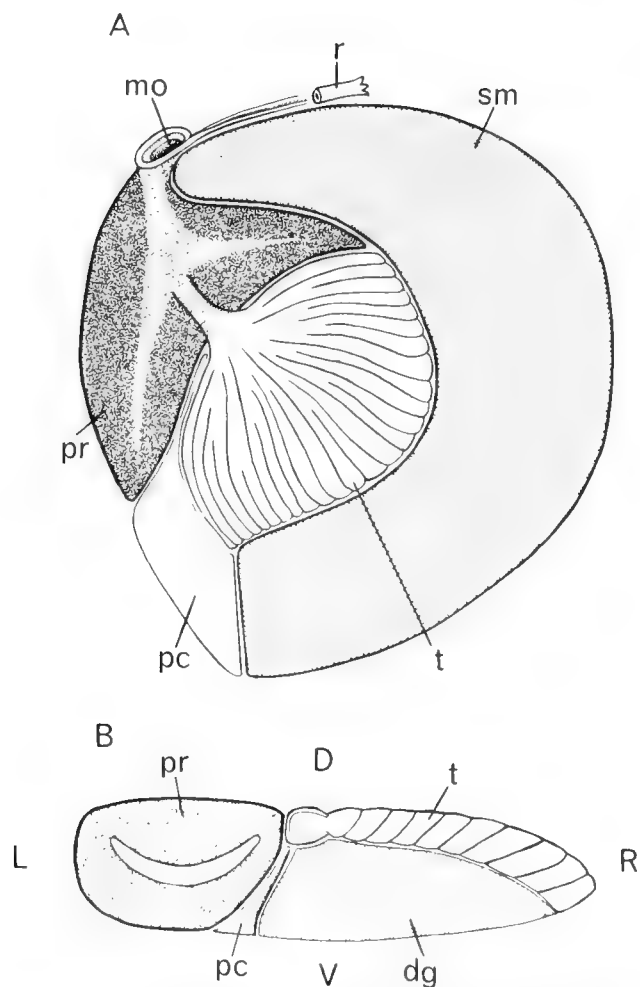


FIG. 12. A, diagram of male reproductive system; dorsal view; B, transverse section. D, dorsal; dg, digestive gland; L, left; mo, male opening; pc, pericardial cavity and its forward extension into the visceral mass; note the glandular epithelium against the digestive gland; pr, prostate gland; R, right; r, rectum by anus; sm, shell muscle; t, testis; V, ventral.

The oviduct starts as a nearly globular chamber with numerous folds on its walls, two folds apparently separating it from the second section of the duct. This runs backwards as a smooth-walled tube along the left side of the ovary but separated from it by the pericardial extension until it is near the main pericardial cavity. Here it turns abruptly through 180° and proceeds forwards, in contact with, and to the left of the proximal section. This distal part of the oviduct, like the initial part, has many folds on its walls. There is also present a richly-ciliated groove on its topographically right-dorsal wall; this may be traced on to the left wall of the proximal section where it opens out to form a flat, ciliated tract running to its inner end. Anteriorly, just in front of the connexion between ovary and duct, the oviduct opens to the mantle cavity, its lips out-turned to form a

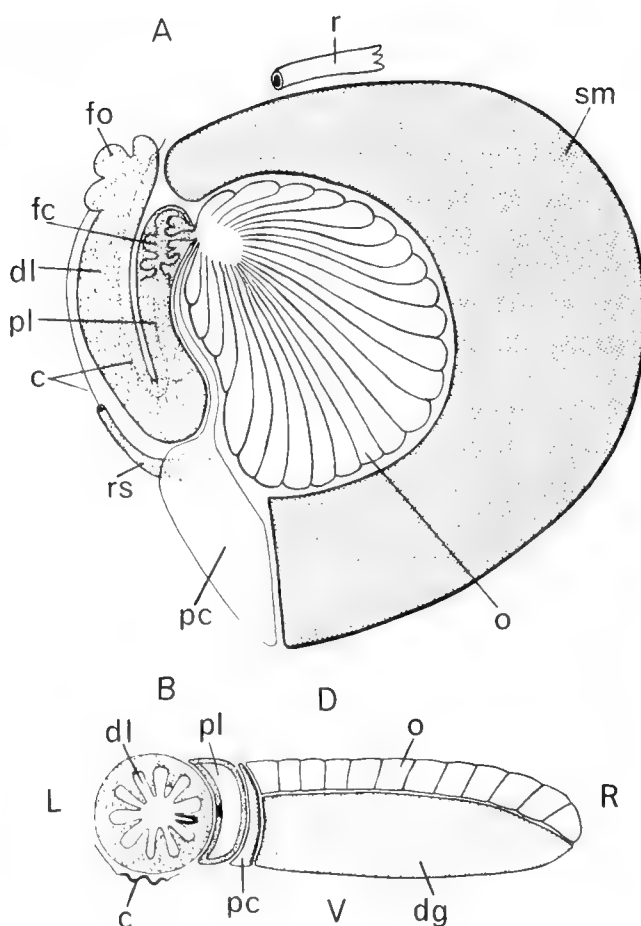


FIG. 13. A, diagram of female reproductive system; dorsal view; B, transverse section. c, ciliary tract in roof of mantle cavity and in female duct; D, dorsal; dl, distal limb of oviduct; dg, digestive gland; fc, fertilization chamber; fo, female opening; L, left; o, ovary; pc, pericardial cavity and its forward extension into the visceral mass, glandular epithelium against the digestive gland; pl, proximal limb of oviduct; R, right; r, rectum by anus; rs, receptaculum seminis; sm, shell muscle; V, ventral.

lobed, bell-shaped structure (Fig. 11B) placed in a position corresponding to that of the male pore.

At a point anterior to and to the right of the pore, between its lips and the shell muscle, the ciliated groove opens to the front end of a short ridged and grooved area which runs back on the wall of the mantle cavity, ventral to the edge of the kidney (Fig. 11B). At the posterior end of this area lies a small opening leading to a receptaculum seminis. Its duct is ciliated and muscular, narrow near the opening but widening as it runs transversely to the right. The receptaculum lies under the anterior end of the pericardial cavity and contains spermatozoa, all lying with their heads against the epithelium lining it (though not apparently embedded in it) and their tails in a central mass. In the mantle cavity of one spe-

cimen sectioned, near the receptacular opening, small clumps of sperm were also found but none were seen in any part of the oviduct. These sperm were not related to any nurse cell, nor were they organized into spermatophores or spermatozeugmata, though they may well have had some prostatic secretion around them.

The prostate gland contains two types of cell, ciliated and glandular, which lie more or less alternately to compose the epithelium. The ciliated cells are wineglass-shaped with long stalks attaching their expanded distal parts, in which the nuclei lie, to the basement membrane. The gland cells have broad bases containing nuclei and some vacuoles, each with a spherule of secretion; the base is connected to a narrower apical part packed with secretory granules. These stain a brilliant orange with eosin and are shed to the lumen of the tubules where they swell, stain red, and ultimately dissolve. Ripe sperm, which have long, narrow heads, fill the vas deferens and parts of the main lumen of the prostate, embedded in material of prostatic origin. In the lumen of the prostate many sperm orientate so that their heads lie towards the epithelium and some, indeed, appear to become embedded in the ciliated cells. The lips of the male pore and its grooved extension alongside the rectum are heavily ciliated.

The ovary of the animals examined seemed active in every case and contained many apparently ripe eggs. Some eggs were also present in the proximal limb of the oviduct, but this was interpreted as a post-mortem effect rather than a normal process of egg shedding. In this situation the eggs had a diameter of 100–150 μm , were moderately rich in yolk but had no external coats. The wall of the oviduct consists throughout of alternating ciliated and gland cells, except in the ciliated groove where gland cells are absent. The details of the cells, and of the secretion they elaborate, however, differ from the one limb to the other. In the proximal the ciliated cells are moderately broad at their free ends and the gland cells rather narrow. The cytoplasm of the latter contains many vacuoles and although much of the secretion seems to have been lost on fixation it is clear that it stained with hematoxylin. In the distal section of the duct the ciliated cells are extremely slender and the gland cells very swollen. Their cytoplasm contains usually only one large vacuole the contents of which (though again mainly dissolved) stain with eosin. Eggs, therefore, presumably re-

ceive two coatings as they pass along the oviduct. Since the ciliated groove originates in a tract related to the receptaculum it may be supposed that sperm received from the male and stored there are passed to the ciliated groove along which they travel up the oviduct, are liberated at the upper end of the proximal limb where the tract to which the groove leads comes to an end. This would represent the site of fertilization, after which event the eggs would be carried down the tract, receiving their two coats as they go.

DISCUSSION

In its anatomy *Neomphalus fretterae* is unique amongst living gastropods, presenting a combination of archaic and advanced features which effectively prevents its association with any living group. It does not fit easily, moreover, into the customary division of prosobranchs into archaeogastropods and mesogastropods (or caenogastropods, to use Cox's (1960) wider term) since, according to the system used as criterion, it falls clearly into the one group or equally definitely into the other. Since this is obvious also in Trochacea and the mesogastropods are not in themselves a markedly coherent group it suggests strongly that the term mesogastropod refers to a particular level of organization rather than a single taxonomic division. In addition *Neomphalus* has many features which relate to its unusual mode of life and may well be peculiar to itself.

Archaeogastropod characters. These are exhibited most clearly in the ctenidium, which is aspidobranch, and in the radula, which is rhipidoglossate, even if in their detailed organization neither is exactly typical. Another external feature linking *Neomphalus* to the archaeogastropods is the presence of epipodial tentacles, though their restriction to the posterior part of the foot is unusual.

In internal anatomy, features of the alimentary and nervous systems most clearly emphasize the archaeogastropod condition. Small glandular pouches in the roof of the buccal cavity are reminiscent of the salivary glands of *Diodora* and are not very different from the small tufts of all archaeogastropods other than Patellacea. The buccal cavity also contains a radular diverticulum from which the radular sac opens. This feature occurs in most archaeogastropods but is absent from

mesogastropods. As in archaeogastropods generally, there are lateral glandular pouches along the whole length of the mid-esophagus which anteriorly overlap the posterior part of the buccal mass, whereas in mesogastropods they lie posterior to it (Amaudrut, 1898). The reduction in the degree of folding of their walls may be partly compensated for by their increased length. This part of the gut, too, which ordinarily shows the effects of torsion by the rotation of the folds on its walls, has come to lie anterior to the region affected by torsion and is symmetrical; this may well also be linked with the elongation of the neck. The presence of an anterior intestinal loop is another archaeogastropod character.

The nervous system is hypoathroid to dys-tenoid and shows many primitive characteristics (Fretter & Graham, 1962). The cerebral ganglia lie well forward in the head and far apart, linked by a long commissure. They connect with the pleural and pedal ganglia by connectives which, even allowing for the extension of the neck, are long. The pleuropedal ganglia form a connected but clearly bilobed mass on each side and the pedal ganglia take the form of elongated cords connected across the mid-line by several commissures. The visceral loop is normal in arrangement except for the tightness of the streptoneury around the esophagus and some points in the distribution of the nerves dealt with later. Many cells lie in nerves.

Mesogastropod characters. In contrast to these features there are some points in the anatomy of *Neomphalus* which agree with mesogastropods rather than with archaeogastropods, and in some systems the arrangement is wholly mesogastropodan. Though the arrangement of muscles in the buccal mass is in some respects—more particularly in relation to the transverse fold—like that of archaeogastropods, it is in total rather more mesogastropod than archaeogastropod in character. This is particularly obvious in the reduced number of muscles which are present by comparison with, for example, a trochid (Nisbet, 1973) or patellid. The gut is also clearly mesogastropod in that the rectum does not enter the pericardial cavity, let alone penetrate the ventricle.

In the nervous system the cerebral ganglia have each a ventrally placed labial lobe, representing the originally separate labial ganglion. In archaeogastropods this fusion has not occurred, and a labial commissure,

absent in *Neomphalus*, is usually present. The statocysts each contain only a single statolith as in mesogastropods, whereas there are normally several in archaeogastropods.

Although the ctenidium is aspidobranch it is single, the right one having apparently all but disappeared, and with it the right auricle of the heart.

The mesogastropod resemblances of *Neomphalus* are clear in the renal and reproductive systems. There is only one kidney, the left; any persistent part of the right kidney has become incorporated in the reproductive tract and has no excretory significance. The left kidney is very similar in organization to that of a monotocardian and is neither a papillary sac as in pleurotomariaceans and trochaceans nor reduced as in patellaceans and fissurellaceans. Indeed the kidney expands (as in some rissoacean mesogastropods) to form a large body cavity into which gut, blood vessels and visceral ganglia project. It forms a space separating shell muscle from viscera and penetrates, along with outgrowths from the pericardial cavity, amongst the viscera, so that there is an extensive coelomic space throughout the visceral mass. Perhaps as a consequence of its increase in area the kidney wall is simple, almost completely lacking the folds common in other prosobranchs, and evidence of excretory activity is largely limited to sites overlying the renal vessels.

The nephridial gland, though conforming in general to the structure it exhibits in prosobranchs, is unusual in that it is much more spongy, the tubular projections of the kidney being inflated and the related vessels reduced in size, though numerous.

The structure of the auricle suggests that a primary urine might be filtered through its walls, and the gland cells which line the pericardial cavity where it abuts against the blood spaces of the digestive gland show signs of nipping off parts of the cell tip. It is surprising, in the light of these facts, that there seems to be no renopericardial opening through which filtrate and secretion might pass to the kidney. Expectation of finding one at the posterior end of the horn-like prolongation of the kidney towards the base of the auricle was high, since that is the position in which it would normally be found, but there is certainly no renopericardial papilla, though it is still possible that some relatively inconspicuous connexion exists which has eluded our search. The explanation of the presence of this poste-

rior extension—if it does not lead to a renopericardial opening—may be to lead the renal efferent to the base of the gill.

The relationship of kidney and vascular system is typically monotocardian with all the blood from head-foot and visceral mass being passed through the kidney; from this it collects into an efferent vessel and passes into the ctenidial axis or a rectal sinus, in both of which places it may be oxygenated. *Neomphalus* differs from mesogastropods in that the breakdown of the afferent renal vessel to form a plexus is less complete and a rather large vessel runs to link with the efferent.

Characters peculiar to Neomphalus. The head has no pretentacular elongation with the result that mouth and tentacles are terminal. There is, however, a very marked post-tentacular elongation which brings these structures far in front of the anterior edge of the foot. This neck region bears lateral expansions reminiscent of the neck lobes of a calyptraeacean, and, to a lesser extent, of a trochacean. The homologies are doubtful. Neck lobes in trochaceans are considered to be forward extensions of the epipodium and in calyptraeaceans of the propodial region of the foot. In *Neomphalus* some posterior parts of the lobes are innervated from the pedal ganglia and others from the subesophageal, but the anterior region is supplied by nerves from the cerebropedal connectives and, to a minor extent, from the cerebral ganglia.

Neck formation has affected internal organs, elongating the cerebropleural and cerebropedal connectives and cephalic artery. It has also affected the course of the protractor muscles of the radular membrane. In most prosobranchs these run posteriorly to join the columellar muscle (as in trochaceans), or the shell muscle (as in patellaceans); in probosciferous forms they shorten and originate in the lateral walls of the head. In *Neomphalus* elongation of the neck seems to have acted like a post-tentacular proboscis and brought about the same result. The mid-esophagus normally lies in the region of torsion: in *Neomphalus* it lies anterior to it. This anterior migration may well have been a consequence of elongation of the neck.

The stomach is relatively simple in organization though most features of prosobranch gastric anatomy apart from sorting areas are present in standard topographical relationships though reduced form. In its histology,

however, an unusual feature is the arrangement of cells involved in the formation of the gastric shield. The small tubular outgrowth at the apex of the stomach has characteristics agreeing with those of a spiral caecum and also has a sufficiently correct spatial relationship with the gastric shield to suggest homology with that structure. Reduction of this part of the stomach also occurs in Fissurellacea and Patellacea and may therefore be connected with the adoption of a limpet shape and simplification of the visceral coils.

The digestive gland is relatively small and is peculiar in being confined to the topographical underside of the visceral mass. Its structure appears unusual in the apparent presence of tubular glands in the tubules.

The ctenidium is unique—a bipectinate gill of extraordinary length, unattached on its afferent side, though the axis is stoutly and broadly fastened to the mantle skirt along most of its length and supported by a hypertrophy of skeletal tissue. The lamellae have elongated into filaments, well ciliated, and the whole adapted for creating and sieving a water stream.

The most outstanding features of *Neomphalus* are its limpet-like form and the enlargement of the mantle cavity and gill to allow ciliary food-collecting, changes which have affected the visceral half of the body to a greater extent than the head-foot.

Three major alterations in organization have accompanied the adoption of the limpet shape: (1) the pallial organs of the animal's right side have disappeared except for a vestigial ctenidium and an associated vessel which remains well developed because it has assumed the drainage of the expanded mantle skirt; (2) the visceral mass has undergone 270° of torsion in relation to the head-foot; (3) the mantle cavity and visceral mass have undergone a leftward rotation about an anteroposterior axis so that structures originally right have moved dorsally and those originally left, ventrally. Much of the palliovisceral anatomy—and some of the cephalopedal—can be explained in terms of these movements.

The loss of topographically right pallial organs is clear so far as osphradium and kidney are concerned. The loss of the right ctenidium is equally as obvious at first sight as it is in the monobranchiate patellaceans, yet a vestige seems to persist. Near the mouth of the mantle cavity, anteriorly and to the left of the midline, a group of 5–10 ciliated lamellae lies over the course of the pallial vein. This vessel runs

posteriorly to the innermost part of the mantle cavity where it turns forward to join the efferent branchial and so the auricle. In typical archaeogastropods only three vessels run to the auricles: two efferent branchials, one to each auricle, with the nephridial gland efferent joining that on the left. In *Neomphalus* there is no right auricle, but two vessels from opposed parts of the mantle skirt enter the left one (the course of the nephridial gland efferent remains unclear but neither vessel can be that). It is, therefore, in view of these relationships, appropriate to assume that the pallial vein is homologous with the right ctenidial efferent, secondarily associated with the left one in view of other changes (see below). The idea of an efferent ctenidial vessel persisting even in the absence of a functional gill is supported by the presence of the right pallial vein in trochids.

There are not many situations in the body of a prosobranch gastropod where one regularly finds a prominent blood vessel and an equally prominent nerve lying alongside one another, especially within the confines of the mantle skirt. The ctenidial axis is one such place and it was initially the close association between the pallial nerve and the pallial vein which first led us to ask whether this vessel might be related to a lost gill.

Two facts bear against this interpretation. In the left ctenidial axis, anteriorly, the ctenidial nerve lies under the efferent vessel; it originates in the supra-esophageal ganglion. Alongside the pallial vein, the putative right ctenidial efferent, there also runs a prominent nerve, as one would expect if this is the correct homology. This nerve, one would suppose, should connect with the subesophageal ganglion. It does not, however, and proves to be a branch from the supra-esophageal. The second fact is the situation of the vessel in the mantle skirt. In Fig. 16A, the morphologically mid-ventral line of the mantle cavity is marked by the esophagus, its morphologically mid-dorsal line by the rectum. The right half of the mantle skirt is compressed to the small part between rectum and esophagus in which the genital duct lies. If the pallial vein were a right ctenidial efferent, and if it retained its original situation, it should be found here too; yet it lies morphologically left of the rectum.

There are thus some points—association of nerve and vessel, lamellae, relationship to heart—which speak for the homology, and others—innervation, situation on mantle skirt—which argue against it. There seems no

way to resolve the matter on present knowledge.

The existence of 270° of torsion instead of the usual 180° has the effect of making the long axis of the visceral mass lie at right angles to that of the head-foot instead of parallel to it, and of bringing the original left edge of the mantle cavity to the posterior end of the body. This is immediately seen on looking at an animal removed from its shell in dorsal view. Then it is obvious that the attachment of the shell muscle is indeed horseshoe-shaped as in other limpets, but its concavity faces left, not anteriorly. When that displacement is allowed for, the disposition of the organs of the visceral mass becomes nearly identical with that of other prosobranchs, the pericardial region alongside one end of the horseshoe, the anus and genital opening alongside the other.

Torsion makes itself evident not just in the orientation of the visceral mass but in the twisting of gut and visceral loop. With increased torsion this effect should be more marked, and this is indeed so, the twisting of the visceral loop round the esophagus being extremely tight and accomplished within a very short distance. This may, perhaps, be an additional factor in bringing about the forward migration of the mid-esophagus, which leaves only the much narrower posterior part to be embraced by the connectives.

It is not, however, possible to explain all the anatomical peculiarities of the visceral and pallial parts of *Neomphalus* on the basis of the two changes just mentioned. They leave unexplained the disposition of the esophagus and visceral nerve loop, the heart, the stomach, the digestive gland, gonad and genital duct, and the position of the ctenidium and (right) pallial efferent. To understand how these have come to be as they are, a third movement has to be introduced—a roll round an anteroposterior axis of visceral mass and mantle to the left, which in effect shifts the mantle cavity from a dorsal to a left lateral position. That this has occurred is clearly shown by examination of the stomach and the heart.

The stomach of a typical prosobranch is fundamentally U-shaped, the concavity facing forwards, the esophagus opening anteriorly to the left limb whilst the intestine runs forward from the right (Fig. 14). The spiral caecum, if present, opens from the apical region. In *Neomphalus* the stomach is still U-shaped but the concavity faces left because of the increased torsion. The positions of esophagus

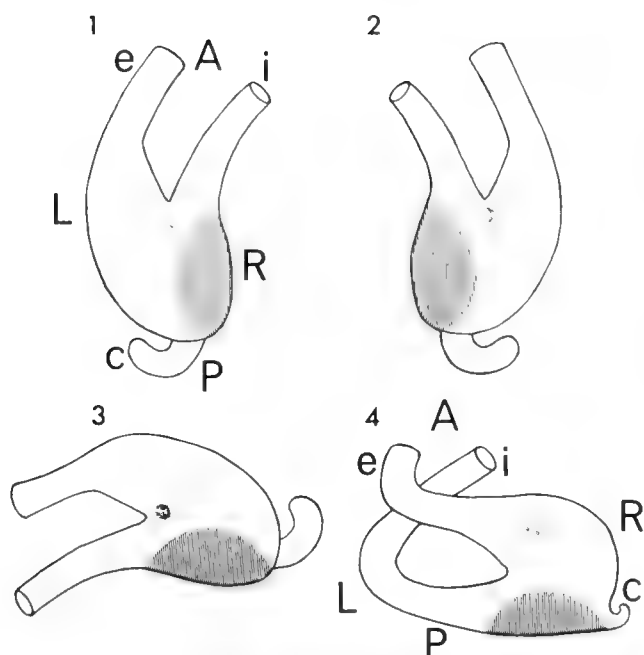


FIG. 14. Diagrams to show the topographical relationships between the stomach of a primitive prosobranch such as a trochacean and that of *Neomphalus*. 1, dorsal view of the stomach of an animal such as *Monodonta*; 2, the same after rotation through 180° on an anteroposterior axis; 3, after a further 90° rotation anticlockwise on a vertical axis, the consequence of increased torsion; 4, diagram of the stomach of *Neomphalus*, comparable to diagram 3 with the intestine running forward to the anus. Gastric shield hatched; area of ducts of digestive gland stippled. A, anterior; c, spiral caecum; e, esophagus; i, intestine; L, left; P, posterior; R, right.

and of rectum and anus, however, remain unchanged—anterior to the stomach, and left and right respectively. The esophagus opens into the anterior limb of the stomach and the intestine arises from the posterior. If the position of the stomach were simply due to a rotary motion these positions would be reversed. The actual anatomy can be explained only on the assumption that the stomach has also turned over so that the original dorsal surface is now underneath. This movement also explains how the dorsal surface of the visceral mass is completely covered by gonad whilst digestive gland is confined to its ventral surface.

There are some unusual features in the organization of the heart region: the auricle lies behind rather than anterior to the ventricle, the ctenidial efferent enters the auricle posteriorly and the bulbus lies at the anterior end of the ventricle. Some of these features (position of auricle and ctenidial efferent) can be attributed to the shift due to increased torsion, but not the details of the ventricle and aortae. In

the more primitive diotocardians with spirally-coiled visceral humps, e.g., *Pleurotomaria*, *Scissurella*, trochids, but not in the modified fissurellaceans, the heart lies across the body with the left auricle on the anterior side, the right posteriorly and the aortae issuing from the left side of the ventricle (Fig. 15). Apply the two movements which have already been described in relation to the stomach to such a heart and an arrangement is reached which differs from that in *Neomphalus* only in that a right auricle is still present, receiving the right ctenidial (or pallial) vessel. To achieve identity with *Neomphalus* it has only to be supposed that this vessel, and perhaps also its auricle, migrate to join the left ctenidial efferent where it enters the pericardial cavity.

This movement also brings the right pallial vessel to a position approximately that occupied in *Neomphalus*. It would also cause the attachment of the left gill to the mantle skirt to lie on the floor of the mantle cavity as it is found to do. It may, too, underlie the un-

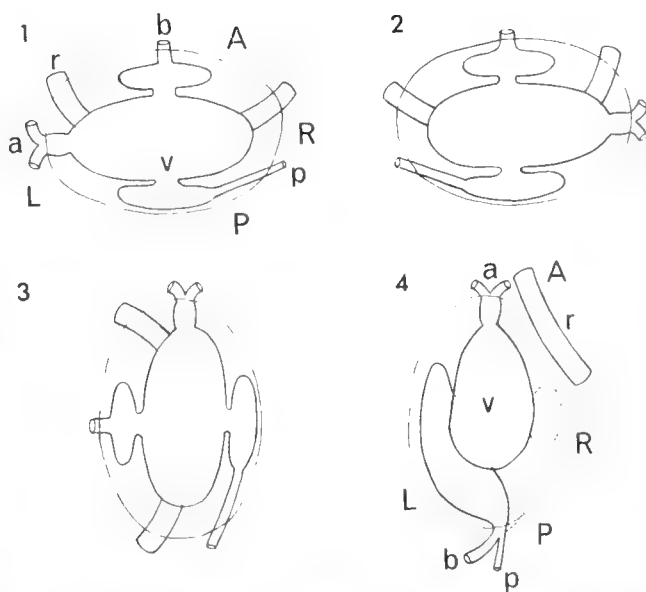


FIG. 15. Diagrams to show the topographical relationships between the heart and associated structures of a primitive prosobranch and those of *Neomphalus*. 1, dorsal view of heart and related organs, based on *Monodonta*; 2, the same after rotation through 180° on an anteroposterior axis; 3, after a further 90° rotation anticlockwise on a vertical axis, the consequence of increased torsion; 4, diagram of *Neomphalus*, comparable to diagram 3, save that the rectum (r) no longer enters the pericardial cavity, the right auricle is lost and its associated vessel (p) now joins the efferent branchial (b). A, anterior; a, anterior and posterior aortae arising from bulbus; b, efferent branchial vessel running to left auricle; L, left; P, posterior; p, pallial vessel; R, right; r, rectum; v, ventricle.

usual course of the large pallial nerve which originates from the subesophageal ganglion. This one would expect to run to the right, whereas it runs to the left in close contact with nerves from the supra-esophageal ganglion. It may, however, still be directed at right pallial organs now on the left because of these topographical changes. One further anatomical peculiarity of *Neomphalus* attributable to this rotary movement shows that it has also affected the posterior end of the head-foot where that passes into the visceral mass. The cephalopodal sinus, with its contained anterior aorta, posterior esophagus and anterior intestinal loop, appears unusually sited along the left side of the shell muscle and the part of the body linking head and visceral mass. Another odd feature of this part of the body is the disposition of the visceral loop, the two halves of which lie, not side by side as is usual, but more or less in a dorsoventral plane, the right half dorsal to the left. This abnormal arrangement is easily understood on the supposition that a leftward rotation of the mantle cavity through about 90° has occurred. The original mid-dorsal surface of the body (the floor of the mantle cavity), marked by the aorta and esophagus, now faces left instead of dorsally and the visceral loop is brought into a vertical instead of a horizontal plane (Fig. 16).

From these points it is clear the *Neomphalus* has followed an evolutionary course quite different from those giving rise to the fissurellacean and patellacean limpets, where the mantle and visceral mass retain an anteroposterior alignment coincident with that of the head-foot, or indeed, from that of any other living mollusc. As a consequence the pallial cavity—and to some extent the viscera—come to lie on an axis parallel to but alongside that of the head-foot, the right side of the cavity in the same dorsoventral plane as the left side of the foot. This gives a lower shell than is encountered in other limpets, perhaps an adaptation to the environment in which the animals live, perhaps a reflection of weaker powers of adhesion.

As might be expected from the common adoption of a ciliary food-collecting mechanism there is a greater resemblance between *Neomphalus* and the hipponicacean and calyptraeacean limpets, but these too retain the basic relationship between head-foot and visceral mass. Elongation of the mantle cavity to permit a longer ctenidium has been achieved by backward growth of its left side only, unaccompanied by rotation or increased

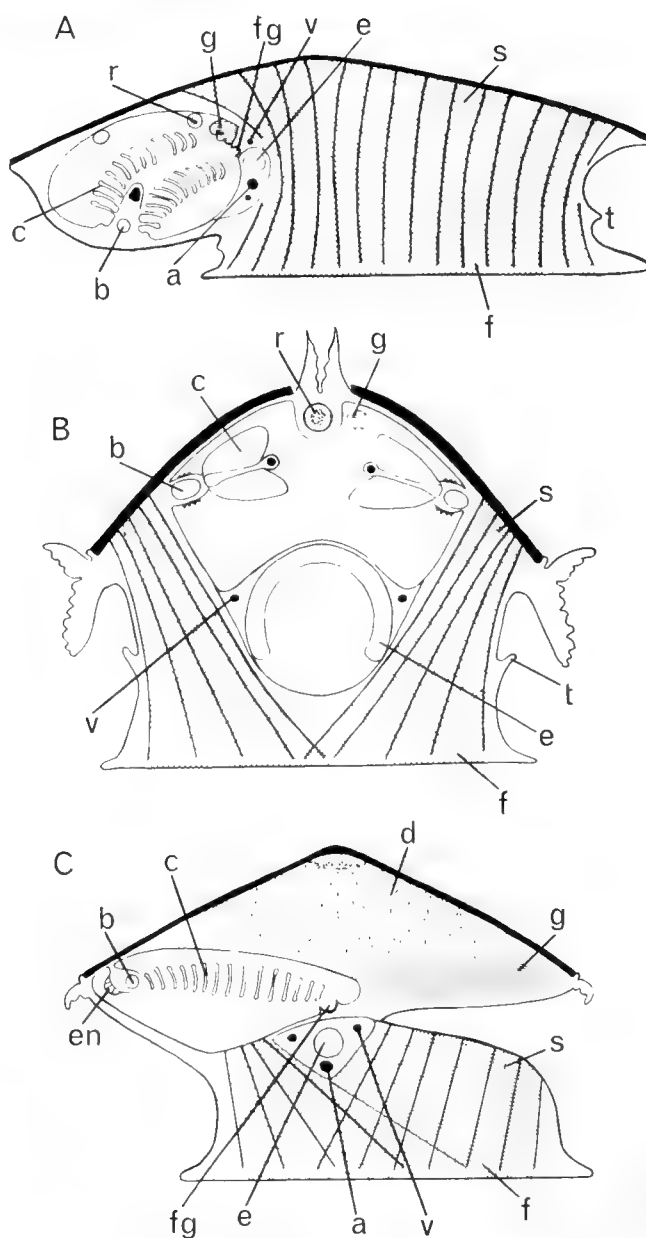


FIG. 16. Diagrammatic transverse sections based on camera lucida drawings to show the relative dispositions of mantle cavity, cephalopodal mass, shell muscle, and certain organs. A, *Neomphalus*; B, *Diodora*; C, *Calyptraea*. a, anterior aorta in cephalopodal sinus; b, efferent branchial vessel in gill axis, the osphradium alongside in A and B; c, ctenidial leaflet; d, digestive gland; e, esophagus in cephalopodal sinus; en, endostyle; f, foot; fg, food groove; g, in A, the female opening; in B, the projection of the urinogenital opening on the plane of the section; in C, the gonadal area of the visceral mass; r, rectum; s, shell muscle; t, epipodial ridge; v, visceral loop in cephalopodal sinus.

torsion. The ventricle has retained its central position whilst the auricle has elongated backwards to keep pace with the growth of the gill. In *Neomphalus* this growth of the left side has not occurred. Indeed in keeping part of the mantle cavity over the head, it is the anterior right part of the pallial margin which

has had to be extended. For this to happen, retention of the right pallial vein may have proved essential.

If the filaments of a ctenidium are to function well as a filter (Yonge, 1938) the axis must be long (to allow filament number to increase) and the filaments must elongate (to allow current force and filtration area to grow). In addition there must be some pathway to carry filtered material to the mouth. In all prosobranch ciliary feeders the collected food is transported to the tips of the filaments and so the pathway to the mouth lies on the side of the body opposite to that from which the ctenidial axis arises. These arrangements are clear in the monotocardian ciliary feeders and in *Umbonium*, the only archaeogastropod so far described with this mode of feeding (Fretter, 1975). *Umbonium*, however, is a trochid and the bulk of its ctenidium is pectinibranch. In all these animals a single rank of filaments connects with a food groove. It seems that these requirements could not be adequately met in any aspidobranch retaining both right and left ctenidia. It is presumably such mechanical difficulties that have led to the suppression of the right ctenidium of *Neomphalus*. Its remaining gill functions well as a filter only because of a modification of the position of its axis so that both sets of filaments can lie across the mantle cavity and their tips reach the food groove. The speculations of Yonge (1947) and Fretter & Graham (1962) that modification of a bipectinate gill for filter feeding was highly improbable and that this had to await the evolution of the monopectinate condition have thus been proved unfounded.

In typical archaeogastropods—not neritaceans—the gonad discharges to the right kidney, and any accessory secretion is produced by the swollen lips of the opening of that organ to the mantle cavity; from this comes the jelly-like material in which the eggs of an animal like *Calliostoma* are deposited. The reproductive system of *Neomphalus*, like that of neritaceans, has reached the mesogastropod level of complexity in that there is a glandular region interposed between the gonad and the genital opening, implying the occurrence of some copulatory process and the laying of some kind of spawn. There is, in conjunction with the former, provision for the reception of sperm by the female and for their transport to an internal site of fertilization, necessitated by the later provision of coatings which would make union of egg and sperm difficult or im-

possible. It is to be noted that the glandular section of the genital duct, in both sexes, is closed, a condition more advanced than that found in a number of mesogastropods.

Some discussion of the homologies of the genital tract is necessary. The position of the gonopericardial duct in the female shows that there is no ovarian duct. And, though there is no gonopericardial connexion in the male (despite the presence of a similar pericardial extension), it may be presumed that there is no testicular duct either; however, absence of a gonopericardial duct is usual in male caenogastropods. Since the testicular duct of mesogastropods is the site of sperm storage, *Neomphalus* has, in its absence, come to use the rather capacious lumen of the prostate for this, and there are indications that some nutrition of the sperm may occur there.

It is difficult to be certain of homologies in the female and of how much, if any, of the oviduct is pallial in origin. The proximal limb, however, may be comparable with the albumen gland of mesogastropods, its expanded upper part acting also as fertilization chamber; the distal limb may correspond to the jelly or capsule gland, with the ciliated groove representing the ventral channel moved to its present position by the roll of the mantle cavity to the left which has already been mentioned.

The homologies of the receptaculum seminis are more obscure and the problem is made more awkward in that the organ appears to act not only as a pouch for the reception of sperm (a bursa copulatrix) but also as a storage place for them (a receptaculum seminis). As an anatomical structure, however, it is probably not homologous with the structures of mesogastropods commonly called receptaculum seminis since they lie in most animals proximal to the oviducal glands. A more likely homology is with the pouch known as the bursa copulatrix. This is usually distal to the glands and is the starting point of the ciliated groove leading sperm to the site of fertilization. The receptaculum of *Neomphalus* shows both these characters and to complete the comparison it has only to be supposed that it happens to have a situation more remote from the female aperture than usual. Though it is unlikely, because of their relationship to the vascular system (Fretter, 1965), that the ducts of neritaceans are strictly homologous with those of *Neomphalus*, separate openings of oviduct and receptaculum are already known in that group. It may in-

deed be that this is the original site of a pouch for reception of sperm and that its commoner association with the oviduct is a secondary position representing a tidying up in the mantle cavity or a consequence of the evolution of the more efficient copulatory organ of the mesogastropods.

A few deductions as to the activities of the living limpet may be hazarded on the basis of its anatomy. The foot is muscular enough to suggest some locomotor as well as adhesive activity. Although the radula is relatively short, its structure and that of the buccal mass, along with the contents of the gut, support the idea that the limpet may supplement the food that it collects on its gill by rasping the substratum.

In considering the mechanics of a copulatory process on the assumption that the left tentacle of the male is a copulatory organ, though not necessarily an erectile one, it has to be remembered that it is not the oviducal opening which the tentacle has to reach, but that of the receptaculum. This lies on the left side of the body in the wall of the kidney and pericardial cavity about level with the anterior end of the bulbus and ventral to it. It is therefore some distance behind the posterior limit of the entrance to the mantle cavity. There are several possible copulatory stances that animals might adopt—alongside one another, heads together or at opposite ends; head on; or, as is usual in prosobranchs, with the male mounted on the shell of the female, both facing in the same direction. Consideration of each of these in relation to anatomy strongly suggests that the last is by far the most likely, and that the natural backward inclination of the tentacle hooked over the thin, flat edge of the shell would then bring it close to the opening of the receptaculum. The vascular supply to the tentacle is not great, indicating little erectile capacity whereas it seems distinctly muscular and it could presumably be pushed further into the mantle cavity by some bending of the neck. Since there is only slight indication of a seminal groove over its surface the prostatic secretion must be sufficiently viscous to prevent its general dispersal by the currents in the mantle cavity.

There remains the problem of how sperm reach the tentacle from the male pore since there seems to be no direct link, and any such would have to cross the food groove. The lips of the pore, however, directly overlie the posterior end of the groove along the left side of the neck which leads to the tentacle, and it seems possible that at copulation the one

could become addressed to the other, allowing sperm to pass. We have, in addition, suspected some extension of this groove on to the dorsal surface of the neck on the left, ventral to the food groove, which might facilitate movement of seminal fluid.

In females the left neck groove is as well marked as it is in males but is almost certainly not involved in the outward passage of eggs. It is not, however, apparently without function since masses of material have been found within it, mainly detrital. The most likely activity—which would occur in both sexes except when copulation is occurring—is the removal of particulate waste which has settled on the floor of the mantle cavity before reaching the ctenidium. This would correspond to the current A described by Yonge (1938). The groove is heavily ciliated and its epithelium is rich in gland cells. Material collected here would be embedded in secretion, led to the left tentacle and dropped on to the substratum.

It seems that fertilization of the eggs must be internal, since a ciliated tract can be traced from the mouth of the receptaculum to the inner end of the proximal limb of the oviduct. The fertilized eggs are then surrounded by first, nutritive albumen, and then a protective coat which seems more likely to be jelly-like rather than of the nature of a capsule. But it is not possible to say whether this is dispersed outside the mantle cavity to free the eggs or whether it is used to attach spawn to the substratum.

Finally, we attempt to assess the taxonomic standing of *Neomphalus* on the basis of its anatomy.

We have noticed only four features of *Neomphalus* that are otherwise found only in animals classified as Archaeogastropoda. These are: the rhipidoglossate radula, the radular diverticulum, the overlap of esophageal pouches anteriorly with the buccal mass, and the anterior loop of the intestine. It possesses, it is true, other characters which are commonly regarded as typical of archaeogastropods but these are actually also found in some or many mesogastropods. The bipectinate ctenidium is one of these—it is also found in Valvatacea; the hypoathroid to dysidenoid nervous system is a second, but this may also be seen in Cyclophoracea and Viviparacea; epipodial tentacles represent a third such character, but these are common in mesogastropods in relation to the opercular lobes, thus showing the same tendency as in

Neomphalus to disappear anteriorly whilst persisting posteriorly. Anterior epipodial vestiges may also perhaps be represented by the neck lobes of cyclophoraceans and viviparaceans. These three characters, therefore, are shared by *Neomphalus* and some of the lowest superfamilies of the mesogastropods. There are, indeed, some other features in which they agree: thus although in the cyclophoracean *Pomacea canaliculata* (Andrews, 1965a, 1965b) there is no anterior loop, the intestine runs so as to project into the cavity of the kidney, as in *Neomphalus*, rather than the digestive gland as is more usual; *Pomacea* also lacks a pretentacular snout and so has a terminal mouth on each side of which lies an oral lobe; in viviparids, as in *Neomphalus*, it is a tentacle which acts as copulatory organ, though the right one rather than the left.

In all other respects the organization of *Neomphalus* is unequivocally mesogastropod and an enumeration of mesogastropod characters would heavily outweigh the archaeogastropod list. In these circumstances it seems necessary to ask—is *Neomphalus* a mesogastropod?

It must be borne in mind that the assumption of mesogastropod characteristics is nothing new in archaeogastropods—this is already evident in trochaceans. But members of that group still retain a large number of features in respect of which they agree with archaeogastropods rather than with mesogastropods: two auricles, two kidneys, epipodial sense organs, little or no development of glandular genital ducts, none of which are seen in *Neomphalus*. The same trend is obvious, and even more marked, in Neritacea, whilst an examination of animals in the lowest superfamilies of prosobranchs normally classified as mesogastropods shows a persistence of features often regarded as archaeogastropod. The requirements of the taxonomist make boundaries between groups more rigid than they really are and there is no hard and fast boundary between the archaeogastropod and the mesogastropod groups. In prosobranch evolution it is clear that numerous and diverse attempts have been made by different phyletic lines to pass from the level of organization described by the term archaeogastropod to that described by the term mesogastropod. Most have ended in failure, pushed into extinction by the radiation of the successful monotocardians. Neritacea are an exception and have succeeded in a radiation

predominantly in brackish and fresh water and on land; Valvatacea have all but disappeared, while Architaenioglossa (Cyclophoracea + Viviparacea) have been modestly successful only by adopting some particular and occasionally difficult habitats. *Neomphalus* seems to represent still another archaic group which has survived by adaptation to a way of life allowing its persistence in a very special habitat. On balance, however, it seems to be further from the archaeogastropod condition than are the groups referred to above and accepted by most malacologists as mesogastropods.

REFERENCES CITED

- AMAUDRUT, A., 1898, La partie antérieure du tube digestif et la torsion chez les mollusques gastéropodes. *Annales des Sciences naturelles, Zoologie*, (7) 8: 1–291.
- ANDREWS, E. B., 1965a, The functional anatomy of the gut of the prosobranch gastropod *Pomacea canaliculata* and of some other pilids. *Proceedings of the Zoological Society of London*, 145: 19–36.
- ANDREWS, E. B., 1965b, The functional anatomy of the mantle cavity, kidney and blood system of some pilid gastropods (Prosobranchia). *Journal of Zoology*, 146: 70–94.
- ANDREWS, E. B., 1979, Fine structure in relation to function in the excretory system of two species of *Viviparus*. *Journal of Molluscan Studies*, 45: 186–206.
- COX, L. R., 1960, Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, 33: 239–261.
- FRETTER, V., 1965, Functional studies of the anatomy of some neritid prosobranchs. *Journal of Zoology*, 147: 46–74.
- FRETTER, V., 1975, *Umbonium vestiarium*, a filter-feeding trochid. *Journal of Zoology*, 177: 541–552.
- FRETTER, V. & GRAHAM, A., 1962, *British Prosobranch Molluscs*. London, Ray Society, xiv + 755 p.
- MCLEAN, J. H., 1981, The Galapagos Rift Limpet *Neomphalus*. *Malacologia*, 21: 291–336.
- NISBET, R. H., 1973, The role of the buccal mass in the trochid. *Proceedings of the Malacological Society of London*, 40: 435–468.
- YONGE, C. M., 1938, Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journal of the Marine Biological Association of the United Kingdom*, 22: 453–468.
- YONGE, C. M., 1947, The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London*, ser. B, 232: 443–517.

EVOLUTION OF LARVAL DEVELOPMENT IN EASTERN ATLANTIC TEREBRIDAE (GASTROPODA), NEOGENE TO RECENT

Philippe Bouchet

*Museum National d'Histoire Naturelle
55, rue Buffon, 75005 Paris, France*

ABSTRACT

Four lineages of eastern Atlantic Terebridae from the Miocene to Recent are discussed. The type of larval development, as determined from observations of protoconchs, shows three kinds of evolution through time: 1. loss of the planktonic stage followed by allopatric speciation; 2. size increase of the veliger larva; 3. planktonic development retained unchanged, followed in one case by allopatric subspeciation.

It is suggested that there is no direct relation between dispersal capacity and a species' temporal longevity. However, the limited evidence presented in the paper supports the idea that allopatric speciation is connected with nonplanktonic larval development.

INTRODUCTION

Gastropod protoconchs yield information on the type of larval development. This information is used in alpha taxonomy by both paleontologists and zoologists and the biological and evolutionary importance of the developmental stages has been the subject of various papers (Thorson, 1946, 1961; Scheltema, 1966, 1971, 1972, 1977a; Robertson, 1976, among others).

It has been suggested (Scheltema, 1977b) that prosobranch gastropods with long duration (teleplanic) planktonic larvae can maintain genetic exchange over long distances and that these species are least liable to change and speciate through time. Furthermore, it has been suggested that prosobranch gastropods with more restricted capacity of dispersal (medium to short duration planktonic larvae) "will show geographic variation and varying degrees of speciation" (Scheltema, 1977b: 317). Finally, species with direct development are held to have a more restricted range through space and time (Hansen, 1980).

There are only six documented cases of intraspecific variation in mode of reproduction among prosobranchs (Robertson, 1976) and in this paper the type of larval development will be considered intraspecifically constant.

The distance factor has been investigated in Recent species and it is known that through planktonic larvae gene flow can be maintained between populations of a species living

on both sides of the Atlantic (Scheltema, 1971; Robertson, 1964).

The time factor has been much less investigated. The primary reason is that few lineages of fossil marine gastropods have been adequately described. Most paleontological studies are concerned with the whole gastropod or mollusc fauna of a given locality, with little or no concern with lineages. The larval shells have been used, mainly in alpha taxonomy, in only a small number of works. It was not until Shuto (1974) and Scheltema (1977b) that protoconchs became a subject of theoretical interest in the study of prosobranch evolution.

In this paper, I will discuss the lineages of Eastern Atlantic Terebridae from Miocene to Recent, with emphasis on the evolution of types of larval development. In all cases, the type of larval development has been determined through protoconch morphology.

In the reconstruction of the lineages I have studied all available material of Recent West African Terebridae (Bouchet & Le Loeuff, in prep.). The fauna consists of 17 species, of which 7 are undescribed; it can be assumed that this is a reasonable coverage of this terebrid fauna. For all species I had specimens with good protoconchs, thus making the type of larval development determinable.

It has been demonstrated throughout the European paleontological literature that the living representatives of the Miocene and Pliocene fossils of Europe are to be sought for on the continental shelf of West Africa. I have

therefore looked for the ancestors of the West African Recent Terebridae mainly in the tropical/subtropical deposits of the Southern European Neogene. I also reviewed the literature on the West Atlantic Neogene. The Miocene and Pliocene Terebridae of Italy have been the subject of special monographs (Sacco, 1891; Davoli, 1977) and I have studied the collections of Istituto di Geologia, Torino; Istituto di Paleontologia, Modena; Institut Royal des Sciences Naturelles de Belgique, Brussels; Museum National d'Histoire Naturelle, Paris; and British Museum (Natural History), London. It has thus been possible to trace back (with some certainty) the ancestors of several West African species, and to determine the type of larval development of each from juveniles retaining good protoconchs.

DESCRIPTIONS OF THE LINEAGES

1. Lineage of *Terebra senegalensis* Lamarck

In the Miocene, this lineage starts with *Terebra plicaria* Basterot which appears in the Burdigalian and is widespread in the Helvetian of all southern and central Europe. At this stage, the shell starts to become more obtuse, with a shallower suture and less distinct subsutural groove. It is the form known as *T. modesta* Tristan in DeFrance, which in the Tortonian tends to replace *T. plicaria* in all of Europe. The two forms can only be separated through biometry (Davoli, 1977: 159).

After the Messinian salinity crisis, this lineage invaded southern Europe once again probably from populations which had survived in the Atlantic. This Pliocene form is more slender than the upper Miocene form, with a rather indistinct subsutural groove; the axial ribs are close set on the first teleoconch whorls and then become more spaced or disappear. This form is called *T. fuscata* Brocchi. The protoconch indicates planktonic larval development.

After the Pliocene, cold waters replaced the tropical waters and *T. fuscata* migrated southward to West Africa, invading the continental shelf south to Angola and the slope of the oceanic Cape Verde seamounts. The last event in the lineage is loss of the planktonic dispersal phase. The Cape Verde populations have thus become isolated and can today be regarded as specifically distinct from the continental populations. The Cape Verde species (as yet unnamed) is very constant, with a glossy, pinkish white shell and axial sculpture

present only on the upper whorls. The continental species, *T. senegalensis* Lamarck is more variable in sculpture, with smooth or ribbed forms although an axial sculpture is always present on the upper whorls. The shell is light yellowish brown with a series of subsutural reddish brown spots and sometimes three series of coloured spiral bands.

2. Lineage of *Terebra corrugata* Lamarck

This lineage is present in the Neogene of Europe with a single species, *T. acuminata* Borson, which spans the period of the Burdigalian to the Pliocene without apparent change. Its living representative is *T. corrugata* Lamarck which shows the same characters as the fossil, except that it is more slender and has a protoconch diameter of 800 μm as compared with 635 μm in lower Pliocene fossils. Both protoconchs are multispiral and of the planktonic type.

3. Lineage of *Terebra (Strioterebrum)* species

The *Terebra (Strioterebrum)* group of species is represented in the Miocene of Italy by three species, of which the type of larval development is known for two: *T. terebrinum* Bellardi & Michelotti had planktonic larvae, but did not appear again in the Pliocene after the Messinian salinity crisis. In the Miocene, this species was absent from the Atlantic Portugal and Aquitanian basins and thus probably became extinct during the drying out of the Mediterranean. *T. basteroti* Nyst also had planktonic larvae and was common in all Miocene basins of central and southern Europe. It gradually evolved into two different forms, *T. reticulare* Pecchioli in Sacco with close-set axial sculpture and strong spiral lines, and *T. pliogenicum* Fontannes with more distant axial ribs and less distinct spirals. Both species retained the planktonic larvae and have survived in the Recent West African fauna without significant change. Recent *T. reticulare* from the Ivory Coast cannot be distinguished from Pliocene fossils of Italy; Recent *T. pliogenicum* from the same locality have the axial sculpture a little more widely spaced than the Pliocene fossils. Today they occupy sympatrically two different niches, *T. reticulare* on soft muddy sand bottoms, while *T. pliogenicum* favours clean sand.

The Miocene *T. basteroti* stock also probably at some stage gave rise to four different

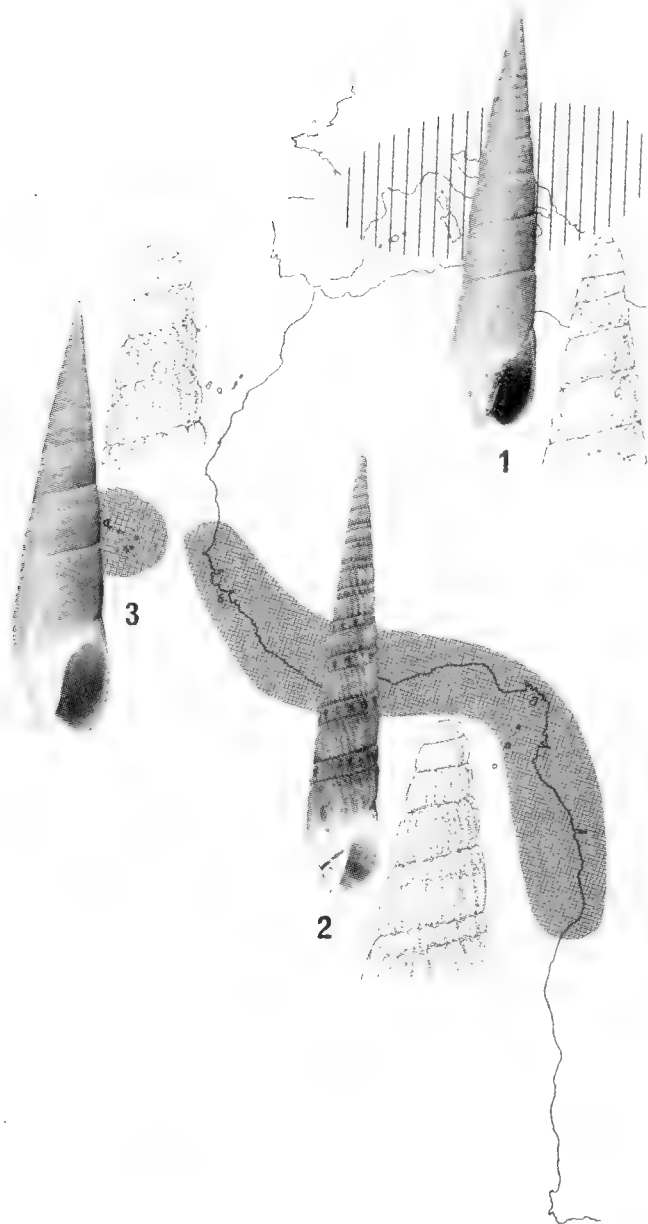


FIG. 2. Distribution, adult and larval shells of *Terebra fuscata* (1), *T. senegalensis* (2), and *T. n. sp.* (3).

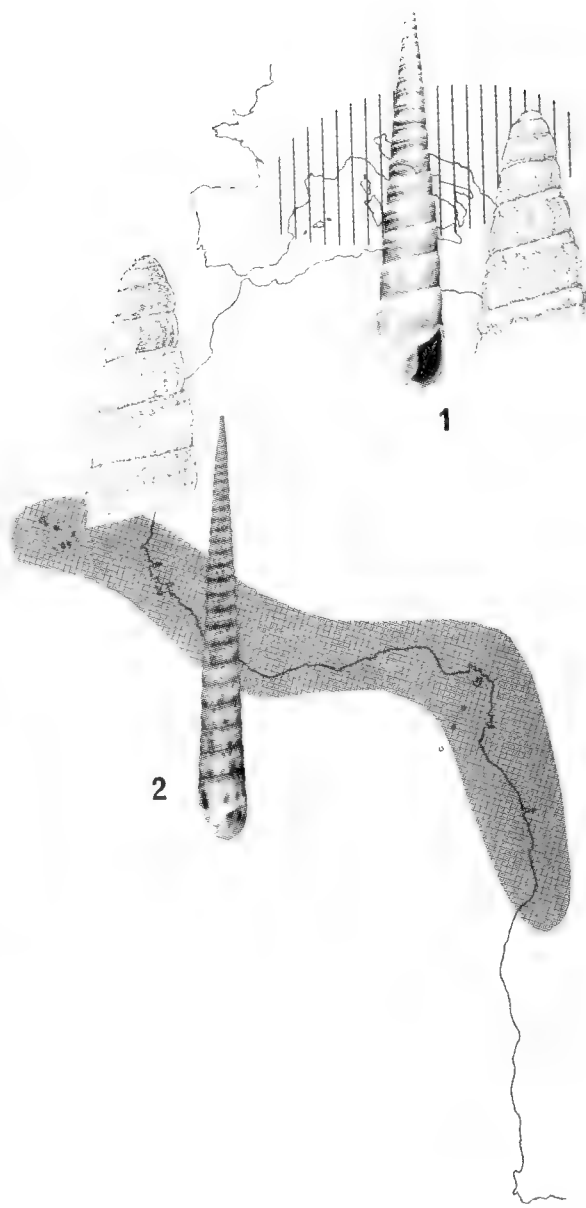


FIG. 3. Distribution, adult and larval shells of *Terebra acuminata* (1) and *T. corrugata* (2).

recent West African species with direct development, but the lack of a fossil record prevents an understanding of this speciation.

4. Lineage of *Hastula* species

There are four described Recent species of *Hastula* in West Africa. Definitely the most common is *H. micans* Hinds, characterized by a very shallow suture and a suprasutural spiral groove. *H. micans* lives in large numbers on the wide open sandy beaches with heavy surf. Surprisingly, no known fossil species can be regarded as the ancestor of *H. micans*. It is possible that this ancestor lived in similar environment in which it was very unlikely to become fossilized as a fresh, identifiable shell.

A second West African *Hastula* is *H. knockeri* Smith, now restricted to the coasts

of Dahomey and Ivory Coast, and about which very little is known.

The other two species are more closely related and apparently shared a common history back into the Paleogene (*H. plicatula* Lamarck). In the Neogene two forms diverged: *H. striata* Basterot and *H. subcinerea* d'Orbigny; the distinction between the two forms becomes more obvious in the mid-Miocene when *H. striata* evolved phyletically into *H. costulata* Borson, with close-set axial ribs. During this time *H. subcinerea* evolved into *H. farinesi* Fontannes with reduced, widely spaced axial sculpture. The separation of the two species is complete in the Pliocene. Both *H. costulata* and *H. farinesi* have planktonic larvae.

From the Pliocene *H. costulata* stock, the Recent *H. lepida* Hinds differs only in having

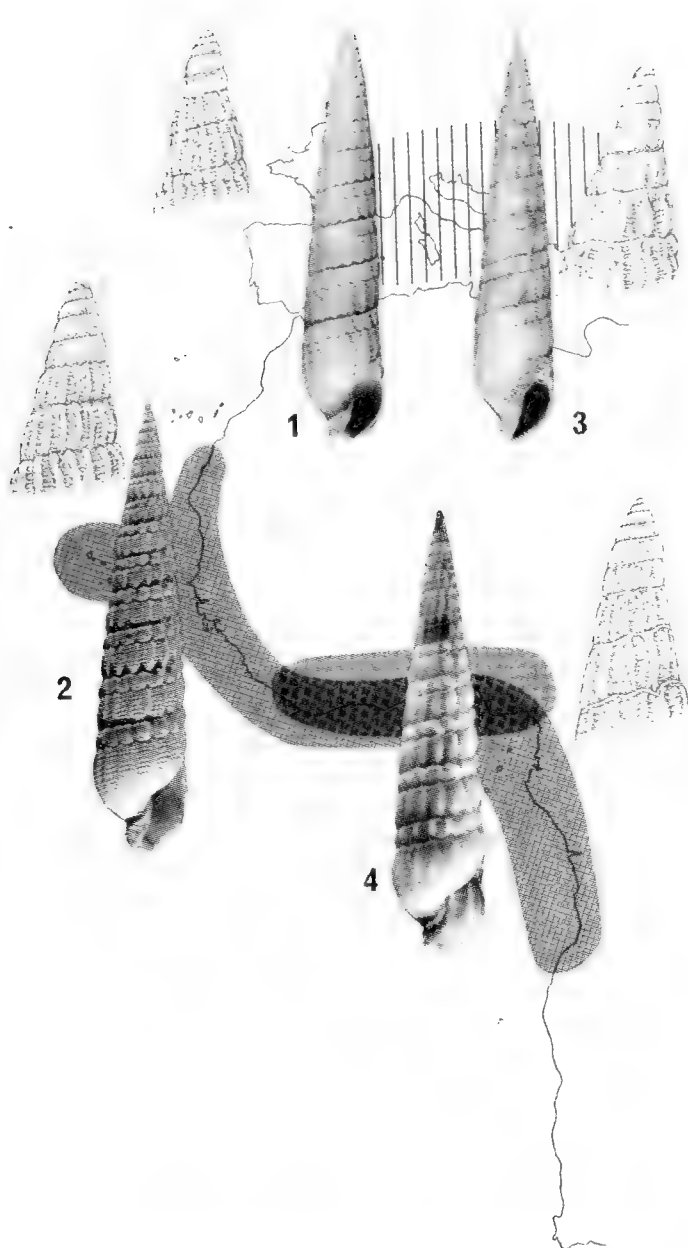


FIG. 4. Distribution, adult and larval shells of Pliocene (1) and Recent (2) *Terebra reticulare*, and of Pliocene (3) and Recent (4) *T. pliogenicum*.

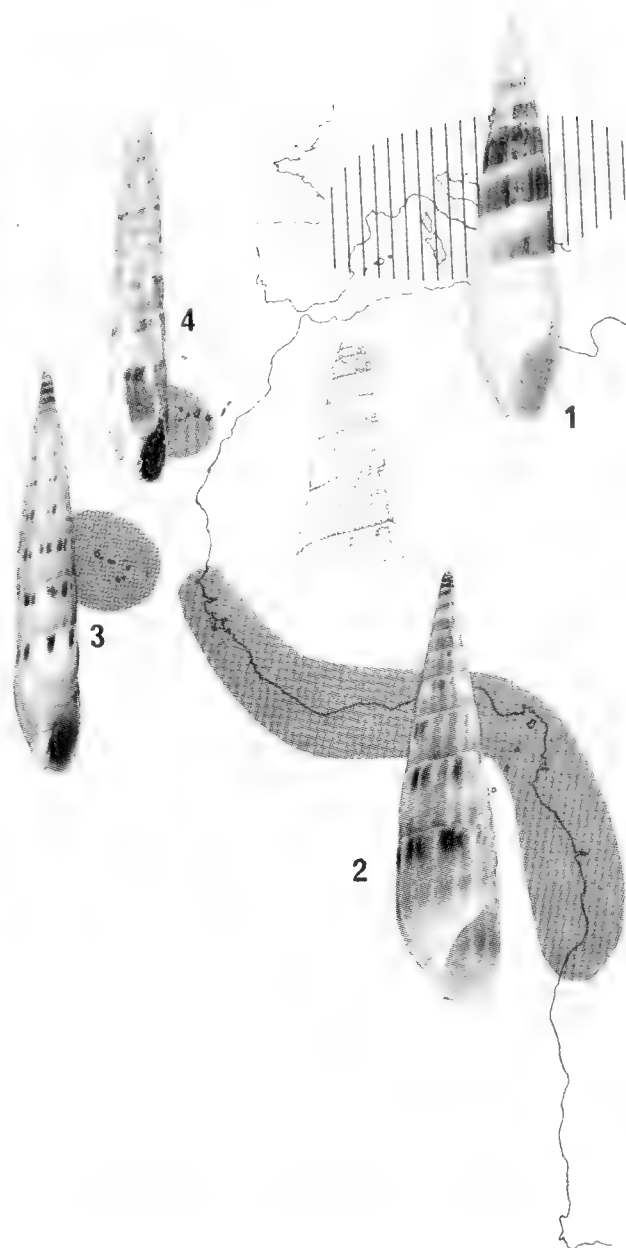


FIG. 5. Distribution, adult and larval shells of *Hastula costulata* (1), *H. lepida* (2) and its Cape Verde (3) and Canarian (4) subspecies.

stronger and more widely spaced axial sculpture. However, the larval shell is retained unchanged as well as the colour marks, still present on some lower Pliocene shells. The dispersal capacity of the *H. lepida* veligers has enabled it to colonize offshore islands where subspeciation has occurred: *H. lepida lepida* lives on the shelf of West Africa from Senegal to Angola while one subspecies (unnamed) is restricted to the Cape Verde Islands and another (unnamed) one lives in the central and western groups of the Canaries. The island subspecies differs from the continental form in being much more slender, with a smaller aperture, and a dark shell in the Canarian subspecies. There are more conchological differences between the different subspecies of *H. lepida* than there are be-

tween *H. lepida lepida* (Recent) and *H. costulata* (lower Pliocene).

The *H. subcinerea-farinesi* stock was apparently amphiatlantic. Only a few *Hastula* taxa have been described in the West Atlantic Neogene, but forms like *H. lissa* Jung from the Miocene of Venezuela are undoubtedly part of this stock. It is known that Pliocene *H. farinesi* had planktonic larvae and probably the Miocene *H. subcinerea-lissa* had similar larval development (it is known for *subcinerea*) through which genetic exchange could occur between each side of the Atlantic. The West African Recent representative of *H. farinesi* is *H. exacuminata* Sacco, which appears to be a mere local variant of *H. salleana* Deshayes, a West Atlantic species with planktonic larvae.

DISCUSSION AND CONCLUSIONS

The main problem in tracing back the origin of the West African Terebridae in particular, and of the Recent West African fauna in general, is the lack of Neogene deposits along the whole West African coast. This lack is compensated for by the rich and well studied Miocene and Pliocene fauna of Europe. The scope of most paleontological studies concerned with this fauna is, however, as stated in the Introduction, limited to a single horizon of a particular basin. Considering that these Neogene deposits have been studied for more than 150 years, the result is an overwhelming mass of names. There are more than 200 specific/subspecific names for the Neogene Terebridae of Europe while the total number of species probably did not exceed 25. To some extent it can be said that the names change with every major geological stage and with every major basin.

The second problem is the lack of adequately preserved juveniles with protoconchs. This is the primary reason in this paper for lack of information on several Miocene Terebridae; the type of larval development is known for most Pliocene species.

It is difficult to compare the results obtained on the evolution of protoconchs with other similar results because they are few and concern prosobranch groups that are only distantly related to Terebridae.

Smith (1945) has shown in West Atlantic *Ficus* (Ficidae) a phyletic evolution from forms with planktonic larvae in the lower Miocene to forms with direct development in the Recent. Gougerot & Le Renard (1980) have shown from protoconch observations an evolution from planktonic to lecithotrophic type of development in *Triforis bitubulatus* Baudon (Triforidae) in the Eocene of the Paris basin. A similar type of evolution is shown here in the *Terebra senegalensis* lineage.

Robertson (1973) remarked that "in the evolution of *Philippia* (Architectonicidae) there are indications that protoconch size and morphology are among the first characters to change" and showed protoconch enlargement in the Cenozoic evolution of the genus. At the species level, this compares with the evolution described here for the *Terebra acuminata-corrugata* series.

The case of the *Hastula* lineage is interesting because it suggests that the rate of appearance or extinction of characters may differ between species stemming from a common ancestor and sharing the same type of

larval development. Geographical isolation seems to act more rapidly than the phyletic change of *Hastula costulata-lepida* over the whole Pliocene.

More generally, we can now turn back to the questions asked by Scheltema (1977b):

What evidence from the fossil records supports the notion that dispersal capability is related to species temporal longevity?

Hansen (1980) and Shuto (1974) have published data on the evolution of Volutacea and Buccinacea, but I think one should be very careful to avoid circular reasoning in the answer to this question. This answer depends on the species concept in a phyletic lineage. When one deals with species with planktonic larvae, one assumes that dispersal is linked with the capacity for a species to become adapted to broad latitudinal and hydrological conditions. Thus an interpopulation variability is interpreted in terms of phenotypical variation. With this in mind, time changes in a lineage will similarly be interpreted as of infraspecific rank.

When considering species with direct development, interpopulation variability is interpreted in connection with the absence of genetic exchange through the larval life. Heterogeneity is interpreted as being genetically determined and thus different morphs along a continuum (geographical or chonal) are frequently given specific rank.

However, the example of Recent species shows that the Arctic shallow water gastropods, which all have direct development, have huge intraspecific variability. Many temperate/tropical species with planktonic larvae have interspecific differences which in paleontology would frequently be interpreted as infraspecific variability.

What evidence supports the idea that allopatric speciation is connected with mode of reproduction and dispersal capability?

The results of this study on Terebridae can be classified into three degrees of speciation since the lower Pliocene:

1. No speciation or phyletic subspeciation: *Terebra acuminata-corrugata* (planktonic); *T. reticulare* (planktonic) and *T. pliogenicum* (planktonic); *Hastula farinesi-salleana* (planktonic).
2. No speciation over time; allopatric subspeciation in Recent: *H. costulata-lepida* (planktonic).
3. Speciation through time and space: *T. fuscata* (planktonic)-*senegalensis* (direct)-n.sp. (direct).

Thus this limited evidence supports the

idea that allopatric speciation is connected with nonplanktonic larval development. But the study of many additional lineages is needed to provide a more statistical answer. In this respect the Neogene of Europe can offer a rich fauna which is reasonably well described, together with good paleogeographic and stratigraphical data.

ACKNOWLEDGEMENTS

I thank especially Dr. G. Pavia (Torino) and Dr. F. Davoli (Modena) who put their collections of respectively Pliocene and Miocene Terebridae at my disposal. I am also grateful to the curators of paleontology of the Institut Royal des Sciences Naturelles (IRSN, Dr. A. DHondt), British Museum (Dr. N. Morris) and Museum National d'Histoire Naturelle (Dr. J. C. Fischer). The drawings of protoconchs have been prepared by Ms. C. Beauchamp and the photos by Mr. A. Foubert.

REFERENCES CITED

- DAVOLI, F., 1977, Terebridae (Gastropoda). In Montanaro Gallitelli, E. (ed.), Studi monografici sulla malacologia miocenica modenese. Parte I. I Molluschi tortoniani di Montegibbio. *Paleontographica Italica*, 70: 135–169, pl. 17–20.
- GOUGEROT, L. & LE RENARD, J., 1980, Clefs de détermination des petites espèces de Gastéropodes de l'Eocene du bassin parisien. XII. La famille des Triphoridae. *Cahiers des Naturalistes*, 35: 41–59.
- HANSEN, T. A., 1980, Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology*, 6: 193–207.
- ROBERTSON, R., 1964, Dispersal and wastage of larval *Philippia krebssii* in the North Atlantic. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 116: 1–27.
- ROBERTSON, R., 1973, On the fossil history and intrageneric relationships of *Philippia*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125: 37–46.
- ROBERTSON, R., 1976, Marine Prosobranch Gastropods: Larval studies and systematics. *Thalassia Jugoslavica*, 10: 213–238.
- SACCO, F., 1891, I Molluschi dei terreni terziarii del Piemonte e della Liguria. Parte X: Cassididae (aggiunte), Terebridae e Pusionellidae. Clausen, Torino, 66 p., 2 pl.
- SCHELTEMA, R. S., 1966, Evidence for trans-Atlantic transport of gastropod larvae belonging to the genus *Cymatium*. *Deep Sea Research*, 13: 83–95.
- SCHELTEMA, R. S., 1971, Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin*, 140: 284–322.
- SCHELTEMA, R. S., 1972, Dispersal of larvae as a means of genetic exchange between widely separated populations of shoalwater benthic invertebrate species. In BATTAGLIA, B., ed., *Fifth European Marine Biological Symposium*, Piccin, Padova, p. 101–114.
- SCHELTEMA, R. S., 1977a, Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. KAUFFMAN, E. G. & HAZEL, J. E. (eds.), *Concepts and Methods of Biostratigraphy*. Dowden, Hutchinson and Ross, Stroudsburg, p. 73–108.
- SCHELTEMA, R. S., 1977b, On the relationship between dispersal of pelagic veliger larvae and the evolution of marine prosobranch gastropods. In BATTAGLIA, B. & BEARDMORE, J. (eds.), *Marine Organisms*. Plenum, New York, p. 303–322.
- SHUTO, T., 1974, Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia*, 7: 239–256.
- SMITH, B., 1945, Observations on gastropod protoconchs. *Paleontographica Americana*, 3(19): 1–48, pl. 21–23.
- THORSON, G., 1946, Reproduction and larval development of Danish marine bottom Invertebrates, with special reference to the planktonic larvae in the Sound. *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser, serie Plankton*, 4(1): 1–523.
- THORSON, G., 1961, Length of pelagic larval life in marine bottom Invertebrates as related to larval transport by ocean currents. *Publications of the American Association for the Advancement of Science*, 67: 455–474.

THE MOLLUSCAN DIGESTIVE SYSTEM IN EVOLUTION

Luitfried v. Salvini-Plawen

Institut für Zoologie, Universität Wien, Dr. Karl Lueger-Ring 1, A1010 Wien I, Austria

ABSTRACT

A comparative analysis of molluscan alimentary conditions including anatomy, way of life, and digestive as well as feeding properties dependent on diets is given with special attention to conditions in the Caudofoveata and Solenogastres which have hardly been considered until now. Such outlines reveal that the original diets of the ancestral molluscs consisted of micro-organisms and/or deposit matter in general, taken up from a fairly firm substratum by means of a broad monoserial radula. The (presumably) initial, intracellular as well as extracellular digestion later on convergently selected the separation of a midgut gland off the straight alimentary canal—single in Caudofoveata, and paired in Placophora-Conchifera—serving for pure secretion (Caudofoveata; Bivalvia-Nuculidae) and even as the restricted site of actual digestion. Further adaptation included the differentiation of a food-mucus column or protostyle in at least two evolutionary lines (Caudofoveata; Conchifera), of a diphyletic gastric shield, and even of a true crystalline style (Tryblidiida, Gastropoda, Bivalvia). Also the chitinous, so-called peritrophic membrane is no monophyletic character. Other, i.e. mostly macrovorous, food taken up predominantly in a predaceous (carnivorous) way does not include such strictly correlated attributes, with the exception of respective pharyngeal conditions (radula; seizing/sucking/swallowing mechanisms, etc.) and of a fairly short alimentary canal (Solenogastres, Scaphopoda, Cephalopoda in general; Gastropoda-Heteropoda, -Neogastropoda, etc.).

Such knowledge facilitates the understanding of selective pressures responsible for supra-specific evolution and enables us to accept 1. an unspecialized microvorous diet on marine deposits as a key character for the Caudofoveata to burrow in soft sediments (subsequently causing other adaptive reorganization: pedal shield, worm-like shape, etc.); 2. a microherbivorous diet on hard bottoms as a key character for special adaptations in the Placophora (esophageal and midgut glands, slender intestine; subradular organ); 3. primitive placophoran conditions also principally existing congenitally in ancestral Conchifera (= Galeroconcha), within which the unselective deposit-feeding may have essentially contributed to the survival of direct descendants: Tryblidiida; 4. microvorous diet also as original (and in part highly specialized) in two of the Galeroconcha offspring, the Gastropoda and the Bivalvia, whereas other descendent groups originated by assuming different diets, such as micro-carnivory in Scaphopoda and the swallowing of carrion to predatory feeding in Cephalopoda; 5. an early alteration from microvorous to Cnidaria-voracious feeding as a key character for the Solenogastres, inducing respective behavioural adaptation in locomotion and therefore narrowing the body shape (followed by other organizational consequences: internalization of the posteriorly limited mantle grooves, regression of gonoducts, etc.). Thus, in avoidance of those adaptations to microvorous feeding (midgut gland, protostyle, gastric shield, etc.), the Solenogastres evidently retained the most conservative configuration of the digestive system in general within the Mollusca.

INTRODUCTION

Comparative analyses of various kinds within animal groups have frequently been based upon information gained only from familiar and quantitatively important subgroups, thus neglecting ones which are less familiar but of equal qualitative importance. Such a biased representation often also con-

cerns the Mollusca, frequently resulting in misleading conclusions especially with regard to primitive conditions of the phylum as a whole.

Increased knowledge and more comprehensive analyses have revealed that the ancestral patterns of molluscs are more closely retained in the still shell-less Caudofoveata and Solenogastres,¹ the synorganization of

¹Because of the characters of the mantle and the gonopericardial system, both classes have formerly been classified as Chaetodermatina, etc., and as solenogastrid Neomeniina, etc., within a single taxon Aplacophora. Since such an assemblage (cf. Scheltema, 1978) negates their evolutionary diphyletic origin and artificially unites two basically independent lines (cf. S. Hoffman, 1949, and others), the Chaetodermatina had been separated from the solenogastrid aplacophorans as a proper class Caudofoveata (cf. Salvini-Plawen, 1969a, 1972c, 1980).

their characters is evidenced to be more conservative than that of *Neopilina*, for example (cf. Vagvolgyi, 1967; Degens et al., 1967; Salvini-Plawen, 1969a, 1972c, 1980, 1981; Peters, 1972; Stasek, 1972; Trueman, 1976). An extensive consideration of molluscan organization in respect to the comparative representation of groups being of equivalent evolutionary levels must also include alimentary conditions (cf. Graham, 1955). In conformity with this purpose, equivalent emphasis should be placed on those minor groups which are not ordinarily discussed because of lack of familiarity or knowledge. Conclusions tracing anagenetic and primitive molluscan patterns onto the already highly developed Gastropoda and Bivalvia only (cf. Graham, 1949; Owen, 1966a, b) must lead to misinterpretation.

An analysis of digestive and feeding properties dependent on diets may not only elucidate specific morphological and physiological conditions, but may well contribute to our knowledge of phyletic trends with respect to behavioural adaptations. Since most organ systems are dependent on each other (form-function complex, cf. Bock & Wahler, 1965), evolutionary pathways can largely be explained by synorganized alterations predominantly following selection pressure for food, habitat, and mode of locomotion (cf. Mayr, 1970). An accurate scrutiny of the alimentary conditions may thus essentially facilitate the understanding of selective pressures responsible for supraspecific evolution.

A) MOLLUSCAN ALIMENTARY CONDITIONS

Information on feeding, anatomical, and digestive properties is fairly detailed as concerns the major groups of gastropods, bivalves, and siphonopods (cephalopods). In the attempt to come to an equivalent basis for all classes with respect to a comparative estimation of the alimentary conditions, special attention is paid to—and a more detailed account is given for—those groups which so far have not been treated.

1. Caudofoveata

The Caudofoveata are still shell-less (aplacophorous), vermiform molluscs of 2 to 140 mm in length, and their mantle is covered by a chitinous cuticle as well as by aragonitic scales and terminal spines; the lateral mantle edges are fused midventrally and the ventral gliding surface is merely characterized by its cerebrally innervated, post- or perioral rudiment, the pedal shield (evolutionary line of Scutopoda; cf. Salvini-Plawen, 1980). The mantle cavity is in a terminal position and contains one pair of ctenidia. The radula is distichous, the alimentary tract straight, and the midgut exhibits posteriorly a narrow intestine and a voluminous ventral midgut sac. The sexes are separate, the conveyance of the sexual products occurs via pericardioducts; fertilization is external. The animals are

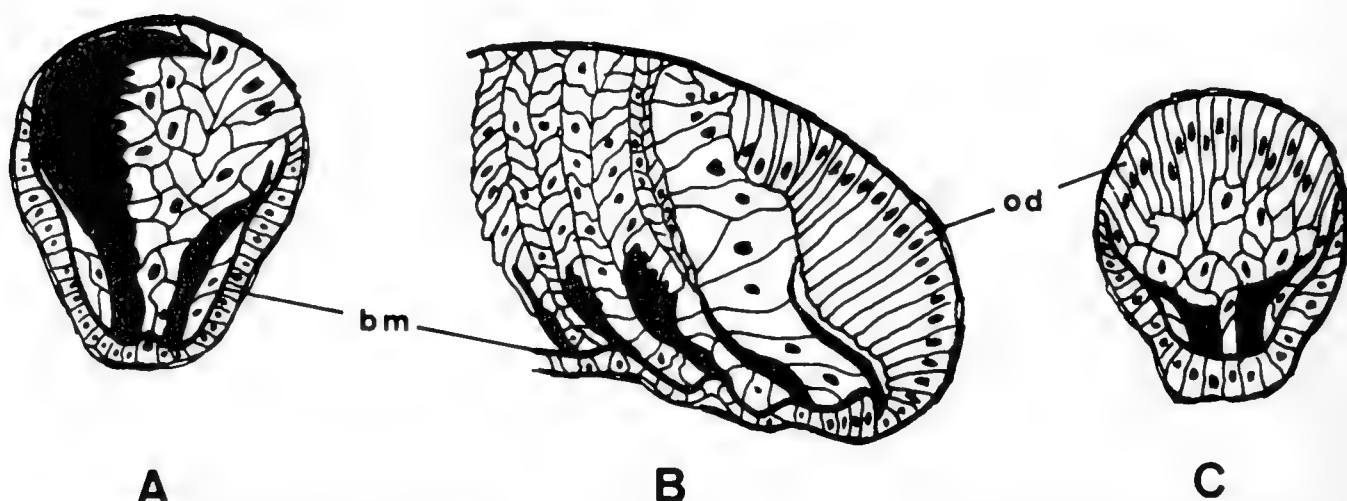


FIG. 1. Caudofoveata: radular sheath of *Scutopus ventrolineatus*; A, in anterior cross section; B, in longitudinal section; C, in posterior cross section. bm = radular membrane (ribbon), od = odontoblasts.

marine burrowers of muddy sediments, feeding on microorganisms and organic matter. There are 66 species in three families.

Digestive system: The digestive system in Caudofoveata begins with a mouth opening surrounded by a distinct muscular sphincter; it leads into the folded, expandible and protrusile buccal cavity provided with some glandular cells. The preradular foregut is cuticularized, or only ciliated in Chaetodermatidae, and there are three sets of predominantly follicular glands: (1) Some unicellular ventral glands just in front of the radula opening on a small papilla ("subradular organ" of Heath; cf. Schwabl, 1963: 261); (2) a pair of lobular lateral organs close to the radula (Chaetodermatidae only?); (3) a mass of dorsal glands above the radula or some distance behind, primitively being epithelial, otherwise but subepithelial follicles in a paired arrangement (*Scutopus robustus*, Chaetodermatidae) which may be correlated with a proper dorsal pouch. In *Prochaetoderma* a pair of chitinized, spatulate and large cuticular elements ("mandibles") are differentiated in oblique position each in a voluminous lateral foregut pouch. *Psilodens* lacks a subradular sac.

The radulae of all Caudofoveata are distichous, viz. two erected curved teeth per row² are differentiated upon a true radular membrane or ribbon (*Scutopus*, *Limifossor*, *Prochaetoderma*; see Fig. 1), proximally underlain by the pharyngeal subradular membrane (cf. also Scheltema, 1978); additionally, in *Prochaetoderma* the sheath produces lateral alate structures. The elaboration of the radula apparatus (denticulation, alae, and supportive elements) is important for the classification³ at the family level (Salvini-Plawen, 1969b, 1975), but exhibits in all members except the Chaetodermatidae a basically typical fashion. In the latter, however, there is only one transverse row of teeth which in *Chaetoderma* is reduced to a pair of simple denticles or is even totally lost. In compensation, the radular membrane is elaborated to form a large conical element (basal plate or cone) associated with one or two pairs of cuticular lateral supports and some smaller elements (cf. Scheltema, 1972; Salvini-Plawen & Nopp, 1974). The typical radula of the more conservative caudofoveates is characteristically

developed within its sheath by distal odontoblasts (Fig. 1), the lower/anterior of which secrete the ribbon and the upper/terminal ones produce the teeth themselves; the dorsal epithelium contributes by hardening the distal portion of the teeth (sclerotization). In Chaetodermatidae the sheath is replaced by a small radular pit and the subsequent tongue-like, cone-producing pouch. In all members a well defined pair of bolsters of muscular as well as connective tissue, and frequently also turgescient cells support the radula. A generically different system of 8–13 muscle groups is associated with the radula apparatus, 6–8 of which can be homologized throughout (K. Deimel, 1981, Diss. Univ. Wien).

The postradular (esophageal) foregut generally shows some ciliated areas, and its opening into the midgut may be equipped with a sphincter. As in the case of the radula apparatus, new investigations demonstrate that the differentiation of the midgut approximately reflects gradual properties at the family level: the more primitive condition is represented in *Psilodens* (*P. elongatus*) and *Metachaetoderma*, both of which possess an extended, somewhat pouched midgut, ventrally and laterally lined by the large inflated cells with a voluminous glandular body escaping into the gut lumen after rupture of the cell wall ('club-shaped' cells or 'Keulenzellen'; Fig. 2). Dorsally the midgut is provided with a simple, cubical epithelium of indifferent appearance, whereas at the rims of the intruding folds, cells varying in shape from cylindrical to club-shaped can be seen to be densely packed with coarse granula ('granula-cells' or 'Körnerzellen'; Fig. 2); the distal portion of the cells are apocrinely cast off to be mixed with the food particles. The histological differentiation can be pursued further to the single, voluminous midgut sac or gland which is ventrally separated from the posterior midgut (or intestine) not before the midbody; the granula-cells are here arranged more broadly beneath the gonad(s) extending dorsally or somewhat laterodorsally. The ciliated intestine is straight and narrow, but very extensible. It begins laterodorsally together with the midgut sac, the transitional region to the former is likewise ciliated, and it leads directly to the mantle cavity.

²The former statement of five elements per transverse row (as recently also accepted by Ivanov, 1979: 9) is due to a misinterpretation of cuticular and ribbon elements.

³Ivanov's classification (1979) cannot be accepted since it is based upon misinterpretations noted above (footnote 2).

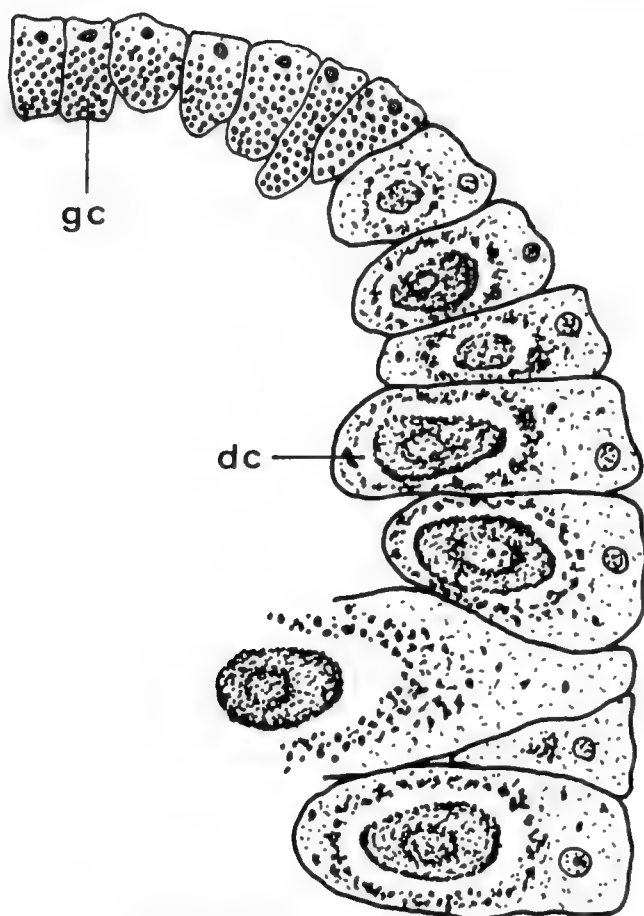


FIG. 2. Caudofoveata: dorsolateral detail of cross section through the midgut sac of *Chaetoderma nitidulum*. dc = club-shaped cells, gc = granula-cells.

Other limifossorids (*Scutopus*, *Limifossor*) possess a comparatively short, pouched midgut lined by an epithelium cubical to columnar in shape and filled with fine granula. The terminal area (with the emergence of the intestine) is also ciliated, but the 'granula-cells' and 'club-shaped' cells are here confined (with identical arrangement) solely to the midgut sac (Fig. 3A) which is already separated in the anterior third of the body. In both described species of *Prochaetoderma*, the short midgut is subdivided histologically into an anterior-dorsal lining of more or less cubical cells with fine granulation and into a posterior-ventral area consisting of densely granulated cells similar to the 'granula-cells' of the midgut gland in other species. The latter organ in *Prochaetoderma* is considerably lobulated and lined by one kind of cell appearing to be a modified 'club-shaped' type.

With the exception of *Falcidens crossotus*, all Chaetodermatidae so far investigated show a distinct separation of the short midgut with cubical, finely granulated cells, and a midgut sac with typical 'club-shaped' cells as well as latero-dorsal 'granula-cells' (Figs. 2, 3B); in *F. crossotus* most of the lining in the midgut gland is made up of 'granula-cells' and the arrangement of the 'club-shaped' cells is confined to a ventral band. In all these

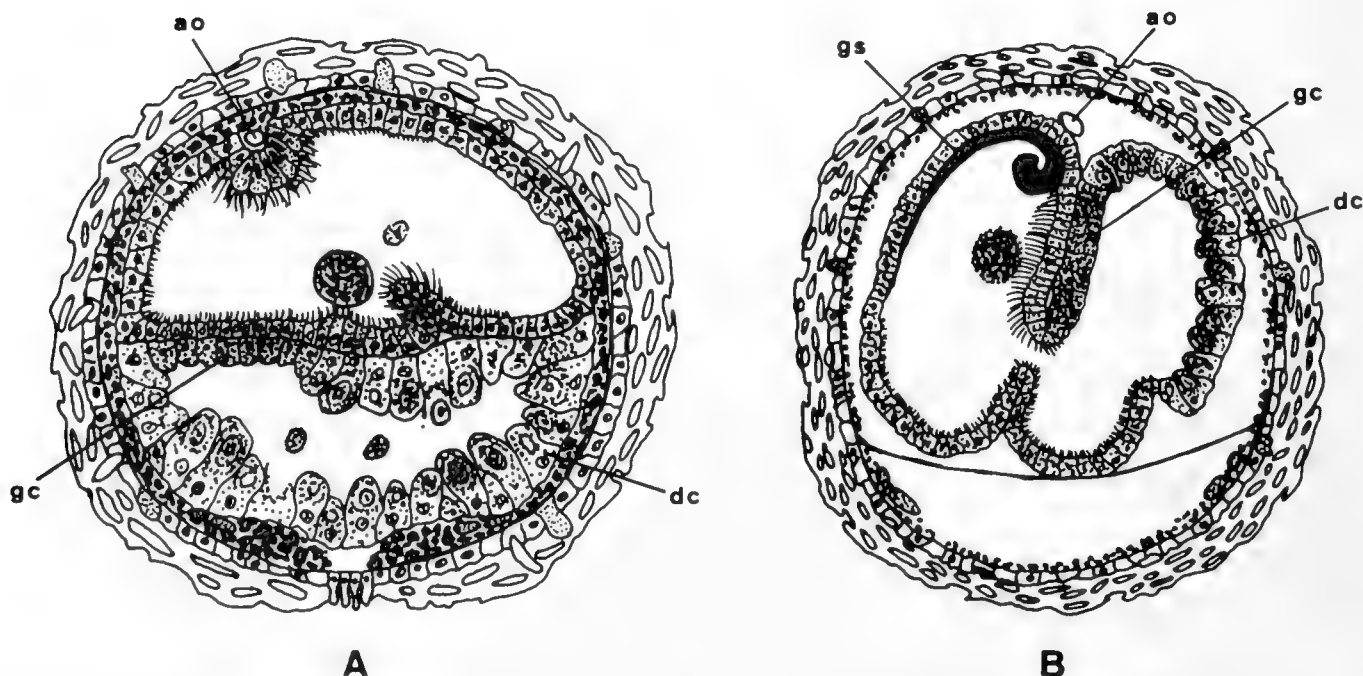


FIG. 3. Caudofoveata: cross section through separation of the midgut sac from the midgut proper, A in *Scutopus ventrolineatus* (Limifossoridae) just after separation, B in *Falcidens aequabilis* (Chaetodermatidae) with gastric shield. ao = aorta, dc = club-shaped cell and gc = granula-cell of midgut sac, gs = gastric shield.

Chaetodermatidae, however (*F. hartmani*, *F. crossotus*, *F. guttuosus*, *F. caudatus*, *F. aequabilis*; *Chaetoderma nitidulum*, *C. canadense*, *C. intermedium*, *C. recisum*, *C. rectum*), the midgut itself differentiates towards a stomach; at its terminal, ciliated section an area close to the entrance into the intestine consists of a cuticular cover with a medially knob-like rim (tooth); this cuticularized area constitutes a primitive gastric shield not present in other Caudofoveata (Fig. 3; see below, also Scheltema, 1978).

Diets: As far as the present information reveals (Table 1), there is surprising homogeneity in the general food of Caudofoveata. In all species examined, the diets consist of microorganisms and/or organic detritus when inferred from gut contents. There are, however, no direct observations on feeding and only the exceptional observations on *Prochaetoderma* (see below) as well as the conditions in *Chaetoderma eruditum* (cf. Heath, 1904) or in *Falcidens caudatus* (Table 1) reflect indirectly on the food itself. This insight as well as some striking differences in the amount of the respective food remnants in the gut point to the evidence that several species might take up their food selectively (e.g. *C. montereyense*). On the other hand, owing to the lack of direct observations, we do not know about diets which undergo total solution without leaving recognizable remains in the gut. We may also point to the establishment of cuticular skeletons obviously coming from entomostracans (*Scutopus ventrolineatus*, *Prochaetoderma californicum*, *Falcidens crossotus*, *F. guttuosus*, *F. aequabilis*, *Chaetoderma canadense*, *C. eruditum*); like those, some other specific food is well imaginable. In accordance with the burrowing manner of living, all diets come from the marine bottom-layer; findings of other particles and/or stated organisms, therefore, may be an accidental by-product.

The most surprising condition is met with regard to the radula. Though they possess typical distichous teeth in several transverse rows, the more conservative Limifossoridae and *Prochaetoderma* obviously do not essentially differ in their diets from the highly specialized Chaetodermatidae (see below). Since we may consider the chaetodermatid radula as an adaptation for the uptake of food, the distichous and partially hooked radula of the more primitive members does not conceivably appear to be a primary adjustment for a similar microphagous diet; present data, however,

do not allow any other conclusions. Surveying the food-relations of the Caudofoveata, there is clear evidence that most if not all Recent members of the group feed on microorganisms and/or deposit matter in general; no principal difference can be seen with respect to the more conservative representatives possessing an allegedly predatory type of radula.

Feeding mechanisms and digestion:

Owing to their concealed manner of life, there are few observations on the food uptake of burrowing Caudofoveata. Kowalevsky (1901: 280–281) reports for *Prochaetoderma raduliferum* that the radula is projected and continuously moves both rows of teeth against each other as if they were searching for some objects to be pushed into the buccal cavity. Nearly identical observations have been made by the present author on the same species: obviously to gather food, the perioral portion of the body becomes shortened and the pharyngeal spatulae (so-called mandibles) spread wide to support it. Simultaneously the radula protrudes and is displayed in order to brush and rake in food particles. Both these observations coincide with the function of the radula, i.e. to brush and seize sediment particles without specific selection. Similar action of the radula apparatus is described by Heath (1905: 714–715) for *Limifossor talpoideus*, although the spread radula itself seems not to be actually protruded out of the mouth opening. There is no further direct evidence on feeding mechanisms. Concerning the Chaetodermatidae with their strongly altered radula apparatus, Heath (1904: 460; 1911: 25) presumes an active food-gathering function of the pedal shield for *Chaetoderma*; this would also correspond to the anatomical condition (musculature, etc.) that the radula here is apparently not brought to the tip of the foregut. Problems arise, however, concerning the function of the radula in *Falcidens*, where the two single, forcep-like teeth appear predestined to seize objects; the respective musculature and the findings in *F. caudatus* (Table 1) concur with that hypothesis, which also would infer radular manipulation of selected food (see above).

The food taken up is carried backwards (presumably) by means of the radula (Heath, 1905) or the chaetodermatid basal cone respectively (Heath, 1911). After being broken up by the enzymatic secretion of the foregut glands, the food is passed through the post-radular foregut by muscular action supported

TABLE 1. Diets in Caudofoveata.

Species	Contents of gut or faecal pellets	Reference
LIMIFOSSORIDAE		
<i>Scutopus ventrolineatus</i> Salvini-Plawen	organic debris (minute fragments of tests, spicules, cuticular skeletons)	Salvini-Plawen (unpubl.)
<i>Scutopus robustus</i> Salvini-Plawen	granular coagulum with some debris	Salvini-Plawen (unpubl.)
<i>Limifossor talpoideus</i> Heath	granular coagulum with some diatoms, sponge spicules, inorganic debris	Heath, 1905, 1911
<i>Psilodens elongatus</i> (Salvini-Plawen)	organic debris (minute skeletal fragments)	Salvini-Plawen (unpubl.)
PROCHAETODERMATIDAE		
<i>Prochaetoderma raduliferum</i> (Kowalevsky)	organic and inorganic debris; one intact turret-like foraminifer (230 μ m \times 200 μ m)	Kowalevsky, 1901; Salvini-Plawen (unpubl.)
<i>Prochaetoderma californicum</i> Schwabl	fragments of radiolaria, diatoms, spicules; crustacean eggs; cuticular skeletons	Schwabl & Salvini-Plawen (unpubl.)
CHAETODERMATIDAE		
<i>Falcidens gutturosus</i> (Kowalevsky)	diatoms, fragments of radiolaria, sponge spicules, cuticular skeletons; organic debris	Salvini-Plawen (unpubl.)
<i>Falcidens crossotus</i> Salvini-Plawen	fragments of arthropod legs and other cuticular skeletons, sponge spicules; organic and inorganic debris; embedded protist parasites	Salvini-Plawen (unpubl.)
<i>Falcidens caudatus</i> (Heath)	one specimen with 5 intact Foraminifera-Textularia (300 μ m–600 μ m) in the foregut	Salvini-Plawen (unpubl.)
<i>Falcidens aequabilis</i> Salvini-Plawen	organic debris with a few cuticular structures, diatoms, and some inorganic matter	Salvini-Plawen (unpubl.)
<i>Chaetoderma nitidulum</i> Lovén	tests of diatoms, foraminifers, some radiolaria; organic and inorganic debris	Wirén, 1892; Salvini-Plawen (unpubl.)
<i>Chaetoderma canadense</i> Nierstrasz	fragments of cuticular skeletons and sponge spicules, organic and inorganic debris	Salvini-Plawen (unpubl.)
<i>Chaetoderma eruditum</i> Heath	organic debris with bits of plants, vegetable spores, foraminifers, sponge spicules; intact Foraminifera-Rotalia; diatoms, fragments of entomostracans	Heath, 1904, 1911
<i>Chaetoderma hawaiiense</i> Heath	diatoms, plant spores, sponge spicules, organic debris	Heath, 1911
<i>Chaetoderma montereyense</i> Heath	diatoms; organic and inorganic debris	Heath, 1911
<i>Chaetoderma argenteum</i> Heath	diatoms; organic and inorganic debris	Heath, 1911
<i>Chaetoderma californicum</i> Heath	radiolaria, diatoms, sponge spicules, organic and inorganic debris; embedded protist parasites	Heath, 1911
<i>Chaetoderma nanulum</i> Heath	fragments of radiolaria and sponge spicules, organic debris	Heath, 1911
<i>Chaetoderma japonicum</i> Heath	diatoms, sponge spicules	Heath, 1911
<i>Chaetoderma bacillum</i> Heath	diatoms, organic and inorganic debris	Heath, 1918
<i>Chaetoderma squamosum</i> Heath	diatoms, sponge spicules, inorganic debris	Heath, 1918

TABLE 1. (Continued)

Species	Contents of gut or faecal pellets	Reference
<i>Chaetoderma intermedium</i> Knipowitsch	granular coagulum mainly with inorganic debris, a few sponge spicules and fragments of radiolaria	Salvini-Plawen (unpubl.)
<i>Chaetoderma</i> (?) <i>militare</i> Selenka	fragments of radiolaria, diatoms, sponge spicules	Salvini-Plawen (unpubl.)

by ciliated areas (when present); there it is mixed with the secretions of the dorsal glands to become a mucous bolus or strand containing the particles (the mucus string is, however, produced even when food material is absent). The midgut is the principal site of digestion which obviously takes place entirely extracellularly—although pinocytosis may occur (compare Owen, 1966b: 65f). Commonly a greater number of the large bodies of the 'club-shaped' cells in the midgut sac is found in the lumen where they undergo slow solution; but they are occasionally found even still in the faeces. The released contents of the apocrine portion of the 'granula-cells' are also found and undergo disintegration. At least in some species (*Scutopus ventrolineatus*, *Falcidens aequabilis*, *F. crossotus*, *F. liosquameus*), food particles bound by the mucus strand are conveyed through the gut by middorsal cilia; they are mixed with the digestive secretions and compacted in the posterior region to a food-mucus column which, in accordance with the arrangement of its components, is rotated there by the cilia usually present. In more conservative members such as *Scutopus* and also *Prochaetoderma*, the mucous food strand is continuous directly into the intestine, at the beginning of which it is divided into pellets. In the chaetodermatids (so far as investigated) there is a primitive gastric shield including a "tooth" (see above), and the compacted food column with a central mucus rod and peripherally bound particles correspond to an ergatulum or protostyle (cf. Owen, 1966b: 61 f). The faecal pellets are conveyed in the long, ciliated intestine and are generally ovoid in form; they measure in *Falcidens crossotus* up to $300\ \mu\text{m} \times 80\ \mu\text{m}$. They contain food remnants and frequently a portion of the mucus column, too; the latter are in *F. crossotus* up to $185\ \mu\text{m} \times 40\ \mu\text{m}$, and even up to $230\ \mu\text{m} \times 40\ \mu\text{m}$ in *Scutopus robustus*. Each pellet is enclosed in a so-called peritrophic membrane which, as in *F. aequabilis*,

may be continuous to form a string of pellets; as identified in *Scutopus ventrolineatus*, *Falcidens gutturosus*, and *Chaetoderma canadense*, that peritrophic membrane is produced in the midgut proper.

2. Solenogastres

The Solenogastres are still shell-less (aplacophorous), laterally narrowed molluscs of 1 mm to 300 mm in length, and their mantle is covered by a chitinous cuticle and aragonitic scales or spicules; the foot is narrowed to a groove usually provided with longitudinal folds and begins with a distinct pedal gland (line of Adenopoda; cf. Salvini-Plawen, 1972c, 1980). The subterminal mantle cavity bears no ctenidia but is often equipped with secondary respiratory formations (plicae, papillae)—the anterolateral sections of the mantle cavity are reduced and the posterolateral ones are internalized. The straight midgut shows serial lateroventral expansions. The animals are hermaphroditic, the gonoducts are usually reduced and the conveyance of the sexual products then occurs via the pericardioducts; there is internal fertilization, and there are accessory genital organs. The animals are marine, mostly cnidariavorous epibionts. There are 180 species in four orders.

Digestive system: The digestive system in Solenogastres appears to be exceptional because it possesses no separate midgut gland, and also has not developed a radular ribbon; both characters, however, can be judged primitive (see below). The mouth opening and/or buccal cavity is located behind or dorsoposteriorly within the atrial sense organ (the remnant of the preoral mantle cavity; cf. S. Hoffman, 1949). It leads into a generally expandible and cuticularized foregut. In its preradular portion, this tube is often provided with an initial sphincter and other distinct musculature, thus representing a pharynx frequently functioning as a suction pump

(Salvini-Plawen, 1967b). When present, a distinct postradular foregut or esophagus serves predominantly a glandular secretive function. Within the Solenogastres four principal sets of foregut glands can be distinguished (cf. Salvini-Plawen, 1978): (1) single subepithelial pharyngeal glands; (2) a distinct dorso-pharyngeal follicle gland; (3) one pair of (ventral) glandular organs, the ducts of which generally open lateroventral to the radula apparatus; (4) single subepithelial esophageal glands. Either the pharyngeal glands (1) or the tubular organs (3) are obligately present and only occasionally substituted by special formations. Most important for classification at the family level, the lateroventral tubular organs (3) in their turn are differentiated in four different types (Salvini-Plawen, 1967b, 1972a, 1978).

The radula apparatus consists of a highly variable radula itself with different numbers of transverse rows, which in general rest upon a direct continuation of the pharyngeal cuticle, the basal cuticle (compare the subradular membrane in other molluscs). A radula bolster may be represented merely by a simple accumulation of muscular and connective tissue forming a median or paired support. More specialized degrees exhibit a distinct muscular concentration sometimes even provided with turgescient cells. Though only rarely observed in the living state, the radula may frequently be protruded towards the mouth due to associated, distinct pro- and retractors. The radula itself is produced as usual in a separate sheath by odontoblasts, and the dorsal epi-

thelium of the sheath contributes to the sclerotization of the teeth (compare Fig. 5). Worn-out teeth are cast off, or retained throughout life in the continuously growing ventral radula sac(s). The shape of the teeth may be categorized in four types of taxonomic value at the family level: (1) monoserial plates with varying denticulation; (2) biserial, serrate plates; (3) biserial, erected teeth with median hooks (distichous type); (4) numerous teeth

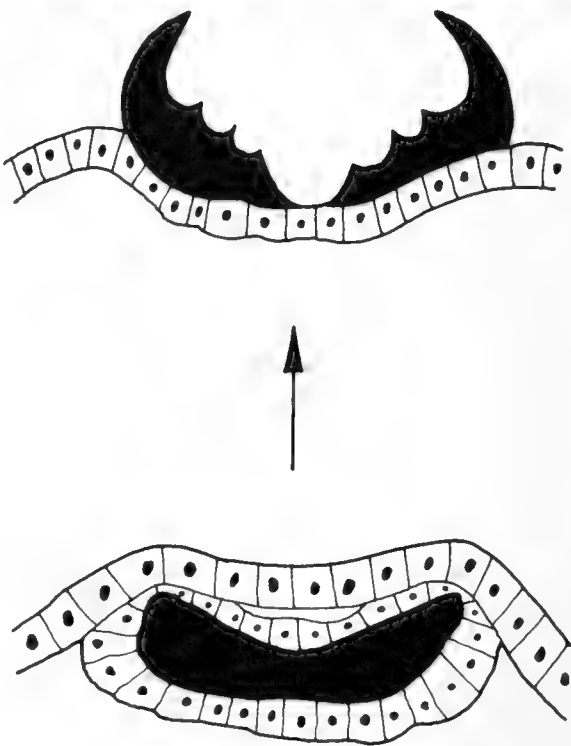


FIG. 4. Solenogastres: morphogenesis of the distichous radula of *Pruvotina impexa* (from Salvini-Plawen, 1972c).

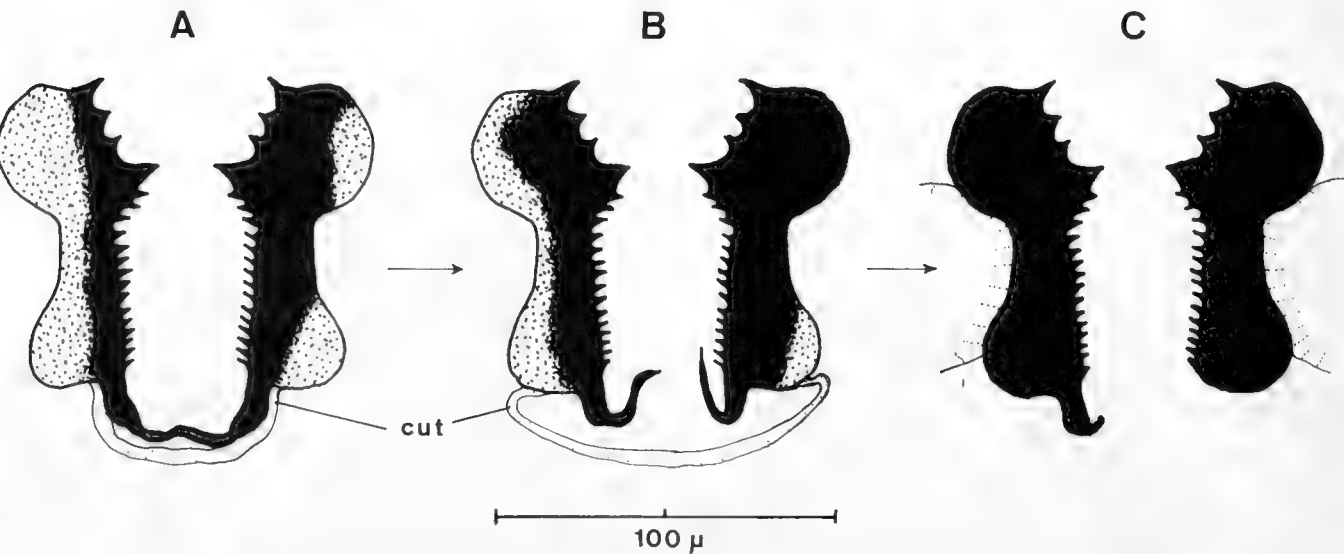


FIG. 5. Solenogastres: morphogenesis of the biserial radula of *Simrothiella schizoradulata* (from Salvini-Plawen, 1978). A, a pair of still medially joined plates enclosed in the sheath; B, separation in the junction of sheath and foregut; C, radula exposed in the pharynx. Black areas are sclerotized. cut = basal cuticle.

per transverse row (polyserial and polystichous types). As concern the presumably primitive type of solenogastrid radula, distinct evidence is found that the biserial and distichous types are derived from the monoserial radula: Figs. 4 and 5 (cf. Salvini-Plawen, 1972c, 1978); the polyserial/polystichous radula being already differentiated only within more specialized families. In different independent evolutionary lines, the radula has been reduced, mostly in connection with sucking up food.

The midgut is generally sharply separated from the foregut, while the latter is often additionally provided with a terminal sphincter. The midgut occupies the whole body cavity with the exception of the middorsal and mid-ventral spaces (dorsal gonads, ventral-sinus); there is often the differentiation of a distinct frontal caecum. Owing to the random serial arrangement of the dorsoventral pair of muscle bundles, the midgut generally exhibits a lateroventrally pouched configuration; in some species (especially very small ones) no pouches are present, since the serial dorsoventral musculature runs alongside the body wall. The midgut is lined by a high, glandular digestive and resorptive epithelium of club-shaped cells with enzymatic granula and bodies; sometimes two different types of cells have been reported which, however, may be due to varying developmental stages. Generally, a middorsal ciliated strip or fold is present; this continues into the short, ciliated rectum which opens dorsally into the mantle cavity.

Diets: Up to the last decade little was known about diets in the Solenogastres; information on the contents of the gut as well as inferences of epizoic condition were summarized in Hoffmann (1930), Graham (1955), and Hyman (1967). Recent investigations, however, resulted in the identification of numerous relations to the food sources summarized in Table 2. This list clearly demonstrates that most Solenogastres are dependent on Cnidaria as a food source, the specialization to which is demonstrated by the Solenogastres' ability to prevent the explosion of nematocysts (Salvini-Plawen, 1967a, 1968). These are obviously embedded within mucous secretions and taken up in an unexploded condition (Salvini-Plawen, 1972b); Moreover, they remain intact and are able to retain their ability to explode (Salvini-Plawen, 1968).

There are a few Solenogastres with diets

other than Cnidaria. Setting aside occasional cases of uptake of diatoms, etc. as well as of organic debris (see *Micromenia fodiens*, *Nematomenia tengulata*, *Archaeomenia prisca*, *Hemeimenia intermedia*, also *Proneomenia sluiteri* and others), only *Dorymenia usarpi* may actually feed on microorganisms by brushing the surface of the sediment with its radula (although one specimen has been recorded in an epizoic condition). A somewhat enigmatic condition is found in *Anamenia gorgonophila*, *Proneomenia sluiteri*, and *Rhipidoherpia copulobursata*, in which arthropods (entomostracans) have been recorded—but at least two species of which are known to be tied to Octocorallia (and one *A. gorgonophila* showed ingested eggs with adjacent tissue). Are those arthropods parasites of the corals, or are these Solenogastres (especially *P. sluiteri*) genuinely omnivorous?

Some of the data given and repeatedly cited in the literature is misleading. Probably due to lack of interest, gut contents simply were not noticed or not looked at accurately enough. This is demonstrated in several reinvestigated species (see Table 2) and is strikingly obvious in some neomeniomorphs: *Archaeomenia prisca* sectioned and described by Thiele (1906) as well as *Neomenia carinata* (cf. Nierstrasz & Stork, 1940) contain a large food mass in their gut lumen within which the numerous spirocysts and nematocysts are clearly discernible. On the other hand, Nierstrasz (1902: 27) reports for *Hemimenia intermedia* that "the animal feeds on sponge; in one of the specimens the alimentary canal is filled with remains of food, amongst which there are numerous sponge spicules." A reexamination of the slides reveals that there is indeed in one specimen an accumulation of sponge spicules. These skeletal elements, however, are totally isolated from the alimentary food mass and not embedded in it; they are found in a location clearly above those of the animal's respective section planes. The actual food mass within the gut in both specimens of *H. intermedia* distinctly contains a large amount of spirocysts and nematocysts, some of which are in ill-defined (semi-digested) condition.

Some special conditions in epizoic species may still be discussed: *Nematomenia banyulensis*, *Rhopalomenia aglaopheniae*, *Anamenia gorgonophila*, and *Strophomenia indica* have been recorded so abundantly upon respective Cnidaria (see Table 2 and references therein) that there can be no doubt

TABLE 2. Diets in Solenogastres.

Species	Recorded habits	Food	Gut contents	Reference
Order PHOLIDOSKEPIA (38 species known)				
<i>Dondersia annulata</i> Nierstrasz	upon Gorgonaria	?	?	Nierstrasz, 1902
<i>Dondersia cnidevorans</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Dondersia stylastericola</i> Salvini-Plawen	upon Stylasteridae (Hydrozoa)	Stylasteridae (Hydrozoa)	nematocysts	Salvini-Plawen, 1978
<i>Dondersia laminata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Micromenia simplex</i> Leloup	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1972a
<i>Micromenia fodiens</i> (Schwabl)	free roving	Hydrozoa	nematocysts; diatoms	Schwabl, 1955; Salvini-Plawen, 1968, 1972a
<i>Nematomenia flavens</i> (Pruvot)	epizoic upon <i>Lafoea dumosa</i>	<i>Lafoea dumosa</i> (Hydrozoa)	nematocysts	Pruvot, 1891; Maluquer, 1917, Salvini-Plawen, 1978
<i>Nematomenia banyulensis</i> (Pruvot)	epizoic upon <i>Lafoea dumosa</i> , <i>Lytocarpia myriophyllum</i> , and <i>Grammaria abietina</i>	tissues of the hydrozoan hosts?	—	Pruvot, 1891, Maluquer, 1917, Nierstrasz & Stork, 1940
<i>Nematomenia platypoda</i> (Heath)	epizoic upon Campanulariidae	Campanulariidae (Hydrozoa)	nematocysts	Heath, 1911
<i>Nematomenia corallophila</i> (Kowalevsky)	on <i>Corallium rubrum</i>	?	?	Kowalevsky, 1881
<i>Nematomenia tegulata</i> Salvini-Plawen	free roving ?	Cnidaria	Nematocysts; diatoms	Salvini-Plawen, 1978
<i>Lyratoherpia carinata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Lyratoherpia bracteata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Heathia porosa</i> (Heath)	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen (unpublished)
<i>Sandalomenia carinata</i> Thiele	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Lepidomenia harpagata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Genitoconia rosea</i> Salvini-Plawen	free roving	Hydrozoa	nematocysts	Salvini-Plawen, 1967a, 1968
<i>Genitoconia atriolonga</i> Salvini-Plawen	free roving	Hydrozoa	nematocysts	Salvini-Plawen, 1967a, 1968
Order NEOMENIAMORPHA (15 species known)				
<i>Archaeomenia prisca</i> Thiele	free roving ?	Hexacorallia	spirocysts and nematocysts; some diatoms, sponge spicules	Salvini-Plawen, 1978

<i>Hemimenia intermedia</i> Nierstrasz	free roving ?	Hexacorallia	spirocysts and nematocysts; some sponge spicules, diatoms	Nierstrasz, 1902; Salvini-Plawen, 1978
<i>Hemimenia dorsosulcata</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
<i>Neomenia carinata</i> Tullberg	burrowing in sediment	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
<i>Neomenia (carinata) affinis</i> (Koren & Danielssen)	burrowing ?	Hexacorallia	nematocysts	Salvini-Plawen (unpublished)
<i>Neomenia dalyelli</i> (Koren & Danielssen)	free roving ?	Hexacorallia	nematocysts	Salvini-Plawen, 1978
<i>Neomenia trapeziformis</i> Salvini-Plawen	free roving ?	Hexacorallia	nematocysts	Salvini-Plawen, 1978
<i>Neomenia permagna</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts	Salvini-Plawen, 1978
<i>Neomenia herwigii</i> Kaiser	free roving ?	Anthozoa ?	nematocysts	Kaiser, 1976
<i>Neomenia labrosa</i> Salvini-Plawen	burrowing ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Neomenia crenagulata</i> Salvini-Plawen	burrowing ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Neomenia laminata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Neomenia proprietecta</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
Order STERROFUSTIA (8 species known)				
<i>Phyllomenia austrina</i> Thiele	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Phyllomenia cornuadentata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Harpagoherpia tenuisoleata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Lituiherpia spermathecata</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
<i>Ocheyoherpia lituifera</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Imeroherpia quadridens</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
Order CAVIBELONIA (119 species known)				
<i>Eleutheromenia sierra</i> (Pruvot)	preying upon the hydroids <i>Lytocarpia myriophyllum</i> , and <i>Nemertesia antennina</i>	?	?	Pruvot, 1891, 1897
<i>Gephyroherpia antarctica</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Pruvotina praegnans</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Pruvotina uniperata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Pruvotina longispinosa</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Pruvotina megathecata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Pruvotina pallioglandulata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978

TABLE 2. (Continued)

Species	Recorded habits	Food	Gut contents	Reference
? <i>Pruvotina cryophila</i> (Pelseneer)	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Labidoherpis spinosa</i> (Thiele)	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Lophomenia spiralis</i> Heath	epizoic upon <i>Cryptolaria operculata</i>	<i>Cryptolaria</i> (Hydrozoa)	nematocysts	Heath, 1911
<i>Metamenia triglandulata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Hypomenia nierstraszi</i> van Lummel	free roving ?	Cnidaria ?	sporadic nemato-cysts	Salvini-Plawen (un-published)
<i>Forcepimena protecta</i> Salvini-Plawen	free roving amongst Cnidaria	Cnidaria	nematocysts	Salvini-Plawen, 1969b
<i>Rhopalomenia aglaopheniae</i> (Kowalevsky & Marion)	epizoic upon <i>Lytocarpia myriophyllum</i>	tissues of the hydro-zoan host	a few nematocysts	Nierstrasz & Stork, 1940; Salvini-Plawen, 1972a and unpublished
<i>Rhopalomenia atlantica</i> (Leloup)	epizoic upon Lafoeidae	Lafoeidae (Hydrozoa)	nematocysts	Salvini-Plawen, 1972a
<i>Rhopalomenia carinata</i> Salvini-Plawen	in part upon Synthechiidae	Synthechiidae (Hydrozoa)	nematocysts	Salvini-Plawen, 1978
<i>Rhopalomenia tricarinata</i> Salvini-Plawen	epizoic (?) upon Synthechiidae	Synthechiidae (Hydrozoa)	nematocysts	Salvini-Plawen, 1978
<i>Rhopalomenia sertulariicola</i> Salvini-Plawen	epizoic upon Sertulariidae	Sertulariidae (Hydrozoa)	nematocysts	Salvini-Plawen, 1978
<i>Rhopalomenia cristata</i> Salvini-Plawen	in part upon <i>Grammaria</i> (Hydrozoa)	Lafoeidae or Coryni-dae (Hydrozoa)	nematocysts	Salvini-Plawen, 1978
<i>Rhopalomenia rhynchopharyngeata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Dinomenia hubrechtii</i> Nierstrasz	upon Gorgonaria	?	?	Nierstrasz, 1902
<i>Pruvotina sopita</i> (Pruvot)	roving upon <i>Sertularella polyzonias</i>	?	?	Pruvot, 1891
<i>Alexandromenia grimaldii</i> Leloup	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1972a
<i>Alexandromenia antarctica</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Alexandromenia latosoleata</i> Salvini-Plawen	free roving	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Alexandromenia acuminata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Spengelomenia polypapillata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Spengelomenia procera</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978

<i>Sputoherpia fissitubata</i> Salvini-Plawen	free roving ?	Zoantharia	tissues, spirocysts and skeleton of Zoantharia; fragments of radiolaria, diatoms, and sponge spicules	Salvini-Plawen, 1978
<i>Sputoherpia laxopharyngeata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Sputoherpia megaradulata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Utraloherpia abyssalis</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Meromenia hirondellei</i> Leloup	epizoic ?	Hexacorallia	spirocysts	Salvini-Plawen, 1972a
<i>Birasoherpia trisialota</i> Salvini-Plawen	free roving ?	?	one buccal radiolarian	Salvini-Plawen, 1978
<i>Sialoherpia aculeitecta</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
<i>Drepanomenia vampyrella</i> Heath	free roving	<i>Epizoanthus</i> (Zoantharia)	tissues of the prey	Heath, 1911
<i>Drepanomenia perticata</i> Salvini-Plawen	free roving ?	Hexacorallia	spirocysts and nematocysts	Salvini-Plawen, 1978
<i>Anamenia borealis</i> (Koren & Danielssen)	free roving ?	Octocorallia	<i>Gersemia</i> -spicules (Alcyonaria)	Odhner, 1921
<i>Anamenia farcimen</i> (Heath)	epizoic upon <i>Acanthogorgia angustiflora</i> and <i>Dendronephthya</i>	Gorgonaria and Alcyonaria	nematocysts and ova of the host	Heath, 1911
<i>Anamenia triangularis</i> (Heath)	epizoic upon <i>Calicogorgia</i>	<i>Calicogorgia</i> (Gorgonaria)	nematocysts and germ cells of the host	Heath, 1911
<i>Anamenia gorgonophila</i> (Kowalevsky)	epizoic upon Gorgonaria (<i>Paramuricea chamaeleon</i>)	tissues of the host ?	Entomostracans; ingulfed eggs	Salvini-Plawen, 1972a and unpublished
<i>Anamenia spinosa</i> (Heath)	epizoic upon <i>Acanthogorgia japonica</i>	tissues of the gorgonarian host ?	?	Heath, 1911
<i>Anamenia agassizi</i> (Heath)	epizoic upon <i>Acanthogorgia armata</i>	tissues of the gorgonarian host?	?	Heath, 1918
<i>Strophomenia lacazei</i> Pruvot	epizoic upon <i>Muricea</i> (Gorgonaria)	tissues of the host ?	?	Pruvot, 1899
<i>Strophomenia debilis</i> (Nierstrasz)	upon Gorgonaria	?	?	Nierstrasz, 1902
<i>Strophomenia indica</i> (Nierstrasz)	epizoic upon Gorgonaria	tissues of the host	a few nematocysts and spicules	Nierstrasz, 1902; Salvini-Plawen (unpublished)
<i>Strophomenia regularis</i> Heath	epizoic (?) upon <i>Dendronephthya</i> (?)	Cnidaria (Gorgonaria?)	nematocysts	Heath, 1911

TABLE 2. (Continued)

Species	Recorded habits	Food	Gut contents	Reference
<i>Strophomenia scandens</i> Heath	epizoic upon <i>Acanthogorgia armata</i>	tissues of the gorgonian host?	—	Heath, 1911
<i>Strophomenia ophidiana</i> Heath	upon <i>Acanthogorgia angustiflora</i> (Gorgonaria)	?	?	Heath, 1911
<i>Proneomenia sluiteri</i> Hubrecht	free roving	Alcyonaria, Entomostraca	Alcyonaria, entomostracans; diatoms	Hubrecht, 1881; Heuscher, 1892
<i>Proneomenia praedatoria</i> Salvini-Plawen	free roving ?	Octocorallia	Octocorallia	Salvini-Plawen, 1978
<i>Proneomenia epibionta</i> Salvini-Plawen	epizoic upon Cryosogorgiidae	Cryosogorgiidae (Gorgonaria)	nematocysts	Salvini-Plawen, 1978
<i>Proneomenia stillerthyrocytica</i> Salvini-Plawen	free roving ?	Cnidaria (Hydrozoa?)	nematocysts, cuticle of prey ?	Salvini-Plawen, 1978
<i>Dorymenia weberi</i> (Nierstrasz)	epizoic upon Gorgonaria	tissues of the host ?	unknown prey; fragments of radiolaria	Nierstrasz, 1902
<i>Dorymenia tricarinata</i> (Thiele)	free roving ?	?	?	Salvini-Plawen, 1978
<i>Dorymenia hoffmani</i> Salvini-Plawen	free roving ?	Gorgonaria	nematocysts, spicules	Salvini-Plawen, 1978
<i>Dorymenia usarpi</i> Salvini-Plawen	free roving ?	microorganisms (organic deposit)	fragments of radiolaria, diatoms, foraminifera, sponge spicules, bryozoan cases	Salvini-Plawen, 1978
<i>Dorymenia harpagata</i> Salvini-Plawen	free roving ?	Cnidaria ?	nematocysts	Salvini-Plawen, 1978
<i>Dorymenia profunda</i> Salvini-Plawen	free roving ?	?	one fragment of radiolaria	Salvini-Plawen, 1978
<i>Dorymenia paucidentata</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Epimenia australis</i> (Thiele)	free roving ?	Alcyonaria	spicules	Thiele, 1902
<i>Epimenia verrucosa</i> (Nierstrasz)	free roving ?	<i>Dendronephthya</i> , <i>Nephtya</i>	portions of the alcyonarian prey	Nierstrasz, 1902; Baba, 1940
<i>Epimenia vixinsignis</i> Salvini-Plawen	free roving ?	Cnidaria	nematocysts	Salvini-Plawen, 1978
<i>Epimenia</i> spec. (dict. <i>australis</i>) (Smith, 1903: 621)	free roving ?	Alcyonaria	part of alcyonarian colony	Salvini-Plawen (unpublished)
<i>Syngenoherpia intergenerica</i> Salvini-Plawen	free roving ?	Cnidaria ?	nematocysts	Salvini-Plawen, 1978
<i>Rhipidoherpia copulobursata</i> Salvini-Plawen	free roving ?	?	arthropods, skeletal fragments of radiolaria, sponges etc.	Salvini-Plawen, 1978

about the biological relation of the solenogaster to the hypobiont. Careful investigation of those solenogastres, however, resulted in the almost total lack of identifiable food particles respective to the cnidarian; only some sporadic nematocysts in one specimen of *R. aglaopheniae* and of *S. indica* confirm the feeding relation, and the single record of ingested eggs in *A. gorgonophila* may likewise point to the hypobiont's tissue. But why don't further individuals and animals of other species likewise possess nematocysts? A closer look at the animals demonstrates that the Solenogastres are generally associated with or coiled around the stem of the cnidarian colony; that portion of the body wall is, however, commonly protected by the theca or by dense skeleton and hence mostly devoid of nematocysts. Moreover, except for *Anamenia*, the species are without radula and presumably take their food up by macerating the body wall and sucking the liquefied tissue of the prey, the chyle of which would therefore only rarely also contain nematocysts and other distinct food particles. For *Anamenia* also an active uptake of cnidarian parasites might be considered (as indicated above). It might therefore be deceptive to infer the diets solely on the basis of epizoic information (see *Eleutheromenia sierra*, *Pruvotina sopita*, and others).

Feeding mechanisms and digestion:

There is little direct information for Solenogastres about the uptake of food. The detection of food appears to be modulated by the preoral sense organ with its chemoreceptive papillae as well as its heavily acting ciliary bands, and the mechanical contact may be effected by sensitive hairs (circum-atrial setae; cf. Pruvot, 1891; Salvini-Plawen, 1968, 1969b). Observations made by Baba (1940) on *Epimenia verrucosa* and by Barnard on *Dorymenia paucidentata* (cf. Salvini-Plawen, 1978) evidence the actual usage of the protruded radula to get food, and inferences from anatomical conditions (Salvini-Plawen, 1967a, b, 1978) likewise suggest the protrusion of the radula to the tip of the foregut. The action and employment of the radula can often be concluded on the basis of its morphological and/or functional type, and in several cases even analogized to conditions found in gastropods: the monoserial-monostichous radula (*Dondersia*, etc.) to the Monostichoglossa (= Saccoglossa), the pectinid and serrate monoserial radulae (*Anamenia*, many Amphimeriidae, etc.) to the Aeolidiacea, the polystichous

radula (*Proneomenia*, etc.) to the Taenioglossa, or the serrate-biserial radulae (*Simrothiella*, etc.) to certain Stenoglossa. The hooked distichous radulae of many solenogastroid genera correspond to jaw formations in Polychaeta or Rotatoria and may be regarded as typical seizing forceps.

With the possible exception of the radula of *Dorymenia usarpi* and some further species which may also feed themselves by brushing microorganisms, all other radula types may serve to attack Cnidaria (Salvini-Plawen, 1967b): first, in most Solenogastres some secretions of the foregut glands brought into direct contact with the prey can prevent the discharge of nematocysts due to hyperviscosity (Salvini-Plawen, 1972b). Only after the cnidarian tissue has been immunized is the prey attacked by the radula or by the enzymatically macerating foregut secretions (see below). The actual uptake of the Cnidaria-food by means of the radula occurs either when larger pieces from the prey are ripped and cut off (cf. Heuscher, 1892; Baba, 1940; Salvini-Plawen, 1978), or when the prey's body wall is forced open and tissue is sucked as also in the case of radula-less representatives (Salvini-Plawen, 1967b, 1972b).

Nearly 50 species (more than 25%) from different families show reduction of the radula. In these animals as in further representatives, the frequent elaboration of a proboscis and/or a sucking pump points to the uptake of liquefied food (cf. Salvini-Plawen, 1967b). As demonstrated in *Drepanomenia vampyrella* (cf. Heath, 1911) and experimentally evidenced in *Epimenia verrucosa* (cf. Baba, 1940) the foregut glands produce secretions which dissolve food into chyle. In radula-less species chyle is already formed when the tip of the foregut touches and even enters the body wall of the Cnidaria (any cuticular or skeletal covering is thereby penetrated). Finally, swallowing of the food takes place either with help of the shovelling radula or by suction, thus conveying the food to the midgut. If present, ciliary movement supports this process. The transport of the food within the midgut itself is realized by the weak but distinct muscularis, as well as by the middorsal ciliation. The epithelial lining generally consists homogeneously of secretive and resorptive club-shaped cells containing numerous granula and larger bodies or droplets. Digestion first takes place extracellularly by means of the contents of the cell portions apocrinely

cast off into the gut lumen. Isolated small particles of the chyle (partly including nematocysts) are then phagocytised and digested intracellularly. The remains of food (nematocysts, spicules, cuticle, fragments of tests, etc.) are conveyed dorsally to the posterior, and are released via the rectum without the formation of a peritrophic membrane (and hence of true faecal pellets).

3. Placophora

The Placophora (or Polyplacophora) are in general dorsoventrally compressed molluscs 3 mm to 330 mm long, and their mantle is covered by a chitinous cuticle and aragonite bodies, middorsally replaced by eight large, generally four-layered plates; the mantle cavity surrounds the flat, ventrally-innervated foot (see Adenopoda) as well as the simple head (head disc), and it produces 6-88 pluralized pairs of ctenidia. The mantle epithelium produces sensory papillae and out of them the specialized so-called aesthetes (cf. Fischer, 1978; Fischer et al., 1980). The alimentary tract is provided with paired esophageal and midgut glands, and the narrowed intestine is variously looped; the uniform radula possesses 17 teeth per transverse row, and there is a distinct subradular sense organ. The pericardioducts are elaborated to function as excretory organs (emunctoria). The sexes are (with few exceptions) separate, and fertilization is external. The Placophora are marine, generally living upon hard bottoms predominantly in the littoral zone, and most members feed microherbivorously by scraping algae. There are about 600 Recent species classified in three orders.

Digestive system: Most information on the placophoran alimentary condition comes from early investigation, essentially supplemented by Fretter's study (1937); surveys are summarized by Hoffmann (1930), Owen (1966a, b), and Hyman (1967).

In the centre of the head disc the mouth leads to a short oral tube, limited towards the actual buccal cavity by a distinct sphincter; both sections are of a cuticularized epithelium with interspersed mucocytes (buccal glands). There is a pair of dorsobuccal foregut glands (salivary glands) of simple to compound sacular configuration, and the subradular sac with its dorsally elaborated bipartite sense organ consists of glandular epithelium, sometimes even terminally forming a seemingly

paired gland proper (cf. Hoffmann, 1930; Salvini-Plawen, 1972c). Beginning with the dorsal foregut glands, the subsequent, entodermal esophagus (cf. Hammarsten & Runnström, 1925: 273) is of an epithelium without cuticle bearing a longitudinal differentiation into ciliated and mucous bands; above the entrance of the radula into the pharynx, the esophagus enlarges to differentiate anteriorly a pair of glandular pouches and to lead posteriorly into the tubular esophagus proper as well as into the paired esophageal glands.

The radula apparatus exhibits an extensive supporting system including a transverse muscle bar, paired bolsters (cartilages and air sacs), and a great variety of muscle bundles (cf. Plate, 1897; Graham, 1973). The radula itself is produced in a very long, straight sheath and rests upon the radular membrane (ribbon). The uniform organ of 17 teeth per transverse row shows the second lateral ones elaborated as a robust, strongly sclerotized hook. As demonstrated by the developmental pattern (cf. Sirenko & Minichev, 1975), those latter hamate teeth are the unique remnants of the originally monoserial radula, whereas the marginal teeth (3rd-8th laterals) as well as the rhachis plus the first laterals arise only later from one radula plate each of which is subsequently fragmented (Fig. 6).

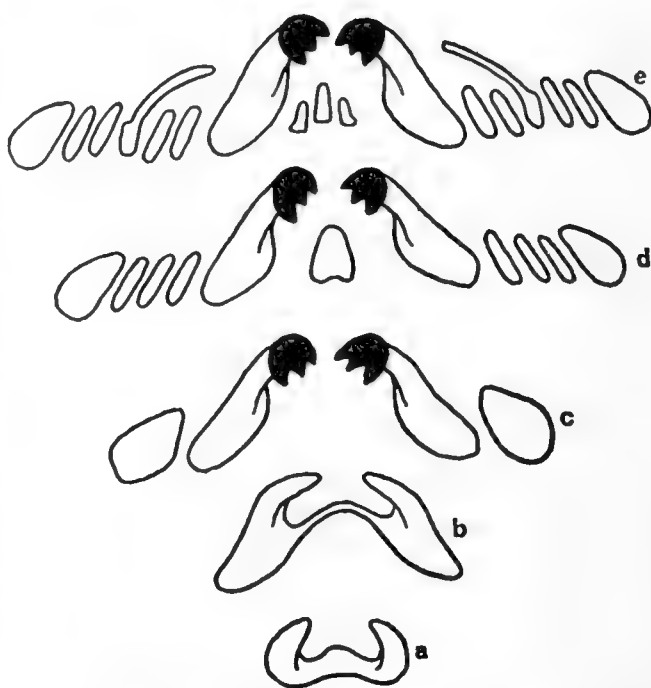


FIG. 6. Placophora: morphogenesis of the radula (from Sirenko & Minichev, 1975); the lateral plate at each side in c and the central plate in d each is fragmented to become six and three teeth respectively.

The extensive esophageal glands or sugar glands extend ventrally and are built up of carbohydrase-secreting cells as well as supporting cells arranged in numerous villi (cf. Fretter, 1937). The short, ciliated esophagus exhibits longitudinal ridges and is limited against the stomach by a sphincter. The stomach demonstrates a fairly unusual configuration from a comparative point of view. In some conservative conditions it represents a scarcely enlarged portion which may be externally delimited merely by an anterior constriction (see esophageal sphincter) and by the openings of the midgut glands. More detailed information is available for the more elaborated types of stomachs in the majority of Placophora which are characterized by the differentiation of a variously shaped enlargement, the ventral sac (cf. Fretter, 1937). The stomach proper appears to be represented by a scarcely extended section directly continuous between the esophagus and the intestine (see Fig. 7A) which corresponds to the above stomach of the conservative type. Its wall is characterized by a dorsal and ventral ciliated band, delimiting the "dorsal channel" at the right side (Fretter, 1937); the wall of the (ventral-) left side is largely expanded to form a voluminous, ventrally-bent sac. This latter organ often has a cuticularized epithelium (Fretter, 1937) or but a ciliated one (Greenfield, 1972) and is underlain by a distinct muscle. The dorsal-left and left areas of the wall of the stomach continues to become—after separation of the ventral sac—together with the now merely gutter-like "dorsal channel" the anterior intestine. This right-sided "gutter"/"dorsal channel" in its turn posteri-

orly receives the (in adults) asymmetrically arranged outlets of the midgut glands; in *Lepidopleuridae* this entire section ("gutter"/"dorsal channel" with orifices of the glands) has become separated from the anteriormost intestine to form the so-called "ductus choledochus" (Plate, 1901: 442).

The paired midgut or digestive glands after metamorphosis become arranged in succession, the right gland being directed dorso-anteriorly and the left one spreading postero-ventrally (cf. Hammarsten & Runnström, 1925); each gland is structured into tubules, the ductules of which join together to form one outlet. Their epithelium consists of two types of cells scantily provided with cilia. The slender to club-shaped digestive cells are characterized by small vacuoles, fatty and lipid droplets, as well as a large distal vacuole provided with an irregular granular mass; the latter is extruded and frequently present in all parts of the midgut as well as the faecal pellets (cf. Fretter, 1937). The second, less frequent type consists of fairly pyramidal cells filled with spherules of calcium deposits (lime cells, excretory cells; cf. Owen, 1966b: 79).

The intestine is increasingly looped according to different levels of differentiation (cf. Plate, 1901: 444 f), and must be divided in two successive sections. The anterior section is continuous from the stomach and extends to the intestinal valve at about one-third of the total length of the intestine. It is characterized by the two longitudinal ciliary bands arising in the stomach, and actually begins behind the orifices of the midgut glands where the "gutter" flattens out ventrally and a transverse ciliated band splits off from the ventral one to

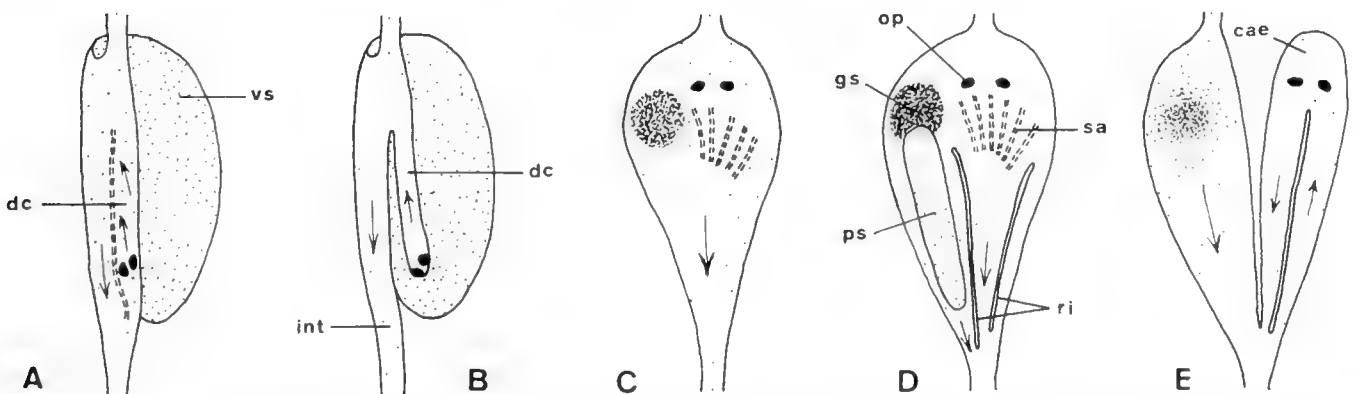


FIG. 7. Schematic diagrams of the main features of the gastric region to compare the basic configuration in A, Placophora in general; B, Placophora-Lepidopleuridae; C, Scaphopoda; D, Bivalvia and Gastropoda; E, Siphonopoda (cephalopods). Arrows indicate movements of contents (save for absorption); cae = caecum, dc = "dorsal channel" and "ductus choledochus," gs = gastric shield, int = intestine, op = openings of the midgut glands, ps = protostyle, ri = ridge (typhlosome), sa = sorting area, vs = ventral sac of stomach.

join the (now equally ventral-positioned) dorsal ciliated band; it is surrounded by inner circular and outer longitudinal muscle fibers. The bipartite intestinal valve is marked by ciliated epithelium underlain by an anterior as well as posterior constrictor muscle, thus functioning as site for the formation of the faecal pellets. The following posterior intestine underlain by weak musculature shows ciliated and glandular cells secreting non-mucous droplets to coat the faecal pellets; they are thus possibly responsible for the elaboration of the peritrophic membrane evidenced in at least some species (cf. Peters, 1968). The longitudinally-ridged epithelium of the rectum shows uniform, densely ciliated cells. The anus is surrounded by a distinct sphincter muscle.

Diets: The majority of Placophora are grazing microherbivores, scraping off incrusting algae, other minute organisms and pieces of larger weeds; hence also nonorganic material, such as sand grains or sponge spicules, may accidentally be taken up with the food.

Some exceptions to the predominant form of feeding are known; there is even carnivory. This has been evidenced especially in the Mopaliidae, within which *Mopalia* grazes on sessile or sedentary organisms such as sponges, Cnidaria, Bryozoa, or even polychaetes and bivalves. *Placiphorella* in the same family has specialized predation by trapping and ingesting free-moving organisms. The anterior mantle region is extended and enlarged to form a flap with which the prey is trapped when stimulating the flap. In addition, a tentacled mantle lobe in front of the head disc functions as the posterior limitation of the trap cavity; when prey is captured (small crustaceans, polychaetes, etc.), the mantle-lobe is raised and the flap curled inward which brings the prey nearer to the mouth region to be seized (cf. McLean, 1962). Probably some other species have also attained a special diet such as *Hanleya hanleyi* (Lepidopleuridae), abyssal specimens of which feed on sponges (cf. Plate, 1899: 74).

Feeding and Digestion: The only detailed information comes from Fretter (1937: 151 f.) who gives a comparative account of the condition in *Lepidochitona cinerea* (L.) and *Acanthochitona fascicularis* (L.) or *A. communis* (Risso). Before feeding starts, the subradular organ of the animal firmly pressed to the bottom is protruded through the mouth to test the substratum for food; in case of a positive result, the sensory organ is withdrawn

and the radula is projected to become fully exposed and pressed upon the substratum. Since the teeth are directed backwards, the rasping effect is on the return pull of the radula, drawing the food particles into the buccal cavity. That subsequent testing and rasping action is repeated with every bite. The rasped particles are pressed dorsally by the retracting radula, mixed with the mucus of the buccal glands and lubricated by the secretion of the so-called salivary glands. Transferred to the ciliated roof of the foregut, the food string is conveyed along the esophagus by ciliary currents and mixed up with the amylolytic enzyme from the esophageal glands. Entering the stomach, the food string is directed by the ciliary bands into the ventral sac, into which likewise the proteolytic secretion of the digestive glands is transported by the opposite beat of the cilia on the posterior bands of the stomach (via the "dorsal channel"; Fig. 1A). Thus the food string and the enzymes are mixed and disintegrated in the ventral sac by its muscular action; there is no rotation of a food-mucus column.

The ventral sac and the anterior intestine is the predominant site of digestion which is purely extracellular (except for some phagocytosis by amoebocytes). Due to the lack of cellulase, certain quantities of unbroken and hence unattacked algal cells remain undigested. The products dissolved by digestion and undigested food-mucus material is forced by muscular activity from the ventral sac into the intestine, where it is rotated by ciliary action and dragged backwards. Owing to the musculature of the anteriormost intestine and the intestinal valve, the mucus-food material is squeezed in between both regions, so that the dissolved products are separated and pressed anteriorly (!) into the ducts of the midgut glands; there absorption takes place by the digestive cells. The intestinal valve itself fragments the undigested material to faecal pellets which in the posterior intestine are more compacted and provided with a peritrophic membrane.

4. Galeroconcha-Tryblidiida (Monoplacophora)

The Tryblidiida are shell-bearing Mollusca 1.5 mm to 37 mm long, the mantle with shell of which covers the whole body; the mantle cavity extends peripodally and houses 5–6 pairs of modified ctenidia; the ventrally-

innervated foot (see Adenopoda) is flat and there is a distinct head with tentacle formations. The excretory organs (emunctoria), gonads, and heart-auricles are pluralized. The alimentary tract is provided with extensive, paired esophageal and midgut glands, and the narrowed intestine is coiled; the radula has 11 teeth per transverse row. The sexes are separate, and fertilization is external. The Tryblidiida are marine, bottom-dwelling deposit-feeders including 7–11 Recent species; they constitute the grade of a mere order of the class Galeroconcha with predominantly extinct members, also including the order Bellerophontida (or Belleromorpha) accepted to be likewise untorted (cf. Salvini-Plawen, 1980).

Digestive system: Available information on the anatomy, including the digestive system of the group is restricted to *Neopilina galathea* (cf. Lemche & Wingstrand, 1959) supplemented by some notes on other representatives. The mouth opening with its dorsal and ventral lip is bordered by flapped tentacles and leads into a cuticularized buccal cavity, the dorsocaudal portion of which is differentiated into a subradular pouch with a naked, glandular epithelium and the distally elaborated subradular sense organ. The adjacent pharyngeal foregut produces a dorso-frontal, cuticular plate or single jaw, a frontal diverticulum with epithelial glands, as well as the caudally-extending radula apparatus.

Resting upon a supporting apparatus similar to that of the Placophora by exhibiting a strong transverse muscle bar and a pair of rod-like cartilages, the radula itself inserts on the ribbon which is proximally underlain with the pharyngeal subradular membrane. Produced in a slightly coiled sheath, the radula consists of 11 teeth in each transverse row (cf. McLean, 1979). Except in *N. (Vema) hyalina*, the three median teeth are fairly slender, rod-like structures, while the second, third, and fifth lateral teeth are broad hooks with a blunt free end (as are also the first ones in *V. hyalina*). The fourth lateral (or first marginal) teeth are more delicate structures having a distal, aborally curved comb or brush of about 30–45 slender, fringe-like denticles (for details cf. McLean, 1979).

The transition from the pharyngeal foregut to the ciliated esophagus is characterized by a pair of lateral diverticula extending as flat sacs beneath the dorsal body wall; they include three pair of pouches as well as the so-called "dorsal coeloms" which, however,

in *N. (Vema) ewingi* are shown to be direct continuations of those diverticula (Lemche & Wingstrand, 1959: 56 footnote, and 1960: 1820). These extensive sacs are homogeneously lined with secretory epithelium, and due to their identical configuration in Placophora (cf. Fretter, 1937: fig. 1), they may be homologized with the esophageal pouches as well as esophageal or sugar glands in these organisms (Lemche & Wingstrand, 1960: 1798 and 1820; Salvini-Plawen, 1972c: 279 f). The roughly triangular stomach receives the outlets of the extensively ramified, paired digestive glands through a slit-like opening at each side. The intestine, which is overlain by a blind pocket, starts at the mid-posterior. In the pocket a true crystalline style seems to be produced, which possesses a concentric structure and is directed towards the esophageal opening; however, no formation of a gastric shield is said to exist. The midgut or digestive glands are homogeneously lined with a high epithelium, the cells of which contain several large peripheral granules and often also more basal, smaller granula. These cells would therefore correspond to the secretive-absorptive, digestive cells of other Conchifera (cf. Owen, 1966b: 80). The long, ciliated intestine is coiled to form a flattened cone (Lemche & Wingstrand, 1959; Menzies & Layton, 1962: 406; Rokop, 1972; Cesari & Guidastri, 1976: 235; McLean, 1979); in *N. galathea* it consists of six loops arranged counter-clockwise. The short, likewise ciliated rectum opens middorsally on a low papilla into the posterior mantle cavity.

Diets: Information on the diets of *Neopilina* comes only from analysis of gut contents. In *N. galathea* it included "a high proportion of radiolarians, scattered centric diatoms, etc. mixed up with much undefined detritus matter" (Lemche & Wingstrand, 1959: 63), and "a faecal pellet removed from the hindgut of a specimen of *Neopilina (Vema) ewingi* showed the presence of diatom frustules, a radiolarian skeleton, pelagic foraminiferal tests and innumerable bacteria-size particles as well as sponge spicules" (Menzies et al., 1959: 179); one *V. hyalina* also contained "diatom frustules and sponge spicules in the gut" (McLean, 1979: 13), and a South Atlantic specimen contained the test of a foraminifer shown by transmitted light (probably within the esophageal gland; cf. Rosewater, 1970). Filatova et al. (1974) briefly discuss the food conditions of those representatives which adhere to hard substrates as recorded by

Filatova et al. (1968) in situ from the surface of a large basalt rock, or also by Lowenstam (1978) and McLean (1979). Accordingly, one can accept that the diets in these animals consist of the bacterial film and the layer of organic debris "usually existing on the surface of such hard substratum" (Filatova et al., 1974: 675). All this evidence (cf. also Wolff, 1961) suggests that *Neopilina* in general is a non-selective deposit feeder (cf. also Menzies et al., 1959: 179/180). The probability of deposit-feeding is further supported by the dark-coloured content within the intestine of *N. oligotropha* and another Central-North Pacific specimen (Filatova et al., 1968; Rokop, 1972).

Feeding mechanisms and digestion: No observation is available on food uptake by *Neopilina*. Owing to the analysis of the musculature of the radula apparatus given by Lemche & Wingstrand (1959: 39 f), there is indication "that the radula carries the food inwards by simply moving to and fro, without being protruded through the mouth for real rasping movements" (*loc. cit.*: 46). Hence, the gathering of food is proposed to be realized by the preoral tentacle apparatus (Lemche & Wingstrand, 1959: 24; Wolff, 1961: 135; Cesari & Guidastrì, 1976: 238); the distance of the head from the bottom in living animals (cf. Lowenstam, 1978) supports that suggestion. However, with respect to the proximity of the radula to the mouth opening as well as to the structure of the radula teeth, there may well be an additional brushing and/or shoveling function of the only slightly protruded and displayed radula in gathering deposit material (cf. also Filatova et al., 1974).

The food taken up is transported backwards to the esophageal foregut where it is conveyed farther by the cilia. According to the likewise ciliated stomach, this organ may merely function to mix up the food particles with enzymes of the crystalline style and to sort out the faecal material. The real site of digestion may therefore be the digestive diverticula, the peripheral end of the cells of which often project like a tongue into the lumen (Lemche & Wingstrand, 1959: 30) and may thus indicate phagocytosis. Additionally, the highly lobulated gland configuration also points to intracellular digestion within these organs; there are no allusions as to whether extracellular digestion also takes place (cf. also Owen, 1966b: 65 f).

With regard to the continuous faecal mass within the intestine of *Neopilina galathea*, *N.*

oligotropha, and *V. hyalina* (Lemche & Wingstrand, 1959; Rokop, 1972; McLean, 1979), as well as to the photographed faecal 'pellet' of *V. ewingi* (Menzies et al., 1959: 179), there seems to be no peritrophic membrane.

5. Other Conchifera

As mentioned, the alimentary conditions in Gastropoda, Bivalvia, and Siphonopoda (cephalopods) are in general more intensively investigated and knowledge about them is more broadly distributed, so that a summary recalling the main features (as far as known) will be sufficient.

Gastropoda: As concerns a comparative analysis within the gastropods, especially the conditions in Prosobranchia are of importance; essential studies on them come from Graham (1939, 1949), Fretter & Graham (1962), and Morton (1953, 1955); a most valuable summary is given by Owen (1966a, b).

The anterior alimentary tract is provided with some scattered glands in the oral tube (buccal glands), with a subradular sac to which in Neritopsina (and several Neogastropoda?) ventral foregut glands are associated (cf. Fretter & Graham, 1962: 156 and 165; Starmühlner, 1959; Ponder, 1973), with lateral buccal pouches, with diffuse (zeugobranchs) or paired-distinct dorsal foregut glands (salivary glands), and in most archaeogastropods as well as mesogastropods with glandular esophageal pouches; these esophageal gland(s) in Neogastropoda are differentiated to the unpaired gland of Leiblein and poison gland (Toxoglossa) respectively (cf. Ponder, 1973). There is a distinct dorsal jaw, paired or single (cf. Fretter & Graham, 1962: 169), and some species possess a subradular organ (cf. Hyman, 1967: 247). The primitive radula of Gastropoda is rhipidoglossate; morphogenetic data may suggest, however, a distichous to biserial radula as original for gastropods (cf. Kerth, 1979; also Sirenko & Minichev, 1975), whereas the larval radula in *Patella* is triserial with a three-cusped median tooth (Smith, 1935) and in *Onchidella* the median teeth precede the others (cf. also Raven, 1958: 235).

The features of the stomach of the conservative members of the gastropods (see archaeogastropods) are characterized by a proximal globular region provided with a coiled caecum, with the openings of the

paired midgut glands, with a cuticularized area (gastaric shield) against which the food-mucus column (protostyle) is rotated and mixed with enzymes, and with a ridged, ciliated sorting area; the distal tubular region or style sac contains the major part of the protostyle to become distally fractionated, and the intestinal groove bounded by the two longitudinal ridges or typhlosoles to convey non-absorbed material to the intestine. More advanced microherbivorous Gastropoda (especially if provided with ciliary feeding mechanisms) have differentiated a true crystalline style, a purely hyaline rod with a more liquid core; the style sac then being functionally no more continuous with the intestine but solely by way of the intestinal groove. Digestion is in part extracellular (stomach) and partly intracellular (midgut glands; amoebocytes). Constant herbivorous members show predominantly intracellular digestion, whereas in other prosobranchs extracellular digestion appears to predominate (cf. Owen, 1966b); investigated Fissurellidae obviously perform solely extracellular digestion (cf. Owen, 1958).

Macrofeeding, carnivorous or sucking gastropods have generally abandoned the style sac stomach (as have the algae-scraping Patellida; cf. Fretter & Graham, 1962: 225 f) and replaced it by mechanically acting organs (muscular and cuticular equipments: gizzards), by histolytic secretions, or simply by a thorough radular trituration of the food (see Heteropoda, Ptenoglossa, Neogastropoda, etc.). At least in some gastropods the existence of peritrophic membranes has been evidenced (cf. Peters, 1968).

Bivalvia: With respect to the evolutionary differentiation found in Recent bivalves, four main developmental levels correlated with feeding conditions can be discerned: Ctenidiobranchia (Nuculida), Palaeobranchia (Solemyida), Autobranchia (Lamellibranchia s. str.), and Septibranchia (Poromyida; cf. Salvini-Plawen 1980, 1981). As concerns the alimentary tract and its special function, Owen (1955, 1956), Yonge (1928, 1939), Purchon (1956, 1957, 1958), Reid (1965) and Judd (1979) have contributed greatly to the present knowledge which is surveyed in detail by Owen (1966a, b).

Since the Bivalvia have lost the buccal mass including the radula, jaw, subradular organ, and pharyngeal glands, the most elaborated region of the gut is seen in the stomach; rudimentary esophageal glands, however, have been reported to exist in Nuculidae

(cf. Pelseneer, 1891: 235–236; Salvini-Plawen, 1972c: 279–280). The stomach exhibits a similar elaboration of its complexity as in gastropods (cf. summary by Nevesskaya et al., 1971). The pyriform style sac organ of protobranchs (Ctenidiobranchia and Paleobranchia) differentiates a food-mucus column or protostyle with its functional and structural attributes as in conservative Prosobranchia, but there is no caecum (see Fig. 7D); in Nuculidae digestion takes place extracellularly (cf. Owen, 1956 and 1966b: 67). The great majority of bivalves, the Autobranchia, on the contrary have a true crystalline style with an at least functional isolation of its distal portion from the adjacent intestine. Among those two principal types of elaboration, there is a certain variety according to the arrangement of the single structures (as presented comparatively by Nevesskaya et al., 1971) which generally also correspond to systematic groupings.

In contrast to Yonge (1928) and Purchon (1963), however, the similarities of the stomach in Septibranchia to that in protobranchs are—at least in Verticordiacea—due to secondary conditions. The investigations of Allen & Turner (1974) and of Bernard (1974) convincingly demonstrate that the Verticordiacea belong to the autobranch Anomalodesmata. On the other hand, the septum as well as the similarly modified configuration of the stomach in Verticordiacea and Septibranchia s. str. (Poromyida) are clear analogies due to a similar carnivorous diet (cf. Salvini-Plawen, 1980: 263).

Scaphopoda: In comparison to the major conchiferan groups, there are only a few investigations of the alimentary condition in Scaphopoda about which general information can be discussed (cf. Morton, 1959; Sahlmann, 1973).

The head is scarcely elaborated (rather than “reduced”), but there is an enlarged, contractile but not retractile conical snout (oral cone, but not “proboscis”) with the central mouth and the two captacula-bearing bulges at its base. The horizontally slit-like mouth opening leads to a short buccal cavity provided with glandular lateral pouches. The subsequent pharynx is characterized by a strong, horseshoe-shaped jaw, by a small subradular organ with ventrolaterally adjacent, subepithelial gland cells, and by the strong radula uniformly provided with five teeth per transverse row. The esophagus with ciliated cells and mucocytes demonstrates lobed en-

largements, the esophageal glands, and continues without distinct limitation in the fairly thin-walled stomach. It is a muscular organ the ventral and lateral epithelium of which is cuticularized to be raised at one point to a small tooth (gastric shield), but is devoid of mucocytes and ciliated cells (cf. Morton, 1959). The midgut glands open proximally by means of two large symmetrical orifices at each side of a small ciliated caecum (*Dentaliida*) or but by one single left opening (*Siphonodentaliida*). A series of ciliated ridges radiates over the proximal end of the stomach (sorting area). The intestine without mucocytes performs a few (generally three) loops and terminates in an enlarged rectum to which a rectal gland is associated; it possibly serves for excretion of lipid-containing metabolic products (Sahlmann, 1973).

The Scaphopoda feed on small organisms, especially Foraminifera, but *Dentalium entale* feeds also on Ostracoda and small molluscs (*Kelliella*, *Rissoa*; Sahlmann, 1973). The food is collected by the terminal, sensitive and even adhesive bulb of the hydrostatically extended captacula (cf. Dinamani, 1964; Gainey, 1972; Sahlmann, 1973). Larger prey is grasped by the tip of the captaculum and directly brought to the mouth by retraction of the tentacle; smaller particles are conveyed by ciliar tracts along the captaculum to the mouth (not confirmed by Sahlmann, 1973), or may also be taken up by the cone-like foot via a dorsally formed groove. Ciliated labial lappets pass the food material to the mouth opening and from there by muscular action of the oral cone into the buccal cavity. The food is seized and thoroughly triturated by the powerful radula (the counterpart of the jaw), so that all organisms are fractured and only the broken remains can subsequently be observed. Peristaltic movements of the foregut aided by the radula transfer the food mass to the esophagus where it is provided with glandular products and passed by ciliary action to the stomach. There the material is provided with the secretion from the midgut glands and mixed up by means of the muscular action of the stomach. Digestion is extracellular and the contractions of the stomach also press the dissolved products into the digestive glands where they are resorbed. Peristaltic movements finally squeeze the in-

digestible remains periodically into the intestine. The faeces are not compacted into separate firm pellets, so that no peritrophic membrane appears to be produced.

Siphonopoda (cephalopods)⁴: With respect to the accurate synopsis by Bidder (1966) and the clearance of the morphogenesis of the alimentary canal by more recent studies (cf. Boletzky, 1967; Fuchs, 1973; Meister & Fioroni, 1976), only some principal conditions need be summarized.

Most living Siphonopoda are active macrophagous feeders, taking even carrion (*Nautilus*), thus being predatory or scavengers. Some lesser known members, such as the Cirromorpha, collect small, planktonic food and may be regarded as microvorous (cf. also the loss of the radula). The prominent buccal apparatus includes the characteristic jaws (mandibles), the radula organ, and one (*Nautilus*) or three to four sets of foregut glands. The radula itself bears 13 teeth or plates per transverse row in *Nautilus*, and nine or seven elements in the Coleoidea; during radulogenesis in *Loligo* and *Ozaena* (= *Eledone*) the median teeth precede the lateral ones (cf. Fuchs, 1973). The ventrolateral glandular lobes in *Nautilus* may correspond to the paired anterior foregut glands of others which open above the radula in the lower portion of the dorsal buccal cavity; the posterior foregut glands (poison glands) secrete to a median duct which opens on a large papilla below the subradular pouch, and the sublingual as well as also dorsal buccal glands (if present; cf. Fuchs, 1973) constitute median masses of the ventral and dorsal portion respectively of the central buccal mass. In *Nautilus* a subradular organ is present.

The posterior esophagus, in *Nautilus* and Octobranchia enlarged to form a crop, is of entodermal origin as is all the subsequent alimentary tract subdivided into stomach, spirally coiled caecum with initially paired midgut gland, intestine and ink sac. Except in *Nautilus*, the fused midgut glands are subdivided into two portions referred to as digestive gland ("liver"; distal section) and digestive appendages ("pancreas"; proximal section) (cf. Bidder, 1976). There are two grooves separated by a so-called columellar ridge which convey from the midgut gland opening through the caecum, Esophagus, crop, and

⁴Since the more recent re-establishment of earlier findings demonstrated that the arms are in fact cerebrally-innervated organs and hence head-tentacles (rather than derivatives of the foot), the erroneous term "Cephalopoda" should be suppressed in favour of Siphonopoda Lankester, 1877 (cf. Salvini-Plawen, 1980a: 265, 1980b).

stomach have a cuticular lining, the caecum and the intestine are at least partially ciliated. Movement of the food along the alimentary canal is performed by muscular action (Bidder, 1966: 111). Digestion by enzymes coming from the digestive gland(s) appears to be completely extracellular and is carried out in the gastric as well as caecal section. Absorption of digested food products occurs in the digestive gland ("liver") and caecum (*Nautilus*, *Sepia*, *Octopus*), but in *Loligo* only the caecum (and part of the intestine) serves for absorption.

B) EVOLUTIONARY PATHWAYS

Although there are still gaps in our knowledge of the detailed alimentary conditions, the configuration as well as principal function of this organ system can be compared. In contrast to most previous considerations, the present study also includes for the first time equivalent data on the lower molluscs and can thus more adequately enter into a discussion from the phylogenetic point of view.

1. Comparative analysis

In an earlier study (Salvini-Plawen, 1972c) the organization of the molluscan groups has already been compared with special reference to the Caudofoveata and Solenogastres in the attempt to trace the homologous derivatives of the different organ systems including the alimentary tract. Greater knowledge now permits me to give more precise information and to contribute more essentially to the estimation of conservative and advanced characters.

Beginning with the radula, there is no doubt about the principal homology of the organ throughout the phylum. Except for the Solenogastres (and Bivalves), all other groups also demonstrate a radular membrane or ribbon upon which the teeth are inserted during radulogenesis; in Caudofoveata, Placophora, *Neopilina*, Prosobranchia, and Coleoida the ribbon is formed by the lower/anterior odontoblasts, and the teeth themselves by the terminal ones (cf. also Raven, 1958: 233). The roof epithelium of the radula sheath also contributes in general as concerns special hardening processes. The condition in Solenogastres—solely possessing a basal cuticle continuous with the pharyngeal

cuticle, as is the elastic subradular membrane in other molluscs (cf. Hyman, 1967: 236; Scheltema, 1978: fig. 2)—at the first view may either express a more conservative, or rather a specialized state; the poorly elaborated radula support in many species suggests a primitive condition. On the other hand, it must be pointed to the developmental pattern of radulae in Solenogastres and Placophora (compare Figs. 5 and 6) which exactly coincide in their originally monoserial configuration, independent of the later radiative specialization (esp. in Solenogastres, cf. Figs. 4 and 5). As is argued by Sirenko & Minichev (1975: 432), the polyserial radula of the Conchifera may morphogenetically be subsequent to the actual (advanced) placophoran condition—as appears indeed supported by the radulogenesis in Pulmonata (cf. Kerth, 1979); the preceding formation of the central teeth in Coleoida (*Loligo*, *Ozaena*) and Gymnomorpha (*Onchidella*) may reflect an advanced condition.

The formation of a single or divided jaw (or mandible) despite its different elaboration respective to the groups doubtlessly is homologous throughout; it constitutes a principal character of the level of Conchifera.

Immediately associated with the radula to house its ventrally-bent section, a subradular pouch or sac may be differentiated. This is not only likewise the site for the subradular sense organ in Placophora and more conservative Conchifera, but is also correlated to glandular organs. This can be stated in Placophora, *Neopilina*, Gastropoda-Neritopsina, Scaphopoda (rudimentary), and perhaps even in Siphonopoda-Coleoida (posterior foregut glands); the ventral foregut glands in Solenogastres as well as the ventral glandular follicles in Caudofoveata (opening with a papilla) correspond exactly to such (at least distally) paired glandular formations ventral to the radula. Secondly, also the dorsal foregut glands in Caudofoveata, Solenogastres, Placophora, and Tryblidiida (frontal gland) can be compared. With regard to the lack of dorsal glands in Neritopsina and to their diffuse arrangement in many other Archaeogastropoda, however, doubts must be expressed about the homology of the gastropod dorsal glands (salivary glands) with those of the Aculifera; rather they constitute new differentiation within the gastropod level.

There is some difficulty as concerns the homology of the esophagus and its derivatives. There is essential identity of the whole

configuration of esophageal pouches and glands in *Neopilina* (pouched "pharyngeal diverticula" including the "dorsal coeloms") and in Placophora that there can be no serious doubt about their mutual correspondence; in Placophora, however, the esophagus clearly originates from the entoderm (Hammarsten & Runnström, 1925: 273, which in this respect fully coincides also with Kowalevsky's figures, 1883). On the other hand, these esophageal elaborations far-reachingly coincide with the glandular esophageal pouches (archaeogastropods, mesogastropods) and the unpaired esophageal gland (neogastropods) in Prosobranchia being, however, of ectodermal origin (cf. Raven, 1958: 157 and 229/230); there is no information about the derivation of the esophageal pouches/glands in Scaphopoda. As pointed out elsewhere (Salvini-Plawen & Splechna, 1979), homology does not forcibly depend on the germ layers (identical origin), since substitutions and shifts of materials may occur without cancelling the original differentiation; thus homology is not always defined by the formative material, but rather due to identical hereditary information. With this respect, we may perhaps also homologize all the post-pharyngeal/pre-gastric gut sections in Siphonopoda (cephalopods) with the esophagus (being configured as such anyway) and the entodermal crop as a modified esophageal pouch (entodermal in Placophora, ectodermal in Prosobranchia).

The gastric region including the stomach and the midgut glands needs a more detailed discussion: (a) The comparability of the gastric area is especially high in Gastropoda and Bivalvia (cf. Graham, 1949), since it coincidentally includes a proximal globular region with the gastric shield, the orifices of the midgut glands, and the sorting area, as well as a tubular region including two typhlosoles which limit the intestinal groove, and the style sac with the protostyle (Fig. 7D). There is no agreement, however, whether the spiral caecum in archaeogastropods (and vestigial in scaphopods?) is a primitive feature (cf. Graham, 1949); it might well be differentiated in connection with the uptake/digestion of more selected algal food. Further gastric elaboration, most obvious by the differentiation of a true crystalline style, must clearly be seen as convergence in gastropods and bivalves. (b) Moreover, the characters in the stomach of Scaphopoda (cf. Morton, 1959) permit derivation of the conditions from an

outlined organ common to Gastropoda and Bivalvia (Figs. 7C and D), but which abandons the protostyle again; the small gastric diverticulum may with doubt correspond to the spiral caecum in archaeogastropods, or rather constitute a roughly analogous formation. (c) Reducing the complicated conditions in Siphonopoda (cephalopods) to the most simplified scheme for equivalent comparison, there is fair probability that it likewise derived from a style-sac stomach (Fig. 7E). The caecum would then represent the distally elongated and separated section of the intestinal groove including the (major?) typhlosole (columellar ridge; cf. Graham, 1949) as well as the orifices of the midgut glands; on the other hand, the cuticularized stomach would be the section of the style sac including the relic of the gastric shield. (d) In addition, the Placophora demonstrate some allusions to a similar principal configuration (cf. Graham, 1949) including the two ridges of the anterior-most intestine with the "dorsal channel"/"gutter" between as typhlosoles with intestinal groove, and with the cuticularized sac as relic of the gastric shield area; to this interpretation, however, we cannot agree. The basic configuration of the placophoran stomach is distinctly different (Fig. 7A), since the outlets of the midgut glands open into the terminal section of the stomach proper ("dorsal channel"/"gutter"); moreover, both the ridges bordering the "dorsal channel"/"gutter" appear to be nothing but the separations for the two one-way systems (Fig. 7A, arrows), viz. the digested food material moving posteriorly towards the intestine, and the digestive enzymes from the midgut glands anteriorly to the anterior stomach (and ventral sac) as well as the dissolved products from the anterior intestine forward to the gland orifices (cf. Fretter, 1937). Also, there is no food-mucus column rotating against a cuticularized area, and the ventral sac does not correspond in its position to a function as gastric shield (even when cuticularized) relative to the style sac. Thus, the ventral sac simply appears to represent an enlargement for storage and digestion in more advanced Placophora, comparable to the crop in many pulmonates and opisthobranchs (cf. Owen, 1966b: 55). Such different configuration when compared to Gastropoda/Bivalvia is underlined by the more specialized condition in Lepidopleuridae, where the "dorsal channel" is in fact separated to form a "ductus choledochus" (Fig. 7B). (e) As far as knowledge of the gastric condition in Tryblidi-

ida permits evaluation of comparative analysis (cf. Lemche & Wingstrand, 1959), there is an independently-formed style-sac stomach in *Neopilina*, dissimilar to other molluscan configuration. The dorsally separated true crystalline style, the scarcely differentiated, ciliated stomach with lateral openings of the midgut glands, as well as the already stated lack of cuticularization (gastric shield) are different characters to those in Placophora as well as higher Conchifera. (f) Whereas all groups discussed above (Conchifera and Placophora) principally coincide in their basic midgut organization by the synorganized differentiation of a stomach, a pair of lateral midgut glands, an intestine, and even also of esophageal glands, the organization in Caudofoveata appears to be quite apart. There is an extensive, unpaired sac which—due to the condition in *Psilodens* and *Metachaetoderma*—can be stated as a longitudinal (!) separation of a once homogeneous organ; secondly, there is a developmental series of midgut elaboration in recent levels of organizations which functionally parallels the evolutionary differentiation of a stomach with a protostyle. (g) Finally, the midgut system of Solenogastres stands totally isolated among the molluscs and coincides at most with that of Nemertini or several Turbellaria.

The straight intestine in Caudofoveata is the minor section separated off from the once homogeneously voluminous midgut and thus represents an analogous formation to the looped organ in Placophora and Conchifera, these being homologous throughout and having differentiated by a narrowing and elongation of the whole posterior midgut (adaptation to microherbivory). There is no intestine in Solenogastres. Faecal pellets surrounded by a peritrophic membrane are known in Caudofoveata, Placophora, and Gastropoda; they are definitely absent in Solenogastres and very probably absent in Tryblidiida.

2. Adaptive conditions

The original differentiations of all those alimentary configurations outlined are a reflection of feeding conditions. In consideration of correlations between diets and organization of the alimentary tract, there is clear mutual dependence of the style-sac type of stomach from microvory (cf. Yonge, 1930); moreover, there is even distinct co-existence of micro-

vory with the elaboration of midgut glands. These relations hold good for the Caudofoveata, the Placophora, the Tryblidiida, the Gastropoda and the Bivalvia. Within the Scaphopoda, the basic configuration of the stomach—by heredity being without doubt ancestrally similar to that of Gastropoda-Bivalvia (see Fig. 7)—accordingly has altered secondarily and abandoned the differentiation of a (proto-)style; such a condition can be principally confirmed likewise in Siphonopoda. Consequently, we cannot attribute to the Scaphopoda a factual “(omni-)microvorous” diet rather than “(micro-)carnivorous” feeding, a statement which fully coincides with the findings by Sahlmann (1973) and which might explain the total lack of the style (cf. also Yonge, 1930). In Placophora, the actual lack of a (proto-)style, however, can be accepted as being a primary condition due to their evolutionary *status nascendi* of respective adaptations; in addition, the special algae-scraping diet of tidal forms obviously does not adaptively imply the elaboration of a (proto-)style (compare also Patellida, p. 391).

In consideration of the special condition in Solenogastres, they are clearly predatory-carnivorous animals. With respect to the likewise carnivorous Siphonopoda (cephalopods), Prosobranchia-Heteropoda, -Neogastropoda, etc., or even Bivalvia-Septibranchia, that diet does not involve or cause an involution or loss of the midgut glands. Moreover, the progressive adaptation of the midgut microvory in Caudofoveata distinctly points to an originally homogeneous organ before the longitudinal separation of an intestine and a midgut sac occurred. We may thus positively accept that the homogeneous, straight midgut of Solenogastres, merely provided with lateral expansions due to the serial arrangement of the dorsoventral muscle bundles, corresponds to an original configuration conservatively retained because of carnivory. Such an estimation parallels the primitive state of the radula (basal cuticle, support) likewise to be judged as conservative; it also coincides with the presumed original digestion. It was thought for a long time that primitive digestion in Mollusca was intracellular (cf. Graham, 1955; Owen, 1966b: 65); several more conservative groups however, show predominant or exclusive extracellular digestion (Caudofoveata, Placophora, Prosobranchia-Fissurellidae, Bivalvia-Nuculidae). This led to the acceptance of an originally intraplus extra-cellular digestion—as in Soleno-

gastres—with subsequent trends either leading to an increase of intracellular digestion (phagocytosis) or to a predominance of extracellular digestion (cf. Owen, 1966b: 65 f).

In transferring these results into a phylogenetic scheme, the evolutionary differentiation of the radula as such, as well as the basically gliding-creeping habits of the archimolluscan organization (cf. Salvini-Plawen, 1972c, 1980, 1981; Trueman, 1975, 1976) distinctly point to a primitively microvorous manner of living of the ancestral molluscs (cf. also Graham, 1955) which gathered their food by means of an eversible brushing or scraping pharyngeal cuticle (radula rudiment). On the other hand, there is clear evidence that both the recent microvorously-feeding lines, the Caudofoveata and the Placophora-Conchifera, adapted independently restricted midgut sacs for respective secretion of digestive enzymes. In connection with their organization this brings us to the qualified conclusion that diet must be attributed a principal key character in the basic molluscan radiation (cf. Salvini-Plawen, 1972c, 1980, 1981): (1) some ancestral molluscs still provided with an aculiferan mantle cover (chitinous cuticle, aragonitic scales) adopted a burrowing mode of life in an attempt to exploit sediments rich in food without much change of their diets. Such adaptation involved changes towards a worm-like shape—with the differentiation of a hydrostatic muscular tube for burrowing, the reduction of the ventrally-innervated gliding surface and mere differentiation of the cerebrally-innervated section to become the pedal shield, as well as further anatomical consequences (cf. Salvini-Plawen, 1972c, 1980, 1981); they thus represent a separate evolutionary branch of Scutopoda, viz. the infaunal-microvorous Caudofoveata. Their recent organization can hence be attributed to a great extent to the positive selection pressures upon the preference for a new habitat with better food exploitation. (2) Other populations continued to live epibenthically and separated a rudimentary head for better food uptake (Adenopoda; cf. Salvini-Plawen, 1972c, 1980, 1981). The exploitation of microorganisms in the littoral zone subsequently included not only the formation of more protective shell plates (arranged serially to enable rolling-up), but also the selection of a stomach with paired midgut gland and a slender intestine, of esophageal glands, as well as of a subradular organ. Such adaptive organization to micro(herbi)vorous feeding gave rise

to the level of Placophora. (3) Early placophoran organization presumably invaded sublittoral bottoms to enlarge the range of food, which released the animals from rolling-up protectively and enabled formation of a homogenous shell: Conchifera (cf. Salvini-Plawen, 1972c: 263, 1981). Nonselective deposit-feeding by means of the brushing radula was supplemented by tentacle formations (characteristic for all Conchifera, cf. Salvini-Plawen, 1980: 268, 1981) and the differentiation of a jaw rudiment. Such feeding might also have been one of the decisive properties for the survival of the Tryblidiida. The organizationally more successful early gastropods and primitive bivalves also supplanted the ancient tryblidiids ecologically, the latter having been forced to withdraw into biotopes where they could stand the competition. Nonselective deposit-feeding as performed by *Neopilina* in this respect appears to be a favourable prerequisite, since it is that food-source in most benthic biotopes—including otherwise obviously oligotrophic areas (cf. Rokop, 1972)—which is found in sufficient abundance for the tryblidiids and other deposit- and filter-feeding organisms to live on (cf. Menzies et al., 1959; Filatova et al., 1968, 1974). (4) Nonselective deposit-feeding also performed in ancestral Gastropoda (radula; cf. Owen, 1966a: 20) and in primitive Bivalvia (labial flaps; cf. Salvini-Plawen, 1980a: 262, 1980b) favoured a presumably monophyletic differentiation of a food-mucus column or protostyle in Conchifera, subsequently adaptively elaborated along three different lines to become a crystalline style (Tryblidiida, Gastropoda and Bivalvia); there is no confirmation, however, as concerns a possible (secondary) modification of other gastric characters in recent *Neopilina*. (5) Micro-carnivorous, macrovorous, and other predatory diets as assumed in Scaphopoda, Siphonopoda (cephalopods), Bivalvia-Septibranchia, and several advanced groups in Gastropoda (Heteropoda, Neogastropoda, Gymnosomata, etc.) involved independent abandonment of the congenital style-sac type of stomach to become respectively modified within the given frame of basic conchiferan midgut configuration. (6) The food relations of Solenogastres to Cnidaria in general indicate that the whole group adapted in its origin to the cnidarian food source, supported by the fact that other diets are only recognizable within the higher members (Cavibelonia). Originating in still aculiferan Adenopoda (cf. Salvini-Plawen,

1972c, 1980, 1981), that evolutionary line presumably adapted at an early stage to secondary hard bottoms rich in Cnidaria (Cnidaria-'meadows,' coral reefs), thus developing a wriggling-winding locomotion assuming a laterally narrowed shape (with its respective anatomical consequences; cf. Salvini-Plawen, 1972c, 1980, 1981). Their straight midgut devoid of a differentiation into stomach, digestive glands, and intestine, as well as their primitive character of a radular basal cuticle and radula support (or also the lack of a subradular organ) are therefore due to the early evolutionary deviation from microphagy (and respective adaptations) towards Cnidaria-vory. Within the molluscs, the Solenogastres have thus obviously retained the most conservative general configuration of the digestive system.

SUMMARY

A comparative analysis of the molluscan alimentary condition reveals that 1. The Caudofoveata are microvorous animals which differentiated a longitudinal separation of the more posterior midgut into a large single midgut sac and a slender, straight intestine; they perform extracellular digestion. 2. The midgut in Caudofoveata demonstrates a gradual adaptation to microfeeding conditions resulting in the presence of a food-mucus column (protostyle) and a primitive gastric shield in advanced members (Chaetodermatidae). 3. The Solenogastres are Cnidaria-vorous predators with a straight, merely pouched midgut performing intra- and extracellular digestion, and they are devoid of a true radular membrane (ribbon). 4. The Tryblidiida are nonselective deposit feeders by means of a brushing radula and assisting tentacle formations as well as a distinct jaw formation. 5. The Scaphopoda are (micro-)carnivorous animals rather than being (omni-)microvorous. 6. The basic elaboration of the midgut developed independently twice, viz. in Caudofoveata (midgut sac, intestine) and in Placophora-Conchifera (esophageal glands, stomach, midgut glands, intestine). 7. The gastric elaboration in Placophora is a differentiation *sui generis*. 8. The gastric configuration in Scaphopoda and Siphonopoda (cephalopods) can be deduced from the basically similar condition in Gastropoda and Bivalvia. 9. The general configuration of the digestive system in Solenogastres (see item 3 above) reflects the most con-

servative condition within the molluscs. 10. The digestive system largely reflects basic behavioural selection pressures (with subsequent morphological adaptations) in evolutionary pathways of molluscan radiation.

REFERENCES CITED

- ALLEN, J. & TURNER, J., 1974, On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. *Philosophical Transactions of the Royal Society of London*, ser. B, 268: 401-536.
- BABA, K., 1940, The mechanisms of absorption and excretion in a solenogastre, *Epimenia verucosa* (Nierstr.). *Journal of the Department of Agriculture, Kyushu Imperial University*, 6(4): 119-166.
- BERNARD, F., 1974, Septibranchs of the Eastern Pacific (Bivalvia Anomalodesmata). *Allan Hancock Monographs in Marine Biology*, 8: 1-279.
- BIDDER, A., 1966, Feeding and digestion in Cephalopods. In WILBUR, K. & YONGE, C. M., *Physiology of Mollusca*, Academic Press, New York, 2: 97-124.
- BIDDER, A., 1976, New names for old: the cephalopod "mid-gut gland." *Journal of Zoology*, 180: 441-443.
- BOCK, W. & WAHLERT, G. v., 1965, Adaptation and the form-function complex. *Evolution*, 19: 269-299.
- BOLETZKY, S. v., 1967, Die embryonale Ausgestaltung der frühen Mitteldarmanlage von *Octopus vulgaris* Lam. *Revue Suisse de Zoologie*, 74: 555-562.
- CESARI, P. & GUIDASTRI, R., 1976, Contributo alla conoscenza dei Monoplacofori recenti. *Conchiglie*, 12: 223-250.
- DEGENS, E., JOHANNESSEN, B. & MEYER, R., 1967, Mineralization processes in molluscs and their paleontological significance. *Die Naturwissenschaften*, 54(24): 638-640.
- DINAMANI, P., 1964, Feeding in *Dentalium conispicum*. *Proceedings of the Malacological Society of London*, 36: 1-5.
- FILATOVA, Z., SOKOLOVA, M. & LEVENSTEIN, R., 1968, Mollusc of the Cambro-Devonian class Monoplacophora found in the Northern Pacific. *Nature*, 220(5172): 1114-1115.
- FILATOVA, Z., VINOGRADOVA, N. & MOSKALEV, L., 1974, New finding of the ancient primitive mollusc *Neopilina* in the Atlantic part of the Antarctic. *Nature*, 249(5458): 675.
- FISCHER, F., 1978, Photoreceptor cells in chiton aesthetes (Mollusca, Polyplacophora, Chitonidae). *Spixiana*, 1: 209-213.
- FISCHER, F., MAILE, W. & RENNER, M., 1980, Die Mantelpapillen und Stacheln von *Acanthochiton fascicularis* L. (Mollusca, Polyplacophora). *Zoomorphologie*, 94: 121-131.

- FRETTER, V., 1937, The structure and function of the alimentary canal of some species of Polyplacophora (Mollusca). *Transactions of the Royal Society of Edinburgh*, 59, part I (4): 119–164.
- FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs*. Ray Society, London, 144: xvi & 755 p.
- FUCHS, E., 1973, Organo- und Histogenese des Darmsystems, embryonale Blutbildung und Dotterabbau bei *Eledone cirrosa* Lam. (Cephalopoda, Octopoda). *Zoologisches Jahrbuch, Abt. Anatomie*, 91: 31–92.
- GAINEY, L., 1972, The use of the foot and the captacula in the feeding of *Dentalium*. *Veliger*, 15: 29–34.
- GRAHAM, A., 1939, On the structure of the alimentary canal of style-bearing prosobranchs. *Proceedings of the Zoological Society of London*, ser. B, 109: 75–112.
- GRAHAM, A., 1949, The molluscan stomach. *Transactions of the Royal Society of Edinburgh*, 61: 737–778.
- GRAHAM, A., 1955, Molluscan diets. *Proceedings of the Malacological Society of London*, 31: 114–159.
- GRAHAM, A., 1973, The anatomical basis of function in the buccal mass of prosobranch and amphineuran molluscs. *Journal of Zoology*, 169: 317–348.
- GREENFIELD, M., 1972, Feeding and gut physiology in *Acanthopleura spinigera* (Mollusca). *Journal of Zoology*, 166: 37–47.
- HAMMARSTEN, O. & RUNNSTRÖM, J., 1925, Zur Embryologie von *Acanthochiton discrepans* Brown. *Zoologisches Jahrbuch, Abt. Anatomie*, 47: 261–318.
- HEATH, H., 1904, The habits of a few Solenogastres. *Zoologischer Anzeiger*, 27: 457–461.
- HEATH, H., 1905, The morphology of a solenogastre. *Zoologisches Jahrbuch, Abt. Anatomie*, 21: 701–734.
- HEATH, H., 1911, Reports on the scientific results of the expedition to the tropical Pacific, XIV: the Solenogastres. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 45: 1–182.
- HEATH, H., 1918, Solenogastres from the Eastern coast of Northern America. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 45: 183–263.
- HEUSCHER, J., 1892, *Proneomenia sluiteri*. *Jenaische Zeitschrift für Naturwissenschaften*, 27: 477–512.
- HOFFMAN, S., 1949, Studien über das Integument der Solenogastren... *Zoologiska Bidrag från Uppsala*, 27: 293–427.
- HOFFMANN, H., 1930, Amphineura und Scaphopoda. BRONN's *Klassen und Ordnungen des Tierreichs*, 3, Abt. 1 (Nachtrag): 1–453.
- HUBRECHT, A., 1881, *Proneomenia sluiteri* gen. et sp. n. *Niederländisches Archiv für Zoologie*, Suppl. 1(9): 1–75.
- HYMAN, L., 1967, Mollusca I. *The Invertebrates*, 6: 1–792. McGraw-Hill.
- IVANOV, D., 1979, On the system of Caudofoveata (Mollusca, Aplacophora). *Abstracts of Communications, sixth meeting on the Investigation of Molluscs, USSR Academy of Sciences, Zoological Institute, LIKHAREV, I. (ed.)*, 8–9 (in Russian).
- JUDD, W., 1979, The secretions and fine structure of bivalve crystalline style sacs. *Ophelia*, 28: 205–233.
- KAISER, P., 1976, *Neomenia herwigii* sp. n., ein bemerkenswerter Vertreter der Solenogastren (Mollusca, Aculifera) aus argentinischen Schelfgewässern. *Mitteilungen des Hamburger zoologischen Museums und Institutes*, 73: 57–62.
- KERTH, K., 1979, Phylogenetische Aspekte der Radulamorphogenese von Gastropoden. *Malacologia*, 19: 103–108.
- KOWALEVSKY, A., 1881, *Neomenia corallophila* i *Coeleplana metschnikowii*. *Nachrichten der kaiserlichen Gesellschaft der Freunde der Naturkunde, Moskau*, 43: 1–5 (in Russian).
- KOWALEVSKY, A., 1883, Embryogénie du *Chiton polii* (Philippi). *Annales du Musée d'Histoire Naturelle de Marseille, Zool.* 1(5): 1–46.
- KOWALEVSKY, A., 1901, Sur le genre *Chaetoderma*. *Archives de Zoologie expérimentale et générale*, sér. 3, 9: 261–283.
- LEMICHE, H. & WINGSTRAND, K., 1959, The anatomy of *Neopilina galathea* Lemche, 1957 (Mollusca, Tryblidiacea). *Galathea Report*, 3: 9–72.
- LEMICHE, H. & WINGSTRAND, K., 1960, Classe des Monoplacophores. GRASSÉ (ed.), *Traité de Zoologie*, 5: 1787–1821.
- LOWENSTAM, H., 1978, Recovery, behaviour and evolutionary implications of live Monoplacophora. *Nature*, 273(5659): 231–232.
- MALUQUER, J., 1917, Notes para l'estudi dels Solenogastres (Molluscos amfineures) de Catalunya. *Treballs de la Institució d'Història Natural (Barcelona)*, 3: 9–53.
- MAYR, E., 1970, Evolution und Verhalten (Evolution and behaviour). *Zoologischer Anzeiger*, Suppl. 34: 322–336.
- MCLEAN, J. H., 1962, Feeding behaviour of the chiton *Placiphorella*. *Proceedings of the Malacological Society of London*, 35: 23–26.
- MCLEAN, J. H., 1979, A new monoplacophoran limpet from the continental shelf off Southern California. *Contributions in Science, Natural History Museum of Los Angeles County*, 307: 1–19.
- MEISTER, G. & FIORONI, P., 1976, Zur Darmentwicklung bei coleoiden Tintenfischen. *Zoologisches Jahrbuch, Abt. Anatomie*, 96: 394–419.
- MENZIES, R., EWING, E., WARZEL, L. & CLARKE, A., 1959, Ecology of the recent Monoplacophora. *Oikos*, 10: 168–182.
- MENZIES, R. & LAYTON, W., 1962, A new species of monoplacophoran mollusc, *Neopilina* (Neo-

- pilina*) *veleronis* from the slope of the Cedros Trench, Mexico. *Annals and Magazine of Natural History*, ser. 13, 5: 401–406.
- MORTON, J. E., 1953, The functions of the gastropod stomach. *Proceedings of the Linnean Society of London*, 164: 240–246.
- MORTON, J. E., 1955, The functional morphology of the British Ellobiidae (Gastropoda, Pulmonata) with special reference to the digestive and reproductive systems. *Philosophical Transactions of the Royal Society*, ser. B, 239: 89–160.
- MORTON, J. E., 1959, The habits and feeding organs of *Dentalium entalis*. *Journal of the Marine Biological Association of the United Kingdom*, 38: 225–238.
- NEVESSKAYA, L., SKARLATO, O., STAROBOGATOV, Ya. & EBERSIN, A., 1971, New ideas on bivalve systematics. *Paleontological Journal*, 5: 3–20.
- NIERSTRASZ, H., 1902, The Solenogastres of the Siboga-Expedition. *Siboga-Expedition, Monograph* 47: 1–46.
- NIERSTRASZ, H. & STORK, H., 1940, Monographie der Solenogastren des Golfes von Neapel. *Zoologica* (Stuttgart), 36(99): 1–92.
- ODHNER, N., 1921, Norwegian Solenogastres. *Bergens Museums Aarbok* 1918–19, *Naturvidenskabelig raekke*, 3: 1–86.
- OWEN, G., 1955, Observations on the stomach and digestive diverticula of the Lamellibranchia. I. The Anisomyaria and Eulamellibranchia. *Quarterly Journal of Microscopical Science*, 96: 517–537.
- OWEN, G., 1956, Observations on the stomach and digestive diverticula of the Lamellibranchia. II. The Nuculidae. *Quarterly Journal of Microscopical Science*, 97: 541–567.
- OWEN, G., 1958, Observations on the stomach and digestive gland of *Scutus breviculus* (Blainville). *Proceedings of the Malacological Society of London*, 33: 103–114.
- OWEN, G., 1966a, Feeding. In WILBUR, K. & YONGE, C. M., *Physiology of Mollusca*, Academic Press, New York, 2: 1–51.
- OWEN, G., 1966b, Digestion. Ibidem, 2: 53–96.
- PELSENEER, P., 1891, Contribution à l'étude des Lamellibranches. *Archives de Biologie*, 11: 147–312.
- PETERS, W., 1968, Vorkommen, Zusammensetzung und Feinstruktur peritrophischer Membranen im Tierreich. *Zeitschrift für Morphologie der Tiere*, 62: 9–57.
- PETERS, W., 1972, Occurrence of chitin in Mollusca. *Comparative Biochemistry and Physiology*, 41B: 541–550.
- PLATE, L., 1897, Die Anatomie und Phylogenie der Chitonen. Teil A. *Zoologisches Jahrbuch*, Suppl. 4: 1–243.
- PLATE, L., 1899, Die Anatomie und Phylogenie der Chitonen. Teil B. *Zoologisches Jahrbuch*, Suppl. 5: 15–216.
- PLATE, L., 1901, Die Anatomie und Phylogenie der Chitonen. Teil C. *Zoologisches Jahrbuch*, Suppl. 5: 281–600.
- PONDER, W., 1973, The origin and evolution of the Neogastropoda. *Malacologia*, 12: 295–338.
- PRUVOT, G., 1891, L'organisation de quelques Néoménien des côtes de France. *Archives de Zoologie expérimentale et générale*, sér. 2, 9: 699–810.
- PRUVOT, G., 1897, Les fonds et la faune de la Manche occidentale (côtes de Bretagne) comparés à ceux du Golfe du Lion. *Archives de Zoologie expérimentale et générale*, sér. 3, 5: 511–660.
- PRUVOT, G., 1899, Sur deux Néoménien nouveaux de la Méditerranée. *Archives de Zoologie expérimentale et générale*, sér. 3, 7: 461–509.
- PURCHON, R., 1956, The stomach in the Protobranchia and Septibranchia (Lamellibranchia). *Proceedings of the Zoological Society of London*, 127: 511–525.
- PURCHON, R., 1957, The stomach in the Filibranchia and Pseudolamellibranchia. *Proceedings of the Zoological Society of London*, 129: 27–60.
- PURCHON, R., 1958, The stomach in the Eulamellibranchia, stomach type IV. *Proceedings of the Zoological Society of London*, 131: 487–525.
- PURCHON, R., 1963, Phylogenetic classification of the Bivalvia, with special reference to the Septibranchia. *Proceedings of the Malacological Society of London*, 35: 71–80.
- RAVEN, Ch., 1958, *The analysis of molluscan development. Morphogenesis*. Pergamon Press, London, 2: 1–311.
- REID, R., 1965, The structure and function of the stomach in bivalve molluscs. *Journal of Zoology*, 147: 156–184.
- ROKOP, F., 1972, A new species of monoplacophoran from the abyssal North Pacific. *Veliger*, 15: 91–95.
- ROSEWATER, J., 1970, Monoplacophora in the South Atlantic Ocean. *Science*, 167: 1485–1486.
- SAHLMANN, B., 1973, *Untersuchungen zur Histologie und Nahrungsbiologie der Scaphopoden*. Dissertation, Mathematische-Naturwissenschaftliche Fakultät der Universität Kiel, Institut für Meereskunde, 107 p.
- SALVINI-PLAWEN, L. v., 1967a, Neue skandinavische Aplacophora (Mollusca, Aculifera). *Sarsia*, 27: 1–63.
- SALVINI-PLAWEN, L. v., 1967b, Über die Beziehungen zwischen den Merkmalen von Standort, Nahrung und Verdauungstrakt bei Solenogastres (Aculifera, Aplacophora). *Zeitschrift für Morphologie und Ökologie der Tiere*, 59: 318–340.
- SALVINI-PLAWEN, L. v., 1968, Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia*, 31: 131–142.
- SALVINI-PLAWEN, L. v., 1969a, Solenogastres

- und Caudofoveata (Mollusca, Aculifera), Organisation und phylogenetische Bedeutung. *Malacologia*, 9: 191–216.
- SALVINI-PLAWEN, L. v., 1969b, Faunistische Untersuchungen am Roten Meer im Winter 1961/62: V. Caudofoveata und Solenogastres (Mollusca, Aculifera). *Zoologisches Jahrbuch, Abt. Systematik*, 96: 52–68.
- SALVINI-PLAWEN, L. v., 1972a, Revision der monegassischen Solenogastres (Mollusca, Aculifera). *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 10: 215–240.
- SALVINI-PLAWEN, L. v., 1972b, Cnidaria as food-sources for marine Invertebrates. *Cahiers de Biologie marine*, 13: 385–400.
- SALVINI-PLAWEN, L. v., 1972c, Zur Morphologie und Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie*, 184: 205–394.
- SALVINI-PLAWEN, L. v., 1975, Mollusca Caudofoveata. *Marine Invertebrates of Scandinavia*, 4: 1–54.
- SALVINI-PLAWEN, L. v., 1978, Antarktische und subantarktische Solenogastres (eine Monographie: 1898–1974). *Zoologica* (Stuttgart), 44(128): 1–305.
- SALVINI-PLAWEN, L. v., 1980, A reconsideration of systematics in the Mollusca (Phylogeny and higher classification). *Malacologia*, 19: 249–278.
- SALVINI-PLAWEN, L. v., 1981, On the origin and evolution of the Mollusca. *Atti dell'Accademia nazionale dei Lincei*. In press.
- SALVINI-PLAWEN, L. v. & NOPP, H., 1974, Chitin bei Caudofoveata (Mollusca) und die Ableitung ihres Radulaapparates. *Zeitschrift für Morphologie der Tiere*, 77: 77–86.
- SALVINI-PLAWEN, L. v. & SPLECHTNA, H., 1979, Zur Homologie der Keimblätter. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 17: 10–30.
- SCHELTEMA, A., 1972, The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 72: 361–370.
- SCHELTEMA, A., 1978, Position of the class Aplacophora in the phylum Mollusca. *Malacologia*, 17: 99–109.
- SCHWABL, M., 1955, *Rupertomenia fodiens* n.g. n.sp., eine neue Lepidomeniidae von der Südwestküste Schwedens. *Österreichische zoologische Zeitschrift*, 6: 90–146.
- SCHWABL, M., 1963, Solenogaster mollusks from Southern California. *Pacific Science*, 17: 261–281.
- SIRENKO, B. & MINICHEV, Y., 1975, Développement ontogénétique de la radula chez les polyplacophores. *Cahiers de Biologie marine*, 16: 425–433.
- SMITH, F. G. W., 1935, The development of *Patella vulgata*. *Philosophical Transactions of the Royal Society of London*, ser. B, 225: 95–125.
- STARMÜHLNER, F., 1969, Die Gastropoden der madagassischen Binnengewässer. *Malacologia*, 8: 1–434.
- STASEK, Ch., 1972, The molluscan framework. *Chemical Zoology*, 7: 1–44.
- THIELE, J., 1902, Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie*, 72: 249–466.
- THIELE, J., 1906, *Archaeomenia prisca* n.g. n.sp. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition Valdivia 1898/1899*, 9: 317–324.
- TRUEMAN, E., 1975, *The locomotion of soft-bodied animals*. Arnold, London, 200 p.
- TRUEMAN, E., 1976, Locomotion and the origins of Mollusca. *Perspectives in Experimental Biology*, 1 (Zool.): 455–465.
- VAGVOLGYI, J., 1967, On the origin of molluscs, the coelom, and coelomatic segmentation. *Systematic Zoology*, 16: 153–168.
- WIREN, A., 1892, Studien über Solenogastres I. *Konglige Svenska Vetenskaps-Akademien Handlingar*, 25(12): 1–66.
- WOLFF, T., 1961, Animal life from a single abyssal trawling. *Galathea Report*, 5: 129–162.
- YONGE, C. M., 1928, Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Philosophical Transactions of the Royal Society of London*, ser. B, 216: 212–263.
- YONGE, C. M., 1930, The crystalline style of the Mollusca and a carnivorous habit cannot normally co-exist. *Nature*, 125(3151): 444–445.
- YONGE, C. M., 1939, The protobranchiate Mollusca. *Philosophical Transactions of the Royal Society of London*, ser. B, 23: 79–147.

ZUSAMMENFASSUNG

ZUR EVOLUTION DES ERNÄHRUNGSSYSTEMS DER MOLLUSKEN

Luitfried v. Salvini-Plawen

Eine vergleichende Darstellung von Darmtrakt, Nahrung und Verdauung bei Mollusken bringt folgende Ergebnisse: 1. Die Caudofoveata ernähren sich mikrovor und weisen eine Längs-Unterteilung des hinteren Mitteldarmes in einen langen, umfangreichen Mitteldarmsack und in ein gerades Intestinum auf. Die Verdauung erfolgt extrazellulär. 2. Die Mitteldarm-Verhältnisse innerhalb der Caudofoveata zeigen eine zunehmende Anpassung an die Mikrovorie, welche

letztlich zur Ausbildung eines verfestigten Nahrungs-Schleimstranges (Protostyl) und eines Magenschildes führt (Chaetodermatidae). 3. Die Solenogastres sind Cnidaria-vore Räuber mit einem einheitlichen, nur mit serialen Lateralausbuchtungen versehenen Mitteldarm, worin intra- wie extrazelluläre Verdauung erfolgt. Als einzige Molluskengruppe weisen sie keine Radular-Membran auf und ihre Radulapölster sind meist sehr einfach. 4. Die Tryblidiida ernähren sich unselektiv von Bodensatz (Mikroorganismen und Detritus), welchen sie mit Hilfe der kehrenden Radula und der Tentakelbildungen aufnehmen. 5. Auf Grund der Ernährungs- und Mitteldarm-Verhältnisse sind die Scaphopoden nicht als (omni-)mikrovor, sondern als (mikro-)carnivor zu beurteilen. 6. Der Mitteldarm-Ausbau in Caudofoveata (Mitteldarmsack, Intestinum) und in Placophora-Conchifera (Oesophagealdrüsen, Magen, Mitteldarmdrüsen, Intestinum) ist voneinander unabhängig aus einem einheitlichen Organ ohne Abschnittbildungen erfolgt. 7. Der Ausbau des Magens bei Placophora ist als gruppeneigen festzustellen. 8. Die Mitteldarm-Verhältnisse der Scaphopoda wie der Siphonopoda (Cephalopoden) können von einer Ausprägung abgeleitet werden, wie sie prinzipiell bei Gastropoden und Muscheln vorliegt (Fig. 7). 9. Die allgemeinen Verhältnisse des Darmtraktes der Solenogastres (Punkt 3) spiegeln die ursprünglichste Ausprägung innerhalb der Mollusken wider, welche durch einen frühzeitigen Übergang zur räuberischen Lebensweise erhalten blieb. 10. Das Ernährungssystem der Mollusken lässt weitgehend den Selektionsdruck auf grundsätzliche Verhaltensweisen (mit davon abhängigen morphologischen Veränderungen) erkennen, welche wesentlich zur evolutiven Differenzierung in Grossgruppen beigetragen haben.

NOTES ADDED IN PROOF

While the present paper was in press, two studies of interest appeared, viz. "Structure and functional morphology of radular system in *Chaetoderma*" (in Russian) by D. Ivanov (*Zool. Zhurn.*, 1979, 58: 1302–1306) and "Comparative morphology of the radulae and alimentary tracts in the Aplacophora" by A. Scheltema (*Malacologia*, 1981, 20: 361–383). Ivanov's analysis based upon whole mount sections of preserved material appears only restrictively reliable and contrasts to the histological investigations as concerns the musculature and configuration of the radula apparatus (see pp. 373 and 375, and K. Deimel, 1981, Dissertation University Wien: "Die Muskulatur des Radulaapparates bei Caudofoveata").

The study by Scheltema (1981) generally coincides with and corroborates the conditions presented here. There are, however, some discrepancies and/or errors which should be clarified: 1) There is a distinct difference between a radular membrane (ribbon) and the basal cuticle of Solenogastres: the basal cuticle is a direct continuation of the pharyngeal cuticle (as is the subradular membrane of other molluscs possessing a ribbon), and it is hence not independently formed at the bottom or blind end of the radula sheath. There are different grades of elaboration of the basal cuticle (cf. H. Nierstrasz, 1905, in *Zool. Jahrb. Anat.*, 21: 655–701, and 1909, in *Ergebn. Fortschr. Zool.*, 1: 239–306)

which may even totally lack or but be elaborated towards a ribbon-like structure as in *Epimenia verrucosa* (cf. Nierstrasz, 1905: 684; 1909: 267).—2) Also Salvini-Plawen (1972c, 1978) regards the possession of tubular foregut glands (ventral organs type A) as primitive for Solenogastres (error by Scheltema, 1981: table 1); and in contrast to the statement by Scheltema (1981: 362), within the primitive Solenogastres (order Pholidoskepia) the Dondersiidae are regarded as belonging to the conservative level (monoserial radula, foregut glands, mantle scales, development) rather than the Wireniidae (Salvini-Plawen, 1978, 1980).—3) The argumentation by Scheltema (1981: 378) as concerns the (non-)homology of the pedal shield in Caudofoveata fails, since the homology refers to the position, structure, synorganization, and innervation of the pedal shield relative to an overall ventral gliding sole (cf. S. Hoffman, 1949, and the corrected version in Salvini-Plawen, 1972c) with which the scattered/diffuse mucous cells fully correspond (sole glands; arranged to lateral clusters in most Caudofoveata and Solenogastres respectively; cf. Salvini-Plawen 1972c: 225 and 294f, 1978: 16). The cuticle of the pedal shield (main argument by Scheltema, 1981) in any case represents a secondary (!) character and has nothing to do with the advanced homology.

EVOLUTION OF CALCAREOUS HARDPARTS IN PRIMITIVE MOLLUSCS¹

Winfried Haas

*Institut für Paläontologie der Universität Bonn,
Nussallee 8, D-5300 Bonn 1, Germany*

ABSTRACT

Our considerations on the evolution of molluscan calcareous hardparts are primarily based on the placophorans because of their systematic position between the Conchifera and the "Aplacophora" (Solenogastres and Caudofoveata). Shell formation in the Placophora is significantly more primitive than in the Conchifera. Calcium carbonate secretion takes place without the aid of a true periostracum underneath a rather unstable glycoproteinaceous cuticle. A differentiated periostracal groove is not developed but is present in its primordial stage. The epithelium secreting the shell plates does not show any relevant differences from the epithelium of the perinotum. This can also be seen as a primitive evolutionary stage. Thus, the Conchifera must be derived from the Placophora and not vice versa as is often supposed, especially by paleontologists. In view of these considerations, the condition with eight isolated shell plates in the Placophora must be seen as a phylogenetically original character. In our view, the conchiferan shell must be interpreted as a fusion of the eight shell plates of the placophorans. The larval valves of the chitons are formed in a markedly more primitive way than the concha of the conchiferans with their highly differentiated shell gland. The formation of the calcareous spines or scales of the placophoran girdle takes place in cell invaginations of the epithelial papillae. In that way, a crystallization chamber is provided, protecting the biomineralizate against external influences. The spines or scales in the mantle of the Solenogastres and Caudofoveata are formed in the same way. Their mantle epithelium with the calcareous hardparts is homologous with the perinotum epithelium and its mineralizates of the placophorans. The hypothesis that the shell plates of the Placophora can be derived from the anlagen of primitive spines in the original molluscan mantle is discussed. The acquisition of the shell plates of the Placophora respectively, the concha of the Conchifera is a new development in the phylogeny of the molluscs.

INTRODUCTION

The early phylogeny of molluscs can hardly be recognized by means of their fossil record because the subdivision of the phylum must have already taken place in the Precambrian. On the one hand, we know few fossils and on the other it is supposed that most primitive molluscs did not possess hardparts easily recognized to be of molluscan origin. So we are mainly restricted to speculations based on Recent forms. In this paper, the somewhat neglected aspects of the formation of calcareous hardparts by the mantle with respect to evolution will be discussed.

OBSERVATIONS AND INTERPRETATIONS

We begin with the Placophora which hold a key position as we examine the problem of molluscan shell evolution. A normal chiton has eight shell plates encircled by a girdle or

perinotum which bears, in most cases, calcareous spines or scales and which is covered by a glycoproteinaceous cuticle. The structure of the placophoran shell plates (Fig. 1) has been described in detail by Haas (1972, 1976). A shell plate consists of three layers. There is a very thin and incompletely polymerized organic cover, which is not a true periostracum, and two calcareous layers, the tegmentum and the hypostracum, which consist of aragonite. The tegmentum is made up of rods of spherulite sectors (Fig. 1C) running in its uppermost part parallel to the surface. Further ventrally, the tegmentum is formed by spherulitic sectors directed ventrolaterally. The tegmentum contains canals for the esthetes. The hypostracum is constructed of crossed lamellae (Fig. 1D). Compared with the crossed lamellar structures of the Conchifera, this has some special features: the bundles of the crystal fibres are combined in such a way that their crystallographic c-axis coincides with the bisectrix of

¹Dedicated to Prof. H. K. Erben at his sixtieth birthday.

these crossing fibres. In the Conchifera, the c-axes of neighbouring fibre bundles enclose an angle of about 110°. Here the elements of the third order (third order lamellae) are mostly combined into sheet-like second order

elements (second order lamellae) which are never present in the Placophora. In modern chitons (Neoloricata Bergenhayn) the articulamentum (Fig. 1B) is developed as an intercalation within the hypostracum. It is built up

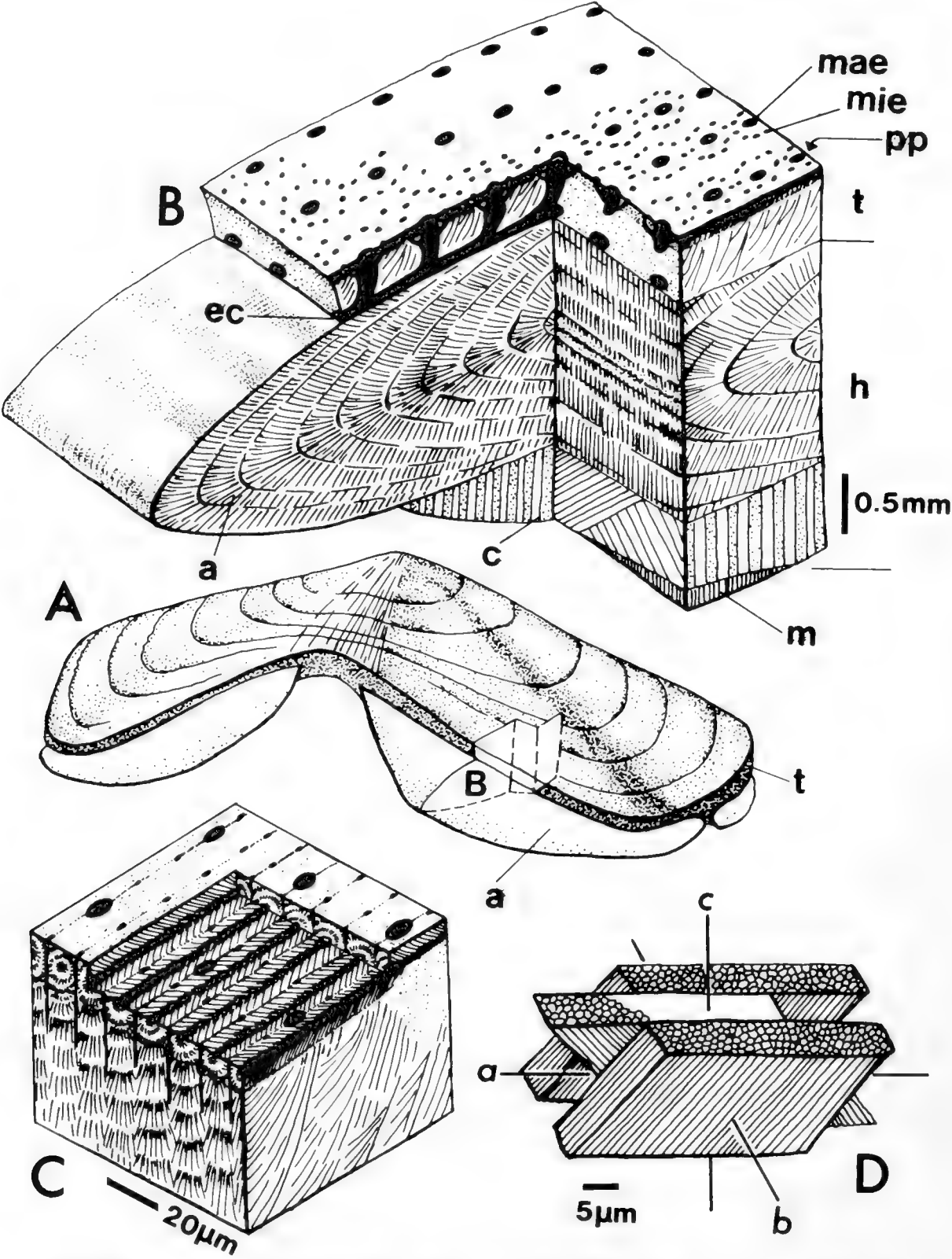


FIG. 1. Morphology of an intermediate shell plate of a chiton (after Haas, 1976). A, whole plate; B, block diagram showing the shell layers (for location see A); C, block diagram of the tegmentum; D, crossed lamellar structure of the hypostracum with crystallographic axes (a, b, c). a, articulamentum; c, crossed lamellar structure of the hypostracum; ec, esthete canal; h, hypostracum; m, myostracum; mae, macres-thete; mie, micresthete; pp, properiostracum; t, tegmentum.

of spherulitic bundles. It serves for a better insertion of the shell plates in the perinotum. The myostracum, a prismatic layer, present in all chitons, is a modification of the hypostracum for muscle attachment (Haas, 1972).

The perinotal spines or scales have a rather complicated outer shape with differentiated ornamentation in most living chitons. All are constructed of a simple spherulitic sector of aragonite, showing a primitive mineralogic structure. The mantle and its epithelia secrete two products: the shell plates and the cuticula of the girdle with the spiculae or scales (Fig. 2).

There is only a very small degree of differentiation between the epithelium forming the shell plates and the perinotal epithelium. A primitive kind of periostracal groove (Fig. 3) shows, to a certain extent, differentiation of its wall proximal to the shell plate. The distal wall, in contrast, is covered by normal perinotal epithelium. The cells of the proximal wall of the periostracal groove may play a role in providing tanning agents for the inner parts of the cuticle forming the properiostracum.

In this context, some remarks must be made concerning the definition of a periostracum. A true periostracum as it appears in

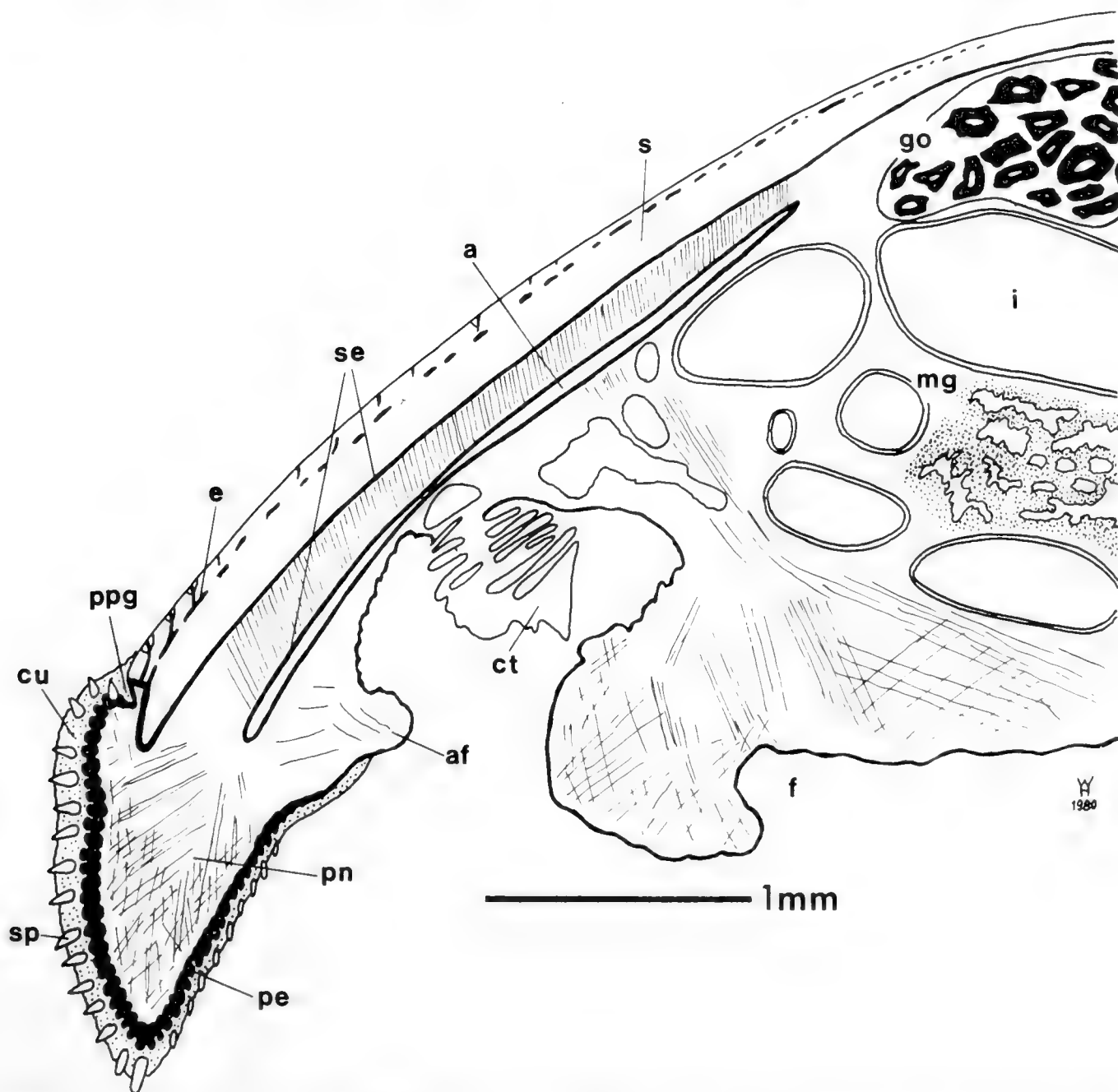


FIG. 2. Cross section through the middle part of *Lepidochitona cinerea* (L.), showing the situation of the shell and mantle. a, articulamentum of the succeeding shell plate; af, accessory fold of the perinotum; ct, ctenidium; cu, cuticle; e, esthetes and esthete canals; f, foot; go, gonad; i, intestine; mg, midgut gland; pe, perinotal epithelium; pn, perinotum; ppg, properiostracal groove; s, shell plate; se, epithelium secreting the shell plates; sp, calcareous spine.

the Conchifera is a pellicle covering the calcareous part of the shell consisting of polymerized organic material (tanned proteins), which is formed in a periostracal groove encircling the shell border. The shell plates of the Placophora are covered by a rather insignificant organic pellicle, but it seems to be only weakly polymerized. Its existence is rather difficult to prove. This can be done if one briefly decalcifies a shell plate. Then a pellicle on which the distribution of the esthete caps adhering to it show their original distribution pattern (Haas, 1972) can be stripped off. From morphological observations, it appears that a stabilization, perhaps by tanning, of the proteinaceous content of the inner part of the cuticle takes place on the shell plate at some distance from the mantle edge. Because of technical difficulties, we have failed to demonstrate the presence of tanning agents by means of the DOPA-reaction. Beedham & Trueman (1968) obtained a positive Millon reaction for proteins at the site of the properiostracum. From its morphological

nature and because the properiostracal groove in Placophora never contains any polymerized pellicle, the organic cover of the shell plates can only be seen as a first evolutionary stage of a periostracum. Accordingly, it should be called the "properiostracum." In contrast to the true periostracum in Conchifera, it does not play an important role in shell formation but may merely provide a protection of the shell plates against corrosion.

The mode of calcium carbonate precipitation in the tegmentum of the Placophora is rather primitive. The cells of the mantle edge surrounding the valves are covered with long whip-like processes (microvilli) adjacent to the shell margin (Fig. 4). Also, the cuticle from the periostracal groove, which may be tanned to a certain degree, covers the margin of the valves. Thus, a crystallization chamber (Haas & Kriesten, 1974; Haas, 1976) is provided which, on the one hand, prevents any influence from the external environment and, on the other hand, prevents calcium carbonate secretion into the cuticular material covering

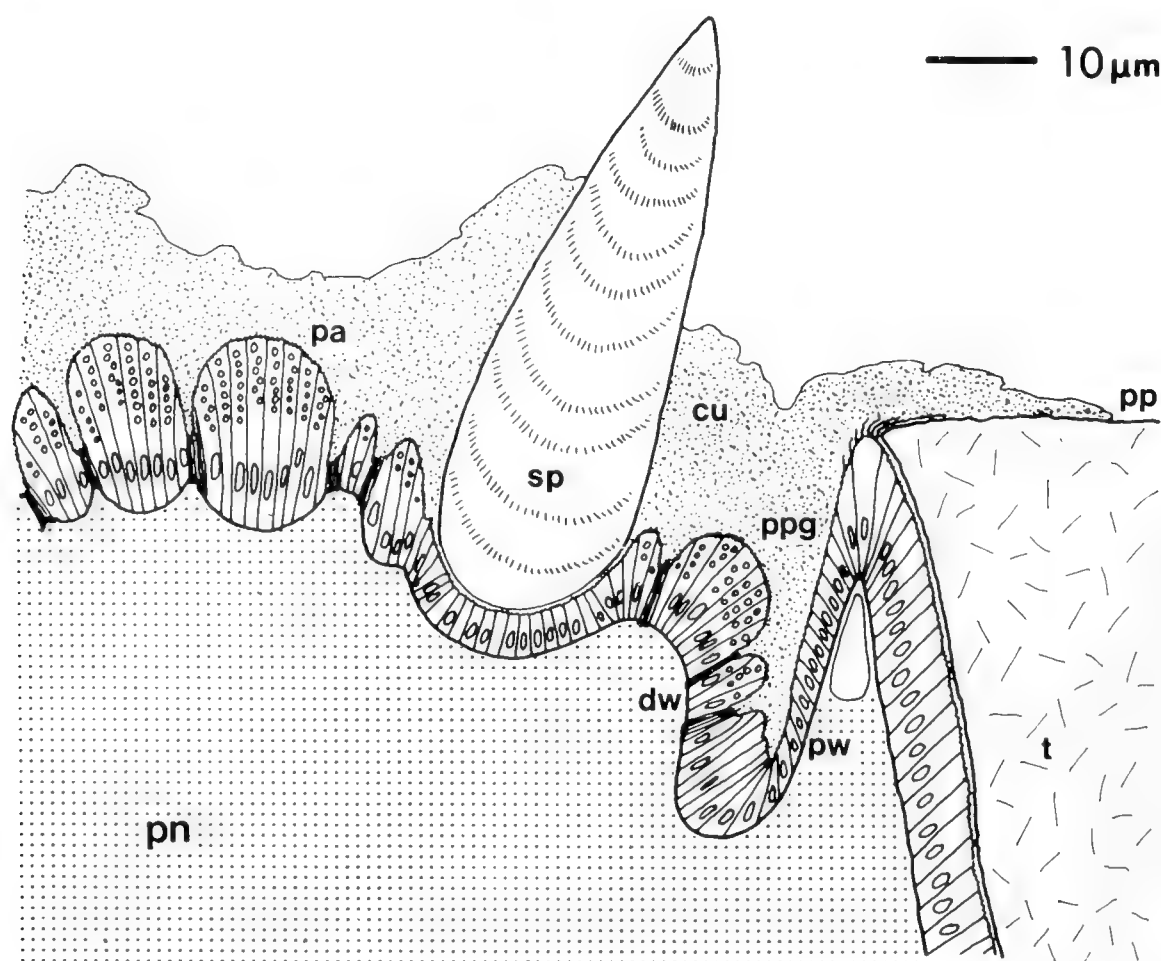


FIG. 3. Cross section through the shell and mantle near the shell margin in *Acanthopleura granulata* (Gmelin), cu, cuticle; dw, distal wall of the properiostracal groove; pa, epithelial papilla of the perinotum; pn, perinotum; pp, properiostracum; ppg, properiostracal groove; pw, proximal wall of the properiostracal groove; sp, calcareous spine; t, tegmentum.

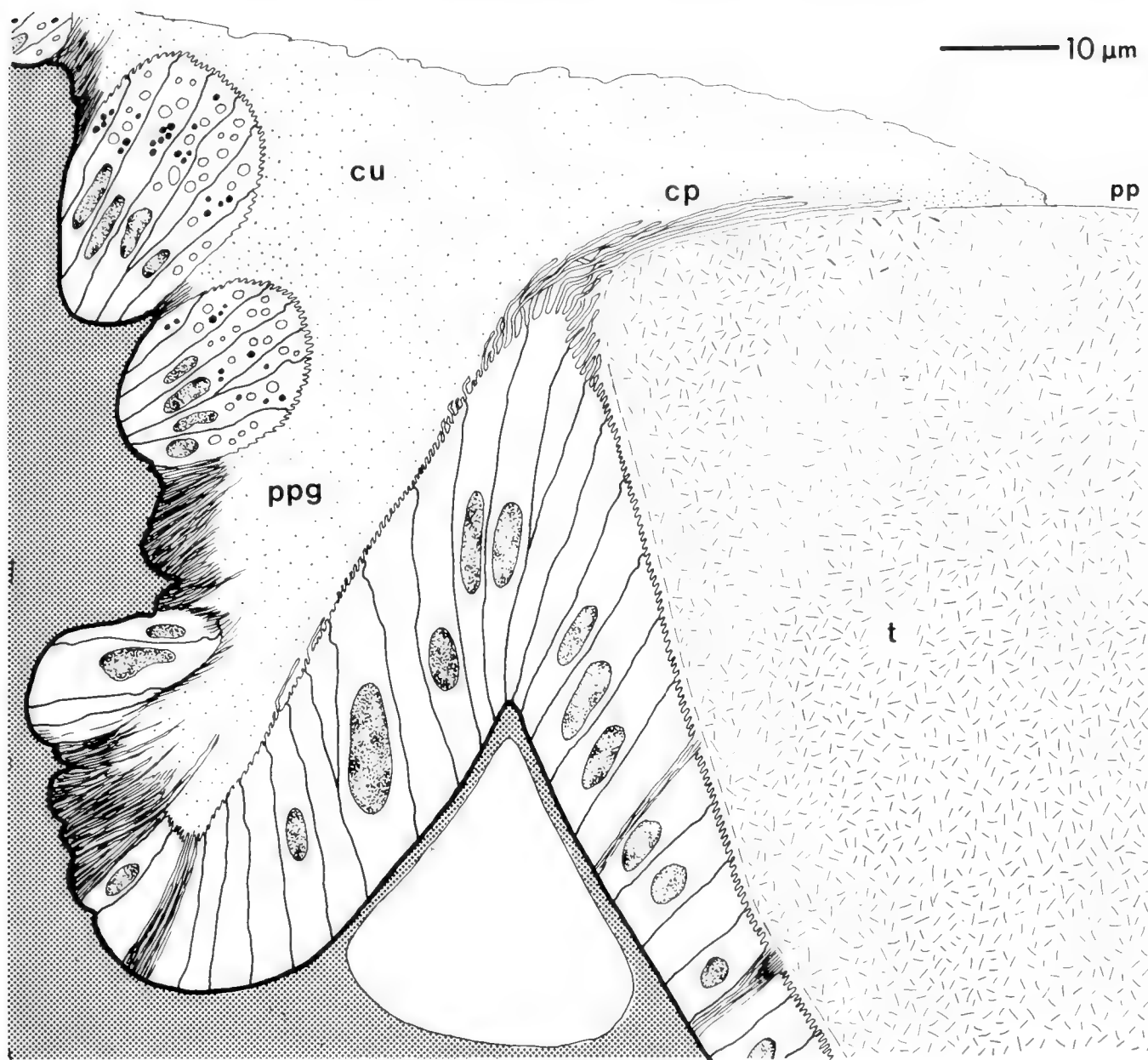


FIG. 4. Cross section through the shell and mantle near the shell margin in *Lepidochitona cinerea* (L.). Cuticle and cell processes of the mantle edge protect the growing shell margin. cp, cell processes; cu, cuticle; pp, periostracum; ppg, properiostracal groove; t, tegmentum.

the valve margin. Although we cannot observe a true periostracal groove with the high degree of differentiation of the Conchifera (Fig. 5), nor a true periostracum, nor the high degree of differentiation of the shell-secreting conchiferan epithelium, we must state that the Placophora possess around each shell plate a primitive periostracal groove. The latter has been called by Haas & Kriesten (1974) the properiostracal groove. In Placophora, the region between the proximal wall of the properiostracum groove (Figs. 4, 5) and the shell edge can be homologized with the outer mantle fold of the Conchifera (Haas, 1972). Then, following this line of thinking, the perinotum is homologous with the inner mantle folds of the Conchifera (Haas, 1972).

As already noted, the shape of the perinotal calcareous hardparts may be rather complicated, although the structure itself is a simple spherulitic sector of aragonite. The calcareous part of a spine or scale can be secreted by a single cell (Haas & Kriesten, 1975; Haas, 1976) or by an epithelial layer within an epithelial papilla (Haas & Kriesten, 1977). But also in the latter case, spine formation begins with a one-cell stage. Fig. 6 shows the formation of the calcareous part of a spine by a single cell. At the beginning (Fig. 6A), this cell is deeply invaginated and the calcium carbonate is precipitated extracellularly in the chamber thus formed. Later (Fig. 6B), the growing spine protrudes from the epithelial papilla and the neighbouring cells are in close

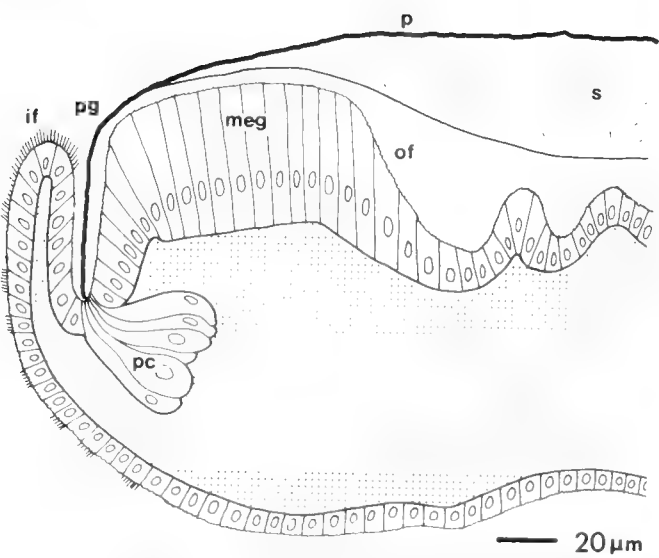


FIG. 5. Situation of shell and mantle in the gastropod *Helisoma duryi* (Wetherby) (after Chan & Saleuddin, 1974). if, interior mantle fold; meg, mantle edge gland; of, outer mantle fold; p, periostracum; pc, periostracal cells; pg, periostracal groove; s, shell.

contact with it forming a collar around the shaft of the spine. They secrete an organic pellicle onto the spine. Thus, a crystallization chamber is provided. At the final stage of spine formation, the neighbouring cells and the cell which secretes the calcium carbonate form the organic cup at the proximal end of the spine. This cup is identical to the cup of the macrosthetes (Haas & Kriesten, 1975, 1977, 1978). Recently, Fischer, Maile & Renner (1980) proved conclusively that nearly all the elements of the esthete apparatus can be shown in certain epithelial papillae of the perinotum. These observations support strongly our assumption that differentiation of the perinotal epithelium and the epithelium secreting the shell plates, especially the tegumentum, is minimal.

Fig. 7 shows the epithelium forming a large calcareous spine (megaspine) in *Acanthopleura granulata*. The formation begins with

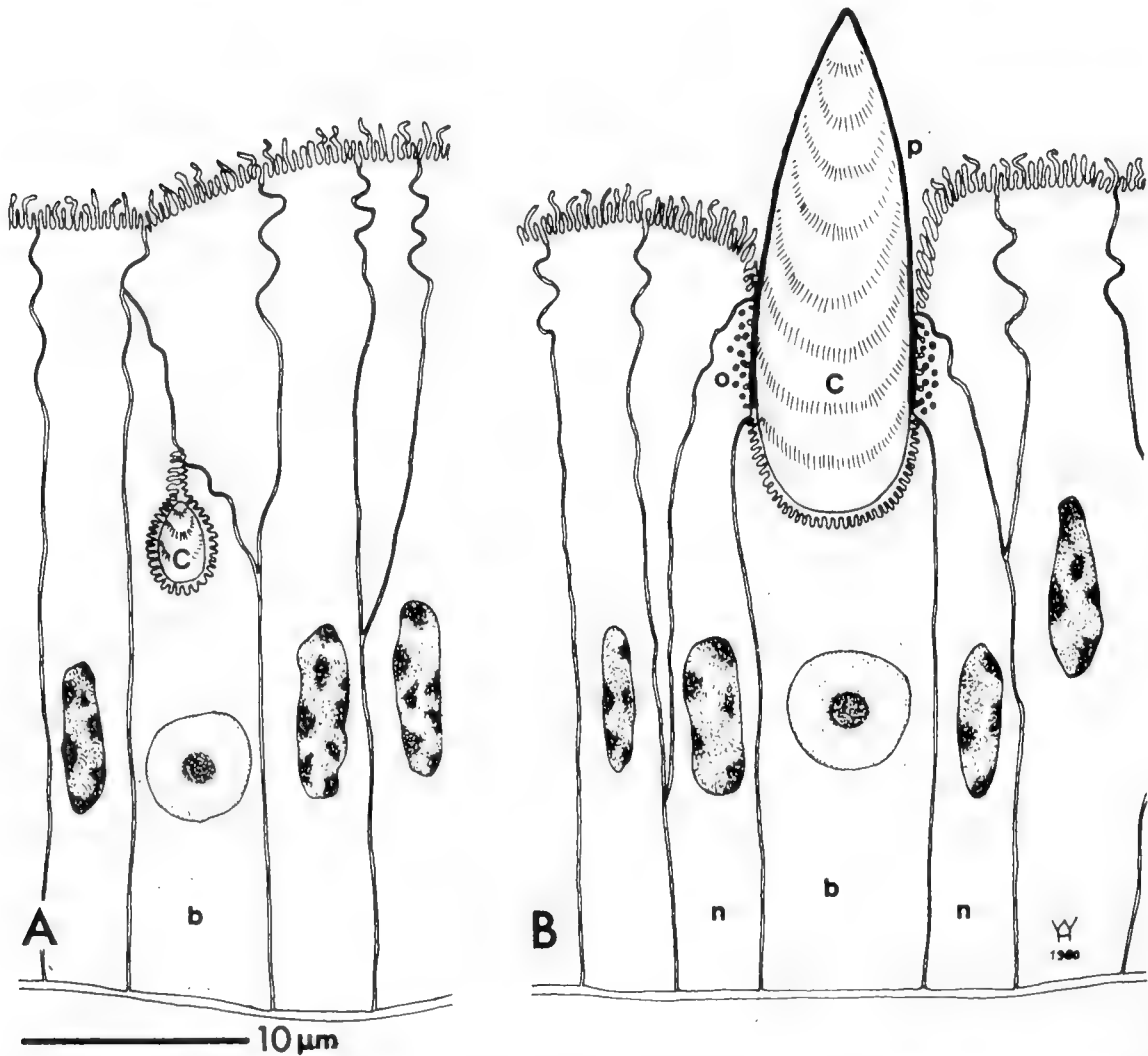


FIG. 6. Schematic diagrams of two different stages of spine formation in *Lepidochitona cinerea* (L.). The calcareous part of the spine is formed by a single cell. A, early stage; B, advanced stage. b, basal, calcium carbonate-secreting cell; c, calcareous part of the spine; n, neighbouring cell; o, vesicles filled with organic material which form the organic pellicle of the spine; p, organic pellicle of the spine.

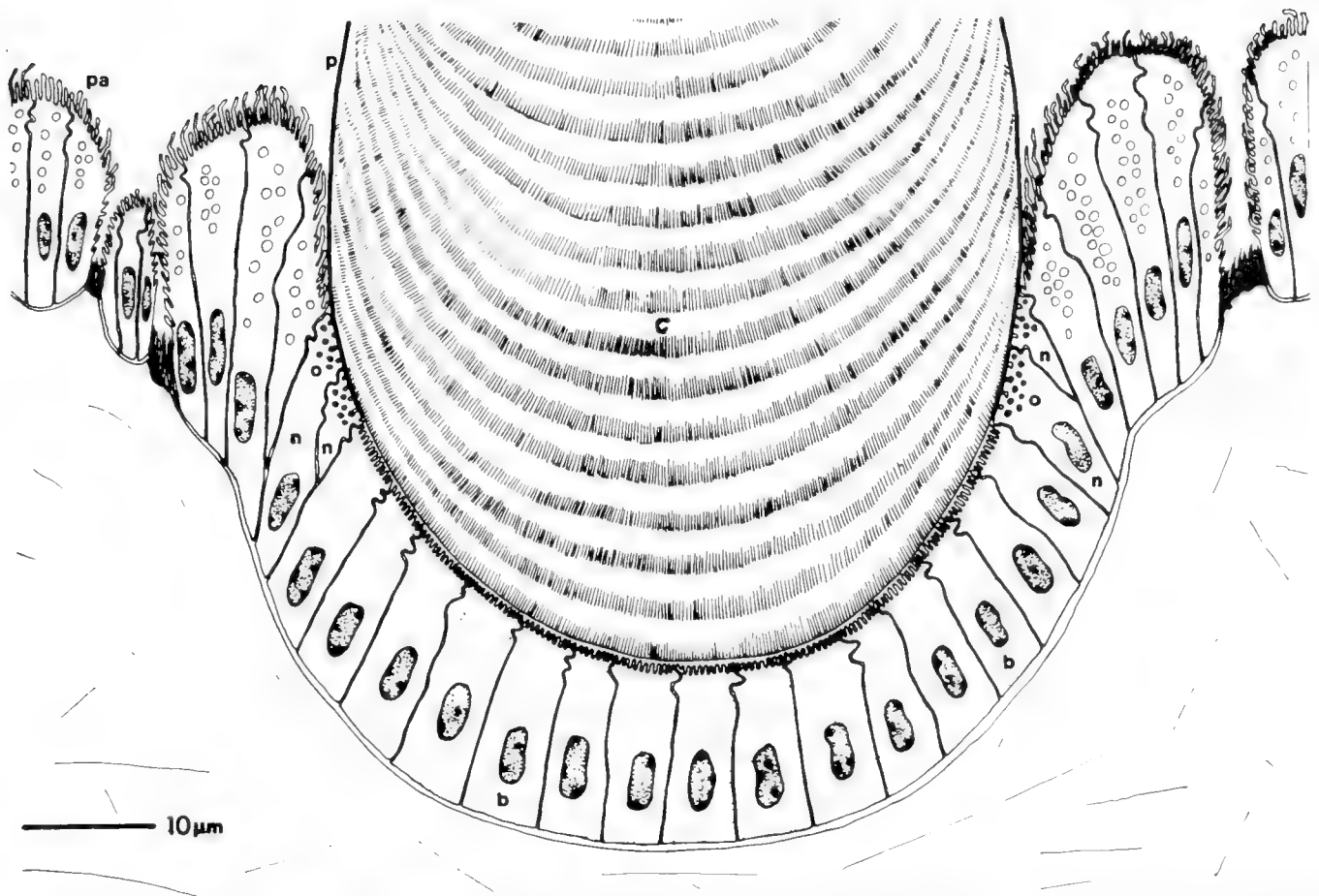


FIG. 7. Advanced stage in spine formation in *Acanthopleura granulata* (Gmelin). The calcareous part of the spine is formed by many calcium carbonate-secreting cells. Symbols as in Fig. 6; pa, epithelial papilla of the perinotum.

an invagination in a single cell as in the case described above. Later this initial cell divides and an epithelium secreting calcium carbonate is formed. Some spines in living chitons attain rather large size and continue to grow throughout the animal's life (Plate, 1901). The neighbouring cells play the same role in closing the crystallization chamber and producing an organic pellicle as in spine formation by a single cell. In the same way, an organic cup may be formed as described above. The initial papilla concerned with the spine formation degenerates and other cells divide and produce new perinotal epithelium. As a whole, the spine-secreting epithelium of the multicellular type resembles very much the epithelium secreting the tegmentum of the shell plates. Obviously, one can compare to a certain extent spine formation with shell formation and can, in principle, attribute to each spine its own periostracal groove as Kniprath (1979) suggests. But, in our view this is not reasonable because one can properly speak of a periostracal groove only if it derived from the true periostracal groove of the Conchifera.

There is an even more primitive mode of calcareous spine formation observed in young bottom-living larvae (Fig. 8) which may also occur in the adults of certain primitive chitons like *Hanleya* (Plate, 1901; modern observations are lacking). Here the calcareous spine is formed within a deep invagination of a papillar cell. In that case the apical part of the cells forms a collar which closes the crystallization chamber at the basal part of the invagination. There is no evidence that an organic pellicle is formed. The neighbouring cells do not seem to be involved in spine formation.

Shell formation in chiton larvae is also very instructive with respect to our assumption that shell formation in the Placophora is more primitive than in the Conchifera (Haas, Kriesten & Watabe, 1979, 1980; Kniprath, 1979). Here too, a crystallization chamber is provided to keep the biomineralizate free from external influences and to guarantee proper localization of calcium carbonate precipitation. In young free-swimming larvae, the dorsal epithelium is differentiated into bulges and grooves. At the site of the grooves, formation

of the shell plates occurs later (Figs. 9, 10). As we interpret this situation, the neighbouring cells of the groove complex produce a type of mucous cuticle which is rather unstable and which covers the site of later calcium carbonate precipitation, closing it against external influences. The dorsal covering of the mantle in

chiton larvae consists of a mucous layer of rather low electron density which we consider to be identical with the cuticle. At the apices of some cells within the region between the groove complexes, electron dense pillow-like masses of organic material can be observed. They seem to dissolve in the cuticle. This phenomenon has been described by Hammarsten & Runnström (1925) and by Kniprath (1979). We have the impression that this condensed organic material is transported on the grooves where later calcium carbonate precipitation takes place to achieve a better sealing of the future crystallization chamber. The organic material cannot be compared with the organic material forming the spine pellicle which is secreted from small vesicles (see Haas & Kriesten, 1975). We do not accept Kniprath's (1979) opinion that only the electron dense material represents the cuticle. It has not yet been observed in the formation of the perinotal cuticle. On the other hand, it does appear in some sections through the adult animals near the mantle edge where it seems to be involved in the formation of the organic cover of the shell plates. On the other hand, we must admit that the dorsal covering of chiton larvae is rather incompletely consistent. But, while the first calcium carbonate secretion appears, the entire valves are covered with a fibrous cuticle. However, little is known about the formation of the placophoran cuticle.

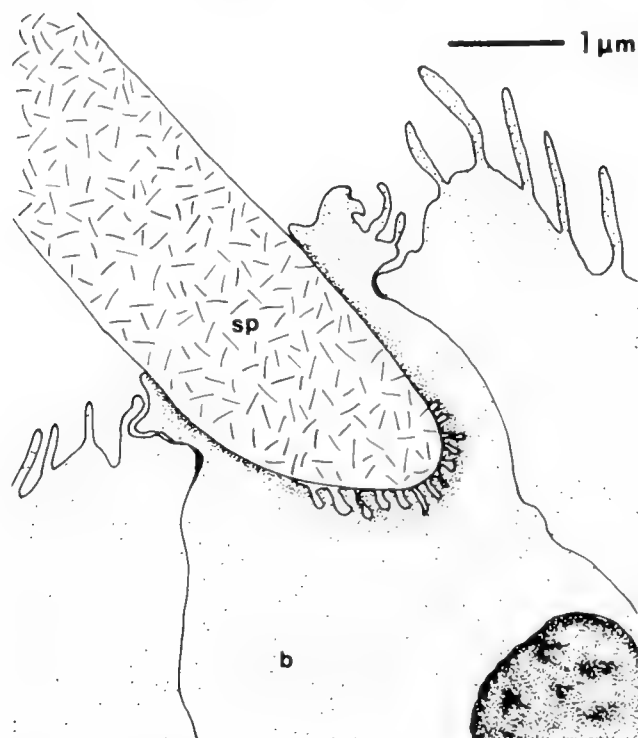


FIG. 8. Spine formed by a single cell in the perinotum of larval *Lepidochitona cinerea* (L.). b, basal, calcium carbonate-secreting cell; sp, spine.

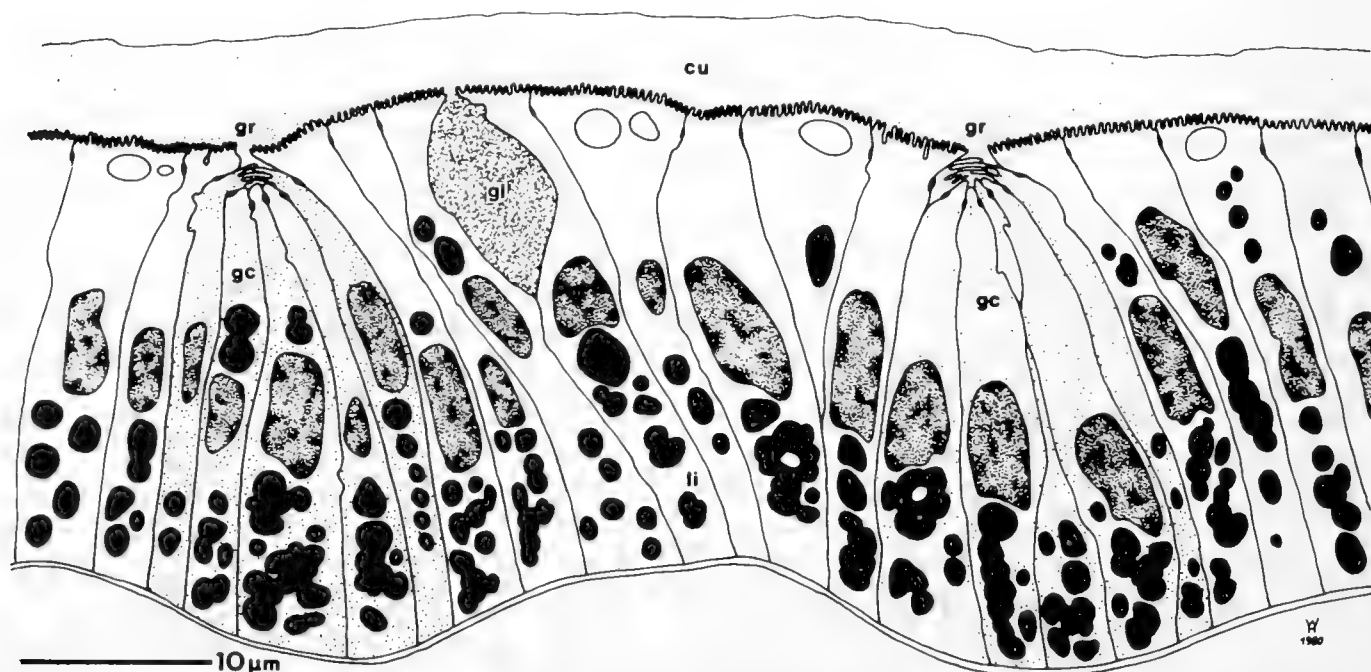


FIG. 9. Median section through the mantle of a free-swimming larva of *Lepidochitona cinerea* (L.), showing two groove complexes (after Haas, Kriesten & Watabe, 1980). cu, cuticle; gc, groove cell; gl, gland cell; gr, groove; li, lipid granulum.

Later the groove complex proliferates, and long cell processes (microvilli) interdigitate from the edges of the crystallization chamber forming a cage and keeping the biomineralizate in place (Fig. 11). The larval shell shows spherulitic growth of aragonite. Later, a simple crossed lamellar layer is secreted and the first two esthetes appear in the shell.

Compared with the highly complicated and well programmed shell field development in the Conchifera (Kniprath, 1977, 1979), the development of the shell field in the Placophora is primitive. In the conchiferan larvae, a pellicle is formed at the distal edge of the invaginated shell gland which must be designated a periostracum. In this way, a crystallization chamber is provided which is obviously

more perfect than the cuticle and microvilli cage method in placophorans. A true periostracum in larvae as well as in adults has the main advantage for shell formation because the first respectively lateral mineralizates of the shell no longer need to be separated against a cuticle. Consequently, the microvilli cage can be given up. The outer shell layer can now be directly precipitated against the periostracum which provides a perfect closing of the mineralization chamber against exterior influences.

For our considerations the shape of the periostracal groove itself is not so relevant as is its differentiated proximal wall. From this point of view, homologization of the periostracal grooves of Placophora and Conchifera is

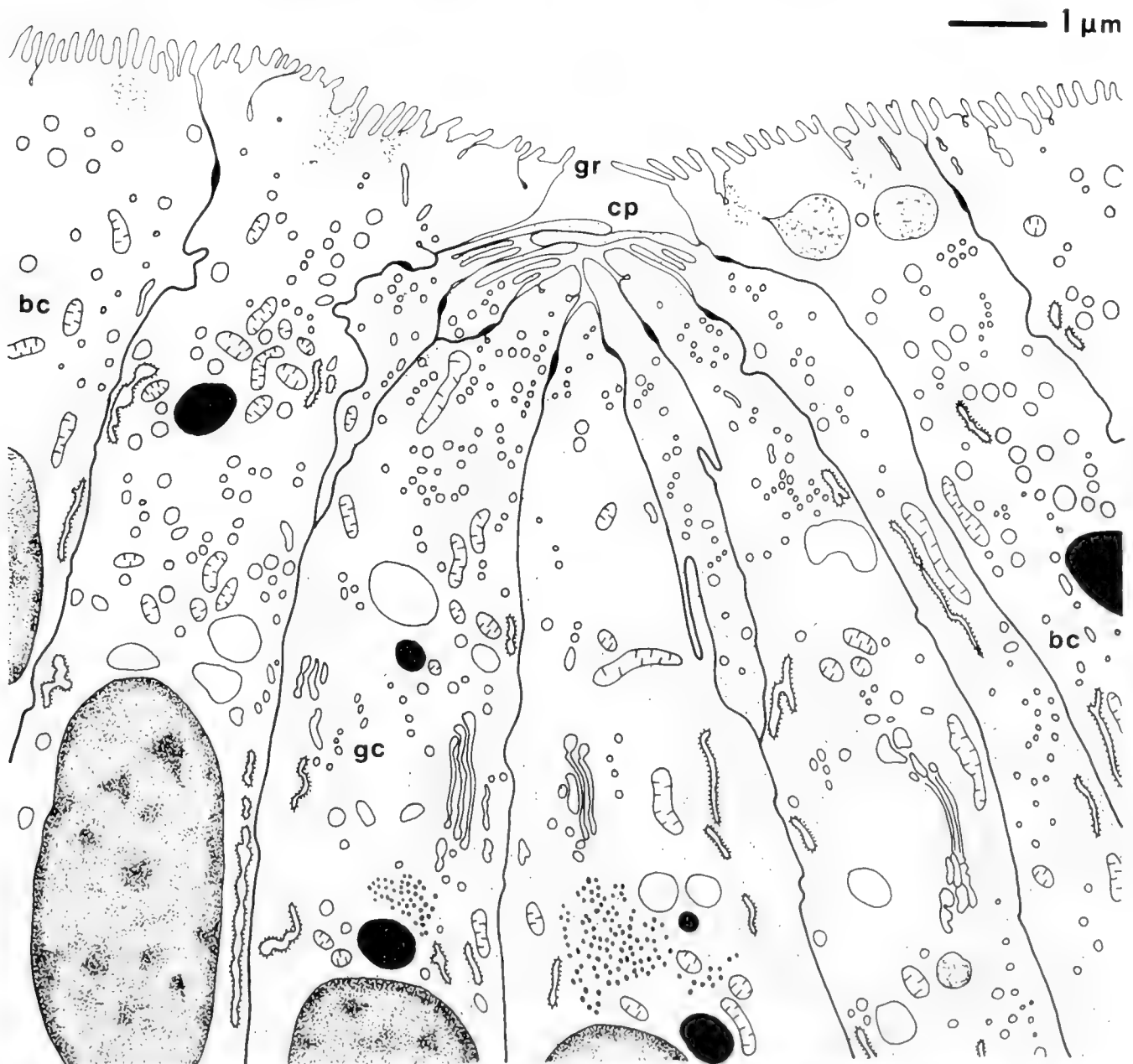


FIG. 10. Groove cell complex of a free-swimming larva of *Lepidochitona cinerea* (L.); detail of Fig. 9. bc, bulge cell; cp, cell processes; gc, groove cell; gr, groove.

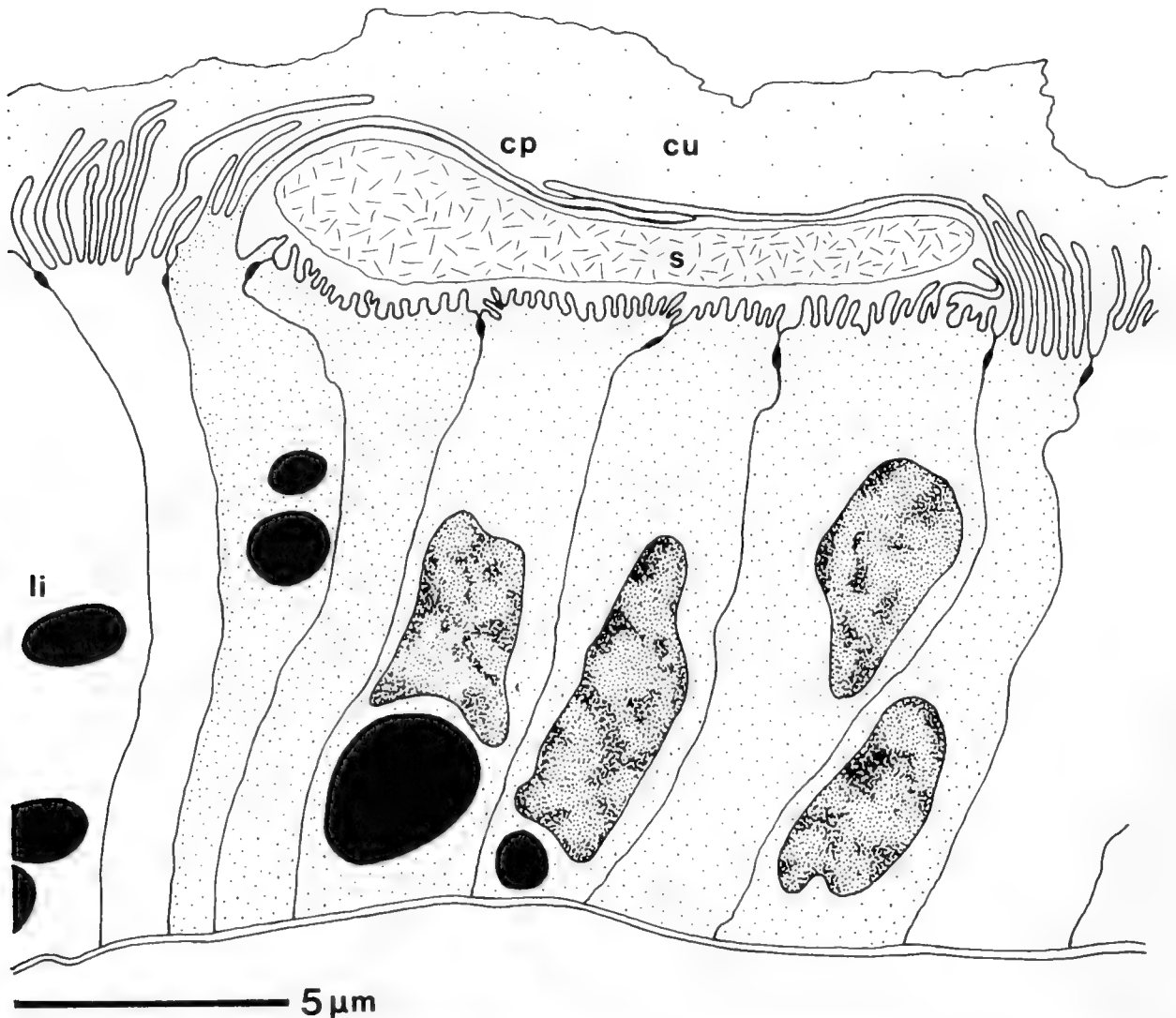


FIG. 11. Median section through a bottom-dwelling larva of *Lepidochitona cinerea* (L.), showing calcium carbonate secretion in an intermediate shell plate (after Haas, Kriesten & Watabe, 1980). cp, cell processes; cu, cuticle; li, lipid granule; s, shell plate.

possible. For this question it is more significant that the proximal wall of the periostracal groove, or the properiostracal groove and the epithelium secreting the shell, form a mantle fold enabling lateral growth of the shell. This occurs both in the Placophora and the Conchifera. Due to their manner of secreting their outer shell layers, the inclination of the proximal wall of the outer mantle fold is fundamentally different in both groups. In the Placophora it is directed mesioventrally, whereas in the Conchifera it is mostly horizontally displayed.

We have presented some observations and speculations which suggest that shell formation in Placophora is more primitive than in Conchifera. Next we must seek animals which, with respect to their calcareous hardparts, are more primitive than the Placophora. These are represented in the living Solenogastres and Caudofoveata, comprised in the

stage group Aplacophora. In the living fauna, these animals are highly adapted to special life conditions (ciliary gliding and sediment boring, respectively). According to Hoffman (1949) and Boettger (1955), both are homologous in several respects with the Placophora. The mantle of the Solenogastres and Caudofoveata is covered with a cuticle containing calcareous scales or spicules. Both groups show in their papillate mantle epithelium and in their calcareous hardparts considerable similarities to the perinotal epithelium of the Placophora. The spicules and scales also consist of aragonitic spherulite sectors which are in some cases covered with an organic pellicle. In some Solenogastres, the spicules bear an organic cup at their proximal end (Hoffman, 1949). Some of the spiculae in more highly evolved Solenogastres are hollow, whereas primitive forms possess massive scales, spines or needles. The for-

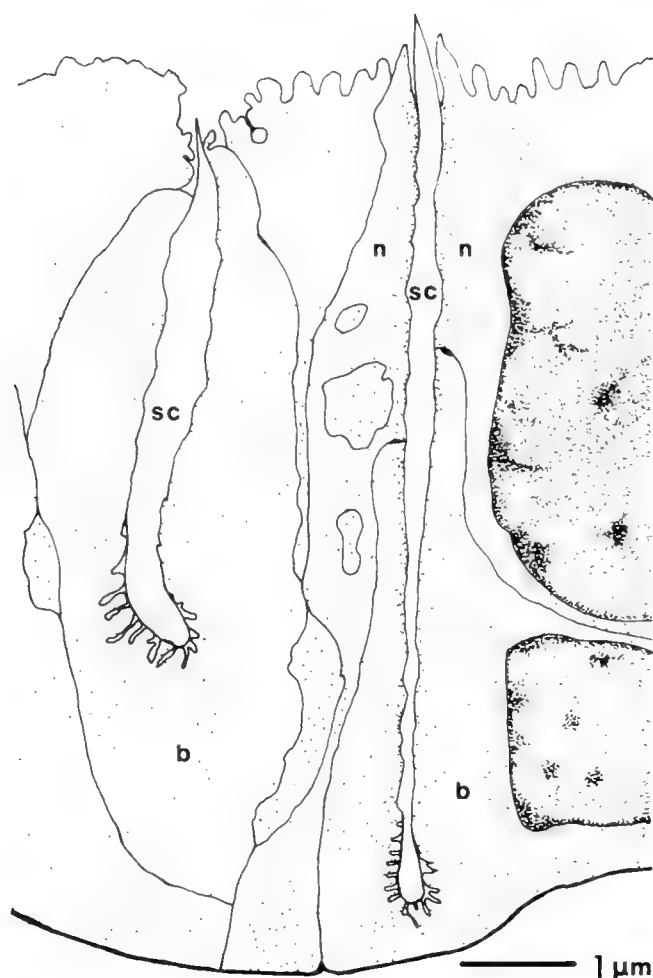


FIG. 12. Longitudinal section through the mantle of a primitive solenogastre (gen. et sp. nov.), with developing calcareous scales. b, basal, calcium carbonate-secreting cell; n, neighbouring cell; sc, calcareous scale.

mation of the calcareous hardparts in both classes, despite some differences in the morphology of the mantle epithelium, takes place in nearly the same way (Figs. 12, 13) as has been described above in the perinotal hardparts of the Placophora, especially in the spines of larvae or of very young metamorphosed animals (Fig. 8). It is out of the question that the aplacophoran classes Solenogastres and Caudofoveata are phylogenetically closely related to the placophorans. Considering hardpart formation, such a relationship is not possible.

DISCUSSION

Many of the problems we have discussed in the previous section must be viewed in the context of the molluscan phylogenetic tree. Fig. 14 is based on the author's arguments on the evolution of molluscan calcareous hard-

parts; it incorporates some features of the soft body. In nearly all respects, this phylogenetic tree conforms with the representation of molluscan evolution conceived by Salvini-Plawen (1972, 1980). For our purposes, we have introduced combinations of taxonomic names with the prefixes Archi- and Eu-, thus indicating that there are hypothetical stem groups and existing groups. These names are of no taxonomic significance.

It has long been debated whether the Placophora descended from the Tryblidiida, which are without any doubt Conchifera, by subdivision of the concha into eight shell plates, or whether the Conchifera stem from the Placophora by unification of their eight shell plates into one concha. The former view has been advocated recently mainly by paleontologists (Knight, 1952; Runnegar & Pojeta, 1974). It is more reasonable to think that Placophora are the ancestors of Conchifera. For it is obvious—a point having been stressed by Boettger (1955) and Salvini-Plawen (1972)—that the dorsoventral muscles of the chitons are arranged serially into 2×8 pairs and that in the Tryblidiida there

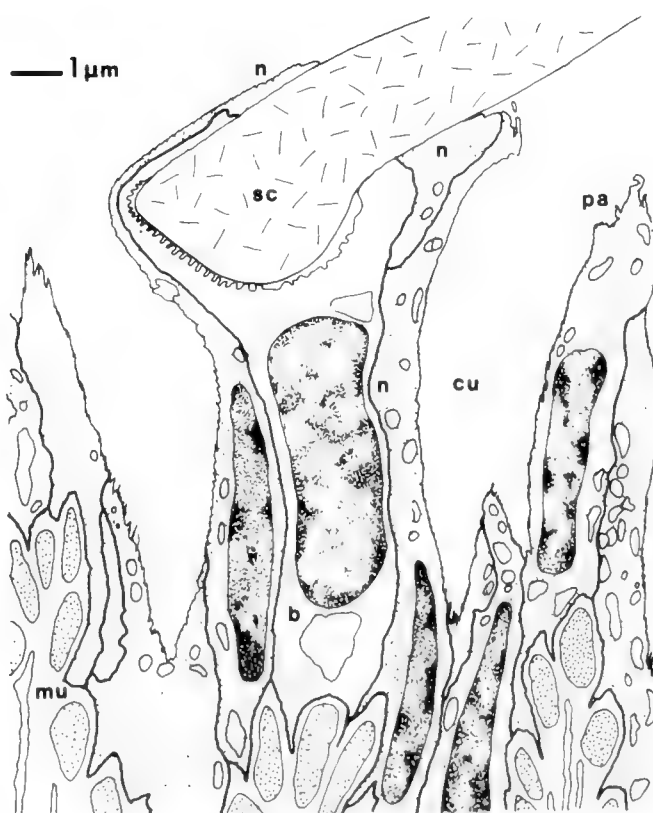


FIG. 13. Longitudinal section through the mantle of *Falcidens guttuerosus* (Kowalevsky) with a developing calcareous scale. b, basal, calcium carbonate-secreting cell; cu, cuticle; mu, muscle bundle; n, neighbouring cell; pa, epithelial papilla; sc, calcareous scale.

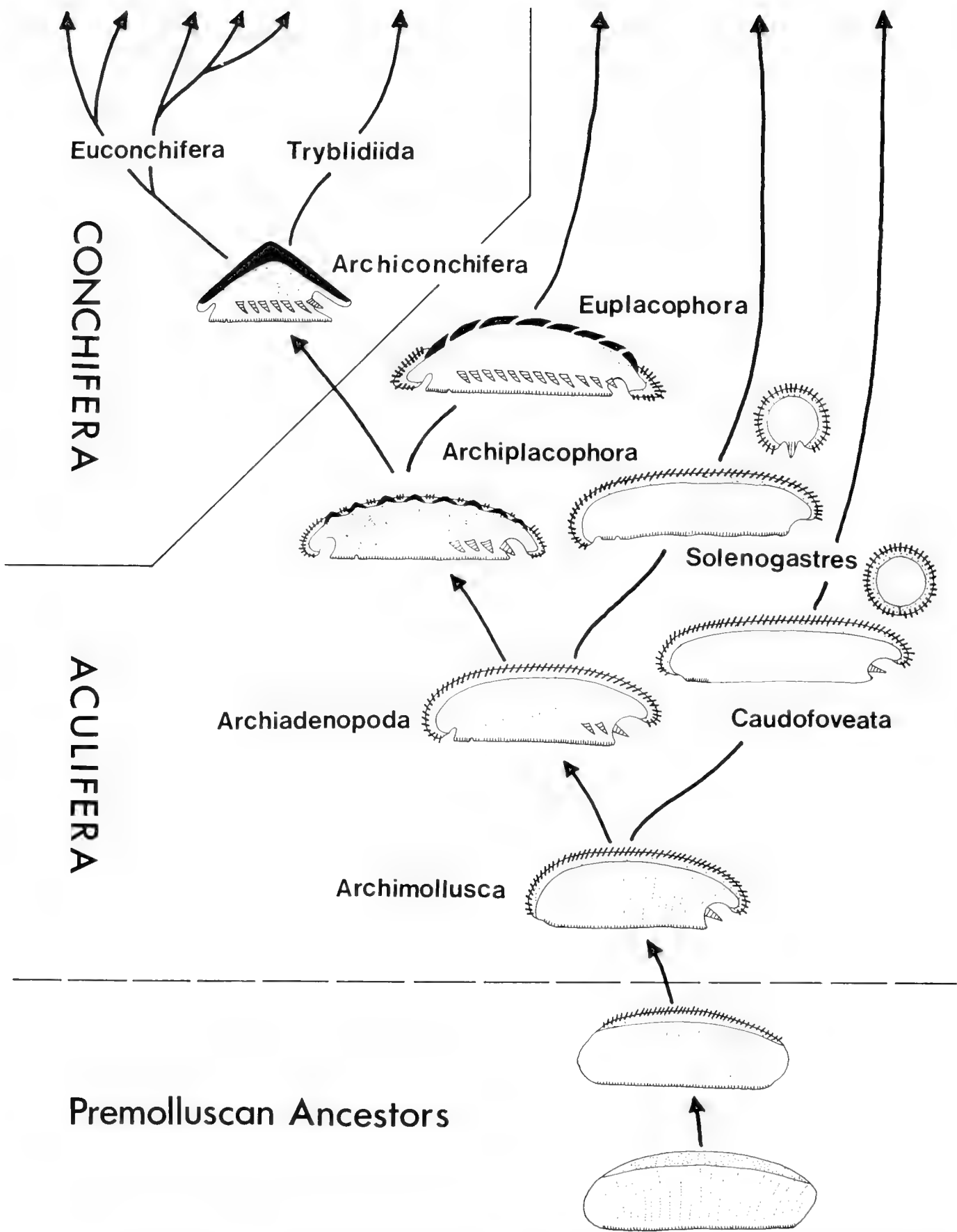


FIG. 14. Phylogeny of the primitive Mollusca based on the evolution of the calcareous hard parts of the mantle. Features of the soft body are taken from other authors, mainly from Salvini-Plawen (1972, 1980). I did not follow the arguments of Boettger (1955) and Salvini-Plawen (1972, 1980) according to which all primitive molluscs had only one pair of ctenidia.

are, in spite of the uniform concha, eight pairs. In this latter case, the double cords of the Placophora have been concentrated into single cords. It is difficult to imagine why a uniform concha should have, preadaptively referring to polyplacophory, multiplied its dorso-ventral muscles as in the case of the Tryblidiida. The evolution from the Tryblidiida into the different euconchiferan classes shows an obvious reduction or concentration of the dorso-ventral muscles. This is by far the best technical solution for animals which elevate their shell above the substrate [as also *Neopilina* does (Lowenstam, 1978)] and which can withdraw their body into the shell. In this context, the capacity for rolling up in the Placophora would not be understandable in an evolutionary way of a subdivision of the concha. It is more convincing that the loss of the placophoran longitudinal muscles appeared during the evolution from the Placophora in the direction of the Conchifera rather than vice versa. This means that the rolling up ability and the possession of longitudinal muscles must be inherited from the ancestors of the Placophora (Archiadenopoda). These considerations, often presented by other authors (see Salvini-Plawen, 1972, 1980), are supported by shell formation in larvae as well as in adults, and the low degree of differentiation of the mantle epithelium in the Placophora is obviously more primitive than in the Conchifera.

An important problem in the hypothesized derivation of the Conchifera from the Placophora is the possession of crossed lamellar structure in the chitons and, on the other hand, the possession of the nacreous structure in the Tryblidiida. The nacreous structure has been thought by various authors to be the most primitive structure of the inner layer of molluscan shells. This shell type is present in the Tryblidiida and in all basal stocks of the euconchiferan classes. In most of the latter, the nacreous structure is abandoned in more advanced phylogenetic stages in favour of a crossed lamellar structure. Without referring to some adventurous speculations arising from lumping together the placophoran and conchiferan crossed lamellar structures, we come to the following conclusions. As we have demonstrated earlier (Haas, 1972, 1976) and discussed in this paper, the crossed lamellar structure of the placophorans is in its mineralogical properties decidedly different from the crossed lamellar structure of the Placophora as a unique

apomorphic acquisition which has nothing to do with similar structures in the Conchifera. It is best to imagine that the Archiplacophora have had a rather undifferentiated inner shell layer which probably was made up of spherulitic sectors. From such a structure there have evolved on the one hand the crossed lamellar layer of the Placophora and the nacreous layer of the Conchifera on the other.

Starting from our conclusion that the epithelium secreting the shell plates and the epithelium of the perinotum are not very different, we may suppose that one can postulate a genetic relation between the calcareous hardparts of the placophoran mantle.

As mentioned above, several authors (Blumrich, 1891; Runnegar, Pojeta, Taylor & Collins, 1979) have proposed that the placophoran shell plates must have been derived in some way from megaspines. But megaspines are only present in highly evolved chiton taxa so that they must be supposed to be phylogenetically younger than shell plates. The close similarity of the epithelia secreting both shell plates and megaspines is therefore an expression of the fact that the differentiation of the respective mantle epithelia is rather limited. It would also be difficult to understand how the esthetes, which are specialized perinotal papillae, could be incorporated into a megaspine.

It can be more easily imagined that the shell plates of the Placophora have developed from the anlagen of simple spines or scales as we have described in the case of the perinotum of larvae and young metamorphosed animals in chitons or from the mantle of the Aplacophora. However, derivation of the placophoran shell plates from definite spines or scales, especially from the highly specialized calcareous perinotal hardparts in most chitons, cannot be admitted. The evidence against this view is their formation in a cell invagination and the sealing of the crystallization chamber by the collar mechanism provided by the cell apices or the neighbouring cells. We must rather suppose that within eight median areas of the mantle of those Placophora (which we prefer to call Archiplacophora), the calcium carbonate-secreting cells do not invaginate as deeply as in normal spine or scale formation. Consequently, a collar mechanism which serves the shaping of a single spine did not operate. Thus, calcium carbonate precipitation could take place underneath the cuticle from several calcium carbonate-secreting sites, forming a plate-like

biomineralizate. The deposited mineral could incorporate sensitive papillae (now transformed into esthetes). To give a definite shape to such a primordial shell plate, a mantle edge, in order to enable lateral growth and formation of new esthetes, and a seam of cell processes, in order to prevent irregular crystal growth into the cuticle, have become necessary. It is to be supposed that early in phylogeny, increasing thickness of the shell plates occurred with the result that a double layered calcareous shell developed. This situation is also reflected to a certain degree in the ontogeny of living chitons, where shell formation begins with a calcium carbonate secreting epithelium which later proliferates, forming an epithelium of a perinotal aspect with papillae now transformed into esthetes.

Kniprath (1979) interprets shell formation in the Placophora, as Blumrich (1891) did earlier, to be a simple lateral growth of perinotal spines and he does not see any relevant differences between perinotal spines and shell plates. Accordingly, he does not accept any homologies between the shell plates of the Placophora and the shell of the Conchifera. As a consequence, he denies the existence of a properiostracal groove in the placophorans, and he also cannot interpret the perinotum as a mantle fold. He does not take into account the above mentioned arguments which, primarily on the basis of the number of the dorsoventral muscles, support the hypothesis that the concha of the Conchifera is a product of the unification of the eight shell plates of the Placophora. To argue that a simple lateral growth of perinotal spines forms the shell plates with accepting the argument that the shell plates of the Placophora are in a phylogenetic connection with the concha of the Conchifera is not consistent with the incorporation of the esthetes.

It could well be that the first shell formations in chitons have been covered by the cuticle. But this cuticle did not contain spines as Beedham & Trueman (1967, 1968) proposed in their reconstructions. As a consequence of the origin of the placophoran shell plates from the anlagen of spines or scales which correspond to formations of the perinotum, it must be concluded that the predecessors of the Placophora possessed a mantle which corresponded totally to the present placophoran perinotum. These animals, which we wish to call Archiadenopoda, must have been of a chiton-like appearance but without plates. They must have been covered by a mantle

with calcareous spines or scales and with a broad creeping foot. The eight shell plates in Placophora (seven in Septemchitonida) are the first acquisition of shells in the Mollusca. After the formation of these shell plates in Archiplacophora, the dorsoventral muscles attached to them.

According to the fossil record, the Paleozoic Placophora had posteriorly flattened conical shell plates (*Chelodes*). (In general, a cone seems to be the most primitive shape of a shell with lateral and thickened growth.) The supposed earliest chiton *Matthevia* from the Upper Cambrian (Runnegar, Pojeta, Taylor & Collins, 1979) with long conical shell plates seems to be an extreme variant. If this animal was indeed a chiton, the deep, mesially arranged holes in the inner shell must have each contained a pair of dorsoventral muscles diverging ventrolaterally to provide space for the inner organs. The living chitons and most of their fossil representatives have developed clasp-like shell plates which are adapted to the animal's life on hard substrata.

The question we have already discussed in a previous section is the evolutionary direction of the well-established relationship of the Placophora with the Solenogastres and Caudofoveata. The concept that the Aplacophora stem from the Placophora by loss of the shell plates, advanced by Pelseneer (1890), cannot be supported (Boettger, 1955) for we only observe a reduction of the outer, but not the inner, shell layer in certain taxa of relatively high phylogenetic rank. From this it is to be assumed that the Aplacophora never possessed shell plates at all. Their ancestors, which certainly must have been less highly specialized than the living representatives of the Solenogastres and Caudofoveata, must be considered the predecessors of the Placophora.

But in this context, the assumption that the shell plates of the Archiplacophora have formed directly from the transverse rows of spiny scales of the Aplacophora (see Salvini-Plawen, 1972) as they appear in the larvae of the Solenogastre *Nematomenia banyulensis* (Pruvot, 1890) must be rejected. Perhaps one can interpret these conditions, as we have already discussed, as a pre-archiplacophoran division into several areas of the dorsal mantle with respect to later shell plate areas. That would mean that there is some vestige of the predecessors of the Archiplacophora. It must be said, however, that the observation of Pruvot (1890) needs reinvestigation. The above

reported speculations on the derivation of the Placophora from the Aplacophora are supported by many of Salvini-Plawen's (1972, 1980) arguments concerning the anatomy of the soft body, and there is no contradiction from the point of view of the calcareous hard parts.

We can close our considerations with the hypothetical Archiadenopoda and Archimollusca (Salvini-Plawen, 1972, 1980) which mainly represent stages in the evolution of the molluscan foot. By these arguments the Caudofoveata are the most primitive group next to the Archimollusca.

From the concept of evolution of molluscan calcareous hardparts, in all cases the most primitive mollusc must have had a cuticle and calcareous spicules or scales. Whether it had a turbellarian ancestor as has been supposed by various authors (Stasek, 1972; Stasek & Williams, 1974; Salvini-Plawen, 1972, 1980) or whether it was a preannelid (Boettger, 1955; Remane, Storch & Welsch, 1974; Siewing, 1976) is still open to question. The possession of calcareous spicules in certain turbellarians (Rieger & Sterrer, 1975) has been used by some authors (Runnegar, Pojeta, Taylor & Collins, 1979; Salvini-Plawen, 1972; Stasek, 1972; Stasek & McWilliams, 1973) as an argument for a turbellarian ancestor of the molluscs. This conclusion is not yet convincing for these spicules are not situated in the epithelium but underneath it. Their formation is still unclear.

ACKNOWLEDGEMENTS

I thank my colleagues, Prof. Dr. N. Watabe of the University of South Carolina at Columbia, South Carolina and Prof. Dr. K. M. Wilbur of Duke University, Durham, North Carolina for reading the manuscript.

REFERENCES CITED

- BEEDHAM, G. E. & TRUEMAN, E. R., 1967, The relationship of the mantle and shell of the Polyplacophora in comparison with that of other Mollusca. *Journal of Zoology*, 151: 215–231.
- BEEDHAM, G. E. & TRUEMAN, E. R., 1968, The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. *Journal of Zoology*, 154: 443–451.
- BLUMRICH, J., 1891, Das Integument der chitonien. *Zeitschrift für wissenschaftliche Zoologie*, 52: 404–476.
- BOETTGER, C. R., 1955, Beiträge zur Systematik der Urmollusken (Amphineura). *Zoologischer Anzeiger, Supplement*, 19: 223–256.
- CHAN, J. Y. & SALEUDDIN, A. S. M., 1974, Acid phosphatase in the mantle of the shell-regenerating snail *Helisoma duryi duryi*. *Calcified Tissue Research*, 15: 213–220.
- FISCHER, F. P., MAILE, W. & RENNER, M., 1980, Die Mantelpapillen und Stacheln von *Acanthochiton fascicularis* L. (Mollusca, Polyplacophora). *Zoomorphologie*, 94: 121–131.
- HAAS, W., 1972, Untersuchungen über die Mikro- und Ultrastruktur der Polyplacophorenschale. *Biomineralization*, 5: 1–52.
- HAAS, W., 1976, Observations on the shell and mantle of the Placophora. In WATABE, N. & WILBUR, K. M., The mechanisms of mineralization in the invertebrates and plants. *Belle W. Baruch Library in Marine Science*, 5: 389–402.
- HAAS, W. & KRIESTEN, K., 1974, Studien über das Mantelepithel von *Lepidochitona cinerea* (L.) (Placophora). *Biomineralization*, 7: 100–109.
- HAAS, W. & KRIESTEN, K., 1975, Studien über das Perinotum-Epithel und die Bildung der Kalkstacheln von *Lepidochitona cinerea* (L.) (Placophora). *Biomineralization*, 8: 92–107.
- HAAS, W. & KRIESTEN, K., 1977, Studien über das Epithel und die kalkigen Hartgebilde des Perinotums bei *Acanthopleura granulata* (Gmelin) (Placophora). *Biomineralization*, 9: 11–27.
- HAAS, W. & KRIESTEN, K., 1978, Die Ästheteten mit intrapigmentärem Schalenauge von *Chiton marmoratus* L. (Mollusca, Placophora). *Zoomorphologie*, 90: 253–268.
- HAAS, W., KRIESTEN, K. & WATABE, N., 1979, Notes on the shell formation in the larvae of the Placophora (Mollusca). *Biomineralization*, 10: 1–8.
- HAAS, W., KRIESTEN, K. & WATABE, N., 1980, Preliminary note on the calcification of the shell plates in chiton larvae. In OMORI, M. & WATABE, N., The Mechanisms of Biomineralization in animals and plants. *Proceedings of the Third International Biomineralogical Symposium*: 67–72. Tokai University Press, Tokyo.
- HAMMARSTEN, O. & RUNNSTRÖM, J., 1925, Zur Embryologie von *Acanthochiton discrepans* Brown. *Zoologisches Jahrbuch, Anatomie*, 47: 262–318.
- HOFFMAN, S., 1949, Studien über das Integument der Solenogastres. *Zoologiska Bidrag från Uppsala*, 27: 293–427.
- KNIGHT, J. B., 1952, Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections*, 114: 1–56.
- KNIPRATH, E., 1977, Zur Ontogenese des Schalenfeldes von *Lymnaea stagnalis*. *Roux Archiv für Entwicklungsmechanik der Organismen*, 181: 11–30.
- KNIPRATH, E., 1979, Ontogenèse de la région coquillière des mollusques. *Thèse présentée*

- devant l'Université Pierre et Marie Curie, Paris, 185 p.
- LOWENSTAM, H. A., 1978, Recovery, behavior and evolutionary implications of live Monoplacophora, *Nature*, 273: 231–232.
- PELSENEER, P., 1890, Sur le pied de *Chitonellus* et des Aplacophora. *Bulletin de Science France et Belgique*, 22: 489–495.
- PLATE, L., 1901, Die Anatomie und Phylogenie der Chitonen, Teil C. *Zoologisches Jahrbuch, Supplement*, 5: 281–600.
- PRUVOT, G., 1890, Sur le développement d'un Solénogastre. *Comptes Rendus de l'Académie des Sciences*, Paris, 111: 689–692.
- REMANE, A., STORCH, V. & WELSCH, U., 1974, *Kurzes Lehrbuch der Zoologie*. Stuttgart, Fischer, 492 p.
- RIEGER, R. M. & STERRER, W., 1975, New spicular skeletons in Turbellaria, and the occurrence of spicules in marine meiofauna. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 13: 207–248.
- RUNNEGAR, B. & POJETA, J., 1974, Molluscan phylogeny: The paleontological viewpoint. *Science*, 186: 311–317.
- RUNNEGAR, B., POJETA, J., TAYLOR, M. E. & COLLINS, D., 1979, New species of the Cambrian and Ordovician *Matthevia* and *Chelodes* from Wisconsin and Queensland. Evidence for the early history of polyplacophoran molluscs. *Journal of Paleontology*, 53: 1374–1394.
- SALVINI-PLAWEN, L. v., 1972, Zur Morphologie und Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie*, 184: 205–394.
- SALVINI-PLAWEN, L. v., 1980, A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, 19: 249–278.
- SIEWING, R., 1976, Probleme und neuere Erkenntnisse in der Grosssystematik der Wirbellosen. *Verhandlungen der Deutschen zoologischen Gesellschaft*, 1976: 59–83.
- STASEK, C., 1972, The molluscan framework. *Chemical Zoology*, 7: 1–44.
- STASEK, C. R. & MCWILLIAMS, W. R., 1973, The comparative morphology and evolution of the molluscan mantle edge. *Veliger*, 16: 1–19.

INDEX TO SCIENTIFIC NAMES IN VOLUME 21

An asterisk (*) denotes a new taxon

- abietina*, *Grammaria*, 380
abyssalis, *Utravhoherpia*, 383
abyssicola, *Limopsis*, 89
abyssicola, *Lyonsiella*, 44
abyssorum, *Xylophaga*, 136, 143
Acanthinulinae, 157, 158
Acanthochitona, 388
Acanthogorgia, 383, 384
Acanthopleura, 406, 408, 409
Achatinacea, 157
aculeitecta, *Sialoherpia*, 383
Aculifera, 414
acuminata, *Alexandromenia*, 382
acuminata, *Parapholas*, 130, 136, 143
acuminata, *Terebra*, 365, 366, 368
acuta, *Jullienia*, 217, 218
adamsiana, *Limopsis*, 72
Adelopoma, 177
Adenopoda, 377, 386, 389, 396
aegypos, *Teredo*, 144
aequabilis, *Falcidens*, 374–377
affinis, *Limopsis*, 63, 68, 83, 84
affinis, *Lyrodus*, 144
affinis, *Neomenia*, 381
africana, *Xylophaga*, 130, 136, 143
agassizi, *Anamenia*, 383
aglaopheniae, *Rhopalomenia*, 379, 382, 385
alabastrina, *Hydrobia*, 261
alabastrina, *Tomichia*, 222
alatus, *Euomphalopterus*, 313
albiensis, *Limopsis*, 66, 71
Alcithoe, 285
Alcyonaria, 383, 384
Alexandromenia, 382
alfredensis, *Barnea*, 144
altenai, *Xylopholas*, 130, 136, 143
amandae, *Limopsis*, 71
Amberleya, 335, 336
Amberleyacea, 292, 293, 311, 330, 334, 335
Amberleyidae, 335
Amberleyinae, 335
americanus, *Spondylus*, 27, 32
Amphidromus, 175
Amphimeniidae, 385
Amphiscapha, 313, 315, 317, 320
Amphitomaria, 314
Ampullariidae, 315, 323
Amusium, 23, 27, 28
anacarina, *Turbinilopsis*, 316
Anamenia, 379, 383, 385
anatina, *Laternula*, 42
Anculosa, 211
Ancylus, 12
anechoensis, *Bankia*, 144
Angaria, 336
angasi, *Offadesma*, 41, 42, 44, 53
angustiflora, *Acanthogorgia*, 383, 384
Anisostoma, 314, 334, 335
annulata, *Dondersia*, 380
Anomalodesmata, 35–60, 391
Anomia, 29
Anomiacea, 23, 24, 26, 27, 31
Anomphalacea, 292, 311, 314, 330, 333
Anomphalidae, 333
anserifera, *Laternula*, 42
antarctica, *Alexandromenia*, 382
antarctica, *Gephyroherpia*, 381
antennina, *Nemertesia*, 381
Anthozoa, 381
antillensis, *Limopsis*, 62, 73, 89
aperta, *Tricula*, 215, 216, 218, 220, 222
Aplacophora, 371, 377, 401, 403, 412, 415–417
Aquidauania, 211, 212, 221
Arca, 62
Arcacea, 62, 72
Archaeogastropoda, 170, 291–336, 353, 354, 359–361, 393, 394
Archaeomenia, 379, 380
Archaicinae, 150
Architaenioglossa, 361
Architectonicidae, 285, 315, 317, 368
Arcidae, 72, 75
Arcoidea, 61–93
arctatum, *Mesodesma*, 96, 97, 101, 102, 104, 107, 108
arechavalettoi, *Mesodesma*, 96
argenteum, *Chaetoderma*, 376
Ariantinae, 150
Arionidae, 157, 158
Ariophantacea, 157
Ariophantidae, 157, 158, 164
armata, *Acanthogorgia*, 383, 384
Armenica, 162
Arthrocnemum, 232
Arthropoda, 384
Asaphis, 104
Aspella, 268
Aspidobranchia, 359
Aspidopholas, 117, 144
Assimineae, 225, 233, 261
Asthenothaerus, 41
Atactodea, 96, 105, 107
atlantica, *Rhopalomenia*, 382
atlantica, *Xylophaga*, 122, 130, 136, 143
atriolonga, *Genitoconia*, 380
augustae, *Limopsis*, 71, 75
Aulacopoda, 157, 158
aurita, *Limopsis*, 62, 66, 67, 69, 71, 74, 83–85
aurita, *Xylophaga*, 136, 143
australasiae, *Barnea*, 144
australis, *Bankia*, 130, 133, 144
australis, *Epimenia*, 384
Australonema, 333
austrina, *Phyllomenia*, 381
Autobranchia, 391
azorica *azorica*, *Leptaxis*, 175
bacillum, *Chaetoderma*, 376
Bactronophorus, 117, 123, 130, 133, 134, 137, 143
Balcis, 284
Balea, 169

- Bankia*, 111–148
Bankiinae, 115–117, 124, 127, 134, 138, 139, 144
banyulensis, *Nematomenia*, 379, 380, 416
Barnea, 115, 117, 130, 135, 136, 138, 143, 144
barthelowi, *Bankia*, 144
bartschi, *Teredo*, 112, 116–122, 138–141, 144
bassi, *Limopsis*, 65, 69, 88, 90, 93
basteroti, *Terebra*, 364, 365
bathonica, *Amberleya*, 335
Bathyarca, 69
Bathybembix, 335
bavayi, *Pachydrobia*, 215
belcheri, *Limopsis*, 62, 81
Bellatara, 283
Bellerophontacea, 296, 314, 323
Beraunia, 313, 315, 316
bicallosa, *Perforatella*, 151
binneyi, *Pomatiopsis*, 239
bipalmulata, *Bankia*, 144
bipartita, *Lyrodus*, 144
bipennata, *Bankia*, 144
Birasoherpia, 383
birmanica, *Barnea*, 144
bitubulatus, *Triforis*, 368
Bivalvia, 23–34, 61–93, 95–110, 371, 387, 390, 391, 393–397
Blanfordia, 211, 212, 221, 239
Boettgeria, 169
bollingi, *Tricula*, 215, 222
borealis, *Anamenia*, 283
boschasina, *Laternula*, 42
**boucheti*, *Palaina*, 179, 182, 185–192, 195–198, 201, *202, 203
bracteata, *Lyratoherpia*, 380
Bradybaena, 173
Bradybaenidae, 150, 157, 158, 163, 164, 172, 174, 175
branchiata, *Parapholas*, 136, 143
brandti, *Paraprosiothenia*, 217
brazieri, *Limopsis*, 70, 72, 74, 92, 93
Brechites, 36, 43, 52, 57
brevis, *Bankia*, 144
brevis, *Pachydrobiella*, 217, 218
Brochidium, 334
bruuni, *Xylophaga*, 136, 143
Bryozoa, 388
Buccinacea, 368
Bulimulidae, 172, 175
Bulinus, 233, 234
burchi, *Tricula*, 222
Burmesiididae, 50, 54
Burnupia, 234
Bythograea, 307
Caecella, 95, 101, 102, 104, 106, 108
Caenogastropoda, 353
caldeirarum, *Leptaxis*, 175
Calicogorgia, 383
californica, *Parapholas*, 130, 136, 143
californicum, *Chaetoderma*, 376
californicum, *Prochaetoderma*, 375, 376
Calliostoma, 315, 359
Calliotropis, 335
calva, *Parapholas*, 136, 143
Calyptogena, 292
Calyptraea, 211, 214, 220, 358
Calyptraeacea, 355, 358
Calyptraeidae, 211, 284, 286, 291–336
Camaenidae, 175
campanellata, *Bankia*, 130, 133, 144
Campanile, 263–289
Campanilidae, 263–289
Campanilopa, 280, 281, 283
Campanilinae, 280
Campanulariidae, 380
campechiensis, *Pholas*, 130, 136, 143
canadense, *Chaetoderma*, 375–377
canaliculata, *Pomacea*, 361
Canariella, 168
cancellata, *Limopsis*, 62, 90
candida, *Barnea*, 130, 136
candida, *Pholadomya*, 36, 45, 46, 48–57
Candidula, 151
capensis, *Burnupia*, 234
Cardiomya, 51
Carditacea, 73, 75
carinata, *Bankia*, 144
carinata, *Lyratopherpia*, 380
carinata, *Neomenia*, 379, 381
carinata, *Rhopalomenia*, 382
carinata, *Sandalomenia*, 380
Caucasotachea, 162
caudatus, *Falcidens*, 375, 376
Caudofoveata, 371–375, 393, 395–397, 400, 401, 403, 412–414, 416, 417
Cavibelonia, 381, 396
cawstoni, *Tomichia*, 221, 222, 225, 230, 234, 261, 262
Cecina, 211, 212, 221
ceiba, *Bankia*, 144
centrifuga, *Serpulospira*, 313
Cepaea, 151
Cephalopoda, 291, 321, 371, 372, 387, 390, 392, 394–400
Ceratomyacea, 55
Ceratomyopsidae, 50
Ceratopea, 331
Ceratophallus, 234
Ceratoptilus, 280, 281
Cerion, 2
Cerithiacea, 263–289
Cerithiidae, 280, 285–287
Cerithiopsidae, 286, 287
Cerithium, 280–282, 285
Cernuella, 150, 151
Cetoconcha, 51
Chaceia, 117, 130, 135, 136, 143
Chaenomyidae, 50
Chaetoderma, 373–377, 401
Chaetodermatidae, 373–376, 397, 400
Chaetodermatina, 371
chamaeleon, *Paramuricaea*, 383
Chamidae, 37, 38
Chara, 234
Chelodes, 416
cheveyi, *Aspidopholas*, 144
chiloensis, *Pholas*, 130, 136, 143

- chinensis*, *Caecella*, 101, 102, 104, 106, 108
Chlamys, 25–29
 Chondrinidae, 157, 158
 Chondrulinae, 157, 158
chuni, *Limopsis*, 80, 81
Cidarina, 335
cinnaminiensis, *Pomatiopsis*, 232
cinerea, *Lepidochitona*, 388, 405, 407, 408, 410–412
 Cionellacea, 157
 Cionellidae, 157, 158
 Cirridae, 313, 335
Cirrus, 335, 336
clappi, *Lignopholas*, 136, 143
clappi, *Teredo*, 130, 133, 144
 Clausiliacea, 157
 Clausiliidae, 157–162, 164, 169, 171, 174, 175
 Clausiliinae, 157, 158, 161, 162
Clavagella, 36, 43, 52
 Clavagellacea, 35, 36, 42–44, 48, 50, 52–57
 Clavagellidae, 36, 42–44, 50, 54, 56, 57
clavus, *Uperotus*, 130, 133, 134, 144
 Cleidothaeridae, 36–40, 50, 52–54, 56
Cleidothaerus, 36, 38, 40, 53, 56
clenchi, *Xylophaga*, 136
Clisospira, 331
 Clisospiracea, 292, 311, 330, 331, 334
 Clisospiridae, 331, 332
 Cnidaria, 371, 379–385, 388, 396, 397, 400
cnidevorans, *Dondersia*, 380
Cocculina, 325
 Cocculinacea, 325
 Cocculinidae, 296
 Cocculinoidea, 325
cochleata, *Mimospira*, 331
Cochlicella, 151, 174
 Cochlicopidae, 157
Cochlodesma, 39, 41, 49, 53
 Cochlodininae, 157, 158
 Cochlostomatidae, 177
 Cochlostomatinae, 181, 182
 Codonochelidae, 334
coemansi, *Limopsis*, 66, 71
 Coleoidea, 392, 393
communis, *Acanthochitona*, 388
compacta, *Lecanospira*, 324
compacta, *Montacutona*, 55
complanata, *Mesodesma*, 103
complex, *Dichostasia*, 335
compressa, *Limopsis*, 90
concava, *Xylophaga*, 136, 143
 Conchifera, 371, 389, 390, 393, 395–397, 400, 403–418
Concholepas, 310
conica, *Lacunopsis*, 218
conicum, *Microdoma*, 333
conicus, *Hipponix*, 279
conradi, *Penitella*, 130, 136, 143
conspurcata, *Xerotricha*, 174
convexa, *Xylophaga*, 130
copulobursata, *Rhipidoherpia*, 379, 384
corallensis, *Limopsis*, 71
 Coralliophilidae, 314
Corallium, 380
corallophila, *Nematomenia*, 380
Corbicula, 139
Corbula, 97
cornea, *Mesodesma*, 98
cornuadentata, *Phyllomenia*, 381
coronata, *Hubendickia*, 217, 218
coronata, *Lacunopsis*, 214
coronatum, *Oriostoma*, 313
corrugata, *Terebra*, 365, 366, 368
 Corynidae, 382
Cosa, 75
costata, *Cyrtopleura*, 130, 136, 143
costata, *Jullienia*, 217, 220
costulata, *Hastula*, 364, 366–368
Coxiella, 209, 211, 212, 221, 238
 Craspedopomatinae, 170
Craspedostoma, 334–336
 Craspedostomatacea, 291–336
 Craspedostomatidae, 334
Crassostrea, 99, 108
Cratis, 62, 75
crenagulata, *Neomenia*, 381
Crepidula, 303
crispata, *Zirfaea*, 136, 143
cristata, *Limopsis*, 63, 68, 71, 83
cristata, *Rhopalomenia*, 382
crooki, *Hubendickia*, 217
crooki, *Jullienia*, 217
crooki, *Pachydrobia*, 215
 Crossostomatidae, 334
crossotus, *Falcidens*, 374–377
cruciger, *Cyrtopleura*, 130, 136, 143
 Crustacea, 75
cryophila, *Pruvotina*, 382
Cryptolaria, 382
 Crysogorgiidae, 384
 Ctenidiobranchia, 391
cumingi, *Limopsis*, 67, 82, 83
cumingiana, *Caecella*, 106, 108
cumingii, *Jouannetia*, 136, 143
cuneiformis, *Martesia*, 136, 143
curta, *Diplothyra*, 136, 143
Cuspidaria, 45, 50, 51, 56
 Cuspidariacea, 35, 54–57
 Cuspidariidae, 36, 38, 44, 45, 47, 49–52, 54, 56, 57
cuspidata, *Cuspidaria*, 51
Cycas, 184
 “Cyclonema,” 333
Cyclopecten, 27, 28
 Cyclophoracea, 177, 180, 181, 360, 361
Cyclosporgia, 316
cylindrica, *Hubendickia*, 218
Cylindropalaina, 180, 200
Cylindrus, 151, 175
 Cypraeacea, 284
 Cyrtodontidae, 75
Cyrtopleura, 117, 130, 134–136, 143
dactylus, *Pholas*, 130, 136, 143
dalli, *Limopsis*, 81
dalyelli, *Neomenia*, 381
Danilia, 334, 335
dannevigi, *Limopsis*, 93

- darwini*, *Nettastomella*, 136, 143
Daudebardiinae, 157, 158
davisi, *Karelainia*, 216–218
debilis, *Strophomenia*, 383
decussata, *Nipponolimopsis*, 67, 71
Delavaya, 212, 216
Dendronephthya, 383, 384
Dendropoma, 284
Dentaliida, 392
Dentalium, 392
destructa, *Bankia*, 144
Dialidae, 286
Diastomidae, 286, 287
diazii, *Limopsis*, 83
Dichostasia, 334, 335
dichotoma, *Asaphis*, 104
Dicyathifer, 117, 123, 130, 133, 134, 137, 143
diegensis, *Limopsis*, 63, 68, 83, 84, 86
differentis, *Tomichia*, 209–262
dilatata, *Barnea*, 144
Dimyidae, 23
Dinomenia, 382
Diodora, 353, 358
Diozoptysis, 282
Diplommatina, 177, 178, 180, 199, 203, 204
Diplommatinidae, 177–208
Diplommatininae, 177, 182
Diplothyra, 117, 130, 135, 136, 143
Dirocerithium, 283
Discinae, 157, 158
Discohelix, 314
Discula, 151, 175
Discus, 169
docens, *Beraunia*, 313
dominicensis, *Teredothyra*, 130, 133, 143
Donax, 96, 101–105, 107, 108
Dondersia, 380
Dondersiidae, 401
dorsalis, *Xylophaga*, 122, 130, 136, 143
dorsosulcata, *Hemimenia*, 381
Dorymenia, 379, 384, 385
Drepanomenia, 383
Drosophila, 221, 239
drouetina, *Leptaxis*, 175
dryas, *Nausitora*, 144
duchassaingii, *Jouannetia*, 130, 136, 143
dumosa, *Lafoea*, 380
dunlopei, *Nausitora*, 130, 133, 144
duplicata, *Xylophaga*, 136, 143
duryi, *Helisoma*, 408
Ecologarinia, 180
edax, *Nototeredo*, 130, 133, 144
Edmondiidae, 50
elachista, *Limopsis*, 64, 68, 71
Eledone, 392
elegans, *Hydrorissoia*, 217, 218
elephantina, *Odontomaria*, 324
Eleutheromenia, 381, 385
elliptica, *Laternula*, 42
elongatus, *Psilodens*, 373, 376
emarginata, *Thais*, 12
enderbyensis, *Limopsis*, 93
Endodontacea, 157
Endodontidae, 157, 158, 168, 169
Enidae, 157–159, 169–171, 174, 175
Eninae, 157, 160, 164
Enigmonia, 24
Ensis, 97
ensis, *Ensis*, 97
entale, *Dentalium*, 392
Entodesma, 36, 37
Entomostraca, 379, 383
epibionta, *Proneomenia*, 384
Epimania, 384, 385, 401
Epizoanthus, 383
erecta, *Xylophaga*, 136, 143
erosa, *Geloina*, 52
erosa, *Polymesoda*, 52
eruditum, *Chaetoderma*, 375, 376
Euciroa, 50
Euconulidae, 157, 158
eucosmus, *Limopsis*, 65, 69, 72, 90, 93
Euomphalacea, 291–336
Euomphalidae, 312–314, 317, 323
Euomphaliinae, 150
**Euomphalina*, 292, 293, 312, 324, *325
Euomphalopteridae, 312, 313
Euomphalopterus, 313, 314
Euomphalus, 284, 313, 317
Euthyneura, 283
ewingi, *Neopilina*, 389
ewingi, *Vema*, 389
exacuminata, *Hastula*, 364, 367
excavata, *Teredothyra*, 143
eximia, *Poromya*, 50
expansa, *Halewisia*, 215, 218
explanata, *Talona*, 130, 136, 143
Falcidens, 374–377, 413
farciimen, *Anamenia*, 383
farinesi, *Hastula*, 364, 366–368
fascicularis, *Acanthochitona*, 388
Fenouillia, 216
Ferussaciidae, 157, 158, 169
Ficidae, 368
Ficus, 368
fimbriatula, *Bankia*, 111, 112, 117–121, 144
fischeriana, *Pachydrobia*, 215
fischerpietti, *Lacunopsis*, 214, 220
fissitubata, *Sputoherpia*, 383
Fissurellacea, 354
Fissurellidae, 296, 304, 391, 395
fitchi, *Penitella*, 130, 136, 143
flavens, *Nematomenia*, 380
flexuosa, *Halicardia*, 50
floridana, *Lyrodus*, 112, 118–121, 130, 133, 138, 139, 144
flumineae, *Corbicula*, 139
fluviatilis, *Ancylus*, 12
fodiens, *Micromenia*, 379
foliata, *Xylophaga*, 136, 143
Foraminifera, 392
forbesianus, *Hemipecten*, 23–34
Forcepimania, 382
formosa, *Lyonsiella*, 45, 47, 51
forskali, *Limopsis*, 90
forteradiata, *Limopsis*, 69, 90

- Fossarus*, 216, 217
fosteri, *Bankia*, 144
foveatus, *Fossarus*, 216, 217
fragilis, *Barnea*, 144
fragilis, *Lyonsiella*, 44, 45, 47, 50, 51
fragilis, *Martesia*, 130, 136, 143
fragilis, *Parilimya*, 46, 47, 49–51, 55
**fretterae*, *Neomphalus*, 291–*294–361
fruticum, *Bradybaena*, 173
fucifera, *Teredo*, 130, 133, 144
Fukuia, 211, 212, 221
fulleri, *Teredo*, 133, 144
fuscata, *Terebra*, 364–366, 368
fusticula, *Nausitora*, 130, 133, 135, 144
gabbi, *Penitella*, 130, 136, 143
gaederopus, *Spondylus*, 32
galathea, *Neopilina*, 389, 390
galathea, *Xylophaga*, 136, 143
Galeoconcha, 371, 388–390
Gastrocoptinae, 163
Gasterodontinae, 157, 158
Gastropoda, 5–13, 263–289, 291–361, 363–369, 371, 387, 390, 391, 393–397, 400
Geloina, 52
Genitoconia, 380
Geomitrinae, 150, 151, 153, 154, 158, 168, 170, 171
Gephyroherpia, 381
gerda, *Xylophaga*, 136
Gersemia, 383
gerstfeldti, *Perforatella*, 151
giganteum, *Campanile*, 264, 268, 280
giganteum, *Cerithium*, 281
gigas, *Campanile*, 282
gigas, *Cerithium*, 281
gigas, *Ostrea*, 108
gigas, *Telescopium*, 280
glabrata, *Atactodea*, 105, 107
globosa, *Jouannetia*, 130, 136, 143
globosa, *Lacunopsis*, 214
globosa, *Xylophaga*, 122, 136, 143
Glycymerididae, 61, 62, 74
Glycymeris, 62, 69
glycymeris, *Glycymeris*, 62
gochenouri, *Hubendickia*, 218
gomphoceras, *Campanile*, 282, 283
Gorgonaria, 382–384
gorgonophila, *Anamenia*, 379, 383, 385
gouldi, *Bankia*, 111, 112, 117–122, 127, 130, 133, 139, 140, 144
Gourmya, 285
gourmyi, *Gourmya*, 285
gowllandi, "*Eclogarinia*," 180
gracilis, *Bankia*, 144
gracilis, *Hydrorissioia*, 217
Grammaria, 380, 382
Grammysidae, 50
granulata, *Acanthopleura*, 406, 408, 409
granulata, *Poromya*, 47
grevei, *Xylophaga*, 136, 143
guineensis, *Xylophaga*, 144
Guianadesma, 35, 53, 55
gutta, *Hydrocena*, 170
gutturosus, *Falcidens*, 375–377, 413
Gymnomorpha, 393
Gymnosomata, 396
hadalis, *Xylophaga*, 136, 143
Halewisia, 210–212, 215, 218
Halicardia, 50
Haliotidae, 296
Haliotis, 35
Hanleya, 388, 409
hanleyanus, *Donax*, 96, 101–104, 107
hanleyi, *Hanleya*, 388
hanseni, *Paraprososthenia*, 216, 217
harmandi, *Jullienia*, 217, 218
harmandi, *Lacunopsis*, 214, 220
harpagata, *Dorymenia*, 384
harpagata, *Lepidomenia*, 380
hartmani, *Falcidens*, 375
Hastula, 364, 366–368
hawaiiense, *Chaetoderma*, 376
healdi, *Psiloterdeo*, 130, 133, 140, 144
Heathia, 380
hedleyi, *Nausitora*, 130, 133, 144
helenae, *Limopsis*, 71
Helicacea, 157
Helicella, 150
Helicellinae, 149–176
Helicidae, 149–176
Helicigoninae, 150–153, 155, 158
Helicinae, 150, 151, 153, 155, 158, 162, 168
Helicodontidae, 150
Helicodontinae, 150, 151, 153, 155, 158, 168
Helicoidea, 150
Helicopsis, 150
Helicostylinae, 175
Helicotoma, 314, 324
Helicotomidae, 314
Helisoma, 408
Helix, 153, 169
Helixena, 151, 174, 175
Hemicycla, 168, 171
Hemimenia, 379, 381
Hemipecten, 23–34
hendrickxi, *Hydrobia*, 233, 234
herwigi, *Neomenia*, 381
Heterodonta, 115
Heteropoda, 371, 391, 395
Heterurethra, 157, 158
Hexacorallia, 380–383
Hinnites, 23, 26, 27, 31, 32
Hippocampoides, 314
Hipponicacea, 358
Hipponix, 279
hirondellei, *Meromenia*, 383
hirtella, *Limopsis*, 93
hoeninghausii, *Limopsis*, 66, 71
hoffmani, *Dorymenia*, 384
Holopea, 333
Holopeidea, 333
Holopoda, 157, 158
Holopodopes, 157, 158
horrida, *Laevicordia*, 47
hortensis, *Cepaea*, 151
hospitalis, *Hydrorissioia*, 218

- Hubendickia*, 209–262
hubrechtii, *Dinomenia*, 382
humilior, *Palaina*, 200
Humphreyia, 43
hupensis, *Oncomelania*, 218, 230, 239
hyalina, *Neopilina*, 389
hyalina, *Vema*, 389, 390
Hydrobia, 209–262
Hydrobiidae, 218, 222, 236
Hydrobiinae, 218
Hydrocena, 170
Hydrorissoia, 211, 212, 216–218, 230
hydrorissoidea, *Karelainia*, 217
Hydrozoa, 380, 382, 384
Hygromiidae, 150
Hygromiinae, 150, 151, 153, 155, 158–160, 162–164, 174
Hypomenia, 382
Hystericella, 151
idonea, *Limopsis*, 83
Ilaira, 334
Imeroherpia, 381
impexa, *Pruvotina*, 378
inaequivalvis, *Pandora*, 37, 38, 55
incerta, *Pachydrobia*, 215
indica, *Limopsis*, 81, 83
indica, *Strophomenia*, 379, 383, 385
indica, *Xylophaga*, 136, 143
infundibulum, *Lesueurilla*, 324
ingolfia, *Xyloredo*, 130, 136
Inoceramidae, 75
inornata, *Barnea*, 144
insperata, *Danilia*, 335
intergenerica, *Syngenoherpia*, 384
intermedia, *Hemimenia*, 379, 381
intermedia, *Limopsis*, 83
intermedium, *Chaetoderma*, 375, 376
Isognomostoma, 150, 164
Jaminiinae, 157, 158
janeiroensis, *Limopsis*, 81, 83
Janulus, 169
japonica, *Acanthogorgia*, 383
japonica, *Nettastomella*, 130, 136, 143
japonica, *Xylophaga*, 144
japonicum, *Chaetoderma*, 376
johnsoni, *Teredo*, 144
Jouannetia, 117, 124, 130, 135, 136, 143
Jouannetiinae, 117, 123, 124, 126, 127, 143
juarezi, *Limopsis*, 86
Jullienia, 211, 212, 216–218, 220
Jullieniini, 210–212, 214–218, 222
Karelainia, 211, 212, 216–218, 222
kearneyi, *Palaeotrochus*, 333
Kelliella, 392
knockeri, *Hastula*, 366
knoxii, *Nototeredo*, 130, 133, 144
knudseni, *Xylophaga*, 144
**kuniorum*, *Palaina*, 186–190, 200, *204
Kuphinae, 112, 115–117, 124, 126, 127, 143
Kuphus, 111–148
Labidoherpis, 382
labrosa, *Neomenia*, 381
lacazei, *Strophomenia*, 383
Lacunopsini, 210–212, 214, 215, 218
Lacunopsis, 211, 212, 214, 218, 220
laeve, *Cerithium*, 218, 282
laeve, *Pyrazus*, 282
laeve, *Telescopium*, 282
Laevicordia, 47
laevis, *Ceratoptilus*, 282
laevis, *Straparollus*, 313, 317
Lafoea, 380
Lafoeidae, 382
Lambis, 287
Lamellaria, 306
Lamellibranchia, 391
lamellosa, *Barnea*, 130, 136, 143
lamellosa, *Thais*, 12
laminata, *Dondersia*, 380
laminata, *Neomenia*, 381
lanceolata, *Cyrtopleura*, 130, 136, 143
lanceolata, *Limopsis*, 83
Lanistes, 315, 323, 332
lapidaria, *Pomatiopsis*, 230, 232, 249
lata, *Limopsis*, 89
Laterrula, 42, 53
Laternulidae, 36, 39–42, 49, 50, 53–56
latosoleata, *Alexandromenia*, 382
laxopharyngeata, *Sputoherpia*, 383
Lecanospira, 323, 324, 331
Leiostyla, 169
Lejeania, 151
Lepetellacea, 325
lepida, *Hastula*, 364, 366–368
Lepidochitona, 388, 405, 407, 408, 410–412
Lepidomenia, 380
Lepidopleuridae, 387, 388
Leptaxinae, 150–153, 158, 168, 170, 174
Leptaxis, 175
Leptonacea, 55
Lesueurilla, 292, 314, 323, 324
Levantina, 162
levayi, *Paraprososthenia*, 217
leve, *Cerithium*, 280, 282
Lignopholas, 115, 117, 124, 130, 134–136, 140, 143
lilliei, *Limopsis*, 65, 70, 72, 73, 75, 82, 91, 93
lilydalensis, "*Cyclonema*," 333
Limacidae, 157, 158
Limidae, 26, 46
Limifossor, 373, 375, 376
Limifossoridae, 374, 376
Limnoria, 111
Limopsacea, 73
Limopsidae, 61–93
Limopsis, 61–93
Lindholmiolinae, 150
linsa, *Sallya*, 333
Liomphalus, 314–316
liosgameus, *Falcidens*, 377
lirata, *Assimineia*, 225, 261
Liotia, 336
Liotiidae, 292, 314, 317, 334–336
Liotiinae, 334
lirata, *Tomichia*, 225
lissa, *Hastula*, 367

- Lithoglyphopsis*, 212, 215
 Litiopidae, 286
Littorina, 211, 220
 Littorinacea, 335
 Littorinidae, 211, 215, 285
lituifera, *Ocheyoherpia*, 381
Lituiherpa, 381
lobata, *Xylophaga*, 136, 143
logani, *Maclurites*, 331
Loligo, 392, 393
longipilosa, *Limopsis*, 83
longispinosa, *Pruvotina*, 381
Lophomenia, 382
loringi, *Limopsis*, 62, 65, 69, 70, 72, 73, 90, 93
loscombiana, *Pholadidea*, 106, 108, 130, 136, 143
lubbocki, *Weeksia*, 313
Lutraria, 95, 101
lutraria, *Lutraria*, 101
Lymnaea, 5–13
Lyonsia, 36, 37, 44, 52
Lyonsiella, 44, 45, 47, 50, 51
Lyonsiellidae, 36, 51
Lyonsiidae, 36–39, 53–56
Lyratoherpia, 380
Lyrodus, 111–148
Lytocarpia, 380–382
mabillana, *Limopsis*, 83
macgillivrayi, *Limopsis*, 90
macgillivrayi, *Palaina*, 178, 180
 Macluritacea, 291–336
Maclurites, 330, 331
 Macluritida, 318
 Macluritidae, 313, 323, 331
 Macluritina, 293, 310, 325
 Macluritoidea, 325
 Macropalaina, 180, 210, 204
Mactra, 95, 101, 106–108
 Mactracea, 95
 Mactridae, 56, 104
mactroides, *Mesodesma*, 95–110
mactroides, *Tivela*, 98, 103, 107
maggae, *Limopsis*, 72
 Magilinidae, 314
magnifica, *Calyptogena*, 292
malleolus, *Teredora*, 130, 133, 144
Malleus, 24
manilensis, *Barnea*, 144
manni, *Dicyathifer*, 130, 133, 143
maorianus, *Cleidothaerus*, 40
**mareana*, *Palaina*, 182, 186–190, 200, 204, 205,
 *206, 207
 Margaritariidae, 50
Margarites, 311
mariei, *Cylindropalaina*, 200
mariei, *Diplommatina*, 200
mariei, *Palaina*, 177–208
marionensis, *Limopsis*, 62, 63, 67, 74, 80, 81
martensi, *Bankia*, 144
Martesia, 111–148
 Martesiinae, 111–148
massa, *Lyrodus*, 130, 133, 134, 144
massei, *Lacunopsis*, 214, 220
Matthavia, 416
matocotana, *Teredothyra*, 130, 133, 143
maximus, *Pecten*, 26, 28
medilobata, *Lyrodus*, 130, 133, 144
mediterranea, *Corbula*, 97
 Megadesmidae, 50
megaradulata, *Sputoherpia*, 383
 Megaspiridae, 175
megathecata, *Pruvotina*, 381
megotara, *Psiloteredo*, 127, 130, 133, 134, 144
melanoides, *Neodiasoma*, 287
melanura, *Pholadidea*, 130, 136, 143
mera, *Mactra*, 106–108
Meromenia, 383
mesenterina, *Turbinaria*, 29
Mesodesma, 95–110
 Mesodesmatidae, 95–110
 Mesogastropoda, 170, 180, 209–263, 284, 286,
 292, 310, 323, 353–355, 359–361, 390, 394
 Mesurethra, 157, 158
Metachaetoderma, 373, 395
 Metafruticicolinae, 150
Metamenia, 382
mexicana, *Xylophaga*, 136, 143
micans, *Hastula*, 366
Microdoma, 333
 Microdomatacea, 292, 311, 330, 333
 Microdomatidae, 333
Micromenia, 379, 380
microps, *Limopsis*, 72
 Milacidae, 157, 158
militare, *Chaetoderma*, 377
Mimospira, 331, 332
mindanensis, *Teredo*, 144
minima, *Limopsis*, 66, 70, 71
minima, *Oncomelania*, 239
minor, *Leptaxis azorica*, 175
minuta, *Limopsis*, 63, 64, 68, 69, 87–89
misjae, *Limopsis*, 71
modesta, *Terebra*, 364, 365
 Modiolidae, 75
 Modiomorphacea, 75
 Modulidae, 285, 286
 Mollusca, 1–4, 371–418
Monacha, 150, 153, 155, 158
 "Monachines," 150
Monilearia, 168, 171
Monodonta, 357
 Monoplacophora, 321, 388–390
 Monostichoglossa, 385
 Monotocardia, 323, 355, 361
Montacutona, 55
montereyense, *Chaetoderma*, 375, 376
montrouzieri, *Diplommatina*, 199
montrouzieri, *Palaina*, 181, 182, 185–196, 198–
 201, 204, 205
Mopalia, 388
 Mopaliidae, 388
multirugosus, *Hinnites*, 27, 31, 32
multistriata, *Limopsis*, 65, 69, 82, 88, 89, 90
munensis, *Jullienia*, 217
 Murchisonioidea, 325
Murella, 151
 Muricacea, 383

- muroaki*, *Xylophaga*, 136
murrayi, *Xylophaga*, 136, 143
mutabilis, *Strombus*, 287
Mya, 15
Myadora, 37–39, 52
Myochama, 36, 37, 52
Myochamidae, 36–40, 52–54, 56
Myoida, 115
myriophyllum, *Lytocarpia*, 380–382
Mytilacea, 23–25
Mytilidae, 75, 293, 309
Mytilimeria, 37
Mytilus, 15, 19
naceli, *Xyloredo*, 136, 143
nanae, *Limopsis*, 71
**nanodes*, *Palaina*, 182, 187–190, *203
nanulum, *Chaetoderma*, 376
Napaestinae, 157, 158, 170
Napaeus, 169, 174, 175
natalensis, *Ceratophallus*, 234
natalensis, *Tomichia*, 209–262
natalis, *Limopsis*, 64, 87, 89
Nausitora, 116, 117, 123, 130, 133–135, 140, 144
Nautiloidea, 321
Nautilus, 392, 393
navalis, *Teredo*, 112, 117–122, 127, 130, 133, 144
Nematomenia, 379, 380, 416
Nemertesia, 381
Nemertini, 395
Neobankia, 116
Neodiastoma, 287
Neogastropoda, 263, 286, 310, 371, 390, 391, 394–396
Neolepas, 321
Neoloricata, 404
Neomenia, 379, 381
Neomeniamorpha, 380
Neomeniina, 371
**Neomphalacea*, 292, 293, *294, 312, 324
**Neomphalidae*, 292, *294, 309, 320–322
**Neomphalus*, 291–*294–361
Neopilina, 137, 372, 389, 390, 393–396, 415
Neopilinidae, 321
Neoteredo, 117, 123, 127, 130, 133, 134, 137, 143
Neotrigonia, 287
Nephthya, 384
Nerineidae, 282, 283
Neritacea, 292, 323, 330, 359, 361
Neritidae, 215, 296, 316
Neritina [suborder], 325
Neritopsina, 390, 393
Nettastomella, 117, 124, 130, 134–136, 143
Nevadispira, 317
neztalia, *Bankia*, 144
nierstraszi, *Hypomenia*, 382
niphas, *Leptaxis*, 175
nipponense, *Halicardia*, 50
Nipponolimopsis, 67, 71
Nipponopanacca, 46, 47
**nissidiophila*, *Palaina*, 182, 186–193, 195, 196, 198, 201–*203
nitidulum, *Chaetoderma*, 374–376
Nododelphinulidae, 335, 336
Noetiidae, 72
nooi, *Xyloredo*, 136, 143
nordenskioldii, *Zenobiella*, 151
northi, *Liomphalus*, 315, 316
norvagica, *Nototeredo*, 127, 130, 133, 144
norvegica, *Lyonsia*, 36, 37
Nototeredo, 116, 130, 133, 134, 138, 144
novaezealandiae, *Mesodesma*, 103
nucula, *Jullienia*, 217
Nuculidae, 371, 391, 395
nuttalli, *Schizothaerus*, 107
obesa, *Diplommatina*, 201
obesa, *Macropalaina*, 201
obesa, *Palaina*, 186–190, 196, 201, 202
obliqua, *Limopsis*, 83
oblonga, *Limopsis*, 68, 70, 84, 87
obtecta, *Aspidopholas*, 144
obturatorium, *Barnea*, 144
obtusa, *Spathoteredo*, 130, 133, 144
obtusa, *Xylophaga*, 136
obtusata, *Xylophaga*, 143
obtusatus, *Cylindrus*, 151, 175
Ocheyoherpia, 381
Octobranchia, 392
Octocorallia, 379, 383, 394
Octopus, 393
Odontomaria, 314, 324
Offadesma, 41, 42, 44, 53, 55
Oleacinacea, 157
Oleacinidae, 157, 158
oligotropha, *Neopilina*, 390
Omphalocirridae, 312–314, 316, 317
Omphalocirrus, 313, 331
Omphalotrochidae, 312–315, 323
Omphalotrochus, 313, 316
Onchidella, 390, 393
Oncomelania, 211, 212, 218, 221, 230, 239, 254
Onychochilidae, 331, 332
Onychochilus, 331, 332
oolithica, *Limopsis*, 66, 70
**opaoana*, *Palaina*, 182, 185–192, 195–198, 200, 201, 204–*205–206
opercularis, *Chlamys*, 28
operculata, *Cryptolaria*, 382
ophidiana, *Strophomenia*, 384
Opisthobranchia, 310, 394
Opisthostoma, 182
Orculidae, 157, 158, 163
orcutti, *Bankia*, 144
orientalis, *Pholas*, 144
Oriostoma, 313, 314, 316
Oriostomatacea, 311, 330
Oriostomatidae, 312–317, 323
Orthurethra, 158
Ostracoda, 392
Ostrea, 15, 74, 108
Ovalarca, 72
ovoidea, *Chaceia*, 130, 136, 143
Oxychilus, 169
Ozaena, 392, 393
Pachydrobia, 210–212, 215, 216, 218, 220, 236
Pachydrobiella, 211, 212, 216–218
pachyptila, *Riftia*, 292, 307

- pacifica*, *Euciroa*, 50
Paedhoplitinae, 150
Palaeobranchia, 391
Palaeotaxodonta, 50, 54
Palaeotrochacea, 292, 311, 330, 333
Palaeotrochidae, 333
Palaeotrochus, 333
Palaina, 177–182, 185–207
pallioglandulata, *Pruvotina*, 381
Paludina, 225
Panacca, 46, 47
panamensis, *Limopsis*, 86
panamensis, *Uperotus*, 130, 144
panamensis, *Xylophaga*, 136, 143
Pandanus, 178
Pandora, 37, 38, 55
Pandoracea, 35–39, 42, 44, 50, 52–57
Pandoridae, 36–39, 50, 54, 56
Papuinae, 175
paradoxa, *Limopsis*, 81
Paragalerus, 309
Paramuricaea, 383
Parapholas, 117, 130, 135, 136, 143, 144
Paraprososthenia, 211, 212, 216, 217
Parapyrgula, 212, 216
Pararhytida, 203
Parilimya, 36, 45–47, 49–53, 55–57
Parilimyidae, 45, 47, 50, 56
parksii, *Teredo*, 144
Parmacellidae, 157, 158
Partula, 2
parva, *Barnea*, 130, 136, 143
Patella, 2, 315, 390
Patellacea, 296, 310, 314, 353, 354, 358
Patellida, 391, 395
Patellina, 310
paucidentata, *Dorymenia*, 384, 385
Pecten, 23, 25, 26, 28, 29
Pectinacea, 23–23
pectinata, *Jouannetia*, 136, 143
Pectinibranchia, 359
Pectinidae, 23, 26–28, 32, 42, 46
pectunculoides, *Bathyarca*, 69
pedicellatus, *Lyrodus*, 139, 144
Pedum, 23, 26–31
Pelagiella, 331
pellucida, *Hubendickia*, 218
penelevis, *Limopsis*, 93
Penicillus, 43
penis, *Brechites*, 43
penita, *Penitella*, 136, 143
Penitella, 117, 130, 135, 136, 143, 144
pentangulatus, *Euomphalus*, 313
peregra, *Lymnaea*, 5–13
Perforatella, 151
perieri, *Limopsis*, 83
Periploma, 53
Periplomatidae, 36, 39–42, 49, 50, 53–56
permagna, *Neomenia*, 381
Perna, 74
Pernopectinidae, 27
perroquini, *Diplommatina*, 204
perroquini, *Macropalaina*, 204
perroquini, *Palaina*, 180, 182, 186–190, 204, 205
perticata, *Drepanomenia*, 383
Petalococonchus, 284
Phaedusinae, 157, 158, 161
phaseolina, *Thracia*, 39–41
Phasianellidae, 296, 311
Phenacolepadidae, 296
philippii, *Bankia*, 144
Philippia, 368
Philobrya, 75
Philobryidae, 61, 62, 71, 75
Pholadacea, 111–148
Pholadidae, 111–148
Pholadidea, 106, 108, 117, 130, 135, 136, 143
Pholadina, 115
Pholadinae, 117, 126, 138, 143
Pholadomya, 36, 45–57
Pholadomyacea, 35, 36, 45–48, 50, 52, 53, 55–57
Pholadomyidae, 45–49, 53, 56
Pholadomyoida, 35, 36, 50, 56
Pholas, 117, 130, 135, 136, 143, 144
Pholidoskepia, 380, 401
Phyllomenia, 381
physa, *Onychochilus*, 331
pilsbryi, *Zirfaea*, 130, 136, 143
Pinctada, 23, 24
Pinnacea, 75
pisana, *Theba*, 174
Placiphorella, 388
Placophora, 371, 385–388, 393–397, 400, 403–418
Placuna, 24, 31
plana, *Scrobicularia*, 15–21
Planaxidae, 286, 287
planetica, *Cardiomya*, 51
planispira, *Saduniella*, 217
planulata, *Helicotoma*, 324
Platyacridae, 313, 335
Platyceras, 333
Platyceratacea, 311, 314, 330, 333
Platyceratidae, 333
platypoda, *Nematomenia*, 380
Pleuroceridae, 286
Pleuromyidae, 50
pleuronectes, *Amusium*, 28
Pleurotomaria, 357
Pleurotomariacea, 292, 310, 312, 314, 323, 324, 331, 354
Pleurotomariidae, 292, 296, 298, 304, 310, 312, 321, 331
Pleurotomariina, 331
Pleurotomarioidea, 325
plicaria, *Terebra*, 354, 365
plicatula, *Hastula*, 364, 366
Plicatulacea, 23, 32
Plicatulidae, 23
pliocenicum, *Terebra*, 364, 365, 367, 368
poculifer, *Teredo*, 130, 133, 140, 144
Pododesmus, 27
Poiretia, 160, 161
poirieri, *Paraprososthenia*, 217
Poleumitidae, 313
polita, *Hubendickia*, 217, 218, 220
Polygyracea, 157

- Polygyridae, 150, 157
Polymesoda, 52
polypapillata, *Spengelomenia*, 382
 Polyplacophora, 386–388
polythalamia, *Kuphus*, 130, 133, 137, 143
polyzonias, *Sertularella*, 382
Pomacea, 361
Pomatias, 170
 Pomatiopsidae, 209–262
 Pomatiopsinae, 209–262
Pomatiopsis, 209–262
Porites, 28
Poromya, 45, 47, 50, 51, 56
 Poromyacea, 35, 36, 39, 44, 45, 48–50, 53–57
 Poromyida, 391
 Poromyidae, 36, 38, 44–47, 49–51, 54, 56
porosa, *Heathia*, 380
portoricensis, *Teredo*, 144
 Potamididae, 283, 286, 287
praedatoria, *Proneomenia*, 384
praegnans, *Pruvotina*, 381
praestans, *Xylophaga*, 122, 136, 143
praetenue, *Cochlodesma*, 41
princesae, *Teredora*, 130, 133, 134, 144
prisca, *Archaeomenia*, 379, 380
procera, *Spengelomenia*, 382
Prochaetoderma, 373–377
 Prochaetodermatidae, 376
Procrucibulum, 309
producta, *Tomichia*, 225, 230, 262
profunda, *Dorymenia*, 384
profunda, *Xylophaga*, 136
 Progalerinae, 332
Progalerus, 309
Proneomenia, 379, 384
 Propeamussiidae, 23, 26–28, 32
Propeamussium, 27, 28
proprietecta, *Neomenia*, 381
 Prosobranchia, 177–289, 292, 354, 360, 363, 368, 390, 391, 393–395
protecta, *Forcepimena*, 382
 Protobranchia, 391, 395
Protocalyptraea, 309
Pruvotina, 378, 381, 382, 395
Pseudomalaxis, 334
 Pseudophoracea, 292, 311, 314, 330, 332, 333
 Pseudophoridae, 333
Psilodens, 373, 376, 395
Psiloteredo, 116, 117, 123, 130, 133, 134, 137, 140, 144
 Ptenoglossa, 391
 Pteriacea, 23, 24, 26, 75
 Pteriidae, 24
 Pterioidea, 24, 35, 53–55, 57
 Pteriomorpha, 24
pulchella, *Teredo*, 116
 Pulmonata, 5–13, 310
 Punctinae, 157, 158
Punctum, 168
 Pupillacea, 157
 Pupillidae, 157, 158, 169
 Pupillinae, 163
 Pyramidulidae, 157, 158
Pyrasmus, 282
quadra, *Pholadidea*, 130, 136
quadridens, *Imeroherpia*, 381
quadrizonata, *Parapholas*, 144
quillingi, *Jouannetia*, 136, 143
radians, *Calyptraea*, 214, 220
raduliferum, *Prochaetoderma*, 375, 376
ravni, *Limopsis*, 71
recisum, *Chaetoderma*, 375
rectum, *Chaetoderma*, 375
reedsii, *Amphiscapha*, 313
regularis, *Strophomenia*, 383
renschii, *Teredo*, 144
reticulare, *Terebra*, 364, 365, 367, 368
Retinella, 169
reynei, *Neoterodo*, 130, 133, 137, 143
 Rhipidoglossa, 325
Rhipidoherpia, 379, 384
Rhopalomenia, 379, 382, 385
rhynchopharyngeata, *Rhopalomenia*, 382
Riftia, 292, 295, 307, 308
rikuzenica, *Xylophaga*, 136, 143
Rissoa, 392
 Rissoacea, 354
 Rissoidae, 285
rivicola, *Lignopholas*, 130, 136, 143
Robertsiiella, 212
robustus, *Scutopus*, 373, 376, 377
rochi, *Bankia*, 144
rogersi, *Hydrobia*, 262
rogersi, *Tomichia*, 209–262
rolfbrandti, *Jullienia*, 217
rolfbrandti, *Lacunopsis*, 214
rosea, *Genitoconia*, 380
rostrata, *Nettastomella*, 130, 136, 143
rubiginosa, *Zenobiella*, 151
rubrum, *Corallium*, 380
ruizana, *Limopsis*, 81
 Saccoglossa, 385
Saduniella, 211, 212, 214, 217
Salicornia, 231–233
salleana, *Hastula*, 367, 368
Sallya, 332, 333
sanctaemariae, *Helixena*, 151, 174, 175
Sandalomenia, 380
sansibarica, *Limopsis*, 81
saulii, *Nausitora*, 144
saxicola, *Entodesma*, 37
scalaris, *Limopsis*, 72
scandens, *Strophomenia*, 384
 Scaphopoda, 387, 391, 393–397, 400
schizoradulata, *Simrothiella*, 378
Schizothaerus, 107, 108
schneideri, *Nausitora*, 144
Scissurella, 357
 Scissurellidae, 296, 331
scotiana, *Limopsis*, 93
Scrobicularia, 15–21
 Scutopoda, 372, 396
Scutopus, 372, 374–377
 Seguenziacea, 325
 Seguenziidae, 296, 311, 315
senegalensis, *Psiloteredo*, 130, 133, 144
senegalensis, *Terebra*, 364–366, 368
Sepia, 393

- Septemchitonida, 416
septemradiatus, *Chlamys*, 28
 Septibranchia, 391, 395, 396
 Septibranchioidea, 36, 50
Serpulorbis, 284
Serpulospira, 313, 315, 317
Sertularella, 382
sertulariicola, *Rhopalomenia*, 382
 Sertulariidae, 382
 setacea, *Bankia*, 130, 133, 144
Sialoherpia, 383
siamensis, *Hubendickia*, 218
siberutensis, *Limopsis*, 81
sierra, *Eleutheromenia*, 381, 385
Sigmurethra, 157, 158
similis, *Barnea*, 144
simplex, *Micromenia*, 380
Simrothiella, 378
sinuosum, *Guianadesma*, 35, 53
 Siphonodentaliida, 392
 Siphonopoda, 372, 387, 390, 392–397, 400
 Skeneidae, 296, 311
sluiteri, *Proneomenia*, 379
smithi, *Diplothyra*, 130, 136
smithi, *Teredothyra*, 144
soboles, *Limopsis*, 62, 69, 93
Solemyda, 391
 Solenidae, 56
 Solenogastres, 371, 377–379, 385, 393, 395–397, 400, 401, 403, 413, 414, 416
solidissima, *Mactra*, 101
somersi, *Teredo*, 144
sopita, *Pruvotina*, 382, 385
soyoe, *Limopsis*, 90
spatha, *Spathoteredo*, 130, 133, 144
Spathoteredo, 117, 123, 130, 133, 134, 144
Spengelomenia, 382
spermathecata, *Lituiherpia*, 381
sphaerica, *Lacunopsis*, 214
Sphaeroma, 111
 Sphincterochilinae, 150, 151, 153, 158, 174
spicata, *Limopsis*, 83
spinosa, *Anamenia*, 383
spinosa, *Labidoherpia*, 382
spinosa, *Pachydrobia*, 215
spinulosum, *Craspedostoma*, 335
spiralis, *Hubendickia siamensis*, 218
spiralis, *Lophomenia*, 382
Spisula, 95, 101
 Spondylidae, 23, 26, 27, 32, 46
spondyloideum, *Pedum*, 27–29
Spondylus, 26, 27, 32
Sputoherpia, 383
squamosum, *Chaetoderma*, 376
Stenzelia, 72
Sterrofustia, 381
stillerthrocytica, *Proneomenia*, 384
stimpsoni, *Limopsis*, 83
 Stomatellidae, 310, 311, 333
strangei, *Palaina*, 205, 207
Straparollus, 313, 317
 Streptaxidae, 173, 175
 Striarcinae, 72
striata, *Hastula*, 364–366
striata, *Martesia*, 112, 116–121, 130, 136, 138, 143
striata, *Myadora*, 37, 39
Strioterebrum, 364, 365
 Strobilopsinae, 157, 158
 Strombidae, 263, 287
Strombus, 287
Strophomenia, 379, 380, 383–385
stylastericola, *Dondersia*, 380
 Stylasteridae, 380
 Stylommatophora, 149, 171, 173
subcinerea, *Hastula*, 364, 366, 367
subpersonatum, *Isognomostoma*, 150, 164
subtruncata, *Barnea*, 130, 136, 143
 Subulinidae, 157, 158, 175
 Succineacea, 157
 Succineidae, 157, 158
suessi, *Anisostoma*, 335
sulcata, *Hubendickia*, 217, 218, 220
sulcata, *Limopsis*, 83
supplicata, *Xylophaga*, 136, 143
surinamensis, *Limopsis*, 81
symbolicum, *Campanile*, 263–289
symmetrica, *Holopea*, 333
 Syncyclonemidae, 27
Syngenoherpia, 384
 Syntheciidae, 382
Tacheocampylaea, 151
tajimae, *Limopsis*, 81
takanoshimensis, *Lyrodus*, 133, 144
Talona, 117, 130, 135, 136, 143
talpoideus, *Limifossor*, 375, 376
tasmani, *Limopsis*, 83
Teiichispira, 330
Telescopium, 280–282
 Tellinacea, 15–21, 46
tenella, *Limopsis*, 62, 63, 67, 74, 81, 82
tengulata, *Nematomenia*, 379, 380
tenisoni, *Limopsis*, 90
tenuiradiata, *Limopsis*, 90
teramachii, *Xylophaga*, 144
terceirana, *Leptaxis*, 175
Terebra, 364–368
Terebralia, 281, 282
 Terebridae, 363–369
terebrinum, *Terebra*, 365
Teredina, 115, 116
 Teredinidae, 111–148
 Teredininae, 115–117, 124, 127, 138, 139, 143
Teredo, 111–148
Teredora, 116, 117, 123, 130, 133, 134, 135, 144
Teredothyra, 117, 123, 130, 133, 134, 137, 143, 144
 Testacellacea, 157
 Testacellidae, 157, 158
tetragona, *Arca*, 62
Thais, 12
Theba, 174
thermydron, *Bythograea*, 307
 Thiariidae, 287
thoracites, *Bactronophorus*, 130, 133, 137, 143
Thracia, 39–42, 49, 54, 55
 Thraciacea, 35, 36, 39–42, 44, 49, 50, 53–57
 Thraciidae, 36, 39–42, 49, 53–57
Tibia, 287

- Tivela*, 98, 103, 107
Tomichia, 209–262
tomlini, *Xylophaga*, 144
tornata, *Poromya*, 47
torresi, *Limopsis*, 90
totteni, *Hydrobia*, 218, 219
trapeziformis, *Neomenia*, 381
triangularis, *Anamenia*, 383
triangularis, *Teredo*, 144
tricarinata, *Dorymenia*, 384
tricarinata, *Rhopalomenia*, 382
Trichiinae, 150
Tricula, 209–262
Triculinae, 209–262
Triculini, 209–262
Triforidae, 368
Triforis, 368
triglandulata, *Metamenia*, 382
Trigoniacea, 35, 53
Trigoniidae, 287
Trigonochlamydidae, 157, 158
Trinacriinae, 72
trisialota, *Birasoherpia*, 383
tristis, *Hydrobia*, 225
tristis, *Tomichia*, 209–262
Trochacea, 291–336, 353–355, 361
Trochidae, 296, 311, 317, 335, 359
Trochina, 310, 311, 314, 325, 333
Trochita, 332
Trochoidea, 151
Trochoidea, 325
Trochonematacea, 334
tropicus, *Bulinus*, 234
truncata, *Barnea*, 136, 143
truncata, *Laternula*, 42
Truncatella, 225
truncatum, *Cerithium*, 282
Tryblidiida, 371, 388–390, 393, 395–397, 400, 413–415
tuberculata, *Hubendickia*, 217
tubifera, *Pholadidea*, 130, 136, 143
tubulata, *Xylophaga*, 136, 143
Turbellaria, 395
Turbinaria, 29
Turbinidae, 296, 311, 316, 317, 334
Turbinilopsis, 316
turnerae, *Penitella*, 144
turnerae, *Xylophaga*, 130, 136, 143
turricula, *Discula*, 151, 175
turricula, *Hystericella*, 151
Turritella, 319, 321, 322, 332
Turritellidae, 285–287, 291, 321, 322
Tyrodiscus, 169
Umbonium, 311, 324, 333, 359
uniperata, *Pruvotina*, 381
Uperotus, 117, 123, 130, 133, 134, 135, 143, 144
usarpi, *Dorymenia*, 379, 384
Utralvoherpia, 383
vaginata, *Limopsis*, 62, 63, 67, 80, 82
Valloniidae, 157, 158
Valloniinae, 157, 158
Valvata, 285
Valvatacea, 360, 361
vampyrella, *Drepanomenia*, 383
varia, *Chlamys*, 28, 29
variabilis, *Pachydrobia*, 215, 218
Velepallaina, 180
Velutina, 284
Vema, 389, 390
Veneroida, 35, 53–55, 57
ventricosa, *Tomichia*, 209–262
ventricosa, *Truncatella*, 225
ventrolineatus, *Scutopus*, 372, 374–377
Vermetidae, 285–287
Vermetus, 284
verrucosa, *Epimenia*, 384, 385, 401
Verticordiacea, 35, 50, 51, 54–57, 391
Verticordiidae, 36, 39, 44, 45, 47, 49–51, 54–56
Vertiginidae, 157, 158
Vetigastropoda, 325
vetusta, *Leptaxis*, 175
vetustum, *Platyceras*, 333
villosiuscula, *Thracia*, 39–41
virginica, *Crassostrea*, 99, 108
Vitreinae, 157, 158
Vitrinidae, 157, 158, 169
vittatus, *Donax*, 101, 102, 105, 108
Viviparacea, 360, 361
Viviparus, 323
vixinsignis, *Epimenia*, 384
vixornata, *Limopsis*, 65, 70, 72, 91
Volutacea, 368
Volutidae, 285
Vulsella, 74
washingtona, *Xylophaga*, 122, 130, 136, 143
weberi, *Dorymenia*, 384
Weeksia, 313, 314, 316, 320
Weeksiidae, 312, 314, 320
whitneyi, *Omphalotrochus*, 313
whoi, *Xylophaga*, 136
Wireniidae, 401
wolffi, *Xylophaga*, 136, 143
woodwardi, *Limopsis*, 90
Xenophoridae, 317
Xeropicta, 150
Xerosecta, 150
Xerotricha, 174
xylophaga, 111–148
Xylophagainae, 111–148
Xylophaginae, 115
Xylopholas, 115, 117, 124, 130, 135, 136, 143
Xylophoma, 115
Xyloredo, 115–117, 124, 130–137, 143
yoshimurai, *Aspidopholas*, 144
Zachsia, 117, 130, 133, 139, 144
Zebrina, 160
zenkewitschi, *Zachsia*, 130, 133, 139, 144
Zenobiella, 151, 173
zeteki, *Bankia*, 144
zevinae, *Neolepas*, 321
zilchi, *Pachydrobia*, 215
Zirfaea, 117, 130, 135, 136, 143
Zoantharia, 383
zonalis, *Limopsis*, 81
Zonitinae, 157, 158, 160, 162
Zonitacea, 157
Zonitidae, 157–159, 169
zwellendamensis, *Paludina*, 225
zwellendamensis, *Tomichia*, 209–262

INSTRUCTIONS FOR AUTHORS

MALACOLOGIA publishes original studies on the Mollusca that are of international interest and are of high scholarly standards. Both descriptive and experimental research results are acceptable provided they are primarily or exclusively concerned with the phylum. Contributions include long monographs as well as moderately short research papers. Brief papers are not acceptable. MALACOLOGIA provides a forum for such different aspects of malacology as anatomy, comparative physiology, ecology, medical malacology, paleontology and systematics. Papers of only biochemical or physiological interest should be submitted elsewhere. Review articles are more appropriately submitted to *Malacological Review* (P.O. Box 801, Whitmore Lake, Michigan 48189, U.S.A.). All manuscripts submitted are reviewed by at least 2 malacologists. Articles are accepted with the firm understanding that they have not been submitted or published elsewhere in whole or in part.

Manuscripts may be in English, French, German or Spanish, and should follow MALACOLOGÍA style. They must contain a concise but informative Abstract summarizing not only the content but the results. Papers in languages other than English should include a translation of the Abstract into English. Authors desiring their abstracts translated into other languages must provide these. Care should be taken to include all necessary foreign accents. Manuscripts must be typed on one side of good quality white paper, double-spaced throughout, with ample margins, and are to be submitted in triplicate. Illustrations are likewise to be in triplicate (the 2 copies may be photocopies, etc.). Tables, figure captions and all footnotes are to be grouped (in this order) at the end of a manuscript, and all Ms pages (including the Abstract) are to be numbered sequentially. Avoid internal page references (which have to be added in page proof). Make the hierarchy of headings within the text simple and consistent. Suggest an abbreviated running title to be used at the top of each right hand page.

Contributors in English are asked to use the *Council of Biology Editors (CBE) Style Manual* (Ed. 3, 1972), obtainable for \$6.00 from the American Institute of Biological Sciences,

1401 Wilson Boulevard, Arlington, Virginia 22209, U.S.A. MALACOLOGIA follows most of the recommendations in this *Manual*. In particular, simplified particles such as the following are used: numbers above ten should not be written out except at the beginning of a sentence; percentages following a number are expressed as %, and abbreviations of measures (after a number): mm, ml, kg, etc. have no period (full stop), nor an "s" in the plural. Note that the international symbol for micron is now μm , not μ .

Illustrations must be carefully prepared and so planned that they can be printed in 1 column or the full width of a page of the journal. The maximum size of a printed figure is 13.5×20.0 cm (preferably not as high as this so that the caption does not have to be on the opposite page). Drawings and lettering must be in dark black on white, blue tracing, or blue-lined paper. Lines and dots should be thick enough to allow reduction by $\frac{1}{2}$ or $\frac{1}{3}$. This should be taken into consideration also in relation to the lettering. Letters and numbers must not be less than 2 mm in height, preferably larger, after reduction. Several drawings or photographs may be grouped together to fit a page, but drawings are not to be grouped with photographs. Photographs are to be glossy and high contrast. All illustrations are to be numbered sequentially as figures (not grouped as plates), and are to be arranged as closely as possible to the order in which they are first cited in the text (Each figure must be cited in the text.) All original illustrations should be mounted, numbered, labeled or lettered and ready for the engraver. Scale lines are required for all figures and should be convenient lengths (e.g., "200 μm ," not "163 μm "). Magnifications in captions are not acceptable, and neither are photographic reductions of line drawings.

Captions should summarize what is shown in an illustration, and should not duplicate additional information given in the text. Each lettered abbreviation labeling an individual feature in a figure must either be explained in each caption (listed alphabetically), or be grouped in one alphabetic sequence in a section near the beginning of the text (use the latter method if many abbreviations are repeated on different figures).

Tables are to be used sparingly, and should be planned to fit 1 or 2 columns on 1

page. Each table must be submitted double-spaced throughout on a separate manuscript page. Do not use vertical lines.

All **References** cited in the text must be listed (bibliographies including uncited items are unacceptable). Each reference should be cited accurately (the Editors will spot check for accuracy) and should be in the style used in recent issues of MALACOLOGIA—except that beginning with Vol. 16 journal titles will be cited complete and unabbreviated. For all manuscripts submitted henceforth, disregard the abbreviations in MALACOLOGIA, 1972, 11(2): 415–426. The journal uses the ampersand (&) for “and”; “et al.” may be used in the text, but not in the References. In addition to the volume number, complete page numbers of articles and books must be cited. If plates or maps, etc., are not included in the pagination they too must be cited. For books, the publisher and city are required. In systematic papers, synonymies should not give complete citations but should relate by author, date and page to the References.

Voucher specimens. In systematic papers, all new type-specimens must be deposited in museums where they may be consulted by other scientists. Beginning with Vol. 16 and when appropriate, MALACOLOGIA will also require that voucher specimens from other kinds of research be deposited in museums.

Reprints. When they order 50 or more reprints, authors will receive 25 additional reprints gratis; additional copies may be ordered at the time proof is returned to the Editorial Office. Later orders cannot be considered.

PAGE COSTS

MALACOLOGIA requests authors with grant support to help pay publication costs. MALACOLOGIA requires subsidization for extra long papers.

SUBSCRIPTION COSTS

For Vol. 22, personal subscriptions are U.S. \$17.00 and institutional subscriptions are U.S. \$27.00. For information on Vol. 23, address inquiries to the Subscription Office.

CONTENTS

SECOND INTERNATIONAL SYMPOSIUM ON EVOLUTION
AND ADAPTIVE RADIATION OF MOLLUSCA

SPONSORED BY

UNITAS MALACOLOGICA

SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS

PERPIGNAN, FRANCE. 31 August-7 September 1980

G. M. DAVIS	Introduction to Symposium	1
P. CALOW	Adaptational aspects of growth and reproduction in <i>Lymnaea peregra</i> (Gastropoda: Pulmonata) from exposed and sheltered aquatic habitats	5
E. R. TRUEMAN and H. B. AKBERALI	Responses of an estuarine bivalve, <i>Scrobicularia plana</i> (Tellinacea) to stress	15
C. M. YONGE	On adaptive radiation in the Pectinacea with a description of <i>Hemipecten forbesianus</i>	23
B. MORTON	The Anomalodesmata	35
P. G. OLIVER	The functional morphology and evolution of Recent Limopsidae (Bivalvia, Arcoidea)	61
W. NARCHI	Aspects of the adaptive morphology of <i>Mesodesma mactroides</i> (Bivalvia Mesodesmatidae)	95
K. E. HOAGLAND and R. D. TURNER	Evolution and adaptive radiation of shipworms (Bivalvia, Teredinidae)	111
A. J. CAIN	Variation in shell shape and size of helicid snails in relation to other pulmonates in faunas of the Palaearctic region	149
S. TILLIER	Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs)	177
G. M. DAVIS	Different modes of evolution and adaptive radiation in the Pomatiopsidae (Prosobranchia: Mesogastropoda)	209
R. S. HOUBRICK	Anatomy, biology and systematics of <i>Campanile symbolicum</i> with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia)	263
J. H. McLEAN	The Galapagos rift limpet <i>Neomphalus</i> : relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation	291
V. FRETTER, A. GRAHAM and J. H. McLEAN	The anatomy of the Galapagos rift limpet, <i>Neomphalus fretterae</i>	337
P. BOUCHET	Evolution of larval development in eastern Atlantic Terebridae (Gastropoda), Neogene to Recent	363
L. v. SALVINI-PLAWEN	The molluscan digestive system in evolution	371
W. HAAS	Evolution of calcareous hardparts in primitive molluscs	403
INDEX TO VOLUME 21, No. 1-2		419

ACME
BOOKBINDING CO., INC.

MAY 15 1984

100 CAMPBELL STREET
CHARLESTON, MASS.



DATE DUE

~~AUG 05 2002~~

