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COMPARATIVE ANATOMY AND PHYLOGENY
OF THE RECENT ARCHAEOGASTROPODA
(MOLLUSCA: GASTROPODA)

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Contents

Abstract

Comparative descriptions were made for 23 species belonging to 23 genera of 17 families of Archaeogastropoda. Using data from new observations and previous literature, cladistic analyses were carried out based on *a priori* homology assumptions.

The analysis resulted in cladograms (length=209, CI=0.660, RI=0.881, RCI=0.582) having the following topology: Outgroups+(Patellogastropoda+(Caenogastropoda+(Neritopsina+(*Neomphalus*+(*Cocculina*+(*Seguenzia*+(*Lepetodrilus*+(Zeugobranchia+Trochoidea))))))))). Their relationships are summarized as follows: (1) In agreement with recent theories, Patellogastropoda are regarded as the earliest gastropod offshoot, because of retained plesiomorphies shared with outgroups. Especially, their stereoglossate radula and two-layered jaw in common with Tryblidiida or Cephalopoda suggest a basal position within Gastropoda. (2) Non-Patellogastropoda are united as the monophyletic group, Orthogastropoda Ponder and Lindberg, 1996. They are further divided into Rhipidoglossa and Caenogastropoda. (3) A robust clade is formed by genera of Neritopsina diversified from marine to terrestrial environments. (4) *Neomphalus* represents an early offshoot within the rhipidoglossate clade. Similarities were found between *Neomphalus* and Vetigastropoda in buccal musculature. (5) The position of Cocculinidae is suggested to be closer to Vetigastropoda than to Neritopsina. Monophyly of Cocculiniformia was not tested. (6) Monophyly is supported for Seguenzioidea, Lepetodriloidea, Zeugobranchia, and Trochoidea, and they are defined as Vetigastropoda. (7) Architaenioglossa cannot be included in "Archaeogastropoda" because of apomorphies shared with Neotaenioglossa, so that they are united as the caenogastropod clade. (8) "Archaeogastropoda" are considered here as a "pre-taenioglossate" grade, including patellogastropod and rhipidoglossate clades.

Transformations in character evolution were revealed by *a posteriori* character evaluation under parsimony criteria: (1) Symmetry of the pallial complex in Zeugobranchia must be interpreted as secondary due to reversal. This view is supported by the ontogeny of the complex. The gastropod common ancestor probably developed asymmetrical pallial and internal organs similar to those of Patellogastropoda. (2) An amphineurous-type of primitive buccal musculature is retained in archaeogastropods, but in contrast well-organized compact type evolved in the common ancestor of Caenogastropoda including Architaenioglossa. Digestive tract and radular teeth also show patterns for simplification from "Archaeogastropoda" to Caenogastropoda. Dietary change and proboscis formation probably played an important role in the evolution of the gastropod digestive system. (3) Heart and coelomic organs were independently reduced on the right side, which generated a mosaic pattern of character states among archaeogastropods. Therefore, unpaired "mesogastropod" characters no longer imply the non-archaeogastropod nature of the taxa having such states.

By comparison with the anatomy-based hypothesis of relationships, phylogenetic evaluation of characters of the shell's protoconch was made: (1) Morphology of the archaeogastropod protoconch was categorized into four basic morphotypes, namely, symmetrically uncoiled, paucispiral, multispiral, and globular (modified terrestrial). Patellogastropods have characteristic mode of septal formation and loss of the protoconch. The internal resorption of the columella in protoconch and teleoconch is also a specific feature of Neritopsina. (2) Torsion at the larval stage has no relationship with shell coiling at least in the case of the symmetrical protoconch of Patellogastropoda. (3) The above categorization of protoconch morphology is

largely consistent with categorization by anatomical characters, and therefore morphotypes of the proto-conch (especially mode of coiling) can be regarded as phylogenetically essential shell characters. (4) The gastropod protoconch is presumed to have undergone evolution through longitudinal elongation from a cap-like conchiferan type (Patellogastropoda) into coiling forms by asymmetrical mechanical deformation (non-neritopsine Rhipidoglossa), and acquisition of the multispiral form by accretionary growth (Neri-topsina and Caenogastropoda).

I. Introduction

"Archaeogastropoda" is a large gastropod group with a long and successful history from the late Cambrian to the Recent. More than eighty extinct and extant families have been described as archaeogastropods (Knight *et al.*, 1960), and recent members are assigned to about forty families (see Appendix). Anatomically, some archaeogastropods have been thought to exhibit many primitive features within Gastropoda. Especially, symmetry of various pallial and internal organs (ctenidia, osphradia, hypobranchial glands, auricles, and kidneys) has been regarded as one of the plesiomorphies retained from the original molluscan plan (e.g. Graham, 1985). Therefore, "Archaeogastropoda" plays an important role in phylogenetic studies as a key taxon in considering the origin and subsequent radiation of gastropod groups.

The traditional concept of Archaeogastropoda has been greatly modified as a consequence of phylogenetic analyses based on various anatomical characters. (1) *Thiele (1925, 1929):* Thiele's classical concept of Archaeogastropoda included Zeugobranchia, Docoglossa, Trochaecea, Neritacea, and Cocculinacea, among which Zeugobranchia was considered to be most primitive. (2) *Cox (1960), Cox and Knight (1960), Knight et al. (1960):* These authors basically followed Thiele's scheme, and divided Recent members into four suborders, Pleurotomariina, Patellina, Trochina, and Neritopsina. (3) *Golikov and Starobogatov (1975):* Drastic changes in gastropod systematics were proposed by these authors. The prosobranch gastropods were split into three subclasses, Cyclobranchia (including Docoglossa), Scutibranchia (including zeugobranchs), and Pectinibranchia (including Turbinimorpha, Neritimorpha, and caenogastropods). (4) *Salvini-Plawen (1980):* Vetigastropoda was proposed for Zeugobranchia, Trochoidea, and Cocculinoidea based on the predominance of the right shell muscle. Effectiveness of this original definition was denied by Haszprunar (1985 c), but later the taxon was justified by several synapomorphies. (5) *Salvini-Plawen and Haszprunar (1987), Haszprunar (1988 a, b; 1993), and Salvini-Plawen and Steiner (1996):* The phylograms by these authors differ from others in sequential derivation of Docoglossa, Cocculiniformia, Neritopsina, Vetigastropoda, hot-vent taxa (Peltospiroidea and Neomphaloidea), Seguenziina, Architaenioglossa, and the remaining higher groups (Apogastropoda). A hypoathroid-type of nervous system was employed as diagnostic character of Archaeogastropoda, including Architaenioglossa. (6) *Hickman (1988):* From a phylogenetic (rather than taxonomic) viewpoint, Archaeogastropoda was restricted to Pleurotomarioidea, Fissurelloidea, and Trochoidea. This narrow definition has not been followed by any subsequent authors. (7) *Ponder and Lindberg (1996: 1997):* A cladistic analysis form all gastropod groups was carried out based on outgroup comparison with testarian taxa. The names "Eogastropoda" (=Patellogastropoda + possible coiled ancestor) and "Orthogastropoda" (=all remaining gastropods) were proposed by these authors to signify explicitly distinct states of two basic clades of Gastropoda. Hot vent-taxa and Vetigastropoda were united as Archaeogastropoda (*s. s.*).

As is suggested by historical review, one of most significant changes in recent theories is that the pleurotomarioidean-like gastropod ancestor of the traditional view become no longer supported, and Patellogastropoda are regarded as most primitive. It has also been revealed that the relationships among "Archaeogastropoda" are more complex than traditionally known. These advances have been provided mainly by the following innovations in the anatomical approach as noted by Haszprunar (1988 a, b). (1) *New material:* Totally unknown new taxa of higher rank have been discovered from deep-sea environments, especially from the hydrothermal vents. The range of "Archaeogastropoda" was markedly extended from tradi-

tional one. (2) *Microscopic anatomical observation:* Microscopic or submicroscopic techniques have been applied to observations of soft anatomy. Most typically, observations with transmission electron microscopy (TEM) on the osphradial sense organ (Haszprunar, 1985 a, b) and sperm morphology (e.g. Koike, 1985; Healy, 1988, 1996; Hodgson, 1995) revealed a number of new phylogenetic characters. (3) *Advances in phylogenetic methodology:* Cladistic analysis has been almost universally adopted over a traditional empirical approach (Salvini-Plawen and Steiner, 1996; Ponder and Lindberg, 1996; 1997). Phylogenetic relationships among taxa are interpreted based on the distinction between apomorphy and plesiomorphy, synapomorphy and homoplasy, and monophyly and poly-/paraphyly rather than simply based on the degree of similarity or dissimilarity. Only monophyletic taxa defined by synapomorphic homologues are regarded as acceptable in cladistics.

Several major problems, however, still remain unsolved in gastropod phylogeny as pointed out by Ponder and Lindberg (1996). It is very apparent that further advance will rely upon filling gaps in knowledge of morphological characters by new observations. Biased information on characters known from limited taxa is especially problematic. It is often difficult to fill gaps in a data matrix from information based only on earlier literature. Lengthy classic descriptions are often ineffective, when important characters in current systematics are not described according to required standards. Thus, additional comparative studies covering a wide range of characters and taxa are indispensable for the morphological approach toward resolving relationships.

This study has its aim particularly on the following four subjects, taking the above-mentioned background and problems into consideration. (1) *New anatomical observations:* In this study, attempts were made to reveal new anatomical information useful for higher phylogenetic studies. (i) Internal anatomy in addition to external anatomy was directly observed with scanning electron microscopy (SEM). This method helps to eliminate artifacts in reconstructing complex three-dimensional structures. (ii) In macroscopic anatomy, special attention was paid to unexplored organs. In particular, comparative anatomy of the buccal mass successfully revealed a number of useful characters. (2) *Cladistic analysis:* Based on anatomical observations, discrete homologous characters were used for cladistic analysis. All characters were unordered and unweighted *a priori* to carry out an "assumption-free" analysis. The relationships of taxa including outgroups were determined by calculation based on parsimony criteria. The analysis was performed on operational taxonomic units (OTUs) at the generic level. (3) *Hypotheses of character state transformation:* This study also aims to present hypotheses on the pathways of morphological evolution. The polarity of transformation series was traced on cladograms *a posteriori* to suggest how respective morphological states have evolved. (4) *Relationships between shell and soft parts:* Phylogenetic congruence of protoconch characters was tested by comparing the relationships inferred from non-shell characters.

II. Material and Methods

(1) Material

A total of 52 species belonging to 43 genera of 19 families were selected as material to include diverse groups of Archaeogastropoda (Table 1). Observations were made on anatomical characters of 23 species (23 genera and 17 families) and protoconchs of 38 species (33 genera and 15 families).

Most specimens were collected in the intertidal or subtidal zone except some deep-sea and terrestrial taxa. Living specimens were relaxed in solution of magnesium chloride of various concentration to prevent the head-foot from retracting into the shell. Then animals were fixed in 10% formalin for several days or weeks. In the case of spiral forms, shells were broken with a hammer before fixation or dissolved in hydrochloric acid after fixation to enhance the effect of the fixative. Fixed animals were finally preserved in 70% ethanol. Protoconch samples were picked up from various sediments (shell sands) which were collected from inter-tidal or subtidal zones or from deeper habitats by dredging.

Specimens used in this study were registered and preserved in the University Museum, University of To-kyo.

(2) Morphological Observations

Soft parts: The anatomy was reconstructed by a combination of the following three methods. (i) Ani-mals were dissected under a binocular microscope. In fresh animals, some organs could be distinguished by color. Morphology of tentacles and lappets were also observed in anesthetized living animals. In the case of preserved specimens, dissected animals were observed by staining with methylene blue. (ii) Microanatomi-cal details that were not observable by optical microscopy were investigated by scanning electron micro-scope (Hitachi S-2400, at 12-20 kV acceleration voltage). Dissected parts were dehydrated in a graded se-ries of ethanol and t-butyl alcohol (2-methyl-2-propanol), and dried using a freeze dryer (Hitachi ES-2030). Pieces were coated with platinum vanadium using an ion coater (Eiko IB-5). Some minute speci-mens were embedded in paraffin as for usual histological sectioning and cut at 0.1-0.5 mm with a steel knife. The soft parts were deembedded with xylene and freeze-dried for SEM observation. (iii) Serial sec-tions were prepared to supplement gross dissection in *Scutus, Sulculus, Chlorostoma, Nerita, Cinnalepeta, and Lepetodrilus*. Paraffin-embedded serial sections were made at intervals of 6-10 μm and stained with haematoxylin and eosin.

Radula: Radulae were removed from the buccal mass by soaking in sodium hypochlorite for several minutes and air-drying, following slight dehydration in 70% ethanol. The radular ribbon was cut into sev-eral pieces to reveal the basal morphology and relationships of overlapping teeth. SEM observation was carried out at 5-6 kV acceleration voltage.

Protoconch: Morphological features of protoconchs were observed with SEM, with special reference to shape, number of whorls, sculpture, and boundary with the teleoconch. Morphology of the early teleoconch was also described by contrasting it to that of the protoconch. SEM observations were made at 12-15 kV acceleration voltage.

(3) Description

Organ systems: Arrangement and division of some characters are somewhat modified from conventional

Table 1. Localities of material. A = anatomy, P = protoconch.

Family	Genus and Species	A	P	Locality	Register Number
Patellidae	Patella flexosa	X		Banda, Tateyama, Boso Peninsula	RM27611
Nacellidae	Cellana toreuma	X	X	Banda, Tateyama, Boso Peninsula	RM27612, RM27613
Lepetidae	Limalepeta lima	X		Off Kushiro, Hokkaido	RM27614
Lepetidae	Iothia sp.		X	Suruga Bay	RM27615
Acmaeidae	Pectinodonta orientalis	X		Tosa Basin, 1034-1036m (KT-90-13, Sta. T2)	RM27616
Lottiidae	Niveotectura pallida	X		Otsuchi, Iwate Prefecture	RM27617
Lottiidae	Erginus sybaritica	X		Akkeshi, Hokkaido	RM27618
Lottiidae	Erginus moskalevi		X	Kamui-misaki, Esashi, Hokkaido	RM27619
Lottiidae	Lottia tenuisculpta		X	Ito, Izu Peninsula	RM27620
Lottiidae	Lottia tenuisculpta		X	Goshikinohama, Tosa, Kochi Prefecture	RM27621
Lottiidae	Nipponacmea schrenckii	X		Kashiwajima Island, Kochi Prefecture	RM27622
Pleurotomariidae	Mikadotrochus beyrichii		X	Takase, Izu Islands	RM27623
Pleurotomariidae	Mikadotrochus beyrichii	X		Hyotanse, Izu Islands, 119-121m (KT-95-17, Sta. TW-1)	RM27624
Pleurotomariidae	Mikadotrochus beyrichii	X		Sagami Bay	RM27625
Pleurotomariidae	Mikadotrochus beyrichii	X		Off Boso Peninsula	RM27626
Pleurotomariidae	Mikadotrochus beyrichii	X		Off Choshi, Chiba Prefecture	RM27627
Haliotidae	Sulculus diversicolor aquatilis	X	X	Banda, Tateyama, Boso Peninsula	RM27628, RM27629
Fissurellidae	Scutus (Aviscutum) sinensis	X		Chojagasaki, Miura Peninsula	RM27630
Fissurellidae	Scutus (Aviscutum) unguis		X	Bise, Motobu, Okinawa	RM27631
Fissurellidae	Tugali decussata		X	Banda, Tateyama, Boso Peninsula	RM27632
Fissurellidae	Tugali decussata		X	Goshikinohama, Tosa, Kochi Prefecture	RM27633
Fissurellidae	Zeidora calcaeolina		X	Off Nijima Island, Izu Islands	RM27634
Fissurellidae	Emarginula sp.		X	Tsuchihama, Amami-Oshima	RM27635
Fissurellidae	Rimula sp.		X	Yudomari, Yakushima Island	RM27636
Fissurellidae	Diodora sp.		X	Tsuchihama, Amami-Oshima	RM27637
Fissurellidae	Macroschisma dilatatum	X	X	Banda, Tateyama, Boso Peninsula	RM27638, RM27639
Fissurellidae	Macroschisma dilatatum		X	Goshikinohama, Tosa, Kochi Prefecture	RM27640
Fissurellidae	Macroschisma dilatatum		X	Mishima Island, Hagi, Yamaguchi Prefecture	RM27641
Scissurellidae	Anatoma sp.	X	X	Off Daiozaki, 422-425m (KT-86-6, Sta. KN-4)	RM27642, RM27643
Scissurellidae	Anatoma japonica		X	Off Shimoda, Izu Peninsula	RM27644
Scissurellidae	Sinezona sp.		X	Goshikinohama, Tosa, Kochi Prefecture	RM27645
Scissurellidae	gen. et sp.		X	Goshikinohama, Tosa, Kochi Prefecture	RM27646
Turbinidae	Turbo (Marmarostoma) stenogyrum	X		Banda, Tateyama, Boso Peninsula	RM27647
Turbinidae	gen. et sp.		X	Goshikinohama, Tosa, Kochi Prefecture	RM27648
Turbinidae	Homalopoa nocturnum		X	Banda, Tateyama, Boso Peninsula	RM27649

Table 1. (continued)

Family	Species			Locality	Registration
Turbinidae	*Homalopoa nocturnum*	x		Tsunoshima Island, Yamaguchi Prefecture	RM27650
Turbinidae	*Tricolia* sp.	x		Bise, Motobu, Okinawa	RM27651
Turbinidae	*Tricolia megastoma*	x		Banda, Tateyama, Boso Peninsula	RM27652
Trochidae	*Chlorostoma lischkei*		x	Otsuchi, Iwate Prefecture	RM27653
Trochidae	*Chlorostoma* sp.	x		Goshikinohama, Tosa, Kochi Prefecture	RM27654
Trochidae	*Euchelus pauperculus*	x		Tatsukushi, Kochi Prefecture	RM27655
Trochidae	*Stomatia phymotis*		x	Sotodomari, Nishiumi, Ehime Prefecture	RM27656
Trochidae	*Broderipia iridescens*		x	Shirahama, Wakayama Prefecture	RM27657
Trochidae	*Broderipia iridescens*		x	Maajiro, Yawatahama, Ehime Prefecture	RM27658
Trochidae	*Broderipia iridescens*	x		Tsuchihama, Amami-Oshima	RM27659
Trochidae	*Broderipia iridescens*	x		Goshikinohama, Tosa, Kochi Prefecture	RM27660
Trochidae	*Cantharidus* sp. cf. *callichroa*	x		Tsunoshima Island, Yamaguchi Prefecture	RM27661
Trochidae	*Cantharidus* sp. cf. *callichroa*	x		Banda, Tateyama, Boso Peninsula	RM27662
Trochidae	*Calliostoma* sp.	x		Off Shimoda, Izu Peninsula	RM27663
Trochidae	*Lirularia? minima*	x		Tsunoshima Island, Yamaguchi Prefecture	RM27664
Skeneidae	*Pondorbis japonicus*	x		Goshikinohama, Tosa, Kochi Prefecture	RM27665
Skeneidae	*Cyclostremiscus* sp. 1	x		Miyako Island, Okinawa	RM27666
Skeneidae	*Cyclostremiscus* sp. 2	x		Miyako Island, Okinawa	RM27667
Lepetodrilidae	*Lepetodrilus nux*		x	Izena Hole, Okinawa Trough, 1340m (Shinkai 2000, Dive 364)	RM27668
Seguenziidae	*Seguenzia* sp.		x	Hyuga Basin, off Bungo-suido,1092-1094m (KT-86-16, Sta. C)	RM27669, RM27670
Cocculinidae	*Cocculina nipponica*		x	Off Okushiri Island, Hokkaido, 650-660m (KT-92-12, Sta. OS-4)	RM27671, RM27672
Neritidae	*Nerita (Theliostyla) albicilla*		x	Banda, Tateyama, Boso Peninsula	RM27673
Neritidae	*Nerita (Theliostyla) albicilla*	x		Tsuchihama, Amami-Oshima	RM27674
Neritidae	*Nerita (Puperita) bensoni*	x		Tsuchihama, Amami-Oshima	RM27675
Neritidae	*Nerita* sp.	x		Tsuchihama, Amami-Oshima	RM27676
Neritidae	*Septaria porcellana*		x	Uken, Amami-Oshima	RM27677
Neritidae	*Septaria porcellana*		x	Hirajo, Misho, Ehime Prefecture	RM27678
Neritidae	*Pisulina adamisiana*	x		Tsuchihama, Amami-Oshima	RM27679
Phenacolepadidae	*Cinnalepeta pulchella*		x	Tassha, Sado Island, Niigata Prefecture	RM27680
Phenacolepadidae	*Cinnalepeta pulchella*		x	Futahama, Tosashimizu, Kochi Prefecture	RM27681
Phenacolepadidae	*Cinnalepeta pulchella*		x	Hirajo, Misho, Ehime Prefecture	RM27682
Phenacolepadidae	*Phenacolepas* sp.	x		Befu, Tabuse, Yamaguchi Prefecture	RM27683
Hydrocenidae	*Georissa japonica*	x		Sakai, Okutama, Tokyo	RM27684
Helcinidae	*Waldemaria japonica*		x	Gongendani, Shiga Prefecture	RM27685
Ampullariidae	*Pomacea canaliculata*		x	Usa, Tosa, Kochi Prefecture	RM27686
Pleuroceridae	*Biwamelania reticulata*		x	Lake Biwa, Shiga Prefecture	RM27687

usage for convenience. (i) Various features on the exterior surface of the body are treated collectively as "external characters." Similarly, organs in the pallial cavity are allocated to the "pallial complex." Therefore, tentacles, lappets and other external sense organs are described as external characters, whereas the osphradium is assigned to the pallial complex. (ii) Buccal muscles are treated within the digestive system rather than the muscular system. This treatment stresses the unity of buccal-mass characters as a functional unit of the feeding apparatus.

Terminology: Terminology and abbreviations adopted in this study are listed in Table 2. Terms are derived from anatomical texts on malacology for the most part (e.g. Fretter and Graham, 1962; 1994; Voltzow, 1994), but some additional notes are necessary. (i) Nomenclature of buccal musculature follows functional naming that divides muscles into protractor, retractor, levator, depressor, sphincter, dilator, and constrictor (e.g. Graham, 1964, 1973; Fretter, 1965; Nisbet, 1973), rather than naming based on sites of insertion (e.g. Lemche and Wingstrand, 1959; Wingstrand, 1985). (ii) For the excretory organ, the term "kidney" is used in place of "nephridium" because of popularity (e.g. Fretter and Graham, 1962; 1994), although it is inappropriate zoologically (Haszprunar, 1988 b: 383). (iii) Terms for some characters specific to Neritopsina (e. g. annex and basal glands in the reproductive organ) follow Berry *et al.* (1973) and Thompson (1980). (iv) Descriptive terms of orientation follow Ponder and Lindberg (1997) to compare non-gastropod "pretorsional" and gastropod "post-torsional" states. This distinction is particularly important in discussion considering the evolution of characters relative to anterior-posterior or right-left axes.

(4) Claditstic Analysis

Outgroups: Nautilus (Cephalopoda), *Neopilina* (Monoplacophora : Tryblidiida) and a generalized polyplacophoran were selected as outgroups of Archaeogastropoda, following Ponder and Lindberg (1996; 1997). Anatomical information of outgroups was mainly derived from Griffin (1900) for *Nautilus*, and Lemche and Wingstrand (1959) and Wingstrand (1985) for *Neopilina* (or *Vema* for several characters). The generalized characters of Polyplacophora were coded (under the name *"Chiton"*) from various sources, mainly Hyman (1967), Salvini-Plawen (1985), and Eernisse and Reynolds (1994). Within Conchifera, Diasoma (Bivalvia and Scaphopoda) were eliminated from outgroups, because of entire loss of the buccal mass in the former and lack of data on buccal structures in the latter. In Gastropoda, two caenogastropod genera (*Pomacea* and *Biwamelania*) were added to test the relationship between Archaeogastropoda and the root of Caenogastropoda. Their states were determined by personal observations on *Pomacea canaliculata* (Lamarck, 1819) and *Biwamelania reticulata* Kajiyama and Habe, 1961 and partly by data from Berthold (1991). In the search for trees, Polyplacophora was designated as outgroup and others were included in the ingroup.

Ingroup: The OTUs used in the cladistic analysis include 23 archaeogastropod genera selected to represent various families or superfamilies extensively. All patellogastropod families were anatomically investigated except Neolepetopsidae. Among the ten known families of two superfamilies of "Cocculiniformia," only Cocculinidae are represented (by *Cocculina*) in this study; other families were not treated because material was unavailable. Among vetigastropod groups, Crypeosectidae and Skeneidae were not used in the analysis, but all taxa at superfamilial level were considered. Seguenzioidea was not investigated in detail due to limited quality and quantity of material. States of several characters were supplemented by previously published data in literature (Quinn, 1983; Ponder and Lindberg, 1997). Among deep-sea limpet taxa, data for *Neomphalus fretterae* McLean, 1981 were constructed from the descriptions by Fretter *et al.* (1981) and McLean (1981). Peltospiroidea and *Melanodrymia* were not used, because character states have not been fully elucidated for characters required by this analysis. Lepetodriloidea were represented by *Lepetodrilus nux* (Okutani, Fujikura and Sasaki, 1993). In the neritopsine groups, only Neritoidea (Neritidae and Phenacolepadidae) and Helicinoidea (Helicinidae) were used in the analysis.

Table 2. Abbreviations used in the figures.

a = anus	cpg = capsule gland
aa = anterior aorta	cpn = circumpallial nerve
ab = anterior band of jaw	cpv = circumpallial vessel
aca = anterior cartilage of odontophore	crm = retractor muscle of ctenidium
acm = afferent ctenidial membrane	cs = crystal sac
acv = afferent ctenidial vein	ct = cephalic tentacle
acx = afferent ctenidial axis	dag = dorsal albumen gland
ae = anterior esophagus	dbt = dorsal buccal tensor muscle
afc = abfrontal cilia of ctenidial lamella	dca = posterodorsal cartilages of
afv = afferent pallial vein	odontophore
ah = apical hole	dcl = dorsal ctenidial lamellae
ahg = accessory lobe of hypobranchial	ddf = dilator muscle of dorsal food channel
gland	ddg = duct of digestive gland
ahv = afferent hypobranchial vessel	de = dilator muscle of esophagus
al = anterior levator muscle of odontophore	df = dorsal fold of esophagus
alc = anterolateral cartilage of odontophore	dfc = dorsal food channel of anterior
alp = anterior loop of intestine	esophagus
ang = annex gland	dg = digestive gland
apn = anterior pedal nerve	dgo = opening of digestive gland to
aps = anterior pallial streak	stomach
apv = anterior pallial vein	dl = dorsal levator muscle of odontophore
ark = anterior lobe of right kidney	dp = dorsal protractor muscle of
arv = afferent renal vein	odontophore
at = anterior tensor muscle of odontophore	drd = dilator muscle of radular
au = auricle	diverticulum
aw = anterior wing of jaw	drm = dorsal part of retractor muscle of
ba = bulbous aorta	subradular membrane
bc = buccal commissure	drs = duct of receptaculum seminis
bcp = bursa copulatrix	dsg = duct of salivary gland
bct = buccal constrictor muscle	e = eye
bcv = buccal cavity	ecm = efferent ctenidial membrane
bd = buccal dilator muscle	ecv = efferent ctenidial vein
bg = buccal ganglion	ecx = efferent ctenidial axis
br = bursicle	ed = enigmatic duct
bs = buccal sphincter muscle	edo = opening of enigmatic duct
bsg = basal gland	eo = opening of esophagus to stomach
bsn = buccal sinus	ep = esophageal pouch
bt = buccal tensor muscle	epd = epipodium
C = central tooth	epf = epipodial flap
c = ctenidial lamella	ept = epipodial tentacle
ca = odontophoral cartilage	epv = efferent pallial vein
cbc = cerebrobuccal connective	erv = efferent renal vein
cc = cerebral commissure	es = eyestalk
cdc = cerebropedal connective	eso = epipodial sense organ
cg = cerebral ganglion	ev = esophageal valve
clc = cerebrolabial connective	f = foot
clp = cephalic lappet	fal = foot autotomy line
cm = columellar muscle	fc = frontal cilia of ctenidial lamellae
cn = ctenidial nerve	fo = female opening of gonoduct
co = copulatory organ	g = gonad
cpc = cerebropleural connective	gbc = glandular part of buccal cavity

Table 2.   (continued)

gbr = groove of bursicle
gc = gastric caecum
gd = gonoduct
gk = glandular part of kidney
gs = gastric shield
gst = tooth of gastric shield
hg = hypobranchial gland
hr = head retractor muscle
i = intestine
if = inner fold of mantle margin
ig = intestinal groove
il = inner lip
ilm = inner lamella of beak
ir = inner retinal cell
ivp = inner ventral protractor muscle of
    odontophore
j = jaw
ja = muscular attachment to jaw
k = kidney
ko = kidney opening
L = lateral teeth
la = left auricle
lbc = labiobuccal connective
lc = labial commissure
lca = labial cartilage
lct = left ctenidium
lep = lateral pouch of anterior esophagus
lg = labial ganglia
lhg = left hypobranchial gland
lic = licker
lk = left kidney
lko = opening of left kidney
LMP = lateromarginal plate
ln = labial nerve
lp = lateral protractor muscle of
    odontophore
lpr = lateral protractor muscle of subradular
    membrane
lps = lateral pallial streak
lrp = left renopericardial duct
lsm = left shell muscle
lsp = lateral sublingual pouch
ltc = lateral cilia of ctenidial lamella
M = marginal teeth
m = mouth
mca = median cartilage of odontophore
me = mid-esophagus
ml = median levator muscle of
    odontophore
mm = mantle margin
mo = male opening of gonoduct

mp = mandibular protractor muscle
mpc = median pedal commissure
mpr = median protractor muscle of
    subradular membrane
mr = mandibular retractor muscle
mrs = median retractor of radula sac
ms = mantle slit
mt = major typhlosole
mtl = mantle
na = nerve to anus
nae = nerve to anterior esophagus
ng = nerve to gonoduct
ngk = non-glandular part of kidney
nk = nerve to kidney
nl = neck lobe
nlk = nerve to left kidney
nme = nerve to mid-esophagus
nog = nerve to osphradio-ctenidial
    ganglion
npc = nerve to pericardium
npm = nerve to posterior buccal
    musculature
nrk = nerve to right kidney
nsg = nerve to salivary gland
nsm = nerve to shell muscle
nsp = nerve to sublingual pouch
nt = minor typhlosole
oap = outer approximator muscle of
    cartilages
od = oral disk
of = outer fold of mantle margin
ol = outer lip
ola = oral lappet
olm = outer lamella of beak
on = oral nerve
op = attachment area of operculum
opl = outer posterior levator of
    odontophore
opn = optic nerve
or = outer retinal cell
os = osphradium
osg = osphradio-ctenidial ganglion
ov = ovary
ovd = oviduct
ovp = outer ventral protractor muscle of
    odontophore
pa = posterior aorta
pag = secondary pallial gill
pc = pericardium
pca = posterior cartilage of odontophore
pcd = pedal cord

Table 2. (continued)

pcv = pallial cavity
pd = posterior depressor muscle of
  odontophore
pda = pedal artery
pdc = pedal commissure
pdg = pedal ganglion
pdn = pedal nerve
pdt = postdorsal buccal tensor muscle
pe = posterior esophagus
peg = posterior esophageal gland
pen = penis
pg = periostracal groove
pl = posterior levator muscle of
  odontophore
plc = pleural commissure
plg = pleural ganglion
pm = pallial retractor muscle
pn = pallial nerve
pov = pallial oviduct
ppg = pseudoplicate gill
pr = prostate
prk = posterior lobe of right kidney
prn = parietal nerve
prp = prostate pouch
prs = postmedian retractor muscle of
  radular sac
pt = pallial tentacle
pvs = provaginal sac
pw = posterior wing of jaw
r = rectum
ra = right auricle
rct = right ctenidium
rd = radula
rda = radular artery
rds = radular sac
rdv = radular diverticulum
rhg = right hypobranchial gland
rk = right kidney
rko = right kidney opening
rov = retractor muscle of esophageal valve
rpd = renopericardial duct
rrd = retractor muscle of radular
  diverticulum
rrp = right renopericardial duct
rrs = retractor muscle of radular sac
rs = seminal receptacle
rsm = right shell muscle
rsr = retractor muscle of subradular
  membrane
rve = rectum passing through ventricle
sa = sorting area

sbg = subesophageal ganglion
sbv = subesophageal part of visceral loop
sct = subcephalic tentacle
sg = salivary gland
sgo = opening of salivary gland
slc = sublingual cartilage
slg = sublingual gland
slp = sublingual pouch
sm = shell muscle
smg = seminal groove
sn = snout
sp = spermatophore
spg = supraesophageal ganglion
sps = spermatophore sac
spv = supraesophageal part of visceral loop
sr = skeletal rod
srm = subradular membrane
ss = style sac region of stomach
st = stomach
sta = statocyst
stc = commissure of statocyst
sv = seminal vesicle
t = testis
tac = tensor muscle of anterior cartilage
tc = terminal cilia of ctenidial lamellae
tlm = transverse labial muscle
tn = tentacular nerve
tot = tensor muscle of oral tube
tpv = transverse pallial vein
tr = terminal ridge of ctenidial lamellae
trs = ventral tensor muscle of radular sac
ugo = urogenital opening
v = ventricle
va = vagina
vag = ventral albumen gland
vap = ventral approximator muscle of
  cartilages
vb = vitreous body
vcl = ventral ctenidial lamellae
vd = vas deferens
vf = ventral fold of esophagus
vg = visceral ganglion
vgl = vestigial gill leaflets
vlc = ventrolateral cartilage of odontophore
vo = V-organ
vp = ventral protractor muscle of
  odontophore
vrm = ventral part of retractor of
  subradular membrane
wo = wart organ

Character selection: Unless clearly rejected by homology criteria, characters were not excluded from the phylogenetic analysis, even if they were expected to be homoplastic according to traditional view. In some cases, morphologically similar structures of doubtful homology were tentatively treated as homologous. Homology was tested mainly by similarity and congruence in position, innervation, and microstructure.

In contrast, the following characters were eliminated from phylogenetic analysis. (i) Non-discrete, qualitative characters were all excluded. Examples are the depth of pallial cavity, the length of the ctenidial membrane, the length and configuration of the radular sac, all of which show continuous degree of development. (ii) The shell (protoconch) characters were not included in order to evaluate phylogenetic congruence with anatomical characters based on the result of the analysis. (iii) In spite of their potential for resolving a higher phylogeny, all submicroscopic characters were excluded because of the lack of real data in the majority of OTUs. (iv) Even among macroscopic and microscopic characters, some well-known characters were not used in the analysis because of the lack of data for most OTUs. Examples include pericardial and nephridial glands (Fretter, 1990; Ponder and Lindberg, 1997), egg structure (Amio, 1963: figs. 5, 9), cleavage pattern (Biggelaar, 1996; Haszprunar and Biggelaar, 1997), and contents of statocysts (statoliths or statoconia) (Haszprunar, 1988 b). (v) In the female reproductive organ, glands associated with the oviduct and sperm storage sac are not used except for Neritopsina. There seem to be no definite criteria to test their homology across distant higher gastropod taxa (Ponder and Lindberg, 1997).

Character coding: Division of character states was discussed in detail prior to the analysis (IV−1). All multistate characters were coded as unordered. No characters were constrained as irreversible and assumed to follow Dollo's parsimony. In the data matrix, unknown or uninvestigated states were scored as "?", and inapplicable states of missing characters or uncertain homology were represented by "−". Equal weighting was applied to all characters except in the analysis using scaled characters.

Search for phylogenetic trees: The data matrix was edited using MacClade ver. 3.04 (Maddison and Maddison, 1992) and analyzed with PAUP ver. 3.1.1 (Phylogenetic Analysis Using Parsimony; Swofford, 1993). The search for phylogenetic trees was carried out by the heuristic search option, but not by branch-and-bound or exhaustive search, because of excessively long calculation time caused by the large data matrix (93 characters for 29 taxa). To increase the likelihood of finding the shortest tree, a random addition sequence of 30 replicates was employed in heuristic analysis with swapping algorithms of tree bisection reconnection (TBR). Steepest descent was not in effect in the analysis. Because the analysis did not produce a single most-parsimonious tree, a strict consensus tree was computed.

In further steps, three different methods of analysis, (i) heuristic analysis by scaled weighting, (ii) bootstrap analysis, and (iii) clade decay analysis, were performed to evaluate the robustness of tree topology. In the scaled analysis, 1000 base weights were applied to all characters based on the rescaled consistency index (RCI) using the scale option to assess the effect of multistate characters on tree topology.

Character trace: Polarity of character evolution was traced following tree calculation, although some character changes were also determined *a priori* by outgroup comparison (see Ponder and Lindberg, 1997). Change of character states and synapomorphies for clades were identified in most-parsimonious trees using both ACCTRAN (accelerated transformation) optimization which favors reversals over parallelisms and DELTRAN (delayed transformation) optimization which favors parallelisms over reversals. This procedure was performed using the reconstruction option in PAUP and the character trace option on tree window in MacClade.

Taxon names for major gastropod clades: Taxon names for higher gastropod categories in this study followed the schemes of Ponder and Warén (1988) and Ponder and Lindberg (1997). Therefore, Caenogastropoda is equivalent to Cox's (1960) original definition (= "Mesogastropoda" + Neogastropoda, = Architaenioglossa + Neotaenioglossa + Neogastropoda). This definition is different from Haszprunar's (1988 a, b) Caenogastropoda in which Architaenioglossa is not included.

(5) Summary of Archaeogastropod Taxonomy

A review of diagnostic characters and included taxa was presented for archaeogastropod higher taxa at order to family levels in Appendix. It was constructed by literature searches for previous anatomical descriptions in addition to the results of this study. Original literatures were not necessarily cited for the character states verified in this study, but in the case of taxa and characters not treated in descriptive part, references were always shown in the section of included taxa, or directly in each character state.

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III. Descriptions

Family Patellidae Rafinesque, 1815
Patella (Penepatella) flexuosa Quoy and Gaimard, 1834
(Figs. 1 a-b, 2 a-d)

External Anatomy: Mantle margin (mm) provided with numerous short circumpallial tentacles (pt) (Figs. 1 a, b). Shell muscle (sm) horseshoe-shaped, divided into about sixteen bundles by blood vessels from visceral hemocoel to circumpallial vessel (Fig. 1 a). Pallial retractor muscle connecting shell muscle anteriorly.

Head with short rounded snout (sn) and pair of smooth cephalic tentacles (ct) without papillae (Figs. 1 a, b). Margin of outer lip (ol) lacking microtentacles and oral lappets (Fig. 1 b). Eyes (e) open, longitudinally invaginated, black pigmented within bases of cephalic tentacles.

Epipodial region lacking tentacles and sensory projections. Operculum absent. Two distinct sensory streaks present on lateral walls of shell muscle (Fig. 1 b). Lateral pallial streaks (lps) extending posteriorly on sides of foot. Anterior pallial streaks (aps) much shorter than lateral ones, attached to anterior ends of shell muscle; inner ends turning slightly inward to pallial cavity.

Pallial Complex: Pallial cavity shallow, restricted to narrow area of nuchal region, containing "secondary" pallial gills, paired kidney openings, anus, and paired osphradia. Ctenidium and hypobranchial gland absent. Pallial gills (pag) arising from circumpallial vessel by evagination (Fig. 1 b). Respective leaflets triangular, feather-like, with tips directed to outside. Outer edge of leaflets thicker and more stiffen than inner margin. Floor of pallial cavity with pair of osphradia on inner sides of anterior shell muscle ends. Tuberculate wart-organ well developed in outer part of osphradia.

Digestive System: Buccal sphincter and constrictor not clearly developed. Very thin pairs of mandibular protractors and retractors inserted on jaw plate. Movement of inner lips (il) controlled by transverse labial muscles. Extrinsic muscles of odontophore comprising dorsal protractors, lateral protractors, ventral protractors, and anterior levators. Depressors absent. Posterior part of buccal mass lacking tensor muscle.

Jaw simple single plate, consisting of larger posterior and smaller anterior wings (aw, pw, Fig. 2 a); their overlapping area thickened to form smooth anterior band (ab). Posterior wings affixed to odontophore by muscle attachments.

Radular sac long, turning in a few loops. Posterior end of radula sac simple. Radular formula 3−(1+2)−1−(2+1)−3 (see Sasaki *et al.*, 1994 for SEM micrographs). Radular row symmetrical. Central tooth extremely thin, represented only by chitinous ridge between innermost lateral teeth, without any trace of mineralization. Lateral teeth consisting of two pairs of slender inner teeth with simple cusps and one greatly enlarged pair of outer teeth each with four denticles. Inner two marginals vertically aligned. Outermost marginals broader, situated more posteriorly than inner teeth. Basal plates complexly sculptured by thick ridges that continue to bases of teeth.

Muscles of subradular membrane and radular sac exhibiting characteristically complicated configuration. Subradular membrane controlled by six muscles: (1) Median protractors of subradular membrane, with markedly asymmetrical arrangement. Anteriorly right and left muscle strands running backward between cartilages along radular sac. In posterior area of buccal mass, right muscle bending sharply toward right, penetrating membrane separating cephalic and visceral sinuses, finally merging into right shell muscle. Left
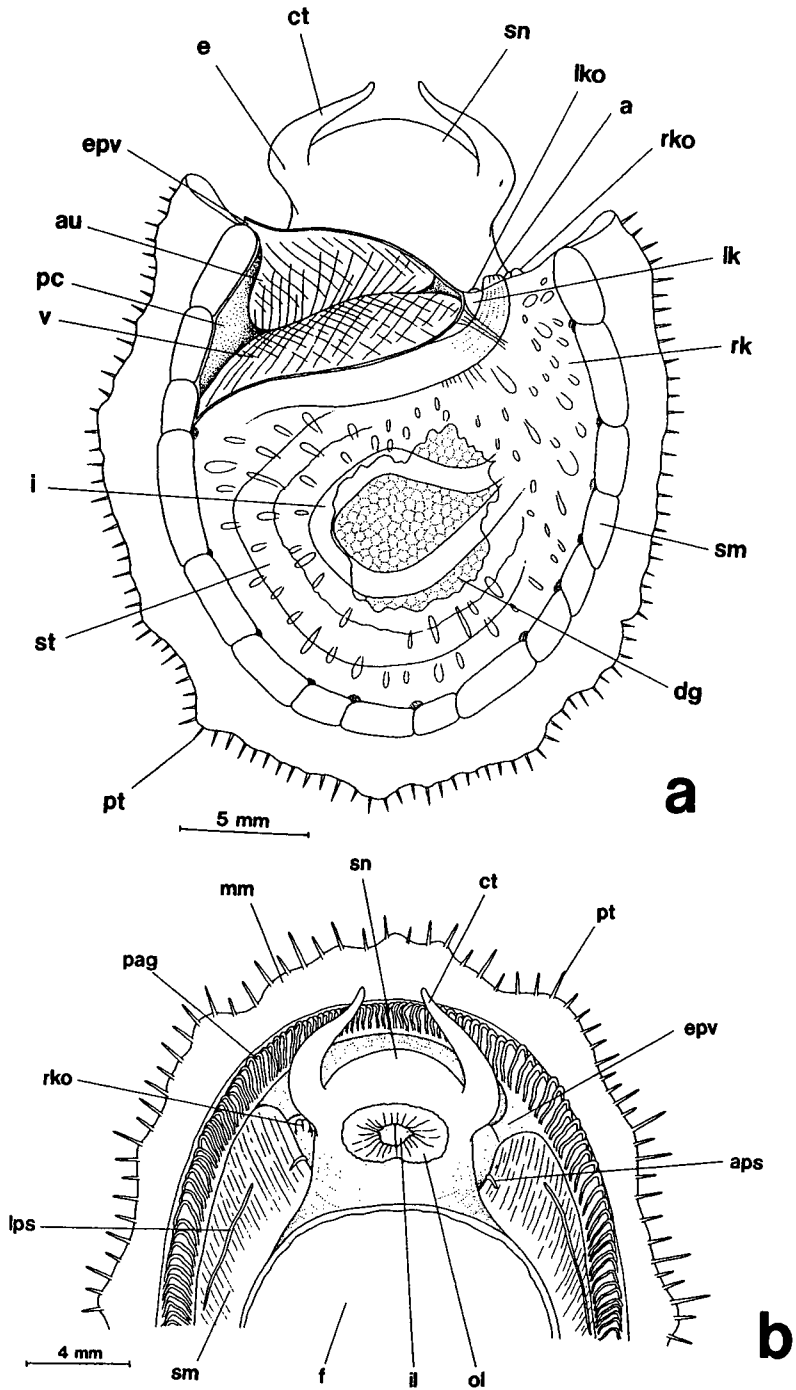
Fig. 1. *Patella (Penepatella) flexuosa*. **a**, Dorsal view of the body after removal of the shell and mantle. **b**, Ventral view of the anterior part of the animal.
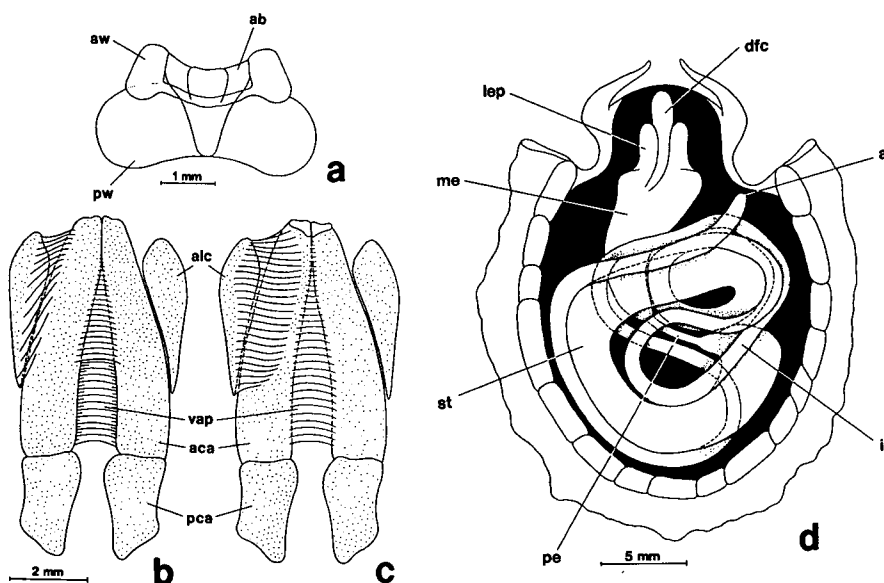
Fig. 2. *Patella* (*Penepatella*) *flexuosa*. **a**, Dorsal view of the jaw. **b**, Dorsal view of the odontophoral cartilages.
c, Ventral view of the odontophoral cartilages. Approximator muscle on the right side is removed. **d**,
Configuration of the alimentary tract.

muscle running straight posteriorly along radular sac. (2) Lateral protractors of subradular membrane, origi-
nating at anterior end of subradular membrane, inserting onto posterior cartilages (pca). (3) Retractors of
subradular membrane composed of two layers (dorsal and ventral) on ventral side. (4) Retractors of radular
sac, connecting to ventral side of radular sac and posterior end of radular cartilages. (5) Tensor of radular
sac, originating from ventral surface of radular sac far behind buccal mass, inserting in dorsal part of retrac-
tors of subradular membrane. (6) Median retractor of radular sac (mrs), running along left strand of median
protractor (mpr).

Odontophoral cartilages mainly consisting of three pairs (Figs. 2 b, c). Anterior cartilages (aca) longitudi-
nally elongated, slightly curved outward. Posterior cartilages (pac) half as long as anterior cartilages, sub-
equal in width. Anterolateral cartilages (alc) contacting but not overlapping with anterior cartilages. Ventro-
lateral and dorsal posterior cartilages (vlc, dca) greatly reduced. Labial cartilages (as in *Cellana*, below) ab-
sent.

Anterior cartilages connecting to two-layered ventral approximator (vap). Insertion of dorsal layer re-
stricted to anterior half of anterior cartilages, while that of ventral layer extending along length of anterior
cartilages (Figs. 2 b, c).

Sublingual pouch lacking outgrowths of sublingual gland. Licker sharply lamellate. Radular diverticulum
wide and deep between anterior esophagus and radular sac. Paired salivary glands completely fused as sin-
gle glandular mass behind buccal mass. Two pairs of salivary ducts extending from anterior margin of sali-
vary glands. Inner ducts running along anterior esophagus, emptying at posterior end of buccal cavity.
Outer ducts running along outer sides of buccal mass, opening into lateral walls of buccal cavity.

Anterior esophagus divided into median dorsal food channel (dfc) and lateral esophageal pouches (lep)
over buccal mass by ventral and dorsal folds (Fig. 1 d). Lateral pouches extended to form well-expanded
mid-esophagus (me). Mid-esophagus gradually curving to right, reducing its width toward central part of
visceral mass, then sharply constricting into narrow posterior esophagus. Mid-esophagus densely septated

internally by transverse septum-like evagination of glandular epithelium. Posterior esophagus (pe) striated internally by longitudinal ridges whose pattern is visible from outside.

Stomach (st) curving in C-shape along posterior and left shell muscle (Fig. 1 d). Digestive glands opening into initial chamber of stomach through paired ducts. Stomach totally lacking gastric caecum, sorting area, tooth of gastric shield. Very thin typhlosoles running along length of stomach. Intestine (i) with four loops, two of them anteriorly shifted. Rectum running along pericardium without penetration. Anus (a) opening at right posterior corner of pallial cavity.

Circulatory System: Heart containing single auricle, ventricle, and muscular bulbous aorta (Fig. 1 a). Auricle (au) receiving blood only from left side via efferent pallial vessel (epv). Anterior margin of auricle fixed to anterior wall of pericardium, its left wall more prominently expanded than right wall. Ventricle (v) obliquely posterior to auricle, connected to posterior wall of pericardium by connective tissues. Bulbous aorta completely ventral to ventricle. Venous blood flowing from kidneys to circumpallial vessel through afferent pallial vessels penetrating shell muscle. Circumpallial vessel extending to anterior pallial cavity as complete circle, provided with secondary pallial gills (pag) (Fig. 1 b). Efferent pallial vessel (epv) entering auricle only from left side.

Excretory System: Excretory organs consisting of right and left kidneys (Fig. 1 a). Left kidney (lk) much smaller than right, restricted to small area between rectum and pericardium. Right kidney (rk) very large, entirely enclosing digestive glands both dorsally and ventrally. Both kidneys with papillate opening (rko, lko) on either side of anus. Papilla of right opening more prominently extended than that of left opening. Right opening vertically slit-like; left simple.

Reproductive System: Gonad developing below digestive system, emerging dorsally on left side when gravid. Gonoduct arising from left side, passing below rectum, discharging into right kidney independent of left renopericardial duct. Right kidney opening functioning as urinogenital opening. Sexes separate. Testis creamy in color; ovary reddish brown.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia at bases of cephalic tentacles. Pleural and pedal ganglia below posterior end of buccal mass, connected to cerebral ganglia by long connectives. Oral region containing labial ganglia with distinct labial commissure. Buccal ganglia connected to labial ganglia through labiobuccal connectives. Supraesophageal, subesophageal, and visceral ganglia fused as tightly twisted visceral loop on right side. Supra- and subesophageal parts of visceral loop supplying nerves to osphradial ganglia. Zeugoneury absent. Circumpallial nerve forming complete circle. Pedal cords with many incomplete pedal commissures. Statocysts on outer ventral sides of pedal ganglia.

Family Nacellidae Thiele, 1891
Cellana toreuma (Reeve, 1854)
(Figs. 3 a-c, 4 a-b, 5 a-d, 6, 7 a-b, 8 a-b, 9 a-b, 10 a-h, 11 a-h,)

Protoconch: Protoconch pear-shaped with well-inflated apex, entirely symmetrical along longitudinal axis (Figs. 3 a-c). Adapertural part elongated, somewhat constricted. Exterior surface with reticulate sculpture creating pit-like appearance between ridges. On dorsal side, network ridges anastomosing to exhibit denser sculpture. Eight longitudinal streaks (one dorsal and ventral in midline, three on each side), arising and radiating from posteroventral tip of protoconch.

External Anatomy: Animal limpet-shaped without visceral coiling. Mantle margin (mm) fringed with series of circumpallial tentacles (Fig. 4 a, pt) consisting of regularly alternating longer and shorter ones. Tentacles pigmented by gray circular bands (Fig. 4 b). Under SEM observation, clusters of cilia scattered on surface of tentacles (Figs. 10 a, b). Attachment of shell muscle (sm) horseshoe-shaped, constricted into about sixteen bundles penetrated by vessels (Fig. 4 a). Pallial muscle connecting right and left ends of shell muscle beyond head.
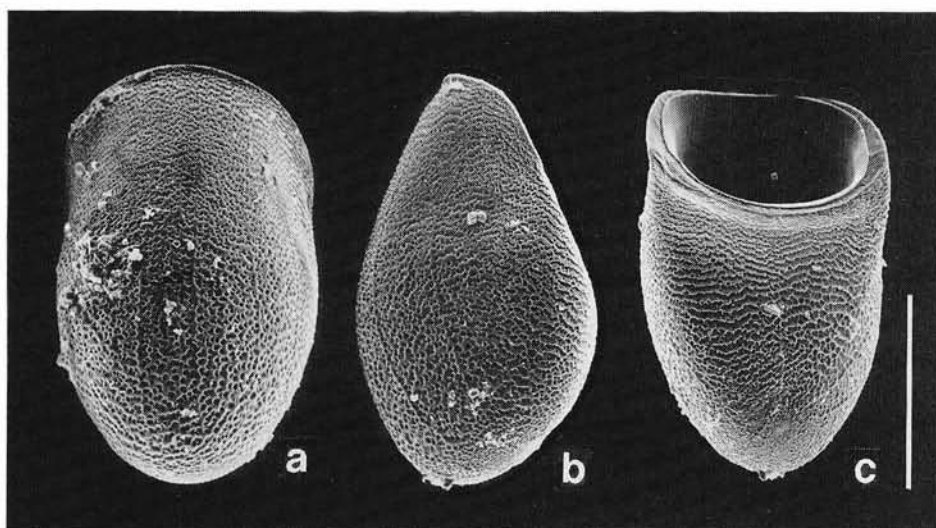
Fig. 3. Protoconch of *Cellana toreuma*. RM 27612. **a**, Dorsal view. **b**, Right lateral view. **c**, Ventral view.
Scale = 100 μm.

Head with short snout (sn) and pair of non-papillate cephalic tentacles (ct). Snout always directed ventrally, fitting mouth to substratum. Outer lip (ol) of mouth fringed with minute tentacles (Fig. 10 e). Inner lips (il) arising from inner lateral wall of oral tube, with only median parts exposed. Oral lappets absent. Eyes open, simply invaginated cups, with inner basal portions black-pigmented; presence clearly indicated externally by short slits.

Tentacles, sense organs, and operculum absent. Only one pair of sensory streaks in pallial groove; anterior pallial streaks (aps) running along both ends of shell muscle, extending slightly backward in pallial groove. Lateral pallial streaks (as in *Patella*, above) absent.

Pallial Complex: Pallial cavity shallow, restricted to small space in nuchal region, containing "secondary" pallial gills, anus, paired kidney openings, and paired osphradia. Ctenidium and hypobranchial gland absent.

Pallial gills (pag) developing from circumpallial vessel (Fig. 10 c), with cilia arising irregularly from its surface (Fig. 10 d). Gills very characteristically absent in front of head where circumpallial vessel interrupted (Fig. 4 b).

Paired osphradia symmetrically situated on floor of pallial cavity near anterior end of shell muscle; right and left osphradia of subequal size. Surface of wart-organ (wo) smooth, lacking ciliated zone, with spongy structure in cross-section (Figs. 9 e, f, SEM observation).

Digestive System: Oral tube not surrounded by circular buccal sphincter and constrictor, but instead covered by jaw. Inner lateral walls of oral cavity giving rise to thickened inner lips which are fixed by transverse labial muscles (tlm, Fig. 5 c).

Odontophore connected to wall of body cavity by dorsal, lateral, and ventral protractors, and anterior levators (Figs. 5 a-d, 6): (1) Dorsal protractors (dp) occupying most dorsal part of buccal mass, running obliquely along anterior esophagus, inserting on posterior cartilages. (2) Lateral protractors (lp) running along outer sides of odontophore over retractors of subradular membrane (rsr). (3) Ventral protractors (vp) distinctly divided into two layers. Outer ventral protractors (ovp) as most ventral part of musculature, connected to body cavity floor beneath sublingual pouch. Inner ventral protractors (ivp) widely enveloping ventral side of odontophore, attached to posterior end of sublingual pouch, margin or inner surface of ante-
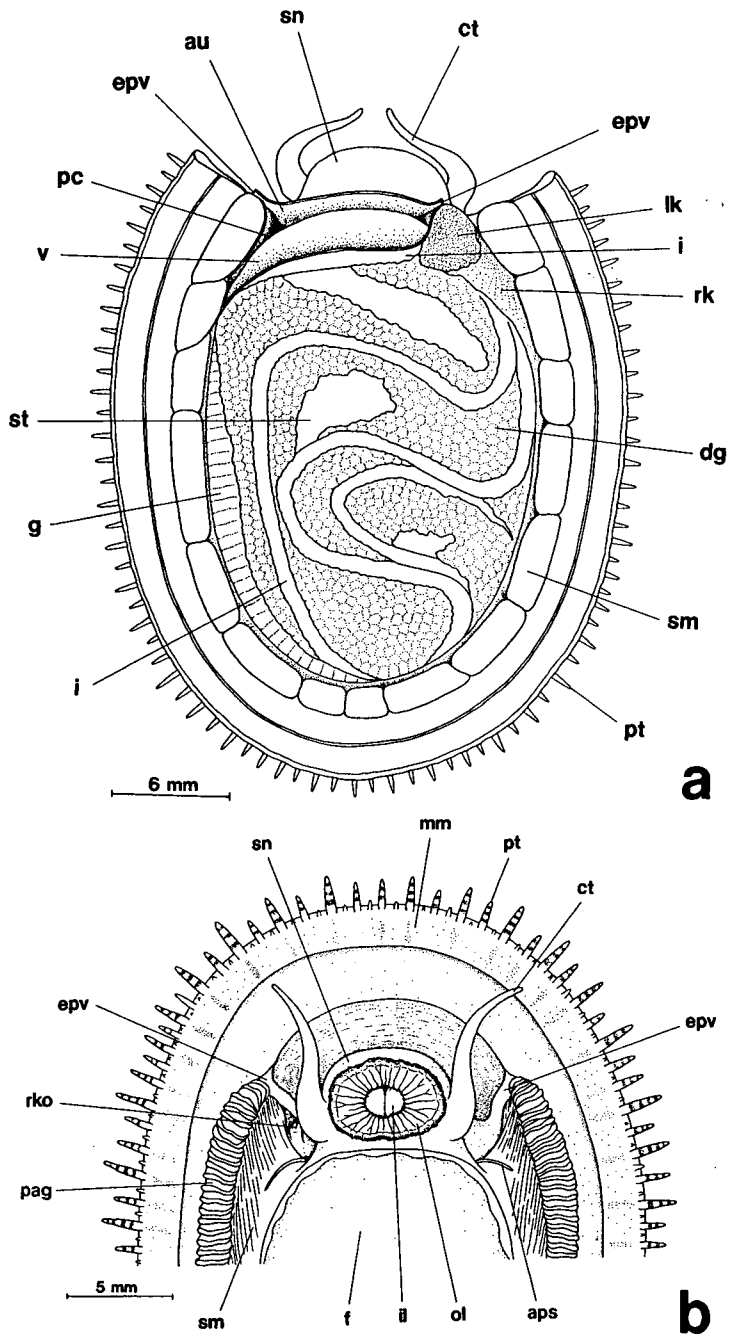
Fig. 4. *Cellana toreuma*. **a**, Dorsal view of the body after removal of the shell and mantle. **b**, Ventral view of the anterior part of the animal.
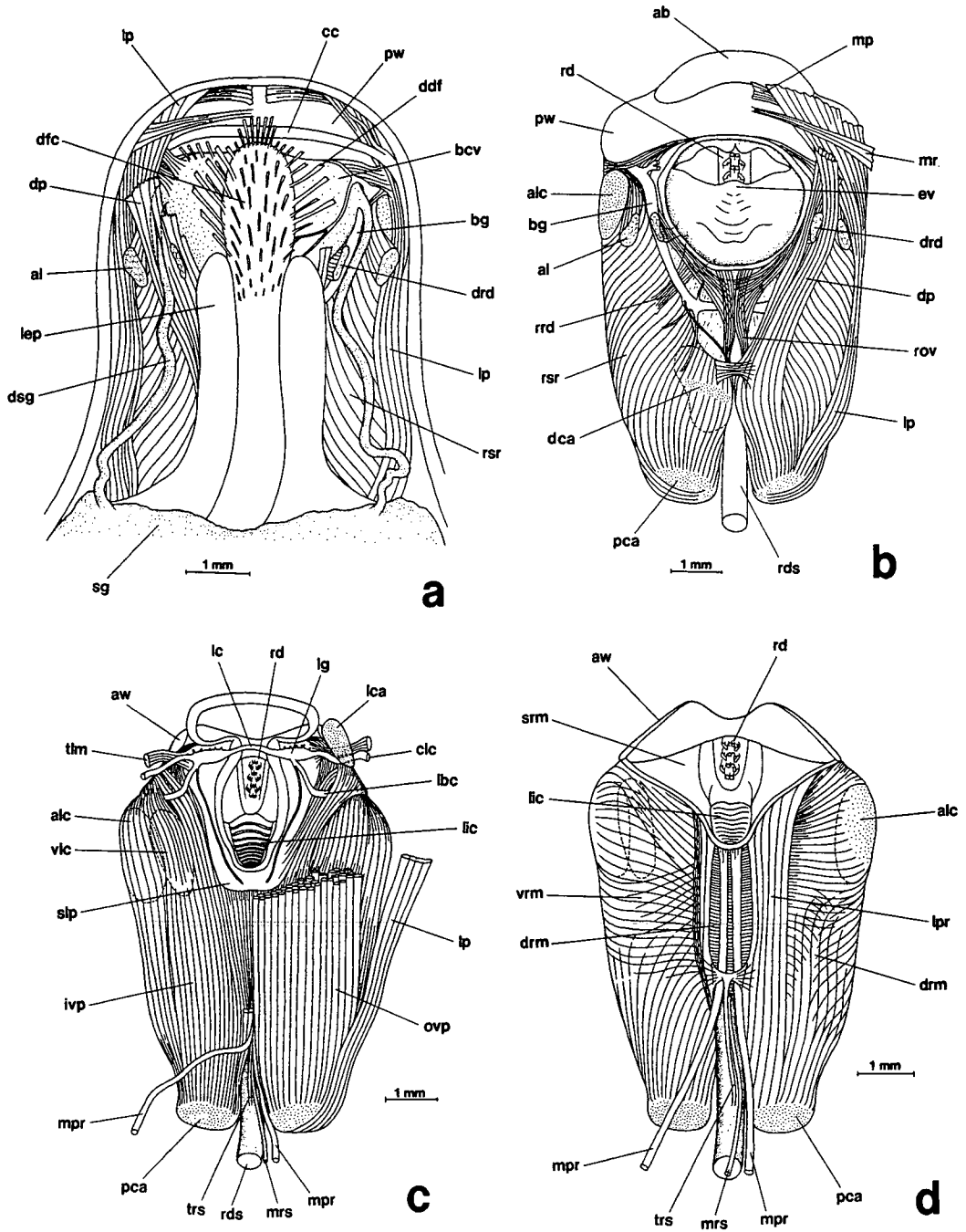
Fig. 5.   *Cellana toreuma*. **a**, Dorsal view of the buccal region. Some muscles on the right side are removed. **b**, Dorsal view of the buccal mass after removal of the esophagus and muscles on the left sides. **c**, Ventral view of the buccal mass. The floor of sublingual pouch is cut to expose the licker. Some muscles on the left side are removed. **d**, A deeper dissection of the buccal mass. Ventral part of the retractor muscle of the subradular membrane (vrm) is wholly removed on the right side.
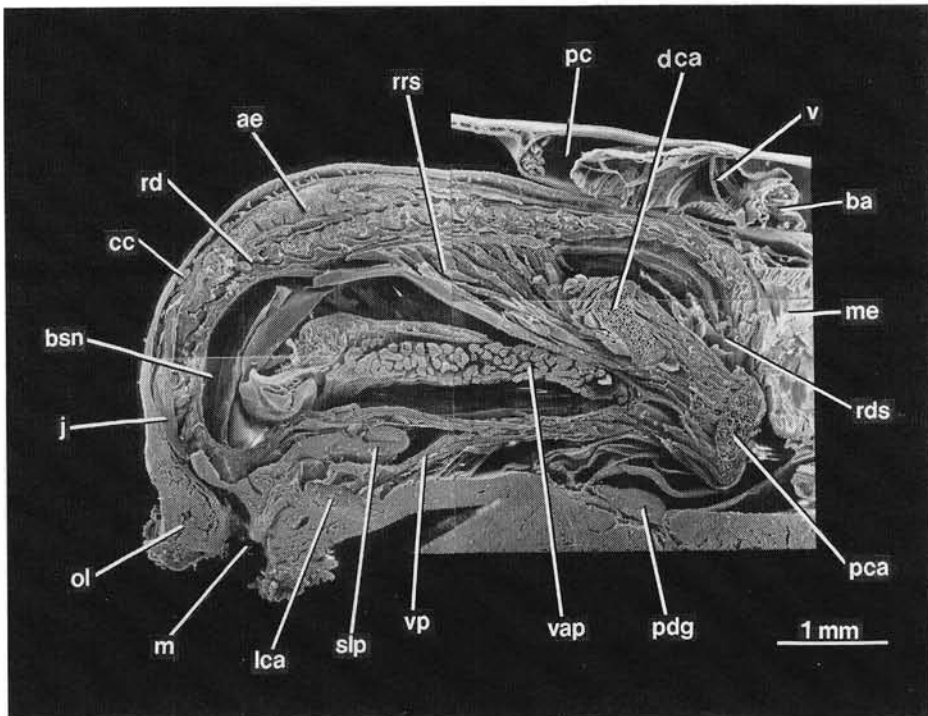
Fig. 6.   *Cellana toreuma*. SEM micrograph of longitudinal section of head region. RM 27613 a.
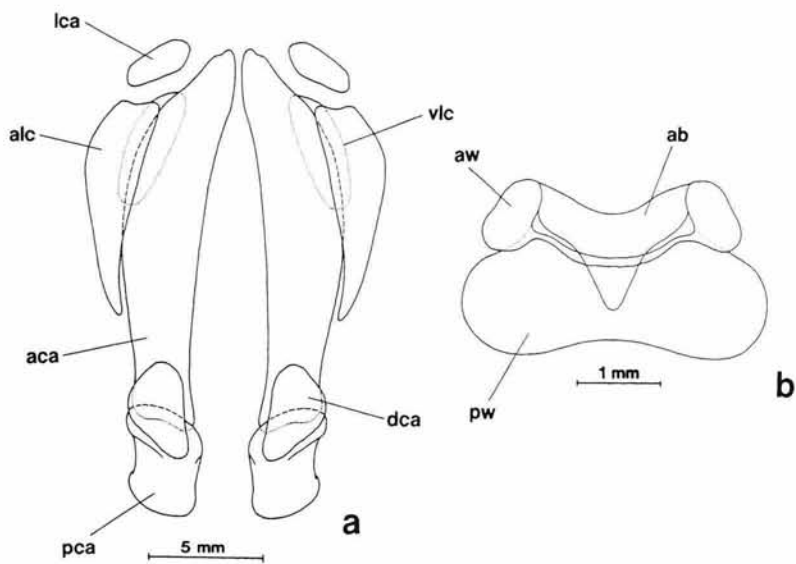

Fig. 7.   *Cellana toreuma*. **a**, Dorsal view of the odontophoral cartilages. Approximator muscles are omitted. **b**, Dorsal view of the jaw.
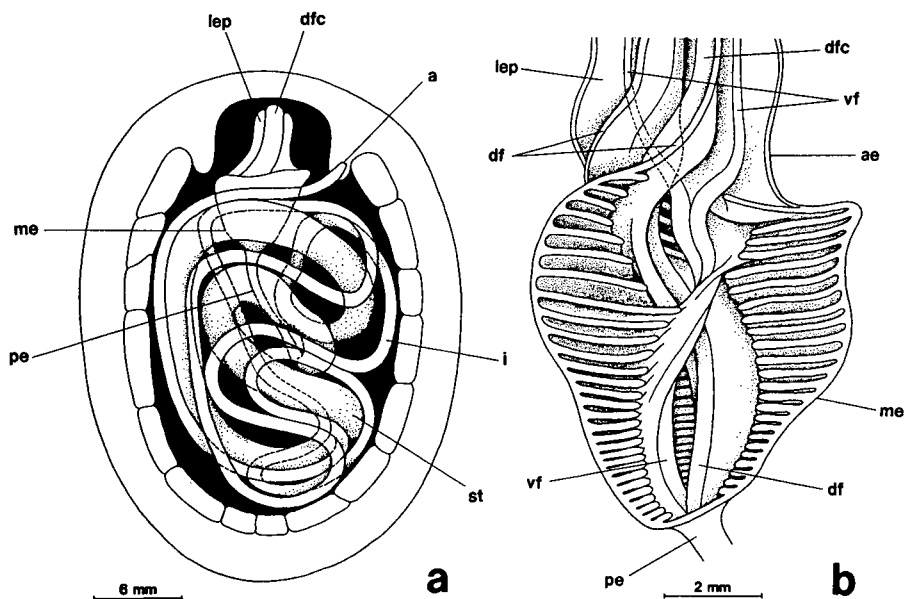
Fig. 8.   *Cellana toreuma*. **a**, Configuration of the alimentary tract. **b**, Internal structure of the anterior and mid-esophagi. Dorsal wall is removed, and lateral wall is slightly opened.
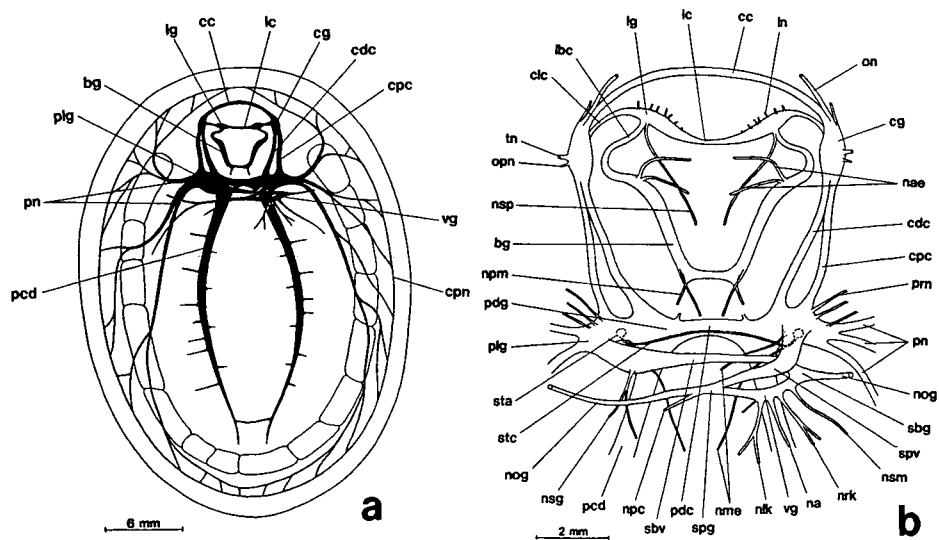

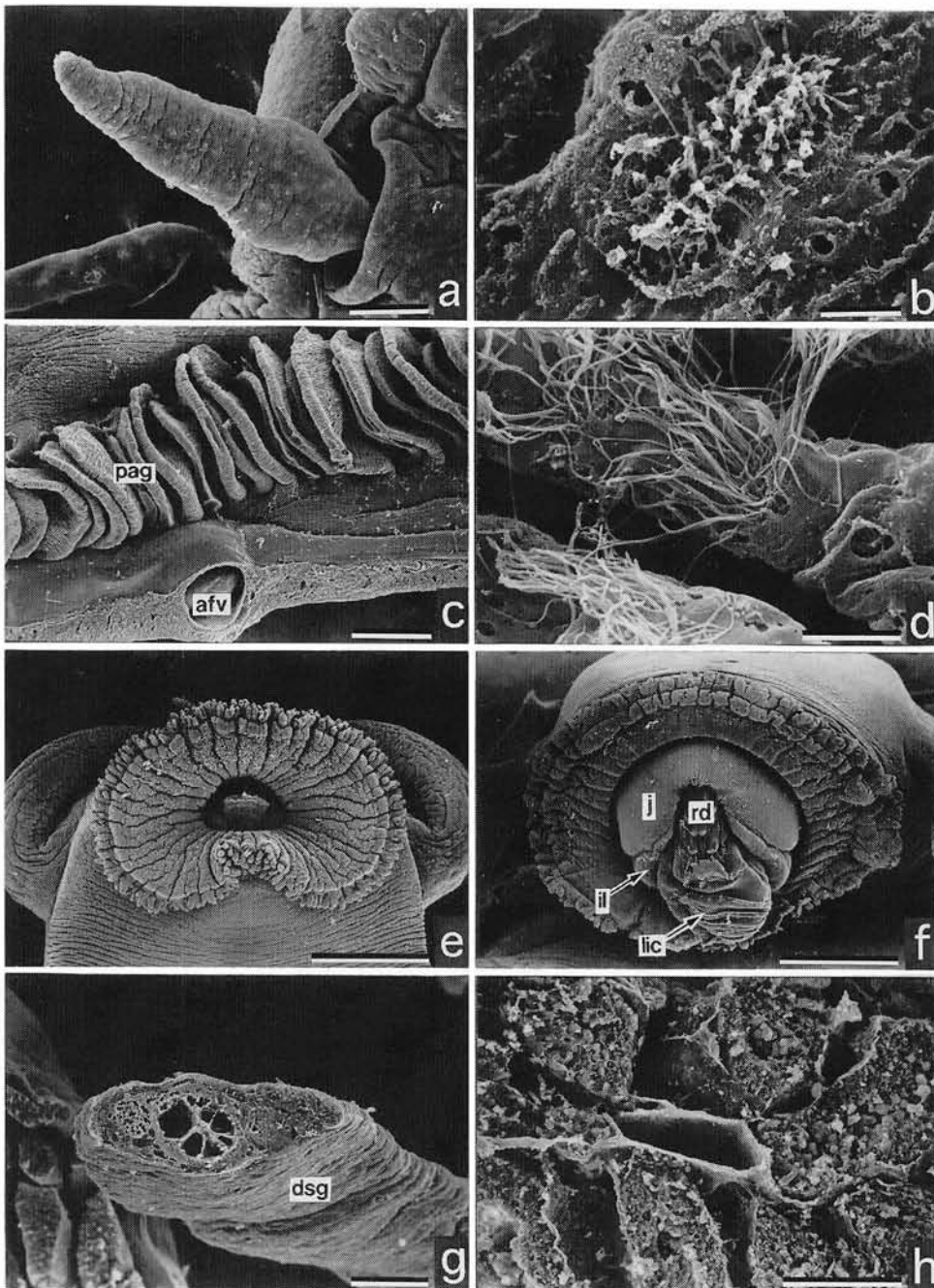Fig. 9.   *Cellana toreuma*. **a**, Whole view of nervous system. **b**, Nervous system in the head region.

Fig. 10. *Cellana toreuma*. SEM micrographs of soft parts. **a-d**, RM 27613 b. **e-f**, RM 27613 c, **g**, RM 27613 d. **h**, RM 27613 a. **a**, Retractile pallial tentacles of mantle margin. Scale = 100 μm. **b**, Surface of pallial tentacle. Scale = 5 μm. **c**, Secondary pallial gills. Scale = 500 μm. **d**, Cilia on secondary gills. Scale = 5 μm. **e**, Outer lip of mouth. Scale = 1 mm. **f**, Licker and anterior part of jaw protruding in the mouth. Scale = 1 mm. **g**, Cross-section of salivary duct. Scale = 50 μm. **h**, Vertical section of digestive gland. Scale = 100 μm.
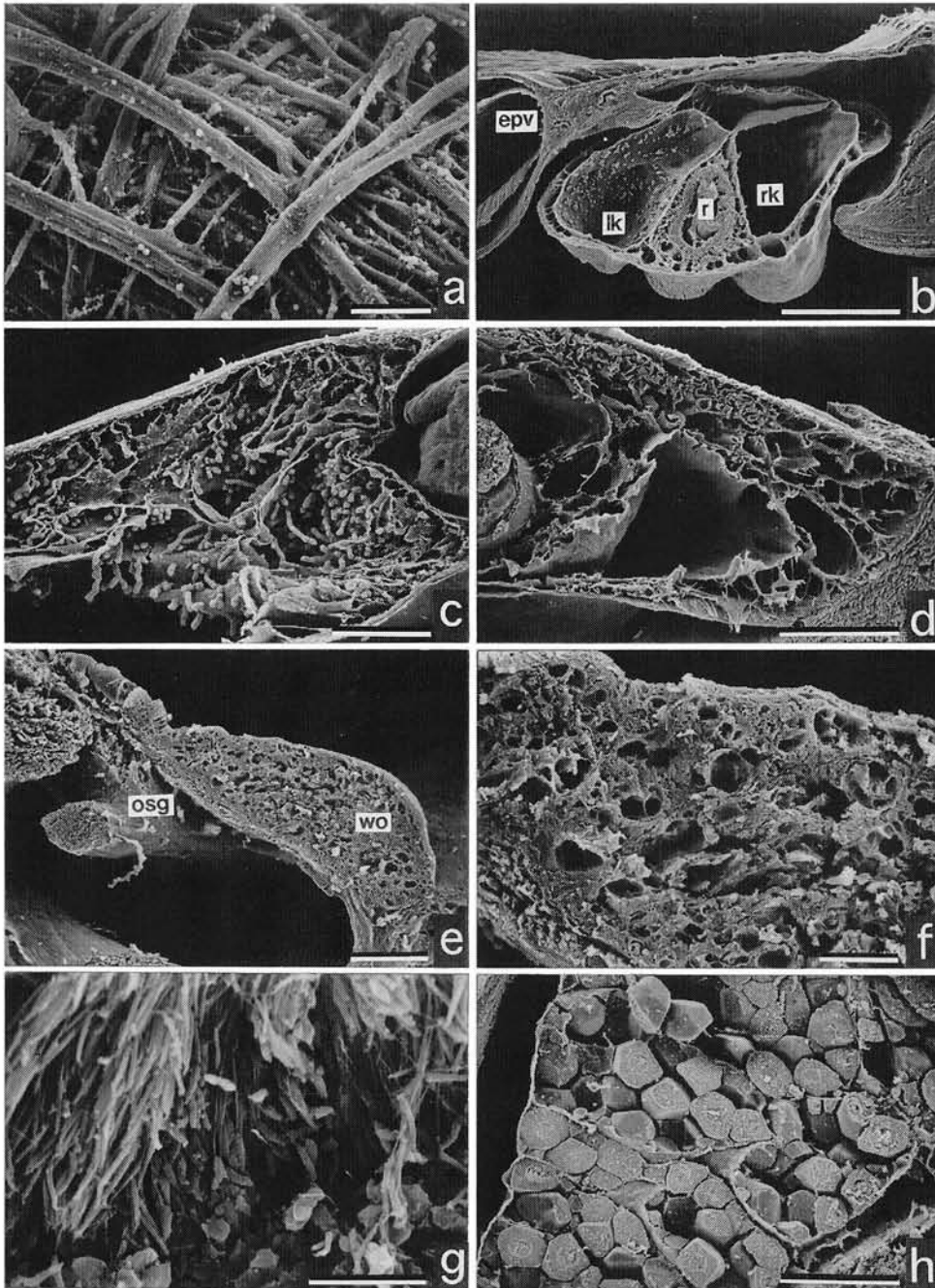
Fig. 11.   *Cellana toreuma*. SEM micrographs of soft parts. **a**, **g**, RM 27613 a. **b**, RM 27613 b. **c**, RM 27613 e.
d-f, RM 27613 d. **h**, RM 27613 f. **a**, Inner wall of ventricle with muscle fibers. Scale = 50 μm. **b**,
Cross-section of anal region with terminal chambers of kidneys. Scale = 500 μm. **c**, Inner wall of left
kidney. Scale = 250 μm. **d**, Cross-section of right kidney. Scale = 500 μm. **e**, Cross-section of right
osphradium with ganglion and wart-organ. Scale = 100 μm. **f**, Enlarged view of cross-section of wart-
organ. Scale = 25 μm. **g**, Spermatozoa in testis. Scale = 10 μm. **h**, Ova in ovary. Scale = 300 μm.

rior and posterior wings of jaw, ventral side of oral tube, and part of retractors of subradular membrane. (4) Anterior levators (al) inserting on anterolateral sides of odontophoral cartilages, running along anterior end of cartilages below labiobuccal connective, rising dorsally toward origin on roof of body cavity. Depressors and tensors absent in posterior part.

Jaw forming single plate composed of smaller anterior and larger posterior wings (aw, pw) (Fig. 7 b). Anterior margin thickened into smooth anterior band (ab). Most parts of jaw covering dorsal side of oral tube. Posterior wings firmly fixed to odontophore by muscle attachment.

Radular sac very long, forming more than three loops. Posterior end of radular sac not bifurcated. Radular formula 1?–2–1–2–1?. Inner lateral teeth thin with acute cusp and central ridge. Cusp of outer lateral teeth divided into two lateral parts; acutely pointed inner cusp with median ridge; blunt outer cusp smoothly continued to outer margin of shaft, forming excavated longitudinal cleft. Marginal teeth represented by thin plates adhered to radular membrane. Basal plates sharply sculptured.

Subradular membrane fixed by thick retractors and two relatively thin pairs of odontophoral protractors: (1) Retractors of subradular membrane (rsr) extending from lateral margin of subradular membrane, entirely enclosing cartilages, ventrally divided into two layers (Fig. 5 d): dorsal layer (drm) between two pairs of subradular membrane protractors and ventral approximator of odontophoral cartilages; ventral layer (vrm) fused between inner ventral protractors of odontophore and two pairs of subradular membrane protractors. (2) Median protractors of subradular membrane (mpr) extending backward along midline; left protractor running straight, but right one more or less sharply bending left, ventrally penetrating buccal membrane, ultimately attaching to right shell muscle (Figs. 5 c, d). (3) Lateral protractors of subradular membrane (lpr) lying laterally to median protractors, inserting onto posterior cartilages (pca) (Fig. 5 d).

Ventral side of radular sac inserted by (1) paired retractors of radular sac (rrs) (Fig. 6), (2) unpaired median retractor of radular sac (mrs), and (3) unpaired ventral tensor of radular sac (trs) (Figs. 5 c, d).

Odontophore containing five pairs of cartilages: anterior (aca), posterior (pca), anterolateral (alc), ventrolateral (vlc), and posterodorsal cartilages (dca) (Fig. 7 a). In addition, pair of labial cartilages (lca) on ventral floor of buccal region (Fig. 6). Odontophoral part of cartilages interconnected by sheet-like muscles to each other to form firm core of buccal mass. Among them, anterior cartilages especially tied by well-developed, two-layered ventral approximator muscle (vap).

Anterior part of buccal cavity giving rise to ventral branch of deep sublingual pouch (slp) without outgrowths (Fig. 5 c). Licker (lic) provided with 9–10 transverse lamellae (Figs. 5 d, 10 f). Radular diverticulum narrow, longitudinally elongated below esophageal valve. Salivary glands (sg) pouch-like, widely extended over post-buccal region (Fig. 5 a). Paired long salivary ducts (dsg) arising from outer anterior part of glands, discharging into buccal cavity bilaterally (Figs. 5 a, 10 g).

Inner portion of anterior esophagus distinctly partitioned into dorsal food channel (dfc) and lateral pouches (lep) by inner ventral folds (vf) and outer dorsal folds (df) (Figs. 8 a, b). Mid-esophagus (me) bending toward left in visceral region. Boundary between anterior and mid-esophagi clearly delimited by internal structural difference (Fig. 8 b). Dorsal and ventral folds of mid-esophagus prominently rotated counterclockwise. Right and left dorsal folds fused into single fold posteriorly; both ventral folds fused at beginning of mid-esophagus. Mid-esophagus ending with distinct constriction. Posterior esophagus (pe) internally corrugated by longitudinal grooves.

Stomach (st) consisting of smaller proximal part of sigmoidal loop and larger C-shaped distal part (Fig. 8 a). Only initial chamber of stomach with small openings of ducts from digestive glands. Sorting area indistinct; gastric caecum and tooth of gastric shield totally absent. Intestinal groove between typhlosoles very shallow. Intestine (i) consisting of more than ten loops, coiling complexly within digestive glands. Rectum not penetrating ventricle or pericardium. Anus (a) opening at right anterior corner of pallial cavity.

Circulatory System: Heart composed of auricle, ventricle, and muscular bulbous aorta (Fig. 4 a). Very

characteristically, auricle (au) receiving efferent pallial vessels from both right and left sides, plus capillary vessels from pallial cavity roof (Figs. 4 a, b). Left posterior side of auricle with narrowly expanded space, rendering its outline asymmetrical. Ventricle (v) muscular compared to auricle. Inner wall of ventricle wholly covered with granules (Fig. 11 a). Wall of auricle fixed by connective tissue to wall of pericardium (pc) on right side. Bulbous aorta obliquely elongated, ventrally connected to ventricle through very long narrow slit, leading to anterior aorta on right anterior side and to posterior aorta on left posterior side.

Anterior aorta running ventrally into buccal region below salivary glands. Behind buccal mass, anterior aorta entering radular artery which encloses whole radular sac and extends back to visceral region. Anterior aorta further extending anteriorly as buccal artery between right and left cartilages, expanding to form buccal sinus (bsn) in center (Fig. 6), separated from surrounding cephalic sinus by buccal membrane but partly continuous through lacunae.

Posterior aorta bifurcating beyond pericardium. Ventral branch supplying blood to gonad; dorsal branch supplying digestive system. Branches divaricating complexly within visceral mass, associated with right kidney surrounding visceral mass circularly both dorsally and ventrally. Venous blood vessels from visceral sinus passing though shell muscle toward circumpallial vessel, finally entering auricle through paired efferent pallial vessels.

Excretory System: Paired asymmetrical kidneys on either side of terminal part of intestine (Figs. 4 a, 11 b). Both kidneys lying on right side of pericardium. Left kidney (lk) extremely small relative to right, its inner wall covered densely with vermiform projections (Fig. 11 c). Opening of left kidney papillate with longitudinal slit (Fig. 4 b). Right kidney (rk) extending widely along shell muscle, surrounding digestive glands and stomach, its lumen spacious and partitioned by membranous structure (Fig. 11 d). Opening of right kidney (rko) forming simple pore. Left renopericardial duct opening as horizontally elongated slit at base of right posterior wall of pericardium. Right renopericardial duct opening into right wall of pericardium through minute pore.

Reproductive system: Reproductive organ consisting of very simple gonad and gonoduct. Gonad (g) situated within ventral side of visceral mass; left side extending to dorsal surface as it becomes gravid and increases its volume (Fig. 4 a). Gonoduct connected to right kidney independent of renopericardial duct. Because of its thinness, gonoduct often difficult to trace in macroscopic observation in non-breeding condition, but packed with gametes in gravid phase.

Sexes separate; consecutive hermaphroditism not observed. Male and female identified by texture of gonadal contents: granular in female (ovary), cotton-like in male (testis); this difference reflecting morphology of clusters of gametes within gonad. Spermatozoa with long head and thread-like tail (Fig. 11 g). Ova covered by thick layer of yolk (Fig. 11 h). Gametes discharged through right kidney; fertilization free in sea water.

Nervous system: Circumesophageal nerve ring hypoathroid (Figs. 9 a, b). Cerebral ganglia (cg) at bases of cephalic tentacles, interconnected to cerebral commissure (cc) running in front of posterior wings of jaw. Pleural and pedal ganglia (plg, pdg) juxtaposed along posterior margin of buccal mass, each connected to cerebral ganglion by long connective (cdc, cpc). Both lying not in visceral region, but within cephalic sinus separated from visceral sinus by membrane.

Cerebral ganglia innervating laterally cephalic tentacles via tentacular nerves, eyes via optic nerves, and anteriorly to oral region of snout. Inner sides of ganglia also providing thin but distinct nerves to ventral side of buccal cavity. Labial ganglia (lg) supplying nerves anteriorly to labial region through about 7 labial nerves and posteriorly to sublingual pouch and its vicinity (Figs. 5 c, 9 b), connected by labial commissure (lc). Elongated buccal ganglia (bg) between esophagus and radular diverticulum, providing nerves to buccal cavity roof, dorsal food channel, and muscles of buccal mass. Buccal and labial ganglia connected through labiobuccal connectives (lbc) running between posterior wings of jaw and lateral protractor muscles of

odontophore.

Very tight visceral loop formed by fusion of visceral (vg), supraesophageal (spg), and subesophageal (sbg) ganglia just behind buccal mass on right side. Loop prominently slanted against horizontal plane of body with subesophageal side placed more ventrally. Ganglia of loop innervating kidneys (nrk, nlk), anus (na), digestive glands and tracts, and pericardium (npc). Thin nerve particularly extending to shell muscle from subesophageal side (nsm, Fig. 9 b). Connectives with osphradial ganglia also arising from sides of visceral loop.

Pleural ganglia close to lateral body walls, giving off several thin parietal nerves (prn) and thicker pallial nerves (pn). Latter nerves dividing into anterior and posterior branches on both right and left sides, penetrating shell muscles, extending into thin mantle, reaching cord of circumpallial nerve (cpn). Fine branches from pallial nerves forming complex nerve plexus by anastomosing in mantle margin. Zeugoneury absent on both sides.

Pedal ganglia not very concentrated, emitting thick pedal cords to pedal musculature. Statocysts (sta) located lateral to pedal but ventral to pleural ganglia, united by very thin commissure (stc) (Fig. 9 b).

Family Lepetidae Dall, 1869
Limalepeta lima (Dall, 1918)
(Figs. 12 a-b, 13 a-b, 14 a-c)

External Anatomy: Circumpallial tentacles of mantle margin not visible in fixed specimen; living specimens not observed. Shell muscle (sm) horseshoe-shaped with pallial retractor muscle, divided into bundles by blood vessels. Head with short snout, and non-papillate cephalic tentacles (ct) without eyestalks. Outer lip (ol) of mouth surrounded by oral lappets (olp) (Fig. 12 b). Eyes of simple invaginated type within bases of cephalic tentacles. Foot lacking lateral epipodial tentacles and sense organs, and operculum. Anterior and lateral pallial streaks also absent.
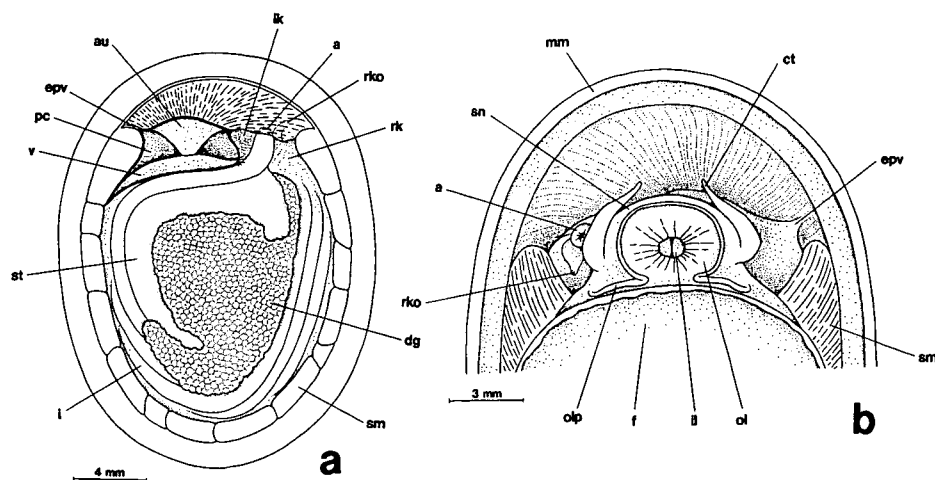
Fig. 12.   *Limalepeta lima.* **a,** Dorsal view of the body after removal of the roof of pericardium. **b,** Ventral view of the anterior part of the animal.

Pallial Complex: Pallial cavity shallow, containing only anus and paired kidney openings on posterior wall (Fig. 12 a). No true ctenidia or "secondary" gills. Osphradia and osphradial ganglia absent. Hypobranchial gland absent.

Digestive System: Movement of inner lips controlled by transverse labial muscles (tlm) running below
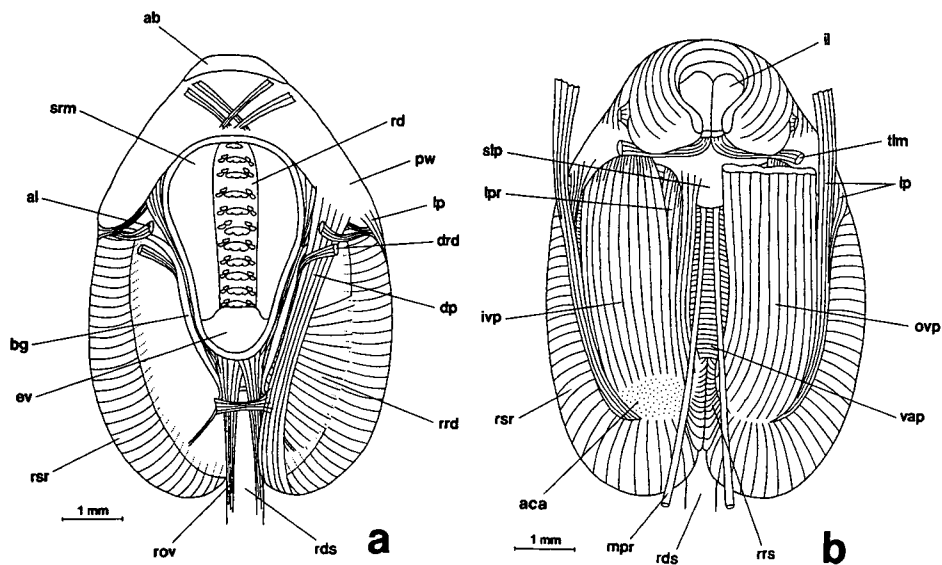
Fig. 13. *Limalepeta lima.* **a,** Dorsal view of the buccal mass after removal of some left muscles. **b,** Ventral view of the buccal mass. Outer ventral protractor muscle of odontophore (ovp) is removed on the left side.
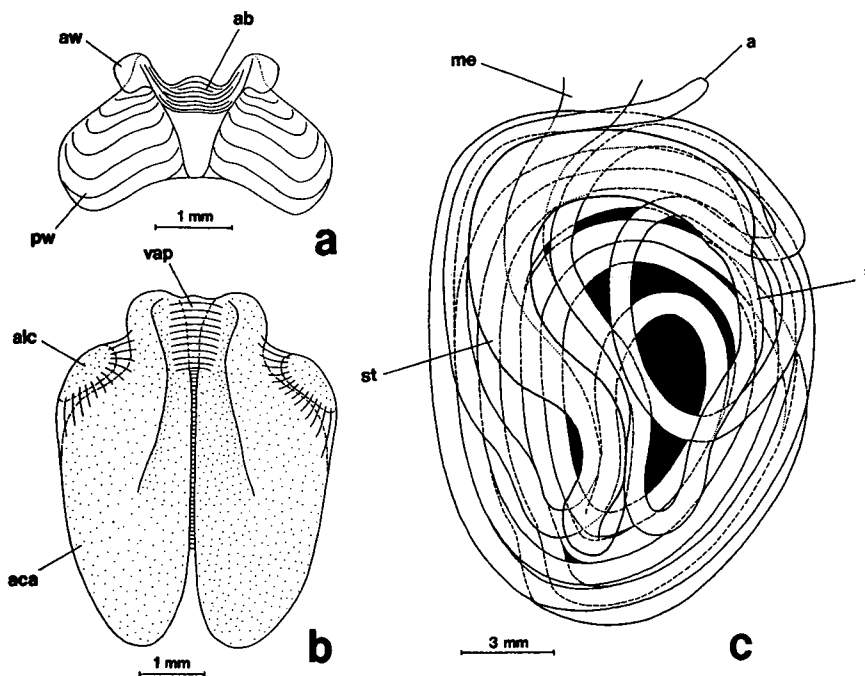

Fig. 14. *Limalepeta lima.* **a,** Dorsal view of the jaw. **b,** Dorsal view of the odontophoral cartilages. **c,** Configuration of the post-buccal alimentary tract.

anterior wings of jaw toward origin of lateral wall of snout. Muscles of odontophore consisting of following muscles (Figs. 13 a, b): (1) Dorsal protractors (dp) running from end of posterior cartilages, passing between anterior levators and dilators of radular diverticulum (drd), attaching to margin of posterior wings of jaw. Behind buccal cavity, right and left muscles connected by thin transverse muscle tissues over retractors of esophageal valve (rov). (2) Lateral protractors (lp) rather thin, restricted to outer ventral sides of ventral protractors of odontophore, inserted on posterior wings of jaw and anterior wall of snout. (3) Ventral side of odontophore covered by thick layers of outer and inner ventral protractors of odontophore (ovp, ivp), the former originating on floor of snout including sublingual pouch, while the latter arising from sides of oral tube and posterior wings of jaw. Both protractors inserting on posterior cartilages, overlapping in distribution. (4) Anterior levators (al) inserted on sides of anterolateral cartilages, passing between connective muscles on posterior wings of jaw and retractors of subradular membrane. Depressors and tensor absent posteriorly.

Jaw (j) thick, marking clear incremental lines in parallel to margin (Fig. 14 a), consisting of larger posterior and smaller anterior wings (pw, aw) with weekly toothed anterior band (ab). Posterior wings attached to odontophore by muscles; anterior wings fixed on inner lips of oral region.

Radular formula 2–0–1–0–2. Radular row symmetrical. Central tooth paddle-shaped, nearly square, attached to radular membrane in smaller area; cusp divided into three portions of equal width. Marginal teeth broadly spatulate, gently curved. Attachment area of teeth on radular membrane small. Basal plates absent.

Subradular membrane firmly fixed to cartilages by retractors of subradular membrane (rsr), which are not divided into dorsal and ventral parts, but clearly shows paired condition (Fig. 13 b). Protraction of membrane caused by two pairs of protractor muscles. Median protractors (mpr) thin, extending toward posterior side of buccal mass. Configuration of right and left muscles completely symmetrical. Lateral protractors (lpr) thick, inserted on anterior ventral surface of subradular membrane, running above inner ventral protractors. Radular sac controlled only by retractors of radular sac (rrs). Median retractors of radular sac (mrs) and ventral tensor of radular sac (trs) (corresponding to those of *Patella* and *Cellana*) absent.

Odontophore containing two pairs of cartilages (Fig. 14 b). Anterior cartilages (aca) extending over whole length of odontophore, expanding laterally, connected by two layered ventral approximator (vap); ventral layer widely connecting to anterior cartilages, while dorsal layer restricted to anterior region between grooved parts of cartilages. Anterolateral cartilages (alc) small. Labial cartilages (as in *Cellana*) absent.

Sublingual pouch (slp) deep, lacking pouch-like projections and glandular outgrowths on sides (Fig. 13 b). Licker weakly sculptured by divaricate furrows. Radular diverticulum widely spread over odontophore, covered by sheet-like retractors of radular diverticulum (rrd, Fig. 13 a). Salivary glands arising directly from lateral walls of buccal cavity, extending obliquely toward outer posterior corners of buccal mass.

Anterior esophagus depressed over odontophore, with dorsal food channel and lateral pouches. Midesophagus (me) septate internally, not strongly inflated, with rather gradual counterclockwise rotation in this part. Posterior esophagus (pe) marked by internal furrows; its initial part not distinctly constricted.

Stomach (st) basically C-shaped, but its anterior part distorted posteriorly (Fig. 14 c). Openings of digestive glands restricted to small area of initial part. Gastric caecum, sorting area, and tooth of gastric shield absent. Intestinal groove between typhlosoles very shallow. Intestine (i) extremely long, complicated in configuration. Rectum passing pericardium along posterior wall, terminating at right corner of pallial cavity.

Circulatory System: Heart consisting of auricle, ventricle, and muscular bulbous aorta (Fig. 12 a). Auricle (au) receiving blood from efferent pallial vessel on right side and also directly from roof of pallial cavity. Ventricle (v) elongated along posterior wall of pericardium, leading ventrally into muscular bulbous aorta (ba) which has similar form to that of ventricle.

Excretory System: Paired kidneys of extremely unequal size on right side of pericardium (Fig. 12 a).

Left kidney (lk) in area between anus and pericardium; lumen filled with minute digitiform projections. Left kidney opening (lko) projected as small papilla. Course of renopericardial ducts not determined. Right kidney (rk) encircling alimentary tract along shell muscle, also widely extending into base of visceral mass; lumen spacious with membranous partitions. Right kidney opening (rko) extended as long tapering tube (Fig. 12 b).

Reproductive System: Gonad lying on ventral side of digestive tracts and glands. Gonoduct arising from left side of gonad, communicating with right kidney anteriorly, passing below rectum; relationship with right renopericardial duct not determined. Right excretory pore prolonged as urogenital opening.

Nervous System: Circumesophageal nerve ring hypoathroid. Pleural and pedal ganglia very closely connected. Right and left pedal ganglia widely spaced. Labial ganglia united by labial commissure. Buccal ganglia arising from posterior sides of labial ganglia. Visceral loop originating from left and right pleural ganglia. Supraesophageal, visceral, and subesophageal ganglia fused into tight loop behind buccal mass. Osphradioctenidial ganglia and zeugoneury absent. Pedal cords widely spaced. Statocysts lying on outer sides of pedal ganglia below pleural ganglia.

Iothia sp.
(Figs. 15 a-d)

Protoconch: Protoconch completely symmetrical, longitudinally elongated. Lateroventral wall extending outward to form lateral pouches and corresponding constrictions on either side. Densely reticulated sculpture and several longitudinal streaks visible on side, although detailed structure not observed in specimens examined due to erosion. Protoconch symmetrically positioned relative to sagittal axis of teleoconch throughout ontogeny.

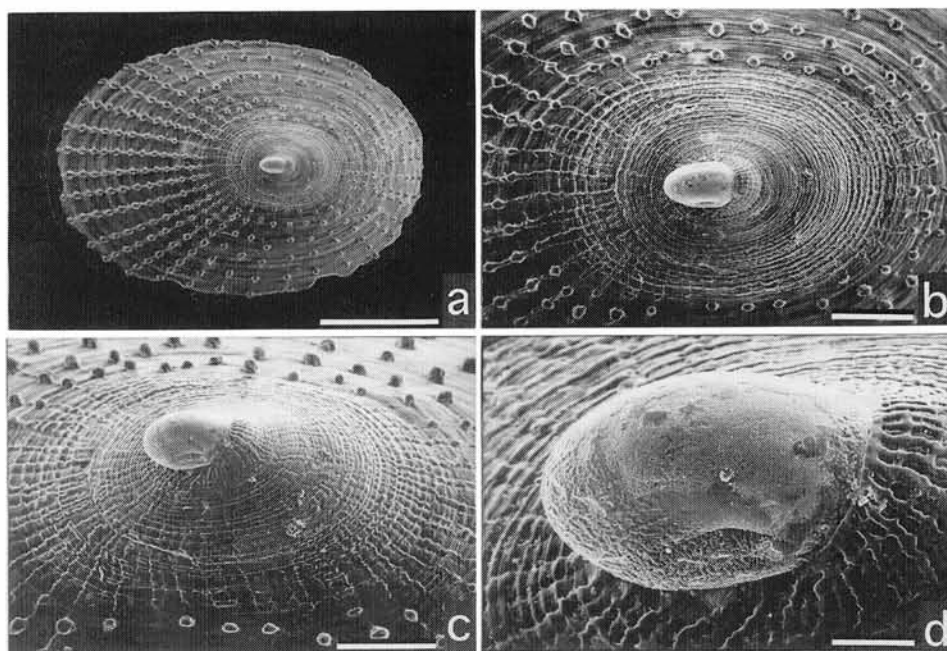Fig. 15.   Protoconch of *Iothia* sp. RM 27615. **a**, Dorsal view. Scale = 1 mm. **b**, Dorsal view of apical area. Scale = 250 μm. **c**, Oblique lateral view of apical area. Scale = 250 μm. **d**, Right lateral view of protoconch. Scale = 50 μm.

Family Acmaeidae Forbes, 1850
Pectinodonta orientalis Schepman, 1908
(Figs. 16 a-d, 17 a-e)

External Anatomy: Mantle margin (mm) apparently lacking definite microtentacles in preserved specimens; living specimens not observed. Shell muscle (sm) horseshoe-shaped, constricted into about eighteen bundles. Head with short snout and non-papillate cephalic tentacles (ct) without eyestalks. Outer lip of mouth surrounded by oral lappets. Presence or absence of eyes not ascertained. Epipodial region smooth, lacking sensory streaks on shell muscles. Epipodial tentacles and sense organs, and operculum also absent.

Pallial Complex: Pallial cavity shallow, restricted to nuchal region, containing left ctenidium, paired kidney openings, and anus (Fig. 16·a). Osphradium and hypobranchial gland absent. Feather-like bipectinate ctenidium (c) arising from left side in front of pericardium. Ctenidial membrane not developed on both afferent and efferent sides. Ctenidial lamellae lacking sense organs and skeletal rods.

Digestive System: Inner lips of mouth (il) pulled outside by transverse labial muscles (tlm). Oral tube not surrounded by buccal sphincter and constrictor. Muscles of odontophore include the following (Figs. 16 b-d): (1) Dorsal protractors (dp) inserting on posterior end of posterior cartilages. (2) Lateral protractors (lp) occurring anteriorly on posterior cartilages, extending to lateral walls of snout and posterior wings of jaw; insertion slightly overlapping ventral protractors. (3) Outer ventral protractors (ovp) as most prominent muscle on ventral side, covering entire ventral side. Inner ventral protractors (ivp) inserted on posterior cartilages, connecting to posterior end of sublingual pouch (slp), ventral side of oral tube, and anterior wings of jaw (aw). (4) Anterior levators (al) on dorsal side between strands of dorsal protractors inserted on anterolateral cartilages (alc). Depressors and postdorsal and dorsal buccal tensors absent.

Jaw situated posterolaterally over oral tube, composed of anterior and posterior wings (aw, pw) connected by smooth anterior band (ab) (Fig. 17 c); posterior wings attached to anterolateral projections of anterior cartilages.

Radular sac not very long, forming two loops behind buccal mass, posterior end not bifurcated. Radula formula 0-1-0-1-0. Radular row symmetrical. Lateral teeth widely lobate, prominently serrated with ten denticles. Cusp divided by faint line into two portions, i.e. innermost and remaining denticles. First denticle most prominent, with remaining ones becoming shorter distally. Basal plates very solid with oblique tooth attachment scars; anterior margin concave; posterior margin convex; anterior outer corner projecting anteriorly, articulating with posterior margin of adjacent plates.

Muscles of subradular membrane consisting of the following (Fig. 16 d): (1) Median protractors (mpr) very thin, extending to ventral body cavity posterior to buccal mass. Both right and left strands running straight, exhibiting symmetrical configuration (unlike *Patella* and *Cellana*). (2) Lateral protractors (lpr) attached to subradular membrane on inner tip along with median muscle, obliquely extending posteriorly to origin of posterior cartilages. Muscle occurring just beneath inner ventral protractors (ivp). (3) Subradular membrane widely attached dorsally by retractors (rsr) that constitute main part of buccal mass. Right and left halves clearly divided into paired condition, not fused ventrally (unlike *Patella* and *Cellana*). Ventral side of radular sac connected to posterior cartilages by retractors of radular sac (rrs). Radular sac manipulated only by retractors of radular sac. Median retractor and ventral tensor of radular sac absent.

Odontophoral cartilages consisting of larger anterior and smaller anterolateral cartilages (aca, alc) (Figs. 17 a, b). Anterior pair united by two-layered ventral approximator (vap).

Sublingual pouch (slp) provided with triangular sac on sides (lsp) (Fig. 16 d); wall very thin, probably not glandular. Licker not sharply lamellate but sculptured by furrows. Radular diverticulum (rdv) widely spread over odontophore. Salivary glands obliquely extending from lateral part of buccal cavity toward outer posterior corners of buccal mass. Salivary ducts absent.

Anterior esophagus dorsoventrally depressed, divided into median dorsal food channel and lateral
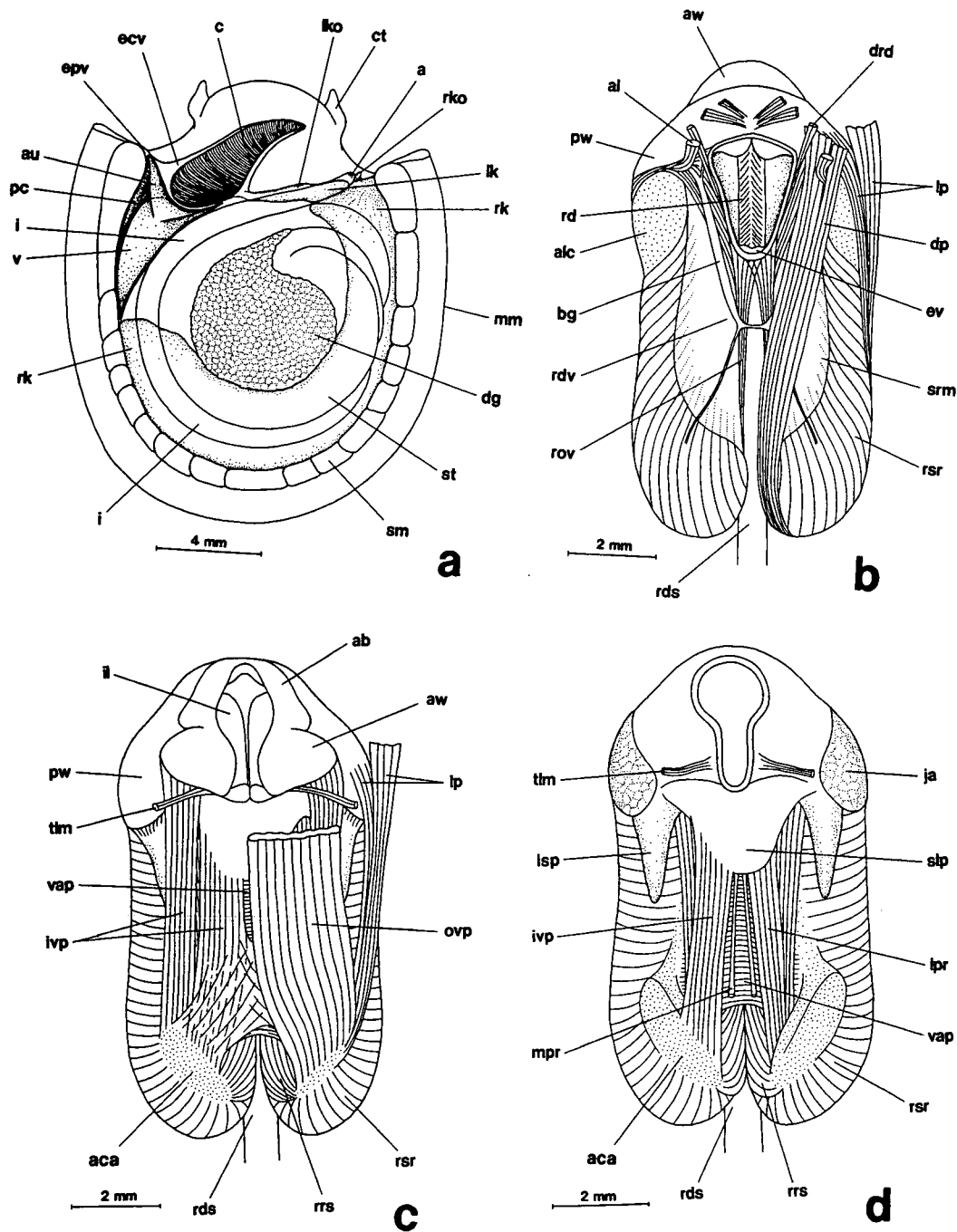
Fig. 16.   *Pectinodonta orientalis*. **a**, Dorsal view of the animal after removal of the shell and mantle. **b**, Dorsal view of the buccal mass after removal of some left muscles. **c**, Ventral view of the buccal mass after removal of some left muscles. **d**, Deeper dissection on the ventral side of the buccal mass.
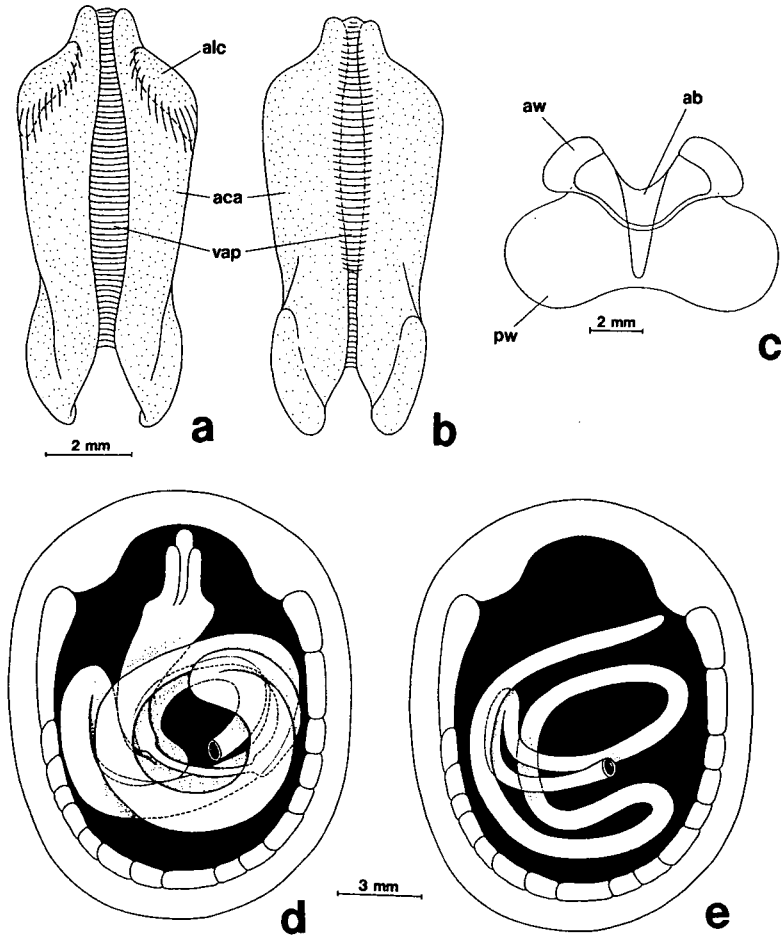
Fig. 17. *Pectinodonta orientalis*. **a**, Dorsal view of the odontophoral cartilages. **b**, Ventral view of the odontophoral cartilages. **c**, Dorsal view of the jaw. **d**, Configuration of the alimentary tract from esophagus to stomach. **e**, Configuration of the intestine.

esophageal pouches on outer sides by dorsal and ventral folds. Inner wall of mid-esophagus densely septated. Dorsal and ventral folds twisted counterclockwise internally in this section. Posterior esophagus becoming narrower, directed to right side.

Stomach with complexly folded configuration (Fig. 17 d). Proximal and distal sections curving once or twice below C-shaped dorsal median part. Openings of digestive glands very narrow, restricted to initial part of stomach. Gastric caecum, corrugated sorting area, and tooth of gastric shield absent. Intestinal groove not distinct. Intestine coiled three times, terminating at anterior right corner of visceral mass after running along posterior margin of pericardium and left kidney (Fig. 17 e).

Circulatory System: Pericardium (pc) posterior to base of ctenidium, longitudinally elongated into triangular form (Fig. 16 a). Heart consisting of single auricle and ventricle. Auricle (au) connected to efferent pallial and efferent ctenidial vessels. Ventricle (v) larger and more extensively muscular than auricle, opening ventrally into muscular bulbous aorta through long slit. Afferent ctenidial vessel connected to blood space of left kidney. Efferent ctenidial vessel (ecv) emptying directly into auricles together with efferent pallial vessel (epv) from circumpallial vessel.

Excretory System: Two extremely unequal kidneys on right of pericardium. Left kidney (lk) much smaller than right. Left kidney opening (lko) non-papillate, consisting of small transverse slit. Renopericardial ducts not observed. Right kidney (rk) encircling digestive system dorsally and ventrally. Right kidney opening (rko) projecting forwards as papilla.

Reproductive System: Gonad lying ventral to digestive tract and glands. Gonoduct arising from left side, connecting to right kidney.

Nervous System: Three major ganglia of circumesophageal nerve ring hypoathroid. Pleural-pedal complex concentrated. Pedal ganglia almost fused in midline. Labial ganglia present; labial commissure below sublingual pouch. Pedal cords very thick. Statocysts on outer sides of pedal ganglia.

Family Lottiidae Gray, 1840
Niveotectura pallida (Gould, 1859)
(Figs. 18 a-c, 19 a-c)

External Anatomy: Pallial tentacles on edge of mantle margin present in living condition, but so minute and sparse that they can be hardly observed in preserved specimens. Shell muscle horseshoe-shaped, very thick, divided into approximately fourteen bundles by blood penetration. Head with pair of thick non-papillate cephalic tentacles (ct) without eyestalks. Mouth encircled by oral lappets, smooth, without microtentacles. Eyes (e) deeply pitted, black-pigmented within bases of cephalic tentacles. Epipodial part lacking tentacles and sense organs. Operculum absent. Pallial streaks absent on shell muscle.

Pallial Complex: Shallow pallial cavity contains left ctenidium, paired kidney openings, and anus (Fig. 18 a). Osphradium and hypobranchial gland absent. Ctenidium (c) triangular, not very long. Ctenidial membrane not developed. Lamellae lacking sense organs and skeletal rods.

Digestive System: Inner lips connected to transverse labial muscles on inner and ventral sides. Odontophore narrower in anterior half, expanded laterally in posterior region, fixed by three pairs of protractors and one pair of levators (Fig. 18 b). (1) Dorsal protractors (dp) originating from dorsal wall of snout covering posterior wings of jaw, running along radular sac and esophagus, inserting on posterior cartilages. (2) Lateral protractors (lp) arising from outer ventral sides of, and attached to, anterolateral sides of buccal mass. (3) Ventral protractors composed of thick muscles covering major part of most ventral area of buccal mass, extending to posteroventral end of posterior cartilages. (4) On dorsal side, anterior levators (al) suspending buccal mass dorsally, originating from ventrolateral part of anterolateral cartilages, partly overlapping with inner section of lateral protractors and dorsal protractors. Depressors, and dorsal and postdorsal buccal tensors absent.

Jaw with well-rounded anterior and posterior wings (aw, pw) and smooth anterior band (ab). Anterior wings of jaw connected to inner lips. Posterior wings fixed to odontophore by muscular attachment from anterolateral cartilages.

Radular sac short, forming two small loops, with posterior end simply rounded. Radula formula 0-3-0-3-0. Radular row symmetrical. Lateral teeth arranged in inverted V-shape. Blunt cusp of each tooth strongly bent straight backward. Innermost laterals on anterior inner sides. Middle laterals rectangular in frontal view, wider than innermost teeth distally. Middle and outermost teeth continuously situated posterolaterally. Basal plates much wider than long.

Anterior area of subradular membrane connected to paired thin median and thicker lateral protractors (mpr, lpr). Subradular membrane attaching to thick bundles of retractors. Median protractors with symmetrical configuration; retractors of subradular membrane not fused ventrally. Ventral side of radular sac directly tied to inter posterior portion of posterior cartilages by its retractors. Median retractor of radular sac and ventral tensor of radular sac absent on ventral side of radula sac.

Odontophore containing two pairs of cartilages. Anterior cartilages (aca) inflated, broadened posteriorly,
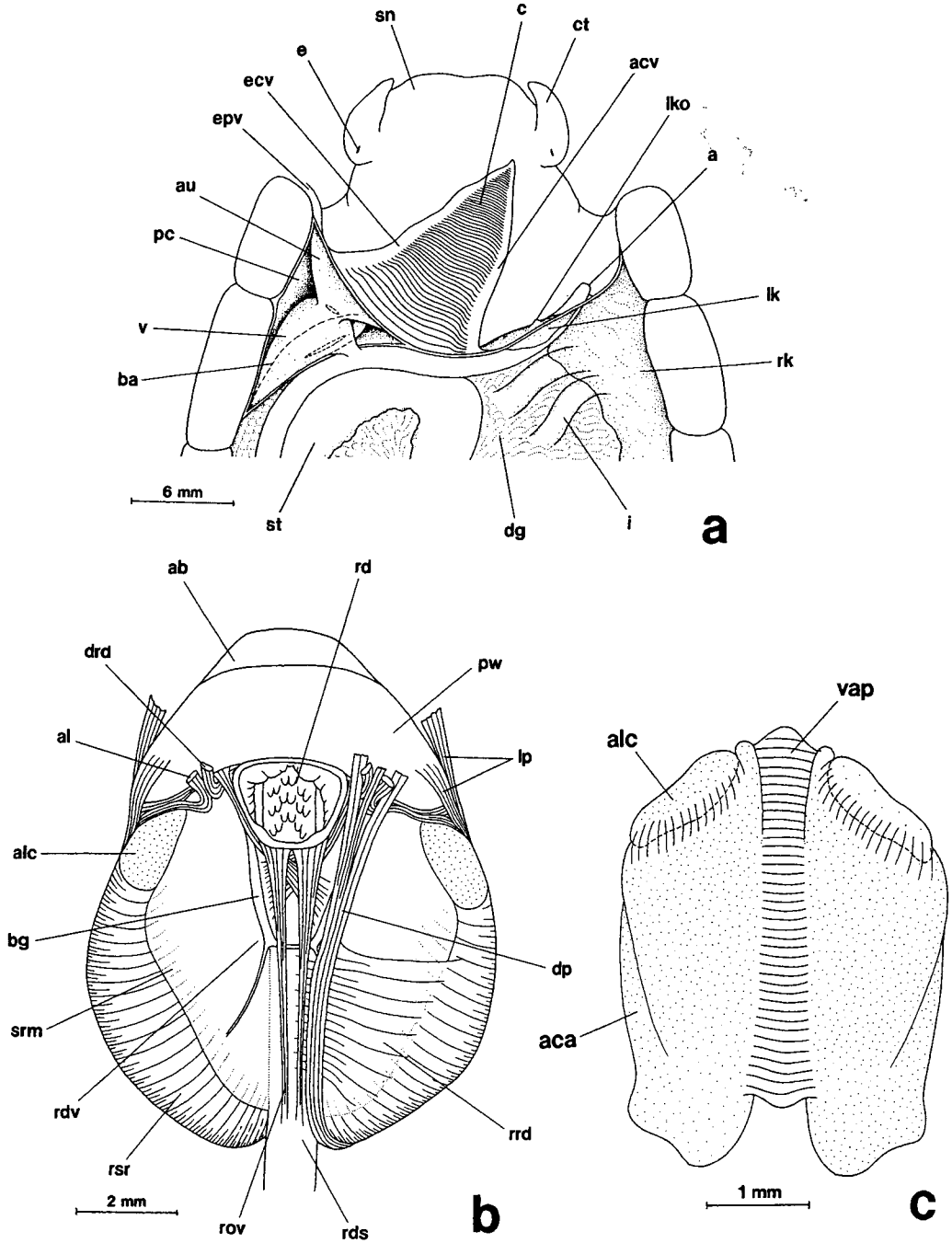
Fig. 18. *Niveotectura pallida.* **a**, Dorsal view of the anterior half of the animal after the removal of the mantle. **b**, Dorsal view of the buccal mass. Several left muscles are removed. **c**, Dorsal view of the odontophoral cartilages.
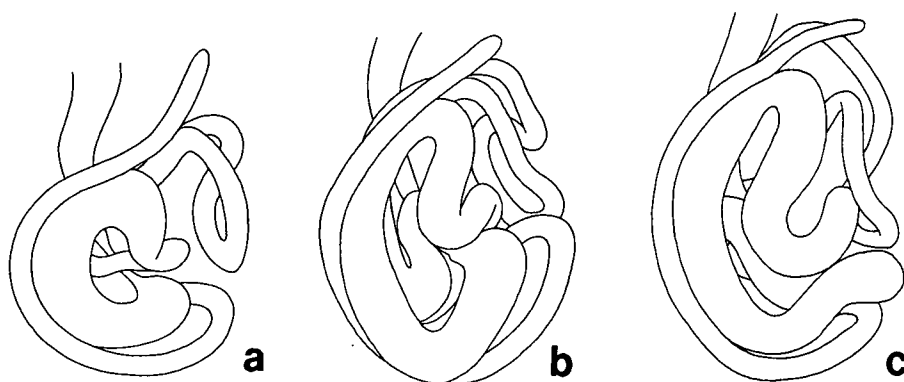
Fig. 19.   *Niveotectura pallida*. Ontogenetic change in configuration of alimentary tract. Shell length 2.6 mm (**a**),
9.8 mm (**b**), 22.0 mm (**c**).

connected by two-layered ventral approximator (vap). Anterolateral cartilages (alc) small and rounded (Fig. 18 c).

Sublingual pouch deep and smooth. Outgrowths of sublingual gland and sac-like projections absent on sides of sublingual pouch. Radular diverticulum very widely spread over odontophore. Licker sculptured by several V-shape clefts. Salivary glands obliquely elongated, directly opening into buccal pouch without duct.

Anterior esophagus partitioned into dorsal food channel and lateral pouches by thick dorsal and ventral folds. Ventral folds subdivided by two longitudinal grooves at proximal portion of mid-esophagus. Both dorsal and ventral folds clearly twisted counterclockwise. Wall of mid-esophagus bearing numerous transverse lateral folds. Posterior esophagus narrowing in posterior region, distinguished by bands of longitudinal muscles.

Configuration of stomach and intestine becoming increasingly complicated with growth (Figs. 19 a-c). Stomach initially C-shaped, changing with growth to coil in posterior terminal part, finally exhibiting at least five loops. Digestive glands opening into stomach through small paired pores at beginning of stomach. Gastric caecum and tooth of gastric shield absent. Sorting area not clearly formed. Typhlosoles and intestinal groove ill-defined. Intestine forming numerous small irregular loops which fill large space of visceral region (Fig. 19 c). Rectum not penetrating pericardium or ventricle.

Circulatory System: Heart consisting of unpaired auricle, ventricle, and bulbous aorta (Fig. 18 a). Auricle (au) triangular, narrowed posteriorly, connected to anterior end of pericardium and ventricle posteriorly, receiving efferent pallial vessels, capillary vessels of nuchal cavity roof, and efferent ctenidial vessel. Ventricle (v) well-expanded, attached to pericardial wall on right and posterior corners, suspended by connective tissue from pericardial wall and roof. Bulbous aorta (ba) swelling beneath ventricle, dividing into anterior and posterior aortae.

Excretory System: Two extremely unequal kidneys on each side of rectum (Fig. 18 a). Left kidney (lk) much smaller than right, connected to pericardium by renopericardial canal. Right kidney (rk) surrounding stomach, broadly spreading over base of visceral region. Right renopericardial duct not found. Right opening of kidney papillate; while left opening (lko) represented by simple, transverse slit.

Reproductive System: Gonad in ventral part of visceral region, extending thin gonoduct to right kidney. Red ovary clearly distinguishable in color from creamy testis.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia lying laterally near buccal mass at bases of cephalic tentacles, giving connectives laterally to labial ganglia and posteriorly to pleural and pedal ganglia. Cerebral commissure running in front of jaw. Labial ganglia embedded in ventral part of

mouth, innervating lips of mouth. Labial commissure connecting labial and cerebral ganglia.

Right pleural ganglion connected to supraesophageal ganglion at left; left pleural ganglion associated with subesophageal ganglion at right. Visceral ganglion lying over anterior aorta, fused with supraesophageal and subesophageal ganglia to form narrow visceral loop. Visceral ganglion innervating pericardium, digestive glands, and tract. Subesophageal ganglion supplying branches to kidney and right side of shell muscles. Supraesophageal ganglion associated with ctenidium and left side of shell muscle.

Pleural ganglia attached to ventrolateral body wall, linked with pedal ganglia by thick connective tissue, laterally giving rise to anterior and posterior pallial nerves which innervate mantle margin through shell muscle. Pedal ganglia very closely situated, extending thick pedal cords. Statocysts at ventral sides of pleural ganglia.

Erginus sybaritica (**Dall, 1871**)

(Figs. 20 a-f)

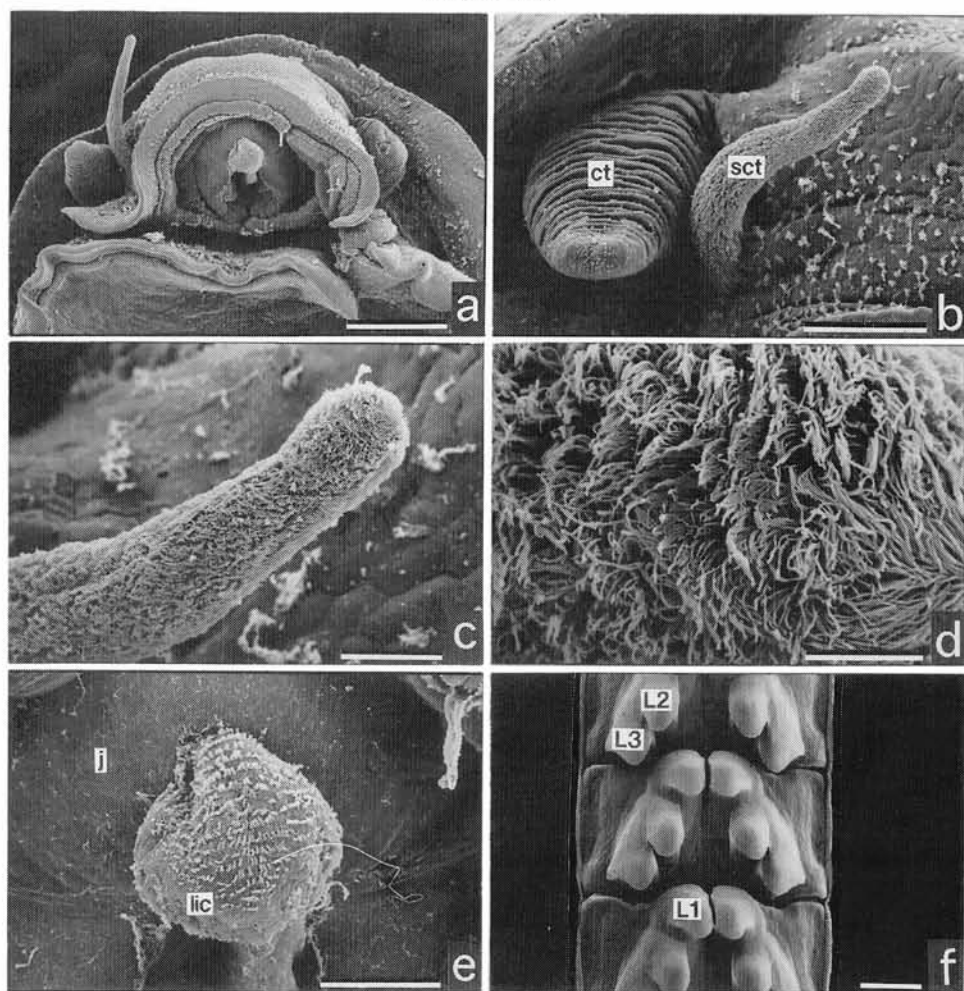Fig. 20. *Erginus sybaritica*. SEM micrographs of soft parts. **a-e**, RM 27618 a, **f**, RM 27618 b. **a**, Ventral view of head region. Scale = 500 µm. **b**, Right cephalic tentacle and subcephalic tentacle. Scale = 200 µm. **c**, Tip of subcephalic tentacle. Scale = 50 µm. **d**, Cilia covering subcephalic tentacle. Scale = 10 µm. **e**, Licker. Scale = 100 µm. **f**, Radula. Scale = 50 µm.

External Anatomy: Mantle margin with crowded series of minute circumpallial tentacles in living animal, which are completely retracted when preserved. Attachment of shell muscle horseshoe-shaped, divided into about fourteen segments by vessels. Thin pallial muscle connecting anterior ends of shell muscle. Head provided with pair of non-papillate cephalic tentacles with invaginated eyes on their outer bases. Outer lip of mouth with laterally swollen oral lappets. Prominent subcephalic tentacle (sct) beneath right cephalic tentacle (Figs. 20 a, b), with surface entirely covered by dense cilia (Figs. 20 c, d). Internally, tentacle with muscular fibers, narrow blood space, and nerve from right cephalic ganglion, without tubular duct-like structure. Sensory projections and pallial streaks absent in pedal region.

Pallial Complex: Pallial cavity relatively deep, attaining nearly half of body length, containing paired kidney openings and anus, but lacking ctenidium, osphradium, and hypobranchial gland. "Secondary gills" also absent. Pallial cavity deeply developing into brooding chamber during breeding season.

Digestive System: Oral region provided with inner lips associated with transverse labial muscles and anterior wings of jaw. Oral tube not clearly surrounded by buccal sphincter and constrictor. Muscles of odontophore consisting of dorsal protractors, lateral protractors, ventral protractors, and anterior levators. Depressors and levators absent in posterior part. Dorsal and postdorsal buccal tensors also absent.

Jaw consisting of small anterior wings, large posterior wings, and medially thickened smooth anterior band. Anterior part of jaw covering oral tube; posterior wings with connection to anterolateral projections of cartilages.

Radular sac forming single loop in visceral mass; posterior end inflated with development of odontoblasts, but not bifurcated. Radula formula 0–3–0–3–0 (Fig. 20 f). Radular row symmetrical. Three lateral teeth arranged in inverted V-shape. Innermost laterals with blunt cusp and longest base. Middle laterals situated posterolaterally to innermost; cusp blunt and elongate. Outermost laterals fused anterolaterally with middle teeth; cusp blunt, triangular, with outward lateral projection. Basal plates thick, wider than long, with smooth surface.

Muscles of subradular membrane consisting of lateral protractors, median protractors, and retractors of subradular membrane. Median protractors not asymmetrical. Retractors not fused ventrally. Muscles of radular sac composed of retractors of radular sac. Both median retractor of radular sac and ventral tensor of radular sac absent.

Buccal mass containing two pairs of cartilages: anterior and anterolateral. The former connected by two-layered ventral approximator. Sublingual pouch deep, simple, without projections of sublingual gland. Licker smooth in macroscopical observation, but with microprojections in transverse arrangement under SEM observation (Fig. 20 e). Radular diverticulum widely developed, depressed over odontophore.

Salivary glands not well developed, elongated longitudinally on outer posterior sides of buccal mass. Paired salivary ducts running along anterior esophagus from anterior ends of salivary glands to lateral extensions of buccal cavity.

Anterior esophagus provided with inflated dorsal food channel and depressed lateral pouches, internally divided by conspicuous dorsal and ventral folds. Mid-esophagus partitioned by lamellate projections. Posterior esophagus narrow, longitudinally corrugated internally. Stomach C-shaped, simple in internal structure; gastric caecum, tooth of gastric shield, and corrugated sorting area absent. Intestine with four complex loops. Rectum (fourth loop of intestine) not penetrating pericardium or ventricle, directly contacting posterior pericardial wall in non-breeding individuals due to reduction of gonad.

Circulatory System: Heart consisting of single auricle and ventricle. Auricle laterally elongated, connected with efferent pallial vessel in left corner and with numerous capillary vessels from nuchal cavity roof throughout anterior margin. Ventricle posterolaterally elongated, connected with auricle anteriorly, leading into bulbous aorta ventrally. Pericardium heavily compressed posteriorly with development of nuchal cavity as brooding pouch.

Excretory System: Asymmetrically paired kidneys present. Left kidney much smaller than right, extremely elongated along left side of rectum. Left kidney opening narrow and simple. Right kidney widely spreading over base of visceral mass, distinguishable from visceral organs by yellowish hue in living animal. Right kidney opening prolonged as very thin tube. Left renopericardial canal extending along posterior limit of pallial cavity; right renopericardial canal could not be confirmed.

Reproductive System: Gonad widely spreading below digestive glands, with thin connective duct to right kidney. Hermaphroditism not confirmed. Relatively large, few eggs directly deposited in nuchal cavity. As eggs develop, nuchal cavity becoming enlarged as brooding pouch to accommodate juveniles, pushing visceral region backward.

Nervous System: Configuration of ganglia and nerves similar to that in *Niveotectura*.

Erginus moskalevi (Golikov and Kussakin, 1972)
(Figs. 21 a-c)

Protoconch: Protoconch symmetrical, oval, shield-shaped. External surface sculptured by tiny pits, each 1.25–5 μm in diameter (Fig. 21 c). Protoconch-teleoconch boundary clearly demarcated by abrupt change in sculpture; exterior surface of early teleoconch finely punctate. Protoconch situated in symmetrical position relative to sagittal axis of teleoconch. Young snails brooded in pallial cavity of parent, remaining there until at least 460 μm in shell length. In brooded condition intact protoconch still retained; septum beginning to seal inside of apex. Inside of protoconch and early teleoconch seem to have small shell pores not found in adult shell.

Lottia tenuisculpta Sasaki and Okutani, 1994
(Figs. 21 d-h)

Protoconch: Protoconch symmetrically elongated, cup-shaped, lateroventrally inflated, exhibiting small constriction and slight lateral extensions (so-called lateral pouches). Outer surface entirely covered with undulating striae. Apertural lip of protoconch nearly straight. Protoconch generally lost at very early stage with shell length of 0.5–1 mm after inside of apex sealed off by septum, easily detached from apex by mechanical shock.

Nipponacmea schrenckii (Lischke, 1868)
(Figs. 22 a–b)

Gross anatomy of this species described by Sasaki and Okutani (1993 a). Additional observations on buccal mass described below.

Digestive System: Oral tube dorsally covered by jaw, not clearly surrounded by buccal sphincter and constrictor. Inner lips linked with transverse labial muscles (tam) running along inner sides of anterior wings toward lateral walls of snout (Fig. 22 b).

Odontophore fixed on body wall by following four muscles (Figs. 22 a, b): (1) Dorsal protractors (dp) inserted on posterior end of posterior cartilages, extending forward between anterior levators and dilators of radular diverticulum, attaching to posterior margin of posterior wings of jaw. (2) Lateral protractors (lp) composed of two layers, both of which inserting on lateral posterior end of posterior cartilages and extending along outer lateral margin of odontophore. Outer muscle originating in wall of snout over posterior wings of jaw; inner muscle directly connected with lateral margin of posterior wings. (3) Ventral protractors consisting of two layers. Outer ventral protractors (ovp) as most prominent odontophoral muscles; in width almost equal to that of odontophore. Inner ventral protractors (ivp) narrower than outer, connected to posterior cartilages and ventral surface of sublingual pouch. Anteriorly right and left sides linked with transverse sheet of muscle. (4) Anterior levators (al) inserted on outer sides of anterolateral cartilages, ex-
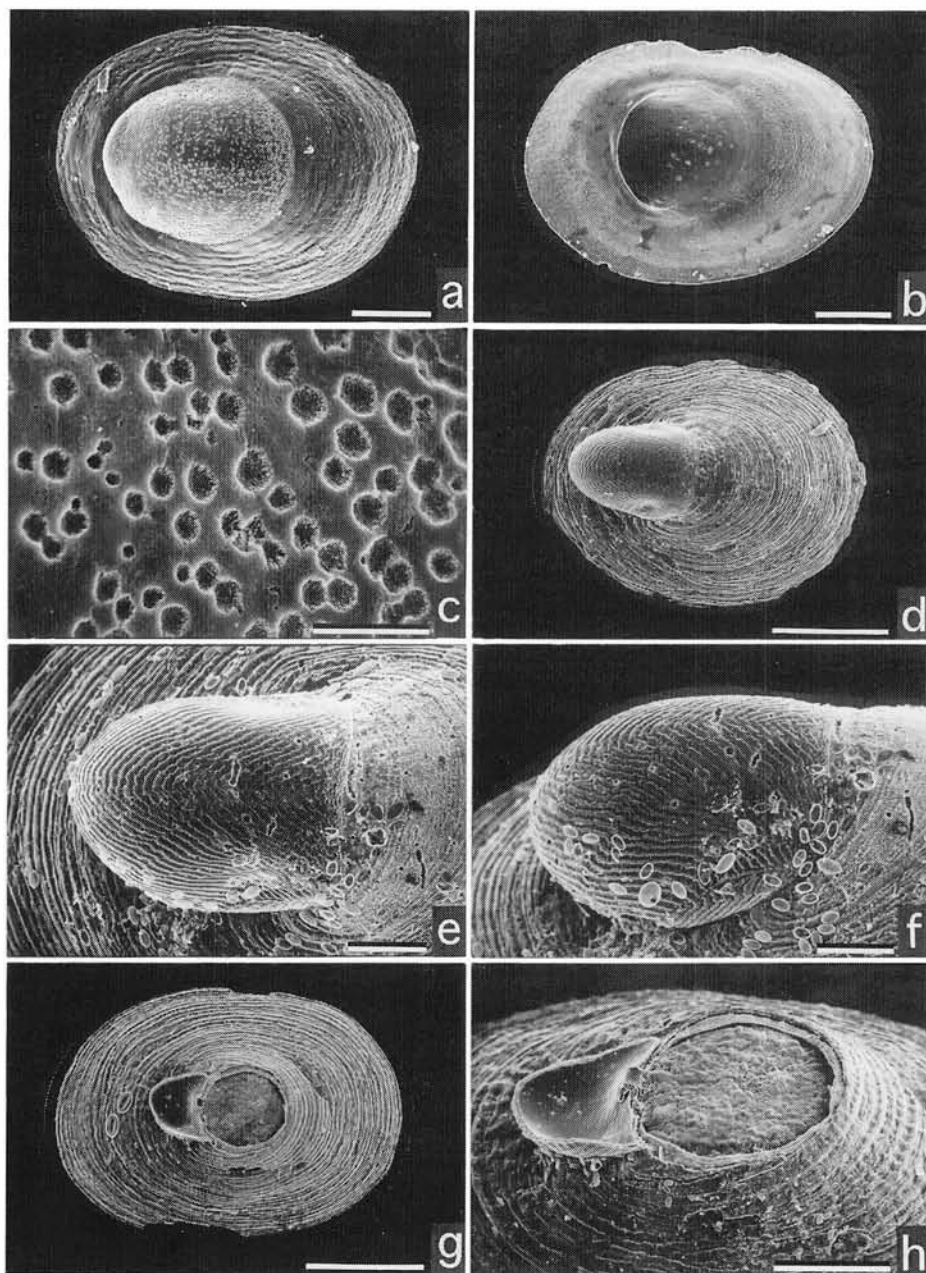
Fig. 21. Protoconch of Lottiidae. **a-c**, *Erginus moskalevi*. RM 27619. **a**, Dorsal view of a brooded shell from brooding pouch of the adult. Scale = 100 μm. **b**, Ventral view. Scale = 100 μm. **c**, Surface sculpture of protoconch. Scale = 10 μm. **d-h**, *Lottia tenuisculpta*. **d, g-h**, RM 27620. **e-f**, RM 27621. **d**, Dorsal view of a juvenile shell. Scale = 250 μm. **e**, Dorsal view of protoconch. Scale = 50 μm. **f**, Right lateral view of protoconch. Scale = 50 μm. **g**, Juvenile shell with protoconch detached and apex sealed with septum. Scale = 250 μm. **h**, Oblique view of apical area. Scale = 100 μm.

Fig. 22. *Nipponacmea schrenckii*. **a**, Dorsal view of the buccal mass after removal of several extrinsic muscles. **b**, Ventral view of the buccal mass. Left side of the outer ventral protractor muscle of odontophore (ovp) is removed.

tending dorsally beneath labiobuccal connective, attaching to origin of dorsal wall of snout. Depressors and levators absent in posterior part.
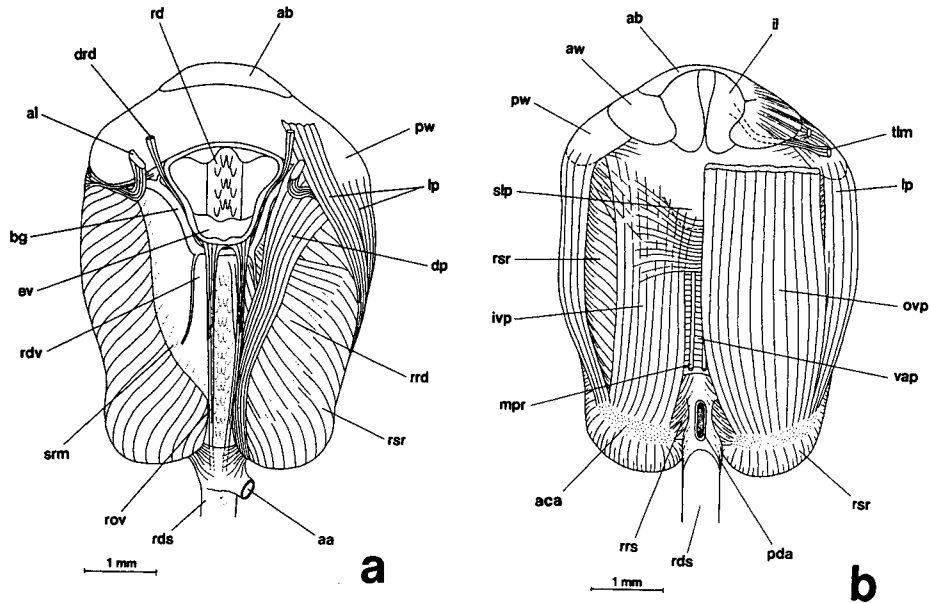
Muscles of subradular membrane consisting of three pairs: (1) Median protractors of subradular membrane (mpr) very thin, symmetrically positioned. (2) Lateral protractors (lpr) much thicker than median pairs. (3) Subradular membrane affixed to odontophore by retractors of subradular membrane (rsr), clearly divided into pair, not fused ventrally.

Radular sac pull only by retractors of radular sac (rrs) running between ventral side of radular sac and posterior cartilages. Both median retractor of radular sac and ventral tensor of radular sac absent.

Odontophoral cartilages consisting of elongated anterior and triangular anterolateral cartilages. Anterior cartilages medianly connected by ventral approximator muscle. Labial cartilages (as in *Cellana*) absent.

Family Pleurotomariidae Swainson, 1840
Mikadotrochus beyrichii (Hilgendorf, 1877)
(Figs. 23 a-d, 24 a-b, 25 a-d, 26 a-d, 27 a-h)

Protoconch: Protoconch tightly coiled in 1.25 whorls, its direction slightly hyperstrophic against teleoconch (Figs. 23 a-c). Observed shell empty and eroded, with irregular fine granulous deposits and two fine spiral threads clearly visible in apical view (Figs. 23 c-d). Protoconch-teleoconch boundary marked by abrupt appearance of spiral riblets on teleoconch. Slit not formed in protoconch but inserted between spiral riblets in early teleoconch (Fig. 23 a).

External Anatomy: Animal trochiform. Mantle deeply sinuate in midline (Figs. 24 a, b). Mantle margin (mm) divided into two folds by periostracal groove (pg) (Fig. 27 b). Outer fold (of) smooth, sharply edged. Inner fold (if) thicker than outer, provided with several layers of densely overlapping microtentacles. Inner surface of inner fold finely denticulated by longitudinal furrows (Fig. 24 b). Attachment of columellar muscle (cm) restricted to narrow subrectangular area. Muscle not divided into bundles.
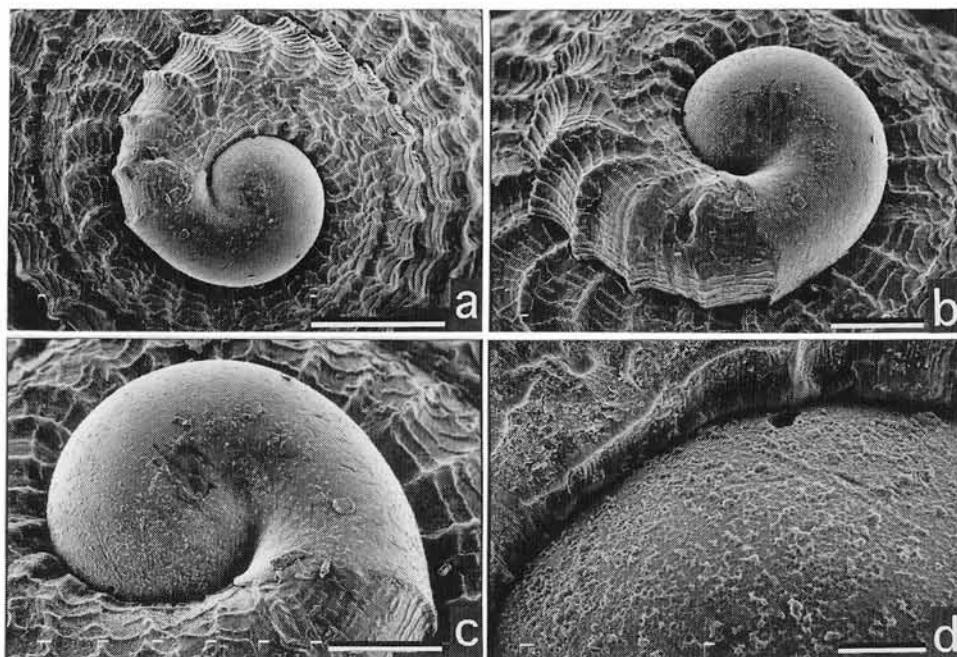
Fig. 23.   Protoconch of *Mikadotrochus beyrichii*. RM 27623. **a**, Apical view of protoconch. Scale=500 μm. **b**-
c, Oblique view of apical area. Scale=200 μm. **d**, Surface sculpture of protoconch. Scale=50 μm.

Head with cylindrical snout (sn), and pair of thick cephalic tentacles (ct) without papillae. Cephalic lap-
pets absent. Outer lip (ol) thickened as oral disk, covered by numerous papillate projections (Fig. 25 b).
Eyes open, at bases of cephalic tentacles, without eyestalks. Inner layer of retina containing tall black-
pigmented cells.

Foot (f) very large, inflexible, folded longitudinally (rather than anteroposteriorly) when retracted.
Epipodial region comprising several (3?) pairs of epipodial flaps (epf) (Fig. 24 a). Ventral margin of flaps
fringed by tuberculate microprojections, which presumably represent epipodial sense organs (Fig. 27 c).
Posterior side of epipodium with multispiral operculum. Attachment for operculum thickened, reflected as
opercular lobe. Surface of head-foot region somewhat papillate, covered by layer of tall columnar cells (Fig.
27 a).

Pallial Complex: Pallial cavity very deep, occupying one-half volution of body whorl, including paired
ctenidia, paired osphradia, paired kidney openings, anus, and paired hypobranchial glands (Fig. 24 b). Or-
gans of columellar side slightly shorter than those of peripheral side.

Ctenidial lamellae bipectinate. Efferent ctenidial axes attached to outer ventral sides of pallial wall by
long efferent ctenidial membranes (ecm); afferent sides totally lacking membrane connecting to mantle.
Both ctenidial axes containing well expanded ctenidial vessels, nerves, and paired retractor muscles. Free
portions of afferent axes also bearing skeletal supports. Each lamella elongated triangular, with tip of termi-
nal ridge directed toward inside, stiffened by skeletal rods, with surface of zones of cilia. Bursicles evi-
dently lacking on efferent sides of leaflets; no trace of knobby structures or associated grooves of typical
bursicles in SEM observation (Fig. 27 d).

Osphradia (os) situated at free portions of efferent ctenidial axes, paired in agreement with ctenidia (Fig.
27 d). Surface of osphradium sporadically covered with cilia (Fig. 27 e).

Large area of mantle skirt covered by hypobranchial glands (Fig. 24 b), divided into right and left glands
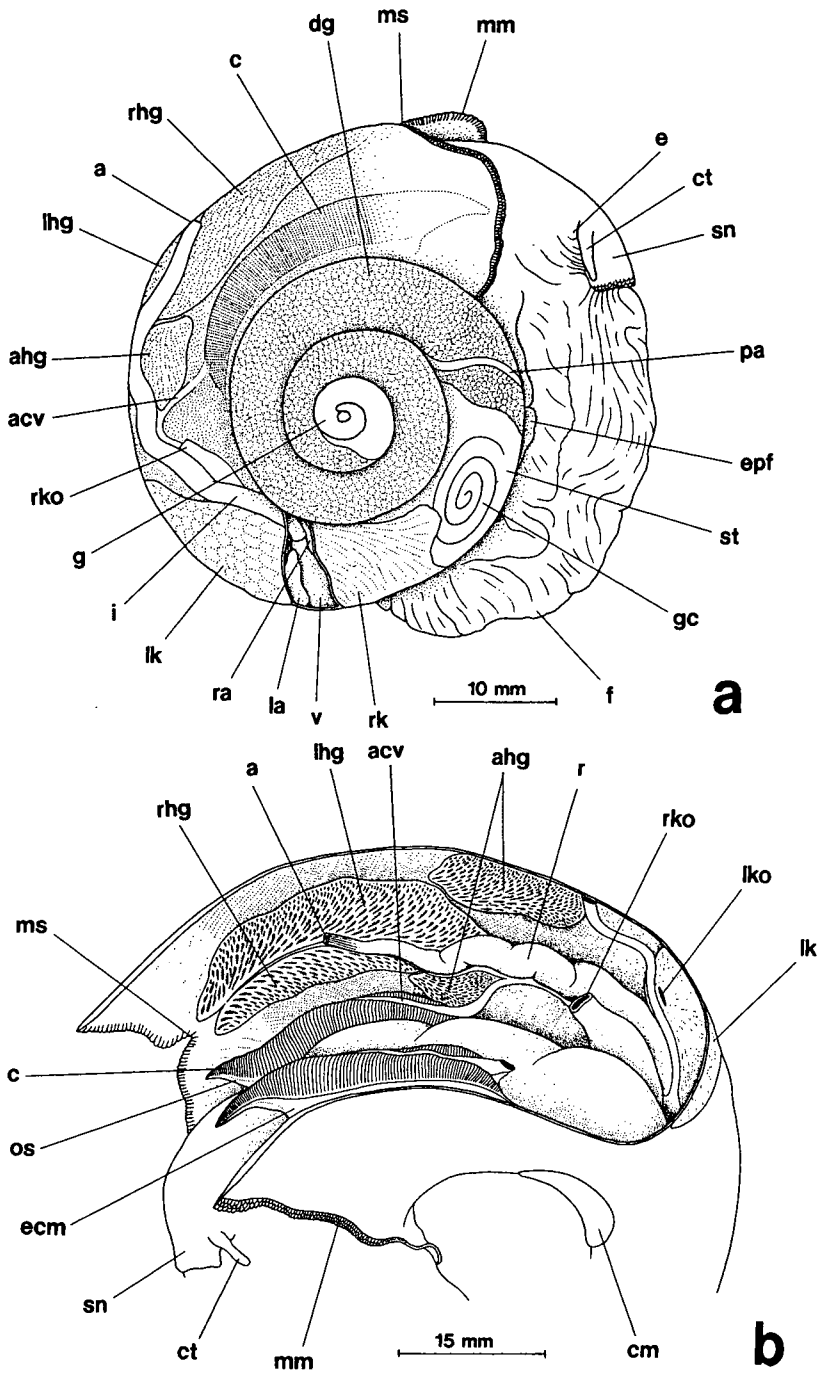
Fig. 24. *Mikadotrochus beyrichii.* **a,** Apical view of the animal with shell removed. **b,** Left lateral view of the animal after the opening of pallial cavity.
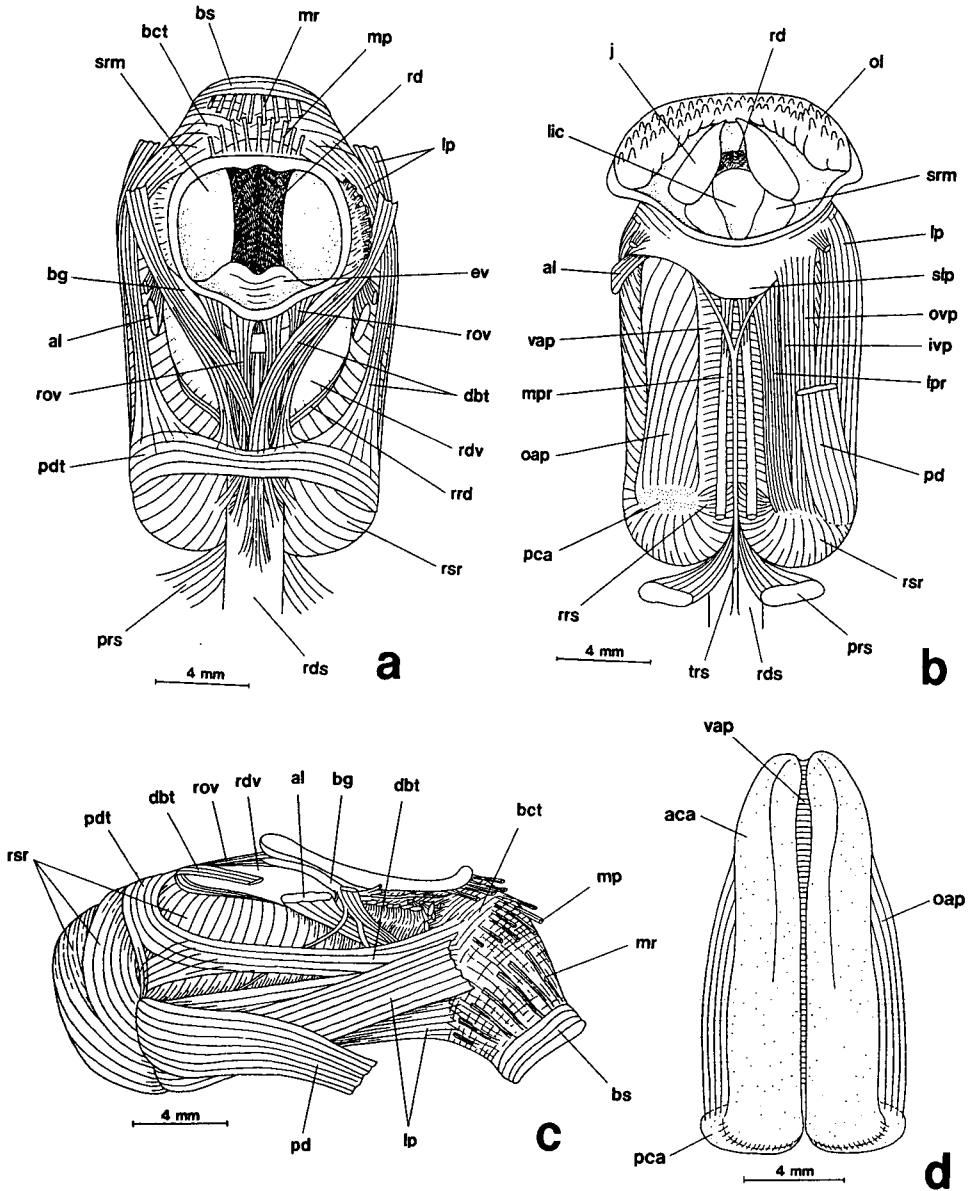
Fig. 25.   *Mikadotrochus beyrichii*. **a**, Dorsal view of the buccal mass. **b**, Ventral view of the buccal mass. Some ventral muscles are removed on the left side. **c**, Right lateral view of the buccal mass. **d**, Dorsal view of the odontophoral cartilages.
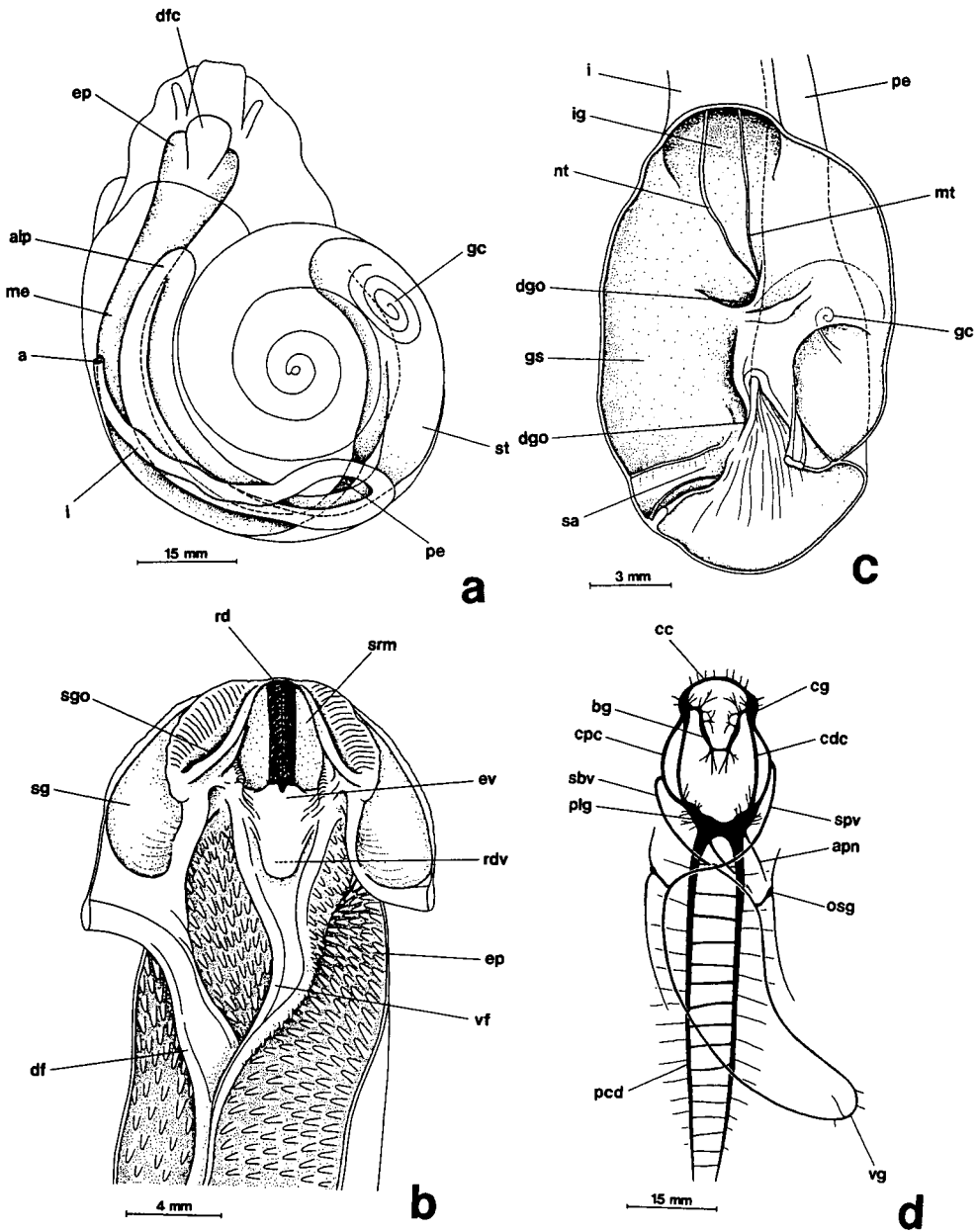
Fig. 26. *Mikadotrochus beyrichii.* **a**, Configuration of the alimentary tract. **b**, Internal structure of the anterior alimentary tract. Buccal cavity and dorsal food channel are cut sagitally and extended laterally. **c**, Internal structure of the stomach. The dorsal side of the distal part is reflected over the proximal part. **d**, Nervous system.
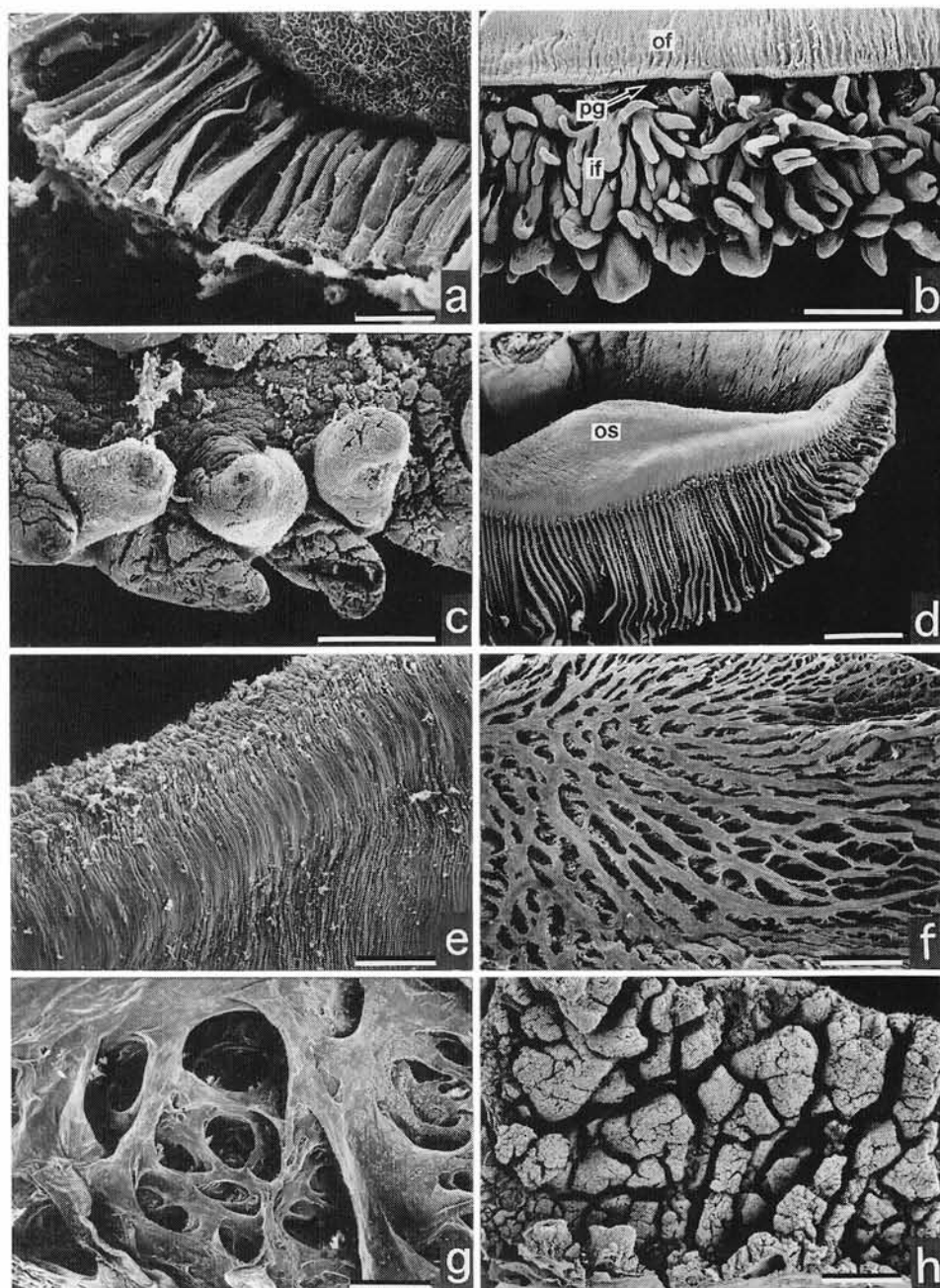
Fig. 27. *Mikadotrochus beyrichii*. SEM micrographs of soft parts. **a**, **d-e**, RM 27625 a. **b**, RM 27625 b. **c**, **f**, **h**, RM 27625 c. **g**, RM 27625 d. **a**, Columnar epidermal cells of epipodium. Scale = 10 μm. **b**, Dorsal view of mantle margin with periostracal groove. Scale = 500 μm. **c**, Sense organs on ventral margin of epipodial flap. Scale = 200 μm. **d**, Free portion of dorsal lamellae of left ctenidium. Scale = 1 mm. **e**, Surface of osphradium. Scale = 100 μm. **f**, Inner surface of hypobranchial gland. Scale = 1 mm. **g**, Inner wall of right kidney. Scale = 1 mm. **h**, Inner wall of left kidney. Scale = 1 mm.

(rhg, lhg) by rectum in posterior half. Each paired gland with accessory lobe posteriorly (ahg, Fig. 24 b), structurally identical in having network of vessels and glandular epithelium (Fig. 27 f). Both main and accessory glands somewhat reduced on right side.

Digestive System: Oral tube surrounded by buccal sphincter and constrictor (bs, bct) with mandibular protractors and retractors (mp, mr). Buccal mass fixed by lateral protractors (lp), outer and inner ventral protractors (ovp, ivp), anterior levators (al), posterior depressors (pd), and dorsal buccal tensors (dbt) (Figs. 25 a-c). Posterior part of odontophore tightly bound by thick band of postdorsal buccal tensor (pdt). Dorsal buccal tensors (dbt) consisting of outer and inner parts: outer part connecting to buccal constrictor; inner part uniting with dorsal wall of snout. Separate levator muscles absent; outer part of lateral protractors probably providing antagonistic function for depressors.

Paired jaws projecting from dorsal side of oral tube. Very characteristically, entire jaw plate fleshy, not cuticularized; surface and anterior margin completely smooth.

Radular sac rather long along right side of mid-esophagus, straight in configuration. Surface surrounded by thick connective tissue of radular artery. Posterior end deeply bifurcated. Radular formula roughly ca. 60 –ca. 40–1–ca. 40–ca. 60, but tooth arrangement cannot be exactly categorized because of aberrant derivation. Radula divisible into inner central tooth field with shorter teeth and outer marginal field with longer teeth. Each transverse radular row symmetrical in marginal tooth fields but clearly asymmetrical in central tooth field. Central tooth elongated, with thin shaft, without cusp; outline of shaft and base distorted by asymmetry together with several neighboring teeth. First and second pairs of lateral teeth especially filamentous, undulate, skewed to either right or left, greatly asymmetrical. Following teeth lamellate, with inverted V-shaped configuration. Within inner zone of marginal fields, teeth elongated with sickle-shaped cusps; teeth becoming shorter toward outside, with tip of cusp acutely pointed in spinous form; pointed cusp divided into three branches, with dorsal side giving rise to filaments. Outermost teeth smooth, lacking projection or filamentous structure.

Subradular membrane inserted by median and lateral protractors (mpr, lpr) and retractors of subradular membrane (rsr). Radular sac pulled back by retractors (rrs) originating from posterior odontophoral cartilages and by postmedian retractors of radular sac (prs) from floor of body cavity. Thin tensor muscle (trs) arising from dorsal side of sublingual pouch, extending in median line backward, ending behind insertion of postmedian retractors.

Odontophore containing two pairs of cartilages (Fig. 25 d). Anterior cartilages (aca) longitudinally elongated with weak anterolateral extension. Posterior cartilages (pca) much smaller than anterior, attached to posterior end of anterior cartilages ventrally. Anterior pair of cartilages united by ventral approximator (vap). Anterior and posterior pairs longitudinally connected by outer approximators (oap) on outer sides.

Sublingual pouch (slp) not generating glandular outgrowth (Fig. 25 b). Licker (lic) thickened on anterior part of subradular membrane. Salivary glands (sg) spreading over buccal cavity, discharging into it through longitudinally slit-like openings without ducts. Surface of glands split into numerous minute branches. Inner margin of opening of salivary glands (sgo) especially thickened (Fig. 26 b).

Anterior esophagus expanded laterally to form esophageal pouches (ep) that enclose greater posterior part of buccal mass except ventral side. Dorsoventrally depressed lateral pouches not formed. Sac-like projection formed posterior to esophageal valve (ev) over radular diverticulum (Fig. 26 b). Interior of esophageal pouches and entire mid-esophagus lined with glandular epithelium with long papillate projections. Mid-esophagus (me) extremely elongated, as long as one-half volution of body whorl (Fig. 26 a). Dorsal folds (df) fused into broad band; similarly paired ventral folds (vf) united into single fold over buccal mass. Both folds gradually twisted counterclockwise in mid-esophagus. Posterior esophagus (pe) distinctly constricted, much shorter than mid-esophagus.

Stomach (st) strongly bent, divided into proximal and distal regions (Fig. 26 c). Spiral gastric caecum

(gc) prominently developing on dorsal surface. Most of stomach occupied by smooth-surfaced gastric shield (gs). Tooth of gastric shield not found. Ridge-like structures rather unclear throughout interior of stomach: partition of sorting area (sa) not very apparent; two ridges continued into spiral caecum until they disappear near tip of caecum. Digestive glands opening by two distantly separated openings (dgo). Posterior (topologically anterior) opening leading to dorsal lobe of glands, while anterior (topologically posterior) opening connecting with ventral lobe. From right side of posterior digestive opening, major and minor typhlosoles (mt, nt) extending into intestine. Intestinal groove (ig) between two typhlosoles very broad.

Intestine (i) running forward along right side of body wall, bending back to trace same course on left side, forming single very long anterior loop (Fig. 26 a). Intestine then curving dorsally, penetrating pericardium and ventricle, entering pallial cavity. Rectum running along mid-line, ending at anus (a) at anterior two-thirds of pallial cavity.

Circulatory System: Pericardium on posterior side of left kidney (Fig. 24 a). Heart consisting of smaller right and larger left auricles and single ventricle. Left auricle (la) on anterolateral side of ventricle; right one (ra) on posterolateral side.

Aorta divided into anterior and posterior aortae within pericardium. Aortic bulb indistinct. Posterior aorta (pa) transporting blood to stomach and digestive glands. Initial part of anterior aorta running within mantle skirt, near posterior end of ctenidium, bending to lead into anterior visceral region along esophagus. In head region, aorta opening into cephalopedal sinus through buccal and pedal arteries. Radular sac enclosed posteriorly by radular artery.

Excretory System: Two greatly asymmetrical kidneys on posterior and anterior sides of pericardium (Fig. 24 a). Right kidney (rk) much larger than left; its inner wall attached by fenestrated lamellae; its posterior lobe exposed on dorsal surface posterior to pericardium; anterior lobe deeply spreads over right side of anterior visceral region (Fig. 27 g). Terminal part near right kidney opening especially enlarged to form long tube of urogenital papilla (Fig. 24 b), but histological nature (pallial origin?) not observed. Presence of sexual dimorphism in terminal part not verified because of immaturity and incompleteness of available individuals. Right renopericardial duct opening to pericardium beneath right auricle.

Left kidney (lk) lying within pallial cavity, overhanging pallial roof, its inner wall covered by papillate projections, being shorter in anterior section but longer in posterior (Fig. 27 h). Slit-like left kidney opening (lko) lying on inner anterior side of kidney (Fig. 24 b). Left renopericardial duct opening near right limit of left auricle.

Reproductive System: Structure of reproductive system not adequately determined because gonads of available specimens were immature or visceral hump was torn off within upper whorls of shell.

Nervous System: Circumesophageal nerve ring basically hypoathroid (Fig. 26 d). Cerebral ganglia (cg) well developed at bases of cephalic tentacles. Pleural ganglia (plg) on outer anterior sides of pedal ganglia, completely fused with pedal ganglia. Characteristically, cerebropleural and cerebropedal connectives (cpc, cdc) with fused origin at their base.

Cerebral ganglia laterally emitting tentacular and optic nerves (tn, opn). Inner anteroventral sides innervating labial region. Ganglia dorsally connected to cerebral commissure (cc) which gives rise to fine nerves toward oral tube. On ventral side, labial ganglia and commissure absent. Cerebrobuccal connectives (cbc) arising from inner ventral sides of cerebral ganglia. Buccal ganglia (bg) lying over odontophore, innervating entire buccal musculature, anterior esophagus, radula, and associated structures.

Visceral loop originating (unusually) from cerebropleural connectives (cpc), rather than directly from pleural ganglia (Fig. 26 d). Supraesophageal part of loop (spv) on right side arising from nearer anterior end than subesophageal part (sbv) of left side. Cerebropleural connectives running more dorsally than cerebropedal connectives (cdc), being pulled up by initial parts of visceral loop. Visceral loop extremely long, correlating with depth of pallial cavity. Ganglionation of supraesophageal, subesophageal, and visceral sec-

tions all indistinct, and therefore loop seems to be of simple cord-type throughout its length. Nerves originating from sub- and supraesophageal parts to osphradio-ctenidial ganglia (osg), kidneys, rectum, and pericardium.

Pedal cords (pcd) exhibiting well-developed, ladder-like configuration. At least sixteen distinct pedal commissures between pedal cords toward posterior end of foot (Fig. 26 d). Disposition of commissures not always parallel, their thickness also varying slightly. Pedal cords also with thin pedal or epipodial nerves on each outer side. From anterior sides of pedal ganglia, more or less thick pair of anterior pedal nerves extending into pedal musculature. Statocysts lying on anterodorsal sides of pedal ganglia.

Family Haliotidae Rafinesque, 1815
Sulculus diversicolor aquatilis (Reeve, 1846)
(Figs. 28 a-d, 29 a-b, 30 a-b, 31 a-f, 32 a-d, 33 a-b)

Protoconch: Protoconch planispirally coiled, inrolled by early teleoconch (Figs. 28 a-b). Neither lateral pouch nor suture of protoconch clearly formed; only slight constriction in center representing trace of spiral coiling. Sculpture on protoconch consisting primarily of irregular deposits with round pits and several spiral lirae that develop subtly (Figs. 28 b-c). Boundary between protoconch and teleoconch marked by simple axial line (Figs. 28 d).
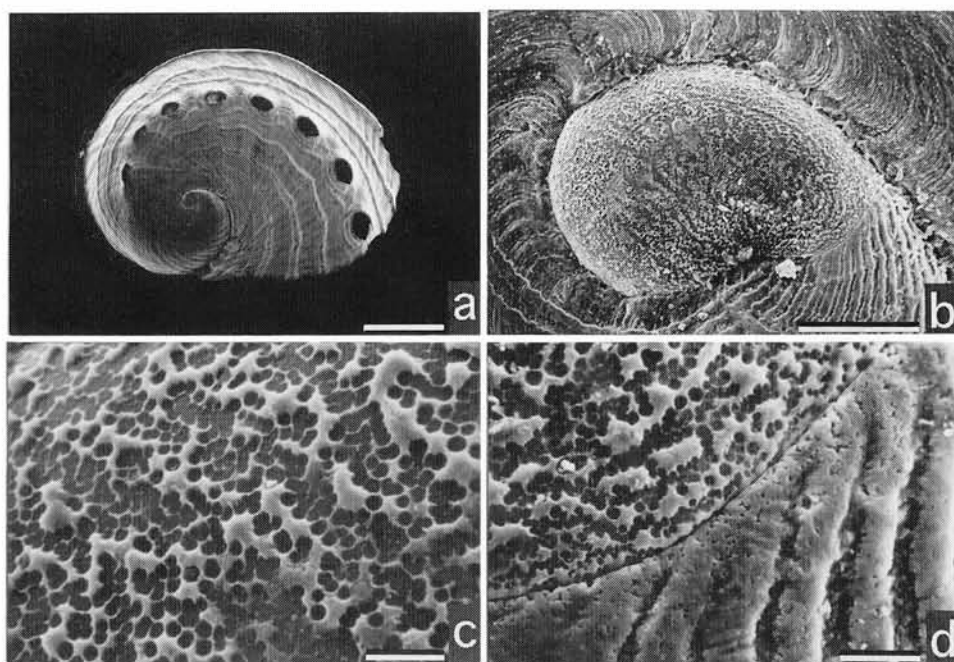
Fig. 28.   Protoconch of *Sulculus diversicolor aquatilis*. RM 27628. **a**, Dorsal view of juvenile shell. Scale = 1 mm. **b**, Dorsal view of protoconch. Scale = 100 μm. **c**, Surface sculpture of protoconch. Scale = 10 μm. **d**, Boundary between protoconch and teleoconch. Scale = 10 μm.

External Anatomy: Animal markedly depressed dorsoventrally with small spiral visceral hump. Mantle deeply sinuated along midline of pallial cavity (Figs. 29 a, b). Mantle margin (mm) lacking circumpallial microtentales; three long pallial tentacles (pt) projecting from mantle margin. Median one arising from posterior end of mantle slit; anterior two lying over head region anteriorly. Left tentacle situated slightly anterior to right one.
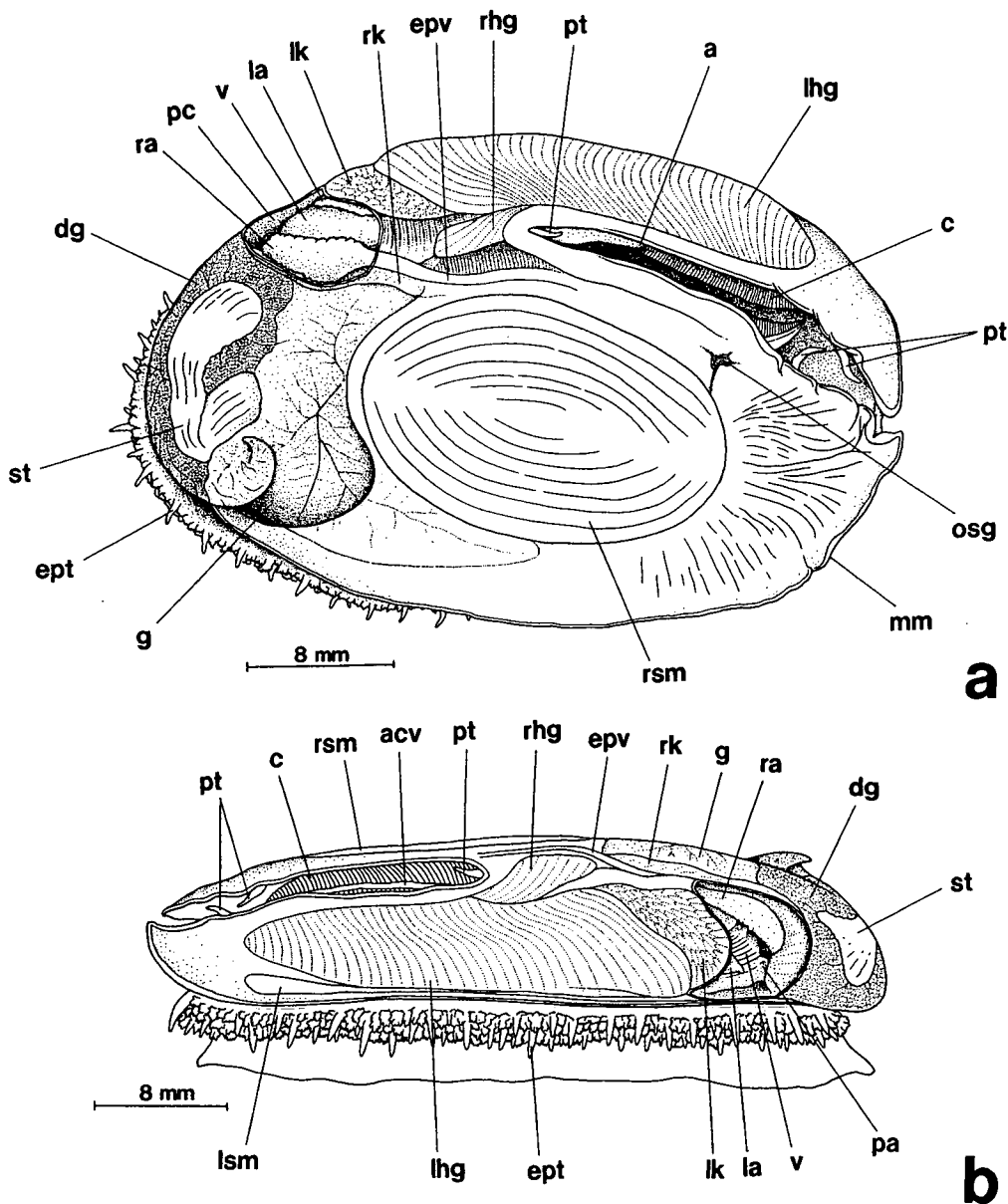
Fig. 29. *Sulculus diversicolor aquatilis*. a, Dorsal view of the animal after removal of the shell and roof of pericardium. b, Left lateral view of the animal.

Shell muscles composed of paired muscles of extremely unequal size. Right shell muscle (rsm) large, oval, in center of body. Left muscle (lsm) thinly elongated below anterior part of left hypobranchial gland, not visible from dorsal side.

Head provided with papillate cephalic tentacles (ct), eyestalks (es), and cephalic lappets (clp). Cephalic lappets fused with each other in midline and also with inner margin of eyestalks, extending over bases of cephalic tentacles. Eyes open, filled with vitreous body at tip of eyestalks. Neck lobes absent.

Foot very large, reaching almost entire body length. Epipodium circularly fringed by epipodial tentacles

Fig. 30. *Sulculus diversicolor aquatilis*. **a**, Pallial complex and head region. **b**, Inner view of the posterior part of pallial cavity and pericardium.

(ept), consisting of long papillate and short dendritic tentacles. Epipodial sense organs present only at bases of long tentacles, taking form of simple ciliary tuft. Operculum absent.

Pallial Complex: Pallial cavity very deep, reaching two-third of body length, containing paired ctenidia with osphradia, paired kidney openings, anus, and paired hypobranchial glands.

Paired bipectinate ctenidia (c) in pallial cavity in slightly asymmetrical arrangement (Fig. 30 a). Efferent ctenidial axes fixed on pallial wall by long efferent membranes (ecm) except at free anterior portion. Afferent side entirely lacking afferent membrane. Ctenidial axes containing well-developed efferent and afferent ctenidial vessels (ecv, acv), nerves, and paired retractor muscles. Free portion stiffened by skeletal rods.

Ctenidial lamellae depressed, triangular, with three zones of cilia on exterior surface and skeletal rods at efferent sides internally. Efferent sides of both dorsal and ventral lamellae (dcl, vcl) with longitudinal row of bursicles (br) near efferent axes.

Osphradial epithelia covering free portions of efferent ctenidial axes (os, Fig. 30 a). No distinct zonation observed on outer surface; surface sparsely covered with cilia in SEM observation.

Hypobranchial glands attached to roof of pallial cavity. Right and left glands greatly unequal in size. Right gland (rhg) lying in posterior end of mantle cavity over rectum. Left gland (lhg) elongated anteriorly along left pallial cavity wall, finely branched into many transverse sections by pallial vessels, with inner wall prominently lamellate. Right and left glands in contact with each other over midline of rectum.

Digestive System: Oral tube surrounded by thick layers of buccal sphincter and constrictor (bs, bct) with mandibular protractors and retractors (mp, mr). Buccal mass fixed on body wall by lateral protractors (lp), outer and inner ventral protractors (ovp, ivp), anterior levators (al), posterior levators (pl), posterior depressors (pd), and dorsal buccal tensors (pdt) (Figs. 31 a, b). Lateral and ventral protractors elaborated into especially thick muscle strands, but posterior pairs of depressors and levators much thinner than protractors. Posterior levators arising from inner ventral end of posterior cartilages, crossing under posterior depressors. Anterior levators located outside of inner part of lateral protractors, but inside of outer part of lateral pro-
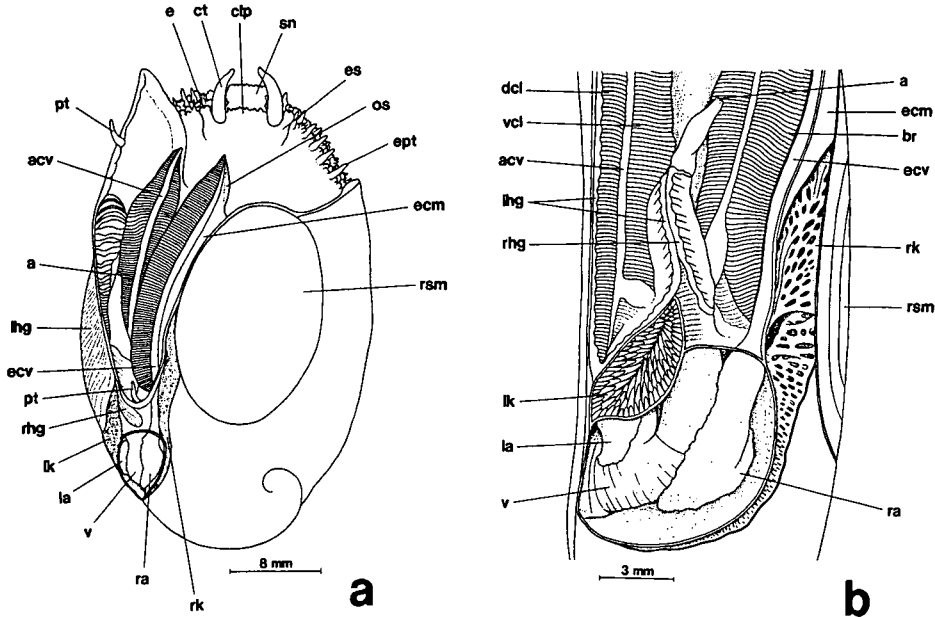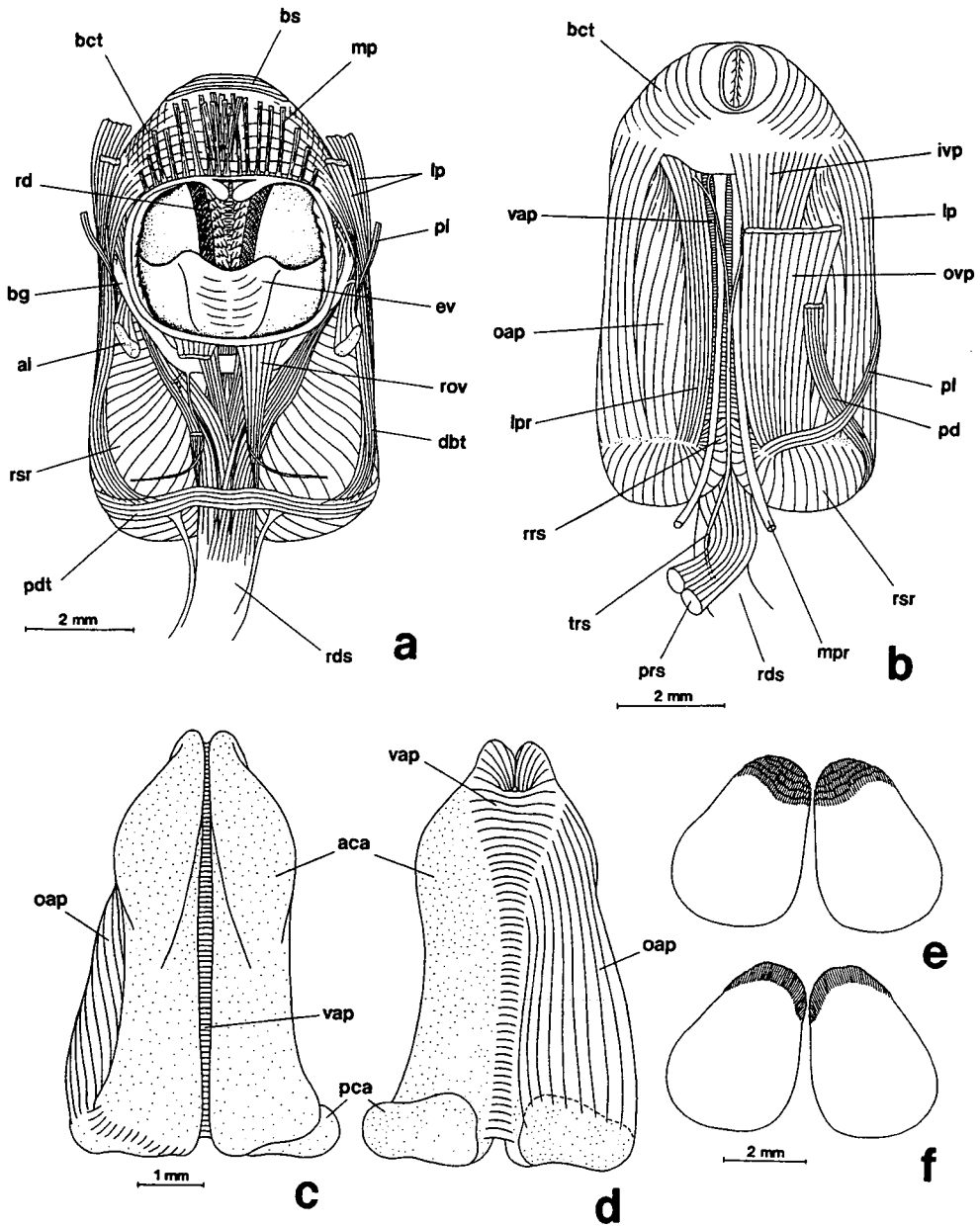
Fig. 31. *Sulculus diversicolor aquatilis*. **a**, Dorsal view of the buccal mass. **b**, Ventral view of the buccal mass. Ventral protractor of odontophore (ovp) is removed on the left side. **c**, Dorsal view of the odontophoral cartilages. Right outer approximator muscle is removed. **d**, Ventral view of the odontophoral cartilages. **e**, Dorsal view of the jaws. **f**, Ventral view of the jaws.
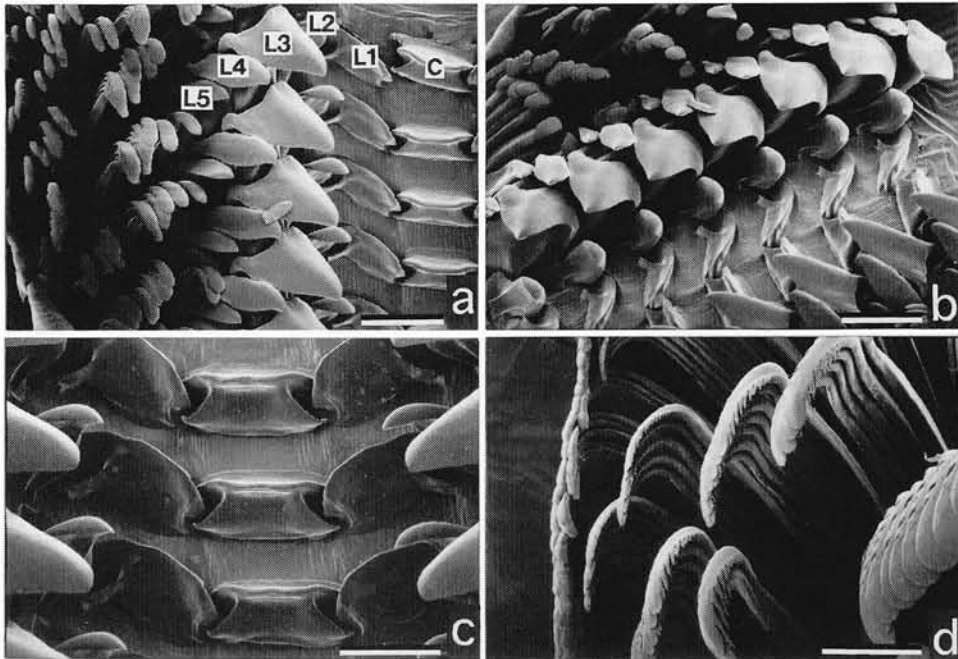
Fig. 32. *Sulculus diversicolor aquatilis*. SEM micrographs of radula. RM 27629. **a**, Left row of radular teeth. Scale = 250 μm. **b**, Oblique view of left row of central and inner marginal teeth field. Scale = 250 μm. **c**, Inclined view of central teeth field. Scale = 200 μm. **d**, Left outer marginal teeth. Scale = 100 μm.
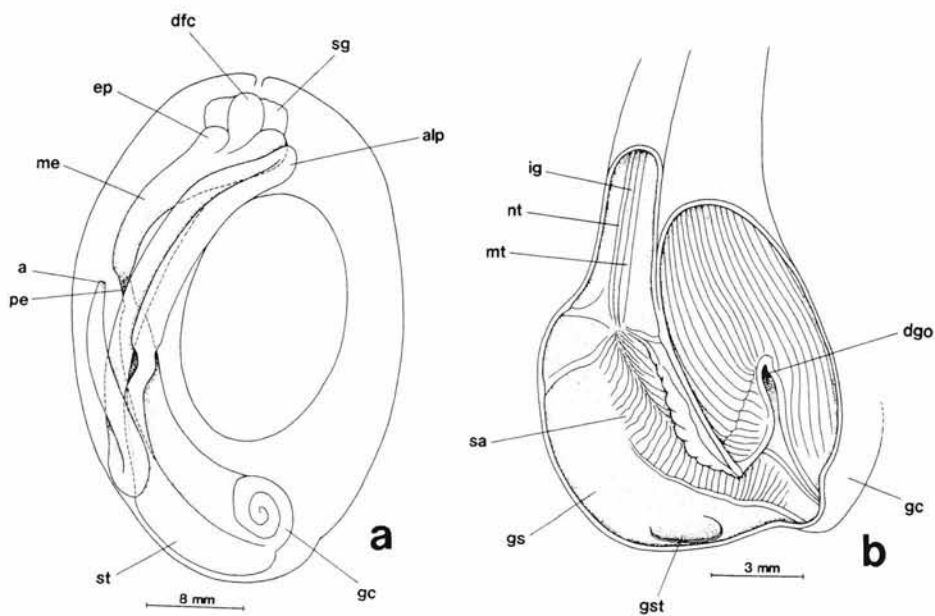
Fig. 33. *Sulculus diversicolor aquatilis*. **a**, Configuration of the alimentary tract. **b**, Internal structure of the stomach.

tractors and dorsal buccal tensors. Paired odontophoral cartilages fixed by postdorsal buccal tensor. Dorsal buccal tensors (dbt) running within space between outer and inner parts of lateral protractors, attached to anterolateral extensions of anterior cartilages.

Jaws (j) separated into distinct pair (Figs. 31 e, f). Anterior margin fimbriate, with fine chitinous rods denser on dorsal side than on ventral side. Posterior two-thirds of jaw attached to wall of oral tube, while remaining anterior section free from oral cavity.

Subradular membrane controlled by lateral and median protractors (lpr, mpr) and retractors (rsr). Median pair attaching to floor of body wall behind buccal mass, while lateral pair inserting on posterior cartilages. Radular sac pulled back by retractors (rrs) within odontophore and by postmedian retractors (prs) behind odontophore. Very thin tensor muscle (trs) running medially from site near sublingual pouch to ventral side of radular sac behind buccal mass: its anterior portion bifid; its posterior end running to right side of post-median retractors, not between them.

Radular sac straight in configuration, attaining half of body length. Posterior end of radular sac deeply bifurcated. Radular formula n–5–1–5–n (Figs. 32 a, d). Transverse radular row asymmetrical; left side skewed more anteriorly than right. Central tooth with broad trapezoidal base and non-denticulate cusp; form of tooth itself symmetrical, but its disposition skewed asymmetrically toward left. Inner two pairs of lateral teeth also constituting central tooth field that has spacious zone of short-stalked teeth. First laterals also oblong; its width almost equal to that of central tooth. Second laterals situated more anteriorly, smaller than first laterals. Outer three laterals much more elongated than inner two; third teeth largest in radular row. Lateromarginal plates absent. Marginals with thin elongated shafts and finely serrated cusps.

Odontophore supported by two pairs of cartilages (Figs. 31 c, d). Anterior cartilages (aca) longitudinally elongated with anterolateral extensions; anterior tip forming hook ventrally. Posterior cartilages (pca) attached to posterior end of anterior cartilages ventrally and projecting laterally. Median side of anterior pair connected by ventral approximator (vap). Anterior and posterior pairs united by outer approximators (oap).

Sublingual pouch represented by shallow simple sac. Smooth licker clearly formed on anterior end of subradular membrane. Radular diverticulum deep below well-developed esophageal valve. Salivary glands (sg) spreading over roof of buccal cavity, discharging directly through longitudinal slits. Surface of salivary glands finely ramified by vermiform outgrowths.

Anterior esophagus terminating over buccal mass. Inner wall of esophageal pouches (ep) and mid-esophagus (me) extensively covered with papillate projections of glandular epithelium. Ventral folds fused in middle part; dorsal folds running independently through mid-esophagus. Both ventral and dorsal folds progressively twisting counterclockwise inside mid-esophagus. Posterior esophagus (pe) characterized by reduction in diameter and by many longitudinal grooves.

Stomach (st) strongly folded into proximal and distal regions near apex of visceral mass (Figs. 33 a, b). Distal part bending anteriorly along left margin of proximal part. Dorsal side of folded region bearing large spiral gastric caecum (gc). Ducts from digestive glands (dgo) opening on floor of proximal region and inner dorsal side of distal region. Internally, pair of longitudinal folds continuing to interior of spiral caecum. Ciliated sorting area (sa) between two folds exhibiting transversely corrugated sculpture. Tooth of gastric shield (gst) lying on posterior wall of gastric shield. Intestinal groove on ventral side marked by major and minor typhlosoles (mt, nt) toward intestine. Protostyle (formed by consolidation of gut contents in rod form) contained in distal region and initial part of intestine.

Intestine passing over stomach, extending anteriorly beside shell muscle, reaching buccal region to form long anterior loop that partly overlaps right esophageal pouch (Fig. 33 a), following same course in opposite direction, bending to penetrate pericardium and ventricle, finally ending anteriorly as anus. Within pallial cavity rectum attached to right and left hypobranchial glands posteriorly, but remaining anterior part freely projecting within the cavity.

Circulatory System: Pericardium lying on posterior side of pallial cavity. Heart consisting of large right auricle, small left auricle, and median ventricle (Fig. 30 b).

Venous blood from kidneys entering expanded space at bases of ctenidia (basibranchial sinus). Right and left sides of sinuses communicating beneath rectum, followed by afferent ctenidial vessels (acv). Blood passing through ctenidial lamellae entering efferent ctenidial vessels (ecv) together with those transported via pallial and hypobranchial vessels, draining into auricles. On left side, efferent renal vessel from left kidney joining before entering auricle.

Excretory System: Excretory system consisting of paired but greatly asymmetrical kidneys (Fig. 30 b). Right kidney (rk) developed along right posterior parts of pallial cavity and pericardium, also widely spreading toward anterior visceral region over intestine. Lumen spacious, inner wall partitioned by perforated lamellae. Left kidney (lk) much smaller than right kidney, lying on anterior left side of pericardium. Inner wall thickly covered with finger-like projections representing so-called papillary sac. Each kidney with renopericardial duct.

Reproductive System: Gonochoristic gonad (g) situated over digestive system, beginning near right kidney, covering anterior half of visceral hump dorsally, finally extending into cavity on outer side of right shell muscle. Gonoduct (gd) opening into right kidney in both sexes. Urogenital opening not greatly enlarged into papillae in female.

Nervous System: Circumesophageal nerve ring of hypoathroid. Cerebral ganglia at bases of cephalic tentacles connected with thick cerebral commissure over buccal constrictor of oral tube in front of buccal cavity. Pleural and pedal ganglia tightly juxtaposed. Connectives between cerebral ganglia and pedal/pleural ganglia also running toward ventral side of buccal mass. Pedal ganglia almost fused with short commissure.

Cerebral ganglia innervating cephalic tentacles, eyestalks, circumoral region (intensively), but not connected by labial commissure. Labial ganglia also absent. Cerebrobuccal connectives arising from ventral sides of cerebral ganglia, extending along lateral wall of odontophore inside lateral protractors. Buccal ganglia lying between radular diverticulum and floor of anterior esophagus.

Pleural ganglia laterally providing nerves to lateral wall of body musculature including columellar muscles. Visceral nerve loop arising from both right and left pleural ganglia. Supraesophageal part of loop passing over esophagus toward anterior limit of ctenidial attachment. Subesophageal part of loop running beneath esophagus, penetrating part of right shell muscle, emerging in right. From supraesophageal and subesophageal ganglia, relatively thick nerve extending toward osphradioctenidial ganglia and mantle margin. Osphradioctenidial ganglia innervating osphradia on inner anterior sides and efferent ctenidial axes on outer posterior sides. Pallial nerves derived from supra-/subesophageal nerves, uniting with nerves from pleural ganglia through zeugoneury. Supraesophageal-visceral connective innervating mid-esophagus by very thin nerves. Subesophageal-visceral connective innervating anterior lobe of right kidney. Visceral ganglion weakly developed between right and left kidney openings beneath rectum; innervation not clearly observed, but at least thin nerves proceeding to both kidneys.

Pedal cords well-developed, connected to several distinct commissures, exhibiting scalariform configuration. Thin anterior pedal nerves extending from pedal ganglia into pedal musculature. Statocysts lying on anterodorsal sides of pedal ganglia.

Family Fissurellidae Fleming, 1822
Scutus (Aviscutum) sinensis (Blainville, 1825)
(Figs. 34, 35 a-c, 36 a-f, 37 a-f)

External Anatomy: Mantle clearly divided into three folds, with outer fold always extending dorsally over shell margin. Anterior part of mantle bearing longitudinal mantle slit (Fig. 36 d), although its presence
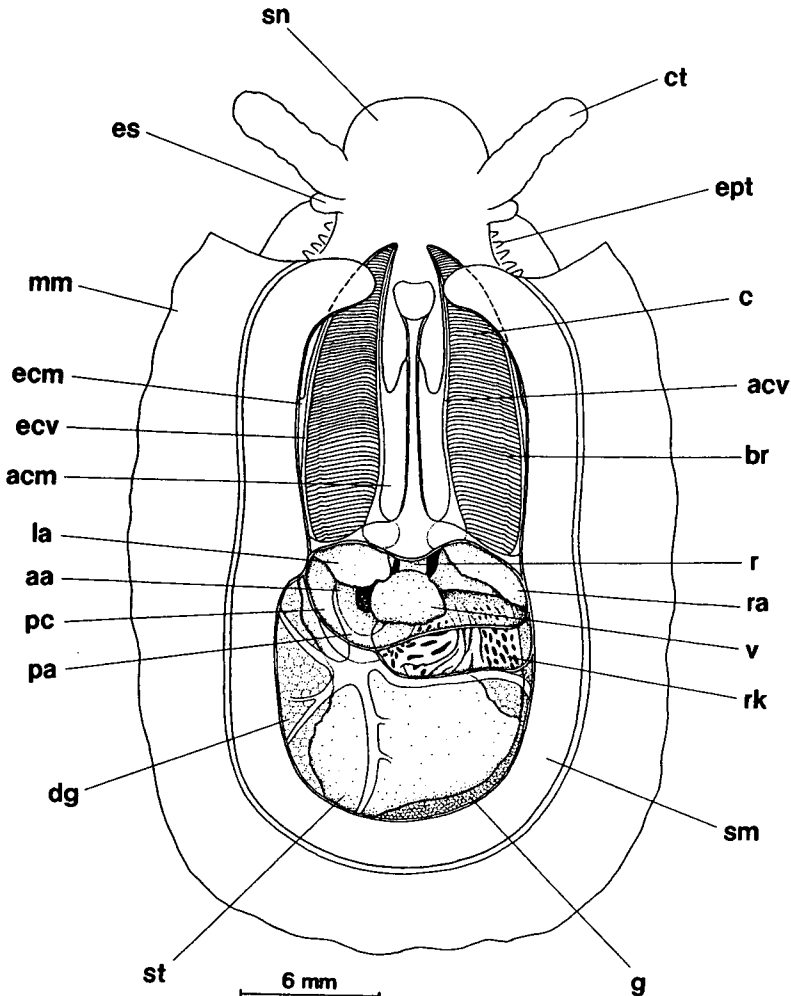
Fig. 34.   *Scutus (Aviscutum) sinensis*. Dorsal view of the animal after removal of the shell, mantle, and anterior
          mantle margin.

hardly reflected in shell morphology. Mantle margin without circumpallial tentacles and long pallial tenta-
cles.

Head with truncated snout, thick non-papillate cephalic tentacles (ct), and small eyestalks (es) (Fig. 34).
Circumoral area thickened by smooth outer lip. Eyes on eyestalks closed by epithelium, with vitreous body
inside (Fig. 37 a). Retina composed of two layers of tall cells (Fig. 37 b); inner cell layer darkly pigmented
in black; outer layer unpigmented in histological sections. Oral and cephalic lappets and neck lobes not de-
veloped.

Epipodium with circle of triangular non-papillate epipodial tentacles. Epipodial sense organs (eso) lying
on ventral surface of tentacles, not at base (Fig. 37 c). Operculum absent.

Shell muscle (sm) elongated horseshoe-shaped, not divided into bundles. Form of shell muscle asymmet-
rical by weak inward projection on left side of pericardium (Fig. 34). Pallial retractor muscle forming dis-
tinct attachment to shell. Head retractor muscle without independent attachment area.

Pallial Complex: Depth of pallial cavity reaching half length of area surrounded by shell muscle, includ-
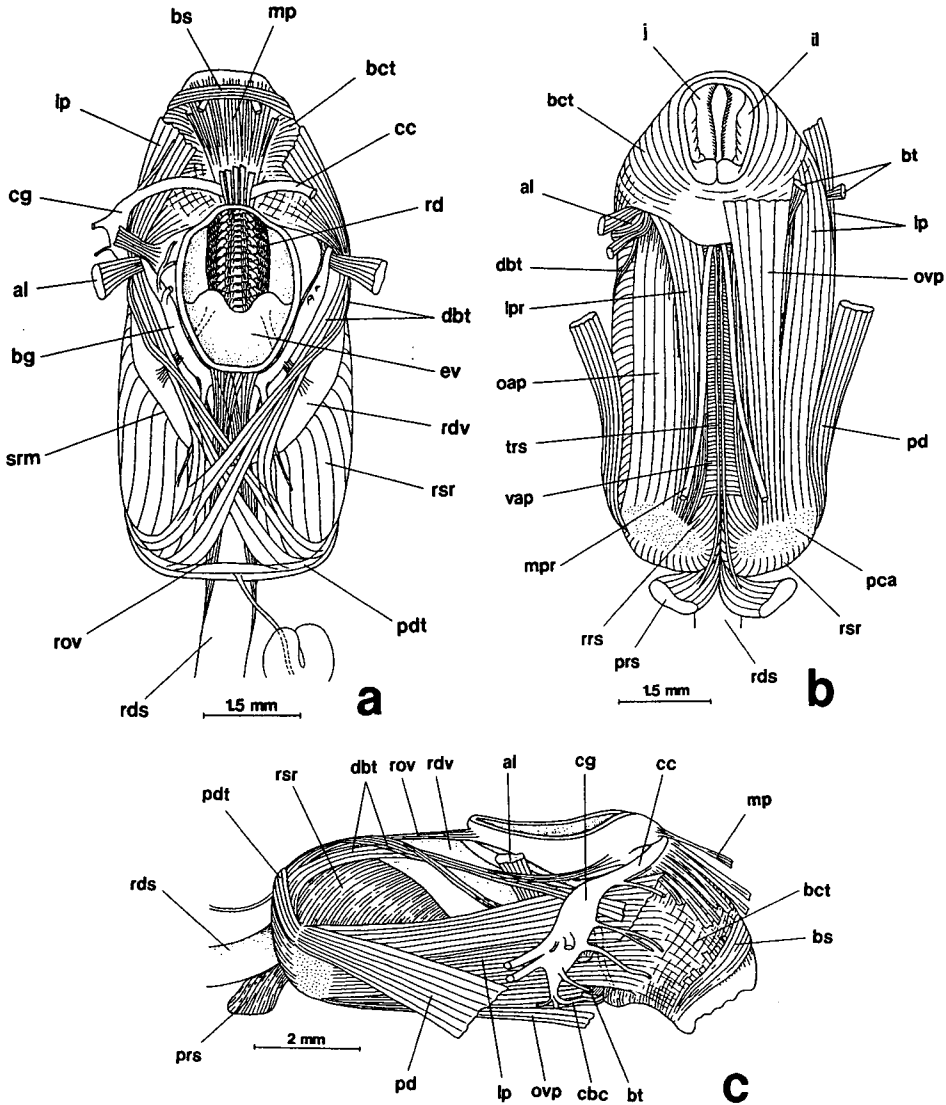
Fig. 35. *Scutus* (*Aviscutum*) *sinensis*. a, Dorsal view of the buccal mass. b, Ventral view of the buccal mass. Several extrinsic muscles are removed on the left side. c, Right lateral view of the buccal mass.

ing paired ctenidia with osphradia, anus, and kidney openings (Fig. 34). Hypobranchial glands absent.

Ctenidia (c) bipectinate, truly symmetrical in form and position. Ctenidial axes suspended on lateral pallial wall by efferent ctenidial membrane (ecm) and on roof of pallial cavity by afferent ctenidial membrane (acm). Each axis containing typical ctenidial structures of vessel, nerve, and retractor muscles. Lamellae triangular in outline, forming prominent terminal ridges (tr) projecting inside (Fig. 37 d). Efferent sides of lamellae with longitudinal array of bursicles (br) (Fig. 37 d). Surface of lamellae covered by three zones of ciliation. Lamellae supported by skeletal rods on efferent sides. Osphradia covering free portions of efferent axes.

Digestive System: Oral tube surrounded by sphincter and constrictor with mandibular protractors (mp)
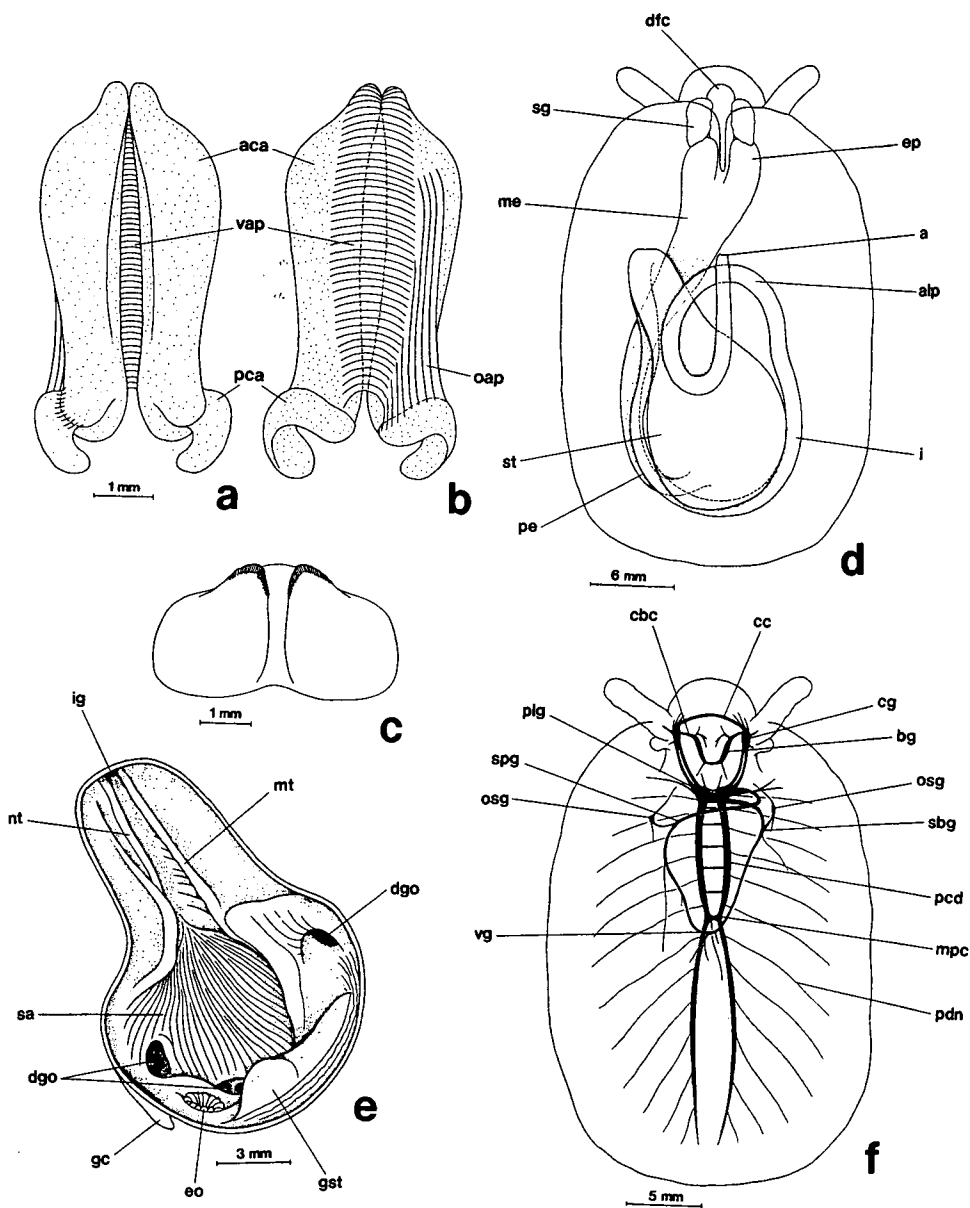
Fig. 36.   *Scutus* (*Aviscutum*) *sinensis*. **a**, Dorsal view of the odontophoral cartilages. Right outer approximator
muscle is removed. **b**, Ventral view of the odontophoral cartilages. **c**, Ventral view of the jaw. **d**, Con-
figuration of the alimentary tract. **e**, Internal structure of the stomach. **f**, Nervous system.

and retractors (mr). From sides of oral tube, two distinct tensor muscles arising below layers of constrictors.

Muscles controlling orientation of odontophore comprising lateral protractors (lp), outer and inner ven-
tral protractors (ovp, ivp), anterior levators (al), and posterior depressors (pd) (Figs. 35 a-c). Posterior leva-
tors absent. Posterior part of odontophore fixed by two kinds of tensor muscles. Dorsal buccal tensors (dbt)
consisting of two distinct strands that fuse posteriorly. Inner strand originating from body wall, passing be-
tween lateral protractor and cerebral ganglion. Outer strand extending over inner strand, attaching to margin
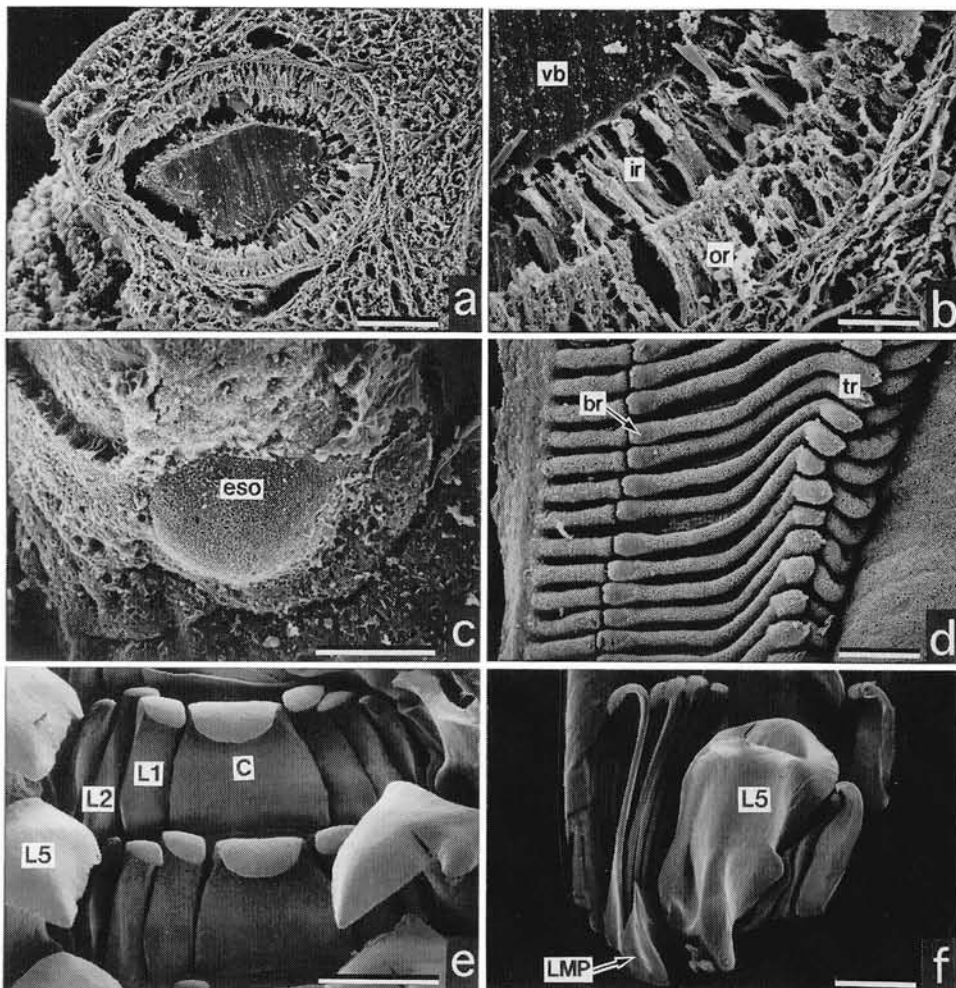
Fig. 37.   *Scutus (Aviscutum) sinensis.* SEM micrographs of soft parts. **a-b**, RM 27630 a. **c-d**, RM 27630 b. **e-f**, RM 27630 c. **a**, Vertical section of eye. Scale = 100 μm. **b**, Enlarged view of retina. Scale = 25 μm. **c**, Epipodial sense organs on ventral surface of tentacle. Scale = 100 μm. **d**, Dorsal view of ctenidial lamellae. Scale = 250 μm. **e-f**, Radula. **e**, Central teeth complex. Scale = 100 μm. **f**, Basal view from inner lateral to inner marginal teeth. Scale = 200 μm.

of subradular membrane. Postdorsal buccal tensor (pdt) inserting on both sides of posterior cartilages.

Jaws (j) wholly attached to inner wall of oral tube except fimbriate anterior tip (Fig. 35 b), divided into independent pair, but median zone connected by cuticularized membrane (Fig. 36 c).

Radular sac forming single loop to ventral side. Posterior end deeply bifurcated, connected to postdorsal buccal tensor (pdt) by thin muscle string (Fig. 35 a). Radular formula $(n+1)-(1+4)-1-(4+1)-(1+n)$ (Figs. 37 e, f). Each teeth row almost symmetrical in central field, but outer lateral teeth asymmetrically interdigitated when radula closed by retraction. Central tooth trapezoidal, slightly asymmetrical, skewed to right side; cusp semicircular, lacking denticles; base also simple without lateral extension. Inner three pairs of inner laterals equal in length, but becoming more slender outside; cusps indistinct. Fourth teeth most slender among four paired inner laterals, concealed under inner margin of enlarged outer laterals. Outer (fifth) laterals sharply projecting with acutely pointed tip and subsidiary denticle at outer side of cusp; basal

part of shaft with thick ridge and lobate extension on each side. Lateromarginal plates strongly keeled; inner margin with close interaction with basal extension of outer laterals (Fig. 37 f). Marginals greatly elongated into filamentous form with finely serrated cusps.

Muscles controlling radular action consisting of median and lateral protractors of subradular membrane (mpr, lpr), retractors of subradular membrane (rsr), retractors of radular sac (rrs), and postmedian retractors of radular sac (prs) (Fig. 35 b). Tensor muscle of radular sac (trs) divided into right and left strands, their posterior ends attached to inner sides of postmedian retractors of radular sac (prs), not to ventral side of radular sac.

Odontophore containing two pairs of cartilages showing somewhat specialized form (Figs. 36 a, b). Anterior cartilages (aca) longitudinally elongated with weak anterolateral extensions. Posterior cartilages (pca) curving inside, attaching to posterior ends of anterior cartilages. Boundary between two cartilages connected by thin muscles dorsally, partially fused ventrally. Anterior cartilages ventrally inserted by ventral approximator (vap). Anterior and posterior pairs united by outer approximator muscles (oap).

Sublingual pouch shallow. Licker simple. Radular diverticulum present. No caecum (as in *Diodora*; Fretter and Graham, 1962: fig. 96, pdm) found between paired odontophoral cartilages. Salivary glands (sg) developed over buccal cavity (Fig. 36 d); opening not through ducts, but through longitudinal slits; dorsal surface ramified into vermiform outgrowths.

Anterior esophagus dilated to form esophageal pouches (ep), covering posterior end of buccal mass entirely. Dorsal folds paired along length of mid-esophagus; ventral folds fused in middle part. Wall of mid-esophagus extensively papillate. End of mid-esophagus marked by completion of twisting of dorsal folds and by disappearance of glandular papillae. Posterior esophagus (pe) very short.

Proximal part of stomach (st) well-inflated; outline pyriform (Figs. 36 d, e). Digestive glands opening into stomach through three large pores (dgo); two lying near opening of esophagus on posterior side, remaining one on right side. Gastric caecum (gc) small, crescent-shaped. Dorsal inner surface covered by gastric shield. Tooth of gastric shield (gst) projecting on posterior side. Sorting area (sa) and typhlosoles (nt, mt) well developed on ventral inner surface. Distal part of stomach and initial part of intestine elongated toward anterior left side, projecting over mid-esophagus.

Intestine (i) running along stomach posteriorly, forming anterior loop (alp) on right side of mid-esophagus (Fig. 36 d). Posterior part of intestine making another smaller loop above stomach, penetrating pericardium and ventricle, finally opening into pallial cavity along median line.

Circulatory System: Pericardium lying slightly posterior of center of body, enlarging laterally to contact shell muscle (Fig. 34). Heart consisting of larger right and smaller left auricles (ra, la), and median ventricle (v).

Aorta emerging from left side of ventricle, bifurcating into anterior and posterior aortae. Anterior aorta (aa) running beneath pericardium and esophagus, finally entering buccal region. Posterior aorta (pa) dividing into three main vessels. Right branch extending along posterior margin of right kidney, reaching gonad. Middle branch extending posteriorly, supplying blood mainly to stomach. Left branch penetrating into digestive glands.

Venous system around digestive organs well-developed, connected to kidneys. In front of kidneys, efferent renal vessels expanding to form small basibranchial sinus. Blood then flowing from afferent to efferent ctenidial vessels (acv, ecv), returning to right and left auricles.

Excretory System: Two extremely unequal kidneys (Fig. 34). Enlarged right kidney (rk) lying under pericardium, extending to dorsal surface on right posterior side of pericardium, also ventrally spreading over mid-esophagus; inner wall comprising of folded lamellae with irregular perforation. Renopericardial canal arising from right side, opening into pericardium near excretory pore of right kidney. Right kidney opening into pallial cavity via large papilla with longitudinal slit.

Left kidney (lk) greatly reduced, restricted to narrow space between posterior wall of pallial cavity and left auricle. Left kidney opening simple small pore without papilla. Left renopericardial canal from left kidney apparently absent.

Reproductive System: Gonad (g) mostly located beneath stomach and digestive glands; right margin tending to swell toward dorsal surface as gonad becomes mature (Fig. 34). Sexes distinguished by granular appearance of ovary in females and by non-granular homogeneous surface of testis in males. Gonoduct extending along left kidney, connecting to right kidney via renopericardial duct. Gametes discharging into sea water through right kidney opening.

Nervous System: Circumesophageal nerve ring hypoathroid (Fig. 36 f). Cerebral ganglia (cg) lying at bases of cephalic tentacles, connected by thick commissure (cc). Pedal and pleural ganglia juxtaposed closely, almost fused.

Cerebral ganglia (cg) sending several nerves to labial region, lacking clear labial commissure below oral tube. Labial ganglia also absent. Cerebrobuccal connectives (cbc) directly arising from inner ventral sides of cerebral ganglia.

Visceral loop not very long, arising from right and left pleural ganglia. Visceral ganglion (vg) under right excretory pore, innervating both kidneys and pericardium. Connectives between visceral and supra-/subesophageal ganglia sending thin nerves to digestive tract. Supra- and subesophageal ganglia (spg, sbg) connected with osphradioctenidial ganglia (osg) that occur at bases of efferent ctenidial axes.

Pedal cords (pcd) developed into very characteristic form, not buried within pedal musculature, but exposed throughout their length beneath visceral mass, medianly connected with specially thick commissure (mpc) (Fig. 36 f). In anterior portion of median commissure, pedal cords connected with thick commissures at constant intervals, but similar commissures lacking in posterior part. Thin long pedal nerves extended from outer sides of cords in ventral membrane of visceral mass to pedal musculature. Statocysts attached to anterodorsal parts of pedal ganglia, visible from dorsal side.

Scutus (Aviscutum) unguis (Linnaeus, 1758)
(Figs. 38 a-b)

Protoconch: Protoconch paucispiral, planispirally coiled. Lateral pouch indistinct; suture of protoconch very clear. Surface of protoconch covered by weak spiral threads and strong wavy axial ridges. Discordant rib also present on lateral pouch. Protoconch-teleoconch boundary clearly demarcated by distinct band.

Tugali decussata (A. Adams, 1852)
(Figs. 38 c-f)

Protoconch: Protoconch paucispiral, discoidal, slightly orthostrophic. Outer surface ornamented with fine net-like sculpture consisting of ten regular-spaced spiral riblets. Lateral pouch on apical side marked by three or more oblique ribs in discordant direction to spiral sculpture. Protoconch-teleoconch boundary demarcated by thick apertural lip of protoconch.

Zeidora calceolina A. Adams, 1860
(Figs. 39 a-b)

Protoconch: Protoconch nearly symmetrical, planispiral, longitudinally elongated. Exterior sculpture mostly abraded in specimen investigated; fine granules observed at least in apical area. Protoconch-teleoconch boundary clearly demarcated, from which radiating thread-like sculpture appears near selenizone. Protoconch slightly inclined to right relative to growth axis of teleoconch.
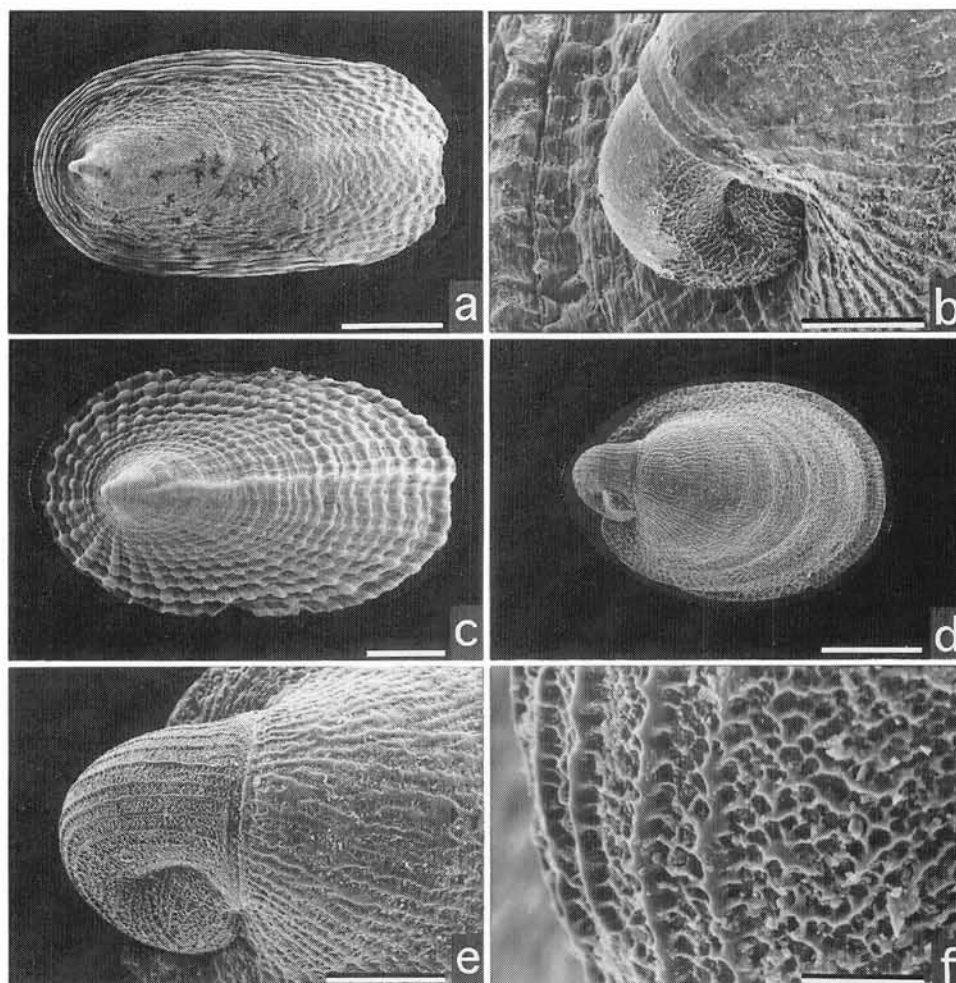
Fig. 38.   Protoconch of Fissurellidae. **a-b**, *Scutus (Aviscutum) unguis*. RM 27631. **a**, Dorsal view of young shell. Scale=1 mm. **b**, Right lateral view of apical area. Scale=100 μm. **c-f**, *Tugali decussata*. **c**, RM 27632. **d-f**, RM 27633. **c**, Dorsal view of subadult shell. Scale=1 mm. **d**, Dorsal view of early juvenile shell. Scale=250 μm. **e**, Protoconch and early teleoconch. Scale=100 μm. **f**, Sculpture of protoconch. Scale=20 μm.

Emarginula sp.
(Figs. 39 c-d)

Protoconch: Protoconch elongated, paucispiral, almost planispiral. Lateral pouch clearly formed laterally; suture of protoconch very clear. Outer surface ornamented with fine frame-like, irregular deposits arranged axially at constant intervals. Protoconch-teleoconch boundary demarcated by strong axial ribs.

Rimula sp.
(Figs. 39 e-f)

Protoconch: Protoconch paucispiral, planispiral. Outer surface ornamented by rough reticulated sculpture consisting of irregular axial and regular spiral ribs. Protoconch-teleoconch boundary clearly demarcated by distinct apertural lip of protoconch.
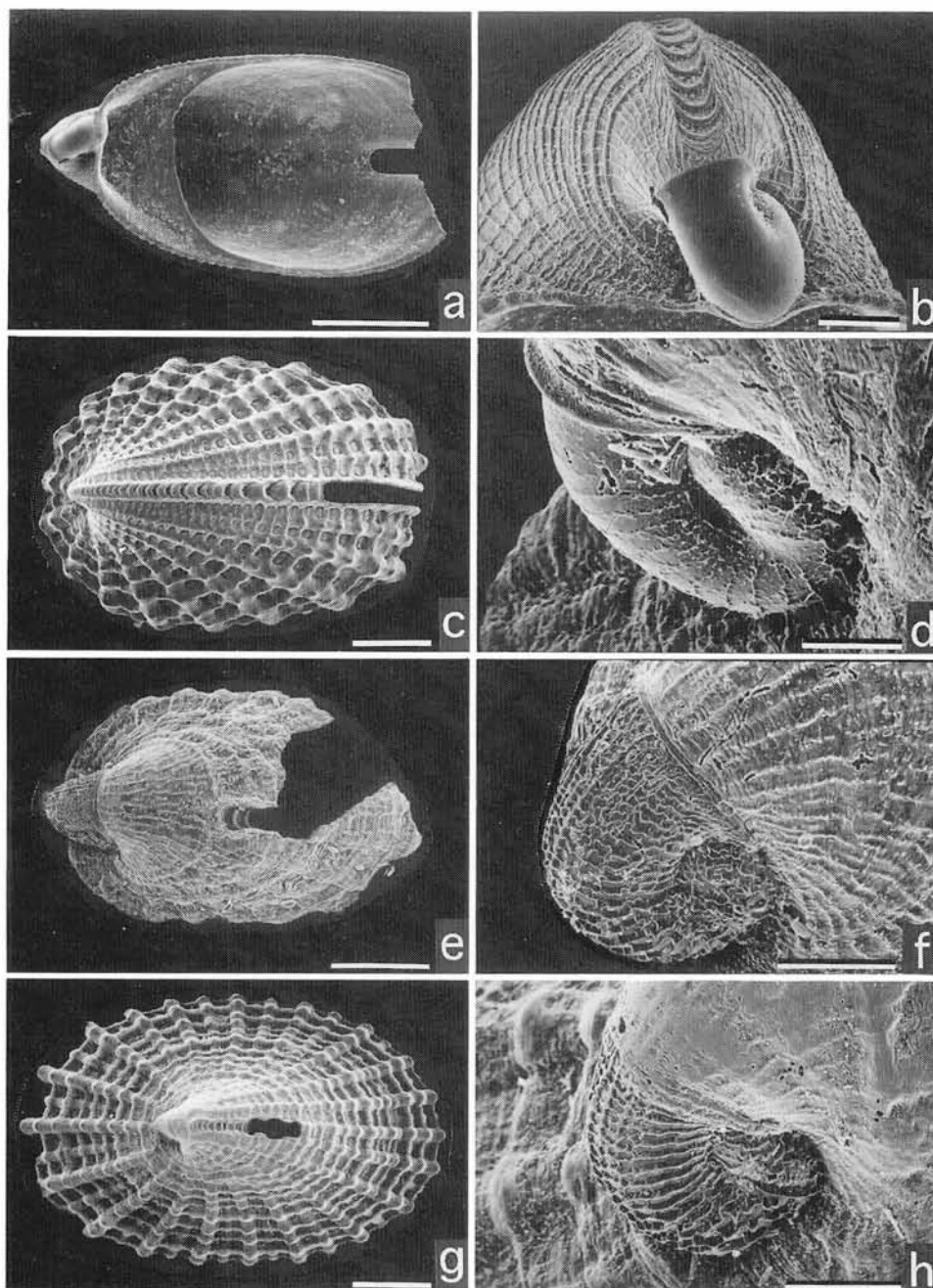
Fig. 39.   Protoconch of Fissurellidae. **a-b**, *Zeidora calcaeolina*. RM 27634. **a**, Ventral view of adult shell. Scale = 500 μm. **b**, Apical view seen from posterior side. Scale = 100 μm. **c-d**, *Emarginula* sp. RM 27635. **c**, Dorsal view. Scale = 500 μm. **d**, Right lateral view of protoconch. Scale = 50 μm. **e-f**, *Rimula* sp. RM 27636. **e**, Dorsal view. Scale = 250 μm. **f**, Right lateral view of protoconch. Scale = 100 μm. **g-h**, *Diodora* sp. RM 27637. **g**, Dorsal view. Scale = 500 μm. **h**, Right lateral view of protoconch. Scale = 100 μm.

Diodora sp.
(Figs. 39 g-h)

Protoconch: Protoconch nearly paucispiral, planispiral. Lateral pouch weakly constricted, producing deep sutural line. Sculpture consisting of many prominent axial ribs crossed by several spiral cords on periphery. Discordant rib formed on apical side. Protoconch-teleoconch boundary unclear in specimen examined due to abrasion.

Macroschisma dilatatum (A. Adams, 1851)
(Figs. 40 a-h, 41 a-c)

Protoconch: Protoconch completely symmetrical, with posterior end strikingly projecting outward as keel (Figs. 40 b-g). Lateral pouch well-inflated, marking bilaterally deep longitudinal depression (Figs. 40 e-g). Most of surface entirely smooth. Lateral pouches striated by nearly parallel linear sculpture; dorsalmost one more distinctly prominent than others (Figs. 40 g-h).

Teleoconch: At shell length of 0.6 mm, median apertural margin reflected to form foramen by immediate closure. Perforation centrally maintained by forward resorption and backward re-secretion of shell materials (Figs. 40 a-d).

External Anatomy: Shell and soft body completely limpet-shaped. Animal more than twice as large as shell in length. Because post-pericardial region wholly covered by extended epipodium, visceral hump not visible from dorsal surface.

Mantle skirt perforated by longitudinal apical hole (ah, Fig. 41 a). Mantle skirt suspended from shell by pallial retractors that mark several attachments. Mantle margin (mm) slightly reflected over shell margin with irregular microprojections.

Head with short snout (sn), non-papillate cephalic tentacles (ct), and eyestalks. Oral and cephalic lappets absent. Cephalic tentacles non-papillate. Eyes closed.

Surface of epipodium (epd) bearing tuberculate texture. Some enlarged tubercles on lateral area perhaps representing minute epipodial tentacles. Presence or absence of epipodial sense organs unclear. Operculum absent. Shell muscle (sm) horseshoe-shaped, undivided into bundles.

Pallial Complex: Pallial cavity containing paired ctenidia and osphradia, paired kidney openings, and anus. Hypobranchial glands absent. Ctenidia bipectinate, symmetrically paired in pallial cavity. Afferent and efferent ctenidial axes connected by long membranes to pallial roof along apical hole and to inner side of shell muscle, respectively. Ctenidial lamellae depressed dorsoventrally with apices projected on afferent side. Lamellae provided with bursicles and skeletal rods on efferent side. Osphradia at efferent axes of anterior free portions.

Digestive System: Composition of buccal musculature (oral, odontophoral, and radular muscles) essentially as in *Scutus*. Jaws paired on dorsal side of oral tube, with brush-like projections at anterior margin. Odontophore containing longer anterior and smaller posterior cartilages, connected by ventral and outer approximator muscles.

Radular sac short, posterior end deeply bifurcated. Radular formula (n+1)–(1+4)–1–(4+1)–(1+n). Transverse tooth row asymmetrically distorted, left half more strongly skewed anteriorly than right side. Central tooth plate-like, remarkably asymmetrical in both configuration and tooth morphology, without distinct shaft and cusp. Four inner lateral teeth of almost equal width, also asymmetrical in configuration; cusps non-denticulate, becoming smaller toward outside; each lateral tooth except innermost with inward basal projection. Outer (fifth) lateral teeth much more robust than others; cusp tri-denticulate; base with prominent extension on inner side. Lateromarginal plates triangular, strongly carinated by prominent acute keel. Marginal teeth very thin with finely serrated denticles.

Sublingual pouch shallow, simple. Licker smooth. Radular diverticulum deeply developed. Caecum not
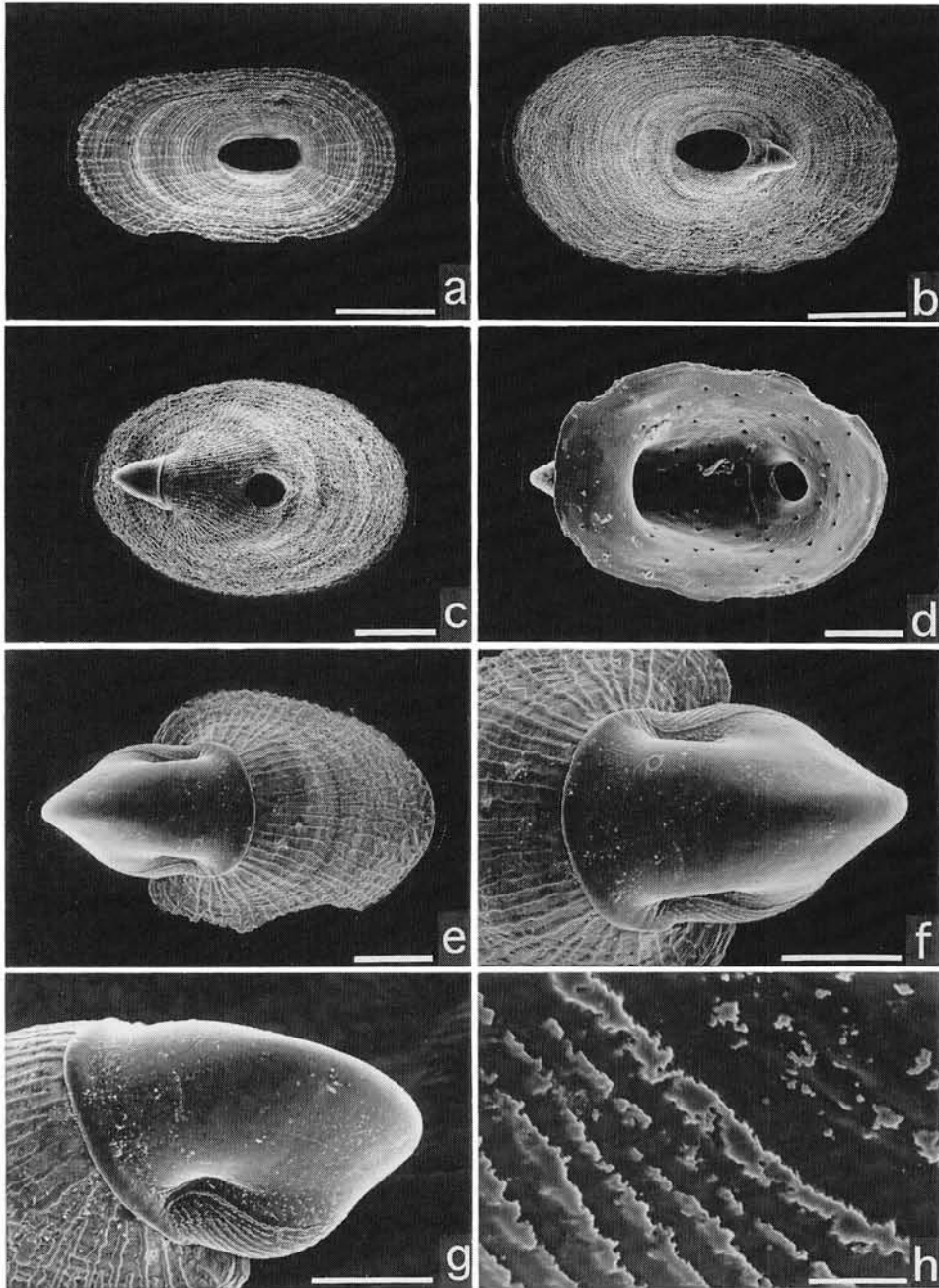
Fig. 40. Protoconch of *Macroschisma dilatatum*. **a**, RM 27639. **b-c**, RM 27640. **d-h**, RM 27641. **a**, Dorsal view of subadult shell. Scale = 1 mm. **b**, Juvenile shell with oval foramen and intact protoconch. Scale = 500 μm. **c**, Juvenile shell with small circular foramen. Scale = 250 μm. **d**, Ventral view of juvenile shell with foramen and shell pores of canal structure. Scale = 200 μm. **e**, Dorsal view of early juvenile shell. Scale = 100 μm. **f**, Dorsal view of protoconch. Scale = 50 μm. **g**, Left lateral view of protoconch. Scale = 50 μm. **h**, Sculpture on lateral pouch. Scales = 10 μm.
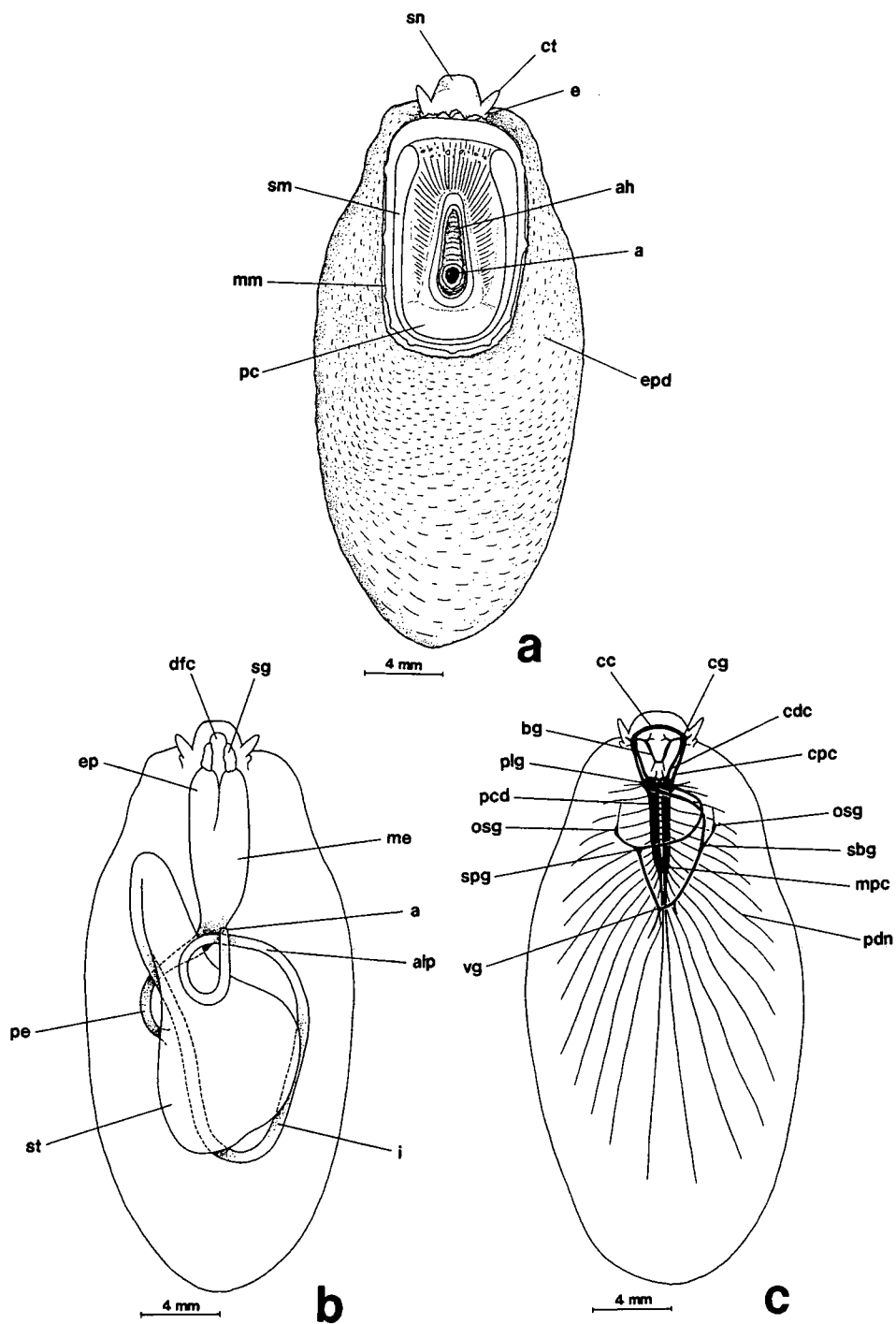
Fig. 41. *Macroschisma dilatatum*. **a**, Dorsal view of the animal after shell removed. **b**, Configuration of the alimentary tract. **c**, Nervous system.

found between paired odontophoral cartilages. Paired salivary glands (sg) opening into buccal cavity through longitudinal slits without ducts.

Posterior half of odontophore covered by enlarged esophageal pouches (ep) (Fig. 41 b). Mid-esophagus cylindrical. Rotation of dorsal and ventral folds gradual. Ventral folds fused in middle part of mid-esophagus. Inner wall covered by papillae throughout its length. Posterior esophagus (pe) opening into stomach on left side.

Proximal chamber of stomach (st) swelling to become pyriform (Fig. 41 b). Digestive glands opening on lateral area separately. Diminutive crescent-shaped gastric caecum projecting ventrally at posterior end. Large gastric tooth arising on posterior wall. Sorting area and typhlosoles well developed on ventral inner surface. Distal tapering area containing tip of protostyle. Intestine (i) extending backward beneath stomach, curving forward to produce single anterior loop (alp) (Fig. 41 b); rectum penetrating pericardium and ventricle; anus (a) opening in posterior median end of pallial cavity.

Circulatory System: Pericardium (pc) lying between apical hole and posterior margin of horse-shape shell muscle (Fig. 41 a). Heart consisting of paired auricles and median ventricle. Right auricle slightly larger than left one.

Excretory System: Kidneys paired. Right kidney spreading into posterior and anterior right sides of pericardium. Left kidney greatly reduced, in front of left auricle. Opening of right kidney papillate, with longitudinal slit; that of left kidney minute simple pore. Right renopericardial duct extending from right side of right kidney. Left renopericardial duct not found.

Reproductive System: Gonochoristic gonad beneath digestive glands and stomach. Gonoduct ascending dorsally from right side, connecting with right renopericardial duct. Testis fine cotton-like; ovary granulate with yolk-rich eggs.

Nervous System: Circumesophageal nerve ring hypoathroid (Fig. 41 c). Labial ganglia and commissure absent. Short visceral loop arising from right and left pleural ganglia. Pedal cords (pcd) closely juxtaposed, connected with especially thick median pedal commissure (mpc). Cords on anterior side of medial commissure markedly thickened, united by about eleven thin commissures. Posterior part of cords rather abruptly attenuating. Fine thread-like pedal nerves radiating toward margin of foot. Pedal cords and most part of pedal nerves not buried in pedal musculature. Statocysts present on anterodorsal part of pedal ganglia.

Family Scissurellidae Gray, 1847
Anatoma sp.
(Figs. 42 a-d, 43 a-h, 44 a-b)

Protoconch: Protoconch paucispiral, nearly planispiral. Weak constriction generating rather unclear suture near aperture on apical side (Fig. 44 b). Surface covered with regular net-like sculpture formed by anastomosis of fine ridges. Protoconch-teleoconch boundary demarcated by faintly thickened lip.

External Anatomy: Animal trochiform. Mantle deeply sinuate in median line (Fig. 42 a). Inner fold of mantle margin fringed by densely papillate, short microtentacles (Figs. 43 b, c). Papillae composed of long stalks and distal tuft of cilia, both of which indistinguishable from those of cephalic and epipodial tentacles. Posterior limit of mantle slit giving rise to long pallial tentacle (pt) with similar papillae (Fig. 42 a). Attachment of shell muscle trapezoidal, restricted to columellar side within body whorl.

Head with pair of cephalic tentacles and eyestalks. Cephalic lappets absent. Cephalic tentacles papillate laterally. Eyestalks short with closed eyes at top. Neck lobes absent.

Epipodium bearing five pairs of papillate epipodial tentacles (ept) (Figs. 43 a, d). Anterior three pairs large, tentacular; fourth pair with extended tip. Fifth pair slightly slender.

Pallial Complex: Deep pallial cavity containing paired ctenidia, paired kidney openings, coiled intestinal loops with anus, and right hypobranchial gland (Fig. 42 a). Position of osphradium not identified.
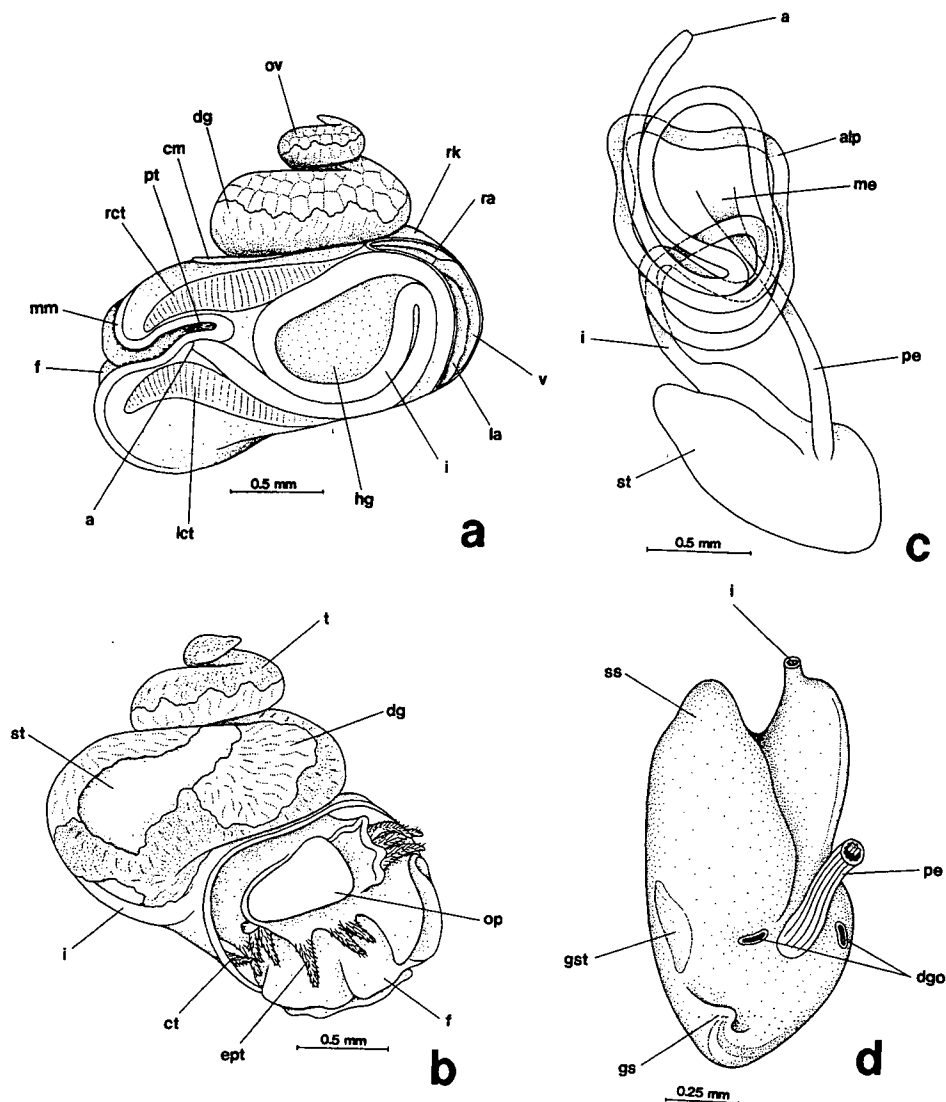
Fig. 42. *Anatoma* sp. **a**, Dorsal view of the animal with shell removed. **b**, Ventral view of the animal. **c**, Con-
figuration of the post-buccal alimentary tract. **d**, Stomach.

Ctenidia (rct, lct) slightly asymmetrical, composed of about thirty monopectinate lamellae. Lamellae
covered by cilia zoned laterally. Bursicles (br) prominently developed near efferent axis (Fig. 43 e). Open-
ing of lumen slit-like, continued to lateral cilia. Few tufts of cilia on exterior part of bursicle. Hypobranchial
gland (hg) lying within pallial loop of intestine, restricted to right side relative to rectum, consisting of tall
cells containing spherules.

Digestive System: Oral tube surrounded by buccal sphincter and constrictor (bs, bct), fixed by mandibu-
lar protractors and mandibular retractors. Muscles of odontophore comprising lateral protractors (lp), ante-
rior levators (al), posterior depressors (pd), and ventral protractors (ovp, ivp) (Fig. 43 f). Posterior levators
absent. Dorsal posterior part united by postdorsal (pdt) and dorsal buccal tensors (dbt).

Jaws consisting of paired elements attaching to oral tube posteriorly but projecting into mouth anteriorly.
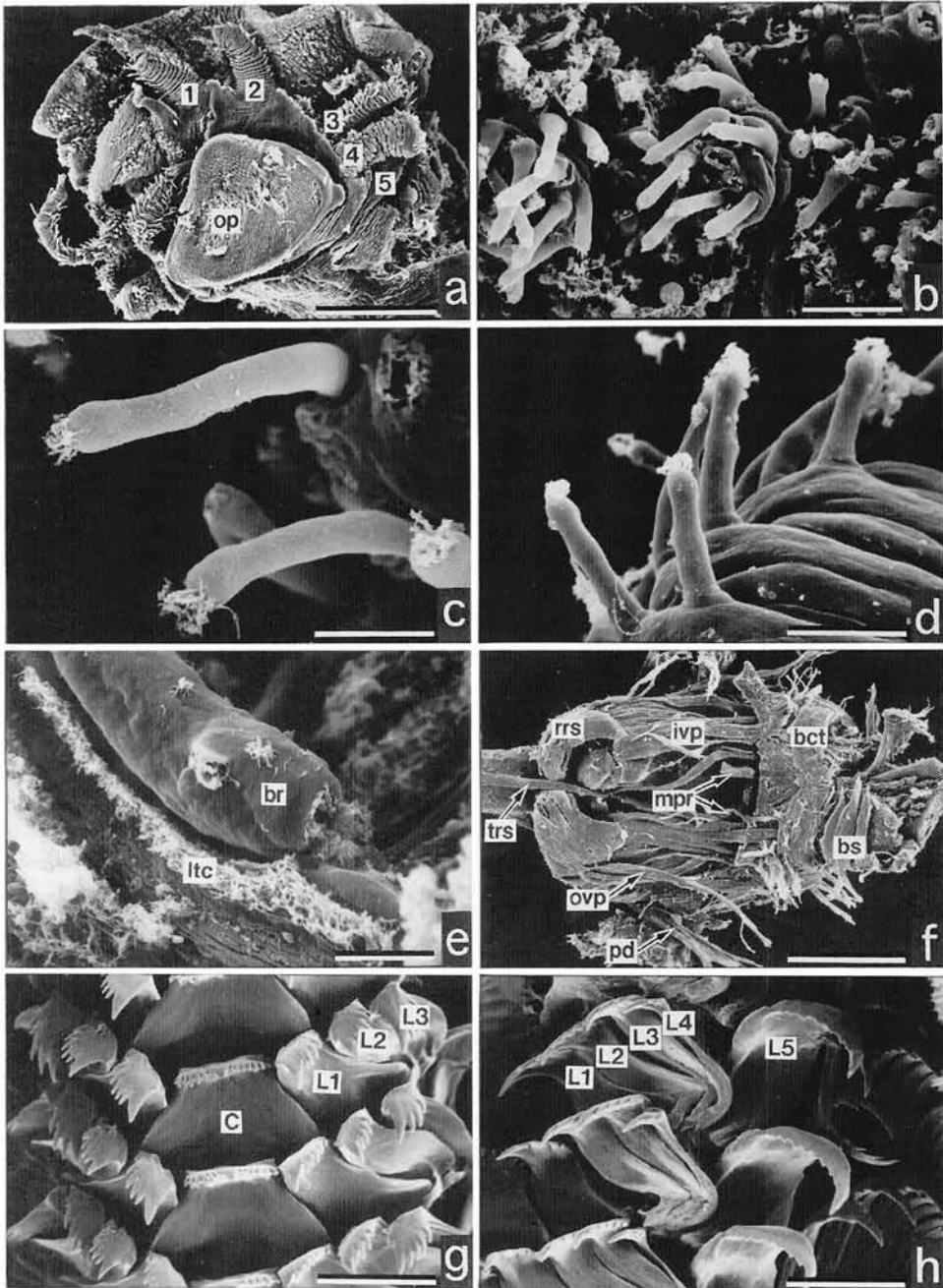
Fig. 43. *Anatoma* sp. SEM micrographs of soft parts. **a-c, e**, RM 27642 a. **d**, RM 27642 b. **f**, RM 27642 c. **g-h**, RM 27642 d. **a**, Ventral view of anterior part with opercular lobe and epipodial tentacles. Scale = 250 μm. **b**, Microtentacles on mantle margin. Scale = 25 μm. **c**, Enlarged view of ciliated papillae of microtentacles. Scale = 10 μm. **d**, Ciliated papillae on epipodial tentacle. Scale = 20 μm. **e**, Bursicle on ctenidial lamella. Scale = 25 μm. **f**, Ventral view of buccal mass. Scale = 100 μm. **g**, Central tooth and inner lateral teeth. Scale = 10 μm. **h**, Lateral teeth and inner marginal teeth field. Scale = 10 μm.

Fig. 44.   Protoconch of Scissurellidae. **a-b**, *Anatoma* sp. RM 27643. **a**, Ventral view of adult shell. Scale = 1
mm. **b**, Oblique apical view of protoconch. Scale = 100 μm. **c-d**, *Anatoma japonica*. RM 27644. **c**,
Dorsal view of subadult shell. Scale = 250 μm. **d**, Apical view of protoconch. Scale = 50 μm.

Anterior margins indented with scaly projections.

Radular sac form single vertical loop behind buccal mass. Posterior end clearly bifurcated. Radular for-
mula n−(1+4)−1−(4+1)−n (Figs. 43 g, h). Transverse radular row symmetrical. Central tooth broadest of
all radular teeth; base broad, extending over innermost lateral teeth; shaft tapering distally, cusp indented by
one thick median and seven thinner lateral denticles. Inner lateral teeth progressively reducing in width out-
wardly; shafts strongly bent at base; cusps triangular-shaped, sharply denticulate; inner three laterals of
common shape with five or six denticles, but slender outermost one with only three denticles. Outer (fifth)
laterals with broad base, articulating with bases of inner laterals; cusp sharply hooked along outer margin,
finely serrated by small denticles. Lateromarginal plates absent. Marginal teeth slender, thread-like, with
less than six denticles on cusps.

Subradular membrane connected to lateral and median protractors (lpr, mpr) and retractors (rsr). Thin
tensor muscle of radular sac (trs) running from dorsal part of sublingual pouch to ventral side of radular sac
posterior to buccal mass (Fig. 43 f). Postmedian retractors of radular sac absent.

Odontophore containing elongated anterior and small posterior cartilages connected by ventral and outer
approximator muscles.

Sublingual pouch shallow, simple. Radular diverticulum deeply developed. Salivary glands attached to
buccal cavity dorsally without ducts. Anterior esophagus inflated posterior to buccal mass. Mid-esophagus
(me) not very long; counterclockwise rotation of dorsal and ventral folds apparent. Inner wall covered with
papillae except in ciliated dorsal food channel. Posterior esophagus (pe) extending along columella on right
side, corrugated by several longitudinal furrows internally.

Stomach (st) large for body size, visible from dorsal surface of visceral hump (Fig. 42 b). Posterior apex
slightly curving to form short gastric caecum (Fig. 42 d). Paired folds and median groove visible through

outside of caecum. Digestive glands (dg) opening on either side of end of posterior esophagus. Distal portion of stomach distinctly divided into isolated style sac region (ss) and preintestinal extension. Tooth of gastric shield (gst) lying at base of style sac region; paired typhlosoles running through extended part of preintestinal region.

Intestine (i) running complicated course through both visceral and pallial regions (Fig. 42 c). Anterior loop (alp) formed beyond mid-esophagus. After penetrating into pericardium and ventricle, pallial section forming large loop anteriorly. Loop in pallial cavity recurving once, finally terminating on left side of mantle slit.

Circulatory System: Pericardium elongated along posterior limit of pallial cavity. Heart consisting of right auricle (ra) lying at right posterior side, left auricle (la) on left anterior side, and median ventricle (Fig. 42 a).

Excretory System: Kidneys asymmetrically paired. Right kidney (rk) lying on right side of right auricle along columella; presence indicated by light brown color in fixed material. Left kidney (lk) on left side of pericardium; lumen lacking distinct papillae.

Reproductive System: Gonad (ov, t) lying on dorsal side of digestive glands in spiral part of visceral hump (Figs. 42 a, b). Sexes apparently separated, distinguished by texture of granulation of gonadal tissue. Pathway of gonoduct to pallial cavity not determined. Copulatory organ absent.

Nervous System: Circumesophageal nerve ring hypoathroid. Pedal ganglia nearly fused in midline. Pedal cords buried in pedal musculature without median connection (unlike in *Scutus* and *Macroschisma*). Labial ganglia and commissure not found. Visceral loop originating directly from pleural ganglia. Statocysts on anterior sides of pedal ganglia.

Anatoma japonica (A. Adams, 1862)
(Figs. 44 c-d)

Protoconch: Protoconch paucispiral, almost planispiral. Suture unclear, represented only by spiral depression. Outer ornament consisting of irregularly arranged granules. Protoconch-teleoconch boundary margined by delicate axial line.

Sinezona sp.
(Figs. 45 a-c)

Protoconch: Protoconch spirally coiled, hyperstrophic. Terminal part of protoconch oriented more dorsally over initial part at distinct angle. Surface very strongly sculptured. On dorsal side, at least fifteen tall varices arranged in parallel to apertural margin. Characteristically, most centrally situated rib with quite different angle to remaining ribs. This rib much longer than others extended from dorsal to ventral centers. Ribs formed as aggregations of tall spicular prisms.

Scissurellidae gen. et sp.
(Figs. 45 d-f)

Protoconch: Protoconch paucispiral, with coiling direction nearly planispiral but slightly hyperstrophic. Surface covered with dense series of axial ribs transversely connected with weak spiral ridges. Interspaces between axial ribs entirely filled with fine granules. In central part of protoconch, aggregation of granules forming distinct ridge-like structure on both apical and basal sides. Protoconch-teleoconch boundary marked by thicken axial lip.
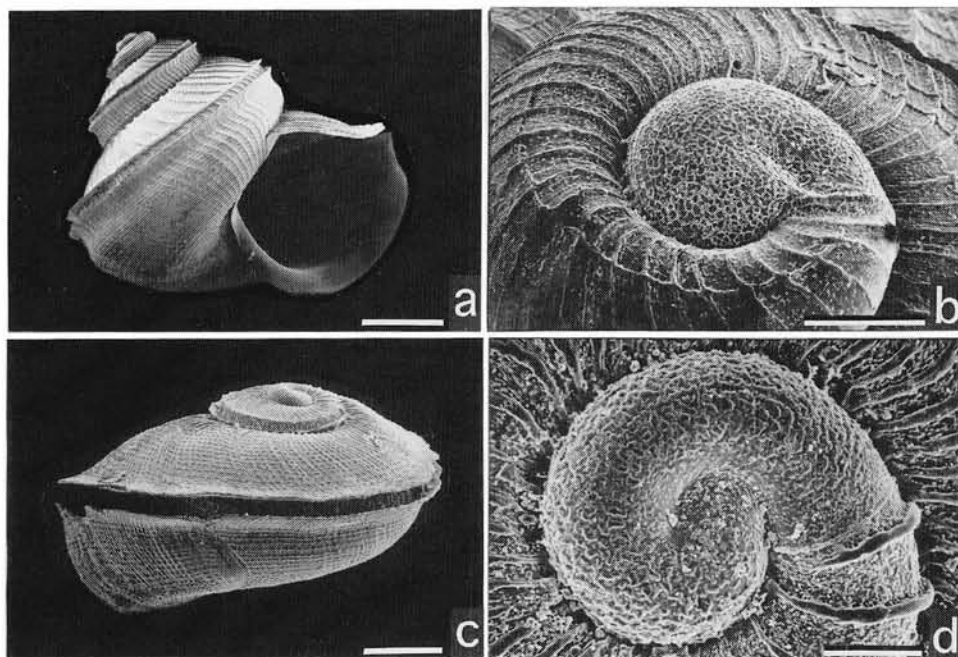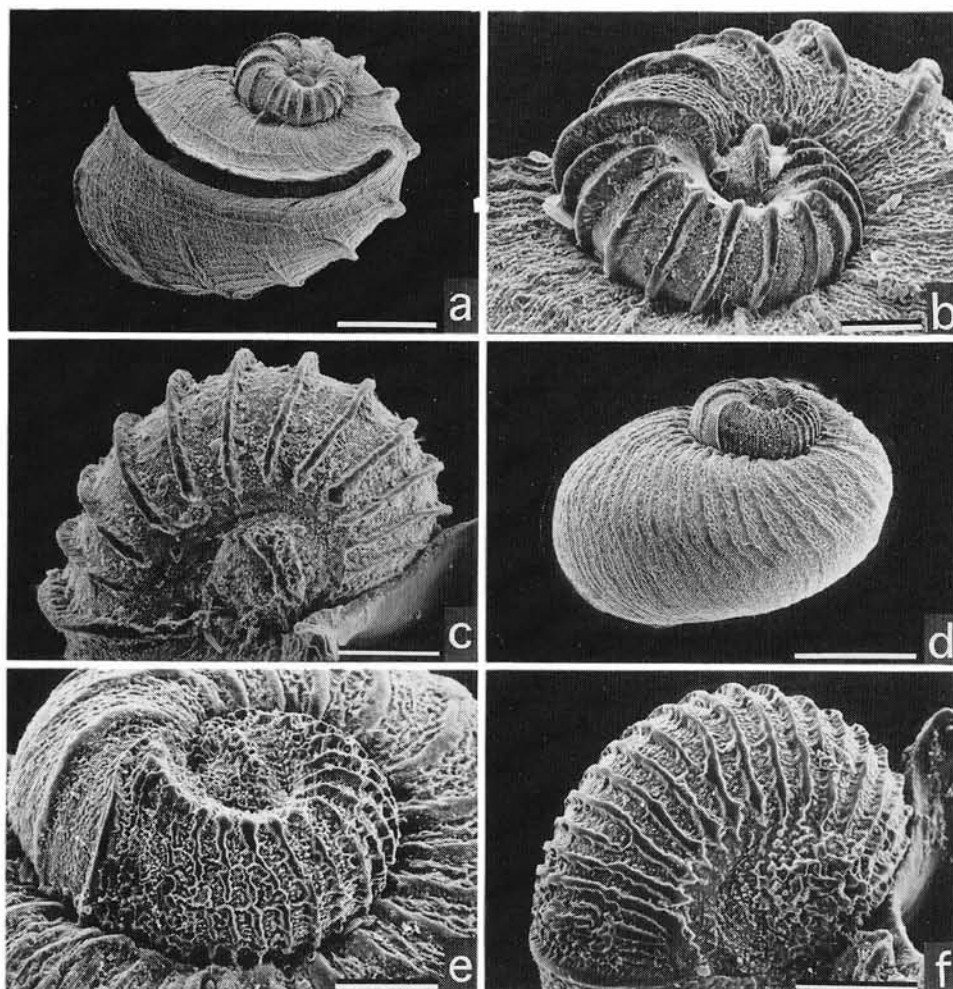
Fig. 45.   Protoconch of Scissurellidae. **a-c**, *Sinezona* sp. RM 27645. **a**, Apical view of young shell. Scale = 250
μm. **b**, Oblique apical view of protoconch. Scale = 50 μm. **c**, Basal view of protoconch. Scale = 50 μm.
d-f, Scissurellidae gen. et sp. RM 27646. **d**, Oblique apical view of subadult shell. Scale = 200 μm. **e**,
Oblique apical view of protoconch. Scale = 50 μm. **f**, Basal view of protoconch. Scale = 50 μm.

Family Turbinidae Rafinesque, 1815
Turbo (Marmarostoma) stenogyrum (Fischer, 1873)
(Figs. 46 a-b, 47 a-f, 48 a-b)

External Anatomy: Mantle margin (mm) lacking microtentacles. Shell muscle consisting of single undi-
vided columellar muscle (cm).

Head with snout (sn), cephalic lappets (clp), papillate cephalic tentacles (ct), and eyestalks (es). Outer lip
of mouth forming thick oral disk. Eyes (e) open, plugged with vitreous body at tips of eyestalks. Inhalant
(left) and exhalant (right) neck lobes present in neck region.

Foot (f) with four pairs of long papillate epipodial tentacles, each with knobby epipodial sense organ at
base. Head-foot folding anteroposteriorly when retracted. Calcareous operculum attached to opercular lobe
of epipodium.
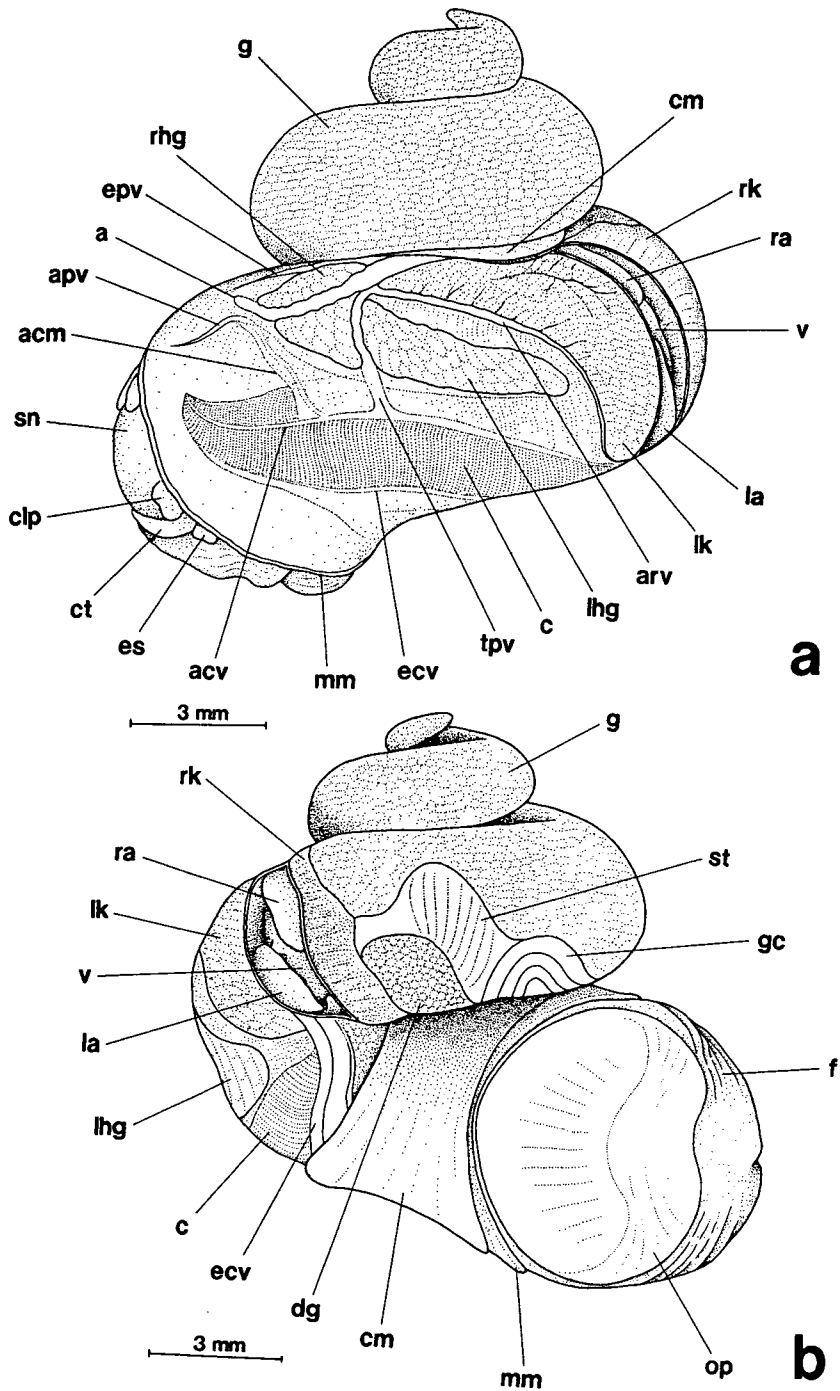
Fig. 46. *Turbo (Marmarostoma) stenogyrum.* a, Dorsal view of the animal with shell removed. b, Ventral view of the animal.
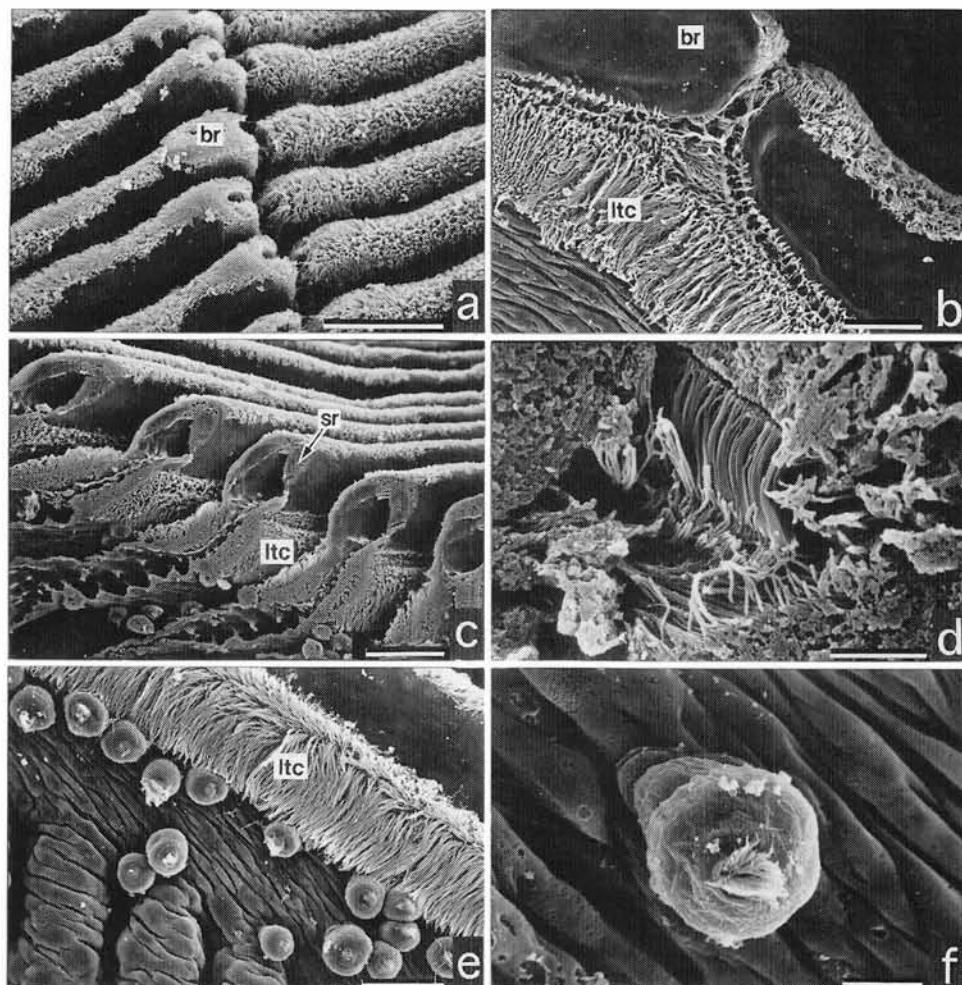
Fig. 47. *Turbo* (*Marmarostoma*) *stenogyrum*. SEM micrographs of ctenidium. RM 27647. **a**, Dorsal view of bursicles. Scale = 100 μm. **b**, Lateral view of bursicles with lateral cilia. Scale = 50 μm. **c**, Cross-section of efferent side of ctenidial lamella. Scale = 100 μm. **d**, Cross-section of ciliated lumen of bursicles. Scale = 5 μm. **e**, Lateral view of ctenidial lamella with ciliated papillae. Scale = 50 μm. **f**, Enlarged view of ciliated papilla. Scale = 10 μm.

Pallial Complex: Pallial cavity extending more than half of body whorl, including left ctenidium, left osphradium, paired kidney openings, anus, and paired hypobranchial glands (Figs. 46 a, b).

Ctenidium (c) extending almost entire length of pallial cavity, attached to left wall of pallial cavity by efferent ctenidial membrane and to pallial roof by afferent ctenidial membrane (acm). Left dorsal area of pallial cavity divided by afferent ctenidial membrane, generating isolated pocket space dorsally. Ventral ctenidial lamellae more enlarged and projecting to right side than dorsal lamellae. Efferent side of lamellae provided with series of bursicles (br, Fig. 47 a) and skeletal rods (sr) internally (Fig. 47 c).

Bursicles prominent, arrayed longitudinally along efferent ctenidial axis. Presence of bursicle marked by dorsally expanded knob and deep ciliated groove (Figs. 47 a, b). Inside of bursicle with pocket lumen, heavily ciliated with long (7–8 μm) simple cilia (Fig. 47 d). Exit of pocket lumen visible from dorsal side as vertical slit. On sides of ctenidial filament, ciliated micropapillae (ca. 20 μm in diameter) occurring be-
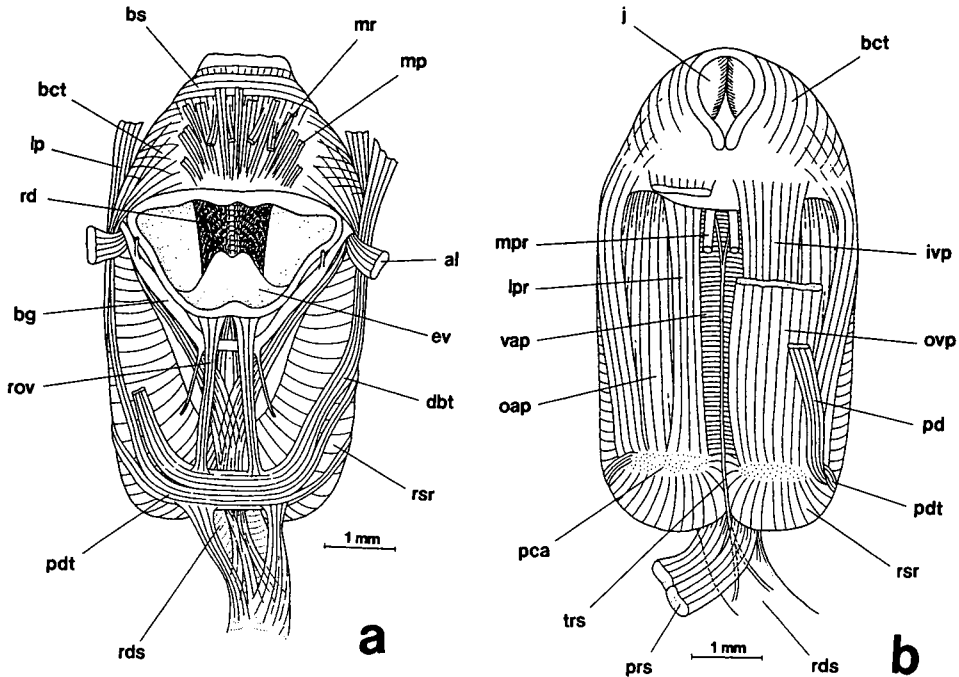
Fig. 48. *Turbo (Marmarostoma) stenogyrum.* a, Dorsal view of buccal mass after removal of the esophagus. b, Ventral view of buccal mass. Some muscles of left side are removed to show the inner part.

neath strip of lateral cilia (Figs. 47 e, f).

Osphradium covering free position of efferent ctenidial axis. Paired hypobranchial glands on pallial roof on either side of rectum. Right gland (rhg) much smaller than left gland. Left gland (lhg) intersected by transverse pallial vessel dorsally.

Digestive System: Oral tube surrounded by buccal sphincter (bs) and constrictor (bct) with mandibular protractors (mp) and retractors (mr). Movement of odontophore controlled by lateral protractors (lp), inner and outer ventral protractors (ovp, ivp), anterior levators (al), and posterior depressors (pd) (Figs. 48 a, b). Posterior levators absent. Right and left sides tightly held by postdorsal buccal tensor (pdt) and dorsal buccal tensors (dbt).

Jaws (j) divided into symmetrical pairs on dorsal side of oral tube. Anterior edge fimbriate, projecting into oral cavity.

Radular sac forming coiled loops behind buccal mass, posterior end clearly bifurcated. Radular formula n−5−1−5−n. Radular tooth row symmetrical. Central tooth subrectangular, plate-like, with indistinct cusp. Inner four lateral teeth slender with reduced cusps and outward projection at bases. Outermost laterals spatulate, almost straight without basal projection. Bases of laterals overlapping from inner to outer teeth. Protolateromarginal plates not well-developed. Inner marginals prominently elongated, but outer teeth gradually diminishing in size.

Manipulation of radula controlled by median and lateral protractors of subradular membrane (mpr, lpr), retractors of subradular membrane (rsr), retractors of radular sac (rrs), and postmedian retractors of radular sac (prs) (Fig. 48 b). Radular sac connected to sublingual pouch ventrally by tensor muscle (trs) which arises from space between paired postmedian retractors (prs).

Buccal mass containing two pairs of cartilages. Anterior cartilages elongated, connected to ventral ap-

proximator. Posterior cartilages small, extending laterally. Both cartilages united longitudinally by outer ap-
proximators.

Sublingual pouch shallow without glandular outgrowth. Radular diverticulum present. Buccal cavity
overlain directly by salivary glands without ducts, followed by large esophageal pouches overlapping pos-
terior part of buccal mass. Mid-esophagus long, gradually reduced in width posteriorly. Dorsal and ventral
folds clearly formed within it. Inner wall covered with papillate esophageal glands except in dorsal food
channel. Posterior esophagus short.

Stomach bent, divided into small proximal and large distal sacs. Posterior apex of stomach with promi-
nent spiral caecum (gc) visible from surface of visceral hump (Fig. 46 b). Distal portion including openings
of digestive glands, toothed gastric shield, paired typhlosoles, and intestinal groove. Corrugated pattern of
sorting area visible from exterior. Intestine coiling complexly with single anterior loop. Rectum penetrating
ventricle, running along pallial roof, opening anteriorly.

Circulatory System: Pericardium within visceral hump along posterior limit of pallial cavity (Figs. 46 a,
b) containing paired auricles and median ventricle. Right auricle (ra) narrowly elongated; left auricle (la)
well inflated. Aortae bifurcated within pericardium without forming bulbous aorta.

Anterior aorta running along efferent ctenidial vessel on pallial wall, entering head region. Posterior
aorta passing within digestive glands.

Blood from right kidney draining posteriorly into left afferent renal vein (arv), anteriorly into transverse
pallial vessel (tpv) penetrating left hypobranchial gland, reaching afferent axis of ctenidium. Afferent cteni-
dial vessel (acv) supplying blood to afferent side of ctenidial lamellae, also giving rise to branch into ante-
rior pallial vessel (apv) along margin of afferent ctenidial membrane (acm). Blood from ctenidial lamellae
and mantle skirt entering efferent ctenidial vessel (ecv), leading to ventricle. Efferent renal vessel also en-
tering ventricle from left posterior end of left kidney.

Excretory System: Excretory system consisting of right and left kidneys (Figs. 46 a, b). Right kidney
(rk) within visceral hump, also extending to right side of anterior visceral region over mid-esophagus; inner
wall lamellate. Right kidney opening short papilla. Left kidney (lk) occurring dorsally within pallial cavity,
inner wall papillate. Left kidney opening represented by longitudinal slit.

Reproductive System: Gonad (g) on dorsal side of digestive glands (Figs. 46 a, b), when ripe, reaching
posterior margin of right kidney. Gonoducts connected to right kidney, but relationship with renopericardial
duct not identified. Sexes distinguished by external appearance. Ovary clearly granular; testis exhibiting un-
clear granulation.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia at bases of cephalic tenta-
cles; pleural and pedal ganglia on posteroventral sides of buccal mass. Cerebral commissure overlapping
frontal margin of buccal cavity. Labial ganglia and labial commissure absent. Buccal ganglia connected to
ventral extension of cerebral ganglia.

Paired pleural ganglia sending nerves to outer sides of body musculature including columellar muscle. In
left anterior pallial wall, nerves from supraesophageal to osphradioctenidial ganglia united by distinct
nerves of zeugoneury from anterior pallial nerve. Visceral loop originating from right and left pleural gan-
glia, elongated along pallial cavity wall. Differentiation of supraesophageal and subesophageal ganglia not
very apparent. Pedal cords well developed with commissures. Statocysts on anterior dorsal sides of pedal
ganglia.

Turbinidae gen. et sp.

(Figs. 49 a-f)

Protoconch: Protoconch paucispiral, planispiral. Lateral pouch not clearly formed. Suture of protoconch
short, clear. Sculpture consisting of discontinuous spiral thread and zigzag ridge-like deposits both of which
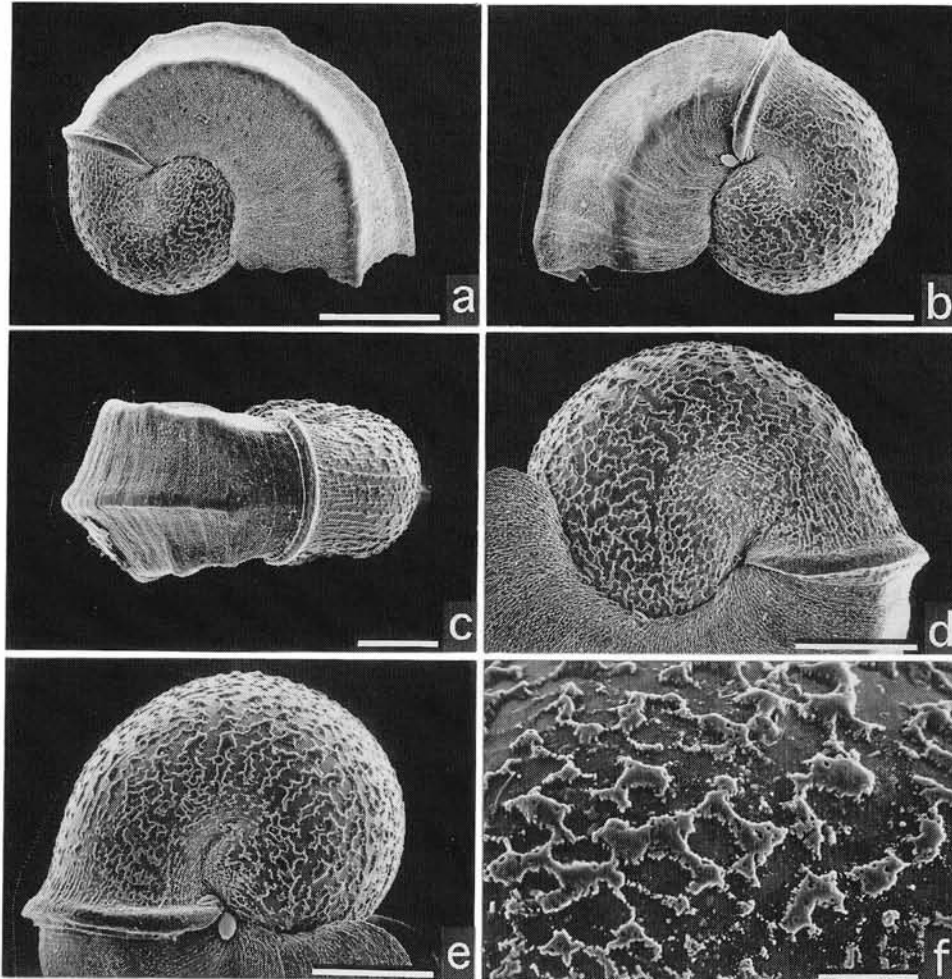
Fig. 49. Protoconch of Turbinidae gen. et sp. RM 27648. **a**, Apical view of juvenile shell. Scale=200 μm. **b**, Basal view of juvenile shell. Scale=100 μm. **c**, Dorsal view of juvenile shell. Scale=100 μm. **d**, Apical view of protoconch. Scale=100 μm. **e**, Basal view of juvenile shell. Scale=100 μm. **f**, Sculpture of apical side of protoconch. Scale=25 μm.

partly anastomose to form reticulate pattern; interspace powdered with minute grains. Sculpture of central area finer than that of periphery both on apical and basal sides. Protoconch-teleoconch boundary clearly demarcated by prominent axial ridge.

Homalopoma nocturnum (Gould, 1861)
(Figs. 50 a-d)

Protoconch: Protoconch paucispiral, almost planispiral, slightly hyperstrophic. Lateral pouch not inflated; constriction of suture producing shallow depression. Outer surface ornamented with fine irregular microtubercles that aggregate to construct axial sculpture. Fine striae also formed in radial direction on both apical and basal sides. Protoconch-teleoconch boundary marked by constriction.
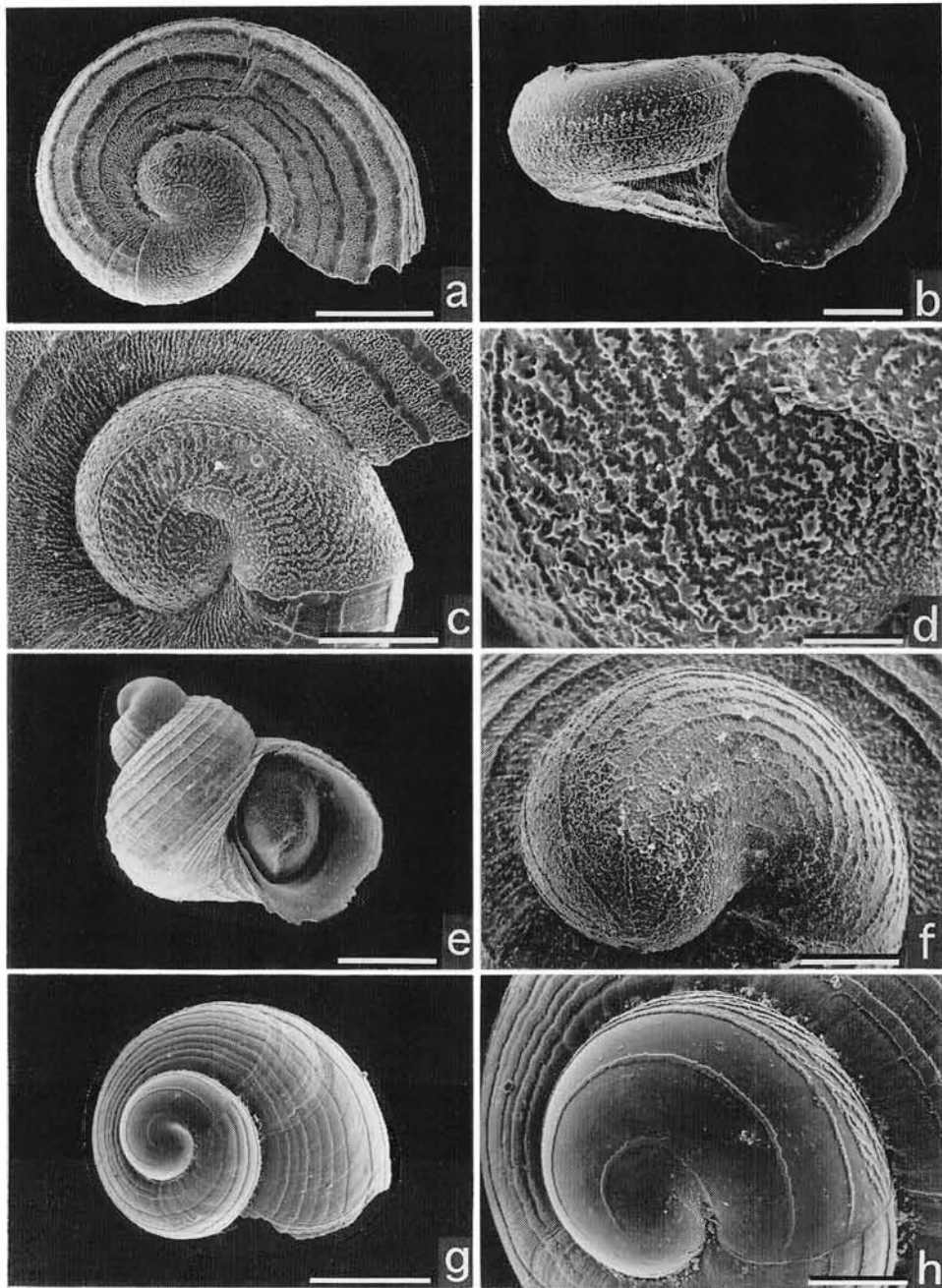
Fig. 50. Protoconch of Turbinidae. **a-d**, *Homalopoma nocturnum*. **a**, RM 27649. **b-d**, RM 27650. **a**, Apical view of juvenile shell. Scale = 200 μm. **b**, Ventral view of juvenile shell. Scale = 100 μm. **c**, Apical view of protoconch. Scale = 100 μm. **d**, Sculpture of protoconch. Scales = 25 μm. **e-f**, *Tricolia* sp. RM 27651. **e**, Ventral view of juvenile shell. Scale = 250 μm. **f**, The apical view of protoconch. Scale = 50 μm. **g-h**, *Tricolia megastoma*. RM 27652. **g**, Apical view of juvenile shell. Scale = 300 μm. **h**, Apical view of protoconch. Scale = 80 μm.

Tricolia sp.
(Figs. 50 e-f)

Protoconch: Protoconch oblong, conispirally coiled. Extension of lateral pouch indistinct. Suture marked by shallow constriction occurring inside apertural area. Protoconch sculptured by clear spiral ridges; number initially five, increasing with growth, attaining ten at protoconch aperture. Interspace of ridges forming reticulation with ridge-like deposits and round pit-like depressions. Apertural margin of protoconch weakly thickened, clearly distinguished from spiral cords of early teleoconch.

Tricolia megastoma (Pilsbry, 1895)
(Figs. 50 g-h)

Protoconch: Protoconch discoidal, paucispiral, well-inflated. Lateral pouch on apical side not prominent. Coiling direction orthostrophic in both protoconch and teleoconch. Sculpture showing very characteristic pattern of three distinct spiral ridges in peripheral margin. Each ridge gradually bifurcating, obliquely directing toward outer periphery. Interspace between two ridges totally smooth even at high magnification. Protoconch-teleoconch boundary delimited by simple axial line.

Family Trochidae Rafinesque, 1815
Chlorostoma lischkei (Tapparone-Canefri, 1874)
(Figs. 51 a-b, 52 a-b, 53 a-e)

External Anatomy: Visceral hump spirally coiled in 2.5 volutions. Mantle margin (mm) simple, lacking microtentacles. Columellar muscle (cm) longitudinally elongated, narrowly restricted to columellar side.

Head with short snout, cephalic lappets, cephalic tentacles, and eyestalks. Outer lip of mouth thickened, forming circular oral disk. Cephalic lappets transversely elongated, divided into distinct pairs. Eyestalks on posterior sides of cephalic tentacles. Eyes opening externally. Neck lobes present on inhalant (left) and exhalant (right) sides.

Epipodium provided with four pairs of very long epipodial tentacles (ept) extensible over periphery of body whorl. Surface of tentacles papillate with ciliary crown. Base of each tentacle with knobby projection on which epipodial sense organ lies. Multispiral corneous operculum on epipodium.

Pallial Complex: Pallial cavity reaching more than one-half volution of body whorl, containing left ctenidium with osphradium, paired kidney openings, anus, and paired hypobranchial glands (Figs. 51 a, b).

Ctenidium (c) bipectinate, long, extending along left wall of pallial cavity. Efferent (left) side supported by long efferent ctenidial membrane except anterior free portion; afferent side suspended by afferent membrane, attached to mantle skirt along left margin of hypobranchial glands.

Afferent and efferent axes include afferent and efferent ctenidial vessels, also paired retractor muscles and median nerve. Efferent side of anterior free portion stiffened by skeletal rods that are distinguished by reddish staining in histological sections.

Ctenidial lamellae depressed in form like acute-angled triangle; apex of lamellae directed and projected to afferent side. Surface with frontal, abfrontal, and lateral cilia. Efferent side of lamellae supported by paired skeletal rods. Bursicles prominent on efferent side of lamellae. Osphradium on outer surface of anterior free portion of efferent axis.

Hypobranchial glands paired, extremely unequal in size. Right gland (rhg) elongated along rectum. Left gland (lhg) extending in posterior median direction, contacting anterior part of left kidney. Transverse pallial vein running below left gland.

Digestive System: Oral tube surrounded by buccal sphincter (bs) and constrictor (bct) with mandibular protractors (mp) and retractors (mr). Odontophore fixed by lateral protractors (lp), outer and inner ventral protractors (ovp, ivp), anterior levators (al), posterior levators (pl), and posterior depressors (pd) (Figs. 52 a,
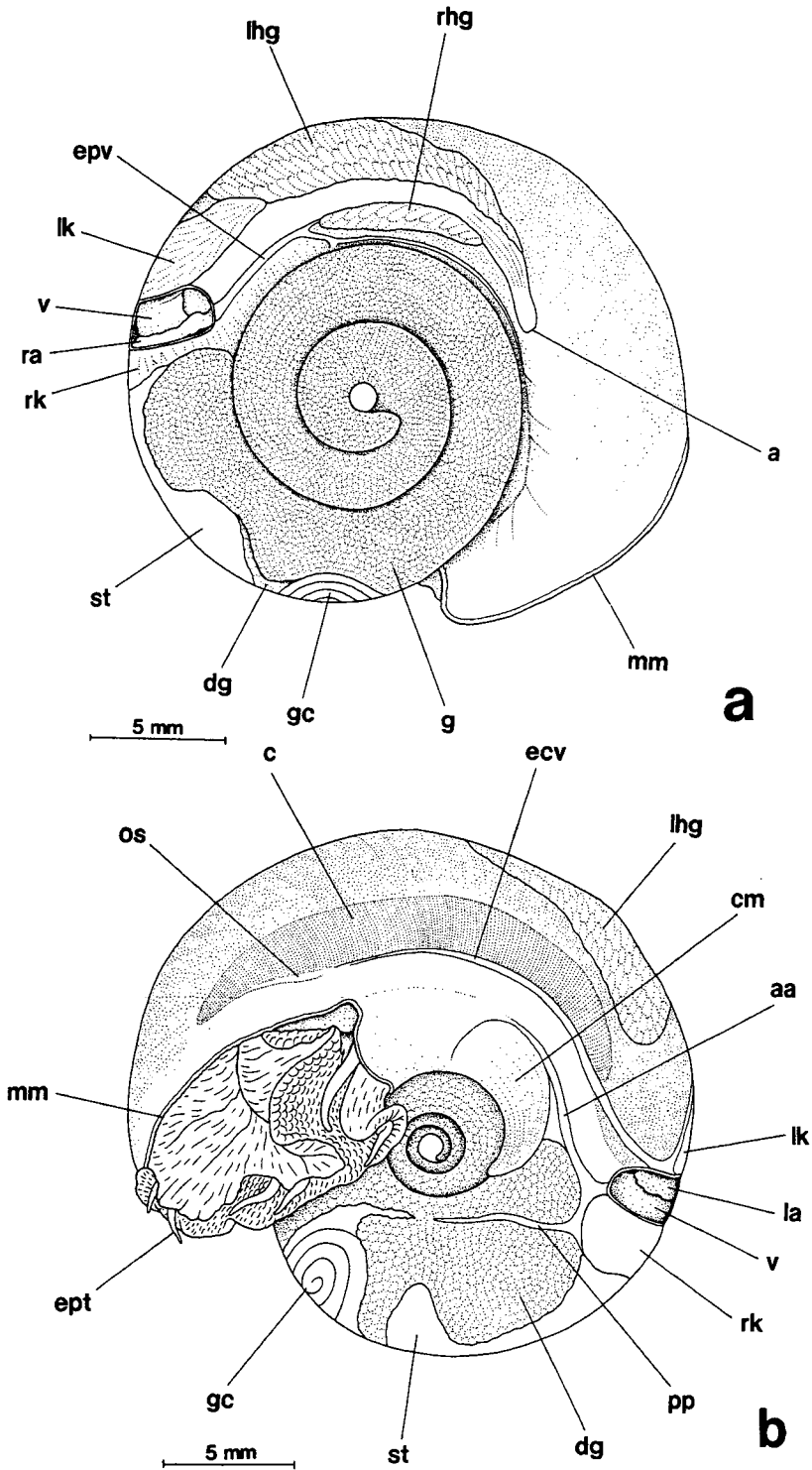
Fig. 51. *Chlorostoma lischkei*. **a**, Apical view of the animal after shell removed. **b**, Basal view of the animal.
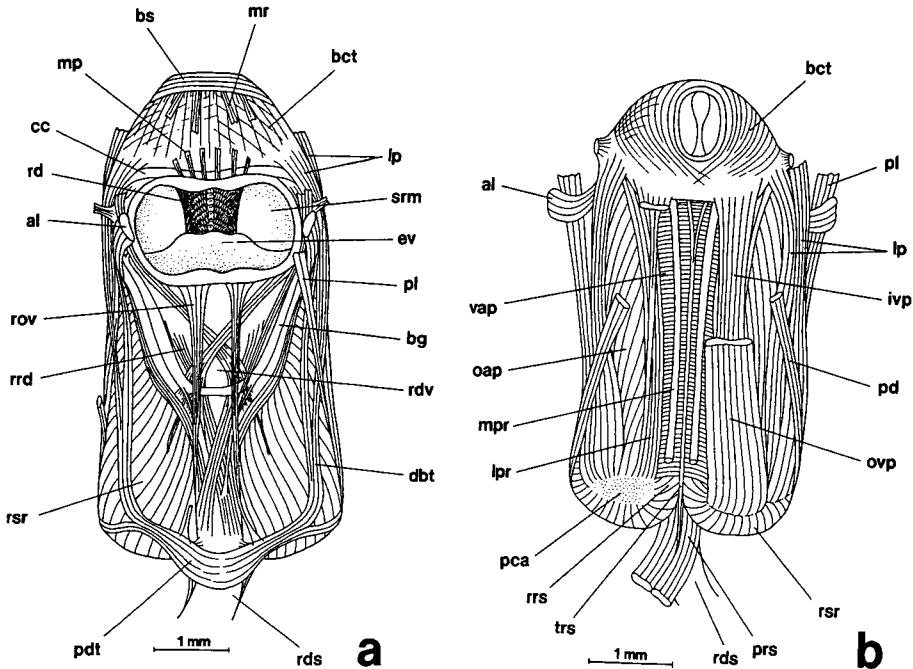
Fig. 52. *Chlorostoma lischkei*. **a**, Dorsal view of the buccal mass after removal of the esophagus. **b**, Ventral view of the buccal mass. Some muscles on left side are removed to show the inner part.

b). Posterior side of odontophore bound by postdorsal buccal (pdt) and dorsal buccal tensors (dbt).

Jaws paired, subtrapezoid, thin, nearly entirely attached to wall of oral tube. Anterior margin and inner surface totally smooth (Fig. 53 c).

Radular sac forming loops with few volutions on right ventral side of mid-esophagus. Posterior end clearly bifurcated. Radular formula n–5–1–5–n. Tooth row symmetrical. Central tooth subrectangular, plate-like, with lateral extensions and slightly reflected cusp. Lateral teeth with keeled shafts and acute cusps; bases with prominent outward projection and intimate articulation with each other. Protolateromarginal plates smoothly extended from bases of innermost marginals. Marginal teeth all very long; cusps with weak median ridge and serration on outer side.

Subradular membrane attached by median and lateral protractors (mpr, lpr) on anterior side and by retractors (rsr) on lateral and posterior sides (Fig. 52 b). Radular sac ventrally inserted by retractors (rrs) and postmedian retractors (prs). Tensor of radular sac (trs) running from dorsal side of sublingual pouch to ventral side of radular sac between paired postmedian retractors (prs).

Odontophore containing two pairs of cartilages (Figs. 53 a, b). Anterior cartilages (aca) longitudinally elongated, posterior cartilages (pca) transversely extended. Ventral sides of anterior cartilages connected by single-layered ventral approximator along length. Anterior and posterior pairs united by outer approximators (oap).

Sublingual pouch shallow, lacking glandular projection. Licker smooth on anterior end of subradular membrane. Radular diverticulum present. Salivary glands without well-developed ducts over dorsal surface of buccal cavity, partly overlapping dorsal food channel.

Dorsal food channel well-inflated, merging into mid-esophagus. Initial part of mid-esophagus (me) enlarged by esophageal pouches. Inside of mid-esophagus entirely covered by papillate glandular epithelium
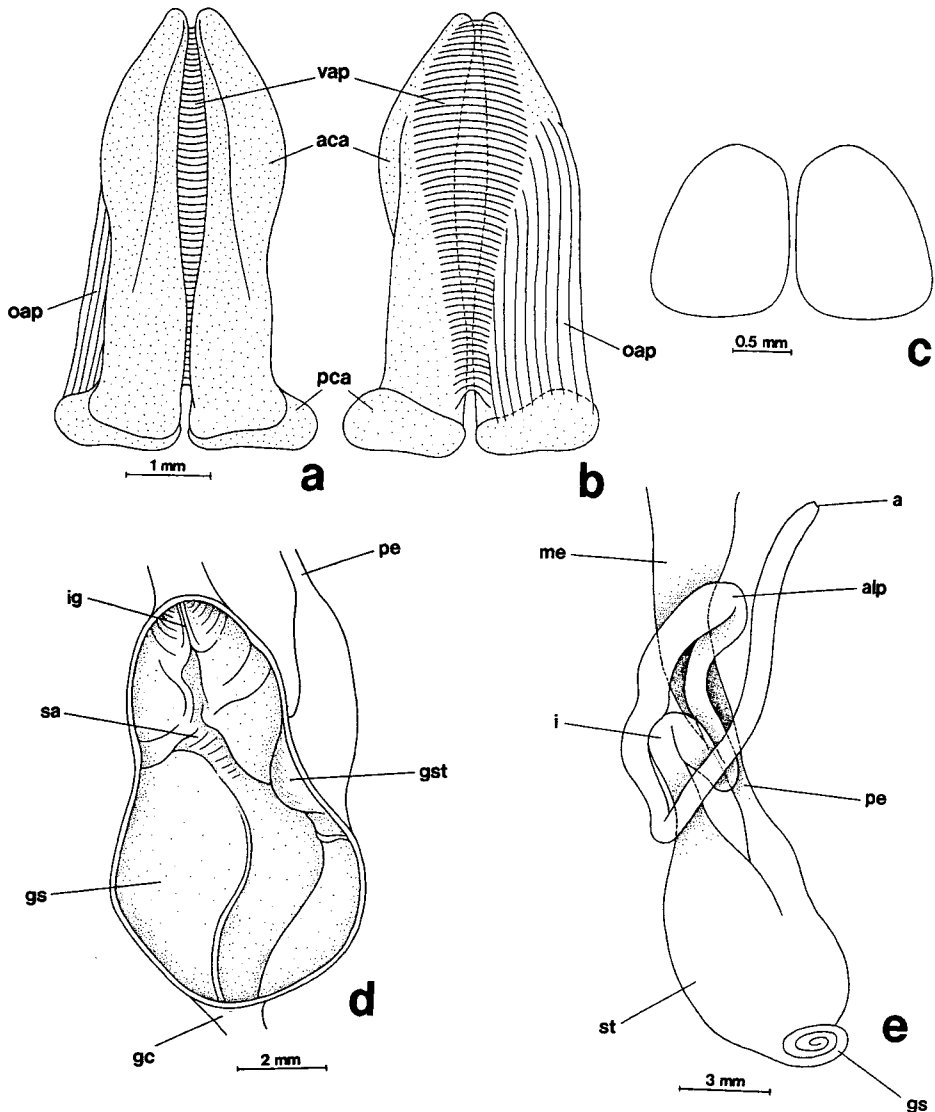
Fig. 53.   *Chlorostoma lischkei*. **a**, Dorsal view of the odontophoral cartilages. Right outer approximator muscle is removed. **b**, Ventral view of the odontophoral cartilages. **c**, Ventral view of the jaws. **d**, Internal structure of the stomach. **e**, Configuration of the post-buccal alimentary tract.

except in ciliated zone between paired dorsal and ventral folds. Posterior esophagus (pe) formed by constriction of mid-esophagus; inner surface longitudinally corrugate.

Stomach (st) large, well-expanded (Fig. 53 e), strongly bent in V-shape, divided into right proximal and left distal parts. Both ventral and dorsal surfaces of stomach covered by digestive glands (dg); lateral wall of distal parts widely exposed on surface of visceral hump (Figs. 51 a, b). Posterior apex giving rise to spiral gastric caecum (gc) consisting of three volutions. Inside of proximal part mainly occupied by smoothly cuticularized gastric shield (gs) (Fig. 53 d). Tooth of gastric shield (gst) on dorsal side of openings of esophagus and digestive glands. Sorting area (sa) weakly developed in median area. Typhlosoles and intestinal groove (ig) well-defined in distal end of stomach.

Intestine (i) forming single anterior loop on right side (Fig. 53 e). Rectum penetrating pericardium and ventricle, running on roof of pallial cavity between paired kidneys and hypobranchial glands.

Circulatory System: Pericardium lying transversely along posterior wall of pallial cavity, containing paired asymmetrical auricles and single ventricle (Figs. 51 a, b). Right auricle (ra) thinly elongated on right dorsal side. Left auricle (la) on left ventral side larger than right one. Right auricle receiving blood only from efferent pallial vein; left auricle connecting efferent ctenidial vessel and efferent renal vein.

Excretory System: Excretory system consisting of paired kidneys of different form and histology (Figs. 51 a-b). Right kidney (rk) lying posterior to pericardium on dorsal surface, also extending internally toward anterior right visceral region. Right kidney opening projecting as short papilla. Left kidney (lk) entirely lying in pallial cavity, internally exhibiting condition of so-called papillary sac; left kidney opening represented by longitudinal short slit. Renopericardial ducts paired.

Reproductive System: Gonochoristic gonad (g) lying over digestive glands, extending over stomach and part of right kidney when ripe (Fig. 51 a). Gonoduct running inner columellar side, opening into right kidney. Gametes discharged into pallial cavity through right excretory pore.

Nervous System: Circumesophageal nerve ring hypoathroid. Labial region innervated by several nerves from cerebral ganglia, lacking distinct labial commissure and ganglion. Visceral loop arising from right and left pleural ganglia. Left nerve from supraesophageal to osphradioctenidial ganglia connected by nerve from left pleural ganglion (zeugoneury). Pedal cords scaraliform. Statocysts on anterior part of pedal ganglia.

Chlorostoma. sp.
(Figs. 54 a-c)

Protoconch: Protoconch coiled in slightly hyperstrophic direction with about 1.25 volutions. Lateral pouch insignificant on apical side, with unclear suture. Basal side weakly inflated, with lateral pouch forming ventral extension. Protoconch surface totally covered with reticulate sculpture that is denser in apical and basal regions than at periphery. Protoconch-teleoconch boundary marked by thin axial rib followed by few spiral cords of early teleoconch.

Euchelus pauperculus (Lischke, 1872)
(Figs. 54 d-f)

Protoconch: Protoconch planispirally coiled, discoidal. Extension of lateral pouch inconspicuous. Outer surface of protoconch sculptured by irregular ridge-like deposits showing reticulate pattern. Interspaces of ridges finely granulated. Protoconch-teleoconch boundary delimited by gently convex rim of protoconch aperture.

Stomatia phymotis Helbling, 1779
(Figs. 55, 56 a-b)

External Anatomy: Animal much larger than shell, incapable of retracting completely. Visceral hump with only small spiral tip inside shell apex. Mantle margin fringed by irregularly-shaped microtentacles. Shell muscle (sm) horseshoe-shaped, completely continued posteriorly by thin, filmy muscles below visceral hump. Both terminal parts of muscle enlarged, not divided by blood vessel penetration.

Head with slightly tapering snout, cephalic lappets, cephalic tentacles, eyestalks. Outer lip of mouth weakly developed, lacking micropapillae and oral lappets (Fig. 55). Cephalic lappets (clp) isolated as independent pair, finely fringed. Cephalic tentacles (ct) thinner than well-developed eyestalks. Surface of cephalic tentacles papillate. Eyestalks totally free from papillae. Eyes (e) open with vitreous body inside. Neck region extending to form broad neck lobes (nl) on both left and right sides; exhalant side connected
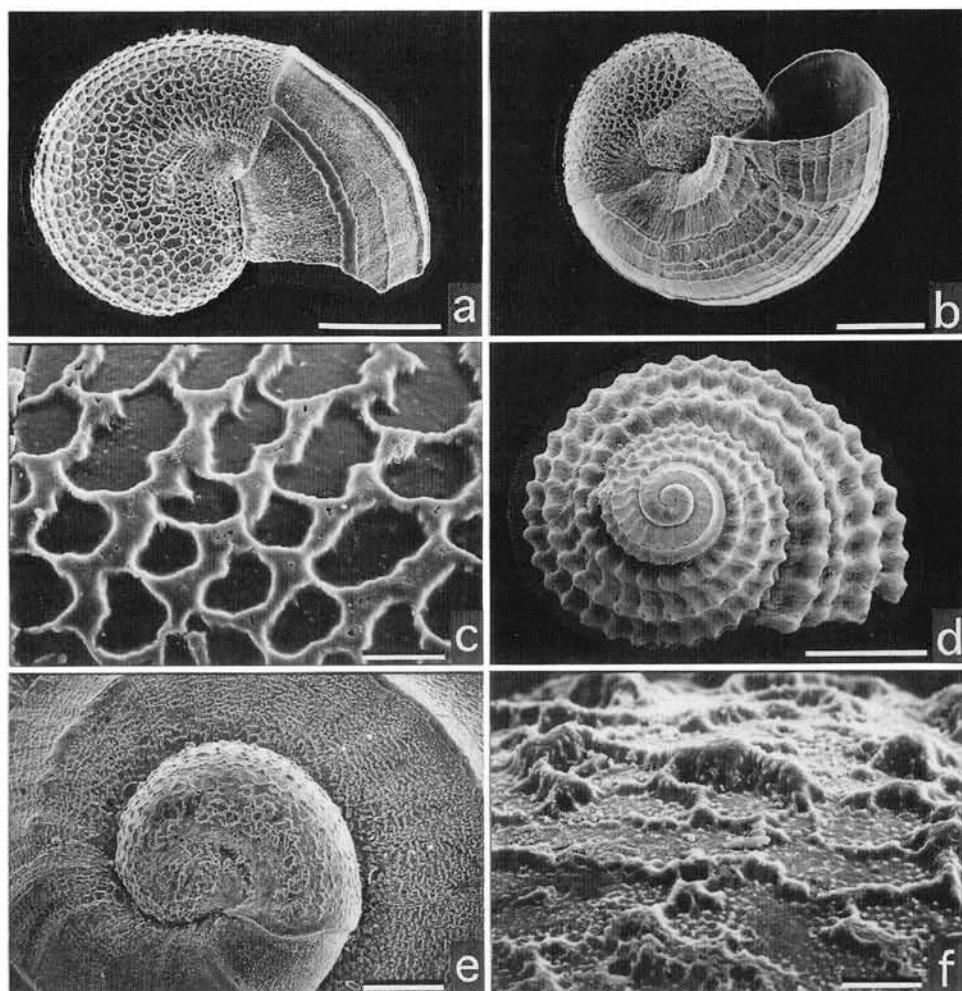
Fig. 54. Protoconch of Trochidae. **a-c**, *Chlorostoma* sp. RM 27654. **a**, Apical view of early juvenile shell. Scale = 100 µm. **b**, Basal view of juvenile shell. Scale = 100 µm. **c**, Sculpture of protoconch. Scale = 10 µm. **d-f**. *Euchelus pauperculus*. RM 27655. **d**, Apical view of subadult shell. Scale = 1 mm. **e**, Apical view of protoconch. Scale = 100 µm. **f**, Sculpture of protoconch. Scales = 10 µm.

with bases of eyestalks, enrolled to create siphonal structure.

Foot greatly hypertrophied relative to shell size. Top of propodium divided by median cleft into right and left lobes below head. Metapodium detachable by autotomy when animal is threatened. Autotomy line (fal) visible on exterior surface in fixed specimen (Fig. 55). Epipodium entirely covered by spinous protrusions, but relationship to typical epipodial tentacles unclear. In living condition, several (probably four) relatively large dendritic tentacles protruding on epipodium; knobby structures at bases probably functioning as epipodial sense organs. Operculum absent.

Pallial Complex: Pallial cavity half as deep as postcephalic visceral region, containing left ctenidium with osphradium, paired kidney openings, anus, and paired hypobranchial glands (Fig. 55).

Ctenidium bipectinate, crossing pallial cavity obliquely from posterior left to anterior right side. Efferent side connected to shell muscle by long efferent membrane (ecm); afferent side suspended from mantle skirt
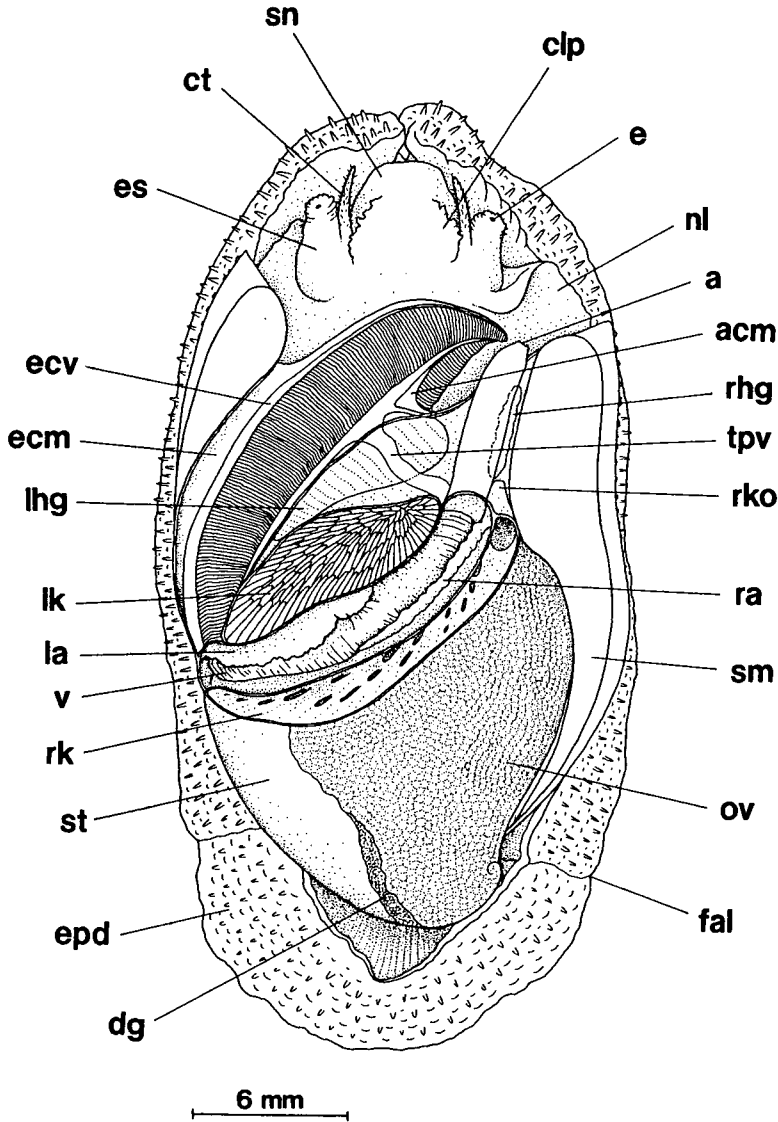
Fig. 55. *Stomatia phymotis*. Dorsal view of the animal after removal of the shell and mantle.

by short afferent membrane (acm).

Ctenidial lamellae dorsoventrally depressed. Ventral lamellae wider than dorsal lamellae. Right edge of ventral lamellae partly extended, visible in dorsal view (Fig. 55). Both lamellae provided with row of bursicles near efferent ctenidial axis. Lamellae supported by skeletal rods on efferent side. Afferent membrane penetrated by transverse and anterior pallial veins (tpv, apv). Efferent axis of anterior free portion covered by osphradium.

Left hypobranchial gland (lhg) lying on mantle skirt in right portion of ctenidium, intersected dorsally by transverse pallial vessel. Right hypobranchial gland (rhg) attaching to right side of pallial section of rectum, greatly reduced into narrow strip.

Digestive System: Composition of oral, odontophoral, and radular muscles as those in *Chlorostoma*.
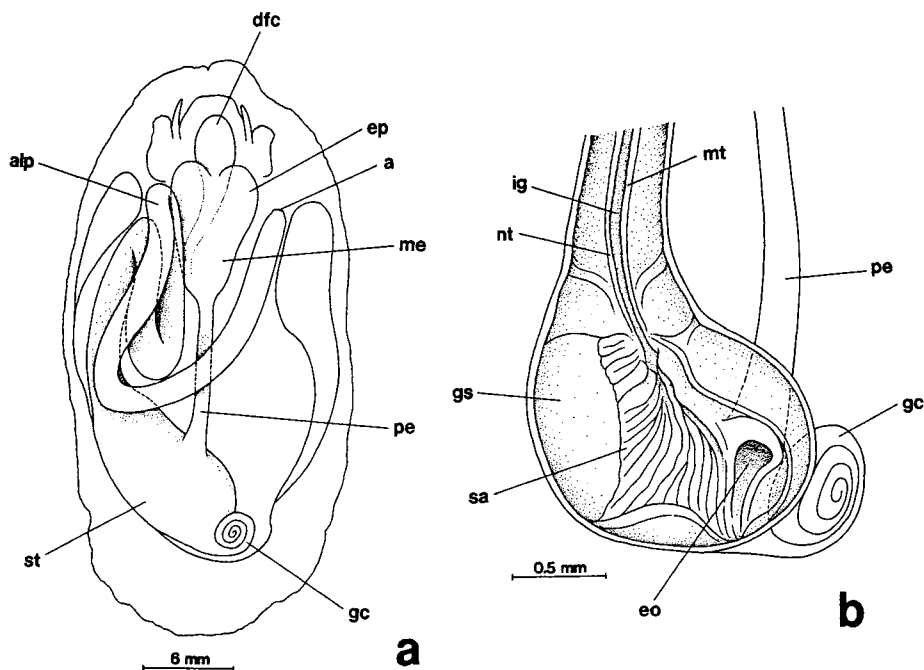
Fig. 56. *Stomatia phymotis*. **a**, Configuration of the alimentary tract. **b**, Internal structure of the stomach.

Postdorsal buccal tensor (pdt) and dorsal buccal tensors (dbt) present. Postmedian retractors (prs) and thin tensor muscle (trs) inserting on ventral side of radular sac. Jaws paired in oral tube. Anterior margin simple. Odontophoral cartilages consisting of longer anterior and shorter posterior pairs, united by ventral and outer approximator muscles.

Radular sac bifurcated at posterior end. Radular formula n−5−1−5−n. Tooth row symmetrical. Central tooth with short shaft, distinctly serrated cusp, and base forming broad and rounded lateral extensions. Inner four laterals with broad cusps with outer serration and enlarged bases with smooth outward extension. Outermost laterals similar to inner teeth in cusp morphology, but shaft straight without extension. Bases of all laterals overlapping. Protolateromarginal plates smooth, well-developed. Marginal teeth elongated with deep food groove below serrated cusps.

Sublingual pouch shallow, simple. Licker smooth. Radular diverticulum present. Salivary glands over buccal pouch, opening though longitudinal slits. Esophageal pouches (ep) enlarged on posterior side of buccal mass. Inner wall of mid-esophagus (me) papillate; dorsal and ventral folds twisted counterclockwise interiorly. Mid-esophagus constricted, followed by posterior esophagus (pe). Stomach (st) well-inflated, unfolded (Fig. 56 a); esophagus and ducts of digestive glands opening on right posterior side (Fig. 56 b); posterior apex giving rise to spiral gastric caecum (gc) with more than three volutions. Tooth of gastric shield on dorsal side of esophageal opening. Sorting area (sa) well-developed ventrally. Major and minor typhlosoles (mt, nt) continuing from posterior part of stomach into intestine. Intestine (i) bent four times to form two anterior loops on left side of mid-esophagus; rectum penetrating pericardium and ventricle; anus (a) opening beside right anterior rim of shell muscle.

Circulatory System: Pericardium extending along border of pallial cavity and visceral hump between paired kidneys (Fig. 55). Heart consisting of asymmetrically paired auricles and median ventricle. Right auricle (ra) extremely elongated along pericardial wall, connected to efferent pallial vessel through narrow part of anterior end. Outlet to ventricle opening from left anterior side. Left auricle (la) more developed

than right one. Irregular margin of filtration chamber well-developed. Connection with ventricle arising from right side. Ventricle (v) greatly elongated throughout pericardium. Aorta bifurcating into anterior and posterior aortae without forming distinct bulbous aorta at their dividing point. Transverse pallial vessel (tpv) very clearly crossing left hypobranchial gland from right kidney to afferent ctenidial vessel.

Excretory System: Excretory system consisting of two kidneys (Fig. 55). Right kidney (rk) narrowly elongated along posterior margin of pericardium, extending ventrally to right anterior visceral region; lumen spacious; lamellate wall irregularly fenestrated. Right kidney opening (rko) projecting as short papilla. Left kidney (lk) lying within pallial cavity; lumen densely filled with long spicular papillae (Fig. 55). Left kidney opening simple short slit.

Reproductive System: Gonochoristic gonad lying on dorsal side of digestive glands (Fig. 55). At maturity, gonad also extending over stomach. In dissected specimens, gonoduct not distinct, but well developed gonad directly reaching anterior section of right kidney. Urogenital papilla not well differentiated in female.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral commissure running over dorsal food channel. Labial ganglia and commissure absent. Visceral loop arising from right and left pleural ganglia. Statocysts on anterodorsal margin of pedal ganglia.

Broderipia iridescens (Broderip, 1834)
(Figs. 57 a-b, 58 a-f, 59 a-d)
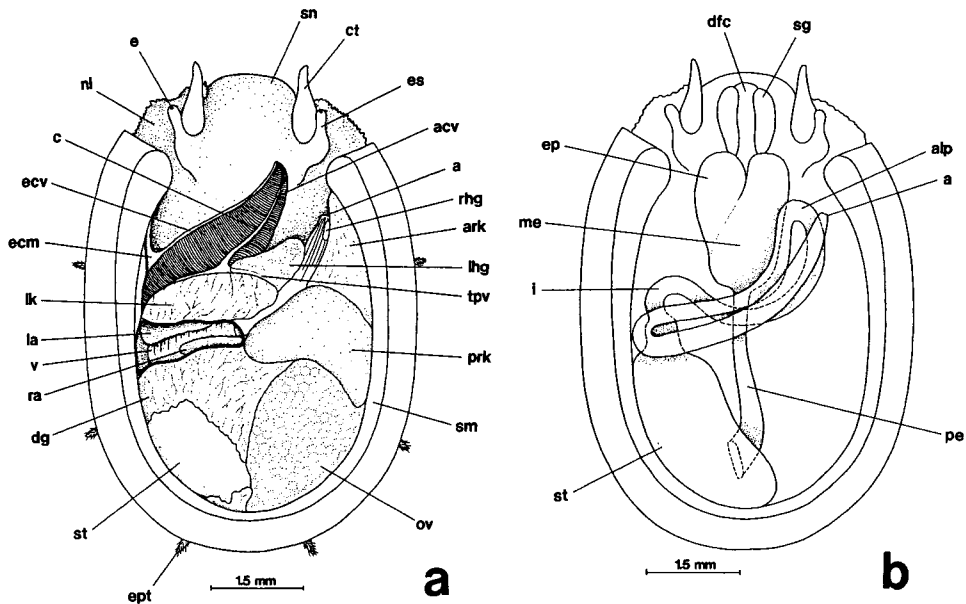
Fig. 57. *Broderipia iridescens*. **a**, Dorsal view of the animal after removal of the mantle. **b**, Configuration of the alimentary tract.

Protoconch: Protoconch trochispiral, longitudinally elongate, well-inflated (Figs. 59 b-c). Surface of protoconch covered by characteristic reticulation, divided into four distinct zones in apical area. Lateral pouch of apical side with fine reticulate ridge sculpture.

External Anatomy: Soft parts completely limpet-form without spiral visceral hump. Mantle margin lacking specific sensory tentacles. Shell muscle (sm) horseshoe-shaped, not divided into bundles.

Head with snout (sn) and pair of papillate cephalic tentacles (ct), lacking cephalic lappets between ce-
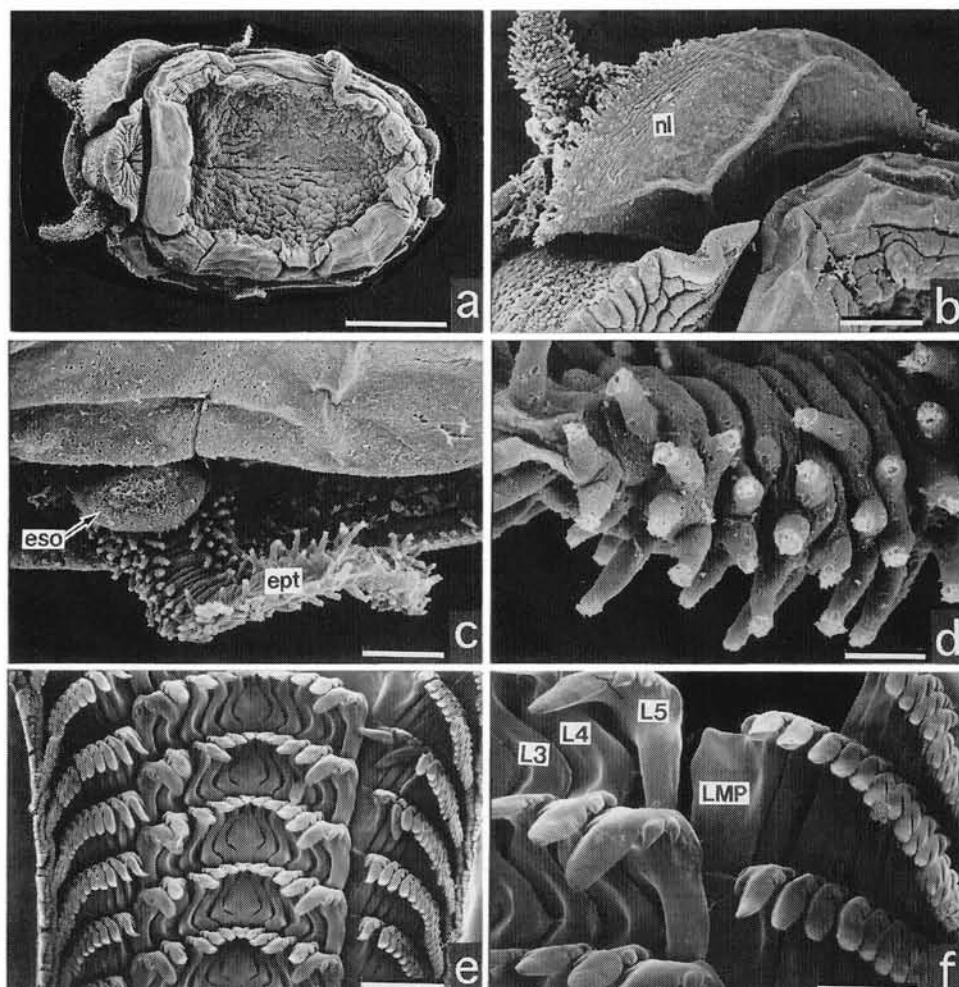
Fig. 58.   *Broderipia iridescens*. SEM micrographs of soft parts. **a-d**, RM 27657. **e-f**, RM 27658. **a**, Ventral
view of whole animal. Scale = 1 mm. **b**, Left neck lobe. Scale = 250 μm. **c**, Epipodial tentacle and
sense organ. Scale = 100 μm. **d**, Enlarged view of micropaillae on epipodial tentacle. Scale = 20 μm. **e**,
Whole row of radular teeth. Scale = 50 μm. **f**, Transitional area between lateral and marginal teeth,
showing protolateromarginal plate. Scale = 25 μm.

phalic tentacles. Outer lip of mouth thickened into oral disk, without microtentacles (Fig. 58 a). Surface of
snout weakly papillate. Neck region with inhalant (left) and exhalant (right) neck lobes (nl), both slightly
papillate with ciliary crown (Fig. 58 b). Eyes (e) open at tip of eyestalks.

Foot sole marked by weak mid-ventral cleft. Epipodium in pallial groove provided with three pairs of
epipodial tentacles (ept): two lateral, one posterior near midline (Fig. 58 a). Cephalic and epipodial tenta-
cles bearing dense rows of ciliated microtentacles (Fig. 58 d). Base of each epipodial tentacle with large,
knob-shaped epipodial sense organ (eso) (Fig. 58 c). Foot autotomy line and operculum absent.

Pallial Complex: Pallial cavity reaching one-half body length, containing left ctenidium with osphra-
dium, paired kidney openings, and paired hypobranchial glands (Fig. 57 a).

Ctenidium bipectinate, dorsoventrally depressed. Efferent ctenidial membrane (ecm) barely evident
along inner side of shell muscle. Afferent membrane reduced. Dorsal ctenidial lamellae narrower than ven-
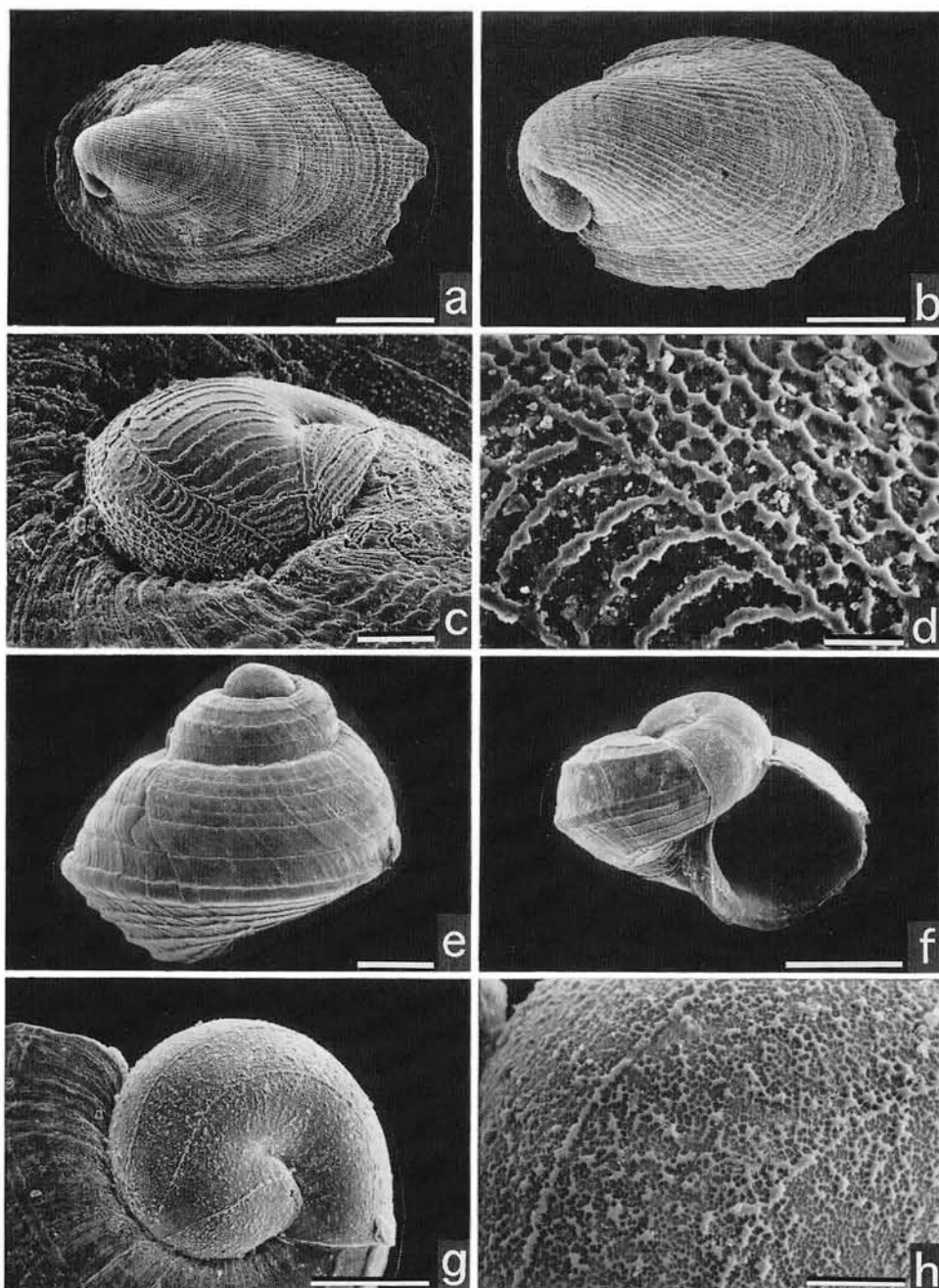
Fig. 59. Protoconch of Trochidae. *Broderipia iridescens*. **a**, **c-d**, RM 27659. **b**, RM 27660. **a**, Dorsal view of juvenile shell. Scale=500 μm. **b**, Dorsal view of early juvenile shell. Scale=250 μm. **c**, Enlarged view of protoconch. Scale=50 μm. **d**, Sculpture of peripheral side of protoconch. Scale=10 μm. **e-h**, *Cantharidus* sp. cf. *callichroa*. **e-f**, RM 27661. **g-h**, RM 27662. **e**, Dorsal view of juvenile shell. Scale=250 μm. **f**, Ventral view of juvenile shell. Scale=200 μm. **g**, Apical view of protoconch. Scale=100 μm. **h**, Sculpture of protoconch. Scale=25 μm.

tral lamellae, so that extended part of ventral lamellae visible on right side. Both lamellae with bursicles on efferent side. Lamellae and efferent free axis supported by skeletal rods. Osphradium lying on efferent free axis.

Hypobranchial glands paired, not well-developed. Right gland (rhg) greatly reduced, situated on right side of rectum near anus. Left gland (lhg) larger than right, lying far removed from right gland on pallial roof, contacting left side of rectum and anterior margin of left kidney posteriorly.

Digestive System: Composition of oral, odontophoral, and radular muscles identical to that in *Chlorostoma*. Postdorsal buccal tensor and dorsal buccal tensors present. Postmedian retractors and tensor muscle inserting on ventral side of radular sac.

Jaws divided into paired plates, distinguished by dark color on oral tube, anterior margin smooth. Odontophoral cartilages consisting of elongated anterior and nodular small posterior pairs connected with ventral and outer approximators.

Radular sac with clearly bifurcated posterior end. Radular formula n−5−1−5−n (Figs. 58 e, f). Tooth row symmetrical. Central tooth with short, constricted shaft below well-developed cusp; base with triangular lateral projections. Lateral teeth with cusps similar to that of central, becoming prominent toward outermost laterals. Bases of inner four laterals overlapping with basal extensions; that of outermost teeth smooth. Protolateromarginal plates (LMP) broadly developed, originating from base of innermost marginals. Marginals elongated with distinct cusps.

Sublingual pouch lacking glandular outgrowth, very shallow. Licker small and smooth. Radular diverticulum present. Salivary glands (sg) without ducts, lying on dorsolateral sides of buccal cavity, partly overlapping dorsal food channel of anterior esophagus (Fig. 57 b). Mid-esophagus (me) marked by enlargement of esophageal pouches, twisting counterclockwise, terminating in constriction. Posterior esophagus (pe) straight, extending posteriorly on floor of visceral mass.

Stomach (st) pyriform, lying on left posterior side of visceral mass (Fig. 57 b). Posterior esophagus and ducts of digestive glands opening on right posterior side, intestine on left anterior end. Posterior apex of stomach with non-spiral, small gastric caecum. Interior of stomach clearly defined by sorting area, gastric shield, tooth of gastric shield, and intestinal groove between major and minor typhlosoles.

Intestine (i) coiling only twice, generating single anterior loop along right side of mid-esophagus. Rectum penetrating pericardium and ventricle. Anus (a) opening near anterior right end of shell muscle.

Circulatory System: Pericardium forming part of visceral hump, contacting posterior limit of pallial cavity behind left kidney (Fig. 57 a). Heart consisting of right and left auricles (ra, la) and single ventricle (v), all markedly transversely elongated.

Excretory System: Two kidneys facing each other on each side of rectum (Fig. 57 a). Right kidney enlarged, composed of two clearly separated sections. Posterior lobe (prk) hollow, with smooth interior surface; gonoduct opening posteriorly. Anterior lobe (ark) lamellate internally, opening ventrally. Anterior and posterior lobes connected to each other through narrow canal. Right renopericardial duct opening into pericardium beneath right auricle. Opening of right kidney slightly papillate. Left kidney (lk) composed of papillary sac. Left renopericardial duct opening in median part of anterior pericardial wall. Opening of left kidney slit-like.

Reproductive System: Gonad (g) spreading over posterior dorsal surface in both sexes. Gonoduct opening into central part of posterior lobe of right kidney (Fig. 57 a).

Nervous System: Circumesophageal nerve ring hypoathroid. Pedal and pleural ganglia markedly concentrated. Cerebral commissure running over anterior part of dorsal food channel. Labial ganglia and commissure absent. Visceral loop arising from right and left pleural ganglia. Pedal cords scalariform. Statocysts attached to anterior sides of pedal ganglia.

Cantharidus sp. cf. *callichroa* (Philippi, 1850)
(Figs. 59 e-h)

Protoconch: Protoconch nearly discoidal, inflated, paucispiral. Coiling direction orthostrophic. Lateral pouch on apical side projecting to apertural side, with extension producing clear suture as deep cleft. Pouch on basal side projecting, marking distinct pouch-like region. Surface on apical side ornamented by irregularly scattered crystal deposits coalescing to form several spiral threads becoming gradually convergent adaperturally. Protoconch-teleoconch boundary marked by thickened axial lip.

Calliostoma sp.
(Figs. 60 a-d)

Protoconch: Protoconch longitudinally elongated, well-inflated. Adapertural part tightly coiled to orthostrophic direction with distinct suture line. Lateral pouch clearly visible on apical side. Protoconch forming distinct angle to teleoconch, exhibiting heterostrophic appearance. Ornament on protoconch represented by wholly regular hexagonal network composed of vertically aligned columnar prismatic crystals superimposed vertically on smooth base. Boundary between protoconch and early teleoconch distinct, with thickened axial ridge.

Lirularia? minima (Golikov in Golikov and Scarlato, 1967)
(Figs. 60 e-h)

Protoconch: Protoconch initially planispiral, becoming slightly hyperstrophic in final stage, so that protoconch situated at quite different orientation against axis of orthostrophic, conispiral teleoconch. Surface covered by sharp net-like sculpture; some spiral threads visible in ventral view. Protoconch-teleoconch boundary marked by broad axial band.

Family Skeneidae Clark, 1851
Pondorbis japonicus Ando and Habe, 1980
(Figs. 61 a-d)

Protoconch: Protoconch longitudinally elongated, strongly distorted, heavily heterostrophic. Apex pointed ventrally; ventral side of protoconch well inflated. Sculpture almost homogeneously pitted or with polygonal network sculpture. Ridges partially emphasized. Protoconch-teleoconch boundary marked by axial ridge.

Cyclostremiscus sp. 1
(Figs. 61 e-f)

Protoconch: Protoconch almost planispiral, well-inflated. Lateral pouch not appearing differentiated with globular protoconch outline. Well-inflated abapertural part marking very clear sutural line as deeply cleft groove. Surface of median apical area mostly smooth, free from sculpture except for very minute vermicular deposit. Remaining area roughly sculptured by flat ridge with densely pitted depressions. Protoconch-teleoconch boundary marked by thick ribs that are completely continuous with spiral ribs of teleoconch.

Cyclostremiscus sp. 2
(Figs. 61 g-h)

Protoconch: Protoconch planispiral. Apical area almost flat. Lateral pouch on apical side small, not extended laterally. Suture of protoconch clear. Sculpture of protoconch continuous, consisting of widely radiating spiral ridges occurring only on apical side. Lateral pouch on apical side delimited by short spiral ridge
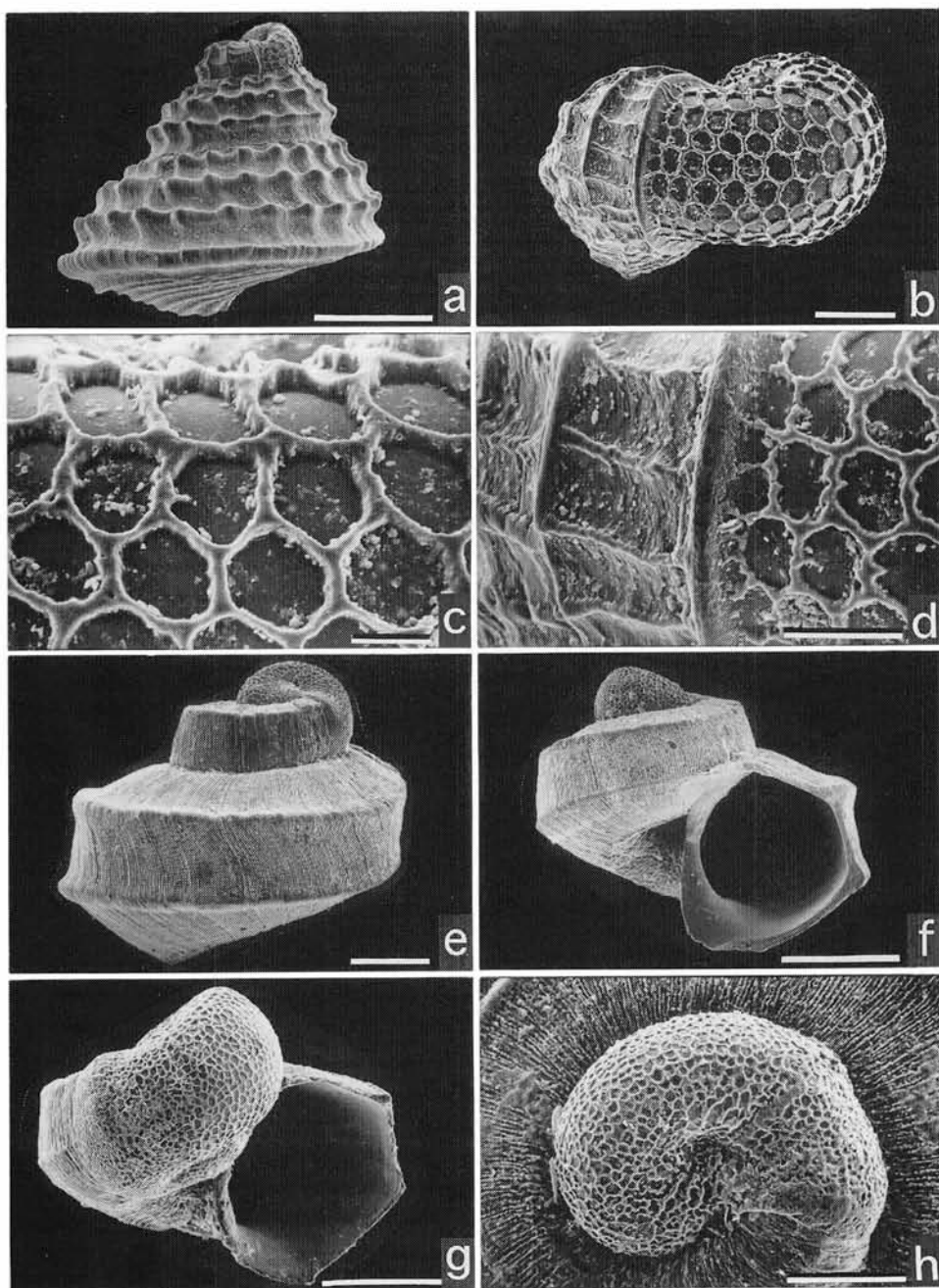
Fig. 60.   Protoconch of Trochidae. **a-d**, *Calliostoma* sp. RM 27663. **a**, Dorsal view of juvenile shell. Scale =
500 μm. **b**, Protoconch and early teleoconch. Scale = 100 μm. **c**, Sculpture of protoconch. Scale = 25
μm. **d**, Boundary between protoconch and teleoconch. Scale = 50 μm. **e-h**, *Lirularia? minima*. RM
27664. **e**, Dorsal view of subadult shell. Scale = 100 μm. **f**, Ventral view of juvenile shell. Scale = 200
μm. **g**, Ventral view of early juvenile shell. Scale = 200 μm. **h**, Apical view of protoconch. Scale =
100 μm.
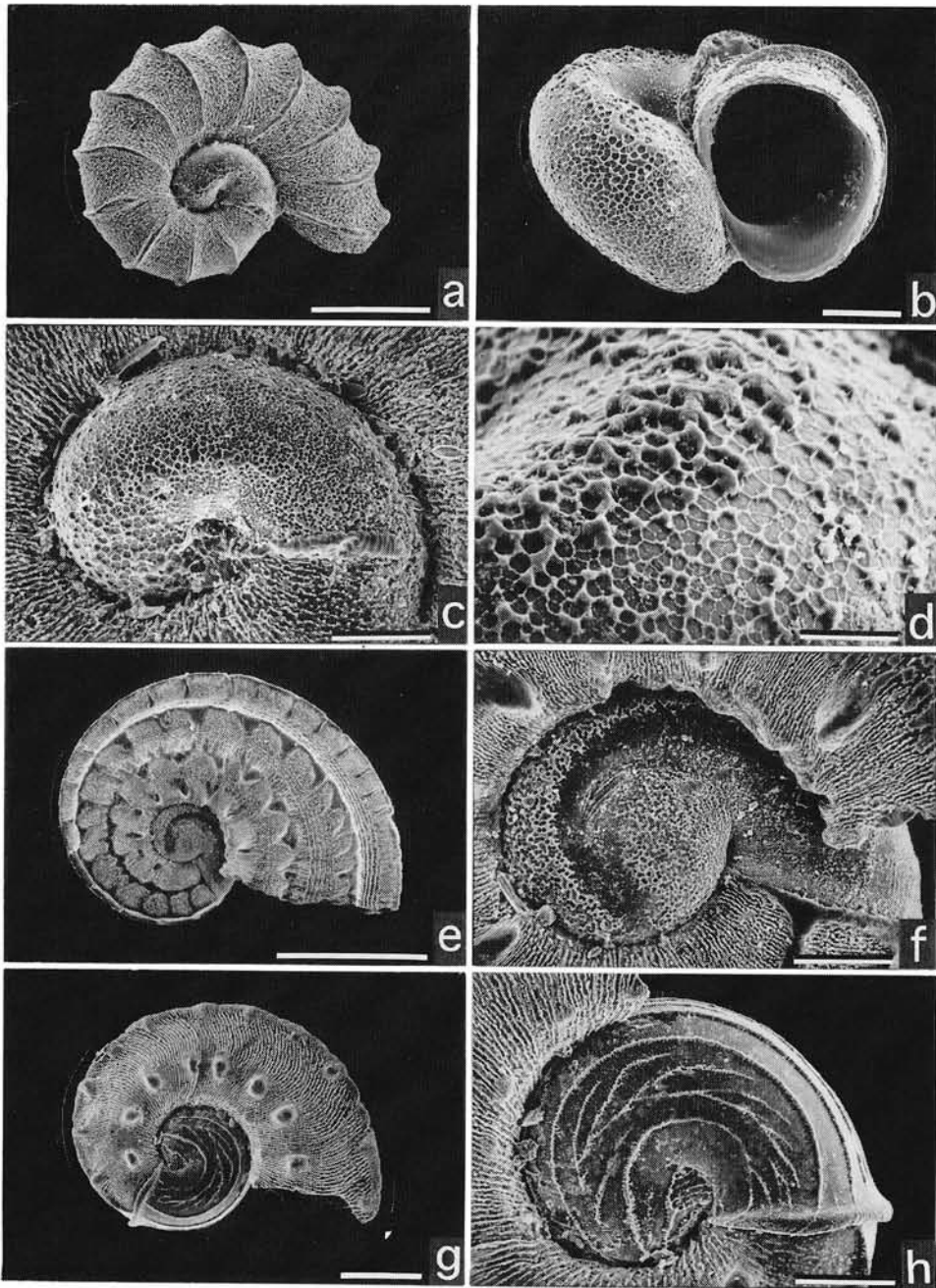
Fig. 61. Protoconch of Skeneidae. **a-d**, *Pondorbis japonicus*. RM 27665. **a**, Apical view of subadult shell. Scale = 200 μm. **b**, Ventral view of very early juvenile shell. Scale = 50 μm. **c**, Apical view of protoconch. Scale = 50 μm. **d**, Sculpture of shoulder of protoconch. Scale = 10 μm. **e-f**, *Cyclostremiscus* sp. 1. RM 27666. **e**, Apical view of subadult shell. Scale = 250 μm. **f**, Apical view of protoconch. Scale = 50 μm. **g-h**, *Cyclostremiscus* sp. 2. RM 27667. **g**, Apical view of subadult shell. Scale = 100 μm. **h**, Apical view of protoconch. Scale = 50 μm.

crossed by six or more fine oblique ribs. Apertural margin of protoconch very thick, inflected.

Family Lepetodrilidae McLean, 1988
Lepetodrilus nux (Okutani, Fujikura and Sasaki, 1993)
(Figs. 62, 63 a-e, 64 a-d, 65 a-h)

External Anatomy: Soft parts limpet-shaped with apex projecting posteriorly. Mantle margin divided into two folds by deep periostracal groove (pg). Outer fold (of) thinner and smoother; inner fold (if) thicker, fringed by numerous microtentacles (Fig. 65 a).

Head with snout (sn), and pair of non-papillate cephalic tentacles (ct). Snout short; neck region prolonged forward. Outer lip of mouth smooth, without sensory projection, lacking oral lappets. Posterior bases of cephalic tentacles extended laterally; eyes not located in serial sections. Neck lobes and cephalic lappets absent. Penis in male not confirmed (material examined all female).
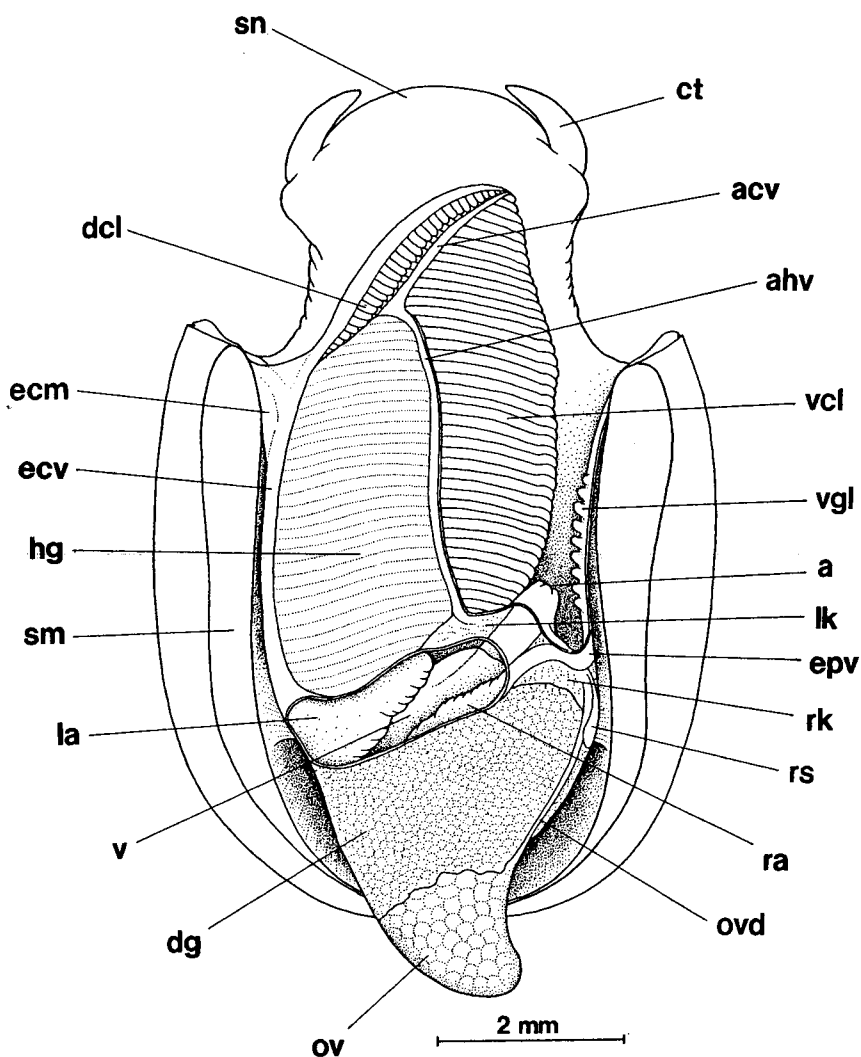
Fig. 62 *Lepetodrilus nux*. Dorsal view of the body after removal of the shell and mantle.
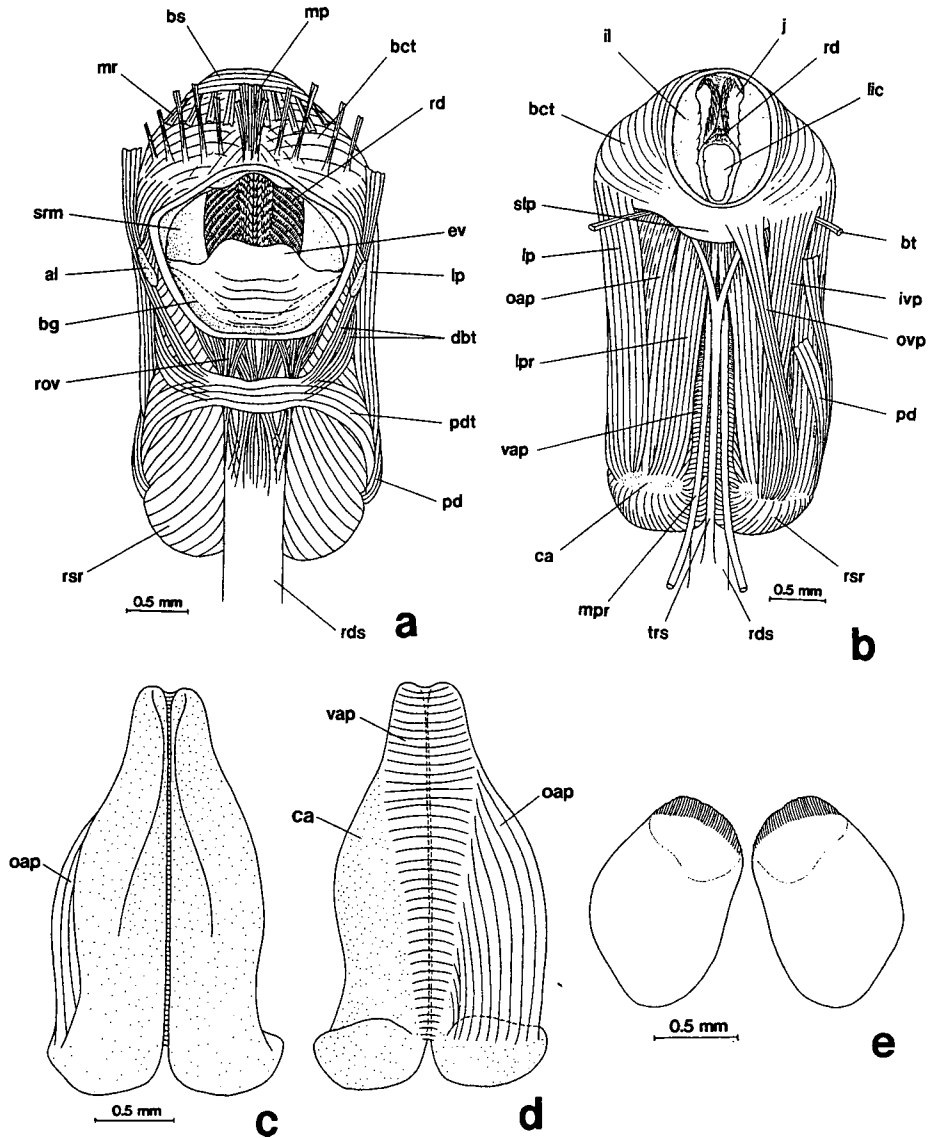
Fig. 63. *Lepetodrilus nux*. **a**, Dorsal view of the buccal mass after removal of the esophagus. **b**, Ventral view of the buccal mass. Some muscles on the left side are removed to show internal structure. **c**, Dorsal view of the odontophoral cartilages. The right outer approximator muscle is removed. **d**, Ventral view of the odontophoral cartilages. **e**, Ventral view of the jaws.

Anterior margin of ventral foot sole demarcated by groove marking opening of anterior pedal gland. Non-papillate epipodial tentacles represented by long folds with three pairs of protrusions on sides of foot. Tuberculate epipodial sense organs at pointed tip of epipodial tentacles. Operculum absent.

Paired shell muscles (sm) horseshoe-shaped, posteriorly connected to filamentous muscles below visceral hump, not divided into bundles or penetrated by blood vessels (Fig. 62).

Pallial Complex: Pallial cavity attaining two-thirds of body length, containing left ctenidium, left osphradium, gill leaflets on right side, paired kidney openings, anus, and left hypobranchial gland.
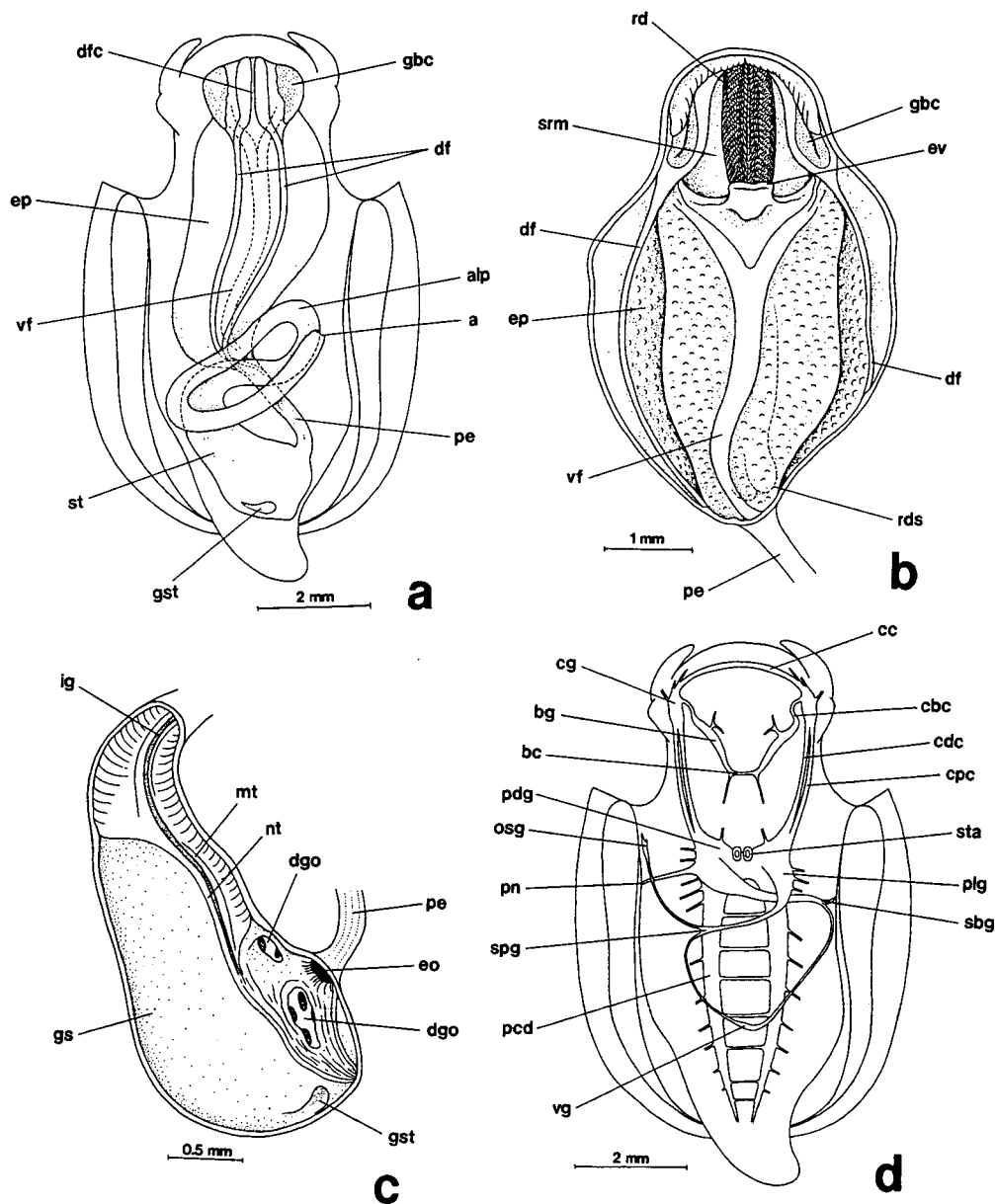
Fig. 64. *Lepetodrilus nux*. **a**, Configuration of the alimentary tract. **b**, Inner view of the anterior alimentary tract. **c**, Internal structure of the stomach. **d**, Nervous system.

Ctenidium greatly modified from typical bipectinate ctenidium. Lamellae bipectinate in anterior third but monopectinate in remaining posterior area. Ctenidial axes not supported by membrane, directly attached to mantle skirt in monopectinate area. In bipectinate part, dorsal lamellae (dcl) very short, restricted to narrow outer crescent-shaped zone of bipectinate area (Figs. 62, 65 b). Ventral lamellae (vcl) dorsoventrally depressed, fused with base of hypobranchial gland (Fig. 62). Respective ventral lamellae elongated feather-shaped. Each ctenidial axis containing paired muscles and median nerve. Each leaflet with frontal, abfrontal, lateral, and terminal cilia; efferent side internally supported by paired skeletal rods; leaflets with series of
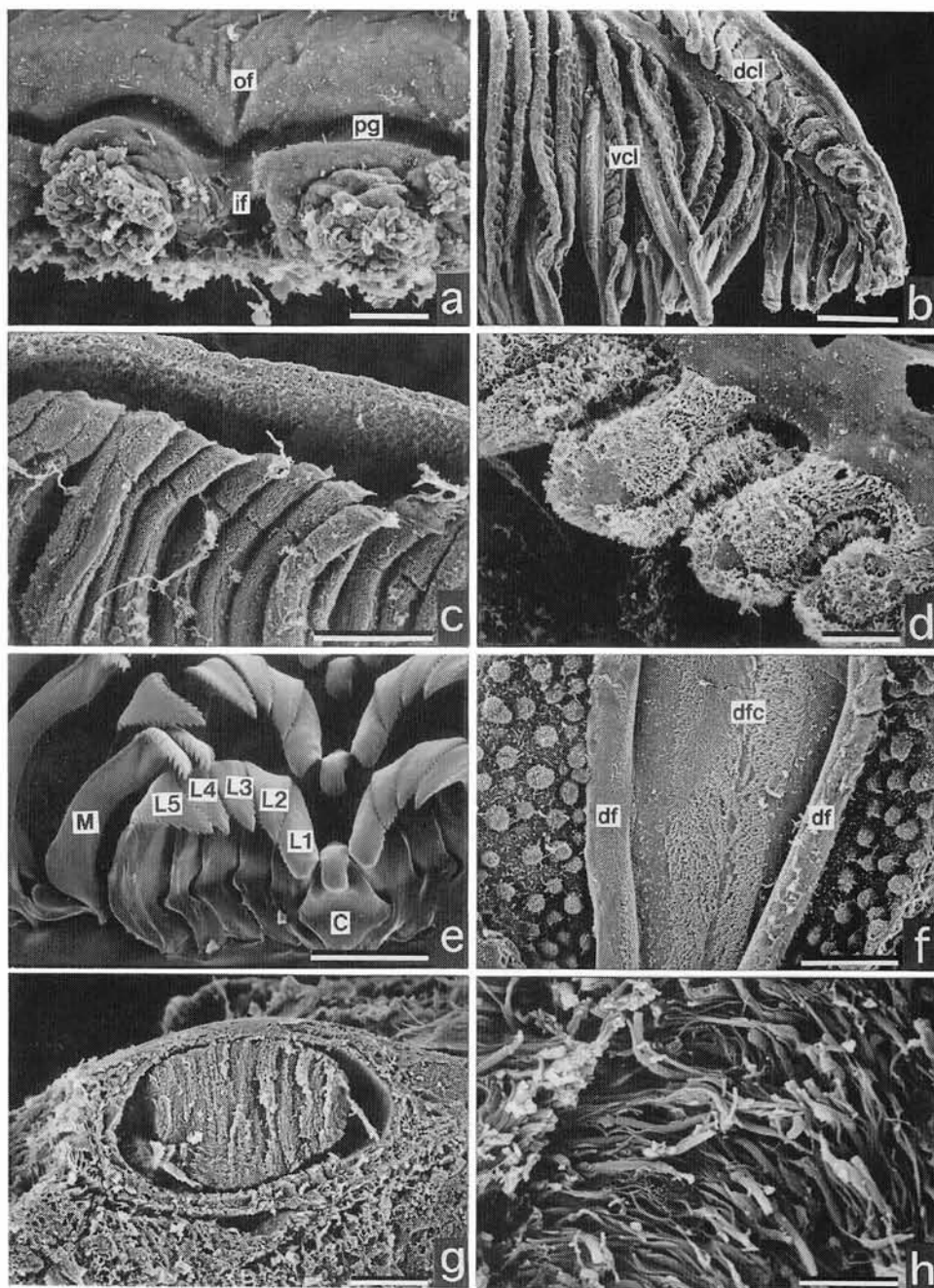
Fig. 65. *Lepetodrilus nux*. SEM micrographs of soft parts. **a-b**, RM 27668 a. **c-d**, **f-h**, RM 27668 b. **e**, RM 27668 c. **a**, Microtentacles on inner fold of mantle margin. Scale = 25 μm. **b**, Dorsal view of bipectinate part of ctenidium. Scale = 250 μm. **c**, Ventral view of ventral lamellae with a series of grooves. Scale = 200 μm. **d**, Vestigial gill leaflets on right efferent pallial vessel. Scale = 50 μm. **e**, Central teeth field of the radula. Scale = 20 μm. **f**, Dorsal inner wall of mid-esophagus. Scale = 250 μm. **g**, Cross-section of receptaculum seminis. Scale = 50 μm. **h**, Spermatozoa stored in receptaculum seminis. Scale = 10 μm.

shallow grooves near apex in ventral view (Fig. 65 c). [These cannot be identified as bursicles, because of absence of interiorly ciliated lumen.]

Right side of pallial cavity lacking true ctenidium. Nine to twelve gill leaflets projecting from efferent pallial vessel (epv) which runs along interior shell muscle (Fig. 62). Surface entirely covered with cilia that appear weakly organized into zones (Fig. 65 d).

Osphradium not distinguishable in superficial observation, but histological thin sections revealed dark-stained sensory epithelium covering free portion of efferent ctenidial axis, extending along anterior end of left shell muscle. Osphradial epithelium including tall cells with elongated nuclei. Osphradium not located on right side.

Well-developed hypobranchial gland (hg) widely attached to left half of mantle skirt, partitioned into narrow transverse sections by vessels from afferent to efferent hypobranchial vessels (Fig. 62). Venous blood transported from transverse pallial vessel to afferent vessels of ctenidial lamellae through hypobranchial glands. Therefore, intervals of sectors of hypobranchial glands completely corresponding to those of vessel of ctenidial lamellae.

Digestive System: Oral tube surrounded by circular buccal sphincter and constrictor (bs, bct). Buccal tensors (bt) extending from ventral side of sublingual pouch to wall of snout between inner ventral protractors and lateral protractors. Mandible protractors (mp) arising from surface of buccal constrictor, and mandibular retractors (mr) appearing from inside of buccal sphincter. Retractors of esophageal valve (rov) inserted on dorsal side of radular sac, covered by postdorsal buccal tensor (pdt).

Odontophores fixed by lateral protractor, posterior depressor, anterior levator, ventral protractor muscles (Figs. 63 a, b). (1) Lateral protractors (lp) arising from posterior cartilages, running along sides of odontophore, attaching dorsolaterally to buccal constrictor. (2) Posterior depressors (pd) inserted near outer lateral corners of posterior cartilages, crossing over postdorsal buccal tensor (pdt), directed downward, united with floor of body cavity. (3) Anterior levators (al) occurring in anterolateral extensions of anterior cartilages, ascending along cartilages on inner sides of lateral protractors and dorsal buccal tensors, emerging dorsally just beside buccal cavity. (4) Inner and outer ventral protractors (ovp, ivp) inserted on ventral surface of posterior cartilages, extending to sublingual pouch.

Left and right halves of odontophore united by two kinds of tensors. (1) Postdorsal buccal tensor (pdt) originating from sides of posterior cartilages under insertions of posterior depressors. (2) Dorsal buccal tensors (dbt) consisting of two parts: dorsal part extending over lateral protractor; outer ventral part running downward, fusing with lateral margin of subradular membrane.

A pair of dark brownish jaws (j) attached to dorsal walls of oral tube at posterior two-third. Finely split, rod-bearing anterior edge exposed to opening of mouth (Figs. 63 b, e).

Radular sac short, straight; posterior end deeply bifurcated (Fig. 64 b). Radular formula 25+−5−1−5−25 +(Fig. 65 e). Tooth row asymmetrical. Central tooth with bilateral basal extensions overlaid on bases of innermost lateral teeth; cusp longitudinally rectangular with very minute serration of denticles. Five pairs of lateral teeth of almost even width; cusps fringed by fine serrated denticulation; shafts almost straight. Base of outer teeth interlocked by inner teeth. Cusps of innermost lateral teeth longer than those of second to fifth teeth, showing steep V-shaped arrangement. Lateromarginal plates absent. Marginal teeth with broadly elongated shafts.

Subradular membrane attached by paired thin median protractors (mpr) and thick lateral protractors (lpr) (Fig. 63 b). Lateral protractors terminating in origin on posterior cartilages. Median protractors elongated along radular sac, anchored on pedal musculature below mid-esophagus.

Retractors of radular sac extending from origin on inner sides of posterior cartilages to insertion on ventral mid-part of radula between anterior cartilages. Tensor of radular sac (trs) as thick as median protractor muscles (Fig. 63 b), arising from underside of radular sac just behind posterior end of buccal mass, running

straight forward along mid-line, bifurcated anteriorly into symmetrical strands, fixed to floor of sublingual pouch, crossing over median and lateral protractors of subradular membrane. Postmedian retractors of radular sac absent.

Buccal mass containing single pair of odontophoral cartilages (ca), connected by ventral and outer approximator muscles (vap, oap) (Figs. 63 c, d).

Sublingual pouch (slp) shallow, lacking glandular outgrowth (Fig. 63 a). Licker (lic) on anterior tip of subradular membrane elongated, smooth (Fig. 63 b). Salivary glands totally absent around buccal cavity, but sides of buccal cavity lined by tall glandular cells.

Beginning of esophagus marked by esophageal valve (ev), separated from deep radular diverticulum. Anterior esophagus extended laterally to form large esophageal pouches of mid-esophagus, remarkably dilated laterally, also extended ventrally to completely enclose posterior part of radular sac (Fig. 64 b). Interior of esophagus provided with paired longitudinal folds (Figs. 64 b, 65 f). Dorsal folds (df) paired throughout anterior to mid-esophagus. Ventral folds (vf) beginning from sides of esophageal valve, converging to fuse into thick single fold, extending almost straight back, only posterior part twisted counterclockwise. Inner surface of mid-esophagus (me) wholly covered with papillate projections of esophageal gland, except in ciliated dorsal food channel (dfc) (Fig. 65 f). Posterior esophagus (pe) greatly narrowed, obliquely postured on right side.

Stomach (st) pyriform, on bottom of visceral mass (Fig. 64 a). Paired ducts from digestive glands entering near opening of esophagus (eo). Posterior apex of stomach weakly projecting as small gastric caecum. Internally, most area of left side occupied by smooth cuticularized gastric shield (gs) (Fig. 64 c). Tooth of gastric shield (gst) projecting on posterior wall of stomach. Right side narrowly sculptured by folds; sorting area not well-developed. In posterior half, intestinal groove (ig) deeply formed between major and minor typhlosoles.

Intestine folded twice to form single anterior loop (alp) on posterior right side of mid-esophagus (Fig. 64 d). Rectum penetrating pericardium and ventricle (v). Anus (a) opening into posterior right corner of pallial cavity.

Circulatory System: Heart consisting of right and left auricles and single ventricle (Fig. 62). Right auricle (ra) smaller than left (la). Initial part of aorta not enlarged into bulbous aorta.

Efferent pallial vessel (epv) on right side draining into pallial cavity along shell muscle, running over right kidney, finally entering right auricle. Circulation in left pallial cavity beginning from transverse pallial vein arising from anterior margin of left kidney, soon connecting to afferent hypobranchial vein (ahv). Branches from the vessel supplying hypobranchial gland, entering afferent side of ctenidium, finally joining efferent ctenidial vessel (ecv). Therefore, blood necessarily entering ctenidium via hypobranchial gland. Afferent hypobranchial vessel extending anteriorly along right margin of hypobranchial gland, becoming afferent ctenidial vessel (acv) at termination of hypobranchial gland. Efferent ctenidial vessel extending from free tip to entire length of ctenidium. At anterior base of efferent ctenidial membrane, left efferent pallial vessel joining efferent ctenidial vessel, entering left auricle.

Excretory System: Excretory system consisting of right and left kidneys (Fig. 62). Right kidney (rk) extending to dorsal surface of visceral mass, also continuing ventrally. Oviduct in female discharged within dorsal lobe. Opening of right kidney (rko) slit-like.

Left kidney (lk) overhanging in pallial cavity, receiving blood from blood space below kidney. Left kidney opening into pallial cavity ventrally through minute slit-like opening. Renopericardial duct present on both right and left sides.

Reproductive System: Specimens studied all females. Ovary (ov) lying over digestive glands in pointed visceral hump under shell apex (Fig. 62). Thin oviduct extending from right side of ovary, passing over exterior surface of visceral mass. Oviduct connected to kidney though short pathway of renopericardial canal.

Ova discharged into pallial cavity through right kidney opening. Floor of pallial cavity on right side lined with tall ciliated cells, perhaps serving for transportation of gametes.

Right pallial wall deeply excavated outside of right kidney into deeply elongated sac that acts as receptaculum seminis (rs) (confirmed by optical and scanning electron microscopy of serial sections that this structure fills with spermatozoa) (Figs. 65 g, h).

Nervous System: Circumesophageal nerve ring hypoathroid (Fig. 64 d). Cerebral ganglia at bases of cephalic tentacles; pleural and pedal ganglia (plg, pdg) tightly fused behind buccal mass. Cerebral commissure (cc) running in front of jaw plates. Cerebropleural and cerebropedal connectives (cdc, cpc) very long, correlated with elongation of neck region.

Several pairs of labial nerves extending from ventral part of cerebral ganglia but not fusing to form labial commissure. Labial ganglia absent. Cerebrobuccal connectives (cbc) arising from inner ventral sides of cerebral ganglia.

Visceral loop originating from both right and left pleural ganglia. In spite of great depth of pallial cavity, visceral loop not very long because of posterior location of pleuro-pedal ganglia. Connectives from right and left pleurals to subesophageal and supraesophageal ganglia (sbg, spg) rather thick; posterior connectives becoming extremely thin toward visceral ganglion beneath left kidney.

Left pleural ganglia laterally providing nerves to pallial, parietal, and pedal regions. Ctenidia innervated by nerve from supraesophageal ganglion. Corresponding nerve on right side extending toward shell muscle. Osphradial ganglion (osg) only on left side. Right side of equivalent nerve and ganglion reduced. Zeugoneury not confirmed.

Pedal ganglia extending backward to thick pedal nerve cords. Pedal commissure well-developed, forming scalariform pedal nerve system. Statocysts (sta) attached to inner anterodorsal sides of pedal ganglia.

Family Seguenziidae Verrill, 1884
Seguenzia sp.
(Figs. 66 a-f, 67 a-h)

Protoconch: Protoconch well-inflated, conispiral. Lateral pouch smooth, without disjunct extension (Figs. 66 b-d). Suture of protoconch very clearly demarcated. Growth direction of protoconch not hyperstrophic, but orthostrophic ventrally. Surface homogeneously covered with somewhat spirally arranged, irregular elongated deposits (Fig. 66 f). Protoconch-teleoconch boundary gently thickened by broad apertural ridge (Fig. 66 e).

External Anatomy: Shell and animal trochiform. Mantle with paired (inhalant and exhalant) slits located in corresponding positions of sinuses of shell aperture. Mantle margin mamillate with microtentacles having ciliary corona (Fig. 67 a). Long pallial tentacles absent. Attachment of shell muscle single, slightly coiling along columella of shell. Muscle not divided into bundles.

Head with elongated snout and pair of papillate cephalic tentacles (ct) (Fig. 67 b). Cephalic lappets and neck lobes absent. Snout simple. Outer lip of mouth without oral lappets. Cephalic tentacles thicker than epipodial tentacles, with ciliated microtentacles shortened near bases but becoming longer toward tips of cephalic tentacles. Subocular peduncle and "accessory cephalic process" (Quinn, 1983) arising from outer base of right cephalic tentacle and from right side of neck region, respectively.

Foot sole not divided by mid-ventral cleft. Ventral surface of foot densely ciliated. Opening of pedal gland present anteriorly. Epipodium with three pairs of papillate epipodial tentacles (Fig. 67 b) with microtentacles on which ciliary crowns occur (Fig. 67 c). Paucispiral corneous operculum present on epipodium.

Pallial Complex: Pallial cavity very deep, occupying more than one-half whorl, containing left ctenidium, anus, and left hypobranchial gland. Ctenidium completely monopectinate, consisting of nearly 30 ctenidial filaments attached to mantle (Fig. 67 d). Ctenidial filaments heavily ciliated. Presence of bursi-
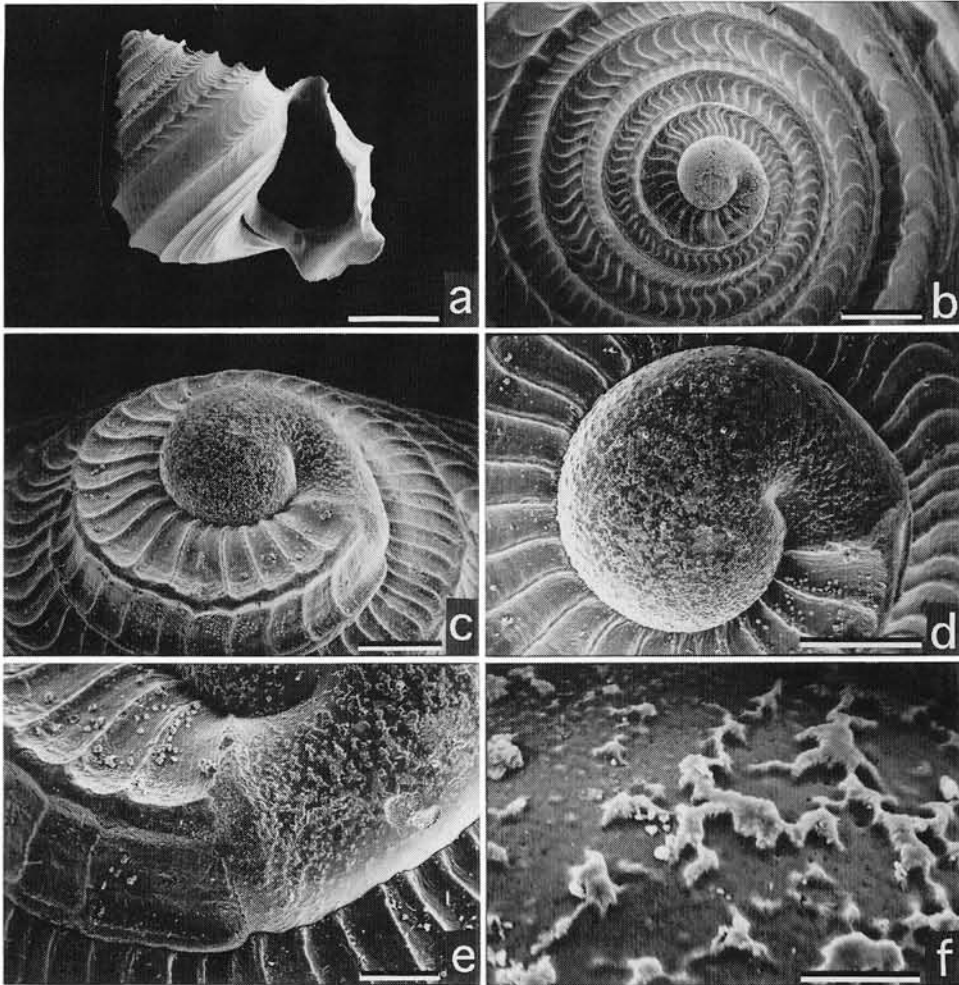
Fig. 66.   Protoconch of *Seguenzia* sp. RM 27669. **a**, Ventral view of adult shell. Scale = 1 mm. **b**, Apical view.
Scale = 250 μm. **c**, Slightly inclined view of apex. Scale = 100 μm. **d**, Apical view of protoconch.
Scale = 100 μm. **e**, Boundary between the protoconch and teleoconch. Scale = 50 μm. **f**, Sculpture of
protoconch. Scale = 10 μm.

cles suggested by ciliated groove (Fig. 67 d). Presence of osphradium not verified. Hypobranchial gland on
left pallial roof composed of tall columnar cells containing numerous granules (Fig. 67 e).

Digestive System: Muscles of odontophore consisting of lateral protractors, ventral protractors, and ante-
rior levators. Presence of posterior levators, posterior depressors, postdorsal buccal tensor, and dorsal buc-
cal tensors unverified.

Jaw plates bilaterally paired, attaching to oral tube dorsally, with inner surface characterized by scaly
sculpture in anterior half.

Radular sac short and straight. Posterior end of radular sac not observed. Radular formula 5?-1-1-1-5?
(Fig. 67 f). Radular tooth row symmetrical. Central tooth broadest, with base thickened by trapezoidal basal
processes; cusp equilaterally triangular in outline, sharply serrated with spicular denticles. Lateral teeth in-
termediate in width between central and marginal teeth; length of shaft almost same as that of central tooth;
cusp provided with about five denticles on both outer and inner sides. Marginal teeth thin, thread-like; both
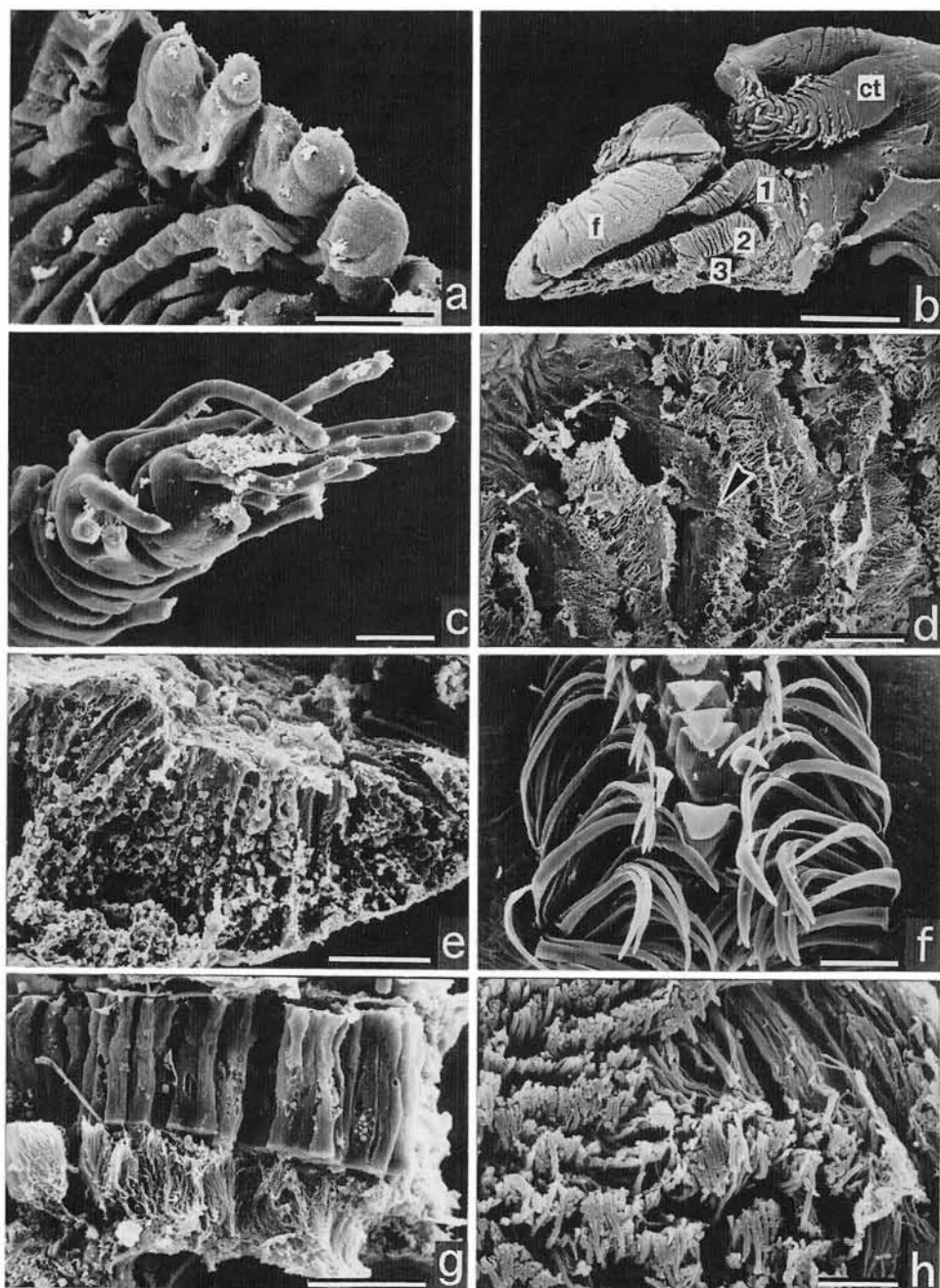
Fig. 67.   *Seguenzia* sp. SEM micrographs of soft parts. **a**, **d**, RM 27670 a. **b**, RM 27670 b. **c**, **h**, RM 27670 c. **e**-**g**, RM 27670 d. **a**, Inner view of mantle margin with microtentacles. Scale=20 μm. **b**, Left lateral view of head-foot. Scale=250 μm. **c**, Top of epipodial tentacle. Scale=25 μm. **d**, Ctenidial lamellae. Arrowhead indicates lateral groove of bursicle. Scale=25 μm. **e**, Vertical section of hypobranchial gland. Scale=50 μm. **f**, Radular teeth. Scale=25 μm. **g**, Ciliated columnar epithelium of intestine. Scale=20 μm. **h**, Spermatozoa stored in receptaculum seminis in female. Scale=10 μm.

outer and inner margins provided with spinous denticles progressively diminishing toward smooth shaft.

Muscles of subradular membrane consisting of lateral and median pairs of protractors and retractors. Presence or absence of postmedian retractors of radular sac (prs) unverified. Buccal mass containing anteriorly pointed, single pair of odontophoral cartilages, united by ventral approximator muscle.

Radular diverticulum present. Glandular outgrowth not found in sublingual pouch. Presence of salivary glands unverified. Esophagus with both ventral and dorsal folds. Ventral folds fused into single median ridge behind buccal mass. Inner structures of mid- to posterior esophagi and stomach not determined. Small gastric caecum present. Intestine extremely long, forming a few loops, with posterior part running on pallial roof and complexly coiled. Epithelium of intestine composed of tall cells bearing long cilia on their interior surface (Fig. 67 g). Rectum terminating as anus on right side of anterior pallial cavity.

Circulatory System: Pericardium lying on posterior left side of pallial cavity. Structure of heart not sufficiently observed due to heavily contracted condition.

Excretory System: Inner structure of excretory organs and position of excretory openings not observed.

Reproductive System: Gonad dorsally extending into spiral visceral mass. Sexes probably separate; hermaphroditic state not observed. Female with large yolk-rich eggs in ovary. Course of gonoduct not ascertained. Females with receptaculum seminis on left side of posterior pallial wall, visible through thin epithelium of mantle as whitish hue nearly circular in cross-section. Sperm cells stored in receptaculum very long with elongated head (Fig. 67 h). Males not found in material.

Nervous System: Circumesophageal nerve ring hypoathroid. Cephalic ganglia well-developed, near bases of cephalic tentacles. Pedal ganglia below posterior end of buccal mass. Other structures not observed.

Family Cocculinidae Dall, 1882
Cocculina nipponica Kuroda and Habe, 1949
(Figs. 68 a-f, 69 a-d, 70 a-b, 71, 72 a-f)

Protoconch: Protoconch planispiral, symmetrical in dorsal view (Figs. 68 a-c). Surface ornamented with network pattern, coarser laterally, denser dorsally (Figs. 68 d-f). Protoconch-teleoconch boundary marked by very thin, slightly undulated apertural lip. Growth direction of protoconch parallel to anterio-posterior axis of teleoconch.

External Anatomy: Animal limpet-shaped. Mantle margin lacking circumpallial microtentacles. Shell muscle (sm) horseshoe-shaped, penetrated by afferent mantle vessels (Fig. 69 a), thickened at anterior ends by fusion with head retractor muscles, forming somewhat incurved rounded projections.

Head bearing short snout (sn) and non-papillate cephalic tentacles (ct). Mouth surrounded by bristles. Outer lip with broad oral lappets (ola) laterally. Eyes absent. Copulatory organ on right neck region (co, Fig. 69 b).

Paired, ciliated, non-papillate epipodial tentacles (ept) present on posterior part of epipodium (Fig. 69 b). Epipodial sense organs absent. Operculum absent.

Pallial Complex: Pallial cavity shallow, occupying less than half of body length, containing pseudoplicate gill on left side, left osphradium, single kidney opening, anus, and left hypobranchial gland. Most of area of posterior mantle roof occupied by pericardium on left and kidney on right. Folded, pseudoplicate gill (ppg) arising on right mantle roof (Fig. 69 a), covered by somewhat irregular ciliation. Hypobranchial gland (hg) on left side of gill.

Digestive System: Odontophore fixed by lateral and ventral protractors (Figs. 70 a, b): (1) Outer part of lateral protractors (lp) running from posterior ends of cartilages to wall of snout. Inner part of muscle connecting with ventral extensions of cartilages and buccal constrictor covering oral tube. (2) Outer ventral protractors (ovp) originating from body musculature below buccal mass, inserting on posterior extensions of cartilages. Inner ventral protractors (ivp) on dorsal side of outer protractors, similar in configuration to
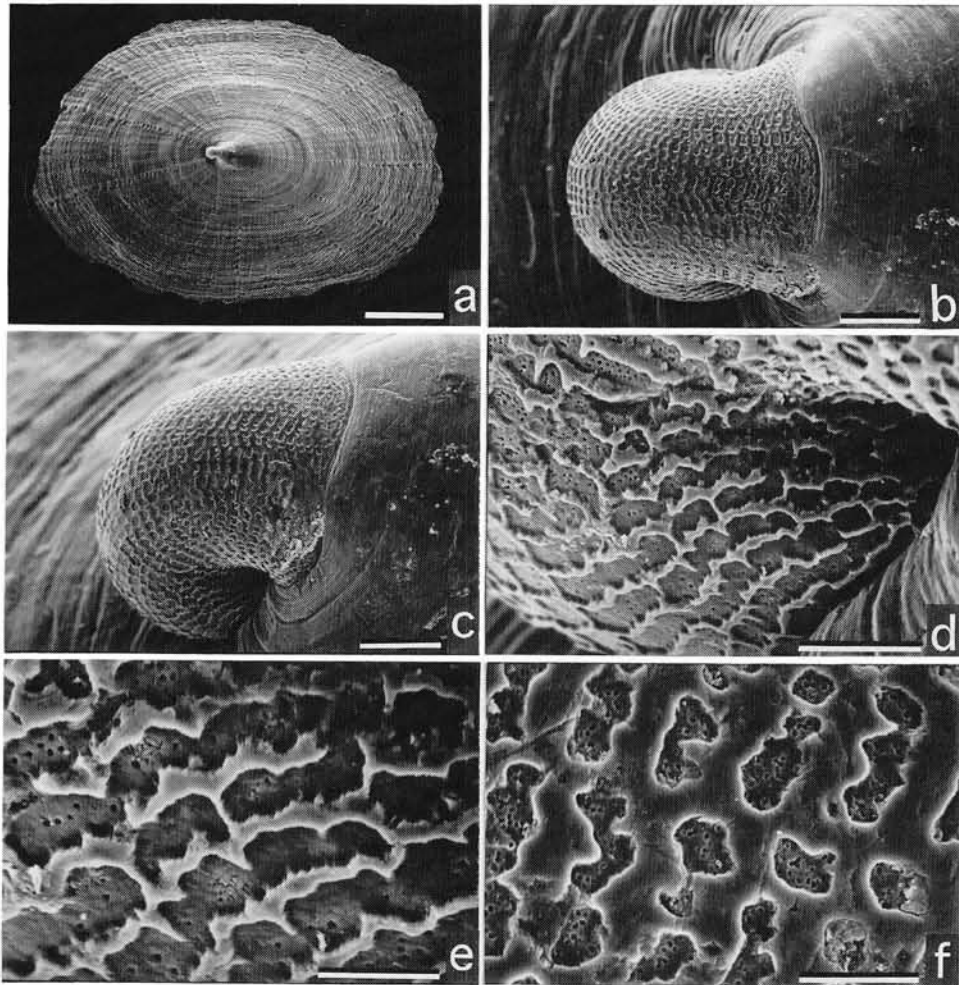
Fig. 68.   Protoconch of *Cocculina nipponica*. RM 27671. **a**, Dorsal view of adult shell. Scale = 1 mm. **b**, Dorsal view of protoconch. Scale = 50 μm. **c**, Right oblique view of protoconch. Scale = 50 μm. **d**, Right lateral view of the central part of the protoconch. Scale = 20 μm. **e**, Sculpture of lateral part of protoconch. Scale = 10 μm. **f**, Sculpture of adapertural part of protoconch. Scale = 10 μm.

outer ventral protractors. Left and right halves of odontophore united by postdorsal buccal tensor (pdt) and dorsal buccal tensors (dbt). Levators and depressors of odontophore absent.

Paired jaw plates (j) distinguished by darker color from adjacent area of oral tube, with smooth anterior margin and inner surface lacking scale-like sculpture.

Radular sac (rds) bent ventrally behind buccal mass (Fig. 71). Posterior end bifurcated to form globular lateral projections (Figs. 70 a, b). Radular formula n−(1+3)−0−(3+1)−n. Each transverse row symmetrical. Central area of radula lacking teeth, with broad exposed space on radular membrane marked by longitudinal ridges, corresponding to radular segments. Inner lateral teeth narrowly elongated. Second laterals with shorter shaft and more extended base than innermost laterals; cusp tri-denticulate with innermost denticle longest. Third laterals elongated, sickle-like; cusp with single acute hook. Outer (fourth) laterals elongated, stout; dorsal surface of cusp streaked by fine longitudinal lirae converging distally; inner basal corner articulating with base of third lateral teeth. Lateromarginal plates absent. Marginal teeth broad basally, taper-
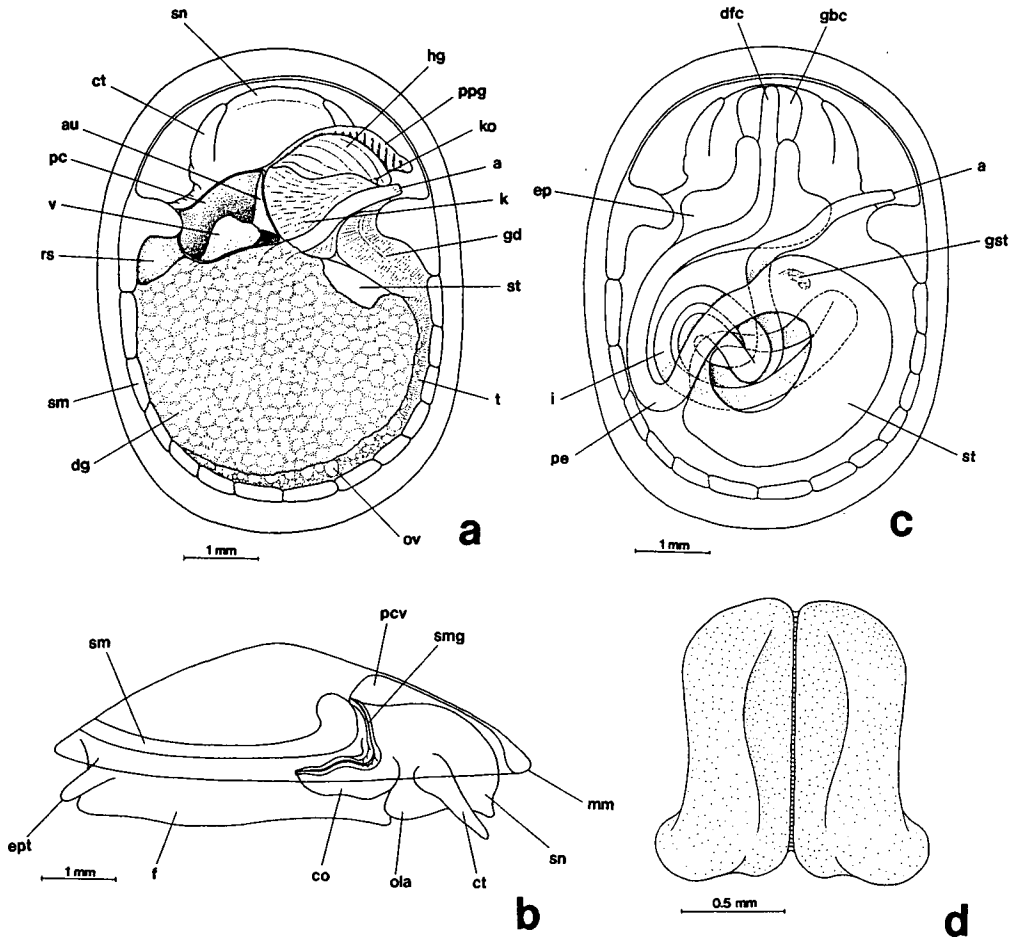
Fig. 69. *Cocculina nipponica.* **a**, Dorsal view of the body after removal of the shell and mantle. **b**, Semischematic representation of the right lateral view. **c**, Configuration of the alimentary tract. **d**, Dorsal view of the odontophoral cartilages.

ing in distal third; cusps sickle-shaped, denticulate, with sharply elongated denticles.

Action of radula controlled by two pairs of protractors and single pair of retractors of subradular membrane. Due to development of odontophoral cartilages and retractor muscles, buccal mass markedly swelling in posterior part. Median protractors (mpr) emerging from ventral side of subradular pouch, attaching to ventral body musculature. Lateral protractors (lpr) originating from posterior extensions of cartilages.

Buccal mass containing pair of odontophoral cartilages (ca) (Figs. 69 d, 71, 72 a, b) connected by single-layered ventral approximator muscle. Tensor of cartilages absent.

Ventral side of oral tube forming simple sublingual pouch (slp) without lateral glandular outgrowths (Fig. 70 b). Buccal cavity extending laterally, its wall lined by single layer of tall glandular cells. Radular diverticulum narrow. Salivary glands absent.

Anterior esophagus depressed over odontophore. Interior clearly divided into dorsal food channel (dfc) and lateral pouches by dorsal and ventral folds. Behind buccal mass, lateral pouches developing into large, flat pouches (ep). Both dorsal and ventral folds disappearing in posterior esophagus (pe). Inner wall of mid-
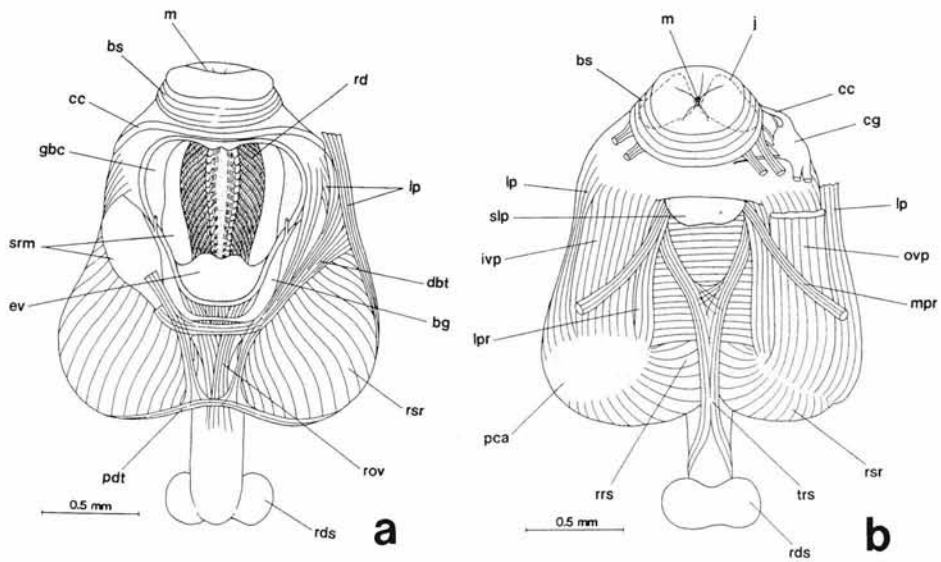
Fig. 70.   *Cocculina nipponica*. **a**, Dorsal view of the buccal mass after removal of the esophagus and some muscles. **b**, Ventral view of the buccal mass. Some muscles and cephalic ganglion of left side are removed.
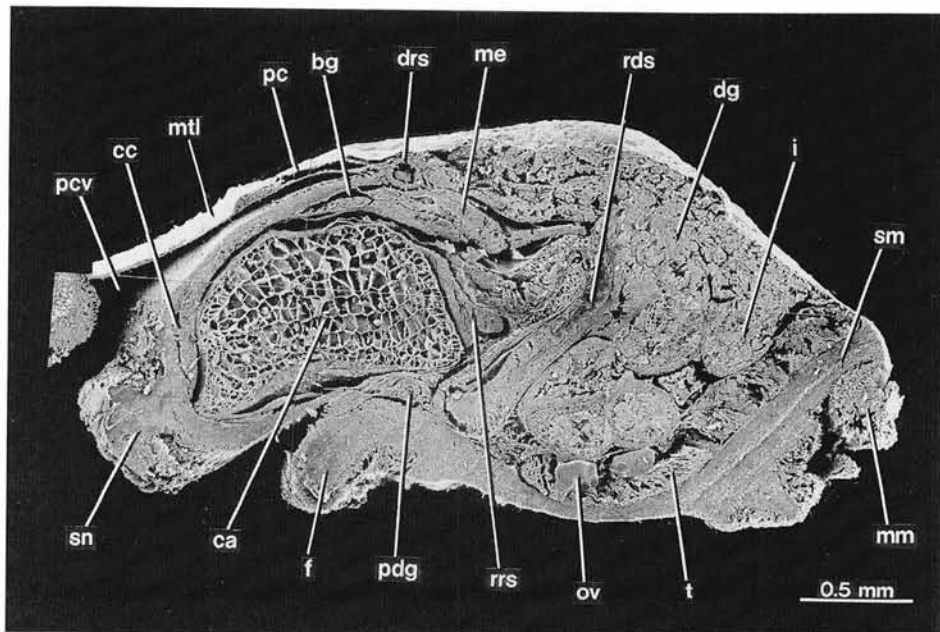
Fig. 71.   *Cocculina nipponica*. SEM micrograph of the animal in longitudinal section. RM 27672 a.

esophagus smooth. Esophagus gradually curving left, recurving anterodorsally toward stomach.

Stomach (st) inverted C-shaped (Fig. 69 c). Part of stomach appearing on dorsal surface of visceral hump, mostly embedded within digestive glands (dg). Digestive glands opening into stomach through single pore at initial dorsal part. Inside of stomach ventrally curved by typhlosoles and corrugated sorting area. Dorso-
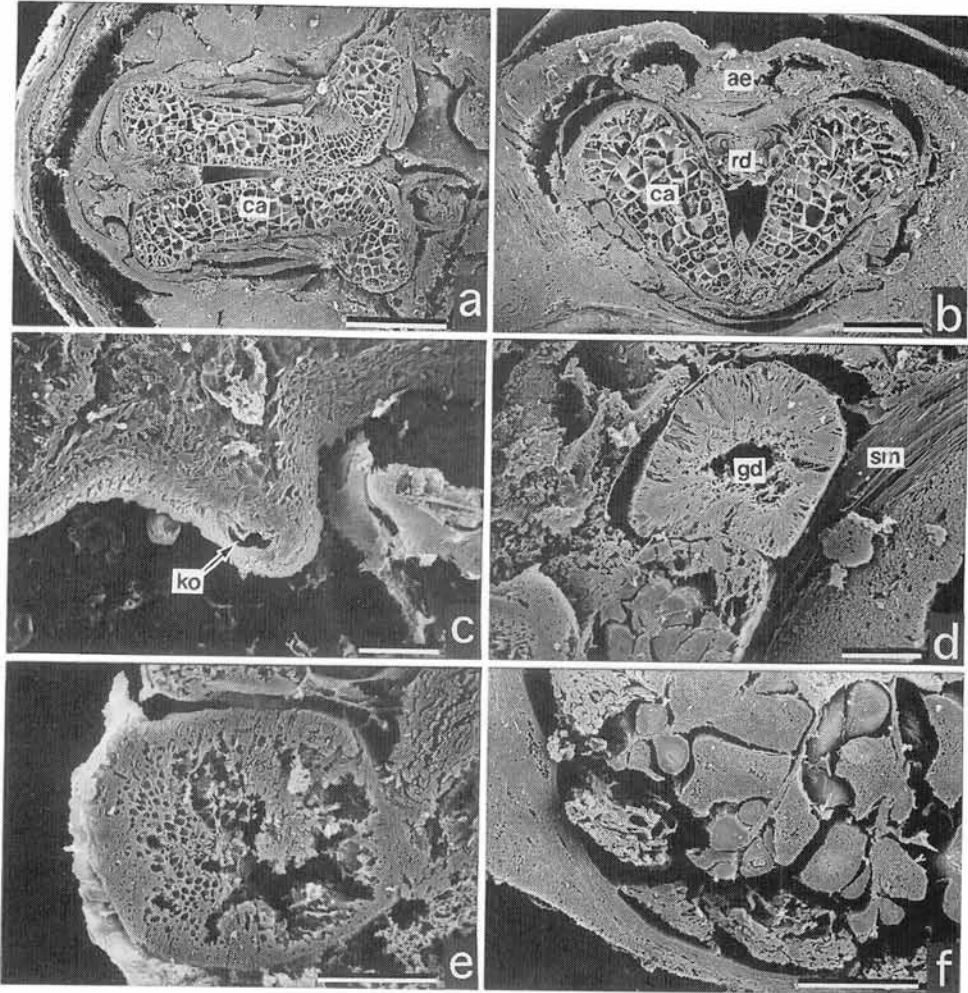
Fig. 72. *Cocculina nipponica*. SEM micrographs of soft parts. **a, c, e,** RM 27672 a. **b, d, f,** RM 27672 b. **a,**
Horizontal section of buccal mass. Scale=500 μm. **b,** Cross-section of buccal mass and anterior
esophagus. Scale=250 μm. **c,** Opening of kidney. Scale=50 μm. **d,** Cross-section of glandular part
of gonoduct. Scale=100 μm. **e,** Horizontal section of receptaculum seminis. Scale=100 μm. **f,** Hori-
zontal section of clusters of oocytes and growing ova. Scale=200 μm.

lateral wall entirely smooth with cuticularized gastric shield. Tooth of gastric shield (gst) projecting on dor-
sal part just behind opening of digestive glands. Intestine (i) bending four times at more ventral level than
posterior esophagus and stomach; only terminal part running along dorsal surface. Recum not penetrating
pericardium or ventricle. Anus (a) exceeding right anterior limb of shell muscle.

   Circulatory System: Pericardium (pc) on left side just posterior to pallial cavity. Heart consisting of sin-
gle auricle and single ventricle (Fig. 69 a). Auricle (au) lying on right anterior side, connecting with ventri-
cle through narrow opening. Auricle receiving blood from pseudoplicate gill. Connection with kidney un-
certain. Ventricle (v) rather freely fixed within pericardium on left posterior side of auricle. No clear bound-
ary identified between anterior and posterior aortae.

   Excretory System: Single kidney (k) on right side of pericardium. Anterior part of kidney mainly at-
tached to mantle skirt (Fig. 69 a). Posterior part overrun by rectum. Small kidney opening (ko) to left side

of anus beneath hypobranchial gland (Fig. 72 c). Internal microstructure not observed histologically.

Reproductive System: Hermaphroditic gonad on ventral side of visceral mass (Fig. 71). Testis (t) and ovary (ov) partly separated, but intermingled with each other on ventral side (Figs. 71, 72 f). Gonoduct (gd) originating from right side of gonad, extending along shell muscle. Distal part of gonoduct dilated, highly glandular (Fig. 72 d). Near genital opening, another duct extending toward left side under pericardium. Terminal part of duct enlarged to form receptaculum seminis (rs), partly appearing on left dorsal surface between pericardium and shell muscle (Figs. 69 a, 72 e). Near genital opening, deep seminal groove (smg) running along edge of shell muscle, extending to verge of copulatory organ (co) continuously. Copulatory organ arising behind base of right cephalic tentacle.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia at bases of cephalic tentacles, connected by cerebral commissure. Pleural and pedal ganglia (pdg) under buccal mass (Fig. 71), united with cerebral ganglia (cg) by separate, short cerebropleural and cerebropedal connectives.

Cerebral ganglia provided with at least four branches to oral region, but lacking labial commissure and ganglia (Fig. 70 b). Cerebrobuccal connectives arising from inner ventral sides of cerebral ganglia, running along anterolateral edges of cartilages. Buccal ganglia (bg) visible over retractors of subradular membrane (rsr) when esophagus removed dorsally (Fig. 70 a), mainly innervating esophagus anterodorsally and buccal musculature both ventrolaterally and posteriorly.

Structural details of visceral nerve loop and innervation to pallial organs not observed. Pedal ganglia extending thick pedal cords, apparently lacking commissures. Statocysts attached to inner anterodorsal sides of pedal ganglia.

Family Neritidae Rafinesque, 1815
Nerita (Theliostyla) albicilla Linnaeus, 1758
(Figs. 73 a-b, 74 a-d, 75 a-e, 76 a-d, 77 a-h, 78 a-b)

Protoconch: Protoconch globular, multispiral, convoluted in orthostrophic direction (Figs. 78 a, b). Outer surface free of prismatic deposits, completely smooth except for fine growth lines. Protoconch-teleoconch boundary clearly demarcated. Margin of protoconch aperture slightly thickened.

External Anatomy: Head-foot nearly symmetrical. Visceral hump not spirally coiled, with apex directed toward anterior. Mantle margin smooth, without microtentacles.

Head with short snout (sn), non-papillate cephalic tentacles (ct), eyestalks (es), and right cephalic penis (pen) in male. Outer lip of mouth smooth, laterally extended to form oral lappets. Eyestalks with lateral extension arising from outside of cephalic tentacles. Closed eyes on tips of eyestalks. Flap-like penis to inside of right cephalic tentacle.

Epipodial region of foot lacking epipodial tentacles and sense organs. Attachment of shell muscle divided into right and left portions (lsm, rsm), each subdivided into nine or ten bundles (Figs. 73 a, b). Right muscle attaching to inside of apical area; left muscle to basal side of columella.

Pallial Complex: Pallial cavity very deep, reaching almost entire body length, containing left ctenidium, right "vestigial gill," left osphradium, left kidney opening, anus, genital opening(s), and right hypobranchial gland.

Single (left) bipectinate ctenidium arising from left posterior pallial wall. Ctenidium supported by short afferent and efferent ctenidial membranes. Afferent and efferent ctenidial axes containing afferent and efferent ctenidial vessels, ctenidial nerves, and retractor muscles (Fig. 77 a). Ctenidial lamellae triangular-shaped in alternating arrangement. Midline of lamellae projecting vertically, generating ridged appearance. Efferent side of ctenidial lamellae lacking skeletal rods (Fig. 77 b). Surface of ctenidial lamellae covered with zoned series of frontal, abfrontal, and lateral cilia. Bursicles absent.

Marked tuberculation of "vestigial gill" (Fretter, 1965) on right side of kidney opening (Fig. 77 c). Cili-
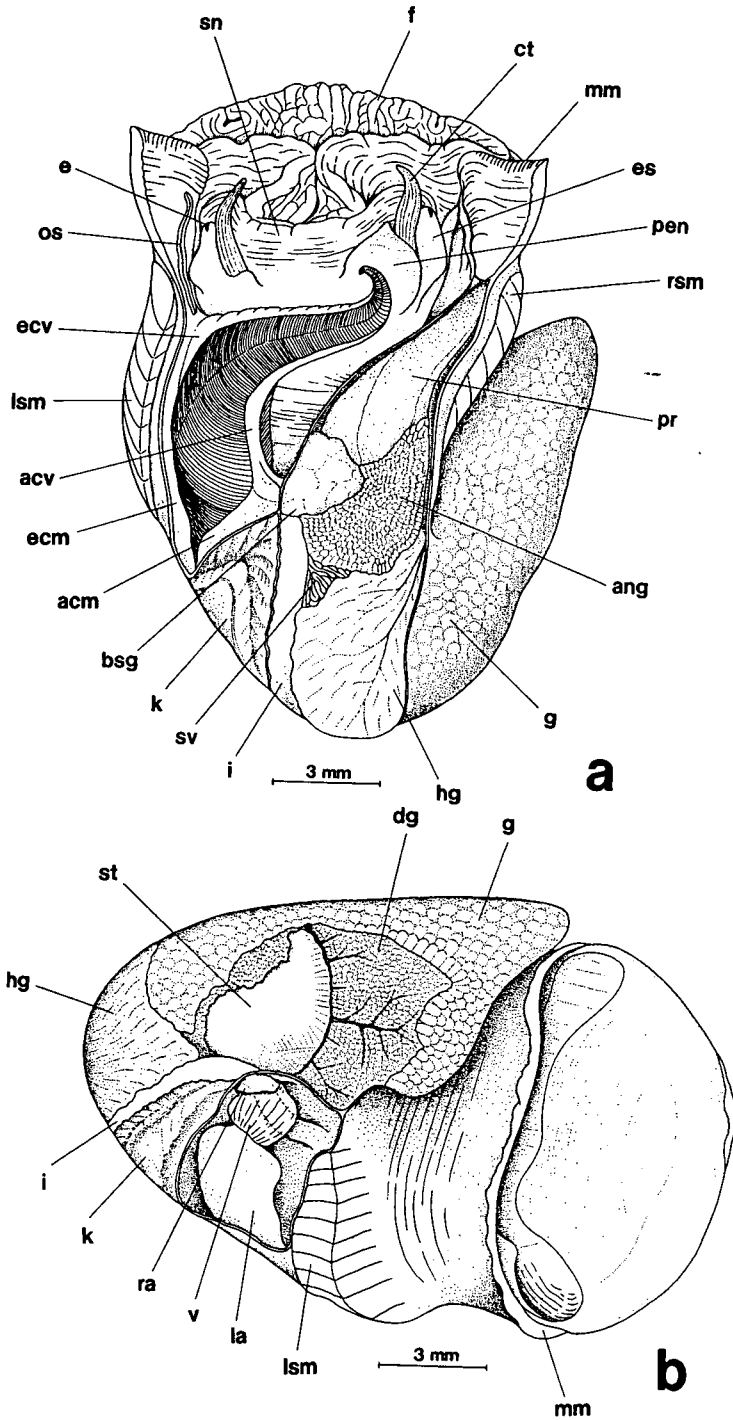
Fig. 73. *Nerita* (*Theliostyla*) *albicilla*. **a**, Dorsal view of the animal after shell and mantle removed. **b**, Ventral view of the animal.
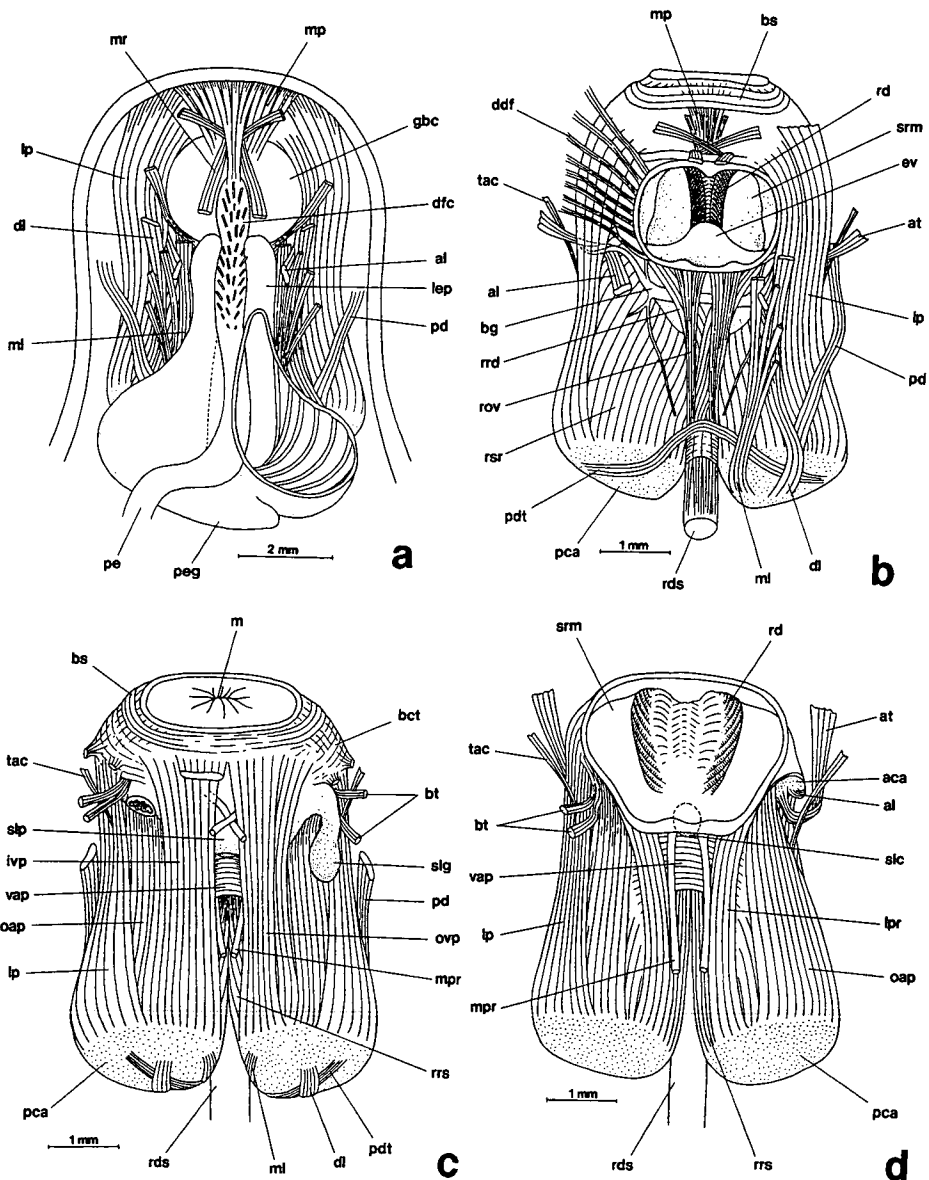
Fig. 74. *Nerita (Theliostyla) albicilla*. **a**, Dorsal view of the buccal region. Right esophageal pouch is cut to expose internal septate structure. **b**, Dorsal view of the buccal mass after removal of the esophagus and some muscles on the left side. **c**, Ventral view of the buccal mass. **d**, A deeper ventral dissection of the buccal mass. Some muscles on the right side are removed.

ary bands on surface of gill absent. Gill internally connected with large space of efferent pallial vessel.

Osphradium (os) resting on mantle skirt on anterior side of attachment of efferent ctenidial axis (Fig. 73 a), with long vermiform ridge accompanied by furrow and ciliated band on each side (Fig. 77 d). Hypobranchial gland (hg) well-developed on right side, associated with genital duct.

Digestive System: Oral tube surrounded by buccal sphincter and constrictor (bs, bct), mandibular protractors and retractors (mp, mr), and buccal tensor muscles (bt).
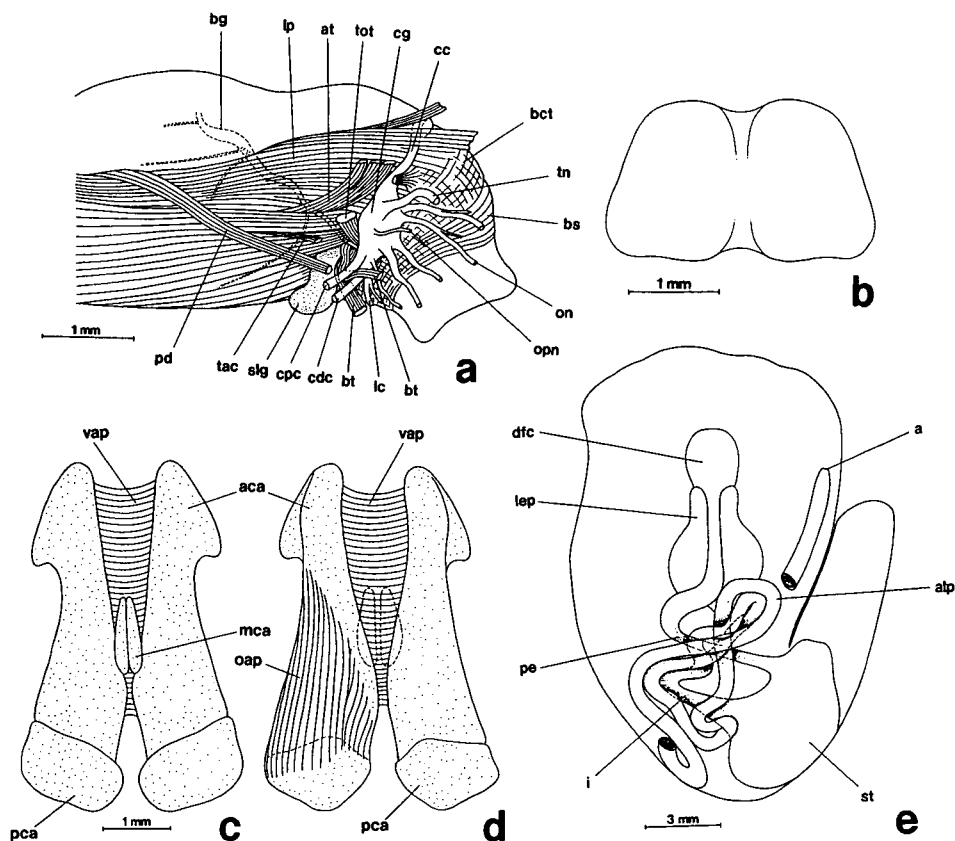
Fig. 75.   *Nerita (Theliostyla) albicilla*. **a**, Right lateral view of the anterior part of the buccal mass. **b**, Ventral view of the jaws. **c**, Dorsal view of the odontophoral cartilages. **d**, Ventral view of the odontophoral cartilages. Left outer approximator muscle is removed. **e**, Configuration of the alimentary tract. A part of rectum is cut to reveal intestinal loop.

Buccal mass anchored on musculature of body wall by lateral protractors (lp), ventral protractors (vp), median and dorsal levators (ml, dl), posterior depressors (pd), anterior levators (al), and anterior tensors (at) (Figs. 74 a-d, 75 a). Posterior part of odontophore united by postdorsal buccal tensor (pdt). Posterior levator and dorsal buccal tensor absent.

Jaws (j) completely adhered to dorsal area of oral tube, composed of distinctly paired translucent plates fused by median cuticularized zone (Fig. 75 b). Each plate subrectangular with rounded edge. Anterior margin and inner surface lacking sculpture and projection.

Radular sac very long, coiling at least three times. Posterior end of radular sac not clearly divided. Radular formula n−(1 + 3)−1−(3 + 1)−n. Radular row symmetrical. Central tooth laterally rectangular. First lateral teeth with inner margin completely fitting into central tooth; cusp small, reflected in flap-like, triangular form at outer anterior corner. Second and third laterals in narrow groove between first inner lateral and outer lateral teeth. Outer (fourth) laterals greatly enlarged transversely; cusp thickened, smooth, shield-shaped; base inflated with deep pit on outer side. Lateromarginal plates absent. Marginals with long shafts and smooth cusps.

Subradular membrane attached anteriorly with two pairs of protractors, median and lateral protractors (mpr, lpr), and laterally with well-developed retractor muscles (rsr). Retractors of radular sac (rrs) originat-
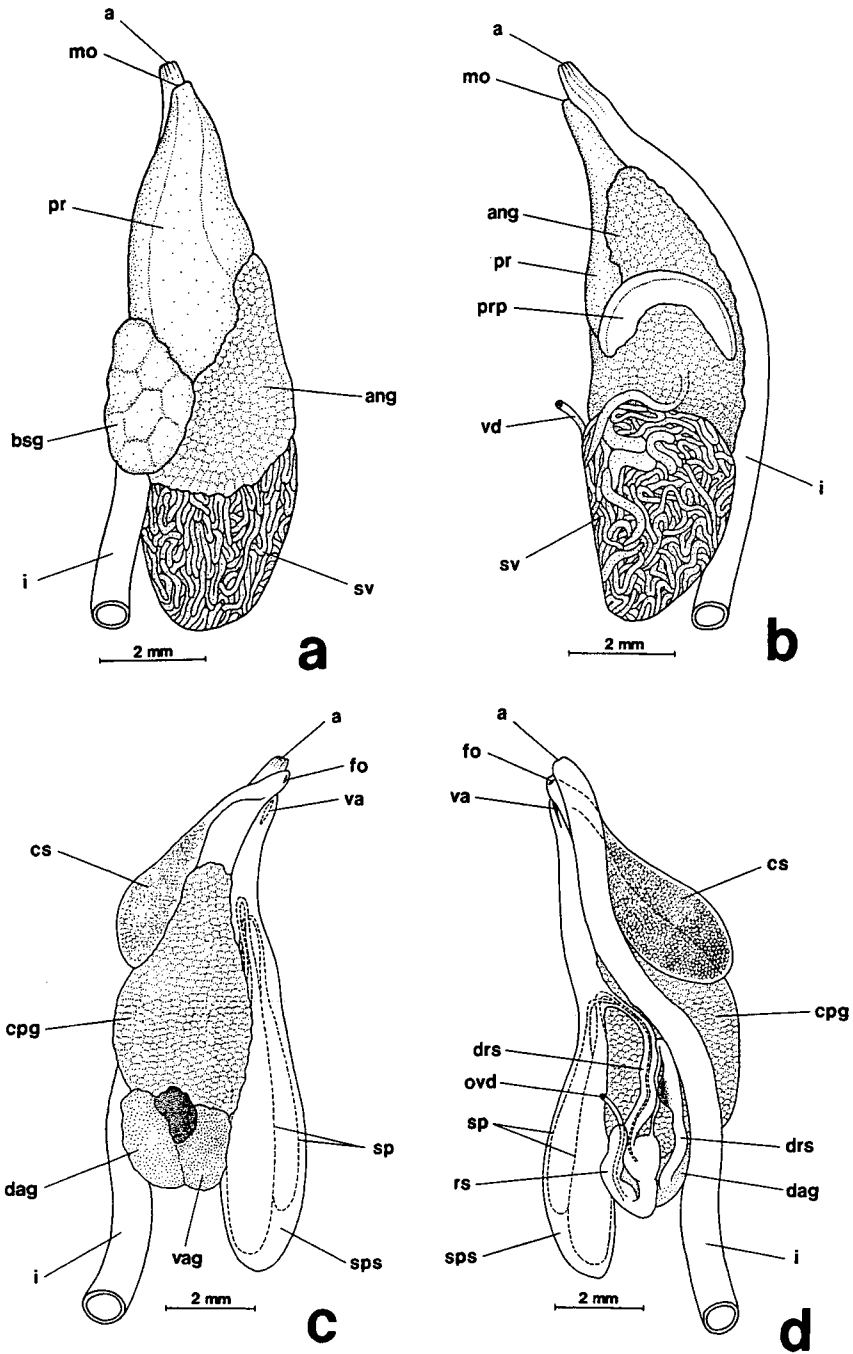
Fig. 76. *Nerita* (*Theliostyla*) *albicilla*. **a**, Dorsal view of the male pallial gonoduct. **b**, Ventral view of the male pallial gonoduct. **c**, Dorsal view of the female pallial gonoduct. **d**, Ventral view of the female pallial gonoduct.
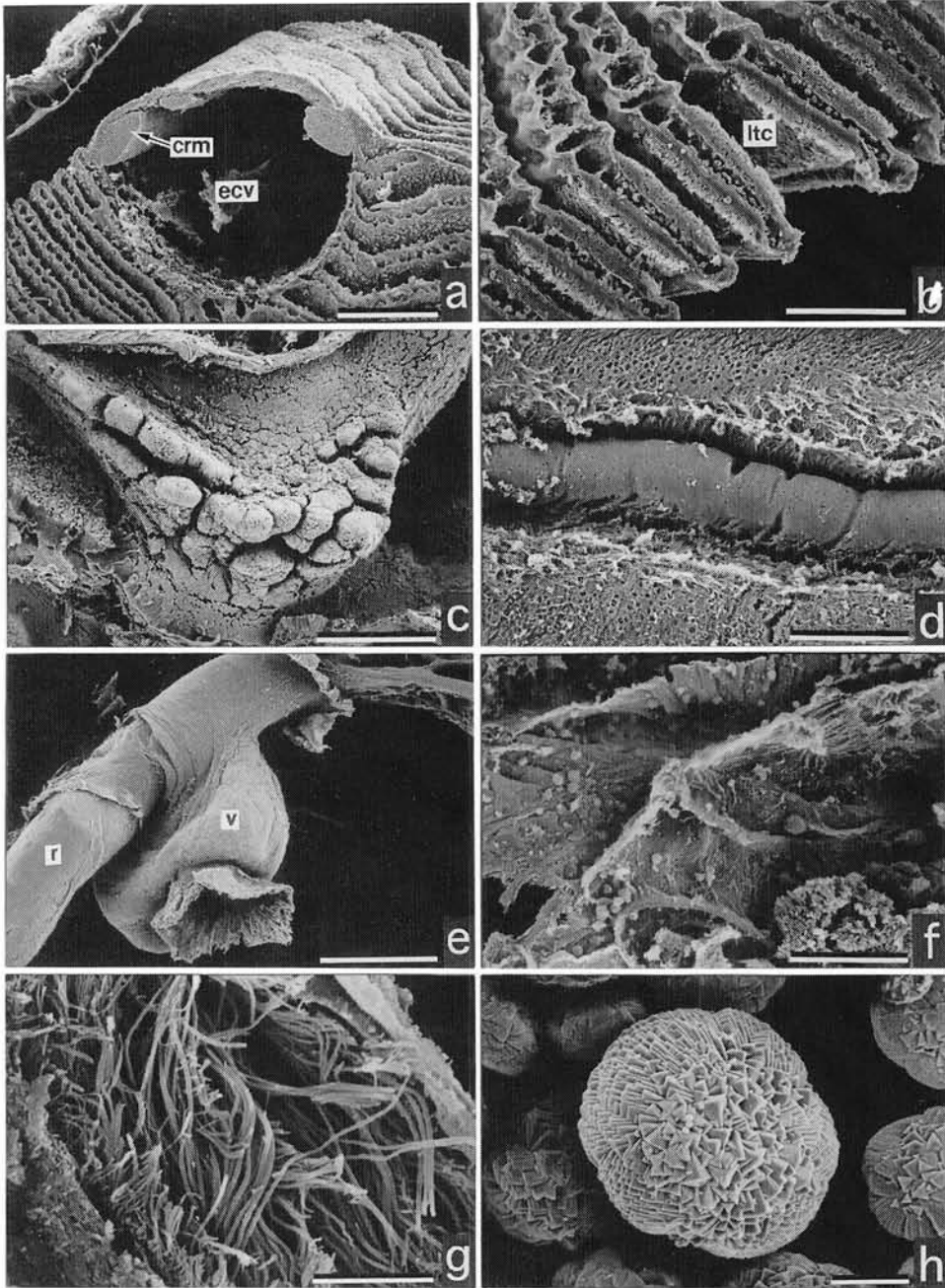
Fig. 77. *Nerita (Theliostyla) albicilla*. SEM micrographs of soft parts. **a-b**, RM 27673 a. **c-e**, RM 27673 b. **f-g**, RM 27673 c. **h**, RM 27673 d. **a**, Cross section of efferent ctenidial axis. Scale = 500 μm. **b**, Cross section on the efferent side of ctenidial lamellae, showing absence of skeletal rods. Scale = 100 μm. **c**, Vestigial gill on right pallial wall. Scale = 500 μm. **d**, Enlarged view of osphradium and its ciliated zones. Scale = 100 μm. **e**, Ventricle penetrated by rectum. Scale = 1 mm. **f**, Inner wall of glandular part of kidney. Scale = 50 μm. **g**, Spermatozoa within seminal vesicle of male. Scale = 10 μm. **h**, Egg reinforcement crystals removed from crystal sac of female. Scale = 25 μm.
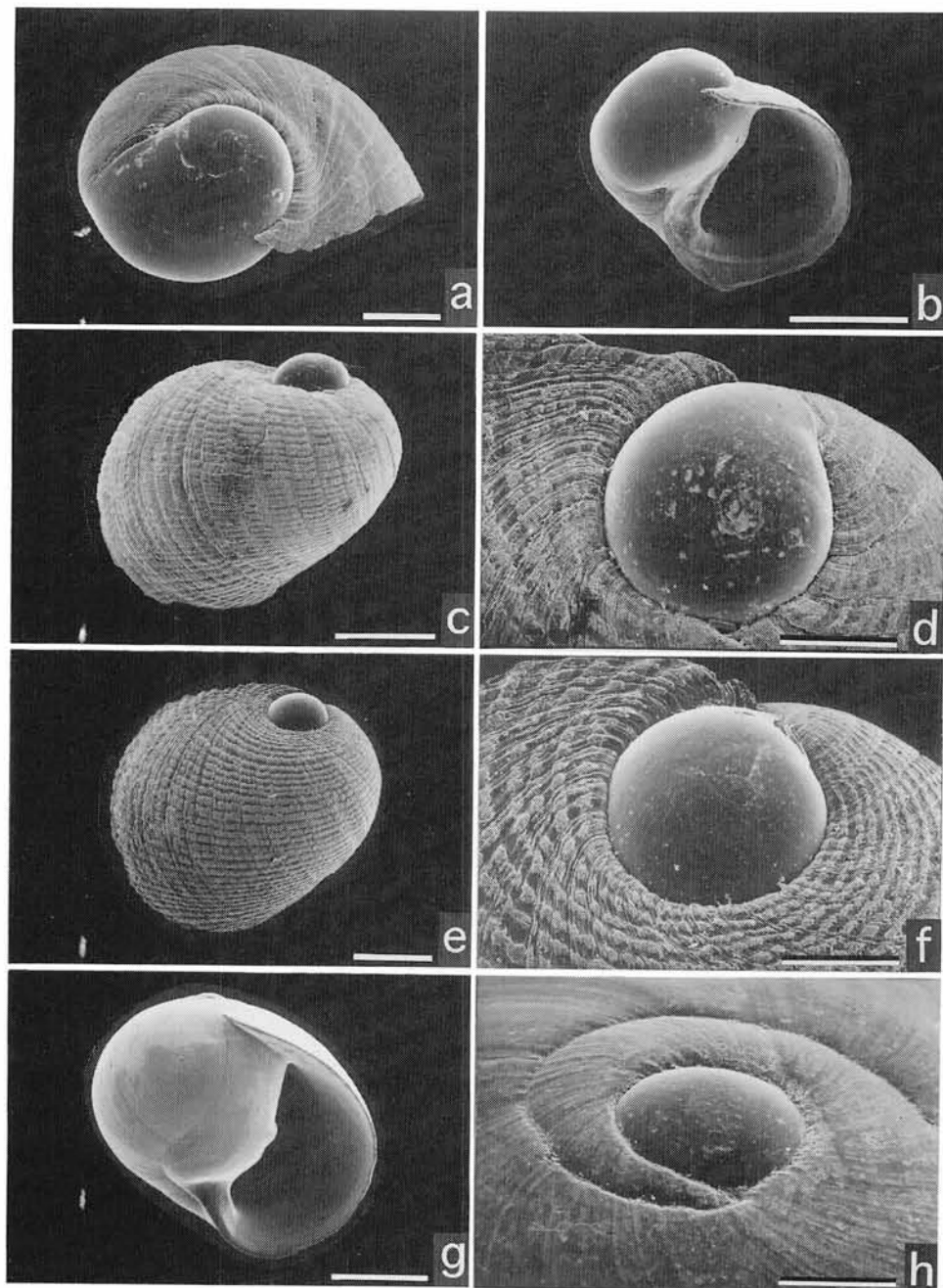
Fig. 78.   Protoconch of Neritidae. **a-b**, *Nerita (Theliostyla) albicilla*. RM 27674. **a**, Apical view. Scale = 250 μm. **b**, Ventral view. Scale = 500 μm. **c-d**, *Nerita (Puperita) bensoni*. RM 27675. **c**, Dorsal view of juvenile shell. Scale = 500 μm. **d**, Apical view of protoconch. Scale = 200 μm. **e-f**, *Nerita* sp. RM 27676. **e**, Dorsal view of juvenile shell. Scale = 500 μm. **f**, Apical view of protoconch. Scale = 200 μm. **g-h**, *Pisulina adamsiana*. RM 27679. **g**, Ventral view of subadult shell. Scale = 500 μm. **h**, Oblique apical view of protoconch. Scale = 100 μm.

ing from inner sides of posterior cartilages, inserting on ventral plane of radular sac. Postmedian retractors and tensor of radular sac absent.

Odontophoral cartilage consisting of anterior, posterior, and median pairs (Figs. 75 c, d). Anterior cartilages (aca) elongated, attached posteriorly to posterior cartilages (pca). Unpaired median cartilage (mca) lying on median grooves between paired anterior cartilages. Small sublingual cartilage (slc) below anterior tip of subradular membrane (Fig. 74 d).

Ventral sides of anterior cartilages connected to ventral approximator (vap). Anterior and posterior cartilages longitudinally linked with outer approximators (oap). Sides of anterior cartilages attached to body wall by thin tensor muscles (tac) (Figs. 74 b-d, 75 a).

Licker absent on anterior tip of subradular membrane (Fig. 74 d). Inside of oral tube thickened by cuticularized epithelium. Sides of buccal pouches especially thickened by glandular epithelium composed of tall columnar cells. Salivary glands not differentiated around buccal cavity. Paired sublingual glands (slg) projecting on sides of sublingual pouch (Fig. 74 c). Radular diverticulum deeply formed.

Anterior esophagus dorsoventrally depressed with paired lateral esophageal pouches (lep) and median dorsal food channel (dfc). Lateral esophageal pouches gradually increasing in width posteriorly, forming large spaces; inner wall covered with separate posterior esophageal glands (peg) (Fig. 74 a). Posterior part of pouches truncated from main trunk of esophagus. Remaining part of esophagus reducing in diameter, forming posterior esophagus (pe) with inner surface sculptured by longitudinal furrows.

Stomach (st) well-inflated, oval (Fig. 75 e), with right side exposed on surface of visceral hump in ventral view. Corrugated pattern of sorting area partly visible externally as fine lines (Fig. 73 b). Gastric caecum small, crescent-shaped. Interior of stomach containing paired openings of digestive glands, large cuticularized gastric shield, tooth of gastric shield, ciliated sorting area, and intestinal groove between major and minor typhlosoles. Opening to intestine lying on left posterior side of stomach.

Intestine (i) with complicated course, forming anterior loops twice over posterior esophagus (Fig. 75 e). Rectum penetrating pericardium and ventricle (Fig. 77 e), running along genital ducts, ending as anus (a) on anteroventral side of genital pore.

Circulatory System: Posterior end of pericardium deeply elongated into visceral region along left shell muscle. Heart consisting of paired unequal auricles and median ventricle (Fig. 73 b). Right auricle (ra) reduced but functional, connected to renal wall. Left auricle (la) well-developed, receiving blood from ctenidium and mantle skirt. Inner wall of ventricle firmly supported by muscular strands. Blood vessel from ventricle bifurcating into anterior and posterior aortae. Bulbous aorta not formed.

Excretory System: Single kidney (k) on posterior side of ctenidium (Fig. 73 a). Internal wall distinctly partitioned into two portions. Glandular part on right side filled with folded walls (Fig. 77 f), extending gradually toward anterior right corner; left side of non-glandular area forming larger smooth space. Renopericardial duct running toward right side of kidney; renopericardial pore perforating anterior section of glandular zone of kidney. Opening of kidney represented by vertical slit.

Reproductive System: Gonad lying on dorsal end of visceral hump (Figs. 73 a, b). Sexes separate. In both testis and ovary, gametes aggregating into cylindrical clusters of similar form; ovary distinguished by black epithelium in contrast to non-pigmented epithelium of testis. Gonoduct not connected to kidney. Pallial gonoduct showing remarkable sexual dimorphism.

Male Gonoduct (Figs. 76 a, b): Vas deferens (vd) from testis totally covered with dark gray epithelium, distal part especially forming very complicated entangled mass of ducts below hypobranchial glands, serving as seminal vesicle (sv). Extended part of seminal vesicle including completed spermatozoa (Fig. 77 g) packed within spermatophore, exhibiting whitish hue. Course of seminal vesicle completely random; terminal part of vas deferens invariably opening into pallial gonoduct from ventral side. Most of pallial gonoduct covered ventrally by prostate gland (pr), divided by ridges internally. Middle part of prostate twisted to

form crescent-shaped prostate pouch. Dorsal side of prostate attached by so-called basal gland (bsg) composed of translucent gelatinous tissue of large glandular cells. Posterior half of prostate covered by so-called annex gland (ang) both ventrally and dorsally. Ventral lobe of annex gland covering larger area of prostate than dorsal side. Ciliated sperm groove between gonopore and cephalic penis absent.

Female Gonoduct (Figs. 76 c, d): Female gonoduct with two genital openings (diaulic), consisting of three major parts: (i) spermatophore sac (sps) and receptaculum seminis (rs) for reception and storage of sperm; (ii) oviduct (ovd) as conduit of egg cells; (iii) pallial oviduct for production of egg capsule enclosing fertilized eggs.

Spermatophore sac opening as vagina (va). After copulation, spermatophores conveyed into spermatophore sac with rounded part directed posteriorly. Long filamentous tip penetrating far back into chamber of receptaculum seminis. Ducts of receptaculum seminis (drs) composed of three parts: (i) Proximal part arising anteriorly from spermatophore sac, posteriorly followed by receptaculum seminis. (ii) Middle part becoming extremely thin compared to other parts. (iii) Distal part recurved, becoming thick again, leading to ventral albumen gland (vag), inflating in middle to form right-directed extension pigmented black internally (Fig. 76 d), of unknown function.

Posterior end of pallial gonoducts comprised of albumen glands divided into two parts. Ventral albumen gland (vag) mainly lying on ventral side, receiving sperm from ducts of receptaculum seminis. Dorsal albumen gland (dag) partly overlying ventral gland, connected to oviduct from ovary. Boundary between ventral and dorsal glands with particular glandular zone staining darkly in methylene blue. More anteriorly, pallial oviduct mainly consisting of capsule gland (cpg). Crystal-secreting sac (=crystal sac) (cs), attached to termination of gonoducts, connected to gonoduct only near female opening anteriorly. Sac distended in breeding season by egg reinforcement crystals (Fig. 77 h), becoming clearly visible from dorsal surface by whitish color. Female opening (fo) simple pore; opening of vagina slit-like.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia (cg) situated at bases of cephalic tentacles. Pleural and pedal ganglia fused, forming massive complex. Pedal ganglia closely located; pedal commissure represented by short and broad contact zone. Right and left pleural ganglia connected by thick pleural commissure.

In buccal region, cerebral ganglia connected to cerebral commissure (cc) in front of buccal cavity (Fig. 75 a). Cerebral ganglia giving off branches of oral nerve (on) anteriorly, and tentacular and optic nerves (tn, opn) laterally. Nerve to cephalic penis arising from beneath sublingual pouch; labial commissure (lc) connecting right and left cerebral ganglia. Labial ganglia absent. Cerebrobuccal connectives branching from labial commissure, not directly from ventral extension of cerebral ganglia. Buccal ganglia (bg) connected with buccal commissure over odontophore between anterior esophagus and radular diverticulum.

Visceral loop forming very loose loop in accordance with deep pallial cavity. Origin of loop only from right pleural ganglion. Subesophageal part of loop much thicker than supraesophageal part, the latter arising from more anterior part of right pleural ganglion than the former. Below pallial gonoduct and "vestigial gill," subesophageal ganglion supplying nerves to genital duct, gonad, and right shell muscle. Loop further continuing to visceral ganglion lying below kidney opening, innervating kidney, pericardium, and digestive tract.

Very thin supraesophageal loop ascending to right side of buccal mass, passing over esophagus, finally reaching base of ctenidium where it diverges into anterior and posterior parts. Anteriorly directed part entering base of efferent ctenidial membrane, also innervating ctenidium and osphradium. Posteriorly directed part representing viscero-supraesophageal connective, running along floor of pallial cavity, uniting with visceral ganglion.

Lateral body walls receiving dense innervation directly from pleural ganglia. Thick nerves especially penetrating anterior rims of shell muscles, extending mantle margin circularly, forming zeugoneury with

supraesophageal loop on left side.

Pedal ganglia with thick pedal cords with many fine pedal nerves to pedal musculature. From anterior part of pedal ganglia, pair of thin anterior pedal nerves extending toward pedal region below head. Statocysts on dorsal sides of pedal ganglia.

Nerita (Puperita) bensoni (Récluz, 1850)
(Figs. 78 c-d)

Protoconch: Protoconch globular, multispiral, orthostrophic. Surface completely smooth except for fine growth lines. Protoconch terminating in clear line, followed by teleoconch sculptured by axial growth lines and about 40 spiral cords.

Nerita sp.
(Figs. 78 e-f)

Protoconch: Protoconch globular, multispiral, with fine growth lines. Coiling direction orthostrophic. Early teleoconch sculptured by about 35 thick, rough, granulose radial riblets.

Pisulina adamsiana G. and H. Nevill, 1869
(Figs. 78 g-h)

Protoconch: Protoconch globular, multispiral, orthostrophic. Fine growth lines visible on exterior surface, details unclear in worn empty shells examined. Protoconch mostly covered by teleoconch, with only small apical area exposed.

Septalia porcellana (Linnaeus, 1758)
(Figs. 79 a-d, 80 a-b)

External Anatomy: Animal limpet-shaped. Mantle margin simple, without microtentacles. Attachment area of shell muscle horseshoe-shaped, interrupted posteriorly (Fig. 79 a). Muscle not divided into bundles or penetrated by blood vessels.

Head with short snout (sn), paired non-papillate cephalic tentacles (ct), eyestalks (es), and right cephalic penis (pen) in male. Outer lip enlarged into broad disk with extended oral lappets. Eyestalks laterally extended, broader than cephalic tentacles. Eyes (e) closed with cornea. Cephalic penis arising from right side; anterior ventral margin marked by deep groove.

Epipodium lacking sensory projections of epipodial tentacles and sense organs. Calcified operculum in space between foot and visceral hump, buried in pedal musculature anteriorly.

Pallial Complex: Pallial cavity very deep, reaching 80% of body length in deepest section, containing left ctenidium, left osphradium, left kidney opening, anus, genital opening(s), and right hypobranchial gland (Fig. 79 a). "Vestigial gill" absent on right side (unlike in *Nerita*).

Ctenidium (c) bipectinate. Both afferent and efferent axes widely supported by broad afferent and efferent membranes. Ctenidial lamellae depressed, with apices revealing weak ridges medially. Efferent side of lamellae lacking skeletal rods and bursicles.

Osphradium (os) with lateral ciliated zones lying along anterior end on right side of shell muscle in extension line of efferent ctenidial membrane. Hypobranchial gland (hg) associated with genital duct on right side.

Digestive System: Buccal musculature identical in composition with that in *Nerita*. Jaws composed of paired plates on dorsal side of oral tube, connected medially to filmy inner surface. Surface and anterior margin smooth.

Radular sac long, with several loops; posterior end simple. Radular formula n–(1 + 3)–1–(3 + 1)–n.

Fig. 79. *Septaria porcellana*. **a**, Dorsal view of the animal after removal of the shell and mantle. **b**, Configuration of the alimentary tract. **c**, Internal structure of the stomach. **d**, Nervous system.

Radular row symmetrical. Central tooth rectangular with shortly stalked base; non-denticulate cusp clearly formed by thick reflection. First inner laterals transversely elongated; posterior margin of base concave, with backward extension near outer corner; cusp triangular with rounded tip. Second and third laterals extremely reduced relative to other teeth, longitudinally narrow with indistinct cusps. Outer (fourth) laterals largest in radular row; cusp laterally thickened in shield-like shape; cutting edge lacking denticles; shaft stout, robust, with deep basal hole; cusp continuing to membranous extension of shaft whose margin sigmoidally bent. Lateromarginal plates absent. Marginal teeth with elongated shafts and finely denticulate
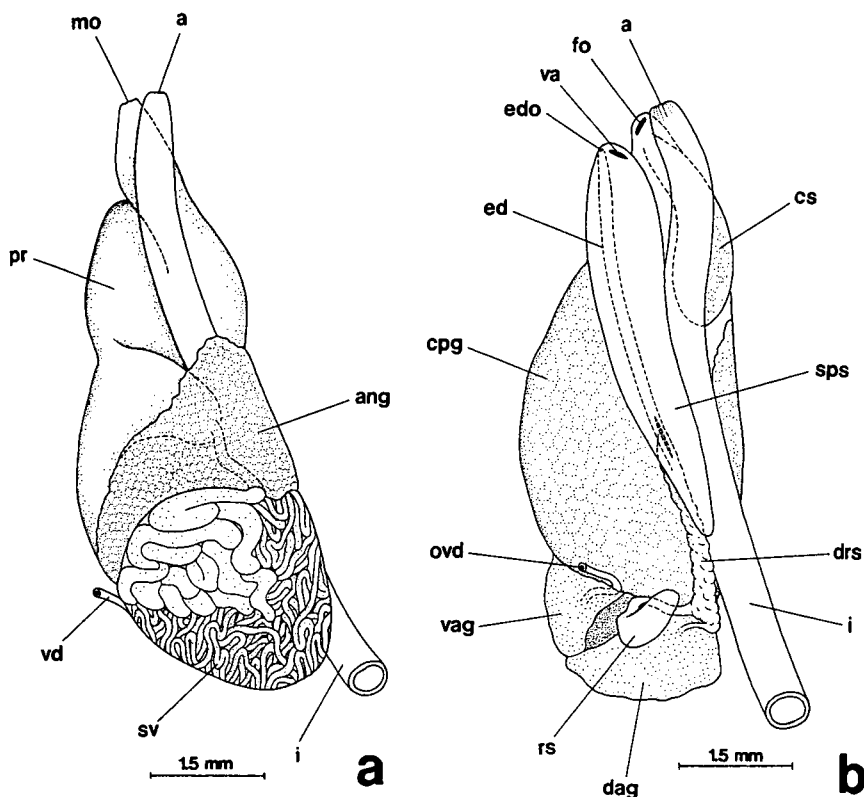
Fig. 80.   *Septaria porcellana*. a, Ventral view of the male pallial gonoduct. b, Ventral view of the female pallial gonoduct.

cusps.

Odontophore containing paired anterior, posterior, and median odontophoral cartilages. Sublingual cartilage absent (unlike in *Nerita*).

Licker absent. Sublingual pouch well-developed, with sublingual glands projecting on outer sides. Radular diverticulum clearly present. Salivary glands not differentiated around buccal cavity. Anterior esophagus depressed over odontophore. Lateral pouches (lep) followed by enlarged and septated posterior esophageal glands (peg) (Fig. 79 b). Mid-esophagus not clearly distinguished. Posterior esophagus (pe) very long, extending almost straight toward stomach at end of visceral region. Paired digestive glands (dg) with couple of ducts from stomach. Posterior wall of stomach giving rise to short gastric caecum (gc) (Fig. 79 c). Tooth of gastric shield (gst) lying on dorsal side. Sorting area (sa) and intestinal groove (ig) between major and minor typhlosoles (mt, nt) well defined on ventral side. Intestine (i) forming double loops anteriorly (alp), penetrating pericardium and ventricle, finally ending as anus (a) on left side of gonoduct.

Circulatory System: Pericardium lying in triangular area between ctenidium and kidney (Fig. 79 a). Posterior part of pericardium extending below visceral hump as tubular sac. Heart consisting of greatly asymmetrical pair of auricles and median ventricle. Left auricle (la) well-developed, receiving blood from ctenidium. Right auricle greatly reduced to thin string-like form.

Excretory System: Kidney (k) mostly occupying posterior part of mantle roof, extending into visceral region along rectum (Fig. 79 a). Lumen divided into lamellate glandular area on right side and smooth nonglandular area on left side. Renopericardial duct passing from anterior right corner of pericardium into ante-

rior chamber of glandular part of kidney. Kidney opening short slit.

Reproductive System: Gonad lying over digestive glands mainly on right side. Gonoduct not connected with kidney, showing extreme sexual dimorphism.

Male Gonoduct (Fig. 80 a): Vas deferens (vd) folded complexly as mass of innumerable loops in posterior end of pallial gonoduct. Proximal loops distended with sperm, where vas deferens functioning as seminal vesicle (sv). Most of pallial gonoduct occupied by prostate gland (pr). Seminal vesicle leading ventrally into prostate; their connection invisible externally due to covering of annex gland (ang). Basal gland (as in *Nerita*) absent. Prostate curving twice before opening in anterior pallial cavity. Ciliated sperm groove between gonopore to cephalic penis absent.

Female Gonoduct (Fig. 80 b): Female gonoduct with three genital openings (triaulic). Vagina (va) opening at tip of spermatophore sac (sps). From posterior lateral wall, duct arising through elongated slit, bifurcating at base into enigmatic duct (ed) anteriorly and duct of receptaculum seminis (drs) posteriorly. Enigmatic duct running anteriorly along spermatophore sac, discharging into pallial cavity at minute pore (edo). Duct of receptaculum roughly nodose on external surface, posteriorly branching into receptaculum seminis (rs) and duct to ventral albumen gland. Dorsal and ventral albumen glands (dag, vag) divided by median zone staining darkly in methylene blue. Most of pallial oviduct occupied by capsule gland (cpg). Crystal sac (cs) communicating with oviduct at distal end. Opening of gonoduct (fo) lying beside anus.

Nervous System: Circumesophageal nerve ring hypoathroid (Fig. 79 c). Cerebral ganglia (cg) at bases of cephalic tentacles. Cerebral commissure (cc) in front of buccal cavity. Pedal and pleural ganglia (pdg, plg) united as large paired mass behind buccal mass. Pedal ganglia connected by thick commissure. Pleural ganglia dorsally united by distinct pleural commissure (plc) whose right origin lies more posteriorly than that of left side.

In buccal region, labial ganglia absent, but distinct labial commissure (lc) connecting to cerebral ganglia ventrally behind mouth. Buccal ganglia (bg) arising from labial commissure, not directly from cerebral ganglia. Nerve to cephalic penis arising from inner part of right cephalic ganglion.

Visceral loop arising only from right pleural ganglion. Supraesophageal part of visceral loop much thinner than subesophageal part. The former running over buccal mass, while the latter extending along lateral body wall. Visceral ganglion (vg) lying on right side of kidney opening. Extremely thin viscero-supraesophageal connective forming complete visceral loop.

Pedal cords (pcd) giving off few branches. Pedal commissure indistinct. Statocysts (sta) attached to dorsal sides of pedal ganglia below pleural commissure.

Family Phenacolepadidae Pilsbry, 1895
Cinnalepeta pulchella (Lischke, 1871)
(Figs. 81 a-b, 82 a-b, 83 a-c, 84 a-b, 85 a-f)

External Anatomy: Animal limpet-shaped. Mantle margin clearly divided into inner and outer folds by deep periostracal groove. Inner fold of mantle margin with mamillate microtentacles (Figs. 85 a, b). Head with short snout (sn), pair of long non-papillate cephalic tentacles (ct), and short eyestalks (es) at outer bases (Fig. 81 a). Outer lip of mouth smooth, extended laterally with oral lappets. Eyes (e) closed on eyestalks. In males, long tentacular penis (pen) arising from ventral side of base of right cephalic tentacle (Fig. 85 b). Epipodium lacking epipodial tentacles and sense organs. No trace of internal operculum located in pedal musculature in serial sections. Shell muscle horseshoe-shaped without division or penetration by blood vessels.

Pallial Complex: Pallial cavity deepened in anterior two-thirds of body, containing left ctenidium, left kidney opening, anus, and genital opening(s) (Fig. 81 a). Hypobranchial gland and "vestigial gill" absent on right side.
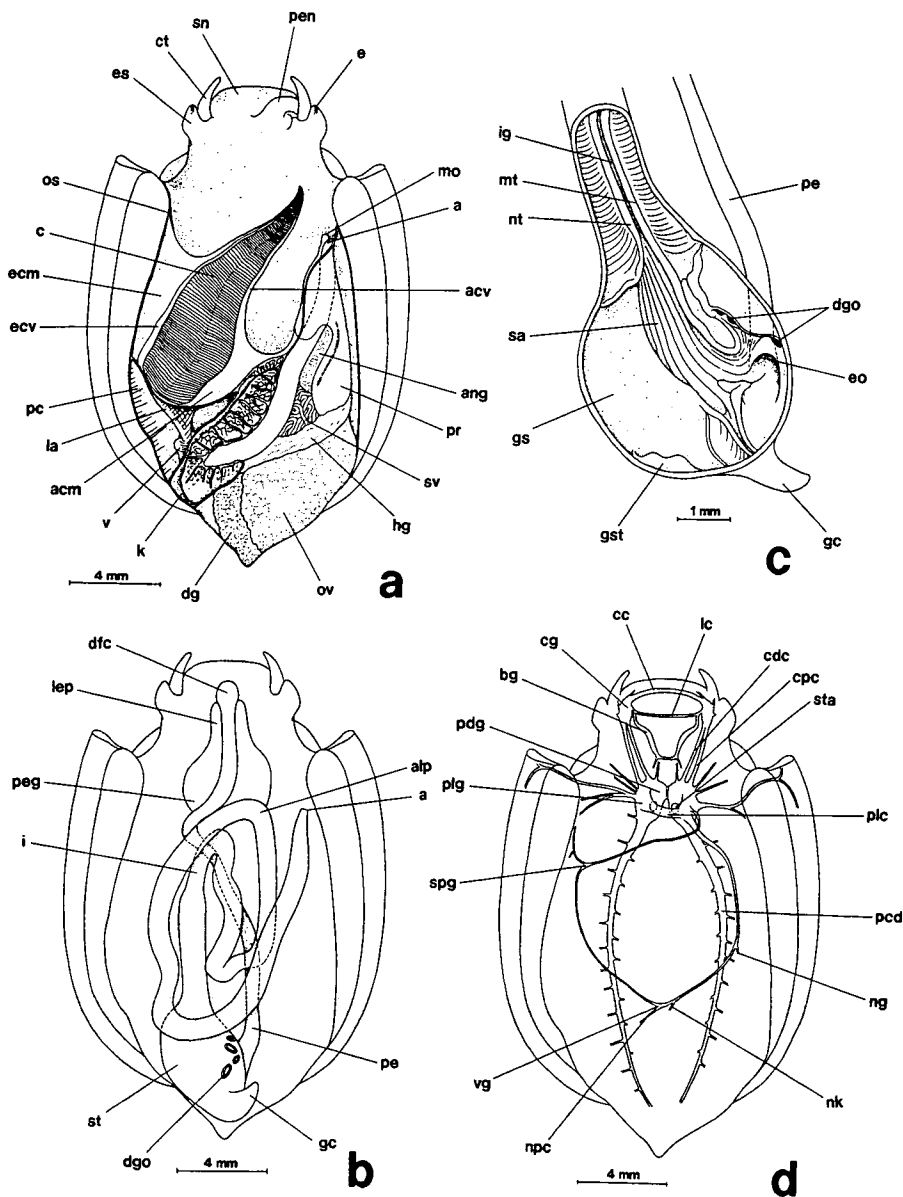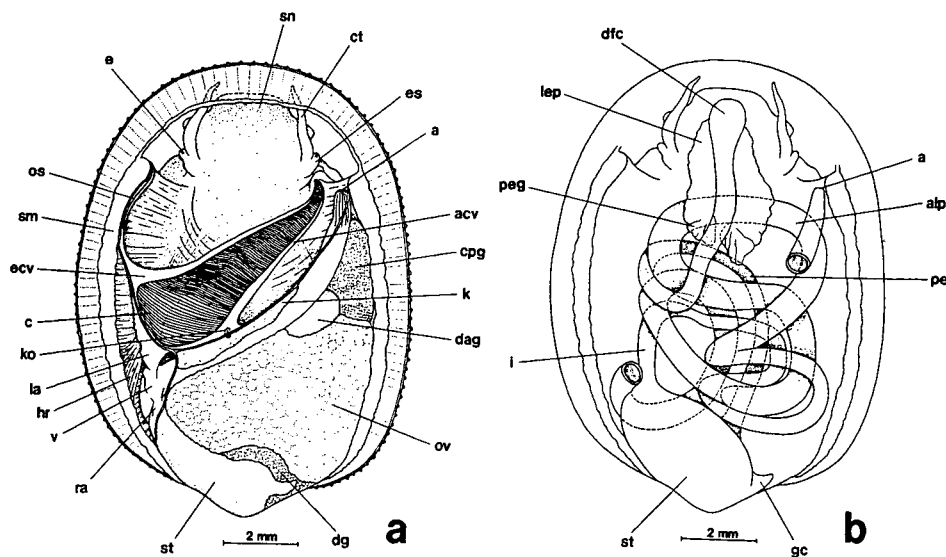
Fig. 81. *Cinnalepeta pulchella.* **a**, Dorsal view of the animal after removal of the shell and mantle. **b**, Configuration of the alimentary tract.
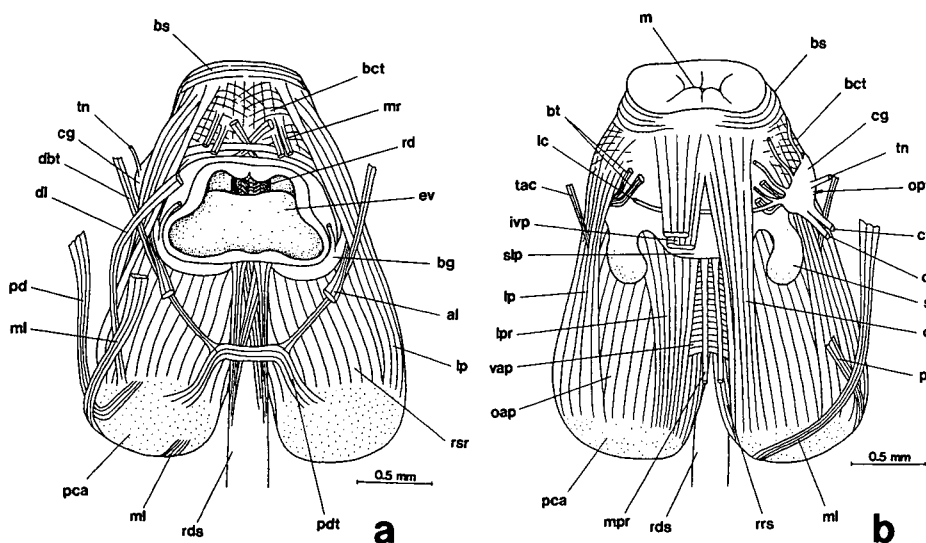
Fig. 82. *Cinnalepeta pulchella.* **a**, Dorsal view of the buccal mass. **b**, Ventral view of the buccal mass.

Ctenidium (c) bipectinate. Greater portion of ctenidial axes lacking ctenidial membranes. Internal structure of axes and surface cilia identical to those in *Nerita*. Ctenidial lamellae depressed, with centrally projecting terminal ridges. Efferent side lacking bursicles and skeletal rods. Osphradium (os) attached to inner margin of shell muscle, provided with lateral ciliated zones.

Digestive System: Odontophore connected to body wall by median and posterior levators (ml, dl), posterior depressors (pd), anterior levators (al), lateral protractors (lp), ventral protractors (ovp, ivp), and dorsal
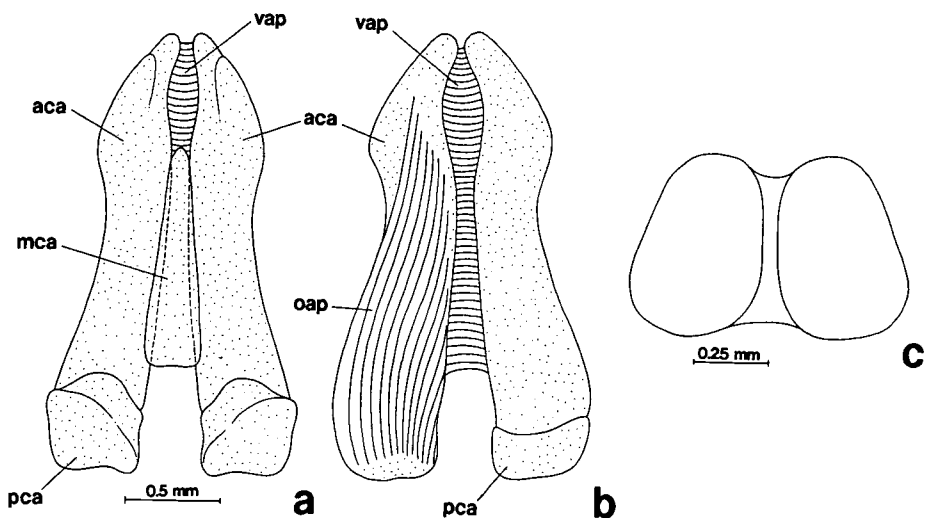
Fig. 83. *Cinnalepeta pulchella*. a, Dorsal view of the odontophoral cartilages. b, Ventral view of the odonto-phoral cartilages. The left outer approximator muscle is removed. c, Ventral view of the jaws.
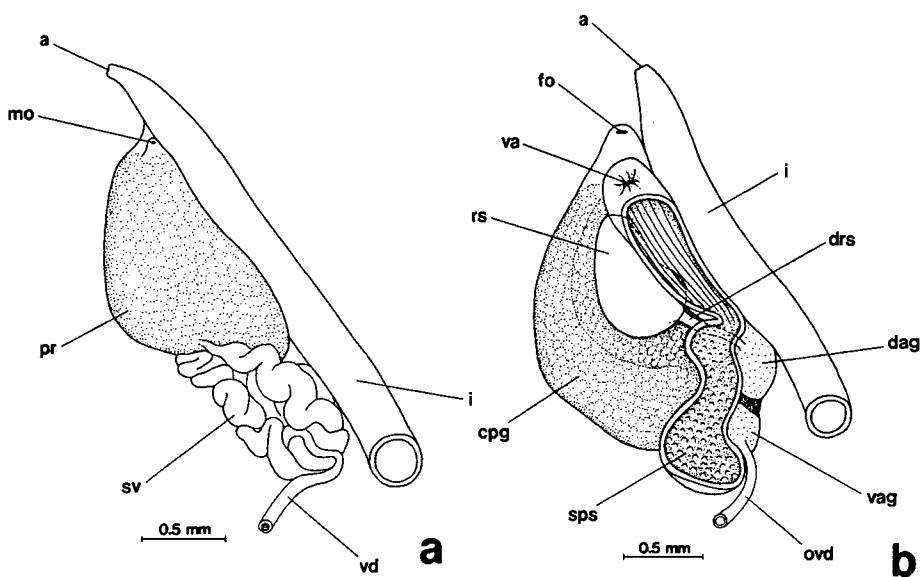
Fig. 84. *Cinnalepeta pulchella*. a, Ventral view of the male pallial gonoduct. b, Ventral view of the female pal-lial gonoduct. Part of spermatophore sac is cut to show the inner wall.

buccal tensors (dbt), (Figs. 82 a, b). Postdorsal buccal tensor (pdt) connecting right and left sides of poste-rior cartilages.

Jaws consisting of paired thin plates attached to dorsal side of oral tube (Fig. 83 c). Radular sac almost straight, not coiled. Posterior end simple. Radular formula n−(1 + 3)−1−(3 + 1)−n (Figs. 85 e, f). Tooth row symmetrical. Central tooth nearly square in frontal view, with slightly extended basal margins, without dis-tinct cusp. First inner lateral teeth greatly obliquely elongated; outer corner situated more anteriorly than in-
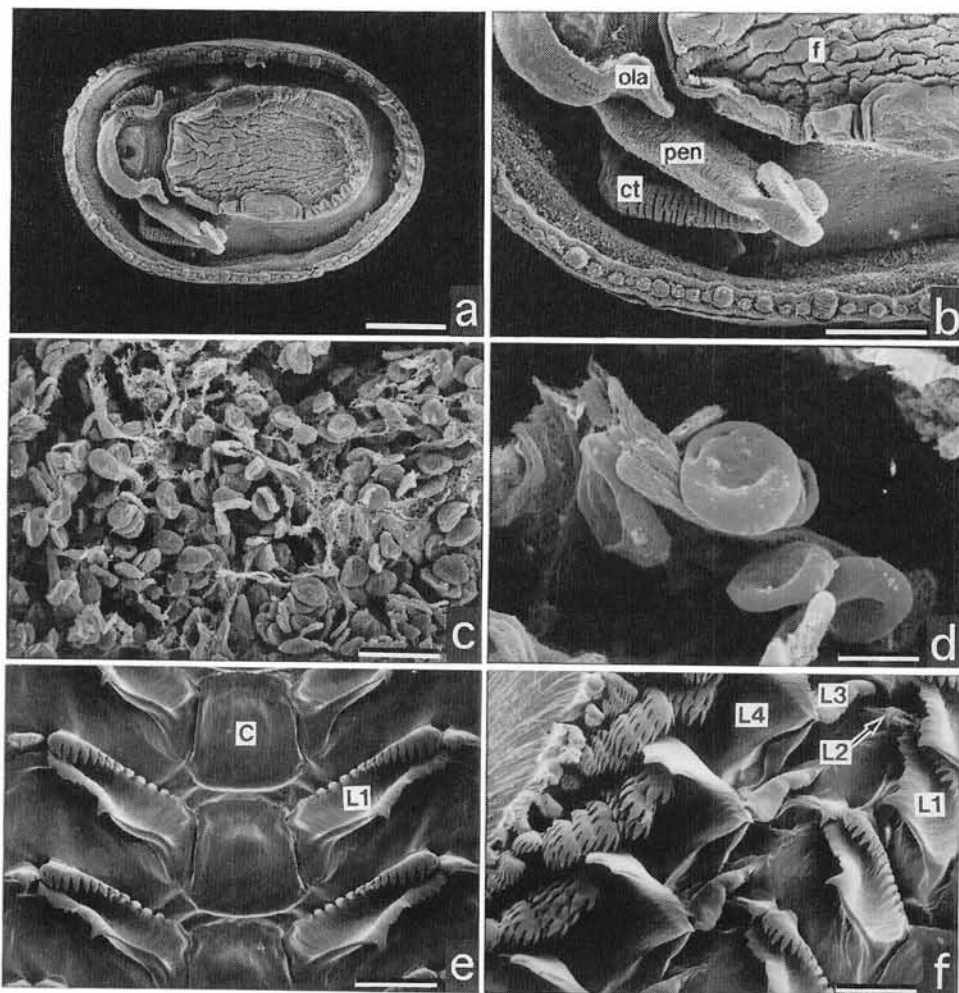
Fig. 85. *Cinnalepeta pulchella.* SEM micrographs of soft parts. **a-b**, RM 27681 a. **c-d**, RM 27681 b. **e-f**, RM 27682. **a**, Ventral view of animal. Scale=1 mm. **b**, Cephalic penis and right cephalic tentacle. Scale =500 μm. **c**, Erythrocytes in sinus of mantle margin. Scale=25 μm. **d**, Enlarged view of erythrocytes. Scale=5 μm. **e**, Central and innermost lateral teeth. Scale=25 μm. **f**, Oblique view of left innermost lateral to marginal teeth. Scale=25 μm.

ner corner; cusp saw-like, with fifteen sharp denticles; base with reflected flaps projecting as sharp median denticle. Second inner laterals small, almost fused with first teeth. Third laterals enrolled inside, with posteriorly elongated base. Outer (fourth) laterals longitudinally straight; cusp angulate with three weak denticles. Lateromarginal plates absent. Marginal teeth thin, long, with sharply denticulate cusps.

Subradular membrane controlled anteriorly by median and lateral protractors (mpr, lpr), and posteriorly by retractors (rsr). Radular sac controlled by retractor muscles (rrs) between pairs of cartilages. Tensor and other retractors absent in radular sac.

Odontophore cartilages consisting of longer anterior and smaller posterior pairs of cartilages (aca, pca) and unpaired median cartilage (mca) (Figs. 83 a-b). Paired anterior cartilages united by ventral approximator (vap); anterior and posterior cartilages connected by outer approximators (oap). Tensor muscles of anterior cartilage (tac) originating from body wall, inserting on sides of anterior cartilages, passing between lat-

eral protractors (lp) (Fig. 82 b). Sublingual cartilage absent.

Sublingual pouch (slp) deep, with outgrowth of sublingual gland (slg) on each side (Fig. 82 b). Radular diverticulum shallow. Licker absent at anterior part of subradular membrane. Salivary glands absent. Anterior esophagus accompanied by long lateral pouches (lep) in septate posterior esophageal glands (peg) (Fig. 81 b). Terminal section of glands posteriorly separated from main channel of esophagus, extending ventrally along posterior slope of buccal mass. Posterior esophagus (pe) running along base of visceral mass, opening into stomach on right side.

Stomach (st) provided with pair of openings to digestive glands, small gastric caecum (gc), toothed gastric shield, narrow sorting area, and intestinal groove between major and minor typhlosoles. Intestine (i) forming complicated course of about five loops (Fig. 81 b); rectum penetrating pericardium and ventricle, anus (a) opening beside right end of shell muscle.

Circulatory System: Pericardium compressed along inner wall of shell muscle on left side. Posterior part of pericardium extending into ventral part of stomach as narrow tube. Heart consisting of asymmetrically paired auricles and single ventricle. Left auricle (la) connected to efferent ctenidial vessel; reduced right auricle (ra) apparently lacking circulatory function.

Mantle margin thickened to develop into spongy space as respiratory surface (Fig. 85 c). Side of foot also with particular blood space. Discoidal erythrocytes, each 8 μm in diameter and 1.6 μm thick (Fig. 85 d), densely distributed throughout vascular system. Because of their presence, animal entirely reddish in living condition, immediately turning pale after fixation.

Excretory System: Single left kidney (k) in elongated area of pallial cavity wall along rectum (Fig. 81 a). Lumen divided into glandular and non-glandular areas. Kidney opening (ko) below origin of afferent ctenidial vessel as non-papillate, simple, longitudinal slit.

Reproductive System: Gonochoristic gonad (g) lying over digestive glands and stomach. Gonoduct not connected to kidney, exhibiting sexual dimorphism.

Male Gonoduct (Fig. 84 a): Vas deferens (vd) from ventral side of testis coiling complexly to form seminal vesicle (sv), leading anteriorly to prostate (pr) covered by another glands histologically identical to those of annex gland in *Nerita*. Basal gland absent. Opening (mo) lying at ventral tip of gonoduct. Ciliated sperm groove between gonopore and cephalic penis absent.

Female Gonoduct (Fig. 84 b): Female gonoduct with two genital openings (diaulic). Vagina (va) opening on top of anterior section; posterior section functioning as spermatophore sac (sps). Two sections distinguished externally by constrictions and internally by corrugated or papillate sculpture. Anterior section leading through narrow slit into neighboring receptaculum seminis (rs), which extends to pallial oviduct by short duct. Oviduct connected to ventral albumen gland (vag); dorsal albumen gland (dag) receiving duct from receptaculum seminis. Dorsal and ventral albumen glands separated by distinct median glandular zone. Capsule gland (cpg) well-developed throughout pallial oviduct. Crystal sac absent. Opening (fo) lying on anterodorsal side of vagina.

Nervous System: Circumesophageal nerve ring hypoathroid. Pedal and pleural ganglia concentrated. Right and left pleural ganglia connected by pleural commissures. Cerebral ganglia (cg) ventrally united by labial commissure (lc) without labial ganglia (Fig. 81 b). Connectives to buccal ganglia originating in labial commissure, not in cerebral ganglia. Supra- and subesophageal portions of visceral loop both arising from pleural ganglia. Viscero-supraesophageal connective not clearly traceable. Pedal cords apparently lacking distinct commissures. Statocysts on dorsal sides of pedal ganglia below pleural commissure.

Phenacolepas sp.
(Figs. 86 a-d)

Protoconch: Protoconch globular, multispiral. Apex projecting to right due to orthostrophic growth. In-
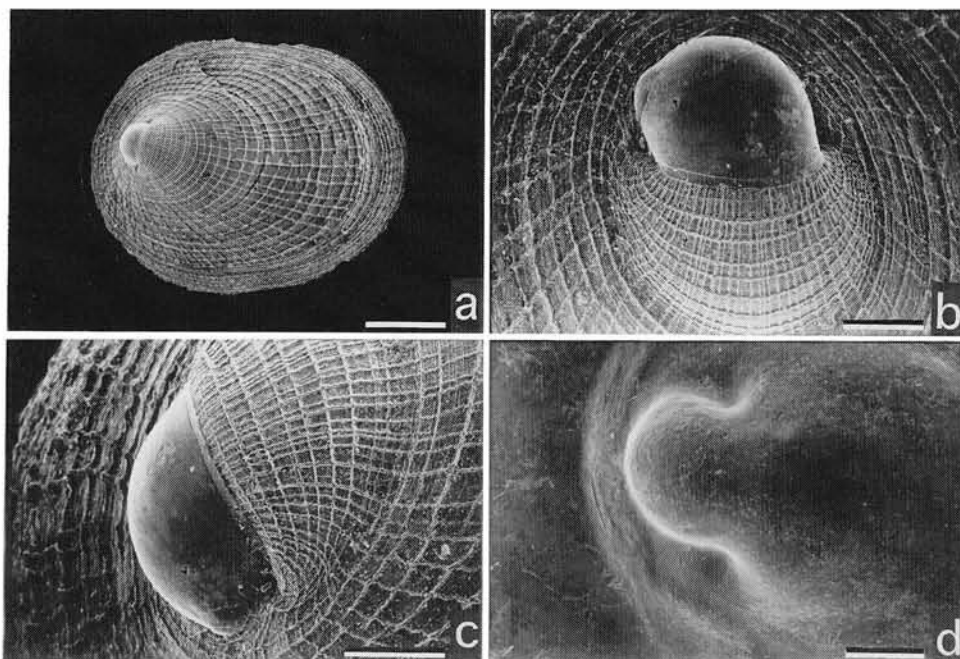
Fig. 86. Protoconch of *Phenacolepas* sp. RM 27683. **a**, Dorsal view of subadult shell Scale=1 mm. **b**, Dorsal view of apical area. Scale=250 μm. **c**, Right oblique view of apical area. Scale=250 μm. **d**, Reabsorbed inner side of protoconch. Scale=250 μm.

ner side of protoconch completely absorbed (Fig. 86 d); exterior part of protoconch including coiled suture retained in shell apex.

Family Hydrocenidae Troschel, 1856
Georissa japonica Pilsbry, 1900
(Figs. 87 a-d)

Protoconch: Protoconch completely globular. Narrow aperture formed anteroventrally, generating short deep suture. Surface covered with irregular depressions in addition to circular lines. Protoconch-teleoconch boundary expressed as smoothly thickened lip.

Family Helicinidae Féussac, 1882
Waldemaria japonica (A. Adams, 1861)
(Figs. 88 a-b, 89 a-e, 90 a-d, 91 a-b)

External Anatomy: Animal discoidal, lacking spiral visceral hump, although shell spirally coiled. Axial cleft formed for columellar septum (Figs. 88 a, b).

Mantle margin lacking circumpallial tentacles. Head with short snout, non-papillate cephalic tentacles, eyestalks. Outer lip of mouth simple, without oral lappets or microtentacles. Eyes lying on eyestalks outside bases of cephalic tentacles, closed by cornea. Male lacking cephalic penis on right side.

Foot rather clearly divided into lateral and ventral portions in fixed specimens. Ventral part smooth, with opercular attachment (op). Surface of dorsal part with rough appearance. Surface of epipodium tuberculate, lacking sensory projections. Calcareous operculum present.

Shell muscles paired, completely divided into dorsal (right) and ventral (left) portions (rcm, lcm). Mus-
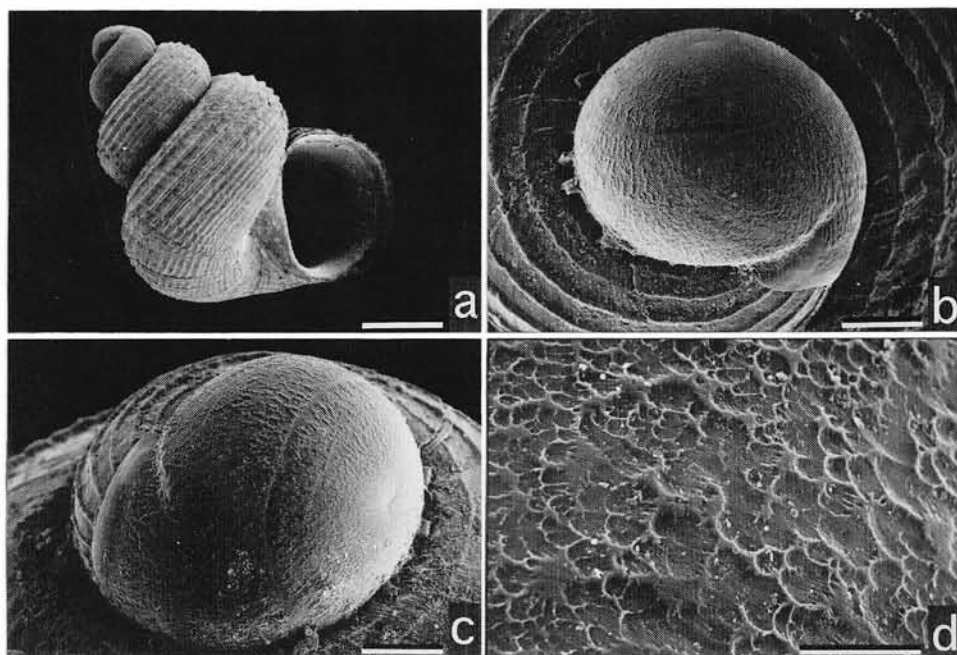
Fig. 87.   Protoconch of *Georissa japonica*. RM 27684. **a**, Ventral view of adult shell. Scale=500 μm. **b**, Apical view of protoconch. Scale=100 μm. **c**, Oblique view of protoconch. Scale=100 μm. **d**, Sculpture of side of protoconch. Scale=20 μm.

cles not divided or penetrated by blood vessels. Head retractor muscle indistinct.

Pallial Complex: Pallial cavity deep, attaining more than half of body whorl, containing kidney opening, pallial gonoduct, anus, and right hypobranchial gland (Figs. 88 a, b). Ctenidium absent, replaced by vascularized mantle skirt. Blood vessels densely developed, especially near efferent and afferent pallial vessels. Osphradium absent. Hypobranchial gland (hg) well-developed in deepest region of pallial cavity roof, discharging into pallial cavity via short hypobranchial duct on posterior side of vaginal opening.

Digestive System: Oral tube surrounded by buccal sphincter and constrictor (bs, bct) with mandibular protractors and retractors (mp, mr). From ventrolateral sides near outer margin of jaws, thin buccal tensors (bt) extending ventrally to ventral body wall.

Muscle controlling odontophore including posterior depressors (pd), anterior levators (al), outer posterior levators (opl), lateral protractors (lp), and outer and inner ventral protractors (ovp, ivp) (Figs. 89 a, b). Median and dorsal levators and dorsal buccal tensor absent. Posterior part of cartilages united by postdorsal buccal tensor (pdt).

Jaws composed of simple translucent plates entirely adhering to dorsal side of oral tube. Inner surface and anterior margin not sculptured.

Radular sac almost straight, terminating near opening of esophagus to stomach. Posterior end simple without bifurcation. Radular formula n–(1+3)–1–(3+1)–n (Figs. 90 a-d). Radular row symmetrical. Central tooth longitudinally rectangular, with weak lateral extensions and simple plate-like cusp. First and second inner lateral teeth similar in size to central tooth; cusps serrated with four to six denticles. Third lateral teeth reduced, plate-like, situated at base of outer lateral teeth. Outer (fourth) lateral teeth greatly enlarged, exhibiting very characteristic complex form; cusp prolonged on inner anterior sides, where sharply serrated with five denticles; base strongly projecting backward in median part, also extending toward outside.
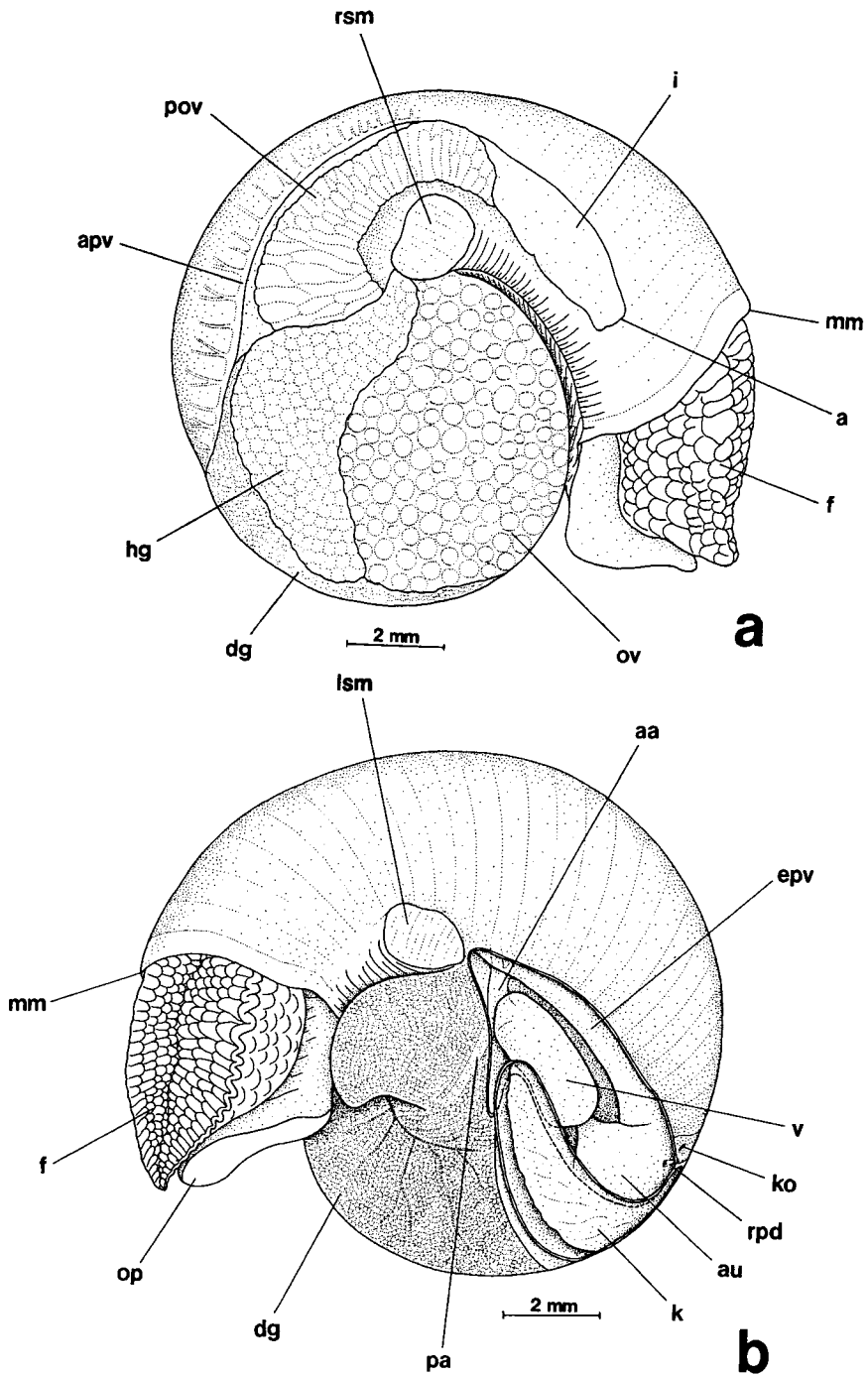
Fig. 88. *Waldemaria japonica*. **a**, Apical view of the animal. **b**, Basal view of the animal.
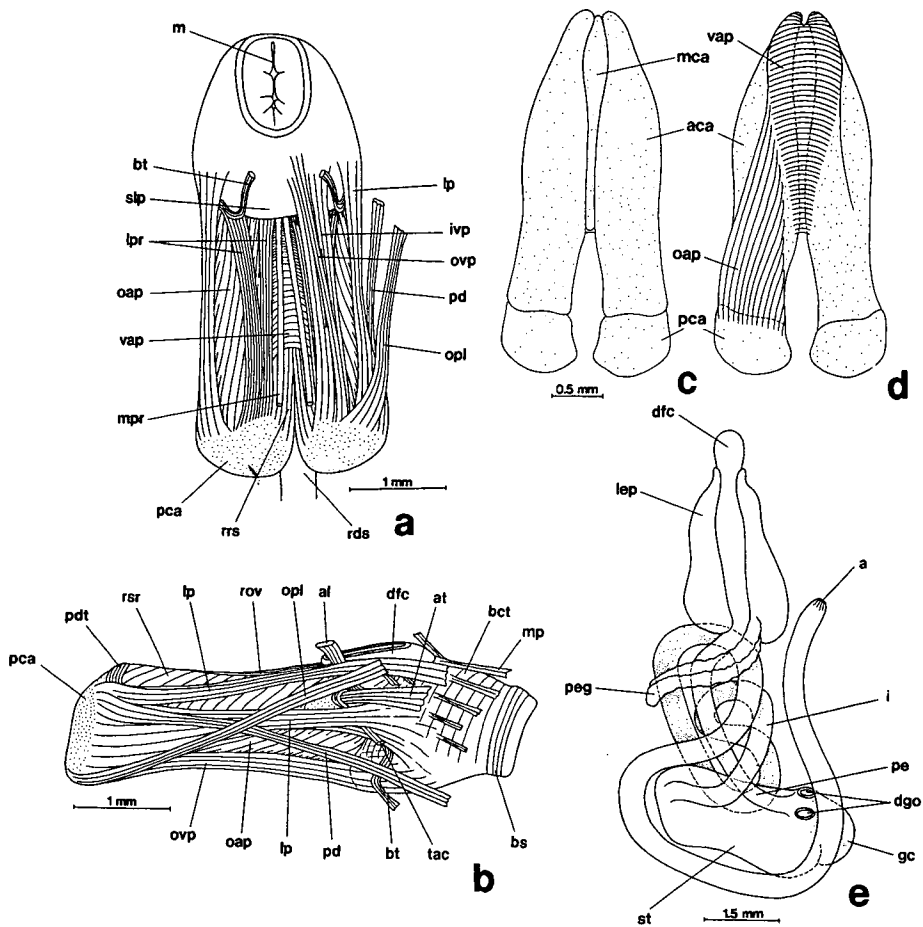
Fig. 89. *Waldemaria japonica.* a, Ventral view of the buccal mass. Some left muscles are removed. b, Right lateral view of the buccal mass. c, Dorsal view of the odontophoral cartilages. d, Ventral view of the odontophoral cartilages. The left outer approximator muscle is removed. e, Configuration of the alimentary tract.

Lateromarginal plates absent. Marginal teeth with two to six acute denticles from inner to outer sides.

Muscles inserting on radular sac and subradular membrane consisting of median protractors (mpr), lateral protractors (lpr), retractors of subradular membrane (rsr), and retractors of radular sac (rrs) (Figs. 89 a, b). Postmedian retractors and tensor of radular sac absent.

Odontophore containing anterior, posterior, and median cartilages (Figs. 89 c, d). Anterior cartilages (aca) extremely elongated; posterior cartilages (pca) small. Pair of anterior cartilages connected by ventral approximator (vap). Anterior and posterior cartilages connected by outer approximator muscles (oap). Single rod-like median cartilage (mca) present between anterior cartilages above ventral approximator. Sublingual cartilage (as in *Nerita*) absent. Lateral extensions of anterior cartilages inserted by tensor muscles (tac) (Fig. 89 b). Anterior tensors of odontophore (at) arising from more anterior part than it.

Sublingual pouch (slp) lacking particular outgrowths of sublingual gland (Fig. 89 a). Licker absent. Radular diverticulum definitely present. Salivary glands not developed as distinct glands outside buccal cavity. Anterior esophagus dorsoventrally depressed, accompanied by lateral esophageal pouches (lep) over
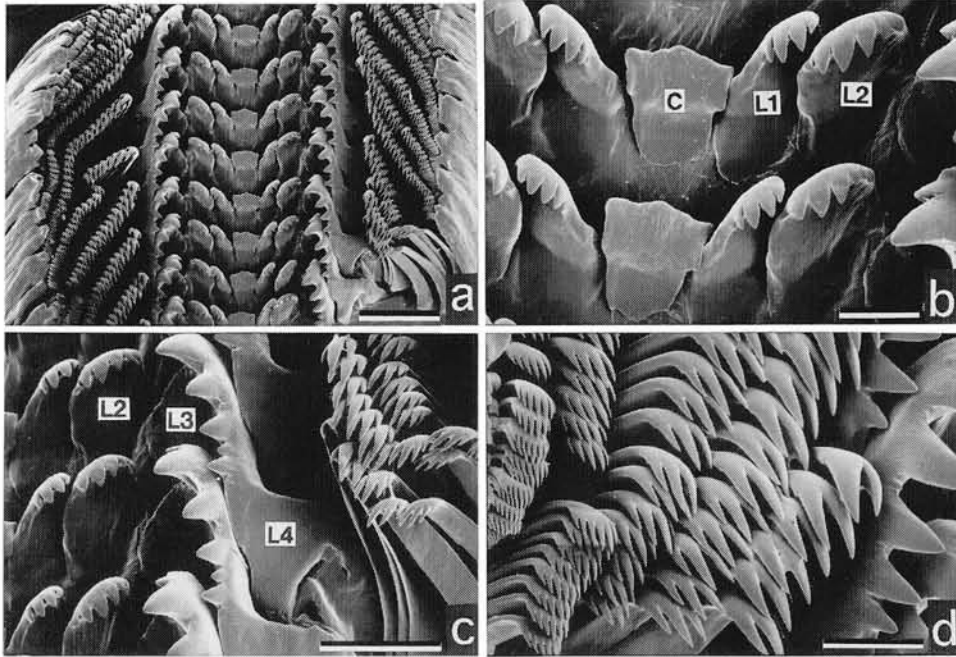
Fig. 90. *Waldemaria japonica*. SEM micrographs of radula. RM 27685. **a**, Whole row of radular teeth. Scale = 100 μm. **b**, Central and inner lateral teeth. Scale = 25 μm. **c**, Inner lateral to marginal teeth. Scale = 50 μm. **d**, Cusps of marginal teeth. Scale = 25 μm.

buccal cavity region. Esophagus curving toward left; posterior section of esophageal pouches arising from it, forming extremely elongated posterior esophageal glands (peg) over intestinal loops (Fig. 89 e). Mid-esophagus not differentiated. Paired ducts from digestive glands connecting with stomach on posterior side. Stomach provided externally with short crescent-shaped gastric caecum (gc) and internally with gastric shield, tooth of gastric shield, sorting area, major and minor typhlosoles, and intestinal groove. Intestine (i) tightly coiling, forming several loops. Rectum passing kidney ventrally, but not passing through pericardium or ventricle. Anus (a) opening on anterior right side of pallial cavity together with genital opening.

Circulatory System: Pericardium situated on left half of posterior end of pallial cavity. Heart consisting of single auricle and single ventricle (Fig. 88 b). Auricle (au) triangular, attached to efferent pallial vessels widely. Ventricle (v) almost free except for narrow vascular connection. Within pericardium, aorta dividing into anterior and posterior aortae (aa, pa). Bulbous aorta not formed. Afferent pallial vein (apv) from kidney running along gonoducts. Efferent pallial vein running along pericardium, directly connecting with ventricle.

Excretory System: Single left kidney (k) lying on posterior side of pericardium (Fig. 88 b), internally divided into glandular part on anterior side and non-glandular part on posterior side. Distal part of kidney extending to right of pericardium, opening into pallial cavity though small slit-like pore (ko). Renopericardial duct (rpd) extending left from distal region to pericardium.

Reproductive System: Gonochoristic gonad lying on dorsal surface of uncoiled visceral hump (Fig. 88 a). In both sexes, tissues of gonads aggregating into cylindrical form, appearing as rounded patterns on dorsal surface. Therefore, sexes not distinguishable according to granulation of gonadal tissue. Gonoduct not connected with kidney, exhibiting sexual dimorphism.

Male Gonoduct: Male gonoduct developing into prostate within pallial cavity. Vas deferens entering
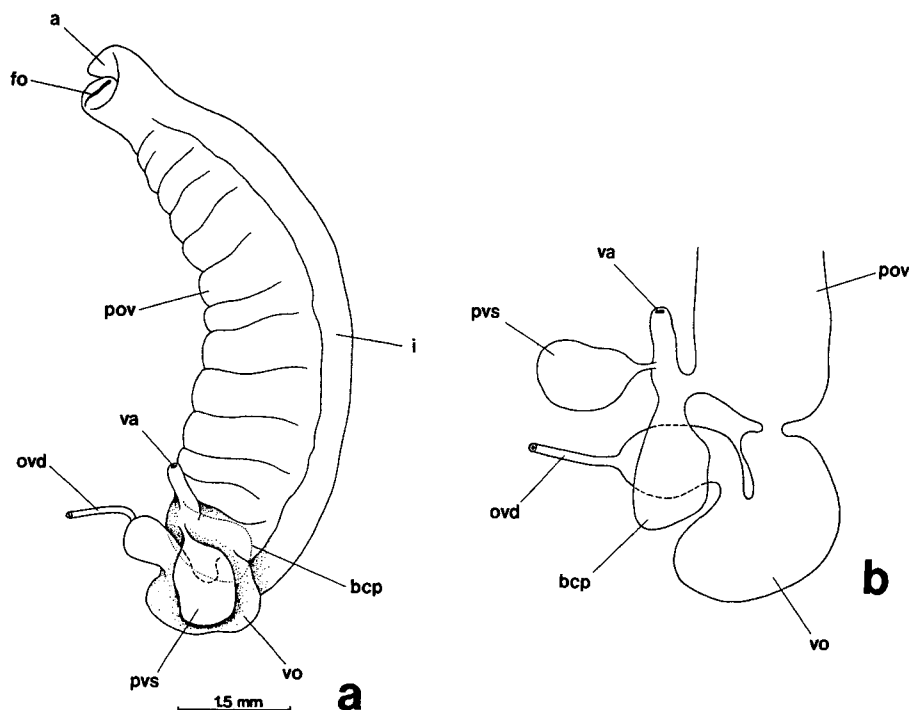
Fig. 91. *Waldemaria japonica.* a, Ventral view of the female gonoduct. b, Schematic representation of the connection of the posterior part of the female reproductive system.

prostate from posteroventral end of pallial gonoduct. Seminal vesicle not developed in any section of vas deferens. Prostate divided into anterior and posterior sections by constriction. Anterior portion of prostate with long prostate pouch on dorsal surface. Annex gland and basal gland absent on pallial gonoduct. Gonopore opening in association with anus. External copulatory organ absent. Production of spermatophores not found.

Female Gonoduct (Figs. 91 a, b): Female gonoduct with two genital openings (diaulic). Vaginal opening (va) lying in posterior end of pallial cavity, followed posteriorly by bursa copulatrix (bcp) which approaches dorsal surface over pallial oviduct (pov) and is visible through mantle. Between vagina and bursa, "provaginal sac" (pvs) (Thompson, 1980) connected by way of narrow ducts; function not detected. Bursa copulatrix entering pallial oviduct from right side.

Oviducts from ovary expanding and twisting to form "V-organ" (vo) (Thompson, 1980). V-organ lying between dorsally sifted bursa copulatrix and ventrally positioned provaginal sac (Fig. 91 a). Distal part of V-organ communicating with pallial gonoducts on left side. From there pallial gonoducts running along rectum, terminating in anterior pallial cavity. Opening of pallial gonoducts incorporated with anus into common chamber.

Nervous System: Circumesophageal nerve ring hypoathroid. Cerebral ganglia at bases of cephalic tentacles. Cerebral commissure running in front of buccal cavity over oral tube. Pleural and pedal ganglia completely fused behind buccal mass with long cerebropedal and cerebropleural connectives. Pleural ganglia connected by pleural commissure.

Cerebral ganglia united ventrally by labial commissure, and dorsally by cerebral commissure. Labial ganglia absent. Buccal ganglia connected to labial commissure through labiobuccal connectives.

Visceral nerve loop arising only from right pleural ganglion. Thinner supraesophageal part of visceral loop originating more anterior than that of thicker subesophageal part. Supraesophageal and subesophageal ganglia weakly developed. Statocysts on dorsal sides of pedal ganglia, connected by short nerve.

IV. Phylogenetic Analysis

IV-1. Character States

To facilitate reference to state in OTUs, abbreviated generic names are listed after each character state. Abbreviations used in this section are as follows: *Chiton = Chi, Neopilina = Nep, Nautilus = Nau, Patella = Pat, Cellana = Cel, Pectinodonta = Pec, Niveotectura = Niv, Nipponacmea = Nip, Erginus = Erg, Limalepeta = Lim, Mikadotrochus = Mik, Sulculus = Sul, Scutus = Scu, Macroschisma = Mac, Anatoma = Ana, Turbo = Tur, Chlorostoma = Chl, Stomatia = Sto, Broderipia = Bro, Lepetodrilus = Lep, Seguenzia = Seg, Cocculina = Coc, Neomphalus = Nem, Nerita = Ner, Septalia = Sep, Cinnalepeta = Cin, Waldemaria = Wal, Pomacea = Pom*, and *Biwamelania = Biw.*

1. External Characters
1. Mantle slit/hole: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Tur, Chl, Sto, Bro, Lep, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) single** [*Mik, Sul, Scu, Mac, Ana*], **(2) double** [*Seg*]

The mantle margin of some archaeogastropods is deeply sinuate. In the zeugobranch genera (Pleurotomariidae, Haliotidae, Scissurellidae, most Fissurellidae), there is a single slit between the paired pallial complexes as an exhalant sinus associated with the anal region. Members of *Macroschisma* have an apical hole instead of slit (Fig. 41 a), but it is functionally identical to the general zeugobranch condition. In Haliotidae, the shell has a series of pores but the mantle of the corresponding position has a simple slit. In *Seguenzia*, the mantle margin has two separated notches, viz. an inhalant sinus on the left side and an exhalant one on the right side. Their presence is also reflected in morphology of the shell aperture.

2. Retractile circumpallial tentacles: (0) absent [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel, Lim, Niv, Erg, Nip*], **(?) unknown** [*Pec*]

In patellogastropod genera, the mantle margin is fringed by numerous microtentacles. The length of microtentacles is variable, from long in *Cellana*, to minute in *Patella* and *Nipponacmea*, to greatly diminutive in *Niveotectura, Erginus,* and *Limalepeta*. The microtentacles can almost completely be retracted into the inner fold of the mantle margin (Fretter, 1990), and therefore, they are often hardly visible and difficult to find in preserved specimens. Sensory projections are also elaborated on the mantle margins of members of various archaeogastropods, such as *Mikadotrochus* (Fig. 27 b), *Lepetodrilus* (Fig. 65 a), *Cinnalepeta* (Fig. 85 b), *Seguenzia* (Fig. 67 a), and *Anatoma* (Fig. 43 c). However, they lack retractility unlike those of patellogastropod limpets.

3. Pallial tentacles: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Scu, Mac, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Sul, Ana*]

In some zeugobranch gastropods, the margin of the mantle slit is provided with a few long tentacles, which are much more prominent than the circumpallial microtentacles. In *Sulculus* there are three tentacles, one in the posterior end of the slit and two on anterior sides situated asymmetrically (Fig. 29). In *Anatoma*, only a median tentacle is present (Fig. 42).

4. Snout: (0) absent [*Chi, Nep, Nau*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

It is a common character of Polyplacophora and Tryblidiida that the head region is less flexible with a muscular attachment to the shell or shell plate (Wingstrand, 1985). In contrast, Cephalopoda and Gastropoda have a free head that is liberated from dorsal shell covering. They differ, however, in the structure of the oral region. The mouth of Cephalopoda is deeply surrounded by a crown of arms/tentacles, whereas the archaeogastropod head is prolonged anteriorly as a snout so as to reach the substratum.

5. Cephalic tentacles: (0) absent [*Chi, Nep, Nau*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

A pair of cephalic tentacles is always present in gastropods on the sides of the head; no non-gastropod mollusk has a homologous structure. In Archaeogastropoda the cephalic ganglia are always situated near the bases of these tentacles.

6. Position of cephalic eyes: (0) absent [*Chi, Nep, Lep, Seg, Coc, Nem*], **(1) within lateral walls of head** [*Nau*], **(2) within bases of cephalic tentacles** [*Pat, Cel, Lim, Niv, Erg, Nip*], **(3) at posterior outside of cephalic tentacles (with or without eyestalks)** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Ner, Sep, Cin, Wal, Pom, Biw*], **(?) unknown** [*Pec*]

Several kinds of photoreceptors are often developed in various parts of the molluscan body. However, a pair of eyes innervated by the cerebral ganglia is shared only by Cephalopoda and Gastropoda. In other cases (e.g. pallial eyes of pectinid bivalves and valve eyes of Polyplacophora) receptors are innervated by pallial nerves from the pleural ganglia.

The position of the eyes is slightly variable in several types. In *Nautilus*, they are invaginated in the lateral walls of the head (Young, 1987). In Patellogastropoda, they are housed within the bases of the cephalic tentacles. However, in members of non-patellogastropod genera, the eyes are always located on the outer bases of the tentacles, and are often provided with eyestalks of variable length. Eyes were not found in *Lepetodrilus, Seguenzia, Cocculina*, and *Neomphalus* (Fretter *et al.*, 1981). A vestige of the original eyes has been identified as so-called "basitentacular glands" in Cocculinidae (Haszprunar, 1987 a).

7. Eyestalks: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Lep, Seg, Coc, Nem*], **(1) present** [*Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Ner, Sep, Cin, Wal, Pom, Biw*]

The outer bases of the cephalic tentacles may be evaginated to generate eyestalks and to carry the eyes at their distal tips. Eyestalks are not formed in Patellogastropoda but are present in members of rhipidoglossate and caenogastropod genera except in deep-sea eye-less taxa. *Mikadotrochus* lacks eyestalks even though eyes are present on the outer sides of the cephalic tentacles. The length of eyestalks is variable among the various gastropod groups.

8. Eye structure: (0) open, hollow [*Nau, Pat, Cel, Lim, Niv, Erg, Nip*], **(1) open with vitreous body** [*Mik, Sul, Tur, Chl, Sto, Bro*], **(2) closed with vitreous body** [*Scu, Mac, Ana, Ner, Sep, Cin, Wal, Pom, Biw*], **(-) inapplicable** [*Chi, Nep, Lep, Seg, Coc, Nem*], **(?) unknown** [*Pec*]

Cephalic eyes are divided into several discrete grades of development. Among the outgroups, *Nautilus* has open pin-hole eyes (in contrast to lens eyes of other cephalopods) (Barber, 1987). Of Gastropoda, patellogastropod limpets have simply invaginated eyes, hollow internally, without contents of secreted materials (Fig. 92). The retina consists of a single layer of cells containing a pigmented zone (Marshall and Hodgson, 1990). In the remaining groups, the lumen of the optic cup is filled with a vitreous body (so-called "lens"). The pupil is covered with an epithelium in neritopsine genera and in Caenogastropoda but remains un-

a   b   c
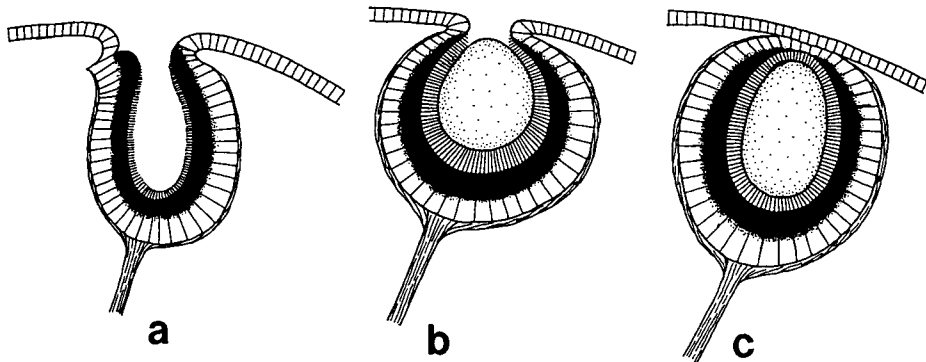
Fig. 92.   Character states of eyes. a, Open hollow eye. b, Open with vitreous body. c, Closed with vitreous
body.

closed in others.

9. Cephalic lappets: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Scu, Mac, Ana, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Sul, Tur, Chl, Sto*]

A pair of flap-like extensions is present on the dorsal surface of the snout between the cephalic tentacles in *Sulculus* and in trochoidean genera excluding *Broderipia*. They are finely fringed and seem to be fused along the midline with each other and with the bases of the eye stalks on the outer sides. The cephalic penis in Neritidae may be comparable to this structure due to similarity in position (Ponder and Lindberg, 1997), but I do not treat them as homologous because of the asymmetrical condition of the neritoidean penis (character #82).

10. Neck lobes: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Tur, Chl, Sto, Bro*]

The epithelia of the right and left neck regions variously develop to form flap-like structures in the genera of Trochoidea. Such structures never occur in non-trochoidean gastropods and outgroups. They function as a guide for the inlet (left) and outlet (right) of water currents (Hickman and McLean, 1990).

11. Anterior pallial streaks: (0) absent [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel*]

Long strips termed "anterior pallial streaks" are situated at the anterior ends of the shell muscle in *Patella* and *Cellana*. Another pair of strips called "lateral pallial streaks" is absent in *Cellana* and restricted to *Patella* in patellogastropods (Fretter and Graham, 1962: fig. 50; Stüzel, 1984: pl. 21). They are said to be innervated from osphradial and pleural ganglia and to have sensory function (Haszprunar, 1985 a). Other groups of patellogastropod limpets and archaeogastropods lack structures homologous to these streaks.

12. Epipodial tentacles: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem*]

The surface of the epipodial region in archaeogastropods has various forms of tentacles that are innervated from the pedal ganglia (Crisp, 1981). Their morphology is greatly variable and difficult to categorize into discrete subtypes in terms of form, number, and position: (i) The most typical subtype is one with several pairs (mostly four symmetrical pairs) of long tentacles found in the trochoidean genera, *Anatoma* and

Seguenzia. Neomphalus also has several pairs on posterior side, although numbers are different between right and left sides (McLean, 1981). (ii) *Cocculina* has only a single posterior pair of simple rod-like tentacles. (iii) In *Mikadotrochus* long tentacles are absent, but instead, several longitudinally elongated flaps are present (Fig. 24 a). Thick flaps similarly occur on the sides of the foot in *Lepetodrilus*. (iv) *Scutus* of Fissurellidae has small triangular flaps along the epipodial margin (Fig. 34). However, in *Macroschisma* of the same family, vestigial tentacles are represented by tubercular processes on sides of the epipodium (Herbert, 1988). (v) In *Sulculus*, the tentacles are extremely hypertrophied to surround the entire epipodial region (Fig. 29). In the outgroups, cephalopod arm/tentacles may be comparable to gastropod epipodial tentacles, but their homologous relationship is rejected by the criteria of innervation (Salvini-Plawen, 1980; Salvini-Plawen and Steiner, 1996).

13. Epipodial sense organs (ESO): (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Tur, Chl, Sto, Bro, Lep, Seg*], **(?) unknown** [*Mac, Ana*]

The epipodial tentacles of many archaeogastropods are provided with special sensory structures at their bases. The epipodial sense organs are homologized by common position with the tentacles and by common innervation from the pedal nerves (Crisp, 1981), although the exterior form of the organ shows wide variation, from prominent knobs with cilia to simple tufts of cilia. These variations are divisible as follows: (i) The most typical form is knobby projections at the bases of the tentacles in trochoidean genera. (ii) Members of Fissurellidae have the sense organs on the ventral surface of each flap-like epipodial tentacles, although its presence or absence is unclear when the epipodial tentacles have degenerated. (iii) The presence of this organ in Pleurotomariidae has been questioned (Woodward, 1901; Fretter, 1964, 1966; Hickman, 1996), but tuberculate protrusions were observed with SEM during this study along the ventral margin of the epipodial flaps (Fig. 27 c). These are morphologically similar to the ESOs in Fissurellidae, and are hence considered to be homologous. (iv) Members of Haliotidae has a crown of cilia at the bases of epipodial tentacles. (v) In Scissurellidae, presence of sense organs is questionable. Similarly, *Seguenzia* has papillate epipodial tentacles but sensory organs could not be observed. The states in these taxa must still be considered dubious, because detailed observation was not successful during this study. For the analysis, the state in *Seguenzia* was scored as "present," following the data matrices of Ponder and Lindberg (1996, 1997). (vi) *Lepetodrilus* has tuberculate ESOs as projections on the epipodial flaps. (vii) *Cocculina* has a pair of posterior tentacles, but ESOs are lacking. None of Patellogastropoda, *Neomphalus* (*fide* McLean, 1981), Neritopsina, or Caenogastropoda possess similar sense organs in the epipodial region.

14. Micropapillae on cephalic and epipodial tentacles: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Scu, Mac, Lep, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Sul, Ana, Tur, Chl, Sto, Bro, Seg*]

The tentacles of some archaeogastropods are provided with papillae, each composed of a long stalk with a ciliary crown at the distal tip. They have been considered to function as sensory organs (Crisp, 1981) and termed "micropapillae" (Hickman and McLean, 1990). Micropapillae were found in *Sulculus*, all trochoidean genera, *Anatoma* (Fig. 43 d), and *Seguenzia* (Fig. 67 c). The absence of such microscopic structures was verified in other genera by SEM observation. The epipodial tentacles of *Cocculina* do not have micropapillae and are simply covered with cilia.

15. Number of shell muscle attachments: (0) eight pairs [*Chi, Nep*], **(1) two pairs** [*Nau*], **(2) single pair** [*Sul, Lep, Ner, Wal*], **(3) unpaired (including horseshoe-shaped)** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Seg, Coc, Nem, Sep, Cin, Pom, Biw*]

Polyplacophora and Tryblidiida share the state of muscular structure consisting of eight longitudinally replicated pairs of three muscle sets (oblique, longitudinal, and transverse muscles) (Wingstrand, 1985). *Nautilus* has two distinctly separated pairs of head retractors (Griffin, 1900), although other cephalopods (Coleoidea) have a single pair of dorsoventral muscles consisting of head and funnel retractors (Wells, 1988). A single pallial adductor is also present in octopods but is absent in squids. Among Archaeogastropoda, muscle attachments are clearly separated only in Haliotidae, *Lepetodrilus*, some Neritidae (*Nerita*, but not *Septalia*), and Helicinidae.

16. Muscle constriction into bundles: (0) absent [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Coc, Ner*]

Division of each shell muscle into a continuous series of bundles occurs in all patellogastropod genera, *Cocculina*, and *Nerita*. In the former two taxa, blood vessels from the visceral haemocoel penetrate the shell muscle to reach the circumpallial vessel, which is clearly observable in living animals. The site of penetration corresponds to that of muscular constriction but is partly incongruent. In *Nerita*, the vessel penetration is poorly developed, but muscle division is very clear. Other neritopsine genera do not exhibit such a condition (e.g. *Septalia*). In view of outgroup comparison, the constricted muscles of archaeogastropods cannot be regarded as fused as in amphineuran muscles, because the latter are composed of distinctly paired sets that are longitudinally replicated, while gastropod muscle bundles do not have paired counterparts on both right and left sides.

2. Pallial Complex
2-1. Ctenidia
17. Number of ctenidia: (0) multiple pairs [*Chi, Nep*], **(1) two pairs** [*Nau*], **(2) single pair** [*Mik, Sul, Scu, Mac, Ana*], **(3) left only** [*Pec, Niv, Nip, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Ner, Sep, Cin, Pom, Biw*], **(4) absent** [*Pat, Cel, Lim, Erg, Coc, Wal*]

It is generally accepted that the primitive molluscan ctenidium is a single symmetrical pair like that in Caudofoveata (Salvini-Plawen, 1988), to be secondarily multiplied or reduced in various taxa. All three outgroups have larger number of ctenidia than Gastropoda. They are numerous in Polyplacophora (Eernisse and Reynolds, 1994), 3-6 pairs in Tryblidiida (6 in *Vema*, 5 in *Neopilina*) (Haszprunar, 1997), and 2 pairs in *Nautilus* (Griffin, 1990).

The ctenidia of Archaeogastropoda are categorized into three states: (i) paired, (ii) left ctenidium only, and (iii) absent or replaced by "secondary gills." The paired right and left ctenidia are present in Zeugobranchia (=Pleurotomariidae, Haliotidae, Fissurellidae and Scissurellidae), but the remaining archaeogastropods as well as the Caenogastropoda have a single left ctenidium only. The ctenidium is absent in *Limalepeta*, *Erginus*, and *Waldemaria*, in which the vascularized mantle skirt serves as the primary respiratory surface. In other cases the ctenidium is replaced by a secondary structure: in *Patella* and *Cellana* by leaflets in the pallial groove, in *Cocculina* by a pseudoplicate gill in the pallial cavity.

18. Ctenidial filaments: (0) bipectinate [*Chi, Nep, Nau, Pec, Niv, Nip, Mik, Sul, Scu, Mac, Tur, Chl, Sto, Bro, Lep, Nem, Ner, Sep, Cin, Wal*], **(1) monopectinate** [*Ana, Seg, Pom, Biw*], **(-) inapplicable** [*Pat, Cel, Lim, Erg, Coc, Wal*]

Molluscan ctenidia generally have bipectinate structure (Fig. 93). Most archaeogastropods retain this original condition, but "higher" groups (e.g. all Caenogastropoda) are invariably monopectinate, namely, with the ctenidial axis completely attached to the mantle skirt and only ventral lamellae retained. However, monopectinate ctenidia are also found in *Anatoma* and *Seguenzia* (Fig. 67 d). Seemingly an intermediate condition is observed in *Lepetodrilus* whose ctenidial lamellae are monopectinate in the posterior two-
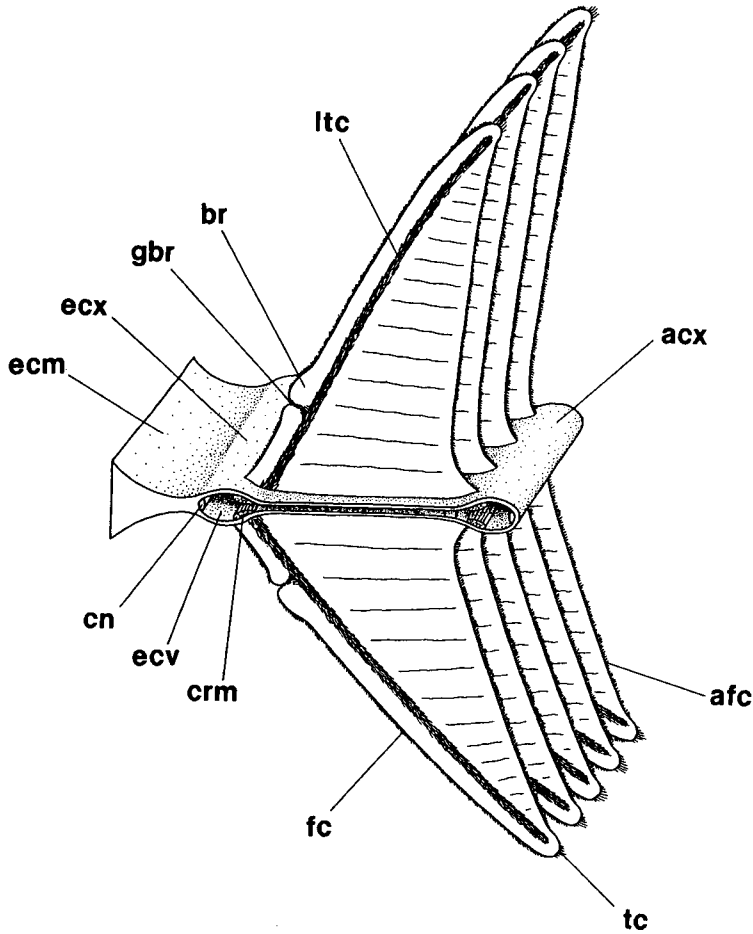
Fig. 93.   Generalized ctenidium of Vetigastropoda.

thirds but bipectinate in the remaining anterior part. In this analysis this condition was scored as bipectinate because it is clearly retained as such in the anterior portion. Partial change into a posteriorly monopectinate condition also occurs in some trochoid groups (Hickman and McLean, 1990).

19. Skeletal rods on efferent side of ctenidial filaments: (0) absent [*Chi, Nep, Nau, Pec, Niv, Nip, Ner, Sep, Cin*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Pom, Biw*], **(-) inapplicable** [*Pat, Cel, Lim, Erg, Coc, Wal*]

Each leaflet in a molluscan ctenidium is often provided with a supporting tissue called a skeletal rod. In the outgroups, the rod is absent in both Polyplacophora (Salvini-Plawen, 1988) and Tryblidiida (Lemche and Wingstrand, 1959; Haszprunar, 1997). The ctenidial leaflets of Cephalopoda (including *Nautilus*) have a similar supporting structure on the afferent side, not on the efferent side (Young, 1947). Thus, the cephalopod skeletal rod is not considered homologous to those of other molluscs but to be of independent origin (Haszprunar, 1988 b; Ponder and Lindberg, 1997). Among Gastropoda, the efferent rod is absent in both patellogastropod and neritopsine genera but present in the remaining taxa having ctenidia.

20. Bursicles (=**ctenidial sense organs**): **(0) absent** [*Chi, Nep, Nau, Pec, Niv, Nip, Mik, Lep, Nem, Ner, Sep, Cin, Pom, Biw*], **(1) present** [*Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Seg*], **(-) inapplicable** [*Pat, Cel, Lim, Erg, Coc, Wal*]

Some archaeogastropod groups are known to have a special sense organ on the efferent side of each ctenidial lamella (Fig. 93). This organ, called a bursicle, was experimentally demonstrated to have a chemosensory function in Trochidae by Szal (1971). Later Haszprunar (1987 c) investigated the microstructure of this organ and also revealed its phylogenetic significance as a synapomorphy for Vetigastropoda. In this study I also confirmed (using SEM) that the taxonomic distribution of ctenidial sense organs is restricted to Vetigastropoda (including *Seguenzia*). Exceptionally within this group, bursicles were not found in *Mikadotrochus* (Fig. 27 d), although Haszprunar (1987 c) reported their presence in *Perotrochus* of the same family, Pleurotomariidae.

The homology of this organ with other 'bursicle-like' structures is easily demonstrated by comparing internal and external structures. A true bursicle has a ciliated groove that connects with the lateral cilia and ciliated lumen (Haszprunar, 1987 c; Fig. 49 d). Using this criterion, it is without doubt that *Lepetodrilus* lacks bursicles. A row of grooves are found on the ctenidial leaflets in *Lepetodrilus* (Fig. 65 c), but these never contain a ciliated pocket lumen. The groove on the leaflets presumably represents the depressed terminal ridge of the ctenidial lamellae due to unusual depression and modification of the ctenidial attachment in this case. *Neomphalus* also seems to lack bursicles (McLean, 1981: fig. 8).

2–2. Osphradia

21. Number of osphradia: (0) paired [*Chi, Pat, Cel, Nip, Mik, Sul, Scu, Mac*], **(1) single left** [*Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Pom, Biw*], **(2) absent** [*Nep, Lim, Pec, Niv, Erg, Wal*], **(?) unknown** [*Nau, Ana*]

In the outgroups, osphradia are represented by strips on the pallial roof on the posterior sides of the ctenidia in Polyplacophora (Haszprunar, 1987 d), while they were unknown or absent in Tryblidiida (Lemche and Wingstrand, 1959; Haszprunar, 1997). In *Nautilus*, so-called "interbranchial papillae" may represent an osphradium, but its homology is uncertain (Ponder and Lindberg, 1997). In archaeogastropods, there are both paired and unpaired conditions. (i) Paired osphradia are developed in the patellogastropod limpets (*Patella, Cellana*, and *Nipponacmea*) and zeugobranchs (Pleurotomariidae, Haliotidae, and Fissurellidae). (ii) Only the left osphradium is developed in other gastropods. The osphradium of *Neomphalus* is also regarded as a single left one as discussed by Ponder and Lindberg (1997). The state in *Seguenzia* was also coded as single left, following Ponder and Lindberg's (1997) data matrix (character 100). (iii) The organ is absent in some patellogastropods (*Limalepeta, Pectinodonta, Niveotectura*, and *Erginus*) and *Waldemaria* (Helicinidae). The state is unknown in *Anatoma*.

22. Position of the osphradia: (0) on pallial roof [*Chi, Pom, Biw*], **(1) on pallial floor** [*Pat, Cel, Nip*], **(2) on free portion of efferent ctenidial axis** [*Mik, Sul, Scu, Mac, Tur, Chl, Sto, Bro*], **(3) at base of efferent ctenidial membrane** [*Lep, Coc, Nem, Ner, Sep, Cin*], **(-) inapplicable** [*Nep, Lim, Pec, Niv, Erg, Wal*], **(?) unknown** [*Nau, Ana, Seg*]

The position of osphradia exhibits four states in outgroups and ingroups. (i) The osphradia of the Polyplacophora and Caenogastropoda are separated from the ctenidium and adhere to the pallial roof. (ii) In the patellogastropod genera, they are always on the floor of the pallial cavity just inside the anterior end of the shell muscle attachment. (iii) In the vetigastropod genera, they are on the efferent axis of the free tip of the bipectinate ctenidium. (iv) In Neritopsina, *Lepetodrilus*, *Neomphalus*, and *Cocculina*, the osphradium is associated with the base of the efferent side of the ctenidium.

23. Morphology of the osphradia: (0) single-zoned [*Chi, Mik, Sul, Scu, Mac, Tur, Chl, Sto, Bro, Lep, Coc, Nem, Ner, Sep, Cin, Pom, Biw*], **(1) two-zoned with wart-organ** [*Pat, Cel, Nip*], **(-) inapplicable** [*Nep, Lim, Pec, Niv, Erg, Wal*], **(?) unknown** [*Nau, Ana, Seg*]

In archaeogastropods, two discrete states occur in the external morphology of the osphradium (Fig. 94). (i) In patellogastropod genera, osphradia consist of two distinct areas, viz. inner and outer zones ("Osphradium s. str." and "Ctenidienrudiment" of Stützel, 1984). According to Haszprunar (1985 a) the inner zone is directly innervated by the osphradial ganglia; its epithelium lacks sensory cells and is associated with free nerve endings only; the outer tuberculate zone (=wart-organ) includes numerous "cilia star cells." The wart-organ has sometimes been considered as gill rudiments (e.g. Stützel, 1984), but this idea is rejected because of the coexistence of wart-organ and ctenidium in some lottiid genera (e.g. *Lottia* and *Nipponacmea*). (ii) In the remaining groups of gastropods, osphradia lack such specific structures externally. In the outgroups, polyplacophoran osphradia consist of long vermiform strips without distinct zonation (Eernisse and Reynolds, 1994; Haszprunar, 1987 d).
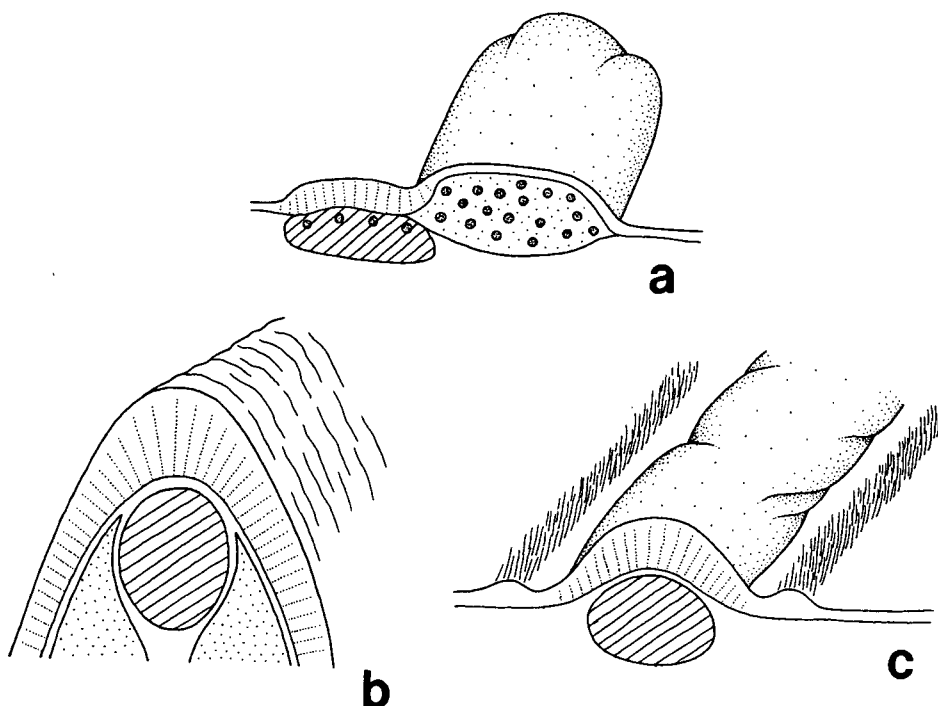
Fig. 94.   Character states of the osphradium. Cross-section is based on Haszprunar (1985 a). a, Double-zoned with wort-organ. b, Single-zoned without cilated zone. c, Single-zoned with ciliated lateral zone.

24. Lateral ciliated zones: (0) absent [*Chi, Pat, Cel, Nip, Mik, Sul, Scu, Mac, Tur, Chl, Sto, Bro, Lep, Coc, Nem*], **(1) present** [*Ner, Sep, Cin, Pom, Biw*], **(-) inapplicable** [*Nep, Lim, Pec, Niv, Erg, Wal*], **(?) unknown** [*Nau, Ana, Seg*]

Ciliated zones on sides of osphradium are found in neritopsine genera (except *Waldemaria*) and in caenogastropod genera, but are absent in other groups. In neritopsines and *Biwamelania* ciliated zones are parallel to elongated simple ridge of central zone of osphradium (Fig. 94 c). *Pomacea* has ciliated zones in grooves of lamellate osphradium. Polyplacophora lack the division of ciliated zones (Haszprunar, 1987 d).

2-3. Hypobranchial Glands

25. Number of hypobranchial glands: **(0)** paired [*Chi, Nep, Mik, Sul, Tur, Chl, Sto, Bro*], **(1)** single right [*Ana, Ner, Sep, Wal*], **(2)** single left [*Lep, Seg, Coc, Pom, Biw*], **(3)** absent [*Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Scu, Mac, Nem, Cin*]

The molluscan pallial cavity is often provided with mucus-secreting glands. They are particularly well-developed as a prominent glandular area, the hypobranchial gland. In the outgroups, paired elongated strips are present in the pallial groove of Polyplacophora (Salvini-Plawen, 1988) and in *Neopilina* (Lemche and Wingstrand, 1959), whereas glands are unknown in *Nautilus* (Griffin, 1990).

Within archaeogastropods, several states are distinguishable: (i) Paired glands are generally well-developed on either side of the rectum in most Vetigastropoda. In the dextrally coiling forms, the left gland is always larger than the right one that is suppressed on the columellar side. (ii) Most neritopsine genera are unique in having only the right gland which is attached dorsally to the gonoduct at the posterior end of the pallial cavity. The scissurellid *Anatoma* also has only the right gland (relative to the rectum) (Fig. 42 a). (iii) The mantle skirt completely lacks the glands in patellogastropods, Phenacolepadidae, Fissurellidae, and *Neomphalus* (McLean, 1981). (iv) All of the remaining archaeogastropods and caenogastropods examined have a single left hypobranchial gland.

3. Alimentary System

3-1. Muscles of Oral Region

26. Transverse labial muscles: **(0)** absent [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1)** present [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*]

In Patellogastropoda, the paired inner lips of the mouth are closely associated with the anterior wings of the jaw, and their movement is controlled by "transverse labial muscles" (Graham, 1964) that are unique to the group. In the remaining archaeogastropods and outgroups, the inner lips are free from the jaw plates, and this muscle is absent.

3-2. Muscles of Odontophore

27. Dorsal protractor muscles of the odontophore: **(0)** absent [*Chi, Nep, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1)** present [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(?)** unknown [*Nau*]

The protractor muscles running between the posterior end of the cartilage and the wall of the snout on the dorsal side of odontophore is called the dorsal protractor muscle of the odontophore (Graham, 1964; 1973). This paired muscle is shared by all patellogastropod genera but is absent in all other groups including outgroups. The state in *Nautilus* is unknown in previous descriptions (Griffin, 1900; Young, 1991).

28. Anterior levator muscles of the odontophore: **(0)** present [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Ner, Sep, Cin, Wal*], **(1)** absent [*Coc, Pom, Biw*]

The levator muscles running from the anterolateral sides of the odontophore to the wall of the snout has been described in Polyplacophora and Tryblidiida (Graham, 1973; Wingstrand, 1985, as "Muscle IIIc = *m. cartilaginis anterolateralis*"). In Gastropoda, it is also present in all patellogastropod, vetigastropod, and neritopsine genera, but is absent in *Cocculina* and caenogastropod genera. A homologous muscle is also absent in *Nautilus* (Griffin, 1990). The "odontophoral levator" in *Neomphalus* (Fretter *et al.*, 1981: figs. 3-4) is homologous with this muscle.

29. Dorsal levator muscles of the odontophore: **(0)** absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg,*

Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Pom, Biw], **(1) present** [*Ner, Sep, Cin, Wal*]

This levator muscle originates from the anterodorsal wall of snout and inserts at the posteroventral end of the cartilage, pulling the odontophore anterodorsally. It is crossed transversely by the postdorsal buccal tensor muscle but for the most part lies on the dorsal surface of the buccal mass. Presence of this muscle is restricted to the neritopsine genera.

30. Median levator muscles of the odontophore: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

From the median sides near the dorsal levator muscles, the thinner muscle strands of the levator muscle are extended from the ventral end of the posterior cartilage to the dorsal wall of the snout. This muscle appears dorsally from the outside of the lateral pouch of the anterior esophagus and lies in the most dorsal position among all muscles. As in the former muscles, this occurs only in the neritopsine genera, but is absent in *Waldemaria* (Fig. 89 b).

31. Posterior depressor muscles of the odontophore: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Coc, Nem, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Ner, Sep, Cin, Wal*], **(?) unknown** [*Seg*]

Some archaeogastropods have well-developed depressor muscles from the posterodorsal sides of the odontophore to the floor of the body cavity. It is present in vetigastropod and neritopsine genera but absent in the outgroups, patellogastropods, *Cocculina*, and *Neomphalus* (Fretter *et al.*, 1981). An antagonistic levator muscle is, however, found only in some trochoid genera and *Mikadotrochus*.

32. Postdorsal buccal tensor muscle: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Nem, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc, Ner, Sep, Cin, Wal*], **(?) unknown** [*Seg*]

The posterior dorsal part of the odontophore has a transverse tensor muscle to prevent the right and left cartilages from splitting apart (Fretter and Graham, 1962: fig. 108; Nisbet, 1973: fig. 6, as "postdorsal tensor of cartilages"). It always lies over the radular sac, the retractor muscles of esophageal valve, and the radular diverticulum. This muscle is present only in Vetigastropoda (including *Lepetodrilus*), and Neritopsina. *Neomphalus fretterae* lacks this muscle (Fretter *et al.*, 1981).

33. Dorsal buccal tensor muscles: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc*], **(?) unknown** [*Seg*]

This tensor muscle is extended obliquely from the posterodorsal surface of odontophore to the anterodorsal area over the buccal mass. The posterior part of this muscle is often attached to the postdorsal buccal tensor muscle, forming a tensor muscle complex. Presence of this muscle is restricted to Vetigastropoda (including *Lepetodrilus*), and *Cocculina* in this analysis. In most vetigastropod genera, the distal portion of this muscle is divided into two muscle bands; the upper band originates from the wall of the snout, while the lower band is inserted on the anterolateral extension of the anterior cartilages. The "net muscle" of cocculinid *Coccopigya* (Haszprunar, 1987 a) represents a complex of dorsal and postdorsal buccal tensor muscles.

3-3. Jaws

34. Number of the jaws: (0) absent [*Chi*]**, (1) single** [*Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip*]**, (2) dorsoventrally paired** [*Nau*]**, (3) bilaterally paired** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

The presence of jaw(s) is a synapomorphy of Conchifera except bivalves lacking buccal mass (Wingstrand, 1985: 51), but their number and morphology vary greatly among them. Jaws are absent in Polyplacophora (Wingstrand, 1985), single in Tryblidiida (Wingstrand, 1985), and dorsoventrally paired as "beaks" in Cephalopoda (Tanabe and Fukuda, in press). The gastropod jaw can be clearly distinguished as one of two types: an unpaired jaw in patellogastropods, or a paired jaw in non-patellogastropod groups, including *Neomphalus* (Fretter *et al.*, 1981) (Fig. 95).
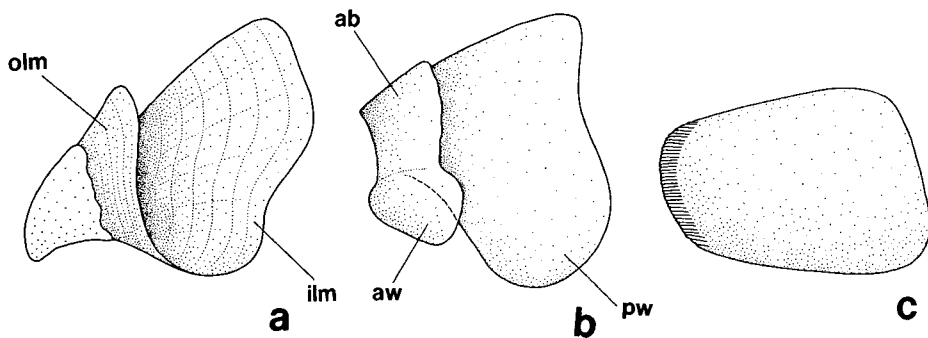
Fig. 95.   Character states of jaws. **a**, Beak-like jaw (upper beak of *Nautilus*; from Tanabe and Fukuda, in press). **b**, Two-layered, laterally undivided jaw (Patellogastropoda). **c**, Paired simple plates.

35. Structure of the jaws: (0) simple sheet-like [*Nep, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]**, (1) two-layered** [*Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip*]**, (-) inapplicable** [*Chi*]

The cephalopods have dorsoventrally paired beaks with acute anterior tips as a primary feeding apparatus. Each of the upper and lower beaks consists of two layers: inner and outer lamellae (Tanabe and Fukuda, in press). In contrast, gastropod jaws always lie only on the dorsal side of the buccal mass. They are further divisible into two essentially different types: the patellogastropod jaw differs from that in other gastropods in having the form of a single plate with a double structure of anterior wings on the anterodosal sides and posterior wings on posteroventral sides. In the remaining groups, jaws consist of a pair of simple sheet-like plates. Tryblidiida also has a simple filmy jaw (Wingstrand, 1985).

36. Position of the jaws: (0) attached to the oral tube and free from the buccal mass [*Nep, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]**, (1) fixed on the odontophore by a muscle attachment** [*Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip*]**, (-) inapplicable** [*Chi*]

Despite of great differences in jaw morphology (dorsoventrally paired or unpaired), cephalopod and patellogastropod jaws share a common structural feature. Cephalopod beaks are embedded in a membranous muscle sheet covering the buccal mass, and the inner and outer lamellae of the upper and lower beaks are attached to the buccal mass by thick muscles via a thin chitin-secreting cell layer (Dilly and Nixon, 1976). In the Patellogastropoda, a single jaw plate is also fixed on the dorsal side of the odontophore. The inner surface of the posterior wing has an attachment of muscles that are inserted on the anterolateral cartilages. In contrast to these groups, jaws are entirely attached to the oral tube independent of the buccal musculature in all of the other gastropod groups (Fig. 96) and Tryblidiida (Wingstrand, 1985).
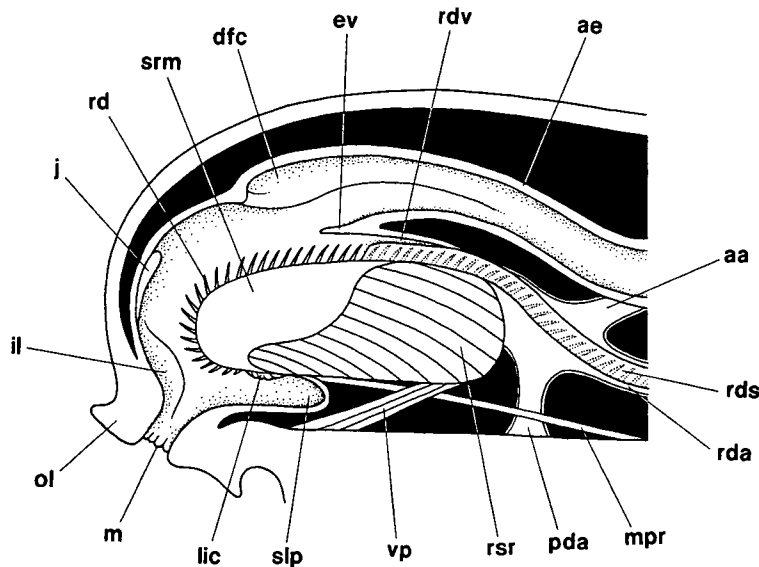
Fig. 96. Schematic sagittal section of head region of Archaeogastropoda.

37. Anterior edge of the jaws: (0) simple [*Nep, Mik, Chl, Sto, Bro, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) calcified** [*Nau*], **(2) thickened into an anterior band** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(3) fimbriate** [*Sul, Scu, Mac, Ana, Tur, Lep, Seg*], **(-) inapplicable** [*Chi*]

The anterior edges of the jaws of archaeogastropods and other molluscs exhibit several characteristic states: (i) The edges are simply smooth in *Neopilina* (Wingstrand, 1985), some of Trochidae (e.g. *Chloros-toma*, Fig. 53 c), *Neomphalus* (Fretter *et al.*, 1981), *Cocculina*, Neritopsina, and Caenogastropoda. (ii) In *Nautilus*, the anterior tip of both beaks are heavily calcified (Okutani and Mikami, 1977; Saunders *et al.*, 1978; Tanabe and Fukuda, in press). The upper beak has a pointed tip, and the corresponding margin of lower beak is denticulate. (iii) In the Patellogastropoda, the central part of the jaw covering the radular teeth is particularly thickened, and the anterior edge develops into a distinct zone called the anterior band (Walker, 1968). (iv) In most vetigastropods, including *Lepetodrilus* and *Seguenzia*, the edges are fimbriate with chitinous bristles or scaly projections.

3-4. Radular Sac
38. Posterior end of the radular sac: (0) simple [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) bifurcated** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc, Nem*], **(?) unknown** [*Seg*]

Ponder and Lindberg (1996; 1997) introduced a new character of the radula that has been completely neglected in previous studies of gastropod phylogeny. It was also confirmed by this study that the end of radular sac is markedly bifurcated in some archaeogastropod groups, but it is quite simple in others. The former type is found in all vetigastropod genera (including *Lepetodrilus*, Fig. 64 b), *Neomphalus* (Fretter *et al.*, 1981: fig. 3), and *Cocculina* (Fig. 70), while all remaining groups including the outgroups exhibit the latter condition. The states in *Seguenzia* was scored as "unknown" by Ponder and Lindberg (1997) and was also not revealed during this study.

3-5. Muscles of the Subradular Membrane and Radular Sac
39. Retractor muscles of the subradular membrane: (0) divided into bilateral pair [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) fused ventrally** [*Pat, Cel*]

An identical topological position of the retractor muscle of the subradular membrane is shared by the cartilage-bearing molluscan groups. The subradular membrane is fixed on the odontophore by paired retractor muscles along the lateral margin. However, in *Patella* and *Cellana*, the muscles are extended ventrally to fuse at the midline (Graham, 1964: fig. 13) and are furthermore split into dorsal and ventral sections. It is also a common pattern in these two genera that the median and lateral protractors of the subradular membrane run between dorsal and ventral layers of the muscles (Fig. 5 d).

40. Symmetry of the median protractor muscles of the subradular membrane: (0) symmetrical [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) asymmetrical** [*Pat, Cel*], **(?) unknown** [*Seg*]

Patella and *Cellana* share a specialized configuration of this paired muscle, which greatly differs from the typical archaeogastropod pattern. In these genera, the left muscle runs almost straight into the body cavity behind the buccal mass; the right muscle bends abruptly to the right and further extends to the shell muscles (Graham, 1964: fig. 12; Figs. 5 c, d). This pattern does not occur in Polyplacophora, Tryblidiida, *Nautilus*, and other gastropod genera. *Neomphalus* is likewise reported to have symmetrical muscles as "protractor muscle of radular membrane" (Fretter *et al.*, 1981: fig. 5, prm).

41. Postmedian retractor muscles of the radular sac: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Ana, Lep, Coc, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Tur, Chl, Sto, Bro, Nem*], **(?) unknown** [*Seg*]

Characteristically paired retractor muscles are found in all vetigastropod genera except *Anatoma*. The fairly thick and paired muscle bundles originate from the floor of the body cavity behind the buccal mass. They are inserted on the ventral surface of the radular sac immediately posterior to the insertion of the retractor muscles of the radular sac. It is also a common pattern that the median protractor muscle of the subradular membrane ends near the origin of this muscle and that the median tensor of the radular sac is attached to the area near the insertion of this muscle. A homologous muscle in *Neomphalus* was described as "radular retractor muscle (rr)" by Fretter *et al.* (1981: figs. 3-5). It is absent in patellogastropod and neritopsine genera, *Anatoma* (Fig. 43 f), *Cocculina* (Fig. 70), *Lepetodrilus* (Fig. 63 b), and Caenogastropoda. Its condition in *Seguenzia* is unknown.

42. Median tensor muscle of the radular sac: (0) absent [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) inserted on the retractor muscle of the subradular membrane** [*Pat, Cel*], **(2) inserted on the sublingual pouch** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc*], **(?) unknown** [*Seg*]

A very thin but distinct muscle strand is inserted on the ventral surface of the radular sac in various archaeogastropod genera. Its origin is on the ventral side of the sublingual pouch in vetigastropod genera, *Cocculina*, and *Lepetodrilus*. In *Patella* and *Cellana*, a similar muscle is present, but its origin shifts slightly to the posterior margin of the fused ventral section of the retractor muscle of the subradular membrane (Fig. 5 d). Therefore, it may not be homologous but was tentatively identified here as this muscle because of the similarity in configuration. Other taxa, including *Neomphalus* (Fretter *et al.*, 1981: fig. 5), lack a corresponding muscle. The state in *Seguenzia* is unknown.

43. Median retractor muscle of the radular sac: (0) absent [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel*]

Between the paired median protractor muscles of the subradular membrane, a thin retractor of the radular sac extends straight toward the posterior side in *Patella* and *Cellana* (Figs. 5 c, d). This characteristic muscle is shared only by these two genera, but is absent in all other groups.

3–6. Radular Teeth

44. Functional type of radula: (0) stereoglossate [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(1) flexoglossate** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

In Gastropoda, the radula can be divided into two functional types that are referred to as "stereoglossate" and "flexoglossate" (Salvini-Plawen, 1988). The outgroups and patellogastropods have the former type, in which the teeth are moved only in parallel to the sagittal direction over the bending plane during feeding action. Gastropods other than patellogastropods all have the latter type radula in which the teeth exhibit flexible rotatory movement over the odontophore and are folded between paired cartilages when the radula is retracted.

45. Teeth mineralization: (0) mineralized [*Chi, Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(1) non-mineralized** [*Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

In the outgroups, the polyplacophoran and tryblidiid radulae are darkly mineralized with iron (McLean, 1979; Wingstrand, 1985), but that of *Nautilus* is chitinous (Lowenstam *et al.*, 1984; Tanabe and Fukuda, in press). In Archaeogastropoda, tooth mineralization with iron occurs only in patellogastropod genera (except Neolepetopsidae; McLean, 1990 b); all other gastropods have non-mineralized teeth.

Ponder and Lindberg (1997) excluded this character from their phylogenetic analysis, because of uncertainty in homology concerning mineral contents. However, the recent results of chemical analysis show that the mineral composition is significantly different between dark (mineralized) and opaque (non-mineralized) teeth (Okoshi, 1996). Mineralized docoglossate radulae with a dark hue contain more than 1000 times more iron than non-mineralized flexoglossate teeth (Okoshi, 1996: table 1). Thus, a distinction between dark and opaque teeth is consistent with the result of chemical analysis, and the difference in color is useful to indicate the presence or absence of intensive mineralization with iron.

46. Basal plates: (0) absent [*Chi, Nep, Nau, Lim, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel, Pec, Niv, Erg, Nip*]

Patellogastropod radular teeth (lateral teeth) generally rest on the specially thickened basal plates. They are morphologically complex in form and sculpture in *Patella* and *Cellana*, or represented by solid simple plates in Acmaeidae and Lottiidae (Lindberg, 1981 a, 1988 a; Lindberg and McLean, 1981; Sasaki and Okutani, 1993 a, b, 1994 a, b). Basal plates are totally absent in Lepetidae (Moskalev, 1977), all outgroups, and all remaining gastropods.

47. Symmetry of tooth row: (0) symmetrical [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) asymmetrical** [*Mik, Sul, Scu, Mac*]

The alignment of the right and left portions of a tooth row is generally symmetrical in the molluscan radula. In some rhipidoglossate radulae, however, asymmetrical arrangement of teeth is prominently developed, in Pleurotomariidae, Haliotidae, Fissurellidae (Hickman, 1981; 1984 a, c). In other taxa, the radula

does not show clear asymmetry.

48. Central tooth: (0) present [*Chi, Nep, Nau, Pat, Lim, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) absent** [*Cel, Pec, Niv, Erg, Nip, Coc*]

The radula of Testaria (Polyplacophora+Conchifera) normally has a medianly situated tooth termed central or rachidian tooth. However, there are some exceptional groups lacking it in archaeogastropods. (i) Acmaeid and lottiid genera and nacellid *Cellana* completely lack any trace of the central tooth. (ii) *Cocculina* also lacks the central tooth, and the radular membrane is widely exposed in the spacious area in the center.

Among Patellogastropoda, *Patella*'s central tooth is represented by a vestigial chitinous ridge between the basal plates (Sasaki et al, 1994). In Lepetidae, there is a large plate-like central tooth that is presumed to be fused with several pairs of lateral teeth (Moskalev, 1977).

49. Number of lateral teeth: (0) 3 pairs (including basal fusion) [*Nep, Pat, Cel, Pec, Niv, Erg, Nip*], **(1) 4 pairs** [*Coc, Nem, Ner, Sep, Cin, Wal*], **(2) 5 pairs** [*Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep*], **(3) multiple pairs** [*Mik*], **(4) single pair** [*Seg, Pom, Biw*], **(5) absent** [*Lim*], **(-) inapplicable** [*Chi, Nau*]

The number of lateral teeth is variable in archaeogastropods and outgroups. (i) Patellogastropod genera normally have three pairs of lateral teeth (Lindberg, 1981 b, 1988 a; McLean, 1990 b), but often these teeth are fused at their bases. The apparent single pair of lateral teeth in Acmaeoidea can be regarded as three pairs because each tooth has three cusps which are still distinctly separated as in *Pectinodonta* (Tsuchida and Ishida, 1977; Hickman, 1983; Marshall, 1985 b). The lateral teeth of Tryblidiida is also regarded as three pairs (McLean, 1979). (ii) The number of lateral tooth pairs is four in *Cocculina, Neomphalus* (McLean, 1981), and neritopsine genera. (iii) There are uniformly five pairs in the Haliotidae, Fissurellidae, Scissurellidae, Trochoidea, and Lepetodrilidae. (iv) *Mikadotrochus* has markedly multiplied lateral teeth (ca. 40 pairs). (v) *Seguenzia* and Caenogastropoda have only a single pair. (vi) The lateral teeth of Lepetidae are probably involved in fusion, but its relationship with a plate-like central tooth is unknown. (vii) In the Polyplacophora and *Nautilus*, lateral and marginal teeth are nominally discriminated for description, but they are not sharply differentiated morphologically unlike the inner lateral and outer marginal tooth fields of Gastropoda.

50. Outer lateral teeth: (0) not differentiated [*Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Pom, Biw*], **(1) fourth teeth enlarged** [*Coc, Ner, Sep, Cin, Wal*], **(2) fifth teeth enlarged** [*Scu, Mac, Ana*], **(-) inapplicable** [*Chi*]

One pair of outermost lateral teeth can be especially enlarged and differentiated. In fissurellid genera and *Anatoma*, the fifth teeth are much more prominent than other lateral teeth. A similar condition is found in the fourth teeth in *Cocculina* and neritopsine genera. Other groups of Archaeogastropoda, Cephalopoda, and Tryblidiida lack such specialization. The second lateral teeth of Polyplacophora are also enlarged, but their homology is uncertain.

51. Lateromarginal plates: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Ana, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) true plate** [*Scu, Mac*], **(2) basal extension of innermost marginal tooth (protolateromarginal plate)** [*Tur, Chl, Sto, Bro*]

The rhipidoglossate radula can have plate-like teeth that interact with outermost lateral and innermost marginal teeth at their base. Fissurellidae all have independent plates, but in Trochoidea they are in most cases continuous basally with the innermost marginal teeth. The simple plate of the latter form is considered to have arisen from the basal extension of the marginal teeth and is called "protolateromarginal plate"

(Hickman and McLean, 1990; Hickman, 1996). Their homology can be difficult to definitely establish but they are treated here as such based upon similarity in morphology and position. The complete plate in Margaritinae of Trochidae (Hickman and McLean, 1990: fig. 50) may support this assumption.

52. Number of marginal teeth: (0) 3 or fewer pairs [*Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Pom, Biw*], **(1) multiple pairs (normally more than 20 pairs)** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal*], **(-) inapplicable** [*Chi, Nau*]

It is very characteristic that non-patellogastropod archaeogastropods have many teeth of similar form in the marginal tooth field. In contrast, patellogastropods and the outgroups possess no more than three pairs of marginal teeth. Similarly, caenogastropod genera (*Pomacea* and *Biwamelania*) have only two pairs of marginal teeth. Tooth homology is uncertain for Polyplacophora and *Nautilus* in which comparable differentiation is not found in the outer teeth field.

53. Morphology of the marginal teeth: (0) plate-like [*Nep, Pat, Cel, Lim*], **(1) inconspicuous or absent** [*Pec, Niv, Erg, Nip*], **(2) elongated with long shaft** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(-) inapplicable** [*Chi, Nau*]

The marginal teeth in archaeogastropods and the outgroups are divided into three states on the basis of the morphology of their shaft. (i) Tryblidiida, Patellidae, Nacellidae, and Lepetidae of Patellogastropoda share teeth with broad, plate-like cusp (Wingstrand, 1985). In these groups, each tooth is tightly attached to the radular membrane. (ii) The marginal teeth are greatly inconspicuous or completely absent in acmaeid and lottiid genera. (iii) The remaining archaeogastropod and two caenogastropod genera have teeth with a long shaft, small base, and slender cusp.

3–7. Odontophoral Cartilages

54. Posterior cartilages: (0) absent [*Chi, Nep, Nau, Lim, Pec, Niv, Erg, Nip, Lep, Seg, Coc, Nem, Pom, Biw*], **(1) present** [*Pat, Cel, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Ner, Sep, Cin, Wal*]

The possession of paired odontophoral cartilages in buccal mass is one of possible synapomorphies of Testaria (Polyplacophora + Conchifera), although it is absent in Bivalvia and Cephalopoda (Young, 1991). Among them, gastropods especially exhibit a diversity in the number of cartilages (Fig. 97). (i) Cartilages include anterior and posterior pairs in Patelloidea (*Patella* and *Cellana*), most vetigastropods, and neritopsines. (ii) Most simple type is found in *Lepetodrilus, Seguenzia, Cocculina, Neomphalus* (Fretter *et al.*, 1981), and caenogastropods in which only a single pair is present. Patellogastropods excluding Patelloidea also do not have posterior cartilages. In outgroups, Polyplacophora and Tryblidiida have two pairs ("medial" and "lateral") of cartilages and a single pair of fluid-filled vesicles (Wingstrand, 1985). Among these pairs, medial cartilages are regarded as homologous with anterior cartilages of gastropods based on similar insertion of ventral approximator (= muscle IIIa, *m. radulae impar*, Wingstrand, 1985: fig. 16). The homology of the remaining pairs with cartilages of gastropods is difficult to establish, although some possibilities have been proposed (Wingstrand, 1985: 61–64).

55. Anterolateral cartilages: (0) absent [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*]

Odontophoral cartilages of lepetid, acmaeid, and lottiid genera consist of two pairs (anterior + anterolateral, not anterior + posterior). Cartilages of *Patella* and *Cellana* also exhibit a similar state in the anterolateral pair, although these genera are specialized in total number of cartilages (three or five pairs). Therefore, odontophoral cartilages of all patellogastropods clearly differ from those of other molluscs in having anterolateral cartilages.
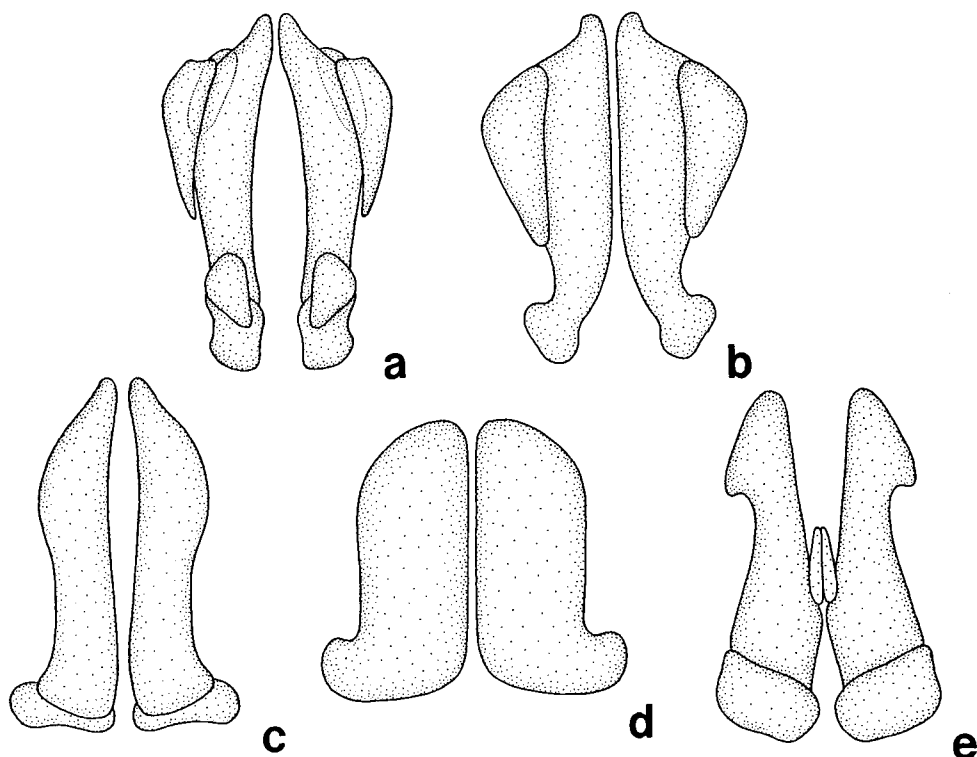
Fig. 97.   Character states of the odontophoral cartilages. **a**, 5 (anterior + posterior + anterolateral + anteroventral + posterodorsal) pairs. **b**, 2 (anterolateral + anterior) pairs. **c**, 2 (anterior + posterior) pairs. **d**, single pair. **e**, 3 (anterior + posterior + median) pairs.

56. Median cartilages: (**0**) **absent** [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Pom, Biw*], (**1**) **present** [*Ner, Sep, Cin, Wal*]

All neritopsines genera investigated have a fused or unfused pair of median cartilages between anterior cartilages, and other gastropod genera totally lack this characteristic pair. "Median cartilages" in neritopsines are evidently different from "medial cartilages" described in Polyplacophora and Tryblidiida (Wingstrand, 1985), because the former are not inserted by the ventral approximator muscle. Thus, no other mollusks possess homologous cartilages.

3–8. Muscles of the Odontophoral Cartilages

57. Ventral approximator muscle of the odontophoral cartilages: (**0**) **single-layered approximator** [*Chi, Nep, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], (**1**) **two-layered approximator** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*], (**-**) **inapplicable** [*Nau*]

The inner sides of the anterior cartilages (Gastropoda) or the "medial cartilages" (Polyplacophora and Tryblidiida) are connected by a horizontal sheet of muscle (Graham, 1973; Wingstrand, 1985). This is always present in molluscan groups having paired cartilages. In the patellogastropod genera, the muscle is composed of ventral and dorsal layers; the ventral layer is fused horizontally below the cartilages but the dorsal one is inserted medially between the cartilages (Graham, 1964: fig. 13). Such a condition is not found in the approximator of the outgroups (e.g. Wingstrand, 1985: fig. 16, Muscle IIIa) and all of non-patellogastropod gastropods, including *Neomphalus* (Fretter et al, 1981: fig. 3).

58. Outer approximator muscles of the odontophoral cartilages: (0) absent [*Chi, Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Nem, Pom, Biw*], **(1) present** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc, Ner, Sep, Cin, Wal*], **(-) inapplicable** [*Nau*], **(?) unknown** [*Seg*]

In vetigastropod genera (including *Lepetodrilus*), *Cocculina*, and all neritopsine genera, thick bundles of longitudinal muscles connect the outer ventral sides of the anterior and posterior pairs of odontophoral cartilages or the anterior and posterior sides of a single pair of cartilages. This muscle is absent in Patellogastropoda, *Neomphalus* (Fretter et al., 1981: fig. 5), Caenogastropoda, and the outgroups. The state in *Seguenzia* is unknown.

59. Tensor muscles of the anterior cartilages: (0) absent [*Chi, Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Pom, Biw*], **(1) present** [*Ner, Sep, Cin, Wal*], **(-) inapplicable** [*Nau*]

In neritopsine genera, a pair of thin muscles insert in the small area of anterior cartilage behind the anterolateral extension of the anterior cartilages. The topological relationship with other muscles exhibits a common pattern; i.e. this tensor emerges between the strands of lateral protractor muscle and extends to the origin in the inner wall of snout. No other molluscan genera have this muscle.

3–9. Alimentary Tract and Glands

60. Outgrowths of sublingual gland: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

The sublingual pouch between the floor of the snout and the anteroventral side of the buccal mass (Fig. 96) has particular bilateral outgrowths in some groups. Species of *Nerita* have a pair of glandular pouches (Fretter, 1965: fig. 8; Figs. 74 c, 75 a). Among neritopsine genera, *Septalia* (Neritidae) and *Cinnalepeta* (Phenacolepadidae) also possess these pouches, but they are not present in *Waldemaria* (Helicinidae). Functionally, the absence of the salivary glands is compensated by the development of this gland in Neritidae (Fretter, 1965). However, in *Cocculina japonica* and *Lepetodrilus nux*, similar outgrowths are not found, although distinct salivary glands are absent.

Of the patellogastropods, only *Pectinodonta orientalis* has pouches in a similar position (Fig. 16 d). However, very thin triangular sacs in this species are greatly different in appearance from round glandular sacs of Neritoidea. These structures are not regarded as homologous with the glandular pouches of neritopsines in this analysis. The functional significance of the triangular pouch of *Pectinodonta* is unknown, but it may be concerned with feeding on submerged logs in deep water.

61. Salivary glands: (0) simple, sack-like glands [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Pom, Biw*], **(1) ramified glands** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro*], **(2) absent** [*Lep, Coc, Nem, Ner, Sep, Cin, Wal*], **(?) unknown** [*Seg*]

The salivary glands of Gastropoda and other molluscs are greatly variable in form and size. Although the glands of outgroups and patellogastropods can be split into a number of subtypes, they are divided into the following three states in this analysis. (i) In outgroups salivary glands are simple and sac-like without ducts in Polyplacophora (Fretter, 1937), Tryblidiida (Wingstrand, 1985), and *Nautilus* (Griffin, 1990: fig. 70). Patellogastropod glands are greatly diversified in terms of size of the glands and number and length of the salivary ducts, but they are regarded as essentially identical. The detailed differences were not applied to the analysis (see discussion in section V–2). (ii) In Vetigastropoda, the glands are ramified into numerous vermiform tubes and discharge into the buccal cavity through narrow longitudinal openings without duct. (iii) *Cocculina, Lepetodrilus, Neomphalus* (Fretter et al., 1981), and all neritopsine genera lack salivary glands. The state in *Seguenzia* is unknown.

62. Esophageal pouches: (0) dorsoventrally depressed lateral pouches [*Chi, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Coc, Nem, Ner, Sep, Cin, Wal*], **(1) absent** [*Nep, Nau*], **(2) expanded pouches** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg*], **(3) posteriorly separated pouches with narrow duct** [*Pom, Biw*]

The anterior esophagus is morphologically variable in molluscan groups (Fig. 98). (i) In Polyplacophora, Patellogastropoda, Neritopsina, and *Cocculina*, the dorsal food channel of the anterior esophagus is accompanied by dorsoventrally depressed, lateral pouches on either side (Salvini-Plawen and Haszprunar, 1987; Salvini-Plawen, 1988). The lateral pouch is elaborated from the central to the posterior region of the buccal mass. The pouches of *Neomphalus* are also depressed type (Fretter *et al.*, 1981). (ii) *Nautilus* has a simple tubular canal (Griffin, 1900). Esophagus of *Neopilina* is also simple, but it develops large paired esophageal diverticula (initially described as a coelom) (Wingstrand, 1985). (iii) In the vetigastropods (including *Lepetodrilus* and *Seguenzia*), large pouches expand to cover the posterior part of the buccal mass. (iv) In Ampullariidae (*Pomacea*) and Pleuroceridae (*Biwamelania*), the esophageal pouches are separated from anterior esophagus as an oblique sac posterior to the buccal mass.
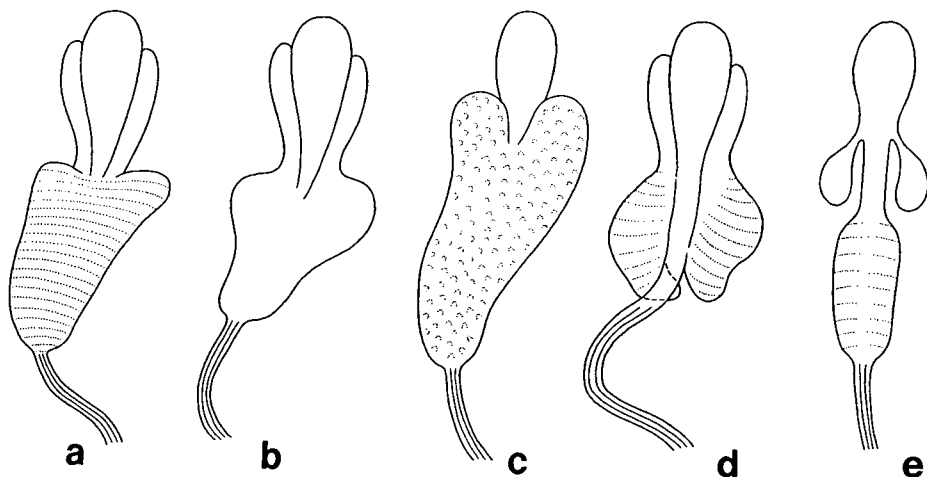
Fig. 98.   Character states of esophagus. a, Dorsoventrally depressed pouches and septate gland. b, Dorsoventrally depressed pouches and simple gland c, Expanded pouches and papillate gland. d, Dorsoventrally depressed pouches and septate glands separated posteriorly from esophagus. e, Posteriorly separated pouches and simple gland.

63. Esophageal gland of mid-esophagus: (0) simple and non-papillate [*Chi, Nep, Nau, Coc, Nem, Pom, Biw*], **(1) septate within mid-esophagus** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(2) papillate** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg*], **(3) septate and separated posteriorly from esophagus** [*Ner, Sep, Cin, Wal*]

Generally, the gastropod mid-esophagus shows a twisted condition due to the torsion, and the interior is lined by glandular epithelium. In the archaeogastropods, the wall of the esophagus expands and develops outgrowths in various ways to increase surface area (Fig. 98). (i) In the outgroups, *Cocculina, Neomphalus* (Fretter *et al.*, 1981), Ampullariidae (*Pomacea*), and Pleuroceridae (*Biwamelania*), the esophageal wall is a simple tube lacking the projecting structure. (ii) In Patellogastropoda, the mid-esophagus is greatly dilated and septated with lamellae. (iii) In all vetigastropod genera, the inner wall of esophagus pouch is papillate. It is also slightly papillate in *Seguenzia*. (iv) The neritopsine genera have posteriorly separated esophageal glands (=posterior glands of Fretter, 1984 a) that are septated internally.

64. Gastric caecum: (0) absent [*Chi, Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Coc, Pom, Biw*], **(1) large and bulbous** [*Nau*], **(2) large and spiral** [*Mik, Sul, Tur, Chl, Sto*], **(3) small and crescent-shaped** [*Scu, Mac, Ana, Bro, Lep, Seg, Nem, Ner, Sep, Cin, Wal*]

The stomach of many molluscs is provided with a caecum of various grade of development. Its variation is divided into the four discrete states. (i) The gastric caecum is absent in Polyplacophora (Fretter, 1937; Salvini-Plawen, 1988) and Tryblidiida (Lemche and Wingstrand, 1959), Patellogastropoda *Cocculina, Pomacea* (Andrews, 1965; Berthold, 1991) and *Biwamelania*. (ii) In *Nautilus*, the caecum is a simple sac but well developed (Griffin, 1990: fig. 23). (iii) Multispiral type is prominent in the stomach of Pleurotomariidae, Haliotidae, and most trochoids (*Turbo, Chlorostoma*, and *Stomatia*). (iv) Short, crescent type is found in Fissurellidae, *Anatoma, Seguenzia, Lepetodrilus, Broderipia, Neomphalus* (Fretter *et al.*, 1981), and in all neritopsine groups.

65. Style sac region, including sorting area and tooth of gastric shield: (0) absent [*Chi, Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(1) present** [*Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

The style sac region of the stomach generally consists of a cuticularized gastric shield and its tooth, plus a ciliated sorting area between the typhlosoles. In Polyplacophora, the ciliated area is present in the stomach, but is not as well organized as in the distinct area (Fretter, 1937; Salvini-Plawen, 1985, 1988). It is totally absent in the modified stomach of Tryblidiida (Lemche and Wingstrand, 1959). In the stomach of *Nautilus*, there are two longitudinal ridges with transverse furrows between them (Griffin, 1900: fig. 32). These ridges are continuous with the entrance of the caecum, suggesting that they are homologous with the typhlosoles of other mollusks (the topological right is the minor typhlosole, the left is the major typhlosole). Likewise, the median corrugated area is homologous with the sorting area of other groups. In gastropods, this region is well-developed and shows rather similar morphology at least within archaeogastropods except Patellogastropoda (Fig. 99). The stomach of all patellogastropod genera lacks a style-sac region almost completely. The absence of all inner structure except typhlosoles suggests the only the proximal part of the stomach is retained near the openings of the digestive glands, and that the initial part of the intestine is expanded to form most of the "stomach" (Fretter, 1990).

66. Anterior loop of intestine: (0) absent [*Chi, Nep, Nau, Biw*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom*]

The so-called anterior loop, a particular course of gut convolution, is shared by archaeogastropod genera. After departure from the stomach, the intestine extends anteriorly to the right posterior region of the buccal mass, crossing over the esophagus. This general pattern is maintained in archaeogastropods, including *Neomphalus* (Fretter *et al.*, 1981), but does not occur in "higher" Caenogastropoda. Ampullariidae of Architaenioglossa also possess a short loop over the esophagus, which is comparable to the archaeogastropod condition. In the outgroups, the intestine is coiled only posteriorly in Polyplacophora (Fretter, 1937) and *Neopilina* (Lemche and Wingstrand, 1959), or is simply bent apart from the anterior region in *Nautilus* (Griffin, 1900).

67. Course of the rectum relative to the pericardium: (0) rectum penetrating neither ventricle nor pericardium [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) rectum penetrating both ventricle and pericardium** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Ner, Sep, Cin*]

The relationship between the pericardium and the course of the rectum (=posterior region of the intestine) is variable in molluscan groups. The rectum runs freely on the ventral side of pericardium in Polypla-
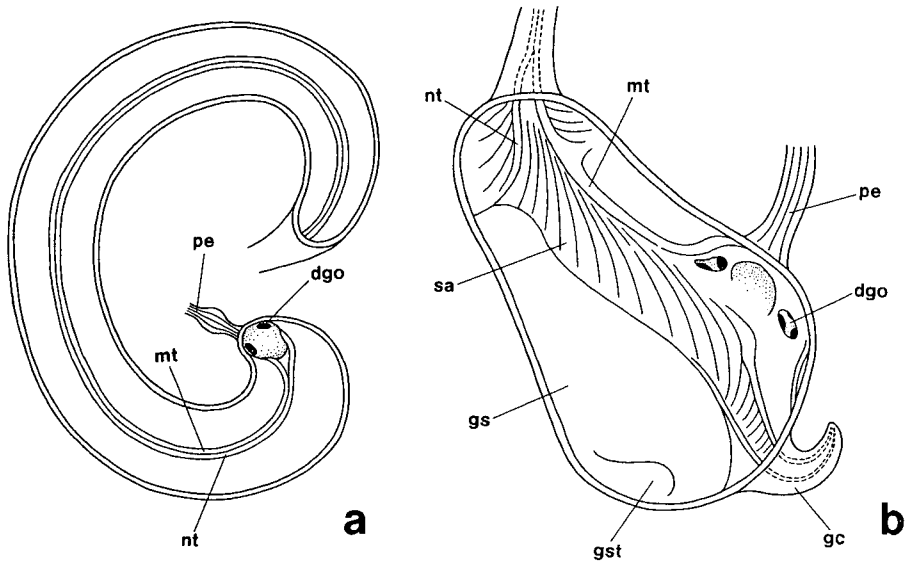
Fig. 99.   Two types of stomach in Archaeogastropoda. a, Patellogastropoda. b, Non-Patellogastropoda.

cophora (Hyman, 1967; Salvini-Plawen, 1985; Eernisse and Reynolds, 1994) and in *Nautilus* (Griffin, 1900). In *Neopilina*, the rectum passes between two isolated pericardial sacs, each of which includes a ventricle and two atria (Lemche and Wingstrand, 1959: fig. 143). Among gastropods, the rectum does not pass through the pericardium in Patellogastropoda, *Cocculina*, *Waldemaria*, *Neomphalus* (Fretter *et al.*, 1981) and Caenogastropoda, whereas penetration occurs in all zeugobranchs, Trochoidea, *Lepetodrilus*, and neritopsine genera excluding *Waldemaria*. It is a general pattern that the rectum always passes through the ventricle when it penetrates the pericardium in the latter groups.

4. Circulatory System

68. Number of auricles: (0) single pair [*Chi, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep*], **(1) two pairs** [*Nep, Nau*], **(2) single pair with right auricle nonfunctional** [*Ner, Sep, Cin*], **(3) single left auricle (unpaired)** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Seg, Coc, Nem, Wal, Pom, Biw*]

Molluscs generally have a median ventricle and paired auricles, but the number of auricles is variable among different taxa. Among the outgroups, Polyplacophora have a pair of auricles (Hyman, 1967; Salvini-Plawen, 1985; Eernisse and Reynolds, 1994). *Nautilus* has two pairs of auricles that are associated with two paired ctenidia and efferent ctenidial vessels (Griffin, 1900). *Neopilina* also has two pairs of auricles (Lemche and Wingstrand, 1959). Among Gastropoda, Patellogastropoda, *Cocculina*, *Seguenzia* (Quinn, 1983; Ponder and Lindberg, 1997), *Neomphalus* (Fretter *et al.*, 1981), *Waldemaria*, ampullariids, and Caenogastropoda have a single auricle (monotocardian condition). Only the vetigastropod genera and *Lepetodrilus* have a truly diotocardian heart with two functional auricles, but neritopsine genera excluding monotocardian *Waldemaria* have a single pair with right auricle nonfunctional.

69. Bulbous aorta: (0) undifferentiated or simple extension of aorta [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) developed into muscular sac** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*]

The muscular aortic bulb is elaborated within the pericardium of Patellogastropoda. It rhythmically contracts to send blood to both anterior and posterior aortae as an accessory pump of the heart (Jones, 1968).

The development of such a contractile apparatus is not found in the aorta of any other group. The ampulla of Ampullariidae is a clearly independent structure because it originates from part of the anterior aorta and has no relationship to the posterior aorta.

70. Basibranchial sinus: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) developed** [*Mik, Sul, Scu, Mac*], **(?) unknown** [*Ana*]

The blood space occurring in the anterior portion of the efferent renal vessel is specially expanded as a 'basibranchial sinus' in zeugobranch genera (Fretter and Graham, 1962: fig. 147). The state in *Anatoma* (with paired ctenidia) could not be verified.

71. Transverse pallial vein: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Tur, Chl, Sto, Bro, Lep*], **(?) unknown** [*Seg*]

In some vetigastropods, the vessel from the right kidney to the afferent ctenidial vessel crosses the mantle skirt and the left hypobranchial gland transversely (e.g. Fig. 46 a). This particular section of the vessel is termed the transverse pallial vein (Fretter and Graham, 1962). It is present in Trochidae, Turbinidae, and *Lepetodrilus*, but is absent in all other groups. The state in *Seguenzia* could not be verified.

5. Excretory System

72. Number of kidneys: (0) single symmetrical pair [*Chi*], **(1) six pairs** [*Nep*], **(2) two pairs** [*Nau*], **(3) single asymmetrical pair** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg*], **(4) left only** [*Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

The number of kidneys (nephridia) and kidney openings (nephridiopores) is extremely variable in the outgroups: a single pair in Polyplacophora (Eernisse and Reynolds, 1994) and two pairs in *Nautilus* (Schipp and Martin, 1987). In Tryblidiida, excretory organs comprise six pairs in *Neopilina*, seven pairs in *Vema*, and three to four pairs in *Micropilina* (Lemche and Wingstrand, 1959; Wingstrand, 1985; Haszprunar, 1997). In general, the paired right and left sides of molluscan excretory organs are bilateral and not differentiated in form and function. Exceptionally, gastropods have an asymmetrically paired or unpaired kidney. Most Archaeogastropoda have paired kidneys, whereas *Cocculina* (and generally Cocculinoidea; Haszprunar, 1988 c), *Neomphalus*, Neritopsina, and Caenogastropoda have single left kidney. The state in *Seguenzia* was scored as "paired," following Ponder and Lindberg's (1997) data matrix (character 29).

73. Position of the kidneys relative to the pericardium: (0) left and right kidneys on either side of pericardium [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg*], **(1) both left and right kidneys on the right side of the pericardium** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*], **(2) post-torsional left kidney on the right side of the pericardium** [*Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

Ponder and Lindberg (1997) pointed out that the position of kidney and pericardium show discrete states throughout molluscan groups. In Patellogastropoda, both kidneys characteristically lie on the right side of the pericardium. In Vetigastropoda, including *Lepetodrilus*, the left kidney is suspended from the mantle skirt on the anterior left side of the pericardium, while the right kidney is extended to visceral region on posterior right side of the pericardium. Similarly, the outgroups have paired kidneys located symmetrically on either side of the pericardium. The remaining groups have a single left kidney on the right side of the pericardium.

74. Papillary sac: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Lep, Seg, Coc, Nem, Ner,*

Sep, Cin, Wal, Pom, Biw], (1) developed [*Mik, Sul, Tur, Chl, Sto, Bro*], (2) small with indistinct papillae [*Scu, Mac*], (?) unknown [*Ana*]

In most vetigastropod groups, the inner surface of the left kidney is evaginated to form papillate surface (the so-called papillary sac). Functionally, this specialization generates a high surface-volume ratio of epithelia to lumen of the kidney. This state is present in Pleurotomariidae, Haliotidae, Turbinidae, and Trochidae, but is not differentiated in the remaining ingroup taxa and the outgroups. In Fissurellidae, the left kidney is greatly reduced in size, but histologically regarded as homologous with the typical papillary sac (Andrews, 1985; 1988). The state in *Seguenzia* was scored as "absent" based on Ponder and Lindberg's (1997) data matrix (character 26). Histological aspects were have not been adequately investigated in *Anatoma*.

6. Reproductive System
6-1. General Characters
75. Position of gonad: (0) dorsal to digestive glands [*Chi, Nau, Mik, Sul, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], (1) ventral to digestive glands [*Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Scu, Mac, Coc*]

The position of the gonad within the visceral mass has been regarded as a phylogenetic character for higher-level molluscan phylogenetics (Ponder and Lindberg, 1996; 1997). The gonad is most of ten located dorsal to the digestive glands and therefore occupies the highest position within the visceral mass. Polyplacophora, *Nautilus*, and most Gastropoda all retain such a topological relationship. However, the reversed position occurs in Tryblidiida (Lemche and Wingstrand, 1959), Patellogastropoda, Fissurellidae, and *Cocculina* (Fig. 71). The gonad is ventrally spread and concealed by the overlapping digestive glands in these forms. In *Neomphalus*, the gonad is situated dorsally (Fretter *et al.*, 1981: figs. 12, 13).

76. Number of gonads and gonoducts: (0) paired [*Chi, Nep*], (1) pre-torsional right only [*Nau*], (2) post-torsional right (=pre-torsional left) only [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

The numbers of the gonads and gonoducts are variable in molluscs at higher taxonomic levels (Ponder and Lindberg, 1996; 1997). Polyplacophora have a single median gonad with bilaterally separated gonoducts (Hyman, 1967). *Neopilina* have two pairs of gonads, each of which is connected with the excretory organ through its own gonoduct (Lemche and Wingstrand, 1959). In *Nautilus*, the gonad itself is symmetrical, but the gonoduct exists only on the pre-torsional right side in both sexes. However, the gonoduct may be originally paired because there is vestigial structure that is indicative of originally paired condition (Arnold, 1987). In all Gastropoda, both the gonad and gonoduct are asymmetrical, being an the posttosional right side only.

77. Opening site of the gonoducts: (0) directly into pallial cavity [*Chi, Nau, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], (1) through kidney into pallial cavity [*Nep, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep*]

Polyplacophora and *Nautilus* have gonoducts which are independent of the kidney, while those of Neopilinidae have a direct connection with distal section of the excretory organ (Lemche and Wingstrand, 1959). Among Gastropoda, most archaeogastropods including *Lepetodrilus* discharge gametes through the right kidney (Fig. 100). However, hermaphroditic *Cocculina* has a separated glandular gonoduct (Figs. 69 a, 72 d), and all neritopsines and caenogastropods have an independent, well-developed pallial gonoduct. The gonoduct of *Seguenzia* was scored as independent of kidney, following Ponder and Lindberg's (1997) data matrix (character 33). *Neomphalus* also has an isolated gonoduct in both sexes (with a gonopericardial duct only in female) (Fretter *et al.*, 1981).
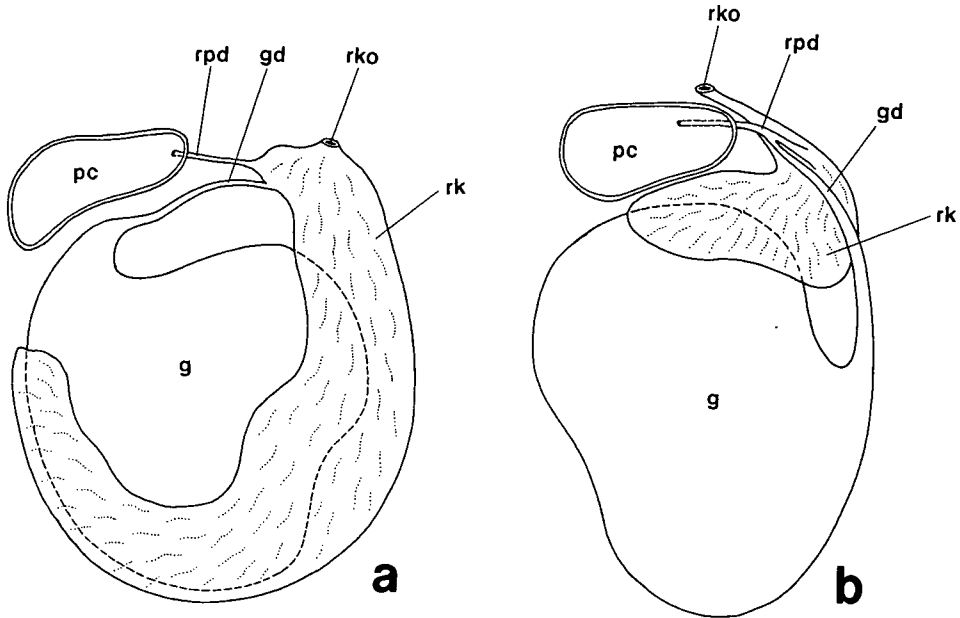
Fig. 100.   Connection and topological relationships of right kidney, pericardium, and gonad. Left kidney is omitted. a, Patellogastropoda. b, Fissurellidae.

6–2. Female Organ

78. Pallial oviduct composed of paired albumen glands and capsule gland: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

Most archaeogastropods (excluding neritopsine genera) release gametes through the right kidney, and accordingly females lack a well-developed pallial gonoduct. In contrast, the female gonoducts in Neritopsina and Caenogastropoda are elaborated into a glandular oviduct, consisting of a proximal albumen gland and a distal capsule gland. However, it is very difficult to establish the homology of individual structure constituting pallial oviduct throughout gastropod higher taxa, as pointed out by Ponder and Lindberg (1997). Exceptionally only some neritopsine genera within Archaeogastropoda seem to share a characteristic and homologized set of paired albumen glands and capsule gland (Fig. 101). In other archaeogastropods, the true (not urogenital) oviduct of *Neomphalus*, *Cocculina*, and Seguenziidae do not develop glands comparable to those of neritopsines.

79. Number of female genital openings: (0) monaulic [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Pom, Biw*], **(1) diaulic** [*Ner, Cin, Wal*], **(2) triaulic with enigmatic duct** [*Sep*]

A vaginal opening independent of the female gonopore is a common and unique feature in neritopsine genera within Archaeogastropoda (Fig. 101). Especially in the genus *Septalia*, an additional accessory duct of unknown function (so-called "*ductus enigmaticus*") is separated from the vaginal duct and extended back to the pallial cavity (Fig. 101 b, ed). Therefore, the gonad is monaulic with a single reproductive opening in all non-neritopsine groups, but diaulic in most Neritopsina and uniquely triaulic in *Septalia*. Ampullariidae have a semi-closed monaulic pallial oviduct (Andrews, 1964; Berthold, 1991), whereas Cerithioidea including Pleuroceridae have an open pallial oviduct with a longitudinal cleft (Houbrick, 1988).
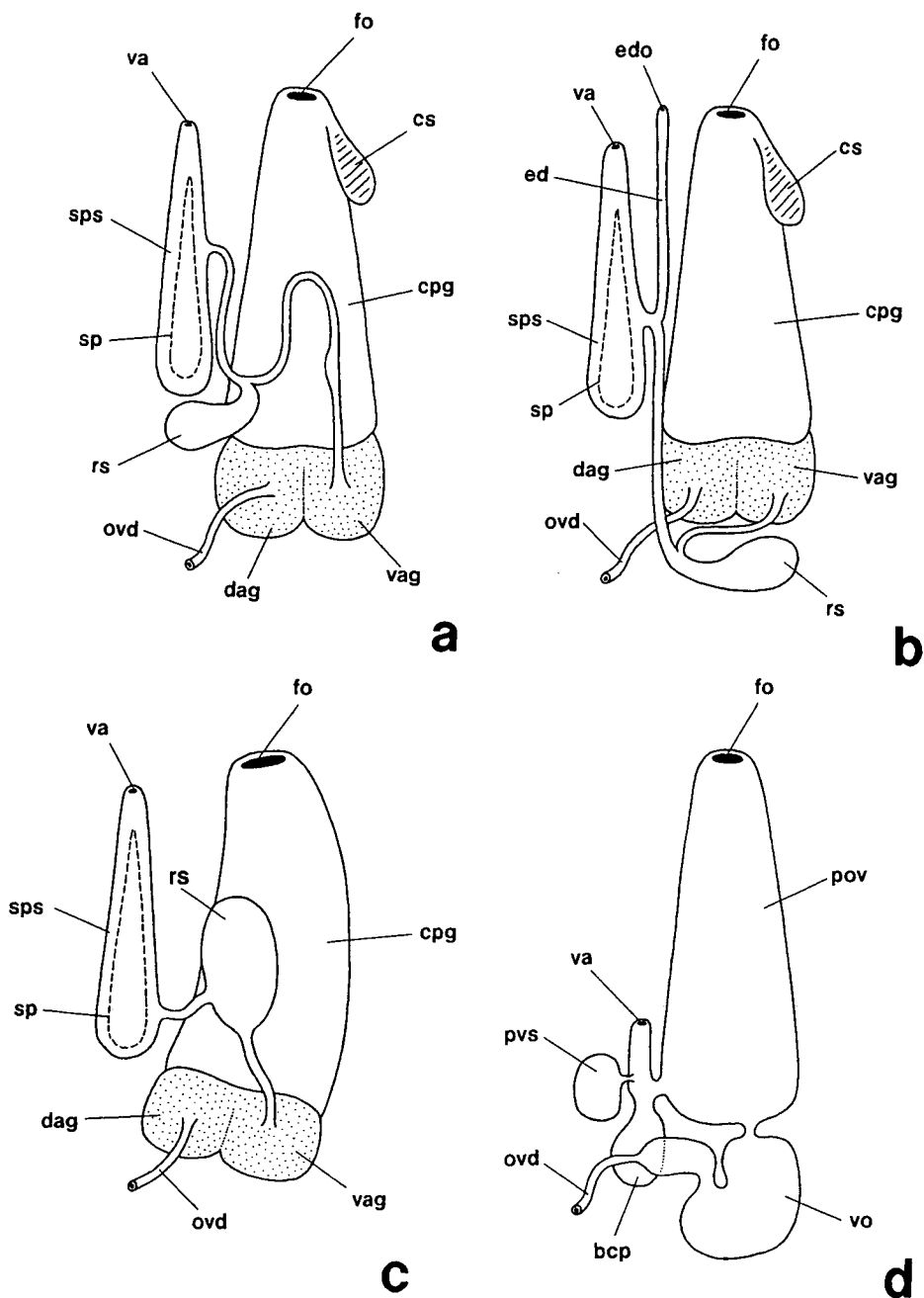
Fig. 101.   Pallial oviduct of Neritopsina. **a**, *Nerita*. **b**, *Septalia*. **c**, *Cinnalepeta*. **d**, *Waldemaria*.

80. Spermatophore sac: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

    In neritopsine genera except for *Waldemaria* (Helicinidae), a special bursa for the reception of a spermatophore is developed within the gonoducts. The sac is distended by the spermatophore after copulation during the breeding season. In *Nerita*, the thin tip of the spermatophore extends from this sac into the duct to

seminal receptacle for sperm transfer (Fig. 76 d). This structure is functionally identical to the "bursa copulatrix" of other groups, but homologies are doubtful among gastropod higher taxa (Ponder and Lindberg, 1997).

81. Crystal sac: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Cin, Wal, Pom, Biw*], **(1) present** [*Ner, Sep*]

The neritid genera (*Nerita* and *Septalia*) deposit lenticular egg capsules with reinforcement minerals (Andrews, 1935; Fretter, 1946; Fretter and Graham, 1978; Bandel, 1982; Houston, 1990). The minerals are secreted by and stored in the crystal sac of the gonoduct. When minerals are being stored, this sac is easily recognized through the thin mantle by the color of minerals. Other groups, including Phenacolepadidae and Helcinidae, do not possess such a mineral-secreting organ.

6–3. Male Organ
82. Cephalic penis on the inner side of the right cephalic tentacle: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

Most neritopsine genera (except *Waldemaria*) have a cephalic penis on the inner side of the right cephalic tentacle. Although various archaeogastropods, especially deep-sea taxa, develop a copulatory apparatus in the head region, they are not homologous with the penes of neritopsines due to a difference in position. The so-called "penis" of *Erginus* (Golikov and Kussakin, 1972; = "subcephalic tentacle" in this study; Fig. 20) is the only structure comparable topologically to neritopsine penes. However, they are not homologous because of great differences in structure (ciliated tentacle without duct or groove in *Erginus* vs. smooth penis with lateral groove in Neritoidea). ·

83. Seminal vesicle derived from vas deferens: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

In the neritopsine genera except *Waldemaria*, the vas deferens is heavily coiled to form a mass of folded ducts which acts as a seminal vesicle. The formation of a spermatophore seems to be initiated in this structure. The seminal vesicle of *Lepetodrilus* (Fretter, 1988) is not regarded as homologous because it has much less coiling form than those of Neritoidea. Males of *Neomphalus* (Fretter *et al.*, 1981) and other taxa do not exhibit such a specialization.

84. "Annex gland" on the prostate: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Wal, Pom, Biw*], **(1) present** [*Ner, Sep, Cin*]

The prostate is widely covered by a gland called the "annex gland" in neritoid genera (Berry *et al.*, 1973). No other groups are found with a comparable glandular area, but the functional significance of the gland is still unknown. Another gland in the male neritid pallial gonoduct, the "basal gland" (Berry *et al.*, 1973), is found only in the genus *Nerita* even within Neritidae, and therefore it is not concerned with the analysis at the suprafamilial level.

7. Nervous System
7–1 Nerve Ring
85. Position of pleural ganglia: (0) pleural ganglia not clearly separated [*Chi, Nep, Nau*], **(1) hypoathroid (pleural ganglia in ventral position)** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom*], **(2) epiathroid (pleural ganglia in**

dorsal position) [*Biw*]

The circumesophageal nerve ring of the outgroups is markedly differentiated as compared with those of gastropods, although they consist of comparable parts. Polyplacophora and Tryblidiida have the amphineurous-type nervous system composed of a circumesophageal nerve ring and lateral and ventral nerve cords. The central nervous system of *Nautilus* is less concentrated than typical coleoid brain, but it is made of a tight nerve ring and short palliovisceral cord (Griffin, 1900). In any case, the pleural ganglia of the outgroups are not distinctly separated from other ganglia.

All genera of Archaeogastropoda investigated have the so-called hypoathroid condition in which pleural ganglia are distant from cerebral ganglia and juxtaposed to pedal ganglia (Fretter and Graham, 1962). In the architaenioglossate groups, an intermediate "dystenoid" condition is known in Viviparidae (Fretter and Graham, 1962), but the Ampullariidae have typical hypoathroid condition (Fig. 102). In Neotaenioglossa of Caenogastropoda, the central nervous system is epiathroid in which the pleurals are closely associated with the cerebrals rather than the pedals.

7–2. Buccal Region
86. Labial ganglia: (0) absent [*Chi, Nep, Nau, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip*]

Labial ganglia are present in all patellogastropod limpets hitherto investigated (e.g. Figs. 4 c, 9). They are positioned beneath the entrance to the sublingual pouch and give off nerves anteriorly toward the ventral labial region and posteriorly to the labiobuccal connectives. Homologous ganglia have not been found in other molluscan groups.

87. Labial/subcerebral commissure: (0) present [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Ner, Sep, Cin, Wal, Pom*], **(1) absent** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Coc, Nem, Biw*], **(?) unknown** [*Seg*]

A labial commissure is clearly present in all species of Patellogastropoda, *Neritopsina* and Ampullariidae, but it is absent in other groups of Archaeogastropoda and Caenogastropoda. *Neomphalus* also lacks this commissure (Fretter *et al.*, 1981). The states in *Seguenzia* is unknown.

Compared with nervous system of outgroups, labial commissure of gastropods can be regarded as homologous with the "subcerebral commissure" (Eernisse and Reynolds, 1994) of the amphineurans. They originate from the cerebral ganglia and are connected ventral to the alimentary canal.

7–3. Lateral/Visceral Loop
88. Position of lateral/visceral nerve loop: (0) outside shell muscles [*Chi, Nep*], **(1) inside shell muscles** [*Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

In the amphineuran nervous system of Polyplacophora and Tryblidiida, the lateral nerve cord runs outside of the shell muscles and is connected transversely with the ventral cords by commissures. In *Nautilus* and gastropod genera, the corresponding visceral loop lies inside the shell muscles (Haszprunar, 1988 b; Ponder and Lindberg, 1997).

89. Streptoneury of lateral/visceral nerve loop: (0) absent [*Chi, Nep, Nau*], **(1) present** [*Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*]

The twisted visceral nerve loop is one of the manifest results of gastropod torsion. This condition is restricted to gastropods and is shared at least by all archaeogastropods and other "prosobranchs." The con-
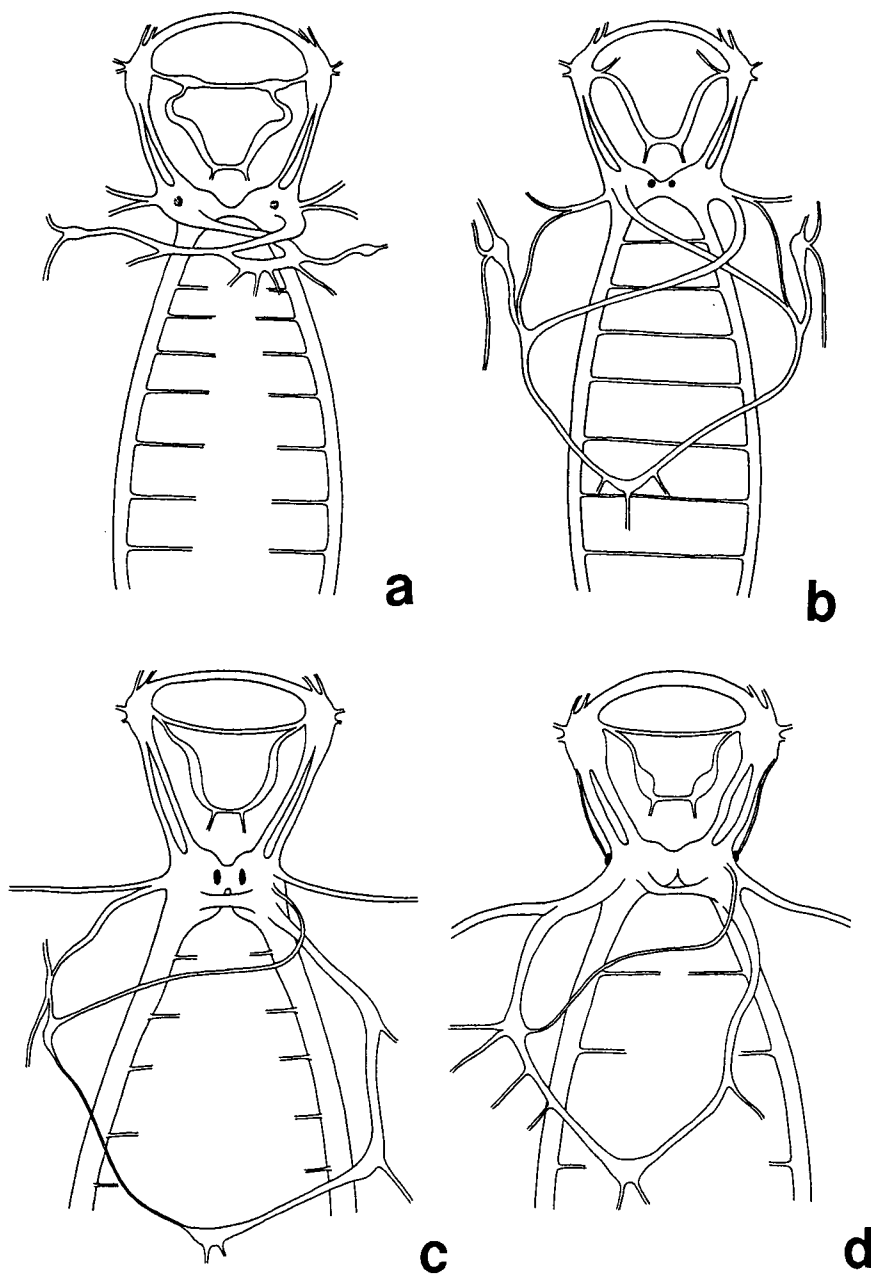
Fig. 102.   Generalized view of nervous system. **a**, Patellogastropoda. **b**, Zeugobranchia. **c**, Neritopsina. **d**, Ampullariidae.

trasting state is, however, found in Heterobranchia as untwisted configuration of visceral loop which is caused by "detorsion" and/or several other secondary modifications (Brace,1977; Schmekel, 1985; Haszprunar, 1988 b: Mikkelsen, 1996). In archaeogastropods, streptoneury occurs regardless of shell form and size, as is shown in purely symmetrical patellogastropod limpets.

90. Origin of lateral/visceral loop: (0) from left and right pleural ganglia [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Biw*], **(1) only from right ganglion** [*Ner, Sep, Cin, Wal, Pom*]

The lateral/visceral nerve loop of various molluscan groups normally arises from both right and left pleural ganglia. However, all neritopsine genera and ampullariids (Berthold, 1991) have a quite different pattern of the visceral nerve loop (Figs. 102 c, d). The loop originates only from the right pleural ganglion, and is seemingly untwisted for the most part. This unusual condition was interpreted to have been achieved by the anterior shift and fusion of the subesophageal ganglion with the pleural ganglion (Berthold, 1991: figs. 344–347). In *Mikadotrochus*, the loop is connected to cerebropleural connectives rather than to pleural ganglia directly. This state in *Mikadotrochus* is probably caused by a partial fusion of cerebropleural connectives and visceral loop and represents a slightly modified condition of normal two-sided origin.

7–4. Pedal Region

91. Median commissure of the pedal cords: (0) absent [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) present** [*Scu, Mac*]

Scutus and *Macroschisma* of Fissurellidae share a special condition in the pedal cords. The left and right cords are connected by a thick transverse connection in the central part of the foot in addition to typical pattern of thin commissures (Figs. 36 f, 41 c). No similar configuration of the pedal nervous system is found in other molluscan groups.

92. Position of the pedal (ventral) cords: (0) embedded in pedal musculature [*Chi, Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Mik, Sul, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal, Pom, Biw*], **(1) exposed on pedal musculature** [*Scu, Mac*]

Other unusual aspects of the nervous system are seen in Fissurellidae. The entire pedal cords are naked on the pedal musculature beneath visceral mass, and so that parallel thin pedal nerves are also exposed on the musculature in the visceral cavity. Such conditions never occur in other molluscan groups. "Normally" the pedal cords are buried completely in the foot.

93. Position of statocysts: (0) absent [*Chi*], **(1) lateral to pedal ganglia on outer sides** [*Nep, Nau, Pat, Cel, Lim, Pec, Niv, Erg, Nip, Pom, Biw*], **(2) anterodorsal or dorsal to pedal ganglia** [*Mik, Sul, Scu, Mac, Ana, Tur, Chl, Sto, Bro, Lep, Seg, Coc, Nem, Ner, Sep, Cin, Wal*]

The possession of statocysts is a shared character of the conchiferan classes. They are commonly innervated from the cerebral ganglia regardless of their position (Wingstrand, 1985). Among the outgroups, *Neopilina* has statocysts on the outer sides of the nerve ring (Lemche and Wingstrand, 1959). In *Nautilus*, they are situated on the outer posterolateral sides of pedal ganglia (Young, 1987: figs. 2,4). In archaeo- and caenogastropods, two different positions are observable (Fig. 102). (i) Statocysts occur on the outer sides of the pedal ganglia in patellogastropod limpets, Ampullariidae (*Pomacea*), and Pleuroceridae (*Biwamelania*). (ii) Statocysts are attached to the dorsal or anterodorsal surfaces of the pedal ganglia in Vetigastropoda, *Cocculina, Neomphalus* (Fretter *et al.*, 1981), and Neritopsina.

IV-2. Cladistic Analysis

Most parsimonious trees: The cladistic analysis, using a heuristic search on the data matrix (Table 3; unordered and unweighted data) yielded four equally parsimonious trees of length 209 steps (CI=0.660, RI =0.881, RCI=0.582) (Fig. 103). All trees obtained were of similar topology with only slight differences. In the resulting strict consensus tree (Figs. 104), polytomies were caused by three unresolved relationships, namely relationships among Acmaeoidea, Zeugobranchia, and Trochoidea. All other parts of the tree were fully resolved.

The relationships of the clades are summarized as follows (Fig. 104): (1) Monophyly of **Gastropoda** (node 3) is supported. (2) The Gastropoda is divided into **Patellogastropoda** (node 4) and non-patellogastropod groups, namely, **Orthogastropoda** (node 9). (3) Within Patellogastropoda, Lepetidae (*Limalepeta*) branches off first. Then the remaining groups (node 5) form two small clades, Patelloidea (node 6), and Acmaeoidea (node 7). (4) The orthogastropod clade bifurcates into two clades, **Rhipidoglossa** (node 10) and **Caenogastropoda** (node 24). (5) The Rhipidoglossa is composed of **Neritopsina** (node 21) and non-neritopsine (node 11) clades. The latter group does not have a taxon name, but corresponds to Archaeogastropoda (*s.s.*) of Ponder and Lindberg (1997). (6) Within Neritopsina, Helcinidae (*Waldemaria*) is separated as an independent clade. The remaining three genera (*Cinnalepeta*, *Nerita*, and *Septalia*) form another clade, Neritoidea (node 22). *Nerita* and *Septaria* are united as a clade corresponding to Neritidae (node 23). (7) The remaining rhipidoglossate groups, excluding *Neomphalus* and *Cocculina*, are united as **Vetigastropoda** (node 13) which consists of *Seguenzia*, *Lepetodrilus*, and a clade (node 15) of **Zeugobranchia** (node 16) plus **Trochoidea** (node 19). (8) Within Zeugobranchia, clades are always formed by Fissurellidae (*Scutus* and *Macroschisma*) (node 18) and pleurotomarid-haiotid genera (*Mikadotrochus* and *Haliotis*) (node 17). The position of *Anatoma* was not resolved.

Scaled analysis: The characters coded by more than two character states theoretically have greater influence on tree topology than binary characters, in proportion to the number of assigned states (Swofford and Begle, 1993). In this analysis, 66 characters are binary, but the data set includes 16 characters having 3 states and 11 characters having more than 3 states. Therefore, multistate characters in this analysis are expected to have significant effects. An analysis was performed based on the characters given 1000 base weight to estimate their effect on tree topology. They were all changed into equally weighted state by scale option.

The scaled analysis resulted in two most-parsimonious trees. Their strict consensus tree (Fig. 105 a) is congruent with that of the unscaled analysis (Fig. 104), and all the major clades retained the same topology as that of unscaled analysis. This indicates that influence of multistate characters was insignificant for tree topology.

Bootstrap analysis: Bootstrapping probabilities were calculated to show which nodes of the cladogram are significantly supported by the data presented. It should be noted that this method includes some assumptions to accept the result as an effective estimate of confidence limits (Felsenstein, 1985; Sanderson, 1989, 1995): (i) Character state changes must be independent. (ii) The observed data set must represent a universal pattern of distribution. However, changes in morphological character states are not always independent, and morphological data always contain bias due to subjective observation and limited taxonomic coverage. Thus, the probabilities derived from this analysis should not be overestimated as an indicator of confidence.

100 bootstrap replicates were attempted by heuristic analysis with random addition sequence of 30 replicates and branch-swapping by tree bisection reconnection (TBR). In the 50% majority-rule consensus tree of the bootstrapping (Fig. 105 b), monophyly of Patellogastropoda, Orthogastropoda, Neritopsina, Vetigastropoda, "Zeugobranchia+Trochoidea," Trochoidea, and Caenogastropoda were all confirmed by high val-

Table 3.   Data matrix.

```
                    1 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 999
Taxon               1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 123

Chiton              0000000-00 0000000000 0000000000 0000—000 00000000— 0—0000000 0000000000 0000000000 0000000000 000
Neopilina           0000000-00 0000000000 2—000000 0001000000 0000000000 0000000000 0100000100 0100101000 0000000000 001
Nautilus            0000010000 0000101000 ????30?000 0002111000 00001000—0 0—000—0 0101100100 0200010000 0000000100 001
Patella             0101120000 1000314— 0110311000 0001112011 0001101000 0001101000 0010010310 0310121000 0000110110 001
Cellana             0101120000 1000314— 0110311000 0001112011 0001101000 0001101000 0010010310 0310121000 0000110110 001
Limalepeta          0101120000 0000314— 2—311000 0001112000 0000000050 0000101000 0010010310 0310121000 0000110110 001
Pectinodonta        0701170700 0000313000 2—311000 0001112000 0000010100 0010101000 0010010310 0310121000 0000110110 001
Niveotectura        0101120000 0000313000 2—311000 0001112000 0000010100 0010101000 0010010310 0310121000 0000110110 001
Erginus             0101120000 0000314— 2—311000 0001112000 0000010100 0010101000 0010010310 0310121000 0000110110 001
Nipponacmea         0101120000 0000313000 0110311000 0001112000 0000010100 0010101000 0010010310 0310121000 0000110110 001
Mikadotrochus       1001130100 0110302010 0200000000 1113000100 1201101030 0121000100 1222111001 0301021000 0000101110 002
Sulculus            1011131110 0111202011 0200000000 1113003100 1201101020 0121000100 1222111001 0301021000 0000101110 002
Scutus              1001131200 0110302011 0200300000 1113003100 1201101022 1121000100 1223111001 0302121000 0000101110 002
Macroschisma        1001131200 0170302011 0200300000 1113003100 1201101022 1121000100 1223111001 0302121000 0000101110 112
Anatoma             1011131200 0171302111 ????100000 1113003100 0201100022 0121000100 1223111007 0307021000 0000101110 112
Turbo               0001131111 0111303011 1200000000 1113003100 1201100020 2121000100 1222111000 1301021000 0000101110 002
Chlorostoma         0001131111 0111303011 1200000000 1113000100 1201100020 2121000100 1222111000 1301021000 0000101110 002
Stomatia            0001131111 0111303011 1200000000 1113000100 1201100020 2121000100 1222111000 1301021000 0000101110 002
Broderipia          0001131101 0111303011 1200000000 1113000100 1201100020 2121000100 1223111000 1301021000 0000101110 002
Lepetodrilus        0001100-00 0110203010 1300200000 1113003100 0201100020 0120000100 2223111000 1300021000 0000101110 002
Seguenzia           2001100-00 0111303111 10??200000 ????3030? ??01100040 0120000?00 7223110300 7300020000 0000107110 002
Cocculina           0001100-00 0100314— 1300200100 0113000100 0201100111 0120000100 2000110300 0420120000 0000101110 002
Neomphalus          0001100-00 0100303010 1300300000 0003000100 1001100010 0120000000 2003110300 0420020000 0000101110 002
Nerita              0001131200 0000213000 1301100011 1103000000 0001100011 0121010111 2033111200 0420020111 1111100111 002
Septalia            0001131200 0000303000 1301100011 1103000000 0001100011 0121010111 2033111200 0420020121 1111100111 002
Cinnalepeta         0001131200 0000303000 1301300011 1103000000 0001100011 0121010111 2033110300 0420020111 0111100111 002
Waldemaria          0001131200 0000204— 2—100010 1103000000 0001100011 0121010110 2033110300 0420020010 0000100111 002
Pomacea             0001131200 0000303110 1001200100 0003000000 0001100040 0020000000 0300110300 0420020000 0000100111 001
Biwamelania         0001131200 0000303110 1001200100 0003000000 0001100040 0020000000 0300100300 0420020000 0000201110 001
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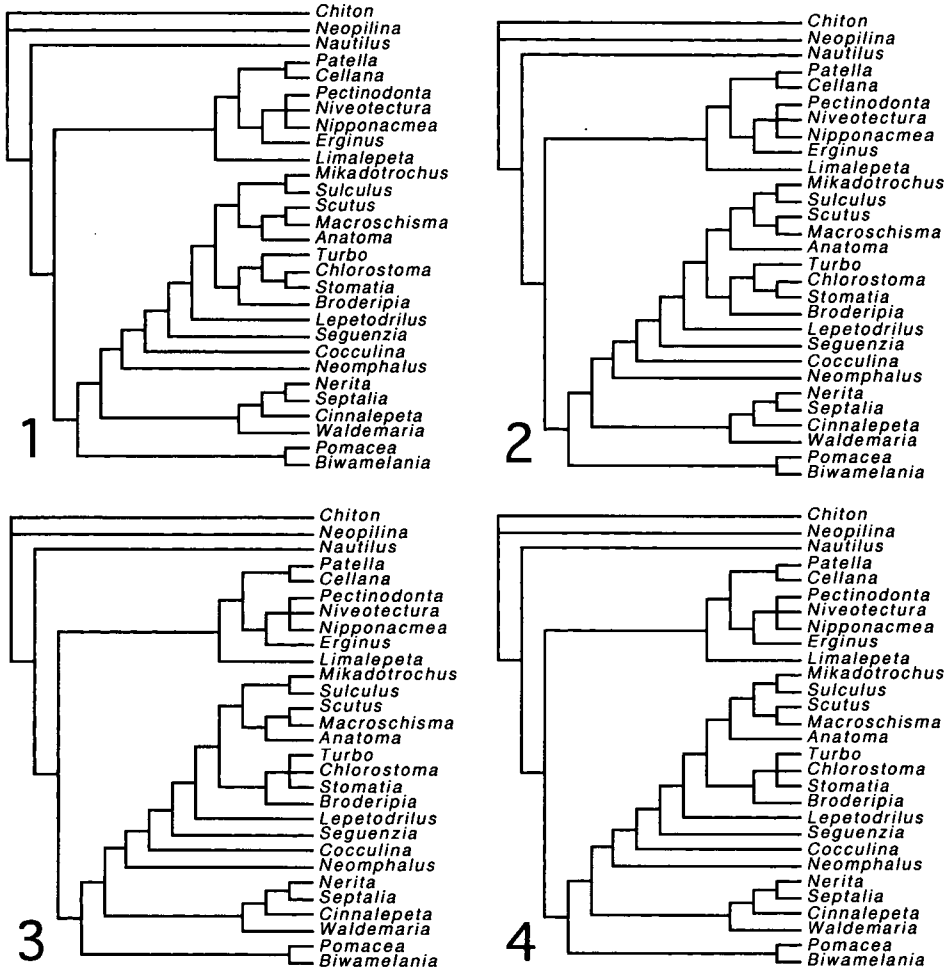
Fig. 103. Four most parsimonious trees (length=209) obtained by heuristic search.

ues between 93 and 100. Clades representing Rhipidoglossa, "*Cocculina* + Vetigastropoda" and "*Lepeto-drilus* + Zeugobranchia + Trochoidea" were relatively well supported by values between 79 and 70. In contrast, subclades within Patellogastropoda, non-neritopsine Rhipidoglossa, and Zeugobranchia had relatively low bootstrap values.

Decay analysis: Cladograms of one or two steps longer than the shortest were calculated to assess the relative robustness of the topology. The analysis yielded 187 trees of length 210 and 2418 trees of length 211.

(1) Trees with one additional step (length=210) (Fig. 105 c): Patellogastropoda, Rhipidoglossa, Neritopsina, "*Cocculina* + Vetigastropoda," Vetigastropoda, "Zeugobranchia + Trochoidea," and Caenogastropoda were supported as monophyletic groups. In contrast, the relationships within patellogastropods and vetigastropods and the basal part of Rhipidoglossa collapsed into polytomies, except for three terminal clades of Patelloidea (*Patella* and *Cellana*) and Fissurellidae (*Macroschisma* and *Scutus*), and Trochoidea (*Turbo*, *Chlorostoma*, *Stomatia*, and *Broderipia*).

(2) Trees with additional two steps (length=211) (Fig. 105 d): Compared with the former tree, some

Chiton
Neopilina
Nautilus
Patella
Cellana
Pectinodonta
Niveotectura
Nipponacmea
Erginus
Limalepeta
Mikadotrochus
Sulculus
Scutus
Macroschisma
Anatoma
Turbo
Chlorostoma
Stomatia
Broderipia
Lepetodrilus
Seguenzia
Cocculina
Neomphalus
Nerita
Septalia
Cinnalepeta
Waldemaria
Pomacea
Biwamelania

Patellogastropoda
Trochoidea
Zeugobranchia
Vetigastropoda
Rhipidoglossa
Orthogastropoda
Archaeogastropoda
Nerititopsina

Fig. 104.   Strict consensus tree of four most parsimonious trees. Higher taxonomic names are indicated on the right side of the tree.

parts of tree topology showed major changes. Further clade decays occurred (i) in basal part of Orthogastropoda (Caenogastropoda + Neritopsina + *Neomphalus* + *Cocculina* + Vetigastropoda) and (ii) in "Zeugobranchia + Trochoidea." These were collapsed into a complete polytomy.

Robustness of tree topology: The results using different analysis options did not reveal surprising differences or significant contradictions. The suggested relationships are summarized as follows: (1) Strong support was obtained for monophyly of Patellogastropoda and for a basal division of gastropods into Patellogastropoda and Orthogastropoda. (2) The bifurcation of Orthogastropoda into Caenogastropoda and Rhipidoglossa clades is possible with relatively high reliability. (3) Neritopsina are united as a very robust clade. (4) The monophyly of non-neritopsine Rhipidoglossa is not very reliable. Position and relationships
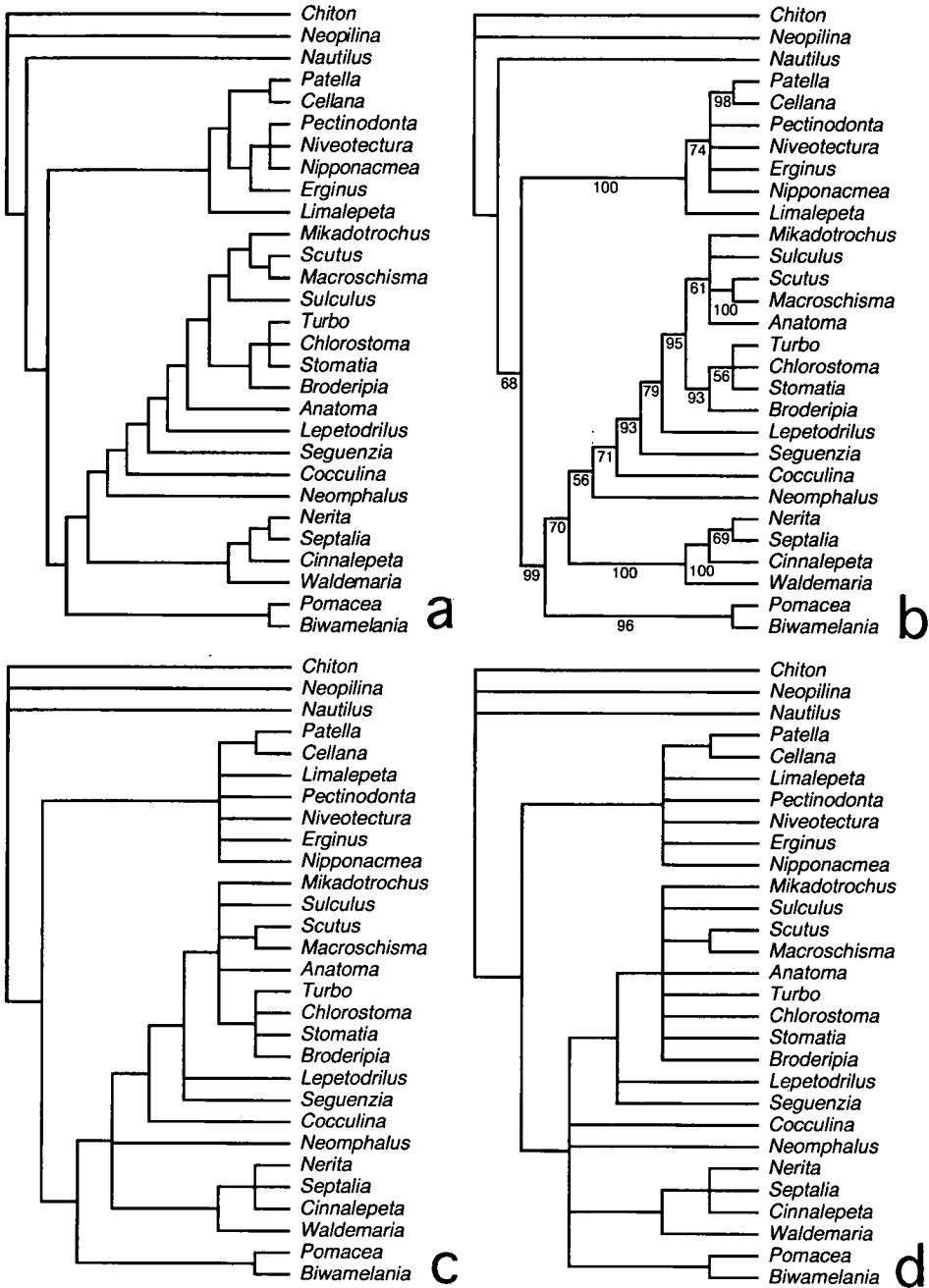
Fig. 105. Cladograms produced by different search options. **a**, Strict consensus tree of two most parsimonious trees obtained by heuristic search based on characters scaled with 1000 base weight. **b**, 50% majority-rule consensus tree based on 100 bootstrap replicates. Percentages are indicated below nodes. **c**, Strict consensus tree of trees one step longer than the shortest (length=210). **d**, Strict consensus tree of trees two steps longer than the shortest (length=211).

of *Neomphalus* and *Cocculina* also cannot be taken as conclusive. (5) Vetigastropoda and "Zeugobranchia +Trochoidea" form a robust clade. (6) The two caenogastropod genera were monophyletic and independent of archaeogastropod genera.

V. Discussion

V-1. Relationships of Major Archaeogastropod Subgroups

Archaeogastropoda Thiele, 1925: From the results of this study, the following comments are proposed on the status of Archaeogastropoda and Architaenioglossa: (i) Archaeogastropoda is defined as a "patellogastropod clade + rhipidoglossate clade," namely as a "pre-taenioglossate grade." (ii) "Archaeogastropoda" is undoubtedly a paraphyletic taxon, and therefore should not be used as a formal taxon name in phylogenetic classification. However, as a long-established group not easily discarded, "Archaeogastropoda" is retained as a collective name for gastropods with primitive radular morphology and buccal mass structure. (iii) Architaenioglossa is independent from the "Archaeogastropoda" and belongs to the Caenogastropoda clade. The hypoathroid condition is a plesiomorphic state of Gastropoda, and accordingly, it should not be overly stressed. Caenogastropoda is defined by synapomorphies such as a taenioglossate radula, compact buccal musculature, distinct esophageal structure, and a monopectinate ctenidium without bursicles. (iv) Neotaenioglossa is separated from Architaenioglossa by synapomorphies such as loss of the radular diverticulum, retractor muscles of the odontophore, and an epiathroid nervous system.

Patellogastropoda Lindberg, 1986: The monophyletic separation of Patellogastropoda (node 4) from other gastropods was strongly supported in this study by unambiguous synapomorphies such as retractile circumpallial tentacles (character #2), a transverse labial muscles (#26), dorsal protractors of the odontophore (#27), anterior band of the jaw (#37), anterolateral cartilages (#55), a two-layered ventral approximator muscle (#57), a septate mid-esophagus (#63), a muscular bulbous aorta (#69), and labial ganglia (#86). Other suggested synapomorphies include osphradia on the floor of the pallial cavity (#22), teeth mineralization (#45) and a simplified stomach (#65) by ACCTRAN optimization, and eyes within the cephalic tentacle (#6), double-layered structure of the jaw attaching to buccal mass (#35, 36), paired kidneys on the right side of the pericardium (#72, 73) by DELTRAN optimization. Division of the shell muscle (#16), ventral position of the gonad (#75), and connection of the gonoduct with the kidney (#77) are unambiguous synapomorphies, but homoplasies with other clades. The loss of the ctenidium (#17) occurred prior to the split of Patellogastropoda.

In relationship to other gastropods, Patellogastropoda are regarded as the earliest gastropod offshoot in accordance with recent theories (Ponder and Lindberg, 1996; 1997). Their suggested position has been based mainly on the stereoglossate radula and symmetrical limpet-shaped shell without helical coiling of teleoconch, both of which are shared with Tryblidiida (Golikov and Starobogatov, 1975; McLean, 1979; Salvini-Plawen, 1981; Wingstrand, 1985; Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988 a, b). In addition, the basal position of Patellogastropoda has also been suggested by the shallow mantle cavity, ctenidium without skeletal rods, paired excretory system, simple eye type, position of statocysts, lowest number of chromosomes (n = 9–10) (Haszprunar, 1988 b), primitive-type sperm morphology (Koike, 1985; Healy, 1988; 1996), and an osphradium lacking true sensory cells (Haszprunar, 1985 a). Furthermore, the double-layered jaw plate shared by Patellogastropoda and Cephalopoda possibly supports primitiveness of Patellogastropoda (see section V-2). Thus, anatomical characters strongly support the basal position of Patellogastropoda.

Orthogastropoda Ponder and Lindberg, 1996: All remaining non-patellogastropod groups (node 9) are

here regarded as a clade. Monophyly of this large group is supported by unambiguous synapomorphies such as eyes with a vitreous body (#8), unpaired osphradium (#21), paired jaws (#34), the position of the jaws free from the buccal mass (#36), and a flexoglossate radula (#44), the elongation of marginal teeth (# 53), and a single kidney on the right side of pericardium (#72, 73). In addition, eyes outside bases of cephalic tentacles (#6), eyestalks (#7), skeletal rods, (#19), lateral ciliated zones of osphradium (#24), a single left hypobranchial gland (#25), single-layered jaws on oral tube (#35, 36), and 4 pairs of lateral teeth (#49) by ACCTRAN and an unpaired ctenidium (#17), the absence of teeth mineralization (#45), a style sac region in the stomach (#65) by DELTRAN are possible synapomorphies that discriminate this clade from patellogastropods.

The Orthogastropoda is further divided into rhipidoglossate and non-rhipidoglossate clades. These relationships are greatly different from those of recent studies (Haszprunar, 1988 a, b; Salvini-Plawen and Steiner, 1996; Ponder and Lindberg, 1996, 1997). The separation of caenogastropod genera (node 24) from rhipidoglossate archaeogastropods is supported by unambiguous synapomorphies such as monopectinate ctenidial filaments (#18), the absence of anterior levator muscles (#28), a single pair of lateral teeth (#49), and posteriorly separated esophageal pouches (#62). Eyes outside of cephalic tentacles (#6), eyestalks (#7), skeletal rods (#19), lateral ciliated zones of osphradium (#24), a single left hypobranchial gland (#25) are all homoplastic with some rhipidoglossate taxa by DELTRAN optimization.

Rhipidoglossa Mörch, 1865: In contrast to recent theories, rhipidoglossate groups (node 10) form a distinct clade. Its monophyly is justified by unambiguous changes such as the position of the osphradium associated with the ctenidial membrane and axis (#22), numerous pairs of marginal teeth (#52), the loss of salivary gland (#61), the presence of a gastric caecum (#64), and statocysts on the anterolateral sides of the pedal ganglia (#93). Other possible synapomorphies for this clade include the postdorsal buccal tensor (# 32) and outer approximator (#58) muscles in ACCTRAN optimization, and four pairs of lateral teeth (#49) in DELTRAN optimization.

Neritopsina Cox and Knight, 1960: The result of the present cladistic analysis strongly supported the robust monophyly of neritopsine groups (node 21) that are diversified from marine to terrestrial habitats. Although some external characters are secondarily modified according to various life habits, they retain astonishingly common organization in the internal organs, especially in buccal musculature, odontophoral cartilages, the anterior alimentary tract, and nervous system. Synapomorphies with unambiguous changes include the dorsal levator (#29) and posterior depressor (#31) muscles, the median cartilages (#56), the tensor muscle of the anterior cartilages (#59), posterior esophageal glands (#63), a diaulic female gonoduct (# 79). Enlargement of the fourth lateral teeth (#50), the presence of posterior cartilages (#54), origin of the visceral loop from the right side only (#90) are all homoplastic with some other groups. Also, the absence of ctenidial rods (#19), and the hypobranchial gland on the right side (#25) in ACCTRAN, and the postdorsal buccal tensor (#32) and outer approximator (#57) muscles in DELTRAN may be independently acquired in this clade.

Concerning the systematic position of Neritopsina within "Archaeogastropoda," many authors (e.g. Yonge, 1947; Cox, 1960; Fretter, 1965, 1984 a; Graham, 1985) have historically favored an intermediate position between primitive rhipidoglossate groups and Caenogastropoda based on the closed pallial gonoduct and single left kidney (="loss of right one"). Meanwhile, Haszprunar (1988 a, b) advocated its more basal position between Vetigastropoda and Cocculiniformia, emphasizing the primitive state of the ctenidium without skeletal rods. The results of the present cladistic analysis did not support such a basal position, but indicated more intimate relationships with other rhipidoglossans than with any other taxa.

"Non-neritopsine Rhipidoglossa": The unity of this group (node 11) is suggested by unambiguous synapomorphies such as epipodial tentacles (#12), a bifurcated posterior end of the radular sac (#38), and absence of a labial commissure (#87). Absence of a ciliated zone in the osphradium (#23) (in ACCTRAN)

and the presence of skeletal rods (#19) (in DELTRAN) may have uniquely evolved in this clade. This clade is equivalent to Archaeogastropoda (*s.s.*) as restricted by Ponder and Lindberg (1997). As in their analysis, this clade was weakly supported in this study.

"Vent Taxa" =*Peltospiroidea McLean, 1988* +*Neomphaloidea McLean, 1981:* Among specialized taxa specific to a deep-sea environment, Neomphaloidea and Peltospiroidea are not closely related with other traditionally known archaeogastropods. Since their discovery in the 1980 s, they have been variously allocated to positions around Vetigastropoda as paraphyletic taxa (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988 a, b; Salvini-Plawen and Steiner, 1996). Their relationships were also poorly resolved in the cladistic analysis of Ponder and Lindberg (1997).

At first sight these vent taxa seem related to "higher" gastropods because they share certain "advanced" gastropod characters, such as a single left auricle, a ventricle independent of the rectum, and a gonoduct independent from the right kidney (Fretter, 1989). On the other hand, characters such as the rhipidoglossate radula, buccal musculature, and the anterior loop of the intestine suggest their affinities to other rhipidoglossate groups of "Archaeogastropoda." Although their systematic positions are still uncertain, they are probably associated with Vetigastropoda according to an osphradium associated with the efferent ctenidial axis, enlarged esophageal pouches with papillae glands, and the postmedian retractor muscle of the radula (in *Neomphalus*). At present, these two specialized superfamilies can be preliminarily grouped as a vernacular name, "vent taxa." The resolution of these groups is an important subject for further studies in gastropod phylogeny.

"Cocculiniformia" Haszprunar, 1987: This taxon was proposed for deep-sea limpets with a secondary respiratory organ (a pseudoplicate gill or several pallial/subpallial leaflets), a modified rhipidoglossate radula, and a specialized feeding mode in the deep-sea environment (Haszprunar, 1987 a, 1988 c; see Appendix). The characteristic reproductive system configuration (hermaphroditic gonad and copulatory organ on the right side) is also assumed to support the monophyly of this taxon (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988 c). Members of this group were allocated to a position between the Patellogastropoda and Neritopsina (first offshoot of Orthogastropoda), emphasizing the primitiveness of limpet-like forms with a shallow mantle cavity and divided shell muscle (also shared with Patellogastropoda) (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988 a, b; Salvini-Plawen and Steiner, 1996).

In contrast to these considerations, the monophyly of Cocculiniformia was clearly rejected by the cladistic analysis of Ponder and Lindberg (1996). Cocculinidae were united with Neritopsina, while Lepetelloidea were allocated to a first offshoot of Vetigastropoda. They assumed that the modifications (mostly reduction) were caused by paedomorphosis.

(1) *Monophyly of Cocculiniformia:* As discussed by Ponder and Lindberg (1997), characters listed as synapomorphies for Cocculiniformia by Haszprunar (Haszprunar, 1987 a, 1988 c) are, in fact, not truly specific to this group, nor universally shared within the group. For example, the absence of (post-torsional) right pallial organs and a monotocardian heart are not diagnostic only for this group. Possible synapomorphies are the hermaphroditic reproductive system and a copulatory organ derived from the right side. Some similarities between Cocculinoidea and Lepetelloidea also found in other taxa of archaeogastropods as synplesiomorphies, and accordingly do not support their monophyly.

(2) *Cocculinoidea-Neritoidea:* According to analysis of Ponder and Lindberg (1996, 1997), Cocculinidae and Neritidae are united by synapomorphies such as 1) a divided shell muscle, 2) absence of salivary glands, 3) jaw structure, 4) sublingual glands, 5) enlarged fourth lateral teeth, 6) a shift in the position of the anus from the posterior half to the anterior half of the pallial cavity, and 7) absence of the right kidney (in contrast to that in Lepetelloidea). In addition, internal copulation, a single ctenidium (if the pseudoplicate gill is homologous with a ctenidium), and absence of skeletal rods in the gills do not seem to contradict this relationships.

Based on my own observations, however, these characters do not plausibly suggest the close relationships of these two taxa: (i) Jaw structure is neither unique to these two nor similar between them. (ii) Sublingual glands projecting from the sublingual pouch are very prominent in neritoid genera, but are not found in *Cocculina nipponica* in comparable form. These results contradict Ponder and Lindberg's (1996; 1997) character coding. Meanwhile, it is possible that the enlarged outer lateral (fourth) teeth and division of the shell muscle by blood vessels may have evolved in the common ancestor of these taxa. Therefore, only the latter two characters can support the monophyly of *Cocculina* and *Nerita*. In buccal characters there is no evidence for close relationship.

(3) *Lepetelloidea-Fissurelloidea:* Positive evidence was presented for a relationship between these two groups by Ponder and Lindberg (1996; 1997). The fourth lateral teeth are markedly enlarged in Cocculinoidea, whereas in the Pseudococculinidae it is the fifth lateral teeth as in Fissurellidae. In addition, some states found in Lepetelloidea (two kidneys, and rectum penetrating ventricle) are shared with Vetigastropoda rather than with Cocculinoidea (see Table 4). Thus, it may not be unlikely that Lepetelloidea are greatly modified vetigatropods, although the relation is not very robust (Ponder and Lindberg, 1997).

(4) *Cocculiniformia-Vetigastropoda:* In contrast to previous works, *Cocculina* is more closely related to Vetigastropoda than to *Neomphalus* (vent-taxa) and Neritopsina in this study. These relationships (node 12) are directly supported by the presence of a dorsal buccal tensor (#33) and a median tensor of the radular sac (#42). Postdorsal buccal tensor (#32) and outer approximator (#58) muscles are also possible synapomorphies for this clade in DELTRAN optimization. If this position is true, all cocculiniform groups, including Cocculinoidea and Lepetelloidea, may form a sister group with Vetigastropoda, independent of Neritopsina. However, as the robustness of this clade is not very high, this is only one of several possibilities.

Vetigastropoda Salvini-Plawen, 1980: The name Vetigastropoda has previously been used for Zeugobranchia + Trochoidea + Cocculinoidea (Salvini-Plawen, 1980) or Lepetodriloidea + Zeugobranchia + Trochoidea (Haszprunar, 1988 a, b; Salvini-Plawen and Steiner, 1996). The definition is here extended to include Seguenzioidea + Lepetodriloidea + Zeugobranchia + Trochoidea in agreement with Ponder and Lindberg (1997).

These taxa (node 13) are united by many synapomorphies, such as epipodial sense organs (#13), fimbriate anterior edge of the jaw (#37), expanded esophageal pouches (#62), papillate esophageal glands (#63), paired kidneys on either side of pericardium (#72, 73). In addition, micropapillae on the tentacles (#14), the posterior depressor muscles (#31), five pairs of lateral teeth (#49), paired auricles (#67), a transverse pallial vein (#71) are also possible synapomorphies in ACCTRAN optimization.

(1) *Zeugobranchia + Trochoidea:* This clade (node 15) is united by unambiguous synapomorphies including the osphradium on the free tip of the ctenidium (#22), paired hypobranchial glands (#25), ramified salivary glands with slit-like openings into the buccal cavity (#61), and presence of a papillary sac (#74). Bursicles (#20) and paired postmedian retractor muscles of the radular sac (#42) occur independently in this clade under DELTRAN optimization.

(2) *Zeugobranchia:* Zeugobranchs (node 16) uniquely share two unambiguous synapomorphies, a median mantle slit (#1) and paired ctenidia (#17). Paired osphradia (#21), asymmetry of the radular teeth (#47) and enlargement of the fifth outer lateral teeth (#50), and basibranchial sinus (#70) are also specialized within this clade in ACCTRAN optimization.

Within Zeugobranchia, four superfamilies (Pleurotomarioidea, Haliotoidea, Fissurelloidea, and Scissurellidae) are recognized as extant forms. They share the following character states: (i) Pleurotomariidae and Haliotidae are linked by open eyes (#8), unenlarged outer lateral teeth (#51), and a spiral gastric caecum (#63) originating from the large U-shaped stomach. They differ in external anatomy (epipodial tentacles, cephalic lappets, eye stalks) and radular morphology (hystricoglossate vs. typical rhipidoglossate). (ii) Fissurellidae and Scissurellidae are related by closed eyes (#8) and a short gastric caecum (#63), but differ in

symmetry of the radular teeth (#47), morphology of the epipodial tentacles, presence or absence of micropapillae (#14), and the pedal nervous system (#91, 92). (iii) Pleurotomariidae, Haliotidae, and Fissurellidae share asymmetrical radular teeth (#47) only, although their radular morphologies are distinctly different. (iv) Haliotidae and Scissurellidae have pallial tentacle(s) (#3). (v) Other combinations of the four families reveal no shared character states.

Recently Harasewych *et al.* (1997) discussed the position of Pleurotomariidae based on cladistic analyses using 18 S rDNA. Their results indicate that Pleurotomariidae is split first within Vetigastropoda and non-pleurotomarid zeugobranchs plus Trochoidea form another clade. This relationship is not consistent with the results of this study in which zeugobranchs form a clade.

(3) *Trochoidea:* The monophyly of Trochoidea (node 19) is supported by unambiguous synapomorphies of neck lobes (#10), and protolateromarginal radular plates (#51). The relationships within trochoidean families, Turbinidae, Trochidae, and Skeneidae, are not clearly established, but Turbinidae was regarded as most primitive by Hickman and McLean (1990) and Hickman (1996). The distinction between Turbinidae and Trochidae is given primarily by basal morphology of central tooth of the radula, and therefore, Trochidae is diagnosed as a "non-turbinid" group (Hickman and McLean, 1990).

(4) *Lepetodriloidea:* Lepetodriloidea is more closely related to "Zeugobranchia + Trochoidea" than to Seguenzioidea. Unambiguous synapomorphies for "Lepetodrilus + Zeugobranchia + Trochoidea" (node 14) are in having the rectum penetrating the ventricle (homoplasy with Neritoidea) (#67), paired auricles (#68), and a connection of the gonoduct with the kidney (homoplasy with Patellogastropoda) (#77). This relationship was also supported by the posterior depressor muscle (#31) and five pairs of lateral teeth (#49) in DELTRAN optimization. Paired kidneys with renopericardial ducts, papillate esophageal glands, and epipodial sense organs are also general vetigastropod characters. Thus, inclusion of this taxon in Vetigastropoda is confirmed, as discussed by Haszprunar (1988 a, b), Fretter (1989), and Ponder and Lindberg (1997).

(5) *Seguenzioidea:* Historically, this family has been variably treated by different authors. (i) It was assigned to "Mesogastropoda" based on the taenioglossate-like radula with a single pair of lateral teeth (e.g. Golikov and Starobogatov, 1975). (ii) It was separated from other gastropod groups as a distinct archaeogastropod taxon 'Seguenziina' by Salvini-Plawen and Haszprunar (1987) and Haszprunar (1988 a, b), stressing the peculiarity of the internal structure of the esophagus. (iii) It was regarded as "archaeogastropods with trochoidean affinity" based on the trochispiral shell form, a nacreous shell layer, a trochoid-like protoconch, epipodial tentacles, and an anterior loop of the intestine (Bandel, 1979; Quinn, 1983). Also in the phylogenetic scheme of Ponder and Lindberg (1996, 1997), the family was considered closely related to Trochoidea.

The present phylogenetic analysis suggests that the family can be placed within Vetigastropoda because of possession of papillate epipodial tentacles (#14), bursicles (#20), and slightly papillate esophageal gland in enlarged esophageal pouches (#62, 63). In contrast, the monopectinate ctenidium (#18) and gonoduct independent of the kidney (#77) are atypical for Vetigastropoda among currently known members. However, for resolution of phylogenetic relationships, there are still many problems in the details of character states in this group. In previous studies, Quinn (1983) described the basic organization of *Seguenzia*, but his observations were limited to the macroscopic level. Haszprunar (1988 b) schematically showed the configuration of several pallial and coelomic organs in *Flexinella*, but did not show details. In this study, some features were observed by SEM but the histological details were unsatisfactory. Thus, many features still remain to be investigated.

V–2. Evolution of Anatomical Characters

1. Symmetry of Pallial Organs

Condition of the archaeogastropod pallial complex: The gastropod pallial cavity generally contains (i) true ctenidium (-a) and/or one of several types of secondary gill, (ii) osphradium (-a) probably derived from the dorsoterminal sense organ of primitive molluscan groups, (iii) hypobranchial gland (s) probably elaborated from the mucus tracts in the primitive pallial groove, and (iv) anal, excretory and genital openings (the latter two incorporated as a urogenital opening in most archaeogastropods). Very interestingly, "Archaeogastropoda" is unusual among Mollusca in that the pallial complex and its associated organs exhibit a mosaic pattern of symmetrically paired, asymmetrically paired, and unpaired conditions (Table 4). However, Caenogastropoda invariably exhibit unpaired monopectinate ctenidium, an unpaired osphradium, an unpaired hypobranchial gland, a monotocardian heart not traversed by the rectum, and an unpaired kidney.

The asymmetry of these organs in gastropods may be caused by differential growth between right and left sides as a coiling effect. However, causes and mutual relationships among animal asymmetry, shell coiling, and torsion are not very evident. At least the relationship between torsion and shell coiling is independent as exemplified by some patellogastropod limpets bearing truly symmetrical shells (see section V–4). Conversely, symmetrical patellogastropods have asymmetrical organ arrangements except for paired osphradia. Only the fissurellid pallial cavity is seemingly completely bilateral as in non-gastropod molluscs, but condition is secondary as revealed by shell ontogeny (see section V–4).

Possible secondary origin of the zeugobranch condition: Historical review shows that the primitiveness and irreversibility of the paired zeugobranch ctenidia and pallial complex have long been considered unquestioned dogma (Young, 1947; Fretter and Graham, 1962; Golikov and Starobogatov, 1975; Salvini-Plawen, 1980; Haszprunar, 1988 b; Ponder and Lindberg, 1996, 1997). Only Haszprunar (1990) considered the possibility of its secondary origin but original paired condition was still favored.

The phylogeny reconstructed in this study shows that paired ctenidia are a logically reversed secondary state which occurs only in the zeugobranch clade independent of the outgroups (Fig. 106). This result may seem "unnatural" or "impossible" in a traditional view. However, assumptions favoring irreversibility in the gastropod ctenidium must postulate multiple independent changes from paired to unpaired states in many taxa throughout Gastropoda under constructed tree topology.

If the reversal is accepted, there are several lines of supporting evidence for the secondary, apomorphic state of zeugobranch ctenidia. (i) The number of molluscan ctenidia is variable and not very conservative as is typically found in non-gastropod groups. Often structurally homologous ctenidia are added or reduced at different sites. (ii) Ontogenetically the left ctenidium is initially predominant in contrast to the equally paired condition in adults (Crofts, 1937; Ino, 1952). Thus, ontogenetic criteria guarantee that the asymmetrical condition is original, not secondary. (iii) The presence of paired ctenidia is always reflected in apertural morphology of the shell in Recent members. The available fossil record shows that the earliest gastropod *Aldanella* had a slit-less trochoid shell (Runnegar and Pojeta, 1985), and pleurotomaroids with a slit appeared later. This suggests that zeugobranchs derived from coiled form with unpaired ctenidium. (iv) The ctenidia of vetigastropods exhibit not ancestral but rather derived states in the presence of skeletal rods, bursicles, and a long efferent membrane (Salvini-Plawen, 1980; Haszprunar, 1988 b). Thus, the osphradio-ctenidial complex (including their ganglion) could have arisen secondarily on the right side as a character complex.

Patellogastropod "ctenidium": The scenario obtained in this analysis (Fig. 106) includes another confusing situation. Although the acmaeoid "ctenidium" was assumed to be homologous to other molluscan ctenidia in the character analysis, the reconstruction suggests that it was an independently acquired struc-

Table 4. Character states of the pallial complex and associated internal organs in Archaeogastropoda and outgroups. See Appendix for references. *1, *Larochea* has an unpaired (left) ctenidium (Marshall, 1993 b). *2, *Hendersonia* has a vestigial right auricle (Thompson, 1980). *3, Gonoduct of *Rhyncopelta* is urogenital only in female (Fretter, 1989). *4, Genital opening is urogenital (Haszprunar, 1988 c).

	Pallial Complex			Heart		Coelomic Organs	
	Ctenidium	Osphradium	Hypob. Gl.	Auricle	Penetration	Kidney	Gonoduct
Polyplacophora	paired	paired	paired	paired	-	paired	genital
Tryblidiida	paired	-	-	paired	-	paired	urogenital
Nautilidae	paired	?	-	paired	-	paired	genital
Patellidae	-	paired	-	left	-	paired	urogenital
Nacellidae	-	paired	-	left	-	paired	urogenital
Lepetidae	-	-	-	left	-	paired	urogenital
Acmaeidae	left	-	-	left	-	paired	urogenital
Lottiidae	left	paired	-	left	-	paired	urogenital
Neolepetopsidae	-	-	-	left	-	paired	urogenital
Pleurotomariidae	paired	paired	paired	paired	+	paired	urogenital
Haliotidae	paired	paired	paired	paired	+	paired	urogenital
Fissurellidae	paired	paired	paired	paired	+	paired	urogenital
Crypeosectidae	paired	paired	paired	paired	+	paired	urogenital
Scissurellidae	paired *1	paired	paired	paired	+	paired	urogenital
Turbinidae	left	left	paired	paired	+	paired	urogenital
Trochidae	left	left	paired	paired	+	paired	urogenital
Skeneidae	left	left	paired	paired	+	paired	urogenital
Lepetodrilidae	left	left	left	paired	+	paired	urogenital
Gorgoleptidae	left	left	left	paired	+	paired	urogenital
Seguenziidae	left	left	left	left	-	paired	genital
Peltospiridae	left	left	-	left	-	paired	*3
Neomphalidae	left	left	-	left	-	left	genital
Cyathermiidae	left	left	-	left	-	left	genital
Cocculinidae	-	left	left	left	-	left	genital
Bathysciadiidae	?	?	?	left	-	left	genital
Lepetellidae	-	?	?	left	+	paired	genital *4
Pyropeltidae	-	left	-	left	+	paired	genital *4
Pseudococculinidae	-	-	-	left	+	paired	genital *4
Osteopeltidae	-	-	-	left	+	paired	genital
Bathyphytophilidae	?	?	?	?	?	?	?
Cocculinellidae	-	left	-	left	+	paired	genital
Addisoniidae	-	left	-	left	-	paired	genital
Choristellidae	-	left	-	left	-	paired	genital
Neritopsidae	?	?	?	?	?	?	?
Neritidae	left	left	right	paired	+	left	genital
Phenacolepadidae	left	left	-	paired	+	left	genital
Shinkailepedidae	left	left	-	paired	+	left	genital
Titiscaniidae	left	?	?	paired	+	left	genital
Hydrocenidae	-	-	?	left	-	left	genital
Ceresidae	-	-	right	paired	-	left	genital
Proserpinidae	-	-	right	left	-	left	genital
Helcinidae	-	-	right	left *2	-	left	genital
Caenogastropoda	left	left	left	left	-	left	genital
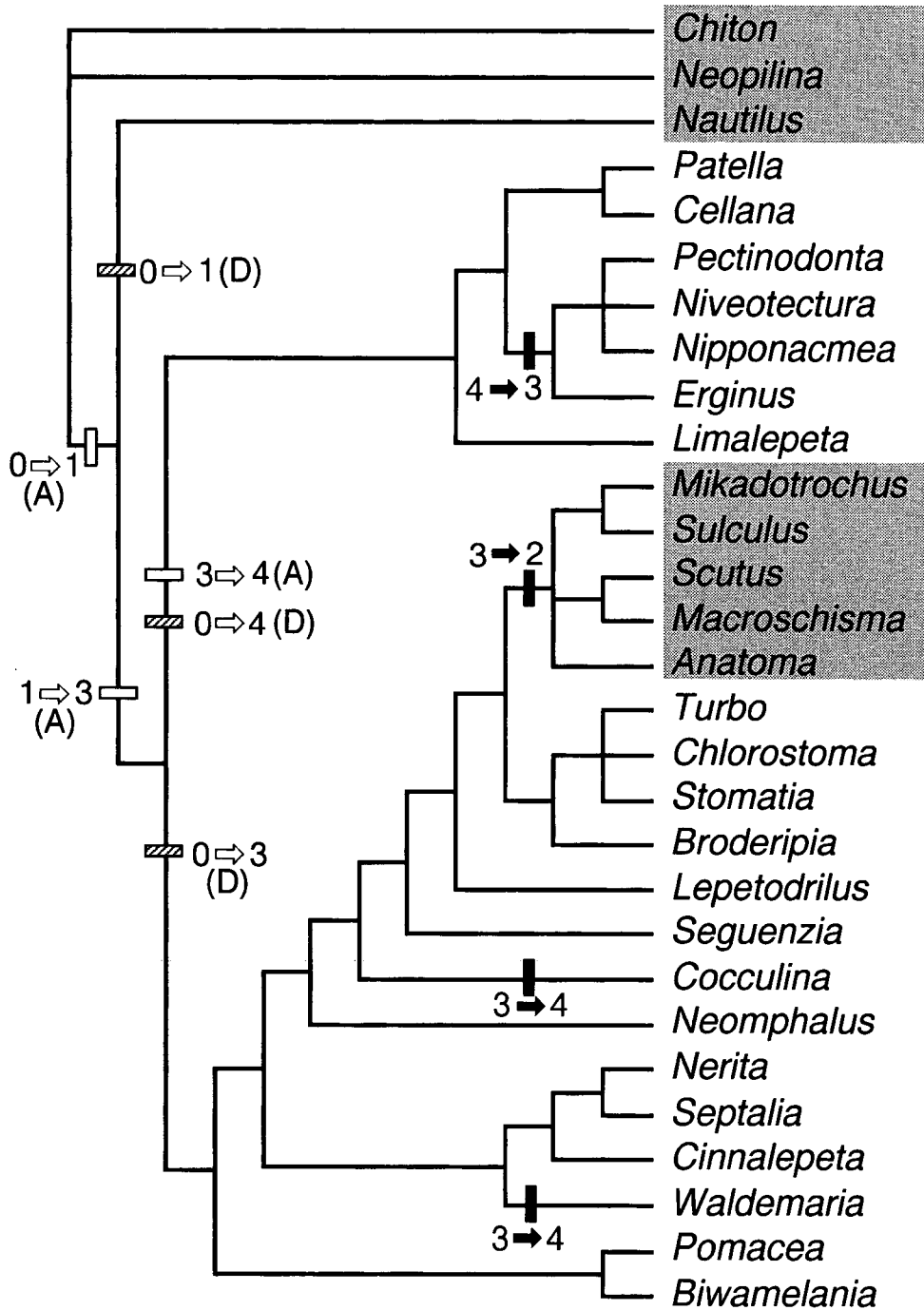
Fig. 106. Reconstruction of the number of ctenidia (character #17) on strict consensus tree (Fig. 104). States: 0 =multiple pairs, 1=two pairs, 2=single pair, 3=post-torsional left only, 4=absent. Character changes are unambiguous (black arrow) or ambiguous (while arrow) under ACCTRAN (A) and DELTAN (D) optimizations. Shading indicates taxa with paired ctenidia.

ture. However, this result seriously contradicts the theory of ctenidial homology about which general agreement has been established (Young, 1947; Fretter and Graham, 1962; Salvini-Plawen, 1980; Graham, 1985; Haszprunar, 1988 b; Ponder and Lindberg, 1997). It would be difficult to infer that such a complex structure was regained in an identical position with similar form, once it has been lost (Dollo's law). No clear solution for this problem can be presented from the results of this study.

Patterns in other pallial organs: Under most-parsimonious reconstruction (Fig. 104), transformations of other pallial organs can be traced and are summarized as follows. These results exhibit a general pattern from paired to unpaired conditions.

(1) *Number of osphradia:* The reconstruction resulted in the scenario that the osphradium was not present in early Gastropoda, because it is of questionable state in *Nautilus* and is absent in some Patellogastropoda. Paired osphradia arose on the pallial floor in some Patellogastropoda. In the Orthogastropoda, the left osphradium was retained (as in Neritopsina, *Cocculina*, *Neomphalus*, and Apogastropoda), and it was regained in paired condition in Vetigastropoda.

(2) *Number of hypobranchial glands:* The hypobranchial gland is absent in *Nautilus* and in ancestral Gastropoda (presumably) plus Patellogastropoda (=Eogastropoda). The left gland arose in Orthogastropoda as is found in *Cocculina*, *Seguenzia*, *Lepetodrilus*, and Apogastropoda. The paired condition was re-acquired by common ancestor of Zeugobranchia and Trochoidea. The state having right gland only was evolved independently by Neritopsina and *Anatoma*.

(3) *Number of auricles:* Two pairs of auricles (in the outgroups) were presumably reduced to the left one only in gastropod ancestor. This condition was inherited by Patellogastropoda and the orthogastropod ancestor (as in *Neomphalus*, *Cocculina*, *Waldemaria*, and Apogastropoda). The paired condition was independently re-evolved nearly symmetrically in Vetigastropoda and extremely asymmetrically in Neritoidea.

(4) *Number of kidneys:* The symmetrically paired kidneys of the outgroups were converted into a single asymmetrical pair in Patellogastropoda and the left one in orthogastropod ancestor. Only Vetigastropoda evolved paired condition (and papillary sac) independently.

These results show that all components of the pallial complex represent reversed, apomorphic conditions in zeugobranchs. This suggestion is "implausible" and may be difficult to accept in a traditional sense. Nevertheless, there is no theoretical reason why the unpaired condition in gastropod organs should be absolutely irreversible. These possibilities should be tested again in future works as should assumptions of homology problem.

2. Respiratory Organs

Polarity of ctenidial characters: Archaeogastropod ctenidia are characterized by the following features: (i) ctenidial leaflets or lamellae attached to ctenidial axes alternately on either side (bipectinate condition); (ii) each axis contains afferent and efferent ctenidial vessels and nerves; (iii) ctenidial axes are also provided with retractor muscles, and therefore the ctenidium is contractile when the skeletal rods are absent; (iv) triangular leaflets are stiffened by the skeletal rods in some but not in others; (v) each leaflet has three (frontal, abfrontal, and lateral) zones of cilia; (vi) the ctenidium is attached to the mantle skirt by efferent and afferent membranes; (vii) ctenidial sense organs (bursicles) may be present.

Polarity of ctenidial characters were determined as follows by outgroup comparison (Salvini-Plawen, 1980; Haszprunar, 1988 b; Ponder and Lindberg, 1997): (i) the paired condition is primitive and a single left ctenidium is apomorphic; (ii) the bipectinate condition is plesiomorphic, and the monopectinate condition is apomorphic; (iii) presence of a long efferent membrane and of bursicles is apomorphic; (iv) presence of skeletal rods is apomorphic, while absence of skeletal rods (with ctenidial contractility) is plesiomorphic. Skeletal rods are an apomorphic character because of their absence in acuriferan ctenidia (Salvini-Plawen, 1980, Haszprunar, 1988 b) and are considered to be of independently origin in Bivalvia, Cephalopoda

(uniquely in afferent axis), and Gastropoda (Young, 1947).

In the reconstruction, the above-mentioned transformations are supported with two exceptions. (i) The paired condition may not be plesiomorphic as discussed above. (ii) The two equally supported transformations are possible regarding the presence of skeletal rods. Skeletal rods may evolved independently in non-neritopsine Rhipidoglossa and Caenogastropoda or lost by reversal in Neritopsina once obtained in the orthogastropod ancestor.

Archaeogastropod monopectinate ctenidium: It is a general feature of prosobranch gastropods that the ctenidium is bipectinate in "Archaeogastropoda" but monopectinate in Caenogastropoda. However, there are some exceptions to this rule among archaeogastropods. A monopectinate condition is found in Lirulariinae and Umboniinae of Trochidae (Fretter, 1975; McLean, 1986; Hickman and McLean, 1990; Herbert, 1992), Larocheinae of Scissurellidae (Marshall, 1993 b), Anatominae of Scissurellidae (this study), Seguenziidae (Quinn, 1983; this study), and Skeneidae (Hickman and McLean, 1990; Warén, 1991 a). Such a ctenidial modification in trochoids is known to be correlated with suspension feeding with ctenidial cilia (McLean, 1986), but in most cases (except *Umbonium*) it also appears to be convergent related to small body size. Elongation of the ctenidial filaments is also the common convergent feature in various filter-feeding gastropods and also occurs in "Mesogastropoda" (e.g. Calyptraeidae and Vermetidae) (Declerck, 1995). These homoplastic phenomena between Vetigastropoda and Caenogastropoda are distinguished by the presence or absence of bursicles on ctenidial lamellae.

Gills of Cocculiniformia: An unusual form of gill is markedly developed in "Cocculiniformia," and they can be divided into three types (Haszprunar, 1988 c). (i) Cocculinoidea (Cocculinidae and Bathysciadiidae) have a pseudoplicate gill whose position, innervation (from the osphradial ganglion), and blood supply are as for a true ctenidium. (ii) "Lower" Lepetelloidea (Lepetellidae, Osteopeltidae, Pyropeltidae, and Psudococculinidae) have several leaflets within the right subpallial and/or pallial cavities. The leaflets are provided with sensory pockets (except in Osteopeltidae). (iii) "Higher" Lepetelloidea (Addisoniidae and Choristellidae) have gills with a proximal glandular area and skeletal rods at the efferent axis.

The question still remains whether the above gills are independent structures or modified ctenidia (Ponder and Lindberg, 1997), although Haszprunar (1988 b, c) regarded them as completely secondary. In the Cocculinoidea, homology with the ctenidium may be suggested by a lateral zone of cilia on the gill leaflets (McLean and Harasewych, 1995: fig. 19) in addition to similarity in position, innervation, and blood supply. In the Lepetelloidea, Ponder and Lindberg (1997) assumed secondary enlargement after reduction, because (i) skeletal rods are present in Addisoniidae and Choristellidae, and (ii) a bursicle-like pocket structure is found in Pyropeltidae, Lepetellidae, and Pseudococculinidae. Zoned ciliation on gill lamellae is also reported in Pseudococculinidae (Hasegawa, 1997 b: fig. 15). Gill reduction into a ciliary spot in Cocculinellidae may be correlated with extreme elongation of subpallial cavity.

One of the difficulties in relating the lepetelloidean gill to a ctenidium is its position on the right side. However, it can be interpreted as a left organ based on the innervation from osphradial ganglion derived from left pleural ganglion (Ponder and Lindberg, 1997). Another problem is the paired condition of Caymanabyssiinae of Pseudococculinidae (Haszprunar, 1988 c, fig. 1). If the gill in Pseudococculinidae is a modified ctenidium, it follows that this represents independent conversion from unpaired to paired condition in this subfamily.

Other types of vestigial gills: Aside from the gills of some Cocculiniformia, two other types of vestigial gills are known in archaeogastropods. (i) *Nerita* has a tuberculate expansion in a position similar to that of the true (right) ctenidium (Fretter, 1965: fig. 1 c; Fig. 77 c). However, this is not a general neritid character and therefore of minor significance to higher systematics of that family. At least *Septalia* do not have such a gill. (ii) Several leaflet-like processes are found in the right efferent pallial vessel of *Lepetodrilus nux* (Fig. 65 d; but undescribed in other lepetodrilids) and of *Neomphalus fretterae* (described but unillustrated, Fret-

ter *et al.*, 1981). Each of these may represent an intermediate state from azeugo- to zeugobranch organization, but the nature of these gills has not yet been fully elucidated. At least the lepetodrilid gill on the right side may be associated with the ctenidium because of its position and ciliation on the lamellae.

Patellogastropod secondary gills: Secondary gills in a circumpallial arrangement are developed in three patellogastropod groups, namely Patellidae, Nacellidae, and three genera of Lottiidae (*Scurria, Tectura* and *Lottia*) (Lindberg, 1988 a). This type of gill has have probably evolved several times, namely, once in the common ancestor of Patellidae and Nacellidae and at least three times within Lottiidae. In Patelloidea, the presence of this kind of gill seems to be a strictly phylogenetic phenomenon because all species have this structure. The difference in configuration of patellid and nacellid gills was probably caused by the autapomorphic change in the circulatory system of Nacellidae. In contrast, the presence of secondary gills in lottiid genera is considered to be an ecologically controlled phenomenon. The secondary gills are generated convergently by increased body size in *Lottia gigantea* (*fide* Lindberg, 1986 b, 1988 a), or by physiological stress in the tropical waters in *Lottia, Tectura*, and *Scurria* (Lindberg and McLean, 1981; Lindberg, 1988 a). Therefore, the presence or absence of such gills cannot be used as systematic character in the Lottiidae (Lindberg, 1988 a).

Absence of the gill: In terrestrial neritopsines (Helicinoidea and Hydrocenoidea), the ctenidium is completely lost and replaced by the vascularized lung that is analogous to that of architaenioglossate and pulmonate land snails. Apparently, it is a common convergent pattern that terrestrial gastropods have also lost this distinct respiratory organ.

In Patellogastropoda, neither ctenidium nor secondary gills are present in Lepetidae (Young, 1960; Angerer and Haszprunar, 1996) and *Erginus* (Golikov and Kussakin, 1972; this study). The absence of a distinct respiratory organ may be attributable to small body size and utilization of the pallial cavity as a blood pouch in the latter group. On the other hand, the absence of gills in Lepetidae is difficult to explain except as a result of phylogenetic constraint. Ecologically a correlation may be found with habitat on stones in muddy bottoms in cold waters of the subtidal zone to the deep-sea (Young, 1960). Body size seems to have no relationship with this phenomenon as exemplified by *Limalepeta lima* which attains more than 30 mm in shell length.

3. Buccal Mass

Jaws: Archaeogastropod jaws are clearly differentiated into two distinct types (see section IV-1). Their evolutionary development can be traced as follows: (i) the number of jaws changed from primitively unpaired to dorsoventrally paired in Cephalopoda or bilaterally paired in Orthogastropoda; (ii) the cephalopod and gastropod ancestors shared the double-layered structure with muscular attachments to buccal mass by ACCTRAN optimization, but the similarity arose independently according to DELTRAN optimization. Thus, at least it is without doubt that the double-layered, undivided jaw fixed on the odontophore vs. single-layered, bilaterally divided jaws on the oral tube supports a major basic division of Gastropoda into Patellogastropoda and Orthogastropoda as proposed by Ponder and Lindberg (1996; 1997).

Although it has not been conceived in previous comparative studies, the cephalopod upper beak and the patellogastropod jaw share some comparable states. As discussed in the character analysis section, they share a medially fused single plate consisting of anterior and posterior sections, which are associated with the odontophore by muscle attachment, unlike those of other gastropod groups. Therefore, the anterior and posterior wings of the patellogastropod jaw can be assumed to be homologous with the outer and inner lamellae of the cephalopod upper beak, respectively. These characters possibly reflect the primitiveness of Patellogastropoda as retained through common ancestry of Gastropoda and Cephalopoda.

Odontophoral cartilages: The transformation of this character has not been discussed in detail in previous phylogenetic studies of Gastropoda. The following changes are expected to have occurred in the five

types of archaeogastropod odontophoral cartilages. (i) Ancestral Gastropoda had a single pair of cartilages. This state was inherited by the "vent taxa," Cocculinidae, Seguenziidae, Lepetodrilidae, and Caenogastropoda. (ii) The cartilages were split into two (anterior and posterior) pairs independently in "Zeugobranchia + Trochoidea," in Neritopsina, and in Patelloidea (*Patella* and *Cellana*). (iii) Two (anterior and anterolateral) pairs of cartilages are the basic patellogastropod pattern, from which more complicated cartilages have arisen in Patelloidea. It is difficult to establish the direct homology between two pairs in Patellogastropoda (anterior and anterolateral cartilages) and Polyplacophora-Tryblidiida (medial and lateral cartilages). (iv) Neritopsine uniquely evolved median pair of cartilages. Therefore, it is concluded that single pair as in some archaeogastropods and Caenogastropoda is original gastropod state, and the number of cartilages increased variously by secondary division in several lines of archaeogastropods.

Common plan of archaeogastropod buccal musculature: Archaeogastropod buccal musculature consists of several common muscle elements (Table 5). They include: (i) lateral and ventral protractor muscles of the odontophore, (ii) anterior levator of the odontophore, (iii) two pairs (lateral and median) of protractors of the subradular membrane, (iv) the retractors of the subradular membrane and radular sac, and (v) ventral approximator of the odontophoral cartilages. These muscles are all present in Polyplacophora and Tryblidiida, and therefore, their presence is plesiomorphic in Gastropoda. The radular muscle (*m. radula longus*) connecting with the shell in Polyplacophora and Tryblidiida (Wingstrand, 1985) is absent at least in Cephalopoda and Gastropoda.

Buccal musculature of Neomphalus: The buccal mass of the enigmatic vent-taxon, *Neomphalus*, was described and illustrated by Fretter *et al.* (1981: figs. 3–5). According to their description, composition of the musculature in this genus is basically of archaeogastropod-type with the above-mentioned basic set of muscles, although pallial and coelomic organs exhibit "mesogastropod-like" states. Most importantly, the ventral side of the radular sac behind the buccal mass is connected to the floor of the body cavity by a "radular retractor muscle (rr)" (= posterior retractor muscle of radular sac in this study). The presence of this muscle suggests the relationship with Vetigastropoda.

Evolution from archaeogastropod to caenogastropod buccal musculature: Comparative anatomy of the buccal musculature reveals several "trends" from archaeo- to caenogastropod levels of organization: (1) *Reduction in muscle number:* The number tends to decrease from Polyplacophora to Gastropoda, and also from "Archaeogastropoda" to Neogastropoda. (2) *Reduction of extrinsic muscles:* The muscles extending from the surface of the odontophore to the wall of the snout are reduced in number in Caenogastropoda. This change increases freedom of the buccal mass and plays an important role in the development of active carnivorous predation and proboscis formation. (3) *Development of intrinsic muscles:* In contrast to the reduction of extrinsic muscles, intrinsic muscles elaborate into a more compact muscular unit. In this respect, the buccal mass of Ampullariidae (Berthold, 1991: figs. 242–246) is closer to those of lower Neotaenioglossa such as Littorinidae (Fretter and Graham, 1962: fig. 14) rather than "Archaeogastropoda," supporting the advanced state of Architaenioglossa over "Archaeogastropoda." (4) *Loss of levators and depressors:* Unlike amphineurans and archaeogastropod groups, Caenogastropoda generally lack a set of levator and depressor muscles. (5) *Development of retractors of the odontophore:* In "Archaeogastropoda," the retraction of the odontophore is a simply passive returning movement by relaxation of the protractor muscles (Graham, 1973). However, a pair of retractors are developed on the ventrolateral sides of the buccal mass in Caenogastropoda except Ampullariidae (e.g. Fretter and Graham, 1962: fig. 14; Davis, 1967; Carriker, 1943) and in Heterobranchia (e.g. Hubendick, 1956; Hurst, 1965; Hembrow, 1973).

Proboscis formation in "higher" caenogastropods: The above-mentioned changes are all explained by morphological changes in the entire feeding apparatus and in the mode of feeding. In grazers of the archaeogastropod level, the buccal mass is fixed in the snout, and feeding is regulated by orientation of the snout and cyclic movements of the radula over the odontophore. In Caenogastropoda, the simple snout is further

Table 5. Taxonomic distribution of buccal muscles. References: *1, Graham (1973) and Wingstrand (1985), *2 Fretter et al. (1981), *3 Berthold (1991).

	Polyplacophora *1	Trybliidae *1	Patellidae	Nacellidae	Lepetidae	Acmaeidae	Lottiidae	Pleurotomariidae	Haliotidae	Fissurellidae	Scissurellidae	Turbinidae	Trochidae	Leptodrilus	Seguenzia	Cocculina	Neomphalus *2	Neritidae	Phenacolepadidae	Helicinidae	Ampullariidae *3
Transverse labial muscle (tlm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lateral protractor of odontophore (lp)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ventral protractor of odontophore (vp)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dorsal protractor of odontophore (dp)	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Retractor of odontophore from posterior side	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anterior levator of odontophore (al)	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Posterior levator of odontophore (pl)	-	-	-	-	-	-	-	-	+	+	-	+	-	-	?	-	-	-	-	-	-
Dorsal levator of odontophore (dl)	-	-	-	-	-	-	-	+	-	-	-	-	-	-	?	-	+	+	+	+	+
Median levator of odontophore (ml)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Posterior depressor of odontophore (pd)	-	-	-	-	-	-	-	+	+	+	+	+	+	+	?	+	-	+	+	+	+
Postdorsal buccal tensor (pdt)	-	-	-	-	-	-	-	+	+	+	+	+	+	+	?	+	-	+	+	+	+
Dorsal buccal tensor (dbt)	-	-	-	-	-	-	-	-	-	-	-	-	-	+	?	-	-	-	-	-	-
"Musculus radulae longus"	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lateral protractor of subradular membrane (lpr)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Median protractor of subradular membrane (mpr)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Retractor of subradular membrane (rsm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Retractor of radular sac (rrs)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Postmedian retractor of radular sac (prs)	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-
Median tensor of radular sac (trs)	-	-	+	+	+	-	-	-	-	-	-	-	-	+	?	+	-	-	-	-	-
Median retractor of radular sac (mrs)	-	-	+	+	+	-	+	-	-	-	-	-	-	-	?	-	-	-	-	-	-
Ventral approximator of odontophoral cartilages (vap)	+	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Outer approximator of odontophoral cartilages (oap)	-	-	-	-	-	-	-	-	-	-	-	-	+	-	?	-	-	+	+	+	-
Tensor of anterior cartilages (tac)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+

elaborated into an extensile proboscis. The tube of the proboscis can be everted and prolonged to contact prey, and buccal mass moved longitudinally in the elongated proboscis. The development of retractors is essential to the control of movement of buccal mass in proboscidiferous, active predators. The evolution from an acrembolic to a narrowly elongated pleurembolic proboscis caused the elongation of cartilages and reduction of radular tooth number from "Mesogastropoda" to Neogastropoda (Graham, 1973).

4. Radula

Basic number of gastropod radular teeth: The importance of the number of radular teeth has long been emphasized in phylogenetic studies in Gastropoda. The rhipidoglossate radula was considered primitive in classic studies, probably because of the ancient image of zeugobranchs and the contrasting state in "higher" stenoglossate taxa, but the idea has not been supported in recent studies. The primitiveness of the patellogastropod radula is elucidated by outgroup comparison. In the outgroups, tooth number is 17 $(8+1+8)$ in Polyplacophora, 11 $(5+1+5)$ in Tryblidiida, and 5–7 in Scaphopoda (Salvini-Plawen, 1988). In Cephalopoda, each row of the radula consists of 13 elements (central$+2$ laterals$+2$ marginals$+2$ marginal plates) in Nautiloidea or 9 elements (central$+2$ laterals$+1$ marginal$+1$ marginal plate) in Coleoidea and Ammonoidea (Nixon, 1995; Tanabe and Fukuda, in press). Therefore, the tooth number of 5–13 in Patellogastropoda is closer to the outgroups than to the higher numbers in rhipidoglossate radulae (McLean, 1979; Wingstrand, 1985; Salvini-Plawen, 1988; Lindberg, 1988 a; McLean, 1990 b).

Common characters among Polyplacophora, Tryblidiida, and Patellogastropoda: In addition to similarity in tooth number, these three groups share several common features in radular morphology: (i) functional type is stereoglossate; (ii) teeth are mineralized with magnetite (Salvini-Plawen, 1988; Okoshi, 1996); (iii) the central tooth is small or lost; (iv) the cusp of the inner marginals is plate-like and comb-shaped in some Polyplacophora (the fifth teeth) and in Tryblidiida (the fourth teeth). A similar state is present only in Lepetidae within Patellogastropoda (McLean, 1979; Wingstrand, 1985); (v) The basal plate is absent. This state is likewise found only in Lepetidae and Neolepetopsidae within Patellogastropoda. These shared states strongly support the basal position of Patellogastropoda in Gastropoda, and also the primitive status of Lepetidae within Patellogastropoda. Therefore, outgroup comparison in morphology again suggests that the hystrichoglossate radula of Pleurotomariidae is far from the archetype (see also Hickman, 1984 c).

Changes in archaeogastropod radulae: In "Archaeogastropoda," the following changes are revealed by character tracing on the given cladograms. (i) The flexoglossate condition evidently evolved in the common ancestor of Orthogastropoda. (ii) Concerning tooth mineralization, two different interpretations are possible. In ACCTRAN optimization, mineralization was lost once in the common ancestor of Gastropoda and Cephalopoda and re-acquired by reversal in Patellogastropoda. In DELTRAN optimization, mineralized teeth were inherited by ancestral gastropods, and later demineralized in Orthogastropoda. (iii) The presence of basal plates is an unquestionable synapomorphy of Patellogastropoda except Lepetidae and Neolepetopsidae. (iv) The central tooth was lost independently in Acmaeoidea (Acmaeidae and Lottiidae) and Cocculinidae. (v) The number of lateral teeth is mostly three pairs or less in the primitive state and is retained in Patellogastropoda. In Orthogastropoda, tooth number was reduced to a single pair in Caenogastropoda or increased to four to five pairs in rhipidoglossate taxa. Tooth reduction occurred in *Seguenzia* in convergence state with Caenogastropoda. (vi) The number of marginal teeth increased markedly in the ancestor of Rhipidoglossa. (vii) Plate-like or vestigial marginal teeth are retained in Patellogastropoda. A further apomorphic state was created by elongation of the shaft of the marginal teeth in the ancestor of Orthogastropoda.

Specialization in rhipidoglossate radulae: As revealed by the reconstruction, the following four changes must have taken place in the course of evolution from the basic docoglossate type to the rhipido-

glossate condition: (i) loss of mineralization, (ii) increase in tooth number towards five pairs of laterals and toward many pairs of marginals, (iii) elongation of marginal shafts (manifest change into basal flexoglossate condition), and (iv) acquisition of marked articulation through the development of basal extension of the teeth.

Due to a combination of the above characters, the radula of Neolepetopsidae was considered to represent an intermediate condition between docoglossate and rhipidoglossate radulae (McLean, 1990 b). However, other anatomical characters suggest the independence of this family from the rhipidoglossate type, therefore, this may represent a change in this state in Patellogastropoda rather than a gradual change.

Several other specializations occur in some rhipidoglossate radulae as suggested by this analysis. (i) Enlargement of prominent outer lateral teeth evolved independently in *Cocculina*, some Zeugobranchia, and Neritopsina. (ii) Asymmetry in teeth row become prominent in a part of Zeugobranchia (Hickman, 1981). (iii) Independent specialization also generated lateromarginal plates in Fissurellidae and protolateromarginal plates in Trochoidea.

Aberrant rhipidoglossate forms: A modified or completely transformed type of rhipidoglossate radula occurs in various archaeogastropod taxa. Some Seguenziidae with taenioglossate-like teeth have, therefore, been previously considered as "Mesogastropoda" (e.g. Golikov and Starobogatov, 1975). Highly specialized aberrant morphology is found in trochoid subfamilies of unknown affinities (Hickman and McLean, 1990) and in "higher" Lepetelloidea (e.g. Addisoniidae and Choristellidae, Hickman, 1983; McLean, 1985 a; Marshall, 1996). In such cases, investigations on buccal mass structure (cartilages and muscles) may be very informative in clarifying their systematic position as suggested above.

5. Alimentary Tract and Glands

Salivary glands: It is extremely difficult to generalize archaeogastropod salivary glands due to diversification into several subtypes. They variably open into the buccal cavity directly or through long ducts, and the form of glands is also greatly variable.

(1) *Patellogastropoda:* Great diversification in both the glands and the ducts has occurred extensively within Patellogastropoda. (i) The glands are large and separated from the buccal cavity behind the buccal mass. They are connected by a pair of long salivary ducts in *Cellana* and most Lottiidae (*Nipponacmea*, *Lottia*, and *Patelloida*) (Sasaki and Okutani, 1993 a; this study; Sasaki, unpublished data). (ii) *Erginus* and *Yayoiacmea* have small glands with a pair of long ducts (Sasaki and Okutani, 1993 b; this study). (iii) The glands of *Patella* are unusual among Gastropoda in having two pairs of ducts from single pair of large glands. (iv) Within Patellogastropoda, *Limalepeta*, *Pectinodonta*, and *Niveotectura* share obliquely tubular glands on the buccal mass without ducts. Subdivision of these states were not used in the analysis because of complexity.

(2) *Gland-less groups:* The reconstruction indicates that the loss of salivary glands occurred in ancestor of Rhipidoglossa. In some neritopsine genera, the absence of the glands is functionally compensated by the extensive lining of glandular epithelium of the buccal cavity and the sublingual glands (Fretter, 1965). In other groups lacking salivary glands (*Cocculina*, *Neomphalus*, and *Lepetodrilus*), specialization of sublingual glands does not occur.

(3) *Vetigastropoda:* The glands of Zeugobranchia and Trochoidea are unique in having ramified lumen and longitudinally slit-like openings to buccal cavity in contrast to sack-like glands and small pore-like openings of others. The result of the analysis shows that these glands arose secondarily after the original glands were lost in basal Rhipidoglossa.

Radular diverticulum: The presence of this character is plesiomorphic for all of archaeogastropods including all vent taxa. It is also present in Architaenioglossa (Ampullariidae), while it is lost in Neotaenioglossa and Neogastropoda (Fretter and Graham, 1962). This character evidently supports the basal position

of Architaenioglossa and the derivation of the remaining "higher" gastropod groups within Caenogastropoda.

Esophagus: The primitive archaeogastropod esophagus is generalized by the following features (Salvini-Plawen and Haszprunar, 1987; Salvini-Plawen, 1988; Fig. 98): (i) division into three portions, *viz.* anterior, mid-, and posterior esophagi; (ii) dorsoventral depression of the anterior esophagus; (iii) a ciliated dorsal food channel and a ventromedian ciliary tract between the dorsal and ventral folds; (iv) lateral pouches on the outer sides of the anterior esophagus; (v) an esophageal valve projecting over the radular diverticulum; and (v) a counterclockwise twist in the mid-esophagus as a consequence of torsion. Most "Archaeogastropoda" retain these primitive features, but the anterior esophagus is simplified in Caenogastropoda and greatly modified in Vetigastropoda. In esophageal characters, Vetigastropoda clearly exhibits an apomorphic state in the inner structure of the anterior and mid-esophagi (papillate glands covering enlarged esophageal pouches).

Stomach: The generalized non-patellogastropod archaeogastropod stomach comprises a toothed gastric shield, a protostyle (= "food-mucus rod"), a ciliated sorting area, major and minor typhlosoles, and a gastric caecum. According to outgroup comparison, the patellogastropod stomach has lost the style sac region and gastric caecum completely, and as such is apomorphic. In this phylogenetic reconstruction, it is equally possible that the gastric caecum arose independently in *Nautilus* and Rhipidoglossa, or that it was lost separately in Patellogastropoda and Caenogastropoda. The latter case seems more likely, because similar (probably homologous) gastric structures are also found in bivalves (Owen, 1966; Purchon, 1977).

"Cocculiniformia" have a specialized stomach which appears to be correlated with the unusual mode of feeding in the deep-sea environment (Haszprunar, 1988 c: fig. 3). In Caenogastropoda, gastric anatomy becomes more simplified in connection with carnivorous feeding (Fretter and Graham, 1962). These forms were most likely derived from the above-mentioned basic type.

Gastric caecum: The presence of simple caecum is regarded as the primitive state in Conchifera because it is also found in Cephalopoda and lamellibranch Bivalvia (Salvini-Plawen, 1988). Therefore, the presence of a large spiral caecum or total loss of the caecum represent more advanced states. Vetigastropoda generally have a large coiled caecum, but it is absent in limpets (Fissurellidae, *Broderipia*, and *Lepetodrilus*). Especially in Trochoidea, members with a trochispiral shell always have a large caecum (e.g. Figs. 53 e, 56 b), whereas only limpet-shaped *Broderipia* lacks it (Fig. 57 b). This example strongly indicates that a large coiled caecum is markedly reduced in association with the limpet shape as suggested by Graham (1939, 1985). In the case of Neritopsina, both coiled and uncoiled forms have the simple short caecum.

Crystalline style: In Gastropoda and Bivalvia the crystalline style is probably developed independently from the primitive protostyle (Salvini-Plawen, 1988). Typically, herbivorous and deposit- or suspension feeding "mesogastropods" elaborate the crystalline style, but such specialization does not occur in archaeogastropods (Declerck, 1995).

Loops of the intestine: Generally the archaeogastropod intestine is long and forms a so-called anterior loop on the right posterior side of the buccal mass. In Caenogastropoda, the intestine becomes shortened, and the anterior loop is lost. Although configuration of the archaeogastropod gut is greatly diversified into complicated forms, they have probably originated in a common pattern phylogenetically and ontogenetically. Interestingly, gut coiling in juveniles of *Patella* (Smith, 1935: fig. 27) is quite similar to that in adults of vetigastropods (e.g. Figs. 33 a, 53 e, 64 a). Therefore, the gut folding twice to form a single anterior intestinal loop must reflect an original archaeogastropod coiling pattern. Within "Prosobranchia," the intestine may have evolved from a complex type to simple one, correlated with a change in feeding from herbivorous to carnivorous as in the case of the stomach (Fretter and Graham, 1962).

6. Reproductive System

Connection of the gonoduct with the kidney: The intimate coordination of the excretory and reproductive systems in Patellogastropoda and Vetigastropoda has been regarded as primitive gastropod condition (Graham, 1985; Haszprunar, 1988 b). However, this connection is the apomorphic state in the most-parsimonious reconstruction obtained by this analysis. The connection of the gonoduct with the kidney occurred independently three times in Tryblidiida, Patellogastropoda, and Vetigastropoda. A similar case also is apparent regarding the supposed primitiveness of paired kidneys. Because the evolution of the gonoduct is probably correlated with the condition of the kidney, reconsideration of homology may be necessary for both the renal organ and the associated gonoduct at the ultrastructural level.

Pallial gonoduct of Neritopsina: By contrasting the archaeogastropod condition with those of "higher" gastropods, the elaboration of the pallial gonoduct is regarded as an irrefutable major change in gastropod evolution. This change can be briefly summarized as follows. (1) *Female organ:* Females of "higher" gastropods developed apparatuses for reception and storage of sperm and as well as secretion of egg covering material (Fretter and Graham, 1962; Fretter, 1984 b). (i) The "bursa copulatrix" receives sperm at copulation, which are then passed to the "seminal receptacle," where they are stored in alignment with their heads buried in the epithelial wall. (ii) The proximal "albumen gland" and distal "capsule gland" of the pallial gonoduct serve for the formation of encapsulated eggs. (2) *Male organ:* In male organs, the following apomorphic states evolved. (i) A "seminal vesicle" may be formed for the storage of mature sperm. (ii) A "prostate gland" is developed on the pallial gonoduct. (iii) A penis is formed and connected with the gonopore via a ciliated sperm duct or groove.

A functionally similar set of the above components is possessed by Neritopsina and various "higher" Gastropoda. However, the pallial gonoduct of Neritopsina can be distinguished from that of Caenogastropoda in some respects (Fretter, 1965): (i) it is wholly enclosed within the anterior pallial vein; (ii) there is no gonopericardial duct in the renal section of the gonoduct; (iii) the right hypobranchial gland is confluent with the pallial gonoduct. Based on these differences, the origin of the neritopsine pallial gonoduct is assumed to be independent. It is highly problematic that no clear criteria of homology are applicable to the gonoducts of entire groups of gastropods at higher levels (Ponder and Lindberg, 1997).

Much of the information available for Neritopsina is actually based upon descriptions of Neritoidea which therefore may not always represent general neritopsine conditions. For example, crystals for reinforcement of the egg capsule is restricted only to some Neritidae. There seem to be greater differences between neritoidean and non-neritoidean groups than are currently recognized, and further investigation is needed on the extensive non-neritoidean groups.

Modification in deep-sea taxa: Internal (or semi-internal) fertilization and brooding in the pallial cavity are common strategies in deep-sea archaeogastropods. Various accessory apparatuses are developed as independent structures. (1) *Seminal receptacle in female:* Development of a receptaculum seminis is the most common strategy in deep-sea taxa and has apparently evolved several times. It is found in *Neomphalus* (Fretter *et al.*, 1981), *Melanodrymia* (Haszprunar, 1989 b), Cocculinidae and Bathysciadiidae (Haszprunar, 1987 a; this study), Addisoniidae and Choristellidae (Haszprunar, 1987 b, 1992), Seguenziidae (Haszprunar, 1988 b; this study), and Lepetodrilidae (Fretter, 1988; this study). (2) *Copulatory organ in male:* Deep-sea archaeogastropods often develop copulatory organ variously from cephalic, neck, and epipodial regions. In "Cocculiniformia," *Seguenzia*, Lepetodrilidae, and Neritoidea (including shallow-water taxa), the organ arises from the right side, whereas *Neomphalus fretterae* and its coiled relatives (*Cyathermia* and *Lacunoides*) (Fretter *et al.*, 1981; Warén and Bouchet, 1989), and Gorgoleptidae (Fretter, 1988) all use the left cephalic tentacle or left oral lappet. In Trochoidea, the epipodial penis from the right side occurs in Skeneidae (Fretter and Graham, 1977; Warén, 1991 a) and *Bathymargarites* (Warén and Bouchet, 1989). Most of the above examples are functionally analogous, but morphologically and positionally not homologous.

7. Nervous System

Changes from archaeogastropods to "higher" gastropods: It is well accepted that concentration of the nervous system is a major event in gastropod evolution (Fretter and Graham, 1962: 307-308; Haszprunar, 1988 b; Ponder and Lindberg, 1997). Especially, the prosobranch circumesophageal nerve ring must have been evolved through the change from a hypoathroid (adjacent pleural and pedal ganglia) to an epiathroid (adjacent pleural and cerebral ganglia) condition. By tracing this character on the phylogenetic reconstruction proposed here and by contrasting archaeo- and caenogastropods, the following process can be proposed for the evolution of the nervous system: (i) the shift of the cerebral and pleural ganglia toward the posterior dorsal side; (ii) the reduction in length of the cerebral commissure and formation of a compact nerve ring; (iii) the loss of the labial commissure; (iv) the development of zeugoneury to enhance innervation of the well-developed left pallial organs; and (v) the development of pedal ganglia and the shift from pedal cords to pedal nerves. These phenomena are explained primarily by the shift of three major ganglionic pairs (Fretter and Graham, 1962; Haszprunar, 1988 b) and are associated with proboscis formation in "higher" caenogastropod groups (Graham, 1973).

It is clearly evident that the hypoathroid circumesophageal nerve ring with a streptoneurous visceral loop and scaraliform pedal cords represent the primitive gastropod nervous configuration of the common ancestor. In Gastropoda, this state is possessed by all archaeogastropods and Ampullariidae of Architaenioglossa. Therefore, retention of the hypoathroid condition clearly supports the primitive status of the latter group within the Caenogastropoda.

Labial ganglia and commissure: The labial commissure is present in both Patellogastropoda, Neritopsina and Architaenioglossa. Because it can be regarded as a homologue of the subcerebral commissure of amphineurans, its presence must indicate a primitive state, and loss of the commissure is clearly apomorphic in non-neritopsine Rhipidoglossa and "higher" gastropods. In contrast, the development of labial ganglia is found only in Patellogastropoda, and therefore the presence of these ganglia is without doubt apomorphic within Mollusca. Thus, the labial commissure is of early origin, whereas the presence of labial ganglia is highly innovative.

Neritopsina-Architaenioglossa condition: Although the phylogenetic relationships as reflected by anatomical characters between Neritopsina and Ampullariidae have never been discussed in detail, these two taxa have a similar nervous system configuration (Figs. 101 c, d). The most prominent similarities are the one-sided origin of the visceral loop, the presence of a pleural commissure, the very thin supraesophageal-cerebral parts of the visceral loop, and a labial commissure without labial ganglia. Therefore, these character sets except plesiomorphic labial commissure may represent one synapomorphic state that links these two groups. However, these states are completely homoplastic according to the most-parsimonious reconstruction. They were probably created by the shift of subesophageal part of visceral loop to right side (Berthold, 1991) independently in these groups.

A similar but somewhat deconcentrated configuration of the nervous system is also reported in the naticid-like *Globularia fluctuata* (*fide* Kase, 1990). This type of nervous system will be an important phylogenetic character in phylogenetic studies of "lower" Caenogastropoda.

V–3. Phylogenetic Evaluation of Protoconch Characters

1. Phylogenetic Characters of Protoconch

Morphotypes of archaeogastropod protoconchs: In terms of the number of whorls and symmetry, the protoconchs of "Archaeogastropoda" can be clearly classified into four types, each of which corresponds to a higher taxonomic category defined by anatomical characters (Fig. 107, Table 6).

(1) *Symmetrically uncoiled type:* Truly symmetrical, bottle-shaped protoconchs are found in patellogastropod genera. The surface is generally covered with finely reticulate, wavy sculpture, although it is modified in the protoconch of brooded *Erginus*. The aperture of the protoconch is sealed by a septum after teleoconch formation.

(2) *Paucispiral type:* Vetigastropoda and their relatives (=non-neritopsine Rhipidoglossa) generally have a symmetrically or asymmetrically paucispiral protoconch. This type is further divided into four subtypes: (i) a planispiral type in Cocculinoidea, (ii) a trochispiral type in Pleurotomariidae, Haliotidae, Crypeosectidae, Scissurellidae, Trochoidea, Seguenzioidea, Peltospiroidea, Neomphaloidea, and some of Fissurellidae (e.g. *Rimula*, *Diodora*, *Tugali*, and *Scutus*), (iii) an elongated type in some of Lepetelloidea (e. g. Psudococculinidae) and Fissurellidae (e.g. *Emarginula, Zeidora, Puncturella*, and *Fissurella*), and (iv) a symmetrical type in *Macroschisma* of Fissurellidae (Fig. 40). It is common to all of these subtypes that the surface is covered with prismatic (typically net-like) deposits of various form.

(3) *Multispiral type:* Aquatic neritopsine groups have a multispiral protoconch regardless of the shell form of the teleoconch. Protoconch morphology is also unaffected by habitat differences as exemplified by various taxa from brackish (*Septalia*) to deep-sea (Shinkailepadidae) environments. This type differs markedly from the other in that the multispiral Protoconch II is formed by accretionary growth in the planktotrophic veliger stage (Bandel, 1982). Resorption occurs in the inside of the protoconch. The surface is never adorned by prismatic deposits.

(4) *Globular type:* Terrestrial neritopsines (e.g. *Georissa* of Hydrocenidae, Fig. 87) have a specialized dome-shaped protoconch. However, it is common to all neritopsine groups that the internal columella is reabsorbed and that the protoconch eventually becomes hollow. This characteristic of protoconch structure suggests derivation from aquatic forms due to secondary modifications to terrestrial life.

Sculpture of protoconch: Within archaeogastropods, a sculpture specific to particular suprageneric taxa is found in only a few cases. Examples are restricted to thick transverse (axial) ribs in Scissurellinae of Scissurellidae, a hexagonal pattern in Calliostomatinae and Thysanodontinae of Trochidae, and a regular net-like pattern with a pitted surface in Cocculinidae. Therefore, in general, detailed differences in protoconch sculpture have little significance in higher-level systematics, but they are very useful in distinguishing closely related taxa at lower taxonomic levels such as a species-complex or genus. At the higher level, irregular prismatic (typically net-like) sculpture is not found in the protoconchs of Caenogastropoda (e.g. Bandel, 1975). Thus, such sculpture may be an important feature suggesting primitiveness retained in Patellogastropoda and non-neritopsine rhipidoglossate groups.

Septal formation in Patellogastropoda: Formation of a septum and loss of the protoconch are common features in Patellogastropoda. The aperture of the protoconch is sealed by a septum from the inside, and ultimately the dorsal part of the protoconch is cut off usually at the stage of less than 1–2 mm in total shell length. A small pit remains at the center of the septum after the absorption of the internal visceral hump (Morse, 1910; Smith, 1935: fig. 29). Also characteristically, a protoconch detachment scar in the shape of a figure-eight remains at the apex of the teleoconch (Sasaki and Okutani, 1993 a; Figs. 21 g, h).

In other limpet-shaped gastropods, the protoconch is always retained at the apex except in fissurellids with foramen and some Lepetelloidea (e.g. *Lepetella* and *Addisonia*; Dantart and Luque, 1994). An internal septum is not known to occur in most non-patellogastropod groups. Pseudococculinidae produce a septum

symmetrically uncoiled   **multispiral**   **globular**

planispiral   **trochispiral**   **elongated**
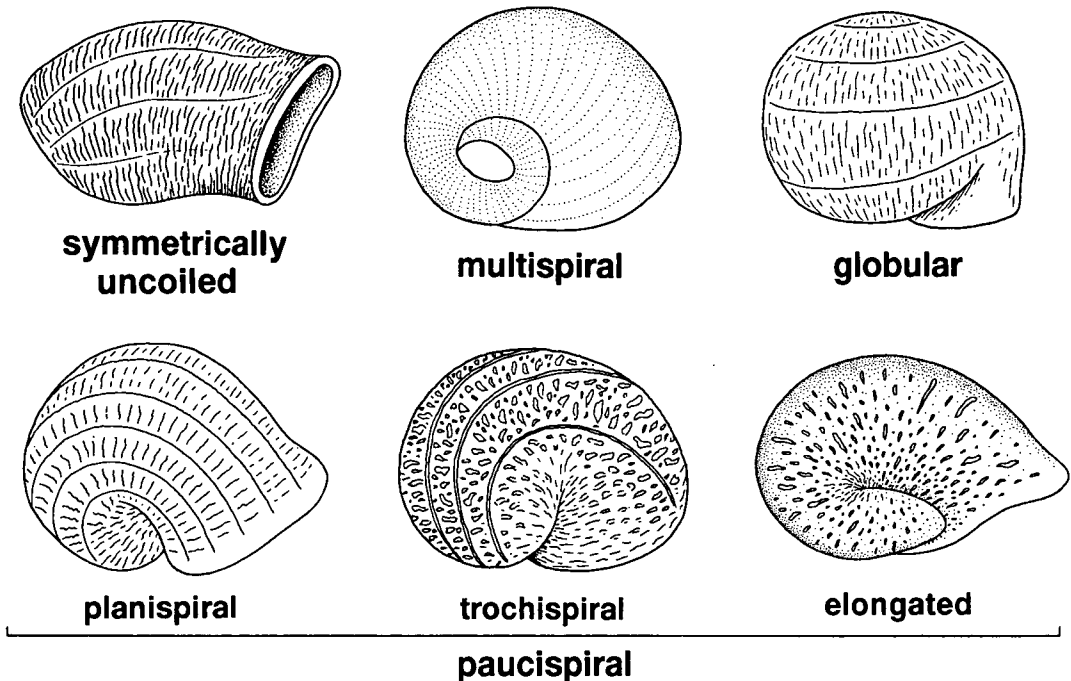
paucispiral

Fig. 107.   Morphotypes of protoconch of Archaeogastropoda.

with an obliquely slit-like opening (Marshall, 1985 a: fig. 10 N; McLean and Harasewych, 1995: figs. 78, 82) but this exhibits a different mode of shell growth.

Mechanical deformation in the paucispiral type: Bandel (1982) suggested that the asymmetrical shell in a paucispiral-type protoconch is formed by a process called mechanical deformation. According to his interpretation, the protoconch is formed by the following successive events (see also Hickman, 1992). (i) A bilaterally symmetrical, cup-shaped organic shell is formed by the shell gland. (ii) The organic shell is mechanically modified into an asymmetrical form by the retractor muscle. Consequently, the apex is directed to the left, and the "lateral pouches" and corresponding dimple-like depressions are emphasized in the asymmetrical form. (iii) The organic shell is rapidly mineralized by the mantle following this deformation. Deformation prior to mineralization is supported by the presence of non-incremental lines that are discordant to spiral sculpture (e.g. Fig. 59 g).

Heterostrophy in Trochoidea: In some genera of Trochoidea, the coiling axis of the protoconch is markedly tilted compared to that of the teleoconch, as is found in *Lirularia? minima* (Fig. 60 g) and *Pondorbis japonicus* (Fig. 61 b). Such a relationship is caused by the formation of a hyperstrophic protoconch and orthostrophically coiled teleoconch. This change in the direction of shell coiling at metamorphosis is termed "heterostrophy" (Haszprunar, 1985 d; Bieler, 1993).

Heterostrophy is well-known as a synapomorphy of the Heterobranchia (Haszprunar, 1985 d). Apparent heterostrophy in Trochoidea differs from that in Heterobranchia in the following respects (Haszprunar, 1988 b; Bieler, 1992): (i) In Heterobranchia, the angle of heterostrophy ranges from 90 to 180 degrees (the extreme form is specially termed anastrophy or coaxial heterostrophy). In Trochoidea, the tilt of the protoconch axis is normally less than 45 degrees. (ii) The hyperstrophic state of the protoconch is formed by mechanical deformation prior to mineralization in Trochoidea, but by accretionary growth in Heterobranchia, as inferred from surface sculpture. Therefore, the similarity in these two distant groups represents an analo-

Table 6. References to descriptions of intact archaeogastropod protoconch using SEM micrographs.

Family	Genus and References
Patellidae	*Patella* (Robson, 1986; Warén, 1988)
Nacellidae	*Cellana* (this study)
Lepetidae	*Propilidium* (Bandel, 1982, as *Cocculina*; Dantart and Luque, 1994), *Iothia* (this study)
Lottiidae	*Lottia* (this study), *Erginus* (Lindberg, 1979; this study)
Neolepetopsidae	*Neolepetopsis* (McLean, 1990b; Gustafson and Lutz, 1994)
Pleurotomariidae	*Mikadotrochus* (this study)
Haliotidae	*Nordotis* and *Sulculus* (Hayashi, 1983a), *Haliotis* (Bandel, 1982)
Fissurellidae	*Emarginula* (McLean, 1984a; Herbert and Kilburn, 1986; this study), *Nesta* (Bandel, 1982), *Zeidora* (Herbert, 1987a; this study), *Puncturella* (Herbert and Kilburn, 1986), *Rimula* (this study), *Tugali* (Herbert, 1987a), *Scutus* (Herbert, 1987a; this study), *Diodora* (Bandel, 1982; McLean, 1984a; Pernet, 1997), *Fissurella* (Bandel, 1982; McLean, 1984a), *Macroshisma* (this study).
Crypeosectidae	*Clypeosectus* (McLean, 1989b; Mullineaux et al., 1996), *Pseudorimula* (McLean, 1989b)
Scissurellidae	*Scissurella* (Bandel, 1982; Herbert, 1986), *Sinezona* (Yaron, 1983; Herbert, 1986; Warén and Bouchet, 1989; Burnay and Rolan, 1990; Leal, 1991a; this study), *Anatoma* (Batten, 1975; Herbert, 1986; this study), *Larochea* and *Larocheopsis* (Marshall, 1993b), *Sutilizona* (McLean, 1989b)
Turbinidae	*Arene* (Bandel, 1982; Leal, 1991a, b), *Cinysca* (Leal, 1991a), *Angaria* (Marshall, 1979), *Astraea* (Leal, 1991a), *Turbo* (Hayashi, 1983b), *Leptothyra* (Marshall, 1979; Hickman, 1992), *Homalopoma* (this study), *Leptocollonia* (Dell, 1990; Numanami, 1996), *Gabrielona* (Hikaman, 1992; Hasegawa, 1997a), *Tricolia* (Gofas, 1993; this study).
Trochidae	*Chlorostoma* (this study), *Euchelus* (Marshall, 1979; this study), *Calliotropis* (Hickman, 1992), *Bathymargarites* (Warén and Bouchet, 1993), *Kaiparathina* (Marshall, 1993a), *Margarites* (Dobberteen and Ellmore, 1986; Hadfield and Strathmann, 1990), *Gibulla* (Bandel, 1982), *Cantharidus* (this study), *Broderipia* (this study), *Synaptocochlea* (Leal, 1991a), *Calliostoma* (Bandel, 1982; Ramón, 1990; Hadfield and Strathmann, 1990; Marshall, 1995a; this study), *Ilanga* (Herbert, 1987b), *Solariella* (Warén, 1993; Herbert, 1987b; Leal, 1991a), *Lirularia* (Hadfield and Strathmann, 1990), *Acremodonta* (Marshall, 1983a; Marshall, 1995b), *Trochaclis* (Warén, 1989; Warén, 1991a; Marshall, 1995b), *Herbertia* (Marshall, 1988b; Herbert, 1995), *Thysanodonta* (Marshall, 1988b)
Skeneidae	*Brookula* (Numanami, 1996), *Lissotesta* (Warén, 1991a; Numanami, 1996), *Cyclostremiscus* (Leal, 1991a; this study), *Pondorbis* (this study), *Lodderena, Cirsonella, Akritogyra, Anekes, Moelleriopsis, Granigyra,* and *Lissomphlia* (Warén, 1991a), *Skenea* (Warén, 1991b, 1993), *Xyloskenea* (Marshall, 1988a; Warén, 1996), *Mikro* (Warén, 1996), *Dillwynella, Leptogyra, Leptogyropsis, Xyleptogyra,* and *Batyxylophila* (Marshall, 1988a)

Table 6. (continued)

Family	Genus and References
Skeneidae	*Protolira* and *Ventsia* (Warén and Bouchet, 1993), *Solutigyra* (Warén and Bouchet, 1989), *Bruceiella* (Warén and Bouchet, 1993; Marshall, 1994)
Pendromidae	*Rugulina* (Warén, 1991b)
Lepetodrilidae	*Lepetodrilus* (Turner et al., 1985; Mullineaux et al., 1996)
Gorgoleptidae	*Gorgoleptis* (Turner et al., 1985; Mullineaux et al., 1996)
Peltospiridae	*Depressigyra* (Turner et al., 1985; Warén and Bouchet, 1989), *Pachydermia* (Turner et al., 1985; Warén and Bouchet, 1989, 1993), *Leptogyra* (Warén and Bouchet, 1989), *Lirapex* and *Melanodrymia* (Turner et al., 1985; Warén and Bouchet, 1989; Mullineaux et al., 1996), *Rhynchopelta* (Turner et al., 1985; McLean, 1989a; Mullineaux et al., 1996), *Nodopelta* (McLean, 1989a), *Peltospira* (Lutz et al., 1986; McLean, 1989a Mullineaux et al., 1996), *Echinopelta* (Gustafson and Lutz, 1994), *Ctenopelta* and *Helicrenion* (Warén and Bouchet, 1993)
Neomphalidae	*Neomphalus* (McLean, 1981; Turner et al., 1985; Warén and Bouchet, 1989; Mullineaux et al., 1996), *Symmetromphalus* (Warén and Bouchet, 1989; McLean, 1990a)
Cyathermiidae	*Cyathermia* (Warén and Bouchet, 1989; Mullineaux et al., 1996), *Lacunoides* (Warén and Bouchet, 1989)
Seguenziidae	*Basilissa* (Quinn, 1983), *Carenzia* (Marshall, 1983b; 1991a) *Seguenzia* (Bandel, 1979; Quinn, 1983; Marshall, 1983b; 1988c; 1991; this study), *Sericogyra* (Marshall, 1988c), *Anxietas, Asthelys, Ancistrobasis, Calliobasis, Fluxinella*, and *Halystina* (Marshall, 1991)
Cocculinidae	*Cocculina* (Marshall, 1985a ; McLean and Harasewych, 1995; Hasegawa, 1997b; this study), *Coccopigya* (Marshall, 1985a; McLean and Harasewych, 1995; Dantart and Luque, 1994; Hasegawa, 1997b), *Dedikovella* (McLean and Harasewych, 1995)
Bathysciadiidae	*Xenodonta* and *Bathysciadium* (Warén, 1993)
Lepetellidae	*Lepetella* (Warén, 1991b)
Pseudoccocculinidae	*Notocrater* (Marshall, 1985a; McLean and Harasewych, 1995), *Copulabyssia* (Haszprunar, 1988d; Dantart and Luque, 1994), *Amphiplica, Punctabyssia*, and *Caymanabyssia* (McLean, 1991), *Kaiparapelta* (Marshall, 1985a; Warén and Gofas, 1996), *Tentaoculus, Mesopelex, Kurilabyssia, Caymanabyssia*, and *Colotrachelus* (Marshall, 1985a)
Osteopeltidae	*Osteopelta* (Marshall, 1994)
Cocculinellidae	*Cocculinella* (Marshall, 1983c; 1985a)
Addisoniidae	*Addisonia* (Dantart and Luque, 1994), *Helcopelta* (Marshall, 1996)
Choristellidae	*Choristella* (McLean, 1992a)
Neritidae	*Nerita* (Bandel, 1982; this study), *Septalia* (Bandel, 1991), *Smaragdia* (Robertson, 1971; Bandel, 1982), *Pisulina* (Herbert, 1991), *Bathynerita* (Warén and Bouchet, 1993)
Phenacolepadidae	*Phenacolepas* (Bandel, 1982; this study)
Shinkailepadidae	*Shinkailepas* and *Olagasolaris* (Beck, 1992b)
Hydrocenidae	*Georissa* (this study)

gous condition caused by different mechanisms of protoconch formation.

Relationships between shell coiling and torsion: In the larval stage, the gastropod visceral mass is rotated counterclockwise by 180 degrees relative to the antero-posterior axis of the head-foot complex. This process is called torsion. The effects of torsion appear as asymmetry of rotation of the mid-esophagus, streptoneury of the visceral nerve loop, and spiral coiling of the larval operculum (Haszprunar, 1988 b). However, in shell morphology, some of patellogastropods (Lepetidae and Lottiidae) have a bilaterally symmetrical relationship between protoconch and teleoconch throughout ontogeny (Figs. 15, 21), although their soft parts are asymmetrically twisted. Therefore, it is clear that torsion of the visceral mass and asymmetry of protoconch and teleoconch are independent at least in the case of Patellogastropoda. Independence of torsion and shell coiling is also evidenced by the wide variety of coiling directions (from orthostrophic to hyperstrophic) in paucispiral protoconchs produced by similarly torted animals.

2. Correlations with Reproductive Biology

Effect of benthic vs. pelagic development on protoconch morphology: The mode of reproduction and spawning of archaeogastropods can be divided into several basic types (Table 7). Because the protoconch morphology is known to be affected by the ecological differences in reproductive and developmental strategies in Caenogastropoda (e.g. Lima and Lutz, 1990), it is important to discuss the relationships between morphotypes and ecological phenomena. In archaeogastropods, larvae are in most cases pelagic, but benthic development (=ecological definition of "direct development" by Thorson, 1950) has been reported in the following groups.

(1) *Benthic egg mass:* Larval development occurs within gelatinous egg masses in *Margarites, Lirularia* and *Cantharidus* (Amio, 1963; Hadfield and Strathmann, 1990; Ming and Sung, 1994). They deposit an egg mass, but its fertilization is still external. Larvae develop within the thick coating of the egg mass. Nevertheless, their protoconch morphology cannot be distinguished from those of species with pelagic development. These instances strongly indicate that developmental mode (pelagic or benthic) does not influence the morphology of the protoconch.

(2) *Brooding:* Benthic development by brooding is known to occur among various archaeogastropods, especially in small-sized species of higher latitudes and of the deep-sea (Thorson, 1965; Hickman, 1992). Fertilization takes place within the pallial cavity, and larvae spend their entire developmental process there until they emerge at the crawling juvenile stage. (i) In Patellogastropoda, species of *Erginus* and *Rhodopetala* (Lottiidae) are known to brood (Thorson, 1935; Golikov and Kussakin, 1972; Lindberg, 1979: this study). The protoconch of *Erginus* formed in the brooding pouch of the pallial cavity is greatly modified from the general patterns of other Patellogastropoda in form and sculpture (Figs. 72 a, b). In this case, the changes in form and sculpture may be attributable to brooding habit, because similar modification is not

Table 7. Basic modes of reproduction and development in "Archaeogastropoda" (excluding specialized deep-sea and terrestrial taxa).

Fertilization	Spawning	Development	
internal	egg capsule	pelagic	planktotrophic
external	broadcast		non-planktotrophic (lecithotrophic)
	benthic egg mass	benthic	
	brooding		

found in non-brooded patellogastropods. (ii) In Vetigastropoda, brooding is known in *Larochea* of Scissurellidae (Marshall, 1993 b), *Clanculus, Margarites, Arene, Muditia*, and *Tricolia* of Trochoidea (Robertson, 1985, table 7). However, these protoconchs do not differ dramatically in morphology compared to those of closely related, non-brooding species. (iii) In "Cocculiniformia," brooding is found in Cocculinidae and Pseudococculinidae (Haszprunar, 1988 d), Bathyphytophilidae (Moskalev, 1978), and *Lepetella* (Warén, 1972; Dantart and Luque, 1994). Among these, the existence of brooding protection also cannot be detected from protoconch morphology.

According to the above examples, protoconch morphology is, in general, not affected by differences in life position during the larval stages. Thus, similarities in protoconch morphology can be assumed to reflect phylogenetic relationships in Archaeogastropods.

Protoconchs I and II: In "higher" gastropods, it is well accepted that a clear demarcation of sculpture at the boundary between protoconch I (PI) and protoconch II (PII) reflects a difference between planktotrophic and non-planktotrophic development (the so-called "apex theory") (Thorson, 1950; Shuto, 1974; Jablonski and Lutz, 1983; Lima and Lutz, 1990). Generalization for the relationship between protoconch features and reproductive strategies is summarized as follows (Hadfield and Strathmann, 1990; Hickman, 1992): (1) Species with planktotrophy have a small PI derived from a small egg. Their protoconchs have high spired multispiral whorls, on which an abrupt change of sculpture occurs at the PI/PII boundary. In Caenogastropoda, sinusigeral notch is often developed at apertural margin of PII (Bandel, 1975). (2) Species with non-planktotrophy (lecithotrophy, benthic development, and ovoviviparity) have a large protoconch (mostly PI) derived from a large egg, consisting of paucispiral whorls without distinctive sculpturing. Therefore, initial size, number of volutions, and presence or absence of the demarcation are used as criteria to distinguish planktotrophic and non-planktotrophic mode of development.

In archaeogastropods, definite planktotrophic development has been verified only in aquatic neritopsines (Bandel, 1982; Robertson, 1985; Hickman, 1992). Non-planktotrophy is also anatomically indicated by the absence of the larval feeding organ, or metatroch (=post-oral ciliary band), and the ciliated food groove (Fretter and Graham, 1962; Hickman, 1992). Therefore, a dichotomy seems to hold between planktotrophic neritopsines and non-planktotrophic non-neritopsines within archaeogastropods. If this is true, the presence or absence of planktotrophy (and PII) is constrained phylogenetically in the case of archaeogastropods. Thus, the difference between multispiral (with PII) and paucispiral (without PII) protoconchs represents a phylogenetically essential character for archaeogastropods.

3. Evolution of Protoconch Characters

Protoconchs of outgroups: The formation of protoconch by shell gland is one of the manifest synapomorphies of Conchifera (Wingstrand, 1985: 51). It is therefore very important for the inference of ancestral state of gastropod protoconch to compare the protoconch morphology among conchiferan classes. (i) Tryblidiida has a circularly cap-shaped protoconch (Warén, 1988, 1992). (ii) Protoconch of Scaphopoda is elongated, tubular and longitudinally symmetrical (Engeser *et al.*, 1993; Steiner, 1995). Right and left parts are distinguished by a longitudinal suture. (iii) Prodissoconch of Bivalvia greatly differs in paired condition from protoconch of other molluscs, but each of two valves is symmetrically shield-like (e.g. Waller, 1981). (iv) *Nautilus* has symmetrically cap-shaped embryonic shell. The central part of the surface is marked by depressions called "cicatrix" (Arnold *et al.*, 1987; Tanabe and Uchiyama, 1997). Thus, the comparison among outgroups reveals that at least symmetrical protoconch is a general pattern of conchiferan molluscs except for most gastropods.

Is protoconch asymmetry original or secondary?: Golikov and Starobogatov (1975) and Lindberg (1981 c, 1988 a) regarded that Patellogastropoda evolved from a conchologically coiled ancestor based on the asymmetrical growth pattern of the early teleoconch of *Patella* in which the protoconch is rotated by 20

degrees to the anterior-posterior axis of the teleoconch. SEM observations by Robson (1986) revealed that the somewhat sinistral appearance in the initial teleoconch of *Patella* (Smith, 1935: fig. 27) is caused by allometric growth of the apertural margin. This seemingly sinistral shell is, in fact, dextrally hyperstrophic shells produced by anatomically dextral animals. However, asymmetrical growth of the early teleoconch is not a general pattern in Patellogastropoda, but is very clear only in Patellidae (though the state of Nacellidae is unknown). The protoconch is almost symmetrically located in Lepetidae (Fig. 15), Lottiidae (Fig. 21), and Neolepetopsidae (McLean, 1990 b). This means that the coiled state in early teleoconch as in *Patella* is not necessarily regarded as original.

Meanwhile, Haszprunar (1988 b) speculated that the gastropod archetype was a primarily symmetrical limpet ("primary limpet") like Patellogastropoda, so that helical coiling of most gastropod shells is a derived state. However, I regard that evolution of shell symmetry should be considered separately in regarding the protoconch and teleoconch. Concerning protoconch, outgroup comparison suggests the presence of a symmetrical protoconch in a gastropod ancestor independent of asymmetrically torted viscera, as is found in extant Patellogastropoda. On the other hand, variations in the degree of symmetry observed in early teleoconchs of Patellogastropoda mean that both coiled and uncoiled states were possible in the teleoconch of the gastropod ancestor. Thus, these facts indicate that a primitively symmetrical protoconch is likely, but the coiling direction of the ancestral teleoconch is not determinable.

Evolutionary processes in archaeogastropod protoconchs: The taxonomic distribution of protoconch morphotypes (Fig. 107, Table 6) and inferred phylogeny (Fig. 104) suggest that the protoconch morphology of archaeogastropods are determined rather rigidly by phylogeny --- (i) symmetrically uncoiled type in Patellogastropoda clade, (ii) paucispiral type in "non-neritopsine Rhipidoglossa" clade, (iii) multispiral type in aquatic groups of Neritopsine clade, and (iv) globular type in terrestrial groups of Neritopsine clade. Among them only multispiral type of protoconch is produced by planktotrophic larvae.

Concerning the evolutionary pathways of protoconch characters, two ways of reconstruction are possible based on the inferred phylogenetic relationships: (i) Ancestral gastropods were non-planktotrophic, and bipartite protoconchs with planktotrophy evolved independently in Neritopsine and Caenogastropoda (at least two apomorphic changes). (ii) Ancestral gastropods were non-planktotrophic, and ancestral Orthogastropoda evolved planktotrophy from this. Non-planktotrophy was re-acquired in non-neritopsine Rhipidoglossa and some Caenogastropoda (single apomorphic change and more than two reversals).

These opposing views are equally plausible. The former case becomes more likely, if emphasis is placed on sculptural similarities between protoconchs of patellogastropods and non-neritopsine Rhipidoglossa (as plesiomorphic) and on structural differences between neritopsine and caenogastropod protoconchs (as apomorphic). In this view, the following scenario can be presented for the evolution of protoconchs in "Archaeogastropoda." (i) The symmetrically uncoiled protoconch of Patellogastropoda evolved from the symmetrically cap-shaped protoconch as in outgroups. (ii) Subsequently, protoconch morphology become paucispially coiled by asymmetrical mechanical deformation, as is observed in the "non-neritopsine Rhipidoglossa" clade. (iii) Finally, the paucispirally coiled protoconch was independently modified into the multispiral form in Neritopsina and in Caenogastropoda, as a result of accretionary shell growth of Protoconch II during the pelagic feeding veliger stage.

Recently, the independent origin of planktotrophy between Neritopsina and Caenogastropoda has also been proposed by Haszprunar (1995) and Ponder and Lindberg (1997) based on different hypotheses on phylogeny. However, this conclusion presented here and by previous studies is still dependent on insufficient quantity and quality of data on archaeogastropod development. To test this hypothesis in more detail, more extensive observations are needed on larval morphology of various groups. At this point, evolution in gastropod protoconchs can be summarized by an initial change from symmetrical to asymmetrical form and a subsequent modification from paucispiral to multispiral form.

VI. Conclusions

1. Anatomical descriptions in this study especially focused on three-dimensional morphological data at the gross and SEM levels. As a result, a number of new characters were revealed in the buccal apparatus and other organs. These characters clearly show discrete states and distinct taxonomic distribution, suggesting potential for contributing toward resolving phylogeny. Thus, some of the vast gaps in gastropod anatomy have been filled by the descriptions in this study.

2. Character tracings on the cladogram resulted in "acceptable" changes in some characters, but "implausible" transformations in others. One example is the change in most pallial characters from unpaired to paired conditions. Although this pattern is opposite to the traditional view, there is no positive theoretical reason why the symmetry of gastropod organs should be assumed absolutely irreversible. In any case, assumptions of homology should be reconsidered, as with any homoplastic result.

3. Other major aspects of gastropod evolution are represented by transformations from complex to simple, from opened to closed, or from weakly organized to well-organized conditions (especially in digestive, reproductive, and nervous system). These share the common feature that primitively intricate conditions are elaborated into functionally sophisticated, compact forms through re-organization.

4. Among shell characters, protoconch morphotypes are relatively consistent with the phylogeny inferred from soft parts. This is in clear contrast to the general observation that macroscopic characters of the gastropod teleoconch are less useful to higher-level phylogeny. More extensive studies should be made relative to larval anatomy and reproductive biology.

5. For future works, microstructural investigations will increase in importance not only in anatomical descriptions but also in conchological and paleontological research. Anatomical observations should also be extended to the larval stages of various taxa in terms of ontogeny and phylogeny or heterochrony. Progress toward better understanding of molluscan evolution can be achieved by a rich accumulation of high-quality data, as well as technical advances in analytical methodology.

VII. Acknowledgments

VIII. References

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Appendix: Diagnostic Characters of Archaeogastropod Subgroups

Order PATELLOGASTROPODA Lindberg, 1986

Diagnostic characters: 1) anteriorly pointed shell apex, 2) symmetrical protoconch, 3) shallow pallial cavity restricted to head region, 4) operculum absent in post-larval stage, 5) horseshoe-shaped shell muscle that is constricted into bundles and connected anteriorly by pallial muscle, 6) shell muscle penetrated by blood vessels from visceral sinus, 7) retractile pallial tentacles, 8) eyes within cephalic tentacles, 9) open eyes without vitreous body, 10) symmetrically paired osphradia of "wart-organ" type on pallial floor (absent in Lepetidae, Acmaeidae, and Neolepetopsidae), 11) ctenidium post-torsional left only (in Acmaeoidea), 12) ctenidium (if present) lacking skeletal rods, 13) hypobranchial gland absent, 14) secondary circumpallial gills (in Patelloidea and some lottiids), 15) single bilamellate, double-layered jaw, 16) anterior wings of jaw associated with inner lips, 17) posterior wings of jaw bound to odontophore, 18) licker well-developed, 19) dorsal protractor muscles of odontophore present, 20) ventral approximator muscle of odontophore cartilages two-layered, 21) transverse labial muscles present, 22) docoglossate (=stereoglossate) radula that is longitudinally inflexible on bending plane, 23) greatly reduced or completely lost central tooth, 24) lateral teeth with broad bases firmly fixed on basal plates (except Lepetidae and Neolepetopsidae), 25) mid-esophagus with lamellar folds, 26) simplification of stomach (loss of gastric shield and gastric caecum; reduction of sorting area), 27) single auricle, 28) rectum not passing through pericardium or ventricle, 29) muscular bulbous aorta within pericardium, 30) two unequal kidneys (smaller left and much larger right), 31) gonoduct extending from left side and connected to right kidney, 32) labial ganglia interconnected by labial commissure, and 33) statocysts on outer sides of pedal ganglia.

Included taxa: Patellina von Ihering, 1876, and Lepetopsina McLean, 1990.

Suborder PATELLINA von Ihering, 1876

Diagnostic characters: 1) radular teeth articulation absent, and 2) radula mineralized with magnetite.

Included taxa: Patelloidea Rafinesque, 1815; Lepetoidea Dall, 1869; and Acmaeoidea Forbes, 1850. Lindberg (1988 a, c) assumed paedomorphic trends within Patellogastropoda from Patellidae to Lottiidae: (i) reduction of body size, (ii) reduction in number of radular teeth, (iii) reduction in complexity of gut, and (iv) evolution of reproductive trait from K- to r-strategist. Similarly, the radular teeth show trends from thin complex to thick simple basal plates, and from broad to narrow marginal field (Lindberg, 1986 a).

Superfamily PATELLOIDEA Rafinesque, 1815

Diagnostic characters: 1) long circumpallial tentacles, 2) anterior pallial streaks present, 3) osphradia present, 4) 3 major odontophoral cartilages (anterior, anterolateral, and posterior pairs), 5) pluricuspid lateral teeth, 6) licker lamellate, 7) basal plates complexly sculptured, 8) marginal field of radula broad, 9) retractor muscles of subradular membrane ventrally fused, 10) median protractor muscles of subradular membrane asymmetrical, and 11) median tensor and retractor muscles of radular sac present.

Included taxa: Patellidae Rafinesque, 1815, and Nacellidae Thiele, 1891. Lindberg (1988 a) and Lindberg and Hedegaard (1996) considered an independent lineage for Patellidae within Patellogastropoda because of the absence of an outermost prismatic shell layer. However, a monophyletic relationship between Nacellidae and Acmaeoidea (Suborder Nacellina Lindberg, 1988) is not anatomically supported in this

study, and therefore, the superfamily Patelloidea are here re-defined to include Patellidae and Nacellidae. Two families are united by many synapomorphies listed above.

Family Patellidae Rafinesque, 1815

Diagnostic characters: 1) 4–6 shell layers composed of crossed-foliated, crossed-lamellar and/or complex crossed-lamellar structures [=MacClintock's (1967) groups 6–10], 2) circumpallial gills continuous anteriorly, 3) anterior and lateral pallial streaks present, 4) radula formula 3–(1+2)–1/0–(2+1)–3, 5) at least 3 pairs (anterior+posterior+anterolateral) of odontophoral cartilages, 6) two pairs of long salivary ducts (in *Patella*), 7) gut configuration simple to complex, and 8) efferent pallial vessel left only.

Included taxa: Patella Linnaeus, 1758, and *Helcion* Montfort, 1810. The central tooth was reported as lost in British species of *Patella* (Jones *et al.*, 1984) but it is clearly present in Japanese species (Sasaki *et al.*, 1994).

Family Nacellidae Thiele, 1891

Diagnostic characters: 1) 4 shell layers (prismatic+foliated+myostracal+foliated) in *Nacella* [= MacClintock's (1967) group 11] or 5 shell layers (prismatic+foliated+crossed-lamellar+myostracal+foliated) in *Cellana* [=MacClintock's (1967) groups 12–14], 2) circumpallial gills interrupted anteriorly, 3) anterior pallial streak present, but lateral pallial streak absent, 4) radular formula 3–2–1–2–3, 5) labial cartilages in addition to 5 pairs (anterior+posterior+anterolateral+ventrolateral+posterodorsal) of odontophoral cartilages, 6) single pair of long salivary ducts, 7) gut configuration complex, and 8) characteristic pathways of efferent pallial vessels entering pericardium from both right and left sides independently.

Included taxa: Cellana H. Adams, 1869, and *Nacella* Schumacher, 1817.

Superfamily LEPETOIDEA Dall, 1869
Family Lepetidae Dall, 1869

Diagnostic characters: 1) 5 shell layers (prismatic+foliated+crossed-lamellar+myostracal+crossed-lamellar) [=MacClintock's (1967) group 15], 2) circumpallial tentacles greatly reduced, 3) pallial streaks absent, 4) oral lappets present, 5) ctenidium and secondary gills absent, 6) osphradia and osphradial ganglia absent, 7) radular formula 2–0–1–0–2 with fusion of central and lateral into single complex, 8) basal plates absent, 9) 2 pairs (anterior and anterolateral) of odontophoral cartilages, 10) obliquely tubular salivary glands without duct, and 11) gut configuration complex.

Included taxa: Lepeta Gray, 1847; *Bathylepeta* Moskalev, 1977; *Iothia* Forbes, 1849; *Limalepeta* Moskalev, 1977; *Maoricrater* Dell, 1956; *Cryptobranchia* Middendorff, 1851; *Propilidium* Forbes and Hanley, 1849; and *Sagamilepeta* Okutani, 1987 (Vaught, 1989). Genera are defined primarily on radular characters (Moskalev, 1977; Okutani, 1987). Anatomy of *Lepeta, Iothia* and *Propilidium* was summarized by Angerer and Haszprunar (1996).

This family has been allocated to the superfamily Acmaeoidea together with Acmaeidae and Lottiidae (Lindberg, 1988 a; Lindberg and Hedegaard, 1996), but anatomical characters do not support their monophyly. Because pallial and radular characters (ctenidium, central tooth, and basal plates) support clear separation from "Acmaeidae plus Lottiidae," this family is here treated as independent superfamily.

Superfamily ACMAEOIDEA Forbes, 1850

Diagnostic characters: 1) short circumpallial tentacles, 2) pallial streaks absent, 3) ctenidium present, 4) radular formula typically 2/1/0–3–0–3–2/1/0, 4) well-developed, simple basal plates, 5) simple licker, and 6) 2 pairs (anterior and anterolateral) of odontophoral cartilages.

Included taxa: Acmaeidae Forbes, 1850, and Lottiidae Gray, 1840.

Family Acmaeidae Forbes, 1850

Diagnostic characters: 1) 5 shell layers (prismatic + foliated + crossed-lamellar + myostracal + crossed-lamellar) in *Acmaea* and *Pectinodonta* (Lindberg and Hedegaard, 1996) [=MacClintock's (1967) group 15], 2) oral lappets present, 3) osphradium absent, 4) radular formula 0–3–0–3–0 (Acmaeinae) or 0–1–0–1–0 (Pectinodontinae) with 3 basally fused cusps, 5) radula arranged in inverted-V configuration, 6) well-developed basal plates with anteriorly projected outer corner, 7) obliquely tubular salivary glands without ducts, and 8) gut configuration complex.

Included taxa: Members are allocated to two subfamilies (Marshall, 1985 b; Lindberg, 1986 b): (1) **Acmaeinae Forbes, 1850** (*Acmaea* Eschscholtz, 1833), and (2) **Pectinodontinae Pilsbry, 1891** (*Pectinodonta* Dall, 1882; *Cerradonta* Okutani, Tsuchida, and Fujikura, 1992; and *Bathyacmaea* Okutani, Tsuchida, and Fujikura, 1992). *Niveotectura*, that has been placed in Lottiidae, is anatomically more closely related to the members of this family in view of pallial character (absence of osphradium), gut morphology (salivary glands and complexly folded stomach), and a radula especially similar to *Acmaea mitra* (Habe, 1944).

Family Lottiidae Gray, 1840

Diagnostic characters: 1) osphradia present, 2) radular formula 0/1/2–3–0–3–2/1/0, 3) radular teeth in stepped configuration (except *Rhodopetala* and *Erginus*), 4) a pair of long salivary ducts, 5) stomach C-shaped, and 6) 4 intestinal loops.

Included taxa: Three subfamilies are defined mainly on the basis of shell structure and radular characters (MacClintock, 1967; Ponder and Creese, 1980; Lindberg, 1981 a, b, 1986 b, 1988 a, b, 1990; Lindberg and McLean, 1981; Lindberg and Vermeij, 1985; Sasaki and Okutani, 1993 a, b, 1994 a, b).

(1) **Rhodopetalinae Lindberg, 1981** (*Rhodopetala* Dall, 1921): 1) shell composed of 5 layers (prismatic + foliated + crossed-lamellar + myostracal + complex crossed-lamellar) [=MacClintock's (1967) group 12], and 2) radular formula 0–3–0–3–0.

(2) **Patelloidinae Chapman and Gabriel, 1923** (*Patelloida* Quoy and Gaimard, 1834 and *Potamacmaea* Peile, 1922): 1) shell consisting of 4 layers (prismatic + crossed-lamellar + myostracal + crossed-lamellar) [=MacClintock's (1967) group 2], 2) radular formula 2–3–0–3–2, and 3) well-developed, spoon-like marginal teeth. Inclusion of *Erginus* Jeffreys, 1877 (=*Problacmea* Golikov and Kussakin, 1972) and *Niveotectura* Habe, 1944 within this subfamily is suggested by characters of shell structure but anatomically problematic.

(3) **Lottiinae Gray, 1840:** 1) fibrous structure present, 2) radular formula 0/1–3–0–3–0/1, and 3) marginal teeth vestigial, lost ontogenetically, or totally absent. Circumpallial secondary gills developed independently in some species of *Lottia*, *Scurria*, and *Tectura* within this subfamily (McLean and Lindberg, 1981; Lindberg, 1988 a: fig. 2). Based on a difference in shell structure, this subfamily can be divided into three groups: (i) Lotiiini (*Lottia* Gray, 1833; *Tectura* 1847; and *Nipponacmea* Sasaki and Okutani, 1993) with 5 shell layers (thin prismatic + thick fibrous + crossed-lamellar + myostracal + crossed-lamellar) [=MacClintock's (1967) group 1]; (ii) Scuriini (*Scurria* Gray, 1847 and *Disscurria* Lindberg, 1986) with 5 shell layers (thick prismatic + thin fibrous + crossed-lamellar + myostracal + crossed-lamellar) [=MacClintock's (1967) group 3]; and (iii) "*Notoacmea*-group" (e.g. *Notoacmea*, Iredale, 1915 and *Atalacmea* Iredale, 1915) with 6 shell layers (prismatic + fibrous + crossed-lamellar + crossed-lamellar + myostracal + crossed-lamellar) [=MacClintock's (1967) groups 4+5].

Suborder LEPETOPSINA McLean, 1990

Diagnostic characters: 1) articulation of radular teeth, and 2) non-mineralized radula.

Included taxa: Lepetopsoidea McLean, 1990

Superfamily LEPETOPSOIDEA McLean, 1990
Family Neolepetopsidae McLean, 1990

Diagnostic characters (based mainly on *Eulepetopsis*): 1) foliated structure present, 2) circumpallial tentacles short, 3) oral lappets present, 4) eyes absent, 5) anterior pallial streaks present, 6) ctenidium absent, 7) osphradium absent, 8) 3 pairs of odontophoral cartilages, 9) radular formula $2-(1+2)-1-(2+1)-2$, 10) central tooth well-developed, 11) absence of basal plates in radula, 12) salivary glands present, 13) mid-esophagus not affected by torsion, 14) stomach C-shaped, and 15) 3 intestinal loops.

Included taxa: The extant members include three genera: *Neolepetopsis* McLean, 1990; *Eulepetopsis* McLean, 1990; and *Paralepetopsis* McLean, 1990. These limpets were previously called "hot-vent group-C" (Hickman, 1983) or "symmetrical limpets" (McLean, 1985 b). Anatomical descriptions were given by Fretter (1990) and McLean (1990 b).

Order VETIGASTROPODA Salvini-Plawen, 1980

Diagnostic characters: 1) columnar nacreous structure (except Lepetodriloidea, Fissurelloidea, Scissurellidae, Tricoliinae, Phasianellinae, Halistylinae, and Skeneidae), 2) micropapillae on tentacles (except Pleurotomarioidea, Fissurelloidea and Lepetodriloidea), 3) epipodial tentacles, 4) epipodial sense organs, 5) ctenidial axes attached by afferent and efferent membranes to mantle skirt (except Pleurotomariidae and Haliotidae lacking afferent membrane), 6) ctenidial axes and lamellae both with skeletal rods, 7) bursicles on efferent side of ctenidial leaflets (except *Mikadotrochus* and *Lepetodrilus*), 8) osphradium(-a) on efferent ctenidial membrane, 9) paired hypobranchial glands, 10) fimbriate anterior edge of jaws (except some trochoids), 11) posterior depressor muscles of odontophore, 12) radular formula typically $n-5-1-5-n$, 13) posterior retractor muscles of radular sac present (except *Anatoma* and *Lepetodrilus*), 14) ramified salivary glands with longitudinal slit-like openings to buccal cavity (except *Lepetodrilus*), 15) salivary ducts absent, 16) expanded esophageal pouches with papillate glands, 17) spiral gastric caecum (reduced in limpet form), 18) rectum penetrating ventricle, 19) paired auricles, 20) two kidneys of different structure and function, 21) left kidney modified into papillary sac (degenerated in Fissurellidae), 22) gametes released through right kidney, 23) labial ganglia and commissure absent, 24) scalariform pedal cords, and 25) statocysts on anterodorsal sides of pedal ganglia.

Included taxa: Zeugobranchia von Ihering, 1876 (Pleurotomarioidea Swainson, 1840; Haliotioidea Rafinesque, 1815; Fissurelloidea Fleming, 1882; and Scissurelloidea Gray, 1847) and Trochoidea Rafinesque, 1815; Lepetodriloidea McLean, 1988; and Seguenzioidea Verrill, 1844.

Superfamily PLEUROTOMARIOIDEA Swainson, 1840
Family Pleurotomariidae Swainson, 1840

Diagnostic characters: 1) pallial tentacles absent, 2) papillate oral disk, 3) open eyes with vitreous body, 4) eye stalks absent, 5) cephalic lappets absent, 6) epipodial flaps with numerous epipodial sense organs, 7) tentacles non-papillate, 8) afferent ctenidial membrane absent, 9) bursicles present in *Perotrochus* (Haszprunar, 1987 c) but absent in *Mikadotrochus*, 10) accessory pair of hypobranchial glands present, 11) uncuticularized jaws, 12) radular formula $(6-10+n+11-21)+(24-26+3-4)+1+(3-4+24-26)+(11-21+n +6-10)$ (Hickman, 1984 c), 13) asymmetrical arrangement of radular teeth (direction of skewness infraspecifically variable), 14) asymmetrical central tooth, 15) smaller inner laterals and larger outer laterals ("lamellate teeth"), 16) three types of teeth in marginal field, i.e. sickle-shaped teeth, filament-tipped teeth (so-called bristle teeth representing "hystricoglossate" condition of Hyman, 1967), and paddle-shaped teeth (Hickman, 1984 c), 17) voluminous U-shaped stomach, 18) multispiral gastric caecum, 19) enlarged urogenital papilla, and 20) visceral loop originating from cerebropleural connectives (not from pleural ganglia).

Included taxa: *Entemnotrochus* Fischer, 1885; *Mikadotrochus* Lindholm, 1927; and *Perotrochus*

Fischer, 1885.

Superfamily HALIOTOIDEA Rafinesque, 1815
Family Haliotidae Rafinesque, 1815

Diagnostic characters: 1) shell with several holes, 2) three pallial tentacles, 3) open eyes with vitreous body, 4) eye stalks present, 5) cephalic lappets present, 6) enlarged right and thin left shell muscles, 7) circumpedal epipodial tentacles, 8) tentacles papillate, 9) afferent ctenidial membrane absent, 10) asymmetrical disposition of central tooth, 11) outermost lateral teeth not enlarged, 13) stomach U-shaped, 14) multispiral gastric caecum, and 15) urogenital papilla not enlarged.

Included taxa: Haliotis Linnaeus, 1758, and thirteen subgenera (or genera) (Vaught, 1989).

Superfamily FISSURELLOIDEA Fleming, 1882

Diagnostic characters: 1) nacreous layer absent, 2) pallial tentacles absent, 3) cephalic lappets absent, 4) tentacles non-papillate, 5) hypobranchial gland lying around mantle-slit/hole area (or absent), 6) greatly reduced left kidney (but same histology as papillary sac of other Vetigastropoda; Andrews, 1985), 7) presence of anal gland (Haszprunar, 1989 a), and 8) gonoduct opening into right renopericardial duct, not directly into right kidney.

Included taxa: Fissurellidae Fleming, 1822, and Clypeosectidae McLean, 1989. Their diagnostic characters were given by McLean (1989 b) and Haszprunar (1989 a).

Family Fissurellidae Fleming, 1822

Diagnostic characters: 1) shell pores formed by canal structure (Reindl and Haszprunar, 1994, 1996), 2) mantle margin three-folded (Stasek and McWilliams, 1973) in contrast to the general gastropod two-folded scheme, 3) closed eyes, 4) eye stalks present, 5) unique hook-shaped termination of shell muscle present in Emarginulinae, but absent in Fissurellinae (e.g. MacClintock, 1963; McLean, 1984 a), 6) many triangular epipodial tentacles (vestigial in *Macroschisma*), 7) epipodial sense organs at ventral sides of epipodial tentacles, 8) radula strikingly asymmetrical (direction of skewness variable among genera; Hickman, 1981; Herbert and Kilburn, 1986), 9) asymmetrical attachment of teeth, 10) outer lateral teeth enlarged, 11) well-developed lateromarginal plates, 12) stomach pyriform, 13) gastric caecum short, crescent-shaped, and 14) pedal cord exposed on pedal musculature and connected by thick median commissure.

Included taxa: This family is often divided into two subfamilies based on characters of shell slit/hole, shell muscle, and radula (Thiele, 1929; McLean, 1984 a, b; McLean and Kilburn, 1986; Herbert and Kilburn, 1986). In other classifications, Diodorinae Wenz, 1938, is sometimes separated from Emarginulinae (e.g. Knight *et al.*, 1960). However, such a distinction is not justified, because no prominent difference is found at least in the following shell and radular characters.

(1) **Emarginulinae Gray, 1834**: 1) selenizone formed, 2) shell muscle with hook-shaped inward process, 3) central tooth rhomboidal, and 4) enlarged fifth laterals bicuspid.

(2) **Fissurellinae Fleming, 1822**: 1) selenizone absent, 2) shell muscle lacking inward process, 3) central tooth tapered at the tip, and 4) enlarged fifth laterals with four cusps.

Family Clypeosectidae McLean, 1989

Diagnostic characters: 1) shell muscle without hook-shaped process, 2) eyes absent, 3) epipodial tentacles 3 pairs in *Clypeosectus* and 4 pairs in *Pseudorimula,* 4) radular formula n + (5–9) + 1 + (5–9) + n (laterals 6–9 pairs in *Clypeosectus*, 5 pairs in *Pseudorimula*), 5) radular teeth symmetrical, 6) outer lateral teeth not enlarged, 7) seminal vesicle present, 8) prostate present, 9) ciliated genital process at base of right cephalic tentacle and ciliated band along right neck present both in male and female of *Clypeosectus*, but ab-

sent in *Pseudorimula*, and 10) receptaculum seminis on right side present in female of *Clypeosectus*, but absent in *Pseudorimula*.

Included taxa: *Clypeosectus* McLean, 1989, and *Pseudorimula* McLean, 1989. Anatomical descriptions were given by Haszprunar (1989) and McLean (1989 b; 1992 c).

Superfamily SCISSURELLOIDEA Gray, 1847
Family Scissurellidae Gray, 1847

Diagnostic characters: 1) pallial tentacle present, 2) mantle edge papillate, 3) eye closed (or absent), 4) very short eye stalks, 5) cephalic lappets absent, 6) several pairs (usually 3–4) of epipodial tentacles: "single pair of separated epipodial sense organs (ESO) tentacles or several ESO-tentacles alone (Haszprunar, 1989 a)," 7) tentacles papillate or non-papillate, 8) two bi- or monopectinate ctenidia or single monopectinate ctenidium (Larocheinae), 9) radular formula $n+(2-5)+1+(2-5)+n$, 10) symmetrical radula, 11) central tooth with large broad base, 12) outer lateral teeth enlarged or not, 13) lateromarginal plate absent, and 14) short gastric caecum.

Included taxa: Anatomy has been described in *Incisura lytteltonensis* (*fide* Bourne, 1910), *Anatoma crispata* (*fide* Fretter and Graham, 1976), *Anatoma yaroni* (*fide* Herbert, 1986), and *Anatoma* sp. (this study). Diagnoses of subfamilies have been given by Herbert (1986), McLean (1989), and Marshall (1993 b).

(1) **Larocheinae Finley, 1927** (*Larochea* Finlay, 1927, and Larocheopsis Marshall, 1993): 1) shell without anal slit or foramen; inner lip of shell enlarged to form brood chamber in females, 2) inoperculate, 3) right subpallial cavity utilized as brood pouch, 4) cephalic and epipodial tentacles non-papillate, 5) radular formula $n-5-1-5-n$, with fifth lateral enlarged, and 6) single left monopectinate ctenidium.

(2) **Scissurellinae Gray, 1847** (*Scissurella* d'Orbigny, 1824; *Incisura* Hedley, 1904; and *Sinezona* Finlay, 1927): 1) shell with slit (in *Scissurella* and *Inscisura*) or foramen (in *Sinezona*), 2) radular formula $n-5-1-5-n$, with enlarged fifth lateral tooth, 3) cephalic and epipodial tentacles papillate, and 4) ctenidia bipectinate.

(3) **Anatominae McLean, 1989** (*Anatoma* Woodward, 1859, and Sukashitrochus Habe and Kosuge, 1964): 1) shell with unclosed slit (in *Anatoma*) or closed forming foramen at maturity (in *Sukashitrochus*), 2) open umbilicus, 3) papillate cephalic and epipodial tentacles, 4) paired mono- or bipectinate ctenidia, and 5) radular formula $n-5-1-5-n$, with enlarged fifth lateral.

(4) **Temnocinclinae McLean, 1989** (Temnocinclis McLean, 1989, and Temnozaga McLean, 1989): 1) nearly symmetrical subpatelliform, with long slit and selenizone, 2) multispiral operculum, 3) radular formula $n-3-1-3-n$, without enlarged outer lateral teeth, 4) paired monopectinate ctenidia, 5) non-papillate cephalic and epipodial tentacles, 6) 3 pairs (in *Temnociclis*) or 4 pairs (in *Temnozaga*) of epipodial tentacles, and 7) eyes absent.

(5) **Sutilizoninae McLean, 1989** (*Sutilizona* McLean, 1989): 1) asymmetrical limpet form with long slit that is closed at maturity, 2) radular formula $n-2$ $(-4?)-1-2$ $(-4?)-n$, without enlarged outer lateral teeth, 3) paired monopectinate ctenidia, 4) one pair of posterior epipodial tentacles, 5) non-papillate cephalic and epipodial tentacles, and 6) eyes absent.

Superfamily TROCHOIDEA Rafinesque, 1815

Diagnostic characters: 1) cephalic lappets present, 2) open eyes on eye stalks, 3) inhalant (left) and exhalant (right) neck lobes, 4) several (typically four) pairs of epipodial tentacles, 5) tentacles with sensory micropapillae, 6) right ctenidium absent, 7) transverse pallial vein present, 8) radular formula $n-5-1-5-n$ (except some subfamilies, e.g. Trochaclidinae and Thysanodontinae), 9) protolateromarginal plates formed by extension of bases of innermost marginal teeth, 10) outer lateral teeth not greatly enlarged, 11) food-

collecting groove in marginal field, and 12) multispiral gastric caecum (except *Broderipia*).

Included taxa: Turbinidae Rafinesque, 1815; Trochidae Rafinesque, 1815; and Skeneidae Clark, 1851. Turbinidae and Trochidae are distinguished by (i) presence or absence of secondary cusps or attachment flap and (ii) length of growing edge of operculum (Hickman and McLean, 1990). Subgroups are classified by characters of snout (outer lip, pseudoproboscis), cephalic lappets, neck lobes, epipodium, epipodial tentacles, ctenidium (afferent and efferent membrane, bursicles, free tip), and radular morphology (base, attachment, shaft, cusp asymmetry, relative size to other teeth, and presence or absence of extension at base, etc.) (Hickman and McLean, 1990; Hickman, 1996).

Family Trochidae Rafinesque, 1815

Diagnostic characters: 1) growing edge of operculum long, and 2) secondary cusp or attachment flap on central tooth present.

Included taxa: 9 subfamilies in 4 informal groups: (1) "Liotiinae Adams and Adams, 1854+Angariinae Thiele, 1921," (2) "Moelleriinae Hickman and McLean, 1990+Colloniinae Cossmann, 1916," (3) "Prisogasterinae Hickman and McLean, 1990+Turbininae Rafinesque, 1815," and (4) "Gabrieloninae Hickman and McLean, 1990+Tricoliinae Woodring, 1928+Phasianellinae Swainson, 1840" (Hickman and McLean, 1990).

Family Turbinidae Rafinesque, 1815

Diagnostic characters: 1) growing edge of operculum short, and 2) secondary cusp or attachment flap on central tooth absent.

Included taxa: 10 subfamilies in 3 informal groups and 3 subfamilies of uncertain affinity: (1) "Tegulinae Kuroda, Habe, and Oyama, 1971+Eucyclinae Koken, 1897+Margaritinae Stoliczka, 1868," (2) "Trochinae Rafinesque, 1815+Stomatellinae Gray, 1840+Calliostomatinae Thiele, 1924+Solariellinae Powell, 1951," (3) "Halistylinae Keen, 1958+Lirulariinae Hickman and McLean, 1990+Umboniinae Adams and Adams, 1854," and (4) Cataeginae McLean and Quinn, 1987, Trochaclidinae Thiele, 1928 (=Acremodontinae Marshall, 1983), and Thysanodontinae Marshall, 1988 (Hickman and McLean, 1990).

Family Skeneidae Clark, 1851

Diagnostic Characters: 1) non-pigmented trochiform shell lacking nacreous layer, 2) ctenidium monopectinate, 3) radular formula $n+(2-6)+1+(2-6)+n$, 4) simultaneous hermaphrodites, and 5) penis at right epipodium.

Included taxa: The family was reviewed by Hickman and McLean (1990) and redefined by Warén (1991 a). Hickman and McLean (1990) classified it into four groups, *viz.* (1) *Parviturbo-Haplocochlias group*, (2) Austral microliotiform group, (3) *Crosseola* group, and (4) deep-water skeneiform group. Anatomical information for the family was given by Fretter and Graham (1977) and Warén (1991 a).

This family includes exclusively small-sized animals, so that their character states are often unclearly defined because of difficulty of observation. Warén (1991 a) stated that some taxa currently included in this family are more similar in radular morphology to Turbinidae or Trochidae, but others to Seguenziidae.

Superfamily uncertain
Family Pendromidae Warén, 1991

Diagnostic characters: 1) teleoconch with net-type and axial or spiral sculpture, 2) radula absent, and 3) large receptaculum seminis on left side of pallial cavity in female.

Included taxa: Pendroma Dall, 1927, and *Rugulina* Palazzi, 1988. The family is anatomically of the archaeogastropod type but is different from other families in the absence of the radula (Warén, 1991 b). Con-

chologically they may be related to Skeneidae with a small trochoid shell.

Superfamily LEPETODRILOIDEA McLean, 1988

Diagnostic characters: 1) nacreous layer absent, 2) eyes and eye stalks absent, 3) tentacles non-papillate, 4) single left ctenidium that is bipectinate at anterior free tip but monopectinate posteriorly, 5) ctenidium without bursicles, 6) single left hypobranchial gland, 7) hypobranchial gland fused with ctenidium, 8) paired jaws with chitinous rods, 9) radular formula n–5–1–5–n, 10) inner lateral teeth aligned in V-shape configuration, 11) marginal teeth about 18 pairs (in *Lepetodrilus*) or 10 pairs (in *Gorgoleptis*), 12) outer lateral teeth not enlarged, 13) lateromarginal plates absent, 14) salivary glands absent, 15) glandular pouches of mid-esophagus greatly enlarged and overlapping posterior part of buccal mass, 16) esophageal wall papillate, 17) spiral gastric caecum absent, 18) intestine with anterior loop, 19) two auricles, 20) rectum passing through ventricle, 21) two kidneys of dissimilar histology, each linked to pericardium by renopericardial duct, 22) gonad discharging into right kidney, 23) gonochoristic, 24) cephalic penis present, 25) vas deferens functioning as seminal vesicle, 26) prostate present, 27) receptaculum seminis present, 28) ciliated genital groove in female, and 29) statocysts with numerous statoconia.

Included taxa: Lepetodrilidae McLean, 1988, and Gorgoleptidae McLean, 1988. Anatomical observations were made by McLean (1988) and Fretter (1988). The two families are distinguished by the following five anatomical criteria, 1) configuration of the shell muscles, 2) presence or absence of the operculum, 3) elaboration of the epipodial tentacles, and 4) structure and position of the penis. This group of limpets was formerly called "hot-vent group-B" (Hickman, 1983) or "dimorphic limpets" by McLean (1985 b).

Family Lepetodrilidae McLean, 1988

Diagnostic characters: 1) horseshoe-shaped shell muscle attachment, 2) operculum absent in adult, 3) three pairs of epipodial tentacles, one pair on anterolateral side of foot and two pairs posteriorly, 4) esophageal pouches enclosing radular sac, 5) postmedian retractor muscle of radular sac absent, and 6) penis with deep seminal groove near base of right cephalic tentacle (absent in *Lepetodrilus schrolli* Beck, 1993).

Included taxa: *Lepetodrilus* McLean, 1988.

Family Gorgoleptidae McLean, 1988

Diagnostic characters: 1) separate pair of shell muscle attachments, 2) multispiral operculum present in adult, 3) epipodial tentacles long, five on left and four on right, and 4) penis developed from left side of snout.

Included taxa: *Gorgoleptis* McLean, 1988.

Superfamily SEGUENZIOIDEA Verriill, 1884
Family Seguenziidae Verrill, 1884

Diagnostic Characters: 1) inhalant and exhalant pallial slits, 2) eyes and eye stalks absent, 3) cephalic lappets absent, 4) subocular peduncle on base of right cephalic tentacle (Quinn, 1983), 5) accessory cephalic process (Quinn, 1983), 6) neck lobes absent, 7) several pairs of epipodial tentacles, 8) micropapillae on cephalic and epipodial tentacles, 9) epipodial sense organ absent (Salvini-Plawen and Haszprunar, 1987) or present (Ponder and Lindberg, 1997), 10) monopectinate ctenidium, 11) ctenidium with skeletal rods and bursicles, 12) single left hypobranchial gland, 13) radula modified rhipidoglossate, with formula as (4–12) + 1 + 1 + 1 + (4–12) (Quinn, 1983), 14) radula diverticulum present, 15) esophagus with ventral mucous pockets (Salvini-Plawen and Haszprunar, 1987), 16) small crescent-shaped gastric caecum, 17) intestine with anterior loop, 18) intestine without penetrating ventricle (Quinn, 1983), 19) monotocardian heart (Quinn, 1983), 20) paired kidneys, 21) true gonoduct discharging directly into pallial cavity (Haszprunar,

1988 b), 22) penis with ciliated sperm groove arising from right posterior neck region (Quinn, 1983), and 23) receptaculum seminis opening at left side of pallial cavity.

Included taxa: According to the classification of Marshall (1991), this taxon consists of 20 genera in 3 subfamilies, (1) **Asthelysinae Marshall, 1991**, (2) **Seguenziinae Verrill, 1884** (including tribes Seguenzi-ini Veriill, 1884, and Fluxinellini Marshall, 1991), and (3) **Guttulinae Goryachev, 1987**. Marshall (1991) assumed the evolutionary pathways from Asthelysinae to Seguenziini through Fluxinellini. If this assumption is accepted, there are some consistent "trends" in character evolution. (i) Central and lateral teeth become thinner and more flexible. (ii) Marginal teeth become more slender. (iii) Number of radular teeth is reduced from up to about 20 pairs (Fluxinellini) to up to about 7 pairs (Seguenziini). (iv) Deep notches are elaborated in shell aperture.

"Vent Taxa" = Peltospiroidea + Neomphaloidea
Superfamily PELTOSPIROIDEA McLean, 1989
Family Peltospiridae McLean, 1989

Diagnostic characters (based mainly on *Rhynchopelta*): 1) snout tapered (except in Hirtopelta), 2) eyes absent, 3) epipodial tentacles not long, 4) tentacles non-papillate, 5) single left bipectinate ctenidium, 6) skeletal rods present (except *Melanodrymia*), 7) osphradium along left shell muscle, 8) hypobranchial gland absent, 9) paired jaws, 10) radular formula n$-$4$-$1$-$4$-$n, 11) single pair of cartilages, 12) sac-like salivary glands without ducts, 13) enlarged esophageal pouches, 14) single left auricle, 15) auricle lacking filter chambers, 16) ventricle not penetrated by rectum, 17) left and right kidneys, 18) nephridial gland in diverticulum of left kidney, 19) right renopericardial canal present in both sexes, 20) left renopericardial canal found only in female, 21) gonopericardial duct absent, 22) gonad with glandular pallial gonoduct, 23) gonoduct urogenital in female, but separated from right kidney in male, 24) seminal vesicle and prostate in male, 25) cephalic penis absent, 26) receptacular duct in female, 27) sperm-ingesting epithelium in ovary, and 28) fertilization within ovary.

Included taxa: Melanodrymia Hickman, 1984; *Depressigyra, Pachydermia*, and *Lirapex*, all Warén and Bouchet,1989; *Echinopelta, Peltospira, Nodopelta, Rhynchopelta*, and *Hirtopelta*, all McLean, 1989 a; *Ctenopelta, Planorbidella*, and *Helicrenion*, all Warén and Bouchet,1993. *Solutigyra* Warén and Bouchet, 1989 was originally described as a member of this family but transferred to Skeneidae based on the similarities to *Xyloskenea* Marshall, 1988 in radula and to *Leptogyropsis* Marshall, 1988 in soft parts and protoconch (Warén and Bouchet, 1993). The internal anatomy of *Rhynchopelta, Peltospira, Nodopelta, Echinopelta*, and *Hirtopelta* was described in detail by Fretter (1989). Some additional information was given by McLean (1989 a) and Warén and Bouchet (1989, 1993). These taxa were previously called "hot-vent group-A" (Hickman, 1983) or "taper-snout limpets" (McLean, 1985 b).

Melanodrymia is represented by *M. aurantiaca* Hickman 1984 and *M. brightae* Warén and Bouchet, 1993. Hickman (1984 b) tentatively placed this genus in Trochoidea. Haszprunar (1989 b) described the anatomy of the species, and Warén and Bouchet (1989) documented additional anatomical information and revealed its higher-level taxonomic position. Diagnostic characters of genus *Melanodrymia* are given as follows: 1) several epipodial tentacles, 2) skeletal rods absent, 3) sensory pockets on ctenidial lamellae, 4) jaw absent, 5) single left kidney, 6) cephalic tentacles ciliated and used as copulatory organ, 7) ciliated seminal groove present, 8) receptaculum seminis on the left side, and 9) statocysts bearing single statolith.

Superfamily NEOMPHALOIDEA McLean, 1981

Diagnostic characters: 1) eyes absent, 2) tentacles non-papillate, 3) single left ctenidium bipectinate, 4) afferent ctenidial membrane absent or very short, 5) skeletal rods present, 6) bursicles absent, 7) radular formula n$-$4$-$1$-$4$-$n, 8) single left auricle, 9) ventricle not penetrated by rectum, 10) left kidney only, 11)

gonad with glandular gonoducts, 12) left cephalic tentacle of male used as penis, and 13) open or closed sperm groove in male.

Included taxa: Neomphalidae McLean, 1981 and Cyathermiidae McLean, 1990

Family Neomphalidae McLean, 1981

Diagnostic characters (based mainly on *Neomphalus*): 1) shell penetrated by microtubules (Batten, 1984 b), 2) neck long, 3) epipodial tentacles along posterior side of foot, 4 to 9 on right and 5 or 6 on left (in *Neomphalus*), or up to 20 in number (in *Symmetromphalus*), 4) paired jaws, 5) central and lateral teeth non-serrated, 6) single pair of odontophoral cartilages, 7) salivary gland absent, 8) overlap of esophageal pouches on buccal mass, 9) nephridial gland present at anterior right side of kidney, 10) gonopericardial duct present in female, 11) male gonoduct with prostate, 12) open seminal groove in left cephalic tentacle, 13) cirri at tip of penis (as in Cyathermiidae) absent, 14) fertilization chamber in proximal part of oviduct, 15) receptaculum seminis unconnected to oviduct, and 16) statocysts containing single statolith.

Included taxa: *Neomphalus* McLean, 1981, and *Symmetromphalus* McLean, 1990. Anatomical description was given by McLean (1981), Fretter *et al.* (1981), McLean (1990 a) and Beck (1992 a). Two genera differ in the following characters: 1) operculum absent (in *Neomphalus*), or present in adult (in *Symmetromphalus*), 2) shell muscle crescent-shaped (in *Neomphalus*), or symmetrically paired (in *Symmetromphalus*), and 3) food groove present (in *Neomphalus*), or absent (in *Symmetromphalus*).

Family Cyathermiidae McLean, 1990

Diagnostic characters: Cyathermiidae are separated from Neomphalidae by the following characters (McLean 1990 b): 1) neck short, 2) serration of central and lateral teeth, 3) enlargement of central tooth, 4) closed sperm groove running in left cephalic tentacle, and 5) two cirri at tip of cephalic tentacles.

Included taxa: The family was proposed for coiled neomphaloids and consists of two genera: *Cyathermia* Warén and Bouchet, 1989, and *Lacunoides* Warén and Bouchet, 1989. Soft parts of *Cyathermia* were described by Warén and Bouchet (1989).

"COCCULINIFORMIA" Haszprunar, 1987

Diagnostic characters: 1) ciliated epipodial tentacles, 2) epipodial sense organ absent, 3) pseudoplicate gill (in Cocculinoidea) or secondary subpallial leaflets (in Lepetelloidea), 4) osphradium left only, 5) secondary respiratory organs at right innervated by osphradial ganglion at left side of pallial roof, 6) modified rhipidoglossate radula, 7) alimentary tract variously modified, 8) gastric caecum absent, 9) single left auricle, 10) pericardium connected only with left kidney, 11) right and left kidneys present (in Lepetelloidea), or left only (in Cocculinoidea), 12) hermaphroditic (except in gonochoristic Choristellidae), 13) copulatory organ at right side, and 14) open seminal groove (except closed duct in *Pseudococculina* and *Notocrater*; Haszprunar, 1988 d).

Included taxa: According to the phylogenetic classification of Haszprunar (1988 c), "Cocculiniformia" are divided into two basic phyletic lines, Cocculinoidea Thiele, 1909 and Lepetelloidea Thiele, 1908. Their relationship is summarized as follows: (i) Cocculinoidea and Lepetelloidea are distinguished by division of shell muscle, types of secondary gill, paired or unpaired kidney, and contents of statocysts. (ii) Within Lepetelloidea, Lepetellidae, Pyropeltidae, and Psudococculinidae have single gonoduct, and gonopore connected with excretory opening. (iii) Addisoniidae and Choristellidae share gill leaflets with proximal glandular zone and skeletal rods, reduction of stomach (also with Cocculinellidae), and gonoduct free from excretory opening (also with Osteopeltidae and Cocculinellidae). (iv) The above-mentioned two groups of Lepetelloidea form a single lineage linked by Osteopeltidae and Cocculinellidae.

Superfamily COCCULINOIDEA Thiele, 1909

Diagnostic characters: 1) shell muscle divided into bundles, 2) pseudoplicate gill, 3) subpallial glands (except *Cocculina* and *Coccocreter*; Haszprunar, 1987 a), 4) paired jaws, 5) single pair of radular cartilages, 6) central radular tooth vestigial or absent, 7) ventricle not penetrated by rectum, 8) single left kidney, 9) hermaphroditic gonad with fused ovary and testis, 10) single glandular gonoduct, 11) gonopore independent of kidney opening, 12) copulatory organ from right neck, 13) receptaculum seminis present, and 14) statocysts with single statolith.

Included taxa: Cocculinidae Dall, 1882, and Bathysciadiidae Dautzenberg and Fischer, 1900 (Haszprunar, 1988 c).

Family Cocculinidae Dall, 1882

Diagnostic characters: 1) oral lappet present, 2) bristles around mouth, 3) eyes modified to basitentacular gland, 4) one pair of posterior epipodial tentacles (except *Coccopigya* lacking tentacles; Haszprunar, 1987 a), 5) osphradium present, 6) left hypobranchial gland present, 7) anterior levator muscle absent, 8) radula n−4−1/0−4−n, 9) fourth lateral teeth enlarged, 10) salivary glands absent, 11) esophagus with pouches, 12) stomach with gastric shield, 13) single mid-gut gland opening, 14) three intestinal loops, and 15) one or two receptaculum seminis with separate ducts.

Included taxa: Cocculina Dall, 1882; *Paracocculina* Haszprunar, 1987; *Coccocrater* Haszprunar, 1987; *Coccopigya* Marshall, 1986; *Fedikovella* Moskalev, 1976; and *Teuthirostria* Moskalev, 1976. Anatomical descriptions and diagnoses were given by Haszprunar (1987 a).

Family Bathysciadiidae Dautzenberg and Fischer, 1900

Diagnosti characters: 1)eys absent, 2) radular formula 1−3−1−3−1 (in *Bathysciadium*) 1−3−0−3−1 (in *Bonus*), 3) salivary glands present, 4) esophageal glands enlarged, 5) stomach with gastric shield, 6) midgut gland absent, and 7) short intestine.

Included taxa: Bathysciadium Dautzenberg and Fischer, 1900; *Bathypelta* Moskalev, 1971; and *Bonus* Moskalev, 1973 (Moskalev, 1973; Haszprunar, 1988 c). Anatomical information on pallial, gonopericardial, and alimentary system was given by Haszprunar (1988 c).

Superfamily LEPETELLOIDEA Thiele, 1908

Diagnostic characters: 1) undivided horseshoe-shaped shell muscle or single columellar muscle (in Choristellidae), 2) secondary gill-leaflets in right pallial and/or subpallial cavities, 3) sensory pocket in gill leaflets present (in Lepetellidae, Pyropeltidae, and Pseudococculinidae), or absent (in Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae), 4) proximal glandular area in gill leaflets absent, or present (in Addisoniidae and Choristellidae), 5) skeletal rods within efferent axis absent, or present (in Addisoniidae and Choristellidae), 6) hypobranchial gland absent, 7) subpallial glands absent, 8) well-developed central tooth, 9) salivary glands present (except Lepetellidae), 10) ventricle penetrated by rectum (except in Addisoniidae and Choristellidae), 11) two kidneys (smaller left kidney connected with pericardium; larger right kidney isolated without renopericardial duct), 12) right kidney ramified into branches (except simple kidney in Lepetellidae), 13) hermaphroditic (except gonochoristic Choristellidae), 14) testis and ovary clearly separated (ventral testis and dorsal ovary), 15) gonoducts simply ciliated without glands, 16) vas deferens and oviduct fused into common genital duct (in Lepetellidae, Pyropeltidae, and Pseudococculinidae), or separated (in Osteopeltidae, Cocculinellidae, and Addisoniidae), 17) right kidney opening and gonopore fused into urogenital opening (in Lepetellidae, Pyropeltidae, and Pseudococculinidae) or separated (in Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae), 18) right cephalic tentacle used as copulatory organ, and 19) statocysts with several or many statocones.

Included taxa: 8 families are included in this superfamily: Lepetellidae Dall, 1882; Pyropeltidae McLean and Haszprunar, 1987; Pseudococculinidae Hickman, 1983; Osteopeltidae Marshall, 1987; Bathyphytophilidae Moskalev, 1978; Cocculinellidae Moskalev, 1971; Addisoniidae Dall, 1882; and Choristellidae Bouchet and Warén, 1979 (Haszprunar, 1988 c).

Family Lepetellidae Dall, 1882

Diagnostic characters: 1) oral lappets absent, 2) unpaired papilla on posterior end of foot (Dantart and Luque, 1994), 3) jaws absent, 4) one pair of odontophoral cartilages, 5) radular formula 3–1–3 (Dantart and Luque, 1994), 6) salivary glands absent, 7) greatly enlarged esophageal pouches, 8) stomach without gastric shield, 9) several openings of digestive gland into stomach, and 10) short intestine.

Included taxa: Lepetella Verrill, 1880; *Tectisumen* Finlay, 1927; and *Tecticrater* Dell, 1956 (Haszprunar, 1988 c). Anatomical information on pallial cavity, gonopericardial system, and alimentary tract was given by Haszprunar (1988 c).

Family Pyropeltidae McLean and Haszprunar, 1987

Diagnostic characters: 1) oral lappets absent, 2) eyes absent, 3) one pair of posterior epipodial tentacles, 4) osphradium present, 5) paired jaws with tooth-like elements, 6) two pairs of odontophoral cartilages, 7) radular formula n–5–1–5–n, 8) esophageal pouches present, 9) stomach with gastric shield, 10) paired mid-gut glands, and 11) several intestinal loops.

Included taxa: The family consists only of a single genus, *Pyropelta* McLean and Haszprunar, 1987 (McLean and Haszprunar, 1987; McLean, 1992 b).

Family Pseudococculinidae Hickman, 1983

Diagnostic characters: 1) sensory papillae on mantle edge, 2) oral lappets present, 3) eyes present or absent, 4) one pair of posterior epipodial tentacles, 5) osphradium absent, 6) paired jaws, 7) two pairs of odontophoral cartilages, 8) radular formula n–5–1–5–n, 9) esophagus with pouches, 10) stomach with gastric shield, 11) single mid-gut gland, and 12) several intestinal loops.

Included taxa: Two subfamilies, (1) **Pseudococculininae Hickman, 1983** (*Pseudococculina* Schepman, 1908; *Bandabyssia* Moskalev, 1976; *Kurilabyssia* Moskalev, 1976; *Mesopelex* Marshall, 1986; *Notocrater* Finlay, 1927; and *Tentaoculus* Moskalev, 1976) and (2) **Caymanabyssinae Marshall, 1985** (*Caymanabyssia* Moskalev, 1976; *Amphiplica* Haszprunar, 1988; *Colotrachelus* Marshall, 1986; *Copulabyssia* Haszprunar, 1988; and *Yaquinabyssia* Haszprunar, 1988). Anatomical descriptions and diagnoses were given by Haszprunar (1988 d).

Family Osteopeltidae Marshall, 1987

Diagnostic characters: 1) oral lappets absent, 2) eyes present, 3) single pair of epipodial lappets, 4) sensory pocket absent in gill leaflets, 5) osphradium absent, 6) paired jaws, 7) single pair of odontophoral cartilages, 8) radulae similar to those of Pseudococculinidae, 9) narrow anterior esophagus without pouches, 10) stomach with gastric shield, 11) paired mid-gut glands, and 12) short intestine.

Included taxa: Osteopelta Marshall, 1987, only. This genus was defined as cocculiniform limpets with pseudococculinid-like shell and radula with an addisoniid-like animal (Marshall, 1987; Haszprunar, 1988 c, e).

Family Bathyphytophilidae Moskalev, 1978

Diagnostic characters: 1) outer lateral teeth enlarged, 2) filamentous marginal teeth, and 3) one pair of marginal plates present.

Included taxa: Two genera (*Bathyphytophilus* Moskalev, 1978, and *Aenigmabonus* Moskalev, 1978) were assigned to this family (Moskalev, 1978), but their anatomy and taxonomic relationships have not been clearly understood (Haszprunar, 1988 c).

Family Cocculinellidae Moskalev, 1971

Diagnostic characters: 1) oral lappets absent, 2) eyes absent, 3) epipodial tentacles absent, 4) reduction of gill into two ciliary spots, 5) osphradium present, 6) jaws absent, 7) radular formula 7–1–1–1–7 (Marshall, 1983 c), 8) 2 paired and 2 unpaired odontophoral cartilages, 9) narrow anterior esophagus without pouches, 10) stomach reduced with vestigial gastric shield, 11) unpaired mid-gut gland, and 12) intestine enlarged.

Included taxa: Cocculinella Thiele, 1909. The anatomy was described for *Cocculinella minutissima* by Haszprunar (1988 e).

Family Addisoniidae Dall, 1882

Diagnostic characters (based mainly on *Addisonia*): 1) oral lappets absent, 2) eyes absent, 3) epipodial tentacles absent, 4) single left osphradium present, 5) jaws absent, 6) two pairs of odontophoral cartilages, 7) radular formula 7–1–7, 8) narrow anterior esophagus without pouches, 9) stomach completely reduced, 10) paired mid-gut glands, 11) intestine forming pseudostomach, and 12) receptaculum seminis present.

Included taxa: The family consists of two subfamilies, (1) **Addissoninae Dall, 1882** (*Addisonia* Dall, 1882), and (2) **Helicopeltinae Marshall, 1996** (*Helicopelta* Marshall, 1996). Details on shell, external and internal anatomy, radula, and life habit were described by Hickman (1983), McLean (1985 a), Haszprunar (1987 b), Dantart and Luque (1994), and Marshall (1996).

Family Choristellidae Bouchet and Warén, 1979

Diagnostic characters: 1) operculum present, 2) oral lappet present, 3) eyes absent, 4) one to two suboptic tentacles posterior to right cephalic tentacle, 5) several epipodial tentacles (up to 4 pairs), 6) osphradium present, 7) jaws fused dorsally, 8) two pairs of odontophoral cartilages, 9) radular formula 5–1–5, 10) anterior esophagus without pouches, 11) stomach completely reduced, 12) single opening of mid-gut glands, 13) intestine forming pseudostomach, 14) gonochoristic, and 15) receptaculum seminis present.

Included taxa: Choristella Bush, 1897, and *Bichoristes* McLean, 1992. Systematics reviewed by McLean (1992 a). The anatomy was described by Haszprunar (1992).

Order NERITOPSINA Cox and Knight, 1960

Diagnostic characters: 1) protoconch multispiral or globular, 2) inside of upper whorls resorbed, 3) closed eyes with vitreous body, 4) visceral mass without spiral coiling (true columella absent), 5) ctenidium lacking skeletal rod, 6) right hypobranchial gland present (absent in some members), 7) osphradium left only (absent in terrestrial forms), 8) osphradium with ciliated zones, 9) three (anterior, posterior, and median) pairs of odontophoral cartilages, 10) dorsal levator muscles of odontophore present, 11) tensor muscles of anterior cartilages present, 12) radular formula typically n–(1+3)–1/0–(3+1)–n, 13) salivary glands absent, 14) esophageal glands septate and separated posteriorly from mid-esophagus, 15) gastric caecum small, crescent-shaped, 16) ventricle penetrated by rectum (except Helcinoidea and Hydrocenoidea), 17) single left kidney composed of glandular and non-glandular parts (Little, 1972), 18) pallial gonoduct developed within anterior pallial vein, 19) gonopericardial canal absent, 20) prostate present in male gonoduct, 21) female gonoduct monaulic, diaulic, or triaulic, 22) bursa copulatrix or spermatophore sac present, 23) receptaculum seminis present, 24) internal fertilization, 25) egg-capsules produced, 26) labial commissure present, without labial ganglia, 27) one-side origin of visceral loop from right side, 28) su-

praesophageal part of visceral loop reduced or absent, and 29) pleural comissure present.

Included taxa: Neritoidea Rafinesque, 1815; Titiscanioidea Bergh, 1890; Hydrocenoidea Troschel, 1856; and Helcinoidea Thompson, 1980.

Superfamily NERITOIDEA Rafinesque, 1815

Diagnostic characters: 1) oral lappets present, 2) sublingual glands evaginated from sublingual pouch, 3) median levator muscles of odontophore present, 4) two auricles (right auricle functional but vestigial), 5) cephalic penis originating from inner side of right cephalic tentacle, 6) spermatophore in male and spermatophore sac in female, 7) female gonoduct typically diaulic, and 8) capsule and albumen glands in female.

Included taxa: Neritopsidae Gray, 1847; Neritidae Rafinesque, 1815; Phenacolepadidae Thiele, 1929; and Shinkailepadidae Okutani, Saito, and Hashimoto, 1989.

Family Neritopsidae Gray, 1847

Diagnostic characters: 1) calcified operculum with strong inner projection, and 2) radular formula $n-(1+3)-0-(3+1)-n$ (three pairs of slender laterals and enlarged fourth teeth) (Baker, 1923; Warén and Bouchet, 1993: fig. 3 D).

Included taxa: Extant members are represented only by a single genus, *Neritopsis* Grateloup, 1932, which includes Indo-Pacific *N. radula* (Linnaeus, 1758) surviving from the Eocene (Batten, 1984 a) and the recently discovered western Atlantic species, *N. atlantica* Sarasua, 1973 (Rosenberg, 1992). Details of anatomy are unknown.

Family Neritidae Rafinesque, 1815

Diagnostic characters: 1) calcified operculum with interior apohysis, 2) paired attachments of columellar muscles (divided into bundles in *Nerita*), 3) right hypobranchial gland present (absent in *Neritina* and *Theodoxus*; Fretter, 1965), 4) vestigial gill on right side (in *Nerita*), 5) radular formula $n-(1+3)-0/1-(3+1)-n$, 6) "annex gland" of Lessen (1899) in male, and 7) crystal sac in female organ (except Neritilinae).

Included taxa: The family is divided into 4 subfamilies based on characters of radula and reproductive organ (Baker, 1923; Andrews, 1937; Knight et al, 1960; Stramühlner, 1976, 1983; Komatsu, 1986).

(1) **Neritinae Rafinesque, 1815** (*Nerita* Linnaeus, 1758; *Neritina* Lamarck, 1816; *Neritodryas* von Martens, 1869; and *Theodoxus* Montfort, 1810): 1) radular formula $n-(1+3)-1-(3+1)-n$, 2) first laterals transversely elongated, 3) fourth teeth transversely thickened with indistinct denticles on shield-shaped cusp, 4) many marginals of similar form, 5) basal gland present in male, 6) cephalic penis present, 7) female gonoduct diaulic without enigmatic duct, and 8) crystal sac present in female.

(2) **Septariinae Golikov and Starobogatov, 1975** (*Septaria* Férussac, 1807): 1) limpet-shape, 2) semiinternal operculum, 3) radular formula $n-(1+3)-1-(3+1)-n$, 4) teeth morphology similar to that of Neritinae, 5) basal gland absent, 6) cephalic penis present, 7) female gonoduct triaulic with enigmatic duct, and 8) crystal sac present.

(3) **Smaragdiinae Baker, 1923** (*Smaragdia* Issel, 1869; *Magadis* Melville and Standen, 1899; and *Pisulina* Nevill, 1869): 1) radular formula $n-(1+3)-1-(3+1)-n$, 2) first laterals not enlongated, 3) fourth laterals transversely prominent with a few distinct denticles, and 4) several pairs of marginals with innermost teeth differentiated, 5) cephalic penis present, and 6) crystal sac present.

(4) **Neritiliinae Baker, 1923** (*Neritilia* von Martens, 1879, and *Septariellina* Bequaert and Clench, 1936): 1) radular formula $n-(1+3)-0-(3+1)-n$, 2) first laterals elongated, 3) fourth laterals enlarged and obliquely aligned with saw-like denticles, 4) many marginals of similar form, 5) cephalic penis absent, 6) female gonoduct monaulic, and 7) crystal sac absent.

Bathynerita Clarke, 1989 in uncertain subfamilial position was reported from hydrocarbon seeps south

of Luisiana, 540–722 m (Warén and Bouchet, 1993).

Family Phenacolepadidae Thiele, 1929

Diagnostic characters: 1) corneous operculum with vestigial apohysis embedded in foot in *Phenaco-lepas* (Fretter, 1984 a), but absent in *Cinnalepeta*, 2) mantle margin with numerous papilla, 3) cephalic lappets absent, 4) epipodial papillae absent, 5) hypobranchial gland absent, 6) radular formula n–(1+3)–1–(3 +1)–n (first laterals transversely elongated with sharp cusps; fourth laterals longitudinally elongated, and marginals with comb-like cusps), 7) erythrocytes present, 8) finger-shaped cephalic penis, 9) female gonoduct diaulic, 10) spermatophore sac and receptaculum seminis present, and 11) crystal sac absent.

Included taxa: *Phenacolepas* Pilsbry, 1891 with 3 subgenera (or genera: *Amapileus* Iredale, 1929; *Cinnalepeta* Iredale, 1929; and *Zacalantica* Iredale, 1921) and *Plesiothyreus* Cossmann, 1888 (Vaught, 1989). The anatomy of *Phenacolepas omanensis* was described by Fretter (1984 a).

Family Shinkailepadidae Okutani, Saito, and Hashimoto, 1989

Diagnostic characters: 1) internal operculum consisting of anterior calcareous and posterior corneous layers, 2) mantle margin with numerous papillae, 3) cephalic lappets absent in *Shinkailepas* (Okutani *et al.*, 1989: fig. 10) but present in *Olgasolaris* (Beck, 1992 b: pl. 5, fig. 5), 4) epipodial papillae present posteriorly, 5) radular formula n–(1+3)–1–(3+1)–n (n=ca. 80 in *Shinkailepas tufari*, 70 in *Olgasolaris toll-manni*; Beck, 1992 b), 6) cephalic penis present, 7) female gonoduct diaulic, and 8) spermatophore sac, receptaculum seminis, and crystal sac absent (Beck, 1992 b: fig. 4).

Included taxa: Two deep-sea genera, *Shinkailepas* Okutani, Saito, and Hashimoto, 1989, and *Olgasolaris* Beck, 1992. Anatomical descriptions was given by Okutani *et al.* (1989) and Beck (1992 b). Beck (1992 b) synonymized this family with Phenacolepadidae, but these two families differ in the morphology of operculum, the presence or absence of epipodial papillae, and the structure of female gonoduct.

Superfamily TITISCANIOIDEA Bergh, 1890
Family Titiscaniidae Bergh, 1890

Diagnostic characters: 1) shell absent, 2) bipectinate ctenidium present, 3) radular formula n–3–0–3–n (first laterals small, second laterals slightly enlarged, third laterals enlarged; Saito and Tsuchiya, 1990), 4) two auricles, 5) ventricle penetrated by rectum, 6) vas deferens not coiled, 7) accessory gland absent in prostate, 8) ciliated groove on right side of head, 9) cephalic penis absent, 10) female gonoduct diaulic with spermatophore sac, 11) oviduct with albumen and capsule glands, 12) receptaculum seminis present, and 13) crystal sac absent.

Included taxon: Monotypic genus *Titiscania* Bergh, 1890, represented by *Titiscania limacina* Bergh, 1890 (=? *T. shinkishihataii* Is. Taki, 1955) distributed from the Philippines to Baja California (Bergh, 1890; Taki, 1955; Keen, 1971; Saito and Tsuchiya, 1990). Anatomical descriptions were given by Bergh (1890) and Houston (1990).

Superfamily HYDROCENOIDEA Troschel, 1856
Family Hydrocenidae Troschel, 1856

Diagnostic characters: 1) calcified operculum with interior apohysis, 2) ctenidium absent and replaced by "lung," 3) single columellar muscle, 4) jaws absent, 5) salivary glands absent, 6) central and lateral radular teeth reduced, 7) single left auricle, 8) ventricle not penetrated by rectum, 9) prostate gland in two portions, 10) cephalic penis absent, 11) female gonoduct monaulic, and 12) receptaculum seminis present.

Included taxa: *Hydrocena* Pfeiffer, 1847; *Georissa* Blanford, 1864; and *Lapidaria* Kang, 1986 (Vaught, 1989). Anatomy of *Hydrocena cattaroensis* was described by Thiele (1910).

Superfamily HELICINOIDEA Thompson, 1980

Diagnostic characters: 1) non-operculate (in Ceresidae and Proserpinidae) or operculate (calcified operculum without apohysis in Helcinidae), 2) gill absent and replaced by "lung," 3) osphradium absent, 4) hypobranchial gland discharging into mantle cavity via hypobranchial duct, 5) radular formula n−(1+3)−1−(3+1)−n, 6) ventricle not penetrated by rectum, 7) cephalic penis absent, 8) female gonoduct diaulic or triaulic, 9) spermatophores absent, 10) "provaginal sac" (Thompson, 1980) always present in female, and 11) "V-organ" and accessory sperm sac (Thompson, 1980) in female.

Included taxa: Ceresidae Thompson, 1980; Proserpinidae Gray, 1847; and Helcinidae Férussac, 1882 (*fide* Thompson, 1980).

Family Ceresidae Thompson, 1980

Diagnostic characters: 1) operculum absent, 2) foot "holopod" (without mucous groove), 3) heart with two functional, nearly equal-sized auricles, 4) prostate not divided into upper and lower divisions, 5) provaginal sac absent in males, and 6) crystalline gland absent on pallial oviduct.

Included taxa: *Ceres* Gray, 1856; *Archecharax* Thompson, 1980; *Linidiella* Jousseaume, 1889; *Proserpinella* Bland, 1865; and *Staffola* Dall, 1905 (Thompson, 1980).

Family Proserpinidae Gray, 1847

Diagnostic characters: 1) operculum absent, 2) foot "aulacopod" (side of foot demarcated by mucus groove as in Pulmonata), 3) single left auricle, 4) prostate divided into prostate-I and -II, 5) vestigial provaginal sac present within prostate-I, and 6) crystalline gland present at base of pallial oviduct.

Included taxa: *Proserpina* Sowerby, 1839 (Thompson, 1980).

Family Helcinidae Férussac, 1882

Diagnostic characters: 1) operculum present, 2) foot "holopod" (without mucus groove), 3) single left auricle (paired in *Hendersonia*; Thompson, 1980), 4) prostate divided into prostate-I and -II, 5) provaginal sac absent in male, and 6) crystalline gland absent.

Included taxa: 28 genera (Vaught, 1989) in 3 subfamilies, (1) **Helcinnae Férussac, 1882**, (2) **Hendersoniinae Baker, 1926**, and (3) **Vianinae Baker, 1922** (Thompson, 1980). Anatomy of some genera was described by Bourne (1911) and Thompson (1980). According to Thompson (1980), several "evolutionary trends" seem to occur in this family: 1) modification of operculum from paucispiral to concentric, 2) increasing complexity of shell sculpture, 3) reduction and loss of right auricle, 4) increase in lengths of pallial gonoduct and hypobranchial duct, 5) simplification and elongation of female primary oviduct, 6) shift of accessory sperm sacs on pedicel, 7) reduction of cusps on radular teeth, 8) fourth lateral ("D-lateral") teeth changing from comb-shaped to T-shaped, and 9) reduction in structural complexity of accessory plate of fourth lateral teeth ("E-lateral"). Presence of the operculum is only discrete character to distinguish this family from others.

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