ANCESTORS AND DESCENDENTS: RELATIONSHIPS OF THE APLACOPHORA AND POLYPLACOPHORA

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ABSTRACT

Four organ systems, pericardium of primitive mollusks, shell ontogeny and spicule formation in chitons and aplacophorans, chaetoderm oral shield, and aplacophoran radula, are described and their relationships discussed. The discussion suggests: (1) a coelomate ancestor of the mollusks; (2) a polyphyletic origin of shell, one for Conchifera and another for chitons; (3) a single class Aplacophora containing two taxa, the Chaetodermomorpha and Neomeniomorpha; (4) an archimolluscan radula with a pair of separate radular membranes bearing rows of single teeth. Evidence is presented that contradicts the following hypotheses: (1) an acoelomate origin of mollusks; (2) the division of aplacophorans into two classes; (3) the derivation of the univalved molluscan shell from a common stem with the eight-shelled chitons. The concept of a subphylum Aculifera is rejected as unnecessary since it holds no essential information.

Hypotheses of early molluscan evolution in the last fifteen years have proposed an acoelomate, turbellariomorph pre-molluscan ancestor with a mucoid dorsal cover and a broad, ciliated locomotory sole through which opened a mouth (Fig. 1) (Salvini-Plawen, 1972, 1980, 1985; Haas, 1981; Boss, 1982; Poulicek and Kreusch, 1983; see also Fretter and Graham, 1962; Stasek, 1972). According to such theories, this pre-mollusk gave rise to an archimollusk with a spiculose integument, an unpaired radular membrane, and a mouth that opened through the ventral locomotory surface. The archimollusk then gave rise to two major taxa, the burrowing aplacophorans (Chaetodermomorpha = Caudofoveata) and an "adenopod", with seven transverse rows of scales and a head separated from the sole. The second group of aplacophorans, the footed Neomeniomorpha (= Solenogastres *sensu* Salvini-Plawen), have split off from the hypothetical "adenopod", the latter giving rise to an "archiplacophoran" with plates formed from coalesced scales. The "archiplacophoran" in turn was the precursor of the Polyplacophora on one hand and the rest of the shelled mollusks, the Conchifera, on the other (for recent accounts and bibliographic references, see Runnegar and Pojeta, 1985; Wingstrand, 1985; Salvini-Plawen, 1985). The subphylum Aculifera, recognized by Haas (1981) and formerly, but no longer, by Salvini-Plawen (cf. 1972, 1980), includes the extant Aplacophora and Polyplacophora as well as the hypothetical archimollusk, adenopod and archiplacophora; all other mollusks form the subphylum Conchifera. Salvini-Plawen (1980) considers the Chaetoder-
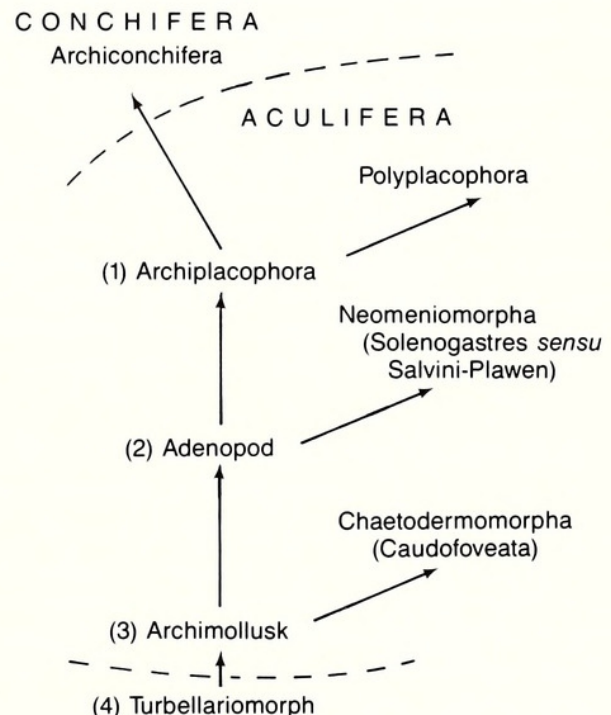

Fig. 1. Phylogeny of the Mollusca (adapted in part from Salvini-Plawen, 1980; Haas, 1981; Poulicek and Kreusch, 1983). Questioned in the text is the validity of: (1) an archiplacophoran origin of the Conchifera; (2) separation of the aplacophoran taxa Chaetodermomorpha and Neomeniomorpha by the existence of an Adenopod; (3) an archimolluscan radula with an undivided radular membrane; (4) an acoelomate ancestor. Compare with figure 14.

momorpha to belong to the subphylum Scutopoda; all remaining mollusks, including the Neomeniomorpha, constitute the subphylum Adenopoda.

Evidence presented here draws on recent observations or experiments on shell and radula formation, the structure of the oral shield of the burrowing aplacophorans, and the size of pericardial spaces in three primitive molluscan classes. The evidence raises questions about the validity of four hypotheses: (1) there is a monophyletic (archiplacophoran) origin of chitons and conchiferan mollusks; (2) the two aplacophoran taxa belong to two separate classes; (3) the most primitive molluscan radula had an undivided radular membrane; (4) the ancestor of mollusks was acoelomate (Fig. 1).

SHELL AND SPICULES

APLACOPHORA AND POLYPLACOPHORA

The Aplacophora and Polyplacophora have been classified together either as the Amphineura because of their similar ladder-like nervous systems (not examined here), or as the Aculifera because of their similar integumental structures: papillae, spines, and cuticle. Indeed, these anatomical relationships between the two groups have been used to justify the inclusion of Aplacophora within the Mollusca (for historical reviews, see Hyman, 1967; Scheltema, 1978),

although they are better regarded as symplesiomorphic traits, shared primitive states that do not necessarily show close evolutionary relationships.

Beedham and Trueman (1968) found similarities in the histochemistry of aplacophoran and chiton integumental cuticle and concluded that "the cuticle of the Aplacophora is tentatively equated with an early mucoid stage in the evolution of the molluscan shell... [The cuticle of *Acanthochiton*] has in addition a discrete inner cuticular layer which may act as a semi-conducting membrane in the deposition of calcareous plates" (p. 443). The papillae of Aplacophora and Polyplacophora are probably homologous (F. P. Fischer, pers. comm.); the papillae and aesthetes of Polyplacophora are likewise homologous (Fischer *et al.*, 1980; Fischer, 1988).

The process of calcareous spicule formation, most recently investigated by Haas (1981), is alike in aplacophorans and chitons (Fig. 2). In both taxa, a spine is secreted extracellularly within an invagination of a single cell. A basal cell secretes calcium carbonate, and as the spicule grows beyond this cell, a crystallization chamber is sealed off by a collar of neighboring cells. The megaspines in chitons, which do not occur in Aplacophora, are formed by a proliferation of the original single basal cell.

The attempt to find further similarities in calcium carbonate deposition that would link the Aplacophora and Polyplacophora by examining embryogenesis has led to less conclusive comparisons. Larval development in the two
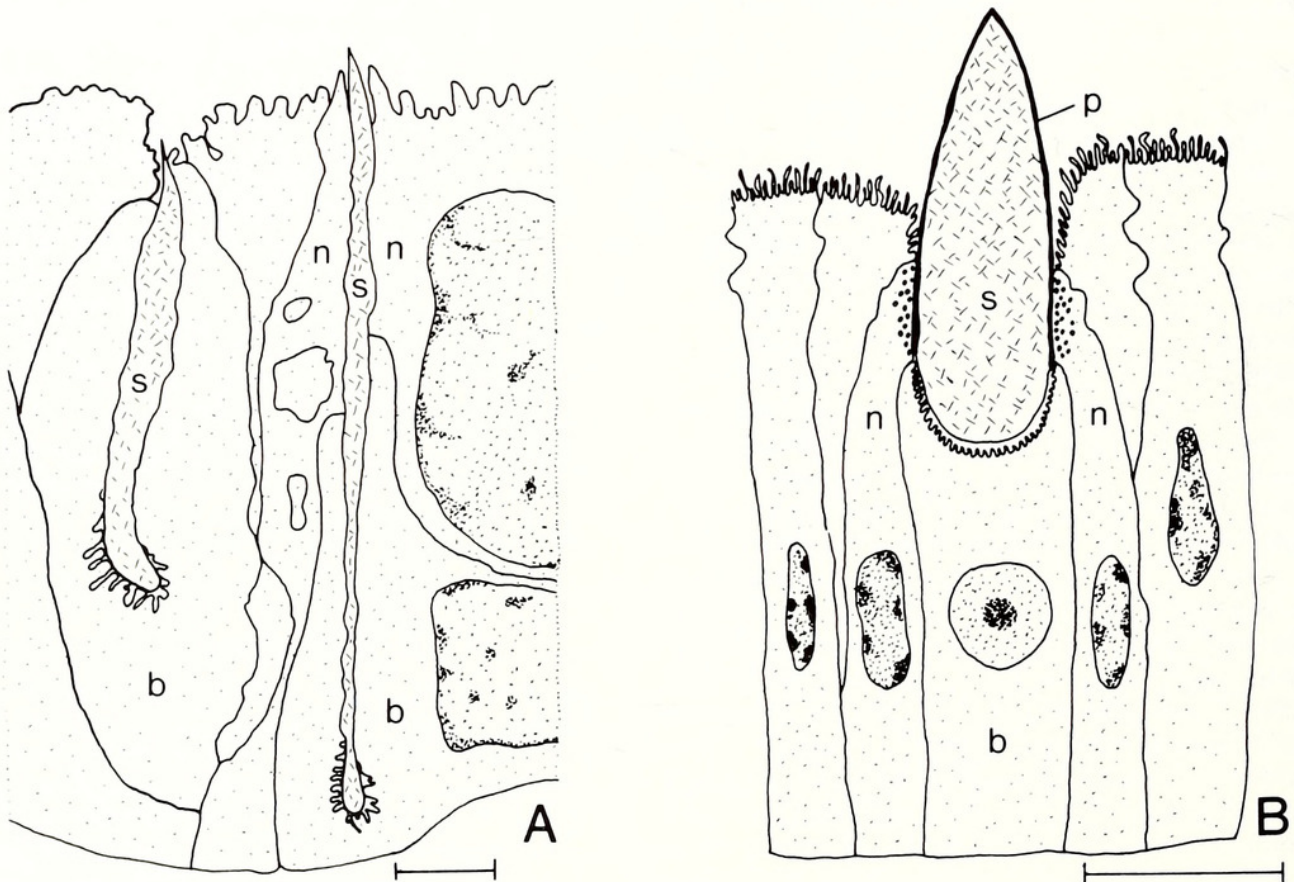

Fig. 2. Spicule formation in Aplacophora and Polyplacophora. **A.** Primitive Neomeniomorpha. **B.** *Lepidochitona cinerea* (Linnaeus). An organic pellicle has not been demonstrated around spicules of the Aplacophora. (After Haas, 1981.) (b, basal cell; n, neighboring cell; p, organic pellicle; s, spicule). Scale bars = 1 μm.
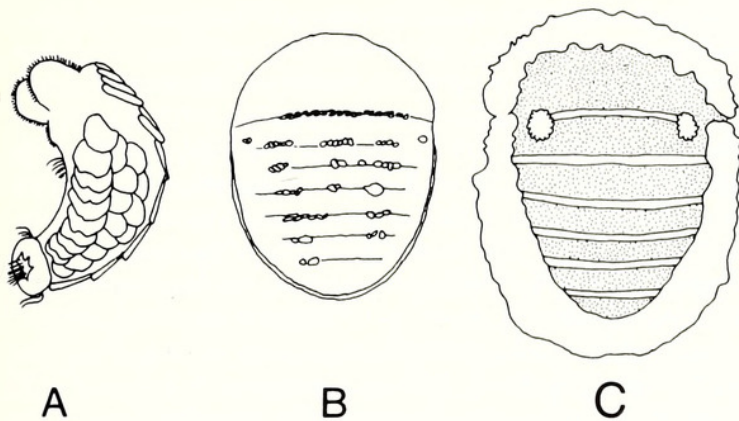
A   B   C

Fig. 3. Reported ontogeny in an aplacophoran, *Nematomenia banyulensis* Pruvot, and a chiton, *Lepidochitona corrugata* Reeve [= *Middendorffia caprearum* (Scacchi)]. **A.** Pruvot's larva, a single observation, lateral view, of a metamorphosing larva of *Nematomenia* with seven dorsal calcareous '"plaques', slightly imbricated and formed of rectangular, plainly juxtaposed spicules" (translated from Pruvot, 1890). The larva did not survive to a juvenile stage. **B.** Defective shell formation in *Lepidochitona corrugata* (= *Chiton polii* (Philippi) as illustrated by Kowalevsky (1883) with separate granules of calcium carbonate deposited along seven plate fields. Coalescence of these granules does not lead to normal growth of shell plates (see Kniprath, 1980). **C.** Birefringence under cross-polarized light in a normally developing *Lepidochitona corrugata* larva. Noncalcareous areas are stippled; the birefringent spicular girdle and six straight, uninterrupted anlagen of the shell plates are without stippling, as are the birefringent rosette-shaped larval eyes. (A and B after Salvini-Plawen, 1972: Fig. 29, after comparison with the original drawings of Pruvot, 1890, and Kowalevsky, 1883; C drawn after photograph by Kniprath, 1980: Fig. 1b.). Scales not known.

groups is dissimilar, but Salvini-Plawen [1972, 1980, 1985 (with qualifications)] argues for homology between seven rows of spicules seen once in a single aplacophoran larva [*Nematomenia banyulensis* Pruvot, Pruvot (1890)] and the development of shell in the larva of the chiton *Lepidochitona corrugata* (Reeve) (= *Chiton polii* Philippi) by a coalescence of granules (Fig. 3A, B) (Kowalevsky, 1883). The rows of spicules observed by Pruvot have not subsequently been seen in any other aplacophoran larvae [*Epimenia verrucosa* (Nierstrasz), *Halomenia gravida* Heath, *Neomenia carinata* Tullberg; see Hadfield (1979) for a summary]. Pruvot's drawing is a lateral view, and the often-copied dorsal view showing seven rows of spicules is a hypothetical reconstruction (Salvini-Plawen, 1972; Wingstrand, 1985).

Recently, Kniprath (1980) reported from rearing experiments that in the larvae of both *Lepidochitona corrugata* [=*Middendorffia caprearum* (Scacchi] and *Ischnochiton rissoi* (Payraudeau) the anlagen of the plates are secreted as uninterrupted rods along narrow transverse depressions, the shell or plate fields, after the development of girdle spicules (Fig. 3C). When *Lepidochitona* larvae were reared at temperatures of 14°-16°C, shell development was normal, but all larvae raised at higher temperatures of 18°-21°C were abnormal and developed granules similar to those reported by Kowalevsky (1883). These granules, even when they coalesced, produced defective shell plates.

The seven "plaques" of Pruvot's larval aplacophoran specimen are said to reflect the number of plates in the early fossil chiton *Septemchiton* (Hyman, 1967; Salvini-Plawen, 1980) and the seven "larval" plaques of chitons (Salvini-Plawen, 1985). However, Rolfe (1981) has shown that the most anterior plate of *Septemchiton*, a burrowing form, although greatly reduced is indeed present and that *Septemchiton* therefore has a full complement of eight plates. Although the caudal plate in chitons is usually added last during development, sometimes only after an extended period of five weeks (Pearse, 1979), it is not clear whether this time lapse reflects an ancestral chiton with only seven plates or is simply a result of development as a chiton elongates. In many adult aplacophorans with single overlapping layers of flat, leaf-like spicules, the bases of the spicules are aligned in rows that are transverse to the long axis of the animal (unpub. data); it would therefore not be surprising to find spicules lined-up in metamorphosing larvae that could be mistaken for "plaques".

Evidence for the coalescence of spines is said to be shown by three sets of broad spicules, or shields, on the head of the juvenile aplacophoran *Nematomenia protecta* (Thiele, 1913). This conclusion is based on spicule shape only, without reference to the underlying epithelium; the number of cells involved in secreting a "shield", a single cell or more than one cell, is not known, despite the inferred epithelial connection constructed by Salvini-Plawen (1985: Fig. 36D). The evidence for coalescence therefore remains unsubstantiated.

Both aplacophorans and chitons retain in common a phylogenetically early mode of calcium carbonate deposition in the form of spicules, but until further observations on aplacophoran embryogenesis prove to the contrary, close evolutionary relationship between the formation of aplacophoran spicules and chiton shells is considered undemonstrated. There is no evidence within chitons themselves that spicules have coalesced to form shell plates.

POLYPLACOPHORA AND THE OTHER SHELLED MOLLUSKS (CONCHIFERA)

The process of shell formation in chitons is argued here to be unique among mollusks. In those gastropods, bivalves, and cephalopods for which the entire shell ontogeny has been studied, earliest calcium carbonate deposition is preceded, first, by formation of a shell-field and shell-field invagination from part of the dorsal ectoderm and, second, by the secretion of an organic pellicle, usually equated with periostracum, over the invagination (Fig. 4A) (Kniprath, 1981; Eyster and Morse, 1984). [In the Cephalopoda, yolk interferes with invagination and, instead, ectoderm builds up in an elevated ring (Kniprath, 1981)]. Calcium carbonate is then secreted beneath the organic pellicle. In the nudibranch *Aeolidia papillosa* (Linnaeus), the early organic pellicle is overlain by long cytoplasmic processes that presumably seal off the crystallization chamber under the pellicle (Fig. 4B) (Eyster and Morse, 1984).

In chitons, no shell field invagination forms (Fig. 4C).

Deposition of a shell plate anlage takes place within a transverse depression bounded and sealed off by long, overlapping microvilli that lie beneath a gelatinous mucoid substance, certainly not periostracum, and questionably equated with a cuticle (Fig. 4C, D) (Kniprath, 1980; Haas *et al.*, 1980; Haas, 1981).

Not only are the ontogenetic processes of shell formation different in chitons and the Conchifera, but structures of the fully formed shells are also unlike and homologies are difficult to discover. Periostracum in the Conchifera, a structure conservative in manner of its secretion and in composi-

tion (Grégoire, 1972), does not exist in chitons, although Haas (1981) has demonstrated the presence of a thin cuticle, or pro-periostracum, overlying the tegmentum and a properiostracal groove surrounding each shell plate. There is no nacreous layer in chiton shells as found in other mollusks, and the cross-lamellar structure of the shell plates is crystallographically unique, with bundles of crystal fibers in the lamellae ordered so that their c-axis "coincides with the bisectrix of these crossing fibers" (Haas, 1981: 403) and the "whole complex acts crystallographically as a single crystal" (Haas, 1977: 392). In other molluscan cross-lamellar structures, the angle between crystal fibers is about 110^0; in gastropods they lie between 90^0-130^0 (Wilbur and Saleuddin, 1983). Haas (1981) considered the cross-lamellar structure of chitons to be homologous with the nacreous layer of other shelled mollusks and imagined that both arose from an undifferentiated inner layer of the "archiplacophoran" plates. The shell of the Conchifera became univalved he believed by fusion of the shell and shell fields. There is no evidence, however, that the dynamics involved in the process of earliest shell deposition through the interplay of shell-field invagination and pellicle in Conchifera could have evolved from the very different process of shell-plate production found in chitons.

Thus, recent work on the ontogeny and structure of shell in chitons and Conchifera shows such major differences between them that it can be questioned whether there was a monophyletic origin of molluscan shell, or rather one origin for chitons and a second for the remaining extant and extinct Conchifera. Tubules in the shells of the monoplacophoran *Neopilina* (Schmidt, 1959), bivalves (e.g. Waller, 1980), and gastropods have sometimes been considered homologous with the aesthete canals of chitons and argued as a support for a monophyletic origin of molluscan shell (e.g. Salvini-Plawen, 1985), but the homology is so far uncertain. When the ontogenetic development of *Neopilina* becomes known, perhaps a basis will be found for deciding whether molluscan shell has a monophyletic or polyphyletic origin.

Fig. 4. Larvel shell deposition in (A, B) the gastropod *Aolidia papillosa* (Linnaeus) and (C, D) the chiton *Ischnochiton rissoi* (Payaudreau). In A, an organic pellicle (arrows) covers the lumen of the shell field invagination (L); in B, the edge of the pellicle can be seen to be overlain by a cytoplasmic extension (e). Calcium carbonate has not yet been deposited. (Drawn after photographs in Eyster and Morse, 1984: Figs. 1, 2). In C, calcium carbonate of the shell plate (p) has been deposited under the overlapped microvilli (s, "stragulum"); a mucus layer (m) covers the stragulum. In D, microvillar processes (s) have pulled apart and a cuticle (c) with a contrasted outer layer is beginning to form; M is perhaps a mucus cell (C and D after Kniprath, 1980.) Scale bars: A = 10 μm; B = 0.5 μm; C; D approximately 6 μm.

CHAETODERM ORAL SHIELD AND THE ARCHIMOLLUSK

One of the original arguments for dividing the Aplacophora into two classes and, ultimately, into two subphyla depends on the hypothesis that mollusks have a turbellariomorph, or flatworm, ancestry. This phylogeny is based on a supposed homology and similarity in mode of locomotion between mollusks and flatworms by means of a "ventral mucociliary gliding surface" (Salvini-Plawen, 1972, 1980: Fig. 5, 1985; see also Trueman, 1976). The molluscan archetype, like the flatworms, is said not to possess a separation of the head from the foot, and the mouth consequently opens through the sole; innervation of the sole is said to be from both the cerebral ganglia and ventral nerve cord. [Stasek (1972) has illustrated but not discussed a head separate from the locomotory sole in the turbellariomorph molluscan precursor.]

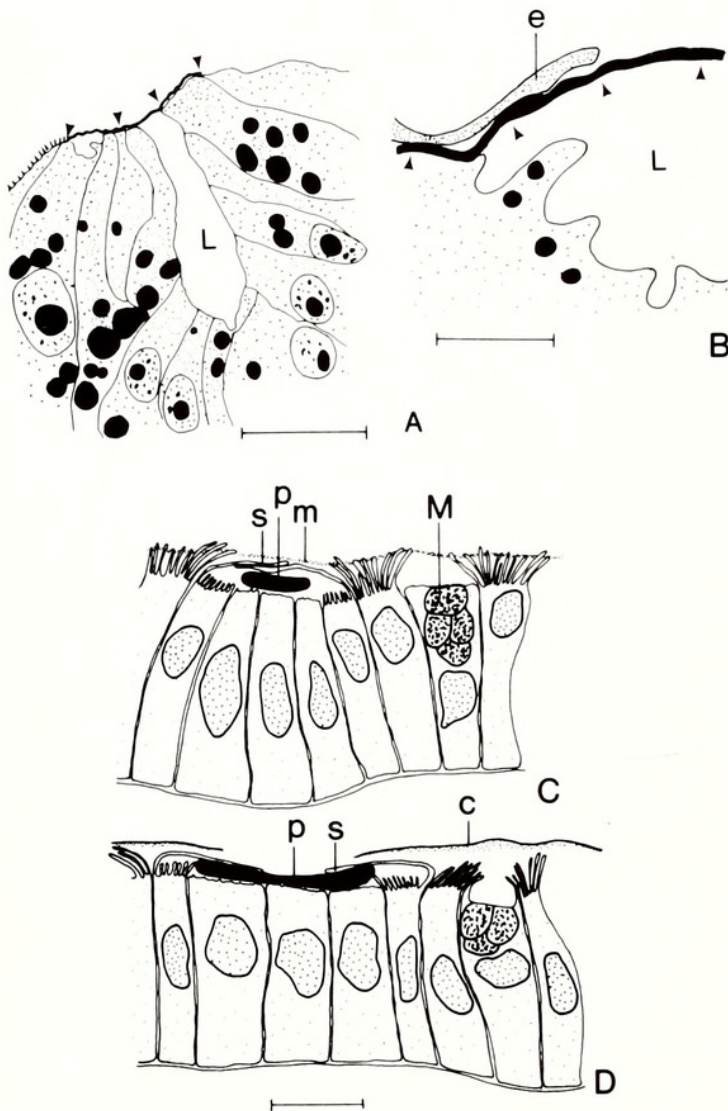Support for the flatworm-like archimolluscan locomo-

tory ventral surface is said to be shown by the cerebrally innervated oral shield of the burrowing Chaetodermomorpha (= Caudofoveata) (Fig. 6A); that is, the shield is regarded as a remnant of the original gliding surface (Salvini-Plawen, 1972, 1980, 1985). The homology with a creeping sole was originally based on histologic similarities in the morphology and arrangement of nerve and mucous cells that lie in the epidermis beneath the oral shield cuticle of chaetoderms and the spiculeless cuticle within the foot-furrow of the creeping neomeniomorphs [Hoffman, 1949; for a translation and explanation, see Scheltema (1983)]. The homology, however, is spurious since molluscan ectoderm, with or without cuticle, is richly supplied with both nerve and mucous cells. Furthermore, Salvini-Plawen (1985) has described (but not illustrated) the specialized ultrastructure of the oral shield, consisting of interdigitated microvilli with glycocalyxes and supporting fibers.

The oral-shield cuticle and epithelium in six genera (*Scutopus*, *Limifossor*, *Prochaetoderma*, *Metachaetoderma*, *Falcidens*, and *Chaetoderma*) representing all families of chaetoderms are continuous with pharyngeal (oral tube) cuticle and epithelium (Scheltema, 1981, 1983). Light microscopy does not reveal a border where the oral shield cuticle joins the pharyngeal cuticle (Figs. 5, 6B), but ultrastructural studies would define this area better. *Scutopus* is considered to be the most primitive chaetoderm because of its least differentiated midgut (Scheltema, 1981) and because of the evidence of ventral fusion of the cuticle (Salvini-Plawen, 1972). In this genus only scattered pyriform mucous cells open through the
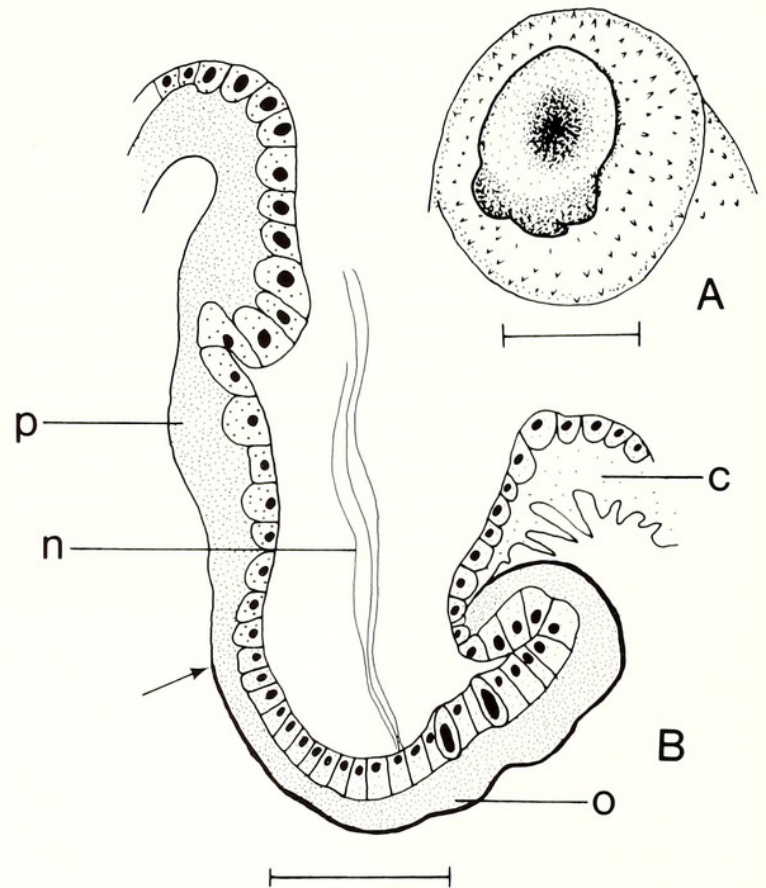

Fig. 6. Oral shield of *Scutopus megaradulatus*. **A.** Anterior view of oral shield *in situ* surrounding darkened mouth in center. **B.** Semischematic drawing of area between large arrowheads in figure 5 showing histology of pharyngeal and oral shield cuticle (lettering and small arrow as in Fig. 5). Scale bars: A = 0.3 mm; B = 0.05 mm.
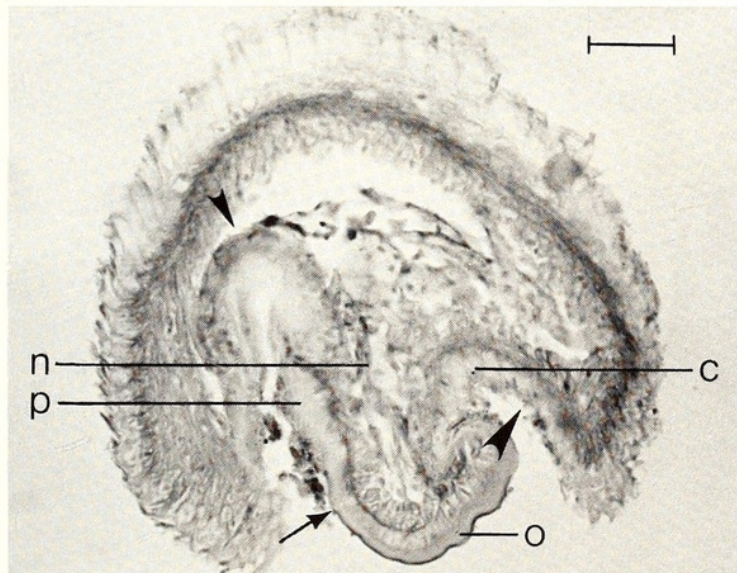

Fig. 5. Oral shield of a Chaetodermomorpha: section through the mouth, pharynx, and oral shield of *Scutopus megaradulatus* Salvini-Plawen showing continuous cuticle of pharynx and oral shield (from 650 m off Cape Hatteras, North Carolina, U. S. A., 34°14.8'N, 75°46.7'W; fixed in formalin, preserved in alcohol, stained with haemotoxylin/Gray's double contrast, sectioned at 0.7 μm.) (c, spiculose cuticle of integument; n, nerve fibers from precerebral ganglion; o, cuticle of oral shield; p, cuticle of pharynx). Small arrow indicates change from oral shield cuticle with a thickened outermost layer to homogeneous cuticle of pharynx. Scale bar = 0.05 mm.

oral shield, further refuting Hoffman's homology, which likened the lobes of mucous cells opening at the lateral edges of the oral shield in advanced Chaetodermatidae with the pedal gland of Neomeniomorpha. This important aspect of Hoffman's homology linking lobed mucous cells of the oral shield and foot furrow was ignored by Salvini-Plawen (1980) while retaining the homology itself. Definitive evidence that the oral shield is a part of a vestigial ventral sole would require innervation from the ventral (= pedal) nerve cord rather than from the cerebral ganglia.

Thus, the oral shield of the Chaetodermomorpha is considered here to be an autapomorphy, a cerebrally innervated external continuation of pharyngeal cuticle like a lip belonging to the head, not to a ventral sole. There is no convincing evidence that it is a remnant of an original creeping sole homologous to the ventral surface of a turbellarian flatworm. The separation of the Aplacophora into two classes based on the supposed (1) plesiomorphy of ventral innervation of the chaetoderm oral shield by the cerebral ganglia and (2) apomorphy of a head separate from the foot in the neomenioids and all other mollusks except chaetoderms is unsatisfactory. A head separate from the foot is considered here to be a plesiomorphy shared by mollusks generally but lost in the bivalves and, because of their burrowing habit, also in the chaetoderms.

RADULA

APLACOPHORAN RADULA

Evidence from the radula morphology of aplacophorans and from the ontogeny of gastropod and chiton radulae suggests that the molluscan radula orginated as a paired structure.

The radula in chitons, the monoplacophoran *Neopilina*, gastropods, and scaphopods is a chitinous structure formed of a single continuous ribbon, or radular membrane, which bears serial rows of teeth; both ribbon and teeth are continually secreted at the proximal end of a pharyngeal diverticulum, the radular sac (Fretter and Graham, 1962; Kerth, 1983; Scheltema, unpub. data). Each row of teeth has left and right sides and usually a central, or median, tooth. The radula is bilaterally symmetrical around the central tooth, that is, the teeth of each side are mirror images of one another. Along the length of the ribbon each tooth has the same shape as the tooth in front of and behind it, that is, the rows of teeth are serially repeated.

In the Aplacophora, the radula is formed in the usual manner and is likewise bilaterally symmetrical and serially repeated (Figs. 7A, 8A, C). The radula has been called monostichous or monoserial if there is only a single tooth in a row; with two mirror-image teeth in each row, distichous or biserial; and with more than two mirror-image teeth, polystichous or polyserial (Nierstrasz, 1905).
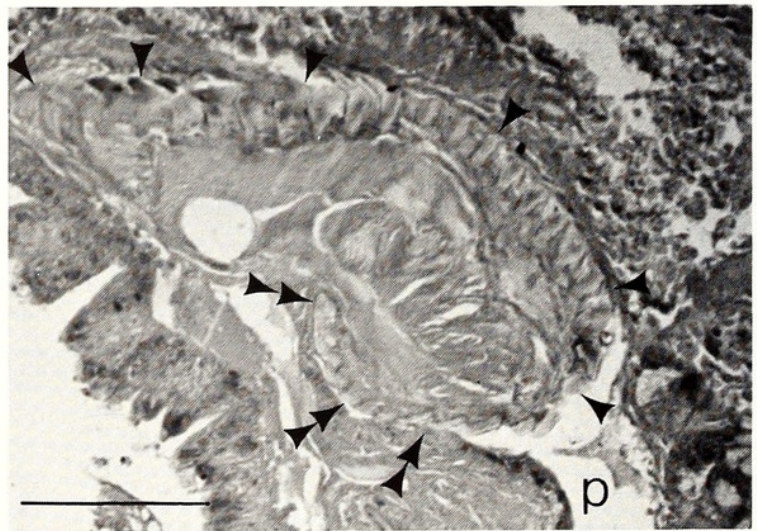
The usual type of radula in the Aplacophora is distichous; a central tooth is lacking in nearly all species. Unique among mollusks the radular membrane itself is divided down the middle so that the entire radula is a bipartite, bilaterally symmetrical, serial structure consisting of two strips
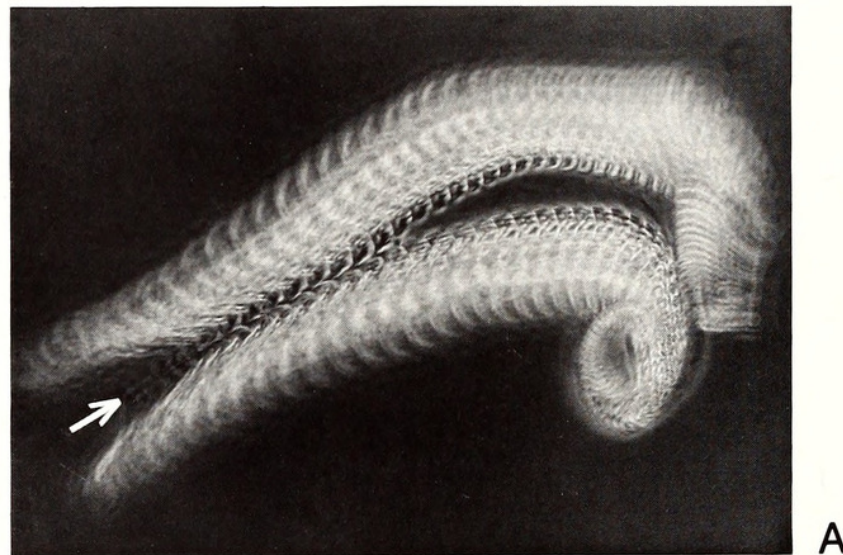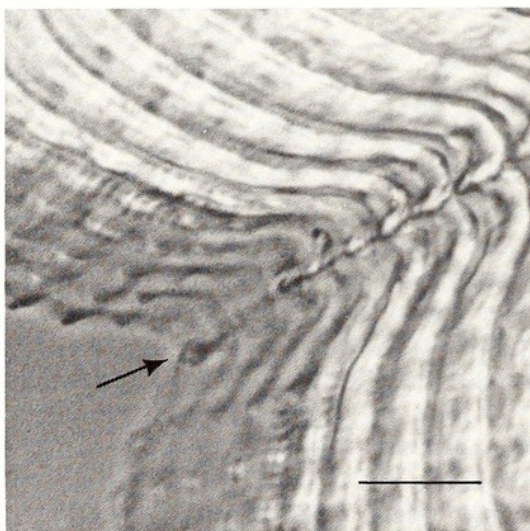
Fig. 7. Aplacophoran radula of *Simrothiella* species. **A.** *Simrothiella* sp. *b* (undescribed); at left are the newest, proximal teeth and fused radular membrane (arrow); distally (on the right) the membrane is bipartite and spirals ventrally down into two ventral pharyngeal pockets. **B.** Close-up of fused, proximal end of radula shown in A. (Whole amount in glycerine; see Scheltema, 1981, for dissecting technique). **C.** *Simrothiella* sp. *a* (undescribed), sagittal section through one side of radula, indicated by single arrowheads; double arrowheads show radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20°50'N, 109° 0.6'W; sections treated as in Fig. 5). Scale bars: A = 100 μm; B = 30 μm; C = 100 μm.

of continuous ribbon, each strip with rows of single denticulate teeth which are the mirror image of the opposed teeth (Figs. 7A, 8A, C). The two parts of the radular membrane are fused to a greater or lesser extent lengthwise along their medial (inner) edges forming a one-piece, unipartite radular ribbon along part of its length (Figs. 7B, 8A; Scheltema, 1981).

The structure of the radula is clear only when it is dissected and isolated from surrounding tissue (Scheltema, 1981). Reconstructions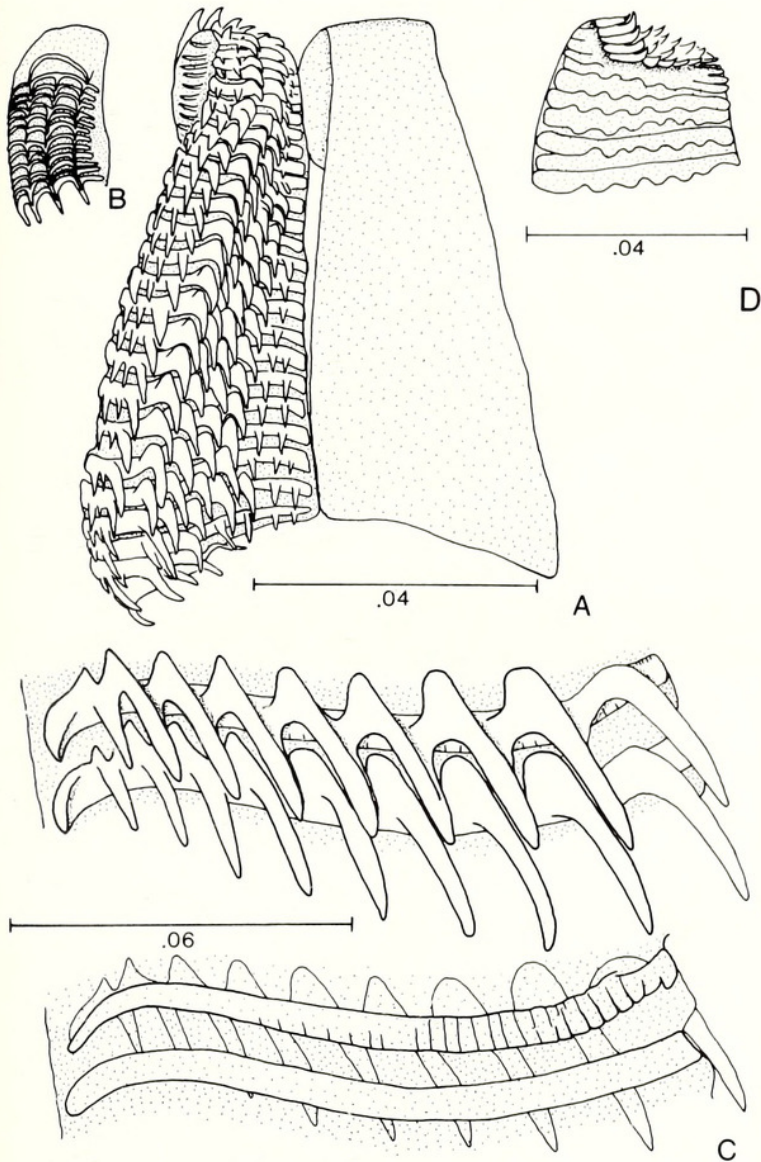 from histologic sections have resulted in misconceptions of actual structure and probable modifications during its evolution [e.g. Nierstrasz, 1905; Salvini-Plawen, 1972, 1978 (*Simrothiella*), 1985].

In order to differentiate the two states that exist for the radular membrane among mollusks, the terms "bipartite" and "unipartite" are used here, and the terms using "—stichous" are reserved for descriptions of the radular teeth only. Thus, a distichous radula can be either uni- or bipartite, but a monostichous radula is necessarily unipartite. The terms with "—serial," which should mean "arranged in series," are not used here, thus obviating the confusion of such a description as "monoserial with paired teeth."

As in other radulate Mollusca, the radular membrane in Aplacophora appears to migrate forward as teeth are added by the odontoblasts; in most species the membranes turn anteroventrally into paired or unpaired ventral pharyngeal pockets, where dissolution of the radula apparently occurs (Figs. 7C, 8D). Unlike grazing gastropods and chitons, in all but one family of Aplacophora the teeth show no wear and thus do not rasp.

The entire radula of juvenile specimen of *Simrothiella* (0.9 mm in length) has been examined. Within each ventral pharyngeal pocket is preserved the earliest ontogenetic development; the first tooth is a nondenticulate bar on a wide expanse of radular membrane (Fig. 8B). As the radula grows in length and width, denticles are added to the teeth medially, i.e. at their inner edges (Fig. 8A). Histologic cross-sections through the proximal, blind end of the radular sac show odontoblasts in two discrete groups, each presumably bound by basement membrane (Figs. 9, 10). The two groups lie within a single sac, surrounded in the usual manner by muscle.

Within the Aplacophora, the radula has evolved at least twice from having a bipartite, distichous radula (Figs. 7, 8) to a radula with a unipartite radular membrane. In the Dondersiidae (Fig. 11), the radula is altogether absent or consists of
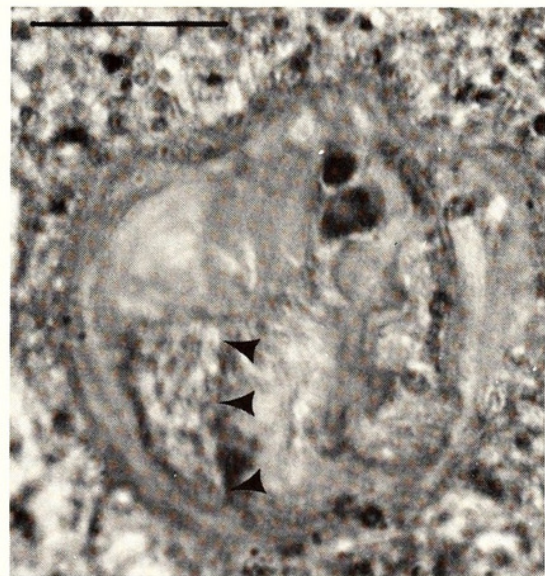

Fig. 8. Radula of *Simrothiella* sp. *b* (undescribed), radular membrane indicated by stippling. **A.** Entire radula of a juvenile specimen, dorsal view, anterior (oldest teeth) at top. Teeth of only left half of radula shown; teeth on the right are the mirror-image of those on the left. Denticles are added to the teeth medially as the radula widens and lengthens. **B.** Distal, oldest part of left radular strip shown folded under in A from ventral pharyngeal pocket; original, first-formed tooth is retained. **C.** Two views of the same two adjacent teeth from an adult specimen: upper teeth drawn in dorsal view as if they were on the right side of the radula, medial denticles on left; lower teeth from left side of radula drawn from beneath radular membrane. **D.** Most anterior part of the same adult radula from which teeth in C were drawn; comparison with juvenile radula B indicates that there is dissolution at the distal end of the radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20°50'N, 109°06'W). Scale bars in mm.

Fig. 9. Radular sac of *Simrothiella* sp. *a* (undescribed). Anterior view of somewhat oblique cross-section through proximal end showing membranes (arrowheads) bounding right and left groups of radula secretory cells (Specimen from 2,633 m at 20°50'N, 109°06'W). Scale bar = 35 μm.
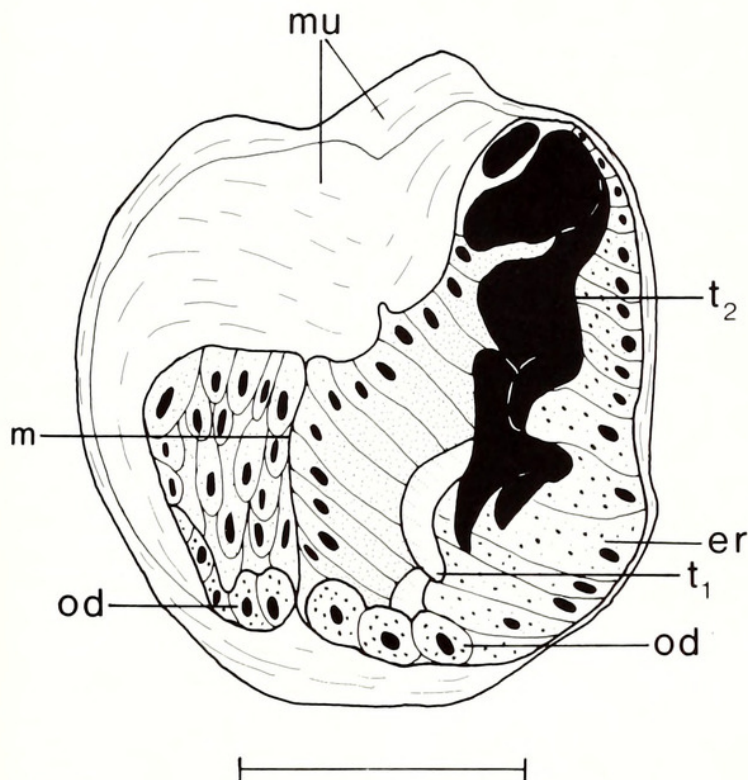
Fig. 10. Semischematic representation of radular sac cross-section shown in figure 9 (er, epithelium of radular membrane; m, membranes bounding left and right groups of radula secretory cells; mu, muscle; od, odontoblasts; t_1, early tooth, or perhaps denticle, not yet staining with haemotoxylin; t_2, older tooth stained by haemotoxylin). Scale bar = 35 μm.

Fig. 11. Monostichous aplacophoran radula of an undescribed species of Atlantic Dondersiidae, four aspects; radular membrane not shown. One denticle is missing from the teeth in the lower two drawings (Specimen from 805 m, 39º51.3'N, 70º54.3'W). Scale in mm.

only a few rows of single teeth, usually 6 or fewer. Its monostichous form appears to be the result of reduction and fusion of a distichous radula, with two of its paired denticles fused at tip and base. In the Prochaetodermatidae, the radula has evolved into a rasping structure with a unipartite radular membrane and a central tooth, or plate (Fig. 12) (Scheltema, 1981,1985).

There are no distinctive radula characteristics, synapomorphies, held in common or uniquely by the Aplacophora and Polyplacophora, the latter with rows of usually 17 teeth on a unipartite radular membrane.

ONTOGENY OF GASTROPOD AND CHITON RADULAE

Vestiges of an original distichous molluscan radula exist in the ontogenetic development of the chiton, pulmonate, opisthobranch, and prosobranch radula. The details of the developing chiton radula are treated by Eernisse and Kerth (1987) and Kerth (this symposium). The radula starts as rarely one to usually three pairs of lateral teeth on a unipartite radular membrane with a central tooth added later. In the ontogenetic development in five families and seven species of pulmonates, the radula begins as a distichous structure with two longitudinal rows of lateral teeth on a unipartite radular membrane; further laterals are then added, and finally a central tooth, which originally may be paired, is secreted thereby uniting the cross-rows (Kerth, 1979). Pruvot-Fol (1926) figured the earliest radular teeth of the opisthobranch *Polycera*,
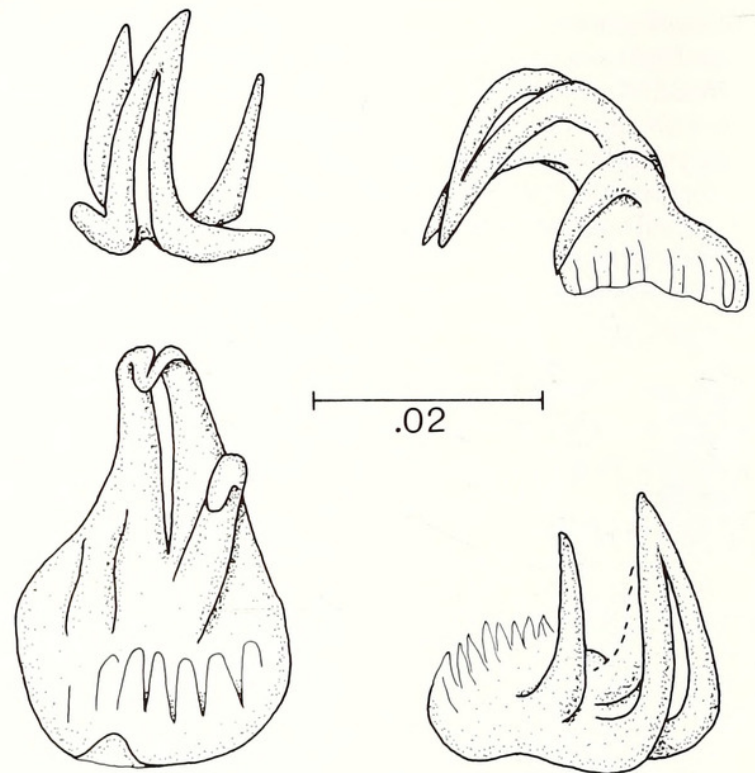

Fig. 12. Undivided, unipartite radular membrane of an undescribed species of Prochaetodermatidae; view of ventral surface (Specimen from 1,624 m 10º30.0'N, 17º51.5'W). Scale = 250 μm.

distichous with a "gouttiere" between them. The radular sac in the opisthobranch *Rhodope* (Riedl, 1960) and in the pulmonate *Physa* (Wierzejski, 1905) originates as a pair of invaginations. In *Rhodope*, lacking a radula, the paired invaginations are lost; in *Physa*, they unite to form a single sac. The developing radular sac in prosobranchs is often bifid (Fretter and Graham, 1962: 173).

To summarize, the most generalized aplacophoran radula is unique because it has a bipartite radular membrane with distichous teeth. Distichous teeth on a unipartite radular membrane exist ontogenetically in other molluscan groups.

PERICARDIUM

The pericardium is a space lined by mesoderm arising embryologically from cell 4d; therefore, it may be considered to be coelom. Raven (1966) questioned, however, whether coelomic cavities among mollusks arise from mesodermal bands (schizocoels) as they do among the annelids. [For an extensive overview of gonopericardial complexes within mollusks, see Wingstrand (1985)].

Salvini-Plawen (1968) hypothesized that the pericardial space evolved within the mesenchyme after the heart, surrounding it and thereby improving its function. Stasek (1972: Fig. 1A, B) illustrated such a situation in the molluscan precursors. Although the pericardium is relatively small in most gastropods and bivalves, in the three primitive classes Aplacophora, Monoplacophora, and Polyplacophora it is spacious relative to the size of the heart (Fig. 13). In *Neopilina* the pericardium is paired, and in the aplacophoran Chaetodermomorpha and most Neomeniomorpha it has either small or large, paired lateral extensions ("horns" in early literature), whose function is not known. Ontogenetically, in the single species of aplacophoran for which size during development is mentioned (Baba, 1938), the pericardium is already large before the heart develops.

How the pericardium functionally could have evolved in a pre-mollusk as a small space, then have become spacious and probably paired, and finally again become reduced in size, is difficult to imagine. Moreover, during organogenesis, the pericardium develops before the heart and the heart arises
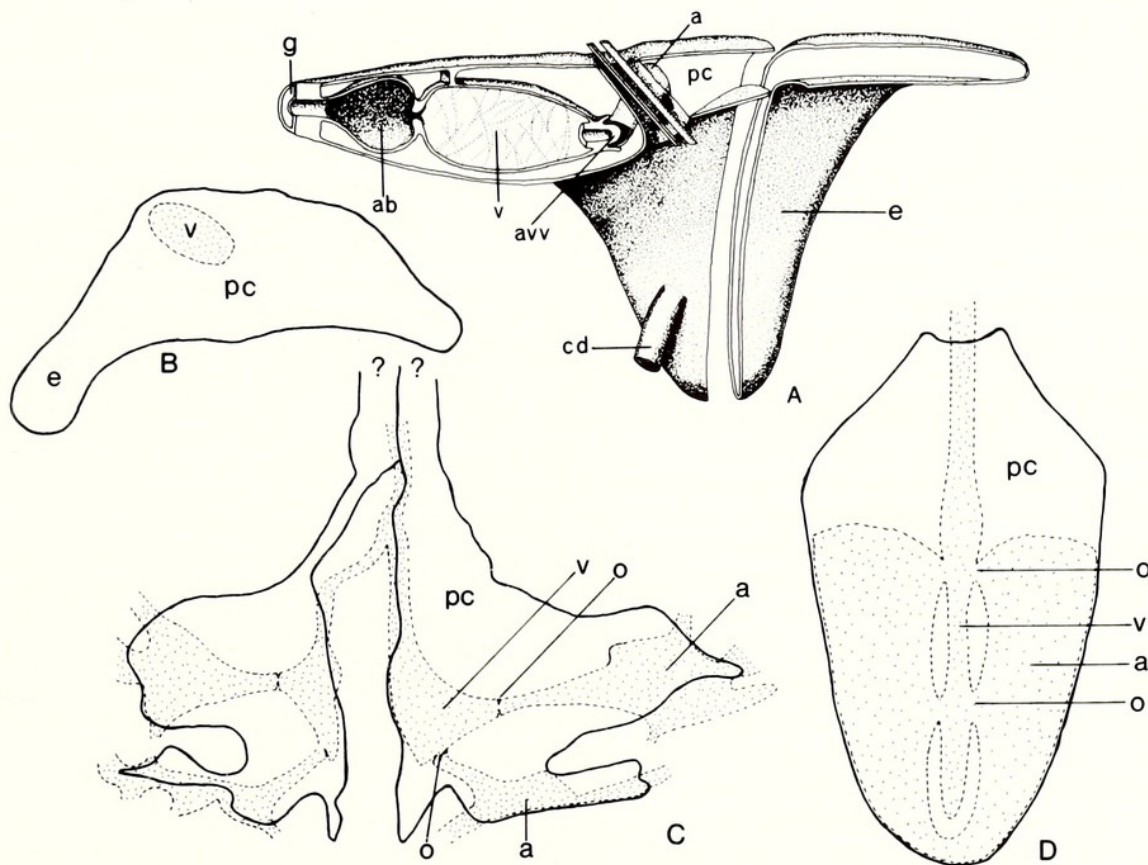

Fig. 13. Heart and pericardium in the primitive molluscan classes Aplacophora (A, B), Monoplacophora (C), and Polyplacophora (D) showing large pericardial spaces in relation to the size of the heart. In B, C, and D the heart is stippled and the pericardium is blank. **A.** *Chaetoderma nitidulum* Lovén, sagittal section through pericardium, heart, and gonopericardial duct (after Scheltema, 1972). Paired auricles (a) open into the ventricle on each side of an atrioventricular valve (avv). Gonads empty through paired ducts (g) into the pericardium (pc), and coelomoducts (cd) lead from the pericardium to the cloaca (not shown). The large paired lateral extensions of the pericardium (e) are known as "horns" in the older literature. **B.** *Simrothiella* sp. *a* (original drawing), same specimen as in figure 9. Somewhat oblique cross-section through the pericardium (pc), ventricle (v), and lateral extension of the pericardium (e). **C.** *Neopilina galatheae* Lemche, dorsal view (after Lemche and Wingstrand, 1959). The pericardium (pc) and ventricles (v) are paired; two pairs of auricles (a) open into each ventricle. It is not known whether there is a connection between the pericardia and gonads (see Wingstrand, 1985). **D.** *Acanthopleura echinata*, dorsal view (after Plate, 1898). Two pairs of ostia (o) open on each side into the ventricle (v); the number of ostia varies from one to four pairs, according to species (a, auricle; ab, aortal bulb; avv, atrioventricular valve; cd, coelomoduct; e, lateral extension of pericardium; g, gonopericardial duct; o, opening between auricle and ventricle; pc, pericardium; v, ventricle). Scales not indicated.

from the dorsal or inner epithelium of the pericardium (Baba, 1938; Raven, 1966), suggesting that evolution of the pericardium probably preceded that of the heart. The large pericardial spaces in the Aplacophora, Monoplacophora, and Polyplacophora point to a coelomate rather than to an acoelomate, turbellariomorph ancestor and lead one to re-examine the evidence for ancestral relationship between the annelids and mollusks (see Vagvolgyi, 1967; Wingstrand, 1985).

DISCUSSION

ACOELOMATE VERSUS COELOMATE MOLLUSCAN ORIGINS

The hypothesis that the ancestor of mollusks was acoelomate is rejected in favor of a coelomate origin because: (1) primitive molluscan taxa have large pericardial spaces; (2) evidence is lacking that the pericardial space began as a small opening in mesenchyme lined by mesoderm; (3) Wingstrand's evidence (1985) strongly suggests a molluscan "derivation from advanced oligomeric Spiralia ('proto-annelids' or 'proto-articulates')" (p. 8) (Fig. 14).

The existence of large pericardial spaces in the primitive extant mollusks has not been considered in hypotheses of an acoelomate molluscan origin. Rejection of the hypothesis of reduced metamery as the origin of molluscan coelom is probably correct (Salvini-Plawen, 1968); however, one need not suppose, therefore, a total absence of either coelom or metamery. Reiger (1985), after careful comparative studies of the fine structure of acoel connective tissue, argued that the acoelomate Bilateria themselves are derived through progenesis from a coelomate ancestor.

SHELL AND SPICULES

The Aplacophora probably evolved from a shell-less rather than from a shelled ancestor. Evidence for this assertion comes from properties of the cuticle (see SHELL AND SPICULES above) and from a comparison of numbers of dorsoventral muscles that run between the outer body wall and foot among various mollusks. In the Neomeniomorpha, two bilateral sets of oblique bands are repeated serially along the body; they are considered homologous to the dorsoventral pedal muscles in other mollusks (Salvini-Plawen, 1972). The evolution of dorsoventral musculature, which coevolved with the shell, has been toward reduction in number, from eight in Polyplacophora and tryblidian Monoplacophora to one in most Gastropoda. The serial arrangement of numerous bands in the Neomeniomorpha is considered therefore to be a plesiomorphy that preceded shell development and its consequent reduction of dorsoventral musculature.

No convincing published evidence links the process of extracellular spicule formation by a single cell (Haas, 1981) with the development of shell fields and shell deposition. The only common attribute of spicule and shell formation is that both are extracellular deposits of calcium carbonate.

Three types of calcium carbonate coverings are found in the Mollusca: spicules in Aplacophora and Polyplacophora; the shell plates of the Polyplacophora with a thin
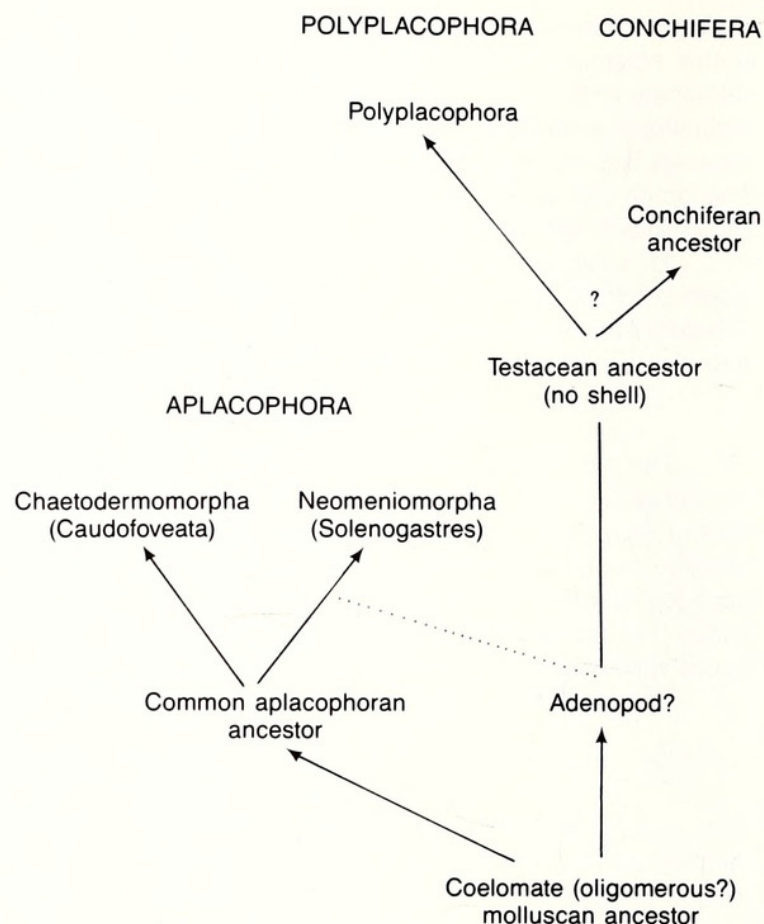

Fig. 14. Phylogeny of the Mollusca (adapted from Wingstrand, 1985). The questioned Adenopod can be dropped (see argument in section "Chaetoderm oral shield and the archimollusk"). The text raises questions about a common testacean ancestor in comparing chiton and conchiferan shell formation and structure (see argument in section "Shell and Spicules"). A coelomate molluscan ancestor, whether or not oligomerous, is corroborated here (see section "Pericardium"). A common aplacophoran ancestor descended directly from the stem mollusk is indicated (see sections "Chaetoderm oral shield and the archimollusk" and "Aplacophora, a monophyletic group"). The stem mollusk had a paired radula with a two-part radular membrane and distichous teeth (see section "Radula").

(nonperiostracal) organic cover, tegmentum, and hypostracum; and the conchiferan shell with periostracum, prismatic layer, and nacreous layer. The trend has been to treat these calcium carbonate structures as homologous, with a morphocline leading from spicules to plates by coalescence in chitons (e.g. Salvini-Plawen, 1972), and from the 8 shell fields in chitons to the single shell field of univalves and bivalves (e.g. Haas, 1981). From the evidence of structure and ontogeny, and discounting the problematic "Pruvot's larva," the existence of this morphocline is seriously questioned.

Is there a single ancestor for polyplacophorans and the remaining shelled mollusks? Wingstrand (1985) makes a strong case for such a hypothetical testacean ancestor, equivalent to the archiplacophoran of figure 1, based on synapomorphies of radula with its supports and musculature, oral flaps, digestive system, pharyngeal diverticula, 8 pairs of pedal retractors, and, possibly, the number and position

of atria (Fig. 13). The shells in chitons are considered to be autapomorphies, but the shell fields and the mineralization process are homologous and monophyletic in chitons and Conchifera. Reasons have been stated above (section on Shell and Spicules) for doubting this homology (Fig. 14). Answers to questions about Pruvot's larva and the relationship of polyplacophoran plates to conchiferan shells could lie in the unknown embryology of *Neopilina* and with the yet-to-be reexamined Pruvot's larva.

RADULA

The direction of evolutionary change in the structure of the aplacophoran radula appears to be from a paired, or bipartite, radular membrane to a single, unipartite ribbon. The rationale for this polarity is based on several points. (1) Rasping seems a more advanced, complicated function for a radula over a simple ability to grasp as found in most Aplacophora. Rasping probably requires the integration of structure provided by a unipartite radular membrane. Only among the Prochaetodermatidae is there wear of the anterior teeth, i.e. evidence of rasping (Scheltema, 1981, 1985), and here the radular membrane is also unipartite. (2) All other radulate aplacophorans except the Dondersiidae and Chaetodermatide with reduced and specialized teeth (Fig. 11; Scheltema, 1972) have a bipartite radular membrane with a fused, unipartite section that often retains visible evidence of fusion; the region of this fused section is not fixed but varies among families and genera (Scheltema, 1981). It is possible, but not parsimonious, to imagine that the radular membrane was originally unipartite, then divided into two, and finally fused again; however, if so, the odontoblasts producing such a secondarily derived, paired radula would have to evolve from a single into a paired group of cells. (3) During ontogeny of the radula in chitons and gastropods, the central tooth is added only after several rows of one or more pairs of lateral teeth have been formed. Presumably the median part of the ribbon is where an originally paired ribbon became unified; subsequently odontoblasts for the central tooth could come into being.

The paired structure of the aplacophoran radula is considered to be the primitive form in mollusks because the direction of evolution, distichous bipartite to distichous unipartite in Aplacophora, is continued in the ontogeny of the gastropod radula, from distichous unipartite to polystichous. Since aplacophorans probably evolved from a shell-less ancestor (see above), the distinctive molluscan structure of a radula was already present when shell evolved (Fig. 14). The aplacophoran plesiomorphic bipartite radula does not form a basis for linking the Aplacophora closely to any other taxon of mollusks.

APLACOPHORA, A MONOPHYLETIC GROUP

The Aplacophora should not be separated into two classes or subphyla on the erroneous homology of the chaetoderm oral shield with a turbellariomorph creeping sole. The oral shield is an autapomorphy of the Chaetodermomorpha. The Neomeniomorpha and Chaetodermomorpha form a monophyletic group with the following probable synapomorphies: a rounded worm shape; a dorsoterminal sensory organ [a chemoreceptor lying external to the mantle cavity, and not known to be ontogenetically or functionally homologous to the osphradium within the mantle cavity of other mollusks (Haszprunar, 1987)]; three to six pairs of precerebral ganglia or swellings (Salvini-Plawen, 1978, 1985); a reproductive system in which the gonads empty into the pericardium through gonopericardial ducts and the pericardium is emptied into the cloaca through coelomoducts (Fig. 13A) (but see Salvini-Plawen, 1972, 1985). An adenopod ancestor becomes a superfluous construct (Fig. 14). As the direction of evolution of organ systems within the Aplacophora becomes clear, new insights into the evolution of mollusks should come to light.

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