

POSITION OF THE CLASS APLACOPHORA IN THE PHYLUM MOLLUSCA¹

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ABSTRACT

The Aplacophora are shell-less, vermiform mollusks found from the continental shelf regions of the world to depths of 9,000 m. They are grouped into a single class with 2 subclasses: Chaetodermomorpha (= Caudofoveata) and Neomeniomorpha (= Ventroplicida; Solenogastres sensu Salvini-Plawen), a classification which preserves early nomenclature based on *Chaetoderma* Lovén, validated by the International Commission on Zoological Nomenclature. The name "solenogaster" is reserved as a common noun like "clam" or "snail."

The Aplacophora have several typical molluscan characters, namely a radula with associated buccal structures; a style sac and mucoid style; a coelom restricted to gonads, a dorsal pericardium, and kidneys; a heart consisting of a ventricle and 2 auricles; laterodorsal-ventral musculature; ventral musculature that bends the body and contained organs dorsally; a dorsal gut; mantle cavity and gills; a vestigial foot which secretes a slime trail; a nervous system of paired ganglionated cords, ladderlike, with pharyngeal ring and buccal ganglia; and finally a development which includes spiral cleavage and a protobranch-like larva. Most of these molluscan characters are not structurally like those of chitons with which they have often been classified; therefore, the Aplacophora are classified separately from the Polyplacophora.

The 2 aplacophoran taxa resemble each other in their nervous system, coelom, haemocoel, musculature, and shape. Differences in integument between the 2 taxa may be due to reduction in the burrowing Chaetodermomorpha, and in the digestive system due to the obligate coelenterate feeding in the Neomeniomorpha.

It is of phylogenetic importance that several characteristic molluscan structures have evolved in the Aplacophora independent of a shell.

INTRODUCTION

The Aplacophora are worm-shaped mollusks surrounded by a cuticle bearing calcareous spicules; they inhabit the deep ocean basins and continental shelf and slope regions of the world. Observations from more than 380 collections made by the Woods Hole Oceanographic Institution, Oregon State University, Scripps Institution of Oceanography, and Centre National de Tri d'Océanographie Biologique show that their greatest species radiation has been in the deep sea. They burrow into or creep on mud; some wrap themselves around alcyonarians upon which they feed. They are common in the deep sea, occurring in nearly all small-meshed epibenthic dredge hauls (Hessler & Sanders, 1967) and box cores taken from all depths to 9,000 m. In recent years the number of biological surveys of the deep sea has increased, and the discovery of numerous new aplacophoran

species has rekindled interest in this group. Although most species are still to be described, some recent taxonomic works are those of Salvini-Plawen (1972, bibliography, for his papers), Schwabl (1963) and Scheltema (1976).

CLASSIFICATION

The 2 classifications given in Table 1 are currently in use for living mollusks. Both classifications retain the 2 distinct taxa that have been recognized since the 19th century: one taxon (Neomeniomorpha = Ventroplicida = Solenogastres sensu Salvini-Plawen) is distinguished by a ventral groove containing a narrow foot, the other (Chaetodermomorpha = Caudofoveata) lacks a ventral groove and has an oral shield and a pair of ctenidia. It should be stressed that there has been no modification of membership in the 2 aplacophoran taxa in either of

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the classifications; only the hierarchical rank has been shifted, and in the second, names have been changed.

The first classification is recommended for 3 reasons: 1) it conserves nomenclature in use since the early 1900's; 2) it separates the Aplacophora and Polyplacophora; and 3) it gives a hierarchical ranking to the 2 aplacophoran taxa that fits well with the arrangement of equally similar taxa in other molluscan classes.

NOMENCLATURE

Nomenclatural changes in the Aplacophora started in the 1930's with the belief that the genus *Chaetoderma* Lovén 1844 was a junior homonym of *Chaetoderma* Swainson 1839 (Pisces). The next available name was *Crystallophrisson* Möbius 1875, an orthographic horror variously spelled in the literature. Heppell (1963), who showed that Swainson used multiple spellings, requested and obtained from the International Commission on Zoological Nomenclature (ICZN) validation of the genera *Chaetoderma* Lovén 1844 and *Chaetodermis* Swainson 1839 (Opinion 764, ICZN, 1966).

Previous to the ICZN ruling, Boettger (1956), wishing to avoid an ordinal name based on "*Crystallophrisson*," used *Caudofoveata* to replace *Chaetodermatoidea*; he also changed the name *Neomeniida* to *Ventroplicida*. As *Chaetoderma* Lovén is a valid name, there is historical reason for preserving Pelseneer's names *Chaetodermomorpha* and *Neomeniomorpha* for the 2 major taxa of Aplacophora. The use of *Solenogastres* Gegenbaur 1878 for the *Neomeniomorpha* alone is particularly confusing, as Gegenbaur included the only 2 genera then known, *Chaetoderma* and *Neomenia*, under this name, which appears throughout the literature as synonymous with Aplacophora. "*Solenogaster*" is best used with lower case and anglicized spelling, a term equivalent to "clam" or "snail."

APLACOPHORA AS MOLLUSKS

The molluscan affinities of the Aplacophora, first noticed in the mid-1870's, have long been discussed (see Hyman, 1967: 2-3, 68-70, for a review). The Aplacophora have

been placed back and forth within and outside the phylum Mollusca for nearly a century; when considered true mollusks, it has usually been because of supposed similarities to chitons. Even Hyman, who recognized the chitons and aplacophorans as separate classes, stated that such similarities "justify the inclusion of solenogasters in Mollusca" (1967: 69), and Fretter & Graham considered that the solenogasters are "undoubtedly related in some way to the chitons" (1962:8), although they placed them outside the Mollusca. The latter returned them to Mollusca in 1976 (p. 548) without discussion. Salvini-Plawen (Table 1) has grouped chitons and aplacophorans as a separate subphylum. The chitons and aplacophorans together have been known as *Amphineura*, *Aculifera*, or *Isopleura*.

At the time that Hoffman (1949) carefully described the integument of the Aplacophora, they had not been considered mollusks by Thiele (e.g., 1925: 12-14), one of the strongest voices of the preceding decades, because they seemed to him to lack the important molluscan characters of "shell, mantle, foot, and nephridia; further, in other mollusks the gonoducts do not issue from the pericardium" (as summarized by Hyman, 1967: 68). Hoffman compared chiton and aplacophoran integuments in both mantle and foot, and by certain homologies between them, brought the 2 aplacophoran taxa back within the concept of mollusks. Two doubtful homologies that he proposed are (1) that the slime tracts of chitons equal the "shell glands" of aplacophorans, a homology that calls for an impossible reorientation of gills in the aplacophorans as noted by Hoffman himself (1949: 407), and (2) that the gland cells of the chiton foot equal the glands of the chaetodermomorph oral shield. However, he concluded that "In spite of my view that the *Neomenioidea* and *Chaetodermatida* were thus early separated from each other and that their common stem was chiton-like in respect to the mantle and foot, I do not feel justified in regarding the *Neomenioidea*, *Chaetodermatida*, and chitons as 3 equivalent groups in the class *Amphineura*. The *Neomenioidea* and *Chaetodermatida* resemble each other exactly in more respects (e.g., in regard to the nervous system and coelom) than either resembles the chitons" (1949: 424, here translated).

Boettger (1956) elaborated on Hoffman

TABLE 1. Classification of the living Mollusca.¹

I Phylum Mollusca	II Phylum Mollusca ²
Class Monoplacophora Wenz 1940 Class Aplacophora von Ihering 1876 [= Solenogastres Gegenbaur 1878] Subclass Chaetodermomorpha Pelseneer 1906 Subclass Neomeniomorpha Pelseneer 1906 [= Ventro- plicida Boettger 1956] Class Polyplacophora [ex Polyplacophores] de Blainville 1816	Subphylum Aculifera Hatschek 1891 [= Amphineura von Ihering 1876] Class Caudofoveata Boettger 1956 Class Solenogastres Gegenbaur 1878 [<i>partim</i>] Class Placophora von Ihering 1876 Subphylum Conchifera Class Tryblidiida Wenz 1939 [= Monoplacophora] (Classes Gastropoda, Bivalvia, Scaphopoda, Cephalopoda)
(Classes Gastropoda, Pelecypoda, Scaphopoda, Cephalopoda)	

¹A recent classification including the extinct mollusks is in Runnegar & Pojeta (1974), who place the Aplacophora and Polyplacophora by themselves in 2 separate subphyla.

²From Salvini-Plawen (1972).

in a theoretical paper on early mollusks, and Salvini-Plawen (1967: 399) stated that from Hoffman's work "der Placophoran-Verwandschaft der aplacophoran Gruppen nicht mehr zu Zweifeln ist."

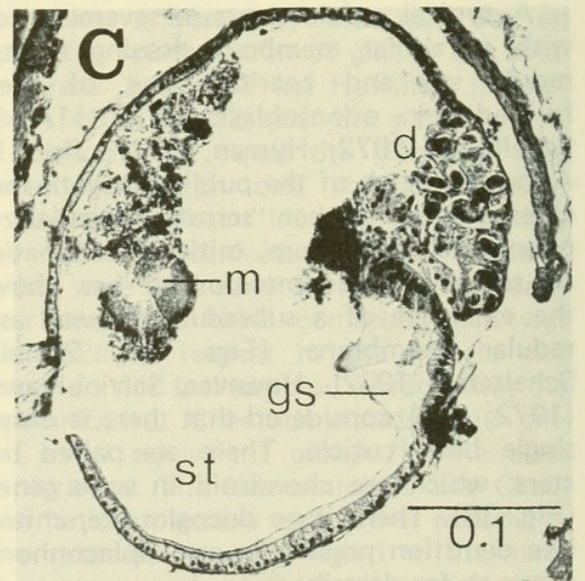
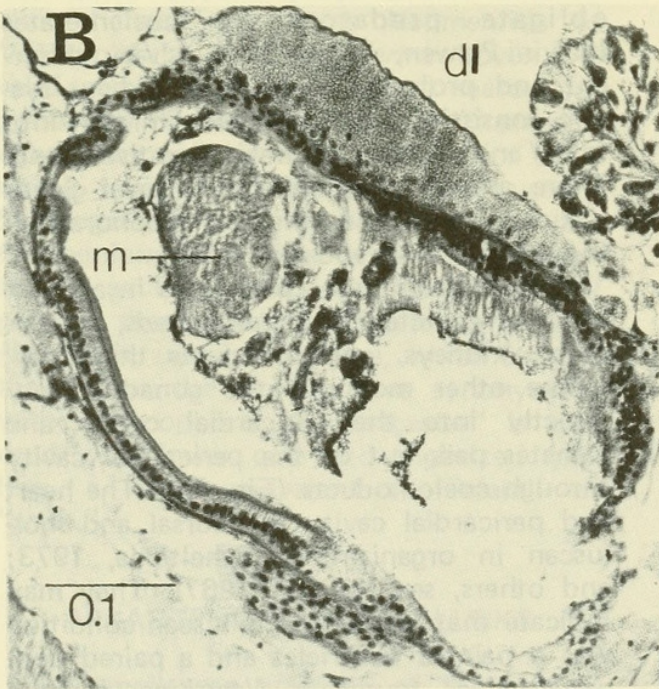
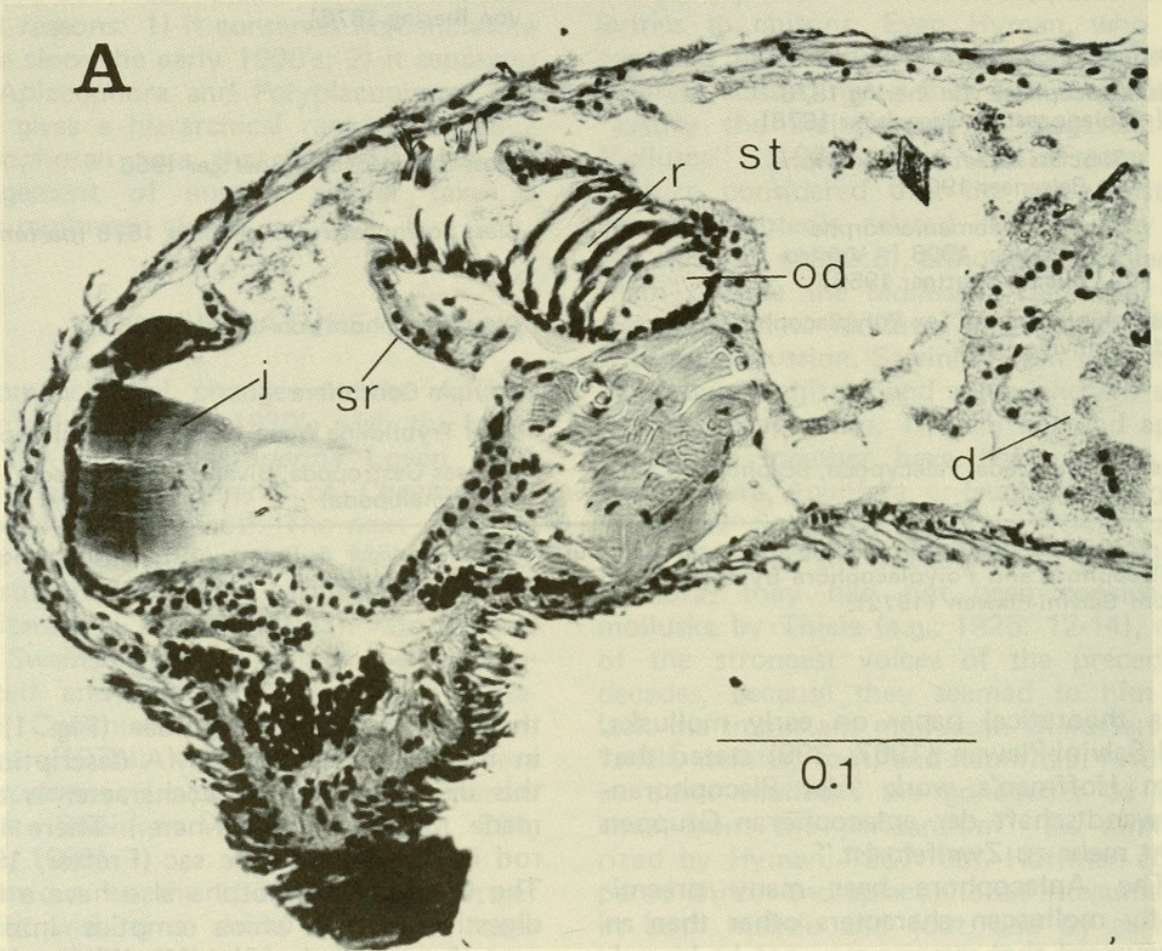
The Aplacophora bear many preeminently molluscan characters other than an integument that may or may not be homologous to that of the chitons (see below). Despite their specialized vermiform shape, they have many archaic, or conservative, molluscan characters.

A typical radula exists in several genera with a radular membrane issuing from a radula sac and bearing rows of teeth formed by odontoblasts (Figs. 1A, 2; Scheltema, 1972; Hyman, 1967, fig. 15). Although much of the published work indicates no more than serrate cuticularized pharyngeal epithelium, critical examination of some Chaetodermomorpha has shown the existence of a subradular as well as a radular membrane (Figs. 1A, 2; also Scheltema, 1972). However, Salvini-Plawen (1972: 240) considered that there is only a single basal cuticle. There are paired bolsters, which are chondroid in some genera (Fig. 3B). There is no docoglossate, chiton-like dentition present in any Aplacophoran genus so far described.

A style sac occurs in the Chaetodermomorpha; a style in the form of a mucoid rod and gastric shield are present as well in

the family Chaetodermatidae (Fig. 1) and in the genus *Limifossor*. (A description of this uniquely molluscan character is to be made more fully elsewhere.) There is no rod in the chiton style sac (Fretter, 1937). The Chaetodermomorpha also have a blind digestive gland, which empties into the posterior stomach (Fig. 1C; Wirén, 1892). The Neomeniomorpha, many of which are obligate predators on coelenterates (Salvini-Plawen, 1967), have a very different and probably specialized mid-gut system consisting of a wide tube thrown into folds and lack a separate digestive gland. There are no chiton-like esophageal glands ("sugar-glands") in the Aplacophora, although salivary glands are found.

The aplacophoran coelom, as in all mollusks is restricted to paired gonads, pericardium, kidneys, and the ducts therefrom; unlike other mollusks, the gonads empty directly into the pericardial cavity and gametes pass out of the pericardial cavity through coelomoducts (Fig. 4A). The heart and pericardial cavity are dorsal and molluscan in organization (Scheltema, 1973; and others, see Hyman, 1967). They may indicate that the early molluscan condition was a pair of ventricles and a paired pericardium, as found in *Neopilina*, for the heart is bilobed during diastole and there are 2 large V-shaped lateral extensions of the pericardium (Chaetodermatidae: Fig.



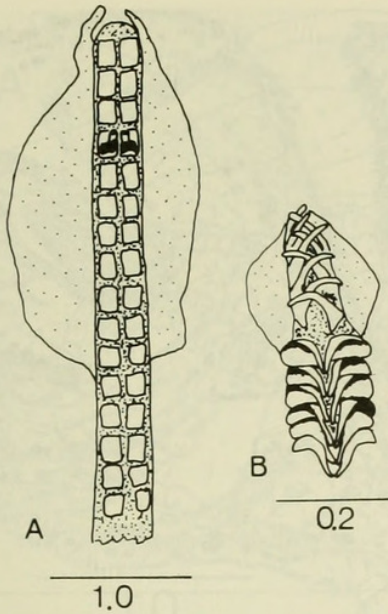


FIG. 2. Radula ribbon (heavy stippling) and subradular membrane (light stippling) of the limpet *Acmaea testudinalis* (A) and *Prochaetoderma* sp. (B; cf. Fig. 1). The position of the teeth in *Acmaea* is indicated; one transverse row is drawn. Scales in mm.

4C; also Scheltema, 1973, figs. 1, 2). The chiton pericardial cavity, also large, does not receive gametes from the gonads.

Histological evidence suggests functional kidneys in the Chaetodermatidae; the cells of the C-shaped coelomoducts, emptying the pericardium to the outside, are similar to the kidney cells in the protobranch *Nucula* (Fig. 3A, 3C). There are no experimental data on the function of the aplacophoran coelomoducts.

Laterodorsal-ventral musculature, expressed serially in the Neomeniomorpha and in restricted body areas in the burrowing Chaetodermomorpha, may preserve the condition leading to reduction in pedal retractors of shelled mollusks including chitons (Salvini-Plawen, 1969). Ventral longitudinal muscles, found in both chitons and

aplacophorans, produce a dorsal bend (Fig. 5A-D). In the burrowing chaetoderms these muscles are weak (Fig. 4B). The digestive system is dorsally placed with a ventral mouth and anus (Figs. 1A, 3A, 4B). The dorsal bend appears during development in the late embryos of 2 species of neomeniomorphs (Pruvot, 1890; Thompson, 1960).

The molluscan head-foot is not in great evidence in the vermiform Aplacophora. However, vestiges remain in both taxa. The Neomeniomorpha produce a sticky slime track along which they creep by the ciliary action of a greatly reduced foot; the head is free of the substrate and moves about by hydrostatic action (personal observation). The Chaetodermomorpha retain a ventral (= pedal) sinus (Fig. 4B), and the genus *Scutopus* still has an external indication of a lost foot (Salvini-Plawen, 1972). In both taxa there is "a malleable 'haemoskeleton' that can be manipulated by the muscles of the body wall" as described by Morton (1967: 17) for the ancestral condition.

A mantle is present in the sense that the epithelium which covers the outer body secretes a mucoid substance and calcium carbonate and forms a fold over a mantle cavity (Fig. 4A, 4C). Histochemical staining indicates that the cuticle of *Proneomenia* is composed of a glucoprotein complex "tentatively equated with an early mucoid stage in the evolution of the molluscan shell" but it is not the same as chiton cuticle, which is more specialized (Beedham & Trueman, 1968: 443). Both Hoffman (1949) and Salvini-Plawen (1972) considered the spicular part of the chiton cuticle to be homologous to aplacophoran cuticle; however, Stasek (1972: 18) and Stasek & McWilliams (1973) pointed out that the homologous parts may be the spiculose integument of the dorsally turned mantle of the chitons and the nonspiculose mantle integument bordering the foot-fold

FIG. 1. A: Sagittal section, anterior of *Prochaetoderma* sp. The most recently formed radula tooth lies adjacent to the odontoblasts at the blind end of the radula sac. The empty space in the head is that part of the pharynx lying between the paired "jaws" that protect and open the ventral mouth (not shown in section). B: Cross-section through mucoid style lying at anterior end of the style sac in *Chaetoderma nitidulum*. Two digestive cell types line the digestive gland lumen ("Körnerzellen" and "Keulenzellen"; Wirén, 1892). C: Cross-section of anterior end of 100 μ m mucoid style projecting from style sac (not shown) and gastric shield in *Falcidens caudatus*; the digestive gland opens into the stomach. Scales in mm.

d	digestive gland	od	odontoblasts
dl	digestive gland lumen	r	radula sac
gs	gastric shield	sr	subradular membrane
j	"jaws"	st	stomach
m	mucoid style		

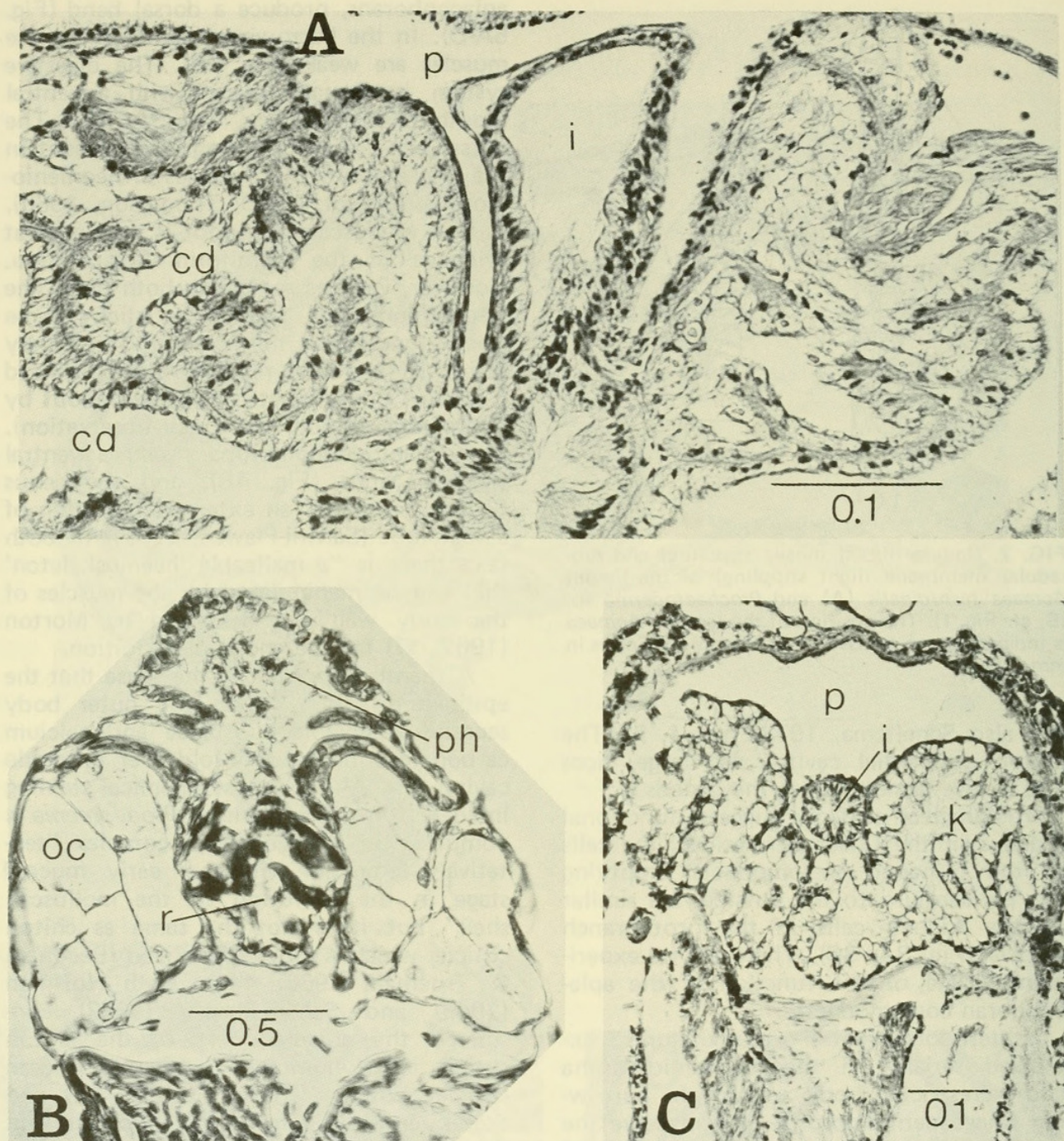


FIG. 3. A: Coelomoducts of *Chaetoderma nitidulum* show great histological similarity to the kidneys of the protobranch *Nucula annulata* (C). Both upper and lower limbs of the C-shaped coelomoducts of *Chaetoderma* are evident, as well as the ventral bend of the intestine. B: Paired odontophore cartilages lie on either side of the radula sac with radula teeth in *Prochaetoderma* sp. C: Kidneys of the protobranch *Nucula annulata*. Scales in mm.

cd	coelomoducts
i	intestine
k	kidney
oc	odontophore cartilage

p	pericardial cavity
ph	pharynx
r	radula sac

and lying within the ventral groove of the Neomeniomorpha.

The shape of the aplacophorans has greatly affected the extent of the mantle cavity, but typical molluscan characters are still evident in the posterior cavity into which the anus and coelomoducts empty

and which contains paired gills in the Chaetodermomorpha. The Neomeniomorpha also retain the mantle cavity in the form of a groove on either side of the vestigial foot.

The nervous system is composed of paired cerebral ganglia and paired lateral and ventral cords with cross commissures, a

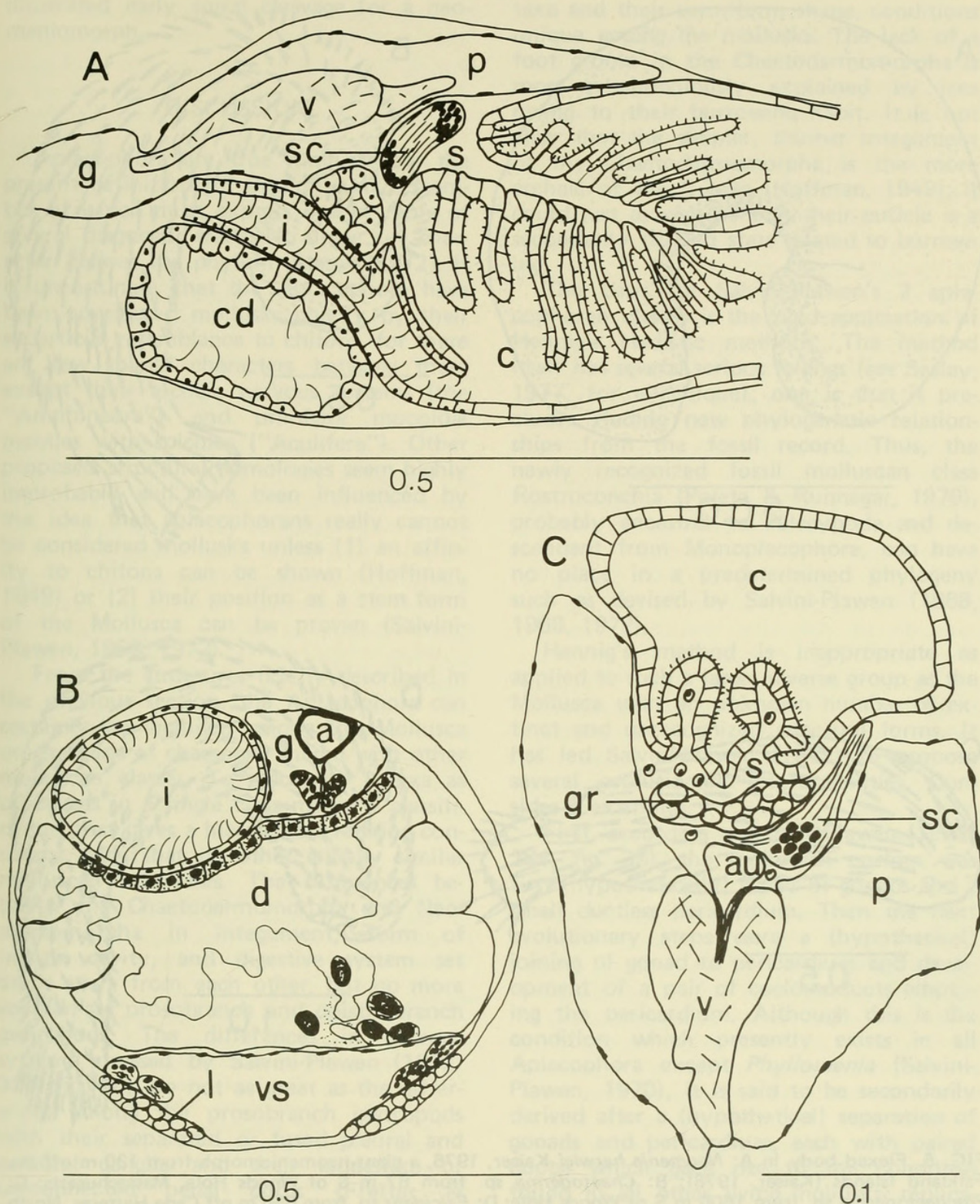


FIG. 4. A: Sagittal section through posterior region of *Falcidens caudatus*. The gonad empties into the pericardial cavity, which is emptied by C-shaped coelomoducts (connection not shown). The intestine, above which lies a suprarectal commissure, bends ventrally to empty into the mantle cavity between a pair of gills. Muscles are not shown. B: Cross-section through the posterior half of a *Chaetoderma nitidulum* juvenile. The gonads, fused in adults, are still paired; the intestine is dorsal. There are 2 types of cell in the digestive gland (cf. Fig. 1B). The ventral sinus is probably homologous to the pedal sinus; a slight thickening of the muscle wall on either side is weakly expressed ventral longitudinal bands causing dorsal bending (Fig. 5). C: Dorsal frontal section through the posterior end of *Falcidens caudatus*. Both the ventricle in diastole and the pericardial cavity are bilobed. Scales in mm.

a	aorta	g	gonad	s	gill sinus
au	auricle	gr	gill retractor	sc	suprarectal commissure
c	mantle cavity	i	intestine	v	ventricle
cd	coelomoducts	l	longitudinal bands	vs	ventral sinus
d	digestive gland	p	pericardial cavity		

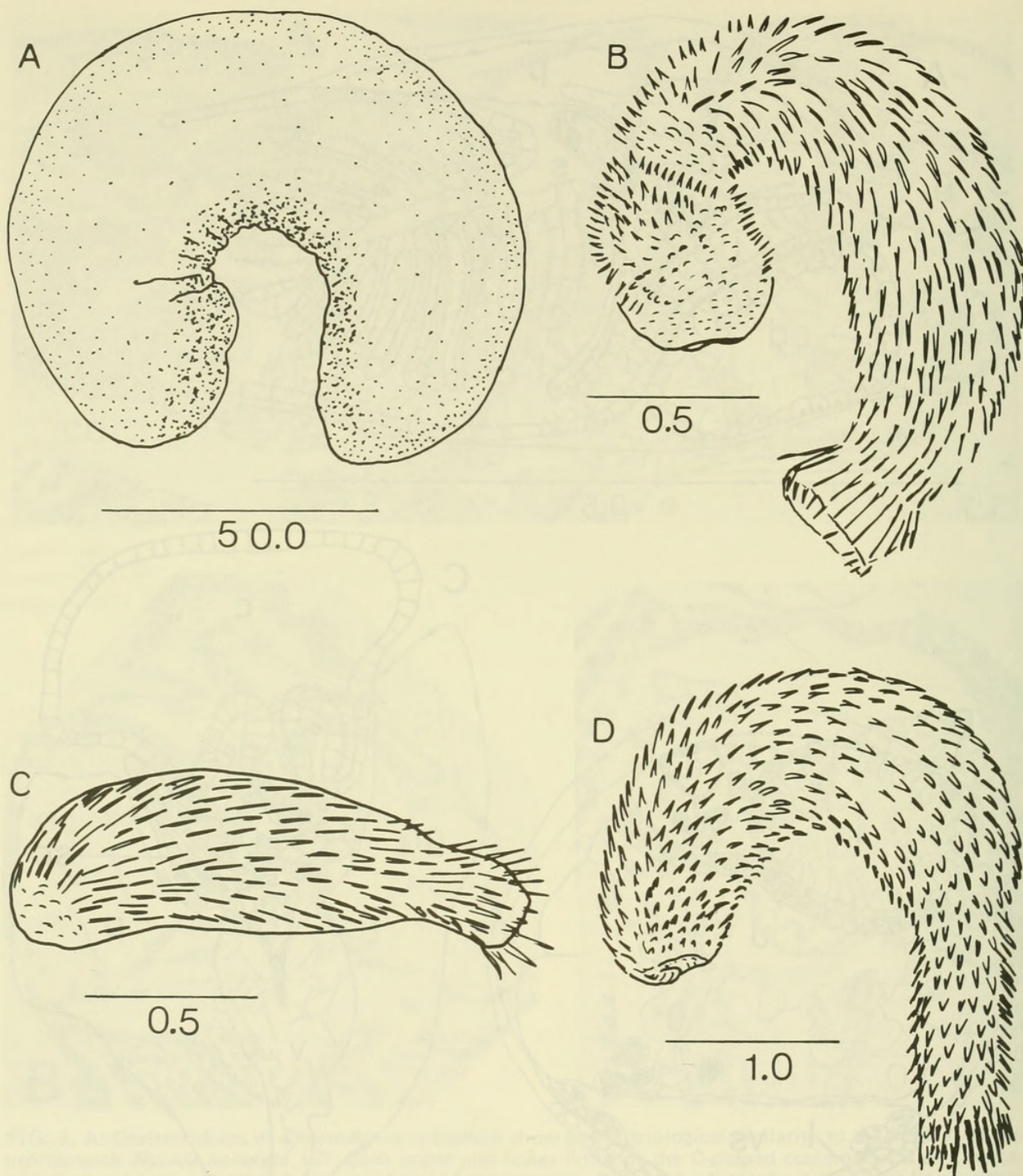


FIG. 5. Flexed body in A: *Neomenia herwigi* Kaiser, 1976, a giant neomeniomorph from 130 m off the Falkland Islands (Kaiser, 1976); B: *Chaetoderma* sp. from 67 m S of Woods Hole, Massachusetts; C: *Prochaetoderma* sp. from 1600 m S of Woods Hole; D: *Falcidens* sp. from 650 m off Cape Hatteras, North Carolina. Scales in mm.

primitive ladderlike plan as in chitons and Monoplacophora, but it is ganglionated rather than medullary (see review in Bullock & Horridge, 1965). The differences in the 2 aplacophoran taxa are given in Salvini-Plawen (1972). There is a typical molluscan buccal innervation and, like chitons, a suprarectal commissure.

Thompson (1960), who observed the development of the late egg, early embryo and settlement stages of *Neomenia*, has published the most comprehensive account of the later development of an aplacophoran, which is remarkably like that of proto-branchs and scaphopods and not at all like that of chitons. Baba (1951) described and

illustrated early spiral cleavage for a neomeniomorph.

DISCUSSION

Aplacophora are true mollusks by the present definitions of that phylum, a member of which must express one or more of several diagnostic traits. No single key character defines the phylum (Stasek, 1972). It is unfortunate that the Aplacophora have been considered mollusks chiefly by their superficial resemblance to chitons, for there are few shared characters between them except their archaic nervous systems (the "Amphineura") and primitive mucoidal mantles with spicules ("Aculifera"). Other proposed structural homologies seem highly improbable and have been influenced by the idea that aplacophorans really cannot be considered mollusks unless (1) an affinity to chitons can be shown (Hoffman, 1949) or (2) their position as a stem form of the Mollusca can be proven (Salvini-Plawen, 1969, 1972).

From the structures briefly described in the previous section, the Aplacophora can certainly be included among the Mollusca on the basis of characters shared with other molluscan classes. To place the 2 taxa as subclasses in a single class makes a classification that gives a hierarchical ranking consistent with that of other equally similar molluscan subclasses. The differences between the Chaetodermomorpha and Neomeniomorpha in integument, form of mantle cavity, and digestive system set them apart from each other, but no more so than are prosobranch and opisthobranch gastropods. The differences in nervous systems stressed by Salvini-Plawen (1972: 320, fig. 50) are not as great as the differences among the prosobranch gastropods with their separated or fused pleural and cerebral ganglia and their ladderlike or unconnected pedal cords (Fretter & Graham, 1962). In fact, it is exactly the similarity in nervous systems in the 2 aplacophoran taxa—ladderlike paired lateral and ventral cords which are ganglionated, and a suprarectal commissure (Fig. 4A, 4C)—that shows the close relationship between them; moreover, there is a dorsoterminal sensory organ in both.

Equally important indications of similarity are the connection between gonads, pericardium, and coelomoducts in both

taxa and their vermiform shape, conditions unique among the mollusks. The lack of a foot groove in the Chaetodermomorpha is most parsimoniously explained by loss owing to their burrowing habit. It is not clear that the simpler, thinner integument of the Chaetodermomorpha is the more archaic of the 2 taxa (Hoffman, 1949); it could just as well be that their cuticle is a secondarily derived state related to burrowing.

The basis for Salvini-Plawen's 2 aplacophoran classes is the rigid application of Hennig's cladistic methods. The method itself has several serious failings (see Szalay, 1977, for a critique); one is that it precludes finding new phylogenetic relationships from the fossil record. Thus, the newly recognized fossil molluscan class Rostroconchia (Pojeta & Runnegar, 1976), probably ancestral to Pelecypoda and descendant from Monoplacophora, can have no place in a predetermined phylogeny such as devised by Salvini-Plawen (1968, 1969, 1972).

Hennig's method is inappropriate as applied to such a large, diverse group as the Mollusca with an unknown number of extinct and unrecognized ancestral forms. It has led Salvini-Plawen (1972) to propose several evolutionary improbabilities. Consider 2 examples.

First, according to Salvini-Plawen (1972: 284, fig. 35), the molluscan coelom was first (hypothetically) a pair of gonads and a small ductless pericardium. Then the next evolutionary steps were a (hypothetical) joining of gonad to pericardium and development of a pair of coelomoducts emptying the pericardium. Although this is the condition which presently exists in all Aplacophora except *Phyllomenia* (Salvini-Plawen, 1970), it is said to be secondarily derived after a (hypothetical) separation of gonads and pericardium, each with paired ducts, which gave rise to the condition found in all other living mollusks; replication of the coelom then took place in the Monoplacophora. Only in the aplacophoran taxa are the gonads considered again to open into the pericardium in 2 separate evolutionary events.

The original state of the molluscan coelom is conjectural, and its organogenesis is unknown in the Aplacophora and Monoplacophora. However, the large pericardium of the Monoplacophora, Aplacophora, and Polyplacophora, the bilaterality of all coe-

lomic spaces in the former 2, and the paired monoplacophoran ventricles, seem to argue against an original small, single coelomic widening simply to protect the heart. The matter of where the gonads emptied originally in the evolutionary history of the mollusks is left open; it may be that the unique gonad-pericardium connection of the Aplacophora is a derived state arising from their vermiform shape. In that case, *Phyllomenia* would be the 1 genus retaining a more ancestral condition.

The second example of an improbable evolutionary event proposed by Salvini-Plawen (1972) is that the oral shield of the Chaetodermomorpha is a remnant of the molluscan foot. This singular homology forms the basis for making 2 classes of the Aplacophora and relates the occurrence of mucous gland cells that open beside the oral shield in *Chaetoderma* to those along the foot groove in *Proneomenia* (Hoffman, 1949). The chaetoderms are burrowing forms, moving headfirst by hydrostatic action. Gland cells are ubiquitous in the outer epithelium throughout the mollusks and appear wherever lubrication is needed functionally. The specialized innervation (Salvini-Plawen, 1972) and cuticularization of the chaetoderm oral shield seem to discount that it is part of an original gliding sole; one should not argue generalized gland cells beside the oral shield and at the same time specialized innervation to it.

The phylogenetic position of the Aplacophora is not easy to ascertain. There is general agreement that the group is primitive and probably very old geologically. There must have been innumerable trials at calcification of a mucoid integument among precambrian forms for which we now have no direct evidence. The Aplacophora were the only forms to survive that did not produce a point—or points—of calcification from which a shell could grow; each calcareous spicule is produced by a single cell (Hoffman, 1949). However, the aplacophoran integument with its spicules, although primitive, should not be considered identical with the original molluscan integument, for it, too, must be the result of selection.²

The most interesting phylogenetic information to be obtained from the Aplacophora is that several characteristic molluscan structures have evolved independent of a shell. The notion that the adaptive functional possibilities of the mantle cavity have led to great diversity in the mollusks is upheld, for in becoming worms, aplacophorans have not exploited this structure and retain quite a uniform morphological pattern. However, their unique specialization of a worm shape has been well adapted to the deep sea benthos.

ACKNOWLEDGEMENTS

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²A recent comparative account on the integument by Rieger & Sterrer, not available to me at this writing, stated that "spicular skeletons . . . are, in some cases (Turbellaria and Mollusca), possibly relics indicating phylogenetic relationship." *Biological Abstracts*, 62, No. 15000: RIEGER, R. M. & STERRER, W. 1975, New spicular skeletons in Turbellaria, and the occurrence of spicules in marine meiofauna. II. *Zeitschrift für die zoologische Systematik und Evolutionsforschung*, 13: 249-278.)

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