

COMPARATIVE MORPHOLOGY OF THE RADULAE AND ALIMENTARY TRACTS IN THE APLACOPHORA¹

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ABSTRACT

The alimentary tract was studied in one genus of Neomeniomorpha and in five genera of Chaetodermomorpha.

The cuticular oral shield of the Chaetodermomorpha is part of the foregut cuticle.

A dorsal ciliated tract or typhlosole, an unarticulated radula on a radular membrane, an odontophore with bolsters within the haemocoel, and paired tubular salivary glands are conservative molluscan characters. It is not certain whether an undivided stomach-digestive gland (Neomeniomorpha) or separate stomach and digestive diverticulum (Chaetodermomorpha) represents the primitive midgut in the Aplacophora. The molluscan style may primitively have been formed throughout the stomach and anterior intestine (*Scutopus*). A style sac with protostyle and a gastric shield have evolved together independently in one family of carnivorous Aplacophora (Chaetodermatidae).

The genera studied here exhibit an evolution of the radula from rows of distichous teeth firmly affixed to a divided or fused radular membrane to (1) a gastropod-like articulated radula and (2) a highly specialized pincers-like radula. The odontophore has evolved from a structure scarcely protruded into the buccal cavity to one with the tip lying free, surrounded by deep buccal pouches and sublingual cavity. A carnivorous diet is related both to a primitive radula (*Gymnomenia*) and to the specialized radulae of *Prochaetoderma* and the Chaetodermatidae (*Chaetoderma* and *Falcidens*).

Evolution to a gastropod-like radula combined with jaws which hold the mouth open in *Prochaetoderma* has made possible a diet which is independent of particle size. A broad food source may be one reason that some species of *Prochaetoderma* are numerically dominant members of the fauna in the deep sea, where food may be limiting.

INTRODUCTION

The alimentary tract of the Aplacophora, excepting the radula, has generally received less attention than other organ systems. The radula itself has usually been described from histologic preparations; isolated radulae with complete radular membranes have been figured for only a few species in the subclass Chaetodermomorpha (= Caudofoveata) (Kowalevsky, 1901; Scheltema, 1972, 1976; Ivanov, 1979) and for only two species of *Epimenia* in the subclass Neomeniomorpha (= Solenogastres *sensu* Salvini-Plawen) (Baba, 1939, 1940). Gut morphologies have usually been described as part of species descriptions; no integrated overview exists for the class as a whole outside of literature reviews in the standard invertebrate treatises. The literature on feeding and digestion in the

Neomeniomorpha was reviewed by Salvini-Plawen (1967b), who has recently proposed evolutionary sequences in the digestive system in the mollusks (1980). The only developmental studies on the alimentary tract are for *Epimenia verrucosa* (Baba, 1938) and *Neomenia carinata* (Thompson, 1960).

This paper examines the morphologies of the radula and fore- and mid-guts of certain aplacophoran families and relates these morphologies to the feeding type and the ecologic importance of these families in the deep-sea benthos. Possible phylogenetic relationships of the aplacophoran radula and gut morphologies are proposed and the bearing of these relationships to understanding molluscan evolution is discussed. Primary consideration is given to the Chaetodermomorpha, but one primitive neomeniomorph is examined (Fig. 1).

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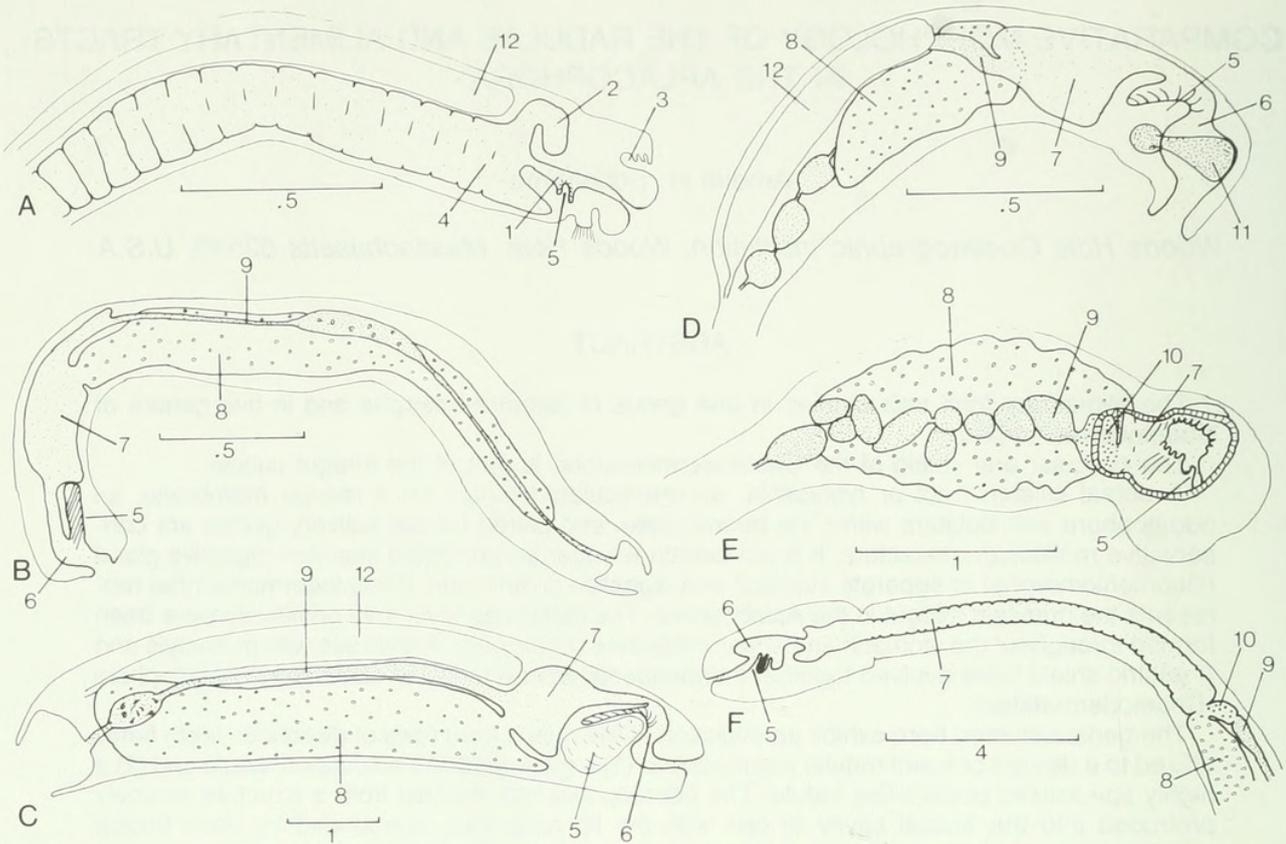


FIG. 1. Alimentary tract of Aplacophora, semi-schematic. A: *Gymnomenia* n. sp., anterior two-thirds only; B: *Scutopus robustus*; C: *Limifossor talpoideus*; D: *Prochaetoderma* sp. y, posterior end not shown; E: *Falcidens caudatus*, posterior end not shown; F: *Chaetoderma nitidulum*, anterior half only. A, F from sagittal sections; B-E from cleared specimens. Gonad not indicated in B, E, or F. Scales in mm. 1, foregut; 2, dorsal caecum; 3, atrium; 4, midgut of undifferentiated stomach and digestive gland; 5, odontophore and radula; 6, buccal cavity; 7, stomach; 8, digestive diverticulum; 9, intestine; 10, style sac; 11, jaws; 12, gonad.

MATERIALS AND METHODS

Thirteen species in four families and six genera were examined, two species by histologic sections only, three by isolated radula preparations only, and eight by both histologic and radula preparations. All unnamed species or species identified by letter only will be formally described elsewhere.

Subclass Neomeniomorpha

Fam. Wireniidae (regarded as primitive on basis of spicule shape, thin integument, and lack of ventral foregut glands, Salvini-Plawen, 1978).

(1) *Gymnomenia* n. sp. 620 m, off Walvis Bay, Namibia, Africa (23°00'S, 12°58'E). 4 specimens (cross and sagittal sections, 2 radula preparations).

Subclass Chaetodermomorpha

Fam. Limifossoridae (regarded as primitive on basis of vestige of ventral foot furrow in *Scutopus*, Salvini-Plawen, 1972a).

(2) *Scutopus megaradulatus* Salvini-Plawen, 1972. 650 m, off Cape Hatteras, North Carolina, U.S.A. (34°14.8'N, 75°46.7'W); 2 specimens (cross sections and radula preparation).

(3) *Scutopus robustus* Salvini-Plawen, 1970. 660 m, Bay of Biscay (48°56'N, 11°02'W); 4 specimens (sagittal sections, 2 gut dissections, and 1 radula preparation).

(4) *Limifossor talpoideus* Heath, 1904. 508-572 m, Alaska; 3 specimens (type material) (cross and sagittal sections, whole mount).

(5) *Limifossor* n. sp. 188-195 m, off east Florida, U.S.A. (27°25'N, 79°53'W); 3 specimens (cross sections, 2 radula preparations).

(6) *Limifossor ?fratula* Heath, 1911. Location unknown. 1 specimen (sagittal sections; Heath material).

Fam. Prochaetodermatidae

(7) *Prochaetoderma* sp. y. (a) 805–811 m, S of Woods Hole, Massachusetts, U.S.A. (39°51.3'N, 70°54.3'W); 6 specimens (radula preparations). (b) 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 21 specimens (9 cross and sagittal sections, 12 radula preparations). (c) 1546–1559 m, off Walvis Bay, Namibia, Africa (23°05'S, 12°31'E); 1 specimen (radula preparation).

(8) *Prochaetoderma* sp. c. (a) 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 4 specimens (radula preparations). (b) 2178 m, S of Woods Hole (39°38.5'N, 70°36.5'W); 2 specimens (radula preparations). (c) 2091 m, off Scotland (57°59.7'N, 10°39.8'W); 1 specimen (radula preparation).

(9) *Prochaetoderma* sp. p. 1624–1796 m, off Dakar, West Africa (10°30.0'N, 17°51.5'W); 6 specimens (2 cross and sagittal sections, 4 radula preparations).

Fam. Chaetodermatidae

(10) *Falcidens* n. sp. 650 m, off Cape Hatteras (34°14.8'N, 75°46.7'W); 1 specimen (radula preparation).

(11) *Falcidens caudatus* (Heath, 1911). 1102 m, S of Woods Hole (39°48.7'N, 70°40.8'W) and 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 5 specimens (sagittal and cross sections).

(12) *Chaetoderma nitidulum* Lovén, 1844 (= *C. canadense* Nierstrasz, 1902; Scheltema, 1973). 74 m, St. Margaret's Bay, Nova Scotia (44°33'01"N, 65°58'09"W). 4 specimens (sagittal and cross sections) and numerous radula preparations.

(13) *Chaetoderma abidjanense* Scheltema, 1976. 80 m, off Ivory Coast, West Africa (5°02.5'N, 3°47'W); 1 specimen (radula, redrawn from Scheltema, 1976).

Most specimens were fixed as part of an entire washed sample in 10% buffered formalin and changed for preservation to 70 or 80% ethyl alcohol within 24 hr. *Chaetoderma nitidulum* was fixed in Bouin's for histologic sections; all others were refixed in HgCl₂ and acetic acid before sectioning. Stains employed were Delafields' haematoxylin, with eosin, Gray's double contrast, or Ponceau S

as counter-stains. Radulae were isolated by dissecting out the buccal mass and treating with 5% sodium hypochlorite (household bleach) to remove the tissue. The isolated radulae were washed in distilled water and examined in glycerin using a Zeiss interference contrast microscope. Drawings were made with the aid of a camera lucida. One radula of a *Prochaetoderma* species was examined with a scanning electron microscope.

COMPARATIVE MORPHOLOGY OF ALIMENTARY TRACTS

Mouth

The external tissue surrounding the mouth in Aplacophora is usually supplied with mucous cells and nerve strands and the mouth is closed by a sphincter muscle. In some Neomeniomorpha there is a peri-oral fold; in *Gymnomenia* this fold bears numerous cuticular processes, which are extensions of the peri-oral cuticle and presumably receive tactile stimuli (Fig. 2M, N). The cuticle of the peri-oral fold is a continuation of the foregut cuticle, and both are supplied by large mucous glands or masses of mucous cells (ducts were not clearly seen).

The Chaetodermomorpha all have a cuticularized oral shield, divided or undivided and more or less surrounding the mouth opening (Fig. 2D, E, J, L). The cuticle of the oral shield is not part of the epidermal, integumental cuticle (Hoffman, 1949) (Fig. 2A), but is a thickened continuation of the cuticle of the oral tube and buccal cavity in *Scutopus*, *Limifossor*, and *Prochaetoderma* (Fig. 2B, G, K). Nierstrasz (1903) noted the same condition in *Metachaetoderma challengerii*, and Schwabl (1961) considered the oral tube epithelium to be a continuation of the oral shield epithelium in *Falcidens hartmani*. In *Chaetoderma nitidulum* and *Falcidens caudatus* the cuticle of the shield joins that of the oral tube; the latter continues for only a short distance before grading into very dense, long cilia (Fig. 2H, I), which in turn shorten and continue into the buccal cavity (see also Schwabl, 1961).

The epithelial cells underlying the oral shield vary in detail among genera, but certain generalizations seem to hold. There is an abrupt change in epithelial cell type between the cells of the oral shield and those of the oral tube (Fig. 2C, F, arrow); however, the

cuticle itself appears to be homogeneous except for a thickened outermost layer of the oral shield and a zone of fibrils running between the epithelial cells of the oral shield and the cuticle (Fig. 2A, 7; C). The epithelial

cells of the oral shield contain vacuoles and secretory granules (Fig. 2A, F). In *Scutopus* the cuticle is pierced by channels and by scattered pyriform mucous cells which are not grouped into lobes (Fig. 2A). In *Chaetoderma*

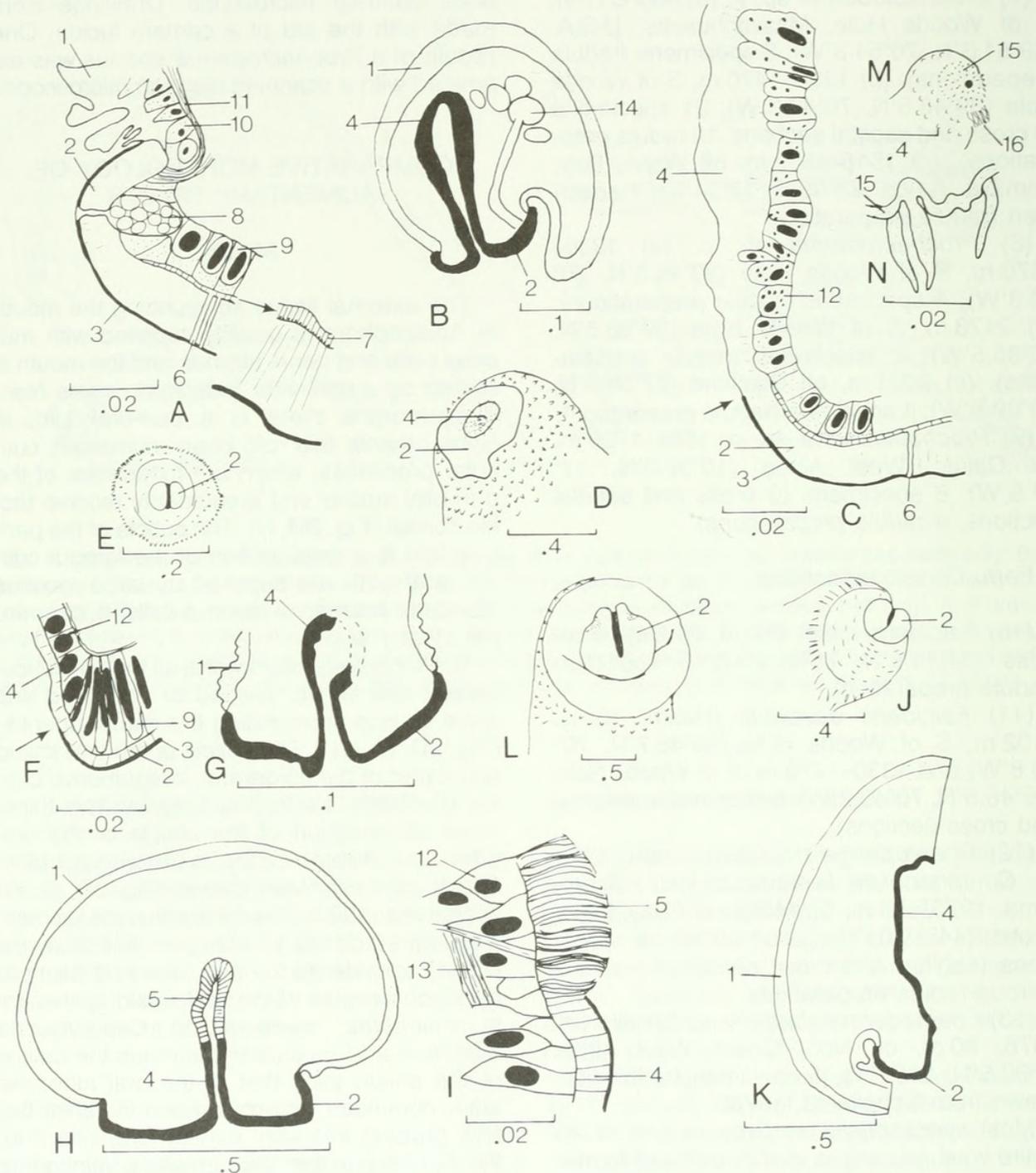


FIG. 2. Mouth of Aplacophora. A-D: *Scutopus megaradulatus*; E-G: *Prochaetoderma* sp. y; H, I, L: *Chaetoderma nitidulum*; J: *Limifossor* n. sp.; K: *Limifossor talpoideus*, one half of section; M, N: *Gymnomenia* n. sp.; B, G, H, K, cross-section through oral shield and oral tube, cuticle of gut black, cuticle of integument stippled; D, E, J, L, M, external views of mouth; A, detail of oral shield and integument; C, F, histologic detail of change from oral shield to oral tube (arrow); I, histologic detail of oral tube; N, tactile extensions of peri-oral cuticle. Scales in mm. 1, epidermal cuticle; 2, oral shield cuticle; 3, outer thickened layer of oral shield cuticle; 4, cuticle of oral tube; 5, cilia of oral tube; 6, channel; 7, zone of fibrils; 8, mucous cell; 9, vacuole; 10, epidermal cell; 11, muscle of body wall; 12, epithelial cell of oral tube; 13, muscles; 14, precerebral ganglion; 15, cuticular peri-oral fold; 16, cilia of pedal pit.

nitidulum the mucous cells form lobes which open at the lateral edges of the oral shield (Hoffman, 1949, and confirmed here).

The oral shield seems to serve both in locomotion and as a sensory organ; it is highly innervated by several precerebral ganglia (Hoffman, 1949; Salvini-Plawen, 1972a) (Fig. 2B).

One specimen of *Scutopus megaradulatus* shows that although the thickest part of the oral shield bends away ventrally from the mouth, it is continuous with and surrounds the mouth opening (Fig. 2D), an observation that does not agree with the original description (Salvini-Plawen, 1972b).

Buccal Cavity

Gymnomenia n. sp. As in many Neomeniomorpha, the foregut appears to be suctorial and a buccal cavity as such is not distinct from the rest of the foregut (Fig. 1A). Two sphincters and numerous circular muscles surround the foregut, in addition to the anterior sphincter that closes the mouth. The radula lies between the two posterior sphincters; the posteriormost one defines the juncture of fore- and midgut. Masses of goblet cells surround the foregut, but there is no ventral pair of salivary glands (Fig. 4F). Between the mouth and the first sphincter the secretory cells are basophilic; between the first and second sphincters they stain orange (Orange II counterstain).

Scutopus (*S. megaradulatus*). The dorsal half to two-thirds of the buccal cavity is lined by tall goblet cells bearing a thick striated cuticle (Fig. 3A). The goblet cells secrete large yellow granules and empty through the cuticle; they occur in all stages of vacuolization (Fig. 3I). A pair of simple tubular salivary glands 150 μm in length lies ventral to the buccal cavity; they empty near their posterior ends laterally into the buccal cavity at the level of the anterior end of the radula. The tip of the buccal mass does not lie free in the buccal cavity; thus there is no sublingual cavity, and the odontophore remains within the main space of the haemocoel (Figs. 1B, 3A).

Limifossor (*L. talpoideus*). The large odontophore tip lies free in the cuticle-lined buccal cavity, and there is a spacious sublingual cavity (Figs. 1C, 3B). Tall goblet cells with large yellow granules similar to those in *Scutopus* line the buccal cavity laterally and dorsally; ventrally the goblet cells are scat-

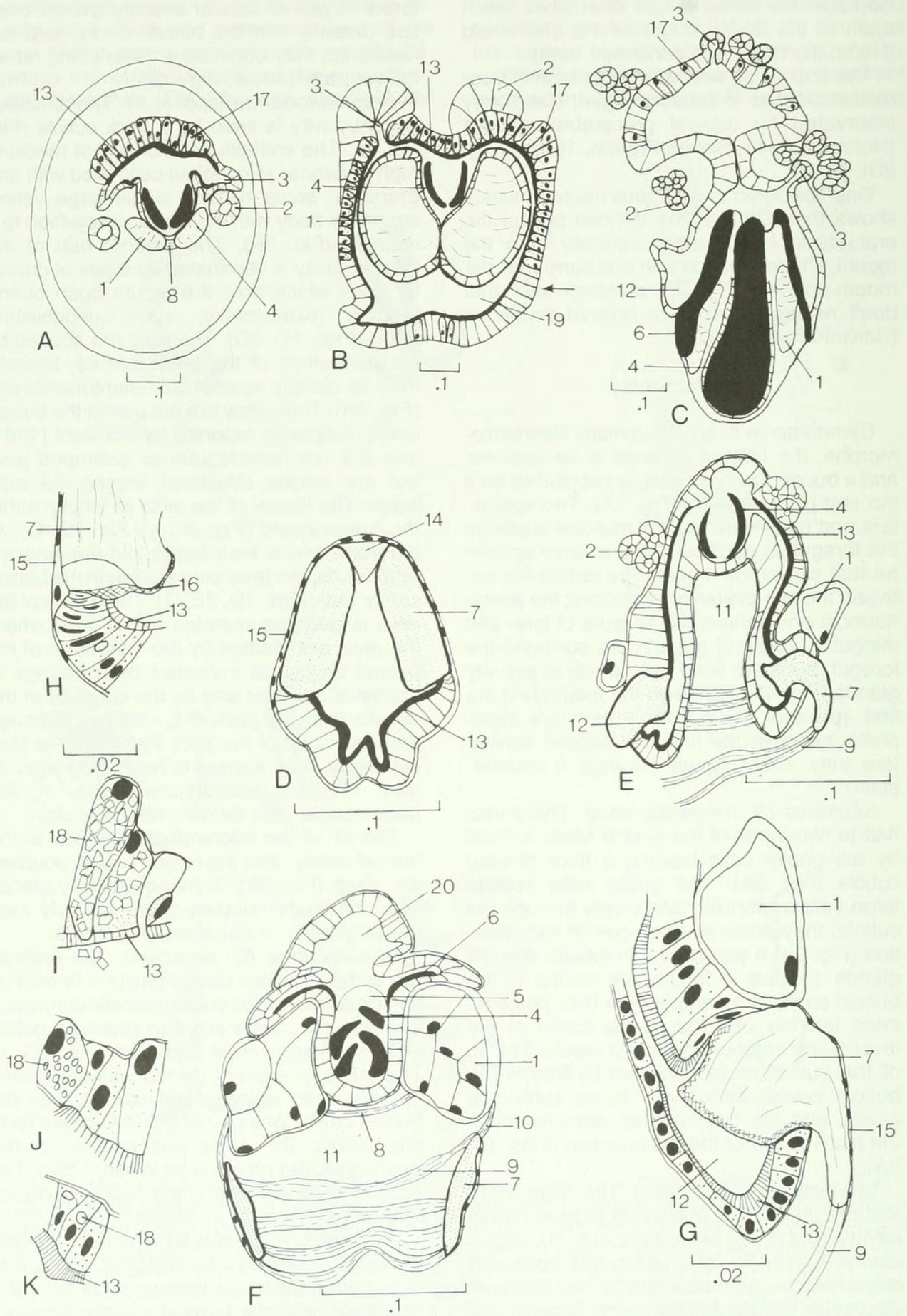
tered. A pair of tubular salivary glands empties dorsally into the buccal cavity near the radula tip; they originate anteriorly and rather far ventrally (arrow, Fig. 3B).

Prochaetoderma (spp. *y*, *p*). The spacious buccal cavity is lined by a thick cuticle (Fig. 3D, E). The epithelium is formed of medium-high columnar to cuboidal cells filled with fine granules; some have a single large yellow secretory body with or without connection to a vacuole (Fig. 3K). The anterior part of the buccal cavity is dominated by a pair of cuticular jaws which hold the mouth open during feeding (Kowalevsky, 1901; unpublished data) (Figs. 1D, 3D). The jaws are abutted by the epithelium of the buccal cavity; laterally they lie directly against basement membrane (Fig. 3H). Thus, they are not part of the buccal cavity cuticle as reported by Schwabl (1961) and are not homologous to gastropod jaws but are unique structures among the molluscs. The bases of the jaws lie wholly within the haemocoel (Fig. 3F; cf. Fig. 7B, C). At the point where their bases join the long anterior ends, the jaws pierce through the buccal cavity wall (Figs. 1D, 3E, G). The cuticle of the jaws is perhaps secreted at the point where the jaws are abutted by the epithelium of the buccal cavity, as indicated by a change in epithelial cell type and by the direction of the striations in the jaws (Fig. 3G, H). Although the major part of the jaws lies within the buccal cavity, they appear to have originated as part of the odontophore mass in the haemocoel (see below under *Radula*).

The tip of the odontophore lies free in the buccal cavity, and the lateral buccal pouches are deep (Fig. 3E). A pair of salivary glands with compound tubules opens dorsally near the beginning of the short esophagus.

Chaetoderma (*C. nitidulum*). The epithelium of the spacious buccal cavity is formed by tall, brush-bordered columnar cells containing fine granules; there are also scattered goblet cells with large yellow secretions (Fig. 3C, J). Two pairs of salivary glands with compound tubules open laterally and dorsally into the buccal cavity, one pair at the level of the tip of the radula, the other just anterior to the esophagus (as reported by Wirén, 1892). The odontophore lies free in the buccal cavity for one-half or more of its length.

Falcidens (*F. caudatus*). The buccal cavity is similar to that of *Chaetoderma*, but is less capacious. There are perhaps also two pairs of salivary glands; however, ducts were not clearly seen for the dorsalmost pair.



Radula

The aplacophoran radula has been shown throughout the literature to be very diverse in form, and far more plastic than the gastropod radula. However, there are certain structures common both to aplacophorans and other mollusks.

All isolated radulae that I have studied, except those of the Chaetodermatidae, have a discrete radular membrane with attached distichous rows of teeth issuing from a radular sac, which is a diverticulum of the buccal cavity known to secrete the radular membrane and teeth in gastropods (Fretter & Graham, 1962) and appearing to do so in Aplacophora. There is no evidence for a primitive so-called "basal membrane" that is part of the foregut cuticle and different in some way from a true radular membrane (Boettger, 1956; Salvini-Plawen, 1972a). The radular membrane is supported by an odontophore which lies in the haemocoel. There are one or more pairs of bolsters formed of connective tissue and muscle, or of chondroid tissue, or perhaps of collagen and muscle; in one case there is cuticularization. Protractor and retractor muscles run between the odontophore mass and the body wall, and presumably all aplacophoran radulae can be protracted to, or through, the mouth. In gastropods, muscles that run between a subradular membrane and the bolsters move the radula itself (Graham, 1973); in Aplacophora a subradular membrane is usually, but not always, lacking. The radula musculature has been described for only a few aplacophoran species and will not be described here except for a few particular cases. A bending plane may be either present or lacking; if present, there is no fixed position along the odontophore from genus to genus where it is situated.

Gymnomenia n. sp. The tiny radula of *Gymnomenia* was overlooked in the original description of the genus (Odhner, 1921) (Fig. 4); it is considered to be secondarily reduced by Salvini-Plawen (1978). There are about 28

rows of hooked distichous teeth, each with two median denticles in various stages of being tanned. None of the teeth show wear. Each tooth is attached to the radular membrane for one-half its length (Fig. 4B, C). In interference contrast, the radular membrane was seen to be continuous (a) between the teeth of each row as a slight ridge (Fig. 4B, C), which in turn runs down the length of the radula; (b) along and slightly below the base of the teeth lengthwise along the radula (Fig. 4A); and (c) lengthwise along the radula at the level of the denticle in the middle of each tooth (Fig. 4D). Thus, the radular membrane is a continuous sheet which appears to be fused medially; it bears two longitudinal rows of well-affixed teeth. Teeth attached so firmly to the radular membrane can have only limited movements.

The orientation of the radula is similar to that described for *Genitoconia* (Salvini-Plawen, 1967a). The fore-end of the radula is positioned dorsoventrally, where it lies in a blind sheath (Fig. 4E, F). About two-thirds of the distance towards the newest formed teeth in the radular sac there is a bending plane, over which the teeth open into the foregut. The short dorsal radular sac is perhaps bifid as in other Wireniidae, as indicated by the medial ridge of the radular membrane, but further histologic material is needed for substantiation.

The base of the fore-end of the radula lies against the connective tissue (? and commissure), defining the pedal sinus (Fig. 4F); directly beneath this, in the sinus, are about seven calcareous statoliths, each produced by a statocyst (Fig. 4G). In *Genitoconia*, Salvini-Plawen (1967a) described a pedal commissure sac with vesicles which he considered perhaps to be a balancing organ ("ein statisches Organ").

The odontophore protractors and retractors have been described for *Genitoconia* (Salvini-Plawen, 1967a), but the exact manner in which they operate the radula is not clear. The function of the enclosed fore-end of the radula

FIG. 3. Buccal cavity in Chaetodermomorpha. A, I: *Scutopus megaradulatus*; B: *Limifossor talpoideus*, arrow indicates level of blind end of salivary gland; C, J: *Chaetoderma nitidulum*; D-H, K: *Prochaetoderma* sp. y. Scales in mm. 1, bolster; 2, salivary gland; 3, opening of salivary gland into buccal cavity; 4, radular tooth (diagrammatic); 5, radular membrane; 6, subradular membrane; 7, jaw; 8, ventral approximator of bolsters; 9, ventral approximator of jaw; 10, tensor between bolster and base of jaw; 11, lumen of odontophore; 12, buccal pouch; 13, cuticle of buccal cavity; 14, dorsal cuticular membrane between distal end of jaws; 15, basement membrane; 16, deeply staining portion of jaw cuticle; 17, goblet cell; 18, large yellow granule; 19, sublingual cavity; 20, esophagus.

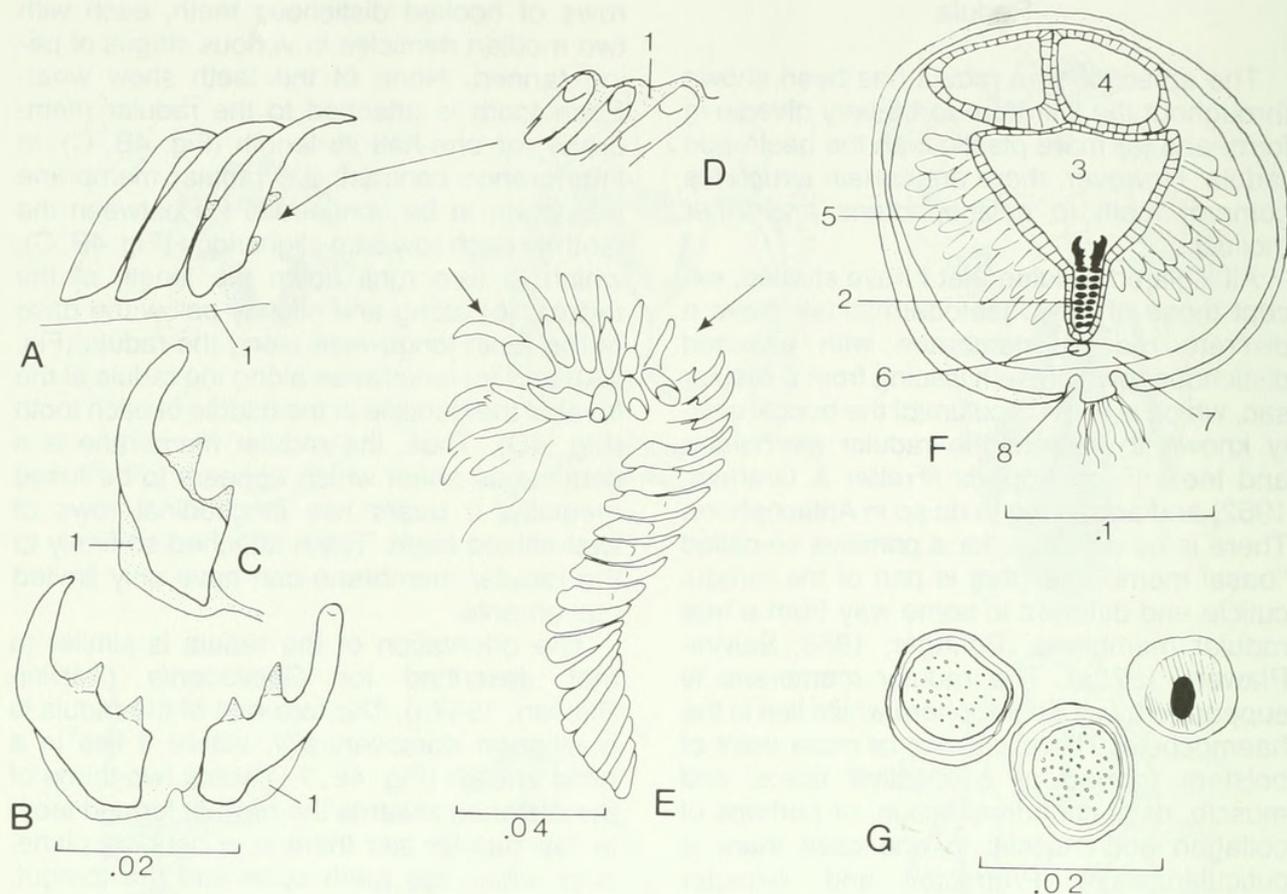


FIG. 4. Radula and statoliths of *Gymnomenia* n. sp. A-D: radular teeth; A, lateral view; B, C, anterior view; D, median view at level of middle denticle indicated by arrow on A; E: radula, lateral view, dorsal at top, anterior to right, most recently formed teeth to left, teeth between arrows exposed in pharynx; F: cross-section showing exposed teeth in foregut and sheath around fore-end of radula resting against statocyst. G: two statoliths and a statocyst cell filled with amorphous substance. Scales in mm, A-D at same scale. 1, radular membrane; 2, radula; 3, foregut; 4, paired dorsal caecum of midgut; 5 goblet cells; 6, statocyst; 7, pedal sinus; 8, pedal pit.

is not known; it may act as a supporting rod-like structure. The proximity of the radula to the statocysts of the pedal sinus may or may not indicate a direct relationship between them. The exposed teeth perhaps are able weakly to tear at soft tissue as it is sucked into the foregut, and very probably serve to move food backwards toward the midgut.

Scutopus (*S. robustus*, *S. megaradulatus*). The radula is formed of seven or more pairs of teeth in a straight, nearly anteroposterior position, with the distal ends of the teeth lying anteriorly to the proximal ends (Figs. 5A, B, 11D). Thus, the older of any two rows of teeth lies beneath and anterior to the younger, and the odontoblasts lie on the dorsal side of the radular sac. There is no bending plane. The teeth of *S. megaradulatus* and *S. robustus* are thick and massive, with pointed tips and many large median denticles which curve ventrally and posteriorly (Fig. 5D). From histo-

logic sections and whole preparations the radular membrane was seen to be formed of two longitudinal bands connected only between each pair of teeth (Fig. 5C). Each band extends laterally along the side of each tooth, but these extensions are not connected (Fig. 5C, D). Thus, the teeth are free to slide past each other, perhaps moved by the ventral tensor (Fig. 5A); they can also be closed by a large dorsal approximator muscle running between the anterior pair of bolsters (Fig. 5A, B). These rather limited possibilities for movement combined with the absence of a bending plane and of a sublingual cavity suggest a simple shovelling or pulling in of food. The radula probably cannot be protruded very far beyond the end of the radular sac, and the teeth do not show any wear.

Limifossor (*Limifossor* n. sp., *L. talpoides*). The radula with its massive odontophore was well described by Heath (1905),

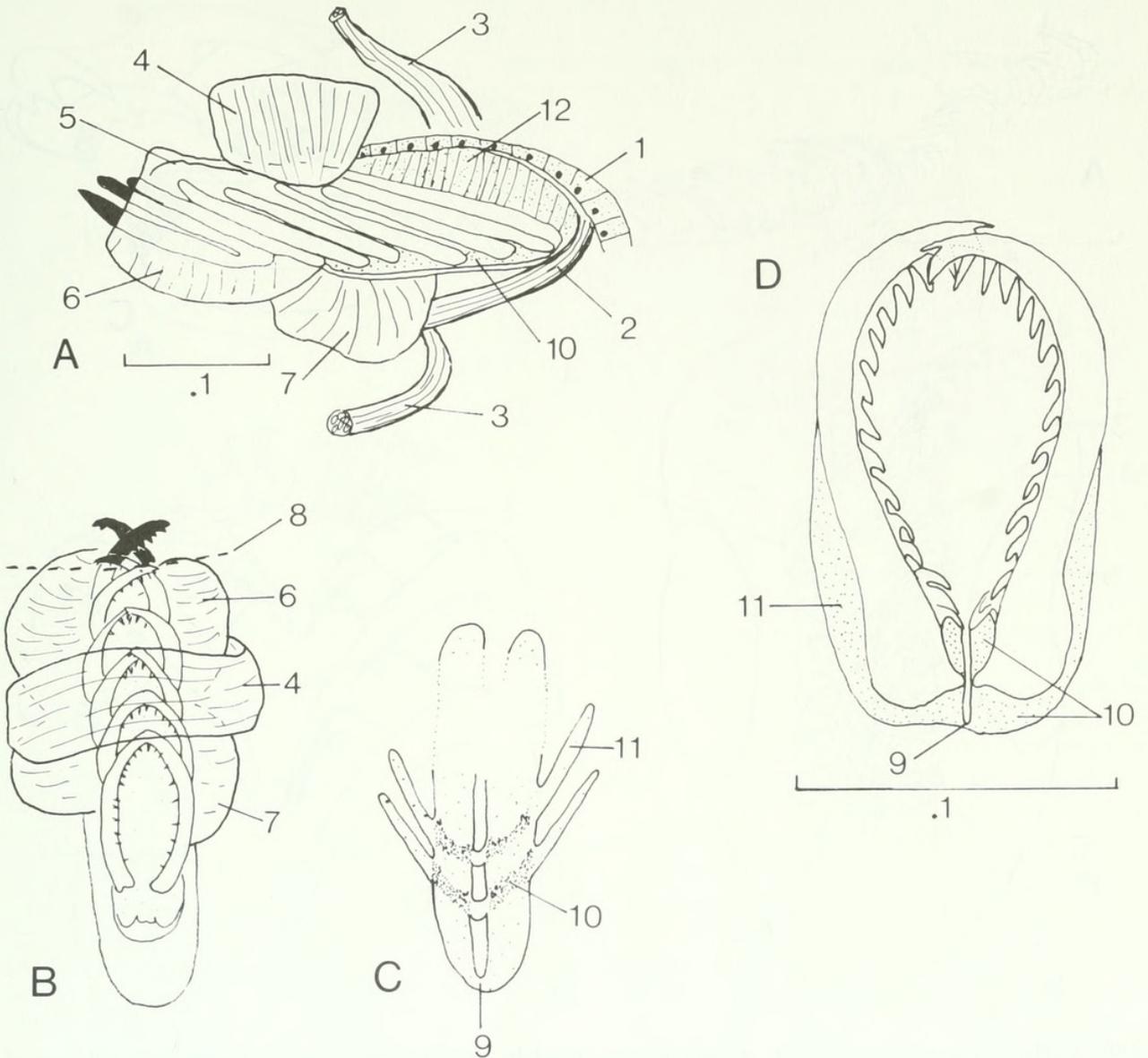


FIG. 5. Radula of *Scutopus*. A, B, D: *S. robustus*; C: *S. megaradulatus*. A, lateral view of buccal mass, anterior to left, teeth beyond radular sheath black; B, dorsal view, anterior end at top; C, diagrammatic representation of radular membrane; D, pair of radular teeth. Scales in mm, A and B at same scale. 1, midgut epithelium; 2, ventral tensor muscle; 3, protractors; 4, dorsal approximator of bolsters; 5, radular sac; 6, anterior bolster; 7, posterior bolster; 8, anterior limit of radular sac; 9, radular membrane connecting pair of teeth; 10, radular membrane attached to base of teeth; 11, lateral extension of radular membrane; 12, odontoblasts of radula.

who illustrated the musculature and watched the radular movements of living animals. A few observations may be added to his.

As Heath noted, the radular membrane is a continuous sheet only at the posterior end of the radula; farther anteriorly it splits along the midline (arrow, Fig. 6B) and continues as two bands. The radular membrane extends for a short distance up the lateral side of each tooth, and these lateral extensions are in connection along the radula (Fig. 6A, C). The teeth are massive, with long lateral hooks and shorter median hooks turned posteriorly (Fig.

6C, D); the bases have a thickened ridge posteriorly. The teeth are set close to each other along the radula; each tooth thus appears to act as a fulcrum for the next posterior one (Fig. 6C, D). There is a large mass of muscle fibers, the tooth adductor, that Heath (1905) found to be responsible for moving the opposed teeth toward each other (Fig. 6B); there is a dorsal approximator of the bolsters, present as in *Scutopus*, which is also probably important in bringing the two rows of teeth together (Fig. 6B). None of the teeth show wear.

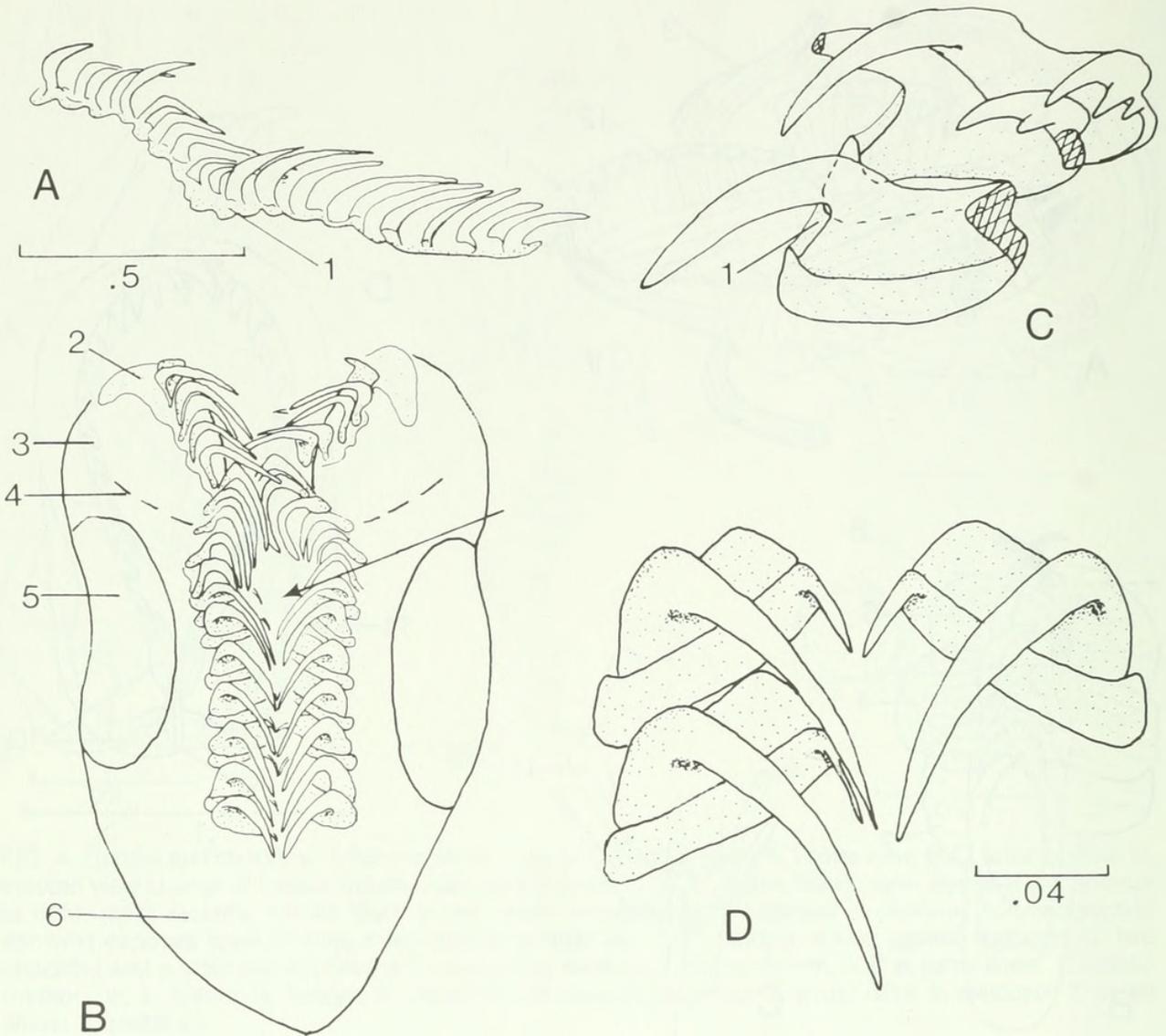


FIG. 6. Radula of *Limifossor* n. sp. A: lateral view of radula, dorsal at top, anterior to left; B: dorsal view of radula and odontophore, anterior at top; arrow indicates point where radular membrane splits into two bands; C, D: oblique and dorsal views of teeth in natural position. Scales in mm, A-B and C-D at same scales. 1, radular membrane; 2, subradular membrane?; 3, odontophore mass; 4, anterior limit of radular sac; 5, attachment of dorsal approximator of bolsters; 6, area of large tooth adductor muscle.

A certain amount of rotation of the teeth is possible, as shown in Figure 6B. These movements are made possible by (a) the median split in the radular membrane, which frees the two longitudinal rows anteriorly, (b) the use of each tooth as a fulcrum by the next posterior one, (c) the presence of a rudimentary bending plane, (d) the possible existence of a subradular membrane for tensor insertion, and (e) a deep sublingual cavity, which frees the entire buccal mass from the haemocoel (Fig. 3B). Heath reported that the odontophore swept past the teeth when the mouth was open. Certainly the radular teeth are able to go through a more complicated set

of movements than can those of *Scutopus* or *Gymnomenia*. Less certain is whether the radula is used for tearing or simply is an improved form of rake.

Prochaetoderma (spp. y, p, c). Kowalevsky (1901) figured the isolated distichous radula of *Prochaetoderma raduliferum*; some details can be added.

Most noticeable are the two large cuticular jaws that nearly fill the space in the head (Fig. 7A-C). Anteriorly they are connected by a membrane (Figs. 3D, 7C); posteriorly within the haemocoel a large bundle of muscle fibers runs between their bases, and a small fiber runs between each base and the chon-

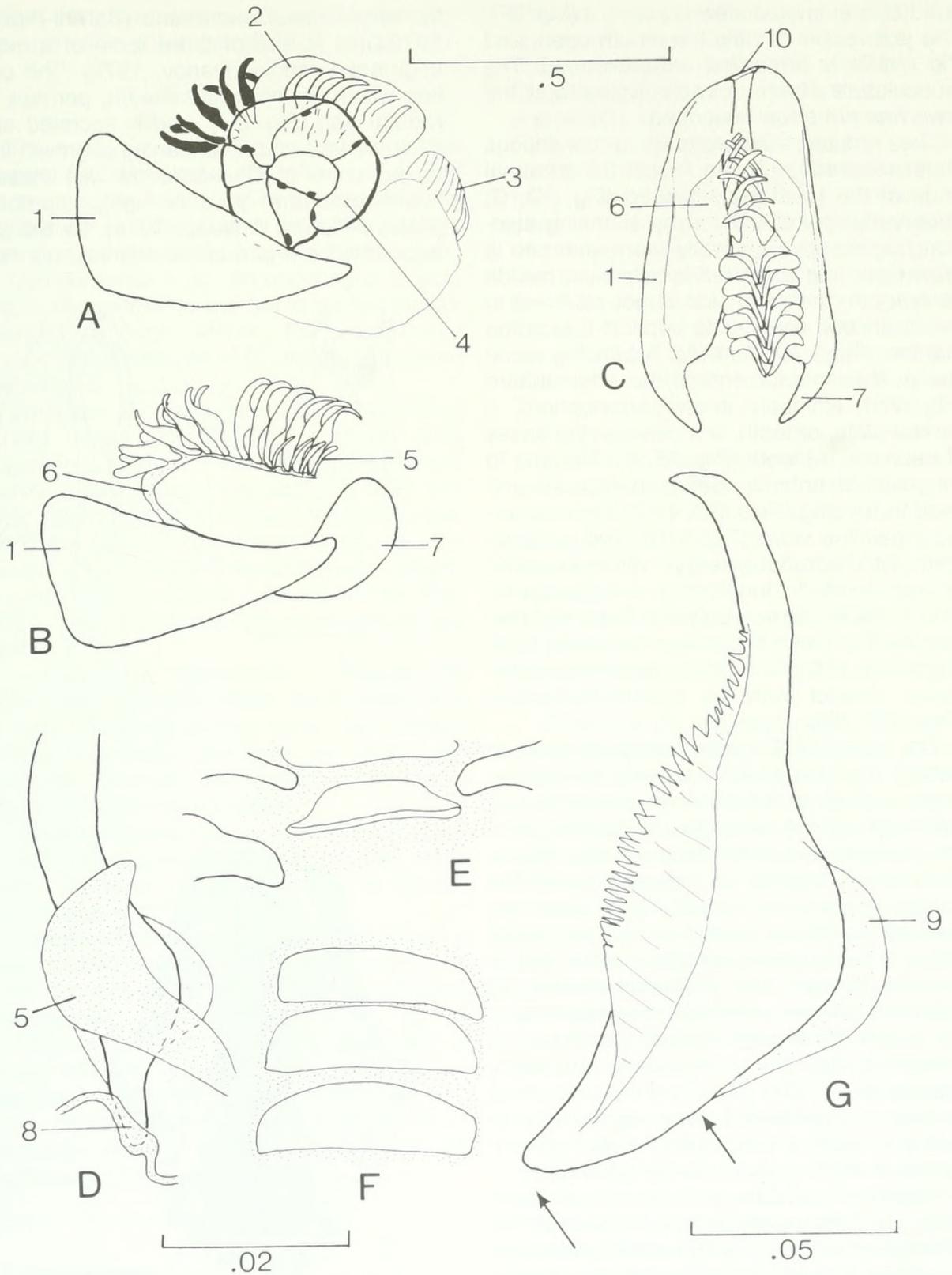


FIG. 7. Radula of *Prochaetoderma*. A-F: *Prochaetoderma* sp. y; G: *Prochaetoderma* sp. p. A, lateral view of jaws, radula, and odontophore, anterior to left; B, same as A, tissue removed; C, dorsal view of B, anterior at top; D, base of tooth, with lateral tooth-like extension and radular membrane in darker stippling; E: oblique view of central plate, or tooth, in relation to proximal ends of teeth; F: row of central plates, anterior at top; G: single radular tooth with membranous denticulate medial brush and lateral membranous wing, attachment to radular membrane between arrows. Scales in mm, A-C and D-F at same scales. 1, cuticular jaw; 2, radular sac; 3, tensor muscles between jaws; 4, chondroid bolster; 5, toothlike lateral extension of radular membrane; 6, subradular membrane; 7, case of jaw which lies within haemocoel; 8, radular membrane; 9, membranous wing of radular tooth; 10, dorsal cuticular membrane.

droid bolster immediately dorsal to it (Fig. 3F). The jaws serve to hold the mouth open, and the radula is protruded between them. The musculature which protracts and retracts the jaws has not been described.

The radular membrane is a continuous sheet to which only the tips of the proximal ends of the teeth are attached (Fig. 7D, G; observation substantiated by scanning electron microscopy). Laterally the membrane is drawn out into a tooth-like extension beside each tooth; the extension is not attached to the tooth but appears to support it in some manner (Figs. 7B, D, 11A). A bending plane lies at the anterior end of the odontophore (Fig. 7B). Uniquely in the Aplacophora, a central plate, or tooth, lies between the bases of each pair of teeth (Fig. 7E, F). The four to six pairs of anterior teeth are crossed and used in feeding (Figs. 7C, 11C); the anterior-most pair are worn (Fig. 11B). The posterior teeth, which probably remain within the radular sac, seem to function as a backstop for food particles carried between the membranous median brush-like extensions of the teeth (Figs. 7G; 11C). There is a subradular membrane, distinct from the radular membrane (Figs. 3F, 7B).

The radula of *Prochaetoderma* appears to reduce the size of food material by rasping before ingestion on the following evidence: (a) the mouth can be held open by the jaws probably independent of radular protrusion; (b) the teeth can articulate, for they are free of the radular membrane laterally and there are median supportive teeth; (c) the chondroid tissue of the bolsters provides a stiff structure to work beneath the protruded radula; (d) there is a bending plane at the anterior end of the odontophore over which the teeth can be articulated; (e) the anterior teeth are worn. Kowalevsky (1901) described the protracted, anterior crossed teeth in living animals as projecting through a wide-open mouth and constantly in motion as if to seize something.

Falcidens and *Chaetoderma* (several species). The very specialized radulae of the Chaetodermatidae (Fig. 8) have already been described in detail from isolated preparations (Scheltema, 1972). Paired denticles or lateral projections attached to the end of a cone-shaped rod presumably act as grasping pincers; tensors run between them and the bolsters (Schwabl, 1961; Ivanov, 1979) (Fig. 8C). There are three published interpretations of the cone-shaped structure: it represents a fused radula (Scheltema, 1972); it is a greatly

thickened basal membrane (Salvini-Plawen, 1972a); it is one of three teeth of a monosegmental radula (Ivanov, 1979). The cone lies within an epithelial sheath, perhaps the radular sac (Fig. 8C), and is secreted at its thick, ventral end. The identity of growth lines in the cone of *Chaetoderma* with those in *Prochaetoderma* jaws is highly improbable (Salvini-Plawen & Nopp, 1974), for the jaws appear to be a part of the odontophore mass

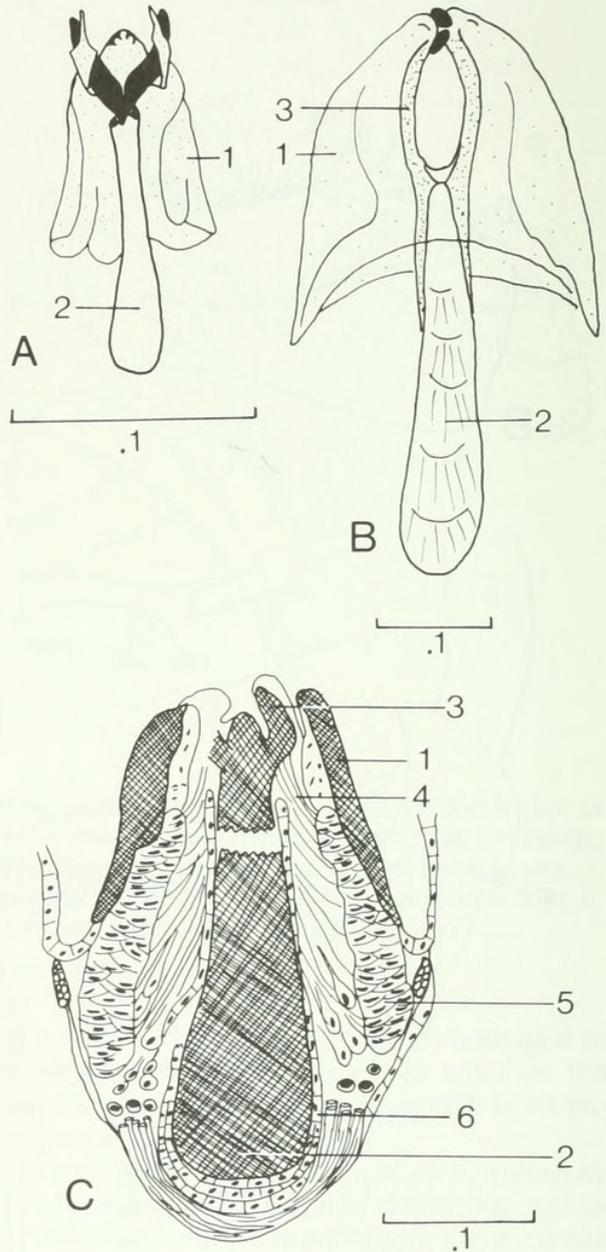


FIG. 8. Radulae of *Chaetoderma* and *Falcidens*. A: *Falcidens* n. sp.; B: *C. abidjanense* (from Scheltema, 1976); C: *C. nitidulum*, histologic section. Scales in mm. 1, cuticle surrounding buccal mass (subradular membrane?) 2, cone-shaped tooth; 3, lateral projection; 4, tensors of lateral projection; 5, bolster; 6, epithelium surrounding cone-shaped tooth (radular sac?).

within the haemocoel and are not underlain by epithelium (cf. Figs. 3D, E, F, 8C).

Esophagus

The esophagus is defined as that part of the foregut forming a tube above the radula and connecting the buccal cavity and stomach. Its epithelium is differentiated from the epithelium of both the buccal cavity and the stomach.

Gymnomenia n. sp. An esophagus is lacking in *Gymnomenia* but not in all Neomeniomorpha, although Odhner (1921) considered the posterior pharynx of *G. pellucida* to be an esophagus.

Scutopus (*S. megaradulatus*). The buccal cavity opens dorsally into a short, wide esophagus formed of low cuboidal epithelium with a brush border; the cells are filled with fine, yellow granules. A short distance posteriorly the lateral walls acquire folds, and the ventral wall thickens. The folds merge dorsally and become ciliated; posteriorly they coalesce into a typhlosole that continues into the stomach.

Limifossor (*L. talpoideus*, *L. ?fratula*). As described by Heath (1905), the esophagus is a long, ciliated, narrow tube with several longitudinal folds; the cells are filled with granules. Dorsally the ciliated epithelium is continued into the stomach.

Prochaetoderma (sp. *y*, *p*). The esophagus is extremely short and bears no cilia; however, Schwabl (1963) reported a ciliated esophagus in *P. californicum*.

Falcidens (*F. caudatus*). The esophagus is discernible from the buccal cavity only by its long, slender goblet cells which lie between the buccal cavity and stomach.

Chaetoderma (*C. nitidulum*). Cells with a brush border line a muscular esophagus. At the entrance to the stomach there are very long, slender goblet cells but no cilia; these coalesce dorsally and become the ciliated typhlosole in the stomach.

Midgut

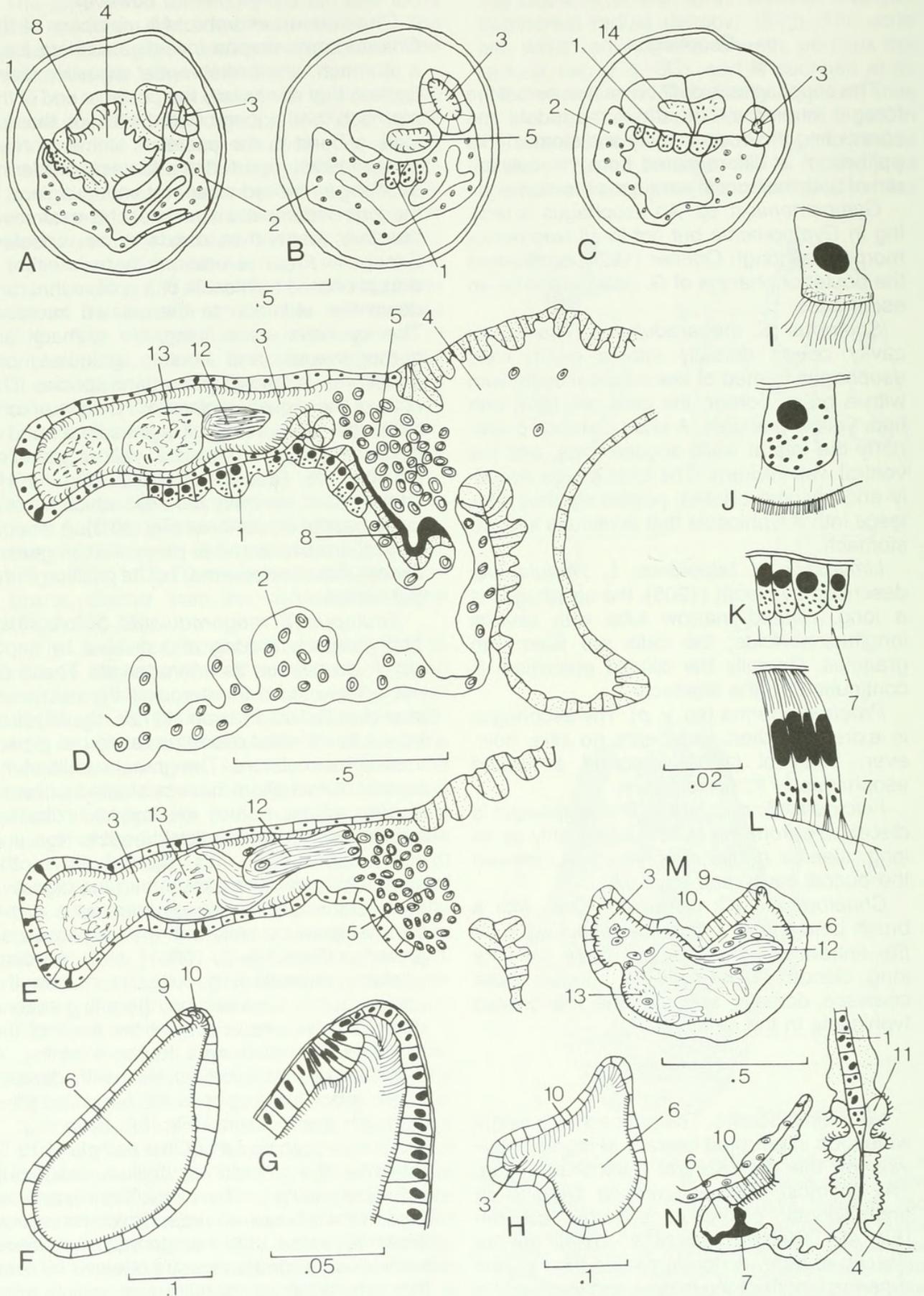
Neomeniomorpha. The stomach is a single wide tube interrupted laterally at regular intervals by the dorsoventral musculature (Fig. 1A). In most Neomeniomorpha there is an antero-dorsal paired or unpaired caecum (Fig. 4F). The cell types of the midgut are not described here. A dorsal ciliated tract or fold runs the length of the midgut and leads into a short, posteriorly placed, ciliated intestine

(Pruvot, 1891; Salvini-Plawen, 1978); it was not seen in *Gymnomenia*, however.

Chaetodermomorpha. All members of the Chaetodermomorpha investigated here have a stomach, a sac-like ventral digestive diverticulum that opens into the posterior end of the stomach, and a long ciliated intestine that follows a bend in the posterior stomach. Nierstrasz (1903) reported that *Metachaetoderma challengerii* lacked a separate midgut gland in the one incomplete specimen he examined, but this observation needs to be repeated. Except in *Prochaetoderma* there is either a dorsal ciliated typhlosole or a groove that runs down the stomach to the ciliated intestine. The epithelial cells lining the stomach are homogeneous and contain granules; cell shape varies among genera and species. The cells of the digestive gland are unique among mollusks: the dorsal wall is lined by a band of cells packed with coarse yellow granules (lacking in *Prochaetoderma*) (Fig. 10H); laterally and ventrally are cells which secrete large basophilic spheres (Fig. 10G). A mucoid or proteinaceous rod is present in all genera except *Prochaetoderma*, but its position in the gut varies.

Scutopus (*S. megaradulatus*, *S. robustus*). The stomach is long and divided by septa which do not run its entire length. These do not appear to be the same as the outpouchings that Salvini-Plawen (1972a, fig. 16) illustrated for *S. ventrolineatus* related to dorsoventral musculature. The granular cells of the stomach epithelium have a striated or brush border; anteriorly they are low and cuboidal, but farther posteriorly they become high and club-shaped (Fig. 10A, B). A strip of the stomach epithelium passes into the digestive diverticulum and continues there as a dorsal band of granular cells with greatly coarsened granules (Figs. 9A–C, 10B, H, 11D). A dorsal ciliated typhlosole (Fig. 10A, C) runs from the esophagus to the intestine; there is a second ciliated typhlosole arising at the base of the stomach that also runs to the intestine. A patch of ciliated cuboidal cells with densely staining borders opposes the bend that joins stomach and intestine (Fig. 9A, I).

In three specimens out of a sample of 19 *S. robustus*, the stomach epithelium was nearly colorless owing to the lack of cell granules. Dissection of two of these colorless specimens revealed that the stomach contained several solid, proteinaceous (stained by rose Bengal), acellular, parallel rods which were presumably formed by secretions from the



septate stomach (Fig. 11E). Crystals of about 40 μm adhered to the outsides of the rods; these crystals became more densely packed posteriorly. Both rods and crystals passed into the anterior intestine; farther posteriorly the crystals, but not the rods, formed part of a fecal mass. The crystals may be organic, as they dissolved in dilute HCl (but not NH_4OH) and broke down into an amorphous yellow mass when subjected to pressure by squeezing them beneath a glass coverslip. In *S. megaradulatus* sections, the stomach was empty and the stomach cells were packed with granules; there was only a short mucoid rod at the anterior end of the intestine.

Fecal material in *Scutopus* is formed into a long spindle-shaped mass along a straight intestine (Fig. 1B).

Limifossor (*L. talpoideus*, *L. ?fratula*). The epithelium of the very short (*L. talpoideus*, Fig. 1C) or very long (*L. ?fratula*) stomach are formed of tall (former) or short (latter) cuboidal granular cells with a striated or brush border. A dorsal typhlosole runs from the esophagus to the intestine. At the posterior bend between the stomach and intestine in *L. talpoideus* the cells are thickly ciliated (?brush border) and have a thick amorphous border resembling cuticle (Fig. 9D, J). Within the anterior ciliated intestine (interpreted originally as a style sac, Scheltema, 1978) is a mucoid rod (Fig. 9D, E). The digestive diverticulum is long. Fecal material is formed into oblong masses along a straight intestine.

Prochaetoderma (spp. *y*, *p*). The stomach is lined by low cuboidal cells probably with a cuticular border; cilia are lacking. The short digestive diverticulum lacks a dorsal band of granular cells and is formed only of secretory cells which are modified from the type found in other chaetoderms; the cell granules are eosinophilic and there are few basophilic, spherical secretions. There is no mucoid rod. The short anterior section of the intestine may

be bent or straight. Fecal material is formed into discrete spherical masses strung out along a long, convoluted intestine (Fig. 1D).

Chaetoderma (*C. nitidulum*). The stomach and digestive diverticulum are long (Fig. 1F). A dorsal typhlosole starts just posterior to the esophagus and runs the length of the stomach and into a style sac (Fig. 9N); only the medial cells of the typhlosole are ciliated anteriorly (Fig. 10E). The stomach epithelium is formed of low cuboidal cells with a striated or brush border; the granular cells of the dorsal band in the digestive diverticulum are very tall with a striated border and were not seen to be in connection with the stomach epithelium. At the base of the stomach there is a thick, hooklike cuticular gastric shield underlain by tall columnar cells which are granule-filled distally and striated basally; fibrils run between the cuticle and cell walls (Fig. 9L, N). The ciliated style sac runs between the stomach and the intestine transversely to the long axis of the body; it contains a mucoid rod in some specimens (Fig. 9M) (see also Scheltema, 1978, fig. 1B). The rod appears to rotate against the gastric shield, inasmuch as food material between the rod and the shield occurs in spiral swirls. The style sac is formed of granular cells with dense, short cilia; a broad ridge borders a groove with longer cilia which continues into the intestine (Fig. 9F-H, M). Fecal material is formed into oblong masses; the intestine is straight.

Falcidens (*F. caudatus*). The stomach is short and bilobed (Fig. 1E); its epithelium is formed of low cuboidal cells with yellow granules and a cuticular border (Fig. 10D). A strip of these cells continues, without a cuticular border, into the digestive diverticulum where it becomes the dorsal band of granular cells of that organ. The digestive diverticulum extends broadly to where the body narrows into a "tail."

A dorsal ciliated groove, rather than typhlo-



FIG. 9. Posterior stomach, anterior intestine, and opening of digestive diverticulum in Chaetodermomorpha. A-C, I: *Scutopus megaradulatus*; D, E, J: *Limifossor talpoideus*; F-H, L-N: *Chaetoderma nitidulum*; K: *Falcidens caudatus*. A-C, cross-section from anterior to posterior, viewed anteriorly; D, E, nearly adjacent sagittal sections, anterior to right; F-H, M, oblique sections through style sac of two specimens, one showing groove (enlarged in G) running into intestine (H) and one with protostyle (M); I-L, morphocline of cells from ciliated to cuticularized at bend between stomach and intestine (I enlarged from A, 8; J from D, 8; K from N, 7). N, oblique view anterior to M at junction of stomach and style sac, showing gastric shield. Scales in mm, A-C, D-E, I-L, M-N, at same scales. 1, dorsal band of granular cells; 2, secretion cells with basophilic spheres; 3, intestine; 4, stomach; 5, bend between stomach and intestine; 6, style sac; 7, gastric shield; 8, specialized cells at bend between stomach and intestine; 9, style sac ridge; 10, style sac groove; 11, dorsal typhlosole; 12, mucoid rod (protostyle); 13, bolus entering intestine; 14, gonad.

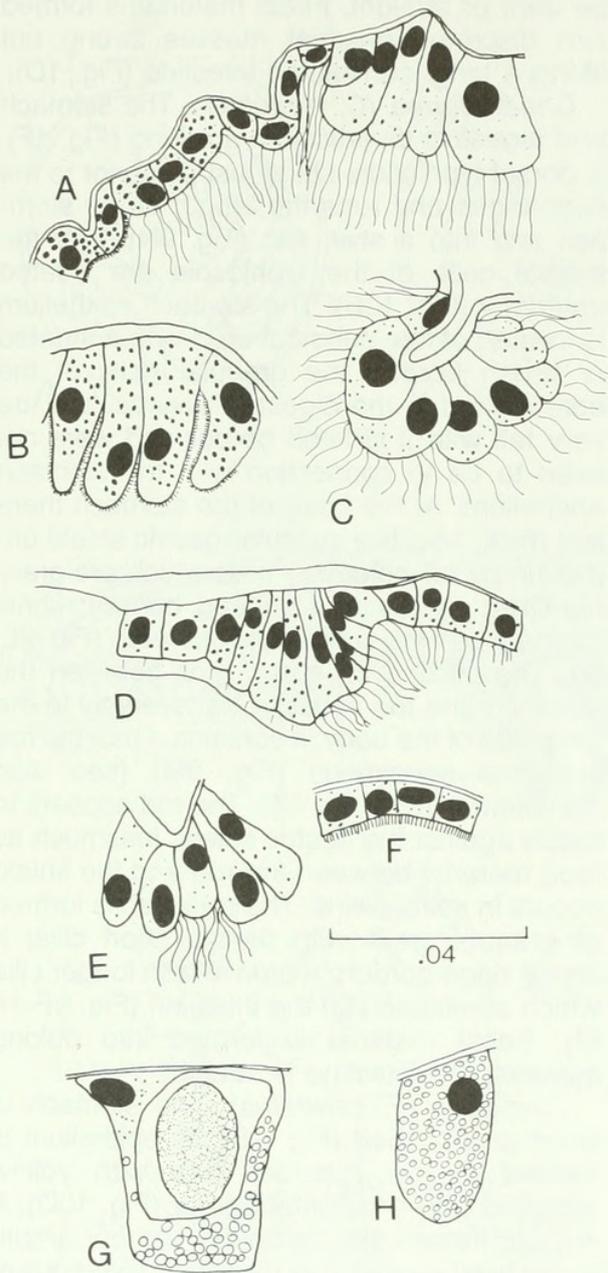


FIG. 10. Cells of alimentary tract in Chaetodermomorpha. A-C, H: *Scutopus megaradulatus*; D: *Falcidens caudatus*; E-G: *Chaetoderma nitidulum*. A-F, granular stomach cells and dorsal ciliated typhlosole or groove (B, C posterior to A); G, digestive gland secretory cell with basophilic sphere; H, cell from dorsal band of granular cells of digestive gland.

sole (Fig. 10D), starts about half way down the length of the stomach and leads to a hook-like gastric shield (Scheltema, 1978, fig. 1C), and thence continues into a style sac. A second, ventral ciliated band starts at about the level of the gastric shield and joins the dorsal typhlosole to form a style sac with a mucoid rod and ciliated ridge bordering a groove. The rod appears to rotate against the gastric shield. Schwabl (1961) described and figured

schematically the gastric shield and style sac for *F. hartmani* without considering them as such, although referring to the style sac as "caecum-like"; a mucoid rod is not mentioned. The cells underlying the gastric shield are cuboidal with large granules distally (Fig. 9K). The style sac is transverse to the body axis (Fig. 1E).

The intestine is convoluted and filled with spherical fecal masses.

Diet

The diet of the species under discussion is based on stomach contents. Not available to me at this time of writing is Salvini-Plawen's work (in press) on diet (see Literature Cited).

Gymnomenia n. sp. As in most Neomeniomorpha, there are many unexploded nematocysts within the cells of the midgut; *Gymnomenia* is therefore considered to feed on Cnidaria.

Scutopus. The diet is not known; fecal material contains organic (?) crystals and perhaps sediment particles. The radula morphology suggests that the diet is particle-size dependent, probably detritus.

Limifossor. The diet is not known. Fecal material contains very small bits of unidentified frustules, spicules and other hard parts of organic origin. Although *Limifossor* has usually been considered a carnivore (Heath, 1905; Salvini-Plawen, 1975), it seems quite as likely from radula morphology that it is a detritivore and possibly particle-size dependent.

Prochaetoderma. The diet seems to be a wide variety of both prey and organic debris. The stomach of several specimens hold Foraminifera with sand tests (?*Saccorhiza*), crustacean parts, radular teeth of smaller *Prochaetoderma*, and bits of unidentified organic remains; much of the food material still contains stained cytoplasm. There are very few sand grains.

Chaetoderma and *Falcidens*. The Chaetodermatidae are considered to be selective carnivores, taking in entire Foraminifera, "worms," small snails and other unidentified organisms which are found in the stomach with stained cytoplasm. Ivanov (1979) has figured the action of feeding. *C. nitidulum* can be a contaminant in laboratory cultures of living Foraminifera upon which they will feed (B. Christensen, personal communication). It is not known whether members of the Chaetodermatidae also feed on organic debris. There are few sand grains in the gut.

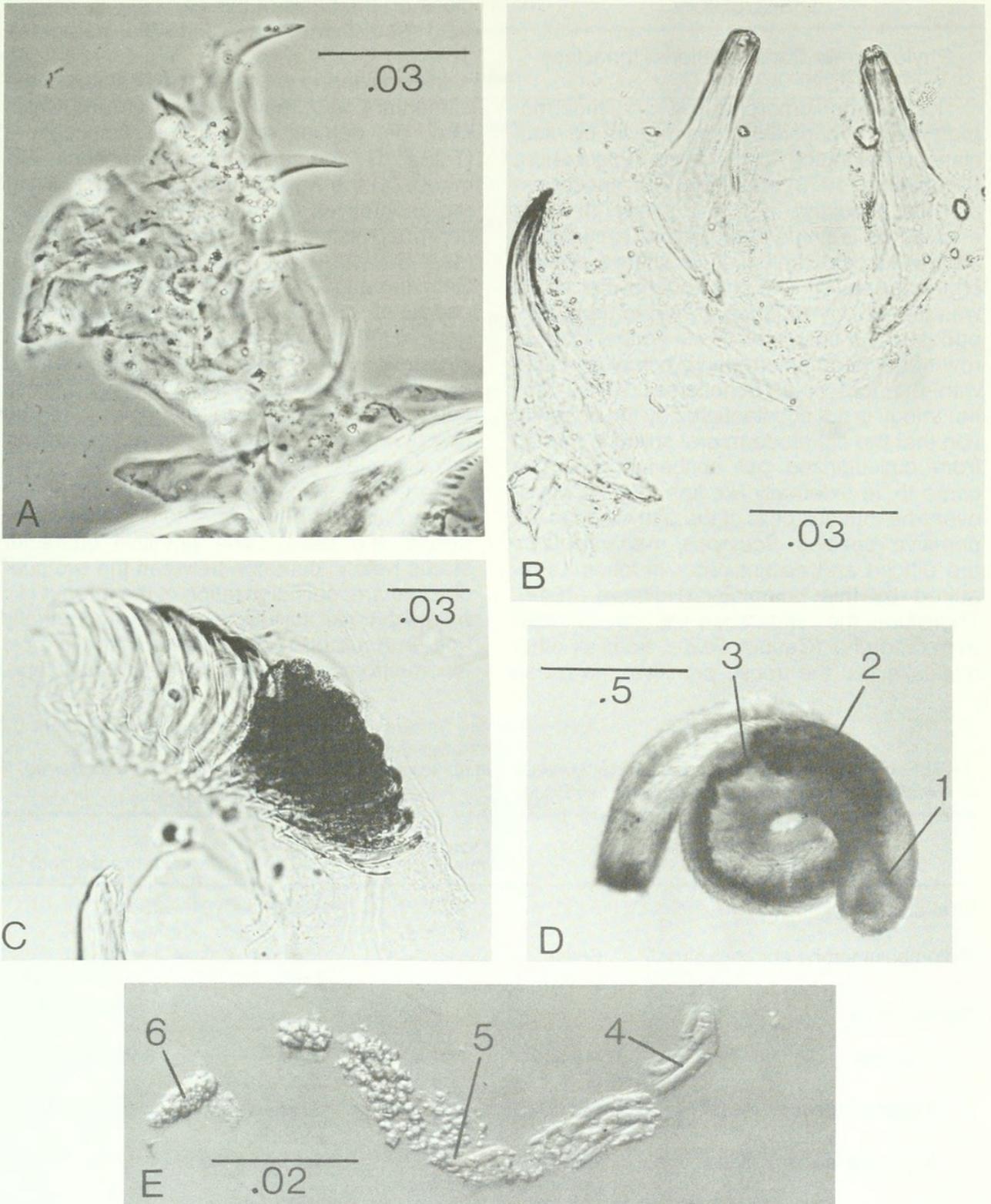


FIG. 11. Radula of *Prochaetoderma* sp. y (A-C) and alimentary tract of *Scutopus robustus* (D, E). A: lateral tooth-like extensions of radular membrane; B: worn anterior pair of denticles; C: food material caught in crossed pairs of anterior teeth, held against posterior 6-7 pairs touching at distal tips; note darkened, tanned distal tips; D: entire preserved specimen in transmitted light; E: proteinaceous rods with adhered crystals dissected from stomach and intestine of a specimen without dark granules evident in D. Scales in mm. 1, radula; 2, darkly pigmented stomach; 3, band of granular cells passing from stomach to dorsal wall of digestive gland; 4, rods from anterior stomach; 5, rods and crystals at base of stomach and entrance into intestine; 6, fecal material.

DISCUSSION

Phylogenetic Considerations: Intraclass

The Neomeniomorpha and Chaetodermomorpha are considered by me to be subclasses belonging to the class Aplacophora (Scheltema, 1978) and their great specialization of acquiring a worm shape to have evolved as a single event before evolution of the molluscan shell (i.e., a shared derived character state). The chaetoderm oral shield was thought by Hoffman (1949) to be homologous to the outer wall of the ventral foot furrow of the neomeniomorphs (homology is not with the foot sole, Scheltema, 1978). This homology is not substantiated by the observation that the chaetoderm oral shield is formed from cuticularized gut epithelium that has come to lie externally like lips (Fig. 2). Moreover, the mucous cells of the oral shield in the primitive species *Scutopus megaradulatus* are diffuse and do not occur in lobes as required by this homology (Hoffman, 1949). Therefore the separation of the Chaetodermomorpha (Caudofoveata) from all other mollusks as the most primitive molluscan

class on the basis of this homology is not upheld (see Salvini-Plawen, 1972a, paragraph 16).

In considering which character states of the alimentary tract may be primitive and which may be derived among the Aplacophora (Table 1), the following assumptions are made: (a) the Aplacophora are the sole living representatives of the primitive pre-placophorous mollusks and geologically very old (see Stasek, 1972; Salvini-Plawen, 1972a; Scheltema, 1978); (b) the least differentiated character state is usually the most primitive, unless there is some evidence for loss of structure; (c) a character state shared by most or all members is usually primitive, unless some evidence points to the contrary; (d) the radula capable of the least amount of manipulation is most primitive.

From the table certain relationships are clear (numbers below refer to character number in the table). The primitive character states held in common between the two subclasses are: cuticularization of the foregut (1); paired tubular salivary glands (lying ventrally both in *Scutopus megaradulatus* and in most Neomeniomorpha; perhaps secondarily lack-

TABLE 1. Primitive and derived character states of the aplacophoran alimentary tract (C = *Chaetoderma*, F = *Falcidens*, G = *Gymnomenia*, L = *Limifossor*, P = *Prochaetoderma*, S = *Scutopus*).

| Character | Primitive | Derived (a, b, independently derived) |
|---------------------------------|--|---|
| <u>Oral shield</u> | | |
| (Neomeniomorpha not considered) | Entire S, F, C | Divided L, P |
| <u>Buccal cavity</u> | | |
| 1. Cuticle | Present G, S, L, P | Absent F, C |
| 2. Goblet cells | Dominant G, S, L | Scattered P, F, C |
| 3. Tubular salivary glands | One pair (most Neomeniomorpha) S, L, P | (a) Two pairs (F?), C (b) ¹ Lacking G |
| 4. Buccal sublingual pouch | Absent, or nearly so G, S | Present L, P, F, C |
| <u>Radula</u> | | |
| 5. Radular membrane | Divided or partially so, or line of fusion G, S, L | Entire P, (F?, C?) |
| 6. Subradular membrane | Absent G, S | Present (L?), P, (F?, C?) |

TABLE 1 (Continued).

| Character | Primitive | Derived (a, b, independently derived) |
|--|---|---|
| 7. Dentition | Distichous, without central plate G, S, L | (a) Distichous, with central plate P (b) Reduced F, C |
| 8. Relationship of teeth to radular membrane | Not articulated G, S, L | (a) Articulated P (b) Reduced F, C |
| 9. Bolster tissue | Connective tissue, muscle (G?), S, L, F, C | Chondroid-like P |
| 10. Cuticular structure derived from odontophore | Absent G, S, L, F, C | Present P |
| 11. Dorsal approximator of bolsters | Present (primitive?) S, L | Absent (derived?) G, P, F, C |
| <u>Esophagus</u> | | |
| 12. Length | Long, short S, L, C | (a) Extremely short P, F (b) Absent (derived?) G |
| 13. Ciliation | Ciliated S, L | Not ciliated P, F, C |
| <u>Midgut</u> | | |
| 14. Ciliated dorsal band, groove, or typhlosole | Present (nearly all Neomeniomorpha) S, L, F, C | Absent (G?), P |
| 15. Digestive diverticulum | Absent (primitive?) G (and all other Neomeniomorpha) | Present (derived?) S, L, P, F, C (and all other Chaetodermomorpha) |
| <u>Chaetodermomorpha only:</u> | | |
| 16. Dorsal granule cells, digestive diverticulum | Present S, L, F, C | Absent P |
| 17. Lining of stomach | Not cuticular S, L, C | Cuticular (P?), F |
| 18. Gastric shield | Absent S, L, P | Present F, C |
| 19. Style sac | Absent S, L, P | Present F, C |
| 20. Mucoïd or protein rod(s) | Present throughout stomach and anterior intestine S | (a) Present, restricted location L, F, C (b) Absent P |
| <u>Feeding, diet</u> | | |
| 21. Feeding type | Detritivore-omnivore S, L, P | Selective carnivore G, F, C |
| 22. Particle size | Dependent S, (L?) F, C | Independent (a) Suctorial G (b) Rasping P |

¹Considered primitive by Salvini-Plawen (1978).

ing in *Gymnomenia*) (3); a distichous radula lacking articulation (7, 8); a divided or fused radular membrane and lack of a subradular membrane (5, 6); and a ciliated dorsal band, groove, or typhlosole that runs the length of the midgut to a ciliated intestine (14). The foregut goblet cells (2) may not be homologous (cf. Figs. 3A, B, 4F).

The greatest difference between the two subclasses lies in the presence or absence of a digestive diverticulum (15). The undivided midgut of the Neomeniomorpha has been interpreted as primitive on the basis of (a) the lack of digestive adaptations (digestive gland, protostyle, gastric shield) for microphagous feeding (Salvini-Plawen, 1980) and (b) the presence of regular outpouchings caused by serially arranged dorso-ventral musculature (Boettger, 1956; Salvini-Plawen, 1969). (These outpouchings were first considered to be primitively lacking in *Genitoconia*, a member of the Wireniidae which includes *Gymnomenia* [Salvini-Plawen, 1967a], but later the lack of lateral pouches was considered to be secondarily derived [Salvini-Plawen, 1978]). Most neomeniomorphs have a very specialized cnidarian diet and thus the undivided midgut may be a specialized or reduced state, and not a primitive one. The single digestive diverticulum of the chaetoderms appears to have developed as a lobe from the stomach; it retains the evidence of its origin in the dorsal band of granular cells which can be traced forward to the stomach epithelium.

Among the Chaetodermomorpha there are two lines of evolutionary change from the least differentiated and therefore presumed primitive state found in *Scutopus*. One direction has been toward increased elaboration of the stomach into a posterior style sac, restriction of the protostyle to this sac, and increased cuticularization at the base of the stomach to form a gastric shield; morphoclines of these character states exist from *Scutopus* through *Limifossor* to *Falcidens* and *Chaetoderma* (Fig. 9). The other direction has been toward reduction as found in *Prochaetoderma*, with a single type of digestive cell in a shortened digestive diverticulum, no dorsal ciliated typhlosole, and no protostyle. The gastric shield is not correlated with general cuticularization of the stomach epithelium (Table 1: 17, 18). A convoluted intestine is found independently in the two genera that have long, thin "tails," *Prochaetoderma* and *Falcidens* (Fig. 1D, E).

The aplacophoran radula has evolved to-

wards freeing the teeth from their primitively broad attachment to the radular membrane and toward development of a sublingual pouch (4, 8). The result has been increased ability to manipulate or break down the food source.

In *Gymnomenia* the radula appears to be one of the most primitive among the Aplacophora (Fig. 4), but much work remains to be done on the diverse radular types found in other Neomeniomorpha (Nierstrasz, 1905; Salvini-Plawen, 1967b, 1978). Among cnidarian feeders with a suctorial foregut, reduction and specialization could be expected; nevertheless, a primitive type of radula occurs in carnivores in the Aplacophora.

The radulae among chaetoderm genera differ greatly in morphology and cannot readily be derived from a primitive type or from each other except in terms of function. Primitively, teeth are affixed to the radular membrane and the odontophore is scarcely free in the buccal cavity; only a sliding motion combined with closing opposed teeth is possible (*Scutopus*, Fig. 5). More complicated movements can occur in *Limifossor* with a split radular membrane and a relatively enormous odontophore (Figs. 1C, 6B; Heath, 1905). A rasping gastropod-like radula has evolved only in *Prochaetoderma* (Fig. 7). The reduced, highly modified radula of *Falcidens* and *Chaetoderma* is probably capable of precise movement in prey capture (Ivanov, 1979). The two most highly evolved radulae occur in the two groups which are carnivorous or carnivorous-omnivorous and which also have the most modified midguts: *Prochaetoderma* with the most complex radula and most reduced midgut and the Chaetodermatidae (*Falcidens* and *Chaetoderma*) with the most modified radula and most complex midgut. There does not appear to be a morphocline in radula type in the Chaetodermomorpha (see Salvini-Plawen, 1975).

Phylogenetic Considerations: Interclass

The style sac and gastric shield are shown by the Aplacophora to have evolved more than once in the Mollusca. In the Aplacophora, a protostyle has evolved before a style sac, and a style sac and gastric shield occur only in a carnivorous family (Chaetodermatidae).

A radula capable of rasping seems to require a single radular membrane, a subradular membrane, a bending plane, firm bolsters,

and some way for the teeth to articulate on the radular membrane. There also must be some way to keep the mouth open during rasping. In gastropods the mouth opens as part of radula protraction (Graham, 1973), but in *Prochaetoderma*, which uses its head for locomotion (burrowing) as well as for feeding, unique jaws have evolved which can keep the mouth open during rasping. The significance of rasping as a feeding mechanism is that feeding is not particle-size dependent (Table 1: 22); large pieces of food can be broken down and manipulated before ingestion, whether the food be a large algal mat on a hard surface, prey, or large pieces of detritus. The ability to manipulate food before ingestion may be one of the reasons for the great success of the gastropods.

It is not possible on the evidence presented here to determine the structure of the archimolluscan alimentary tract. Certainly it had a nonarticulated radula with protractors, retractors, and bolsters, paired tubular salivary glands, a cuticular foregut, and a dorsal ciliated tract running down the midgut. If the Neomeniomorpha have retained a primitive midgut even though they have become food specialists, then a digestive gland must have been derived more than once in the mollusks. On the other hand, if the neomeniomorph midgut is reduced, then a protostyle without a style sac or gastric shield and a digestive diverticulum could have been primitively present in the mollusks, a condition that would lead more directly to parallel evolution in the molluscan midgut of a style sac and gastric shield. The two studies on aplacophoran gut development for two Neomeniomorpha did not have this question in mind (Baba, 1938; Thompson, 1960), but Baba observed that the intestine arises from endoderm and that the midgut epithelium when it first forms is thickest laterally and ventrally, as it is in the chaetoderm digestive diverticulum.

The evidence from entire, isolated radulae of Aplacophora indicates for the mollusks an original state of distichous rows of teeth on a divided radular membrane. The evidence for an original single basal membrane with rows of broad monoserial teeth rests on reconstructions from histologic sections of the neomeniomorph radula of *Dondersia* (Nierstrasz, 1905), on histologic sections of *Simrothiella* (Salvini-Plawen, 1972a), and on ontogenetic studies on chitons (Minichev & Sirenko, 1974). Kerth (1979) has shown, on the other hand, that distichous teeth on a sin-

gle membrane develop ontogenetically in the pulmonates.

The questions of whether the archimolluscan radula was a single or paired structure and whether or not the midgut had a digestive diverticulum is left open for further observations on isolated aplacophoran radulae, comparative histologic studies and studies on development.

Ecological Considerations

Although Aplacophora are ubiquitous in the deep sea from the edge of the continental shelf to the deepest abysses and hadal depths, they seldom are numerically an important constituent of the macrofauna. The two chaetoderm genera described here which are the most primitive also have the fewest known species: *Scutopus* (4) and *Limifossor* (4). The number may be doubled, at most, from existing collections not yet described. The carnivorous species belonging to *Falcidens* and *Chaetoderma* are far more numerous, although their total numbers in any one sample are never great (unpublished data).

Species of *Prochaetoderma* are numerous (unpublished data) and can be the numerically dominant macrofaunal animals in quantitative samples. *Prochaetoderma* sp. *y* was the dominant species in a total of twenty-five 35-cm² tubular cores taken at one 1,760-m station off Woods Hole (Grassle, 1977), although dominance was not high (6.0%; discrepancy from Grassle's data due to recent recognition of a sibling species). The next four most numerous species were polychaete worms (5.1%, 4.4%, 4.2%, and 3.7%) (nematodes, ostracods, and copepods excluded). Actual density of *Prochaetoderma y* was 309 m⁻². In a ¼-m² spade box core taken in the same area, this species was the fourth most numerous species with a density of 192 m⁻². In other quantitative samples in the same area, *Prochaetoderma y* ranged in numbers up to 237 m⁻², and in grab samples taken between 1141 and 2148 m depths it ranged up to 400 m⁻².

In a ¼-m² spade box core taken in the remarkably productive Aleutian Trench off Alaska at a depth of 7298 m, another *Prochaetoderma* was one of the dominant species at a density of 124 m⁻² (Jumars & Hessler, 1976).

The numerical success of some species of *Prochaetoderma* may be attributable in part

to their efficient gastropod-like rasping radula, which has made a wide size range of food sources available to them in an environment where food is probably a limiting factor.

CONCLUSION

The Aplacophora exhibit a wide variation in morphology of the alimentary tract. Comparative studies of these morphologies give insight into evolutionary events and function among the Mollusca and lead to a greater understanding of feeding in the deep sea.

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