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Comparative ultrastructural study of the posterior suckers of four species of symbiotic Platyhelminthes, *Temnocephala* sp. (Temnocephalida), *Udonella caligorum* (Udonellidea), *Anoplodiscus cirrusspiralis* (Monogenea: Monopisthocotylea), and *Philophthalmus* sp. (Trematoda: Digenea)

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Key words: *Temnocephala* sp., *Udonella caligorum*, *Anoplodiscus cirrusspiralis*, *Philophthalmus* sp., ultrastructure, sucker, haptor, phylogeny, homology

Abstract. The posterior attachment organ (sucker) of *Temnocephala* sp. is located ventrally attached to the posterior end of the body by a well defined stalk; those of *Udonella caligorum* Johnston and *Anoplodiscus cirrusspiralis* Roubal, Armitage et Rohde are extensions of the posterior end facing posteriorly. In *Philophthalmus*, the sucker is ventrally embedded in the main body. The sucker of *Temnocephala* is lined by an epidermis, its ventral part separated from the adjacent epidermis by a septate junction. The epidermis resembles that of the body proper, containing nuclei and numerous dense bodies, its surface enlarged by short microvilli, traversed by glandular ducts of two types and by sensory receptors, and based on a basal lamina with a thick underlying fibrous matrix. The stalk of the sucker contains many muscle fibres extending from the main body into the sucker. The posterior surface of the sucker of *Udonella* is separated from the adjacent tegument by a septate junction; it consists of numerous microvilli arising from the basal lamina and does not represent a tegument; glandular ducts of two types open through it, and muscle fibres extend from the body proper into the sucker. The posterior surface of the sucker of *Anoplodiscus* consists of a thin tegument not separated from the adjacent tegument by a septate junction, drawn out into a very large number of densely packed, long microvilli, some branching from a thick cross-striated base; large glandular ducts open postero-laterally. The ventral sucker of *Philophthalmus* is embedded in the body proper but clearly bounded by a "capsule" of basal lamina; it is lined by a tegument continuous with that of the main body and lacking microvilli except in a small band around the ventral sucker opening. There is no evidence from ultrastructure that the suckers of the four taxa are homologous. Since there is no convincing other evidence for the homology of the posterior attachment organs of the major groups of parasitic Platyhelminthes (Neodermata) and the Temnocephalida, a "cercomer theory" assuming such homology cannot be accepted as proven.

Many authors have postulated homology of the posterior attachment organs (the so-called "cercomer") of the various groups of parasitic Platyhelminthes and the Temnocephalida. For example, Brooks and McLennan (1993, earlier references therein) accept the taxa Cercomeria (temnocephalids plus all parasitic platyhelminths) and Cercomeridea (trematodes, monogeneans, gyrocotylids, amphilinids, eucestodes), the former defined, in addition to other synapomorphies, by supposedly homologous posterior attachment organs. However, a critical evaluation of the literature shows that detailed comparative studies, including ultrastructural ones, of the suckers of "Cercomeria" have not been made. Likewise, the development of the organs has not been studied. Hence, homology of the organs has not been established. We therefore examined the suckers of a temnocephalid, udonellid, monopisthocotylean monogenean and digenean trematode with the aim of finding evidence for the homology of the organs of different groups. The species of monogenean was chosen because its sucker is relatively simple, lacking elaborate accessory structures like hooks, septa etc., found in many other monogeneans, which might obscure basic structures useful in a homology analysis. Both the temnocephalid and *Udonella* are attached to similar hosts, crustaceans, and *Anoplodiscus* is permanently attached to the fins of a teleost fish, the sparid *Chrysophrys auratus*. Cercariae of *Philophthalmus* develop in marine snails, the final host of the species

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examined is not known, but other species parasitize various organs of birds (and occasionally man).

MATERIALS AND METHODS

Specimens of an undescribed species of *Temnocephala* were collected from the freshwater crayfish *Cherax destructor* from an Armidale (NSW) pond, specimens of *Udonella caligorum* were collected from the copepod *Caligus epidemicus* on the bream *Acanthopagrus australis* (Sparidae) in Moreton Bay (Qld), and specimens of *Anoplodiscus cirrusspiralis* were collected from the snapper *Chrysophrys auratus* from an aquaculture pond at Cronulla, Sydney, NSW. They were fixed in 3% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.3 (made with seawater for the last two species) for 2 h, 8 days and 2 h respectively at 4°C. The *Temnocephala* specimens were initially put into fixative at 60°C, cooled to room temperature and then transferred to 4°C. Rediae and cercariae of *Philophthalmus* sp. were dissected out of the marine snail *Pyrazus ebeninus* collected at Deception Bay, Queensland, fixed for 2 h at 4°C in 3% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2. Specimens of all species were washed in the same buffer as used for fixation, postfixed in 1% OsO_4 in the same buffer for 1 h, 1.25 h, 0.5 h and 0.5 h respectively before dehydration in an alcohol series and embedding in Spurr resin. The suckers of *Temnocephala*, *Udonella* and *Philophthalmus* cercaria were sectioned transversely. A juvenile specimen of *Anoplodiscus* was sectioned sagittally.

RESULTS

Temnocephala

The posterior attachment organ of *Temnocephala* is located ventrally to the main body, attached to its posterior end by a well defined stalk (Fig. 1A). It is lined by

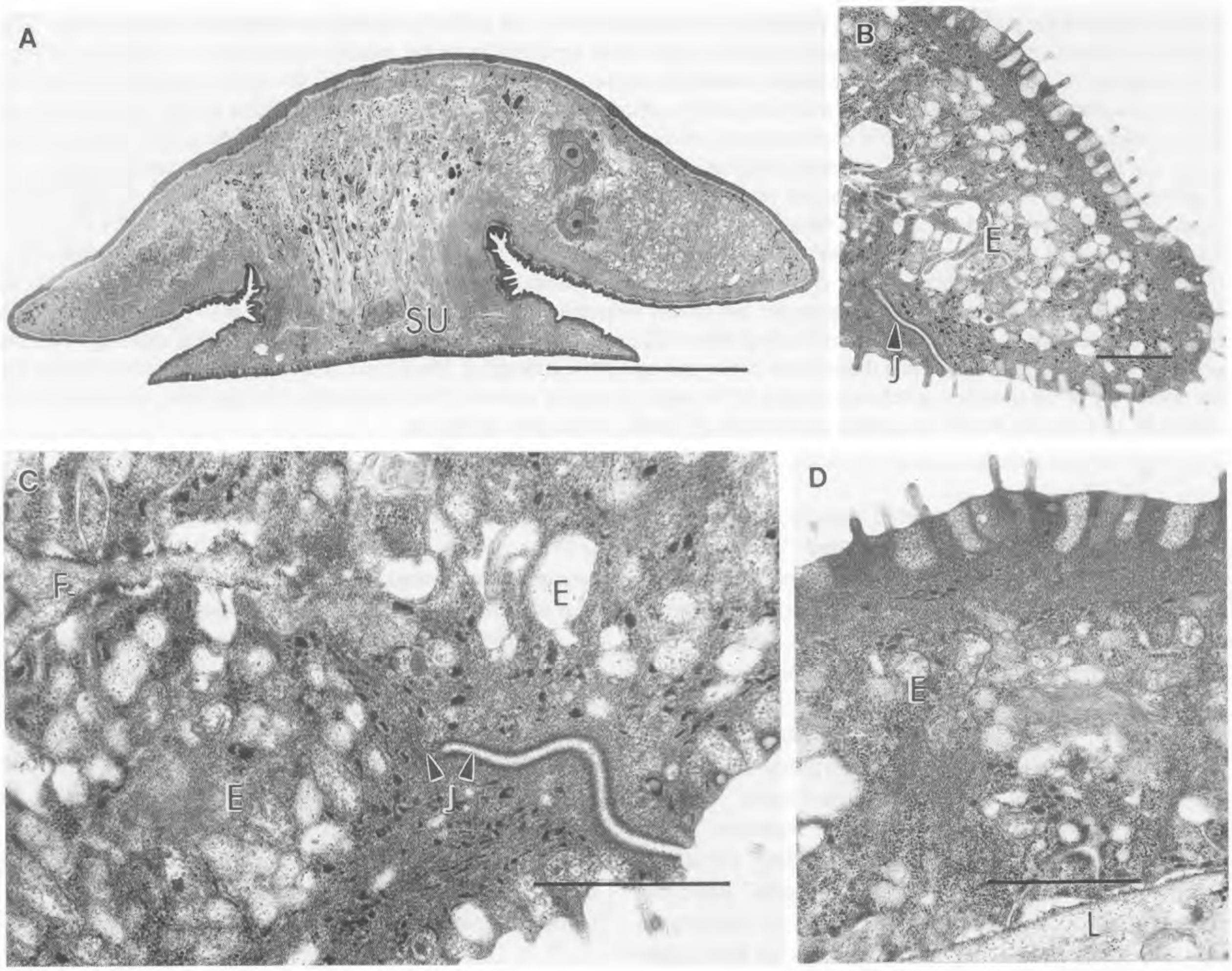

Fig. 1. *Temnocephala* sp. **A** – semithin cross-section through posterior part of body and sucker. **B–D** – E. M. graphs of cross-sections through sucker wall. **B, C** – Margin of sucker with junction (arrowheads). **D** – dorsal sucker wall. Scales 0.1 mm (A), 1 µm (B-D). Abbreviations: see p. 27.

a syncytial epidermis with many short microvilli (Figs. 1B–D, 2A,D–E, 3C) and contains numerous vacuoles scattered through it and arranged in a regular row just beneath the apical membrane (Figs. 1B–D, 3C), xtensions of the basal cell membrane into it (Fig. 1D), as well as many dense bodies (Figs. 1C–D, 2D, 3C). The epidermis is based on a distinct basal lamina with a thick underlying fibrous matrix (Fig. 2D) and is nucleated (Fig. 2A,D). Its ventral part, i.e. the part lining the surface attached to the crustacean host, is separated from the adjacent epidermis by a septate junction (Fig. 1B–C), contains sensory receptors (Fig. 2B), and is traversed by glandular ducts containing two types of secretion (large grana with many very electron dense inclusions in a medium-dense matrix, which break up into a loose reticulum in the ducts near the surface (Fig. 2C–D), and small dense granules, Fig. 2D–E)). The epidermis of the stalk is much thickened, based on a basal

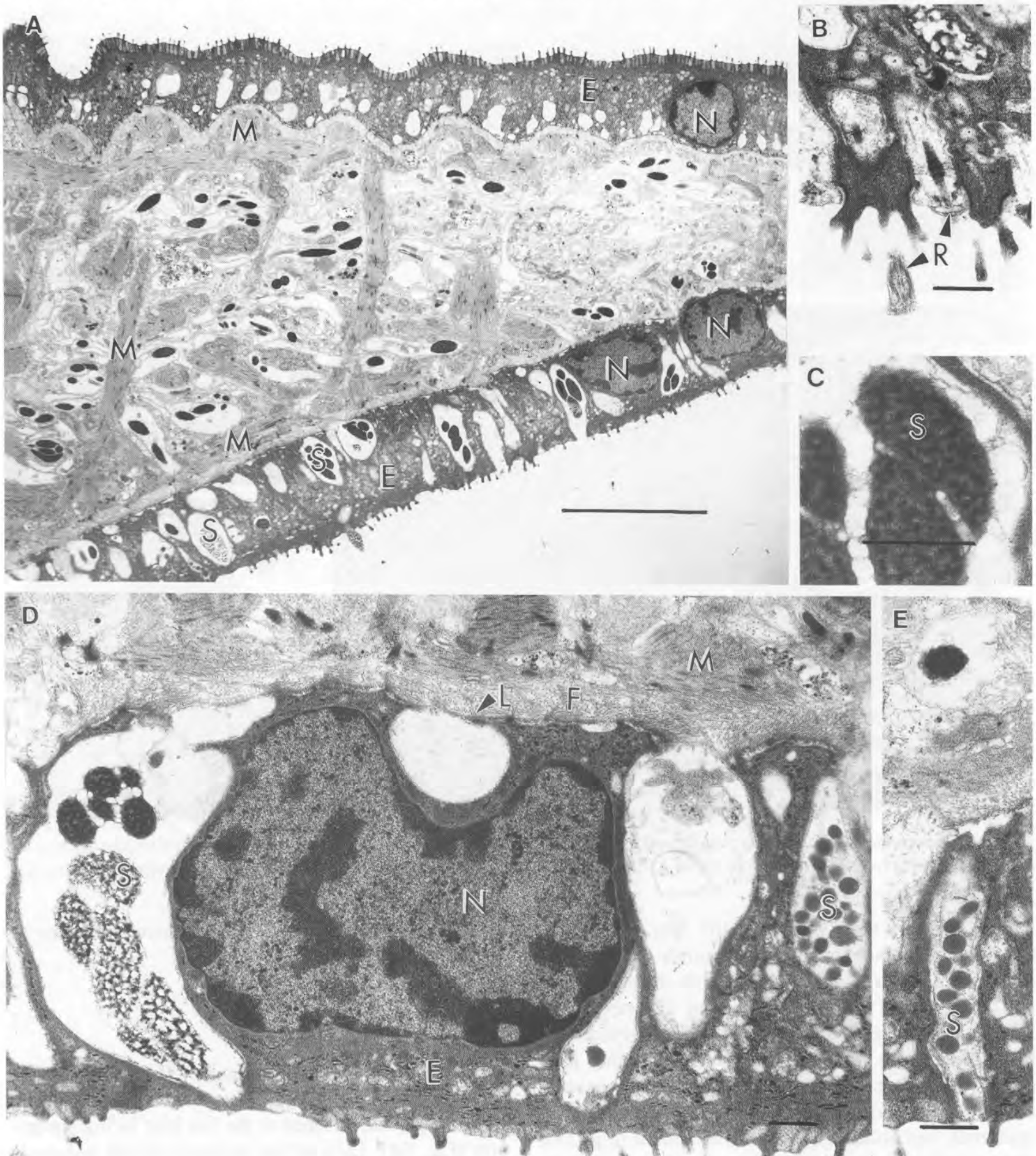

Fig. 2. *Temnocephala* sp. Cross-sections through sucker. Note circular, longitudinal and dorso-ventral muscle filaments in **A**, sensory receptors in **B**, two types of secretion in **C–E**, and epidermal nuclei in **A** and **D**. Scales 5 μm (A), 0.5 μm (B–E).

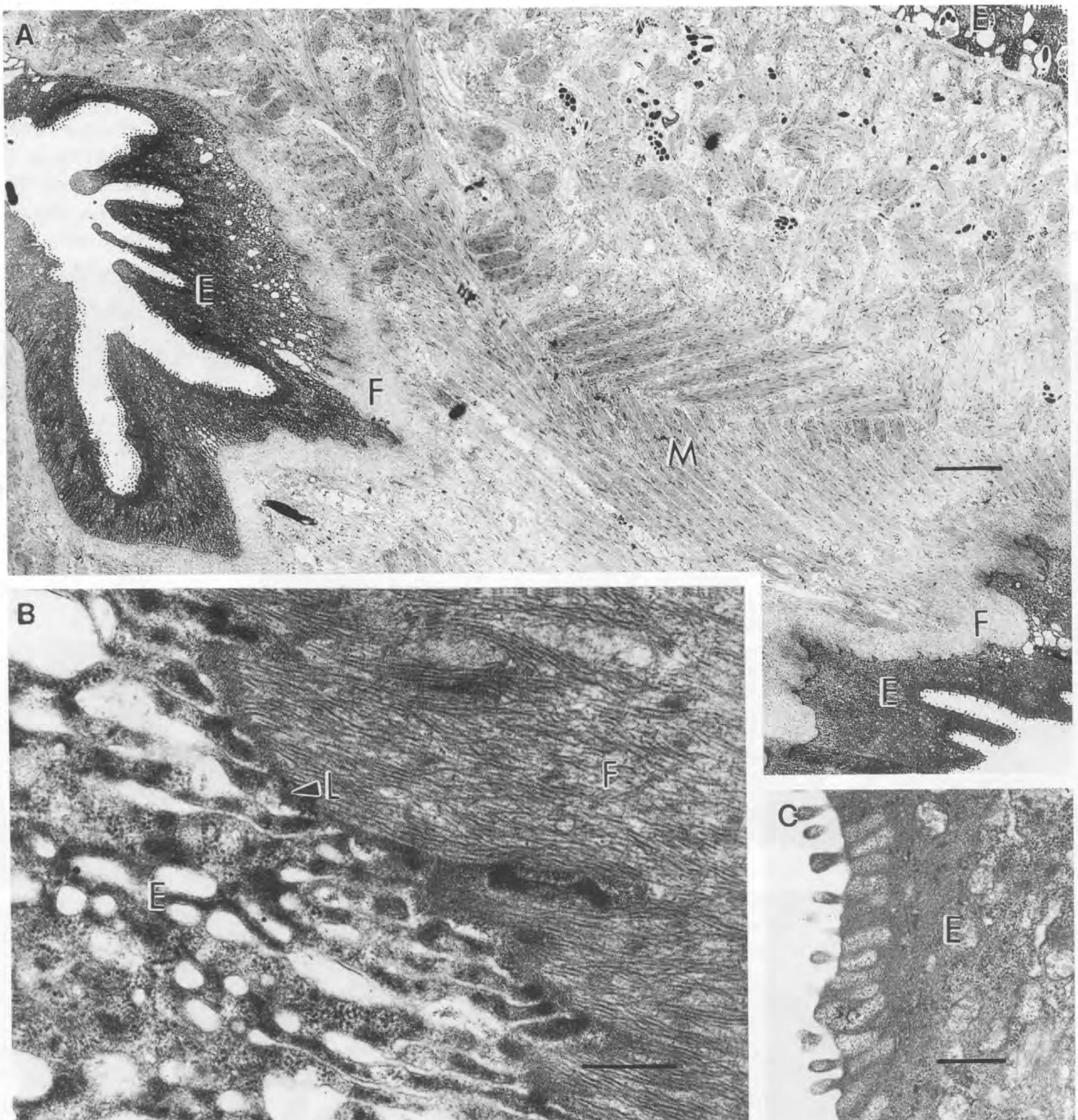

Fig. 3. *Temnocephala* sp. Cross-section through stalk of sucker. Note densely packed oblique muscles extending from main body on top right into stalk on bottom left in **A**, dense fibrous matrix below epidermis in **A** and **B**, and microvilli of epidermis in **C**. Scales 5 µm (A), 0.5 µm (B–C).

lamina and very thick fibrous matrix (Fig. 3A–B); the basal cell membrane forms a large number of extensions into the epidermis, communicating with the vacuoles in the interior thus forming a reticulum of spaces (Fig. 3A–B). Densely packed muscle fibres extend from the body proper into the stalk and sucker, crossing each other (Fig. 3A); in the sucker itself, they extend beneath and along the epidermis, between the dorsal and ventral epidermis, and obliquely in several directions (Fig. 2A). The epidermis close to the sucker resembles that of the sucker, with nuclei, surface microvilli, vacuoles, dense bodies, extensions of the basal cell membrane into it, and glandular ducts (Fig. 4A–B).

Udonella

The posterior attachment organ of *Udonella* is a posterior extension of the body proper, with an indistinct stalk, the surface attached to the fish host facing posteriorly (Fig. 5A). Parts of the tegument of the anteriorly directed wall of the sucker have densely packed stubby

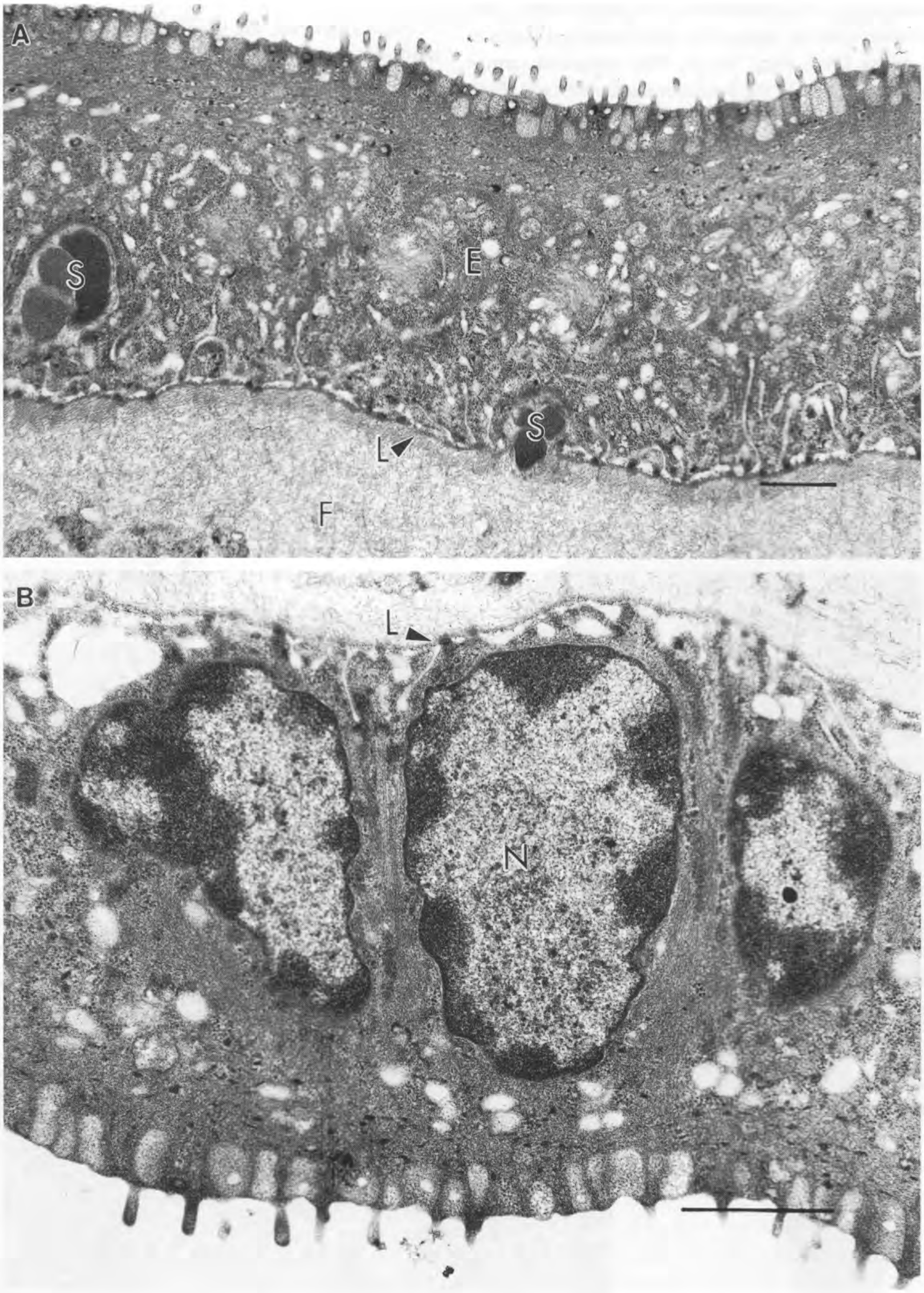

Fig. 4. *Temnocephala* sp. Epidermis of main body near sucker. **A** – dorsal epidermis. **B** – ventral epidermis. Note intraepidermal nuclei, microvilli at surface, basal lamina with underlying thick fibrous matrix, numerous extensions of basal cell membrane into epidermis, numerous vacuoles and small dense bodies in epidermis, row of vacuoles with loose granular contents below surface, and secretory ducts. Scales 1 µm.

microvilli (Fig. 7D), others have interconnected surface extensions (Fig. 7C), resembling the tegument of the body proper with its numerous interconnected surface extensions or loops (Fig. 7A–B). The tegument terminates at the margins of the posterior sucker surface (Fig. 6A–B), connected to it by a septate junction (Fig. 6A–B). This posterior surface is formed by a layer of densely packed microvilli, extensions not of the tegument but of the basal lamina (Fig. 6B–D). Between them open many glandular ducts containing either large or small dense ovoid inclusions (Fig. 6C–D). The interior of the sucker is subdivided into many compartments by interconnected branches of connective tissue (Figs. 5A–B, 6C). Muscle fibres extend from the body proper into the sucker and traverse it in various directions (Figs. 5A–B, 6C), many of them enclosed by branches of connective tissue (Fig. 6C).

Anoplodiscus

As in *Udonella*, the sucker of *Anoplodiscus* is a posterior extension of the body proper without a well defined stalk (Fig. 8A). It is lined by tegument. The tegument of the anterior sucker wall is thick, containing many dense and lucent bodies (Fig. 8B), resembling the body tegument. The posterior sucker wall, attached to the fish host, is formed by a layer of thin tegument (Figs. 9A–C, 10A–B) continuous with the adjacent tegument (Fig. 10A–B) and containing many dense and lucent inclusions (Figs. 9B–C, 10A–B). It is drawn out into numerous long densely packed microvilli (Figs. 8A,C, 9A–D). Many of the microvilli arise by branching from a cross-striated base (Fig. 9B–C). In cross-section, they are seen to contain a dense, irregular core (Fig. 9D). Near the margins of the sucker, they are shorter and more irregular (Fig. 10A–B). Invaginations

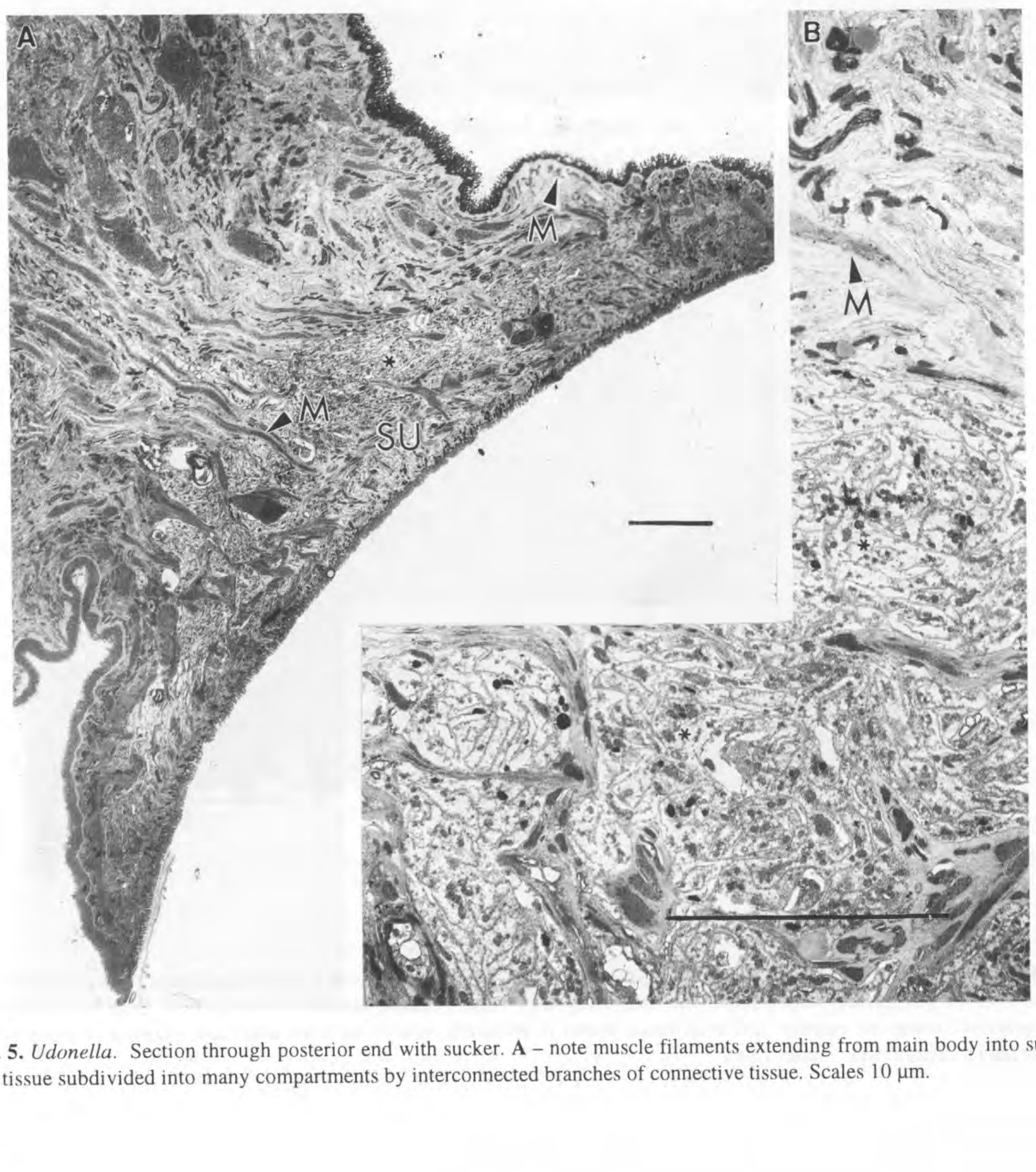

Fig. 5. *Udonella*. Section through posterior end with sucker. **A** – note muscle filaments extending from main body into sucker. **B** – tissue subdivided into many compartments by interconnected branches of connective tissue. Scales 10 µm.

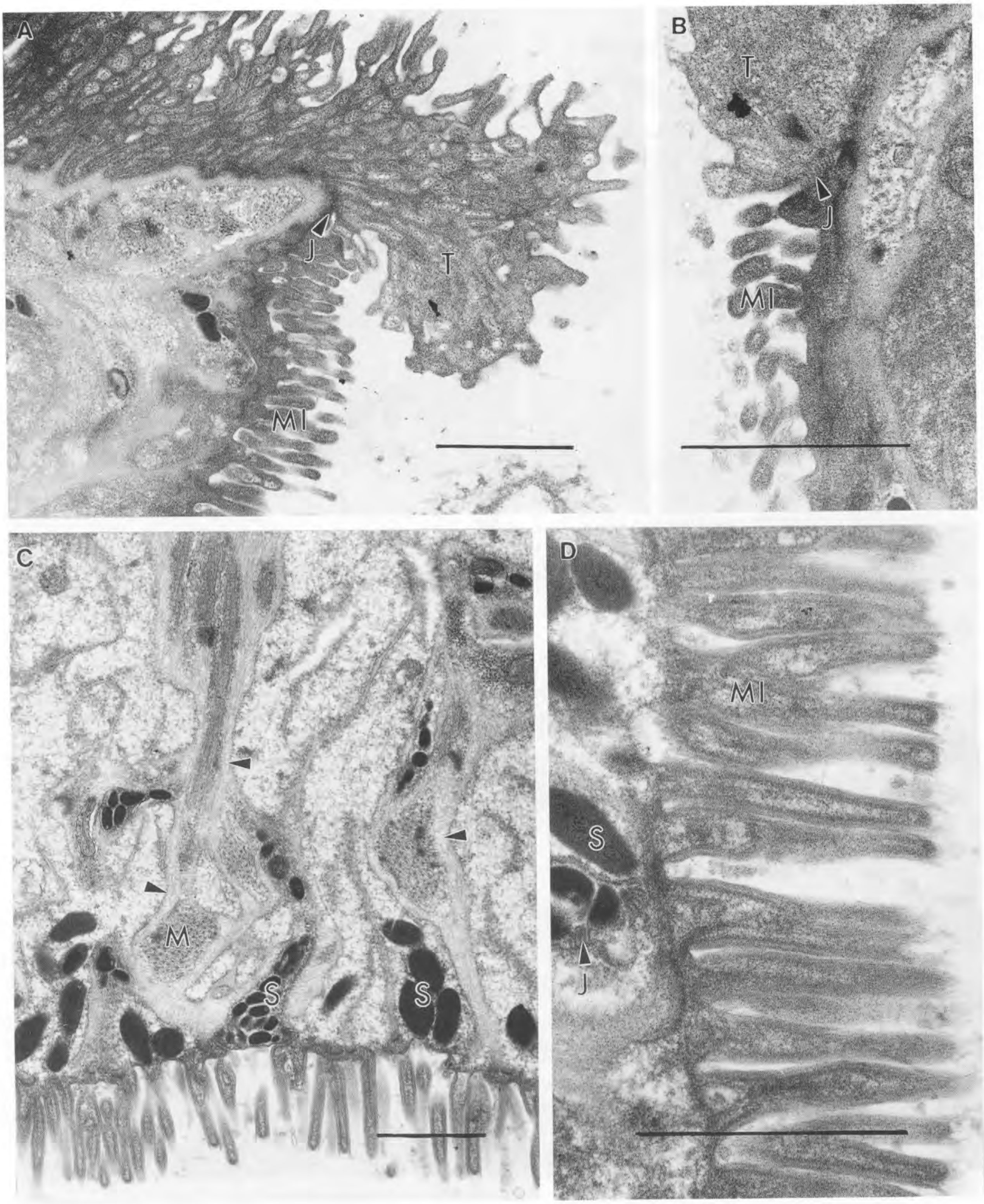

Fig. 6. *Udonella.* Sucker. **A–B** – lateral part of sucker, in contact with tegument of dorsal part of sucker by septate junction. Note densely packed microvilli of sucker. **C–D** – two types of secretion in secretory ducts in contact with surrounding tissue by septate junctions opening between microvilli of sucker. Interconnected branches of connective tissue around muscle filaments and secretory ducts. Scales 1 μm.

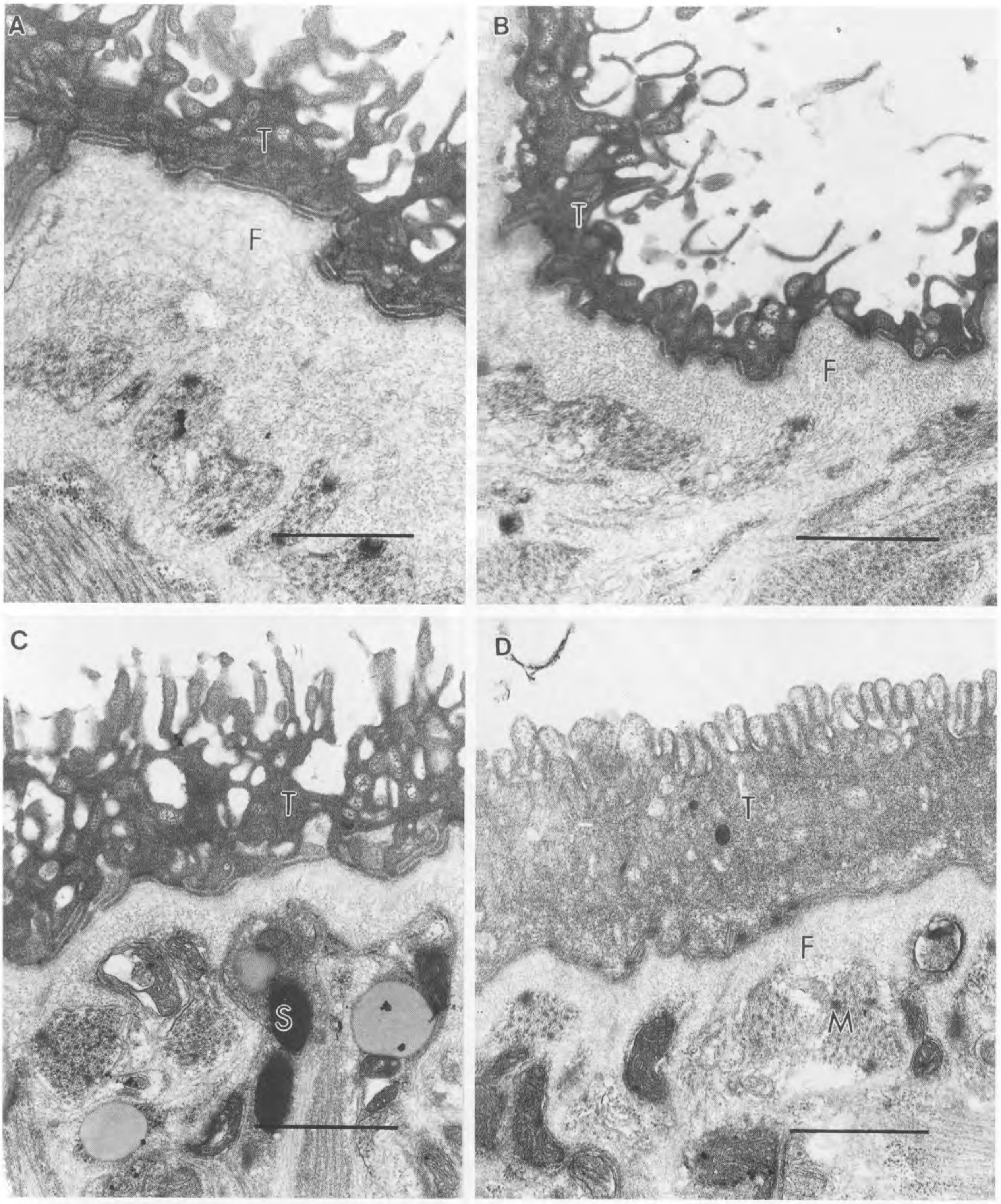

Fig. 7. *Udonella.* **A–B** – tegument of posterior part of body near sucker. Note irregularly shaped and interconnected microvilli and thick fibrous layer below basal lamina. **C–D** – tegument of anterior part of sucker. Note interconnected tegumental microvilli in C and short stubby microvilli in D. Scales 1 μm.

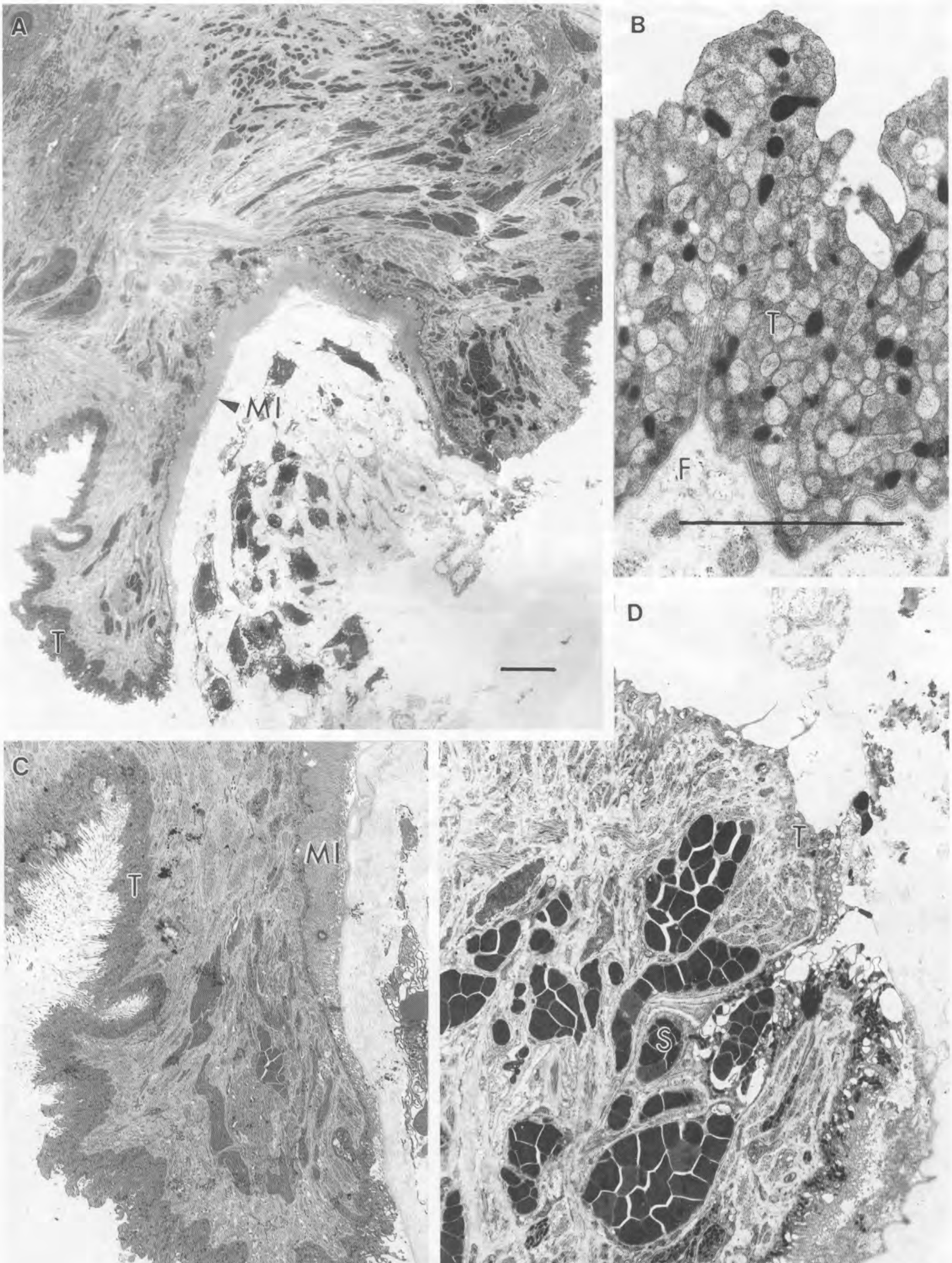

Fig. 8. *Anoplodiscus*. **A** – sucker with dense layer of long microvilli, lateral and anterior parts of sucker with "normal" tegument; **B** – tegument of anterior part of sucker; **C** – lateral part of A at higher magnification. Note layer of microvilli passing over into "normal" tegument; **D** – glandular ducts opening through lateral part of sucker. Scales 2 μm.

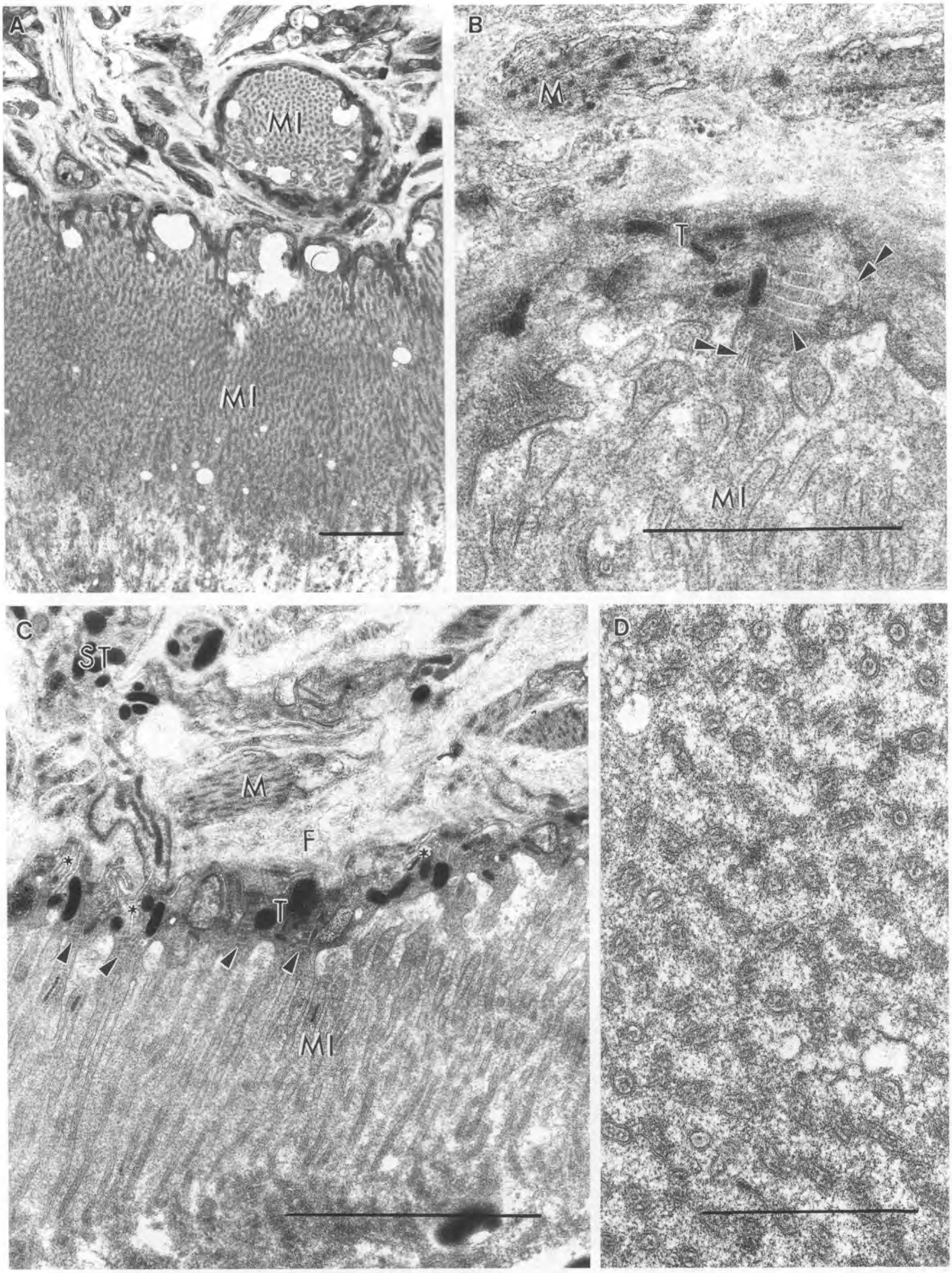

Fig. 9. *Anoplodiscus*. Microvilli of sucker. Note thin layer of tegument continuous with microvilli which may branch near their base and often have a cross-striated base (arrowheads in **B–C**), bundles of fine filaments extending into the microvilli (double arrowheads in **B**), and invaginations of basal cell membrane (asterisks in **C**). Note dense core of microvilli in cross-section (**D**). Scales 2 µm.

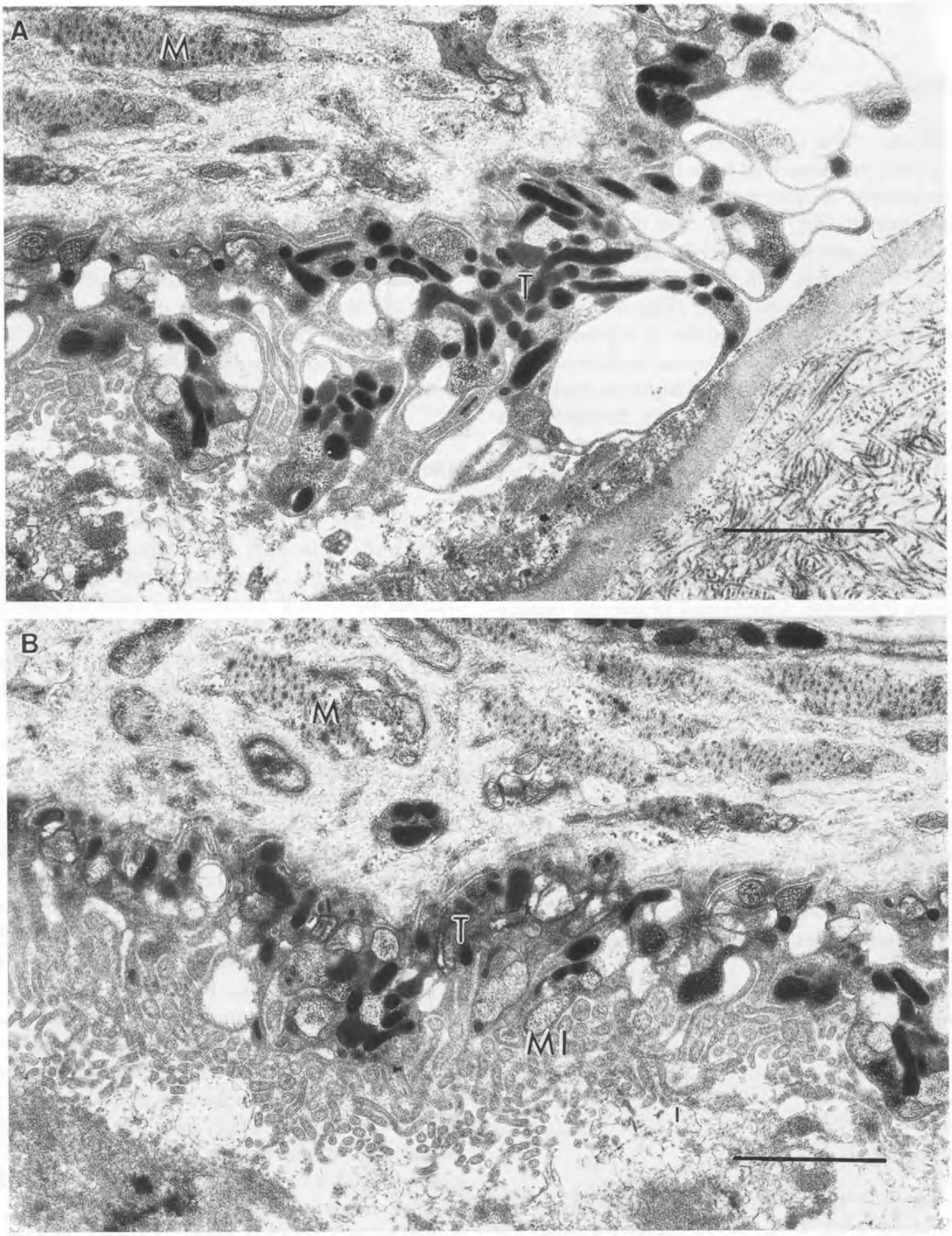

Fig. 10. *Anoplodiscus*. Transitional tegument in lateral parts of sucker. Note large vacuoles, dense bodies of tegument, and irregularly shaped microvilli in **A** (left) and **B**, which become longer, denser and more regular in the more central parts of the sucker cup. Scales 1 μm.

of the basal cell membrane are common (Fig. 9C), and fine filaments extend from the tegument into the microvilli (Fig. 9B). Several glandular ducts with densely packed dense grana open near the margins of the sucker (Fig. 8A, D).

Philophthalmus

The sucker of the cercaria is ventrally embedded in the main body and separated from it by a sheath identical at the electron-microscopic level with that below the surface tegument (Fig. 11A,C). The tegument of the sucker is continuous with that of the main body. A narrow band of tegument with microvilli extends around the ventral opening of the sucker (Figs. 11A–B, 13C), and just outside it is a thickened rim of tegument (Figs. 11A–B, 13C). The lateral and dorsal tegument of the main body differs from that of the sucker in having numerous large, electron-dense secretory droplets (Figs. 11A, 13D). There are no septate junctions between the various types of tegument (Fig. 13C–D). The sucker is a heavily muscular organ, containing densely packed radial muscles (Figs. 11A–B, 12A–C, 13C), attached to the basal lamina by hemidesmosomes (Fig. 11C), and inner and outer layers of filaments which have a predominantly transverse, longitudinal or circular orientation in the section passing through the middle of the sucker (Figs. 12A–C, 13B–C). The various cell types include secretory cells (Fig. 12D), cells with dense cytoplasm (possibly of the same type) (Fig. 12C), and cells whose nuclei are scattered between the muscle filaments and probably represent myocytes (Fig. 12A,C). Receptors in the sucker or close to it include a type with a large electron-dense rootlet (Fig. 13A), a type with a long cross-striated rootlet (Fig. 13A, C), and possibly other types which were not examined in detail. At least some of the receptors have a free cilium (Fig. 13B). All receptors have at least one electron-dense collar (Fig. 13A–C).

Diagrams with the main characteristics of the suckers of the four species examined are given in Fig. 14.

DISCUSSION

Temnocephala

In a series of papers, Williams (1975, 1977, 1978, 1979, 1980a,b, 1982, 1985, 1991) studied the epidermis of some species of *Temnocephala*. As in our species, it contains many vacuoles and there are many microvilli at the surface. Likewise, invaginations of the basal cell membrane are common. Using scanning electron-microscopy, she demonstrated a ridge and associated groove around the periphery of the posterior sucker (Williams 1982, 1991), as well as many openings of glandular ducts on the sucker (Williams 1978). A peripheral ridge and associated groove around the perimeter of the sucker, corresponding to our septate junction, was also demonstrated by scanning electron microscopy in the temnocephalid *Craspedella* sp. by Sewell and Cannon (1995). Sewell and Whittington (1995) studied locomotion in *Craspedella* and presented diagrams of muscles extending from the body proper into the sucker, similar to those found in our study.

Udonella

Ivanov (1952) made a detailed light microscopic study of *Udonella*. The sucker is terminal, an extension of the posterior part of the main body, and perikarya of glands which open on the sucker are located anteriorly to the sucker.

Anoplodiscus

Roubal and Whittington (1990) studied attachment of *A. australis* to its host, the bream *Acanthopagrus australis*, using light, transmission and scanning electron microscopy. A few transmission electron micrographs permit comparison with some aspects of our findings. As in *A. cirrusspiralis*, a thin tegument with dense bodies is drawn out into microvilli. The authors illustrate bundles of "microtubules" which do not show a lumen and appear to correspond to the "bundles of fine filaments" extending from the tegument into the microvilli of *A. cirrusspiralis*. Cross-striated components branching into microvilli are not illustrated in *A. australis*, instead the authors describe small "desmosome-like junctions" (with a weak striation) in the tegument.

Other monogeneans have a great variety of posterior attachment organs (haptors). Generally, the Polyopisthocotylea among them have clamps and hooks, whereas the Monopisthocotylea have hooks of various kinds, and some have "squamodiscs" and other accessory structures for attachment. Many species lack well defined suckers (e.g. Gyrodactylidae, Microcotyloidea), others have muscular suckers attached ventrally or terminally to the posterior end (e.g. Monocotylidae, Capsalidae). We have made ultrastructural studies of the posterior sucker of the monocotylid *Monocotyle helicophallus*. It has an extremely complex structure, to be described in a separate paper. However, presence of a typical tegument and various substructures not found in *Temnocephala* clearly indicate that it is not homologous with the temnocephalid sucker. Even within the Monogenea, homology of the haptor of various orders must be doubtful.

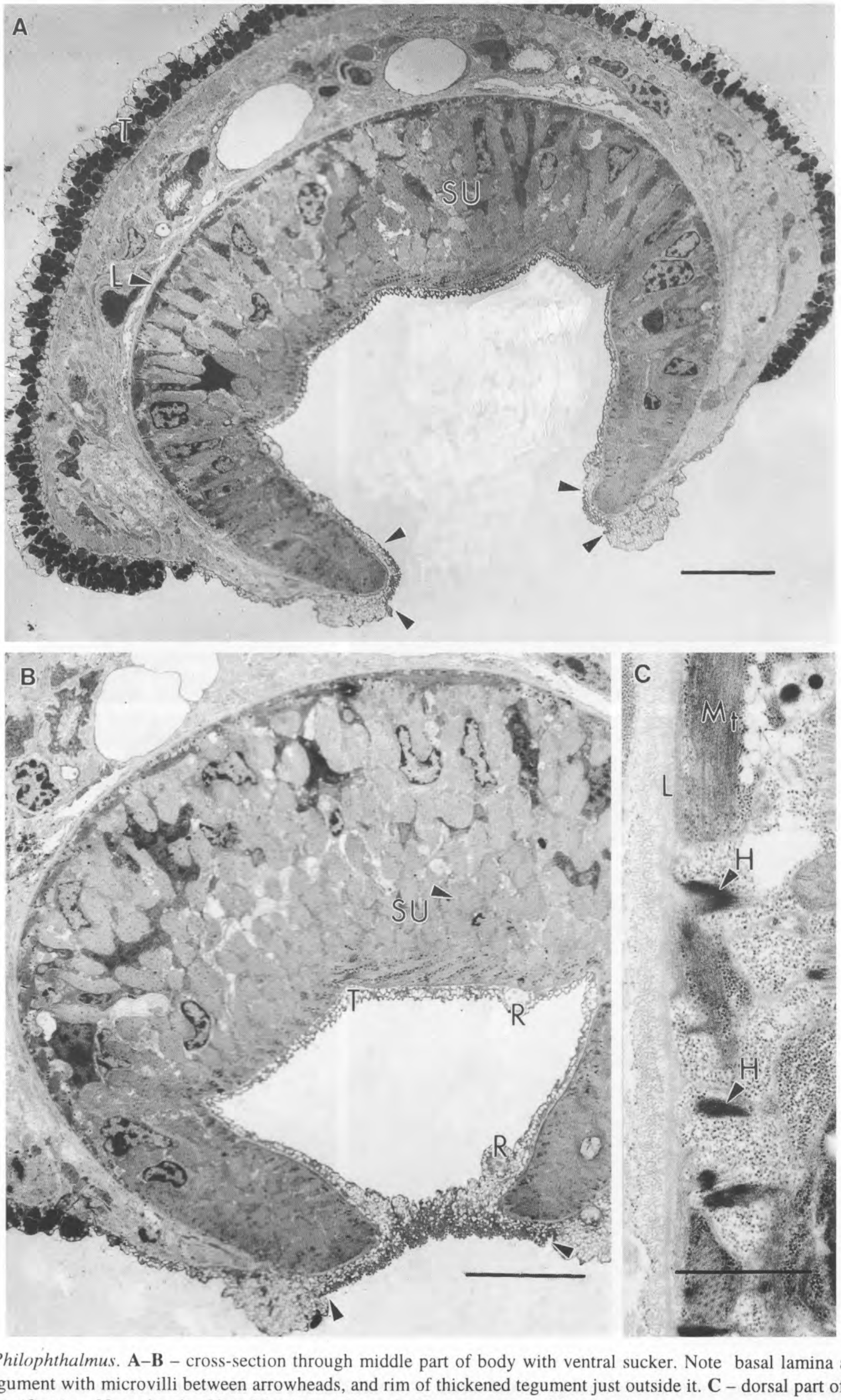

Fig. 11. *Philophthalmus.* **A–B** – cross-section through middle part of body with ventral sucker. Note basal lamina all around sucker, tegument with microvilli between arrowheads, and rim of thickened tegument just outside it. **C** – dorsal part of sucker at higher magnification. Note sheath of basal lamina and muscle filaments attached by hemidesmosomes to basal lamina. Scales 1 µm.

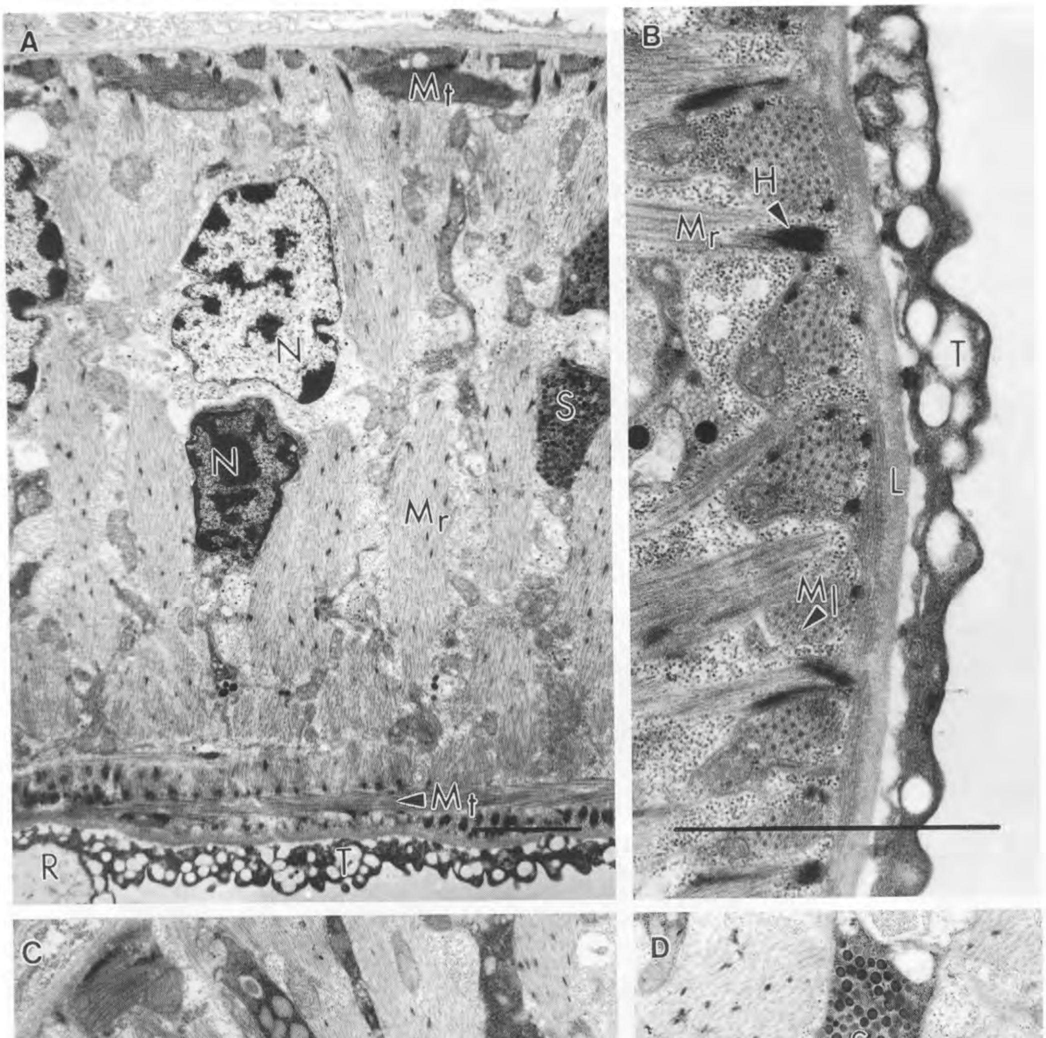

Fig. 12. *Philophthalmus.* Cross-section through ventral sucker. Note basal lamina and tegument lining the lumen of the sucker in **A–C**, densely packed radial muscles, longitudinal and transverse muscles, nuclei of cells, and secretory cell in **D**. Scales 2 µm.

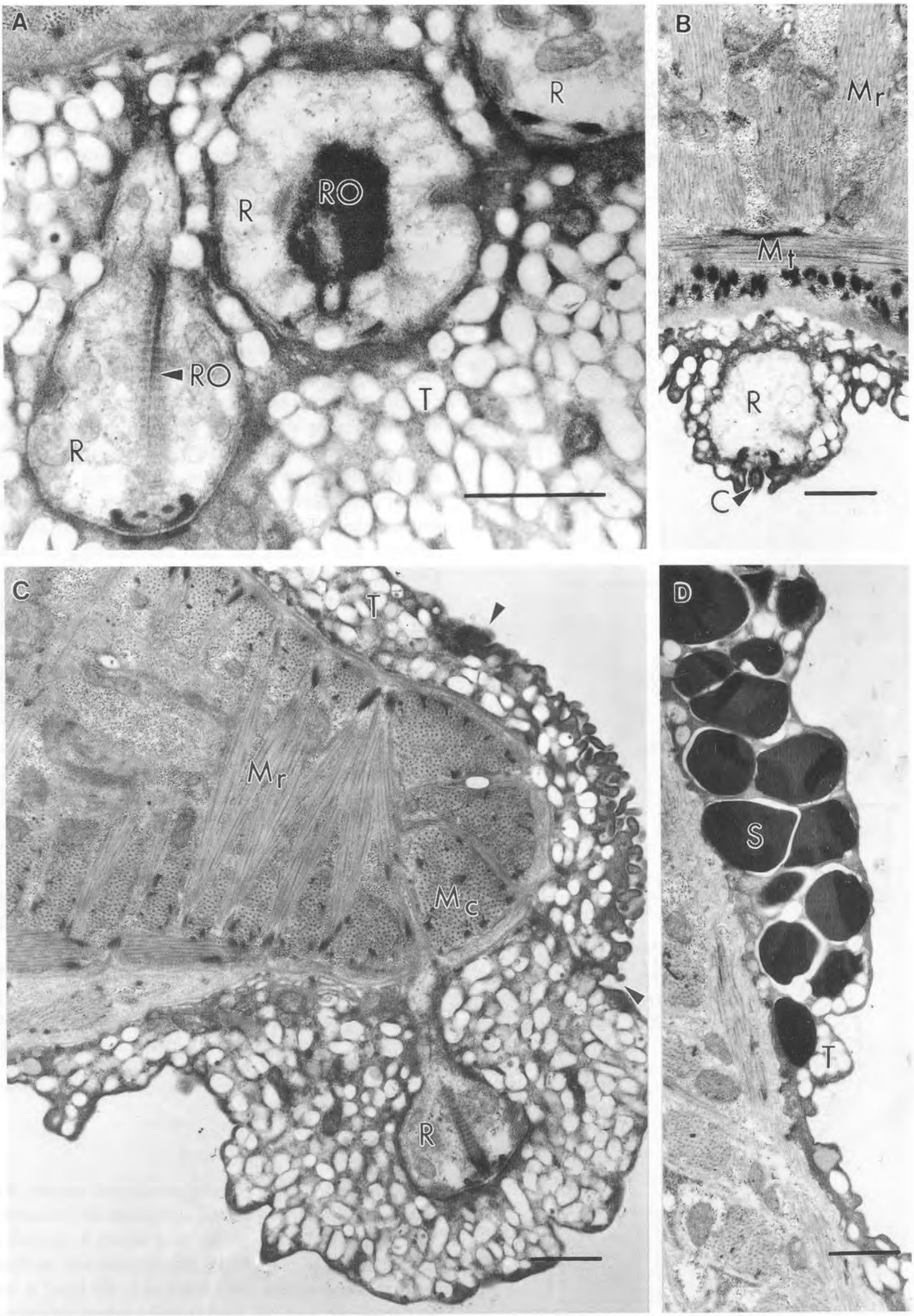

Fig. 13. *Philophthalmus.* **A–C** – sensory receptors. Also note rim of tegument with microvilli between arrowheads in C; **D** – transition between thin tegument near sucker to thick lateral and dorsal tegument with large secretory droplets. Note lack of a septate junction between the two types of tegument. Scales 1 μm.

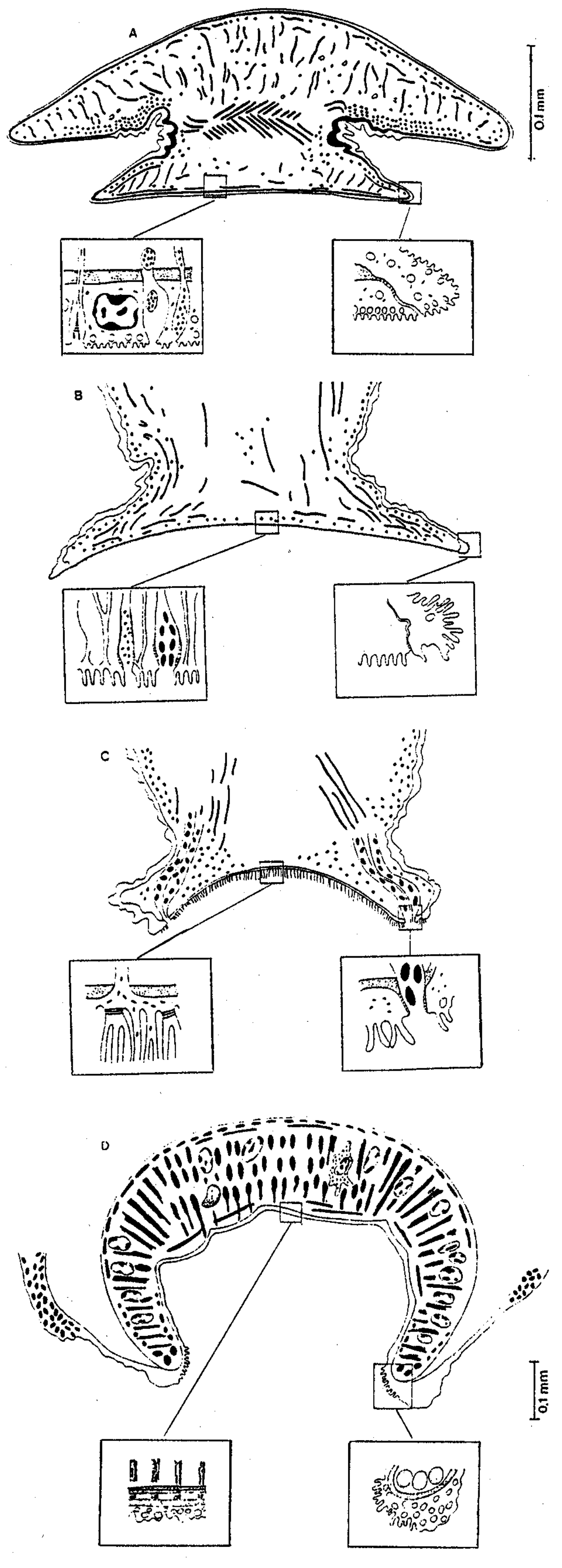

Fig. 14. Diagrams of suckers of *Temnocephala* (**A**), *Udonella* (**B**), *Anoplodiscus* (**C**) and *Philophthalmus* (**D**).

Philophthalmus

Unlike the sucker of the other species examined in this paper, that of *Philophthalmus* is well separated from the adjacent parenchyma by a "capsule" of basal lamina. The wall facing the lumen is formed by a tegument characteristic of the Neodermata, i.e. it is a syncytial surface layer connected to subtegumental perikarya (not examined in this paper). A specialized band of tegument around the ventral opening of the sucker has many microvilli, but this band is continuous with the tegument lining the main body and the inner surface of the sucker, not separated from it by septate junctions. Its function may be to bring about more effective adhesion to host tissue, helping to suck in host tissue when the muscles of the sucker cause expansion of the sucker lumen, by sealing the sucker margin. In the other three species, the suckers do not form such large cavities suitable for sucking in host tissue. Sewell and Whittington (1995) demonstrated that attachment to the host in a temnocephalid is brought about by combined action of adhesion and suction, the latter not resulting in sucking tissue into a cavity.

Morphological evidence does not support the view that the ventral sucker of Digenea is homologous with that of the other species examined. However, there is evidence for homology of the suckers of digeneans and aspidogastreans. The ventral sucker of the aspidogastrean *Rugogaster hydrolagi,* as that of the digenean *Philophthalmus,* is separated from the adjacent parenchyma by a capsule formed by a basal lamina (Rohde and Watson 1992). A tegument lines the lumen, and muscle filaments extend in various directions. Main differences between *Rugogaster* and *Philophthalmus* are as follows: in the former species, "rugae" (transverse ridges) are formed at the posterior end of the sucker, the sucker is less muscular, and the tegument possesses many surface "microtubercles" (short microvilli characteristic of all aspidogastreans examined). Rohde and Watson (1992) concluded that the ventral sucker plus rugae of *Rugogaster* must be considered homologous with the ventral disc of the Aspidogastridae within the Aspidogastrea, and with the ventral sucker of the Digenea.

CONCLUSIONS

Comparison of the posterior attachment organs of the four species examined shows significant differences. In the temnocephalid, the sucker is attached by a well defined stalk to the main body, the epidermis is nucleated and that of the ventral part (attached to the host) is separated from the adjacent epidermis by a complete septate junction around the periphery of the sucker. Numerous glandular ducts open on the sucker. In *Udonella* and

Anoplodiscus there is no well defined stalk and the sucker is a posterior, terminal extension of the body proper. Its posterior surface is lined by the basal lamina drawn out into microvilli in the former species, attached to the adjacent tegument by a septate junction; gland ducts open on the sucker. In the latter species, a thin tegument continuous with the tegument of the main body is drawn out into numerous long microvilli, and large glandular ducts open on the sides of the sucker. In *Philophthalmus*, the sucker is well separated from the main body by a capsule of "basal lamina". It is lined by a tegument without microvilli, continuous with that of the body proper.

Structure of the suckers does not provide evidence that the posterior attachment organs of the four species are homologous, representing a so-called cercomer, as assumed for example by Brooks (1989a, b) and Brooks et al. (1989), who include the synapomorphy "cercomer" in their characterization of the taxon "Cercomeria" (Temnocephalida plus Neodermata). In other words, there is no justification for a "cercomer-theory" that implies homology of the posterior adhesive organs of all the Neodermata and the Temnocephalida. In view of the likely monophyly of the Monogenea plus Cestoda, homology of their hooks (but not necessarily their haptors) may seem more likely.

Rohde (1990, 1991) and Rohde et al. (1993, 1995), mainly using ultrastructure of the protonephridia and analysis of 18S ribosomal DNA sequences, have shown that the Temnocephalida is unlikely to be the sister group of the parasitic Platyhelminthes, i.e. that the taxon "Cercomeria" is invalid. Blair (1993), on the basis ofREFERENCES DNA studies, also concluded that temnocephalids do not represent the sister group of the Neodermata. This conclusion is confirmed by our finding that the posterior attachment organ of *Temnocephala* has no close similarities with those of the parasitic species examined in this paper.

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Abbreviations: E - epidermis; F - fibrous matrix; J - junction; H - hemidesmosome; L - basal lamina; M - muscle filament; Mc - circular muscle filament; Ml - longitudinal muscle filament; Mr - radial muscle filament; Mt - transverse muscle filament; Mi - microvilli; N - nucleus; R - sensory receptor; RO - rootlet; S - secretion; ST - subtegumental cell; SU - sucker; T - tegument.

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