
The Fine Morphology of the Osphradial Sense Organs of the Mollusca. IV. Caudofoveata and Solenogastres

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THE FINE MORPHOLOGY OF THE OSPHRADIAL SENSE ORGANS OF THE MOLLUSCA. IV. CAUDOFOVEATA AND SOLENOGASTRES

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The fine morphology of the osphradial (= dorsoterminal) sense organs of seven Caudofoveata and two Solenogastres is described. In the Caudofoveata the organ forms a longitudinal groove bordered by swellings. It is well developed in the Chaetodermatidae, less developed in the Limifossoridae and vestigial in the Prochaetodermatidae. Within the Solenogastres there occurs great variation in number (total lack up to six) and structure, and no correlation with systematics or ecological factors could be found. Owing to special structures (paddle cilia) the osphradial sense organs of the aplacophoran classes are regarded as chemoreceptors. A role in sexual biology (coordination of spawning) is suggested for the Caudofoveata. The role of the organs in the Solenogastres remains still unclear.

INTRODUCTION

The two aplacophoran classes Caudofoveata and Solenogastres have received little attention so far from malacologists, although the animals are fairly common in deeper waters. Moreover, all investigators of these worm-like animals have emphasized the fact that both groups are the

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most primitive of all molluscs, although highly specialized (Thiele 1902; Hoffman 1949; Scheltema 1978; Salvini-Plawen 1969, 1972*a*, 1980, 1981*a*). Whereas most authors unite both groups in a single taxon Aplacophora, Salvini-Plawen (1969, 1972*a*, 1980, 1981*a*) distinguishes two classes, Caudofoveata and Solenogastres, only the latter being synapomorphously united with all other molluscan classes by the presence of a pedal gland and a locomotor organ (foot) pedally innervated. These taxa are used in his sense in this paper.

This is the fourth of a series of papers concerning the fine morphology of osphradial sense organs. It has been shown that the fine structure of osphradia is very useful in gastropod systematics (Haszprunar 1985*a, b*), whereas there is great uniformity in the Bivalvia. In the Placophora, orders can be distinguished (Haszprunar 1987). In all classes so far investigated the osphradium shows only structures characteristic of chemoreceptors, especially the so-called 'paddle-cilia' (Matera & Davis 1982; Haszprunar 1985*a*). Therefore, the mechanoreceptive hypothesis of Yonge (1947) has to be rejected and a primary function of the osphradium in sexual biology (coordination of spawning, searching for a mate) is suggested (Haszprunar 1987).

Salvini-Plawen (1972*a*, 1981*a*) pointed out the homology of the single dorsoterminal sense organ of the Caudofoveata and the Solenogastres with the paired osphradia of other classes, mainly based on identical innervation (see Haszprunar 1987). These sense organs are therefore called osphradial sense organs in this paper, although there are so far neither ontogenetic nor functional results to support this hypothesis.

The histology of aplacophoran osphradia has been described in some detail by Heath (1911) and Salvini-Plawen (1972*a*, 1978). So far, no fine-structural data have been published.

MATERIAL AND METHODS

Seven Caudofoveata, representing the three known families, and two members of the Solenogastres, representing two orders (see Salvini-Plawen 1978, 1980) have been investigated (table 1).

All Caudofoveata and many small Solenogastres live on deep (50–3000 m), muddy bottoms (larger Solenogastres live epizoically on Cnidaria). *Neomenia carinata* is said to burrow in mud by means of its proboscis (Wirén 1892). All specimens were dredged by boat, washed in fine (250–500 µm) nets and were carefully located under the stereomicroscope.

Fixation for electron microscopy was by glutaraldehyde–osmium (for details see Haszprunar 1985*a*); embedding was in an Epon–Araldite mixture (Mollenhauer 1964). Two methods of decalcification were used: (i) after fixation en bloc by ascorbic acid (see Haszprunar 1985*a*); (ii) after a cut on the block, made by a razor blade, with 15% (by volume) acetic acid for 5 min. In this case it was necessary to wait another 10 min after decalcification, since the tissue was a little swollen. Both methods showed good results, but the first was more practicable. Thin sections were cut with a diamond knife. Staining for light microscopy was with 1% (by mass) toluidine blue (pH 10 by adding borax); staining for electron microscopy was with uranyl acetate and lead citrate.

TABLE 1. SPECIES INVESTIGATED

systematics	species	source
Caudofoveata		
Chaetodermatida		
Limifossoridae	<i>Scutopus ventrolineatus</i> Salvini-Plawen, 1968	Atlantic (Bergen)†
	<i>Scutopus robustus</i> Salvini-Plawen, 1970	Atlantic (Bergen)†
Prochaetodermatidae	<i>Prochaetoderma raduliferum</i> (Kowalevsky, 1901)	Mediterranean Sea (Banyuls-sur-mer)
Chaetodermatidae	<i>Chaetoderma nitidulum</i> Lovén, 1844	Atlantic (Bergen)†
	<i>Falcidens crossotus</i> Salvini-Plawen, 1968	Atlantic (Bergen)†
	<i>Falcidens guttuosus</i> (Kowalevsky, 1901)	Mediterranean Sea Banyuls-sur-mer)
	<i>Falcidens sagittiferus</i> Salvini-Plawen, 1968	Atlantic (Bergen)†
Solenogastres		
Pholidoskepia		
Lepidomeniidae	<i>Aesthoherpia glandulosa</i> Salvini-Plawen, 1985	Atlantic (Bergen)†
Neomeniomorpha		
Neomeniidae	<i>Neomenia carinata</i> Tullberg, 1875	Mediterranean Sea (Banyuls-sur-mer)

† Specimens supplied by Mr W. Pekny.

RESULTS

Scutopus ventrolineatus Salvini-Plawen, 1968

Scutopus robustus Salvini-Plawen, 1970

(Caudofoveata–Chaetodermatida–Limifossoridae)

As in all Caudofoveata, the osphradial (= dorsoterminal) sense organ of both *Scutopus* spp. investigated forms a dorsomedian longitudinal groove some distance in from the edge of the mantle cavity. In *Scutopus ventrolineatus* the cuticle of the body is fairly thick (about 30 µm), and the scales are densely arranged, so that the groove is not visible in the living animal. In *S. robustus* the cuticle is thinner (about 10 µm), therefore the sense organ is visible, although it is covered by a roof-like arrangement of scales.

A transverse section of the anterior mantle cavity (figure 5, plate 1) shows the osphradial sense organ to consist of a double swelling with a central cleft. The sense organ is innervated by paired nerves originating in the suprarectal commissure somewhat lateral to the ctenidial nerves. The swellings are twice as high (30 µm) as the adjacent epithelium (15 µm). They consist of several supporting cells and sometimes mucous cells are also found (figures 1 and 11). At the top of each swelling the cells form projections which penetrate the cuticle and are filled with mitochondria. No scale-bearing cells are found in the epithelium of the swellings.

The median sides of the swellings, which are covered by a very thin cuticle (1 µm), form the central cleft. No sensory elements could be found at the surface of the cleft epithelium, the cells only bear some small microvilli. Below its surface, however, the epithelium becomes less electron-dense, nuclei are rarely found and there is connection with nervous tissue, originating

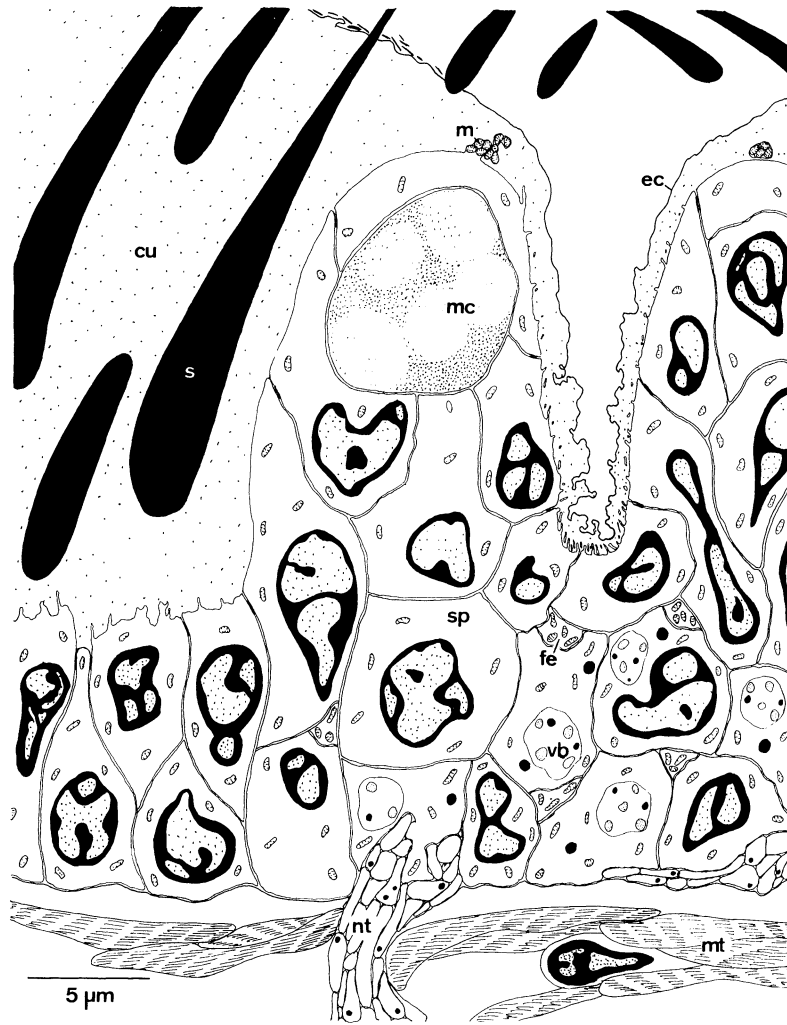


FIGURE 1. Transverse section of the osphradial (= terminal) sense organ of a *Scutopus* sp. (semischematic). cu, (Endo-)cuticle; ec, epicuticle; fe, free nerve process; m, mitochondria; mt, muscle tissue; nt, nervous tissue; s, scales; sp, supporting cell; vb, vesicular body.

in the paired osphradial nerve. Some of these cells include special areas (vb) with granules and mitochondria surrounded by a membrane. Free nerve processes (fe), characterized by their small diameter (1.5 μm) and by many mitochondria, are found between these less electron-dense cells.

There is no special basal lamina developed. A strong layer of (ring) muscle tissue, which is perforated only by the supplying nerves, underlies the epithelium of the osphradial sense organ as well as the whole epidermis. At the posterior end of the organ longitudinal muscles are also present.

Prochaetoderma raduliferum (Kowalevsky, 1901)

(Caudofoveata–Chaetodermatida–Prochaetodermatidae)

The position of the osphradial sense organ of *Prochaetoderma raduliferum* is the same as described for the *Scutopus* spp. above. It is not visible in living animals. The cuticle (20 μm) in which the

bases of the scales are embedded consists as in all Caudofoveata of two layers (figures 12 and 13, plate 2): (i) the epicuticle (ec) is very thin (50 nm) and is covered by small (1 μm) plates which look like microscales in thin sections; (ii) this epicuticle is underlain by the less electron-dense endocuticle (cu) which forms the greater part of the whole cuticle.

In sections (figures 7, 8 and 12) the osphradial sense organ of *Prochaetoderma* is shown to be vestigial. The paired swellings are very small and hardly higher (10 μm) than the adjacent epithelium (8 μm). Below the cuticular cleft (still present), the epithelium is extremely thin (1.5 μm). There are neither microvilli nor other special cell structures. No nervous tissue could be discerned, nor innervation traced. Again there is no basal lamina.

Chaetoderma nitidulum Lovén, 1846

Falcidens crossotus Salvini-Plawen, 1968

Falcidens guttuosus (Kowalevsky, 1901)

Falcidens sagittiferus Salvini-Plawen, 1968

(Caudofoveata–Chaetodermatida–Chaetodermatidae)

The osphradial sense organs of these chaetodermatid species are likewise elongated dorso-medial grooves. Each is always visible, although laterally situated scales again form a roof to protect the groove against mechanical disturbances.

In all species studied the osphradial nerves originate lateral to the ctenidial nerves from the suprarectal commissure; this is in contrast to *Falcidens hartmani*, where a more medial origin of the osphradial nerves is reported (Salvini-Plawen 1981a).

The epithelium of the epidermis (7–8 μm) consists mainly of cylindrical cells with oval nuclei and often with mucous vesicles. Sometimes scale-bearing cells are found that are somewhat higher (10 μm) and include a scale base. This base is characterized by a ring of very small (100 nm), electron-dense vesicles (figures 2 and 12).

As in the *Scutopus* spp. described above, there is a swelling on either side of the central sensory zone. The cuticle of these swellings is very thin (1 μm), and the epicuticle forms certain small knobs. In this zone the cuticle is covered by a layer of mucous material (figures 2 and 13).

The cleft or central zone of the chaetodermatid osphradia shows very different conditions from those of the other families (figure 2). There is no cuticle, but a high (4 μm) microvillous border. The epithelium, which is only 3 μm high, mainly consists of supporting cells (sp). However, two types of sensory cell are also found: (i) cells with slender projections up to the surface of the microvillous border (figures 2 and 15); (ii) cells bearing cilia with very short roots (figures 2 and 14). These cilia can form paddles as described in detail by Haszprunar (1985a). Both cell types are in contact with basal nervous tissue originating in the osphradial nerves.

A very thin basal lamina is present.

Aesthoherpia glandulosa Salvini-Plawen, 1985

(Solenogastres–Pholidoskepia–Lepidomeniidae)

Although this species lives on muddy bottoms and is very small (4–9 mm), its sense organs (preoral sense organ, osphradial sense organ) are well developed (see the generic name). The osphradium forms a large knob dorsally located some distance from the posterior end of the body. The mantle cavity shows eight to ten respiratory lamellae (figure 9, plate 1). The knob

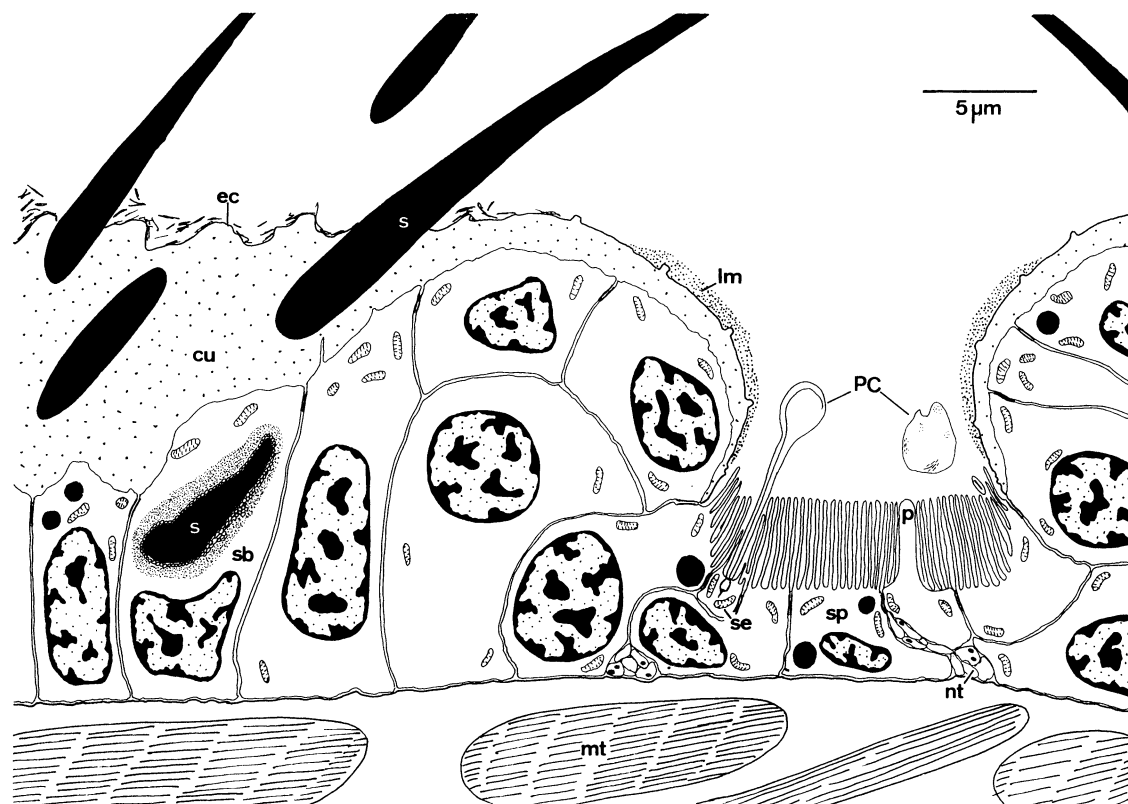


FIGURE 2. Transverse section of the osphradial (= terminal) sense organ of a chaetodermatid (semischematic). cu, (Endo-)cuticle; ec, epicuticle; lm, layer of mucus; mt, muscle tissue; nt, nervous tissue; p, process (sensory); PC, paddle cilia; s, scales; sb, scale-bearing cell; se, sensory cells; sp, supporting cell.

looks like a volcanic cone, its top bent slightly backwards. It can be retracted and expanded. The sense organ is supplied by a single large nerve originating in the suprarectal commissure.

The knob is laterally covered by a thin (5–7 μm) cuticle bearing centripetally arranged scales, which form a roof when the knob is retracted. In contrast to the epithelium of the body, where many mucous cells are found (see the specific name), these are very rare in the epithelium of the knob. The top of the knob, called the central zone, lacks cuticle but shows a complex microvillous border (figure 3). These microvilli belong to supporting cells which are additionally

DESCRIPTION OF PLATE 1

FIGURES 5–10. Semithin sections of the posterior end of caudofoveates and solenogastres. All scale bars: 50 μm .

FIGURE 5. *Scutopus ventrolineatus*.

FIGURE 6. *Falcidens sagittiferus*.

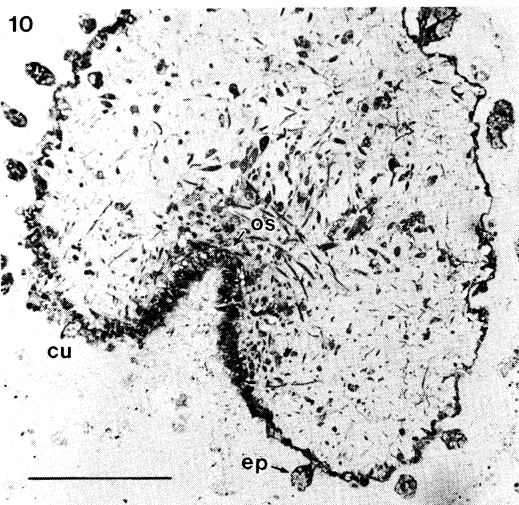
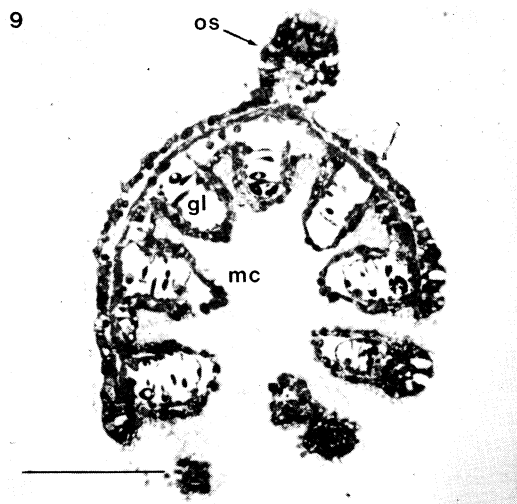
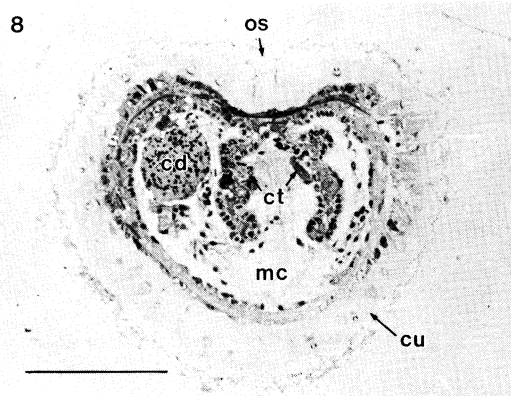
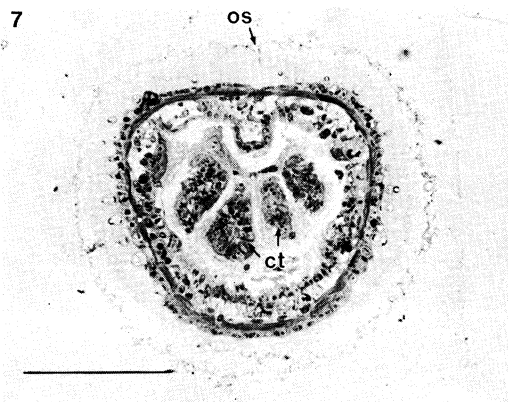
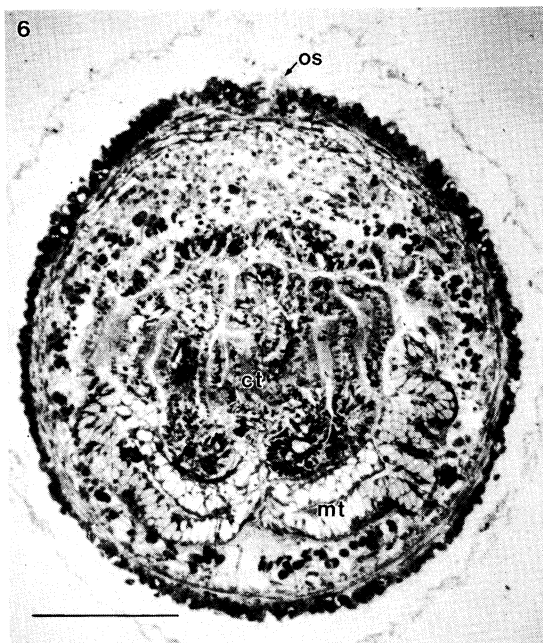
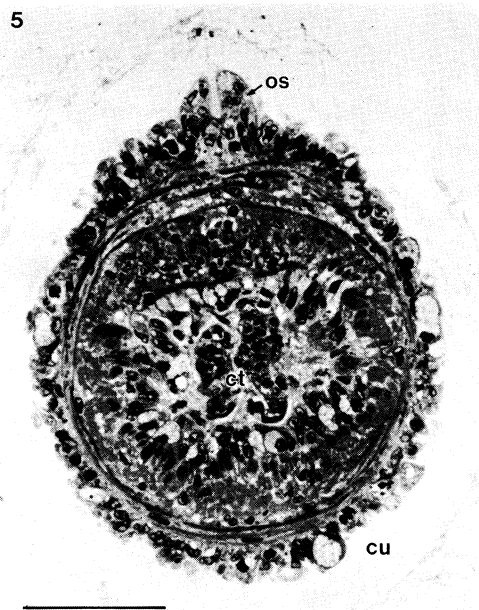
FIGURE 7. *Prochaetoderma raduliferum*: posterior mantle cavity.

FIGURE 8. *Prochaetoderma raduliferum*: anterior mantle cavity.

FIGURE 9. *Aesthoherpia glandulosa*.

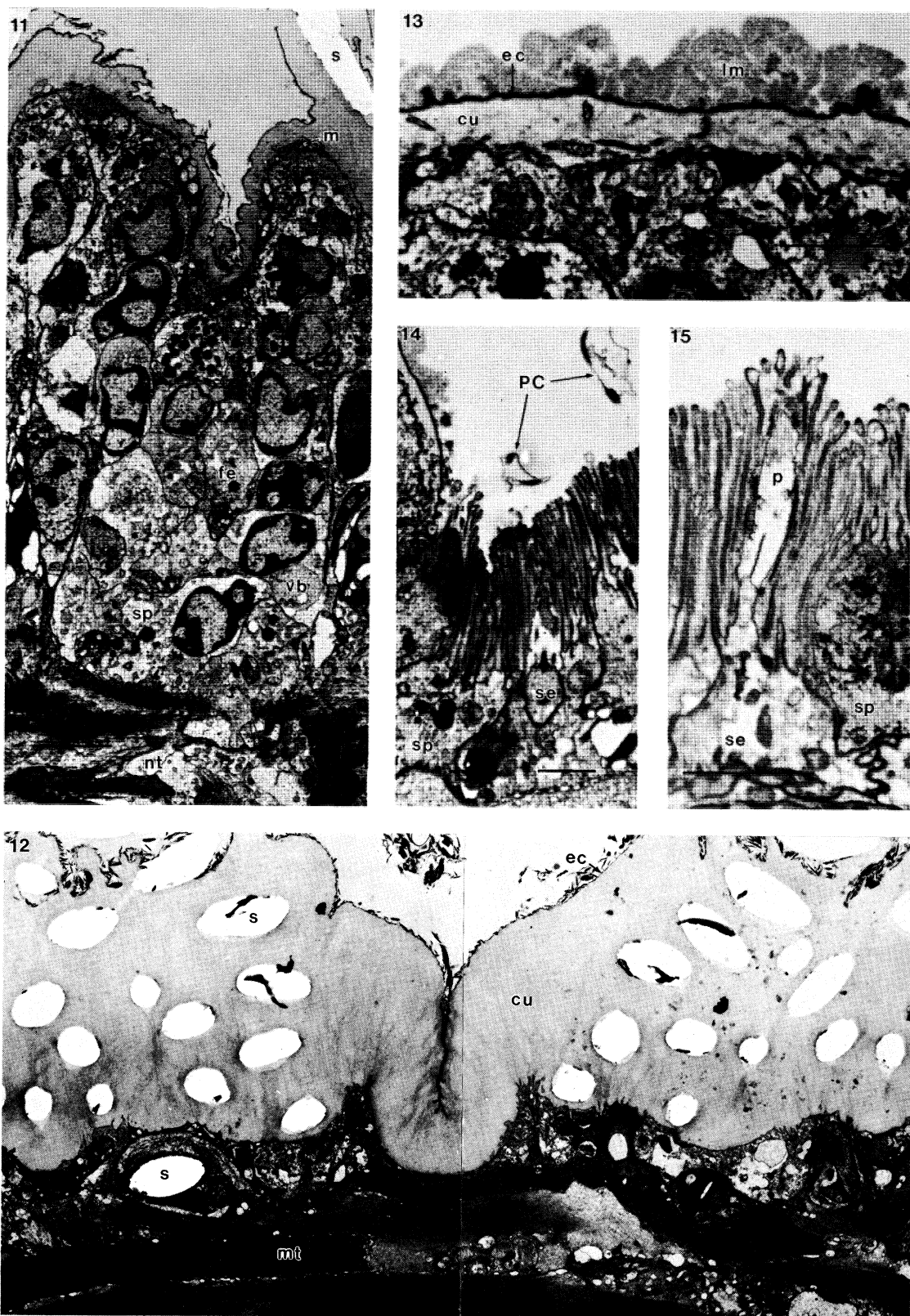
FIGURE 10. *Neomenia carinata* (juv.): immediately behind the mantle cavity.

cd, Coelomoduct (anterior genital duct); ct, ctenidia; cu, cuticle; ep, epidermal papillae; gl, gill lamellae; mc, mantle cavity; mt, mucous tract (posterior genital groove); os, osphradial sense organ.



FIGURES 5–10. For description see opposite.

(Facing p. 68)



FIGURES 11–15. For description see opposite.

DESCRIPTION OF PLATE 2

FIGURES 11–15. Ultrathin sections of caudofoveate osphradia.

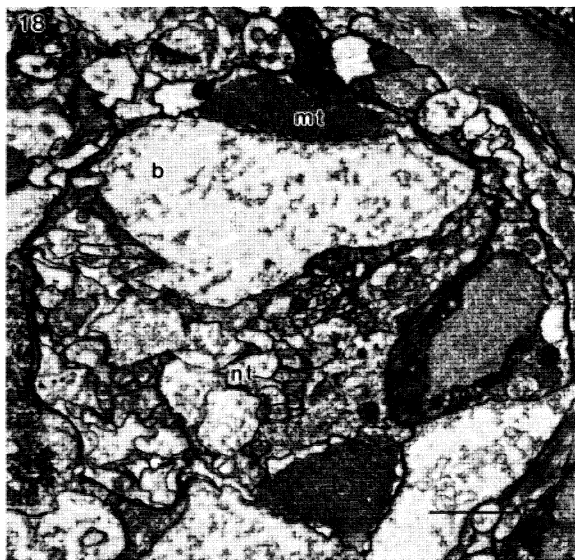
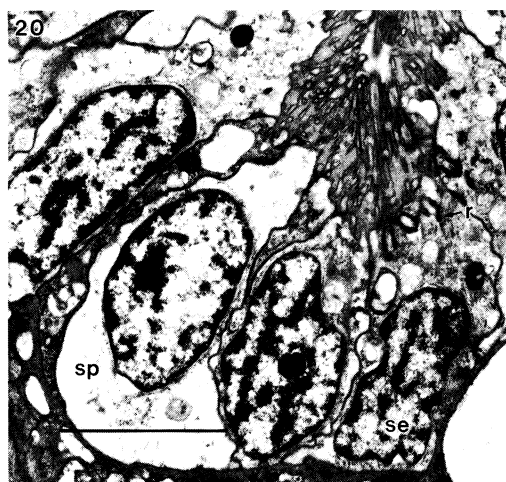
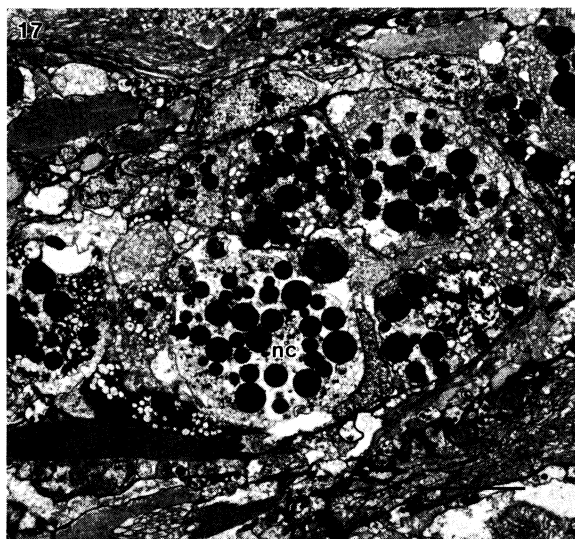
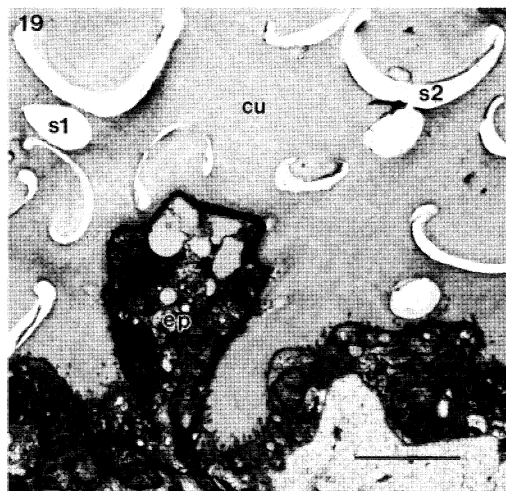
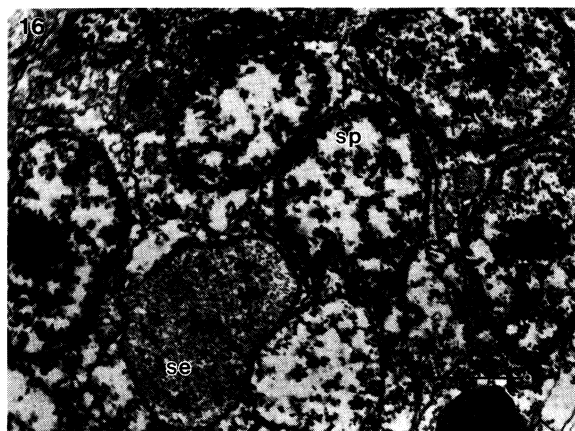
FIGURE 11. *Scutopus ventrolineatus* (scale bar: 5 μm).

FIGURE 12. *Prochaetoderma raduliferum* (scale bar: 5 μm).

FIGURE 13. *Falcidens guttuosus*: detail of the inside of the lateral swellings (scale bar: 2 μm).

FIGURES 14 AND 15. *Falcidens guttuosus*: details of the central zone (scale bars: 2 μm).

cu, (Endo-)cuticle; ec, epicuticle; fe, free nerve ending; lm, layer of mucus; m, mitochondria; mt, muscle tissue; nt, nervous tissue; p, process (sensory); PC, paddle cilia; s, scales; sc, sensory cell; sp, supporting cell; vb, vesicular body.



FIGURES 16–21. For description see opposite.

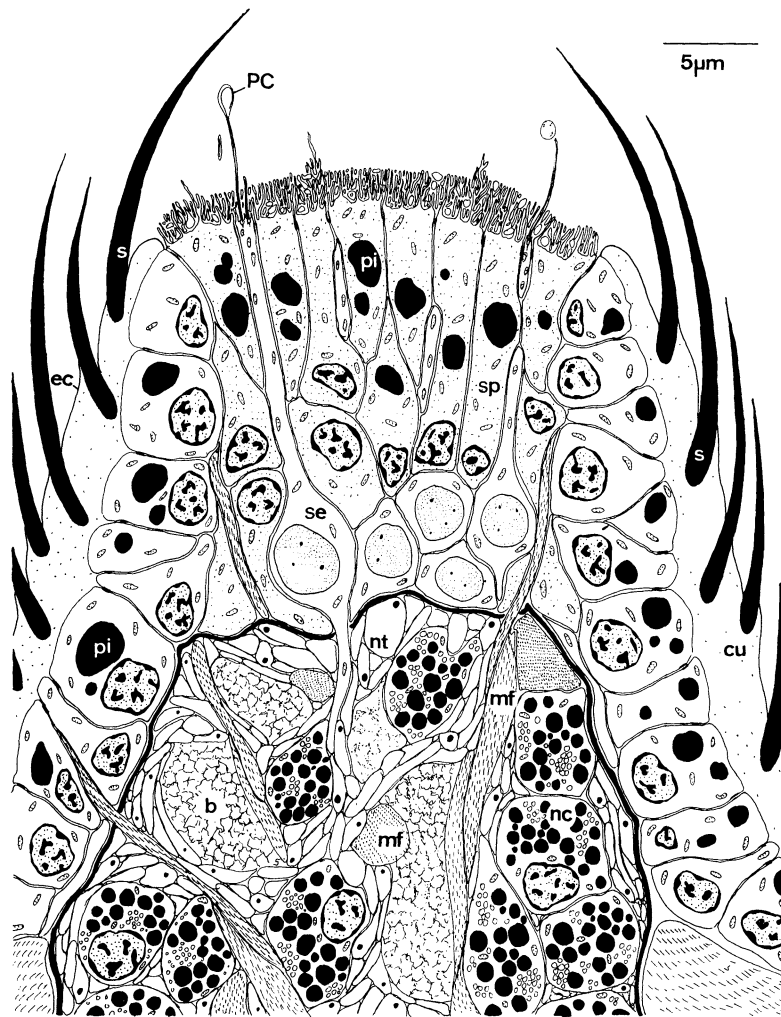


FIGURE 3. Transverse section of the osphradial (= terminal) sense organ of *Aesthoherpia glandulosa* (semischematic). b, Blood lacuna; cu, (endo-)cuticle; ec, epicuticle; mf, muscle fibril; nc, nerve cell; nt, nervous tissue; pi, pigment granules; PC, paddle cilia; s, scales; se, sensory cell; sp, supporting cell.

DESCRIPTION OF PLATE 3

FIGURES 16–21. Ultrathin sections of osphradial sense organs and adjacent epithelia of solenogastres.

FIGURE 16. *Aesthoherpia glandulosa*: nuclei of sensory and supporting cells (scale bar: 2 μm).

FIGURE 17. *Aesthoherpia glandulosa*: nerve cells of the osphradial nerve (scale bar: 5 μm).

FIGURE 18. *Aesthoherpia glandulosa*: mixed tissue of the osphradial nerve (scale bar: 2 μm).

FIGURE 19. *Neomenia carinata*: epithelium with epidermic papillae adjacent to the osphradial sense organ (scale bar: 5 μm).

FIGURE 20. *Neomenia carinata*: sensory cleft of the osphradial sense organ (left = outside) (scale bar: 2 μm).

FIGURE 21. *Neomenia carinata*: supporting cells of the osphradial sense organ (scale bar: 2 μm).

b, Blood lacuna; cu, cuticle; ep, epidermic papillae; mt, muscle tissue; nc, nerve cell; nt, nervous tissue; r, root of sensory cilium; s1, needle-like scale; s2, scale with longitudinal groove; se, sensory cell; sp, supporting cell.

characterized by oval nuclei and large pigment granules. Between them slender processes run up to the surface of the central zone, bearing one to three cilia which can form paddles and have short roots. The perikarya of these sensory cells are situated somewhat deeper than those of the supporting cells. They lack pigment granules and their nuclei are well characterized, since the heterochromatin is nearly dissolved (figures 3 and 16). The axons of the sensory cells run to the osphradial nerve. All epithelia of the knob lack a basal lamina.

Fine structural analysis shows that the osphradial nerve is a mixture of nervous tissue (with nerve cells), muscle tissue and blood spaces (figures 3, 17 and 18). There can be no doubt that this complex is used to retract and expand the knob as well as for sensory reception. This mixed tissue is surrounded by a strong basal lamina. The lamina is penetrated not only by the axons of the sensory cells, but also by slender muscle fibrils which run into the lateral, cuticle-covered epithelium of the knob.

Neomenia carinata Tullberg, 1875

(Solenogastres–Neomeniomorpha–Neomeniidae)

As in many other species of the genus, the osphradial sense organ of *Neomenia carinata* is a somewhat sunken oval sensory area medioterminally placed immediately outside the mantle cavity (Salvini-Plawen 1978). Since the mantle cavity is often retracted, the organ is found in sections in a ventral arrangement (see figure 10). The mantle cavity itself is provided with several large folds which are used as respiratory organs. The osphradial sense organ is supplied by paired nerves originating in the suprarectal commissure.

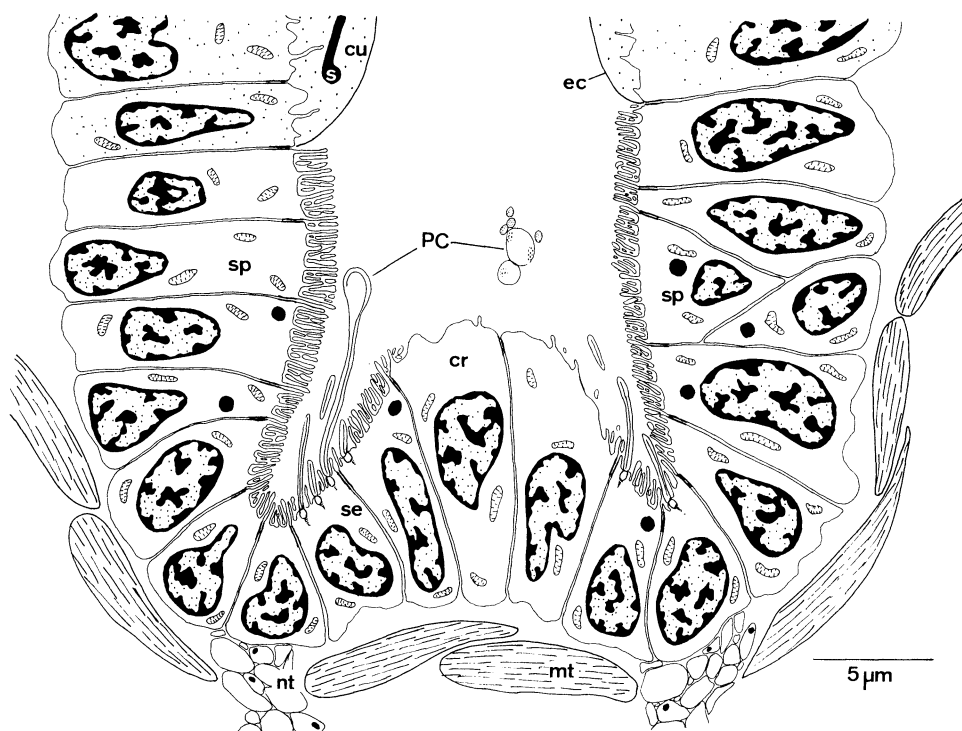


FIGURE 4. Transverse section of the osphradial (= terminal) sense organ of *Neomenia carinata* (semischematic); the figure is oriented upside down (relaxed condition) to make comparisons easier: cr, Crest; cu, (endo-)cuticle; ec, epicuticle; mt, muscle tissue; nt, nervous tissue; PC, paddle cilia; s, scale; se, sensory cell; sp, supporting cell.

Ultrastructurally, the organ shows a symmetrical arrangement (figure 4). It consists of two clefts separated by a small crest. The cells of the adjacent epithelium, which form several epidermal papillae, are covered by a well developed ($10\ \mu\text{m}$) cuticle and bear two types of scales (figure 19, plate 3). In contrast, the cells of the osphradial sense organ are more electron-bright and bear microvilli (figure 21). The cells of the clefts, being in contact with the nervous tissue of the supplying nerves, additionally bear cilia with short roots forming paddles (figures 4 and 20). Thus, they can be regarded as sensory. There is no basal lamina.

Paddle cilia are likewise found on the pedal folds, confirming notes by Thiele (1894) and Hoffman (1949), who described sensory cells in the foot of several Solenogastres.

DISCUSSION

Systematics

When comparing both aplacophoran classes, one is first impressed by many similarities in external shape as well as by some traits of the anatomy. The osphradial sense organs appear in both to be derived from the primitive molluscan condition (paired organs at the edge of the mantle cavity; see Salvini-Plawen (1981*a*), Haszprunar (1987)). In both Caudofoveata and Solenogastres the osphradia are fused and are situated mediadorsally outside the mantle cavity. In all Caudofoveata and many Solenogastres, however, the primitive condition can be traced through the paired nerves and by the symmetrical structure of the organs.

Salvini-Plawen (1969, 1972*a*, 1980, 1981*a*) strengthened the view that all similarities between the classes are either the result of symplesiomorphies (retained primitive characters, for example cuticle with scales, muscle system, nervous system, radula) or of convergences (for example worm-like shape, gonopericardial system). This can be shown by differences in their detailed structure. There is some evidence that the migration and fusion of the osphradial sense organs are due to different processes in Caudofoveata (terminalization of the mantle cavity accompanying a burrowing mode of locomotion) and Solenogastres (lateral narrowing of the mantle cavity accompanying a gliding, winding mode of locomotion) (Salvini-Plawen 1969, 1972*a*, 1981*a*). Thus, the common aberrant modification of the osphradial sense organs in both classes appears to be the result of convergence. In addition, there are differences in structure: a longitudinal groove in the Caudofoveata, erect or sunken knobs in the Solenogastres. Since, however, great differences of osphradial structure are also found within other molluscan classes (for example Gastropoda, Placophora; see Haszprunar (1985*a, b*, 1987)), only ontogenetical studies can possibly decide this question.

Since all three families of the Caudofoveata are represented by the species investigated, it is evident that the structure of the osphradial sense organ is characteristic for families. As shown by identical position, innervation and common derived structure (a dorsomedian longitudinal groove bordered by swellings), the organ has been synapomorphously modified from its basal molluscan configuration (see above) within the Caudofoveata. It is fully developed in the Chaetodermatidae, less developed in the Limifossoridae and vestigial in the Prochaetodermatidae. Thus, the formation of the sense organ fully corresponds with the classification so far used. However, differences in gill-structure (ctenidial axis reduced, two main lamellae only, see figures 7 and 8 and Salvini-Plawen (1969, figure 12)) and radular musculature (Deimel 1982) indicate a separate derivation of the Prochaetodermatidae from a basal caudofoveate type.

As summarized by Salvini-Plawen (1972*a*, 1978), there is some variation in the Solenogastres with respect to the number of osphradial sense organs as well as to their innervation by paired or fused nerves. The presence or absence of the organ is generally regarded as characteristic for the genus level. However, there seems to be an ecological factor involved, since most of the large, epizoic species have an osphradial sense organ, whereas it is reduced in many small mud-living species (in the Norwegian material examined only two of ten species have one, but note the well developed organ in *Aesthoherpia glandulosa*). In contrast, the organ is multiplied in several species and also intraspecific variation in number is reported (for example, *Dorymenia* spp., *Dondersia* spp. (Salvini-Plawen 1978)). In most of these species the multiplied organs are serially arranged, but *Paragymnomenia richardi* Leloup, 1947 (with six organs) also shows lateral ones (Salvini-Plawen 1972*b*). Thus, correlation of presence, absence or multiplication of the osphradial sense organs in the Solenogastres with systematics or ecological factors, or both, remains rather obscure.

Function

Earlier (Haszprunar 1985*a*; also Davis & Matera 1982) it has been pointed out in detail that the so-called paddle cilia are probably genuine and dynamic structures which within Mollusca are characteristic of chemoreceptors. Such paddle cilia are present in the osphradial epithelia of all marine molluscs so far investigated, and in those of the aplacophoran classes. They are also present in the foot of *Neomenia carinata* and a second undescribed species (Pararhopaliidae), confirming former reports of Thiele (1894) and Hoffman (1949) describing sensory cells in the epithelium of the foot of several species of the Solenogastres.

The osphradial sense organ in the caudofoveate Chaetodermatidae appears fully developed and functional. In contrast, the sense organ of *Prochaetoderma* is vestigial and surely not used in sensory reception. Although the osphradial sense organs of the *Scutopus* spp. are not in direct contact with the surrounding water, the very thin (1 µm) cuticle may allow molecules to pass through. A different epithelium, nerve processes, neural contact of the cells being located below of the central cleft, and a rich supply of nervous tissue provide structural evidence for a functional, but somewhat reduced (or specialized?) organ. This may be correlated with the fact that *Scutopus* (no data on *Prochaetoderma*) burrows to some depth (2–5 cm), whereas at least some of the chaetodermatid species live close to the surface of the mud and are thus terminally in contact with the free water (W. Pekny, personal communication).

As outlined elsewhere (Haszprunar 1987), the molluscan osphradium is suggested to be used primarily in sexual biology (coordination of spawning, search for a mate). Such a role of the sense organ appears possible also in the Caudofoveata, since W. Pekny (personal communication) reports a so-called 'stimulatory effect' in spawning for *Scutopus ventrolineatus*. In addition, the osphradial sense organs of both classes are certainly not involved in the search for food, as the Solenogastres have a special, preoral (so-called atrial) sense organ to locate their cnidarian food. Caudofoveata feed on microorganisms or organic detritus, or both, and at most use the highly sensitive pedal shield as a sense organ (Salvini-Plawen 1981*b*).

The Solenogastres are hermaphrodites with internal fertilization. Since their voluminous pedal gland produces large quantities of mucus (Salvini-Plawen 1968; personal observation), they might meet their sexual partner by a trail-following mechanism as described for many gastropods (see Haszprunar 1987). Thus, as in the higher gastropods (see Haszprunar 1985*a*, 1987) the osphradial sense organ could change its primary function. This hypothesis would

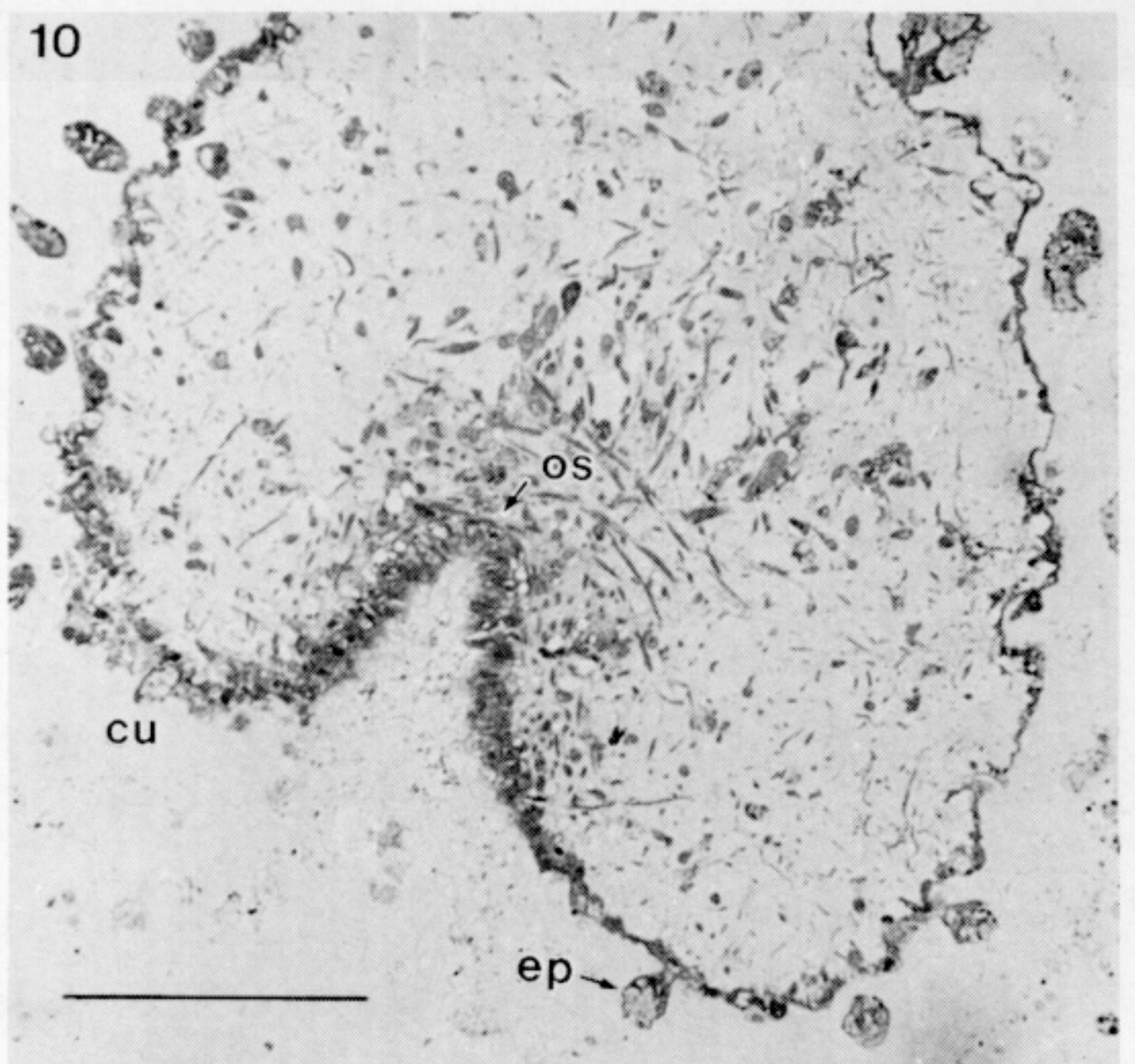
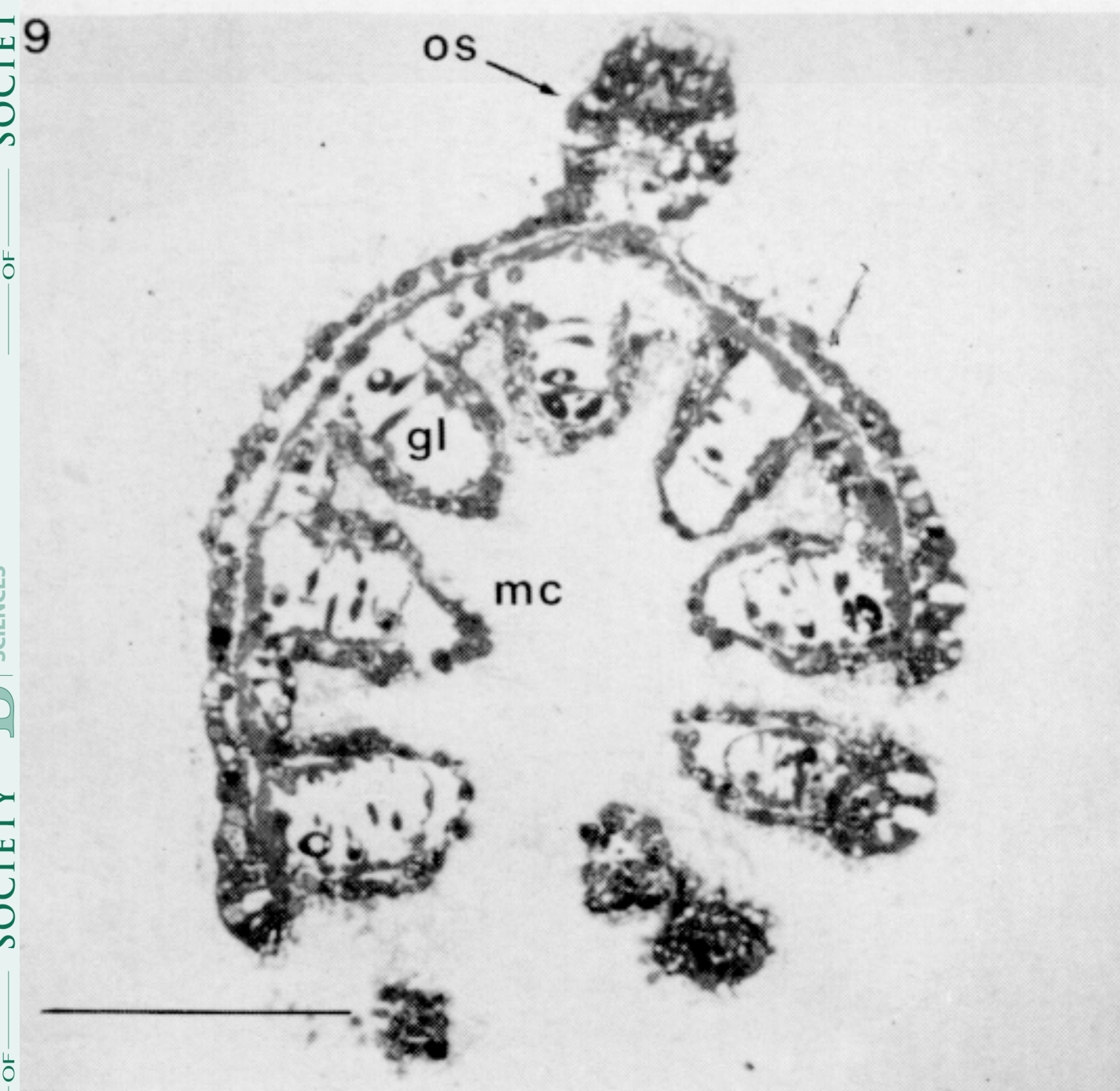
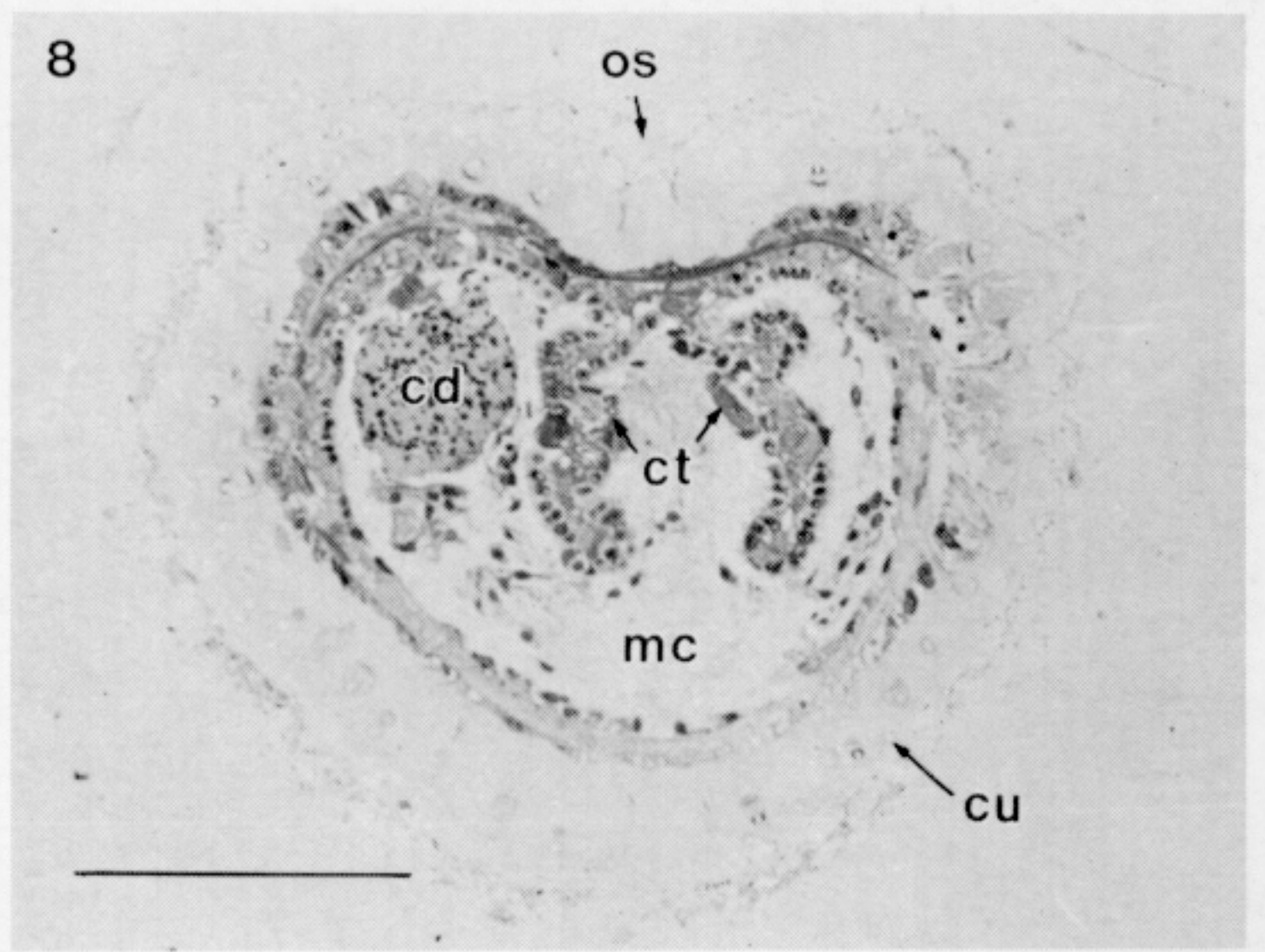
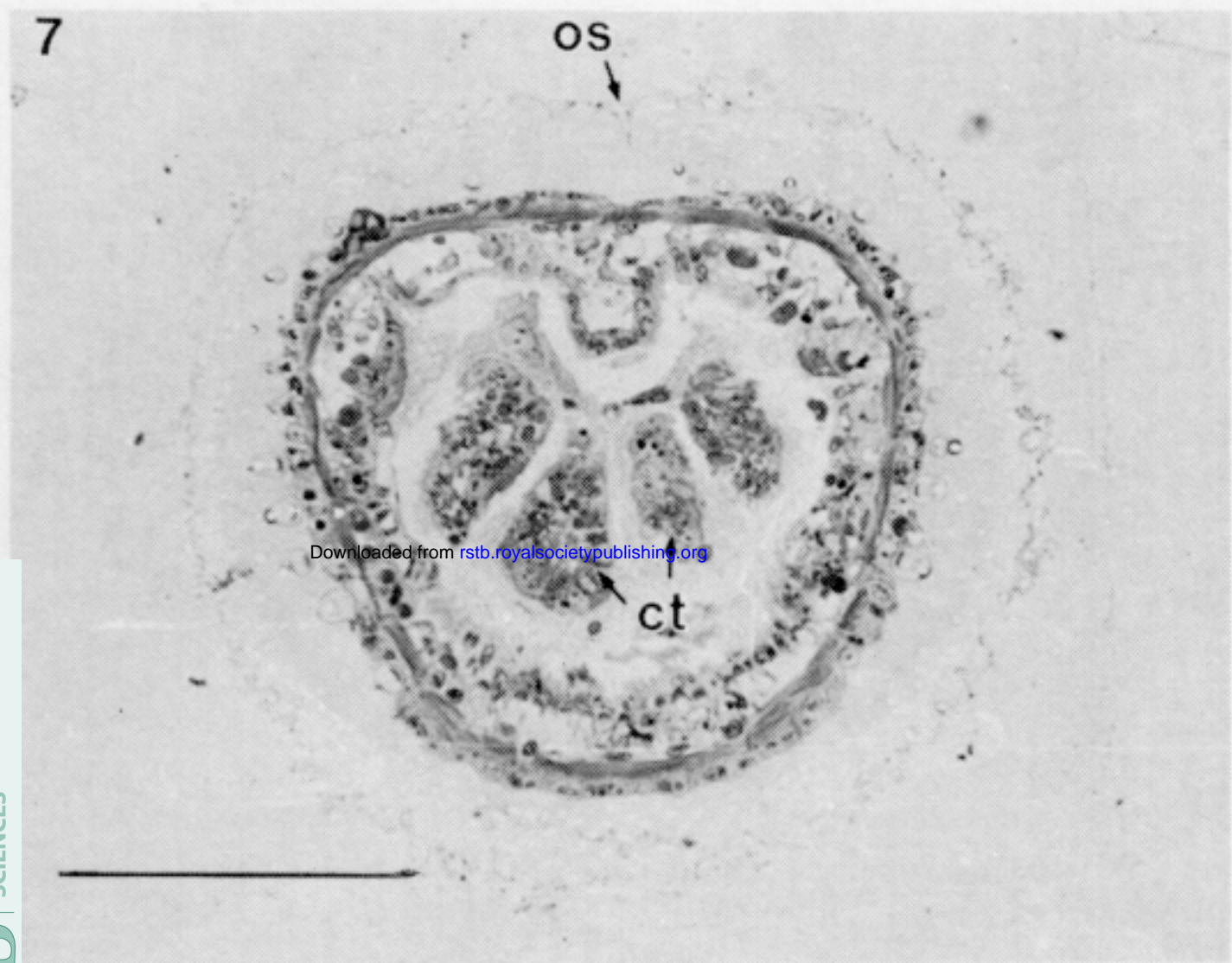
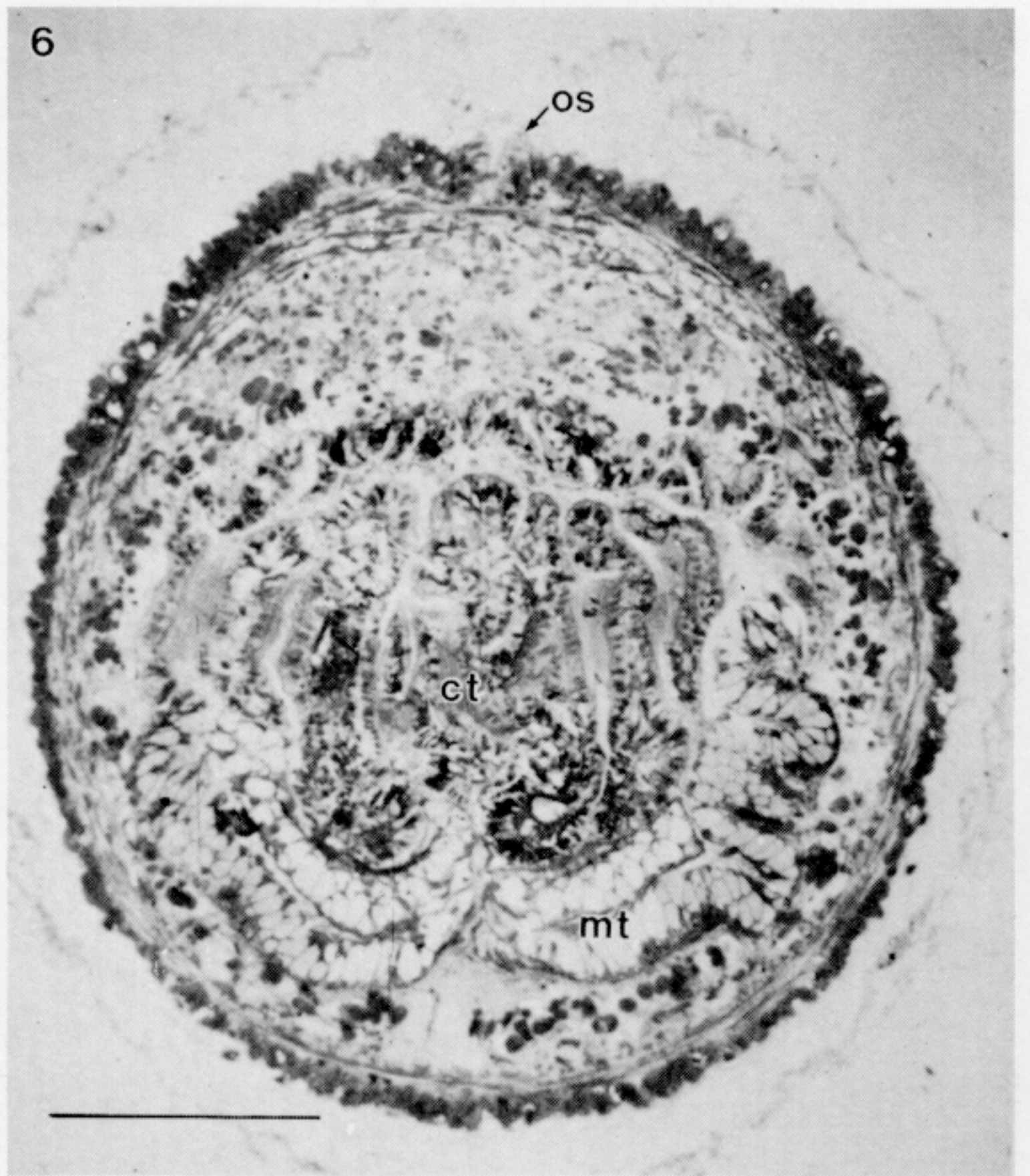
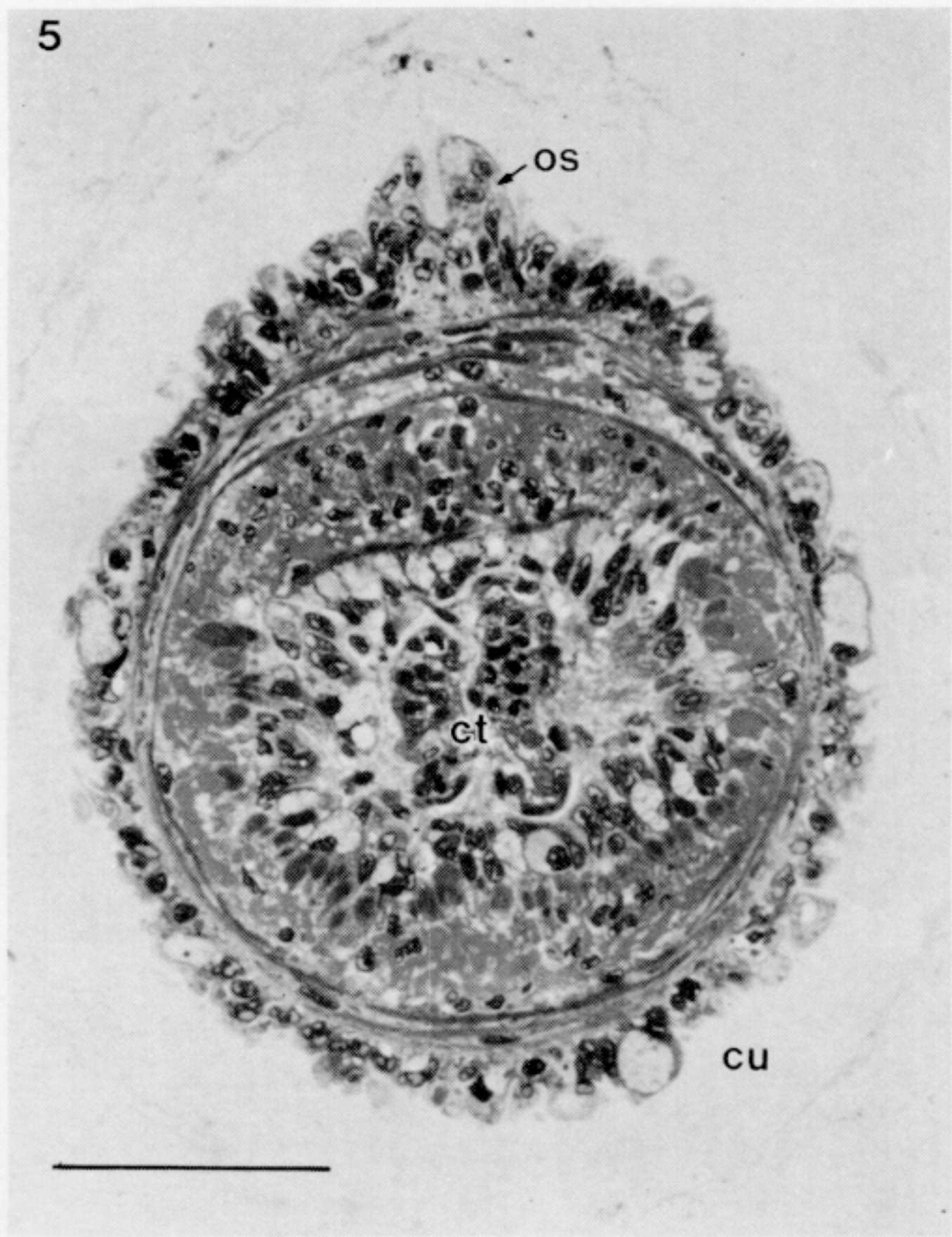
explain the great variation of the organs within the Solenogastres. However, further observations are necessary to correlate their presence, absence and multiplication with either systematics or ecological and functional conditions.

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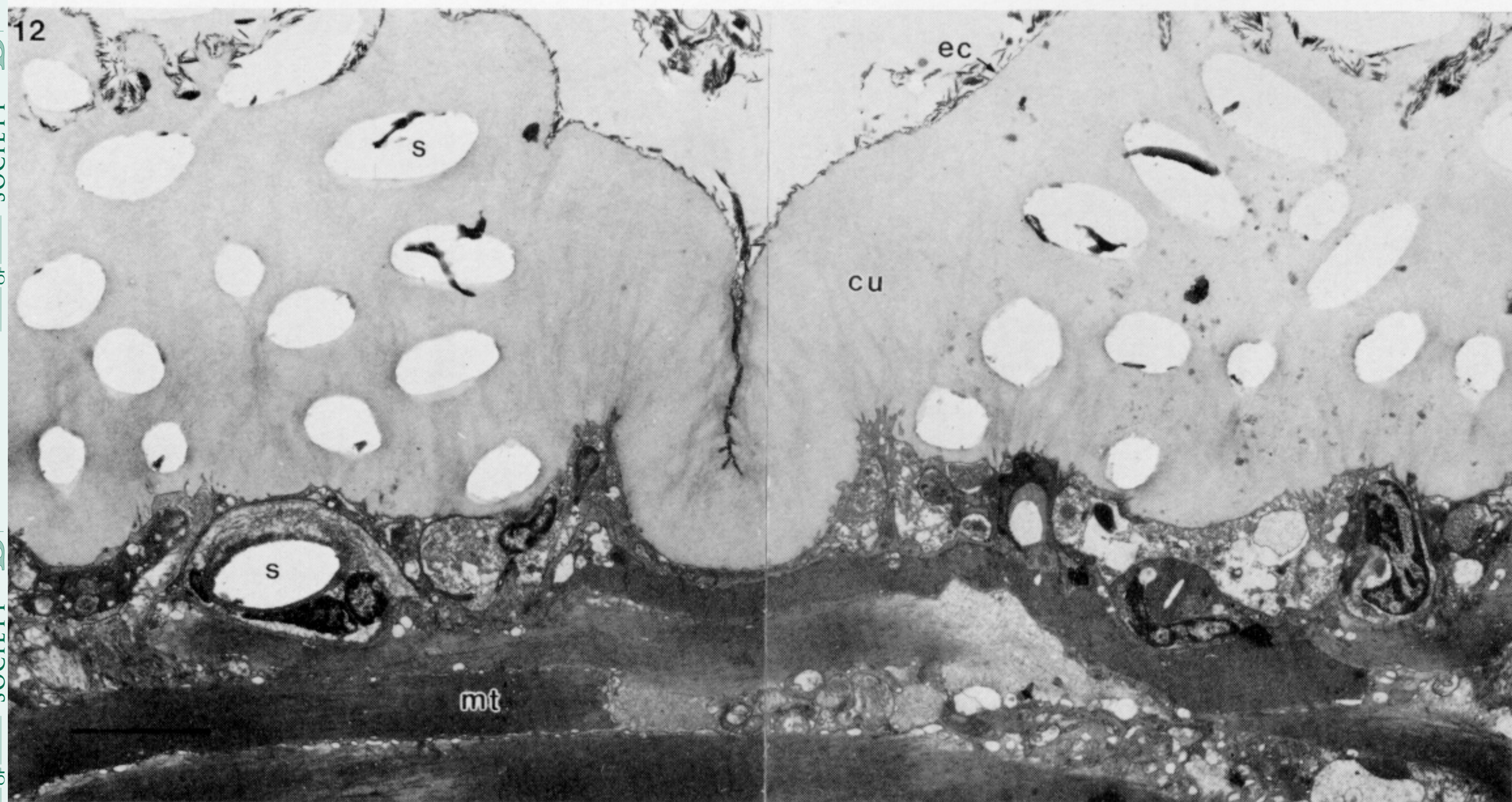
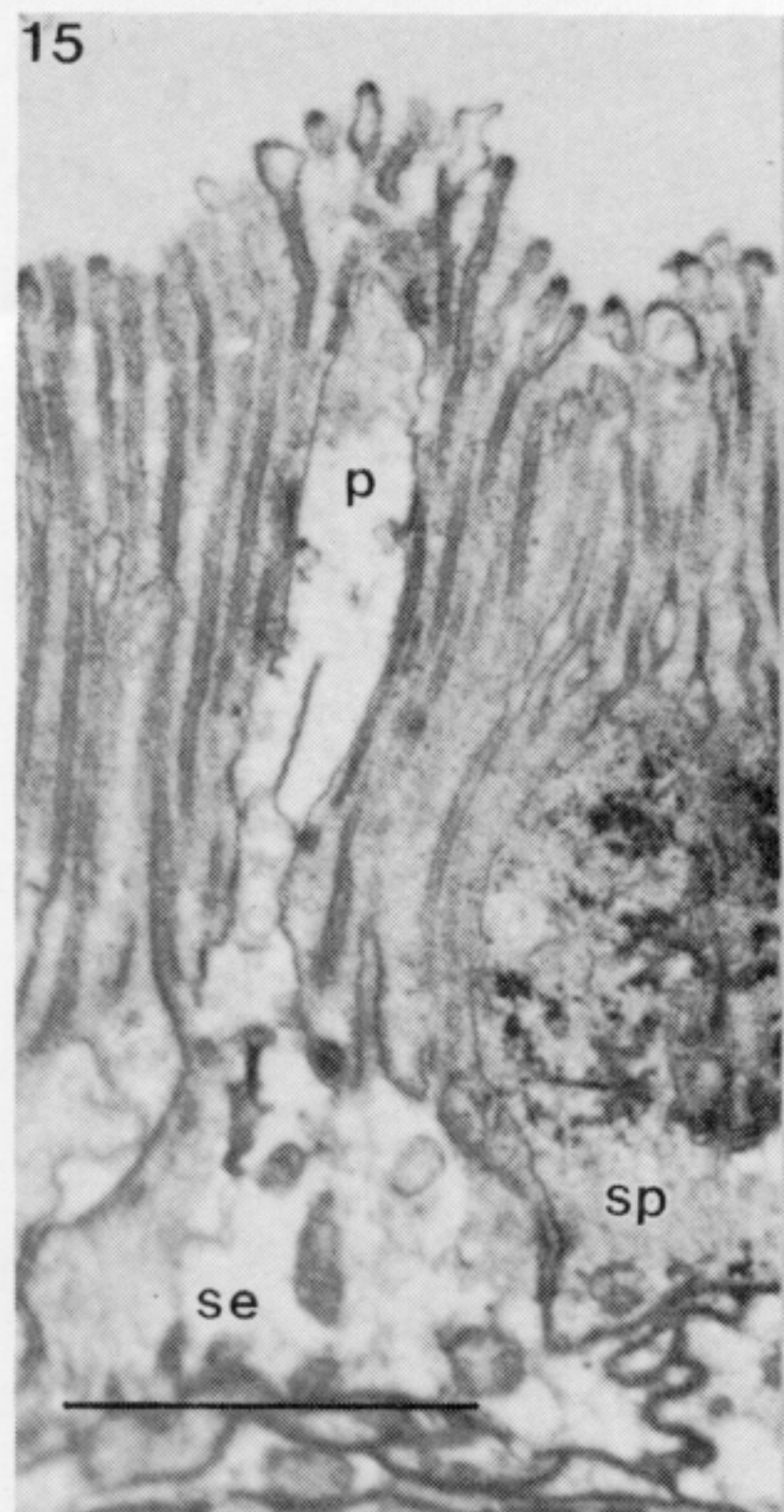
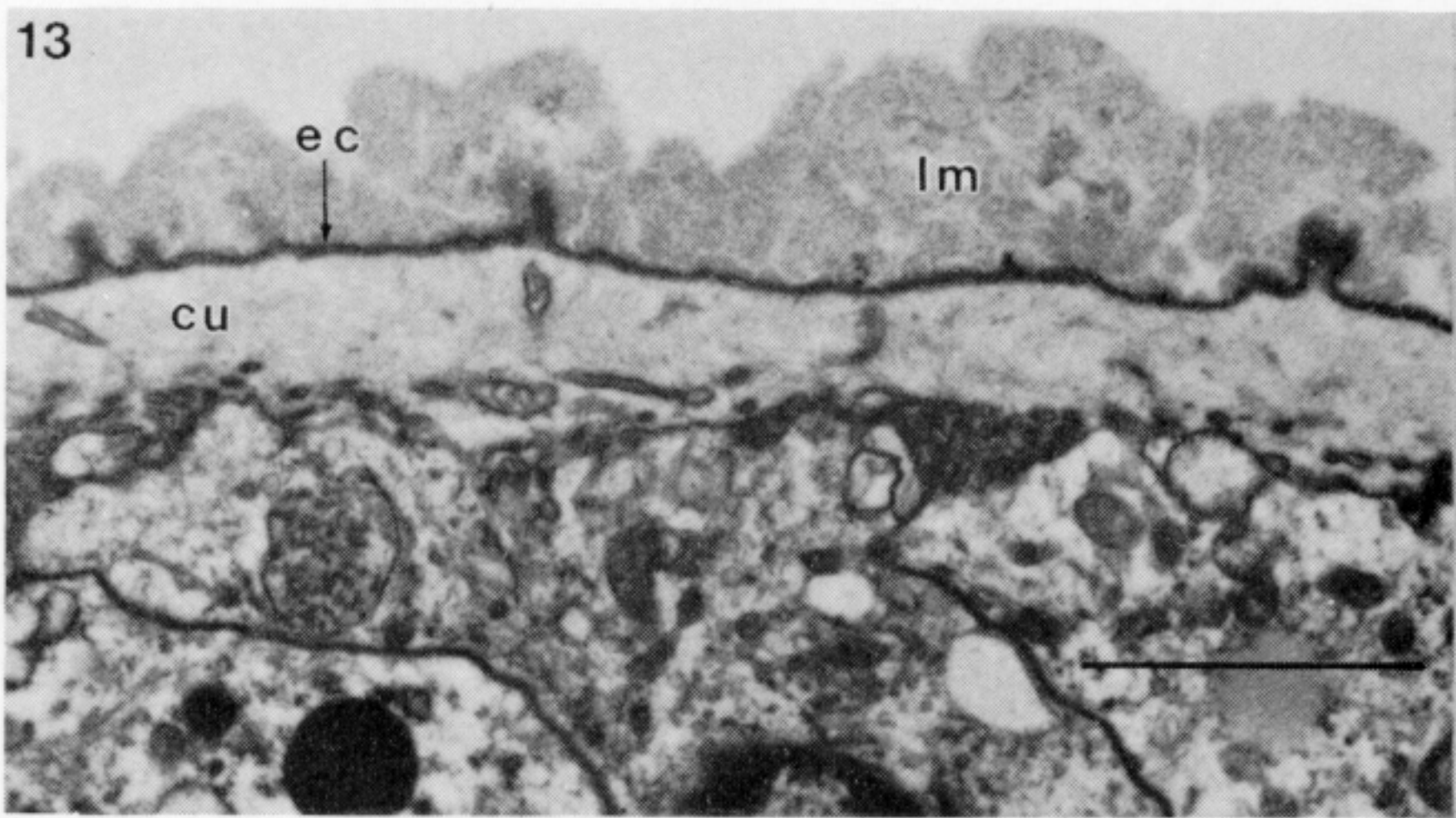
I thank Mr W. Pekny (University of Vienna) for collecting and sending the majority of the material investigated in this paper as well as for information about their behaviour. I am indebted to Professor L. v. Salvini-Plawen (University of Vienna) for determining the species as well as for critical reading of the manuscript.

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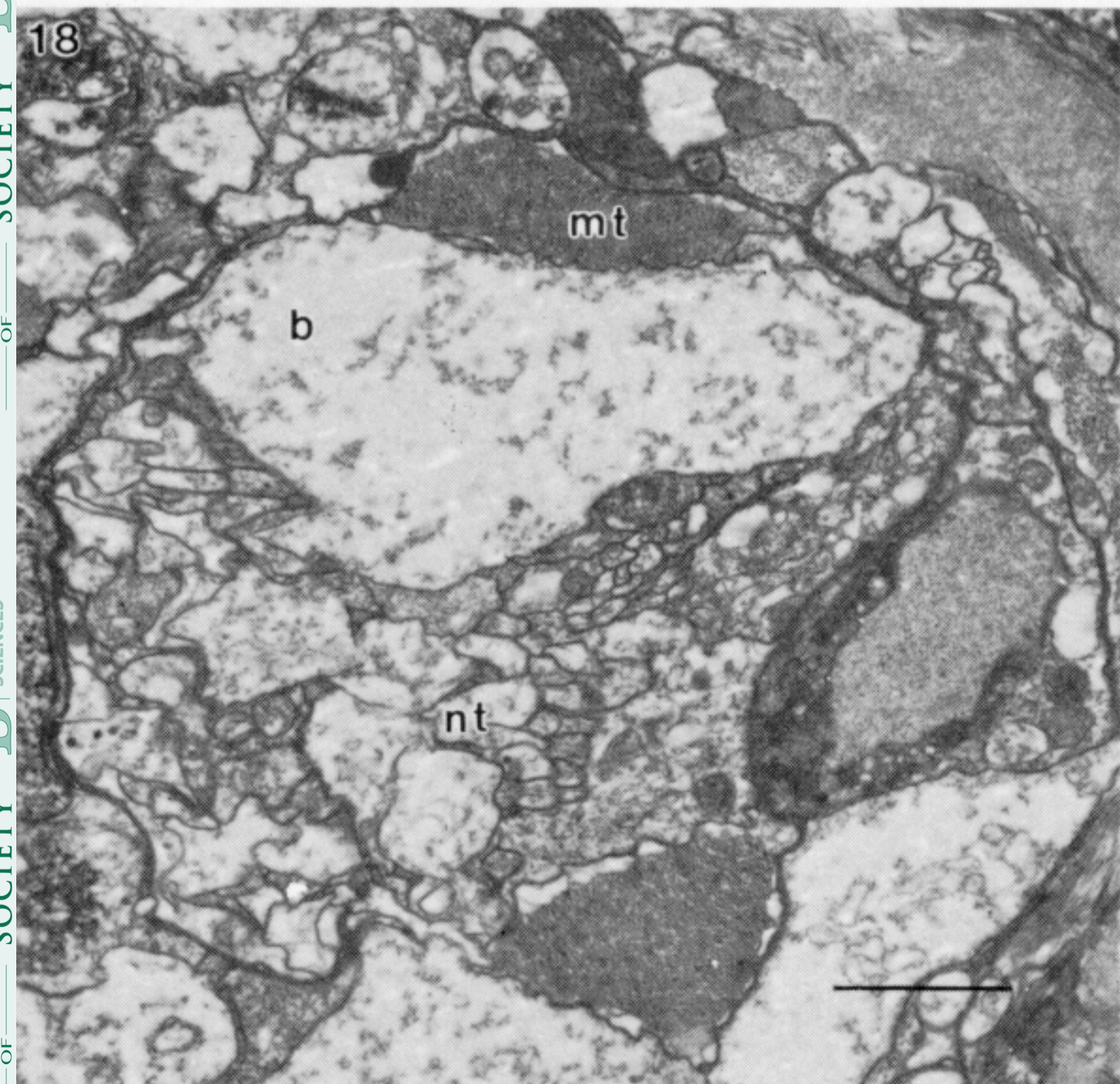
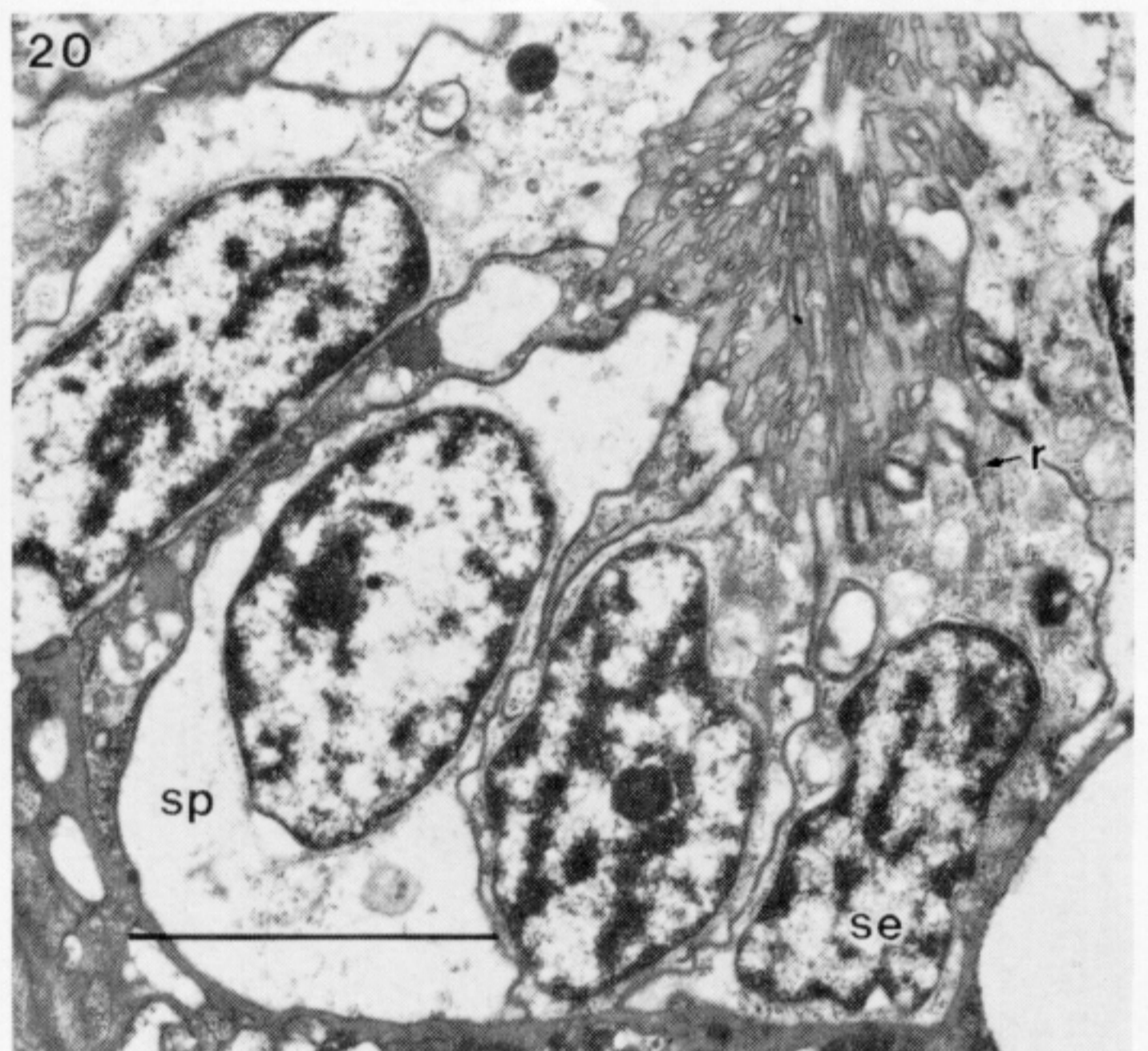
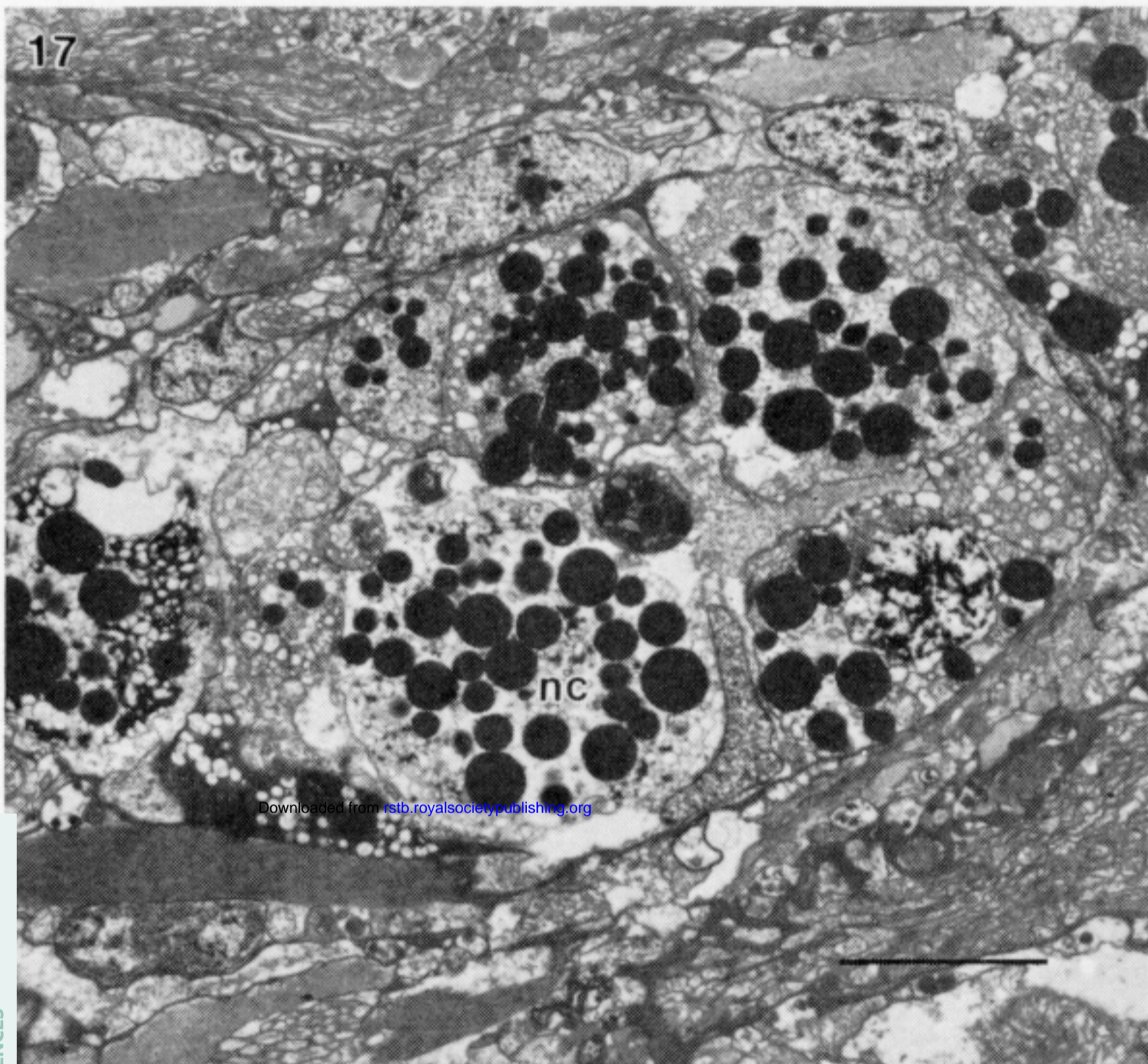
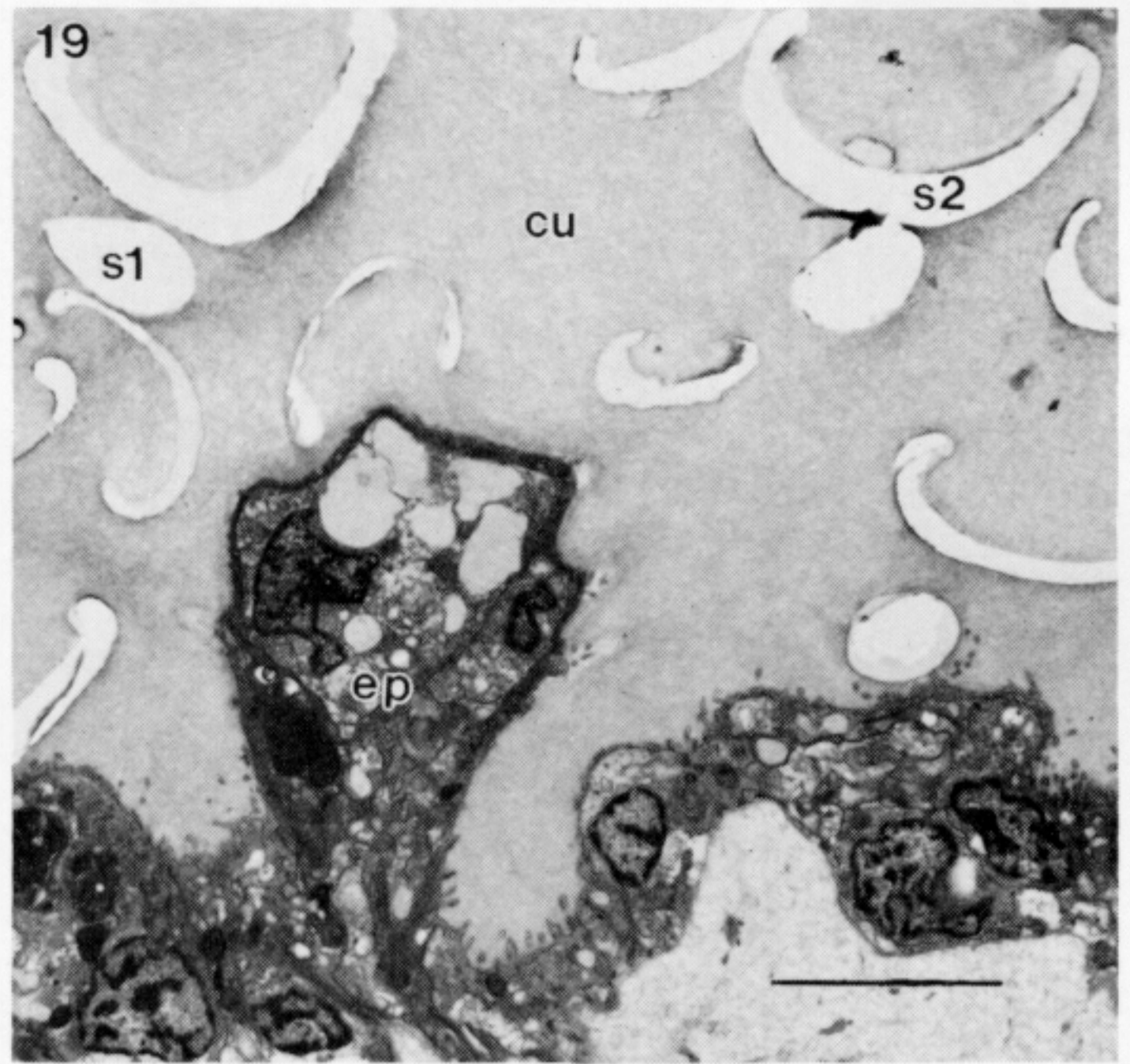
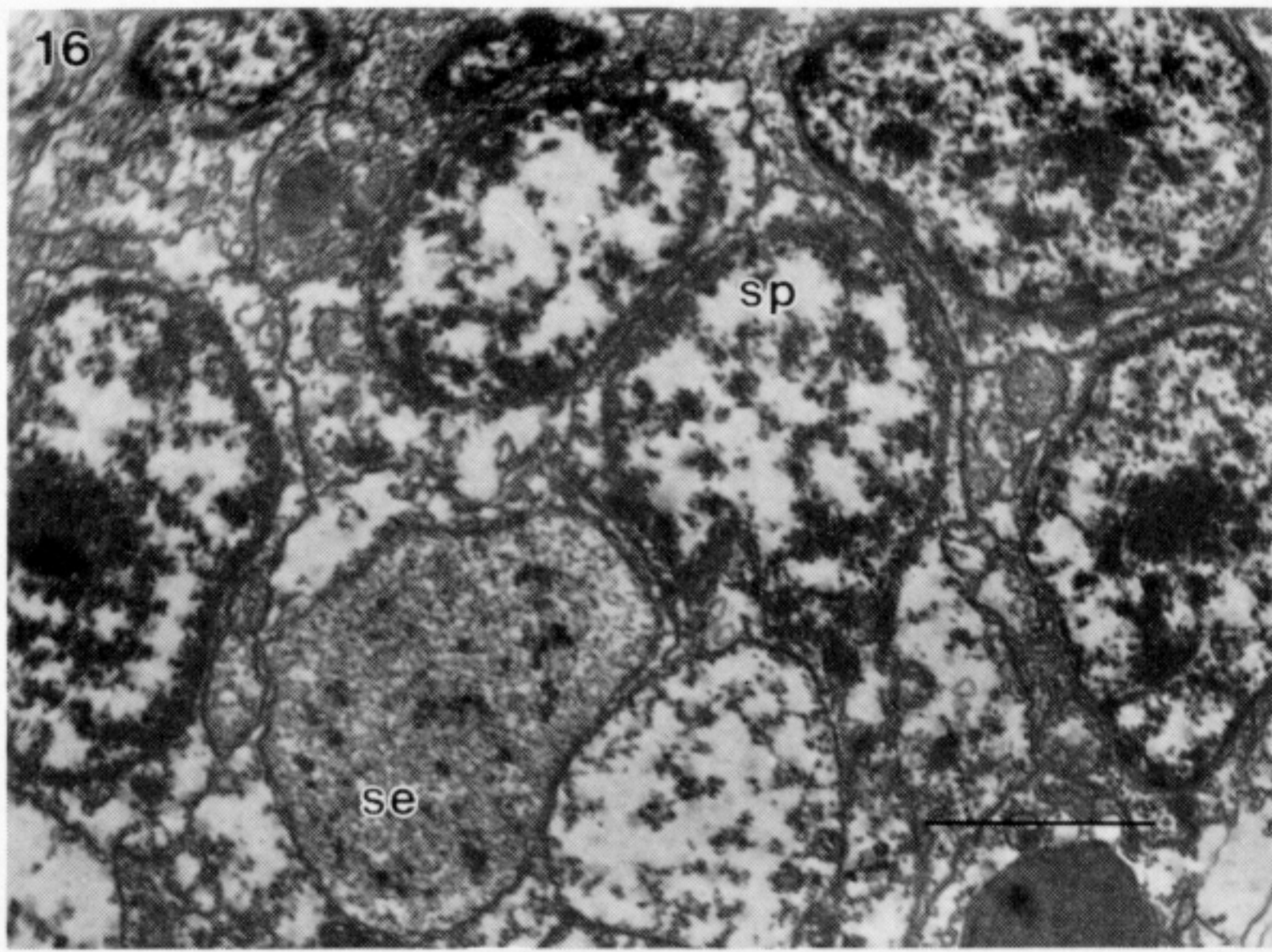


FIGURES 5-10. For description see opposite.



FIGURES 11-15. For description see opposite.

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FIGURES 16–21. For description see opposite.