PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Fine Morphology of the Osphradial Sense Organs of the Mollusca. III. Placophora and Bivalvia

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Phil. Trans. R. Soc. Lond. B 1987 **315**, 37-61
doi: 10.1098/rstb.1987.0002

Phil. Trans. R. Soc. Lond. B **315**, 37–61 (1987) [37]
Printed in Great Britain

THE FINE MORPHOLOGY OF THE OSPHRADIAL SENSE ORGANS OF THE MOLLUSCA.
III. PLACOPHORA AND BIVALVIA

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(*Communicated by A. Graham, F.R.S. – Received* 9 *May* 1985)

[Plates 1–3]

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[Published 12 February 1987

The fine morphology of the osphradia of six placophorans and eight bivalves, representing all major subgroups of both classes, is described. In addition, the branchial and lateral sense organs of *Lepidopleurus cajetanus* (Placophora) have been investigated ultrastructurally.

Whereas osphradial fine structure is very uniform within the Bivalvia, there are differences between Ischnochitonina and Acanthochitonina, supporting the separation of both groups. Major differences in the conditions of the mantle cavity divide Recent Placophora into the orders Lepidopleurida and Chitonida.

The homology of the molluscan osphradium throughout the phylum is discussed in detail. It is concluded that the terminal sense organ (Caudofoveata, Solenogastres), the adanal sensory stripes (Placophora–Chitonida), the interbranchial and post-anal papillae of *Nautilus* (Cephalopoda), and the organ of Lacaze (Gastropoda–Basommatophora) are homologous with the organs of Spengel (Prosobranchia, Opisthobranchia, Bivalvia), all to be called osphradial sense organs (or osphradia).

After discussion it is concluded that the osphradium is a chemoreceptor and not a mechanoreceptor as suggested by many authors. This is shown by the physiological evidence so far reported but mainly by the existence of paddle cilia in the osphradial epithelia throughout the Mollusca, which are typical of molluscan chemoreceptors. It is suggested that the osphradium is primarily used in sexual biology (coordination of spawning, search for a mate), a role altered within the Gastropoda (search for food, osmoreceptor, p_{O_2}-receptor).

INTRODUCTION

Compared with the distinctly prominent osphradia of prosobranch gastropods, the osphradia of placophorans and bivalves are only weakly developed. This may be the reason why the gastropod osphradium has been given much more attention than the osphradium of these two latter classes.

Spengel (1881) was the first who described the osphradia of a bivalve (*Arca noae*), and homologized them with the 'Geruchsorgane' of the Gastropoda. Plate (1897, 1899, 1901) and Pelseneer (1899) described the osphradia of the Placophora histologically and regarded them as homologous with the gastropod osphradia. In contrast to the situation in gastropods, the osphradia of these two classes (as well as of *Nautilus*, figure 4*d*, *e*, *f*) are located on the roof of the mantle cavity, and thus in the exhalant current of water, a rather strange location for a sense organ.

Yonge (1939*a*) has described water currents and several kinds of sense organs in the mantle cavity of the Placophora.

(i) In the Lepidopleurida there are so-called lateral and branchial sense organs. The latter were homologized by Burne (1896) with the osphradia, a point of view which was not shared by Plate (1901, p. 428) and Yonge (1939*a*).

(ii) In the Chitonida there are so-called anterior olfactory organs and adanal sensory stripes, the latter being regarded by all authorities as homologous with the gastropod osphradia.

There are no recent histological data on the chitonid osphradium, nor has an ultrastructural study been published so far. The function of the chitonid osphradium is also a matter of debate because no experiments have been done. Plate (1901) suggested an olfactory function; but Yonge (1939*a*) regarded it as a tactile organ, used to estimate the amount of sediment in the mantle cavity.

The osphradia of the Bivalvia have been studied with more attention than those of the

Placophora. Stork (1934) has summarized and extended knowledge of the histology and innervation of the bivalve osphradium. Recently, Kraemer (1979, 1981) and Zaitseva & Sokolov (1981) have described the histology and neuroanatomical context of the osphradia of freshwater bivalves, the former denying a homology with the gastropod osphradium. So far there are no data on the fine structure of bivalve osphradia.

Owing to the lack of experiments (there are only the recent results of Sokolov & Zaitseva (1982) on freshwater bivalves) the question of the function of the bivalve osphradium remains a matter of speculation. Whereas Spengel (1891) suggested it to be a 'Geruchsorgan' for testing water, Yonge (1947, 1977) still regarded it as a tactile organ. This point of view was extended by Aiello & Guideri (1964, 1965) who hypothesized that the osphradium of the bivalves could aid in the regulation of the ciliary activity of the gills. In contrast, Kraemer (1981) has suggested the bivalve osphradium to be a light sensor regulating seasonal behaviour or reproductive physiology in addition to a possible role in controlling fluid movement or the adduction of the shell valves.

This is the third of a series of papers concerning the fine morphology of the molluscan osphradium. It presents:

(i) the fine morphology of the osphradia of members of all major taxa of the Placophora and Bivalvia;

(ii) the fine morphology of the pallial sense organs of *Lepidopleurus cajetanus* to compare them with the 'true' osphradia of other chitons;

(iii) a discussion on the systematic significance of the osphradial fine structure in Placophora and Bivalvia;

(iv) a discussion on the homology of the osphradium throughout the Mollusca;

(v) a discussion on the possible primary function of the osphradium based on ultrastructural data given.

MATERIAL AND METHODS

The species of which the osphradia (or other pallial sense organs) have been ultrastructurally investigated are listed in table 1, including additional information about their provenance. These species represent all major subgroups of both classes (in the case of the Bivalvia–Anomalodesmata osphradia have not yet been described, and also personal investigations on *Cuspidaria* sp. have not been successful).

The same methods were used for the ultrastructural studies as described in the first part of the series (Haszprunar 1985*a*).

RESULTS

General remarks

All photographs and drawings of the described sensory epithelia are oriented so that the external milieu (mantle cavity) is always located above. In the case of the osphradia of both Placophora and Bivalvia, the situation is in reality inverted, but they are presented in this way to facilitate comparison especially with the osphradia of gastropods.

In all investigated species the 'cuticula' of former authors has been shown to be in reality a microvillous border. Thus, the term 'cuticula' is omitted in the descriptions.

Table 1. Species investigated

systematics	species	source
Placophora		
Lepidopleurida	*Lepidopleurus cajetanus* (Poli, 1791)	Adriatic Sea (Rovinj)
Chitonida		
Ischnochitonina	*Ischnochiton rissoi* (Payraudeau, 1827)	Adriatic Sea (Krk)
	Lepidochitona cinereus (Linné, 1766)	Atlantic (Helgoland)
	Middendorffia caprearum (Scacchi, 1836)	Mediterranean Sea (Villefranche)
	Chiton olivaceus Spengler, 1797	Adriatic Sea (Rovinj, Krk)
	Chiton corallinus Risso, 1826	Adriatic Sea (Piran)
Acanthochitonina	*Acanthochiton communis* (Risso, 1826)	Adriatic Sea (Rovinj, Krk)
Bivalvia		
Protobranchia		
Nuculida	*Nucula sulcata* (Bronn, 1831)	Atlantic (Helgoland)
	Yoldiella lucida (Lovén, 1846)	Atlantic (Bergen)
Autobranchia		
Pteriomorpha	*Mytilus edulis* Linné, 1758	Adriatic Sea (Rovinj)
	Arca noae Linné, 1758	Adriatic Sea (Rovinj)
Palaeoheterodonta	*Anodonta cygnea* Linné, 1758	Lower Austria (Laxenburg)
Heterodonta	*Dreissena polymorpha* Pallas, 1771	Burgenland (Neufelder See)
	Venus verrucosa Linné, 1758	Adriatic Sea (Rovinj)
	Pholas dactylus Linné, 1758	Adriatic Sea (Piran)

As in the osphradia of many gastropods (Storch 1972; Haszprunar 1985*a*, *b*) here also there occur the so-called paddle cilia (or disco cilia) which have been described in detail in the first part of the series (Haszprunar 1985*a*), and thus are only illustrated here (figure 16, plate 3).

Lepidopleurus cajetanus (Poli, 1791)

(Placophora–Lepidopleurida–Lepidopleuridae)

As in all members of the Lepidopleurida the mantle cavity of *Lepidopleurus cajetanus* is characterized by the adanally positioned multiple ctenidia (most of them situated behind the openings of the excretory and genital systems, see Yonge (1939*a*)), the development of which has probably caused the reduction of the osphradia. There are two kinds of pallial sense organs: the branchial and lateral sense organs.

(*a*) *The branchial sense organs*

The branchial sense organs were originally described by Burne (1896) in *Hanleya hanleyi* and later by Plate (1899, p. 98), also in the Lepidopleuridae. They are located at the efferent side of the ctenidial axis (outer, upper side) and are thus situated in the inhalant chamber of the mantle cavity. Each of them is innervated by the underlying efferent ctenidial nerve, which originates in the lateral cord and forms an accessory ganglion at the base of each ctenidium.

The histology of the branchial nerve organs was described by Burne (1896) and by Plate (1899, p. 98). Ultrastructural investigation shows that the branchial sense organs of *Lepidopleurus cajetanus* are only weakly developed and can therefore hardly be regarded as a sense 'organ'. The sensory epithelium is somewhat higher than the adjacent epithelium (20 μm compared with 15 μm) and consists mainly of supporting cells bearing microvilli, only some which also bear cilia. There are also some mucous cells in the epithelium. However, sensory cells have not been found. Situated between the supporting cells are free nerve processes, which arise from nerve cells within the efferent ctenidial nerve and bear short cilia with an irregular pattern (9+0, 8+0) and short roots. There is a thick basal lamina.

(*b*) *The lateral sense organs*

The lateral sense organs were first described by Thiele (1895) in *Lepidopleurus cajetanus* and later found in all investigated species of the Lepidopleurida (Plate 1899; Yonge 1939*a*). They consist of a series (up to 35 in *L. cajetanus*) of small patches on the outer wall of the mantle cavity anterior or external to the ctenidia and thus located in the inhalant water current. They are all innervated by nerves from the lateral cord.

The histology of the lateral sense organs was described in some detail by Plate (1899, p. 98). The sensory epithelium, which is much higher than that of the adjacent mantle (40 μm compared with 20 μm), consists of four cell types:

(i) supporting cells, bearing only microvilli, have their oval nuclei distally located;

(ii) very rare mucous cells, with large mucous vesicles, are found within the sensory epithelium;

(iii) between the supporting cells, small processes reach the surface of the sensory epithelium, bearing one or two short cilia with an irregular pattern of axoneural tubules and a short root. Their round nuclei, the euchromatin of which is less electron-dense than that of the supporting cells, is located basally. Their perikarya are in direct contact with the nervous tissue located at the base of the sensory epithelium: they are therefore regarded as sensory.

(iv) A second type of sensory cell occurs at the edge of the sensory epithelium. These are also in direct contact with the intra-epithelial nervous tissue (figure 15, plate 3). The plasma and the euchromatin of the oval nuclei are electron-dense. These cells bear several cilia which can form paddle cilia.

The basal lamina is again very thick.

Ischnochiton rissoi Payraudeau, 1827
Lepidochitona cinereus Linné, 1766
(Placophora–Chitonida–Ischnochitonina–Ischnochitonidae)
Middendorffia caprearum (Scacchi, 1836)
(Placophora–Chitonida–Ischnochitonina–Callistoplacidae)

As in most members of the Ischnochitonina the osphradia of the three species investigated are located on the roof of the mantle cavity between the anus and the last ctenidium. They are easily visible because of their yellow-brownish pigmentation and they form characteristically longish ridges of heightened epithelium under the suprarectal commissure, from which they are supplied by many small nerves. As described by Plate (1899, pp. 107, 123, 152) for other *Ischnochiton* and for *Nuttalochiton hyadesi* (Callistoplacidae) the pallial mucous tract is immediately adjacent to the sensory epithelium of the osphradium (figure 6, plate 1).

The sensory epithelium, which is about 40 μm high, consists of two cell types (figure 1 and figure 12, plate 2).

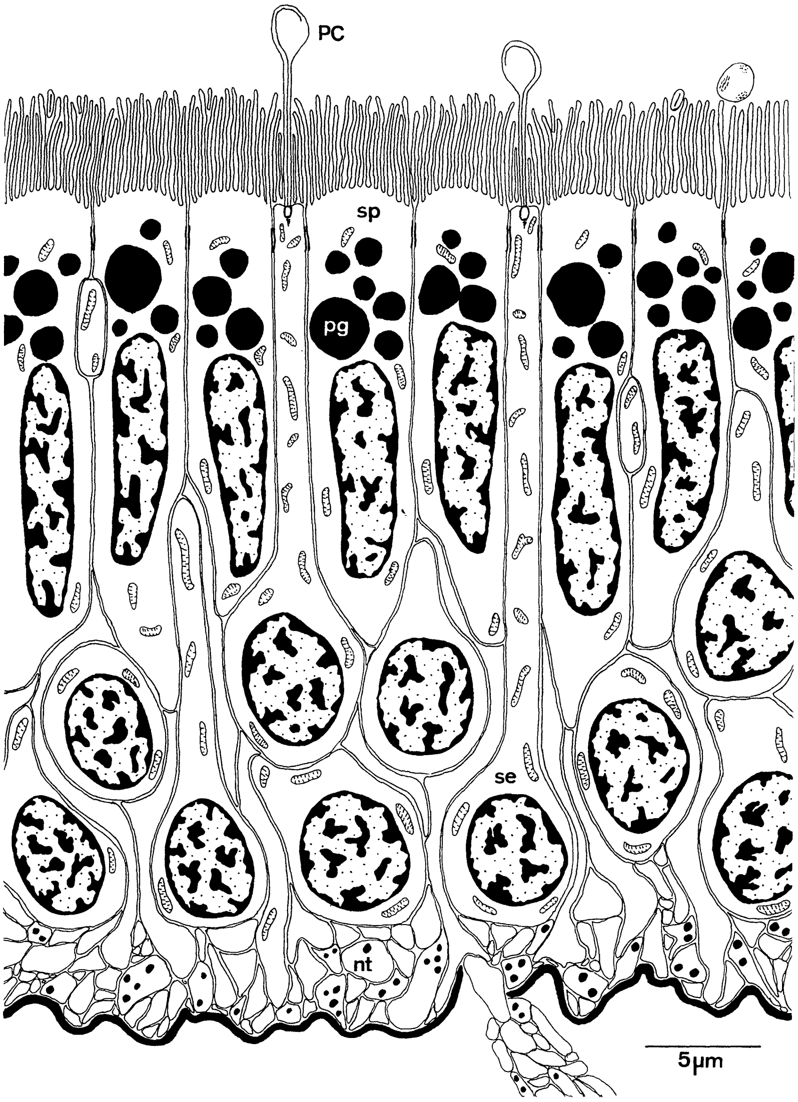

Figure 1. Section of the osphradium of a member of the Ischnochitonina (semischematic). nt, Nervous tissue; pc, paddle cilia; pg, pigment granules; se, sensory cells; sp, supporting cell.

(i) The supporting cells, characterized by large pigment granules, a high microvillous border, and distally located oval nuclei. In *Ischnochiton rissoi* the most distal part of these supporting cells lacks organelles and is somewhat arched (figure 12).

(ii) Between these supporting cells small processes reach the surface of the epithelium bearing one or two cilia which form paddle cilia and have very short roots. Their perikarya with round nuclei are basally situated and are placed immediately above a dense layer of intra-epithelial nervous tissue which is connected with the suprarectal commissure by small nerves, penetrating the thick basal lamina. This intra-epithelial nervous tissue is also found in the epithelia of the adjacent mantle and mucous tract (see also figure 13, plate 2).

Chiton olivaceus Spengler, 1797
Chiton corallinus Risso, 1826
(Placophora–Chitonida–Ischnochitonina–Chitonidae)

The osphradia of these *Chiton* species are found between the anus and the last but one ctenidium. Owing to a brownish pigmentation they are clearly visible in *Chiton olivaceus*, whereas in *C. corallinus* osphradia are found only in serial sections.

Differences arise in the position of the mucous tract which is not placed adjacent to the osphradial epithelium (figure 7; see also Plate 1899, p. 40). In contrast, the sensory epithelium itself strongly resembles that of the other Ischnochitonina described above. Again there are supporting cells and sensory cells with paddle cilia (figure 16), and intra-epithelial nervous tissue in the adjacent mantle epithelium (figure 13).

Acanthochiton communis (Risso, 1826)
(Placophora–Chitonida–Acanthochitonina–Acanthochitonidae)

The osphradia are placed beneath the anus, being nearly invisible due to the weak pigmentation. Plate (1901) did not describe the histology of an acanthochitonid osphradium, the epithelium of which shows great differences to that of the Ischnochitonina (figures 2*a*, *b*, 8 and 14):

The sensory epithelium is divided into a mucous zone (mantle side) and a sensory groove (pedal side). The mucous zone has a high epithelium (up to 70 μm) which consists mainly of mucous cells showing different kinds of plasma and mucous vesicles. Type A has an electron-dense plasma, its small mucous vesicles are distally located and are so densely packed that it resembles a honeycomb pattern. Type B is characterized by a very electron-dense plasma. Its mucous vesicles are larger, loosely packed and often show an electron-dense centre. Type C (figure 14) is zoned: mucous vesicles like type B are distally or centrally located. Between them or basally situated there is a zone of plasma which forms a labyrinth of tubules including mitochondria and which is granulated like the plasma of the basally located perikaryon. None of the mucous cell types bears microvilli which are (together with the presence of cilia) characteristic of the supporting cells lying between them. Their nuclei are located distally and they have several pigment granules. There is a layer of basally situated nervous tissue, but no sensory cells or free nerve endings could be found in this zone of the osphradium.

The epithelium of the sensory groove (figure 2*b*) is much lower (20–30 μm) and consists of two cell types, which are (i) supporting cells with microvilli only; or (ii) sensory cells with an electron-dense plasma and paddle cilia, being in contact with basal nervous tissue. Both types have pigment granules and oval nuclei.

As usual in Placophora, the basal lamina is very thick.

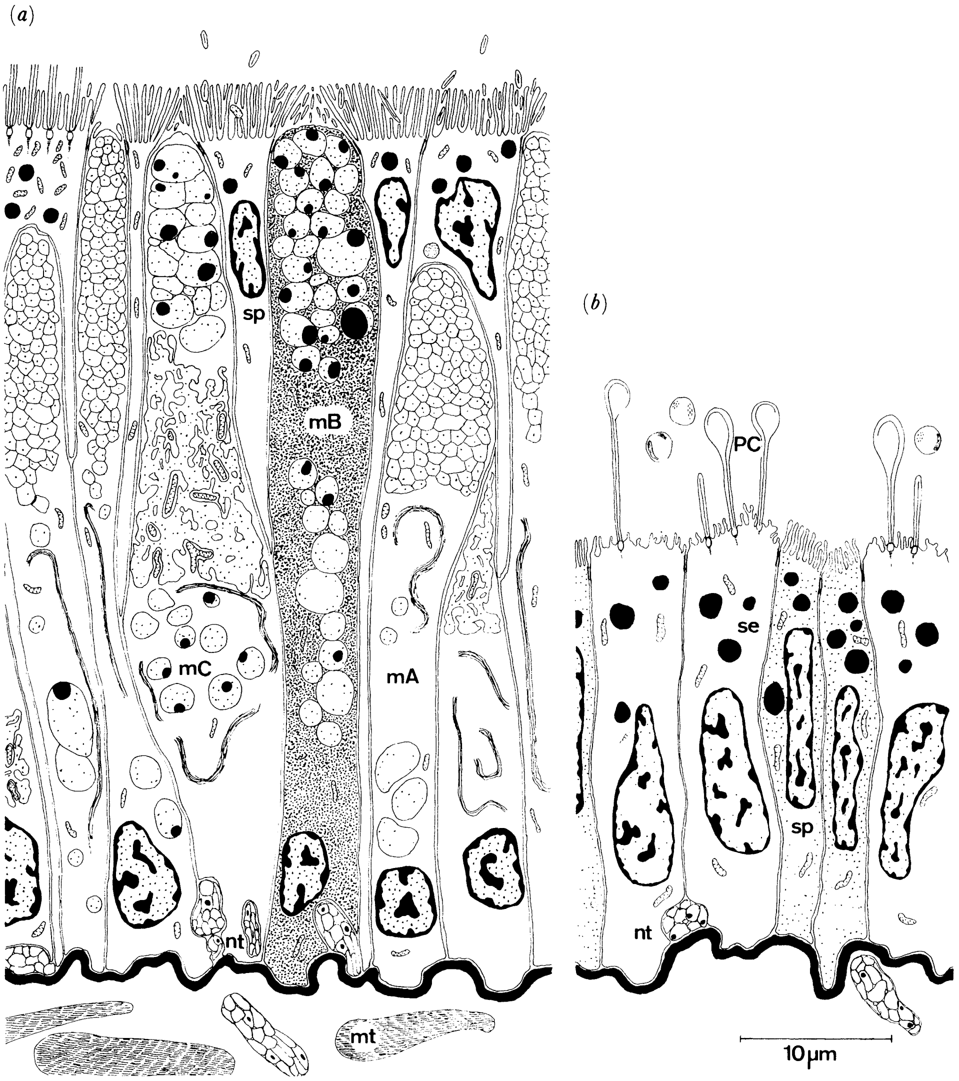

FIGURE 2. Section of the osphradium of *Acanthochiton* (semischematic). (*a*) Mucous zone, (*b*) sensory groove. mA, mB, mC, mucous cell of type A, B, C; mt, muscle tissue; nt, nervous tissue; PC, paddle cilia; se, sensory cell; sp, supporting cell.

Nucula sulcata (Bronn, 1831)
(Bivalvia–Protobranchia–Nuculida–Nuculidae)

Ever since Yonge's (1939*b*, 1947, 1959) studies the mantle cavity of the Protobranchia (especially the genus *Nucula*) has been known to represent one of the most archaic types within the Conchifera; it comprises a pair of true ctenidia (see figure 5*e*), hypobranchial glands and a conservative (anterior–posterior) water current. The position of the osphradia, lying at the inner side of the ctenidial axis in the exhalant current (Pelseneer 1891; Yonge 1939*b*, 1947) also appears to be conservative. In *Nucula sulcata* they are easily visible owing to their yellow-brown pigmentation. They are innervated by the branchial nerve which forms a small ganglion.

The histology of the osphradium of *Nucula* has not been investigated up to now. The sensory epithelium is somewhat higher (10–15 μm) than the adjacent mantle epithelium (6–10 μm) and is additionally characterized by a very high (5 μm) microvillous border. It consists of two elements (figure 17, plate 3):

(i) the supporting cells, which are cylindrical in shape, have round mitochondria, round nuclei and many, distally located pigment granules;

(ii) between them, narrow (2 μm) sensory processes, originating from nerve cells within the osphradial ganglion, reach the surface of the epithelium, bearing up to three cilia. These cilia do not leave the microvillous border, but run parallel to the surface within and have an irregular axonemal pattern (9+0, 8+1). These processes are also characterized by many microtubules running between the elongated mitochondria.

There is no basal lamina.

Yoldiella lucida (Lovén, 1846)

(Bivalvia–Protobranchia–Nuculida–Nuculanidae)

As described by Stempell (1898, p. 407) in *Leda sulculata* (Nuculanidae) and *Malletia chilensis* (Malletiidae), the osphradia of *Yoldiella lucida* are located at the inner side of the base of the ctenidial axis. They are situated in the exhalant current despite the development of siphons (as in all Autobranchia), and are only visible in sections, owing to the lack of pigmentation. They are innervated by the branchial nerve, forming a small ganglionic layer.

The histology and fine structure of the osphradial epithelium resemble those of *Nucula sulcata* in all respects (supporting cells, free nerve processes with abnormal cilia).

Mytilus edulis Linné, 1758

(Bivalvia–Autobranchia–Pteriomorpha–Mytilidae)

The osphradia of *Mytilus edulis* are, as in all mytilids, (List 1902; Clasing 1923) nearly unpigmented swellings situated ventral to the visceral ganglion and the beginning of the branchial nerve which forms a distinct ganglionic area. They are crossed by the ciliary tracts typical of mytilid species.

The histology of mytilid osphradia has been described by List (1902) and Clasing (1923), whereas White (1937) apparently mistook them for the ciliary tracts.

In contrast to the conditions described above for *Nucula sulcata*, there are two kinds of sensory elements in the osphradial epithelium of *Mytilus edulis* (figures 3 and 18):

(i) as in *Nucula* there are free nerve processes with irregular cilia;

(ii) additionally sensory cells are found within the osphradial epithelium, projecting long axons to the ganglionic area of the branchial nerve underneath (figure 18). They also bear cilia which run parallel to the surface of the epithelium, but can also form paddle cilia.

(iii) the supporting cells have only few pigment granules.

There is only a very thin basal lamina.

Arca noae Linné, 1758

(Bivalvia–Autobranchia–Pteriomorpha–Arcidae)

The strongly pigmented and thus easily visible osphradia of *Arca noae* were first described by Spengel (1881), who regarded them as homologous with those of the gastropods. They are

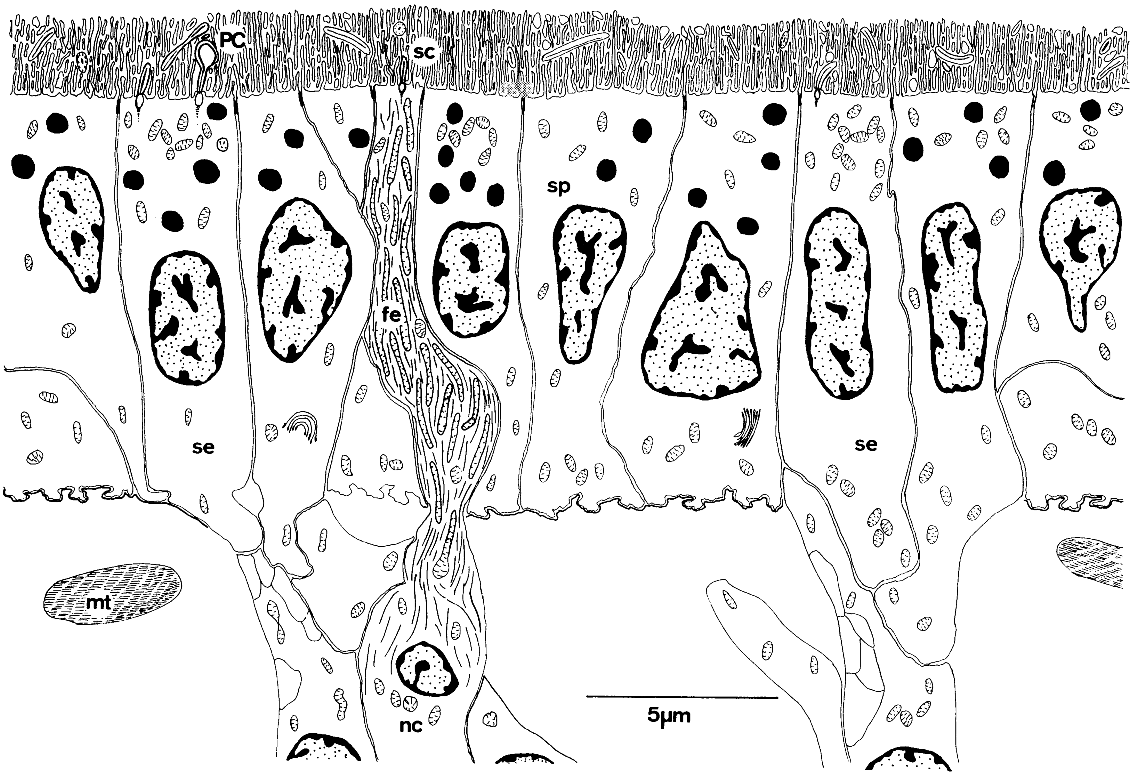

Figure 3. Section of the osphradium of a (marine) bivalve (semi-schematic). fe, Nerve process; mt, muscle tissue; nc, nerve cell; PC, paddle cilia; sc, sensory cilium; se, sensory cell; sp, supporting cell.

located ventral to the visceral ganglion and follow the branchial nerves, which form distinct ganglia.

The histology of the osphradium of *Arca noae* has also been described by Dakin (1910), who paid attention especially to the innervation. There is a large cord of nervous tissue within the high (30 μm) sensory epithelium (figure 10, plate 1), which is connected with the osphradial ganglion by a series of strong nerves. The cell types are the same as those described in *Mytilus*; the sensory elements (sensory cells or free nerve processes) are innervated, in most cases, by the intraepithelial nervous cord, but are occasionally directly supplied by the osphradial ganglion.

Anodonta cygnea Linné, 1758

(Bivalvia–Autobranchia–Palaeoheterodonta–Unionidae)

As described by Freidenfelt (1897) the osphradia of *Anodonta* are supplied by the branchial nerve which forms a distinct ganglion. The sensory epithelium, which has been described histologically by Zaitseva & Sokolov (1981), is unpigmented and thus only visible in sections. In contrast to the marine species described above, the microvillous border is low. Free nerve processes, characterized by a more electron-dense plasma and many mitochondria, bear only short straight cilia which do not extend beyond the microvillous border. Sensory cells and paddle cilia have not been found, and there is no basal lamina.

Dreissena polymorpha Pallas, 1771

(Bivalvia–Autobranchia–Heterodonta–Dreissenidae)

Probably owing to total lack of pigmentation and to the low epithelium, the osphradia of *Dreissena polymorpha* have not been found by most previous investigators (for example, Meisenheimer 1900; Morton 1969). Only Babor (1895) has described the innervation that originates in an accessory ganglion anterior and adjacent to the visceral ganglion. The osphradial epithelium is located as usual ventral to the branchial nerve which is fused with the nerves from the accessory ganglion.

The sensory epithelium resembles that of *Anodonta* in all respects (low microvillous border, free nerve endings with short straight cilia, no sensory cells).

Venus verrucosa Linné, 1758

(Bivalvia–Autobranchia–Heterodonta–Veneridae)

The osphradia of *Venus verrucosa* are weakly pigmented, soft swellings ventral to the branchial nerves that supply them with many small nerves, as described in *Venus casina* by Dakin (1910).

The sensory epithelium strongly resembles that of *Mytilus* (two sensory elements, paddle cilia).

Pholas dactylus Linné, 1758

(Bivalvia–Autobranchia–Heterodonta–Myina–Pholadidae)

Owing to lack of pigmentation the osphradia of *Pholas dactylus* are found only in sections, lying ventral to the branchial nerves. There is some confusion over the innervation, since the results of different authors do not agree.

(i) Pelseneer (1891) stated that the osphradium is only supplied by nerves from the cerebrovisceral connective.

(ii) Dakin (1910) found additional innervation by the visceral ganglion as in other members of the Myina.

(iii) Förster (1914) investigated the visceral ganglion and its nerves in great detail, describing a direct connection between the osphradium and the pallial nerves in addition to the other connections. Thus, the neuroanatomy has reached its highest degree of complexity within the Bivalvia so far investigated.

A transverse section of the branchial nerve in the osphradial region shows that the whole forms a ledge-like structure (figure 11, plate 1). This ledge shows two zones: (i) inside anterior (right in figure 11) there are many mucous cells and supporting cells, forming a zone which is not innervated by the branchial nerve; (ii) outside, posterior (left in figure 11) the sensory epithelium is elaborated as described for *Mytilus* (two kinds of sensory elements, paddle cilia). The supporting cells are the same in both zones; a basal lamina is not present.

DISCUSSION

Systematic significance of osphradial structure in Placophora and Bivalvia

Since Haszprunar (1985*a*) has shown the prosobranch osphradium to be an important character for classification at the suborder level, similar conditions could also be expected in placophorans and bivalves. The results show, however, that the systematic significance of the osphradial fine structure is very different in each class.

Placophora

As stated by nearly all authors (for example, Plate 1901; Knorre 1925; Yonge 1939*a*, Bergenhayn 1930, 1855; Starobogatov & Sirenko 1975; Salvini-Plawen 1980), the Lepidopleurida appear as the earliest offshoot of Recent placophorans on the basis of anatomical and plate characters. In contrast to the Chitonida, their ctenidia are (independently) multiplied mainly posterior to the (original) post-renal gill, and thus the osphradia are suppressed, being replaced by the branchial (?) and lateral sense organs (for homology of osphradia and branchial sense organs, see below), which show a similar structure to the osphradia of the Ischnochitonina.

The entirely different structure of the osphradial epithelium of *Acanthochiton* supports the separation of the Acanthochitonidae (and Cryptoplacidae) in a suborder Acanthochitonina distinct from the Ischnochitonina, as is done by most modern authors. Both suborders, however, should be united in an order Chitonida (Thiele 1929; Starobogatov & Sirenko 1975), because of the common presence of true osphradia, coordinated with a common mode of ctenidial multiplication (mainly anterior to the post-renal gill which is first developed during ontogeny, see Heath (1899), Hammarsten & Runnström (1926), Minichev & Sirenko (1984) and a similar arrangement of the pallial mucous tracts (two, instead of three as in the Lepidopleurida).

The identical structure of the osphradial epithelium of all Ischnochitonina investigated (members of Ischnochitonidae, Callistoplacidae, and Chitonidae) is additional evidence for the phylogenetic unity of this taxon (contrasting with Starobogatov & Sirenko (1975) who divided it in two groups). There are, however, differences in the relative position of the mucous tracts: whereas in Ischnochitonidae and Callistoplacidae the tract is adjacent to the osphradial epithelium (see figure 6 and also Plate (1899), pp. 107, 123, 152), this is not the case in the Chitonidae (see figure 7 and also Plate (1901) p. 407). Since most of the families of the Ischnochitonina have not been investigated in this respect, it remains uncertain, whether or not this is of systematic significance.

Bivalvia

In contrast to the conditions in prosobranchs and placophorans, the osphradia of bivalves are very uniform in structure and thus do not show any systematic significance within this class. Only members of the heterodont suborder Myina (Mactroidea, Myoidea, Adesmoidea) appear to be characterized by a more or less cerebral part of osphradial innervation (see also Pelseneer 1891).

The homology of the osphradia throughout the Mollusca

Placophora and Bivalvia (especially Protobranchia) are said to have retained many archaic conditions of the molluscan mantle cavity. Their osphradial features, together with data on Archaeogastropoda (Haszprunar 1985*a*) and on the aplacophoran classes (Haszprunar 1981, 1987) form a well founded basis on which to discuss osphradial homology throughout the Mollusca. Since the osphradial sense organs are largely involved in nearly all modifications of the molluscan mantle cavity, it is not surprising that there is a great variation in their position, number, size, and function (figure 4). Despite these differences there are remarkable similarities in innervation and in their position relative to the ctenidia (figure 5). Such a homology must be proven by 'classical' comparative anatomy alone, since osphradial structure is very different even within those groups (for example, Prosobranchia, Chitonida) where there is no doubt about their homology. In broad agreement with Salvini-Plawen (1981) it will be shown that the terminal sense organs (Caudofoveata, Solenogastres), the adanal sensory stripes (Placophora–Chitonida), and also the organ of Lacaze (Gastropoda–Basommatophora) are homologous with the organs of Spengel (Prosobranchia, Opisthobranchia, Bivalvia, *Nautilus*), and all may be termed osphradial sense organs (or osphradia only).

The archetypal condition (*figures* 4*a*, 5*a*)

From conditions in Recent classes, the mantle cavity of a hypothetical molluscan archetype is suggested to be located lateroterminally, having one pair of ctenidia, homogeneous mucous tracts, and a pair of osphradial sense organs (Salvini-Plawen 1972, 1980, 1981). The osphradia were probably placed on the roof of the mantle cavity, as they still are in the Chitonida and Bivalvia, or, with respect to the conditions in the aplacophoran classes, at the mantle edge, always lying in the exhalant current. They are assumed to be supplied by paired nerves from the terminal portion of the lateral cords or from the suprarectal commissure close to the base of the ctenidial nerve.

Caudofoveata (*figures* 4*b*, 5*b*i, 5*b*ii):

Owing to a burrowing mode of life, the mantle cavity has been shifted terminally and partly inverted, having a pair of primitive ctenidia and mucous tracts (= spawning grooves in females). The osphradial (= terminal) sense organs are fused to a single sensory groove which is placed in the inhalant current at the dorsoterminal edge of the mantle cavity. However, the paired innervation is retained by nerves originating from the suprarectal commissure. There is variation with the respect that in *Falcidens hartmanni* the osphradial nerves originate inside the ctenidial nerves (figure 5*b*i), whereas in all other species investigated, they originate outside (figure 5*b*ii) (Salvini-Plawen 1972, 1981). The osphradial sense organs appear to be reduced in the Prochaetodermatidae (Haszprunar 1981, 1987*b*).

Solenogastres (*figures* 4*c*, 5*c*)

Owing to a winding and wriggling locomotion (indicating an independent evolution), the hermaphroditic Solenogastres possess a mantle cavity restricted to a small terminal cavity and to a pair of internalized tubes (mucous tracts = spawning ducts) directed anteriorly. Ctenidia are totally reduced. The osphradial (= terminal) sense organ is situated outside the mantle cavity, being fused to a single, circular groove or pit, but generally still supplied by paired nerves from the suprarectal commissure. There are certain variations in the occurrence of osphradia within the Solenogastres: they may be multiplied in species of some genera, showin innervation also from the lateral cords, or they may be reduced, mainly in small species (Salvini-Plawen 1969, 1972, 1978). Their position with respect to the water current is not certain.

Placophora: *Lepidopleurida*

Whether or not the branchial sense organs of the Lepidopleurida can be regarded as osphradia is a matter of debate (Burne 1896; Salvini-Plawen 1981 compared with Plate 1901; Yonge 1939*a*).

Since branchial sense organs are found at the efferent side of each ctenidial axis, this correlation must have been evolved before the ctenidia were multiplied. The alternative hypothesis, that there is a secondary correlation by subdivision of a single original osphradium

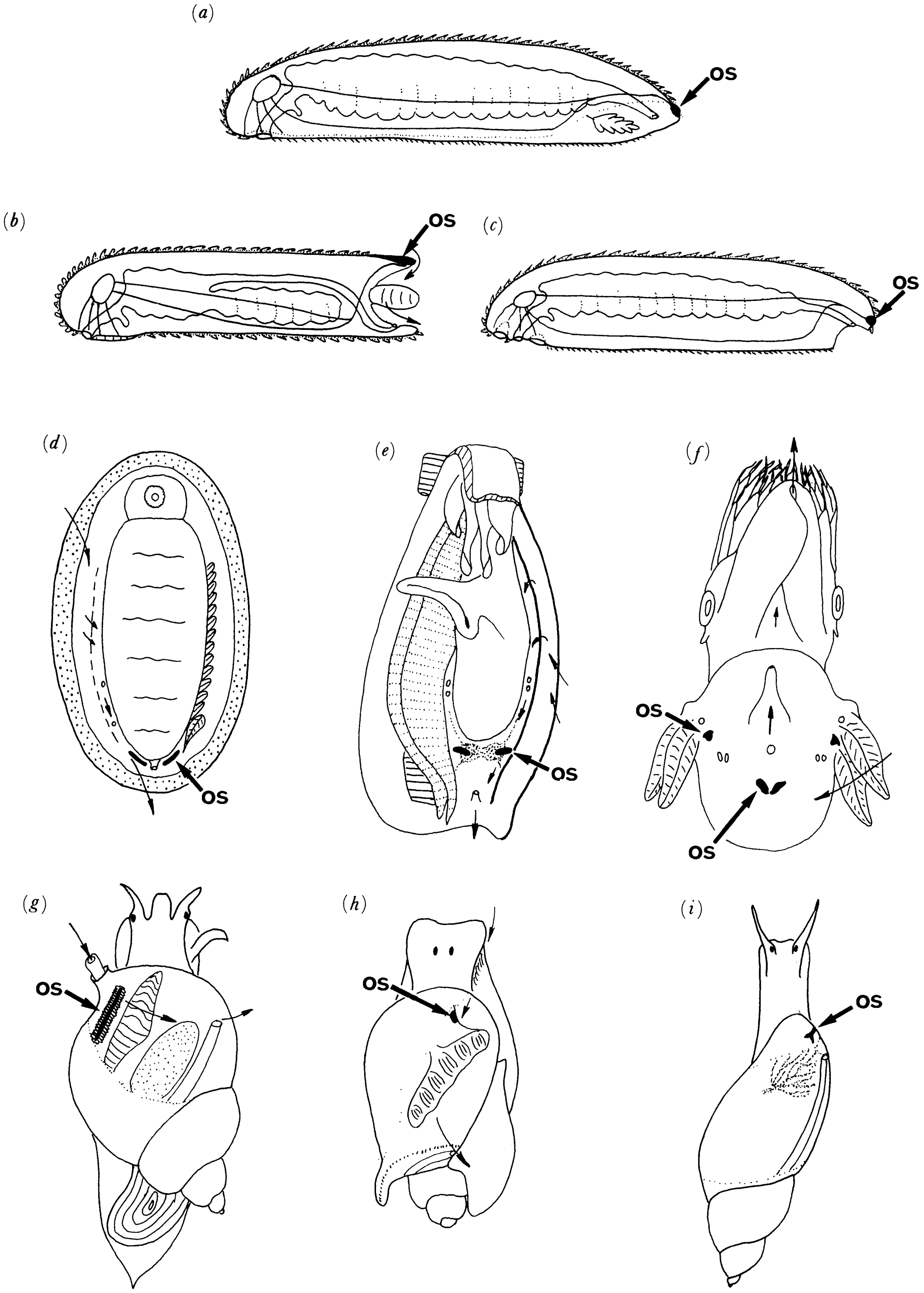

FIGURE 4. Position of the osphradium (os) in the molluscan classes (water currents are indicated by weak arrows). (*a*) Archetype (hypothetical) lateral view (after Salvini-Plawen 1981). (*b*) Caudofoveata: lateral view (after Salvini-Plawen 1981). (*c*) Solenogastres: lateral view (after Salvini-Plawen 1981). (*d*) Placophora: ventral view of a chitonid (after Yonge 1939*a*). (*e*) Bivalvia: ventral view of a mytilid (original). (*f*) Cephalopoda: ventral view of *Nautilus* (after Lankester & Bourne 1883). (*g*) Gastropoda – Prosobranchia: dorsal view of a neogastropod (after Lang & Hescheler 1900). (*h*) Gastropoda – Opisthobranchia: dorsal view of a philinid (after Hyman 1967). (*i*) Gastropoda – Pulmonata: dorsal view of a lymnaeid (original).

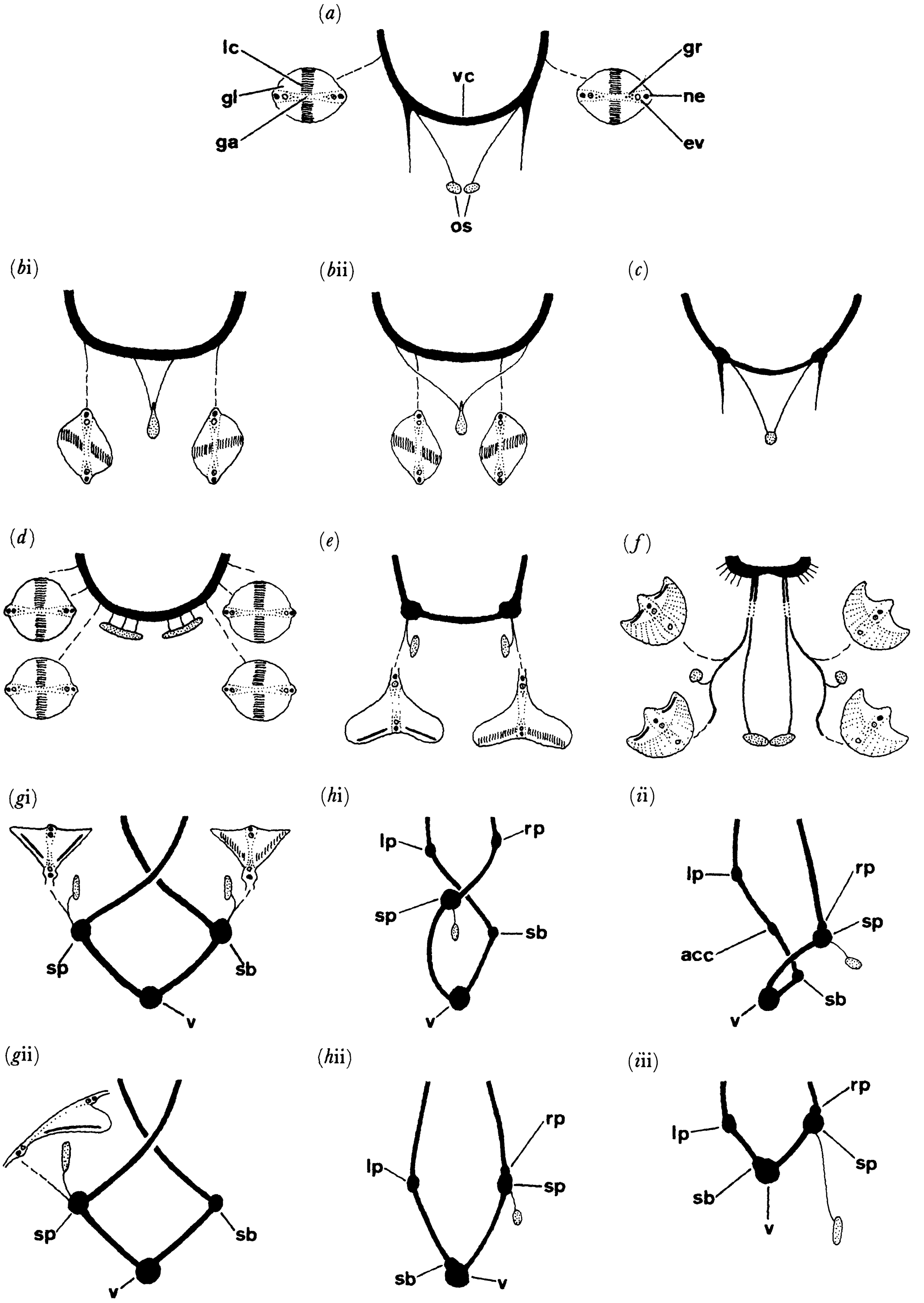

Figure 5. Innervation of the osphradium in the molluscan classes and its position relative to the ctenidia (all drawings are of dorsal view; skeletal rods of ctenidia are included always in the left one). (*a*) Archetypes (hypothetical). (*bi*) *Falcidens hartmanni* (Caudofoveata). (*b*ii) Rest of Caudofoveata. (*c*) Solenogastres. (*d*) Chitonida. (*e*) Nuculida. (*f*) *Nautilus* (Cephalopoda). (*gi*) Zeugobranchia (Prosobranchia 1). (*g*ii) Caenogastropoda (Prosobranchia 2). (*hi*) *Acteon* (*Opisthobranchia* 1). (*h*ii) *Philine* (Opisthobranchia 2). (*ii*) *Chilina dombayana* (Pulmonata 1). (*i*ii) *Lymnaea stagnalis* (Pulmonata 2). (*a*), (*bi*), (*b*ii), (*c*), (*d*), (*e*), (*f*), (*gi*) after Salvini-Plawen (1981); (*g*ii), (*hi*), (*h*ii), (*i*ii) after Hyman (1967); (*ii*) after Plate (1895)). acc, Accessory ganglion; ev. efferent vessel; ga, gill axis; gl, gill lamella; gr, gill retractor muscle; lc, lateral cilia; lp, left parietal ganglion; ne, efferent gill nerve; os, osphradium; rp, right parietal ganglion; sb, suboespophageal ganglion; sp, supraoesophageal ganglion; v, visceral ganglia; vc, visceral commissure.

(Plate 1901, p. 428), appears improbable in the light of the largely accepted theory of a multiplication of ctenidia. Ontogenetical results are needed for elucidation, but there are two main arguments to deny a homology of the branchial sense organs with the osphradia.

(i) Hammarsten & Runnström (1926) described branchial sense organs in juvenile *Acanthochiton discrepans* which also has a true osphradium.

(ii) Fine ultrastructural observations have shown that the sensory epithelium is very weakly developed. It is obvious that the efferent ctenidial nerve also supplies its overlying epithelium, and this has been found likewise in ctenidia of other chitons (*Chiton olivaceus* and *Acanthochiton communis*, personal observation). In addition, the efferent side of the ctenidial axis of Acmaeidae (Thiem 1917) and Valvatidae (Bernard 1890) were also erroneously said to be osphradia, although there are true osphradia present in these prosobranchs (see Haszprunar 1985*a*).

Thus, the branchial sense organs of the Lepidopleurida are suggested to be secondary structures. Together with the lateral sense organs, both situated in the inhalent current, they might have substituted the function of the osphradium, whatever this may be (see below).

Placophora: *Chitonida* (*figures* 4*d*, 5*d*)

Despite multiplication of the ctenidia, the conditions of the chitonid mantle cavity appear to be very primitive. This also refers to the paired osphradia (= adanal sensory stripes) located on the roof of the mantle cavity in the exhalant current left and right of the anus. They are innervated by a series of nerves from the suprarectal commissure. They are said to be reduced in some species (Plate 1901, p. 426).

Galeroconcha: *Neopilina*

Lemche & Wingstrand (1959) did not describe osphradia in *Neopilina galatheae*: possibly they overlooked them. Further investigations on other species of the Tryblidiida also, will show whether they are really absent; whether there is only one pair of osphradia (as in the Chitonida), or whether they have been multiplied together with the ctenidia and excretory organs (as in *Nautilus*, see below).

Bivalvia (*figures* 4*e*, 5*e*)

The Bivalvia (especially the genus *Nucula*) have retained several primitive conditions of the mantle cavity (one pair of ctenidia, homogeneous mucous tracts = hypobranchial glands). The paired osphradia are situated lateral or ventral to the ctenidial nerve or the visceral ganglion.

Recently, Kraemer (1979, 1981) denied a homology of the bivalve osphradium with that of other molluscs: owing to the somewhat modified conditions found in the freshwater species (*Corbicula*, *Lampsilis*) that she studied, the sense organs would not be comparable to the osphradia in the gastropods. This neglects, however, the fact that the osphradial conditions of the most primitive Protobranchia are almost identical to those found in the Chitonida (figures 4*d*, *e* and 5*d*, *e*, and Salvini-Plawen 1981): both are placed on the roof of the mantle cavity, are supplied by nerves from the visceral commissure, are located in the exhalant current, and are still paired.

There is some variation within the Bivalvia in the innervation of the osphradia. Primitively supplied by a ganglionic layer of the ctenidial nerve, they are in many species directly innervated by the visceral ganglion (see Stork 1934; Kraemer 1981), and in the Myina cerebral nerves also take part on the innervation of the osphradia (Pelseneer 1891; Dakin 1910). Nevertheless, the conditions represented in *Nucula* and other Protobranchia strongly support the homology of the bivalve osphradia with those of the other classes. Osphradia are not found in the septibranchs (personal observation) and are possibly reduced in all Anomalodesmata.

Scaphopoda

Distaso (1906) described an osphradium in several *Dentalium* species; however, there are at present no confirmatory reports by other authors. My own investigations of *Dentalium dentale* (Dentaliidae), *Entalina quinquangularis*, and *Cadulus subfusiformis* (Siphonodentaliidae) have also failed to detect any sensory epithelium in the respective area. Therefore scaphopods are thought to lack osphradial sense organs.

Cephalopoda: *Nautilus* (*figures* 4*f*, 5*f*)

Since the original description by Lankester & Bourne (1883) there is general agreement that the interbranchial papillae of *Nautilus* are true osphradia. They are situated in the exhalant current and are supplied by a side-branch of the ctenidial nerve.

Whether or not the fused postanal papillae can be regarded as osphradia, as by Willey (1898), is still a matter of debate. Lankester & Bourne (1883) and Pelseneer (1899) denied such a homology, but without stated arguments. There is a difference in that the postanal papillae are supplied by nerves directly originating from the visceral commissure. Since, however, all (paired) organs and openings of the nautilid mantle cavity (ctenidia, mucous tracts = nidamental glands, nephroducts, coelomoducts) are doubled, it is very probable that the osphradia are likewise doubled. Nevertheless, further fine structural comparative investigations on the interbranchial and postanal papillae are needed to decide this question.

Gastropda: *Prosobranchia* (*figures* 4*g*, 5*g*i, 5*g*ii):

By torsion of the mantle cavity the osphradia have become situated at the anterior end of the animal, lying there in the inhalant current. It is to be stressed that the Gastropoda (but not the other classes) are the exception in that respect, and this is also the reason for the great elaboration of the osphradium in this group. The osphradia are still paired in the Zeugobranchia and Docoglossa: in all other groups the (post-torsional) right osphradium has been reduced together with the right ctenidium, probably independently evolved in Trochoidea, Neritoidea and Pectinibranchia (Salvini-Plawen 1980). Since it is placed beneath the ctenidial axis in Docoglossa, Neritopsina and Pectinibranchia, its position at the efferent side of the ctenidial axis in the Vetigastropoda (Fissurelloidea, Pleurotomarioidea, Trochoidea, see Salvini-Plawen (1980), Salvini-Plawen & Haszprunar (1987)) appears a secondary phenomenon. Within the higher Caenogastropoda it forms a large organ, formerly also called false gill (fausse branchie).

The paired osphradia are innervated (as are the ctenidia) by nerves from the supra- and suboesophageal ganglion (all ganglia of the visceral = lateral cord of the Conchifera are together homologous with the visceral commissure of the lower classes, but cannot be homologized among each other, because they represent independent concentrations. Consequently the remaining left osphradium is supplied by the supraoesophageal ganglion (figure 5*g*ii). Owing to the increasing importance of the osphradium within the gastropods this correlation is very strongly fixed throughout the class.

Gastropoda: *Opisthobranchia* (*figures* 4*h*, 5*h*i, 5*h*ii)

Owing to a burrowing mode of life, the mantle cavity in primitive Opisthobranchia is detorted step by step (the genus *Acteon* shows a very archaic condition, see figure 5*h*i), and the original left osphradium becomes located to the right side, but still placed in the inhalant current. In all species where present (it is reduced in many higher opisthobranchs) it is innervated by the supraoesophageal ganglion. Functionally, it is more and more replaced by the organ of Hancock, of similar structure (Edlinger 1980), or by the rhinophores.

Gastropoda: *Pulmonata* (*figures* 4*i*, 5*i*i, 5*i*ii)

In any attempt to trace the evolution of the pulmonate mantle cavity and nervous system, the interpretation of the homology of the osphradium (= organ of Lacaze) must be considered. Thus Hubendick (1947, 1978) favouring the so-called zygosis hypothesis, has denied the homology of the pulmonate osphradium with the left osphradium of the Prosobranchia. Recently, however, it has been shown in detail (Haszprunar 1985*c*) that:

(i) the mantle cavity of the basommatophorous Pulmonata is homologous with that of opisthobranchs and thus also with that of prosobranchs (mainly on the basis of common ciliary tracts and a pallial kidney);

(ii) the pulmonate mantle cavity can be regarded as semi-detorted: only the inhalant chamber is shifted, whereas the exhalant one is still placed as in prosobranchs owing to a functional pneumostome; this is especially demonstrated by the intermediate conditions found in the nervous system of *Chilina dombayana* (figure 5*i*i, and Plate 1895);

(iii) the osphradium as well as the gill (regarded as homologous with that of siphonariids and basal opisthobranchs) have shifted outside the mantle cavity in the Branchiopulmonata (= higher limnic Basommatophora); this is demonstrated by ontogenetical differentiation (Pelseneer 1901).

Within the Pulmonata, the osphradium is thus always supplied by the supraoesophageal ganglion; this is also true in Stylommatophora where it can still be seen during embryogenesis (Pelseneer 1901).

On the function of the molluscan osphradium

The opinions advanced so far on the function of the molluscan osphradium are listed in table 2, mainly including such as are historically important or based on experimental data. It appears beyond question that the osphradium of the higher Caenogastropoda is used in the search for food. The osphradium in all other classes is placed, however, at the posterior end of the body of the animals and located in the exhalant current, a condition which is most probably primitive (see figure 4). Accordingly, it is obvious (i) that the osphradium must have another primary function and (ii) that there has been a change (or enlargement) of function within the gastropods.

The opinon of Yonge (Hulbert & Yonge 1937; Yonge 1939*a*, 1947, 1977; Kraemer 1981) who regards the osphradium primarily as a mechanoreceptor to detect sediment liable to block the mantle cavity, has strongly influenced other workers. There are, however, several arguments contradicting the hypothesis of a mechanoreceptive function of the osphradium.

(i) A protection receptor located in the exhalant current (as in Chitonida, Bivalvia, and *Nautilus*) is ineffective. In addition, there are other sense organs in the inhalant current (anterior

Table 2. Dates and opinions on the function of the osphradium

systematics: genus	basis of data	suggested receptor type	suggested function	references
ollusca general	water currents within the mantle cavity	primarily a mechanoreceptor	detecting invaded sediment	Hulbert & Yonge (1937), Yonge (1939*a*, 1947, 1977)
acophora general	anatomy, histology	chemoreceptor	testing water	Plate (1901)
valvia				
Mytilus	electrophysiological experiments	?	regulating activity of gill cilia	Aiello & Guideri (1964, 1965)
Unio, *Anodonta*	electrophysiological experiments	chemoreceptor, osmoreceptor	?	Sokolov & Zaitseva (1982)
Lampsilis, *Corbicula*	anatomy, histology	light receptor	regulating reproductive season	Kraemer (1981)
astropoda general	anatomy, histology	chemoreceptor	testing water	Spengel (1881)
osobranchia general	anatomy, histology	chemoreceptor	testing water	Bernard (1890)
Viviparus	anatomy, histology, behavioural experiments	chemoreceptor	detecting food, detecting a mate	Wölper (1950)
Viviparus, *Bithynia*, *Valvata*	anatomy, histology	mechanoreceptor	detecting invaded sediment	Starmühlner (1952)
Alectrion, *Busycon*	behavioural experiments	chemoreceptor	detecting food	Copeland (1918)
Nassa	behavioural experiments	chemoreceptor	detecting food	Henschel (1932)
Nassarius	behavioural experiments	chemoreceptor	detecting food	Carr (1967)
Bullia	behavioural experiments	chemoreceptor	detecting food	Brown & Noble (1960)
Buccinum	behavioural experiments	chemoreceptor	detecting food	Brock (1936)
Buccinum	electrophysiological experiments	chemoreceptor	detecting food	Bailey & Laverack (1963, 1966)
pisthobranchia				
Aplysia	electrophysiological experiments	chemoreceptor, osmoreceptor	measuring osmotic stress	Stinnakre & Tauc (1969)
Aplysia	electrophysiological experiments	chemoreceptor, osmoreceptor	inducing neurosecretion	Jahan-Parvar *et al.* (1968, 1969)
Aplysia	electrophysiological experiments	chemoreceptor	detecting food	Downey & Jahan-Parvar (1972)
ulmonata				
Biomphalaria	behavioural experiments	chemoreceptor	detecting food	Michelson (1960)
Biomphalaria	behavioural experiments	chemoreceptor	?	Townsend (1973*b*)
Planorbarius	electrophysiological experiments	?	?	Bailey & Benjamin (1968)
Lymnaea	electrophysiological experiments	chemoreceptor, p_{O_2}-receptor	inducing air-breathing	Kamardin (1976), Sokolov & Kamardin (1977)

sense organs in Chitonida, siphonal papillae in Bivalvia), which are more suitably located for such a mechanoreceptive function.

(ii) Such a receptor would be strange in cases where the mantle cavity is filled with air (terrestrial Caenogastropoda, higher Basommatophora) or is reduced (Gymnosomata). In all these cases the osphradium is modified in shape, but in no way reduced (Haszprunar 1985*a*, and unpublished).

(iii) All experimental data known so far (see table 2) demonstrate the osphradium not to be a mechanoreceptor, but a chemoreceptor (for bivalves see also Sokolov & Zaitseva 1982).

(iv) In *Arca noae* (and several other Bivalvia–Pteriomorpha) the abdominal sense organs have been shown to be actual mechanoreceptors (Zhadan & Semenkov 1982; Haszprunar 1985*d*). They exhibit an entirely different structure, such as in other mechanoreceptors.

(v) In nearly all osphradia of marine molluscs so far investigated (Haszprunar 1985*a*, *b*, 1987, this paper) paddle cilia are present which are typical of molluscan chemoreceptors (see also Barber & Wright 1969; Storch 1972; Matera & Davis 1982; and for detailed discussion Haszprunar 1985*a*); such paddle cilia are never found in mechanoreceptors.

Recently Kraemer (1981) suggested that the bivalve osphradium is a photoreceptor to regulate seasonal behaviour or reproductive physiology. This hypothesis cannot be accepted, since:

(i) eyes occur in several bivalve groups (also in *Lampsilis*) which appear to be more suitable in that respect;

(ii) Sokolov & Zaitseva (1982) have demonstrated that the bivalve osphradium is chemoreceptive;

(iii) there is no fine structural evidence of photosensory elements.

The suggestion that the osphradium is involved in reproductive biology, however, might be correct, but based on chemoreception rather than on photoreception.

Summing up these arguments it is stressed that:

(i) the osphradium is a chemoreceptor in all classes;

(ii) it is probably not used as a protection receptor, but induces a 'positive' reaction;

(iii) it is primarily not used as a food detector except in higher prosobranchs.

Wölper (1950) was the first to suggest a possible role of the osphradium in sexual biology, based on her experiments with *Viviparus* (Prosobranchia). Later, this has also been discussed by Townsend (1973*a*, *b*) for aquatic pulmonates and by Kraemer (1981, see above) for bivalves, and this hypothesis might well be valid for all molluscan groups (except higher Gastropoda).

There is no doubt that molluscs are primarily gonochoristic and that fertilization primitively occurs outside the animal in the water. Such a gonochoristic organism *must* know whether or not there are gametes of its sexual partner in the surrounding water, since the genital products would be so rapidly dispersed that a high fertilization rate would not be possible. A sense organ, detecting the presence of specific genital products in the water, is not limited in its location within the water current, since spawning (and not a protective reaction) can be induced.

There are no confirmatory experimental results, but some conditions in Placophora and Bivalvia support this hypothesis: in both classes a stimulatory effect has been reported in many cases (summarized by Pearse 1979; Sastry 1979; Andrews 1979). Nelson (1936; Nelson & Allison 1940) showed that sperm proteins influence the frequency of the ciliary beat on the gill of the oyster. Aiello & Guideri (1964, 1965) additionally reported evidence that this frequency is induced by nerve impulses from the visceral ganglion and the branchial nerve. The hypothesis of a pheromone-sensitive osphradium would explain both results. Recently, Munro *et al.* (1983) suggested that the substance inducing sperm release in tridacnid clams is a protein. Also the close connection of the osphradium with the posterior adductor muscle (which was stressed by Kraemer (1981)) may explain the fact that spawning in bivalves is often supported by rhythmic contractions of this muscle (Sastry 1979).

This primary function of the molluscan osphradium appears to be retained in those archaeogastropods which have retained external fertilization: Vetigastropoda, Docoglossa. In some species a stimulation effect has been reported (summarized by Webber 1977), although this was denied by Gersch (1936) and Medem (1945), the latter suggesting a tactile induction. Since both groups are mainly herbivorous, having retained the subradular organ to test food, the osphradium is probably not used as a food-detector. Ctenidial bursicles in the Vetigastropoda (Szal 1971; Haszprunar 1987*a*) and tentacles of the mantle edge in Docoglossa (Phillips 1975) have shown to be responsible for chemical detection of predators, so that this function is also improbable for the osphradia.

With the differentiation of internal fertilization (Cocculinoidea, Neritoidea, Pectini-

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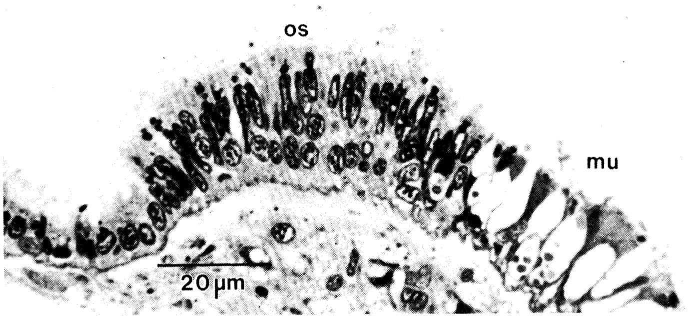

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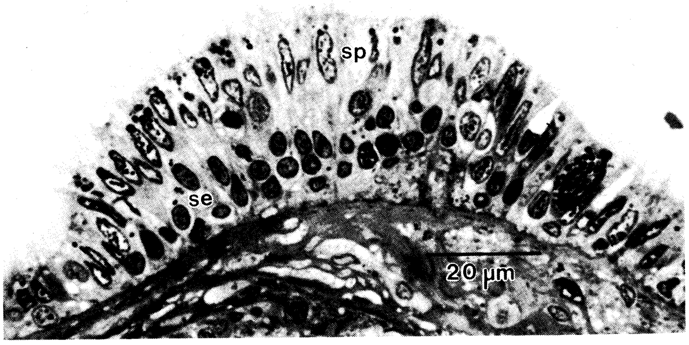

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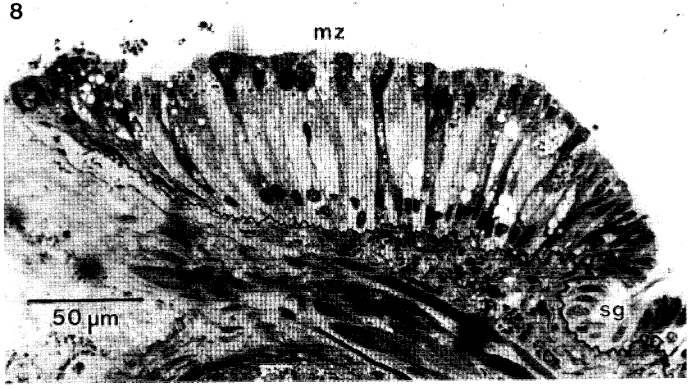

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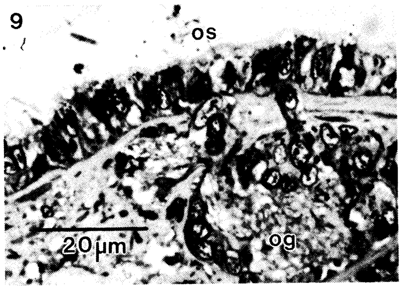

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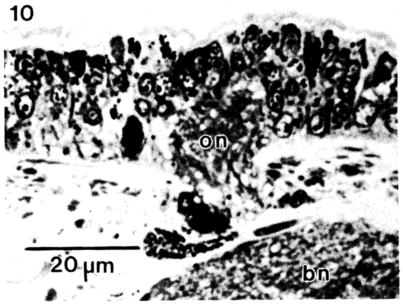

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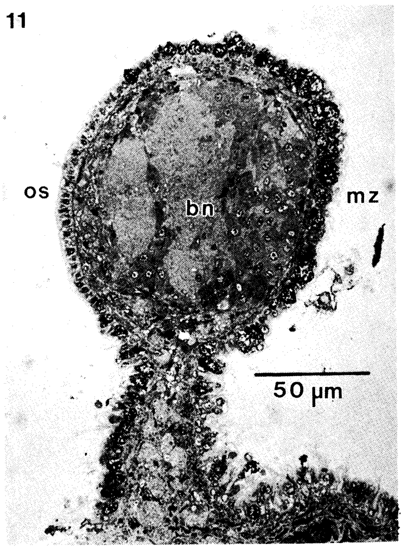


Figures 6–11. Semithin sections of osphradial epithelia.

Figure 6. *Ischnochiton rissoi*.

Figure 7. *Chiton olivaceus*.

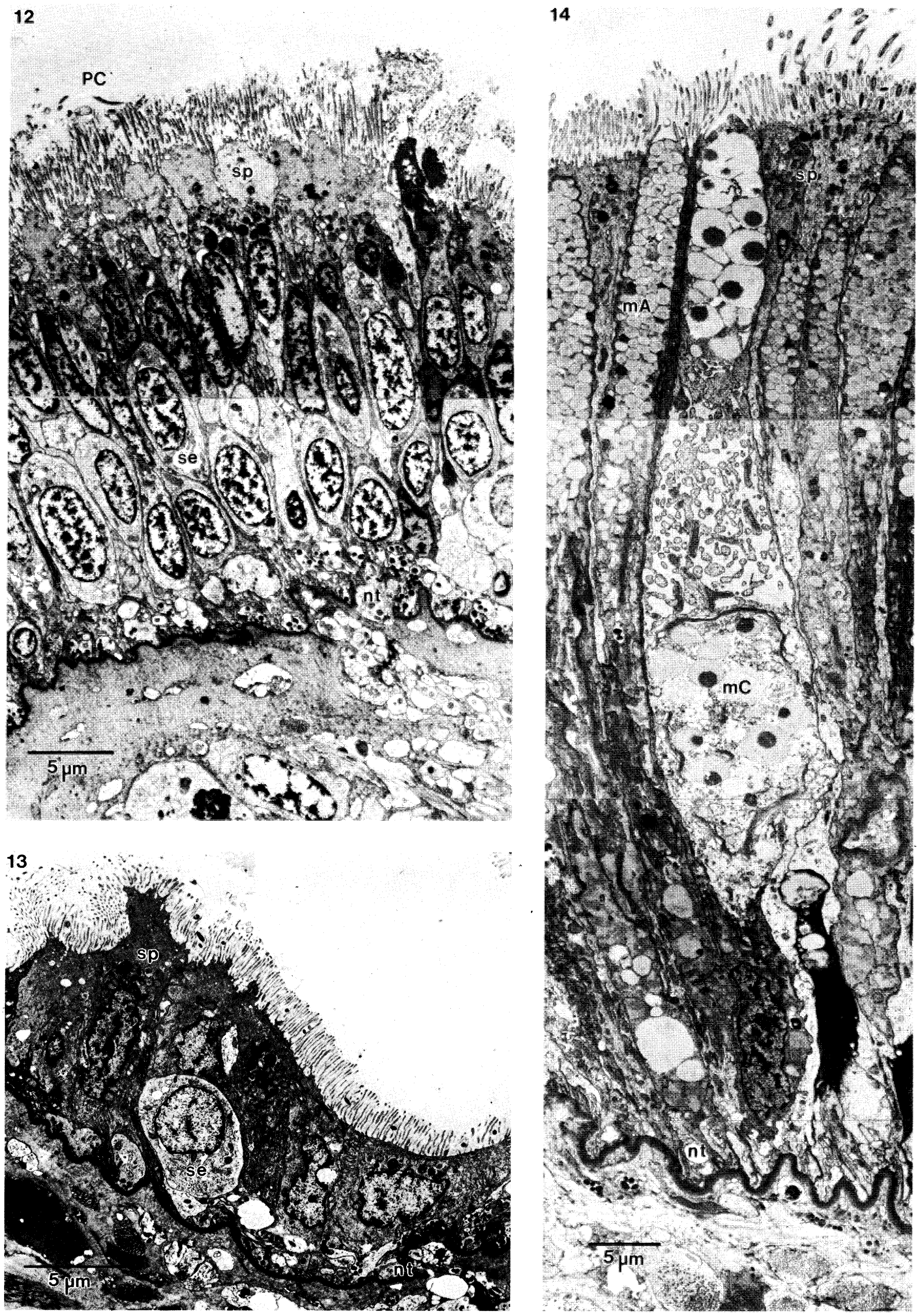
Figure 8. *Acanthochiton communis*.

Figure 9. *Mytilus edulis*.

Figure 10. *Arca noae*.

Figure 11. *Pholas dactylus*.

bn, Branchial nerve; mu, mucus tract; mz, mucus zone; og, osphradial ganglion; on, osphradial nerve; os, osphradial epithelium; se, sensory cells; sg, sensory groove; sp, supporting cells.



FIGURES 12–14. For description see opposite.

Description of plate 2

Figure 12. Section of osphradial epithelium of *Ischnochiton rissoi*.

Figure 13. Section of mantle epithelium of *Chiton olivaceus*.

Figure 14. Section of mucus zone of the osphradium of *Acanthochiton communis*.

mA, mC, Mucous cell of type A, C; nt, nervous tissue; pc, paddle cilia; se, sensory cells; sp, supporting cells.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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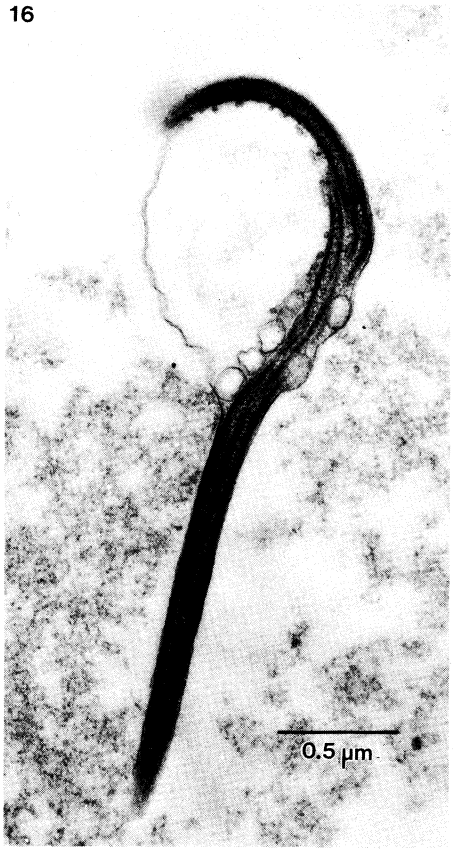

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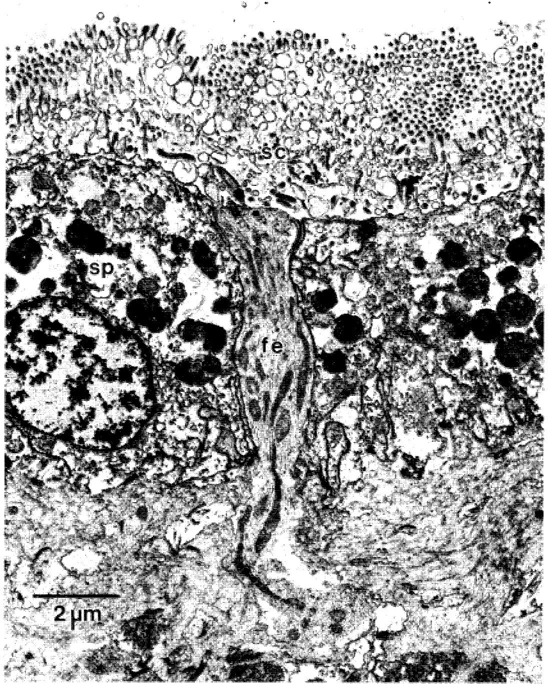

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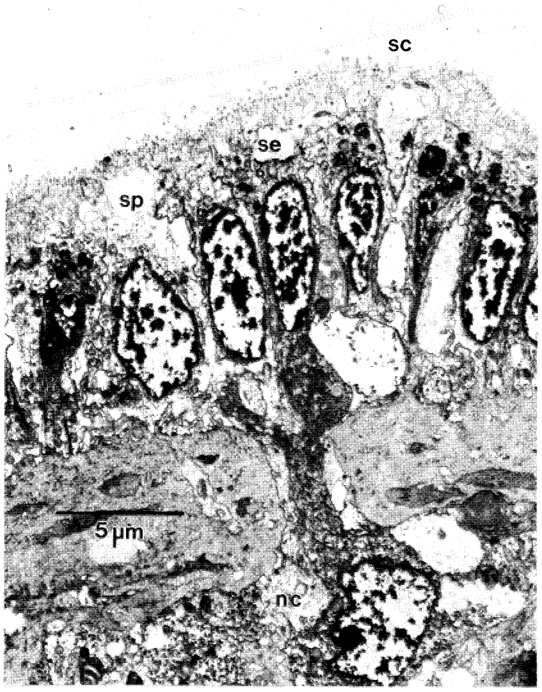

Figures 15–18. For description see opposite.

branchia), the osphradium can additionally or alternatively be used in search of food. Its role in sexual biology is still retained in basal groups (for example *Viviparus*, see Wölper 1950), now in the search for a mate. In higher Caenogastropoda sexual pheromones have been found in several species (Cate 1968; Snyder & Snyder 1971; Dinter 1974; Webber 1977). However, the function of searching for a mate is more or less taken over by the trail-following mechanism of the head tentacles (Peters 1964; Crisp 1969; Wells & Buckley 1972). The osphradium is now predominantly (or exclusively) used as a food detector as demonstrated in many Stenoglossa (see table 2). Such a change of function without a change of the general mode of the receptor (as implied by the hypothesis of Yonge 1977) appears easily possible during evolution.

Owing to the detorsion in the opisthobranchs, the osphradium is functionally replaced by the organs of Hancock (Edlinger 1980) or by rhinophores (Wolter 1967). The conditions in *Aplysia*, the osphradium of which has been shown to be additionally an osmoreceptor (see table 2) are not to be expected in other Opisthobranchia, many of which live deep enough not to be stressed by osmotic changes. Recently, Willan (1983, p. 224) described a special pedal gland in *Pleurobranchaea maculata* which produces pheromones and so draws (by a trail-following mechanism?) sexual partners together to mate. This could explain the reduction of the osphradium in all Eleutherobranchia (= Acoela: Pleurobranchomorpha, Nudibranchia, Anthobranchia) except *Tylodina* (which lacks such glands).

The role of the pulmonate osphradium is still doubtful. The search for a mate in most cases is performed by using the trail-following mechanism (Wells & Buckley 1972; Townsend 1974*a*,*b*). A role as a food-detector, suggested by Michelson (1960), has been denied by Townsend (1973*b*). Bailey & Benjamin (1968) failed to show any special function by electrophysiological methods. Kamardin (1976), and Sokolov & Kamardin (1977) have shown that the osphradium of *Lymnea* measures dissolved-oxygen concentration in the water, controlling air-breathing, but many aquatic pulmonates always live submerged and thus do not need such a receptor. Within more primitive pulmonates (Siphonariidae, Amphibolidae, Chilinidae) the function of the osphradium is unknown.

The presence of the osphradium in the cephalopod genus *Nautilus* alone can be explained in the light of this hypothesis as in all other Cephalopoda the search for a mate is performed visually (Arnold & Williams-Arnold 1977; Wells & Wells 1972, 1977). The pin-hole camera eye of *Nautilus* is certainly more primitive and might usefully be supplemented by a chemical system.

To sum up, the hypothesis presented here, regarding the osphradium as a chemoreceptor primarily used in sexual biology (coordination of spawning, search for a mate) agrees with all the facts so far known. Nevertheless 'experimental work with modern techniques on the osphradium is overdue' (Yonge 1947; p. 512) especially in the lower classes.

Description of plate 3

Figure 15. Section of the epithelium of the lateral sense organ of *Lepidopleurus cajetanus*.

Figure 16. Longitudinal section of a paddle cilium of *Chiton olivaceus*.

Figure 17. Section of osphradial epithelium of *Nucula sulcata*

Figure 18. Section of osphradial epithelium of *Mytilus edulis*.

fe, Nerve process; nc, nerve cell; nt, nervous tissue; pc, paddle cilia; sc, sensory cilia; se, sensory cells; sp, supporting cells.

This work was supported by the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich. I thank Professor L. v. Salvini-Plawen (University of Vienna) for the initiation of the study and for much support throughout. I also acknowledge the kindness of Professor A. Graham (University of Reading), who kindly criticized the manuscript.

Notes added in proof (24 *October* 1986). Salvini-Plawen & Haszprunar (1982) suggested a distinct relationship between the Myina (with cerebrovisceral innervation of their osphradia) and certain Anomalodesmata (with cerebrovisceral innervation of the septum). This view has been recently supported by Morris & Morris (1986) from the palaeontological point of view.

Wingstrand (1985) does not even mention the presence and absence of osphradia in Recent Tryblidiia.

The recent electrophysiological results of Croll (1985) suggest a distinct role of the osphradium of *Aplysia* in regulating respiration by detecting the pH of the sea water near the gill. Thus, there might be a general role of the osphradium with respect to respiration in the euthyneurous gastropods.

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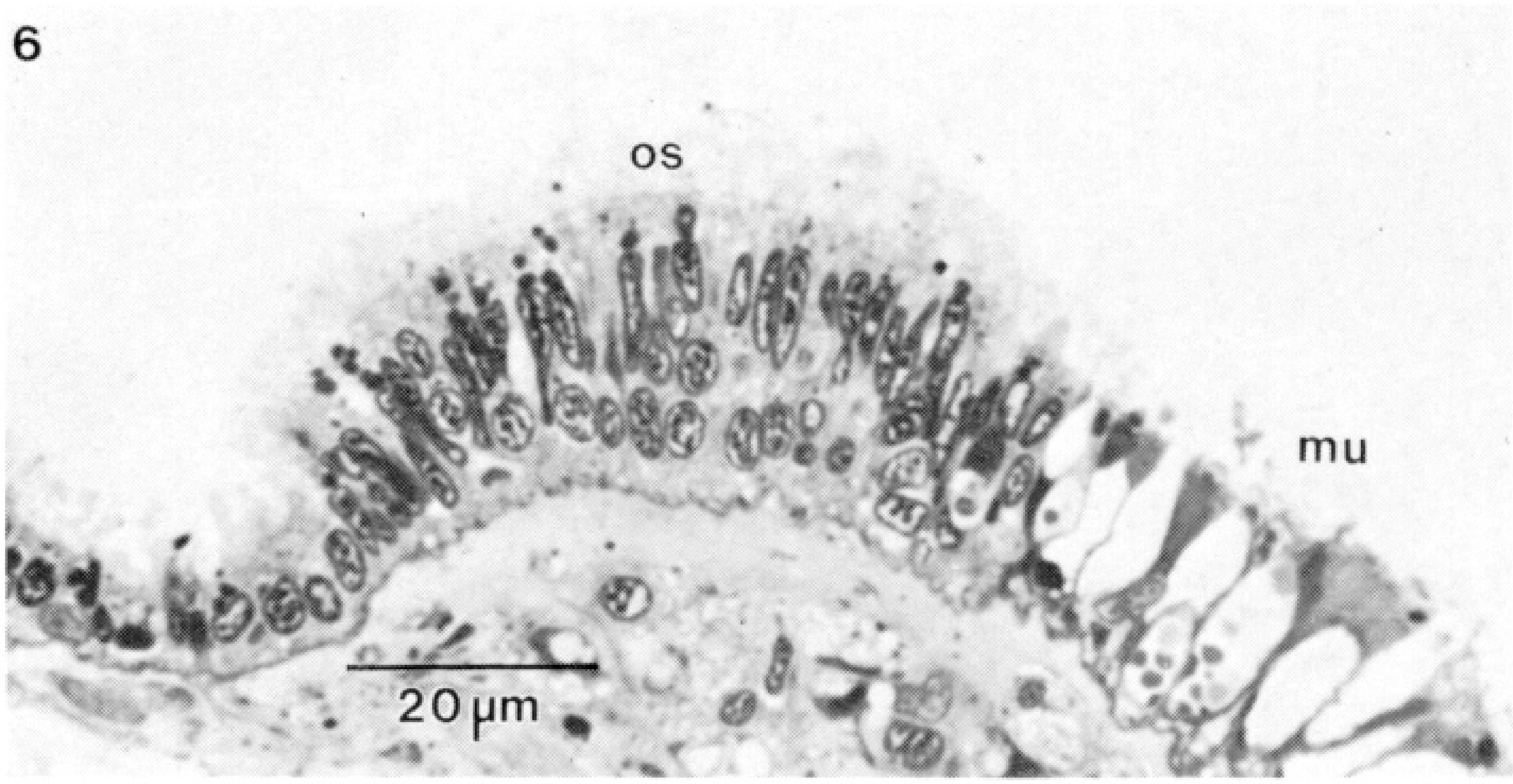

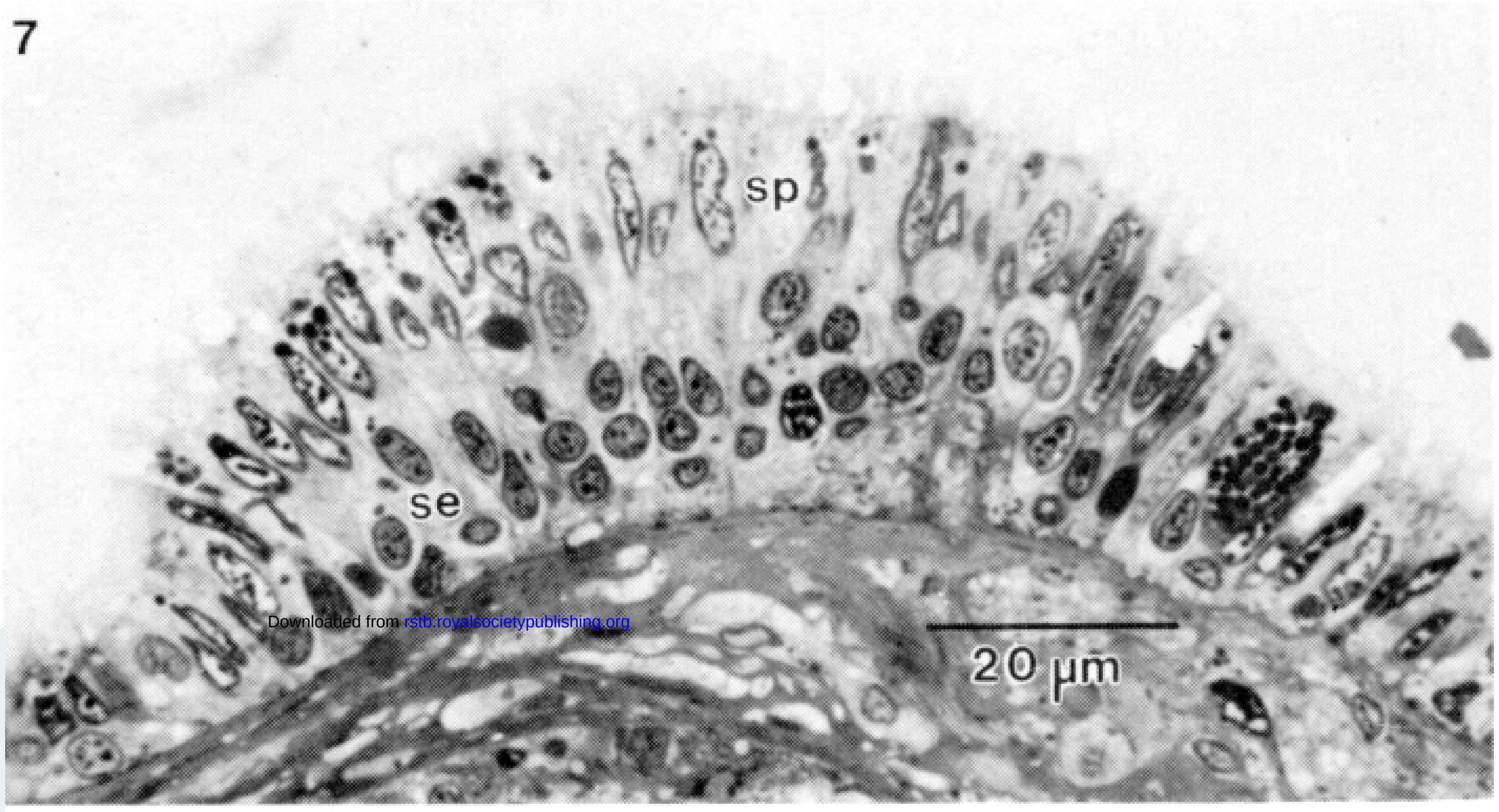

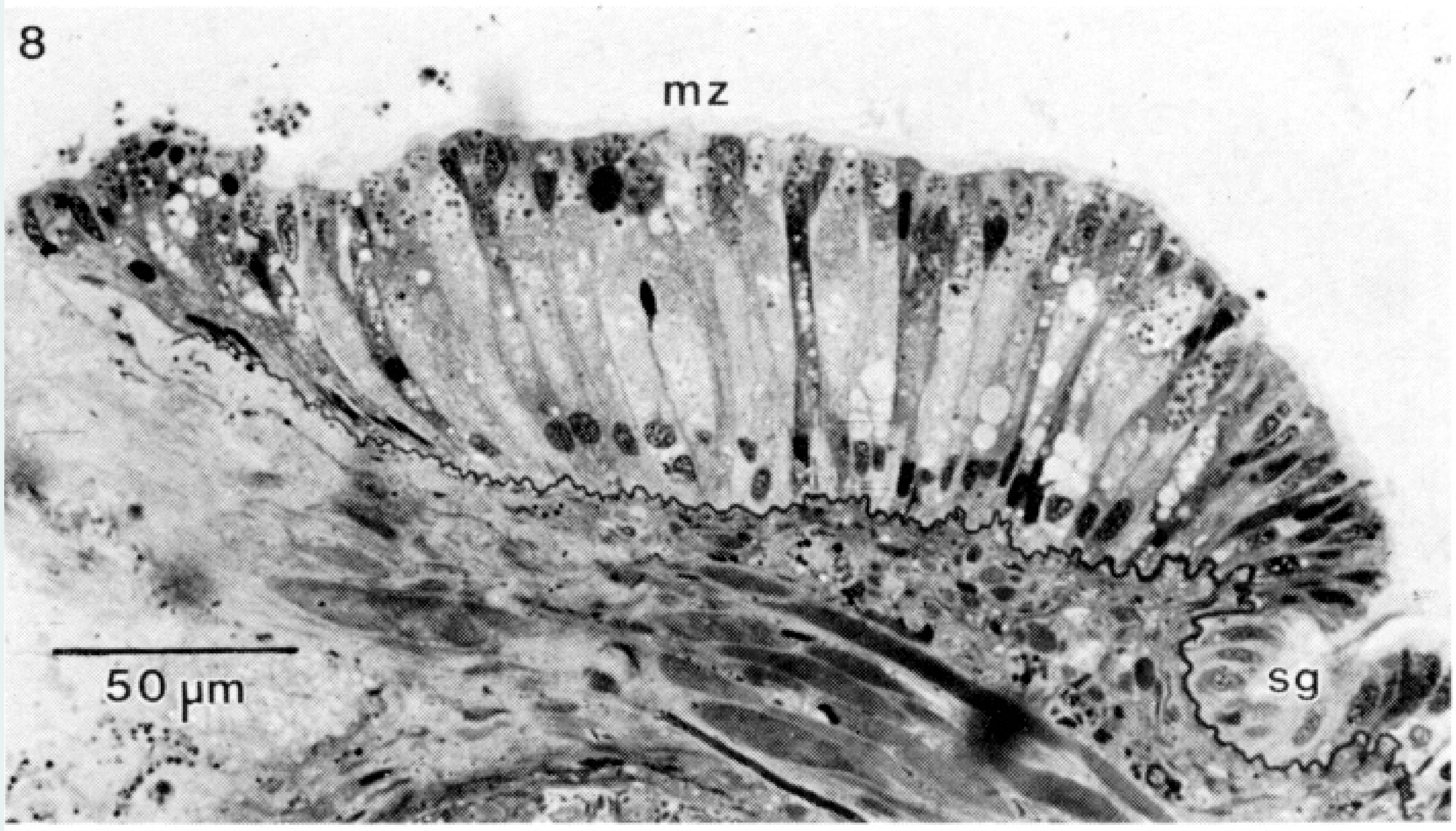

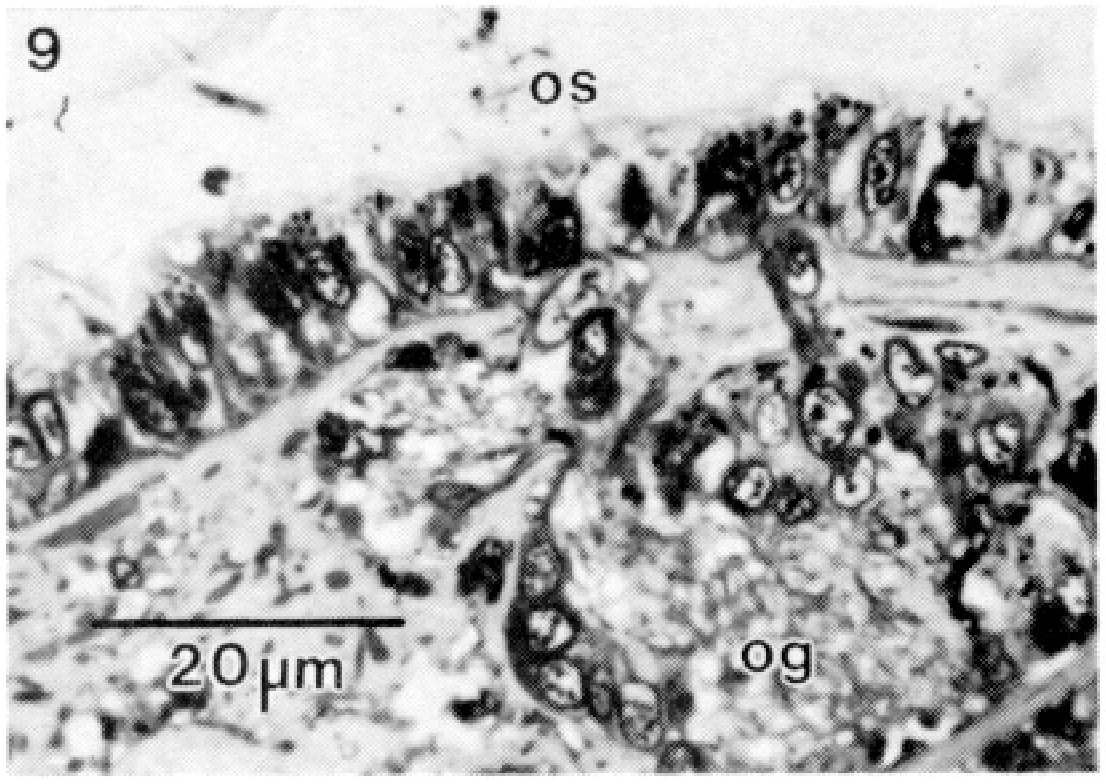

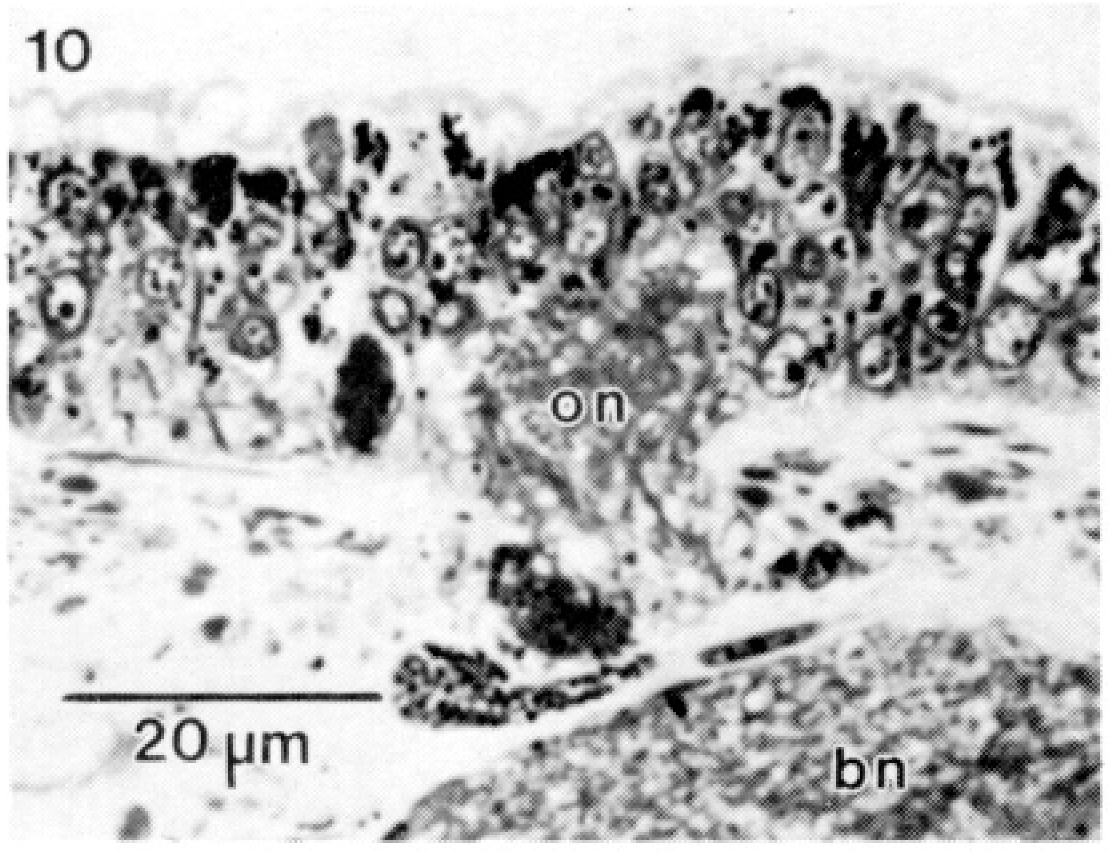

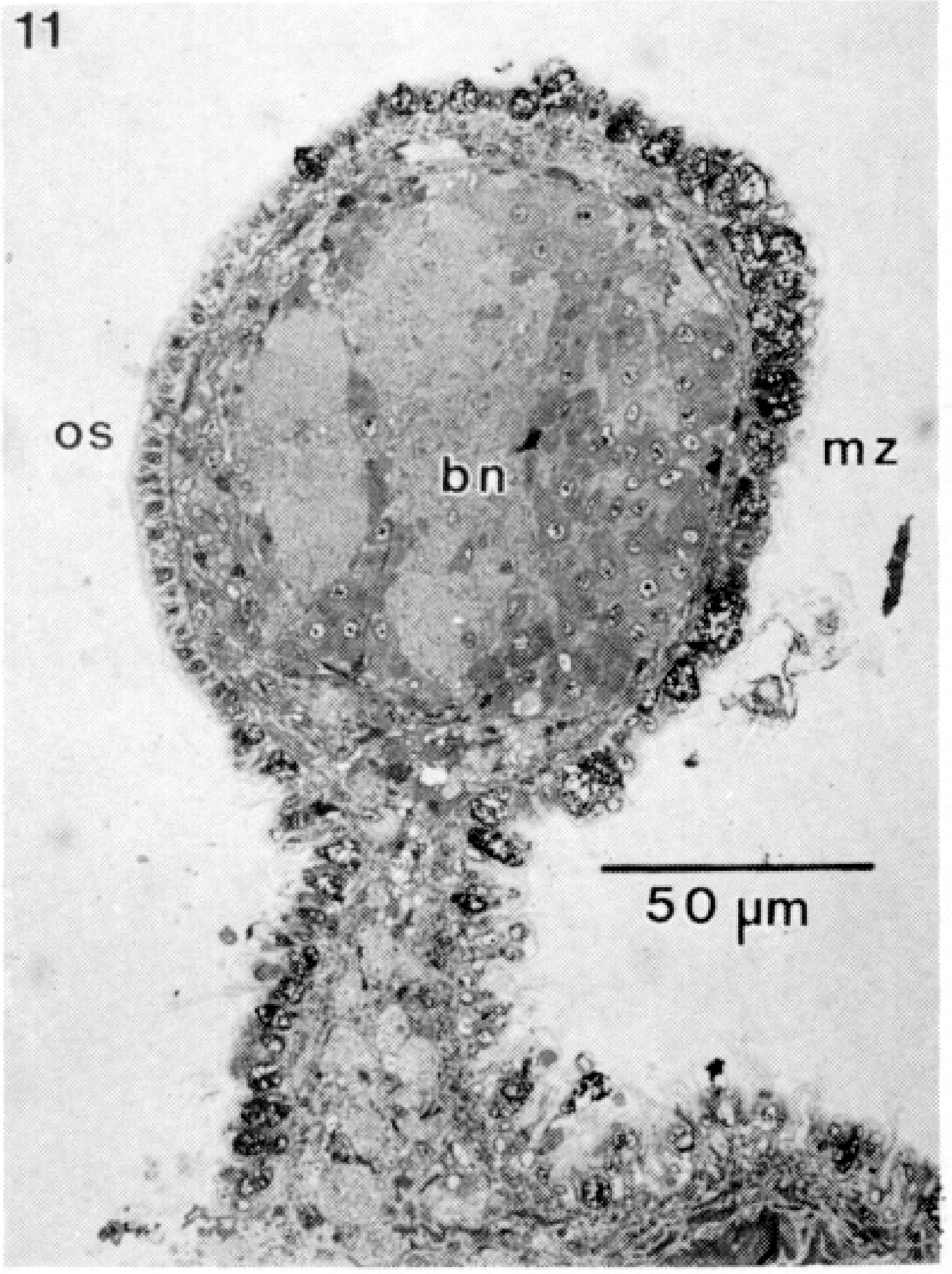

FIGURES 6–11. Semithin sections of osphradial epithelia.

FIGURE 6. *Ischnochiton rissoi.*

FIGURE 7. *Chiton olivaceus.*

FIGURE 8. *Acanthochiton communis.*

FIGURE 9. *Mytilus edulis.*

FIGURE 10. *Arca noae.*

FIGURE 11. *Pholas dactylus.*

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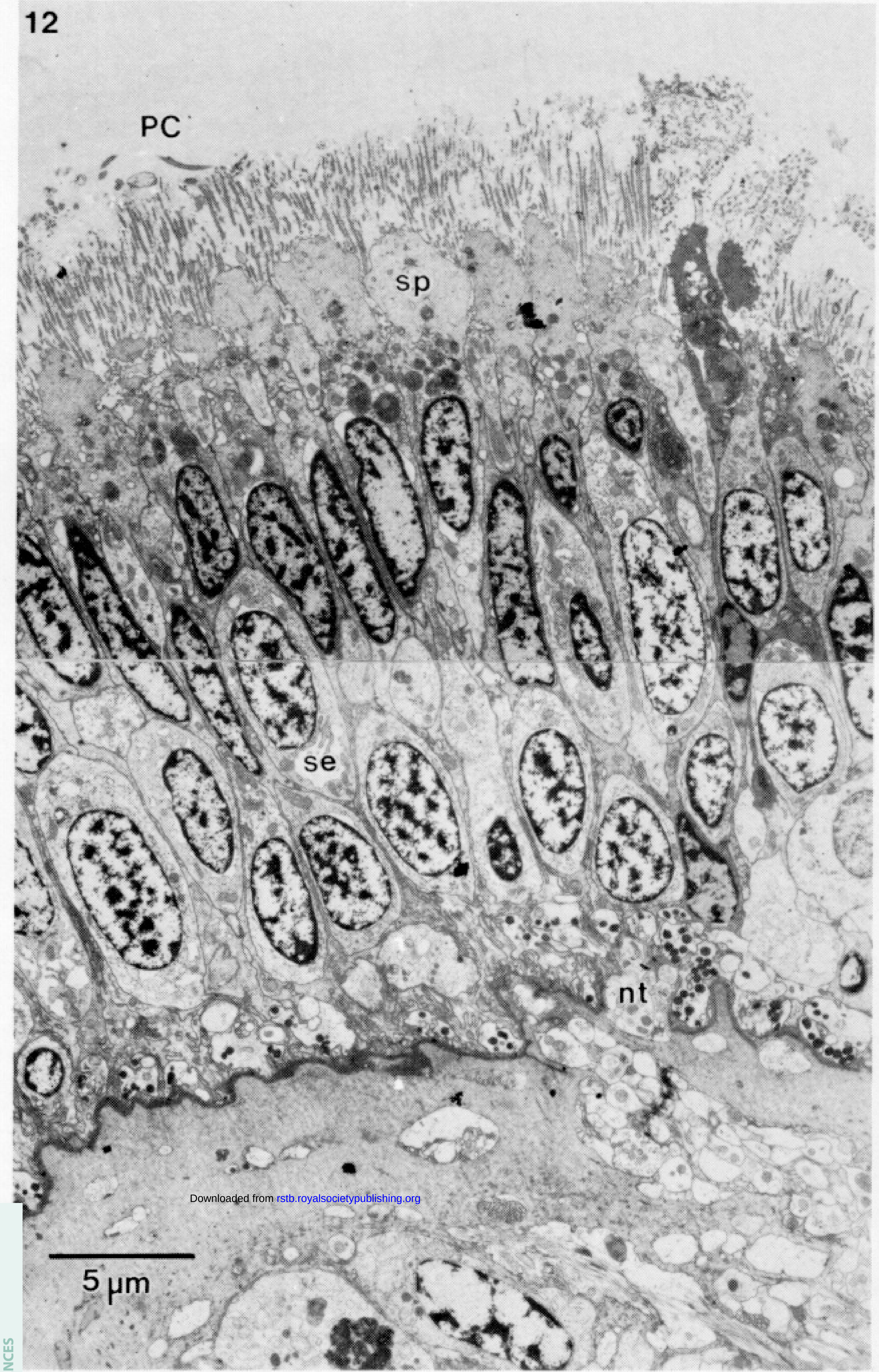
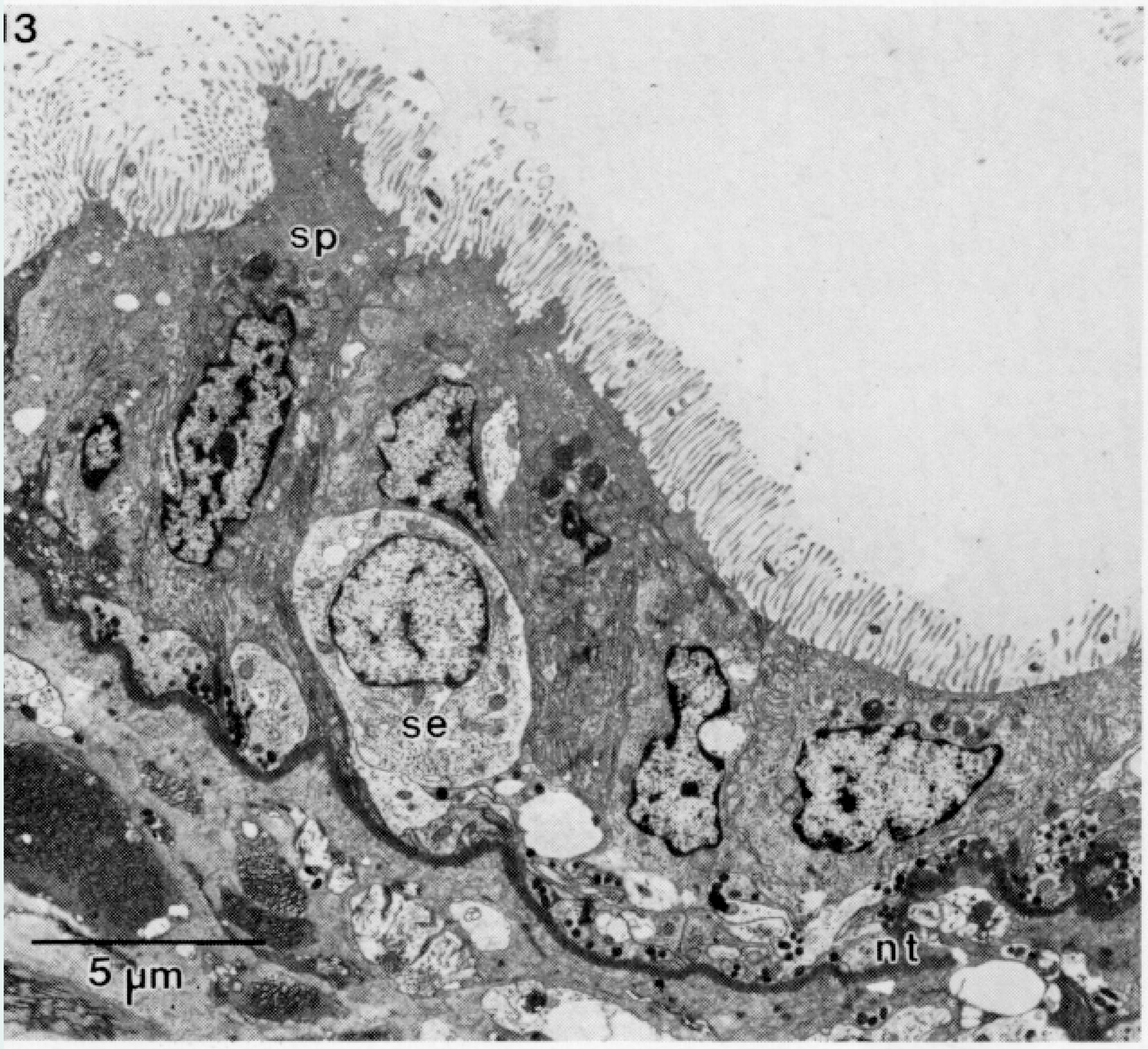
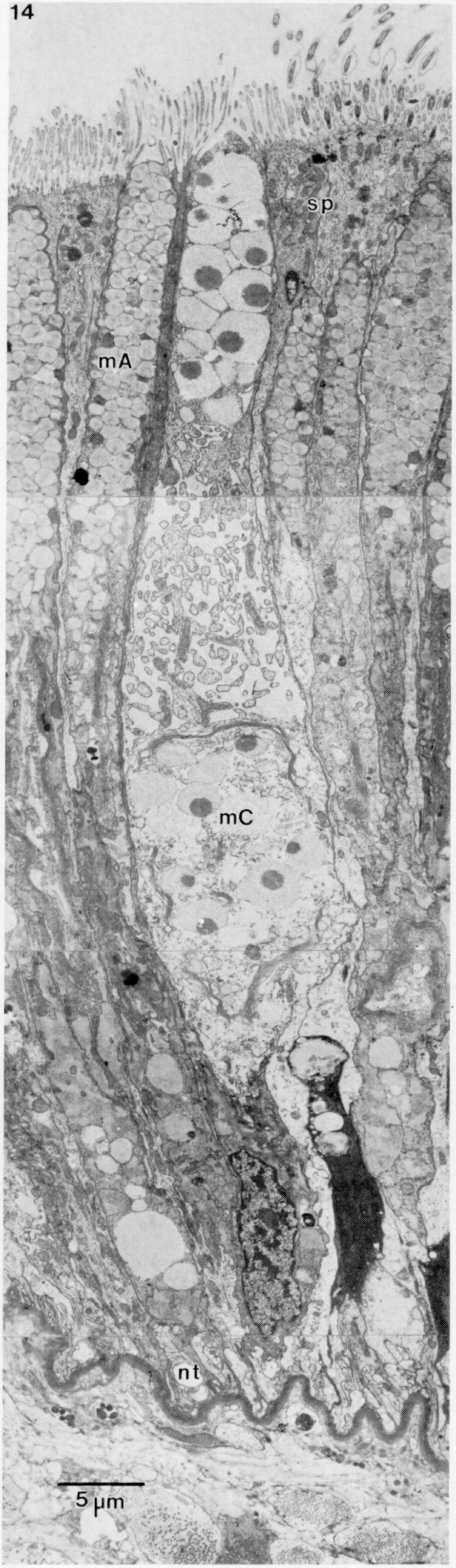


13

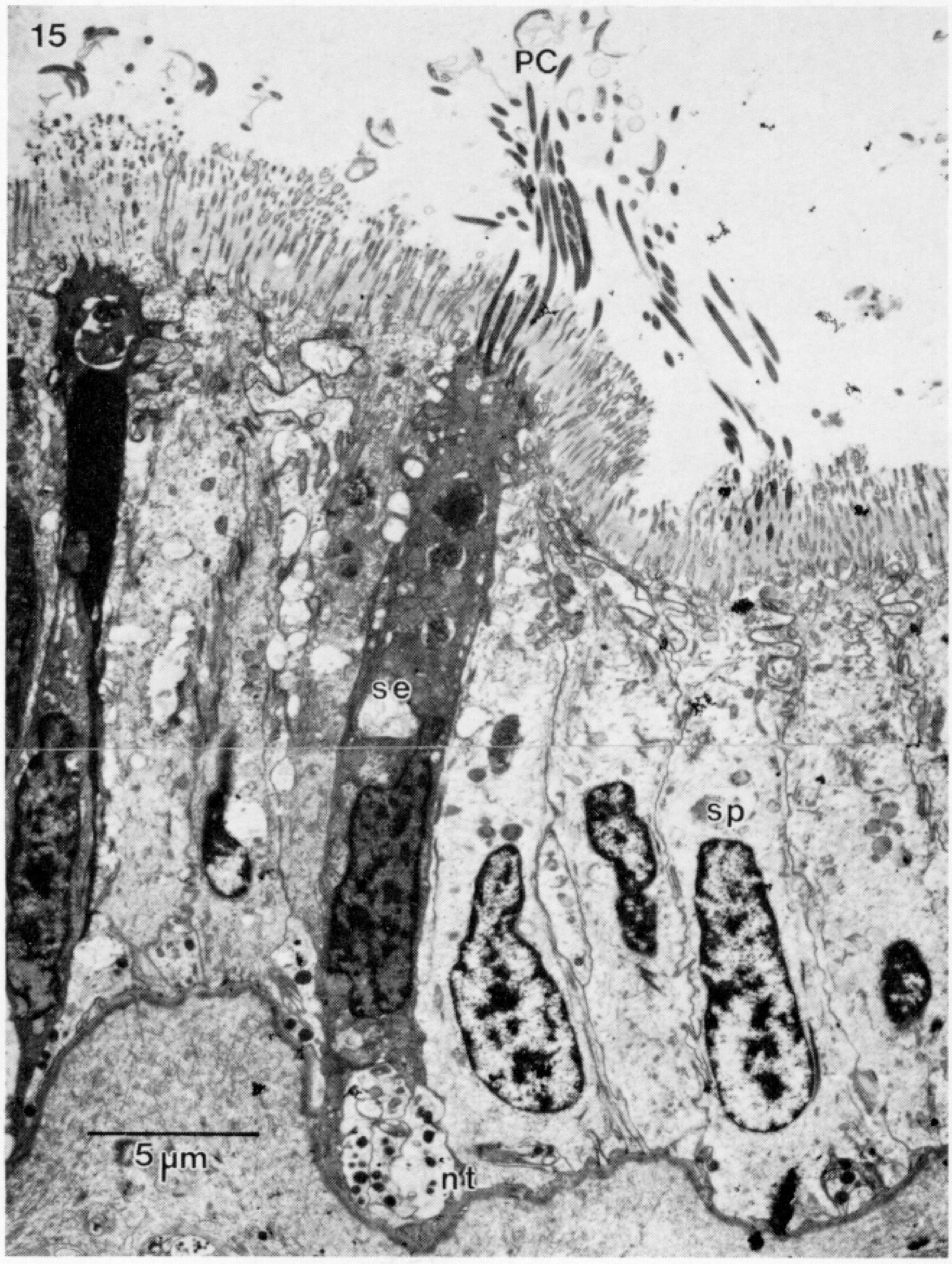


14

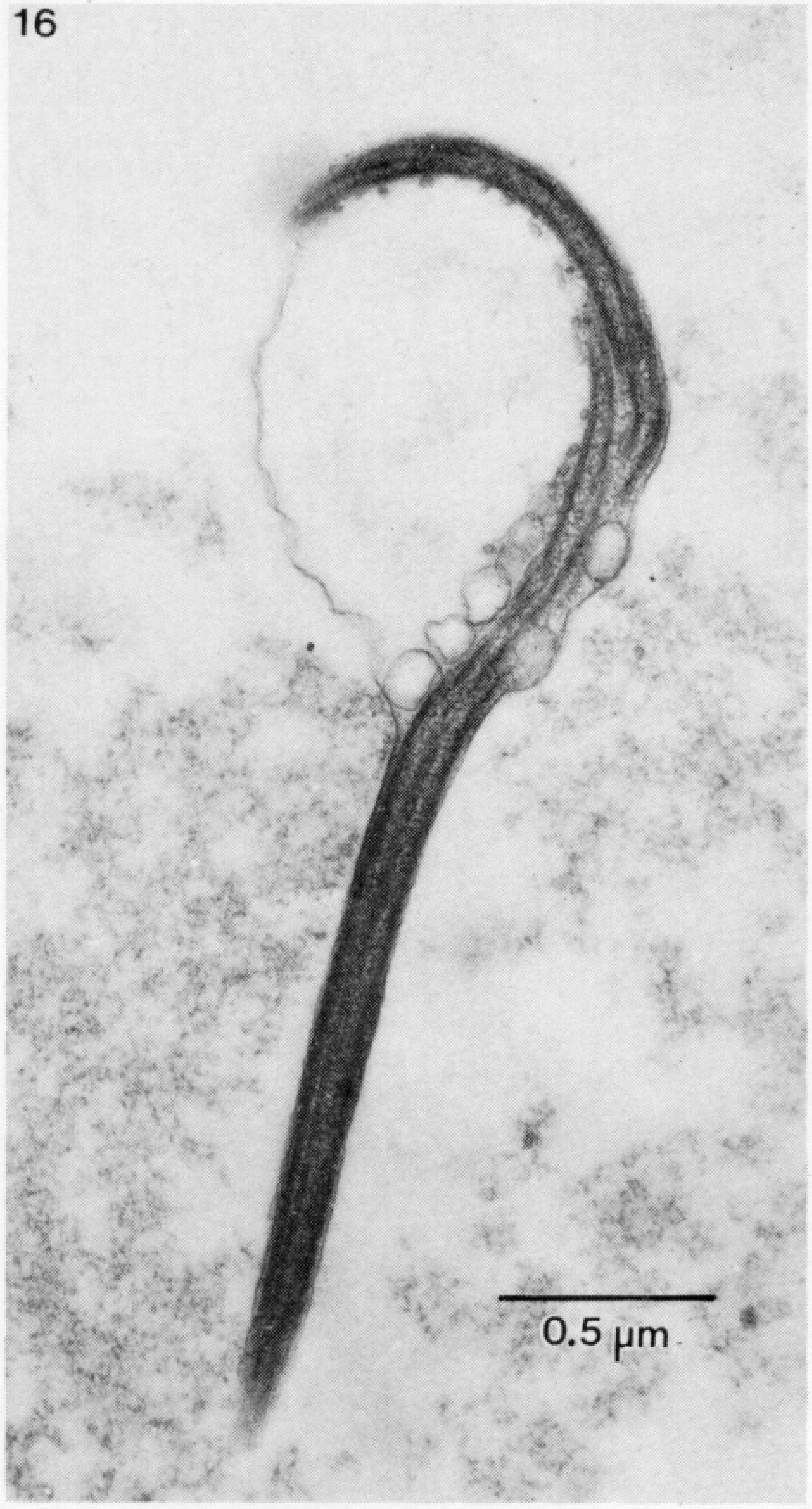


FIGURES 12–14. For description see opposite.

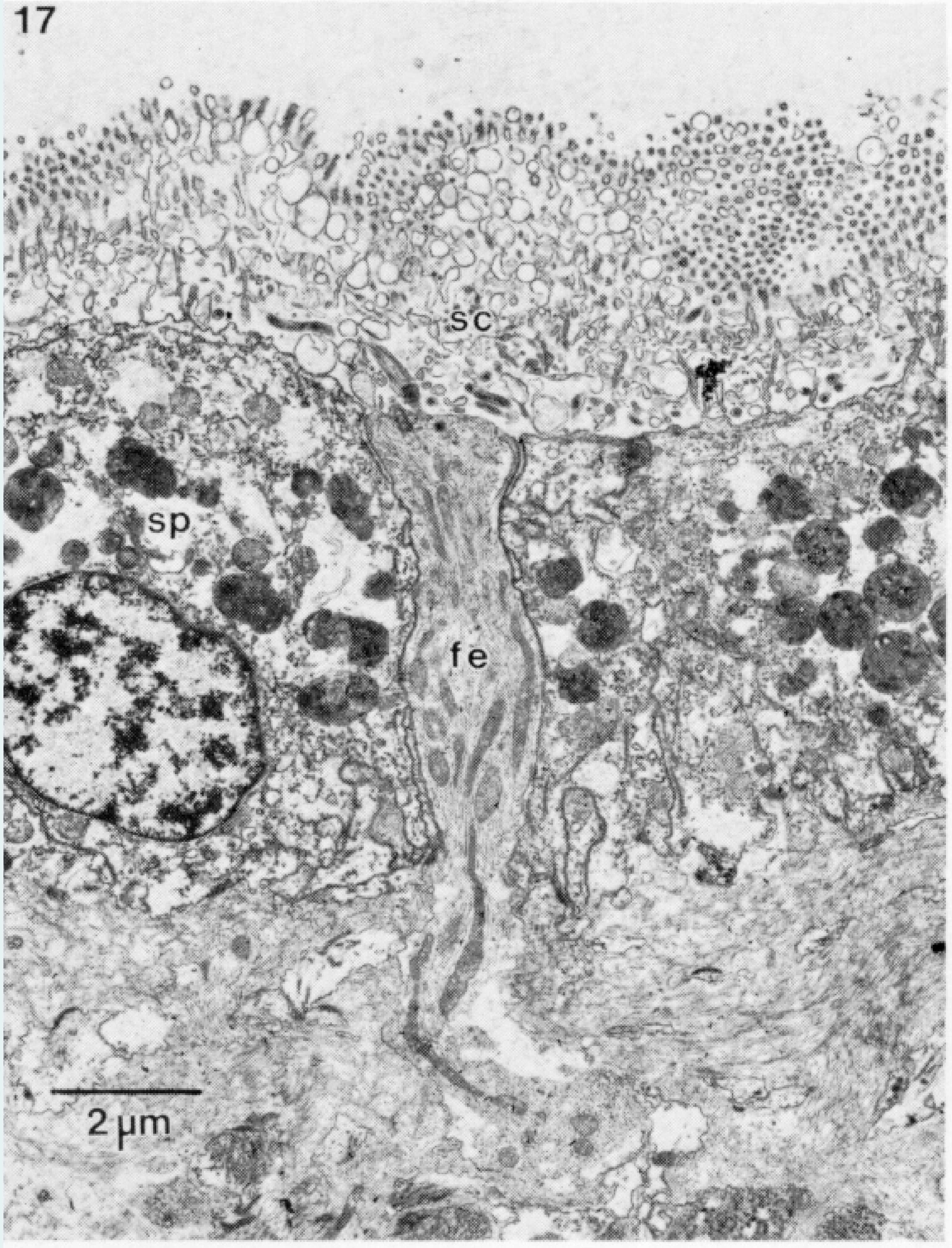
15



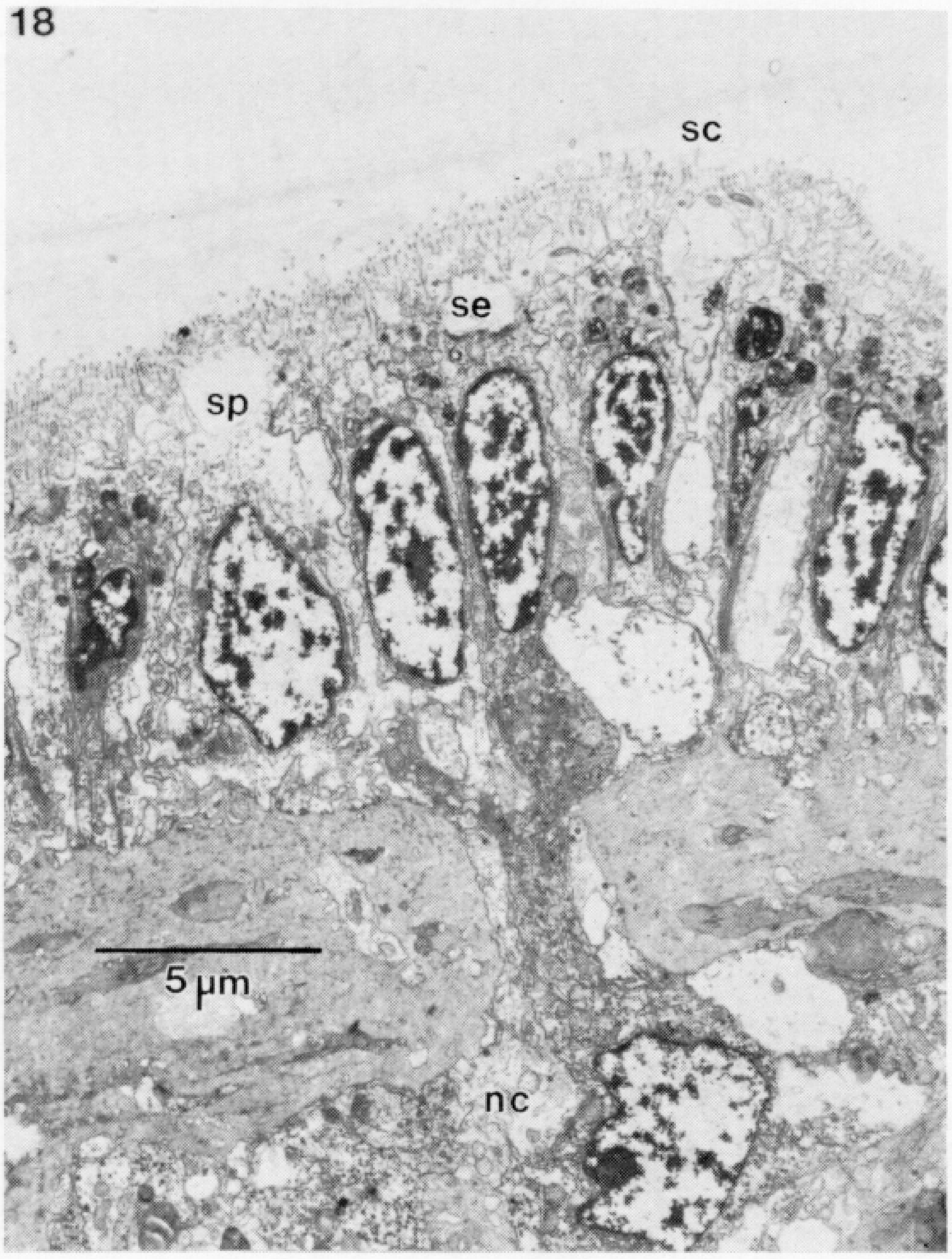
16



17



18



FIGURES 15–18. For description see opposite.