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THE FINE MORPHOLOGY OF THE OSPHRADIAL SENSE ORGANS OF THE MOLLUSCA.
I. GASTROPODA, PROSOBRANCHIA

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[Plates 1–5]

CONTENTS

The comparative ultrastructure of osphradia is investigated in 51 species of prosobranch gastropods, representative of nearly all superfamilies as well as of various habits and environments.

The essential results show that the sensory epithelium of the osphradium as a whole may reflect environmental conditions, whereas the ultrastructure of osphradial cell types reflects actual taxonomic relations. Accordingly, the following taxa can be differentiated on the basis of osphradial fine structure:

(i) the validity of the recently established taxon Vetigastropoda (Pleurotomarioidea, Fissurelloidea, and Trochoidea) is confirmed;

(ii) the Docoglossa appear as a very isolated group;

(iii) the osphradia of the Neritopsina are similar to those of the Caenogastropoda with respect to the organization of the sensory epithelium, but differ in cell types;

(iv) in Valvatoidea the osphradium is indifferently elaborated, and no close relationship to other groups can be stated;

(v) the Viviparoidea possess a special type of osphradium distinct from that of other taenioglossan groups;

(vi) Neotaenioglossa (= Mesogastropoda partly), Heteroglossa (Cerithiopsoidea, Triphoroidea, Epitonioidea, Eulimoidea), and Stenoglossa (= Neogastropoda) represent an (unnamed) monophyletic stock which is characterized by three special cell types with a constant mutual positional relationship within the osphradial epithelium.

On the basis of its structure the function of the osphradium is suggested to be chemoreceptive (also in Archaeogastropoda).

INTRODUCTION

Since the study of prosobranchs by Fretter & Graham (1962), many new data have been collected, providing new theories about prosobranch phylogeny and the origin of the higher subclasses (see, for example, Taylor & Sohl 1962; Golikov & Starobogatov 1975; Salvini-Plawen 1980; Gosliner 1981). New methods have been used to get additional information with respect to anatomy, but in most cases the results do not allow a definite evaluation of systematic relations (for example, Ghiselin *et al.* 1967; Patterson 1967). Recent ultrastructural data on spermatid development have brought new results useful for phylogenetic estimations (Thompson 1973; Healy 1982).

In any attempt to prove that the structure of osphradia will help us to understand prosobranch evolution, it is necessary to demonstrate that:

(i) there are characters that do not depend on ecological factors;

(ii) these characters are sufficiently complex to form a taxobase;

(iii) a taxonomic system based on osphradial structure can be supported by other characters.

This paper shows that the ultrastructure of prosobranch osphradia meets these requirements and thus becomes an important new taxobase for a natural classification of Prosobranchia.

HISTORICAL REVIEW

The osphradium has been described up to this century as a 'false gill' (fausse branchie), but was demonstrated by Spengel (1881) to be a sense organ. The position and innervation of the osphradium were the basic arguments for Spengel's theory that prosobranch streptoneury is due to torsion. Later the osphradium always played an important role in discussions of gastropod phylogeny (for example, Thiem 1917*a*, *b*; Hubendick 1947), but since the attention has been predominantly directed to the structure of the digestive tract and the genital system (for example, Fretter & Graham 1949; Morton 1955; Robertson 1973), and there is no comparative study of osphradia in recent decades to continue the work of Spengel (1881), Bernard (1890), Yonge (1947) and Demal (1955). Although there is some information about the fine structure of prosobranch osphradia (see table 2), most of it relates to the highly specialized Stenoglossa. Up to now there has been no use of osphradial structure in systematics.

The function of the prosobranch osphradium is still uncertain. In the Stenoglossa it has been demonstrated to be chemoreceptive, playing an important role in the search for food (Copeland 1918; Brock 1936; Brown & Noble 1960; Bailey & Laverack 1963, 1966; Carr 1967). The results of Wölper (1950) on *Viviparus* also support this function at the taenioglossan level. There are no results, however, relating to Archaeogastropoda. In contrast to the majority of authors Yonge (1947, 1962, 1977; Hulbert & Yonge 1937) maintains his theory of the primary mechanoreceptive function of the osphradium which appears to be uncontradicted up to now although there are no experimental results to support his opinion.

With respect to all these open questions the present paper gives an account of

(i) the comparative fine structure of osphradia of nearly all prosobranch superfamilies;

(ii) its ecological significance;

(iii) the osphradial cell types, and the systematic significance of these new characters, leading to a better understanding of phylogenetic pathways in Prosobranchia;

(iv) the ultrastructure of the receptor elements and the receptor quality of the prosobranch osphradium.

Material and methods

The species, the osphradia of which have been ultrastructurally investigated, were selected so that (i) they should represent as many superfamilies as possible; (ii) they should include families of uncertain systematic position, and (iii) members of related families or superfamilies should be different in habitat or environment.

The species are listed in table 1, including additional information about their provenance. All species that had already been ultrastructurally investigated by earlier authors are added in table 2 to give complete information on the data available.

The specimens were generally dissected in ice-water (1–4 °C), and pre-fixed for 5 h or, if necessary, up to seven days in a 2.5 % phosphate-buffered glutaraldehyde. After a wash in buffer (Sörensen: NaH_2PO_4-Na_2HPO_4, 0.1 M, pH = 7.3) they were post-fixed for 2 h in a 1–2 % phosphate-buffered osmium tetroxide, rinsed in buffer again, dehydrated in the ethanol series, infiltrated with propylene oxide (twice, 10 min) and embedded in an Epon-Araldite mixture (Mollenhauer 1964).

Very small animals (for example, *Caecum*, *Skeneopsis*) were fixed whole after narcotization or cracking the shells. Pre- and post-fixation were done as described above, but the osmic acid was washed out by a salt solution (NaCl; 0.14 M). To decalcify specimens the method of Dietrich & Fontaine (1975) was adapted: decalcification was done with 1 % ascorbic acid buffered by 0.14 M salt solution for 12–18 h, depending on the thickness of the shell. It is necessary to avoid light during the process, to change the fluid two or three times, and to stir the solution during the decalcification process, otherwise the ascorbic acid will oxidize quickly.

In the case of marine species the local salinity was imitated by adding pure saccharose or salt.

Semi-thin sections (0.5 μm) were stained by 0.1 % toluidine blue; ultra-thin sections (gold–silver interference colour) cut with glass knives, were stained by uranyl acetate and lead citrate and examined by using a Zeiss EM9/S2.

Table 1. Species whose osphradia were investigated

superfamily family	species	source
Pleurotomarioidea		
Haliotidae	*Haliotis lamellosa* Lamarck, 1822	Adriatic Sea (Rovinj)
Fissurelloidea		
Fissurellidae	*Diodora italica* (Defrance, 1820)	Adriatic Sea (Rovinj)
	Scutus unguis (Linné, 1758)	Pacific (aquarium)
	Emarginula elongata O. G. Costa, 1829	Adriatic Sea (Piran)
Trochoidea		
Trochidae	*Gibbula varia* (Linné, 1767)	Adriatic Sea (Rovinj)
Turbinidae	*Astraea rugosa* (Linné, 1767)	Adriatic Sea (Piran)
Phasianellidae	*Tricolia pullus* (Linné, 1768)	Adriatic Sea (Piran)
Patelloidea		
Acmaeidae	*Acmaea virginea* (Müller, 1776)	Atlantic (Plymouth)
Patellidae	*Helcion pellucidum* (Linné, 1767)	Atlantic (Plymouth)
	Patella coerulea Linné, 1758	Adriatic Sea (Rovinj)
Neritoidea		
Neritidae	*Nerita undata* Linné, 1758	Pacific (Samoa)
	Nerita plicata Linné, 1758	Pacific (Samoa)
	Nerita textilis Gmelin, 1791	Pacific (Samoa)
	Puperita pupa (Linné, 1767)	Pacific (aquarium)
	Theodoxus prevostianus (Pfeiffer, 1828)	Lower Austria (Bad Vöslau)
Valvatoidea		
Valvatidae	*Valvata piscinalis* (Müller, 1774)	Lower Austria (Lunz am See)
Viviparoidea		
Viviparidae	*Viviparus contectus* (Millet, 1813)	Lower Austria (Marchegg)
Ampullariidae	*Marisa cornuarietis* (Linné, 1758)	South America (aquarium)
	Ampullarius sp.	South America (aquarium)
Littorinoidea		
Littorinidae	*Littorina littorea* (Linné, 1758)	Atlantic (Plymouth)
	Littorina obtusata (Linné, 1767)	Atlantic (Plymouth)
	Littorina saxatilis (Olivi, 1792)	Atlantic (Plymouth)
	Littorina neritoides (Linné, 1767)	Mediterranean Sea (Naples)
Pomatiasidae	*Pomatias elegans* (Müller, 1774)	Jugoslavia (Krk)
Rissoidea		
Hydrobiidae	*Hydrobia ulvae* (Pennant, 1777)	Adriatic Sea (aquarium)
Bithyniidae	*Bithynia tentaculata* (Linné, 1758)	Lower Austria (Fischament)

Table 1 (*cont.*)

superfamily family	species	source
Rissoidae	*Rissoa* sp.	Mediterranean Sea (aquarium)
Caecidae	*Caecum glabrum* (Montagu, 1803)	Adriatic Sea (Rovinj)
Skeneopsidae	*Skeneopsis planorbis* (O. Fabricius, 1780)	Atlantic (Plymouth)
Cerithioidea		
Turritellidae	*Turritella communis* Risso, 1826	Adriatic Sea (Piran)
Thiaridae	*Fagotia acicularis* Férussac, 1823	Lower Austria (Bad Vöslau)
	Melanoides tuberculata (Müller, 1774)	Tropic (aquarium)
Cerithiidae	*Bittium reticulatum* (Da Costa, 1778)	Adriatic Sea (aquarium)
Stromboidea		
Aporrhaidae	*Aporrhais pespelecani* (Linné, 1758)	Adriatic Sea (Piran)
Lamellarioidea		
Capulidae	*Capulus ungaricus* (Linné, 1767)	Adriatic Sea (Piran)
Triviidae	*Erato voluta* (Montagu, 1808)	Mediterranean Sea (Naples)
Calyptraeoidea		
Calyptraeidae	*Crepidula moulinsi* (Michaud, 1829)	Atlantic (Helgoland)
Cypraeoidea		
Cypraeidae	*Monetaria annulus* (Linné, 1758)	Pacific (aquarium)
	Mauritia arabic (Linné, 1758)	Pacific (aquarium)
	Mauritia scurra (Gmelin, 1791)	Pacific (aquarium)
	Lyncina pantherina (Lightfoot, 1786)	Pacific (aquarium)
	Lyncina lynx (Linné, 1758)	Pacific (aquarium)
	Erosaria caput-serpentis (Linné, 1758)	Pacific (aquarium)
Ovulidae	*Simnia spelta* (Linné, 1758)	Mediterranean Sea (Naples)
	Pseudosimnia sp.	Pacific (aquarium)
Atlantoidea		
Atlantidae	*Atlanta inflata* Souleyet, 1852	Mediterranean Sea (Villefranche)
Naticoidea		
Naticidae	*Polinices guillemini* (Payraudeau, 1826)	Adriatic Sea (Piran)
Triphoroidea		
Triphoridae	*Triphora perversa* (Linné, 1758)	Mediterranean Sea (Naples)
Eulimoidea		
Eulimidae	*Eulima glabra* (Da Costa, 1778)	Adriatic Sea (Rovinj)
Epitonioidea		
Epitoniidae	*Epitonium clathrus* (Linné, 1758)	Adriatic Sea (Rovinj)
Muricoidea		
Muricidae	*Truncularíopsis trunculus* (Linné, 1767)	Adriatic Sea (Rovinj)

Table 2. Prosobranchia species whose osphradia had been ultrastructurally investigated by former authors

superfamily family	species	references
Pleurotomarioidea		
Haliotidae	*Haliotis* sp.	Yatchmenoff 1979
Littorinoidea		
Littorinidae	*Littorina littorea* (Linné, 1758)	Crisp 1973
Muricoidea		
Muricidae	*Nucella lapillus* (Linné, 1758)	Crisp 1973
	Thais haemastoma (Linné, 1758)	Garton, Caprio, Roller 1981
Buccinidae	*Buccinum undatum* Linné, 1758	Welsch & Storch 1969, Crisp 1973
	Neptunea antiqua (Linné, 1758)	Welsch & Storch 1969
Nassariidae	*Nassarius reticulatus* (Linné, 1758)	Crisp 1973
	Bullia digitalis Meuschen	Newell & Brown 1977
Melongenidae	*Busycon* sp.	Anderson 1963
Conoidea		
Conidae	*Conus flavidus* Lamarck, 1822	Alexander & Weldon 1975
	Conus spp.	Crisp 1973

RESULTS

General remarks

In describing and schematizing the sensory epithelia, the external milieu (mantle cavity) was oriented always 'above' to make comparisons easier. The correct location of the osphradia is given at the beginning of each description.

It has been shown that all previous observations of alleged 'cuticula' are due to a microvillous border. Therefore the term 'cuticula' is not used.

In many osphradia so-called 'paddle cilia' (or discocilia) occur, which have been recently described in several phyla (see table 7). But there are such great differences in configuration among them that it will in the future be necessary to define more exactly what a paddle cilium is. For instance, the paddle cilia described by Berquist *et al.* (1977) in sponge larvae and by Bone *et al.* (1982) in tunicates are clearly different from those described in molluscs. In the sensory epithelia described below, each paddle cilium bears a discoid, biconcave or round swelling at its tip (figure 26). The microtubular complex, running up to the swelling with its normal configuration, is enrolled several times, forming a spiral. In this spiral it loses its normal configuration and shows abnormal features (9+1, 9+0, 8+0, 7+0). Paddle cilia, where present, always project from sensory elements. They never occur in cells of the adjacent, likewise ciliated mantle epithelium.

Haliotis lamellosa Lamarck, 1822

(*Pleurotomarioidea*, *Haliotidae*)

As in all Vetigastropoda (Pleurotomarioidea, Fissurelloidea and Trochoidea, after Salvini-Plawen 1980) the osphradia of *Haliotis lamellosa* are placed on the free part of the efferent edge of each gill axis with their ganglion inside the efferent membrane of the gill. The osphradia occur as yellow-brown ridges without a central cleft (in contrast to the description by Crofts (1929)). They are innervated by a number of paired branches of the osphradial nerve, which runs parallel to the branchial nerve on the efferent side of each gill axis. These fine processes reach the sensory epithelium, which does not show any zonation.

On each side of, but beyond the sensory epithelium is a zone of a highly grooved epithelium, its surface bearing densely arranged microvilli. Cilia are absent. Within the epithelium there is some nervous tissue but this makes no contact with the surface.

The histology of the osphradium of *Haliotis* has been previously described by Bernard (1890), Crofts (1929), Demal (1955) and Yatchmenoff (1979). Within the sensory epithelium, which is up to 60 μm in height, several cell types can be distinguished (figure 1).

(i) Supporting cells (sp.) with microvilli, pigment granules and oval nuclei, which are

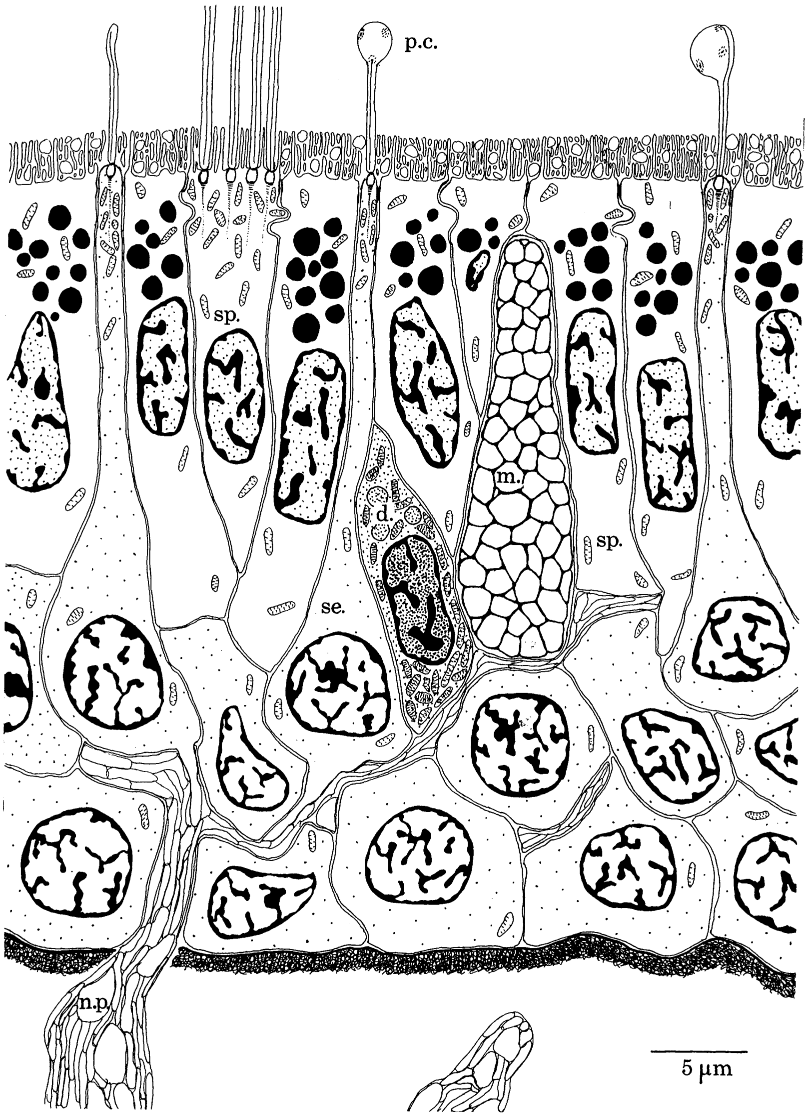


FIGURE 1. Section of the osphradium of a vetigastropod (mainly after the conditions of *Haliotis lamellosa* – semischematic). d., Dark cell; m., mucous cell; n.p., neural process; p.c., paddle cilium; se., sensory cell; sp., supporting cell.

situated distally, possessing electron-dense euchromatin. Sometimes a second type of supporting cell with cilia occurs and this is correlated with an increase of distally located mitochondria.

(ii) Mucous cells (m.), which are filled with different kinds of secretory granules and have elongate shape.

(iii) 'Dark cells' (d.) with extremely electron-dense nuclei, possessing very many mitochondria.

(iv) Sensory cells (se.), resembling in shape and structure the cells of the osphradial nerve, being characterized by a granular plasma as well as by proximally located, more or less round nuclei with electron-lucent euchromatin. They possess thin processes that reach the surface of the epithelium and bear one or two cilia, which can form paddle cilia. Near the edge of the epithelium these cells can reach the surface with full breadth. In this case they bear many cilia, which may be paddle cilia. The sensory cells send their axons into the osphradial nerve.

(v) 'Cilia bottles' (figure 20, plate 3). Close to the edge of the sensory area, but still within it, there are often cells showing a fluid-filled lumen filled by specialized cilia. These cilia show all variations from the normal 9+2 to an 8+0 microtubular pattern. They are very densely packed, and sometimes their membranes are swollen. The lumen is closed, thus the cilia do not make contact with the surface (this is in contrast to similar cells described by Emery (1975, 1976) in olfactory organs of cephalopods). The surface of the lumen has also complexes of microvilli in different positions.

The basal lamina is composed of two components (figure 20): (i) a 60 nm compact and electron-dense zone and (ii) an underlying net-like structure 1 μm thick which ends at the edge of the sensory epithelium. Both layers are interrupted by the associated nerves.

The findings of Yatchmenoff (1977, 1979) do not agree with the data given here in respect of the shape of the sensory epithelium as a whole as well as the existence of special cell types.

Diodora italica (*Defrance*, 1820)
(*Fissurelloidea*, *Fissurellidae*)

The osphradia are located on the free part of each efferent gill axis and are slightly yellowish. In contrast to conditions in *Haliotis*, there is a zonation of the sensory area (figures 7*b* and 9): in the centre are cells with only cilia, whereas laterally most of the cells bear only microvilli. The osphradial nerve is fused with the branchial nerve. On both sides of the sensory area is a zone of grooved epithelium as in *Haliotis*.

As a whole the osphradial epithelium is similar in composition to that in *Haliotis* (supporting cells, mucous cells, dark cells, sensory cells). There are only few differences:

(i) there are no cilia bottles;

(ii) the cilia of the central cells possess special membranes, which swell up immediately beyond the microvillous border (figure 21). The microtubular complex does not change its configuration, showing the normal 9+2 pattern even distal to the swellings.

(iii) There is a uniform and compact basal lamina.

Scutus unguis (*Linné*, 1767)
(*Fissurelloidea*, *Fissurellidae*)

Position, innervation and zonation of the osphradium of *Scutus* are identical with those of the osphradium of *Diodora*.

The fine structure of the sensory epithelium is nearly identical with that of *Diodora*. The single difference is in the cilia of the central cells, which do not form swellings. All other characters of *Diodora* (supporting cells, mucous cells, dark cells, sensory cells) are likewise found in *Scutus*.

Emarginula elongata O. G. Costa, 1829

(*Fissurelloidea*, *Fissurellidae*)

The arrangement and innervation of the osphradium of *Emarginula* are identical with conditions in *Diodora* and *Scutus*; there is, however, no zonation of the sensory epithelium. The osphradia are not visible because of their lack of coloration

Compared with the osphradia of *Diodora* and *Scutus*, the sensory area appears to be somewhat reduced. There are only few sensory cells and dark cells, but many mucous cells. As in all members of the Fissurelloidea investigated, there are no cilia bottles.

Gibbula varia (*Linné*, 1767)

(*Trochoidea*, *Trochidae*)

As in all Vetigastropoda, the left osphradium (the right gill and right osphradium are reduced in the Trochoidea) is located on the free part of the efferent gill axis, with its ganglion within the efferent membrane of the gill (see Fretter & Graham 1962, p. 96). It is yellowish and thus clearly visible. As in *Haliotis* there is a special osphradial nerve to the sensory epithelium, which is not zoned in any way. As in *Haliotis*, *Diodora*, *Scutus*, and *Emarginula* there is a grooved epithelium beyond the sensory area (figure 10, plate 1).

The osphradial epithelium is similar in its histology and fine structure to that of *Haliotis*. There are all the cell types described in *Haliotis*, including the very special type of cilia bottles. These cilia bottles were also found by Crisp (1981) in the epipodial sense organs of trochids, and are thus not limited to the osphradia in this family. With the exception of the basal lamina, which is very thin in *Gibbula* (50 nm), the sensory epithelia of *Haliotis* and *Gibbula* are identical.

Astraea rugosa (*Linné*, 1767)

(*Trochoidea*, *Turbinidae*)

The arrangement and innervation of the osphradium is as in *Gibbula*, but there is a zonation similar to that described for *Diodora* and *Scutus*. There is also the lateral, grooved epithelium.

Most of the cell types described for *Gibbula* are likewise found in *Astraea* (supporting cells, mucous cells, dark cells, sensory cells), but there are no cilia bottles. The cilia of the central zone do not form swellings like those of *Diodora*. As in *Gibbula*, the basal lamina is very thin.

Tricolia pullus (*Linné*, 1768)

(*Trochoidea*, *Phasianellidae*)

The macroscopically invisible osphradium is located and innervated as in the other members of the Trochoidea described above (see Fretter & Graham 1962, p. 124). As in all Vetigastropoda, there are lateral zones of grooved epithelium.

The osphradium of *Tricolia* appears to be somewhat reduced, similar to the conditions of *Emarginula*. There are few sensory cells, but many mucous cells. Dark cells and cilia bottles could not be found. Again, the basal lamina is very thin.

Helcion pellucidum (*Linné*, 1758)
(*Patelloidea, Patellidae*)

Up to the beginning of this century there was great confusion about conditions in the mantle cavity of the Docoglossa (cf. Spengel 1881; Bernard 1890; Thiele 1893; Haller 1894; Davis & Fleure 1903; Fisher 1904; Schuster 1913), but with the comparative study by Thiem (1917*a*, *b*) the configuration appears to have been cleared up: although the author combined his results with a very dubious hypothesis with respect to homology and phylogeny (1917*b*, p. 509).

There are three kinds of special sensory epithelium in the mantle cavity of the juvenile specimens of *Helcion pellucidum* investigated.

(i) The paired subpallial sensory strips, first described by Thiele (1893), running around the anterior edge of the shell muscle, but not reaching the osphradia. They are innervated by nerves from the osphradial ganglion as well as from the pleural ganglion (Thiele 1893; Thiem 1917*a*, p. 391). The sensory epithelium is fairly large where it surrounds the muscle, but becomes smaller running back within the lateral pallial groove. Between the supporting cells, which have microvilli only, slender processes of sensory cells reach the surface of the epithelium. They bear cilia that originate somewhat more distally than the microvilli of the adjacent supporting cells, and they are surrounded by eight to ten strong microvilli with electron-dense central fibrillae. These characters are similar to those described by Haszprunar (1984*a*) in the mechanoreceptors of bivalves, but different from the conditions in the osphradial epithelium (see below). Thus a homology with an osphradium as suggested by Thiem (1917*b*, p. 509) cannot be accepted. The sensory cells, additionally characterized by a more granula plasma than that of the supporting cells, have axons connecting them with the nerve.

(ii) Thiele (1895, p. 222, 1902; p. 327) described a streak of sensory epithelium in several docoglossan species on the roof of the nuchal cavity, immediately adjacent to the anterior left part of the shell muscle. Although denied by Thiem (1917*a*, p. 391), it has been found here and investigated ultrastructurally. A sensory epithelium, characterized by higher cells and innervation, is developed only on the left side. The associated nerve originates from the osphradial ganglion, and runs in the edge of the mantle cavity. The supporting cells in part bear cilia with long roots and they have small, distally located pigment granules; they are much higher (10 μm) than the cells of the adjacent mantle epithelium (5 μm). There are free nerve-endings between them, arising from nerve cells within the nerve and bearing short cilia with short roots which have an irregular microtubular pattern ($9+0$, $8+0$).

(iii) The paired, true osphradia are located far back in the nuchal cavity. Large osphradial ganglia lie underneath which innervate the sensory epithelia. A so-called 'rudimentary gill' or 'Nackenwarze' is not developed in *Helcion pellucidum*. Here, the sensory epithelium is expanded above the whole area of the osphradial ganglion. The sensory epithelium is formed like that of the dorsal sensory streak described above (figure 2). The supporting cells never bear cilia, but are more or less pigmented. There are also free nerve-endings with short cilia, but some of the cilia are longer forming paddle cilia.

Patella coerulea Linné, 1758
(*Patelloidae, Patellidea*)

The paired osphradia of *Patella coerulea* are located far back in the nuchal cavity and are of yellow-brown colour. Just beside them there are brilliant red spots, representing the so-called

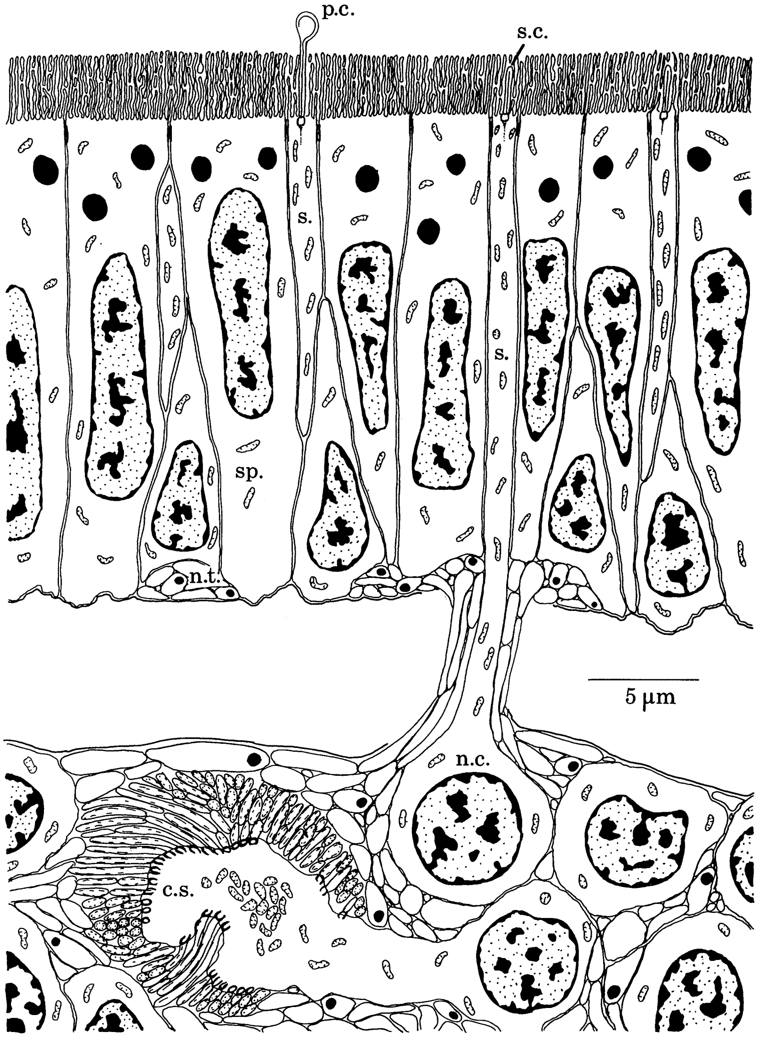


FIGURE 2. Section of the osphradium of a docoglossan (mainly after the conditions of *Patella coerulea*, semischematic). c.s., Cilia star cell; n.c., nerve cell; n.t., nervous tissue; p.c. paddle cilium; s, sensory process; s.c., sensory cilium; sp., supporting cell.

tubercle organ (= Nackenwarze of Thiem 1917*a*, *b*), which has not always been distinguished from the osphradium by authors (for example, Bernard 1890; Schuster 1913; Fretter & Graham 1962). The subpallial sensory strip and the dorsal sensory streak occur in the same positions as in *Helcion*; they have not been investigated in *Patella*.

The osphradial sensory epithelium is identically developed as described for *Helcion*. Again there exist free nerve-endings with short cilia or paddle cilia and no special sensory cells are present. Within the osphradial ganglion, there are peripherally located special cilia, called cilia star cells (figures 2, 7*c* and 11). Their perikarya, having a lot of mitochondria, bear numerous cilia without roots, filling completely the (haemal?) space outside the cells. The pattern of the microtubuli of the cilia is abnormal, showing arrangements from 9+1 to 7+0. Ten to fifteen such cilia star cells may be found in a single section of the osphradial ganglion.

These cilia star cells likewise occur in great numbers (up to 60 in a single section) within the adjacent tubercle organ, also innervated by the osphradial ganglion. Between them there is a mixture of nervous tissue, haemal lacunae, and connective tissue, forming a peculiar organ, the external shape of which is very variable (Thiem 1917*a*, p. 387; personal observation). Because of this structure, homology with any prosobranch gill (Thiem 1917*a*, *b*) must be denied.

Acmaea virginea (*Müller*, 1776)

(*Patelloidea*, *Acmaeidae*)

Whereas most members of the Acmaeidae have retained their osphradia, they are reduced in *Acmaea virginea* (Thiem 1917*b*, p. 509; personal observation). Thiem (1917*b*) described sensory epithelia on the efferent side of the gill axis of several acmaeid species, regarding them as osphradia. In *Acmaea virginea* no trace of such an epithelium has been found.

The left dorsal sensory streak is present (described by Thiele 1902, p. 327), showing the same structure as in *Helcion*. In no acmaeid are there subpallial sensory strips.

Nerita plicata Linné, 1758

(*Neritoidea*, *Neritidae*)

As in all Neritidge the (left) osphradium of *Nerita plicata* is located between the efferent membrane of the gill and the anterior edge of the mantle cavity (see Fretter & Graham 1962, p. 95). It is a yellow-brown epithelial ridge, showing a zonation into laterally situated ciliary areas, with a central ridge above the osphradial nerve. The innervation of the neritid osphradium as well as its homology to the osphradia of other Prosobranchia has been much debated in earlier literature (compare Bouvier 1892; Boutan 1893; Lenssen 1903; Bourne 1908), but is now cleared up: linked by a zygosis with the left pleural ganglion, the supra-oesophageal ganglion sends out a nerve to the osphradial ganglion, from which a nerve runs just beneath the left columellar muscle. Above this osphradial nerve the sensory epithelium is elaborated.

So far, the histology of a nerited osphradium has been described in detail only by Bourne (1908) and Starmühlner (1969). The sensory epithelium is built up of several cell types (figures 3 and 7*a*).

(i) Supporting cells, characterized by oval nuclei with electron-dense euchromatin, are the predominant elements of the central zone. Distal to their nuclei, there are granular bodies, sometimes provided with a concentric arrangement of electron-dense granules within a matrix (figure 23). These cells bear microvilli only.

(ii) Between these supporting cells slender processes filled with mitochondria reach the surface of the sensory epithelium; they have one or two short cilia bent to run parallel to the epithelial surface amongst the microvilli of the adjacent cells. The perikarya of the processes are located more basally than those of the supporting cells and have nuclei with electron-lucent euchromatin. These cells are connected with the osphradial nerve by axons, proving them to be sensory.

(iii) Very rarely cells with elongate, basally located nuclei are found within the central zone (figure 3, x). They reach the surface of the epithelium by a slender process with one or two cilia at its tip. Axons were not found, but each perikaryon is placed in close relation to some nervous tissue.

(iv) The same condition is found in another rare cell type of the central zone, characterized by a particularly massive elaboration of its tip, which reaches beyond the microvillous border (figures 3(y) and 24).

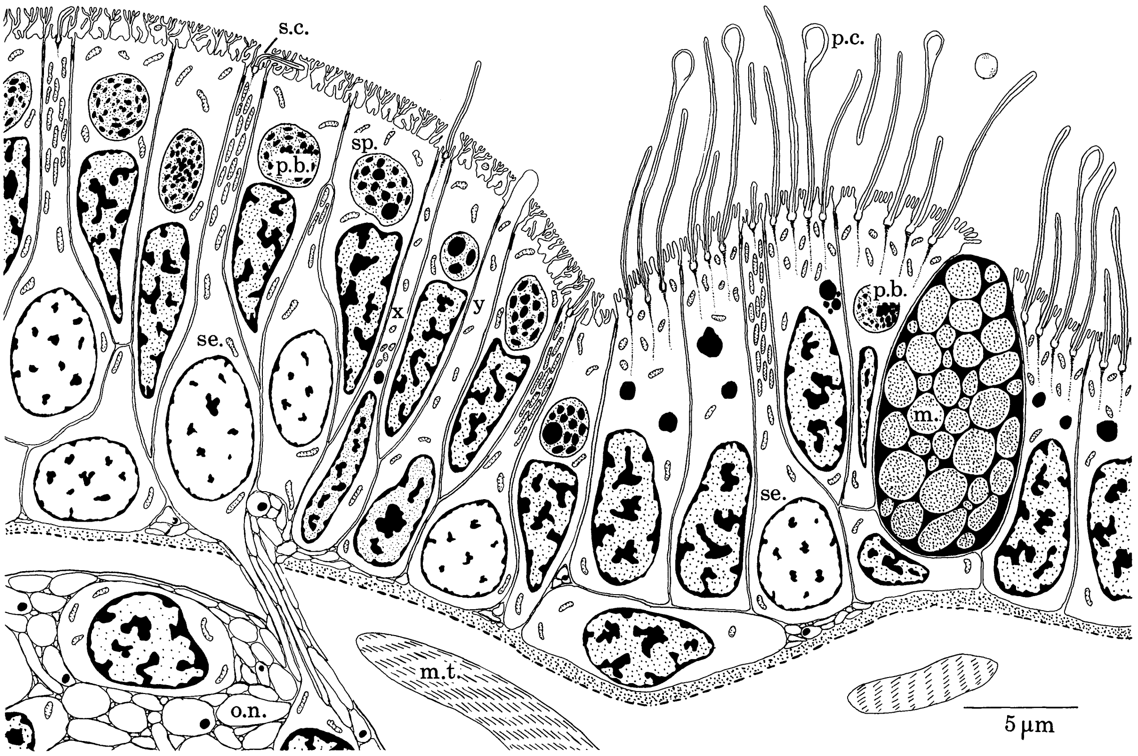


FIGURE 3. Section of the osphradium of a marine neritid (semi-schematic). m., Mucous cell; m.t., muscle tissue; o.n., osphradial nerve; p.b., pigment body; p.c., paddle cilium; s.c., sensory cilium; se., sensory cell; sp., supporting cell; x, y, special (sensory?) cells (see text).

(v) The lateral ciliary zones are formed by cylindrical cells with many cilia, which may form paddle cilia, at their tips. In some cases also granular bodies can be seen within these cells. There are also some sensory cells.

(vi) Occasionally large mucous cells are present within the lateral zone. The may prevent drying of the epithelium, if the mantle cavity is filled with air to function as a lung (Fretter 1965; a similar condition is found in the terrestrial *Pomatias elegans*).

The basal lamina consists of two parts: distally there is a continuous layer, which is limited basally by an interrupted electron-dense membrane.

Nerita undata Linné, 1758
Nerita textilis Gmelin, 1791
(*Neritoidea*, *Neritidae*)

Innervation, histology, and fine structure of the osphradia of *Nerita undata* and *Nerita textilis* are identical with the conditions described for *N. plicata*.

Puperita pupa (*Linné*, 1758)
(*Neritoidea*, *Neritidae*)

The osphradial epithelium of *Puperita pupa* is very low (figures 7*f* and 12), but shows the typical neritid arrangement with the same cell types.

Theodoxus prevostianus (*Pfeiffer*, 1828)

In this freshwater species the osphradium is traceable only in serial sections, but it shows, nevertheless, the typical zonation of all neritids.

The central zone is built up merely of supporting cells (without granula bodies) and sensory cells, and there are no mucous cells within the ciliated zones. In addition, the cilia of the ciliated zones never form paddle cilia. In all other respects the osphradium of *Theodoxus prevostianus* repeats the characters of the marine species.

Valvata piscinalis (*Müller*, 1774)

(*Valvatoidea*, *Valvatidae*)

The special characters of the mantle cavity in the genus *Valvata* have long been a matter of interest. Even after the studies of Bernard (1888, 1890), Yonge (1947), Starmühlner (1952), and Cleland (1954) the systematic position of this family is still dubious, mainly because of the special elaboration of the gill which, according to Salvini-Plawen (1981), represents (as in Acmaeidae and Neritidae) primitive gastropod conditions. Only the left osphradium is retained, located just behind the inhalant opening of the mantle cavity. It forms a small elevation of taller cells, which can be observed only in serial sections, and it is innervated from the osphradial ganglion. As already stated by Starmühlner (1952) and Yonge (1947), no special sensory epithelium could be found on the gill axis.

The histology of the osphradium of *Valvata* spp. was investigated by Bernard (1888, 1890) and Starmühlner (1952). It is very weakly elaborated, showing no trace of zonation. The epithelium consists of cells mostly with cilia, but otherwise without any special character. Between them, processes of sensory cells reach the surface of the sensory epithelium bearing short cilia (figure 4). Paddle cilia are not developed.

Viviparus contectus (*Millet*, 1813)

(*Viviparoidea*, *Viviparidae*)

The (left) osphradium of *Viviparus* is located beneath the pectinibranch gill, lying exactly in the inhalant current of the mantle cavity. It forms a clearly visible, brownish and nearly cylindrical ridge, extending along the anterior third of the gill (see Fretter & Graham 1962, p. 290). It is innervated by a large osphradial nerve which contains nerve cells.

The microanatomy and histology of the osphradium of *Viviparus* species have been described by several authors (Bernard 1890; Wölper 1950; Starmühlner 1952; Demal 1955; Benjamin 1971). The osphradium of *Viviparus* is characterized by a series of pits at each side, lined by ciliated cells only; they are likewise innervated by the osphradial nerve (figure 13). These pits are also present in late embryos (4 mm shell height).

The epithelium of the central ridge is organized in two layers (figure 5). The distal layer (about 25 μm thick) mainly consists of cells with elongate nuclei and microvilli, though some possess cilia. Between these cells there are big mucous cells (basophilic). The basal layer (about 12 μm thick) is formed by the perikarya of the sensory cells, possessing axons that connect with the osphradial nerve. They project slender processes that run between the epithelial cells up to the surface of the epithelium, bearing short cilia with short roots and an abnormal pattern of microtubules (9+0, 8+0).

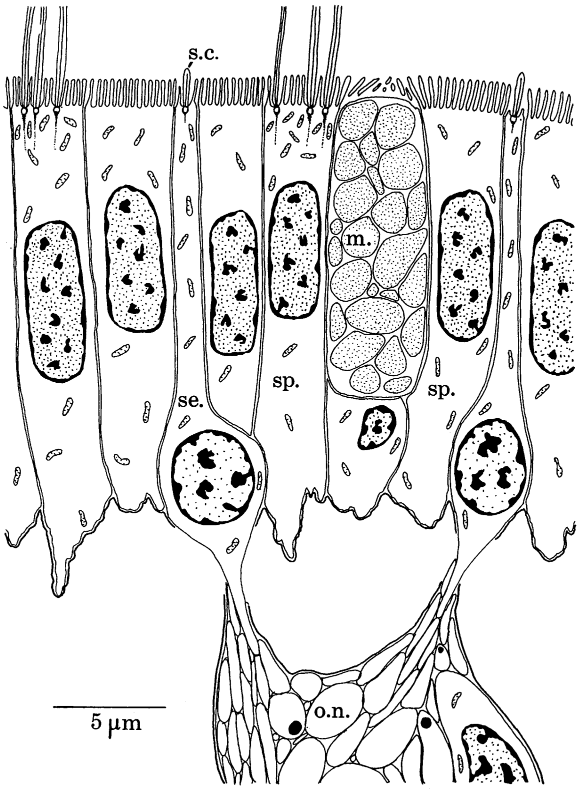


FIGURE 4. Section of the osphradium of *Valvata piscinalis* (semi-schematic). m., Mucous cell; o.n., osphradial nerve; s.c., sensory cilium; se., sensory cell; sp., supporting cell.

The ciliated epithelium of the osphradial pits is similar to that of the central ridge. In contrast to the sensory cells, the cilia-bases of the epithelial cells lie somewhat deeper. There are no mucous cells and there is no trace of a basal lamina.

Marisa cornuarietis (*Linné*, 1758)
(*Viviparoidea*, *Ampullariidae*)

As in all ampullariids, the osphradium of *Marisa cornuarietis* is located at the base of the siphon, being transferred here from the typical caenogastropodan situation alongside the gill through the development of the lung-sac (Demian 1965; Demian & Yousif 1973). It constitutes a gill-like structure by in-foldings of the epithelium. These in-foldings become pits, very similar to the conditions in *Viviparus* (figure 14). This character was also described by Starmühlner (1969, p. 152) in *Pila ceillei*. The osphradial ganglion is placed immediately below the central epithelium, the lateral pits being sunk in it.

The histology of the ampullariid osphradium has been described by Prashad (1925) and Starmühlner (1969). The sensory epithelium as well as the epithelium of the pits is very similar to those described above for *Viviparus*. This refers to the two-layered organization as well as to the cell types, but there are more ciliated epithelial cells in the central ridge than in *Viviparus*. Again there is no basal lamina.

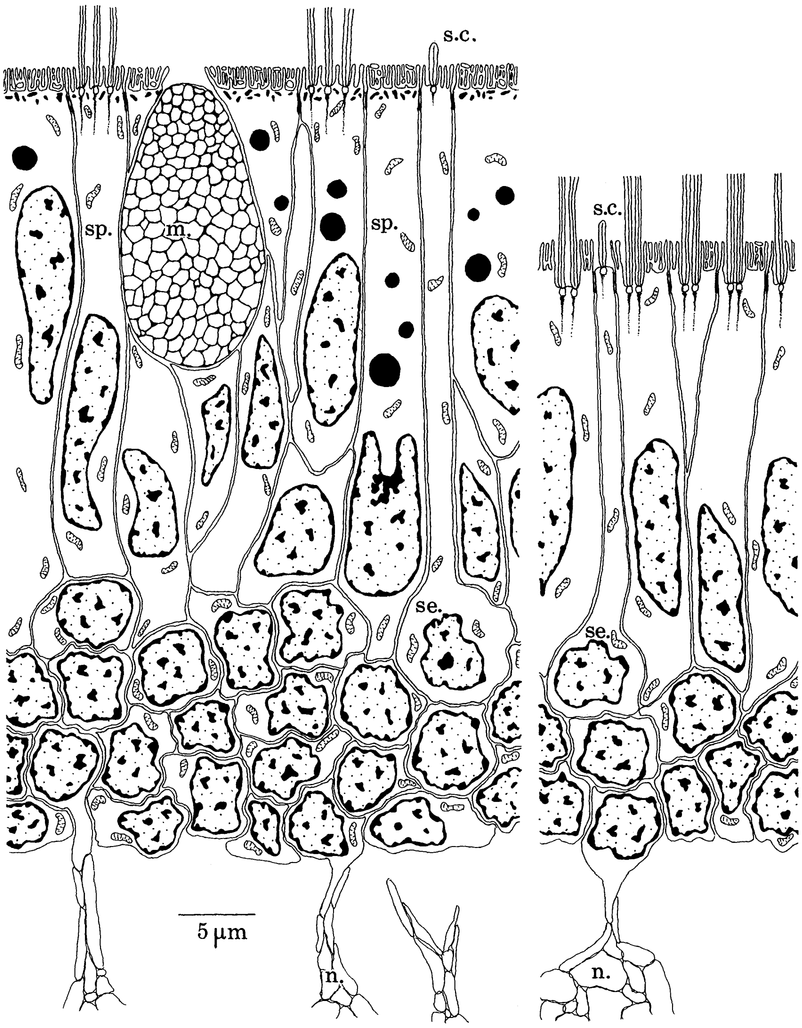


FIGURE 5. Section of the osphradium of a viviparoidean (semi-schematic). Left side epithelium of the central ridge; right side, epithelium of the grooves. m., Mucous cell; n., neural process; s.c., sensory cilium; se., sensory cell; sp. supporting cell.

Ampullarius sp.

(*Viviparoidea*, *Ampullariidae*)

The osphradial characters of *Ampullarius* are almost identical with those described for *Marisa*. This refers to the configuration, organization, histology and ultrastructure. Within the ciliated epithelial cells there are many small electron-dense pigment granules.

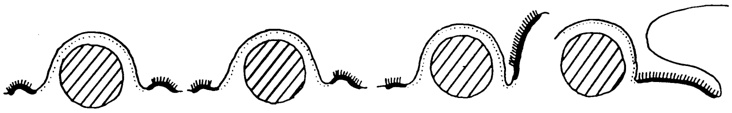
Littorina littorea (*Linné*, 1758)

(*Littorinoidea*, *Littorinidae*)

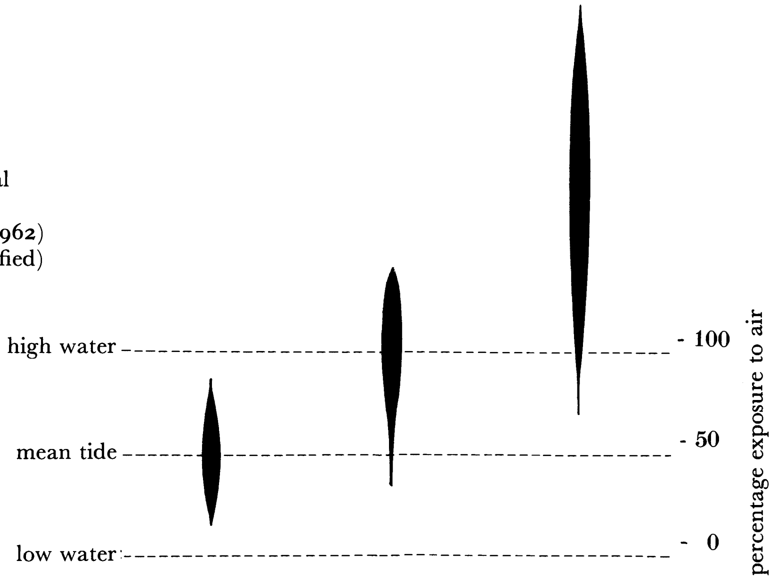
As is typical of lower Caenogastropoda the osphradium occurs as an elongated ridge beneath the pectinibranch gill (see Fretter & Graham 1962, p. 21). It is innervated by nerves from the osphradial ganglion, lying within the ridge.

The histology and ultrastructure of the osphradium of *Littorina littorea* have been previously described by Crisp (1973), and I agree with most of her results; in some cases another interpretation will be given. As described by Crisp, the osphradium has a central zone (= sensory zone of Dakin (1912) and Crisp (1973)), bordered by two strips of ciliated epithelium (= transitional zone) representing the lateral zones, which in *Littorina littorea* are developed symmetrically (see table 3).

Table 3. Evolution from the primitive type to the groove type of osphradium within the Littorinoidea in relation to ecological factors

species	*Littorina littorea* *Littorina obtusata*	*Littorina saxatilis*	*Littorina neritoides*	*Pomatias elegans*
diagrams of the osphradium (in transverse section) central zone lateral zone				
ratio of the number of Si2 cells from the left and right lateral zone (left:right)	1:1	2:3	1:3	0:*n* terrestrial

ecology:
diagram relating the vertical range of the *Littorina* species (after Fretter & Graham (1962) and Daguzan (1976) simplified)



The lateral zones consist of characteristic cell types (figure 6):

(i) The Si1 cells (after Welsch & Storch 1969) are always located beneath the central zone, lying in a depression of the epithelium. In contrast to the descriptions of Welsch & Storch (1969) and of Crisp (1973), but correctly figured by the latter, the distal surface of the Si1 cell is marked by massive extensions rather than by clefts. This is made obvious by the correlated positions of the desmosomes; by the continuity of the outer margin with that of neighbouring cells; and by the fact that within these extensions there are never any organelles (figure 31, plate 5). Thus they are to be regarded as specialized 'columnar microvilli'.

(ii) The Si2 cells are similar to the Si1 cells, but bear cilia, which project between the columnar microvilli and are characterized by an additional basal plate (figures 28 and 29, plate 4). Many of them form paddle cilia (figure 26). Their position is constantly to one side of the Si1 cells. There is some nervous tissue between the basal parts of the Si2 cells and also of the Si1 cells, but no axons could be found.

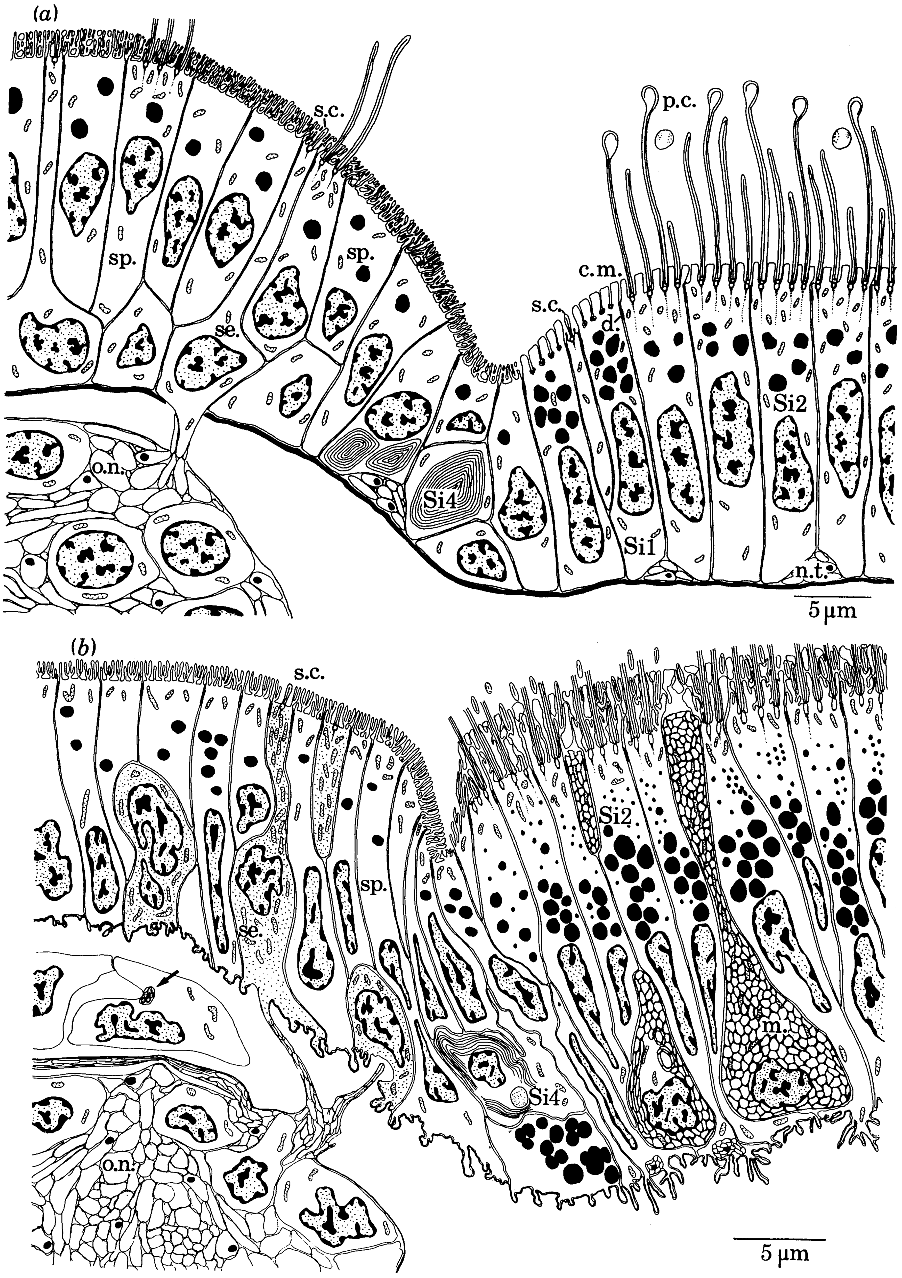


FIGURE 6. (*a*) Section of the osphradium of a marine neotaenioglossan, heteroglossan, or stenoglossan (semischematic). c.m., Columnar microvilli; d., desmosome; n.t., nervous tissue; o.n., osphradial nerve; p.c., paddle cilia; s.c., sensory cilium; se., sensory cell; Si1, Si2, Si4, see text; sp., supporting cell. (*b*) Section of the osphradium of *Pomatias elegans* (semi-schematic). m., Mucous cell; o.n., osphradial nerve; s.c., sensory cilium; se., sensory cell; Si2, Si4, see text; sp., supporting cell; arrow: encapsuled cilia.

(iii) Between the Si1 cells there are often slender neural processes running upwards from the basal region and bearing short cilia with short roots. They have an irregular pattern of microtubules, losing their central tubules and in part also the surrounding ones, thus showing a 9+0, 8+0 and even a 7+0 arrangement at some distance from the basal body.

The epithelium of the central zone is higher than that of the lateral zones and mainly consists of cells which bear microvilli only (figure 30). There are also some cells with cilia. Close to the lateral zones there is a special cell type called the Si4 cell by Welsch & Storch (1969) and Crisp (1973), and characterized by an onion-like pattern of smooth endoplasmic reticulum (figure 32). In contrast to Crisp (1973) I found no processes (but compare *Rissoa*). Between the epithelial cells, slender processes reach the surface of the epithelium, bearing one short cilium with a short root and with irregular microtubular pattern (9+0, 8+1, 7+1, 8+0, 7+0). Their perikarya have axons that connect to the underlying osphradial ganglion. With the exception of the Si4 cells the central zone is as a whole very similar to that of the Neritopsina and the Viviparoidea.

There is a strong, electron-dense basal lamina, interrupted only by nervous tissue.

Littorina obtusata (*Linné*, 1767)†
(*Littorinoidea*, *Littorinidae*)

The osphradium of *Littorina obtusata* is identical to that of *L. littorea* in position, organization, and cell types (Si1, Si2, Si4 cells).

Littorina saxatilis (*Olivi*, 1792)†
(*Littorinoidea*, *Littorinidae*)

Position and ultrastructure of the osphradium of *Littorina saxatilis* are identical to those of *L. littorea* except that the right lateral zone is more developed than the left (see table 3).

Littorina neritoides (*Linné*, 1767)
(*Littorinoidea*, *Littorinidae*)

Although the gill of *Littorina neritoides* is reduced to only a few lamellae, the osphradium is well developed. The asymmetry of the lateral zones is more obvious than in *L. saxatilis* (see table 3), the right lateral zone forming a groove together with the right part of the central zone. The cell types are as described for *L. littorea.*

Pomatias elegans (*Müller*, 1774)
(*Littorinoidea*, *Pomatiasidae*)

The osphradium of *Pomatias elegans* is located in the anterior third of the mantle cavity, and is easily visible by its pigmentation (see Fretter & Graham 1962, p. 592). Since the innervation is identical to that of the other Caenogastropoda, there is no doubt about its homology.

The histology has been described by Garnault (1887) and Demal (1955). They stated that, in contrast to the terrestrial members of Neritopsina and Cyclophoroidea, the osphradium of *Pomatias* (and of all other terrestrial members of the Littorinoidea and Rissoidea) is well developed.

A transverse section through the osphradium demonstrates it as an asymmetrical grooved structure (figure 15, plate 2) formed of the same elements as the osphradia of *Littorina* spp. (figure 6*b*).

Only the right part of the central zone is developed, lying above the osphradial nerve. The epithelial cells with oval nuclei bear microvilli and have an electron-dense plasma. The sensory

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† After Fretter & Graham (1980).

cells, with basally located, round nuclei, electron-lucent plasma, and axons to the osphradial nerve, have processes that run upwards to the surface of the epithelium; they bear short cilia with abnormal microtubular configuration. Close to the lateral zone, occasional Si4 cells are found. Between the basal lamina of the epithelium and the osphradial nerve there is a special layer of cells, one of which was found to have incorporated few cilia (9+2 pattern) (e.c., figure 34).

Within the lateral zone there occur two cell types: strongly pigmented Si2 cells, the cilia of which have never been observed to form paddle cilia, and bottle-like mucous cells between them (figure 25). There is some nervous tissue at the bases of the Si2 cells.

Hydrobia ulvae (*Pennant*, 1777)

(*Rissoidea*, *Hydrobiidae*)

The osphradium is elaborated in the typical caenogastropod position ventral to the efferent gill sinus. It is visible in section only and the osphradial ganglion is placed below the central ridge.

The organization is similar to that described for the *Littorina* spp. There is an asymmetry such that the right lateral zone is twice as large as the left one, representing a configuration similar to that described for *L. saxatilis*.

The sensory epithelium consists of the same cell types as in *L. littorea* (Si1, Si2, Si4 cells).

Bithynia tentaculata (*Linné* 1758)

(*Rissoidea*, *Bithyniidae*)

Location and innervation of the osphradium of this fresh-water species is typical for Caenogastropoda (see Fretter & Graham 1962, p. 99). The osphradium is obvious through its pigmentation.

The histology has been briefly described by Starmühlner (1952). The organization is identical to the condition of *Littorina littorea*. Differences occur, however, in that there is no Si4 cell, and the cilia of the Si2 cells do not form paddle cilia.

Rissoa sp.

(*Rissoidea*, *Rissoidae*)

The osphradium of *Rissoa* is located and innervated as in most Caenogastropoda. It is clearly visible by its pigmentation, and its division into central and lateral zones is also macroscopically obvious.

The lateral zones are strongly developed, rising to the same height as the central zone (figures 7*k* and 16). From the osphradial ganglion two strong nerves emerge having only few cells.

There are the same cell types as described for *Littorina littorea*. In some cases the Si4 cells fully reach the surface of the epithelium (figure 32). Si1 and Si2 cells occur in their usual arrangement; the cilia of the Si2 cells may form paddle cilia (figure 27).

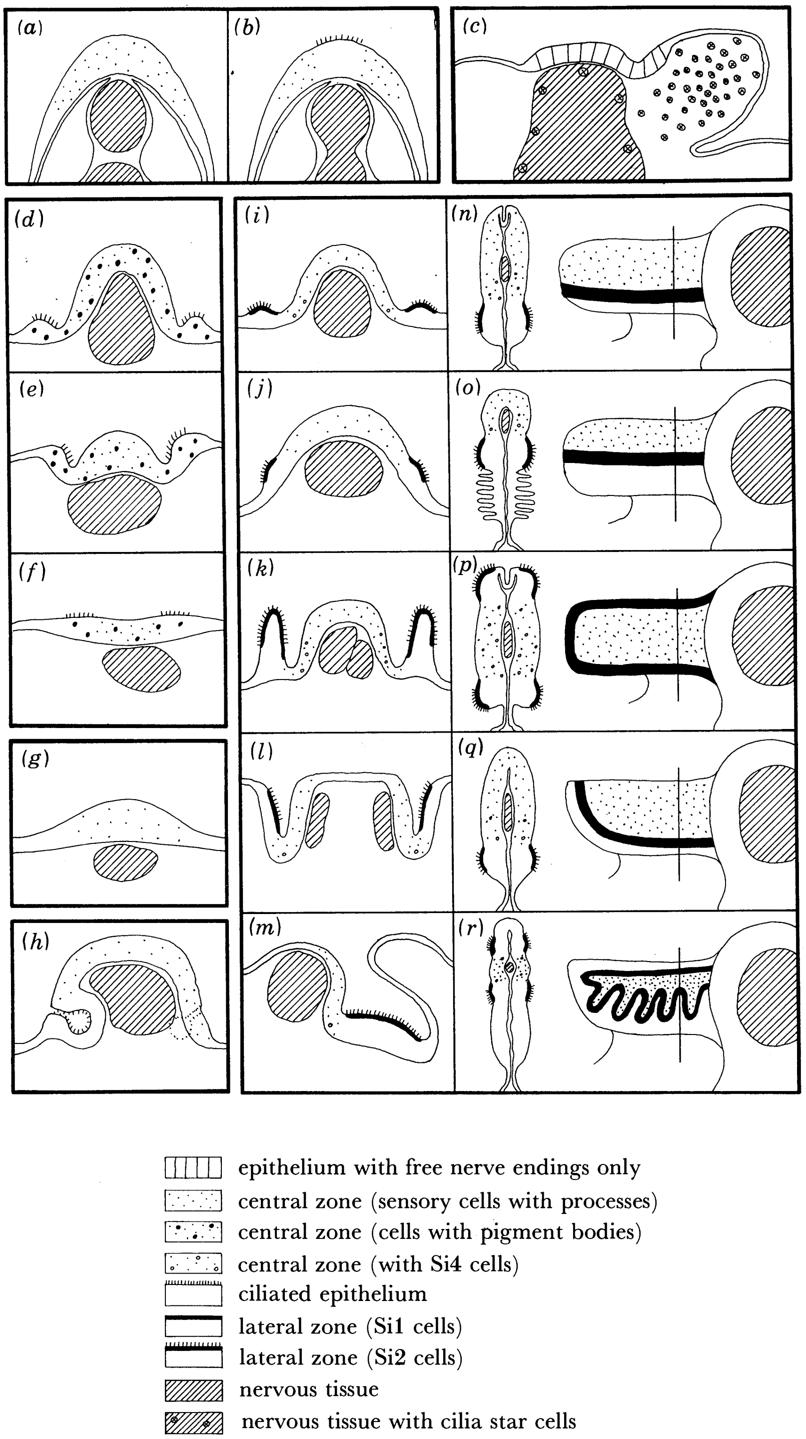

FIGURE 1. Comparative view of prosobranch osphradia, all in transverse section. Figures (*n*)–(*r*) show, left, a transverse section of a lamella; right, a transverse section of the axis with a surface view of a lamella.

Vestigastropoda-type, (*a*) *Haliotis*, *Gibbula*, (*b*) *Diodora*, *Scutus*, *Astraea*. (*c*) Docoglossa-type (*Patella*). Neritopsina-type; (*d*) *Nerita* sp.; (*e*) *Nerita plicata*; (*f*) *Puperita*. (*g*) Valvatoidea-type (*Valvata*). (*h*) Viviparoidea-type (*Viviparus*, *Marisa*, *Ampullarius*).

Si1–Si2–Si4-type, (*i*) *Littorina littorea*, *Turritella*, *Bittium*, *Aporrhais*, *Triphora*; (*j*) *Bithynia*, *Fagotia*, *Melanoides*; (*k*) *Rissoa*; (*l*) *Eulima*; (*m*) *Pomatias*; (*n*) *Capulus*, *Crepidula*, *Erato*, *Monetaria*, *Mauritia*, *Lyncina*, *Erosaria*, *Simnia*; (*o*) *Pseudosimnia*; (*p*) *Polinices*; (*q*) *Truncularioрsis*, *Buccinum*, *Nassarius*, *Bullia* (after Welsch & Storch 1969; Crisp 1973; (*r*) *Conus* (after Crisp 1973).

Caecum glabrum (*Montagu*, 1803)

(*Rissoidea*†, *Caecidae*)

The osphradium of *Caecum* is located on the left side deep in the mantle cavity, which lacks a gill. As described by Goetze (1938) it is prominently developed and easily seen by the strong pigmentation of the lateral zones, forming a horseshoe-like organ around the osphradial ganglion. The innervation starts from the supra-oesophageal ganglion.

Goetze (1938) described the histology of the osphradial epithelium, which consists of very low cells and is organized into a central zone and the semicircular contiguous lateral zones. The central zone is differentiated as in *Littorina littorea*, including Si4 cells. There is no pigmentation. The Si1 and Si2 cells of the lateral zones have large pigment granules (as large as the nuclei), which are responsible for the visibility of the organ. There is a weakly elaborated basal lamina.

Skeneopsis planorbis (*O. Fabricius*, 1780)

(*Rissoidea*, *Skeneopsidae*)

In contrast to other small rockpool-living snails (such as *Rissoella* and *Omalogyra*), the mantle cavity of *Skeneopsis planorbis* has a typically caenogastropod elaboration. The external shape of the osphradium is similar to that described by Ponder (1968, figure 30) for small rissoids. Located at the left side in the mantle cavity, the osphradium is much larger than the poorly developed gill. The lateral zones are as high as the central zone, giving the apparently bipectinate character seen in cross section (Fretter 1948), though in reality solid throughout. As in *Caecum glabrum* the epithelium of the osphradium is very low.

Ultrastructural investigation show similar results as described for *Caecum*. The Si1 and Si2 cells of the lateral zones have large pigment granules, whereas the cells of the central zone do not. Si4 cells were not observed.

Turritella communis Risso, 1826

(*Cerithioidea*, *Turritellidae*)

As in most members of the Cerithioidea, the osphradium of *Turritella communis* occurs as a yellow-brownish pigmented ridge along the efferent gill vessel. Innervation and zonation are typical of higher Caenogastropoda.

In fine structure the osphradium closely resembles *Littorina littorea*. The lateral zones are built up of Si1 and Si2 cells (with paddle cilia), and Si4 cells are found within the central zone.

Fagotia acicularis Férrusac, 1823

(*Cerithioidea*, *Thiaridae*)

Position, innervation, and external shape are as in *Turritella*. The histology of the osphradia of four thiarid species has been described by Starmühlner (1969, pp. 178, 197, 221, 238), who showed their division into central and lateral zones. In *Fagotia acicularis* the epithelium does not form folds, but the lateral zones lie immediately left and right of the central zone (figure 17).

Ultrastructural osphradial characters are similar to the conditions in *Bithynia tentaculata* (also

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† After Moore (1962).

freshwater). There are no Si4 cells, and the cilia of the Si2 cells do not form paddle cilia. In all other respects the sensory epithelium is as in *Littorina littorea*.

Melanoides tuberculata (*Müller*, 1774)
(*Cerithioidea*, *Thiaridae*)

All osphradial characters of *Melanoides tuberculata* are identical to those of *Fagotia acicularis*.

Bittium reticulatum (*Da Costa*, 1778)
(*Cerithioidea*, *Cerithiidae*)

In contrast to the pectinate shape of the osphradium of *Cerithium vulgatum*, the osphradium of *Bittium reticulatum* is a simple brown ridge ventral to the gill (see Fretter & Graham 1962, p. 367). There is the usual division into central and lateral zones all with a low epithelium.

The ultrastructure of the sensory epithelium is typical of Cerithioidea (see above). The Si2 cells bear paddle cilia.

Aporrhais pespelecani (*Linné*, 1758)
(*Stromboidea*, *Aporrhaidae*)

The osphradium is a brownish ridge, running in a winding configuration beneath the gill (see Fretter & Graham 1962, p. 179). The zonation and innervation are as in the Cerithioidea.

The sensory epithelium is nearly identical with that described for *Littorina littorea*. Again, there are Si4 cells within the central zone close to the lateral zones which are built up of Si1 and Si2 cells. The columnar microvilli of the Si2 cells, bearing paddle cilia, are largely fused (figure 26).

Capulus ungaricus (*Linné*, 1767)
(*Lamellarioidea*, *Capulidae*)

As described by Yonge (1938), the osphradium of *Capulus* is located between the left anterior edge of the horseshoe-like columellar muscle and the efferent vessel of the gill (see Fretter & Graham 1962, p. 104). The pectinate organ is asymmetrically developed, the lamellae of the gill side are three times larger than those of the muscle side, so that the organ appears to be monopectinate (in the related Trichotropidae both mono- and bipectinate osphradia occur, see Yonge 1962). The osphradium is innervated by a nerve originating from the supra-oesophageal ganglion, which forms a dialyneury with a pallial nerve from the left pleural ganglion. This condition is typical for the Capulidae and the Calyptraeidae, but does not exist in the Trichotropidae (Graham 1954).

A transverse section through a lamella of the osphradium presents an organization similar to that of the more primitive types described above (figure 7*n*). Each lamella is connected to the mantle cavity by a proximal thin membrane, consisting of low cells with microvilli only. In the proximal portion of the lamella there are symmetrically developed lateral zones which are built up of Si2 cells (with paddle cilia) and Si1 cells more distally. The distal half of the lamella can be homologized with the central zone by the existence of sensory cells with processes, bearing short, abnormal cilia, and by the occurrence of Si4 cells close to the lateral zones. The distal margin of the lamella forms a cleft, in which ciliated cells produce a water current. There is a well-developed basal lamina which includes the lamellar nerve.

Erato voluta (*Montagu*, 1808)

(*Lamellarioidea*, *Triviidae*)

In contrast to members of the Cypraeoidea (see below), the osphradium of the Triviidae is bipectinate; this character, together with the existence of an echinospira larva and the lack of pedal cords, has established the classification of the Triviidae within the Lamellarioidea (see Fretter & Graham 1962, p. 629). It is elaborated at the right of the persistent left columellar muscle beneath the gill, and is supplied with a ganglionated nerve from the supra-oesophageal ganglion (see Fretter & Graham 1962, pp. 210, 329).

The histology and fine structure of the sensory epithelium are identical to the conditions found in *Capulus*.

Crepidula moulinsi (*Michaud*, 1829)

(*Calyptraeoidea*, *Calyptraeidae*)

The osphradium of *Crepidula* is developed behind the inhalant opening of the mantle cavity, lying beneath the gill and bordered by the so-called food pouch. Compared with the hypertrophied gill, the osphradium is weakly elaborated, being represented by a nearly monopectinate structure. The innervation is similar to that of *Capulus* (Graham 1954).

External shape and histology of calyptraeid osphradia have been described by several authors (Osborn 1887; Haller 1892; Scheidig 1913; Kleinsteuber 1913; Werner & Grell 1950). The osphradial lamellae of *Crepidula* have the same ultrastructure as those of *Capulus* (which applies also to the cell types Si1, Si2, Si4, see figures 18 and 31).

Monetaria annulus (*Linné*, 1758)

(*Cypraeoidea*, *Cypraeidae*)

The unique conditions of cypraeid anatomy have received attention for a long time (Bouvier 1887; Haller 1890; Vayssière 1923, 1927; Riese 1930; Rau 1934; Risbec 1937; Kay 1960). The mantle cavity is characterized by a special arrangement of its organs; owing to a secondary 90° rotation to the right, the normal (left–right) horizontal arrangement of pallial organs has changed into a longitudinal (anterior–posterior) one. Most anteriorly there is the large triradiate osphradium at the base of the siphon, behind the small left columellar muscle. It is in part surrounded by the semicircular, pectinibranch gill. Behind the gill the large hypobranchial gland is placed, followed by the rectum. The innervation of the osphradium has been described in most detail by Riese (1930, p. 396): projecting from the large supra-oesophageal ganglion which has been shifted by the rotation to a position above the right cerebropleural ganglion, there are three osphradial nerves; two small ones that directly originate from the ganglion, and a large one that is fused with the branchio-pallial nerves.

The organization, histology, and fine structure of the osphradium are as described for *Capulus*. The lateral zones are proximally located, consisting of Si1 and Si2 cells. A special leaflet nerve runs between the basal lamina of the sensory epithelia.

Mauritia arabica (*Linné*, 1758)

(*Cypraeoidea*, *Cypraeidae*)

Position, innervation, and organization of the osphradium are identical to those of *Monetaria annulus*. The lateral zones are very weakly elaborated and thus poorly visible. Within the lamellar nerve large granular bodies occur. In all other respects the sensory epithelium resembles that of *Monetaria annulus*.

Mauritia scurra (*Gmelin*, 1791)
Lyncina pantherina (*Lightfoot*, 1786)
Lyncina lynx (*Linné*, 1758)
Erosaria caput-serpentis (*Linné*, 1758)
(*Cypraeoidea*, *Cypraeidae*)

Position, innervation, and organization of the osphradium of these four cypraeid species are as described in *Monetaria annulus*. In contrast to *Mauritia arabica*, the lateral zones, consisting as usual of Si1 and Si2 cells (with paddle cilia) are well developed in these species.

Simnia spelta (*Linné*, 1758)
(*Cypraeoidea*, *Ovulidae*)

The anatomy of the Ovulidae is very similar to that of the Cypraeidae (Fretter & Graham 1962, p. 629), and the osphradium is likewise triradiate. There are no detailed data on the innervation of the osphradium.

The organization and structure of the osphradial leaflets are identical to the conditions described above for *Capulus* and the cypraeid species.

Pseudosimnia sp.
(*Cypraeoidea*, *Ovulidae*)

Whereas the external shape and position of the osphradium of *Pseudosimnia* are identical to what is described above for the other members of the Cypraeoidea, the organization of the leaflets differs in some points (figure 7*o*). Proximal to the lateral zones a special zone is developed, the epithelium of which is highly folded; it consists of cells with microvilli only and with many electron-dense pigment granules (figure 33). The adjacent lateral zones are formed as usual (Si1, Si2 cells), but the central zone, which has no distal cleft, is smaller than in the other cypraeoid species.

Atlanta inflata Souleyet, 1852
(*Atlantoidea*, *Atlantidae*)

In most species of the Atlantidae the conditions of the mantle cavity are typical for caenogastropods (Yonge 1942) (in the higher Atlantoidea the mantle cavity is more and more reduced, but the osphradium is retained). In *Atlanta inflata* the gill is completely reduced, probably owing to the smallness of the species (shell length 2 mm). In contrast the osphradium is well developed; it is an asymmetrical ridge because of the reduction of the right lateral zone. A big osphradial ganglion innervates the sensory epithelium.

Spengel (1881) described the histology of the osphradium in *Pterotrachea mutica*, where it is built up symmetrically. In *Atlanta inflata* the conditions of the sensory epithelium are typical for higher Caenogastropoda. The lateral zones consist of Si1 and Si2 cells, Si4 cells and sensory cells with processes are found in the central zone. The basal lamina is very thin.

Polinices guillemini (*Payraudeau*, 1827)

(*Naticoidea*, *Naticidae*)

The osphradium of *Polinices* is a pectinate structure alongside the efferent gill vessel, showing a bend of nearly 90° at its anterior end (similar features have been described by Haller (1892) and Risbec (1956) in other naticid species). The leaflets on the gill-side are somewhat longer than those on the other side.

Only Haller (1892) has described the histology of a naticid osphradium. In contrast to his findings on *Sigaretus neritoides* in which there occur tubule-like clefts with different epithelia, the osphradial leaflets of *Polinices guillemini* occur as rounded rectangles built up as follows (figures 7*p* and 19).

The edges consist of lateral zones which are oriented so that the Si1 cells are placed on the long side. The columnar microvilli of the Si2 cells are very high and are connected by handles with the cells (figures 28 and 29). In the middle of each long side of the rectangle, a central zone is developed, consisting of a high epithelium which contains many Si4 cells. The distal short side bears a cleft, which is built up of low cells with microvilli only. This applies also to the basal lamella, uniting the basal short side with the mantle epithelium. Nervous and muscle tissue is placed between the basal laminae of each leaflet.

Triphora perversa (*Linné*, 1758)

(*Triphoroidea*, *Triphoridae*)

The family Triphoridae is unique among the prosobranchs in being characterized by a *situs inversus* of its anatomy. Thus the osphradium is located at the right in the mantle cavity, being a brownish ridge, which runs far back beneath the pectinate gill. It is innervated by the (right) supra-oesophageal ganglion.

The organization and the fine structure of the sensory epithelum is nearly identical to the conditions described in *Littorina littorea*. The lateral zones consist of Si1 and Si2 cells (with paddle cilia), the central zone is characterized by Si4 cells and has typical sensory cells with processes. Only a thin basal lamina is present.

Eulima glabra (*Da Costa*, 1778)

(*Eulimoidea*, *Eulimidae*)

In contrast to other members of the eulimidae which have a pectinate osphradium (Fretter & Graham 1962, p. 257), that of *Eulima glabra*, located at the usual position, is represented by a pigmented double groove on the left mantle roof. A transverse section shows its organization (figure 7*l*).

Compared with the osphradium of *Littorina littorea*, the sensory epithelium is divided into two symmetrical parts. The abaxial side of each groove is built up by lateral zones with Si1 and Si2 cells, whereas the adaxial side represents one half of the central zone. As usual, Si4 cells are found in each half of the central zone. The osphradial nerve also occurs as two parallel nerves, each running under one half of the central zone.

Epitonium clathrus (*Linné*, 1758)

(*Epitonioidea*, *Epitoniidae*)

The family Epitoniidae has additional interest, since it is said to be a link between prosobranchs and opisthobranchs (Fretter 1979; Robertson 1973, 1983). However, the conditions of the mantle cavity are typical of caenogastropods.

The osphradium is a brownish ridge, located at the usual position beneath the pectinibranch gill. It shows the typical zonation into central and lateral zones. The central zone is built up as described in *Littorina littorea*. The lateral zones consist of Si1 and Si2 cells (with paddle cilia), but differ from the usual type in having some strongly ciliated cells (without paddle cilia) adjacent to the Si2 cells. Only a thin basal lamina is present.

Truncularioposis trunculus (*Linné*, 1767)

(*Muricoidea*, *Muricidae*)

As in all Stenoglossa the osphradium of *Truncularioposis* is bipectinate and greatly developed. The fine structure of osphradia of members of the Stenoglossa has been described by several authors (see table 2). The organization of the osphradial leaflets is as described by Crisp (1973) (figure 7*q*). At the base there are lateral zones that turn up at the end of each leaflet. A central zone is distally developed. The leaflet nerve runs between the strong basal laminae.

Discussion

General remarks

The facts given above are discussed from three aspects:

(i) the osphradium as a whole structure which may reflect different ecological conditions, especially a terrestrial mode of life or a carnivorous habit;

(ii) osphradial structure and cell types reflecting actual relationships;

(iii) the fine structure of the receptive elements (cilia) proving the chemoreceptive (and not the mechanoreceptive) role of the osphradium.

Ecological significance

With regard to the shape and configuration of the osphradia as a whole, three main types can be recognized.

(i) The primitive type, appearing merely as a ridge of cells higher than those of the adjacent mantle epithelium: found in Vetigastropoda, Docoglossa, Neritopsina, Architaenioglossa, some Neotaenioglossa, many Heteroglossa (for taxa see table 6).

(ii) The groove type, an asymmetrical groove in the wall of the mantle cavity: terrestrial Neotaenioglossa.

(iii) The lamellar type, showing a lamellate structure: found in Ampullariidae, many Neotaenioglossa and some Heteroglossa, all Stenoglossa (correlated in most cases with the presence of a siphon).

There is no correlation of these types with any taxonomic position, and even within some families two types may occur (for example, Cerithiidae, Eulimidae).

Within the Littorinoidea the evolution from the primitive type to the groove type can be outlined, since the development of the groove type parallels a higher degree of exposure to air (see table 3).

(i) *Littorina littorea* and *L. obtusata* possess osphradia of the primitive type which are completely symmetrical.

(ii) In *L. saxatalis* there is the same type, but with an asymmetrical configuration (as demonstrated by the ratio of the Si2 cells of the left to those of the right lateral zone).

(iii) In *L. neritoides* the osphradium exhibits a more obviously asymmetrical shape, and the right lateral zone forms a groove.

(iv) In *Pomatias elegans* the left lateral zone of the osphradium is reduced completely. The right one, however, forms a deep groove and includes large mucous cells, probably to prevent drying when the epithelium is exposed to air.

Within the Rissoidea *Hydrobia ulvae*, which lives partly exposed to air, possesses an asymmetrical osphradium of the primitive type (but without mucous cells), and in *Pseudocyclotus* (Assimineidae, terrestrial) Thiele (1927, p. 140, figure 17) described an osphradium 'very similar to that of *Pomatias*'.

There is an interesting difference between the terrestrial members of the Neritopsina and the Cyclophoroidea on the one side, all of which have completely lost their osphradium, and terrestrial members of the Littorinoidea and Rissoidea on the other, whose osphradia are retained and transformed. This may be due to the much earlier penetration into terrestrial habitats of the former groups.

There is no doubt that the lamellar type of osphradium evolved convergently several times within different lines (only within the Stenoglossa may it be monophyletic). This is demonstrated by a different arrangement of the hypertrophied lateral zone (see figure 7*n*, *p*, *q*, *r*), whereas the central zone is even reduced in some cases (for example from Muricoidea to Conoidea, cf. Crisp 1973). The lamellar type is normally found in carnivorous species, but also in the filter-feeding Calyptraeoidea.

Hulbert & Yonge (1937) and Yonge (1947) emphasized the fact that the lamellar type of osphradium is correlated with life on soft sediments in favour of their theory of a mechanoreceptive osphradium. This correlation, however, is because a distance chemoreceptor is useful only in water with oriented currents (Ankel 1938), conditions often correlated with a more or less soft sediment (but found likewise in the phytal). In most cases the lamellar type is correlated with the presence of the pallial siphon, which is used to detect the (orientated) water current. The osphradium itself will be shown to be a chemoreceptor only (see below).

Systematic significance

To use a new character such as osphradial structure as a taxobase it is necessary to check which characters depend on ecological factors and which do not. This has been taken into account in the selection of related species, especially within the Neotaenioglossa, which are, moreover, found in many different habits and environments.

The results, summarized in table 4, in most cases coincide with the current systematic scheme and, moreover, in some cases demonstrate that osphradial fine structure can help to answer open questions.

Vetigastropoda

The great similarity of the osphradia of Pleurotomarioidea, Fissurelloidea and Trochoidea, particularly with regard to their very special cell types (for example, cilia bottles) supports the ideas of Salvini-Plawen (1980) who united these superfamilies on the bases of their comparative anatomy and ontogeny into a single group, Vetigastropoda. The uniform special position of the osphradia (on the free part of the efferent gill axes) as well as their common structure are in agreement with their placement in this systematic unit.

Docoglossa

The special features of the mantle cavity (three kinds of sensory epithelium, tubercle organs) as well as other anatomical characters demonstrate the isolated position of the Docoglossa within the Gastropoda (Fretter & Graham 1962, p. 615; Golikov & Starobogatov 1975; Salvini-Plawen 1980).

The weakly organized osphradia are similar to those of the primitive Vetigastropoda in being devoid of zonation. They are, however, uniquely different by reason of a special fine structure not present in any other prosobranch taxon (free nerve endings only, without sensory cells in the epithelium). The function of the cilia star cells in the osphradial ganglion and the tubercle organ is unknown. It may perhaps be neuroendocrine, since Herbert (1982) described similar ciliary derivates in the (probably) neuroendocrine juxtaganglionar organ of the Trochidae.

Neritopsina

Marine as well as freshwater members of the Neritopsina possess an identical osphradial type. The osphradium, however, is evidently more highly organized than those of the Vetigastropoda and the Docoglossa, since the sensory epithelium is divided into a central zone and lateral zones with ciliated cells (see also Starmühlner 1969, p. 108) in the same manner as in all Caenogastropoda (except *Valvata*). In contrast to this similarity, the cell types of the osphradia of the Neritopsina are different to those of the Caenogastropoda. These facts coincide with the ideas of Fretter (1946, 1965), Bandel (1982), and Giusti & Selmi (1982) that the Neritopsina represent a very early offshoot on the way from the archaeogastropod to the caenogastropod level of organization.

Architaenioglossa

The osphradium of *Valvata* is so insignificantly differentiated that it is impossible to base any relation upon it. The question whether this simple organization of the osphradium is primary or secondary, still remains open.

Although the external features of the osphradia are different in Viviparidae (primitive type) and Ampullariidae (lamellar type), the similarities of their structure support the monophyly of the taxon Viviparoidea. In both families the lateral zones are differentiated to deep grooves, and the epithelium is two-layered. Some authors (Demal 1955; Benjamin 1971) have argued for relations between Viviparoidea and Basommatophora, in which the osphradium (= Lacaze's organ) likewise shows a grooved structure. But basal Pulmonata (*Siphonaria*, *Chilina*) do not have a grooved osphradium (Haeckel 1913; Hubendick 1947; Harry 1964) and they appear to be related to basal Opisthobranchia and Allogastropoda (Architectonicoidea, Pyramidelloidea, see Haszprunar 1984*b*, *c*). Recently Boss (1982) placed the Bithyniidae within the Viviparoidea. Since *Bithynia* possesses, however, osphradial characters like those of the Neotaenioglossa (see below), but not of the Viviparoidea (with which they only share some convergences with regard to a similar habit, that is, facultative filter-feeding), the Bithyniidae are replaced within the Rissoidea.

Because of the conservative characters in their nervous system or their mantle cavity,

Table 4. Occurrence and distribution of osphradial features within the Prosobranchia in relation to systematic and ecological factors

Superfamily							Character						
genus	1	2	3	4	5	6	7	8	9	10	11	12	13
Pleurotomarioidea													
Haliotis	·	·	+	+	·	·	·	·	·	·	·	m	h
Fissurelloidea													
Diodora	·	·	+	·	·	·	·	·	·	·	·	m	h
Scutus	·	·	+	·	·	·	·	·	·	·	·	m	h
Emarginula	·	·	+	·	·	·	·	·	·	·	·	m	h
Trochoidea													
Gibbula	·	·	+	+	·	·	·	·	·	·	·	m	h
Astraea	·	·	+	·	·	·	·	·	·	·	·	m	h
Tricolia	·	·	+	·	·	·	·	·	·	·	·	m	h
Patelloidea													
Helcion	+	·	·	·	·	·	·	·	·	·	·	m	h
Patella	+	+	·	·	·	·	·	·	·	·	·	m	h
Neritoidea													
Nerita	·	·	+	·	+	+	·	·	·	·	·	m	h
Puperita	·	·	+	·	+	+	·	·	·	·	·	m	h
Theodoxus	·	·	+	·	+	+	·	·	·	·	·	l	h
Valvatoidea													
Valvata	·	·	+	·	·	·	·	·	·	·	·	l	h
Viviparoidea													
Viviparus	·	·	+	·	+	·	+	+	·	·	·	l	h/f
Marisa	·	·	+	·	+	·	+	+	·	·	·	l	h/c
Ampullarius	·	·	+	·	+	·	+	+	·	·	·	l	h/c
Littorinoidea													
Littorina	·	·	+	·	+	·	·	·	+	+	+	m	h
Pomatias	·	·	+	·	+	·	·	·	·	+	+	t	h
Rissoidea													
Hydrobia	·	·	+	·	+	·	·	·	+	+	+	m	h
Rissoa	·	·	+	·	+	·	·	·	+	+	+	m	h
Bithynia	·	·	+	·	+	·	·	·	+	+	·	l	h/f
Caecum	·	·	+	·	+	·	·	·	+	+	+	m	h
Skeneopsis	·	·	+	·	+	·	·	·	+	+	·	m	h
Cerithioidea													
Turritella	·	·	+	·	+	·	·	·	+	+	+	m	f
Fagotia	·	·	+	·	+	·	·	·	+	+	·	l	h
Melanoides	·	·	+	·	+	·	·	·	+	+	·	l	h
Bittium	·	·	+	·	+	·	·	·	+	+	+	m	h/c
Stromboidea													
Aporrhais	·	·	+	·	+	·	·	·	+	+	+	m	f
Lamellarioidea													
Capulus	·	·	+	·	+	·	·	·	+	+	+	m	f
Erato	·	·	+	·	+	·	·	·	+	+	+	m	c
Calyptraeoidea													
Crepidula	·	·	+	·	+	·	·	·	+	+	+	m	f
Cypraeoidea													
Monetaria	·	·	+	·	+	·	·	·	+	+	+	m	c
Mauritia	·	·	+	·	+	·	·	·	+	+	+	m	c
Lyncina	·	·	+	·	+	·	·	·	+	+	+	m	c
Erosaria	·	·	+	·	+	·	·	·	+	+	+	m	c
Simnia	·	·	+	·	+	·	·	·	+	+	+	m	c
Pseudosimnia	·	·	+	·	+	·	·	·	+	+	+	m	c
Atlantoidea													
Atlanta	·	·	+	·	+	·	·	·	+	+	+	m	c
Naticoidea													
Polinices	·	·	+	·	+	·	·	·	+	+	+	m	c
Triphoroidea													
Triphora	·	·	+	·	+	·	·	·	+	+	+	m	c

TABLE 4 (*cont.*)

Superfamily genus	Character 1	2	3	4	5	6	7	8	9	10	11	12	13
Eulimoidea													
Eulima	·	·	+	·	+	·	·	·	+	+	+	m	c
Epitonioidea													
Epitonium	·	·	+	·	+	·	·	·	+	+	+	m	c
Muricoidea													
Truncularioppsis	·	·	+	·	+	·	·	·	+	+	+	m	c
Buccinum†	·	·	+	·	+	·	·	·	+	+	+	m	c
Conoidea													
Conus†	·	·	+	·	+	·	·	·	+	+	+	m	c

+, Present. † After Crisp (1973).
1, Epithelium without sensory cells (free nerve endings only).
2, Cilia star cells.
3, Epithelium with sensory cells, having processes (= central zone).
4, Cilia bottles.
5, Laterally situated ciliated epithelium (= lateral zones).
6, Occurrence of pigment bodies.
7, All epithelia two-layered.
8, Lateral zones formed as grooves.
9, Si1 cell within the lateral zone.
10, Si2 cell within the lateral zone.
11, Si4 cell within the central zone.
12, Habitat (m, marine; l, freshwater; t, terrestrial).
13, Diet, (h, herbivorous; c, carnivorous; f, filter feeding).

Valvatoidea, Viviparoidea and Cyclophoroidea are suggested to represent early offshoots of the Caenogastropoda (Fretter & Graham 1962, p. 623). Accordingly, these three independent lines of a similar low level of organization are classified here within the suborder Architaenioglossa.

Neotaenioglossa, Heteroglossa and Stenoglossa

The Si1, Si2, and Si4 cells, described first by Welsch & Storch (1969) and later by Crisp (1973) in the osphradia of Stenoglossa, are likewise present in the majority of the former Mesogastropoda. This predominantly mesogastropod stock is classified here as Neotaenioglossa and Heteroglossa (see below and table 6). The cells, identified by Edlinger (1980) as Si1, Si2 and Si4 cells in the osphradium and the Hancock's organ of *Haminea navicula* (Opisthobranchia, Bullomorpha) are, however, entirely different (see Haszprunar 1984*b*).

On the basis of investigation of species which are marine, freshwater, and terrestrial as well as of different habits, it is possible to discriminate between the basic systematic character and those versions of it owing to difference in habit and habitat (see also table 4).

Neotaenioglossa, Heteroglossa, and Stenoglossa agree in possessing the highly specialized Si2 cells, which predominantly contribute to the lateral zone. Welsch & Storch (1969) described axons of this cell type, but neither their own scheme nor the diagram given by Crisp (1973) show axons, rather than nervous tissue, between the Si2 cells. These characters, also present in the species described here, lead to the opinion that the Si2 cell is a secondary sensory cell. This is supported by the fact that the lateral zone, but not the central zone proper, is multiplied in some higher groups. The existence of paddle cilia, although only in marine species, additionally supports this opinion (see below).

A second character that unites Neotaenioglossa, Heteroglossa, and Stenoglossa is present in the Si1 cell, always located between the Si2 cells and the central zone. They do not exist in the terrestrial *Pomatias elegans*, but are equally present in freshwater and marine species. Compared with the number of Si2 cells, few Si1 cells can be found within each lateral zone. This may be because Si1 cells develop into Si2 cells during morphogenesis.

The third character linking the three suborders is represented by the Si4 cells that exist in all superfamilies investigated, but only in the marine forms. This cell type also exists in the terrestrial *Pomatias elegans*, and may thus be reminiscent of its marine ancestors (Fretter & Graham 1962, p. 621). The Si4 cells are always arranged within the central zone close to the Si1 cells. They show some variation in having processes that reach the surface of the sensory epithelium as described by Crisp (1973) and here confirmed in *Rissoa*, but such processes do not occur in all the species investigated (for example, *Polinices*). The Si4 cell is likewise suggested to be chemosensitive by Crisp (1973).

These three special cell types support the evolutionary unity of Neotaenioglossa, Heteroglossa, and Stenoglossa, since a convergent differentiation of three such specialized cell types and their constant arrangement within the osphradial epithelium appears to be impossible. Accordingly, it is to be stressed that the Stenoglossa did not evolve independently from the Archaeogastropoda as suggested by Ponder (1973), but are a monophyletic branch with roots within the basal Neotaenioglossa, rather than among advanced ones (see Ponder 1973). The Heteroglossa, nom.nov.†, are considered as a separate suborder of the Caenogastropoda. Their caenogastropodan nature is shown not only by the existence of the Si1-Si2-Si4-cell types of their osphradia, but also by their possession of a true pectinibranch gill and a prosobranch mode of spermiogenesis (Healy 1982). Thus, they have nothing to do with the Architectonicoidea, with which they are usually united (see table 5), the latter being not even Prosobranchia (see

TABLE 5. THE TAXON 'HETEROGASTROPODA' AS RECENTLY USED BY DIFFERENT AUTHORS

systematic position	included groups	references
suborder of Caenogastropoda	Triphoroidea Architectonicoidea Epitonioidea	Kosuge 1966 Habe & Kosuge 1966
order of Opisthobranchia	Triphoroidea Architectonicoidea Epitonioidea	Climo 1975
suborder of Caenogastropoda	Triphoridae Cerithiopsidae Epitoniidae Mathildidae Architectonicidae	Fretter 1979
superfamily of Caenogastropoda	Triphoridae Architectonicidae Mathildidae Pyramidellidae	Boss 1982
suborder of Caenogastropoda	Cerithiopsoidea Triphoroidea Epitonioidea Eulimoidea Architectonicoidea	Fretter & Graham 1982,

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† Instead of Heterogastropoda, to get '-glossa' as an ending for the names of all suborders of the Caenogastropoda, to avoid the different senses in which this word (Heterogastropoda) has been used (see Table 5), and to emphasize the various types of radula which its members possess.

Haszprunar 1984*b*, *c*). According to Kosuge (1966), the Heteroglossa appear to represent another offshoot from basal Neotaenioglossa.

Prosobranchia

Figure 8 outlines relations within the Prosobranchia with respect to the points of emergence of each new type of osphradium. Table 6 tabulates the prosobranch superfamilies in the way discussed above. The few superfamilies the osphradia of which were not investigated are placed therein according to the opinion of the majority of authors.

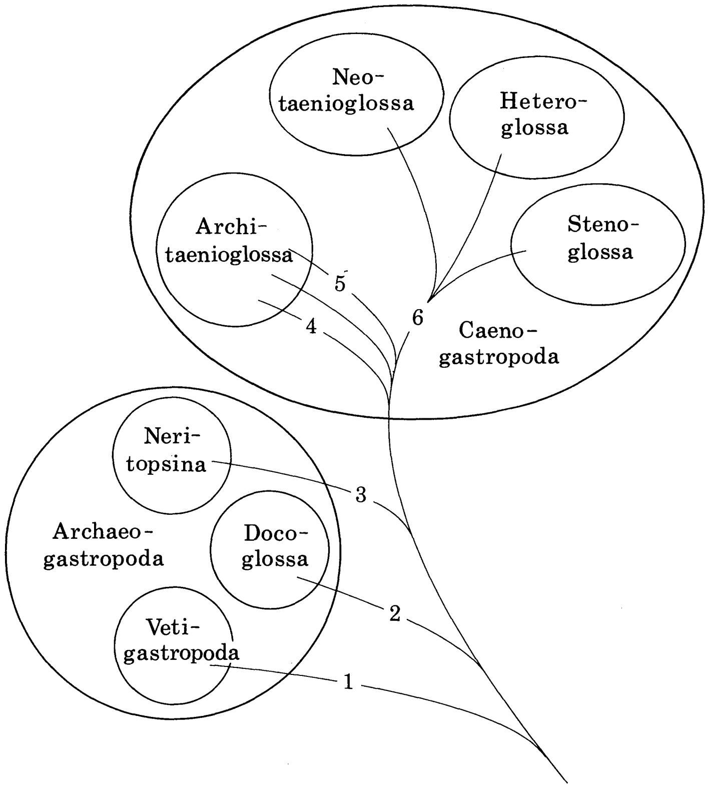


FIGURE 8. Proposed interrelations of the Prosobranchia in the light of osphradial fine structure types: 1, Vetigastropoda-type; 2, Docoglossa type; 3, Neritopsina type; 4, *Valvata* type; 5, Viviparoidea type; 6, Si1/Si2/Si4 type.

The main consequence of the present results is the abandonment of the taxon Mesogastropoda: it is split up into Architaenioglossa (three independent early offshoots), Neotaenioglossa, Heteroglossa (forming with Stenoglossa a monophyletic assemblage), and the Allogastropoda (Architectonicoidea, Pyramidelloidea) which, evidence suggests, are not even prosobranchs (see Haszprunar 1984*b*, *c*).

Functional significance

All physiological and ecological investigations into the prosobranch osphradium so far have suggested a probably chemoreceptive role for the organ. Nevertheless, the opinion of Yonge (1947, 1962, 1977; Hulbert & Yonge 1937), claiming that the osphradium is mainly

TABLE 6. CLASSIFICATION OF THE PROSOBRANCHIA PROPOSED HERE

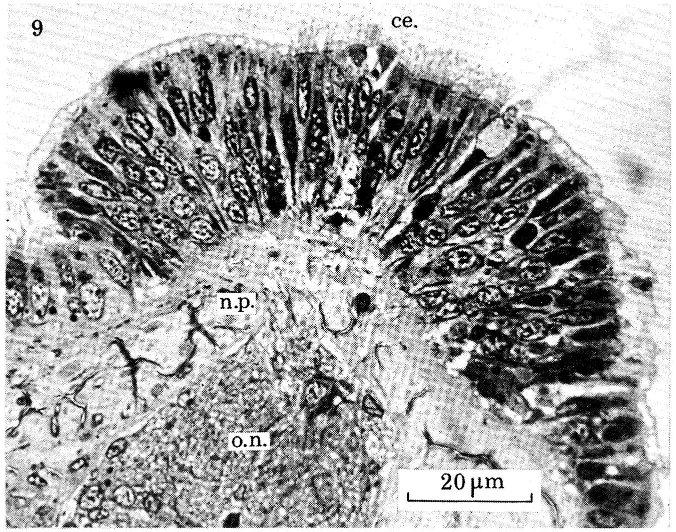
Subclass Prosobranchia Milne-Edwards, 1848	
Order Archaeogastropoda Thiele, 1925	
Suborder Vetigastropoda Salvini-Plawen, 1980	
Superfamily	Pleurotomarioidea
	Fissurelloidea
	Trochoidea
Suborder Docoglossa Troschel, 1866	
Superfamily	Patelloidea
Suborder Neritopsina Cox, 1960	
Superfamily	Neritoidea
Incertae sedis:	
Superfamily	Neomphaloidea
	Cocculinoidea
	Seguenzioidea
Order Caenogastropoda (= Pectinibranchia) Cox, 1960	
Suborder Architaenioglossa Haller, 1892 emend.	
Superfamily	Valvatoidea
	Cyclophoroidea
	Viviparoidea
Suborder Neotaenioglossa Haller, 1892 emend.	
Superfamily	Littorinoidea
	Rissoidea
	Rissoelloidea (?)
	Loxonematoidea
	Cerithioidea
	Stromboidea
	Hipponicoidea
	Calyptraeoidea
	Lamellarioidea
	Cypraeoidea
	Atlantoidea
	Naticoidea
	Tonnoidea
Suborder Heteroglossa (nov.)	
Superfamily	Cerithiopsoidea
	Triphoroidea (= Rhiniglossa)
	Epitonioidea (= Ptenoglossa)
	Eulimoidea (= Aglossa)
Suborder Stenoglossa (= Neogastropoda) Bouvier, 1887	
Superfamily	Muricoidea (= Rhachiglossa)
	Cancellarioidea (= Nematoglossa)
	Conoidea (= Toxoglossa)

mechanoreceptive, has strongly influenced the literature. Up to now there are no physiological investigations of Archaeogastropoda, but the structural data described here help to solve this question.

During the last 15 years so-called paddle cilia (or discocilia) have been described in several phyla of the Metazoa (see table 7). Comparison shows that the similarly named ciliary derivatives described by Berquist *et al.* (1977), Heimler (1978) and Bone *et al.* (1982) are entirely different in their structure (no swellings or no spiral configuration of the microtubular complex). Although many authors accept that paddle cilia are genuine structures (most recently Matera & Davis 1982), there are still those who regard them as artefacts. The data given here agree with the facts described by former authors with respect to the following points.

(i) True paddle cilia occur only in zones of sensory cells, and do not occur in adjacent non-sensory ciliated epithelia.

9



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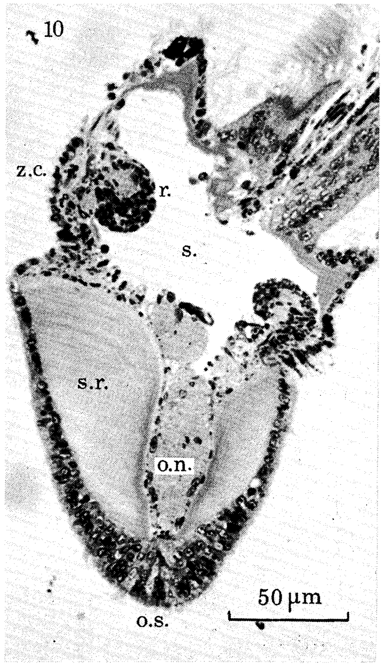

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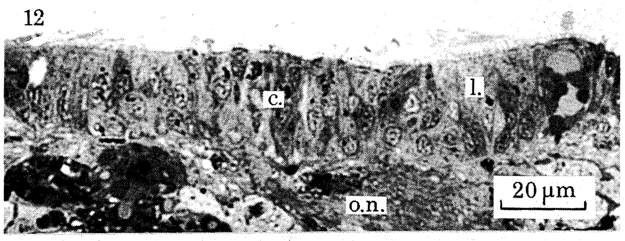

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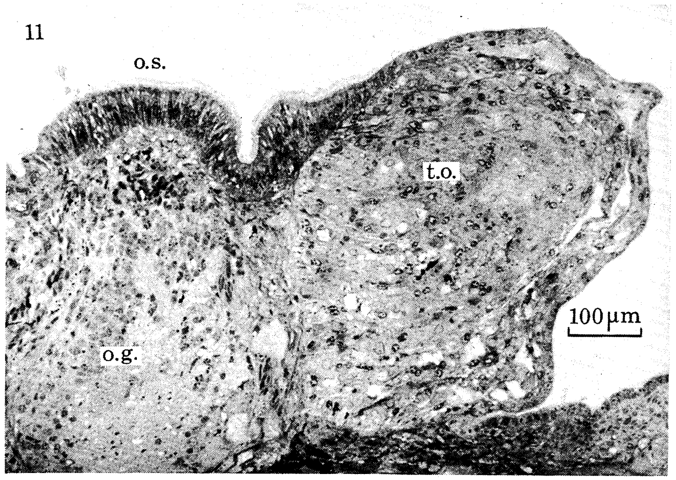

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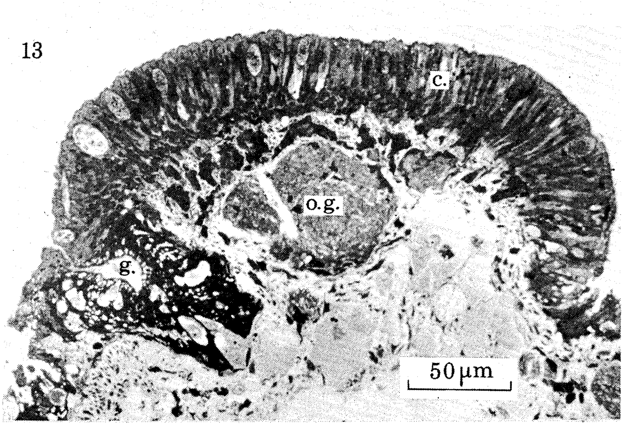

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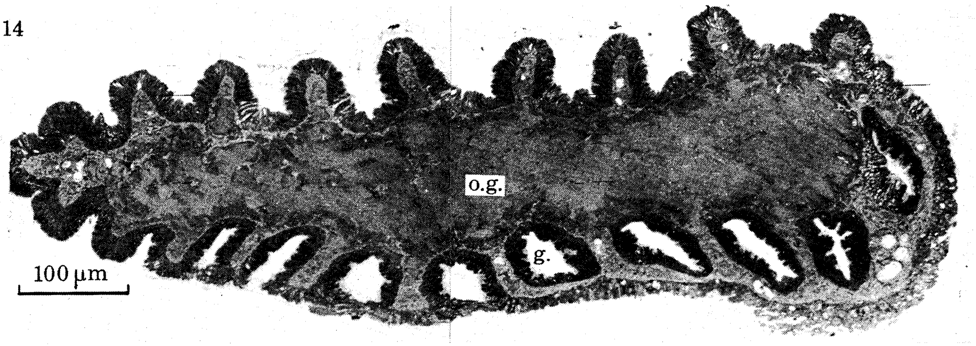


FIGURES 9–14. Semithin sections of osphradia of types 1–5 ('Archaetypes'). c., Central zone; ce., central ciliary zone; g., groove; l., lateral zone; n.p., neural process; o.g., osphradial ganglion; o.n., osphradial nerve; o.s., osphradial sensory epithelium; r., gill retractor (with nerve); s., efferent vessel of the gill; s.r., skeletal rod; t.o., tubercle organ; z.c., zone of grooved epithelium.

FIGURE 9. *Diodora italica.*

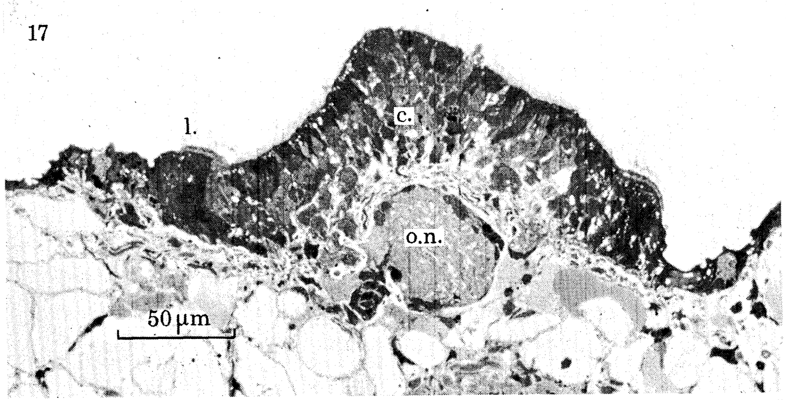
FIGURE 10. *Gibbula varia.*

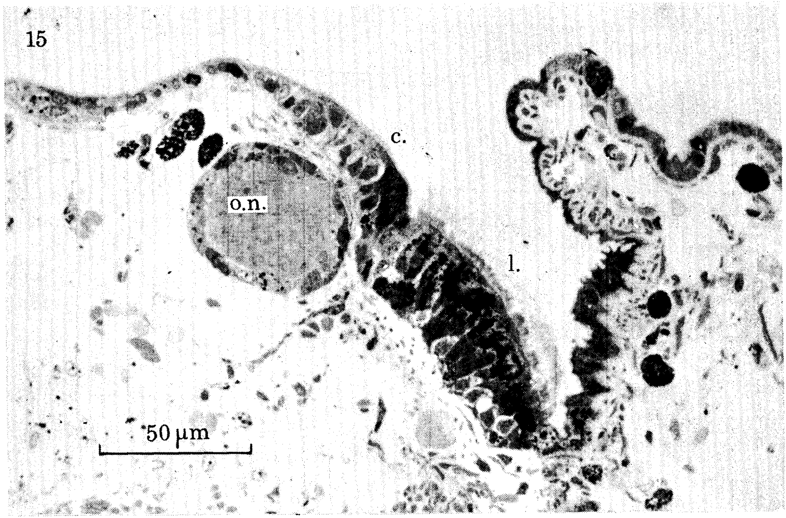
FIGURE 11. *Patella coerulea.*

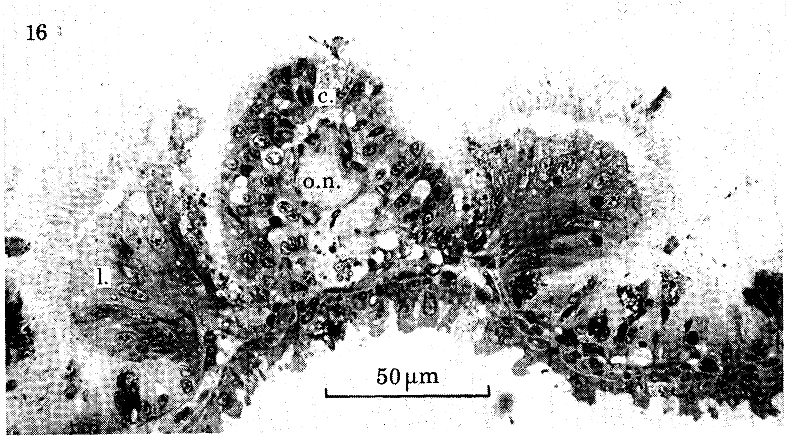
FIGURE 12. *Puperita pupa.*

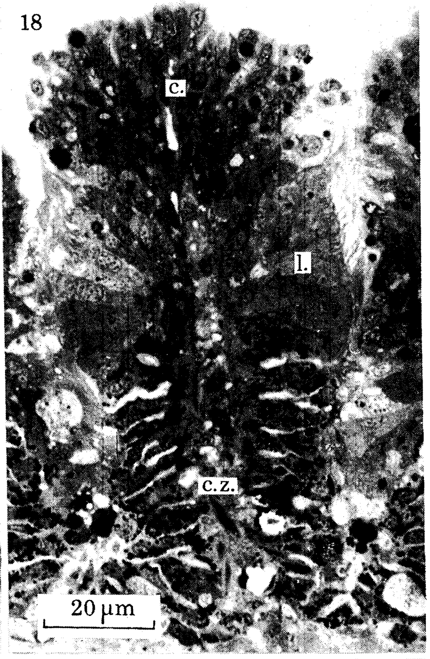
FIGURE 13. *Viviparus contectus.*

FIGURE 14. *Marisa cornuarietis* (nearly horizontally sectioned).









FIGURES 15–19. Semi-thin sections of osphradia of the Si1–Si2–Si4 type. c., Central zone; c.z., zone of pigmented, folded epithelium; l., lateral zone; o.n., osphradial nerve.

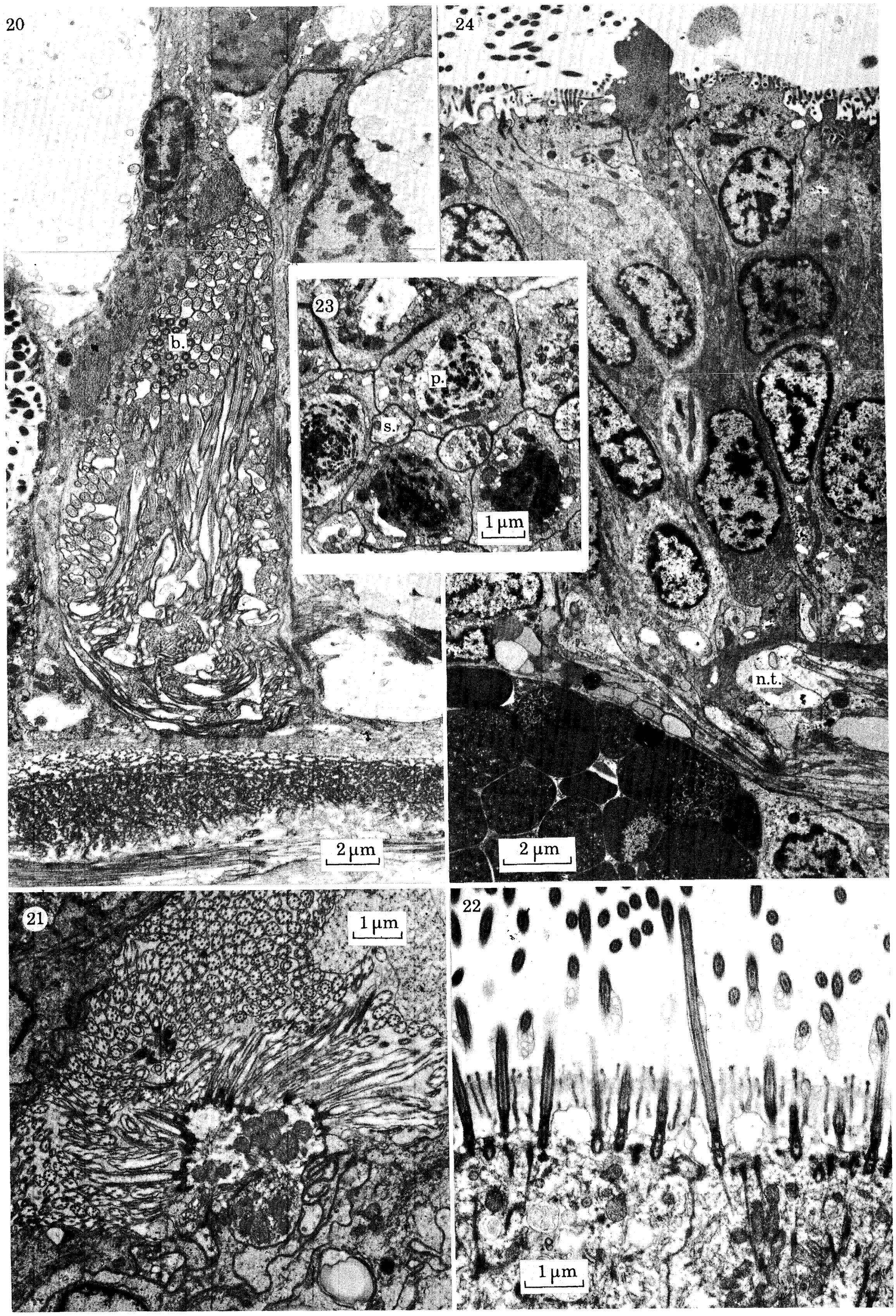
FIGURE 15. *Pomatias elegans.*

FIGURE 16. *Rissoa* sp.

FIGURE 17. *Fagotia acicularis.*

FIGURE 18. *Pseudosimnia* sp. (one leaflet).

FIGURE 19. *Polinices guillemini* (one leaflet).



FIGURES 20–24. b., Basal bodies; n.t., nervous tissue; p., pigment body; s., process of sensory cell.

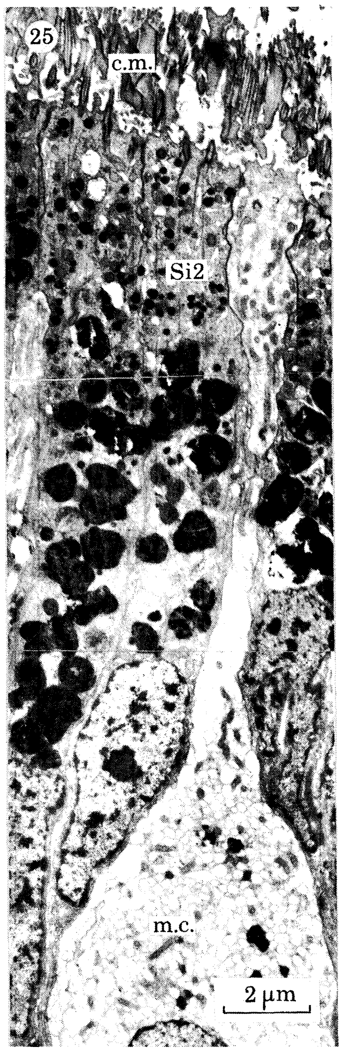
FIGURE 20. *Haliotis lamellosa*; cilia bottle.

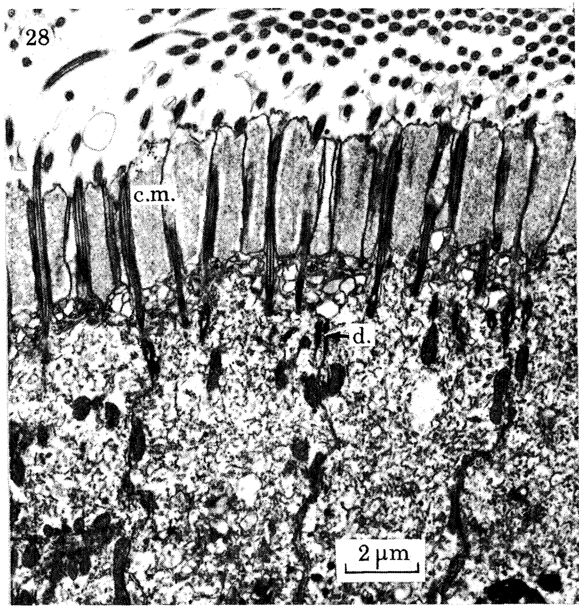
FIGURE 21. *Patella coerulea*: cilia star cell (osphradial ganglion).

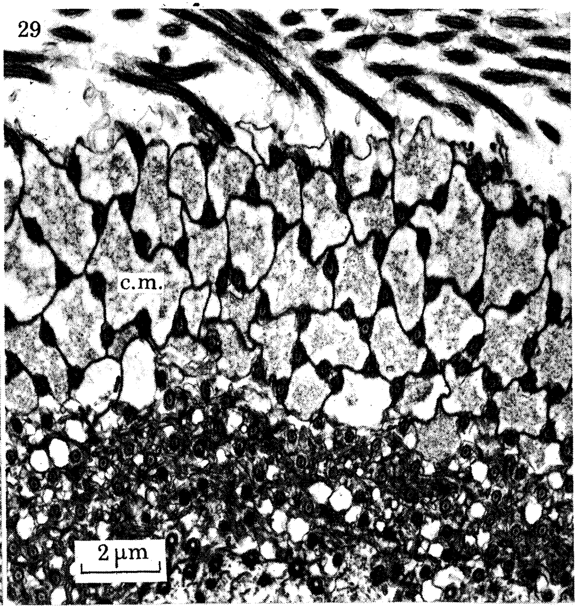
FIGURE 22. *Diodora italica*: extended ciliary membranes (central ciliated zone).

FIGURE 23. *Nerita plicata*: horizontally sectioned part of the central zone.

FIGURE 24. *Puperita pupa*: special cell 'y'.







FIGURES 25–29. c.m., Columnar microvilli; d., desmosomes; m.c., mucous cell; n.t., nervous tissue; p.c., paddle cilia.

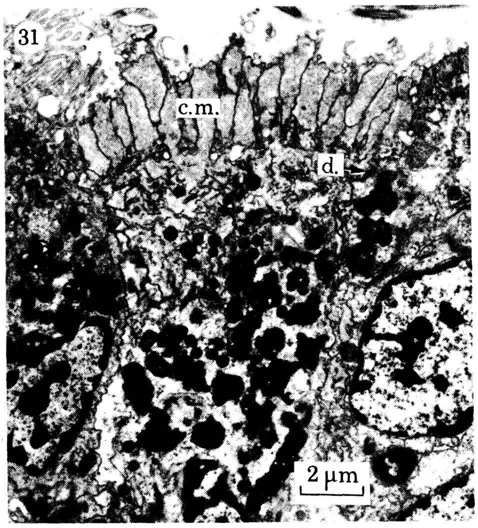
FIGURE 25. *Pomatias elegans*: lateral zone.

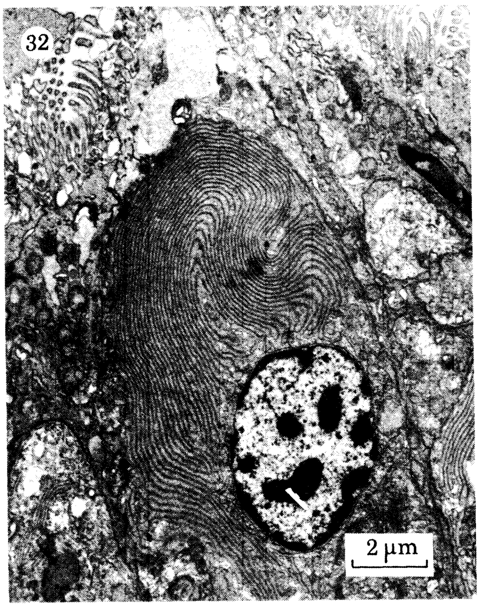
FIGURE 26. *Aporrhais pespelecani*: Si2 cell with paddle cilia.

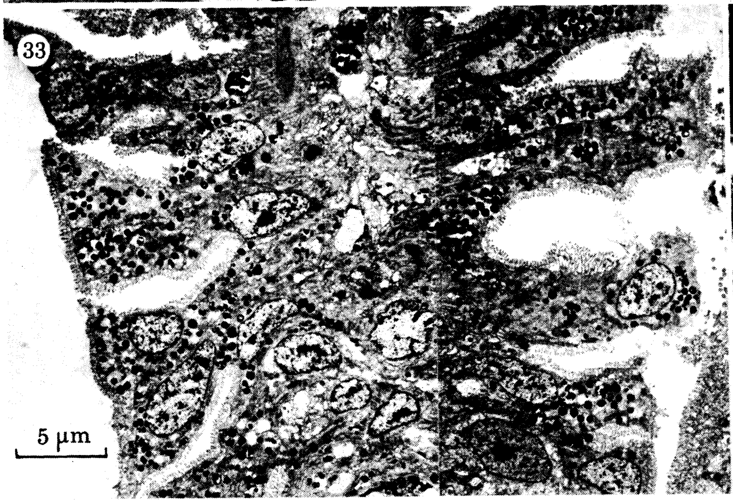
FIGURE 27. *Rissoa* sp.: Si2 cells with paddle cilia.

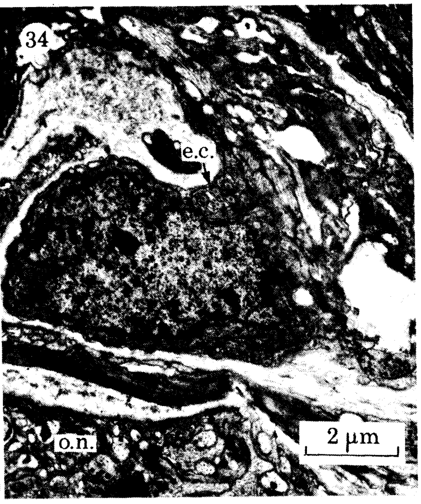
FIGURE 28. *Polinices guillemini*: Si2 cells (vertical section).

FIGURE 29. *Polinices guillemini*: Si2 cells (oblique section).









FIGURES 30–34. c.m., Columnar microvilli; d., desmosome; e.c., encapsuled cilia; s.c., sensory cilium; se., sensory cell; sp., supporting cell.

FIGURE 30. *Littorina neritoides*: central zone.

FIGURE 31. *Crepidula moulinsi*: Si1 cells.

FIGURE 32. *Rissoa* sp.: Si4 cell.

FIGURE 33. *Pseudosimnia* sp.: zone of pigmented, folded epithelium.

FIGURE 34. *Pomatias elegans*: cell with encapsuled cilia (arrow).

Table 7. Occurrence of the so-called paddle cilia so far investigated

Phylum – class	location	suggested function	references
Porifera, Demospongia			
12 species	nearly all larval cilia	?	Berquist *et al.* 1977
Plathelminthes, Turbellaria			
29 species	epidermal sensory cells	artefact	Ehlers & Ehlers 1978
Gnathostomulida			
several species	epidermal cells	artefact	Sterrer 1968
Mollusca, Caudofoveata			
Falcidens gutturosus	terminal sense organ (= osphradium)	chemoreceptive	Haszprunar 1981
Mollusca, Solenogastres			
2 species	terminal sense organ, foot	chemoreceptive	Haszprunar 1981
Mollusca, Placophora			
Lepidopleurus cajetanus	lateral sense organ	chemoreceptive	Haszprunar unpubl.
Chitonida: 4 species	osphradium	chemoreceptive	Haszprunar 1981, 1984*c*
Acanthochiton communis	osphradium	chemoreceptive	Haszprunar 1981, 1985
Mollusca, Gastropoda			
Prosobranchia: 35 species	osphradium	chemoreceptive	Haszprunar (this paper)
Terebra sp.	siphon	chemoreceptive	Storch 1972
Neptunea antiqua	osphradium	chemoreceptive	Storch 1972
Haminea navicula	Hancock's organ	chemoreceptive	Haszprunar (unpublished)
Pleurobranchaea californica	rhinophores	chemoreceptive	Matera & Davis 1982
Mollusca, Bivalvia			
Mytilus californianus	byssus attachment plaque forming region	as spatula	Tamarin *et al.* 1974
5 species	osphradium	chemoreceptive	Haszprunar 1985
Mollusca, Cephalopoda			
Nautilus pompilius	rhinophores	chemoreceptive	Barber & Wright 1969
Loligo pealei (embryo)	external yolk sac, mantle cavity	?	Arnold & Williams-Arnold 1980
Echiurida, Echiurinea			
Bonellia viridis	proboscis	?	Jaccari & Schembri 1979
Annelida, Polychaeta			
Lanice conchilega	epidermal cells	produce water currents	Heimler 1978
9 species	gills	?	Storch & Alberti 1978
Tentaculata, Brachiopoda			
Lingula unguis	lophophore	chemoreceptive	Storch & Welsch 1976
Echinodermata, Echinoidea			
Psammechinus miliaris	globiferous pedicellariae	chemo-, mechanoreceptive	Oldfield 1975
Hemichordata, Pterobranchia			
Rhabdopleura compacta	cephalic shield, tentacles	water current, ionic transport	Dilly 1977*a*, *b*
Rhabdopleura nordmanni	tentacles		Welsch 1983
Chordata, Tunicata			
Ciona intestinalis	endostyle	artefact	Bone *et al.* 1982

(ii) Paddle cilia occur only in marine organisms.

(iii) Paddle cilia are not always found, and there is great difference in their number in different specimens.

On combining the arguments of Ehlers & Ehlers (1978) and Matera & Davis (1982) it becomes obvious that these special cilia are very dynamic structures (the enrolling process, but not the microtubular pattern, has been shown to be reversible). They thus *may* assume the appearance of paddle cilia on fixation, but if present, they are typical only of chemoreceptors, especially in molluscs (see table 7), where they are found to be present also in other chemoreceptors than osphradia. The pseudopaddle cilia described by Berquist *et al.* (1977), Heimler (1978) and Bone *et al.* (1982) have never been suggested to be chemoreceptive.

The existence of paddle cilia, not only in the certainly chemoreceptive osphradia of higher Prosobranchia, but also in the Archaeogastropoda, as well as their lack of mechanoreceptive structures such as are present in the subpallial sensory strips of the Patellidae, indicate a purely chemoreceptive function for the osphradium also in Archaeogastropoda. Its role as a food-detector, however, is certainly less important than in the Caenogastropoda, although there are some carnivorous forms (for example, some species of *Calliostoma*). It appears possible that another function may be still more typical of archaeogastropod osphradia, and this function may be the primitive one within the Mollusca in general. It may be that it is used in the search for a sexual partner or to coordinate spawning, as is indicated by the results of Wölper (1950). There are also some results in other molluscan classes that agree with this hypothesis. In the Placophora and Bivalvia the likewise chemoreceptive osphradia are located at the end of the body beneath the anus in the exhalant current. Thus, they are with certainty not used as food-detectors, see Haszprunar (1985).

Summing up, the osphradia of Prosobranchia are demonstrated to be chemoreceptive, mainly indicated by the presence of paddle cilia. Their role in Archaeogastropoda also relates to their sexual biology (coordination of spawning, search for a mate), a role altered within the Caenogastropoda so that they become important distance-chemoreceptors in the search of food.

I thank Professor L. v. Salvini-Plawen (University of Wien) for the initiation of this study as well as for many discussions about this contribution. I also acknowledge the kindness of Dr Vera Fretter (University of Reading) and Professor F. Giusti (University of Siena), who criticized the manuscript. I am deeply indebted to Professor A. Graham (University of Reading), who so kindly added his comments and corrections to the manuscript. The work was supported by the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich (project number P4751) and by the Kulturamt der Stadt Wien (grant number MA7/1781/79).

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Note added in proof (17 August 1984). A recently published paper by Maeda (1983, Types of osphradia in the Prosobranchia with special reference to the relation of feeding habits. *Venus* (*Jap. Jl Malac.*) **41**, 264–273) completes external morphology of prosobranch osphradia. Lacking structural investigations, the author fails in describing six types of osphradia in prosobranchs (differing from those described in this paper).

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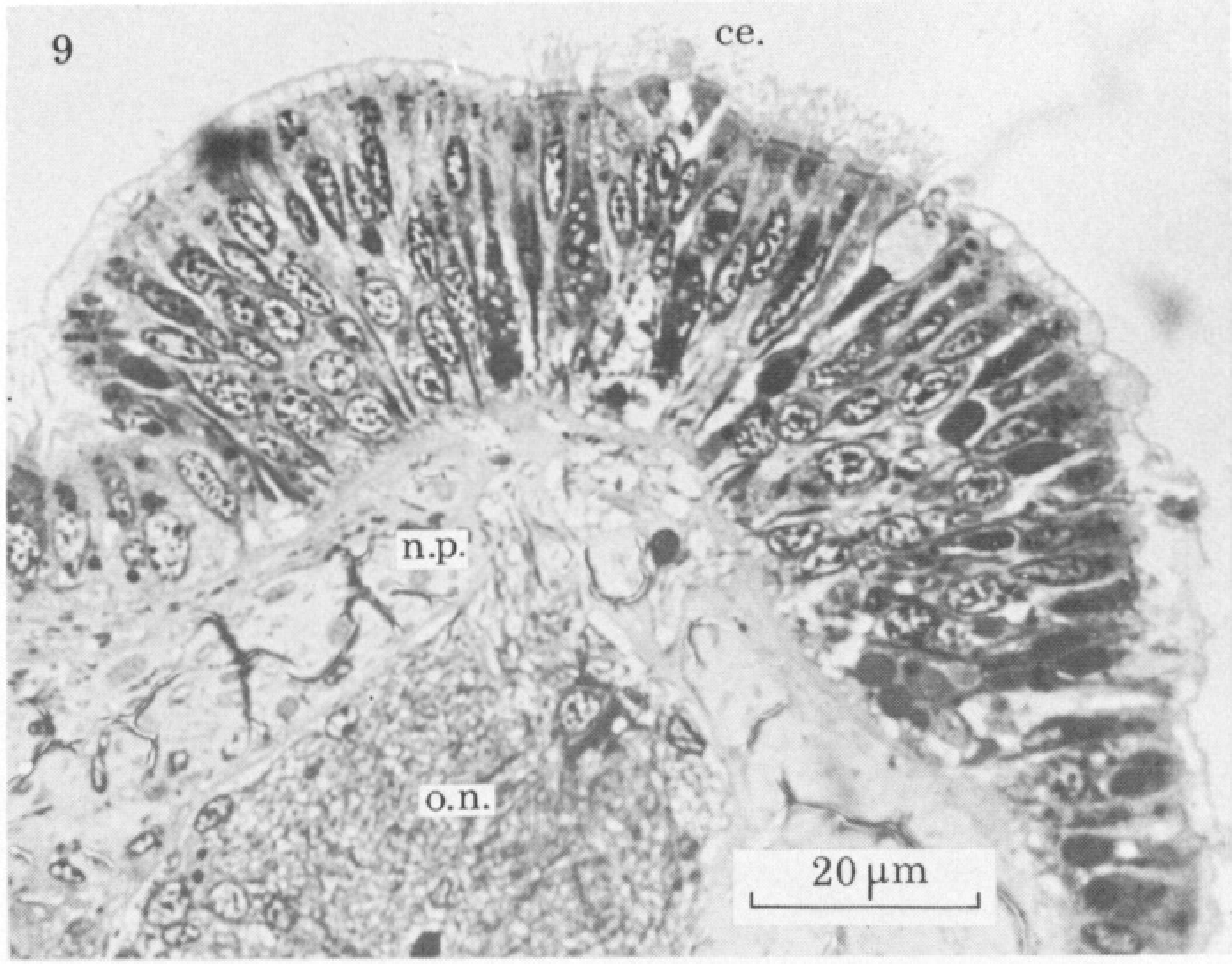

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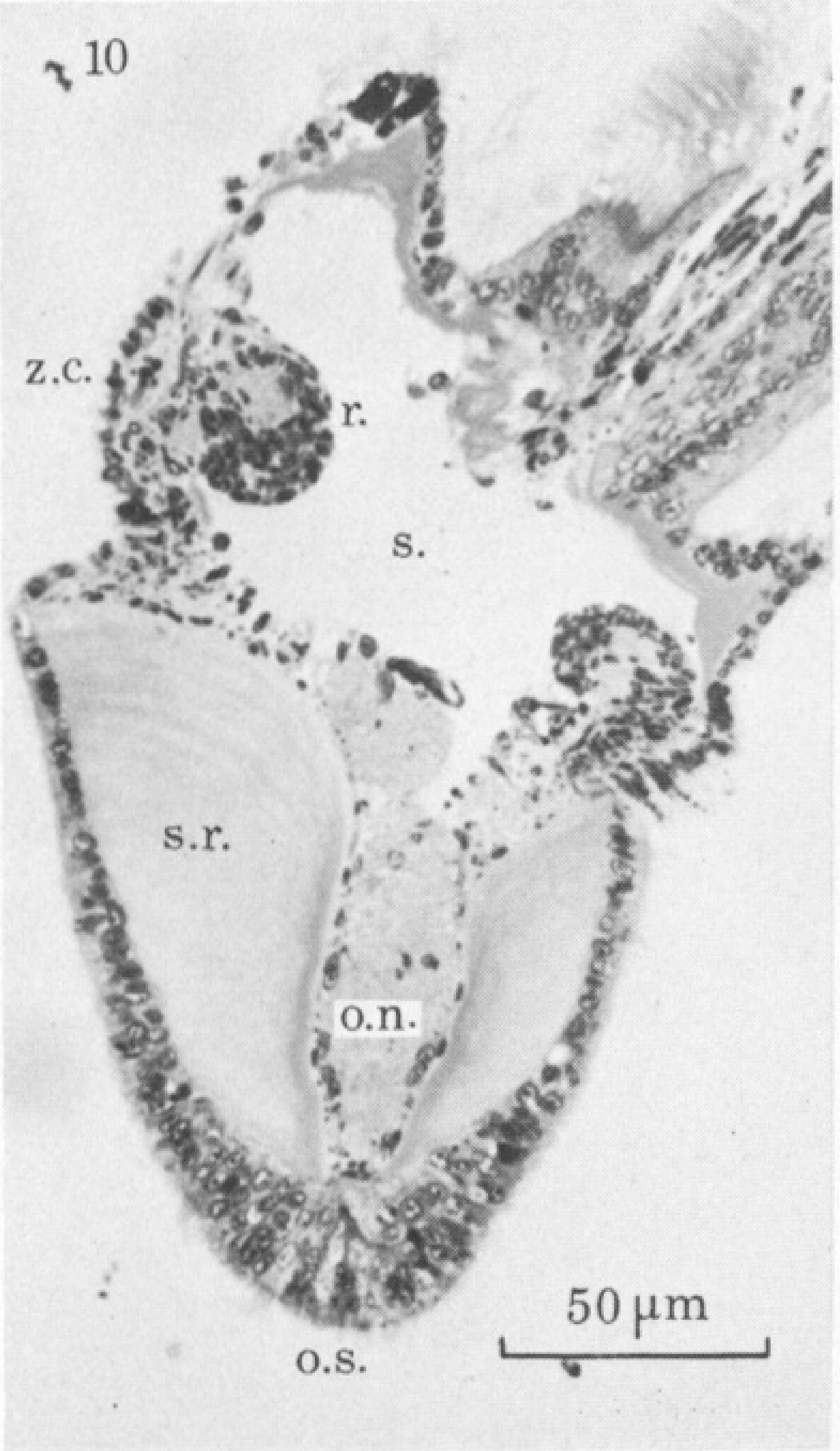

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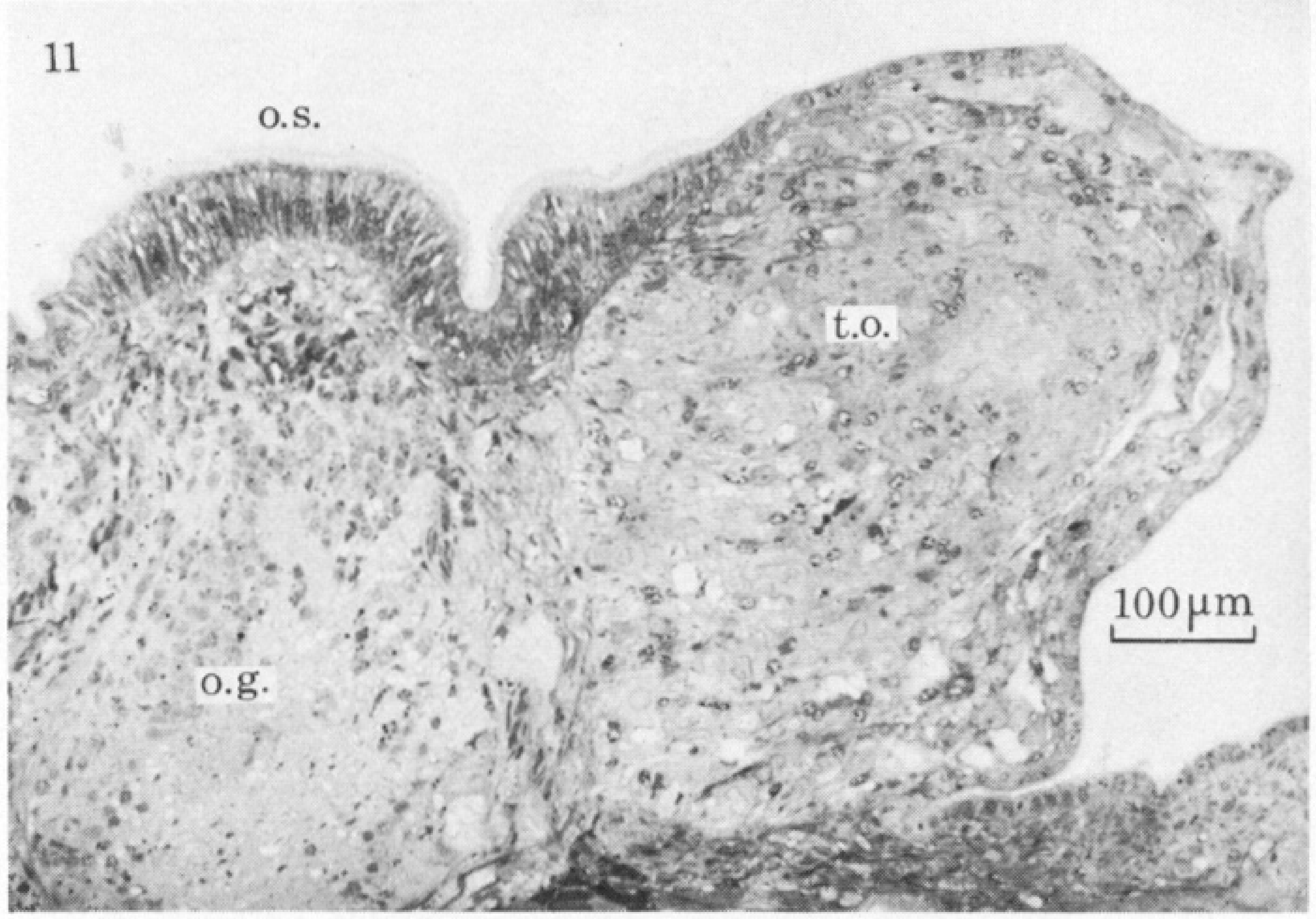

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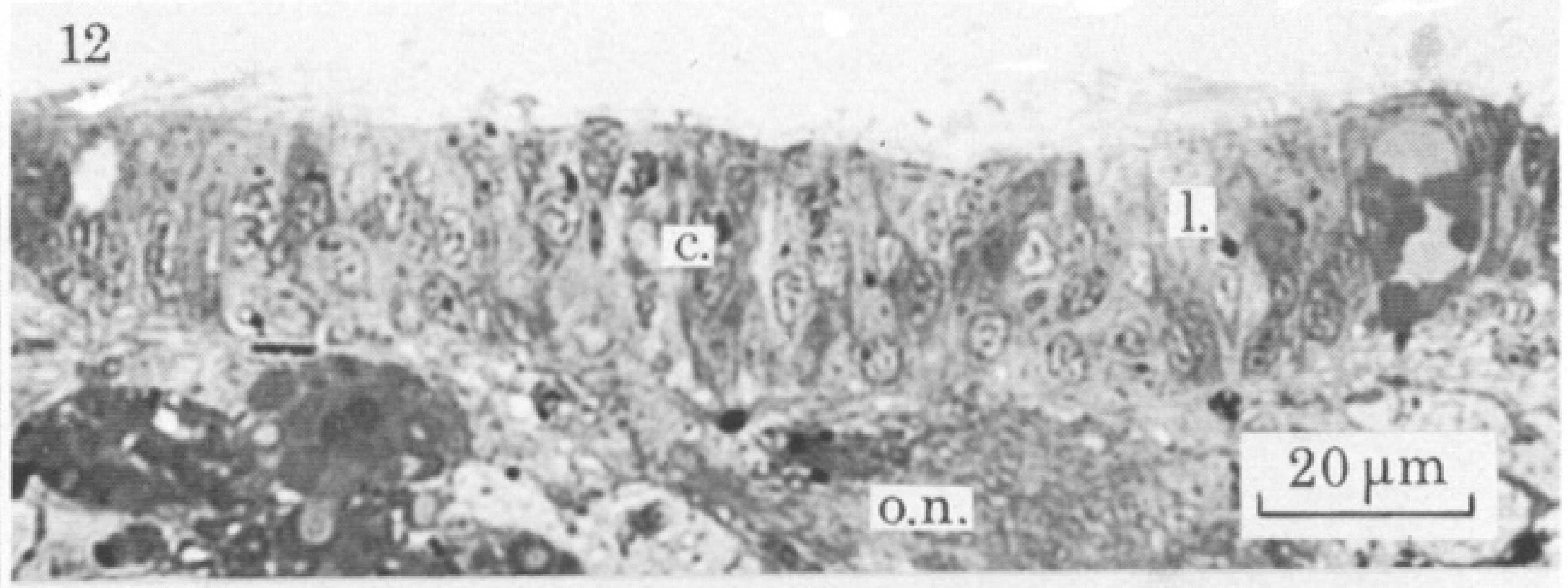

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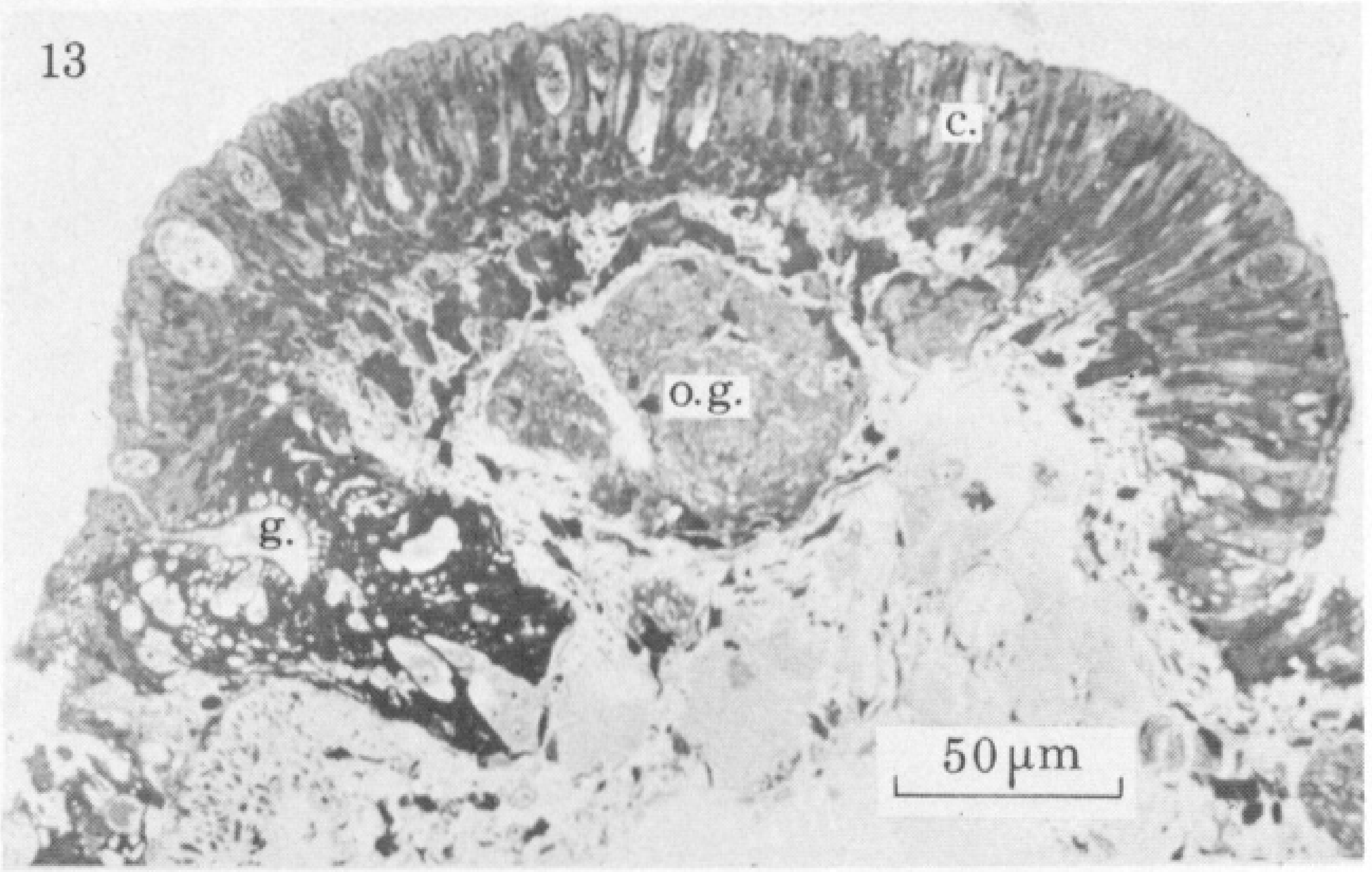

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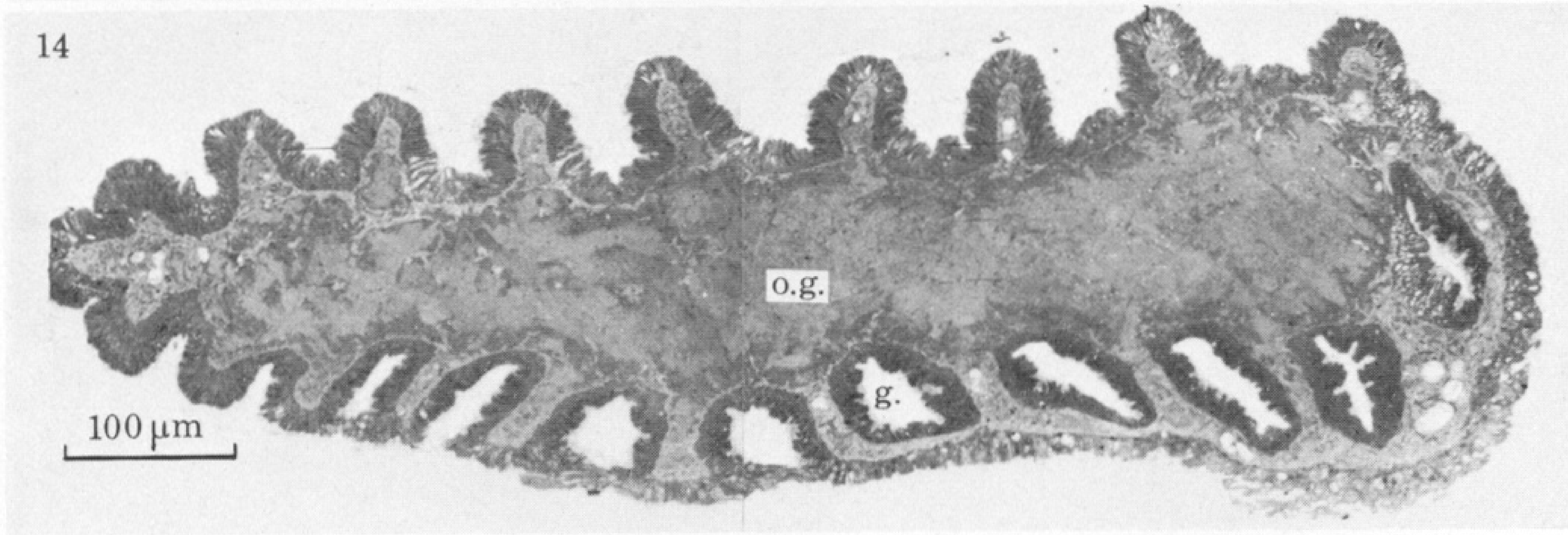


FIGURES 9–14. Semithin sections of osphradia of types 1–5 ('Archaetypes'). c., Central zone; ce., central ciliary zone; g., groove; l., lateral zone; n.p., neural process; o.g., osphradial ganglion; o.n., osphradial nerve; o.s., osphradial sensory epithelium; r., gill retractor (with nerve); s., efferent vessel of the gill; s.r., skeletal rod; t.o., tubercle organ; z.c., zone of grooved epithelium.

FIGURE 9. *Diodora italica*.

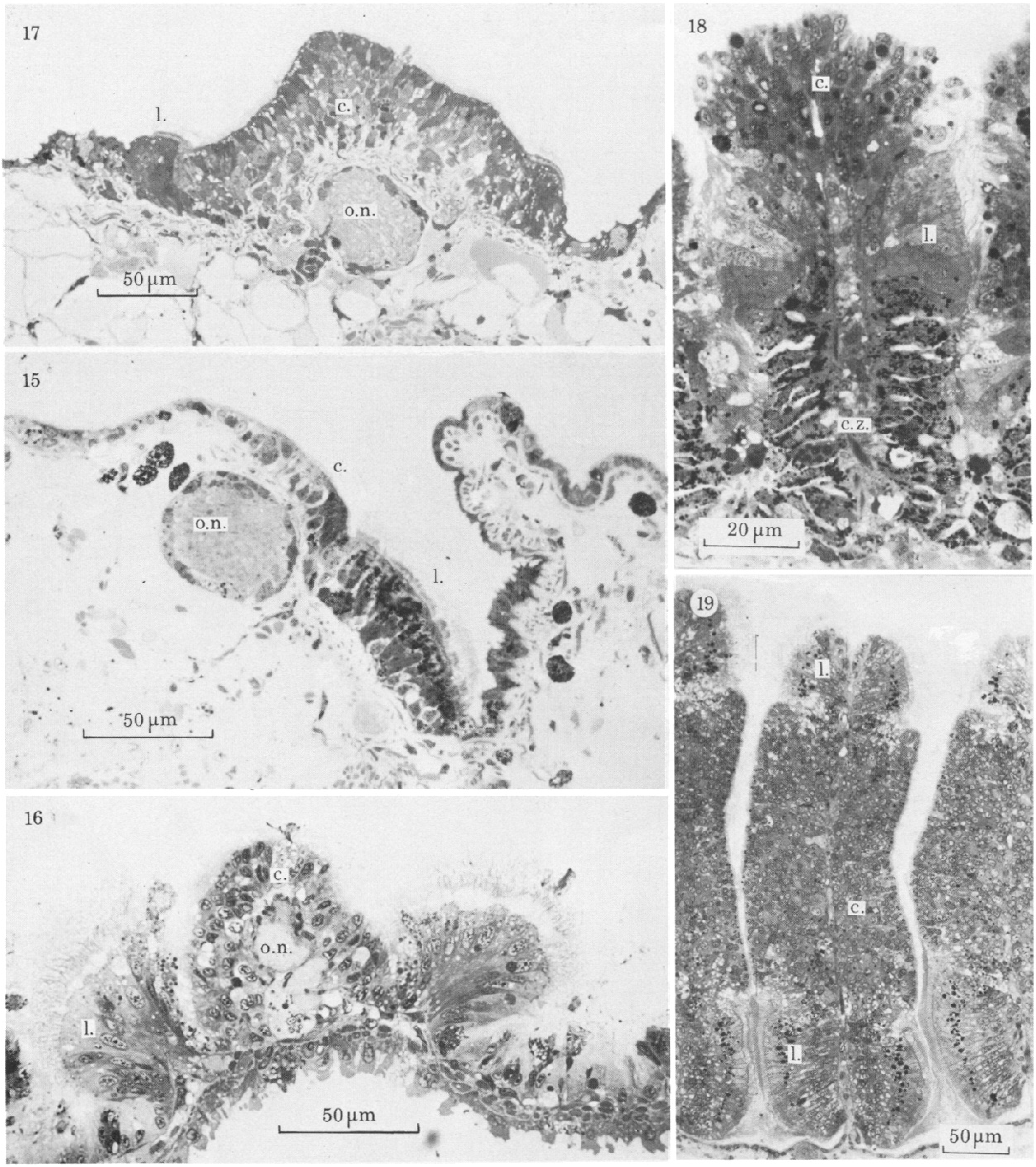
FIGURE 10. *Gibbula varia*.

FIGURE 11. *Patella coerulea*.

FIGURE 12. *Puperita pupa*.

FIGURE 13. *Viviparus contectus*.

FIGURE 14. *Marisa cornuarietis* (nearly horizontally sectioned).



FIGURES 15–19. Semi-thin sections of osphradia of the Si1–Si2–Si4 type. c., Central zone; c.z., zone of pigmented, folded epithelium; l., lateral zone; o.n., osphradial nerve.

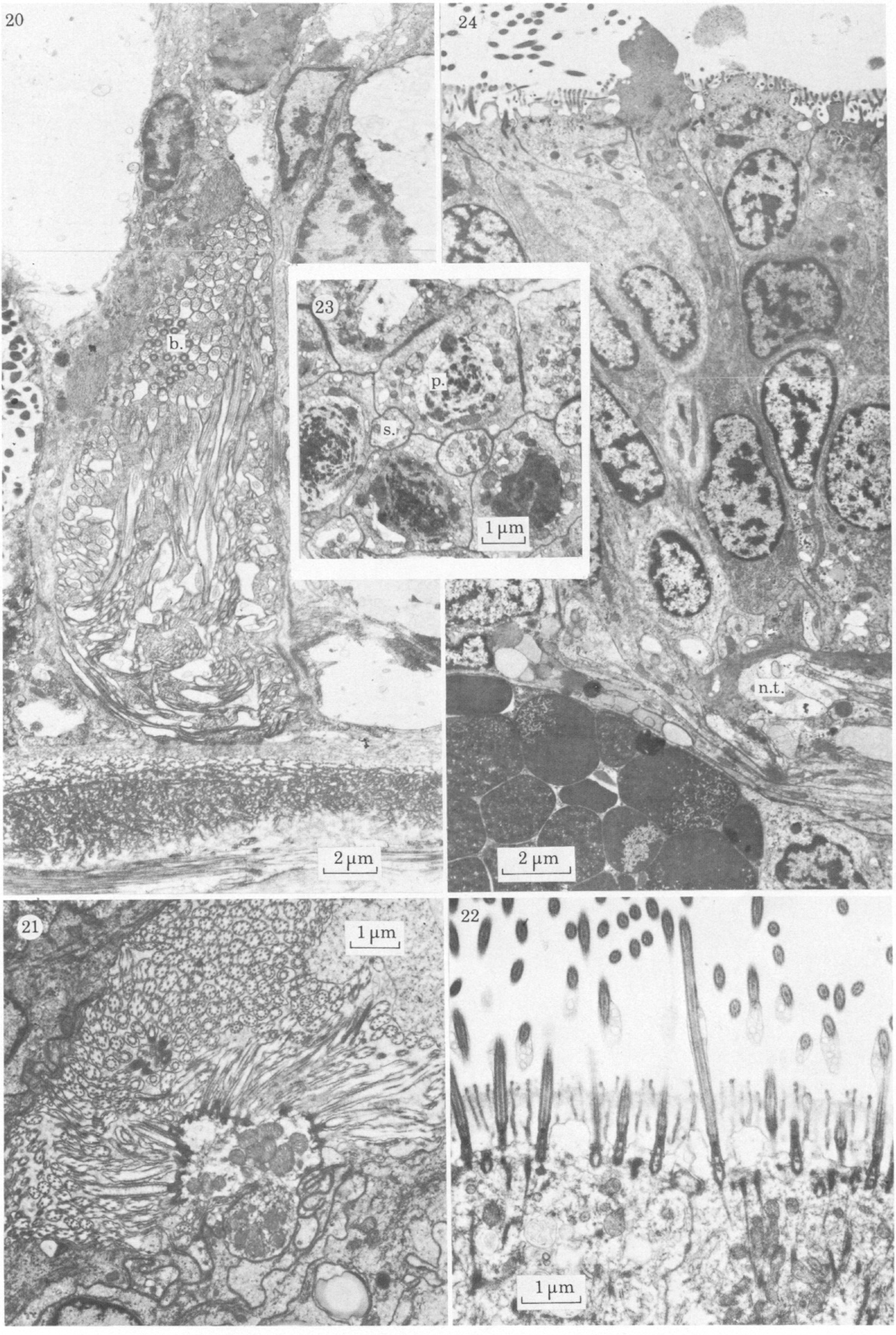
FIGURE 15. *Pomatias elegans.*

FIGURE 16. *Rissoa* sp.

FIGURE 17. *Fagotia acicularis.*

FIGURE 18. *Pseudosimnia* sp. (one leaflet).

FIGURE 19. *Polinices guillemini* (one leaflet).



Figures 20–24. b., Basal bodies; n.t., nervous tissue; p., pigment body; s., process of sensory cell.

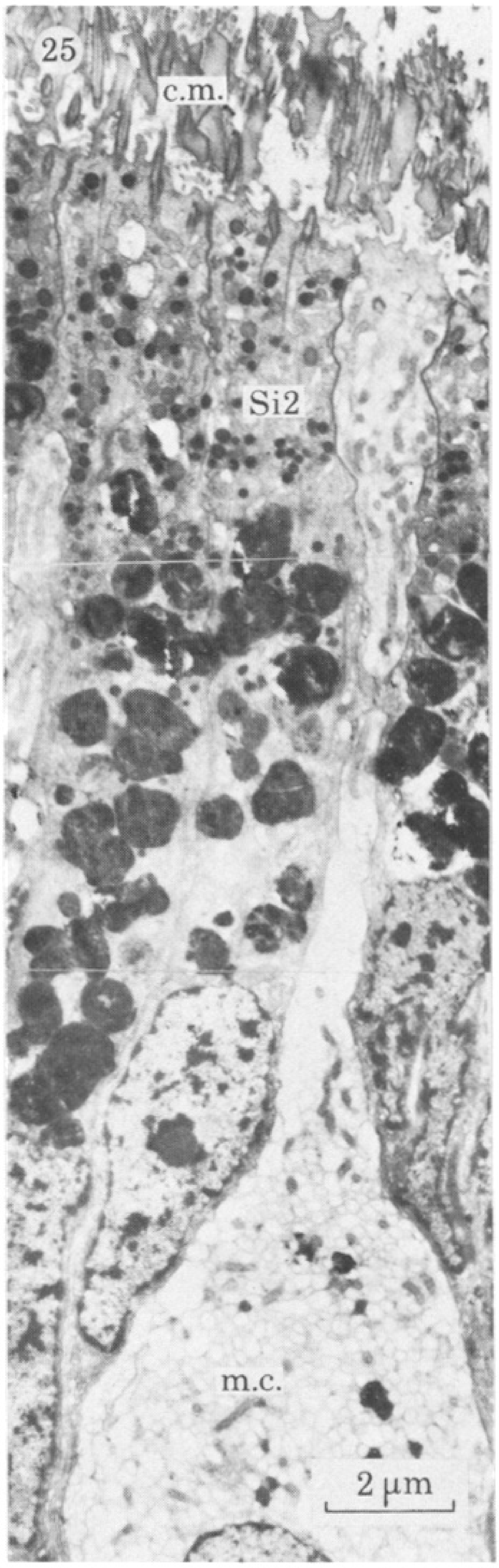
Figure 20. *Haliotis lamellosa*; cilia bottle.

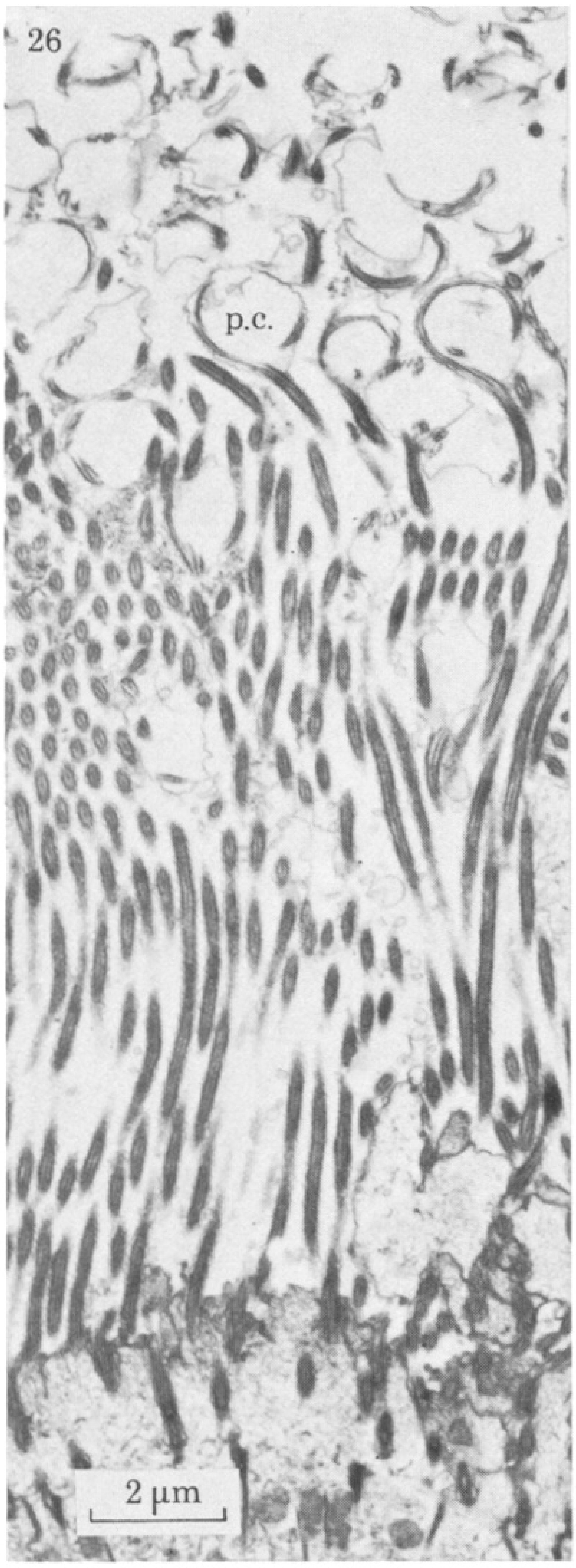
Figure 21. *Patella coerulea*: cilia star cell (osphradial ganglion).

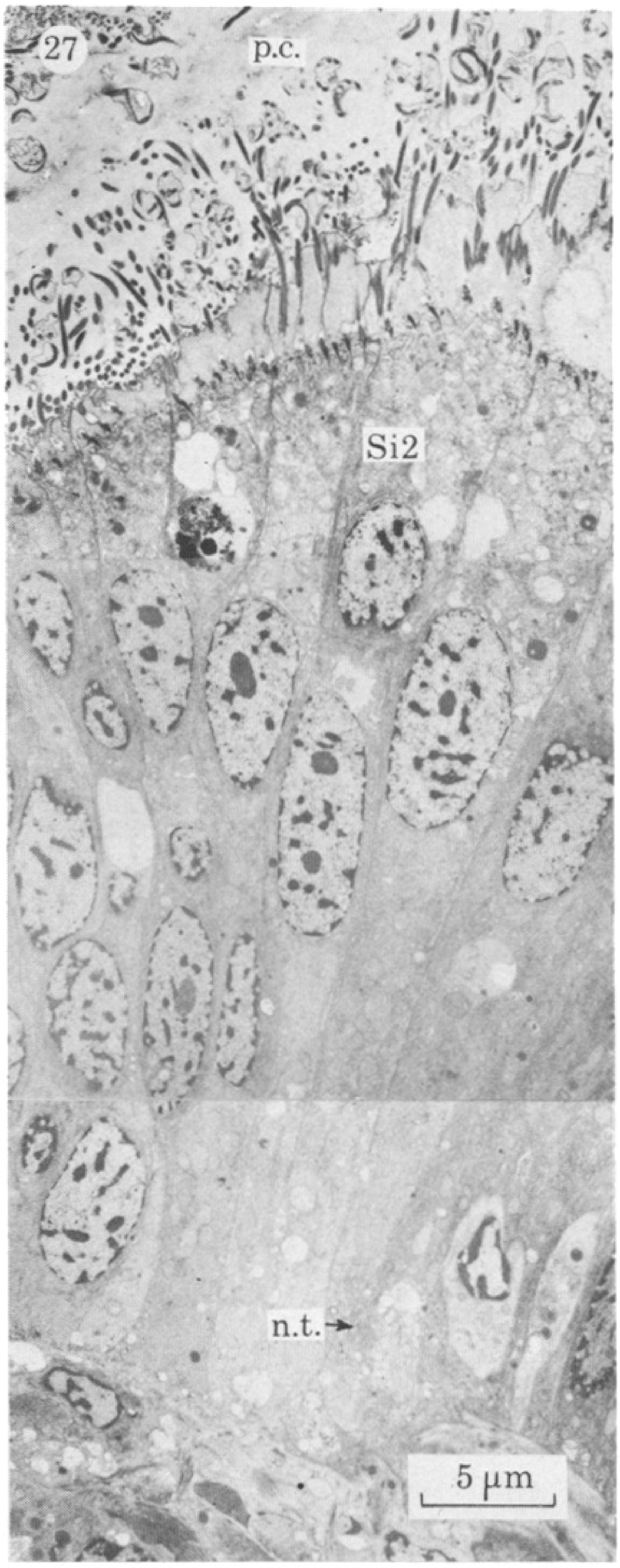
Figure 22. *Diodora italica*: extended ciliary membranes (central ciliated zone).

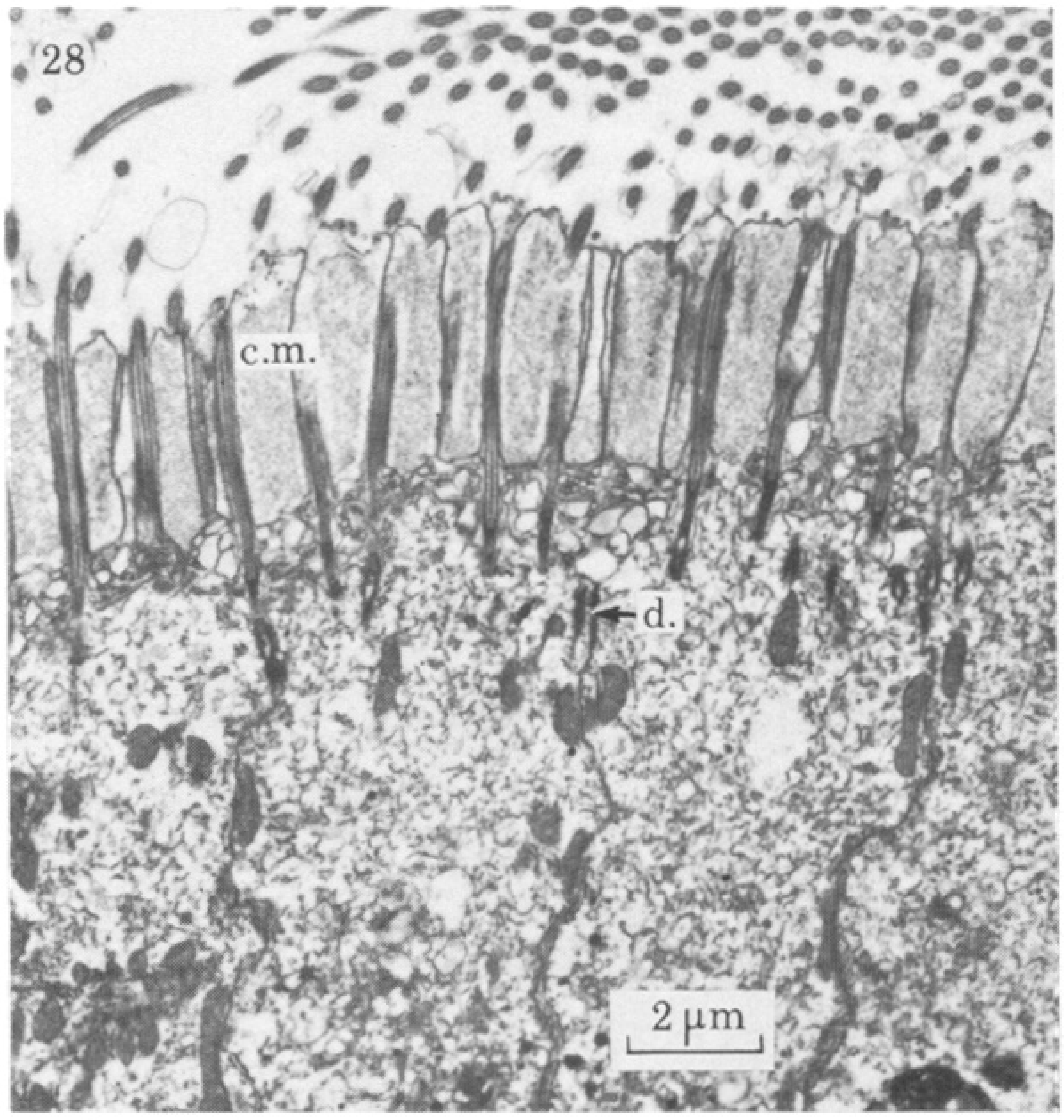
Figure 23. *Nerita plicata*: horizontally sectioned part of the central zone.

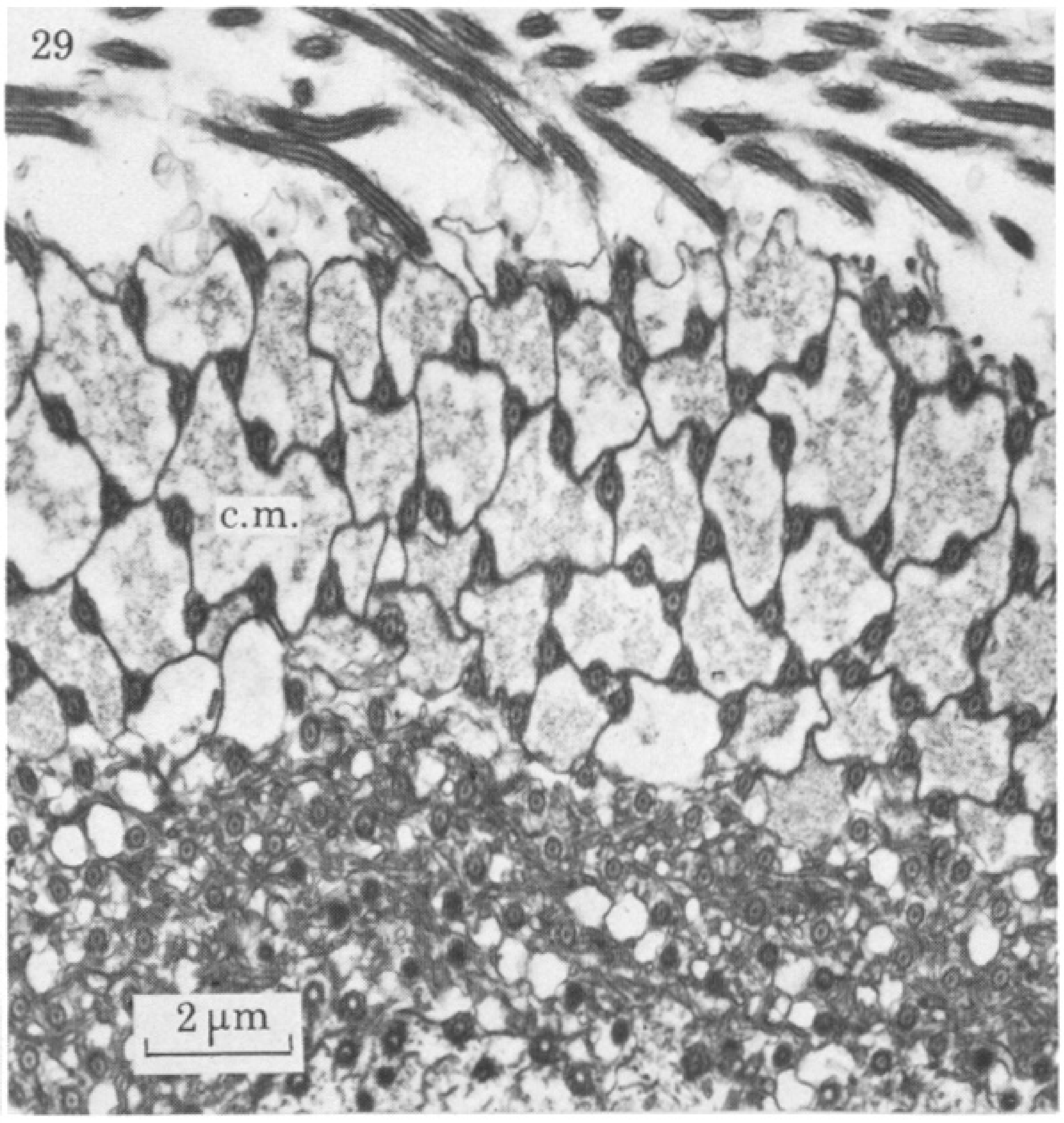
Figure 24. *Puperita pupa*: special cell 'y'.











FIGURES 25–29. c.m., Columnar microvilli; d., desmosomes; m.c., mucous cell; n.t., nervous tissue; p.c., paddle cilia.

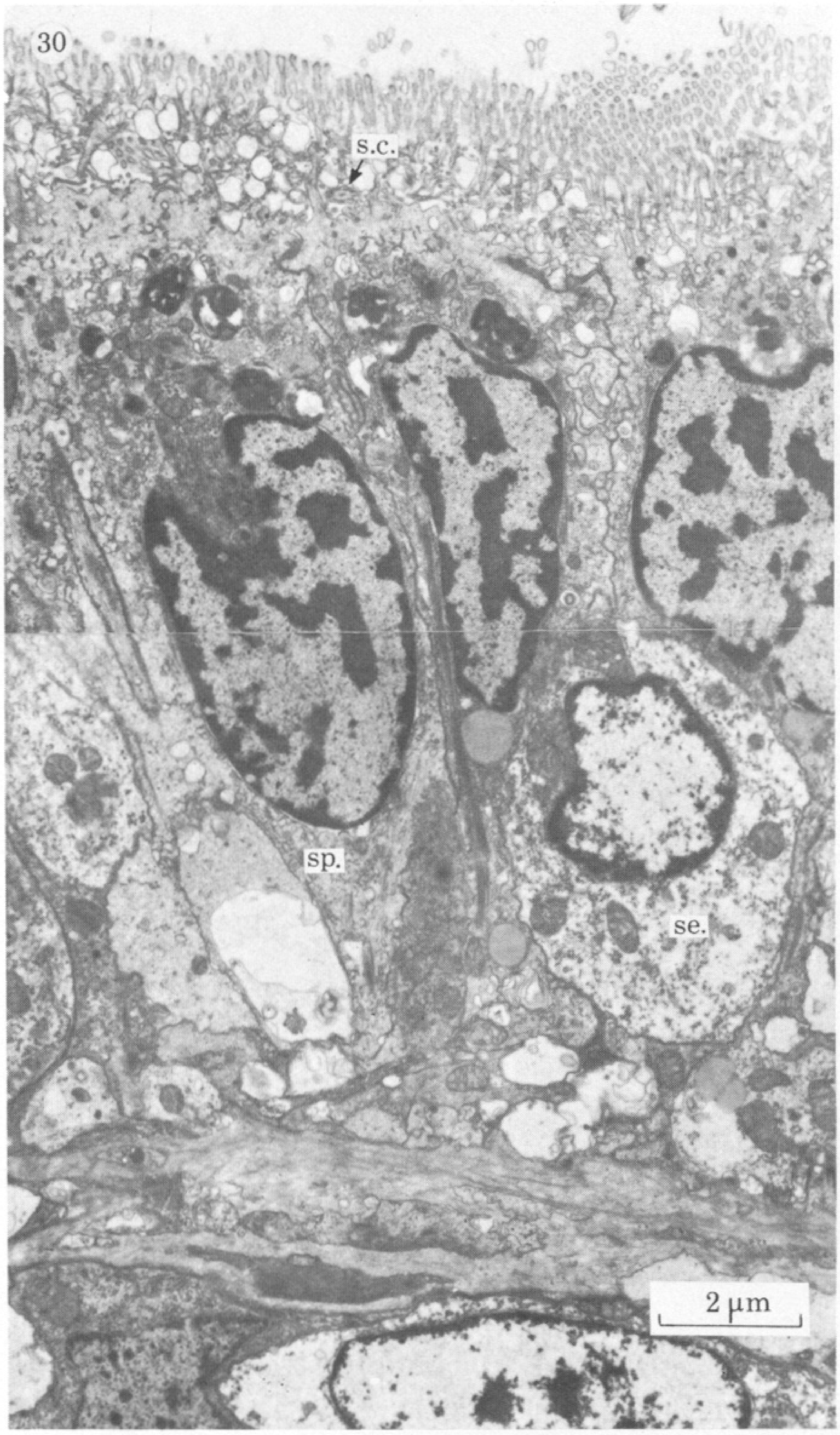
FIGURE 25. *Pomatias elegans*: lateral zone.

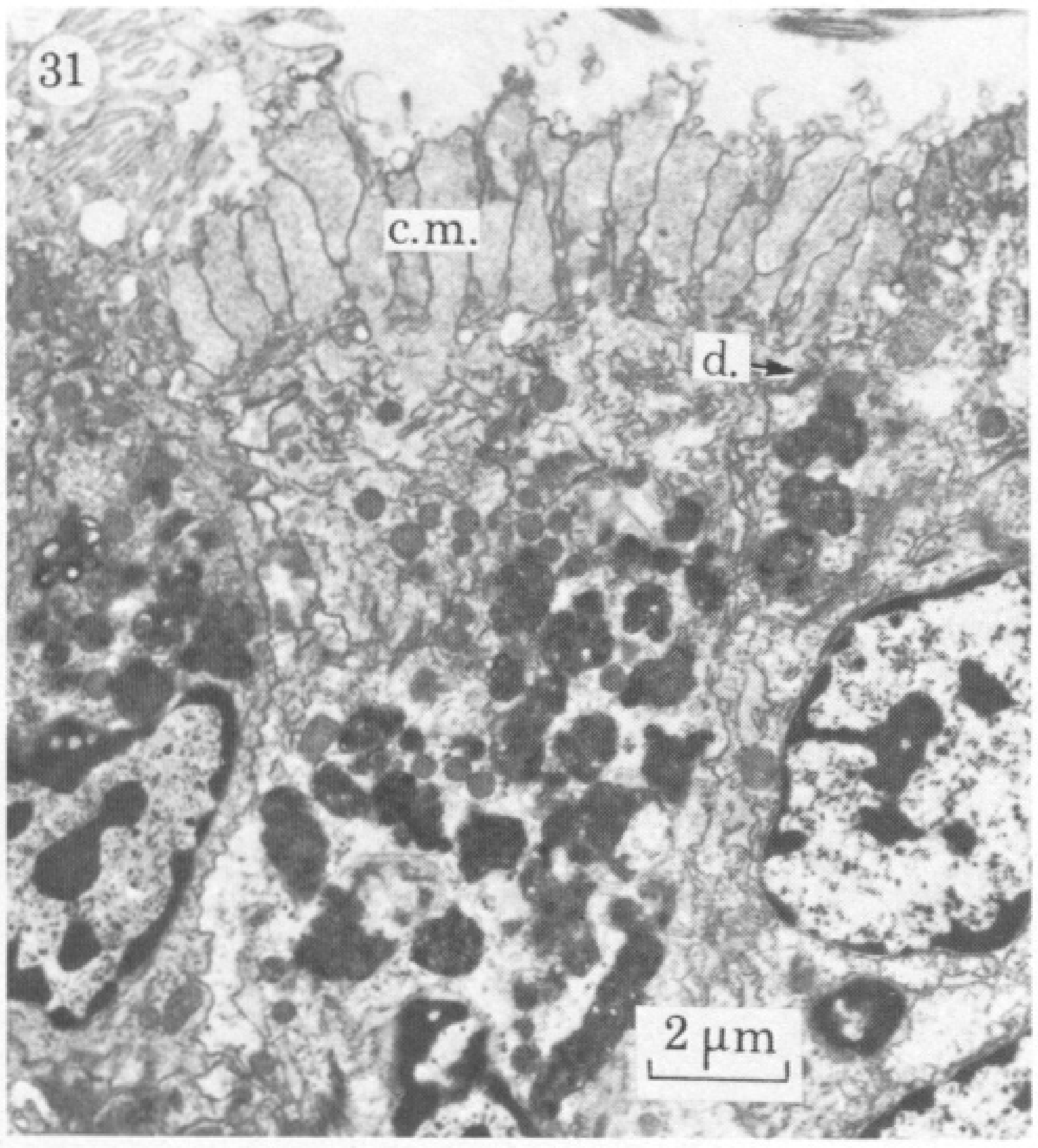
FIGURE 26. *Aporrhais pespelecani*: Si2 cell with paddle cilia.

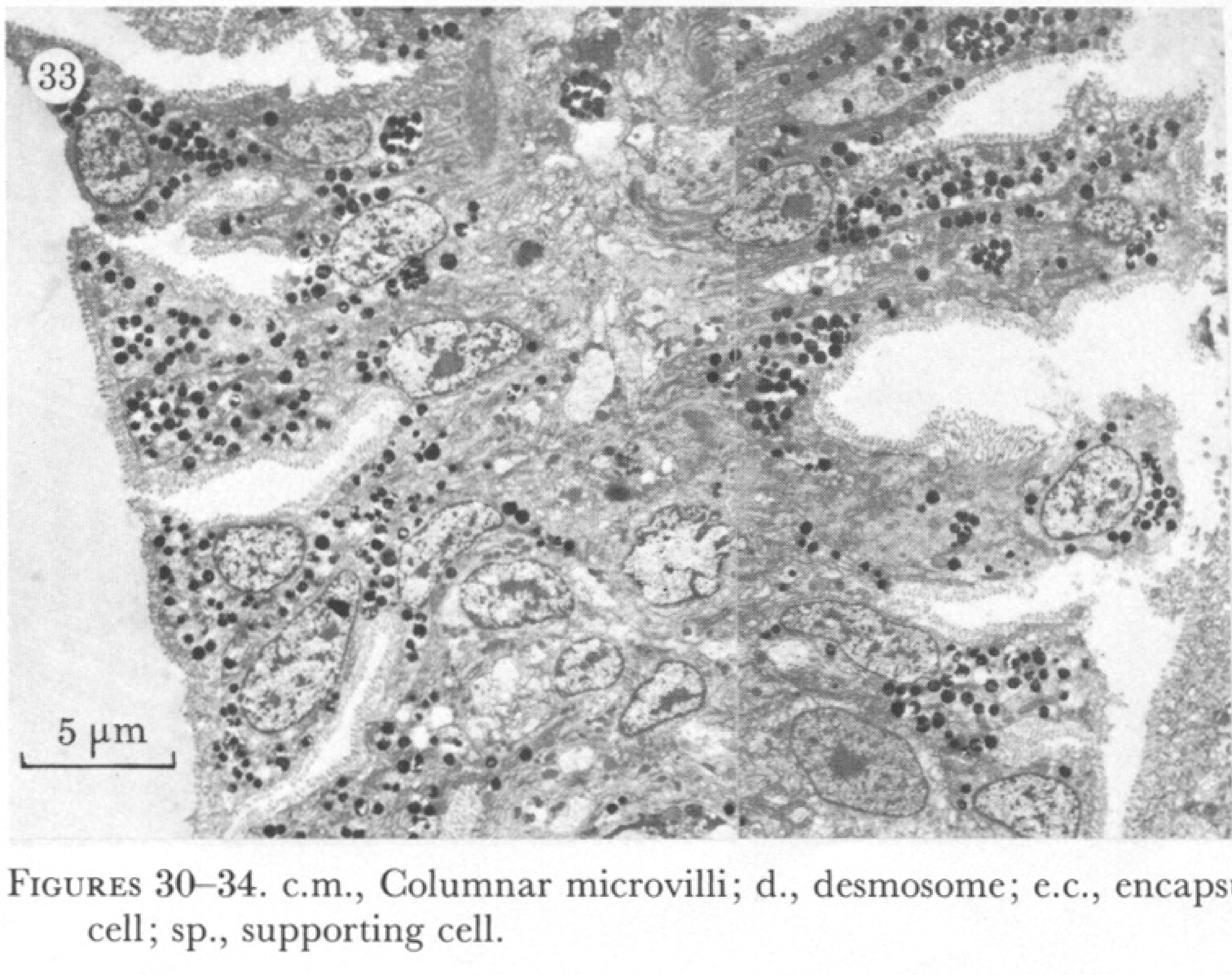
FIGURE 27. *Rissoa* sp.: Si2 cells with paddle cilia.

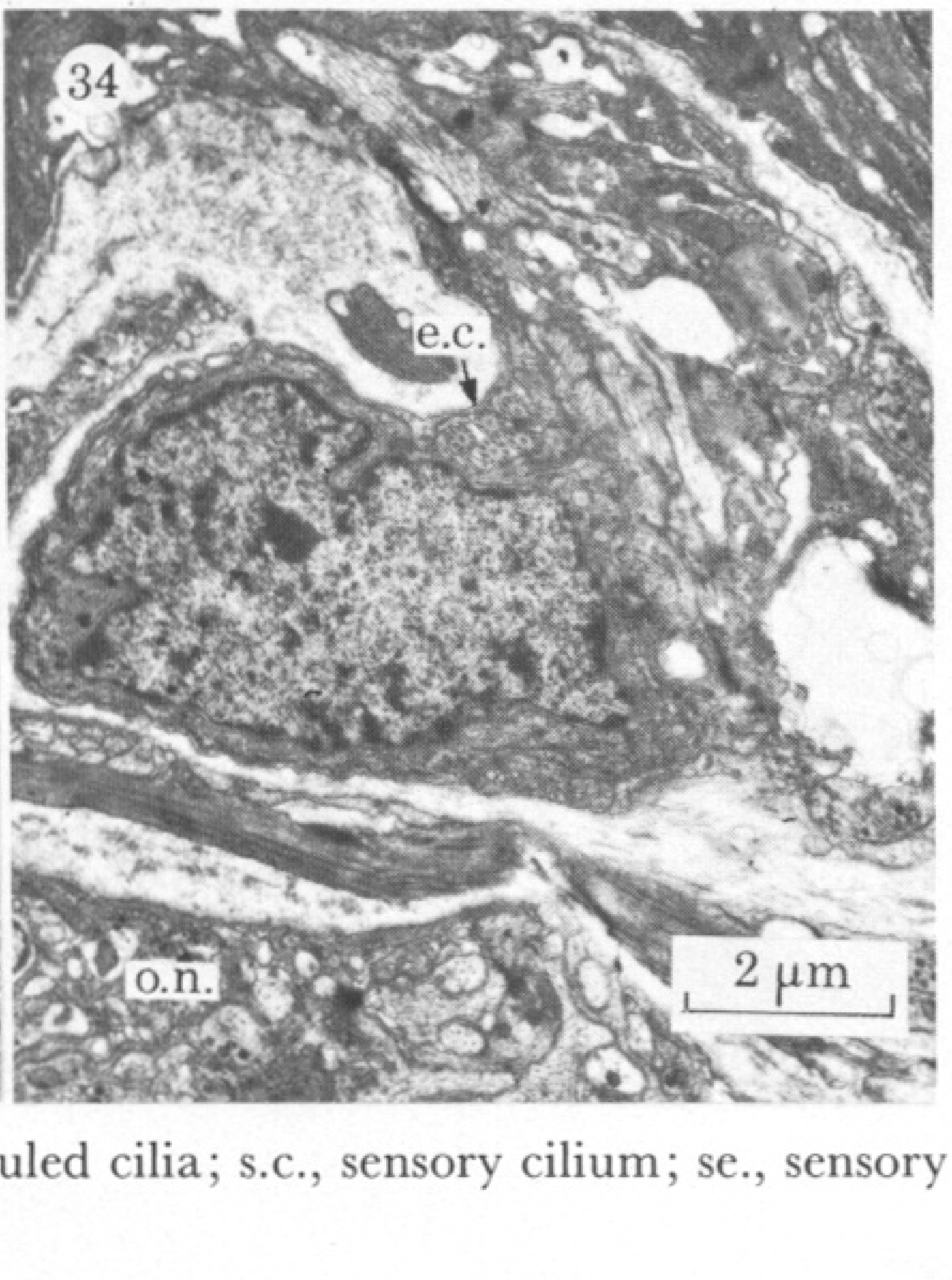
FIGURE 28. *Polinices guillemini*: Si2 cells (vertical section).

FIGURE 29. *Polinices guillemini*: Si2 cells (oblique section).









Figures 30–34. c.m., Columnar microvilli; d., desmosome; e.c., encapsuled cilia; s.c., sensory cilium; se., sensory cell; sp., supporting cell.

Figure 30. *Littorina neritoides*: central zone.

Figure 31. *Crepidula moulinsi*: Si1 cells.

Figure 32. *Rissoa* sp.: Si4 cell.

Figure 33. *Pseudosimnia* sp.: zone of pigmented, folded epithelium.

Figure 34. *Pomatias elegans*: cell with encapsuled cilia (arrow).