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# The Fine Morphology of the Osphradial Sense Organs of the Mollusca II. Allogastropoda (Architectonicidae, Pyramidellidae)

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# THE FINE MORPHOLOGY OF THE OSPHRADIAL SENSE ORGANS OF THE MOLLUSCA. II. ALLOGASTROPODA (ARCHITECTONICIDAE, PYRAMIDELLIDAE)

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(*Communicated by A. Graham, F.R.S. – Received* 18 *January* 1984)

[Plate 1]

## CONTENTS



The fine structure of the osphradia of Architectonicidae and Pyramidellidae is described. In contrast to their different external shape, the sensory epithelium of the osphradium of both families is very similar, but entirely different from that of all true prosobranchs. There are, however, similarities with the osphradia of basal Opisthobranchia (Bullomorpha).

Based on these osphradial characters and supported by several additional anatomical characters, the systematic position of both families is regarded as outside the Prosobranchia, but representing the common basal niveau for Opisthobranchia and Pulmonata.

## Introduction

The families Architectonicidae and Pyramidellidae are of doubtful systematic position, since the studies of Fretter & Graham (1962) and Robertson (1973) have shown that the classification of Thiele (1929), within the Cerithioidea and Eulimoidea respectively, is not an adequate one,

and they relate them more or less with the Opisthobranchia. Recently the Architectonicidae (together with the related Mathildidae) or Pyramidellidae, or both, have been brought by several authors (Kosuge 1966; Climo 1975; Gosliner 1981; Boss 1982) into relation with Heteroglossa, that is, the Cerithiopsoidea, Triphoroidea, Epitonioidea, and Eulimoidea. Depending on the point of view, all these super-families may be regarded either as prosobranchs or as opisthobranchs (see Haszprunar 1984*a*, table 5).

In this paper the fine structure of the osphradia of the Architectonicidae and Pyramidellidae is compared with that of Heteroglossa and basal Opisthobranchia. Based on the osphradial characters, the relations of both families are discussed briefly (this subject is elaborated in detail in Haszprunar 1984*b*).

## Material and methods

*Heliacus areola* (Gmelin) and two other *Heliacus* spp. (Architectonicidae), *Odostomia eulimoides* Hanley, and for comparison the basal opisthobranch *Scaphander lignarius* (Linné) were used in the investigations.

For ultrastructural research the same methods were used as described by Haszprunar (1984*a*).

In addition, serial sections were made of the species investigated, of *Turbonilla elegantissima* (Montagu) and of *Pyramidella acuta* (Gmelin) to get information about the innervation of the osphradium and other anatomical characters of the mantle cavity. The specimens were fixed in formaldehyde buffered with sea water or in Bouin's fluid, dehydrated in an ethanol series, embedded in Paraplast and cut into 5–10 μm sections. The sections were stained by Heidenhain's Azan method leading to useful results in all tissues.

## Results

### *Heliacus areola* (*Gmelin*, 1791), *Heliacus spp.* (*Architectonicidae*)

To date, the characters of the mantle cavity of the Architectonicidae have been described only by Bouvier (1886). Recently Robertson (1973) has added some details. The mantle cavity of the Architectonicidae is unique, combining prosobranch as well as basal opisthobranch and pulmonate characters.

The mantle cavity is well developed, extending back as far as half of the last whorl of the animal. It is longitudinally divided by a high crest, bearing at its edge a strongly ciliated tract. On the left side of the most anterior part of the mantle cavity a very prominent osphradium is formed by several radiating finger-like ridges, the centre of which is marked by the osphradial ganglion. The most posterior ridge runs back to the inner end of the mantle cavity underlain by its nerve. Right of the osphradium a second ciliary tract occurs and it is located opposite to the ventral one. Both produce a strong current from left to right. The main part of the mantle cavity is occupied by the greatly developed hypobranchial gland the epithelial folds of which have elongated to form respiratory lamellae (figure 1). Thus, the gill of the Architectonicidae is a secondarily developed organ. The rectum, the voluminous oviduct, and the vas deferens are placed at the right side of the mantle cavity.

The osphradial ganglion is connected by a short nerve with the nearby supra-oesophageal ganglion.


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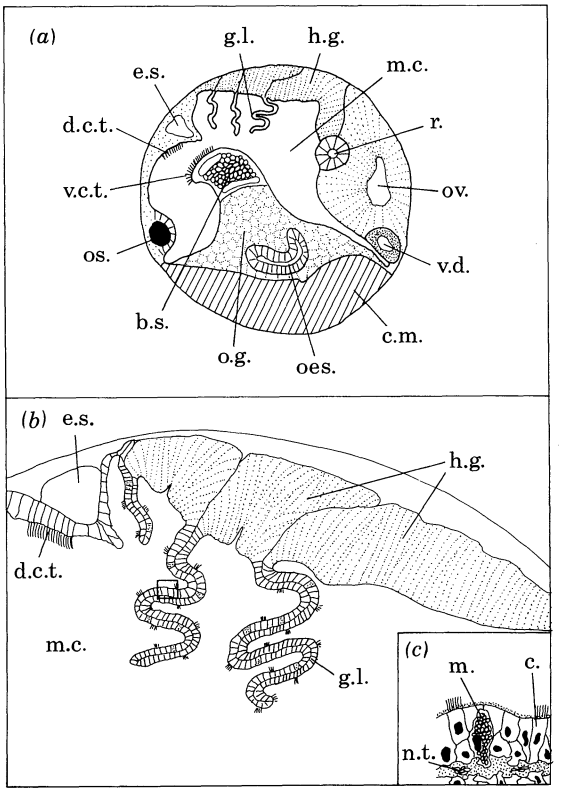


FIGURE 1. *Heliacus areola* (Architectonicidae): transverse sections to show organization of the mantle cavity and gill. (*a*) Mantle cavity and its organs. (*b*) Hypobranchial gland and its respiratory lamella. (*c*) Detail of gill-lamellae. Abbreviations: b.s., blood vessel; c., ciliated cell; c.m., columellar muscle; d.c.t., dorsal ciliary tract; e.s., efferent vessel; g.l., gill lamella; h.g., hypobranchial gland; m., mucous cell; m.c., mantle cavity; n.t., nervous tissue; oes., oesophagus; o.g., oesophagus glands; o.s., osphradial ganglion; o.v., oviduct; r., rectum; v.c.t., ventral ciliary tract; v.d., vas deferens.

The epithelium of the osphradial ridges comprises several cell types (figure 2).

(i) Most cells bear complex microvilli forming a high layer which appears in two portions: distally the microvilli lie parallel to one another, whereas proximally they form a very complex pattern. These cells, which are supporting cells, have many pigment granules distal as well as proximal to their nuclei (figure 8, plate 1).

(ii) Sometimes a second type of supporting cell occurs having cilia (figures 2 and 8). They have many mitochondria close to the basal bodies of the cilia and shorter microvilli.

(iii) Between these supporting cells another cell type (se.) occurs having a proximally placed nucleus. A slender process reaches the surface of the epithelium bearing a very short cilium which ends within the microvillous layer and has a short root. These cells are in contact with basally placed nervous tissue which originates in the underlying nerve, and they are thus regarded as sensory cells.

(iv) Within the sensory epithelium some big mucous cells are found, filled with prominent secretory granules.

(v) In the narrow spaces between the ridges, especially close to the osphradial ganglion, there are many densely packed cilia running parallel to the epithelial surface of the ridges. The most distal of these form paddle cilia which have also been described in many other gastropod

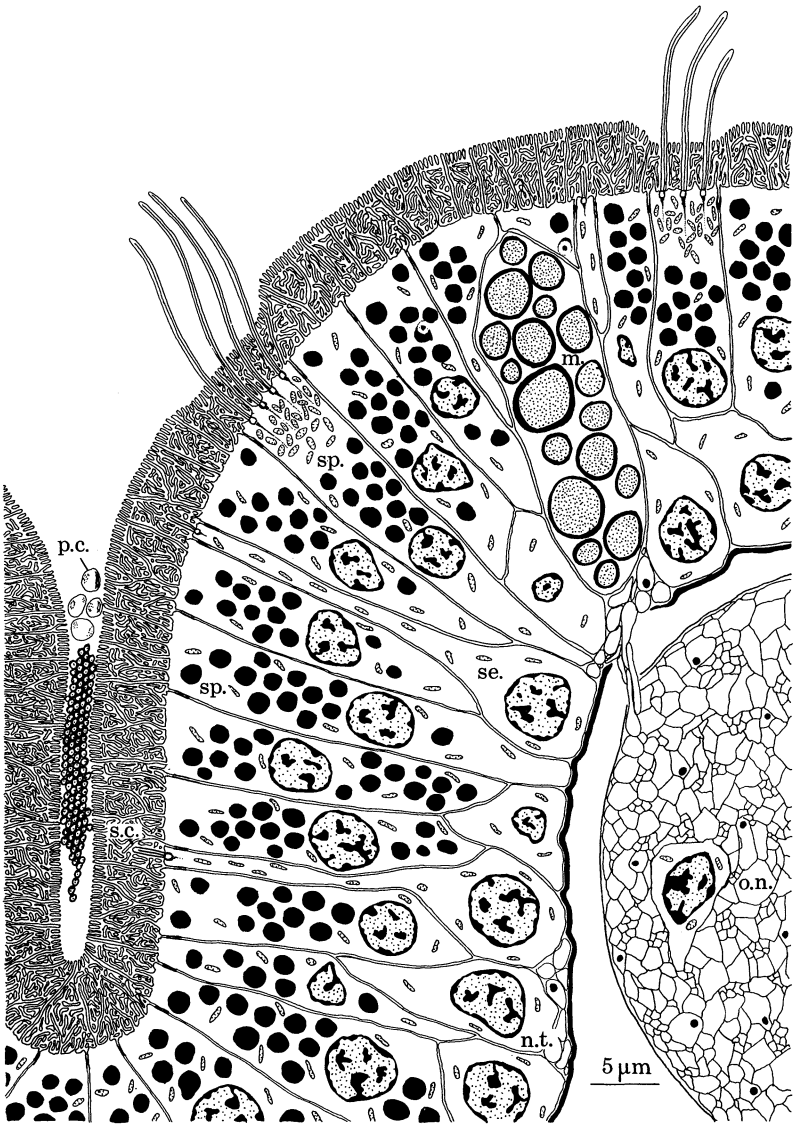


FIGURE 2. Section of the osphradial lamellae of an architectonicid (semischematic). m., Mucous cell; o.n., osphradial nerve; p.c., paddle cilium; s.c., sensory cilium; s.e., sensory cell; s.p., supporting cell; n.t., nervous tissue.

osphradia (Storch 1972; Haszprunar 1984*a*). These cilia originate from sensory cells of the epithelium above the osphradial ganglion which are similar to the sensory cells of the ridges.

There are few nerve cells within the osphradial nerve.

### *Odostomia eulimoides Hanley*, 1844 (*Pyramidellidae*)

The mantle cavity of pyramidellid species has been described by Fretter & Graham (1949, 1962, p. 126) and shows remarkable similarities with that of the Architectonicidae. As in that family there are two apposed ciliary tracts, but lying more to the right side of the mantle cavity. Left of the dorsal tract the osphradium is placed, formed by a ridged epithelium (figure 6). Right of the dorsal tract the voluminous hypobranchial gland occupies the main part of the mantle skirt. In the small species so far investigated there is no gill, but in *Pyramidella acuta*

(Gmelin) a gill was found, just right of the dorsal ciliary tract, with the same structure and position as that of the Architectonicidae. In contrast, the gills of the Siphonariidae and of the Opisthobranchia are placed left of the dorsal ciliary tract. The rectum and the gonoduct are located on the right side of the mantle cavity.

The osphradium is innervated by a nerve coming from the osphradial ganglion located on the left side, and so crossing two thirds of the mantle cavity, since, owing to the concentration of the nervous system, the supra-oesophageal ganglion is placed on the right side (in *Turbonilla elegantissimia* it is placed more or less directly over the oesophagus (personal observation). The long supra-oesophageal–osphradial connective is characterized by a distinct neuroendocrine portion that originates in a 'dorsal body' of the supra-oesophageal ganglion. This character was also found in *Pyramidella acuta*.

The sensory epithelium is built up of cells of different height, so that ridges and grooves are formed (figure 3).

(i) Most cells of the epithelium bear only microvilli forming a layer that looks double. These supporting cells have many pigment granules distal to their elongated nuclei (figure 9).

(ii) At the base of the grooves another cell type occurs, characterized by an oval nucleus and cilia. These cilia are densely packed in the groove and may form paddle cilia, showing a pattern very similar to that described for the Architectonicidae. There are many mitochondria close to the basal bodies of the cilia. Nervous tissue is found adjacent to them; thus they are regarded as sensory.

There are no nerve cells within the osphradial nerve.

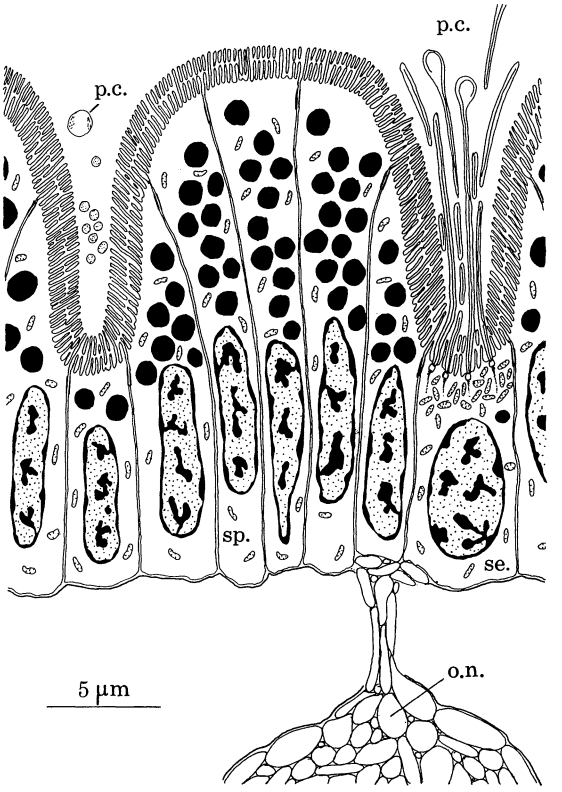


FIGURE 3. Section of the osphradium of a pyramidellid (semischematic). o.n., Osphradial nerve; p.c., paddle cilium; s.e., sensory cell; s.p., supporting cell.


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*Scaphander lignarius* (*Linné*, 1784) (*Bullomorpha*, *Scaphandridae*)

The characters of the mantle cavity are typical of Bullomorpha, showing a stage of about 90° detorsion (Hoffmann 1939; Brace 1977*a*, *b*). The yellow-brown pigmented and thus easily visible osphradium is placed on the anterior membrane of the plicate gill, thus being located in the inhalant stream of water. Behind the gill there are two opposed ciliary tracts and finally the rectum (there is no pallial gonoduct).

The osphradium, which forms a slight, round groove with a somewhat heightened margin, is innervated by the underlying osphradial ganglion which sends many fine nerves into the sensory epithelium.

The osphradial epithelium is divided into two zones: the central zone and the margin (figure 7). The epithelium of the central zone shows very narrow clefts whereas the margin forms a ciliated ridge surrounding the groove. The epithelium consists of several cell types.

(i) The supporting cells of the central zone are very similar to those described in *Heliacus* and *Odostomia*. Bearing a high microvillous layer that appears double; they have elongated nuclei and many distally placed pigment granules (figure 10).

(ii) At the bottom of the clefts slender processes reach the surface of the sensory epithelium, each bearing a short, rootless cilium which ends among the microvilli. The perikarya of these processes are basally located and have oval nuclei. Nervous tissue is found adjacent to them and shows that the cells are probably sensory.

(iii) Most of the epithelium of the margin is built up of cells with cilia. Their cytoplasm appears to be darker than that of the supporting cells which are likewise found in the epithelium of the margin. Correlated with the presence of cilia there are many distally located mitochondria.

(iv) There are some mucous cells within the marginal epithelium.

## Discussion

*Comparison between Architectonicidae and Pyramidellidae*

Though the external shape and the position of the osphradia within the mantle cavity differ markedly, osphradial fine structure in both families is very similar; both are, however, different from any type of prosobranch osphradium so far investigated (Haszprunar 1984*a*). This conflicts with the suggestions of most authors who classify the two families even in different subclasses. A closer relationship was suggested by Risbec (1955), Robertson (1973), and Boss (1982). This close relationship of both families is in addition indicated by the coincident existence of a mixture of prosobranch characters (solid shell with operculum, heart position,

## Description of plate 1

Figures 5–7. Semithin sections of osphradial epithelium.

Figures 8–10. Ultrathin sections of osphradial epithelium.

Figure 5. *Heliacus* sp.

Figure 6. *Odostomia eulimoides*.

Figure 7. *Scaphander lignarius*.

Figure 8. *Heliacus areola*.

Figure 9. *Odostomia eulimoides*.

Figure 10. *Scaphander lignarius*.



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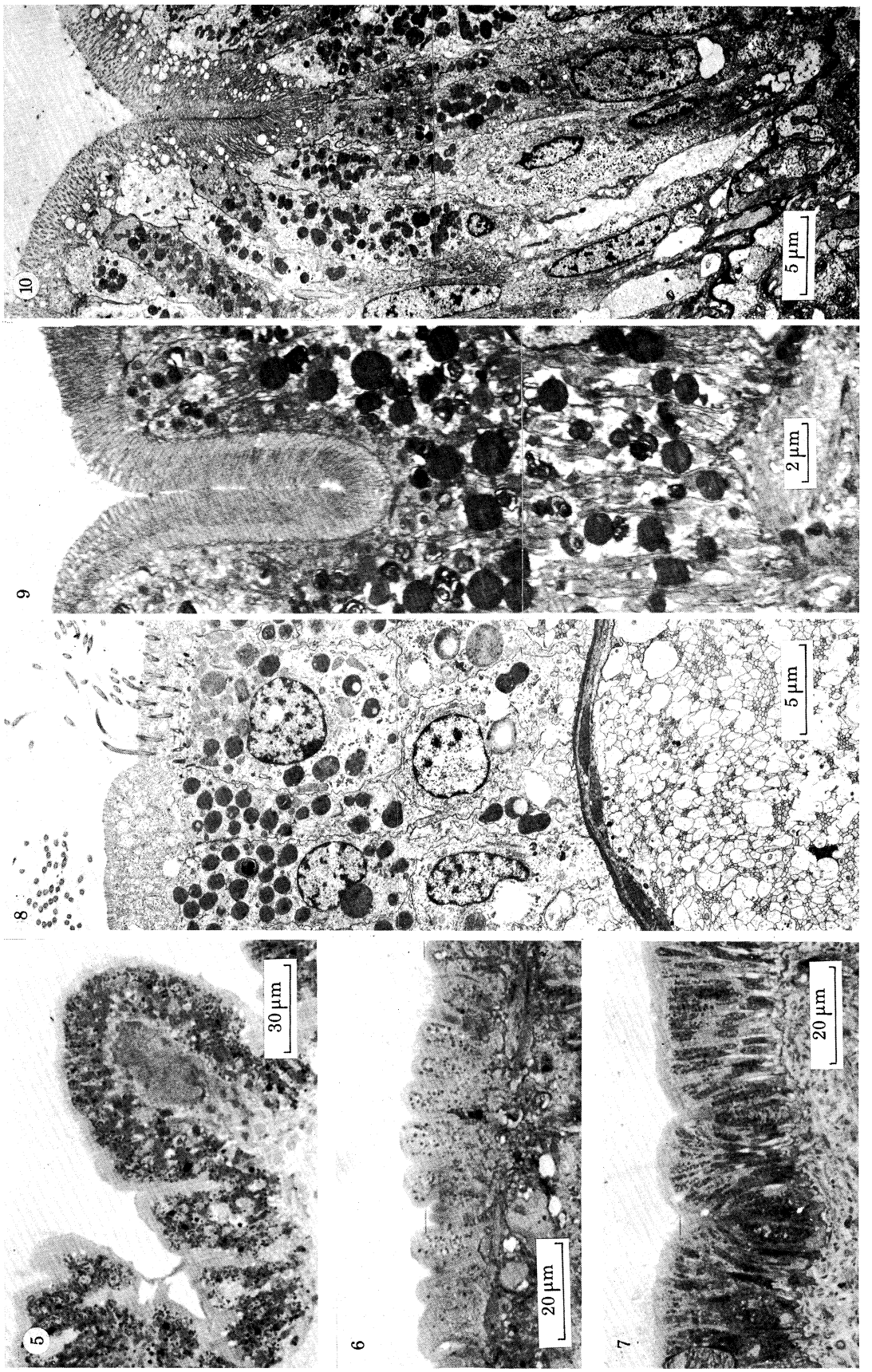


FIGURES 5–10. For description see opposite.

(*Facing p.* 502)



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triganglionate condition of the visceral loop) as well as opisthobranch and pulmonate characters (heterostrophy, ciliary tracts, spiral sperms: for details see Haszprunar (1984*b*)). Moreover, in both families there exists a very similar alimentary tract (Risbec (1955), and personal observation), and (if present) an identical type of gill (see above).

### *Comparison with Heteroglossa*

As extensively discussed in the foregoing paper (Haszprunar 1984*a*), the fine structure of the prosobranch osphradia reflects presumed relations. The higher Caenogastropoda are, in particular, characterized by their distinctive osphradial organization (three special cell types with constant position within the osphradial epithelium).

In contrast to the elaboration in Architectonicidae and Pyramidellidae, the osphradia of *Triphora perversa* (Triphoridae), *Eulima glabra* (Eulimidae) and *Epitonium clathrus* (Epitoniidae) possess the characteristic Si1–Si2–Si4 type of the Neotaenioglossa–Stenoglossa (Haszprunar 1984*a*). The results of Healy (1982) on spermiogenesis also suggest that the Triphoridae and Epitoniidae–Janthinidae are Caenogastropoda, whereas the spermiogenesis in Architectonicidae and Pyramidellidae is entirely different. Haszprunar (1984*a*) created a new taxon Heteroglossa, including Cerithiopsoidea, Triphoroidea, Epitonioidea, and Eulimoidea as a suborder of the Caenogastropoda. The caenogastropodan nature of these Heteroglossa is additionally evidenced by the existence of a true pectinibranch ctenidium. In the light of their synapomorphous, very special type of osphradium, the Heteroglossa are regarded as monophyletic, together with the Neotaenioglossa and the Stenoglossa.

The gill of the Architectonicidae and of some Pyramidellidae (Risbec 1955, p. 70, and this paper) is known to be a secondary elaboration developed from folds of the hypobranchial gland (figure 1). Both families should therefore be separated from the Prosobranchia (see below).

### *Comparison with the Opisthobranchia–Pulmonata*

Although Edlinger (1980) described the osphradium of *Haminea navicula* (Bullomorpha) using terms applicable to the caenogastropodan Si1–Si2–Si4 type (see Haszprunar 1984*a*), this osphradium is entirely different to those of the Caenogastropoda (see his published photos), but is nearly identical to that of *Scaphander lignarius*. There is a remarkable similarity in the fine structure of the osphradial epithelium of the Bullomorpha and that of the Architectonicidae and Pyramidellidae, although the external shape is different. There appears to be a tendency to decrease the height of the sensory epithelium, the spaces between the ridges (Architectonicidae, figure 5) becoming clefts in the Bullomorpha (figure 7), with the osphradium of the Pyramidellidae (figure 6) representing an intermediate condition.

Gosliner (1981) presented good reasons for excluding the pyramidellids from the Opisthobranchia and the same might be true for the Architectonicidae. Nevertheless, there are strong relations between the Architectonicidae–Pyramidellidae and the Opisthobranchia, and also with the Pulmonata and the Gymnomorpha (separated after Salvini–Plawen 1970, 1980). This is because all the 'opisthobranch' characters found in Architectonicidae and Pyramdiellidae do also exist within the basal Pulmonata and partly, also, within the Gymnomorpha. This applies to the heterostrophic apex, the two ciliary tracts within the mantle cavity, the black larval kidney, the chalazae, and the mode of spermiogensis leading to a spiral type of sperm (for details see Haszprunar 1984*b*), and suggests that all these groups have a monophyletic origin. The older term Heterobranchia Gray, 1840 should be preferred to Spengel's (1881)


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taxon Euthyneura, because of the convergence of the euthyneury in several lines (Salvini-Plawen 1980; Haszprunar 1984*b*). For the Architectonicidae and Pyramidellidae, which are regarded as the most primitive members of recent Heterobranchia, the new taxon Allogastropoda is proposed; they represent the common ancestral level of Opisthobranchia as well as of Gymnomorpha and Pulmonata (figure 4).

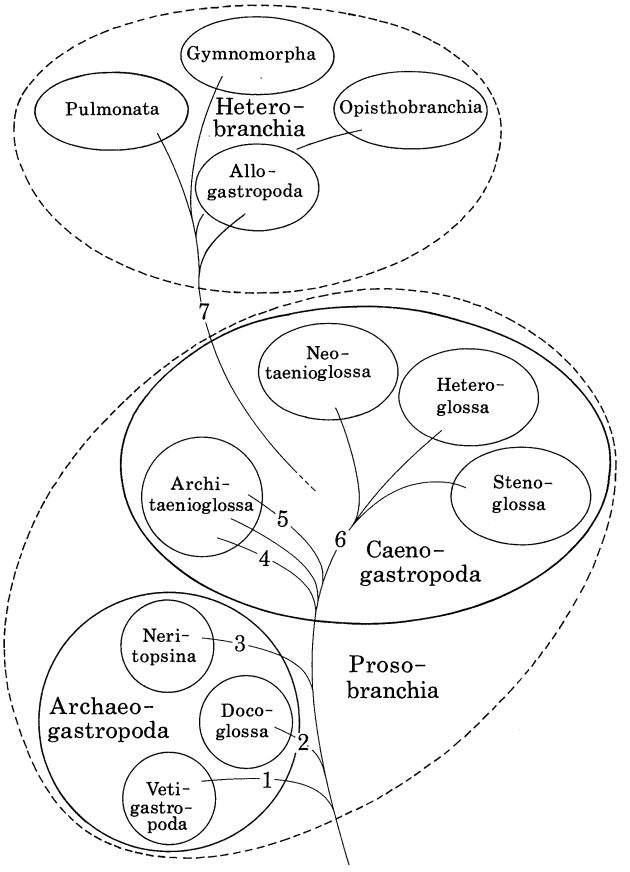


FIGURE 4. Proposed interrelationships of the Gastropoda in the light of osphradial fine structure (compare Haszprunar 1984*a*, *b*): 1, Vetigastropoda type; 2, Docoglossa type; 3, Neritopsina type; 4, *Valvata* type; 5, Viviparoidea type; 6, Si1–Si2–Si4 type; 7, Heterobranchia type.

I thank Professor L. v. Salvini-Plawen (University of Wien) for the initiation of this study as well as for critical advice. I am indebted to Professor A. Graham (University of Reading) who critically commented on and corrected the manuscript. The work was supported by the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich (project number P4751).

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*Note added in proof* (17 August 1984). A detailed anatomy of Architectonicidae is presented by the author Haszprunar (1985 Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). *Zool. Scr.* (in the press)), presenting much additional evidence for the systematic suggestions presented in this paper.



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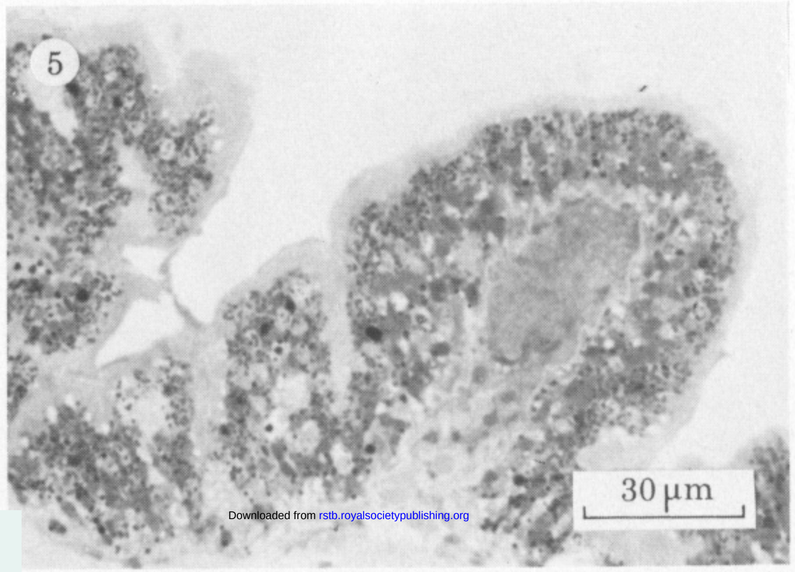




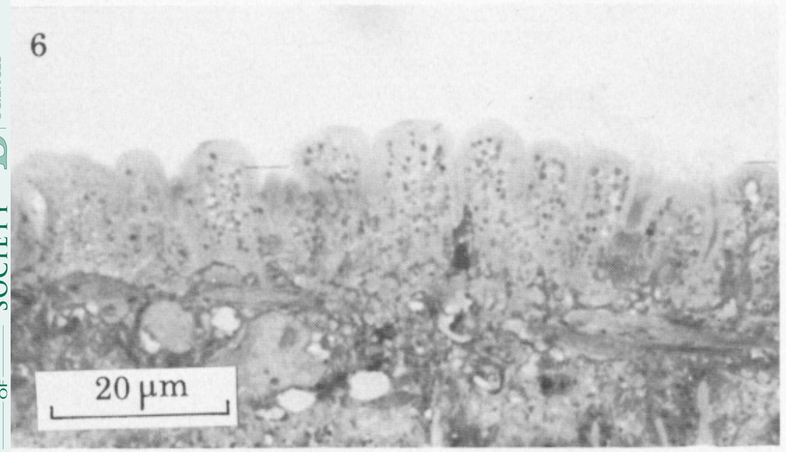


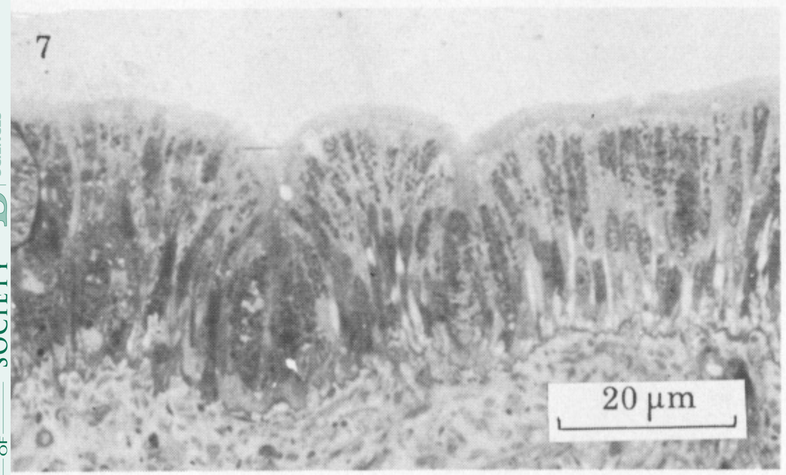


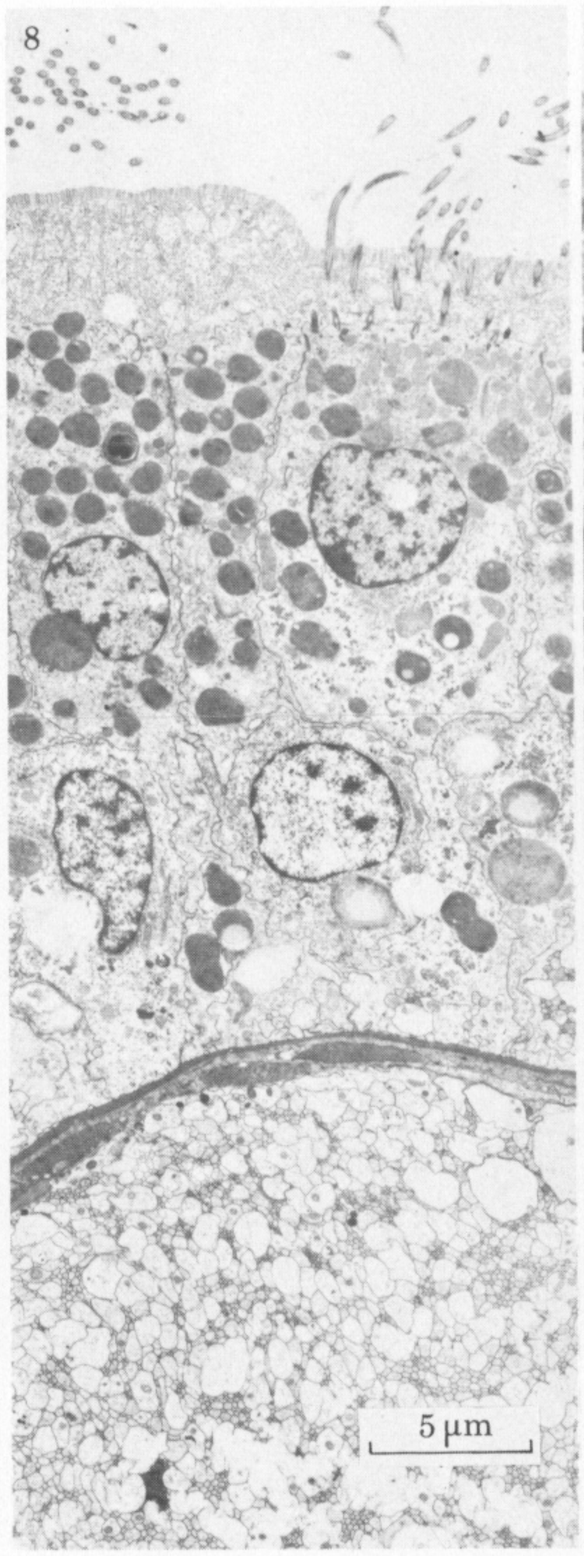


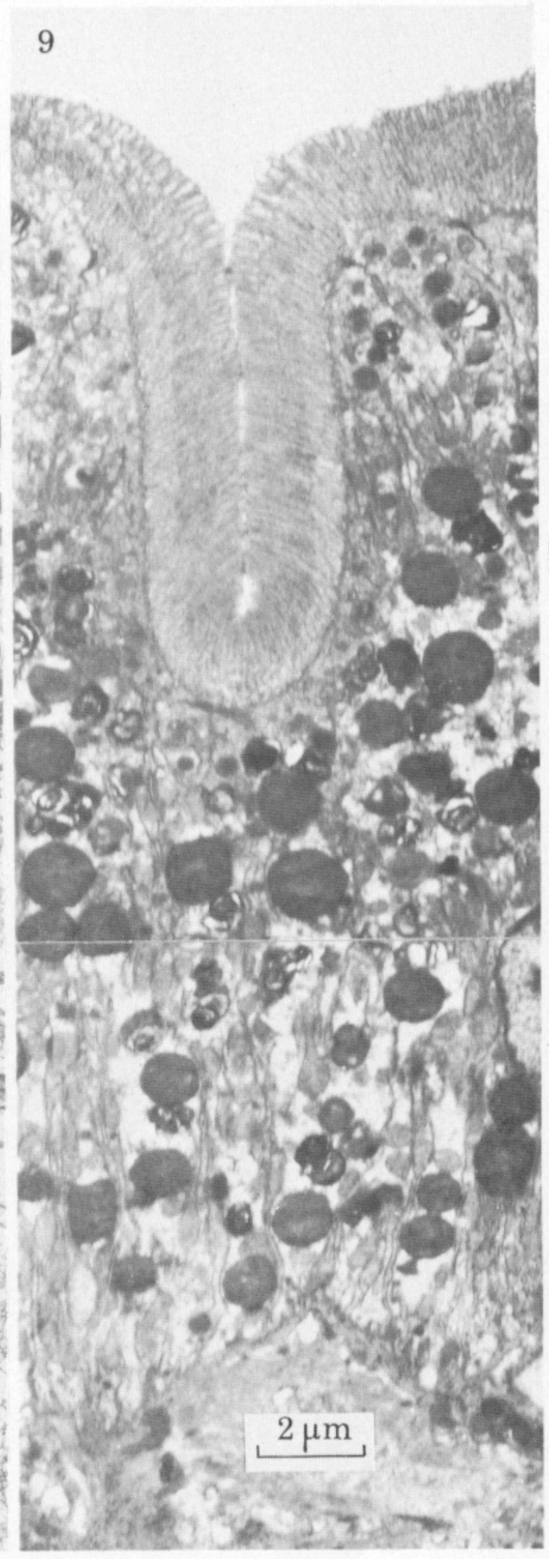


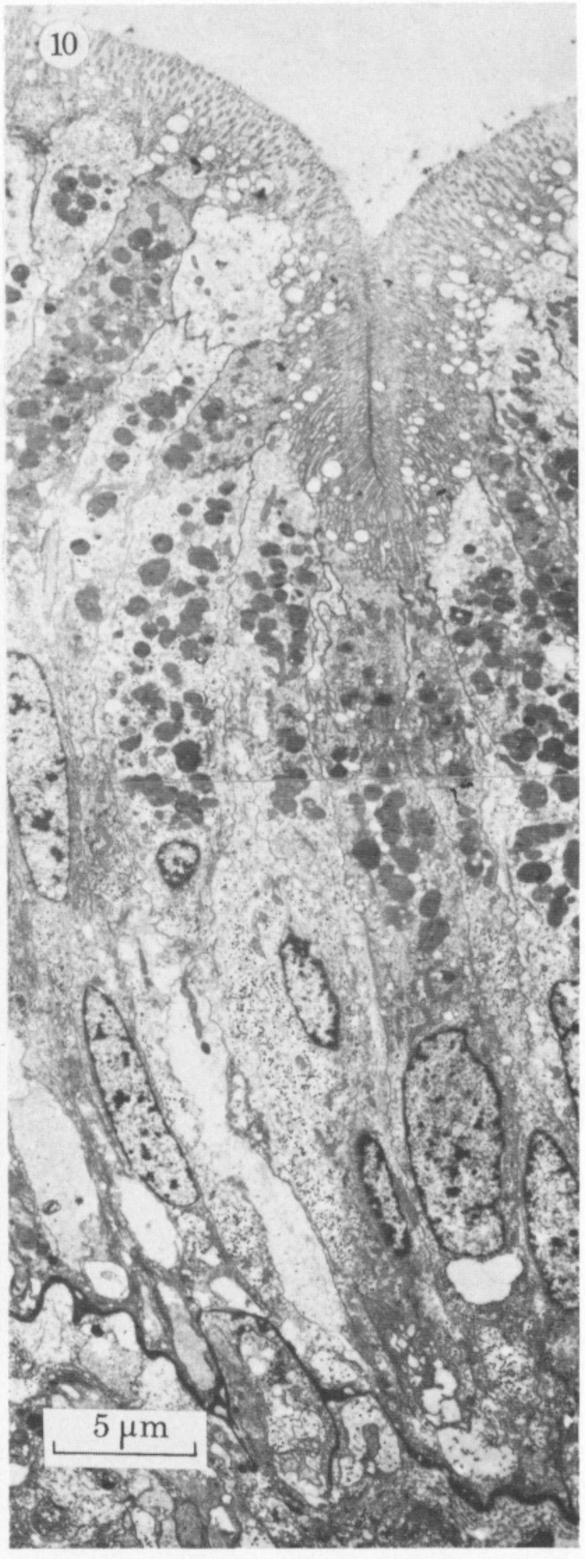


FIGURES 5–10. For description see opposite.