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# Functional anatomy and histology of the digestive tract of fingernail clams (Sphaeriidae, Bivalvia)

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The structure of the digestive tract in Sphaeriidae conforms well to the bivalve general pattern. Intergeneric variation was found in the length of the alimentary canal (2.5 times shell length in *Sphaerium*, 2.0 times in *Pisidium*). Interspecific variation occurred in the structure of e.g. the labial palps and the digestive diverticulae, mainly between the neotenic *Pisidium conventus* and other members of the genus.

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## 1. Introduction

The food and feeding biology of bivalves, mainly of marine species but also of large freshwater species like *Dreissena* and *Anodonta*, have been reviewed by Owen (1974), Winter (1978), Alimov (1981) and Morton (1983). The food and feeding mode of the small bivalves in the family Sphaeriidae is not as well known. Meier-Brook (1969) described their general position (umbo down, approx. 5 mm below sediment surface) during filtration and Efford & Tsumura (1973) noted the only minor importance of dissolved materials in their diet. Lopez & Holopainen (1987) suggested that *Pisidium* feed by the filtration of suspended microorganisms from interstitial water.

The general structure of the bivalve digestive tract has been well described by many workers (e.g. Owen 1955, Reid 1965, Purchon 1958, 1960, 1977 and Morton 1973), as recently reviewed by Morton (1983). However, the only previous description we know of the alimentary canal of *Pisidium* is given by Odhner (1929), who presents some simple drawings of the appearance and general side view of the stomach from oesophagus to hindgut in four species. The structure and function of the stomach of *Sphaerium corneum* has been described in detail by Purchon (1958).

Some features of the general anatomy (including the digestive tract) and histology of *Sphaerium* and *Musculium* are given by Monk (1928) and Okada (1935). Histological sections of *Pisidium* have been presented by Meier-Brook (1970), Maciorowski et al. (1977) and Holopainen (1987), and of *Sphaerium* by Purchon (1977: Fig. 106) and Holopainen (1987).

Our aim here is to give a more detailed description of various parts of the digestive tract of three *Pisidium* species in comparison with *Sphaerium corneum*.

## 2. Materials and methods

The bivalves *Pisidium casertanum* (Poli), *P. conventus* Clessin and *P. amnicum* (O. F. Müller) were collected from Lake Pääjärvi, southern Finland, 61°04'N, 25°08'E (Ruuhijärvi 1974, Holopainen 1979) and *Sphaerium corneum* L. from the littoral of the eutrophicated small lakes Lovojärvi (approx. 4 km from L. Pääjärvi, see Ilmavirta et al. 1974) and Varaslampi (in Joensuu, eastern Finland, 62°37'N, 29°45'E; see Holopainen 1987). The clams were relaxed with pentobarbital (Meier-Brook 1976) and fixed in alcoholic Bouin. For histological studies they were embedded in paraffin or polyester wax, sliced to 7 µm sections and stained with the allochrome system (Lillie 1951). For scanning electron microscopy the samples were dissected and transferred to absolute alcohol and critical point dried before coating with a 400 Å gold film. During dissection the details were carefully drawn using a camera lucida.

## 3. Functional anatomy of the digestive tract

In *Pisidium* and *Sphaerium* the mouth is situated immediately below the mid-part of the anterior adductor muscle and is surrounded by two pairs of labial palps (Fig. 1). On both sides the anterior margin of the inner gill filament ends between the inner and outer palp. The slender, tubular oesophagus runs to the stomach, which has large openings to the digestive diverticulae of the midgut gland or liver. The midgut starts ventrally from the stomach and proceeds downward and forward along with the style sac. The hindgut starts with a coil, which is again situated close to the mouth. After the coil the gut runs back posteriodorsally, goes through the heart ventricle and descends as the rectum behind the posterior adductor muscle to end just below it in the cloacal chamber.

The shell length represents 50.5% ($n$=8, shell lengths 5.8–8.0 mm) of the length of the digestive tract in *P. amnicum* but 40.5% in *S. corneum* ($n$=8, SL 7.7–11.6 mm). This difference is significant ($t$=5.67, $P$<0.001; arcsine square root transformation). In *P. casertanum* and *P. conventus* the length of the tract relative to the shell length is the same as in *P. amnicum*, or seems to be characteristic of the genus.

The structure and function of different parts of the tract are described below.

*Labial palps and mouth.* The slit-like mouth is surrounded by two pairs of labial palps, small flap-like projections on both sides of the base of the anterior edge of the ctenidium. The slit between the bases of the outer and inner palp forms the oral groove, a functional extension of the food-carrying groove on the anterior margin of the ctenidium. The outer surface of the outer palp rests against the mantle and the inner surface of the inner palp is in close contact with the base of the foot (Figs. 2–3). The oral grooves from both sides join at the mouth, the upper lip is formed from the extensions of the anterior parts of the outer palps and the lower lip from a ridge joining the anterior margins of the inner palps. The surfaces of the palps facing each other, and the gill, all have ciliated ridges. The length and shape of the palps varies between species. In both *P. casertanum* and *P. conventus* the outer palps are broad and rather immobile structures with only a short projectile tip. *P. conventus* has 2–3 and *P. casertanum* 3–4 ciliated ridges on the surface of the outer palp facing the inner palp. *P. amnicum* (Fig. 2) and *S. corneum* have more mobile outer palps with 7 to 11 ridges. The inner palps are longer, more slender and mobile than the outer ones but are again shorter and broader in *P. conventus* and in *P. casertanum* when compared to *P. amnicum* and *S. corneum* (Figs. 2–3).

The function of the palps between the gill and the mouth is that of conveying, sorting and selecting particles to be ingested as food or rejected as pseudofaeces. Only non-mineral particles with diameters of up to 5 µm in *Pisidium* and 30 µm in *Sphaerium* are ingested (Lopez & Holopainen 1987, Holopainen, unpubl.). In general the length of the palps is related to the feeding mode: deposit feeders and those living in turbid waters have very long and mobile palps, whereas the filter-feeders in clear waters have small palps (Morton 1983).

*Oesophagus.* In cross section the oesophagus is round outside but has a horizontally flattened and ciliated (slit-like) lumen in *P. casertanum* (Fig. 10). In *P. conventus* the lumen is round, too (Figs. 8–9). The length of the oesophagus is about 18% of the total tract in *Pisidium amnicum* but slightly shorter (13%) and oval in *Sphaerium corneum* (Fig. 4).

The role of the oesophagus is simply by ciliary activity to pass particles to the stomach, an act which in *P. conventus* is seen to take place in just a few seconds (Holopainen unpubl.).

*Stomach.* The stomach is a flattened sac with a dorsal hood (blind curve) to the left (Figs. 5–6). The structures inside contain ciliary tracts and grooves, as well as a hard gastric shield and anterior openings from vestibulae on both sides to the digestive diverticulae system. The diameter of the stomach is about 5–7% of the total tract length in both genera. The structure of the stomach of *Sphaerium corneum* was described in detail and defined by Purchan (1958, 1960) as belonging to bivalve stomach type IV. The stomach in *Pisidium* appears to be identical with this.

The function of the stomach is largely that of sorting. Other possible functions (mechanical grinding and extra-cellular digestion) are performed by the revolving action of the crystalline style projecting into the lumen of the stomach (Reid 1965, Morton 1973, 1983, Judd 1979).

*Digestive diverticulae.* The space dorsal and lateral to the stomach, that posterior to the oesophagus, and that between the mid-gut and the oesophagus is filled with digestive diverticulae of the midgut gland or liver (Fig. 5). In *P. casertanum* and *S. corneum* these consist of several bunches of branching tubules with spherical blind end-cavities or lobes and a common opening to the vestibulae of the stomach. The number of lobes is in the order of 200 and their outer diameter is 0.1 mm in a 3–4 mm (shell length) animal (Figs. 5 and 7). The diameter of the lobes is the same

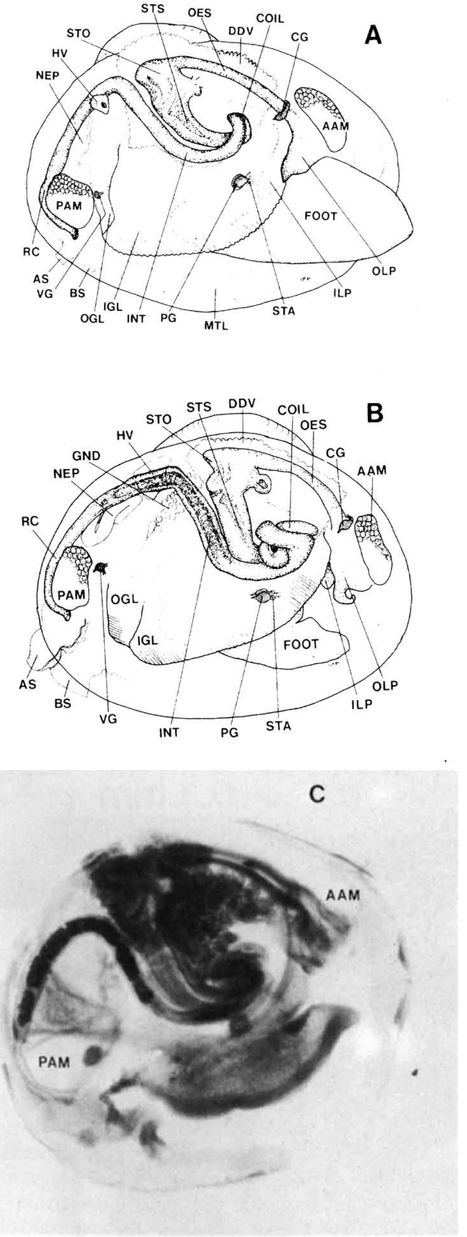


Fig. 1. Drawings of *Pisidium amnicum* (A) and *Sphaerium corneum* (B), together with a photograph of *S. corneum* (C) dissected to show the digestive tract. — AAM, PAM: anterior and posterior adductor muscles; OLP, ILP: outer and inner labial palps; CG, PG and VG: cerebral, pedal and visceral ganglia; STA: statocyst; OES: oesophagus; DDV: digestive diverticulae; STO: stomach; STS: style sac; HV: heart ventricle; NEP: nephridium; RC: rectum; AS, BS: anal and branchial siphons; OGL, IGL: inner and outer gills; INT: intestine (hindgut); MTL: mantle.

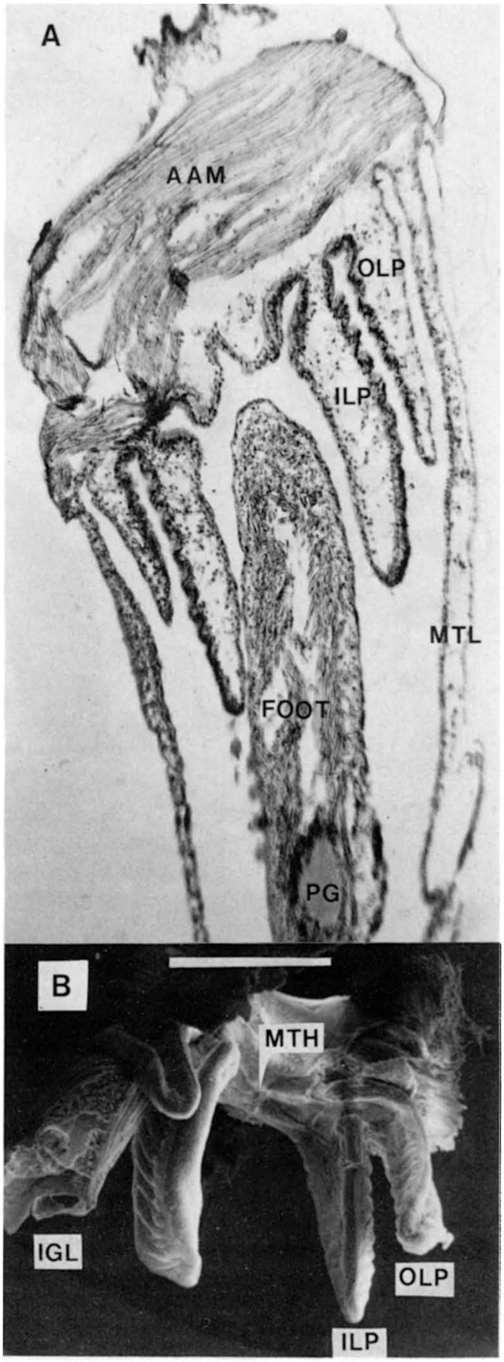


Fig. 2. A section through (A), and a photograph of (B) the labial palps of *P. amnicum*. — MTH: mouth; for other abbreviations see Fig. 1. Scale bars: 1 mm.

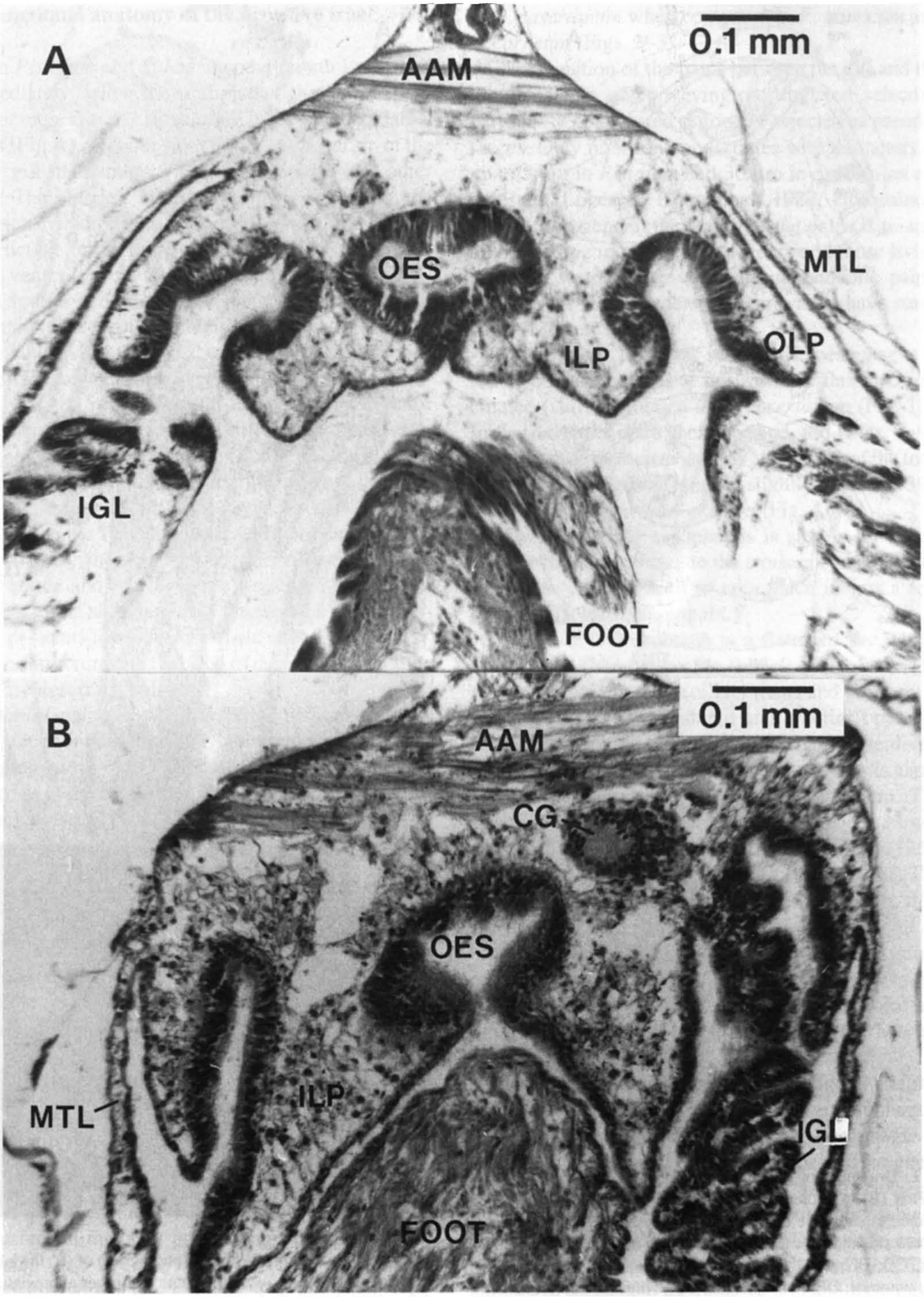


Fig. 3. Transverse sections of the labial palps of *P. conventus* (A) and *P. casertanum* (B). For abbreviations see Fig. 1.

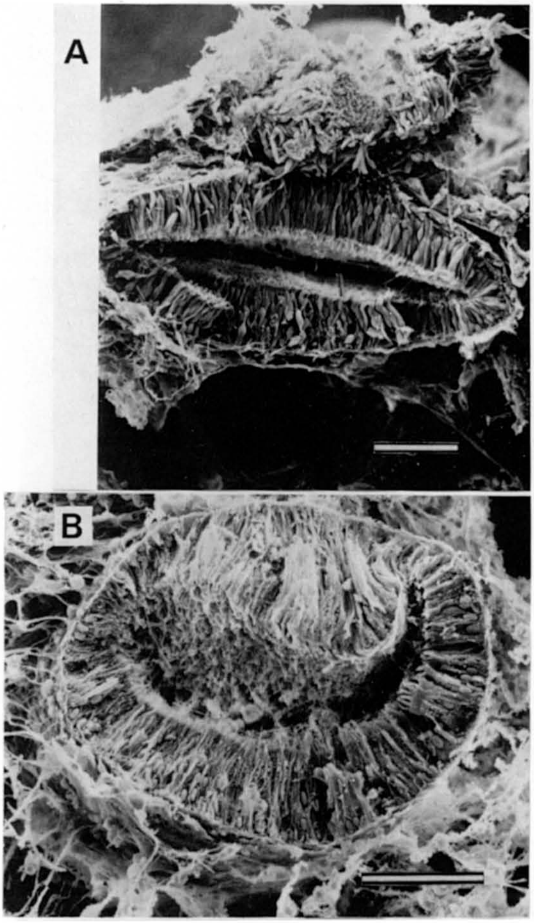


Fig. 4. Transverse sections of the oesophagus (A) and rectum (B) of *S. corneum* (8 mm). Scale bars: 100 μm.

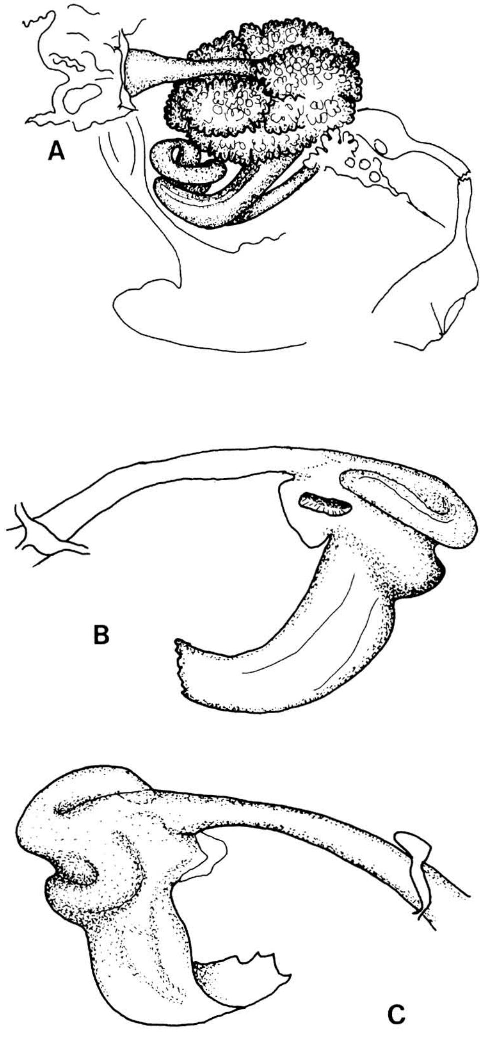
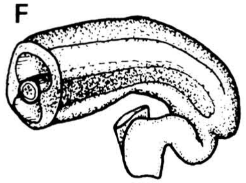
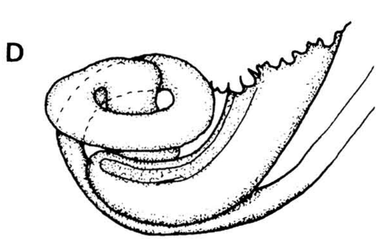
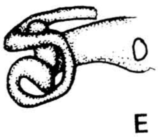
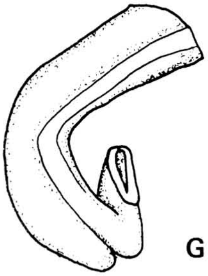


Fig. 5. Detailed drawings of the stomach and coil regions of *S. corneum*. — A: dorsolateral view of the digestive diverticulae, midgut and coil regions. B: left and C: right side of the stomach-midgut region. D: details of the coil. E: dorsal view of the coil. F, G: midgut and style sac. For abbreviations see Fig. 1. The drawings are not all to the same scale.









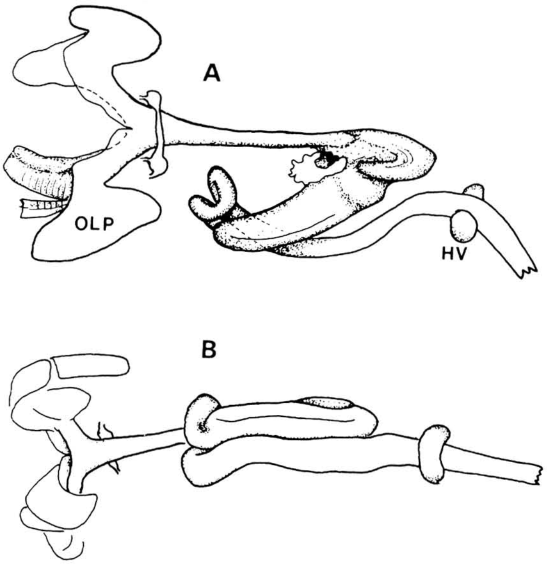


Fig. 6. Detailed drawings of the stomach and coil regions of *P. amnicum*. — A: dorsolateral view. B: ventral view.

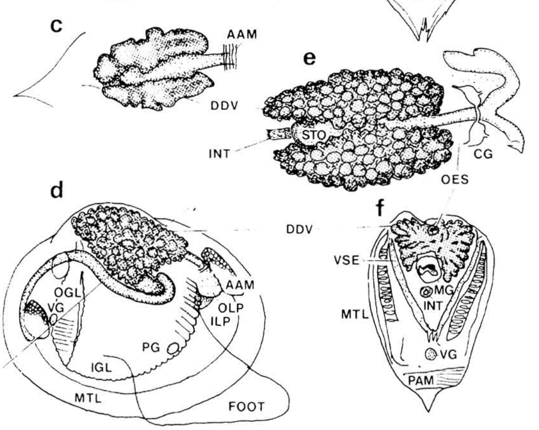


Fig. 7. Drawings of *P. conventus* (a–c) and *P. casertanum* (d–f) to show the digestive diverticulae. Dorsal views in the middle (c, e). — VSE: visceral septum; for other abbreviations see Fig. 1.

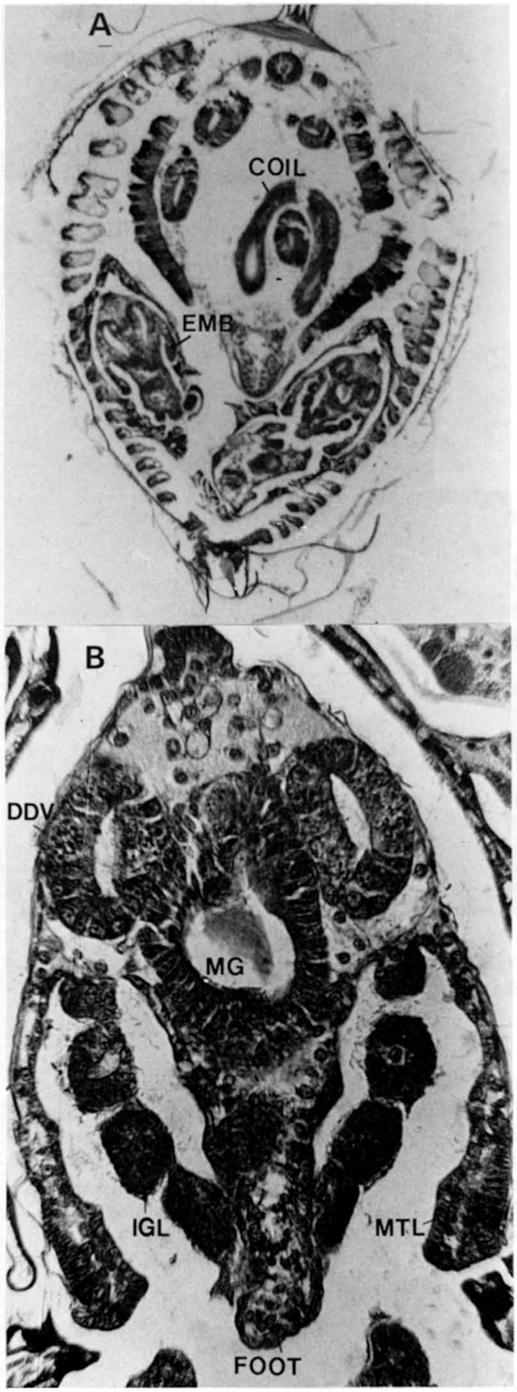


Fig. 8. A transverse section (A) of a gravid *P. conventus* at the coil region, together with that of the embryo or larva (B) to show the developing digestive diverticulae at the simple tube stage. For abbreviations see Fig. 1.

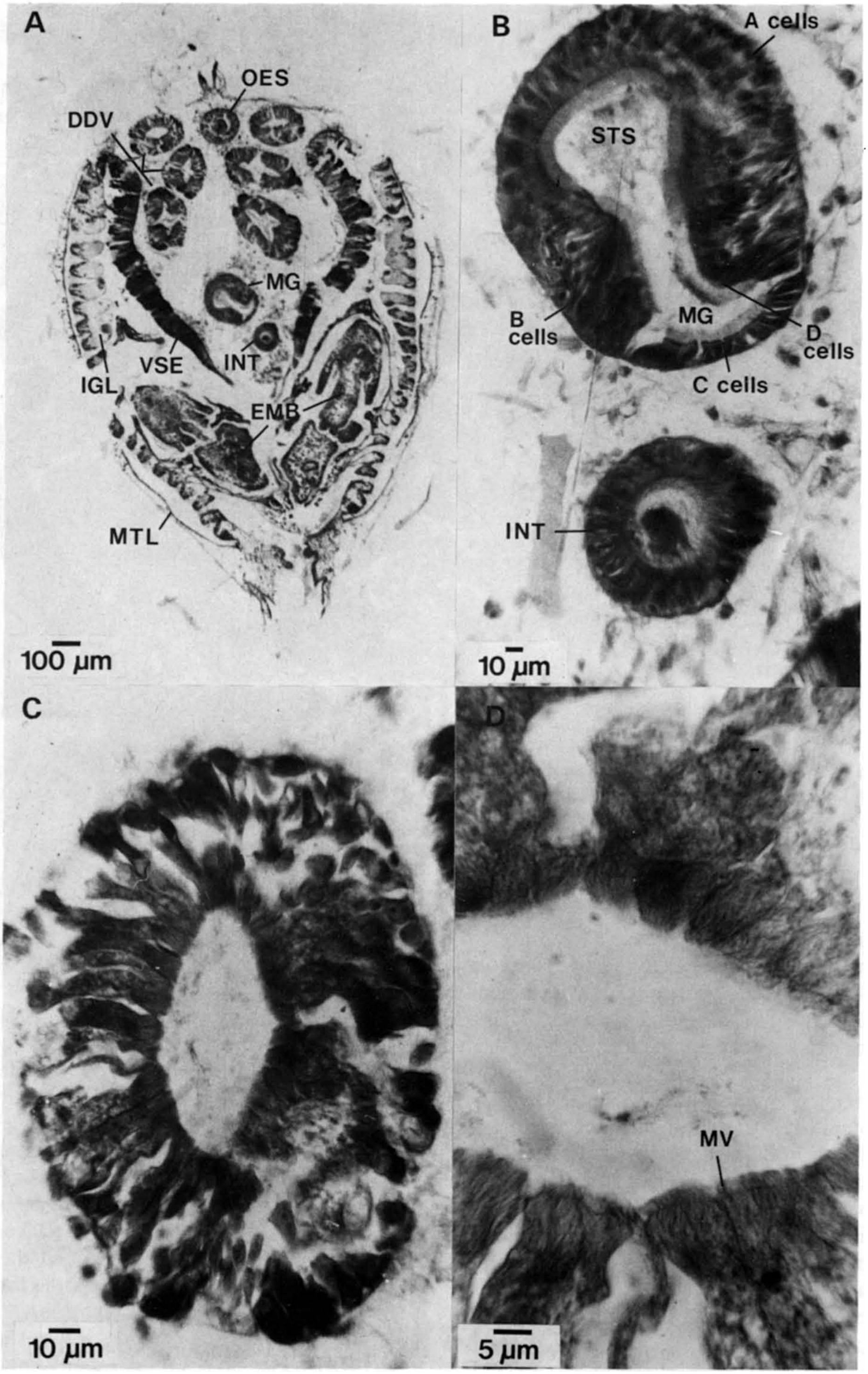


Fig. 9. A transverse section of *P. conventus* (A) and details of the midgut and intestine (B), as well as of one tubule (uppermost right in A) of the digestive diverticulae (C D). Lake Pääjärvi 17 July 1984. — MV: microvilli; for other abbreviations see previous figures.

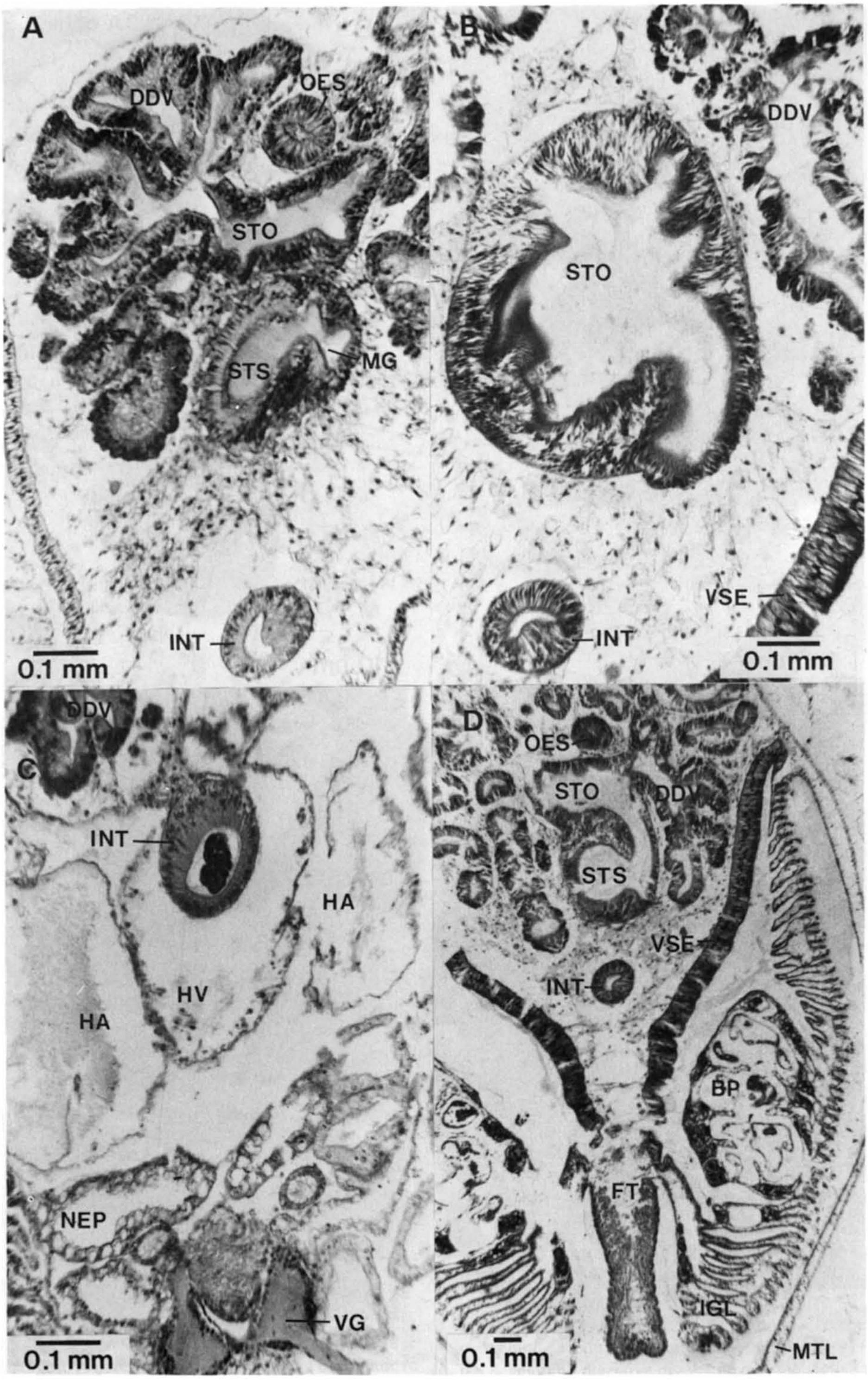


Fig. 10. Transverse sections of *P. casertanum* to show the digestive diverticulae, stomach and intestine. — FT: foot; MG: midgut; HA: heart auricle; VSE: visceral septum; BP: brood pouch; for other abbreviations see Fig. 1.

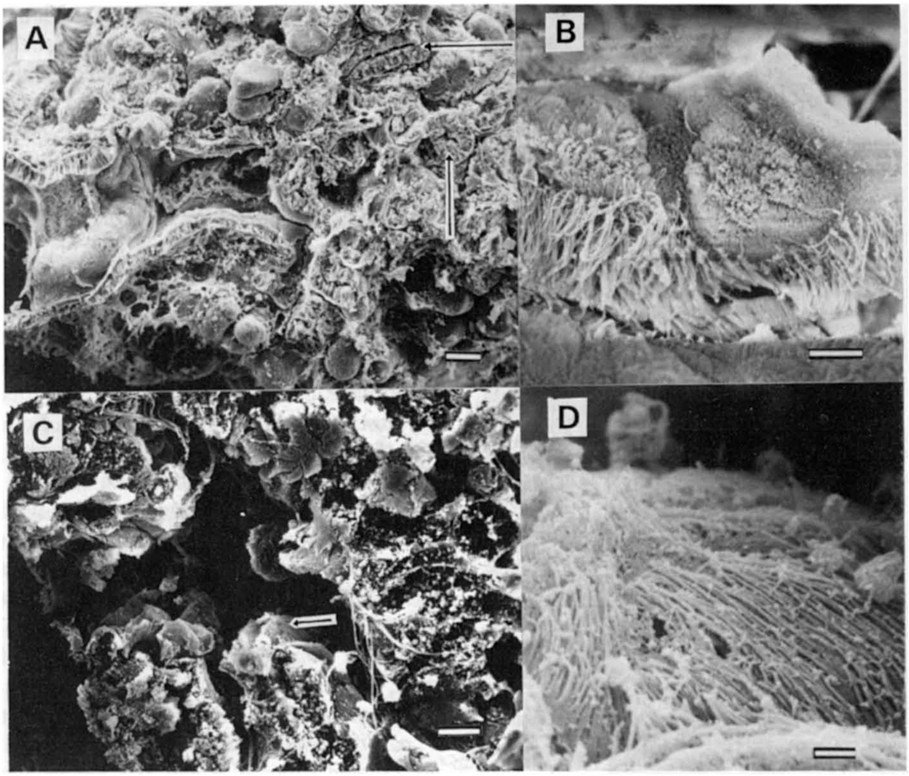


Fig. 11. A primary duct and part of the digestive diverticulae (A) of *S. corneum*. Details of the secondary duct are shown in (B), and those of the tubule in (C). D is part of the inner ciliation of the tubule (C). — FLA: flagellae of the crypt cells in the invaginations of the tubule. Scale bars: A: 100 µm; B, C: 10 µm; D: 1 µm. The sites of the enlargements (B, C) are shown in A and that of D in C.

even in an 11 mm *S. corneum*, but their number may reach one thousand. The spheres are hollow but have thick walls, leaving only narrow cavities. Clusters of crypt cells with flagellae can be seen in Fig. 11 (for details of the function see Morton 1983).

*P. conventus* has a much simpler structure with only ten large lobes which have relatively large and simple inner cavities (Fig. 7) furnished with microvilli (Fig. 9). Meier-Brook (1967) has pointed out that in the neotenic species of the subgenus *Neopisidium*, the differentiation of the gland (digestive diverticulae) is limited and the maximum lobe number in the dorsal portions of the gland is 4 to 8, e.g. in *P. conventus*. According to Meier-Brook (1970) the number of lobes is generally small (only a few) in embryos inside the parent (or at the larval stage; see also Fig. 8) but increases to hundreds in the adults of *P. obtusale*, for example. The neotenic, simple structure of the main or only site of absorption and intracellular digestion (Owen 1955, Morton 1983) probably sets certain requirements for food quality and quantity and hence habitat selection in the species in question (see Lopez & Holopainen 1987).

*Style sac and crystalline style.* The mid-gut is joined to the style sac and ventrally or anterioventrally to the stomach, forming a fairly straight, thick and in cross section rounded part before the coil (Figs. 9, 10 and 12). The inner cavity is, however, reduced to a broad T-shape by two folds or typhlosoles on the right side, leaving a thin wall between them at the base of the 'T'. The wider part of the cavity (top of the 'T') is the style sac furnished with transverse folds and lined with heavily ciliated cells (A cells, Figs. 9 and 12) for rotating the style contained in the sac. The posterior typhlosolis is larger, with dark staining cells

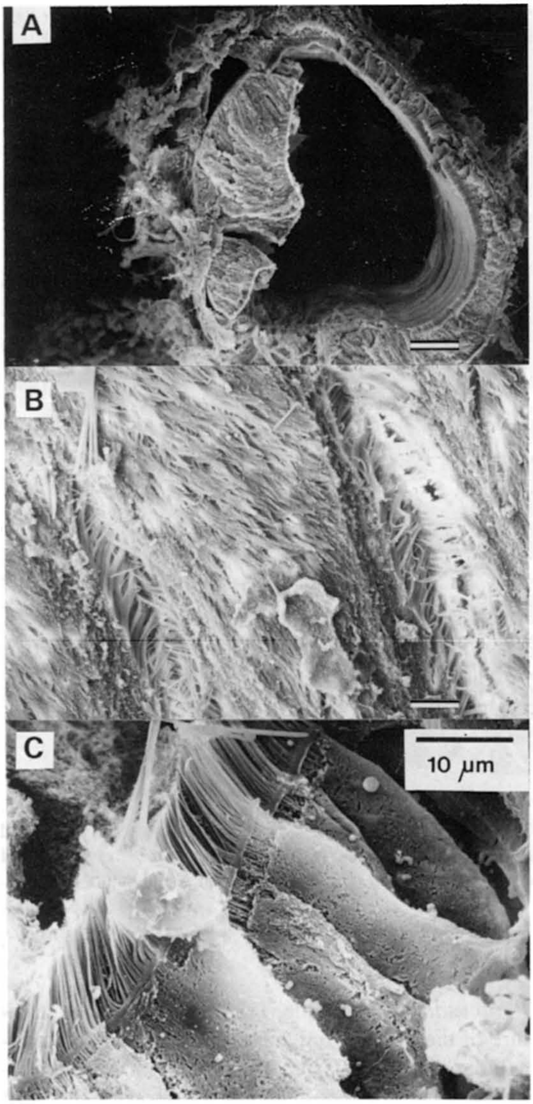


Fig. 12. Dorsal view of the style sac (A) and details of the layers (B) of A-cells (C) in *P. casertanum*. Scale bars: A: 100 µm; B, C: 10 µm.

(B cells) which probably play a part in the secretion of the style. The style sac ends blindly but the gut continues from the "thin wall" or food groove side (C and D cells, Fig. 9) and is looped into a coil. The length of the style sac and the mid-gut is 9–12% of the total tract length. The crystalline style is a transparent hyaline rod, round in cross section and with a sheath and a clearer outer part (Judd 1979). The diameter of the style was 0.11 mm in *P. amnicum* (shell length 7 mm), 0.08 mm in *P. casertanum* ( 3 mm) and as much as 0.12 mm in *P. lilljeborgi* (3 mm). We have not been able to detect or measure the style in *P. conventus* but the overall stomach anatomy suggests a similar size and structure. Judd (1979) and Morton (1983) give a detailed description of the bivalve design and composition of the style and style sac.

*Coil and hindgut.* In *Pisidium* the next part of the gut is a broadly U-shaped coil (length ca. 13% of total tract) projecting anteriodorsally and serving to turn the gut backward again. In *S. corneum* the coil is more complicated, flat in the first part and much longer (approx. 30% of the total tract, Fig. 5). Following the coil the gut ascends posteriodorsally parallel to the style sac, runs through the heart ventricle and then descends as the rectum along the body wall and proceeds in a flattened form behind the posterior adductor muscle, to end through a papilla or thickened tissue ring in the cloacal chamber just below the muscle and close to the visceral ganglion. The length of the gut from coil to anus is about 40% of the total tract, the heart being located half way along it. A longitudinal dorsal fold or typhlosolis runs in the gut of *P. casertanum* (but not in *P. conventus*) and the walls are ciliated (Figs. 4, 9 and 10). Defaecation is performed by the ciliary activity in the rectum. The hindgut (following the coil) and the rectum form the only part of the canal where the gut contents (rejected material and waste from that ingested) can be found accumulated (Lopez & Holopainen 1987). In *P. conventus* the contents of the hindgut and rectum form a spiral coil if the gut is not completely and tightly filled.

*Visceral septum.* Another interesting anatomical feature in *Pisidium* is the prominent visceral septum or epithelium of the visceral sac (Figs. 9–10). Especially in gravid individuals of both *P. conventus* and *P. casertanum* the septum is constructed of a thick columnar epithelium with a high glycogen content (PAS-positive histochemical reaction causing the black coloration in the figures) and suggestive of some metabolic function. Meier-Brook (1970) has described this change in the thickness and cell type of the septum during gravidity in some *Pisidium* species. He also noticed a quick return to the former state after the release of embryos unless another period of reproduction followed immediately. Meier-Brook (1970) suggested that this thickened septum was a mechanical support against the pressure from the increasing brood sac.

## 4. Conclusions

In summary, the design and structure of the alimentary canal in Sphaeriidae closely resembles the general bivalve pattern (e.g. Morton 1983). The stomach represents stomach type IV as described by Purchon (1958, 1960).

The intergeneric differences in Sphaeriidae include the longer and more mobile palps and clearly longer coil portion of the gut of *S. corneum* compared to *Pisidium*. Usually lengthening of the gut is in relation to an increased proportion of vegetable material in the diet. In the case of *Sphaerium* and *Pisidium* no detailed information on the diet (assimilated food) exists but some results suggest higher filtration rates (Hinz & Scheil 1972) and the ingestion of larger particles in *Sphaerium* (Holopainen, unpubl.). This, together with the anatomical evidence given above, could indicate that the ingestion of plant detritus or herbivory on diatoms and green algae is more important in *Sphaerium*, whereas *Pisidium* species rely mostly on microbes (Lopez & Holopainen 1987).

*Pisidium casertanum* is a typical representative of its genus but *P. conventus*, on the other hand, shows some distinctive features in the anatomy of the digestive tract: short labial palps, round oesophagus, simple midgut gland, no typhlosolis in the hindgut. The most interesting feature is the simple (neotenic) structure of the digestive diverticulae system, the most important organ of absorption and intracellular digestion. *P. conventus* is a small, stenoecious species with low metabolic demands (Holopainen & Hanski 1979, 1986). It most probably feeds on an interstitial suspension of microbes (Lopez & Holopainen 1987), which constitute an adequate, high quality food easily digested even by simple machinery.

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