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## COMPARATIVE ANATOMY OF THE ALIMENTARY CANAL OF HYPERIID AMPHIPODS

*Charles Oliver Coleman*

### ABSTRACT

The foregut and midgut glands of hyperiids are strongly aberrant in comparison with gammaridean amphipods. In hyperiids, the stomach has a reduced filter capability. In the genus *Cylopus*, there is only a one-step filter developed, which is of different origin from the filter structures of gammaridean stomachs. In all other hyperiids, the stomach has lost its filter function. In the genus *Phrosina*, the stomach cavity is completely reduced. Corresponding to the reduction of stomach filtration, the anatomy of the midgut gland is transformed from the plesiomorphic condition of blind-ending tubes to large saclike digestion chambers. The stomach connects with the midgut gland. There is a constriction between the midgut gland and the midgut. Food morsels were found in the stomach and the midgut gland but not in the midgut of these species. The role of the midgut remains obscure. This investigation yielded synapomorphies for the otherwise not well-justified taxon Hyperiidea.

The anatomy of the alimentary canal of amphipods is remarkably diverse. The foregut especially has been studied in detail (Thiem, 1942; Siewing, 1963; Martin, 1964; Kannevorff and Nicolaisen, 1969; Keith, 1974; Icely and Nott, 1984; Coleman, 1990a, 1991, 1992) and its functional morphology is relatively well understood. In gammaridean, ingolfiellidean, and caprellidean amphipods the functional roles of the foregut are essentially the same. However, development of certain foregut structures and relative stomach length differ in certain taxa, apparently because of differences in food preference and the systematic position (Coleman, 1991).

The greatest variations in stomach structure evolved in food specialists. The necrophagous (see Presler, 1986) *Waldeckia obesa* (Chevreux, 1905) (Lysianassoidea) has an oversized stomach, possibly as an adaptation to long intervals between short periods of active feeding (Coleman, 1992). Other lysianassids use their extendible midgut as a food reservoir (Dahl, 1979; Barnard and Ingram, 1986). The Antarctic species *Bathypanoploea schellenbergi* Holman and Watling, 1983 (Stilipedidae) feeds on holothurians (Coleman, 1990b) and has a dilated stomach (Coleman, 1992) that shows some resemblance to conditions found in the possibly related *Parandania boeckii* (Stebbing, 1888) (Stegocephalidae) that feeds on medusae of the genus *Atolla* (see Moore and Rainbow, 1989; Coleman, 1990a). Such investigations show that anatomy can pro-

vide details for a better understanding of the ecology and the phylogeny of these amphipods.

Alimentary canals of various hyperiids have been studied (Claus, 1887; Ide, 1892; Garbowski, 1896; Woltereck, 1904, 1927; Agrawal, 1967; Evans and Sheader, 1972; Sheader and Evans, 1975; Brusca, 1981; Diebel, 1988), but no comparative examinations were carried out. Thus, it is understandable that structures of the aberrant hyperiid alimentary canal could not be homologized until now and that many functional aspects remained undetermined.

Moore (1992) discussed the possibility that stegocephalids and hyperiids might be closely related, since both taxa, having a similar mode of living and morphological features of the hyperiid infraorder Physosomata, "are certainly reminiscent of stegocephalids" (Moore, 1992). Like the stegocephalids, many hyperiids are food specialists and are considered to be "parasitoids associated with gelatinous zooplankton" (see review in Laval, 1980). The parasitoid habit was questioned by Sheader and Evans (1975). They viewed *Parathemisto gaudichaudii* as a free-living predaceous hyperiid. In *Hyperia galba*, one of the best-studied hyperiid amphipods, controversy persists as to the specific food preference. Some investigators regard this species to be parasitic, but others regard it to be commensal (see reviews in Laval, 1980; Ditrach, 1992). Von Westernhagen (1976) found that *Hyperoche medusarum* might be

a predator feeding mainly on copepods and larvae of herring.

Whatever may be true, all three of the above species belong to a single hyperiid family and certainly do not represent the Hyperiidea as a whole. Despite some very promising observations of live hyperiids carried out by divers (Madin and Harbison, 1977; Harbison *et al.*, 1977), the biology of most species is still poorly understood.

The investigation of the functional anatomy of the alimentary canals of selected hyperiid species might suggest what kind of food is preferred. Aside from the hypothesis that many hyperiids feed on gelatinous plankton, there is another point that requires investigation, namely, the uncertainty whether the Hyperiidea are a monophyletic group or a polyphyletic assemblage (Pirlot, 1932). The aim of this study is to describe the gut anatomy in order to throw light on this phylogenetic problem.

#### MATERIALS AND METHODS

Specimens of *Cylopus lucasi* Bate, 1862, were collected during the RV *Polarstern* cruises during 1987 and 1992 near Elephant Island (South Shetland Islands, Antarctica). Collections were made with a rectangular midwater trawl at unknown depth. *Brachyscelus globiceps* (Claus, 1887) was examined from the collections of the Museum für Naturkunde (Berlin). This species was collected during the Dana expedition at station 3814 IV (9.9.1929, 4°38'S 99°24'E, MW 50, S200). *Platyscelus armatus* (Claus, 1879), also from the Museum für Naturkunde (Berlin), was collected on the Dana expedition at station 1168 (12.11.1921, MW 300). *Lanceola sayana* Bovallius, 1885, was collected during a cruise of the MV *Delaware* (det. T. E. Bowman, 17 July 1958, 36°16'N 70°00'W) from *Alepisaurus* sp. provided by the National Museum of Natural History (Washington, D.C.). Specimens of *Phronima sedentaria* Forskål, 1775, *Scina crassicornis* Fabricius, 1775, and *Phrosina semilunata* Risso, 1822 were collected from the Mediterranean at unknown locations at a depth of 200 m. Collected material was fixed in approximately 4% Formalin; material from the museums was stored in 70% ethanol.

Specimens were dissected using a pair of microsurgical scissors and forceps to remove most of the tergites. The alimentary canal was extricated and examined with a Wild M3 dissecting microscope.

Foreguts from each species were heated for 30 min in concentrated potassium hydroxide solution to remove tissue. The unstained cuticle of the foreguts were transferred into glycerol or water. All structures were seen easily through the transparent cuticle. Small pieces of glass were used to stabilize the stomachs in a watch-glass. Drawings were made with a Wild M3 dissecting microscope and an Olympus BH-2 microscope, both fitted with a camera lucida. In the drawings of the foreguts, thick lines indicate structures on the surface

of the cuticle, fine lines inner structures, and dashed lines depict contours of the lowest plane.

For histological examinations, specimens were embedded in methylmethacrylate (Technovit 7100, Kulzer). The polymerization of the methylmethacrylate was retarded in a refrigerator for several hours. Sections of 4  $\mu$ m were obtained with a Reichert-Jung microtome (Cambridge Autocut 1140). Sections were stained with toluidine blue (0.1% approximately 30 s). Photomicrographs were made with an Olympus OM-2 camera on an Olympus BH-2 microscope.

For SEM examinations, parts of the foreguts were dissected, dried in an alcohol series, critical-point-dried, sputter-coated with gold (4 min at 10 mA) and examined on a Hitachi S 450 scanning electron microscope.

Terminology of foregut structures is that of Scheloske (1976a, b).

#### RESULTS

##### *Cylopus lucasi*

As in gammaridean amphipods, the foregut of *Cylopus lucasi* is differentiated into esophagus, stomach chamber, and funnel region (the fused lamina dorsalis and lamella ventralis; cf. Scheloske, 1976b), the latter protruding deeply into the midgut. The inner surface of the esophageal cuticle is covered with short setae, especially dense on the cuticular plates located just behind the mouth opening (Fig. 1A). The stomach chamber lacks lateralia and is divided into a dorsal cavity and two ventral channels. The ventral channels are formed by a large ventral invagination (Fig. 1B a-c: IM, inferomedianum) and lateral infoldings (Fig. 1B a-c: IL, inferolateralia).

The inferomedianum is not subdivided as in gammaridean amphipods into anterior and posterior regions. However, there is a large undivided inferomedianum that is significantly produced caudally. It is wide anteriorly, tapering posteriorly, and has a deep depression anteriorly, so that the inferomedianum appears as a bilobed structure in transverse sections (Fig. 1B a). More posteriorly, this depression becomes shallower (Fig. 1B b, c) and terminates in a narrow keel (Figs. 1B d, 2A). Nearly halfway between the beginning and the posterior apex of the inferomedianum the cuticle of the dorsal region is sclerotized to form a pair of narrow and medially directed straps of unknown function (Fig. 2A). There are dense rows of short spines on the dorsolateral part of the inferomedianum that extend over the ventral channels to the lateral side of the

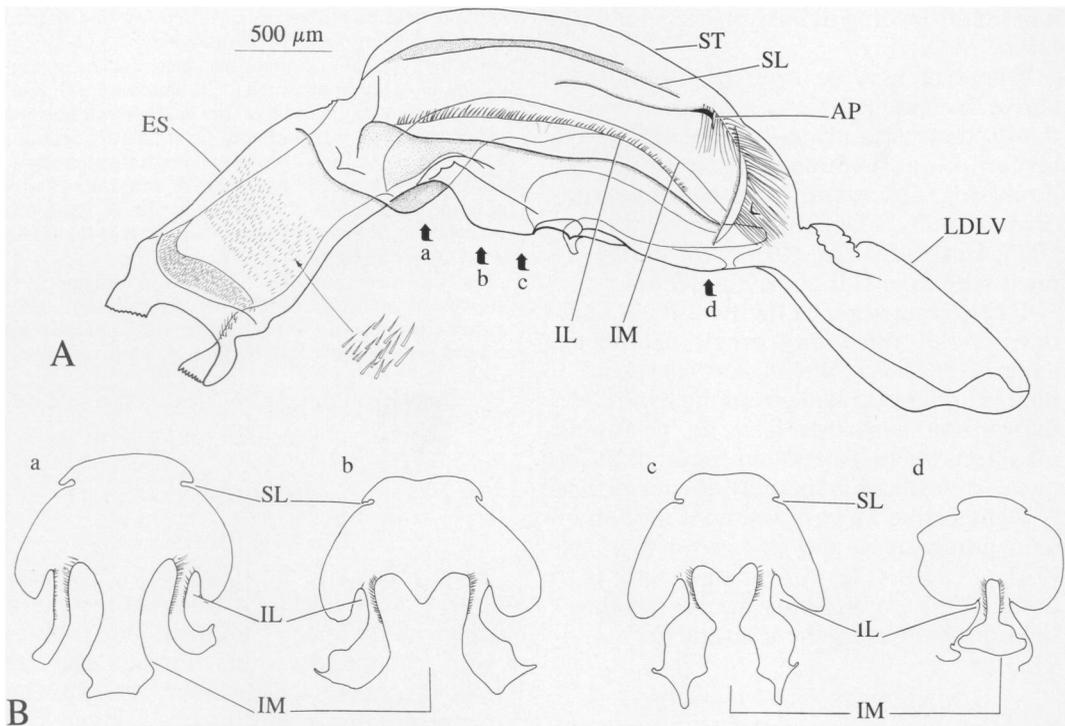


Fig. 1. *Cyllopus lucasi*. A, left lateral view of macerated foregut; arrowheads indicating planes of histological sections in B. AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, SL = superolaterale. ST = stomach.

inferolateralia (Fig. 3A). The middorsal region of the inferomedianum is covered with groups of setae (Fig. 3A).

The inferolateralia are curved dorsally and bear a row of dorsally directed setae extending nearly throughout the whole stomach cavity (Fig. 3A).

In the dorsal stomach cavity, there is another pair of short lateral invaginations, the superolateralia (Fig. 1A, B a–c). In gammaridean amphipods these infoldings are bordered with long setae, but in *Cyllopus lucasi* they are developed only in the posterior part of the stomach chamber (Fig. 1A). The lateral internal stomach cuticle is densely covered with rows of setae (Fig. 3B, D).

The ventral channels of the stomach of *Cyllopus lucasi* course into the atrium of the midgut gland (Fig. 4C). The atrium communicates with two blind-ending tubes that extend into the pleon region. Each cecum bears a lobe anterodorsally that comes near the esophagus (Fig. 4A, C). The midgut has two short anterodorsal ceca. At the border

of the hindgut, the midgut is expanded and bears two laterally directed ceca and two additional ceca pointing posteriorly. The hindgut narrows to a dorsoventral slit that may be dilated by groups of extrinsic muscles attached laterally.

#### *Brachyscelus globiceps*

The foregut of *Brachyscelus globiceps* is of unique shape within amphipods. The esophagus enters the stomach ventrally. The anterodorsal cuticle consists of a sclerotized convex shield, whereas the posterior cuticle is thin and folded. The stomach exit is small and there is no lengthy funnel region (Fig. 5B; arrowhead). A pair of ventral infoldings are the only structural elements extending into the stomach cavity. These infoldings are in contact with the lateral stomach cuticle. There is no inferomedianum, and ventral channels are absent. Only the inferolateralia separate lateral channels. These infoldings are serrate dorsally and bear teeth dorsomedially. The internal lateral stomach

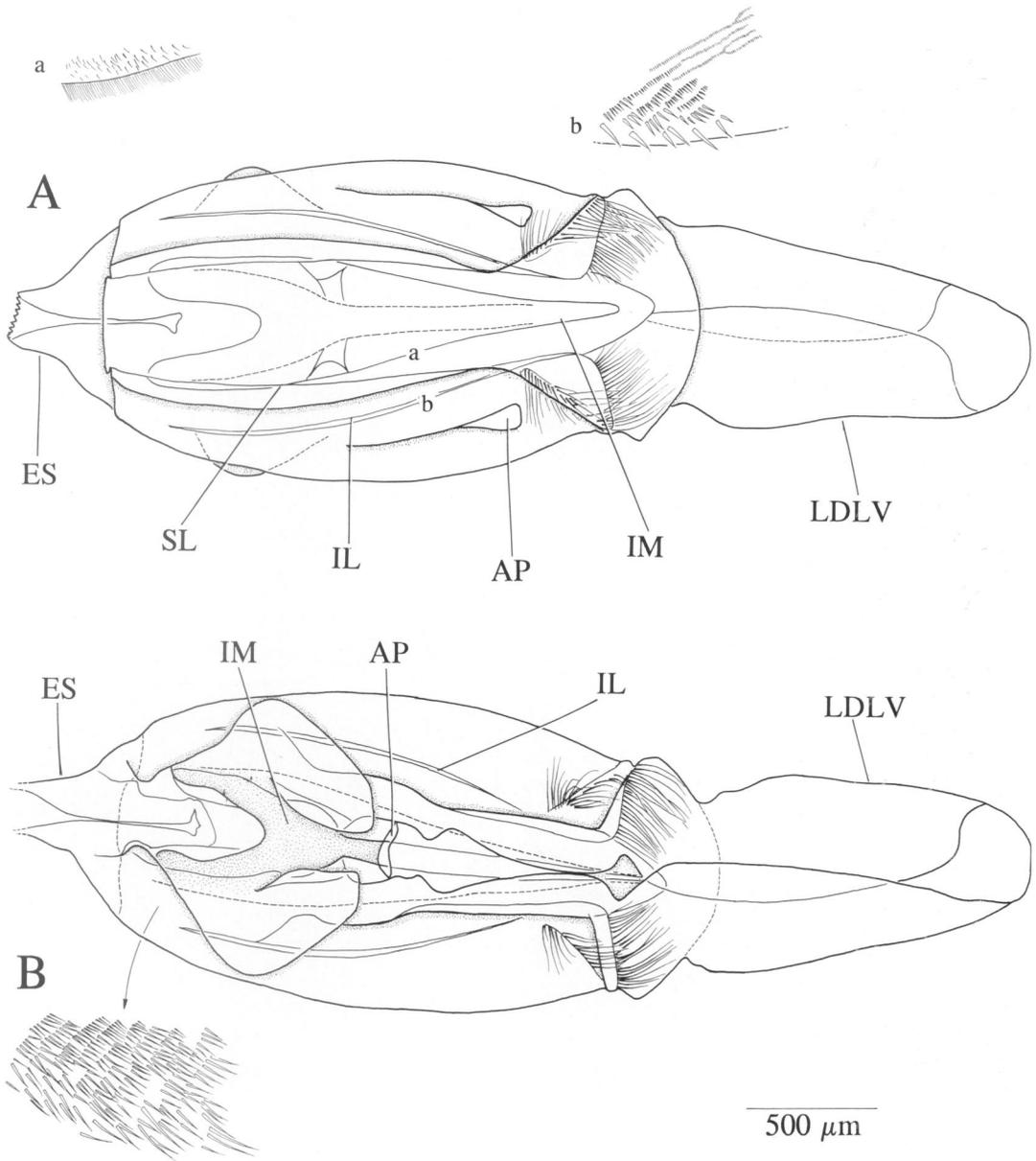


Fig. 2. Foregut of *Cyllopus lucasi*. A, dorsal view. a, detail of inferomedianum; b, medial face of inferolaterale; B, ventral view, detail showing enlarged spinules of internal lateral stomach cuticle. AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, SL = superolaterale.

wall bears rows of posteriorly directed short spines (Fig. 9A).

The exit from the stomach cavity is connected to the spacious atrium of the midgut gland (Fig. 6C: arrowhead). The midgut gland has a pair of anteroventral lobes, as in *Cyllopus lucasi* (Fig. 6A), and two ceca

with conspicuous lateral protrusions (Fig. 6A–C). The midgut is embedded between the ceca of the midgut gland. The midgut is constricted at the junction to the atrium of the midgut gland (Fig. 6C). Food morsels are present in the stomach and the midgut gland, but not in the midgut.

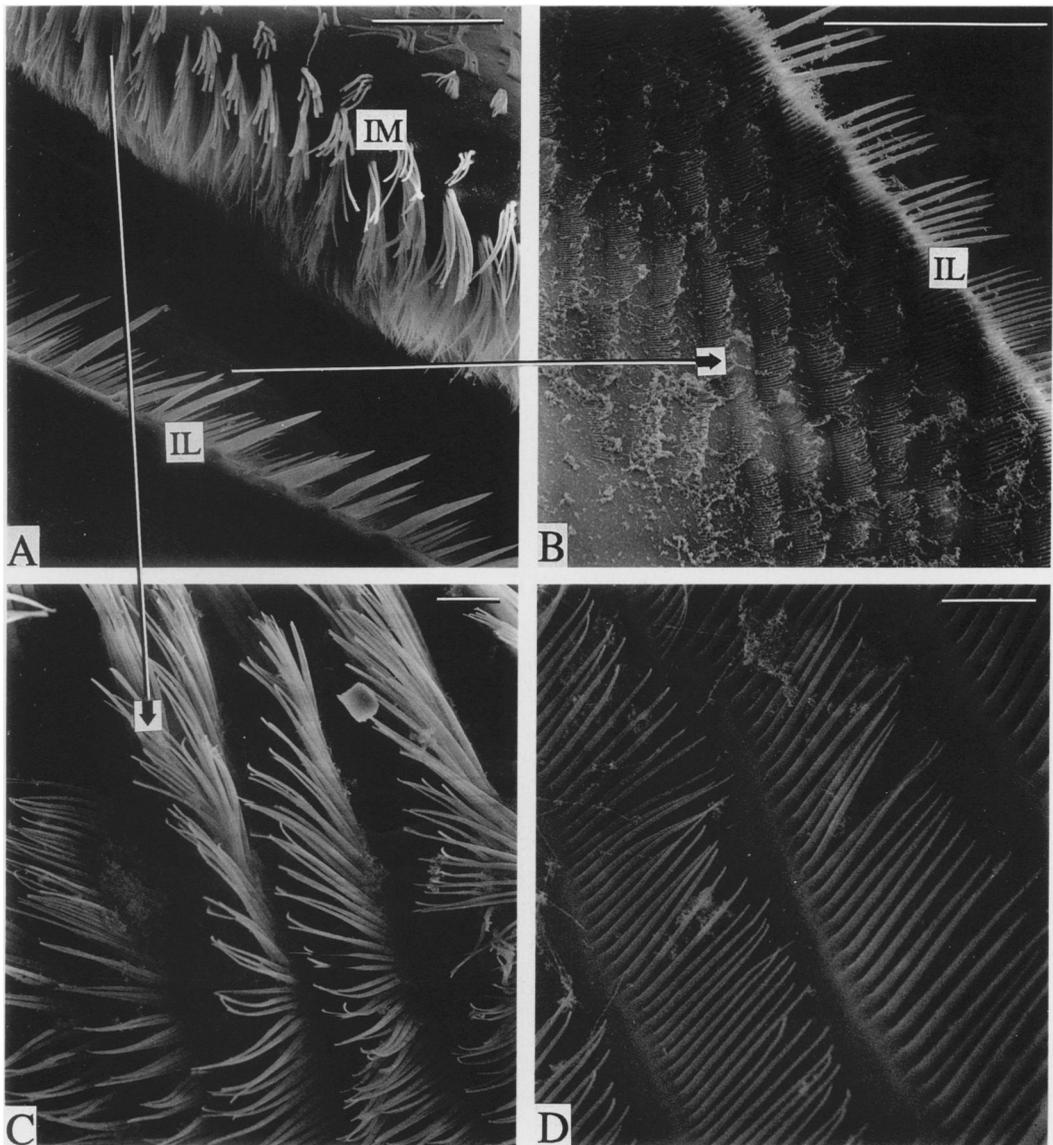


Fig. 3. SEM photomicrographs of stomach of *Cyllopus lucasi*. A, inferomedianum (above) and left inferolaterale (below). Note dorsally directed setation on inferolaterale, homologous to rough filter setae in gammaridean amphipods; B, detail of inner face of left inferolaterale; C, groups of lateral setae on inferomedianum; D, rows of small setae on lateral face of inferolaterale. IL = inferolaterale, IM = inferomedianum. Scale bars A, B = 50  $\mu\text{m}$ ; C, D = 5  $\mu\text{m}$ .

### *Platyscelus armatus*

The foregut of *Platyscelus armatus* has a large esophagus (Figs. 7, 8B). Its walls are narrowed considerably, so that the lumen is restricted in diameter. The cuticle of the esophagus is sclerotized and thickened halfway between the mouthparts and the stomach chamber (Figs. 7, 8B: arrowhead). The stomach cavity is rather short with only in-

ferolateralia infolded from the ventral side. Their dorsal margins are somewhat serrate and small spines are present on the lateral side of the infoldings (indicated as dashed lines in Fig. 9B). Furthermore, the internal lateral stomach wall is covered by a crescent-shaped field of minute spines. There is a tongue-like lobe midventrally that is produced and rounded dorsally, and may be the vestigial inferomedianum. As in

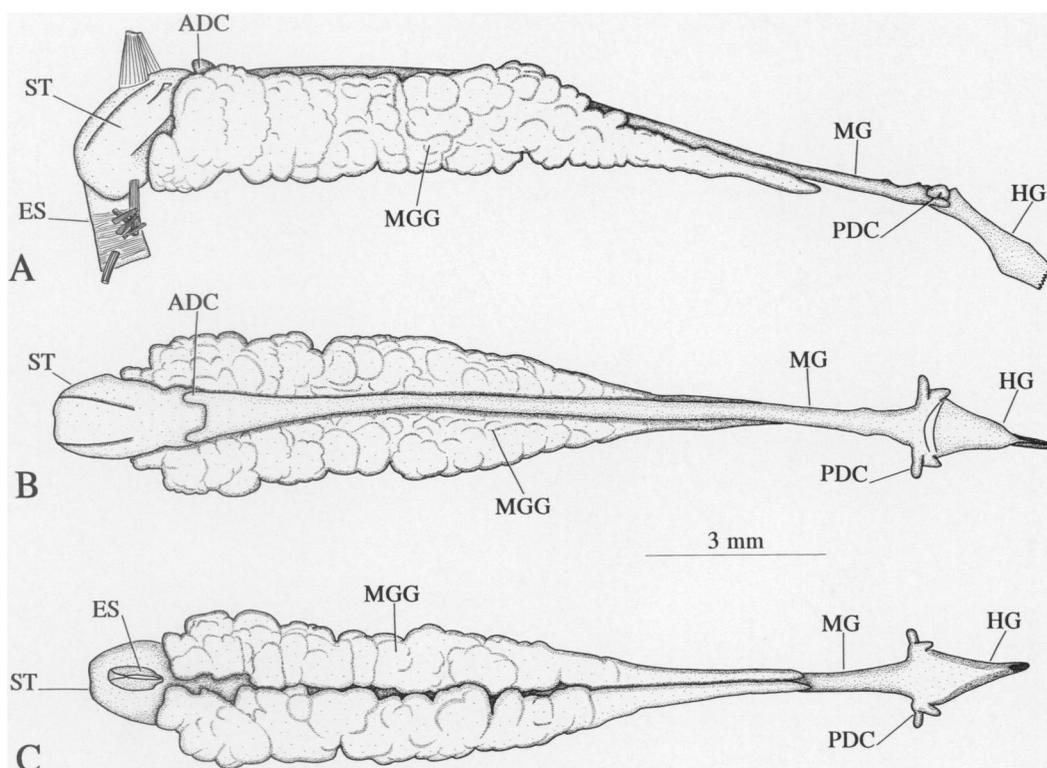


Fig. 4. Dissected alimentary canal of *Cyllopus lucasi*. A, left lateral aspect; B, dorsal view; C, ventral side. ADC = anterodorsal cecum, ES = esophagus, HG = hindgut, MG = midgut, MGG = midgut gland, PDC = posterodorsal cecum, ST = stomach.

*Brachyscelus globiceps*, the stomach is connected to the midgut and not to the midgut. The exit of the stomach cavity to the midgut gland is conspicuous. Food is not filtered in the stomach and enters the midgut gland as large particles.

The midgut gland consists of a cavernous atrium and a pair of bulky ceca with lateral protrusions (Fig. 8A). The midgut gland reaches into the front of the sixth pereonite. The stomach is located at the front of the atrium and to a limited extent projects into its lumen. The midgut is linked with the posterior wall of the atrium. The lumen of the midgut is constricted close to its junction to the midgut gland, similar to the condition in *Brachyscelus globiceps*.

#### *Phronima sedentaria*

The slender esophagus of *Phronima sedentaria* leads into a short stomach cavity, which is drawn out posteriorly into a unique, long-bowed, hoodlike structure (Figs. 10A, 11B, C). Comparable to the stomachs of

*Cyllopus lucasi*, *Brachyscelus globiceps*, and *Platyscelus armatus*, the inferolateralia project dorsally into the stomach cavity (Fig. 14A, B). They bear a row of stout teeth (Fig. 10B), each of which has microspines posteromarginally. The midventral stomach cuticle is weakly elevated (Fig. 11B, C: IM). This structure may be homologous with the inferomedianum. The exit of the stomach chambers is located posteroventrally.

The midgut gland and the stomach are restricted to the head and the first two pereonites (Fig. 12A, B). The midgut gland envelopes the stomach laterally (Figs. 12, 13, 14A, B). Lobes of the midgut gland extend ventrally to the entrance of the esophagus into the stomach cavity; dorsally the stomach cavity remains partly unoccupied. The posterior hoodlike projection extends deeply into the midgut gland, but does not reach the midgut. There are no paired midgut gland ceca, but a pair of short anteroventral lobes (Figs. 11A, 13A). Posteriorly, the midgut gland is curved into a canal of

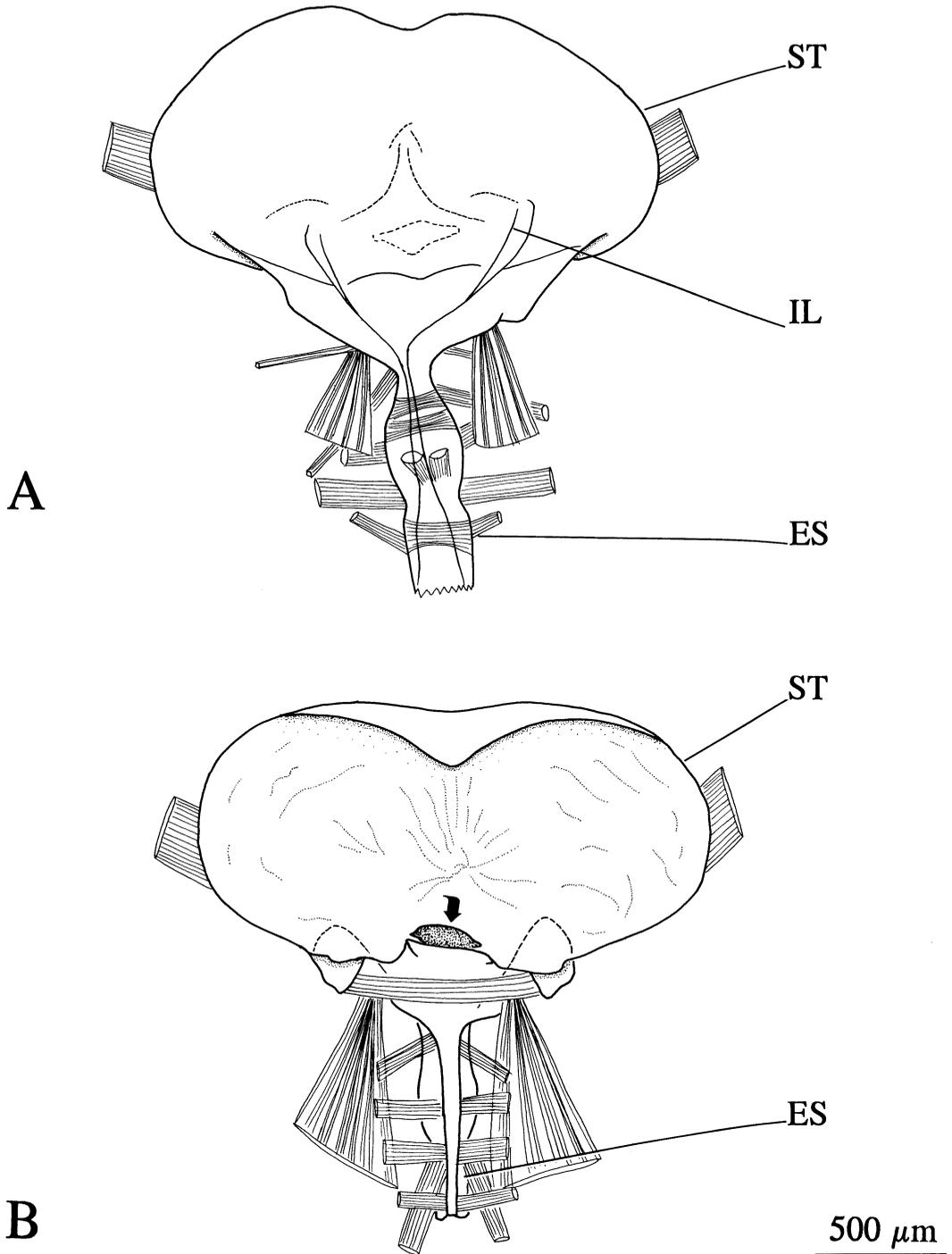


Fig. 5. Foregut of *Brachyscelus globiceps*. A, seen anteriorly, and B, posteriorly. Arrowhead indicating outlet of stomach cavity to midgut gland. ES = esophagus, IL = inferolaterale, ST = stomach.

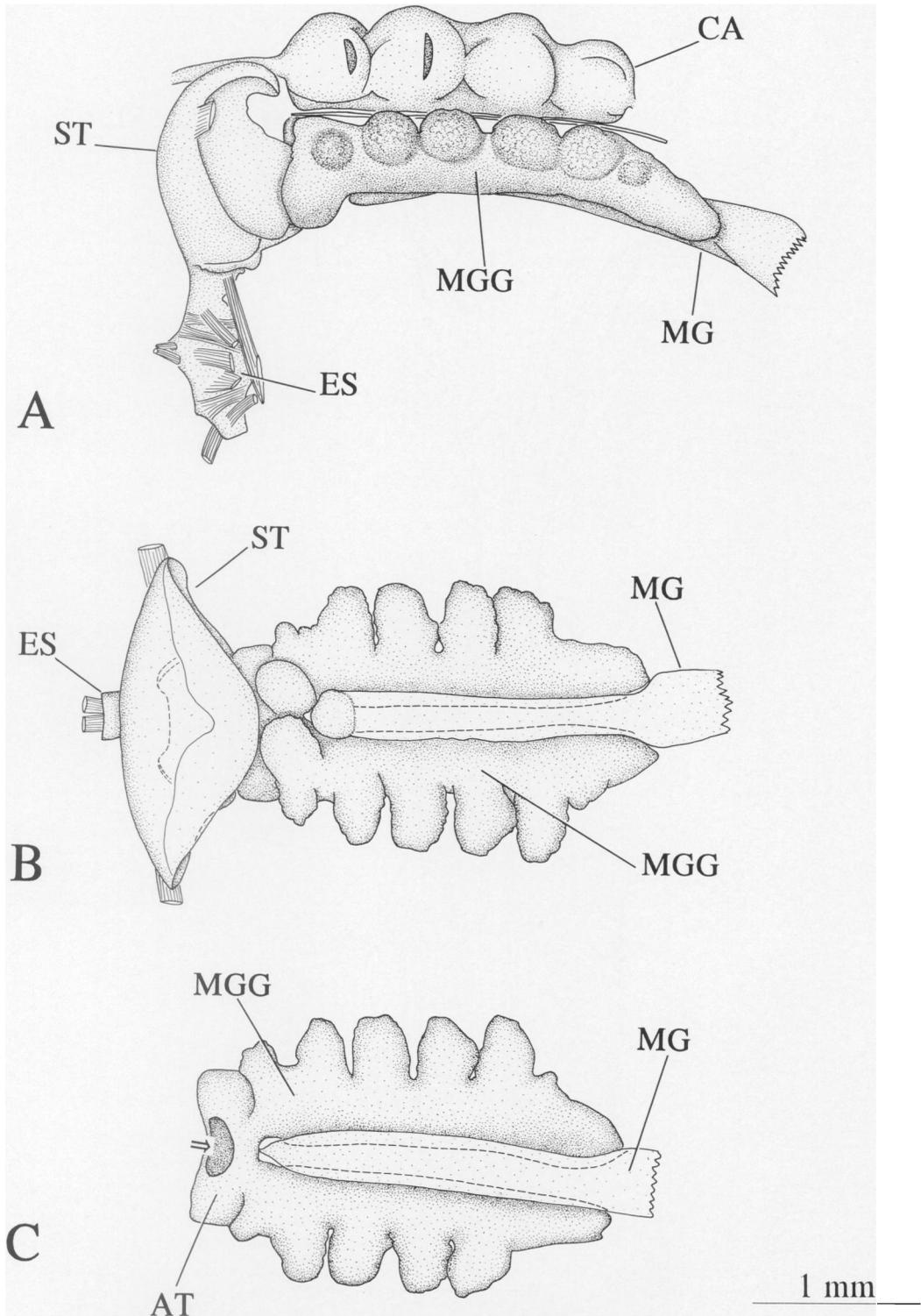
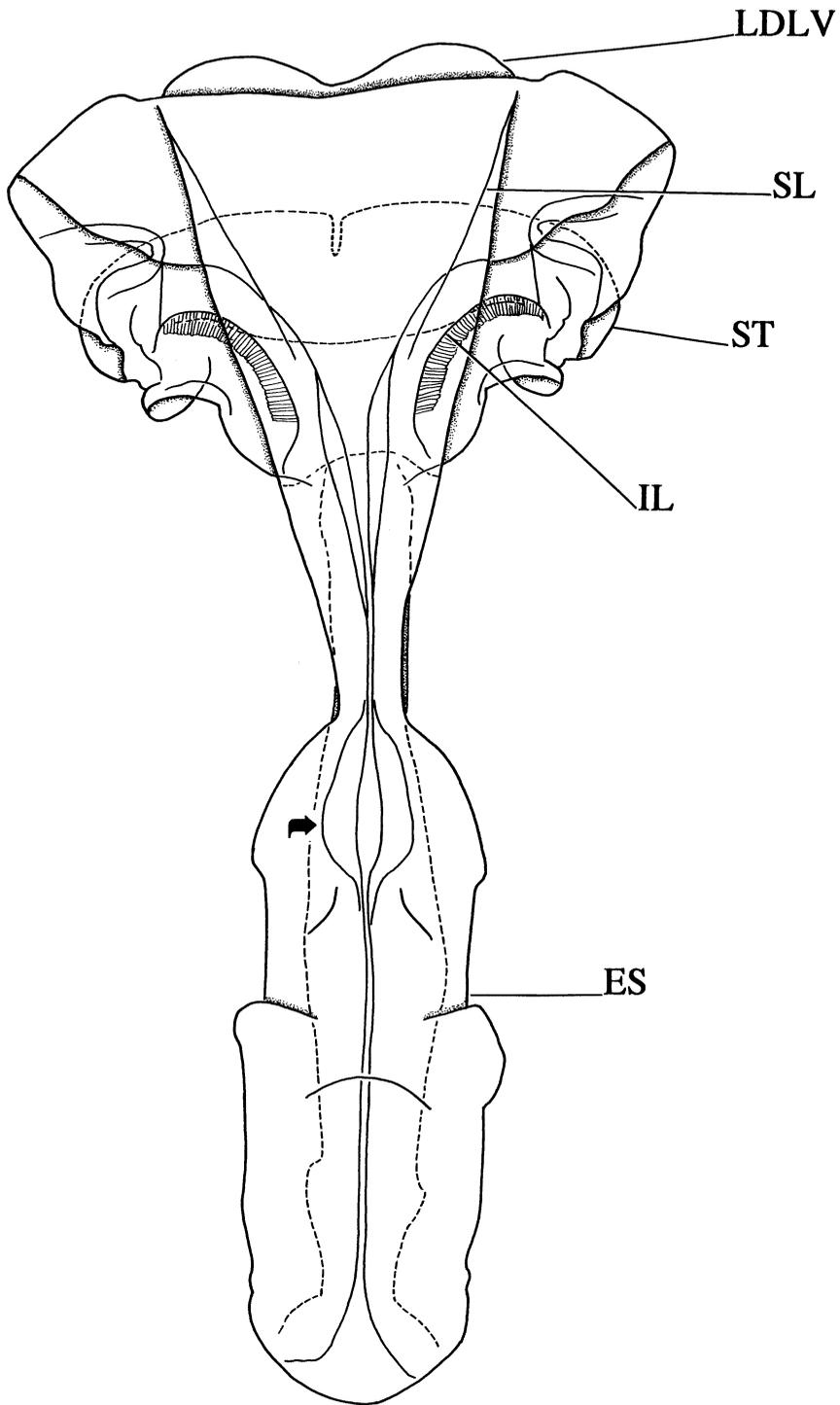


Fig. 6. Dissected alimentary canal of *Brachyscelus globiceps*. A, left lateral view; B, dorsal; C, ventral. Arrowhead indicating inlet of stomach into midgut gland. AT = atrium of midgut gland, CA = heart, ES = esophagus, MG = midgut, MGG = midgut gland, ST = stomach.



500 μm

Fig. 7. Foregut of *Platyscelus armatus*, viewed dorsally. Arrowhead indicating sclerotized cuticular region. ES = esophagus, IL = inferolaterale, LDLV = fused lamina dorsalis and lamella ventralis, SL = superolaterale, ST = stomach.

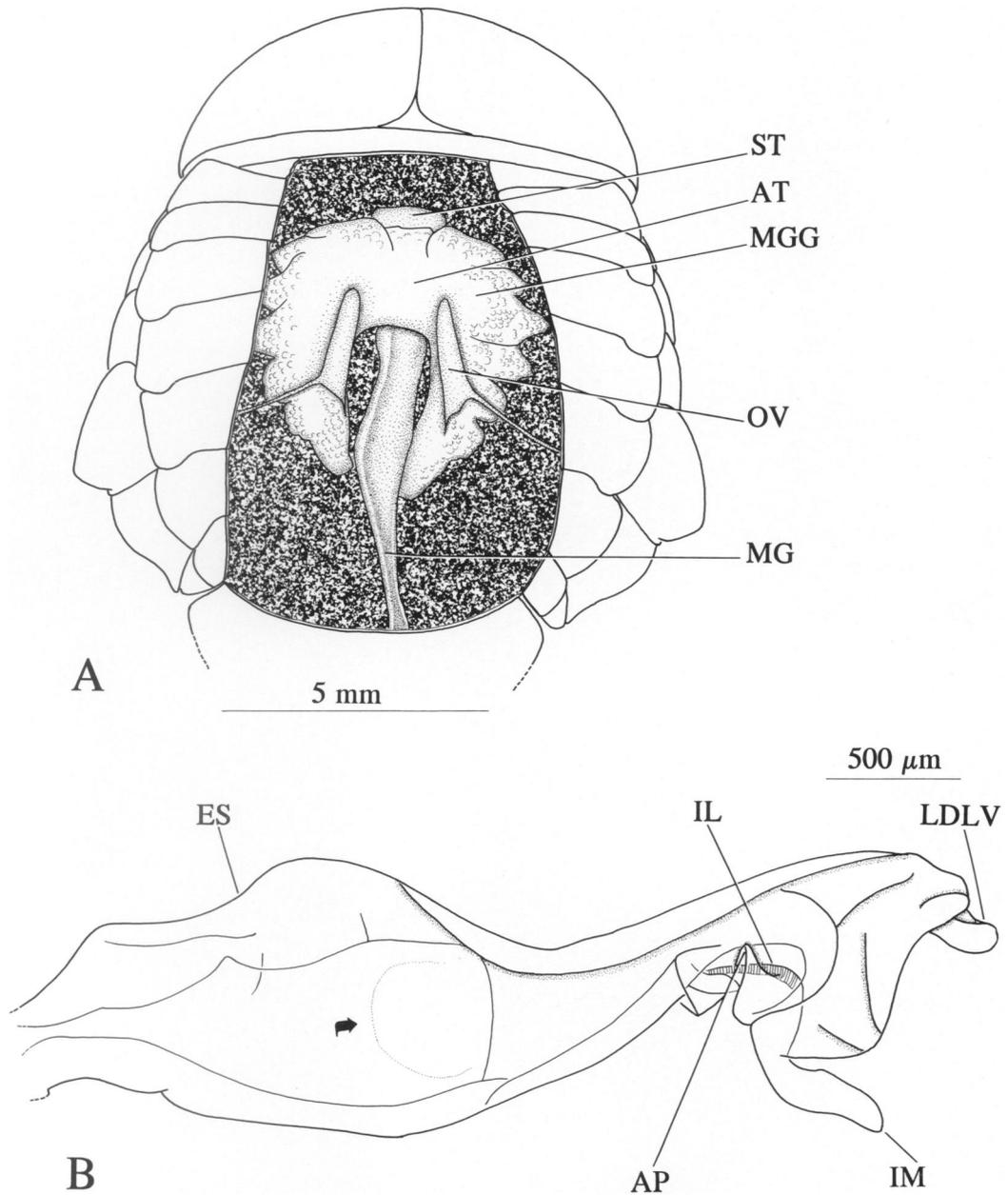


Fig. 8. *Platyscelus armatus*. A, dorsally dissected specimen; B, right lateral view of foregut, arrowhead indicating sclerotized cuticular region. AT = atrium of midgut gland, AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, MG = midgut, MGG = midgut gland, OV = ovary, ST = stomach.

small diameter that is connected to the midgut (Figs. 12, 13, 14D). Between the midgut gland and the midgut there is no abrupt change in histology, but the cells gradually become shorter and extended (Fig. 14C, D),

and less intensively stained. The nuclei are spherical in the cells of the midgut gland but oval in those of the midgut itself. The midgut is transparent and dorsoventrally compressed.

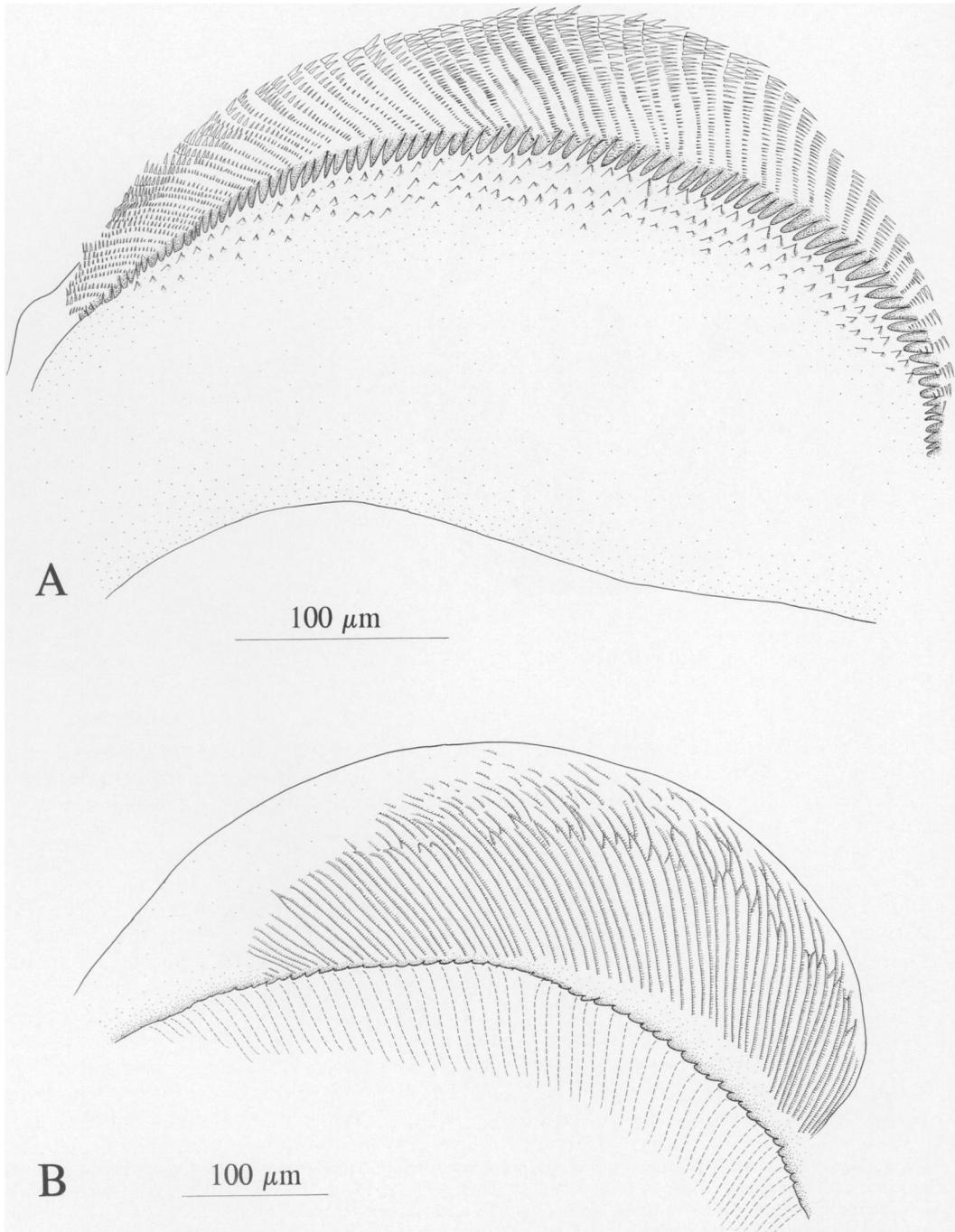


Fig. 9. Medial face of inferolateralia and internal lateral stomach cuticle of A, *Brachyscelus globiceps*, and B, *Platyscelus armatus*. Dashed lines indicating rows of short setae on lateral side of inferolateralia.

#### *Lanceola sayana*

The foregut of *Lanceola sayana* is a large flexible sac (Fig. 15A) that fills most of the pereon. At the opening of the esophagus

into the stomach cavity, there is a pair of lateral folds that are continuous with folds of the ventral stomach wall, the so-called ventral groove (cf. Woltereck, 1927). This groove has a ladder-shaped pattern because

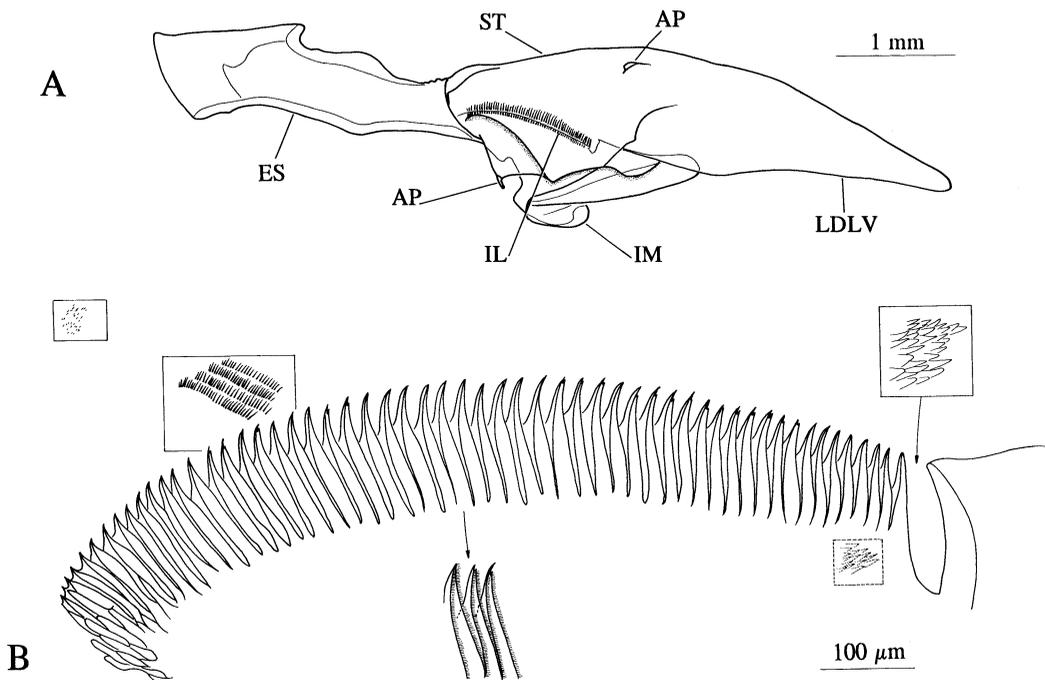


Fig. 10. *Phronima sedentaria*. A, left lateral aspect of foregut; B, enlarged armature of inferolaterale, details in boxes illustrating different setae of internal lateral stomach cuticle. AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, ST = stomach.

of small cuticular transverse folds. The lateral folds of the ventral groove deviate posteriorly; close to the opening of the stomach cavity into the midgut gland these folds are drawn dorsally. Dorsal to the esophagus, the stomach cuticle is depressed, and ventrally a tonguelike structure is formed (Fig. 15D). Although homologies are difficult to interpret, the lateral infoldings might be inferolateralalia and the ventral tongue the inferomedianum.

The midgut gland is remarkably short and restricted to pereionites 6 and 7. The stomach is attached to the anteriormost cell layer of the midgut gland and is not inserted deeply into it. The anterior opening of the midgut gland is broad, and large soft food morsels are present in its cavity. The surface of the midgut gland is deeply infolded. Posteriorly the midgut gland narrows drastically. It is not clear whether the midgut gland and the midgut are connected. The midgut epithelium is thin and translucent. There is a rather broad dorsal midgut cecum directed anteriorly that overlaps the midgut gland and lateral midgut bulges (Fig. 15C). No food particles were found in the midgut, although

the stomach chamber and midgut gland were filled with soft tissue. Higher magnification of the stomach contents revealed numerous nematocysts.

#### *Scina crassicornis*

The esophagus and stomach cavity of *Scina crassicornis* are short (Figs. 16A–C, 17). Inferolateralalia are developed as lateral invaginations, and a conspicuous ventromedial invagination of the stomach cuticle may correspond to the inferomedianum. These invaginations form ventral channels. The lateral invaginations do not bear filter setae. However, there are patches of minute spines on the inferolateralalia, the dorsal stomach cuticle, and the dorsal region of the inferomedianum. The dorsal stomach cuticle is produced into two long and two short apodemes. Dorsal and ventral cuticular lamellae protrude into the midgut gland. The exit of the stomach to the midgut gland is large (Fig. 16C).

Comparable to *Lanceola sayana*, the midgut gland is developed as a sac without ceca. The midgut gland length is variable among specimens, reaching into pereionites

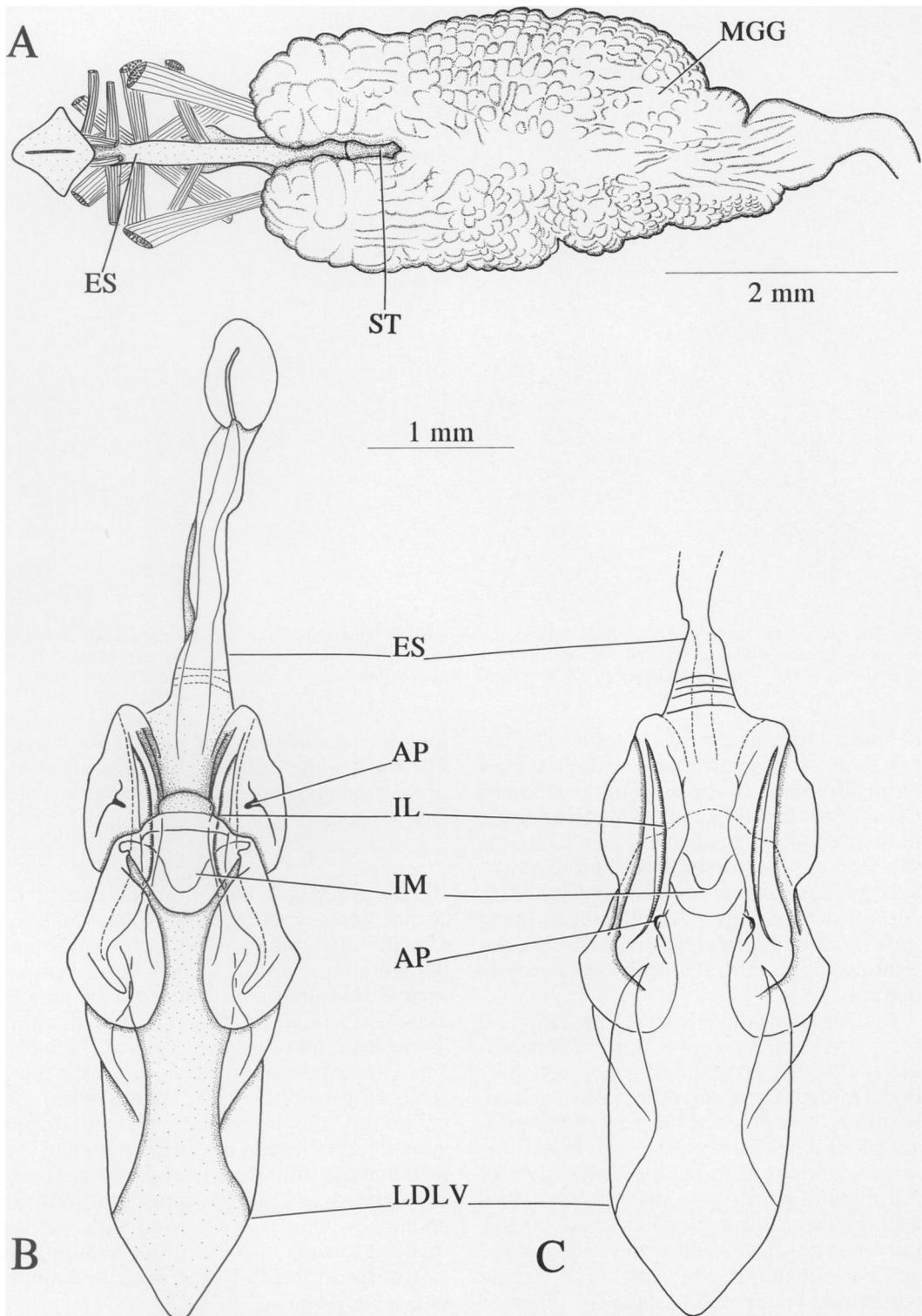


Fig. 11. *Phronima sedentaria*. A, foregut and midgut gland, ventral; B, foregut seen from ventral, and C, from dorsal side. AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, MGG = midgut gland, ST = stomach.

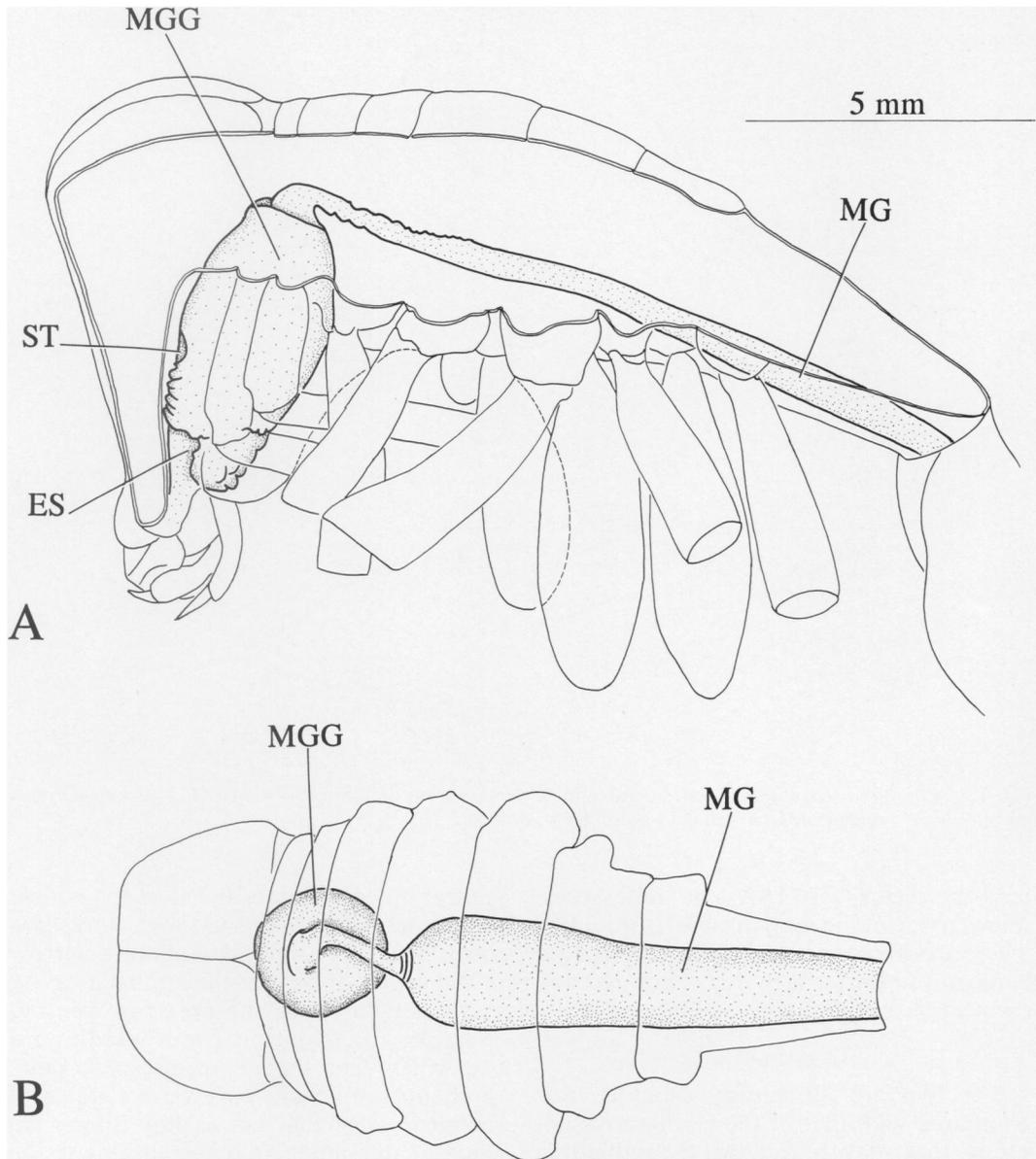


Fig. 12. *Phronima sedentaria*. A, partially dissected specimen displaying alimentary canal; B, dorsal aspect of alimentary canal. ES = esophagus, MG = midgut, MGG = midgut gland, ST = stomach.

4–7. The midgut overlaps the midgut gland dorsally, but to a lesser extent ventrally. The midgut gland bears a constriction posteriorly.

#### *Phrosina semilunata*

The stomach is entirely reduced in this species. Only the esophagus is retained (Fig. 18C). The part of the esophagus that borders on the mouthparts is normally developed;

however, the diameter of the esophagus is reduced considerably posteriorly. Cuticular folds are present. The terminal region of the esophagus is attached to the tissue of the midgut gland, but does not noticeably project into the lumen.

The foregut and midgut gland of *Phronima sedentaria* are restricted to the head and the anterior pereionites, whereas in *Phrosina semilunata* the midgut gland reaches

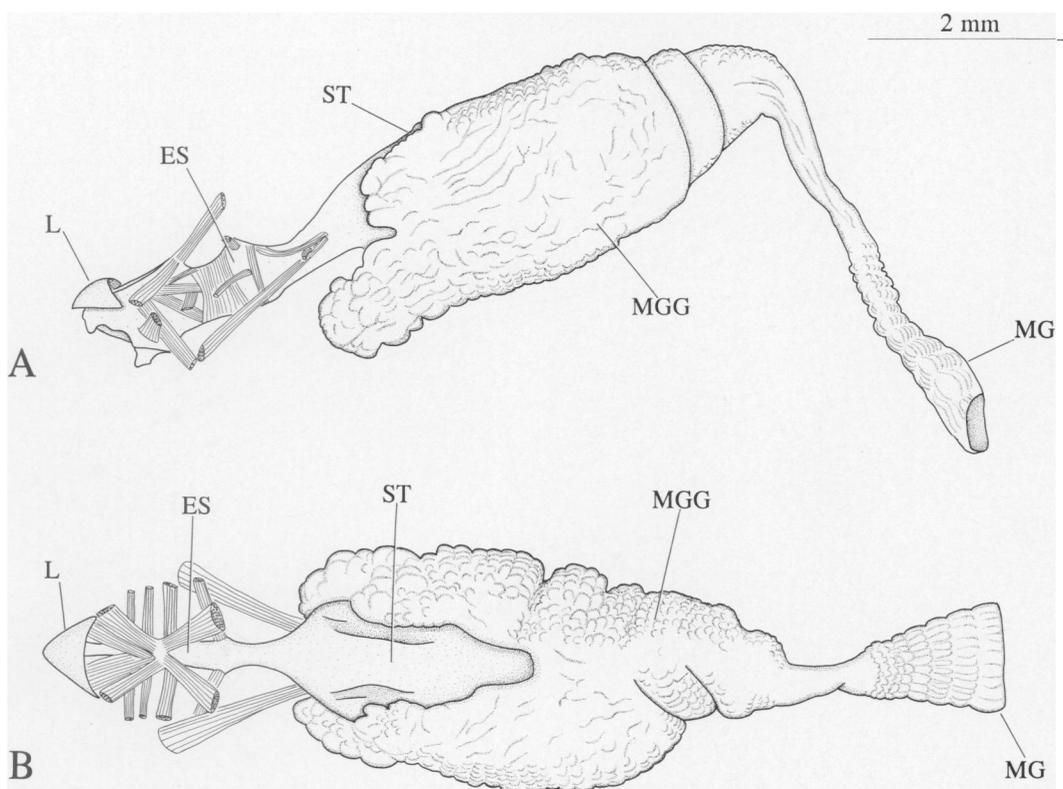


Fig. 13. *Phronima sedentaria*. A, left lateral, and B, dorsal aspect of alimentary canal. ES = esophagus, L = labrum, MG = midgut, MGG = midgut gland, ST = stomach.

into the pleon (Fig. 18A). In some specimens, tissue of the midgut gland is infolded. There are no ceca present. The midgut gland is narrowed posteriorly (Fig. 18B) and any connection to the midgut is obscure.

#### DISCUSSION

The hyperiid alimentary canal is here compared with that of the Gammaridea, a group that may reflect the groundpattern within the Amphipoda. For this reason, a short survey on the functional morphology of the gammaridean foregut is given below.

At the inlet of the esophagus into the stomach cavity are lateral setose invaginations, the so-called lateralialia, which press food morsels into the stomach chamber and prevent food fragments from entering back into the esophagus (Icely and Nott, 1984). The stomach cuticle is infolded into two pairs of lateral (dorso- and ventrolateral) and two ventral ridges. The anterior ventrolateral ridges (inferolateralialia anteriores) are setose. These setae overpass the anterior

ventral invagination of the stomach cuticle (inferomedianum anterius) and work as a rough filter. The inferolateralialia are narrow in the posterior part of the stomach cavity and meet dorsal to the posterior ventral, ridgelike invagination (inferomedianum posterius). This ridge comprises two pairs of channels that are covered by grates of setulated setae that act as fine filters. An effect of the cuticular invaginations is the division of the stomach cavity into a food storage and digestion chamber and ventral channels formed by the inferolateralialia and the inferomedianum.

Food particles are pressed through the rough filter, enter these ventral channels, are transported posteriorly, and finally are filtered a second time at the fine filter. The filtrate enters the atrium of the midgut gland and from there into one or two pairs of midgut gland ceca. Generally these ceca extend into the pleon. The two-step filtration ensures that only very small particles or fluids enter the midgut gland, and thus prevent

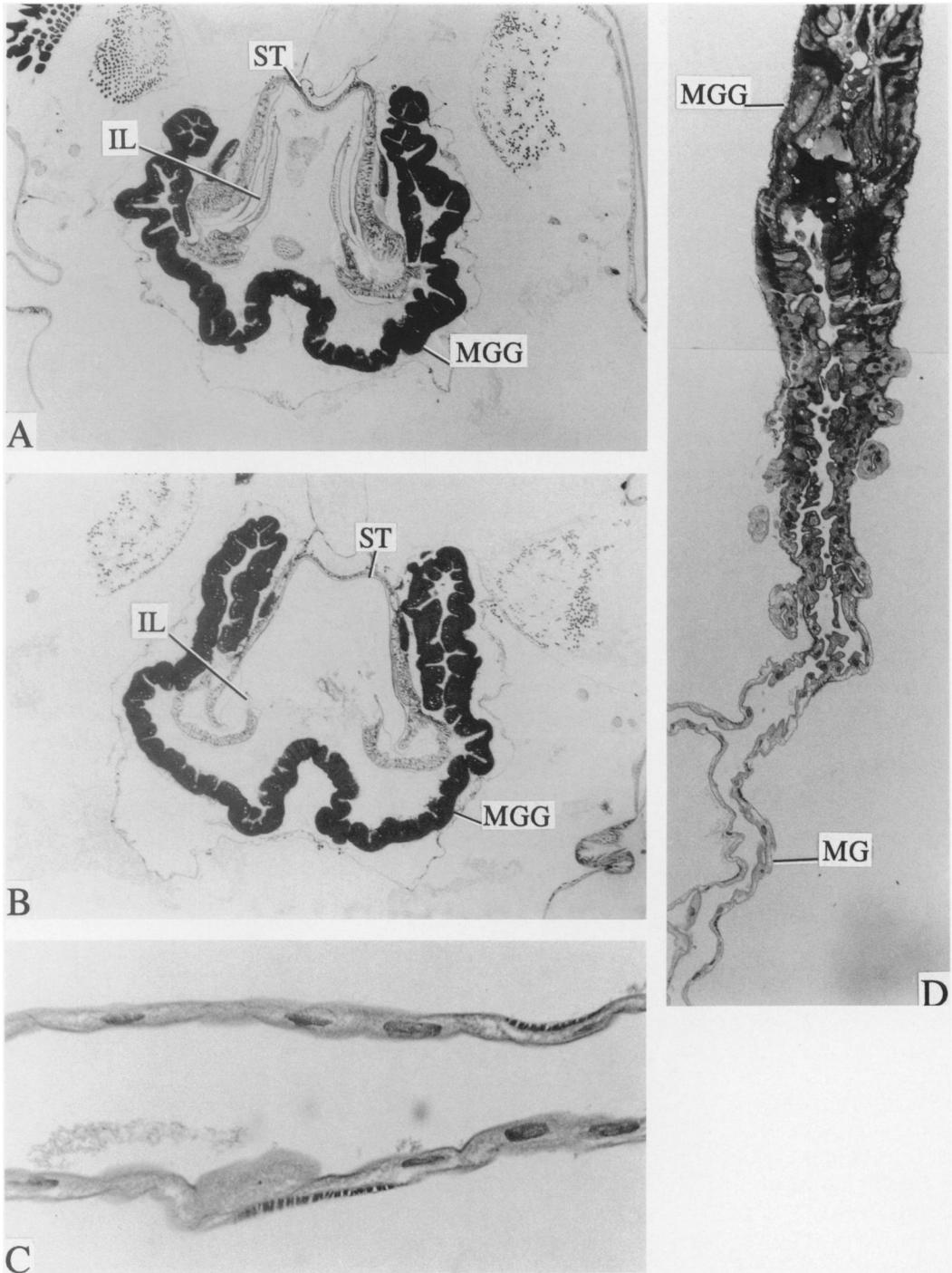


Fig. 14. Photomicrographs of histological sections of alimentary canal of *Phronima sedentaria*. A and B, anterior region of stomach chamber showing inferolateralia and midgut gland epithelium enveloping stomach; C, midgut epithelium; D, constriction of midgut gland toward midgut. MG = midgut, MGG = midgut gland, ST = stomach, IL = inferolaterale.

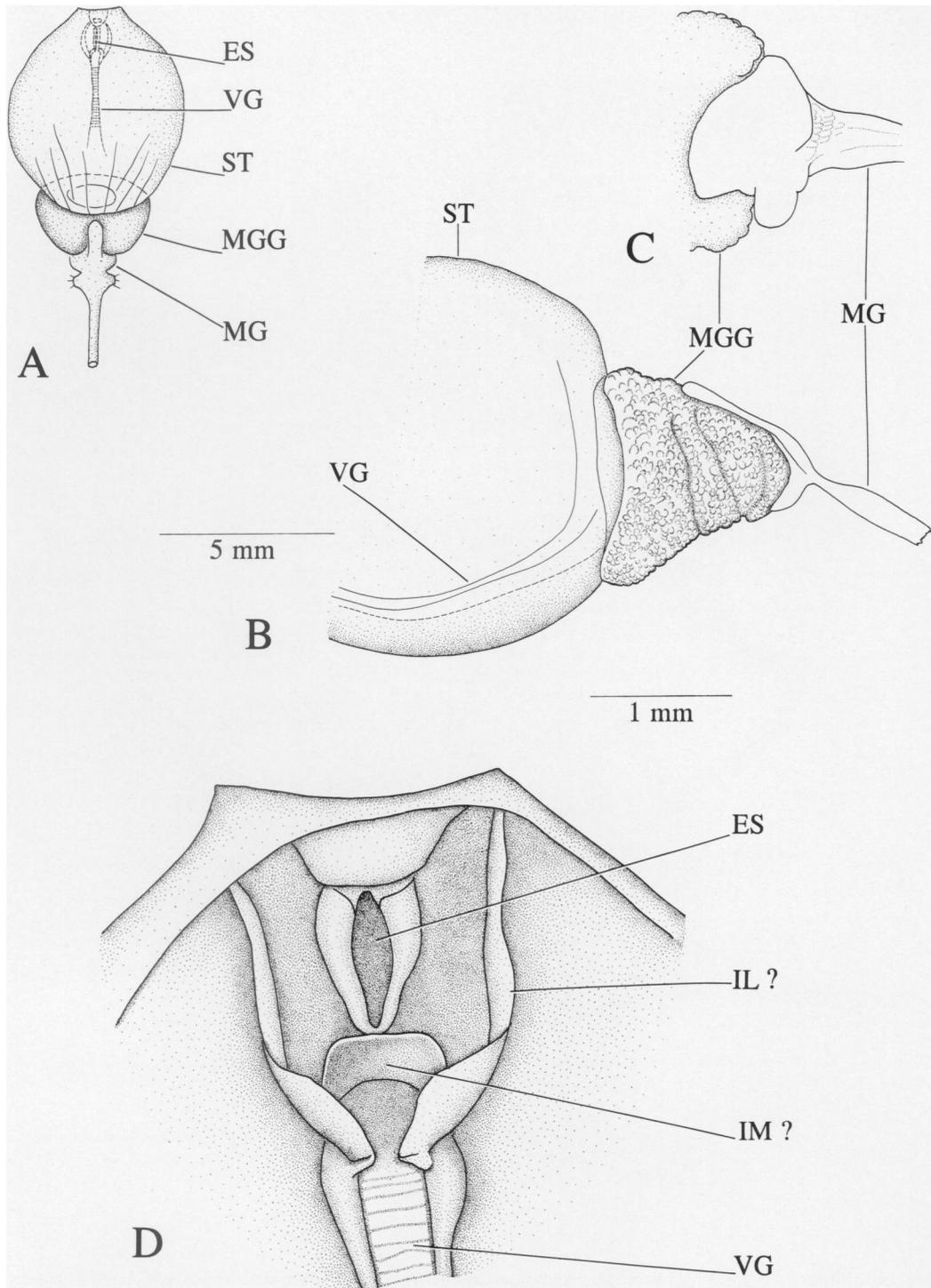


Fig. 15. *Lanceola sayana*. A, schematic drawing modified after Woltereck (1927); B, posterior region of stomach connected to midgut gland; C, dorsal process of midgut; D, anterior area of dissected stomach, seen posteriorly. ES = esophagus, IL? = possibly inferolaterale, IM? = possibly inferomedianum, MG = midgut, MGG = midgut gland, ST = stomach, VG = ventral groove.

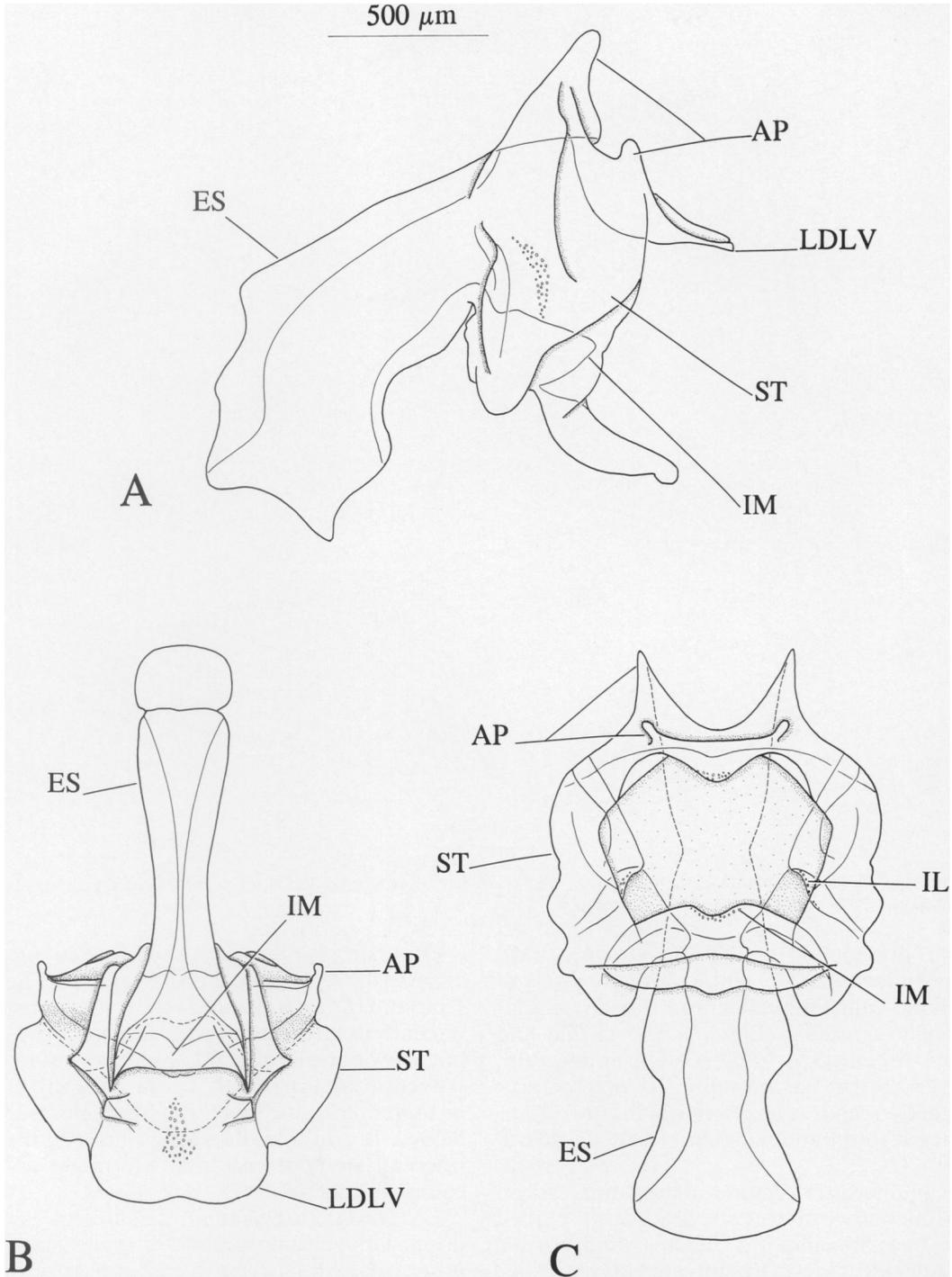


Fig. 16. Foregut of *Scina crassicornis*. A, left lateral aspect; B, dorsal view; C, seen posteriorly. AP = apodeme, ES = esophagus, IL = inferolaterale, IM = inferomedianum, LDLV = fused lamina dorsalis and lamella ventralis, ST = stomach.

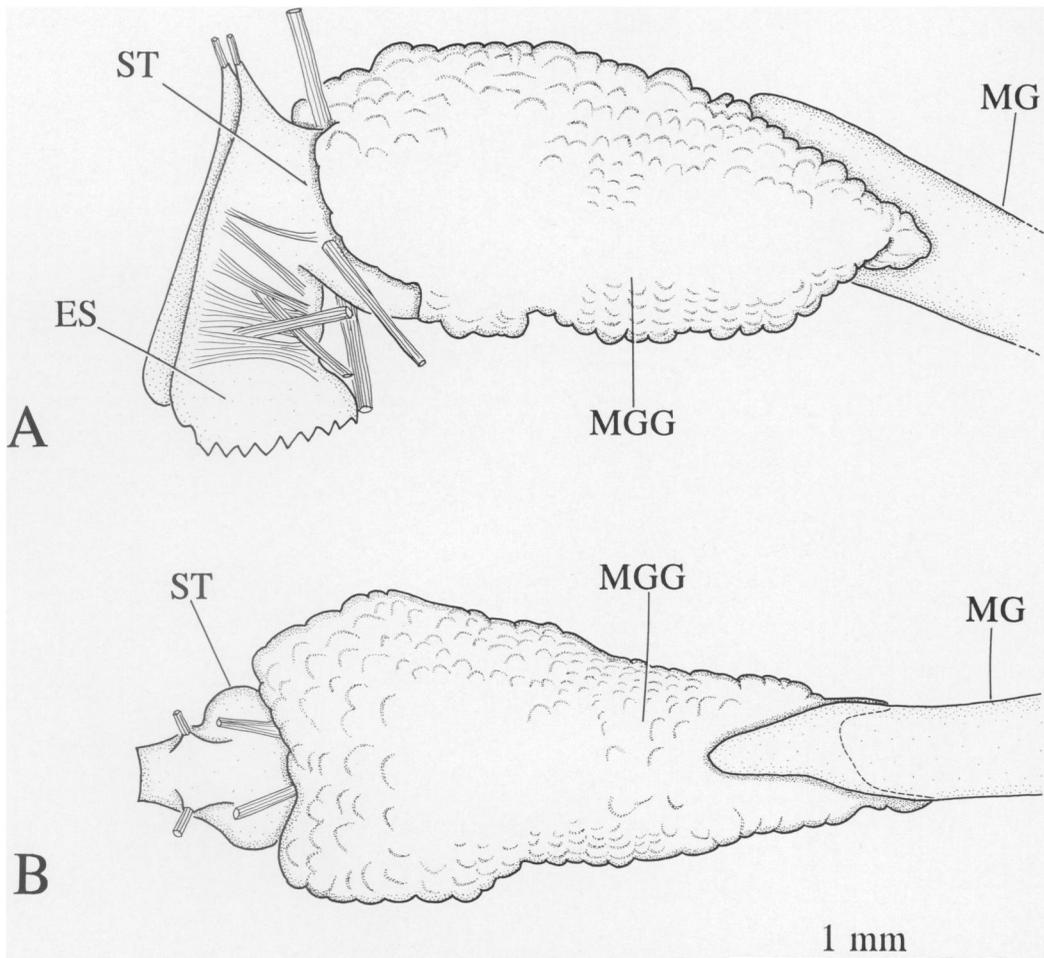


Fig. 17. Alimentary canal of *Scina crassicornis*. A, left lateral aspect; B, dorsal view. ES = esophagus, MG = midgut, MGG = midgut gland, ST = stomach.

the obstruction of the narrow ceca. Indigestible remains enter the midgut by way of the so-called funnel (lamina dorsalis and lamella ventralis; cf. Scheloske, 1976a) and are discharged over the hindgut and rectum. The midgut has only limited enzyme production and resorption capabilities compared to the midgut gland (Icely and Nott, 1985).

Numerous structures of the gammaridean alimentary canal are so reduced or modified in hyperiids that it is difficult or impossible to decide if these structures are homologous. The characteristics of hyperiid alimentary canals are the following:

(1) Lateralia are wanting. Dorsolateral infoldings of the stomach cavity (the so-called superolateralia) are, if present, rudimentary and lack setae.

(2) Inferolateralia are not subdivided into an anterior region and a posterior part. The setae and the inferolateralia are not directed medially as filter elements, as in gammarids, but show dorsally and are obviously not involved in filtering food. These setae might be used to triturate larger food particles (see below). In addition, the small spines on the internal lateral stomach cuticle might accomplish this role.

(3) The inferomedianum is, if present, not divided into an anterior infolding and a posterior ridge. In *Cylopus lucasi*, it protrudes deeply into the stomach cavity and forms a lobe posteriorly, and bears dorsolateral groups of setae that are directed laterally and reach the medial side of the inferolateralia. Thus, they pass over the ventral channels, different from the condition in

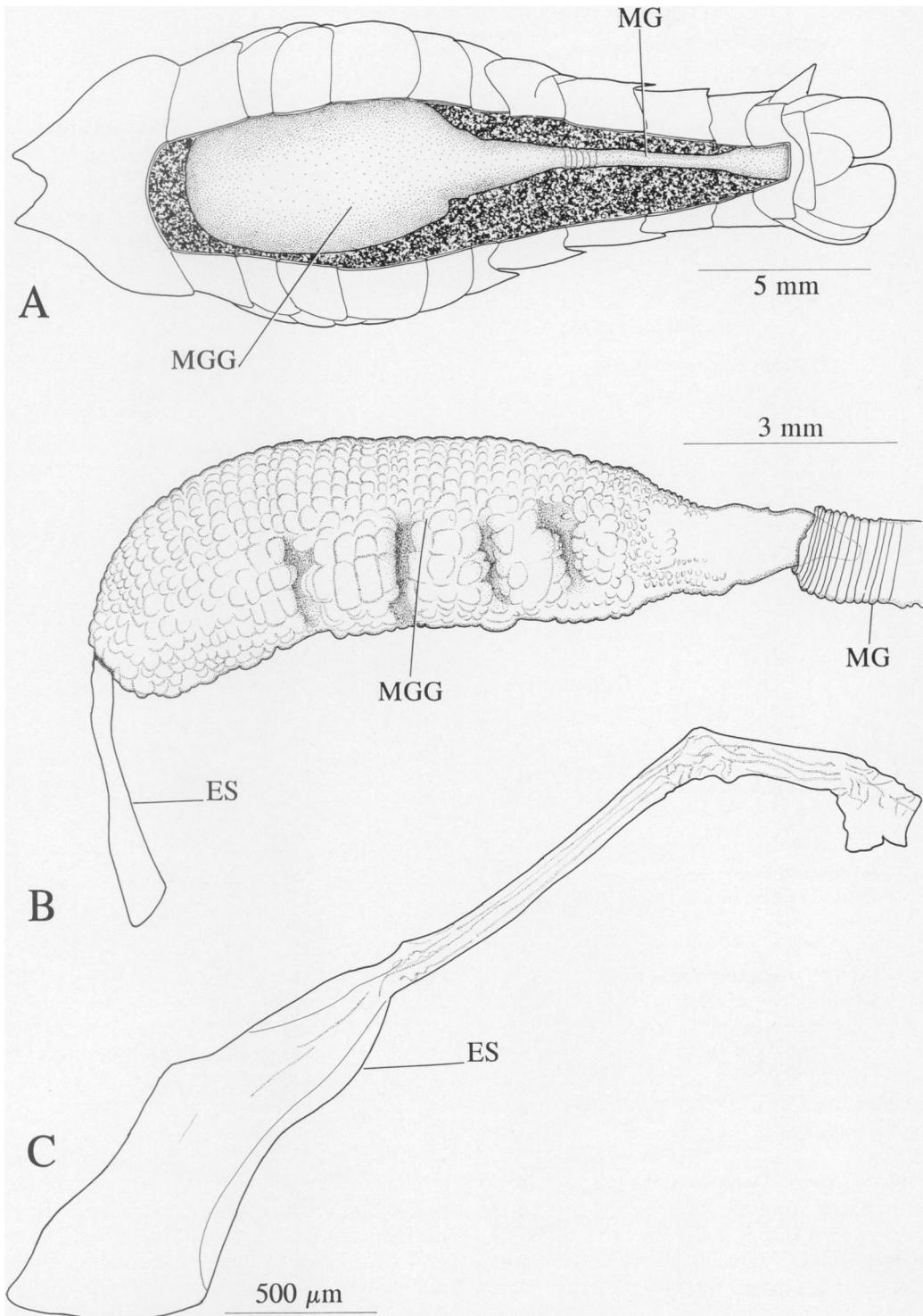


Fig. 18. *Phrosina semilunata*. A, dorsally dissected specimen showing dominant midgut gland extending through entire pereion; B, dissected alimentary canal; C, rudimentary foregut, only esophagus retained. ES = esophagus, MG = midgut, MGG = midgut gland.

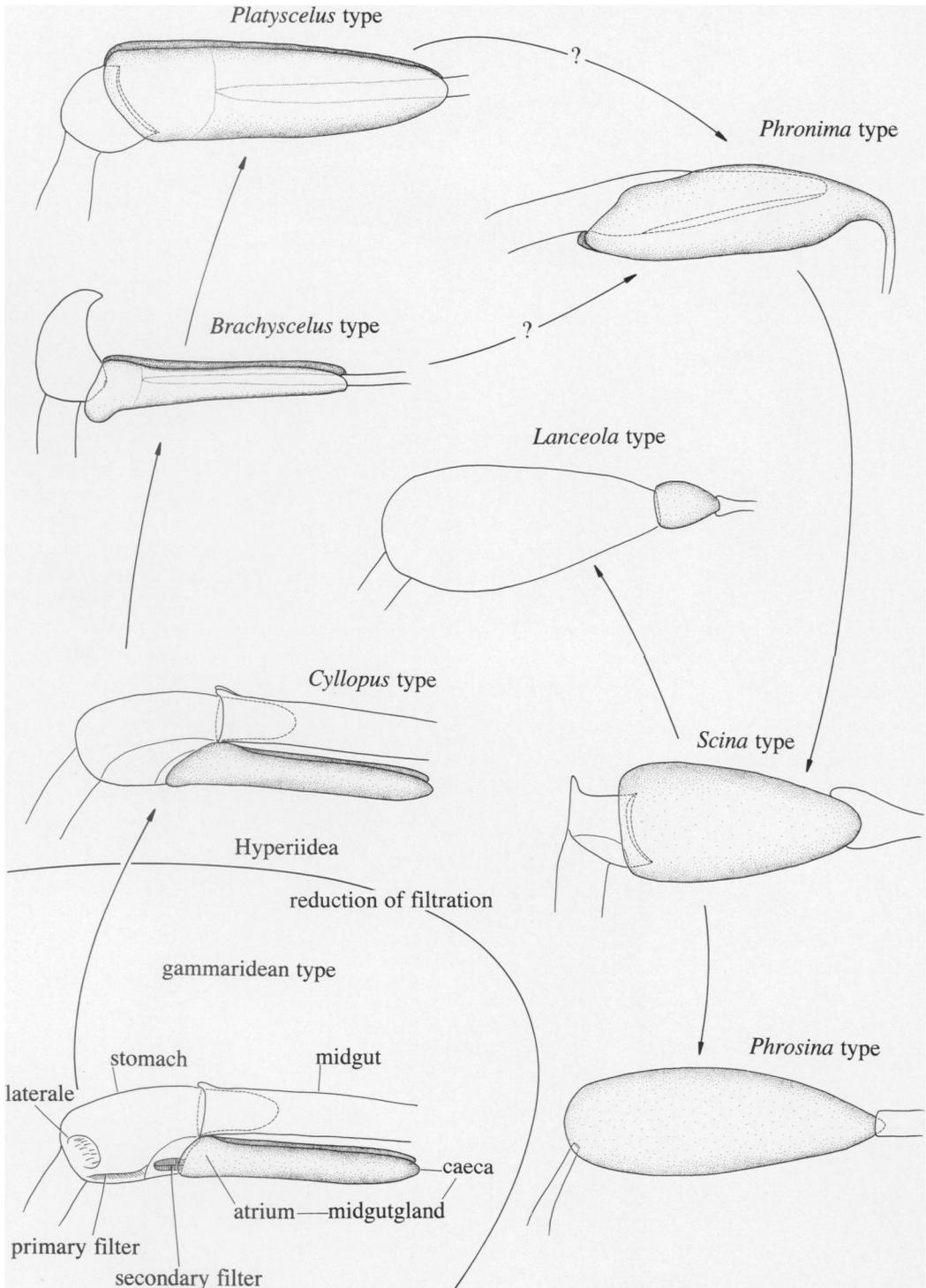


Fig. 19. Schematic drawings of hyperiid stomachs and midgut glands arranged in morphocline. Types on left side have paired midgut gland caeca; apomorphic condition (saclike midgut gland) shown on right side.

gammaridean amphipods where the filter setae insert on the inferolateralia and are directed medially. The comparison with gammaridean and other peracaridan stomachs confirms that the filter mechanism of *Cylopus* is certainly secondarily formed. In all other hyperiid stomachs studied, these groups of setae are missing and the inferomedianum is shallow. Thus, there are no channels in which filtrate could be transported separately.

(4) The evolution of the midgut gland and the midgut probably results from reduction of filtration potential of the foregut. *Cylopus lucasi* still has a limited filtration capability and the filtrate is transported into the midgut gland by way of ventral channels.

Corresponding to reduction of filtration capabilities of the stomachs in other known hyperiids, there must have occurred a major transformation of the midgut gland and midgut. Quite different from the Gammaridea, in these hyperiids the stomach opens exclusively into the atrium of the midgut gland, and the midgut is not directly connected to the foregut. The midgut is posterior to the midgut gland atrium, being separated from it by a unique sphincterlike constriction. Because there is no filtering by the stomach, larger food particles enter the atrium of the midgut gland and ceca, if present.

Anatomical states of the hyperiid species for which information is available may be arranged in a morphocline (Fig. 19) that may reflect phylogenetic relationships:

(1) Filtration of food in the stomachs is reduced primarily (e.g., *Cylopus*) and is completely absent secondarily. With loss of filtration capabilities the stomach becomes smaller.

(2) The atrium of the midgut gland is enlarged, and the midgut is connected to the midgut gland (e.g., *Brachyscelus* and *Platyscelus*).

(3) Ceca of the midgut gland are completely reduced, but the atrium of the midgut gland is retained (e.g., *Phronima*).

(4) The atrium of the midgut gland is enlarged significantly (e.g., *Scina* and *Phrosina*).

Separation of fine particles by means of filtration in the stomach is reduced, so that even large food particles enter the midgut

gland. The hyperiid alimentary canal probably evolved with utilization of food that may be digested without leaving remains which might obstruct or injure the midgut gland.

Feeding habits of hyperiids remain for the most part unknown (Bowman and Gruner, 1973). Most species appear to be associated with gelatinous zooplankton, such as medusae, siphonophores, or salps, at least during a phase of their life, and may feed on them (Madin and Harbison, 1977; Harbison *et al.*, 1977; Laval, 1980). Examinations of hyperiid food preference on the basis of gut contents may be misleading because food taken up by the hyperiid might have been ingested by the host (Laval, 1980). Small amounts of recognizable remains, such as crustacean fragments, are more conspicuous than large amounts of mesoglea that would appear in the alimentary canal as an unidentifiable matrix, which would lead to a wrong impression of the food preference. On the other hand, undigested nematocysts in the gut indicate preying on cnidarians. However, nematocysts might be ingested incidentally, without cnidarians being the food preferred (Laval, 1980). Evidence of the food preferences may be obtained through direct observation of the animals by SCUBA diving or in aquaria. This was done by Laval (1966, 1972, 1980), Madin and Harbison (1977), and Harbison *et al.* (1977). They reported data relative to associations of hyperiids with gelatinous plankton, confirming that in many cases food of their hosts or the host tissue itself was consumed.

Anatomical findings support the impression that soft-bodied food is preferred by the hyperiids examined. Since large food particles may enter the midgut gland (except in *Cylopus*), only food that is digested more or less completely would not obstruct it. Structure of the much reduced mouthparts (Bowman and Gruner, 1973) indicate that cutting and reducing of tough food to small pieces is limited. The lumen of the esophagus and the beginning of the midgut are reduced and prevent the early escape of food from the stomach-midgut gland complex.

Anatomy of the midgut gland is aberrant in some species. The atrium of the midgut gland is thought to have been enlarged during hyperiid evolution. Unfortunately, no

intermediate states are known that might suggest an explanation for the unique junction of the midgut gland and midgut in hyperiids.

There is some controversy about the origin of the cavity between the stomach and the midgut constriction. I am convinced that this cavity represents the atrium of the midgut gland for the following reasons: (1) The surface of this organ is structured and ridged as is typical for midgut glands; (2) The above-mentioned transformation series illustrates hypothetical evolution from a pleiomorphic condition (with ceca) to an apomorphic state where no ceca are present; (3) The origin of the midgut is defined where a peritrophic membrane is secreted (Icely and Nott, 1985). There is no peritrophic membrane in this chamber, but it was found by Sheader and Evans (1975) near the midgut constriction; and (4) It is very unlikely that hyperiid species without midgut gland ceca would have reduced the midgut gland completely. They would have lost the functions of the midgut gland, namely, enzyme secretion, resorption, and storage of lipids and glycogen (Moritz *et al.*, 1973).

My view was shared by Brusca (1981), who examined three species of the genus *Cystisoma*, and described this chamber as the "caecum," the constriction that leads to the anterior midgut as the "caecal duct" (see also Schmitz, 1992). The anatomy of *Cystisoma* is reminiscent of the conditions found in *Phronima*, except that in *Cystisoma* the foregut-midgut gland complex is much smaller and a dorsal outgrowth of the midgut gland is developed.

Diebel (1988) examined *Phronima sedentaria* and homologized the "caecum" with the midgut that is connected by a narrow tube (the "midgut tube") to the hindgut. This is an erroneous interpretation. What was thought by Diebel (1988) to be the hindgut is located within the pereion and lacks any cuticular lining of its epithelium (Fig. 14C). This error traces to Claus (1879) who also described the cecal mass of *Phronima sedentaria* as the "Magendarm" (stomach-gut, part of the midgut); the ventral lobes of which were recognized as the "Leberlappen" (midgut gland ceca) which are not differentiated histologically from the "Magendarm" (cf. Frenzel, 1884). However, I would

homologize these lobes of the midgut gland of *Phronima sedentaria* with the ventral lobes in *Brachyscelus globiceps*, *Cylopus lucasi*, or even in the stegocephalid *Parandania boeckii* (Stebbing) (see Coleman, 1990a); all these species have lobes and a pair of midgut gland ceca.

Far more complicated is the homology of the epithelium that envelopes the foregut in the genus *Parathemisto* Boeck (see Sheader and Evans, 1975). These authors designate this structure as the anterior part of the midgut. A pair of midgut gland ceca are connected to this cavity. A posterior portion of the midgut is located posterior to a constriction (designated "sphincter" by Sheader and Evans, 1975). I believe that at least part if not all of this "midgut" cavity that envelopes the stomach of *Parathemisto* is derived from the atrium of the midgut gland, although no histological evidence is apparent. However, Sheader and Evans (1975) described a peritrophic membrane secreted near the "sphincter" region. This site of formation of the peritrophic membrane in gammaridean amphipods generally defines the beginning of the midgut (Martin, 1964; Icely and Nott, 1985).

Anatomical diversity of hyperiid alimentary canals is fascinating and in no other crustacean groups so impressive. The heterogeneity ranges from foreguts that are oversized in *Lanceola sayana* to complete reduction of the stomach chamber in *Hyperoche medusarum* (Krøyer) (cf. Evans and Sheader, 1972) and in *Phrosina semilunata* (Fig. 19).

It is difficult to evaluate the functional significance of the foregut structures of hyperiids. In all stomachs, except in *Cylopus lucasi*, filtration is obviously reduced; the stomach contents are directed into the midgut gland, and there is no direct connection of the stomach to the midgut as is generally the case in the other amphipod suborders. The only known analogy, and probably a convergence to this hyperiid pattern within the Gammaridea is in the stegocephalid *Parandania boeckii*. In this species, the filtrate flows into the midgut gland. The midgut does not seem to be connected to the stomach and seems to begin blindly (Coleman, 1990a). *Parandania boeckii* feeds on deep-water medusae of the genus *Atolla* (Moore and Rainbow, 1989; Coleman,

1990a), and thus has a similar food as many hyperiids. Although the stomach of hyperiids and stegocephalids look completely different, the esophagus of both is narrowed to a slit. This might be an adaptation to digest soft mucous food and prevent food losses via the esophagus. The muscles of the esophagus of these taxa allow drastic enlargement of its lumen to swallow large food morsels, or perhaps to disgorge indigestible remnants (cf. Coleman, 1990a).

The inferolateralia of hyperiids are infoldings of the ventral stomach cuticle and are curved dorsally (except in *Scina crassicornis*). They form lateral channels between the lateral sides of the inferolateralia and the lateral stomach cuticle that are open to the posterior stomach cavity. Perhaps the setae or spines on the dorsal edge of these infoldings are involved in triturating food. Contractions of the muscles attached to anterolateral apodemes may enlarge the space between the inferolateralia and the stomach cuticle. This arrangement might result in sucking of food alongside the armature of the inferolateralia into these channels. This action would not be filtration, in that the lateral channels do not conduct finer food particles from larger particles separately into the midgut gland or midgut. Food returns into the stomach chamber posteriorly.

It is remarkable that the midgut glands of the hyperiids examined exhibit quite differing dimensions. In the suspected plesiomorphic species, *Cylopus lucasi*, *Brachyscelus globiceps*, and *Platyscelus armatus*, there are paired midgut gland ceca that extend through the pereion, whereas the apomorphic condition is developed in *Lanceola sayana*, *Phronima sedentaria*, and *Cystisoma* (cf. Brusca, 1981) where the midgut glands are minute and without ceca. In *Scina crassicornis* or *Phrosina semilunata*, the midgut gland extends through the entire pereion, as perhaps a secondary prolongation.

The role of the midgut remains obscure. With the exception of *Cylopus lucasi*, the midgut was empty, even when the stomach and midgut gland were filled with food. This may be influenced by the constricted junction of midgut gland and midgut. Perhaps at certain times this constriction widens, letting food remain pass quickly. This action

was observed by Shearer and Evans (1975) in *Parathemisto gaudichaudii* (Guérin).

Despite the anatomical diversity of the hyperiid alimentary canal, there seems to be a common pattern indicating that at least the species examined have a monophyletic origin. The only exception is *Cylopus lucasi*. This species bears some plesiomorphic (and many apomorphic) characters in its alimentary canal that suggest a gammaridean condition. However, there are no synapomorphies to confirm inclusion in a monophylum of all other hyperiids examined.

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