Histomorphology of the digestive tract of *Chonopeltis australis* (Crustacea: Branchiura)

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The morphology and histology of the digestive tract of the branchiuran crustacean, *Chonopeltis australis* Boxshall, 1976 are described from serial sections. The foregut is differentiated into a preoral cavity, containing the mandibles and tongue, an ascending oesophagus, with an H-shaped lumen invested with longitudinal, circular and dilator muscles, a horizontal oesophagus with a star-shaped lumen and lacking longitudinal and dilator muscles, and an oesophageal funnel consisting of inner and recurrent walls. The midgut is differentiated into anterior and posterior chambers, separated by an S-shaped muscular tube. The arborescent midgut glands open laterally into the anterior part of the anterior midgut. Columnar epithelial cells line the anterior midgut whereas tall, papilliform cells are present in the epithelium of the posterior midgut. The transition from posterior midgut to hindgut is marked by the presence of very tall epithelial cells. The terminology describing the various parts of the digestive tract of branchiurans is discussed.

Die morfologie en histologie van die spysverteringskanaal van *Chonopeltis australis* Boxshall, 1976, 'n verteenwoordiger van die Branchiura (Crustacea), word beskryf vanaf seriesneë. Die voorderm is gedifferensieer in 'n pre-orale holte, waarbinne die mandibels en tong voorkom; 'n stygende esofagus met 'n H-vormige lumen omring deur lengte, kring- en dilatorspiere; 'n horisontale esofagus met 'n stervormige lumen wat slegs deur kringspiere omring is; en 'n esofageale tregter wat uit 'n binneste en 'n teruggevoude wand bestaan. Die middelderm bestaan uit 'n voorste en agterste kamer, geskei deur 'n S-vormige buis. Die boomvormige middeldermkliere open lateraal in die voorste deel van die voorkamer. Die voorkamer van die middelderm is uitgevoer met silinderepiteelselle terwyl lang, papilvormige selle die epiteel van die agterkamer uitmaak. Die oorgang vanaf die agterkamer van die middelderm na die agterderm word deur die aanwesigheid van besonder lang silinderepiteelselle gekenmerk. Terme wat gebruik word om die onderskeie dele van die spysverteringskanaal te beskryf, word bespreek.

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Branchiuran crustaceans of the genus *Chonopeltis* are ectoparasites of African freshwater fishes (Fryer 1968) and to date 12 species have been described (Avenant-Oldewage 1991. Although Thiele (1900) described the first species, *C. inermis*, more than 90 years ago, no information on the histomorphology of any of the internal structures is available for this genus. The same applies to the genus *Dipteropeltis*, of which only one species, *D. hirundo*, has been described (Calman 1912). On the other hand, the morphology of some of the internal structures in representatives of the other two branchiuran genera, *Argulus* and *Dolops*, has received ample attention from previous workers (Claus 1875; Leydig 1889; Thiele 1904; Maidl 1912; Martin 1932; Debaisieux 1953; Madsen 1964; Swanepoel & Avenant-Oldewage 1992). The histological structure of the digestive tract of *A. foliaceus* was investigated by Claus (1875) and Madsen (1964), whereas Maidl (1912) and Avenant-Oldewage & Van As (1990) described that of *Dolops longicauda* and *D. ranarum* respectively.

Here information is supplied on the morphology and histology of the digestive tract in *Chonopeltis australis* Boxshall, 1976, based on light microscopical observations.

Material and Methods

About 30 *Chonopeltis australis* specimens were collected from their fish hosts, *Labeo umbratus* (Smith, 1841) and *L. capensis* (Smith, 1841), in Boskop Dam, near Potchef-stroom, Transvaal, and transported live to the laboratory. After positioning a specimen on a clean microscope slide containing a drop of water, a small amount of petroleum jelly was placed on either side of the drop of water. The slide was then transferred to a Petri dish for viewing with a dissecting microscope. The specimen was manipulated with a fine camel's hair brush to ensure correct orientation of the appendages. A small coverslip was then placed onto the petroleum jelly and gently pressed down to ensure that the specimen remained flat. Using a medicine dropper, fixative was then dropped between the coverslip and microscope slide. Some specimens were fixed in a 10% solution of phosphate buffered neutral formalin (Romeis 1968), others in either Bouin's fluid (Humason 1979), or in Tellyesniczky's acetic acid alcohol formalin solution (Lillie & Fullmer 1976).

Following fixation, the specimens were dehydrated in a series of ethanol solutions, transferred to propylene oxide, infiltrated with the low viscosity aliphatic epoxy resin, Transmit LM (TAAB), for 24 h in a vacuum chamber, and cured in fresh Transmit LM for 18 h at 70°C.

Longitudinal, transverse or frontal serial sections, at a thickness of 5 μm, were obtained by cutting whole embedded animals with glass knives fixed to a rotary microtome. Following removal of the embedding medium with a saturated solution of sodium hydroxide in absolute ethanol, the sections were stained either with Mayer's haematoxylin,
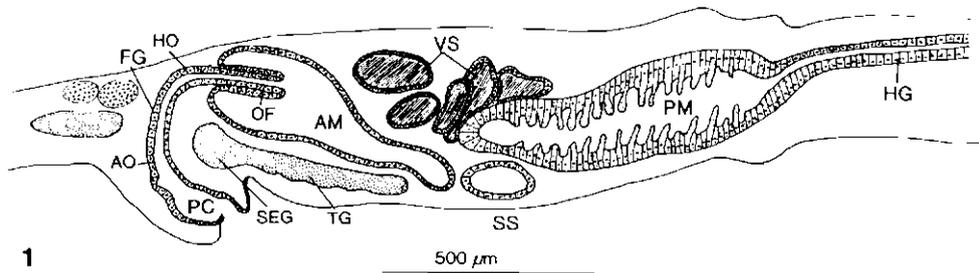
Figure 1 *Chonopeltis australis*. Mid-sagittal section through male 3,6 mm total length. AM anterior midgut; AO ascending oesophagus; FG foregut; HG hindgut; HO horizontal oesophagus; OF oesophageal funnel; PC preoral cavity; PM posterior midgut; SEG suboesophageal ganglion; SS S-shaped duct; TG thoracic ganglia; VS coils of seminal vesicle.

counterstained with eosin (Humason 1979), azocarmine, counterstained with Heidenhain's azan solution (Romeis 1968), or with periodic acid-schiff solution (PAS) (Pearse 1985) followed by haematoxylin and light green, or PAS, followed by azocarmine, aniline blue and orange-G.

Histochemical characteristics of the epithelial walls of the digestive tract were ascertained by staining buffered formalin sections (either with periodic acid-schiff reagent (PAS), or with Diazotization coupling (Diazo) or with alcian blue at pH 1,0 or 2,5 (Pearse 1985).

Contractions of the walls of the digestive tract were studied in live animals. These were kept for up to 2 h in a 5% solution of the vital stain neutral red, in dam water. Compressed air was bubbled through the staining solution to prevent anoxia. Specimens were then rinsed in dam water and positioned on a microscope slide as previously described. Because the epithelial lining of the digestive tract took up the stain faster than the thick, cuticle-lined external body wall, the outline of the digestive tract could easily be observed through the transparent body wall.

Results

The constituent parts of the digestive tract of *Chonopeltis australis* are illustrated in Figure 1. In a 3,6-mm male, the digestive tract is 2,87 mm in length and comprises a cuticle-lined foregut (0,65 mm), a midgut (1,42 mm) and a cuticle-lined hindgut (0,80 mm).

Foregut

The foregut is differentiated into four distinct histomorphological regions, viz. a preoral cavity (100 μm), an ascending oesophagus (150 μm), a horizontal oesophagus (150 μm) and an oesophageal funnel (125 μm) (Figure 2).

The preoral cavity, which is lodged in the proboscis, is lined by cuboidal epithelial cells, resembling those of the hypodermis, and likewise covered by a cuticle (Figure 3A). No muscular coat surrounds the epithelial wall of the preoral cavity (Figure 3A). The mandibles project from the lateral walls into the lumen and a tongue (see discussion) is present in the roof (posterior wall) of the preoral cavity. Four tongue muscles bisect a glandular mass (Figure 3A), the ducts of which drain into the preoral cavity. The gland cells gave negative results with PAS and alcian blue (pH 1,0 and 2,5), but moderately positive results with Diazo. The cuticular coat of the tongue contains numerous seta-like
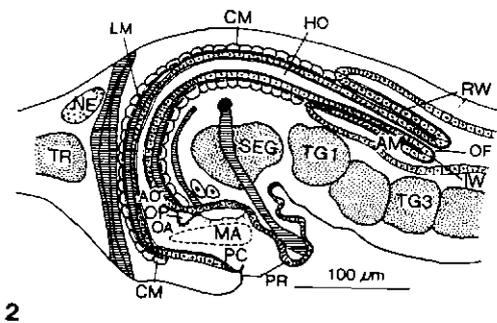

Figure 2 *Chonopeltis australis*. Mid-sagittal section through foregut of a male 3,11 mm total length. AM anterior midgut; AO ascending oesophagus; CM circular muscles; LM longitudinal muscle; IW inner wall of oesophageal funnel; HO horizontal oesophagus; MA position of mandible; NE nauplius eye; OA oral aperture; OF oesophageal funnel; OP oral plate; PC preoral cavity; PR proboscis; RW recurrent wall of oesophageal funnel; SEG suboesophageal ganglion; TG1, TG3 first and third thoracic ganglia; TR tritocerebrum.

projections which probably function in cleaning the mandibles.

The cuticular wall of the oral aperture contains five dentigerous plates (Figure 3B) which may function in filtering aliment. Opening and closure of the oral aperture is regulated by two pairs of dilator muscles and a well-developed constrictor muscle (Figure 3B).

The ascending oesophagus, which passes through the circumoesophageal nerve ring, has an H-shaped, cuticle-lined lumen (Figure 3C). The epithelial wall consists of cells of the cuboidal type which stain positively with PAS, but negatively with alcian blue, indicating the presence of glycoproteins. External to the epithelial wall some longitudinal (dorso-ventral) muscle fibres, as well as a battery of constrictor muscles, are present (Figures 2, 3C).

The horizontal oesophagus runs parallel to the mid-dorsal body wall and its muscular wall consists of constrictor muscles only (Figures 2, 3D). Its lumen is star-shaped, owing to the cuticle being thrown into a number of longitudinal ridges (Figure 3D). It enters the midgut by way of the oesophageal funnel (Figure 2) originating by intussusception of the foregut into the anterior midgut. The oesophageal funnel has an inner wall of tall, columnar epithelial cells and a recurrent wall of squamous cells (Figures 2, 3E). Both epithelial walls are lined by cuticle. The epithelial cells of

the inner and recurrent walls contain vacuoles, the contents of which stain positively with PAS, but negatively with alcian blue. Between the basement membranes of the inner and recurrent epithelial walls, some longitudinal muscle fibres are present (Figure 3F) contracting the funnel into a bell-shaped structure or extending it into a tubular structure.

Midgut

The midgut is differentiated into anterior and posterior chambers (Figures 1, 4A,B). Depending on the stage of sexual maturity, the shape of both chambers is affected by either the number of ripe eggs present or the extent of evaginations of the seminal vesicle invading the haemocoelic spaces surrounding the midgut. In one male the posterior part of the anterior midgut was reduced to a narrow duct (Figures 1, 4A), whereas in a female, containing a few ripe eggs, the shape of the anterior part of the posterior midgut was clearly deformed (Figure 4B).

The anterior midgut is situated above the suboesophageal and thoracic ganglia (Figure 1). In a 7-mm female this tubular sac is 1,42 mm in length with a diameter of 0,4 mm (Figure 4B). The epithelial wall of the anterior midgut consists of closely packed columnar epithelial cells (Figure 3E) which vary in height from 12–20 μm. The taller cells are predominant along the anterior wall, close to the oesophageal funnel (Figure 3E). The nuclei are situated basally to centrally within the cells and vacuoles appear to be absent (Figure 3E). Scattered among the epithelial cells of the midgut wall, are cells which stain moderately positive with Diazo and intense purple with azan (Figure 3G). These cells probably correspond to the F-B-transitional cells found in the midgut of decapods (Dall & Moriarty 1983). In azan-stained sections, a distinct basement membrane can be observed between the epithelium and the single layer of circular muscle fibres. In parts of the digestive tract where the muscles are in a contracted condition, the basement membrane displays a zig-zag pattern (Figure 3G). Characteristically the fibrous parts of the muscle cells lie close to the basement membrane of the epithelium, whereas the sarcoplasm, containing the nuclei and being three to four times the volume of the muscle cells, lies externally (Figures 3J, 5A).

The two ducts of the midgut glands (enteral diverticules) open laterally into the anterior midgut, more or less halfway along its length (Figures 4A,B), and in the same transverse plane as the fourth thoracic ganglion. Each midgut gland consists of numerous finger-shaped tubuli (50–100 μm in diameter) branching through the haemocoelic spaces within the carapace at random. The tubuli drain into larger ducts uniting with others to form the main duct. The epithelial lining of the midgut glands contains two distinctly different cell types: columnar epithelial cells (12 μm), with small basally situated nuclei, resembling those of the anterior midgut wall, and large spindle-shaped cells (18 μm), with large, centrally situated nuclei (6 μm), and granular cytoplasm (Figure 3G). The apical granules of the large cells stain negatively with PAS and alcian blue, but moderately positive with Diazo, indicating the presence of protein, probably enzymes.

Azan-stained sections of the midgut glands reveal a very thin layer of mauve-stained circular muscle fibres surrounding the intensely blue-stained basement membrane (Figure 3G). In vitally stained specimens contraction of the walls of the tubular midgut glands is often observed. Although numerous hypodermal gland cells fill the spaces within the carapace between the tubuli of the midgut glands, these glands, some staining positively with PAS, do not drain into the lumen of the tubuli, but to the exterior via minute ectodermal ducts.

The posterior midgut is a tubular sac measuring 1,2 mm × 0,5 mm in a 7-mm female and 0,7 mm × 0,3 mm in a 3,6-mm male (Figures 4A,B). The anterior and posterior walls of the posterior midgut are lined by columnar epithelial cells (20 μm) resembling those of the anterior midgut, whereas the remaining walls contain two distinctly different cell types: papilliform cells (30–40 μm) with apically situated vacuoles and centrally situated nuclei, and columnar epithelial cells (12 μm) with basally situated nuclei (Figures 3H, I). The apical portion of some of the papilliform cells stain strongly positive with Diazo but negative with PAS, indicating the presence of protein, probably digestive enzymes.

An isthmus, in the form of a thick-walled, S-shaped duct, separates the anterior and posterior chambers of the midgut (Figures 3I, 5A,B). The duct is spirally orientated, with its

Figure 3 *Chonopeltis australis.* A–L: sections through various parts of digestive tract. All sections are transverse except C and J which are frontal. Scale bars 50 μm. A. Proboscis showing preoral cavity (PC) lined with cuboidal epithelial cells (EP) and associated gland cells (GC), mandible (M) and tongue (T). B. Oral aperture showing oral constrictor muscle (CM), oral dilator muscle (DM) and dentigerous plates (TP). C. Ascending oesophagus with surrounding circular muscles (CM), H-shaped lumen (L) and longitudinal muscles (LM). D. Horizontal oesophagus showing epithelial folds (EP) around star-shaped lumen and constrictor muscle (CM). E. Oesophageal funnel at point of entering anterior midgut (AM). The inner wall (IW) of tall columnar cells and recurrent wall (RW) of squamous cells. Note basement membranes (BM) between recurrent wall and epithelial wall (EP). F. Oesophageal funnel showing layer of longitudinal muscle fibres (LM) between inner wall (IW) and recurrent wall (RW). G. Main duct of midgut gland (TMG) showing spindle-shaped cell (SC) with large nucleus and thin circular muscle layer (CM). Part of wall of anterior midgut (AM) showing Diazo-positive cells (DP) and zig-zag basement membrane (BM). H. Posterior midgut showing papilliform cells (PC). I. S-shaped duct (SS) showing circular muscle layer (CM) and tall epithelial cells (EP) reducing lumen to a slit-like passage. Note relatively shorter columnar cells (EPM) of anterior midgut wall. Papilliform cells (PC) of posterior midgut also labelled. J. Transition from posterior midgut (PM) to hindgut (HG) showing tall epithelial cells (EP), thoracic part of hindgut (TPH) and circular muscle (CM) with small fibrous part and large nucleated sarcoplasm. K. Thoracic part of hindgut showing circular muscle layer (CM), small star-shaped lumen lined by cuticle (CT) and tall epithelial cells (EP). L. Abdomen showing dorsal (DB) and ventral (VB) body walls, dorso-ventral muscles (DV) and circular muscle layer (CM) of hindgut.
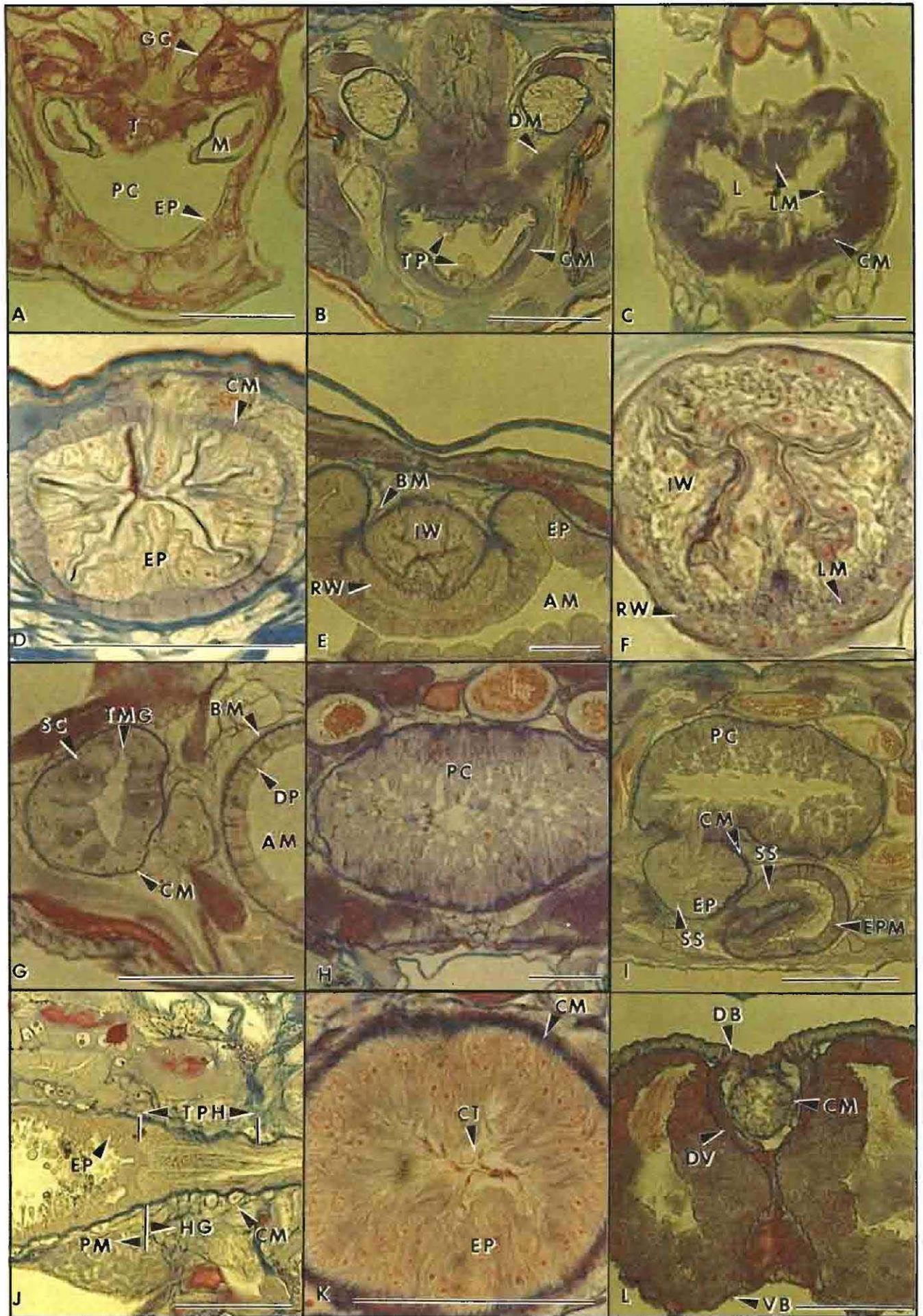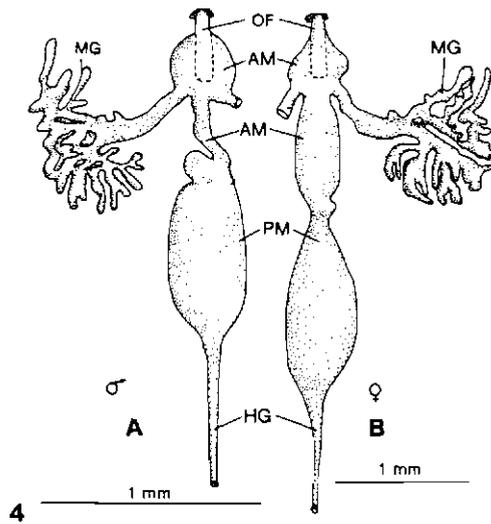
Figure 4 *Chonopeltis australis.* Reconstructions of the digestive tracts. A. Male, 3,6 mm total length. B. Female, 7 mm total length. AM anterior midgut; HG hindgut; MG midgut glands; OF oesophageal funnel; PM posterior midgut.
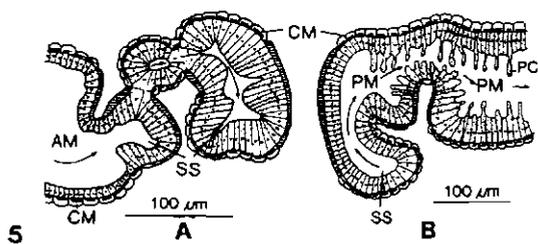

Figure 5 *Chonopeltis australis.* A. Frontal section through junction between anterior midgut and S-shaped duct. B. Longitudinal section through junction between S-shaped duct and posterior midgut. Arrows indicate path of foregut fluid through S-shaped duct. AM anterior midgut; CM circular muscles; PC papilliform cell; PM posterior midgut; SS S-shaped duct.

anterior part in the same horizontal plane as the floor of the anterior midgut (Figure 5A). Its posterior part, which opens into the dorsally situated anterior end of the posterior midgut, lies in a vertical plane (Figures 3I, 5B). In comparison with the low (12 μm) columnar epithelial cells lining the anterior midgut, the epithelial cells of the S-shaped duct are exceptionally tall (30 μm), resulting in the lumen of the isthmus being reduced to a narrow passage (Figures 3I,. 5A). No longitudinal muscle fibres could be observed external to the thick basal membrane of the isthmus, but it is surrounded by a battery of circular muscle fibres, resembling those of the anterior midgut (Figure 5A). Since no additional muscle layers could be observed in the transition from anterior midgut to isthmus and from the isthmus to posterior midgut, it appears that the entire S-shaped duct functions as a sphincter in regulating the flow of food entering the posterior midgut or preventing it from flowing back into the anterior midgut.

Hindgut

The cuticle-lined hindgut is a straight tube, 0,8 mm in length in a 3,6-mm male. Histologically, the hindgut is differentia-

ted into three regions, a thoracic part (70 μm), an anterior abdominal part (70 μm) and a longer posterior abdominal part (660 μm) (Figures 3J, 6A). The latter runs posteriorly, between the abdominal lobes, and opens posterodorsally at the anus, where the abdominal lobes separate.

The transition from posterior midgut to hindgut is marked by a very tall epithelium (Figures 3J, 6A,B). The epithelial wall of the thoracic part of the hindgut, with its tall columnar epithelial cells, is covered externally by a coat of circular muscles (Figures 3K, 6A,C), which are a continuation of the muscle coat of the posterior midgut (Figure 6A). The anterior abdominal part of the hindgut is smaller in diameter than the thoracic part and also has a layer of circular muscle fibres (Figure 6D). Dorsoventrally-orientated muscles, which lie external to the circular muscles (Figs 6A,D), originate from the body wall cuticle and extend between the dorsal and ventral walls of the abdominal lobes (Figure 3L). In the remainder of the abdominal part of the hindgut, muscles are absent (cf. Figures 6A,E). Concerning the arrangement of muscles in the abdominal part of the hindgut, it is conspicuous that the main abdominal nerves initially run between the circular and dorsoventral muscles (Figures 6A,D), but farther back, where the circular muscles are absent, the nerves proceed laterally to the dorsoventral muscles (Figures 6A,E).

The cells constituting the epithelial wall of the hindgut contain many vacuoles, the content of which stain positively with PAS, but negatively with alcian blue or Diazo.

Discussion

In the literature concerning the morphology of the digestive tract of branchiurans, inconsistent and sometimes confusing terminology has been used to describe the different parts of the digestive tract. Heller (1857) described in *Gyropeltis* (=Dolops) a 'Russelhöhle' (proboscis cavity) which is connected to the 'Magendarm' (stomach) by a bow-shaped tube. The stomach is followed by a wide 'Darm' (gut), which is followed by the rectum. Thorell (1864) called the bow-shaped tube between the buccal cavity (proboscis cavity) and the stomach in *Argulus foliaceus* an oesophagus and observed that it passes through the nerve ring to open into the stomach by means of a cup-like organ, which probably acts as a sucking pump. Leydig's (1889) description of the digestive tract of *A. foliaceus* was more accurate when he distinguished three regions, viz. an 'Anfangsdarm' (foregut) or 'Schlund' (oesophagus), a 'Mitteldarm' (midgut) which is differentiated into a 'Magen' (stomach) and 'eigentlichen Darm' (gut proper), and the 'Enddarm' (hindgut). Maidl (1912) accepted Leydig's (1889) terminology, but gave preference to the term 'Dünndarm' (intestine) when describing that part of the digestive tract preceeding the hindgut. Martin (1932) did not describe the digestive tract in the three *Argulus* species she studied and used the term crop when labelling that part of the digestive tract containing the midgut glands, i.e. the stomach of earlier workers. Madsen (1964) followed Martin's (1932) terminology, but substituted the term midgut for intestine, implying that the crop is not part of the midgut. However, in *Chonopeltis australis* and other branchiurans hitherto investigated (Madsen 1964; Avenant-Oldewage & Van As 1990), the so-called crop is
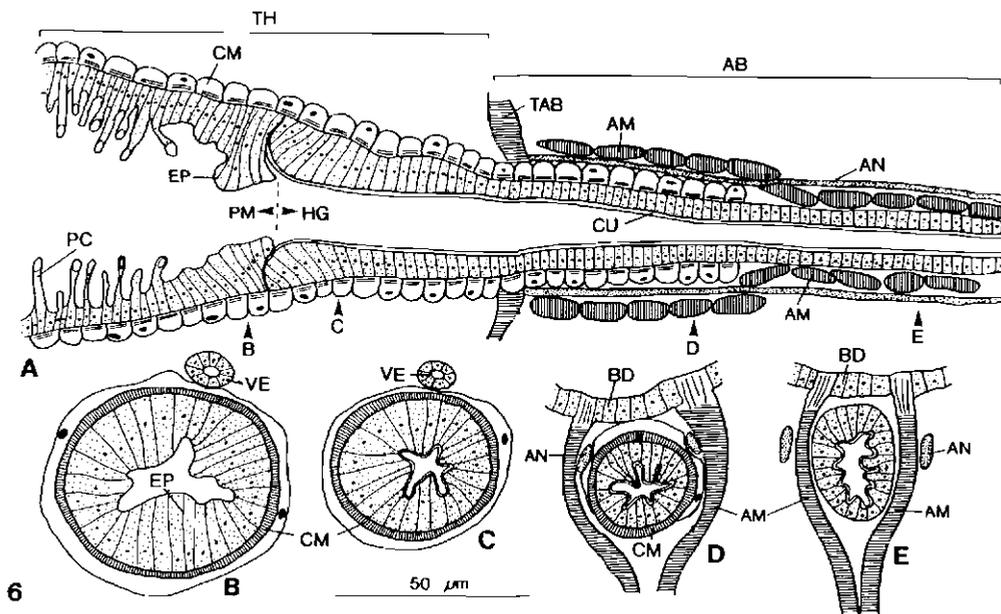
Figure 6 *Chonopeltis australis*. A. Frontal section through posterior part of midgut and anterior part of hindgut. *Arrows* B–E indicate positions of transverse sections. B–E. Transverse sections at various levels of posterior midgut and hindgut. AB abdominal region; AM dorso-ventral abdominal muscle; AN main abdominal nerve; BD dorsal abdominal wall; CM circular muscle; CU cuticle; EP epithelium; HG hindgut; PC papilliform cell; PM posterior midgut; TAB transverse muscle between thorax and abdomen; TH thoracic region; VE vas efferens.

not lined by cuticle, and, therefore, belongs to the midgut. It is evident that the term 'crop', used to describe the anterior part of the midgut in branchiurans, is a misnomer, since the crop in insects is an oesophageal caecum, derived from the ectodermal foregut (Meglitsch 1972). Since the midgut in branchiurans is differentiated into a distinct anterior and posterior chamber, we propose that the terms crop and intestine be replaced with respectively anterior and posterior midgut, as suggested by Leydig (1889) more than a hundred years ago.

The branchiuran foregut is a bow-shaped tube connecting the proboscis cavity to the midgut (Heller 1857). The nature of the proboscis cavity as well as the position of the true oral aperture, were discussed by a number of early workers. Vogt (1845), Leydig (1850) and Claus (1875) referred to the proboscis cavity as the 'Mundhöhle' (oral cavity) and regarded the oral aperture in *Argulus* as being situated terminally in the proboscis, where the free ends of the upper and lower lips meet. Leydig (1889) later changed his opinion regarding the oral aperture in *A. foliaceus*, stating that it lies proximally between the mandibles where their serrated margins meet. In his comparative study of some of the proboscis muscles of *A. foliaceus* and *Dolops longicauda*, Maidl (1912) concluded that the distal end of the oesophagus, which in both species is characterized by the absence of circular muscles, is not to be found terminally in the proboscis, but at its base, where the oral aperture is therefore situated. Maidl (1912), however, still referred to the cavity in front of the oral aperture, i.e. the proboscis cavity, as the 'Mundhöhle' (oral cavity). Martin (1932) observed in *A. viridis* that three delicate chitinous lamellae guarded the 'mouth opening' and proposed the term 'buccal cavity' for the cavity in front of (distally to) the mouth opening, a term accepted by later workers (Madsen 1964;

Avenant-Oldewage & Van As 1990). However, since the external (distal) opening of the buccal cavity is usually called an oral aperture, the cavity which in branchiurans lies in front of (proximal to) the oral aperture should be referred to, more aptly, as a preoral cavity.

Apart from housing the mandibles, the preoral cavity also contains an eminence or 'Wulst' projecting medially from its roof (labium, posterior wall of proboscis). This structure, first referred to as the 'Zunge' (tongue) by Maidl (1912) when investigating the nature of the proboscis in *Dolops longicauda* and *Argulus foliaceus*, is very prominent in *D. longicauda*. Maidl (1912) did not describe the finer detail of the tongue in these species, but in *A. viridis* two spines, termed labial spines by Martin (1932), are situated at the tip of the tongue. In *A. japonicus* two of the four efferent ducts from some giant gland cells, located ventrally to the optic tracts, terminate in these spines (Swanepoel & Avenant-Oldewage 1992). The cuticle of the tongue in *Chonopeltis australis* shows numerous setose projections which probably function in cleaning the mandibles. Furthermore, the four retractor muscles of the tongue in this species bisect a group of gland cells draining into the pre-oral cavity. Maidl (1912) mentioned two glandular complexes ('Munddrüsen') in *D. longicauda*, one of which is situated dorsal to the tongue in a more or less similar position to that in *C. australis*, the other located in front of the oesophagus and ventral to the tritocerebrum. Both glands drain into the 'Mundhöhle' (= preoral cavity). Nothing is known concerning the origin of the tongue in branchiurans. Since the tongue is intimately associated with the posterior wall of the proboscis, it is clear that information on its origin depends on a thorough investigation of the early development of the proboscis. The only relevant study, that of Martin (1932) on *A. viridis*, indicates that the basal parts of the mandibles form the main

portion of the proboscis. She did not, however, make any mention of a tongue.

In all branchiurans hitherto investigated the epithelial wall of the oesophagus is covered externally by a muscular coat consisting of inner longitudinal muscles and an outer layer of circular muscles (Claus 1875; Madsen 1964). The ascending oesophagus (distal part of the oesophagus) in *Chonopeltis australis* also has some dilator muscles, originating from the proboscis skeletal bars and the ventral body wall, whereas the horizontal oesophagus (proximal part) contains circular muscles only. The oesophagus enters the midgut by way of the oesophageal funnel, first observed by Thorell (1864) in *Argulus foliaceus* and later by Maidl (1912) in *Dolops longicauda*. A similar structure was observed in Caligidae (Copepoda) by Kabata (1974). The oesophageal funnel in *Chonopeltis australis* originates by intussusception of the foregut into the midgut and consequently consists of a cuticle-lined inner and recurrent wall.

An isthmus divides the midgut of branchiurans into roughly equal-sized parts. In both *Argulus* and *Dolops* the isthmus is a short, simple, narrow tube invested with strong sphincter muscles (Claus 1875; Maidl 1912; Madsen 1964). In *Chonopeltis australis*, however, it is a relatively long S-shaped tube with exceptionally thick epithelial wall. The circular muscles are of the same thickness as those of the remainder of the midgut and it appears that the entire S-shape tube functions as a sphincter. The fact that the epithelial wall of the anterior midgut contains columnar epithelial cells, whereas that of the posterior midgut contains papilliform cells, was first observed by Claus (1875), later described in *A. foliaceus* by Grobben (1908) and by Maidl (1912) in *Dolops longicauda*. In *C. australis* these epithelial cells can be so tall and numerous that they nearly fill the lumen of the posterior midgut. Overstreet, Dykova & Hawkins (1992) suggested that the papilliform cells in the epithelial wall of the posterior midgut of branchiurans appear to produce digestive enzymes. In *C. australis* we noticed that the free ends of the papilliform cells, projecting into the midgut lumen, are engulfed by (digested?) food particles. Furthermore, the size of the papilliform cells appears to be affected by the degree of starvation. Specimens, sectioned soon after removal from their hosts, have tall (40 μm) papilliform cells, whereas individuals, sectioned after being starved for 3–4 days, show rather small (20 μm) papilliform cells. John & Nair (1975) suggested that the globular ends of the elongated cells in the midgut of the copepod *Hermilius longicirnis* break off as spherical vesicles bursting open so that their fluid becomes mixed with the food content of the lumen. In the copepod *Paranthessius anemoniae* the epithelial cells of the midgut are amoeboid in nature (Briggs 1977). The apical surfaces of these amoeboid cells bulge into the midgut in pseudopodial fashion to enclose the midgut contents. From these observations he deduced that these cells function phagocytically.

The hindgut of branchiurans is a straight tube with the cuticle-lined epithelium, like that of the oesophagus, folded longitudinally, resulting in a star-shaped lumen (Grobben 1908; Madsen 1964). In the transitional area between midgut and hindgut the posterior wall of the midgut in *Chonopeltis australis* is marked by the presence of a very thick epithelium. However, in the three *Argulus* species

examined by Madsen (1964) the epithelium of the posterior wall of the midgut is differentiated into four or more finger-like papillae whereas in *Dolops ranarum* papillae are absent (Avenant-Oldewage & Van As 1990). Furthermore, in comparison with the posterior part of the hindgut, the anterior portion of the hindgut wall, in all branchiurans hitherto investigated, is exceptionally thick, reducing the lumen to a narrow passage. Since no observable sphincter muscles, other than the ordinary circular muscles, envelop the epithelial wall in the transitional area between midgut and hindgut (Madsen 1964; Avenant-Oldewage & Van As 1990), the anterior part of the hindgut could effectively be closed off by contraction of the circular muscles.

Comparison of the digestive tracts of *Argulus*, *Dolops* and *Chonopeltis* reveals many morphological and histological similarities. There are, however, differences in the foregut, where the tongue differs in morphology and in function in the three genera.

Acknowledgements

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