THE ANATOMY OF *PACHYDERMIA LAEVIS* (ARCHAEOGASTROPODA: 'PELTOSPIRIDAE')

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ABSTRACT

The anatomy of *Pachydermia laevis* Warén & Bouchet, 1989 is investigated. It is a deep-sea gastropod and restricted to hydrothermal vents of the East Pacific Rise. Its anatomy resembles that of *Melanodrymia aurantiaca* Hickman, 1984 (Melanodrymiidae) in most respects, except that its gonopericardial duct opens into the renopericardial duct, not into the pericardial chamber, and that it lacks a copulatory organ. Examination of *M. aurantiaca* main confirms earlier work. The two species have a cerebral buccal connective fused with the cerebral ganglion (not free from it), a synapomorphy that has not been described for any other archaeogastropod. The investigation suggests that *Melanodrymia* and *Pachydermia* are closely related and together with Cyathermiidae and Neomphalidae form a monophyletic group within the Neomphalina. No evidence was found to support earlier speculations about close relations of Neomphalina to Viviparoidea.

INTRODUCTION

The Archaeogastropoda has been regarded as either a monophyletic taxon or the stem group of gastropods (Haszprunar, 1993). The name was introduced by Thiele (1925) for the 'lowest' level of gastropod organisation. This paraphyletic definition was supported by the fact that the diagnostic characters of Archaeogastropoda, such as a streptoneurous and hypoathroid nervous system, are plesiomorphic. Recently, the discovery of new archaeogastropods, such as hydrothermal vent species, and re-examination of poorly known taxa, such as the Cocculiniformia, have opened the discussion of the status of Archaeogastropoda. However, it is still regarded as a paraphyletic taxon (Ponder & Lindberg, 1996, Salwini-Plawen & Steiner, 1996).

The Neomphalina is a group of archaeogastropods, only known from hydrothermal vents in the Pacific Ocean, with both coiled and limpet-shaped species. They have internal fertilization; some have copulatory organs but such are not always present. The taxon has been divided into the families Cyathermiidae, Neomphalidae, Peltospiridae and Melanodrymiidae (the last family introduced by Salvini-Plawen & Steiner, 1996). The cyathermiids and neomphalids are characterized by having an enlarged ctenidium and a left cephalic tentacle which is modified into a penis (Fretter, Graham & McLean, 1981; McLean, 1981, 1990). The Peltospiridae is probably a polyphyletic assemblage of species (Warén & Bouchet, 1989; Warén, pers. comm.). Table 1 lists the described taxa and morphological investigations of neomphalines. This paper is restricted to two rather unmodified peltospirids. The other peltospirids together with the cyathermiids and the neomphalids will be treated later (Israelsson, in prep.).

Species of Neomphalina exhibit plesiomorphic archaeogastropod characters such as simple sac-like salivary glands; mid-oesophageal pouches (actually gutter-like longitudinal folds); ctenidia supported by skeletal rods; streptoneurous and hypoathroid nervous system; and presence of ctenidial bursicles (Haszprunar, 1993), but also apomorphic characters such as lack of a nacreous layer in the shell, internal fertilization, and absence of a labial commissure. This combination of plesiomorphic and apomorphic characters led Sitnikova & Starobogatov (1983) to the conclusion that they are mesogastropods within the order Vivipariformes. However, the apomorphic characters are present also in some other archaeogastropod taxa.

Haszprunar (1993, 1996) and Ponder & Lindberg (1996) analysed the phylogeny of Gastropoda and regarded Neomphalina as a monophyletic group of uncertain position within the Archaeogastropoda. However, Salvini-Plawen & Steiner (1996) suggested a polyphyletic origin of the neomphalines. I believe that the ambiguous results of the phylogenetic

Table 1. List of species of Neomphalina.

Taxa	Reference	Comment
Cyathermiidae McLean, 1990		
Cyathermia naticoides Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology
Lacunoides exquisitus Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology
Neomphalidae McLean, 1981		
Neomphalus fretterae McLean, 1981	McLean (1981)	Shell, radula, external morphology
	Fretter *et al.* (1981)	Shell, radula, external morphology, detailed anatomy
Symmetromphalus hageni Beck, 1992	Beck (1992)	Shell, radula, external morphlogy, notes about anatomy
Symmetromphalus regularis McLean, 1990	McLean (1990)	Shell, radula, external morphlogy,
Peltospiridae McLean, 1989		
Ctenopelta porifera Warén & Bouchet, 1993	Warén & Bouchet (1993)	Shell, radula, external morphology
Depressigyra globulus Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology
Echinopelta fistulosa McLean, 1989	McLean (1989)	Shell, radula, external morphology
Hirtopelta hirta McLean, 1989	McLean (1989)	Shell, radula, external morphology
	Fretter (1989)	Notes about anatomy
	Warén & Bouchet (1993)	Shell
Lirapex granularis Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell
Lirapex humata Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology
Melanodrymia aurantiaca Hickman, 1984	Hickman (1984)	Shell, radula,
	Warén & Bouchet (1989)	Shell, radula, external morphology
	Haszprunar (1989)	Detailed anatomy
Melanodrymia brightae Warén & Bouchet, 1993	Warén & Bouchet (1993)	Shell, radula, external morphology
Nodopelta heminoda McLean, 1989	McLean (1989)	Shell, radula, external morphology
	Fretter (1989)	External morphology, notes about anatomy
Nodopelta subnoda McLean, 1989	McLean (1989)	Shell, radula, external morphology
	Fretter (1989)	Notes about anatomy
Pachydermia laevis Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology
Pachydermia sculpta Warén & Bouchet, 1993	Warén & Bouchet (1993)	Shell, radula, external morphology
Peltospira delicata McLean, 1989	McLean (1989)	Shell, radula, external morphology
	Fretter (1989)	External morphology, anatomy
Peltospira lamellifera Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell
Peltospira operculata McLean, 1989	McLean (1989)	Shell, radula, external morphology
	Fretter (1989)	External morphology,
Planorbidella planispira (Warén & Bouchet, 1989)	Warén & Bouchet (1989)	Shell, radula, external morphology
	Warén & Bouchet (1993)	External morphology
Rhynchopelta concentrica McLean, 1988	McLean (1988)	Shell, radula, external morphology
	Fretter (1989)	External morphology, anatomy
Rhynchopelta nux Okutani, Fujikura & Sasaki 1993	Okutani *et al.* (1993)	Not a peltospirid (Warén, personal communication)
Solutigyra reticulata Warén & Bouchet, 1989	Warén & Bouchet (1989)	Shell, radula, external morphology

analyses are caused by lack of detailed information.

Despite the number of species involved (Table 1), only two of them have been investigated thoroughly (*Melanodrymia* and *Neomphalus*). The lack of information and the importance other authors have given the neomphalines for establishing the phylogeny of Archaeogastropoda, causes a need for further anatomical investigations. I here report the result of a more detailed investigation of the anatomy of *Pachydermia laevis* Warén & Bouchet, 1989 and a re-examination of *Melanodrymia aurantiaca* Hickman, 1984, which will form a basis for comparison with several other species classified in Cyathermiidae, Neomphalidae and Peltospiridae (Israelsson, in prep.).

MATERIAL AND METHODS

The examined specimens of *Melanodrymia aurantiaca* and *Pachydermia laevis* are part of the material reported by Warén & Bouchet (1989). They were fixed in 4% formalin buffered with borax and stored in 80% ethanol. Four female and three male specimens were dehydrated through absolute ethanol and therpeneol, embedded in Histowax, serially sectioned at 5 μm or 7μm thickness, and stained with Ehrlich's haematoxylin and eosin. The section series are deposited at the Swedish Museum of Natural History, Stockholm.

RESULTS

Pachydermia laevis

Head-foot and pallial complex. The radula, the shell, and the external morphology of the soft parts of *Pachydermia laevis* were described by Warén & Bouchet (1989). The only noticeable feature of the shell is that the protoconch is covered by a fine net-sculpture that becomes finer and more indistinct towards the aperture. In general, the anatomy resembles that of *M. aurantiaca* (Haszprunar, 1989, and own observations). None of the males exceeded half the size of an adult female. No other sexual dimorphism was found and the species is probably gonochoristic since none of the examined individuals shows signs of sex reversal or have hermaphroditic gonads.

The foot is muscular and well-developed. Figure 1A-B shows the exterior of the head-foot. The propodium is distinct and separated from the mesopodium by a transverse furrow. There are five small epipodial tentacles at each side of the foot. They are gradually smaller

forwards, surround the posterior 2/3 of the operculum, and lack sensory papillae. The epithelium of the sole is separated from the muscle layer by a thin layer of connective tissue. The anterior portion of the foot is filled by the large anterior pedal gland, which is innervated by the anterior pedal nerves. The gland is lobed and composed of irregularly rounded, strongly staining gland cells, and opens in the furrow between the mesopodium and propodium. The epithelium of the foot contains scattered mucous cells resting on connective tissue and horizontal muscle fibres. There is no posterior pedal gland.

The head has a tapering snout and a pair of laterally placed, conical cephalic tentacles, almost twice as long as the snout in preserved specimens, and of equal size and shape in both sexes. There are no sensory papillae, oral lappets or neck lobes. The epithelium of the head and the base of the tentacles contains scattered mucous cells resting on connective tissue and horizontal muscle fibres. The interior of the tentacles is filled with cartilaginous cells. Some papilliform structures are located at the base of the tentacle and may be a result of contraction of the head, but their epithelium differs from the epithelia of both the head and the tentacles. These papillae are covered by a layer of poorly staining cells.

The body consists of three whorls of which 2.6 constitute the visceral mass. The outer half of the visceral mass is occupied by the digestive glands, the inner half by the gonad. The columellar muscle occupies a semicircular area starting slightly behind each corner of the pallial cavity. The columellar shell gland (Fig. 2, shgl) is located between the muscle and the posterior part of the pallial edge, close to the outer pallial fold (opf), and it continues towards the columellar muscle (col). The gland consists of two cell types, inner gland cells and outer, smaller cells. The gland cells are irregularly rounded, poorly staining, about 10 μm in diameter and scattered in connective tissue. The smaller outer cells are elongated and stain more intensely. Near the shell, the attachment zone of the columellar muscle consists of very flattened cells (epcol). The epithelium of the visceral mass towards the shell is even thinner (only 2 μm) than that covering the columellar muscle.

The pallial cavity occupies one third of a whorl in preserved specimens. A cross-section of the pallial margin is shown in Figure 2. The cavity contains a small bipectinate ctenidium with an osphradium at its efferent side and a
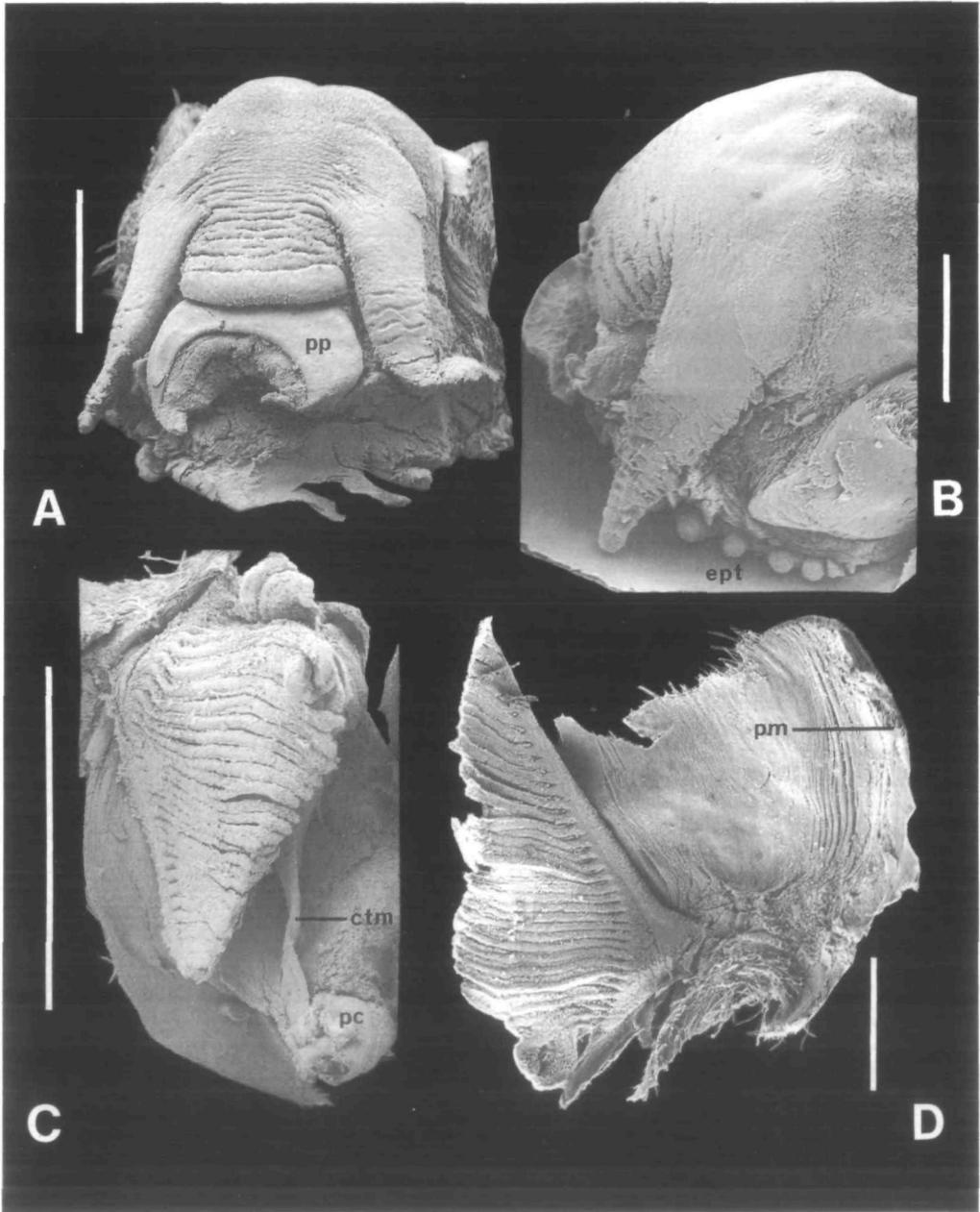
Figure 1. *Pachydermia laevis.* External morphology. A-B. Anterior (A) and lateral (B) view of the anterior part of the body. C-D. Posterior (C) and anterior (D) view of the pallial roof showing the ctenidium and ctenidial membrane. Scale bars = 500 μm. Abbreviations: ctm, ctenidial membrane with the efferent branchial vein; ept, epipodial tentacles; pc, pericardium; pm, pallial margin; pp, propodium.

large afferent vein in a ctenidial membrane, a nephropore, a gonopore, an anus, and a pair of hypobranchial glands. The anus opens at the posterior third of the pallial cavity immediately to the left of and in front of the anterior part of the right columellar muscle. The most distal part of the rectum is free from the pallial roof. The gonopore is located to the right of the
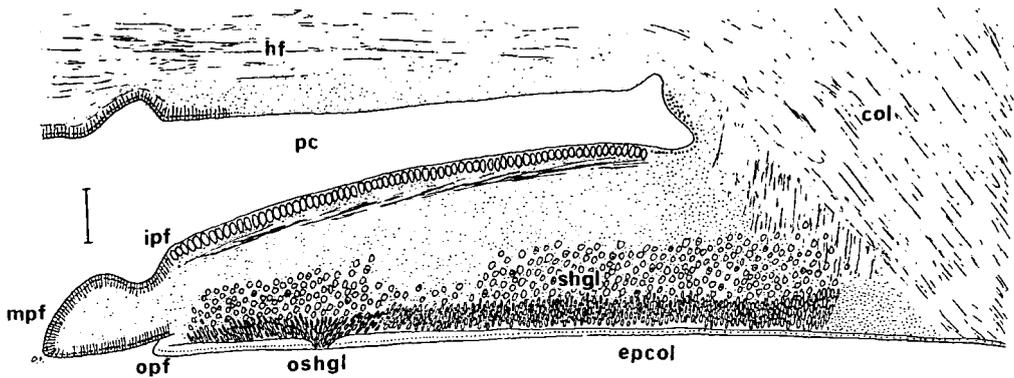
Figure 2. *Pachydermia laevix.* Cross-section through the posterior part of the pallial edge, above the foot. Scale bar = 50 μm. Abbreviations: col, columellar muscle; epcol, epithelium of attachment area of columellar muscle; hf, head-foot; ipf, inner fold of pallial margin; mpf, median fold of pallial margin; opf, outer fold of pallial margin; oshgl, opening of shell gland; pc, pallial furrow; shgl, shell gland.

rectum, just behind the posterior part of the columellar muscle. The epithelium of the pallial cavity is about 10 μm thick and consists of elongated, ciliated cells with apical nuclei. The roof of the pallial cavity contains mucous cells overlaying the muscle layer. The pallial edge is smooth and has three folds. The outer and inner folds of the pallial edge (opf, ipf) are poorly developed, but the middle fold (mpf) is well-developed and its epithelium contains scattered, strongly staining, rounded cells.

The single, bipectinate ctenidium (Fig. 1C–D) is small and occupies the posterior half of the pallial cavity. It consists of about 35 pairs of leaflets which lack cartilaginous support. The proximal quarter of the efferent side of the gill axis is fused with the pallial wall, then curves abruptly over toward the anus; the afferent side is fused correspondingly. The ventral leaflets are triangular, free and their ventral corners are drawn out into a short tongue. The dorsal leaflets are smaller, proportionally lower, and their free corners form an obtuse angle. No sensory bursicles have been found. The efferent axis of the leaflets (Fig. 4B) is broader and more densely ciliated than the afferent axis. The efferent axis consists of somewhat elongated, ciliated cells around a blood sinus and contains scattered mucous cells. All the cells at the tip of the efferent axis are narrow; their nuclei are located close together. The afferent axis is thinner and covered by a thinner epithelium with more squarish and less richly ciliated cells around a blood sinus. There are no mucous cells in the abfrontal end.

There are two hypobranchial glands. The left one is well developed while the right one is considerably smaller. The left hypobranchial gland

(Fig. 5A, lhgl) covers the pallial roof to the left of and over most of the rectal sinus. The gland consists of four types of cells: gland cells, mucous cells of the hypobranchial type, sparse ciliated cells, and indistinct cells with strongly staining vesicles. The gland contains three histologically different zones, a left zone with only gland cells, a middle zone with mucous and gland cells, and a right zone with only indistinct cells. The right hypobranchial gland is located on the pallial wall to the right of the rectal sinus and has a histological structure similar to that of the right region of the left hypobranchial gland.

Alimentary system. The alimentary system consists of a buccal mass with a bilobed jaw, a pair of salivary glands and a radula; an oesophagus with a pair of oesophageal pouches; a stomach; digestive glands; an intestine; and a rectum; the latter two both lack accessory organs.

The mouth (Fig. 3A, mo) is subterminally to ventrally located on the snout. The jaw is bilobed and consists of prismatic rods. The subradular pouch is small and lacks a sense organ. The epithelium of the posterior buccal cavity consists of ciliated, agranular, squarish cells. The radula rests on a pair of odontophore cartilages which are interconnected by a ventrally situated horizontal muscle. The radular morphology was described by Warén and Bouchet (1989). The radular sac (rs) is straight, long and runs ventral to the oesophagus. Its posterior end is bifid.

A pair of small salivary glands (sgl) open laterally and posteriorly in the buccal cavity. The glands form invaginations of the dorsal wall of the buccal cavity and are situated immediately behind the cerebral commissure.
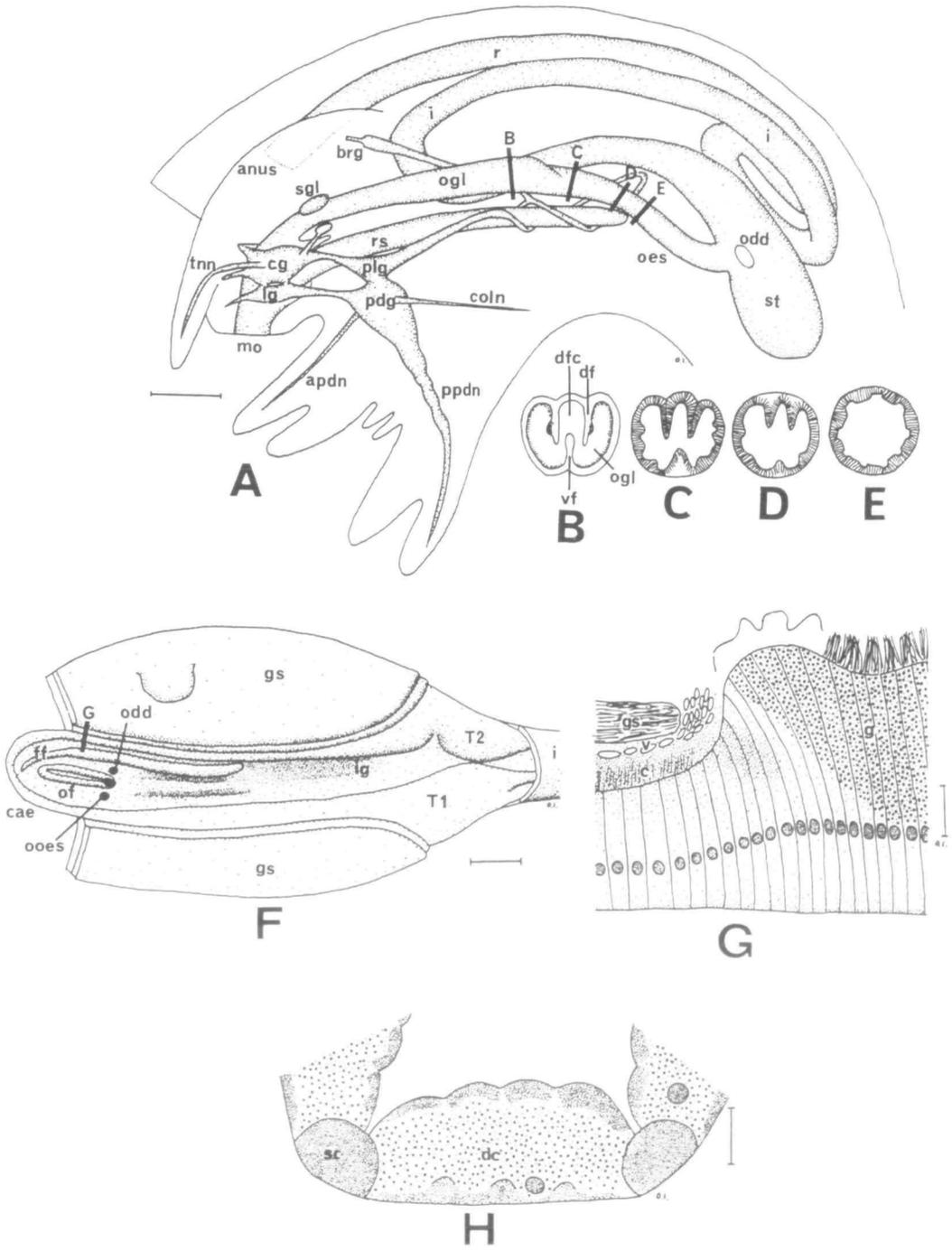
Figure 3. *Pachydermia laevis.* Alimentary system. A. Reconstruction of the alimentary and nervous system. The digestive glands are omitted from the figure but they occupy the outer half of the whorls. The locations of the cross-sections shown in B-E. Cross-sections through mid-oesophagus (B) and posterior oesophagus (C-E). F. Stomach opened up dorsally along the midline, from intestine to caecum. Scale bar = 100 μm. G. Cross-section of the caecal fold towards the gastric shield in stomach (position indicated by G in F). Scale bar = 10 μm. H. Part of cross-sectioned tubule of the digestive diverticulae. Scale bar = 10 μm. Abbreviations: apdn, anterior pedal nerve; brg, branchial ganglion; c, cilia; cae, caecum; cg, cerebral ganglion; coln, columellar muscle nerve; dc, digestive cell; df, dorsal fold; dfc, dorsal food channel; ff, caecal fold; g, granules; gs, gastric shield; i, intestine; ig, intestinal groove; lg, labial ganglion; mo, mouth; odd, left opening of digestive diverticulae; oes, oesophagus; of, fold from oesophagus; ogl, oesophageal gutters; ooes, opening of oesophagus into the stomach; pdg, pedal ganglion; plg, pleural ganglion; ppdn, posterior pedal nerve cord; r, rectum; rs, radular sac; sc, secretory cell; sgl, salivary gland; st, stomach; T1, major typhlosole; T2, minor typhlosole; tnn, tentacular nerve; v, vesicles; vf, ventral fold.

Each gland has a broad opening not developed as a duct. The epithelium of the glands is composed of about 10 μm high, fairly broad, ciliated cells with granular contents. There are no accessory salivary glands.

Between the buccal mass and the stomach three histologically different parts of the oesophagus can be distinguished:

(1) The short anterior oesophagus without appendages. Its epithelium is folded and has a smooth internal surface composed of elongated cells.

(2) The mid-oesophagus, which has two dorsal and one ventral fold (Fig. 3B, df and vf). The former ones demarcate a dorsal food channel (dfc), and all three demarcate two glandular, lateral oesophageal gutters (ogl) (= oesophageal pouches in Haszprunar, 1989). The gutters are lined by two regions: (1) a major glandular portion with the gland cells forming irregular stalked clumps, and (2) a minor ciliated portion. (3) The long posterior oesophagus. The folds of the mid-oesophagus transform gradually into eight longitudinal folds (Figs 3C-E). The epithelium of the posterior oesophagus consists of ciliated cells. No mucous cells are visible.

The oesophagus opens into the large stomach (Figs 3A, st) ventrally and between the openings of the digestive glands (Fig. 3A, odd). The stomach is embedded in the digestive glands and surrounded by the posterior visceral haemo-coel. The stomach, oesophagus and intestine contain detritus, polychaete bristles, sponge spicules, grains of iron sulphide and unicellular algae. The stomach consists of three sections (Fig. 3F): (1) the small posteriorly situated part with a short caecum (cae; considered homologous to the spiral caecum of vetigastropods); (2) the mid-stomach, which is demarcated posteriorly by the openings of the oesophagus and the digestive glands and anteriorly by the conversion of the intestinal groove into a narrow cleft; (3) the anterior part, which corresponds to the style sac region and is gradually transformed into the intestine.

From the opening of the oesophagus two folds emerge (Fig. 3F, of) and continue into the posterior stomach. The folds are surrounded by the major typhlosole (T1) and a caecal fold (ff). The caecal fold ends in the mid-stomach. The major typhlosole splits at the left opening of the digestive gland into an anterior fold that is confined to the style sac region and a posterior one which is restricted to the caecal region. Anterior to the opening of the oesophagus, the major typhlosole and the caecal fold mark the intestinal groove (ig). This is a thin-walled groove surrounded by much broader ciliated areas. The intestinal groove is plicated into two grooves in the mid-stomach. In the anterior stomach (the style sac region) the intestinal groove forms a narrow cleft surrounded by the major and the minor typhlosole (T2). Both the typhlosoles continue into the intestine as narrow folds.

The epithelium of the caecal fold (Fig. 3G) consists of narrow, granulated and ciliated cells with compressed nuclei. These cells are about three times as high as the epithelial cells of the gastric shield area, but they have about the same volume. At the borders of the fold, the cells lack cilia, are less granulated and covered by an irregular, non-staining, translucent layer. The epithelium of the typhlosoles resembles that of the caecal fold, except that it lacks the un-ciliated type of cells. The epithelium of the intestinal groove is about 3 μm thick and ciliated. The major part of the mid-stomach is covered by the gastric shield (Fig. 3F, gs), which protrudes near the middle of the left side as a prominent boss. The cells of the epithelium under the gastric shield have structures that look like cilia (Fig. 3G, c). Between the epithelial cells and the gastric shield, there is a layer with scattered vesicles. The gastric shield is surrounded by a narrow fold.

The two digestive glands occupy the outer half of the whorls of the visceral mass. The

glands are composed of numerous branched tubules of angular cross-section which open through two openings into the stomach; the right opening is larger than the left one. The epithelium of the intestinal groove continues into the openings of the digestive glands. The tubules are surrounded by the visceral haemocoel. The digestive glands contain two types of cells: secretory and digestive cells. The secretory cells (Fig. 3H, sc) are large, rounded, strongly staining, and are situated at the corners of the tubules. The digestive cells (dc) are indistinctly separated from each other so that they form a mass filling the area between the secretary cells. The digestive cells have numerous granules. Their surface towards the lumen is strongly staining, homogenous and agranular; their surface toward the visceral haemocoel has irregular bodies with histological appearance similar to that of the secretory cells.

The intestine (Fig. 3A, i) is coiled, forming two turns, a proximal coil which approaches the cephalopedal haemocoel and a posterior loop at the level of the stomach. There are no intestinal, rectal or anal appendages or glands. Both typhlosoles continue into the intestine where they gradually disappear. The epithelium of the intestine differs from that of the style sac region and consists of non-ciliated cells. The rectum (r) is surrounded by a large blood sinus, and its most distal part is free from the pallial roof. The rectum consists of two histologically different parts. The proximal part of the rectum has a ciliated, undulated, but not folded epithelium. The distal part of the rectum has eight longitudinal folds. The epithelial cells are similar in the two parts but are less uniformly shaped in the posterior rectum due to the internal folding. The anus opens immediately to the left of and in front of the anterior right part of the columellar muscle.

Circulatory system. The circulatory system (Fig. 4A) consists of (1) a vein system with an anterior and a posterior collecting sinus joining into a transverse pallial vein, in turn branching into branchial, pallial and renal veins, (2) a monotocardian heart with a bulbus, and (3) an arterial system with a bifurcated aorta and an open circulation through the cephalopedal and visceral haemocoels.

All internal organs are embedded in haemocoels. The cephalopedal haemocoel surrounds the internal organs of the head and the foot. The visceral haemocoel surrounds the organs of the visceral hump. These two haemocoels are distinctly separated from each other by a thick muscular septum located between the head-foot and the visceral mass.

The aorta (a) emerges from the ventricle and divides, dorsally to the oesophagus, into the anterior and the posterior aorta. The anterior aorta (aa) follows the supraoesophageal ganglion and the pleural-supraoesophageal connective, and supplies the cephalopedal region. The posterior aorta (pa) follows the right visceral nerve and supplies the posterior visceral sinus. Its course could be followed only for a short distance.

The major part of the venous system is composed of blood sinuses and more well defined vessels; these are not true blood vessels since they lack endothelial lining and are formed by thin septa, about 2 μm thick, with scattered nuclei. The blood from the head and foot is collected in an anterior collecting sinus (acs); the blood from the visceral mass is drained by a posterior collecting sinus (pcs); these join and form a common transverse pallial vein (tpv). This vein branches off: (10 three afferent renal veins (arv) to the left nephridium, (2) a thin hypobranchial vessel (hbv) to the vestigial right hypobranchial gland, (3) a rectal sinus (rs), (4) an afferent pallial vein (apv), and (5) a large afferent branchial view (abv).

There are no vessels visible between the left hypobranchial gland and the transverse pallial vein but these organs are situated close to each other. The afferent branchial vein, as described by Warén & Bouchet, (1989), runs in a skin fold hanging down from the pallial roof, originating close to the anus. It joins the afferent side of the ctenidium at the distal part of the fusion of the ctenidium with the pallial wall. The gonoduct is surrounded by a sinus, the gonoduct sinus (gds), that is connected to the visceral haemocoel and the anal sinus. A distinct but very thin septum separates the rectal and the gonoduct sinuses. From the afferent branchial vein several branchial vessels (bv) and pallial veins (pv) emerge. The pallial veins run through the mantle and join the efferent pallial vein (epv); the latter becomes increasingly wider and fuses with the efferent branchial vein (ebv). The internal pallial nerve follows the efferent and afferent pallial veins. The afferent branchial vein passes through the ctenidial membrane and enters the ctenidium, where it branches into the branchial veins. From the ctenidium, the blood runs through the efferent branchial vein (ebv) to the heart. This vein receives several efferent renal veins (erv). The left nephridium (lk) is supplied by three afferent renal veins (arv) and drained by several
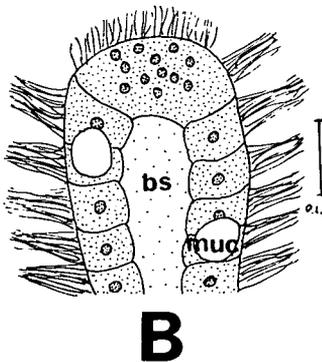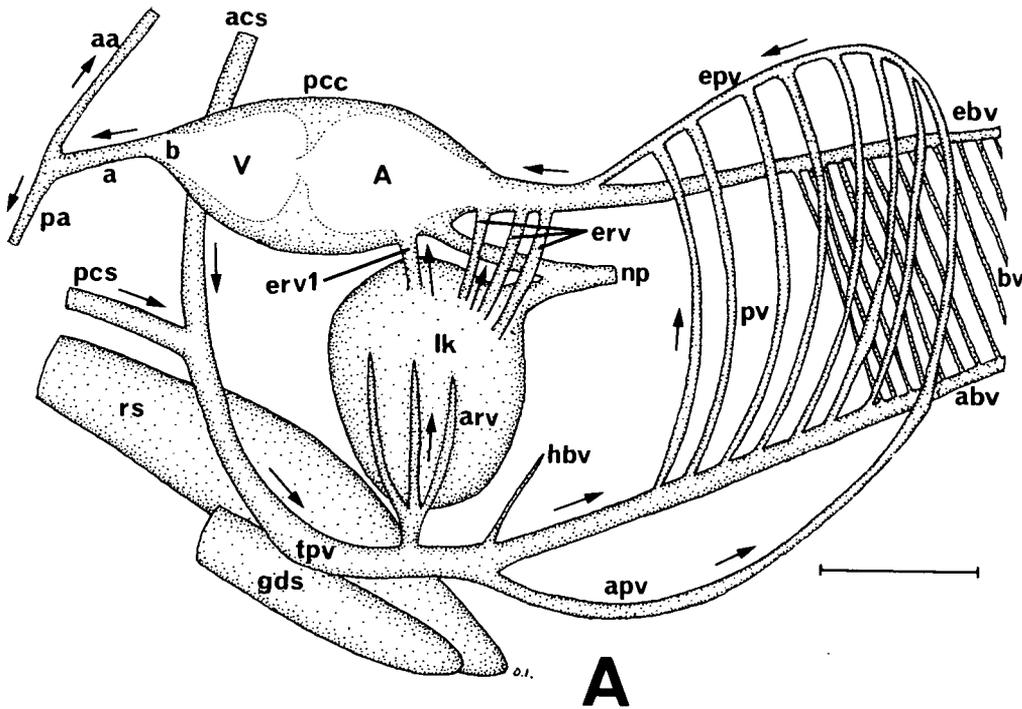
Figure 4. *Pachydermia laevis*. Circulatory and respiratory system. A. Reconstruction of the circulatory system. Scale bar = 200 μm. B. Frontal end of a branchial filament. Scale bar = 10 μm. Abbreviations: a, aorta; A, auricle; aa, anterior aorta; abv, afferent branchial vein; acs, anterior collecting sinus; apv, afferent pallial vein; arv, afferent renal vein, b, bulbus; bs, blood sinus; bv, branchial vessel; ebv, efferent branchial vein; epv, efferent pallial vein; erv, efferent renal vein; erv1, efferent nephridial gland vein; gds, gonoduct sinus; hbv, hypobranchial vessel; lk, left nephridium; muc, mucous cell; np, nephropore; pa, posterior aorta; pcc, pericardial chamber; pcs, posterior collecting sinus; pv, pallial vein; rs, rectal sinus; tpv, transverse pallial vein; V, ventricle.

efferent renal veins (erv). The region corresponding to the nephridial gland is connected directly to the auricle through the efferent nephridial gland vein (erv1).

The heart lies at the left side immediately behind the posterior end of the pallial cavity. The single auricle (A) is larger than the ventricle (V). The ventricle terminates in a bulbus (b) that is surrounded by the same muscular lining as the ventricle. The bulbus opens posteriorly into the aorta. The pericardium (Figs 5A and 6, pcc) is large and its epithelium contains strongly staining, solitary cells in an unicellular layer, especially in the vicinity of the opening of the

renopericardial duct. The pericardium is not wrapped around the rectum.

Excretory system. The excretory system consists of the pericardium, a renopericardial duct, a single (left) nephridium with a large nephridial cavity, and a nephropore. The right nephridium is reduced and incorporated in the gonoducts.

The left nephridium (Figs 5A and 6) consists of a large cavity surrounded by blood sinuses, an excretory area, a ciliated groove and a smooth area. A folded area, drained by a vein directly into the auricle (Fig. 4A, erv1), may be the nephridial gland. A groove runs from the
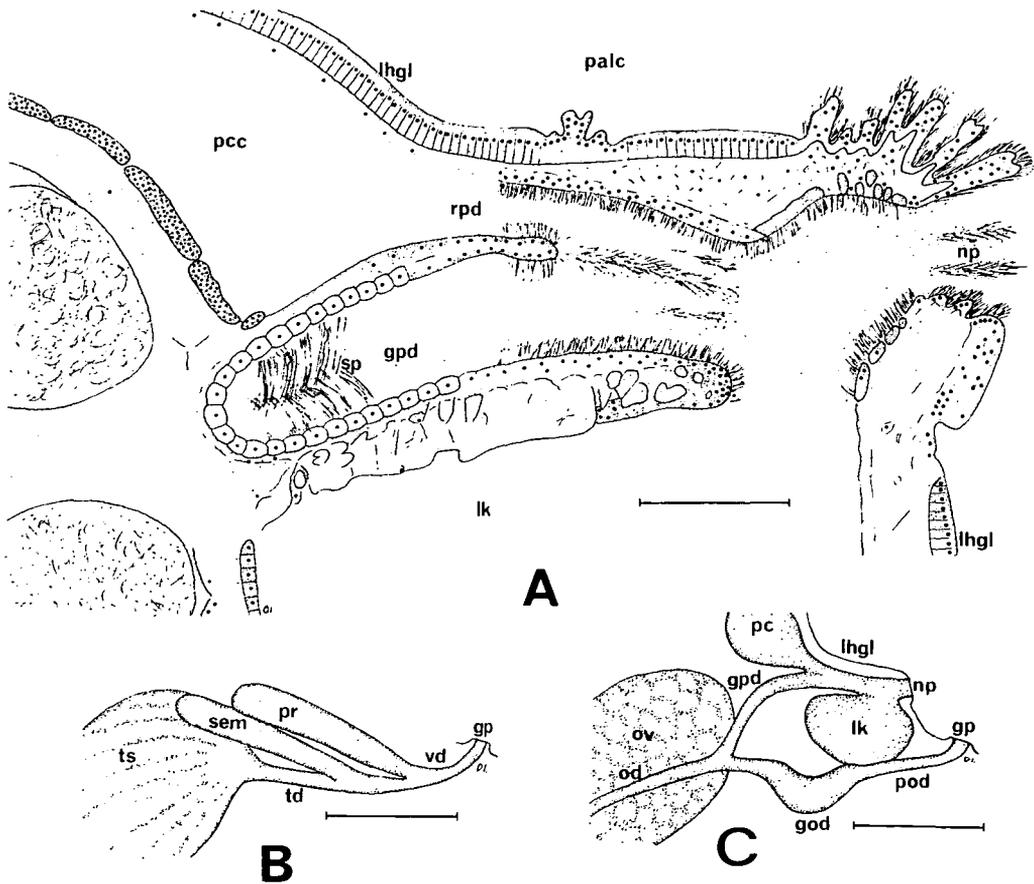
Figure 5. *Pachydermia laevis*. Excretory and reproductive systems. A. Reconstruction of the pericardial ducts, showing the connection between the gonopericardial duct, renopericardial duct, pericardium, nephridium and the nephropore. Figure 6 shows one of the sections that the reconstruction is based on. Scale bar = 100 μm. B. Reconstruction of the male reproductive system. C. Reconstruction of the female reproductive system. Scale bars = 500 μm. Abbreviations: god, glandular oviduct; gp, gonopore; gpd, gonopericardial duct; lhgl, left hypobranchial gland; lk, left kidney; np, nephropore; od, ovarian duct; ov, ovary; palc, pallial cavity; pc, pericardium; pcc, pericardial chamber; pod, pallial oviduct; pr, prostate gland; rpd, renopericardial duct; sem, seminal vesicle; sp, spermatozoa; td, testicular duct; ts, testis; vd, vas deferens.

opening of the renopericardial duct to the nephropore. The epithelium of the groove is ciliated and contains strongly staining cells, similar to the excretory cells in the pericardial wall. The smooth area has a thin, non-ciliated epithelium towards the rectal sinus, the transverse pallial vein and the posterior visceral haemocoel. The cells are agranular, non-ciliated and squarish with a flat surface towards the blood sinus and a concave surface towards the nephridial cavity. The nephridial cavity occupies the main part of the nephridium. It contains vesicles and free, very large cells. The free cells have a single, large vacuole containing a crystal of stored waste material; their

cytoplasm is radially striated. The nephridial cavity opens through the radially folded nephropore into the pallial cavity.

The renopericardial duct (Figs 5A and 6 rpd) connects the left nephridium with the pericardial chamber and opens into the nephridium near the nephropore. Its epithelium is ciliated and consists of indistinctly separated cells. The gonopericardial duct (gpd) (absent in males) opens into the renopericardial duct, not into the pericardial chamber (Fig. 5A and 6). The epithelium of the duct is similar to that of the ovarian duct and consists of large, squarish, uniform cells, clearly different from the epithelium of the renopericardial duct.
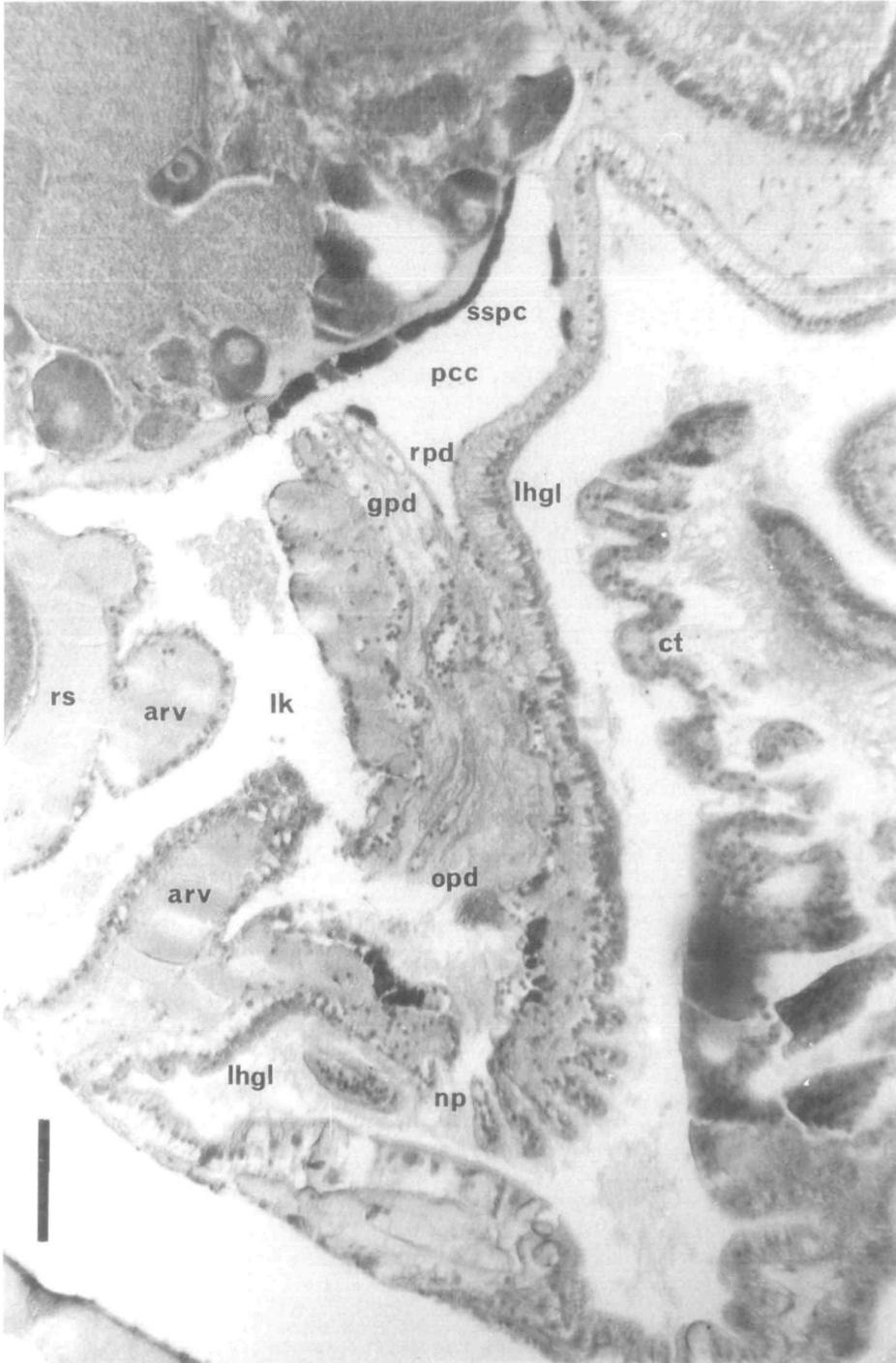
Figure 6. *Pachydermia laevis.* Cross-section through the pericardial ducts. Figure 5A shows a reconstruction. Scale bar = 100 μm. Abbreviations: arv, afferent renal vein; ct, ctenidium; gpd, gonopericardial duct; lhgl, left hypobranchial gland; lk, left nephridium; np, nephropore; pcc, pericardial chamber; rpd, renopericardial duct; rs, rectal sinus; sspc, strongly staining cells of the pericardium.

Reproductive system. Pachydermia laevis is gonochoristic and has internal fertilization, as indicated by the presence of spermatozoa in the female ducts in all females.

The female reproductive system (Fig. 5C) consists of an ovary, an ovarian duct which sends off a gonopericardial duct, a glandular oviduct, and a short pallial oviduct between the glandular oviduct and the gonopore. There is no bursa copulatrix or receptaculum seminis. The large ovary (ov) occupies the ventral half of the apical whorls. The ovarian duct (od) starts posteriorly in the ovary and runs along the columellar side of the ovary, before leaving it. The ovarian duct is thin with a very narrow lumen covered by an epithelium of large cells. The gonopericardial duct branches off, shortly before the ovarian duct enters the glandular oviduct. The glandular oviduct (god) forms a distinct bend, and consists of two histologically different parts: (1) a proximal thick-walled part with elongated, ciliated secretory cells, and (2) a distal thin-walled part with ciliated cells and secretory cells. The pallial oviduct (pod) runs parallel to the rectum in a separate sinus and opens through the gonopore (gp) on a papilla to the right of the rectum, just behind the posterior part of the columellar muscle in the pallial cavity. The epithelium of the pallial oviduct consists of narrow, tall cells. Sperm are attached in bundles centrally on the surface of epithelial cells in the gonopericardial duct and the oviduct (Fig. 5A, sp), except the glandular part.

All stages of the oogenesis are present simultaneously in the ovary. The smallest oogonia are ovate and the cytoplasm and nucleolus stain uniformly and weakly; the chromatin is condensed. Later, the oogonia become rounded. They increase in size (from a diameter of 10 to 20 μm), as do the nucleus (diameter increases from 5 to 15 μm) and nucleolus (diameter from 2 to 10 μm). Scattered yolk granules appear in the yearly vitellogenous oocytes, at the vegetative pole and in the centre of the cytoplasm. The nucleolus has small granules along its margin. During vitellogenesis, the yolk granules increase in number; the animal pole is still clear. Finally, the granules fill three quarters of the cytoplasm. The granules of the nucleolus grow in size and become fewer. The cytoplasm (at a cell diameter of 30 to 50 μm) continues to grow in size, but the sizes of the nucleus (≈20μm) and nucleolus ≈10–15 μm) increase only slightly. During late vitellogenesis, yolk granules appear at the animal pole and finally fill the whole cytoplasm. During the later stages, in contrast to the earlier ones, the cytoplasm (diameter 50 to 100 μm), nucleus (diameter 20 to 30 μm), as well as nucleolus (from 15 to 20 μm) all grow in size. The large postvitellogenous oocytes have an irregularly rounded nucleus with an indistinct membrane. In the mature egg, the diameter of the cytoplasm is ≈130 μm, that of the nucleus ≈40 μm, and that of the nucleolus ≈25 μm.

The male reproductive system (Fig. 5B) consists of a testis, a testicular duct leading to the seminal vesicle and the prostate gland, and finally a vas deferens leading to the gonopore. There is no penis or seminal groove at the gonopore. The testis (ts) is large, lobed and occupies the inner half of the whorls. The lobes consist of small rounded cells and a lumen filled with sperm. Only euspermatozoa were found. The testicular duct (td) connects the testis with the seminal vesicle (sem). Both the seminal vesicle and testicular duct are separated from the posterior visceral haemocoel by a thin layer of connective tissue. The seminal vesicle and the testicular duct contain masses of sperm. The testicular duct continues to the opening of the prostate gland. The prostate gland (pr) is an elongated bladder with a thick epithelium of columnar, apically granulated gland cells. The vas deferens (vd) connects the testicular duct and the prostate with the gonopore. Its epithelium is similar to that in the prostate gland. The gonopore (gp) of the male is similar to the female one. Spermatophores have not been found in *Pachydermia*, only in *Melanodrymia* sp. (Warén, pers. comm.).

Nervous system. The large cerebral ganglia (Figs 3A and 7A, cg) rest on the wall of the buccal mass well behind the cephalic tentacles, more posteriorly than usual among archaeogastropods. Anteriorly the cerebral ganglia are interconnected by a distinct cerebral commissure. Each cerebral ganglion is ventrally connected to the much smaller labial ganglion through the two cerebral-labial connectives (Fig. 7A, pclc and aclc). I believe the anterior (aclc) one to be homologous with the labial-buccal connective in other gastropods, since it follows the cerebral ganglion and exits posteriorly as the cerebral-buccal connective. The posterior cerebral-labial connective (pclc) corresponds to the cerebral-labial connective in other gastropods. The following nerves, commissures and connectives emerge from the cerebral and labial ganglia: (1) two snout nerves (snn), (2) a tentacular nerve (Figs 3A and 7A, tnn), (3) the cerebral commissure (Fig.

7A, cc), (4) the cerebral-pleural connective (cplc), (5) the cerebral-buccal connective (cbc), and (6) the labial-pedal connective (lpdc). The cerebral-pleural connective is straight. The cerebral-buccal connective is thinner than the cerebral-pleural connective but still well-developed. The labial-pedal connective is as long as the cerebral-pleural connective. There are no visible nerves from the connectives. The small buccal ganglia (bg) are interconnected bia a short buccal commissure (bc) and they are connected with the labial ganglia through the cerebral-buccal connective. There are no visible buccal nerves.

The pleural ganglion (Figs 3A and 7A, plg) is connected with the cerebral ganglion via the cerebral-pleural connective (Fig. 7A, cpls). The pleural-pedal connective is so short that the ganglia are abutting. The suboesophageal and the supraoesophageal ganglia (sbg and spg) emerge from the pleural ganglia. There are no visible nerves from the pleural ganglion and its connectives. The suboesophageal ganglion (sbg) lies to the left of the radular sac and is not separated from the left pleural ganglion. The median pallial nerve (mpn) and left visceral nerve (lvn) emerge from the suboesophageal ganglion. The supraoesophageal ganglion (spg) is connected with the right pleural ganglion via a connective that runs dorsally along the right side of the radula sac continuing at the right side of the oesophagus together with the anterior aorta. It is wider and longer than the suboesophageal ganglion. From the supra-oesophageal ganglion emerges (1) a connective to the osphradial ganglion (osg) and (2) a right visceral nerve (rvn). The right visceral nerve follows the posterior aorta backwards. There is also a very thin nerve that possibly interconnects the suboesophageal ganglion with the supraoesophageal ganglion, but it was too poorly developed for any certain conclusions. The visceral ganglia are small and connected via the visceral commissure (vc). The right visceral ganglion (rvg) is situated behind the pallial cavity.

The osphradial ganglion (osg) is located close to the osphradium at the base of the ctenidium. It has two connectives, dorsally to the equally sized branchial ganglion (brg) and ventrally to the larger supraoesophageal ganglion (spg). The branchial ganglion is located close to the osphradial ganglion, separated only by a short connective. From the branchial ganglion emerges the branchial nerve (brn). The mantle is innervated by: (1) an internal pallial nerve (ipn), which emerges frm branchial ganglion

and innervates the posterior left side of mantle (anteriorly it is connected by a transverse connective to the median pallial nerve); (2) a median pallial nerve (mpn), which is connected to the suboesophageal ganglion, and innervates the anterior part of the inside of the mantle. (Anteriorly at both side of the mantle it is connected to the external pallial nerve by a transverse connective, one at each side); (3) an external pallial nerve (epn), which innervates the pallial margin.

The large pedal ganglia (Figs 3A and 7A, pdg) are located below the pleural ganglia. They are connected with the labial and pleural ganglia, and to each other via a short pedal commissure (Fig. 7A, pdc). The pedal ganglia send out: (1) an anterior pedal nerve (Figs 3A and 7A, apdn), which innervates the anterior pedal gland and the propodium; (2) a posterior pedal nerve cord (ppdn), which is confluent with the pedal ganglion, and consists of five swellings, each with one outwardly and one inwardly directed nerve (the latter are probably interconnections or at least directed as interconnectives but only the most posterior one could be verified); this nerve cord innervates the median and posterior part of the foot; (3) a shell muscle nerve (coln), which emerges near the starting point of the pleural-pedal connectives; (4) a thin nerve (Fig. 7A, n) whose end point could not be determined.

Sense organs. Eyes, optic nerves, subradular organ, ctenidial bursicles, and sensory papillae are absent. The osphradium (Fig. 7B, os) consists of some inconspicuous ridges ventrally and dorsally on the efferent ctenidial base. It contains a strongly staining layer of sensory cells overlaying the osphradial ganglion (7A and 7B, osg); the osphradium is innervated by several nerves from the ganglion. The two statocysts (Fig. 7A, stc) are partly embedded in the pedfal ganglia and are about 70–90 μm in diameter. Each statocyst has a single statolith that is cellularly embedded. The statocysts are lined with a unicellular layer of ciliated, flattened sensory cells. The innervation of the statocysts could not be found.

Melanodrymia aurantiaca

The anatomy of *Melanodrymia aurantiaca* was described in detail by Haszprunar (1989). My examination confirmed his detailed description with a single discrepancy; I found a jaw to be present. Another difference is that no septa could be detected in the visceral haemocoel.
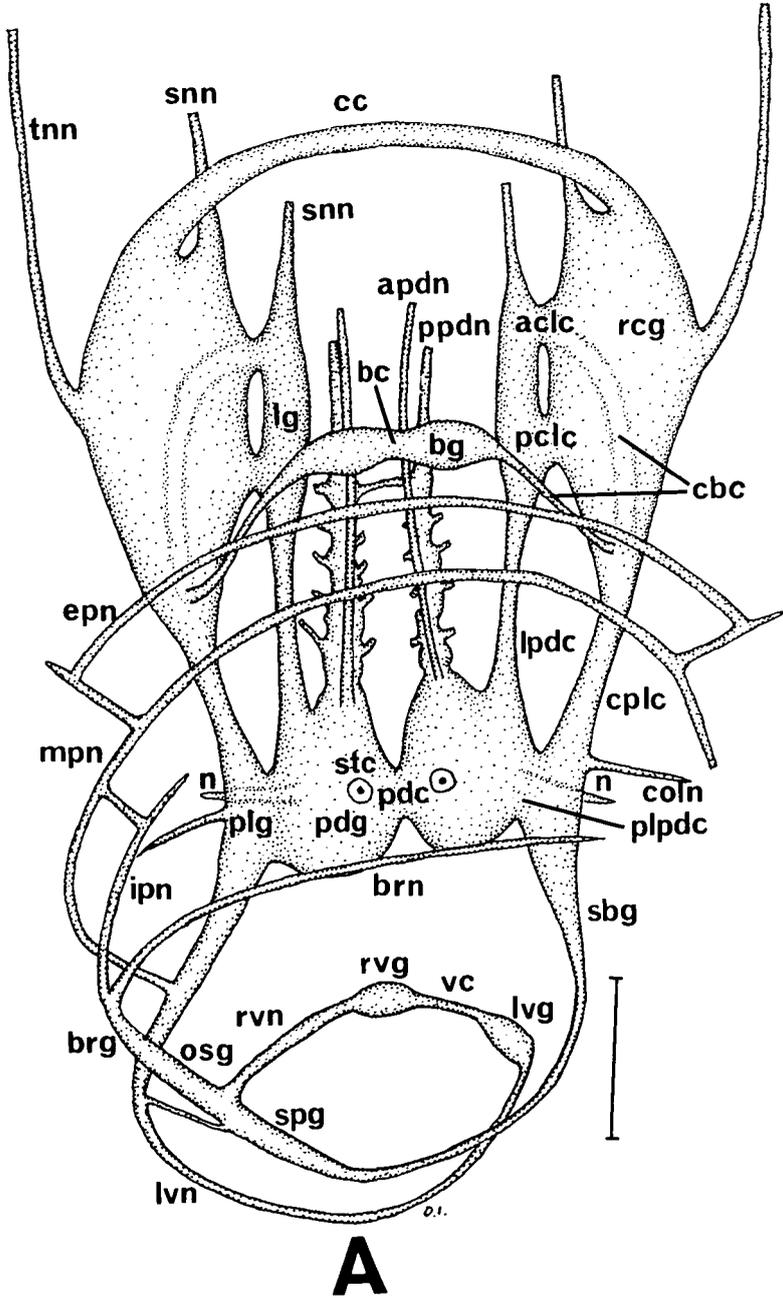
A

This may be due to the small size of the animals.

DISCUSSION

The discussion will be restricted to a brief comparison with *Melanodrymia aurantiaca* and some notes about other neomphalines. A more exhaustive evaluation of the relationships will have to wait until more comparative information is available, a work now in progress (Israelsson in prep.)

McLean (1989) described the family Peltospiridae and classified it in a monotypic superfamily, Peltospiroidea, related to *Neomphalus*
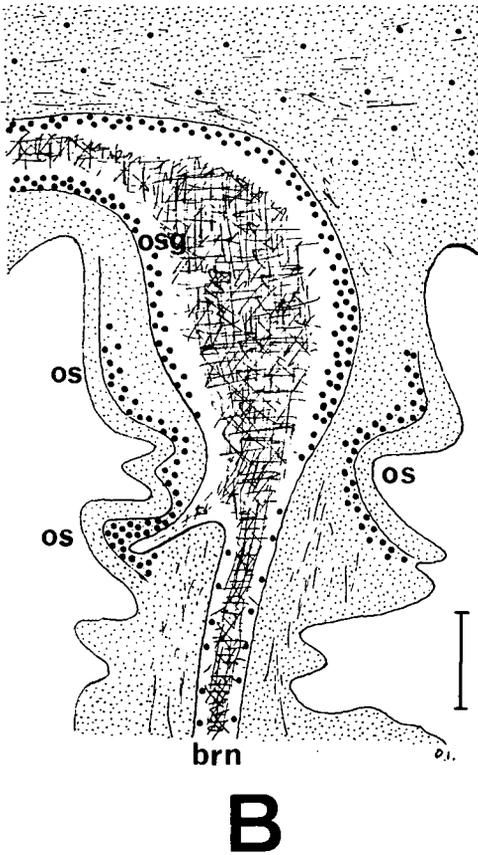
Figure 7. *Pachydermia laevis.* Nervous system and sense organs. A. Reconstruction of the nervous system in contracted state. For a lateral view, see Fig. 3A. Scale bar = 200 μm. B. Cross-section through basal part of ctenidium with osphradium. Scale bar = 20 μm. Abbreviation: aclc, anterior cerebral-labial connective; apdn, anterior pedal nerve; bc, buccal commissure; bg, buccal canglion; brg, branchial ganglion; brn, branchial nerve; cbc, cerebral-buccal connective; cc, cerebral commissure; coln, columellar muscle nerve; cplc, cerebral-pleural connective; epn, external pallial nerve; ipn, internal pallial nerve; lg, labial ganglion; lpdc, labial-pedal connective; lvg, left visceral ganglion; lvn, left visceral nerve; mpn, median pallial nerve; n, nerve from pedal ganglion; os, osphradium; osg, osphradial ganglion; pclc, posterior cerebral-labial connective; pdc, pedal commissure; pdg, pedal ganglion; plg, pleural ganglion; plpdc, pleural-pedal connective; ppdn, posterior pedal nerve cord; rcg, right cerebral ganglion; rvg, right visceral ganglion; rvn, right visceral nerve; sbg, suboesophageal ganglion; snn, snout nerve; spg, supraoesophageal ganglion; stc, statocyst; tnn, tentacular nerve; vc, visceral connective.

but without placing it into a higher classification. Warén & Bouchet (1989, 1993) classified an array of small coiled gastropods (among them *Pachydermia*) in this family but admitted that this was a provisional arrangement and that the group, as used by them, probably was polyphyletic. Their reason for this arrangement was lack of information; there was a confusing distribution of characters including the fine net sculpture on the protoconch, radulae and soft part morphology. This overlap of characters also involved the Neomphalidae (Warén & Bouchet, 1989, 1993; Warén, pers. comm.).

Melanodrymia aurantiaca was classified as 'Trochacea?' (Hickman, 1984), based on the rhipidoglossate radula. Warén & Bouchet (1989, 1993) provisionally placed *Melanodrymia* in the Peltospiridae. Haszprunar (1991) described the anatomy of *Melanodrymia aurantiaca* in detail and found it difficult to classify *Melanodrymia* due to the lack of synapomorphies.

McLean (1990) introduced an additional family in the Neomphaloidea for the genus *Cyathermia* (classified by Warén & Bouchet (1989) in the Neomphalidae), basing his decision on differences in the radula and the male copulatory organ.

Salvini-Plawen & Steiner (1995) discussed the classification of the Neomphalina, concluding that the group is polyphyletic, and recognized a new family for *Melandrymia aurantiaca*. Their decision was based only on a reinterpretation of already published information and they emphasized the absence of skeletal rods in the gill filaments of *Melanodrymia*. This absence of a single character made them consider *Melanodrymia* and *Neomphalus* to be independently derived from an original dibranchiate condition.

My examination of *Pachydermia laevis* and *Melanodrymia aurantiaca* shows (as concluded by McLean, 1990) that the suggestions by Sitnikova & Starobogatov (1989) about relations between Neomphalina and Architaenioglossa are poorly founded. Instead all available information clearly supports a position among the Archaeogastropoda *sensu* Haszprunar (1993): streptoneurous, hypoathroid nervous system; pedal cords connected by several commissures; eyes without a cornea; pouch-like salivary glands; longitudinal glandular gutters in the mid-oesophagus; rhipidoglossate radula with bifid radular sac; bipectinate ctenidium; a ventricle with a bulbus; and epipodial tentacles [not metapodial tentacles, which occur among caenogastropods].

Some details in the morphology are unusual for Vetigastropoda, for example: (1) lack of nacre; (2) strongly developed periostracum; (3) lack of sensory papillae; and (4) internal fertilization. These characters are shared not only with other neomphalines, but with almost all obviously unrelated vent vetigastropods and I therefore consider them environmental adaptations, as did Warén & Bouchet (1989, 1993) with the three first mentioned characters.

The examination of the anatomy of *Pachydermia* and *Melanodrymia* supports Warén & Bouchet (1989) classification of the two genera in the same family. The anatomy is very similar and the following characters are considered of importance to emphasise this: (1) cerebral-buccal connective fused to cerebral ganglion (not known from other gastropods); (2) transversal pallial vein running in a skin fold; (3) radular details, for example similar shape and number of the teeth in the central and lateral fields and the same demarcation of the lateral from the marginal field by a broad, very oblique tooth (Warén pers. comm.); (4) protoconch sculpture (shared with Neomphalidae and *Leptogyra*, see Warén & Bouchet, 1989, figs 82, 84 and 85; 1993, fig. 32A).

There are, however, certain differences between the two genera that give support for maintaining them as two distinct taxa: (1) thick, ornamented shell with thin periostracum in *Melanodrymia*, thin and simple shell with thick periostracum in *Pachydermia*, (2) sensory bursicles present in gill of *Melanodrymia*, missing in *Pachydermia*; (3) epipodial tentacles well developed in *Melanodrymia*, small in *Pachydermia*, (4) right hypobranchial gland present (although reduced) in *Pachydermia*, absent in *Melanodrymia*; (5) intestine with one additional coil in *Pachydermia*; (6) copulatory organ (modified cephalic tentacle) and receptaculum seminis present in *Melanodrymia*, absent in *Pachydermia*; (7) gonopericardial duct of *Pachydermia* opens into renopericardial duct (not known from any other gastropod).

Any more detailed evaluation of these characters will need information about further neomphaline taxa and access to related species from non-vent environments.

The results failed to support a classification together with *Peltospira* as suggested by Warén & Bouchet (1989, 1993). The examination did not reveal a single apomorphy shared with this genus, which seems to be well characterized by a distorted protoconch equipped with strong spiral ridges, a male reproductive system with a large prostate gland, and a smoothly tapering

snout. These synapomorphies draw the attention to the two coiled genera *Lirapex* and *Depressigyra* (classified in Peltospiridae by Warén & Bouchet (1989) which have a protoconch similar to *Peltospira* and a comparable radular and epipodial arrangement but due to lack of anatomical information I refrain from further speculation.

The relations to the Neomphalidae and Cyathermiidae are presently difficult to discuss in any detail. Only a single species of Neomphalidae has been described anatomically and no information is available abvout the anatomy of *Cyathermia*. Some features, however, suggest relations (Beck, 1992; Fretter *et al.*, 1981; Warén & Bouchet, 1989): (1) net-like protoconch sculpture; (2) the left tentacle of the male is modified into a copulatory organ in both *Melanodrymia*, the cyathermiids and the neomphalids. This will be elaborated in a paper in preparation, dealing with the anatomy of *Cyathermia* (Israelsson, in prep.).

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REFERENCES

BECK, L.A. 1991. *Symmetromphalus hageni* sp. n., a new neomphalid gastropod (Prosobranchia: Neomphalidae) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). *Annalen des Naturhistorischen Museums in Wien*, **93B**: 243-257.

FRETTER, V. 1989. The anatomy of some new archaeiogastropod limpets (Superfamily Peltospiracea) from hydrothermal vents. *Journal of Zoology, London*, **218**: 123-169.

FRETTER, V. & GRAHAM, A. 1994. *British prosobranch molluscs*. Ray Society, London.

FRETTER, V. & GRAHAM, A. & McLEAN, J.H. 1981. The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae*. *Malacologica*, **21**: 337-361.

HASZPRUNAR, G. 1989. The anatomy of *Melanodrymia aurantiaca* Hickman, a coiled Archaeogastropod from the East Pacific hydrothermal vents (Mollusca, Gastropoda). *Acta Zoologica*, **70**: 175-186.

HASZPRUNAR, G. 1993. The Archaeogastropoda. A clade, a grade or what else? *American Malacological Bulletin*, **10**: 165-177.

HASZPRUNAR, G. 1996. The Mollusca: Coelomate turbellarians or mesenchymate annelids? In *Origin and evolutionary radiation of the Mollusca* (J. Taylor, ed.), 1-28. Oxford University Press.

HICKMAN, C.S. 1986. A new archaeogastropod (Rhipidoglossa, Trochacea) from hydrothermal vents on the East Pacific Rise. *Zoologica Scripta*, **13**: 19-25.

MCLEAN, J.H. 1981. The Galapagos Rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacologia* **21**: 291-336.

MCLEAN, J.H. 1989. New Archaeogastropoda limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. *Zoologica Scripta*, **18**: 49-66.

MCLEAN, J.H. 1990. A new genus and species of neomphalid limpet from the Mariana vents with a review of current understanding of relationships among Neomphalacea and Peltospiracea. *Nautilus*, **104**: 77-86.

OKUTANI, T., FUJIKURA, K. & SASAKI, T. 1993. New taxa and new distribution records of deepsea gastropods collected from or near the chemosynthetic communities in the Japanese waters. *Bulletin of the National Museum (Tokyo), Ser. A.*, **19**: 123-143.

PONDER, W.F. & LINDBERG, D.H. 1996 Gastropod phylogeny – Challenges for the 90s. In: *Origin and evolutionary radiation of the Mollusca* (J. Taylor, ed.), 135-154. Oxford University Press.

PONDER, W.F. & LINDBERG, D.H. 1997. Towards a phylogeny of gastropod molluscs – a preliminary analysis using morphological characters. *Zoological Journal of the Linnean Society of London*, **119**: 83-265.

SALVINI-PLAWEN, L.V. & STEINER, G. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. In *Origin and evolutionary radiation of the Mollusca* (J. Taylor, ed.), 29-51. Oxford University Press.

SITNIKOVA, T.Y. & STAROBOGATOV, Y.I. 1983. On the taxonomic position of the genus *Neomphalus* McLean, 1981. In: *Abstracts of communications, seventh meeting on the investigation of molluscs*. (I.M. Likharev, ed.), 23-26. U.S.S.R. Academy of Sciences, Zoological Institute.

THIELE, J. 1925. Gastropoda. In: *Handbuch der Zoologie* (Kükenthal, W., ed.), Vol. 5, 38-155. De Gryter, Berlin.

WARÉN, A. & BOUCHET, P. 1989. New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta*, **18**: 67-102.

WARÉN, A. & BOUCHET, P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta*, **22**: 1-90.