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Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropoda

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Midgut morphology of gastropod molluscs has been underutilized as a resource of characters for phylogenetic analysis. The exclusion of these features reflects the inference that they will be uninformative in determining phylogenetic relationships because they are functionally correlated. In general, it has been hypothesized that the style sac form of midgut is an adaptation to microphagy and becomes secondarily simplified in taxa that have adopted a macrophagous/carnivorous habit with a corresponding increase in extracellular digestion (i.e. radular trituration, gizzards and/or foregut glands). This assumption has resulted in the formulation of adaptive scenarios concerning gastropod alimentary systems, which are mapped onto phylogenetic hypotheses derived from other characters. However, any conclusions regarding phylogenetic utility, and therefore homology, must be realized within a cladistic context. For this analysis, a multi-organ system anatomical data set was assembled for 16 caenogastropods and two outgroups. The data matrix comprises 64 characters and includes many systems poorly represented in previous broad-based comparative surveys, such as the alimentary and reno-pericardial systems. In addition, several taxa were included for which no comprehensive anatomical studies have been available (Cyclophoroidea, Ptenoglossa). Phylogenetic analysis with NONA 1.6 resulted in two most-parsimonious trees with length 188, CI = 0.53 and RI = 0.63, differing only in the placement of *Prunum apicinum* and *Conus jaspideus*. The topology of the strict consensus (*Macleaniella Theodoxus*((*Neocyclotus Marisa*)((*Lampanella*((*Petaloconchus Strombus*)(*Crepidula Bithyia*)))(*Littorina*(*Neverita*(*Cypraea*(*Nitidiscala*(*Panarona*(*Prunum Conus*(*Ilyanassa Urosalpinx*)))))))))), is largely congruent with several independent estimates based on both morphological and molecular data, supporting caenogastropod monophyly and monphyly of the Architaenioglossa, Sorbeoconcha and Neogastropoda. To evaluate phylogenetic utility of the midgut, a broad sampling of taxa was included representing a diversity of feeding modes, food preferences and alimentary morphologies. Character optimization revealed that the evolution of midgut structure is highly mosaic, cutting broadly across patterns of feeding, diet and foregut complexity, to a degree previously unappreciated. In addition, features from the foregut (subradular organ, oesophageal folding) and midgut (position of gastric shield) are broadly distributed among large clades of caenogastropods, providing critical basal synapomorphies within the group. This demonstrates that the gut is an unexploited resource for important and informative characters in higher order systematics of caenogastropods. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **137**, 447–554.

ADDITIONAL KEYWORDS: anatomy – cladistics – feeding – foregut – gastropods – homology – kidney – midgut – nerves – reproduction.

INTRODUCTION

The Caenogastropoda is an extremely large and diverse superorder presently including over 120 families of marine, freshwater and terrestrial gastropods (Ponder & Warén, 1988). Encompassing the traditional ‘mesogastropod’ and neogastropod ‘prosobranchs’, the Caenogastropoda as originally constituted was thought to be a polyphyletic assemblage of unrelated taxa (Cox, 1960; Graham, 1985). Although composition of the group has undergone considerable refinement over the past 30 years (Bieler, 1992), recent cladistic analyses generally support its

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monophyly and are beginning to converge on a broad outline of its evolutionary history (Haszprunar, 1985c, 1988a,b; Tillier *et al*., 1992; Rosenberg *et al*., 1994; Winnepenninckx, Backeljau & deWachter, 1996; Harasewych *et al*., 1997a,b; Ponder & Lindberg, 1996; 1997; Rosenberg *et al*., 1997; Harasewych *et al*., 1998; Winnepenninckx *et al*., 1998; Colgan, Ponder & Eggler, 2000).

The restructuring of gastropod classification marks a significant departure from the scheme devised earlier this century by Thiele (1929), that remained largely unchanged for over half a century. This revolution in the higher order systematics of gastropod molluscs was facilitated, in part, by new suites of ultrastructural and molecular characters (Haszprunar, 1985a,b; Healy, 1988, 1996; Tillier *et al*., 1992). But equally important has been the reformulation and refinement of classical molluscan anatomical homologies (Ponder & Lindberg, 1996, 1997). However, one aspect of gastropod biology that remains underutilized in this context is the gastropod midgut (Ponder & Lindberg, 1996, 1997).

Structurally and functionally, the midgut is one of the most complex regions of the gastropod digestive tract and is generally divisible into two chambers; the proximal or gastric chamber (Fig. 1, gc) and the distal chamber, or style sac (Fig. 1, ss). The gastric chamber bears the openings of the oesophagus (Figs 1, e) and the digestive gland ducts (Fig. 1, dgd), and its walls have numerous ciliated folds that direct the flow of gut contents. In addition, a portion of the gastric epithelium commonly possesses a chitinous cuticle that is developed into a prominent tooth, or gastric shield (Fig. 1, gs). A part of the gastric chamber also may be elaborated into a sorting area (Fig. 1, sa) composed of parallel ciliated ridges and grooves (Morton, 1952b, 1953; Fretter & Graham, 1962; Owen, 1966).

The more distally located style sac region (Fig. 1, ss) is a narrow chamber lying between the gastric chamber and the pyloric region of the intestine (Graham, 1949). This region is characterized by the presence of two prominent folds, or typhlosoles: the major typhlosole (Fig. 1, t1) and the minor typhlosole (Fig. 1, t2). These folds bound the intestinal groove (Fig. 1, ig), forming the main rejection tract of the midgut, and the style sac, sometimes containing a proteinaceous rod, or crystalline style (Graham, 1985).

With the advent of cladistic methodology to reconstruct phylogeny, claims of large amounts of homoplastic or parallel evolution among gastropods have led to a priori assumptions regarding the phylogenetic utility of specific features, inevitably resulting in the exclusion of presumably homoplastic characters from evolutionary studies (e.g. Gosliner & Ghiselin, 1984; Haszprunar, 1998b). However, any conclusions regarding phylogenetic utility, and consequently homology, ultimately must result from cladistic analysis. In the absence of such a test, features of gastropod anatomy have been assayed inconsistently as to their systematic importance. For example, due to a presumed mutual interdependence between feeding mode, diet and structure (Salvini-Plawen, 1981), midgut characters have been regarded as useful in defining groups (Haszprunar, 1988a) but otherwise of little value in higher order systematics of gastropods (Graham, 1949, 1955; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988a; Salvini-Plawen, 1988). In particular, the style sac form of midgut has been viewed as the plesiomorphic gastropod 'bauplan' asso-

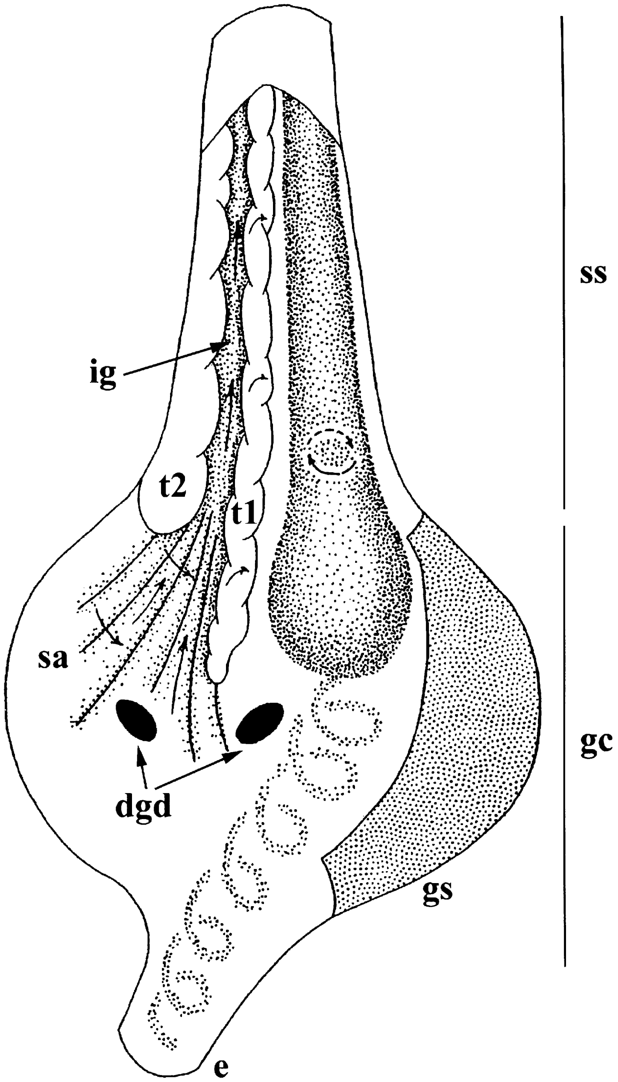

Figure 1. Midgut morphology of 'typical prosobranch'; adapted from Smith (1967). Abbreviations: dgd, digestive gland duct; e, oesophagus; gc, gastric chamber; gs, gastric shield; ig, intestinal groove; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

ciated with microphagy (Morton, 1952b, 1953; Salvini-Plawen, 1981, 1988), with simplifications of this configuration mirroring macrophagy and/or carnivory and an accompanying emphasis on extracellular digestion (Graham, 1939, 1949, 1955; Morton, 1953; Salvini-Plawen, 1988). Although some correlation between structure and function is apparent, it remains untested whether this interdependency is so advanced as to render alimentary characters obsolete for the purposes of reconstructing historical patterns.

Thus, similar to other organ systems, the midgut has remained underutilized as a source of phylogenetic information within the Gastropoda at all taxonomic levels. At lower taxonomic levels, this information has not been integrated into morphologic cladistic analyses (e.g. Houbrick, 1988), despite the existence of a comparatively rich descriptive literature of midgut anatomy for several groups (e.g. Cerithioidea). Phylogenetic studies at higher taxonomic levels have fared little better. Most commonly, midgut anatomy has been simply mapped onto branching schemes devised from other characters (Salvini-Plawen, 1988) or only a few midgut characters are included in the analysis (e.g. three characters, Ponder & Lindberg, 1997; two characters, Sasaki, 1998).

The paucity of cladistic analyses at lower taxonomic levels that incorporate midgut data is particularly surprising. At these levels, midgut morphology is relatively conservative, facilitating comparisons, and thus putative homology statements between taxa (Graham, 1949, 1985; Haszprunar, 1988a; pers. obs.). At higher taxonomic levels, patterns of simplification and loss render comparisons difficult (Ponder & Lindberg, 1997). In addition, much of the available information concerning midgut morphology comprises scattered descriptions by numerous authors who commonly do not provide adequately detailed descriptions and/or do not follow consistent methodological procedures to facilitate comparisons (e.g. ventral and dorsal incisions; Graham, 1939, 1949). Moreover, existing comparative studies are rather limited in scope (e.g. four caenogastropod families, Graham, 1949; four neogastropod families, Smith, 1967; five neogastropod families, Medinskaya, 1993), further complicating efforts to place this information into a consistent framework. Consequently, available descriptions suggest a significant, untapped resource of characters suitable for phylogenetic analysis, but generally preclude rigorous homology statements across the Gastropoda. Thus, detailed, broad-based comparative surveys are required (Ponder & Lindberg, 1996) to synthesize midgut morphology into a coherent framework, with explicit and consistent hypotheses of homology.

Although a thorough reanalysis of phylogenetic relationships within the Caenogastropoda is beyond the scope of this single analysis, the goal of this study is to evaluate the putative homology and phylogenetic utility of the complex and diverse modifications of caenogastropod midguts. This study synthesizes classic descriptions of midgut morphology with new data into characters that are combined with morphological information from many organ systems. The resulting cladistic analysis is used to evaluate hypotheses of homology and several long-standing controversies concerning the phylogenetic utility of the caenogastropod digestive tract.

MATERIAL AND METHODS

Anatomical reconstructions combine standard dissection supplemented with serial histological sections. Living and preserved material was dissected using a Zeiss binocular microscope with *camera lucida*. Animals to be sectioned were maintained in aquaria for ≥24 h, allowing the contents of the midgut and hindgut to clear. Tissues were preserved in alcoholic Bouin's or 10% salt-water formalin for 24 h, transferred to 70% ethanol, dehydrated to 100% ethanol, and embedded in paraplast. Serial sections were cut at 6–8 μm, mounted, and stained with haematoxylin and eosin phloxine (Humason, 1967). A minimum of two males and two females per species were sectioned for gonochoristic and sequential hermaphroditic species, one in cross section and one in sagittal section. Two specimens of the simultaneous hermaphrodite *Macleaniella moskalevi* were sectioned, one in cross section and one in sagittal section. Institution acronyms are as follows: BMSM – Bailey-Matthews Shell Museum, Sanibel, Florida; USNM – Smithsonian Insitution, National Museum of Natural History, Washington DC.

Midguts were opened by a dorsal longitudinal incision and examined shortly after collection to establish the presence or absence of a crystalline style/protostyle; carmine particles were used to observe the direction of ciliary currents. The midgut and surrounding viscera were then excised and the midgut pinned open, using the surrounding tissue for support and to hold the pins; the epithelium was cleared of mucus and debris using a pipet and small brush. The water was replaced with a fixative of 5% glutaraldehyde in 0.1 M cacodylate buffer; pH was adjusted to 7.4 with 0.2 M HCl and milli-osmolarity for marine specimens was adjusted with sucrose. Tissues were fixed for 30–60 min depending on size, transferred to 30% ethanol and gradually dehydrated to 100% to minimize shrinkage, remaining in each alcohol dilution for a minimum of 30 min. Following dehydration, tissues were critical-point dried, mounted on stubs with adhesive tabs, and photographed using an AMRAY 1810 scanning electron microscope at the SEM laboratory, Smithsonian Institution, National Museum of Natural History.

Ciliary current direction and topological relations such as 'left' and 'right', describe features of the midgut as opened along a mid-dorsal (exposed surface) longitudinal incision with the flaps opened laterally and the style sac uppermost (except *Theodoxus fluviatilis*, see below). Cilia within the style sac region are recognizable as one of two distinct types: similar to those lining the intestinal groove (uniform), or forming a tall, compact brush border (differentiated). The term 'base' refers to the morphologically posterior end of a structure (e.g. mantle cavity, buccal cavity); the terms proximal and distal are used to describe distance relative to the origin (i.e. mouth or gonad). Following Fretter & Graham (1962), direct connections between the right pleural and subesophageal, or left pleural and supra-oesophageal ganglia are referred to as right or left zygoses, respectively; peripheral connections are referred to as right and left dialyneuries.

ANATOMICAL DESCRIPTIONS

Anatomical descriptions are provided for all taxa included in the phylogenetic analysis. In instances where previous descriptions exist (see Remarks, below), the anatomy has been redescribed to verify existing descriptions and/or elaborate on aspects that were insufficiently detailed. Most importantly, consistent terminology is used to facilitate comparisons and homology assessment between taxa.

FAMILY COCCULINIDAE

MACLEANIELLA MOSKALEVI LEAL & HARASEWYCH 1999

Material Examined

Puerto Rico Trench (BMSM 1000). Two preserved paratypes were sectioned for anatomical reconstructions (see details in Leal & Harasewych, 1999; Strong & Harasewych, 1999). No specimens were available for scanning electron microscopic investigations of midgut morphology; midgut morphology is inferred from sections. Ciliary currents within the midgut are unknown.

External anatomy and mantle cavity

Weakly developed anterior pedal gland opening anteriorly and laterally to foot sole. Operculum absent. Mantle penetrated by haemal sinuses. Hypobranchial gland weakly developed, comprising several large cells in pallial roof. Pseudoplicatid gill forming small ciliated papilla present in front of anus in right mantle roof.

Reproductive system

Adults simultaneous hermaphrodites. Gonopericardial canal absent. Gonad forming voluminous sac, containing both eggs and sperm. Sac-like portion of gonad connecting to visceral glandular gonoduct by non-ciliated duct. Glandular gonoduct opening to enclosed duct of seminal receptacle under base of mantle cavity. Duct of seminal receptacle opening to seminal receptacle posteriorly and mantle cavity anteriorly. Receptacle containing mass of unorientated sperm. Seminal groove absent. Copulatory organ formed by enlarged right cephalic tentacle.

Alimentary System

Foregut. Radula rhipidoglossate. Single pair of odontophoral cartilages present. Subradular region cuticularized; subradular organ absent. Sublingual cavity bearing two lateral, glandular pouches. Salivary glands comprising small pouches. Small, unpaired jaw above ventral mouth. Jaw homogeneous, not composed of rods. Ventral ciliary tract beginning within posteriormost buccal cavity as weakly glandular, ciliated thickening. Ventral tract elaborated into large T-shaped, mid-ventral fold for short distance upon emerging from buccal cavity. T-shaped, mid-ventral fold rapidly becoming obscured by underlying mass of glandular tissue (Fig. 8A, vf); large mass lens-shaped, not bilobed. Similar to ventro-lateral folds (Fig. 9A, vlf), mid-ventral fold and glandular mass not continuing posteriorly into mid-oesophagus. Paired oesophageal pouches present. Two glandular, ventro-lateral folds present at inner margin of pouch ducts, persisting only short distance within anterior oesophagus. Oesophageal pouches histologically differentiable into two regions. Anteriorly, pouches simple and weakly glandular. Tissue of the pouches first becoming more significantly glandular along ventral surface, forming convoluted epithelium. Convoluted glandular tissue expanding posteriorly, completely lining pouches as mid-ventral glandular mass diminishing. Glandular tissue of mid-oesophageal pouches and mid-ventral fold histologically distinct; the former comprising low, vacuolated cells, the latter dense, elongate prismatic cells.

Midgut. Posterior oesophagus entering midgut postero-dorsally. Extensive cuticle lining gastric chamber, elaborated into prominent gastric shield mid-dorsally. Grooved tract across midgut roof continuous with oesophagus; sorting area absent. Paired digestive gland ducts opening to posterior oesophagus. Caecum absent.

Hindgut. Intestine exiting midgut posteriorly. Style sac and intestinal groove absent. Hind gut completing three, large loops.

Reno-pericardial system

Single, left, sac-like kidney; excretory lamellae absent. Nephridial gland absent.

Nervous system and sensory structures

Broad circum-oesophageal nerve ring lacking secondary connections between ganglia; nerve ring weakly dystenoid. Buccal connectives passing anteriorly to buccal ganglia lying below oesophageal pouches. Single commissure connecting pedal ganglia. Supra-oesophageal ganglion innervating osphradial ganglion within mantle roof. Possibly sensory, ciliated, prismatic cells overlying osphradial nerve. Single visceral ganglion present. Tentacular nerve single. Eyes modified into basitentacular gland on small stalks at outer bases of cephalic tentacles. Statocysts containing single statolith in one animal, several tiny statocones (~3) in another.

Remarks

Internal anatomy was described by Strong & Harasewych (1999); the shell, radula, and external aspects of the copulatory organ were described by Leal & Harasewych (1999). This redescription uses terminology to promote homology comparisons in a higher order framework and elaborates on the salivary glands, ventral folding of the foregut, the ventral glandular mass, and the histological differentiation of the oesophageal pouches. Given the histological differentiation between the anterior and posterior portion of the oesophageal pouches, these structures are interpreted as continuous buccal pouches and non-sepatate oesophageal glands.

Discussion

The family Cocculinidae is remarkably morphologically diverse, considering that so few comprehensive anatomical accounts exist. All cocculinids have a highly vascularized pallial roof, most likely playing a significant role in gas exchange. The mantle cavity bears the apertures of the genital system and alimentary system on the right and a hypobranchial gland in the centre of the pallial roof that may be weakly developed or well-developed and contained within a pocket, ventrally enclosed by the kidney. Just in front of the anus is a pseudoplicatid gill that ranges from large and foliated to small and papillate. Other species lack a gill, bearing only a ciliary tract or a series of leaflets (Haszprunar, 1987, 1988c, 1998a; unpublished data; Sasaki, 1998; Strong & Harasewych, 1999).

All cocculinids are simultaneous hermaphrodites. A pallial glandular gonoduct is lacking, instead the gonoduct that conveys gametes from the gonad to the base of the mantle cavity is glandular. A seminal groove may be present or absent, and leads from the genital aperture to a copulatory organ formed by or associated with the right cephalic tentacle, the foot, or the oral lappet. There may be one or two ‘seminal receptacles’ that store unorientated sperm (Haszprunar, 1987, 1988c, 1998a; Sasaki, 1998; Strong & Harasewych, 1999).

Radular cartilages comprise a single pair. Jaws typically consist of a single, small, unpaired plate on the anterior buccal cavity roof, or may be robust and weakly paired. The jaws are homogeneous and lack rods (Haszprunar, 1987, 1988c, 1998a). Although early studies reported cocculinoidean salivary glands as absent (Haszprunar, 1987, 1988c; Strong & Harasewych, 1999), it is now recognized that the salivary glands form simple, glandular pouches in most taxa (Haszprunar, 1998a). However, some possess prominent, tubular salivary glands (Haszprunar, unpublished data). In those species with pouch-like salivary glands, the sublingual cavity is highly glandular (Haszprunar, 1987, 1988c; Strong & Harasewych, 1999). Outpocketings of the cocculinid oesophagus have been referred to as ‘oesophageal pouches’ and/or ‘oesophageal glands’ (Haszprunar, 1987, 1988c, 1998a; Salvini-Plawen, 1988; Sasaki, 1998; Strong & Harasewych, 1999). Due to the internal differentiation of the pouches (anteriorly simple, posteriorly convoluted), they are here interpreted as representing continuous buccal pouches and oesophageal glands.

The Cocculinoidean circulatory system is characterized by a rectum that does not penetrate the ventricle. A nephridial gland is lacking (Haszprunar, 1987, 1988c; Strong & Harasewych, 1999).

The nervous system of cocculinoideans may be hypoathroid with un-fused supra-esophageal and visceral ganglia or weakly dystenoid with fused or unfused visceral and supra-esophageal ganglia. No secondary connections are formed between the pleural and oesophageal ganglia. Sensory structures include osphradia and statocysts. The osphradium is present or absent; in some the osphradium lacks a discrete sensory epithelium, consisting only of ciliated cells overlying the osphradial nerve. Cocculinoideans possess statocysts bearing a single statolith. However, *Macleaniella* is polymorphic for this feature. Eyes rarely contain pigment and are typically modified into a mucus-secreting basitentacular gland (Haszprunar, 1987, 1988c, 1998a; Strong & Harasewych, 1999).

FAMILY NERITIDAE

THEODOXUS FLUVIATILIS (LINNAEUS 1758)

Material examined

Poitiens, France (USNM 836154). Only preserved material was available for study. Consequently, scanning electron micrographs of complete midgut morphology were difficult to obtain and were supplemented with *camera lucida* drawings of dissected material. In *Theodoxus fluviatilis*, the midgut is rotated ~45° counter-clockwise within the visceral mass relative to caenogastropods (see Discussion). Thus, to facilitate topological comparisons with ingroup taxa, the midgut of was opened by a longitudinal incision along the left side.

External anatomy and mantle cavity

Anterior pedal gland opening anteriorly to shallow flap along broad propodium. Operculum present. Vestigial right gill present at base of mantle cavity below pallial glandular gonoduct.

Reproductive system

Gonopericardial canal absent. Proximal tip of glandular gonoduct embedded in visceral mass. Pallial portion of glandular gonoduct closed and diaulic. One genital opening leading to connected copulatory bursa and seminal receptacle; the former storing unorientated sperm, the latter orientated sperm.

Distal vas deferens forming highly coiled seminal vesicle. Prostate closed with distal genital aperture. Open seminal groove leading from genital aperture to penis lying on cephalic lappet to left of right cephalic tentacle.

Alimentary system

Foregut. Radula rhipidoglossate. Three paired odontophoral cartilages and one unpaired sublingual cartilage present. Subradular membrane completely covering odontophore to base of deep sublingual cavity; subradular organ absent (Fig. 4A). Paired glands opening ventrally to sublingual cavity. Dorsal epithelium of buccal cavity cuticularized. Discrete jaw and salivary glands absent. Mid-ventral fold low in buccal cavity (Fig. 8B, vf), continuous with dorsal lip of radular sac. Paired lobes of glandular tissue developing below mid-ventral fold within anterior oesophagus. Low, weakly glandular ventro-lateral folds present along inner aspect of ducts to oesophageal pouches (Fig. 9B, vlf). Glandular mid-ventral fold persisting within anterior and mid-oesophagus, through region of torsion, before diminishing. Paired oesophageal pouches present, simple anteriorly, becoming increasingly folded and glandular posteriorly, comprising continuous buccal pouches (Fig. 9B, bp) and oesophageal glands (Fig. 8B, eg).

Midgut. Oesophageal aperture (Fig. 12A, e) and posterior digestive gland duct lying to left of gastric shield (gs); anterior digestive gland duct (dgd) within deep pocket between gastric shield and style sac. Gastric shield dorsal, functionally separating oesophageal aperture and posterior digestive gland duct from gastric lumen. Ciliated fold (cf) beginning at proximal tip of minor typhlosole (t2), extending posteriorly to left of oesophagus. Ciliated fold and glandular pad (gp) curving into caecum (c) lying behind shield. Major typhlosole (t2) and several folds continuous with intestinal groove terminating at oesophageal aperture. Raised ciliary tract on major typhlosole absent (Fig. 21A). Deep sac (Fig. 12A, ds) present, bounded posteriorly by lip of style sac and anteriorly by second fold, both continuous with minor typhlosole. Mouth of sac surrounded by differentiated style sac cilia. Crystalline style absent.

Hindgut. Intestine completing approximately two loops. Rectum penetrating ventricle.

Reno-pericardial system

Transverse pallial vein extending dorsally from cephalopedal sinus, splitting into afferent branchial vein and afferent renal vein. Afferent branchial vein traversing anterior wall of kidney to afferent ctenidial membrane; afferent renal vein passing through thin-walled ventral chamber of kidney (= bladder), supplying dorsal chamber containing mass of excretory lamellae. Vestigial right gill present. Blood sinus of vestigial right gill communicating directly with cephalopedal sinus. Nephridial gland absent.

Nervous system and sensory structures

Circum-oesophageal nerve ring surrounding buccal mass anteriorly, with buccal connectives passing posteriorly to buccal ganglia. Nervous system hypoathroid, right zygoneurous and left dialyneurous, with paired visceral ganglia. Labial commissure present. Single pedal commissure connecting pedal ganglia. Pedal cords present. Tentacular nerve single. Statocysts with single statolith present dorsally and medially, just behind pedal commissure. Eyes on tips of short ocular peduncles.

Remarks

This species has been the subject of many anatomical investigations, emphasizing the mantle cavity, reproductive and alimentary systems. Gilson (1896), Fretter & Graham (1962) and Fretter (1946) provided information for reproductive anatomy; the latter account is the most comprehensive and details gross morphology as well as histological fine structure for both males and females.

Lenssen (1899), Bourne (1908), Graham (1939) and Whitaker (1951) provided information for the foregut. Whitaker's account, describing the structure and function of the foregut, is the first to suggest that the outpocketings of the foregut represent continuous buccal pouches and oesophageal glands; these structures had been variously interpreted as salivary glands (Lenssen, 1899) or simply as oesophageal pouches (Bourne, 1908; Graham, 1939). Whitaker was also the first to recognize the presence of paired sublingual glands in this species. Whitaker acknowledges the presence of the mid-ventral fold, but does not describe the presence of ventro-lateral folds. The species possesses a seventh unpaired cartilage (Lenssen, 1899; Bourne, 1908; Fretter, 1946); however, this supports the cuticle of the sublingual pouch and is not considered to represent part of the odontophore (*cf.* Sasaki, 1998).

Preliminary observations on midgut and hindgut anatomy were provided by Lenssen (1899) and were described more completely by Graham (1939) and Fretter & Graham (1962); Graham clarified the absence of the crystalline style in this species. Several findings obtained here for midgut morphology differ subtly from those reported previously (Graham, 1939; Fretter & Graham, 1962). In the present analysis, the oesophageal aperture and one digestive gland duct were found immediately to the left of the gastric shield such that, when the midgut is closed, the shield separates them from the gastric chamber. A second digestive gland duct is present within the deep pocket between the gastric shield and style sac.

Landsburg (1882) and Lenssen (1902) provided the main points of reno-pericardial morphology and circulation, which were elaborated by Bourne (1908); Fretter (1965) primarily described blood flow through the mantle and associated organs. Blood supply to the vestigial right gill, an organ first noted by Lenssen (1902), has been attributed to a diverticulum off the transverse pallial vein (Bourne, 1908; Fretter, 1965). However, as described above, histological sections revealed that the vestigial gill sinus opens directly to the cephalopedal sinus.

Lenssen (1902) provided a relatively thorough account of the nervous system which was refined by Bourne (1908).

Discussion

Reproductive anatomy of most neritids is highly complex, particularly among females. The pallial oviduct is typically diaulic, one aperture leading to the bursa and seminal receptacle, the second leading to the glandular oviduct, which is posteriorly embedded in the visceral mass and subdivided into capsule and albumen glands (Bourne, 1908; Fretter, 1946, 1965; Starmühlner, 1969; Berry, Lim & Sasekumar, 1973; Houston, 1990; Haynes, 1991; Sasaki, 1998). These two parallel portions of the oviduct communicate posteriorly via a narrow duct. Some neritids possess a triaulic pallial oviduct. The third aperture is referred to as the ductus enigmaticus (Bourne, 1908) and, as the name implies, is of uncertain function but has been suggested to regulate internal pressure by allowing water into the oviduct or excess sperm to escape (Bourne, 1908; Fretter, 1965; Houston, 1990; Haynes, 1991). In addition, some neritids have a small duct that leads from the renal oviduct and opens to the posterior end of the mantle cavity adjacent to the vestigial right gill (Fretter, 1965). The presence of this duct, its position within the body and its positional relationship to the vestigial gill has been interpreted as evidence that the right kidney has been integrated into the glandular reproductive tract (Fretter, 1965), rather than forming the seminal receptacle, as suggested by Thiele (1902). This connection between gonoduct and mantle cavity is absent in *Theodoxus fluviatilis* (Fretter, 1946). Bourne (1908) described the so-called oviduco-coelomic funnel (= gonopericardial canal), which connects the gonoduct with the extensive pericardial coelom. Despite careful searching, Fretter (1965) was unable to confirm this.

Male reproductive anatomy typically consists of a testis, a distal vas deferens that is highly coiled and functions in the storage of sperm, and a highly glandular prostate that forms the spermatophore. The prostate is closed, discharging through an aperture adjacent to the anus, and is subdivided into two distinct masses of glands. The penis, when present, lies on the cephalic lappet, to the left of the right cephalic tentacle (Bourne, 1908; Andrews, 1937; Starmühlner, 1969; Houston, 1990; Sasaki, 1998).

The relatively conservative foregut anatomy consists of paired sublingual glands opening ventrally to the buccal cavity, and confluent buccal pouches and oesophageal glands lying anterior to the region of torsion; salivary glands are absent (Thiele, 1902; Bourne, 1908; Whitaker, 1951; Fretter, 1965). There are typically three sets of paired cartilages (Lenssen, 1899; Bourne, 1908; Fretter, 1946; Salvini-Plawen, 1988); the median cartilages may be fused or unfused and a seventh unpaired cartilage may be present below the anterior tip of the subradular membrane (Sasaki, 1998).

In general, the neritid midgut consists of a globular gastric chamber that bears a highly variable number of digestive gland duct openings; a small, textured pouch posterior to the gastric shield may be present (Haller, 1894; Bourne, 1908; Fretter & Graham, 1962; Fretter, 1965). A prominent fold associated with the minor typhlosole passes posteriorly into the caecum; this fold may be absent or elaborated into a well-developed sorting area (Fretter, 1965). *Theodoxus fluviatilis* remains the only neritid described possessing a small transverse pouch just within the lip of the style sac (Graham, 1939). However, a similar pouch has been observed in *Neritina reclivata* (pers. obs.).

The neritid reno-pericardial system comprises an enlarged pericardial coelom, a heart with two auricles, and a long, ciliated reno-pericardial canal that opens to the dorsal, glandular portion of the two-tiered kidney (Fretter, 1965). The ventral portion of the kidney forms a bladder into which the nephropore opens (Lenssen, 1902; Thiele, 1902; Bourne, 1908; Sasaki, 1998; Estabrooks, Kay & McCarthy, 1999). The intestine pierces not only the ventricle, but the lumen of the kidney as well (Thiele, 1902), posteriorly separating a portion of the reno-pericardial coelom.

The neritid nervous system is right zygoneurous and left dialyneurous, with paired visceral ganglia – one lying in the transverse pallial vein and the second adjacent to the vestigial gill (Bouvier, 1892; Bourne, 1908). The pedal ganglia are united by a single commissure (Bourne, 1908; Sasaki, 1998). The identity and homology of the subintestinal ganglion, while previously in question (Haller, 1894), consists of a swelling lying between and just behind the pleural ganglia (Bouvier, 1892; Bourne, 1908; Starmühlner, 1969).

FAMILY CYCLOPHORIDAE

NEOCYCLOTUS DYSONI AMBIGUUM (MARTENS 1890)

Material examined

Yucatan, Mexico (USNM 890933).

External anatomy and mantle cavity

Foot broad with narrow opening of anterior pedal gland. Operculum with outer calcareous layer and chitinous basal plate. Pallial roof well vascularized, ctenidium absent. Hypobranchial gland forming thick pad, narrowing anteriorly. Hypobranchial gland composed of subepithelial gland cells penetrated by ciliated ducts discharging to ciliated excretory groove. No differentiation of hypobranchial gland into two distinct regions.

Reproductive system

Gonad dorsally overlying digestive gland, extending to posterior end of midgut. Gonopericardial connection absent. Oviduct extending anteriorly past proximal tip of glandular pallial oviduct, looping back upon itself, broadening into lobulate seminal receptacle; receptacle lying along left, ventral wall of glandular oviduct bearing orientated sperm. Oviduct extending anteriorly from receptacle, sending off dorsal branch to large, saculate bursa copulatrix lying above receptacle, containing unorientated sperm. Oviduct continuing forward, gradually increasing in diameter and becoming more glandular, closely appressed to ventral side of glandular oviduct. Oviduct, opening to capsule gland short distance back from genital aperture.

Pallial oviduct partially embedded in viscera behind base of mantle cavity, extending to mantle edge. Albumen gland forming proximal end of glandular oviduct, alongside seminal receptacle and bursa, with gradual transition anteriorly to cells comprising capsule gland. Lumen of pallial oviduct divided longitudinally forming two chambers, more or less dorsal and ventral, communicating posteriorly via short ventro-lateral slit extending from bursa to near base of pallial oviduct. Dorsal chamber surrounding ventral chamber dorsally and on left. Oviduct opening to ventral chamber. Ventral chamber ending blindly anteriorly, becoming highly complexly folded posteriorly. Dorsal chamber bearing genital aperture at anterior end, with simpler internal structure, becoming less glandular posteriorly.

Seminal vesicle derived from vas deferens absent. Closed prostate lying along base of mantle cavity. Seminal groove leading from distal end of prostate to penis lying on side of head in centre of nape. Seminal groove secondarily closed with superficial groove overlying the duct.

Alimentary system

Foregut. Transverse mouth opening at tip of short snout to large buccal mass (Fig. 6A). Radula taenioglossate. Buccal cavity walls bearing pair of prominent jaws with saw-like teeth, lying well forward of dorsal folds. Jaw composed of outer homogeneous layer and inner rod layer (Fig. 5A, j). Subradular organ present (Figs 4B, 5A, sro). Organ long and well developed with shape of flattened cone projecting between jaws into mouth opening. Shallow horizontal clefts marking sides of organ. Short ventral fold present, beginning in buccal cavity (Fig. 8C, vf). Ventral trough replacing ventral fold, flanked by two ventro-lateral folds (Fig. 9C, vlf) running along inner edges of ducts of buccal pouches (bp). Pouches short, broad (Fig. 6A, bp); pouch ducts lined with basophilic epithelium. Salivary gland ducts (sgd) opening dorso-laterally, under cerebral commissure. Salivary glands massive, overlying portions of mid- and posterior oesophagus to back of cephalic haemocoel. Mid-oesophageal epithelium uniformly folded after separation of pouches, with broad, flattened and longitudinally folded lumen; septate oesophageal gland absent (Fig. 11B, me).

Midgut. Posterior oesophagus opening to left limb of U-shaped gastric chamber (Fig. 13A). Distal portion of midgut almost completely lined by cuticle, leaving only a ventral ciliated strip (cs). Ciliary currents flowing anteriorly within ciliated zone. Cuticle elaborated into small gastric shield (gs) ventrally on right, adjacent to oesophageal opening (e). Large groove horizontally subdividing gastric lumen posterior to style sac. Deep, rounded posterior portion of groove forming vestibule receiving numerous digestive gland ducts (dv). Anterior tip ending in blind pouch (gap) next to intestinal groove; no secretion observed emanating from pouch. Shallow intestinal groove bounded by two low typhlosoles (t1, t2). Intestinal groove turning briefly to right at distal end of style sac. Transverse segment of intestinal groove bounding mouth of single pyloric caecum (pyc); caecum extending short distance posteriorly under style sac. Style sac epithelium smooth and unfolded, bearing well differentiated cilia. Raised ciliary tract on major typhlosole and crystalline style absent.

Hindgut. Intestine exiting style sac, extending short distance posteriorly alongside style sac, completing three full loops embedded in digestive gland.

Reno-pericardial system

Kidney and pericardium lying within pallial roof (Fig. 22A). Kidney large, overhanging pericardium; thick mass of excretory tubules almost completely filling lumen, roughly divided into several lobes. Nephridial gland absent. Nephropore (np) opening posteriorly to narrow vertical extension of mantle cavity behind kidney. Afferent renal vessel extending short distance back from cephalopedal sinus, turning dorsally, running along back wall of pericardium (per) to enter kidney from below, near nephropore. Afferent renal vessel entering kidney lobe overhanging pericardium. Reno-pericardial canal (rpc) opening dorsally near afferent renal vessel. Pericardial lumen narrow, extending short distance posterior to kidney.

Nervous system and sensory structures

Nervous system hypoathroid, right zygoneurous, left dialyneurous (Fig. 24A). Circum-oesophageal nerve ring surrounding anterior buccal mass at level of ocular peduncles (Fig. 6A, nr). Labial commissure absent. Single, thick tentacular nerve innervating tentacle (tn). Pallial nerve arising from left pleural ganglion bearing small ganglion with several small branches, lying at base of pallial roof (osg). Pedal ganglia (Fig. 24A, pdg) connected by one commissure with two cross connections between pedal cords (pc). Statocysts (sc) with numerous statoconia on postero-dorsal surface of pedal ganglia. Buccal ganglia (Fig. 6A, bg) lying behind circum-oesophageal nerve ring at base of buccal cavity, just above buccal pouch ducts. Long connective leading to supra-oesophageal ganglion (sp) lying near back of cephalic haemocoel. Paired visceral ganglia (vg) lying under kidney, to right of pericardium, within cephalopedal sinus. Visceral commissure double. Osphradium absent. Eyes on tips of short ocular peduncles.

Remarks

Thompson (1969) described the reproductive anatomy of this species. While the gross morphology of that description is essentially identical to the one provided here, the interpretation of homologies is not. Thompson described the oviduct as persisting anteriorly along the distal end of glandular oviduct, with a short recurvent segment forming an albumen gland. However, as described above, the simple loop of the oviduct forms a seminal receptacle containing orientated sperm. Thompson also described a large, well-developed seminal receptacle closely appressed to the glandular oviduct, communicating with the oviduct distal to albumen gland. A bursa copulatrix was cited as lacking. However, the structure identified as the receptacle, is, in fact, a large bursa copulatrix with unorientated sperm. The glandular pallial oviduct was described as comprising only a capsule gland. However, the glandular pallial oviduct comprises both an albumen gland and a capsule gland. While not externally separable, these glands are distinguishable histologically. The description of male reproductive anatomy presented above is congruent with that of Thompson.

Discussion

There are few comprehensive anatomical studies of cyclophorids. Much of available comparative data concerns their reproductive anatomy, with only scattered accounts of nervous, alimentary and reno-pericardial anatomy. However, it seems clear that all cyclophorids share a unique combination of modifications to the mantle cavity. The pallial roof forms a highly vascularized respiratory surface (Kasinathan, 1975). The ctenidium and osphradium have been lost, and the kidney, while lacking the ureter found in some terrestrial forms, has been displaced anteriorly and occupies a position within the pallial roof (Tielecke, 1940; Andrews & Little, 1972; Kasinathan, 1975). The hypobranchial gland is modified into a thick pad penetrated by ducts and appears to have become an accessory excretory organ (Andrews & Little, 1972). The size of the gland varies greatly among cyclophorid species, and may be differentiated into two distinct regions (Thompson, 1969; Andrews & Little, 1972). However, the hypobranchial gland of *Murdochia pallidum* has been described as similar histologically to other marine 'prosobranchs' (Morton, 1952a).

Descriptions of the reproductive system account for the majority of comparative studies among cyclophorids (e.g. Weber, 1924; Tielecke, 1940; Morton, 1952a; Berry, 1964; Thompson, 1969; Kasinathan, 1975; Jonges, 1980). The female is typically characterized by a pallial gonoduct divided into albumen and capsule glands, with a bursa and receptacle opening to the inner end of the albumen gland. In some species, the receptacle is not a separate pouch, but forms an enlarged section of the renal oviduct (Morton, 1952a; present study). The pallial oviduct may open broadly to the mantle cavity (Thompson, 1969; Kasinathan, 1975) or form a closed tube with a distal genital aperture (Tielecke, 1940; Morton, 1952a; Berry, 1964; Thompson, 1969; Kasinathan, 1975). Male cyclophorids typically possess a prostate at the base of the mantle that may be open or closed (Tielecke, 1940; Berry, 1964; Thompson, 1969; Kasinathan, 1975). A seminal groove, similarly open or closed, leads from the prostate to the penis lying behind the right cephalic tentacle or in the middle of the nape (Tielecke, 1940; Morton, 1952a; Morrison, 1955; Berry, 1964; Thompson, 1969; Kasinathan, 1975). In some species, as in *Neocyclotus dysoni ambiguum*, the seminal groove may be secondarily coalesced by a raphe with a superficial groove overlying the duct (Thompson, 1969).

A notable exception to this rather consistent picture is the reproductive anatomy of neotropical cyclophorids in the Aperostominae and Neocyclotinae (Thompson, 1969). Thompson reported that all neotropical species studied lack a bursa copulatrix and possess an albumen gland formed by a simple loop in the oviduct, justifying unification of the two subfamilies in a new family, the Neocyclotidae. One of the species studied by Thompson included *Neocyclotus dysoni ambiguum*. The reanalysis of reproductive homologies for this species provided here are congruent with previous descriptions of cyclophorid reproductive anatomy and do not support recognition of a separate family for the neotropical genera.

There are virtually no published accounts of alimentary anatomy in cyclophorid species, and those that are available are contradictory. For example, buccal pouches may be present (Amaudrut, 1898; Kasinathan, 1975) or absent (Morton, 1952a). Amaudrut (1898) clearly figured a prominent subradular organ projecting between the jaws of *Cyclophorus vulvulus*. Morton (1952a) neither confirmed nor denied the presence of the subradular organ, but a schematic diagram of the foregut does not show a subradular organ. Similarly, Kasinathan (1975) did not report a subradular organ. The mid-oesophagus is narrow (Kasinathan, 1975) or forms a voluminous crop (Amaudrut, 1898).

Morton (1952a) described several features of the midgut of *Murdochia pallidum* congruent with the present description including a cuticularized epithelium with a ventral ciliated channel and the presence of a protostyle. However, Morton described no outpocketings of the gastric chamber nor style sac, the digestive gland is stated to open via a single duct near the style sac, and the intestine is reported as simple and S-shaped. Kasinathan (1975) described the gastric chamber as cuticularized only anterior to the oesophageal aperture; the presence of pyloric caecae or gastric pouches is neither confirmed nor denied, but a single digestive gland duct is reported in a position similar to that of the gastric pouch described here for *Neocyclotus dysoni ambiguum*.

Most cyclophorids share a similar reno-pericardial morphology (Andrews & Little, 1972; Kasinathan, 1975). All except *Murdochia pallidum* (Morton, 1952a) have a largely pallial kidney. This shift has been accompanied by a change in the topological relationships of features associated with the reno-pericardial complex such that the nephropore, afferent renal vessel and reno-pericardial canal all lie in a posterior position, with the nephropore opening to a posterior extension of the mantle cavity. The exact position of these features varies considerably among cyclophorid taxa (Andrews & Little, 1972).

Although few accounts detail all aspects of cyclophorid nervous system morphology, those available converge on a consistent picture of a hypoathroid, right zygoneurous, left dialyneurous nervous system, lacking a labial commissure and possessing well-developed pedal cords (Bouvier, 1887; Tielecke, 1940; Kasinathan, 1975). There are some conspicuous exceptions. For example, there are no reports of a small ganglion on the nerve from the left pleural ganglion. Given that osphradial innervation is primarily pleural among architaenioglossans (Bouvier, 1887; Annandale & Sewell, 1921; Prashad, 1925; Berthold, 1991; Ponder & Lindberg, 1997), the ganglion is undoubtedly an osphradial ganglion, despite loss of the osphradium. Bouvier (1887) and Kasinathan (1975) reported the presence of a single visceral ganglion and numerous cross-connections between the pedal cords in two species of *Cyclophorus*.

FAMILY AMPULLARIIDAE

MARISA CORNUARIETIS (LINNAEUS 1758)

Material Examined

Ft. Meyers, Florida (USNM 890932); San Juan, Puerto Rico (USNM 795555); Charlotteville, St. John, Tobago (USNM 836135).

External anatomy and mantle cavity

Mantle roof forming well vascularized lung with pneumostome opening alongside ctenidium. Pedal gland opening to anterior margin of propodium. Operculum present. Anterior kidney chamber extending into pallial roof.

Reproductive system

Gonopericardial connection absent. Seminal receptacle with orientated sperm formed by distal oviduct, embedded in glandular oviduct. Proximal tip of glandular oviduct invading viscera.

Seminal vesicle derived from vas deferens absent. Pallial vas deferens closed along entire length, opening to mantle cavity via small aperture at distal end of prostate. Penis present on edge of pallial skirt with vas deferens opening at tip.

Alimentary system

Foregut. Radula taenioglossate. Single pair of odontophoral cartilages present. Large, complexly folded subradular organ present (Fig. 4C). Paired jaws composed of outer homogeneous layer and inner rodlet layer (Fig. 5B, j). Anterior salivary gland ducts lying under circum-oesophageal nerve ring. Buccal pouches opening to posterior buccal cavity and anterior most oesophagus. Mid-ventral fold beginning in buccal cavity and continuing into anterior oesophagus. Two ventro-lateral folds present, bounding inner buccal pouch ducts. Mid-ventral fold diminishing after separation of buccal pouches. Mid-oesophagus uniformly folded, lacking septate oesophageal gland.

Midgut. Oesophagus opening broadly to S-shaped gastric chamber. Epithelium of gastric chamber coarsely folded and cuticularized. Gastric cuticle thickened to right of oesophageal aperture. Sorting areas absent. Three digestive gland ducts opening to vestibule at proximal end of style sac. Paired gastric pouches present, adjacent to lip of style sac, bordering extension of intestinal groove into gastric chamber. Ciliary currents flowing clockwise around lip of style sac. Currents flowing from digestive gland vestibule into intestinal groove. Paired typhlosoles running length of style sac. Style sac epithelium transversely folded bearing differentiated cilia. Pyloric caecae present at distal end of style sac.

Hindgut. Intestine exiting style sac, curving a short distance posteriorly alongside distal style sac, and completing approximately three loops below kidney lumen.

Reno-pericardial system

Kidney comprising posterior, visceral lobe and anterior lobe within pallial roof. Kidney communicating with auricle; nephridial gland absent at site of connection.

Nervous system and sensory structures

Nervous system hypoathroid, left and right zygoneurous. Nerve ring lying anteriorly, with buccal connectives passing posteriorly to buccal ganglia lying near emergence of buccal pouches. Single pedal and pleural commissure present, with single anastomosis between pedal nerves. Single visceral ganglion present. Statocysts with numerous statoconia present dorso-laterally on pedal ganglia. Osphradium bipectinate. Eyes on tips of ocular peduncles. Tentacular nerve single.

Remarks

The anatomy of this species is well documented in several publications, most notably a detailed study on ampullariids (Berthold, 1991), as well as several papers on the reproductive system (Mello, 1988; Schulte-Oehlmann *et al.* 1994), digestive system (Demian, 1964) and a series on organogenesis (Demian & Yousif, 1973a,b, 1975). Minor omissions from existing descriptions include precise descriptions of ventral folding within the anterior oesophagus, the ciliary currents within the midugt and the branching patterns of the tentacular nerve. Berthold (1991) did not describe the presence of the subradular organ in his morphological investigations of ampullariids, including *Marisa cornuarietis*; the structure was thoroughly described by Demian (1964) and Lufty & Demian (1967).

Discussion

Available descriptions provide a rather conservative picture of ampullariid morphology. Ampullariids are the only gastropods to possess a well-developed lung in conjunction with a ctenidium (e.g. Bouvier, 1888; Scott, 1943; Starmühlner, 1969; Demian & Yousif, 1973c).

All described ampullariids possess a glandular oviduct comprising a closed tube that lies partially behind the base of the mantle cavity; the distal oviduct forms a receptaculum seminis, bearing orientated sperm, just prior to the junction with the albumen gland (Berthold, 1991). A bursa copulatrix may be present or absent; a ‘pseudo bursa copulatrix’ may be present, comprising the efferent duct of the receptaculum seminis (Berthold, 1991). The penis lies within the mantle roof and is equipped with a diverse and variable array of accessory glands (Bouvier, 1888; Scott, 1943; Starmühlner, 1969; Berthold, 1991).

The glandular apparatus of the foregut comprises massive salivary glands, buccal pouches, and a subradular organ; the jaws are large (Scott, 1943; Starmühlner, 1969; Berthold, 1991). The voluminous mid-oesophagus forms a crop. The midgut is U-shaped, highly muscular and cuticularized (Graham, 1939); the digestive gland ducts open to a common vestibule, a pyloric caecum is present and the gastric pouches may be single or paired (Starmühlner, 1969; Berthold, 1991).

The kidney of ampullariids comprises two distinct chambers, with the anterior chamber, or 'ureter', lying within the pallial roof and bearing the nephropore (Bouvier, 1888; Prashad, 1925; Fretter & Graham, 1962; Hägler, 1963; Andrews, 1965b; Starmühlner, 1969); the homologies of these two chambers and their precise connection with each other and the mantle cavity was historically a source of confusion (see Demian & Yousif, 1973b for review). The relative sizes of the chambers varies considerably within the family (e.g. Berthold, 1991).

The Ampullariidae are characterized by a nerve ring that is hypoathroid, left zygoneurous, with a single visceral ganglion and fused right pleural and suboesophageal ganglia, rendering the identity of the latter virtually undistinguishable; a labial commissure is present (Bouvier, 1887; Prashad, 1925; Ranjah, 1942; Scott, 1943; Starmühlner, 1969). Pedal ganglia with one commissure, two cross connections between the pedal nerves, and a pleural commissure are also present (Berthold, 1991), but the latter is commonly identified as a pedal commissure (e.g. Starmühlner, 1969).

For an analysis of ampullariid morphology, phylogeny and biogeography, see Berthold (1991), and Bieler (1993) for a cladistic reanalysis and critique.

FAMILY BATILLARIIDAE: *LAMPANELLA MINIMA* (GMELIN 1791)

Material Examined

Missouri Key, Florida (USNM 890934).

External anatomy and mantle cavity

Propodium bearing deep opening to anterior pedal gland. Operculum corneous, thin, multispiral with central nucleus. Mantle margin papillate with short, thin, widely spaced papillae arising just inside mantle rim (Fig. 6B). Inhalant margin marked by scalloping of mantle edge; exhalent margin thickened, and bearing two papillae (Fig. 6B). Hypobranchial gland well developed.

Reproductive system

Gonad spreading dorsally over digestive gland to posterior end of midgut. Renal oviduct contacting pericardium (Fig. 2A, per); gonopericardial canal absent. Oviduct discharging to glandular pallial oviduct at base of mantle cavity. Pallial oviduct open along entire length, composed of lateral (inner) and medial (outer) laminare, with deep intervening oviductal groove. Medial lamina edge bearing deep, ciliated sperm gutter, running from distal tip and terminating short distance before base of mantle cavity. Large spermatophore bursa (spb) dorsally overlying broad, flat seminal receptacle (rcs) embedded in albumen gland (ag) of medial lamina. Bursa and receptacle communicating posteriorly via narrow, ciliated duct and opening to sperm gutter anteriorly, with broad aperture of bursa just anterior to narrow receptacle aperture. Degenerating spermatophores commonly found within bursa. Shallow, ciliated groove traversing side of foot from tip of pallial oviduct to ovipositor.

Straight distal vas deferens swollen with ripe sperm, functioning as seminal vesicle. Renal vas deferens narrowing shortly behind base of mantle cavity, contacting pericardium with connective tissue, but gonopericardial canal absent (Fig. 3A, per). Vas deferens opening to prostate (pr) at base of mantle cavity, composed of parallel, glandular laminae with deep intervening groove. Free edge of medial lamina with low, longitudinal, glandular ridge running along inner border. Tissue of medial lamina forming deep transverse cleft, comprising spermatophore forming organ (Fig. 3A). Glandular tissue of lateral lamina extending short distance onto pallial floor at base of mantle cavity (Fig. 3A).

Alimentary system

Foregut. Radula taenioglossate. Paired jaw present at anterior end of dorsal folds; jaw composed of rods with laterally overlapping homogeneous layer. Subradular membrane incompletely covering odontophore. Subradular organ present, comprising broad, glandular shield with transverse ridges (Fig. 4D). Radular sac long and somewhat coiled, lying alongside mid-oesophagus. Tube-like salivary glands (Fig. 6B, sgl) passing through circum-oesophageal nerve ring. Ventral fold present (Fig. 8D, vf), running length of anterior oesophagus and terminating at initiation of oesophageal gland. Paired ventro-lateral folds (Fig. 9D, vlf) emerging within posterior most buccal cavity, at inner aspect of two lateral outpocketings (bp) lined with acidophilic epithelium. Weakly glandular, septate oesophageal gland present (Fig. 6B, eg) within enlarged mid-oesophagus, composed of bilaterally symmetrical septate folds and an open, ventral food groove. Septae terminating short distance before end of mid-oesophagus; posterior mid-oesophagus comprising short, crop-like compartment.

Midgut. Oesophagus entering midgut ventrally on left (Fig. 13B, e). Well-developed sorting area (sa), extending posteriorly from intestinal groove, past oesophageal aperture, along floor and wall of gastric chamber. Ciliated fold (cf) V-shaped, forming margin of sorting area, extending anteriorly from oesophageal aperture to intestinal groove, then turning posteriorly. Ciliary currents flowing toward intestinal groove within sorting area. Hypertrophied glandular pad (gp) with median groove, extending to base of gastric chamber. Single digestive gland duct (dgd) lying to left of glandular pad, posterior to oesophageal aperture. Ventro-lateral gastric shield (gs) present. Style sac region with transversely folded epithelium and well-differentiated cilia. Crystalline style present. Broad, raised ciliary tract (ctr) present along inner (style sac) edge of major typhlosole (t1). Currents flowing clockwise within style sac region when viewed from behind.

Hindgut. Intestine exiting style sac, turning posteriorly alongside style sac to gastric chamber, then turning anteriorly.

Reno-pericardial system

Kidney partially overlying pericardium, extending into pallial roof. Weakly developed nephridial gland present. Reno-pericardial canal opening ventrally, just behind mantle cavity. Afferent renal vessel entering kidney adjacent to reno-pericardial canal, continuing dorsally, ramifying into tubules within roof.

Nervous system and sensory structures

Nervous system epiathroid (Fig. 24B), right and left dialyneurous, lying just behind buccal mass (Fig. 6B, nr). Small buccal ganglia lying at back of buccal mass just in front of cerebral ganglia. Single, large tentacular nerve (tn) with several small branches, one innervating snout and others innervating tentacle. Supra-oesophageal (sp) and sub-oesophageal (Fig. 24B, sb) connectives long. Single visceral ganglion (Fig. 6B, vg) overlying oesophagus at posterior end of cephalic haemocoel, under pericardium. Statocysts with numerous statoconia (Fig. 24B, sc), present on postero-dorsal surfaces of pedal ganglia. Osphradium (Fig. 6B, os) forming long, narrow ciliated ridge, approximately two-thirds length of ctenidium.

Remarks

Histological sections revealed that *Lampanella minima* (Fig. 9D) possesses glandular expansions of the anterior most oesophagus (bp) that are similar in position (below the dorsal folds (df), adjacent to the buccal ganglia (bg)) and histological detail (strongly acidophilic – unlike the basophilic foregut epithelium of other caenogastropods) to the buccal pouches of *Littorina littorea*. Thus, although buccal pouches have been reported only rarely (*Melanopsis praemorsa*; Graham, 1939; *Thiara amarula*, *Melanatria fluminea*; Starmühlner, 1969) or as lacking entirely within the superfamily (Houbrick, 1988), these structures are interpreted here as homologous to the buccal pouches of other caenogastropods.

Discussion

The reproductive anatomy of *Lampanella minima* differs from other batillariids (Houbrick, 1988) in the absence of baffles on the lateral lamina and the presence of a sperm gutter only along the medial lamina, and not along the lateral lamina.

The mid-oesophagus of cerithioideans displays a range of morphologies from a simple crop to a well-developed septate oesophageal gland (Graham, 1939; Starmühlner, 1969; Houbrick, 1988). The gut of *Lampanella minima* and other batillariids is intriguing in the presence of a crystalline style in conjunction with an oesophageal gland; a rare co-occurrence among caenogastropods (e.g. Graham, 1939). The midgut of *L. minima* shares many features with other marine cerithioideans, including the presence of a single digestive gland duct, the crystalline style and hypertrophied gastric pad (Graham, 1939; Marcus & Marcus, 1964; Driscoll, 1972; Houbrick, 1974, 1987, 1988, 1991a,b).

The renal organ remains under-represented in descriptions of cerithioidean taxa. Often the presence of the nephridial gland is neither confirmed nor rejected (e.g. Marcus & Marcus, 1964; Houbrick, 1987; Ponder, 1991). Some studies have implied the presence of the gland, figuring a narrow strip of tissue adjacent to the pericardium (Houbrick, 1991a) or a large lobe nearly equal in size to the remaining kidney tissue (Houbrick, 1974). Yet others have stated explicitly that the nephridial gland is absent (Simroth, 1896–1907; Seshaiya, 1934b; Strong & Glaubrecht, 2002). Thus, it appears that presence or absence and development of the gland varies within the group, but the limited information available renders it difficult to evaluate in a comparative context.

The nervous system of *Lampanella minima* is right and left dialyneurous, congruent with studies of batillariids and other cerithioidean families including the Melanopsidae, Pleuroceridae, Potamididae and Cerithideidae (Bouvier, 1887; Marcus & Marcus, 1964; Houbrick, 1988).

FAMILY VERMETIDAE: *PETALOCONCHUS VARIANS* (D'ORBIGNY 1841)

Material Examined

Sebastian Inlet, Florida (USNM 890935).

External anatomy and mantle cavity

Operculum thin and chitinous, shallowly concave, slightly overlapping side of foot. Spiral lamella upstanding for approximately one half volution, forming raised ridge for another one half volution. Single, low, inconspicuous spiral lamina present within shell along columellar surface. Lamina becoming obsolete towards aperture. Body of animal long and slender, appearing as sideways displaced, sometimes irregular, coils. Posterior end of body thinning to long, slender tail comprising only gonadial tissue. Columellar muscle thick anteriorly, thinning to narrow strip running almost complete length of body, unattached to viscera for much of that length. Ctenidial filaments narrowly triangular. Ctenidium extending from mantle edge, not reaching base of mantle cavity. Voluminous branchial vein traversing base of mantle cavity from pericardium to ctenidium. Hypobranchial gland well developed, composed of transverse folds covering rectum and mantle roof from anus to base of mantle cavity. Cephalic tentacles short and thick, lying on either side of broad, flattened head. Two long, slender pedal tentacles lying just under snout, atop reduced foot sole. Pedal gland opening medially under pedal tentacles. Pedal gland large, extending approximately one-half length of cephalic haemocoel, alongside oesophagus. Numerous small, ciliated ducts penetrating secretory portion of gland, coalescing into large ciliated duct under circum-oesophageal nerve ring. Pedal gland duct extending anteriorly along floor of columellar muscle to aperture.

Reproductive system

Gonad displaced posteriorly, comprising long posterior tip of visceral mass. Gonad thinning anteriorly, running along left, ventral aspect of digestive gland. Narrow oviduct emerging from ovary at posterior end of midgut, opening to pallial oviduct at base of mantle cavity. Gonopericardial duct absent. Pallial oviduct thin, short, weakly glandular, traversing basal one-third of elongate mantle cavity (Fig. 2C). Short albumen gland (ag), approximately one-fourth size of capsule gland (cg). Single, ovoid seminal receptacle (rcs) present at anterior end of albumen gland. Oviductal groove closed along proximal albumen gland, opening at level of receptacle. In brooding females, anterior one-third of mantle roof split along midline, accommodating attachment of egg capsules to interior of shell. Egg capsules, attached via narrow thread short distance back from shell aperture, containing numerous small embryos. Attached sacs not arranged in linear series of oldest to youngest, but occurring in mixed groups.

Vas deferens emerging from testis at posterior end of gastric chamber, widening rapidly, engorged with ripe sperm, functioning as seminal vesicle. Seminal vesicle narrowing toward base of mantle cavity and opening to pallial gonoduct (Fig. 3B, pr). Prostate composed of two highly glandular laminae with deep intervening groove, extending approximately one-half length of mantle cavity. Laminae largely open, fused only short distance along proximal end. Laminae flaring widely, exposing glandular surfaces to mantle cavity.

Alimentary system

Foregut. Radula taenioglossate. Paired jaws present at anterior ends of dorsal folds; jaw composed of rods with laterally overlapping homogeneous layer. Sub-radular membrane incompletely covering odontophore. Sub-radular organ present, composed of vertical, glandular crest projecting into mouth opening. Salivary glands passing through circum-oesophageal nerve ring. Radular sac short, curving dorsally around right posterior limit of buccal cavity. Glandular mid-ventral fold present in posterior buccal cavity. Two, short ventro-lateral folds present within anterior oesophagus. Septate oesophageal gland absent.

Midgut. Oesophagus opening ventrally, on left (Fig. 14A, e). Prominent gastric shield (gs) on right, ventro-lateral wall. Well-developed sorting area (sa) extending posteriorly from intestinal groove, straddling oesophageal aperture. Sorting area covering surface of tall, free-standing flap (if) between oesophageal aperture and intestinal groove. Ciliated fold (cf) bounding sorting area and extending posteriorly from sorting area, along left wall of gastric chamber. Ciliary currents flowing toward intestinal groove within sorting area. Single digestive gland duct (dgd) present mid-ventrally. Glandular pad (gp) projecting only short distance past tip of gastric shield. Digestive gland largely resticted posterior to gastric chamber; anterior digestive gland lobe possibly absent. Style sac with paired typhlosoles and transversely folded epithelium bearing differentiated cilia. Crystalline style and raised ciliary tract (ctr) along major typhlosole (t1) present. Raised tract thin, only several cilia thick. Ciliary currents in style sac flowing counter-clockwise when viewed from behind.

Hindgut. Intestine emerging from style sac, curving dorsally to right over posterior end of kidney.

Reno-pericardial system

Kidney lying alongside pericardium, partially overhanging pericardial lumen, extending into pallial roof. Pallial and visceral portions of kidney approximately equal in size (Fig. 22C). Afferent renal vessel entering kidney just behind base of mantle cavity, extending dorsally, branching into two large vessels supplying pallial and visceral excretory tubules in roof. Reno-pericardial canal (rpc) opening ventrally, to left of afferent renal vessel. Region of connective tissue distinct from remaining excretory tissue (ng) present along length of kidney roof. Efferent nephridial vein joining pallial portion of efferent branchial vein.

Nervous system and sensory structures

Nervous system epiathroid, right and left dialyneurous. Nerve ring lying short distance behind buccal mass. Supra-oesophageal connective long; sub-oesophageal connective very short. Buccal ganglia lying at base of buccal mass, anterior to circum-oesophageal nerve ring. Tentacular nerve bifid. Visceral connectives extremely long, extending along columellar muscle to single visceral ganglion at base of mantle cavity. Small statocysts with single statoliths present on postero-lateral surfaces of pedal ganglia. Eyes small, present at lateral bases of cephalic tentacles. Osphradium comprising short, thin, ciliated ridge along anterior portion of ctenidium.

Remarks

Although Sebastian Inlet vermetids have been identified as *Petaloconchus varians* (Mikkelsen, Mikkelsen & Karlen, 1995), this identification should be viewed with caution. D'Orbigny's type material includes two thin and chitinous operculae, but they are crushed and the presence of upstanding spiral lamellae could not be determined, nor could the presence of internal spiral laminae be assessed (Keen, 1961). Moreover, much of the original description included features that may fall within the realm of intraspecific variation, notably, variations in colour and colour pattern of the mantle, foot and cephalic region (d'Orbigny, 1834–46).

Olsson & Harbison (1953) described a new species of *Petaloconchus* from Florida that ranges from the Pliocene to the Recent, *P. floridanus*. They claimed that specimens of this species are commonly confused in museum collections for *P. varians*. They criticized the type material of *P. varians* as being too fragmentary and insufficient for purposes of identification, but paradoxically described the new species on the basis of coiling habit and shell ornament, features notoriously variable within vermetid species, with no mention of diagnostic features of the operculum, internal aspects of the shell, or of internal anatomy. Moreover, they did not cite unique features that could serve to distinguish *P. floridanus* from *P. varians*. Thus, the description for *P. floridanus* is equally inadequate for purposes of identification as the original type material for *P. varians*. Consequently, positive identification of the current material examined awaits re-description of the type material and comprehensive anatomical descriptions for both *P. varians* and *P. floridanus*.

Discussion

Given this important caveat, the specimens identified here as *Petaloconchus varians* possess many characters diagnostic of the genus which distinguish it from other operculate vermetid genera. These include the sideways displaced, spiral growth form, an elongate columellar muscle, spiral opercular lamellae and spiral laminae within the shell (Carpenter, 1856; Keen, 1961; Morton, 1965). *Petaloconchus varians* is unique among described members of the genus because only a single, low lamina is present – the number and development of laminae in the genus are variable, but are often paired and sufficiently prominent to partially occlude the lumen of the shell (Keen, 1961; Morton, 1965).

The reproductive anatomy of *P. varians* presents some unusual features. Of particular interest is the presence of a mantle slit in females and brooding of egg capsules attached to the shell. Several taxonomic revisions and comparative studies have emphasized the fact that the operculate genera, *Petaloconchus* and *Dendropoma*, lack both of these features and brood unattached egg capsules within the mantle cavity (Morton, 1954, 1965; Keen & Morton, 1960; Keen, 1961; Hadfield, 1970; Hughes, 1978). With rare exception, egg capsules are ordered in a linear series from oldest to youngest in these genera (Hughes, 1978). However, *P. varians* was found to brood egg capsules attached to the inner surface of the shell by a fine thread. Egg capsules were not arranged in a linear series, but occurred in mixed clusters. Egg capsules were also observed within the mantle cavity. However, it is unclear whether these were being brooded or were newly formed egg capsules awaiting attachment to the shell. In comparison to other vermetid genera, both *Serpulorbis* and *Vermetus s.s.* reportedly brood attached sacs and bear a deeply incised mantle (Morton, 1951a,b,c, 1965; Hadfield, 1970; Hughes, 1978).

Morphology of the capsule gland also distinguishes *Petaloconchus varians*, forming a long, thin organ at the base of the mantle cavity. The anterior tip of the capsule gland lies well back of the posterior limit of the mantle slit. In *Serpulorbis* and *Vermetus*, Morton, 1965) speculated that the pouch-like capsule gland comes directly into contact with the lining of the shell in order to secure the embryo sacs. This does not seem to be possible in all species of *Serpulorbis* (e.g. Hadfield, 1970), nor in *P. varians*, indicating that an alternative method of egg capsule attachment should be explored in these species, possibly via the pedal gland. The presence of a receptacle occurring at the junction of the albumen and capsule glands is common within the Vermetidae (Morton, 1951a, 1965).

The vermetid digestive system has been described by Morton (1965) as offering no distinctive generic features. Existing descriptions, however, suggest that several midgut features vary and could be a potential source of characters within the group. For example, Yonge (1932) described the presence of a fold separating the opening of the intestine from the cavity of the midgut. As described above, this fold is similarly present in *Petaloconchus varians*, its surface bearing an extension of the sorting area. This fold is also present in *Serpulorbis zealandicus* (Morton, 1951a; = S-shaped fold) and *Dendropoma* (*Novastoa*) *lamellosa* (as *Dendropoma lamellosa*) (Morton, 1951c; = strongly projecting fold). The folds in *P. varians* and *S. zealandicus* both bear sorting lamellae.

A second feature of interest is the digestive gland ducts, which vary from two (Morton, 1951a,c) to three (Yonge, 1932). The presence of a single digestive gland duct and the absence of digestive gland tubules anterior to the midgut in *P. varians* suggests that the anterior lobe may have been lost in this species. Confirmation of this character requires detailed study of the digestive gland and digestive gland ducts. One final character is ciliary current direction within the style sac region, which may flow in a clockwise (Morton, 1951a) or counter-clockwise direction (Yonge, 1932; present study). This feature similarly requires further investigation.

Although there are few accounts of vermetid nervous systems, they indicate that the nervous system is epiathroid and right dialyneurous; in contrast to the present description, a left zygoneury may be present (Lacaze-Duthiers, 1860; Hadfield, 1970). Visceral ganglia may be single (Hadfield) or paired (Lacaze-Duthiers); the tentacular nerve may be single and the statocysts lacking (Hadfield).

FAMILY STROMBIDAE: *STROMBUS MUTABILIS* SWAINSON 1821

Material examined

Okinawa, Japan (USNM 890936). Only preserved material was available for study, thus SEM micrographs of complete midgut morphology were difficult to obtain and were supplemented with *camera lucida* drawings of dissected material.

External anatomy and mantle cavity

Anterior pedal gland opening to shallow groove along narrow tip of well-demarcated propodium. Operculum spatulate with free, pointed tip, bearing numerous small cusps along one edge. Head directed toward left, bringing left eye into inhalant margin. Mantle margin smooth with single, small pallial tentacle within exhalent margin. Hypobranchial gland large and well-developed.

Reproductive system

Gonad dorsally overlying digestive gland to base of kidney. Gonopericardial canal absent. Oviduct opening to glandular pallial oviduct at base of mantle cavity (Fig. 2D). Albumen gland (ag) comprising a highly complex and convoluted system of enclosed glandular folds. Capsule gland (cg) short and simple, open along entire length.

Renal oviduct opening to rounded base of albumen gland (= uterine ball) with complex, internally folded structure. Single-groove portion of albumen gland (no dotted line) proceeding anteriorly from uterine ball to base of oviductal groove. Albumen gland turning back upon itself at U-shaped junction with double groove portion (with dotted line) of albumen gland. Double-groove portion of gland, accommodating bi-directional flow of eggs, extending posteriorly, past uterine ball, to uterine apex. Apex simple with no uterine arms. Albumen gland extending anteriorly from apex, terminating blindly past anterior tip of capsule gland. Capsule gland small, composed of two glandular laminae bordering deep oviductal groove. Narrow, ciliated egg groove traversing side of foot from tip of capsule gland to anterior pedal gland.

Bursa copulatrix (bc) and seminal receptacle (rcs) present. Bursa lying between capsule gland and blind tip of albumen gland, containing mass of unorientated sperm. Receptacle lying posterior to U-junction of single- and double-groove portions of albumen gland. Receptacle muscular and lobulate with many rounded chambers containing orientated sperm. Narrow ducts of receptacle and bursa opening to common muscular aperture inside oviductal groove near connection between albumen and capsule glands. Common aperture also opening to albumen gland at U-junction.

Vas deferens emerging from testis, rapidly expanding into large, convoluted seminal vesicle. Seminal vesicle narrowing slightly before discharging to base of pallial gonoduct. Proximal portion of gonoduct forming crescentic prostate (Fig. 3D, pr), composed of two short laminae with open, shallow intervening groove. Seminal groove extending forward from prostate to penis (pe) lying behind right cephalic tentacle on side of neck. Penis long, muscular, with narrow base. Seminal groove continuing along ventral aspect of penis, terminating at bifid tip.

Alimentary system

Foregut. Mouth at tip of long, extensible snout. Paired jaws present at anterior ends of dorsal folds; jaw composed of rods with laterally overlapping homogeneous layer. Sub-radular membrane incompletely covering odontophore. Sub-radular organ present (Fig. 5D, sro) forming small, rounded protuberance within shallow sublingual cavity. Radular sac straight, extending short distance back from buccal cavity. Salivary gland ducts passing through nerve ring. Glandular mid-ventral fold present (Fig. 8E, vf), beginning within buccal cavity, extending into anterior oesophagus. Short ventro-lateral folds present within anterior oesophagus (Fig. 9E, vlf). Glandular outpocketings of anterior oesophagus absent. Dorsal folds long and slender in cross-section, curving medially. Mid-oesophagus expanding into large, sac-like crop, lined with thin, pendulous longitudinal folds; septate oesophageal gland absent.

Midgut. Oesophagus entering midgut ventrally, on left (Figs 12B, e). Lumen of midgut elongate and roughly conical, curving and narrowing to shallow pouch (ce) on left side. Well-developed sorting area (sa) lining left wall, extending posteriorly from oesophageal aperture. Large, free-standing vertical flap (if) separating intestinal and oesophageal apertures. Several low folds (cf) on right side of sorting area, extending posteriorly and terminating near posterior tip of gastric chamber. Digestive gland ducts paired (dgd); anterior duct opening under lip of style sac (ss), posterior duct opening mid-ventrally to left of glandular pad (gp). Prominent gastric (gs) shield present ventro-laterally on right. Glandular pad barely projecting posteriorly past gastric shield. Proximal, free tip of major typhlosole extending into gastric chamber. Style sac (ss) and intestine (int) separate. Suture visible within style sac where typhlosoles have fused; ciliary tract of tall cilia on major typhlosole visible projecting from suture into style sac (Fig. 21C). Style sac epithelium bearing differentiated cilia. Crystalline style present. Ciliary currents unknown.

Hindgut. Intestine exiting directly from gastric chamber, looping under proximal style sac, extending to right through anterior lobe of digestive gland to kidney. Intestine curving dorsally over posterior end of kidney, then turning anteriorly.

Reno-pericardial system

Kidney large, elongate (Fig. 22D). Excretory lamellae extending within kidney roof and along right wall. Nephridial gland (ng) present forming broad, flat, narrowly triangular organ within roof. Afferent renal vessel entering kidney posteriorly, extending forward within kidney floor, supplying approximately four to six clusters of excretory tissue along right wall. Afferent renal vessel emerging from floor near reno-pericardial canal, curving dorsally past nephropore (np), supplying nephridial gland, traversing midline of gland.

Nervous system and sensory structures

Nervous system epiathroid, right and left dialyneurous. Nerve ring lying immediately behind buccal mass at base of snout. Buccal ganglia present at back of buccal mass just anterior to nerve ring. Supra-oesophageal and sub-oesophageal connectives long. Accessory pedal ganglia present. Tentacular nerve bifid, bearing prominent tentacular ganglion at base of tentacle. Paired visceral ganglia present straddling oesophagus near base of cephalic haemocoel. Two statocysts with large, ovoid statoliths lying dorso-laterally on pedal ganglia behind pedal connectives. Large eyes well above tentacle bases. Osphradium long and bipectinate, extending from inhalant margin to base of mantle cavity.

Discussion

In general, existing descriptions of strombid female reproductive anatomy do not allow comparisons to homologous organs found in other caenogastropods. For example, Reed (1995b) described only a single type of glandular cell comprising the ‘uterus’ in six species of *Strombus*. However, there are two types of gland present in *S. mutabilis*, homologues of the albumen and capsule glands of other caenogastropods. The open ‘uterine terminus’ described by Reed (1995b) undoubtedly corresponds to the capsule gland, although this portion of the oviduct is much shorter in *S. mutabilis*.

Similarly, sperm storage organs of *Strombus* species have been rarely described (e.g. Haller, 1893; Woodward, 1894; Bergh, 1895a). While clarifying the presence of both a receptacle and a bursa, Reed (1995b) identified the anterior-most storage structure as a receptacle, the more posterior structure a bursa copulatrix, based on inferred functional criteria. However, the alternative interpretation offered here, based on the presence of orientated vs. unorientated sperm, is consistent with the position of putative homologues in other caenogastropods. *Strombus mutabilis* is noteworthy among strombids in possessing two openings to the albumen gland; one communicating with the joint receptacle/bursa aperture and a second opening broadly to the capsule gland.

Male reproductive anatomy of *Strombus mutabilis* is congruent with previous descriptions (Bergh, 1895a; Risbec, 1927; Reed, 1995a). The penes in *Strombus* species vary in the presence or absence of 'auxiliary prongs' and the size and shape of finger-like projections at the tip of the verge (Bergh, 1895a; Risbec, 1927; Reed, 1995a); alternatively, the penis may be long and narrow with a blunt, deeply incised tip (Woodward, 1894).

The strombid mid-oesophagus is often described as a simple, conducting tube. However, the presence of a voluminous crop (Woodward, 1894; Amaudrut, 1898; Risbec, 1927), as well as the presence of prominent, longitudinal folds (Haller, 1893; Amaudrut, 1898; Graham, 1939) has been reported in several species.

Although existing descriptions are rarely sufficiently detailed to place all aspects of midgut morphology into a comparative context, it is clear that the strombid midgut is characterized by the presence of a separate style sac, a prominent curving gastric shield and two digestive gland apertures (Haller, 1893; Woodward, 1894; Bergh, 1895a; Risbec, 1927). Little's (1965) more detailed description identified several features congruent with the present description, including a sorting area to the left of the oesophagus, folds bounding the sorting area that extend into the gastric chamber, a glandular pad that extends a short distance posteriorly from the gastric shield, and a free major typhlosole tip projecting from the style sac lip. With rare exceptions (Risbec, 1927), position of the digestive gland ducts is rather conservative: one adjacent to the style sac and a second near the gastric shield (Haller, 1893; Woodward, 1894; Bergh, 1895a; Little, 1965).

Anatomical studies including the reno-pericardial system identify the presence of a nephridial gland in *Strombus* (Haller, 1893; Bergh, 1895a; Risbec, 1927). Little's (1965) more detailed investigation of *Strombus gigas* clearly described the dorsal branch of the afferent renal vessel supplying the nephridial gland and is depicted along the midline of the gland.

Strombid nervous systems have been described consistently as dialyneurous, zygoneurous, with two visceral ganglia (Bouvier, 1887; Haller, 1893; Bergh, 1895a; Amaudrut, 1898; Risbec, 1927; Little, 1965). Minor differences include the condition of the tentacular nerve, which may be single (Little, 1965), single with a tentacular ganglion (Risbec, 1927) or bifid and lacking a tentacular ganglion (Bouvier, 1887). Position of the statocysts appears to be variable within strombids, and has been described as anterior (Bouvier, 1887; Haller, 1893; Bergh, 1895a; Little, 1965) or posterior (Woodward, 1894) to the pedal ganglia.

FAMILY CALYPTRAEIDAE: *CREPIDULA PLANA* SAY 1822

Material Examined

Cape Henlopen, Virginia (USNM 890937).

External anatomy and mantle cavity

Foot narrow anteriorly, broadly rounded posteriorly. Duct of pedal gland opening to shallow propodial groove. Head flattened dorso-ventrally. Mantle cavity extending down left side of visceral mass. Hypobranchial gland large and well developed. Mantle edge folded anteriorly to form food pouch. Gill filaments long and slender with skeletal rods. Ctenidial axis glandular, forming endostyle.

Reproductive system

Protandrous hermaphrodites. In male phase, testis lying alongside tubules of digestive gland, extending down sides of visceral mass. Testis opening anteriorly to broad and tightly coiled seminal vesicle lying just behind base of mantle cavity. Short vas deferens emerging from seminal vesicle, opening to seminal groove (Fig. 3C, sg) at base of mantle cavity. Prostate (pr) small, comprising small region of glandular cells at base of mantle cavity, extending short distance along seminal groove. Prostatic tissue forming two distinct concentric layers of basophilic cells. Seminal groove extending down neck and along ventral surface of elongate, narrow penis (pe) with curved terminal papilla.

Ovary dorsally overlying digestive gland. Broad renal oviduct opening to approximately four or five small seminal receptacles (Fig. 2B, rcs) with narrow ducts. Gonopericardial canal absent. Oviduct opening to short, compact pallial oviduct comprising closed albumen (ag) and capsule (cg) glands. Long vagina (v) emerging from capsule gland, terminating in narrow, elongate female opening (fo).

Alimentary system

Foregut. Paired jaw weakly developed at anterior ends of dorsal folds; jaw composed of rods with laterally overlapping homogeneous layer. Subradular membrane incompletely covering odontophore. Small subradular organ present (Fig. 5E, sro) in shallow sublingual cavity. Long, tubular salivary glands (Fig. 6E, sgl) by-passing circum-oesophageal nerve ring. Short mid-ventral fold (Fig. 9F, vf) and flanking ventro-lateral folds (vlf) present in anterior oesophagus. Mid-oesophagus uniformly folded; septate oesophageal gland absent (Fig. 11D, me).

Midgut. Midgut occupying apex of visceral mass. Oesophagus opening mid-ventrally (Fig. 14B, e), near distal end of ventro-lateral gastric shield (gs). Sorting area (sa) well developed anterior to oesophageal aperture. Ciliary currents flowing toward intestinal groove within sorting area. Ciliated fold (cf) extending posteriorly from proximal end of minor typhlosole, passing to left of oesophageal aperture. Glandular pad (gp) extending posteriorly from gastric shield, paralleling ciliated fold to posterior end of midgut. Folds terminating within small caecum (c) on right behind gastric shield. Paired digestive gland ducts (dgd) opening at proximal end of major typhlosole (t1). Style sac region characterized by horizontally folded epithelium bearing differentiated cilia. Raised tract of cilia (ctr) present on both typhlosoles (t1, t2). Crystalline style present. Ciliary currents flowing clockwise within style sac region when viewed from behind.

Hindgut. Intestine exiting style sac and extending from left to right, looping broadly and slightly posteriorly around kidney, then turning anteriorly.

Reno-pericardial system

Kidney anteriorly surrounding pericardium, slightly overhanging pallial cavity. Afferent renal vessel entering kidney floor anteriorly, just in front of renopericardial duct, supplying excretory tissue along floor. Excretory tissue ramifying dorsally within roof and along walls. Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous, left dialyneurous (Fig. 24C). Supra-oesophageal (sp) and sub-oesophageal (sb) connectives extremely short. Circum-oesophageal nerve ring (Fig. 6E, nr) lying well posterior to buccal mass. Tentacular nerve (tn) splitting upon entering tentacle into two nerves of equal size. Visceral loop short bearing two small visceral ganglia (vg) straddling oesophagus. Statocysts with statoliths (Fig. 24C, sc) present on dorso-lateral surfaces of pedal ganglia. Osphradium unipectinate (Fig. 6E, os).

Remarks

In a series of papers on development of the sex organs, emphasizing the transformations that occur during sex change, Gould (1917, 1949, 1952) provided the essential features of reproductive anatomy for *Crepidula plana* which are congruent with those provided above. This includes the presence of a tightly coiled seminal vesicle, seminal groove and penis behind the right cephalic tentacle in males and, in females, the presence of the gonopericardial canal, the presence of the seminal receptacle, and the absence of the bursa copulatrix. However, the detailed morphology of neither the seminal receptacles nor glandular pallial oviduct was described. In contrast to Gould (1917), the presence of a gonopericardial canal could not be confirmed in the present study.

Discussion

The mantle cavity and mechanism of ciliary suspension feeding in the Calyptraeidae has been well studied (e.g. Orton, 1912, 1913; Yonge, 1938; Werner, 1953). Calyptraeids possess a triangular mantle cavity extending over an elongate neck and along the left side of a flattened visceral mass; a large gill bearing skeletal rods is present, with an elaborate mucus-producing ‘endostyle’ along its axis (Orton, 1912, 1913; Kleinstüber, 1913; Yonge, 1938; Graham, 1952). Members of the family are unique among ciliary feeders because they obtain food particles from a food groove on the right side of the neck, in addition to a food pouch that collects particles at the anterior edge of the mantle skirt via a modification of the rejection current of other caenogastropods (Yonge, 1938).

Calyptraeids typically possess seminal receptacles at or near the junction of the renal and pallial oviducts; the number of receptacles and the nature of their connection to the oviduct can vary (single duct or one per receptacle). A gonopericardial canal is present only in females and generates during the transition between male and female phases (Giese, 1915; Ishiki, 1939; Graham, 1952; Fretter & Graham, 1962; Yipp, 1983). The pallial oviduct of calyptraeids is characterized by the absence of a bursa copulatrix and a narrow vagina that can vary greatly in length (Kleinstüber, 1913; Fretter & Graham, 1962; Yipp, 1983). The pallial vas deferens lacks prostatic development (Graham, 1952; Yipp, 1983), but rudiments of female glands in the male phase may have a prostatic function (Giese, 1915; Graham, 1952).

Midgut features are conservative among described calyptraeids, including the development and position of sorting areas, the extension of the minor typhlosole and parallel glandular pad across the midgut floor, the presence of a caecum, the position of the gastric shield, and the concavity of the major typhlosole (Fretter & Graham, 1962; Yipp, 1980; pers. obs.). One variable feature includes the position and number of digestive gland ducts. Graham (1939) found four ducts within the midgut of *Crepidula fornicata* and *Calyptraea chinensis*; two opening at the proximal end of the major typhlosole, and two opening within the caecum. Development of the major typhlosole terminal lappet also varies between species (Fretter & Graham, 1962; pers. obs.). In addition, the ciliary tract on the minor typhlosole, present in *Crepidula plana*, is lacking in *C. fornicata* (pers. obs.).

Calyptraeid nervous systems have been described as right zygoneurous and left dialyneurous (Graham, 1952). A notable exception is *Crepidula fornicata*, which has a connection between the left dialyneury and a nerve from the left visceral ganglion, in addition to a dialyneurous connection between nerves from the right visceral and the sub-oesophageal ganglia (Graham). *Crepidula plana* lacks secondary connections involving nerves from the visceral ganglia. Bouvier (1887) reported the presence of a left zygoneury in *C. fornicata*?. This could not be confirmed by Graham.

FAMILY BITHYNIIDAE: *BITHYNIA TENTACULATA* (LINNAEUS 1758)

Material Examined

Alexandria, Virginia (USNM 890938).

External anatomy and mantle cavity

Mantle edge smooth. Pedal gland opening to shallow flap along anterior margin of propodium. Anterior kidney chamber extending into pallial roof. Short, monopectinate osphradium present along anterior one third of ctenidium. Operculum present.

Reproductive system

Gonopericardial canal present. Renal oviduct forming seminal receptacle bearing orientated sperm. Oviduct opening to posterior bursa just before entering glandular gonoduct. Pallial oviduct closed along entire length, opening anteriorly via short vagina. Bursa copulatrix extending posteriorly along surface of capsule gland, opening anteriorly to vagina. Vas deferens convoluted, functioning as seminal vesicle. Pallial vas deferens closed along entire length, from prostate at base of mantle cavity to tip of penis. Tubular, accessory prostate gland opening to subterminal lateral lobe of penis.

Alimentary system

Foregut. Weakly developed jaws present at anterior ends of dorsal folds; jaw composed of rods with laterally overlapping homogeneous layer. Subradular membrane incompletely covering odontophore. Subradular organ present forming vertical ridge of tissue within long, narrow sublingual cavity. Short, tubular salivary glands (Fig. 6D, sgl) overlying nerve ring (nr). Radular sac short. Anterior oesophagus bearing single mid-ventral fold (Fig. 9G, vf) and two, broad ventrolateral folds (vlf). Mid-ventral fold gradually merging with right glandular field posteriorly within anterior oesophagus, producing paired ventral folds with intervening ciliated groove. Ventral glandular folds diminishing through region of torsion within circum-oesophageal nerve ring. Mid-oesophagus uniformly folded; septate oesophageal gland absent.

Midgut. Oesophagus (Figs 15A, e) opening to midgut ventrally to left of ventro-lateral gastric shield (gs). Paired, ciliated folds emerging from intestinal groove, extending posteriorly to left of oesophageal aperture. Left fold diminishing; right fold (cf) curving to right at posterior end of gastric chamber, terminating within shallow caecum (c) behind gastric shield (gs) on right. Development of fold (cf) variable, in some individuals forming shallow shelf subdividing base of gastric chamber. Glandular pad (gp) projecting only short distance posterior to gastric shield. Paired digestive gland ducts (dgd) present to left of gastric shield. Style sac region characterized by presence of paired typhlosoles (t1, t2), differentiated cilia and crystalline style. Broad tract of raised cilia (ctr) present on major typhlosole.

Hindgut. Intestine emerging from style sac, extending posteriorly beside style sac, curving around distal end of kidney, then turning anteriorly.

Reno-pericardial system

Kidney large and elongate, comprising posterior, visceral chamber and anterior pallial chamber. Visceral lumen large, extending posteriorly past pericardium (Fig. 22B, per) to gastric chamber. Visceral lumen subdivided by vertical septum of excretory tissue beside pericardium. Pallial chamber alongside rectum, extending almost to anus, with weakly developed excretory tissue along walls surrounding large central lumen. Afferent renal vessel entering floor of visceral kidney lumen, at base of mantle cavity, in front of reno-pericardial canal (rpc) and septum. Ventral branches extending anteriorly and posteriorly, supplying excretory tissue within pallial and visceral chambers. Branch of afferent renal vessel extending dorsally, posteriorly passing nephropore (np), supplying small mass of excretory tissue, then entering nephridial gland (ng).

Nervous system and sensory structures

Nervous system epiathroid, right and left dialyneurous. Nerve ring lying just behind base of buccal mass. Tentacular nerve (Fig. 6D, tn) with large basal swelling, splitting into three nerves of approximately equal size (one slightly larger) persisting length of tentacle. Metapodial and propodial ganglia present. Metapodial commissure present. Visceral loop bearing single visceral ganglion to right of posterior oesophagous. Statocysts with single statolith present dorso-laterally on pedal ganglia.

Remarks

There are several published descriptions on the anatomy of this species. Reproductive details have been provided in Krull (1935), Ankel (1936) and a thorough account by Lilly (1953) that is in agreement with the report here. However, Lilly, while noting the presence of sperm in the renal oviduct and unorientated sperm in the posterior bursa, identified the latter as a seminal receptacle; Fretter & Graham (1962) later identified the renal oviduct as a seminal receptacle. The gonopericardial canal has been described as present (Krull, 1935) or absent (Lilly, 1953).

Graham (1939) provided a brief description of the foregut, noting that the walls of the large buccal cavity are cuticularized, the salivary glands are small, and the dorsal folds conspicuous. Within the anterior oesophagus, Graham recorded the presence of paired ventral folds. Krull (1935) remarked that the jaw was composed of small scales. Gross midgut morphology was figured by Krull and elaborated by Graham. There are several discrepancies between these and the present description. Graham described both folds emerging near the minor typhlosole and intestinal groove as curving into the pocket behind the gastric shield; the latter was characterized as being dorsally situated. Digestive gland ducts have been cited as paired (Krull, 1935) or single (Graham, 1939; Fretter & Graham, 1962).

The pallial kidney extension was described by Lilly (1953); Fretter & Graham (1962) discussed the functional significance of this feature.

All basic features of the nervous system have been documented by Bouvier (1887); Krull (1935) made several clarifications, including the presence of a right dialyneury. Krull noted the presence of a bifid tentacular nerve and the absence of the tentacular basal swelling which disagree with the present description. The metapodial commissure has been recorded as absent (Bouvier, 1887) or present (Simroth, 1896–1907; Krull, 1935).

Discussion

Traditionally, bithyniids have been classified near (Wenz, 1938–44) or within (Thiele, 1928a) the Hydrobiidae. However, bithyniids possess a number of features not found in hydrobiids, including features of the head-foot, mantle cavity, operculum, egg capsules, and differ in feeding and reproductive modes (Taylor, 1966). In spite of these differences, Hershler & Thompson (1988) continued to support a close relationship between the Bithyniidae and the hydrobiid subfamilies Amnicolinae and Emmericiinae, based on the shared presence of a unique caecum-like accessory prostate within the penis. A preliminary phylogenetic analysis of rissooidean gastropods placed the Bithyniidae firmly within the superfamily, but suggested that the family is a divergent lineage within the group (Ponder, 1988). Preliminary results of molecular phylogenetic analysis suggest that the Bithyniidae and Hydrobiidae are not closely related (R. Hershler, pers. comm.). In general, relationships of bithyniid gastropods to other rissooideans remains poorly understood. Despite this uncertainty, for comparative purposes discussion will be limited to hydrobiids and bithyniids.

The female reproductive system of hydrobiids consists of a coiled oviduct, a renal oviduct modified into a posterior bursa and seminal receptacle, and a closed pallial oviduct with a ventral channel; a gonopericardial duct may be present or absent (Krull, 1935; Davis, 1980; Hershler & Davis, 1980; Davis, Mazurkiewicz & Mandravvhia, 1982; Davis & Pons da Silva, 1984; Davis & Mazurkiewicz, 1985; Hershler, 1985; Ponder *et al.* 1991; Hershler & Frest, 1996). In addition, much of the albumen gland lies posterior to the base of the mantle cavity. *Bithynia tentaculata* also possesses a coiled oviduct; the recurvent portion, rather than a discrete sac, forming a seminal receptacle as in *B. caerulane* (Beliakova-Butenko, 1974). Only the posterior bursa of *B. tentaculata* is visceral in position.

As in *Bithynia tentaculata*, hydrobiid male reproductive anatomy is characterized by the presence of a seminal vesicle, a closed prostate and pallial vas deferens and a lobate penis with the penial duct opening at its tip (Davis, 1980; Hershler & Davis, 1980; Davis *et al.*, 1982; Davis & Pons da Silva, 1984; Davis & Mazurkiewicz, 1985; Hershler & Frest, 1996). As stated above, bithyniids possess a unique accessory gland that opens to a lateral lobe of the penis (Thiele, 1928a; Beliakova-Butenko, 1974), suggesting an affinity to the hydrobiid subfamilies Amnicolinae and Emmericiinae (Seshaiya, 1930; Hershler & Thompson, 1988).

Hydrobiid and bithyniid foregut morphology is similar in that the salivary glands do not pass through the circum-oesophageal nerve ring, but lie on top of it (Seshaiya, 1930; Hershler & Davis, 1980). Jaws are present (Seshaiya, 1930; Ponder *et al.*, 1991). In hydrobiids, the dorsal folds of the mid-oesophagus are so prominent as to subdivide the lumen of the oesophagus into three longitudinal channels (Graham, 1939; Ponder *et al.*, 1991). In one species, the central channel is completely closed off for a short distance by the fusion of the dorsal folds to the ventral wall of the oesophagus (Bregenzer, 1916). No such subdivision occurs in *Bithynia tentaculata*.

Bithyniid and hydrobiid midgut morphology is rather complex, with diverse patterns of outpocketing and folding (Hershler & Davis, 1980; Davis *et al*., 1982; Davis & Pons da Silva, 1984; Ponder *et al*., 1991; Davis & Mazurkiewicz, 1985 Hershler, 1985). Although sometimes lacking (Seshaiya, 1930; Hershler & Davis, 1980), the caecal extension of other hydrobiids represents an outpocketing of a different part of the midgut as compared to *Bithynia tentaculata*, reaching its deepest dimension posteriorly or along the left side of the midgut (Davis *et al*., 1982; Ponder *et al*., 1991). Several prominent folds originating near the oesophagus and/or intestinal groove extend across the midgut floor; a variable number of these folds terminate within the deepest part of the caecal extension (Davis *et al*., 1982; Ponder *et al*., 1991). However, similar to *B. tentaculata*, one or sometimes two folds may continue around the posterior end of the midgut, terminating on the right behind the gastric shield (Davis *et al*., 1982; Ponder *et al*., 1991).

The kidney of hydrobiids and bithyniids is large with a posterior (Robson, 1920) or both an anterior and posterior extension (Seshaiya, 1930; Krull, 1935). A nephridial gland is present (Seshaiya, 1930; Krull, 1935; Ponder *et al*., 1991). Although Krull did not describe blood supply to the gland in *Lithoglyphus naticoides*, the diagrammatic representation of the kidney suggests that a large branch of the afferent renal vessel supplies the gland as in *Bithynia tentaculata*.

The nervous system of hydrobiids, as *Bithynia tentaculata*, is epiathroid and left dialyneurous (Seshaiya, 1930; Hershler & Davis, 1980); Krull (1935) described also a right dialyneury in *Lithoglyphus naticoides*. Seven characteristic nerves emerge from the cerebral ganglia; the basal swelling of the tentacular nerve varies in size (Krull, 1935; Hershler & Davis, 1980; Ponder *et al*., 1991). Tentacular nerve branching patterns have not been described, thus it is unknown if the trifid tentacular nerve of *Bithynia tentaculata* is typical. The pedal ganglia bear propodial and metapodial swellings. The metapodial commissure may be present (Krull, 1935; Hershler & Davis, 1980) or absent (Seshaiya, 1930).

FAMILY LITTORINIDAE:
LITTORINA LITTOREA LINNAEUS 1758

Material examined

Wood's Hole, Massachusetts (USNM 890939).

External anatomy and mantle cavity

Pedal gland opening to anterior margin of propodium. Operculum present. Mantle margin smooth. Hypobranchial gland well developed.

Reproductive System

Renal oviduct functioning as seminal receptacle, storing orientated sperm. Gonopericardial canal absent. Oviduct opening to glandular gonoduct at base of mantle cavity. Pallial oviduct closed along entire length. Anterior bursa present.

Proximal vas deferens convoluted, forming seminal vesicle. Prostate open to mantle cavity. Open seminal groove extending from prostate to tip of penis lying behind right cephalic tentacle.

Alimentary system

Foregut. Radula taenioglossate. Paired cartilages supporting odontophore. Subradular membrane almost completely covering odontophore. Weakly glandular, narrow papilla, extending forward ventral to radular ribbon (Figs 4E, 5F, sro). Dorsal surface of papilla lined with thin layer of cuticle. Buccal cavity lined with cuticle. Glandular mid-ventral fold (Fig. 8F, vf) beginning in buccal cavity, extending posteriorly to buccal pouches, then diminishing. Mid-ventral fold not continuing into mid-oesophagus. Buccal pouches opening to posterior buccal cavity and anterior oesophagus. Anterior ducts of buccal pouches lined with highly glandular, acidophilic epithelium, expanding dorsally into buccal pouches. Remainder of pouch epithelium strongly basophilic. Apertures of pouches bounded by prominent ventro-lateral folds (Fig. 9H, vlf). Oesophageal gland present within mid-oesophagus, forming transverse septae of glandular tissue partially occluding oesophageal lumen.

Midgut. Oesophagus (Fig. 15B, e) opening near proximal end of minor typhlosole (t2); mucus-secreting pouch at base of minor typhlosole absent. Three ducts of digestive gland (dgd) and surrounding ciliary sorting area (sa) lying at proximal end of major typhlosole (t2). Ciliary currents in sorting area flowing anteriorly toward intestinal groove. Gastric shield (gs) ventrolateral on right. Gastric chamber cuticularized. Ciliated fold (cf) bearing short, dense cilia emerging near minor typhlosole, running posteriorly to left of oesophageal aperture. Ciliated fold bordering grooved tract bearing long cilia. Grooved tract emerging from under lip of ciliated ridge near oesophageal aperture, paralleling ridge posteriorly. Grooved tract curving around posterior periphery of gastric chamber, extending short distance anteriorly along right wall. Currents within ciliary tract flowing posteriorly. Low, ciliated ridge (cs) extending posteriorly along left side of gastric shield. Currents over ciliated ridge flowing posteriorly and towards right side. Crystalline style absent. Raised tract of cilia on major typhlosole absent. Currents flowing clockwise within style sac when viewed from behind.

Hindgut. Intestine emerging from style sac, curving posteriorly around rear wall of kidney before turning anteriorly.

Reno-pericardial system

Afferent renal vessel entering kidney floor anteriorly, extending dorsally and ramifying to supply excretory tissue. Nephridial gland present. Branch from afferent renal vessel supplying nephridial gland absent.

Nervous system and sensory structure

Nervous system epiathroid, left dialyneurous. Nerve ring lying just behind base of buccal mass. Tentacular nerve bifid. Metapodial commissure present. Visceral ganglia paired. Statocysts with single statoliths present postero-dorsally on pedal ganglia, slightly asymmetrical. Small eyes present at lateral bases of cephalic tentacles. Osphradium comprising long, thin, ciliated ridge along base of ctenidium.

Remarks

The anatomy of this species has been well established in several published descriptions, most notably a thorough account by Fretter & Graham (1962). Previous studies include those of Ankel (1936, 1937), who provided information on foregut anatomy and the nervous sytsem, and Johansson (1939) who also provided details on foregut anatomy. Lacking from these accounts are descriptions of the unique, papilla-like subradular organ, and the ventral folding of the anterior oesophagus.

Johansson (1939) and Graham (1949) described midgut anatomy for this species. The present description agrees with these on most major points. However, there are several discrepancies. Both Johansson and Graham described only two ciliary tracts leading posteriorly into the gastric chamber; one bounding the oesophagus to the left and a second passing to the left of the gastric shield. In addition, Graham found a mucus-secreting pouch at the base of the minor typhlosole; ciliary currents were described as flowing anteriorly to the left of the gastric shield.

The metapodial commissure has been reported as present (Fretter & Graham, 1962; Marcus & Marcus, 1963) or absent (Simroth, 1896–1907; Ankel, 1936).

Discussion

The basic layout of the reproductive system and the foregut of littorinids is largely congruent with *Littorina littorea*. Variable features of reproductive anatomy include the presence or absence of a gonopericardial canal, the looping patterns of the gladular oviduct, an open or closed prostate and seminal groove, and the morphology of the penis and accessory glands (e.g. Linke, 1933; Johansson, 1939; Fretter & Graham, 1962; Marcus & Marcus, 1963; Bingham, 1972; Reid, 1986).

All littorinids described possess an elongate, cuticularized gastric chamber, with at least one ciliary tract (e.g. Marcus & Marcus, 1963; Morton, 1975); length of the gastric chamber is variable and is not correlated with habitat (Reid, 1986). The number of ciliary tracts and digestive gland ducts and the size of the sorting area are also variable (e.g. Marcus & Marcus, 1963; Reid, 1986). Despite inconsistencies between the present and previous descriptions as summarized above, the present results are congruent with investigations of *Tectarius muricatus* (pers. obs.) and *L.* (*Austrolittorina*) *unifasciata antipoda* (as *Melarhaphe oliveri*) (Morton, 1975). All three species possess three ciliary tracts; one extending from the oesophageal aperture and curving around the base of the gastric chamber with two flanking tracts. Similar to Graham (1949), Marcus & Marcus (1963) documented a mucus-secreting pouch at the proximal end of the style sac in *L. angulifera*. *Littorina littorea* is intriguing because it lacks a ciliary tract on the major typhlosole; the tract is present in another non-style-bearing littorinid, *T. muricatus* (pers. obs.).

Although much of the detailed information regarding the littorinid nervous system concerns *Littorina littorea* (Bouvier, 1887; Johansson, 1939; Fretter & Graham, 1962), additional studies have found no significant differences in organization in other species (Johansson, 1939; Marcus & Marcus, 1963). One minor exception is the metapodial commissure, which has been reported as present (Johansson, 1939; Fretter & Graham, 1962; Marcus & Marcus, 1963) or absent (Simroth, 1896–1907; Ankel, 1936).

FAMILY NATICIDAE:
NEVERITA DUPLICATA (SAY 1822)

Material examined

Wood's Hole, Massachusetts (USNM 890941). Only immature males and females were available for study. Thus, observations on reproductive anatomy are preliminary.

External anatomy and mantle cavity

Mantle edge smooth with single, small pallial tentacle lying within exhalent margin. Hypobranchial gland weakly folded. Bipectinate osphradium lying near inhalant margin, approximately one-half length of ctenidium. Foot massive with extensive propodium. Anterior edge of propodium sharply indented at midline. Anterior pedal gland opening along junction of propodium and metapodium. Large, horny operculum present. Cephalic tentacles flattened and triangular with shallow, ventral groove extending along outer edges. Two broad, flattened lobes present on either side of cephalic tentacles, bearing recessed eyes along ventral surfaces. Eyes weakly pigmented, retaining lens. Rhynchostome opening ventrally.

Reproductive system

Gonad dorsally overlying digestive gland on right. Vas deferens forming convoluted seminal vesicle. No gonopericardial connection present in females or males. Glandular pallial gonoduct open in both sexes. No sperm storage structures apparent associated with pallial or renal oviduct. Closed pallial vas deferens crossing neck from open prostate to penis behind right cephalic tentacle.

Alimentary system

Foregut. Radula taenioglossate. Foregut modified into short acrembolic proboscis lying over circum-oesophageal nerve ring when retracted. Transverse mouth opening at tip of extended proboscis, surrounded by tumid outer lips with ventral cleft. Accessory boring organ present under lip, forming large flattened pad bearing rodlet border. Large, paired jaws present at distal tips of dorsal folds. Sublingual cavity shallow. Subradular membrane incompletely covering surface of odontophore. Small subradular organ present (Figs 4F, 5G, sro), forming rounded, folded and glandular protuberance. Anterior oesophagus flattened, bearing ciliated dorsal folds and dorsal food groove and non-ciliated ventral channel (Fig. 10A, vc); no ventral folds present. Two small, ciliated ducts emerging from ascinous salivary gland, passing through nerve ring embedded in dorso-lateral walls of oesophagus. Large odontophoral retractor muscle attaching ventrally to buccal mass and splitting, inserting onto lateral walls of cephalic haemocoel. Large, septate oesophageal gland present within mid-oesophagus. Surface of septae sculptured with fine, anastomosing channels. Gland differentiated into small anterior light coloured region and posterior, brown region. Dorsal food groove, u-shaped and enclosed by one of flanking folds.

Midgut. Oesophagus (Fig. 16A, e) entering posterior end of narrow, elongate midgut. Gastric shield absent. Left, ventral wall of gastric chamber lined with well-developed sorting area (sa), extending from oesophageal aperture to intestinal groove (ig). Sorting area flanked on right by single, low ciliated fold (cf). Ciliated fold extending between posterior digestive gland duct (dgd), opposite oesophageal aperture, and anterior duct near minor typhlosole (t2). Sorting lamellae comprising two sets of parallel folds, directed anteriorly and obliquely toward midline of sorting area. Ciliary currents within sorting area flowing toward intestinal groove. Currents within gastric chamber flowing anteriorly along right wall and clockwise along ventral floor. Style sac region (ss) comprising two, low typhlosoles (t1, t2) bounding short, narrow region of transverse folds bearing low, compact cilia. Ciliary tract on major typhlosole absent. Currents flowing clockwise within style sac region, posteriorly within intestinal groove.

Hindgut. Intestine emerging from style sac, curving slightly posteriorly and dorsally along rear wall of kidney and pericardium, then continuing anteriorly.

Reno-pericardial system

Excretory tissue of kidney divisible into three parallel, histologically distinct lobes (Fig. 23A). Right lobe dorsally surrounding intestine, comprising folded, tubular excretory lamellae. Central lobe anteriorly overhanging nephropore, comprising villous, massive excretory lamellae. Lobe bordering pericardium on left side of kidney, comprising hypertrophied nephridial gland (ng). Afferent renal vessel entering kidney floor anteriorly, just behind reno-pericardial canal (rpc). Afferent renal vessel splitting into two large branches, one extending antero-dorsally along front wall of kidney and supplying right lobe, second branch extending postero-dorsally. Postero-dorsal branch supplying both right and central lobes.

Nervous system and sensory structures

Nervous system epiathroid, left zygoneurous. Nerve bundle emerging from each cerebral ganglion containing tentacular and optic nerves. Tentacular and optic nerves becoming distinct short distance from nerve ring. Single tentacular nerve producing numerous, small branches innervating tentacle and cephalic haemocoel. Four nerves from each cephalic ganglion innervating proboscis; one representing long buccal connective. Large pedal ganglia adjacent to cerebral and pleural ganglia; pedal connectives short. Prominent propodial ganglia present at anterior ends of pedal ganglia. Pedal nerves ganglionated. Sub-oesophageal and pleural ganglia adjacent; supra-oesophageal connective long. Pallial nerves from sub-oesophageal and right pleural ganglia contacting, but no dialyneury formed. Visceral loop bearing two asymmetrical visceral ganglia straddling posterior oesophagus. Statocysts with single statoliths lying ventrally and anterior to circum-oesophageal nerve ring.

Discussion

Much of the literature pertaining to naticids concerns their predatory behaviour. Accordingly, anatomical descriptions are largely restricted to foregut anatomy – the radula and accessory boring organ in particular. Thus, few comprehensive anatomical studies are available, with only rare accounts of reproductive, renal, and nerve morphology.

The naticid foregut is characterized by the presence of an acrembolic proboscis, large jaws and an accessory boring organ (Hirsch, 1915; Eales, 1923; Ziegelmeier, 1954; Fretter & Graham, 1962; Marcus & Marcus, 1965). The organ has been found to consist of two distinct epithelia; one secretory and one comprising a microvillous brush border extending through a matrix of protein and chitin (Bernard & Bagshaw, 1969). This and other studies have found a common fine-structural construction between the proboscidial accessory boring organ of naticids and the pedal accessory boring organ of muricids (Carriker, 1981). Glands associated with the foregut include an ascinous salivary gland and a large oesophageal gland (Bouvier, 1887; Hirsch, 1915; Eales, 1923; Ziegelmeier, 1954; Fretter & Graham, 1962; Marcus & Marcus, 1965; Reid & Friesen, 1980). The oesophageal gland is differentiated into two discrete regions and comprises septae which are finely sculptured with radiating canals (Reid & Friesen). The dorsal food groove is u-shaped (Fretter & Graham; Reid & Friesen).

The midgut of naticids is elongate with the oesophageal aperture opening at the posterior tip; a gastric shield is absent (Simroth, 1896–1907; Hirsch, 1915; Fretter & Graham, 1962; Reid & Friesen, 1980). Several aspects of midugt morphology vary within the family. The large sorting area may extend the full length of the gastric chamber along the left (Reid & Friesen), or may be restricted to a rather small area near the intestinal groove (Fretter & Graham). The digestive gland ducts may open at opposite ends of the sorting area (Hirsch; Reid & Friesen), or both may open near the intestinal groove (Fretter & Graham). The ciliated fold to the right of the sorting area is accompanied by a groove that joins the midline rejection tract of the sorting area (Reid & Friesen); no distinct groove is present in *Neverita duplicata*. Fretter & Graham reported that only vestiges of the typhlosoles and style sac region remain. Similarly, Reid & Friesen reported that no trace of a style sac region is apparent, but clearly show ciliary currents flowing in a clockwise direction in this portion of the gut.

The excretory tissue is subdivided into two lobes that are histologically and macroscopically distinct (Simroth, 1896–1907) – the so-called folded and absorbing kidney lobes of Fretter & Graham (1962). A nephridial gland is present; although extremely large in *N. duplicata*, the gland may be restricted to a relatively narrow band along the pericardial wall (Fretter & Graham). The afferent renal vessel splits to supply both lobes (Fretter & Graham).

The naticid nervous system is epiathroid and left zygoneurous with long buccal connectives (Bouvier, 1887; Eales, 1923). Three cerebral nerves innervate the proboscis (Bouvier). Sensory structures include a large bipectinate osphradium with leaflets of a complex structure (Marcus & Marcus, 1965; Maeda, 1988, 1990). Eyes have been reported as lacking (Marcus & Marcus, 1965), although this may be a consequence of the fact that they are recessed within flattened lobes at the outer bases of the cephalic tentacles (present study). Similar lobes have been recorded in several species (e.g. Ziegelmeier, 1957).

FAMILY CYPRAEIDAE:
CYPRAEA ROBERTSI HIDALGO 1906

Material examined

Playa Bique, Panama (USNM 890940).

External anatomy and mantle cavity

Anterior pedal gland opening to deep propodial groove. Mantle surface pustulose with conical papillae; short siphonal fringe. Anterior kidney chamber extending into pallial roof. Osphradium triradiate. Hypobranchial gland extensive, comprising large, pendulous folds. Operculum absent.

Reproductive system

Gonad occupying terminal whorls, anteriorly bounding digestive gland and midgut on right. Gonopericardial canal absent. Vestigial gonopericardial canal present, forming small, blind pericardial diverticulum. Oviduct entering capsule gland near base of mantle cavity. Capsule gland (Fig. 2E, cg) long and crescentic, narrow posteriorly, expanding anteriorly. Albumen gland (dg) lying along dorsal margin of capsule gland, opening to capsule gland anteriorly via narrow duct. Large, lobate seminal receptacle (rcs) opening to blind posterior end of albumen gland. Finely grooved tract extending anteriorly from aperture of albumen gland, expanding at distal end of capsule gland, continuous with narrow vagina (v). Vagina terminating at small female opening (fo).

Vas deferens forming large and complexly coiled seminal vesicle. Seminal vesicle narrowing anteriorly and opening to closed, narrow, glandular, basophilic prostate at base of mantle cavity (Fig. 3E, pr). Vas deferens emerging from pallial roof, opening to large pocket and open seminal groove lined with acidophilic cells. Seminal groove extending across neck and along ventral surface of long, simple, narrowly triangular penis (pe).

Alimentary system

Foregut. Radula taenioglossate. Foregut modified into muscular, acrembolic proboscis (Fig. 6C, ps). Jaw absent; buccal cavity uncuticularized. Subradular membrane completely covering ventral surface of odontophore; subradular organ absent (Fig. 4G). Short mid-ventral fold (Fig. 8G) present forming dorsal lip of radular sac. Paired muscular, non-glandular pouches present opening to anterior oesophagus. Shallow ridge running transversely across floor of oesophagus between pouches; ventro-lateral folds absent. Salivary gland ducts passing through broad nerve ring, under long pedal connectives. Salivary gland massive, filling left side of cephalic haemocoel and overlying oesophageal gland. Radular sac long and coiled. Mid-oesophagus with well-developed, septate oesophageal gland and open dorsal food groove.

Midgut. Oesophagus opening to left limb of large, U-shaped midgut (Fig. 16B, e). Gastric shield absent. One digestive gland duct (dgd) opening near oesophagus, draining small posterior lobe of digestive gland. Second digestive gland duct draining large anterior lobe of digestive gland, forming caecum. Broad mouth of caecum opening ventrally, along anterior wall of midgut. Anterior extension of major typhlosole (t1) bounding caecum on right. Style sac region characterized by single (major) typhlosole and transversely folded epithelium bearing uniform cilia; minor typhlosole absent. Ciliated strip on major typhlosole absent. Ciliary currents flowing clockwise within style sac region. Major typhlosole turning to right at distal end of style sac. Transverse lip of major typhlosole bounding deep pyloric caecum (pyc), extending posteriorly under style sac. Minor typhlosole beginning within pyloric caecum, paralleling major typhlosole straight out of caecum. Posterior digestive gland lobe occupying terminal visceral whorls; anterior lobe extending into pallial cavity.

Hindgut. Major and minor typhlosoles continuing only short distance within proximal intestine. Intestine straight.

Reno-pericardial system

Kidney large, differentiated into posterior and anterior, histologically distinct lobes (Fig. 23B). Posterior lobe (pl) overlying visceral kidney lumen. Anterior lobe (al) long and narrow, extending within pallial roof under intestine (int), along digestive gland and pallial gonoduct. Nephridial gland present (ng). Afferent renal vessel entering kidney posteriorly, extending anteriorly along floor, producing numerous small branches supplying lamellae along ventral surface of digestive gland. Afferent renal vessel splitting near nephropore (np) into two large branches of equal size. Ventral branch supplying anterior lobe of kidney. Dorsal branch supplying anterior and posterior lobes.

Nervous system and sensory structures

Nervous system epiathroid, left zygoneurous, possibly right dialyneurous (Fig. 24D). Circum-oesophageal nerve ring (Fig. 6C, nr) lying obliquely within cephalic haemocoel, with concentrated cerebro-pleural complex near left cephalic tentacle. Buccal ganglia present just anterior to buccal pouches (bp). Tentacular nerve (tn) dividing into nerve plexus upon entering tentacle. Long pedal connectives passing over anterior oesophagus. Pedal ganglia (Fig. 24D, pdg) large with pedal cords (pc) forming numerous cross connections. Supra-oesophageal (sp) connective very short; sub-oesophageal (sb) connective long. Single large visceral ganglion (Fig. 6C, vg) lying within cephalopedal sinus. Four smaller accessory visceral ganglia (vg) present straddling posterior oesophagus and along left side of cephalic haemocoel. Statocysts with single statolith (Fig. 24D, sc) present on dorsal surface of pedal ganglia.

Discussion

The foregut of cypraeoideans is modified to form a muscular, acrembolic proboscis (Vayssière, 1923; Kay, 1960). The position, number and glandular development of pouches within the anterior oesophagus is variable. They may be paired (Kay, 1960; present study) or unpaired and thin-walled or glandular (Amaudrut, 1898; Vayssière, 1923; Thiele, 1929; Rau, 1934; Fretter, 1951; Fretter & Graham, 1962). Such unpaired mucus diverticulae have been described as opening to the oesophagus at the origin of the oesophageal gland, slightly posterior to that described here. It seems likely that these glandular and non-glandular diverticulae are homologues (*cf.* Kay, 1960) despite slight differences in position within the anterior oesophagus. In fact, given that twisting of the anterior oesophagus brings the left pouch into a hidden ventral position, it suggests that many of the described single diverticulae may be paired with asymmetrical development of glandular tissue.

Cypraeoideans display an extraordinary conservatism of midgut morphologies. The structure and development of such features as the digestive caecum, the major typhlosole, and the intestinal groove are remarkably similar in many species (Haller, 1890; Rau, 1934; Kay, 1960). *Cypraea robertsi* differs in that it lacks both the gastric shield and the ciliated strip on the major typhlosole, which might otherwise confound attempts to interpret midgut homologies. However, the ovulid *Jenneria pustulata* has a midgut that is similar in overall organization, and also possesses both the shield and the ciliated strip (pers. obs.). Owing to this basic conservatism, midgut morphology of *J. pustulata* permits an interpretation of cypraeoidean midgut homologies and a reinterpretation of the hypotheses offered by Kay (1960), even in those taxa lacking structures such as the gastric shield.

As stated above, *Jenneria pustulata* possesses a gastric shield and a ciliated strip on the major typhlosole. The gastric shield and a prominent horizontal fold distal to the shield (= lip of style sac) in *J. pustulata* are similar to style-bearing caenogastropods in their position and connection to other landmarks. This suggests that the portion of the midgut along the major typhlosole referred to as the 'cuticular area' by Kay (1960), represents the style sac region of other caenogastropods. Kay suggested instead that the region of the gut distal to the transverse segment of the major typhlosole is comparable to the style sac region. This reinterpretation indicates that the transverse segment of the major typhlosole lies at the distal end of the style sac, not at the proximal end as suggested by Kay, confirming the identification of a pyloric caecum at the distal end of the style sac in *C. robertsi*. Kay did not describe a pyloric caecum under the transverse segment of the major typhlosole. However, a depression appears to be visible in the appropriate position. *Cypraea robertsi* is unique in lacking a minor typhlosole in the style sac region.

As in naticids, the excretory tissue of cypraeids is subdivided into two lobes that are histologically and macroscopically distinct (Haller, 1890; Simroth, 1896–1907). Haller's detailed description of the kidney in *C. testudinaria* also clearly documented the branching of the afferent renal vessel to supply the anterior and posterior lobes. Rau (1934) provided a largely erroneous interpretation of the reno-pericardial system of *Cypraea arabica*, referring to the anterior kidney lobe as the right kidney, complete with a rudimentary nephropore near the anus.

Cypraeoidean nervous systems are displaced to the left of the buccal mass, with highly concentrated cerebral and pleural ganglia; the supra-oesophageal and left pleural ganglia are in close proximity, and the sub-oesophageal ganglion is widely separated from the others (Haller, 1890; Amaudrut, 1898; Vayssière, 1923; Riese, 1931). Riese's (1931) detailed analysis of the nervous system of *Cypraea moneta* described at least two anastomoses of the sub-oesophageal and supra-oesophageal ganglia that pass through the mantle roof; presence or absence of these dialyneuries could not be confirmed in sections of the highly glandular mantle roof of *C. robertsi*. Pedal cords with numerous cross connections are present (Haller, 1890; Shaw, 1909; Riese, 1931). In contrast to the present findings, the tentacular nerve typically is shown as a simple, unbranched nerve (Haller, 1890; Vayssière, 1923). The number of visceral ganglia is somewhat inconsistent among existing descriptions. For example, Haller (1890) depicted a single main ganglion with only a single accessory ganglion, while Riese (1931) described one main and three accessory ganglia. The position of the accessory ganglia is also variable. This inconsistency may be due to differing interpretations of the swellings along the visceral loop, several of which were only visible in *C. robertsi* with the aid of histological sections; these are highly variable in size and not all produce nerves.

FAMILY EPITONIIDAE: *NITIDISCALA TINCTUM* (CARPENTER 1864)

Material examined

Venice, California (USNM 890942).

External anatomy and mantle cavity

Mantle edge smooth. Hypobranchial gland thick, bright orange/brown in colour, producing characteristic purple secretion when disturbed. Osphradium (Fig. 7C, os) long, extending length of ctenidium, consisting of broad central axis bordered by two, densely ciliated ridges. Anterior pedal gland composed of basophilic cells, opening to deep cleft along anterior edge of propodium. Mesopodial pedal gland composed of basophilic and acidophilic cells, penetrated by numerous small ciliated ducts coalescing and opening to groove in foot sole via single, broad duct. Groove mid-ventral, extending approximately two thirds length of foot from posterior tip.

Reproductive system

Protandrous hermaphrodites. Gonad dorsally enclosing digestive gland on right. Vas deferens emerging from testis, rapidly enlarging to form seminal vesicle storing spermatozeugmata. Vas deferens narrowing anteriorly, opening to pallial gonoduct at base of mantle cavity. Prostate comprising paired, open laminae with shallow intervening gonoductal groove, densely ciliated anteriorly. Penis absent.

Gonopericardial canal absent. Oviduct opening to glandular pallial gonoduct short distance from its base. Pallial gonoduct comprising paired laminae, open along anterior end of albumen gland and length of capsule gland. Enclosed base of albumen gland bearing ciliated ridges directing sperm back and dorsally to opening of seminal receptacle. Small, ovate receptacle attached to dorsal wall of albumen gland, storing orientated sperm. In many females, degenerating spermatozeugmata visible adhering to floor of pallial cavity adjacent to albumen gland.

Alimentary System

Foregut. Foregut modified into acrembolic proboscis (Fig. 7C, ps). Numerous long, thin branching protractor and retractor muscles connecting proboscis to walls and floor of cephalic haemocoel. Proboscis comprising long proboscis sheath opening to elongate buccal mass. Paired jaws (j) present, consisting of long sheets of cuticle comprised of rods with laterally overlapping, dark-staining homogeneous layer. Jaw supported by muscular, compartmentalized tissue and posteriorly flanking odontophore. Paired, thin, flexible cartilages supporting medially incised odontophore. Cartilages posteriorly L-shaped in cross section, becoming U-shaped anteriorly. Lateral arms of cartilages invading walls of buccal mass, supporting jaw, extending between cuticle and compartmentalized tissue beneath. Ptenoglossate radula extending completely over odontophore into deep sublingual cavity; subradular organ absent. Dorsal folds indistinct. Anterior oesophagus highly folded and uniformly glandular (Fig. 10B). Discrete ventral folds and ventro-lateral folds absent. Dorsal pair of salivary glands (Fig. 7C, sgl) and ventral pair of accessory salivary glands (asg) present. Distal tips of salivary glands and fused distal tip of accessory glands attaching to ventral surface of oesophagus. Ducts of foregut glands extending anteriorly embedded within buccal cavity walls. Dorsal glands opening laterally beside odontophore. Ventral accessory glands, opening labially at base of proboscis sheath, terminating in cuticular stylets. Mid-oesophagus short and broad, with folded glandular walls; septate oesophageal gland absent (Fig. 11H, me). Proximal posterior oesophagus highly muscularized. Distal posterior oesophagus glandular, thin-walled, opening to midgut.

Midgut. Midgut comprising small anterior chamber, and elongate, highly folded, sacculate gastric chamber (Fig. 17A). Oesophagus (e) entering left side of small anterior chamber, bounded by muscular valves. Anterior chamber also receiving single, large digestive gland duct (dgd). Gastric chamber walls densely ciliated; ciliary currents circulating particles posteriorly along left wall and anteriorly along right wall. Style sac region characterized by presence of single (major) typhlosole and longitudinally folded epithelium bearing uniform cilia.

Hindgut. Style sac region emerging from right, anterior end of caecum opposite oesophageal aperture. Intestine straight.

Reno-pericardial system

Kidney small, surrounding pericardium on right. Afferent renal vessel entering kidney floor just behind base of mantle cavity. Afferent renal vessel extending dorsally, branching into two large vessels that ramify to supply excretory tissue. Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, left zygoneurous (Fig. 24E). Circum-oesophageal nerve ring (Fig. 7C, nr) lying far anterior to buccal mass, surrounding elongate proboscis sheath (ps). Long buccal connectives extending posteriorly to buccal ganglia lying ventrally at back of buccal mass, flanking short radular sac. Tentacular nerve (tn) single with small tentacular ganglion near base of nerve. Long pedal connectives extending around proboscis sheath to small pedal ganglia (Fig. 24E, pdg) partially embedded in mesopodial mucus gland. Supra-oesophageal (Fig. 7C, sp.) and sub-oesophageal (sb) connectives long. Pallial nerve from left pleural ganglion producing two small nerves before merging with supra-oesophageal ganglion. Single visceral ganglion (vg) under pericardium within cephalopedal sinus. Statocysts with single statoliths (Fig. 24E, sc) present on postero-dorsal surfaces of pedal ganglia.

Discussion

The Epitoniidae is currently classified in the Superfamily Janthinoidea with the Aclididae and Janthinidae. The anatomy of the family Epitoniidae, as well as of the superfamily to which it belongs, has been insufficiently investigated. Of the three families, the Aclididae is the least known; little more is established than the fact that they possess an acrembolic proboscis with a ptenoglossate radula, the males are aphallate and there are paired pedal folds that cover the base of the shell when the foot is extended (Fretter & Graham, 1982; Bouchet & Warén, 1986).

Considerably more is known about the two remaining families. The foot of *Janthina janthina* is modified, reflecting its pelagic life habit with a so-called funnel into which numerous glands empty (Simroth, 1896–1907). But like *Nitidiscala tinctum*, other epitoniids possess a foot that is indented posteriorly and bears a central groove (Fretter & Graham, 1982) into which a mesopodial pedal gland opens (in both males and females) and secretes the mucus thread that connects egg capsules (Robertson, 1983).

Pallial cavity anatomy is fairly conservative within the Janthinoidea, consisting of an elongate ctenidium, a thick hypobranchial gland that releases a characteristic purple secretion, and a long osphradium (Bouvier, 1886; Thiele, 1928b; Clench & Turner, 1950; Taki, 1956, 1957; Robertson, 1963; Warén, 1980). Robertson (1983) suggested that the purple dye is repugnatorial. The description of Bouvier (1886) for *Janthina globosa* suggested a regionation of the osphradium as described here.

There has been some controversy surrounding the reproductive mode of janthinoideans (see Fretter & Graham, 1962, 1982 and Robertson, 1981a for discussion and review). However, it seems clear that most are protandrous hermaphrodites with only a single sex change (Ankel, 1930; Graham, 1954; Breyer, 1980; Robertson, 1981a,b, 1983; Fretter & Graham, 1982; Smith & Breyer, 1983), but sex reversal may occur in some species (Ankel, 1936). Due to the absence of copulatory organs in the Janthinoidea, sperm are transferred via spermatozeugmata which are stored in the seminal vesicle and distal end of the male genital tract (Ankel, 1930; Graham, 1954; Bulnheim, 1968; Robertson, 1981a, 1983; Fretter & Graham, 1982). While abundant in the seminal vesicle, no spermatozeugmata were found in the pallial gonoduct in *Nitidiscala tinctum*. However, spermatozeugmata were routinely found at the base of the pallial cavity alongside the proximal pallial oviduct. In the absence of a bursa copulatrix, this most likely represents the site of spermatozeugmata degeneration whereupon sperm are passed to the seminal receptacle.

Available descriptions of epitoniids reveal that both open (Fretter & Graham, 1982) and closed (Taki, 1956, 1957) gonoducts are present. *Janthina janthina* (Graham, 1954) possesses a closed pallial gonoduct that functions as a prostate during the male phase; posterior to the prostate is a blind sac with tubular glands that stores spermatozeugmata (Graham). During the female phase in *J. janthina*, the proximal portion of the pallial oviduct bears a highly villous appearance, similar to the glandular sac found in the same position during the male phase (Graham). No tubular glands were evident in female *Nitidiscala tinctum*. *Janthina janthina* (Graham) and other epitoniids (Taki, 1956, 1957) apparently lack a seminal receptacle.

Epitoniids possess a long acrembolic proboscis (Thiele, 1928b; Taki, 1956, 1957; Fretter & Graham, 1962, 1982; Warén, 1980; Robertson, 1981b, 1983) with two pairs of salivary glands (Bouvier, 1886; Thiele, 1928b; Taki, 1956, 1957; Fretter & Graham, 1962). Janthinids possess only a short extensible snout (Graham, 1965) equipped with two (Bouvier, 1886; Simroth, 1902; Risbec, 1953; Graham, 1965) or three pairs of glands (Thiele, 1928b; Marcus, 1956). All janthinoideans have an odontophore supported by U-shaped cartilages that extend into the buccal walls and support the jaw (Thiele, 1928b; Marcus, 1956; Graham, 1965). In some, the jaw is massive (Taki, 1956, 1957). However, most janthinoideans lack the thick, muscular, compartmentalized tissue supporting the jaw (Thiele, 1928b; Marcus, 1956; Graham, 1965). Other species possess only small cuticular plates at the anterior end of the buccal cavity, with glands in the buccal cavity walls that may correspond to the compartmentalized tissue described here (e.g. *Clathrus clathrus*; Fretter & Graham, 1962). Terminal stylets on the ventral salivary gland ducts may be present (Simroth, 1902; Thiele, 1928b; Ankel, 1936, 1949; Fretter & Graham, 1962, 1982; Robertson, 1963; Warén, 1980) or absent (Thiele, 1928b); the presence of stylets was neither confirmed nor denied by Taki (1956, 1957).

Janthinoideans possess a simple midgut (Taki, 1956, 1957; Fretter & Graham, 1982), but there is some minor variability in the posterior oesophagus and in the position of intestinal, oesophageal and digestive gland apertures. The distal, glandular portion of the posterior oesophagus of *Nitidiscala tinctum* corresponds to the so-called cardiac chamber of other epitoniids (Taki, 1956, 1957); the chamber varies from small and poorly developed, to large and muscular (Taki). In addition, the cardiac chamber may open separately to the gastric chamber (Taki), rather than to the caecum as in *N. tinctum*. Digestive gland ducts may be paired or single (Taki).

Similar to *Nitidiscala tinctum*, *Janthina* is epiathroid and left zygoneurous (Bouvier, 1886; Thiele, 1928b). Bouvier also described the nervous system of *Scala communis* (as *Scalaria communis*) as epiathroid but lacking secondary connections between ganglia. However, his preparation was apparently compromised by the purple secretions of the hypobranchial gland (Thiele, 1928b). Statocysts with single statoliths are present between the pedal ganglia (Bouvier, 1886; Marcus, 1956).

FAMILY CANCELLARIIDAE: *PANARONA CLAVATULA* (SOWERBY 1832)

Material examined

Playa Bique, Panama (USNM 890943).

External anatomy and mantle cavity

Mantle edge papillate (Fig. 7A). Hypobranchial gland well-developed with pendulous, folded epithelium. Osphradium (os) large and bipectinate, lying behind inhalant margin. Siphon short and broad. Right cephalic tentacle bifid. Left tentacle bearing lateral flaps; flaps curving dorsally, becoming juxtaposed with siphon. Anterior pedal gland opening to moderately deep cleft along front of large propodium. Ventral pedal gland present in females, opening to elongate slit short distance back from anterior edge of foot sole. Operculum absent.

Reproductive system

Gonad extending along right from tip of viscera to kidney, penetrating tubules of digestive gland. Gonopericardial connection present behind base of mantle cavity (Fig. 2F, gpc). Pallial oviduct closed. Albumen gland short with U-shaped lumen (ag). Approximately four, small, ciliated ducts emerging dorsally, along crest of gland, opening to small seminal receptacles bearing orientated sperm (rcs). Albumen gland lumen narrowing anteriorly to non-glandular, muscular duct connecting albumen and capsule glands. Connecting duct opening dorsally to ingesting gland (igl) containing unorientated sperm. Capsule gland (cg) large, composed of two parallel laminae with regionated epithelium. Large, deep, muscular bursa lying at anterior end of capsule gland, opening broadly to pallial cavity (fo). Bursa and capsule gland connected by small, ciliated duct, opening short distance back from female aperture.

Vas deferens emerging from testes, expanding into somewhat straight, lobulate seminal vesicle. Vas deferens narrowing behind base of mantle cavity, extending short distance across pallial floor, opening to glandular prostate. Prostate comprising convoluted tube opening proximally to mantle cavity via short, tubular diverticulum. Pallial vas deferens crossing neck, entering penis lying behind right cephalic tentacle. Penis long and spatulate with narrow base and pointed terminal papilla. Coiled penial duct running down midline of penis and opening to tip.

Alimentary system

Foregut. Foregut modified into large, muscular pleurembolic proboscis (Fig. 7A). Proboscis sheath (ps) attaching to walls of cephalic haemocoel near cephalic tentacles. Numerous protractor and retractor muscles connecting proboscis sheath to walls of head. Single, large retractor, originating ventro-laterally on left side of proboscis sheath, attaching to columellar muscle at back of head. Small mouth opening at tip of proboscis to short oral tube, rapidly becoming lined with cuticle. Cuticular tube gradually widening posteriorly to buccal mass. Buccal mass hanging free from posterior end of retracted proboscis. Odontophore narrow and elongate with deep sulcus, incompletely lined by subradular membrane (Fig. 4H). Anterior odontophore forming muscular, non-glandular, U-shaped shelf supporting long, slender nematoglossan teeth. Radular sac short, thin and slightly curved (Fig. 7A, rs). Paired, ascinous salivary glands (sgl) with short ducts opening to buccal cavity posteriorly and dorsally. Paired accessory salivary glands (asg) long and tubular. Muscular ties attaching posterior tips of accessory glands to proboscis sheath. Accessory salivary glands narrowing upon entry to retracted proboscis sheath, to long, ciliated ducts running along cuticular tube, entering alimentary canal near transition between cuticle and oral tube.

Short anterior oesophagus; ventral folds absent (Fig. 10C). Valve of Leiblein (Fig. 7A, vl) present short distance back from buccal mass. Long, slender mid-oesophagus bearing ventral, U-shaped strip of glandular epithelium liberating brown secretory droplets into oesophageal lumen. Transition from glandular mid-oesophagus to posterior oesophagus occurring at base of cephalic haemocoel, marked by narrowing of oesophageal lumen.

Midgut. Midgut small, U-shaped, partially embedded in digestive gland at back of kidney (Fig. 17B). Oesophagus (e) opening to midgut on left. Walls simple, lined with parallel, well-ciliated folds. Digestive gland opening via single large duct (dgd) to back wall. Two parallel, asymmetrical folds running along back wall of midgut, connecting oesophageal aperture with opening of digestive gland. Major typhlosole (t1) extending across floor of midgut and terminating adjacent to digestive gland duct. Style sac region bearing paired typhlosoles (t1, t2) and longitudinally folded epithelium with undifferentiated cilia. Ciliary currents flowing linearly within gastric chamber from oesophageal aperture to style sac region.

Hindgut. Intestine straight, narrow. Anal gland present along distal portion of rectum, terminating just before anus. Anal gland confluent with rectum along entire length of gland, secreting small, brown-black, granular concretions into lumen of rectum.

Reno-pericardial system

Kidney large (Fig. 23C), lumen internally subdivided into large posterior chamber and smaller anterior chamber. Anterior chamber extending into pallial roof, bearing nephropore (np) along anterior wall. Incomplete dorsal septum restricting communication between chambers, formed by excretory tissue and the dorsal afferent renal vessel (DARV). Afferent renal vessel entering kidney floor at anterior end of posterior chamber to right of reno-pericardial canal, behind base of mantle cavity. Ventral afferent renal vessel (VARV) running posteriorly within floor, supplying narrow strip of primary tubules along right wall and roof. DARV curving dorsally and to left from kidney floor, supplying secondary tubules along left side of kidney and in roof of anterior chamber. Three small branches near origin of DARV supplying primary tubules as well, along right wall and within anterior chamber roof on right. Primary and secondary tubules meronephridial. Nephridial gland present (ng).

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous, left dialyneurous, with all ganglia except visceral and supra-oesophageal ganglia concentrated in circum-oesophageal nerve ring. Long buccal connectives originating from large nerve bundle innervating proboscis sheath and accessory salivary gland ducts. Buccal ganglia lying at posterior end of buccal cavity (Fig. 7A). Single, thick tentacle nerve (tn) splitting near eye into four nerves approximately equal in size, extending in parallel down centre of tentacle. Supra-oesophageal ganglion lying to left of proboscis short distance behind cephalic tentacle. Small siphonal ganglion (sig) present at point of dialyneury between pallial nerve and branch from osphradial nerve. Siphonal nerve immediately bifurcating into two prominent nerves. Propodial ganglia present at anterior ends of pedal ganglia. Visceral loop bearing paired visceral ganglia (vg), straddling posterior oesophagus. Statocysts with large statoliths lying ventral to circum-oesophageal nerve ring, adjacent to ventral pedal gland duct.

Discussion

Female reproductive anatomy is rather consistent among described species; in females, a gonopericardial canal may be present or absent (Graham, 1966; Harasewych & Petit, 1982, 1984, 1986). One notable exception is the description by Graham (1966) who described two glandular structures, an ingesting gland and a seminal receptacle, posterior to the large capsule gland. Given the position of the gonopericardial canal, it seems likely that Graham confused the albumen gland for a receptacle. This inference is particularly likely given the numerous receptacles lining the dorsal crest of the albumen gland in *Panarona clavatula*. This interpretation would render the conditions of *Cancellaria cancellata* equivalent to other cancellariids in the presence of a single ingesting gland between the capsule and albumen glands. No receptacles were described by Harasewych & Petit (1982, 1984, 1986). Male reproductive anatomy seems somewhat more variable; the prostate may open to the inner end of the pallial cavity via a small diverticulum (Graham, 1966) or a narrow slit (Harasewych & Petit, 1982, 1986). In addition, the length of the prostate varies and may be convoluted or straight (Graham, 1966; Harasewych & Petit, 1982, 1984, 1986).

All cancellariids share a nematoglossan radula consisting of a single row of teeth. As the radula travels forward, the teeth become divided into a posterior set and an anterior set, the latter projecting forward into the cuticular, tubular jaw (Bouvier, 1887; Barnard, 1957; Olsson, 1970; Ponder, 1973; Oliver, 1982; Petit & Harasewych, 1986). Proboscis morphology and the glandular structures associated with the foregut are highly consistent in all species studied, with only subtle variations in the relative lengths of the salivary glands, oral tube, and jaw, with the two latter determining the placement of the buccal cavity within the proboscis sheath; the retracted proboscis may be tubular or ventrally flattened and papillose (Bouvier, 1887; Amaudrut, 1898; Simroth, 1902; Graham, 1966; Harasewych & Petit, 1982, 1984, 1986). Several authors (Ponder, 1973; Taylor & Morris, 1988; Kantor, 1996), apparently following Graham (1966), stated that the mid-oesophagus of Cancellarioideans occurs exclusively anterior to the nerve ring. In *Panarona clavatula*, the mid-oesophagus extends to the posterior end of the cephalic haemocoel. The midgut is typically small and sac-like bearing parallel folds (Harasewych & Petit, 1982, 1984, 1986) and a single duct of the digestive gland (Graham, 1966). The anal gland may be present or absent (Harasewych & Petit, 1982, 1984, 1986). The precise connection between anal gland and rectum remain undescribed for other cancellariids. Thus, it is unknown if *P. clavatula* is unique, or if all cancellariids possess an anal gland that forms a glandular strip confluent with the rectum, rather than a separate tube opening via a duct to the rectum or pallial cavity as in other neogastropods (e.g. Ponder, 1973).

A nephridial gland is present; size of the kidney can vary substantially between species (Harasewych & Petit, 1982, 1984, 1986).

The nervous system of cancellariids is known in detail only from *Cancellaria cancellata* (Bouvier, 1887), with some general information given by Graham (1966); with minor exceptions, both studies are in agreement with the description provided above. One exception is the number of visceral ganglia, and may be paired (Bouvier) or single (Graham). The long cerebro-buccal connectives are bound in nerve bundles from the cerebral ganglia that innervate the proboscis. However, there are two separate bundles in *Panarona clavatula* (present study) and *C. cancellata* (Bouvier), and only a single median bundle in *C. reticulata* (Graham). The tentacular nerve is single (Bouvier).

FAMILY MARGINELLIDAE: *PRUNUM APICINUM* (MENKE 1828)

Material examined

Missouri Key, Florida (USNM 890944).

External anatomy and mantle cavity

Smooth mantle covering shell. Anterior pedal gland opening to shallow lip under propodium. Ventral pedal gland present in females, opening to elongate slit near front of foot sole. Long, slender siphon lying between cephalic tentacles, left margin fused to side of head (Fig. 7D, si). Root of siphon lacking basal flaps. Extensive hypobranchial gland composed of smooth, unfolded epithelium with two distinct regions. Operculum absent.

Reproductive system

Gonad lying along right side of body, not penetrating tubules of digestive gland. Gonopericardial canal absent. Oviduct opening to anterior end of large albumen gland (Fig. 2G, ag); albumen gland visceral in position, closely appressed to side of kidney. Albumen gland opening anteriorly to single ingesting gland (igl) containing unorientated sperm. Ciliated, S-shaped duct near base of mantle cavity connecting ingesting gland and capsule gland (cg). Capsule gland bearing distinctly regionated glandular epithelium with anterior and posterior zones of mucus secreting cells. Capsule gland opening to highly folded vestibule. Vestibule curving around base of muscular bursa copulatrix (bc) and opening dorsally to bursa. Bursa narrowing to short vagina, terminating in simple female aperture (fo).

Broad, straight, ciliated vas deferens functioning as seminal vesicle. Gonopericardial canal absent. Vas deferens narrowing before entering long, glandular prostate (Fig. 3F, pr). Prostate lying at base of mantle cavity, across exhalent margin. Proximal prostate bearing slit-like opening to pallial cavity. Pallial vas deferens (pvd) extending anteriorly along side of head to base of large penis (pe) lying short distance behind right cephalic tentacle. Penial duct extending straight down centre of penis to open at tip. Penis broad, muscular, dorso-ventrally flattened, unilobed, narrowing from broad base to fine tip.

Alimentary system

Foregut. Mouth lying at tip of large pleurembolic proboscis (Fig. 7D, ps), opening to short, strongly folded buccal cavity. Paired salivary glands (sgl) opening laterally, single accessory salivary gland (dasg) opening ventrally to buccal cavity. Jaw absent. Buccal pouch opening ventrally to posterior end of buccal cavity. Buccal pouch housing modified buccal mass, supported by thin, flexible radular cartilage fused anteriorly and posteriorly. Anterior end of cartilage forming gutter bearing uniserial, multicusped radula. Duct of poison gland (gland of Leiblein, gl) opening to floor of oesophagus at junction of buccal pouch and buccal cavity. Glandular ventral folds absent (Fig. 10D). Salivary gland ducts lying free within proboscis, becoming attached anteriorly to lateral walls of buccal cavity. Paired salivary glands comprising large mass lying to left of proboscis; ducts not penetrating nerve ring. Single, tubular accessory salivary gland embedded within ventral wall of proboscis. Poison gland duct extending posteriorly attached to floor of oesophagus. Oesophagus and poison gland duct penetrating nerve ring. Narrow poison gland duct expanding into large, glandular tube upon passing through nerve ring. Poison gland terminating in pointed, muscular bulb. Oesophagus widening abruptly into large, saculate oesophageal caecum upon passing through nerve ring. Valve of Leiblein absent.

Midgut. Simple, sac-like midgut present behind pericardium (Fig. 18A). Paired digestive gland ducts (dgd) and oesophageal aperture (e) opening on left. Walls of midgut simple and lined with uniformly ciliated folds. Finely grooved tract running along anterior wall, continuous with intestinal groove. Two typhlosoles present in style sac region. Major typhlosole (t1) continuous with folds forming posterior boundary of finely grooved tract. Style sac region longitudinally folded with uniform and undifferentiated cilia. Ciliary currents flowing clockwise within midgut lumen.

Hindgut. Straight, short intestine. Small anal gland forming simple branched tubule under hypobranchial gland. Anal gland opening directly to mantle cavity just in front of anus.

Reno-pericardial system

Kidney large (Fig. 23D). Afferent renal vessel entering kidney floor anteriorly behind reno-pericardial canal (rpc). VARV extending back within floor, supplying numerous clusters of primary tubules lining right wall and roof. DARV curving dorsally behind nephropore (np), attached to front wall of kidney. Secondary tubules reduced to small region at front of kidney roof. Primary and secondary tubules not interdigitating. Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous and left dialyneurous. All ganglia except visceral ganglia concentrated in large nerve ring (Fig. 24F). Tentacular nerve continuously bifurcating, upon entering tentacle, into numerous small nerves of equal size (Fig. 7D, tn). Buccal ganglia (Fig. 24F, bg) fused to ventral surface of cerebral ganglia (ceg). Large siphonal ganglion (Fig. 7D, sig) present near base of siphon (si), at point of dialyneury between pallial nerve and branch from osphradial nerve. Propodial ganglia (Fig. 24F, ppg) present at anterior ends of pedal ganglia. Paired visceral ganglia (Fig. 7D, vg) present straddling oesophagus. Statocysts (Fig. 24F, sc) lying short distance below and behind pedal ganglia, each containing single, large, ovoid statolith. Osphradium (Fig. 7D, os) large, bipectinate, lying behind base of siphon. Eyes at outer bases of slender cephalic tentacles.

Remarks

Little has been published on the anatomy of *Prunum apicinum*. The description of the external anatomy and radula presented here are congruent with those provided by Coovert (1987) and Coovert & Coovert (1990), respectively.

Discussion

Reproductive anatomy of marginellid species remains poorly known compared to the extensive studies of radulae, external anatomy and, to a lesser degree, foregut anatomy discussed below. The oviduct typically joins the albumen gland near its anterior extent (Ponder, 1970; Harasewych & Kantor, 1991). Similar to other neogastropods (Fretter, 1941), the capsule gland has a distinctly regionated glandular epithelium. There may be an anterior and posterior zone of mucus secreting cells (Ponder, 1970; present study) or only a posterior zone (Ponder). There are usually two, rarely one or three, glandular structures for the storage of sperm between the albumen and capsule glands (Ponder, 1970; Fretter, 1976; Harasewych & Kantor, 1991). However, the presence of orientated or unorientated sperm is not always specified. Thus, it is not clear if these comprise ingesting glands, receptacles, or both. From those descriptions that do note sperm orientation, it appears that some taxa possess only ingesting glands (Ponder, 1970), with orientated sperm within the ingesting gland ducts. It should be noted that Ponder (1970, 1973) inferred these structures to be receptacles despite the presence of unorientated sperm, based on the fact that ingestion was not observed. Other marginellids possess both receptacles and ingesting glands (e.g. Fretter, 1976).

Graham (1966) observed an unusual connection between the genital duct and kidney in *Marginella desjardini*, as well as an ingesting gland and a seminal receptacle proximal to the combined albumen/capsule gland; he found no evidence of a bursa copulatrix. Ponder (1970) offered a reinterpretation of Graham's description and suggested that the posterior-most glandular structure Graham described as a seminal receptacle was in fact homologous to the albumen gland. Ponder further suggested that the structure described as an ingesting gland, with its numerous vesicles was homologous to the seminal receptacles of other marginellids.

However, based on the reproductive anatomy of *Prunum apicinum* an alternative interpretation of Graham's findings is possible. Of particular importance is the nature of the connection between the albumen and capsule glands, as well as the close disposition of albumen gland and kidney. Because Graham's 'unusual' connection between oviduct and kidney in *Marginella desjardini* strongly resembles the sinuous, S-shaped duct connecting the ingesting gland and capsule gland in *P. apicinum*, this suggests that Graham did not differentiate the kidney from the underlying albumen gland. Thus, the capsule/albumen gland of *Marginella desjardini* is homologous to the capsule gland of other marginellids. This reinterpretation renders the configuration of sperm storage structures in *M. desjardini* more easily interpretable. As is common within the family, *M. desjardini*, in fact, possesses two storage structures between the capsule and albumen glands. This interpretation of *M. desjardini* also renders the configuration in *Prunum apicinum* that much more unique, the latter being one of two described marginellids to possess a single sac (*Granula* sp.; Ponder, 1970).

Male reproductive anatomy is somewhat less variable than females. The vas deferens connecting testis with prostate may be straight (present study) or convoluted (Graham, 1966; Ponder, 1970; Harasewych & Kantor, 1991). Pallial connections of the prostate gland may comprise a slit (Marcus & Marcus, 1968; Ponder, 1970) or a tubular duct (Ponder, 1970; Fretter, 1976). The prostate may lie across the exhalent margin (Marcus & Marcus, 1968; Ponder, 1970; Harasewych & Kantor, 1991) or within the penis (Ponder, 1970; Fretter, 1976). The penis is oval to spatulate, uni- or bilobed, with the vas deferens opening at its tip (Eales, 1923; Graham, 1966; Marcus & Marcus, 1968; Ponder, 1970; Fretter, 1976).

Of all the organ systems, foregut morphology is best known among marginellid taxa. All marginellids share a large or small (Eales, 1923) pleurembolic proboscis that commonly contains a unique buccal pouch. The pouch has been shown to be derived from the radular sac and houses a highly modified odontophore supported by cartilages that are fused anteriorly, posteriorly, or both (Graham, 1966; Ponder, 1970; Ponder & Taylor, 1992; Coovert & Coovert, 1995). The buccal mass may be lacking (Eales, 1923; Graham, 1966; Ponder, 1970).

The foregut glandular apparatus is highly variable. Salivary glands may be ascinous or tubular, the salivary gland ducts may be free or attached to the oesophageal walls, the accessory salivary gland may be absent or present, the poison gland (gland of Leiblein) may have a pointed or blunt muscular, terminal bulb, and the poison gland duct may open midventrally or laterally to the buccal cavity, or to the mid-oesophagus (Eales, 1923; Graham, 1966; Marcus & Marcus, 1968; Ponder, 1970; Fretter, 1976; Ponder & Taylor, 1992; Coovert & Coovert, 1995). In some species, the poison gland lacks a terminal bulb (Ponder, 1970). Alternatively, as in *Marginellona gigas*, the poison gland may be broad and saculate rather than narrow and tubular as in the remaining marginellids (Harasewych & Kantor, 1991). Both the oesophageal caecum and the valve of Leiblein may be present or absent (Graham, 1966; Marcus & Marcus, 1968; Ponder, 1970; Fretter, 1976; Ponder & Taylor, 1992; Coovert & Coovert, 1995). It is interesting to note that the oesophageal caecum and valve of Leiblein lie in a similar position, at the junction of the anterior and mid-oesophagus. While both may be lacking, they are never present simultaneously (except in the disputed description of Marcus & Marcus, 1968), suggesting that they may be homologues. The valve of Leiblein, when present, differs from other neogastropods in that a duct ventrally by-passes the valve (Ponder, 1970; Ponder & Taylor, 1992).

Typically, the midgut is small and sac-like with two digestive gland ducts (Graham, 1966; Ponder, 1970; Fretter, 1976); a single duct or caecum-like duct may be present (Ponder, 1970; Fretter, 1976). Finely grooved tracts commonly connect the intestinal, oesophageal and digestive gland apertures (Ponder, 1970; Fretter, 1976). The intestine is rather straight and no style sac region is apparent (Graham, 1966). The anal gland may be present or absent, often opening to the rectum via a single duct (Ponder, 1970; Harasewych & Kantor, 1991), and rarely to the pallial cavity (Ponder, 1970; Fretter, 1976).

The kidney is a large, elongate organ along the left margin of the viscera. The secondary tubules are restricted to an antero-dorsal region (Ponder, 1970). Ponder was not explicit about the size of the mass of secondary tubules, thus, it is unknown whether the extremely small mass in *Prunum apicinum* is unique. Ponder likened marginellid kidney morphology to that of olivids (Marcus & Marcus, 1959). However, the latter description indicates a long strip of 'villous' secondary tubules extending the length of the kidney roof, and is not comparable to the conditions in *P. apicinum*.

The circum-oesophageal nerve ring is highly concentrated (Eales, 1923; Marcus & Marcus, 1968; Ponder, 1970); paired visceral ganglia are present near the left side of the asymmetrical cephalic haemocoel (Bouvier, 1887; Graham, 1966; Fretter, 1976).

FAMILY CONIDAE: *CONUS* (*LEPTOCONUS*) *JASPIDEUS* GMELIN 1791

Material Examined

Little Duck Key, Florida (USNM 890945). Only immature males were available; female anatomy is unknown, and male reproductive anatomy is preliminary.

External anatomy and mantle cavity

Mantle edge scalloped. Siphon short and broad with asymmetrical basal flaps. Left flap large, lying against side of head. Ctenidium and large bipectinate osphradium (Fig. 7E, os) lying short distance behind base of siphon. Large, folded hypobranchial gland present. Anterior pedal gland opening to slit under thick propodial flap. Ventral pedal gland unknown. Operculum present.

Reproductive system

Gonad occupying tip of viscera, posteriorly bordering digestive gland. Vas deferens emerging from testis, rapidly developing into highly convoluted seminal vesicle. Prostate opening to mantle cavity via proximal slit. Closed pallial vas deferens traversing mantle floor and side of neck to penis behind right cephalic tentacle. Penial duct opening at tip of penis.

Alimentary system

Foregut. Proboscis intraembolic (Fig. 7E, ps). Rhynchostome with sphincter opening to spacious rhynchocoel. Tentacles surrounding rhynchostome absent. Entire surface of rhynchocoel lined with tall, glandular, basophilic folds; discrete snout gland absent. Proboscis wall folded upon itself where sheath attaches to head wall. Proboscis sheath extending only short distance beyond base of rhynchocoel. Approximately six to eight large retractor muscles extending from base of proboscis, to wall of cephalic haemocoel. Proboscis telescopically folded within rhynchocoel, with true mouth at tip, and intermediate sphincter short distance behind mouth. Single tooth present within proboscis tip. Buccal lips surrounding slit-like opening at tip. Short buccal tube leading to muscular buccal mass lying at base of proboscis; odontophore absent. Radular sac (rs) and poison gland duct (gl) entering buccal mass on right side, latter just posterior to former. Radular sac (rs) subdivided into long and short arms. Posterior, long arm secreting radular teeth, connecting to radular caecum via small constriction. Radular caecum small, lined with cuticle, storing numerous mature teeth within lumen. Paired salivary gland ducts extending from mass comprising paired ascinous salivary gland (sgl), around anterior oesophagus, one on each side, opening to caecum. Long, narrow, glandular poison gland duct, opening to large, muscular bulb (gl). Accessory salivary gland absent. Short, broad anterior oesophagus uniformly folded (Fig. 10E).

Midgut. Midgut small, U-shaped, embedded in digestive gland just posterior and to left of kidney. Lumen lined with longitudinal, uniformly ciliated folds

(Fig. 18B). Paired digestive gland ducts present (dgd). One duct draining posterior lobe, opening to back wall on right. Second duct draining anterior lobe, opening near intestinal aperture. Major typhlosole (t1) extending posteriorly into gastric chamber, proximal tip expanding into large pad near anterior most digestive gland duct. Style sac region bearing paired, glandular typhlosoles and longitudinally folded epithelium bearing undifferentiated cilia. Ciliary currents flowing linearly within gastric chamber from oesophageal aperture to style sac region.

Hindgut. Intestine straight. Anal gland forming narrow, muscular, unbranched tubule, opening to rectum short distance behind anus.

Reno-pericardial system

Kidney long. Afferent renal vessel entering kidney floor anteriorly, adjacent to nephropore and reno-pericardial canal. VARV extending posteriorly within floor, supplying primary tubules along right wall and roof. DARV extending postero-dorsally, running along right margin of roof, supplying secondary tubules within roof. Primary and secondary tubules pycnonephridial, interdigitating within kidney roof along narrow band extending approximately three-quarters length of kidney; primary tubules exclusively lining posterior one-quarter of kidney roof. Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous, and left dialyneurous. Nerve ring lying obliquely within cephalic haemocoel near base of proboscis (Fig. 7E, nr). Single nerve branching near cephalic tentacle, giving rise to tentacular and optic nerves. Single tentacular nerve splitting rapidly into three nerves of equal size near eye (tn). Long buccal connectives innervating buccal ganglia lying between anterior oesophagus and radular caecum. Double commissure present between buccal ganglia. Pedal and suboesophageal connectives long, extending around spacious anterior oesophagus. Supra-oesophageal ganglion lying near nerve ring innervated by short connective. Small siphonal ganglion (sig) present at point of dialyneury between branch of anterior osphradial nerve and pallial nerve. Single stout siphonal nerve emerging from ganglion. Pedal ganglia large with propodial ganglia lying at their anterior bases. Visceral loop bearing three visceral ganglia (vg). Large statocysts with single, large statoliths present ventrally and anterior to pedal ganglia.

Discussion

The pallial cavity of conids is dominated by a long and complex bipectinate osphradium (Taki, 1937; Alexander, 1970, 1973; Alexander & Weldon, 1975; Taylor & Miller, 1989). Size and orientation of the structure and complexity of individual leaflets has been shown to vary. Several variables, including curvature and density of leaflets showed no correlation with ecological factors suggesting a possible utility in phylogenetic studies (Spengler & Kohn, 1995).

There exists a rather large body of comparative data on conid radular morphology (e.g. Nybakken, 1970a,b, 1990; James, 1980; Shimek & Kohn, 1981; Kohn, Nishi & Pernet, 1999), particularly in the context of feeding ecology. Indeed, shifts in feeding have occurred rarely within *Conus*, with radular types cutting across patterns of feeding biology. This indicates that, in general, radular tooth morphology is a rather reliable indicator of phylogeny (Duda, Kohn & Palumbi, 2001).

Prososcis structure is rather uniform in the Conidae compared to other families in the Conoidea (e.g. Miller, 1989), and comprises an intraembolic proboscis with a buccal mass at its base; the valve of Leiblein is lacking. A poison gland consisting of a large, muscular bulb and a long, glandular duct, opens to the buccal mass. Radular teeth are formed in the long arm of the radular sac and passed to the short arm for storage before being transferred to the proboscis tip. Much of the variability of foregut anatomy concerns the accessory glands. A snout gland that opens to the rhynchocoel may be present or absent; accessory salivary glands may be present or absent, single or paired (e.g. Bergh, 1895b; Amaudrut, 1898; Shaw, 1914; Alpers, 1931; Jaeckel, 1952; Abbott, 1967; Marsh, 1971, 1977; Greene & Kohn, 1989; Miller, 1989). *Conus jaspideus* corresponds to Feeding Mechanism 4 in the classification scheme of Kantor (1990). Several comparative surveys of neogastropod and/or toxoglossan foregut anatomy also are available (Taylor & Morris, 1988; Miller, 1989; Kantor & Taylor, 1991; Medinskaya, 1992; Kantor, 1996); Taylor, Kantor & Sysoev (1993) provided a review of foregut structures within the Conoidea and a revised classification of the Conidae based largely on this system.

The midgut of conids is small and undifferentiated, lacking caecae and sorting areas (Shaw, 1914). A discussion of the presence or absence of the anal gland within the Conidae is a notable exception in discussions of neogastropod phylogeny, despite being commonly reduced or lost in many neogastropods (e.g. Ponder, 1973; Taylor & Morris, 1988); Shaw (1914) did not figure or describe an anal gland in *Conus tulipa* or *C. textile*. There are no descriptions of renal morphology within the Conidae.

Available descriptions converge on a consistent view of the nervous system as zygoneurous, dialyneurous, with long subesophageal, buccal and pedal connectives. The supra-oesophageal ganglion is incorporated in the nerve ring and there are three visceral ganglia along the visceral loop. The tentacular nerve gives rise to the optic nerve, then branches into three nerves of equal size. The statocysts lie ventral to the circum-oesophageal nerve ring (Bouvier, 1887; Shaw, 1914).

FAMILY NASSARIIDAE: *ILYANASSA OBSOLETUS* (SAY 1822)

Material examined
Cape Henlopen, Delaware (USNM 890946).

External anatomy and mantle cavity
Mantle edge smooth. Siphon long with basal flaps (Fig. 7B, si), opening to bipectinate osphradium (os). Anterior pedal gland opening under thick propodial flap. Ventral pedal gland present in females, opening mid-ventrally via small slit, just behind front edge of foot. Operculum present.

Reproductive system
Gonad dorsally overlying digestive gland on right, to base of gastric chamber. Gonopericardial canal present behind base of mantle cavity (Fig. 2I, gpc); small flap marking entrance of canal to pericardium. Oviduct opening to small albumen gland with U-shaped lumen (ag). Three to four small pouches along crest of albumen gland possibly functioning in storage of sperm; no sperm present. Albumen gland narrowing and opening to ventral channel of capsule gland (cg), dorsally giving off narrow duct leading to lobate ingesting gland (igl). No sperm present in duct of ingesting gland. Capsule gland comprising paired, glandular laminae bearing regionated epithelium, enclosing tall, narrow lumen. Proximal capsule gland bordering albumen gland turning briefly to left, then turning anteriorly and continuing towards female opening. Ventral channel opening at anterior end of capsule gland, to short, narrow vagina, terminating in simple female opening (fo). Muscular bursa and vestibule absent; glandular tissue of distal capsule gland forming shallow pocket, possibly functioning as bursa.

Vas deferens emerging from testis and expanding into large, convoluted seminal vesicle. Vas deferens narrowing near back wall of kidney. Several strands of connective tissue connecting vas deferens and pericardial wall; gonopericardial canal absent. Vas deferens opening to narrow, convoluted prostate at base of mantle cavity (Fig. 3G). Small diverticulum from proximal prostate ending blindly. Pallial vas deferens crossing neck and entering base of penis (pe). Penis long and dorso-ventrally flattened with spatulate tip. Penial duct (ped) running subcentrally to tip of penis.

Alimentary System
Foregut. Salivary gland ducts (Fig. 7B, sgd) bypassing nerve ring, embedded anteriorly within dorsal folds, then curving around base of buccal cavity, opening ventrally under elongate odontophore. Accessory salivary glands and jaws absent. Three nerves from each buccal ganglion and each cerebral ganglion innervating large pleurembolic proboscis. Nerves and buccal artery entering proboscis ventrally, passing through proboscis basal septum.

Paired cartilages fused anteriorly. Lateral edges of cartilages curving dorsally, forming gutter supporting radular ribbon. Deep sulcus dorsally enclosing rachiglossate radula. Odontophore long, narrow, and dorso-ventrally flattened. Radula passing over bending plane of anterior tip, extending posteriorly into deep sublingual cavity. Subradular organ absent. Unfused posterior tips of cartilages, becoming enveloped in thick sheath of muscle fibres, flanking long, straight radular sac. Paired retractor muscles connecting each bolster tip and radular sac to ventral proboscis wall (ps). Thick muscular sheet dorsally connecting bolsters. Two large sets of retractors, connecting inner sides of bolsters to dorso-lateral proboscis walls. Single, unpaired set of retractors attaching ventrally to buccal mass and posterior proboscis sheath. Two large protractors attaching laterally to posterior ends of bolsters and anteriorly to sides of proboscis. Large buccal mass filling cephalic haemocoel when retracted, projecting well past posterior end of proboscis sheath.

Dorsal folds beginning just behind mouth, continuing into anterior oesophagus, gradually migrating ventrally. Ventral folds absent within anterior most oesophagus (Fig. 10F). Walls of distal anterior oesophagus becoming uniformly highly folded. Valve of Leiblein (Fig. 7B, vl) present proximal to nerve ring; gland of Leiblein present with terminal ampulla. Dorsal folds weakly developed within mid-oesophagus.

Midgut. Oesophagus opening ventrally on left (Fig. 19A). Well-developed sorting area present to left of oesophagus (sa). Paired digestive gland ducts (dgd) opening to right of oesophagus. Long, narrow glandular fold (gp), separating digestive gland ducts from small, ventro-lateral gastric shield (gs). Posterior gastric chamber extremely elongate (ce), lined with textured, knobby epithelium roughly arranged in longitudinal folds; irregular tufts of cilia crowning crests of folds. Ciliary currents within gastric chamber flowing posteriorly on left and anteriorly on right. Ciliary currents flowing clockwise in sorting area and adjacent to intestinal groove. Large, well-developed style sac region bearing two large typhlosoles, each possessing ciliated strip of raised cilia along inner (style sac) margins (Figs 19A, 21H). Typhlosoles flanking extensive region of transversely folded epithelium with differentiated cilia. Ciliary currents flowing clockwise within style sac. Crystalline style present.

Hindgut. Intestine exiting style sac, curving dorsally and slightly posteriorly around rear wall of kidney. Anal gland absent.

Reno-pericardial system

Kidney lumen elongate, projecting slightly into pallial cavity (Fig. 23E). Afferent renal vessel entering kidney floor anteriorly, to right of reno-pericardial canal (rpc). VARV extending posteriorly within floor, supplying numerous clusters of primary tubules along right wall. DARV extending dorsally attached to front wall of kidney, turning posteriorly within centre of kidney roof, supplying secondary tubules. Primary and secondary tubules pycnonephridial, broadly interdigitating along right side of roof. Simple, narrow, thin-walled gland of Leiblein ampulla present within afferent renal vessel, extending within DARV (Fig. 7B, gl). Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous, left dialyneurous (Fig. 24G). All ganglia except visceral ganglia concentrated in circum-oesophageal nerve ring. Cerebral (ceg) and pleural (plg) ganglia broadly fused. Single nerve splitting near nerve ring into tentacular and optic nerves. Tentacular nerve giving off several small branches before splitting into two nerves of equal size, extending length of tentacle (Fig. 7B, tn). Buccal ganglia (Fig. 24G, bg) present at anterior ends of cerebral ganglia. Large siphonal ganglion present (Fig. 7B, sig) at dialyneury between nerve from left pleural and branch from anterior osphradial nerve. Posterior osphradial nerve giving rise to left arm of visceral loop. Propodial ganglia (Fig. 24G, ppg) present at anterior ends of pedal ganglia (pdg). Paired, asymmetrical visceral ganglia (Fig. 7B, vg) straddling posterior oesophagus. Highly asymmetrical statocysts with single statoliths present ventral to nerve ring (Fig. 24G, sc).

Remarks

Dimon (1905) provided some preliminary observations on the external anatomy and mantle cavity, reproductive and alimentary systems. Brown (1969) gave a more detailed description of the alimentary system. The present description is congruent with that of Brown in many respects with several minor exceptions. For example, Brown described the salivary gland ducts as entering the buccal cavity dorso-laterally. Histological sections revealed here that fine ducts, embedded within the walls of the buccal mass, enter ventrally under the odontophore. Brown figured the gland of Leiblein as lacking a terminal ampulla. The ampulla was found here to enter the dorsal branch of the afferent renal vessel and is thin-walled and simpler than those in some muricids (e.g. Carriker, 1943).

Within the midgut, Brown (1969) indicated that ciliary currents adjacent to the intestinal groove flow towards the intestine. Here, these currents were found to flow transversely in the direction of the sorting area or, more posteriorly, toward the oesophageal aperture itself. In addition, Brown did not acknowledge the presence of an elongate glandular fold bounding the gastric shield.

Discussion

Like other nassariids, *Ilyanassa obsoletus* bears weak dorsal folds in the anterior oesophagus (= glande framboisée) (Graham, 1941). A valve of Leiblein and a small gland of Leiblein are present; accessory salivary glands and the anal gland are lacking (Graham, 1941). The kidney is pycnonephridial (Ponder, 1973).

Female reproductive anatomy of *Ilyanassa obsoletus* is consistent with described nassariids in the presence of a gonopericardial connection and an ingesting gland, but is unique in lacking a bursa (Fretter, 1941; Johansson, 1957; Houston, 1976). Houston (1976) described the presence of an opening within the oviduct to the mantle cavity in *Nassarius incrassatus*, an aperture recorded only in several muricids (Houston, 1976) and unknown among nassariids. Houston (1976) did not find a seminal receptacle or an ingesting gland, structures reported as present in a different analysis of the same species (Johansson, 1957). The present study noted several outpocketings of the albumen gland. Although their function could not be confirmed, similar outpocketings are known to store sperm in other neogastropods (e.g. Kool, 1993).

In male nassariids, a diverticulum connecting the base of the prostate with the mantle lumen may be open (Fretter, 1941), fused shut (present study), or lacking entirely (Houston, 1976). The penial duct within the dorso-ventrally flattened penis may be subcentral (present study) or centrally located (Fretter, 1941).

There appear to be two types of midgut organization within the Nassariidae. The midgut structure of *N. incrassatus* (Smith, 1967) and *Tritia fratercula* (Medinskaya, 1993) is congruent in many respects with that of *Ilyanassa obsoletus*, with several minor exceptions. For example, in the two former taxa, the depression bearing the paired ducts of the digestive gland is more pronounced than in *I. obsoletus*, and the sorting area to the left of the oesophagus is lacking. The ‘ciliary sorting area’ (Smith) of *N. incrassatus* is homologous to the style sac region, and the ‘posterior sorting area’, occurring ventrally in front of the intestinal groove, has no equivalent in *I. obsoletus*. The 'posterior sorting area' (Medinskaya) of *T. fratercula* is not equivalent to the structure of the same name in *N. incrassatus*, but is homologous to the style sac region. In contrast, the midgut organization of of *Nassarius reticulatus* (Graham, 1949) and *Cyclope neritea* (Morton, 1960) is characterized by an elongate fold bounding the oesophageal aperture to the left, separating the oesophagus from the sorting area; this fold is lacking in the other nassariids. In addition, the digestive gland ducts open to the sorting area to the left of the oesophagus and there is no fold bounding the gastric shield on the left.

The nervous system of *Ilyanassa obsoletus* differs from described nassariids only in minor detail (Risbec, 1952; Fretter & Graham, 1962; Brown, 1982). For example, in *I. obsoletus* the left arm of the visceral loop branches from the posterior osphradial nerve near the osphradium; in other nassariids, the visceral loop arises much closer to the circum-oesophageal nerve ring (Brown) or from the nerve ring itself (Fretter & Graham). Three or five pairs of buccal nerves innervate the proboscis (Brown). The propodial ganglia may be lacking; a single visceral ganglion with two accessory ganglia may be present (Brown).

FAMILY MURICIDAE:
UROSALPINX CINEREA (SAY 1822)

Material examined

Indian River, Delaware (USNM 890947).

External anatomy and mantle cavity

Mantle edge smooth. Siphon opening to bipectinate osphradium approximately one half length of ctenidium. Anterior pedal gland opening under flap along broad margin of propodium. Paired ventral openings to foot sole comprising ventral pedal gland (in females) and accessory boring organ. Operculum present.

Reproductive system

Oviduct entering anterior end of large albumen gland (Fig. 2H, ag). Posterior portion of albumen gland visceral, lying alongside kidney (Fig. 2H). Small, blind diverticulum present at junction between renal and glandular oviducts, representing vestigial gonopericardial canal, but not contacting pericardium. Capsule gland (cg) composed of regionated epithelium, comprising right, left and antero-ventral (right) lobes. Ventral channel extending anteriorly to vestibule at anterior end of capsule gland. Small duct connecting ventral channel with large, muscular bursa copulatrix (bc) lying below glandular oviduct. Vestibule narrowing to long vagina. Vagina curving around bursa, opening to mantle cavity via simple female opening (fo).

Proximal vas deferens convolute, functioning as seminal vesicle. Broad base of large, glandular prostate opening to mantle cavity via narrow slit. Prostate narrowing anteriorly. Closed pallial vas deferens crossing neck to short, narrowly triangular, spatulate penis lying behind right cephalic tentacle. Penial duct extending subcentrally to tip, connected to surface by visible suture.

Alimentary system

Foregut. Radula rachiglossate. Large pleurembolic proboscis present. Radular ribbon lying in deep sulcus between paired cartilages. Robust sclerite, composed of homogeneous cuticle, dorsally lining buccal cavity, juxtaposed with grooved, ventral cuticle. Salivary glands by-passing nerve ring, entering buccal cavity dorso-laterally. Accessory salivary glands present, opening via common duct. Ventral folds within anterior oesophagus absent (Fig. 10G).Valve of Leiblein present. Gland of Leiblein large and complex. Ampulla of gland of Leiblein entering afferent renal vessel.

Midgut. Midgut lying short distance behind kidney. Gastric lumen small, U-shaped (Fig. 19B). Oesophagus opening to posterior tip of gastric chamber from left (e). Posterior-most oesophagus elongating dorsoventrally, folds diminishing. Dorsal oesophageal roof becoming rounded, ventral floor becoming narrow, V-shaped channel. Ventral channel continuous with deep vestibule containing two large, asymmetrical ducts of digestive gland (dgd). Vestibule lying to right of oesophageal aperture, along inner wall of gastric chamber. Low fold (gp) bounding lip of vestibule continuous with major typhlosole (t1). Posterior tip of gastric chamber terminating in shallow pouch (po) ventral to oesophageal aperture. Gastric shield absent. Ciliary currents in vestibule flowing into intestinal groove. Ciliary currents flowing from left to right out of blind pouch, and clockwise in main gastric chamber, toward vestibule along ventral floor. Style sac region (ss) bearing paired typhlosoles (t1, t2), and long, broad region of irregularly transverse folds bearing differentiated cilia. Currents flowing clockwise in style sac. Crystalline style absent.

Hindgut. Intestine exiting style sac region (Fig. 19B, int), extending anteriorly and towards left along surface of viscera. Intestine crossing from left to right ventrally behind pericardium and kidney, then turning anteriorly at right side of kidney. Branching anal gland lying under well-developed tissue of hypobranchial gland, opening to rectum just behind anus.

Reno-pericardial system

Afferent renal vessel entering kidney floor anteriorly, to right of nephropore in front of reno-pericardial canal. VARV extending posteriorly within floor, supplying approximately three main vessels that ramify along right wall. DARV branching soon after emerging from floor, supplying excretory tissue along front wall and in roof. DARV turning posteriorly near roof, continuing back alongside nephridial gland. Primary and secondary tubules pycnonephridial, interdigitating broadly within roof. Nephridial gland present.

Nervous system and sensory structures

Nervous system epiathroid, right zygoneurous, left dialyneurous. All ganglia except visceral ganglia concentrated in circum-oesophageal nerve ring. Many fine branches of single tentacular nerve innervating cephalic haemocoel and tentacle. Single, dominant tentacular nerve running to tip of tentacle. Small siphonal ganglion present at point of dialyneury between nerve from left pleural ganglion and nerve from anterior osphradial nerve originating from supra-oesophageal ganglion. Visceral loop bearing two visceral ganglia overlying posterior oesophagus. Statocysts with single statoliths just below circum-oesophageal nerve ring, near pedal ganglia.

Remarks

Houston (1976) provided an analysis of reproductive morphology of this species that is congruent in most respects to the description here. But Houston reported a centrally placed penial duct and did not describe the vestigial connection to the mantle cavity in the male, nor the vestigial gonopericardial canal in the female. Houston also found orientated spermatozoa attached to the ventral channel of the capsule gland; this could not be confirmed in the material examined here.

Carriker (1943) provided a thorough description of proboscis structure and function, foregut anatomy and the circum-oesophageal nerve ring, with the exception of tentacular nerve branching patterns and the siphonal ganglion.

Discussion

A wealth of anatomical data is available for muricids, revealing a rich source of variability in all organ systems. For example, in females, a gono-pericardial connection may be present (Fretter, 1941; Houston, 1976) or absent (Houston, 1976). Unlike other neogastropod families, the albumen gland displays two distinct morphologies, either linear or U-shaped (Kool, 1993). There may be a connecting duct between the capsule and albumen glands, or only a simple constriction may separate the two (Houston, 1976). Sperm storage structures between the albumen and capsule glands may comprise a single ingesting gland with the duct acting as a seminal receptacle (Fretter, 1941), or paired storage structures, an ingesting gland anteriorly and a seminal receptacle posteriorly. The duct of the ingesting gland typically arises from the capsule gland (Houston, 1976). In addition, orientated spermatozoa may be attached to the unciliated, columnar epithelium of the capsule gland's ventral channel (Fretter, 1941; Houston, 1976), or lie within outpocketings of the albumen gland (Kool, 1993). The anteroventral lobe of the capsule gland may be present or absent (Wu, 1973). The bursa copulatrix may be continuous with the capsule gland (Kool, 1993) or separate from it, lying dorsally or ventrally to the oviduct (Fretter, 1941; Houston, 1976; Kool, 1993). In females, the foot bears an accessory boring organ located within a pore that may or may not be separate from the ventral pedal gland (Fretter, 1941; Ponder, 1973; Kool, 1993).

In males, the vas deferens is highly convoluted (Fretter, 1941) or rather straight (Houston, 1976). There may be a small diverticulum off the vas deferens that is connected to the pericardium by connective and muscle tissue, or there may be no trace of a gonopericardial connection (Fretter, 1941). Communication between the prostate and mantle cavity is absent, or present via a slit or a short ciliated duct (Fretter, 1941; Houston, 1976; Kool, 1993). The penis is dorso-ventrally flattened with ducts either centrally or subcentrally located (Fretter, 1941; Houston, 1976); the pallial vas deferens may be open (Kool, 1993) or closed with a visible suture connecting the duct to the surface (Fretter, 1941; Kool, 1993).

The Muricidae is one of only several neogastropod families to possess a cuticular lining of the buccal epithelium (Ponder, 1973), rendering homology of this structure to the jaws of other caenogastropods uncertain (Ponder & Lindberg, 1997). Typically, the dorsal salivary glands are massive, but the accessory salivary glands are present or absent, paired or single, with paired accessory glands typically sharing a common duct (Haller, 1888; Amaudrut, 1898; Wu, 1965; Ponder, 1973; Wu, 1973; Kool, 1993).

Muricids possess a large, complexly folded gland of Leiblein, with a well-developed terminal ampulla that varies in length (Haller, 1888; Amaudrut, 1898; Hirsch, 1915; Wu, 1965; Kool, 1993) but is commonly described as lying within the afferent renal vein (Haller, 1882; Carriker, 1943; Kool, 1993). The mid-oesophagus contains a region of highly glandular dorsal folds that also varies in length, which passes into the duct of the gland of Leiblein (Haller, 1888; Hirsch, 1915; Graham, 1941; Wu, 1965; Ponder, 1973; Kool, 1993).

The midgut is U-shaped with paired ducts opening to an often large and deep vestibule (Haller, 1888; Hirsch, 1915; Wu, 1965; Smith, 1967; Kool, 1993;

Medinskaya, 1993). Similar to the present findings, Haller (1888) and Smith (1967) found a deep oesophageal groove that opens directly to the vestibule. The lip of the vestibule is formed by a fold of variable height, functionally separating the ducts from the gastric chamber. The fold passes more or less directly into the major typhlosole (Wu, 1965; Kool, 1993; Medinskaya, 1993) and may bear a remnant of the gastric shield (Smith, 1967).

The style sac region, comparable to the so-called 'zone of compaction' (Smith, 1967; Medinskaya, 1993) or 'intestine' (Kool, 1993), is characterized by the presence of parallel, transverse folds bearing differentiated cilia (present study), but has been reported to be cuticularized (Medinskaya, 1993). The region of horizontal folding in the style sac varies considerably in length between species (Wu, 1965; Smith, 1967; Kool, 1993; Medinskaya, 1993). Previous studies have consistently reported that ciliary currents beat out of the oesophagus and toward the duct vestibule (Wu, 1965; Smith, 1967), clockwise within the gastric lumen and compacting area (Wu, 1965; Smith, 1967; Medinskaya, 1993), and out of the vestibule into the intestinal groove (Wu, 1965; Medinskaya, 1993).

Graham (1949) examined several muricids, including *Urosalpinx cinerea*. However, Graham's description of the muricid midgut differs fundamentally from those discussed above; the major typhlosole bounds the inner edge of the duct vestibule, whereas in all other muricids, this typhlosole bounds the outer edge of the vestibule. This reversal of topological relationships may be a printing error. Moreover, ciliary currents flow away from, rather than toward, the duct vestibule along the ventral floor of the gastric chamber (Fig. 19B) and only a single duct of the digestive gland is present.

Muricid nervous systems are epiathroid, dialyneurous and zygoneurous (Haller, 1882, 1888; Bouvier, 1887). A siphonal ganglion is present at the site of dialyneury (Haller, 1882). All major ganglia except the visceral ganglia are incorporated in the circum-oesophageal nerve ring, with the buccal ganglia separated from the nerve ring by short connectives (Bouvier); the supra-oesophageal connective may be somewhat long (Haller, 1882). Two (Bouvier) or three (Haller, 1882) visceral ganglia may be present.

PHYLOGENETIC ANALYSIS

A data matrix comprising 18 taxa and 64 characters was edited with DADA 1.97 (Nixon, 1995) (Table 1). Ingroup taxa were chosen to represent a broad diversity of feeding modes (e.g. grazing, suspension feeding), diets (e.g. microherbivory, carnivory) and alimentary morphologies. Outgroups were chosen based on the results of Ponder & Lindberg (1997), indicating that cocculinids and neritids may form a clade sister to the Apogastropoda (Caenogastropoda plus Heterogastropoda; Fig. 27).

Table 1. Data matrix for 16 caenogastropods and two outgroups. '–' indicates inapplicable cells; '?' indicates unknown data

	Character number (× 10)
Taxa	0 1 2 3 4 5 6
Macleaniella	1000110115100014?-00101110-0110101010000001000102 20-0001010-0231
Theodoxus	0000--000-1010110-00101110-000010100 0?00??0?0000220-1000000-?231
Neocyclotus	10011100031111102000111 10--00001112000110010010 0220-0021010-10-1
Marisa	1001110002?11110200011110--00001112000110010010 0220-0010010-1011
Lampanella	1000000010011110100011111 1-0010111110000011010202 2111100010-1030
Petaloconchus	1000000010011110100011010--00101110110000110102022111100110-0030
Strombus	1000000110111111010001101 0--0011111011?0001101020221 01101110-0010
Crepidula	000110001011111011001100 0--011011101000001101020221 12101110-0000
Bithynia	101110011311111011001101 0--01101110000000110102022 101110210-0030
Littorina	100110011011111 14?000111111-0011111210000000100020221 11111100-0030
Neverita	100?00??1411111010030-0011-001?0-0-1000000000020011 11101000-0110
Cypraea	000010001511100--003111011-00000-0-0010010000130011111234?0-0020
Nitidiscala	1?000000100210101213 0-000--00000-0-0010010010030221131 00000-0030
Panarona	0110101111131213?1120-0013-10000-130020000010031011121 0131100110
Prunum	010011111111 4100--1120-0012100000-13001000001003100112101 41110110
Conus	1???????1115--0--1010-0012100000-13002000001003110111102 21100110
Ilyanassa	111010101316100--1020-00120100111131010001101020101121 011111011 0
Urosalpinx	1100111111161012?1120-001201000 0-1300101001000211011210101110110

The terminals coded in this analysis are species level examplars. Although this approach is repeatable, it has a number of limitations; the exemplar may be morphologically derived relative to the group it represents, and the method limits the amount of data that can be incorporated into an analysis if there is data disjunction, i.e. data from different species cannot be spliced together to form a composite terminal (Nixon & Carpenter, 1996). However, alternatives often incur more serious liabilities. The intuitive groundplan approach has been severely criticized on the basis that it is unrepeatable and subjective (Yeates, 1995). The splicing and fusing of terminals has been justified on the grounds that the amount of data included in an analysis is maximized, and ambiguity is decreased through the removal of '?', thereby strengthening the parsimony criterion. Despite these advantages, the trade-off between ambiguity and repeatability is clearly acknowledged (Nixon & Carpenter, 1996 and Carpenter & Wheeler, 1999) and carries the additional liability of the assumption of monophyly among the fused terminals. Thus, all methods currently available to cope with the problems of large numbers of terminals and/or data disjunction have advantages as well as liabilities.

Heuristic studies have demonstrated that when absence is coded in a multistate character, it becomes informative in determining the placement of taxa characterized by loss relative to other taxa (Strong & Lipscomb, 2000). This issue is important in phylogenetic analyses of a group dominated by numerous parallel trends of reduction and loss (Ponder & Lindberg, 1997). Thus, morphological characters were coded using reductive coding (Wilkinson, 1995) and analysed using NONA 1.6 (Goloboff, 1993) which suppresses persistent arbitrary resolutions, using the heuristic search option 'hold 100; hold/25; mult*20.' All characters were analysed as unordered. Bremer support was calculated with TreeRot (Sorenson, 1996) using a heuristic search option with ten random addition sequences and tree-bisection-reconnection branch swapping. To evaluate correlations between gut morphology and feeding, character optimizations were examined in CLADOS (Nixon, 1993) under DELTRAN and compared to feeding biology, which was mapped onto the consensus cladogram.

CHARACTERS

The following is a description of characters used in this analysis with a comparison and discussion of putative homologies, variability and distribution among the taxa. Species names are given in brackets after each state description in the order that they appear in the text. '?' indicates unknown data, '–' indicates inapplicable data. State assignments do not reflect a priori polarization of characters. Abbreviations are as follows: *Mac* = *Macleaniella*; *The* = *Theodoxus*; *Neo* = *Neocyclotus*; *Mar* = *Marisa*; *Lam* = *Lampanella*; *Pet* = *Petaloconchus*; *Str* = *Strombus*; *Cre* = *Crepidula*; *Bit* = *Bithynia*; *Lit* = *Littorina*; *Nev* = *Neverita*; *Cyp* = *Cypraea*; *Nit* = *Nitidiscala*; *Pan* = *Panarona*; *Pru* = *Prunum*; *Con* = *Conus*; *Ily* = *Ilyanassa*; *Uro* = *Urosalpinx*.

EXTERNAL ANATOMY

1. Adult operculum

(0) Absent [*Mac*, *Cre*, *Cyp*, *Pan*, *Pru*] (1) Present [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Bit*, *Lit*, *Nev*, *Nit*, *Con*, *Ily*, *Uro*].

This feature has been included in this analysis despite the likelihood that most gastropods possess at least a larval operculum that has been lost independently in the adult in many groups (Ponder & Lindberg, 1997).

2. Ventral pedal gland

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*] (1) Present [*Pan*, *Pru*, *Ily*, *Uro*].

The ventral pedal glands of female neogastropods play a role in formation of the egg capsule, moulding the egg case and attaching it to the substrate (Ankel, 1936; Fretter, 1946). Many basal caenogastropods also possess metapodial and/or mesopodial accessory pedal glands that similarly play a role in reproduction (e.g. Ponder, 1965, 1967; Ponder & Yoo, 1980; Houbrick, 1987) or in anchoring the animal to the substrate (Houbrick, 1993). For example, epitoniids possess a mesopodial pedal gland that functions in forming the string of egg capsules (e.g. Robertson, 1983; present description). The gland opens through a ciliated duct, near the anterior one third of the foot sole, to a longitudinal groove running posteriorly to the sole tip. Although the origin and homologies of the neogastropod ventral pedal gland have received little attention, Fretter (1946) described the presence of a 'ventral' pedal gland in *Trivia monacha* that moulds the egg capsules. Because the gland is present only in females, Fretter (1946) suggested that the gland was homologous to that in the Neogastropoda. In the present analysis, the feature in *Nitidiscala tinctum* is coded with '?' to indicate homology uncertain pending a more detailed analysis of pedal gland homologies.

REPRODUCTIVE SYSTEM

3. Gonopericardial canal

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pru*, *Uro*] (1) Present [*Bit*, *Pan*, *Ily*].

This feature is notoriously variable at lower taxonomic levels within the gastropods, having been lost independently many times (Fretter & Graham, 1962), and may be polymorphic within species as well (e.g. *Bithynia tentaculata*; Krull, 1935; Lilly, 1953; present analysis). Moreover, there is a range of gonopericardial 'connections' or remnants of such connections, the presence of a discrete canal being only one. Given this variability, it is possible to subdivide this feature into many states, including: connection between pericardium and gonoduct via connective tissue (*Lampanella minima*; Fig. 2A), small blind diverticulum off oviduct (*Urosalpinx cinerea*; Fig. 2H), small blind diverticulum off pericardium (*Cypraea robertsi*). These features were autapomorphic and not coded in the present analysis.

4. Seminal receptacle derived from renal oviduct

(0) Absent [*Mac*, *The*, *Lam*, *Pet*, *Str*, *Cyp*, *Nit*, *Pan*, *Pru*, *Ily*, *Uro*] (1) Present [*Neo*, *Mar*, *Cre*, *Bit*, *Lit*].

Structures responsible for storing sperm can be differentiated as seminal receptacles or copulatory bursae on the presence of orientated sperm; the former storing orientated and the latter storing unorientated sperm. This distinction is not always made in descriptions of caenogastropod reproductive anatomy, confounding broad based hypotheses of homology (e.g. Lilly, 1953; Reed, 1995b). Moreover, all pouches and/or portions of the oviduct that store orientated sperm are uniformly referred to as receptacles in the absence of detailed comparative studies to confirm or reject the putative homology of such structures. One notable exception is the analysis of Ponder & Lindberg (1997), which suggested that receptacles associated with the albumen gland within the pallial oviduct are not homologous to receptacles derived from the renal oviduct.

In the present analysis, a striking diversity of receptacles associated with the pallial glandular oviduct was encountered (see Fig. 2, rcs), rendering hypotheses of homology tenuous at best. Furthermore, given differences in position and derivation, homology between receptacles of the renal and pallial oviduct is unlikely. Thus, only receptacles formed by the renal oviduct are hypothesized to be homologous here. The seminal receptacle of *Macleaniella moskalevi* is not considered to be homologous because it contains unorientated sperm and opens to the gonoduct behind the base of the mantle cavity (Strong & Harasewych, 1999). The present study reinterpreted oviduct homologies of some cyclophorids (Thompson, 1969), thereby revealing the presence of orientated sperm within the renal oviduct of *Neocyclotus dysoni ambiguum*; a seminal receptacle formed by the renal oviduct is also present in *Marisa cornuarietis* (Berthold, 1991; Schulte-Oehlmann *et al.*, 1994). Ponder & Lindberg (1997) coded receptacles derived from the renal oviduct as absent in architaenioglossans.

5. Pallial oviduct

(0) Open [*Lam, Pet, Str, Nev, Nit*] (1) Closed [*Mac, Neo, Mar, Cre, Bit, Lit, Cyp, Pan, Pru, Ily, Uro*].

The pallial oviduct may form a deep, open oviductal groove (e.g. *Lampanella minima*, Fig. 2A) or it may be closed along its length (e.g. neogastropods, Fig. 2F–I) opening only at the anterior tip (fo). *Macleaniella moskalevi* does not possess a pallial gonoduct (Strong & Harasewych, 1999); this taxon is scored as inapplicable.

6. Albumen gland

(0) Pallial [*Lam, Pet, Str, Cre, Bit, Lit, Nev, Cyp, Nit, Pan, Ily*] (1) Visceral [*Mac, Neo, Mar, Pru, Uro*].

In caenogastropods, the glandular oviduct typically lies entirely within the mantle cavity. However, in a number of taxa, the albumen gland is partially or completely behind the base of the mantle cavity (e.g. Fretter, 1946; Davis *et al.*, 1982; Ponder, 1984; Hershler, 1985; Schulte-Oehlmann *et al.*, 1994; present study). It is uncertain without ontogenetic data whether this pattern is the result of a common mechanism. In rissoids, this phenomenon has been attributed to the secondary glandularization of the renal oviduct (Ponder, 1988; Ponder & Lindberg, 1997).

According to the present study, the albumen gland lies partially behind the base of the mantle cavity in *Theodoxus fluviatilis* (Fretter, 1946), *Neocyclotus dysoni ambiguum* (Thompson, 1969), and *Marisa cornuarietis* (Schulte-Oehlmann *et al.*, 1994). In *Prunum apicinum* (Fig. 2G) and *Urosalpinx cinerea* (Fig. 2H), the albumen gland (ag) lies wholly behind the base of the mantle cavity alongside the kidney. Although many hydrobiids and rissoids possess a partially to wholly visceral albumen gland, in *Bithynia tentaculata* only the posterior bursa is visceral in position (Lilly, 1953). The visceral glandular gonoduct of *Macleaniella moskalevi* (Strong & Harasewych, 1999) is not considered homologous to the pallial glandular gonoduct of caenogastropods here and is coded as inapplicable. The pallial glandular gonoduct of neritopsines has been considered a parallel invention to that of caenogastropods (Haszprunar, 1988a). However, a re-evaluation and test of the homologies of the glandular oviduct in *T. fluviatilis* are beyond the scope of this analysis and are treated tentatively as homologous. Thus, the glandular oviduct of *T. fluviatilis*, the posterior tip of which is embedded in the viscera, has been coded state '1'.

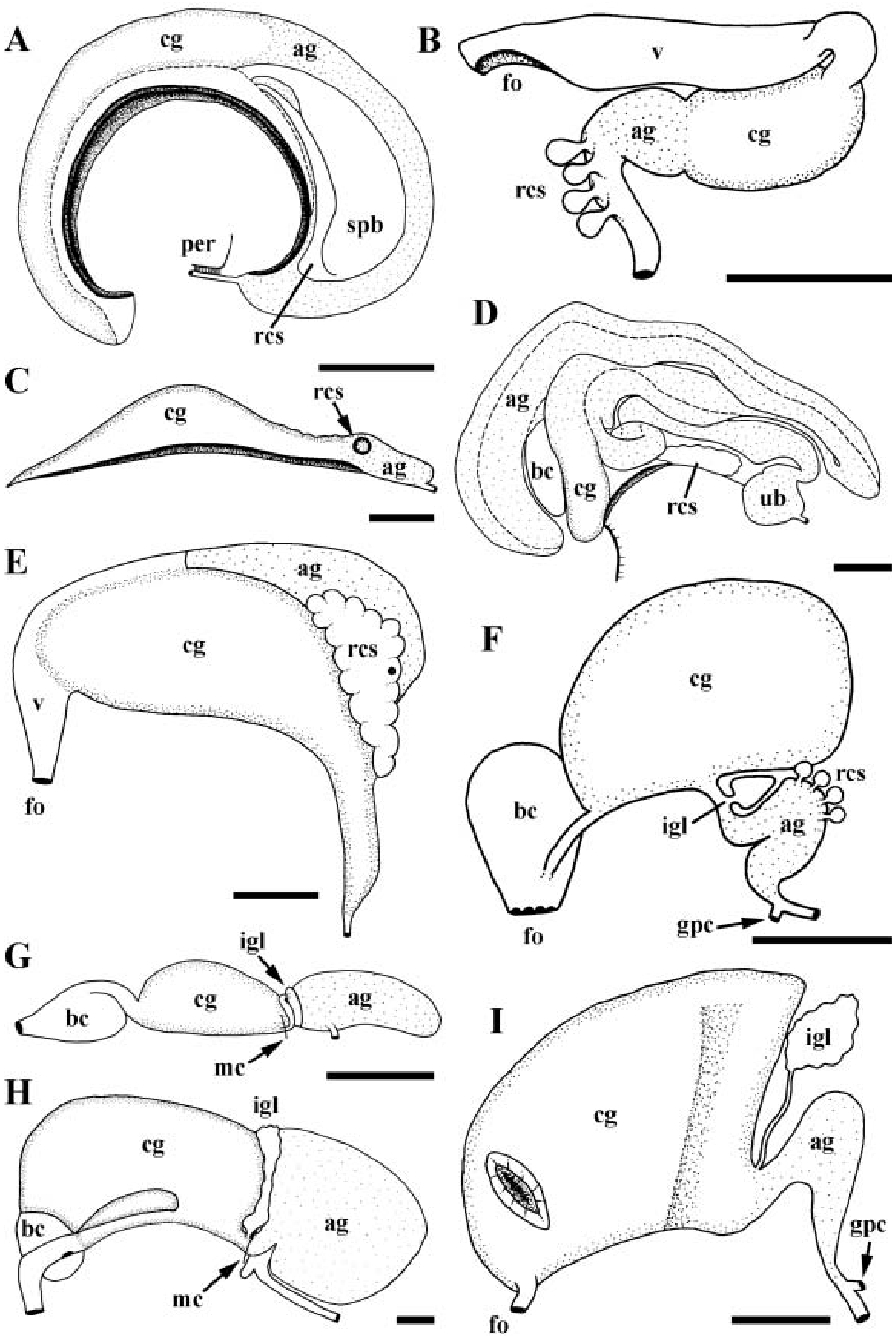

Figure 2. Female reproductive morphology. (A) *Lampanella minima*. Note connective tissue between renal oviduct and pericardium. (B) *Crepidula plana*. (C) *Petaloconchus varians*. (D) *Strombus mutabilis*. Note egg groove from capsule gland down side of foot. Dotted line indicates double-groove portion of albumen gland. (E) *Cypraea robertsi*. Note duct of receptacle at posterior end of albumen gland. (F) *Panarona clavatula*. (G) *Prunum apicinum*. Note that base of mantle cavity lies between the capsule and albumen glands. (H) *Urosalpinx cinerea*. Ventro-lateral lobe of capsule gland is shown by transparency. Note blind diverticulum off renal oviduct and small aperture connecting vestibule and bursa copulatrix. Base of mantle cavity indicated by arrow. (I) *Ilyanassa obsoletus*. Note shallow pocket in distal end of capsule gland, perhaps functioning as bursa. Scale bar = 1 mm. Abbreviations: ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; fo, female opening; gpc, gonopericardial canal; igl, ingesting gland; mc, base of mantle cavity; per, pericardium; rcs, seminal receptacle; spb, spermatophore bursa; u, uterine ball; v, vagina.

7. Ingesting gland

(0) Absent [*Mac, Neo, Mar, Lam, Pet, Str, Cre, Bit, Lit, Cyp, Nit*] (1) Present [*Pan, Pru, Ily, Uro*].

The ingesting gland (Fig. 2F–I, igl), a sac storing unorientated sperm, lies between the albumen (ag) and capsule glands (cg) of neogastropods (Fretter, 1941; Ponder, 1973). Ponder & Lindberg (1997) suggested that it is likely homologous to the posterior bursa of some neotaenioglossans.

8. Anterior bursa

(0) Absent [*Mac*, *Neo*, *Mar*, *Lam*, *Pet*, *Cre*, *Cyp*, *Nit*, *Ily*] (1) Present [*The*, *Str*, *Bit*, *Lit*, *Pan*, *Pru*, *Uro*].

A muscular bursa copulatrix (Fig. 2, bc) at the anterior end of the pallial oviduct is present in many caenogastropods, and functions in the storage of unorientated sperm. Of course, a bursa copulatrix is lacking in species that do not copulate. However, even in those that do copulate, the bursa may be absent (e.g. *Cypraea robertsi*, Fig. 2E; *Ilyanassa obsoletus*, Fig. 2H). The anterior bursa is not considered here homologous to other 'bursae' in different positions along the pallial oviduct. For example, *Lampanella minima* (Fig. 2A) possesses a spermatophore bursa (spb) of uncertain homology, embedded within the albumen gland (ag). *Bithynia tentaculata* possesses a posterior bursa that lies behind the posterior tip of the glandular gonoduct (Lilly, 1953).

9. Seminal vesicle derived from vas deferens

(0) Absent [*Mac*, *Neo*, *Mar*] (1) Present [*The*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Cyp*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

A highly convoluted vas deferens that functions in the storage of mature sperm is lacking in architaenioglossans, but is present in all sorbeoconchans (all caenogastropods to the exclusion of the Architaenioglossa; see Fig. 27). In the former, a straight vas deferens connects the testis with the base of the glandular gonoduct lying behind the base of the mantle cavity (e.g. Berthold, 1991) and does not store sperm. Ponder & Lindberg (1997) did not consider the distal seminal vesicle of neritopsines (e.g. *Theodoxus fluviatilis*, Fretter, 1946) to be homologous to the proximal seminal vesicle of sorbeoconchans. Because *T. fluviatilis* is an outgroup taxon, testing the homology of these structures is beyond the scope of this analysis. In the present analysis they are treated tentatively as homologous.

10. Pallial vas deferens

(0) Open along entire length [*Lam*, *Pet*, *Str*, *Cre*, *Lit*, *Nit*] (1) Closed along entire length with small opening at proximal end of prostate [*Pan*, *Pru*, *Con*, *Uro*] (2) Closed along entire length with small opening at distal end of prostate [*Mar*] (3) Completely closed and no communication with mantle cavity [*Neo*, *Bit*, *Ily*] (4) Proximal pallial vas deferens open (along prostate) and closed distally [*Nev*] (5) Proximal pallial vas deferens closed (along prostate) and open distally [*The*, *Cyp*].

The pallial vas deferens conducts sperm from the base of the mantle cavity to the tip of the copulatory verge (when present). The pallial vas deferens can be subdivided into several distinct regions, not all of which may be present: a glandular prostate (Fig. 3, pr), an open groove (sg) or closed tube (pvd) connecting the prostate (pr) and the penis (pe), and a duct (ed) running the length of the penis. In all taxa included in this analysis, prostatic development occurs along the proximal pallial vas deferens and is considered to be homologous. However, *Crepidula plana* (Fig. 3C) lacks the characteristic elongate prostate, possessing only a small glandular area (pr) restricted to the opening of the pallial vas deferens to the mantle cavity. It has been suggested that these glands are rudiments of the female glandular gonoduct and have a prostatic function in the male phase (Giese, 1915; Graham, 1952).

The various regions of the pallial vas deferens show a highly mosaic pattern of fusion. In some taxa it is open along its length, from base of mantle cavity to tip of penis (e.g. *Crepidula plana*, Fig. 3C; *Strombus mutabilis*, Fig. 3D). In others, the pallial vas deferens is fused only along the prostate (e.g. *Cypraea robertsi*, Fig. 3E), only distal to the prostate (e.g. *Neverita duplicata*), or along its entire length (e.g. *Ilyanassa obsoletus*, Fig. 3G). In several taxa with a completely closed pallial vas deferens, there may be a small duct that allows communication between the lumen of the prostate and the mantle cavity (e.g. *Prunum apicinum*, Fig. 3F).

11. Penis

(0) Absent [*Lam*, *Pet*, *Nit*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lit*, *Bit*, *Str*, *Cre*, *Nev*, *Cyp*, *Pan*, *Ily*, *Uro*, *Pru*, *Con*].

A copulatory verge may be present or absent. Among the architaenioglossans, the verge occurs on the neck in *Neocyclotus dysoni ambiguum* (Thompson, 1969) and on the mantle edge in *Marisa cornuarietis* (Schulte-Oehlmann *et al.*, 1994). The latter also occurs in some pilids (Andrews, 1964); *Marisa* has been scored with '?' to indicate homology uncertain. Within sorbeoconchans, the verge typically is associated with the neck or foot and is pedally innervated (Fretter & Graham, 1962; Graham, 1985). Several ingroup taxa lack a verge, including *Lampanella minima* (Fig. 3A),

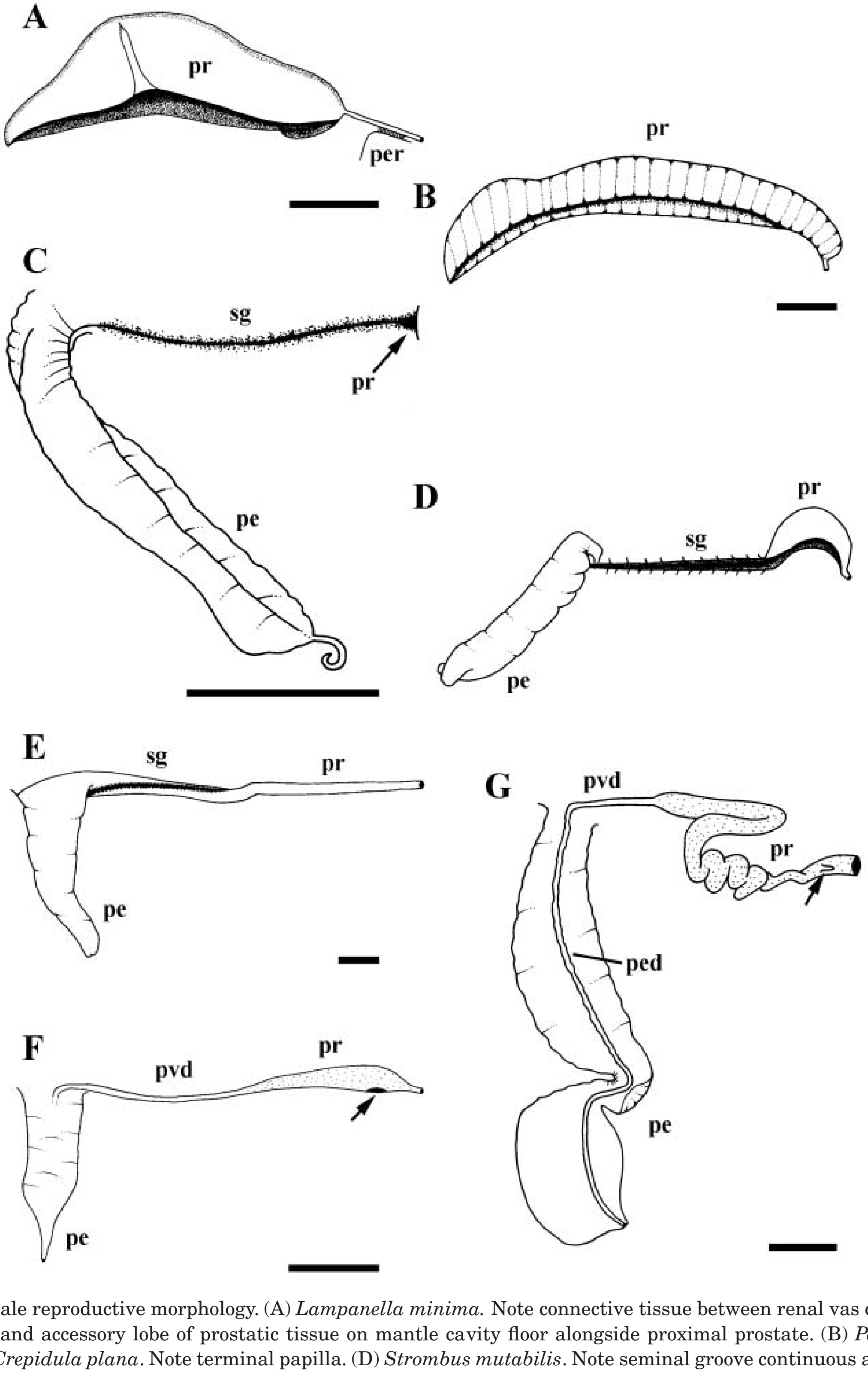

Figure 3. Male reproductive morphology. (A) *Lampanella minima.* Note connective tissue between renal vas deferens and pericardium and accessory lobe of prostatic tissue on mantle cavity floor alongside proximal prostate. (B) *Petaloconchus varians*. (C) *Crepidula plana*. Note terminal papilla. (D) *Strombus mutabilis*. Note seminal groove continuous along ventral aspect of penis. (E) *Cypraea robertsi*. Note seminal groove continuous along ventral aspect of penis. (F) *Prunum apicinum*. Penial duct not shown. Arrow indicates slit-like communication between proximal prostate and mantle cavity. (G) *Ilyanassa obsoletus*. Arrow indicates fused, tube-like communication between proximal prostate and mantle cavity. Scale bar = 1 mm. Abbreviations: ped, penial duct; pe, penis; per, pericardium; pr, prostate; pvd, pallial vas deferens; sg, seminal groove.

Petaloconchus varians (Fig. 3B) and *Nitidiscala tinctum*.

Among outgroup taxa, *Theodoxus fluviatilis* possesses a penis on the cephalic lappet to the left of the right cephalic tentacle (Fretter, 1946). In *Macleaniella moskalevi*, the right cephalic tentacle is modified to function as a copulatory organ (Strong & Harasewych, 1999). Thus, in outgroup taxa, the copulatory organ is cerebrally innervated.

All the various penes in the aforementioned groups are unlikely to be homologous and a second character is required to evaluate the homology of these copulatory verges with differing positions and innervations. However, such a character would serve only to differentiate ingroup from outgroup taxa, is autapomorphic within the ingroup (*Marisa cornuarietis*), and was not included in the analysis. The intent of this 'presence/absence' character is to evaluate whether absence of a verge is primary or secondary.

ALIMENTARY SYSTEM: FOREGUT

12. Radular configuration
(0) Rhipidoglossate [*Mac*, *The*] (1) Taenioglossate [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*] (2) Ptenoglossate [*Nit*] (3) Nematoglossate [*Pan*] (4) Uniserial [*Pru*] (5) Toxoglossate [*Con*] (6) Rachiglossate [*Ily*, *Uro*].

Homologies of radular teeth, particularly in instances of tooth reduction and loss, classically have been postulated on the basis of tooth morphology and position, coupled with information derived from hypothesized intermediate forms. Ponder & Lindberg (1997) clearly outline the limitations of this approach. The issue is particularly problematic when attempting to recognize homology across the Gastropoda, but can be equally problematic within caenogastropods, i.e. within groups such as ptenoglossans and neogastropods that have deviated from the taenioglossate condition (Ponder & Lindberg, 1997). For example, it is unclear whether the ptenoglossate condition is the result of multiplication of only marginal teeth or marginal and lateral teeth (Ponder & Lindberg, 1997). In addition, the distinctive nematoglossan teeth of cancellariids, '. . . do not have any obvious homology with other neogastropods' (Taylor & Morris, 1988), but have been suggested to be derived from the rachidian and lateral teeth (Harasewych & Petit, 1982). Thus, only gross radular configurations are coded here; more rigorous analyses of homology in cases of complex patterns of tooth fusion and/or loss await detailed studies of radular ontogenies.

13. Odontophoral cartilages
(0) Six [*The*] (1) Two [*Mac*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Ily*, *Uro*].

Within caenogastropods, the number of odontophoral cartilages is uniform, typically comprising a single pair. In a number of taxa, these two cartilages may show various patterns of fusion (e.g. *Prunum apicinum*, *Ilyanassa obsoletus*). In *Conus jaspideus*, the odontophore and cartilages are lacking.

Among outgroup taxa, *Theodoxus fluviatilis* and other neritids possess three pairs of cartilages (Salvini-Plawen, 1988; Sasaki, 1998). *Macleaniella moskalevi* and all cocculinids described thus far (Haszprunar, 1987, 1988c; Sasaki, 1998; Strong & Harasewych, 1999) possess only a single pair. Indeed, this is one feature that distinguishes the Cocculinoidea from other basal gastropods (Ponder & Lindberg, 1997).

14. Subradular region
(0) Cuticularized [*Mac*, *The*, *Nit*, *Cyp*, *Pru*, *Ily*, *Uro*] (1) Glandular [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*] (2) Muscular [*Pan*].

The subradular organ, or licker, is recorded in peltospirids, patellogastropods, and other basal gastropods (Haszprunar, 1988a; Salvini-Plawen, 1988; Ponder & Lindberg, 1997). In these taxa, the subradular organ usually bears cuticular scales and is inferred to have a sensory function based on a common, but not universal, co-occurrence with the labial commissure. The only report of a subradular organ among caenogastropods is in *Marisa cornuarietis* (Demian, 1964) and *Pila globosa* (Prashad, 1925). Amaudrut (1898) was the first to figure the subradular organ; Simroth (1896–1907) copied Amaudrut's (1898) plate and misidentified the structure as a muscular pad (Prashad, 1925). Andrews' (1965a) anatomical study neither confirms nor rejects the presence of a subradular organ in *Pomacea canaliculata*. Berthold (1991) does not describe the presence of a subradular organ in his detailed morphological investigations of ampullariids, including *Marisa cornuarietis*.

In architaenioglossans (Fig. 4B,C), the subradular organ (sro) is prominent with a non-cuticularized, complexly folded, high prismatic epithelium bearing numerous goblet cells (Fig. 4A,B; Prashad, 1925; Demian, 1964; present study). It lies below the radula (r) and projects into the mouth opening (mo) when the odontophore is retracted; no nerve fibres were observed innervating the organ in either *Neocyclotus dysoni ambiguum* or *Marisa cornuarietis*.

During the present study, glandular elaborations of the subradular odontophoral epithelium projecting into the mouth, were discovered in a number of sorbeoconchans (Figs 4D–F, 5C–E,G). The evidence is sufficient to hypothesize homology of all such subradular organs; all are similar in position and share a high prismatic epithelium with numerous goblet cells

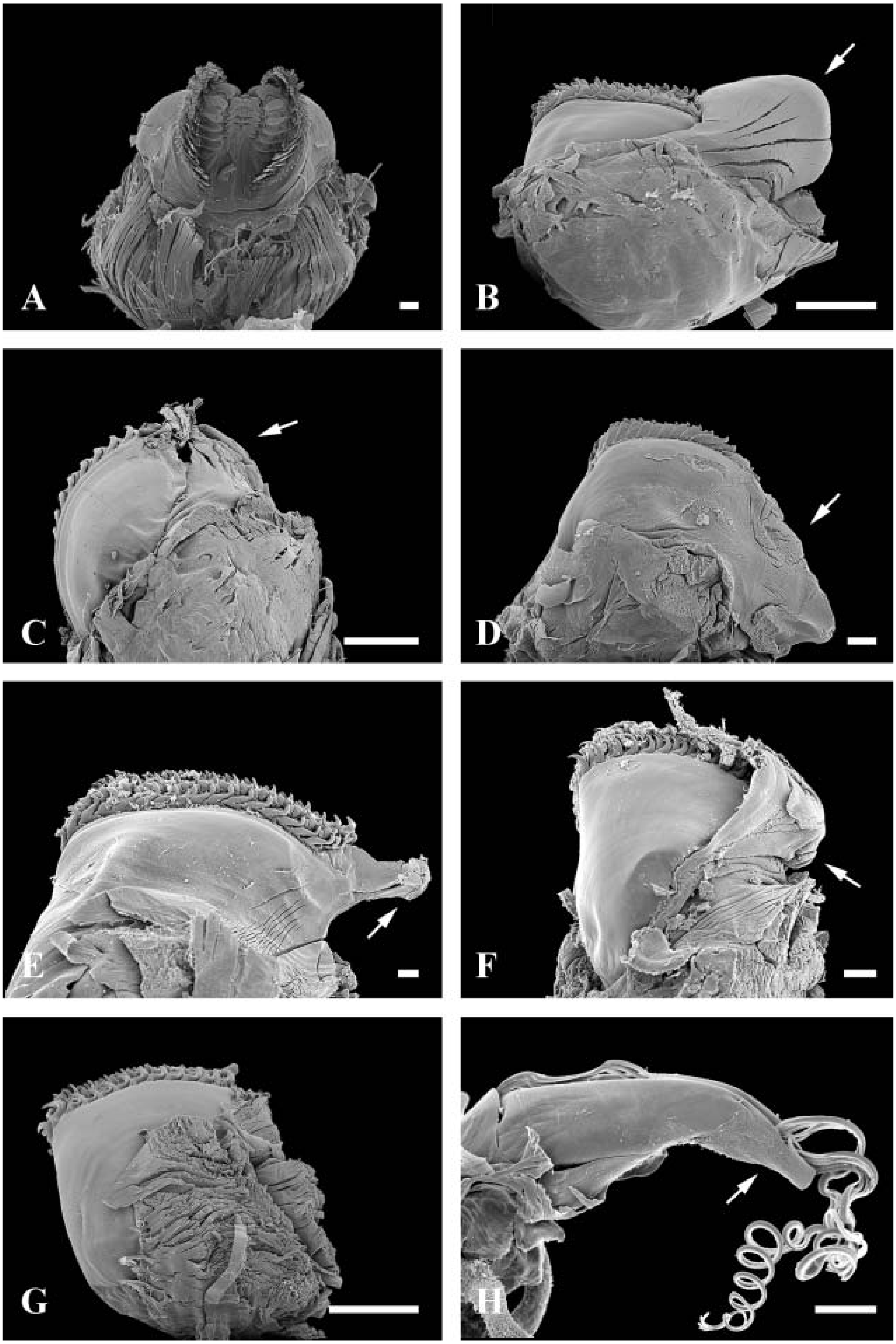

Figure 4. Morphology of odontophore; subradular organ (indicated by arrows). Except when noted, view is from the side and ventral is to the right. (A) *Theodoxus fluviatilis*, ventral view. Subradular organ absent. Scale bar = 100 µm. (B) *Neocyclotus dysoni ambiguum*. Scale bar = 1 mm. (C) *Marisa cornuarietis*. Scale bar = 1 mm. (D) *Lampanella minima*. Scale bar = 100 µm. (E) *Littorina littorea*. Scale bar = 100 µm. (F) *Neverita duplicata*. Scale bar = 100 µm. (G) *Cypraea robertsi*. Subradular organ absent. Scale bar = 1 mm. (H) *Panarona clavatula*. Ventral is down. Scale bar = 100 µm.

(except *Panarona clavatula*, see below). Among non-neogastropod sorbeoconchans, it appears that these structures are lubricatory and not sensory as they are not associated with a labial commissure and have a high prismatic, glandular epithelium dominated by mucus cells. Similarly among architaenioglossans, as suggested by Demian (1964) and Lufty & Demian (1967), it seems likely that the subradular organ has a lubricatory rather than a sensory function, despite the presence of a labial commissure in ampullariids (Prashad, 1925; Berthold, 1991; Sasaki, 1998), because no labial nerves have been observed innervating the epithelium (Prashad, 1925: 111; present study) and considering the predominating mucus cells of the subradular epithelium.

In contrast to many of the sorbeoconchans included here (e.g. Figure 4B–D), the radula of *Littorina littorea* extends far down over the frontal face of the odontophore. In this species (Figs 4E, 5F), the subradular organ (sro) is restricted to the base of the odontophore, forming a long, narrow projection that is less glandular than those of other species and is cuticularized along its dorsal surface. The overall appearance of the odontophore in *L. littorea* is similar to *Cypraea robertsi* (Fig. 4G). However, in the latter, the radula extends to the base of the sublingual cavity, and a subradular organ is lacking. It is important to note that the presence or absence of a subradular organ is independent of the presence of a proboscis. *Cypraea robertsi* (Fig. 4G) possesses a short acrembolic proboscis, but lacks a subradular organ; *Neverita duplicata* (Figs 4F, 5G) possesses an acrembolic proboscis in conjunction with a small, rounded subradular organ (sro).

The only neogastropod to possess a non-cuticularized subradular extension of the odontophore is *Panarona clavatula* (Figs 4H, 5H). In this taxon, this portion of the odontophore forms a muscular shelf supporting the nematoglossan radula and is lined with cuboidal epithelium. This 'subradular organ' cannot play a role like that of other sorbeoconchans because the epithelium is non-secretory and the odontophore is never extruded from the mouth (Petit & Harasewych, 1986).

The homology of the subradular organ of caenogastropods to those of patellogastropods and other gastropods is beyond the scope of this analysis, but has been hypothesized by several authors (e.g. Prashad, 1925; Ponder & Lindberg, 1997).

15. Cuticular lining of buccal epithelium

(0) Absent [*Cyp*, *Pru*, *Con*, *Ily*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Nit*, *Pan*, *Uro*].

Any cuticular lining of the caenogastropod buccal cavity has been treated as putatively homologous in this analysis. Those taxa lacking definitively developed jaws, as opposed to simple cuticular linings of the buccal epithelium, are coded with a separate state (see below). The coding used here differs slightly from that used by Ponder & Lindberg (1997), who distinguish between jaws and simple cuticular linings, coding the latter as 'jaws absent'.

16. Cuticle condition

(0) Paired jaw elements [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Nev*, *Nit*,] (1) Single, small jaw element [*Mac*] (2) Single, robust 'sclerite' [*Uro*] (3) Tubular cuticle [*Pan*] (4) Cuticularized oral epithelium [*The*, *Lit*].

The plesiomorphic condition of the jaw within the Gastropoda is a pair of elements that are connected dorsally (Ponder & Lindberg, 1997). Most caenogastropods (e.g. *Lampanella minima*, Fig. 5C; *Strombus mutabilis*, Fig. 5D) develop these paired jaw elements (j) at the anterior ends of the dorsal folds flanking the mouth (mo). In *Littorina littorea*, the oral epithelium is cuticularized with no definitive development of jaw plates. Ponder & Lindberg (1997) coded neogastropods as lacking jaws and did not consider the thick, dorsal sclerite of *Urosalpinx cinerea* and other muricids (Carriker, 1943; Wu, 1965) to be homologous to the jaws of other caenogastropods. *Panarona clavatula* (Figs 5H, j) and other cancellariids possess a long tubular cuticle that surrounds the buccal mass with a visible seam running dorsally along the midline (Harasewych & Petit, 1982, 1984, 1986). The cuticular tube narrows anteriorly and connects the buccal mass, at the posterior end of the proboscis, with the oral tube.

Among the outgroups, *Macleaniella moskalevi* possesses a small, unpaired jaw lying at the anterior end of the buccal cavity above the ventrally situated mouth opening (Strong & Harasewych, 1999). *Theodoxus fluviatilis* has a cuticularized dorsal epithelium in a region of transverse folds (Whitaker, 1951) that does not form a jaw.

17. Jaw composition

(0) Homogeneous [*Mac*] (1) Partially bi-layered homogeneous and rods [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Nev*, *Nit*] (2) Wholly bi-layered [*Neo*, *Mar*].

The jaw of outgroup taxa (e.g. *Macleaniella moskalevi*, Strong & Harasewych, 1999) is homogeneous in composition. In contrast, among caenogastropods that possess discrete jaws, the jaws are composed of numerous small rods (Starmühlner, 1969; Ponder & Lindberg, 1997). Architaenioglossans are unique among caenogastropods in possessing a wholly bi-layered jaw with an outer homogeneous layer and an inner layer of rods (Lufty & Demian, 1967; present study) (Fig. 5A,B). The latter has been shown to arise

Figure 5. Histology of subradular organ. (A) *Neocyclotus dysoni ambiguum*. Transverse section. Note bi-layered jaw. Scale bar = 0.5 mm. (B) *Marisa cornuarietis*. Sagittal section. Note bi-layered jaw. Scale bar = 0.5 mm. (C) *Lampanella minima*. Transverse section. Note jaw with exposed rods. Scale bar = 1 mm. (D) *Strombus mutabilis*. Transverse section. Scale bar = 0.5 mm. (E) *Crepidula plana*. Transverse section. Scale bar = 1 mm. (F) *Littorina littorea*. Sagittal section. Scale bar = 1 mm. (G) *Neverita duplicata*. Transverse section. Scale bar = 0.5 mm. (H) *Panarona clavatula*. Transverse section. Scale bar = 1 mm. Abbreviations: c., radular cartilage; j, jaw; mo, mouth; r, radula; srm, subradular membrane; sro, subradular organ.

later in ontogeny than the homogeneous layer in *Marisa cornuarietis* (Lufty & Demian, 1967). Sasaki (1998) coded the Ampullariidae as possessing simple sheet-like jaws.

In fact, in the present study, the jaw of sorbeoconchans was found to be only partially composed of rods, with an outer homogenous layer that laterally overlies the rodlet layer (e.g. *Lampanella minima*, Fig. 5C). But this jaw is, nevertheless, distinct from that of architaenioglossans because the rods are partially exposed. Outgroup and ingroup taxa with a simple cuticular lining of the buccal mass (*Theodoxus fluviatilis*, *Littorina littorea*, *Panarona clavatula*) or a jaw of uncertain homology (*Urosalpinx cinerea*) have been coded as uncertain for this character.

18. Salivary gland/duct position relative to circum-oesophageal nerve ring

(0) Pass through nerve ring [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Lit*, *Nev*,] (1) Overlie/lie alongside nerve ring [*Cre*, *Bit*, *Cyp*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (2) Posterior to nerve ring [*Nit*].

This feature has figured rather extensively in caenogastropod systematics (Bieler, 1992) in differentiating between 'mesogastropods' (e.g. Fig. 6B,C) and neogastropods (e.g. Fig. 7A,B,D,E); the former with salivary glands (sgl) that pass through the nerve ring (nr), the latter with salivary glands that by-pass the nerve ring (Ponder, 1974; Ponder & Lindberg, 1997). However, a number of 'mesogastropods' have salivary glands that do not pass through the nerve ring (Ponder & Lindberg, 1997) (e.g. *Bithynia tentaculata*, Fig. 6D; *Crepidula plana*, Fig. 6E). Only in some cases is this a consequence of the fact that the salivary glands are too short to reach the nerve ring. In addition, the discovery that salivary gland position may be polymorphic within a species (Bieler & Mikkelsen, 1988) has rendered the utility of the feature in higher order systematics doubtful (Bieler, 1992).

Nitidiscala tinctum (Fig. 7C) is unique because the salivary glands (sgl) and buccal mass lie far posterior to the nerve ring (nr); only extension of the acrembolic proboscis during feeding will draw the buccal mass and glands forward to penetrate the nerve ring; this species has been coded with a separate state.

19. Accessory salivary glands

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Con*, *Ily*] (1) Present [*Nit*, *Pan*, *Pru*, *Uro*].

Accessory salivary glands occur in a number of neogastropods (e.g. *Panarona clavatula*, Fig. 7A, asg; *Prunum apicinum*, Fig. 7D, dasg) as well as several non-neogastropod groups including ptenoglossans (e.g. *Nitidiscala tinctum*, Fig. 7C, asg) and tonnoideans (Ball, Taylor & Andrews, 1997). Their sporadic occurrence, even within the Neogastropoda, does not appear to be correlated with diet or feeding mode (Andrews, 1991). Generally acknowledged to be homologous within the Neogastropoda (Ponder, 1974; Haszprunar, 1988a; Ball *et al*., 1997; Ponder & Lindberg, 1997), the question of homology to accessory glands in other caenogastropod taxa is not so straightforward. The question is particularly contentious because of its potential to be informative in the question of sister group relationships to the Neogastropoda.

Andrews (1991) marshalled an argument that the accessory glands of ptenoglossans may be homologous to those of neogastropods because they share similarities in organization, structure (tubular) and position (open labially). Ball *et al*. (1997) suggested that 'accessory salivary glands' of the Neritidae (= sublingual pouches) and Tonnoidea could not be homologous to those of neogastropods based on numerous grounds, including dissimilarity in position and fine structure. However, Ball *et al*. (1997) cited histological differentiation to contest homology of the ptenoglossan and neogastropod accessory glands. Ponder & Lindberg (1997) considered the evidence insufficient to postulate homology of these structures and coded accessory salivary glands as lacking in the Ptenoglossa. In the present analysis, although the glands are not histologically identical across the groups studied, the evidence of similarity based on positional and structural criteria is considered sufficient to warrant testing homology of these structures.

20. Modifications of foregut

(0) Unmodified snout [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Lit*, *Bit*, *Str*, *Cre*, *Pet*] (1) Intraembolic proboscis [*Con*] (2) Pleurembolic proboscis [*Pan*, *Pru*, *Ily*, *Uro*] (3) Acrembolic proboscis [*Nev*, *Cyp*, *Nit*].

Three main modifications of the foregut are recognizable, including the acrembolic (e.g. *Cypraea robertsi*, Fig. 6C), pleurembolic (e.g. *Panarona clavatula*, Fig. 7A; *Ilyanassa obsoletus*, Fig. 7B; *Prunum apicinum*, Fig. 7D) and intraembolic proboscis (*Conus jaspideus*, Fig. 7E). These types differ primarily in the insertion of retractor muscles; muscles insert at the tip of the proboscis in the acrembolic type and at the middle of the sheath in the pleurembolic type. Differences in insertion pattern determine the amount of eversion of the proboscis sheath; in the acrembolic proboscis, the proboscis sheath is wholly everted, but only partially everted in the pleurembolic proboscis. The intraembolic type involves the elongation of the oral tube; the proboscis sheath (Fig. 7E, ps) is fused to the internal walls of the head (= rhynchocoel) and is not

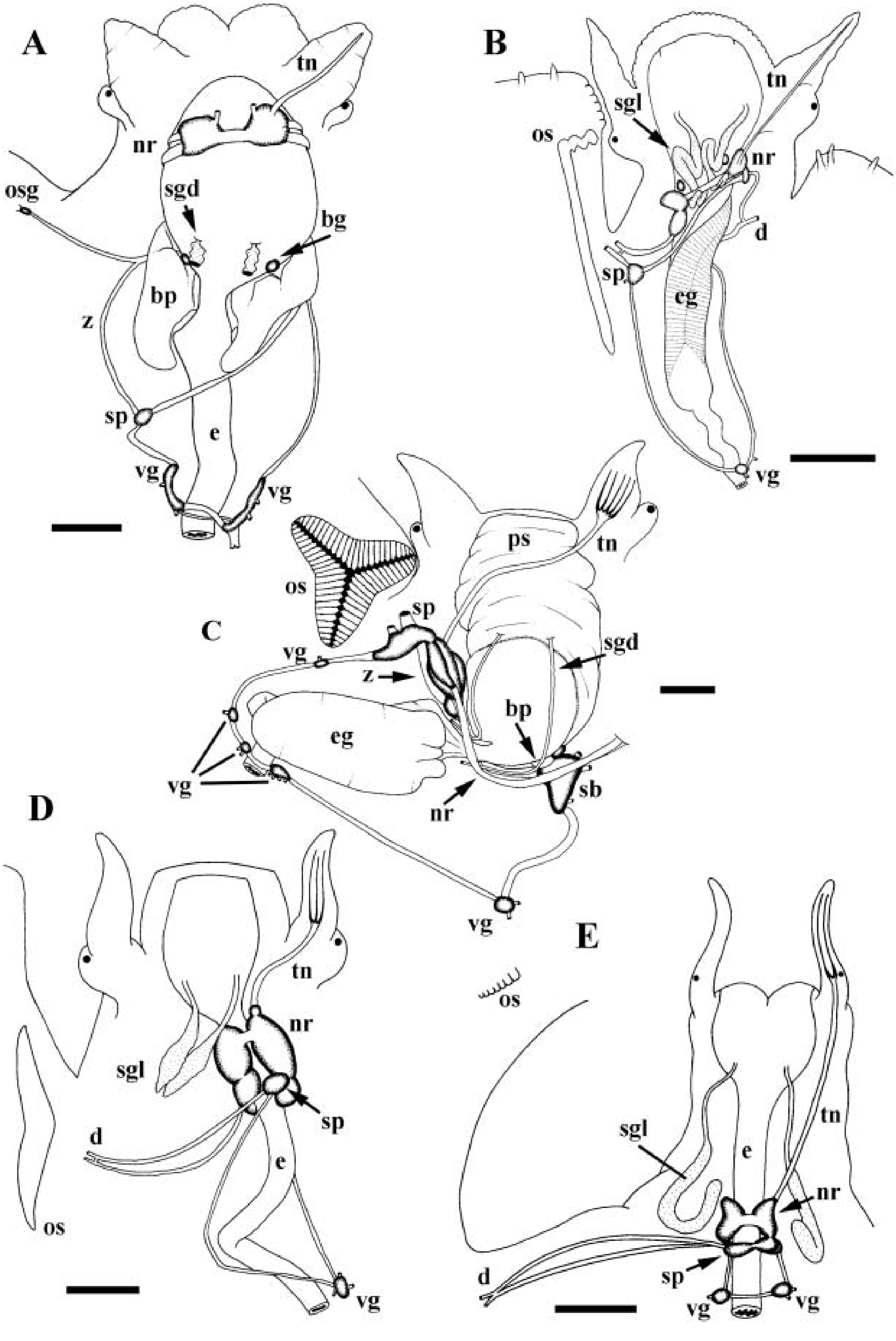

Figure 6. Morphology of cephalic haemocoel among basal caenogastropods. (A) *Neocyclotus dysoni ambiguum*. For simplicity, large salivary glands removed. Scale bar = 1 mm. (B) *Lampanella minima*. Scale bar = 1 mm. (C) *Cypraea robertsi*. For simplicity, large salivary glands removed. Scale bar = 1 mm. (D) *Bithynia tentaculata*. Scale bar = 0.5 mm. (E) *Crepidula plana*. Scale bar = 1 mm. Abbreviations: bp, buccal pouch; d, dialyneury; e, oesophagus; eg, oesophageal gland; nr, circum-oesophageal nerve ring; os, osphradium; osg, osphradial ganglion; ps, proboscis sheath; sb, sub-oesophageal ganglion; sgd, salivary gland duct; sgl, salivary glands; sp., supra-oesophageal ganglion; tn, tentacular nerve; vg, visceral ganglion; z, zygoneury.

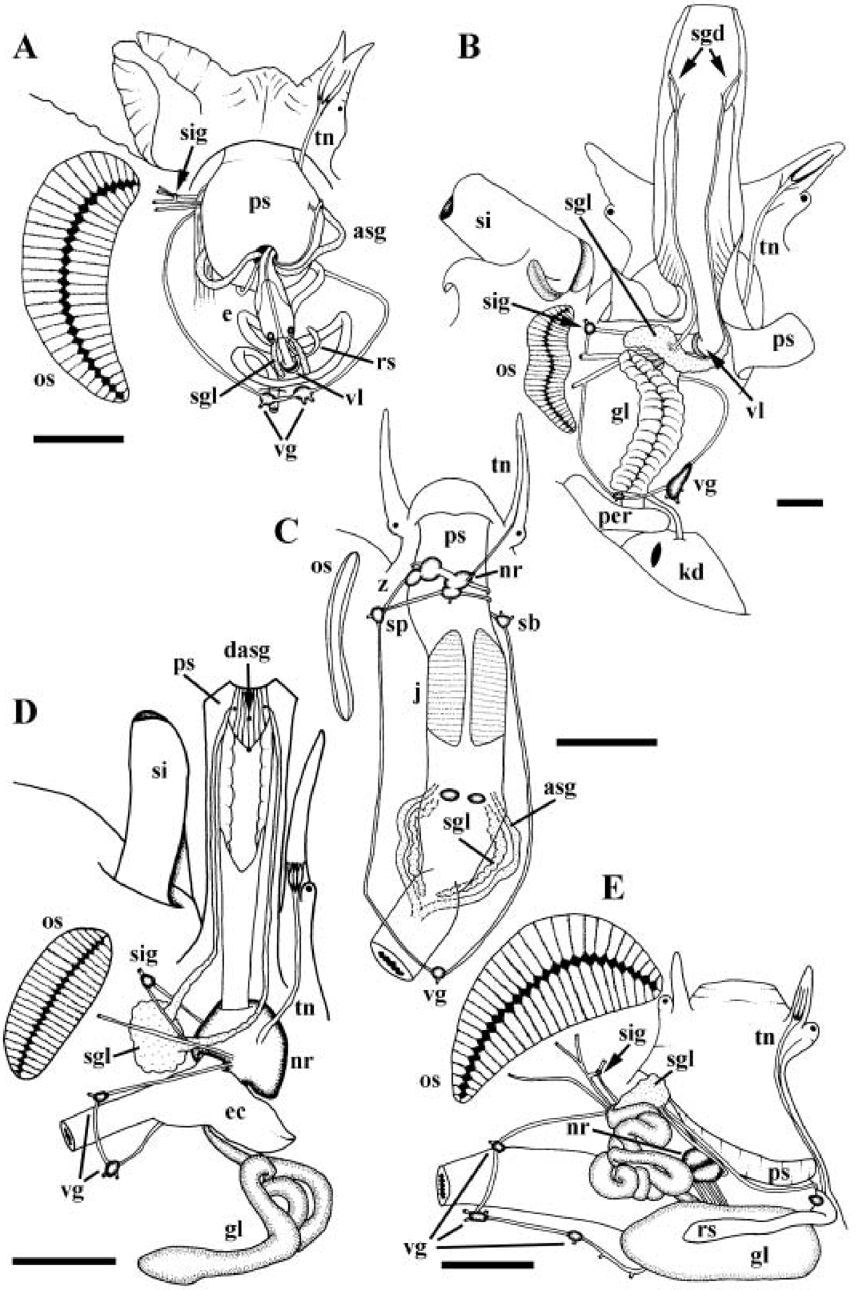

Figure 7. Morphology of cephalic haemocoel among derived caenogastropods. (A) *Panarona clavatula*. Siphon obscured by left cephalic tentacle and is not visible in this view. Note large, modified left cephalic tentacle and large proboscis retractor connecting to columellar muscle. (B) *Ilyanassa obsoletus*. Note second visceral ganglion lying below pericardium and large radular retractors connecting to base of proboscis sheath; ampulla of gland of Leiblein visible within afferent renal vessel. Duct of gland of Leiblein stippled. (C) *Nitidiscala tinctum*. Note compartmentalized tissue supporting jaw and buccal ganglia lying between salivary glands where the latter enter buccal cavity. (D) *Prunum apicinum*. Note duct of poison gland opening mid-ventrally to base of buccal cavity, just behind opening of accessory salivary gland. (E) *Conus jaspideus*. Siphon not visible in this view. Note long coiled duct of poison gland; buccal ganglion visible where short arm of radular sac enters buccal cavity. Base of proboscis sheath is shown, but rhynchocoel has not been opened. Scale bar = 1 mm. Abbreviations: asg, accessory salivary gland; dasg, duct of accessory salivary gland; e, oesophagus; ec, oesophageal caecum; gl, gland of Leiblein; j, jaw; kd, kidney; nr, circum-oesophageal nerve ring; os, osphradium; per, pericardium; ps, proboscis sheath; rs, long arm of radular sac; sb, sub-oesophageal ganglion; sgd, salivary gland duct; sgl, salivary glands; si, siphon; sig, siphonal ganglion; sp, supra-oesophageal ganglion; tn, tentacular nerve; vg, visceral ganglion; vl, valve of Leiblein; z, zygoneury.

everted (Fretter & Graham, 1962; Miller, 1989; Kantor, 1990; Ponder & Lindberg, 1997).

As succinctly summarized by Ponder & Lindberg (1997), the proboscis is correctly viewed as a complex comprising numerous characters. These general categories disguise significant amounts of variability in organization, including musculature, muscle insertion and elongation patterns, not only between, but within categories. For example, Kantor (1990) hypothesized that the pleurembolic proboscis has been convergently derived in neogastropods and cassids, citing differences in musculature. Indeed, within the neogastropods, the pleurembolic proboscis has been alternatively cited as being synapomorphic of the group (Haszprunar, 1988a) or convergently derived within the group based on differences in elongation patterns (Ponder, 1974). Thus, homology of the pleurembolic type, even within neogastropods, remains controversial.

Homology of the acrembolic type is similarly contested. Considered to be homoplastic at higher taxonomic levels (e.g. architectonicids vs. ptenoglossans), the homology of this feature even with the Caenogastropoda is uncertain (Haszprunar, 1988a). Differences in position of the circum-oesophageal nerve ring of ptenoglossans (= ctenoglossans) have been cited as supporting several independent derivations of the proboscis within this group (Haszprunar, 1988a). The issue of homology of the ptenoglossan acrembolic proboscis to that of other caenogastropods (e.g. cypraeids, naticids) is also problematic. Although the buccal ganglia lie in comparable positions in all three groups, each displays distinct musculature patterns. Thus, the homologies of the acrembolic proboscis within the Ptenoglossa and to other caenogastropods remains poorly understood.

As a consequence of these issues, and the fact that many observed variations in organization were autapomorphic, this complex has been coded simply in the present study. More detailed studies and improved taxon sampling will shed important light on the homology of these modifications, an issue that is only beginning to be understood.

21. Mid-ventral fold

(0) Absent [*Nev*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Cyp*].

Primitively, gastropods possess dorsal and ventral sets of glandular folds bounding ciliated, non-glandular conducting channels (Fretter & Graham, 1962; Salvini-Plawen, 1988). Development of ventral folds within the oesophagus (characters 21, 22 and 24) has been rather thoroughly described for more basal gastropods by Salvini-Plawen & Haszprunar (1987) who demonstrated that the highly consistent and characteristic folding patterns are of considerable systematic utility as they do not covary with feeding biology. In particular, Salvini-Plawen & Haszprunar distinguished the presence of a mid-ventral ciliary tract and two glandular ventro-lateral folds in the anterior oesophagus; within the mid-oesophagus, the ciliary tract may be elaborated into a prominent T-shaped fold as the glands of the ventro-lateral folds expand and meet at the midline.

Ventral folding within the *mid*-oesophagus among caenogastropods has been widely described and compared (e.g. Graham, 1941; Fretter & Graham, 1962; Ponder, 1973), but folding within the anterior oesophagus is less well understood. Salvini-Plawen & Haszprunar (1987) stated that the ciliary tract is lacking and that ventro-lateral folds may be present, citing Fretter & Graham (1962) and Starmühlner (1969). However, the former citation refers to the conditions of the mid-oesophagus. Starmühlner indeed described ventral folding within the anterior oesophagus among five genera of cerithioideans and one species of ampullariid, but no consistent pattern emerged from these investigations. Salvini-Plawen (1988) noted only that all higher gastropods (Apogastropoda, see Fig. 27) possess an anterior oesophagus circular in cross section, again emphasizing the glandular development of the mid-oesophagus.

The most thorough comparative analysis of oesophageal folding within the Caenogastropoda is the account of Graham (1939). That study noted the complete absence of ventral folding within the anterior oesophagus or, at most, only ‘minor irregularities’ or ‘weak longitudinal folding’. The only exception was the recognition of two longitudinal folds ‘of no great height’ within the anterior oesophagus of *Bithynia tentaculata*. In phylogenetic treatments, Haszprunar (1988a) stated that all higher gastropods lack ventral folding within the anterior oesophagus; Ponder & Lindberg (1997) coded all caenogastropods except cyclophorids and provannids as lacking ventral folds.

However, it is now clear that the buccal cavity and anterior-most oesophagus of many caenogastropods (Figs 8C–G, 9C–H) bear a mid-ventral fold (vf) and two ventro-lateral folds (vlf); these features are far more consistent and widespread than previously acknowledged. The ciliated mid-ventral fold begins on the dorsal lip of the radular sac within the buccal cavity and, although variable in length, is restricted to the anterior oesophagus. Among basal gastropods, as stated above, the ciliary tract may be elaborated into a prominent T-shaped fold within the mid-oesophagus as the glands of the ventro-lateral folds expand and meet at the midline (Salivini-Plawen & Haszprunar, 1987). In contrast to this interpretation, among the

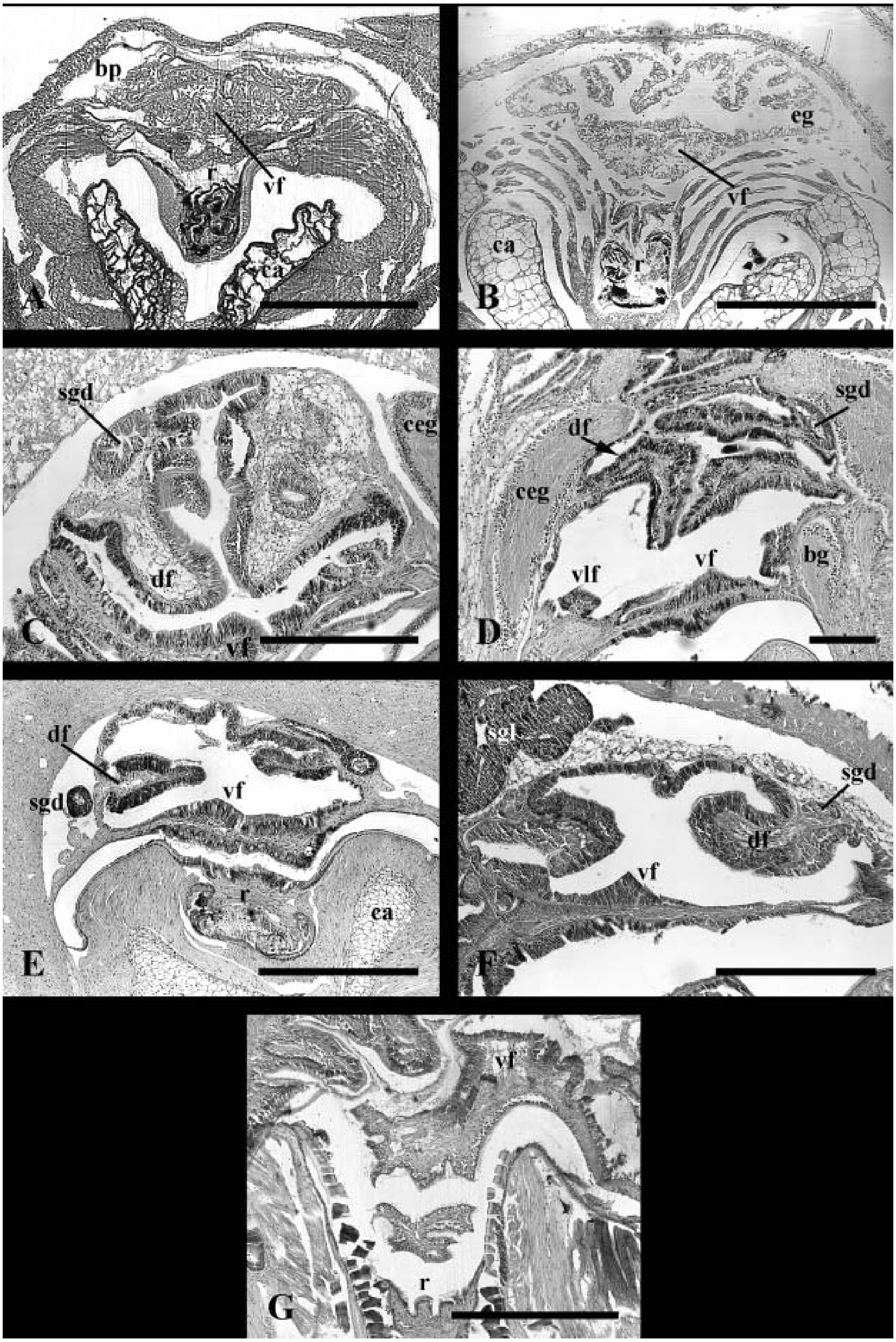

Figure 8. Histology of anterior oesophagus; ventral fold. (A) *Macleaniella moskalevi.* Scale bar = 0.5 mm. (B) *Theodoxus fluviatilis*. Scale bar = 0.5 mm. (C) *Neocyclotus dysoni ambiguum*. Scale bar = 0.5 mm. (D) *Lampanella minima*. Scale bar = 1 mm. (E) *Strombus mutabilis*. Scale bar = 0.5 mm. (F) *Littorina littorea*. Scale bar = 0.5 mm. (G) *Cypraea robertsi*. Note that ventral fold is offset to the right. Scale bar = 0.5 mm. Abbreviations: bp, buccal pouch; bg, buccal ganglion; c., radular cartilage; ceg, cerebral ganglion; df, dorsal fold; e.g. oesophageal gland; r, radula; sgd, salivary gland duct; sgl, salivary gland; vf, ventral fold; vlf, ventro-lateral fold.

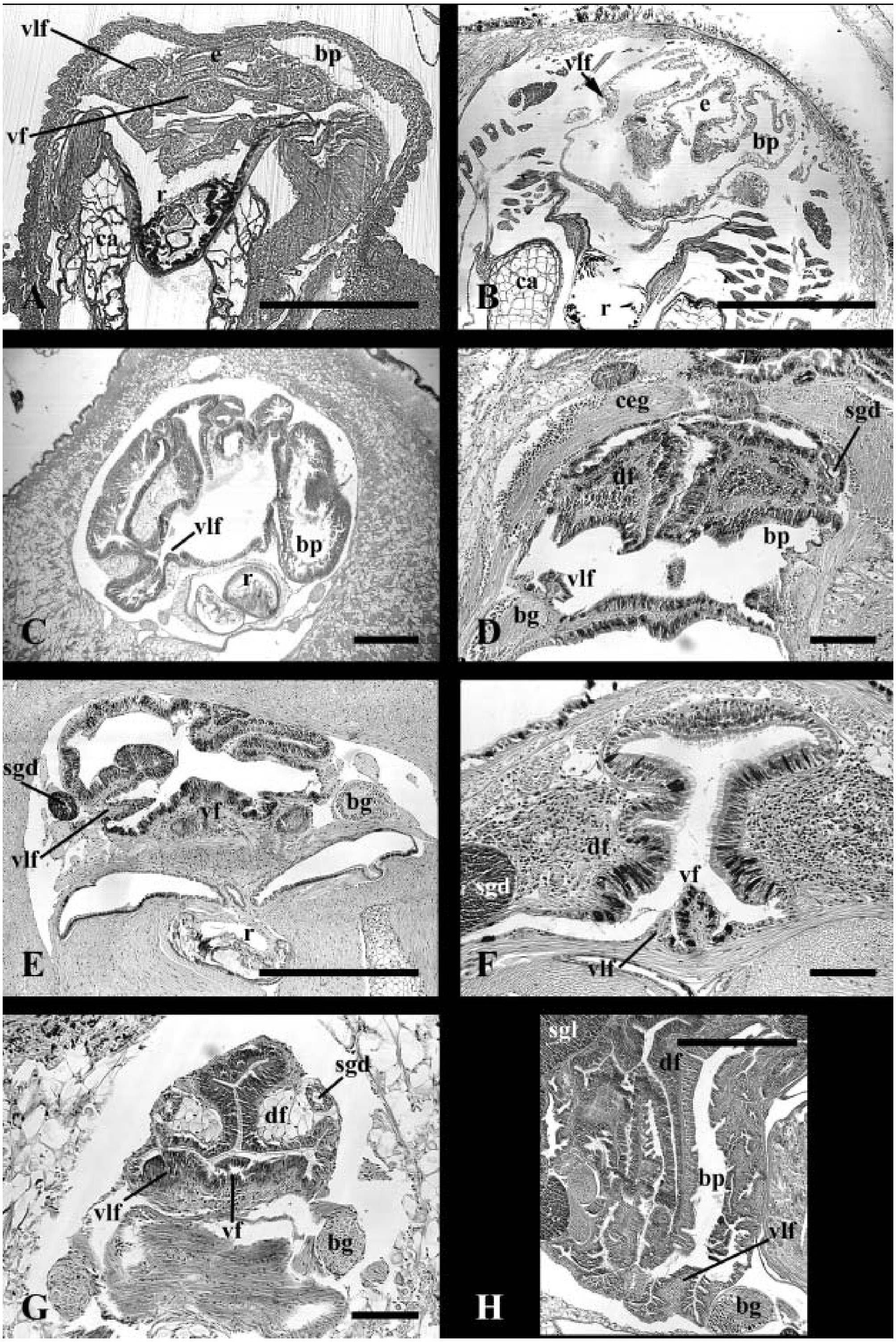

Figure 9. Histology of anterior oesophagus; ventro-lateral folds. (A) *Macleaniella moskalevi.* Scale bar = 0.5 mm. (B) *Theodoxus fluviatilis*. Scale bar = 0.5 mm. (C) *Neocyclotus dysoni ambiguum*. Scale bar = 0.5 mm. (D) *Lampanella minima*. Scale bar = 1 mm. (E) *Strombus mutabilis*. Scale bar = 0.5 mm. (F) *Crepidula plana*. Scale bar = 1 mm. (G) *Bithynia tentaculata*. Scale bar = 1 mm. (H) *Littorina littorea*. Scale bar = 0.5 mm. Abbreviations: bp, buccal pouch; bg, buccal ganglion; ca, radular cartilage; ceg, cerebral ganglion; df, dorsal fold; e, oesophagus; r, radula; sgl, salivary gland; vf, ventral fold; vlf, ventro-lateral fold.

outgroups the mid-ventral ciliary tract was found to be elaborated into a large, T-shaped fold already within the anterior oesophagus. Moreover, the glandular mass associated with the fold is interpreted as being independent of the ventro-lateral folds, as all features co-occur at the same level within the oesophagus. Although differing in shape, the T-shaped fold is interpreted as being homologous to the mid-ventral fold of caenogastropods. Similar to the latter, the T-shaped fold is restricted to the anterior oesophagus in *Macleaniella moskalevi*, but extends through the mid-oesophagus in *Theodoxus fluviatilis*. Although autapomorphic and not coded in the analysis, the persistence of the mid-ventral fold into the mid-oesophagus may be an important feature for the higher order phylogeny of the Gastropoda. Ventral folding is lacking in *Neverita duplicata*, *Nitidiscala tinctum* and all neogastropods examined (Fig. 10A–G).

22. Mid-ventral fold condition

(0) Underlying glandular mass [*Mac*, *The*] (1) Glandular epithelium only [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Cyp*].

As stated above, in outgroup taxa the mid-ventral fold is associated with a large, ventral mass of glandular tissue just behind the separation of the oesophagus from the buccal cavity. This gland is not interpreted to represent the glands of the ventro-lateral folds (*cf.* Salvini-Plawen & Haszprunar, 1987) because all of these features co-occur in the anterior oesophagus. The glandular mass is uniform in *M. moskalevi* (Fig. 8A, vf) and bi-lobed in *T. fluviatilis* (Fig. 8B, vf).

Among ingroup taxa, the epithelium of the fold is glandular, but there is no associated ventral glandular mass (see oesophageal gland, below). Size and shape of the mid-ventral fold is variable (Fig. 8C–G, vf), but in all caenogastropods with ventral folding, the fold is not continuous within the mid-oesophagus.

23. Buccal pouches

(0) Absent [*Pet*, *Str*, *Cre*, *Bit*, *Nev*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Lit*, *Cyp*].

Buccal pouches are lateral outpocketings of the buccal cavity and anterior most oesophagus (Amaudrut, 1898; Fretter & Graham, 1962). The homologies of such outpocketings across the Gastropoda and even among neotaenioglossans remain controversial. For example, Ponder (1983) argued that the buccal pouches of some rissooideans are not homologous to those of other caenogastropods but are derived from the oesophageal gland. Thus, Ponder & Lindberg (1997) restricted their concept of buccal pouches to pockets of the buccal cavity and/or anterior most oesophagus in neotaenioglossans that differ histologically from the oesophageal gland; these were not treated as homologous to pockets of similar position in basal gastropods. Sasaki (1998) treated all anterior pockets (= esophageal pouches) as putative homologues.

Similarly, all such pockets of the buccal cavity and anterior oesophagus are treated as homologous here. Among outgroup taxa, the so-called oesophageal pouches can be differentiated into continuous buccal pouches (*Macleaniella moskalevi*, Fig. 8A; *Theodoxus fluviatilis*, Fig. 9B, bp) and oesophageal glands (*M. moskalevi*, Fig. 11A; *T. fluviatilis*, Fig. 8B, eg) that are distinguishable histologically (Whitaker, 1951; present study). In the ingroup, buccal pouches are present in architaenioglossans (Fig. 6A, bp) and *Littorina littorea* (Fretter & Graham, 1962). Many cypraeoideans have been described with outpocketings of the anterior oesophagus, the so-called oesophageal pockets (e.g. Kay, 1960). Because they are similar in position, these are interpreted as homologous to buccal pouches (Fig. 6C, bp). In contrast, Fretter & Graham (1962) interpreted the unpaired 'mucus diverticulum' of *Erato* (Fretter, 1951) as homologous to the 'mid-oesophageal pouches' (= oesophageal glands) of basal gastropods.

Histological sections of *Lampanella minima* revealed the presence of lateral outpocketings similar in position and histological detail to the buccal pouches of *Littorina littorea*. Based on these criteria, although cerithioideans have been cited as lacking buccal pouches (Houbrick, 1988), *L. minima* is coded here as possessing buccal pouches.

24. Ventro-lateral folds

(0) Absent [*Cre*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Bit*, *Lit*].

Ventro-lateral folds are low to rather high glandular folds that often bound the entrance to the buccal pouches within the anterior oesophagus. In *Macleaniella moskalevi* (Fig. 9A, vlf), they become highly glandular for a short distance then diminish before the transition between the buccal pouches and oesophageal glands. In *Theodoxus fluviatilis* (Fig. 9B, vlf), they remain weakly glandular the length of the buccal pouches and oesophageal glands. The posterior extent of these folds may be significant in the systematics of basal gastropods.

Salvini-Plawen & Haszprunar (1987) stated that ventro-lateral folds may be present or absent in caenogastropods. However, it is now clear that they are present in far more caenogastropods than previously appreciated. Although the folds are nearer the midline

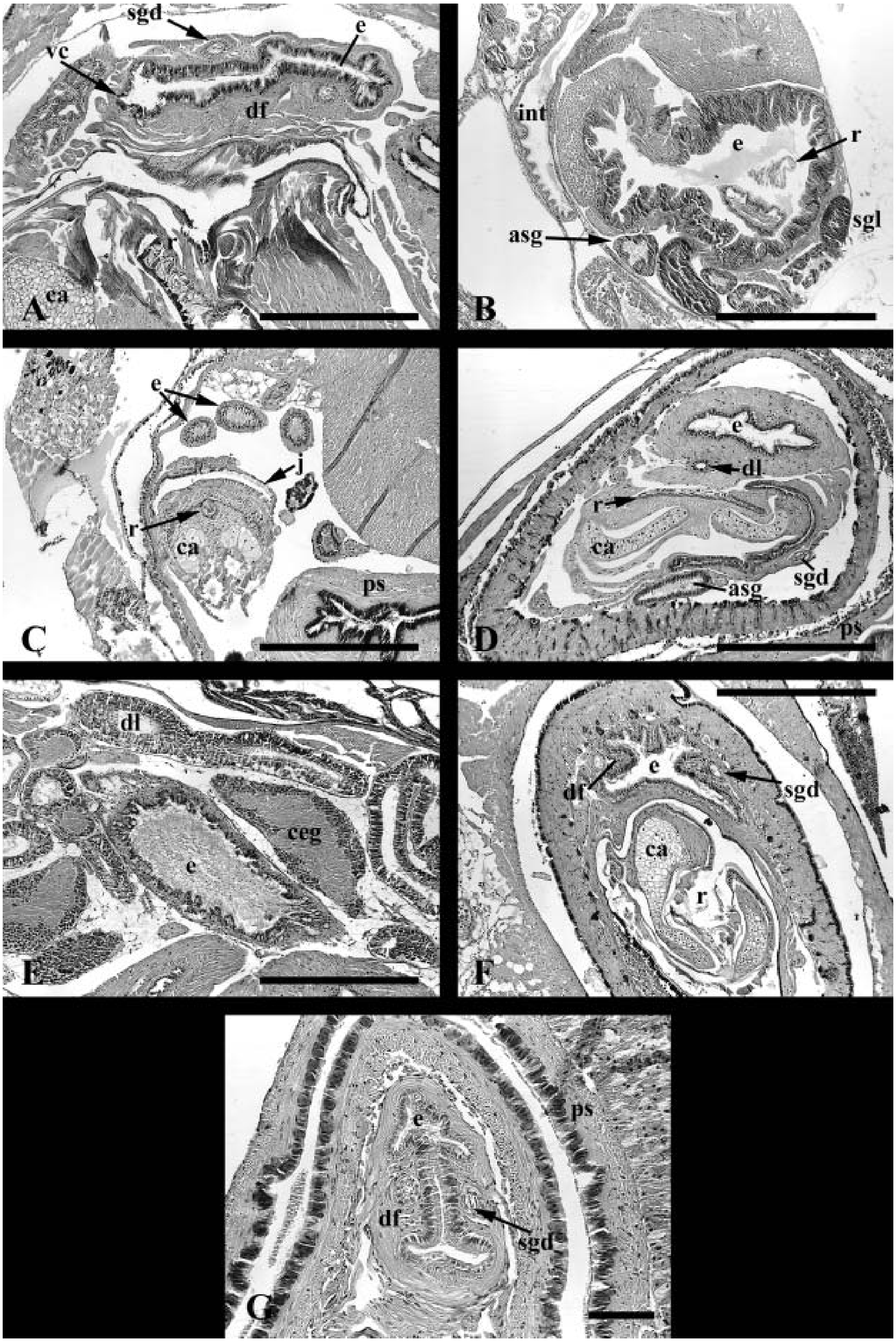

Figure 10. Histology of anterior oesophagus; ventral folding absent. (A) *Neverita duplicata*. Scale bar = 0.5 mm. (B) *Nitidiscala tinctum*. Scale bar = 0.5 mm. (C) *Panarona clavatula*. Scale bar = 0.5 mm. (D) *Prunum apicinum*. Scale bar = 0.5 mm. (E) *Conus jaspideus*. Scale bar = 0.5 mm. (F) *Ilyanassa obsoletus*. Scale bar = 0.5 mm. (G) *Urosalpinx cinerea*. Scale bar = 1 mm. Abbreviations: asg, accessory salivary gland; ca, radular cartilage; ceg, cerebral ganglion; df, dorsal fold; dl, duct of gland of Leiblein; e, oesophagus; int, intestine; j, jaw; ps, proboscis sheath; r, radula; sgd, salivary gland duct; sgl, salivary gland; vc, ventral channel.

in caenogastropods compared to the outgroups, this may be a consequence of the dorso-ventral depression of the oesophagus in the latter. Moreover, the presence or absence of ventro-lateral folds and buccal pouches is independent; the buccal pouches need not necessarily be accompanied by folds, and the folds are retained in many taxa that lack pouches. For example, *Crepidula plana* (Fig. 9F) lacks buccal pouches, but has retained two small ventro-lateral folds (vlf), while the reduced, non-glandular buccal pouches of *Cypraea robertsi* (Fig. 6C, bp) are not associated with ventro-lateral folds.

25. Oesophageal glands

(0) Absent [*Neo*, *Mar*, *Bit*, *Str*, *Cre*, *Pet*, *Nit*] (1) Present [*Mac*, *The*, *Lam*, *Lit*, *Nev*, *Cyp*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

The homologies of the buccal pouches and oesophageal pouches/glands has been an area of confusion due to the interchangeable use of these terms. Following Amaudrut (1898), Whitaker (1951) considered the oesophagus to be a series of outpocketings, comprising the buccal and oesophageal pouches/glands (see also Sasaki, 1998). This interpretation is adopted here. As described above, differences in histology and folding pattern between the anterior and posterior oesophageal pouches of *Macleaniella moskalevi* and *Theodoxus fluviatilis*, suggest that these outpocketings comprise continuous buccal and oesophageal pouches/glands (*cf.* Whitaker, 1951). Sasaki (1998) interpreted the oesophageal pouches of neritopsines as continuous ‘oesophageal pouches’ (= buccal pouches) and oesophageal glands, but described the mid-oesophagus of cocculinids as a simple tube.

The ventral mass of glandular tissue associated with the ventral fold (character 22), paired in *Theodoxus fluviatilis* and forming a solid disc in *Macleaniella moskalevi*, has been interpreted as being continuous with the glands of the oesophageal pouches, collectively forming the oesophageal gland (Salvini-Plawen & Haszprunar, 1987). However, the glandular mass does not extend into the mid-oesophagus in some taxa (e.g. *M. moskalevi*); moreover, the glands of the oesophageal pouches and the ventral glandular mass are histologically distinct. Given the fact that caenogastropods are here revealed to possess a mid-ventral fold in conjunction with an oesophageal gland, but lack this ventral glandular mass, indicates that these features (i.e. ventral glandular mass and oesophageal glands) are independent. Thus, the term ‘oesophageal gland’ should be restricted to the glandular lateral outpocketings of the mid-oesophagus, as coded here.

26. Mid-oesophageal gland condition

(0) Simple/septate lateral pouches [*Mac*, *The*] (1) Transverse septae [*Lam*, *Lit*, *Nev*, *Cyp*] (2) Poison gland/Gland of Leiblein [*Pru*, *Con*, *Ily*, *Uro*] (3) Ventral glandular oesophageal epithelium [*Pan*].

The evolution of the oesophageal glands has received considerable attention (e.g. Fretter & Graham, 1962; Ponder, 1974; Salvini-Plawen & Haszprunar, 1987). As described above, only the glandular posterior portion of the oesophageal pouches is inferred to comprise the oesophageal gland in both outgroups (Figs 8B, 11A) and is independent of the ventral glandular mass. Ponder & Lindberg (1997) consider both the anterior and posterior oesophageal pouches of cocculinids and neritids to comprise the oesophageal gland, consisting of two distinct lobes in the latter.

Within the ingroup, the gland consists of glandular septae that form transverse sheets (Figs 11C,E–G). In contrast to Ponder & Lindberg (1997), architaenioglossans are not considered to possess an oesophageal gland; in these taxa, the mid-oesophagus is longitudinally folded, with no lateral outpocketings nor glandular septae (Fig. 11B), comprising a voluminous crop (Demian, 1964; present study).

Among neogastropods, the oesophageal gland is modified into the gland of Leiblein (Fig. 7, gl; Ponder, 1973). Several neogastropod groups lack a separate, unpaired mid-oesophageal gland, including the Cancellariidae (Ponder, 1974). Instead, these taxa possess a glandular strip within the mid-oesophagus that has been suggested to be homologous to the gland of Leiblein (Graham, 1966; Ponder, 1973). The present study revealed that the glandular strip in *Panarona clavatula* extends through the mid- and posterior oesophagus from behind the valve of Leiblein (Fig. 7A, vl) to the posterior end of the cephalic haemocoel, an apparently unique morphology within the Cancellariidae (Graham, 1966). In marginellids, the large and coiled duct of the unpaired foregut gland is derived from the stripped-off glandular dorsal folds of the oesophagus, with the gland of Leiblein forming the muscular terminal sac (Fig. 7D, gl; Ponder, 1974; Ponder & Taylor, 1992). This structure closely resembles the poison gland of toxoglossans (Fig. 7E, gl); the two are thought to have developed in a similar but parallel fashion and have not been considered homologous (e.g. Ponder, 1974), but are tentatively treated as such here.

27. Terminal Ampulla

(0) Ampulla of gland of Leiblein extends into afferent renal vessel [*Ily*, *Uro*] (1) Ampulla does not extend into afferent renal vessel [*Pru*, *Con*].

In neogastropods, the afferent renal vessel opens to the collecting sinus adjacent to the gland of Leiblein (when present). The terminal ampulla of the gland, termed the ‘ampulle’ by Brock (1936), has been

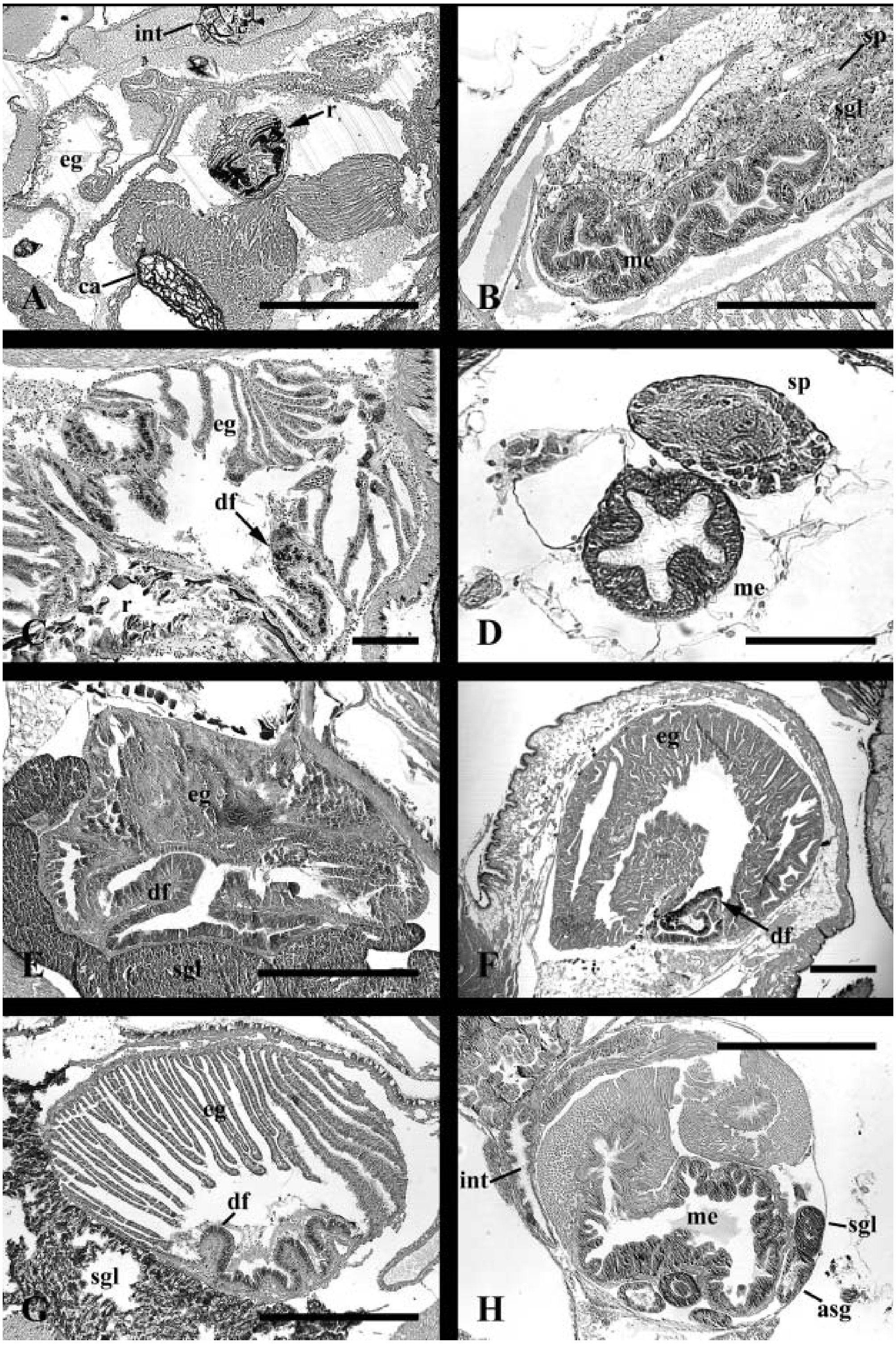

Figure 11. Histology of mid-oesophagus; oesophageal gland. (A) *Macleaniella moskalevi*. Scale bar = 0.5 mm. (B) *Neocyclotus dysoni ambiguum*. Scale bar = 0.5 mm. (C) *Lampanella minima*. Scale bar = 1 mm. (D) *Crepidula plana*. Scale bar = 1 mm. (E) *Littorina littorea*. Scale bar = 0.5 mm. (F) *Neverita duplicata*. Scale bar = 0.5 mm. (G) *Cypraea robertsi*. Scale bar = 0.5 mm. (H) *Nitidiscala tinctum*. Note transition to muscular posterior oesophagus. Scale bar = 0.5 mm. Abbreviations: asg, accessory salivary gland; ca, radular cartilage; df, dorsal fold; eg, oesophageal gland; int, intestine; me, mid-oesophagus; r, radula; sgl, salivary gland; sp, supra-oesophageal ganglion.

described in a number of muricoidean and buccinoidean taxa (e.g. Amaudrut, 1898). Within muricids, the ampulla often lies within the afferent renal vessel, and may reach the dorsal branch of the vessel (Haller, 1882; Carriker, 1943; Kool, 1993). The ampulla similarly extends into the afferent renal vessel in *Ilyanassa obsoletus* (Fig. 7B, gl), but is thin walled and simpler than the ampulla of *Urosalpinx cinerea* (Carriker, 1943).

28. Valve of Leiblein

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pru*, *Con*] (1) Present [*Pan*, *Ily*, *Uro*].

The valve of Leiblein, a pyriform organ lying at the transition of the anterior and mid-oesophagus, is restricted to the Neogastropoda (Ponder, 1974). There is a correlation between presence or absence of the valve and size or placement of the gland of Leiblein; taxa lacking a gland or have duct of the gland of Leiblein that by-passes the oesophagus, lack a valve of Leiblein. This correlation has led to speculation that the valve functions in the retention of the enzymatic secretion of the gland (Ponder, 1974). Consistent with this prediction, the valve of Leiblein is present in *Panarona clavatula* (Fig. 7A, vl), *Ilyanassa obsoletus* (Fig. 7B, vl) and *Urosalpinx cinerea* (Carriker, 1943), all of which possess a gland of Leiblein (gl) that opens to the mid-oesophagus. A valve of Leiblein is lacking in *Conus jaspideus* and *Prunum apicinum* in which the gland of Leiblein (Fig. 7D,E, gl) by-passes the oesophagus and opens near the mouth. A highly folded oesophageal caecum occurs just behind the nerve ring at the transition between the anterior and mid-oesophagus in *P. apicinum* (Fig. 7D, ec) and other marginellids similarly lacking a valve of Leiblein (Coovert & Coovert, 1995). This caecum does not occur in conjunction with a valve and thus, may represent a rudiment of the valve of Leiblein.

MIDGUT

29. Caecum

(0) Absent [*Mac*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*The*, *Cre*, *Bit*]

The gastric caecum is widely distributed within molluscs (Simroth, 1896–1907; Graham, 1949; Fretter & Graham, 1962; Fretter, Graham & McLean, 1981; Salvini-Plawen, 1988; Ponder & Lindberg, 1997; Sasaki, 1998). Among basal gastropods, it is closely associated with the gastric shield and varies from small and crescent-shaped to a large, spiral sorting structure. Until recently, the large spiral caecum was thought to be plesiomorphic for gastropods (Fretter &

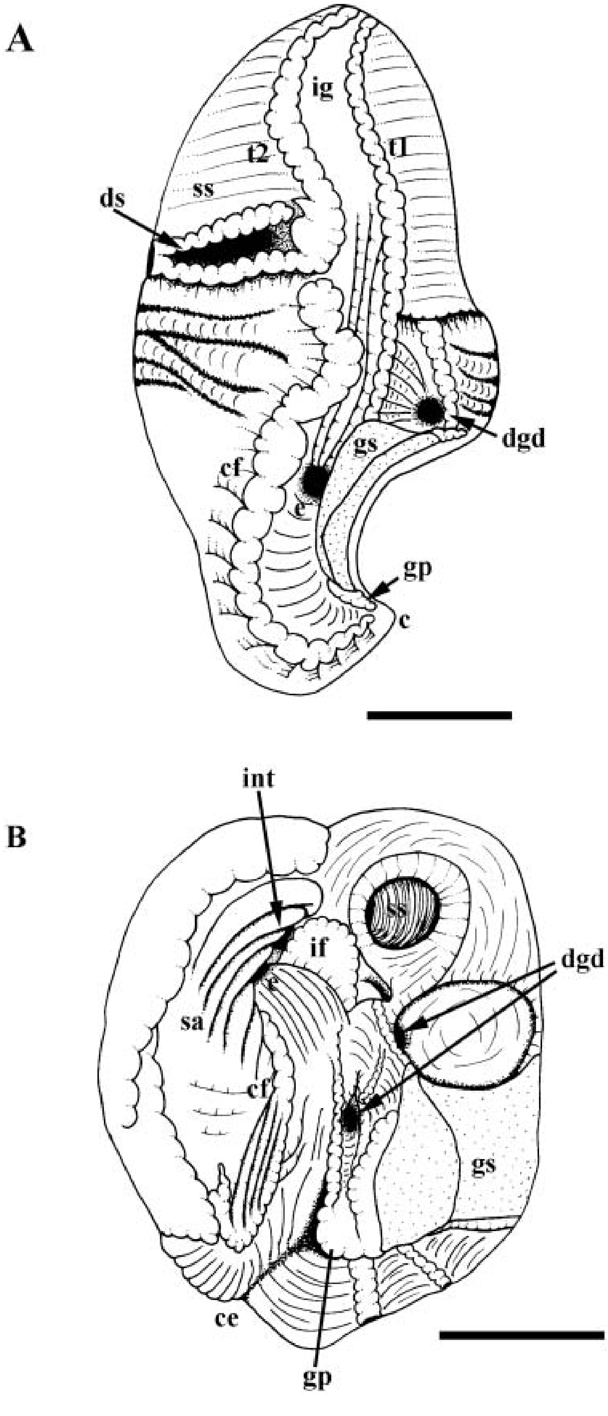

Figure 12. Midgut morphology of taxa examined only from preserved material. (A) *Theodoxus fluviatilis*, left lateral view. Second digestive gland duct to right of oesophageal aperture obscured by gastric shield. (B) *Strombus mutabilis*, dorsal view. Scale bar = 1 mm. Abbreviations: c, caecum; ce caecal extension; cf, ciliated fold; dgd, digestive gland duct; ds, deep sac; e, oesophagus; gp, glandular pad; gs, gastric shield; if, intestinal flap; ig, intestinal groove; int, intestine; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

Graham, 1962; Graham, 1949, 1985), but now it is considered derived within the Vetigastropoda (Salvini-Plawen & Haszprunar, 1987; Ponder & Lindberg, 1997).

In basal gastropods, the caecum opens ventrally near the posterior end of the gastric chamber; more or less continuous extensions of the major (Fig. 1, t1) and minor (Fig. 1, t2) typhlosoles and intestinal groove (Fig. 1, ig) extend across the midgut floor into the caecum (Graham, 1949). In large spiral forms, the sorting area (Fig. 1, sa) to the left of the minor typhlosole extends into the caecum as well.

In some sorbeoconchans, a system of (crescentic) ciliated folds and grooves (Figs 12A, 14B, 15A, cf) extends from the oesophagus (e) in a broad arc, curving into a pocket (c) behind the gastric shield (gs) near the posterior end of the midgut. This type of midgut organization has been described in many species, including cerithioideans (e.g. *Bittium reticulatum*, *Cleopatra bulimoides*, *Pachymelania fusca*, *Paludomus tanschaurica*, *Potadoma vogelii*, *Telescopium telescopium*, *Terebralia sulcata*, *Turritella communis*; Randles, 1902; Seshaiya, 1929; Graham, 1938; Binder, 1959; Fretter & Graham, 1962; Houbrick, 1991b), calyptraeoideans (e.g. *Crepidula fornicata*, *Calyptraea chinensis*; Graham, 1939; Fretter & Graham, 1962), rissooideans (e.g. *Bithynia tentaculata*, *Hydrobia truncata*, *Tatea huonensis*;(Fretter & Graham, 1962; Davis *et al*., 1982; Ponder *et al*., 1991) and stromboideans (e.g. *Aporrhais pespelicani*; Fretter & Graham, 1962). This pattern is also evident in some neritoideans (e.g. *Theodoxus fluviatilis*, *Neritina virginaea*, *Nerita fulgurans*, *Nerita peloronta*; Bourne, 1908; Graham, 1939; Fretter & Graham, 1962; Fretter, 1965).

The homologies of these pockets and crescentic folds have been variously interpreted. Fretter & Graham (1962) suggested that the small pockets lying at the upper end of the midgut in *Bittium reticulatum*, *Crepidula fornicata*, *Calyptraea chinensis*, *Turritella communis*, *Bithynia tentaculata* and *Aporrhais pespelicani* are vestiges of the spiral caecum based on the fact that the pattern of folds and grooves entering the pocket is similar to that in forms possessing a true caecum. On the other hand, Randles (1902) suggested that the crescentic folds themselves, not the pocket, are the homologues of the caecum. Seshaiya (1932) concluded that the crescentic folds on the midgut floor are not a vestigial spiral caecum. Although the folds themselves are homologous, he interpreted the spiral caecum midgut and crystalline style midgut as independent derivations from a common ancestor possessing a plesiomorphic pattern of folds. This argument was based in part on the functional grounds that typhlosolar folding of the gastric epithelium is functionally required to direct particles, either to the caecum or to the head of the style. Houbrick (1991b) concurred with this interpretation in describing midgut morphology of *Terebralia sulcata* and *Telescopium telescopium*.

Complicating the question of homology, any outpocketings and/or extensions of the gastric chamber have been referred to uncritically as a ‘caecum’ and, implicitly or explicitly, considered homologous to the caecum of basal gastropods. These include such features as the neogastropod ‘caecum’ (Simroth, 1896–1907; Smith, 1967; Medinskaya, 1993; Ponder & Lindberg, 1997), a pouch-like extension separated from the main gastric chamber by a horizontal fold, or the long, posterior ‘caecal’ extension of *Littorina littorea* (Graham, 1949; Johansson, 1939; Ponder & Lindberg, 1997).

An indication to the homologies of these structures is offered by a critical examination of folding patterns and position of outpocketings. As described above, the plesiomorphic gastropod caecum opens ventrally at the posterior end of the gastric chamber behind the gastric shield and receives extensions of the major and minor typhlosoles. In *Theodoxus fluviatilis* (Fig. 12A, c), *Crepidula plana* (Fig. 14B, c) and *Bithynia tentaculata* (Fig. 15A, c), the pocket lies above and behind the gastric shield (*laterally* to *dorso-laterally*) on the right. In *T. fluviatilis* (Fig. 12A, cf) and *C. plana* (Fig. 14B, cf), the pocket receives only an extension of the minor typhlosole (passing to the left of the oesophagus) and an extension of the glandular pad (Figs 12A, 14B, gp) supporting the gastric shield; the major typhlosole terminates at the proximal end of the style sac or near the oesophagus (*T. fluviatilis*). In *B. tentaculata*, two folds emerge from the intestinal groove (Fig. 15A, ig) and pass the oesophageal aperture (e) to the left; the left fold rapidly diminishes while the right fold (cf) continues around the posterior end of the gastric chamber into the pocket (c). Thus, in these three species, only folds extending from the minor typhlosole/intestinal groove enter the pocket.

The ‘caecum’ of other rissooideans (e.g. *Hydrobia truncata*, *Tatea huonensis*) occurs in a subtly different position from that described above, forming a posterior extension of the gastric chamber, and reaching its deepest extent on the *left* or in a *median* position. Thus, this ‘caecum’ comprises an elongation of a different portion of the gastric epithelium. This conclusion is supported by an examination of the pattern of folds. In *T. huonensis* (Ponder *et al*., 1991), the pattern of folds is similar to that in *Bithynia tentaculata*, in which a fold curves around the posterior end of the gastric chamber and terminates behind the gastric shield on the right. However, the ‘caecum’ in *T. huonensis* comprises a pouch bordering the posterior edge of the curving fold, not a pocket behind the shield receiving the terminal tip of the fold.

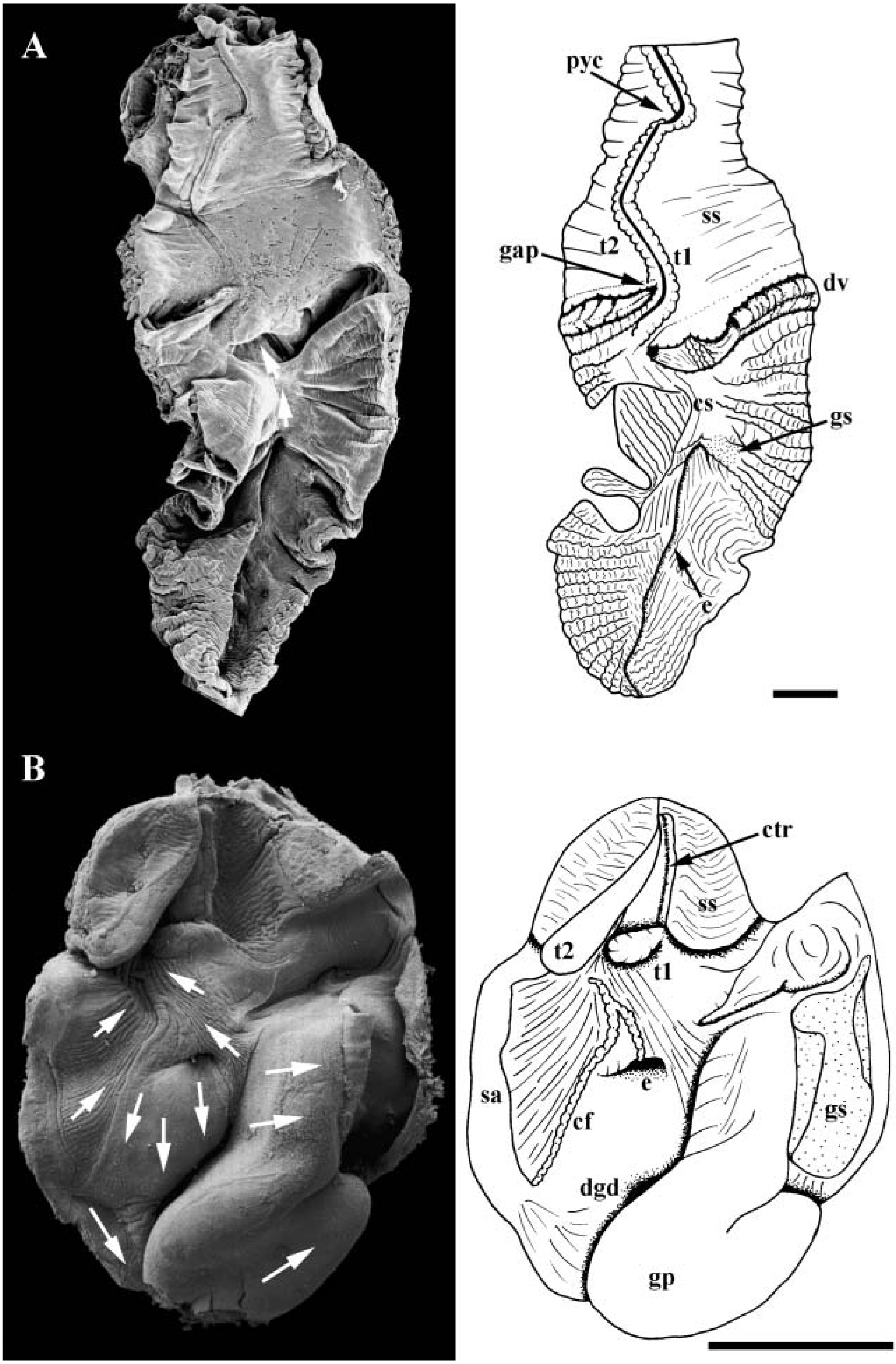

Figure 13. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Neocyclotus dysoni ambiguum*, dorsal view. (B) *Lampanella minima*, dorsal view. Scale bar = 1 mm. Abbreviations: cf, ciliated fold; cs, ciliated strip; ctr, ciliary tract; dgd, digestive gland duct; dv, digestive gland vestibule; e, oesophagus; gap, gastric pouch; gp, glandular pad; gs, gastric shield; pyc, pyloric caecum; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

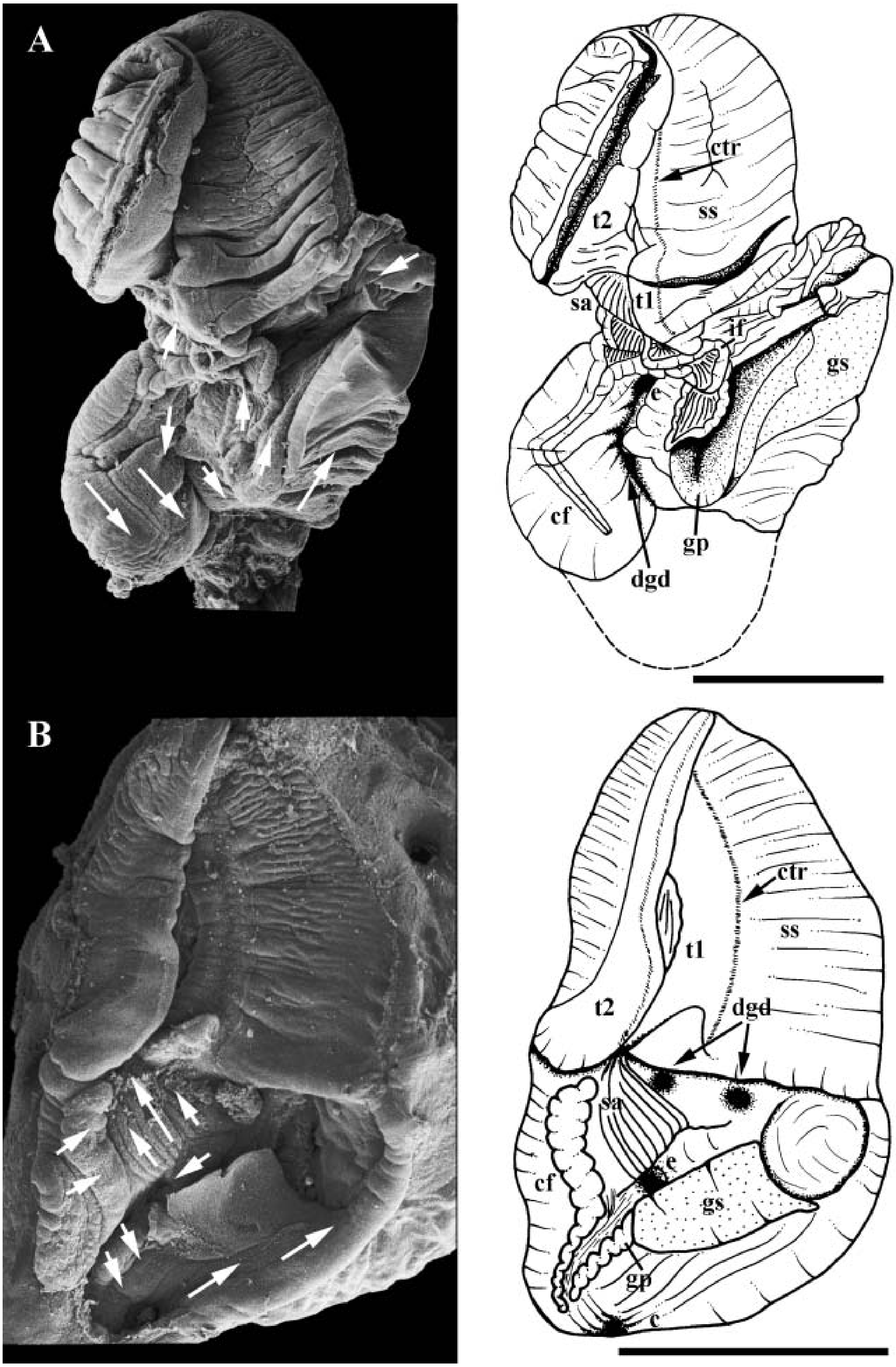

Figure 14. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Petaloconchus varians*, dorsal view. (B) *Crepidula plana*, dorsal view. Scale bar = 1 mm. Abbreviations: c, caecum; cf, ciliated fold; ctr, ciliary tract; dgd, digestive gland duct; e, oesophagus; gp, glandular pad; gs, gastric shield; if, intestinal flap; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

In *Hydrobia truncata*, several folds terminate along the *left* wall of the midgut in the 'caecum' (Davis *et al*., 1982). This configuration is similar to the midgut morphology of *Strombus mutabilis* described below (Fig. 12B). In these two taxa, the ciliated folds (cf) are not crescent-shaped, but run straight along the floor to the left of the oesophagus, terminating in a pocket along the left wall of the midgut. This configuration of typhlosoles indicates that the caecal chamber of strombids (ce) and of various hydrobiids represent yet other elongations of the midgut as compared to those described above.

Thus, the homologies of the diverse assortment of gastric chamber outpocketings among caenogastropods is a complex issue. Critical re-examination of midgut landmarks clearly demonstrates that the 'caecae' of caenogastropods comprises a heterogeneous assortment of structures that represent many independent modifications; nor are they homologous to the vetigastropod caecum. In this analysis, the position and folding patterns in the pocket of *Theodoxus fluviatilis* (Fig. 12A, c), *Crepidula plana* (Fig. 14B, c) and *Bithynia tentaculata* (Fig. 15A, c) is considered sufficiently similar to postulate homology. However, given that this structure occurs in a dorso-lateral position suggests that the caecum of these three species is not homologous to the caecum of vetigastropods (Fretter & Graham, 1962), which opens posteriorly and ventrally. *Macleaniella moskalevi* and other cocculinids lack a caecum (Haszprunar, 1987, 1988c; Strong & Harasewych, 1999).

30. Ciliated oesophageal fold in gastric chamber

(0) Absent [*Mac*, *Neo*, *Mar*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*The*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*].

A prominent ciliated fold (or folds; Figs 12A,B, 13B, 14A,B, 15A,B, 16A, cf) commonly extends from the minor typhlosole (t2), to the left of the oesophageal aperture (e), bounding the intestinal sorting area (sa) when present. In *Theodoxus fluviatilis* (Fig. 12A) and *Crepidula plana* (Fig. 14B), the fold curves around the posterior end of the gastric chamber and terminates within the 'caecum' (c). In *Bithynia tentaculata* (Fig. 15A), a large fold (cf) emerges from the intestinal groove, passes to the left of the oesophagus and curves around the posterior end of the gastric chamber. A second smaller fold emerges from the minor typhlosole and diminishes before reaching the posterior end of the gastric chamber; a sorting area is absent. This double pattern of folds is common in other rissooidean gastropods (Davis *et al*., 1982; Ponder *et al*., 1991). It is not clear if the single fold in other caenogastropods is homologous to one or both of these folds.

In caenogastropods that possess a ciliated fold in the absence of a caecum, the fold terminates along the left wall of the midgut. In *Lampanella minima* (Fig. 13B), the fold (cf) is low and forms the boundary of the sorting area (sa). In *Petaloconchus varians* (Fig. 14A), the fold (cf) similarly runs along the edge of the sorting area (sa), but extends for a short distance posteriorly beyond the sorting lamellae. In *Strombus mutabilis* (Fig. 12B), the fold (cf) is a composite structure and forms an extension of the sorting area, terminating in a short caecal extension of the gastric chamber along the left wall (see below). In *Neverita duplicata* (Fig. 16A), it runs along the right boundary of the sorting area (sa), connecting the oesophageal aperture (e) and the two digestive gland ducts (dgd). The fold is lacking in *Cypraea robertsi* (Fig. 16B), *Nitidiscala tinctum* (Fig. 17A) and the neogastropods (Fig. 17B,19B).

31. Posterior caecal extension

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Cre*, *Bit*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Uro*] (1) Present [*Str*, *Lit*, *Ily*].

Posterior caecal extensions are not considered to be homologous to the 'caecum' of *Theodoxus fluviatilis*, *Bithynia tentaculata* and *Crepidula plana*, but are considered to represent an elongation of a different portion of the gastric chamber. Similarly, Graham (1949) suggested that the posterior caecal extension of the gastric chamber in *Littorina littorea* is not homologous to the spiral caecum, but represents an elongation of a different portion of the gastric chamber. 'The caecum of the trochids has been lost; what the littorinids possess is a new structure, and if its anatomical and functional relationships be considered, it will be found to be a posterior elongation of that area of the midgut of *Monodonta* which lies dorsal to the opening of the caecum, bordered on the left by the groove emerging from the caecum and by the gastric shield, and receiving on its right the ridged tract coming from the oesophagus' (Graham, 1949: 748).

However, this character is difficult to code in some taxa because there is no objective, stationary frame of reference; how does one define a 'posterior' extension when other landmarks are not always stationary? Despite often consistent and predictable associations between midgut features, the anterior migration of the oesophagus (Graham, 1949), variable development of the sorting areas, and variable position of digestive gland ducts (Graham, 1939), render these features problematic in providing a reference point for divergent taxa. At least within caenogastropods, the only seemingly stable landmark is the gastric shield. Despite a shift in the position of the shield with the forward migration of the oesophagus among more basal gastropods (Graham, 1949), the caenogastropod

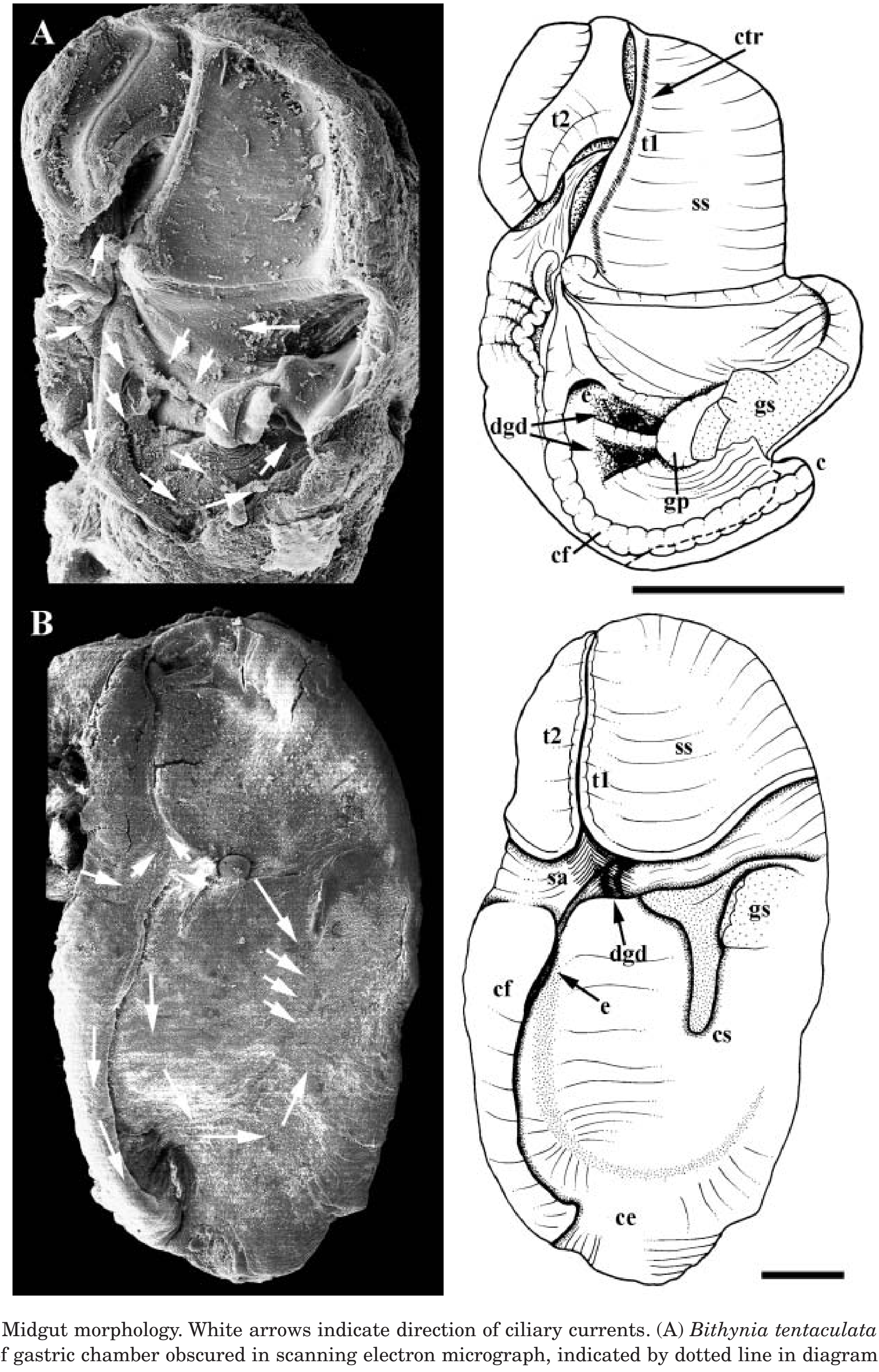

Figure 15. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Bithynia tentaculata*, dorsal view. Distal end of gastric chamber obscured in scanning electron micrograph, indicated by dotted line in diagram on right. (B) *Littorina littorea*, dorsal view. Stippling indicates ciliary tract within gastric chamber extending from oesophageal aperture. Scale bar = 1 mm. Abbreviations: c, caecum; ce, caecal extension; cf, ciliated fold; cs, ciliated strip; ctr, ciliary tract; dgd, digestive gland duct; e, oesophagus; gp, glandular pad; gs, gastric shield; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

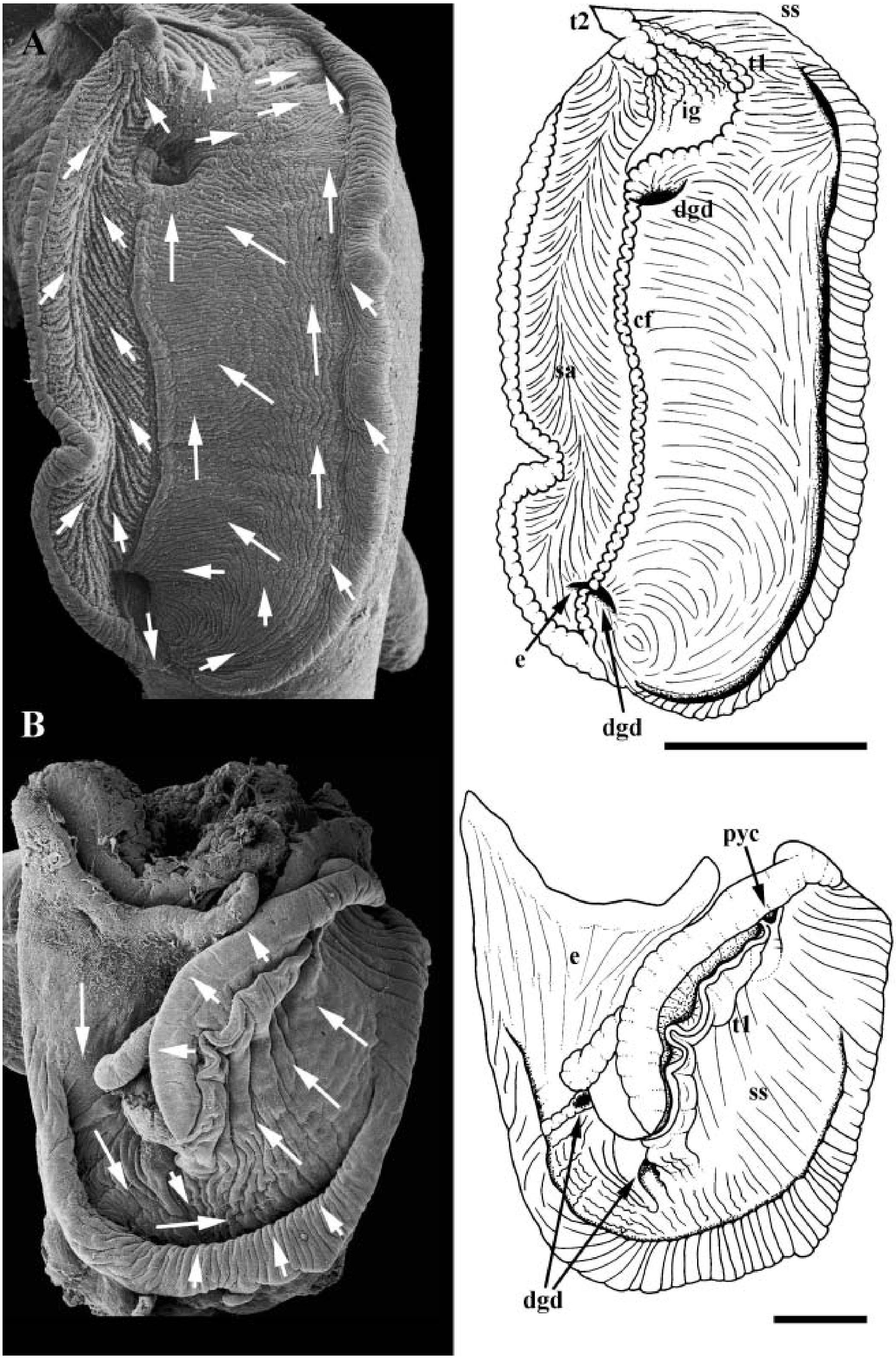

Figure 16. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Neverita duplicata*, dorsal view. Scale bar = 1 mm. (B) *Cypraea robertsi*, dorsal view. Abbreviations: cf, ciliated fold; dgd, digestive gland duct; e, oesophagus; ig, intestinal groove; pyc, pyloric caecum; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

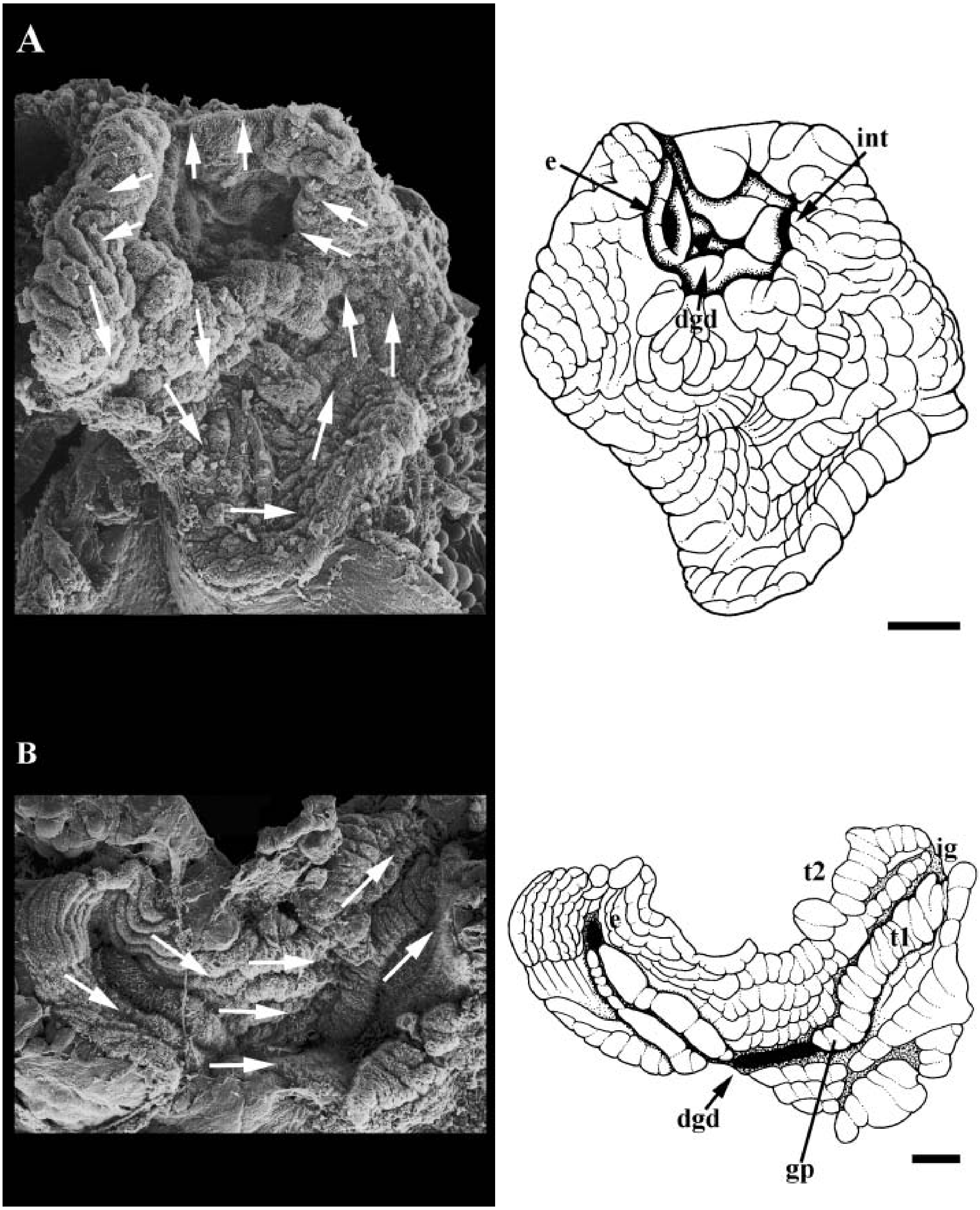

Figure 17. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Nitidiscala tinctum*, dorsal view. (B) *Panarona clavatula*, dorsal view. Note paired folds on midgut floor between oesophageal aperture and large digestive gland duct. Scale bar = 100 µm. Abbreviations: dgd, digestive gland duct; e, oesophagus; gp, glandular pad; ig, intestinal groove; int, intestine; t1, major typhlosole; t2, minor typhlosole.

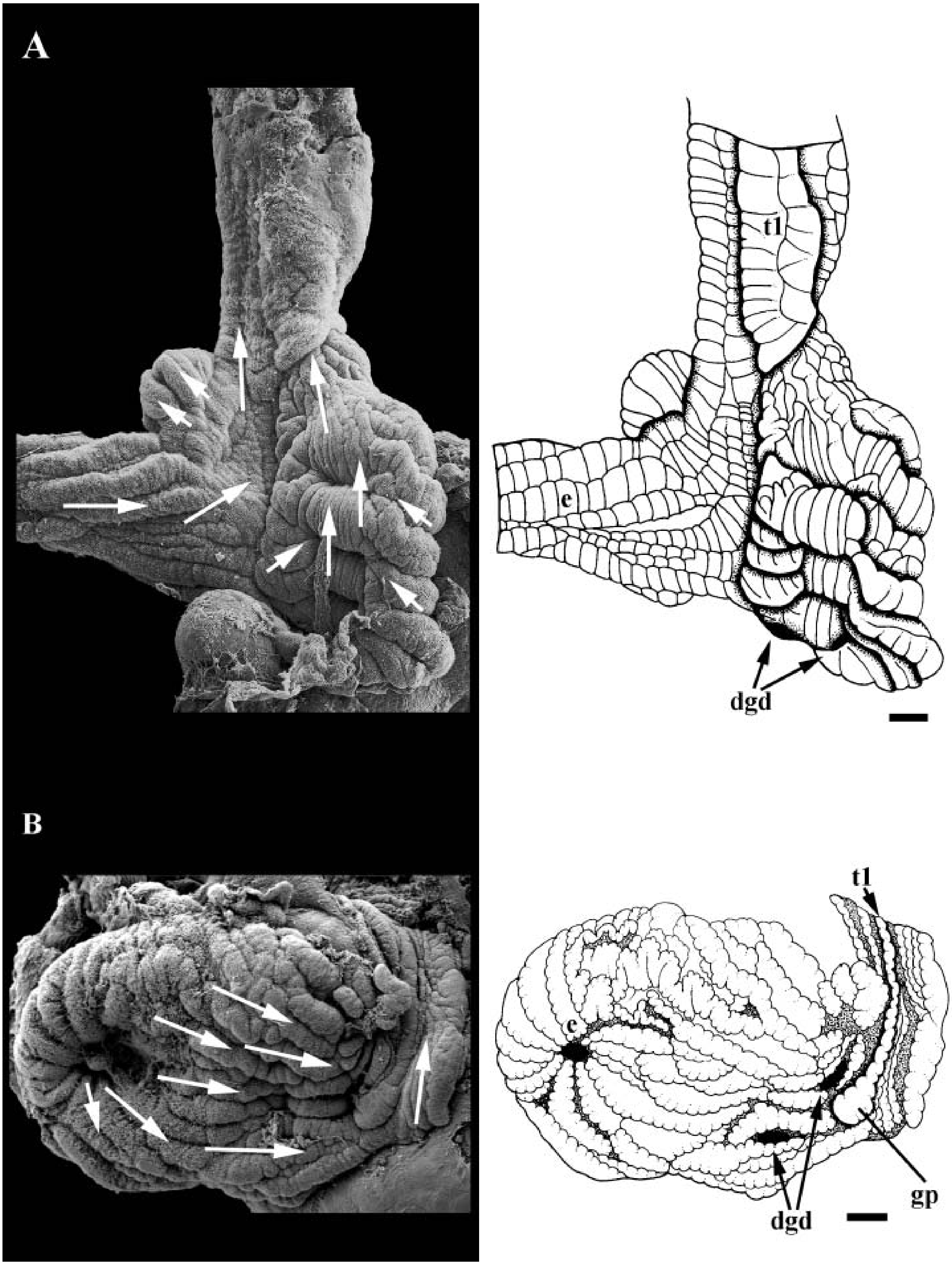

Figure 18. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Prunum apicinum*, dorsal view. (B) *Conus jaspideus*, dorsal view. Scale bar = 100 µm. Abbreviations: dgd, digestive gland duct; e, oesophagus; gp, glandular pad; t1, major typhlosole.

shield occurs in a conservative association with the style sac. In fact, the position of the shield has been cited as an appropriate landmark for documenting other positional shifts, such as non-torsional asymmetries affecting the visceral mass (Fretter *et al*., 1981). Thus, the presence of a small gastric shield adjacent to the style sac in *Littorina littorea* (Fig. 15B) and *Ilyanassa obsoletus* (Fig. 19A) provides a frame of reference, sufficiently similar to other caenogastropods, to evaluate the relative size of their gastric chamber (ce).

However, the shield has been lost in many taxa; *Neverita duplicata* is particularly problematic. No shield is present in this species nor in other naticids (Fretter & Graham, 1962; Reid & Friesen, 1980). The presence of two digestive gland ducts at opposite ends of the gastric chamber suggests that the elongate chamber represents an elongation of the central portion of the midgut wall rather than a posterior extension as in *Ilyanassa obsoletus* and *Littorina littorea*. However, it is not possible to falsify the hypothesis that the gastric chamber of *N. duplicata* represents a posterior caecal extension with a migration of the digestive gland and/or oesophageal apertures. Thus, homologies of this species are uncertain. The small pouch below the oesophageal aperture in *Urosalpinx cinerea* (Fig. 19B, po) is considered to represent yet another independent evagination of the midgut wall.

Ponder & Lindberg (1997) view the architaenioglossan midgut as an elongate chamber, analagous to the gastric chamber of *Littorina littorea*. However, they do not consider this structure to be a 'caecum' on the grounds that it is cuticularized, despite the presence of a ventral ciliary tract (Prashad, 1925; Demian, 1964; Andrews, 1965a; present study). Paradoxically, they do consider the cuticularized gastric chamber of littorinoideans (bearing a longitudinal fold and several ciliary tracts; Johansson, 1939; Graham, 1949; present study) to be homologous to the 'caecum'.

The gastric chamber of architaenioglossans is not considered here to comprise an elongate chamber and, thus, represents neither a 'caecum' nor a 'posterior caecal extension.' In fact, the midgut is U-shaped; the posterior oesophagus continuously broadens, forming a seamless transition from oesophagus to midgut. This is apparent upon opening the midgut along a dorsal, longitudinal incision (Fig. 13A); the oesophagus (e) is seen to open under the reflected flap that extends to the posterior limit of the gastric chamber; the gastric shield (gs) lies opposite the opening.

32. Gastric shield

(0) Absent [*Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Uro*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Ily*].

The gastric shield is the tooth-like portion of the cuticular midgut lining. The cuticle has been suggested to function in protecting the gastric epithelium from the action of the crystalline style and/or hard particles (Graham, 1949). However, as noted in the past, the gastric shield is present in many taxa that do not possess a crystalline style and/or in carnivores that do not ingest abrasive particles (Graham, 1939, 1949; Morton, 1951; Owen, 1966). Early hypotheses of homology of this feature were directly linked to the presence of a crystalline style. For example, Graham (1939) and Demian (1964) argued that absence of a crystalline style in ampullariids precluded homology of the cuticle in these taxa to the gastric shield. Later, Graham (1949) revised this view, considering any thick cuticular covering of the gastric epithelium to be a gastric shield, even in the absence of a crystalline style.

33. Position of gastric shield

(0) Dorsal [*Mac*, *The*] (1) Ventro-lateral [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Ily*].

This survey has revealed that the position of the gastric shield varies between ingroup and outgroup taxa. In *Macleaniella moskalevi* (Fig. 20A) and *Theodoxus fluviatilis* (Fig. 20B), the gastric shield (gs) is dorsal in position. In all caenogastropods that possess a cuticular lining of the gastric epithelium, the shield is predominantly ventro-lateral in position (Fig. 20C–H). Although the cuticular lining often extends over the lateral walls of the midgut, the difference in tooth position between ingroup and outgroup taxa is clearly visible.

It may be possible to subdivide this character more finely with denser taxon sampling across the Gastropoda. Preliminary studies (pers. obs.) show that the exact position of the dorsal gastric shield is variable. For example, in *Macleaniella moskalevi*, the shield is developed left of the midline, while in *Theodoxus fluviatilis*, it is developed to the right of the midline.

34. Glandular pad

(0) Absent [*Nev*, *Cyp*, *Nit*] (1) Present [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

The gastric shield is secreted and supported by a mid-ventral fold referred to as the glandular pad by Houbrick (e.g. 1991b). This pad is highly developed only in members of the Cerithioidea (e.g. *Lampanella minima*, Fig. 13B, gp). In other caenogastropods, it is significantly smaller but nonetheless glandular and referred to as a collar by Ponder *et al*. (1991). In general, the pad terminates shortly posterior to the gas-

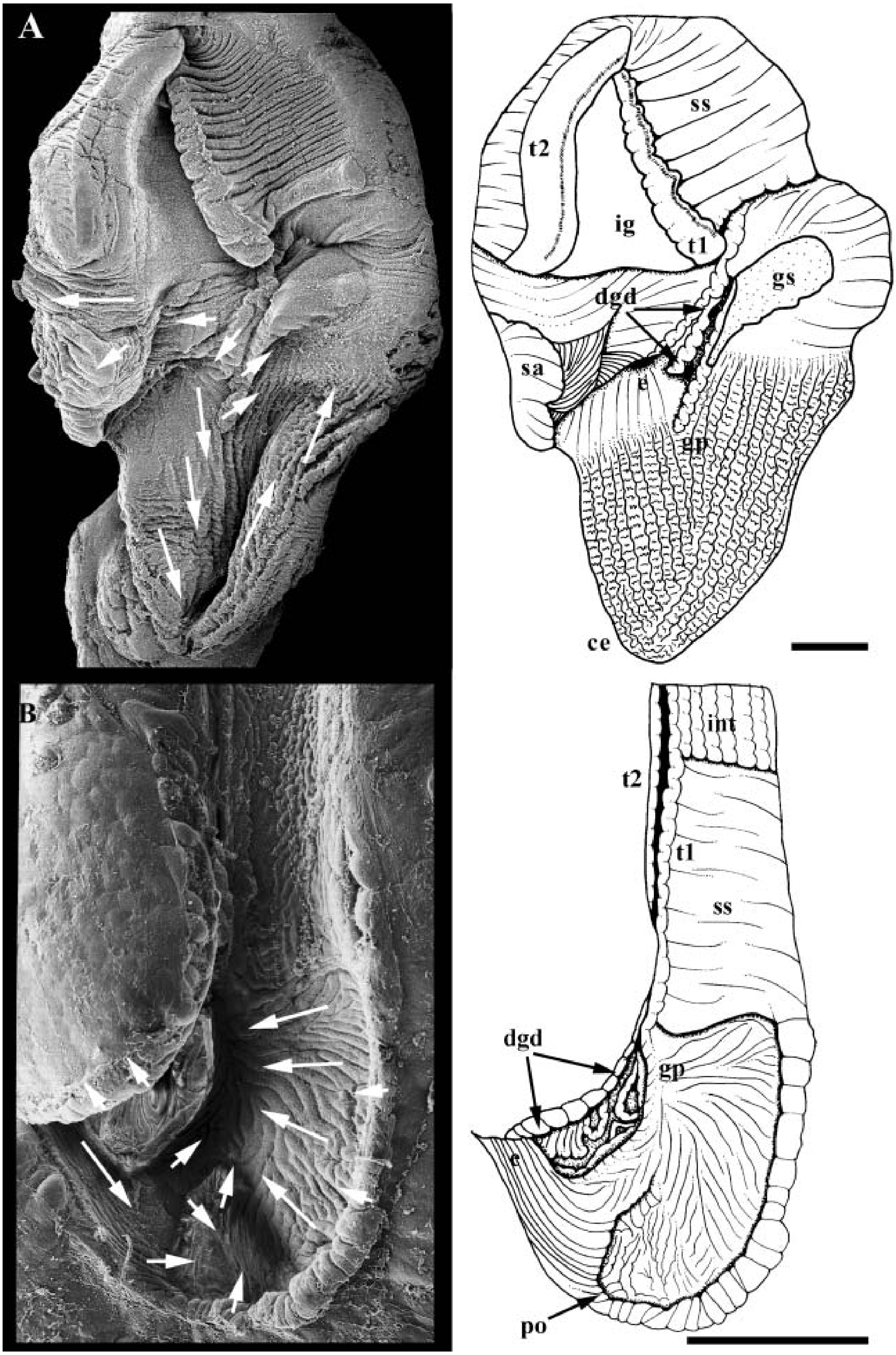

Figure 19. Midgut morphology. White arrows indicate direction of ciliary currents. (A) *Ilyanassa obsoletus*, dorsal view. (B) *Urosalpinx cinerea*, dorsal view. Scale bar = 1 mm. Abbreviations: ce, caecal extension; dgd, digestive gland duct; e, oesophagus; gp, glandular pad; gs, gastric shield; ig, intestinal groove; int, intestine; po, pouch; sa, sorting area; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

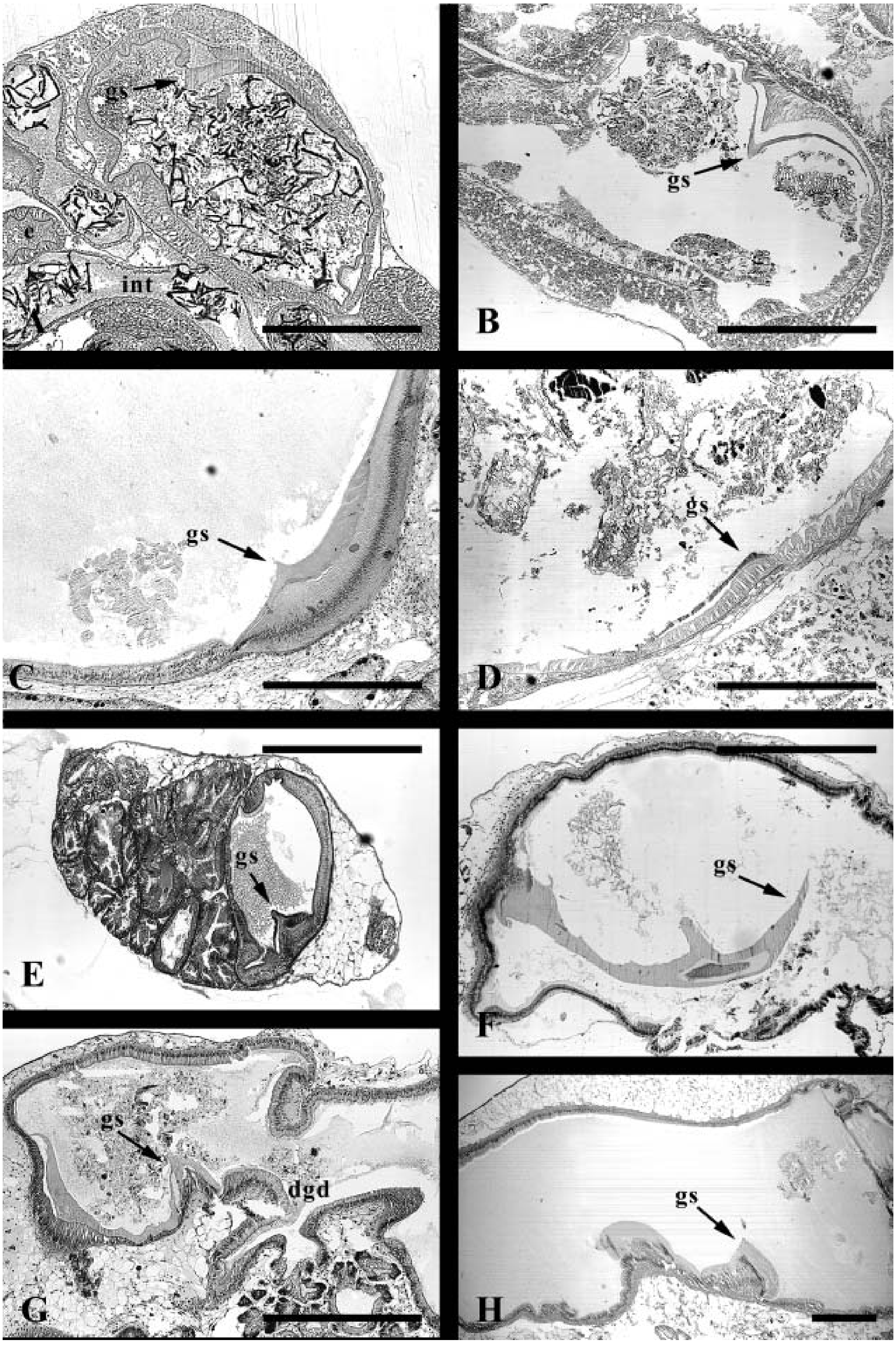

Figure 20. Histology of midgut; position of gastric shield. (A) *Macleaniella moskalevi*, transverse section. (B) *Theodoxus fluviatilis*, saggital section. (C) *Neocyclotus dysoni ambiguum*, transverse section. (D) *Marisa cornuarietis*, saggital section. (E) *Crepidula plana*, transverse section. (F) *Strombus mutabilis*, saggital section. (G) *Bithynia tentaculata*, saggital section. (H) *Ilyanassa obsoletus*, saggital section. Scale bar = 0.5 mm. Abbreviations: dgd, digestive gland duct; e, oesophagus; gs, gastric shield; int, intestine.

tric shield. In *Theodoxus fluviatilis* (Fig. 12A), *Crepidula plana* (Fig. 14B) and *Bithynia tentaculata* (Fig. 15A), the pad (gp) curves to the right, paralleling the extension of the minor typhlosole (t2) into the caecum (c). In other taxa, the pad runs for some distance posteriorly within the gastric chamber (e.g. *L. minima*, Fig. 13B; *Ilyanassa obsoletus*, Fig. 19A). In *Neocyclotus dysoni ambiguum* (Fig. 13A), *Marisa cornuarietis*, *Littorina littorea* (Fig. 15B), and other architaenioglossans (e.g. *Viviparus viviparus*; pers. obs.) the pad is modified into a ciliated strip (cs) (Graham, 1949; present study).

Homology of the glandular pad in the neogastropod midgut is somewhat problematic. Most neogastropods lack a gastric shield. However, some species possess a prominent fold on the floor of the midgut that bears a thin layer of cuticle (Smith, 1967; Medinskaya, 1993). This fold is recognizable when non-cuticularized because it is more or less continuous with the major typhlosole, sometimes forming a direct extension of the major typhlosole across the midgut floor. Consequently, it appears that, in neogastropods, the gastric shield and its supporting pad of tissue occur in a much closer association with the major typhlosole.

Thus, in neogastropods, the fold forming a more or less direct extension of the major typhlosole into the gastric chamber, sometimes bearing a cuticle, is here considered tentatively to be homologous to the glandular pad. This fold often bounds the openings of the digestive gland ducts on the right (Graham, 1949; Smith, 1967; Medinskaya, 1993), but this association may vary. In *Ilyanassa obsoletus* (Fig. 19A) the fold supports a small gastric shield (gs), extends to the base of the major typhlosole (t1), and bounds paired ducts of the digestive gland (dgd) on the right. In *Urosalpinx cinerea* (Fig. 19B), the fold (gp) forms a small lip along the right side of a deep vestibule that bears the paired ducts of the digestive gland (dgd); in other muricids the fold is more prominent (Smith, 1967; Medinskaya, 1993). In *Panarona clavatula* (Fig. 17B), the fold (gp) extends into the gastric chamber to the edge of the single, large digestive gland aperture (dgd). In *Conus jaspideus* (Fig. 18B), the major typhlosole (t1) expands into a large pad (gp) that borders the more distal duct of the digestive gland (dgd), almost reaching the more proximal duct. In *Prunum apicinum*, the major typhlosole is continuous with a prominent ridge that posteriorly bounds a finely grooved tract running along the front wall of the midgut. This feature is tentatively coded as forming an extension of the major typhlosole.

The so-called gastric shield region of Wu (1965) does not correspond to the region observed to be the site of gastric shield secretion in other neogastropods. Based on other landmarks and characteristic transverse folding, the region of cuticle indicated by Medinskaya (1993) is homologous to the style sac region of other gastropods.

In several taxa, the fold is lost completely, including *Neverita duplicata* (Fig. 16A), *Cypraea robertsi* (Fig. 16B) and *Nitidiscala tinctum* (Fig. 17A). In *C. robertsi*, homology of the glandular pad and the major typhlosole extension is not supported based on the observation that lamellarioidean species, with a similar midgut organization, possess a gastric shield that is not closely associated with the major typhlosole extension (Graham, 1949).

35. Glandular pad condition
(0) Simple pad/collar [*Mac*, *The*, *Pet*, *Str*, *Cre*, *Bit*] (1) Hypertrophied [*Lam*] (2) Ciliated Strip [*Neo*, *Mar*, *Lit*] (3) Longitudinal fold/extension of major typhlosole [*Pan*, *Pru*, *Con*, *Ily*, *Uro*].

36. Intestinal groove sorting area
(0) Absent [*Mac*, *Neo*, *Mar*, *Bit*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Uro*] (1) Present [*The*, *Lam*, *Pet*, *Str*, *Cre*, *Lit*, *Nev*, *Ily*].

A well-defined area of ciliated, parallel lamellae is often associated with the intestinal groove. In some taxa (*Lampanella minima*, Fig. 13B; *Petaloconchus varians*, Fig. 14A; *Strombus mutabilis*, Fig. 12A; *Neverita duplicata*, Fig. 16A), the sorting area (sa) expands from the floor adjacent to the intestinal groove (ig) along the left wall and roof. In others (*Crepidula plana*, Fig. 14B; *Littorina littorea*, Fig. 15B; *Ilyanassa obsoletus*, Fig. 19A), it is restricted to the floor immediately adjacent to the intestinal groove. *Bithynia tentaculata* (Fig. 15A) is unique among more basal sorbeoconchans in lacking a sorting area. Although various other regions of the midgut have been designated as having a sorting function (Graham, 1939, 1949; Fretter & Graham, 1962; Smith, 1967; Medinskaya, 1993), they are not similar in position, do not possess the characteristic parallel folding and are not considered homologous.

37. Intestinal groove flap
(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Pet*, *Str*].

The floor adjacent to the intestinal groove may be modified into a flap that most likely prevents ingested particles from passing directly to the intestinal groove. In *Strombus mutabilis* (Fig. 12B) the flap (if) is large and simple; the structure has been noted in other descriptions of strombid midgut anatomy (e.g. Little, 1965). In *Petaloconchus varians* (Fig. 14A), the flap (if) is equally large, but the surface bears lamellae that are continuous with the intestinal groove sorting area; the flap has been observed in other vermetids (e.g. *Vermetus inopertus*, pers. obs.).

38. Ciliary currents within gastric chamber

(0) Bi-directional flow [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Cre*, *Bit*, *Lit*, *Nev*] (1) Clockwise rotation [*Cyp*, *Nit*, *Pru*, *Ily*, *Uro*] (2) Simple, linear [*Pan*, *Con*].

Ciliary current direction within the midgut is highly complex and variable. However, three general patterns of midgut circulation adjacent to the oesophageal aperture may be recognized. In outgroup and many ingroup taxa, there is bi-directional flow near the oesophagus; one current forming a rejection stream that flows into the intestinal groove, the other flowing posteriorly into the gastric chamber. This pattern is evident in *Lampanella minima* (Fig. 13B), *Petaloconchus varians* (Fig. 14A), *Crepidula plana* (Fig. 14B), *Littorina littorea* (Fig. 15B) as well as *Bithynia tentaculata* (Fig. 15A), despite the absence of the sorting area that forms the rejection current in other taxa. Although the posterior position of the oesophagus in *Neverita duplicata* (Fig. 16A) renders this character somewhat difficult to interpret, currents near the oesophagus are split into a rejection current (sa) and a separate current that flows into the main gastric chamber. Architaenioglossans (Fig. 13A) are tentatively coded with this group, despite the presence of a largely cuticularized gastric chamber, because the ventral ciliated strip (cs) directs paticles anteriorly toward the intestinal groove.

In *Cypraea robertsi*, *Nitidiscala tinctum* and several neogastropod taxa, the prevailing currents within the midgut are simpler, flowing in an overall clockwise pattern such that midgut contents are rotated and currents flow transversely adjacent to the intestinal groove. Due to the proximity of the oesophageal and intestinal apertures in *Nitidiscala tinctum*, this character was difficult to interpret. However, in general, currents flow clockwise within the gastric chamber. This pattern is evident in *Prunum apicinum* (Fig. 18A) despite a highly reduced midgut.

In *Panarona clavatula* (Fig. 17B) and *Conus jaspideus* (Fig. 18B), midgut currents are essentially linear. The oesophageal stream passes directly from oesophagus to intestine and is not subdivided or rotated. Only preserved material was available for *Macleaniella moskalevi* and *Strombus mutabilis*; thus, current direction is unknown for these taxa. Current direction for *Theodoxus fluviatilis* is from Graham (1939).

39. Gastric pouches

(0) Absent [*Mac*, *The*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Neo*, *Mar*].

Gastric pouches are small, blind outpocketings of the left midgut wall, adjacent to the intestinal groove, and represent modifications of the style sac pocket – an expansion of the gastric chamber at the opening of the style sac. They secrete a milky white mucus string that is directed by ciliary currents across the midgut floor into the style sac.

These pockets are known primarily from architaenioglossans. Prashad (1925) figured gastric pouches in his description of *Pila globosa*, but inferred them to comprise the opening of the pyloric caecum (see below). In his detailed study of the alimentary canal of *Marisa cornuarietis*, Demian (1964) suggested that previous authors had mistakenly confused gastric pouches for digestive gland apertures based on superficial similarity. In the present study, a pocket was found in *Neocyclotus dysoni ambiguum*, similar in position to those in *Marisa cornuarietis*. Similar pouches have been described in other architaenioglossans, including pilids (Andrews, 1965a). Gastric pouches also occur in the viviparid *Cipangopaludina japonicus* (pers. obs.). However, the pockets occur more posteriorly on the floor of the midgut, near the right wall. Yet they secrete the same milky mucus string that enters the style sac, suggesting that they may be homologous despite differences in position.

Graham (1949) described the presence of a mucus-secreting pouch at the inner end of the minor typhlosole in *Littorina littorea*; Marcus & Marcus (1963) also found a pouch in *L. angulifera*. Based on Graham's (1949) description, Demian (1964) suggested that the pouch in *L. littorea* may by homologous to the gastric pouches of *Marisa cornuarietis*. However, in agreement with the study of Johansson (1939), the presence of a mucus-secreting pouch could not be confirmed here in *L. littorea* (Fig. 15B).

A similar, mucus-secreting 'deep sac', lying at the base of the minor typhlosole, was described in *Theodoxus fluviatilis* (Graham, 1939). An similar structure has been observed in *Neritina reclivata* (pers. obs.). Detailed examination of the latter and a re-examination of *T. fluviatilis* (Fig. 12A, ds) indicate that these sacs are not modifications of the gastric chamber as in architaenioglossans, but lie within the style sac. This is supported by the fact that the minor typhlosole (t2) curves around the mouth of the sac and the characteristic style sac ciliation bounds the opening. In contrast, the paired and single pockets of *Marisa cornuarietis* and *Neocyclotus dysoni ambiguum* (Fig. 13A, gap), respectively, lie outside the lip of the style sac (ss) as modifications of the gastric chamber.

40. Digestive gland duct vestibule

(0) Absent [*Mac*, *The*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*] (1) Present [*Neo*, *Mar*, *Uro*].

The number of digestive gland apertures can vary from one to many, and typically are found near the junction of the gastric chamber and the style sac region and/or near the oesophageal aperture. The most common pattern is the presence of paired ducts, one draining each of the paired lobes of the digestive gland. However, several taxa bear only a single duct (e.g. *Lampanella minima*, Fig. 13B; *Petaloconchus varians*, Fig. 14A; *Nitidiscala tinctum*, Fig. 17A; *Panarona clavatula*, Fig. 17B), or three digestive gland ducts (*Littorina littorea*, Fig. 15B). Architaenioglossans (Fig. 13A) and *Urosalpinx cinerea* are characterized by the presence of two (*Urosalpinx cinerea*), three (*Marisa cornuarietis*) or numerous (*Neocyclotus dysoni ambiguum*) ducts that open to a common vestibule (dv) at the base of the style sac.

Without detailed studies of the digestive gland lobes and ducts, it is impossible to evaluate homology of the ducts, particularly in cases of multiplication or loss. Given this ambiguity, only the presence or absence of the digestive gland duct vestibule is coded at present.

41. Pyloric (style sac) typhlosoles

(0) Two [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) One [*Cyp*, *Nit*].

One characteristic feature of the style sac region is the presence of two typhlosoles separating the midgut rejection tract – the intestinal groove (Graham, 1939, 1949; Morton, 1952b, 1953; Fretter & Graham, 1962; Owen, 1966). However, two taxa (*Cypraea robertsi*, Fig. 16B; *Nitidiscala tinctum*) possess a single typhlosole (t1); in both taxa, it is the major typhlosole that is present.

In those gastropods that possess a style, the two typhlosoles may partially to completely fuse, structurally separating the style sac and intestinal groove. A threefold classification of gastropod style sacs based on the degree of communication between the typhlosoles was formulated by Robson (1922), which was adapted from studies of bivalves (Matthias, 1914). This classification was accepted and expanded by numerous workers (e.g. Mackintosh, 1925; Seshaiya, 1934a; Johansson, 1941; Graham, 1949; Owen, 1966; Salvini-Plawen, 1988). Only *Strombus mutabilis* possesses fused typhlosoles, and was not coded here.

42. Ciliation pattern on major typhlosole

(0) Ciliation homogeneous [*The*, *Neo*, *Mar*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Uro*] (1) Distinct strip of long cilia present along length of typhlosole [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Ily*].

Scanning electron investigation of the style sac epithelium revealed that a distinctive strip of long cilia bounds the inner (style sac) edge of the major typhlosole in many species, and may be present along the minor typhlosole as well. This strip varies in thickness from a few cilia (*Crepidula plana*, Fig. 21D) to a broad, brush-like band (*Bithynia tentaculata*, Fig. 21E). Despite the fusion of the typhlosoles in *Strombus mutabilis* (Fig. 21C), the strip is visible projecting from the fusion scar.

In this analysis, the distribution of this character is identical with the distribution of the crystalline style. However, studies of taxa not included here confirmed the presence of the strip in taxa lacking a style (e.g. lamellarioideans, littorinoideans). Thus, these features are considered to be independent and are coded separately.

The significance of this ciliated strip is not clear. It is generally accepted that the crystalline style is secreted by a region of glandular cells along the inner edges of the typhlosoles (Nelsen, 1918; Graham, 1949; Fretter & Graham, 1962). However, this secretory region appears to be broader than the width of the ciliated strip. Thus, the strip may correspond to the inner boundary of this secretory region. Alternatively, it has been noted that cilia along the typhlosoles are largely responsible for rotating the crystalline style (Salvini-Plawen, 1988). In this case, the strip may function in style sac circulation, and is retained in taxa that have lost the style.

43. Pyloric (style sac) ciliation

(0) Uniform [*Mac*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*] (1) Differentiated [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Ily*, *Uro*].

Even in the absence of a crystalline style, the style sac region can be recognized by the presence of a distinctive high, uniform, ciliary brush border (e.g. Seshaiya, 1929, 1932; Graham, 1939, 1949; Morton, 1951). Immediately obvious in histological section, this ciliary carpet is apparent macroscopically as an iridescent sheen on the style sac epithelium. These characteristic cilia are present in style-bearing gastropods, but are also present in basal gastropods that lack a crystalline style and are retained in a number of derived caenogastropods that have lost the crystalline style. In other taxa, the style sac region is lined with a relatively dense carpet of significantly shorter cilia (e.g. *Neverita duplicata*) or with cilia similar to those found within the intestinal groove (e.g. *Panarona clavatula*).

44. Pyloric folding

(0) Smooth/Transverse [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Ily*, *Uro*] (1) Longitudinal [*Nit*, *Pan*, *Pru*, *Con*].

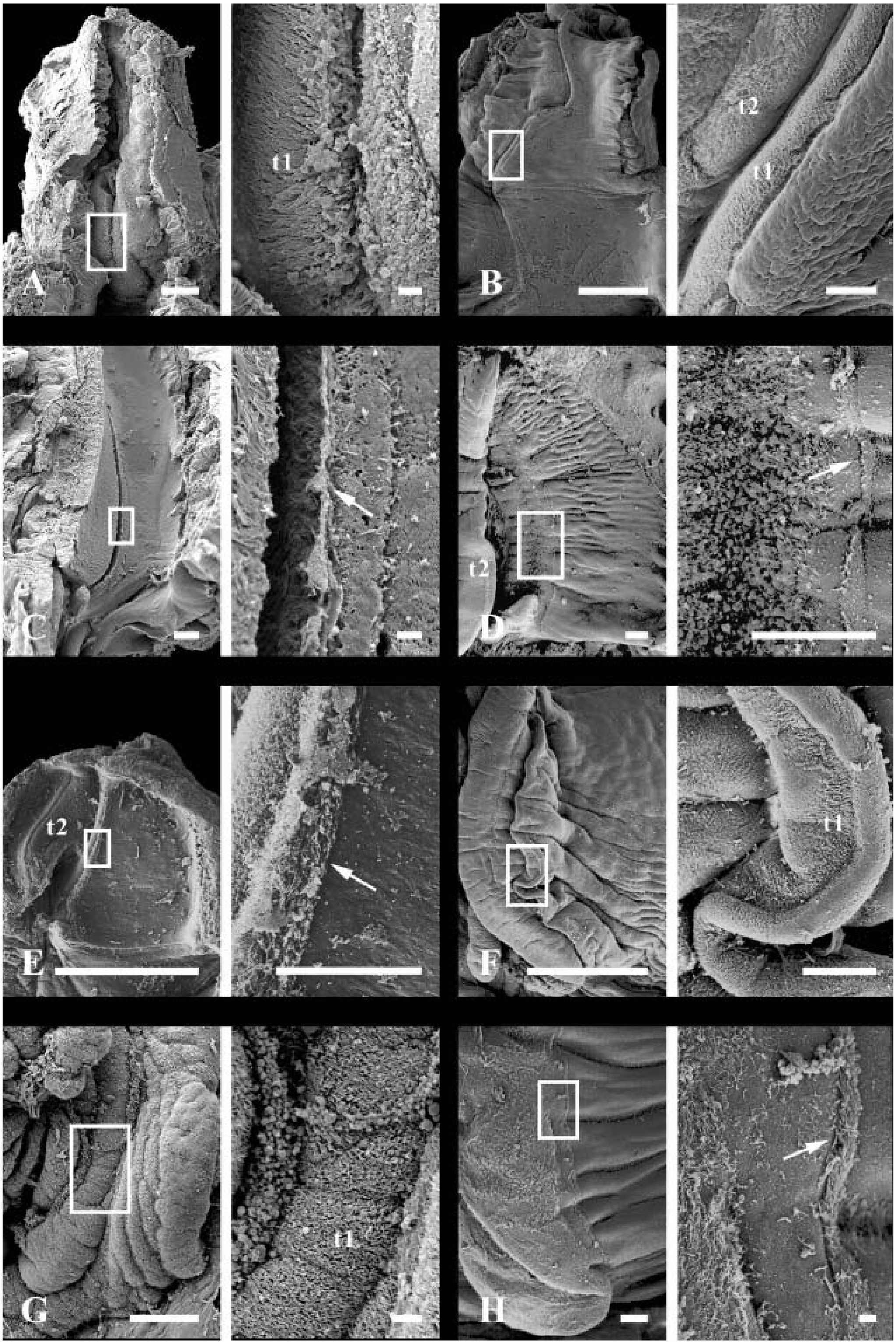

Figure 21. Style sac morphology; major typhlosole and ciliary tract (indicated by arrows). (A) *Theodoxus fluviatilis*. Scale bars (left to right) =100 µm, 10 µm. (B) *Neocyclotus dysoni ambiguum*. Scale bars = 1 mm, 100 µm. (C) *Strombus mutabilis*. Scale bars = 100 µm, 10 µm. (D) *Crepidula plana*. Scale bars = 100 µm, 100 µm. (E) *Bithynia tentaculata*. Scale bars = 1 mm, 100 µm. (F) *Cypraea robertsi*. Scale bars = 1 mm, 100 µm. (G) *Conus jaspideus*. Scale bars = 100 µm, 10 µm. (H) *Ilyanassa obsoletus*. Scale bars = 100 µm, 10 µm. Abbreviations: t1, major typhlosole; t2, minor typhlosole.

In the absence of this distinctive pyloric ciliation, another characteristic feature of the style sac region is the presence of a smooth to transversely folded epithelium and accompanying clockwise circulation patterns (Graham, 1939, 1949; Fretter & Graham, 1962). For example, *Neverita duplicata* (Fig. 16A) lacks the characteristic style sac ciliation, but bears a small region of transverse folds (ss) flanked on either side by the major (t1) and minor typhlosoles. Currents in this region flow clockwise, similar to the style sac region of other caenogastropods. Similarly, despite simplification of the midgut, a region of the neogastropod gut can be identified as homologous to the style sac region based on the position of landmarks such as the gastric shield (Smith, 1967; Wu, 1973). This region of irregularly transverse folds lies between the typhlosoles and varies significantly in development, and can be seen in *Urosalpinx cinerea* (Fig. 19B, ss) despite the absence of a crystalline style. However, many neogastropods, while possessing the major and minor typhlosoles, retain no evidence of this transverse folding of the pyloric epithelium. Instead, the epithelium is longitudinally folded and currents flow posteriorly into the intestine. This pattern is evident in *Panarona clavatula* (Fig. 17B), *Prunum apicinum* (Fig. 18A), and *Conus jaspideus* (Fig. 18B).

45. Crystalline style

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Uro*] (1) Present [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Ily*].

The crystalline style first was described in 1686 by Anton deHeide in *Mytilus*. Mitra (1901) established the important fact that the style is a non-cellular, secretory product of the intestinal epithelium. Although some workers suggested that the style was composed of a globulin or chondrin matrix (e.g. Yonge, 1932), experimental studies identified the style matrix as mucin (Berkeley, 1935). Hypotheses on the role of the style have ranged from reproduction, mechanical support, food reserve, lubrication, and an aid in absorption (see review in Nelsen, 1918). However, now it is accepted that the rod is concurrently rotated and pushed into the gastric chamber, where relatively higher pH levels dissolve the style releasing carbonic acid and enzymes that have been impregnated in the style matrix (Coupin, 1900), ensuring a constant supply of enzymes to the midgut contents, while the carbonic acid acts as a buffer, maintaining pH levels for optimal enzymatic activity (Yonge, 1930). Rotation of the style, in conjunction with currents along the typhlosoles, may play a role in retrieving digestible particles that have escaped the gastric chamber prematurely, as well as compensating for the absence of peristaltic contraction by circulating midgut contents and bringing particles into contact with the sorting area (Yonge, 1926; Graham, 1949; Morton, 1952b, 1953; Fretter & Graham, 1962; Owen, 1966).

In the absence of a crystalline style, the style sac is not involved in the process of digestion but in the formation of faeces. In these species, the style sac contains a fecal rod or ‘protostyle’, a rotating mass of waste particles and mucus that represents the initiation of fecal pellet formation. In contrast to style sacs containing a true hyaline crystalline style, ciliary currents direct the contents of the style sac towards the intestine rather than into the gastric chamber (Morton, 1952b, 1953; Fretter & Graham, 1962; Owen, 1966).

A crystalline style is found in three classes of molluscs: the Gastropoda, Bivalvia and Monoplacophora (see review in Salvini-Plawen, 1981). Among gastropods, true styles are limited primarily to the Caenogastropoda (Fretter & Graham, 1962). Homology of the crystalline style is an issue that is controversial both at higher and lower taxonomic levels. The style has been regarded as a feature uniting gastropods and lamellibranchs (Wingstrand, 1985) or, conversely, as a feature independently derived in these two groups (e.g. Graham, 1949; Salvini-Plawen, 1981). Even within the Gastropoda, the homology of the crystalline style is unclear. Some have observed that the style is not distributed randomly within the Gastropoda, and supported homology of the structure (e.g. Graham, 1939, 1949). Others have supported the view that it is an adaptive feature associated with herbivory (Jenner, 1956; Brown, 1969; Curtis & Hurd, 1981).

The crystalline style was not coded in the analysis of Ponder & Lindberg (1997), because it was considered too homoplastic (W. Ponder, pers. comm.). However, the fact that a feature is homoplastic at higher hierarchical levels, does not deny its potential to resolve relationships at lower hierarchical levels and has been included here.

46. Pyloric caecae

(0) Absent [*Mac*, *The*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Neo*, *Mar*, *Cyp*].

Bouvier (1888) was the first to document the presence of pyloric caecae in *Ampullaria*. Heretofore, the presence of pyloric caecae at the distal end of the style sac has been documented only in architaenioglossans (Prashad, 1925; Demian, 1964; Andrews, 1965a). However, it is clear from the present description (*Cypraea robertsi*, Fig. 16B, pyc) and reinterpretation of Kay's (1960) study above, that cypraeoideans similarly possess pyloric caecae.

The pyloric caecae of architaenioglossans and cypraeoideans are similar in that they extend posteriorly under the style sac, opening to a transverse segment of the intestinal groove at the distal end of the style sac. However, the caecae differ in slight detail. In *Marisa cornuarietis* (Demian, 1964) and *Neocyclotus dysoni ambiguum* (Fig. 13A), the minor typhlosole (t2) parallels the major typhlosole (t1) through the pyloric caecum (pyc). In *Cypraea robertsi* (Fig. 16B), the minor typhlosole is not present in the style sac region (ss) and instead extends from the mouth of the caecum into the intestine. Other cypraeoideans have been described that possess a minor typhlosole within the style sac (Kay, 1960). Pyloric caecae may be present also in lamellarioideans. A transverse segment of the major typhlosole appears to be present at the distal end of the style sac in two triviid species described by Graham (1949).

HINDGUT

47. Intestinal conformation

(0) Three loops [*Mac*, *Neo*, *Mar*] (1) Two loops [The] (2) Single loop [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Ily*, *Uro*] (3) Straight [*Cyp*, *Nit*, *Pan*, *Pru*, *Con*].

Complex intestinal looping is most commonly associated with basal gastropods, with simplifications often cited as accompanying shifts in feeding habit (Fretter & Graham, 1962). Recently, this view has been justifiably criticized (Ponder & Lindberg, 1997). In basal sorbeoconchans (*Lampanella minima*, *Petaloconchus varians*, *Strombus mutabilis*, *Crepidula plana*, *Bithynia tentaculata*, *Littorina littorea*, *Neverita duplicata*) and two neogastropods (*Ilyanassa obsoletus*, *Urosalpinx cinerea*), the intestine emerges from the style sac, turns posteriorly along the style sac and loops around the back of the kidney. In *Cypraea robertsi*, *Nitidiscala tinctum*, *Panarona clavatula*, *Prunum apicinum* and *Conus jaspideus*, the intestine travels straight from the midgut to the mantle cavity.

In contrast, the intestine of basal gastropods and outgroup taxa shows a complex pattern of looping with a first loop that travels far anteriorly (Salvini-Plawen, 1988) and completes approximately two (*Theodoxus fluviatilis*) to three (*Macleaniella moskalevi*) full loops before entering the pallial cavity. In *Marisa cornuarietis* and *Neocyclotus dysoni ambiguum*, an intermediate pattern is apparent; both taxa possess a recurvent segment of the proximal intestine that travels posteriorly along the style sac, in addition to three intestinal loops. In *N. dysoni ambiguum*, the intestinal loops are embedded in the digestive gland posterior to the kidney; in *M. cornuarietis*, the loops lie beneath the kidney lumen. This complex looping pattern has been considered independently derived of that in basal gastropods (Ponder & Lindberg, 1997).

Ponder & Lindberg (1997) noted that the recurvent segment of the proximal intestine alongside the style sac is unique to caenogastropods. However, many caenogastropods have shortened the intestine such that the looped segment curves in a vertical, rather than horizontal, plane. In addition, there is a continuum from a highly recurvent proximal intestine to a straight intestine. Due to this difficulty in quantifying the looping pattern of the proximal intestine, this character is not coded here.

48. Anal gland

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Ily*] (1) Present [*Pan*, *Pru*, *Con*, *Uro*].

The anal gland is an excretory structure (Andrews, 1992) associated with the rectum. It is present in many neogastropods (Ponder, 1973) and may be functionally replaced by the kidney in taxa that have lost the structure (Andrews, 1992). Typically forming a caecal outgrowth of the rectum, the present study revealed that the anal gland of *Panarona clavatula* communicates along its length to the rectum – a previously undescribed configuration. In *Urosalpinx cinerea* and *Conus jaspideus*, the gland opens via a discrete aperture to the intestine near the anus; in *Prunum apicinum*, the anal gland opens directly to the pallial cavity. The gland is lacking in *Ilyanassa obsoletus*. So-called rectal glands are also known in several sorbeoconchan groups; these are considered independently derived (Ponder & Lindberg, 1997).

RENO-PERICARDIAL SYSTEM

49. Renal lamellae

(0) Meronephridial [*Nev*, *Cyp*, *Pan*, *Pru*] (1) Pycnonephridial [*Con*, *Ily*, *Uro*] (2) Undifferentiated [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nit*].

Most caenogastropods (e.g. *Petaloconchus varians*, Fig. 22C) possess a kidney comprised of excretory tissue with a uniform and characteristic vacuolated appearance. However, a number of taxa possess two distinct lobes of excretory tissue that are microscopically and macroscopically distinct, including *Neverita duplicata* (Fig. 23A), *Cypraea robertsi* (Fig. 23B, al, pl), and all the neogastropods (Fig. 23C–E). The traditional bipartite classification of differentiated kidney types (meronephridial vs. pycnonephridial) has been retained here despite the well-justified criticism that even meronephridial kidneys may have lamellae that interdigitate to a small degree (Ponder, 1973). Although this classification has been applied traditionally only to neogastropod taxa, *Neverita duplicata* and *Cypraea robertsi* are here coded as meronephridial to test the hypothesis that differentiated kidney lobes are homologous. Heretofore, homology of the

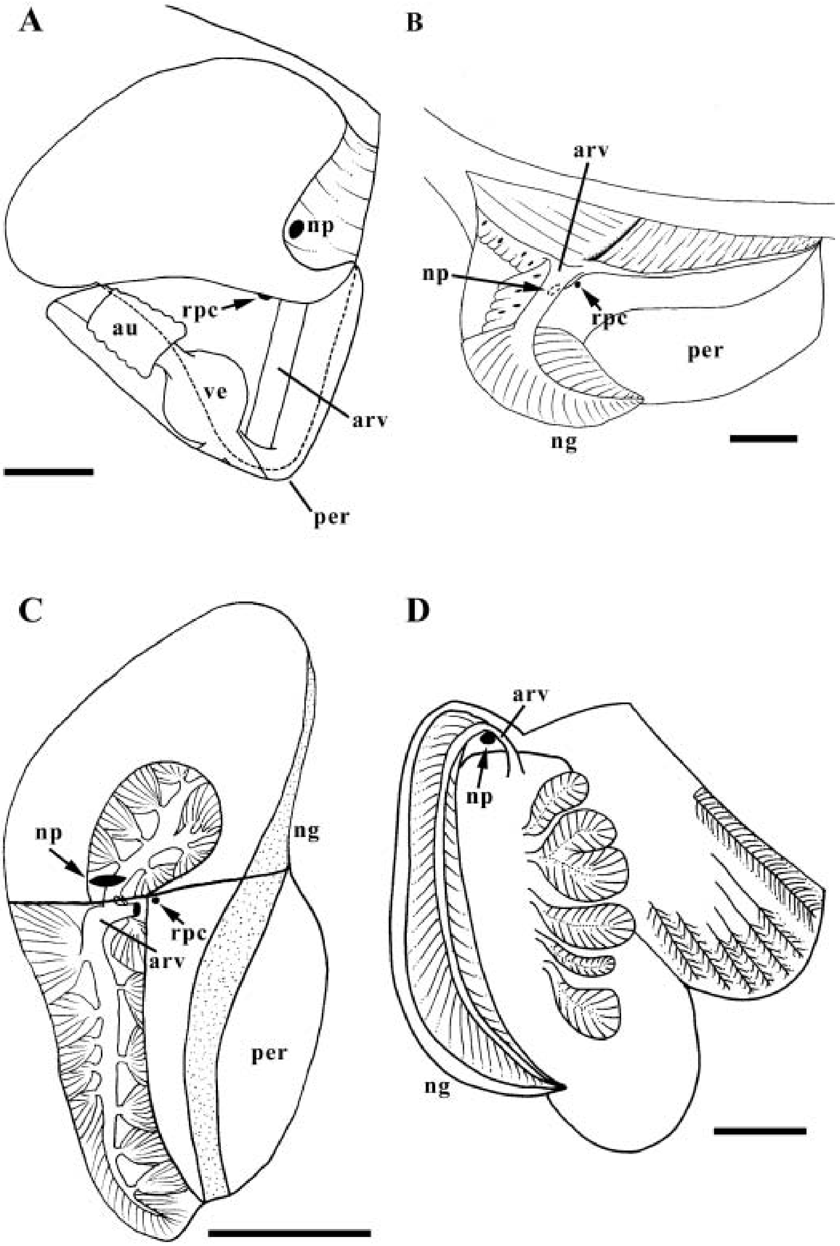

Figure 22. Kidney morphology; basal caenogastropods with undifferentiated lamellae. (A) *Neocyclotus dysoni ambiguum*, lateral view. Dotted line indicates removed lateral lobe overhanging pericardium. Scale bar = 1 mm. (B) *Bithynia tentaculata*, dorsal view. Scale bar = .5 mm. (C) *Petaloconchus varians*, ventral view. Horizontal line indicates base of mantle cavity. Excretory tubules within pallial portion revealed by ventral incision. Scale bar = 0.5 mm. (D) *Strombus mutabilis*. Dorsal view. Scale bar = 1 mm. Abbreviations: arv, afferent renal vessel; au, auricle; ng, nephridial gland; np, nephropore; per, pericardium; rpc, reno-pericardial canal; ve, ventricle.

lobes in naticids and cypraeids to those of the Neogastropoda has not been addressed. However, Fretter & Graham (1962) noted histological similarities between the lobes of *Natica* and those of neogastropods.

In *Macleaniella moskalevi*, the kidney is a simple sac with a single layer of uniform excretory tissue lining the lumen; lamellae are not developed (Strong & Harasewych, 1999). *Theodoxus fluviatilis* has a two-tiered kidney, with a mass of uniform excretory lamellae above and a voluminous 'bladder' below.

50. Dorsal afferent renal vessel

(0) Supplies single differentiated lobe [*Pru*, *Con*, *Ily*, *Uro*] (1) Supplies both differentiated lobes [*Nev*, *Cyp*,

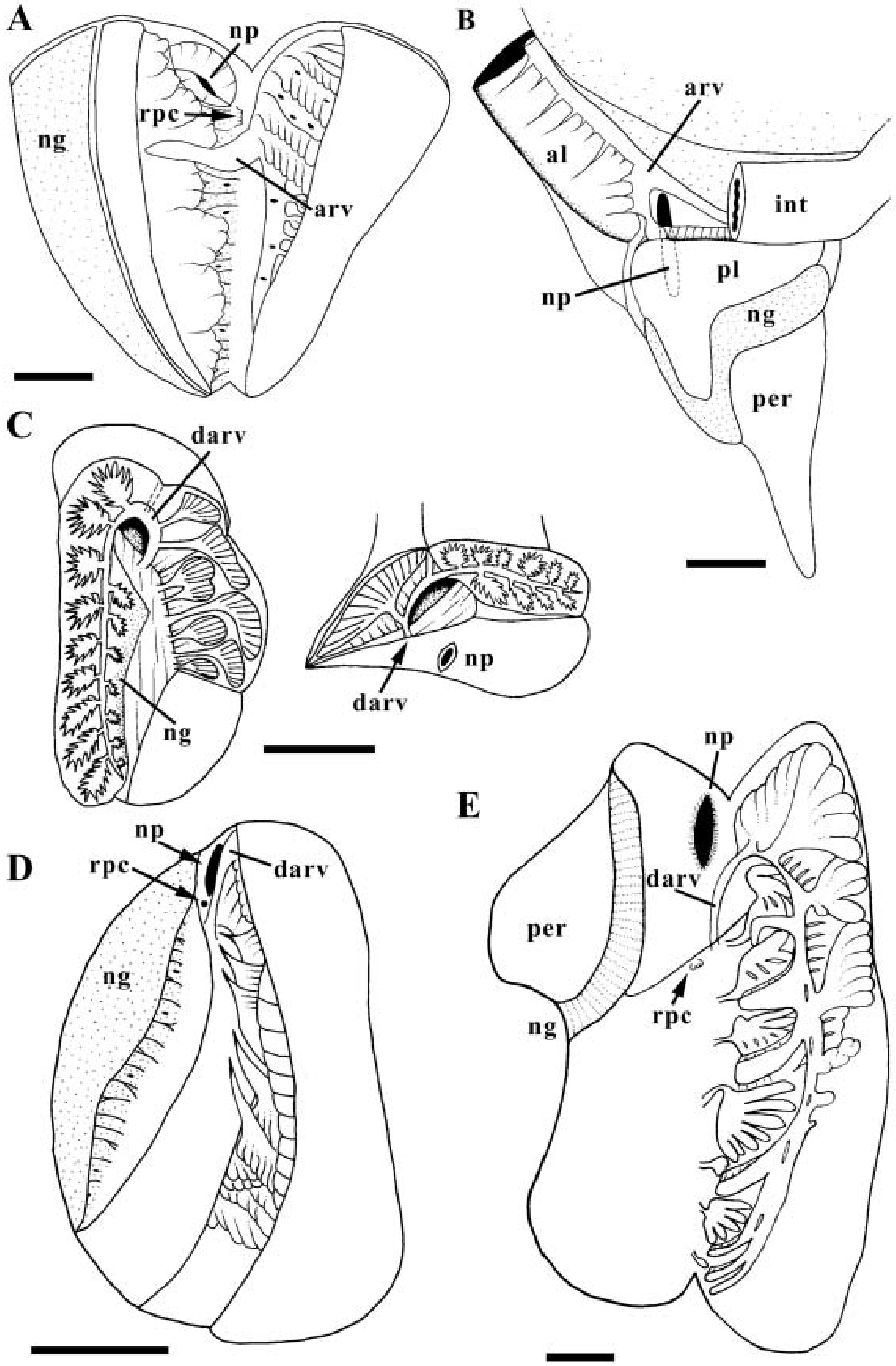

Figure 23. Kidney morphology; derived caenogastropods with two differentiated lobes of lamellae. (A) *Neverita duplicata*, dorsal view. Kidney opened between lobes of differentiated lamellae. (B) *Cypraea robertsi*, dorsal view. Intestine removed to reveal internal details. (C) *Panarona clavatula*, dorsal view, posterior chamber on left, anterior chamber on right. Kidney roof opened between lobes of primary and secondary lamellae. Note meronephridial condition (no interdigitation of lamellae) and that dorsal branch of afferent renal vessel supplies both primary and secondary tubules. (D) *Prunum apicinum*, dorsal view. Note small region of secondary tubules within kidney roof supplied by dorsal branch of afferent renal vessel. (E) *Ilyanassa obsoletus*, dorsal view. Note pycnonephridial condition (interdigitation of lamellae). Scale bar = 1 mm. Abbreviations: al, anterior kidney lobe; arv, afferent renal vessel; au, auricle; darv, dorsal branch of afferent renal vessel; int, intestine; ng, nephridial gland; np, nephropore; per, pericardium; pl, posterior kidney lobe; rpc, reno-pericardial canal; ve, ventricle.

Pan] (2) Supplies undifferentiated tissue [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nit*].

The afferent renal vessel (ARV) is the main conduit of blood into the kidney from the ventral collecting sinus (Fretter & Graham, 1962). In taxa with undifferentiated kidney tissue, the vessel continues dorsally from the cephalopedal sinus, emerges from the kidney floor near the nephropore, and supplies the lamellae that spread across the kidney roof and walls (Fretter & Graham, 1962). In taxa with two differentiated lobes of lamellae, this vessel divides into two to many branches that supply the lobes. In *Neverita duplicata* (Fig. 23A), the ARV splits into an anterior branch, supplying the right lobe, and a posterior branch, supplying both the right and left lobes. In *Cypraea robertsi* (Fig. 23B), the ARV travels anteriorly along the kidney floor, producing small branches that supply excretory tissue along the right wall. Upon reaching the anterior kidney wall, the ARV continues dorsally with several small branches supplying the anterior kidney lobe (al), and eventually entering the left lobe (pl).

In neogastropods, the afferent renal vessel divides into two main branches: the dorsal (DARV) and the ventral (VARV) branch. The ventral branch remains within the kidney floor, while the dorsal branch emerges near the nephropore and is similar in position to the ARV of taxa with undifferentiated kidney lobes. When Perrier (1889) first described renal circulation, he suggested that the two lobes of neogastropod kidneys have separate blood supplies. It has long been known that there is a single blood supply that divides (Fretter & Graham, 1962); the VARV supplies one lobe and the DARV supplies the second (e.g. *Prunum apicinum*, Fig. 23D; *Ilyanassa obsoletus*, Fig. 23E). However, it has been revealed here that in *Panarona clavatula* (Fig. 23C), the VARV supplies the right lobe while the DARV supplies both lobes, similar to *Neverita duplicata* and *Cypraea robertsi*.

51. Nephridial gland
(0) Absent [*Mac*, *The*, *Neo*, *Mar*] (1) Present [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

The nephridial gland is a mass of connective tissue and muscle fibres between the kidney and pericardium, lined with ciliated cells and penetrated by haemocoelic spaces (Fretter & Graham, 1962). Blind invaginations of the gland surface bring blood, on one side, and urine, on the other, into close contact. Blood flows into the haemocoelic sinuses of the gland from the renal lamellae, is collected into the efferent nephridial vein, and subsequently flows to the auricle of the heart (Fretter & Graham, 1962).

Nephridial gland histology is remarkably uniform across the caenogastropods, with one notable exception. In *Petaloconchus varians* (Fig. 22C), the gland (ng) is comprised of spongy, connective tissue, calling into question its excretory function. However, it is similar in position (a narrow strip along the kidney roof adjacent to the pericardium) and circulation (blood flows to the auricle), suggesting that it is indeed homologous.

The development of the gland varies. In most taxa, it occurs as a thickening in the common reno-pericardial wall that extends to some degree into the kidney roof. In *Neverita duplicata*, the gland is hypertrophied and exceeds the size of the individual kidney lobes. In *Bithynia tentaculata* and *Strombus mutabilis*, it occurs in the kidney roof and, in the former, is developed predominantly anterior to the pericardium.

Ponder & Lindberg (1997) cite the absence of a nephridial gland in cerithioideans. However, *Lampanella minima* possesses a small gland lining the common reno-pericardial wall evident only in histological section; sections confirmed its connection to the auricle. The presence of the gland in other cerithioideans is implied by the depiction of a strip of tissue alongside the pericardium in some reports (Houbrick, 1974, 1991a).

52. Nephridial gland blood supply
(0) Receives blood from afferent renal vessel [*Str*, *Bit*] (1) Receives blood from renal lamellae [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Cre*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

Typically, blood flows to the nephridial gland via the kidney lamellae (Fretter & Graham, 1962). However, in some caenogastropods, the gland receives blood directly from the ARV via a distinct branch. The presence of this branch has been noted in several descriptions (e.g. *Strombus gigas*; Little, 1965), but has not been placed in a comparative context. In *Bithynia tentaculata* (Fig. 22B) and *S. mutabilis* (Fig. 22D), a large branch of the ARV enters the nephridial gland (ng) anteriorly, signifying that a comparatively substantial volume of blood enters the nephridial gland and escapes oxygenation before returning to the pericardium; the implications of this circulation pattern are not clear.

Blood circulation patterns in architaenioglossans are similar to that of sorbeoconchans, despite absence of a nephridial gland in the former, with a portion of the blood flowing directly from the kidney to the auricle. In *Theodoxus fluviatilis*, two blood vessels direct blood dorsally away from the cephalopedal sinus: the afferent branchial membrane and the afferent renal vessel. Thus, approximately half the volume of blood that returns to the heart via the ctenidium, escapes the excretory action of the kidney. Detailed patterns of circulation were insufficiently preserved in *Macleaniella moskalevi*.

NERVOUS SYSTEM AND SENSORY STRUCTURES

53. Nerve ring position relative to buccal mass

(0) Overlying buccal cavity [*The*, *Neo*, *Mar*] (1) Just behind buccal cavity [*Mac*, *Lam*, *Pet*, *Str*, *Bit*, *Lit*, *Nev*, *Cyp*, *Con*] (2) Far posterior to buccal cavity [*Cre*, *Pan*, *Pru*, *Ily*, *Uro*] (3) Anterior to buccal cavity [*Nit*].

Position of the circum-oesophageal nerve ring varies with respect to the buccal mass in resting position. In *Theodoxus fluviatilis* and architaenioglossans (e.g. *Neocyclotus dysoni ambiguum*, Fig. 6A), the nerve ring (nr) lies anteriorly such that the buccal connectives pass posteriorly from the cerebral ganglia to the buccal ganglia (bg) at the base of the buccal mass. *Macleaniella moskalevi* possesses a broad nerve ring with lateral cerebral ganglia, rendering comparison difficult. However, the buccal connectives pass anteriorly to the buccal ganglia (Strong & Harasewych, 1999). Among most basal sorbeoconchans (e.g. *Lampanella minima*, Fig. 6B), including those with an acrembolic proboscis (e.g. *Cypraea robertsi*, Fig. 6C), the nerve ring (nr) sits just behind the buccal mass. One exception is *Nitidiscala tinctum* (Fig. 7C) wherein the nerve ring (nr) lies far anterior to the buccal mass (in resting position) as a consequence of the extreme elongation of the oral tube (= proboscis sheath, ps). *Crepidula plana* (Fig. 6E) is unique with a posterior nerve ring (nr) lying near the base of the cephalic haemocoel.

Within the Neogastropoda, the nerve ring is far behind the buccal mass, the latter lying anteriorly (*Prunum apicinum*, Fig. 7D; *Ilyanassa obsoletus*, Fig. 7B; *Urosalpinx cinerea*) or posteriorly (*Panarona clavatula*, Fig. 7A) within the pleurembolic proboscis. The only exception is *Conus jaspideus* (Fig. 7E), wherein the nerve ring (nr) lies shortly behind a highly modified buccal mass at the base of the intraembolic proboscis (ps).

54. Nerve ring

(0) Hypoathroid [*Mac*, *The*, *Neo*, *Mar*] (1) Epiathroid [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

Placement of the pleural ganglia relative to the pedal ganglia has figured prominently in the systematics of the Gastropoda (Spengel, 1881; Golikov & Starobogatov, 1975; Haszprunar, 1985c, 1988a,b). Within caenogastropods, there are several basic configurations, including hypoathroid (*Neocyclotus dysoni ambiguum*, Fig. 24A; *Marisa cornuarietis*), and epiathroid (sorbeoconchans, Fig. 24B–G). *Macleaniella moskalevi* is unique with a nerve ring that is weakly dystenoid (Strong & Harasewych, 1999). Although informative within the Cocculinidae (Strong, Harasewych & Haszprunar, submitted), this species is coded as hypoathroid here because separation between the right pedal and pleural ganglia is only slight.

55. Pedal commissures and cross connections

(0) One [*Mac*, *The*, *Lam*, *Pet*, *Str*, *Cre*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Two [*Mar*, *Bit*, *Lit*] (2) Three or more [*Neo*, *Cyp*].

The presence of pedal cords with numerous cross connections is plesiomorphic within the Gastropoda (Fretter & Graham, 1962), with the reduction to a single commissure uniting the Sorbeoconcha (Ponder & Lindberg, 1997). Among caenogastropods, numerous cross connections are present in cyclophoroideans and cypraeoideans (Fig. 24D, pc; e.g. Bouvier, 1887). Many littorinoideans and rissooideans possess a metapodial commissure (Fretter & Graham, 1962; Hershler & Davis, 1980) which has been considered by some (e.g. Simroth, 1896–1907; Marcus & Marcus, 1963) to be a remnant of the pedal cords. However, the presence or absence of this commissure has been difficult to confirm in some species (e.g. *Littorina littorea*, *Bithynia tentaculata*; Bouvier, 1887; Simroth, 1896–1907; Fretter & Graham, 1962).

56. Visceral ganglia

(0) Single [*Mac*, *Mar*, *Lam*, *Pet*, *Bit*, *Nit*] (1) Paired [*The*, *Neo*, *Str*, *Cre*, *Lit*, *Nev*, *Pan*, *Pru*, *Ily*, *Uro*] (2) Triple [*Con*] (3) Four or more [*Cyp*].

The visceral ganglia (ganglion) are typically located below the pericardium, near the junction of the cephalopedal sinus and the afferent renal vessel (Fretter & Graham, 1962). The number of visceral ganglia, fairly conservative at the familial level, varies from one to four or more. The single ganglion of *Macleaniella moskalevi* lies just below the gonoduct on the right side of the body (Strong & Harasewych, 1999). Within the ingroup, the single ganglion (vg) of *Marisa cornuarietis*, *Lampanella minima* (Fig. 6B), *Petaloconchus varians*, *Bithynia tentaculata* (Fig. 6D) and *Nitidiscala tinctum* (Fig. 7C) lies on or adjacent to the posterior oesophagus (e). In taxa with two ganglia, they straddle the posterior oesophagus, connected by a single or rarely a double (*Neocyclotus dysoni ambiguum*, Fig. 6A) commissure. *Conus jaspideus* (Fig. 7E) possesses three ganglia, with two lying on either side of the posterior oesophagus and the third lying on the right side of the cephalic haemocoel; nerves sporadically branch from the visceral loop, but are not associated with ganglia. In *Cypraea robertsi* (Fig. 6C), two

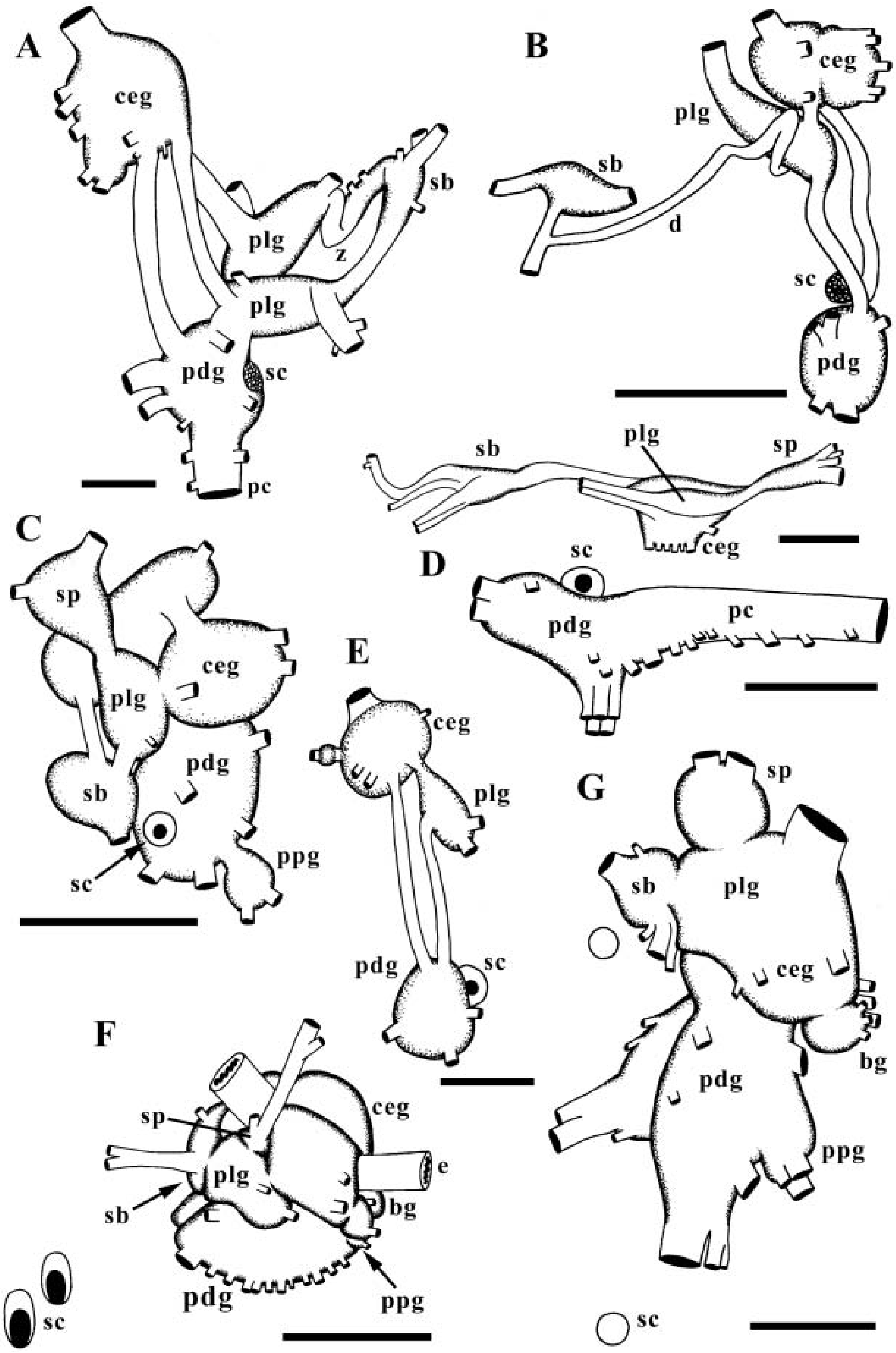

Figure 24. Circum-oesophageal nerve ring morphology. (A) *Neocyclotus dysoni ambiguum*. Scale bar = 0.5 mm. (B) *Lampanella minima*. Scale bar = 0.5 mm. (C) *Crepidula plana*. Scale bar = 0.5 mm. (D) *Cypraea robertsi*. Upper diagram depicts cerebral, pleural, supra-esophageal, and sub-oesophageal ganglia; lower diagram depicts pedal ganglia and pedal cords. Scale bar = 1 mm. (E) *Nitidiscala tinctum*. Scale bar = 0.25 mm. (F) *Prunum apicinum*. Scale bar = 0.5 mm. (G) *Ilyanassa obsoletus*. Scale bar = 0.5 mm. Abbreviations: bg, buccal ganglion; ceg, cerebral ganglion; d, dialyneury; e, oesophagus; pc, pedal cord; pdg, pedal ganglion; plg, pleural ganglion; ppg, propodial ganglion; sb, sub-oesophageal ganglion; sc, statocone; sp, supra-oesophageal ganglion; z, zygoneury.

small ganglia straddling the posterior oesophagus innervate the immediate viscera including the pericardium. A third large ganglion on the right side of the cephalic haemocoel innervates the kidney and the gonoduct. Two smaller ganglia yielding one to two nerves are present along the left side of the head. Several additional swellings were apparent in histological section but did not produce nerves. Thus, the exact number of ganglia is difficult to specify in this species and has been coded as four or more.

57. Tentacular nerve

(0) Single [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Nev*, *Nit*, *Uro*] (1) Bifid [*Pet*, *Str*, *Cre*, *Lit*, *Ily*] (2) Trifid [*Bit*, *Con*] (3) Quadrifed [*Pan*] (4) Nerve plexus [*Cyp*, *Pru*].

This character describes the branching pattern of the tentacle nerve trunk, and not the pattern of branching of fine nerves from the trunk which varies considerably even within species (pers. obs.). The criteria used to specify the number of nerve trunks were (a) the tentacular nerve must branch at the level of the eye, and (b) the branches must persist the length of the tentacle. It must be noted that *Cypraea robertsi* (Fig. 6C) and *Prunum apicinum* (Fig. 7D) have been coded with the same state, despite differences in the exact formation of the nerve plexus, which forms by simultaneous branching in the former, and progressive bifurcation in the latter. This distinction will only become important in analyses with denser taxonomic sampling and/or at lower hierarchical levels

In a phylogenetic context, a bifurcate tentacular nerve has been thought to be typical of the Apogastropoda (Fig. 27; Haszprunar, 1985c, 1988a,b; Salvini-Plawen & Haszprunar, 1987; Salvini-Plawen, 1988; Ponder & Lindberg, 1997). The commonly cited exception is the single dominant nerve in architaenioglossans and some cerithioideans (Bouvier, 1887; Berthold, 1990; Ponder & Lindberg, 1997; present study). However, this analysis revealed an unappreciated diversity of branching patterns including trifid (e.g. *Bithynia tentaculata*, Fig. 6D, tn), quadrifed (e.g. *Panarona clavatula*, Fig. 6A, tn) and multifed patterns (e.g. *Cypraea robertsi*, Fig. 6C; *Prunum apicinum*, Fig. 7D, tn) in addition to the commonly recognized single (e.g. *Neocyclotus dysoni ambiguum*, Fig. 6A, tn) and bifid patterns (e.g. Crepidula, Fig. 6E, tn).

58. Right zygo-, dialyneury

(0) No secondary connections formed [*Mac*, *Lit*, *Nev*, *Nit*] (1) Secondary connections formed [*The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*].

Many gastropods have brought the pleural and oesophageal ganglia into more (zygoneury) or less (dialyneury) direct communication, presumably facilitating neural control of the pallial organs (Fretter & Graham, 1962). The only taxon to lack secondary connections between the left pleural and supra-oesophageal ganglia was *Macleaniella moskalevi* (Strong & Harasewych, 1999); thus, this character was autapomorphic and not included. A number of taxa lack secondary connections between the right pleural and sub-oesophageal ganglia (e.g. *Nitidiscala tinctum*, Fig. 7C). The presence or absence of this feature in *Cypraea robertsi* could not be confirmed.

59. Siphonal ganglion

(0) Absent [*Mac*, *The*, *Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*] (1) Present [*Pan*, *Pru*, *Con*, *Ily*, *Uro*].

The position of secondary connections between the left pleural and supra-oesophageal ganglia varies markedly among most non-neogastropod sorbeoconchans. Within the Neogastropoda, the position of dialyneury is remarkably consistent, with a ganglion present at the site (e.g. Bouvier, 1887; see Fig. 7). This is referred to as the siphonal ganglion (sig) because one to two nerves from this ganglion innervate that part of the pallial margin modified into the inhalant siphon.

60. Siphonal ganglion development

(0) Slight enlargement with few glial cells [*Pan*, *Con*] (1) Large, well-developed ganglion surrounded by glial cells [*Pru*, *Ily*, *Uro*].

Development of the siphonal ganglion varies considerably among neogastropods. In some, the ganglion (sig) is small, supported by few glial cells (e.g. *Panarona clavatula*, Fig. 7A; *Conus jaspideus*, Fig. 7E). Others possess large, well-developed siphonal ganglia, completely surrounded by glial cells (e.g. *Prunum apicinum*, Fig. 7D; *Ilyanassa obsoletus*, Fig. 7B).

61. Statocysts

(0) Statolith [*The*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Statoconia [*Neo*, *Mar*, *Lam*].

Statocysts contain multiple statoconia (e.g. *Neocyclotus dysoni ambiguum*, Fig. 24A; *Lampanella minima*, Fig. 24B) or a single statolith (Fig. 24C–G). Although polymorphic within the species, *Macleaniella moskalevi* is unique among cocculinids in possessing several small statoconia (Strong & Harasewych, 1999). Due to variability at lower taxonomic levels, the phylogenetic utility of this feature at higher levels has been placed in doubt (see Ponder & Lindberg, 1997).

62. Position of statocysts
(0) Lateral [*Neo*, *Mar*, *Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Cyp*, *Nit*] (1) Ventral [*Nev*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (2) Medially [*Mac*, *The*].

There is considerable variability in the position of statocysts relative to the pedal ganglia. In outgroups, statocysts occur medially, along the inner edge of the ganglia; they lie just behind the commissure in *Theodoxus fluviatilis* (Lenssen, 1902) and just in front of the commissure in *Macleaniella moskalevi* (Strong & Harasewych, 1999). In the ingroup, statocysts commonly occur in a lateral position, postero-dorsally alongside or behind the commissure (e.g. *Crepidula plana*, Fig. 24C; *Cypraea robertsi*, Fig. 24D; *Nitidiscala tinctum*, Fig. 24E, sc). There may be some slight asymmetry between the right and left sides (Fretter & Graham, 1962). In *Neverita duplicata* and the neogastropods (e.g. *Prunum apicinum*, Fig. 24F; *Ilyanassa obsoletus*, Fig. 24G), the statocysts (sc) are more ventral in position and may be more anterior (e.g. *N. duplicata*) or more posterior (e.g. *P. apicinum*) relative to the ganglia. Ponder & Lindberg (1997) coded all caenogastropods as possessing statocysts dorsal/postero-dorsal in position.

63. Osphradial morphology
(0) Monopectinate [*Cre*] (1) Bipectinate [*Mar*, *Str*, *Nev*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (2) Triradiate [*Cyp*] (3) Ciliated ridge [*Mac*, *The*, *Lam*, *Pet*, *Bit*, *Lit*, *Nit*].

Scanning and transmission electron microscopic studies have revealed a number of osphradial characters relevant to higher order systematics of the Gastropoda (Haszprunar, 1985a, 1985b; Taylor & Miller, 1989). These features clearly differentiate architaenioglossans from sorbeoconchans (Ponder & Lindberg, 1997). Details of fine structure aside, gross morphology of the osphradium can be informative as well; for example, Ponder & Lindberg (1997) found a general increase in osphradium size within the Sorbeoconcha. The size and complexity of the osphradium has been noted to display a general correlation with feeding habit and food preference. However, several interesting exceptions occur, suggesting some independence between these variables (e.g. *Crepidula plana*, Fig. 6E, os; Taylor & Miller, 1989).

64. Ocular peduncle
(0) Absent [*Lam*, *Pet*, *Str*, *Cre*, *Bit*, *Lit*, *Nev*, *Cyp*, *Nit*, *Pan*, *Pru*, *Con*, *Ily*, *Uro*] (1) Present [*Mac*, *The*, *Neo*, *Mar*].

Eyes at the tips of a distinct peduncle at the base of the cephalic tentacle occur in *Theodoxus fluviatilis* and the architaenioglossans. *Macleaniella moskalevi* does not possess eyes *per se*, but the basitentacular gland, inferred to be a modified eye (Haszprunar, 1987, 1988c), occurs on a low, separate stalk adjacent to the cephalic tentacle.

RESULTS

Two minimum-length trees were obtained with length 188, CI = 0.53 and RI = 0.63; the strict consensus is shown in Figure 25. These differed only in the sister group relationship to *Ilyanassa* and *Urosalpinx*; one topology supported *Prunum* while the other supported *Conus* as the sister group. Two rounds of successive weighting in HENNIG86 (Farris, 1988) produced a single topology with length 580, CI = 0.76 and RI = 0.84, supporting *Prunum* as the sister group to *Ilyanassa* and *Urosalpinx*.

This analysis supports monophyly of the Caenogastropoda, with three main clades recovered within the ingroup: (1) *Neocyclotus* and *Marisa*, (2) *Lampanella*, *Petaloconchus*, *Strombus*, *Crepidula*, *Bithynia*, and (3) *Littorina* as the sister taxon to a group including *Neverita*, *Cypraea*, *Nitidiscala* and the neogastropods

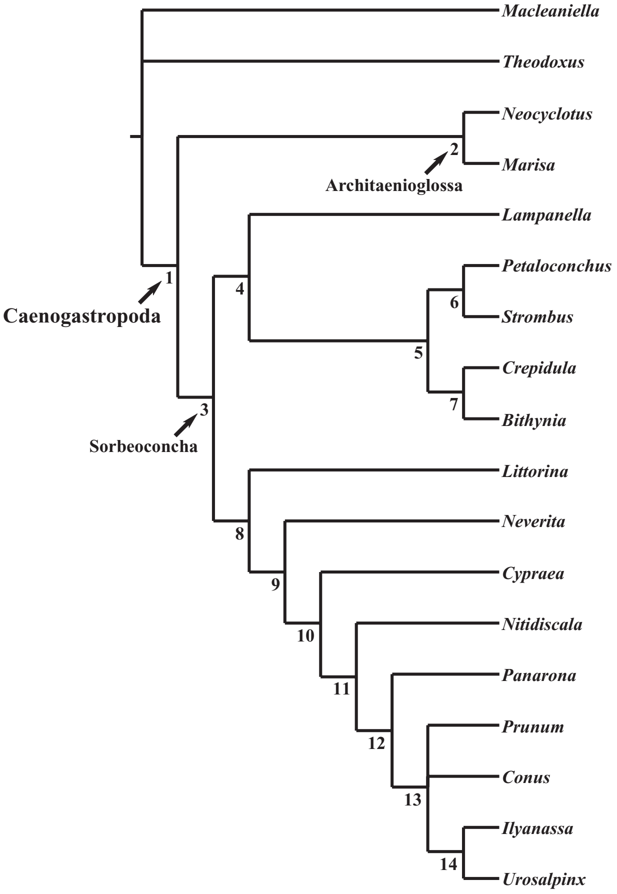

Figure 25. Strict consensus of two MPT's, length = 188, CI = 0.53 and RI = 0.63. Numbers at the nodes refer to discussion in the text.

Panarona, *Prunum*, *Conus*, *Ilyanassa*, *Urosalpinx*. Thus, this analysis supports a monophyletic Architaenioglossa, Sorbeoconcha and Neogastropoda (Fig. 25). *Nitidiscala* was recovered as the sister group to the neogastropods.

Five unambiguous synapomorphies (Fig. 26) support the Caenogastropoda (Fig. 25, node 1), including: a taenioglossate radula (character 12: 1), the presence of a glandular subradular organ (14: 1) and a low mid-ventral fold within the anterior oesophagus that is not associated with a ventral glandular mass (22: 1), a ventral gastric shield (33: 1), and statocysts that lie dorso-laterally along the pedal ganglia behind the pedal commissure (62: 0).

The Architaenioglossa (Fig. 25, node 2) is distinguished by eight synapomorphies (Fig. 26): a renal oviduct modified into a seminal receptacle (4: 1), a wholly bi-layered jaw (17: 2), absence of oesophageal glands (25: 0), presence of a glandular pad represented by a ciliated strip (35: 2), gastric pouches (39: 1), a digestive gland duct vestibule (40: 1), and pyloric caecae (46: 1), and presence of statocysts with numerous statoconia (61: 1).

Monophyly of the Sorbeoconcha (Fig. 25, node 3) is supported by 11 characters (Fig. 26), including: the presence of a pallial albumen gland (6: 0), a seminal vesicle derived from the proximal vas deferens (9: 1), a partially bi-layered jaw (17: 1), a septate oesophageal gland (26: 1), presence of a ciliated fold to the left of the oesophageal aperture within the midgut (30: 0), a distinct intestinal groove sorting area (36: 1), an intestine that completes a single loop (47: 2), a nephridial gland (51: 1), a nerve ring that lies just behind the buccal cavity (53: 1), an epiathroid nerve ring (54: 1), and absence of an ocular peduncle (64: 0).

Two large clades of sorbeoconchans were recovered (Fig. 25, nodes 4 and 8); both are only weakly supported by two forward homoplasies (Fig. 26). Similarly, the sister group relationship between *Nitidiscala tinctum* and the Neogastropoda (Fig. 25, node 11), is only weakly supported by the presence of accessory salivary glands (19: 1) and several secondary reductions or losses including absence of a ventral fold (21: 0) and buccal pouches (23: 0), and the presence of longitudinal folding within the style sac region (44: 1) (Fig. 26).

The Neogastropoda (Fig. 25, node 12) is highly distinct, united by 14 synapomorphies (Fig. 26): the presence of a ventral pedal gland (2: 1), an ingesting gland (7: 1), a bursa copulatrix (8: 1), a closed pallial vas deferens with a prostate that communicates with the mantle cavity via a small duct (10: 1), the presence of salivary glands that by-pass the nerve ring (18: 1), a pleurembolic proboscis (20: 2), a glandular pad that forms a longitudinal fold (34: 1), 35: 3), an anal gland (48: 1), a nerve ring that lies far posterior to the buccal mass (53: 2), a zygosis between the right pleural and sub-oesophageal ganglia (58: 1), a siphonal ganglion (59: 1), statocysts that are ventral in position (62: 1), and a prominent bipectinate osphradium (63: 1).

The cancellariid *Panarona clavatula* forms the sister group to the remaining neogastropods. The latter (Fig. 25, node 13) are united by the shift in dorsal afferent renal vessel circulation from supplying two differentiated kidney lobes to supplying a single lobe (50: 0) (Fig. 26).

DISCUSSION

The broad branching patterns recovered here, comprising a monophyletic Architaenioglossa, Sorbeoconcha and Neogastropoda, are congruent with current estimates of caenogastropod phylogeny based on morphological data (Fig. 27; Ponder & Lindberg, 1997). One significant difference is the division of sorbeoconchans into two large clades. Previous morphological and molecular studies have favoured a predominantly pectinate branching scheme within the Sorbeoconcha (Fig. 27; Haszprunar, 1988a,b; Ponder & Lindberg, 1997; Rosenberg *et al*., 1997; Harasewych *et al*., 1998; Winnepenninckx *et al*., 1998).

A second controversial aspect of this scheme is the relationship among neogastropod taxa, with the placement of the Cancellariidae (*Panarona clavatula*) as the sister group to the remaining neogastropods, and the Buccinidae (*Ilyanassa obsoletus*) and Muricidae (*Urosalpinx cinerea*) in a more distal position. Recent cladistic studies have favoured a more basal position for rachiglossate taxa (Ponder & Lindberg, 1997). Other studies have generated ‘intuitive’ hypotheses (Taylor & Morris, 1988; Taylor *et al*., 1993; Kantor, 1996), with cladistic reanalysis producing largely unresolved topologies (Kantor, 1996; Rosenberg, 1998). With this caveat, it is interesting to note that Kantor (1996), building on the results of Taylor & Morris (1988), tentatively hypothesized a basal position for the Cancellarioidei, with the separation of the gland of Leiblein uniting the remainder of the group. In addition, Kantor (1996) placed rachiglossan taxa distally, with the nassariids forming one of the most derived families of neogastropods, a hypothesis congruent with the present study. Kantor’s (1996) hypothesis differs from the current results in placing muricids basal to marginellids.

Another disputed aspect of this scheme concerns the monophyly and placement of the Architaenioglossa. This issue has been subject to differing interpretation in several recent morphological studies (Haszprunar, 1988a,b; Ponder & Lindberg, 1997), with no clear consensus emerging with molecular data (e.g. Harasewych *et al*., 1998). In the present analysis, several features have been revealed and/or clarified that bring

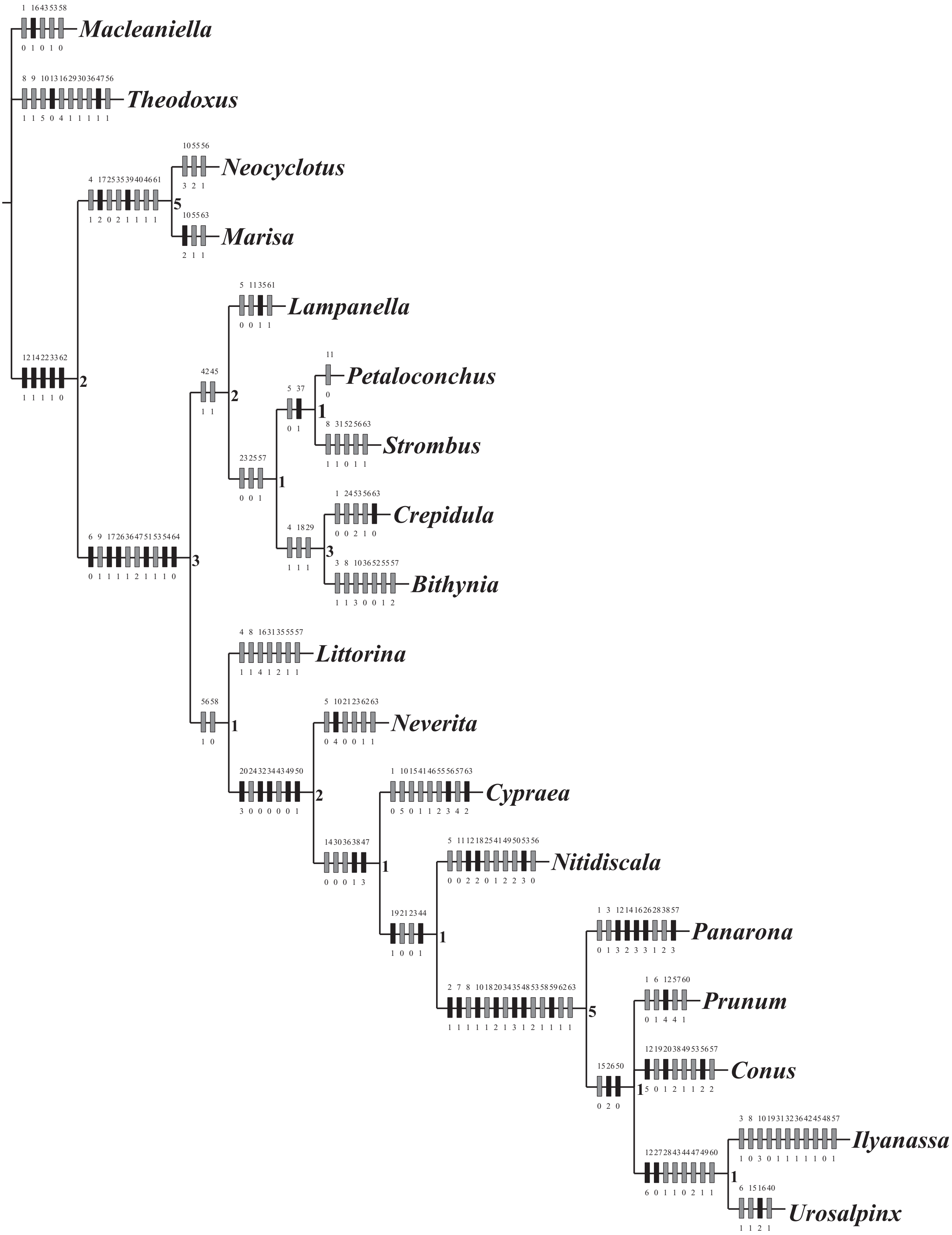

Figure 26. Strict consensus tree showing all character optimizations. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN). Numbers at the nodes indicate Bremer support.

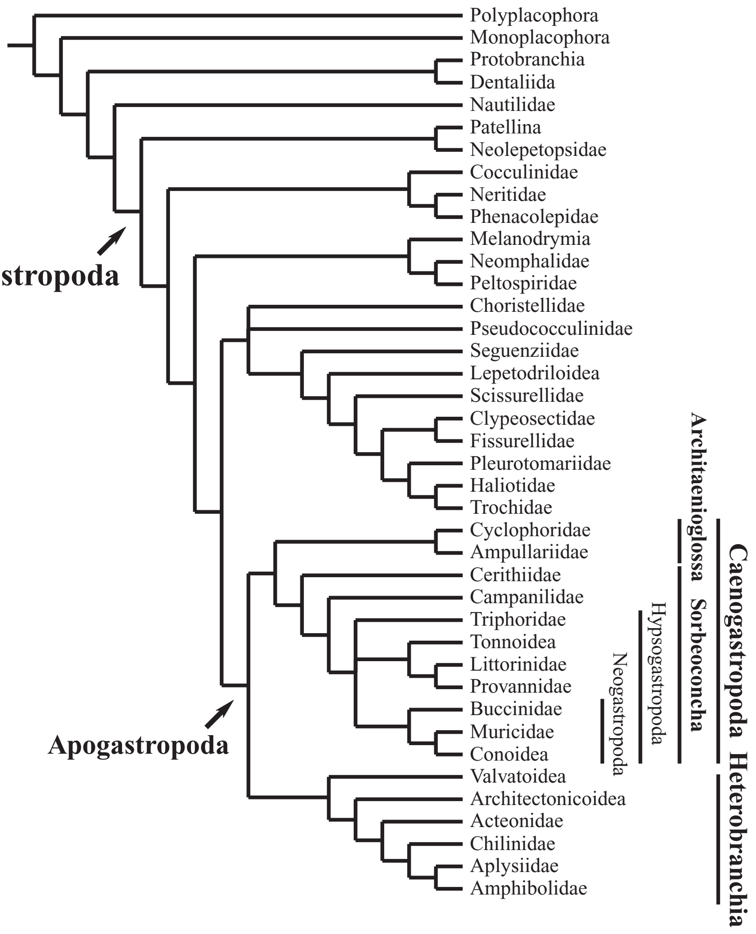

Figure 27. Phylogeny of the Gastropoda; adapted from Ponder & Lindberg (1997).

new evidence to the question of architaenioglossan monophyly and affinity. Features supporting placement of the Architaenioglossa as sister group to the Sorbeoconcha include the presence of a subradular organ, a low mid-ventral fold within the anterior oesophagus not associated with an underlying glandular mass, and a ventral gastric shield. Despite placement as sister group to the remaining caenogastropods, there can be no doubt concerning the considerable 'morphological gap' (Haszprunar, 1988b) separating architaenioglossans from sorbeoconchans, highlighted by the numerous synapomorphies uniting them as a clade (see Results above).

EVOLUTION OF THE REPRODUCTIVE SYSTEM

A number of features have been included in this analysis despite the common perception that they are 'highly variable' and 'potentially misleading' in phylogeny reconstruction. This is particularly true of features relating to reproductive biology. However, such features almost without exception optimized to terminal branches and did not support basal nodes (e.g. three independent derivations of the gonopericardial canal, Fig. 28, character 3; three independent losses of the penis, Fig. 28, character 11). Thus, these features had no influence, misleading or otherwise, on tree topology.

One homoplastic feature interpreted as homologous in the past is the condition of the oviduct (Fig. 28, character 4). A renal oviduct modified to form a seminal receptacle was supported as being independently derived in the architaenioglossans, in *Littorina littorea*, and in (*Crepidula plana*, *Bithynia tentaculata*). This character was found to be a synapomorphy of the Hypsogastropoda in the analysis of Ponder & Lindberg (1997). The change in interpretation is attributable in part to new data for *Neocyclotus dysoni ambiguum*, which provides an important synapomorphy for the Architaenioglossa.

In contrast, several reproductive characters optimized to basal nodes, suggesting fundamental shifts

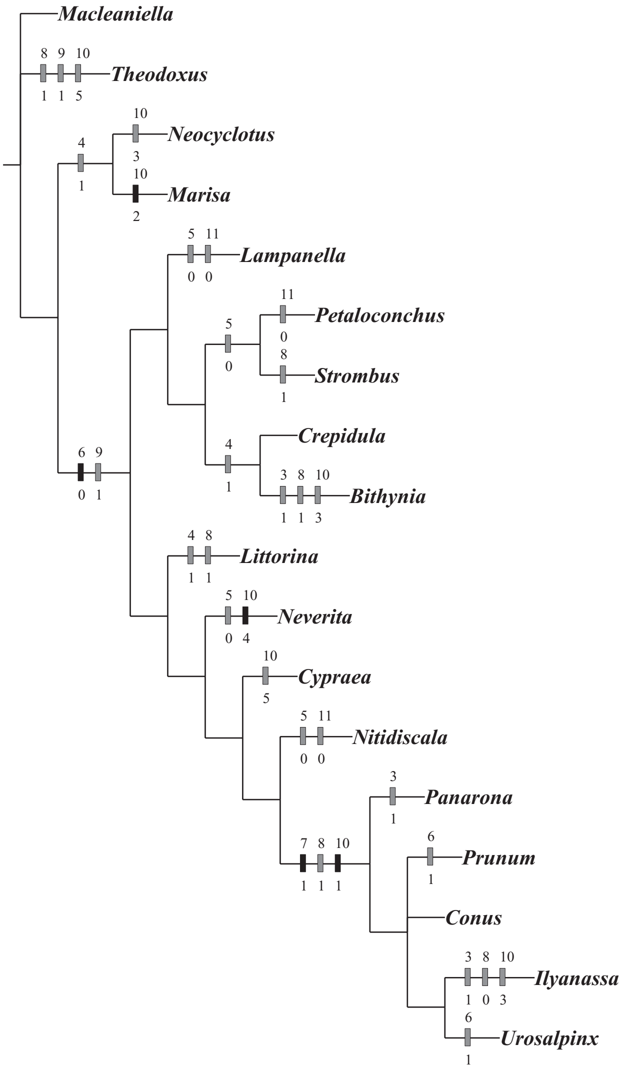

Figure 28. Evolution of the reproductive system. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN).

in reproductive biology. One example is the position of the glandular pallial oviduct (Fig. 28, character 6). In the outgroup *Theodoxus fluviatilis* (the question of homology of these glands aside) and the architaenioglossans, the posterior glandular oviduct invades the viscera. In contrast, all other basal caenogastropods possess a glandular oviduct that is completely pallial in position. Despite homoplasy within neogastropods (two independent derivations of a visceral albumen gland), optimization of this character near the base of the tree supports monophyly of the Sorbeoconcha and highlights the anatomical distinctiveness of architaenioglossans.

A vas deferens modified to form a seminal vesicle also forms a synapomorphy of the Sorbeoconcha (Fig. 28, character 9). Optimization at this node is ambiguous due to the interpretation that *Theodoxus fluviatilis* possesses a seminal vesicle. However, it is not clear if the structures in ingroup and outgroup taxa are homologous (see character 9, above).

EVOLUTION OF THE RENO-PERICARDIAL SYSTEM

Two non-neogastropod taxa with histologically and macroscopically distinct lobes of renal lamellae were included to test the hypothesis that this differentiation is homologous to that of neogastropods; *Neverita duplicata* and *Cypraea robertsi* were coded as meronephridial (Fig. 29, character 49), a term typically restricted to neogastropods. The analysis supports kidney differentiation as homologous, uniting *N. duplicata* and *C. robertsi* in a large clade with the neogastropods.

A new character to caenogastropod systematics is the blood supply to differentiated kidney lobes (Fig. 29, character 50). Historically, it was thought that blood supply to the lobes in the Neogastropoda is separate; one lobe supplied by the dorsal branch of the afferent renal vessel (DARV) and the other supplied by the ventral branch (VARV; Fretter & Graham, 1962). However, it is now clear that the DARV splits to supply both lobes in the cancellariid *Panarona clavatula*. Similarly, the DARV provides blood to both lobes in *Neverita duplicata* and *Cypraea robertsi*. This feature is important in supporting the basal placement of cancellariids within the neogastropods.

A second new character of reno-pericardial anatomy is the blood supply to the nephridial gland (Fig. 29, character 52). In *Bithynia tentaculata* and *Strombus mutabilis*, the afferent renal vessel splits to supply the nephridial gland directly. In all remaining sorbeoconchans, the nephridial gland receives blood indirectly via the renal lamellae. This direct branch to the nephridial gland is supported as a homoplasy. However, details of kidney circulation are known for few other caenogastropods and with improved sampling, this feature may prove to be an informative character for phylogenetic analysis.

Repeated invasion of the pallial cavity is one interesting aspect of reno-pericardial evolution. This is significant in the higher order systematics of the Gastropoda because a single, left, pallialy situated and supplied kidney is a synapomorphy of the Heterobranchia (Fig. 27; Haszprunar, 1985c, 1988a,b; Ponder & Lindberg, 1997). A number of taxa in this analysis have a partially pallial kidney – the diversity of reno-pericardial morphologies underscoring the homoplastic nature of this feature. For example, as in other cocculinids (Haszprunar, 1987, 1988c), *Macleaniella moskalevi* has a kidney that extends forward into the pallial roof, ventrally enclosing the rectum (Strong

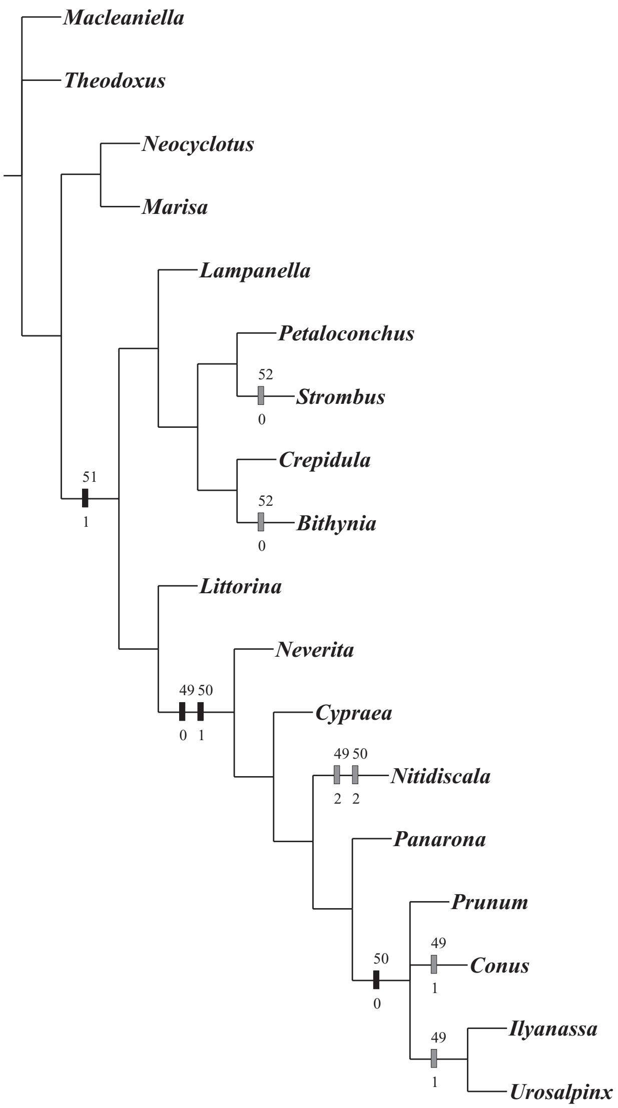

Figure 29. Evolution of the reno-pericardial system. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN).

& Harasewych, 1999). In some cocculinids, the kidney ventrally encloses the hypobranchial gland, forming the 'Manteldrüse' condition described by Thiele (1903).

Architaenioglossans display two markedly different kidney conditions. *Marisa cornuarietis* has an anterior kidney lobe (ureter; Demian & Yousif, 1973b) that swings into position within the pallial roof during torsion (Demian & Yousif, 1973b). This lobe bears the nephropore along its floor near the base of the mantle cavity and is histologically similar to the visceral portion of the kidney; blood supply and other landmarks (e.g. reno-pericardial canal) are similar in position to those of other caenogastropods. On the other hand, the reno-pericardial complex of *Neocyclotus dysoni ambiguum* and other cyclophorids is unusual in that it is almost entirely pallial (Fig. 22A); the positions of the afferent renal vessel, nephropore and reno-pericardial canal have shifted as a consequence of this forward migration. Typically, the afferent renal vessel enters the kidney floor near the reno-pericardial canal and nephropore, just behind the base of the mantle cavity. However, in cyclophorids, the nephropore (np) opens posteriorly to an extension of the mantle cavity behind the kidney (Andrews & Little, 1972). In addition, the reno-pericardial duct (rpc) and afferent renal vessel enter a kidney lobe overhanging the pericardium and are thus, dorsal in position, to the left of the nephropore. Consequently, the afferent renal vessel must travel dorsally from the cephalopedal sinus to the renal lamellae above, actually penetrating the pericardial cavity. This unique disposition of the reno-pericardial system will most likely prove informative in assessing monophyly of the Cyclophoroidea.

Two included sorbeoconchans, *Bithynia tentaculata* and *Cypraea robertsi*, also have partially pallial kidneys, both possessing a long, narrow anterior kidney chamber that ventrally encloses the rectum. However, these taxa differ in the development and histological differentiation of excretory tissue within the pallial extension. In *B. tentaculata*, the anterior kidney lobe is a narrow, laterally compressed chamber with only weakly developed excretory lamellae along its walls surrounding a large lumen. In contrast, the anterior lobe of *C. robertsi* is dorso-ventrally compressed and shifts in position from predominantly left of the rectum at the base of the pallial cavity, to predominantly right of the rectum near the mantle edge. In addition, the lobe is filled with a compact mass of excretory tubules that are distinct from those occupying the visceral portion of the kidney. The conditions in *Cypraea* are significant because they demonstrate that the phenomenon is not restricted to freshwater groups.

EVOLUTION OF THE NERVOUS SYSTEM

Conclusions regarding evolution of the nervous system generally agree with previous hypotheses (Haszprunar, 1985c, 1988a,b; Ponder & Lindberg, 1997). A hypoathroid condition is primitive within the caenogastropods, supporting the basal position of the architaenioglossans. Epiathroidy is a synapomorphy of the Sorbeoconcha (Fig. 30, character 54). One new insight into the evolution of the nerve ring is that the change from hypoathroidy to epiathroidy is accompanied by a shift in the position of the nerve ring; architaenioglossans possess a hypoathroid nerve ring that anteriorly overlies the buccal mass (e.g. *Neocyclotus dysoni ambiguum*, Figs 6A, 24A, nr), while Sorbeoconchans possess an epiathroid nerve ring that lies just behind

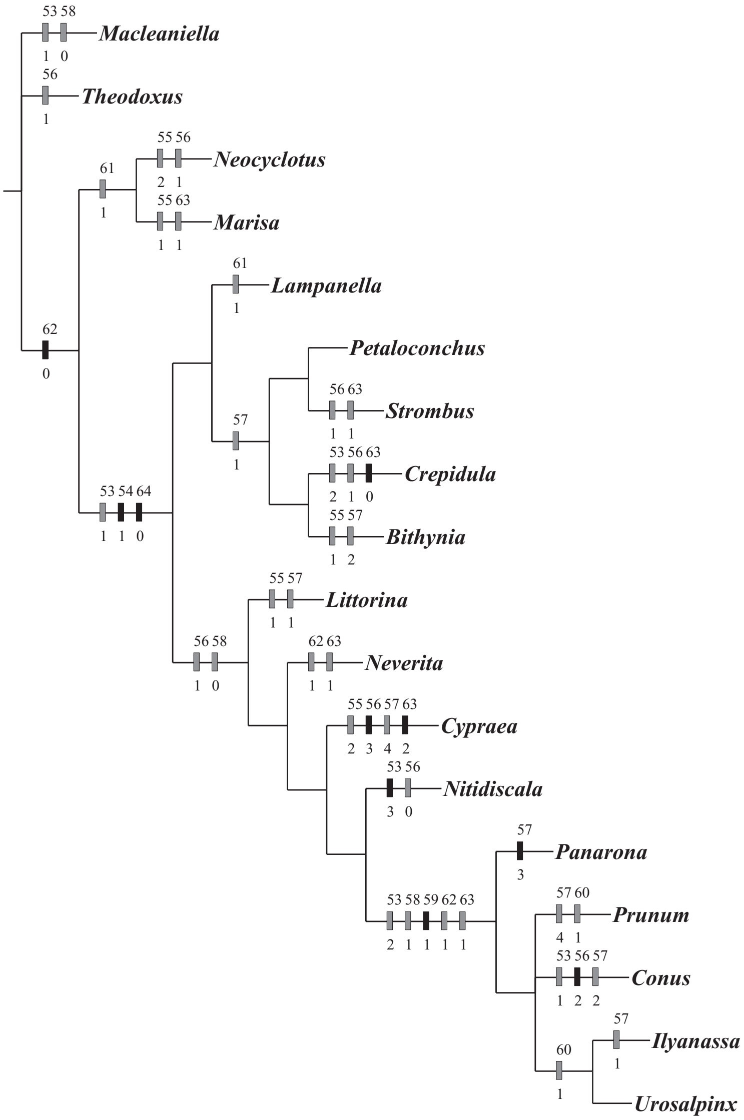

Figure 30. Evolution of the nervous system. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN).

the buccal mass (e.g. *Lampanella minima*, Figs 6B, 24B, nr; Fig. 30, character 53).

Several other nervous system features also optimize to basal nodes and appear to accompany major organizational shifts. For example, albeit of uncertain functional significance, the Caenogastropoda are united by the presence of statocysts that are dorsolateral relative to the pedal ganglia and the neogastropods by the presence of ventral statocysts. The presence of a siphonal ganglion supports monophyly of the Neogastropoda. However, this feature has a more obvious functional significance in predatory neogastropods, suggesting an increase in nervous co-ordination of the inhalant pallial margin. This undoubtedly reflects the increased emphasis on sensing of chemical cues by the osphradium, which lies within the inhalant current.

Outgroup choice in this analysis has had a significant impact on evaluating the evolution of pedal cords with numerous cross-connections (Fig. 30, character 55). Because both outgroups have a single pedal commissure, the numerous cross-connections (≥3) in *Neocyclotus dysoni ambiguum* and *Cypraea robertsi* were concluded to be homoplastic gains; the metapodial commissure in *Bithynia tentaculata* and *Littorina littorea* similarly are concluded to be homoplastic gains. However, with alternative outgroups, numerous cross-connections would be plesiomorphic for the Caenogastropoda with the sorbeoconchans supported by the presence of a single pedal commissure; the conditions in *C. robertsi* would remain a homoplastic gain. Thus, determination of the plesiomorphic condition awaits resolution of the sister group relationship to the Apogastropoda. Irrespective of outgroup choice, the condition in cypreaids is not concluded to represent retention of the plesiomorphic condition (e.g. Simroth, 1896–1907; Fretter & Graham, 1962).

This investigation revealed a diversity of tentacular nerve branching patterns. A bifurcate tentacular nerve has been considered typical of sorbeoconchans (Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1985c, 1988a,b; Ponder & Lindberg, 1997). However, optimization indicates repeated independent derivations of tentacle nerve branches from the plesiomorphic single nerve trunk (Fig. 30, character 57). The only exception is the presence of a bifid nerve uniting (*Petaloconchus*, *Strombus*) with (*Crepidula*, *Bithynia*) (Fig. 30, character 57). Thus, in contrast to the prevaling view, these results support the interpretation that a single tentacular nerve is plesiomorphic within caenogastropods, with numerous independent variations on this theme.

EVOLUTION OF THE GUT

Evolution of the foregut

The subradular organ has been cited as restricted to architaenioglossans, with loss of the feature uniting sorbeoconchans (Ponder & Lindberg, 1997). However, glandular elaborations of the subradular epithelium are indeed present in many sorbeoconchans; all are similar in position with a high prismatic epithelium and scattered goblet cells, providing sufficient evidence to hypothesize homology – a hypothesis that was not rejected in this analysis. A notable exception is the non-glandular pad supporting the nematoglossan radula of *Panarona clavatula*. Not surprisingly, optimization reveals that this feature has arisen independently in cancellariids (Fig. 31, character 14).

Ponder & Lindberg (1997) were first to formalize the significance of jaw composition (homogeneous vs. rods) in gastropod systematics, with jaws composed of simple rods forming a synapomorphy of all higher Orthogastropoda, excluding Neritopsina and Cocculinidae. Their analysis hinted at further significance of the feature in acknowledging the bi-layered jaw of *Marisa cornuarietis* (Lufty & Demian, 1967). The presence of bi-layered jaws in *Neocyclotus dysoni ambiguum* (present study), renders this a synapomorphy of the Architaenioglossa (Fig. 31, character 17). Moreover, the sorbeoconchan jaw is composed, not of simple rods, but of a homogeneous layer partially overlapping a layer of rods – a synapomorphy of the group.

The presence of accessory salivary glands has been considered a neogastropod synapomorphy, independently derived elsewhere (Ponder, 1974; Haszprunar, 1988a; Taylor & Morris, 1988; Ball *et al*., 1997; Ponder & Lindberg, 1997). In contrast, the present analysis did not reject the hypothesis that the accessory salivary glands of ptenoglossans and neogastropods are homologous (Andrews, 1991). In addition, despite some homoplasy, salivary gland ducts that by-pass the nerve ring remains an important character for distinguishing the Neogastropoda.

The anterior oesophagus of caenogastropods has been regarded as largely lacking the ventral folding characteristic of basal gastropods (Graham, 1939; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988a; Ponder & Lindberg, 1997). However, it is now clear that the buccal cavity and anterior-most oesophagus of many basal caenogastropods bear a mid-ventral fold (Fig. 31, character 21) and two ventro-lateral folds (Fig. 31, character 24) comparable to those of basal gastropods; these features are far more widely distributed within the group than previously acknowledged. The ventro-lateral folds, commonly associated with the inner margins of the buccal pouches, are retained in many caenogastropods, even in those lacking buccal pouches (Fig. 31, character 23). The mid-ventral fold is variable in shape but is distinctly present. In contrast to basal gastropods, the fold is not associated with an underlying glandular mass (Fig. 31, character 22) and is a synapomorphy of the Caenogastropoda.

Homology of the oesophageal glands has been subject to conflicting interpretation. Among the outgroups, oesophageal glands comprise paired, glandular outpocketings of the mid-oesophagus (Figs 8B, 11A), and are continuous with the buccal pouches of the anterior oesophagus. The glandular mass of tissue associated with the mid-ventral fold in the anterior oesophagus has been interpreted as being continuous with the glands of the oesophageal pouches (Salvini-Plawen & Haszprunar, 1987). As described above, the glands lining the posterior oesophageal pouches and those of the ventral mass are histologically distinct. Moreover, given the fact that some caenogastropods possess a mid-ventral fold in conjunction with an oesophageal gland but lack this ventral gland, this indicates that the latter are independent characters. Within the ingroup, the oesophageal gland comprises distinctive glandular septae and is a synapormorphy of the Sorbeoconcha. In contrast to some interpretations (e.g. Ponder & Lindberg, 1997), the voluminous mid-oesophagus of architaenioglossans is not considered to comprise an oesophageal gland, highlighting yet another unique aspect of this clade's organization.

Evolution of the midgut

Non-torsional asymmetries

One of the more intriguing aspects of the digestive system investigated in this analysis is the phenomenon of

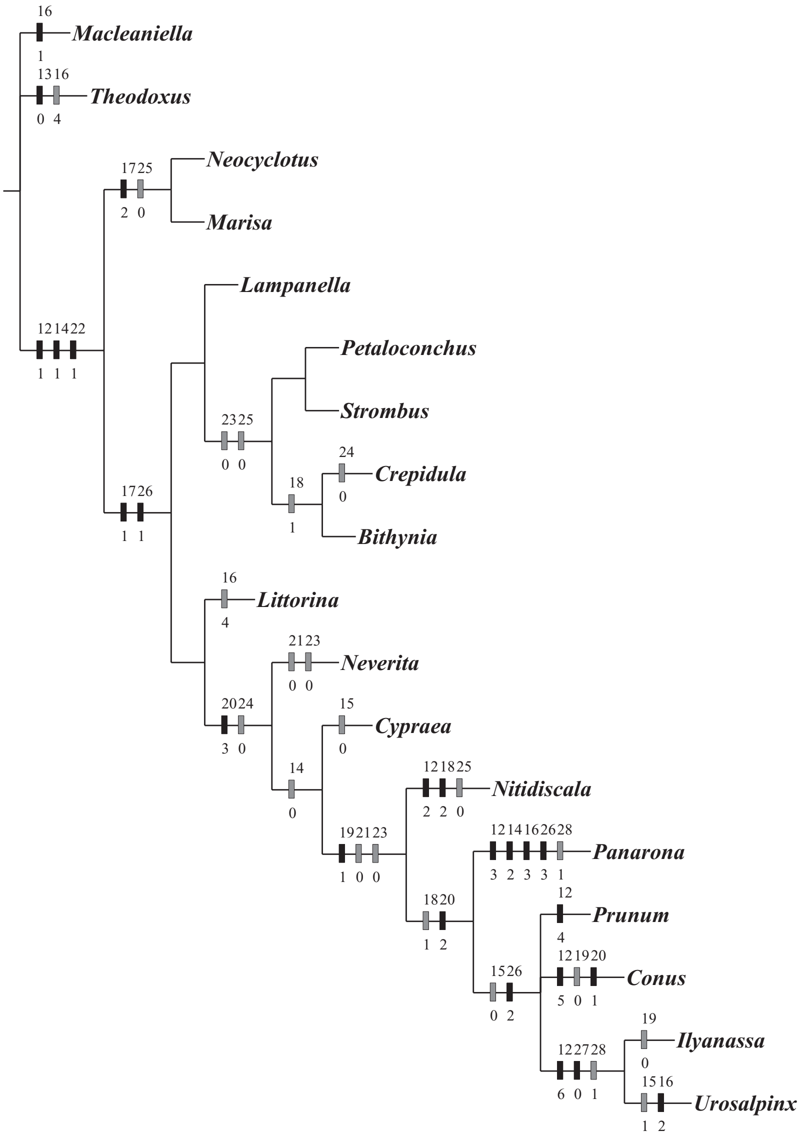

Figure 31. Evolution of the foregut. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN).

non-torsional displacement. This ontogenetic process results in the spatial reorganization of organs or organ systems within the viscera. The manifestations of this process on the digestive system are easily documented by examining the disposition of the midgut relative to other organs or simply the position of the gastric shield. Non-torsional asymmetries are best documented in *Neomphalus fretterae*, in which the asymmetry is apparent, not only in the digestive system, but in the nerves and pericardium as well (Fretter *et al.*, 1981).

In general, non-torsional asymmetries have been more commonly documented among limpet-like taxa. One example is the midgut rotation in the Calyptraeidae – the midgut of *Trochita* and *Calyptraea* has rotated approximately 90° in a horizontal plane relative to that of *Crepidula* (Kleinstüber, 1913). This is most evident in the disposition of the style sac, opening to the intestine posteriorly in the former and anteriorly (as in outgroup taxa) in the latter. Another example is the midgut rotation of the Cocculinoidea. In bathysciadiids (e.g. *Bathysciadium*) and basal cocculinids (*Fedikovella*, *Teuthirostria*) the oesophagus is straight and enters the midgut ventrally (Haszprunar, unpublished data); in all remaining cocculinids, the oesophagus curves dorsally to enter the midgut postero-dorsally (Haszprunar, 1987, 1988c; Strong & Harasewych, 1999). These non-torsional rotations are limited in taxonomic distribution but indeed have phylogenetic utility at lower taxonomic levels (Strong, Harasewych & Haszprunar, 2003). Despite documentation of this phenomenon primarily in limpet-like taxa, Lindberg & Ponder (1996) have emphasized that these rearrangements are unlikely to be restricted to limpets and are not necessary for adoption of a limpet-like habit.

Indeed, the present investigation has confirmed that such asymmetries are not limited to limpet-like taxa and have the potential to provide important phylogenetic information at higher taxonomic levels. This conclusion is based on the observation that the gastric shield is predominantly dorsal in position among outgroup taxa; indeed, a dorsal gastric shield is plesiomorphic within the Mollusca (Graham, 1949; Salvini-Plawen, 1988). However, in all caenogastropods that possess a cuticular lining of the midgut, the gastric shield is ventral in position, suggesting that the entire midgut of caenogastropods has undergone a ~45° clockwise rotation along a longitudinal axis. A rotation rather than a migration, as the mechanism is substantiated by the fact that topological relationships of midgut features (e.g. gastric shield, oesophageal and digestive gland apertures) are virtually identical in *Theodoxus fluviatilis* (Fig. 12A) as compared to ingroup taxa (e.g. *Strombus mutabilis*, Fig. 12B). In fact, Fretter *et al*. (1981) stated that structures such as the gastric shield may be useful in identifying instances of non-torsional asymmetry. A ventral shield is an important synapomorphy, supporting monophyly of the Caenogastropoda including the Architaenioglossa. Moreover, this discussion underscores that rearrangements of many kinds are a dominant theme in the evolution of a Class that historically is defined by asymmetry – the phenomenon of torsion.

Homology of the spiral caecum

As described above, the presence of crescentic ridges and grooves terminating in a pocket behind the gastric shield is common among gastropods. In the present analysis, only *Theodoxus fluviatilis*, *Crepidula plana* and *Bithynia tentaculata* have this configuration. Optimization of presence of the caecum indicates that it is independently derived within the Caenogastropoda, uniting *C. plana* and *B. tentaculata* (Fig. 33, character 29).

Although the caecum is homoplastic, the presence of ciliated folds that direct particles posteriorly into the gastric chamber is plesiomorphic within the Caenogastropoda (Fig. 33, character 30). Reduction or loss of this mechanism for directing particles into the gastric chamber is paralleled closely by simplifications in midgut circulation. Most taxa with gastric folds, regardless of sorting area development, possess a rejection current that directs particles anteriorly into the intestinal groove (Fig. 33, character 36). Indeed, this appears to be the plesiomorphic midgut circulation pattern within the Mollusca (Graham, 1949; Morton, 1953; Salvini-Plawen, 1981, 1988). Taxa with reduced typhlosolar folding, similarly have simplified circulation patterns, with predominantly clockwise to linear circulation and no discrete rejection current (Fig. 33, character 38).

Homology of pyloric caecae

The distribution of pyloric caecae within the Caenogastropoda now has been extended from architaenioglossans (Bouvier, 1888; Prashad, 1925; Demian, 1964; Andrews, 1965a) to cypraeoideans. Although previously unreported, the presence of pyloric caecae in other taxa is implied by the depiction of a transverse segment of the intestinal groove at the distal end of the style sac region (lamellarioideans, Graham, 1949; cypraeoideans, Kay, 1960). This feature is concluded to be independently derived in the two groups (Fig. 33, character 46). The more derived position of *Cypraea robertsi* is supported by a number of features including the subradular organ, kidney differentiation and configuration of the nervous system. However, hypotheses of homology will always remain conjectural, subject to repeated tests of congruence with the addition of new data. More simply, pyloric caecae may be concluded to be homologous in future analyses.

In this context, it is interesting to note the repeated suggested affinity between architaenioglossans and cypraeoideans (e.g. Haller, 1890). This link was formalized in the classification of Sitnikova & Starobogatov (1982) on the basis of radular and reproductive features (Ponder & Warén, 1988). Indeed, cypraeoideans possess a mosaic of putatively plesiomorphic and apomorphic features that present an all-too-common dilemma for molluscan systematists. Among putative plesiomorphies, cypraeoideans are characterized by pedal cords with numerous cross connections. This has been hypothesized to be independently derived within the group, with osphradial structure cited to support their more derived placement (Ponder & Warén, 1988). However, the present investigation adds the presence of buccal pouches and pyloric caecae to the growing list of putative plesiomorphies for the superfamily. Perhaps the solution ultimately will be a bipartite division of the Caenogastropoda similar to the one supported in the present analysis to reconcile these apparently conflicting sets of characters.

Homology of the crystalline style and style sac

The issue of style sac homology has figured most prominently in the higher order systematics of the Gastropoda and Mollusca (e.g. patellogastropods, Ponder & Lindberg, 1997). In contrast, that recent study considered the homologies of the style sac within the Caenogastropoda to be relatively straightforward; all caenogastropods, including neogastropods, were inferred to possess a style sac.

In the past, the homology of the caenogastropod style sac has not been so clear. Although it is now regarded as the anterior chamber of the midgut housing the style, early discussions of homology or nonhomology of the 'style sac' centred on functional hypotheses concerning the site of secretion of the style. Thus, pyloric caecae and gastric pouches have been hypothesized to be 'style saces' based on the inference that they represent the site of secretion of the style (e.g. Robson, 1922; Demian, 1964). Although this early confusion has since been clarified, the correct identification of the style sac region is not always straightforward. This is most apparent in descriptions of neogastropod midgut morphology. The authors of several comparative studies have not recognized the neogastropod homologue of the style sac, but have identified the region on functional grounds as a 'ciliary sorting area' (Smith, 1967), 'posterior sorting area' (Medinskaya, 1993), 'zone of compaction' (Smith, 1967; Medinskaya, 1993) or 'intestine' (Kool, 1993). This failure to identify putative homologies, compounded by inconsistencies in terminology, confounds efforts to make hypotheses of homology that are useful within a broad phylogenetic framework.

Moreover, the traditional view has been to address this portion of the gut as an integrated unit when rendering hypotheses of homology. However, when one considers the manifold macroscopic and microscopic variation of this region of the gut, it becomes increasingly difficult to define what is necessary and sufficient to code 'presence' or 'absence' of a style sac. The view taken here is that the pyloric region of the gut is a character complex – a fact acknowledged (W. Ponder, pers. comm.), but not formalized in a morphological cladistic analysis. This perspective allows the homologies of the structures that comprise the style sac to be assessed individually, including typhlosole number, typhlosole ciliation, pyloric ciliation and folding, and presence or absence of the crystalline style (Fig. 32). Of these five characters, only the presence of a distinct ciliary strip on the major typhlosole is new to caenogastropod systematics; the remaining characters were previously documented within the Caenogastropoda, but their distributions have been clarified for many taxa included.

Subdividing the style sac into its structural elements and analysing the complex mosaic of character change brings new insight into the evolution of this region of the gut (Fig. 32). In many cases, these characters optimize to different nodes, underscoring the (semi) independent nature of change within this character complex. For example, the loss of the minor typhlosole has occurred independently two separate times (under DELTRAN; Fig. 32, character 41). The presence of the raised ciliary tract on the major typhlosole supports the clade including *Lampanella minima*, and is independently derived in *Ilyanassa obsoletus* (Fig. 32, character 42). Differentiated style sac ciliation (Fig. 32, character 43) and smooth to transverse folding within the pylorus (Fig. 32, character 44) are primitive within the Caenogastropoda; both are lost and regained in different subsets of derived sorbeoconchans. The hyaline crystalline style is concluded to be homoplastically derived within caenogastropods (Fig. 32, character 45).

The only two characters that optimize to the same node are the presence of the raised ciliary tract and the presence of the crystalline style. However, as explained above, these features have been observed to vary independently among additional taxa not included in this analysis. Thus, all the varied features of the 'style sac' are not evolving in concert, but are changing independently and providing independent evidence of phylogeny; this highlights the inadequacy of the view of the style sac as an integrated unit (Fig. 32, inset).

Phylogenetic utility of the midgut

The dominant perception is that features of the gastropod midgut are functionally correlated (Graham, 1955; Salvini-Plawen, 1981, 1988) – similarities between taxa reflecting common functional requirements for the ingestion and digestion of food, rather than common ancestry. As such, they may be useful for defining taxa, but are of little use in higher order systematics of gastropods (Haszprunar, 1988a). To support this view, evidence has been assembled that conforms to this prediction, while exceptions have been downplayed. The emphasis on supporting evidence has contributed to the impression that there exists a more or less strict correspondence between complexity of midgut structure and function; complexity of midgut structure reflecting a microphagous diet, and simplicity reflecting a carnivorous or macrophagous diet with a corresponding increase in extracellular digestion (i.e. gizzards, radular trituration, and/or foregut glands; Graham, 1939, 1949, 1985; Morton, 1953; Smith, 1967; Salvini-Plawen, 1988). At first glance, this pattern holds true – microphagous basal caenogastropods possess complex typhlosolar folding of the gastric epithelium, complex ciliary sorting mechanisms, a prominent gastric shield and a crystalline style, while macrophagous and carnivorous forms have secondarily reduced complex midgut structures in several ways. However, there is a far more mosaic pattern of foregut and midgut modification than previously recognized, one that is difficult to correlate with feeding mode and nourishment. This pattern

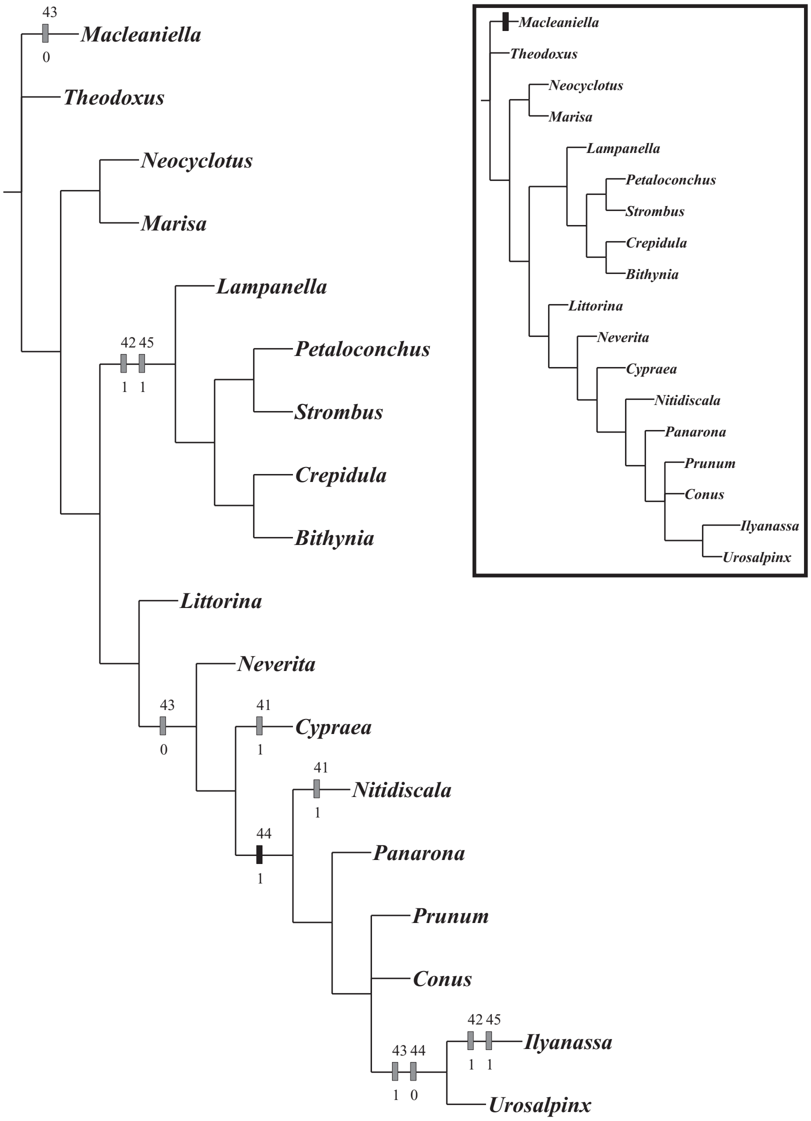

Figure 32. Evolution of the style sac. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN). Inset shows optimization of 'style sac present/absent.' Hashmark indicates 'loss of style sac' in *Macleaniella moskalevi*.

becomes increasingly clear as the distribution and homologies of alimentary structures are refined – exceptions become the rule.

For example, not all microphagous grazers have complex midgut morphologies, independent of the development of foregut glands. *Lampanella minima* has well-devloped ciliated folds, a glandular pad, a large sorting area and a crystalline style in conjunction with buccal pouches and an oesophageal gland. *Littorina littorea*, also a microphagous grazer (Graham, 1949, 1955, 1985; Hawkins *et al.* 1989), possesses a midgut that is simpler in several respects in that the non-muscular gastric chamber is cuticularized, typhlosolar folding reduced, the sorting area small, and a crystalline style sac lacking, but buccal pouches and a mid-oesophageal gland are similarly present. Other microphagous grazers (e.g. *Strombus mutabilis*) have more complex midgut morphologies, similar to *L. minima*, but lack both buccal pouches and the mid-oesophageal gland.

Another example is the alimentary system configuration of the Architaenioglossa. Some architaenioglossans are macrophagous herbivores (Prashad, 1925; Graham, 1955) and have modified the gastric chamber into a U-shaped, cuticularized, highly muscular 'gizzard' (Prashad, 1925; Demian, 1964; Andrews, 1965a; present study) with only a single ventral ciliary tract, no sorting area, and a style sac region lacking a crystalline style; buccal pouches are present but a mid-oesophageal gland is lacking. However, *Viviparus viviparus*, although not included here, retains all essential features of architaenioglossan foregut and midgut morphology (pers. obs.), while adopting a microphagous suspension-feeding habit (Graham, 1955).

Among carnivorous neogastropods, many have nothing more than a sac with simple circulation patterns (e.g. *Panarona clavatula*). Others have more complex circulation patterns (e.g. *Prunum apicinum*) and possess clear landmarks of basal sorbeoconchans such as the style sac or gastric shield (e.g. *Ilyanassa obsoletus*, *Urosalpinx cinerea*). Some members of largely carnivorous neogastropod families (e.g. columbellids), although not included in this analysis, possess a midgut bearing a gastric shield (Kantor & Medinskaya, 1991; deMaintenon, 1999) with style sac ciliation that is undifferentiated (pers. obs.); several reversals to herbivory within the family have not been accompanied by homoplastic gains in complexity of midgut structure.

The mosaic nature of midgut change is highlighted by comparing individual characters with feeding biology. For example, differential development of sorting areas (Fig. 33, character 36) presents no predictable association with feeding mode and diet. The microphagous suspension-feeding omnivores *Petaloconchus varians* (mucus-net suspension feeder) and *Crepidula plana* (ciliary suspension feeder; Fig. 33) display markedly differing degrees of sorting area development, with that in the former being comparable to *Lampanella minima*, a microphagous grazer. Despite comparable sorting areas, *P. varians* lacks an oesophageal gland while *L. minima* possesses one. *Bithynia tentaculata*, a microomnivorous grazer and opportunistic suspension feeder (Graham, 1985), lacks both a ciliary sorting mechanism and an oesophageal gland. Predatory carnivores may have a well developed sorting area (e.g. *Neverita duplicata*) or may lack one (e.g. *Urosalpinx cinerea*; Fig. 33), independent of the presence of an unpaired foregut gland.

The gastric shield has been viewed as an integral part of the gastropod style sac form of midgut, functionally linked to microherbivory and the ingestion of abrasive particles (e.g. Morton, 1953). However, the shield has been retained in many carnivores that do not ingest potentially harmful particles (Fig. 33). Arguably, size of the shield may be linked with herbivory and/or presence of a crystalline style. Indeed, the shield attains its greatest degree of development in style-bearing forms and has been cited as being larger in neogastropods that have secondarily assumed herbivory as compared to closely related carnivores (Kantor & Medinskaya, 1991).

Further exceptions can be found in the structure of the style sac. For example, the presence or absence of the ciliated strip along the ventral typhlosole is independent of feeding – it is present or absent in microphagous basal sorbeoconchans (variable even within the same family, e.g. Littorinidae), and present or absent in carnivores and opportunistic scavengers (Fig. 33). Moreoever, pyloric caecae are here revealed to be present in the macroherbivorous architaenioglossans and carnivorous cypraeoideans (Fig. 33, character 46).

The crystalline style poses yet another exception to the rule. Although originally thought to be associated with herbivory (e.g. Yonge, 1930), as the distinction between the protostyle and true crystalline style was clarified, it was rapidly realized that there was no necessary interdependence between the two, i.e. not all herbivores require a style. The absence of a style in herbivores is typically attributed to sporadic feeding behaviour, the presence of a style being contingent upon a continuous supply of food (Yonge, 1930, 1932; Graham, 1939). However, *Ilyanassa obsoletus* (Curtis, 1980; Curtis & Hurd, 1981) is a deposit feeding, opportunistic scavenger that not only possesses a crystalline style in the presence of extracellular proteases, but exhibits style cycling as a consequence of digestive rhythms (Curtis & Hurd, 1981). This demonstrates that there is no necessary interdependence between the presence of a crystalline style, herbivory and continuous feeding.

Furthermore, previous investigators have supported a mutual dependency between the presence of the crystalline style and the development of the oesophageal glands (Yonge, 1930, 1932; Graham, 1939; Fretter & Graham, 1962). It was widely held that the oesophageal glands degenerate because they are functionally replaced by the style (Graham, 1939; Morton, 1953; Owen, 1966; Salvini-Plawen, 1988). However, as noted in the past, there are numerous exceptions to this apparent correlation (e.g. Woodward, 1899; Ponder, 1967; Houbrick, 1980, 1988). That there is no necessarcy interdependence between the style and mid-oesophageal glands is supported in this analysis by the presence of both in *Lampanella minima* and *Ilyanassa obsoletus*.

On a final note, the apparent reinvention of the crystalline style and gastric shield in *Ilyanassa obsoletus*, an omnivorous, opportunistic scavenger, warrant additional comment. It is clear from the preceeding discussion that these features do not reappear in every neogastropod that is partially or wholly dependent on vegetable matter for nourishment. Although it is possible that both of these traits may be atavistic in *I. obsoletus* as a consequence of its unusual diet, several alternative explanations are equally plausible. For example, it is possible that all sorbeoconchans secrete the style protein, but that the style only polymerizes in those taxa lacking extracellular proteases. Thus, the reappearance of this feature in *I. obsoletus*

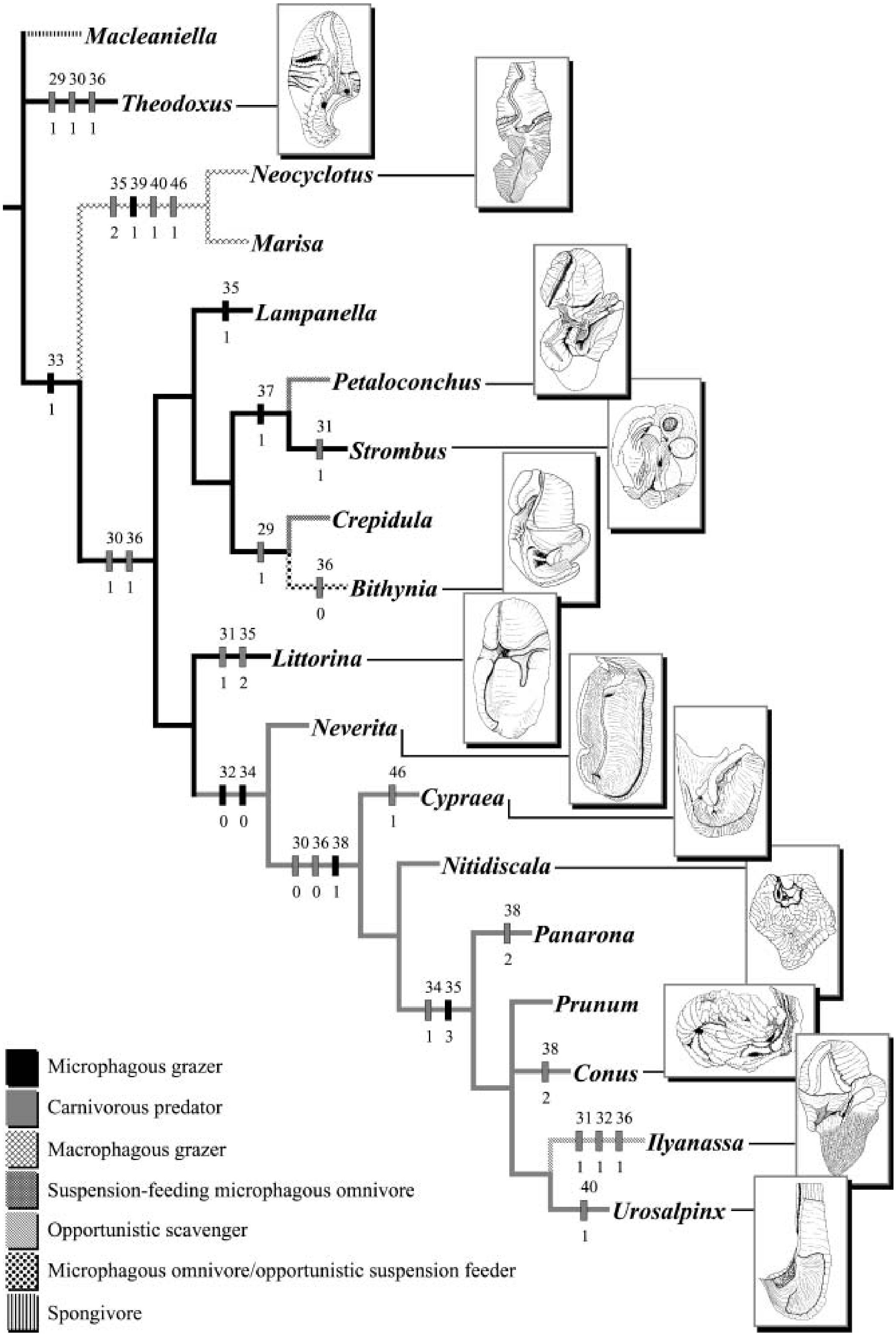

Figure 33. Evolution of the midgut, excluding features of the style sac. Black hashmarks indicate forward changes, grey hashmarks indicate forward homoplasies (DELTRAN). Branches indicate feeding mode and diet of each species. Representative midgut morphologies are shown.

simply may be attributable to the cyclic production of enzymes, corresponding with its well-documented digestive rhythms (Curtis, 1980; Curtis & Hurd, 1981). The ostensible reappearance of the gastric shield may be the consequence of taxon sampling, as many neogastropods are known to possess cuticular linings of the gastric epithelium (Smith, 1967; Medinskaya, 1993). The fact that the gastric shield of *I. obsoletus* occurs in a ventral position similar to other caenogastropods, argues against it being a neomorphic feature. On the other hand, the reappearance of the shield may be due to heterchrony. As summarized by deMaintenon, 1999), some neogastropods possess a gastric shield during larval stages, but lose the structure in the adult. Thus, these structures present two intriguing cases wherein numerous patterns of secondary loss or processes such as heterochrony can confound homology assessment.

Thus, although a general correlation of complexity and microphagy is evident, abundant examples exist that prove exceptions to the rule. Indeed, foregut complexity, feeding mode and diet are weak guides at best to predicting the presence or absence and development of midgut features including typhlosolar folding, sorting areas, number of digestive gland ducts, crystalline style and gastric shield. The vague statement that midgut features will become simplified as a consequence of carnivory cannot be used reliably to predict which features will become modified and in what ways. Similar to the evolution of the style sac discussed above, features of the gastric chamber show a highly mosaic pattern of reduction and loss, one that bears no one-to-one correspondence with feeding biology. Thus, instead of plastically mirroring functional requirements, this suggests that there are many alternative functional pathways for the effective handling of food; as a consequence, the historical, phylogenetic signal is not unravelled with each functional shift.

In this framework, the most straightforward utility of midgut characters is for defining groups (*cf.* Haszprunar, 1988a), like the Architaenioglossa, wherein midgut structure is maintained with high fidelity in spite of functional shifts. However, alimentary morphology retains a utility in recovering deeper caenogastropod nodes as well, despite the many divergent morphologies present in the group. This conclusion is supported by the fact that several foregut and midgut features provide critical basal synapomorphies within the Caenogastropoda. For example, features such as the subradular organ, jaw composition, oesophageal folding, the position of the gastric shield, the presence of the crystalline style, and the presence of a raised ciliary tract, optimize near the base of the tree. In other words, these are relatively conservative, widely distributed features for large clades of caenogastropods, cutting broadly across patterns of feeding biology. In addition, as pointed out above, the evolution of these features is highly mosaic, and does not bear a precise correspondence to feeding mode and nourishment.

Perhaps most significantly, the Caenogastropoda are united by five synapomorphies. Four of these features comprise characters relating to the alimentary system: the presence of a glandular subradular organ, a low mid-ventral fold in the anterior oesophagus not associated with a ventral glandular mass, and a ventral gastric shield. Three of these are characters new to caenogastropod systematics; either they were unknown within the group, their precise taxonomic distribution had been undocumented, or their significance to caenogastropod systematics had not been appreciated. This suggests that features of the gut, as a consequence of assumptions regarding phylogenetic utility, remain inadequately investigated in a comparative context. In other words, the assumption that gut characters will be uninformative or misleading in delineating phylogenetic relationships has caused the significance of the gut and its ability to provide important and informative characters to be ignored.

CONCLUSIONS

1. This study has provided anatomical information for several understudied groups, including cyclophorids and ptenoglossans, as well as a broad comparative survey of many major organ systems among 16 representative caenogastropods.
2. This survey has clarified the distribution and/or homologies of several features (e.g. jaw, subradular organ, buccal pouches), and has revealed several features new to caenogastropod systematics, including characters from the reno-pericardial system (blood supply to differentiated lamellae and to the nephridial gland), nervous system (tentacular nerve branching patterns), and the foregut (e.g. oesophageal ventral folding).
3. This study has attempted to place the complex morphological variability of the midgut into a coherent framework with explicit hypotheses of homology that are not dependant on functional criteria, and to extend hypotheses of homology among more basal caenogastropods to the neogastropods, thereby rendering midgut homologies more useful and consistent in the context of higher order caenogastropod systematics. In so doing, this study has revealed several new midgut characters (e.g. position of the gastric shield, direction of ciliary currents, presence of a ciliary tract).
4. Character optimization has demonstrated that many of these new characters are informative at a number of taxonomic levels within the Caenogastropoda. A comparison of midgut character optimi-

zations, feeding modes and diets has revealed that patterns of change among caenogastropod midgut characters are highly mosaic, to a degree previously underestimated. Thus, there is no strict one-to-one correspondence between midgut morphology and feeding biology, an interdependence emphasized in previous discussions concerning phylogenetic utility of the midgut.

5. This fact, combined with the optimization of several gut features to critical basal nodes, demonstrates that the midgut has an unexploited ability to provide important and informative characters in the higher order systematics of caenogastropods.

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