

## Anatomy of the hadal limpet *Macleaniella moskalevi* (Gastropoda, Cocculinoidea)

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**Abstract.** The anatomy of the hadal, cocculinid limpet *Macleaniella moskalevi* is described. This species has a small, symmetrical, cap-shaped shell with a prominent internal transverse septum. As in other cocculinid genera, broad oral lappets and epipodial tentacles are present. Vestigial eyes are also present, but lack pigment and are modified into the basitentacular gland. The unique aortic vessel and associated hemal gland are present. Mantle cavity morphology is characteristic of cocculinid taxa; the cavity contains a pseudoplicatid gill, hypobranchial gland, and shallow brood pouch. Adults are simultaneous hermaphrodites, possessing a gonad with distinct egg and sperm producing regions; the common gonoduct is glandular. The single receptaculum seminis is connected to the anterior gonoduct via an enclosed duct. An enlarged right cephalic tentacle is inferred to function as a copulatory organ. The digestive gland occupies that part of the visceral mass confined above the septum and opens by way of two ducts into the distal esophagus. The anterior digestive tract is characterized by the presence of extremely well-developed esophageal pouches, a cuticularized sublingual pouch, and an unpaired jaw. A subradular sense organ and salivary glands are lacking. *M. moskalevi* is remarkably unique among previously described cocculinids in the anatomy of the reproductive tract and of the organs associated with the mantle cavity. In particular, the conformation of the nervous system in this species is unknown among cocculinids described thus far.

*Additional key words:* Mollusca, deep-sea

Cocculinids are limpet-like gastropods that are found in deep-sea habitats worldwide and are known primarily from bathyal depths. *Macleaniella moskalevi* LEAL & HARASEWYCH 1999 and *Fedikovella caymanensis* (Moskalev 1976) remain the only cocculinid species to date that are known to inhabit the hadal zone. Apart from the genus *Teuthirostria*, which inhabits chitinous cephalopod beaks, cocculinids are exclusively associated with submerged wooden substrates. Despite this consistent and predictable substrate association, it remains unclear whether cocculinids obtain nourishment directly from their substrate or from microbes, detritus, or other food resources associated with the surfaces on which they are found.

Ever since their discovery and first description (Dall 1882), cocculinid species have intrigued their investigators with unique combinations of features. These features have proven problematic for the taxonomy of cocculinid limpets because they conflict with the suites

of characters thought to be diagnostic at higher taxonomic levels. Difficulty in determining the taxonomic placement of cocculinids has been exacerbated by the common practice of placing any deep-sea limpet with a modified archaeogastropod organization in the same taxonomic group. Thus, the phylogenetic affinities of the family have remained ambiguous, a fact reflected in their fluctuating taxonomic status. Based on his anatomical investigations of *Cocculina*, Thiele (1903), stressed the isolated position of this family, but inferred a close relationship to *Neritopsina*. Later, Thiele (1908) suggested a close relationship between *Bathysciadium* and Cocculinidae and erected the superfamily Cocculinoidea to include the families Cocculinidae (*Cocculina*), Lepetellidae (*Bathysciadium*, *Lepetella*), and Addisoniidae (*Addisonia*). This scheme was expanded with the description of material collected during the latter half of the nineteenth century, but remained largely unchanged for the next 80 years.

By the 1980's the Cocculinoidea had grown to include nine families representing a variety of deep-sea limpet-like forms: Addisoniidae (Dall 1882), Bathypeltidae (Moskalev 1971), Bathyphytophilidae (Mos-

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kalev 1978), Bathysciadiidae (Dautzenberg & Fischer 1900), Cocculinellidae (Moskalev 1971), Cocculinidae (Dall 1882), Lepetellidae (Dall 1882), Osteopeltidae (Marshall 1986), and Pseudococculinidae (Hickman 1983). The first attempts to subdivide this group into monophyletic components came in the late 1980's; based on anatomical studies that supported differences observed between cocculinid and pseudococculinid radulae (Hickman 1983, 1984; Marshall 1986), Haszprunar (1987a, 1988a) erected two superfamilies, the Cocculinoidea and Lepetelloidea, and united them within the Suborder Cocculiniformia. Further review of Cocculiniformia taxonomy can be found in Moskalev (1976), Haszprunar (1987a, 1988a), and Dantart & Luque (1994).

The superfamily Cocculinoidea, as formulated by Haszprunar (1987a), includes the Cocculinidae (*Cocculina*, *Coccopigya*, *Teuthirostria*, *Paracocculina*, *Fedikovella*, and *Cococrater*) and the Bathysciadiidae (*Bathysciadium*, *Bathypelta*?, and *Bonus*). With the description of the genus *Macleaniella*, the Cocculinidae now includes seven genera. These taxa are united by the shared presence of subpallial glands, a pseudoplicatid gill, a single left pallially-situated kidney, hermaphroditism, and statocysts with statoliths (Haszprunar 1988a). Cocculinid external morphology and radulae have been well documented (Dall 1882, 1889; Thiele 1903, 1909; Schepmann 1908; Moskalev 1971, 1976; Hickman 1983, 1984; McLean 1987, 1992; Dantart & Luque 1994; McLean & Harasewych 1995; Leal & Harasewych 1999), but prior to the present investigation, only nine of the ~70 described species of cocculinids had been studied anatomically (Thiele 1903; Haszprunar 1987a). In addition, Thiele's (1908) description of *Bathysciadium pacificum* and Pelseener's (1900) erroneous anatomical account of *Bathysciadium costulatum* (Thiele 1908; Haszprunar 1987a) remain the only published anatomical studies of other cocculinoidean taxa.

## Methods

Three preserved paratypes of *Macleaniella moskalevi* were made available for this study by Drs. Nancy Voss and José Leal, Sanibel Museum. The specimens were collected in 1970 (see Leal & Harasewych for history of specimens); the original fixative is unknown.

The specimens were removed from their shells, post-fixed in Bouin's fixative, dehydrated to 95% ethyl alcohol and embedded in JB-4® plastic. This embedding medium is water soluble and does not require complete dehydration of tissue; consequently, this type of medium has the advantage of causing less distortion

and shrinkage than other embedding procedures including paraffin and epoxy resins (Polysciences 1982). Semi-thin serial sections were cut at 3.5 µm on a conventional rotary microtome with glass knives. Sections were stained with 2% toluidine blue. Anatomical reconstructions are based on transverse and sagittal sections.

## Results

### External structures

For a detailed description of shell morphology in *Macleaniella moskalevi*, see Leal & Harasewych (1999). The shell is unique within the Cocculinidae in possessing an internal transverse septum.

There are two posterior, asymmetrically placed, epipodial tentacles within the subpallial cavity; the left is slightly more posterior than the right. The subpallial cavity is complexly folded and lined by tall (<40 µm), prismatic non-ciliated cells interspersed with densely staining, metachromatial glandular cells. These cells of the subpallial gland (Fig. 1A, sg) are concentrated ventrally within the subpallial cavity, confirming the description by Thiele (1903: pl. 6, fig. 20).

The head bears two broad oral lappets (Fig. 1D, ol) and two lateral cephalic tentacles (Fig. 1B, t), with the enlarged right cephalic tentacle functioning as a copulatory organ (Fig. 1C, co). The epithelium of the oral lappets (Fig. 1C, ol) is composed of tall cells ranging from 20–30 µm in height and is densely ciliated. Scattered flask-shaped mucus cells are found predominantly along the ventral and outer margins of the lappets. A similar epithelium lines the surfaces of the cephalic tentacles, but is sparsely ciliated and mucus cells are scattered more evenly over the dorsal and ventral surfaces.

### Muscle system

The disposition of the musculature in *M. moskalevi* is identical to that in other cocculinid species (Thiele 1903; Haszprunar 1987a). The head retractors insert on the shell dorso-laterally, at the inward anterior-leading edges of the shell muscles. They travel anteriorly and ventrally for a short distance and insert on the back of the head (Fig. 1E, hr). The foot is weakly muscularized and forms the insertion point for the muscle bundles of the horseshoe-shaped shell muscle. Characteristic of cocculinid limpets, the foot sole is relatively small and exhibits two distinct epithelia; an inner non-ciliated region of tall (~20 µm) prismatic cells surrounded by a densely ciliated region of larger cells. The pedal gland (Fig. 1G, pgl) is weakly developed and opens ventrally through an anterior and lateral slit (pd).

## Mantle

As in other cocculinids investigated thus far (Haszprunar 1987a), the mantle forms a highly vascularized organ that likely plays an extensive role in respiration. A large sinus encircles the mantle edge (Fig. 1H, ms). Above the sinus, the inner mantle epithelium is folded (im) while the outer mantle epithelium is smooth and supplied with many fine muscle fibers. The mantle epithelium contains scattered large mucus cells and is primarily non-ciliated.

The mantle cavity (Fig. 1E, mc) is lined by short (~6  $\mu\text{m}$  tall), sparsely ciliated cells. The base of the pallial roof is occupied by the pericardium (per) to the left and the kidney (k) to the right. Thus, these organs bound the base of the mantle cavity dorsally. Ventrally, the mantle cavity is bounded by the enclosed duct of the receptaculum seminis (drs). The slit-like base of the mantle cavity is subdivided by a shallow, longitudinal septum (Figs. 1E, 3, ls).

Situated at the right side of the mantle cavity (Fig. 1I, mc) are the anal aperture (a) and, immediately to its left, the nephridiopore (np). A small pseudoplicatid gill projects into the pallial cavity in front and to the left of the anal papilla. The gill forms a densely ciliated finger-like projection (Fig. 2A,B, g), that likely controls water flow through the mantle cavity. The hypobranchial gland (Fig. 2B,C, hg) occupies only a small area of the mantle roof anterior and to the left of the gill. Right of center in the pallial roof lies a shallow, posteriorly projecting pocket that has been interpreted by Haszprunar (1987a) as a brood pouch, based on the presence of ripe eggs. This pouch did not possess ripe eggs in the two specimens of *M. moskalevi* sectioned for this study. The large glandular cells (>50  $\mu\text{m}$ ) of the hypobranchial gland (Fig. 2C, hg) extend for a short distance into the muscular mouth of the brood pouch (bp).

## Circulatory and excretory system

The single left kidney (Fig. 1E,F, k) is large and sac-like; it expands from a position on the left, behind the heart (Fig. 1E, per), to occupy the right side anteriorly, ventrally enclosing the rectum (Fig. 1F, rec). There is no evidence of a nephridial gland.

The pericardium (Fig. 1E, per) is large and is found near the dorsal and posterior limits of the mantle cavity on the left. A pericardial gland (Fig. 1F, perg) is present but is poorly developed and limited to a small number of glandular cells scattered along the ventral pericardial wall. Detailed investigation of the heart chambers, valves, and reno-pericardial duct was precluded due to inadequate preservation.

An aortic arch (Fig. 2D, aa), a contractile vessel

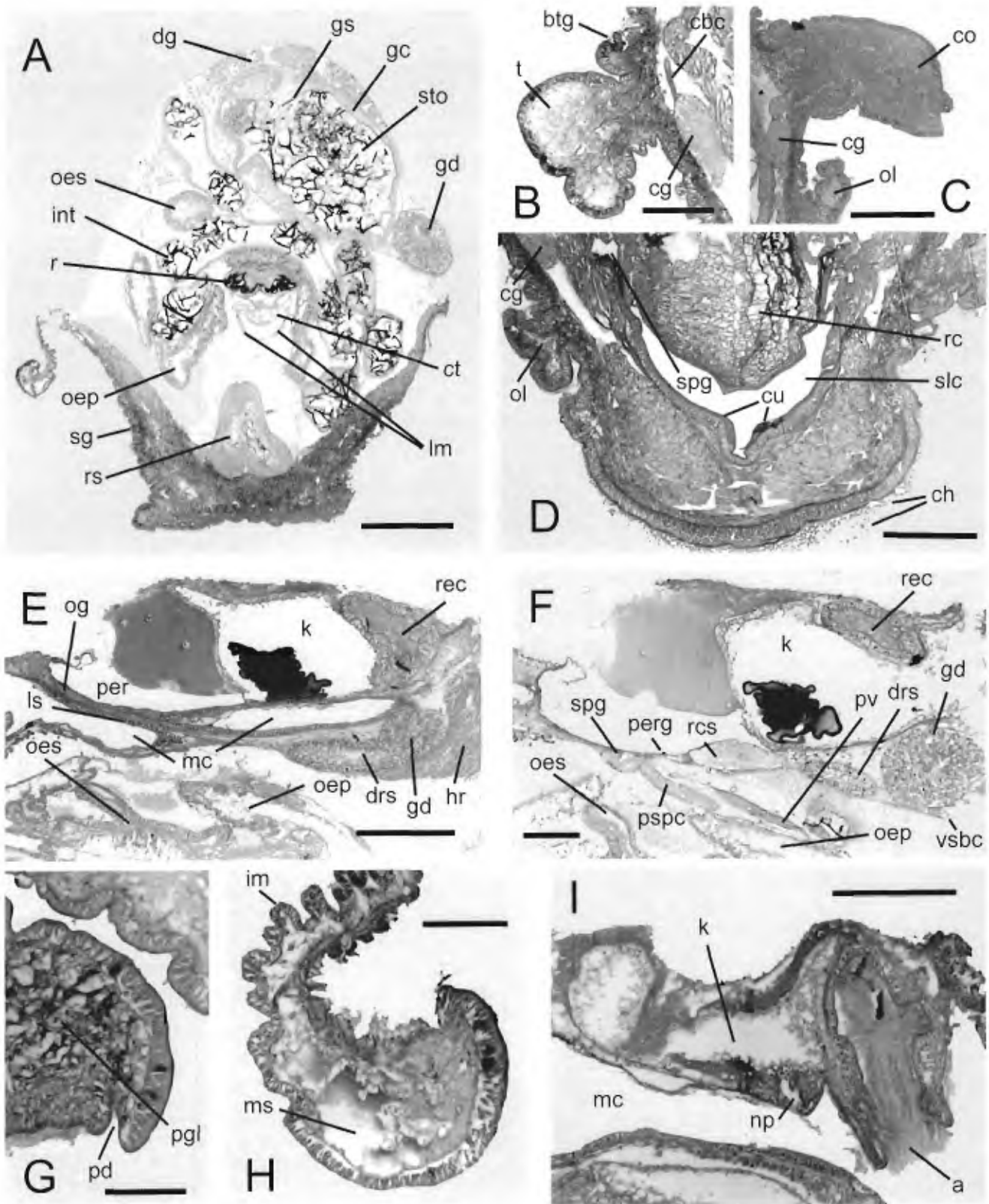
unique among gastropods to cocculinid limpets, is present in *M. moskalevi*. This vessel, with its paired longitudinal muscle bundles (lm), occupies a median position slightly below and between the paired radular cartilages (Fig. 2E, rc). It persists anteriorly to the level of the mouth opening where it splits into two smaller vessels, each with a single muscle bundle that inserts into the buccal musculature along the ventral surface of the cartilages. Posteriorly, the vessel gradually migrates dorsally to the C-shaped bend of the radula within the main body cavity. At the flexure point of the radular sheath, the muscle bundles (Fig. 1A, lm) insert onto the ventral band of chordoid tissue (ct) (Haszprunar 1987a) stiffening the radula (r). This point of flexure, situated at the posterior dorsal wall of the head in other cocculinids, occupies a position within the main visceral hemocoel in *M. moskalevi*. Consequently, the aortic arch does not penetrate the pedal and buccal sinuses as in other cocculinids, but connects the buccal sinus with the visceral hemocoel.

However, the aortic arch maintains communication with the pedal sinus (Fig. 2E, ps). At the level of the pedal ganglia (pg), the arch is connected via two lateral membranes (ltm) to the surface of the pedal musculature. Anteriorly, the membranes do not close to form an enclosed chamber but extend inward, narrowing the chamber. Just anterior to these membranes, the pedal sinus opens and thus lies in direct connection with the space enclosed by the membranes. Behind the opening of the pedal sinus, a small and weakly bilobed gland is found (Fig. 2D, hmg); termed the hemal gland by Haszprunar (1987a), it lies above the fibers of the pedal musculature.

The intra-membrane space below the aortic arch is connected to the pericardium via a large vessel (Fig. 1F, pv) that emerges ventrally from the pericardium near the supraesophageal ganglion. This vessel parallels the pleuro-supraesophageal connective (pspc) ventrally and to the right for a short distance. From here, the vessel turns inward and continues ventrally, travelling forward with the visceral-subesophageal connective (Fig. 2E, vsbc). The vessel (pv) and the visceral-subesophageal connective penetrate the right lateral membrane (ltm) at the level of the statocysts (st).

## Reproductive system

Adults of *M. moskalevi* are simultaneous hermaphrodites. Inadequate preservation has rendered it difficult to determine the precise location of sperm production. However, it is clear that the distal reproductive tract is divided into two morphologically distinct regions. One portion forms a voluminous sac



**Fig. 1.** A. Transverse section through visceral mass anterior to the separation of the digestive gland above the septum. Note insertion of longitudinal muscle fibers of aortic arch on ventral band of chordoid tissue. Scale bar, 500  $\mu$ m. B. Transverse section of left cephalic tentacle and basitentacular gland. Note small duct and surrounding mucus cells opening

(Fig. 3, go) and occupies the posterior-most portion of the visceral mass below the septum. This is the site of egg production and contains approximately four large, yolky eggs (Fig. 2F, e) ~150  $\mu\text{m}$  in diameter, as well as several smaller developing eggs. The eggs are embedded in the glandular epithelium of the gonad walls. In addition, there are a large number of mature sperm (s) free within the lumen of the gland and surrounding the eggs.

This sac-like portion of the gonad is connected to the glandular gonoduct (Figs. 2F, G, 3, gd) postero-dorsally by a non-ciliated narrowing of the gonad walls. At the point of connection between the two, the gonoduct is massive and glandular but rapidly forms a slit-shaped duct with a roughly tubular arrangement of glandular cells. Small, darkly staining, elliptical acrosomes, interspersed among the glandular cells of the gonoduct, indicate that it may function as a vesicula seminalis to store ripe sperm. Mature sperm are also visible within the lumen of the slit-like, ciliated duct. The gonoduct is circular in cross section and varies little in diameter as it proceeds forward along the right side of the body.

The histology of the genital tract changes abruptly where the gonoduct opens to a small flattened chamber lined by ciliated cuboidal epithelium (<18  $\mu\text{m}$ ). This chamber lies under the base of the mantle cavity and represents the enclosed duct of the receptaculum (Figs. 1F, 2G, 3, drs). At the anterior extent of the chamber, the genital opening to the mantle cavity is found on the left. A short distance posteriorly, the chamber opens on the left to a thin-walled pouch containing ripe sperm, the receptaculum seminis (Figs. 1F, 3, rcs). Thus, the receptaculum is not connected directly to the mantle cavity.

The copulatory organ (Fig. 1C, co) is formed by an

enlarged right cephalic tentacle. No ciliated tract or seminal groove leading to the genital opening could be detected. While tentative, these findings parallel those of Haszprunar (1987a), who attributed the apparent absence of an open seminal groove in some cocculinid taxa (*C. agassizii*) to poor preservation.

### Alimentary system

The radula of *M. moskalevi* has been described and illustrated by Leal & Harasewych (1999). These authors have noted that it is virtually indistinguishable from that of *Fedikovella caymanensis*.

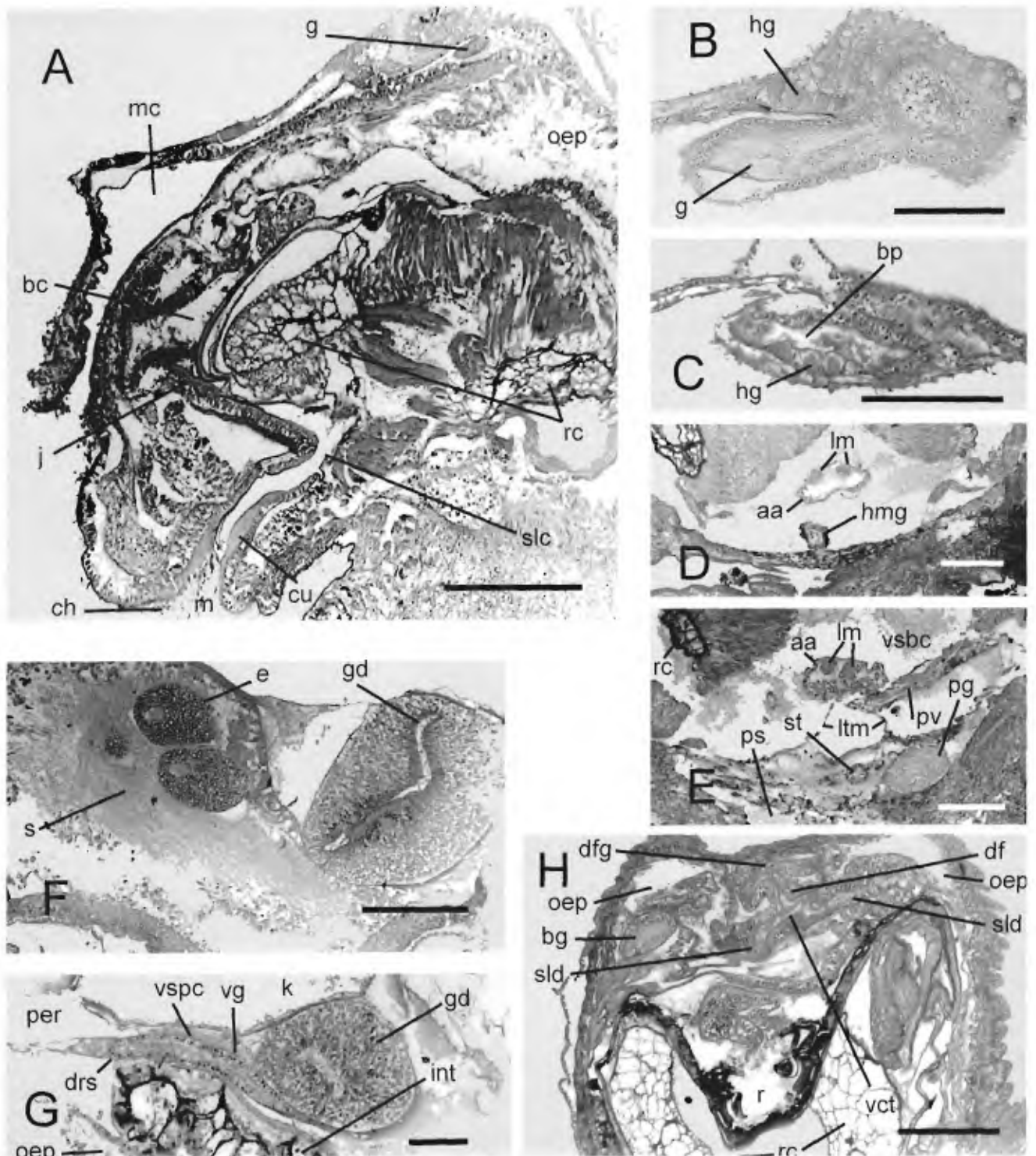
There is a single pair of large, elongate radular cartilages (Fig. 2H, rc). Anteriorly, the cartilages appear C-shaped in transverse section with their concave surfaces facing inward. Just posterior to emergence of the esophagus is a broad, flattened radular diverticulum lying between the esophagus and the radular sheath. As in other cocculinids, this diverticulum is glandular and appears lens-shaped in transverse section. The radular sheath is strengthened along its length by two crescent-shaped bands of cartilaginous chordoid tissue (Fig. 1A, ct) (Haszprunar 1987a), one ventral and one dorsal; the ventral band is more robust. The radular sheath continues posteriorly, to beyond the back of the head, before making a large C-shaped curve (when viewed laterally) such that the radular sac (rs) occupies a ventral position.

A cuticularized epithelium, bearing many cuticular hairs (Figs. 1D, 2A, ch), lines the oral field and surrounds the ventral mouth (Fig. 2A, m). This cuticle extends into the sublingual pouch (Figs. 1D, 2A, slc) and, as in other cocculinid species, forms two ventro-lateral bands (cu) that are separated ventrally by a narrow non-cuticularized glandular groove. A subradular

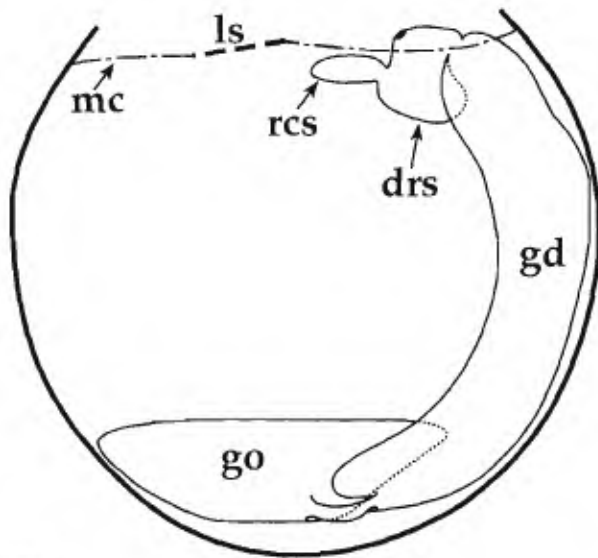
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to dorsal surface. Scale bar, 200  $\mu\text{m}$ . **C.** Transverse section of enlarged right cephalic tentacle. Innervation by the tentacular nerve is visible. Scale bar, 250  $\mu\text{m}$ . **D.** Transverse section through sublingual cavity near mouth. Note thin layer of cuticle on dorsal wall of cavity. Scale bar, 250  $\mu\text{m}$ . **E.** Transverse section near posterior end of mantle cavity showing longitudinal septum at base. Just anterior to plane of section in Fig. F. Scale bar, 250  $\mu\text{m}$ . **F.** Transverse section just behind base of mantle cavity through receptaculum seminis. At this level, esophagus is U-shaped, but dorsal grooves have appeared laterally. Scale bar, 130  $\mu\text{m}$ . **G.** Transverse section of right foot margin. Scale bar, 100  $\mu\text{m}$ . **H.** Transverse section of mantle margin. Scale bar, 100  $\mu\text{m}$ . **I.** Transverse section of mantle roof above head. Scale bar, 250  $\mu\text{m}$ . Abbreviations: (a) anus, (btg) basitentacular gland, (cbc) cerebro-buccal connective, (cg) cerebral ganglion, (ch) cuticular hairs, (co) copulatory organ, (ct) chordoid tissue, (cu) cuticular lining, (dg) digestive gland, (drs) duct of the receptaculum seminis, (gc) gastric cuticle, (gd) gonoduct, (gs) gastric shield, (hr) head retractor, (im) folded inner margin of mantle, (int) intestine, (k) kidney, (lm) longitudinal muscles, (ls) longitudinal septum, (mc) mantle cavity, (ms) mantle sinus, (np) nephridiopore, (oes) esophagus, (oep) esophageal pouches, (og) osphradial ganglion, (ol) oral lappet, (pd) pedal gland duct, (per) pericardium, (perg) pericardial gland, (ppl) pedal gland, (pspc) pleuro-supraesophageal connective, (pv) pericardial vessel, (r) radula, (rc) radular cartilage, (rcs) receptaculum seminis, (rec) rectum, (rs) radular sac, (s) sperm, (sg) subpallial gland, (sgp) sublingual glandular pouch, (slc) sublingual cavity, (spg) supraesophageal ganglion, (sto) stomach, (t) cephalic tentacle, (vsbc) visero-subesophageal connective.



**Fig. 2.** A. Oblique sagittal section through head and anterior visceral mass. Scale bar, 250  $\mu$ m. B. Transverse section through pseudoplicate gill. Scale bar, 200  $\mu$ m. C. Transverse section through brood pouch in mantle roof. Hypobranchial gland cells are visible extending a short distance into the pouch. Scale bar, 200  $\mu$ m. D. Transverse section through hemal gland just anterior to the pedal ganglia. A small portion of the right lateral membrane is still visible. Plane of section just anterior to that in Fig. E. Scale bar, 200  $\mu$ m. E. Transverse section through aortic arch and lateral membranes. Pedal ganglia and statocysts just becoming visible on the right. Scale bar, 200  $\mu$ m. F. Transverse section through gonad in posterior visceral mass, anterior to connecting duct. Slit-like lumen of gonoduct just becoming visible. Scale bar, 250  $\mu$ m. G. Transverse section at level of visceral ganglion. Note darkly staining elliptical acrosomes scattered through glandular



**Fig. 3.** Diagrammatic reconstruction of reproductive system. Dorsal view. Anterior is directed to the top of the page. Scale bar, 250  $\mu\text{m}$ . Abbreviations: (drs) duct of the receptaculum, (gd) gonoduct, (go) gonad, (ls) longitudinal septum, (mc) base of mantle cavity, (rsc) receptaculum seminis.

sensory organ and salivary glands are lacking in *M. moskalevi*, while the lateral glandular pouches are present (Fig. 1D, spg). Dorsally, the sublingual pouch is lined by a thin layer of cuticle.

A vestigial jaw (Fig. 2A, j) is present on the dorsal surface of the buccal cavity near the front of the head. The jaw lies immediately below a pouch-like evagination of the buccal cavity (bc) that occupies the anterior-most portion of the head and represents the initiation of the dorsal folds (Fig. 2H, df). The dorsal folds and intervening dorsal food groove of the buccal cavity continue into the anterior and mid-esophagus, remaining distinct until the separation of the esophageal pouches in the posterior esophagus. At the point of emergence from the buccal cavity, the ventral floor of the anterior esophagus develops a ventral ciliated tract (vct) opposing the dorsal food groove. Additionally, two glandular ventro-lateral folds emerge at the

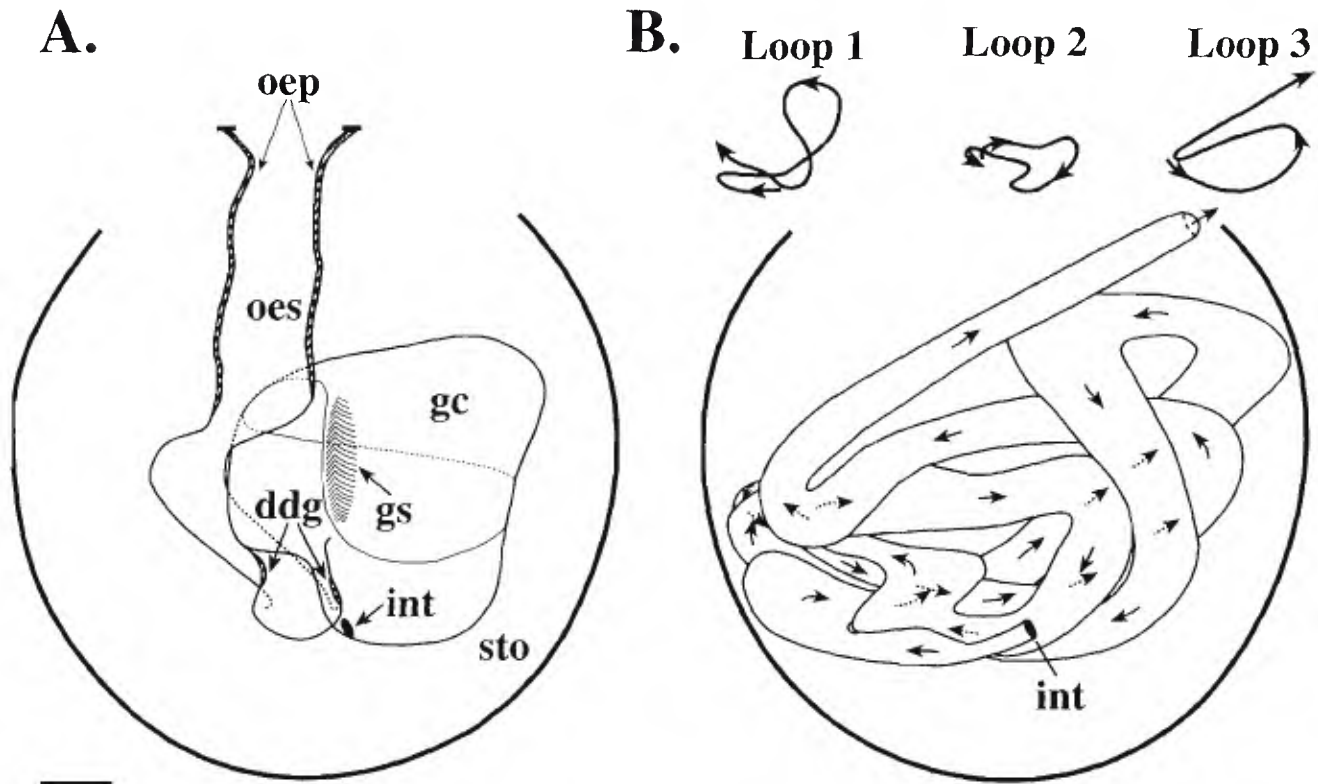
distal junctions between the esophageal pouches and their slit-like ducts. These folds persist posteriorly for only a short distance within the anterior esophagus. At this level, the dorsal food groove appears T-shaped in transverse section and the dorsal folds are equally developed. However, just posterior to the termination of the ventral folds, the right dorsal fold begins to migrate laterally and gradually flattens, so that the dorsal food groove now appears U-shaped in section (Fig. 1F, oes). These stages in the configuration of esophageal folding patterns are typical for cocculinid limpets (Salvini-Plawen & Haszprunar 1987). Posterior to this, two smaller dorsal grooves appear laterally and migrate inward, up the sides of the food groove, so that at the point of separation from the esophageal pouches it appears t-shaped in cross section. After separation, the esophagus rapidly develops approximately eight equal folds (Fig. 1A, oes). The effect of torsion, indicated by a rotation of the dorsal folds into a ventral position, is not evident in the anterior and mid-esophagus.

The paired esophageal pouches (Figs. 1A, 2G, oep) are large and complexly folded. Within the head, they are in a dorsal position and occupy free space between the loops of the hind gut posteriorly. The pouches communicate freely with the anterior and mid-esophagus through long, transverse, slit-like ducts (Fig. 2H, sld). These ducts begin within the buccal mass and continue approximately two-thirds the length of the esophagus. They are demarcated anteriorly by two ventral folds along their outer margins; posteriorly, the ducts become demarcated at their inner margin by two ventral grooves.

The stomach (Fig. 1A, sto) occupies a position on the right side of the visceral mass and expands anteriorly to a more central position. It is overlain by the tubules of the digestive gland (dg) and is bounded to the right by the gonoduct (gd). The esophagus travels posteriorly from the buccal mass, crosses briefly to the left at midlength, then crosses back to the midline. From this ventral position, it arcs dorsally to enter the rear of the stomach (Fig. 4A, oes). Upon entering, the esophagus forms a groove across the roof of the stom-

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tissue of gonoduct. Possible reno-pericardial connection also visible. Scale bar, 130  $\mu\text{m}$ . **H.** Transverse section through buccal mass at point of connection with esophagus. Scale bar, 250  $\mu\text{m}$ . Abbreviations: (aa) aortic arch, (acr) acrosomes, (bc) buccal cavity, (bg) buccal ganglion, (bp) brood pouch, (ch) cuticular hairs, (cu) cuticular lining, (df) dorsal fold, (dfg) dorsal food groove, (drs) duct of the receptaculum, (e) egg, (g) pseudoplicatid gill, (gd) gonoduct, (go) gonad, (hg) hypobranchial gland, (hmg) hemal gland, (int) intestine, (j) jaw, (k) kidney, (lm) longitudinal muscles (ltm) lateral membranes, (mc) mantle cavity, (mn) mantle nerve, (m) mouth, (oep) esophageal pouches, (pc) pedal commissure, (per) pericardium, (pg) pedal ganglion, (ps) pedal sinus, (pv) pericardial vessel, (r) radula, (rc) radular cartilages, (rec) rectum, (s) sperm, (sbg) subesophageal ganglion, (slc) sublingual cavity, (sld) slit-like duct, (st) statocyst, (vct) ventral ciliated channel, (vg) visceral ganglion, (vsbc) viscerosubesophageal connective, (vspc) viscerosupraesophageal connective.



**Fig. 4.** Diagrammatic reconstruction of digestive system. Dorsal view. Anterior is directed to the top of the page. Scale bar, 250  $\mu\text{m}$ . **A.** Esophagus and stomach in isolation. Note position of intestinal aperture in posterior stomach wall corresponding to same in **B.** **B.** Intestinal loops showing visible surfaces only. Arrows indicates direction of flow from proximal intestine to anus at upper right. Dotted arrows indicate pathway of portions hidden from view. Complete loops indicated below from proximal (left) to distal (right). Abbreviations: (ddg) ducts of the digestive gland, (gc) gastric cuticle, (gs) gastric shield, (int) intestine, (oes) esophagus, (oep) esophageal pouches, (sto) stomach.

ach that can be traced forward almost one-third the length of the gastric chamber. An extensive cuticle (Fig. 1A, 4A, gc) covers the entire anterior portion of the gastric chamber. Posteriorly, the cuticle is confined to the right dorsal wall and is elaborated into a prominent gastric shield mid-dorsally (gs). The hind gut leaves the stomach posteriorly (Fig. 4A, int) to the left. Neither a style sac nor a groove (Haszprunar 1987a) could be found in the proximal intestine, although observations were hindered by the gut contents (see below) which significantly deformed the intestinal epithelium. The hind gut (Fig. 1A, int) completes three, large loops (Fig. 4B) before exiting through the papillate anus (Fig. 1I, a).

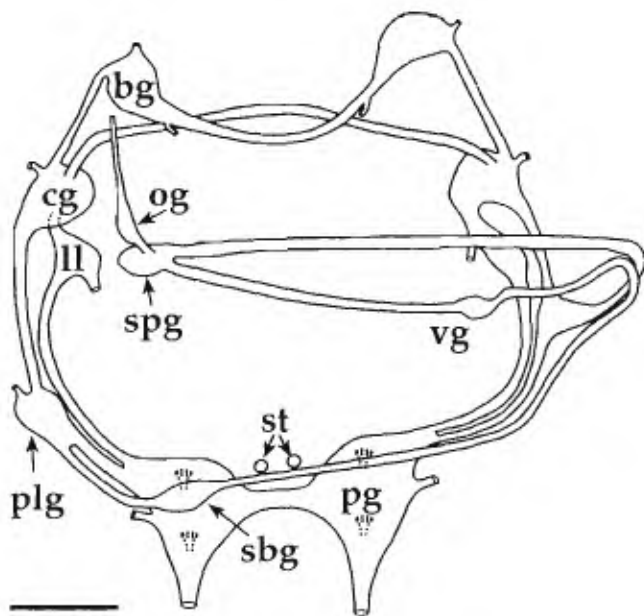
The paired lobes of the digestive gland are situated above the stomach; the right lobe is adjacent to the stomach while the left lobe lies predominantly above the posterior esophagus and the loops of the hind gut. Posteriorly, the digestive gland is the only part of the visceral mass that is confined above the shelf-like septum within the shell. There are two digestive gland ducts (Fig. 4A, ddg) that open into the posterior esophagus

immediately before entering the stomach. The ducts are situated laterally and are asymmetrical, with the right duct being significantly larger.

#### Nervous system and sensory structures

Situated obliquely when viewed from the side, the wide circum-esophageal nerve ring (Fig. 5) overlies the buccal complex anteriorly, with the buccal ganglia (Fig. 2H, bg) lying dorso-laterally below the esophageal pouches (oep) at the emergence of esophagus. These ganglia are connected via a commissure that travels backward and ventrally between the radular sheath and the radular diverticulum behind the buccal mass. Long connectives (Fig. 1B, cbc) run posteriorly and ventrally from the buccal ganglia, around the sides of the head, to the cerebral ganglia (Fig. 1B,C, cg) lying laterally at the ventral margin of the cephalic tentacles. In turn, two connectives run ventrally and posteriorly to the pleural ganglia. The pleuro-pedal connectives on each side are unequal in length. Thus, the pleural and pedal ganglia are dystenoid (unfused)





**Fig. 5.** Diagrammatic reconstruction of nervous system. Dorsal view. Anterior is directed to the top of the page. Scale bar, 250  $\mu$ m. Note mantle nerve exiting osphradial ganglion. Abbreviations: (bg) buccal ganglion, (cg) cerebral ganglion, (ll) labial lobe, (og) osphradial ganglion, (pg) pedal ganglion, (plg) pleural ganglion, (sbg) subesophageal ganglion, (spg) supraesophageal ganglion, (st) statocyst, (vg) visceral ganglion.

on the right and hypoathroid (fused) on the left. A single, long connective runs from the labial lobe of each cerebral ganglion to the pedal ganglia (Fig. 6A, pg). There is a single, stout commissure (pc) connecting the two pedal ganglia.

The visceral loop starts at the left pleural ganglion, which is connected via a short, thin connective (Fig. 6A, psbc) to the subesophageal ganglion (sbg) lying above the left pedal ganglion. From the subesophageal ganglion, a connective (Fig. 2E, vsbc) runs to the right, through the membranes attached to the aortic arch, then turns dorsally. The connective (Fig. 1F, vsbc) then runs a short distance along the base of the esophageal pouches before turning to occupy a position below the gonoduct (gd). Continuing to run posteriorly, the connective curves inward along the ventral base of the gonoduct to the visceral ganglion (Fig. 2G, vg) lying at the left of the gonoduct. A connective (vspc) runs to the left from the visceral ganglion, above the duct of the receptaculum, to the supraesophageal ganglion (Fig. 1E, spg) situated left of center below the pericardium. Two connectives emerge from the supraesophageal ganglion. One leaves dorsally and enters the longitudinal septum (Fig. 1E, ls) at the base of the mantle cavity; this connective innervates the osphradial gan-

gion (og) lying within the pallial roof. The second connective (Fig. 1F, pspc) leaves the supraesophageal ganglion anteriorly to the right. Travelling to the right in a large arc ventrally and anteriorly, the connective comes to occupy a lateral position at the level of the right cephalic tentacle. From here, the nerve runs forward a short distance to the right pleural ganglion.

A thick nerve (Fig. 6B, mn) exits from the osphradial ganglion and runs forward, within the mantle roof. While the mantle nerve crosses to the right to innervate the gill in other cocculinid species, it maintains a position just left of center in *M. moskalevi*. Only at the far anterior portion of the mantle does the nerve narrow and cross slightly to the right, to occupy a more median position. No trace of a nerve branching off the main trunk could be detected.

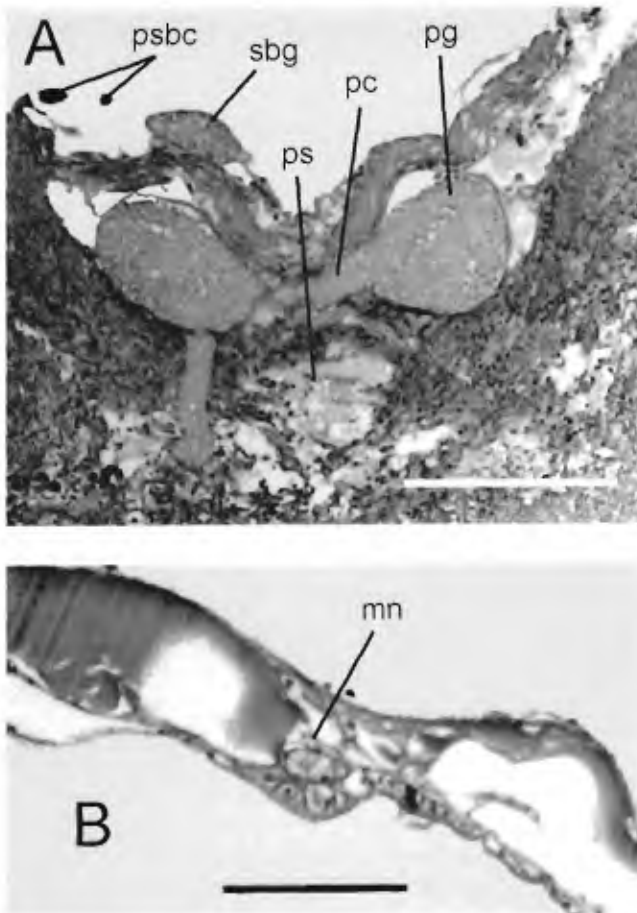
Sensory structures found in cocculinid species include osphradia, vestigial eyes modified to comprise the basitentacular gland (Haszprunar 1987a), and statocysts. No discrete sensory epithelium was found in *M. moskalevi*, apart from tall ( $\sim 20 \mu$ m), ciliated prismatic cells overlying the mantle nerve. Haszprunar (1987a) described the presence of "dimples" at the posterior base of the cephalic tentacles, modified into a mucus-secreting, "basitentacular" gland that is connected to the surface via a narrow or broad duct. The presence of basal pigment in *Cocculina cowani* supports the conclusion that these represent vestigial eyes. A small basitentacular gland (Fig. 1B, btg) is present in *M. moskalevi*. Statocysts (Fig. 2E, st) were found to contain a single statolith in one animal but several tiny statocones ( $\sim 3$ ) were found in another.

### Gut contents

Gut-content analysis of *M. moskalevi* confirmed the presence of dictyoceratid spongin fibers (S. Pomponi, pers. comm.) throughout the gut, almost to the exclusion of all other ingested material. Small quantities of putative fungal spores were also found in small concentrations (D. Lipscomb, pers. comm.).

### Discussion

*Macleaniella moskalevi* displays a number of anatomical features that are consistent with other cocculinid species, but differs in several significant ways (Table 1). While its external shell morphology is very similar to that of *Fedikovella caymanensis* (Moskalev 1976), it is unique among cocculinids in possessing a transverse septum within the shell. Such septae are similarly, but more weakly, developed in some species of *Tentaoculus* (Pseudococculinidae) (Marshall 1986; McLean & Harasewych 1995).



**Fig. 6.** **A.** Transverse section through pedal ganglia. Scale bar, 250  $\mu\text{m}$ . **B.** Transverse section through mantle nerve and possibly sensory overlying cells. Small patch of cilia visible at lower right. Scale bar, 100  $\mu\text{m}$ . Abbreviations: (mn) mantle nerve, (pc) pedal commissure, (pg) pedal ganglion, (ps) pedal sinus, (psbc) pleuro-subesophageal connective, (sbg) subesophageal ganglion.

Within the mantle cavity, *M. moskalevi* differs from other cocculinids in lacking a clearly defined osphradium. Apart from the prismatic ciliated cells (Fig. 6B) overlying the mantle nerve in the pallial roof, no trace of a discrete osphradium could be detected. It is possible that these cells have a sensory function in the absence of a well-defined osphradium located near the gill as in other cocculinid species. In addition, the position of the brood pouch is unique in that it occurs forward of the gill rather than deeper within the mantle cavity. The gill is extremely small and lacks the folded appearance typical of cocculinid pseudoplicatid gills. *M. mosaklevi* differs from some cocculinids in the development of the hypobranchial gland; the gland is uncharacteristically small and not located within a pocket enclosed ventrally by the kidney as in species

of *Paracocculina* and *Coccolpigya* and in *Cocculina cowani*. Thus, it does not conform to the "Manteldrüse" condition originally described by Thiele (1903) for *Cocculina* (*Paracocculina*) *laevis*.

The central position of the receptaculum seminis is unique and renders comparison with the paired or single left receptacula in other cocculinid species difficult. It appears to have a position similar to that of the single receptaculum found in the cocculinoidean genus, *Bathysciadium* (Thiele 1908). However, it differs from the receptaculum of *Bathysciadium pacificum* in that the latter is connected to the mantle cavity via an enclosed duct rather than directly to the gonoduct itself. As stated above, no connection between the receptaculum and the mantle cavity was discernable in *M. moskalevi*.

The right cephalic tentacle functions as a copulatory organ, as in *Coccol crater agassizii* (Haszprunar 1987a). While tentative, these findings parallel those of Haszprunar (1987a), who attributed the apparent absence of an open seminal groove in some cocculinid taxa to poor preservation.

Although several aspects of the circulatory system could not be examined in detail, it is clear that *M. moskalevi* differs considerably in the development of the aortic arch. This vessel connects the buccal and pedal sinuses in all other cocculinids studied to date. In *M. moskalevi* the aortic arch, while communicating directly with the pedal sinus, penetrates the buccal sinus anteriorly and the main visceral hemocoel posteriorly. This implies a much broader role for this vessel in circulation than in other species and indicates a greater potential for the distribution of the products of the hemal gland throughout the circulatory sinuses of the body. The aortic arch of *M. moskalevi* is also unique in the nature of its connection with the pericardium. In no other species is the aortic arch so closely associated with a blood vessel that communicates directly with the pericardium.

*Macleaniella moskalevi* is unique among described cocculinids in the arrangement of the nervous system. Most cocculinids fall into two categories regarding the arrangement of nerves: (1) hypoathroid with distinct visceral and supraesophageal ganglia, the former ganglion situated on the right and the latter on the left side of the body, and (2) dystenoid on the right and hypoathroid on the left with fused visceral and supraesophageal ganglia. *M. moskalevi* shows a dystenoid condition on the right side of the circum-esophageal nerve ring but the visceral and supraesophageal ganglia have remained unfused. However, recent anatomical investigations have revealed that *Fedikovella caymanensis* and *Teuthirostria cancellata* share this same

**Table 1.** Summary of anatomical features for *Macleaniella moskalevi*.

Character	State
<b>Mantle Cavity:</b>	
Brood Pouch	Anterior to gill
Gill	Reduced, papillate
Hypobranchial gland	Small
<b>Circulatory System:</b>	
Aortic arch	Penetrates buccal and visceral hemocoels
Nephridial gland	Absent
Pericardial gland	Weakly developed
Hemal gland	Small
<b>Reproductive System:</b>	
Receptaculum seminis	Single, central
Duct of the receptaculum seminis	Enclosed; no connection to mantle cavity
Copulatory organ	Modified right, cephalic tentacle
Seminal groove	Absent
<b>Alimentary System:</b>	
Salivary glands	Absent
Sublingual cavity	Glandular
Jaw	Reduced
Intestinal groove	Absent
Digestive glad ducts	Paired
<b>Nervous System and Sensory Structures:</b>	
Conformation of pleural ganglia	Dystenoid on the right
Fusion of Visceral/Supraesophageal ganglia	Unfused
Osphradial ganglion	Left
Statocyst	Polymorphic statolith/statoconia
Eyes	Basitentacular gland; narrow duct
Osphradium	Sensory? epithelium overlying mantle nerve

configuration of the nervous system (G. Haszprunar, pers. comm.). Additionally, while polymorphic within the species, *M. moskalevi* is the only known cocculinid to possess several small statocones. Statocones have been reported in lepetelloidean species (Haszprunar 1987a,b, 1988a,b), but cocculinid taxa have heretofore been characterized by the possession of a single statolith (Haszprunar 1987a).

Feeding biology and associated inferred adaptations of the digestive tract have figured prominently in the development of classifications of the Cocculiniformia (Haszprunar 1988a). Within the Cocculinoidea, the predominance of a life-habit strongly associated with wood has led to the conclusion that this represents the primitive substrate of cocculinids (and consequently cocculinoidean) taxa (Haszprunar 1988a). In addition, a highly modified alimentary tract accompanied by the presence of wood within the gut has lead to the conclusion that these animals feed upon the substrates they inhabit. However, not all agree that the wood is being digested; it has been suggested that microbes associated with the wood

may be the source of nourishment (Marshall 1986; McLean 1992).

As noted by Leal & Harasewych (1999), all specimens of *M. moskalevi* were taken from hardwood blocks and logs, in which they produced long, clearly demarcated grooves with semicircular cross-sections. Anemones, sponges, polychaete worms, and crustaceans were taken at the same stations. The overwhelming predominance of spongin fibers in the gut, in conjunction with their substrate association, tentatively supports the conclusion that *M. moskalevi* relies on materials (especially sponges) associated with its substrate as a food source, but occasionally non-selectively ingests its substrate. This represents a previously undescribed instance of spongivory within the Cocculinidae, a well-documented phenomenon among other deep-sea gastropod taxa (Harasewych et al. 1988).

### Conclusions

The description presented here highlights the need for further comprehensive accounts of cocculinid anat-

omy. The 11 species for which such information is available represent only 15% of the ~70 described cocculinoidean species. Although these 11 species represent 5 of 7 genera, the unique combinations of features these species continue to reveal indicates that there remains much to learn about the biology of this understudied group. As our knowledge of deep-sea limpet biology increases, it is likely that they will continue to intrigue us with "... extraordinary and unexpected characters" (Dall 1882).

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