Amer. Malac. Bull. **25**: 51-69 (2008)

Aesthete canal morphology in the Mopaliidae (Polyplacophora)*

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Abstract: The aesthete canals of fourteen chiton species were cast with epoxy, allowing detailed examination and comparison of the entire canal system that infiltrates their valves (shell plates). Some species in this study have been classified without question in the family Mopaliidae (*Mopalia ciliata* (Sowerby, 1840), *Mopalia lignosa* (Gould, 1846), *Mopalia spectabilis* Cowan and Cowan, 1977, *Mopalia swanii* Carpenter, 1864, *Katharina tunicata* (Wood, 1815)), while other species have been placed in that family by some workers but not others (*Dendrochiton flectens* (Carpenter, 1864), *Dendrochiton lirulatus* (Berry, 1963), *Tonicella insignis* (Reeve, 1847), *Tonicella lineata* (Wood, 1815), *Tonicella lokii* Clark, 1999, *Tonicella marmorea* (Fabricius, 1780), *Nuttallochiton mirandus* (Thiele, 1906), *Plaxiphora aurata* (Spalowski, 1795)), and one has never been placed in the Mopaliidae (*Tonicia chilensis* (Frembly, 1827)). The results provide additional evidence that there is high diversity in aesthete canal morphology but also some striking resemblances interpreted here as homologies, reaffirming that aesthete canal characters have considerable potential for phylogenetic analyses and for supporting classification ranks ranging from suborder to species. In this case, the results are broadly consistent with traditional classifications of mopaliids, but *Tonicella* and *Dendrochiton* (taxa not always thought not to be mopaliids) share many aesthete canal synapomorphies with undisputed mopaliids, whereas *Plaxiphora* (typically thought to be a mopaliid) has an aesthete canal system more similar to non-mopaliid members of the Acanthochitonina. These differences are in line with results of recent phylogenetic analyses of the Mopaliidae.

Key words: Chiton, *Mopalia*, valve, tegmentum, esthete

The hard layers of chiton valves consist of the uppermost tegmentum, the articulamentum whose projections form the sutural laminae and insertion plates, and the underlying hypostracum. The tegmentum, which is the visible layer of the chiton shell in life, is infiltrated with a complex, tissue-filled canal system that opens at the dorsal valve surface as sensory or secretory organs known as aesthetes (also *esthetes*) (Marshall 1869). The pores on the dorsal surface are entrances of tiny canals that often pass into bulb-shaped (aesthete) chambers that then connect to larger horizontal canals and eventually exit at the valve's anterior or lateral margin, or in some regions of the ventral valve surface (now known to correspond to the nervous innervation of the aesthetes). Knorre (1925) made detailed schematic drawings of the entire canal system in *Lepidochitona cinerea* (Linnaeus, 1767) (as *Trachydermon cinereus*) that revealed this configuration of canals. Prior to Knorre's (1925) work, Moseley (1885) noticed two size classes of aesthete pores (termed micropores and megalopores) on the dorsal valve surface and coined the term megalaesthete for the organic tissues within the often bulbous chambers near the valve's dorsal surface, and micraesthete for the tissues in the smaller canals that connect from the bulb of the megalaesthete to the valve surface. The organs that occupy the upper portion of the chiton tegmentum include the aesthetes (Blumrich 1891) and in some cases also the extrapigmental and intrapigmental ocelli (Nowikoff 1907, 1909). Although aesthetes have been found in all modern chitons so far examined, ocelli have so far been found only in some members of the Schizochitonidae (Moseley 1885) and Chitonidae (Boyle 1977).

Although there have been numerous studies of aesthetes in many chiton species (see the review in Reindl *et al.* 1997),

* From the symposium "Advances in Chiton Research" presented at the joint meeting of the American Malacological Society and Western Society of Malacologists, held 29 July to 3 August 2006 in Seattle, Washington.

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their function has been debated. Moseley (1885) documented the morphology of ocelli in *Schizochiton incisus* (Sowerby, 1841) (Chitonina: Schizochitonidae). In this species, the ocelli are the largest known for any chiton and are sparsely distributed in relatively huge chambers—presumably enlarged megalaesthete cavities. Boyle (1969a, 1969b) confirmed the presence of photoreceptors in ocelli in *Onithochiton neglectus* Rochebrune, 1861. A photosensory role for aesthetes had initially been proposed by Blumrich (1891) and observations that certain chiton species are either positively or negatively phototactic (*e.g.*, Crozier 1920, Omelich 1967, Boyle 1972, Fischer 1988, Currie 1989) have led many to view photoreception as the primary role of aesthetes. Indeed, Crozier and Arey (1918) observed that a crawling *Chiton tuberculatus* Linnaeus, 1758 (which lacks large conspicuous ocelli) immediately stopped crawling, temporarily, in response to a shadow from a fly about 2 m away. However, the function of most of the aesthetes, besides those with ocelli, has been disputed, with suggestions including mechanoreception (Moseley 1885), chemoreception (Fischer 1988, Baxter *et al.* 1990), periostracum replenishment and secretion (Boyle 1974, Baxter *et al.* 1987, 1990), and secretions for protection, prevention of desiccation, or fouling by epibionts (Fischer 1988). An electron microscopy study of aesthete tissues (Omelich 1967), an immunocytochemical study (Reindl *et al.* 1997), and electrical recordings (Omelich 1967, Fischer, pers. comm. in Eernisse and Reynolds 1994) have all shown that aesthetes contain neuronal structures, demonstrating a sensory function in at least some cases. However, it seems plausible that aesthetes could serve many roles, or the functions differ in different lineages, as suggested by Haas and Kriesten (1978), Fischer (1978, 1988), Sturrock and Baxter (1995), and others.

Because features of the aesthete canal system and the nature of aesthete caps vary between chiton taxa (*e.g.*, Boyle 1974, Baxter and Jones 1981, 1984, Sturrock and Baxter 1993, 1995, Reindl *et al.* 1997, Schwabe and Wanninger 2006), they provide a suite of characters that have been included in phylogenetic and taxonomic studies of chitons (*e.g.*, Hull and Risbec 1930-1931, Leloup 1940, 1942, 1948, Bullock 1985, 1988, O'Neill 1985, Watters 1990, Sirenko 1992, 2001, Saito 1996, 2006). Brooker (2004) included extensive data from the distribution, arrangement, density, shape, and size of ocelli; aesthete pore area, shape, densities, and ratios; and size, density, and shape of large pores in the tegmentum eaves in her cladistic analysis of the *Acanthopleura* Guilding, 1829. Moreover, Schwabe and Wanninger (2006) documented variation among chiton genera in the elevation of aesthete pores, pigmentation in the megalaesthetes, and the arrangement of micraesthetes around the megalaesthetes.

Currie (1989), however, cautioned that there can be much variation in size and density of aesthete pores in different areas of one valve. This point was echoed by Brooker (2004), who found this to be true in the *Acanthopleura* and who emphasized the need to compare data from the same valve area when describing differences in aesthete patterns between species.

Recently, using an approach pioneered by Haas and Kriesten (1978; see Eernisse and Reynolds 1994), Fernandez *et al.* (2007) made epoxy casts of the aesthete canal system in twelve chiton species and demonstrated variation among suborders, families, genera, and species. A cladistic analysis revealed congruence between relationships inferred from aesthete canal characters alone and those derived from other aspects of morphology as well as molecules, suggesting that aesthete canal characters are useful in helping to infer relationships between chitons (Fernandez *et al.* 2007).

This study expands previous work by focusing largely on internal relationships within one family of chitons, Mopaliidae Dall, 1889. This family has conventionally included at least *Mopalia* Gray, 1847, *Placiphorella* Carpenter in Dall, 1879, *Amicula* Gray, 1847, *Katharina* Gray, 1847, *Plaxiphora* Gray, 1847, and *Placiphorina* Kaas and Van Belle, 1994 (*e.g.*, Kaas and Van Belle 1994, Sirenko 2006). The placement of *Nuttallochiton* Plate, 1899 and *Dendrochiton* Berry, 1911 has been less consistent. For example, Thiele (1931) placed *Nuttallochiton* in the Lepidochitonidae, whereas Van Belle (1983) and Kaas and Van Belle (1987) placed it in the Chaetopleurinae (Ischnochitonidae) instead. Sirenko (1993, 1997, 2006) later assigned this genus to the Mopaliidae, although recent molecular phylogenetic analyses (Okusu *et al.* 2003, Eernisse, unpubl. data) suggest that *Nuttallochiton* should be excluded from that family. Berry (1911) originally proposed *Dendrochiton* as a member of Mopaliidae because its members possess girdle setae similar to those of *Mopalia*, but others have instead considered it to belong to Lepidochitonidae (*e.g.*, Ferreira 1982, Van Belle 1983). Van Belle (1983) and Kaas and Van Belle (1985) even considered it to be a subgenus of *Lepidochitona* Gray, 1821 within Lepidochitonidae.

Eernisse (unpubl. data) used mitochondrial 16S rDNA data to discover a previously unrecognized association of some conventional mopaliid genera (*Placiphorella*, *Katharina*, *Amicula*, and *Mopalia*) with genera normally placed in other families (*Cryptochiton*, *Tonicella* Carpenter, 1873, and *Dendrochiton*). Furthermore, these analyses revealed that the more southern genera, *Plaxiphora* and *Nuttallochiton*, are only distantly related to Mopaliidae. This family was previously diagnosed by a posterior caudal sinus in the tail valve, which may instead be interpreted as a convergent trait related to size increase and the enhancement of respiratory currents (Eernisse, unpubl. data). In order to provide evidence for or against this proposed rearrangement, we examined aesthete canal morphology in a number of undisputed

mopaliid taxa in addition to representatives newly embraced into, or excluded from, the Mopaliidae based on this new classification scheme (Eernisse, unpubl. data).

Thus the goals of this study were to: (1) determine if aesthete canal morphology supports this new taxonomic scheme of the Mopaliidae; (2) determine the degree and nature of variation in aesthete canal systems in a larger set of chitons (see Figs. 1 and 2) to better assess the hypothesis in Fernandez *et al.* (2007) that such characters are useful in chiton phylogeny; and (3) use the new data to refine the previous attempt (in Fernandez *et al.* 2007) to define potential characters and states of the aesthete canal system that may be useful in future phylogenetic analyses of chitons.

MATERIALS AND METHODS

All chitons used in this study were adults and most were collected from the Eastern Pacific (collection data: Appendix 1). Valves from at least two individuals from each species were treated, except for the deep-water *Nuttallochiton mirandus*. Two or three intermediate valves of each individual were embedded and examined. All epoxy casts and voucher valves for each species in this analysis have been deposited at the Santa Barbara Museum of Natural History (SBMNH).

Valves were removed from dried or alcohol-preserved specimens using a scalpel, tweezers, and scraping tools. Boiling the chitons to remove the valves was not done because this can break valves into pieces. The isolated intermediate valves of all species were soaked in household bleach for up to 24 hours and placed in a sonicating bath for 20-30 minutes at room temperature to dislodge remnant organic material and other debris. Valves were dehydrated through an ethanol series and then embedded in epoxy using a method modified after Golubic *et al.* (1970). A low viscosity, medium hardness embedding medium was mixed using the Embed 812 kit from Electron Microscopy Sciences. The Embed 812 kit consisted of Embed 812 embedding resin, Dodecenyl Succinic Anhydride (DDSA), Nadic Methyl Anhydride (NMA), and Benzyldimethylamine (BDMA). They were combined in the following proportions: 44.2% Embed 812, 35.4% DDSA, 17.7% NMA, and 2.7% BDMA. The valves were submerged in resin and placed under a vacuum in a desiccating chamber for 24 hours and then cured in an oven at 60 °C for 24 hours. The cured epoxy blocks were trimmed using a rotary hand tool with a thin-bladed saw. Cuts were made around the edges of the valves, making sure to intersect the valve along much of its margin. The epoxy blocks were placed in 10% HCl for another 24 hours, or until all of the calcium carbonate in the valves dissolved away, then rinsed thoroughly with distilled water, cleaned with bleach, and split apart into a dorsal and ventral cast.

In a few cases (*e.g.*, Fig. 3F), after the vacuum stage but prior to curing, valves were drained of most epoxy, with only a shallow pool extending just above the insertion plates. The surface of these valves, still with a coating of epoxy, was then wiped with a Kimwipe dipped in alcohol. This alternative method was included to better see the meglaesthete bulbs and associated micraesthetes near the dorsal valve surface (it allows the aesthete chambers to be visible from the top, rather than from underneath, where they are largely hidden by underlying canals).

The casts were gold sputtered for 90 seconds and examined using a LEO 1430 Scanning Electron Microscope (SEM) with an accelerating voltage (EHT) of 10-15 kV under high vacuum. Many images were taken using backscatter electron detectors (two to four quadrants) at high or variable pressure. The backscatter detectors (QBSD) produced far less charging than occasionally occurred with the secondary electron detector (SE). The number and exact backscatter detectors varied, though the best contrast was usually achieved with 3 of 4 detector quadrants on. In a few cases, charging still occurred, so variable pressure (30-40 Pa) and the Variable Pressure detector (VPSE) were used.

In many species, mopaliids in particular, the dense carpet of horizontal canals on the dorsal casts prevented a clear view of the overlying (in life; in SEM photographs of the dorsal casts, they underlie the horizontal canals), near-surface canal system. In these cases, a thin-tipped needle was used to pull away some of the horizontal canals and reveal the megalaesthete chambers and micraesthete canals that lay below on the casts. In such cases, re-coating with gold was necessary.

Epoxy casts made prior to this study and described in Fernandez *et al.* (2007) were also used in comparative analyses herein. These specimens are: *Mopalia muscosa* (Gould, 1846) (SBMNH 83143 and 83144), *Mopalia acuta* (Carpenter, 1855) (SBMNH 83160 and 369432), *Cyanoplax* (as *Lepidochitona*) *hartwegii* (Carpenter, 1855) (SBMNH 83146 and 83147), *Nuttallina californica* (Nuttall MS, Reeve, 1847) (SBMNH 83148, 83149, and 83156), *Lepidozona cooperi* (Dall, 1879) (SBMNH 83150 and 83151), *Lepidozona mertensii* (Middendorff, 1847) (SBMNH 83145 and 369438), *Lepidozona pectinulata* (Carpenter in Pilsbry, 1893) (SBMNH 83152 and 83153), *Placiphorella velata* Carpenter MS, Dall, 1879 (SBMNH 83161 and 369440), *Nuttallochiton hyadesi* (de Rochebrune, 1889) (SBMNH 83157), *Ischnochiton textilis* (Gray, 1828) (SBMNH 83158 and 369435), *Ischnochiton variegatus* (H. Adams and Angas, 1864) (SBMNH 83159 and 369437), and *Lepidopleurus cajetanus* (Poli, 1791) (SBMNH 83154 and 83155).

While most genera thought to belong in the Mopaliidae (plus a few other families) were included in this study, *Amicula* and *Cryptochiton* were not. *Cryptochiton* adults lack

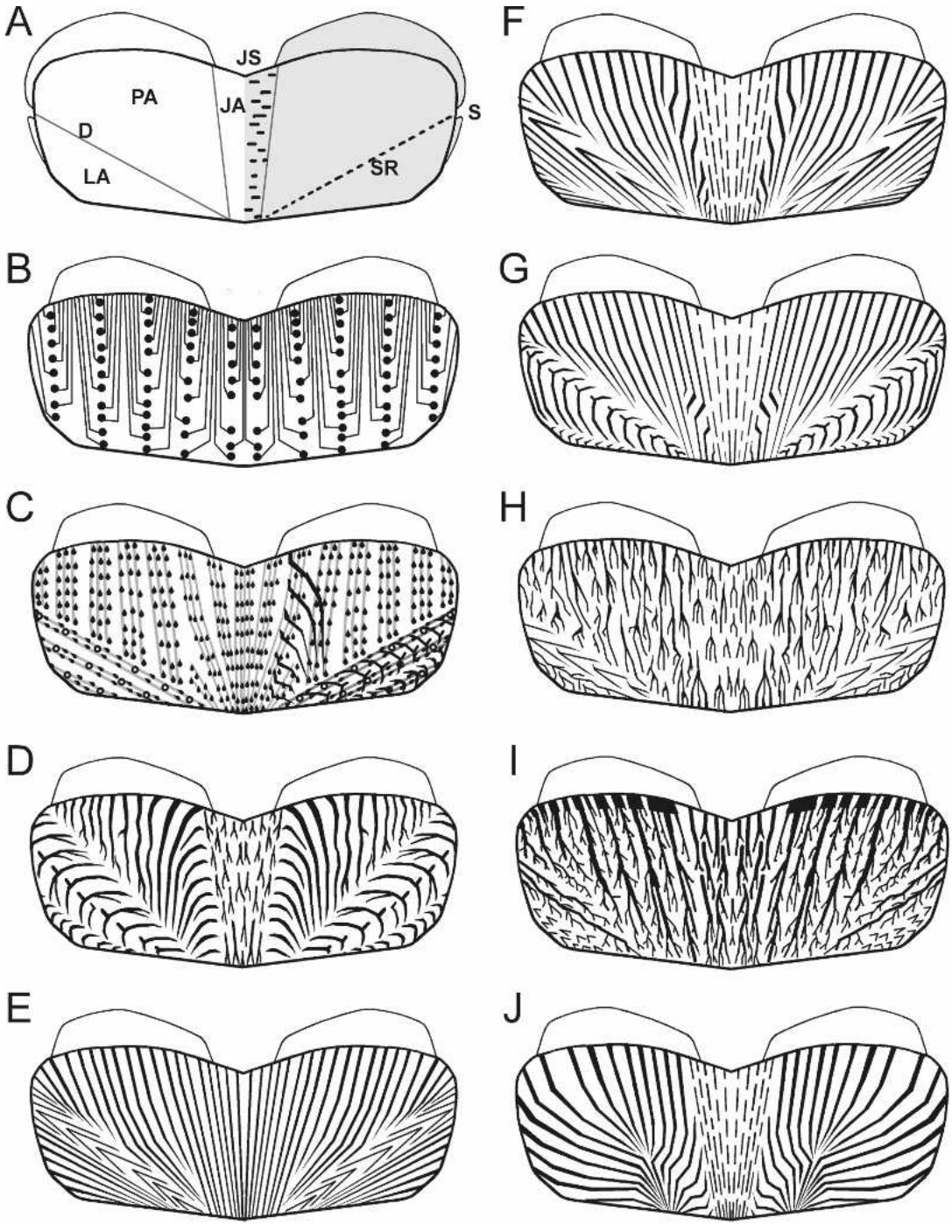

Figure 1. Schematic of the horizontal canal system in different chiton genera. A, Chiton intermediate valve showing dorsal (left side) and ventral (right side) features and terminology: D, diagonal line; JA, jugal area or jugum; JS, jugal sinus; LA, lateral area; PA, pleural area (also referred to as median triangle (Baxter and Jones 1981) or median area (Baxter and Jones 1984)); S, slit; SR, slit ray. B, Schematic of horizontal canals (lines) and megalaesthetes (filled circles) in *Lepidopleurus*, based on the pattern seen in *L. cajetanus*. C, *Lepidozona*, based on *L. cooperi*, *L. pectinulata*, and *L. mertensii*. D, *Ischnochiton*, based on *I. textilis* and *I. variegatus*. E, *Mopalia* type 1, characterizing *M. acuta*, *M. muscosa*, and *M. lignosa*. F, *Mopalia* type 2, characterizing *M. ciliata*, *M. spectabilis*, and *M. swanii*. G, *Tonicella*, based on *T. lokii*, *T. lineata*, *T. insignis*, and *T. marmorea*. H, *Plaxiphora*, based on *P. aurata*. I, *Cyanoplax*, based on *C. hartwegii*. J, *Nuttallina*, based on *N. californica*. The reconstructions in I and J were based on aesthete casts of *Cyanoplax hartwegii* (SBMNH 83146, 83147) and *Nuttallina californica* (SBMNH 83148, 83149, 83156) shown in Fernandez *et al.* (2007).

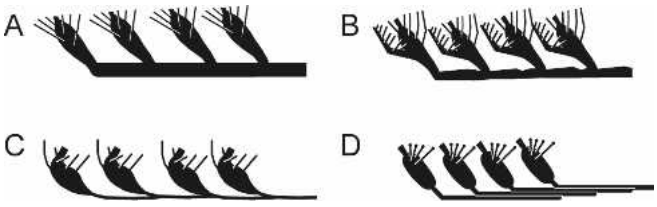

Figure 2. Schematic showing comparative morphology of canals that extend from the dorsal valve surface to the underlying horizontal canals. A, Form characteristic of *Mopalia* spp., *Tonicella* spp., *Dendrochiton* spp., *Placiphorella velata*, and *Katharina tunicata*. B, Form characteristic of *Cyanoplax hartwegii*, *Nuttallina californica*, *Plaxiphora aurata*, and *Nuttallochiton* spp. C, Form characteristic of *Ischnochiton* spp., *Tonicia chilensis*, and *Lepidozona* spp. D, Form characteristic of *Lepidopleurus cajetanus*. Reconstructions of *C. hartwegii*, *N. californica*, *P. aurata*, *Nuttallochiton*, *Ischnochiton*, and *Lepidozona* are based on aesthete canal casts described and photographed in Fernandez *et al.* (2007).

a tegmentum, and adults of *Amicula* have only a small remnant of that shell layer, which limits the extent to which their aesthete canal systems can be compared to those of other mopaliids. Valves of juvenile *Cryptochiton stelleri* Middendorff, 1847 have some tegmentum, but we were not able to obtain juveniles of this species for destructive analysis.

The cladistic analysis using only aesthete canal characters was constructed with PAUP 4.0b10 (Swofford 2002). All taxa from Fernandez *et al.* (2007) as well as those herein (N = 26 total from both studies) were scored for the analysis, although five taxa had the same exact character states as another taxon in the analysis, so these "redundant" taxa were excluded (N = 21 in this analysis) to allow for branch-and-bound analysis over a reasonable time frame. Specifically, *Mopalia lignosa* had the same character states as *Mopalia ciliata*, *Mopalia spectabilis* had the same as *Mopalia muscosa*, *Tonicella marmorea* had the same as *Tonicella lineata*, *Tonicella lokii* had the same as *Tonicella insignis*, and *Lepidozona cooperi* had the same as *Lepidozona mertensii*. All characters were un-weighted and all character states unordered (description of characters and their states in Appendix 2). *Lepidopleurus cajetanus* was used as the outgroup. A branch-and-bound search was completed using maximum parsimony.

All epoxy casts and voucher shell plates from each individual in this study as well as those in the previous one (Fernandez *et al.* 2007) have been deposited at the SBMNH.

RESULTS

Reference to the trend of the canal system in the descriptions to follow is consistent with the flow of sensory information and the direction of valve growth (see Baxter and Jones 1981, 1984), such that the pores on the dorsal tegmentum surface are taken to be the entrance and the sites where the canals enter the body of the chiton (large pores in the anterior and lateral tegmentum eaves, slit rays, and underneath the jugum) the exit. The terms anterior, posterior, dorsal, and ventral refer to the valve in life position. The two pieces of the aesthete canal cast are termed dorsal and ventral, also defined based on life position.

A nearly complete cast of the aesthete canal system was achieved in most relatively un-eroded valves. The few eroded valves (*e.g.*, from one individual of *Plaxiphora aurata*), in contrast, had missing canals and a high incidence of tunnels caused by endolithic organisms. The ventral casts in this study often had at least a few complete vertical canal elements (*i.e.*, extending from the dorsal to ventral surface of the valve), allowing a detailed examination of the megalaesthete-micraesthete complex in certain portions of the valve. The results reveal variation in the horizontal canal system (Fig. 1) as well as megalaesthete-micraesthete morphology (Fig. 2).

Data from the aesthete canal casts of *Mopalia acuta*, *Mopalia muscosa*, and *Nuttallochiton hyadesi*, described in Fernandez *et al.* (2007), are also incorporated into the following descriptions of the canal system in each genus.

The taxonomic assignments are based on Sirenko (1997, 2006) but assignments that differ between Sirenko (2006) and what is suggested by the phylogeny in Eernisse (unpubl. data) are indicated with a question mark. Specifically, Eernisse's phylogenetic hypothesis suggests *Dendrochiton* and *Tonicella* are in the Mopaliidae and *Nuttallochiton* is not.

Mopalia (Acanthochitonina: Mopaliidae) (Figs. 3, 4E-I)

The dorsal casts reveal large (ranging from about 20-75 μm diameter), nearly straight, roughly equal diameter, regularly spaced, primary horizontal canals that run from the posterior to anterior margin through all valve areas (Figs. 3C, 3E, 3H, 4E, 4I; also fig. 2a,b,j in Fernandez *et al.* (2007)). The canals are closely spaced (about 10-40 μm between primary canals) and only rarely do they merge with each other. At least two vertical levels of primary horizontal canals can be seen at their exit near the anterior margin of the valve. In *Mopalia ciliata*, *Mopalia spectabilis*, and *Mopalia swanii*, the horizontal canals on either side of the jugal area fan out laterally (Figs. 3H, 4A, 4I), whereas in the other species of *Mopalia*, the long axes of all horizontal canals in the central area are consistently straight (Fig. 3C; also fig. 2a,j in Fernandez *et al.* (2007)).

There are also many short, smaller-diameter (about 10-20 μm) subsidiary horizontal canals, above (in life) and inclined relative to primary horizontal canals, that merge with the primary canals at regular intervals (Figs. 3A-B, 3D, 4G;

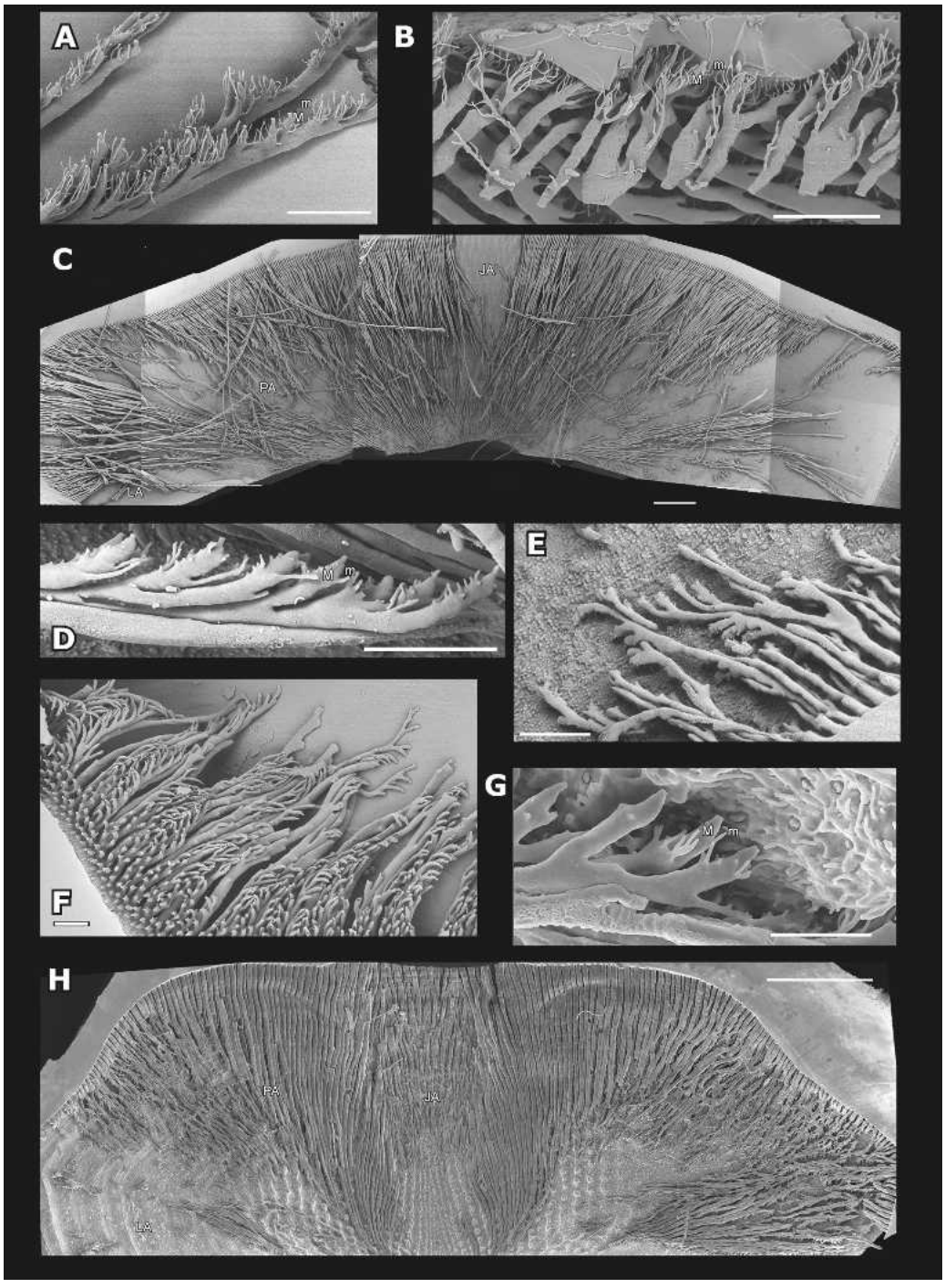

Figure 3. SEM images of casts of aesthete canal systems for *Mopalia spectabilis* (SBMNH 369491) (A-B), *Mopalia lignosa* (C-E), and *Mopalia swanii* (SBMNH 83329) (F-H). All images are of dorsal casts, except A which is of the ventral cast. A-B, *Mopalia spectabilis*. A, Close-up of a complete slit ray canal element on the ventral cast. Scale bar = 200 μm. B, Close-up of lateral area canals along the posterior margin of a different individual than in A. Scale bar = 200 μm. C-E, *Mopalia lignosa*. C, Composite image showing view of much of the system of horizontal canals (SBMNH 83328). Scale bar = 1 mm. D, Close-up of canals in the pleural area (SBMNH 83328). Scale bar = 200 μm. E, Canals in the pleural area along the anterior margin of a different individual (SBMNH 83327). Scale bar = 200 μm. F-H, *Mopalia swanii*. F, Complete canals in the pleural area. Cast was made by draining epoxy off valve prior to curing. Scale bar = 200 μm. G, Close-up of canals in the pleural area. Scale bar = 100 μm. H, Composite image showing horizontal canal pattern. Scale bar = 1 mm. Key: JAc, jugal area channel; M, megalaesthete chamber; m, micraesthete canal; SRc, slit ray channel; all other abbreviations as in Fig. 1A.

also fig. 2i in Fernandez *et al.* (2007)). Gently expanding megalaesthete chambers connect to these subsidiary canals (Figs. 3A, 3D, 3G, 4F-H; also fig. 2c,i in Fernandez *et al.* (2007)). Megalaesthete chambers begin as a short length of canal with a diameter of about 12-15 μm, before gently flaring out as they continue down towards the horizontal canals. At least four micraesthete canals (about 2-4 μm in diameter) trend in a straight, slightly angled to vertical manner to enter each megalaesthete chamber where it first reaches maximum diameter (Fig. 4F). At the top of the casts of the micraesthete canals and megalaesthete chambers are cup-shaped protuberances (Figs. 3G, 4G) that appear to be casts of subsidiary and apical caps, respectively.

In the jugal area of dorsal casts, some horizontal canals have a more flattened appearance and project upward (*i.e.*, turn down towards the ventral valve surface in life). The canals that exit at, or very close to, the jugal sinus, on the other hand, have a circular cross-section. On the ventral casts, the corresponding area (referred to as the ventral jugal triangle in Fernandez *et al.* (2007)) has short lengths of similarly flattened canals. These ventral canals occur in rows that correspond to valve growth lines; about five or more canals along some growth lines can be seen on the casts of species such as *Mopalia ciliata*. Most of the *Mopalia* spp. have a large number of canals that exit below the jugum, but *Mopalia acuta* has only very few jugal area canals that exit ventrally.

In *Mopalia ciliata*, *Mopalia spectabilis*, and *Mopalia swanii*, the horizontal components of the slit ray canals occur through a large portion of the lateral areas (Figs. 4E, 4I), with canals on either side of the slit ray progressing at a low angle relative to each other to meet and then turn downwards towards the slit ray. In contrast, the other species of *Mopalia* have slit ray canals that only extend for a short distance to either side of the slit ray, with the two horizontal components meeting at an even lower angle (Fig. 3C; also Fig. 2a,j in Fernandez *et al.* (2007)).

Tonicella (Acanthochitonina: Tonicellidae?) (Figs. 4A-D, 5)

This genus has large (ranging from about 40-75 μm diameter), long, somewhat wavy, wide, very regularly spaced, main horizontal canals that occur from the anterior to posterior margin of the valves (Figs. 4A, 5A-B, 5F, 5L). The spacing of canals is even more regular than in the *Mopalia* spp., giving the aesthete canal system in this genus the most orderly appearance. The main horizontal canals regularly meet gently-tapering megalaesthete chambers (*e.g.*, Fig. 4B, 4D, 5E, 5G, 5I) that are themselves embedded with numerous micraesthete canals. These megalaesthete chambers are connected obliquely downward by short canals to the main horizontal canals. The micraesthetes tend to be relatively short and straight.

The jugal area canals begin as micraesthetes that connect to gently tapering megalaesthete bulbs that connect to long, occasionally somewhat sprawling (Fig. 4H), canals that after a short distance begin to turn downward. These canals extend for a fair distance before merging with others into a larger canal, which then extends for a distance before merging with an even larger one (Fig. 5J). All the species in this genus had a high number (>30) of canals exiting ventrally below the jugum.

The slit ray canals make up the entire lateral area of the tonicellids, and have a high arc, with a consistent curve towards each other (Figs. 4A, 4C, 5A, 5C, 5F, 5L). On the ventral casts, the slit ray exits can be seen to begin as a line near the apex, but often split up into two or more rows towards the lateral margins of the valve.

Katharina (Acanthochitonina: Mopaliidae) (Figs. 6D-G)

The dorsal casts of *Katharina tunicata* reveal straight, regularly spaced, fairly large (about 30-40 μm diameter), densely packed horizontal canals that are angled towards the posterior apex in the lateral and pleural areas. The jugal area is dominated by canals that exit ventrally ("jugal area channels" of Baxter and Jones (1981)) (Fig. 6F). The jugal area canals have a high rate of merging before exiting at the ventral surface below the jugum. The morphology of the canals that lead into these horizontal canals is quite variable within the two individuals observed. In most cases, the micraesthetes connect to gently tapering megalaesthete chambers that then connect through a short canal into a main horizontal canal. In other cases, a large number of micraesthetes connect to long, narrow, often branching canals that then lead to a main horizontal canal or into a megalaesthete chamber (Fig. 6D). In the jugal area channels, numerous long, straight micraesthetes merge into the large canals either directly or by first merging into short, intermediate sized canals (Fig. 6E).

The apical area canals are quite noticeable on the ventral cast (Fig. 6G), perhaps because the apical area is more extensive in this species than in any other in the study. Many large horizontal canals occur in the apical area, connecting to micraesthetes that originate on the ventral or posterior surface of the apical area. The slit ray canals were not clearly seen in the SEM images of the casts.

Dendrochiton (Acanthochitonina: Tonicellidae?)
(Figs. 7A-F)

The dorsal casts show large (about 40-50 μm diameter), long, fairly dense (about 60 μm between adjacent canals), somewhat wavy main horizontal canals that occur from the anterior to posterior margin of the valve (Figs. 7A, 7E). These canals have regular intersections with gently expanding megalaesthete chambers (Figs. 7C-D, 7F). Numerous straight micraesthetes trend downward and attach at the megalaesthete chamber all along its extent nearly up to its

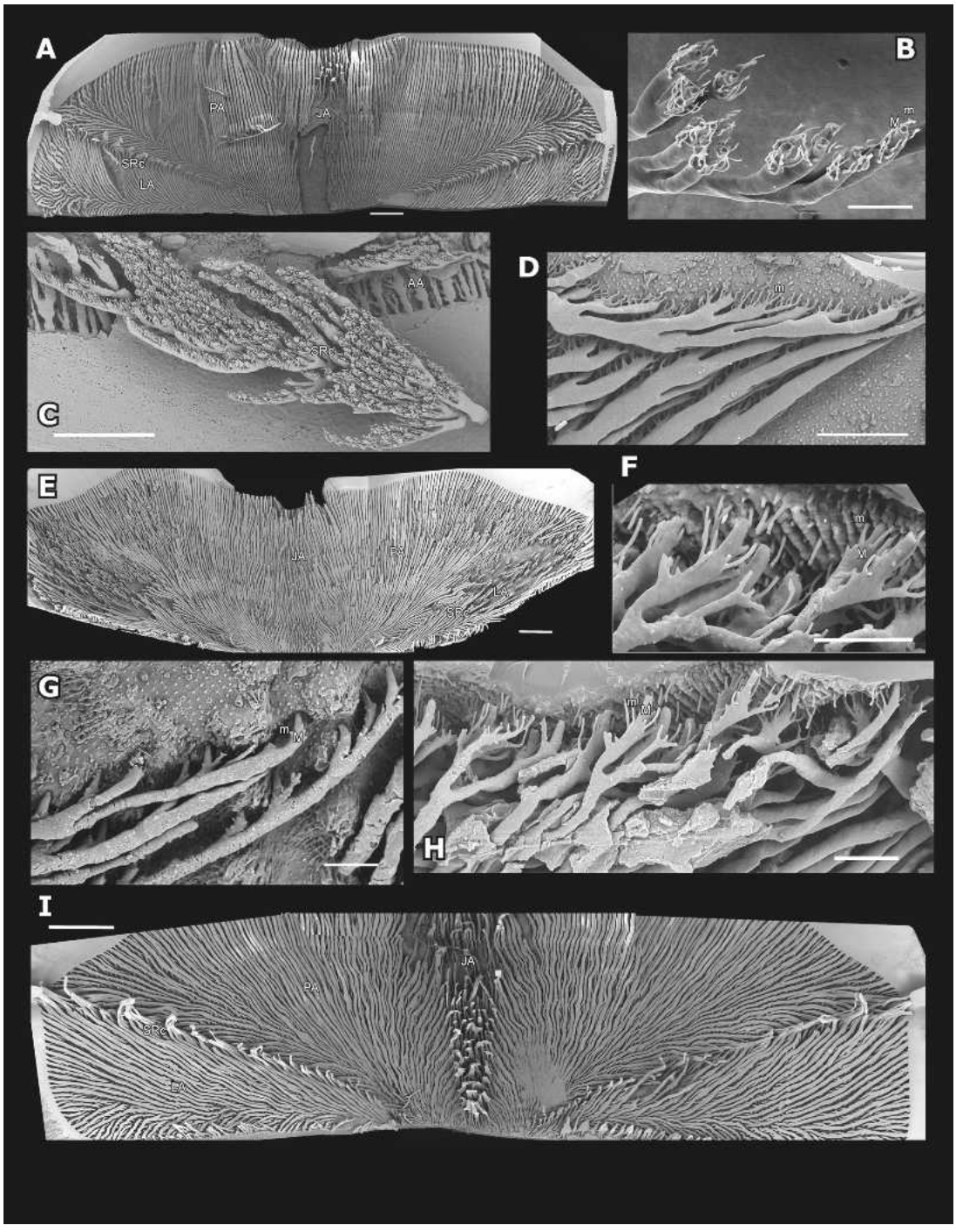

Figure 4. SEM images of casts of aesthete canal systems for *Tonicella insignis* (SBMNH 369497) (A-D), *Mopalia ciliata* (SBMNH 369501) (E-H), and *Mopalia spectabilis* (SBMNH 369501) (I). B and C are photos of ventral casts; all others are dorsal casts. A-D, *Tonicella insignis*. A, Composite image showing the whole horizontal canal pattern. Scale bar = 1 mm. B, Close-up of the near-surface portion of a slit ray canal. Scale bar = 100 μm. C, View of slit ray canals overlying (in this image) apical area canals in a different individual than shown in A-B. Scale bar = 200 μm. D, Close-up of the lateral area near the posterior margin of the valve. Scale bar = 200 μm. E-H, *Mopalia ciliata*. E, Composite image showing the entire horizontal canal system (SBMNH 83326). Scale bar = 1 mm. F, View of canals along the posterior margin (in between the lateral area and apical area) (SBMNH 83325). Scale bar = 100 μm. G, Close-up of canals in lateral area (SBMNH 83325). Scale bar = 100 μm. H, Close-up of canals in jugal area (SBMNH 83325). Scale bar = 100 μm. I, *Mopalia spectabilis*, composite image showing the whole horizontal canal pattern. Scale bar = 1 mm. Key: AA, apical area; others as in Figs. 1A and 3.

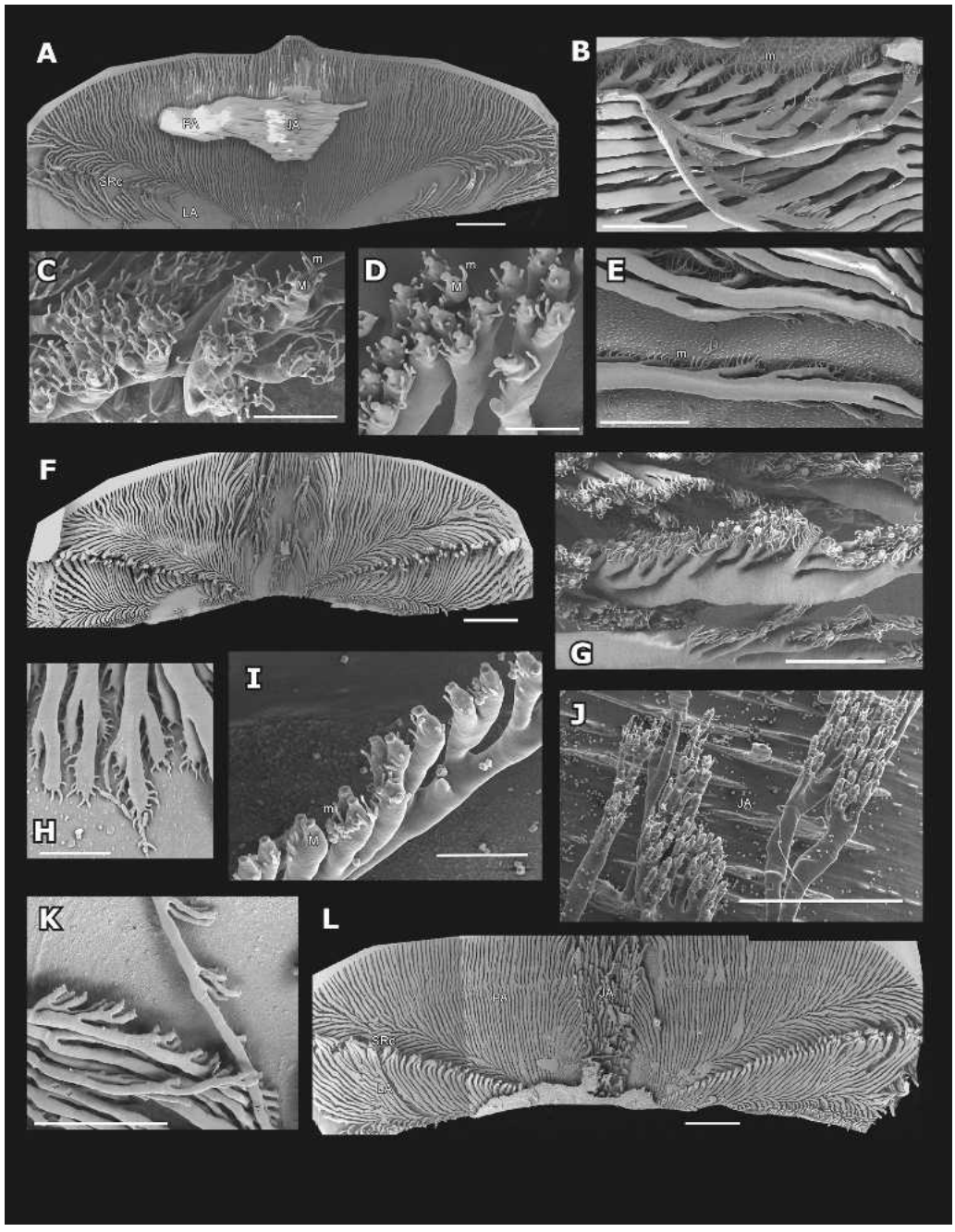

Figure 5. SEM images of casts of aesthete canal systems for *Tonicella marmorea* (SBMNH 369496) (A-D), *Tonicella lineata* (SBMNH 369488) (E-H), and *Tonicella lokii* (I-L). All images are of dorsal casts, except C, D, G, J, and I, which are images of ventral casts. A-D, *Tonicella marmorea*. A, Composite image showing complete horizontal canal system, with some remnant shell material in the middle. Scale bar = 1 mm. B, Close-up of region of pleural area with some horizontal canals scraped aside. Scale bar = 200 μm. C, Close-up of dorsal portion of slit ray canals. Scale bar = 100 μm. D, Close-up of some canals in the apical area. Scale bar = 100 μm. E-H, *Tonicella lineata*. E, Close-up of canals in the pleural area, with some missing adjacent horizontal canals. Scale bar = 200 μm. F, Composite image showing overall horizontal aesthete canal pattern. Scale bar = 1 mm. G, Close-up of canals in the apical area. Scale bar = 200 μm. H, Close-up of jugal area canals. Scale bar = 100 μm. I-L, *Tonicella lokii*. I, Close-up of dorsal portion of slit ray canals on the ventral cast (SBMNH 83319). Scale bar = 100 μm. J, Close-up of jugal area canals on the ventral cast (SBMNH 83319). Scale bar = 500 μm. K, Close-up of canals in the pleural (right) and lateral (upper left) region of the shell, with numerous horizontal canals missing, dorsal cast (SBMNH 83319). Scale bar = 500 μm. L, Composite image showing the overall horizontal aesthete canal pattern of a different individual (SBMNH 83320). Scale bar = 1 mm. Key: same as in Figs. 1A and 3.

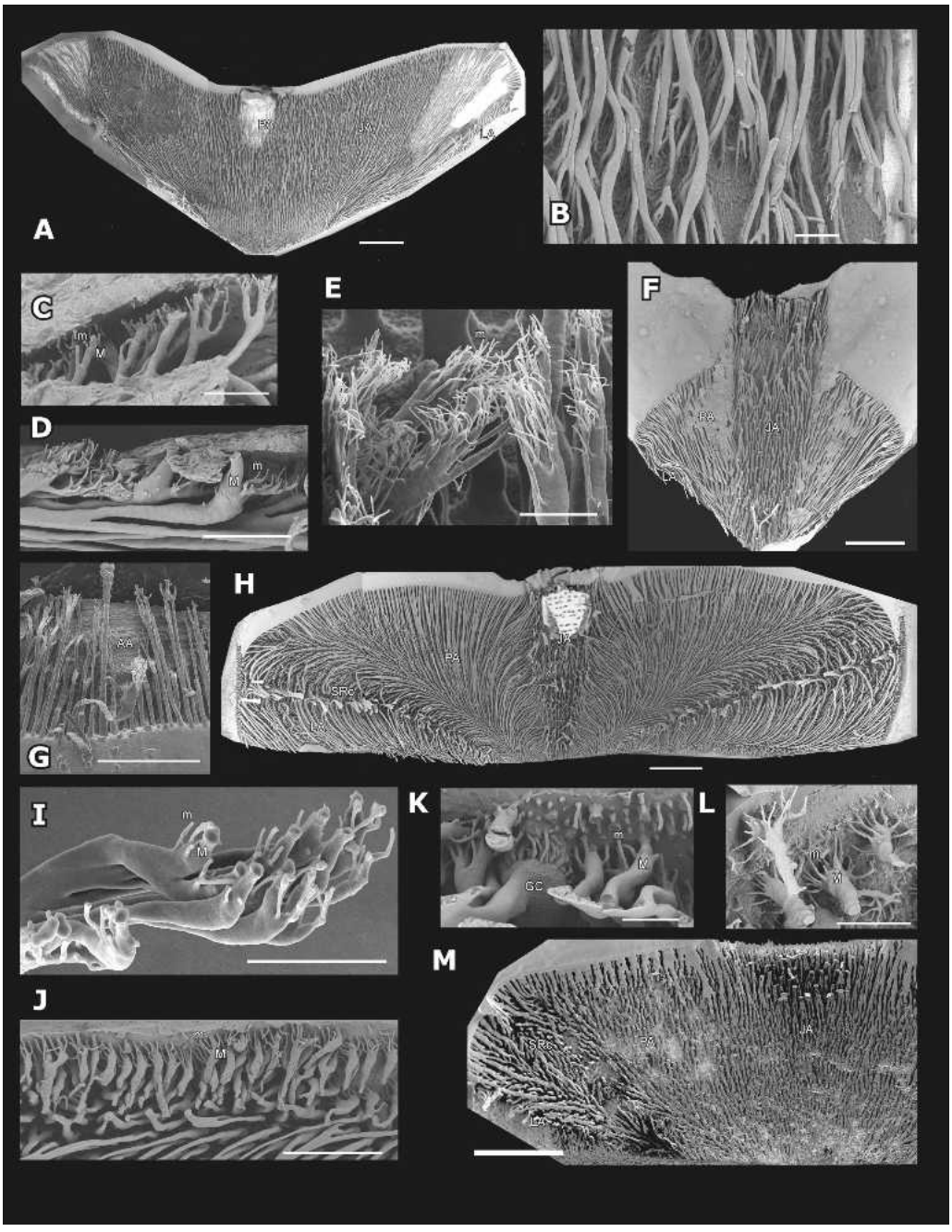

Figure 6. SEM images of casts of aesthete canal systems for *Plaxiphora aurata* (SBMNH 83321) (A-C), *Katharina tunicata* (SBMNH 369494) (D-G), *Tonicia chilensis* (SBMNH 369486) (H-K), and *Cyanoplax hartwegii* (SBMNH 83147) (L-M). Photos E, G, and I are of ventral casts; all others are of dorsal casts. A-C, *Plaxiphora aurata*. A, Composite image showing pattern of the horizontal canal system. Scale bar = 1 mm. B, Close-up of jugal area canals. Scale bar = 100 μm. C, Close-up of canals in the lateral area, near the posterior margin. Scale bar = 100 μm. D-G, *Katharina tunicata*. D, Close-up of canals in the lateral area, along the posterio-lateral margin. Scale bar = 100 μm. E, Close-up of dorsal portion of jugal area canals. Scale bar = 1 mm. F, Composite image showing horizontal canal system. G, Close-up of canals in the apical area. Scale bar = 500 μm. H-K, *Tonicia chilensis*. H, Composite image showing horizontal canal system. Some remnant shell material visible in middle anterior. Scale bar = 1 mm. I, Close-up of slit ray canals. Different individual than in H, J-K. Scale bar = 100 μm. J, Close-up of lateral area along the posterior margin. Scale bar = 200 μm. K, Close-up of pleural area showing large chamber (that presumably contained an ocellus). Scale bar = 50 μm. L-M, *Cyanoplax hartwegii*. L, Close-up of lateral area canals at the posterio-lateral corner. Scale bar = 100 μm. M, Composite image showing horizontal canal pattern. Scale bar = 1 mm. Key: GC, giant chamber, presumably that held an ocellus; others as in Figs. 1A, 3, and 4.

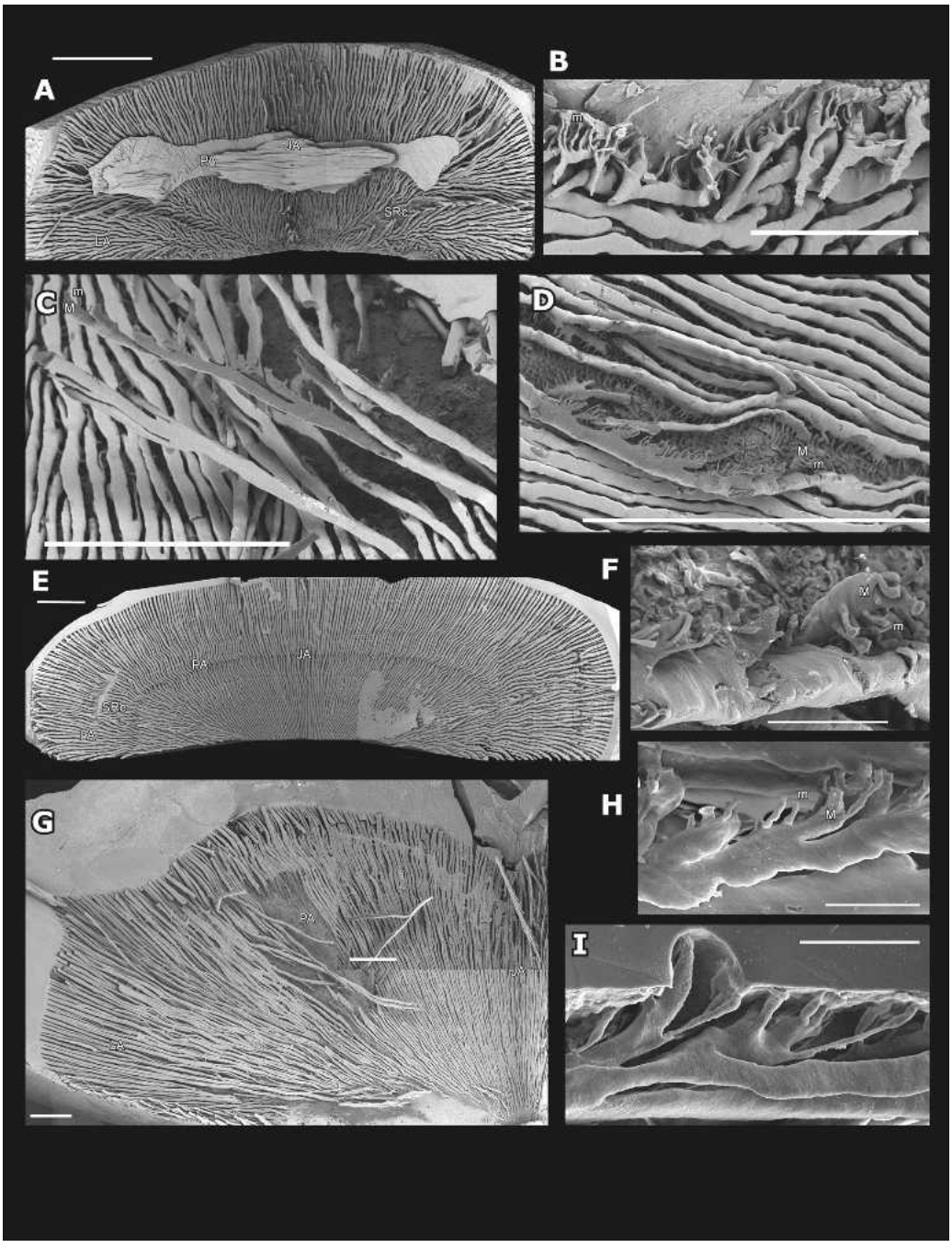

Figure 7. SEM images of casts of aesthete canal systems for *Dendrochiton lirulatus* (SBMNH 369493) (A-C), *Dendrochiton flectens* (SBMNH 369492) (D-F), and *Nuttallochiton mirandus* (SBMNH 83324) (G-I). All images are of dorsal casts. A-C, *Dendrochiton lirulatus*. A, Composite image showing view of much of the system of horizontal canals, with some remnant shell material in the center. Scale bar = 1 mm. B, Close-up of the lateral area near posterior margin. Scale bar = 200 μm. C, View of pleural area, portion of anterior margin in upper right. D-F, *Dendrochiton flectens*. D, View of pleural area showing a region with horizontal canals pulled aside, showing megalaesthete and micraesthete canals. Scale bar = 1 mm. E, Composite image showing view of the complete horizontal canal system. Scale bar = 1 mm. F, Close-up view of region of D. Scale bar = 100 μm. G-I, *Nuttallochiton mirandus*. G, Composite image showing one half of the entire horizontal canal system. Scale bar = 1 mm. H, View of jugal area surface canals along the broken margin. Scale bar = 100 μm. I, View of another region of jugal area surface canals along the broken margin. Scale bar = 100 μm. Key: same as in Figs. 1A and 3.

intersection with the main horizontal canal (Figs. 7B, 7D, 7F).

The jugal area channels are more prominent in *Dendrochiton lirulatus* than in *Dendrochiton flectens* (compare Figs. 7A and 7E). The jugal area channels begin as micraesthetes that connect to sprawling, sub-cylindrical, horizontal canals that then connect to cylindrical canals that turn downwards, merging with others of their kind, before terminating at the ventral valve surface below the jugum.

In one individual of *Dendrochiton flectens*, canals exited at many different places on the ventral surface of the valve, not just below the jugum and in the slit rays. Such a pattern has not been seen in any of the twelve species studied by Fernandez *et al.* (2007) or in the thirteen other species in this study, and likely resulted from abnormal growth. The horizontal components of the slit ray canals have a relatively narrow lateral extent (Figs. 7A, 7E) and form a single prominent line of pores that make up the slit ray.

Plaxiphora (Acanthochitonina: Mopaliidae?) (Figs. 6A-C)

This species is characterized by micraesthete canals that enter small narrow canals or gently tapering megalaesthete chambers (Fig. 6C) that then connect with small horizontal canals (about 15-20 μm diameter), which may merge a few times until becoming relatively narrow, widely spaced, wavy main horizontal canals (Fig. 6B). One individual examined, whose valves were eroded, had a high density of tunnels made by endolithic organisms. There are very few jugal area canals apparent on either the dorsal or ventral casts of either specimen.

The horizontal components of the slit ray canals extend for a short width on either side of the slit ray, meeting at a low angle (Fig. 6A), nearly sub-parallel to the slit ray, before the merged canal trends upward on the dorsal cast (downward in life) towards pores along the slit ray.

The apical area canals, seen on the ventral cast, show relatively widely-spaced horizontal canals running most of the length of the apical area. They originate as micraesthete canals on the ventral surface of the apical area, near or along the posterior margin. These small-diameter canals widen and then, in many cases, merge with another horizontal canal as they progress toward the anterior margin of the apical area.

Nuttallochiton (Acanthochitonina: Mopaliidae?) (Figs. 7G-I)

The dorsal casts reveal primary horizontal canals (about 30-50 μm in diameter) throughout the entire interface between the tegmentum and articulamentum (Fig. 7G; also fig. 2g in Fernandez *et al.* (2007)). There is a spacing of about 20-50 μm between canals, with about 18 canals per mm along the horizontal plane. Micraesthetes (1-3 μm diameter) connect to the elongate, indistinct megalaesthete chambers that regularly connect, after a short distance, to the primary horizontal canals (Fig. 7H; also fig. 2h in Fernandez *et al.* (2007)). The megalaesthete chambers have a diameter of about 10-12 μm before widening to the same diameter as the connecting canals (about 17-20 μm).

Nuttallochiton mirandus appears to have no, or very few, jugal area canals and very few slit ray canals. The latter condition contrasts with *Nuttallochiton hyadesi*, which has a wider lateral extent of the horizontal components of the slit ray canals (compare Fig. 7G with fig. 2g in Fernandez *et al.* (2007)).

Tonicia (Chitonina: Chitonidae) (Figs. 6H-K)

The specimens of *Tonicia chilensis* show relatively narrow (about 30-40 μm diameter), widely spaced (about 50-100 μm between canals), curving horizontal canals that repeatedly intersect canals from megalaesthete chambers. All the megalaesthete chambers consist of bulbs that are embedded with a relatively small number of micraesthete canals (Figs. 6I-J). The main horizontal canals on either side of the jugal area have a very high arc towards the lateral margin. In a few locations, extremely large aesthete bulbs occur (much larger than the typical megalaesthete chambers), that are embedded with an immense number of micraesthete canals (Fig. 6K).

The jugal area canals are abundant and cover most of the valve surface (Fig. 6H). Many of these canals originate in the pleural areas and may even extend to the lateral areas. Such a wide extent of jugal area canals has not been seen in any of the twelve species examined in Fernandez *et al.* (2007) or in any of the other thirteen species in this study. The slit ray canals take up the entire lateral area (Fig. 6H) and have a similar degree of convergence of canals as in the jugal area channels of the central area.

DISCUSSION

Variation in aesthete canal characters

The results provide further evidence for variation in aesthete canal morphology among chiton suborders, families, genera, and often species (Table 1). Building from Fernandez *et al.* (2007), the results herein confirm that many chiton taxa at all taxonomic ranks are unified by synapomorphies (whether a character state is primitive or derived, assessed by the cladistic analysis using *Lepidopleurus cajetanus* as an outgroup) and that aesthete features have considerable potential as phylogenetic characters at a number of levels.

The cladistic analysis herein (Fig. 8) yields a phylogenetic hypothesis based solely on the broad morphology of

the aesthete canal system across a large group of chitons, mostly within the Suborder Acanthochitonina. The cladistic analysis is meant to: (1) show the similarities and differences in the aesthete canal system between a larger set of chitons; (2) refine characters and character states from Fernandez *et al.* (2007), in light of the new information, to make the characters/states more useful for future phylogenetic analyses of a broader range of taxa; and (3) test a recent view of mopaliid phylogeny (Eernisse, unpubl data).

Many other aspects of chiton morphology have been used in phylogenetic studies of chitons, including egg hull characters (Eernisse 1984, 1988, Sirenko 1993, 1997, 2006), sperm morphology (Hodgson *et al.* 1988, Buckland-Nicks 1995, 2006, Buckland-Nicks and Hodgson 2000), radula and radular tooth biomineralization patterns (Bullock 1985, Brooker and Macey 2001, Saito 2003), gill placement characters (Eernisse 1984, Sirenko 1993, 1997, 2006), and girdle and gland characters (Sirenko 2006). Moreover, Okusu *et al.* (2003) have been successful in using molecular sequences to infer chiton phylogeny. Attempts to determine the phylogenetic relationships within the Polyplacophora should of course incorporate as many of these characters as possible (Sirenko 2006), and we would add aesthete canal morphology to this list.

Aesthete canal morphology in the Mopaliidae

Fernandez *et al.* (2007) described how the mopaliids in their study (*Mopalia muscosa*, *Mopalia acuta*, *Placiphorella velata*, and *Nuttallochiton hyadesi*—but see below) are characterized by wide, straight, closely spaced, primary horizontal canals that exist through much of the valve length, as well as regular merging of short, subsidiary branches from the upper tegmentum with these primary canals. The subsidiary branches connect with only slightly expanded megalaesthete "chambers" just below the valve surface that are embedded with a large number of micraesthete canals. This pattern was also seen in all the *Mopalia* spp., *Katharina tunicata*, and some others (see below) in this analysis, strengthening the hypothesis that such aesthete canal characters typify mopaliids.

In addition, the results of this study show how *Mopalia ciliata*, *Mopalia spectabilis*, and *Mopalia swanii* share aesthete canal characters that are absent in *Mopalia acuta*, *Mopalia lignosa*, and *Mopalia muscosa*, based on the observations that the former group has a wider range of the slit ray canals and a more fan-like arrangement of the horizontal canals that flank the jugal area than the latter group.

Katharina tunicata shows the typical mopaliid pattern of long, straight, horizontal canals with gently tapering mega-

Table 1. Aesthete characters used in the PAUP analysis. Descriptions of characters and character states provided in Appendix 2. Key to abbreviations: jug, number of canals that exit ventrally under jugum; lat, nature of slit ray canals in lateral area; lin, linear arrangement and orderly spacing of megalaesthete bulbs; mgc, types of megalaesthete chambers; hgc, huge aesthete chambers; deh, density of horizontal canals; shc, connection between surface and main horizontal canals; flj, divergence of horizontal canals flanking jugal area; hap, straight horizontal canals; reg, regular merging of short canals into main horizontal ones; lam, lateral merging of main horizontal canals.

Species	jug	lat	lin	mgc	hgc	deh	shc	flj	hap	reg	lam
Mopalia ciliata	1	2	0	0	0	1	1	2	1	1	0
Mopalia muscosa	1	2	0	0	0	1	1	0	1	1	0
Mopalia swanii	1	2	0	0	0	1	1	2	1	1	0
Mopalia acuta	1	2	0	0	0	1	1	0	1	1	0
Tonicella lineata	1	1	0	0	0	1	1	2	1	1	0
Tonicella insignis	1	1	0	0	0	1	1	2	1	1	0
Tonicia chilensis	1	0	0	2	1	0	1	0	1	0	0
Placiphorella velata	1	2	0	0	0	1	1	0	1	1	0
Dendrochiton flectens	?	2	0	0	0	1	1	0	1	1	0
Dendrochiton lirulatus	1	2	0	0	0	1	1	0	1	1	0
Katharina tunicata	1	2	0	0	0	1	1	1	1	1	0
Nuttallochiton mirandus	0	1	0	1	0	1	0	0	1	0	0
Nuttallochiton hyadesi	0	2	0	1	0	1	0	0	1	0	0
Plaxiphora aurata	0	3	0	1	0	0	0	0	0	0	1
Ischnochiton textilis	1	0	0	2	?	0	1	0	0	0	0
Ischnochiton variegatus	1	0	0	2	0	0	1	0	0	0	0
Nuttallina californica	1	3	0	1	0	0	0	0	0	0	1
Cyanoplax hartwegii	1	3	0	1	0	0	0	0	0	0	1
Lepidopleurus cajetanus	1	4	1	3	0	0	2	0	0	0	0
Lepidozona mertensii	1	0	1	2	1	0	1	0	0	0	0
Lepidozona pectinulata	1	0	1	2	1	0	1	0	0	0	0

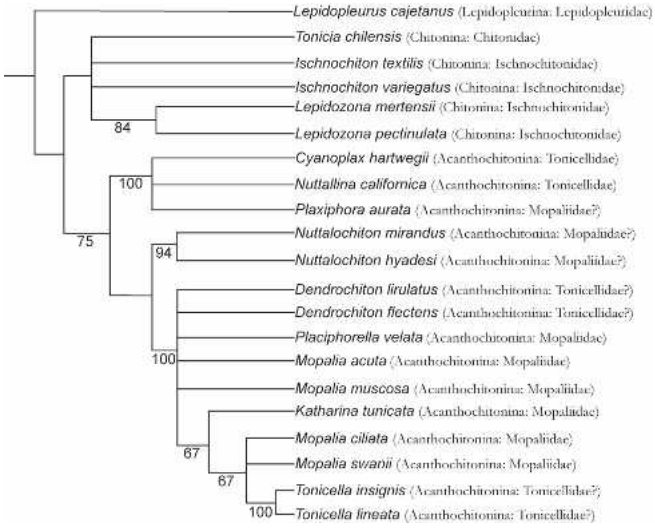

Figure 8. Majority-rule consensus tree of the 96 most parsimonious trees (with 23 steps) that resulted from the cladistic analysis (PAUP) using only aesthete canal morphology. Numbers indicate majority rule consensus values. The data matrix for the analysis is shown in Table 1 and the characters and character states are listed in Appendix 2. The taxonomic assignments are based on Sirenko (1997 and 2006) but assignments that differ between Sirenko (2006) and what is suggested by the phylogeny in Eernisse (unpubl. data) are indicated with a question mark. Specifically, Eernisse's phylogenetic hypothesis suggests *Dendrochiton* and *Tonicella* are in the Mopaliidae and *Nuttallochiton* is not.

laesthete bulbs, but it also has some long, relatively narrow, horizontal, occasionally branching, subsidiary canals just below the surface that are embedded with numerous micraesthetes along their length, a character also seen in *Nuttallina californica* and *Cyanoplax hartwegii* (previously *Lepidochitona hartwegii*) (Fernandez *et al.* 2007).

Our previous study of chiton aesthete canal casts (Fernandez *et al.* 2007) revealed that *Nuttallochiton* bears strong similarities in the aesthete canal system with other members of the Mopaliidae, and the results of this study are not inconsistent with that interpretation. The cladistic analysis suggests that *Nuttallochiton* is either a basal group within the Mopaliidae or is the outgroup to that family (Fig. 8). Regardless of which interpretation is preferred, it is clear that the aesthete canal system of *Nuttallochiton* is intermediate between those of (other) mopaliids and other members of the Acanthochitonina such as *Cyanoplax* and *Nuttallina*. The *Nuttallochiton* species in this analysis and the previous one (Fernandez *et al.* 2007) share the large, closely spaced horizontal canals with mopaliids, but also share with *Cyanoplax* sprawling megalaesthete super-chambers that connect to the main horizontal canals via a canal subparallel to the surface, in addition to regular merging of short horizontal canals in the posterior half of the valve. However, *Nuttallochiton* differs from the members of the Acanthochitonina so far examined in lacking a large number of micraesthetes, and it differs from most other chitons so far examined in having no or very few canals that exit underneath the jugum. Overall, it shares similar aesthete canal characters both with the *Cyanoplax* group and undisputed members of Mopaliidae, but distinguishing between derived and plesiomorphic similarities will be best considered in the context of a more complete analysis of morphological and molecular evidence.

Plaxiphora had been historically placed in the Mopaliidae (*e.g.*, Kaas and Van Belle 1987, Sirenko 2006), but the results of this study suggest, as in Eernisse (unpubl. data), that this genus belongs outside of this family. *Plaxiphora* has a very high ratio of micraesthetes/megalaesthete, and a greater amount of shell material between neighboring horizontal canals than in the mopaliids. It also shares sprawling megalaesthete chambers with *Cyanoplax* and *Nuttallina,* other members of the Acanthochitonina, although a broader study incorporating more members of this suborder and the others is needed to better determine whether these shared characters are primitive or derived within this group. Regardless, *Plaxiphora* lacks the long, densely packed, straight main horizontal canals that characterize all mopaliids.

Tonicella shares many characters with the mopaliids (*e.g.*, large, closely-spaced, straight horizontal canals, same megalaesthete chamber shape, regular merging of short subsidiary canals with the primary horizontal canals). The results of the cladistic analysis are consistent with those of Eernisse (unpubl. data), which suggested *Tonicella* should be classified within the Mopaliidae. All four members of this genus analyzed in this study share remarkably similar aesthete canal systems (in particular, they have the most orderly arrangement of canals), and are each more similar to each other than any is to any of the other species whose aesthete canals have so far been described in detail.

The two species of *Dendrochiton* analyzed in this study share many aesthete characters with other mopaliids, such as the long, straight horizontal canals, non-descript shape of the megalaesthete bulbs, and a relatively large number of micraesthetes per megalaesthete (though not so many as in *Cyanoplax* and *Nuttallina*). Consistent with Kaas and Van Belle (1987), who listed *Dendrochiton* as a subgenus of *Lepidochitona,* the *Dendrochiton* species in this study share some characters of the aesthete canal system with *Cyanoplax hartwegii* and *Nuttallina californica*, such as the presence of long, narrow, horizontal canals that connect with megalaesthete chambers with many micraesthetes. However, *Dendrochiton* shares more synapomorphies with the mopaliids than

it does with *Cyanoplax* and *Nuttallina*, consistent with the results of Eernisse (unpubl. data).

Dendrochiton and the other members of the Mopaliidae share many overall similarities in aesthete canal system with those of fellow members of the Acanthochitonina, *Cyanoplax*, and *Nuttallina*. These similarities include a high density of horizontal canals (though higher in mopaliids), high number of micraesthetes per megalaesthete (though higher in *Cyanoplax*/*Nuttallina*), and a regular merging of subsidiary canals with the main horizontal canal. In fact, the horizontal canal system drawn for *Lepidochitona cinerea* by Knorre (1925, fig. 37, as *Trachydermon cinereus*) is similar to that of mopaliids (Fig. 1F): relatively straight horizontal canals in the pleural area that extend most of the valve's length, with a regular merging of subsidiary canals, and with a relatively wide extent of the slit ray canals. Some of these similarities may provide evidence for grouping Mopaliidae and Lepidochitonidae (*e.g.*, *Lepidochitona*, *Cyanoplax*, *Nuttallina*) as a subclade within Acanthochitonina, or might be plesiomorphic features for Acanthochitonina, with differences noted in *Plaxiphora* and *Nuttallochiton* best considered derived features. Future studies of the aesthete canal system in other members of the Acanthochitonina, and the combination of these data with a wider range of morphological and molecular evidence should reveal which interpretation is more likely.

Conclusions

The results provide further evidence that characters of the aesthete canal system are phylogenetically informative at a number of taxonomic levels. This study approximately doubles the total number of comparisons possible, now 26 species, when these data are combined with those in the study by Fernandez *et al.* (2007). This present study is also significant in providing some of the first morphological evidence corroborating a new proposal based on molecular evidence. Specifically, variation in aesthete canal morphology is largely consistent with the new classification of the Mopaliidae proposed by Eernisse (unpubl. data), which excludes the genera *Plaxiphora* and *Nuttallochiton* from Mopaliidae (although the placement of *Nuttallochiton* is uncertain with respect to the Mopaliidae based on aesthete canal morphology alone) while including *Tonicella* and *Dendrochiton* within this family. Some characters in common between members of Mopaliidae and Lepidochitonidae could reflect synapomorphies for uniting these families within Acanthochitonina. More resolution is expected with the addition of other chiton species in future analyses of aesthete canal morphology, and the combination of these data with other morphological and molecular evidence will help elucidate relationships within Polyplacophora.

ACKNOWLEDGMENTS

Daniel Geiger provided additional and extensive training to MJV and CZF on the SEM and indispensable advice on techniques to improve image quality. Hank Chaney, SBMNH, provided most of the specimens used in this study and permitted the use of the SBMNH SEM. We also thank Kevin McKeegan for his generosity in allowing MJV and CZF to use the SEM at the UCLA Department of Earth and Space Sciences. Michelle Hopkins provided additional help with the SEM at UCLA ESS. Roger Clark previously identified many of the SBMNH chitons used in this analysis. William Hewson helped locate specimens of *Nuttallochiton* and *Plaxiphora*. Susanne Lockhart collected the specimens of *Nuttallochiton* and *Plaxiphora* and sent them to DJE. *Plaxiphora* was collected during the ICEFISH (International Collaborative Expedition to collect and study Fish Indigenous to Sub-antarctic Habitats) cruise led by H. William Detrich, and *Nuttallochiton* was collected during the AMLR (Antarctic Marine Living Resources) cruise led by Dr. Christopher Jones. Boris Sirenko and an anonymous reviewer provided suggestions that greatly improved the general focus and many details of the paper. Comments from the editors Ken Brown and Cynthia Trowbridge also greatly improved the clarity and overall quality of the paper.

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Submitted: 30 January 2007; **accepted:** 24 November 2007; **final revisions received:** 10 February 2008.

Appendix 1. Collecting and locality information for the chitons used in this study.

Species	Accession #(s)	Collector(s)	Date collected	Locality notes
Dendrochiton flectens	SBMNH 369492	George Hanselman	1973	Underside of rocks during a −0.76 m tide, Cactus Island, Washington
Dendrochiton lirulatus	SBMNH 369493	George Hanselman	1971	Intertidal of Ensenada Blanca, Baja California Norte, Mexico
Katharina tunicata	SBMNH 83323	Michael Vendrasco	1999	Rocky intertidal, Cambria, California
Katharina tunicata	SBMNH 369494	George Hanselman	1972	Vancouver Island, British Columbia, Canada
Mopalia spectabilis	SBMNH 369491	Spencer Thorpe	1965	Morro Bay Harbor breakwater, California
Nuttallochiton mirandus	SBMNH 83324	Susanne Lockhart	2006	235 m depth, about 100 km south of Penguin Island, Antarctic
Plaxiphora aurata	SBMNH 83321-83322	Susanne Lockhart	2004	Intertidal, Tristan da Cunha, Sub-Antarctic
Tonicella lokii	SBMNH 83319-83320	Christine Fernandez and Michael Vendrasco	2006	Rocky intertidal, Cambria, California
Tonicella insignis	SBMNH 369497	Roger Clark	2000	Unalaska Island, Aleutian Islands, Alaska, 5-10 m depth
Tonicella lineata	SBMNH 369488	Spencer Thorpe	1965	Anacortes, Washington
Tonicella marmorea	SBMNH 369496	Ron McPeak	1977	Underside of rocks, 5-10 m depth, Seal Island, Nova Scotia, Canada
Tonicella marmorea	SBMNH 369495	Norm Curran	1964	Newagen, Maine
Tonicia chilensis	SBMNH 369486	Hank Chaney	2004	Under small rocks in tidepools, Cobija, Chile
Mopalia ciliata, Mopalia lignosa, and *Mopalia swanii*	SBMNH 83325-83330	George Hanselman	Unknown	California (additional details unknown)

Appendix 2. Description of aesthete characters and character states used in the cladistic analysis

1. Number of canals that exit ventrally under the jugum (jug): (0) 0-30, (1) >30.

Comments: area is the same as the "ventral jugal triangle" of Fernandez *et al.* (2007, fig. 1) and can be seen as the number of "jugal area channels" as defined in Baxter and Jones (1981, 1984). The number of canals in this area can be inferred from the number of pores seen on the ventral surface of valves in this region, the canal pieces in this region of the ventral cast, and in some cases in the dorsal cast, seen as upturned, typically flattened canals in the jugal area.

2. Nature of slit ray canals in lateral area (lat): (0) sparse and highly curved, (1) dense and highly curved, (2) dense and not highly curved, (3) sparse and not highly curved, (4) no slit ray canals.

Comments: refers to the extent of the horizontal portions of the slit ray canals that occur at the tegmentum/articulamentum interface. On the dorsal casts, these canals can be seen to merge parallel to the slit ray before trending downwards (in life; upwards on the dorsal cast) to a slit ray pore. This character is similar to character 8 (hcc: degree of horizontal canal curvature towards diagonal line) in Fernandez *et al.* (2007), although the divisions between character states are herein refined to match natural character state boundaries in the now larger taxon set.

3. Linear arrangement and orderly spacing of megalaesthete bulbs (lin): (0) absent, (1) present.

Comments: refers to well-organized anterior-posterior zones of megalaesthete chambers. This character can best be seen in some photos of *Lepidopleurus cajetanus* in Fernandez *et al.* (2007), which suggests that this character may be primitive in the crown group Polyplacophora. This character is the same as character 9 (apz: canals differentiated into anterior-posterior columns) in Fernandez *et al.* (2007).

4. Types of megalaesthete chambers (mgc): (0) type A, (1) type B, (2) type C, (3) type D.

Comments: the megalaesthete chamber types are illustrated in Fig. 7. Type A is a gently tapering chamber that only has a subtle bulb shape. Type B is a more sprawling chamber whose micraesthetes often merge before entering it. Type C is widest in the middle, with gradual tapering on both ends. Type D has an elongate form tapered sharply on both ends, like a sausage. Note this character refers to the typical shape of the megalaesthete chamber. Most species have at least some variation in the appearance of these chambers. Character 3 (blb: megalaesthete bulbs in central area) from Fernandez *et al.* (2007) makes up a portion of this newly expanded character.

5. Huge aesthete chambers (hgc): (0) absent, (1) present.

Comments: these are much larger than typical megalaesthete chambers and may be modified or merged megalaesthete chambers. These may contain ocelli. They are sparsely and apparently randomly distributed in *Tonicia* and are regularly distributed in large granules in *Lepidozona*. This character is similar to character 7 (hmc: huge aesthete chambers in large granules) in Fernandez *et al.* (2007), but is more broadly defined to allow the large chambers in *Tonicia* and *Lepidozona*—which appear homologous—to be coded the same.

6. Density of horizontal canals (deh): (0) very low (much visible space between canals), (1) low (some visible space between canals), (2) high (little visible space between canals).

Comments: refers to the density of primary horizontal canals at the tegmentum/articulamentum interface. This character is the same as that of the same number and code in Fernandez *et al.* (2007).

7. Typical connection between surface canals (*e.g.*, megalaesthete chambers) and main horizontal canals (shc): (0) long canal that is, in part, parallel to the surface, (1) short canal, oblique to surface, (2) each horizontal canal connects to only one megalaesthete bulb.

Comments: refers to the typical portion of the canal between the surface chambers and horizontal canals at the tegmentum/articulamentum interface. In *Lepidopleurus cajetanus*, each horizontal canal connects to only one megalaesthete bulb, making it difficult to compare with the other taxa (*i.e.*, it is difficult to say where the connecting canal "ends" and the horizontal canal "begins"). For this reason, *L. cajetanus* was coded as having a unique state (2).

8. Divergence of horizontal canals flanking the jugal area (flj): (0) absent, (1) tilted towards apex, (2) tilted away from apex.

Comments: refers to the set of main horizontal canals in the pleural area immediately adjacent to the jugal area. In some cases the angle of divergence (from the bisecting line) is high. Those canals that are tilted away from the apex are often arced and bend back towards the apex. This character is a modification/refinement of character 11 (doc: direction of convergence of horizontal canals in lateral area) in Fernandez *et al.* (2007).

9. Straight (or regularly wavy) horizontal canals from anterior to posterior margins (hap): (0) absent, (1) present.

Comments: this character can also be read as whether main (or primary) horizontal canals extend nearly the entire length of the valve.

10. Regular merging of short canals into main horizontal canals (reg): (0) absent, (1) present.

Comments: refers to whether there is a high rate of merging of obliquely-oriented, connecting canals from the megalaesthete chambers along the length of the main horizontal canals.

11. Lateral merging of main horizontal canals (lam): (0) absent, (1) present.

Comments: refers to a high rate of lateral merging of main horizontal canals, especially in the posterior portion of the valve.

General comments about characters: many of the characters used in Fernandez *et al.* (2007) were modified herein (see above) and some were excluded from this analysis. In some cases character states were modified to better match natural boundaries in the now larger taxon set. Character 1 from Fernandez *et al.* (2007) (agc: aesthete/granule correlation) was excluded because granules in many of the species examined are often indistinct, making it difficult to assess homology. Character 2 from that paper (are: megalaesthete canal morphology/pattern differ by valve area) was not used because it correlates with character 2 (lat) in this analysis and we decided against indirect weighting of that character.

Amer. Malac. Bull. **25**: 71-76 (2008)

Mopalia kennerleyi Carpenter, 1864, a forgotten species and its southern analogue *Mopalia ciliata* (Sowerby, 1840)*

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Abstract: The hairy chiton *Mopalia kennerleyi* Carpenter, 1864 is distinguished from its congener *Mopalia ciliata* (Sowerby, 1840), and the identity of *Chiton wosnessenskii* von Middendorff, 1847 is clarified. *Mopalia kennerleyi* and *M. ciliata* are distinguished by setae structure, valve sculpture, and radular teeth. Their characteristics are illustrated and discussed, and their distributions defined.

Key words: chiton, sibling species, California, Polyplacophora, mollusc

The examination of several hundred lots of what has been regarded as *Mopalia ciliata* (Sowerby, 1840) from throughout its recorded range of Alaska to Baja California revealed that two similar but distinctive species could be distinguished by setae structure: *Mopalia ciliata* from southern California and Baja, and a northern species ranging from central California, north to the Aleutian Islands in Alaska, for which *Mopalia kennerleyi* Carpenter, 1864 appears to be the oldest available name. These distinctions in setae and name for the northern species have already been noted and illustrated by Eernisse *et al.* (2007). Recent molecular work by Kelly *et al.* (2007) and Kelly and Eernisse (2007) have clearly verified this conclusion.

It is not new to consider northern specimens as distinct. Pilsbry (1892: 305) distinguished *Mopalia ciliata,* from what he considered its variety *M. c. wosnessenskii* (von Middendorff, 1847), by the "much fainter sculpture" and by the latter's lack of "white thorns or spines (spicules) near the base of the setae." As Middendorff's name is currently regarded as a synonym of *M. ciliata*, one would first expect that this name should be revived for the northern taxon. However, an examination of the lectotype (Fig. 1; ZISP N834) (designated by Sirenko, pers. comm., October 2007), the larger of two syntypes of Middendorff's *Chiton wosnessenskii* (Fig. 1) revealed that it was instead a specimen of *Mopalia hindsii* (Sowerby MS, Reeve, 1847). The type locality for *C. wosnessenskii* is given as Atka Island in the Aleutians (52°11′57″N, 174°12′48″W); however, *M. hindsii* does not occur in the Aleutians. Middendorff's type specimens were said to have come from both Atka Island and Sitka, Baranof Island, SE Alaska (57°08′N, 135°55′W), the Russian capitol of Alaska during the early 1800s and the type locality of many of Middendorff's types. Undoubtedly both specimens came from Sitka. The western-most distribution of *M. hindsii* is in the vicinity of Kodiak Island, in the Gulf of Alaska (57°N, 154°W). The question of name priority for these two nominal taxa is a matter for further investigation.

Pilsbry (1892) considered *Mopalia kennerleyi* Carpenter, 1864 to be a synonym of *Mopalia ciliata*, an assignment followed by Burghardt and Burghardt (1969), Smith (1977), and Kaas and Van Belle (1994).

Although the type of *Mopalia kennerleyi* is lost (Smith 1977, T. Nickens, USNM, pers. comm. October 2003), there can be little doubt from Carpenter's original description and the type locality of "Puget Sound" as to which species he was referring. *Mopalia kennerleyi* Carpenter, 1864 is thereby reinstated as the oldest available name for northern species.

MATERIALS AND METHODS

Specimens of "*Mopalia ciliata*" from my own collection, comprising more than one hundred lots from the Aleutian Islands to Baja California, were separated into two distinctive types of girdle setae using a dissecting microscope (as in Clark 1991). Setae and radula from each of these two potential species were prepared and examined with a scanning electron microscope (SEM) at the Biology Department of Southern Oregon University, using methods described by

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* From the symposium "Advances in Chiton Research" presented at the joint meeting of the American Malacological Society and Western Society of Malacologists, held 29 July to 3 August 2006 in Seattle, Washington.