NOTES ON THE MORPHOLOGY OF *ADMETE VIRIDULA* (GASTROPODA: CANCELLARIIDAE)

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ABSTRACT

The anatomy and shell morphology of Admete viridula *(Fabricius, 1780), a boreal cancellariid, are described. This species, the type of* Admete *Kroyer, 1842, differs from members of the Cancellariinae and Trigonostominae in having a thinner shell composed of a single aragonitic layer, a reduced kidney and jaw, and a long, expanded prostate gland, as well as in lacking a radula, separate sperm ingesting gland and dorsally recurved albumen gland. Based on cladistic analysis of 20 shell and anatomical characters, we suggest that the family Admetinae is an early offshoot from primitive cancellariid stock, that the subfamily Trigonostominae contains the most primitive cancellariids studied anatomically to date, and that Cancellariinae comprise a comparatively recent radiation with specialized chemosensory capabilities.*

The composition and taxonomic history of the superfamily Cancellariacea have been briefly discussed in previous papers (Harasewych & Petit, 1982, 1984). The relationship of this group to other prosobranchs is still uncertain, as is the phylogenetic arrangement of the nearly 100 nominal supraspecific taxa proposed almost exclusively on the basis of shell characters.

Recent supraspecific taxa have, in general, been clustered around three morphological types, represented by the genera *Cancellaria*, *Trigonostoma* and *Admete*, that have been given subfamily status by Cossmann (1899). Members of the Cancellariinae and Trigonostominae inhabit tropical and temperate waters while Admetinae is generally limited to polar regions with some species inhabiting deeper waters of the temperate zone. The gross anatomy of *Cancellaria reticulata* (Linné, 1767), the type of Cancellariinae, and *Olssonella smithii* (Dall, 1888) a trigonostomine, have previously been described (Harasewych and Petit, 1982, 1984).

No general anatomical studies of any admetine are known to us, although brief descriptions of the animal of *Admete viridula* (Fabricius, 1780) were given by Möller (1842: 88, as *A. crispa* Möller) and Jeffreys (1876: 322). Simple drawings of the living animal were published by H. & A. Adams (1853: pl. 29, fig. 5; copied by Tryon, 1885: pl. 7, fig. 32), Troschel (1865: pl. 4, fig. 14) and Morse (1921: pl. 7, fig. 43). Troschel (1865: pl. 4, figs. 16, 17) figured the jaws of *A. viridula* and the synonymous *A. crispa*, referring to these structures as "hard apparatus" and suggesting that they may be toxoglossan radular teeth. The latter figure was copied by Fischer (1883: 595, fig. 359) and labelled as a radular tooth. Tryon (1885: pl. 7, fig. 33) copied Fischer's figure without comment. Thiele (1904: 172) identified Troschel's figures as jaws and reported the absence of a radula in *A. viridula*. The austral species *A. magellanica* Strebel, 1905, and *Waipaoa marwicki* Dell, 1956, were shown to lack radulae, respectively, by Powell (1951: 167) and Beu and Climo (1974: 327). Not all admetines are without radulae as evidenced by the figures of the radula of *Nothoadmete tumida* Oliver, 1982, that accompanied the description of that species. The gross anatomy and shell morphology of *Admete viridula* (Fabricius, 1780), the type species of *Admete* Möller, 1842 [as *A. crispa* Möller, 1842] are here described and compared to other cancellariid taxa.

The checkered nomenclatural history of this

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species is detailed by Bouchet & Warén (1985: 257), who point out that North American authors have used the junior synonym *Admete couthouyi* (Jay, 1839) for the species, based on incorrect statements by Dall (1887: 298; 1918: 318, 328) contending that the type of *A. viridula* was a turrid. Although this was refuted by Pilsbry (1938), Macpherson (1971: 107), citing Dall, followed other New World malacologists in using *A. couthouyi*.

Admete viridula is exceedingly variable as attested by the synonymy listed by Bouchet & Warén (1985: 258), to which additional nomina will eventually be added. While the Canadian specimens used for this study are not "typical" of the species, in conchological characters, they do fall within the range of variation accepted by Bouchet & Warén (1985: figs. 683-689) who examined thousands of North Atlantic specimens.

Materials and Methods

Anatomical data is based on 2♂ and 1♀ specimens from the Saguenay River, Quebec [48°24′48″N, 70°44′-70°48′W] Voucher Material-National Museum of Natural Sciences, Ottawa 43946.

Shell fragments for ultrastructural studies were broken from the outer lip with pliers. Specimens were then immersed in 10% hydrochloric acid (HCl) until the shells dissolved. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection. Portions of the reproductive systems and anterior proboscis were sectioned at a thickness of 6 μm, and the sections stained in hematoxylin and eosin. Dried shell fragments were powdered in a mortar and pestle, and the X-ray diffraction pattern determined on a Philips APD 3600 Automated X-ray Powder Diffractimeter.

Shell Morphology

External: Shell, reaching 20 mm in length, thin, ovate with conical spire and rounded anterior (Fig. 1). Protoconch (Figs. 3, 4) paucispiral, consisting of 1 whorl, with a smooth, chalky surface incised by fine, spiral lines. Transition to teleoconch marked by beginning of axial growth striae and an increase in shell thickness. Teleoconch with up to 5½ convex whorls. Early whorls (Fig. 2) strongly shouldered, becoming more rounded with increase in shell size. Suture deeply impressed. Spiral sculpture of 16-21 shallow, rounded cords on body whorl and 7-10 on the penultimate whorl. Axial sculpture of 14-24 ribs per whorl, increasing in number but decreasing in prominence as the shell becomes larger. Aperture elliptical, deflected from coiling axis by 20-28°. Outer lip smooth to slightly corrugated. Siphonal canal short but pronounced in juveniles (Fig. 2), commonly indiscernible in large adults (Fig. 1). Inner lip with 2 weak columellar folds and a siphonal fold. Color white to ivory, uniform within and without.

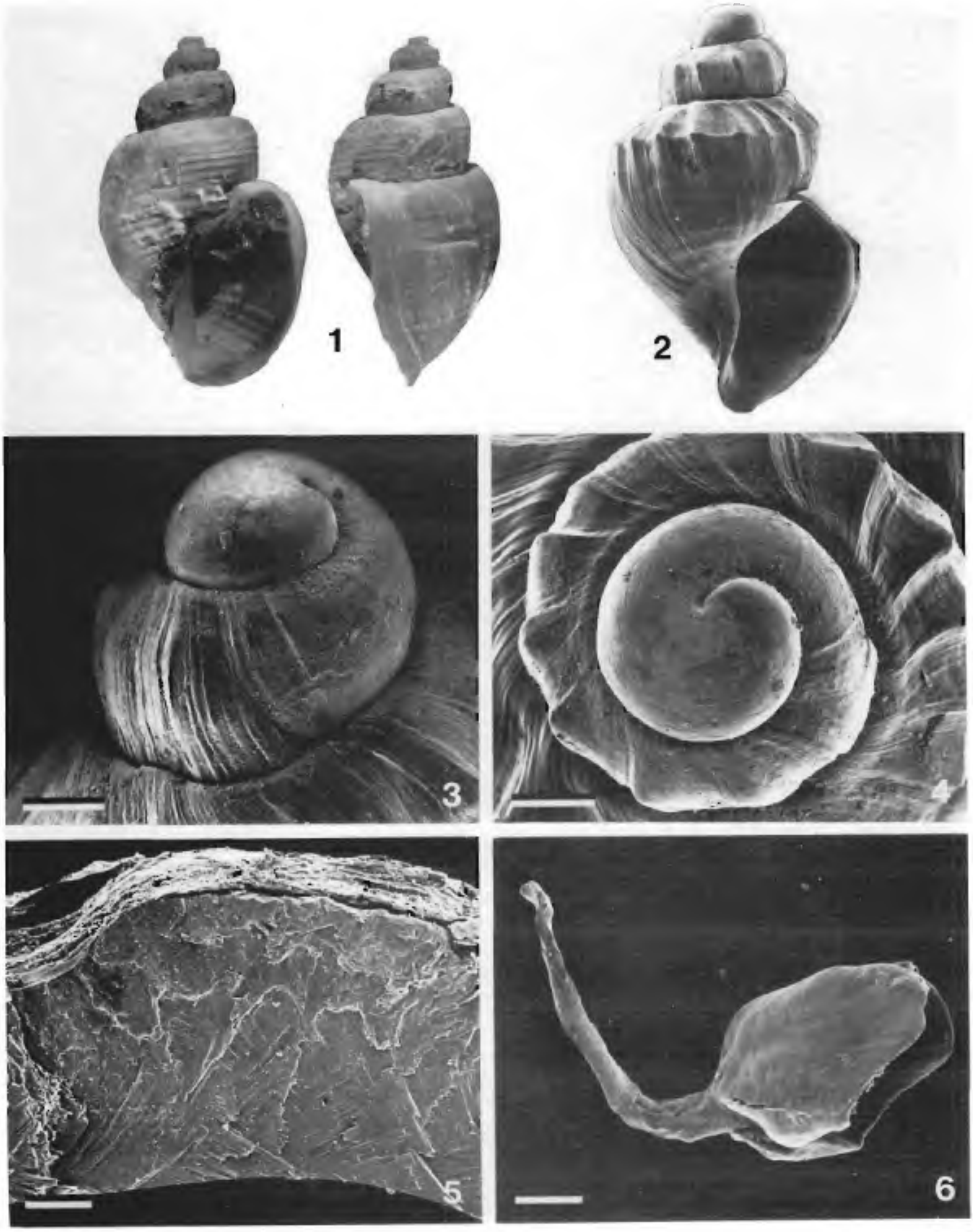
Internal: Fractured shells revealed the internal surfaces to be smooth and continuous, and to lack the apertural lirae and periodic increases in prominence of columellar folds found in other cancellariids (Harasewych and Petit, 1982, 1984).

Ultrastructure: A thin, brownish, lamellose periostracum overlies the shell, which appears to consist of a single layer of crossed-lamellar crystals (Fig. 5), oriented with lamellar planes parallel to the outer lip. X-ray diffraction analysis of powdered shell revealed it to consist primarily (>95%) of aragonite.

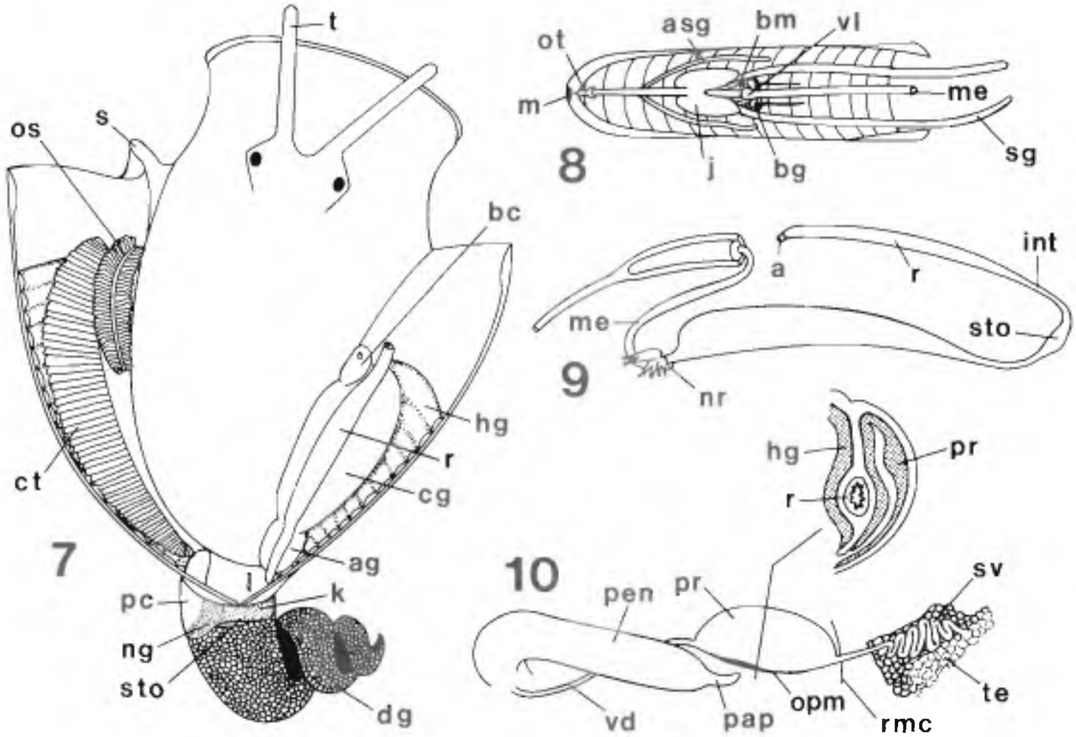
Soft-parts Morphology

External features: The soft-parts comprise 3 to 3⅓ whorls, of which the digestive gland (Fig. 7, dg) occupies about 2¼ whorls, the kidney (Fig. 7, k) less than ⅛ whorl and the mantle cavity just over ½ whorl. Preserved animals were orange tan in color, lacked any discernible markings and were retracted at most ¼ whorl into the aperture. The foot is broad and ovate, lacking an operculum. Tentacles (Fig. 7, t) are long, tubular and symmetrical. The mantle edge is smooth, the siphon (Fig. 7, s) short but distinct.

Mantle cavity: The mantle cavity is shorter and broader than in other cancellariids dissected, with pallial organs situated as in other higher prosobranchs. The osphradium (Fig. 7, os) is broad anteriorly (L/W = 3), tapers posteriorly, and consists of about 35 leaflets per side. Adjacent is the ctendium (Fig. 7, ct), twice as long and slightly narrower than the osphradium, composed of about 70 triangular leaflets. This organ and the voluminous, transversely pleated hypobranchial gland (Fig. 7, hg)



FIGS. 1-6. Features of the shells and jaw of *Admete viridula* (Fabricius). **1**, Apertural and right side views of specimen collected in the Saguenay River, Quebec. [48°24'48"N, 70°44'-70°48'W] sta. 62 30 (NMNS 43946) 3.0 × . **2**, Scanning electron micrograph of juvenile specimen dredged in 673 m, off Martha's Vineyard, Massachussetts, U.S. Fish. Comm. sta. 994-97. (USNM 43232) 20.0 × . **3**, Protoconch of specimen in figure 2, lateral view, scale bar = 200 μm. **4**, Protoconch of specimen in figure 2, axial view, scale bar = 200 μm. **5**, Fracture surface. Plane of fracture parallel to outer lip, scale bar = 100 μm. **6**, Lateral view of jaw, scale bar = 50 μm.



FIGS. 7-10. Anatomical features of *Admete viridula*. **7,** Female specimen removed from shell, partially uncoiled and mantle cavity opened mid-dorsally to display contents. **8,** Dissection of anterior portion of proboscis, opened mid-dorsally. **9,** Diagrammatic representation of the alimentary system. **10,** Male reproductive system.

a, anus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; bg, buccal ganglia; bm, buccal mass; cg, capsule gland; ct, ctenidium; dg, digestive gland; hg, hypobranchial gland; int, intestine; j, jaw; k, kidney; m, mouth; me, mid-esophagus; ng, nephridial gland; nr, nerve ring; opm, opening to mantle cavity; os, osphradium; ot, oral tube; pap, papilla; pc, pericardium; pen, penis; pr, prostate gland; r, rectum; rmc, rear of mantle cavity; s, siphon; sg, salivary gland; sto, stomach; sv, seminal vesicle; t, tentacle; tes, testes; vd, vas deferens; vl, valve of Leiblein.

span the roof of the mantle cavity. The pallial gonoducts and rectum (Fig. 7, r) are located along the right side of the mantle cavity, while its rear is formed by the pericardium (Fig. 7, pc) and kidney (Fig. 7, k). The kidney is small, being only twice the size of the pericardium. The nephridial gland (Fig. 7, ng) occupies nearly half the kidney along the pericardium.

Alimentary system: The broad, tubular pleurombolic proboscis can be extended nearly the length of the shell aperture, and is the same color as the foot. Broad retractor muscles extend from the columellar muscle, while thinner strands originate from the body wall. A short oral tube (Fig. 8, ot) extends from the mouth (Fig. 8, m) to the cuticularized, tubular portion of the jaw (Fig. 8, j), which expands posteriorly to envelope the lateral surfaces of the minute buccal mass (Fig. 8, bm). The longitudinally grooved buccal mass lacks a radula and has only a vestigial subradular membrane. A pair of short, extremely thin accessory salivary glands (Fig. 8, asg) lie alongside the buccal mass, emptying into the posterior portion of the oral tube through fine ducts. The wider and much longer salivary glands (Fig. 8, sg) join the buccal mass laterally, via short ducts, just anterior to the esophageal opening. A small valve of Leiblein (Fig. 8, vl) and a pair of buccal ganglia (Fig. 8, bg) are situated at the rear of the bucal mass. The narrow mid-esophagus (Figs. 8, 9, me) runs posteriorly from the valve of Leiblein, passing through the nerve ring (Fig. 9, nr) before expanding and becoming sacular. The esophagus narrows at the rear of the cephalic sinus and leads to a simple U-shaped stomach (Fig. 7, 9, sto) that is embedded in the anterior face of the digestive gland. Longitudinal folds

TABLE 1. *Admete viridula* (Fabricius), measurements of shell characters. Linear measurements in millimeters. (n = 10).

Character	Mean	Standard Deviation	Range
shell length	16.87	1.91	13.82-19.02
shell width	9.90	1.13	8.18-10.97
aperture length	10.21	1.42	8.13-11.58
aperture length / shell length	0.604	0.023	0.567-0.641
#whorls, teleoconch	4.78	0.35	4.33-5.33
spire angle	55.2°	2.9°	45.5°-58.0°

line the stomach and pass into the intestine (Fig. 9, int), which runs through the kidney and along the right wall of the mantle cavity, expanding slightly to form the rectum (Figs. 7, 9, r). Neither an anal gland nor identifiable gut contents were detected in any of the specimens examined.

Female reproductive system: As the only female specimen available to us was poorly preserved, only the pallial portion of the oviduct is described. The oviduct passes through the kidney and expands to form a broad, laterally compressed albumen gland (Fig. 7, ag), which expands further to form the long, blunt, capsule gland (Fig. 7, cg). A small, ovate, bursa copulatrix (Fig. 7, bc) is situated below the anterior margin of the capsule gland. An ingesting gland was not found. Egg capsules of *Admete viridula* are figured by Bouchet and Waren (1985: fig. 687).

Male reproductive system: The testes (Fig. 10, te) consist of a yellowish mass of ascinous tubules embedded in the right side of the digestive gland and extend nearly a full whorl from its anterior edge. These tubules converge to form a testicular duct that immediately forms a serpentine seminal vesicle (Fig. 10, sv). The duct straightens at the anterior limit of the digestive gland, passes through the kidney and enters the mantle cavity ventral to the rectum. It greatly expands to form the prostate gland (Fig. 10, pr), which extends along the posterior third of the mantle cavity and communicates with it by a long ventral slit (Fig. 10, opm). From the anterior portion of the prostate gland, a tubular vas deferens (Fig. 10, vd) leads to the base of the penis (Fig. 10, pen), which is ovate in cross-section, extends approximately ⅔ the length of the mantle cavity and has a terminal papilla (Fig. 10, pap).

Nervous system: Admete viridula has a typical cancellariid nervous system (Bouvier, 1887: Harasewych and Petit, 1982, 1984), with the cerebral, pedal and pleural and subesophageal ganglia fused into a nerve ring, and the buccal ganglia (Fig. 8, bg) at the rear of the buccal mass.

Discussion

Cladistic analysis of the 20 shell and anatomical characters listed in Table 2 produced the cladogram in Figure 11. Despite the lack of agreement on the relationships of supraspecific taxa, nearly all classifications proposed to date separate the Admetinae from the remaining Cancellariidae (H. and A. Adams, 1853: Troschel, 1865; Fischer, 1883; Tryon, 1885; Cossmann, 1899; Thiele, 1929; Wenz, 1943), and this arrangement is supported by the present study.

Of the characters used to distinguish the Admetinae from other cancellariids, most con-

TABLE 2. Shell and anatomical characters used to distinguish between *Admete viridula, Cancellaria reticulata* and *Olssonella smithii*. Primitive states denoted by (0), derived states by (1).

1) Shell: (0) thick; (1) thin.
2) Internal varices: (0) pronounced; (1) reduced or absent.
3) Shell ultrastructure of: (0) 2 orthogonal layers; (1) 1 layer.
4) Protoconch of: (0) 2 whorls; (1) 1 whorl.
5) Tentacles: (0) symmetrical, unmodified; (1) asymmetrical, left tentacle modified.
6) Osphradium with approximately: (0) 35 leaflets/side; (1) 70 leaflets/side.
7) Ctenidium with: (0) < 125 leaflets; (1) > 200 leaflets.
8) Distance between osphradium and ctenidium: (0) normal; (1) large relative to either organ.
9) Kidney occupying: (0) > ¼ whorl; (1) < ⅛ whorl.
10) Proboscis: (0) tubular; (1) ventrally flattened, papillose.
11) Jaws with: (0) short posterior lobes; (1) long posterior lobes.
12) Buccal mass: (0) small; (1) large, filling retracted proboscis.
13) Radula: (0) present; (1) absent.
14) Outer cusps of radular teeth: (0) simple, smooth; (1) with secondary dentition.
15) Accessory salivary gland: (0) shorter than; (1) longer than; salivary gland.
16) Mid-esophagus posterior to nerve ring: (0) sacular; (1) convoluted tube.
17) Anal gland: (0) present; (1) absent.
18) Sperm ingesting gland: (0) present; (1) absent.
19) Albumen gland: (0) dorsally recurved; (1) laterally compressed.
20) Prostate gland: (0) long, expanded; (1) short, convoluted.

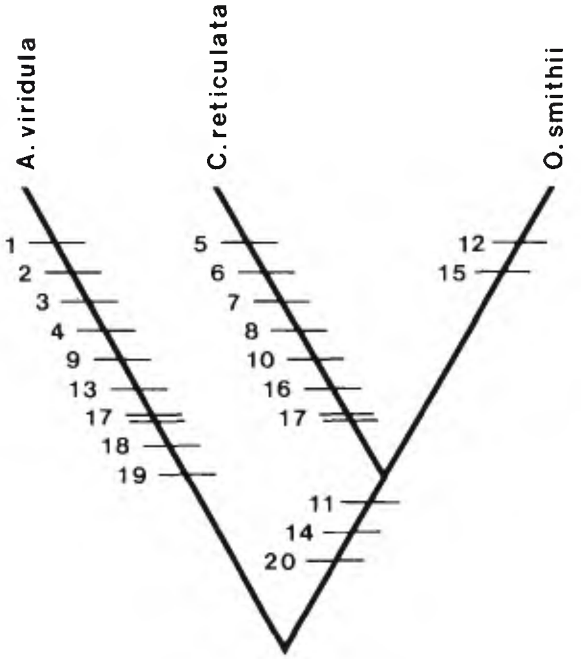


FIG. 11. Cladogram of phylogenetic relationships of cancellariid taxa. Single slashes across tree branches represent transformations of the corresponding character from the primitive (0) to the derived (1) state. Double slashes indicate transformations that occur more than once.

spicuous are their thin shells lacking pronounced surface sculpture and apertural lirae. This is likely a consequence of their polar habitat, as Graus (1974) has shown that decreased calcification in high latitudes is due to reduced availability of calcium carbonate in colder waters. Admetines also lack such antipredatory features as internal varices that are found in tropical and temperate cancellariids. The predominance of aragonite in the shell is plesiomorphic, as calcite is more easily formed (Wilbur, 1964) and more stable (Lowenstam, 1954) at low temperatures.

In terms of anatomical organization, *Admete viridula* differs from ancestral cancellariid morphology, most nearly approximated by *Olssonella smithii* of the taxa studied to date, in having a shallower mantle cavity, a reduced kidney, and in lacking color pattern. At least some of these may also be adaptations to cold water.

Cancellariines and Trigonostomines have uniserial "tricusped" radular teeth with elaborate secondary dentition on the outer cusps and a comparatively simple ventrally recurved central cusp (Harasewych and Petit, 1982, 1984; Petit and Harasewych, 1986). The radula of *Nothoadmete tumida,* the only known radulate admetine, has barbed central cusps and simple bulbous outer cusps (Oliver, 1982: figs. 3, 5). Presence of central cusp barbs in *Cancellaria atopodonta* Petit and Harasewych (1986: figs. 15, 16) suggests that this feature is primitive and occurred in the ancestor of all Recent cancellariids. The jaws of admetines lack the long posterior lobes found in cancellariines and trigonostomines. Although the diet of cancellariids remains unknown, we have suggested that they are piercing suctorial feeders based on the functional morphology of their alimentary systems (Harasewych and Petit, 1982, 1984; Petit and Harasewych, 1986). The loss of radula and reduction in the size of the buccal mass in most admetines suggests that they feed suctorially, but on a different group of prey organisms than other cancellariids.

The lack of an anal gland in *Admete viridula* and *Cancellaria reticulata* is likely a comparatively recent convergence, as this organ has been reported in *Cancellaria cancellata* (Graham, 1966).

Additional differences between admetines and other cancellariids are found in the reproductive systems. The prostate gland of *Admete viridula* is long and greatly expanded, while in *Olssonella smithii* and *Cancellaria reticulata* it is short and convoluted. *Admete viridula* also lacks the separate sperm ingesting gland and dorsally recurved albumen gland found in cancellariines and trigonostomines.

The phylogenetic arrangement in Figure 11 is supported by the fossil record, as several "admetines" have been reported from the Upper Cretaceous, and *Waipaoa,* known to be aradulate in the Recent fauna, dates back to the Oligocene. *Cancellaria, sensu stricto,* first appears in the Miocene and is characterized by modifications to the left cephalic tentacle, proboscis, osphradium and ctendium, organs involved in tactile and distance chemoreception.

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BOOK REVIEW

Washington Public Shore Guide: Marine Waters by James W. Scott and Melly A. Reuling. 1986. 348 pp., numerous photos, maps and habitat sketches. Cloth, $25.00; paperback, $14.95.

If you are planning on studying or visiting the shorelines of the State of Washington, this is a great bargain with many useful facts about the 2,400-mile saltwater shoreline of 14 counties. It largely ignores mollusks, a fact which offers a challenge to conchologists. —*R. T. Abbott.*