

NOTES ON THE MORPHOLOGY OF *OLSSONELLA SMITHII*
(GASTROPODA: CANCELLARIIDAE)¹

M. G. Harasewych and Richard E. Petit

Research Associates

Department of Invertebrate Zoology

National Museum of Natural History

Smithsonian Institution

Washington, D.C. 20560

ABSTRACT

Olssonella smithii (Dall, 1888) is a small cancellariid gastropod that inhabits sand substrates off the southeastern United States, the Gulf of Mexico, Colombia and Venezuela. It resembles *Cancellaria reticulata* (Linné, 1767) in anatomical organization, but differs in having a less specialized anterior alimentary system and an unmodified left cephalic tentacle. Shell ultrastructure is similar in these two species, although *O. smithii* has a thicker periostracum. *Olssonella smithii* also lacks bifurcated columellar folds and has internal varices that differ in periodicity from those of *C. reticulata*. Based on the morphology of radulae and jaws we suggest that the subfamilies Cancellariinae and Trigonostominae are more closely related to each other than either is to Admetinae, in which there is a trend toward loss of the radula.

The Cancellariacea comprise a highly specialized, poorly known and taxonomically enigmatic group of marine gastropods. Although they form a morphologically compact natural assemblage, their relationships to other prosobranchs are less than certain. The group has been included in the Toxoglossa by early workers (eg. Troschel, 1865; Tryon, 1882; Fischer, 1883), in the Volutacea (eg. Thiele, 1929; Wenz, 1938-1944; Taylor and Sohl, 1962) and elevated to ordinal status by Olsson (1970) who proposed the name Nematoglossa. Golikov and Starobogatov (1975) reduced the group to a suborder, but retained the name Nematoglossa. Most recent workers regard this group as a superfamily within Neogastropoda (Ponder, 1973; Keen and Coan, 1974; Taylor *et al.*, 1980; Boss, 1982). Taylor *et al.* (1980) suggest that Cancellariacea are derived from the Purpurinidae (Middle Triassic-Upper Cretaceous), which they resemble in shell morphology.

Various higher level classifications based exclusively on shell characters have been proposed (see Marks, 1949, for a review of the early

work), but phylogenetic relationships have yet to be investigated.

Anatomical studies have, for the most part, been limited to radular morphology (eg. Troschel, 1865; Barnard, 1958; Olsson, 1970; Oliver, 1982; Schremp and Richmond, 1983; Schremp, 1983) or to the anterior alimentary system (Amaudrut, 1898; Graham, 1966). The gross anatomy of *Cancellaria reticulata* (Linné, 1767) has recently been described (Harasewych and Petit, 1982).

We recently obtained several preserved specimens of *Olssonella smithii* (Dall, 1888), a species taxonomically remote from *Cancellaria reticulata*, and examined its shell and soft parts in order to investigate the morphological diversity within Cancellariacea.

There are few literature citations for *Olssonella smithii*. This species was originally described from off Cape Hatteras, North Carolina, a record which probably represents its most northern range. Specimens were reported from the northwestern Campeche Bank, Yucatan Peninsula, Mexico (Rice and Kornicker, 1965) and from the coasts of Colombia and Venezuela [Petuch, 1981, as *Agatrix epomis* (Woodring)]. Other Venezuelan specimens ten-

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tatively identified as *O. smithii* were reported by Princz (1982).

Several authors have placed *Olssonella* as a subgenus of *Agatrix*, an assignment we do not accept as we feel that the two genera are separable and there is no evidence for a subgeneric relationship.

Materials and Methods

The following specimens were used in this study:

1 ♀, trawled in 110-99 meters, E. of Sebastian Inlet, Florida (27°48'N, 79°55'W) on *Oculina* bed (Indian River Coastal Zone Museum 65:585).

1 ♀, dredged in 45.7 meters, about 28 nautical miles NE of Cape Canaveral, Florida (28°44'N, 80°10'W) R/V Delaware II, Cruise 824, sta. 90. (Voucher specimen-National Museum of Natural History, Smithsonian Institution 806986).

1 ♂ and 2 ♀, dredged in 80.4-84.1 meters, about 78 nautical miles E of Savannah River Mouth, Georgia (32°02'N, 79°18'W) R/V Delaware II, Cruise 824, sta. 16.

1 ♂ and 1 ♀, dredged in 45.7-47.5 meters, about 24 nautical miles NE of Cape Canaveral, Florida (28°39'N, 80°09'W) R/V Delaware II, Cruise 824, sta. 91.

Specimens for anatomical and histological studies were immersed in 10% hydrochloric acid (HCl) until the shells dissolved. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection. One male and one female specimen were sectioned at a thickness of 8 µm and the sections stained in hematoxylin and eosin. Dry shells were sectioned with a diamond saw or fractured in a vise for examination of internal structure and ultrastructure.

Shell Morphology

External: Shell small (to 15 mm), heavy, elongate-oval, with conical spire and rounded anterior (Fig. 1). Protoconch deviated by 10-15°, consisting of about 2 dark-brown, inflated glassy whorls. Transition to teleoconch marked by abrupt acquisition of spiral sculpture (Fig. 2). Teleoconch with up to 4²/₃ strongly convex whorls. Suture deeply impressed. Spiral sculpture of 15-19 cords on body whorl and 8 or 9 on penultimate whorl, with or without one fine striae between. Collabral sculpture of 8-11 strong, evenly-spaced, prosocline ribs per whorl.

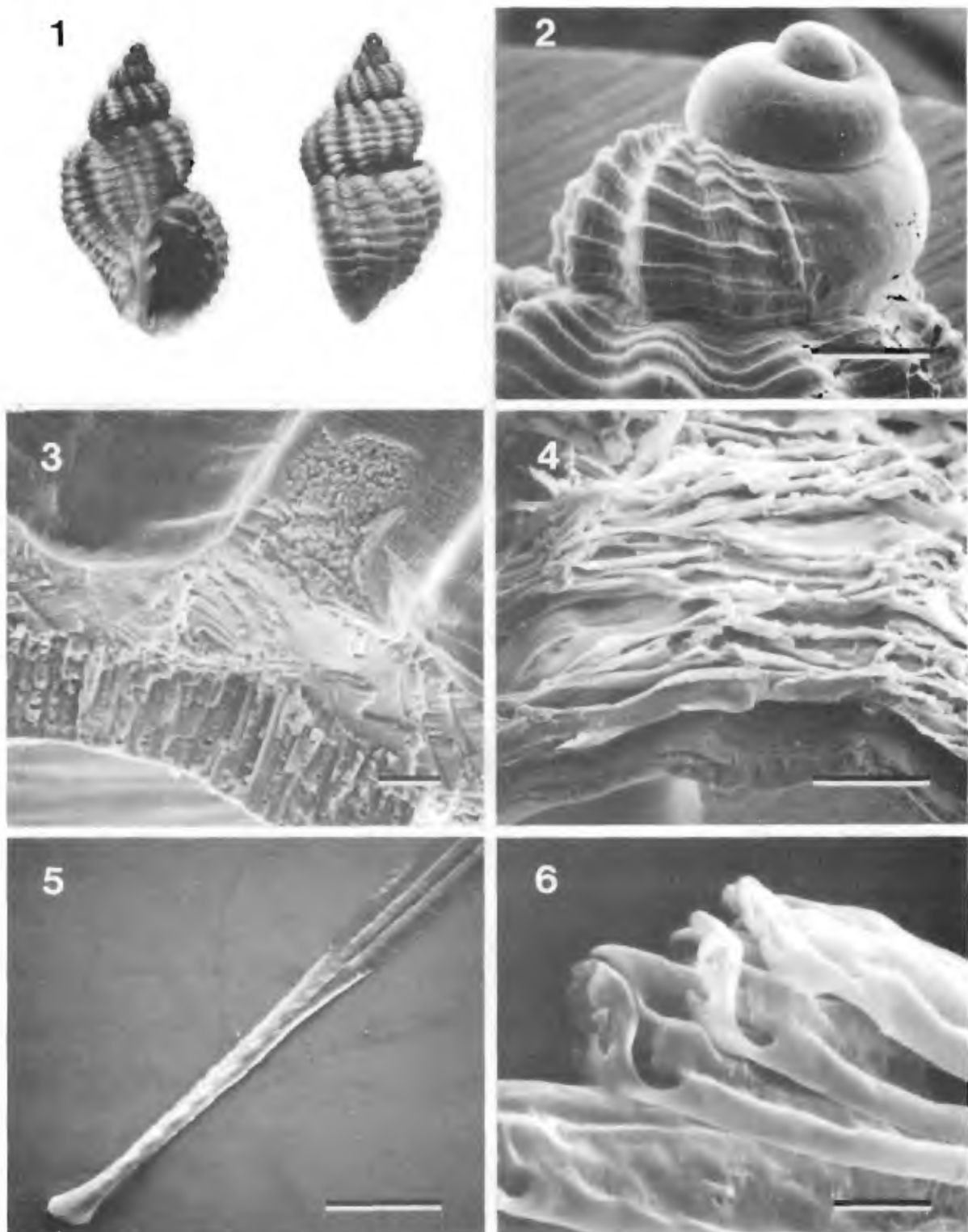
There is a slight increase in number of spiral cords and a decrease in number of axial ribs with increase in shell size. Aperture hemi-elliptical, deflected from coiling axis by 10-15°. A shallow indentation separates the very abbreviated siphonal canal from the outer lip, which contains 8 or 9 spiral lirae that are thickest beneath axial ribs. Inner lip with 2 simple columellar folds and a siphonal fold. Anterior half of inner lip forms a raised inductura beneath which the pseudoumbilicus appears as a narrow fissure. Color creamy tan to purplish brown, lightest on axial ribs, darker between, and darkest along suture. Some specimens have a white band across the middle of the body whorl. Aperture white to purplish brown, columellar folds and apertural lirae white.

TABLE 1. *Olssonella smithii* (Dall), measurements of shell characters (in mm) n=10.

Character	mean	range	standard deviation
Shell length	10.86	6.8-14.9	3.29
Shell width	6.38	4.2-8.7	1.79
Aperture length	5.08	3.3-6.6	1.24
Aperture length / Shell length	0.477	0.438-0.542	0.042
# whorls, protoconch	1.76	1.7-2.0	0.09
# whorls, teleoconch	3.71	3.0-4.7	0.67
# ribs on final whorl	9.1	8-11	0.99
Spire angle	55.9°	53-59°	1.9°

Internal: Sectioned and fractured shells reveal that internal surfaces are smooth and continuous in the early whorls. By the third post-nuclear whorl, apertural lirae develop and columellar folds increase in prominence. Apertural lirae span 3 axial ribs then become reduced or absent for 3 axial ribs before again enlarging and spanning 3 ribs (periodicity roughly 240°). Unlike *C. reticulata*, the location of the apertural lirae is not discernible on the outer surface of the shell. Columellar folds become pronounced every 120°, with every other columellar prominence occurring in opposition to the median of the 3 lirate axial ribs.

Ultrastructure: A thick, yellowish, lamellose periostracum (Fig. 4) overlies the shell, which consists of 2 orthogonal layers of crossed-lamellar aragonite (Fig. 3). The outer layer, in which the lamellar planes are collabral, varies in thickness from 400-800 µm and comprises the



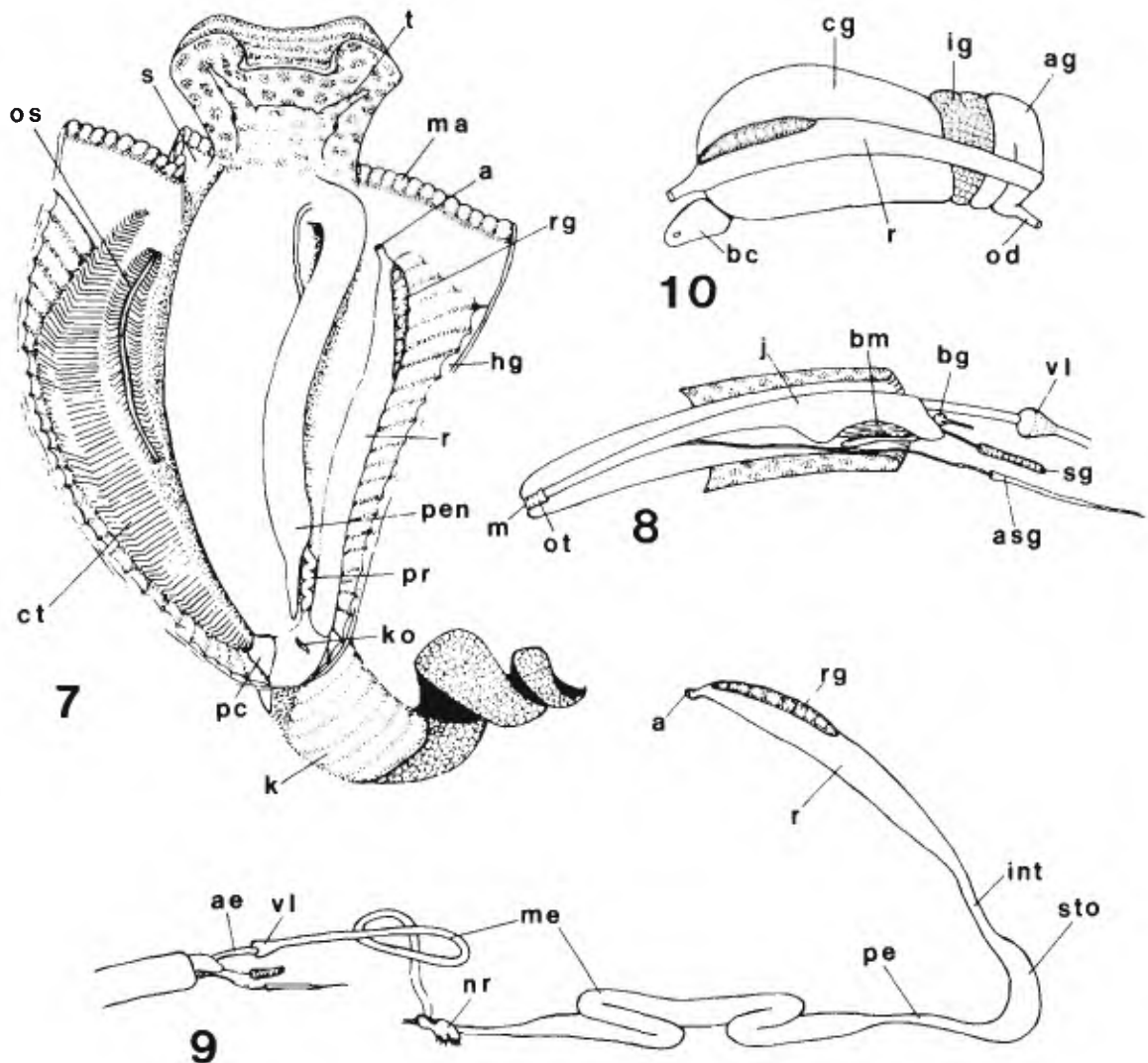
FIGS. 1-6. Shell and radular features of *Olssonella smithii* (Dall). 1, Apertural and right side views of a female specimen dredged in 45.7 meters, about 28 nautical miles NE of Cape Canaveral, Florida. (USNM 806986). $4\times$. 2, Protoconch. Scale bar = $400\ \mu\text{m}$. 3, Fracture surface. Plane of fracture parallel to outer lip. Scale bar = $50\ \mu\text{m}$. 4, Periostracum. Scale bar = $200\ \mu\text{m}$. 5, Proximal end of radular tooth, detached from radular ribbon. Scale bar = $10\ \mu\text{m}$. 6, Side view of distal ends of radular teeth. Scale bar = $3\ \mu\text{m}$.

axial ribs, spiral cords and internal lirae. The inner layer, with transversely oriented lamellar planes, forms a fairly uniform lining (100-150 μ m) along the inner surface of the shell.

Soft Parts Morphology

External features: The shell-less animal consists of approximately $3\frac{1}{2}$ whorls, with the digestive gland comprising 2 whorls, the kidney

$\frac{1}{4}$ whorl and the mantle cavity extending over $\frac{2}{3}$ whorl. Preserved animals were retracted to just within the final set of apertural lirae. Animals were light tan in color, with reddish brown spots that covered the upper and lateral surfaces of the short, rectangular foot and the symmetrical tentacles (Fig. 7, t), but stopped just within the strongly papillose mantle edge (Fig. 7, ma). The siphon (Fig. 7, s) is short and blunt. The opercu-



FIGS. 7-10. Anatomical features of *Olssonella smithii* (Dall). 7. Male specimen removed from shell, partially uncoiled and mantle cavity opened mid-dorsally to display contents. 8. Dissection of retracted proboscis, viewed from left side. 9. Diagrammatic representation of the alimentary system. 10. Diagrammatic representation of the female pallial gonoduct. a, anus; ae, anterior esophagus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; bg, buccal ganglion; bm, buccal mass; cg, capsule gland; ct, ctenidium; hg, hypobranchial gland; ig, ingesting gland; int, intestine; j, jaw; k, kidney; ko, kidney opening; m, mouth; ma, mantle edge; me, mid-esophagus; nr, nerve ring; od, oviduct; os, osphradium; ot, oral tube; pc, pericardium; pe, posterior esophagus; pen, penis; pr, prostate, r, rectum, rg, anal gland; sto, stomach; t, tentacle; vl, valve of Leiblein.

lum is lacking.

Mantle cavity: The arrangement of organs within the mantle cavity is similar to that of other higher prosobranchs. The osphradium (Fig. 7, **os**) ($L/W \cong 3$) consists of 35 leaflets per side. Immediately adjacent is the ctenidium (Fig. 7, **ct**), slightly wider and twice as long as the osphradium and composed of about 115 triangular leaflets. Occupying the roof of the mantle cavity is the voluminous, whitish, transversely pleated hypobranchial gland (Fig. 7, **hg**). To its right lie the rectum (Fig. 7, **r**) and genital ducts. The kidney (Fig. 7, **k**) lines the rear of the mantle cavity and opens into it by a single vertical slit (Fig. 7, **ko**). The pericardium (Fig. 7, **pc**) is embedded in the left side of the kidney, with only a small area bordering the mantle cavity.

Alimentary system: The stout, tubular, pleurobolic proboscis, which can be extended nearly the length of the shell, is the same color as the foot (i.e. tan with reddish brown spots on the dorsal and lateral surfaces). When the proboscis is retracted, the large buccal mass (Fig. 8, **bm**) extends beyond its posterior limits. A short oral tube (Fig. 8, **ot**) leads from the mouth (Fig. 8, **m**) to the cuticularized, tube-like jaw (Fig. 8, **j**), the expanded posterior portion of which surrounds the buccal mass. The dorsal surface of the buccal mass is covered by a broad, medially-grooved cuticle that supports a radular ribbon consisting of a single row of 54-56 ($n=4$) long ($\sim 900 \mu\text{m}$), narrow ($\sim 20 \mu\text{m}$ at base) teeth. Each tooth appears to consist of a recurved ribbon $30 \mu\text{m}$ wide (Fig. 5), the distal end of which has 3 highly modified cusps: the 2 lateral, inwardly directed cusps each have a complex of secondary cusps (Fig. 6). Two pairs of salivary glands lie behind the buccal mass. The larger pair (Fig. 8, **sg**) are tubular, their ducts entering the buccal mass anterior to the esophageal opening. A second longer but narrower pair of glands (Fig. 8, **asg**) empty via ducts into the oral tube. The short anterior esophagus (Fig. 9, **ae**) runs from the roof of the buccal cavity to a large, muscular valve of Leiblein (Figs. 8, 9, **vl**). Posterior to this valve lies the mid-esophagus (Fig. 9, **me**), which becomes convoluted before passing through the nerve ring (Fig. 9, **nr**) and winding posteriorly along the floor of the cephalic sinus. There is no gland of Leiblein, but a narrow glandular strip lines the dorsal surface of a portion of the mid-

esophagus. The straight, narrow posterior esophagus (Fig. 9, **pe**) begins at the rear of the cephalic sinus and leads to a simple, U-shaped stomach (Fig. 9, **sto**). Longitudinal folds run through the stomach and into the intestine (Fig. 9, **int**), which passes through the kidney and continues along the right side of the mantle cavity where it expands to form a rectum (Figs. 7, 9, 10, **r**). A small anal gland (Figs. 7, 9, **rg**) runs along the dorsal anterior portion of the rectum to a point where it detaches from the roof of the mantle cavity to form the anus (Figs. 7, 9, **a**). No identifiable gut contents were found in any of the specimens examined.

Female reproductive system: The female reproductive system is similar in most respects to that of *Cancellaria reticulata* (Harasewych and Petit, 1982). The yellowish, ascinous ovary lies at the posterior-most portion of the visceral mass. From it a thin-walled oviduct (Fig. 10, **od**) runs anteriorly along the columellar side of the digestive gland, kidney and pericardium before entering the rear of the mantle cavity. No gonopericardial duct was found. The pallial portion of the oviduct consists of an albumen gland (Fig. 10, **ag**), a small, tubuliferous ingesting gland (Fig. 10, **ig**), a large, ovate capsule gland (Fig. 10, **cg**) and a triangular bursa copulatrix (Fig. 10, **bc**).

Male reproductive system: The male reproductive system does not differ markedly from that of *Cancellaria reticulata* (Harasewych and Petit, 1982). The testis lines the columellar side of the digestive gland and gives rise to a testicular duct that runs anteriorly along the visceral mass, becoming convoluted when adjacent to the kidney, then straightening and entering the rear of the mantle cavity. Here it expands, becoming convoluted and glandular (Fig. 7, **pr**), then constricts again and leads to the base of a long, cylindrical penis (Fig. 7, **pen**). The penis, ovate in cross-section, contains a coiled penial duct and has a terminal papilla.

Nervous system: As in *Cancellaria reticulata* (Harasewych and Petit, 1982), the nervous system is highly concentrated with the cerebral, pleural, pedal and subesophageal ganglia fused into a nerve ring (Fig. 9, **nr**) that encircles the esophagus and anterior aorta. The buccal ganglia are at the rear of the buccal mass, but neither the proboscis nor the cerebro-buccal

connectives are as long as in *C. reticulata*.

Discussion

Within the cancellariacean framework, *Olssonella smithii* is less specialized than is *Cancellaria reticulata* both in shell structure and in anatomical organization. Table 2 lists major anatomical differences between these two species, with asterisks denoting conditions we consider to be derived.

The diet of cancellariids remains a mystery, as no identifiable gut contents could be found in any species examined. However, the highly modified chemoreceptive organs and anterior alimentary system of *C. reticulata* suggest a more specialized diet for that species. *Olssonella smithii* has a simpler anterior alimentary system, but the very large hypobranchial gland suggests the possibility of toxin production (Halstead, 1965).

Olssonella smithii is also less specialized in shell architecture, lacking the external evidence of internal varices and bifurcated columellar folds of *C. reticulata*. The former species has apertural lirae every 240° rather than every 120° as found in the latter. Shell ultrastructure is similar in both species, although *O. smithii* has a thicker, coarser periostracum.

Attempts to investigate morphological diversity within the Cancellariacea have been hampered by a lack of a phylogenetic arrangement

of the approximately 100 nominal supraspecific taxa within the group. The superfamily has been divided into the Cancellariidae and the extinct Paladmetidae (Sohl, 1964; Ponder, 1973). Cancellariid genera have, in general, been clustered around three morphological types that have been elevated to the subfamilies Cancellariinae, Trigonostominae and Admetinae (Cossmann, 1899).

Cancellaria reticulata, whose anatomy has recently been described (Harasewych and Petit, 1982), is the type species of *Cancellaria* Lamarck, 1799. *Olssonella smithii*, the type species of *Olssonella* Petit, 1970, may serve as exemplar of the Trigonostominae. No general anatomical studies of any species of Admetinae are known to us, although a brief description of a living *Admete viridula* (Fabricius, 1780) is given by Jeffreys (1876) and repeated by Tryon (1885). Thiele (1929), Powell (1951) and Oliver (1982) have published figures or descriptions of radulae and jaws of members of this subfamily. The limited data available show that Cancellariinae and Trigonostominae are more closely related to each other than either is to Admetinae. Representatives of the first two "subfamilies" have radular teeth in which the outer cusps have secondary cusps; indeed, the principle radular differences seem to lie in the patterns of this secondary dentition. In contrast, the outer "cusps" of admetine radular teeth are bulbous

TABLE 2. Anatomical differences between *Olssonella smithii* and *Cancellaria reticulata*. Asterisk denotes derived condition.

Character	<i>Olssonella smithii</i>	<i>Cancellaria reticulata</i>
Left cephalic tentacle	normal	*bilobed
distance between osphradium and ctenidium	normal	*enlarged
hypobranchial gland	*hypertrophied	normal
proboscis shape	tubular, smooth	*ventrally flat, papillose
proboscis	normal, pleurombolic	*posterior portion of retracted proboscis serves as proboscis sheath
buccal mass	large, protrudes posteriorly when proboscis is retracted	*small, contained in anterior portion of proboscis
valve of Leiblein	large, normal	*reduced to bulge on esophagus
middle esophagus	*?expanded	narrow
penis	cylindrical	*?flat
bursa copulatrix	triangular	*?rectangular
cerebro-buccal connective	*long	**very long

and nearly hemispherical, with the central portion of the tooth lined with longitudinally arranged barbs (Oliver, 1982: Figs. 3, 5). Within Admetinae the jaw is shorter (Oliver, 1982: Fig. 4), lacking the posterior lobes present in jaws of Cancellariinae (Olsson, 1970: Fig. 13) and Trigonostominae (Olsson, 1970: Fig. 24).

Admete magellanica (Strebel, 1905) lacks a radula but has a tubular jaw (Oliver, 1982:16) suggesting to us a trend toward loss of radula in Admetinae with the tubular jaw being used as a piercing stylet, as in the pyramidellids.

Admittedly, these interpretations are speculative, being based on minimal data. It is hoped further work will shed more light on some of the hypotheses proposed.

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