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MORPHOLOGY AND SYSTEMATICS OF THE ENIGMATIC VOLUTID *PLICOLIVA ZELINDAE* (PETUCH, 1979) (MOLLUSCA: GASTROPODA)

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ABSTRACT

The morphology of the living animal, anterior alimentary system and nervous system of *Plicoliva zelindae* is described. Presence of paired siphonal appendages, broad cephalic shield and lateral lappets, as well as a long connective between the supraesophageal and right pleural ganglia confirm the assignment of this taxon to the family Volutidae. The subfamily Plicolivinae, characterized by its multicuspid lateral teeth, distinctive sabot-like rachidian teeth, and a gland of Leiblein with greatly enlarged terminal bulb, shares some anatomical features with the volutid subfamilies Haliinae and Volutinae. With certain members of the former (e.g., *Amoria*) it shares a distinctive external pigmentation pattern and similar siphonal appendages and rachidian teeth. Comparisons of Plicolivinae with published data on various species of Volutinae reveal similar shell morphology and the presence of a gland of Leiblein with an enlarged terminal bulb in both subfamilies.

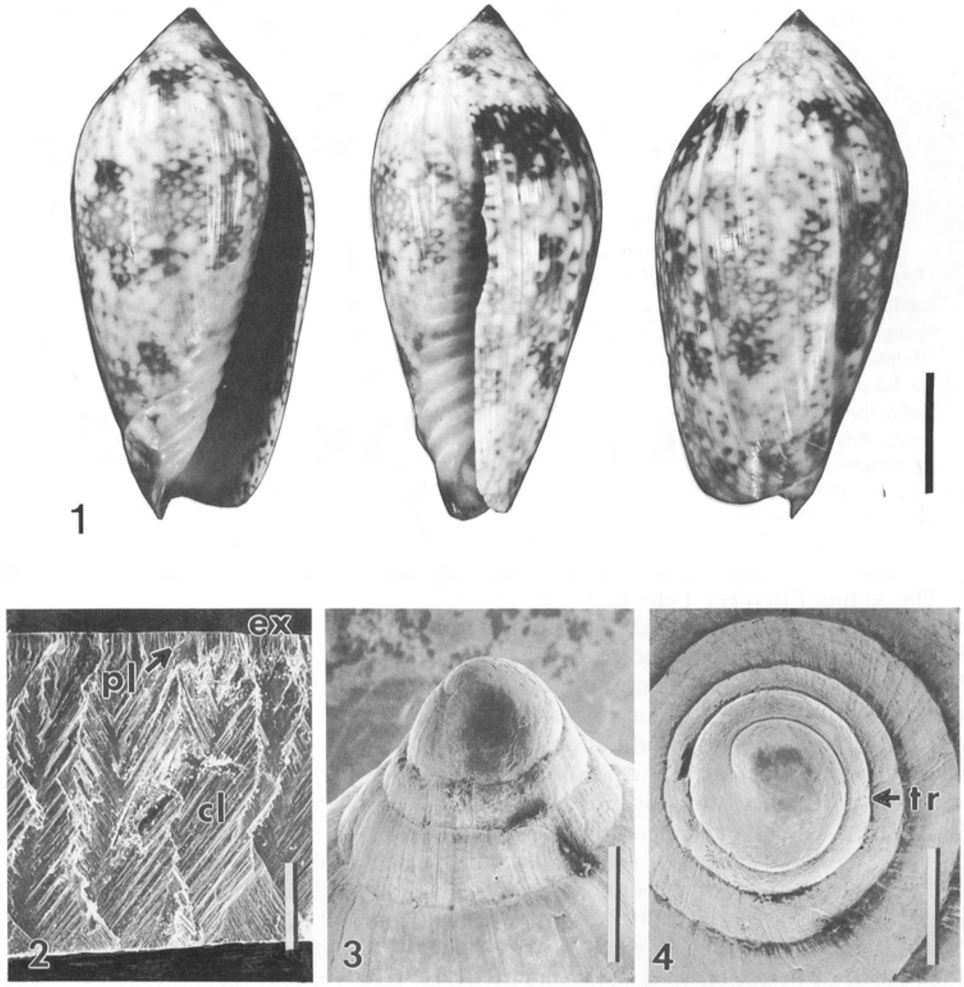
The genus *Plicoliva* Petuch, 1979, contains two shallow-water, geographically restricted species with broadly disjunct ranges. *Plicoliva zelindae* (Petuch, 1979), the type species, is endemic to the vicinity of the Abrolhos Reef Complex and from off Espírito Santo State in eastern Brazil, while *P. ryalli* Bouchet, 1990 is known only from off Ghana, in western Africa.

To date, only shell and radular characters have been used to infer the systematic allocation of *Plicoliva.* Petuch (1979) originally described *Plicoliva zelindae* in the family Olividae, erecting *Plicoliva* as a subgenus of *Oliva.* While noting that *P. zelindae* "resembles volutes in the genera *Lyria* or *Enaeta* more than typical *Oliva* or *Olivella*" (Petuch, 1979: 521), he argued that the shell shape, high gloss, and number of columellar folds favored the inclusion of this taxon in the Olividae. Later, Petuch and Sargent (1986: 16) elevated *Plicoliva* to generic rank and transferred it to the Volutidae without further discussion. More recently, Petuch (1987: 140) reduced *Plicoliva* to a subgenus of *Lyria,* also without discussion.

Bouchet (1990) described a second species of *Plicoliva, P. ryalli,* from 2–40 m depth off the coast of western Africa. Based on an examination of the radulae of both species, he concluded that the peculiar combination of conchological and radular features warranted the introduction of the new subfamily Plicolivinae, within the Volutidae, "although future anatomical work may disprove this placement" (Bouchet, 1990: 9). In this paper we present additional data on the morphology of the animal of *Plicoliva zelindae* and discuss the implications of these findings on the suprageneric systematics of *Plicoliva.*

MATERIAL AND METHODS

Protoconch and ultrastructure data are from the holotype of *Plicoliva zelindae* (USNM 780655) from the south side of Guaratibas Reefs, Abrolhos Reef Complex, Bahia State, Brazil (17°25′S, 039°08′W), 1 m depth, in shell gravel in a tide pool. Live animal observations are based on a single juvenile specimen (MNHN) collected by Bouchet, Métivier and Leal off Espírito Santo State, Brazil (21°37′S, 040°18′W) in 37 m (R/V MARION-DUFRESNE MD55-Brésil Cruise, station DC15, 05/1987). The shell and radula of this specimen are figured in Bouchet (1990: figs. 1, 2 and 14–16 respectively). Anatomical and additional radular data are based on the incomplete soft parts of a single, female specimen collected off Guarapari, Espírito Santo State, Brazil, by J. Coltro and M. V. Coltro, in May 1992, and sent by E. C. Rios.



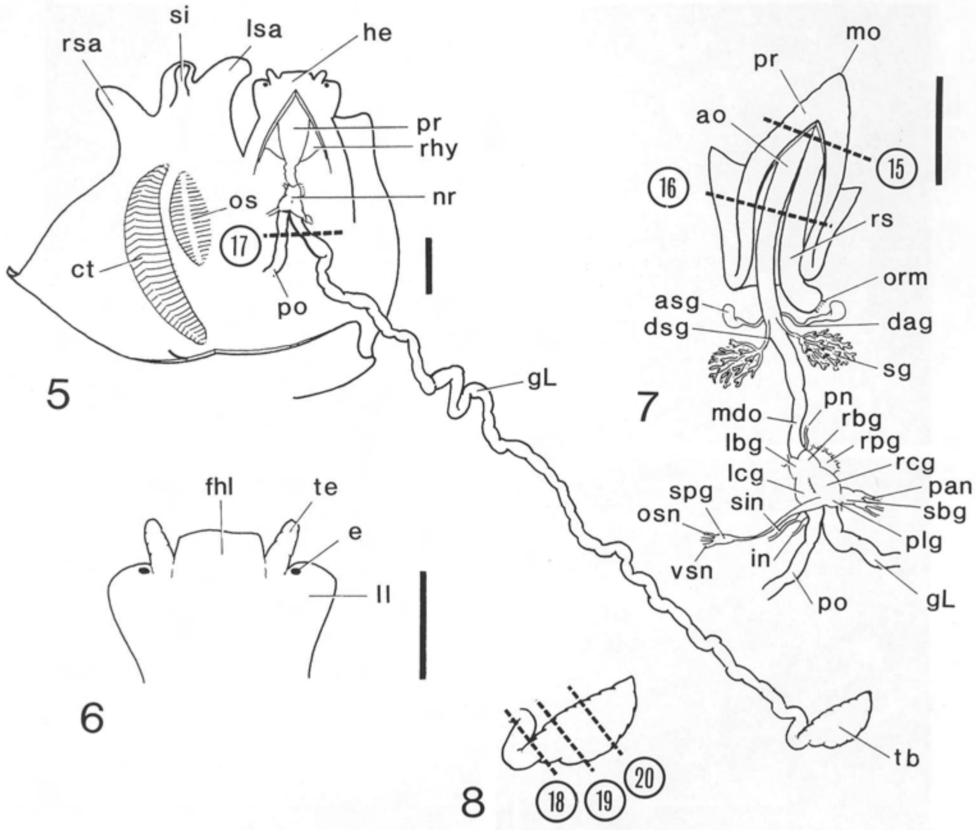
Figures 1–4. *Plicoliva zelindae,* Abrolhos Reef Complex, Brazil, USNM 780655, holotype. 1. Shell. Scale bar = 5 mm; 2. Shell ultrastructure, collabral section at outer lip. Scale bar = 100 μm. 3, 4. Protoconch, lateral and apical views. Scale bars = 2 mm. Abbreviations: cl, cross-lamellar layer; pl, prismatic layer; ex, external shell surface; tr, transition from protoconch to teleoconch.

Toluidine blue stain was used to provide contrast during dissections. The distal tip of the proboscis with everted radula was dehydrated through a standard alcoholic series, and critical point dried using carbon dioxide as the transitional fluid (Lewis and Nemanic, 1973). Critical point dried tissue, radular preparations, and shell fragments were coated with carbon and gold-palladium, and examined under Hitachi S-570, or Cambridge Stereoscan 250 Mk2 scanning electron microscopes. The protoconch of the holotype was examined uncoated under SEM. Tissues for histological examination were excised, paraffin-embedded, sectioned at 6 μm, and stained with Harris haematoxylin and eosin (Humason, 1979).

We add to the conchological data provided by Petuch (1979) and Bouchet (1990) by including brief descriptions and SEM micrographs of the protoconch and shell ultrastructure. These authors should be consulted for full descriptions of shell characters.

RESULTS

Shell Morphology.—Protoconch (Figs. 3, 4) mammillated, smooth, reddish brown, increasing in diameter from 0.85 mm to 1.3 mm in 1½ whorls. Transition to

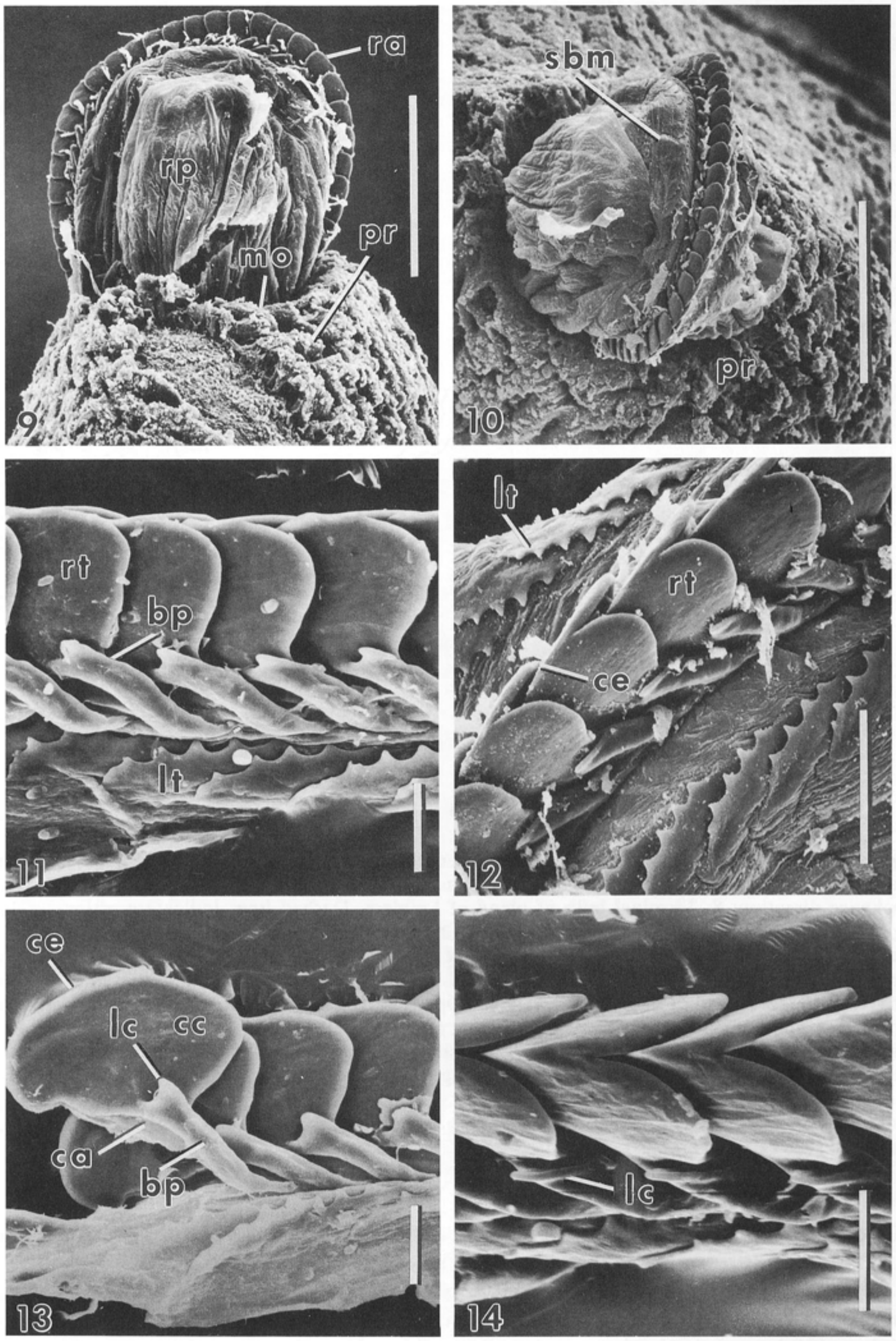


Figures 5–8. *Plicoliva zelindae.* Diagrammatic renditions of: 5. Dissected mantle cavity and cephalic hemocoel; 6. Head; 7. Dissected anterior alimentary system with proboscis rotated 90° in counter-clockwise direction; 8. Terminal bulb of gland of Leiblein. Dashed lines indicate positions of histological sections in Figures 15–20. Scale bars = 2 mm. Abbreviations: ao, anterior esophagus; asg, accessory salivary gland; ct, ctenidium; dag, duct of accessory salivary gland; dsg, duct of salivary gland; e, eye; fhl, frontal head lobe; gL, gland of Leiblein; in, integumentary nerve; lbg, left buccal ganglion; lcg, left cerebral ganglion; ll, lateral lappet; lsa, left siphonal appendage; mdo, mid-esophagus; mo, mouth; nr, circumesophageal nerve ring; orm, odontophore retractor muscle; os, osphradium; osn, osphradial nerve; pan, pallial nerve; plg, pleural ganglion; po, posterior esophagus; pn, proboscis nerve; pr, proboscis; rbg, right buccal ganglion; rcg, right cerebral ganglion; rpg, right pedal ganglion; rs, radular sac; rsa, right siphonal appendage; sg, salivary gland; si, siphon; sbg, subesophageal ganglion; sin, siphonal nerve; spg, supraesophageal ganglion; tb, terminal bulb of gland of Leiblein; te, tentacle; vsn, visceral nerve.

teleoconch (Fig. 4, tr) abrupt, demarcated by slight inflation of whorl and change in surface texture of shell, otherwise almost imperceptible.

A chip from the thin (350 μm), immature outer lip of holotype (Fig. 2) is composed of two layers, a thin (68 μm), outer prismatic layer (Fig. 2, pl), and thicker (280 μm) inner layer of collabrally oriented, crossed-lamellar aragonite (Fig. 2, cl). At least one additional layer is present on the inner surface further within the aperture.

General External Morphology.—Head and foot of living animal dark brownish red, with numerous, closely spaced, creamy white, circular spots that produce a net-like pattern. Along the middle and posterior portions of the foot, the white



Figures 9–14. *Plicoliva zelindae,* scanning electron micrographs of radula. 9–10. Critical point dried proboscis tip with radula everted, 9. lateral and 10. frontal views. Scale bars = 100 μm; 11. Lateral view showing lateral teeth and lateral cusps of rachidian teeth. Scale bar = 10 μm; 12. Dorso-lateral view showing angle between rachidian and lateral teeth. Scale bar = 20 μm; 13. View showing profile of one rachidian tooth and contact area between basal plate and subradular membrane. Scale bar = 10 μm; 14. Dorsal view showing cutting edge of rachidian teeth. Scale bar = 10 μm. Abbreviations:

spots give way to bright-yellow spots each circled by a white ring. Mantle thin, whitish, semi-transparent, almost completely enveloping shell when extended. Extended foot slightly larger than shell, bilobed anteriorly, rounded posteriorly. Operculum absent. Head (Figs. 5, he; 6) broad, flattened, with short, cylindrical tentacles (Fig. 6, te) and truncated, squarish frontal lobe (Fig. 6, fhl) that lacks a median cephalic furrow. Lateral lappets (Fig. 6, ll) rounded anteriorly, tapering posteriorly. Eyes (Fig. 6, e) situated on lateral lappets near their junction with tentacles. Siphon (Fig. 5, si) well developed. Siphonal appendages (Fig. 5, rsa, lsa) equal in size, wider and longer than siphon. Mantle cavity shallow, broad, with large osphradium (Fig. 5, os), ctenidium (Fig. 5, ct) as wide and twice as long as osphradium. Specimen lacking remaining portion of mantle cavity.

Anterior Alimentary System.—Proboscis (Figs. 5, 7, 9, pr) short, anteriorly tapering, strongly muscular, pleurembolic. Rhynchodeum (Fig. 5, rhy) spacious, well defined. Mouth (Figs. 7, 9, mo) small (≈150 μm), situated at apex of proboscis. Anterior esophagus (Figs. 7, 15, 16, ao) broad, highly muscular, lacking conspicuous dorsal folds. Buccal mass and radular sac (Fig. 7, rs) long, extending beyond retracted proboscis.

Radula (Figs. 9–14)extremely long (≈4.5 mm), narrow (60 μm), triserial, comprised of at least 150 rows of teeth. Rachidian teeth tricuspid, sabot-like, V-shaped when viewed dorsally. Central cusps (Fig. 13, cc) greatly enlarged dorso-ventrally, with broad, flat, lateral surfaces that intersect to define a curved cutting edge (Figs. 12, 13, ce). Lateral cusps (Figs. 13, 14, lc) greatly reduced, forming short, conical projections flanking base of central cusp. Basal plate (Figs. 11, 13, bp) narrow, curved, anteriorly concave. Lateral teeth (Figs. 11, 12, lt) elongated, thin, flat, equal in width to rachidian tooth, slightly thickened inner edge with five short cusps giving serrated appearance. Outer edges of lateral teeth directed posteriorly, forming 20° angle with radular axis, with each transverse row approaching an M-shaped configuration.

Salivary glands (Fig. 7, sg) paired, consisting of numerous branching tubules. Ducts of salivary glands (Figs. 7, 15, 16, dsg) running anteriorly along esophagus, becoming embedded in anterior esophageal wall. Accessory salivary glands (Figs. 7, asg) short, tubular, distally expanded, free of salivary glands. Ducts of accessory salivary glands fuse to form single duct (Figs. 15, 16, dag) that runs along the ventral midline of the buccal mass prior to entering the buccal cavity. Valve of Leiblein, greatly reduced, indistinguishable on exterior of esophagus. Mid-esophagus (Fig. 7, mdo) thin, flaccid in preserved animal.

Gland of Leiblein (Figs. 5, 7, gL) extremely long (exceeding shell length), tightly convoluted, entering mid-esophagus just behind nerve ring (Figs. 5, nr; 7). Gland composed of long, narrow (≈500 μm) tube (Fig. 17, gl), wider than posterior esophagus (Figs. 5, 7, 17, po), its lumen filled with amorphous secretion (Fig. 17, am). Terminal bulb (Figs. 5, 18, tb; 8, 19, 20) large (1.6 mm diameter), cardiform, strongly muscular, with outer layer of longitudinal muscles (Fig. 19, lm), inner layer of circular muscles (Figs. 19, 20, cm), sphincter at junction with tubular portion of gland. Lumen of bulb filled with amorphous secretion (Fig. 20, am). Lumen diameter greatest in distal portion of bulb (Fig. 20). Posterior esoph-

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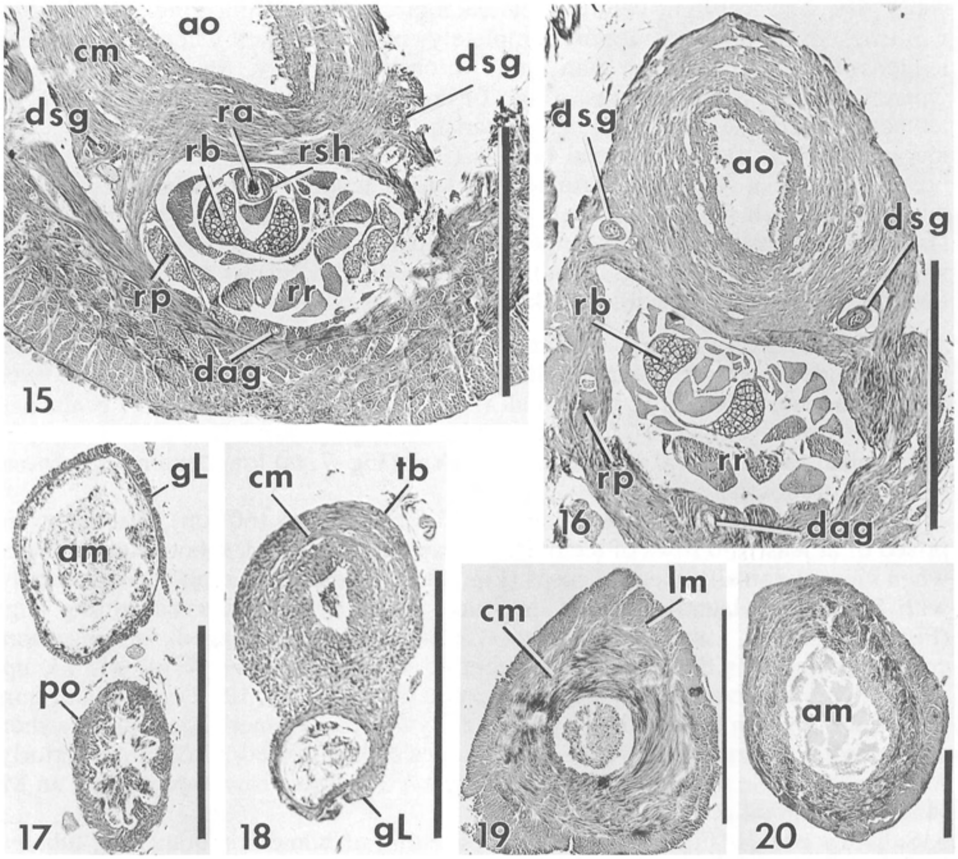
bp, basal plate; ca, contact area of basal plate and subradular membrane; cc, central cusp of rachidian tooth; ce, cutting edge of rachidian tooth; lc, lateral cusp of rachidian tooth; lt, lateral tooth; mo, mouth; pr, proboscis; ra, radula; rp, radular protractor muscle; rt, rachidian tooth; sbm, subradular membrane.



Figures 15–20. *Plicoliva zelindae,* histological sections of anterior alimentary system (see Figs. 5, 7, 8 for position of sections); 15—Anterior third of proboscis; 16—Posterior third of proboscis; 17—Esophagus and gland of Leiblein posteriorly to point of separation; 18—Gland of Leiblein and terminal bulb at junction; 19—Proximal third of terminal bulb of gland of Leiblein; 20—Terminal bulb of gland of Leiblein at region of maximum diameter. All scale bars = 0.5 mm. Abbreviations: ao, anterior esophagus; am, amorphous secretion; cm, circular muscle; dag, duct of accessory salivary gland; dsg, duct of salivary gland; gL, gland of Leiblein; lm, longitudinal muscle; po, posterior esophagus; ra, radula; rb, radular bolster; rp, radular protractor muscle; rr, radular retractor muscle; rsh, radular sheath; tb, terminal bulb of gland of Leiblein.

agus (Figs. 5, 7, 17, po) lined with longitudinal ridges. Remainder of alimentary system lacking in specimen examined.

Nervous System.—Circumesophageal nerve ring (Fig. 5, nr) highly concentrated, except for supraesophageal ganglion (Fig. 7, spg), which is widely separated from right pleural ganglion (Fig. 7, plg). Supraesophageal ganglion situated beneath epithelium of mantle cavity, near osphradium, giving rise to visceral (Fig. 7, vsn) and osphradial nerves (Fig. 7, osn).

DISCUSSION

Although the overall shell morphology of immature specimens of *Plicoliva zelindae* resembles that of the genus *Oliva,* shell morphology of adult *P. ryalli* is recognizably volutid, strongly resembling *Enaeta barnesii* (Gray, 1825) in overall shape, gloss, axial sculpture, columellar dentition and color pattern (Poppe and Goto, 1992: pl. 18). *Plicoliva zelindae* also lacks such conchological and anatomical apomorphies of Olividae as: a channelled suture; pedal lobes; crescent-shaped propodium with longitudinal cleft; posterior mantle lobe; anterior and posterior mantle tentacles (Kantor, 1991). Absence of these characters precludes the inclusion of *Plicoliva* in Olividae.

A broad head with a hood-like frontal lobe and lateral lappets, as well as long, paired siphonal appendages, are characters that are unique to Volutidae, but not ubiquitous within the family. The presence of these characters in *Plicoliva zelindae* supports its inclusion within Volutidae, as does the morphology of its radula. The sabot-like rachidian teeth are very similar to those of *Amoria canaliculata* (Weaver and du Pont, 1970: fig. 33a), but could conceivably be derived by ventral enlargement of the central cusp of the rachidian tooth of *Enaeta cylleniformis* (Sowerby, 1844) (Bouchet, 1990: figs. 21–22). Unlike Bouchet (1990: 8), we do not regard these teeth to be of the "wishbone" type found in *Volutomitra* and *Scaphella,* as the central cusps in these genera are pointed rather than having a broad cutting edge, and likely function by piercing rather than incising prey tissues. Although triserial radulae have been reported within several volutid subfamilies (Aiken and Fuller, 1986: 39), the multicuspid lateral teeth of *Plicoliva* are unique within Volutidae, and a principal diagnostic feature of the subfamily Plicolivinae. Similar multicuspid lateral teeth also occur in Fasciolariidae (Maes, 1967: figs. 1–7) and certain Mitridae (Cernohorsky, 1991: pl. 38, fig. 5), and were regarded as primitive features within the Neogastropoda (Ponder, 1973: 308).

The arrangement of the lateral teeth, with their outer edges directed posteriorly, is nearly perpendicular to the usual orientation of these teeth in neogastropods. Similar orientations of monocuspid lateral teeth have been illustrated for *Volutomitra* (Arnaud and van Mol, 1979: fig. 12B, C), and the volutids *Volutocorbis* (Aiken and Fuller, 1986: 39a) and *Callipara* (Aiken and Fuller, 1986: 39f).

The salivary glands of *Plicoliva zelindae* differ from those of most neogastropods in that the branching structure of the individual tubules is readily apparent. Within the Volutidae, branching salivary glands have been reported only in the genus *Voluta* (Clench and Turner, 1964: 134). The accessory salivary glands are short and do not intertwine with the salivary glands as in some volutids (Clench and Turner, 1964: pl. 82).

The external morphology of the gland of Leiblein of *Plicoliva zelindae,* with a long, convoluted duct associated with a large, terminal muscular bulb, is most similar to those of some specialized marginellids and toxoglossans. As in these taxa, the reduction or loss of the valve of Leiblein in *Plicoliva zelindae* is correlated with the modification of the gland of Leiblein into a long, tubular "poison gland." Although the gland of Leiblein of most volutids consists of a convoluted tube of approximately constant diameter, those of *Voluta musica* (Pace, 1902: 23; Clench and Turner, 1964: pl. 82, fig. 18B), *Voluta ebraea* Linnaeus, 1758 (pers. observ.), and *Ampulla priamus* (Poirier, 1885: pl. 3, fig. 2; Pace, 1902: 29) have been shown to have enlarged, terminal muscular bulbs.

Among rachiglossan neogastropods, the presence of a long connective between the supraesophageal and right pleural ganglia, such as occurs in *P. zelindae,* has been reported only in Muricidae (Marcus and Marcus, 1959: 149) and certain members of the family Volutidae (Ponder, 1973: 322). Within the Volutidae, this type of nervous system (Type 1 following the terminology of Ponder, 1970: 159) has been reported only in the Volutinae, Haliinae, and eastern Atlantic Yetinae.

In Athletinae, Calliotectinae, Zidoninae, and Indo-Pacific Yetinae, these two ganglia are closely fused together (Type 2 nervous system).

Of the nine other Recent subfamilies of Volutidae (Ponder and Warén, 1988: 306), Plicolivinae shares a number of features with the Volutinae and some members of the Haliinae. It shares a Type 1 nervous system and salivary glands with branching ducts with both these subfamilies. Like various species of Volutinae, Plicolivinae has shells with pronounced axial sculpture and numerous (>5) columellar folds, as well as a gland of Leiblein with an enlarged terminal bulb.

Plicolivinae shares the following similarities with species of *Amoria*: glazed shell exterior enveloped by mantle lobes, long siphonal appendages of equal length, rachidian morphology, and a similar pigmentation pattern of white spots containing centered bright-yellow spots on the foot [e.g., *Amoria canaliculata* (McCoy, 1869), see Weaver and du Pont, 1970: pl. 69, top]. Although *Amoria* is included in the subfamily Haliinae, of which the better known name Scaphellinae is a synonym, both *Plicoliva* and *Amoria* differ from *Scaphella* in rachidian morphology, foot pigmentation, siphonal appendage morphology (*Scaphella* has a single appendage on right side), and lack the median cephalic furrow present in *Scaphella* (Clench and Turner, 1964:135).

It is premature to provide a cladistic analysis of the family Volutidae in order to determine the relationships of Plicolivinae, as the literature on the family contains insufficient anatomical data to yield a resolved phylogenetic hypothesis.

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