Copulabyssia riosi, a new deep-sea limpet (Gastropoda: Pseudococculinidae) from the continental slope off Brazil with comments on the systematics of the genus

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ABSTRACT

A new bathyal species of the family Pseudococculinidae is described from samples dredged in 1987 along the continental slope of southeastern-eastern Brazil by the French research vessel *Marion-Dufresne.* The new species, allocated in the genus *Copulabyssia,* differs from the 4 other known congeners by characters of shell, external morphology, mantle cavity, and radula. Descriptions of internal morphology based on microdissections are provided, including the digestive system and the complex muscular apparatus of the odontophore. The distribution of characters of taxonomic significance at the species level in *Copulabyssia* is given in tabular format and discussed.

Key words: Mollusca, Cocculiniformia, Vetigastropoda, Lepetelloidea, bathyal, anatomy, taxonomy, odontophore.

INTRODUCTION

Bathyal samples dredged off E-SE Brazil yielded specimens of an unnamed species of the genus *Copulabyssia,* family Pseudococculinidae. Two live specimens and one empty shell were collected at three stations performed between 960-1320 m. The Pseudococculinidae and other families comprising the superfamily Lepetelloidea Dall, 1882, are included amongst the mollusks living at greatest depths in the ocean (Leal and Harasewych, 1999; Lesicki, 1998; Marshall, 1986; Wolff, 1979). The new taxon exhibits the diagnostic characters of the genus *Copulabyssia* Haszprunar, 1988. *Copulabyssia riosi* new species is herein compared with the 4 other species of the genus named to date (Lesicki, 1998): C. *corrugata* (Jeffreys, 1883) (NE Atlantic); *C. gradata* (Marshall, 1986) (SW Pacific); *C. leptalea* (Verrill, 1884) (N Atlantic); *C. similaris* Hasegawa, 1997 (Japan).

MATERIALS AND METHODS

Two live-collected specimens and one empty shell were available for study. A single specimen was dissected. Microdissection was performed with the specimen immersed in 70% ethanol. The apical (distal) region of visceral mass was damaged; adjacent structures were described and are shown herein based on reconstruction. After dehydration in a standard alcoholic series, the second specimen was chemically dried for 10 min in hexamethyldisilizane (HMDS). Shells, radula, and chemically dried soft parts were coated with carbon and gold and examined and photographed under Hitachi S-570 (at National Museum of Natural History, Smithsonian Institution), Leo 440 (at MZSP), or Philips XL30 ESEM-FEG (Center for Advanced Microscopy, University of Miami) electron microscopes. Institutional abbreviations used are: MNHN, Museum national d'Histoire naturelle, Paris, France; MZSP, Museu de Zoologia da Universidade de Sao Paulo, Brazil; NMNH, Museum of New Zealand Te Papa Tongarewa, Wellington; NSMT, National Science Museum, Tokyo, Japan; SMNH, Natur Historika Riksmuseet, Stockholm, Sweden; USNM, National Museum of Natural History, Smithsonian Institution, Washington. Other abbreviations and text conventions are: **1,** 5, lateral teeth (lateral 5 = pluricuspid tooth); 1, 2, marginal teeth; **ac,** anterior cartilages of odontophore; **an,** anus; **bm,** buccal mass; **br,** subradular membrane; **bs,** buccal sphincter; **df,** dorsal folds of buccal mass; **dg,** digestive gland; **ep,** epipodium; **es,** esophagus; **et,** epipodial tentacles; **gi,** gill; go, gonad; **gp,** genital pore; **if,** inner mantle fold; **in,** intestine; **ir,** insertion of m4 in radular sac; **is,** insertion of m5 in radular sac; **ki,** kidney; **lt,** left cephalic tentacle; **mb,** mantle edge; **mj,** jaw and peribuccal muscles; **mo,** mouth; **mp,** mesopodium; **m2,** pair of buccal mass retractors; **m3,** inner buccal mass protractors; **m4,** pair of antero-dorsal tensors; **m5,** pair of postero-dorsal tensors; **m6,** horizontal muscle; **m7,** pair of odontophore approximators; **m8,** pair of cartilage approximators; **nc,** nuchal cavity; of, outer mantle fold; **pa,** mantle papillae; **pc,** posterior cartilages of odontophore; **pr,** protuberance on right ten-

tacle; **re,** rectum; **ra,** radula; **rn,** radular caecum; **rs,** radular sac; **rt,** right cephalic tentacle; **sc,** subradular cartilage; **sf,** fold along gill; **sg,** seminal groove; **sm,** shell muscle; sn, snout; **st,** stomach; vg, vestigial left gill leaflet. The odontophore muscles examined in this study were also described by Haszprunar (1988: 165-167, fig. 3) for *Kurilabyssia venezuelensis* McLean, 1988. Terminology used herein (boldface) corresponds to the one used by Haszprunar as follows: **mj** = br + otr; bs = bs; m2 = dr2; m4 = rd2; m5 = rr; m6 = ho; *ml* = sr3 (?); m8 = ci. The remaining small muscles described by Haszprunar (1988) could not be observed in the single specimen available for microdissection.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Subclass Orthogastropoda Ponder and Lindberg, 1996
Order Vetigastropoda Salvini-Plawén, 1980

Remarks: The superfamilies Cocculinoidea Dall, 1882, and Lepetelloidea Dall, 1882 have been united under the order Cocculiformia Haszprunar, 1987. Recent studies of gastropod phylogeny based on morphological characters (Ponder and Lindberg, 1996; 1997) suggest that Cocculinoidea is sister taxon to Neritopsina, and that Lepetelloidea is part of the order Vetigastropoda (see also Haszprunar, 1998: 664). This arrangement is followed herein. Harasewych *et al.* (1997) indicated, based on partial 18S rDNA sequences, that Cocculiniformia may not constitute a clade. These latter authors, however, suggested that Cocculinoidea and Lepetelloidea are more closely related to each other and to Patellogastropoda than to Neritopsina or Vetigastropoda.

Superfamily Lepetelloidea Dall, 1882
Family Pseudococculinidae Hickman, 1983
Subfamily Caymanabyssinae Marshall, 1986
Genus *Copulabyssia* Haszprunar, 1988

Type species: *Cocculina corrugata* Jeffreys, 1883, p. 394, pl. 44, figs. 2-2a. Type locality: 59°40'N, 7°21'W, 930 m, *Triton* Expedition station 10.

Diagnosis: Protoconch sculpture of microscopic prismatic crystals; right cephalic tentacle exceptionally large, "swollen"; right cephalic tentacle with deep, open glandular seminal groove situated postero-dorsally; large pedal gland; gills pallial, several well-developed gill leaflets on right side, a single one on left side.

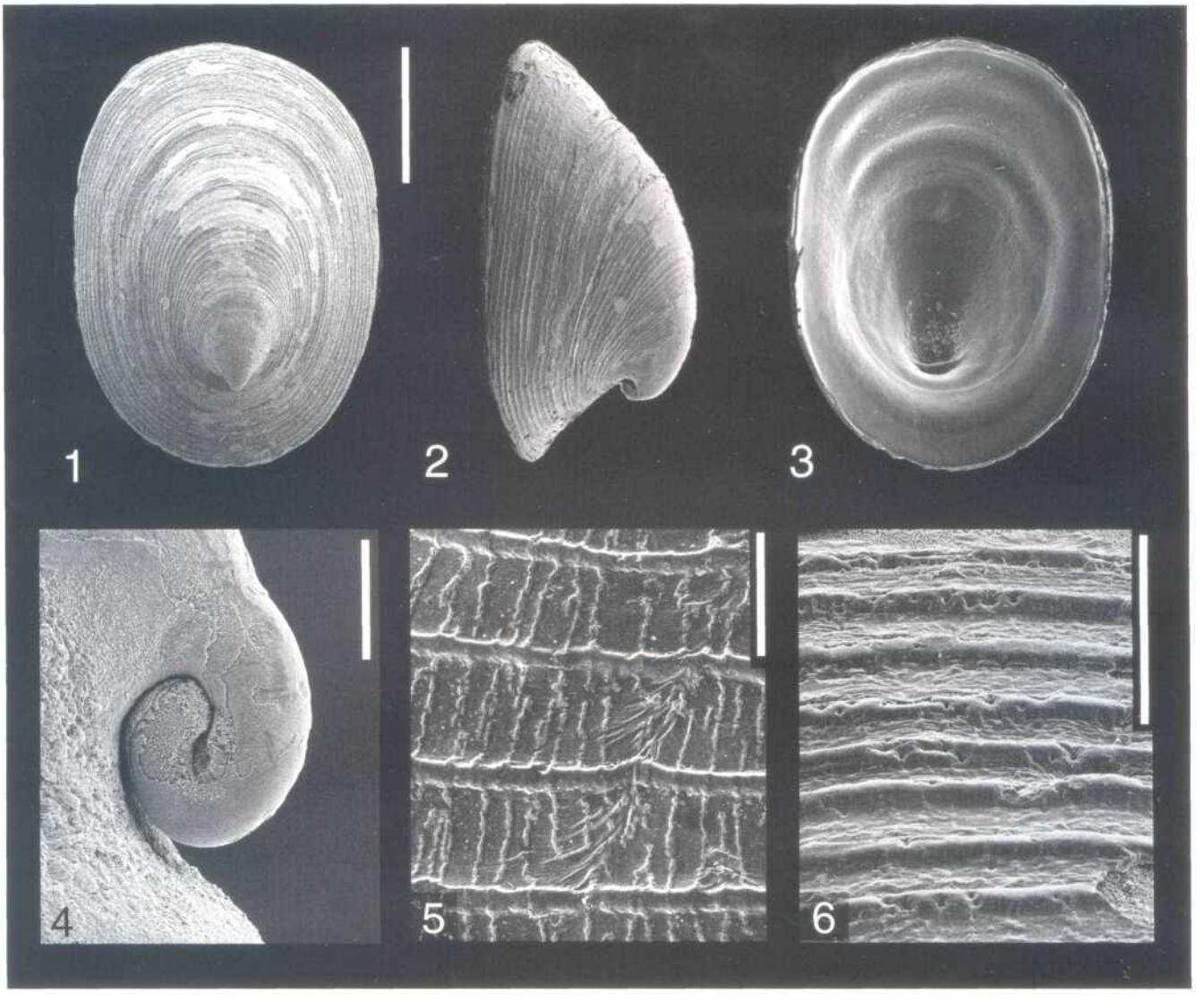
Copulabyssia riosi new species
(Figures 1-24, Table 1)

Diagnosis: Teleoconch at first with radial sculpture then with closely set concentric ribs (interspaces about 25 µm in width); internally with narrow but well-defined anterior apical septum; radial sculpture only on early teleoconch; cutting area of rachidian tooth with blunt cusp; left side of subpallial cavity with small structure that could represent a vestigial gill leaflet; right cephalic tentacle with prominent subterminal protuberance; left cephalic tentacle small for genus; inner branches of epipodial tentacles filamentous.

Description: *Shell (Figures 1-6):* Small (length to 3.50 mm), thin, arched, elevated (height/length about 0.5), with apex at posterior quarter pointing in posterior direction. Anterior slope convex, about 88% of shell length. Posterior slope concave, about 30% of shell length. Shell surface usually lightly eroded, milky white. Protoconch (figure 4) length about 200 µm, surface badly eroded in type material. Teleoconch sculpture of concentric (commarginal) ribs separated by intervals of about 25 µm. Concentric ribs narrow (about 10 µm) and crossed by fine radial lines on early part of teleoconch (figure 5). Concentric ribs on latter part of teleoconch proportionally thicker, radial lines absent (figure 6). Internally with narrow, but well-defined, anterior apical septum. Aperture elliptical (figure 3), not conforming to a planar surface, convex. Shell muscle scar continuous, horseshoe-shaped.

Head-foot (Figures 7, 8, 13, 14, 17): Head prominent and large (about 1/4 foot length) (figures 7, 13, 14, 17). Cephalic tentacles (figures 7, 13, 14, 17, rt, lt) on dorsolateral surface of head. Right tentacle about 4 times larger than left tentacle, modified as copulatory organ (described below). Eyes apparently lacking (unpigmented?). Snout (figures 7, 13, 14, 16, 17, sn) very large, cylindrical on base, gradually becoming slightly flattened dorso-ventrally. Anterior extremity of snout almost flat, broader than region immediately behind it, with pair of small lateral projections. Foot large and flat (figures 7, 13, 14), smaller than shell aperture in preserved animal. Mesopodium (figures 7, 13, 14, mp) flattened. Epipodium (figures 7, 13, 14, ep) flange-like, surrounding entire mesopodium, larger on anterior edge, which covers basoventral region of snout. Pair of epipodial tentacles (figure 7, 9, 13, 14, et) well-developed, projecting from posterior region at both sides of longitudinal axis of animal, slightly dorsal to epipodium, on intersection between mantle and shell muscle. Each epipodial tentacle bifid; outer branch shorter and with broad tip; inner branch longer and pointed. Shell muscle (figures 15-17, sm) horseshoe-shaped (concavity towards anterior region); anterior extremities broader, pointing away from shell apex. Almost all head-foot muscles converge toward insertion of shell muscle.

Mantle cavity (Figures 12-15, 17): Mantle edge (figures 12-14, 17, mb) thick, with 2 folds; outer fold (figures 12, 14, 17, of) covered by slender and very small, translucent papillae (figure 12); inner fold (figures 14, 17, if) about twice as broad as outer fold, richly glandular, white. A small, transparent, yellowish protuberance (figure 13, vg) on inner margin of inner fold, in region adjacent to left cephalic tentacle, may represent vestigial left gill leaflet. Mantle cavity surrounding entire head-foot, somewhat deep, i.e., with ample space be-



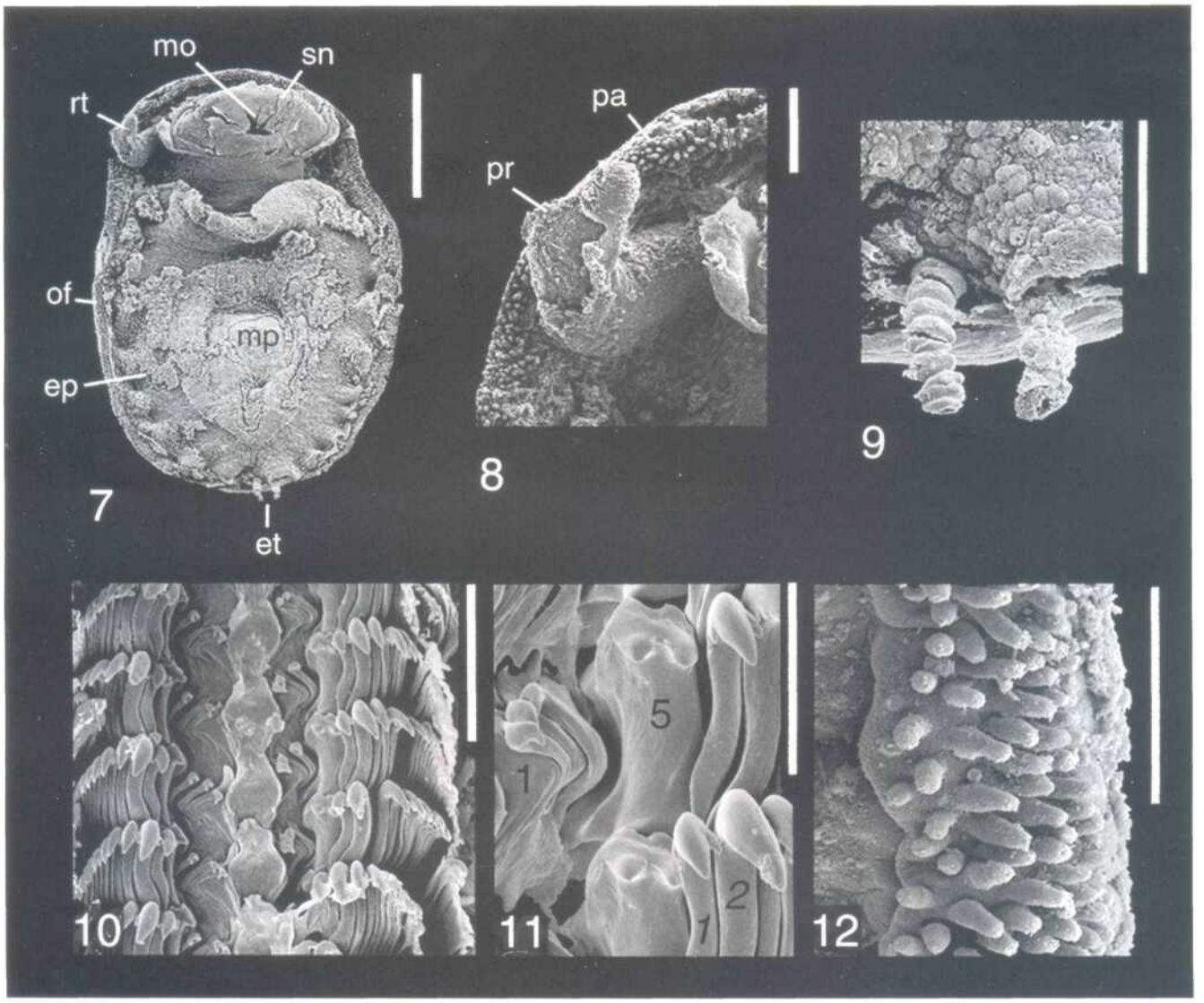
Figures 1-6. *Copulabyssia riosi* new species: shell of holotype, MZSP 32150. 1. Dorsal view. 2. Lateral view. 3. Ventral view. Scale line = 1.0 mm. 4. Protoconch. Scale line = 100 µm. 5-6. Shell sculpture. 5. On early teleoconch. Scale line = 50 m. 6. Close to shell margin. Scale line = 100 m.

tween mantle edge and shell muscle. Nuchal cavity (figures 14, 15, 17, nc) deeper than remainder of mantle cavity. Gill (figures 13, 14, 17, gi) small, situated on right side of mantle cavity, somewhat parallel to mantle edge and extending for about half of foot length, consisting of about 14 successively smaller leaflets. Anterior extremity of gill (figure 5, gi) just posterior to head-foot limit. Each leaflet low and triangular, relatively thick. Most posterior leaflets situated perpendicularly to mantle edge, gradually becoming oblique to it on anterior region. A small, narrow, and low fold (figure 14, sf) runs between gill and shell muscle along posterior half of gill. Anus (figures 15-17, an) and genital pore (figure 17, gp) on right side, at head and foot limit, just anterior to right extremity of shell muscle.

Circulatory and excretory systems (Figures 15-17): Heart not observed. Large blood vessels along thick mantle border. Kidney (figures 15, 17, ki) very small, white, solid, slightly triangular; situated in right-posterior region of head, just posterior to rectum.

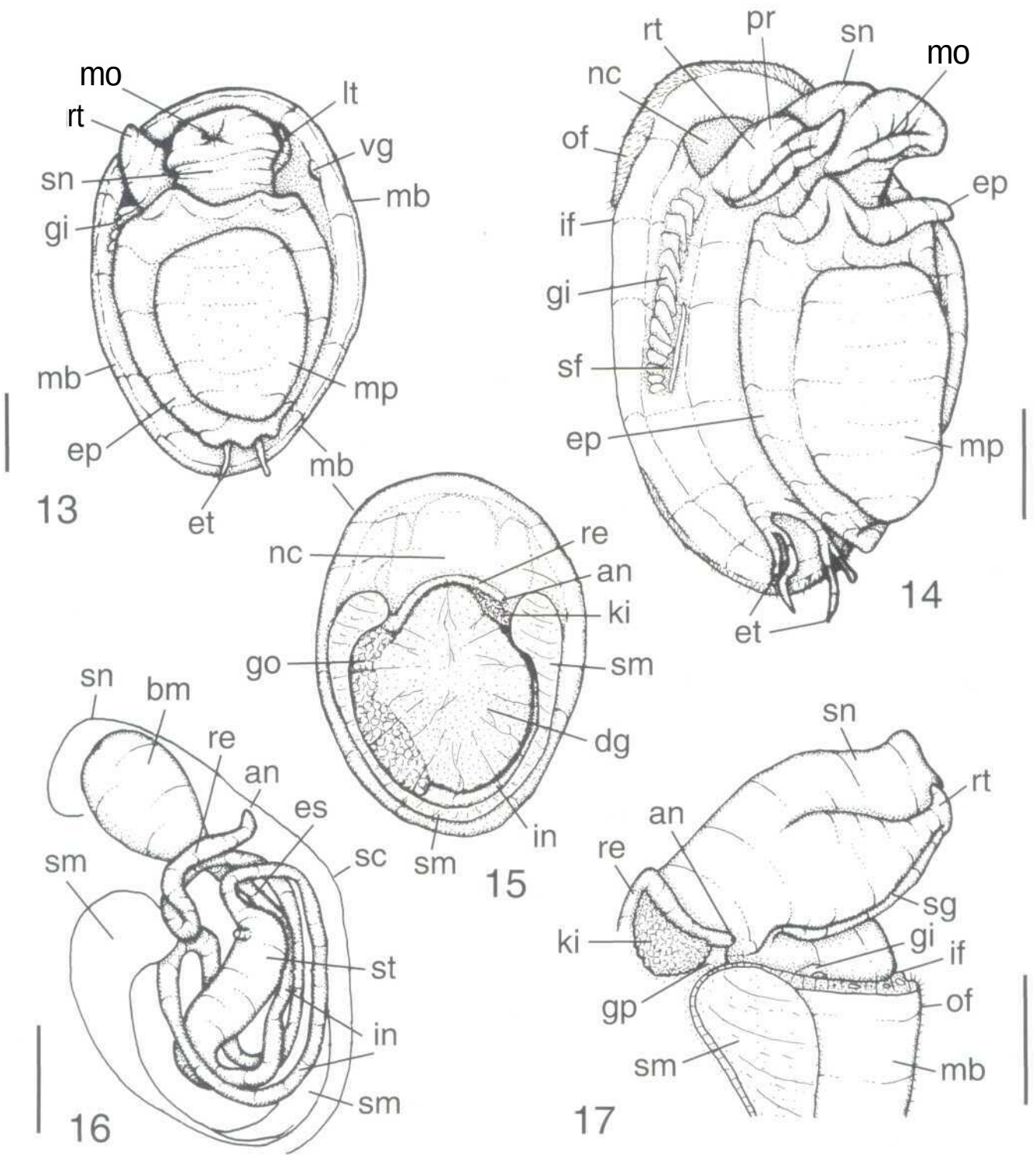
Visceral mass (Figures 15, 16): Round, surrounded by following structures: laterally and in posterior direction by shell muscle, in anterior direction by buccal mass, ventrally by inner surface of mesopodium, and dorsally by central region of mantle and shell. Gonad (figure 15, go) and digestive gland (figure 15, dg) cream in color, intersected by several intestinal loops (figure 16). Gonad situated mainly on left region and digestive gland mainly on central region.

Digestive system (Figures 7, 13-24): Mouth (figures 7, 13, 14, 18, mo) on middle-ventral region of anterior sur-

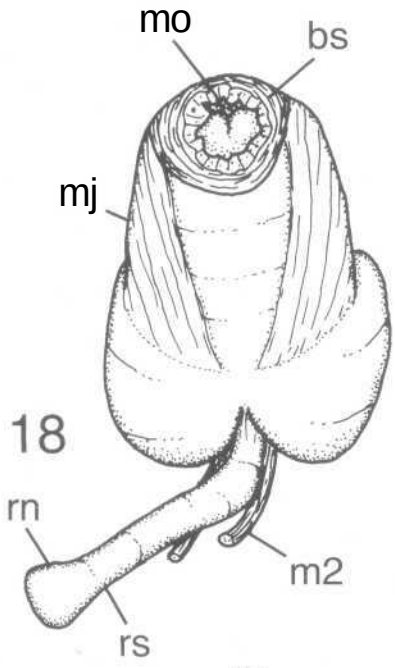


Figures 7-12. *Copulabyssia riosi* new species: paratype, MNHN unnumbered, gross external morphology and radula. 7. Ventral view of animal. Scale line = 500 µm. 8. Detail of right cephalic tentacle (copulatory organ). 9. Inner branches of epipodial tentacles (damaged during preparation). Scale lines = 100 µm. **10-11.** Radula. 10. View of 5 rows. Scale line = 50 µm. 11. Detail of lateral and first marginal teeth. Scale line = 10 µm. 12. Papillae on outer mantle fold. Scale line — 50 µm.

face of snout, oriented transversally. Buccal mass (figure 16, bm) somewhat large, occupying about entire head cavity. Buccal sphincter (figure 18, 19, bs) well developed. Superficial protractor muscle of buccal mass relatively narrow, connected to lateral and dorsal regions of buccal sphincter and adjacent region of snout, running along lateral and dorsal surface of buccal mass, connected to lateral and ventral region of buccal mass. Dorsal wall of buccal mass very thin, with pair of thick longitudinal folds (figure 19, df) that join together in anterior direction at median line, becoming gradually weaker toward esophagus (figures 16, 19, es). Odontophore (figures 18-24) large, comprising most of buccal mass, oval in outline. Odontophore muscles (figures 18-24): (m1) (not illustrated) several small and short fibers connecting buccal mass to adjacent inner lining of snout, more concentrated on dorsal surface; (m2) (figures 18, 19) pair of narrow retractor muscles of buccal mass connected to inner ventral lining of snout just posterior to buccal mass, running parallel to radular sac (figures 19-23, rs), connected to postero-dorsal surface of buccal mass on lateral surface of beginning of esophagus; (m3) (figure 21, 22) pair of thin inner protractor muscles of buccal mass connected to inner lateral lining of mouth, running on (and covering) lateral surface of odontophore, connected to antero-ventral margin of posterior cartilages; (m4) (figures 20-24) pair of antero-dorsal tensor muscles connected in part to outer ventral surface of anterior cartilages and in part to lateral surface of posterior cartilages, running along (and covering) pos-



Figures 13-17. *Copulabyssia riosi* new species: paratype, MZSP 32149, gross morphology. **13.** Ventral view. **14.** Lateral view, right side, margin of mantle deflected to show its inner surface. **15.** Dorsal view. **16.** Digestive system, dorso-lateral view, left side, shown by transparency, only dorsal contour and part of shell muscle shown. **17.** Detail of head, lateral view, right side, adjacent mantle removed by means of an incision around shell muscle. Scale lines = 500 µm.



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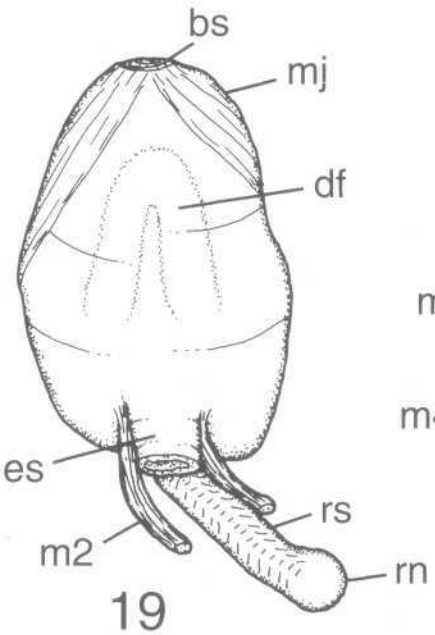

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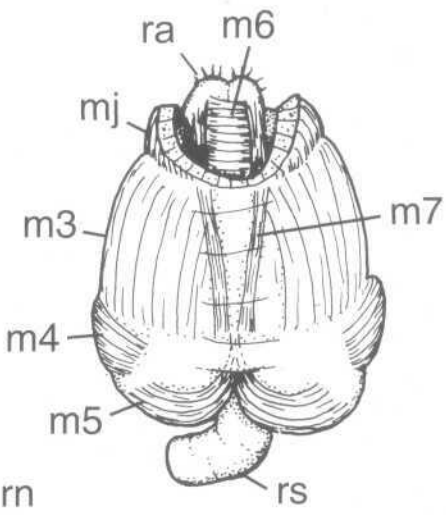

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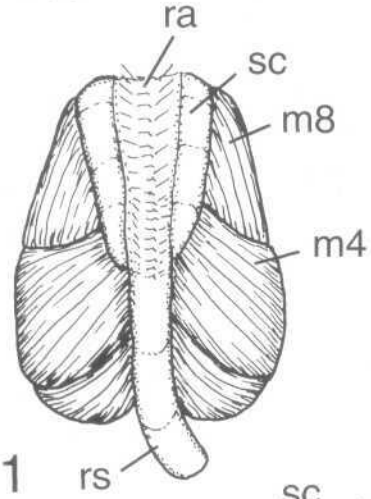

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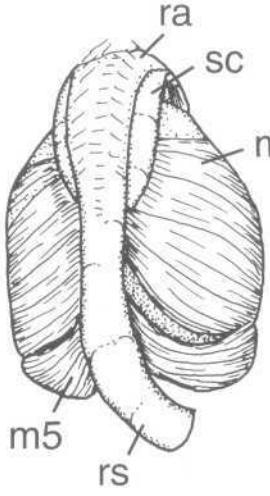

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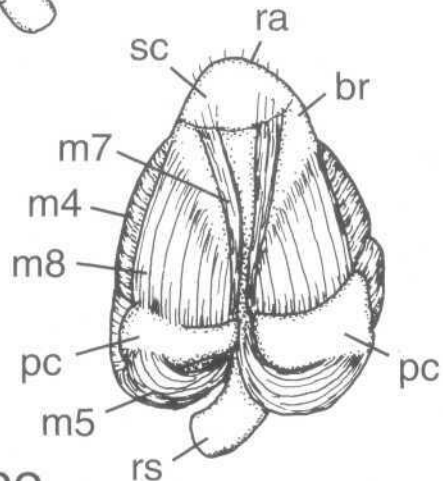

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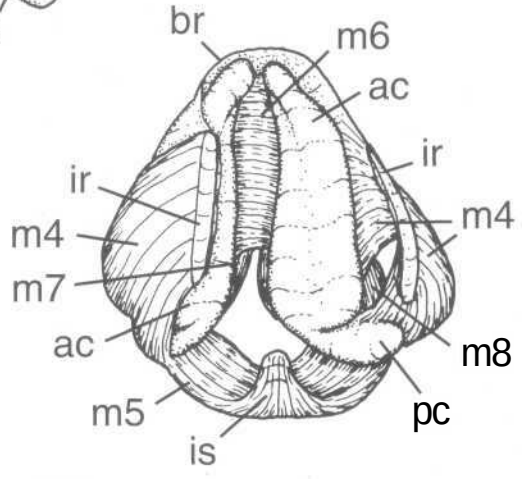

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Table 1. Diagnoses of species of *Copulabyssia*. "Shell length" is maximum size for species. "Rib interspaces" is the distance between concentric ribs on posterior shell slope. "Left gill leaflet" is size of single-leaflet gill in relation to right gill leaflets; medium would be about the same size as right gill leaflets. "Right cephalic tentacle" = copulatory organ ("RT"). Unknown character states indicated by "NA". Degree of development of cephalic tentacles is relative to other congeneric species.

Distribution	C. *riosi* Off SE, E Brazil	*C. leptalea* NW Atlantic	*C. gradata* Off New Zealand	*C. corrugata* NE Atlantic, Med	C. *similaris* Japan
Character					
Shell length (mm)	3.50	2.45	1.95	1.35	3,36
Rib interspaces (µm)	±25	±40	±40	±130	±50
Radial sculpture	early **teleo** only	strong	lacking	present	very weak
Postition of apex	anterior 2/10	anterior 3/10	anterior 3/10	anterior 1/10	variable
Apical septum	present	absent	absent	absent	absent
Rachidian	broad	broad, round sides	broad	elongate	broad
Rachidian cutting area	blunt cusp	long, pointed cusp	cuspless, rounded	cuspless, squarish	cuspless, round
Cusps lateral tooth 5	2-3	4	NA	2	2
Epipodial tentacles	filamentous	NA	NA	stubby	present
Right cephalic tentacle	well-developed	NA	swollen base	swollen base	"bilobed"
Left cephalic tentacle	very reduced	NA	normal	normal	normal
RT protuberance	well-developed	NA	absent	absent	absent
Left gill leaflet	?vestigial	NA	medium	small	?absent
References	this work	Warén, 1991 McLean and Harasewych, 1995	Marshall, 1986 Haszprunar, 1988	Haszprunar, 1988 Dantart and Luque, 1994	Hasegawa, 1997

terior surface of odontophore (figure 24), connected to ventral surface of radular sac on region posterior to emergence of radula; (m5) (figures 20-24) pair of postero-dorsal tensor muscles connected to postero-ventral surface of posterior cartilages, running dorsally and medially along (and covering) posterior surface of odontophore, connected to radular sac just posterior to m4 insertion; m6) (figures 20, 24) horizontal muscle relatively narrow, connected to antero-ventral margin of anterior cartilages along about3/4of their length; m7) (figures 20, 22, 24) pair of narrow ventral tensor muscles connected to meso-ventral margin of posterior region of anterior cartilages, running along meso-ventral surface of odontophore, connected to antero-ventral extremity of subradular cartilage (figures 21-23, sc); m8) (figures 10, 12) pair of broad approximator muscles of cartilages connected to antero-lateral surface of posterior cartilages (figures 22, 24, pc), running toward anterior cartilages, connected along lateral surface of anterior cartilages (figure 24, ac). Anterior cartilages of odontophore flattened, long, narrower in anterior direction, broader in posterior direction. Posterior cartilages short (about 1/5 of anterior cartilage length), semi-spherical. Anterior and posterior cartilages joined together on small area close to median line (figure 24). Esophagus (figures, 16, 19, es) narrow and simple, running toward postero-ventral region of visceral mass, where it suddenly bends in anterior direction to its insertion in stomach (figure 16, st). Stomach large, cylindrical, directed toward shell apex; inner surface uniform, iridescent, greenish. Single duct to digestive gland situated close to shell apex. Stomach suddenly narrows giving origin to intestine (figures 16, in), which runs toward the right and then in posterior direction, surrounding dorsal margin of shell muscle, gradually turning ventrally and in anterior direction to buccal mass, where it suddenly curves in posterior direction, running along dorsal surface of mesopodium dorsally to its posterior edge, looping dorsally to the right, running ventrally back to preceding loop, near posterior region of head, where it crosses transversally from right to left dorsally to left extremity of shell muscle, suddenly turning successively in posterior, dorsal, and anterior directions; last loop represented by rectum (figures 15-17, re) crossing transversally from left to right through kidney along posterior limit of mantle cavity. Anus (figure 15-17, an) small and simple, located on posterior right side of mantle cavity.

Radula (Figures 10-11): Asymmetrical, narrow, relatively short (about twice odontophore length). Rachidian tooth rhomboid, broad for genus, broader at mid-section, and blunt (worn?) cusp. First lateral tooth trian-

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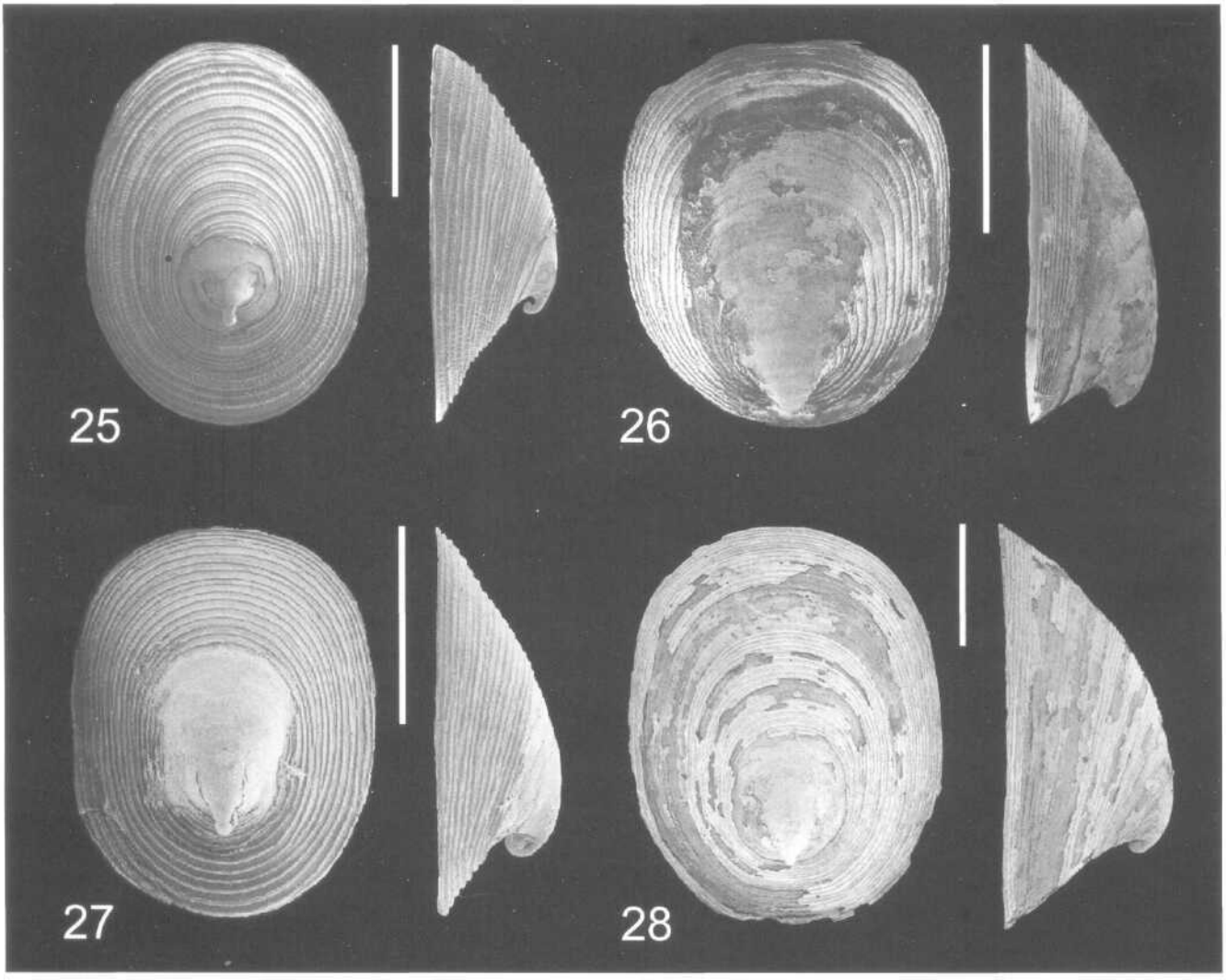
Figures 18-24. *Copulabyssia riosi* new species: paratype, MZSP 32149, buccal mass and odontophore. **18-19.** Buccal mass extracted from snout. **18.** Ventral view. **19.** Dorsal view. **20-24.** Odontophore. **20.** Ventral view, superficial layer of muscles and membranes partially excised. **21.** Dorsal view. 22. Ventral view, superficial layer of muscles and membranes fully excised. 23. Dorsal view. **24.** Dorsal view, radular ribbon and radula sac extracted, most of muscles and cartilages deflected to expose inner surfaces, right-side structures more deflected than those on left side. Scale lines = 500 m.



Figures 25-28. Dorsal and lateral views of shells of other species of *Copulabyssia*. 25. *C. leptalea* (Verrill, 1884). USNM 757345, NE of Norfolk, Virginia, 3080-3090 m, R/V *Gillis* cruise 7508, station 36. 26. *C. corrugata* (Jeffreys, 1883). SMNH unnumbered, SE of Reykjanes Ridge, off southern Iceland, 250-350 m, on sunken wood. 27. *C. gradata* (Marshall, 1986). NMNZ M. 75007, holotype, off White Island, New Zealand, 1075-1100 m, on sunken wood. 28. *C. similaris* Hazegawa, 1997. NSMT-Mo 70822, off Toi, Suruga Bay, Japan, 430-710 m, on sunken wood. Scale lines = 1.0 mm.

gular with outer basal projection that fits into a depression on second lateral tooth, and pointed single cusp. First lateral tooth (figure 11, 1), broad, triangular. Second, third, and fourth lateral teeth strongly curved, with two short cusps. Fifth lateral (pluricuspid) tooth (figure 11, 5) massive, club-like, with 3 subterminal denticle-like cusps. Latero-marginal plate present. Inner marginal teeth pointed, with two denticle-like lateral cusps and thick shafts (e.g., figure 11, *1, 2*), decreasing in size outward. Second marginal tooth largest. Outer marginal teeth with serrations.

Reproductive system (Figures 7, 8, 13, 14, 15, 17): Gonad (figure 15, go) relatively small, on posterior left region of visceral mass, surrounded by left branch of shell muscle, right surface of digestive gland, and some intestinal loops. A very narrow gonoduct on right side (not fully examined), running in anterior direction and apically toward right side of mantle cavity, where it opens. Genital pore (figure 17, gp) turned ventrally, just posterior to anus. Seminal groove (figure 17, sg) beginning on genital pore, running on integument surface for short distance, up to posterior region of base of right tentacle. Right tentacle broad, slightly flattened dorso-ventrally, gradually tapering to flat tip (figures 7, 8, 13, 14, 17, rt). Edges of seminal groove on posterior surface of tentacle, ending on posterior region of tip. A well-developed subterminal protuberance present on anterior surface of tentacle (figure 14).

Type material: Holotype MZSP 32150, 3.25 mm length X 2.50 mm width X 1.60 mm height, from type locality, P. Bouchet, J. Leal, and B. Métivier, 27 May 1987, dead shell. Paratypes: MNHN unnumbered, 3.35

mm length X 2.35 mm width X 1.75 mm height, MZSP 32149 (same specimen, soft parts only), E of Cabo Sao Tome, off Rio de Janeiro State, Brazil, 21°24'S, 39°56'W, 1320°1360 m depth, R/V *Marion-Dufresne* cruise MD55, station CP-04, P. Bouchet, J. Leal, B. Metivier, 9 May 1987, bottom of basaltic gravel and oxidized iron pebbles; MZSP 32151, 3.50 mm length X 2.35 mm width X 1.90 mm height, Doce River Canyon, off Espírito Santo State, Brazil, 19°38'S, 38°43'W, 960 m depth, R/V *Marion-Dufresne* cruise MD55, station CB-95, P. Bouchet, J. Leal, B. Metivier 30 May 1987, bottom of basaltic gravel and oxidized iron pebbles (shell broken during SEM session in Miami).

Type locality: Continental slope SE off Abrolhos coral reef system, off Bahia State, Brazil, 19°00.4'S, 37°48.8'W, 950-1050 m depth, compact dark mud and shell hash bottom, (R/V *Marion-Dufresne* cruise MD55, station DC-72).

Geographic distribution: Continental slope off E-SE Brazil.

Bathymetry: 960-1320 m.

Etymology: Named after Prof. Eliézer de C. Rios, enthusiastic Brazilian author and mentor to an entire generation of malacologists.

DISCUSSION

Specimens of *Copulabyssia riosi* were found apparently removed from the actual organic substrate of the species (see Lesicki, 1998, for a listing of species-specific substrates and food preferences in the family). The new species differs morphologically from the other four species allocated in the genus *Copulabyssia* (see figures 25-28, table 1) by the presence of an apical septum on the inner shell surface, narrow sculptural interspaces, filamentous, longer epipodial tentacles, presence of a structure on the left side of subpallial cavity that could prove to be a vestigial left gill leaflet, and by the presence of an anterior, subterminal protuberance on the right cephalic tentacle. The double insertion of the m4 and the expanded insertion of the m5 are character states unique to *Copulabyssia riosi* when compared to other species of Cocculinoidea and Lepetelloidea for which these characters are known (see Haszprunar, 1987; Simone, 1996); however, the states of these characters are so far unknown for the other four species of the genus *Copulabyssia.*

The mantle organs of *Copulabyssia riosi* are typical of the genus, with nuchal cavity and gill leaflets situated in the right side of the mantle cavity. *Copulabyssia riosi* shows a satellite fold in the inner margin of the gill, and a small protuberance that could represent a vestigial gill leaflet in the left region of the mantle border. In the superfamily Lepetelloidea, similar structures are also present in the *Addisonia enodis* Simone, 1996 (Lepetelloidea, Addisoniidae). The arrangement of loops of the digestive system looks similar to that described by Haszprunar (1988: 167-168, fig. 4) for *Amphiplica knudseni* McLean, 1988 (Lepetelloidea: Pseudococculinidae), but differs by the reduction of salivary glands, jaw plates, and esophageal pouches.

The complex odontophore of *Copulabyssia riosi* presents a combination of apparently plesiomorphic and autapomorphic characters. The presence of 4 odontophore cartilages and their approximator muscle (m8) represents apparently plesiomorphic states present in several species of Patellogastropoda, Vetigastropoda (including Lepetelloidea), Cocculinoidea, and Neritopsina (L. R. L. Simone, personal observation). The well-developed subradular cartilage, the partial connection between the anterior and posterior odontophore cartilages and the horizontal muscle (m6) connected only in a side of the anterior cartilages seem to represent apomorphic characters (at least in relation to Patellogastropoda).

ACKNOWLEDGMENTS

Gerhard Haszprunar (Zoologische Staatssammlung Munchen, Germany), Anders Waren (SMNH), and Bruce Marshall (NMNZ) critically reviewed the manuscript. We are grateful to Philippe Bouchet and Virginie Héros at the original repository institution (National museum d'Histoire naturelle, Paris) for making available the type material. We are also indebted to Suzanne R. Braden (National Museum of Natural History, Smithsonian Institution), for help with some of the SEM illustrations. M. G. Harasewych (National Museum of Natural History, Smithsonian Institution), Anders Waren (SMNH), Bruce Marshall (NMNZ), and Kazunori Hasegawa (NSMT) kindly sent photographs or negatives of relevant species of *Copulabyssia* for illustration. This study was supported in part by FAPESP (Fundação de Amparo a Pesquisa do Estado de Sao Paulo, Brazil) Grant # 96-6756-2 to L. R. L. Simone.

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