

REVISION OF THE GENUS *PARABORNIA* (BIVALVIA: GALEOMMATOIDEA: GALEOMMATIDAE) FROM THE WESTERN ATLANTIC, WITH DESCRIPTION OF A NEW SPECIES FROM BRAZIL

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Abstract *Parabornia palliopapillata* n. sp. (Galeommatidae) is described from small bivalves found attached to the abdomen of the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck) (Lysiosquillidae) from the Rio de Janeiro and São Paulo coasts, Brazil. The shell is thin, flat, white, and smooth. The hinge possesses a pair of small symmetrical cardinal teeth in each valve. The mantle border has 4 marginal folds, the third being entirely papillated, with only the umbonal region lacking papillae. The foot has a small byssus, a ventral furrow and an anterior flower-like organ. The style sac of the stomach is separated from the intestine. The incubation of ova occurs in both demibranchs. A complementary redescription of *P. squillina* Boss, 1965, the single species of the genus up to this time and associated with the same host, is provided, based on paratypes from Panama. The two species differ mainly in details of the mantle border, gill, digestive tract, anterior musculature and shape of the flower-like organ. A discussion of the family assignment of the genus is also provided.

Key words *Parabornia palliopapillata* n. sp., *P. squillina*, Galeommatidae, bivalvia, Brazil, anatomy, Stomatopoda.

INTRODUCTION

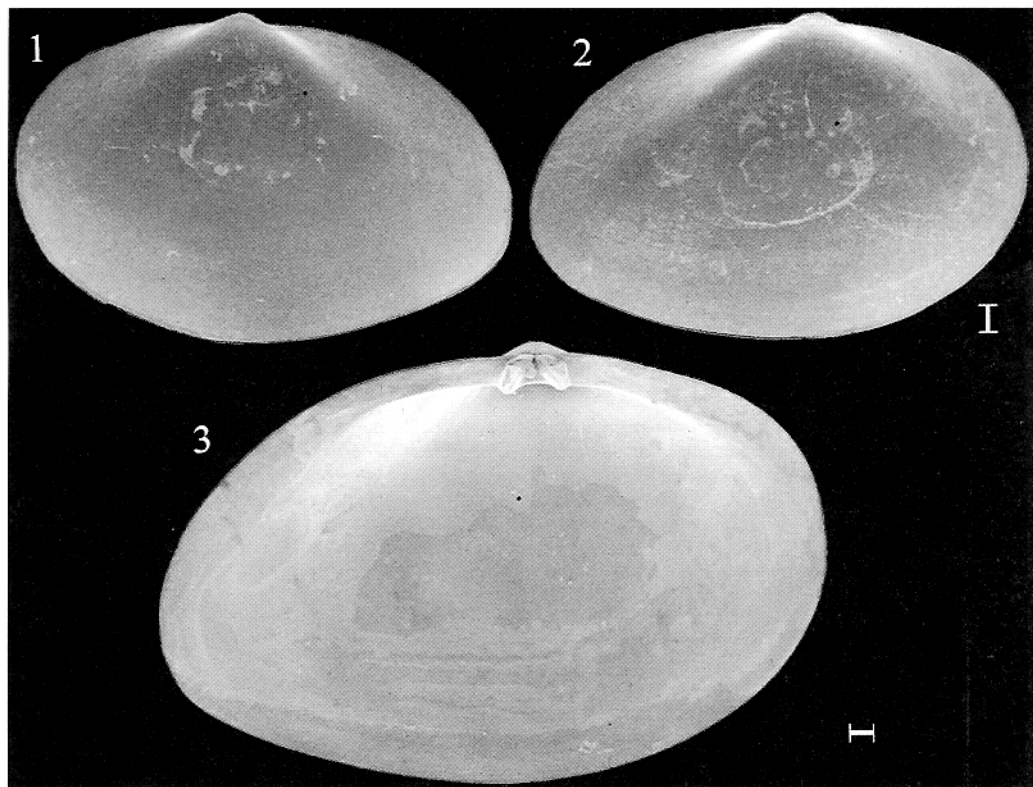
Bivalves living associated with crustaceans are frequently documented (Boss, 1965; Narchi, 1969; Abbott, 1974), including those living attached to their bodies. In the Brazilian malacofauna, however, no bivalves living on crustaceans have previously been detected. According to Abbott (1974), 40 species of galeommatids occur in the Americas, but only 2 species have been reported from Brazilian waters (Rios, 1994). Narchi (1966) described one of them, *Lepton cema* for the São Paulo coast, which is commensal with *Callichirus major* (Say, 1818) (Callinassidae). It is possible that the second species, *L. lepidum* Say, 1826, might not actually occur in Brazil.

The genus *Parabornia* Boss, 1965, encompasses up to this time a single species, *P. squillina* Boss, 1965 (type species by monotypy), with a geographic distribution from western Florida to Panama (Abbott, 1974). This species is found associated with the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck, 1818) (Lysiosquillidae).

At the Museu de Zoologia da Universidade de São Paulo (MZSP), carcinologists discovered small bivalves attached to the abdomen of *L. scabricauda* collected from southeastern Brazilian coast. An analysis of the material preliminarily identified the bivalves as *P. squillina*. However, comparison with paratype specimens of that species showed that, despite the close similarity of the shell and the same host habitat, sufficient anatomical differences exist to consider the Brazilian material as a different species. Although the original description of *L. squillina* is quite complete, including some anatomical aspects, a more complete description of this species is necessary, and is provided herein, emphasizing the differences between the two species.

The systematic arrangement of the Galeommatidae has been relatively unstable, with some taxa of the family sometimes placed in other families (compare, e.g., the classification given by Abbott, 1974, with that of Moore, 1969), a problem reviewed by Ponder (1971a, 1998). Taxonomic problems within the superfamily Galeommatoidae have been

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Figs 1–3 *Parabornia palliopapillata*, shell scanning electron micrographs (MZSP 32192). 1–2 left and right valves, outer view. Scale bar = 300 μ m 3 left valve, inner view. Scale bar = 200 μ m.

clarified by some phylogenies, such as that of Bieler & Mikkelsen (1992). In this paper, the systematics of Ponder (1998) is followed.

MATERIAL AND METHODS

All bivalve specimens received for study were already separated from their crustacean hosts, so details of the life habits were not fully available. However, some young specimens have subsequently been seen still attached to the host and some additional information was obtained from the carcinologists. Some specimens had inexplicably decalcified shells, with only a thin periostracum and remains of the calcareous layers present. The paratype lot of *P. squillina* is preserved in 70% ethanol; 3 of the specimens had already been extracted from the shell and dissected. They were extracted from the shells and dissected by usual techniques and immersed in 70% ethanol under a stereomicroscope. All drawings were done with the aid of a camera lucida. Scanning electron micrographs of the shells were produced in the Microscopy Laboratory of the Museu de Zoologia da Universidade de São Paulo.

Abbreviations of institutions: AMNH: American Museum of Natural History, New York, NY, USA; MZSP: Museu de Zoologia da Universidade de São Paulo, Brazil.

SYSTEMATICS

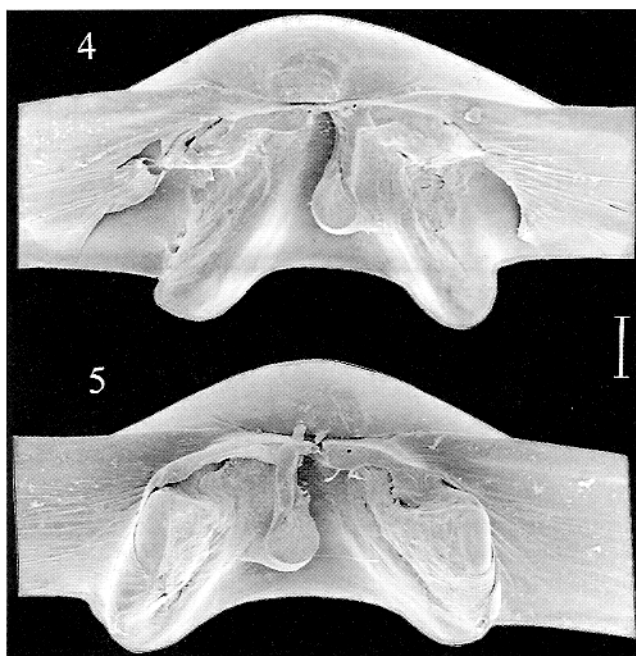
Parabornia palliopapillata new species Figs 1–13

Holotype MZSP 30083 from type locality. Measurements in mm: 7.1 by 5.2 by 1.7 (respectively antero-posterior length, dorsa-ventral height, lateral width).

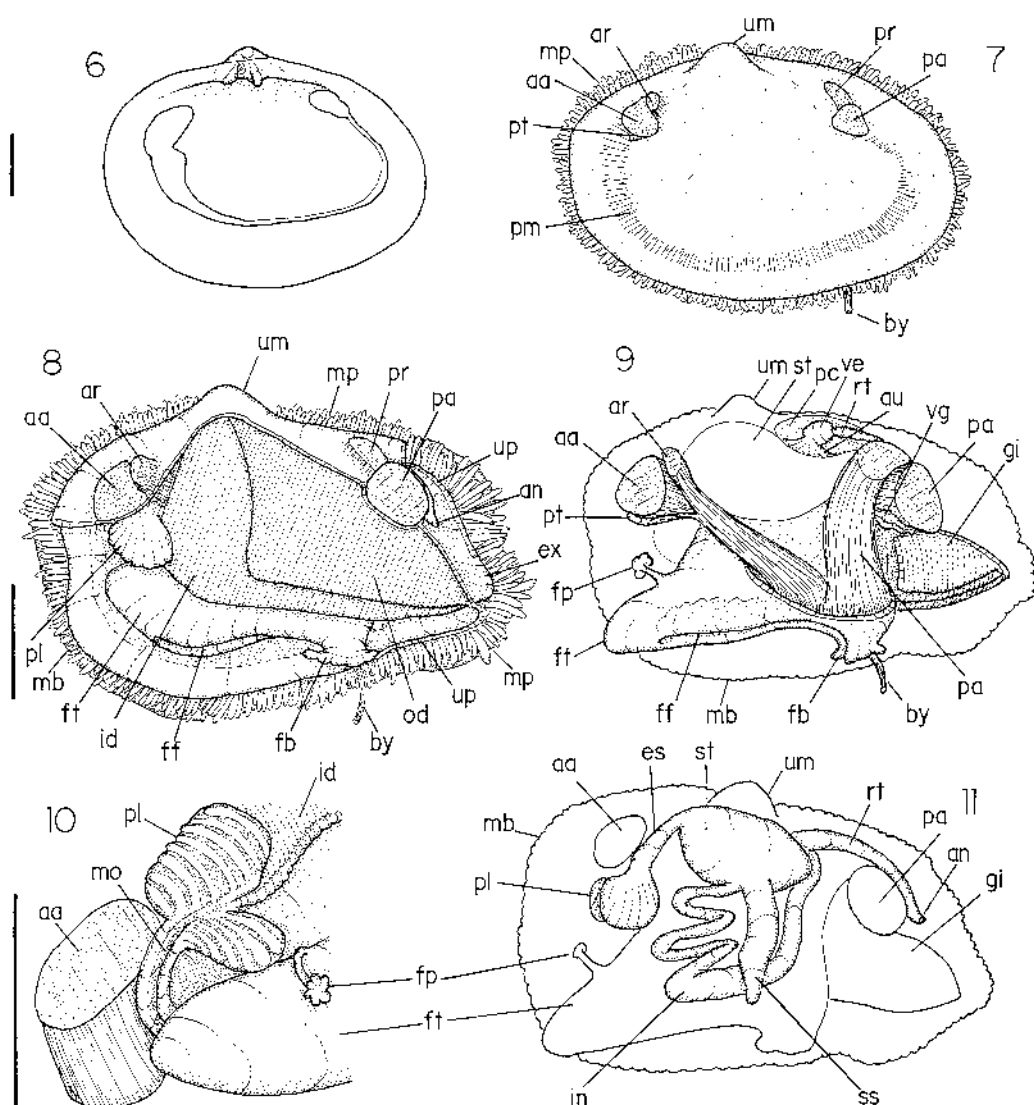
Paratypes BRAZIL. Rio de Janeiro; Ilha Grande, MZSP 30081, 1 specimen, MZSP 32191, 2 young specimens (E. Garbe coll., 1905). São Paulo; Ubatuba, MZSP 30086, 3 specimens with decalcified shells (1983); São Sebastiao, MZSP 30082, 2 specimens with decalcified shells + 1 shell (E. Garbe coll., 1915), MZSP 30084, 3 specimens with decalcified shells (C. M. Silva coll.), Canal, MZSP 32189, 4 young decalcified specimens (M. Silvio col., 7/xi/1959), Buzios Island, MZSP 32187, 1 young specimen (A. Begossi col., xii/1986), Alcatrazes Island (Instituto de Pesca col.), MZSP 32184, 7 young specimens (ix/1965), MZSP 32185, 2 young specimens (v/1964), AMNH 299071, 1 specimen, MZSP 32186, 20 young specimens (iii/1964), MZSP 32192, 4 specimens (iii/1964) (measurements of figured paratype: 6.0 by 4.2 by 1.8), MZSP 32193, 6 young specimens (ix/1965); Santos, Ponta da Praia, MZSP 30085, 3 specimens (2 with decalcified shells), MZSP 32188, 6 young specimens (C. José col., 13/ii/1949), MZSP 32194, 2 young specimens (C. Jesus col.). No locality, MZSP 32190, 2 young specimens.

Type locality Brazil, São Paulo, São Sebastiao, Ilha dos Alcatrazes, 24°05'S, 45°42'W.

Diagnosis Shell subequilateral. Mantle border with 2 layers of large papillae, no anterior differentiated papillae. Flower-like organ on dorsal surface of foot with a narrow stalk. Stomach with a pair of anterior chambers preceding digestive diverticula, and a central pad edging style sac and intestinal apertures. Gastric style sac situated subterminally, long and separated from intestine.



Figs 4–5 *Parabornia palliopapillata*, details of hinge (SEM). 4 right valve 5 left valve, note periostracum surrounding hinge and ligament between the teeth, Scale bar = 100 μ m.



Figs 6–11 *Parabornia palliopapillata*, morphology. 6 right valve, inner view, showing muscle scars. 7 outer view of a specimen extracted from shell, lateral-left view. 8 same, left pallial lobe partly removed. 9 same, further dissected to show foot, main muscles and pericardium 10 detail of anterior region, lateral-left view, palps deflected. 11 digestive tract, digestive diverticula omitted, lateral-left view. Scale bars = 1 mm. Abbreviations as in Figs 12–13.

Description Shell (Figs 1–6). Small (< 10 mm), equivalve, laterally flattened, subequilateral, anterior slightly shorter. Color white. Outer surface smooth, glossy. Sculpture absent except for commarginal undulations and growth lines. Umbones pointed, low, small. Prodissoconch oval, about 110 µm in length (Figs 4, 5). Outline almost elliptical; anterior and ventral margins rounded; ventral and posterior margins slightly produced. Hinge small, restricted to region just below umbo. A pair of small cardinal teeth in each valve (Figs 4, 5), somewhat symmetrical in sagittal and frontal planes. Pair of teeth of right valve articulating with pair of teeth of left valve. Ligament (resilium) small, inter-

nal, situated between hinge teeth, shifted slightly towards dorsal and posterior. Cardinal inner space shallow. Inner surface glossy. Scars of adductor and pedal retractor muscles (described below) situated close to dorsal margin; anterior scar a little larger than posterior scar. Pallial line continuous.

Mantle edge (Figs 7, 8, 13). Entire with 4 distinct folds. Outer fold thin. Third fold consisting of 2 series of papillae, originating between the middle and inner folds (Fig. 13). Papillae long, circular in cross-section, ciliated, closely spaced, present along entire mantle border except in short hinge area. Inner folds fused in posterior $\frac{1}{4}$ of infra-branchial chamber and in dorsal $\frac{1}{2}$ of supra-branchial chamber (Fig. 8: up). Incurrent canal along anterior and ventral region of shell edge. Excurrent canal small, just dorsal to connection of gill and edged by projections of inner folds.

Foot (Figs 8–10, 13). Of medium size. Anterior portion thick and pointed. Foot projection, or flower-like organ, situated in middle region between mouth and distal foot tip (Figs 9, 10: fp); base a slender and tall peduncle; tip a flat, circular, flower-like structure, with folded margins. Ventral edge of foot with a deep byssal groove from just behind distal tip to byssal gland. Posterior end of this furrow edged by undulating folds forming a circle, surrounding byssus fibers (Figs 8, 9: fb). Byssus gland large, white, situated in almost entire ventral region of foot around foot furrow. Byssus pale brown, generally with one or few filaments, rarely with several filaments. Hanging foot morphology, as described by Bieler & Mikkelsen (1992) for galeommatids, present.

Main muscle system (Fig. 9). Adductor muscles subequal, elliptical in section, of relatively small size. Both pairs of foot retractors large and thick, both inserting at posterior region of foot just dorsal to byssus, running dorsally, bulging into visceral mass cavity. Anterior retractor muscles running toward anterior, gradually narrowing, originating just posterior and dorsal to anterior adductor muscle in a small scar (less than $\frac{1}{4}$ of adductor area). Posterior retractor muscles running toward posterior with a somewhat uniform width along their length, originating just posterior and dorsal to posterior adductor muscle with an area equivalent to that of adductor. Paired foot protractors very narrow, almost vestigial; inserting in middle region of anterior retractor muscle, running toward anterior edging of ventral surface of anterior adductor muscle; origin very small, ventral to adductor.

Pallial cavity (Figs 8, 10, 13). Relatively large, about $\frac{1}{4}$ of area surrounding visceral-pedal mass. Ctenidia large, whitish. Gill filaments very narrow, uniform, closely packed. Outer demibranchs inserted only at their dorsal edges, dorsal to inner demibranch insertion. Inner demibranchs larger than outer demibranchs, inserted in dorsal and anterior edges to visceral sac, anterior edge inserted between palps (Fig. 10). Ventral margin of inner demibranchs with food groove. Posterior $\frac{1}{2}$ of inner demibranch length connected ventrally with each other and ending at ventral limit of excurrent canal (Fig. 9). Some specimens with inner cavities of both demibranchs filled with ova (Fig. 13), apparently in same stage of development; outer demibranchs with larger quantity of ova.

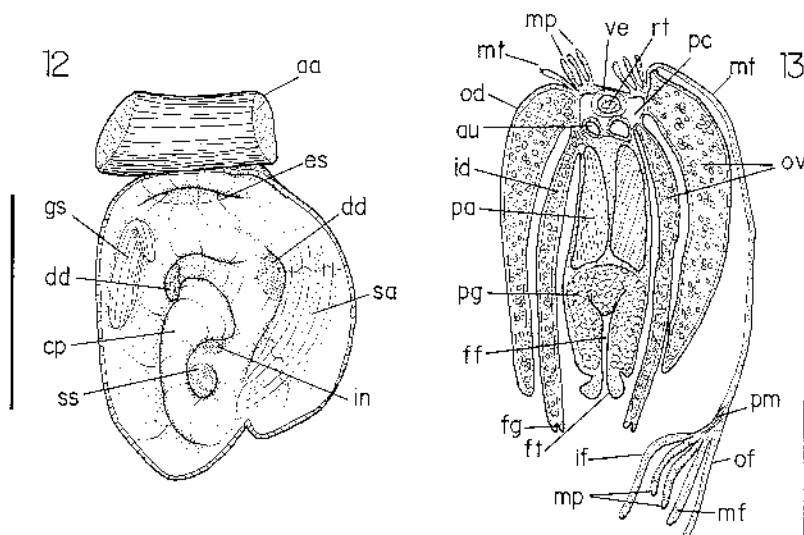
Visceral mass. Greatly compressed by retractor muscles of foot, relatively small. Large stomach dorsal. Digestive diverticula whitish, occupying a small region anterior to stomach. Gonad also whitish, occupying middle and posterior region of visceral cavity surrounding digestive tubes. (No histologic study was made for determining whether or not hermaphrodite.)

Circulatory and excretory systems (Figs 9, 13). Heart relatively small. Pericardium attached to posterior-dorsal surface of stomach. Ventricle spherical, small, surrounding intestine.

Digestive system (Fig. 11). Labial palps relatively small, outline oval, connected to anterior-ventral end of gill and adjacent region of visceral mass. Palp inner surface with few (about 8) broad folds, dorsal edges narrow, ventral edges broad and rounded (Fig.

10). Mouth broad, with thick margins, attached to anterior adductor muscle. Esophagus broad, dorso-ventrally flattened, attached to adductor muscle (Fig. 10). Esophageal inner surface with some longitudinal folds that disappear at the opening of stomach. Stomach (Fig. 12) large, ample, situated ventral to umbones. Central ventral pad curved, broader anteriorly, posterior region narrowing and disappearing. Two openings to digestive diverticula situated in each side of anterior region of ventral gastric wall, at some distance from esophageal insertion, united by a shallow transversal groove. Central pad inner curve surrounds 2 apertures: anterior aperture of intestine, posterior aperture of style sac. Gastric shield chitinous, situated in dorsal-anterior-left gastric region. Remainder of dorsal gastric inner surface with 3–4 longitudinal, low folds. Style sac relatively short (little longer than gastric height), section circular, slightly pointed at distal end. Intestine very slender, traversing 3 small loops toward ventral; third loop becoming broad, transversing dorsal foot surface, passing style sac on the right and suddenly turning dorsally; thereafter, surrounding posterior and dorsal region of stomach and running medially close to dorsal margin. Rectum attached to dorsal and posterior surface of posterior adductor muscle. Anus as a small papilla (Fig. 8) situated close to ventral surface of excurrent chamber.

Nervous system. Not observed in detail, except for a very large pair of visceral



Figs 12–13 *Parabornia palliopapillata*, anatomy. 12 stomach, dorsal view, dorsal gastric wall sectioned at left and deflected to right. 13 transverse section in middle region of animal's body, just posterior to umbo, left mantle lobe removed. Scale bars = 1 mm. Abbreviations: aa anterior adductor muscle; an anal papilla; ar anterior pedal retractor muscle; au auricle; bg byssal gland; by byssus; cp gastric central pad; dd digestive diverticula opening; dg digestive diverticula gland; es esophagus; ex excurrent canal; fb foot region around byssus; ff foot ventral furrow; fg food groove; fp foot anterior projection (flower-like organ); ft foot; gi gill; go gonad; gs gastric shield; id inner demibranch; if inner fold of mantle; in intestine; mb mantle border; mf middle fold of mantle; mo mouth; mp mantle papillae; mt mantle, od outer demibranch; of outer fold of mantle; ov ova inside gill; pa posterior adductor muscle; pc pericardium; pg pedalbyssus gland; pl palp; pm pallial muscles; pr posterior pedal retractor muscle; pt pedal protractor muscle; rt rectum, sa gastric sorting area; sr special region of mantle border lacking papillae; ss style sac; st stomach; um umbonal region; up union (fusion) of mantle lobes by inner folds; ve ventricle; vg visceral ganglia.

ganglion situated on ventral surface of posterior adductor muscles (Fig. 9).

Distribution S. E. Brazil, From Ilha Grande, Rio de Janeiro to Santos, São Paulo.

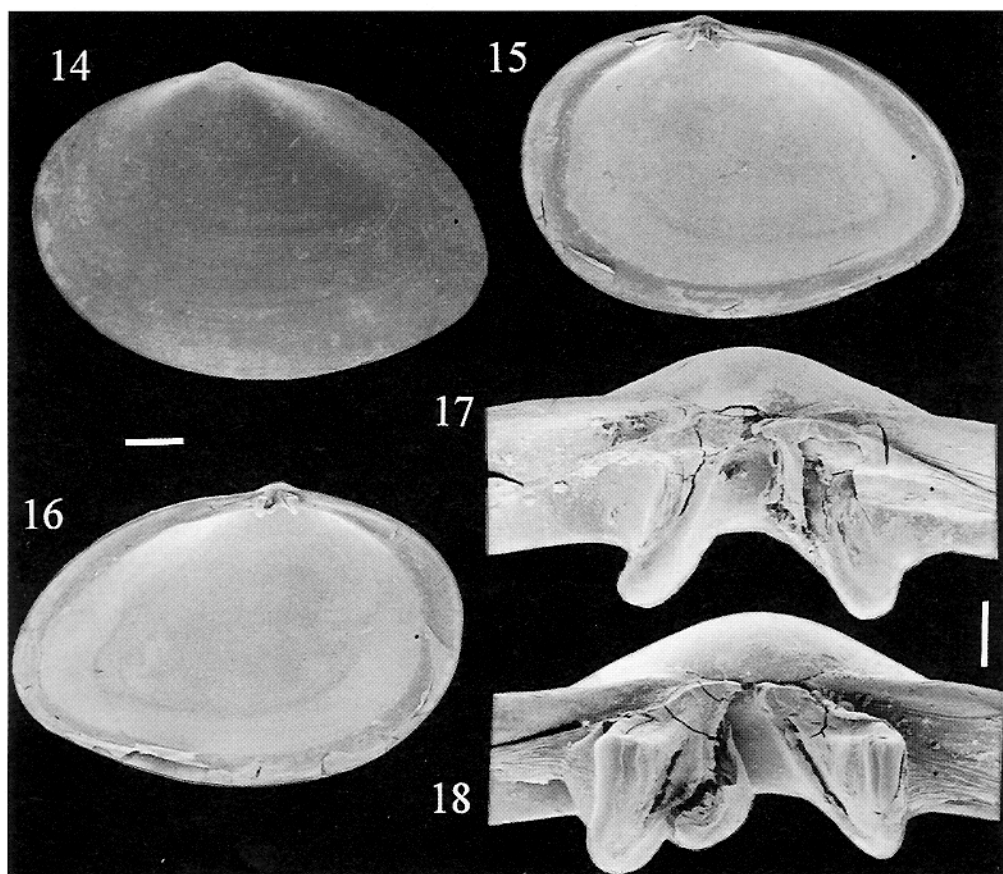
Habitat Attached by byssus in the ventral region of the abdomen of the crustacean *Lysiosquilla scabricauda*, on pleiopod base. Young specimens also occur on maxilipedal bases and under the carapace. Although other species of the lysiosquillids occur in the region, the studied species was found only on *L. scabricauda*.

Etymology The specific epithet refers to the mantle border almost entirely papillated, from Latin *pallium* (mantle) and *papilla*.

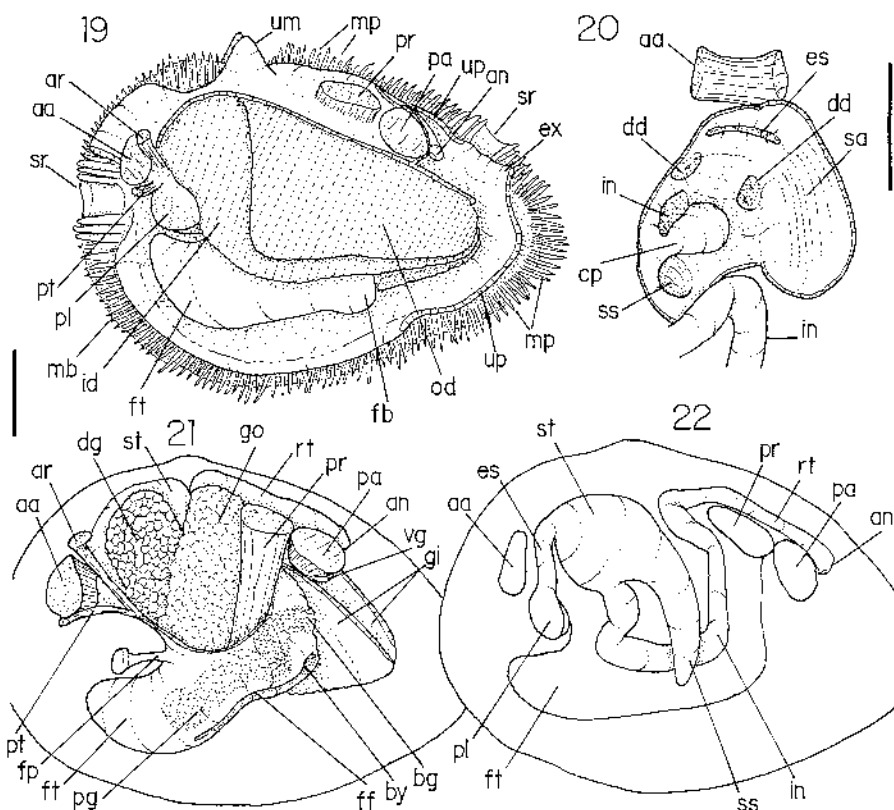
Parabornia squillina Boss, 1965
(Figs 14–22)

Parabornia squillina Boss, 1965: 1–9 (Figs 1–3); Abbott, 1974: 469 (Fig 5415).

Holotype AMNH 112526 (Cristobal, Canal Zone, Panama).



Figs 14–18 *Parabornia squillina* scanning electron micrographs of paratypes (AMNH 112527). 14 left valve, outer view 15 right valve, inner view 16 left valve, inner view. 17 right valve, detail of hinge. 18 same, left valve. Scale bars 14–16 = 0.75 mm, 17–18 = 120 μ m.



Figs 19–22 *Parabornia squillina* anatomy. **19** specimen extracted from shell, lateral-left view, left pallial lobe partly removed. **20** stomach and adjacent structures, dorsal view, gastric dorsal wall cut and deflected to right. **21** visceral mass, foot and main muscles, lateral-left view, integument covering visceral mass and all left pallial structures removed. **22** digestive tract, lateral-left view. Scale bars = 1 mm. Abbreviations as in figs 12–13.

Paratypes AMNH 112527; USNM 653701 (same provenance).

Diagnosis Shell with hinge teeth long. Mantle border possessing 2 regions without papillae, edged by large papillae. Excurrent canal with a short siphon. Flower-like organ with stalk becoming broader (conic) along its length and a tip flat and circular. Anterior foot muscles narrow. Posterior gill end free from mantle. Stomach with style sac situated terminally and central pad separating style sac from intestinal apertures. Few and broad intestinal loops.

Comparative description Shell. Characters closely similar to those of new species, including outline and smooth outer surface. Differs mainly by slightly more rounded outline and relatively longer pair of hinge teeth. Prodissoconch about 105µm in length.

Mantle edge. Most characters similar to those of *L. palliopapillata* including folds and regions of fusion between the lobes. Distinctive or notable features are as follows. Papillae narrower and fewer, not uniform in size (see below), occasionally bifid. Inner fold, in excurrent region, forming a short siphon, longer than that of new species and with edges far from division with infra-branchial chamber. A short region just anterior to palps with about 6 larger papillae in right lobe, and 2 larger papillae bordering a

smooth area in left lobe. A similar region also found in opposed side of animal body, just posterior to excurrent siphon. A short region lacking papillae is also present close to umbones.

Foot. Features similar to those of new species, with following notable attributes. Byssal furrow of similar length, byssal and pedal glands visible through integument, separated from each other (with byssal gland posterior). Flower-like organ similarly situated and sized to that of *P. palliopapillata*, differing by gradual increase of diameter along its length (conic form); and by having apex thicker and circular (without folds).

Main muscle system. Also with similar features than those of new species, differing mainly by more slender anterior pedal muscles (protractor and retractor).

Pallial cavity. Characters similar to those of *L. palliopapillata*, with following distinctive or notable features. Gills virtually identical in form, size and disposition of filaments to those of new species, however differing in having their posterior region free from adjacent mantle wall; i.e., gills connected to each other in region posterior to foot (as in new species), separating supra- and infrabranchial chambers, but their outer edges are not connected to inner surface of mantle at about $\frac{1}{2}$ of posterior gill length. In retracted condition supra- and infrabranchial chambers remain connected with each other at posterior end.

Visceral mass. Inner structures not as compressed as those in new species. Digestive diverticula restricted to anterior half of visceral sac, color white. Gonad occupying posterior visceral half, color pale beige.

Circulatory and excretory systems. Virtually identical to those of new species.

Digestive system. General characters similar to those of *L. palliopapillata*, with the following notable features. Stomach with style sac as terminal-posterior structure. Stomach inner surface with about same distribution of structures, except with more flattened central pad between intestinal origin and style sac aperture (and not surrounding both as in new species). Dorsal sorting area surrounding a proportionally larger and thinner gastric shield. Style sac broader and shorter, with only one loop, mainly anterior to style sac. Intestinal origin turned posteriorly (while new species runs towards anterior). Intestinal loop just posterior and dorsal to stomach crosses from left to right (contrary in relation to that of new species).

Nervous system. Same as new species.

Measurements (in mm) (Same parameters as in new species) AMNH 112527 (1): 6.5 by 4.7 by 2.1; (2): 6.1 by 4.3 by 1.9; (3): 6.3 by 4.5 by 2.0 (specimens labeled in lot).

Distribution Florida to Panama.

Habitat On *Lysiosquilla scabricauda*.

Material examined Paratypes: PANAMA; Canal Zone (Atlantic Ocean), Cristobal, AMNH 112527, 7 specimens, 2 valves (23/viii/1934).

DISCUSSION

Indubitably *Parabornnia palliopapillata* and *P. squillina* are closely related species, with very similar morphological attributes and both commensal with the same stomatopod species. On the other hand, the number and degree of differences between the specimens studied are considered sufficient for specific separation.

Of the described differences, the free portion of the posterior gill region of *P. squillina*

(connected to mantle in *P. palliopapillata*), and the special arrangement of papillae in both anterior and posterior regions of mantle border (with regions lacking papillae, edged by larger papillae in *L. squillina*), are considered most significant. A small region lacking papillae is sometimes found in *P. palliopapillata*, but only in some specimens, the region is of small size, not edged by larger papillae and restricted to the anterior mantle border (never at posterior border). This feature is distinct and was consistently present in all examined specimens of *L. squillina*.

According to Gomes-Correa (1998), the common crustacean host, *Lysiosquilla scabricauda*, occurs from the Atlantic coast of the United States to Santa Catarina, Brazil. However, the *Parabornia* species show a disjunct distribution, *P. squillina* from Florida to Panama and *P. palliopapillata* from south Rio de Janeiro to south São Paulo, with a long gap between the two distributions. *Parabornia palliopapillata* has not been found on *L. scabricauda* from other Brazilian regions nor on other species of the family in a search of the MZSP collections. Several other species of Galeommatoidea occur associated with *L. scabricauda* in Florida, e.g., 5 species of *Divariscintilla* (Mikkelsen & Bieler, 1989, 1992), living detached in the crustacean's burrow.

The anatomical characters of *Parabornia* spp. are somewhat similar to those of the Brazilian species *Lepton cema* (Narchi, 1966), in having a separated gastric style sac (from the intestine), similar gill configuration, and incubation of embryos in the gill. But *Parabornia* spp. differ in having the papillae at the mantle border, a narrow style sac, and a flower-like organ on the foot. The separation of the style sac from the intestine also connects *Parabornia* to other Galeommatoidea, such as *Divariscintilla* spp. (Mikkelsen & Bieler, 1989, 1992), and *Montacutona cerianthia* Ponder, 1971b.

The projection on the foot, or flower-like organ, is a singular feature of *Parabornia* among the Galeommatoidea. However something similar occurs in other species. Species of *Divariscintilla* present flower-like organs, prompting Mikkelsen & Bieler (1989) to coin this good descriptive name, situated in virtually the same foot region. However, the *Divariscintilla* flower-like organs can be multiple (in one of 5 species), and were regarded as a distinct feature of the genus (Bieler & Mikkelsen, 1992). *Pseudopythina maipoensis*, a galeommatoid from Hong Kong, possesses a pair of projections in a comparable situation to flower-like organs (Morton & Scott, 1989).

Boss (1963) provided a comprehensive discussion of *Parabornia* features among the closest galeommatoidean genera. He considered the genus a member of the Erycinidae, but because present knowledge still lacks precise definitions of Galeommatoidea families, the genus *Parabornia* is here provisionally considered in Galeommatoidea (sensu Ponder, 1998). Probably it belongs to the subfamily Erycininae, due to shell and internal anatomy attributes (e.g., flower-like organ, and separation of style sac).

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