The Veliger 50(4):292–304 (December 16, 2008)

THE VELIGER

A New Species of *Fissurella* from São Pedro e São Paulo Archipelago, Brazil (Vetigastropoda, Fissurellidae)

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Abstract. *Fissurella mesoatlantica* n. sp. is endemic to the Saint Peter and Saint Paul Archipelago, Brazil, located approximately in the middle Atlantic (00°55N, 29°20W). The species is very similar to *F. clenchi* from the mainland Brazilian coast, differing in having a taller, more richly sculptured shell and by anatomical details, such as the papillae of mantle border and epipodial tentacles. A complete anatomical description is included.

INTRODUCTION

The Arquipélago de São Pedro e São Paulo, or Saint Peter and Saint Paul Archipelago (ASPSP), is the remotest Brazilian oceanic set of islands. It is the tip of a huge oceanic mountain, with a base of approximately 4 by 2 km in size, its foot at 4 km depth, and an emersed tip of 13,000 m^2. The archipelago is located about 1,010 km off Calcanhar Cape, Rio Grande do Norte State, and about 870 km off Fernando de Noronha, the largest Brazilian oceanic archipelago; it is located approximately in the middle between Brazil and Africa, and close to the Equator line (Souza, 2007); the coordinates are 00°55′00″N 29°20′42″W.

The Archipelago is a strategic point for the Brazilian economy, as it ensures 238,000 km^2 of exclusive economic zone (Gonçalves, 2002). Since 1996, the Archipelago has continuously been occupied by 4-people research teams. Every person is allowed to work in that place only after an in-depth training, provided by the Brazilian Navy in its Rio Grande do Norte Base. Each team is allowed to work in 15-day expeditions.

Despite its biological importance, in being such an isolated place and an important source for the understanding of evolutionary and biological colonization, the local malacofauna has not been the main goal of any projects thus far. The few publications which deal with mollusks from ASPSP are restricted to species lists, with no thorough taxonomical research (e.g., Edwards & Lubbock, 1983, which listed four molluscan species). Even the more classic revision considering the malacofauna of the Brazilian oceanic islands, Leal (1991), did not include ASPSP.

A project supported by the federal Brazilian council of research (CNPq) permitted the collection and study of the ASPSP benthic invertebrate fauna. This paper deals with a common fissurellid in those islands, occurring intertidally, that turned out to be a new species after anatomical and taxonomical investigations. The species have been identified as *F. nubecula* (Linné, 1758) by Edwards & Lubbock (1983), which occurs in the northeastern Atlantic and Mediterranean. Additional data on the fissurellids see McLean (1984).

MATERIAL AND METHODS

The specimens were studied still alive, under a stereomicroscope, on board of Rebocador de Alto-Mar "Almirante Guilhem", commander Captain Antonio Cesar Portela Marques, Brazilian Navy. Later the specimens were preserved in 70% EtOH. The dissections were performed by standard techniques, with specimens immersed in preservative under a stereomicroscope. All drawings were done with the aid of a camera lucida. Most dissection steps were additionally digitally photographed. Radulae of five specimens were additionally examined by scanning electronic microscope (SEM) in the Laboratório de Microscopia Eletrônica of the Museu de Zoologia da Universidade de São Paulo (MZSP). For comparison with *Fissurella clenchi* Farfante, 1943, two lots of this species were examined anatomically: MZSP 80797 from Maceió, Alagoas, and MZSP 39965, from Santos, São Paulo. The data on the anatomy of *F. clenchi* and the further systematics of the Brazilian fissurellids are part of an ongoing project.

Anatomical abbreviations in the figures: **aa**, anterior aorta; **af**, afferent gill vessel; **an**, anus; **au**, auricle; **br**, subradular membrane; **bv**, blood vessel or sinus; **cc**, cerebral commissure; **ce**, cerebral ganglion; **co**, cerebropedal connective; **cv**, ctenidial vein or efferent gill vessel; **df** dorsal fold of buccal mass; **dg**, digestive gland; **eg**, esophageal gland or crop; **ep**, epipodium; **es**, esophagus; **ey**, eye; **fo**, foramen; **fs**, foot sole (mesopodium); **ft**, foot; **gf**, gastric fold; **gi**, gill; **gd**, gonoduct; **go**, gonad; **gs**, gill suspensory stalk; **ha**, head; **if**, inner fold of mantle border; **in**, intestine; **jw**, jaws; **ki**, kidney; **lm**, lateral muscle; **m1–m12**, odontophore muscles; **mb**, mantle border; **mf**, middle fold of mantle border; **mj**, jaw and peribuccal muscles; **mo**, mouth; **mp**, mantle papillae; **mt**, mantle; **ne**, nephrostome; **nv**, nerve; **oc**, anterior odontophore cartilage; **od**, odontophore; **of**, outer fold of mantle border; **om**, ommatophore; **pc**, pericardium; **pg**, anterior furrow of pedal glands; **pl**, pedal-pleural ganglion; **pm**, pallial muscles; **ra**, radula; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, gastric sorting area; **sc**, subradular cartilage; **se**, septum between odontophore and esophagus; **sm**, shell muscle; **sn**, snout; **sp**, gastric spiral caecum (vestigial); **st**, stomach; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **ve**, ventricle.

Abbreviatons of institutions: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; BMNH, The Natural History Museum, London, UK MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil; MORG: Museu Oceanográfico da Fundação Universidade de Rio Grande, RS, Brazil; MZSP: Museu de Zoologia da Universidade de São Paulo, Brazil.

SYSTEMATIC DESCRIPTION

Fissurella mesoatlantica new species

(Figures 1–40)

Fissurella (Cremides) nubecula: Edwards & Lubbock, 1983: 68 (*non* Linné, 1758).

Types: Holotype: MZSP 87462. Paratypes: BRAZIL. **São Pedro e São Paulo Archipelago**; Belmonte Island, 00°55′00″N 29°20′42″W (Simone & Cunha col.), east lagoon, MZSP 86568, 4 specimens, MZSP 86653, 1 specimen (7/xi/2007), Enseada, MZSP 86743, 15 specimens, ANSP A21718, 3 specimens, MNRJ 12476, 3 specimens, MZSP 86515, 2 shells (27/x/2007), MZSP 86518, 14 shells (28/x/2007), MZSP 86520, 9 shells (30/x/2007), MZSP 86528, 7 shells (31/x/2007), MZSP 86636, 7 shells (1/xi/2007), MZSP 87435, 2 shells (2/xi/2007), MZSP 86660, 1 shell (3/xi/2007), MZSP 86570, 9 specimens (4/xi/2007), MZSP 86575, 2 shells (9/xi/2007), northwestern coast, MZSP 86561, 29 specimens, MORG, 3 specimens, BMNH 20080492, 3 specimens (7/xi/2007), north coast, MZSP 86569, 19 specimens (7/xi/2007), canal with São Paulo Island, MZSP 86562, 14 specimens.

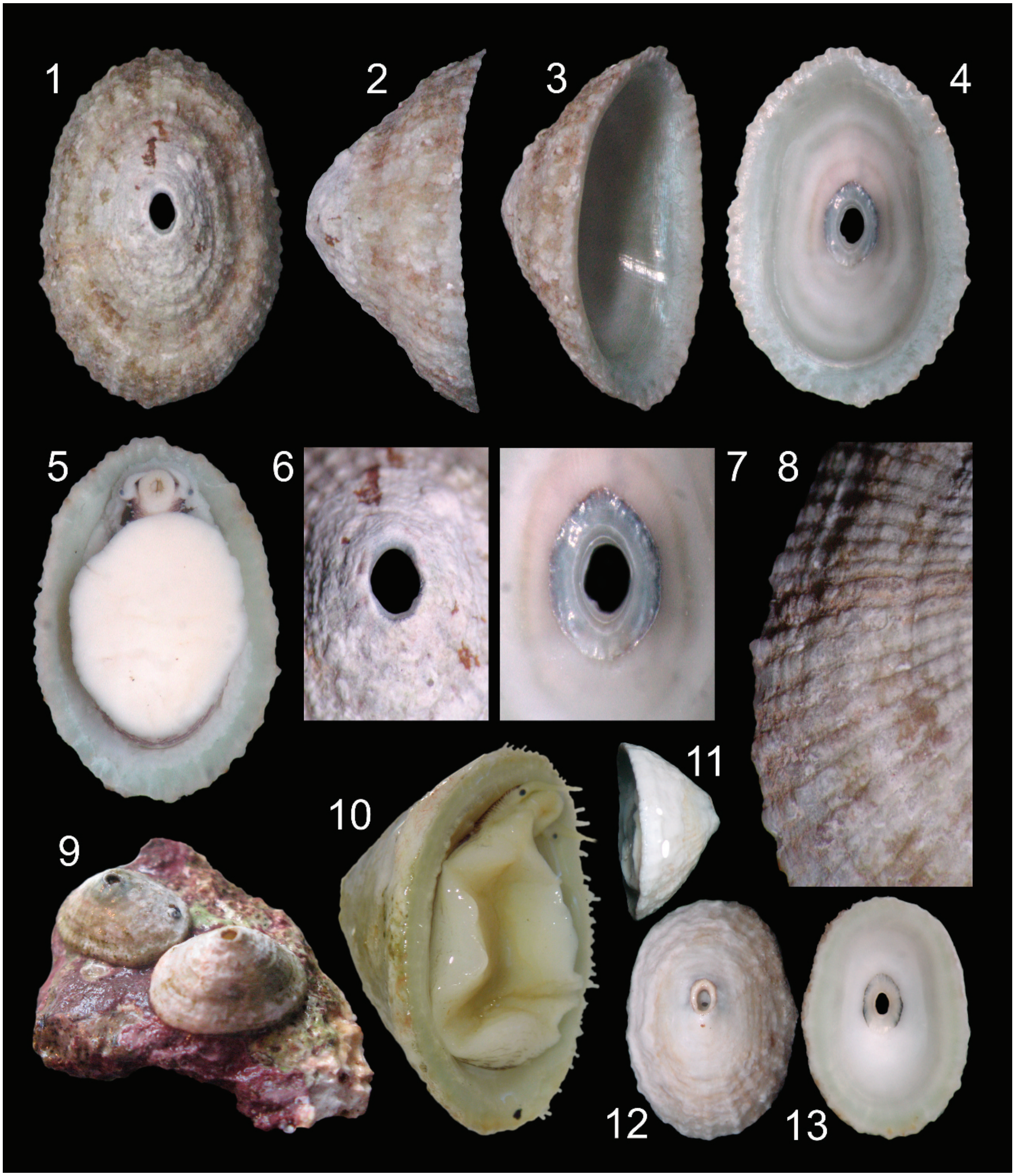
Type locality: BRAZIL. **São Pedro e São Paulo Archipelago**; Belmonte Island, Enseada, 00°55′01″N 29°20′44″W (Simone & Cunha col., 27/x/2007).

Diagnosis: Shell up to 20 mm; about half as high as long; foramen elliptical, central to anterior. Sculptured by about 50 radial, relatively tall ribs, with concentric nodes. Endemic from ASPSP.

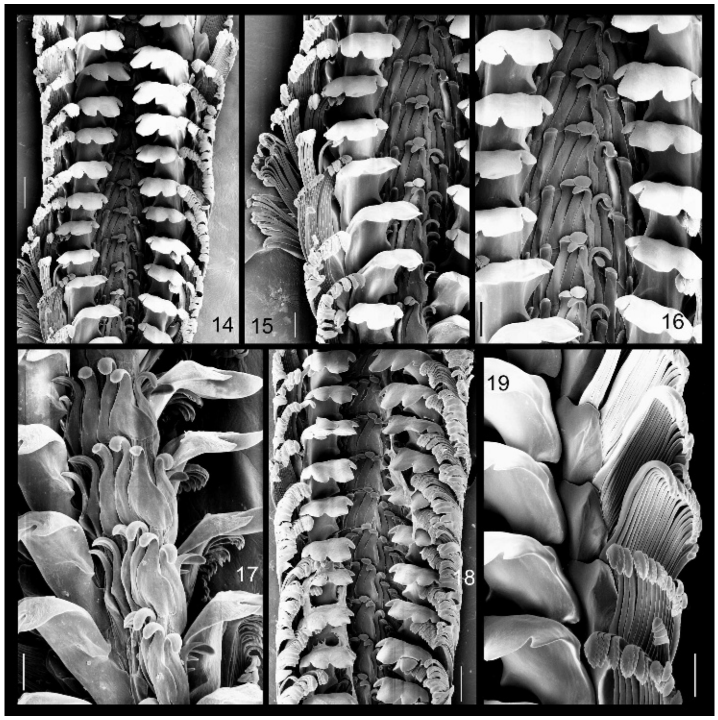
Description: *Shell (Figures 1–13)*. Up to 20 mm. Outline elliptical, width about 70% of length (Figures 1, 4, 5, 12, 13). Normally tall, height more than half of length; profiles straight or slightly convex (Figures 2, 3, 10, 11) in both (anterior and posterior) slopes. Color pale brown, greenish beige and white, with many variations and combinations of these colors, normally in radial mosaic of spots (Figures 1–3, 9, 12). Sculpture consisting of about 50 relatively strong radial ribs (Figures 1, 8, 12); each rib normally three times wider than tall, profile quite rounded, separated from neighboring ribs by interval equivalent to about ¼ of rib's width; cords normally stronger in region closer to edges, arranged normally in pattern consisting of stronger cords separated by three slightly narrower rib (Figure 8). Concentric sculpture normally weak, consisting of undulations and small, commarginally aligned nodes of radial ribs (Figures 1, 8, 12). Apical regions normally eroded (Figures 9, 12). Walls thick (Figure 3). Edges thick (as thick as remainder of shell), bearing small irregular projections corresponding to radial sculpture (Figures 4, 5, 13). Foramen central or displaced anteriorly up to 10% of fraction of shell length (Figures 1, 12); occupying about 1/80 of dorsal shell surface area; outline somewhat elliptical (average length/width ratio = 1.45), with irregular, lateral expansions in middle (Figures 6, 7, 13). Inner surface glossy and whitish-green (Figure 13), reddish region close to apex in some specimens (Figures 4). Blue callus surrounding foramen (Figures 4, 7, 13), occupying about 5% of total inner surface, possessing about same thickness as remaining shell wall, differentiated in being glossier and by scale-like edges. Muscle scar very weak, practically imperceptible.

Young forms (Figure 40) showing smooth, symmetrical, almost planispiral protoconch, of one whorl, white; projected posteriorly and ventrally, slightly placed to left. Protoconch width approximately 0.2 mm. Teleoconch with convex anterior and concave posterior slopes. Foramen about three times longer than wide; located between middle and posterior third between anterior edge and protoconch; middle portion with distinct expansions about a third of whole orifice in size. Sculpture similar to that of large shells, except in being more delicate, and by predominance of radial ribs.

Head-foot (Figures 5, 10, 20, 22, 23, 27). Mostly unpigmented, except region of neck, with transverse dark brown spots (Figures 5, 10), sometimes coalescent. Head preceded by long neck of about half of foot in length and 1/3 of foot's width; almost cylindrical; snout continuous with neck in axis and width. Cephalic tentacles located between middle and anterior thirds, on each side; each tentacle tapering gradually, slightly longer than snout; tip pointed. Ommatophores of approximately same width as tentacles' base and about



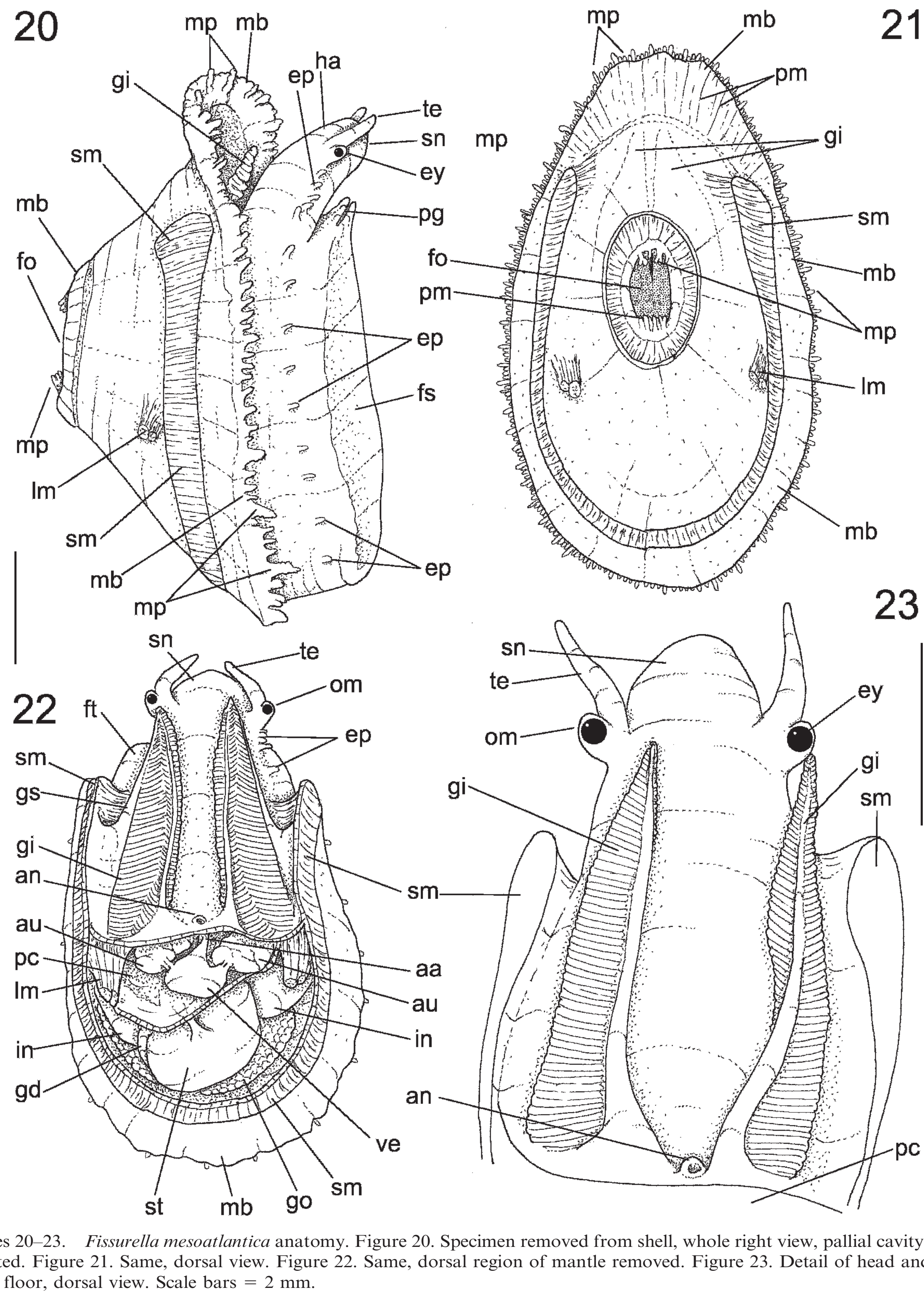
Figures 1–13. *Fissurella mesoatlantica* shell aspects. Figures 1–8. Holotype (length = 14.0 mm). Figure 1. Dorsal view. Figure 2. Right view. Figure 3. Right-slightly ventral view. Figure 4. Ventral-inner view. Figure 5. Whole specimen, ventral view (fixed). Figure 6. Detail of foramen region, dorsal view. Figure 7. Same, ventral-inner view. Figure 8. Detail of sculpture in left-posterior quadrant. Figure 9. Two *in situ* specimens on calcareous algae (MZSP 86743, each with 15 mm). Figure 10. Paratype MZSP 86743, alive, right-slightly ventral view (length = 15.8 mm). Figures 11–13. Paratype MZSP 86562 (length = 14.6 mm). Figure 11. Whole left view (specimens inside). Figure 12. Dorsal view (specimen inside); 13. Ventral-inner view.



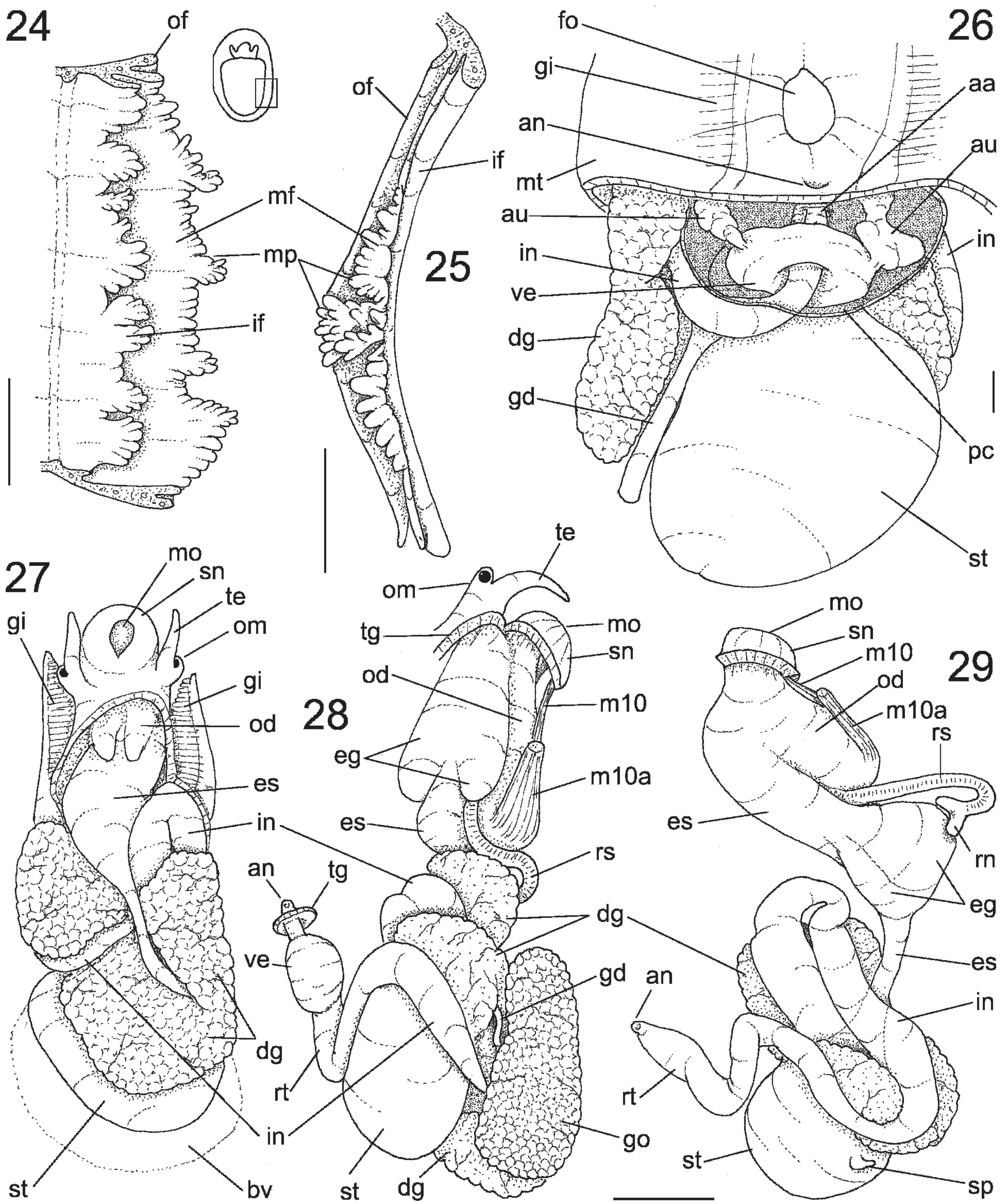
Figures 14–19. *Fissurella mesoatlantica* radulae in SEM. Figures 14–17. Holotype. Figure 14. Whole view in middle region. Figure 15. Detail of marginal area. Figure 16. Detail of central area. Figure 17. Detail of central area in region longitudinally folded; 18–19. Paratype MZSP 86743. Figure 18. Whole view of central region. Figure 19. Detail of marginal area. Scale bars: 14, 18 = 100 μm; remaining = 50 μm.

1/4 tentacles' length; located just posterior to tentacles' origin; tip rounded; eye occupying about half of ommatophore volume (Figure 23: ey). Snout almost cylindrical, weakly tapering towards anterior; anterior end rounded; mouth central, occupying about 1/4 of anterior surface. Epipodium marked only by a series of horizontally aligned tentacles (Figure 20: ep), located approximately in middle between sole and mantle edge; each tentacle about four times as tall as wide, length approximately same as ommatophore and about 1/6 its width; five epipodial tentacles aligned on both sides of neck, just posterior to cephalic tentacles, separated from each other by distance equivalent to their width; remaining epipodial tentacles much more widely spaced, interval equivalent to 6–7 times their width; about 10 pairs of tentacles in region dorsal to foot. No differentiated epipodial sensory organ (ESO) detectable. Foot occupying about 80% of shell aperture, edges simple (Figures 5, 10), thick (central region with about 1/5 of shell height). Anterior furrow of pedal gland about 1/3 of foot width. Propodium about 1/10 of foot's length, touching ventral base of neck. Shell muscle symmetrical; posterior region about 1/7 of shell height; gradually becoming broader towards anterior; anterior region weakly curved dorsally, about 1/4 of shell height (Figures 20, 21); origin in shell located approximately between middle and marginal thirds of shell. Shell muscle protruding inside pallial cavity in anterior region (Figure 22). Pair of longitudinal muscles (Figures 20–22: lm); originating laterally in elliptical area equivalent to 1/100 of inner shell surface, between posterior and middle thirds of shell, just dorsal to adjacent region of shell muscle; running towards anterior; dorsal part inserting in posterior base of gills (Figure 31); ventral part lying along dorsal head integument, splaying along neck base. Haemocoel widely continuous with visceral cavity (Figure 27).

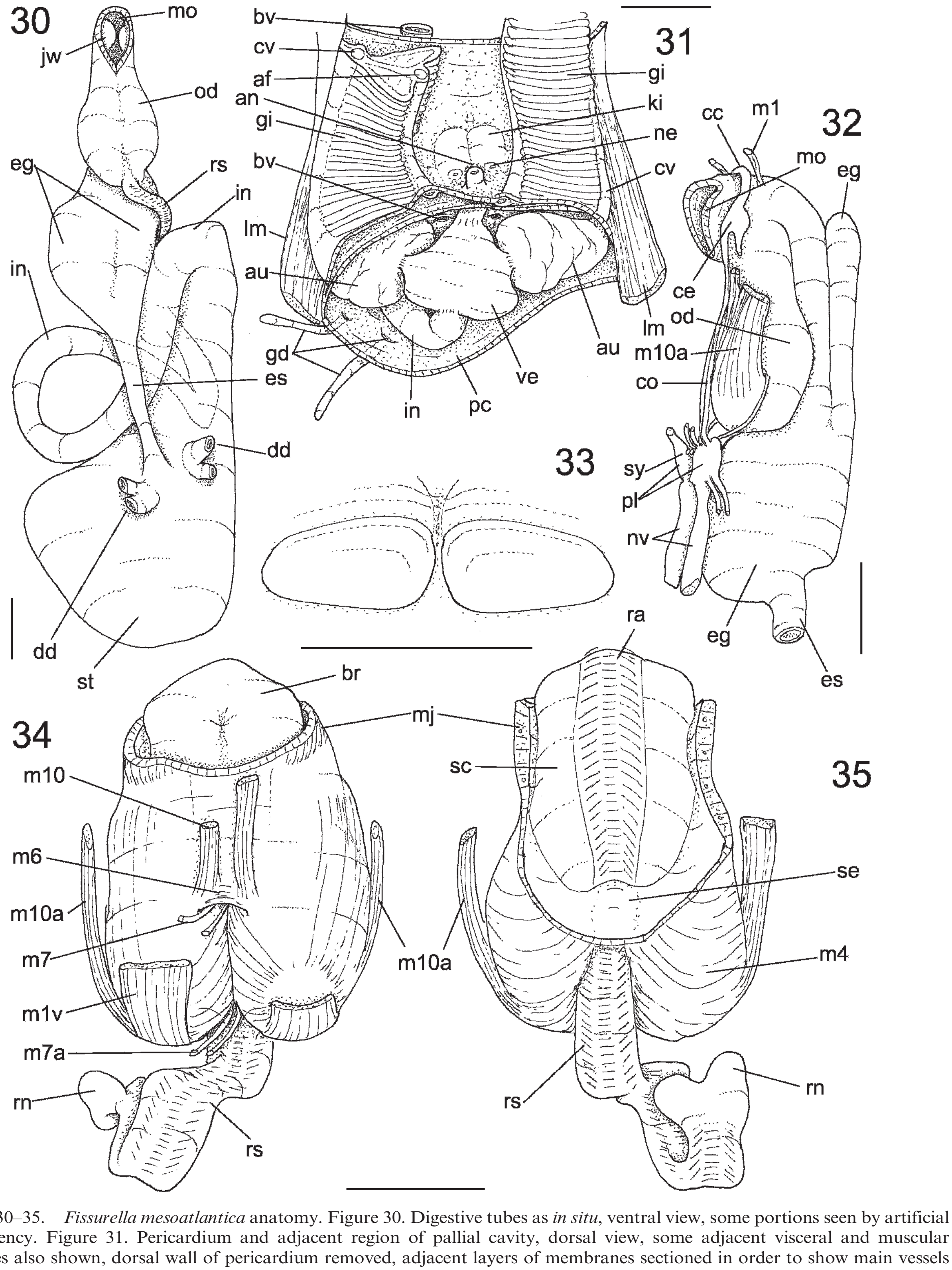
Mantle organs (Figures 22–25, 31). Mantle edge in periphery of shell trifolded (Figures 10, 20, 21, 24). Outer fold smooth, simple, about 1/3 of shell wall thickness; about twice as long as thick. Middle and inner folds similar in size and organization, length about double of outer folds and with about same thickness; all around papillate, each papilla approximately same length of outer fold, about twice as long as wide; both folds possessing regular projections forming longer, papillate small tentacles projecting beyond shell's edge (Figure 10) a distance equivalent to twice of each fold's height; these small and long tentacles arranged somewhat intercalated, interval equivalent to three times their base (Figure 24). Mantle edge in foramen similarly arranged to shell edge; except for



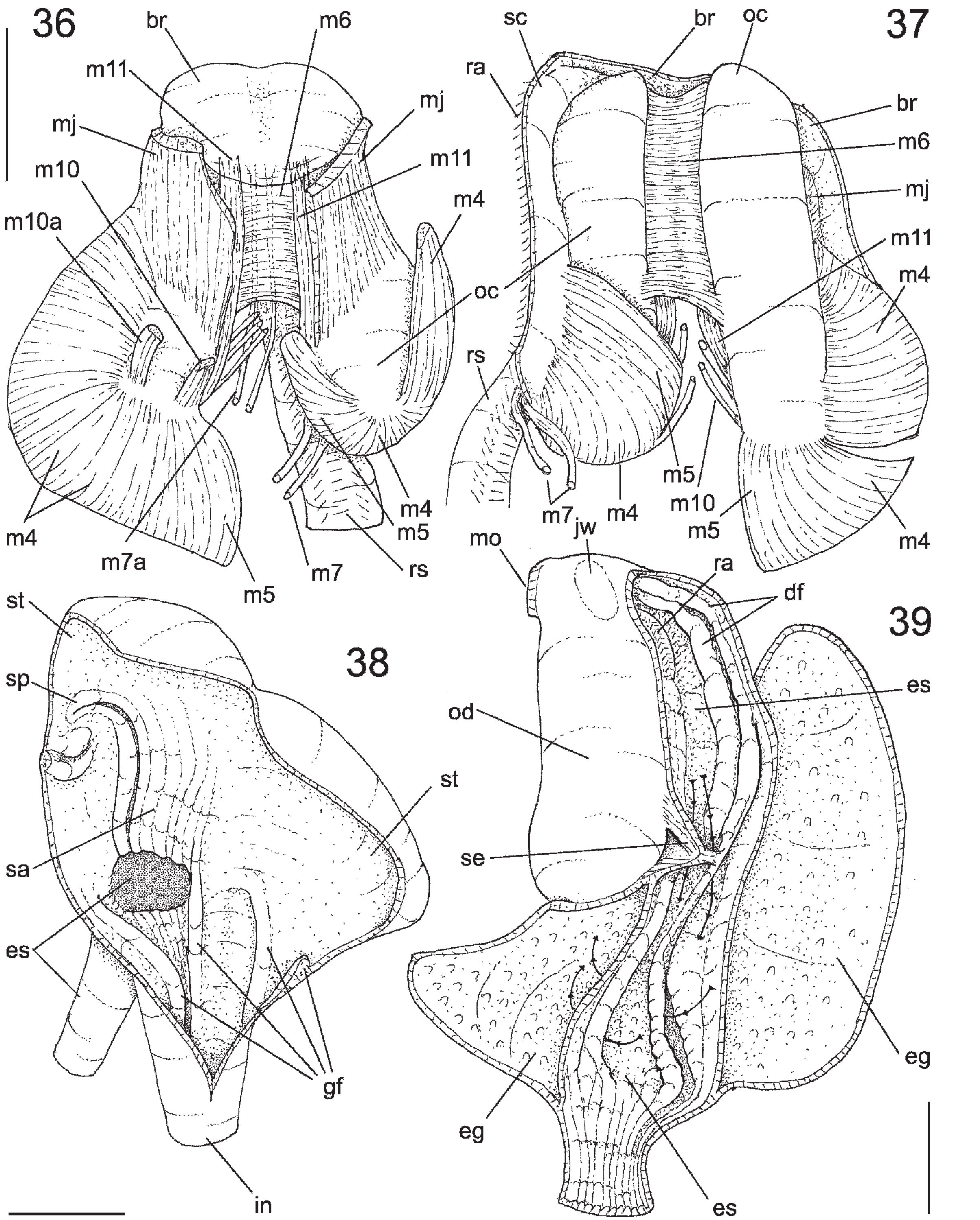
Figures 20–23. *Fissurella mesoatlantica* anatomy. Figure 20. Specimen removed from shell, whole right view, pallial cavity slightly deflected. Figure 21. Same, dorsal view. Figure 22. Same, dorsal region of mantle removed. Figure 23. Detail of head and pallial cavity floor, dorsal view. Scale bars = 2 mm.



Figures 24–29. *Fissurella mesoatlantica* anatomy. Figure 24. Detail of indicated portion of mantle border, inner view. Figure 25. Anterior half of mantle border of foramen, straightened, posterior view. Figure 26. Pericardium and adjacent region of visceral mass and pallial cavity, dorsal view, visceral portion of mantle removed. Figure 27. Haemocoel as *in situ*, ventral view, foot and shell muscle removed, a portion of pallial structures also shown. Figure 28. Same, right view, topology of some adjacent structures also shown. Figure 29. Digestive system as *in situ*, right view. Scale bars = 24–26 = 0.5 mm; 27–29 = 2 mm.



Figures 30–35. *Fissurella mesoatlantica* anatomy. Figure 30. Digestive tubes as *in situ*, ventral view, some portions seen by artificial transparency. Figure 31. Pericardium and adjacent region of pallial cavity, dorsal view, some adjacent visceral and muscular structures also shown, dorsal wall of pericardium removed, adjacent layers of membranes sectioned in order to show main vessels and ducts *in situ*, left gill transversally sectioned to show its constituents. Figure 32. Buccal mass and nerve ring as *in situ*, left view. Figure 33. Jaw plates, inner-ventral view, mouth positioned in inferior side. Figure 34. Odontophore, ventral view. Figure 35. Same, dorsal view. Scale bars = 1 mm.



Figures 36–39. *Fissurella mesoatlantica* anatomy. Figure 36. Odontophore, ventral view, inner layer of structures partially removed, right muscles (left in Figure) deflected, some muscles and radular sac only partially shown. Figure 37. Same, dorsal view, both cartilages deflected, subradular membrane sectioned longitudinally, radular sac and ribbon deflected to left with intrinsic muscles attached to them, right muscles deflected. Figure 38. Stomach, dorsal view, sectioned longitudinally in its intestinal side. Figure 39. Buccal mass and adjacent region of esophagus, left view, esophagus and esophageal gland sectioned longitudinally, inner surfaces exposed, communications among chambers shown by arrows, jaw seen by transparency. Scale bars = 1 mm.

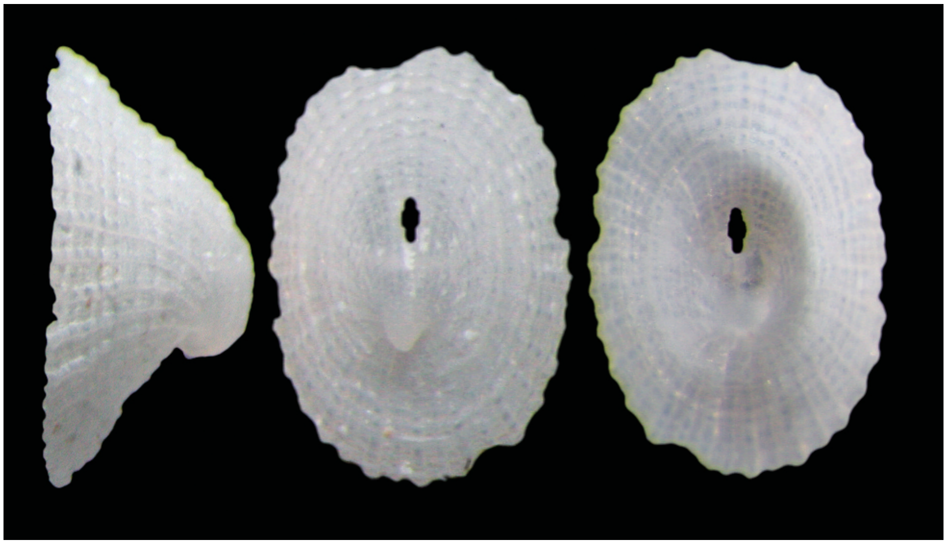


Figure 40. *Fissurella mesoatlantica* shell of young specimen, MZSP 87435; right, dorsal, and ventral views respectively. Length = 2.8 mm.

only middle fold possessing papillae, concentrated in anterior and posterior regions (Figure 21); papillae forming long small tentacles only close to median line, gradually disappearing laterally. Pallial cavity with about half shell's area in depth, symmetrical; its posterior end located just posterior to foramen. Pair of gills symmetrical, each gill about as long as pallial cavity, about 1/4 its width; lateral suspensory stalk (surrounding efferent ctenidial vein) with about half of length attached to shell muscle's dorso-lateral surface (Figures 22, 23, 31); median stalk (surrounding afferent gill vessel) almost completely free, only attached at posterior region close to anus (Figures 22, 26, 31). Gill filaments symmetrical, tip of each leaflet rounded, turned medially (Figure 31). Osphradium inconspicuous. Anus located medially in pallial cavity posterior end (Figures 22, 26, 31). No detectable hypobranchial gland.

Visceral mass (Figures 22, 26–31). Organized as internal mould of shell, more concentrated posteriorly, surrounded ventrally and laterally by shell muscle; continuous with head-foot haemocoel. Volume of visceral sac approximately half of that of shell. Renopericardial area located as most dorsal structure, just posterior to foramen and to pallial cavity; occupying about 1/4 of visceral volume. Stomach occupying central and posterior region, about 1/3 of visceral volume. Digestive gland greenish brown, located in ventral and lateral regions, between stomach and foot, occupying about 1/4 of visceral volume. Gonad white, located mostly in middle of right side; normally about 1/8 of visceral volume. Digestive tubes filling remaining regions of visceral sac, mostly in posterior and dorsal regions (Figures 28, 29). A conspicuous blood sinus surrounding ventral and posterior regions (Figure 27: bv) of visceral sac floor.

Circulatory and excretory systems (Figures 22, 26, 31). Pair of auricles located laterally, receiving in their antero-lateral corner ctenidial vein from outer edge of gills (Figure 31: cv); volume of each auricle approximately 1/4 of that of pericardium; walls thin, translucent. Ventricle central, surrounding short portion of rectum crossing through pericardium (Figure 28: ve); volume equivalent to that of each auricle; walls thick. Connection between ventricle and auricles simple, on each side of ventricle. Afferent gill vessel (Figure 31: af) originating mostly from haemocoel, running along median side of gills. Renal tissue small, only detectable in pallial cavity roof, in region just anterior to anus (Figure 31: ki); possessing central furrow and a volume equivalent to 1/10 of pericardium. Pair of nephrostomes located on each side of anus, located slightly dorsal and at posterior end of renal tissue. Renal tissue solid, white.

Digestive system (Figures 27–39). Buccal mass about 1/8 of haemocoelic volume, located just posterior to mouth (Figures 27, 28). Odontophore occupying about half of buccal mass ventral volume. Pair of jaw plates (Figure 33) thin, translucent, located in middle of buccal cavity's dorsal wall (Figure 39: jw); each plate trapezoidal, located close to median line, anterior edge slightly thicker than posterior edge. Inner surface of dorsal wall of buccal mass possessing a pair of longitudinal folds (Figure 39: df), each fold's width and height about 1/4 of local width; space between both folds equivalent to 1/4 their width; remaining areas smooth. Odontophore muscles (Figures 34–37): **m1v**, pair of posterior protractor muscle of odontophore

(Figure 34), wide and very thin, originating in ventral region of mouth, running posteriorly bordering ventral surface of odontophore, inserting superficially in odontophore's posterior region over area equivalent to 1/4 of odontophore width; **m4**, main pair of ventral tensor muscles of radula (Figures 36–37), originating from lateral and posterior edges of odontophore cartilages; surrounding dorsal lateral portions of cartilages, wide and thick, inserting at ventral surface of radular sac in its portion crossing odontophore, mainly in its posterior and lateral regions; **m5**, pair of auxiliary ventral tensor muscle of radula, wide and thick, as medial continuation of m4 pair, but located more medially, originating from median and posterior edges of odontophore cartilages (Figures 36, 37), inserting along median line in radular sac portion crossing odontophore (Figure 37); **m6**, horizontal muscle, thin and wide, connecting median edges of both odontophore cartilages from their anterior end, up to level between middle and posterior thirds (Figures 36, 37), anterior region placed slightly towards ventral surface of cartilages, with short posterior portion located on dorsal surface (Figure 37); **m7**, pair of small and narrow dorsal tensor muscles of radula (Figure 36), originating from haemocoel's ventral region at posterior level of odontophore, running dorsally, penetrating medial region of odontophore just anterior to radular sac penetration into odontophore, penetrating radular sac, splaying in this region of ventral side of radular ribbon; **m7a**, pair of small and narrow ventral tensor muscles of radula (Figure 36), originating from and initially running with m7 pair, gradually flanking m6 dorsal surface close to median line, inserting in small region of subradular cartilage's ventral end; **m10**, small pair of ventral protractor muscles of odontophore (Figures 29, 34, 36), originating from ventral region of mouth, running posteriorly bordering ventro-anterior region of odontophore, penetrating through ventral membrane of odontophore just anterior to m7 pair penetration, inserting in median region of odontophore cartilages' ventral and posterior surface (Figure 36); **m10a**, pair of narrow ventro-lateral protractor muscles of odontophore (Figures 32, 34–36), originating from same region of pair m10, but more laterally, running posteriorly flanking ventral and lateral region of odontophore, inserting in same region of m10 pair but more laterally (Figure 36); **m11**, main pair of ventral tensor muscles of radula (Figures 36, 37), originating from median-posterior edge of odontophore's cartilages, running along lateral region of m6's ventral surface, inserting in ventral end of subradular cartilage between middle and lateral halves; **mj**, jaw and thick peri-buccal muscles (Figures 34–37), originating from both odontophore cartilages, in their middle and anterior regions of outer surface (Figure 36), running ventrally, partly through subradular membrane (Figure 37), surrounding afterwards mouth opening. Odontophore *non*-muscular structures: **oc**, pair of odontophore cartilages, antero-posteriorly elongated, about four times longer than wide, laterally flattened (about half of their width), about as long as odontophore, anterior end blunt, tip dislocated medially, posterior end rounded; **sc**, subradular cartilage in oral cavity occupying most of expose portion of odontophore (Figure 35) in elliptical outline; **br**, subradular membrane, covering entire region of odontophore exposed into oral cavity (Figures 34–36), thin, translucent, surrounding externally jaw and peribuccal muscles (jw) (Figure 37).

Radular sac with about twice length of odontophore (Figures 28–30, 34, 35), encased between esophageal gland and adjacent portion of intestine; width about 1/5 of odontophore. Radular nucleus blunt, widely bifid, about 1.5 times radular sad width (Figures 34, 35: rn). **Radula** (Figures 14–19): right and left sides asymmetrical, rachidian tooth located at intermediary level between both sides. Rachidian tooth with triangular base, tip blunt, curved posteriorly, base about twice as long as wide (Figures 17, 18); wider portion about 12% of total radular width, length about 20% of radular width; curved tip about 20% of total tooth size. Lateral teeth in six pairs. Four median pairs of lateral tooth similar to rachidian (Figures 16–17), except for narrower base, weakly curved surrounding edge of rachidian's base; this set of four lateral teeth occupying about 20% of radular width in each side. Lateral tooth five, or dominant tooth, much larger, about five times wider and thicker than remaining lateral teeth (Figures 15, 16); base rectangular, with blunt, low cusp in middle region of median edge; tip curved almost perpendicularly, about 20% wider than base, weakly curved inwards, four wide, blunt, terminal cusp occupying about half of tip's width, medial cusps with about 1/5 of terminal cusps' size, both lateral cusps decreasing by a factor of approximate 75% in relation to terminal cusp; lateral tooth five occupying about 15% of radular width. Lateromarginal plate subtriangular (Figure 19); low, lacking projection, cutting edges or cusps, proximal portion narrow, increasing gradually along same distance of any tooth length, producing sinuous distal edges; an oblique, longitudinal thickness ending in base of more distal projection. About 20–22 pairs of marginal teeth, gradually diminishing in size towards periphery (first marginal about twice as large as last one); each one consisting of long rod, with curved distal third (Figures 15, 19); average width of each tooth approximately 5–7% of length; tip pointed, somewhat flat (about 20% wider than proximal rod), each side with 7–8 small, sharp pointed cusps; each cusp about 1/3 of local width of tooth, turned distally, located close to each other, aligned on both sides up to distal end, with a terminal, similar sized cusp; each set of marginal teeth approximately 9–10% of radular width.

Anterior esophagus with dorsal folds gradually crossing to right side (Figure 39). In this region, ventral fold flanking left side of aperture of esophageal gland; dorsal fold flanking dorsal edge of another aperture to esophageal gland, with its pair (flanking ventral edge of this aperture) as another similar sized fold bordering this aperture; between this fold and ventral fold a wide (about half of local esophageal width), longitudinal furrow, connecting oral cavity directly to posterior esophagus; this wide furrow covered by glandular papillae of same fashion of those of esophageal gland. Esophageal gland with two openings from central region of anterior esophagus described above; remaining a blind-sac of approximately same size as odontophore; originated from right side of esophagus, running initially along ventral region of esophagus, surrounding its left side, located afterwards on dorsal side of esophagus, reaching middle level of buccal mass (Figures 32, 39: eg). Inner surface of esophageal gland completely covered by uniform mosaic of papillae; each papilla white, about as tall as thickness of adjacent wall of esophagus, tip rounded, located very close to each other. Posterior esophagus about as long as anterior esophagus (i.e., its portion through esophageal gland) (Figures 29, 30), with about 1/3 of odontophore's width; inner surface bearing 8–10 longitudinal, low, narrow folds, somewhat uniform in size, located close to each other (Figure 39); these inner folds gradually disappearing posteriorly, producing smooth surface (Figure 38: es). Esophageal insertion in middle region of ventral stomach surface (Figures 27–30), in such two pairs of ducts to digestive gland originates (Figure 30: dd), one pair in each side.

Stomach approximately 1/3 of visceral volume, lying about in its central region (Figures 22, 27–30), wide, antero-posteriorly flattened (about twice wide than tall); wide region posterior, gradually narrowing towards anterior and left (Figure 30), reaching posterior level of buccal mass inside haemocoel (Figures 27, 28). Gastric inner surface mostly smooth (Figure 38); a pair of gastric folds originating in posterior region of esophageal insertion, running posteriorly very close to each other along ventral surface, ending in short curve in small, almost vestigial gastric caecum (Figures 29, 38: sp), located in middle level of gastric ventral-right surface; another pair of similar folds originating in right gastric inner surface with similar characters has these folds, but about 1/4 shorter (Figure 38); special sorting area located to left of these longitudinal folds (Figure 38: sa), possessing 4–5 longitudinal, low folds, somewhat uniform in size, very close to each other, about twice as wide as tall, about 2/3 of each longitudinal folds' width, each fold running from esophageal insertion posterior-left, fading at posterior level from gastric caecum. Four pairs of longitudinal folds on intestinal side of stomach (Figure 38) situated about equidistantly from each other; two of them originating on each side of esophagus, running along right side, between these two 6–8 longitudinal, low folds, each about 1/3 size of main folds; other two folds located on opposite sides of main folds, except in having smooth region between (Figure 38: gf). Intestine relatively short, its origin in stomach unclear, relatively short – about as long as stomach if straightened; width uniform along its length, about 1/7 of wider region of stomach; running through digestive gland and gonad (Figures 27–30); inner surface mostly smooth and simple. Rectum short, passing through pericardium (Figures 26, 28, 31). Anus a very short papilla located medially at end of pallial cavity (Figures 23, 28, 31: an).

Genital system. Gonad described above (visceral mass). From it two gonoducts running from ventral to dorsal through digestive gland and stomach (Figures 22, 26, 31); each duct narrow; walls translucent, thin; both simply inserting in ventral-left side of pericardium (Figure 31: gd).

Central nervous system (Figure 32). Nerve ring located between buccal mass and adjacent ventral surface of haemocoel. Pair of cerebral ganglia located in both sides of head; each cerebral ganglion elliptical, about 1/4 of mouth size; cerebral commissure about 1/5 of cerebral ganglion width and 5–6 times longer than it. Pairs of pleural and pedal ganglia located posterior to odontophore, very close to each other. Cerebro-pleural and cerebro-pedal connectives very narrow, running parallel to each other a distance equivalent to eight times cerebral ganglion length. Each pedal and pleural ganglia forming single mass, about 1.5 times cerebral ganglion size, located very close from each other, very short commissure. A particularly large pair of nerves, about half of pedal-pleural ganglia diameter, running posteriorly originating from posterior sides of pedal ganglia (Figure 32: nv).

Measurements (length × width × height in mm). Holotype 14.0 × 9.3 × 6.5. Paratype MZSP 86743#1: 13.3 × 9.1 × 6.6.

Distribution. Only known to the São Pedro e São Paulo Archipelago.

Habitat. Intertidal rocks and calcareous algae.

Material examined. Types.

DISCUSSION

The described species is considered in the genus *Fissurella* Lamarck, 1799 (type species *Fissurella nimbosa* Linné, 1758 by monotypy) because it fits in the definition of the genus (e.g., Farfante, 1943: 1–2; McLean, 1984), such as sub-central apex, radial sculpture, and foramen bounded inside by a callus which is not truncated or excavated. Possibly, the species can belong to the subgenus *Cremides* H. & A. Adams, 1854 [type species *Fissurella barbadensis* (Gmelin, 1791)], because of the radiating sculpture and nodes and crenulated margin. However, as the definition of the fissurellid taxa is poor, mainly related to subgenera, a conservative approach is taken here, considering the species in a wider taxon.

Fissurella mesoatlantica can be easily distinguished from similar species by the height of the shell; normally its shells have a height of about half of their length, a character rarely found in the similar species *F. clenchi* Farfante, 1943; *F. rosea* (Gmelin, 1791) and *F. nubecula* (Linné, 1758). In addition to this character, the following comparisons distinguish these species:

Fissurella nubecula, with which *F. mesoatlantica* has been confused previously (Edwards & Lubbock, 1983), occurs in Mediterranean Sea, West Africa and Canaries Islands (Poppe & Goto, 1991; Ardovini & Cossignani, 2004). *Fissurella mesoatlantica* has a more central foramen, while that of *F. nubecula* is normally placed in posterior third. The sculpture of both species is a quite similar, but *F. nubecula* rarely has nodules along radial ribs, a common feature of *F. mesoatlantica*.

Despite *Fissurella rosea* having been reported from the Brazilian coast (e.g., Rios, 1994), it appears to be only a misidentification related to red-pigmented specimens of *F. clenchi* (pers. obs.). The species appears to be restricted to the Caribbean Sea (Farfante, 1943; Jong & Coomans, 1988). *Fissurella mesoatlantica* lacks the characteristic red or rose stain at the inner area surrounding the foramen of *F. rosea*, and the foramen is usually round without lateral projections. The sculpture of *F. mesoatlantica* is also more robust and irregular than that normally seen in *F. rosea*.

Fissurella clenchi is the only species of *Fissurella* occurring along the Brazilian coast and is most similar to *F. mesoatlantica*. In shell characters, they are difficult to distinguish, except by the above mentioned taller shell of *F. mesoatlantica*. Also, *F. mesoatlantica* normally has fewer radial ribs (about 50 versus about 70 of *F. clenchi*), the shell outline is normally more rounded (length to width ratio of *F. mesoatlantica* is on average 1.4; in *F. clenchi* about 1.7), and its base is normally arched (Figures 2, 11). In addition to the distinguishing shell characters of these two species with disjunct distribution, some additional anatomical features can be enumerated. *Fissurella mesoatlantica* has simpler papillae at the mantle's border (*F. clenchi* has mostly ramified papillae); the papillae in the foramen are generally restricted to the anterior and posterior margins in *F. mesoatlantica* (Figures 21, 25), while they are more uniformly distributed in *F. clenchi*. The epipodial tentacles of *F. mesoatlantica* are more separated from each other and fewer in number compared to *F. clenchi*, which has about 10–12 closely spaced pairs near the head (while *F. mesoatlantica* has five pairs). The anus is papilla-like in *F. mesoatlantica*, but is sessile in *F. clenchi*.

Fissurella emmanuellae Métivier, 1970 (Leal, 1991; Rios, 1994) is an endemic species from Fernando de Noronha archipelago, Brazil, the closest to ASPSP. *Fissurella mesoatlantica* can be easily distinguished by lacking the characteristic brown pigment of the outer surface of the shell, and the green color of the inner shell's surface; additionally, *F. mesoatlantica* has a much more developed sculpture. However, both species have normally a similar height of the shell. Both species are also representative of the tendency for endemism of the genus *Fissurella* on oceanic islands.

From the remaining species occurring in the north Atlantic (Farfante, 1943), *Fissurella mesoatlantica* also differs: from *F. nimbosa* (Linné, 1758), *F. barbadensis* (Gmelin, 1789), *F. angusta* Gmelin, 1789 and *F. nodosa* (Born, 1780) in lacking such raised radial sculpture; from *F. barbouri* Farfante, 1943, in having a much smaller foramen; and from *F. punctata* Fischer, 1857 and *F. fascicularis* Lamarck, 1822 in having an elliptical outline and a sub-central foramen. Based on relative small size and richness of shell sculpture, *F. mesoatlantica* can not be confused with any species from South Atlantic and Pacific coast of South America (McLean, 1984).

It is important to emphasize that the systematics of the genus *Fissurella* is particularly difficult because of the high variability of their shells, which are moldable to the substrate and are, apparently, influenced by other biotic and abiotic features. The anatomy is apparently more conservative and a more stable source for comparative analysis (pers. obs.). Previously, the anatomy of the fissurellids is poorly known, and the knowledge was restricted to a few species (see references below). *Fissurella mesoatlantica* has the normal anatomy of the family, an enigmatic set of plesiomorphic and apomorphic characters in relation to Gastropoda. Among the plesiomorphic states are the pair of symmetrical gills and auricles and the lack of copulatory organs (Lindberg & Ponder, 2001). Of apomorphic states, the more important are the foramen of the shell, separating in two the mantle border (one surrounding the shell and another the foramen); the single pair of odontophore cartilages (Figure 37) (normally the vetigastropods bear a pair of posterior odontophoral cartilages); the shortness of the gastric caecum and of the intestine (Figure 30) (usually very long in vetigastropods) (Ward, 1966); the pair of well-formed gonoducts connecting the gonad with the pericardium (Figure 31) (normally the gonad attaches directly to pericardium); and the fusion of the pair of pleural ganglia with pair of pedal ganglia (Figure 32). The level of these main modifications, whether an autapomorphy of F. mesoatlantica or of another higher taxon (*Fissurella*, Fissurellinae, Fissurellidae), is still unclear. At least some of them are present in most foramen-bearing fissurellids (Boutan, 1886; Ziegenhorn & Thiem, 1925; Trigo, 1930; Odhner, 1932; Fretter & Graham, 1962; Hickman, 1998; Sasaki, 1998). The size of the mantle's edge and complexity of appendages and papillae is much more modest in *Fissurella* than, for example, in *Diodora* Gray, 1821 and *Lucapina* Sowerby, 1835 (Illigworth, 1902; Stasek & McWilliams, 1973). Although differing in some details, the organization of the genital system of *F. mesoatlantica*, with the kidney as part discharge pathway of the gametes, is typical for the family (Bretos et al., 1983; Beninger et al., 2001; Collado & Brown, 2007).

There is apparently a correlation between tallness of shell in limpets and energy of environmental water (waves or flow) (Vermeij, 1974, 2004): the higher the energy, the higher the shell. In *Fissurella mesoatlantica*, the shell is tall in the high energy environment where it was collected. Waves precluded the collection of this species while submerged; the specimens are only collected during very low tide.

Acknowledgments. A special thank to Daniel Geiger and James McLean for the thoughtful correction of the manuscript and for suggestions of references. To the Brazilian Navy, CNPq and Universidade Federal do Rio Grande do Norte (represented by Dr. Jorge Lins), for providing the infrastructure for the training and expeditions. To the team of researchers of MZSP that help in the collect of specimens, Carlos M. Cunha, Eric P. Gonçalves, and William Santana. This project is supported by a governmental grant of CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), process 558436/2005-6.

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