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Article *in* Archiv für Molluskenkunde · June 2021

DOI: 10.1127/arch.moll/150/031-043

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Morphology of two deep-sea *Olivella* from the southwestern Atlantic, with a record of a radula-less Olivellinae species (Neogastropoda: Olivoidea: Olividae)

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Abstract. Two deep-sea species from southeast Brazil, originally assigned to different subgenera of *Olivella*, are anatomically described. *Olivella* (*Olivina*) *klappenbachi* and *Olivella* (*Anasser*) *careorugula*, both described by Absalão & Pimenta (2003), present typical Olivellinae anatomy, with internal absorption of the shell wall and a non-spiralized visceral mass, the absence of a valve of Leiblein and gland of Leiblein, and a large cuticularized and muscular stomach. *Olivella klappenbachi* presents the typical radular morphology of Olivellinae, while *Olivella careorugula* lacks a radula and odontophore, which is unique among known olivids. A well-founded phylogenetic classification of *Olivella* at the generic/subgeneric level is still lacking, and the numerous proposed subgenera are mostly based on the structure of the pillar. A broader taxonomic study incorporating both morphological and molecular data is still necessary.

Key words. Mollusca, Gastropoda, Anatomy, *Anasser*, *Olivina*, radula morphology.

DOI. https://doi.org/10.1127/arch.moll/150/031-043

Introduction

The genus *Olivella* Swainson, 1831 comprises a speciose group of marine neogastropods of the olivid subfamily Olivellinae. Most species occur in the warm waters of tropical and subtropical regions (Olsson 1956), although Pastorino (2009) considered *Olivella* as a temperate group whose diversity decreases in colder waters. The current concept of the genus includes 117 valid species of *Olivella* (MolluscaBase 2020), including 24 species in the western Atlantic.

The systematics and classification of *Olivella* is largely based on the work of Olsson (1956), who established subgenera on the basis of shell characters of American species. However, Pastorino (2009) argued that the shell sometimes can be an unreliable source of characters, and that the present subgeneric concept might be unnatural.

Anatomy provides additional features that might help to clarify the classification. However, knowledge of the anatomy of *Olivella* is scarce, being restricted to the following species: *Olivella verreauxi* (Duclos, 1857) = *Olivella minuta* (Link, 1807) (Marcus & Marcus 1959a, b, including reproduction), *Olivella borealis* Golikov, 1967 (Kantor 1991), *Olivella volutella* (Lamarck, 1811) (Absalão & Garcia 2009), and *Olivella puelcha* (Duclos, 1835) and *Olivella tehuelcha* (Duclos, 1835) (Pastorino 2009, anatomy of the penis).

The radular morphology is better known than the other anatomy. Olsson (1956) examined and briefly described the radulae of 20 species but provided figures only for *Olivella nivea* (Gmelin, 1791), *Olivella columellaris* (G.B. Sowerby I, 1825), *Olivella biplicata* (G.B. Sowerby I, 1825), and *Olivella drangai* Olsson, 1956. Subsequent works described and illustrated the radula of: *Olivella adelae* Olsson, 1956, *O. nivea*, *Olivella dealbata* (Reeve, 1850), *Olivella petiolita* (Duclos, 1835), and *Olivella perplexa* Olsson, 1956 by Bandel (1984); *O. minuta* and *O. puelcha* by Calvo (1987); *O. borealis* by Kantor (1991); *O. puelcha*, *O. tehuelcha*, *Olivella orejasmirandai* Klappenbach, 1986 and *Olivella* cf. *riosi* Klappenbach, 1991 by Pastorino (2009); *O. minuta* and *Olivella exilis* (Marrat, 1871) by Kantor et al. (2017).

 ISSN 1869-0963, eISSN 2367-0622

Kantor (1991) used a morphological analysis of the Olividae to propose Olivellidae as a clade containing *Olivella* species, but this classification is not followed by most taxonomists (e.g., Pastorino 2009; Absalão & Garcia 2009), who maintain Olivellinae within Olividae (MolluscaBase 2020). Recently, Kantor et al. (2017) reinterpreted the phylogeny of the Olividae based on molecular data, which included three *Olivella* species, and concluded that Olivellidae is a clade within Olividae, but they drew no conclusions about the subgeneric division of *Olivella* due to their limited dataset.

Indeed, a revised phylogeny and classification of *Olivella* and its numerous subgeneric names would demand the inclusion of morphological and molecular data of many species. To contribute to the scant information available on the anatomy of *Olivella*, this paper describes the anatomy of 2 deep-sea species from southeastern Brazil, bringing new insights and data about this genus and reporting the first radula-less species.

Material and Methods

The specimens studied were dredged at collecting stations on the Campos Basin continental slope off the states of Rio de Janeiro and Espírito Santo, Brazil (c. 21–24.5° S) in the southwestern Atlantic. These specimens were collected within the framework of an environmental monitoring program for the establishment of deep-sea oil platforms. They were fixed in formaldehyde and preserved in 70% ethanol.

The specimens of *Olivella* were identified to species by comparisons with original descriptions and type series. They were dissected under a stereomicroscope and drawn using a camera lucida following the standard methods of Simone (2011); terminology for odontophore muscles follows Simone (2011). Six specimens of *Olivella careorugula* Absalão & Pimenta, 2003 and 8 of *Olivella klappenbachi* Absalão & Pimenta, 2003 were dissected. In *O. careorugula*, the buccal mass was both dissected manually and dissolved with KOH to be sure about the lack of a radula.

Critical-point drying was used to prepare the penis for scanning electron microscopy (SEM). Penes were rinsed with detergent diluted to 10% in water and placed on an ultrasonic cleaner. Subsequently, they were serially dehydrated in a graded alcohol series, 70%, 80%, and 90%, and twice washed with 100% alcohol. Radulae were cleaned in 10% KOH and subsequently rinsed in water. Shells, radulae, opercula, and penes were analyzed and photographed with a scanning electron microscope (JEOL JSM-6390LV).

The descriptions were written to complement the original conchological descriptions by Absalão & Pimenta (2003) and to present the novel anatomical data for both species. Shell ultrastructure terminology follows Teso & Pastorino (2011).

Anatomical abbreviations: **aa** = anterior aorta; **ae** = anterior esophagus; **am** = anterior mantle tentacle; **an** = anus; **au** = auricle; **bg** = buccal ganglia; **br** = subradular membrane; **ce** = cerebro-pleural ganglion; **cm** = columelar muscle; **co** = cerebro-pedal connective; **cp** = pleuro-pedal connective; **cv** = ctenidial vein; **dd** = duct to digestive gland; **dg** = digestive gland; **ec** = subesophageal comissure; **ep** = posterior esophagus; **es** = esophagus; **fs** = foot sole; **ft** = foot; **gc** = gastric cuticle; **gi** = gill; **hc** = hemocoel; **hg** = hypobranchial gland; **in** = intestine; **ki** = kidney; **kl** = kidney lobe; **lf** = labial flap; **m2**, **m4**, **m5**, **m6**, **m11** = odontophore muscles; **mb** = mantle border; **mj** = peri-buccal and jaw muscles; **ml** = mantle lobe; **mo** = mouth; **mp** = marginal plate of radula; **ne** = nephrostome; **ng** = nephridial gland; **nr** = nerve ring; **oc** = odontophore cartilage; **od** = odontophore; **of** = oral flap; **op** = operculum; **os** = osphradium; **ot** = oral tube; **pb** = proboscis; **pc** = pericardium; **pd** = penis duct; **pe** = penis; **pf** = penis flap; **pg** = pedal gland; **pm** = posterior mantle tentacle; **pp** = penial papilla; **pr** = propodium; **pt** = prostate; **pu** = pedal ganglion; **ra** = radula; **rn** = radular nucleus; **rs** = radular sac; **rt** = rectum; **ry** = rhynchostome; **sb** = stomach muscular belt; **sc** = subradular cartilage; **si** = siphon; **st** = stomach; **su** = subesophageal ganglion; **sv** = seminal vesicle; **sy** = statocyst; **tg** = integument; **ts** = testis; **vd** = vas deferens; **ve** = ventricle; **vm** = visceral mass.

Other abbreviations: **L** = length; **W** = width.

Institutional abbreviations: **ANSP** = Academy of Natural Sciences of Drexel University, Philadelphia; **IBU-FRJ** = Instituto de Biologia, Universidade Federal do Rio de Janeiro; **MNHN** = Muséum national d'Histoire naturelle, Paris; **MNRJ** = Museu Nacional da Universidade Federal do Rio de Janeiro; **MORG** = Museu Oceanográfico da Fundação Universidade de Rio Grande, Rio Grande; **MZSP** = Museu de Zoologia da Universidade de São Paulo.

In the list of examined material, the number inside brackets indicates the number of empty shells or ethanol preserved specimens in each lot. Those specimen lots with an asterisk (*) were destroyed by the fire in the MNRJ.

Results

Family Olividae Latreille, 1825

Subfamily Olivellinae Troschel, 1869

Genus *Olivella* Swainson, 1831

Remarks. As will be discussed, the taxonomic status of the several subgenera of *Olivella* is uncertain, and the subgeneric classification still needs a more robust investigation. In the present approach, we follow MolluscaBase (2020) for the inclusion of the two species studied here in *Olivella* sensu lato.

Olivella klappenbachi Absalão & Pimenta, 2003

Figures 1–4

Olivella (*Olivina*) *klappenbachi* Absalão & Pimenta 2003: 184, fig. 2D, E—Rios 2009: 276, fig. 689.

Description

Shell (Fig. 1A–H). See Absalão & Pimenta (2003), with the following additions: Parietal callus thin, sculptured by minute rather irregular, relatively uniformly distributed threads, almost parallel to inner lip (Fig. 1E, F). Protoconch c. 500 µm (Fig. 1H). Shell ultrastructure composed of 3 layers: a very thin outer layer of prismatic crystals, a middle layer of crossed-lamellar crystals amounting to c. 90% of whole wall thickness, and an inner layer of amorphous structure equal in width to outer layer (Fig. 1G)

Head-foot (Fig. 2A–C). Foot wide, ample, as large as shell; anterior region with bifid thickening, forming anterior propodium (Fig. 2A: pr). Rhynchostome (ry) as transverse, small slit, protected dorsally and slightly to right by bluntly pointed oral flap (Fig. 1B, C: of). Columellar muscle (cm) almost as wide as foot, c. ¼ whorl in length. Hemocoel occupying c. ¼ of middle region (Fig. 2B: hc).

Operculum (Fig. 1I, J). Corneous, thin, creamy yellow, twice as long as wide; slightly larger than foot (Fig. 2B: op); filling whole aperture (Fig. 1A, B). Posterior end bluntly pointed; anterior end rounded. Inner edge with anterior, subterminal notch surrounding subterminal nucleus. Inner scar undulated, flanking inner edge, c. ⅓ of opercular width (Fig. 1I). Outer surface with commarginal growth lines and undulations (Fig. 1J).

Visceral mass (Fig. 2F). Conical, non-spiral, wide, almost as large as head-foot. Stomach (st) occupying c. ⅓ of its volume, located c. ½ whorl posterior to pallial cavity's posterior end (Figs 2A, 3A). Remaining visceral mass consisting of yellowish digestive gland and gonad. Visceral genital tubes very narrow, except for seminal vesicle (Fig. 2F: sv), somewhat tapering anteriorly, occupying c. ⅒ of visceral volume, located ventrally.

Pallial organs (Figs 2D–F, 3A, B). Pallial cavity (Fig. 2F) occupying c. ¾ whorl. Mantle edge (mb) simple, thick. Siphon (si) small, thick, c. ⅓ of pallial cavity's length, edges simple. Posterior mantle tentacle (Fig. 2D, E: pm) as long as pallial cavity, base c. ¼ of length, tapering gradually up to blunt tip; with undulating fold on inner surface; basal mantle lobe (ml) simple, stubby, c. ⅓ tentacle's length. Osphradium (os) elliptical, anterior end slightly more pointed than posterior end, c. ⅓ of pallial cavity's width; central osphradial ganglion wide (Fig. 3B: os); filaments simple, slightly squared, tip rounded, left filaments slightly smaller than right filaments (Fig. 3B: os). Gill (gi) arched (concavity on left), flanking osphradium, about same area as osphradium; both ends pointed; anterior end located c. ¼ of pallial cavity's length posterior to mantle edge; posterior end close to pericardium (Fig. 3A). Gill filaments (Fig. 3B) triangular, as tall as wide, with blunt tips. Hypobranchial gland (hg) low, occupying c. ½ of area between gill and right margin, becoming gradually broader anteriorly. Rectum (rt) and genital tubes lying along right margin. Anus (an) sessile, located between middle and anterior thirds of pallial cavity.

Reno-pericardial structures (Fig. 3A). At anterior end of visceral mass, with c. ¼ of pallial cavity's volume (Fig. 3A: ki, pc). Heart occupying c. ⅓ of reno-pericardial volume; auricle (au) connected subterminally to ctenidial vein (cv), with short portion dorsal to gill. Kidney (ki) mostly hollow, with flattened ventral lobe; broad intestinal portion obliquely crossing kidney and ventrally covered by it. Nephridial gland (ng) narrow, thin, covering the internal surface of the wall dividing kidney, pericardium and pallial cavity. Nephrostome (ne) located close to rectum.

Digestive system (Fig. 3A, C–G, J, K). Proboscis (Fig. 3C: pb) short, c. ½ hemocoel's length and broad (almost as wide as hemocoel); basal walls thin, distal half with thick, muscular wall, as labial flap (Fig. 3C, D: lf). Salivary glands not observed; probably lost during dissections. Odontophore located away from buccal–esophageal axis, connected to labial flap base by ventral orifice (Fig. 3D: od). Odontophore orifice flanked by well-developed buccal sphincter (Fig. 3C, D: sp). Odontophore muscles (Fig. 3C, E–G): m2, pair of narrow retractor muscles of odontophore, originating in ventral surface of hemocoel, passing through nerve ring (Fig. 3C), inserting in latero-posterior surface of odontophore; m4, main pair of dorsal tensor muscles of radula, elongated, relatively thin and narrow, originating along outer-dorsal edge of cartilages, inserting along lateral region of subradular cartilage in its buccal-cavity portion (Fig. 3F); m5, pair of auxiliary dorsal tensor muscles of radula, narrow, thin and long, originating at posterior ends of cartilages, running along medial edges of cartilages, inserting in ventral-median region of subradular cartilage, in its portion along buccal cavity; m6, horizontal muscle, slightly broader than cartilages, connecting ventral edges of both cartilages from their anterior ends up to c. 70% their length (Fig. 3G); m11, pair of ventral tensor muscles of radula, narrow and thin, originating in postero-median corners of cartilages, running anteriorly close to median line, inserting in anterior end of subradular cartilage; mj, peribuccal muscles and protractor muscles of odontophore, immersed in wall connecting latero-anterior surface of odontophore to labial flap (Fig. 3E, F), passing through buccal sphincter (sp). Pair of odontophore cartilages c. 4 times longer than wide, slightly flattened, anterior and posterior ends rounded and similar to each other (Fig. 3G). Radula (Fig. 4): rachidian occupying c. ½ of radular ribbon width, c. 3 times wider

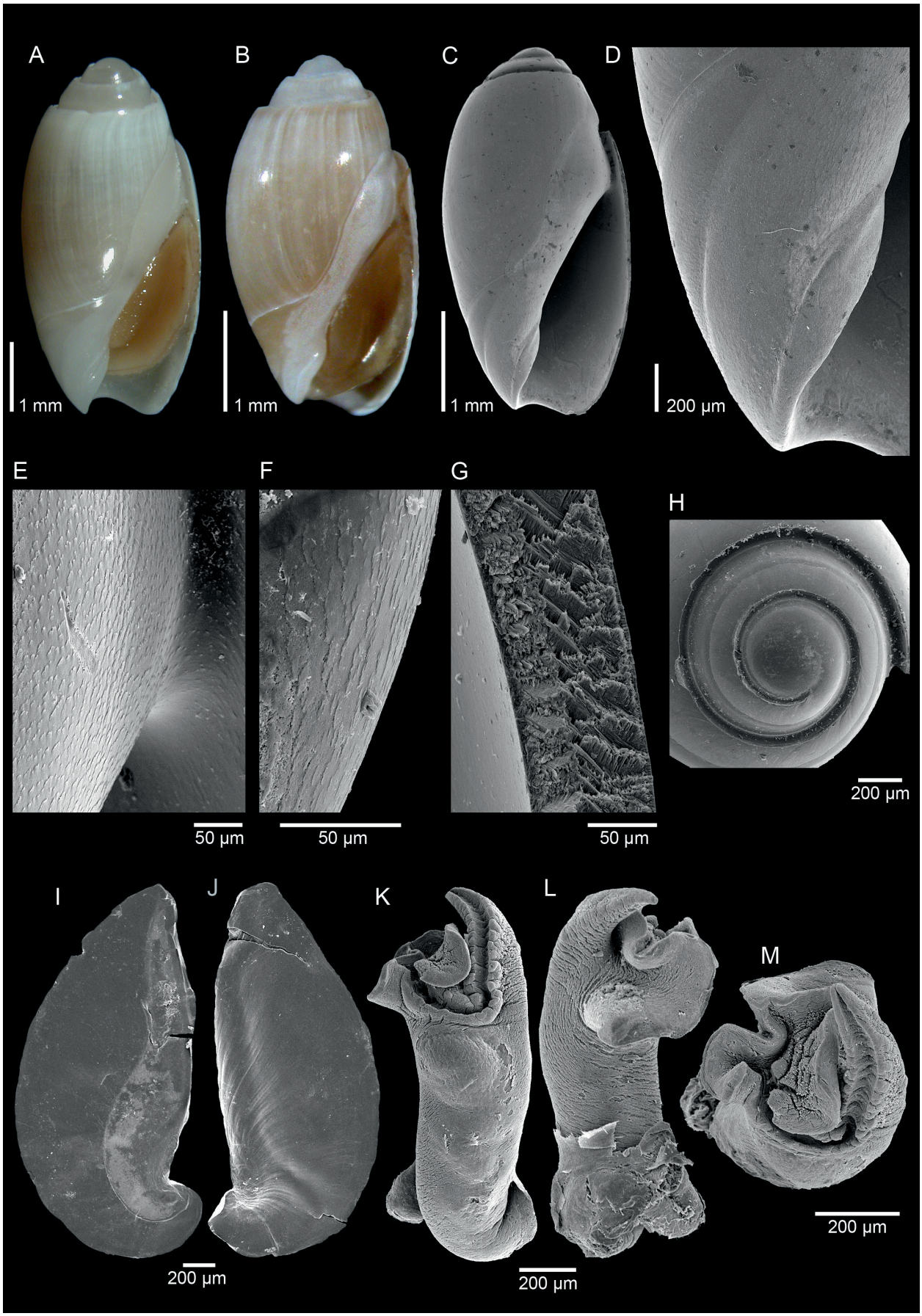


Figure 1. Shell, operculum, and penis of *Olivella klappenbachi*. **A–C.** Shell in frontal view: (**A**) (L 5.2 mm, W 2.6 mm); (**B**) (L 3.6 mm, W 1.9 mm); (**C**) (L 3.6 mm, W 1.9 mm). **D.** Pillar structure. **E, F.** Detail of parietal callus. **G.** Ultrastructure showing commarginal fracture surface. **H.** Shell in apical view. **I, J.** Operculum: (**I**) inner and (**J**) outer views. **K–M.** Penis, dorsal, ventral, and apical views. **A, C–D:** MNRJ 13558; **B, E–M:** MNRJ 13093.

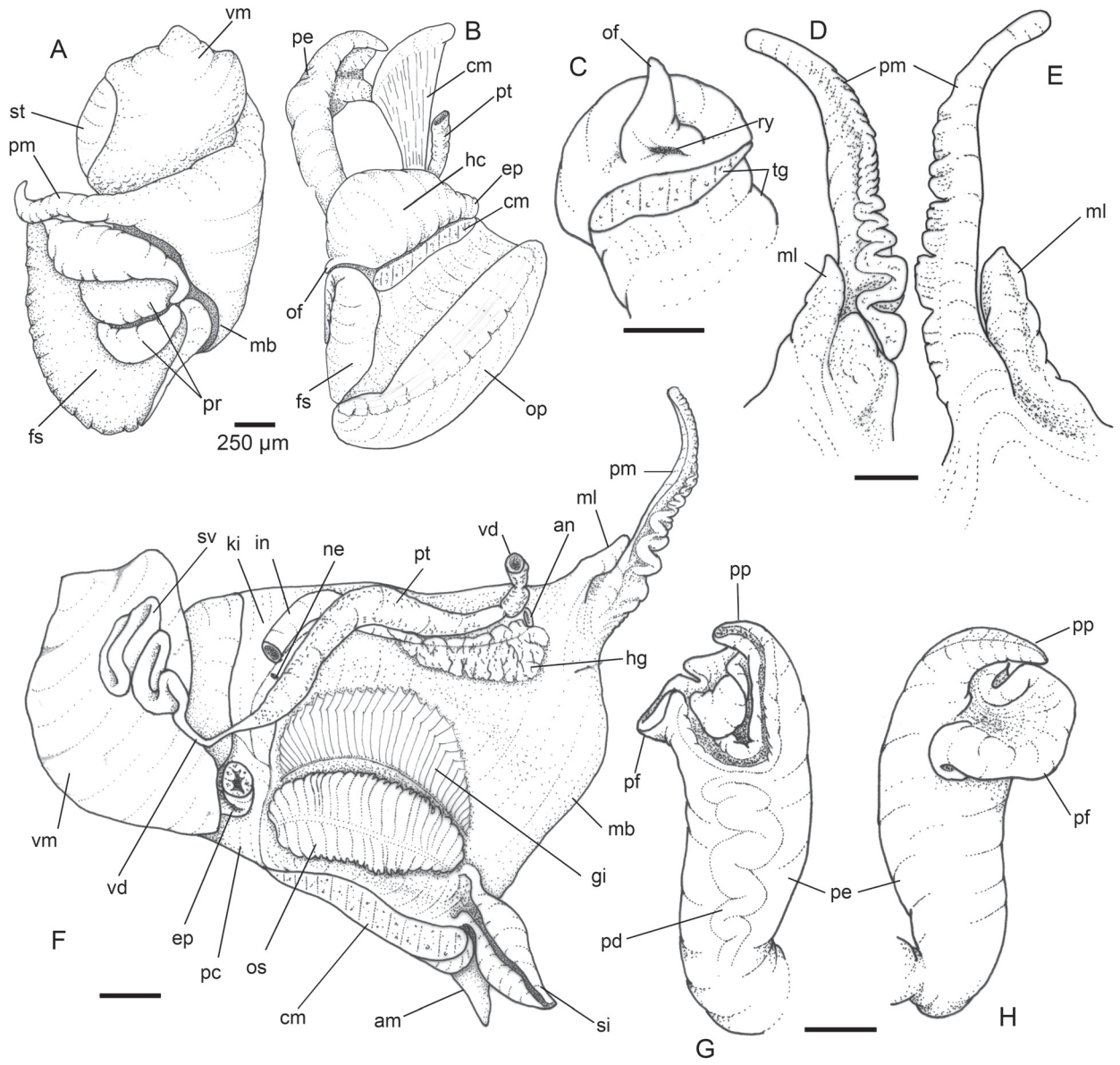


Figure 2. Anatomy of *Olivella klappenbachi*, MNRJ 13093. **A.** Whole male, removed from shell, in dorsal view. **B.** Head-foot, male, in ventral view. **C.** Rhynchostome region of head, in ventral view. **D, E.** Posterior mantle tentacle and adjacent mantle lobe: (**D**) in ventral view; (**E**) in dorsal view. **F.** Pallial cavity and visceral mass, male, mostly ventral view. **G, H.** Penis: (**G**) in dorsal view; (**H**) in ventral view. All scale bars = 250 µm.

than long; cutting edge of rachidian with c. 15 cusps; each cusp narrow, c. 4 times longer than wide, located very close to neighbouring cusps, tip sharply pointed; central cusps larger, slightly irregular in size, gradually decreasing laterally; rachidian base arched; lateral teeth with base slightly concave, c. ½ of rachidian width; large cusp straight or weakly curved outwards, tapering to relatively bluntly pointed tip; marginal plates (mp) rhomboid in outline, c. ½ width of base of lateral teeth. Esophagus (es) as a narrower continuation of oral flap (Fig. 3D), relatively simple, running along c. ½ whorl, inserting in ventro-left side of stomach (Figs 2F, 3A: ep, es). Stomach (st) spherical, narrowly attached to esophagus–intestine axis (Fig. 3A, J, K); stomach walls with large, transverse, thickened area of circular muscle (Fig. 3J: sb); inner gastric surface almost entirely covered by well-developed chitinous layer (Fig. 3K: gc). Intestine (in) and duct to digestive glans (dd) originating close to each other, just anterior to esophageal insertion (Fig. 3A, J); all 3 structures of similar caliber; intestine (in) with single sigmoid loop, crossing renal chamber (Fig. 3A: in), gradually widening. Rectum and anus described above (see pallial organs) (Fig. 2F: in, an).

Genital system. Male (Figs 1K–M, 2F–H). Testis immersed in central region of visceral mass, distinguished with difficultly from digestive gland. Seminal vesicle (sv) with 3 or 4 tight loops, relatively wide; duct narrowing in

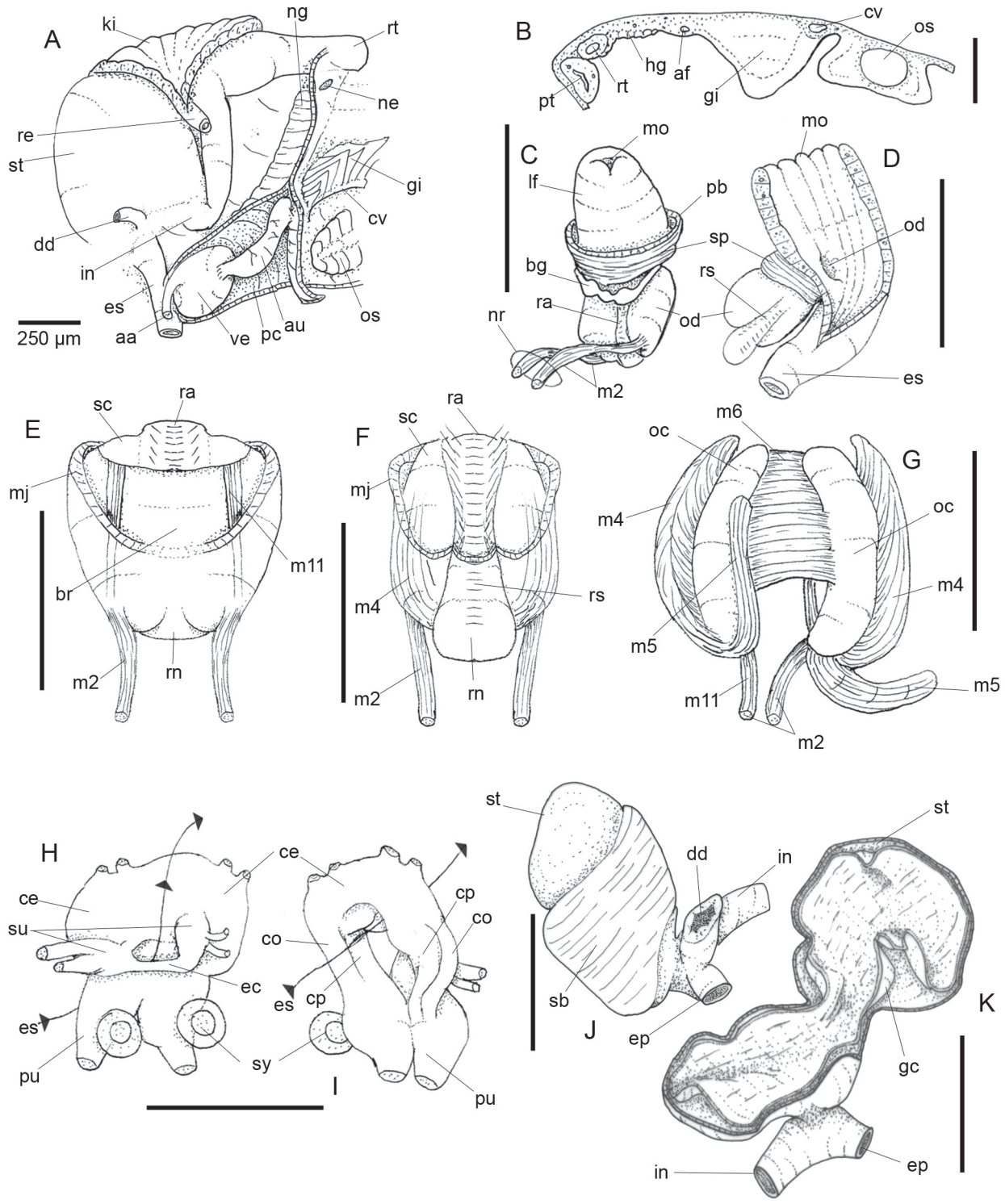


Figure 3. Anatomy of *Olivella klappenbachi*. **A.** Anterior region of visceral mass and adjacent region of pallial cavity, in ventral view, kidney and pericardium opened and deflected. **B.** Pallial cavity roof, transverse section in middle level of osphradium. **C, D.** Foregut: (**C**) dorsal view; (**D**) proboscis partially opened longitudinally. **E–G.** Odontophore: (**E**) in ventral view; (**F**) in dorsal view; (**G**) in dorsal view, with most muscles deflected but leaving m5 still in situ. **H, I.** Nerve ring: (**H**) in ventral view, esophageal topology also shown; (**I**) in dorsal view. **J, K.** Stomach: (**J**) with adjacent ducts in ventral view; (**K**) opened longitudinally. **A–I**: MZSP 121178; **J, K**: MNRJ 13093. All scale bars = 250 µm.

region preceding pallial cavity to form narrow and short vas deferens (vd). In pallial cavity, vas deferens suddenly expanding as prostate gland (pt); part preceding anus becoming narrow, crossing to pallial floor, running short distance up to penis base. Penis (pe) as long as pallial cavity, straight, with base narrower, gradually becoming broader up to complex tip c. twice as wide as base (Figs 1K–M, 2G, H); penis duct broad, zigzagging along

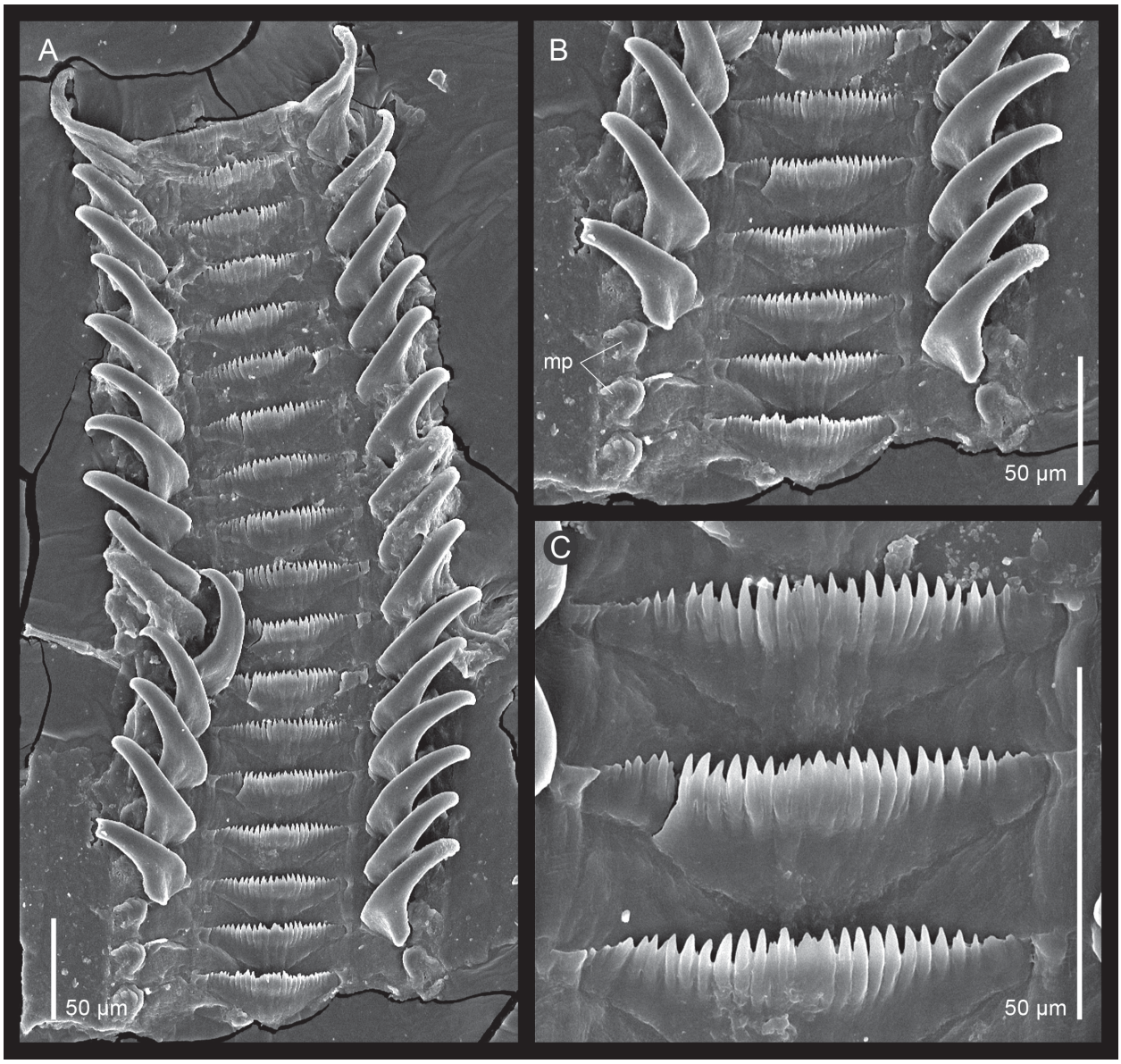


Figure 4. Radula of *Olivella klappenbachi*, MNRJ 13093. **A.** General view of entire radula. **B.** Detail of rows, with some lateral teeth lost and exposing the marginal plates. **C.** Detail of rachidian teeth.

central region of penis (Fig. 2G: pd); penial aperture subterminal, running as transverse groove (Fig. 1M), protected at middle by penis flap (Fig. 2G, H: pf), ending in stubby, pointed terminal penis papilla (Fig. 2G, H: pp). No female specimens available.

Central nervous system (Fig. 3C, H, I). Nerve ring located in posterior region of odontophore in retracted condition (Fig. 3C: nr). Four ganglionic masses of similar size, together c. ½ of odontophore's volume, located very close to each other. Pair of cerebro-pleural ganglia (ce) widely connected with each other, with commissure very short. Pedal ganglia (pu) very close to each other. Both pairs of connectives short and broad (Fig. 3I: cp, co). Subesophageal ganglia forming additional arc connected to both cerebral ganglia (Fig. 3H: ec, su). Statocysts (sy) large, ventral to both pedal ganglia.

Material examined. Paratypes: Brazil, Rio de Janeiro, S of Cabo Frio: MNRJ 8916 [2 shells], MD-55, sta. CB105, −23.7833, −042.1667, 610 m, collected by R/V *Marion Dufresne*.

New material: Brazil, Rio de Janeiro, Campos Basin: MNRJ 13092 [5 specimens*], 500 m, 21–23/xii/2006; MNRJ 17258 [4 specimens*], MZSP 121177 [1 specimen]: −23.2786, −40.9974, 600 m, 19/v/2009, collected by R/V *Gyre*, 19/v/2009; MNRJ 27010 [6 specimens*], MZSP 121179 [2 specimens]: −23.2766, −041.0077, 498 m, collected by R/V *GSO Marechal Rondon*, 26/viii/2013; MNRJ 27086 [6 specimens*], MZSP 121182 [2 specimens]: −23.2789, −041.0101, 498 m, collected by R/V *GSO Marechal Rondon*, 26/viii/2013.

Distribution. North coast of Rio de Janeiro state, southeastern Brazil; deep water, 498–618 m.

***Olivella careorugula* Absalão & Pimenta, 2003**
Figures 5–7

Olivella (*Anasser*) *careorugula* Absalão & Pimenta 2003: 182, fig. 1G–I—Rios 2009: 272, fig. 676.

Differential description

Shell (Fig. 5A–G, I). See Absalão & Pimenta (2003), with the following additions: Protoconch of 630 µm (fig. 5C). Callus narrow (Fig. 5E–G, I), possessing minute, arched striae. Shell ultrastructure (Fig. 5D) as in preceding species.

Head-foot (Fig. 6A–C). Similar characters as preceding species. Oral flap slightly larger (Fig. 6B: of). Columellar muscle narrower and more elongated (cm).

Operculum (Fig. 5H). Most features similar to preceding species, except subterminal inner notch slightly deeper. Proportionally larger, occupying almost entire shell aperture (Figs 5A, H, 6A, C: op).

Visceral mass (Fig. 6A–D). Similar to preceding species, except gonad slightly more distinct from digestive gland (ts).

Pallial organs (Fig. 6D, E). General organization somewhat similar to preceding species. Distinctions and notable remarks follow. Posterior mantle tentacle much longer, almost 1 whorl long (Fig. 6A: pm), slender, simple, lacking undulating fold. Anterior mantle tentacle absent (Fig. 6F). Osphradium (os) slightly broader, anterior-left filaments much smaller, producing anterior asymmetry (Fig. 6D: os); left filaments gradually enlarging up to posterior half. Gill (gi), with anterior end close to mantle edge. Area between gill and rectum narrower. Gill filaments with tips slightly more pointed (Fig. 6E).

Reno-pericardial structures (Fig. 6D). Similar to preceding species.

Digestive system (Figs 6G–I, 7A–E). Mostly similar to preceding species. Salivary glands not observed; probably lost during dissections. Proboscis slightly shorter (Fig. 6G–I: pb). Total absence of odontophore and radula. Labial flap as single structure of buccal mass (Fig. 7A, C), possessing anterior projected flap with 8–10 inner longitudinal folds. Esophagus of uniform width along its length of c. 1 whorl, except for slightly broader anterior region (Figs 6H, I, 7B, C: ae); inner surface lacking clear glands (Fig. 7C). Stomach (st) surrounded by a circular muscular band (Fig. 7D: sb). Duct to digestive gland narrower (Fig. 7E: dd).

Genital system. Male (Figs 5J, K, 6B, D, 7F, G). Testis occupying c. ⅓ of visceral mass, concentrated in superior regions (Fig. 6A, D: ts). Seminal vesicle longer than in preceding species, with more and narrower coils (Fig. 6A, D: sv). Prostate gland and pallial vas deferens narrowly zigzagging on pallial floor, with thick, glandular walls (Figs 6B, 7F: pt). Penis simpler, slenderer, of relatively uniform width along its length (Figs 5J, K, 7F, G), distal region tapering gradually up to a terminal, very small orifice (Figs 5K, 7F, G). Penis duct zigzagging along central penial region, varying from narrow (Fig. 7F) to broad (Fig. 7G) in different specimens. No female specimens available.

Central nervous system (Fig. 7H). Nerve ring's general attributes similar to preceding species, except ganglia farther away from each other. Right cerebral-pleural ganglia smaller than left ones. Cerebral and pedal commissures narrow and more elongated. Subesophageal ganglia connected to pedal ganglia, located at transition between oral tube and anterior esophagus (Fig. 6G, I: nr).

Biological note. Specimens with stomach content of foraminifer testa and shells of small gastropods (Fig. 7E), which were swallowed whole.

Material examined. Paratypes: Brazil, Rio de Janeiro, S of Cabo Frio: MNRJ 8913 [2 shells], MD-55, sta. CB105, −23.7833, −42.1667, 610 m, collected by R/V *Marion Dufresne*.

New material: Brazil, Rio de Janeiro, Campos Basin: MNRJ 13504 [2 specimens*]: −21.8936, −39.8386, 1120 m, 24/viii/2001; MNRJ 13092 [5 specimens*], 500 m, 21–23/xii/2006; MNRJ 17258 [4 specimens*], MZSP 121177 [1 specimen]: −23.2786, −40.9974, 600 m, 19/v/2009, collected by R/V *Gyre*; MNRJ 27026 [2 specimens*], MZSP 121180 [1 specimen*]: −23.2879, −41.0078, 640 m, 31/08/2013, collected by R/V *SGO Marechal Rondon*; MNRJ 27048 [1 specimen*], MZSP 121181 [1 specimen]: −23.2879, −41.0078, 670 m, 29/ix/2013, collected by R/V *SGO Marechal Rondon*.

Distribution. North coast of Rio de Janeiro state, southeastern Brazil; deep water, 500–1120 m.

Discussion

The present anatomical survey has confirmed a set of features that, in combination, are typical of Olivellinae exclusively, some of them also reported by Kantor (1991) and Kantor et al. (2017). These features include some that are apomorphic: the large labial flap making the short proboscis have a blunt, wide distal tip; the stomach positioned away from the esophageal/intestinal axis and bearing a well-developed, surrounding, circular muscle band (Figs 3J, K, 7D, E), which functions as a gizzard; the absence of the gland of Leiblein and the valve of Leiblein; the very large posterior mantle tentacle (Figs 2D–F, 6A). Some features that are plesiomorphic for Olividae are the well-developed operculum, separate odontophore cartilages, and the rachiglossate radula.

Another apparently exclusive olivelline character is the absorption of the inner whorls of the spire, which produces a rather conical, uncoiled visceral mass (Figs

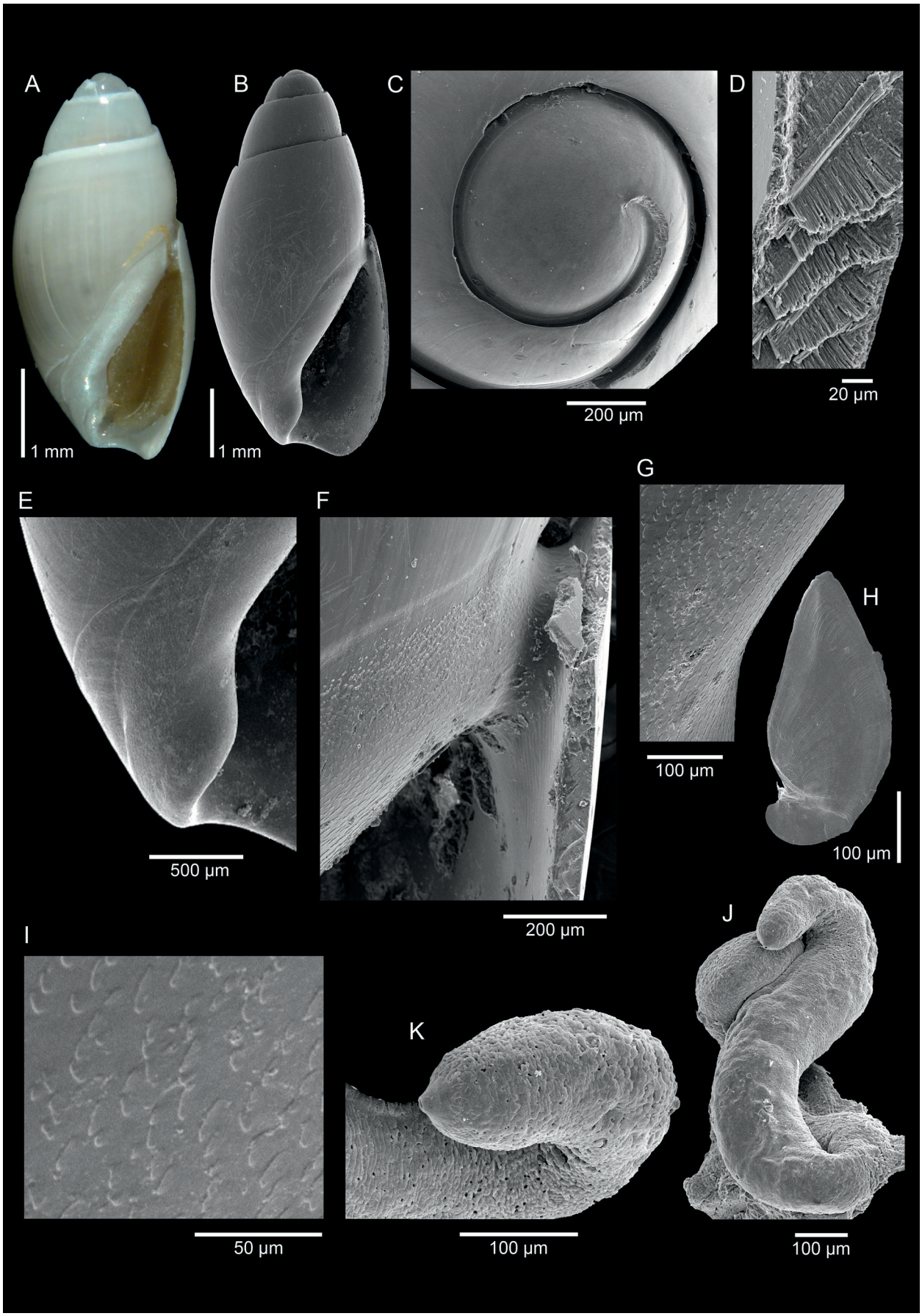
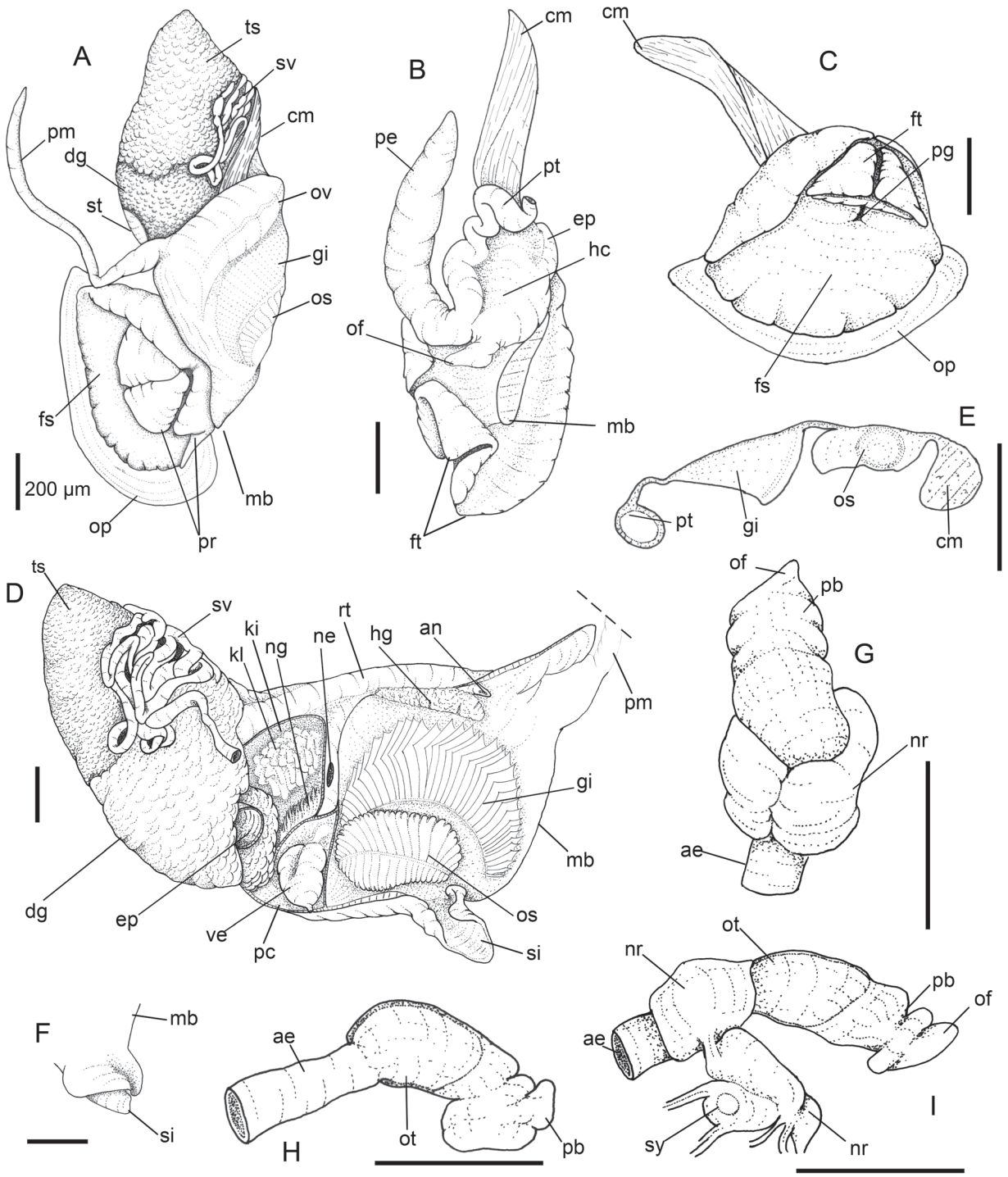


Figure 5. Shell, operculum, and penis of *Olivella careorugula*. **A, B.** Shell in frontal view: (**A**) L 4.3 mm, W 2.0 mm; (**B**) L 5.6 mm, W 2.57 mm. **C.** Shell in apical view. **D.** Ultrastructure, fracture surface commarginal. **E.** Detail of pillar structure. **F, G.** Details of parietal callus. **H.** Operculum, outer view. **I.** Detail of F. **J.** Penis and adjacent region, in whole dorsal view. **K.** Penis, detail of apex. **A, C–D, H, J–K:** MNRJ 13092; **B, E–G, I:** MNRJ 13504.

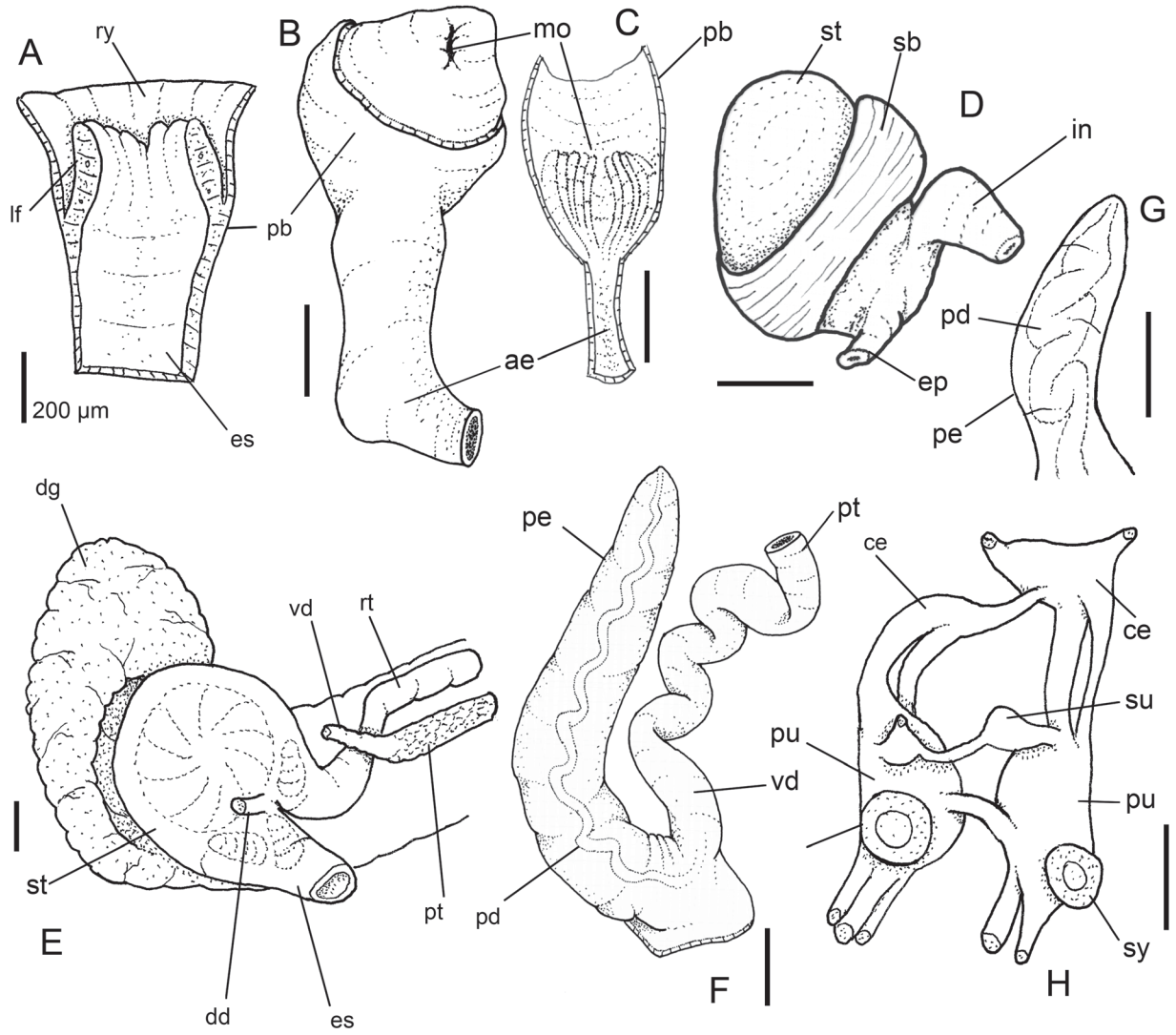


Figures 6. Anatomy of *Olivella careorugula* (MNRJ 13092). **A.** Whole male, removed from shell, in frontal view. **B.** Head-foot, male, in dorsal view. **C.** Foot sole, in ventral view. **D.** Pallial cavity and visceral mass, male, in ventral view with ventral reno-pericardial wall removed. **E.** Pallial cavity roof, transverse section in middle level of osphradium. **F.** Detail of siphon, in dorsal view. **G–I.** Foregut and nerve ring: (**G**) in situ, in dorsal view; (**H**) in right view with nerve ring removed; (**I**) in right view. All scale bars = 200 µm.

2A, F, 6A, D). However, this feature is not found in every species, for example, in *Olivella nivea* a part of the inner shell walls remain, producing a somewhat spiral visceral mass (ADP unpubl. data).

The phylogenetic relevance of these features is still being analyzed. Kantor (1991) recognized some of them as apomorphies of Olivellidae, but in a molecular analysis, Kantor et al. (2017) related them to the subfamily Olivellinae.

Another feature under investigation is the propodium, which is very well developed in olivellines (e.g., Marcus & Marcus 1959a; Pastorino 2007; Troost et al. 2012) (Figs 2A, 6A, C). In some species the propodium has lateral expansions. However, it is not completely clear how



Figures 7. Anatomy of *Olivella careorugula*. **A, B.** Foregut: (**A**) opened longitudinally, in dorsal view; (**B**) in ventral view, with distal portion of proboscis partially removed. **C.** Buccal mass, in ventral view, with proboscis and mouth opened longitudinally. **D.** Stomach, in ventral view. **E.** Visceral mass, in ventral view, with stomach slightly displaced and some adjacent pallial structures also shown in situ; stomach content indicated within. **F, G.** Penis and adjacent genital ducts: (**F**) in dorsal view, with penis duct seen by translucency; (**G**) another specimen. **H.** Nerve ring, in ventral view. **A, E, G, H**: MZSP 121180; **B–D, F**: MNRJ 13092. All scale bars = 200 µm.

the propodium looks in the other olivids. Possibly, it is a feature of the entire family, as all of them are digging animals.

The main anatomical distinctions between *Olivella klappenbachi* and *Olivella careorugula* are explored here. Of the differences, that which appears most interesting is the shape of the penis, which is much more complex in *O. klappenbachi*, with flaps and a papilla at the wide tip (Figs 1K–M, 2G, H), but simple, cylindrical, and with a blunt tip in *O. careorugula* (Figs 5J, K, 7F). The simpler penis of *O. careorugula* has some similarity to that of *Olivella puelcha* (Pastorino 2009: fig 19) and *Olivella minuta* (Petracco et al. 2015). While the penis of *Olivella tehuelcha* has a long terminal papilla (Pastorino 2009: fig 36), it is much less complex than that of *O. klappenbachi*.

Olivella careorugula lacks the anterior mantle tentacle (Fig. 6F), which lies adjacent to the siphon in *O. klappenbachi* (Fig. 2F) and all other *Olivella* species in which this structure has been investigated (*O. nivea*: Marcus & Marcus 1959a; *Olivella borealis*: Kantor 1991; *Olivella volutella*: Absalão & Garcia 2009; *O. tehuelcha*, *Olivella pusilla*, *O. nivea*: ADP unpubl. data).

Shell ultrasctructure (Figs 1G, 5D) follows the same general pattern as described by Teso & Pastorino (2011) for *Olivancillaria* species, in which the middle crossed-lamellar layer is very thick. In *O. puelcha*, in spite of the very similar crossed-lamellar layer, Pastorino (2009) only found 2 layers; Tursch & Macbaete (1995) found a variable number of layers in *Olivella*: 2 in *Olivella japonica* Pilsbry, 1895 and 3 in *O. volutella* and *Olivella biplicata*.

The central nervous system, or nerve ring, of *O. careorugula* (Fig. 7H) is much less concentrated than that of *O. klappenbachi* (Fig. 3H, I) and *O. minuta* (Marcus & Marcus 1959a: fig 19); this feature might be directly related to the absence of an odontophore. Swallowing prey whole in *Olivella* was reported by Marcus & Marcus (1959), and Bandel (1984) stated that the radula of *Olivella* is used to get hold of prey and to pull it into the mouth in one piece.

The radula of *O. klappenbachi* (Fig. 4) is typical of the subfamily, with a broad rachidian tooth. The rachidian tooth has a convex base and several short cusps. The relatively short, hooked lateral teeth curve outwards, and there is a marginal plate of uncertain homology to marginal teeth (Kantor et al. 2017). The rachidian tooth is boat-shaped with a rather convex base and around 20 short cusps of similar size, which agrees with descriptions of other species allocated to the subgenus *Olivina*: *Olivella bullula* (Reeve, 1850) (Olsson 1956), *O. puelcha* and *O. tehuelcha* (Pastorino 2009).

Another remarkable difference is the total absence of an odontophore in *O. careorugula*, in which the oral tube has a direct connection to the anterior esophagus (Figs 6H). In *O. klappenbachi* (Fig. 3C, D) the connection of the oral tube to the odontophore is of the normal shape found in other Neogastropods.

It is not possible to determine if the loss of structures in the buccal mass of *O. careorugula* has a phylogenetic significance until more olivids, especially in *Olivella*, become anatomically known. However, the absence of a radula has also been observed in some species of other neogastropod families that typically have a radula. In some Marginellidae (Souza & Simone 2019) and Raphitomidae (e.g., *Daphnella* Hinds, 1844; Simone 2011), those species that lack a radula have whole polychaetes inside their stomach, which shows that their prey is consumed whole. Other radula-less neogastropods, such Coralliophilinae (Muricidae), are ectoparasites. *Olivella careorugula* apparently is another category of radula-less species, which swallows shelled organisms whole. In such species, the shell might be both chemically dissolved and broken by a muscular stomach.

The subgeneric classification of *Olivella* is largely based on the morphology of the pillar structure, as extensively described by Olsson (1956). On this basis, 2 subgenera were proposed based on the absence of a pillar structure: *Anasser* Absalão & Pimenta, 2003 and *Janaoliva* Sterba & Lorenz, 2005; the latter was also characterized by a small denticle on the outer lip (Sterba & Lorenz 2005).

In spite of the very similar shell morphology of *Olivella* (*Anasser*) and *Olivella* (*Janaoliva*), they belong to separate families. *Janaoliva*, considered a junior synonym of *Olivellopsis* Thiele, 1929, was found to belong to the Bellolividae clade in the molecular analysis by Kantor et al. (2017). In fact, Kantor et al. (2017) described the radula of *Olivellopisis amoni* Sterba & Lorenz, 2005 (type species of *Janaoliva*), as having a rachidian tooth with 3 cusps and the lateral teeth curved inwards, which is typical bellolivid and olivine morphology and is probably plesiomorphic for Olivoidea.

In *Olivella* (*Anasser*) *careorugula*, in spite of the absence of a radula, several anatomical features are confirmed as olivelline-like. Thus, although the above conclusions are not based on the type species of *Anasser*, the similarities of shell morphology in *Anasser* and *Olivellopsis* would appear to be convergent. A subgeneric classification of *Olivella* is a theme for future investigation; in the molecular phylogeny by Kantor et al. (2017), no conclusion was drawn about the subgeneric division of *Olivella* due to their limited dataset. Just which of the 14 subgenera listed by Kantor et al. (2017) will be raised to genus level or synonymized depends on a broader sample for anatomical and molecular studies.

Acknowledgements

We thank Bioconsult Ambiental for the donation of samples, Dr Juliana B. Alvin for her assistance in the critical point procedures, Amanda Veiga and Beatriz Cordeiro for operating the SEM at the Departamento de Invertebrados (MNRJ), and Heike Reise and the 2 anonymous referees for their valuable critics and suggestions on the manuscript.

References

Absalão, R.S. & Garcia, F.J.G. (2009) Anatomy of *Olivella* (*Lamprodoma*) *volutella* (Lamarck, 1811) (Gastropoda, Olividae), a Panamanian Pacific species. *Bollettino Malacologico* **45**: 129–135.

Absalão, R.S. & Pimenta, A.D. (2003) A new subgenus and three new species of Brazilian deep water *Olivella* Swainson, 1831 (Mollusca, Gastropoda, Olivellidae) collected by the RV *Marion Dufresne* in 1987. *Zoosystema* **25**: 177–186.

Bandel, K. (1984) The radulae of Caribbean and other Mesogastropoda and Neogastropoda. *Zoologische Verhandelingen* **214**: 1–188.

Calvo, I.S. (1987) *Rádulas de gastrópodes marinhos brasileiros*. Rio Grande: Editora da FURG.

Kantor, Y.I. (1991) On the morphology and relationships of some oliviform gastropods. *Ruthenica* **1**: 17–52.

Kantor, Y.I., Fedosov, A.E., Puillandre, N. Bonillo, C. & Bouchet, P. (2017) Returning to the roots: morphology, molecular phylogeny and classification of the Olivoidea (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society* **20**: 1–49.

Marcus, Ev. & Marcus, Er. (1959a) Studies on Olividae. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia* **22**: 99–188.

Marcus, Ev. & Marcus, Er. (1959b) On the reproduction of "*Olivella*". *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia* **22**: 189–196.

MolluscaBase (2020) *Olivella* Swainson, 1831. World register of marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=138274 [accessed 2020.viii.1].

Olsson, A.A. (1956) Studies in the genus *Olivella*. *Proceedings of the Academy of Natural Sciences of Philadelphia* **108**: 155–225, pls 8–16.

Pastorino, G. (2007) Sexual dimorphism in shells of the southwestern Atlantic gastropod *Olivella plata* (Ihering, 1908) (Gastropoda: Olividae). *Journal of Molluscan Studies* **73**: 283–285.

Pastorino, G. (2009) The genus *Olivella* Swainson, 1831 (Gastropoda: Olividae) in Argentine waters. *The Nautilus* **123**: 189–201.

Petracco, M., Camargo, R.M., Berenguel, T.A., Arruda, N.C.L.P., Matto, L.A., Amado, L.L., Corbisier, T.N., Castro, I.B. & Turra, A. (2015) Evaluation of the use of *Olivella minuta* (Gastropoda, Olividae) and *Hastula cinerea* (Gastropoda, Terebridae) as TBT sentinels for sandy coastal habitats. *Environmental Monitoring Assess* **187**: 440.

Rios, E.C. (2009) *Compendium of Brazilian seashells*. Rio Grande: Editora Evangraf.

Simone, L.R.L. (2011) Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. *Arquivos de Zoologia* **42**: 161–323.

Souza, Jr, P.J.S. & Simone, L.R.L. (2019) Cladistic analysis of the family Marginellidae (Mollusca, Gastropoda) based on phenotypic features. *Zootaxa* **4648**: 201–240.

Sterba, G.H.W. & Lorenz, F. (2005) *Olivella* (*Janaoliva*) *amoni*, a new subgenus and species from the Bismarck Archipelago and Indonesia (Mollusca: Gastropoda: Olivellidae). *Visaya* **1**(3): 43–46.

Teso, V. & Pastorino, G. (2011) A revision of the genus *Olivancillaria* (Mollusca: Olividae) from the southwestern Atlantic. *Zootaxa* **2889**: 1–34.

Troost, A.I., Rupert, S.D., Cyru, A.Z., Paladino, F.V., Dattilo, B.F. & Peters, W.S. (2012) What can we learn from confusing *Olivella columellaris* and *O. semistriata* (Olivellidae, Gastropoda), two key species in Panamic sandy beach ecosystems? *Biota Neotropica* **12**(2): 101–113.

Tursch, B. & Macbaete, Y. (1995) The microstructure of the shell in genus *Oliva* (Studies on Olividae. 24). *Apex* **10**: 61–78.

Manuscript submitted 15 December 2020
Revised manuscript accepted 9 February 2021