Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2014) **80**: 604–623. doi:10.1093/mollus/eyu063
Advance Access publication date: 3 November 2014

A Special Issue of selected papers from the symposium: 'There's Something About Opisthobranchia', World Congress of Malacology, Ponta Delgada, Azores, July 2013

Taxonomic review of the genus *Pleurobranchaea* (Gastropoda: Pleurobranchoidea) from Brazil, with description of a new species

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(Received 30 December 2013; accepted 13 July 2014)

ABSTRACT

Based on a literature review and anatomical analysis we recognize 17 valid species of the genus *Pleurobranchaea* worldwide and summarize their characters. Many of these species have been insufficiently described and many have numerous synonyms. Four species have been recorded from the western Atlantic: *P. agassizii*, *P. obesa*, *P. tarda* and *P. inconspicua*. *Pleurobranchaea inconspicua* was originally described based on only one specimen from northern Brazil. This study gives a detailed redescription of *P. inconspicua*, based on material from Brazil, and of the similar *P. gela*, based on specimens from West Africa, to clarify their taxonomic validity. A new species from the Brazilian coast, *P. spiroporphyra* n. sp., is described. The traditional characters used in characterization of *Pleurobranchaea* species are evaluated and novel characters proposed. Traditionally, anatomy of the male apparatus, particularly the shape of the cross section of the cuticular stylet, was considered the most useful character to distinguish species. We describe different portions of the cuticular stylet of *P. inconspicua* and show that shape and size vary along its length. These characters seem not to be species-specific if only one portion of the cuticular stylet is examined. Other features, such as the position of the aperture of the salivary duct, the position and presence or absence of extrinsic and intrinsic odontophoric muscles, the configuration of nerves of the cerebropleural and pedal ganglia and the shape of the seminal receptacle, can be used to distinguish species. *Pleurobranchaea spiroporphyra* can be distinguished from other species by having a bright orange labial cuticle in front of the jaws, by a well-developed odontophore muscle m2b, by a laterally flattened, purple cuticular stylet that coils 12–14 times inside the penial sac and shows a thin crest close to the gonopore.

INTRODUCTION

The Pleurobranchaeidae are active hunters of invertebrates and burrow in soft bottoms. The family is considered monophyletic (Martynov & Schrödl, 2009) and comprises three genera: *Pleurobranchaea* Leue, 1813, *Euselenops* Pilsbry, 1896 and *Pleurobranchella* Thiele, 1925; two of them, *Euselenops* and *Pleurobranchella*, are monotypic.

The genus *Pleurobranchaea* currently comprises 15 valid species. Some of these species lack detailed morphological characterization (Ev. Marcus & Gosliner, 1984; Willan, 1987; Dayrat, 2001) and some have numerous synonyms. The genus is represented in temperate to warm waters by species with wide geographical distributions (Muniaín, Ardila & Cervera, 2007).

Only one species, *P. inconspicua* Bergh, 1897, was described from Brazil, based on one specimen from the northeastern coast. Its distribution was subsequently extended based on new records and by the recognition of junior synonyms from several localities in the Western Atlantic Ocean, Mediterranean Sea and West Africa (Muniaín *et al*., 2007). The available published descriptions of *P. inconspicua* and its synonyms are based on features of the external morphology, colouration, radula, jaw and reproductive system (Bergh, 1897; Ev. Marcus & Er. Marcus, 1957; Ev. Marcus & Gosliner, 1984; Muniaín *et al*., 2007).

In the most recent review of the family, Ev. Marcus & Gosliner (1984) pointed out that the classification of Pleurobranchaeidae was, in many cases, based on insufficiently described material. They highlighted that the species were often identified solely on the basis of previous descriptions of material from geographically close regions. Furthermore, although the jaw plates and radula can be used for generic distinction, these features hardly differ within a genus (Vayssière, 1901; Ev. Marcus & Gosliner, 1984). At present, the reproductive system and the penial morphology are considered the most useful characters to discriminate species of

Pleurobranchaea (Ev. Marcus & Gosliner, 1984). However, for most species of the genus these characters have been insufficiently described or are not described at all.

In this study, we redescribe *P. inconspicua* from Brazil, with the aim of improving the taxonomical delimitation of this species. A very similar species, *P. gela* from the Ivory Coast, is compared and a new species from Brazil described. Traditional characters used in the taxonomy of *Pleurobranchaea* are reevaluated and novel ones described.

MATERIAL AND METHODS

The material was obtained from three Brazilian malacological collections: Museu de Zoologia, Universidade de São Paulo (MZSP), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ) and Coleção Malacológica Prof. Henry Ramos Matthews, Universidade Federal do Ceará (CMPHRM). A total of 25 lots and 131 specimens were examined. In the lists of examined material, the number in brackets indicates the number of specimens in each lot, followed by the number of specimens dissected. Specimens of other species of *Pleurobranchaea* were examined for comparison: *P. gela* Ev. Marcus & Er. Marcus, 1966: Grand Bassam, Ivory Coast, MZSP 75368, 29/ix/1966 [1], 19/x/1967 [7]; *P. meckeli* (Blainville, 1825): off Atlit, Israel, MZSP 75485, 06/iv/1968, 64 m depth [1]; Haifa Bay, MZSP 75486, 11/iv/1967 [1]; off Bardawil, MZSP 75487, 14.5 m depth, 03/iv/1978 [1].

Description of external morphology is mainly based upon preserved specimens, except for *P. inconspicua* in order to describe colouration. Dissections and drawings of digestive system, including intrinsic and extrinsic muscles of odontophore, reproductive system, nervous system and circulatory system were done under a stereomicroscope with a drawing tube.

The radula was cleaned in 10% potassium hydroxide, subsequently rinsed in water and mounted for examination in a Jeol JSM-6390LV scanning electron microscope (SEM).

The nomenclature used to name the odontophore muscles follows Ponder *et al.* (2008: 350–351, figs 13.9–13.10). Additional information is added by suffixes (d: dorsal; v: ventral). In the nervous system, when a given ganglion gives rise to different nerves on the left and right sides, these nerves are distinguished as 'l' (left) and 'r' (right); when the nerve bifurcates the number of the nerve is followed by letters (a, b, etc.).

Additional abbreviations: USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMUC-GAS: Statens Naturhistoriske Museum, Copenhagen, Denmark.

SYSTEMATIC DESCRIPTIONS

Superfamily Pleurobranchoidea Gray, 1827
Family Pleurobranchaeidae Pilsbry, 1896

Pleurobranchaea Leue, 1813.

Pleurobranchaea Leue, 1813: 1 (type species *Pleurobranchidium meckeli* Blainville, 1825, by subsequent designation (Blainville, 1825: 471)).
Pleurobranchidium Blainville, 1825: 471 (type species *P. meckeli* Blainville, 1825, by monotypy).
Koonsia Verrill, 1882: 545 (type species *K. obesa* Verrill, 1882, by monotypy).
Pleurobranchillus Bergh, 1892: 27 (type species *Pleurobranchillus morosus* Bergh, 1892, by subsequent designation (Willan, 1977: 153)).
Macfarlandea Ev. Marcus & Gosliner, 1984: 40 (type species *Pleurobranchaea californica* MacFarland, 1966, by monotypy).

Diagnosis (adapted from Thompson, 1970; Willan, 1983, 1987; Ev. Marcus & Gosliner, 1984): body oblong, mantle and head smaller than foot. Oral veil serrated (digitate) in front, extended into expansions laterally. Rhinophores situated far apart on mantle edge. Mouth forming proboscis. Pedal gland in posteroventral part of foot sole in sexually mature specimens; caudal spur on upper surface of tail. Shell absent. Radula without rachidian teeth, lateral teeth bicuspidate, usually with accessory cusp strongly or weakly developed. Odontophore muscles: mj well developed; m5 well developed, covering almost all surface of m4 and median portions of cartilage, extending until dorsal part; pair of m7 (m7l), long and narrow, uniting in posterior portion (radula sac); m7 like tensor ventral muscle of radula, projecting radula forward; m7l connected to oesophagus laterally; m10d a dorsal pair of muscles originating on anterodorsal extremity of snout, connecting to transverse muscle mt. Acid gland large, with network of tubules extending among all organs. Penis sometimes papillate.

Remarks: The generic name *Pleurobranchaea* was established, based on the morphological description of an unnamed species, in an academic dissertation by Leue (1813: 1). In the same work, Leue (1813: 11) used an alternative name, *Pleurobranchidii*, for the same generic concept. Subsequently, Blainville (1825) used *Pleurobranchidium* as the valid generic name and described its type species, *P. meckeli*, on the basis of two specimens sent by Meckel (the academic advisor of Leue); this generic combination was not followed and the name *P. meckeli* (Blainville, 1825) was subsequently used in several publications (e.g. Willan, 1983, 1987; Ev. Marcus & Gosliner, 1984; Cervera & García-Gómez, 1988). In addition, Willan (1983) considered that the epithet *meckeli* should be corrected to *meckelii* and Ev. Marcus & Gosliner (1984) attributed the authority of the name *P. meckelii* to Leue (1813). Blainville (1825) pointed out that *P. meckeli* seems to be the same species as the type species of *Cyanogaster*, a genus proposed by Oken (1823). Subsequently, some authors treated *Cyanogaster* as a synonymy of *Pleurobranchaea* (Willan, 1977; Ev. Marcus & Gosliner, 1984). However, Britz *et al.* (2013) noted that inclusion of the name *Cyanogaster* in a list of synonyms does not make it available, because it does not meet the requirements of Article 12.1 of the International Code of Zoological Nomenclature (ICZN, 1999). Thus, *Cyanogaster* is considered a *nomen nudum*, because in the list by Oken (1823) there is no accompanying description and no distinguishing characters were listed.

Gosliner (1985) reexamined the holotype and paratypes of *Koonsia obesa* Verrill, 1882, type species of *Koonsia* Verrill, 1882, and concluded that the character used to diagnose *Koonsia*, the overhanging mantle, is not unique to this genus and thus could not be used for generic separation. Gosliner (1985) thus confirmed *Koonsia* as a synonym of *Pleurobranchaea*, as previously proposed by several authors (Bergh, 1897; Vayssière, 1901; Willan, 1977, 1983).

Bergh (1892) described *Pleurobranchillus* as a new genus, regarding it as an intermediate between *Pleurobranchus* and *Pleurobranchaea*. However, a few years later, Bergh (1897: 3, note 2; 1898: 64) recognized *Pleurobranchillus* as a synonym of *Pleurobranchaea*.

Ev. Marcus & Gosliner (1984) described *Macfarlandea* as a subgenus of *Pleurobranchaea* based on two diagnostic features: the presence of rudimentary secondary cusps on all radular teeth and a pleurembolic penis with cuticular stylet. Willan (1987) showed that these features are not present in *P. californica* MacFarland, 1966, the type species of *Macfarlandea*, and therefore considered it a synonym of *Pleurobranchaea*.

Pleurobranchaea inconspicua Bergh, 1897.
(Figs 1–4)

Pleurobranchaea inconspicua Bergh, 1897: 49; pl. 8, figs 2–10 (holotype ZMUC-GAS 2148, Cotinguiba river estuary, Sergipe state, Brazil).
Pleurobranchaea hedgpethi Abbott, 1952: 1; pl. 1, figs 1–8.
Pleurobranchaea hamva Ev. Marcus & Er. Marcus, 1957: 21; figs 40–52.

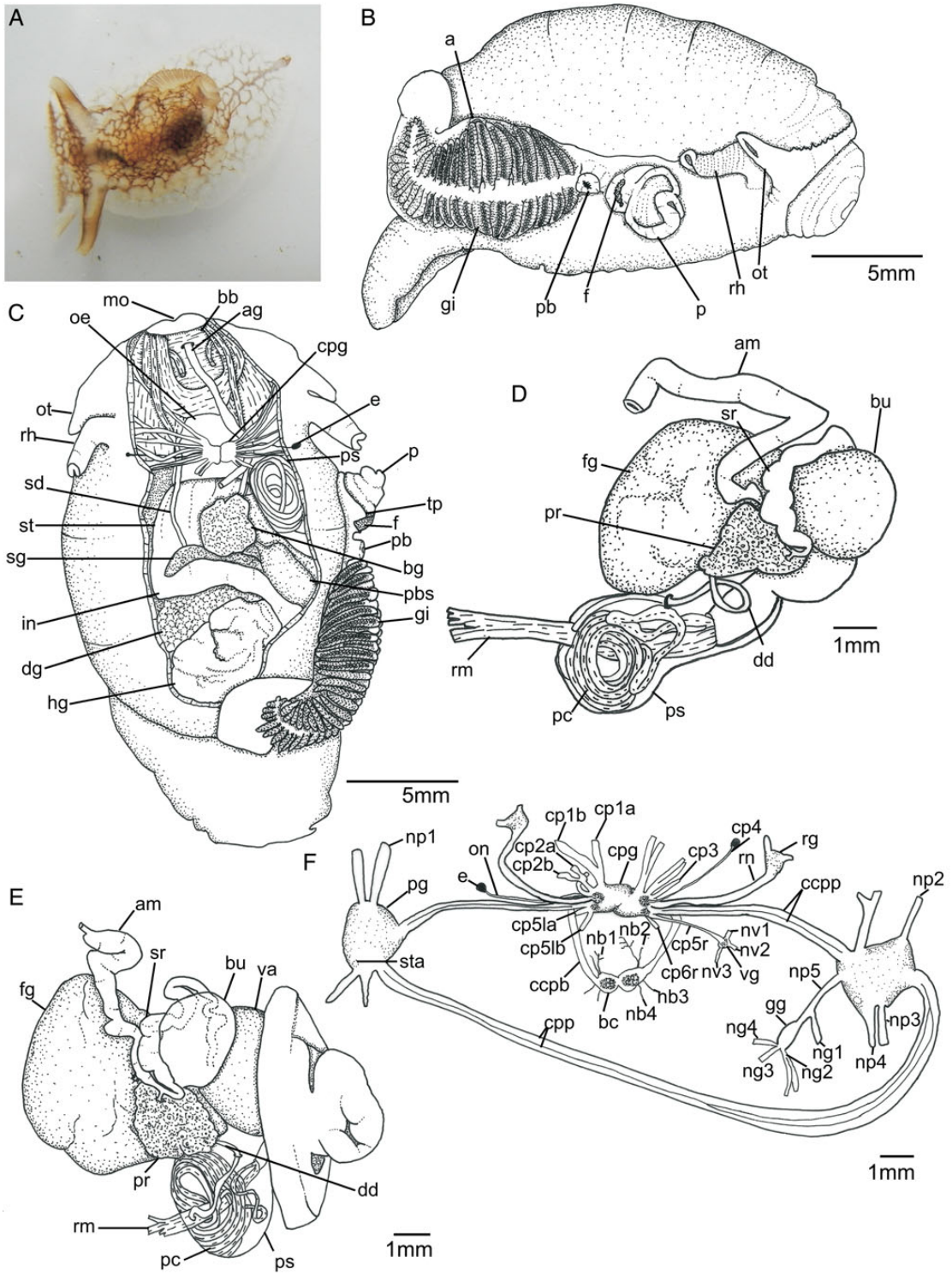

Figure 1. *Pleurobranchaea inconspicua*. **A.** Dorsal view, living specimen (13.0 mm long alive; photo C. M. Cunha). **B.** Lateral view, preserved specimen. **C.** Dorsal view, organization of internal organs. **D, E.** Deflected reproductive system. **F.** Nervous system. **A.** MZSP 103296. **B, C, E.** MNRJ 18227. **D, F.** MNRJ 30558. Abbreviations: a, anus; ag, duct of acid gland; am, ampulla; bb, buccal bulb; bc, buccal ganglion; bg, blood gland; bu, bursa copulatrix; ccpb, connective between the buccal and cerebropleural ganglia; ccpp, connective between the pedal and cerebropleural ganglia; cp, nerves that leave from the cerebropleural ganglion; cpg, cerebropleural ganglion; cpp, commissure between the pedal ganglia; dd, deferent duct; dg, digestive gland; e, eye; f, female opening; fg, female gland; gg, genital ganglion; gi, gill; hg, hermaphrodite gland; in, intestine; mo, mouth; nb, nerves that leave from the buccal ganglion; ng, nerves that leave from the genital ganglion; np, nerves that leave from the pedal ganglion; nv, nerves that leave from visceral ganglion; oe, oesophagus; on, optical nerve; ot, oral tentacle; p, penial papilla; pb, prebranchial aperture; pbs, prebranchial sac; pc, penis (cuticular stylet); pg, pedal ganglion; pr, prostate; ps, penial sac; rg, rhinophoral ganglion; rh, rhinophore; rm, retractor muscle; rn, rhinophoral nerve; sd, salivary duct; sg, salivary gland; sr, seminal receptacle; st, stomach; sta, statocyst; tp, triangular papilla near gonopore; va, vagina; vg, visceral ganglion.

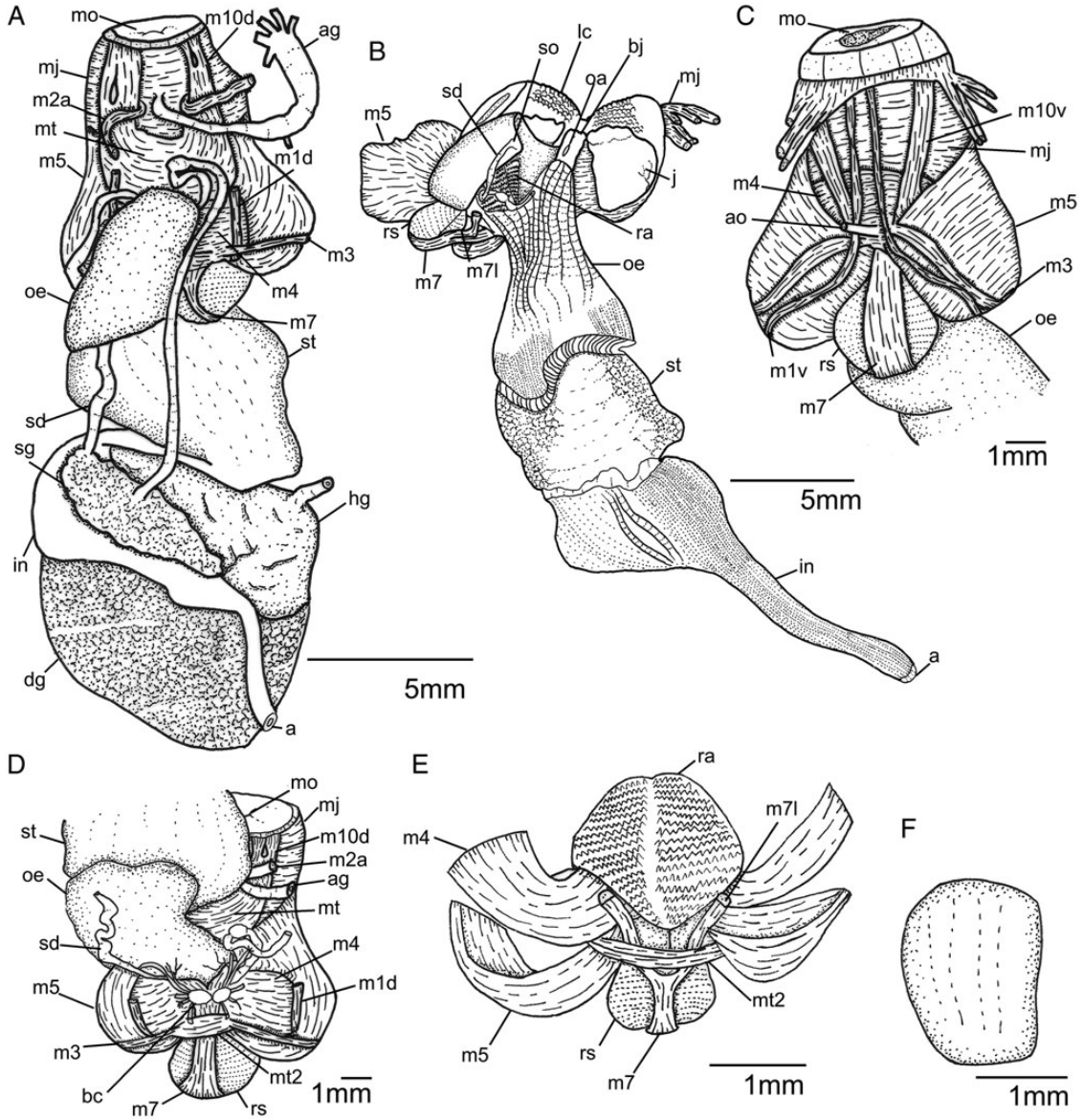

Figure 2. *Pleurobranchaea inconspicua*, digestive system. **A.** Dorsal view. **B.** Foregut sectioned longitudinally from ventral side. **C.** Buccal mass, ventral view. **D.** Buccal mass, dorsal view, detail of posterior region with oesophagus deflected. **E.** Odontophore isolated, dorsal view. **F.** Odontophoral cartilages. **A–D.** MNRJ 30558. **E, F.** MZSP 104842. Abbreviations: a, anus; ag, duct of acid gland; ao, aorta; bc, buccal ganglion; bj, area between jaws; dg, digestive gland; hg, hermaphrodite gland; j, jaw plates; lc, labial cuticle; in, intestine; m1, jugal protractor muscle of odontophore; m2, jugal retractor muscle of odontophore; m3, superficial circular muscle; m4, main dorsal tensor muscle of radula; m5, accessory dorsal tensor muscle of radula; m7, muscle running inside radular sac; m10, protractor muscle of odontophore; mj, jaw muscle; mo, mouth; mt and mt2, transversal superficial muscle; oa, opening of the duct of the acid gland; oe, oesophagus; ra, radula; rs, radula sac; sd, salivary duct; sg, salivary gland; so, opening of the duct of the salivary gland in the oral membrane; st, stomach.

Pleurobranchaea hedgpethi hamva—Er. Marcus, 1961: 141.

? *Pleurobranchaea bonnieae* Ev. Marcus & Gosliner, 1984: 29; figs 1D, 13–14.

Material examined: Brazil: Sergipe state: CMPHRM 676A, 10°42′40″S, 36°18′30″W, 01/ix/1965, 111 m depth [1]; Bahia state: MNRJ 18227, Caravelas, iv/2009 [7; 2 dissected]; Rio de Janeiro state: MZSP 37150, Arraial do Cabo [2]; MNRJ 18212, Baia de Ilha Grande, 19/ii/2006 [4; 1 dissected]; MZSP 32244, Bacia de Campos, 22°59′54″S, 41°51′54″N, 61 m depth [1]; MZSP 32239, Bacia de Campos, 26 m depth [1]; MZSP 29735, Angra dos Reis [2]; São Paulo state: MNRJ 30558, Baia de São Vicente, x/1998 [6; 2 dissected]; MZSP 104842, Baia de São Vicente, x/1998, 10–15 m depth [27; 1 dissected]; MZSP 34857, São Sebastião [6]; MZSP 100486, São Sebastião [1]; MZSP 61560, Praia Grande, Boqueirão, i/1984 [32]; MZSP 75504, Cananéia, 1953 [2]; MZSP 90723, Caraguatatuba [1]; MZSP 34586, Caraguatatuba [1]; MZSP 34856, Caraguatatuba, 22/iv/2001, 45 m depth [1]; MZSP 25344, Santos, Praia do Embaré [1]; MZSP 103296, Pedra da Baleia, Praia do Segredo, 20–21/i/2012 [1]; Santa Catarina state: MZSP 101761, Pontal da Daniela, Florianópolis [4]; Rio grande do Sul state: MZSP 86010 [1]; MZSP 50611, 24/i/1972 [1; 1 dissected].

Diagnosis: Foot translucent white with spur dark brown; seminal receptacle slightly bilobed, difficult to distinguish, appearing as an enlarged portion of duct (Fig. 1D, E); muscular vagina

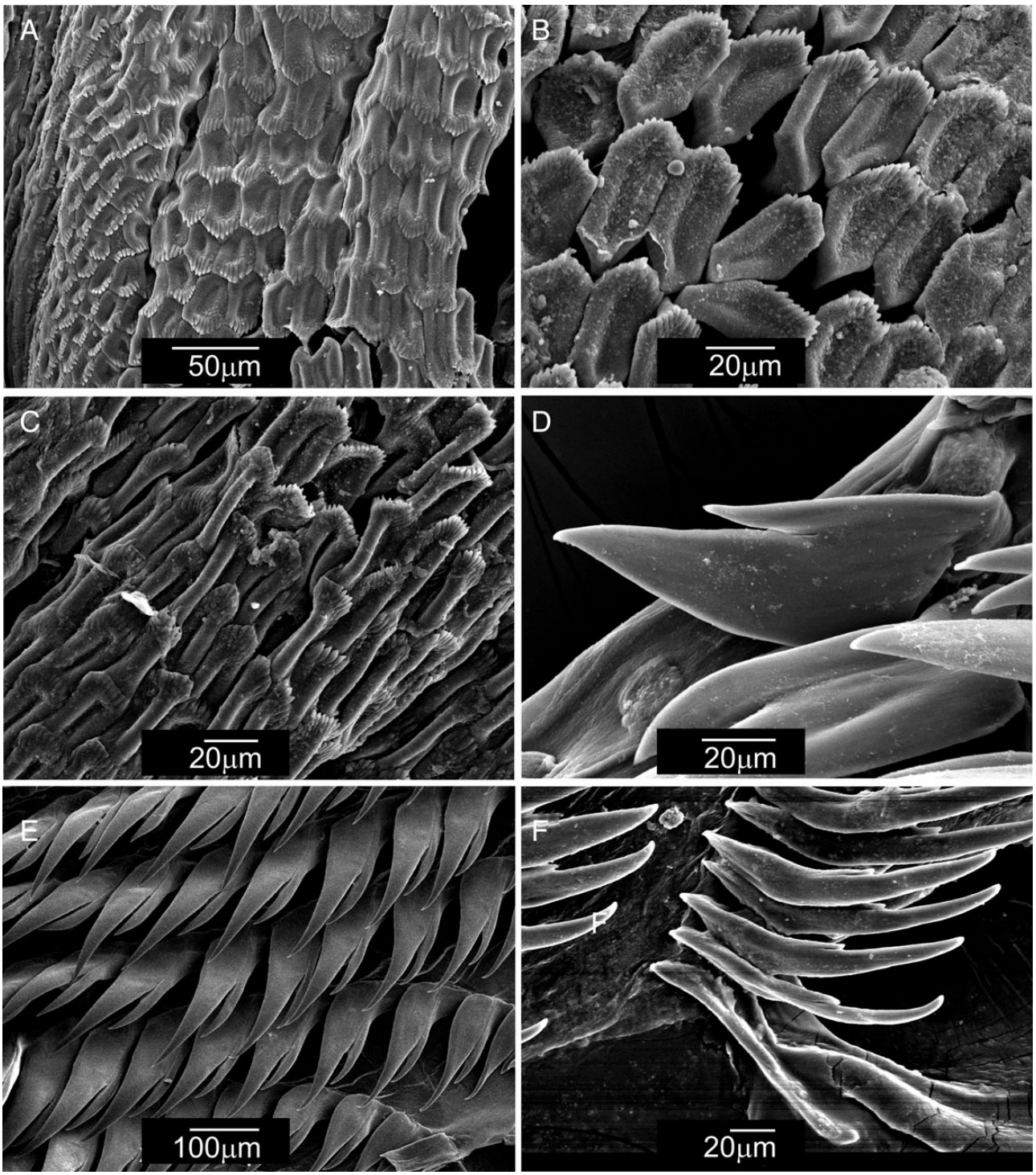

Figure 3. *Pleurobranchaea inconspicua*, SEM of radula and jaw. **A–C.** Jaw. **A.** Anterior portion. **B.** Median portion. **C.** Posterior portion. **D–F.** Radula. **D.** First lateral teeth. **E.** Lateral teeth. **F.** Marginal teeth. **A, F.** MNRJ 30558. **B, C, E.** MNRJ 18212. **D.** MNRJ 18227.

twisting before opening at female pore; cuticular stylet translucent white, coiling 10–11 times inside penial sac; cuticular stylet near deferent duct convex on one side and flattened on other, middle portion with an enlargement and both sides convex, sometimes oval (Fig. 4B, C), decreasing in width near terminal portion until final flat portion (Fig. 4D).

External morphology (Fig. 1A, B): Living specimens translucent white, with reticulate pattern of brown lines and white dots (Fig. 1A); rhinophores and gill translucent brown with some whitish stains; foot translucent white; spur dark brown. Preserved specimens entirely white, except for brown marks on rhinophores edges and reticulate brown pattern on dorsal portion of foot and brown pigment surrounding caudal spur. Length of preserved specimens 17.0–22.0 mm; width 10.0–12.0 mm; length of foot 13.0–18.0 mm, width of foot 7.0–11.0 mm. Body oval, elongated, anterior part and posterior tail rounded. Mantle reduced, not covering foot, tiny flap-like enlargement at end of gill (Fig. 1B). Mantle

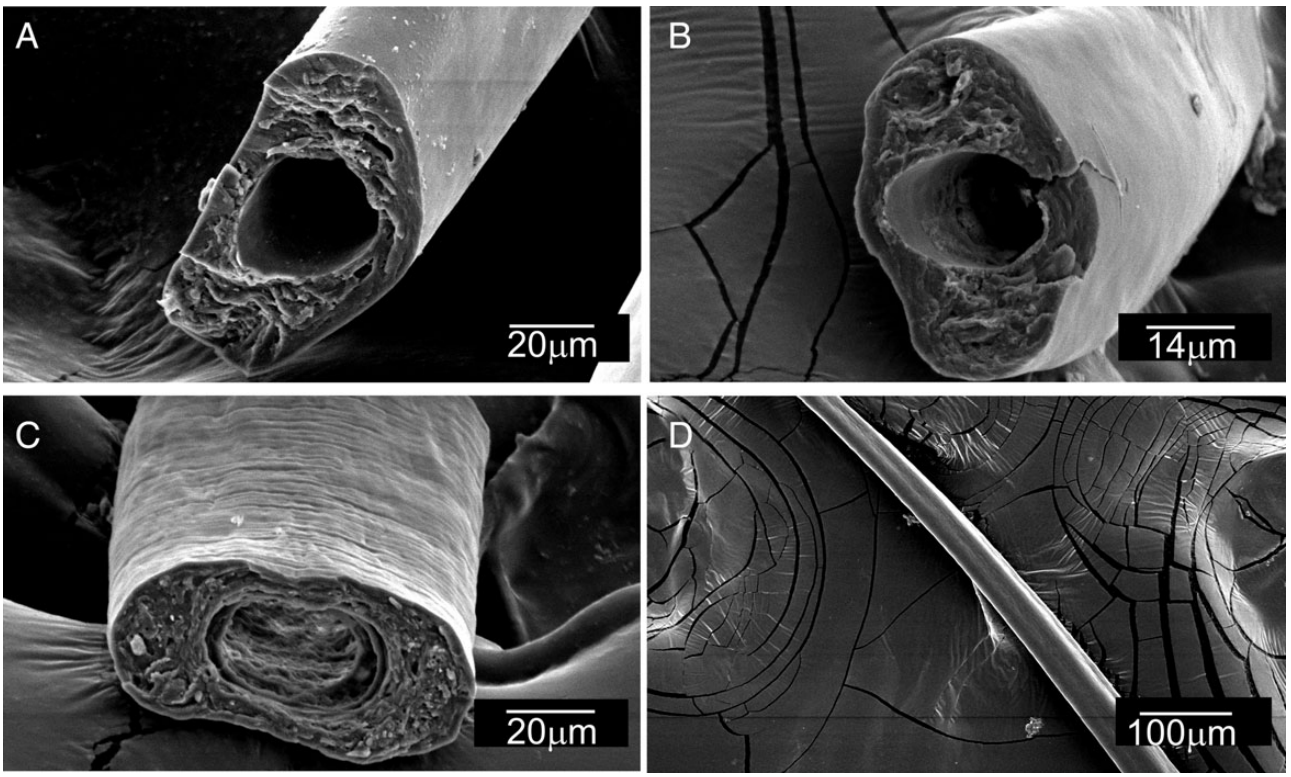

Figure 4. *Pleurobranchaea inconspicua*, SEM of cuticular stylet. **A**. Portion near deferent duct. **B, C.** Middle portion. **D.** Portion near gonopore. **A.** MNRJ 18212. **B, D.** MNRJ 30558. **C.** MNRJ 18227.

surface of preserved specimens smooth in centre; rounded protuberances on mantle edges, with white glandular appearance inside. Oral veil broad, thin, connected to head region; laterally, oral tentacles with deep notch (Fig. 1B); deep notch 0.3–0.5 times length of oral tentacle; several tiny rounded sensory papillae forming approximately two rows of warts on oral veil. Rhinophores rolled, separated. Gill exposed laterally; 0.4–0.6 times length of body (Fig. 1A, B); main rachis smooth, not tuberculate, with glandular tissue; small rounded tubercle on base of each pinnule forming zigzag line; unipinnate; gill with 20–26 pinnules; 7–10 pinnules free from body wall, attached only by branchial membrane. Anal opening always above sixth pinnule (Fig. 1B). Prebranchial pore opening approximately beside main rachis (Fig. 1B). Nephropore under first pinnule. Genital aperture surrounded by thin fold, forming triangular papilla near penial sheath (Fig. 1C). Penis large, cylindrical, sometimes projecting. Foot pointed to round at posterior end; anteriorly bilabiate, upper lip notched, smaller than lower one; metapodial gland posterior, elongated, 0.13–0.17 times foot length.

Circulatory system (Fig. 1C): Pericardium in right and middle parts of visceral sac. Heart under blood gland. Auricle usually much larger than ventricle, both rounded; auricle on right side, ventricle on left. Blood gland close to or joined to aorta; blood gland white, wide, covering left part of pericardium, slightly more anterior, in middle to left portion of body.

Digestive system (Figs 2, 3): Pharyngeal bulb of preserved specimens frequently slightly protruding, resembling a snout. Longitudinal mouth in middle of snout tip. Buccal mass large, muscular, with no distinct oral tube. Buccal and perioral muscles strong. Muscle surrounding jaws (mj) strong, pair of large jaws located in its inner surface, mj originating in lateral and dorsal surfaces of mouth, inserting into lateral and dorsal regions of buccal mass (Fig. 1A, C, D). Tiny tuberculated portion with whitish and black marks, representing labial cuticle anterior to jaws. Jaws pale yellow, of uniform colour; area between jaws white in anterior portion (where opening of duct of acid gland is located) (Fig. 2B), becoming blackish towards posterior portion, near to oesophagus; jaw of two plates surrounding radula inside buccal cavity (Fig. 2B). Jaws transversally elongated; reaching level of radula. Each jaw plate showing rows formed by elements from slightly rounded to slightly elongated (hand-shaped); anterior elements hand-shaped, with 5–11 denticles (Fig. 3A); each element flattened in median part, with thickened border along edge; tiny rounded protuberances on elements; median jaw elements slightly elongated, with same characteristics as others (Fig. 3B); elements more compressed laterally on posterior portion (Fig. 3C). Pair of jugal muscles m1 on dorsal side of buccal mass, inserting between m4 and m5 (Fig. 2A, D), connecting to anterodorsal end of snout. Pair of m2a originating from body wall, passing under pair m10d (Fig. 2A). Pair m10d a dorsal, longitudinal bundle, originating on anterodorsal extremity of snout, connecting to transversal muscle (mt) (Fig. 2A). Pair m4, main dorsal tensor muscle of radula, thin, short, originating in lateral region of cartilages, surrounding them ventrally, inserting into subradular membrane (Fig. 2C). Pair m5, secondary dorsal tensor muscle of radula, large, broad, covering almost entire surface of m4 and median portions of cartilage, extending up to dorsal region (Fig. 2A, C); originating in posterior surface of cartilages, inserting laterally in mj. Pair m7 related to radular sac (Fig. 2D, E), working like m11 as tensor ventral muscle of radula, long, narrow; m7l connected to oesophagus laterally, working like sphincter inside oral tube, joining radular sac. Horizontal muscle mt, connected to m10d on both sides (Fig. 2A); mt2 long, dorsal, divided into two transverse portions (Fig. 2E), connecting in part to both lateral portions of m5, passing under m4

and anterior region of oral membrane (Fig. 2D, E). Pair m3 originating in ventral region of radular sac, surrounding laterally m5 and inserting into mt2 (Fig. 2A, C, D). Pair m1v (ventral jugal muscles) connecting outer surface of m5 to anterior portion of snout (Fig. 2C). Pair m10v inserting in posterior portion of m4. Odontophore cartilage ear-shaped to slightly square (Fig. 2F). Radula purplish-black; formula 30 × 41.0.41 (from preserved specimen 19.0 mm length) and 27 × 45.0.45 (from preserved specimen 11.0 mm length). Rachidian tooth absent. Innermost lateral tooth bicuspid, smaller than other teeth, its smaller cusp slightly rounded (Fig. 3D). Lateral teeth bicuspidate, straight, taller in centre (Fig. 3E). Marginal teeth with tiny secondary cusps (Fig. 3F). Aperture of acid gland located between jaw plates (Fig. 2B). Acid gland wide, long, not convoluted, duct-like, passing within nerve ring, under right cerebropleural ganglion or slightly displaced under nerves of right cerebropleural ganglion (Fig. 2A); branching approximately above reproductive system; its ramifications surrounding digestives organs, penetrating among them; ramifications thin, elongated, usually well developed until posterior portion of digestive gland, sometimes restricted to anterior portion of digestive system near oesophagus. Anterior portion of oesophagus black; internally with longitudinal folds (Fig. 2B). Salivary gland in front of digestive gland, behind stomach (Fig. 2A). Ducts of salivary glands entering pharynx musculature laterally to oesophagus, opening into pharyngeal cavity between radula and jaw plates (Fig. 2A, B); distal to small ampullae, salivary ducts slightly convoluted. Posterior oesophagus flaccid, bulging, beige, of granular appearance; internally folded, with folds more concentrated dorsally. Posterior portion of oesophagus narrowing before entering stomach (Fig. 2B). Stomach curved; translucent beige with granular appearance. Intestine beneath salivary glands and hermaphrodite gland, forming a loop (Fig. 2A). Anus above sixth branchial filament. Salivary, digestive and hermaphrodite glands forming a single aggregate (Fig. 2A).

Reproductive system (Fig. 1D, E, 4): Hermaphrodite gland forming a layer (ventral, lateral) around digestive gland. Ampulla elongate, slightly convoluted (Fig. 1D, E). Spermoviduct branching into two ducts, thinner duct leading to prostate, other duct leading to seminal receptacle. Seminal receptacle slightly bilobed, difficult to distinguish, appearing as an enlarged portion of duct (Fig. 1D, E). Seminal receptacle connected with large, rounded bursa copulatrix by long, convoluted duct (Fig. 1E). Muscular vagina twisting before opening at female pore. Prostate flat, rounded. Deferent duct inserts ventrally into prostate (Fig. 1D, E); first half of deferent duct, sometimes folded, entering penial sac; second half densely convoluted inside penial sac (Fig. 1D, E), passing through posterior portion of penis retractor muscle. Translucent white cuticular stylet, coiling 10–11 times inside penial sac. Cuticular stylet changing in shape and size along its length (Fig. 4); near deferent duct it is convex on one side and flattened on other (height 75–80 μm; width 53–60 μm; Fig. 4A); middle portion with an enlargement, both sides convex (height 69 μm; width 81 μm), sometimes oval (Fig. 4B, C); decreasing in size near terminal portion (width 41 μm); decreasing in width close to gonopore until final flat portion (Fig. 4D). Penial sac attached to wall by retractor penis muscle.

Central nervous system (Fig. 1F): Cerebral and pleural ganglia fused, rhinophoral and optical nerves emerging from anterior protuberance. Nerves leaving cerebropleural ganglia, in anteroposterior order: cp1 bifurcating near origin into anterior branch (cp1a) innervating muscles of snout, posterior branch (cp1b) inserting into dorsal side of snout wall; cp2 bifurcating near base, anterior branch (cp2a) inserting into body wall in direction of velum; posterior branch (cp2b) connecting to lateroventral side of buccal mass; cp3 innervating lateroventral side of body wall; rhinophoral nerve (rn) emerging from protuberance of middle/dorsal part of cerebropleural ganglia, inserting into rhinophoral ganglia. Rhinophoral ganglia small, spherical, bearing two main branched nerves; optical nerves (no) running directly to large black eyes, very long and thin; cp4 optical motor ocular nerve, parallel to optical nerves, branching into tissue around eyes; cerebropleural ganglion connected with pedal ganglion (ccpp) by two connectives; one connective leaves cerebropleural ganglia in anteroventral position, shortly after ccpp, connecting cerebropleural ganglion with buccal ganglion (ccpb). Left and right sides of nerves that leave from cerebropleural ganglia differ. Left side with cp5l that bifurcates near origin, cp5la connecting cerebropleural ganglia with middle portion of notum, just above ramifications of acid gland; cp5lb innervating ramifications of acid gland. Right nerves in anteroposterior order: cp5r leading to visceral ganglion; cp6r, bifurcating near reproductive system into cp6ra inserting into lateral wall of body and cp6rb running into lateroventral portion of body wall and bifurcating (one branch inserting into wall, other running into branchial ganglion). Visceral ganglion bearing three nerves: nv1 in base of penial sac; nv2 and nv3 connecting to buccal bulb. Pedal ganglia almost as large as cerebropleural ganglia, situated near lateral body wall. Pedal nerves in anteroposterior order: np1 innervating anteriorly laterodorsal portion of body, bifurcating; np2 connecting to lateroventral body wall; np3 inserting mediolaterally into body wall; np4 innervating laterally median portion of body wall, with statocyst at its base. Near cerebropleural-pedal connective: np5 leading to genital ganglion. Genital ganglion with four nerves: ng1 running in body wall near gonopore; ng2 branching into many nerves at base of penial sac; ng3 inserting into middle of penial sac near prostate; destination of ng4 not known. Buccal ganglia small, surrounded by translucent tissue, with many thin nerves: nb1 inserting into oesophagus; nb2 innervating salivary glands; nb3 connecting with m4; nb4 inserting into mt2.

Distribution: Northwest Atlantic Ocean: Cape Hatteras, North Carolina (Er. Marcus, 1961); Port Aransas, Texas (Abbott, 1952); Sapelo Island, Georgia (Ev. Marcus & Er. Marcus, 1967a); 27°N, 80°W, Florida (Ev. Marcus & Gosliner, 1984). Southwest Atlantic Ocean: Colombia (Ardila & Rachello, 2004; Muniaín *et al*., 2007); Surinam (Nijssen-Meyer, 1965); Brazil: Ceara state to Rio Grande do Sul state (Rios, 1985); Sergipe state (Bergh, 1897); Rio de Janeiro state (Ev. Marcus & Er. Marcus, 1967b); São Paulo state (Er. Marcus, 1961): Ilhabela (Ev. Marcus & Er. Marcus, 1957); Argentina (Ev. Marcus & Er. Marcus, 1969; Ev. Marcus, 1972; Muniaín *et al*., 2007). A record from Mediterranean Sea, Israel (Ev. Marcus & Gosliner, 1984), requires verification.

Remarks: Bergh (1897) described *P. inconspicua* based on only one preserved specimen from Sergipe state, Brazil. Subsequently, the name was cited in several checklists of Brazilian molluscs (Ihering, 1915; Ev. Marcus & Er. Marcus, 1964; Rios, 1994, 2009) and, before a revision by Ev. Marcus & Gosliner (1984), additional records were made under its junior synonyms. Muniaín *et al*. (2007) gave a redescription of *P. inconspicua* based on specimens from Colombia and Argentina, including SEM micrographs of hard structures and photos of living specimens.

Four species have been listed as synonyms of *P. inconspicua*: *P. hedgpethi*, *P. hamva*, *P. bonnieae* and *P. gela* (Muniaín *et al*., 2007). However, we consider that *P. gela* is a valid species (see below).

Pleurobranchaea hedgpethi Abbott, 1952 has long been listed as a junior synonym (Ev. Marcus & Er. Marcus, 1960; Nijssen-Meyer, 1965; Ev. Marcus & Er. Marcus, 1967a; Ev. Marcus & Er. Marcus, 1969; Ev. Marcus, 1972; Abbott, 1974; Ev. Marcus,

1979), but it was described only briefly. Er. Marcus (1961) considered *P. hamva* Ev. Marcus & Er. Marcus, 1957 as a subspecies of *P. hedgpethi*, because of the shape of the spermatheca, although this could vary according to its degree of filling; the unique difference between these two subspecies was said to be the direction of the flap above the genital aperture. However, Ev. Marcus & Er. Marcus (1967a) abandoned a special designation for specimens with a dorsally directed flap, consequently considering *P. hamva* as a junior synonym of *P. hedgpethi*.

Ev. Marcus & Er. Marcus (1957) gave an extensive description of *P. hamva*, which includes features of the buccal apparatus. We found one specimen in lot MZSP 75504, of which the label reads 'Cananeia, Sao Paulo state, Brazil, 1953'. This matches the date and locality given by Ev. Marcus & Er. Marcus (1957: 25) and we thus conclude that this specimen is part of the type series examined by Ev. Marcus & Er. Marcus (1957). Comparison of the specimens studied here with the illustrations by Ev. Marcus & Er. Marcus (1957: 47; figs 44–46) revealed some differences, such as in the position of the aperture of the acid gland. This aperture is positioned approximately in the middle of the jaw muscle (mj) or a little posteriorly (Figs 1C, 2A), rather than in the anterior portion of the jaw muscle,

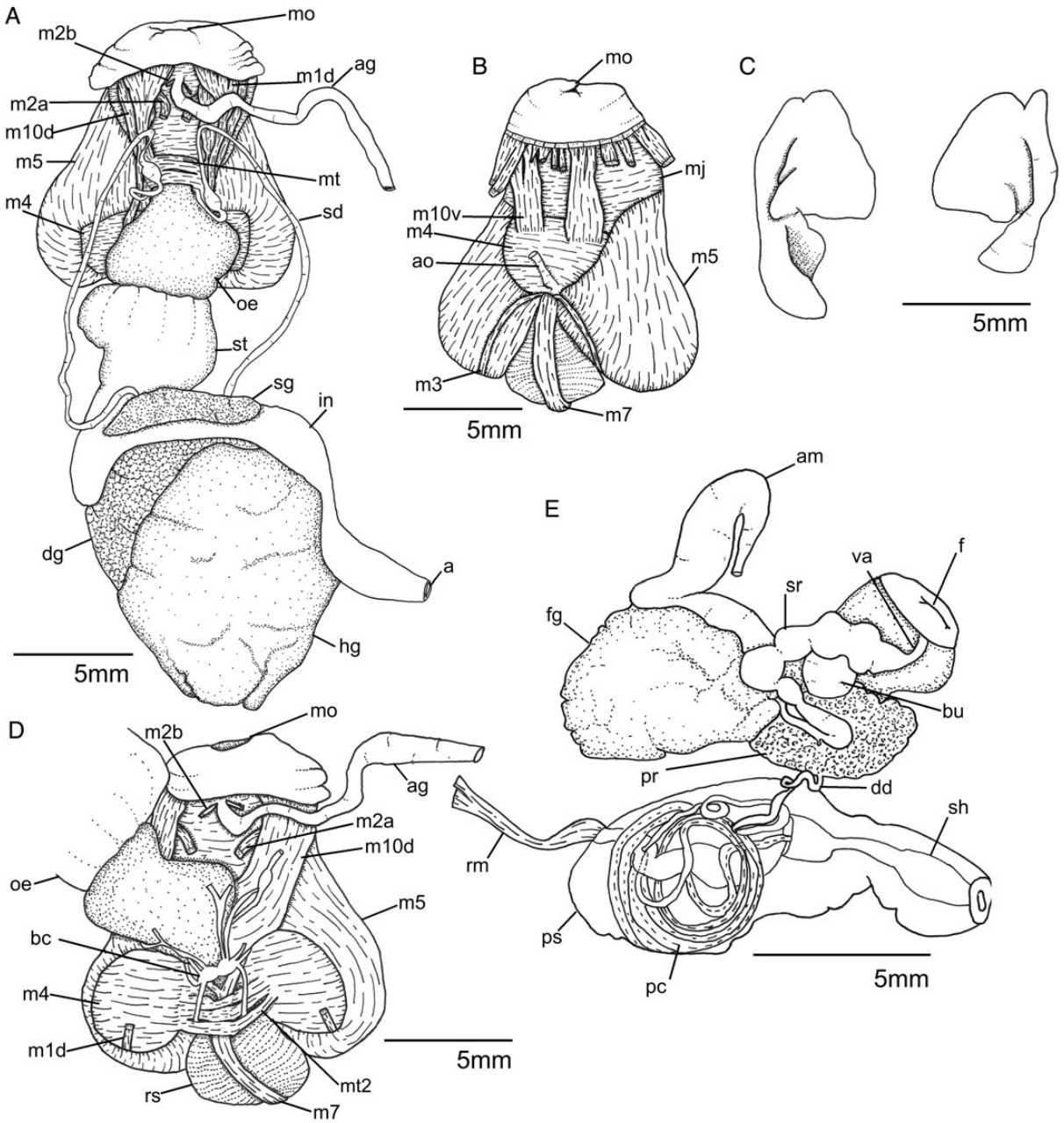

Figure 5. *Pleurobranchaea gela*, internal anatomy (MZSP 75368). **A.** Digestive system as *in situ*, dorsal view. **B.** Buccal mass, ventral view. **C.** Odontophoral cartilages. **D.** Buccal mass, dorsal view, oesophagus deflected. **E.** Reproductive system deflected. Abbreviations: a, anus; ag, duct of acid gland; am, ampulla; ao, aorta; bc, buccal ganglion; bu, bursa copulatrix; dd, deferent duct; dg, digestive gland; f, female opening; fg, female gland; hg, hermaphrodite gland; in, intestine; m1, jugal protractor muscle of odontophore; m2, jugal retractor muscle of odontophore; m3, superficial circular muscle; m4, main dorsal tensor muscle of radula; m5, accessory dorsal tensor muscle of radula; m7, muscle running inside radular sac; m10, protractor muscle of odontophore; mj, jaw muscle; mo, mouth; mt and mt2, transversal superficial muscle; oe, oesophagus; pc, penis (cuticular stylet); pr, prostate; ps, penial sac; rm, retractor muscle; rs, radular sac; sd, salivary duct; sg, salivary gland; sh, penial sheath; sr, seminal receptacle; st, stomach; va, vagina.

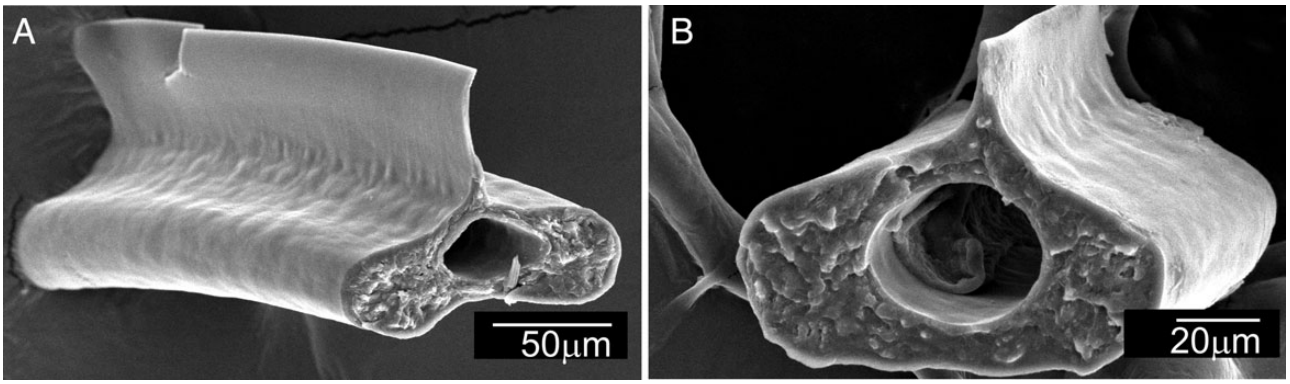

Figure 6. *Pleurobranchaea gela* (MZSP 75368), SEM of cuticular stylet. **A.** Portion near deferent duct. **B.** Median portion.

almost reaching the mouth, as figured by Ev. Marcus & Er. Marcus (1957). Ev. Marcus & Er. Marcus (1957) used a different terminology for the odontophore muscles: the muscle they numbered as 6 and 10 are herein termed m3 and m1v. However, the muscle we name m3 is only partially what Ev. Marcus & Er. Marcus (1957) named 6 and 10, because m3 originates ventrally in m7, near the radular sac, surrounds m5 laterally and inserts on mt2 (Fig. 2C). The other portion of muscle 6, which originates ventrally in mo and surrounds m5, is termed m1v here. This portion inserts in m5 (Fig. 2C). This discrepancy in the pattern of muscles is likely to be attributable to an error by Ev. Marcus & Er. Marcus (1957); we suggest that in their figure 44, the numbers 6 and 10 have been exchanged; if so, the description and illustration by Ev. Marcus & Er. Marcus (1957) fit our description of *P. inconspicua*, confirming that *P. hamva* and *P. hedgpethi* are junior synonyms of *P. inconspicua*.

Ev. Marcus & Gosliner (1984: 9; fig. 1B) described the cuticular stylet of *P. inconspicua* as ovoid in transverse section, with a flattened margin on one side; however, the illustration provided shows that the margin is in fact slightly concave. We examined different portions of the cuticular stylet and found that shape and size change along its length; the cuticular stylet is first convex on one side and flattened on the other, then convex on both sides, then oval and finally flattened in section.

Pleurobranchaea bonnieae is a junior synonym of *P. inconspicua* according to Valdés *et al.* (2006) and Muniaín *et al.* (2007). However, the illustration of *P. bonnieae* by Ev. Marcus & Gosliner (1984: 9; fig. 1D) shows differences from the cuticular stylet observed in *P. inconspicua* in the present study, because the concave portion is very accentuated. The species was described based on only one specimen, which was probably a juvenile, from Florida. Hence, it is impossible to infer the extent of intraspecific variation and whether or not it is a synonym of *P. inconspicua*.

The specimens of *P. inconspicua* studied here agree with previous descriptions of radula and jaws of the genus *Pleurobranchaea* and they have the same number of rows previously described for this species. However, we found fewer teeth (41–45) per row than reported in previous descriptions (50–72 teeth; Bergh, 1897; Ev. Marcus & Er. Marcus, 1957, 1960, 1967b, 1969; Er. Marcus, 1961; Ev. Marcus, 1972; Ev. Marcus & Gosliner, 1984; Muniaín *et al.*, 2007).

Pleurobranchaea gela Ev. Marcus & Er. Marcus, 1966.
(Figs 5, 6)

Pleurobranchaea gela Ev. Marcus & Er. Marcus, 1966: 174; figs 35–37 (syntypes USNM 576245, 4°40′N, 2°00′W to 4°39′N, 2°02′W, 28/v/1964; USNM 576246, 4°57′N, 1°16′W to 4°59′N, 1°16′W, 28/v/1964; USNM 576247, 5°02.5′N, 3°49.5′W to 5°05′N, 3°52′W, 30/v/1964; USNM 576248, 5°07′N, 4°32′W to 5°07′N, 4°36′W, 30/v/1964; USNM 576249, 5°04.5′N, 4°51.5′W, 31/v/1964; USNM 576250, 5°05′N, 4°59.5′W, 31/v/1964; USNM 576251, 4°45′N, 6°13.5′W to 4°44′N, 6°16′W, 01/vi/1964; USNM 576252, 4°35′N, 5°18′E to 4°34′N, 5°19′E, 13/v/1965).

Material examined: Ivory Coast: Grand Bassam: MZSP 75368, 29/ix/1966 [1], 19/x/1967 [7; 4 dissected].

Diagnosis: Black foot sole with light border; m2b thin (Fig. 5A, D); pair m10v inserts in anterior portion of m4 (Fig. 5B); odontophore cartilage triangular with a lateral extension (Fig. 5C); oesophagus beige; cuticular stylet translucent, coiling five to six times inside penial sac; thin, well-developed crest along its cuticular stylet, which decreases in size as it approaches the gonopore (Fig. 6).

Description: Pleurobranchaea gela is very similar to *P. inconspicua* in all investigated organ systems, therefore only differences are given in the following description.

External morphology:Colour of living specimens not observed. Length of preserved specimens 21.0–29.0 mm; width 10.0–21.0 mm; length of foot 15.0–22.0 mm, width of foot 7.0–16.0 mm. Deep notch in apical third of oral tentacles. Gill exposed laterally; 1/2 length of body; main rachis tuberculate; small rounded tubercles on base of pinnules forming zigzag line; gill with 18–26 pinnules; 4–8 pinnules free from body wall, attached only by branchial membrane. Anal opening above sixth or seventh pinnule (Fig. 1B). Nephropore under fourth to fifth pinnule. Metapodial gland posterior, elongated, 0.1 times foot length.

Digestive system (Fig. 5A–D): Anterior borders of jaw and radula plates sometimes visible. Labial cuticle beige with tiny tubercles. Jaws yellowish cream; area between jaws cream in anterior portion. Each jaw plate showing rows formed by polygonal elements ranging from slightly rounded to slightly elongated. Anterior elements of jaws with 8–14 denticles. Two pairs of jugal muscles m2; m2a originating from body wall, passing beside pair m10d; m2b very thin, inserting laterally into mj on sides of duct of acid gland, located in middle of buccal mass (Fig. 5A, D). Pair m1v absent (Fig. 5B). Pair m10v inserts in anterior portion of m4 (Fig. 5B). Transverse muscle mt2 long, dorsal, divided into three transverse portions (Fig. 5D). Odontophore cartilage triangular, with lateral extension longer than triangular portion (Fig. 5C). Radula formula 42 × 57.0.57 (preserved specimen 21.0 mm long). Ramification of acid gland thin, elongated, not well developed. Oesophagus beige; longitudinal folds internally, with transversal ribs.

Reproductive system (Fig. 5E, 6): Seminal receptacle bilobed or trilobed. First quarter of deferent duct initially in visceral cavity,

sometimes folded before entering penial sac. Small, rounded bursa copulatrix. Cuticular stylet translucent purple, coiling five to six times inside penial sac (Fig. 5E); changing in shape and size along its length: near deferent duct convex on both sides, with a crest on one side (height 98 μm; width 124 μm; Fig. 6A); middle portion convex on both sides with well-developed crest (height 80 μm; width 106 μm; Fig. 6B); in final portion crest decreasing in size near gonopore (height 52 μm; width 102 μm).

Central nervous system (Fig. 1F): Cerebropleural ganglia: cp5l leading to lateroposterior part of body; cp6l innervating lateral and ventrolateral wall of body.

Distribution: Nigeria to Ivory Coast (Ev. Marcus & Er. Marcus, 1966; Er. Marcus & Ev. Marcus, 1968).

Remarks: Pleurobranchaea gela Ev. Marcus & Er. Marcus, 1966 was described based on 55 specimens from Ivory Coast to Nigeria. Ev. Marcus & Gosliner (1984) suggested that the differences in the seminal receptacle that distinguish *P. gela* from *P. inconspicua* are a result of differences in their state of contraction and therefore placed *P. gela* in synonymy. However, Ev. Marcus & Gosliner (1984) overlooked differences in external morphology that were given in the original description of *P. gela*. It was described with a black foot sole with light border and a veil with a single row of warts, whereas *P. inconspicua* has a translucent foot sole (Muniaín *et al*., 2007) and a slightly serrated veil with two rows of warts (Ev. Marcus & Er. Marcus, 1957; present study).

Additionally, our anatomical study, based on the specimens of *P. gela* utilized by Er. Marcus & Ev. Marcus (1968) from the Ivory Coast, revealed additional differences, mainly in the odontophore muscles (Table 1). Muscle pair m2b is present but very thin in *P. gela*, whereas m2b is absent in *P. inconspicua* (Fig. 2A); muscle pair m1v is present in *P. inconspicua*, but not in *P. gela* (Fig. 2A); the pair m10v inserts in the anterior portion of m4 in *P. gela* (Fig. 5B), but in the posterior portion of m4 in *P. inconspicua* (Fig. 2C); mt2 is divided into three parts in *P. gela* (Fig. 5D) and two parts in *P. inconspicua* (Fig. 2D). The odontophore cartilage of *P. gela* is triangular with a lateral extension (Fig. 5C), whereas in *P. inconspicua* it is ear-shaped to slightly square (Fig. 2F). The oesophagus is beige in *P. gela* and purplish-black in *P. inconspicua*. The cuticular stylet coils 10–11

Table 1. Comparison among *Pleurobranchaea inconspicua*, *P. gela* and *P. spiroporphyra* n. sp.

	Pleurobranchaea gela Ev. Marcus & Er. Marcus, 1966	*Pleurobranchaea inconspicua* Bergh, 1897	*Pleurobranchaea spiroporphyra* n. sp.
Position of nephropore	Between branchial leaves 4 and 5, usually under leaf 5	Under branchial leaf 1	Under branchial leaf 2
Colour of foot	Black	Translucent white	–
m2b	Present, very thin	Absent	Present
m2a	Present, inserts in mj beside m10	Present, inserts in mj under m10	Present, inserts in mj under m10
m1v	Absent	Present	Absent
m10v	Inserts in anterior portion of m4	Inserts in posterior portion of m4	Bifurcated, one portion inserts in anterior portion of m4 and other in posterior portion of m4
mt2	Divided into three transverse portions	Divided into two transverse portions	Divided into two transverse portions
Elements of jaw	Flattened	Flattened in middle with thickened border	Flattened
Shape of odontophore	Triangular with lateral extension longer than triangular portion	Ear-shaped to slightly square	Ear-shaped
Colour of jaw	Yellow	Yellow	Orange
Colour of oesophagus	Beige	Purplish-black	Purplish-black
Internal surface of oesophagus	Longitudinal folds with transverse crests	Longitudinal folds with transverse crests	Longitudinal folds with rugose (amorphous) appearance
Acid gland	Slightly ramified	Densely ramified	Densely ramified
Opening of duct of salivary gland	Into base to middle portion of oral membrane	Into base of oral membrane	Into apical portion of oral membrane
Colour of cuticular stylet	Translucent, not visible by transparency	Translucent, not visible by transparency	Purple, visible by transparency
Different sizes along cuticular stylet (average per portion in μm)	Near deferent duct: height 98, width 124; median portion: height 80, width 106; near gonopore: height 52, width 102	Near deferent duct: height 77.5, width 56.5; median portion: height 69, width 81; near gonopore: width 32	Near deferent duct: height 39, width 65; median portion: height 52, width 93.5; near gonopore: width 26.75
Number of turns of cuticular stylet	5–6	10–11	12–14
Final portion of cuticular stylet	With rib	Without rib	With rib
Seminal receptacle	Bilobed or trilobed	Bilobed	Many enlargements
Pedal ganglia: nerves in anterior portion	np1 and np2	np1 and np2	np1, np2 and np3
Statocyst	Not seen	Posterior, near np5	Anterior, at base of np1
Cerebropleural ganglia: nerves after pedal commissure	cp5l and cp6l	cp5l (bifurcates into cp5la and cp5lb)	cp5l, cp6l and cp7l

Some information on *P. gela* was taken from Ev. Marcus & Er. Marcus (1966). Measurements in mm.

–, No data available in literature.

times in *P. inconspicua* and 5–6 times in *P. gela*. The latter species always has a thin, well-developed crest along its cuticular stylet, which decreases in size as it approaches the gonopore (Fig. 6); *P. inconspicua* lacks this thin crest (Fig. 4). Ev. Marcus & Er. Marcus (1966) noted that the renal pore of *P. gela* lies under the second pinnule; however, we identified some variation in this character, with the renal pore lying between pinnules four to six in eight of the specimens we examined. In six of these eight individuals, the renal pore lies under the 5th pinnule.

Based on the differences mentioned above, we consider that *P. inconspicua* and *P. gela* are two valid species.

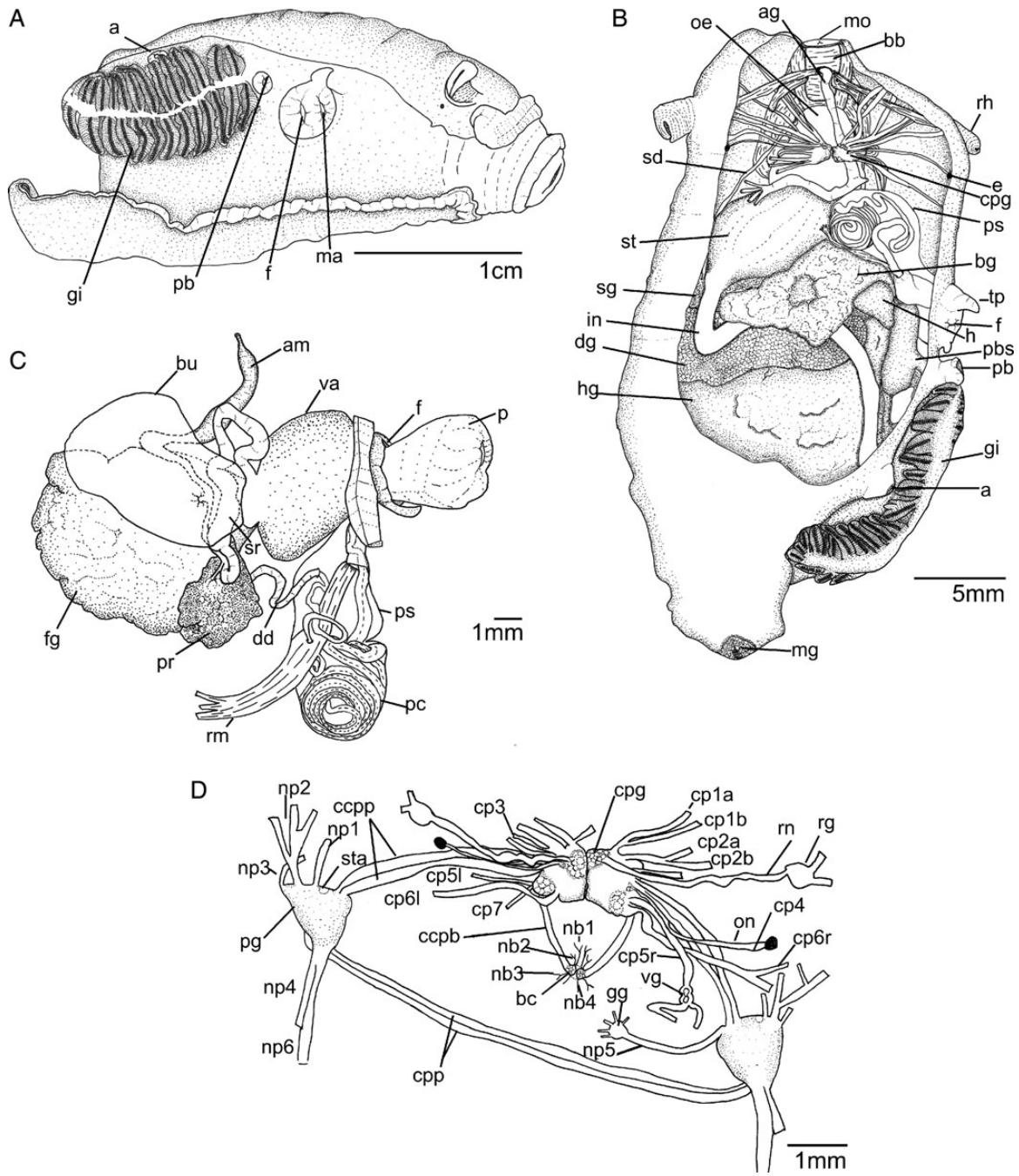

Figure 7. *Pleurobranchaea spiroporphyra* n. sp. (MNRJ HSL7459). **A.** Lateral view, preserved specimen. **B.** Dorsal view, organization of internal organs. **C.** Reproductive system deflected. **D.** Nervous system. Abbreviations: a, anus; ag, duct of acid gland; am, ampulla; bb, buccal bulb; bc, buccal ganglion; bg, blood gland; bu, bursa copulatrix; ccpb, connective between the buccal and cerebropleural ganglia; ccpp, connective between the pedal and cerebropleural ganglia; cp, nerves that leave from the cerebropleural ganglion; cpg, cerebropleural ganglion; cpp, commissure between pedal ganglia; dd, deferent duct; dg, digestive gland; e, eye; f, female opening; fg, female gland; gi, gill; gg, genital ganglion; h, heart; hg, hermaphrodite gland; in, intestine; ma, male opening; mg, metapodial gland; mo, mouth; nb, nerves that leave from the buccal ganglion; np, nerves that leave from the pedal ganglion; oe, oesophagus; on, optical nerve; p, penial papilla; pb, prebranchial aperture; pbs, prebranchial sac; pc, penis (cuticular stylet); pg, pedal ganglion; pr, prostate; ps, penial sac; rg, rhinophoral ganglion; rh, rhinophore; rm, retractor muscle; rn, rhinophoral nerve; sd, salivary duct; sg, salivary gland; sr, seminal receptacle; st, stomach; sta, statocyst; tp, triangular papilla near gonopore; va, vagina; vg, visceral ganglion.

***Pleurobranchaea spiroporphyra* new species**
(Figs 7–10)

Types: Holotype MNRJ 32781, Ponta do Caju (22°53′S; 43°10′W), Baia de Guanabara, Rio de Janeiro state, Brazil, 22/ix/1955; Paratypes MNRJ HSL7459, from type locality [16; 6 dissected].

ZooBank registration: urn:lsid:zoobank.org:act 04844325-8403-47A8-9724-986BF15C3079.

Etymology: spiro, Greek coil; *porphyra*, Greek purple, after the coiled purple penial cuticular stylet that is the most striking feature of this species.

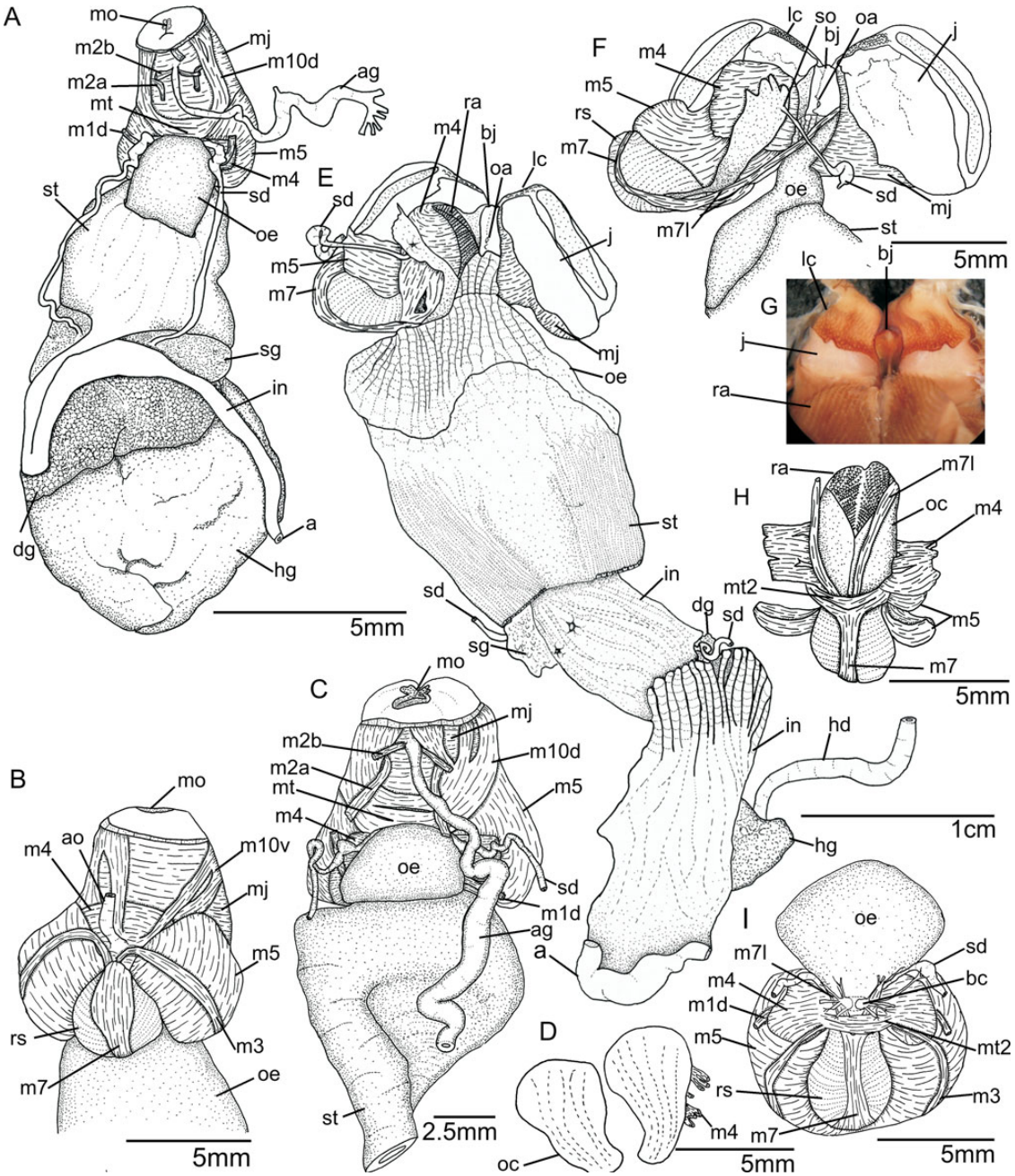

Figure 8. *Pleurobranchaea spiroporphyra* n. sp. (MNRJ HSL7459), digestive system. **A.** Dorsal view as *in situ*. **B.** Buccal mass, ventral view. **C.** Buccal mass, dorsal view. **D.** Odontophoral cartilages. **E–G.** Digestive system opened ventrally. **F, G.** Detail near buccal bulb. **H.** Odontophore isolated, dorsal view. **I.** Dorsal view, oesophagus deflected. Abbreviations: a, anus; ag, duct of acid gland; ao, aorta; bc, buccal ganglion; bj, area between jaws; dg, digestive gland; hd, hermaphrodite duct; hg, hermaphrodite gland; j, jaw plates; lc, labial cuticle; in, intestine; m1, jugal protractor muscle of odontophore; m2, jugal retractor muscle of odontophore; m3, superficial circular muscle; m4, main dorsal tensor muscle of radula; m5, accessory dorsal tensor muscle of radula; m7, muscle running inside radular sac; m10, protractor muscle of odontophore; mj, jaw muscle; mo, mouth; mt and mt2, transversal superficial muscle; oa, opening of the duct of the acid gland; oc, odontophoral cartilage; oe, oesophagus; ra, radula; rs, radular sac; sd, salivary duct; sg, salivary gland; so, opening of duct of salivary gland in oral membrane; st, stomach.

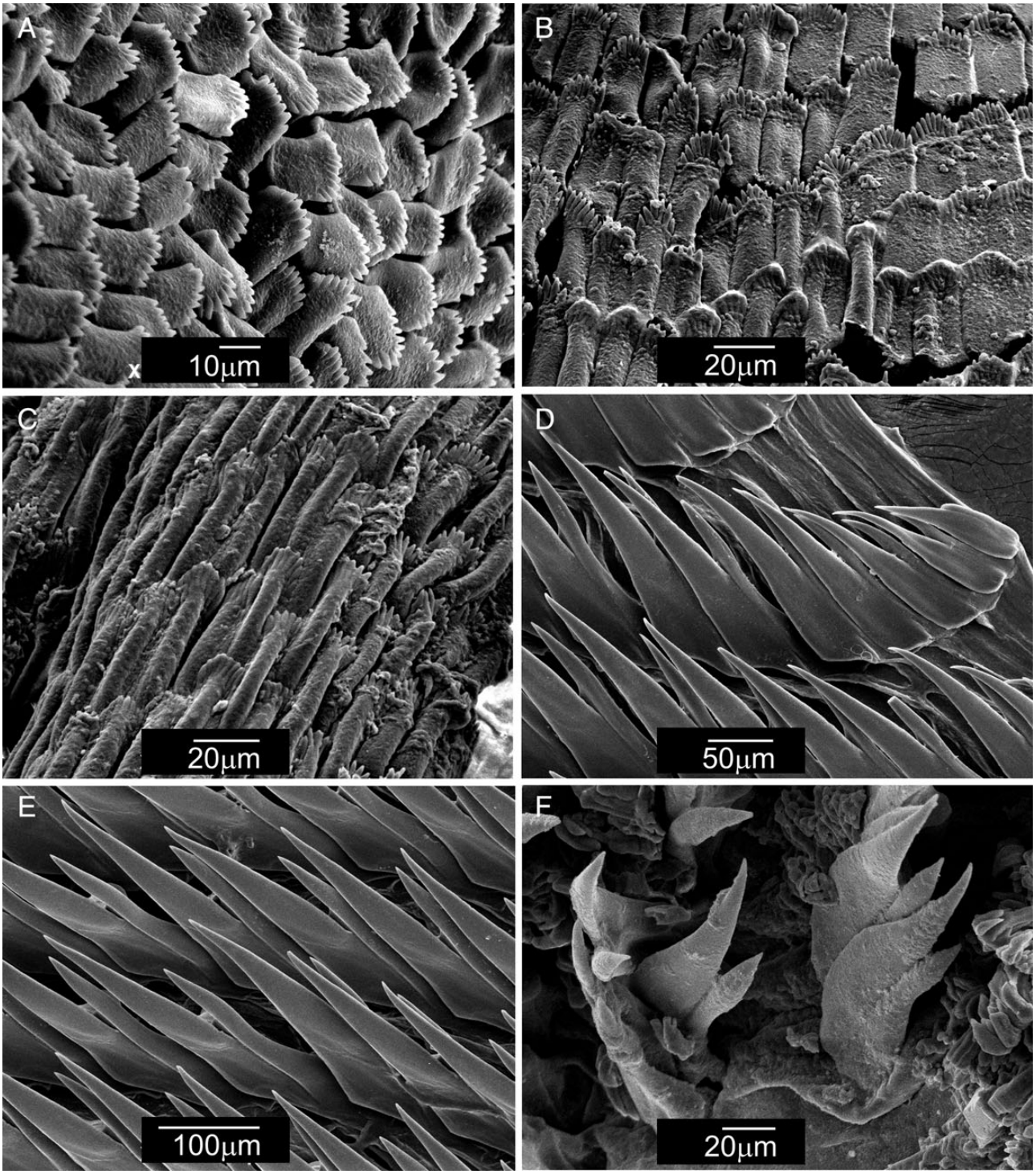

Figure 9. *Pleurobranchaea spiroporphyra* n. sp. (MNRJ HSL7459), SEM of radula and jaw. **A–C.** Jaw. **A.** Anterior portion. **B.** Median portion. **C.** Posterior portion. **D–F.** Radula. **D.** First lateral teeth. **E.** Lateral teeth. **F.** Marginal teeth.

Diagnosis: Labial disc orange (Fig. 8G); jaws pale orange, lighter posteriorly; m2b well developed; cuticular stylet purple, coiling 12–14 times inside penial sac, laterally flattened, with thin crest close to gonopore.

External morphology (Fig. 7A): Living specimens not observed. Preserved specimens: length 23.0–37.0 mm, width 10.0–17.0 mm; foot length 20.0–33.0 mm, width 14.0–7.0 mm; holotype 37.0 mm in length, 15.0 mm in width. Body oval, elongated, anterior part rounded, tapering to rounded tail (Fig. 7A). Mantle margin reduced, not covering foot, mantle with tiny flap at end of gill (Fig. 7A). Mantle surface smooth to rough. Oral veil broad, thin, connected to head region; deep notch in apical third or quarter of oral tentacles; several large

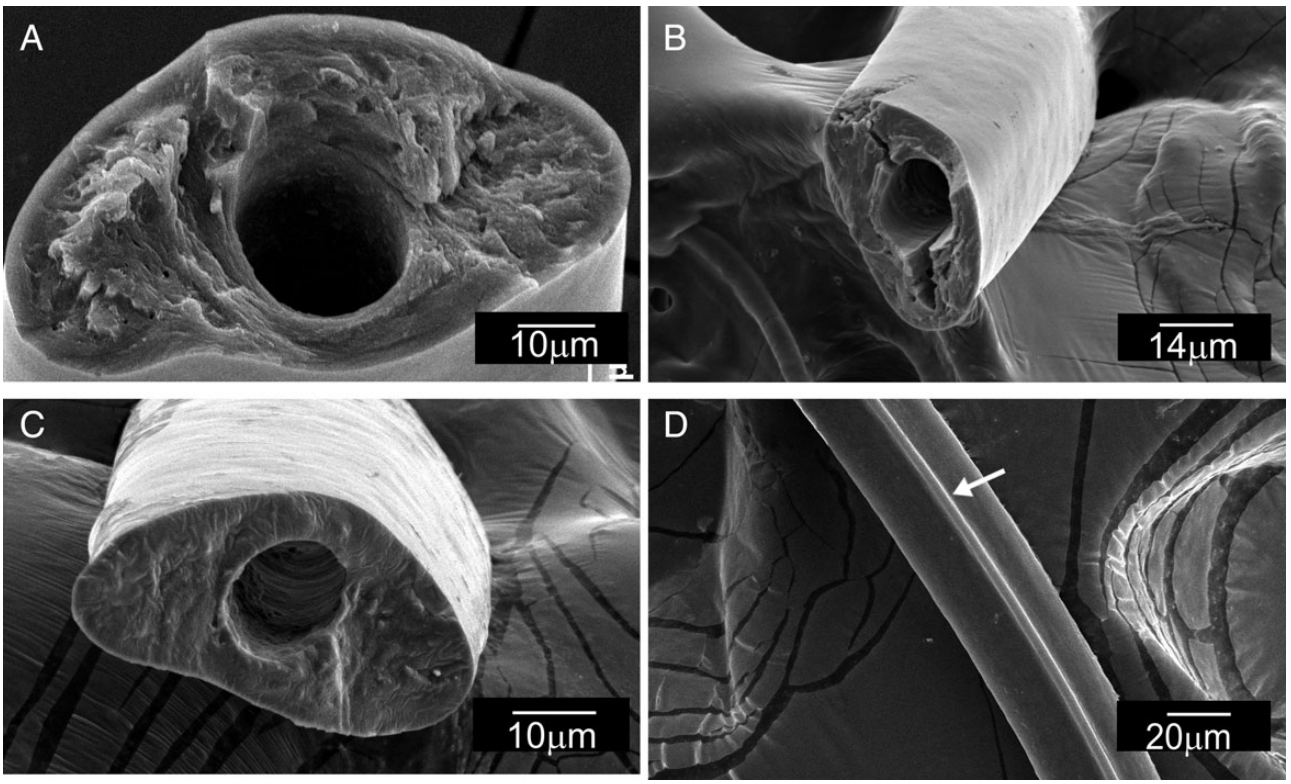

Figure 10. *Pleurobranchaea spiroporphyra* n. sp. (MNRJ HSL7459), SEM of cuticular stylet. **A.** Portion near deferent duct. **B, C.** Median portion. **D.** Portion near gonopore; white arrow indicates crest.

rounded sensory papillae forming one row of warts on oral veil. Rhinophores rolled, separated. Gill exposed laterally, mantle not entirely covering gill; gill 0.3–0.4 times length of body (Fig. 7A); main rachis with tubercles; small rounded tubercles on base of each plume forming zigzag line; unipinnate; gill with 17–23 pinnules; 9 pinnules free from body wall, attached only by branchial membrane. Anal opening above sixth pinnule (Fig. 7A). Prebranchial pore beside first pinnule (Fig. 7A). Nephropore under second pinnule. Genital aperture surrounded by thick fold, with dorsal triangular papilla (Fig. 7A). Penis large, cylindrical, sometimes protruding. Foot pointed or round at posterior end; anteriorly bilabiate, upper lip notched and smaller than lower; metapodial gland posterior, elongated, 0.2 times length of foot.

Circulatory system (Fig. 7B): Very similar to *P. inconspicua* as described above, with following exceptions. Heart lateral to blood gland. Auricle and ventricle approximately of same size. Blood gland cream; when small, then round and in middle of body.

Digestive system (Figs 8, 9): Very similar to *P. inconspicua* as described above, with following exceptions. Labial cuticle orange (Fig. 8G). Jaws pale orange, lighter posteriorly; area between jaws orange in anterior portion (where opening of duct of acid gland is located). Anterior jaw elements hand-shaped, with 5–14 denticles (Fig. 9A); tiny rounded protuberances on elements; jaw elements of median part slightly elongated (foot-shaped) without protuberances (Fig. 9B); elements more compressed laterally on posterior portion (Fig. 9C). Two pairs of jugal muscles m2; m2a originating from body wall, passing under pair m10d; m2b inserting laterally into mj on sides of duct of acid gland, located in middle of buccal mass (Fig. 8A, C). Pair m1v absent (Fig. 8B). Pair m10v bifurcated, one part inserts into anterior portion of m4 and other into posterior portion of m4. Radula formula 30 × 40.0.40 (preserved specimen 32.0 mm) and 32 × 44.0.44 (preserved specimen 37.0 mm). Radula golden brown, lacking rachidian teeth. Innermost lateral tooth bicuspid, smaller than other teeth, its smaller cusp slightly rounded (Fig. 9D). Lateral teeth bicuspid, straight, taller in centre (Fig. 9E). Marginal teeth with smaller cusps (Fig. 9F). Aperture of acid gland between jaw plates (Fig. 8F). Acid gland passing through nerve ring. Salivary ducts with small ampullae; ducts of salivary glands insert into pharynx more posteriorly than in *P. inconspicua*. Stomach with internal folds, sparser than in oesophagus.

Reproductive system (Fig. 7C, 10): Very similar to *P. inconspicua* as described above, with following exceptions. Seminal receptacle with many enlargements. Prostate large. First third of deferent duct with few folds free in visceral sac, before entering penial sac. Cuticular stylet purple, coiling 12–14 times inside penial sac (Fig. 7C); proximal and distal end orange-yellow; changing shape and size along its length; near deferent duct convex on both sides (height 39 µm; width 65 µm; Fig. 10A); in middle portion convex on one side and flattened or concave on the other (height 50–54 µm; width 85–102 µm; Fig. 10B, C); almost in terminal portion, cuticular stylet decreasing in size (height 27 µm; width 40 µm); flat in the last portion with a distinct crest (width 2528.5 µm; Fig. 10D). Male atrium can be everted.

Central nervous system (Fig. 7D): Central nervous system very similar to *P. inconspicua* described above, with following exceptions. Nerve cp5l leading to lateroposterior body; cp6l innervating lateral and lateroventral body wall; cp7l innervating most posterior portion of mantle. Visceral ganglion bearing two nerves that pass under reproductive system. Pedal ganglia

Table 2. Summary of diagnostic features of species of *Pleurobranchaea*.

	Gill	Pairs of gill pinnules	Gill attachment to body wall	Pedal gland	Caudal spur on dorsal surface of tail	Genital aperture	Denticles on jaw elements	
P. agassizii Bergh, 1897	–	32	–	–	Present	–	4–8	
P. augusta Ev. Marcus & Gosliner, 1984	Smooth	20	>0.8 of its length	Weak	Tiny spur	–	Up to 10	
P. brockii Bergh, 1897	May bear knob	30–40	–	Present or absent	Present or absent	Surrounded by circular fold with flaps	Irregular in number and size	
P. bubala Ev. Marcus & Gosliner, 1984	Smooth	26	–	Triangle of pedal gland	Absent	Protruding, with flap on hind border	4–14	
P. californica MacFarland, 1966	Smooth	50–55	$\frac{1}{2}$ > 0.5 of its length	Large, median	Present; irregular, low papillae near tip	–	2–10 small, short, irregular denticles	
P. catherinae Dayrat, 2001	Smooth	40	0.3 of its length	Present	Present	–	–	
P. gela Ev. Marcus & Er. Marcus, 1966	Smooth; alternate tiny knobs on rachis	18–27	$\frac{3}{4}$ > 0.75 of its length	Present	Present	With dorsal flap	10–16 or more	
P. inconspicua Bergh, 1897	Tuberculated	20–26	>0.7 of its length; 7–10 pinnules free from body wall	0.13–0.17 of foot length	Present	Surrounded by fold with triangular papilla	5–11	
P. japonica Thiele, 1925	Alternate knobs on rachis	24–32	–	Present	–	Small genital flap	6–12	
P. maculate (Quoy & Gaimard, 1832)	Main rachis with small, irregular knobs	20–28	$\frac{1}{2}$ > 0.5 of its length	0.7 of foot length	Absent	–	5–11	
P. meckeli Leue, 1813	Alternate knobs on rachis	23–25	>0.8 of its length; six pinnules free from body wall	Well developed	Present	Surrounded by thick fold	–	
P. morula Bergh, 1905	–	36	–	Absent	–	–	3–9	
P. obesa (Verrill, 1882)	Smooth	26–35	–	Present	Present	–	Variable number	
P. spiroporphyra n. sp.	Tuberculated	17–23	>0.7 of its length; nine pinnules free from the body wall	0.13–0.17 of foot length	Present	Surrounded by thick fold, with triangular papillae	5–14	
P. tarda Verrill, 1880	Tuberculated	20–30	–	Rarely developed	Short	With or without flap	–	
P. agassizii Bergh, 1897	32 × 98.0.98	Bicuspid	17 outermost teeth unicuspid	Noncuticularized penis	Deferent duct does not enter the penial sac, except where retractor muscle is attached to it	–	Gulf of Mexico; Florida; Great Bahama Bank	Bergh, 1897; Ev. Marcus & Gosliner, 1984

P. augusta Ev. Marcus & Gosliner, 1984	40 × 70.0.70	Bicuspid	Bicuspid, except for one to two outermost ones unicuspid	Cylindrical, with equally thick walls and sharp crest	Deferent duct winds upwards to and penetrates retractor muscle; together penis and sheath form six loops	Globular	West Africa	Ev. Marcus & Gosliner, 1984
P. brockii Bergh, 1897	40–48 × 65–90.0.65–90	Bicuspid	Sometimes unicuspid	Noncuticularized penis	Penial sac narrow	Coiled	Japan to South Africa	Ev. Marcus & Gosliner, 1984
P. bubala Ev. Marcus & Gosliner, 1984	35 × 100.0.100	Bicuspid	20–30 outermost teeth unicuspid	Similar to *P. tarda*	Penial sac wider in middle than *P. tarda* and less globular than *P. inconspicua*	Bilobed	South Coast of South Africa; Mozambique	Ev. Marcus & Gosliner, 1984
P. californica MacFarland, 1966	52 × 130–145.0–1.130–145	Bicuspid	Bicuspid	No change in diameter within penial sheath	Stylet translucent white; vas deferens makes numerous loops	Saccular enlargements	West coast of North America	MacFarland, 1966
P. catherinae Dayrat, 2001	90 × 45.0.45	Bicuspid	Bicuspid	–	Vas deferens coiled	As two pouches	Tropical Indo-Pacific	Dayrat, 2001
P. gela Ev. Marcus & Er. Marcus, 1966	37–40 × 53–70.0.53–70	Sometimes without a secondary cusp	Sometimes unicuspid	Thin but well-developed crest; in middle convex on one side and concave on other	Translucent white stylet coils five to six times inside penial sac	Trilobed	West Africa	Ev. Marcus & Er. Marcus, 1966; present study
P. inconspicua Bergh, 1897	27–40 × 41–68.0.41–68	Bicuspid	Tiny secondary cusp; unicuspid	Near deferent duct convex on one side and flattened on other; middle portion both sides convex or oval; terminal portion narrowed, flattened	Translucent white stylet coils 10–11 times inside penial sac	Slightly bilobed	Western Atlantic; Israel?	Ev. Marcus & Gosliner, 1984; present study
P. japonica Thiele, 1925	35–45 × 50–80.0–1.50–80	Bicuspid	20 outermost teeth; secondary cusp reduced to spine	–	Deferent duct not coiled	–	Japan; Korea	Tsubokawa, Willan & Okutani, 1992
P. maculate (Quoy & Gaimard, 1832)	40–50 × 70–80.0–1.70–80	Bicuspid	10–15 outermost unicuspid; bicuspid	No cuticular stylet	Vas deferens looped	Absent?	Australia, China, Japan, New Zealand, Sri Lanka	Ev. Marcus & Gosliner, 1984; Willan, 1983
P. meckeli Leue, 1813	46 × 71. 0. 71	Bicuspid	1–5 outermost unicuspid; bicuspid	With high crest	Stylet coiled 6–10 times inside sac	Globular	Cape Verde Is; Mediterranean; Europe	Ev. Marcus & Gosliner, 1984; Cervera & García-Gómez, 1988; present study
P. morula Bergh, 1905	22 × 50.0.50	–	–	–	–	–	Paternoster Is	Bergh, 1905
P. obesa (Verrill, 1882)	31–34 × 75–90.0.75–90	Bicuspid	Unicuspid	–	Stylet present	Lobate and glandular	NW Atlantic	Gosliner, 1985; Ev. Marcus & Gosliner, 1984
P. spiroporphyra n. sp.	30–32 × 40–44.0.40–44	Bicuspid; smaller cusp rounded	Bicuspid with smaller tiny cusp	Near deferent duct convex on both sides; in middle convex on one side and flattened or concave on other; terminal portion laterally flattened with crest	Purple stylet; coiled 12–14 times inside sac	Many enlargements	Rio de Janeiro state, Brazil	Present study
P. tarda Verrill, 1880	–	Bicuspid	Six outermost unicuspid	Rough on outer side	Deferent duct traverses retractor muscle and turn outwards to fundus of atrium	Ciliated and serial	N Atlantic; Angola; Congo; Agulhas Bank	Ev. Marcus & Gosliner (1984)

Pleurobranchaea morosa (Bergh, 1892) and *P. dorsalis* Allan, 1933 are not included because they are poorly described.

–, No data available in the literature.

smaller than cerebropleural ganglia. Pedal nerves: np1 with the statocyst close to base; np6 innervating middle of buccal bulb. Genital ganglion branches into five nerves.

Distribution: known only from type locality.

Remarks: Pleurobranchaea spiroporphyra has the bicuspidate radular teeth (Fig. 9D–F) typical of *Pleurobranchaea*. The genus *Pleurobranchaea* comprises 14 valid species, four of which have been reported from the West Atlantic: *P. tarda* Verrill, 1880 from North America to Cuba and from Ghana to Agulhas Bank, *P. obesa* (Verrill, 1882) from USA to Bahamas, *P. agassizii* Bergh, 1897 from Florida and Great Bahama Bank and *P. inconspicua* (Table 2). *Pleurobranchaea spiroporphyra* clearly differs from *P. tarda* by the muscular penis with a purple cuticular stylet that coils 10–11 times inside the penial sac (Fig. 7C). In *P. tarda* the arrangement of the deferent duct inside the penial sac is different because it turns outwards and reaches the fundus of the atrium, without coiling many times (Ev. Marcus & Gosliner, 1984). The new species differs considerably from *P. obesa* in radula formula and number of branchial leaves. In addition, *P. obesa* has a thick and muscular penial sheath, the penis has an external cuticle over much its length and the tip of the penis bears five to nine tubercles. *Pleurobranchaea spiroporphyra* differs from *P. agassizii* because its deferent duct enters into the penial sac and it has a purple cuticular stylet (Figs 7C, 10), whereas in *P. agassizii* the deferent duct does not enter into a penial sac, but where its retractor muscle is attached, it divides into a sheath and a muscular penis without cuticle (Ev. Marcus & Gosliner, 1984). Additionally, *c.*17 of the outermost marginal teeth lack the secondary cusp in *P. agassizii*, whereas in *P. spiroporphyra* the secondary cusp is always present (Fig. 9F).

Although only preserved specimens of *P. spiroporphyra* were available, some differences from *P. inconspicua* in external morphology could be perceived. *Pleurobranchaea inconspicua* has glandular tissue in the main rachis of the gill, the spur of preserved specimens is rounded and is always surrounded by black pigment, and the renal pore opens under the first pinnule; *P. spiroporphyra*, on the other hand, does not have glandular tissue in the main rachis of the gill, the spur is elongated, without any pigment in preserved specimens, and the renal pore opens under the second pinnule (Table 1). The labial cuticle of *P. spiroporphyra* is orange and the jaws pale orange, becoming lighter posteriorly. By contrast, in *P. inconspicua* the tuberculated portion is whitish with black marks (sometimes almost the same tone as the oesophagus) and the jaws are pale yellow. The elements of the jaw of *P. spiroporphyra* are almost flattened (Fig. 9A, B), with a change in shape towards the posterior portion, whereas in *P. inconspicua* they are flattened in the middle (Fig. 3A, B), with a thickened border. On the dorsal side of the oral tube, *P. spiroporphyra* has m2b positioned near the acid gland base (Fig. 8A, C) and the m1v cannot be seen in the ventral view (Fig. 8B), whereas *P. inconspicua* lacks m2b (Fig. 2A) and m1v is visible in the ventral view (Fig. 2C). The cuticular stylet of *P. spiroporphyra* is purple and conspicuous in all specimens, whereas in *P. inconspicua* it is translucent and therefore difficult to distinguish. SEM images showed that the cuticular stylet of *P. spiroporphyra* is thinner than that of *P. inconspicua*, although both have approximately the same shape. Lateral compression occurs in the cuticular stylet near the gonopore, which generates a crest in *P. spiroporphyra* (Fig. 10D); this does not occur in *P. inconspicua* (Fig. 4D). The deferent duct inside the penial sac exhibits some looping and then passes through the retractor muscle of the penis in both species. In *P. spiroporphyra* the deferent duct passes through the retractor muscle in the middle of the muscle, whereas in *P. inconspicua* it does so distally in relation to the gonopore. *Pleurobranchaea inconspicua* also differs from *P. spiroporphyra* in the configuration of nerves that leave the cerebropleural ganglia. In *P. inconspicua* there is only one nerve in the most posterior portion of the left side, namely cp5l, which bifurcates, whereas *P. spiroporphyra* has three nerves, cp5l, cp6l and cp7l. *Pleurobranchaea spiroporphyra* bears two nerves in the visceral ganglia, whereas *P. inconspicua* has three. Examination of the pedal ganglia shows that *P. spiroporphyra* has a statocyst on the anterior part of the ganglia, whereas in *P. inconspicua* it is in the posterior part; additionally, three main nerves leave from the anterior portion of the pedal ganglia in *P. spiroporphyra* whereas and only two in *P. inconspicua*. There are slight differences in the distribution of the nerves of the genital ganglion; five nerves leave this ganglion in *P. spiroporphyra* whereas and four (one bifurcate) in *P. inconspicua*.

DISCUSSION

Previously, the classification of the Pleurobranchaeidae was based largely on insufficiently described specimens (Table 2). The discrimination of species is difficult because the morphology of the classical hard structures, i.e. radula and jaws, can be used, in most cases, only for generic separation (Vayssière, 1901; Ev. Marcus & Gosliner, 1984). However, we agree with Muniaín *et al.* (2007) that a review of the characters of radular and jaw elements using SEM is desirable, to enable comparison of dubious species. For example, we found a slight difference in the jaws of *P. spiroporphyra* and *P. inconspicua*, the elements of *P. spiroporphyra* being almost flattened (Fig. 9A, B), and those of *P. inconspicua* flattened in the middle with a thickened border (Fig. 3A, B).

Many authors have considered the anatomy of the male reproductive apparatus to be the most useful character. Some have distinguished species by the shape of the cross section of the cuticular stylet (Vayssière, 1901; Ev. Marcus & Gosliner, 1984; Muniaín *et al.*, 2007). In the present study, different portions of the cuticular stylet of *P. inconspicua*, *P. spiroporphyra*, *P. gela* and *P. meckeli* were examined, and it was observed that shape and size vary along its length (Figs 4, 6, 10, 11). This has already been noted by Bergh (1897) for *P. meckeli*, who stated that the diameter of the duct changes abruptly inside the sheath. Therefore, it is necessary to consider variation along the length of the cuticular stylet when comparing species. For example, the illustrations of the stylet of *P. meckeli* by Ev. Marcus & Gosliner (1984: 9; fig. 1E; as *P. notmec*) and the micrographs of this species obtained in the present study (Fig. 12A, B) are similar to some parts of the cuticular stylets of *P. spiroporphyra* (Fig. 9D) and *P. gela* (Fig. 6B), the differences only being apparent when the entire stylet is examined. Thus, we conclude that the cuticular stylet should be reexamined and compared among the species; transverse sections of at least the anterior, middle and posterior portions should be provided.

Some previous descriptions of species of *Pleurobranchaea* have focused on the reproductive system. Cervera & García-Gómez (1988), on the other hand, provided a detailed anatomical study of *P. meckeli*, the type species of the genus. In the present study we examined specimens of *P. meckeli* (Figs 11, 12) from Israel to understand better the general pattern of the genus and facilitate comparisons with *P. inconspicua*, *P. spiroporphyra* and *P. gela*. Although Cervera & García-Gómez (1988: 82, fig. 8) did not describe the buccal bulb in detail, their illustration matches the pattern of muscles described in this paper, thus allowing us to recognize a general pattern in the position and presence/absence of extrinsic and intrinsic odontophoric muscles. This pattern consists of well-developed mj and m5 (secondary dorsal tensor muscle of the radula), the latter covering almost all of the surface of m4 and median portions of the cartilage, and extending to the dorsal part; pair m7 is connected to the

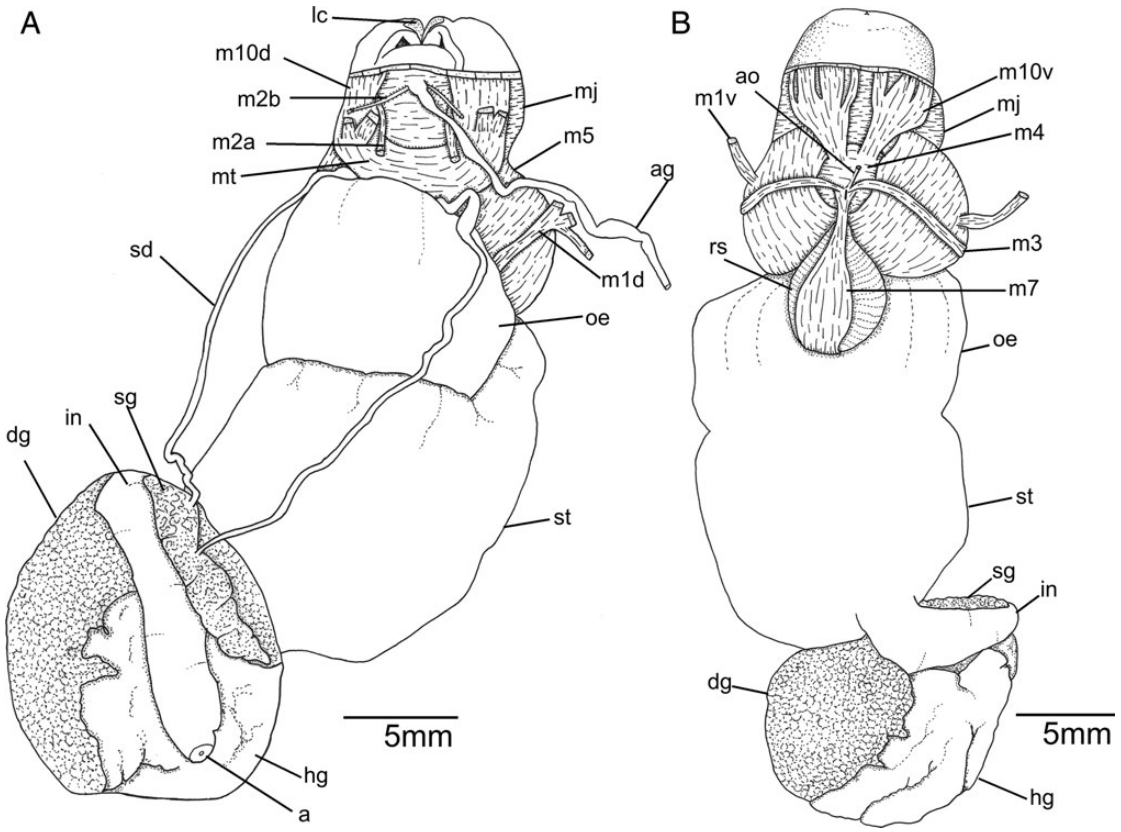

Figure 11. *Pleurobranchaea meckeli*, digestive system (MZSP 75485). **A.** Dorsal view as *in situ*. **B.** Ventral view. Abbreviations: a, anus; ag, duct of acid gland; ao, aorta; dg, digestive gland; hg, hermaphroditic gland; in, intestine; lc, labial cuticle; m1, jugal protractor muscle of odontophore; m2, jugal retractor muscle of odontophore; m3, superficial circular muscle; m4, main dorsal tensor muscle of radula; m5, accessory dorsal tensor muscle of radula; m7, muscle running inside radular sac; m10, protractor muscle of odontophore; mj, jaw muscle; mt, transversal superficial muscle; oe, oesophagus; rs, radular sac; sd, salivary duct; sg, salivary gland; st, stomach.

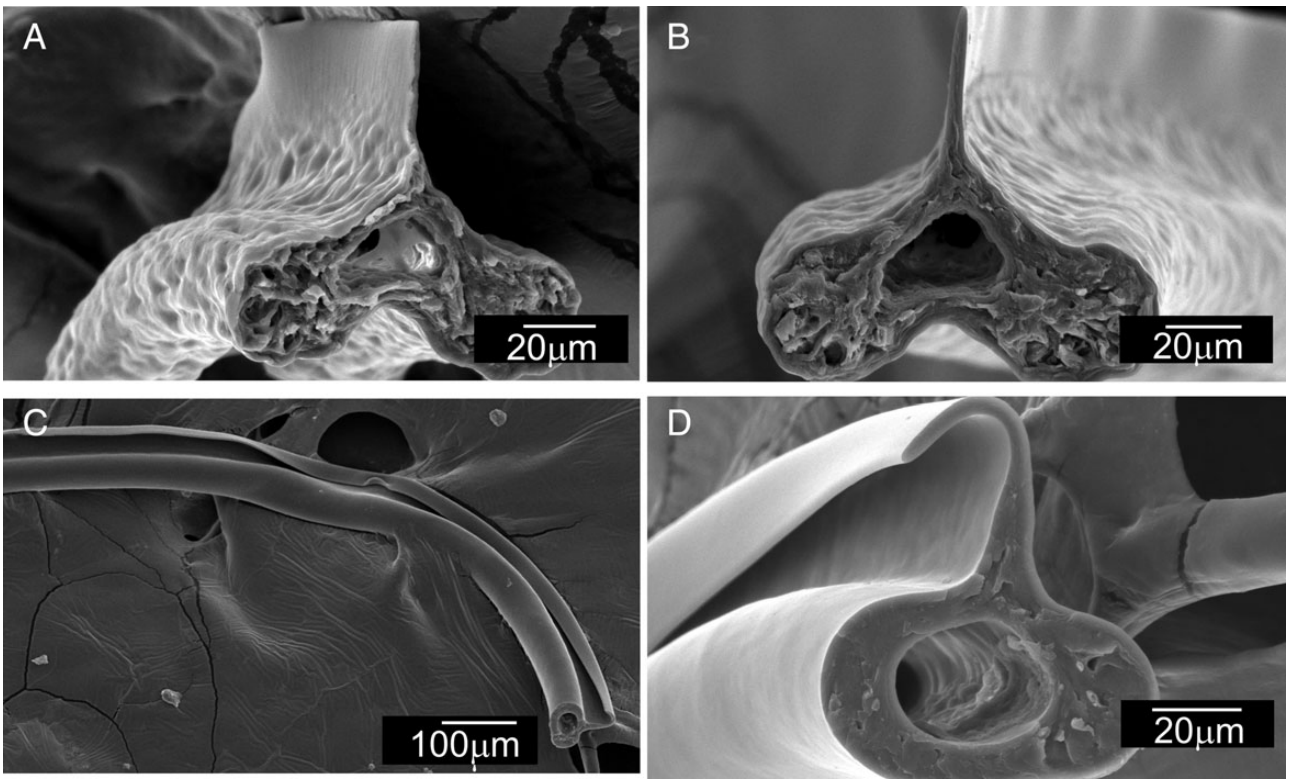

Figure 12. *Pleurobranchaea meckeli* (MZSP 75485), SEM of cuticular stylet. **A.** Portion near deferent duct. **B.** Median portion. **C, D.** Portion near gonopore.

radular sac, and functions like m11 as a tensor ventral muscle of the radula; m7l is connected laterally to the oesophagus, working like a sphincter inside the oral tube and attached to the radula sac; m10d is a dorsal muscle originating on the anterodorsal extremity of the snout and is connected to the transversal muscle mt.

ACKNOWLEDGEMENTS

We were unusually fortunate to have Dr Heike Wägele (Zoologisches Forschungsmuseum Alexander Koenig) as our editor, who spent significant amounts of time on our manuscript and improved it a lot. We are grateful to Dr Carlo M. Cunha for the photograph of *P. inconspicua*, for intellectual support and donations of specimens, to Patrícia O. V. Lima for help with information about the Marcus material in MZSP and to Amanda Garcez da Veiga for help with SEM operation. This work was supported by Conselho de Aperfeiçoamento de Ensino Superior (CAPES) (PhD scholarship to J.A.).

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