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Review of *Baeolidia*, the largest genus of Aeolidiidae (Mollusca: Nudibranchia), with the description of five new species

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Abstract

This paper discusses the systematics of the aeolid genus *Baeolidia* Bergh, 1888. To date, this monophyletic genus is the most diverse within Aeolidiidae with sixteen valid species. Excluding *Baeolidia cryoporos* Bouchet, 1977, the genus is restricted to the Indo-Pacific and Eastern Pacific. Species of *Baeolidia* show a huge intrageneric variability in several morphological characters. Only oral glands, if present, may distinguish *Baeolidia* from other aeolidiids genera. *Aeolidiella occidentalis* Bergh, 1875, *Aeolidiella faustina* Bergh, 1900 and *Spurilla orientalis* Bergh, 1905 are transferred to *Baeolidia* but they are considered *nomina dubia*. Five new species, *Baeolidia rieae* **sp. nov.**, *Baeolidia variabilis* **sp. nov.**, *Baeolidia lunaris* **sp. nov.**, *Baeolidia gracilis* **sp. nov.** and *Baeolidia scottjohnsoni* **sp. nov.** are described.

Key words: Cladobranchia, molluscan diversity, morphology, new species, systematics

Introduction

The aeolidiid genus *Baeolidia* was introduced by Bergh (1888) based on a single preserved specimen of *Baeolidia moebii* from Mauritius. The original description has contradictory information about the cerata arrangement, which has been considered as one of the most important diagnostic characters in Aeolidiidae. Bergh (1888) originally described the cerata in rows and then in arches (page 779 of that contribution). This lack of clarity has produced a great deal of confusion in the literature about the morphological characteristics of this genus. While some authors characterized *Baeolidia* by having the cerata in arches (Miller 2001) others ascribed or transferred species that have rows instead of arches to this genus (Gosliner 1985). Additionally, *Baeolidia* has been considered as a junior synonym of *Spurilla* Bergh, 1864 (Rudman 1982), whereas some authors that have considered *Baeolidia* as a valid genus rejected the validity of *Limenandra* (Gosliner 1980, 1985; Valdés *et al.* 2006; Gosliner *et al.* 2008). Some species have been assigned to *Baeolidia*: *Baeolidia moebii* Bergh, 1888; *Baeolidia major* Eliot, 1903; *Baeolidia japonica* Baba, 1933; *Baeolidia fusiformis* Baba, 1949; *Baeolidia benteva* Er. Marcus, 1958; *Baeolidia cryoporos* Bouchet, 1977 and *Baeolidia palythoae* Gosliner, 1985. Furthermore, *Limenandra nodosa* Haefelfinger & Stamm, 1958; *Aeolidiopsis harrietae* Rudman, 1982 and *Spurilla australis* Rudman, 1982 were also transferred to *Baeolidia* because of their ceratal arrangement or/and the ornamentation of the rhinophores (Gosliner1985; Miller 2001).

The first comprehensive study on Aeolidiidae (Carmona *et al.* 2013) rendered *Baeolidia* as a monophyletic genus once *Spurilla salaamica* Rudman, 1982 and *Aeolidiopsis ransoni* Rudman, 1982 were transferred to *Baeolidia*. The latter contribution also showed that not only the ceratal arrangement but also the rhinophorial ornamentation and the position of the anus lacked of any phylogenetic significance within *Baeolidia*. Additionally, Carmona *et al.* (2013) pointed out the existence of, at least, three undescribed species (Fig. 1). The molecular

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phylogeny of Aeolidiidae (Carmona *et al.* 2013) also showed that *Baeolidia* was closely related with *Spurilla* and *Berghia* Trinchese, 1877, although the relationships among these three genera were not resolved. Recently, the morphological characteristics of *Spurilla*, *Berghia*, and *Limenandra* Haefelfinger & Stamn, 1958 have been re-defined (Carmona *et al*. 2014a, b, c, respectively). While the species of *Spurilla* have a broad body, cerata curved inwards and perfoliate rhinophores, *Berghia* species usually are slender, with papillate rhinophores. Nevertheless the systematics of the genus *Baeolidia* have not been studied. Therefore, the main objectives of the present study are: 1) Undertake a general revision of *Baeolidia* (revising species of all names available, when possible); 2) Describe five new species; 3) Compare the morphological characters of the genus *Baeolidia* with *Spurilla, Berghia* and *Limenandra*.

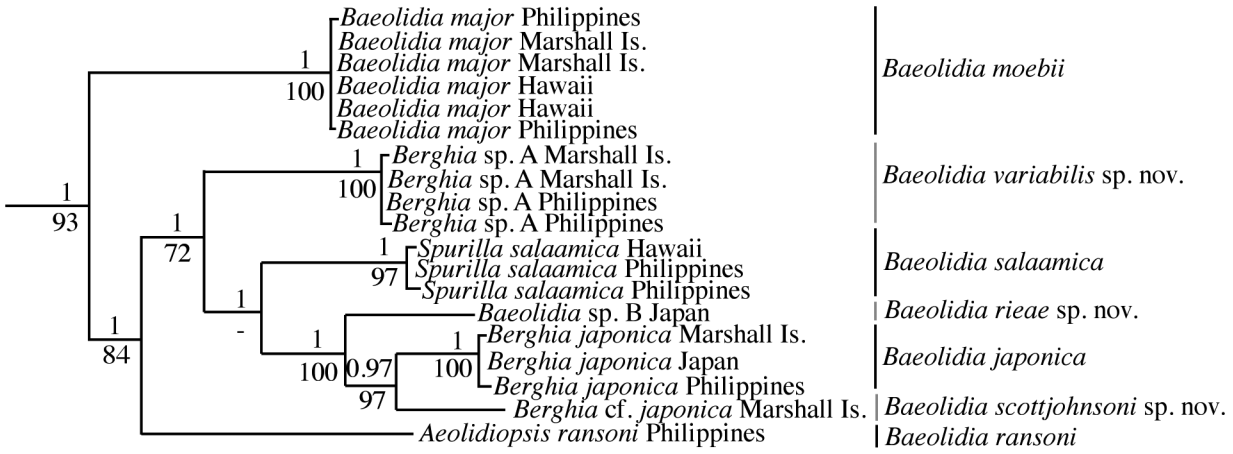

FIGURE 1. Phylogeny of *Baeolidia*, based on Carmona *et al*. (2013). Names on right side of vertical bars refer to revised classification.

Materials and methods

Literature review. A comprehensive review of the literature was conducted to determine the valid names for the species recognized in the present study. After the description of the type species, all available names for *Baeolidia* species are organized and discussed in this paper according to the year of publication. In the synonymy lists, references to the original description of the valid name and all synomyms (basionyms and primary synonyms) as well as the first proposed change of binomen (secondary synonyms) are included, but subsequent references are not.

Morphology. Whenever possible, two or more specimens of each species were examined anatomically. Specimens were dissected by dorsal incision. Their internal features were examined and drawn through a dissecting microscope with the aid of a camera lucida. Special attention was paid to the morphology of the reproductive system and oral and salivary glands. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination by scanning electron microscopy (SEM).

The specimens examined are deposited in the California Academy of Sciences, CASIZ (San Francisco, USA) and the Museo Nacional de Ciencias Naturales, MNCN (Madrid, Spain), being named in agreement to the classification of Aeolidiidae proposed by Carmona *et al.* (2013).

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: LSID urn:lsid:zoobank.org:pub:1DB70C57-A6EB-491D-A0FD-0B1652E5B61E

Results

Systematics

Nudibranchia Cuvier, 1817

Cladobranchia Willan & Morton, 1984

Family Aeolidiidae Gray, 1827

Genus *Baeolidia* Bergh, 1888

Diagnosis of the genus *Baeolidia* based on Bergh (1888). Forma corporis minus depressa quam in Aeolidiis propriis; rhinophoria annulate moriformia, tentacula digitiformia; papillae dorsales non numerosae, compressae, sat breves; margo anterior podarii profunde sulcatus, angulis fortiter productis.- Penis inermis. Mandibulae applanatae: margo masticatorius sublaevis. Radula uniseriata, dentibus simpliciter pectinatis.

Body low. Rhinophores perfoliate. Oral tentacles digitiform. Cerata scarce, compressed, short. Anterior margin grooved. Penis unarmed. Jaws flattened, masticatory border almost smooth. Radula uniseriate, teeth with simple denticulation (translated from Bergh, 1888)

Baeolidia moebii Bergh, 1888

(Figs. 2A–B, 3A, 4A–B, 5, 6A)

Baeolidia moebii Bergh, 1888: 778, pl. LXXIX, Figs. 10–16, pl. LXXX, Figs. 1–4.
Baeolidia major Eliot, 1903: 252.
Baeolidia major amakusana Baba, 1937: 335.
Berghia major (Eliot, 1903): Edmunds 1969, 467, Fig. 10.
Spurilla major (Eliot, 1903): Rudman 1982, 169, Figs. 18–19.

Type locality. Grand Bay, Rodrigues Island, Mauritius.

Type material. To our knowledge no type material remains. We designate the specimen MNCN 15.05/63447 from Mozambique as the neotype in order to avoid confusion with similar species.

Material examined. Neotype: MNCN 15.05/63447, one specimen, dissected, 18 mm in length preserved, Mozambique, Zavora Bay, collected by Yara Tibiriça, January 2012. Other material: CASIZ 177602, one specimen, dissected, 10 mm in length preserved, Philippines, Luzon Island, Batangas Bay, Calumpan Peninsula, collected by Terrence M. Gosliner, 16 April 2008; CASIZ 157017, two specimens, dissected, 25 and 24 mm in length preserved, Philippines, Luzon Island, Batangas Province, Balayan Bay, Seafari Beach, collected by Ángel Valdés and Mary James Adams, 12 May 2001; CASIZ 186211, one specimen, dissected, 10 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, Batangas Bay, collected by Alicia Hermosillo, 04 May 2011; CASIZ 180327, one specimen, dissected, 6 mm in length preserved, Hawaii, Maui, Airport Beach, collected by Cory Pittman, 04 October 2008; CASIZ 076055, one specimen, dissected, 16 mm in length preserved, Mexico, Baja California, Gulf of California, San Jose Island, Punta Colorado, collected by Antonio J. Ferreira 15 July 1971.

Geographical distribution. Originally described from Mauritius (Bergh 1888), it is also known from the Seychelles (Gosliner *et al.* 2008), Tanzania (Eliot 1903; Edmunds 1970), Mozambique (present study), the Reunion Island (Bidgrain 2013), Australia (Cobb & Mullins 2013), Indonesia (Gosliner *et al.* 2008), the Philippines (Gosliner *et al.* 2008), Japan (Baba 1933b, 1937, 1955; Ono 1999, 2004; Nakano 2004) and the Marshall Islands (present study). This species is also found in the Eastern Pacific: Hawaii (Kay 1979; Gosliner 1980), tropical Pacific North America (Gosliner *et al.* 2008) and Mexico (Farmer 1966). Recently, it has also been reported in Turkey (Turk & Furlan 2011).

External morphology (Figs. 2A–B, 3A): Body large, broad, tapering gradually towards posterior end of foot. Foot corners tentaculiform. Body colour variable, commonly greyish white or brownish green (Fig. 2A). Some

specimens reddish (Fig. 2B). Background colour brownish green, overlaid with reticulate ochre pattern. Dorsum usually with bright white patches. Whitish or yellow ring on anteriormost edge of head, continuing towards oral tentacles and forming a distinct light band; both, ring and band, may be interrupted. Rhinophores, oral tentacles and foot corners same as body colour. Rhinophores shorter than oral tentacles. Rhinophores studded with minute knobs (Fig. 3A); apex white. Oral tentacles with white tips.

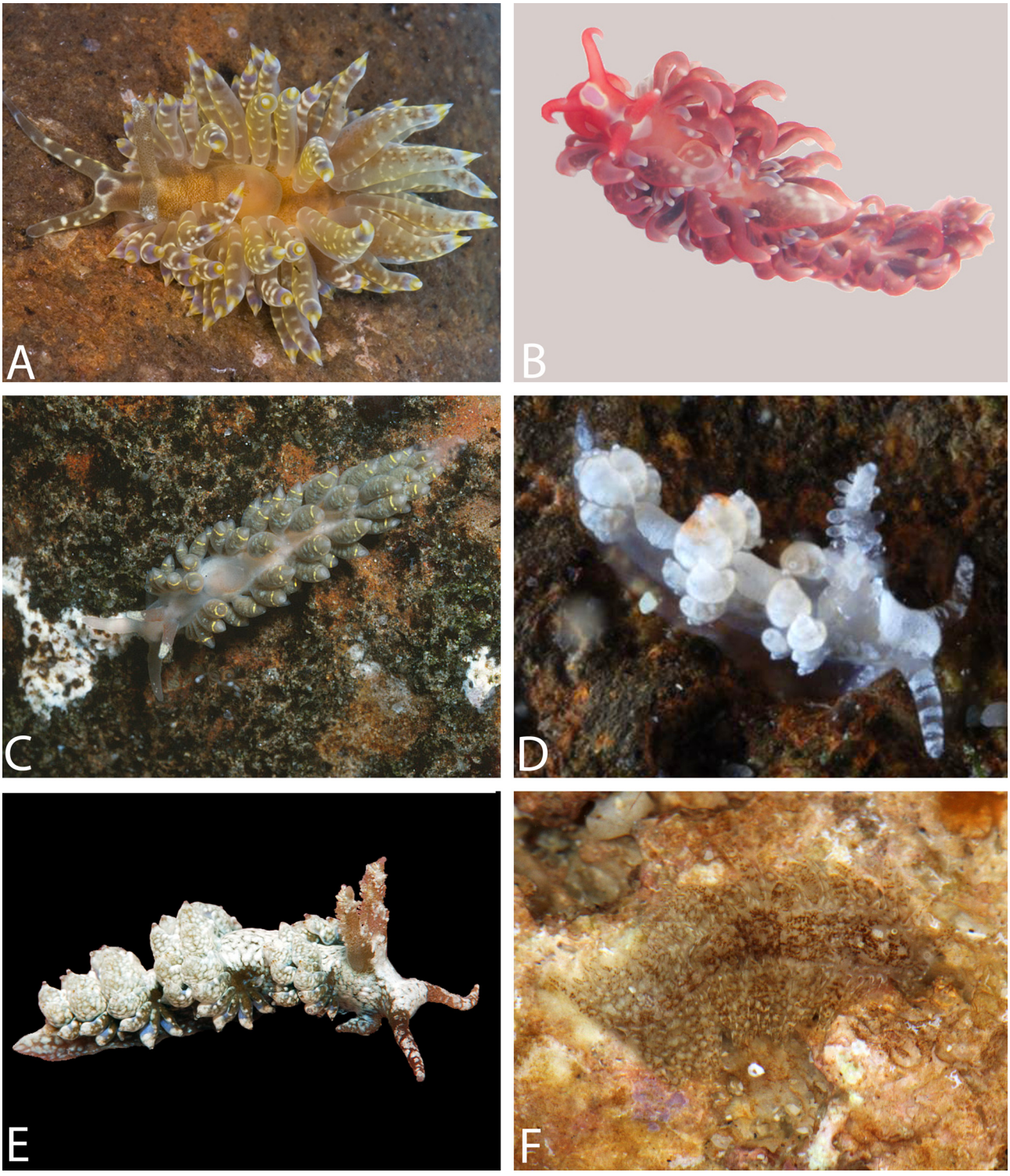

FIGURE 2. Photographs of the living animals. A, B, *Baeolidia moebii*: (A) specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 177602; (B) specimen from Mozambique, photo by Yara Tibiriça, MNCN 15.05/63447; (C) *Baeolidia macleayi,* specimen from Australia, photo by Terrence M. Gosliner, CASIZ 71923; (D-E) *Baeolidia japonica*: (D) specimen from Japan, photo by Akira Kawahara, CASIZ 1814520; (E) specimen from Marshall Islands, photo by Scott Johnson, CASIZ 186795; (F) *Baeolidia ransoni,* specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 186208.

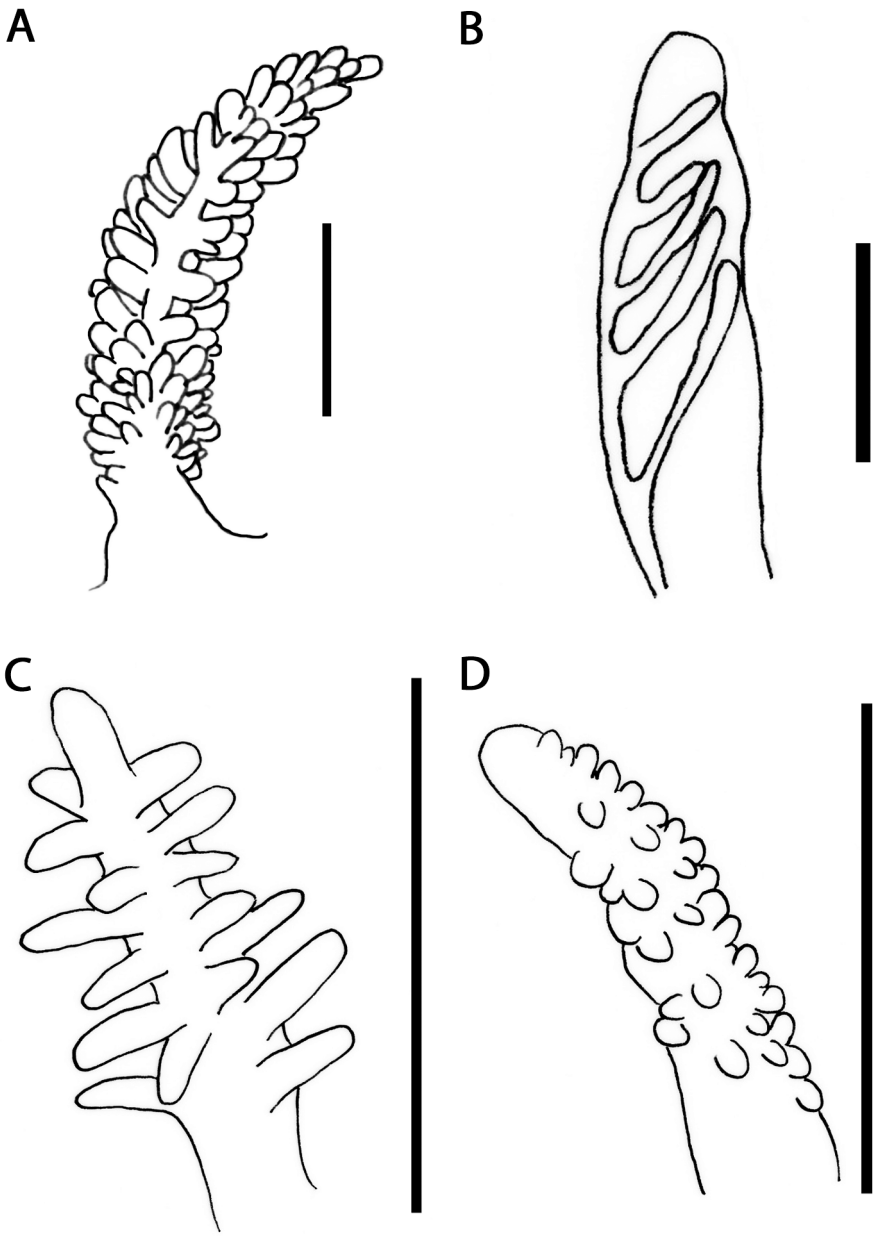

FIGURE 3. Different papillate rhinophores in *Baeolidia*: (A) from Rudman (1982); (B) from Gosliner (1985). Scale bars: A, 3mm; B, 1 mm; C, 1.2 mm; D, 1.5 mm.

Cerata length variable. Cerata flattened, almost leaf-like. Branches of digestive gland brownish-green, shining through translucent body wall. Whitish patches on outer side of cerata, probably with bright yellow marks. Cerata usually with bright yellow subapical band and just below it a purplish area. Apex translucent white. Cerata composed of up to nine arches, leaving a distinct gap between pre and post-pericardial groups. Each arch with 4–15 cerata, decreasing in size towards foot. Anus cleioproctic, within second right arch. Genital opening placed among cerata of anteriormost group on right side.

Anatomy. Masticatory border of jaws smooth (Fig. 4A). Radular formulae 17 x 0.1.0 (MNCN 15.05/63447, 18 mm), 19 x 0.1.0 (CASIZ 076055, 16 mm), 20 x 0.1.0 (CASIZ 177602, 10 mm) and 22 x 0.1.0 (CASIZ 180327, 6 mm). Radular teeth bent upwards with up to 100 elongate, fine and acutely pointed denticles from side to side, without central notch or central cusp (Fig. 4B). Teeth progressively smaller towards posterior region of radula. Oral glands fragile, small and spongy, lying dorso-laterally to buccal bulb (Fig. 5). Oral gland morphology variable, from rounded to elongate. Salivary glands large.

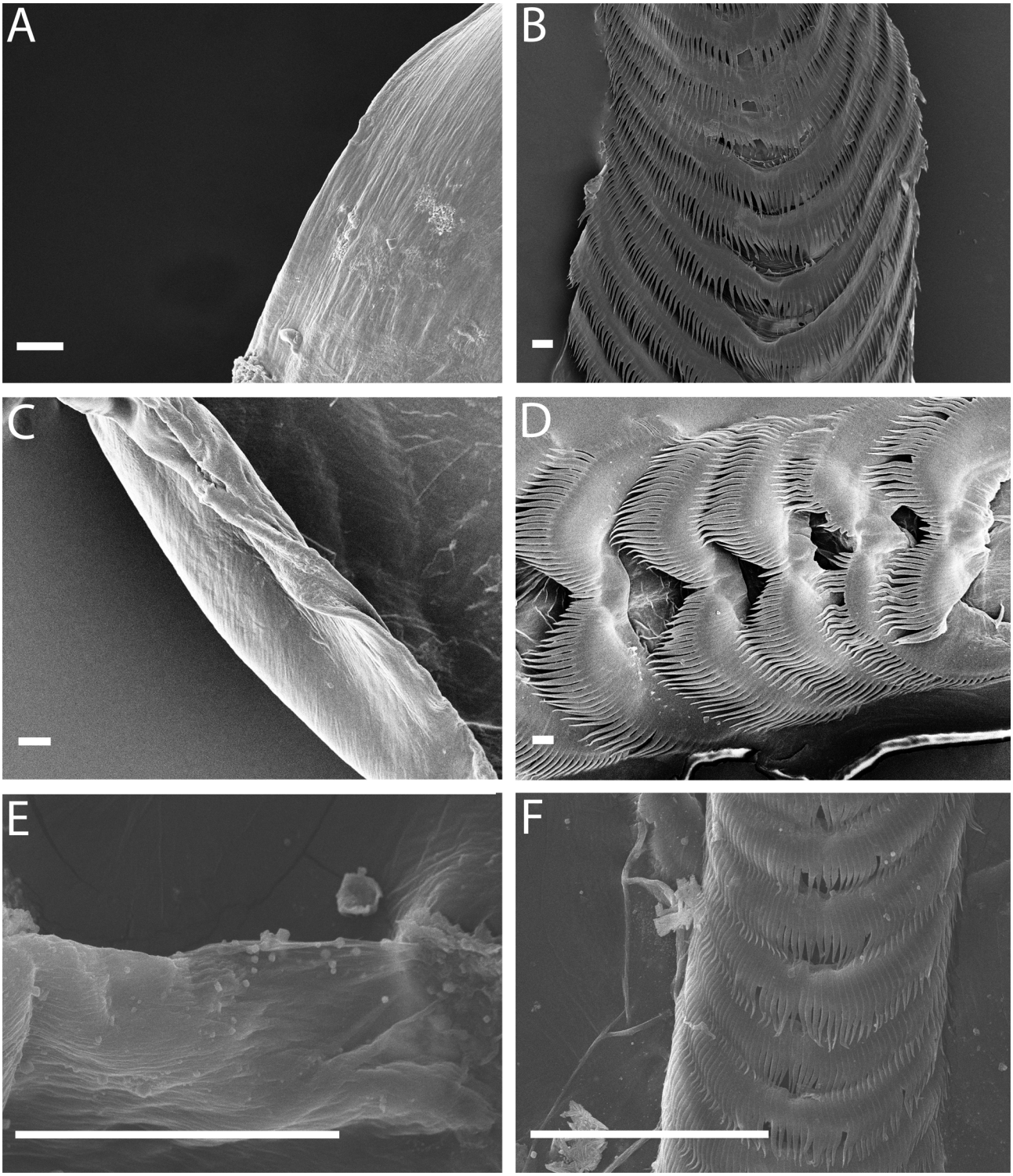

FIGURE 4. Scanning electron photographs. (A–B) *Baeolidia moebii* (CASIZ 180327): (A) Detailed view of the masticatory border; (B) Radular teeth; (C–D) *Baeolidia macleayi* (CASIZ 195247): (C) Detailed view of the masticatory border; (D) Radular teeth; (E–F) *Baeolidia japonica* (CASIZ 181357); (E) Detailed view of the masticatory border; (F) Radular teeth. Scale bars: A, 10 µm; B, 30 µm; C-D, 10 µm; E, 100 µm; F, 150 µm.

Reproductive system diaulic (Fig. 6A). Preampullary duct widening into elongate ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens elongate, moderately wide, penetrating into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis ovoid, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. This species has not been studied under the name of *Baeolidia moebii* since its original description (Bergh 1888). When Eliot (1903) described *B. major*, he pointed out that the latter could be merely a full-grown individual of *B. moebii* since the main difference between both species was the size. Nevertheless, Eliot (1903) finally described *B. major* as a valid species, owing to the ambiguities in the original description of *B. moebii*. Taking into consideration Eliot's statements together with the proximity of both type localities (Mauritius for *B. moebii* and Zanzibar for *B. major*), Carmona *et al.* (2013) considered *B. major* as a junior synonym of *B. moebii*. Neither Bergh (1888) nor Eliot (1903) mentioned the presence of oral glands in *B. moebii*. Only Rudman (1982) pointed out the existence of salivary glands in this species. Two of our specimens possessed oral glands, and salivary glands were found twice. This variability could be an artefact of the state of preservation of these specimens. An alternative hypothesis could be an intraspecific variation for these two characters, which has also been observed in *Limenandra nodosa* (Carmona *et al*. 2014c).

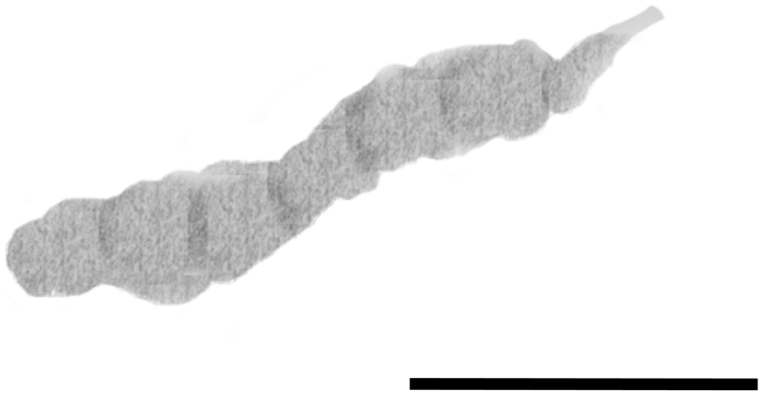

FIGURE 5. Oral glands of *Baeolidia*. Scale bar: 0.5 mm.

Despite the large variability in colouration, our specimens identified as *Baeolidia moebii* match with the information given by Bergh (1888) and Eliot (1903) as well as with more recent descriptions (Edmunds 1969; Gosliner 1980; Rudman 1982). Gosliner (1985) stated the presence of a penial gland in the reproductive system of *B. moebii* (identified as *Berghia major*). The only aeolidiid where this condition has been described is *Limenandra nodosa* (Schmekel 1970), although Carmona *et al.* (2014c) did not find any traces of a penial gland. Since none of the specimens here examined exhibited this structure, the existence of a penial gland for *B. moebii* is not confirmed (Fig. 6A).

Finally, excluding *Baeolidia australis* (see *B. australis* remarks), *B. moebii* colouration is clearly distinguishable from the remaining species of this genus. In terms of internal anatomy, the radular morphology of *Baeolidia moebii* is quite particular since teeth are bent and do not have any central notch or denticle. So far, only *B. australis* and *B. lunaris* **sp. nov.** have similar radular teeth. *Baeolidia moebii* and *B. lunaris* **sp. nov.** differ in size (*B. moebii* is larger than *B. lunaris* **sp. nov.**), and rhinophorial ornamentation (*B. lunaris* **sp. nov.** has elongate papillae instead of minute knobs and colouration). Additionally, the ampulla of *B. moebii* is larger than the ampulla found in *B. lunaris* **sp. nov.** Differences between *B. moebii* and *B. australis* are recorded in *B. australis* remarks.

This species was studied molecularly by Carmona *et al.* (2013) (Fig. 1).

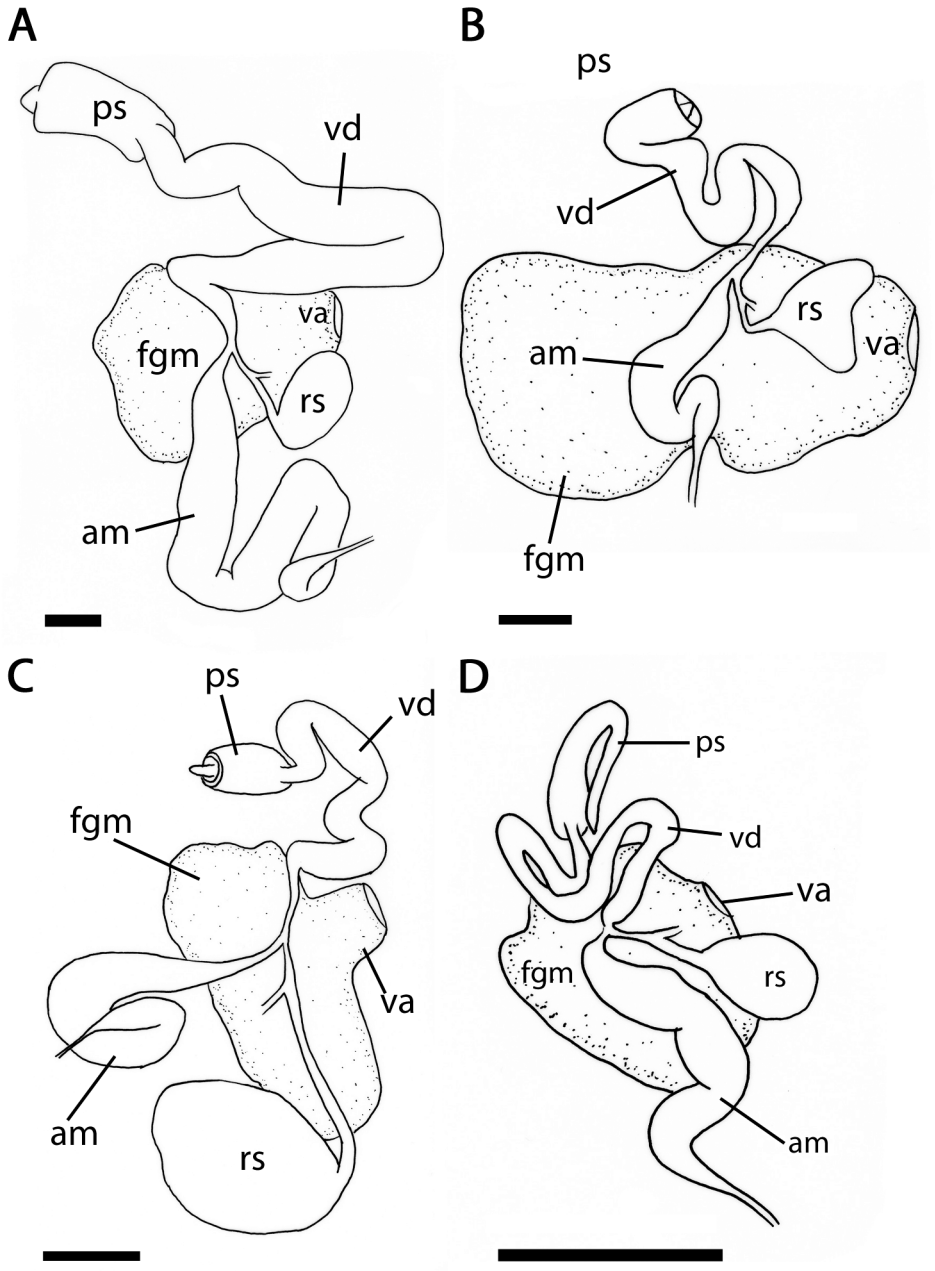

FIGURE 6. Reproductive system. (A) *Baeolidia moebii,* specimen from Mozambique (MNCN 15.05/63447); (B) *Baeolidia macleayi,* specimen from Australia (CASIZ 195247); (C) *Baeolidia japonica,* specimen from Marshall Islands (CASIZ 181357); (D) *Baeolidia ransoni,* specimen from the Philippines (CASIZ 186209). Scale bars: A–D, 0.5 mm. Abbreviations: am, ampulla; fgm, female gland mass; ps, penial sac; rs, receptaculum seminis; va, vagina; vd, vas deferens.

***Baeolidia macleayi* (Angas, 1864)**
(Figs. 2C, 3B, 4C–D, 6B)

Aeolis macleayi Angas, 1864: 65, pl. VI, Fig. 4.
Coryphella macleayi (Angas, 1864): Bergh 1878, 16.
Spurilla macleayi (Angas, 1864): Burn 1969, 96.

Type locality. Port Jackson, New South Wales.

Type material. To our knowledge no type material remains. We designate the specimen CASIZ 071923 (6

mm) from Long Reef, North of Sydney, New South Wales, Australia, as the neotype in order to avoid confusion with similar species.

Material examined. Neotype: CASIZ 195247, one specimen, dissected, 6 mm in length preserved, Australia, New South Wales, North of Sydney, Long Reef, collected by Terrence M. Gosliner, 17 September 1989. Other material: CASIZ 071923, two specimens, dissected, 8 and 6 mm in length preserved, Australia, New South Wales, North of Sydney, Long Reef, collected by Terrence M. Gosliner, 17 September 1989.

Geographical distribution. Originally described from Port Jackson, Australia (Angas 1864), this species is also known from New Zealand (Burn 1962, 1969; Coleman 2001; Miller 2001; Burn 2006; Rudman 2007a).

External morphology (Figs. 2C, 3B): Body fairly short, broad, tapering close to posterior end of foot. Foot corners tentaculiform. Body colour translucent. Some specimens with white and lemon-yellow speckling over dorsum and head. Bright orange mark on pericardium with different intensity; it continues through head and posterior end of foot. Rhinophores ribbed (Fig. 3B), shorter than oral tentacles. Proximal two-thirds reddish or brownish. Distal part of rhinophores with lemon-yellow pigment. Oral tentacles translucent, may have white and lemon-yellow spots.

Cerata elongate and slender, or moderately short and bulb-shaped. Cerata translucent, being visible the brownish or bluish ramifications of digestive gland. Cnidosacs white. Cerata with bright lemon-yellow ring subapically. White spots over ceratal surface might form a second ring below the yellow one. Cerata composed of four arches and three rows, leaving a distinct gap between pre and post-pericardial groups. Each group with 3–10 cerata, decreasing in size towards foot. Anus cleioproctic, below second right row. Genital aperture below first right arch.

Anatomy. Masticatory process smooth (Fig. 4C). Radular formula 16 x 0.1.0 (CASIZ 195247, 6 mm). Radular teeth bilobed with 30–40 elongate and acutely pointed denticles on either side of central cusp (Fig. 4D). Central cusp prominent, elongate. Oral glands spongy, moderately large, delicate, with uniform diameter throughout most of length. Oral glands dorso-laterally to buccal bulb. Salivary glands absent.

Reproductive system diaulic (Fig. 6B). Preampullary duct widening into moderately short ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens inserting into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis heart-shaped, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. We transfer *Aeolis macleayi* to *Baeolidia* because of the type of oral glands, which are exclusive of this genus in Aeolidiidae.

Excluding *Baeolidia faustina* (see *B. faustina* remarks), the colouration and the shape of the cerata distinguish *B. macleayi* from the remaining *Baeolidia* species. Regarding the radular morphology, the teeth found in *B. macleayi* are similar to *B. rieae* **sp. nov.**, *B. variabilis* **sp. nov.** and *B. gracilis* **sp. nov.** Nevertheless, the central cusp of *B. macleayi* is larger than the minute central cusp found in the species mentioned above. Moreover, the shape of the receptaculum seminis is quite different between *B. macleayi* and *B. rieae* **sp. nov.**, *B. variabilis* **sp. nov.** and *B. gracilis* **sp. nov.**: in *B. macleayi* it is heart-shaped; in *B. rieae* **sp. nov.** and *B. variabilis* **sp. nov.** it is bean-like, and the receptaculum seminis of *B. gracilis* **sp. nov.** is ovoid. In addition, it is worth mentioning that *B. macleayi* is a native species from Australia and New Zealand, whereas *B. rieae* **sp. nov.** was found in Japan, *B. gracilis* **sp. nov.** in the Philippines and *B. variabilis* **sp. nov.** is from the Philippines, Papua New Guinea and the Marshall Islands.

The oral glands of *B. macleayi* are first described and reported here.

Baeolidia occidentalis (Bergh, 1874)

Aeolidiella occidentalis Bergh, 1874: 397, pl. VIII, Figs. 9–19.
Spurilla occidentalis (Bergh, 1874): Labbé 1930, 623.

Type locality. The Antilles, not very far from Saint Thomas.

Type material. According to Bergh (1874), the material was deposited in the Museum of Copenhagen. The registration number of the holotype of *Baeolidia occidentalis* is ZMUC-GAS 2042.

Geographical distribution. So far, this species is only known from the Antilles (Bergh, 1874).

External and internal morphology. Not completely described by Bergh (1874). No specimens available for the present study.

Remarks. Bergh (1874) described this species, *Aeolidiella occidentalis*, based on three specimens. Since they were already preserved and in a bad state of conservation, Bergh (1874) did not describe the colouration of the living animal. The radular teeth, the morphology of the cerata and the oral glands described by Bergh (1874) seem to associate this "species" with the genus *Baeolidia.* Although Bergh's original description does not allow identifying this "species", *B. occidentalis* have been reported in some contributions about *Sargassum* and its ecological aspects (e.g. Adams 1960; Thiel & Gutow 2005). However, none of these contributions provided a detailed description of this "species" or of the specimen identified as *B. occidentalis.* The lack of any singular morphological feature in this species leads us to conclude that *Baeolidia occidentalis* should be treated as *nomen dubium*.

Baeolidia faustina (Bergh, 1900)

Aeolidiella faustina Bergh, 1900: 235, pl. 20, Figs. 39–40.
Spurilla faustina (Bergh, 1900): Miller 2001, 641, Figs. 4–5.

Type locality. Tasmania.

Type material. To our knowledge no type material remains.

Geographical distribution. To date, only known from Tasmania (Bergh 1900), New Zealand (Miller 2001), and Australia (Burn 1962, 1969, 2006).

External and internal morphology. Not properly described by Bergh (1900). No specimens available for the present study.

Remarks. Based on the original description and the figure of the radular tooth (Bergh 1900), it is very likely that this species belongs to *Baeolidia*. Nevertheless, Bergh (1900) did not provide any distinctive feature, which has blurred the identity and validity of this species. Since Bergh (1900), only Burn (1962) and Miller (2001) have studied this species but both authors had some difficulties separating *B. faustina* from *B. macleayi*. Burn (1962) distinguished both species mainly by the position of the anus and the external colouration. Seven years later, Burn (1969) transferred all the specimens previously identified as *B. faustina* to *B. macleayi.* Finally, Burn (2006) rendered *B. faustina* as junior synonym of *B. macleayi.* Hence, since this name cannot be assigned to specimens, we conclude that *Baeolidia faustina* should be considered as *nomen dubium*.

Baeolidia orientalis (Bergh, 1905)

Spurilla orientalis Bergh, 1905: 223, pl. XIX, Figs. 29–31.

Type locality. Tual Reef, Kei Island, Indonesia (Station 258 of the Siboga Expedition).

Type material. The material was deposited in the National Museum of Natural History, Leiden. The registration number of the syntype of *Baeolidia orientalis* is ZMA.MOLL.139366

Geographical distribution. To date, this species is only known from the Indo-Pacific (Bergh 1905).

External and internal morphology. Not properly described by Bergh (1905). No specimens available for the present study.

Remarks. Since Bergh (1905), new specimens of *Spurilla orientalis* have not been discovered again. However, its name can be found in the literature as part of the discussion of other *Spurilla* species (e.g. Er. Marcus 1961; García-Gómez 2002). Based on the ceratal insertion (in arches and rows), the figure of the radular tooth (Bergh 1905) and the geographical distribution of *Spurilla* and *Baeolidia* (Carmona *et al.* 2013), this "species" should be ascribed to *Baeolidia*. However, the lack of any singular morphological characters in the original description of *Baeolidia orientalis* leads us to render this species as *nomen dubium*.

Baeolidia japonica Baba, 1933

(Figs. 2D–E, 3C, 4E–F, 6C).

Baeolidia japonica Baba, 1933: 282, Fig. 8.

Spurilla japonica (Baba, 1933): Rudman 1982, 193.
Berghia japonica (Baba, 1933): Gosliner 1985, 261.

Type locality. Tomioka Bay, Japan.

Type material. To our knowledge no type material remains. We designate the specimen CASIZ 1814520 from Ose, Japan, as the neotype in order to avoid confusion with similar species.

Material examined. Neotype: CASIZ 1814520, one specimen, dissected, 2 mm in length preserved, immature, Japan, Ose, collected by Akira Kawahara, 10 February 2010. Other material: CASIZ 186795, one specimen, dissected, 8 mm in length preserved, Marshall Is., collected by Scott Johnson, 12 September 2011; CASIZ 181357, one specimen, dissected, 5 mm in length preserved, Marshall Is., collected by Scott Johnson, 27 December 2008.

Geographical distribution. Originally described from Tomioka Bay, Japan (Baba 1933) it is also known from Shimoda (Nakano 2004), the Ryukyu Is. (Ono 2004), Indonesia (Gosliner *et al.* 2008), the Marshall Is. (present study), Philippines (Gosliner *et al.* 2008), and Papua New Guinea (Gosliner *et al.* 2008).

External morphology (Figs. 2D–E, 3C): Body short, broad, tapering close to posterior end of foot. Foot corners tentaculiform. Body colour brown or translucent white. Bright white spots over dorsum, forming continuous patch from pericardial area to posterior end of foot. Tiny white spots form white mark over head. Rhinophores, oral tentacles and foot corners translucent white. Rhinophores shorter than oral tentacles. Rhinophores full of elongate, white papillae (Fig. 3C); apex white. Oral tentacles with white spots. Cerata moderately short, flattened, almost leaf-like. Cerata usually brownish with white spots, or translucent covered by white pigment; density of white spots varies; some specimens with bluish band on anterior side; a minute white ring on apex. Cerata in two arches followed by rows, leaving a distinct gap between pre and post-pericardial groups. Each group with 4–11 cerata, decreasing in size towards foot. Anus cleioproctic, within right second arch. Gonopore among cerata of anteriormost arch on right.

Anatomy. Masticatory borders smooth (Fig. 4E). Radular formula 33 x 0.1.0 (CASIZ 181357, 5 mm). Radular teeth slightly bilobed with 27–36 elongate, acutely pointed denticles on either side of the inconspicuous central notch (Fig. 4F). Teeth progressively smaller in posterior region of radula. Oral glands small, fragile, spongy. Oral glands dorso-laterally to buccal bulb. Salivary glands long.

Reproductive system diaulic (Fig. 6C). Preampullary duct widening into moderately short ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens entering into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis huge, rounded, short stalk connecting to long oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. When Baba (1933a) described *Baeolidia japonica*, he did not mention anything about colouration. It was sixteen years later (Baba 1949) when the first colour figure of *B. japonica* was published. In that contribution, Baba depicted this species as "ground-colour dark brown, the whole back sprinkled with opaque white spots". This description clearly does not match with our specimens, which are mainly white. Nevertheless, in the same area where Baba described *B. japonica*, both colour types (brownish and whitish) cohabit (Rudman 2002; Nakano 2004; Ono 2004). Since one of our specimens is from the type locality of *B. japonica*, we conclude that both colour types are conspecific.

Excluding *Baeolidia scottjohnsoni* **sp. nov.**, the main internal differences between *B. japonica* and the remaining species of the genus is the shape and the size of the receptaculum seminis. This structure is bigger and more rounded in *B. japonica* than in the remaining *Baeolidia* species. Due to this particular receptaculum seminis, it cannot be confounded with the remaining species of the genus. Its distinction from *B. scottjohnsoni* **sp. nov.** will be discussed in the remarks section for that species.

Carmona *et al.* (2013) studied this species from a molecular approach (Fig. 1).

Baeolidia ransoni (Pruvot-Fol, 1956)

(Figs. 2F, 6D, 7A–B)

Aeolidiopsis ransoni Pruvot-Fol, 1956: 228, Fig. 1.

Type locality. Kaukura Atoll, French Polynesia.

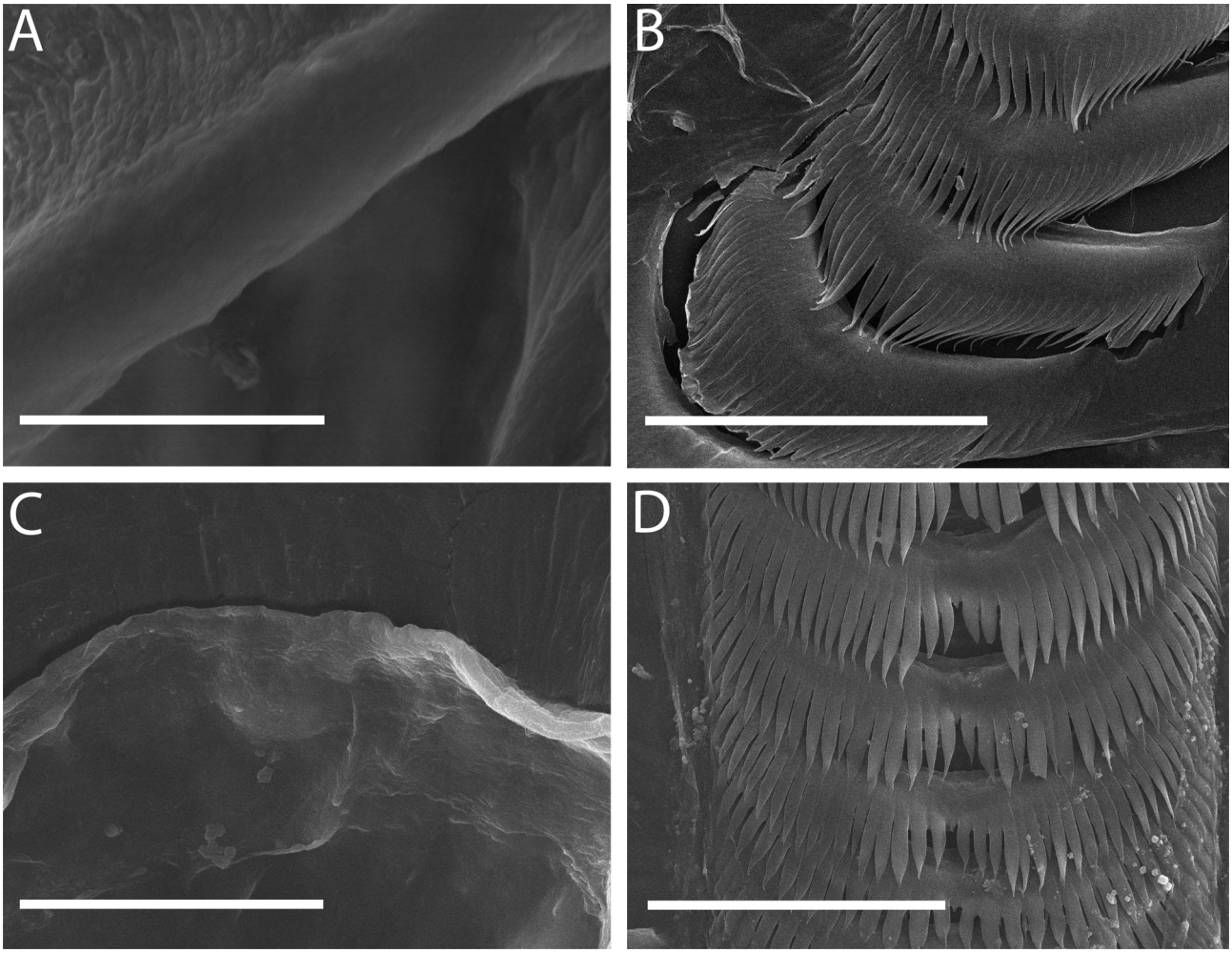

FIGURE 7. Scanning electron photographs. (A–B) *Baeolidia ransoni* (CASIZ 065417); (A) Detailed view of the masticatory border; (B) Radular teeth; (C–D) *Baeolidia salaamica* (CASIZ 184524); (C) Detailed view of the masticatory border; (D) Radular teeth. Scale bars: A, 50 µm; B, 100 µm; C, 50 µm; D, 150 µm.

Type material. To our knowledge no type material exists. We designate the specimen CASIZ 065417 from North of Madang, Papua New Guinea, as the neotype in order to avoid confusion with similar species.

Material examined. Neotype: CASIZ 065417, one specimen, dissected, 3 mm in length preserved, Papua New Guinea, North coast, North of Madang, collected by Richard C. Willan, 31 January 1988. Other material: CASIZ 065300, one specimen, dissected, 10 mm in length preserved, Papua New Guinea, North coast, North of Madang, collected by Richard C. Willan, 31 January 1988; CASIZ 186209, one specimen, dissected, 7 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, Balayan Bay, collected by Terrence M. Gosliner, 28 April 2011; CASIZ 186208, one specimen, Philippines, Luzon, Batangas Province, Calumpan Peninsula, Balayan Bay, collected by Terrence M. Gosliner, 28 April 2011.

Geographical distribution. First described for Kaukura Atoll, French Polynesia (Pruvot-Fol 1956), it is also known from the Indo-Pacific (Australia, Papua New Guinea and the Philippines) (Gosliner *et al.* 2008), Japan (Nakano 2004; Ono 2004) and Hawaii (Pittman & Fiene 2012a).

External morphology (Fig. 2F): Body broad, large, tapering close to posterior end of foot. Foot corners rounded. Body colour translucent with small light ochre and medium bright white spots all over. Density of spots varies. Rhinophores smooth, translucent with ochre pigment. Apex white. Oral tentacles short, slender, tapering near apices. Oral tentacles translucent with small light ochre and medium bright white spots. Cerata flattened, almost leaf-like. Cerata large, closely oppressed to the body surface rather than erect. Cerata translucent with small light ochre and medium bright white spots. Tips translucent. Cerata up to twenty-three rows. Each row contains 1–4 cerata, decreasing in size towards the foot. Anus acleioproctic, dorsally to notal brim. Gonopore located among cerata of anteriormost group on right.

Anatomy. Masticatory edge smooth (Fig. 7A). Radular formulae 11 x 0.1.0 (CASIZ 186209, 7 mm) and 13 x 0.1.0 (CASIZ 065417, 3 mm). Radular teeth pectinate, short with 18–46 elongate, acutely pointed denticles from side to side, without a notch or central cusp (Fig. 7B). Oral glands absent. Salivary glands present.
Reproductive system diaulic (Fig. 6D). Preampullary duct widening into wide ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens elongate, moderately thin, penetrating into wider proximal portion of penial sac, with unarmed penial papilla. Receptaculum seminis rounded, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. The other two *Palythoa* feeders, *Baeolidia harrietae* (Rudman, 1982) and *B. palythoae* Gosliner, 1985, were transferred and ascribed to *Baeolidia* respectively by Gosliner (1985). However, *Aeolidiopsis ransoni* was retained as the sole species of *Aeolidiopsis* because of its acleioproctic anus dorsal to the notal brim (Pruvot-Fol 1956; Gosliner 1985; Miller 2001). Carmona *et al.* (2013) showed that, from a molecular point of view, the position of the anus and the rhinophoral ornamentation are not significant phylogenetically in *Baeolidia*. Hence, *Aeolidiopsis ransoni* was transferred to *Baeolidia*.

Only *B. harrietae* and *B. palythoae* have some resemblance with *B. ransoni* in their colouration, the reticulate pattern of the digestive gland and the cerata lying out the body. However, the smooth rhinophores of the latter species distinguish *B. ransoni* from *B. harrietae* and *B. palythoae*. The teeth of *B. ransoni* are a diagnostic character for this species (Fig. 7B). Teeth of *B. ransoni* lack a central cusp or central notch, are quite arched, pectinate, and have elongate and acutely pointed denticles from side to side. So far, this radular morphology has not been found in any other *Baeolidia* species.

This species was included in the molecular study by Carmona *et al.* (2013) (Fig. 1).

Baeolidia dela (Er. Marcus & Ev. Marcus, 1960)

Berghia dela Er. Marcus & Ev. Marcus, 1960: 924, Figs. 83–86.

Type locality. Addu-Atoll, Maldives Islands.

Type material. To our knowledge no type material exists.

Geographical distribution. So far, this species is only known from the Maldives Islands (Er. Marcus & Ev. Marcus 1960).

External and internal morphology. Described and figured by Er. Marcus & Ev. Marcus (1960). No specimens available for the present study.

Remarks. Ernest & Eveline Marcus (1960) described *Berghia dela*, based on a single specimen. Since this specimen was already preserved, Er. Marcus & Ev. Marcus (1960) could not provide any information about the colouration of the living animal. However, they described and drew the papillate rhinophores, the jaws, the radular tooth and the penis (Er. Marcus & Ev. Marcus 1960, figs. 84–86). The cerata were depicted as cylindrical and were arranged in arches plus rows. Recently, Carmona *et al.* (2014b) stated the main characteristics of the aeolidiid genus *Berghia*. One of the most important is the papillate morphology of the rhinophores, which can be easily distinguished from the rhinophorial ornamentation of *Baeolidia* (see general Discussion). Additionally, based on these authors' investigations, *Berghia* is restricted to the Atlantic and Mediterranean. Therefore, according to these statements, *Berghia dela* should be transferred to *Baeolidia*. Although Er. Marcus & Ev. Marcus (1960) did not give any information about colouration, which is usually critical to recognize and separate species within Aeolidiidae (personal observation), the cylindrical cerata could be the distinctive feature that may help to identify this species if it is ever reported again.

Baeolidia cryoporos Bouchet, 1977

Baeolidia cryoporos Bouchet, 1977: 60, Figs. 26–27.

Type locality. Atlantic Ocean (47º 33 N, 08º 34 W).

Type material. According to Bouchet (1977), the type material was deposited in the Muséum National d'Historie Naturelle, Paris.

Geographical distribution. Deep waters, 2110 m, of the Atlantic Ocean (47º 33 N, 08º 34 W) (Bouchet 1977).

External and internal morphology. Described in detail and figured by Bouchet (1977). No specimens available for the present study.

Remarks. Since Bouchet's description (1977), this species has not been found again. Therefore, the only available information stems from the original description. This deep waters aeolidiid has fusiform cerata in rows and papillate rhinophores. Based on these morphological characters Bouchet (1977) placed this particular member of Aeolidiidae in *Baeolidia*. This author also described the reproductive system, which has an extremely large vas deferens (see figure 27 of Bouchet's contribution), and figured the jaws and one radular tooth. More information about the radula and the oral glands, sometimes absent, would be essential to confirm the allocation of *Baeolidia cryoporos* to this genus. Additionally, this species is the only *Baeolidia* species from the Atlantic and is the only deep-water aeolidiid together with *Aeolidia herculea* Bergh, 1894. The occurrence of this genus in the Atlantic Ocean would need further comparatives studies.

Baeolidia harrietae **(Rudman, 1982)**

(Fig. 8A)

Aeolidiopsis harrietae Rudman, 1982: 157, Figs. 3C, 5D–F, 7–9.
Baeolidia harrietae (Rudman, 1982): Gosliner 1985, 260, Table 1.

Type locality. Lizard Island, Australia.

Type material. The holotype is deposited in the Australian Museum, Sydney (C124689).

Geographical distribution. Originally reported for the Great Barrier Reef of Australia (Rudman 1982), it is also known from Papua New Guinea (Gosliner *et al.* 2008), the Philippines (Gosliner *et al.* 2008) and the Ryukyu Is., Japan (Ono 2004).

External and internal morphology. Figured and described in detail by Rudman (1982). No specimens available for the present study.

Remarks. When Rudman (1982) first described *Aeolidiopsis harrietae*, he pointed out the difficulties of discerning the systematic position of this species within Aeolidiidae. The author finally attributed this species to *Aeolidiopsis* based on the diet similarities with *Aeolidiopsis ransoni*. Gosliner (1985) considered that *Aeolidiopsis harrietae* shares some morphological aspects with *Baeolidia palythoae,* such as the papillate rhinophores, and therefore transferred *A. harrietae* to *Baeolidia.* The molecular phylogeny conducted by Carmona *et al.* (2013) rejected the validity of the genus *Aeolidiopsis*, since *Aeolidiopsis ransoni* clustered within the *Baeolidia* clade. Thus, we agree with Gosliner's (1985) statements and confirm its placement within *Baeolidia.*

Baeolidia ransoni, B. harrietae and *B. palythoae* are very similar from a morphological point of view. However, while *B. harrietae* has papillate rhinophores, *B. ransoni* has smooth ones. *B. palythoae* has two pairs of oral glands, but Rudman (1982) could not find any traces of oral glands in *B. harrietae*.

Baeolidia australis **(Rudman, 1982)**

(Fig. 8B)

Spurilla australis Rudman, 1982, 164, Figs. 12–16.
Berghia australis (Rudman, 1982): Gosliner 1985, 261.
Baeolidia australis (Rudman, 1982): Miller 2001, 633.

Type locality. Long Reef, Australia.

Type material. According to Rudman (1982), the holotype is deposited the Australian Museum, Sydney (C92613).

Geographical distribution. Only reported from New Zealand and Australia (Morton & Miller 1968 as *Baeolidia major*; Powell 1976, 1979; Willan & Morton 1984).

External and internal morphology. Described in detail and figured by Rudman (1982). No specimens available for the present study.

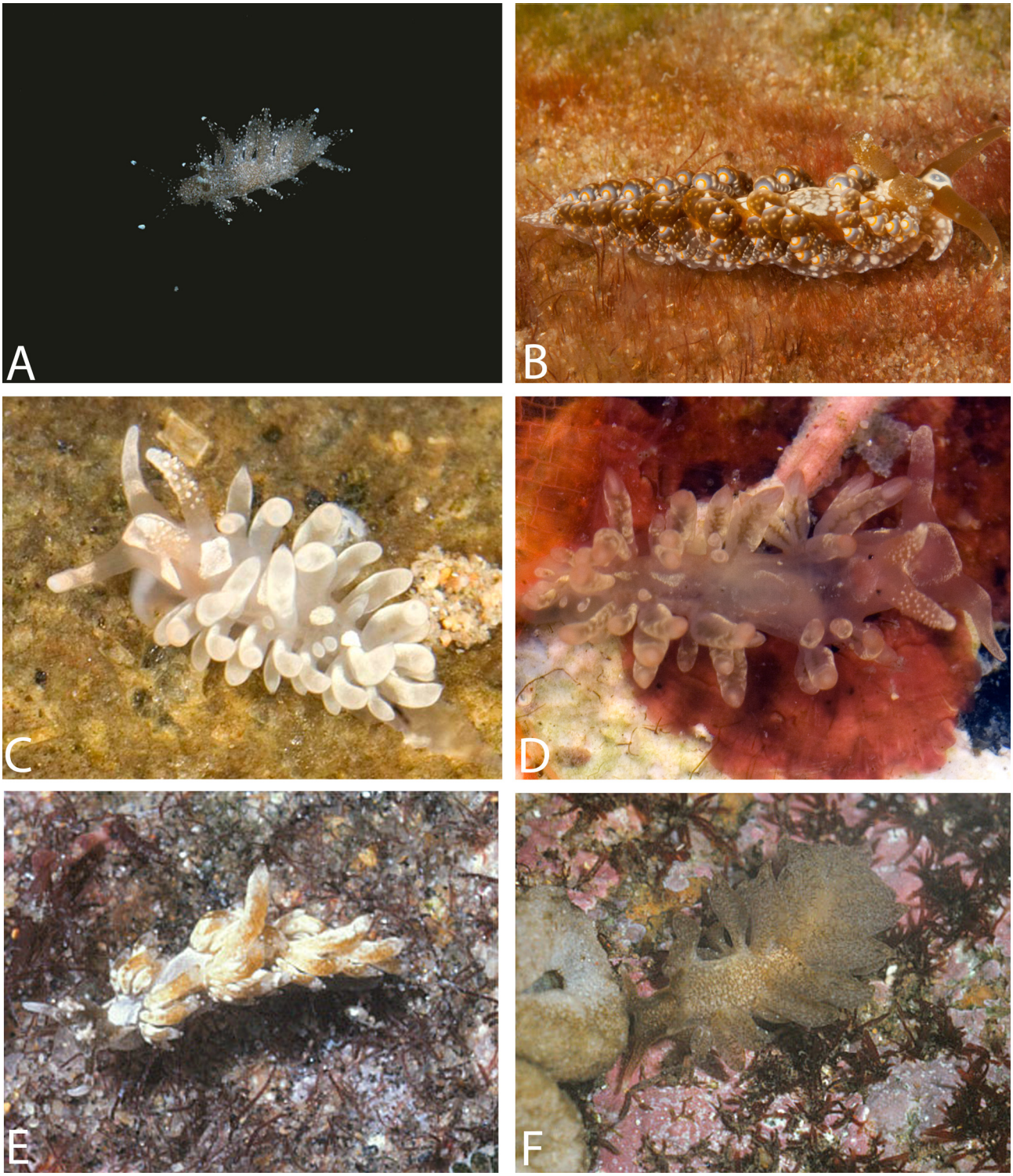

FIGURE 8. Photographs of the living animals. (A) *Baeolidia harrietae*, specimen from Papua New Guinea, photo by Terrence M. Gosliner; (B) *Baeolidia australis,* specimen from Australia, photo by Lean and David Atkinson; (C) *Baeolidia salaamica*, specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 177599; (D) *Baeolidia salaamica*, specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 177397; (E) *Baeolidia chaka*, specimen from South Africa (6 mm), photo by Terrence M. Gosliner; (F) *Baeolidia palythoae*, specimen from South Africa (8 mm), photo by Terrence M. Gosliner.

Remarks. We transfer *Spurilla australis* to *Baeolidia* based on the fact that its rhinophoral papillae (small knobs) are one of the types of *Baeolidia*'s (Fig. 3) and because its morphological similarities with the type species of this genus (*Baeolidia moebii*). Regarding the characteristic of the radula, the teeth of *B. moebii* seem to be wider and have shorter denticles than those of *B. australis*. However, due to the intraspecific variability of this structure

in Aeolidiidae (personal observation), further material of this species would be essential to test the validity of this character. In terms of colouration, *B. australis* has a thin orange sub-apical band above a broad blue band on each cerata, which it is never present in *B. moebii*. *B. australis* looks bluish whereas *B. moebii* is more yellowish or brownish. The body of *B. australis* also seems to have a brown and white reticulate pattern that does not appear to be present in *B. moebii*. Recently Rudman (2007b) questioned the validity of *B. australis*, but until this species could be examined from a morphological and/or molecular point of view we retain *B. australis* as a distinct species.

***Baeolidia salaamica* (Rudman, 1982)**
(Figs. 3D, 7C–D, 8C–D, 9A)

Spurilla salaamica Rudman, 1982: 173, Figs. 21–23.
Berghia salaamica (Rudman, 1982): Gosliner 1985, 261.

Type locality. Dar es Salaam, Tanzania.

Type material. According to Rudman (1982), the material was deposited in the Australian Museum, Sydney (C124695).

Material examined. CASIZ 184524, one specimen, dissected, 6 mm in length preserved, Japan, Manadaru, collected by Rie Nakano, 19 April 2006; CASIZ 177397, one specimen, dissected, 3 mm in length preserved, Philippines, Luzon Island, Batangas Province, Balayan Bay, Anilao, Matotonggil, collected by Terrence M. Gosliner, 18 March 2008; CASIZ 177599, one specimen, 2 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, collected by Terrence M. Gosliner, 16 April 2008.

Geographical distribution. Originally described from Dar es Salaam (Tanzania) (Rudman 1982), this species is also known from Papua New Guinea (Gosliner *et al.* 2008), the Philippines (Gosliner *et al.* 2008), Japan (Ono 1999, 2004; Nakano 2004), Korea (Koh 2006) and Hawaii (Pittman & Fiene 2012b).

External morphology (Fig. 3D, 8C–D): Body short, broad, tapering close towards posterior end of foot. Foot corners tentaculiform. Body colour translucent with white marks scattered over dorsum. White ring, which may have opaque white pigmentation in centre, on head. White diamond-shape mark behind rhinophores. Rhinophores, oral tentacles and foot corners translucent with white marks. Rhinophores shorter than oral tentacles. Rhinophores studded of minute white knobs (Fig. 3D). Apex white. Oral tentacles with white tips.

Cerata moderately long, flattened, almost leaf-like. Branches of digestive gland shining through translucent body wall. Cerata may have white pigmentation (as speckles or covering outer side of cerata) on them. Apex translucent white. Cerata forming two arches plus three rows. Each arch or row contains 2–11 cerata, decreasing in size towards foot. Anus cleioproctic located within second right arch. Genital opening among cerata of anteriormost group on right side.

Anatomy. Masticatory border smooth (Fig. 7C). Radular formulae 13 x 0.1.0 (CASIZ 177397, 3mm) and 19 x 0.1.0 (CASIZ 184524, 6 mm). Radular teeth slightly bi-arched with up to 25 moderately broad, acutely pointed denticles on either side of minute central cusp (Fig. 7D). Teeth progressively smaller towards posterior region of radula. Oral glands small, relatively elongate, spongy. Oral glands dorso-laterally to buccal bulb. Salivary glands absent.

Reproductive system diaulic (Fig. 9A). Preampullary duct widening into ampulla Postampullary duct dividing into oviduct and vas deferens. Vas deferens elongate, entering into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis bean-shaped, connecting to oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. Since Rudman (1982) did not consider *Berghia* and *Baeolidia* as valid genera he described this species as *Spurilla*. Gosliner (1985) transferred *Spurilla salaamica* to *Berghia* based on its papillate rhinophores and cerata in arches. The molecular phylogeny conducted by Carmona *et al.* (2013) showed that *Spurilla/Berghia salaamica* clustered within the *Baeolidi*a clade, breaking the monophyly of *Baeolidia.* Thus, this species was transferred to *Baeolidia,* as the most parsimonious alternative. *Baeolidia salaamica* also shares some morphological features with other members of this genus such as the knob-like papillae of the rhinophores (similar to those found in *B. moebii*), the leaf-like cerata and the cerata arrangement in arches and rows (also in e.g. *B. japonica*). Therefore, we can confirm that *B. salaamica* belongs to this genus.

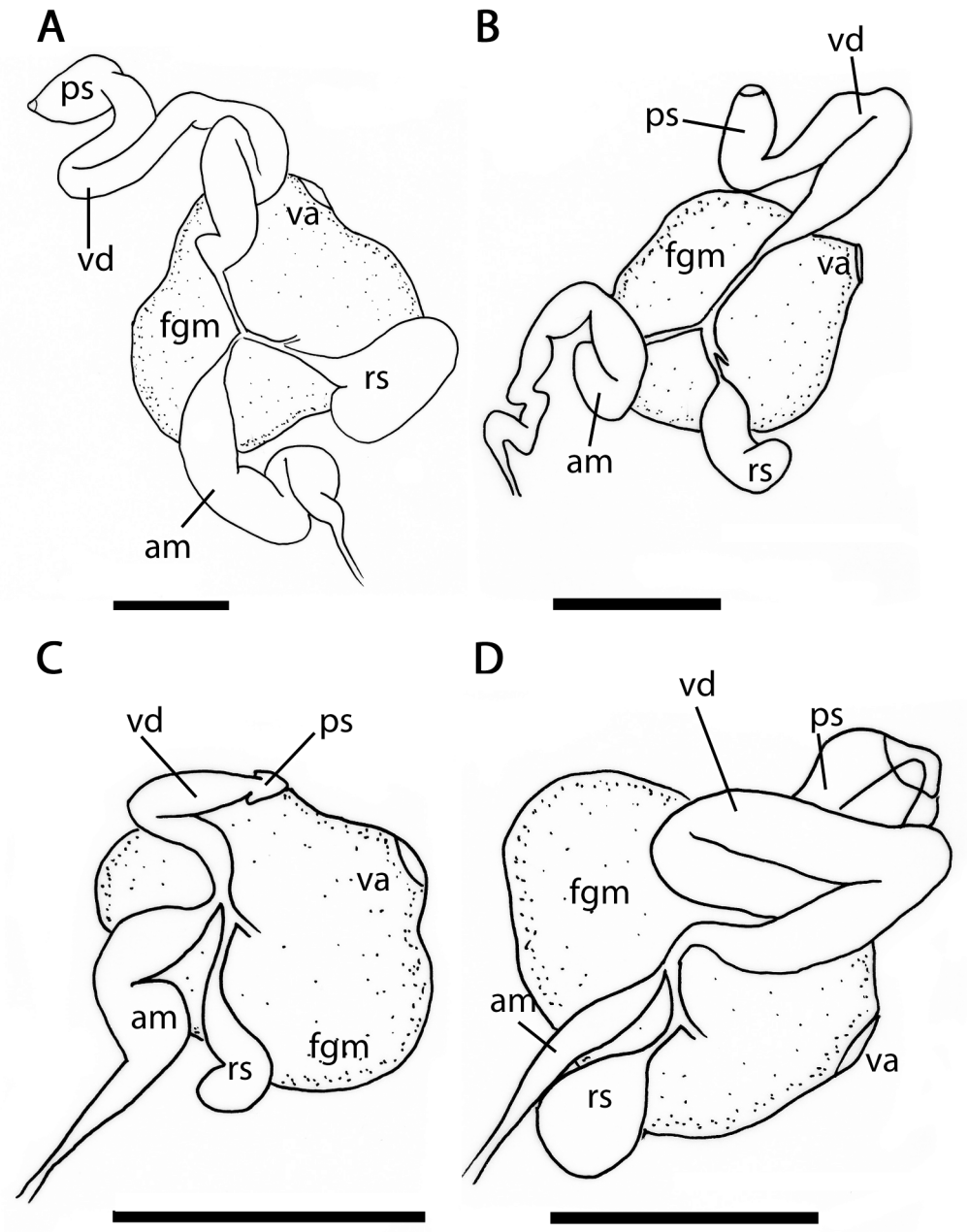

FIGURE 9. Reproductive system. (A) *Baeolidia salaamica,* specimen from Japan (CASIZ 184525); (B) *Baeolidia rieae* **sp. nov.**, specimen from Japan (CASIZ 184525); (C) *Baeolidia variabilis* **sp. nov.**, specimen from the Philippines (CASIZ 177715); (D) *Baeolidia lunaris* **sp. nov.**, specimen from Tanzania (CASIZ 099221). Scale bars: A–D, 0.5 mm. Abbreviations: am, ampulla; fgm, female gland mass; ps, penial sac; rs, receptaculum seminis; va, vagina; vd, vas deferens.

Concerning the original description, only one of our specimens from the Philippines (Fig. 8D) matches completely with Rudman's (1982) diagnosis. Figure 8C shows that the other specimen from the Philippines has somewhat large white patches over the outer side of the cerata. Moreover, none of the specimens here examined bear a denticulate masticatory border (Fig. 7C) as Rudman (1982) stated in the original description. Based on our results in previous studies (Carmona *et al.* 2014a, b, c) we conclude that the latter morphological feature is not significant in Aeolidiidae.

The translucent body, the white ring on the head, the white diamond-shape mark just behind the rhinophores, and mainly the kind of rhinophoral papillae, which is exclusive of *Baeolidia* but being only present in *B. moebii* and *B. australis*, allow us to distinguish *B. salaamica* from other species of this genus. Concerning the anatomical characters, it seems that *B. salaamica* has the wider radular teeth denticles of *Baeolidia* (Fig. 7D). Carmona *et al.* (2013) studied this species from a molecular approach (Fig. 1).

***Baeolidia chaka* (Gosliner, 1985)**
(Fig. 8E)

Berghia chaka Gosliner, 1985, 245, Figs. 11–14.

Type locality. Jesser Point, Sodwana Bay National Park, South Africa.

Type material. The type material was deposited in the South African Museum, Cape Town (Gosliner 1985). The registration number of the holotype of *Baeolidia chaka* is SAM-A35634.

Geographical distribution. So far, only known from South Africa (Gosliner 1985).

External and internal morphology. Described in detail and figured by Gosliner (1985). No specimens available for the present study.

Remarks. *Berghia chaka* was described originally from South Africa (Gosliner 1985). The original description was based on two specimens, both deposited in the South African Museum, Cape Town (SAM). The only available information stems from the original description since this species has not been found again. The body and teeth shape, the flattened cerata and the oral glands described and figured by Gosliner (1985), lead us to transfer *Berghia chaka* to *Baeolidia*.

Gosliner (1985) considered the anteriorly rounded foot as the diagnostic character of *B. chaka*. This species also has some cerata noticeably longer than the rest, which is not very common in *Baeolidia.* In external appearance, *B. chaka* most closely resembles *B. japonica*. However, the latter species possesses tentacular foot corners, a bluish band on the anterior side and cerata uniform in size.

***Baeolidia palythoae* Gosliner, 1985**
(Fig. 8F)

Baeolidia palythoae Gosliner, 1985, 237, Figs. 4–10.

Type locality. Umgazana, South Africa.

Type material. The holotype is deposited in the South African Museum, Cape Town (SAM-A35640).

Geographical distribution. To date, only known from South Africa (Gosliner 1985).

External and internal morphology. Described in detail and figured by Gosliner (1985). No specimens available for the present study.

Remarks. *Baeolidia palythoae* was originally described from South Africa by Gosliner (1985). So far, the only available information about this species is the original description. Gosliner (1985) provided a complete description of this species and figured the rhinophores, the ventral and lateral view of the species, the cerata, the oral glands, the jaws, the central nervous and the reproductive system. This author also presented scanning electron micrographs of the jaws and their masticatory border as well as the radular teeth. The most distinctive features of this species are the second pair of oral glands, which are ovoid in shape and empty on the ventral side of the head, as well as the small tubercles on the masticatory border. *B. palythoae* closely resembles *B. harrietae* in external appearance but both species differ in several features such as the number of cerata per row (4–9 in *B. harrietae* and 3–5 in *B. paylothoae*), the position of the gonopore, the number of oral glands and the ornamentation of the masticatory border (Gosliner 1985).

***Baeolidia rieae* sp. nov.**
LSID urn:lsid:zoobank.org:act:35F88299-66D8-4726-8796-410D907D86F8
(Figs. 9B, 10A, 11A–B).

Baeolidia sp. B: Carmona *et al.* 2013, 6.

Material examined. Holotype: CASIZ 184525, one specimen, dissected, 3 mm in length preserved, Japan, Amami-Ohoshima Island, collected by Rie Nakano, 06 March 2010.

FIGURE 10. Photographs of the living animals. (A) *Baeolidia rieae* **sp. nov.**, specimen from Japan, photo by Jum Imamoto, CASIZ 184525; (B–C) *Baeolidia variabilis* **sp. nov.**: (B) specimen from Marshall Islands, photo by Scott Johnson, CASIZ 187741; (C) specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 177715.

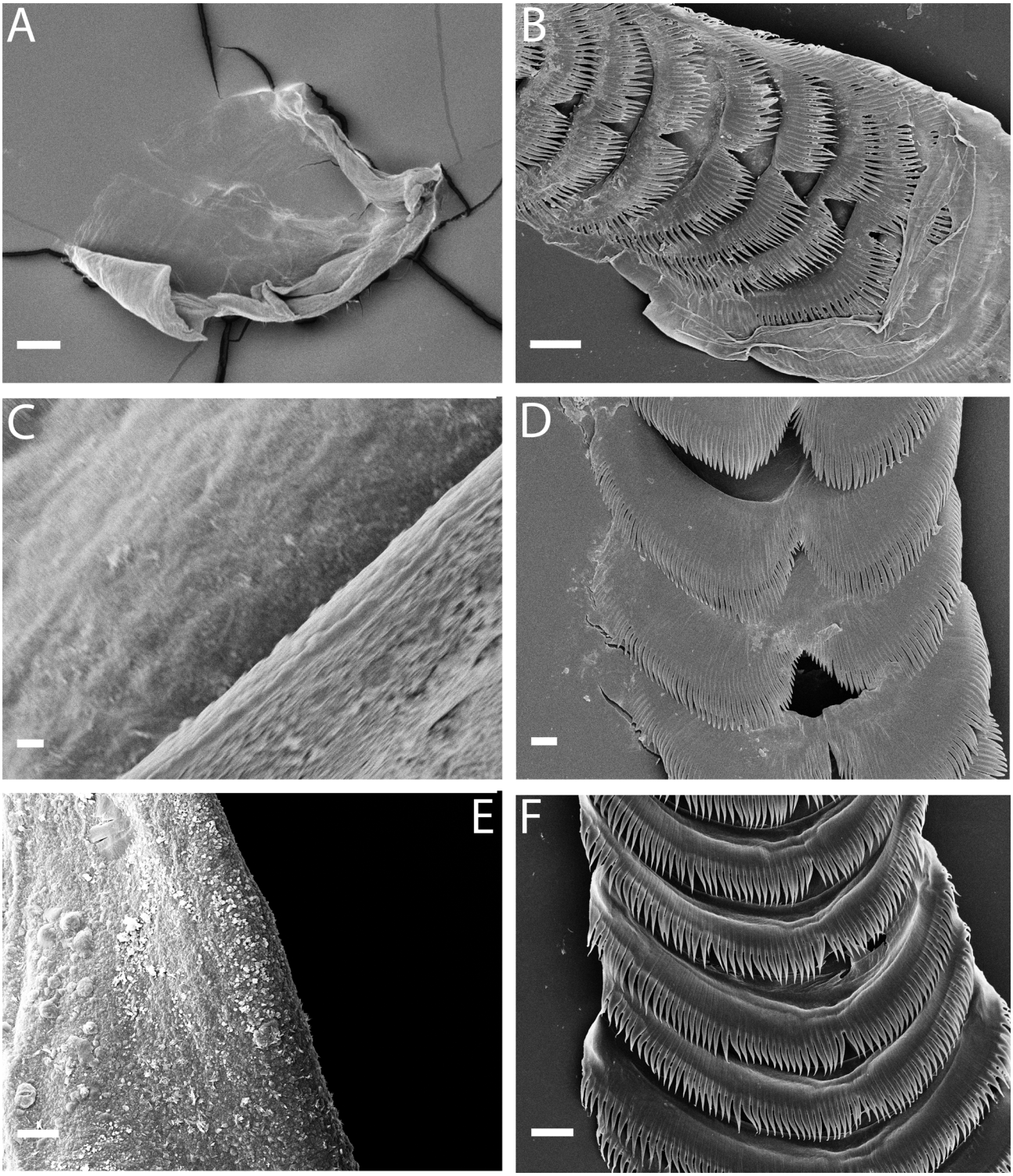

FIGURE 11. Scanning electron photographs. A, B, *Baeolidia rieae* **sp. nov.** (CASIZ 184525); (A) Detailed view of the jaw; (B) Radular teeth; (C–D) *Baeolidia variabilis* **sp. nov.** (CASIZ 177715); (C) Detailed view of the masticatory border; (D) Radular teeth; (E-F) *Baeolidia lunaris* **sp. nov.** (CASIZ 099221); (E) Detailed view of the masticatory border; (F) Radular teeth. Scale bars: A, 30 µm; B, 100 µm; C, 2 µm; D, 10 µm; E, 10 µm; F, 20 µm.

Type locality and habitat. The Amami-Ohoshima Island, Japan. Found in 7 m of water close to green zoanthids.

Geographical distribution. So far, only known from Japan (present study).

Etymology. This species is named after Rie Nakano who kindly provided us material from Japan, including this new species.

External morphology (Fig. 10A): Body short, broad, tapering close towards posterior end of foot. Foot corners rounded. Body colour translucent. Dark ochre and pearly white pigmentation over notum. Rhinophores same colour as ground body colour with inconspicuous papillae. Apex pearly white. Cerata large, flattened, almost leaf-like. Cerata light ochre with pearly white, dark ochre and iridescent green pigmentation. Cnidosacs white. Cerata in one arch followed by three rows, leaving a distinct gap between pre and post-pericardial groups. Each arch with 2–5 cerata, decreasing in size towards the foot. Anus cleioproctic, behind first right row. Gonopore behind the anteriormost row on right.

Anatomy. Ornamentation of masticatory border could not be determined (Fig. 11A). Radular formula 20 x 0.1.0 (CASIZ 184525, 3 mm). Radular teeth bilobed with 31–39 elongate, acutely pointed denticles on either side of minute central cusp (Fig. 11B). Teeth progressively smaller towards posterior region of radula. Oral glands small, spongy, dorso-laterally to buccal bulb. Salivary glands absent.

Reproductive system diaulic (Fig. 9B). Preampullary duct widening into moderately long ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens short, penetrating into wider proximal portion of the penial sac with unarmed penial papilla. Receptaculum seminis bean-shaped, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. *Baeolidia rieae* **sp. nov.** is clearly distinguishable from other members of the genus by its conspicuous iridescent pigmentation. Only *Baeolidia lunaris* **sp. nov.** and *Baeolidia gracilis* **sp. nov.** (see below) have this kind of pigment. Nevertheless, in *B. lunaris* **sp. nov.**, the cerata have a completely different colouration and a very characteristic white spot on their bases. In addition, the body colour of *B. gracilis* **sp. nov.** is much darker than in *B. rieae* **sp. nov.**. *B. gracilis* also has larger cerata with an opaque white line on their inner margin (see below), which is absent in *B. rieae* **sp. nov.**. Anatomically, these three species are similar but some differences could be found. While the radular teeth of *B. lunaris* **sp. nov.** are pectinate, *B. rieae* **sp. nov.** and *B. gracilis* **sp. nov.** have bilobed teeth. In addition, the teeth of *B. rieae* **sp. nov.** show a minute central cusp, but *B. gracilis* **sp. nov.** only has a central notch. *Baeolidia rieae* **sp. nov.** and *B. gracilis* **sp. nov.** also differ in number of oral glands. Regarding the receptaculum seminis, there are differences in shape. While the receptaculum seminis of *B. rieae* **sp. nov.** is bean-like, in *B. lunaris* **sp. nov.** and *B. gracilis* **sp. nov.** it is rounded and ovoid respectively. Moreover, the length of the vas deferens also varies among these species, having an intermediate length in *B. rieae* **sp. nov.**.

This new species was included in the molecular study by Carmona *et al.* (2013) (Fig. 1).

Baeolidia variabilis **sp. nov.**

LSID urn:lsid:zoobank.org:act:B6B01F57-6AD8-49AD-B95D-B7F7EE91C9DC
(Figs. 3C, 9C, 10B–C, 11C–D)

Berghia sp. 1: Gosliner *et al.* 2008, 404.
Berghia sp. 4: Gosliner *et al.* 2008, 405.
Baeolidia sp. A: Carmona *et al*. 2013, 6.

Material examined. Holotype: CASIZ 103739, one specimen, dissected, 4 mm in length preserved, Philippines, Mindoro, Medio Island, collected by Terrence M. Gosliner, 28 February 1995; Paratype: CASIZ 190618, one specimen, dissected, 3 mm in length preserved, Papua New Guinea, North coast collected by Terrence M. Gosliner, 29 January 1988. Other material: CASIZ 177715, one specimen, dissected, 4 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, collected by Terrence M. Gosliner, 21 April 2008; CASIZ 177716, one specimen, dissected, 3 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, collected by Terrence M. Gosliner, 21 April 2008; CASIZ 186210, one specimen, dissected, 2 mm in length preserved, Philippines, Luzon, Batangas Province, Maricaban Island, collected by Terrence M. Gosliner, 21 May 2011; CASIZ 187741, two specimens, dissected, 11 and 10 mm in length alive, Marshall Island, Kwajalein Atoll, collected by Scott Johnson, 24 July 2011.

Type locality and habitat. Medio Island, Mindoro, Philippines. Found in shallow water reefs under coral rubble, where it likely feeds on small sea anemones.

Geographical distribution. So far, only known from the Philippines, the Marshall Islands and Papua New Guinea (present study).

Etymology. In Latin the word "*variabilis*" means variable. The specific name refers to the two colour types of this species.

External morphology (Figs. 3C, 10B–C): Body short, broad, tapering close to posterior end of foot. Foot corners, short and rounded. Body colour translucent with two different colour patterns. First one with opaque white patches on head (its density varies) and notum (Fig. 10B). Light ochre reticulate on both sides of body. Second one with small light ochre spots all over body (Fig. 10C). Rhinophores approximately equal in length to oral tentacles. Rhinophores densely covered by elongate papillae (Fig. 3C). Rhinophores translucent with ochre pigment and white apex. Oral tentacles short, slender, tapering near apices. Oral tentacles same colour as ground colour and white tips.

Cerata flattened, almost leaf-like. In first colour pattern, cerata ochre with white pigmentation on posterior side of basal portion. Some cerata noticeably longer than others. In second colour pattern, cerata recurved inwardly, with some papillae or bulbs. Cerata completely white, usually having bright yellow pigment on posterior side of their distal area. Cerata in two or three arches followed by a couple of rows. Cerata groups leaving a distinct gap between pre and post-pericardial groups. Each group with 1–5 cerata, decreasing in size towards foot. Anus cleioproctic, below second right arch. Genital aperture among cerata of anteriormost group on right.

Anatomy. Masticatory process smooth (Fig. 11C). Radular formulae 8 x 0.1.0 (CASIZ 103739, 4 mm), 14 x 0.1.0 (CASIZ 177715, 4mm). Radular teeth bilobed with 47–52 elongate and acutely pointed denticles on either side of minute central cusp (Fig. 11D). Teeth progressively smaller towards posterior region of radula. Oral glands small, moderately elongate, fragile, spongy, laying dorso-laterally to buccal bulb. Ventral gland present. Salivary glands absent.

Reproductive system diaulic (Fig. 9C). Preampullary duct widening into conspicuous ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens short, entering into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis bean-shaped receptaculum seminis, short stalk connecting to long oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. This particular species highlights how variable the colouration can be within the same species. Gosliner *et al.* (2008) identified both colour patterns as separate species but the molecular analyses undertaken by Carmona *et al.* (2013) showed that they are conspecific. Further studies would help to elucidate if these colour patterns depend on habitat, prey and/or an ontogenetic process.

Both colour patterns differ consistently from the remaining *Baeolidia* species but *B. japonica, B. salaamica*, *B. gracilis* **sp. nov.** and *B. scottjohnsoni* **sp. nov.** (see below) are somewhat similar in external appearance. However, *B. salaamica* is completely translucent, including the cerata, while the body colour of *B. variabilis* **sp. nov.** is opaque white or covered by small ochre flecks. *B. scottjohnsoni* **sp. nov.** and *B. japonica* have a characteristic blue band at the anterior side of the cerata, which is not found in *B. variabilis* **sp. nov.**. Internally, differences in the size of the receptaculum seminis between *B. variabilis* **sp. nov.** and *B. scottjohsoni* **sp. nov.** are also obvious (Fig. 8C and 14B respectively). None of these species has a ventral oral gland except *B. gracilis* **sp. nov.** (see below) but *B. variabilis* **sp. nov.** lacks any traces of the iridescent pigment found on *B. gracilis* **sp. nov.**.
Carmona *et al.* (2013) included this new species in their molecular phylogeny (Fig. 1).

***Baeolidia lunaris* sp. nov.**
LSID urn:lsid:zoobank.org:act:249BBCD0-ED70-4513-8954-BB8566ECFC0E
(Figs. 3C, 9D, 11 E–F, 12A)

Baeolidia sp. 1: Gosliner *et al.* 2008, 405.

Material examined. Holotype: CASIZ 099221, one specimen, dissected, 10 mm in length alive, Tanzania, Mtwara Region, Mana Huanja Island, collected by Terrence M. Gosliner, 01 November 1994.

Type locality and habitat. Mtwara Region, Mana Huanja Island, Tanzania. Found in shallow water feeding on zoanthids.

Geographical distribution. So far, only known from Tanzania (present study).

Etymology. The specific name refers to the white patch present at the base of the cerata, similar to the moon (from latin: *lunaris*, pertaining to the moon).

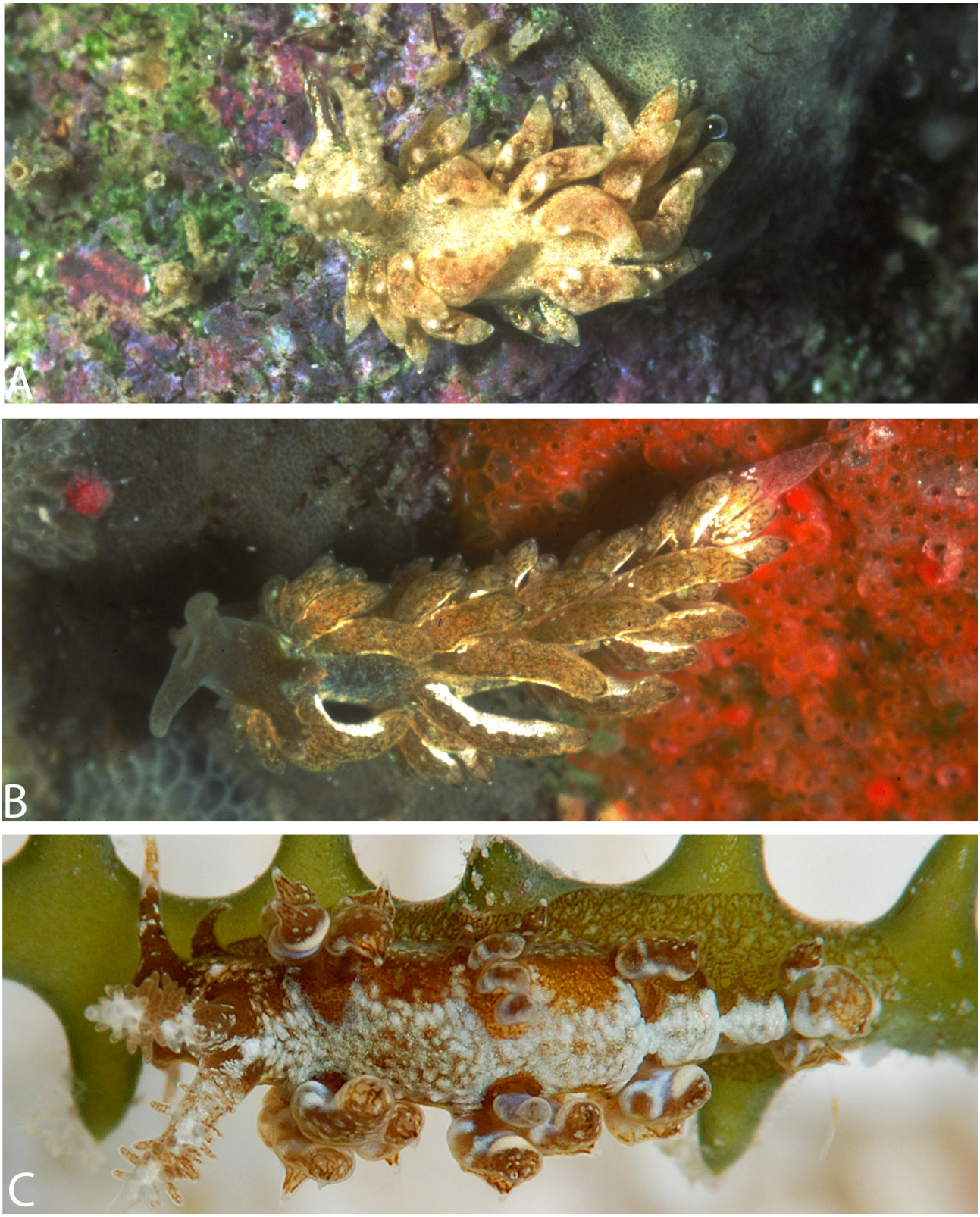

FIGURE 12. Photographs of the living animals. (A) *Baeolidia lunaris* **sp. nov.**, specimen from Tanzania, photo by Terrence M. Gosliner, CASIZ 099221; (B) *Baeolidia gracilis* **sp. nov.**, specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 083766; (D) *Baeolidia scottjohnsoni* **sp. nov.**, specimen from Marshall Islands, photo by Scott Johnson, CASIZ 184503.

External morphology (Figs. 3C, 12A): Body short, broad, tapering close to posterior end of foot. Foot corners rounded. Body colour translucent brownish. Fine iridescent opaque white spots over body. Rhinophores approximately equal in length to oral tentacles. Rhinophores densely covered by elongate papillae (Fig. 3C). Rhinophores translucent brownish with small white spots. Apex white. Oral tentacles translucent brownish short, slender, tapering near apices. Cerata moderately long, flattened, leaf-like. Cerata same colour as ground body colour, but a little bit darker. White spot on anterior side of cerata, close to base. Cerata recurved inwardly. Apex white. Cerata in one arch and four rows, leaving a distinct gap between pre and post-pericardial groups. Each group with 2–5 cerata, decreasing in size towards foot. Anus cleioproctic, below first right row. Gonopore housed among cerata of anteriormost right group.

Anatomy. Masticatory process smooth (Fig. 11E). Radular formula 21 x 0.1.0 (CASIZ 099221, 10 mm). Radular teeth blended with 52–71 elongate, acutely pointed denticles (Fig. 11F). Central cusp absent. Teeth progressively smaller towards posterior radular region. Oral glands small, ovoid, delicate. Salivary glands long. Reproductive system diaulic (Fig. 9D). Preampullary duct widening into short ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens entering into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis rounded, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. Three *Baeolidia* species are known from Tanzania. Only *B. moebii* (Eliot, 1903; Edmunds, 1970), *B. salaamica* (Rudman, 1982) and *B. lunaris* **sp. nov.** (present study) have been reported in that country. In terms of colouration, *B. lunaris* **sp. nov.** differs from *B. moebii* and *B. salaamica* in several features. *B. lunaris* **sp. nov.** lacks the whitish or yellow ring usually present in *B. moebii*. The latter species also has a bright yellow subapical band, which does not appear in *B. lunaris* **sp. nov.**. *B. salaamica* lacks any traces of iridescent pigmentation, being mainly translucent white or brown. Moreover, both species, *B. salaamica* and *B. lunaris* **sp. nov.** differ in the shape of the radular teeth (see Figs. 7C–D and 11E–F respectively). The radular teeth of *B. salaamica* are bilobed while *B. lunaris* **sp. nov.** has pectinate teeth. However, teeth of *B. moebii* and *B. lunaris* **sp. nov.** are very similar (Figs. 4A–B and 11E–F respectively). In terms of reproductive system, *B. lunaris* **sp. nov.** is the only of these three species with rounded receptaculum seminis. The main difference among these species from Tanzania is the morphology of the papillae of their rhinophores. While *B. moebii* and *B. salaamica* have rounded and short papilla, *B. lunaris'* **sp. nov.** are clearly longer.

Regarding the remaining members of this genus, *B. lunaris* **sp. nov.** is similar to *B. rieae* **sp. nov.** and *B. gracilis* **sp. nov.** (see below) in that the three species have iridescent pigment. Neither *B. rieae* **sp. nov.** nor *B. gracilis* **sp. nov.** have a white spot at the base of the anterior side of the cerata. Additionally, the shape of the radular teeth of *B. gracilis* **sp. nov.** and *B. rieae* **sp. nov.** is different of *B. lunaris'* **sp. nov.**. The former species have a radular teeth more bilobed and less bended than the radular teeth of *B. lunaris* **sp. nov.** (see Figs. 11A–B, 11E–F and 13A–B respectively). Because of the lack of material properly conserved for a molecular study, we could not test the validity of this species from a molecular perspective. However, we consider that the morphological and colour characteristics presented here support the validity of *Baeolidia lunaris* **sp. nov.**.

***Baeolidia gracilis* sp. nov.**

LSID urn:lsid:zoobank.org:act:A50C22AD-2E31-4D77-841F-7DEF78087E20

(Figs. 12B, 13A–B, 14A)

Berghia sp. 2: Gosliner *et al.* 2008, 404.

Material examined. Holotype: CASIZ 083766, one specimen, dissected, 9 mm in length preserved, Philippines, Luzon, Batangas Province, Calumpan Peninsula, Maricaban Strait, collected by Terrence M. Gosliner, 22 February 1992.

Type locality and habitat. Arthur's Rock (South West side of Calumpan Peninsula), Maricaban Strait, Calumpan Peninsula, Batangas Province, Luzon, Philippines. Found under coral rubble in 10 m of water.

Geographical distribution. Thus far, known only from the Philippines (present study).

Etymology. The specific name refers to the slender body of this species.

External morphology (Figs. 12B): Body moderately elongate, tapering close to translucent posterior end of

foot. Foot corners rounded. Head and pericardium dark greyish blue. Posterior part of notum and cerata ochre. Iridescent greyish blue and bright ochre pigment over pericardium. Reticulate brown pattern close to foot edges. Rhinophores approximately equal in length to oral tentacles. Rhinophores dark greyish blue with only few moderately short papillae, mainly in posterior part. Oral tentacles short, slender, tapering near apices. Oral tentacles with same colour as rhinophores.

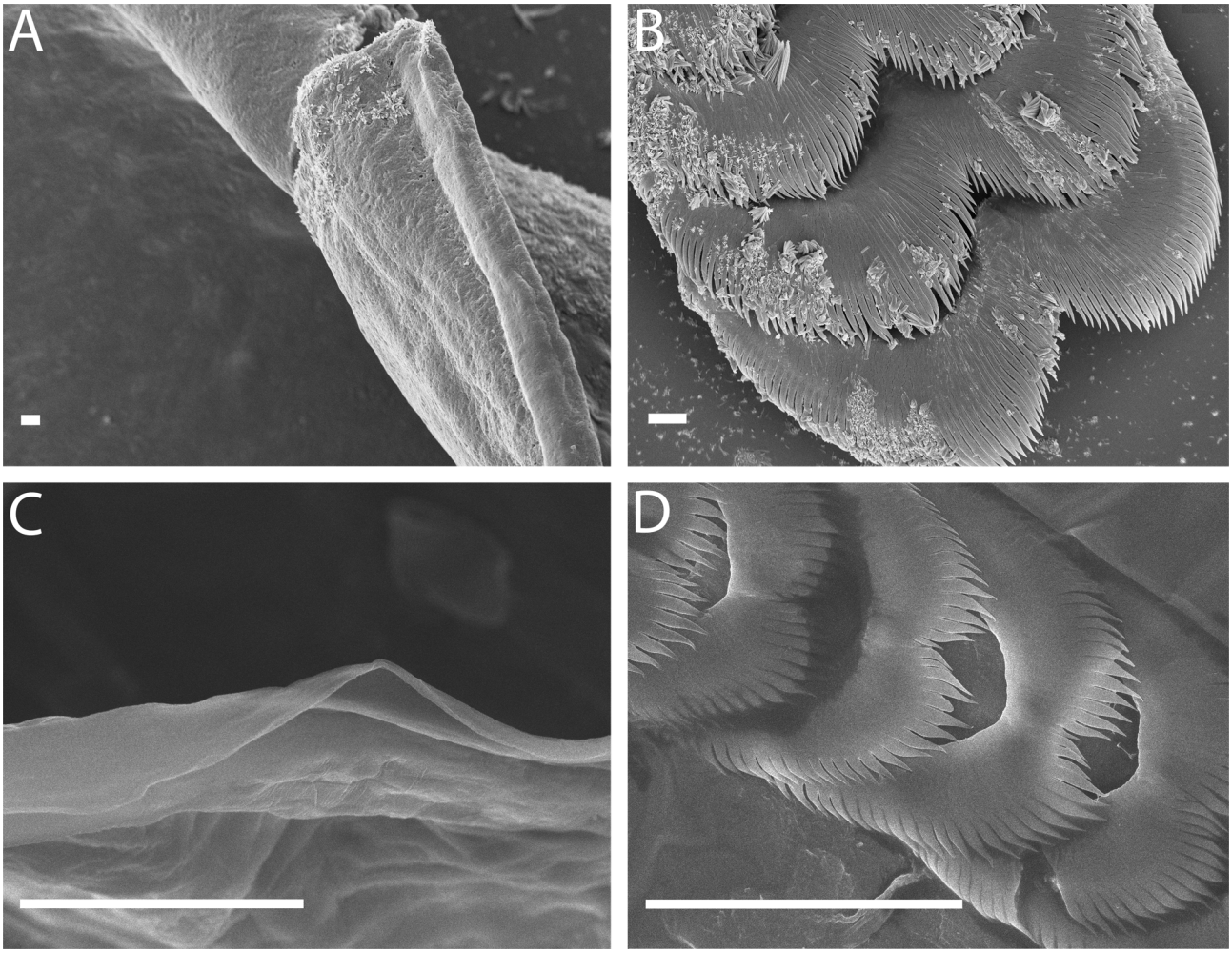

FIGURE 13. Scanning electron photographs. (A–B) *Baeolidia gracilis* **sp. nov.** (CASIZ 083766); (A) Detailed view of the masticatory border; (B) Radular teeth; (C–D) *Baeolidia scottjohnsoni* **sp. nov.** (CASIZ 184503); (C) Detailed view of the masticatory border; (D) Radular teeth. Scale bars: A, 3 µm; B, 10 µm; C, 50 µm; D, 100 µm.

Cerata long, flattened, pod-bean-like. Cerata with greenish ochre net, converging on translucent apex. Inner margin with opaque white line. Cerata in three arches followed by five rows, leaving a distinct gap between pre-pericardial group and post-pericardial groups. Each group with 1–9 cerata, decreasing in size towards foot. Anus cleioproctic, below second right arch. Gonopore among cerata of anteriormost group on right.

Anatomy. Masticatory process smooth (Fig. 13A). Radular formula 9 x 0.1.0 (CASIZ 083766, 9 mm). Radular teeth bilobed with 48–63 elongate, acutely pointed denticles on either side of notch (Fig. 13B). Two pairs of oral glands. Oral glands delicate. First pair elongate, laying dorso-laterally to buccal bulb. Second pair smaller, rounded, emptying on ventral side of head. Salivary glands absent.

Reproductive system diaulic (Fig. 14A). Preampullary duct widening into short ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens inserting into wider proximal portion of penial sac, with unarmed penial papilla. Receptaculum seminis moderately large, ovoid, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. While most of the *Baeolidia* species have a stout body, *Baeolidia gracilis* **sp. nov.** is much more slender than the others members of this genus (see e.g. Fig. 12). The cerata of this species are also particular. They are long, flattened and pod-bean-like rather than being leaf-like. This morphological features and its colour pattern

characterize this species. Regarding colouration, *B. gracilis* **sp. nov.** most closely resembles *B. rieae* **sp. nov.** and *B. lunaris* **sp. nov.**. However, *B. gracilis* **sp. nov.** has a white line on the inner margin of the cerata that is not present in *B. rieae*. **sp. nov.** Moreover, *B. rieae* **sp. nov.** lacks the second pair of oral glands of *B. gracilis* **sp. nov.**. The latter species does not have the white spot close to the base of cerata of *B. lunaris* **sp. nov.**. Both species also differ in the radular morphology (see Fig. 11E–F for *B. lunaris* **sp. nov.** and 13A–B for *B. gracilis* **sp. nov.**). In terms of internal anatomy, in addition to this new species, only *B. variabilis* **sp. nov.** and *B. palythoae* have two pairs of oral glands. *B. variabilis* **sp. nov.** and *B. gracilis* **sp. nov.** have consistent differences in colouration, while *B. palythoae* has papillae over the masticatory border, which is smooth in *B. gracilis* **sp. nov.**.

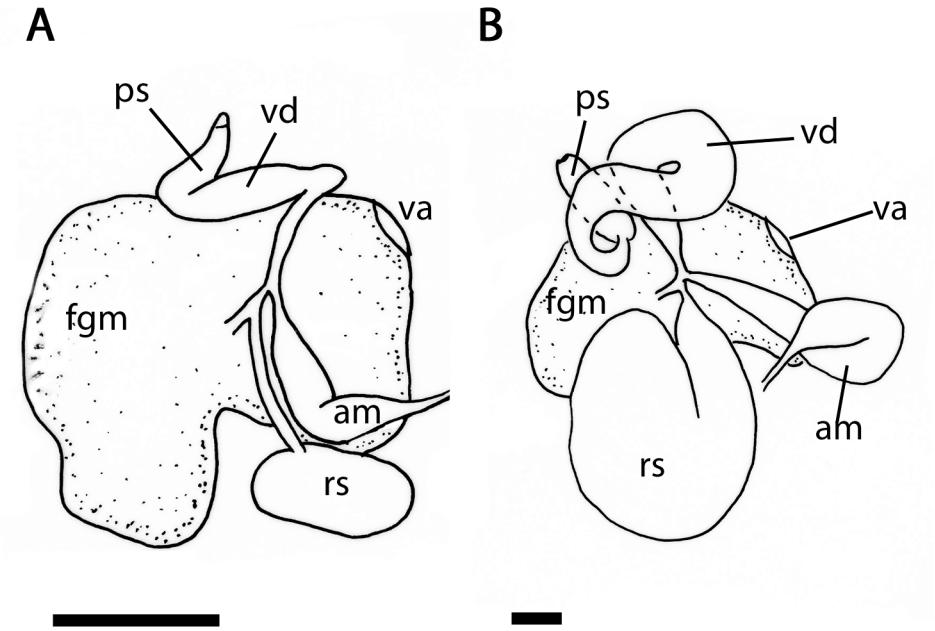

FIGURE 14. Reproductive system. (A) *Baeolidia gracilis* **sp. nov.**, specimen from the Philippines (CASIZ 083766); (B) *Baeolidia scottjohnsoni* **sp. nov.**, specimen from Marshall Islands (CASIZ 184503). Scale bars: A, 0.5 mm; B, 1 mm. Abbreviations: am, ampulla; fgm, female gland mass; ps, penial sac; rs, receptaculum seminis; v, vagina; vd, vas deferens.

***Baeolidia scottjohnsoni* sp. nov.**
LSID urn:lsid:zoobank.org:act:EDE11CBD-6EE9-43D1-9970-158C1FEB2E1A
(Figs. 3C, 12C, 13C–D, 14C)

Baeolidia sp. C: Carmona *et al.* 2013, 6.

Material examined. Holotype: CASIZ 184503, one specimen, dissected, 12 mm in length alive, Marshall Islands, Kwajalein Atoll, Enewetak Pinnacle, collected by Scott Joshnson, 11 October 2010. Paratype: CASIZ 180341, one specimen, dissected, 12 mm in length alive, Hawaii, Maui, Wahikuli, collected by Pauline Fiene, 30 November 2003.

Type locality and habitat. Enewetak Pinnacle, Kwajalein Atoll, Marshall Islands. Found in 10 m of water over *Caulerpa.*

Geographical distribution. So far, only known from the Marshall Islands and the Hawaiian Islands (present study).

Etymology. This species is dedicated to Scott Johnson who kindly provided us with abundant material from the Marshall Islands, including specimens of this new species.

External morphology (Figs. 3C, 12C): Body short, broad, tapering close to posterior end of foot. Foot corners tentaculiform. Body brownish. Bright white spots over head, dorsum and foot. White spots over notum form almost a continuous patch from pericardial area to posterior end of foot, excluding ceratal insertions. Iridescent blue

pigmentation over white spots, more evident on those parts of dorsum where groups of cerata from both sides are closer as well as close to ceratal insertion. Rhinophores, oral tentacles and foot corners brownish with bright white spots. Rhinophores approximately same length of oral tentacles. Rhinophores with elongated papillae (Fig. 3C). Distal papillae whiter. Apex white. Oral tentacles with white spots. Cerata moderately short, flattened, leaf-like. Cerata slightly recurved inwards. Cerata brown with white spots on posterior side. Double subapical band on anterior side of cerata. Upper half of cerata white; second half iridescent blue that may reach their base. Orange or light ochre patch may be found on distal part of posterior side of cerata, being overlaid by bright ochre reticulate. Latter converges on apex. Apex with minute white ring. Cerata in two arches and two rows, leaving a distinct gap between pre and post-pericardial groups. Each group with 2–4 cerata, decreasing in size towards foot. Cleioproctic anus within second right arch. Genital aperture placed within anteriormost arch on right.

Anatomy. Masticatory process smooth (Fig. 13C). Radular formula 14 x 0.1.0 (CASIZ 184503, 12 mm). Radular teeth slightly bilobed with 25 moderately broad and acutely pointed denticles on each side of the small and elongate central cusp (Fig. 13D). Oral glands small, delicate (spongy), elongate. Salivary glands absent.
Reproductive system diaulic (Fig. 14B). Preampullary duct widening into ampulla. Postampullary duct dividing into oviduct and vas deferens. Vas deferens moderately long vas deferens inserting into wider proximal portion of penial sac with unarmed penial papilla. Receptaculum seminis huge, folded, short stalk connecting to short oviduct, before latter forms female glands. Vagina ventral to penis.

Remarks. Excluding *Baeolidia japonica*, *B. scottjohnsoni* **sp. nov.** is easily distinguishable from other members of the genus due to its colouration and the shape and size of its receptaculum seminis. However, the brownish colour pattern of *B. japonica* has some resemblances with *B. scottjohnsoni* **sp. nov.**. Both species have brownish body colour, with white spots all over the notum and a blue band on the posterior side of the cerata. Furthermore, both species have a huge receptaculum seminis (Figs. 6C and 14B). Nevertheless, the molecular phylogenetic analysis conducted by Carmona *et al.* (2013) (see Fig. 1) clearly illuminated the presence of distinct cryptic species that are separated by some morphological differences. The blue pigment over the notum of *B. scottjohnsoni* **sp. nov.**, differences in the radular morphology (denticles of *B. scottjohnsoni* **sp. nov.** are broader than those of *B. japonica*), and the folded receptaculum seminis of *B. scottjohnsoni* **sp. nov.** distinguish these species.

Carmona *et al.* (2013) studied this species from a molecular approach (Fig. 1).

Discussion

Genus *Baeolidia*

Recently, the monophyly of *Baeolidia* was recovered in the first molecular phylogenetic study of Aeolidiidae (Carmona *et al.* 2013). So far, *Baeolidia* is the largest genus within Aeolidiidae with sixteen valid species. Some species traditionally ascribed to *Baeolidia* such as *Baeolidia fusiformis*, *Baeolidia benteva* and *Baeolidia nodosa* belong to other aeolidiid genera but not to *Baeolidia* (Carmona *et al.* 2013; Carmona *et al*. 2014b,c). Moreover, *Baeolidia macleayi*, *Baeolidia dela* and *Baeolidia chaka* are transferred to this genus for the first time. Figure 1 shows the phylogenetic hypothesis for *Baeolidia* presented by Carmona *et al.* (2013.) but showing the final names of the new species on the right side of vertical bars.

Except for the Atlantic species *Baeolidia cryoporos*, this genus is entirely Indo-Pacific with just a few representatives in the Eastern Pacific. Only *B. moebii, B. ransoni, B. harrietae* and *B. salaamica* present populations in the Indo-Pacific as well as in the Eastern Pacific.

The inclusion of *Baeolidia ransoni* and *Baeolidia macleayi,* with smooth and ribbed rhinophores respectively, and the existence of different cerata arrangements within this genus require modifying the diagnosis of the genus *Baeolidia*. All the traditional morphological characters (e.g. the reproductive system and radula) and new morphological traits, such as the oral glands and the rhinophoral papillae, have been deeply studied here. At a generic level, the oral glands, the different types of rhinophoral papillae, the radular morphology and the leaf-shaped cerata were shown to be informative. However, there are species that lack some of these characters. In fact, this genus has the greatest diversity of morphological patterns within Aeolidiidae (see revised diagnosis), which makes it very difficult to determine new synapomorphies at this level based on anatomical data. This situation has also been demonstrated with other heterobranch groups such as *Tambja* and *Roboastra* (Pola *et al.* 2007, 2008) as well as within Aeolidiidae with *Berghia* (Carmona *et al.* 2014b).

Some morphological traits also have intraspecific variation. The ornamentation of the masticatory border (e.g. *Baeolidia salaamica*) and the presence or absence of oral glands (e.g. *Baeolidia moebii*) may vary within the same species. Although the intraspecific varibilty of the precence/absence of the oral glands has not been reported in the literature, this variation has also been observed in *Limenandra nodosa* (Carmona *et al*., 2014c). Thus, in order to separate species, the colouration of the living animal can be considered as the main character in *Baeolidia* together with the ornamentation of the rhinophores (including the different types of papillae) and, in some cases, the radular morphology (Table 1).

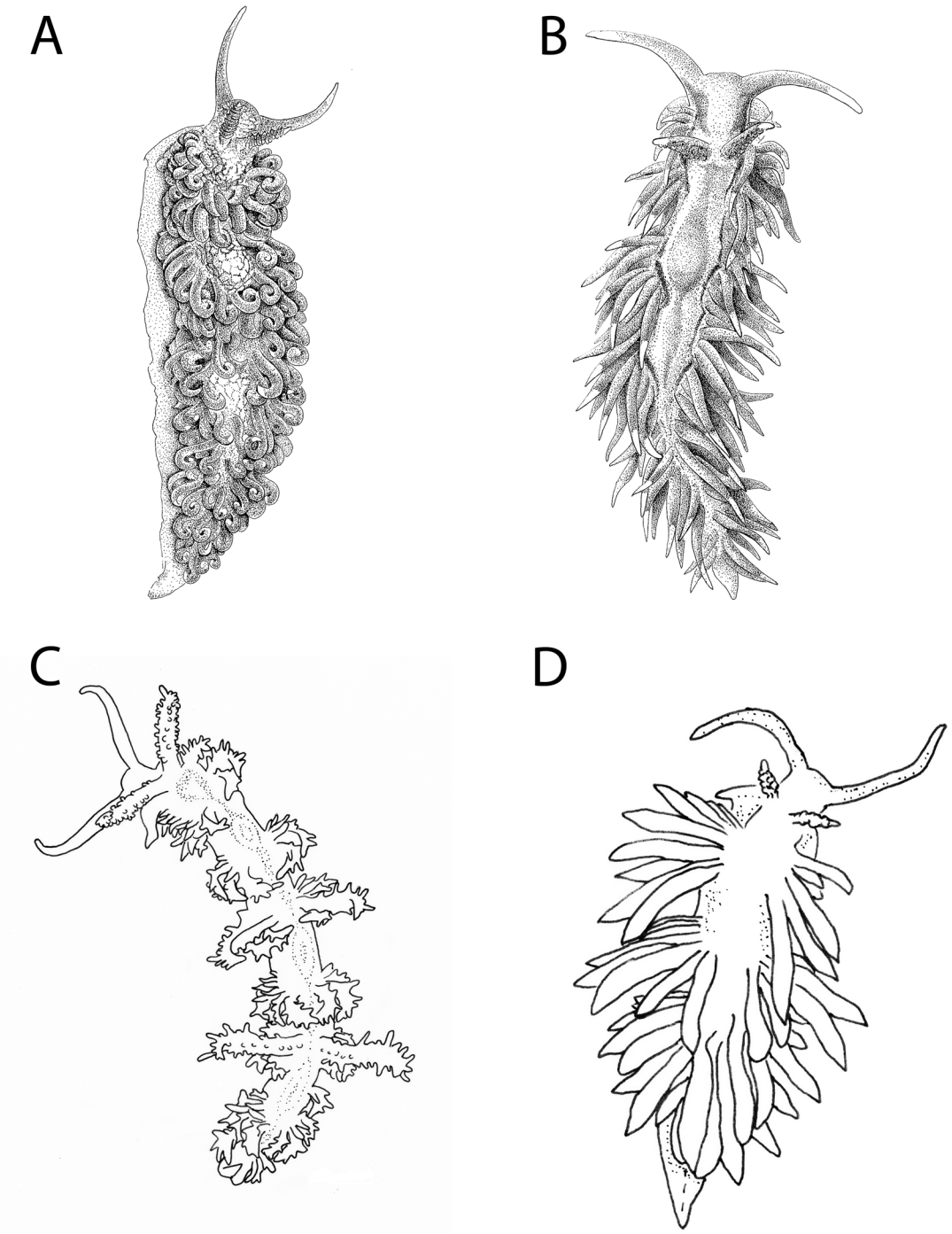

FIGURE 15. Schematic representation of differences of body shape among the genera *Spurilla* (A), drawing of Ascensión Cespedosa; *Berghia* (B), drawing of Ascensión Cespedosa; *Limenandra* (C), taken from Haefelfinger & Stamm (1958); and *Baeolidia* (D), taken from Rudman (1982).

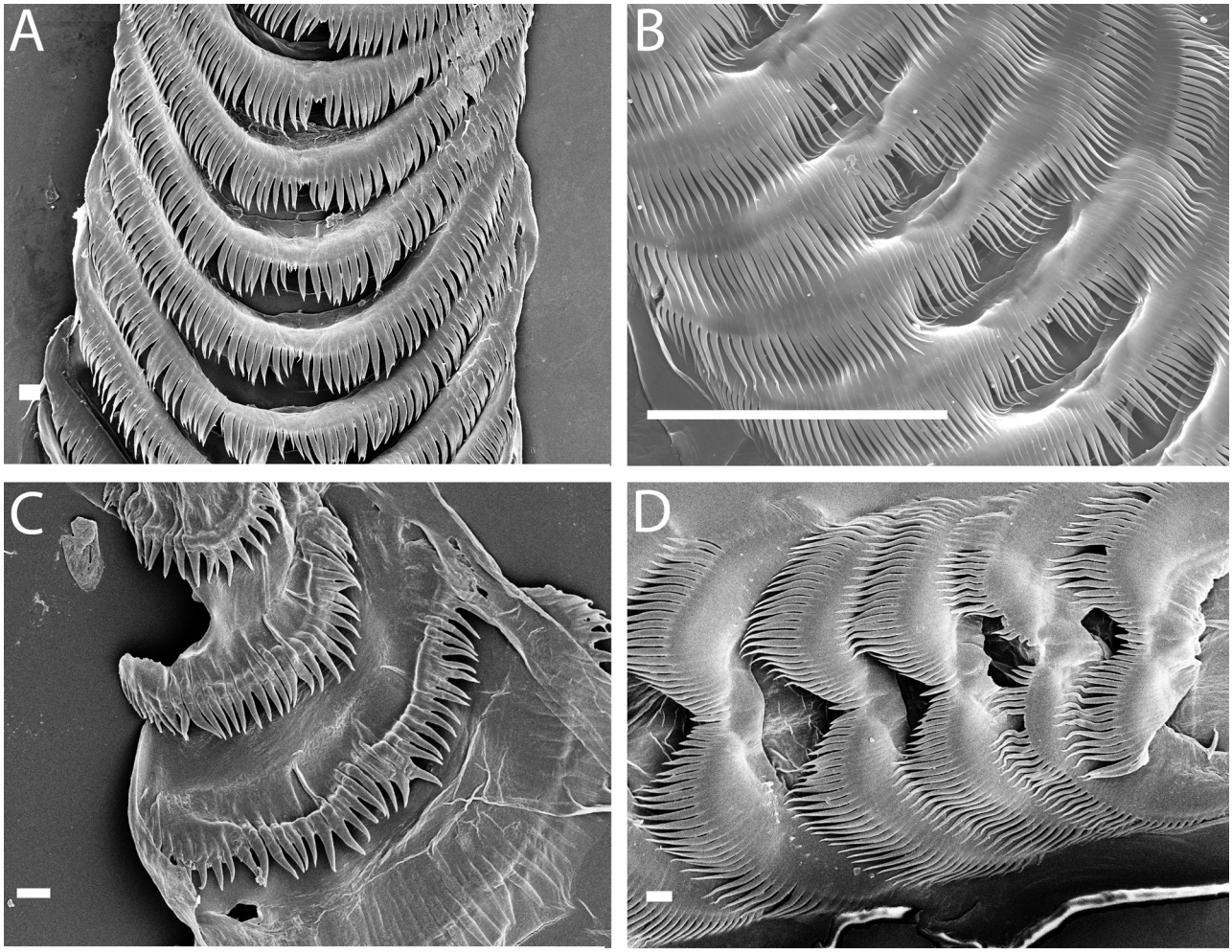

FIGURE 16. Comparison of the radular morphology among the genera *Spurilla* (A), *Berghia* (B), *Limenandra* (C) and *Baeolidia* (D).

Baeolidia* vs *Spurilla, Berghia* and *Limenandra

The aeolidid genera *Spurilla, Berghia* and *Baeolidia* were considered to be closely related. Indeed, Odhner (1939) placed *Spurilla* and *Berghia* in a new family called Spurillidae, including *Baeolidia* ten years later and overlooking *Limenandra* (Odhner in Franc 1968). In the manner of Odhner (in Franc 1968), many authors regarded *Limenandra* as a junior synonym of *Baeolidia*. Recently, the molecular phylogeny of Aeolidiidae (Carmona *et al*. 2013) rejected the validity of Spurillidae sensu Odhner and the synonymy of *Limenandra* with *Baeolidia*. However, the morphological differences among these genera have not been well defined.

Despite difficulties in finding synapomorphies for some genera within Aeolidiidae, it is possible to differentiate *Baeolidia, Spurilla, Berghia* and *Limenandra* based on some features. Regarding body size and morphology, we could divide these genera in two groups: *Spurilla* and *Baeolidia*, and *Berghia* and *Limenandra* (Fig. 15). The body of the members of the first group is quite broad although species of *Baeolidia* are usually smaller and wider than species of *Spurilla*. On the other hand, *Berghia* and *Limenandra* species are both slender but *Limenandra* species are more cylindrical. The rhinophorial ornamentation is also very useful to separate these genera. Although *Berghia*, *Baeolidia* and *Limenandra* were supposed to have papillate rhinophores, we could find consistent differences in the morphology of the papillae. While the rhinophorial papillae of *Berghia* are usually asymmetrical, being more or less rounded on posterior side, and elongate and perpendicular to rhinophores on their lateral sides (see figure 2 of Carmona *et al*. 2014b), in *Limenandra* they are bifurcated (see figure 4 of Carmona *et al*., 2014c). In *Baeolidia*, we find more variability in the morphology of these papillae and in the ornamentation of the rhinophores in general (Fig. 2). However, due to the particular rhinophores together with other morphological features, *Baeolidia* cannot be confounded with *Spurilla, Limenandra,* and *Berghia*. Although the arrangement of

the cerata is not appropriate to separate genera in Aeolidiidae (Carmona *et al.* 2013), the morphology of the cerata may give some information. Our research suggests that all the *Berghia* species have cylindrical cerata, with a round apex and uniform diameter throughout most of their length (Carmona *et al*. 2014b); the cerata of *Limenandra* may have papillae over their surface (Carmona *et al.* 2014c); *Spurilla* has cerata that are recurved inwards (Carmona *et al*. 2014a), which are also present in some species of *Baeolidia*. However, the latter usually have leaf-shaped cerata, being broad at their base and narrowing towards the apices.

Regarding the radular morphology (Fig. 16), only *Limenandra* is easily recognizable from the remaining genera (Fig. 16C). The radular teeth of *Spurilla*, *Berghia* and *Baeolidia* are very similar, corresponding with the radular teeth represented in the Figure 17. Although there is quite a lot of intrageneric variability, Figure 16 depicts the archetypical radular teeth for each genus.

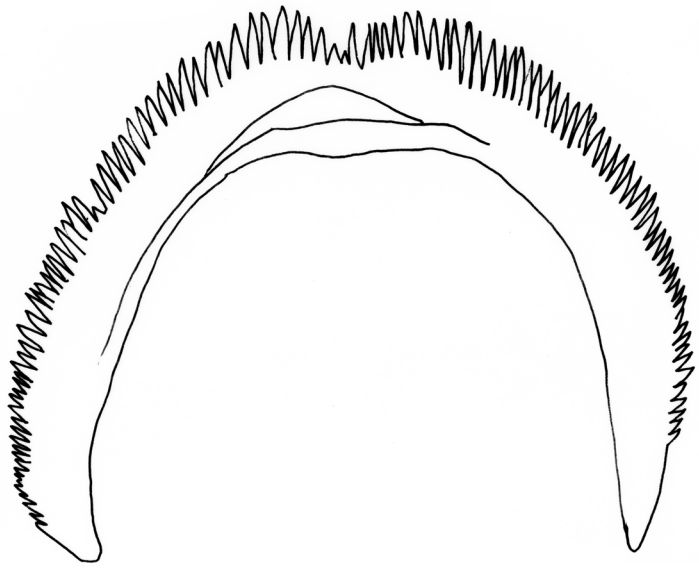

FIGURE 17. Most common radular teeth morphology in Aeolidiidae.

In terms of biogeography, so far *Berghia* is the only genus restricted to one ocean basin (Atlantic-Mediterranean) (Fig. 18A) although the occurrence of otherwise Indo-Pacific *Baeolidia* in the Atlantic Ocean with *B. cryoporos* would need further comparatives studies (Fig. 18B).

In order to facilitate the identification of these four genera, here we present a small key based on external characters and distribution.

1	Rhinophores perfoliate	*Spurilla*
-	Rhinophores ribbed	*Baeolidia macleayi*
-	Rhinophores smooth	*Baeolidia ransoni*
-	Rhinophores papillate	2
2	Notum with colouration pattern of concentric circles	*Limenandra*
-	Notum without colouration pattern of concentric circles	3
3	Cerata cylindrical	4
-	Cerata non-cylindrical	5
4	Indo-Pacific distribution	*Baeolidia dela*
-	Atlantic-Mediterranean distribution	*Berghia*
5	Remaining species of *Baeolidia*.	

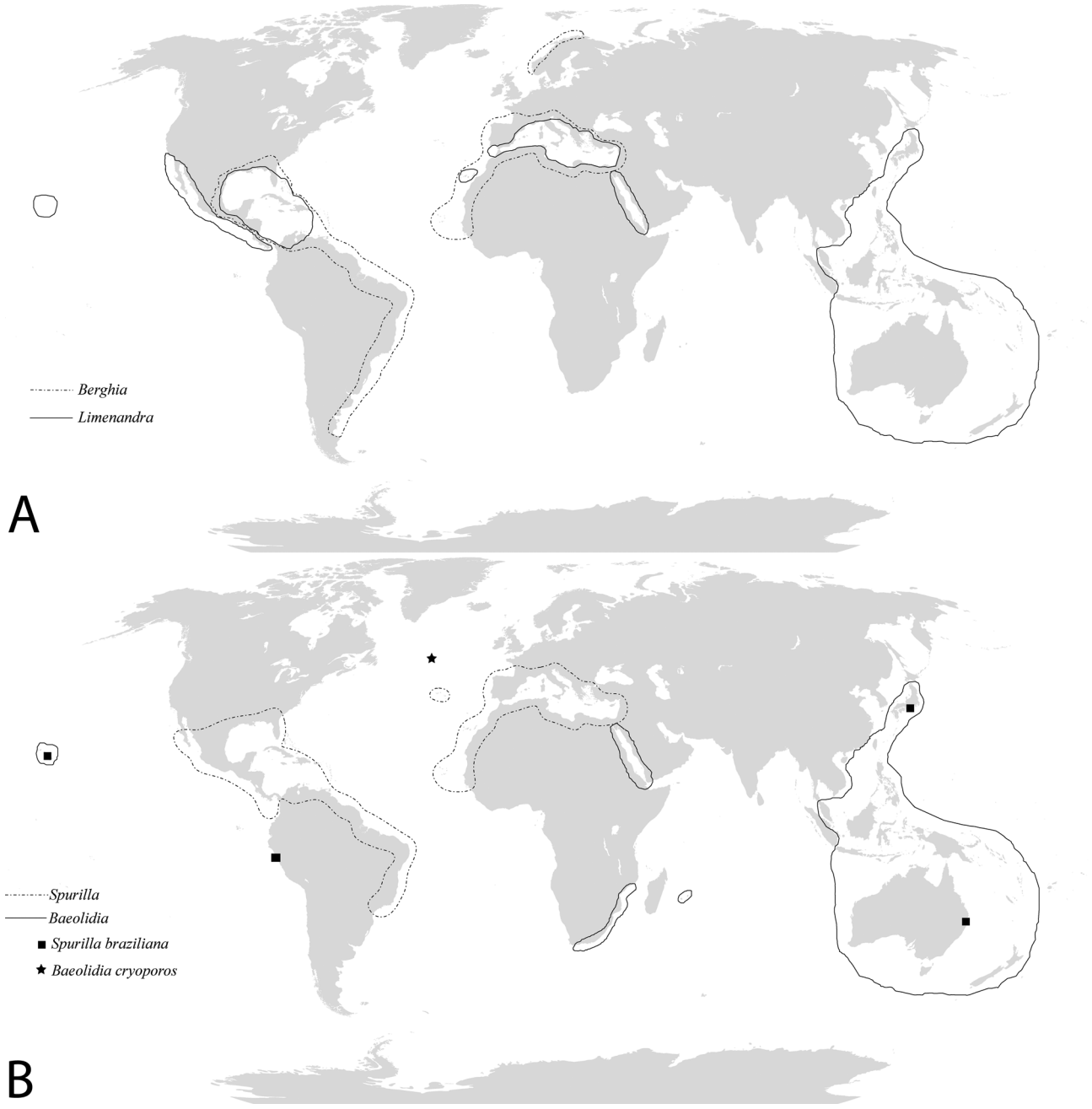

FIGURE 18. Map of the range of the different species of *Spurilla, Berghia, Limenandra,* and *Baeolidia.* A. *Berghia* and *Limenandra.* B. *Spurilla* and *Baeolidia*. Abbreviation: Isolated records of *Baeolidia cryporos* (star) and *Spurilla braziliana* (square).

Revised diagnosis of *Baeolidia*

Body mainly short and broad. Foot corners tentaculiform or rounded. Excluding *B. ransoni* and *B. macleayi*, rhinophores are papillate. Rhinophorial papillae may be elongate or short and rounded. Cerata arranged in arches, rows or both, arches and rows. Cerata dorso-ventrally flattened and normally leaf-like. Radular teeth pectinate, usually bilobed and with a central cusp. Masticatory jaw edge usually smooth. Oral glands, when present, fragile and spongy.

TABLE S1. Distinctive features of Baeolidia species.

Species	Distribution	Body	Rhinophorial ornamentation	Cerata arrangement	Colour of the cerata	Colour of rhinophores	Oral glands	Shape of radular teeth
Baeolidia moebii Bergh, 1888	Indo-Pacific and Eastern Pacific.	Large and broad. Greyish white, brownish green or reddish.	Rounded papillae.	Arches.	Translucent, with whitish patches and bright yellow marks. Bright yellow subapical band.	Ground colour with white spots.	Not always present.	Blended. Teeth progressively smaller in the posterior region of the radula.
Baeolidia macleayi (Angas, 1864)	New Zealand and Australia.	Short and broad. Translucent.	Ribbed.	Arches and rows.	Translucent, with a bright lemon-yellow ring at the third-quarter and white spots.	Proximal two-thirds reddish or brownish. Distal part with lemon-yellow pigments.	Present.	Bi-arched.
Baeolidia japonica Baba, 1933	Indo-Pacific.	Short and broad. Translucent or brown.	Large papillae.	Arches and rows.	Brownish with white spots or translucent with white spots. A bluish band on the anterior side may be present.	Ground colour with white papillae.	Present.	Slightly bi-arched. Teeth progressively smaller in the posterior region of the radula.
Baeolidia ransoni (Pruvot-Fol, 1956)	Indo-Pacific.	Broad and large. Translucent with light ochre and white spots.	Smooth.	Rows.	Translucent with light ochre and white spots	Ground colour with ochre pigments. White apex.	Absent.	Short

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TABLE S1. (Continued)

Species	Distribution	Body	Rhinophorial ornamentation	Cerata arrangement	Colour of the cerata	Colour of rhinophores	Oral glands	Shape of radular teeth
Baeolidia dela (Marcus and Marcus, 1960)	Maldives.	-	Papillate.	-	-	-	-	-
Baeolidia cryoporos Bouchet, 1977	Deep waters of Atlantic Ocean.	-	Papillate.	Rows.	-	-	-	-
Baeolidia harrietae (Rudman, 1982)	Australia, Indian Ocean, Japan and Hawaii.	Large and broad. Translucent overlaid with a reticulate brown pattern	Large papillae.	Rows.	Translucent overlaid with brown reticulate. White tips.	Ground colour. Yellowish white pigments on the apex and ends of the papillae.	Present.	
Baeolidia australis (Rudman, 1982)	New Zealand and Australia.	Large and broad. Brown with white patches.	Rounded papillae.	Arches.	Brown with white patches on the outer side. Below the tip, bright orange band with a broad blue band below it.	Watery-brown.	-	
Baeolidia salaamica (Rudman, 1982)	Indo-Pacific and Eastern Pacific.	Short and broad. Translucent with white marks.	Rounded papillae.	Arches and rows.	Translucent. They may have white patches.	Ground colour with white papillae and apex.	Present.	Slightly bi-arched.
Baeolidia chaka (Gosliner, 1985)	Only from South Africa.	Short and broad. Translucent white with a dense pattern of white	Large papillae.	Arches and rows.	Digestive gland brown. With opaque white pigment.	With chocolate-brown pigment.	Present.	-

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TABLE S1. (Continued)

Species	Distribution	Body	Rhinophorial ornamentation	Cerata arrangement	Colour of the cerata	Colour of rhinophores	Oral glands	Shape of radular teeth
		pigment.						
Baeolidia palythoae Gosliner, 1985	South Africa.	Translucent yellowish with brownish reticulate. Short and broad.	Large papillaa.	Rows.	Translucent yellowish with brownish reticulate.	The same as cerata.	Present. Two pairs.	-
Baeolidia rieae sp. nov.	Japan.	Broad and short. Translucent with ochre and pearly white pigments over the notum.	Large papillae.	Arches and rows.	Light ochre with pearly white, dark ochre and iridescent green pigments.	Translucent with ochre and pearly white pigments.	Present.	Bi-arched. Teeth progressively smaller in the posterior region of the radula.
Baeolidia variabilis sp. nov.	From Philippines, Marshall Island and Papua New Guinea.	Short and broad. Translucent. With white patches or light ochre spots all over the body.	Large papillae.	Arches and rows.	Or ochre with white marks on its posterior side, or completely white with bright yellow pigments on its posterior side.	With ground colour with ochre pigments and white tips.	Present.	Bi-arched. Teeth progressively smaller in the posterior region of the radula.
Baeolidia lunaris sp. nov.	So far, from Tanzania.	Short and broad. Translucent brownish with fine iridescent opaque white spots.	Large papillae.	Arches and rows.	With ground colour and a white spot on its anterior side, close to the base.	Translucent brownish, with iridescent pigments.	Present.	Blended. Teeth progressively smaller in the posterior region of the radula.

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TABLE S1. (Continued)

Species	Distribution	Body	Rhinophorial ornamentation	Cerata arrangement	Colour of the cerata	Colour of rhinophores	Oral glands	Shape of radular teeth
Baeolidia gracilis sp. nov.	Only known from the Philippines.	Moderately elongate. Head and pericardium dark greyish blue. Posterior part of the notum and cerata ochre. Pericardium with iridescent greyish blue and bright ochre pigments.	Elongate papillae.	Arches and rows.	With greenish ochre reticulate and an opaque white line on their inner margin.	Dark greyish blue.	Present.	Bi-arched.
Baeolidia scottjohnsoni sp. nov.	Only known from the Marshall Islands and Hawaii.	Body short and broad. Brownish, with bright white spots over the body. Iridescent blue pigments overlaid the white spots.	Large papillae.	Arches and rows.	Brown with white spots. With a white subapical band followed by a second iridescent blue band. (both in the anterior side of the cerata).	Brownish with white apex.	Present.	Slightly bi-arched.

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