The Linnean Society of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2014, **171**, 108–132. With 14 figures

Systematic review of *Anteaeolidiella* (Mollusca, Nudibranchia, Aeolidiidae) based on morphological and molecular data, with a description of three new species

LEILA CARMONA[1]*, VISHAL BHAVE[2], RAHUL SALUNKHE[2,3], MARTA POLA[4], TERRENCE M. GOSLINER[5] and JUAN LUCAS CERVERA[1]

[1]*Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Campus de Excelencia Internacional del Mar (CEI·MAR), Universidad de Cádiz, Polígono Río San Pedro, s/n, Ap.40. 11510 Puerto Real (Cádiz), Spain*
[2]*Bombay Natural History Society, Hornbill House, Shaheed Bhagat Singh Road, Mumbai 400 001, Maharashtra, India*
[3]*Molecular Biology Unit, National Center for Cell Science, Ganeshkhind, Pune, 411007, Maharashtra, India*
[4]*Laboratorio de Biología Marina, Departamento de Biología, Edificio de Biología, Campus de Excelencia Internacional UAM+CSIC, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049 Madrid, Spain*
[5]*Department of Invertebrate Zoology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, USA*

Received 6 August 2013; revised 16 December 2013; accepted for publication 19 December 2013

Partial sequences of two mitochondrial genes and one nuclear gene from *Anteaeolidiella* specimens collected throughout temperate and tropical areas in the Atlantic, Mediterranean, eastern Pacific, and Indo-Pacific have revealed the existence of a species complex under the name of *Anteaeolidiella indica* (Bergh, 1888). Further examination showed consistent differences in colour pattern and the internal anatomy that became evident only once the molecular outcomes were analysed. Moreover, the original description of *A. indica* suggests that this species has a very particular colour pattern that is not present in any of our specimens. A review of the literature led us to resurrect the names of *Anteaeolidiella cacaotica* (Stimpson, 1855), *Anteaeolidiella saldanhensis* (Barnard, 1927), *Anteaeolidiella takanosimensis* (Baba, 1930), and *Anteaeolidiella lurana* (Ev. Marcus & Er. Marcus, 1967). *Aeolidiella chromosoma* (Cockerell & Eliot, 1905) and *Aeolidiella oliviae* (MacFarland, 1966) are transferred to *Anteaeolidiella* based on our morphological and molecular data. Finally, three new species from the Indo-Pacific are described herein.

© 2014 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2014, **171**, 108–132.
doi: 10.1111/zoj.12129

ADDITIONAL KEYWORDS: cryptic species – Heterobranchia – marine biodiversity – molluscan diversity – morphology – Nudibranchia – systematics.

INTRODUCTION

Miller (2001) erected the genus *Anteaeolidiella*. This author considered as diagnostic characters the wide and bilobed tooth with a central cusp, the nodulose spindle-shaped oral glands, the club-shaped cerata arranged in rows, and the smooth rhinophores. Miller (2001) placed *Aeolidiella indica* (Bergh, 1888a) in this new genus and designed it as the type species. This author also transferred *Baeolidia benteva* Er. Marcus, 1958 to *Anteaeolidiella* based on the ceratal arrangement and the position of the orifices of the latter species.

*Corresponding author. E-mail: leila.carmona@uca.es

Since *Anteaeolidiella indica* was first described (Bergh, 1888a), this species has been reported from the Mediterranean (Schmekel, 1968, 1970; Zenetos *et al*., 2005; Sciberras & Schembri, 2007), the Strait of Gibraltar (García-Gómez, 2002), the Canary Islands (Pérez-Sánchez & Moreno, 1990; Moro *et al*., 1995, 2003; Ortea *et al*., 2001), South Africa (Gosliner & Griffiths, 1981), the Caribbean (Valdés *et al*., 2006; Ortigosa, Simones & Calado, 2013), Brazil (Domínguez, Troncoso & García, 2008; García-García, Domínguez & Troncoso, 2008; Padula *et al*., 2011), the Pacific coast of Costa Rica (Camacho-García, Gosliner & Valdés, 2005), Hawaii (Pittman & Fiene, 2013), Australia (Gosliner, Behrens & Valdés, 2008), New Zealand (Miller, 2001), Japan (Nakano, 2004; Imamoto, 2013), the Kerama Islands (Ono, 1999), the Ryukyu Islands (Ono, 2004), Réunion Island (Bidgrain, 2005), and Ratnagiri, India (Bhave & Apte, 2011). Several species names have been introduced over the years for different colour forms that occur over this biogeographic pattern; however, several of these names have been synonymized with *Anteaeolidiella indica*. Gosliner & Griffiths (1981) compared the latter species with *Aeolidiella orientalis* Bergh, 1888b, *Aeolidiella saldanhensis* Barnard, 1927, *Aeolidiella hulli* Risbec, 1928, *Aeolidiella takanosimensis* Baba, 1930, *Aeolidiella multicolor* Macnae, 1954, and *Aeolidiella lurana* Er. Marcus & Ev. Marcus, 1967, but they concluded that differences were not consistent and therefore attributed them to intraspecific variability. Moreover, *Anteaeolidiella indica* together with some of its synonyms have been considered as junior synonyms of *Anteaeolidiella foulisi* (Angas, 1864) (Burn, 2006; Debelius & Kuiter, 2007). At the same time, Burn (1964, 2006) suggested that the even earlier described *Eolis cacaotica* Stimpson, 1855 could be identical to *Anteaeolidiella foulisi*.

The extreme external and internal similarity of all these species has caused a great deal of confusion and blurred the differences among them. As molecular tools have become more prevalent and cheaper, several heterobranch species with disjunct ranges have proven to be species complexes (Krug *et al*., 2008, 2013; Malaquias & Reid, 2008, 2009; Carmona *et al*., 2011; Gosliner & Fahey, 2011; Jörger *et al*., 2012; Ornelas-Gatdula *et al*., 2012; Pola, Camacho-García & Gosliner, 2012). The molecular phylogeny conducted by Carmona *et al*. (2013) transferred *Aeolidiella oliviae* (MacFarland, 1966) and *Aeolidiella chromosoma* (Cockerell & Eliot, 1905) to *Anteaeolidiella*, resurrected the species *Aeolidiella cacaotica*, *Aeolidiella saldanhensis*, *Aeolidiella takanosimensis*, and *Aeolidiella lurana*, placed them in *Anteaeolidiella*, and highlighted the necessity of reviewing *Anteaeolidiella indica sensu* Bergh (1888a).

Recently collected material from Australia and India allowed us to extend the research by Carmona *et al*. (2013), increasing the number of species studied as well as their range of distribution. In the present contribution, we undertake a systematic revision of *Anteaeolidiella*, based on molecular data (two mitochondrial genes and one nuclear gene) and traditional morphological and anatomical data. We also attempt to clarify the morphological differences between the species of the '*Anteaeolidiella indica*' complex. Moreover, we try to elucidate the identity of *Anteaeolidiella indica sensu* Bergh (1888a) by performing a careful review of the literature. Finally, based on the addition of three new species, we propose a new diagnosis of the genus *Anteaeolidiella*.

MATERIAL AND METHODS

Morphology

A comprehensive review of the literature was conducted to determine the valid names for the species recognized in the molecular and morphological analyses. After the remarks of the type species, all available names for *Anteaeolidiella* species are organized and discussed in this article by year of publication. In the synonymy lists, references to the original description of the valid name and all synomyms, and the first proposed change of binomen, are included, but subsequent references are not.

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 using 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 radula of the specimens from India were examined and drawn using a dissecting microscope.

Voucher specimens are held at the following institutions: AMS, Australian Museum of Sydney, Sydney, Australia; BNHS, Bombay Natural History Society, Mumbai, India; CASIZ, California Academy of Sciences, San Francisco, USA; CNMO, Colección Nacional de Moluscos Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico; LACM, Natural History Museum of Los Angeles County; Los Angeles, USA; MHNSM, Museo de Historia Natural de El Salvador, San Salvador, El Salvador; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MZSP, Museu de Zoologia

da Universidade São Paulo, São Paulo, Brazil; WAM, Western Australian Museum, Perth, Australia; ZMBN, University Museum of Bergen, Bergen, Norway; ZSM, Zoologische Staatssammlung München, Munich, Germany.

Molecular work

Taxon sampling

Samples were obtained using standard scuba-diving sampling techniques for opisthobranchs and through the study of museum collections. Two hundred and fifty-six specimens, including 48 species of Aeolidiidae (20 specimens and nine species of *Anteaeolidiella*), three species of Babakinidae, 32 species of Facelinidae, seven species of Flabellinidae, one species of Fionidae, three species of Piseinotecidae, and four species of Tergipedidae, were used for phylogenetic inference. A total of 197 specimens were successfully sequenced for cytochrome *c* oxidase subunit I (*COI*), 224 specimens were sequenced for *16S* rRNA (*16S*), and 236 specimens were sequenced for histone 3 (*H3*). Thirty-five additional sequences were obtained from GenBank (for a full list of samples, localities, and voucher references, see Supporting Information, Table S1).

Tritonia challengeriana Bergh, 1884 (= *Tritonia antarctica* Pfeffer in Martens & Pfeffer, 1886) was chosen as the out-group for its basal taxonomical position within Cladobranchia (Pola & Gosliner, 2010).

DNA extraction, amplification, and sequencing

DNA was extracted from foot tissue of specimens preserved in 70–100% ethanol, except in the case of small animals, where the whole specimen was used. The Qiagen DNeasy Blood & Tissue Kit was used for DNA extraction (Qiagen, Valencia, CA, USA).

Partial sequences of *COI*, *16S*, and *H3* were amplified by polymerase chain reaction (PCR) using the following primers: LCO1490 (5′-GGTCAACAAATCA TAAGATATTGG-3′) and HCO2198 (5′-TAAACTTC AGGGTGACCAAAAATCA-3′) (Folmer *et al*., 1994) for *COI*; *16S* ar-L (5′-CGCCTGTTTATCAAAAACAT-3′) and *16S* br-H (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi *et al*., 1991) for *16S* rRNA; and H3AD5′3′ (5′-ATGGCTCGTACCAAGCAGACVGC-3′) and H3BD5′3′ (5′-ATATCCTTR GGCATRATRGTGAC-3′) (Colgan *et al*., 1998) for H3. These three gene regions are commonly used in the systematic studies of gastropods (e.g. Meyer, 2003; Williams & Reid, 2004; Dinapoli *et al*., 2006; Frey & Vermeij, 2008; Malaquias & Reid, 2009; Pola & Gosliner, 2010; Claremont *et al*., 2013; Eilertsen & Malaquias, 2013; Ohnheiser & Malaquias, 2013); however, several internal primers for *COI* and *H3* were designed for specimens that did not amplify with the universal primers (Carmona *et al*., 2013: table 1).

Polymerase chain reactions were conducted in 50-μL volume reactions containing 2 μL of both forward and reverse primers (10 mM), 5 μL of deoxyribonucleotide triphosphate (dNTP; 2 mM), a gene-dependent quantity of magnesium chloride (25 mM), 0.5 μL of Qiagen DNA polymerase (5 units μL^{-1}), 10 μL of 'Q-solution' (5×), 5 μL of Qiagen buffer (10×) (Qiagen Taq PCR Core Kit, cat. no. 201225), and 1 μL of genomic DNA. The volumes of magnesium chloride used were 7 μL for *COI* and *16S*, and 4 μL for *H3*. The amplification of *COI* was performed with an initial denaturation for 5 min at 94 °C, followed by 35 cycles of 1 min at 94 °C, 30 s at 44 °C (annealing temperature), and 1 min at 72 °C, with a final extension of 7 min at 72 °C. The *16S* amplification began with an initial denaturation for 5 min at 95 °C, followed by 35 cycles of 30 s at 94 °C, 30 s at 44 °C (annealing temperature), 1 min at 72 °C, with a final extension of 7 min at 72 °C. *H3* amplification was performed with an initial denaturation for 3 min at 95 °C, followed by 40 cycles of 45 s at 94 °C, 45 s at 50 °C (annealing temperature), and 2 min at 72 °C, with a final extension of 10 min at 72 °C.

Successful PCRs were purified by mixing 5 μL of PCR product with 2 μL of ExoSAP-IT (usb.affymetrix.com). Samples were incubated at 37 °C for 15 min followed by an inactivation step at 80 °C for 15 min. Sequence reactions were run on a 3730XL DNA sequencer (Applied Biosystems). All new sequences have been deposited in GenBank.

Sequence alignment and phylogenetic analyses

DNA sequences were assembled and edited using GENEIOUS PRO 4.7.6 (Drummond *et al*., 2009). All the sequences were checked for contamination with BLAST (Altschul *et al*., 1990), implemented in the GenBank database. MAFFT (Katoh, Asimenos & Toh, 2009) was employed to align the sequences. The alignments were checked by eye using MacClade 4.06 (Maddison & Maddison, 2005). Protein-coding sequences were translated into amino acids for confirmation of alignment. Pairwise uncorrected *p*-distance values between each taxon were calculated for the *COI* gene. Uncorrected *p*-distances between all taxa, and level of saturation for first, second, and third codon positions (*p*-distances against transitions plus transversions) were calculated in MEGA 5.0* (Tamura *et al*., 2011) for *COI* and *H3*. No evidence of saturation was found, even in the third codon positions.

The most variable regions from the *16S* rRNA alignment were removed using both the default settings and the standard options for stringent and less stringent selection in GBLOCKS (Talavera &

Castresana, 2007). Excluding 'indel-rich' regions, the tree was in general poorly resolved, with lower node support. Therefore, final analyses were performed including all bases. Sequences of *COI*, *16S*, and *H3* were trimmed to 658, 463, and 327 bp, respectively.

Individual gene analyses and a concatenated analysis were performed. The best-fitting models of evolution for each gene were determined using the Akaike information criterion (Akaike, 1974), implemented in MrModeltest 2.3 (Nylander, 2004). The GTR + I + G model was selected for the three genes.

Maximum-likelihood (ML) analyses were performed using the RAxML 7.0.4 (Stamatakis, 2006), and node support was assessed with non-parametric bootstrapping (BS) with 5000 replicates, random starting trees, and parameters estimated from each data set under the model selected for the original data set. Bayesian inference (BI) analyses were conducted using MrBayes 3.1.2b (Ronquist & Huelsenbeck, 2003) for 45 000 000 generations, with two independent runs and a sampling frequency of 1000. The models implemented were those estimated with MrModeltest 2.3. The combined data set was partitioned among genes and the 'unlink' command was used to allow all parameters to vary independently within each partition.

Convergence was diagnosed graphically by plotting the likelihood against the number of generations for each run using TRACER 1.4.1 (Drummond & Rambaut, 2007). For each analysis, the first 11 250 trees were discarded ('burn-in'), and node support was assessed by posterior probabilities (PPs). Only nodes supported by BS ≥ 75 and PP ≥ 0.90 are discussed. All the alignments and trees published in this study are deposited in TreeBase under project number 15114. urn:lsid:zoobank.org:pub:0D798F9B-102D-4087-9F2F-1751725C9B8D.

Species delimitation

To define species, we used the criteria of divergence and reciprocal monophyly, supported by independent genetic markers (Knowlton, 2000; Wheeler & Meier, 2000; Avise, 2004; Malaquias & Reid, 2009), using cut-off values from Carmona *et al*. (2013) as our reference thresholds (5.5–16%).

We also applied the Automatic Barcode Gap Discovery (ABGD) method (Puillandre *et al*., 2012a). ABGD is a distance-based method designed to detect the so-called 'barcode gap' in the distribution of pairwise distances calculated in a *COI* alignment (Puillandre *et al*., 2012a, b). This method represents progress in avoiding any dependence on a hypothetically defined species. The web-based ABGD program (available at http://wwwabi.snv.jussieu.fr/public/abgd/) was employed with the default settings to generate a preliminary partition of sequences, using the *COI* alignment and excluding the out-group.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank life science identifiers (LSIDs) 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:0D798F9B-102D-4087-9F2F-1751725C9B8D.

RESULTS

Molecular results

The combined data set yielded a sequence alignment of 1448 positions. No saturation was observed across genes and codon positions (not shown). The combined tree provided better resolution than *H3*, *COI*, or *16S* separately, but all of them showed the same species-level topology with high support (not shown). Moreover, although bootstrap values were lower than posterior probabilities in larger clades, the topologies of the ML trees were congruent with the results yielded by Bayesian analyses, and thus ML trees are not shown. Figure 1 only shows the *Anteaeolidiella* phylogenetic hypothesis based on the combined data set represented by BI. The complete tree is given in Supporting Information, Figure S1.

In this study, Aeolidiidae was monophyletic (PP = 0.95, BS = 63), but the relationships among its genera were not resolved. Nevertheless, excluding *Cerberilla*, all the genera were monophyletic and had high support (Fig. S1).

All the *Anteaeolidiella* specimens clustered together in a monophyletic and highly supported group for BI (PP = 1), but this was not supported by the ML analyses (BS = 64). *Anteaeolidiella* was divided into two subclades: one including *Anteaeolidiella oliviae* and *Anteaeolidiella chromosoma* (PP = 1, BS = 89), and the other formed by the remaining species of the genus (PP = 1, BS = 100). Within this latter subclade, *Anteaeolidiella fijensis* sp. nov. appeared as the basal species. All the species were highly supported except for *Anteaeolidiella cacaotica* (PP = 0.91, BS = 63); however, this fact could be explained because only the *16S* sequence was available for the Japanese specimen. The minimum uncorrected p-distance for *COI* among these species was 6.6%.

Applying the ABGD with the standard settings resulted in nine partitions with seven groups each: one for *Anteaeolidiella lurana* specimens, one for *Anteaeolidiella saldanhensis*, one for *Anteaeolidiella cacaotica* specimens, one for *Anteaeolidiella poshitra* sp. nov., one for *Anteaeolidiella takanosimensis*

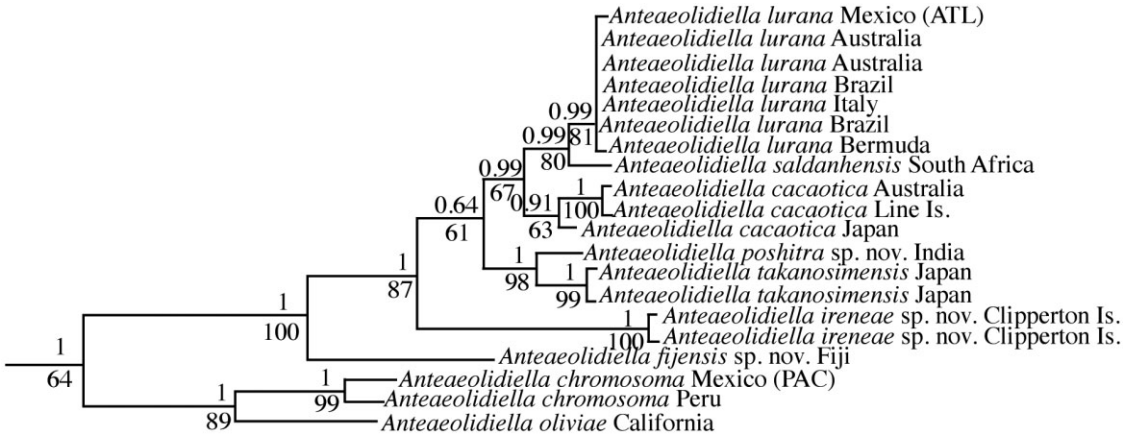


Figure 1. Phylogenetic hypothesis for the genus *Anteaeolidiella* based on the combined data set (*H3* + *COI* + *16S*), inferred by Bayesian inference (BI) analysis. Numbers above branches represent posterior probabilities from BI. Number below branches represent bootstrap values from maximum-likelihood analysis. Abbreviations: ATL, Atlantic Ocean; PAC, Pacific.



Figure 2. Photograph of the putative *Anteaeolidiella indica sensu* Bergh (1888a).

specimens, one for *Anteaeolidiella ireneae* sp. nov. specimens and a final one for *Anteaeolidiella fijensis* sp. nov. The prior maximal distance (p-distance) ranged between 0.001 and 0.06.

SYSTEMATICS

NUDIBRANCHIA CUVIER, 1817

CLADOBRANCHIA WILLAN & MORTON, 1984

FAMILY AEOLIDIIDAE GRAY, 1827

GENUS *ANTEAEOLIDIELLA* MILLER, 2001

Type species: Anteaeolidiella indica (Bergh, 1888a).

Diagnosis of the genus Anteaeolidiella according to Miller (2001): Body low, moderately wide. Cerata in clusters of rows, for the most part sloping downwards and rearwards; rhinophores simple; foot corners triangular; oral glands spindle shaped, with two opposed rows of large nodules (giant secretory cells). Radular tooth moderately wide, strongly bilobed, largest denticles at apex of each lobe, median cusp small yet distinct; jaw masticatory process smooth.

Anteaeolidiella indica (Bergh, 1888a) (Fig. 2)
Aeolidiella indica Bergh, 1888a: 755.

Type locality: Mauritius Islands.

Type material: To our knowledge no type material remains.

Remarks: Bergh (1888a) described this species based on Moebius' drawings and notes. The coloration of the living animal was depicted as white, yellow, and grey, including the oral tentacles and the rhinophores. Miller (2001) designated *Aeolidiella indica* as the type species of *Anteaeolidiella*, although his specimen did not present the coloration described by Bergh (1888a). None of our specimens previously identified as *Anteaeolidiella indica* (Carmona *et al.*, 2013) have the yellow and grey colour pattern. Some photographs of '*Anteaeolidiella indica*' found on web pages could match with Bergh's original description (e.g. Boserelle, Levy & Michenet, 2013), but the localities are quite far from the type locality (Mauritius Islands). We also found one specimen from subtropical South



Figure 3. Photographs of the living animals: A, *Anteaeolidiella cacaotica*, specimen from eastern Australia, photo by O'Grove, MNCN 15.05/63476; B, *Anteaeolidiella chromosoma*, specimen from the Pacific coast of Costa Rica, photo by Yolanda Camacho, MZUCR 8896; C, *Anteaeolidiella saldanhensis*, specimen from South Africa, Western Cape Province, photo by Terrence M. Gosliner, CASIZ 176313; D, *Anteaeolidiella takanosimensis*, specimen from Japan, Manuzuru, photo by Rie Nakano, MNCN 15.05/63479; E, *Anteaeolidiella oliviae*, specimen from California, photo by Gary McDonald; F, *Anteaeolidiella lurana*, specimen from Bermuda, Ferry Reach, photo by Terrence M. Gosliner, ZMBN 82992.

Africa (close to the Mauritius Islands) that seems to be like Bergh's *Anteaeolidiella indica* (Fig. 2). Nevertheless, the specimen is lost (T. M. Gosliner, pers. comm.), and therefore we have not been able to do any dissection or molecular analysis. Because the true *A. indica* clearly differs from the remaining species of *Anteaeolidiella*, we maintain *A. indica* as a valid species, but more material is needed in order to clarify its morphological characteristics.

Anteaeolidiella cacaotica (Stimpson, 1855)
(Figs 3A, 4A, 5A, B, 6)
Eolis cacaotica Stimpson, 1855: 388.
Aeolis foulisi Angas, 1864: 64–65, pl. VI, fig. 3.
Coryphella foulisi (Angas, 1864): Bergh, 1875, 634.
Aeolidiella hulli Risbec, 1928: 262–265, fig. 88, pl. D, fig. 3, pl. X, fig. 7, pl. XII, fig. 4.
Aeolidia foulisi (Angas, 1864): Orr, 1981, 68.
Aeolidiella foulisi (Angas, 1864): Burn, 1964, 89.
Anteaeolidiella foulisi (Angas, 1864): Burn, 2006, 30.

Type locality: Port Jackson, Australia.

Type material: To our knowledge, no type material remains. We designate the specimen MNCN 15.05/63476 from Nelson Bay, New South Wales, Australia, as the neotype.

Material examined: Neotype: MNCN 15.05/63476, one specimen, dissected, immature, 6 mm in length preserved, Australia, New South Wales, Nelson Bay, collected by Dave Harasti, 14.ii.10. Other material: CASIZ 174212, one specimen, dissected, immature,

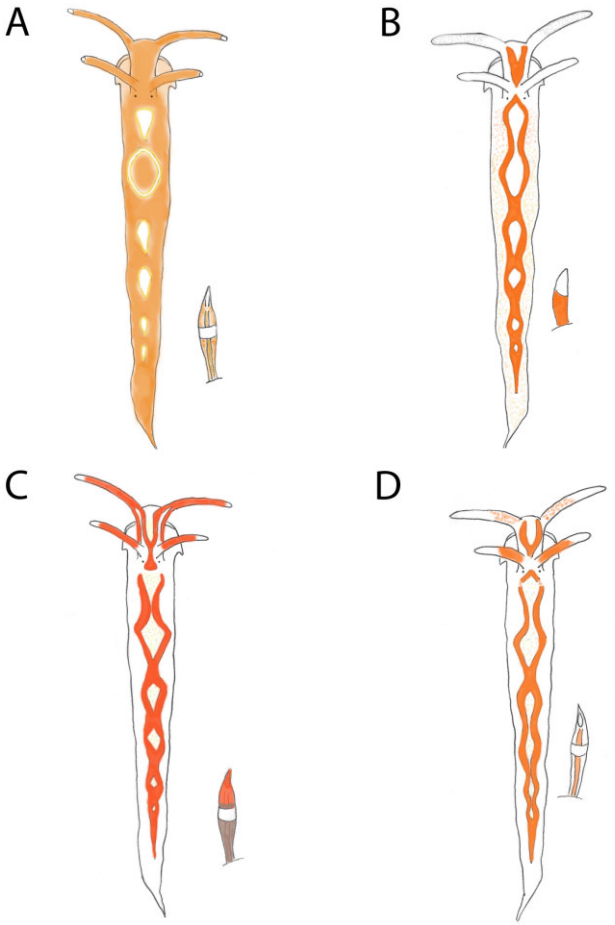


Figure 4. Schematic dorsal color patterns of the '*Anteaeolidiella indica*' species complex: A, *Anteaeolidiella cacaotica*; B, *Anteaeolidiella saldanhensis*; C, *Anteaeolidiella takanosimensis*; D, *Anteaeolidiella lurana.*

4 mm in length preserved, Line Islands, Palmyra Atoll, collected by Christine Huffard, 26.ix.06; MNCN 15.05/63477, one specimen, dissected, immature, 4 mm in length preserved, Japan, collected by Nakano Rie, 10.viii.10.

Geographical distribution: Originally described from Port Jackson, Australia (Stimpson, 1855), it is also known from Kanagawa Prefecture, Japan (Carmona *et al.,* 2013).

External morphology (Figs 3A, 4A): The body is elongate and moderately slender, tapering gradually to the fairly short tail. The anterior foot corners are stout and slightly protruded. The background colour is bright orange, although its intensity varies with the specimen (Fig. 3A). In some specimens, extending posteriorly just behind the rhinophores, an opaque white area in the shape of a teardrop, followed by an opaque white or yellowish circumference, outlining the pericardium, are present. Thereafter, up to four small white teardrops may occur (Fig. 4A). The rhinophores and the oral tentacles have the same colour as the background colour, but with the far end opaque white (Fig. 4A). The rhinophores are stout and taper to a rounded tip. The conical oral tentacles are slightly longer than the rhinophores. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata are long and moderately thick. They extend from the rear of the rhinophores to the tail. The ceratal epithelium is diffusely covered with orange pigment. The ramifications of the digestive gland are greyish brown and terminate in a white cnidosac. A translucent white subapical band is observed (Fig. 4A). The specimens examined here were not very well preserved because the cerata were autotomized. Therefore, the information given below is according to Figure 3A. The cerata are arranged in up to eleven rows. Each row contains between four and seven cerata, decreasing in size towards the foot. The position of the anus and the genital opening could not be determined.

Anatomy: The masticatory border of the jaws is smooth (Fig. 5A). The radular formulae are 9 × 0.1.0 (MNCN 15.05/63476), 11 × 0.1.0 (CASIZ 174212), and 14 × 0.1.0 (MNCN 15.05/63477). The radular teeth are bilobed, with 23 or 24 elongate and acutely pointed denticles on either side of the triangular and elongate central cusp (Fig. 5B). The outermost denticles are larger than the innermost. The large, fusiform, and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). Salivary glands are absent.

As the three specimens studied here were immature, the reproductive system was not studied.

Remarks: The validity of *Eolis cacaotica* has been unknown or omitted by almost all previous authors. Only Burn (1962) pointed out the possibility that *Aeolis foulisi* was its junior synonym. Stimpson (1855) described *Eolis cacaotica* from Port Jackson (Sydney Harbour, eastern Australia), whereas *Aeolis foulisi* was also described from Port Jackson 9 years later (Angas, 1864). As both original descriptions depict the same aeolidiid from the same locality, we render *Aeolis foulisi* as a junior synonym of *Eolis cacaotica*. Because the latter species has the characteristic oral glands described by Miller (2001), which are exclusive of this genus within Aeolidiidae, we transfer *Eolis cacaotica* to *Anteaeolidiella*.

Risbec (1928) erected the species name *Aeolidiella hulli* while studying material from Nou Island, New

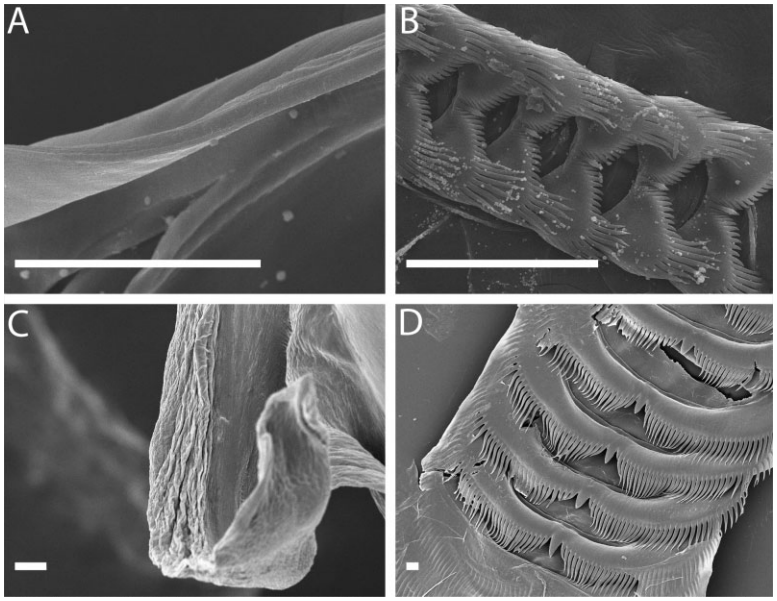


Figure 5. Scanning electron photographs. *Anteaeolidiella cacaotica* (MNCN 15.05/63476): A, detailed view of the masticatory border, scale bar = 100 μm; B, radular teeth, scale bar = 150 μm. *Anteaeolidiella chromosoma* (CASIZ 173060): C, detailed view of the masticatory border, scale bar = 10 μm; D, radular teeth, scale bar = 10 μm.

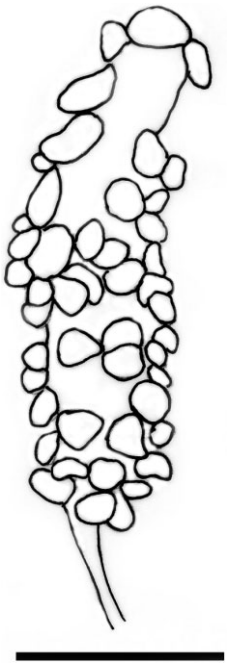


Figure 6. Drawing of the oral gland of *Anteaeolidiella.*

Caledonia. This author attached to the original description two coloured drawings (pl. X, fig. 7, pl. XVII, fig. 4). Both figures illustrate the same coloration pattern shown by *Anteaeolidiella cacaotica*. The type localities of both species are also quite close. Hence, we consider *Aeolidiella hulli* as a junior synonym of *Anteaeolidiella cacaotica*.

Eolis cacaotica has been considered an older synonym of *Austraeolis ornata* (Angas, 1864) by some authors (Coleman, 1989; Rudman & Willan, 1998; R. Willan, pers. comm.), although none of these authors defended this taxonomic position. *Austraeolis ornata* has annulate rhinophores and iridescent blue speckles over the dorsum. Stimpson (1855) did not mention any of these morphological features in the original description of *Eolis cacaotica*, whereas Angas (1864) depicted *Flabellina ornata* presenting these characteristics. Therefore, we concluded that *Eolis cacaotica* could not be an older synonym of *Austraeolis ornata.*

The main external differences among all the species of the *Anteaeolidiella indica* complex are illustrated in the Figures 4 and 7. Therefore, no further comparison with the remaining species is conducted here.

Anteaeolidiella orientalis (Bergh, 1888b)
Aeolidiella orientalis Bergh, 1888b: 673, pl. XVI, figs 8–13.

Eolidina mannarensis Virabhadra-Rao & Alagarswami, 1960: 6, figs 1–4, pl. 1, figs 1–6.

Type locality: 'Noordwaachter' Island, Indian Ocean.

Type material: To our knowledge no type material remains.

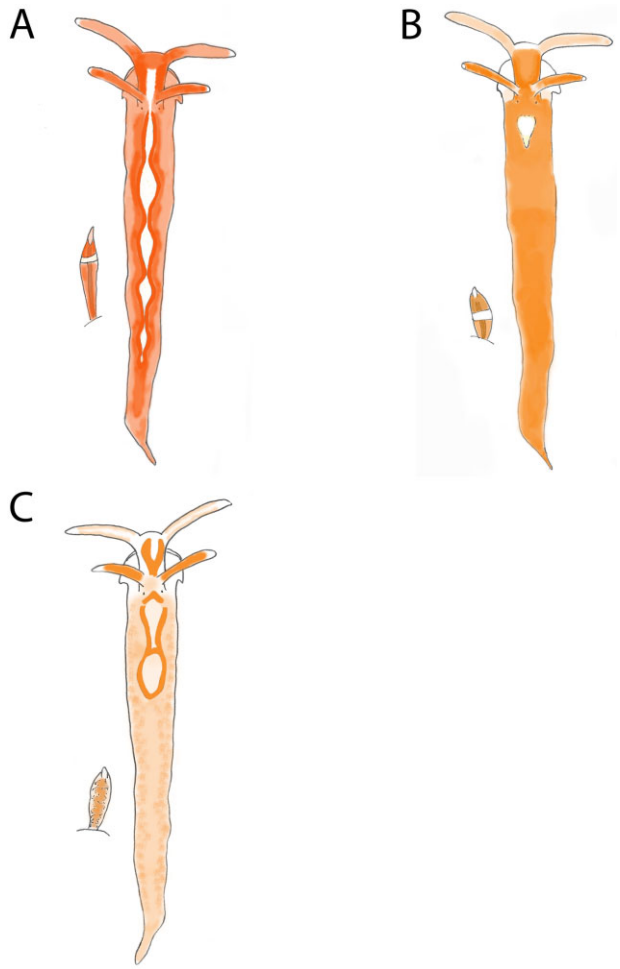


Figure 7. Schematic dorsal color patterns of the '*Anteaeolidiella indica*' species complex: A, ***Anteaeolidiella ireneae* sp. nov.**; B, ***Anteaeolidiella fijensis* sp. nov.**; C, ***Anteaeolidiella poshitra* sp. nov.**

Remarks: Excluding *Anteaeolidiella chromosoma* and *Anteaeolidiella oliviae*, the radular teeth of the remaining species of this genus are strongly bilobed, with elongate and acutely pointed denticles on either side of a prominent central cusp (e.g. Fig. 5B). Bergh (1888b) illustrated this type of radular morphology when he erected *Aeolidiella orientalis*. This author also depicted an oral gland composed of big secretory cells, such as those we found in all *Anteaeolidiella* species. Based on the radular teeth and the oral glands described by Bergh (1888b), we transfer *Aeolidiella orientalis* to *Anteaeolidiella*. Although this species has been considered as a junior synonym of '*A. indica*' (Gosliner & Griffiths, 1981), Bergh (1888b) described the rhinophores as white with red tips that are, so far, exclusive for this species within *Anteaeolidiella*. Edmunds (1969) reported *Aeolidiella orientalis* from Tanzania; however, his specimen showed red rhinophores with white tips, and therefore cannot be identified as *Anteaeolidiella orientalis*.

Eolidina mannarensis was also described as 'pale golden yellow speckled with orange at the tips of the tentacles and rhinophores' (Virabhadra-Rao & Alagarswami, 1960). The radular teeth of this species also correspond to *Anteaeolidiella*. Therefore, we render *Eolidina mannarensis* as a junior synonym of *Anteaeolidiella orientalis*.

Anteaeolidiella chromosoma (Cockerell & Eliot, 1905) (Figs 3B, 5C, D, 6, 8A)
Spurilla chromosoma Cockerell & Eliot, 1905: 51.
Aeolidiella chromosoma (Cockerell & Eliot, 1905): Gosliner, 1985, 259.

Type locality: Deadman's Island, San Pedro, California, USA.

Type material: According to Cockerell & Eliot (1905), in the Natural History Museum, London. The registration number of the holotype of *Anteaeolidiella chromosoma* is NHMUK 1904.7.7.4.

Material examined: CASIZ 173060, one specimen, dissected, 8 mm in length preserved, Mexico, Jalisco, Bahía de Banderas, collected by Jeff Goddard, 26.ii.06; CASIZ 187751, one specimen, dissected, 10 mm in length preserved, Japan, Honshu, Shizuoka Prefecture, Ose Cape, collected by Rie Nakano and A. Kawahara, 20.iii.10.

Geographical distribution: *Anteaeolidiella chromosoma* was first described from Deadman's Island, California, USA. It has also been reported from California (Er. Marcus, 1961), the Pacific coast of Costa Rica (Camacho-García *et al*., 2005), and Japan (Nakano, 2004).

External morphology (Fig. 3B): The body is elongate and moderately broad, tapering gradually to the tail. The anterior foot corners are stout and slightly protruded. The background colour is very variable. Specimens usually have a bright orange background, whereas others are almost translucent white (not shown). Both colour types have white spots all over the notum (from head to tail). Depending on the specimen, the density and size of these spots vary. The rhinophores, the oral tentacles and the foot corners have the same colour as the background coloration. The rhinophores are short and thick. They bear about ten lamellae that are arranged diagonally. The rhinophores have a white apex, white or cream pigmentation in the upper third, or brown pigment on the lamellae. The oral tentacles are long and stout.

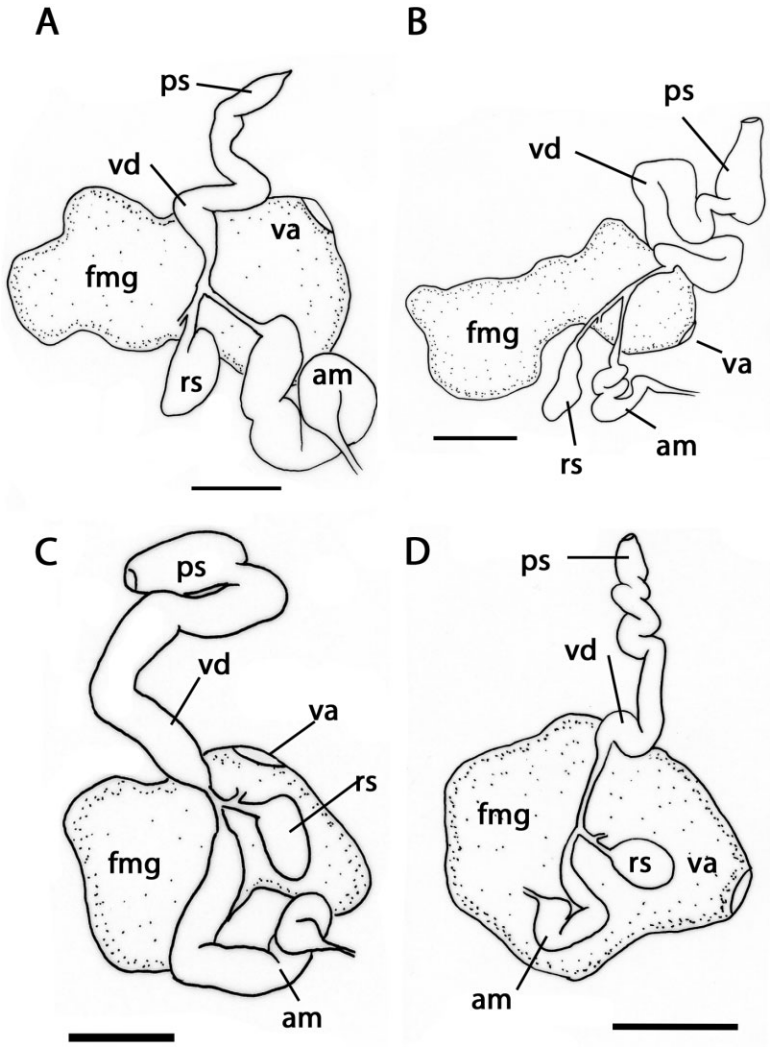


Figure 8. Reproductive system: A, *Anteaeolidiella chromosoma*, specimen from Mexico, Jalisco (CASIZ 173060), scale bar = 1 mm; B, *Anteaeolidiella saldanhensis*, specimen from South Africa, Western Cape Province (CASIZ 176313), scale bar = 1 mm; C, *Anteaeolidiella oliviae*, specimen from California, Monterey (CASIZ 181315A), scale bar = 1 mm; D, *Anteaeolidiella lurana*, specimen from Brazil, Cabo Frio (MZSP 97574), scale bar = 0.5 mm. Abbreviations: am, ampulla; fgm, female gland mass; ps, penial sac; rs, receptaculum seminis; va, vagina; vd, vas deferens.

The coloration of their tips is lighter than background coloration. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata length is variable, but all are long, cylindrical, and uniform in diameter throughout most of their length, and have a round apex. Some specimens have the tips of the cerata recurved inwards. The cerata extend from the rear of the rhinophores to the tail. They are translucent, with brownish green or dark-grey ramifications of the digestive gland visible throughout the body wall. The cnidosacs are white. All specimens have white marks all over the ceratal surface, although its density and size vary. The cerata are arranged in five or six rows in the anterior digestive branch, followed by arches. Each group contains between two and 20 cerata, decreasing in size towards the foot. The anus is cleioproctic, located between the third and the fourth rows. The genital opening is placed among the cerata of the anteriormost group on the right.

Anatomy: The masticatory border of the jaws is smooth (Fig. 5C). The radular formulae are 12 × 0.1.0 (CASIZ 187751) and 24 × 0.1.0 (CASIZ 173060). The teeth are progressively smaller to the posterior region of the radula. They are wide and bilobed, with 16–33 elongate and acutely pointed denticles on either side of the triangular and elongate central cusp (Fig. 5D).

The large, fusiform and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). The salivary glands are absent.

The reproductive system is diaulic (Fig. 8A). The preampullary duct widens into the conspicuous, wide, and long ampulla that narrows again before dividing into the oviduct and vas deferens. The moderately short vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a pyriform receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventral to the penis.

Remarks: Based on the perfoliate rhinophores, Cockerell & Eliot (1905) placed this species within *Spurilla*. Gosliner (1985) rendered *Spurilla chromosoma* as *Aeolidiella* because of the presence of oral glands with large vesicles, together with the anterior digestive branches arranged in rows; however, Carmona *et al*. (2013) transferred this species to *Anteaeolidiella* on the basis of molecular data. The latter outcome agrees with our present study, and it is also supported by the presence of the particular oral glands.

Anteaeolidiella chromosoma differs from the remaining members of the genus by its coloration, its perfoliate rhinophores, and the radular shape. Only *Anteaeolidiella oliviae* presents the latter two morphological characters, but both species have a consistently distinct coloration (see *Anteaeolidiella oliviae* remarks). *Spurilla neapolitana* and *Spurilla braziliana* may have a colour pattern that resembles that of *A. chromosoma*. Nevertheless, *A. chromosoma* presents the anterior digestive branch arranged in rows instead of arches. In addition, the number of lamellae in *A. chromosoma* is low, and they are arranged diagonally, whereas in *S. neapolitana* or *S. braziliana* they are numerous and transverse. Finally, differences between the oral glands of both species (*A. chromosoma* and *S. braziliana*) are also consistent.

Anteaeolidiella saldanhensis (Barnard, 1927)
(Figs 3C, 4B, 6, 8B)
Aeolidiella saldanhensis Barnard, 1927: 201, figs 2, 3.
Aeolidiella multicolor Macnae, 1954: 36, figs 27–29, pl. II, fig. 4.

Type locality: Saldanha Bay, South Africa.

Type material: To our knowledge no type material remains. We designate the specimen CASIZ 176313 from False Bay, Cape Province, South Africa, as the neotype.

Material examined: Neotype: CASIZ 176313, one specimen, dissected, 5 mm in length preserved, South Africa, western Cape Province, False Bay, collected by Terrence M. Gosliner, Ángel Valdés, Marta Pola, Elisabeth Moore, Lakisha Withey, and Carla Stout, 6.i.08.

Geographical distribution: So far, only known from South Africa (Barnard, 1927; Macnae, 1954; Gosliner, 1985; present study).

External morphology (Figs 3C, 4B): The body is elongate and moderately slender, tapering gradually to the fairly short tail. The anterior foot corners are stout and slightly protruded. The background colour is translucent white (Fig. 3C). The head bears a U-shaped orange mark, extending from the rhinophores to the base of the oral tentacles. Up to half of the base of the U is filled with orange pigmentation. Several opaque white diamond-shaped marks can be found beside the rhinophores, along the midline of the dorsum (Fig. 4B). The two anteriormost marks may also be joined. All the diamond-shaped marks are surrounded by orange pigmentation. The latter interrupts the connection among the white marks and extends almost to the tail (Fig. 4B).

Close to the ceratal insertion, orange and/or yellowish white pigmentation are found. The rhinophores and the oral tentacles are translucent with opaque white pigment on them. The rhinophores are stout and taper towards the rounded tip. The conical oral tentacles are slightly longer than the rhinophores. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata are long and moderately thick. They extend from the rear of the rhinophores to the tail and leave a bare zone over the dorsum. The translucent cerata may have two different colorations. The first colour type has white and orange pigmentation on the distal and proximal half, respectively (Figs 3C, 4B). Some other specimens have the ceratal epithelium diffusely covered with orange pigment, and the ramifications of the digestive gland are greyish or bluish in colour (Gosliner, 1985). Both colour types terminate in a white cnidosac. The cerata are arranged in rows: seven rows in the anterior digestive group, followed by up to 20 posterior rows. Each one contains between four and seven cerata, decreasing in size towards the foot. The anus is cleioproctic, located between the second and third rows of the first ceratal group of the right posterior digestive branch. The gonopore is housed ventral to the third row of the anterior digestive group.

Anatomy: Unfortunately, the bucal bulb was lost during the SEM examination process. Therefore, the

masticatory border and the radula could not be studied. The large, fusiform and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). Salivary glands are absent.

The reproductive system is diaulic (Fig. 8B). The preampullary duct widens into the short ampulla that narrows again before dividing into the oviduct and vas deferens. The moderately long vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a pyriform receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventral to the penis.

Remarks: Barnard (1927) erected the species *Aeolidiella saldanhensis* from Saldanha Bay (South Africa), but the original description is very faint. This author only provided some information about the radula and the rounded foot corners. Some years later, Macnae (1954) erected the name *Aeolidiella multicolor*, from False Baye (South Africa). Macnae (1954) could not compare his specimens with Barnard's because the type material of *Aeolidiella saldanhensis* was mislaid (Macnae, 1954). Thus, Macnae (1954) stated that the tentaculiform foot corners of *Aeolidiella multicolor* were significant enough to keep it as a distinct species from *Aeolidiella saldanhensis*. Barnard (1927) depicted the coloration of *Aeolidiella saldanhensis* as 'unknown', probably because the type material was already preserved when Barnard described it, and therefore the rounded foot corners could be an artefact of the preservation of the specimen. Therefore, we do not consider this difference as significant, and render *Aeolidiella multicolor* as a junior synonym of *Aeolidiella saldanhensis*. Because of its radular morphology and its oral glands, we transfer *Aeolidiella saldanhensis* to *Anteaeolidiella*.

As most of the *Anteaeolidiella* species have orange rhinophores, *Anteaeolidiella saldanhensis* is clearly different from the other species because of its white rhinophores and oral tentacles. The main external differences among all the species of the *Anteaeolidiella indica* complex are illustrated in Figures 4 and 7. Therefore, no further comparison with the remaining species is conducted here.

Anteaeolidiella takanosimensis (Baba, 1930)
(Figs 3D, 4C, 6, 9A, B)

Eolis sp. Ijima, 1918: 615, fig. 740.

Aeolidiella takanosimensis Baba, 1930: 122, fig. 4a, b, pl. IV, fig. 5a–c.

Eolidina takanosimensis Baba, 1937: 336.

Type locality: Takanosima, Tateyama Bay, Japan.

Type material: To our knowledge no type material remains. We designate the specimen MNCN 15.05/63479 from Manuzaru, Japan, as the neotype.

Material examined: Neotype: MNCN 15.05/63479, one specimen, dissected, immature, 3 mm in length preserved, Japan, Manuzaru, collected by Rie Nakano, 19.iv.06. Other material: MNCN 15.05/63478, one specimen, dissected, immature, 7 mm in length preserved, Japan, collected by Rie Nakano, 10.viii.10.

Geographical distribution: Only known from Japan (Baba, 1930; Baba, 1979a,b; present study).

External morphology (Figs 3D, 4C): The body is elongate and slender, tapering gradually to the fairly short tail. The anterior foot corners are stout and slightly protruded. The background colour is translucent white (Fig. 3D). The head bears a U-shaped bright coral (PANTONE 1635) mark, extending from the rhinophores to the base of the oral tentacles. Both sides of the head have a conspicuous coral line near the foot edges and extending towards the oral tentacles (Figs 3D, 4C). Extending posteriorly just behind the rhinophores, an opaque white area surrounded by bright coral pigment in the shape of an elongate triangle is found. Over the pericardium there is an opaque white diamond outlined with coral pigment. The latter interrupts the connection among the white marks and extends almost to the tail (Fig. 4C). The rhinophores and the oral tentacles are translucent with bright coral pigment over them (Fig. 4C). The rhinophores are slender, long, and taper towards the white tips. The oral tentacles are conical, slightly longer than the rhinophores, and have white tips. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata are long and moderately thick. They extend from the rear of the rhinophores to the tail and leave a bare zone over the dorsum. The ceratal epithelium is diffusely covered with coral pigment, with a white subapical band, and terminates in a bright coral tip. The ramifications of the digestive gland are greyish or chocolate brown. The specimens examined here were not very well preserved because the cerata were autotomized. Therefore, the information given below is taken from Figure 3D and the original description of *Aeolidiella takanosimensis* (Baba, 1930). The cerata are arranged in up to 28 rows. Each row contains between four and seven cerata, decreasing in size towards the foot. The anus is cleioproctic, located below the second row of the first ceratal group of the right posterior digestive branch. The gonopore is housed between the second and third rows of the anterior digestive group.

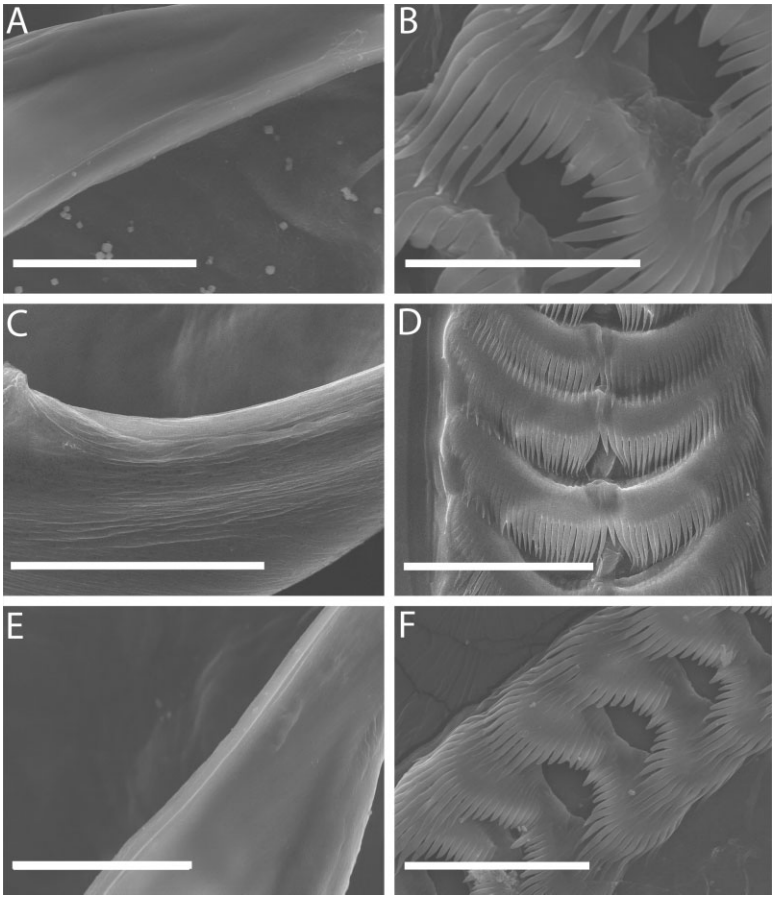


Figure 9. Scanning electron photographs. *Anteaeolidiella takanosimensis* (MNCN 15.05/63478): A, detailed view of the masticatory border, scale bar = 100 μm; B, radular teeth, scale bar = 50 μm. *Anteaeolidiella oliviae* (CASIZ 181315, 10 mm): C, detailed view of the masticatory border, scale bar = 100 μm; D, radular teeth, scale bar = 150 μm. *Anteaeolidiella lurana* (MZSP 97638): E, detailed view of the masticatory border, scale bar = 100 μm; F, radular teeth, scale bar = 100 μm.

Anatomy: The masticatory border of the jaws is smooth (Fig. 9A). The radular formula is 14 × 0.1.0 (MNCN 15.05/63478 and MNCN 15.05/63479). The radular teeth are wide and bilobed, with 14 or 15 elongate and acutely pointed denticles on either side of the triangular and elongate central cusp (Fig. 9B). The large, fusiform, and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). The salivary glands are absent.

The reproductive system could not be studied because all of the specimens available were immature.

Remarks: Baba first described *Aeolidiella takanosimensis* in 1930. During the late 1970s, Baba (1979a, b) depicted the different phases of the coral marks along the development of the specimens (Baba, 1979a), and noted the placement of the anus and the gonopore (Baba, 1979b); however, in the second contribution, Baba (1979b) misidentified some specimens of *Anteaeolidiella takanosimensis*. Based on our morphological and molecular data, we consider that the colour pattern in *Anteaeolidiella*, particularly in the '*Anteaeolidiella indica*' complex, is decisive for distinguishing species. Figure 3 in Baba (1979b) depicts the specimen 'number two' with a uniformly coral-tinted head with no traces of the U-shaped mark. This specimen was also free from the dorsal coral marks. Moreover, Baba (1979b) pointed out that this particular specimen was pleuroproctic instead of cleioproctic. Thus, we consider that specimen number two in Baba (1979b) is not *Anteaeolidiella takanosimensis*, and was probably an undescribed species.

Risbec (1956) identified a preserved specimen from Vietnam as *Aeolidiella? takanosimensis*, although it presented perfoliate rhinophores. This author illustrated the radular teeth that agree with most of the *Anteaeolidiella* species. Some years later, based on

the ornamentation of the rhinophores and differences in the number of radular denticles of *Aeolidiella? takanosimensis*, Ernest Marcus (1961) erected the name *Aeolidiella risbeci* for the specimen found by Risbec in 1956. *Anteaeolidiella chromosoma* and *Anteaeolidiella oliviae* present perfoliate rhinophores, but none of these species have the type of radular teeth illustrated by Risbec (1956). Additionally, the perfoliate rhinophores could be an artefact of the preservation. Although the information given by this author is insufficient for identifying the specimen properly, it seems possible that Risbec's specimen was *Anteaeolidiella takanosimensis*.

Finally, the coloration of our specimens clearly agrees with the original description by Baba (1930). Moreover, the coral colour tips of the cerata and the lateral coral lines can be considered as diagnostic for this species. The main external differences among all the species of the *Anteaeolidiella indica* complex are illustrated in Figures 4 and 7. Therefore, no further comparison with the remaining species is conducted here.

Anteaeolidiella oliviae (MacFarland, 1966)
(Figs 3E, 6, 8C, 9C, D)
Aeolidiella oliviae MacFarland, 1966: 373, pl. 62, figs 4–6, pl. 72, figs 9–14.

Spurilla oliviae (MacFarland, 1966): Sphon & Lance, 1968: 81.

Type locality: San Diego, California, USA.

Type material: To our knowledge no type material remains. We designate the specimen CASIZ 084921 from San Miguel Island as the neotype.

Material examined: Neotype: CASIZ 084921, one specimen, dissected, 20 mm in length preserved, California, Channel Islands, San Miguel Island, collected by Robert Van Syoc, 13.vii.87. Other material: CASIZ 181315, two specimens, dissected, 8 and 10 mm in length preserved, California, Monterey County, Pacific Grove, collected by Gary MacDonald, 26.v.09.

Geographical distribution: So far, known only from California (MacFarland, 1966).

External morphology (Fig. 3E): The body is elongate and moderately broad, tapering gradually to the tail. The anterior foot corners are stout and slightly protruded. The specimens have a bright orange background with white inconspicuous speckles all over the notum (from head to tail). The head of some specimens is completely white (Fig. 3E). The bright orange, almost red rhinophores are short and thick with a white apex. They bear between seven and 16 lamellae that are arranged diagonally, almost vertical. The oral tentacles are long, stout, and translucent white, with white tips. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata length is variable, but all are long, cylindrical, and uniform in diameter throughout most of their length, and have a round apex. Some specimens have the tips of the cerata slightly recurved inwards. They begin at the anterior end of the pericardium to the tail. The cerata are bright orange with white speckles over their surface, mainly at their bases. The cnidosacs are white.

The cerata are arranged in five to 13 rows. Each group contains between three and 17 cerata, decreasing in size towards the foot. The anus is cleioproctic, located between the eighth and ninth rows on the right. The gonopore is between the fourth and fifth rows on the right.

Anatomy: The masticatory border of the jaws is smooth (Fig. 9C). The radular formulae are 14 × 0.1.0 (CASIZ 181315, 8 mm) and 22 × 0.1.0 (CASIZ 181315, 10 mm). The teeth are progressively smaller to the posterior region of the radula. They are also wide and bilobed, with 21–32 elongate and acutely pointed denticles on both sides of the triangular, elongate, and medium central cusp (Fig. 9D). The large, fusiform and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). Salivary glands are absent.

The reproductive system is diaulic (Fig. 8C). The preampullary duct widens into the moderately long ampulla that narrows again before dividing into the oviduct and vas deferens. The elongate vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a pyriform receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female glands. The vagina opens ventral to the penis.

Remarks: Aeolidiella oliviae was described in 1966 by MacFarland. This author provided a detailed description of the external morphology, the coloration, and the buccal bulb of the six specimens of this Californian species. Probably based on the perfoliate rhinophores, Sphon & Lance (1968) transferred *Aeolidiella oliviae* to the genus *Spurilla*, but the molecular phylogeny conducted by Carmona *et al*. (2013) placed this species within *Anteaeolidiella*.

Excluding *Anteaeolidiella chromosoma*, the radular morphology of *Anteaeolidiella oliviae* is consistently different from the rest of *Anteaeolidiella* members, as the radular teeth of the latter species are much wider and are not so strongly bilobed (e.g. Figs 5, 8). More-

over, the bright orange coloration, barely with any other pigment, and the dark orange and perfoliate rhinophores diagnose *Anteaeolidiella oliviae*. The reproductive system is presented here for the first time.

Anteaeolidiella lurana (Ev. Marcus & Er. Marcus, 1967) (Figs 3F, 4D, 6, 8D, 9E, F)
Aeolidiella lurana Ev. Marcus & Er. Marcus, 1967: 115–119, figs 149, 150.

Type locality: Urubuqueçaba, Bay of Santos, Island Brazil.

Type material: According to Ev. Marcus & Er. Marcus (1967) in the US National Museum, Washington DC. The registration number of the holotype of *Anteaeolidiella lurana* is USNM 576293.

Material examined: CASIZ 173060, one specimen, dissected, 8 mm in length preserved, Mexico, Jalisco, Bahia de Banderas, collected by Jeff Goddard, 26.ii.06; CASIZ 071302, four specimens, dissected, 9, 10, 11, and 12 mm in length preserved, Mexico, Pacific Ocean, Islas de Revillagigedo, Isla Socorro, collected by Terrence M. Gosliner, 7–9.xii.88; CASIZ 186820, one specimen, dissected, 3 mm in length preserved, Italy, Gulf of Naples, collected by Guido Villani, x.11; MZSP 97574, one specimen, dissected, 3 mm in length preserved, Brazil, Cabo Frio, collected by Vinicius Padula, 14.xii.08; CNMO 2996, one specimen, dissected, 5 mm in length preserved, Mexico, Yucatán, collected by Jazmin Ortigosa, vii.06; MZSP 97638, one specimen, dissected, 2 mm in length preserved, Brazil, Cabo Frio, collected by Vinicius Padula, 09.xii.07.

Geographical distribution: Anteaeolidiella lurana was originally described from Brazil (Ev. Marcus & Er. Marcus, 1967). This species is also found in the Gulf of Naples [under the names *Aeolidiella takanosimensis* in Schmekel, (1968), *Aeolidiella orientalis takanosimensis* in Schmekel & Portmann (1982), and *Aeolidiella indica* in Sammut & Perrone (1998)], the Lazio coast [*Anteaeolidiella foulisi* in Crocetta *et al*. (2013)], the Balearic Islands (as *Anteaeolidiella indica* in GROC, 2013), the Strait of Gibraltar (as *Aeolidiella indica*, García-Gómez, 2002), the Canary Islands (Pérez-Sánchez & Moreno, 1990; Moro *et al*., 1995, 2003; Ortea *et al*., 2001), the Caribbean [as *Aeolidiella stephanieae* in Ortigosa *et al*., (2013) or as *Aeolidiella indica* in Valdés *et al*. (2006)], Bermuda (present study), and Queensland (Australia, present study).

External morphology (Figs 3F, 4D): The body is elongate and moderately slender, tapering gradually to the fairly short tail. The anterior foot corners are stout and slightly protruded. The background colour is translucent white (Fig. 3F). The head bears a bracket-shaped orange mark, extending from the rhinophores to the base of the oral tentacles. A pair of inconspicuous orange lines, lateral to the head, may be found. Extending posteriorly, just behind the rhinophores, an opaque white area, surrounded by orange pigment, in the shape of an elongate diamond is found. An orange diamond follows the latter mark and outlines the pericardium (Fig. 4D). This orange mark is filled with white pigmentation. Thereafter, two thin orange bands extend almost to the tail, forming teardrops or diamond marks every time they join (Fig. 4D). The rhinophores and the oral tentacles have the same colour as the background. The rhinophores are smooth, stout, and taper towards the rounded tip. They have orange pigment over the proximal two-thirds and white pigmentation on their tips. The conical oral tentacles are slightly longer than the rhinophores. They have white pigmentation on their tips and may also have orange pigment over their dorsal surface. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata are long and thickest in their upper third. They extend from the rear of the rhinophores to the tail. The ceratal epithelium is diffusely covered with orange pigment, interrupted by a white subapical band. The ramifications of the digestive gland are orange and terminate in a white cnidosac. The cerata are arranged in up to 23 rows. Each row contains between two and nine cerata, decreasing in size towards the foot. The cleioproctic anus is usually located between the eighth and ninth rows. The genital opening is housed ventrally to the third row of the anterior digestive group.

Anatomy: The masticatory border of the jaws is smooth (Fig. 9E). The radular formulae are 10 × 0.1.0 (CNMO 2996), 14 × 0.1.0 (CASIZ 186820), 15 × 0.1.0 (MZSP 97574), and 16 × 0.1.0 (MZSP 97638). The radular teeth are wide and bilobed, with 12–22 elongate and acutely pointed denticles on either side of the triangular and elongate central cusp (Fig. 9F). The teeth are progressively smaller in the posterior region of the radula. The large, fusiform, and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). The salivary glands are absent.

The reproductive system is diaulic (Fig. 8D). The preampullary duct widens into the short ampulla that narrows again before dividing into the oviduct and vas deferens. The elongate vas deferens enters the wider proximal portion of the penial sac, which con-

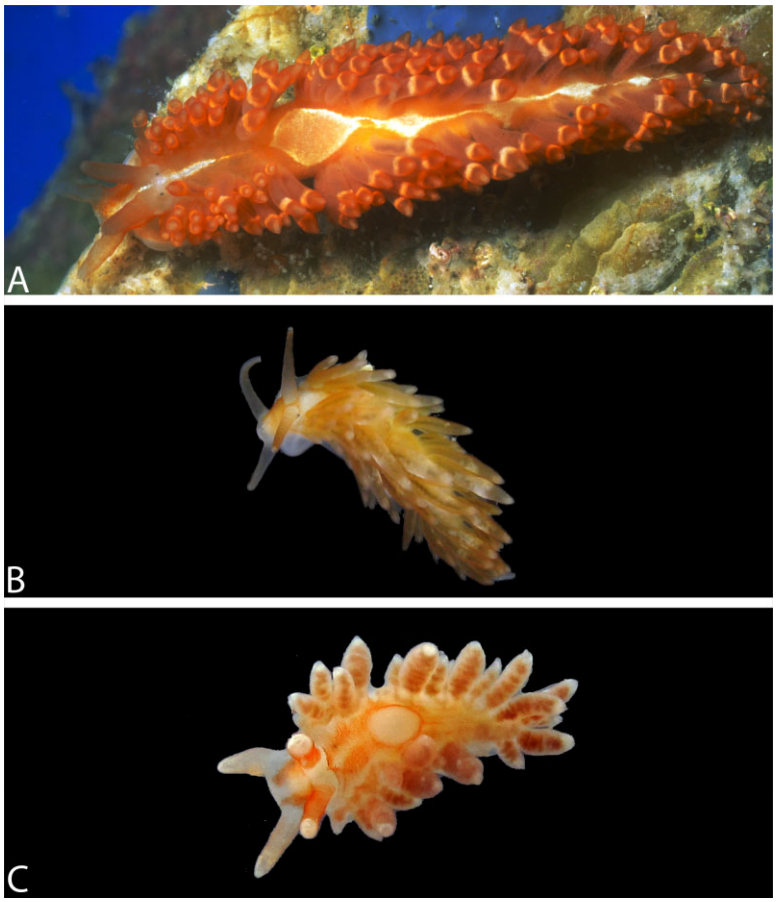


Figure 10. Photographs of living animals: A, ***Anteaeolidiella ireneae* sp. nov.**, specimen from Clipperton Island, photo by K.L. Kaiser, CASIZ 115686; B, ***Anteaeolidiella fijensis* sp. nov.**, specimen from Fiji, photo by Michael Schrödl, ZSM 20130053; C, ***Anteaeolidiella poshitra* sp. nov.**, from India, Gujarat, photo by Vishal Bhave, BNHS-opistho-38.

tains the unarmed penial papilla. The short oviduct connects with a rounded receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventral to the penis.

Remarks: Ev. Marcus & Er. Marcus (1967) described *Anteaeolidiella lurana* with material from the Bay of Santos (Brazil). All our specimens identified as *Anteaeolidiella lurana*, regardless of being from Brazil or not, agree well with the original description. Additionally, the uncorrected *p*-distances for *COI* among these specimens were very close to 0. The translucent body, the bracket-shaped orange mark, the ceratal coloration, and the marks over the notum distinguish this species from other species in the genus (Figs 4, 10).

Thus far, *Anteaeolidiella lurana* is the only amphiatlantic species of this genus. In addition, the presence of this species in the Mediterranean is supposedly caused by shipping transport (Zenetos *et al.*, 2004; García-Gómez, Cervera & García-García, 2011; Crocetta, 2012) or through an unknown vector (Sciberras & Schembri, 2007; Occhipinti-Ambrogi *et al.*, 2011). Moreover, this species has also been recorded from the eastern coast of Australia (present study; minimun uncorrected p-distance = 0% for *COI*).

Anteaeolidiella ireneae sp. nov. LSID urn:lsid:zoobank.org:act:E3B0E8F9-39FB-4254-B9CC-C1C528E7EE40 (Figs 6, 7A, 10A, 11A, B, 12A)
Anteaeolidiella sp. A Carmona *et al.*, 2013: 6.

Material examined: Holotype: CASIZ 115686, one specimen, dissected, 6 mm in length preserved, Clipperton Island, eastern Pacific Ocean, collected by K.L. Kaiser, iv–v.98.

Other material: CASIZ 192421, one specimen, dissected, 12 mm in length preserved, Clipperton Island,

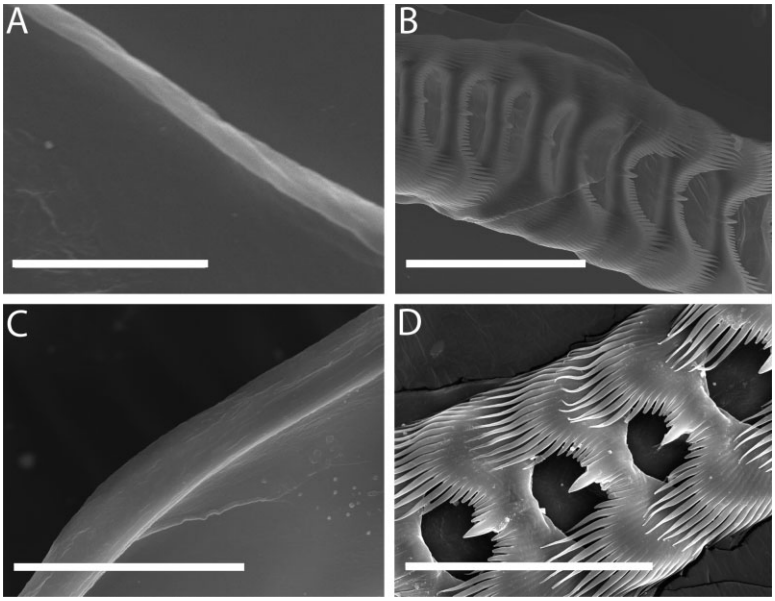


Figure 11. Scanning electron photographs. ***Anteaeolidiella ireneae* sp. nov.** (CASIZ 115686): A, detailed view of the masticatory border, scale bar = 50 μm; B, radular teeth, scale bar = 200 μm. ***Anteaeolidiella fijensis* sp. nov.** (ZSM 20130053): C, detailed view of the masticatory border, scale bar = 50 μm; D, radular teeth, scale bar = 50 μm.

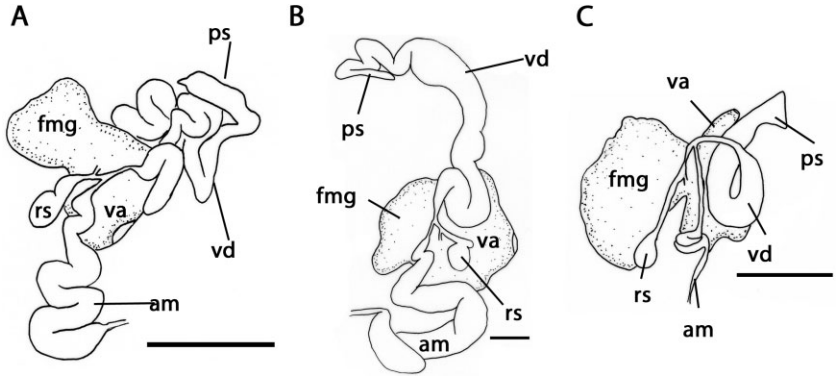


Figure 12. Reproductive system: A, ***Anteaeolidiella ireneae* sp. nov.**, specimen from Clipperton Island (CASIZ 115686), scale bar = 1 mm; B, ***Anteaeolidiella fijensis* sp. nov.**, specimen from Fiji (ZSM 20130054), scale bar = 0.5 mm; C, ***Anteaeolidiella poshitra* sp. nov.**, specimen from India, Guajarat (BNHS-opistho-38), scale bar = 0.5 mm. Abbreviations: am, ampulla; fgm, female gland mass; ps, penial sac; rs, receptaculum seminalis; va, vagina; vd, vas deferens.

eastern Pacific Ocean, collected by K.L. Kaiser, iv–v.98.

Type locality and habitat: Clipperton Island, eastern Pacific Ocean. Under dead coral heads and sand in 15–20 m of deep water.

Geographical distribution: So far, this species is known from Clipperton Island, Isla Canal de Afuera (Panama, PAC), Bahía de San Marte (Mexico, PAC), Isla Socorro (Mexico, PAC; present study), and the Pacific coast of Costa Rica (as *Aeolidiella indica* in Camacho-García *et al*., 2005).

Etymology: This species is dedicated to Irene Cervera, the first daughter of the last author of this article.

External morphology (Figs 7A, 10A): The body is large, elongate, and moderately broad, tapering gradually to the wide tail. The anterior foot corners are stout and slightly protruded. The background colour is translucent white, with orange pigment

scattered over the notum and head (Fig. 10A). The intensity of these orange speckles varies with the specimen, from dull to bright orange. A more or less conspicuous white mark is found over the head that goes through the rhinophores through an opaque white or yellowish area, in the shape of teardrop (Fig. 7A). This white patch may continue over the pericardium as a large whitish yellow diamond or a circle. Posterior to these, up to four pale yellow teardrop marks are found (Fig. 7A). The rhinophores are short, quite thick at their base, and smooth. They can be bright or dull orange, and have a white apex. The oral tentacles are longer than the rhinophores, stout, and translucent orange with white tips. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata length is variable, but all are long, cylindrical, and uniform in diameter throughout most of their length, and have a round apex. They begin at the rear end of the rhinophores to the tail, leaving a bare zone on the dorsum. They might be bright orange or dark grey, both with a white subapical band and white tips.

The cerata are arranged in five to 36 rows. Each group contains between 4 and 12 cerata, decreasing in size towards the foot. The anus is cleioproctic, located between the eighth and ninth rows on the right. The gonopore is between the fourth and fifth rows on the right.

Anatomy: The masticatory process of the jaws is smooth (Fig. 11A). The radular formula is 27 × 0.1.0 (CASIZ 115686). The teeth are progressively smaller to the posterior region of the radula. They are also wide and bilobed, with 24–27 elongate and acutely pointed denticles on both sides of the triangular and elongate central cusp (Fig. 11B). The outermost denticles are larger than the innermost. The large, fusiform and conspicuous oral glands lie dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). The salivary glands are present.

The reproductive system is diaulic (Fig. 12A). The preampullary duct widens into the conspicuous, long, and wide ampulla that narrows again before dividing into the oviduct and vas deferens. The very long and convoluted vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a pyriform-shaped receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventral to the penis.

Remarks: Anteaeolidiella ireneae sp. nov. is clearly distinct from the other *Anteaeolidiella* species. The elongate, large, and broad body, the thick and smooth rhinophores, and the great number of cerata are, thus far, only present in this species. Internally, the morphology of the radular teeth of *Anteaeolidiella ireneae* sp. nov. is also different. Whereas most of the *Anteaeolidiella* species have a few small denticles between the central cusp and the large outermost denticles, *Anteaeolidiella ireneae* sp. nov. doubles the number of small denticles. Regarding the reproductive system, this species has the largest vas deferens among *Anteaeolidiella* species (Fig. 12A).

Anteaeolidiella fijensis sp. nov. LSID urn:lsid:zoobank.org:act:349DA396-370E-4DC3-83EC-EB2D117F5004 (Figs 6, 7B, 10B, 11C, D, 12B)
Anteaeolidiella sp. B Carmona *et al*., 2013: 6.

Material examined: Holotype: ZSM 20130053, one specimen, dissected, 4 mm in length preserved, Fiji, 20.viii.06.

Paratype: ZSM 20130054, one specimen, dissected, 4 mm in length preserved, Fiji, 20.viii.06.

Type locality and habitat: Laucala Bay, Fiji. Under stones in 0–0.5 m of water.

Geographical distribution: So far, only known from Laucala Bay, Fiji (present study).

Etymology: The name *fijensis* refers to the Fiji Republic, where this species is found.

External morphology (Figs 7B, 10B): The body is elongate and moderately slender, tapering gradually to the fairly short tail. The anterior foot corners are stout and slightly protruded. The background colour is translucent white, with bright orange pigment over the dorsum, although the intensity varies with the specimen (Fig. 10B). The head bears an orange mark. The latter extends from the rhinophores to just before the foot edge, leaving the foot edge translucent (Fig. 7B). From the rear of the rhinophores, there is a translucent white area surrounded by an inverted triangle shape (Fig. 7B). The rhinophores are translucent orange and have a white tip end. They are moderately long and stout. The conical and translucent white oral tentacles are slightly longer than the rhinophores. A pair of black eyes is visible at the posterior side of the rhinophores base. The cerata are long and moderately thick. Some of them are *Eubranchus* like. They extend from the rear of the rhinophores to the tail and leave a bare zone over the dorsum. The ceratal epithelium is diffusely covered with orange pigment, and the ramifications of the digestive gland are greenish or brownish. A white subapical band is found. The cnidosacs are white. The cerata are arranged in six rows. Each row contains

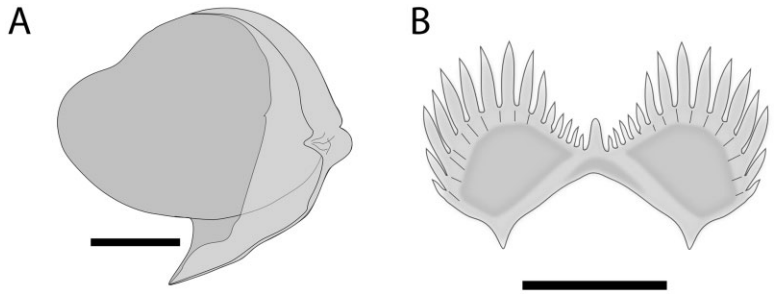


Figure 13. Drawings of the pharyngeal hard structures of ***Anteaeolidiella poshitra* sp. nov.** (BNHS-opistho-38): A, detailed view of the jaw, scale bar = 2 mm; B, radular teeth, scale bar = 50 μm.

between two and 15 cerata, decreasing in size towards the foot. The anus is cleioproctic, located between the second and third rows of the first ceratal group of the right posterior digestive branch. The gonopore is placed ventral to the first row on the right.

Anatomy: The masticatory border of the jaws is smooth (Fig. 11C). The radular formula is 14 × 0.1.0 (ZSM Mol 20130053). The radular teeth are wide and bilobed, with 19–21 elongate and acutely pointed denticles on both sides of the triangular and elongate central cusp (Fig. 11D). The outermost denticles are larger than the innermost. The teeth are progressively smaller in the posterior region of the radula. The large, fusiform, and conspicuous oral glands are arranged dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells (Fig. 6). The salivary glands are absent.

The reproductive system is diaulic (Fig. 12B). The preampullary duct widens into the conspicuous ampulla that narrows again before dividing into the oviduct and vas deferens. The conspicuous vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a rounded receptaculum seminis. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventrally to the penis.

Spawn: The living egg mass (not shown) is white. The number of whorls could not be determined.

Remarks: So far, only three species have a translucent body completely covered by orange pigment: *Anteaeolidiella cacaotica*, *Anteaeolidiella ireneae* sp. nov., and *Anteaeolidiella fijensis* sp. nov. *Anteaeolidiella ireneae* sp. nov. differs from *Anteaeolidiella fijensis* sp. nov. by its large and moderately broad body as well as its thick rhinophores. Externally, the main differences between *Anteaeolidiella cacaotica* and *Anteaeolidiella fijensis* sp. nov. are the coloration of the foot edge and the oral tentacles. The foot edge of the former species is orange instead of white translucent, as in *Anteaeolidiella fijensis* sp. nov. In addition, the oral tentacles in *Anteaeolidiella cacaotica* are usually orange, whereas in *Anteaeolidiella fijensis* sp. nov. they are usually translucent white. Regarding the internal anatomy, *Anteaeolidiella cacaotica* has a shorter vas deferens and a bigger receptaculum seminis than *Anteaeolidiella fijensis* sp. nov. Although the latter species also has a quite large vas deferens, it is not as long as that in *Anteaeolidiella ireneae* sp. nov. Additionally, the receptaculum seminis of *Anteaeolidiella ireneae* sp. nov. is also larger than that in *Anteaeolidiella fijensis* sp. nov. We also find some differences among the radulae of these three species. The central cusp of the radular teeth of *Anteaeolidiella fijensis* sp. nov. is more prominent than that found in *Anteaeolidiella cacaotica*, and *Anteaeolidiella ireneae* sp. nov. has double the number of small denticles between the central cusp and the large outermost denticles.

Anteaeolidiella poshitra sp. nov. LSID urn:lsid:zoobank.org:act:BC321799-0FFE-4585-A617-476FB4ADE19C (Figs 6, 7C, 10C, 12C, 13A, B)

Material examined: Holotype: BNHS-opistho-38, one specimen, dissected, 8 mm in length preserved, India, Gujarat, Jamnagar, Poshitra, Marine National Park, collected by Vishal Bhave and Aditi Nair, 11.xii.09.

Other material: BNHS-opistho-696, one specimen, 8 mm in length preserved, India, Gujarat, Jamnagar, Poshitra, Marine National Park, collected by Amruta Prasade, 27.i.12.

Type locality and habitat: Marine National Park, Poshitra, Jamnagar, Gujarat, India. Found under coral rubble.

Geographical distribution: Thus far, known only from Gujarat, India.

Etymology: The name *poshitra* refers to the shore of Poshitra village in Gujarat, where this species is found.

External morphology (Figs 7C, 10C): The anterior foot corners are stout and slightly protruded. The background colour is translucent white (Fig. 10C). The head bears a bracket-shaped orange mark, from the rhinophores to the base of the oral tentacles. Extending posteriorly, just behind the rhinophores, a pale orange area surrounded by bright orange pigment in the shape of an elongate diamond is found. Over the pericardium there is a pale orange circle outlined with bright orange pigment (Fig. 7C). The rhinophores and the oral tentacles have the same coloration as the background colour. The rhinophores are smooth, stout, and taper towards the rounded tip. They have orange pigment over the proximal two-thirds and white pigmentation on their tips. The conical oral tentacles are slightly longer than the rhinophores. They have white pigmentation on their tips and may have orange pigment over their dorsal surface. A pair of black eyes is visible at the posterior side of the rhinophores base.

The cerata are long and moderately thick, *Eubranchus* like. They extend from the rear of the rhinophores to the tail, and leave a bare zone over the dorsum. The ramifications of the digestive gland are orange, and have several constrictions over its length. They terminate in a white cnidosac. The cerata are arranged in up to six rows. Each one contains between two and six cerata, decreasing in size and number of cerata towards the foot. The anus is cleioproctic, usually located between the eighth and ninth row. The genital opening is placed ventral to the third row of the anterior digestive group.

Anatomy: The masticatory border of the jaws is smooth (Fig. 13A). The radular formula is 15 × 0.1.0 (BNHS-opistho-38). The radular teeth are wide and bilobed, with 13–15 elongate and acutely pointed denticles on either side of the triangular and elongate central cusp (Fig. 13B). The outermost denticles are usually larger than the innermost. The teeth are progressively smaller in the posterior region of the radula. The large, fusiform, and conspicuous oral glands are arranged dorsolaterally to the buccal bulb. Each oral gland comprises rows of giant secretory cells. The salivary glands are absent.

The reproductive system is diaulic (Fig. 12C). The preampullary duct widens into the short and thin ampulla that narrows again before dividing into the oviduct and vas deferens. The conspicuous vas deferens enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The short oviduct connects to a rounded receptaculum seminis with a very long duct. The remaining portion of the oviduct departs from the base of the receptaculum and enters the female gland. The vagina opens ventral to the penis.

Remarks: This new species from India is externally similar to *Anteaeolidiella lurana*, but can be distinguished by several features. The cerata of the specimens from India lack any subapical band, and have constrictions in the digestive gland. In addition, the cerata of *Anteaeolidiella poshitra* sp. nov. are more bulbous than those of *Anteaeolidiella lurana*, resembling the cerata of *Eubranchus*. There are also some consistent differences in the coloration of both species. Whereas *A. lurana* has two dorsal orange and thin bands that extend from the rear of the rhinophores to the tail, forming the pattern depicted in the Figure 3D, *Anteaeolidiella poshitra* sp. nov. also has this kind of band but they disappear when they reach the posterior end of the pericardium (Fig. 7C). Regarding the reproductive system, *Anteaeolidiella lurana* has a quite short ampulla and thin but long vas deferens, whereas in *Anteaeolidiella poshitra* sp. nov. the ampulla is longer and thinner, and the vas deferens is shorter and wider.

DISCUSSION

Our molecular and morphological studies show the monophyletic status of *Anteaeolidiella*, reinforcing the outcomes of Carmona *et al*. (2013) and increasing the number of species from two (Miller, 2001) to ten (present study). These species can be distinguished by a combination of morphological and molecular synapomorphies. Further support for species delimitations was obtained from the ABGD method. The groups proposed by the ABGD were entirely congruent with the molecular phylogeny and the morphological data. The anatomical studies that we have conducted clearly indicate that there are morphological differences between sister species, especially in coloration. This last feature is essential in Aeolidiidae to separate species (pers. observ.). Some *Anteaeolidiella* species also have differences in their reproductive systems and radula. Additionally, different morphological characters such as oral and salivary glands have been examined here, and were found to be informative at the generic level. Although it is currently accepted that some other nudibranch species may have great differences in their colour patterns (e.g. Edmunds, 1969 and Thompson & Brown, 1984 for *Eubranchus farrani*;

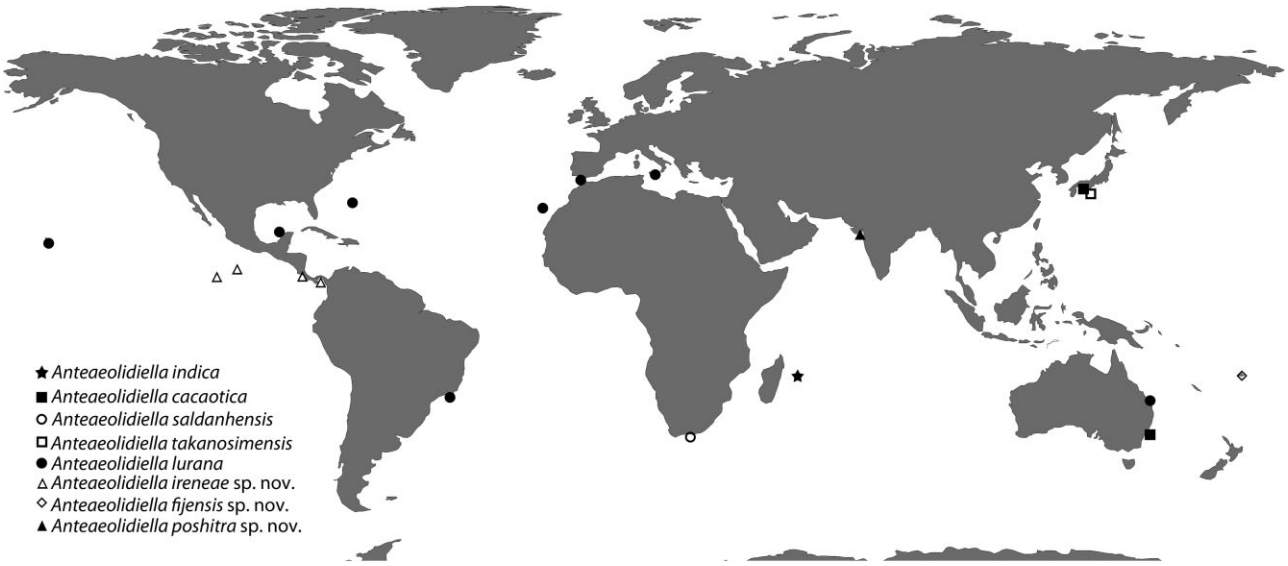


Figure 14. Distribution of the different species of *Anteaeolidiella* indica species complex.

Carmona *et al.,* 2014 for *Spurilla neapolitana*), so far, the species of *Anteaeolidiella* do not have such variability. Figures 4 and 7 illustrate how important the differences in coloration are within this genus. Based on this criterion and upon examining many pictures published on websites and field books, more colour patterns that suggest new putative cryptic species within *Anteaeolidiella* can be found, especially in the Indo-Pacific (e.g. Ono, 2004; Cobb & Mullins, 2013). For instance, in India more than one *Anteaeolidiella* species probably cohabit. Furthermore, when Miller (2001) erected the genus *Anteaeolidiella* and designated *Anteaeolidiella indica* as the type species, this author did not study the real *Anteaeolidiella indica* (with a greyish and yellowish colour pattern). Nevertheless, it is apparent from the locality (West Tamaki Head reef, Auckland, New Zealand), and from his description and figure, that the species actually involved was *Anteaeolidiella lurana*. As Miller's specimen was from New Zealand and the type locality of *Anteaeolidiella lurana* is Brazil, further morphological and molecular studies should be performed in order to clarify the identity of the New Zealand species. Therefore, according to the provisions of ICZN (1999) article 70.3, we maintain *Anteaeolidiella indica* as the type species of this genus.

The identity of *Anteaeolidiella indica* remains an open question. As indicated in the Remarks section of *Anteaeolidiella indica*, we could only find one photograph that matches Bergh's (1888a) original description. Material with this colour pattern is essential to clarify the morphological characteristics of this species and its intraspecific variability.

Our phylogenetic analyses also show how species with similar external coloration are not necessarily closely related. For example, the closest *Anteaeolidiella* species from a chromatic point of view, *Anteaeolidiella lurana* and *Anteaeolidiella poshitra* sp. nov. from India, or *Anteaeolidiella cacaotica* and *Anteaeolidiella fijensis* sp. nov., are not sister species (Figs 1, 3, 4, 9, 10). This tendency, which has also been observed in *Spurilla* (Carmona *et al*., 2014), may suggest an independent evolution of the colour pattern in these taxa.

In terms of biogeography, whereas all the remaining species have a quite restricted distribution (Fig. 14), *Anteaeolidiella lurana* is distributed from the Mediterranean to Brazil, as well as in the Eastern Pacific; however, to test the direction of this spread requires the study of haplotype diversity in Pacific and Atlantic–Mediterranean populations, which is beyond the scope of this study.

Therefore, the morphological and molecular data obtained in this study support the inclusion of *Anteaeolidiella chromosoma* and *Anteaeolidiella oliviae*, previously ascribed to *Spurilla* and *Aeolidiella*, as well as the description of three new species of *Anteaeolidiella*.

Based on the addition of these species in this genus, we propose a new diagnosis: body elongate and usually slender; foot corners stout; rhinophores stout, and usually smooth; coloration orange and/or white; cerata usually in rows; cerata long and moderately thick; radular teeth bilobed, with central cusp; outermost denticles usually larger than the innermost; masticatory border smooth; oral glands large, fusiform, with giant secretory cells.

ACKNOWLEDGEMENTS

We are deeply grateful to all of the individuals that helped to collect and provided specimens and images for this study, such as R. Nakano, D. Harasti, and G. Villani. Many thanks are due to W. Sterrer (Bermuda Aquarium and Museum of Zoology, BAMZ), B. Williams (Bermuda Institute of Oceanographic Sciences), and T.M. Trott (Acting Senior Marine Resources Officer, Bermuda Government), for welcoming, housing, and facilitating permits during the expeditions in Bermuda. We are grateful to Asad Rahmani (Director, BNHS). We are thankful to the Ministry of Environment and Forests, Government of India, who has provided financial support through the All India Co-ordinated Project On Taxonomy (AICOPTAX) and Deepak Apte, Principal Scientist of AICOPTAX and Chief Operating Officer (COO) of BNHS for constant encouragement and funding. We also acknowledge the PCCF (WL) Gujarat and Chief Conservator of Forests, Marine National Park, Gujarat, for the necessary permissions and timely help. We are also grateful to our team in Gujarat who managed and helped our field trips in Gujarat. A. Sellas helped us with some molecular lab work. This work was supported by several research grants: CGL2006-05182/BOS, CTM2008-05228-E/MAR, and CGL2010-17187, Spanish Ministry of Economy and Competitiveness (includes the early Ministry of Sciences and Innovation), to J.L.C.; California Academy of Sciences, National Science Foundation (DEB 0329054 PEET) to T.M. Gosliner; and a research grant from the Malacological Society of London to L. Carmona. This is CEI·MAR journal publication 45.

REFERENCES

Akaike H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19:** 716–723.

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool. *Journal of Molecular Biology* **215:** 403–410.

Angas GF. 1864. Description d'espèces nouvelles appartenant à plusieurs genres de Mollusques Nudibranches des environs de Port-Jackson (Nouvelle-Galles du Sud), accompagnée de dessins faits d'après nature. *Journal de Conchyliologie* **12:** 43–70.

Avise JC. 2004. *Molecular markers, natural history, and evolution, 2nd edn*. Sunderland, MA: Sinauer Associates.

Baba K. 1930. Studies on Japanese Nudibranchs 3. *Venus* **2:** 117–125.

Baba K. 1937. Opisthobranchia of Japan (II). *Journal. Department of Agriculture. Kyushu Imperial University* **5:** 289–344.

Baba K. 1979a. Brief comment on the identification of a nudibranch mollusk, *Aeolidiella takanosimensis* Baba, 1930, from Amakusa, Japan (Eolidoidea: Aeolidiidae). *Publications from Amakusa Marine Biological Laboratory, Kyushy University* **5:** 1–7.

Baba K. 1979b. Short Account of the Anatomy of a Nudibranchiate Mollusk *Aeolidiella takanosimensis* Baba, 1930 from Japan. *The Veliger* **22:** 12–18.

Barnard KH. 1927. South African nudibranch Mollusca, with descriptions of new species and a note on some specimens from Tristan d'Acunha. *Annals of the South African Museum* **25:** 171–215.

Bergh LSR. 1875. Beiträge zur Kenntniss der Aeolidiaden. III. *Verhandlungen der königlichkaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen)* **25:** 633–658.

Bergh LSR. 1888a. Malacologische Untersuchungen. In: Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. *Wissenschaftliche Resultate* **3:** 755–814.

Bergh LSR. 1888b. Beiträge zur Kenntniss der Aeolidiaden. IX. *Verhandlungen der königlichkaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen)* **38:** 673–706.

Bhave VJ, Apte DA. 2011. Illustrated checklist of opisthobranch fauna of Ratnagiri, Maharashtra, India, with eight new records to India. *Journal of the Bombay Natural History Society* **108:** 172–182.

Bidgrain P. 2005. *Anteaeolidiella indica* from Reunion Island [Message in] Sea Slug Forum. Australian Museum, Sydney. Available at: http://www.seaslugforum.net/find/13107

Boserelle P, Levy JM, Michenet F. 2013. *Aeolidiella indica* from Tahiti [Message in] Nudi Tahiti. Available at: http://www.nuditahiti.com/liste-des-esp%C3%A8ces/aeolidiella-indica/

Burn R. 1962. Descriptions of Victorian nudibranchiate Mollusca, with a comprehensive review of the Eolidiacea. *Memoirs of the National Museum, Melbourne* **25:** 95–128.

Burn R. 1964. A centennial commentary and zoogeographical remarks on Angas' Sydney nudibranchs (Molluscs, Gastropoda). *Journal de Conchyliologie* **104:** 85–93.

Burn R. 2006. A checklist and bibliography of the Opisthobranchia (Mollusca: Gastropoda) of Victoria and the Bass Strait area, south-eastern Australia. *Museum Victoria Science Reports* **10:** 1–42.

Camacho-García Y, Gosliner TM, Valdés Á. 2005. *Field guide to the sea slugs of the tropical Eastern Pacific*. San Francisco, CA: California Academy of Sciences.

Carmona L, Lei BR, Pola M, Gosliner TM, Valdés Á, Cervera JL. 2014. Untangling the *Spurilla neapolitana* (Delle Chiaje, 1841) species complex: a review of the genus *Spurilla* Bergh, 1864 (Mollusca: Nudibranchia: Aeolidiidae). *Zoological Journal of the Linnean Society* **170:** 132–154. doi: 10.1111/zoj.12098.

Carmona L, Malaquias MA, Gosliner TM, Pola M, Cervera JL. 2011. Amphi-Atlantic distributions and

cryptic species in sacoglossan sea slugs. *Journal of Molluscan Studies* **77:** 401–412.

Carmona L, Pola M, Gosliner TM, Cervera JL. 2013. A tale that morphology fails to tell: a molecular phylogeny of Aeolidiidae (Aeolidida, Nudibranchia, Gastropoda). *PLoS ONE* **8:** e63000. doi:10.1371/journal.pone.0063000.

Claremont M, Houart R, Williams ST, Reid DG. 2013. A molecular phylogenetic framework for the Ergalataxinae (Neogastropoda: Muricidae). *Journal of Molluscan Studies* **79:** 19–19.

Cobb G, Mullins D. 2013. *Antaeolidiella cacaotica* from Sunshine Coast [Message in] Nudibranchs of Sunshine Coast Australia. Available at: http://www.nudibranch.com.au/pages/2516c.htm

Cockerell TDA, Eliot C. 1905. Notes on a collection of Californian nudibranches. *Journal of Malacology* **12:** 31–53.

Coleman N. 1989. *Nudibranchs of the south Pacific, Vol. 1.* Springwood, Queensland, Australia: Sea Australia Resource Centre.

Colgan DJ, McLauchlan A, Wilson GDF, Livingston S, Macaranas J, Edgecombe GD, Cassis G, Gray MR. 1998. Molecular phylogenetics of the Arthropoda: relationships based on histone H3 and U2 snRNA DNA sequences. *Australian Journal of Zoology* **46:** 419–437.

Crocetta F. 2012. Marine alien Mollusca in Italy: a critical review and state of the knowledge. *Journal of the Marine Biological Association of the United Kingdom* **92:** 1357–1365.

Crocetta F, Macali A, Furfaro G, Cooke S, Villani G, Valdés A. 2013. Alien molluscan species established along the Italian shores: an update, with discussions on some Mediterranean 'alien species' categories. *Zookeys* **277:** 91–108.

Debelius H, Kuiter RH. 2007. *Nudibranchs of the world*. Frankfurt, Germany: IKAN-Unterwasserarchiv.

Dinapoli A, Tamer C, Frassen S, Naduvilezhath L, Klussmann-Kolb A. 2006. Utility of H3-Genesequences for phylogenetic reconstruction – a case study of heterobranch Gastropoda. *Bonner Zoologische Beiträge* **55:** 191–202.

Domínguez M, Troncoso JS, García FJ. 2008. The family Aeolidiidae Gray, 1827 (Gastropoda Opisthobranchia) from Brazil, with a description of a new species belonging to the genus *Berghia* Trinchese, 1877. *Zoological Journal of the Linnean Society* **153:** 349–368.

Drummond AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones-Havas S, Thierer T, Wilson A. 2009. Geneious v4.6. Available at: http://www.geneious.com/

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Edmunds M. 1969. Opisthobranchiate mollusca from Tanzania I. Eolidacea (Eubranchidae and Aeolidiidae). *Proceedings of the Malacological Society of London* **38:** 451–469.

Eilertsen MH, Malaquias MAE. 2013. Systematic revision of the genus *Scaphander* (Gastropoda, Cephalaspidea) in the Atlantic Ocean, with a molecular phylogenetic hypothesis. *Zoological Journal of the Linnean Society* **167:** 389–429.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Journal of Molecular Biology and Biotechnology* **3:** 294–299.

Frey MA, Vermeij GJ. 2008. Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (Genus: *Nerita*): implications for regional diversity patterns on the marine tropics. *Molecular Phylogenetics and Evolution* **48:** 1067–1086.

García-García FJ, Domínguez M, Troncoso JS. 2008. *Opistobranquios de Brasil*. Vigo: Feito S. L.

García-Gómez JC. 2002. *Paradigmas de una fauna insólita. Los moluscos opistobranquios del estrecho de Gibraltar*. (Serie Ciencias) 20: 397 pp. Algeciras, Cádiz, Spain: Instituto de Estudios Gibraltareños.

García-Gómez JC, Cervera JL, García-García F. 2011. *Familia Aeolidiidae*. In: Gofas S, Moreno D, Salas C, coords. *Moluscos marinos de Andalucía*. Málaga: Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga, 508–511.

Gosliner TM. 1985. The Aeolid Nudibranchs family Aeolidiidae (Gastropoda, Opisthobranchia) from tropical Southern Africa. *Annals of the South African Museum* **95:** 233–267.

Gosliner TM, Behrens DW, Valdés Á. 2008. *Indo-Pacific nudibranchs and sea slugs*. Gig Harbor/San Francisco, CA: Sea Challengers/California Academy of Sciences.

Gosliner TM, Fahey S. 2011. Previously undocumented diversity and abundance of cryptic species: a phylogenetic analysis of Indo-Pacific Arminidae Rafinesque 1814 (Mollusca: Nudibranchia) with descriptions of twenty new species of *Dermatobranchus*. *Zoological Journal of the Linnean Society* **161:** 245–256.

Gosliner TM, Griffiths RJ. 1981. Description and revision of some South African Aeolidacean Nudibranchia (Mollusca, Gastropoda). *Annals of the South African Museum* **82:** 102–151.

GROC. 2013. *Anteaeolidiella foulisi a la Reserva Marina del Toro (Mallorca)*. Available at: http://www.opistobranquis.org/ca/noticies/10#sthash.3oBJz77N.dpuf

ICZN. 1999. *International code of zoological nomenclature, fourth edition*. London: International Trust for Zoological Nomenclature.

Ijima I. 1918. *A manual of Zoology*. Tokyo: Dainihontosho Publishing Co., Ltd.

Imamoto J. 2013. *Anteaeolidiella indica. [Message in] Umiushi website.* Available at: http://www.umiushi.info/kanri/photo_sql_eng.php?act=PSP&gakumei1=Anteaeolidiella+%5BOld+Aeolidiella%5D&gakumei2=indica&location_code=000

Jörger MK, Norenburg JL, Wilson NG, Schrödl M. 2012. Barcoding against a paradox? Combined molecular species delineations reveal multiple cryptic lineages in elusive meiofaunal sea slugs. *BMC Evolutionary Biology* **12:** 245.

Katoh K, Asimenos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. In *Bioinformatics for DNA Sequence Analysis* edited by D. Posada. *Methods in Molecular Biology* **537:** 39–64.

Knowlton N. 2000. Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* **420:** 73–90.

Krug PJ, Morley MS, Asif J, Hellyar LL, Blom WM. 2008. Molecular confirmation of species status for the rare cephalaspidean *Melanochlamys lorrainae* (Rudman, 1968), and comparison with its sister species *M. cylindrica* Cheeseman, 1881. *Journal of Molluscan Studies* **74:** 267–276.

Krug PJ, Vendetti JE, Rodriguez AK, Retana JN, Hirano YM, Trowbridge CD. 2013. Integrative species delimitation in photosynthetic sea slugs reveals twenty candidate species in three nominal taxa studied for drug discovery, plastid symbiosis or biological control. *Molecular Phylogenetics and Evolution* **69:** 1101–1119.

MacFarland FM. 1966. Studies of opisthobranchiate mollusks of the Pacific Coast of North America. *Memoirs of the California Academy of Sciences* **6:** 373.

Macnae W. 1954. On some eolidacean nudibranchiate molluscs from South Africa. *Annals of the Natal Museum* **13:** 1–50.

Maddison DR, Maddison WP. 2005. *MacClade 4., v. 4.08 for OSX*. Sunderland, MA: Sinauer Associates.

Malaquias MAE, Reid DG. 2008. Systematic revision of the living species of Bullidae (Mollusca: Gastropoda: Cephalaspidea), with a molecular phylogenetic analysis. *Zoological Journal of the Linnean Society* **153:** 453–543.

Malaquias MAE, Reid DG. 2009. Tethyan vicariance, relictualism and speciation: evidence from a global molecular phylogeny of the opistobranch genus *Bulla*. *Journal of Biogeography* **36:** 1760–1777.

Marcus E. 1958. On Western Atlantic Opisthobranchiate Gastropods. *American Museum Novitates* **1906:** 1–82.

Marcus E. 1961. Opisthobranch Mollusks from California. *The Veliger* **3:** 1–85.

Marcus E, Marcus E. 1967. American Opisthobranch Mollusks. *Studies in Tropical Oceanography, Miami* **10:** 129–203.

von Martens E, Pfeffer GJ. 1886. Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882–83. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **3:** 63–135, pls. 1–4.

Meyer CP. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* **79:** 401–459.

Miller MC. 2001. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Aeolidiidae from New Zealand waters. *Journal of Natural History* **35:** 629–662.

Moro L, Ortea J, Bacallado JJ, Caballer M, Acevedo I. 2003. Anaspidea, Cephalaspidea, Gymnosomata, Notaspidea, Nudibranchia, Sacoglossa y Thecosomata. In: Moro L, Martín JL, Garrido MJ, Izquierdo I, eds. *Lista de especies marinas de Canarias (algas, hongos, plantas y animals)*. Santa Cruz de Tenerife, Spain: Consejería Política Territorial y del Medio Ambiente del Gobierno de Canarias, 93–98.

Moro L, Ortea J, Bacallado JJ, Valdés A, Pérez-Sánchez JM. 1995. Nuevos Aeolidáceos (Gastropoda, Nudibranchia) para la fauna de Canarias. *Revista de la Academia de Canaria de Ciencias* **7:** 63–75.

Nakano R. 2004. *Opisthobranchs of Japan Islands*. Tokyo: Rutles, Inc.

Nylander JAA. 2004. *MrModeltest v2.3*. Program distributed by the author. Uppsala: Evolutionary Biology Centre, Uppsala University. Available at: http://www.abc.se/~nylander/mrmodeltest2/mrmodeltest2.html

Occhipinti-Ambrogi A, Marchini A, Cantone G, Castelli A, Chimenz C, Cormaci M, Froglia C, Furnari G, Gambi MC, Giaccone G, Giangrande A, Gravili C, Mastrototaro F, Mazziotti C, Orsi-Relini L, Piraino S. 2011. Alien species along the Italian coasts: an overview. *Biological Invasions* **13:** 215–237.

Ohnheiser LT, Malaquias MAE. 2013. Systematic revision of the gastropod family Philinidae (Mollusca: Cephalaspidea) in the north-east Atlantic Ocean with emphasis on the Scandinavian Peninsula. *Zoological Journal of the Linnean Society* **167:** 273–326.

Ono A. 1999. *Opisthobranchs of Kerama Islands*. Tokyo: TBS-Britannica Co., Ltd.

Ono A. 2004. *Opisthobranchs of Ryukyu Islands*. Tokyo: Rutles, Inc.

Ornelas-Gatdula E, Camacho-García Y, Schrödl M, Padula V, Hooker Y, Gosliner TM, Valdés A. 2012. Molecular systematics of the '*Navanax aenigmaticus*' species complex (Mollusca, Cephalaspidea): coming full circle. *Zoologica Scripta* **41:** 374–385.

Orr J. 1981. *Hong Kong nudibranchs*. Hong Kong: Urban Council.

Ortea J, Moro L, Bacallado JJ, Herrera R. 2001. Catálogo actualizado de los Moluscos Opistobranquios de las Islas Canarias. *Revista de la Academia Canaria de Ciencias* **12:** 105–136.

Ortigosa D, Simões N, Calado G. 2013. Seaslugs (Mollusca: Opisthobranchia) from Campeche Bank, Yucatan Peninsula, Mexico. *Thalassas* **29:** 59–75.

Padula V, Bahia J, Vargas C, Lindner A. 2011. Mollusca, Nudibranchia: new records and southward range extensions in Santa Catarina, southern Brazil. *Check List* **7:** 1–3.

Palumbi SR, Martin A, Romano S, Owen MacMillan W, Stice L, Grabowski G. 1991. *The simple fool's guide to PCR*. Honolulu: Department of Zoology, University of Hawaii.

Pérez-Sánchez JM, Moreno E. 1990. *Invertebrados Marinos de Canarias*. Las Palmas de Gran Canaria, Spain: Ediciones del Cabildo Insular de Gran Canaria.

Pittman C, Fiene P. 2013. *Aeolidiella indica*. *[Message in] Sea Slugs of Hawaii.* Available at: http://seaslugsofhawaii.com/species/Aeolidiella-indica-a.html

Pola M, Camacho-García YE, Gosliner TM. 2012. Molecular data illuminate cryptic nudibranch species: the evolution of the Scyllaeidae (Nudibranchia: Dendronotina) with a revision of *Notobryon*. *Zoological Journal of the Linnean Society* **165:** 311–336.

Pola M, Gosliner TM. 2010. The first molecular phylogeny of cladobranchian opisthobranchs (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution* **56:** 931–941.

Puillandre N, Lambert A, Brouillet S, Achaz G. 2012a. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* **21:** 1864–1877.

Puillandre N, Modica MV, Zhang Y, Sirovich L, Boisselier C, Cruaud C, Holford M, Samadi S. 2012b. Large-scale species delimitation method for hyperdiverse groups. *Molecular Ecology* **21:** 2671–2691.

Risbec J. 1928. Contribution a l'etude des nudibranches Néo-Calédoniens. Thèse présentée à la faculté des sciences de l'Université de Paris pour obtenir le grade de docteur ès-sciences naturelles. *Faune des Colonies Française* **2:** 1–328.

Risbec J. 1956. Nudibranches du Viet-Nam. *Archives du Muséum National d'Historie Naturelle* **4:** 3–58.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Rudman WB, Willan RC. 1998. Opisthobranchia. In: Beesley PL, Ross GJB, Wells A, eds. *Mollusca: the southern synthesis. Fauna of Australia, Vol. 5, Part B*. Melbourne: CSIRO Publishing. 915–1035.

Sammut CR, Perrone AS. 1998. A preliminary check-list of Opisthobranchia (Mollusca, Gastropoda) from the Maltese Islands. *Basteria* **62:** 221–240.

Schmekel L. 1968. Ascoglossa, Notaspidea und Nudibranchia im Litoral des Golfes von Neapel. *Revue Suisse de Zoologie* **75:** 103–155.

Schmekel L. 1970. Anatomie der Genitalorgane von Nudibranchiern (Gastropoda Euthyneura). *Pubblicacioni della Stazione Zoologica di Napoli* **38:** 120–217.

Schmekel L, Portmann A. 1982. *Opisthobranchia des Mittelmeeres*. Berlin: Springer Verlag.

Sciberras M, Schembri PJ. 2007. A critical review of records of alien marine species from the Maltese Islands and surrounding waters (Central Mediterranean). *Mediterranean Marine Science* **8:** 41–66.

Sphon GC, Lance JR. 1968. An annotated list of nudibranchs and their allies from Santa Barbara County, California. *Proceeding of the California Academy of Sciencies* **36:** 73–84.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22:** 2688–2690.

Stimpson W. 1855. Descriptions of some new marine invertebrata. *Proceeding of the Academy of Natural Sciences of Philadelphia* **7:** 385–395.

Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* **56:** 564–577.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Phylogenetics and Evolution* **28:** 2731–2739.

Thompson TE, Brown GH. 1984. *Biology of opisthobranch molluscs, vol. 2*. London: Ray Society.

Valdés Á, Hamann J, Behrens DW, DuPont A. 2006. *Caribbean Sea Slugs. A field guide to the opisthobranch mollusks from the tropical northwestern Atlantic*. Gig Harbor, WA: Sea Challengers Natural History Books.

Virabhadra-Rao K, Alagarswami K. 1960. An account of the structure and early development of a new species of a nudibranchiate gastropd, Eolidina (Eolidina) mannarensis. *Journal of the Marine Biological Association of India* **2:** 6–16.

Wheeler QD, Meier R, eds. 2000. *Species concepts and phylogenetic theory: a debate*. New York: Columbia University Press.

Williams ST, Reid DG. 2004. Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* **58:** 2227–2251.

Zenetos A, Çinar ME, Panucci-Papadopoulou MA, Harmelin JG, Furnari G, Andaloro F, Bellou N, Streftaris N, Zibrowius H. 2005. Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science* **6:** 63–118.

Zenetos A, Gofas S, Russo G, Templado J. 2004. Vol. 3. *Molluscs*. In: Briand F, ed. *CIESM Atlas of exotic species in the Mediterranean*. Monaco: CIESM Publishers, 1–376.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Phylogenetic hypothesis based on the combined data set (*H3* + *COI* + *16S*), inferred by Bayesian inference (BI) analysis.

Table S1. List of specimens used for phylogenetic analyses. Abbreviations: ATL, Atlantic Ocean; EA, eastern Atlantic Ocean; GB, GenBank; MED, Mediterranean; PAC, Pacific.