

# *Protoeolidiella atra* Baba, 1955 versus *Pleurolidia juliae* Burn, 1966: One or two species?

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**Abstract** *Protoeolidiella atra* Baba, 1955 and *Pleurolidia juliae* Burn, 1966 are two species traditionally regarded as the members of Aeolidiidae but recently attributed to Facelinidae. Because of their apparent similarities, Rudman (J Molluscan Stud 56:505–514, 1990) rendered *P. juliae* as a junior synonym of *P. atra*. In this paper, we conducted a review of both species and completed their descriptions with new data regarding the anatomy of the reproductive system. *P. atra* and *P. juliae* have differences in their colouration, number of cerata and characteristics of their reproductive system. Based on these differences, we conclude that these species are not conspecific and should be regarded as distinct taxa.

**Keywords** Facelinidae · Heterobranchia · Gastropoda · Molluscan diversity · Phylogeny · Taxonomy

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## Introduction

*Protoeolidiella atra* Baba, 1955 and *Pleurolidia juliae* Burn, 1966 are two species considered as the only members of these genera within the aeolid families Protoeolidiellidae Odhner, 1968 and Pleurolidiidae Burn 1966, respectively (Baba 1955; Burn 1966; Odhner 1968). Nevertheless, some authors such as Gosliner and Griffiths (1981), Rudman (1990) and Miller (2001) regarded these species as primitive members of Aeolidiidae Gray, 1827. Because of the similar appearance of these two species, differences between *P. atra* and *P. juliae* have been controversial and raised doubts about the validity of the two species and genera. According to Burn (1966), the triseriate radula of *P. juliae* is the main feature that distinguishes this species from *P. atra*. Almost three decades later, Rudman (1990) did not find any traces of lateral teeth in *P. juliae* and, therefore, concluded that both were conspecific, rendering *P. juliae* as junior synonym of *P. atra*. Baba (1992) rejected this synonymy and maintained both species as valid although he did not examine the radula of *P. juliae*. Recently, the molecular phylogeny of Aeolidiidae (Carmona et al. 2013) transferred *P. juliae* from Aeolidiidae to Facelinidae Bergh, 1889. This outcome concurs with the feeding behaviour of *P. juliae*, since this species, together with *P. atra*, feeds on hydroids (like most facelinids), whereas species of the Aeolidiidae all prey upon sea anemones and other anthozoans, including zoanthids (Gosliner et al. 2008).

In this contribution, we attempt to clarify the conspecificity of *P. atra* and *P. juliae*, using morphology and molecular phylogenetics including specimens from across the geographical range of both species.

## Materials and methods

### Source of specimens and morphology

Samples were collected by SCUBA diving and obtained from wet collections housed at the California Academy of Sciences. Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a stereoscopic microscope with the aid of a camera lucida. Special attention was given 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 under a scanning electron microscopy (SEM). The specimens examined are deposited in the California Academy of Sciences, CASIZ (San Francisco, USA) and National Museum of Nature and Science, NSMT-Mo (Ibaraki Prefecture, Japan).

### Molecular work

#### *DNA extraction, amplification and sequencing*

Two specimens of *P. atra* and one *P. juliae* were studied. Twenty-five additional sequences were obtained from GenBank (see Table 1 for full list of samples, localities and vouchers), including *Tritonia challengeriana* Bergh, 1884 as a distant outgroup because of its basal phylogenetic position within Cladobranchia (Pola and Gosliner 2010). Tissue samples were taken from the foot. Extraction, amplification, purification and sequencing of portions of the COI, 16S rRNA and H3 genes followed the methods described in Carmona et al. (2013, 2014a, b). Sequence reactions were run on a 3730XL DNA sequencer (Applied Biosystems). Sequences were verified by forward and reverse comparisons and have been deposited in GenBank (Table 1).

#### *Sequence alignment and phylogenetic analyses*

Sequences were assembled and edited with Geneious Pro v. 4.7.6 (Drummond et al. 2009), aligned in MAFFT (Katoh et al. 2009) and further checked using MacClade v. 4.06 (Maddison and Maddison 2005). Uncorrected pairwise *p*-distance values between each taxon were calculated for the COI gene. The most variable regions from the 16S rRNA alignment were removed using the default settings in Gblocks (Talavera and 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, 442 and 327 base pairs, respectively.

The best-fit evolutionary model (GTR + I+G for the three genes) was determined in MrModeltest v. 2.3 (Nylander 2004), using the Akaike information criterion (Akaike 1974). MrBayes v. 3.1.2 (Ronquist and Huelsenbeck 2003) was used for Bayesian inference analysis and to estimate posterior probabilities (PP) for node support with two runs of 5,000,000 generations each. Convergence was checked in TRACER v. 1.5 (Drummond and Rambaut 2007) with a burn-in of 25 %. Maximum likelihood (ML) analyses were performed using the software RAxML v7.0.4 (Stamatakis 2006), and node support was assessed with nonparametric bootstrapping (BS) with 5,000 replicates, random starting trees, and parameters estimated from each dataset under the model selected for the original dataset. Only nodes supported by BS  $\geq 70$  (Hillis and Bull 1993) and PP  $\geq 0.95$  (Alfaro et al. 2003) are discussed.

## Results

### Diagnosis of *Protaeolidiella* following Baba (1955)

“A somewhat aberrant genus. The general body-form is roughly as in *Aeolidiella* (smooth rhinophores, simply fusiform gills, broad foot with rounded corners)”. But in the present genus, the branchial papillae are non-caducous and are thickly crowded on the back margins in irregular rows. As there is no distinct mantle flange, the right-sided anal opening in this genus may be considered cleioproctic (not pleuroproctic as in *Coryphella*). “In spite of the degenerative tendency of the jaws and radula, yet they show the fundamental structure of those in *Aeolidiella*. That is, the jaw plates are smooth; the central tooth of the radula is pectinated, with an emargination in the middle”. Provisionally, the present new genus is classified within the family Aeolidiidae.

*Protaeolidiella atra* Baba, 1955

*Protaeolidiella atra* Baba, 1955: 53, pl. XVI, figs. 44–45, text-figs. 52–54.

Type locality: Kasajima, Sagami Bay, Japan (Fig. 1).

Type material: To our knowledge, Baba (1955) designates two syntype lots (NSMT-OpR 0872, NSMT-OpR 0884) at the National Museum of Nature and Science.

Material examined: (NSMT-Mo 78850), one specimen, adult, mature, dissected, 40 mm in length alive, Place Issai, Ohtsuki town Hata-gun, Kochi prefecture, Japan, collected by Rie Nakano, 17.iii.12; (NSMT-Mo 78851), one specimen, adult, mature, dissected, 20 mm in length alive, Place

**Table 1** List of specimens used for phylogenetic analyses

Family	Species	Locality	Collection dates	Voucher	GenBank accession nos.			
					COI	16S	H3	
Tritoniidae	Lamarck, 1809	<i>Tritonia antarctica</i> Pfeffer, 1886	Bouvetoya (EA, GB)	30 Jun 04		HM162718	HM162643	HM162550
Dendronotidae	Allman, 1845	<i>Dendronotus venustus</i> MacFarland, 1966	Santa Monica (California, GB)	Dec 07		HM162709	HM162630	HM162536
Proctonotidae	Gray, 1853	<i>Janolus mirabilis</i> Baba and Abe, 1970	Philippines (GB)	19 May 09		HM162750	HM162674	HM162583
Aeolidiidae	Gray, 1827	<i>Aeolidia papillosa</i> (Linnaeus, 1761)	Sweden	14 Sep 11	MNCN/ADN: 51929	JX087534	JX087462	JX087596
		<i>Berghia coerulescens</i> (Laurillard, 1830)	Croatia	03 Dec 04	ZSM Mol 20041584	JQ997049	JQ996845	JQ996946
Babakiniidae	Roller, 1973	<i>Spurilla neapolitana</i> (delle Chiaje, 1841)	Italy	17 Mar 09	MNCN/ADN: 51976	JX087584	JX087521	JX087659
		<i>Babakina anadoni</i> (Ortea, 1979)	Brazil	Feb 06	MNRJ 10893	HQ616746	HQ616709	HQ616775
		<i>Babakina indopacifica</i> Gosliner, González-Duarte and Cervera, 2007	Philippines (GB)	20 Mar 08	–	HM162754	HM162678	HM162587
Faceliniidae	Bergh, 1889	<i>Cratena peregrina</i> Gmelin, 1791	Senegal	30 May 05	MNCN 15.05/53691	HQ616752	HQ616715	HQ616781
		<i>Facelina annulicornis</i> (Chamisso and Eysenhardt, 1821)	Azores Is. (Portugal)	11 Jun 02	CASIZ 186793	JQ997076	JQ996881	JQ996986
		<i>Favorinus branchialis</i> (Rathke, 1806)	Spain (EA)	26 Jun 07	MNCN 15.05/53695	HQ616761	HQ616724	HQ616790
		<i>Favorinus elenalexianum</i> Garcia and Troncoso, 2001	Costa Rica (EP, GB)	17 Apr 07	–	HM162755	HM162679	HM162588
		<i>Godiva quadricolor</i> (Barnard, 1927)	South Africa (EA, GB)	09 Jan 08	–	HM162692	HM162602	HM162508
		<i>Hermosita hakunamata</i> (Ortea, Caballer and Espinosa, 2003)	Mexico	17 Feb 06	CASIZ 174088	KPI43674	KPI43670	KPI43678
		<i>Moridilla brockii</i> Bergh, 1888	Philippines	29 Apr 11	CASIZ 186245	JQ997083	JQ996888	JQ996994
		<i>Noumeaella isa</i> Marcus and Marcus, 1970	Philippines	01 May 11	CASIZ 186249	JQ997084	JQ996889	JQ996995
		<i>Phidiana lynceus</i> Bergh, 1867	Cuba	21 Jul 08	MNCN/ADN: 51995	JX087562	JX087497	JX087633
		<i>Phylodesmium horridum</i> (Macnae, 1954)	South Africa (EA, GB)	03 Jan 08	–	HM162757	HM162681	HM162590
		<i>Pleurolidia juliae</i> Burn, 1966	Philippines	05 May 05	CASIZ 186217	JQ997094	JQ996899	JQ997007
		<i>Protaeolidiella atra</i> Baba, 1955	Japan	17 Feb 04	NSMT-Mo 78853	KPI43676	KPI43672	KPI43680
		<i>Pruvotfolia longicirrha</i> (Eliot, 1906)	Japan	18 Feb 04	NSMT-Mo 78852	KPI43675	KPI43671	KPI43679
		<i>Pruvotfolia pselliotes</i> (Labbé, 1923)	Cape Verde	Mar 10	MNCN 15.05/53703	HQ616760	HQ616723	HQ616789
		<i>Sakuraeolis enosimensis</i> (Baba, 1930)	France (EA)	05 Sep 04	MNCN 15.05/53705	HQ616762	HQ616725	HQ616791
Fionidae	Alder and Hancock, 1855	<i>Fiona pinnata</i> (Eschscholtz, 1831)	California (GB)	13 Dec 07	–	HM162758	HM162682	HM162591
			Morocco (EA)	22 Dec 10	MNCN/ADN: 51997	JX087558	JX087492	JX087628
Flabelliniidae	Bergh, 1881	<i>Flabellina affinis</i> (Gmelin, 1791)	Balearic Is. (Spain, MED)	14 Jul 07	MNCN 15.05/53696	HQ616753	HQ616716	HQ616782
		<i>Flabellina ischitana</i> Hirano and Thompson, 1990	Morocco (EA)	07 Mar 08	MNCN 15.05/53700	HQ616756	HQ616719	HQ616785
Piscinoteciidae	Edmunds, 1970	<i>Piscinotectus gabinierti</i> (Vicente, 1975)	Spain (MED)	13 Oct 07	MNCN/ADN: 52000	JX087561	JX087495	JX087631

ATL Atlantic Ocean, EA eastern Atlantic Ocean, EP eastern Pacific, GB GenBank, MED Mediterranean

Issai, Ohtsuki town Hata-gun, Kochi prefecture, Japan, collected by Rie Nakano, 17.iii.12; (NSMT-Mo 78852), one specimen, adult, mature, dissected, 40 mm in length alive, Zushi, Japan, collected by Michiaki Homma, 18.ii.12;

Geographical distribution: Originally described from Japan (Baba 1955; Keiu 2000; Nakano 2004), this species has been also reported in South Korea (Koh 2006; Debelius and Kuitert 2007).

External morphology (Fig. 1a, b): The body is elongate, slender and cylindrical with rounded foot corners. The body colour is quite variable, ranging from almost black to burgundy. The dorsal surface has no white pigment. The rhinophores, oral tentacles and foot corners are coloured similarly as the background of the animal. The rhinophores are smooth, shorter than the oral tentacles and have white apices. The oral tentacles are also white tipped.

The cerata densely packed along the edge of the mantle, forming a transverse row. They extend from behind the rhinophores to the posterior end of the body. The ceratal length is variable, but all are slender, cylindrical, with a round apex and uniform diameter throughout most of length. There are around 50–60 cerata per side. They have the same background colour as the body with hyaline white apices. On the right side of the body, the gonopore is situated anteriorly below the beginning of the ceratal row. The anus is on the right side of the body, in a pleuroproct position.

Anatomy (Fig. 1c–e): The radula is uniseriate ( $26 \times 0.1.0$ , NSMT-Mo 78850). The radular teeth are pectinate with 24–60 acutely pointed denticles (Fig. 1c). The latter are flattened laterally, with a similar length. The masticatory border of the jaws is smooth (Fig. 1d). Salivary and oral glands were not observed.

The reproductive system is dialucic (Fig. 1e). The hermaphroditic duct widens into an elongate and wide ampulla, which has moderately thick walls. The ampulla narrows again before dividing into the oviduct and vas deferens. The short vas deferens, which lacks a morphologically well-differentiated prostate, enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The oviduct is moderately elongated and connects to a well-developed receptaculum seminis. The remaining portion of the oviduct separates from the base of the receptaculum and enters the female gland. The vagina opens ventrally relative to the penis.

Diagnosis of *Pleurolidia* following Burn (1966)

Pleuroproct Eolidacea with a triseriate radula (rachidian pectinate, laterals smooth) and smooth masticatory borders;

anus in anterior third of the body length, renal pore a little in front; with rugose rhinophores and cerata, the latter with a low keel or rib on dorsal and ventral sides; penis knob-like, vas deferens prostatic, spermatheca and oviduct with separate apertures (connection probably external); nerve ring with short pedal and parapedal commissures.

*Pleurolidia juliae* Burn, 1966

*Pleurolidia juliae* Burn, 1966: 22, figs. 1–6.

*Protaeolidia juliae* (Burn, 1966): Gosliner et al. 2008: 402.

Type locality: “The Brook”, Lord Howe Island, Australia (Fig. 2).

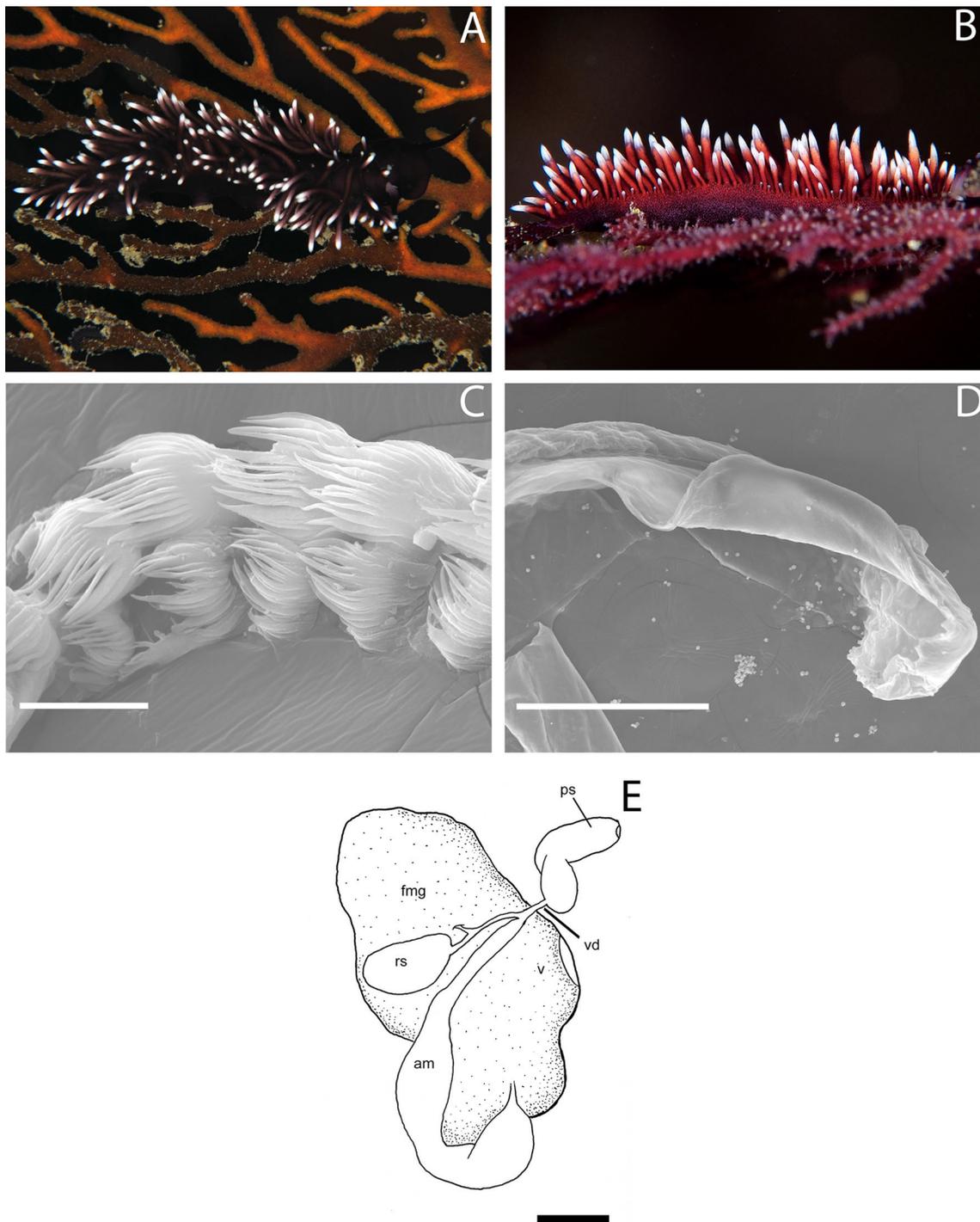
Type material: According to Burn (1966), the material was deposited in the Australian Museum, Sidney. The registration number of the holotype of *P. juliae* is C. 65661.

Material examined: CASIZ 167988, one specimen, adult, mature, dissected, 7 mm in length preserved, Maui, Hawaii, collected by Pauline Fiene-Severns, 12.ix.03; CASIZ 065416, one specimen, adult, mature, dissected, 11 mm in length preserved, Papua New Guinea, collected by Terrence M. Gosliner, 21.i.88.

Geographical distribution: This species was originally described from Lord Howe Island, Australia (Burn 1966), but it can also be found in Madagascar (Gosliner et al. 2008), Papua New Guinea (this study), Indonesia (Gosliner et al. 2008), the Philippines (Gosliner et al. 2008), Palau (Gosliner et al. 2008), and Japan (Baba 1992; Ono 1999, 2004 under the name of *P. atra*; Gosliner et al. 2008).

External morphology (Fig. 2a): The body is slender and cylindrical with rounded foot corners. The body colour is black and may have burgundy pigment over the head and along the back. A broad, irregular white line runs through the dorsal midline, from the head to the posterior end of the body. The oral tentacles and foot corners are coloured similarly to the background of the animal, but the oral tentacles are also tipped with white. The rhinophores are greyish, with white specks over the warts, and have white apices. They have approximately the same length as the oral tentacles.

The cerata are arranged along the edge of the mantle, forming small groups that constitute a transversal row. Sometimes these groups are not symmetrical, having a zigzag arrangement. They extend from behind the rhinophores to the posterior end of the body. The length of the cerata may vary, but all are slender, cylindrical, with round apex and uniform diameter throughout most of their length. There are around 10–20 cerata per side. They have the same background colour of the body with hyaline white

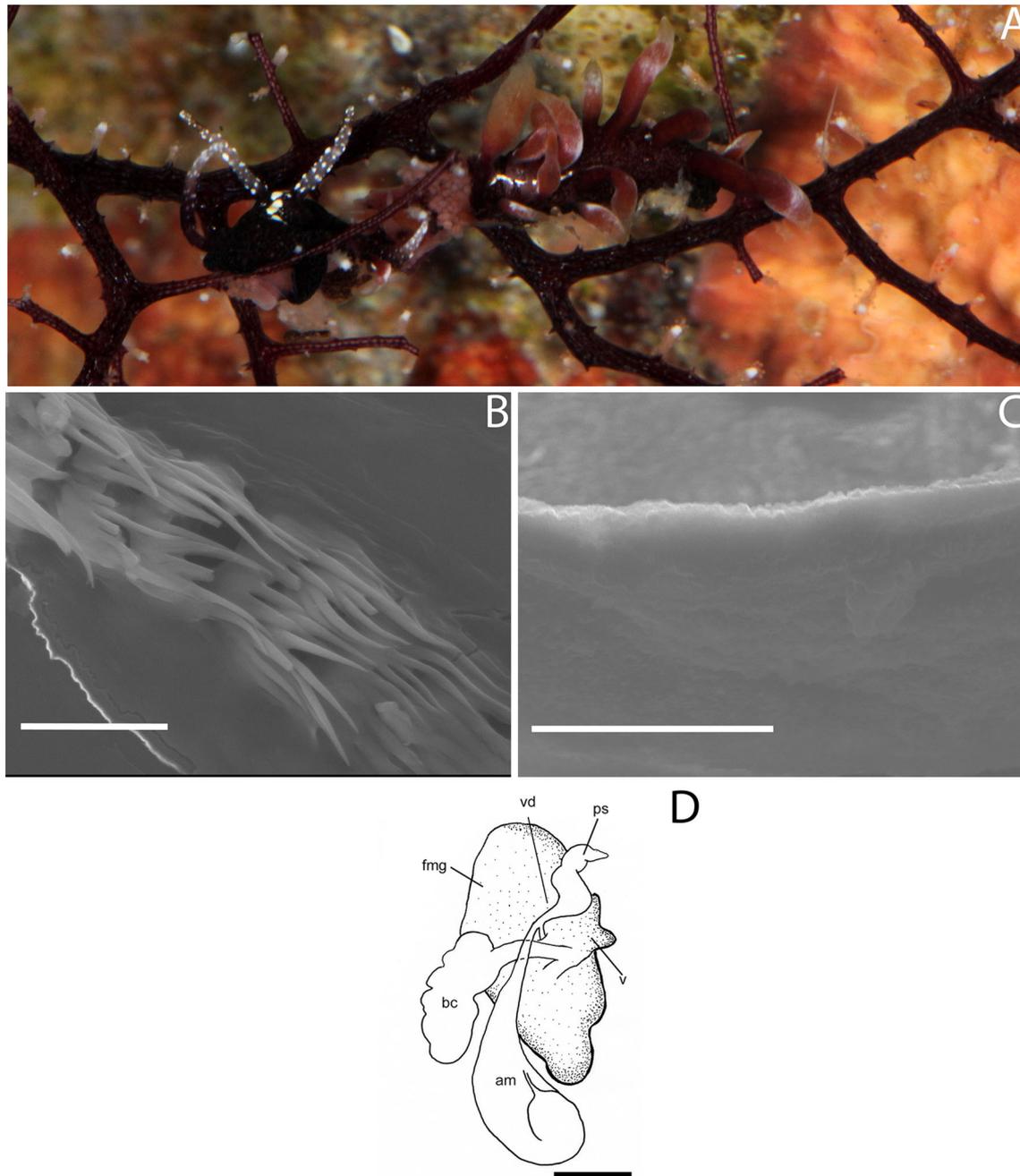


**Fig. 1** *Protaeolidiella atra* Baba, 1955. **a, b** Photographs of living animals. **a** Specimen from Japan, photo by Michiaki Homma, (NSMT-Mo 78852); **b** specimen from Japan photo by Rie Nakano, (NSMT-Mo 78851). **c, d** Scanning electron photographs (NSMT-Mo

78850); **c** radular teeth, *scale bar* 25  $\mu$ m; **d** detailed view of the masticatory border, *scale bar* 250  $\mu$ m; **e** reproductive system (NSMT-Mo 78851), *scale bar* 0.5 mm. *am* ampulla, *fmg* female gland mass, *ps* penial sac, *rs* receptaculum seminis, *v* vagina, *vd* vas deferens

speckles over their surface. The apices are translucent white. On the right side of the body, the gonopore is placed anteriorly below the beginning of the ceratal row. The anus is on the right side of the body, in a pleuroproctic position.

Anatomy (Fig. 2b–d): The radula is uniseriate ( $14 \times 0.1.0$ , CASIZ 167988). The radular teeth are pectinate with 10–12 quite long and acutely pointed denticles (Fig. 2b). The denticles are flattened laterally, with a



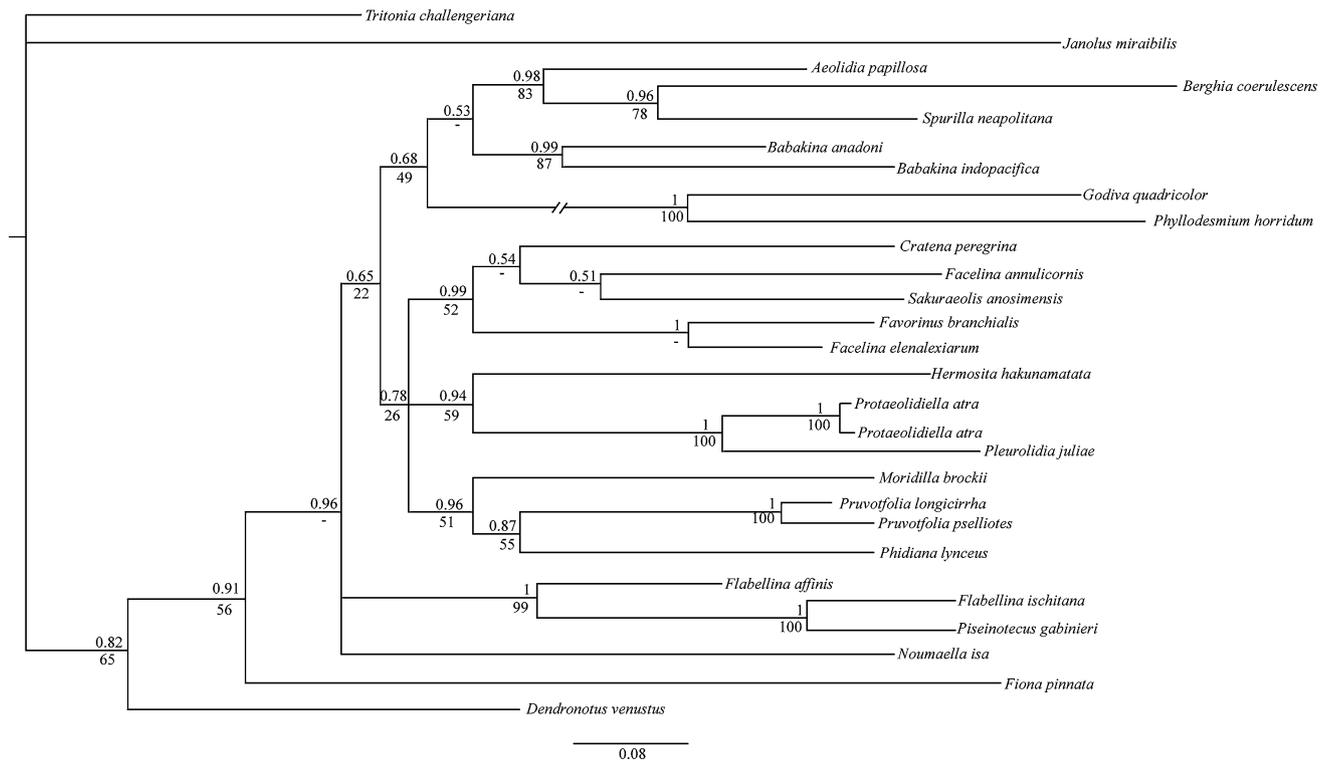
**Fig. 2** *Pleurolidia juliae* Burn, 1966. **a** Photograph of living animal, specimen from the Philippines, photo by Terrence M. Gosliner, CASIZ 186217; **b**, **c** scanning electron photographs (CASIZ 167988), **b** radular teeth, scale bar 25  $\mu$ m; **c** detailed view of the masticatory

border, scale bar 50  $\mu$ m; **e** reproductive system (CASIZ 065416) scale bar 1.5 mm. *am* ampulla, *bc* bursa copulatrix, *fmg* female gland mass, *ps* penial sac, *v* vagina, *vd* vas deferens

similar length. The masticatory border of the jaws is finely denticulate (Fig. 2c). The oral glands are relatively large, consisting of clusters of small and rounded acini. Salivary glands were not found.

The reproductive system is diaulic (Fig. 2d). The pre-ampullary duct widens into a large and wide ampulla, which has moderately thick walls. The ampulla narrows

again before dividing into the vas deferens and the oviduct. The short and wide vas deferens, which lacks a morphologically well-differentiated prostate, enters the wider proximal portion of the penial sac, which contains the unarmed penial papilla. The female gland mass exits at the female genital aperture, adjacent to the bursa copulatrix, which is large and exits via a relatively long, wide duct.



**Fig. 3** Phylogenetic hypothesis for the genera *Protaeolidiella* and *Pleurolidia* based on the combined dataset (H3 + COI + 16S) inferred by Bayesian analysis (BI). Numbers above branches represent

posterior probabilities from BI. Numbers below branches represent bootstrap values from ML

### Phylogenetic analysis

The combined dataset yielded a sequence alignment of 1,427 positions. No saturation was observed across genes and codon positions (not shown). The combined tree provided better resolution than H3, COI or 16S separately (not shown). Bootstrap values were lower than the posterior probabilities in deeper nodes, but the topologies of the ML trees were congruent with the results yielded by the Bayesian analyses, and thus, ML trees are not shown. Figure 3 shows the resulting phylogenetic hypothesis based on the combined dataset represented by BI.

*Protaeolidiella atra* and *P. juliae* were nested among different facelinid species although this relationship was not supported (PP = 0.78, BS = 26). *P. atra* and *P. juliae* formed a single clade (PP = 1, BS = 100) with *Hermosita hakunamatata* as its sister species (PP = 0.94, BS = 59). The minimum uncorrected *p*-distance for COI between *P. atra* and *P. juliae* was 17.93 %.

### Discussion

Despite differences in radular morphology, ceratal arrangement and specialised diet, *Protaeolidiella* and *Pleurolidia* have been considered as primitive aeolidiids

(Tardy 1965; Burn 1966; Gosliner 1985). In addition, Rudman (1990) regarded *P. juliae* as a junior synonym of *P. atra*. Nevertheless, after reassessing Rudman's paper, we are strongly inclined to consider that he only studied specimens of *P. juliae* because none of these specimens were from Japan, the type locality of *P. atra*. More recently, the molecular study conducted by Carmona et al. (2013) placed *P. juliae* within the non-monophyletic Facelinidae, rejecting its traditional placement within the Aeolidiidae. Our anatomical and molecular results agree with those of Carmona et al. (2013) and demonstrated that the presence of morphological and genetic differences between *P. atra* and *P. juliae*. The two species can be distinguished by differences in colouration, since *P. atra* lacks the transverse and dorsal line found in *P. juliae*, as well as by the number of cerata. From an internal anatomical point of view, these species are quite similar but there is an important difference: *P. atra* has a receptaculum seminis, which opens into the proximal region of the gonoduct (Ghiselin 1966; Schmekel 1985; Gosliner 1994), while *P. juliae* possesses a bursa copulatrix that opens into the distal region of the vaginal duct (Ghiselin 1966; Schmekel 1985; Gosliner 1994). Since Baba (1955, 1992) never depicted the reproductive system of *P. atra* and Rudman (1990), likely studied only *P. juliae* (see above), this difference in the reproductive anatomy has not been reported

previously. In addition, we only found oral glands in *P. juliae*. Nevertheless, according to previous studies, oral glands can show some intraspecific variation in other aeolids (Carmona et al. 2014c, d), and therefore, the systematic relevance of this character should be regarded with caution. Considering the anatomical, morphological and genetic differences, we conclude that both genera are valid and monotypic. On the other hand, in order to decide about the validity of the families Protaeolidiellidae and Pleuroliidiidae further information about the phylogeny of the non-monophyletic Facelinidae is needed.

The close relationship among *P. atra*, *P. juliae* and *H. hakumanatata* represents an intriguing case that warrants further study, given that these species are the only aeolids that feed on the hydroid *Solanderia fusca* (Gosliner personal observation). Furthermore, according to Ghiselin (1966), Gosliner (1981), Schmekel (1985) and Mikkelsen (1996), the presence of both, receptaculum seminis and bursa copulatrix, represents the plesiomorphic state in the traditional “Opisthobranchia” and it is interesting to notice that *H. hakumanatata*, the only species with both anatomical structures (Millen and Hermosillo 2012), has a position as sister to the other two species within this clade. The only other species of aeolid nudibranch that has been observed feeding on species of *Solanderia* is *Hermosita sangria* Gosliner and Behrens, 1986. Future studies should examine the phylogenetic relationships of this species to the species discussed above.

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