

Revision of the systematics of *Babakina* Roller, 1973 (Mollusca: Opisthobranchia) with the description of a new species and a phylogenetic analysis

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The genus *Babakina* was first described by Roller in 1973, with *B. festiva* as the type species. Since then a further two species have been described. A review of the literature reveals that many of the original descriptions as well as a few published additional studies offer limited information. This lack of information has produced confusion in the identification of the specimens and the number of valid species. Also, the question as to whether Babakinidae represents a distinct taxon or should be considered as part of the Glaucidae remained unresolved. The results demonstrate that the three described species of *Babakina* Roller, 1973 are differentiated by external and internal anatomical differences. Additionally, *Babakina indopacifica* sp. nov., from several western and central tropical Pacific tropical localities, is here described. Difference in the arrangement of the receptaculum seminis, shape of the penis, and shape and size of the bursa copulatrix are consistent between distinct species from different geographical regions. Radular morphology does not exhibit significant differences between species, with the exception that *B. festiva* and *B. indopacifica* have an asymmetrical distribution of denticles on either side of the central cusp while *B. anadoni* and *B. caprinsulensis* have symmetrical denticles. Preliminary phylogenetic analysis indicates that *Babakina* represents a monophyletic taxon. The phylogeny suggests that Babakinidae should be maintained as a distinct taxon separated from Flabellinidae and Facelinidae by several autapomorphies. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **151**, 671–689.

ADDITIONAL KEYWORDS: aeolid nudibranchs – phylogeny.

INTRODUCTION

Roller (1972) described the aeolid nudibranch genus *Babaina* with the single species, *Babaina festiva* Roller, 1972 from California and temperate Japan. The genus name was a junior homonym of the dorid nudibranch genus *Babaina* Odhner, 1968 and Roller renamed the aeolid genus *Babakina* in 1973. Miller (1974) described a second species, *B. caprinsulensis*, from a single specimen from New Zealand. Ortea (1979) described *Rioselleolis anadoni* from a single

specimen from the northern coast of Spain. This species was later considered to be a species of *Babakina*. Gosliner (1990) questioned whether these taxa are distinct based on similarity of colour pattern. A compilation of all available material from various museums and recent collections of individuals from different parts of the world has now made it possible to provide a comprehensive and detailed comparison of members of this taxon in order to revise the systematics of the genus. Material from the northern and southern Iberian Peninsula, the Canary Islands, the Bahamas, California, the Pacific coast of Mexico, Madagascar, southern Japan, Philippines, Indonesia and the Hawaiian Islands was examined in this

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study. The systematic position of *Babakina* has been the subject of some controversy. Several authors have considered it to be a member of a distinct family. Roller's (1972) description of *B. festiva* included erecting a distinct family Babainidae, later changed to Babakinidae (Roller, 1973) due to homonymy with *Babaina* Odhner, 1968, a genus belonging to the family Chromodorididae.

Some authors consider this genus in a separate family, Babakinidae (Roller, 1973; Behrens, 1991; Rolán *et al.*, 1991; Baba, 2000). Others include the genus within the large family Glaucidae (Miller, 1974; Redfern, 2001; Padula & Absalão, 2005), even the family Facelinidae (Coleman, 2001; Valdés & Bouchet, 2005; CLEMAM, 2006) or Favorinidae (Pérez Sánchez & Moreno, 1990). Moreover, some doubts about the true specific identity have been pointed out by Gosliner (1990).

Babakina shares some features with Facelinidae and Aeolidiidae (uniseriate radula and uniform prostatic diameter), but it lacks two synapomorphies of the Facelinidae/Aeolidiidae clade (lack of a notal brim and cleioproctus anus). For this reason, we have here conducted the first phylogenetic study to test these hypotheses, and give a detailed study of the species included in the genus.

MATERIAL AND METHODS

The material examined for this study is deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), the Museo Nacional de Ciencias Naturales, Madrid (MNCN) and the Universidade Federal do Rio de Janeiro (IBUFRJ).

The specimens were dissected and a morphological examination facilitated by first making a dorsal incision. The internal features were examined using a dissecting microscope with a camera lucida. The buccal mass was dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, and dried and mounted for examination by scanning electron microscopy (SEM). Special attention was paid to the morphology of the reproductive system.

SPECIES DESCRIPTIONS

NUDIBRANCHIA CUVIER, 1817

CLADOBRANCHIA WILLAN AND MORTON, 1984

AEOLIDINA GRAY, 1827

BABAKINIDAE ROLLER, 1973

BABAKINA ROLLER, 1973

Type species: Babaina festiva Roller, 1972: 416, figures 1–9.

Diagnosis: Pleuroproctid Aeolidina, with the cerata arranged in numerous rows along both sides of the body, not in separate groups. Notal brim well developed. Foot corners tentaculiform. Uniseriate radula with triangular rachidian tooth. Rachidian tooth with lateral denticles on either side of the central cusp. Rhinophores sharing a common base. Masticatory border of jaws with 3–4 rows of denticles.

Reproductive system with a diaulic arrangement. Penis unarmed, without penial glands. Prostate uniform, with a proximal receptaculum seminis and a distal bursa copulatrix.

BABAKINA FESTIVA (ROLLER, 1972)

(FIGS 1A, 2, 3A)

Babaina festiva Roller, 1972: 416, figures 1–9.

Babakina festiva (Roller, 1972) – Roller, 1973; Gosliner, 1990; Baba, 2000.

Material examined: CASIZ 070589, one specimen, 28 mm, dissected, California, x.1971, Shane Anderson. CASIZ 071054, one specimen, 17 mm, collected on kelp holdfast, Paradise Cove, Malibu, Los Angeles, California, xi.1971, Shane Anderson. CASIZ 69850, four specimens, two dissected, Matanchen, near San Blas, Nayarit, Mexico, 25.i.1975, Gary McDonald. CASIZ 067110, one specimen, from tide pool, Fitzgerald Marine Reserve, Moss Beach, San Mateo County, 14 June 1987, Terrence M. Gosliner.

Distribution: This species is known from California and middle and northern Japan (Roller, 1972; McDonald, 1983; Gosliner, 1990; Baba, 2000).

External morphology: The body is elongate and slender, with a trailing posterior end of the foot (Fig. 1A). Living animals are 10–32 mm in length. The anterior margins of the foot and tentaculiform foot corners are bilabiate and slightly notched. The body colour can range from a translucent light pink to a purple cast. A short opaque white patch extends medially from the anterior end of the head to just in front of the rhinophores. The moderately long cerata are cylindrical and taper distally. They are translucent white and the deep reddish brown digestive gland is visible in the basal two-thirds followed by a covering of succession of three subapical bands of opaque white, yellow and opaque white. The apex is translucent white. The cerata are densely clustered and continuous throughout the length of the body. There are approximately 100 cerata on either side of the body and they are not clearly divisible into distinct clusters or rows. The largest arch is the most anterior. The red-brown rhinophores share a common base, are perfoliate and have 31–43 lamellae each.

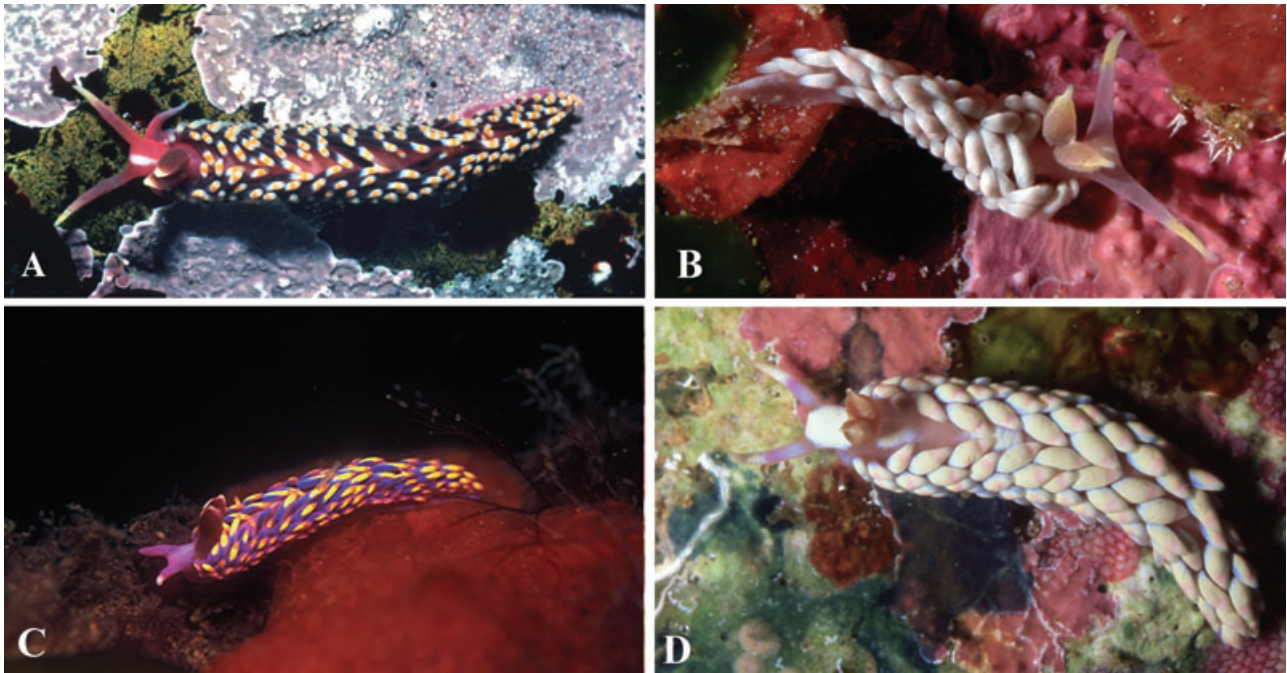


Figure 1. A, *Babakina festiva* (Roller, 1972), living animal, Fitzgerald Marine Reserve, San Mateo County California, photo by T. M. Gosliner. B, *Babakina caprinsulensis* Miller, 1974, living animal, Poor Knights Islands, North Island, New Zealand, photo by I. Skipworth. C, *Babakina anadoni* (Ortea, 1979), living animal, Algarve, Portugal, photo by Jose Augusto Silva. D, *Babakina indopacifica* sp. nov., living animal, Mindanao, Philippines, photo by T. M. Gosliner.

The apex and a line that runs medially along the posterior face of each rhinophore is yellowish white. The oral tentacles are elongate and have a somewhat wrinkled texture. They are the same colour as the ground colour with a lighter tip. The tentacular anterior foot corners are pinkish purple basally with a purple tip. The pleuroproct anus is located ventral to the notal brim about one-third of the body length from the anterior end. The nephroproct is anterior to the anus. The genital aperture is located below notal brim just posterior to the rhinophore base.

Buccal armature: The jaws (Fig. 2A, B) are tan-brown. The masticatory border contains 3–4 rows of numerous irregularly, triangular denticles. The radula formula is $13 \times 0.1.0$ (CASIZ 07589) and $23 \times 0.1.0$ (CASIZ 069850) in two specimens examined. The rachidian tooth (Fig. 2C, D) is broad with wide, triangular central cusp. There are 8–15 elongate, acutely pointed denticles on either side of the central cusp. The number of denticles is not equal on either side. For example, on one tooth there were 12 denticles on the right side and 15 on the left side. Some denticles share a common base and bifurcate above. In some instances denticles are present on the central cusp while in other cases they are only found laterally from the cusp.

Reproductive system: It has an androdiaulic arrangement (Fig. 3A). The narrow elongate preampullary duct widens into the convoluted ampulla. The ampulla consists of 2–3 folds and narrows again before dividing into the oviduct and vas deferens. The vas deferens widens into a glandular prostatic portion that consists of numerous convolutions. The prostatic portion enters the wider proximal portion of the penial sac. The penial papilla is contained within the penial sac. The unarmed penial papilla is elongate and conical in shape. It narrows to a rounded apex and exists adjacent to the elongate bursa copulatrix. The oviduct is elongate and connects to the pyriform receptaculum seminis. The receptaculum is straight in the specimen from California and curved apically in the specimen from Mexico. The other portion of the oviduct emerges from the base of the receptaculum and, after a short distance, enters the small albumen gland. The membrane and the albumen glands are similar in size. The mucous gland is much larger than the other two female glands and exits ventral to the penis and bursa copulatrix.

Remarks: The anatomy of this species fits well with the original description by Roller (1972). Roller did not describe the reproductive anatomy and it is presented here. Its anatomy conforms largely to that

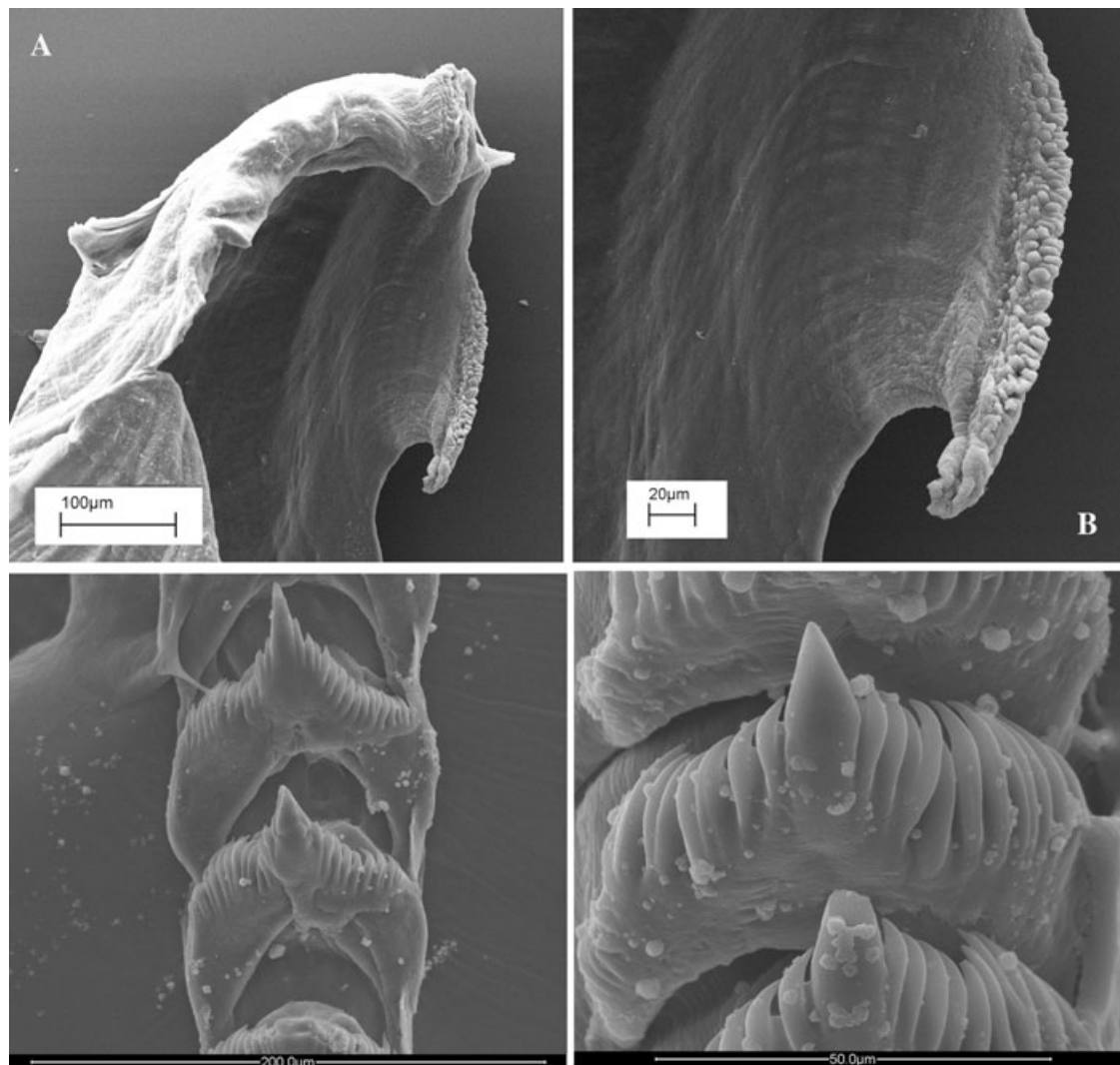


Figure 2. *Babakina festiva* (Roller, 1972), scanning electron micrographs. A, jaw. B, detailed view of masticatory border, from Mexican specimen (CASIZ 069850). C, radular teeth of specimen from Malibu, California (CASIZ 070589). D, radular teeth of specimen from Nayarit, Mexico (CASIZ 69850).

described by Baba (2000). The presence of a curved receptaculum seminis and a thin bursa copulatrix are identical between the Japanese specimen described by Baba and the specimens examined here from California and Mexico. The fundamental arrangement of organs is similar to that described by Miller (1974) for *B. caprinsulensis*, with a proximal receptaculum seminis and a distal bursa copulatrix. This arrangement has been noted as the most plesiomorphic condition found in the Aeolidina (Gosliner & Kuzirian, 1990; Gosliner & Willan, 1991). Some differences in reproductive anatomy between the two species are noted (Table 1). The ampulla of *B. festiva* is much wider and less elongate than that of *B. caprinsulensis*. The penis of *B. festiva* is elongate while that of *B. caprinsulensis* is much shorter. The bursa copula-

trix of *B. festiva* is thin and elongate while that of *B. caprinsulensis* is bulbous and recurved. In *B. festiva*, the receptaculum seminis is pyriform while that of *B. caprinsulensis* is thin and elongate.

BABAKINA CAPRINSULENSIS MILLER, 1974

(FIGS 1A, 3B)

Babakina caprinsulensis Miller, 1974: 37, 1–2.

Distribution: This species is known from Goat Island and Poor Knights Islands, North Island, New Zealand (Miller, 1974; Rudman, 2005a).

Morphology: All morphological characters are known from the original description of this species (Miller,

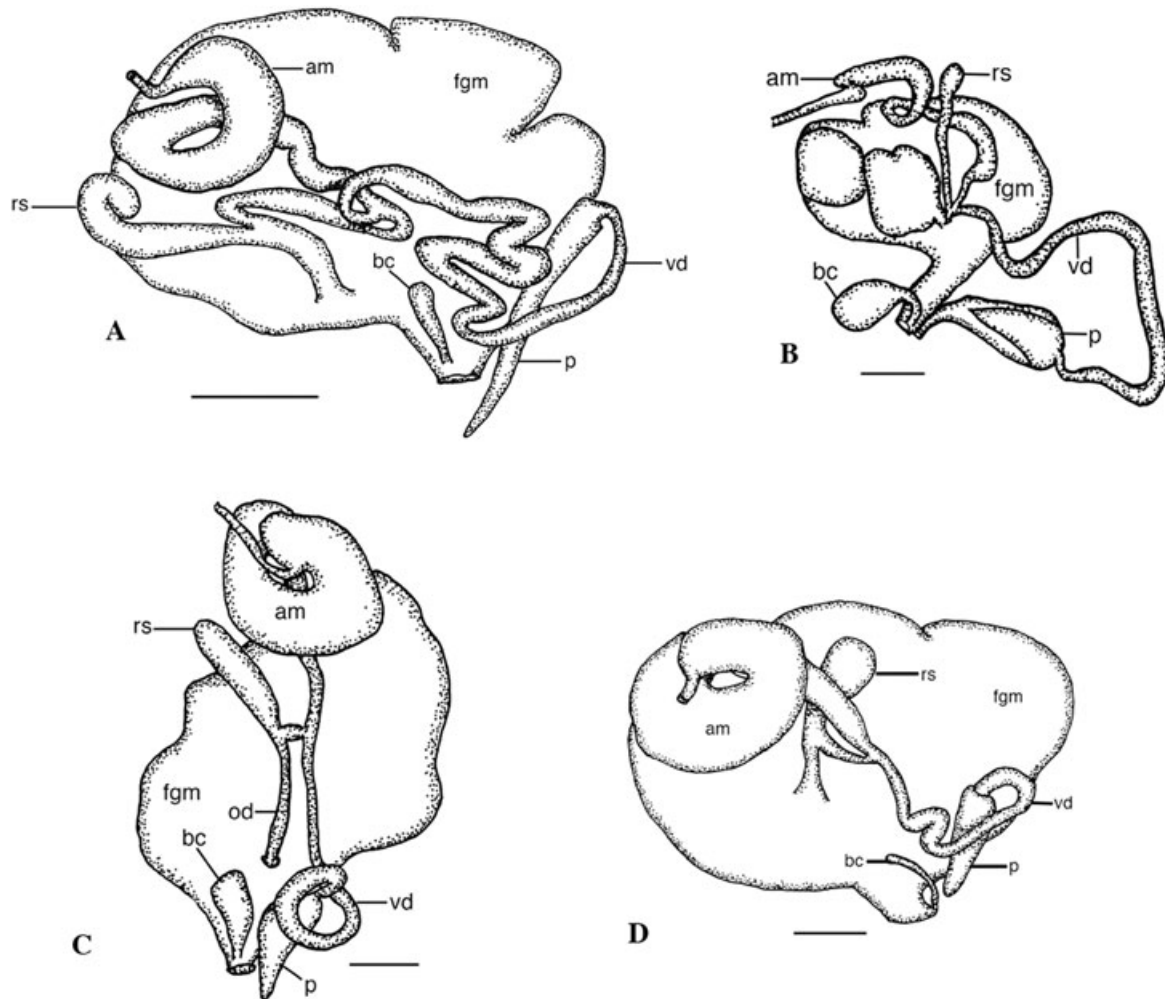


Figure 3. Reproductive anatomy. A, *Babakina festiva* (Roller, 1972), specimen CASIZ 069850, scale = 1.0 mm. B, *Babakina caprinsulensis* Miller, 1974, after Miller (1974). C, *Babakina anadoni* (Ortea, 1979), from Bahamian specimen, MNCN 15/46706. Scale bar = 0.3 mm. D, *Babakina indopacifica* sp. nov., specimen from Mindanao, Philippines. Scale bar = 0.5 mm. Abbreviations: am = ampulla, bc = bursa copulatrix, fgm = female gland mass, od = oviduct, p = penis, rs = receptaculum seminis, vd = vas deferens.

Table 1. Reproductive morphology of *Babakina*

<i>Babakina</i> species	Penial papilla	Bursa shape	Bursa size	Prostate convolutions	Ampulla
<i>B. festiva</i>	Narrow	Long	Large	Many	Wide
<i>B. caprinsulensis</i>	Conical	Round	Large	Many	Narrow
<i>B. anadoni</i>	Conical	Round	Large	Many	Wide
<i>B. indopacifica</i>	Narrow	Long	Small	Few	Wide

1974) and from a subsequent photo of a second specimen from New Zealand (Rudman, 2005a).

Remarks: Miller's (1974) original description of this species provides a complete overview of the anatomy of the species. However, the holotype does not appear

to be present in the National Museum of New Zealand (B. Marshall, pers. comm.). There is one aspect of the morphology of this species that has been amended from the original description. Miller described the rhinophores of *B. caprinsulensis* as being papillate. The photograph of the second specimen from New

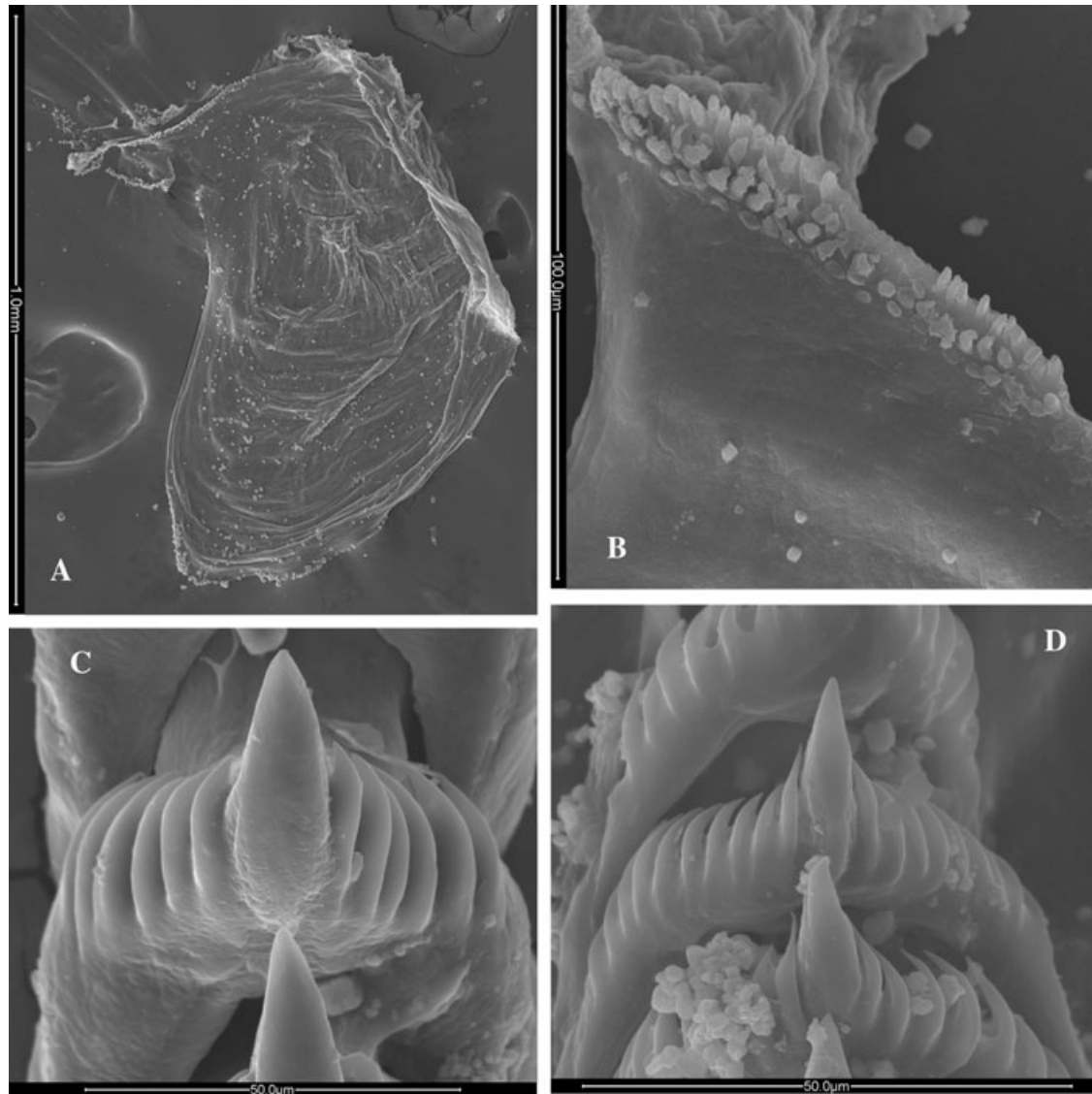


Figure 4. *Babakina anadoni* (Ortea, 1979), scanning electron micrographs. A, jaw, specimen from Tarifa, Spain (MNCN 15.05/46702). B, masticatory border, specimen from Bahamas (MNCN 15./46706). C, radular teeth, specimen from Tarifa, Spain (MNCN 15.05/46702). D, radular teeth, specimen from Bahamas, MNCN 15./46706.

Zealand (Rudman, 2005a) clearly shows that the rhinophores actually consist of a series of incomplete lamellae and represents the only other record of this poorly known species.

BABAKINA ANADONI (ORTEA, 1979)

(FIGS 1C, 3C, 4)

Rioselleolis anadoni Ortea, 1979: 132.

Babakina anadoni – Rolán *et al.*, 1991: 115.

Babakina festiva – misidentification, Padula & Absalão, 2005: 99.

Material examined: MNCN 15.05/46702, one specimen, dissected, 13 mm in length preserved, 15 m depth, Isla de Tarifa, southern Iberian Peninsula (36°00'48"N,; 05°36'W), 5.ix.2003, César Megina. MNCN 15.05/46703, two specimens, 12 and 13 mm in length preserved, one dissected, 10 meters depth, Cabo de Trafalgar, southern Iberian Peninsula (36°11'N, 06°01'W), 25.vi.1994, César Megina. MNCN 15.05/46, one specimen, 25 mm in length alive, Punta Segao, Galicia, northern Iberian Peninsula (43°27'24"N, 8°18'25"W), 25.v.2005, Fátima Martins. MNCN 15.05/46979, one specimen, intertidal zone,

Pedras Negras, Galicia, northern Iberian Peninsula (42°27'N, 08°56'W), 31.iii.2006, A. Luque. MNCN 15.05/46705, two specimens, 2 and 5 mm in length preserved, one dissected, Güimar, Tenerife, Canary Islands (28°18'N, 16°21'W), 30.x.2004, Leopoldo Moro. MNCN 15./46706, one specimen, dissected, 10 mm in length alive, 1 m depth, Thurstone Bay, Abaco, Bahamas (26°42'28"N, 77°18'63"W), 29.vi.1999, C. Redfern. IBUFRJ 14229, one specimen, dissected, 11 mm in length alive, 1 m depth, Praia das Conchas, Cabo Frio, Rio de Janeiro, Brazil (22°52'46"S; 42°01'07"W), 13.xi.2004, V. Padula.

Distribution: Originally described from the northern Spain (Ortea, 1979; Rolán *et al.*, 1991), this species has also been reported from southern Spain (García-Gómez, 1987; Cervera *et al.*, 2006), southern Portugal (Cervera *et al.*, 2006), Canary Islands (Pérez Sánchez & Moreno, 1990; Moro *et al.*, 1995, 2003; Ortea *et al.*, 2001, 2003; present study), Bahamas (Redfern, 2001; present study) and Brazil (Padula & Absalão, 2005).

External morphology: The body is elongate and slender, with a short posterior end of the foot (Fig. 1C). Living animals are 10–25 mm in length. The anterior margin of the foot is elongate, tentaculiform foot corners are bilabiate and slightly notched. The body colour is dull violet but can range from a translucent light pink to purple. A short opaque white or yellowish patch extends medially from the anterior end of the head to just behind the rhinophores. The moderately long cerata are cylindrical and taper distally. They are dark blue, with a yellow upper and unequal dorsolateral surface as well as a subapical orange band. The apex is translucent white. The cerata are densely distributed and are arranged in 22–30 oblique rows, extending from the rear of rhinophores almost to the end of the foot, even continuing along the lateral sides of the pericardial area. Each row contains 2–4 cerata, with the larger ones being situated more dorsally and decreasing in size towards the foot.

The rhinophores have a more intense violet colour than the ground colour of the body, but the apex and the anterior side of the rachis are pale yellow. They share a common base, are perfoliate and have 20–29 lamellae each. The apex and a line that runs medially along the posterior face of each rhinophore is yellowish white. The oral tentacles are elongate and acutely pointed. They are the same colour as the ground colour with an opaque white tip. The tentacular anterior foot corners are pinkish purple throughout. The pleuroproct anus is located ventral to the notal brim about one-third of the body length from the anterior

end. The nephroproct is anterior to the anus. The genital aperture is located below notal brim between the fourth and ninth cerata.

Buccal armature: The jaws (Fig. 4A, B) are tan-brown. The masticatory border of the jaws bears 2–4 rows of denticles that increase in number and size towards the edge. The radular formula of the five dissected specimens is $18 \times 0.1.0$. (MNCN 15.05/46706), $14 \times 0.1.0$ (MNCN 15.05/46705), $14 \times 0.1.0$ (MNCN 15.05/46703), $16 \times 0.1.0$ (MNCN 15.05/46702) and $29 \times 0.1.0$ (IBUFRJ 14229). The rachidian tooth (Fig. 4C, D) is broad with narrow, triangular central cusp. There are 6–10 elongate, acutely pointed denticles on either side of the central cusp. The number of denticles is equal on either side. None of the denticles shares a common base. No denticles are found laterally from the cusp and in no instance extend onto the cusp.

Reproductive system: It has an androdiaulic arrangement (Fig. 3C) and was examined in four specimens (two from the Strait of Gibraltar: MNCN 15.05/46702, MNCN 15.05/46703, one from the Canary Islands: MNCN 15.05/46705, one from the Bahamas: MNCN 15./46706 and one from Brazil: IBUFRJ 14229). All were virtually identical in all aspects of their morphology. The narrow elongate preampullary duct widens into the convoluted ampulla. The ampulla consists of two folds and narrows again before dividing into the oviduct and vas deferens. The vas deferens widens into a glandular prostatic portion that consists of numerous convolutions that cover the penial sac. The prostatic portion enters the wider proximal portion of the penial sac. The unarmed penial papilla is contained within the penial sac, and it is elongate and conical in shape, and the sac is usually curved. It narrows to rounded apex and exists adjacent to the rounded, straight bursa copulatrix. The oviduct is elongate and connects to the pyriform receptaculum seminis. The other portion of the oviduct emerges from the base of the receptaculum and, after a short distance, enters the small albumen gland. The membrane gland is similar in size than the albumen gland. The mucous gland is much larger than the other two female glands and exits ventral to the penis and bursa copulatrix.

Remarks: The external morphology and colouration of *Babakina anadoni* were described from of a single specimen from the northern Spain (Ortea, 1979). Ortea erected the new genus *Rioselleolis* to accommodate this species and considered that this genus should be included in a separate family, without proposing a new family. Rolán *et al.* (1991) transferred this species to the genus *Babakina*, based on

additional material and personal communications with R. Roller.

Our specimens match the external appearance described by Ortea (1979), although some Canarian specimens appear to have a lighter ground body colouration than those from the coast of Spain. Moreover, the features of the radula and jaws described by Rolán, Rolán-Alvarez & Ortea (1991) fit well with those specimens dissected here from eastern and western Atlantic. The reproductive system is described for the first time here, and does not vary significantly in any of the specimens examined. Redfern (2001) collected a single specimen of *Babakina* from Bahamas (western Atlantic), which attributed to *B. festiva*. He described the external appearance only, which is very similar to specimens from the eastern Atlantic. The internal anatomy of Redfern's specimen (present study), as well as that of the Brazilian specimens, agrees with that of *B. anadoni* collected from the eastern Atlantic. Thus, we conclude that his specimen belongs to this species rather than *B. festiva*.

Gosliner (1990) questioned whether the three nominal species of the genus are distinct and may refer only to one biological species. However, after completing a comparative examination of material it is evident that *B. anadoni* is a valid species. Externally, *B. anadoni* can be recognized from other species by the presence of a subapical band of yellow followed by another more distal band of orange. This species has symmetrically arranged denticles on either side of the central cusp as in *B. caprinsulensis*. The other two species have an asymmetrical arrangement of denticles. Several reproductive characters clearly distinguish this species from other *Babakina* (Table 1). The penis of *B. anadoni* is elongate as in *B. festiva*. However, the bursa copulatrix is rounded as in *B. caprinsulensis*, except that the duct is straight in *B. anadoni* rather than curved.

BABAKINA INDOPACIFICA SP. NOV.

(FIGS 1D, 3D, 5)

Babakina festiva – Nakano, 2004: 253.

Babakina festiva – Ono, 2004: 257.

Babakina cf. *festiva* – Rudman, 2005b.

Babakina cf. *festiva* – Rudman, 2005c.

Material examined: Holotype: CASIZ 085891, one specimen, dissected, on sea grass, 1 m depth, near Dipalog, northern Mindanao, Philippine Islands, T.M. Gosliner. Paratypes: CASIZ 088572, one specimen, dissected, 14 mm alive, 18 m depth, crawling at night, Molikini Islet, Maui, Hawaiian Islands, 31.viii.1992, Pauline Fiene. CASIZ 164914, one specimen, in open at night, 1 m depth, Hekili Point, Maui, Hawaiian

Islands, 3.x.2002, Cory Pittman. CASIZ 118804, one specimen, Hekili Point, Maui, Hawaiian Islands, 1 m depth, 3.x.1997, Cory Pittman. CASIZ 120655, one specimen, crawling on bottom at night, 1 m depth, Hekili Point, Maui, Hawaiian Islands, 24.x.1999, Cory Pittman. CASIZ 144040, one specimen, dissected, 5 m depth, off S coast of Gahi Island, Kerama Islands, Ryukyu Islands, Japan, 13.i.2000, Atsushi Ono. One specimen, MNCN 15.05/46741, 12 m depth, Hachijo Island, Japan, 4.v.2005, Nishina Masayoshi. CASIZ 173035, one specimen, dissected (missing buccal mass) Station 14, 14 m depth, barrier reef edge, 14 m depth, W of Nosy Valiha, Radama Islands, Madagascar, 20.x.2005, T. Gosliner.

Distribution: This species is known from southern Japan: Kerama Islands and Hachijo Island (Nakano, 2004; Ono, 2004; and present study), the Philippines, Indonesia, Madagascar and the Hawaiian Islands (present study) and South Korea (Rudman, 2005c).

Etymology: This species is named *indopacifica* for its tropical Indo-Pacific distribution. The remaining three species of *Babakina* are temperate taxa.

External morphology: The body is elongate and slender, with a trailing posterior end of the foot (Fig. 1D). Living animals are 7–18 mm in length. The anterior margins of the foot and tentaculiform foot corners are bilabiate and slightly notched. The body colour can range from a translucent light purple to deep reddish purple. A broad opaque white patch covers most of the head between the rhinophores and the anterior margin of the head. A smaller patch may be present just behind the rhinophores in some specimens. In all specimens observed an additional opaque white patch covers the pericardial region. The relatively short cerata are thick, widest in the middle and taper distally. They are almost entirely opaque white with some bluish purple pigment visible on their posterior face. The apex is translucent white. The cerata are densely clustered and continuous throughout the length of the body, without interruption in the pericardial region. The medial area between the rhinophores and pericardial region is relatively devoid of cerata. There are approximately 15–33 diagonal rows of cerata on either side of the body. Each row contains 2–3 cerata with the innermost cerata of each row being the largest. The bright red rhinophores share a common base, are perfoliate and have up to 28–32 lamellae each. The posterior portion of the rhinophores is covered by a fine dusting of opaque white pigment that extends to the apex. The anterior face lacks opaque white and is uniformly red. The oral tentacles are relatively short, but longer than the rhinophores and have a smooth texture. They are

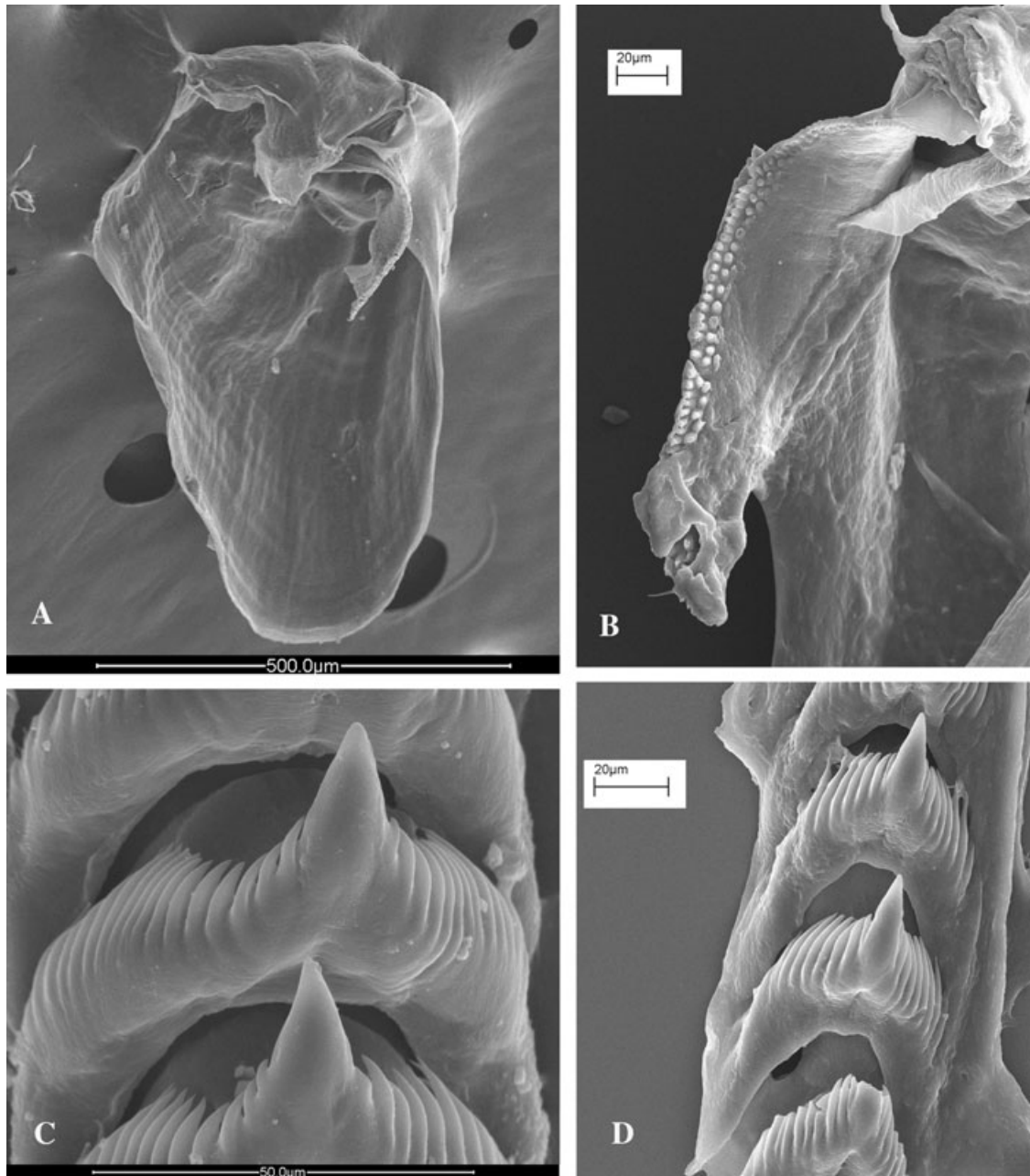


Figure 5. *Babakina indopacifica* sp. nov., scanning electron micrographs. A, jaw, specimen from Mindanao, Philippines (CASIZ 085891). B, masticatory border, specimen from Maui, Hawaii (CASIZ 088572). C, radular teeth, specimen from Mindanao, Philippines (CASIZ 085891). D, radular teeth, specimen from Maui, Hawaii (CASIZ 088572).

pinkish purple basally with a band of opaque white covering the outer one-third to half of the tentacle. The tentacular anterior foot corners are short and are often held close to the body so they are not readily visible. They are pinkish purple throughout their length. The pleuroproct anus is located ventral to the notal brim about one-third of the body length from the anterior end, ventral to the 14th–16th

ceratal row. The nephroproct is anterior to the anus. The genital aperture is located below the notal brim just posterior to the rhinophore base below the seventh ceratal row.

Buccal armature: The jaws (Fig. 5A, B) are tan-brown. The masticatory border contains three rows of numerous irregularly spaced, triangular denticles.

The radula formula is $18 \times 0.1.0$ (CASIZ 085891) and $14 \times 0.1.0$ (CASIZ 088952) in two specimens examined. The rachidian tooth (Fig. 5C, D) is broad with a wide, triangular central cusp. There are 6–12 elongate, acutely pointed denticles on either side of the central cusp in one specimen (CASIZ 088972) and 10–17 denticles in the second (CASIZ 085891). The number of denticles is not equal on either side. For example on one tooth there were 17 denticles on left side and 13 on the right side. No denticles share a common base and none bifurcates above. In some instances denticles are present on the central cusp while in other cases they are only found laterally from the cusp.

Reproductive system: It has an androdiaulic arrangement (Fig. 3D) and was examined in detail in three specimens (CASIZ 085891, CASIZ 088972, CASIZ 173035). The narrow elongate preampullary duct widens into the convoluted ampulla. The ampulla consists of one large fold and narrows again before dividing into the oviduct and vas deferens. The vas deferens widens into a glandular prostatic portion with relatively few convolutions. The prostatic portion enters the wider proximal portion of the penial sac. The penial papilla is contained within the penial sac. The unarmed penial papilla is short and conical in shape. It narrows to an acute apex and exists adjacent to the elongate, very thin bursa copulatrix. The oviduct is elongate and connects to the pyriform receptaculum seminis. The other portion of the oviduct emerges from the base of the receptaculum and, after a short distance, enters the small albumen gland. The membrane gland is about the same size as the albumen gland. The mucous gland is much larger than the other two female glands and exits ventral to the penis and bursa copulatrix.

Remarks: The specimens from the tropical Indo-Pacific can be distinguished easily from other members of *Babakina*. They have opaque white pigment on spindle-shaped cerata and a larger patch of opaque white on the head with an additional pigment patch on the pericardium. The remaining species have thinner, more cylindrical cerata and more elongate anterior foot corners than does *B. indopacifica*. This species shares some radular similarities with *B. festiva*. In both species, the number of denticles on either side of the radular tooth is generally unequal and some denticles are situated on the sides of the primary cusp. *B. indopacifica* is also distinguished by a unique combination of reproductive characters (Table 1). As in *B. caprinsulensis*, *B. indopacifica* has a short, conical penis. It is similar to *B. festiva* in that it has a thin, elongate rather than a short pyriform receptaculum seminis as in *B. caprin-*

sulensis and *B. anadoni*. However, the bursa of *B. indopacifica* is much smaller than that of *B. festiva*. *Babakina indopacifica* also has two unique reproductive characters. The bursa is much reduced and is almost vestigial and the vas deferens has relatively few convolutions compared with the other three species. On the basis of all of these features, the description of *B. indopacifica* as a new species of *Babakina* is supported.

PHYLOGENY OF BABAKINA

Twenty species of aeolid nudibranchs were considered for the present analyses. All were included in the final analysis. Twenty-seven morphological characters were considered for the present study. Table 2 contains a list of all morphological characters considered. The complete character matrix for species of *Babakina* is shown in Table 3. Phylogenetic analyses were performed using the program Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b 10 (Swofford, 2001) using the heuristic algorithm (TBR branch swapping option), set at maximum parsimony. One thousand replicates were run with starting trees obtained using stepwise addition.

In cases where a taxon had two states for a given character they were treated as uncertain. Both ACCTRAN and the DELTRAN optimizations were used for character transformation. In both cases all characters were treated as unordered with the exception of character 11 (radular teeth number) and were polarized using *Notaeolidia gigas* Eliot, 1905 as the outgroup species, as members of the Notaeolidiidae are considered to be among the most basal aeolids (Wägele & Willan, 2000). For a preliminary analysis of the position of the genus *Babakina* within the Aeolidina, we used several species of aeolids of different families. Aeolidiidae: *Aeolidiella alderi* (Cocks, 1852); *Berghia verrucicornis* (Costa, 1864) and *Spurilla neapolitana* (Delle Chiaje, 1823). Facelinidae: *Caloria elegans* (Alder & Hancock, 1845); *Cratena peregrina* (Gmelin, 1791); *Dicata odhneri* (Schmekel, 1967); *Dondice banyulensis* (Portmann & Sandmeier, 1960a), *Facelina auriculata* (Müller, 1776); *Favorinus branchialis* (Rathke, 1806) and *Pruvotfolia pselliotes* (Labbé, 1923). Flabellinidae: *Calmella cavolini* (Vérany, 1846), *Flabellina affinis* (Gmelin, 1791); *Flabellina capensis* (Thiele, 1925) and *Flabellina ischitana* (Hirano & Thompson, 1990). Piseinotecidae: *Piseinotecus gaditanus* Cervera, García-Gómez & García, 1987.

Character 16 (presence or absence of a bursa copulatrix) was excluded from the final analysis as its distribution and homology remain poorly understood within the Aeolidina. The bursa is usually the site of exogenous sperm reception following copulation and

Table 2. Morphological character definitions. The following characters were considered for use in the analyses of *Babakina* and other aeolid groups. The character states are indicated as follows: 0: the presumed plesiomorphic condition; 1, 2: apomorphic condition. For character states that are not applicable, '–' is used and for missing data, '?' is used. Character preceded by an asterisk was deleted from the final analysis. The distribution of plesiomorphic and apomorphic character states is presented in Table 3

- 1 Notal brim: 0 – present; 1 – interrupted; 2 – absent.
- 2 Foot corners: 0 – tentacular; 1 – angular; 2 – rounded.
- 3 Body: 0 – narrow; 1 – wide.
- 4 Cerata: 0 – arise directly from notum; 1 – arise from elevated peduncles.
- 5 Ceratal number: 0 – usually less than 100 cerata per side of the body; 1 – numerous, with many more than 100 cerata per side.
- 6 First ceratal cluster: 0 – rows, present as a series of rows; 1 – arch, forming a horseshoe-shaped arch.
- 7 Second ceratal cluster: 0 – rows, present as a series of rows; 1 – arch, forming a horseshoe-shaped arch.
- 8 Anus: 0 – pleuroproctic; 1 – cleioproctic; 2 – acleioproctic.
- 9 Rhinophoral base: 0 – divided; where both rhinophores have separate point of insertion; 1 – united, where the two rhinophores join and share a common base.
- 10 Rhinophoral ornamentation: 0 – smooth, with no sign or ornamentation, may occasionally appear wrinkled; 1 – annulate, with a series of well-separated rings; 2 – perfoliate, with a series of crowded lamellae; 3 – papillate with series of elongate papillae; 4 – swelling; with one or more inflated areas along the rhinophoral length.
- 11 Radula: 0 – multiseriate with several row of lateral teeth; 1 – triseriate with a lateral tooth flanking either side of the rachidian row; 2 – uniseriate, with only a single rachidian row.
- 12 Lateral teeth: 0 – denticulate, with a series of denticles along the inner masticatory edge; 1 – smooth, with no denticles along cutting edge.
- 13 Rachidian tooth shape: 0 – cuspidate, with a series of denticles flanking a triangular cusp; 1 – pectinate, forming a series of comb-like denticles without a larger central cusp.
- 14 Rachidian tooth: 0 – denticulate; 1 – smooth, without denticles.
- 15 Radular teeth: 0 – symmetrical, with the same number of denticles on either side of the primary cusp; 1 – asymmetrical, with different numbers of denticles on other side of the cusp.
- 16 Jaw denticles: 0 – numerous rows, with multiple rows of denticles along the masticatory margin; 1 – single row, with only one row of denticles; 2 – absent, with no denticles along margin.
- 17 Receptaculum seminis arrangement: 0 – proximal, in closer proximity to the hermaphroditic gland than to the genital aperture; 1 – distal, near the genital aperture.
- 18 Receptaculum seminis shape: 0 – simple; 1 – bilobed.
- 19 *Bursa copulatrix: 0 – present; 1 – absent.
- 20 Bursa copulatrix duct: 0 – straight; 1 – bent.
- 21 Bursa copulatrix shape: 0 – pyriform; 1 – narrow.
- 22 Bursa copulatrix size: 0 – large; 1 – small.
- 23 Penis: 0 – unarmed, without cuticular structures; 1 – armed, with cuticular hooks.
- 24 Penial papilla: 0 – narrow, 1 – conical, 2 – bulbous.
- 25 Penial glands: 0 – absent, devoid of any auxiliary glandular structures; 1 – present, with secondary glandular structures.
- 26 Prostate diameter: 0 – wider in some parts; 1 – uniform diameter throughout.
- 27 Food: 0 – hydroids; 1 – sea anemones; 2 – eggs, with opisthobranch eggs as the primary food source.

may also serve a gametolytic function. The wall of the bursa is lined with columnar endothelial cells. There are both secretory and resorptive cells (Schmekel, 1971). The bursa is present in some aeolids (Gosliner, 1994) but this was not confirmed histologically. Schulze & Wägele (1998) give a detailed description of the internal anatomy and the histology of organs and systems of *Flabellina affinis*. According to these authors, this species has two receptacula, but neither of them shows a gametolytic activity. Some years before, Medina *et al.* (1988) described the ultrastr-

structure of the bursa copulatrix and receptaculum seminis in *Hypselodoris midatlantica* Gosliner, 1990 (as *H. tricolor*). These authors confirmed a gametolytic function in the bursa copulatrix, with a single epithelium lining a lumen filled with a heterogeneous material including remnants of degenerative gametes. A thin layer of connective tissue externally surrounds the epithelium. In the luminal material sperm tails, myelinic formations and homogeneously electron-dense bodies are distinguished. In the case of the receptaculum seminis, it is pyriform and the

Table 3. Morphological character states used for phylogenetic analysis

Characters																												
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
<i>Notaeolidia gigas</i>	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	2	-	-	0	0	0	0	0	0	2	0	1	0
<i>Flabellina capensis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0
<i>Flabellina ischitana</i>	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Flabellina affinis</i>	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	-	-	-	0	0	0	0	0	0
<i>Calmella cavolini</i>	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	0	0	0	0	0	0
<i>Piseinotectus gaditanus</i>	1	1	0	1	0	0	0	2	0	0	2	-	0	0	0	0	0	0	1	-	-	-	0	0	0	0	0	0
<i>Spurilla neapolitana</i>	2	0	1	0	1	1	1	1	0	2	2	-	1	0	0	1	0	0	1	-	-	-	0	2	0	0	1	1
<i>Berghia verrucicornis</i>	2	0	1	0	1	1	1	1	0	3	2	-	1	0	0	1	0	0	1	-	-	-	0	0	0	0	1	1
<i>Aeolidiella alderi</i>	2	1	1	0	1	0	0	1	0	0	2	-	1	0	0	2	0	0	1	-	-	-	0	1	0	0	1	1
<i>Dicata odhneri</i>	2	0	0	0	0	1	1	1	0	0	2	-	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
<i>Facelina auriculata</i>	2	0	0	0	0	0	0	1	0	1	2	-	0	0	0	1	0	0	1	-	-	-	1	2	1	0	0	0
<i>Cratena peregrina</i>	2	1	0	0	0	1	0	1	0	0	2	-	0	0	0	1	0	0	1	-	-	-	0	2	0	1	0	0
<i>Pruvotfolia psellotes</i>	2	0	0	0	0	0	0	1	0	1	2	-	0	0	0	1	0	0	1	-	-	-	1	1	0	0	0	0
<i>Caloria elegans</i>	2	0	0	0	0	0	0	1	0	0	2	-	0	0	0	2	0	0	1	-	-	-	0	2	0	0	0	0
<i>Favorinus branchialis</i>	2	0	0	0	0	1	1	1	0	4	2	-	0	1	0	0	0	0	1	-	-	-	0	2	0	1	2	0
<i>Dondice banyulensis</i>	2	0	0	0	0	1	1	1	0	1	2	-	0	0	0	1	0	0	1	-	-	-	0	1	0	1	0	0
<i>Babakina festiva</i>	0	0	0	0	0	0	0	0	1	2	2	-	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
<i>Babakina anadoni</i>	0	0	0	0	0	0	0	0	1	2	2	-	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
<i>Babakina caprinsulensis</i>	0	0	0	0	0	0	0	0	1	2	2	-	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0
<i>Babakina indopacifica</i>	0	0	0	0	0	0	0	0	1	2	2	-	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0

lumen is filled with abundant spermatozoa that are orientated radially. The sperm heads are embedded in the lining epithelium and the tails are directed toward the centre of the lumen. In this chromodoridid species an histological description for these structures exists, but it is necessary to carry out additional studies to clarify possible homologies within Nudi-branchia, prior to a phylogenetic analysis.

Morphological data were compiled using MacClade, version 4.08 (Maddison & Maddison, 2005). Synapomorphies were mapped using the character trace option in MacClade using the majority rule tree from the PAUP analysis. Bremer analyses were performed on the strict consensus tree to estimate branch support (Bremer, 1994).

CHARACTERS

To determinate the phylogenetic relationships of species of the genus *Babakina*, 27 characters were examined for 20 taxa. The character states are indicated as follows: 0: the presumed plesiomorphic condition; 1, 2, 3: apomorphic conditions. For character states that are not applicable '–' is used and, for character states that are very variable in a taxa, '?' is used. The character states for the data examined for the present study can be found in Table 2.

1. **Notal brim:** 0 – present; 1 – interrupted; 2 – absent. The presence of a rim of tissue along the dorsolateral margins of the body has been considered as a plesiomorphic feature within the Aeolidina (Odhner, 1939). This feature is present in *Babakina* and *N. gigas* (0). These taxa are considered very primitive within Aeolidina. Members of the genus *Flabellina* Voigt, 1834, *Calmella cavolini* and *Piseinotecus gaditanus* have a discontinuous notal brim (1) and they group together in the same clade. In the remaining taxa, no vestige of the notal brim remains (2).
2. **Foot corners:** 0 – tentacular; 1 – angular; 2 – rounded. The anterior region of the foot in *Notaeolidia* is rounded (2). In the case of the genera *Piseinotecus*, *Aeolidiella* and *Cratena*, this region is angular (1). In the rest of the species in study, the foot corners are tentacular (0).
3. **Body:** 0 – narrow; 1 – wide. The species of Aeolidiidae and *Notaeolidia* possess a wide body (1). The rest of the species in this study possess a narrow body (0).
4. **Cerata:** 0 – arise directly from notum; 1 – arise from peduncles. In *F. ischitana*, *Calmella cavolini* and *Piseinotecus gaditanus*, the ceratal cluster emerges from stalked clusters, which are well elevated from the notum. The other taxa have the cerata arranged in linear rows. In the case of the

Flabellina affinis, there is considerable variability; the arrangement of the cerata can be arranged separately or in rows and/or groups that are either placed on the notal ridge or on peduncles (Schulze & Wägele, 1998).

5. **Ceratal number:** 0 – usually less than 100 cerata per side of the body; 1 – numerous, with many more than 100 cerata per side. The cerata of the species of *Spurilla*, *Berghia* and *Aeolidiella* are far more numerous than in the other taxa.
6. **First ceratal cluster:** 0 – rows, present as a series of rows; 1 – arch, forming a horseshoe-shaped arch. In the case of the genera *Spurilla*, *Berghia*, *Dicata*, *Cratena*, *Favourinus* and *Dondice*, the first ceratal cluster forms a horseshoe-shaped arch (1). The remaining species in study have the first ceratal cluster arranged in rows (0).
7. **Second ceratal cluster:** 0 – rows, present as a series of rows; 1 – arch, forming a horseshoe-shaped arch. The vast majority of ingroup taxa that have the arrangement of the first ceratal cluster arranged in an arch, and have the second ceratal cluster in arch as well. Only *Cratena* has a first ceratal cluster in arch with the second cluster forming a row (0).
8. **Anus:** 0 – pleuroproct; 1 – cleioproct; 2 – acleioproct. In the species of Notaeolidiidae and the most primitive species of Flabellinidae, the anus is situated in the pleuroproct position (Gosliner & Willan, 1991). The species of *Flabellina*, *Calmella*, *Notaeolidia* and *Babakina* are pleuroproct (0). Of the taxa included in this analysis only *Piseinotecus* has the anus in an acleioproct position (2). The remaining taxa are cleioproct (1).
9. **Rhinophoral base:** 0 – divided; where both rhinophores have a separate point of insertion into the dorsal surface of the head; 1 – united, where the two rhinophores join and share a common base. This character is an external feature typical of genus *Babakina*.
10. **Rhinophoral ornamentation:** 0 – smooth, with no sign of ornamentation, may occasionally appear wrinkled; 1 – annulate, with a series of well-separated rings; 2 – perfoliate, with a series of crowded lamellae; 3 – papillate with series of elongate papillae; 4 – swelling; with one or more inflated areas along the rhinophoral length. The simple condition, a smooth rhinophore, is considered to represent the ancestral state (0), as it has less sensory surface area. The rhinophores in derived species are generally ornamented. *Flabellina ischitana* and *F. affinis*, as well as in *Dondice*, *Pruvotfolia* and *Facellina*, possess annulate rhinophores (1). *Spurilla neapolitana* and

members of the genus *Babakina* have perfoliate rhinophores (2). *Babakina caprinsulensis* has incomplete lamellae on its perfoliate rhinophores. Species of *Berghia* have papillate rhinophores (3), and in the case of *Favorinus* the rhinophores have a subapical inflated area (4).

11. **Radula:** 0 – multiseriate with several rows of lateral teeth; 1 – triseriate, with a lateral tooth flanking either side of the rachidian row; 2 – uniseriate, with only a single rachidian row. The multiseriate radula is considered to represent the plesiomorphic state (0); *Notaeolidia* has a multiseriate radula. The species of *Flabellina* and *Calmella cavolini* have a triseriate radula (1). The uniseriate radula is the apomorphic state (2). This character was treated as ordered in the analysis based on the fact that the successive loss of lateral teeth has been well documented in aeolid phylogeny (Wägele & Willan, 2000).
12. **Lateral teeth:** 0 – denticulate, with a series of denticles along the inner masticatory edge; 1 – smooth, with no denticles along cutting edge. In most species of *Flabellina*, the lateral radular teeth bear a series of denticles along their inner edge. The absence of denticles on the lateral teeth is considered to represent a derived feature within *Flabellina* (Gosliner & Willan, 1991). *Notaeolidia* bears denticles along the inner masticatory edge of the lateral teeth (0). This character is treated as non-applicable in species with uniseriate radula.
13. **Rachidian tooth shape:** 0 – cuspidate, with a series of denticles flanking a triangular cusp; 1 – pectinate, forming a series of comb-like denticles without a larger central cusp. In species of *Spurilla*, *Berghia* and *Aeolidiella*, the rachidian teeth are pectinate, with denticles on each side of a triangular central cusp.
14. **Rachidian tooth:** 0 – denticulate, 1 – smooth, without denticles. Only *Favorinus* has a rachidian tooth with a single denticle, with no denticles on either side of the central denticle. The rest of the species included in the analysis have a denticulate rachidian tooth.
15. **Rachidian radular teeth:** 0 – symmetrical, with the same number of denticles on either side of the primary cusp; 1 – asymmetrical, with different numbers of denticles on either side of the cusp. In *Babakina festiva* and *B. indopacifica*, the number of denticles is not equal on either side of the rachidian tooth.
16. **Jaws denticles:** 0 – with multiple rows of denticles along the masticatory margin; 1 – single row, with only one row of denticles; 2 – absent, with no denticles along margin. Jaws with several rows of denticles on the masticatory border are considered plesiomorphic (0), whereas those with only one row of denticles (1), or no denticles (2), are apomorphic (Wägele & Willan, 2000). *Spurilla*, *Berghia*, *Cratena*, *Dondice* and the clade including *Pruvotfolia* and *Facelina* have a single row of denticles in the masticatory border (1). *Notaeolidia*, *Aeolidiella*, *Dicata* and *Caloria* lack denticles along the margin of the masticatory border (2).
17. **Receptaculum seminis arrangement:** 0 – proximal, in closer proximity to the hermaphroditic gland than to the genital aperture; 1 – distal, near the genital aperture. A proximal receptaculum seminis is considered plesiomorphic (0). *Flabellina affinis* is the more derived species of *Flabellina* in the analysis and it is the only one with a distal receptaculum seminis (1).
18. **Receptaculum seminis shape:** 0 – simple; 1 – bilobed. A bilobed receptaculum is considered apomorphic (1). *Flabellina affinis* is the only taxon with a bilobed receptaculum in this study. One lobe is not stalked and another one is smaller and stalked.
19. **Bursa copulatrix:** 0 – present; 1 – absent. The presence of a proximal receptaculum seminis and a distal bursa copulatrix is considered a plesiomorphic state (Ghiselin, 1966; Gosliner, 1981; Schmekel, 1985; Mikkelsen, 1996). *Notaeolidia*, *Flabellina capensis*, *F. ischitana*, *Dicata* and the species of *Babakina* have a bursa copulatrix, and are considered plesiomorphic (0). The remaining species included in the analysis lack a bursa (1). This character was deleted from the final analysis owing to the fact that the bursa has often been overlooked and homology of this structure remains open to some question.
20. **Bursa copulatrix duct:** 0 – straight; 1 – bent. In two species, *Flabellina capensis* and *Babakina caprinsulensis*, the bursa has a sharp bend. This is considered plesiomorphic (0). In remaining species the duct is simply curved or straight (1). In the species with bursa copulatrix absent, this character is treated as non-applicable.
21. **Bursa copulatrix shape:** 0 – pyriform; 1 – narrow. In *Babakina festiva* and *B. indopacifica*, the bursa copulatrix has a narrow shape (1). In the remaining species with bursa copulatrix, it has a pyriform shape (0). In those species with bursa copulatrix absent, this character is treated as non-applicable.
22. **Bursa copulatrix size:** 0 – large; 1 – small. Presence of a small bursa is a feature typical of *B. indopacifica*, where the bursa copulatrix is reduced (1). In the species lacking a bursa

copulatrix, this character is treated as non-applicable.

23. **Penis:** 0 – unarmed, without cuticular structures; 1 – armed, with cuticular hooks. The absence of spines within the vas deferens is considered the plesiomorphic state (0) (Gosliner, 1994; Wägele & Willan, 2000). *Pruvotfolia pselliotes* and *Facelina auriculata* (Alder & Hancock, 1855) have a penis with cuticular spines (1). The rest of the species in the study have an unarmed penis.
24. **Penial papilla:** 0 – narrow; 1 – conical; 2 – bulbous. The species *Berghia verrucicornis*, the clade including *Flabellina ischitana*, *F. affinis*, *Calmella* and *Piseinotecus*, as well as the clades including *Babakina festiva* have a narrow penial papilla (0). *Aeolidiella*, *Dicata*, *Pruvotfolia*, *Dondice*, *Babakina caprinsulensis* and *B. anadoni* have a conical penial papilla (1). The remaining species in this study present a bulbous penial papilla (2).
25. **Penial glands:** 0 – absent, devoid of any auxiliary glandular structures; 1 – present, with secondary glandular structures. A simple penis, without penial glands is considered plesiomorphic (0). *Facelina auriculata* is the only taxon in this analysis that has penial glands (1).
26. **Prostate diameter:** 0 – wider in some parts; 1 – uniform diameter throughout. *Notaolidia*, *Cratena*, *Favorinus*, *Dondice* and the species of *Babakina* have a uniform diameter of the prostate (1); the other species have a well-differentiated prostatic section divided into several parts (0).
27. **Food:** 0 – hydroids; 1 – sea anemones; 2 – eggs. The vast majority of species included in the analysis feed on hydroids (0). *Spurilla*, *Berghia* and *Aeolidiella* feed on sea anemones (1) while *Favorinus* feeds on opisthobranch eggs (2).

In the analysis presented (Fig. 6), The heuristic search of the data matrix set produced 16 most parsimonious trees, obtained with 58 steps, and had a consistency index (CI) of 0.63, a retention index (RI) of 0.75 and a homoplasy index (HI) of 0.36.

The resulting phylogeny shows phylogenetic relationships that are rather weakly supported by Bremer values of 1 or 2 (Fig. 7). *Babakina* represents a clade that is moderately well supported by two synapomorphies: united rhinophores (9) and perfoliate rhinophores (10) and has a Bremer support value of 2. The clade including *B. festiva* and *B. indopacifica* is supported by two synapomorphies: different numbers of denticles on other side of the cusp of the rachidian tooth (15) and bursa copulatrix with narrow shape (21). Additionally, *B. indopacifica* has an auto-

pomorphic feature: a reduced bursa copulatrix that is characteristic of this species (22). *Babakina caprinsulensis* has one autapomorphy: a bent bursa duct (20). Within *Babakina*, *B. anadoni* and *B. caprinsulensis* form a trichotomy with the clade containing *B. festiva* and *B. indopacifica*. The sister group relationship of *B. festiva* and *B. indopacifica* has a Bremer support value of 2.

Babakina is the sister group to Aeolidiidae plus Facelinidae. Aeolidiidae is a monophyletic group and is weakly supported as a clade (Bremer support value of 2). Aeolidiidae is supported by four synapomorphies: a broad body (3), a high number of cerata (5), a pectinate rachidian tooth (13) and feeding on sea anemones (27). However, Facelinidae is not supported as a clade in the present analysis. Relationships within Facelinidae are not supported, most probably due to incomplete taxon sampling.

The *Babakina*/Aeolidiidae/Facelinidae clade is supported by one synapomorphy: uniseriate radula (11), and has a Bremer support value of 1. The clade including Aeolidiidae and Facelinidae is supported by a Bremer value of 1 and two synapomorphies: absence of a notal brim (1) and a cleioproct anus (8).

Flabellinidae is weakly supported (Bremer support value of 1), but monophyletic when *Calmella* and *Piseinotecus* are included as members of this taxon. They are supported by the presence of a single synapomorphy: presence of an interrupted notal brim (1). The clade including *Flabellina ischitana*, *F. affinis*, *Calmella* and *Piseinotecus* is supported by a Bremer value of 1 and two synapomorphies: cerata arising from peduncles (4) and a narrow penial papilla (24).

DISCUSSION

The present study permits us to conclude that the three previously described species of *Babakina* and the species described here have consistent external and internal morphological differences and represent distinct species. This conclusion is contrary to Gosliner's (1990) assertion that several of these species may represent synonyms of each other. *Babakina indopacifica* and *B. festiva* are both found in Japanese waters. *B. indopacifica* is found in tropical and subtropical regions while *B. festiva* is found in cold temperate waters in central Japan and California and the subtropical waters of Mexico. In the original description of *B. festiva*, Roller (1972) compared Japanese specimens with California animals and found no consistent differences between the material examined. If additional Japanese material becomes available, it would be valuable to further compare reproductive anatomy with California specimens as well as contrast mitochondrial genome distances such as using

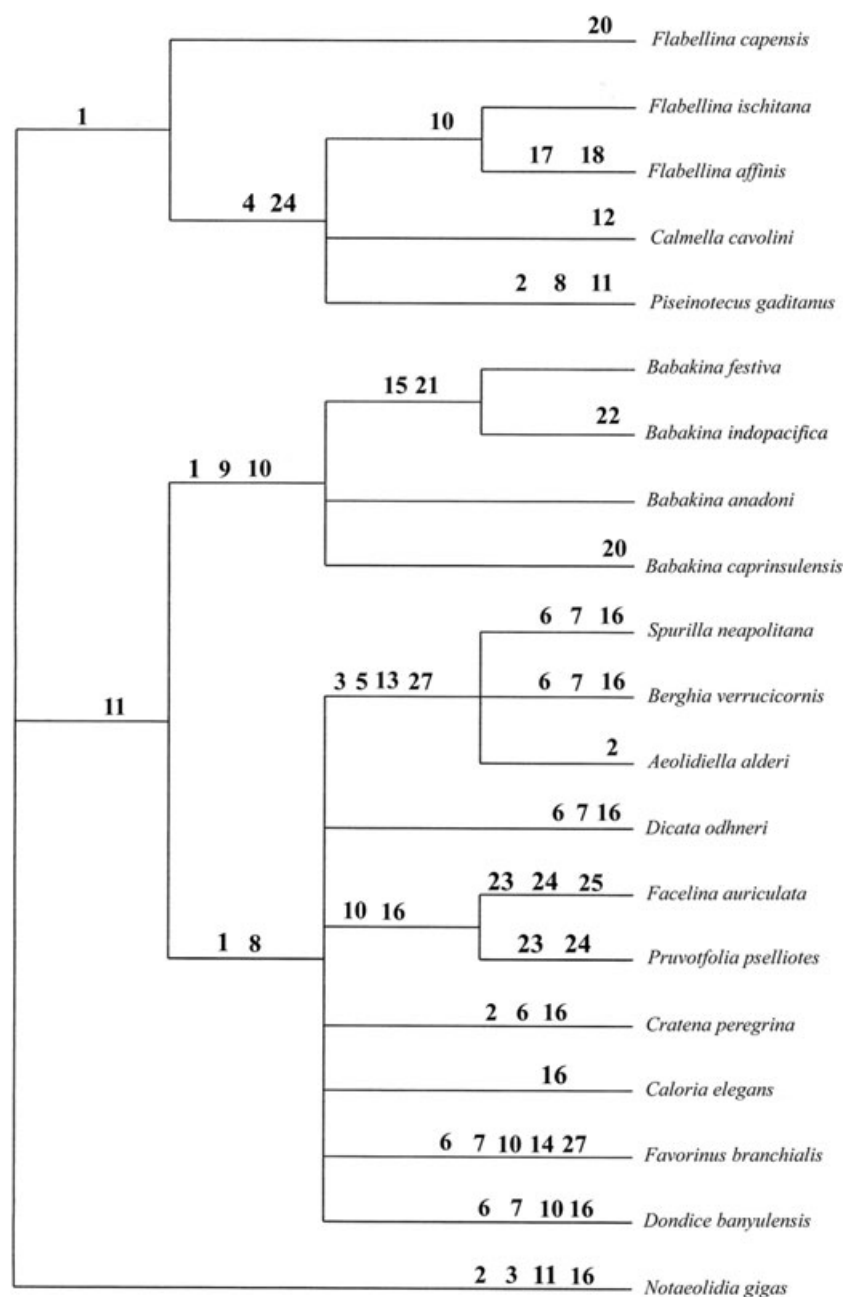


Figure 6. Strict consensus tree of 30 most parsimonious trees. Character numbers correspond to characters listed in Table 2.

partial sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) or the mitochondrial large subunit (16S).

The present lack of resolution within the Facelinidae/Aeolidiidae clade, where taxa traditionally included in the Facelinidae form a polytomy, presents inconclusive results. This is most probably due to incomplete taxon sampling and is beyond the scope of this paper. The inclusion of *Calmella* and

Piseinotecus within the Flabellinidae represents an intriguing suggestion of relationships that warrants further study, given that *Piseinotecus* has been included in a separate family (Edmunds, 1970).

Further studies also need to focus on closer examination of reproductive characters, especially the presence, position and structure of the bursa copulatrix and receptaculum seminis. Such studies would provide a much better understanding of homology and

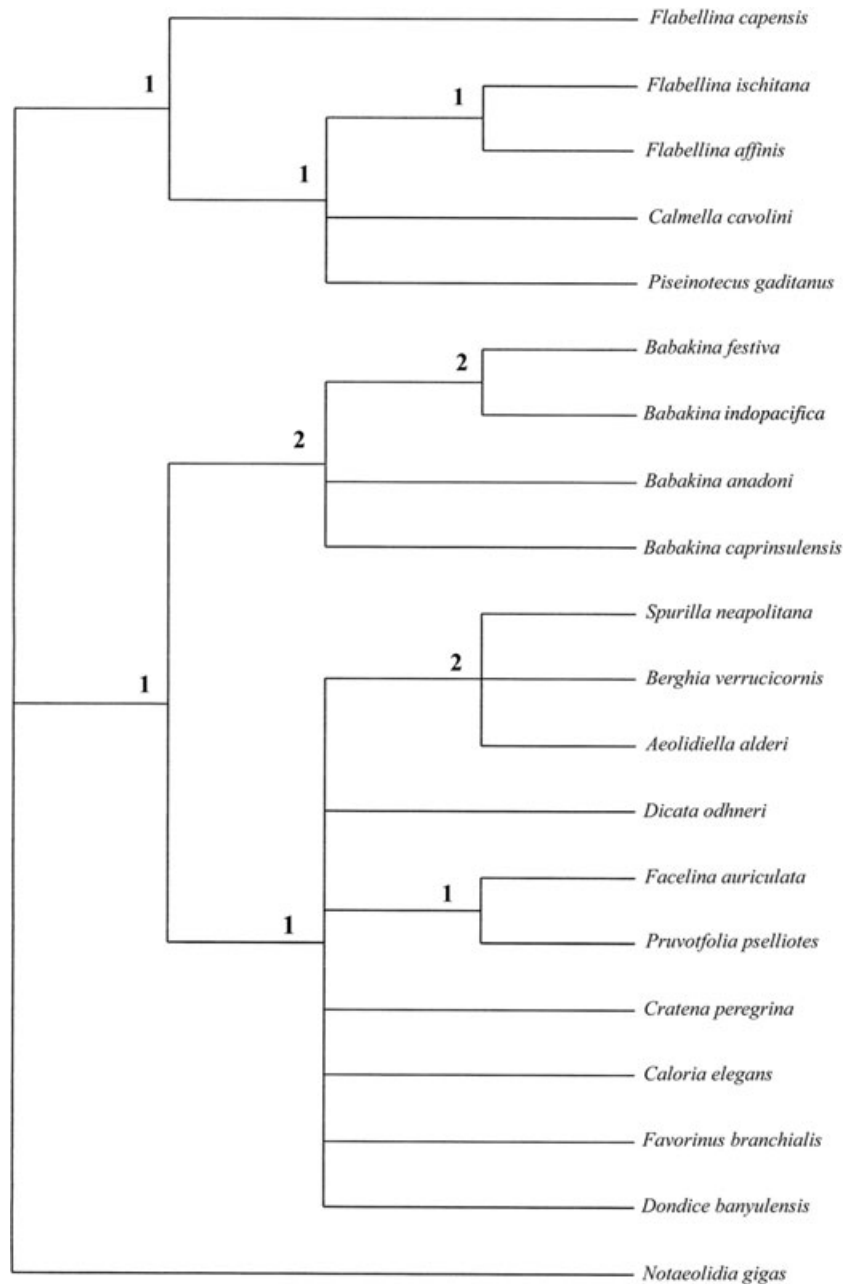


Figure 7. Bremer support values for clades included in strict consensus tree.

character distribution of these structures in aeolids. It is very likely that this would expand our understanding of aeolid phylogenetic relationships.

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