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# A Phylogenetic Analysis of the Aegiridae Fischer, 1883 (Mollusca, Nudibranchia, Phanerobranchia) with Descriptions of Eight New Species and a Reassessment of Phanerobranch Relationships

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**The phylogenetic relationships among the Aegiridae are examined based upon morphological characters of all presently described species and eight new species. The Aegiridae are a monophyletic clade of phanerobranch dorids, a paraphyletic group previously united by the absence of a retractable dorsal gill, which is a pleisomorphic character. There are three traditionally recognized genera within the Aegiridae, *Aegires* Loven, 1844, *Notodoris* Bergh, 1875 and *Triopella* Sars, 1878. Most species of each genus were examined anatomically and some previously undescribed characters were included in the analysis such as details of the central nervous system. Published literature descriptions were utilized in cases where no specimens were available for examination. From the literature review and anatomical examinations, sixty-four characters were considered. These characters were polarized using *Bathydoris* and the type species of several phanerobranch genera. Additionally, four cryptobranch dorids were included in the analysis for comparative purposes. The phylogeny obtained supports both the monophyly of Aegiridae and that *Notodoris* is a monophyletic clade nested within *Aegires*. *Triopella incisa*, the type species of a monotypic genus, is nested within *Aegires* and is the sister species of *Aegires sublaevis*. This phylogeny necessitates inclusion of *Notodoris* and *Triopella* as junior synonyms of *Aegires* to preserve the monophyly of *Aegires*. This also renders *Aegires citrinus* Pruvot-Fol, 1930 as a junior homonym of *Aegires citrinus* (Bergh, 1875). The new name *Aegires pruvotfolae* is given to this former species. The following are new species of *Aegires*: *A. execches* sp. nov., *A. flores* sp. nov., *A. hapsis* sp. nov., *A. incusus* sp. nov., *A. lemoncello* sp. nov., *A. malinus* sp. nov., *A. ninguis* sp. nov. and *A. petalis* sp. nov. All these new taxa are found in the Indo-Pacific except *A. ninguis*, which is found in temperate South Africa. Unique combinations of morphological characters distinguish these as new species of *Aegires*.**

**The present phylogeny supports the notion that the Phanerobranchia represents a paraphyletic group. The Suctoria are the sister group to the Cryptobranchia. Aegiridae is the sister group to Cryptobranchia plus Suctoria. Polyceratidae is the sister group to Cryptobranchia plus Suctoria plus *Aegires*. *Hexabranchus* is basally situated to all of these other taxa but is more derived than *Bathydoris*.**

Aegiridae Fischer (1883) is one of the families of the traditional group Phanerobranchia (Fischer 1880–1887). The classification of the family Aegiridae (= Notodorididae Eliot, 1910) has an interesting, although convoluted history and is presented in detail below and summarized in

Table 1 (see Appendix). According to the most recently published classification of the Aegiretidae [*sic*] (Rudman and Willan 1998) there are only two recognized genera within the group: *Aegires* Lovén, 1844 and *Notodoris* Bergh, 1875. However, *Triopella* Sars, 1878 is also a genus that has been overlooked by most researchers.

The primary character that unites all Phanerobranchia, including Aegiridae, is the presence of a non-retractable dorsal gill. As a result of having an unprotected gill, these animals have developed protective appendages for the gill leaves. This adaptation provides some important information for phylogenetic analyses, which is discussed in detail in a later section. Thompson (1976) described the protective appendage in his characterization of the Superfamily Anadoridoidea (Odhner's [1939]), Suborder Anadoridacea. Fischer et al. (1968) were the first to equate Anadoridacea with the Phanerobranchia Fischer, 1883. The Phanerobranchia are now thought to be paraphyletic (Valdés 2002).

Historically, the Suborder Anadoidacea was divided into two tribes (Bergh 1890), the Suctoria and Non-suctoria. Aegiridae is one of the three currently recognized families within the tribe Non-suctoria along with Triophidae Odhner, 1941 and Polyceratidae Alder and Hancock, 1855 (amended from the original authors' spelling) (Rudman 1998). While these three families have a widely variable external anatomy there are also some similarities. These include the anus and the gill situated medio-dorsally, a well-developed radula usually lacking a rachidian tooth, the edge of the mantle more or less reduced, and a contractile gill that is not retractile. Some of the internal differences between the families include genital organs that may have small hooks on the vas deferens or be unarmed and either a smooth jaw or a jaw having rods (Fischer et al. 1968).

The characters that unite Aegiridae (as noted first by Thiele 1931, although he had called the Family Notodoridinae) include: "a hard body with calcareous spicules, gills that have a separate integumental fold, rhinophores that retract and in most cases, are not lamellate, radula without a rachidian tooth and all lateral teeth hook- or arch-shaped."

Several of the species of both *Aegires* and *Notodoris* were originally described in very abbreviated terms, or based on single specimens. Some entire organ systems were never described either initially or by subsequent workers. In the present study, specimens of each species were examined when available and when not available, all published literature was reviewed. Anatomical details are described for all known species of each genus, some of these details for the first time.

The present study provides an in-depth look at the Aegiridae and presents a phylogenetic analysis of the placement of this family within the Phanerobranch dorids (the Anadoridoidea). The name Phanerobranchia is the most widely used and recognized name, and it is used here instead of the synonymous Anadoridoidea.

Eight new species are described based on examination of material lodged at the California Academy of Sciences and the South African Museum.

## History of Aegiridae Classification

Lovén (1844) introduced the new genus *Aegires* without designating a family affiliation. For the type species of his new genus, he selected *Polycera punctilucens* (D'Orbigny 1836–1842).

Alder and Hancock (1845–1855) labeled the first Suborder in their classification of the Nudibranchia, Anthobranchia. In the early years of the monograph (1845) they placed *Aegires* within Family #1, Doridídae, (Sub-Family Polycerinae), along with *Thecacera, Polycera* and *Idalia.* Later, in 1855, they proposed to use a classification originally suggested by Gray, which now named Family #2 the Doridídae, and which now included *Aegires* with *Doris, Goniodoris* and *Ceratosoma.*

Bergh (1875) introduced the new genus *Notodoris* and drew some anatomical features of the type species *Notodoris citrina*. However, he did not designate a familial association.

Sars (1878) described and drew the type species for his new genus *Triopella* (*incisa*). He mentions the radular similarities between *Triopella* and *Aegirus* in the discussion of the new species.

Fischer (1880–1887) divided the Nudibranchia into 5 suborders: Anthobranchiata, Inferobranchiata, Polybranchiata, Pellibranchiata and Parasita. He further divided the Anthobranchiata into Aglossa and Glossophora. The Aglossa had one family, Doridopsidae, while the Glossophora were subdivided into three groups: the Cryptobranchiata (with one family, Doridiidae), the Phanerobranchiata (Family Polyceridae) and the Abranchiata (Family Heterodoridiidae). Fischer, noting that *Triopella* and *Aegires* (which, like Sars, he spelled *Aegirus*) were closely related, placed both these genera in the Phanerobranchiata (Family Polyceridae) with no mention of *Notodoris*. Fischer did acknowledge that his Polyceridae corresponded to Bergh's "Doris phanerobranchs", so although Fischer left out *Notodoris* he was evidently aware of Bergh's 1875 publication. Fischer further separated the Polyceridae into three sub-families, Acanthodoridinae, Polycerinae and Aegirinae.

Bergh (1890) acknowledged Fischer's group Phanerobranchiata when he placed his two newly described species, *Plocamopherus amboinensis* Bergh, 1890 and *Plocamopherus indicus* Bergh 1890 into the Subfamily Phanerobranchiata (Suborder Nudibranchiata Holohepatica, Family Doridiidae).

Two years later, when Bergh described the systematics of the Nudibranchia (1892:141) he placed *Aegires*, *Notodoris* and *Triopella* within the Polyceridae (Subfamily Doridiidae Phanerobranchiatae Non Suctoriae). He used the spelling *Aegires* not *Aegirus* as Fischer did in 1883. This may have been in recognition of the indexed generic names published in *Nomenclator Zoologicus* (Scudder 1882).

Eliot (1903) placed his newly described *Notodoris gardineri* within the Family Doridiidae Phanerobranchiatae (his spelling). He described the Phanerobranchiatae as those dorids that have no dorsal cavity into which the branchia can be retracted. Eliot acknowledged Bergh's (1875) division of the Phanerobranchiata into the Goniodoridiidae (which possesses a buccal gizzard) and Polyceradae (no gizzard), but stated that a more "natural" division would be Polyceradae (having limaciform bodies, sometimes bearing appendages) and Pseudodoridiidae (flat dorid-like forms). Eliot also noted in his study that *Notodoris* is closely related to *Aegires* and the little known *Triopella* because all three had a hard consistency and had branchiae and rhinophores protected by tubercles.

Eliot (1910:65) in *A Monograph of British Nudibranchiate Mollusca*, Part 8, went on to establish the Family Notodoridiidae for *Notodoris*, *Aegires*, and *Triopella*. He united these genera based upon their simple, hook-shaped teeth, branchial valves and smooth rhinophores. Eliot did not reference Fischer's 1883 family name Aegiridae at this time.

However, thirteen years later, in their classification, Iredale and O'Donoghue (1923) also used the family name Aegiretidae for *Aegires, Notodoris* and *Triopella* but without providing a diagnosis for this group. Apparently these authors were aware that Aegiretidae (Aegiridae) was an older name than Notodoridiidae.

In 1926, Odhner recognized that the Family Notodoridiidae = Aegiretidae, Iredale and O'Donoghue, incorrectly attributing the name Aegiretidae to these authors (and maintaining the incorrect spelling of the family name). Odhner provided two distinguishing characters for Notodoridiidae (Phanerobranchia): "Radular teeth hooked, uniform and tentacles small, inconspicuous".

Risbec (1928) provided a diagnosis for the Family Aegiridés [*sic*] using the genus *Aegirus*

Lovén 1844 as his model. In this document he also provided a lengthy description of *A. leuckartii* Verany, 1853 and synonymized *A. albopunctatus* MacFarland, 1905 with this species. This synonymy was later questioned by Schmekel and Portmann as will be discussed later in the present paper.

Pruvot-Fol (1930) placed a new species she described as *Aegires citrinus* into the Family Aegiretidae, with this particular spelling.

The following year, Thiele's classification (1931) placed *Aegires, Notodoris* and *Triopella* within the Subfamily Notodoridinae (Stirps Doridacea (= Holohepatica) Family Polyceridae). Thiele's diagnosis of the Notodoridinae follows: "Body hard, with calcareous spicules; gills with a separate integumental fold; rhinophores retractile, in most cases not lamellate; radula without central plate, all lateral plates hook- or arch-shaped."

Odhner (1934) established a new genus *Anaegires* with *A. protectus* as the type species. However, this new genus was based upon characters that were later found by Wägele (1987) to be within the realm of intraspecific variation. Wägele justifiably synonymized *A. protectus* with *A. albus* Thiele, 1912. Odhner also commented that Iredale and O'Donoghue (1923) should not have changed the family name to Aegiretidae without justification. Odhner stated that *Notodoris* may be kept as the type genus of the Family and thus Eliot's family name Notodorididae is valid. He completely overlooked the fact that the name Aegiretidae (Aegiridae) was used twenty-seven years prior to Notodorididae.

Pruvot-Fol (1954) placed *Aegires* in Aegiretidae noting that Thiele (1931) erroneously called the subgroup Notodorididae when he grouped *Notodoris* and *Aegires* in the family Polyceradae. Pruvot-Fol correctly pointed out that *Aegires* Lovén, 1844 is an older name than *Notodoris* Bergh, 1875. In this paper, Pruvot-Fol also synonymized *Aegires hispidus* (*Polycera hispida* Hesse, 1872) and *A. leuckartii* Verany, 1853 with *A. punctilucens* (*Polycera* d'Orbigny, 1837). However, she did not mention Risbec's previous (1928, 1953) synonymy of *A. hispidus* and *A. leuckartii* with *Aegires albopunctatus*.

In 1966, MacFarland classified the Notodoridinae (*sic*) as a subfamily of Polyceridae.

Fischer et al. (1968) placed Aegiretidae into the Anadoridacea Odhner (1968) in the tribe nonsuctoria (one of two tribes first identified by Bergh [1892]). Aegiretidae were considered Family #2 of the Anadoridacea (Family 1 = Triophidae Odhner *nov* and Family 3 = Polyceridae Alder and Hancock 1845). Fischer et al. wrongly attributed the name Notodorididae to Odhner, 1926, when in fact Eliot first established this group in 1910.

Nordsieck (1972) established a new genus *Serigea* naming *Aegires* (*Serigea*) *sublaevis* as the type species. He presented the following brief diagnosis of *Serigea*: "Features like *Aegires*, but without tubercles (papillae); rhinophore sheaths low, smooth. Only a few tubercles behind the rhinophores."

Notably, Nordsieck did not mention *Notodoris* in his manuscript on European marine molluscs when he grouped *Aegires*, *Triopella* and *Serigea* nov. gen. within the Family Aegiretidae Fischer, 1883. This is most likely because there are no known *Notodoris* species found in European marine habitats. He did pronounce as Pruvot-Fol did in 1954, that Aegiretidae = Notodorididae Odhner, 1926. Nordsieck thus continued the incorrect attribution of the name Notodorididae to Odhner, 1926 and the incorrect spelling of the family name.

Thompson (1976) changed the name Anadoridacea to Anadoridoidea, in which he included the Family Notodorididae. Thompson listed only *Notodoris* and *Aegires* as the genera in this family. He did not cite the authors of any family names. (see Valdés 2002 for a discussion of the Family name Anadoridacea).

Schmekel and Portmann (1982) used Thompson's name Anadoridoidea but erroneously attrib-

uted the name to Odhner (1959); a non-existent publication that was also omitted in their literature cited.

Gosliner and Behrens (1997) incorrectly attributed the name Notodorididae to Bergh (1897) in their description of the new *Notodoris serenae*. Bergh never used this name to categorize the new genus *Notodoris*. It wasn't until Eliot (1910) wrote the text for Part 8 of Alder and Hancock's monograph of the British nudibranchiate molluscs that this name was first used.

In the most recently published classification of Aegiretidae, Rudman (1998) placed *Aegires* and *Notodoris* in the Family Aegiretidae, Superfamily Anadoridoidea, suborder Doridina. *Triopella* was once again left out of the family and the incorrect spelling of the family name was continued. The correct spelling, Aegiridae is discussed in detail by Willan (2000). Table 1 (see Appendix) summarizes the historical classification of Aegiredae.

## Material and Methods

Twenty-two species of Aegiridae were included in the analysis. This includes all known species of the recognized genera, *Aegires*, *Notodoris* and *Triopella* as well as eight additional, previously unidentified species of *Aegires*. In some cases, the complete published description of certain features of a species allowed the extraction of data from the literature, which was then verified by direct examination of a specimen when available. Type material and additional non-type material was obtained from the following sources: the California Academy of Sciences (CAS), the Los Angeles County Natural History Museum (LACM), the Natural History Museum of Norway, Oslo (D), the South African Museum (A) and the Museo National de Ciencias Naturales Madrid (MNCN). Specimens were drawn under a dissecting microscope using a camera lucida then dissected by dorsal incision. The internal anatomy was drawn as described and then examined either by compound or scanning electron microscope (SEM). External features were examined directly when specimens were available, by photographs, or by literature review. Special attention was given to the reproductive anatomy, the central nervous system and the circulatory system, as some of these features were infrequently (or cursorily) described in the literature. Dorsal tubercles of available specimens were drawn and examined by SEM. Table 2 (see Appendix) shows the list of character states derived from dissections and from the literature reviewed for the present study. Ten additional species were selected for outgroup comparison as discussed below.

### Phylogenetic analytical methods

Phylogenetic analyses were performed using the program Phylogenetic Analysis Using Parsimony (PAUP) version 4.0 (Swofford 2001) using the heuristic algorithm (TBR branch swapping option). One hundred random start trees were obtained by stepwise addition. Bremer analyses were performed to estimate branch support (Bremer 1994). Characters were unordered and were polarized using *Bathydoris abyssorum* Bergh, 1884 as the outgroup. This type species was selected based on the analysis of the cryptobranch dorids by Valdés (2002), which showed that *Bathydoris* is sister to the dorids. Additionally, Wägele (1989a) and Wägele and Willan (2000) demonstrated that *Bathydoris* is the most basal member of the Anthobranchia and is the sister group to the rest of the dorid nudibranchs. *Polycera quadrilineata* (Müller 1776), *Okenia elegans* (Leuckart, 1828), *Onchidoris bilamellata* (Linnaeus, 1767), *Holoplocamus papposus* Odhner, 1926, *Diaphorodoris luteocinta* (Sars, 1870) and *Calycidoris guentheri* Abraham, 1876 were also tested as outgroup taxa in the analyses. These five additional genera are phanerobranchs and basally situated relative to the rest of the dorids. Four cryptobranch dorids were included in the analysis for comparative purposes. The genera were chosen from the most recent analysis of the crypto-

branch dorids (Valdés, 2002) and are the type species and represent the most basal taxa of their particular clade. Those genera are *Actinocyclus* Ehrenberg, 1831; *Conualevia* Collier and Farmer, 1964; *Hexabranchus* Ehrenberg, 1831 and *Mandelia* Valdés and Gosliner, 1999, which has been included in the Cryptobranchia in the most recent classification of the Doridina (Rudman 1998). The source of the information on the outgroup species included in the present analysis is shown in Table 3 (see Appendix). Synapomorphies were examined using MacClade and the character-trace option, using the majority rule tree from PAUP analyses.

## Species Descriptions

### Family Aegiridae Fischer, 1883

#### Genus *Aegires* Lovén, 1844

Type species: *Polycera punctilucens* d'Orbigny, 1837, by monotypy.
Type species: *Aegires albus* Thiele, 1912, by original designation.

Synonyms of *Aegires*: *Anaegires* Odhner, 1934:241, type species *Anaegires albus* Odhner, 1934 by monotypy; *Notodoris* Bergh, 1875:64, type species *Notodoris citrina* Bergh, 1875 by monotypy, syn. nov.; *Serigea* Nordsieck, 1972, type species *Serigea sublaevis* Nordsieck, 1972 by subsequent designation; *Triopella* Sars, 1878:310, type species *Triopella incisa* Sars, 1878 by monotypy, syn. nov.

**Diagnosis.—** Diagnoses of this genus have been provided by multiple authors: Lovén (1844), Schmekel and Portmann (1982), and Thompson and Brown (1984). A summary of these authors' diagnoses follows: The body is firm, with a reduced, indistinct mantle skirt. The dorsum is covered with numerous blunt, pedunculate dorsal tubercles. The rhinophores extend from cylindrical pallial sheaths that have tubercles around the rims. The gill is protected by tuberculate lobes. A median dorsal cuticular plate or jaw is present in the buccal mass. The radular teeth are simple, hamate and not bifid.

#### *Aegires albopunctatus* MacFarland, 1905

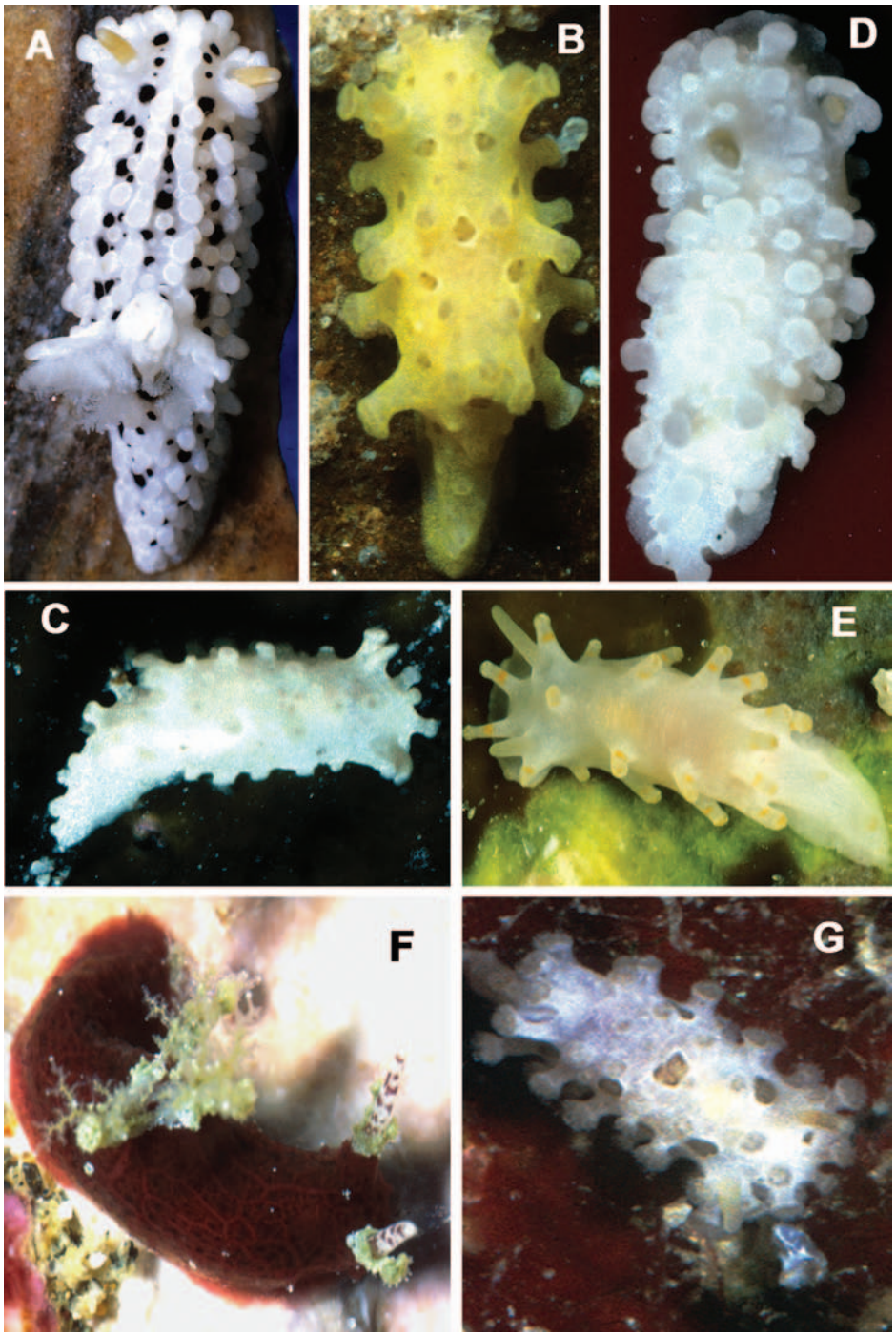
(Figs. 1A, 2–6)

*Aegires albopunctatus* MacFarland, 1905:35-54, pl. 18, Figs 5-8.

**Type material.**— Syntype: Monterey Bay, California, No. 181,281. U.S. National Museum.

**Material examined.**— LACM 127330, one specimen, 18 mm, dissected, Rio San Ysidro, Baja California, collected 28 June 1946, C. Johnson. LACM 71-36, one specimen, 18 mm, dissected, Point Dume, Southern California, collected 8 February 1971, G. Sphon. LACM 90-2.3, one specimen, 7 mm, dissected, Cabo Colnett, Baja California, collected 10 February 1990, collector not specified. CASIZ 118550, one specimen, 20 mm, dissected, Pacific Coast, Baja California North, collected 3 February 1963, W. Farmer. CASIZ 068347, nineteen specimens, one specimen, 20 mm dissected, Corona del Mar, Southern California, collected 4 May 1946, F. MacFarland. CASIZ 068349, five specimens, one specimen, 20 mm, dissected, Cannery Row, Monterey Bay, California, collected 28 September 1968, A. Smith.

Figure 1. Living animals. (A) *Aegires albopunctatus* MacFarland, 1905. CASIZ 118550, photo by A. Ferreira, Monterey Bay, California, 19 mm. (B) *Aegires pruvotfolae* nom. nov. CASIZ 097449, photo by T. Gosliner, Napili Bay, Maui, Hawaii, 6 mm. (C) *Aegires gomezi* Ortea, Luque and Templado, 1990. CASIZ 077315, photo by T. Gosliner, Grand Cayman Island, 5 mm. (D) *Aegires ninguis*.sp. nov. CASIZ 073982, photo by T. Gosliner, Cape Province, South Africa, 8 mm. (E) *Aegires lemoncello* sp. nov. CASIZ 086465, photo by T. Gosliner, Pig Island, Papua New Guinea, 4 mm. (F) *Aegires malinus* sp. nov. CASIZ 085889, photo by T. Gosliner, Bebbit, Philippines, 8 mm. (G) *Aegires incusus* sp. nov. CASIZ 156668, photo by T. Gosliner, Cemetary Beach, Luzon, Philippines, 5 mm.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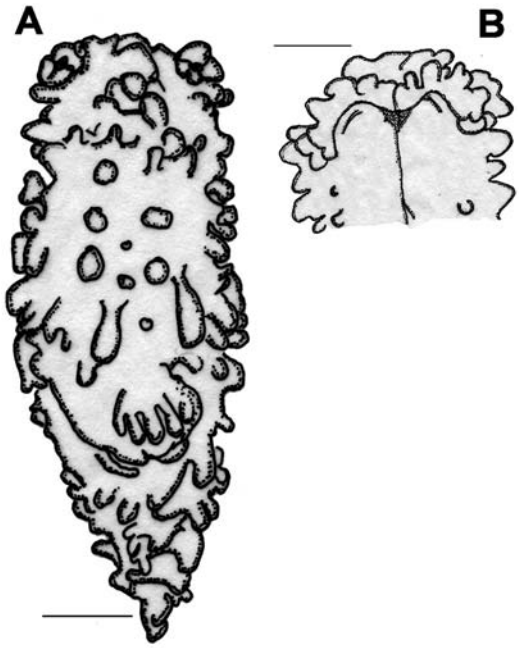



FIGURE 2. *Aegires albopunctatus* MacFarland, 1905. CASIZ 118550. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view of head. Scale = 7 mm.

**DISTRIBUTION.**— West coast of North America from British Columbia to Baja California ([Behrens 1991] Rudman, SeaSlug Forum, accessed Sept. 2004).

**EXTERNAL MORPHOLOGY.**— MacFarland (1905, 1906, 1966) gave thorough descriptions of the external morphology of this species. The specimens examined for the present study matched his descriptions and thus there is no additional information to present. See Fig. 1A for a photo of a living animal from the type locality and Fig. 2 for a drawing of a preserved specimen from Baja California.

**DIGESTIVE SYSTEM.**— *Aegires albopunctatus* shares the same general digestive anatomy as other *Aegires* species (Fig. 3). The buccal bulb is nearly round, with four large muscles attached; two per side. The buccal bulb is shorter and more round than the oral tube (Fig. 3A). There are two glands at the side of the oral tube, near the mouth (Fig. 3B). The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is

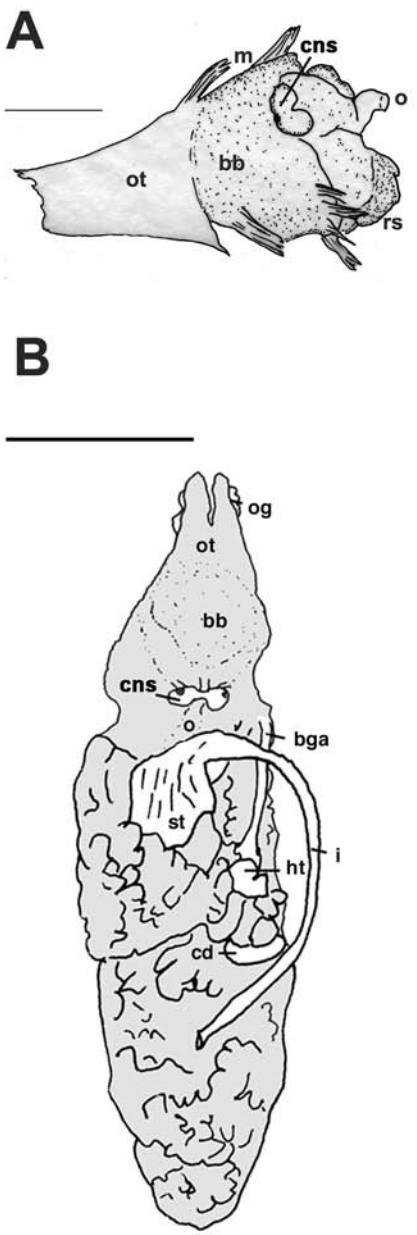



FIGURE 3. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. (A) Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, o = esophagus, rs = radular sac, scale = 0.3 mm. (B) Digestive system: bb = buccal bulb, bga = blood gland artery, cd = collecting ducts, cns = central nervous system, ht = heart, i = intestine, o = esophagus, og = oral gland, ot = oral tube, st = stomach, scale = 3 mm.

lined with a thick cuticle. There is a thick plate at the top of the opening, with thick rods at the edge (Fig. 4A). The radular formula (CASIZ 118550) is 19 × 21.0.21, with all teeth as described by MacFarland. That is, they are simple, hooked and similar in form (Figs. 4B–D). The esophagus is short and connects directly to the stomach (Fig. 6). The intestine makes a simple, wide curve along the outside of the digestive gland.

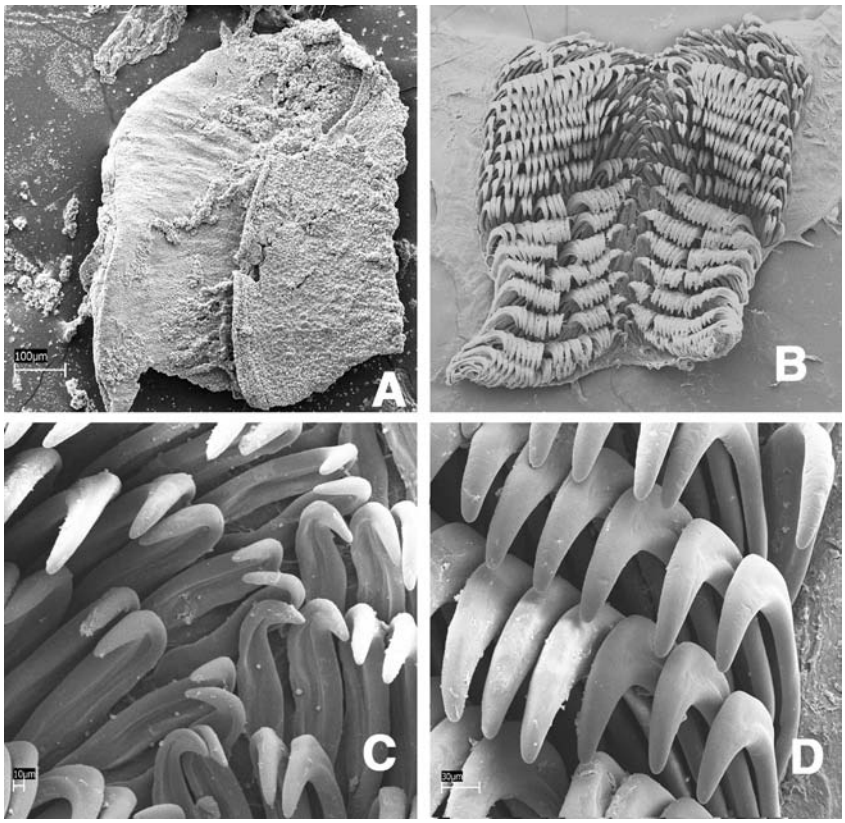



FIGURE 4. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Buccal morphology. (A) Jaw, scale =100 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 30 µm.

**REPRODUCTIVE SYSTEM.**— The ampulla is large and ovoid (Fig. 5). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is differentiated into two parts, the proximal portion being a flattened mass and the distal portion being a long thickened tube. The distal portion folds once after exiting the flattened mass and narrows into the coiled deferent duct. The penis is wider than the deferent duct and terminates into a common genital atrium. The penis contains minute, closely set penial hooks throughout the length of the penis. The vaginal duct is short and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed.

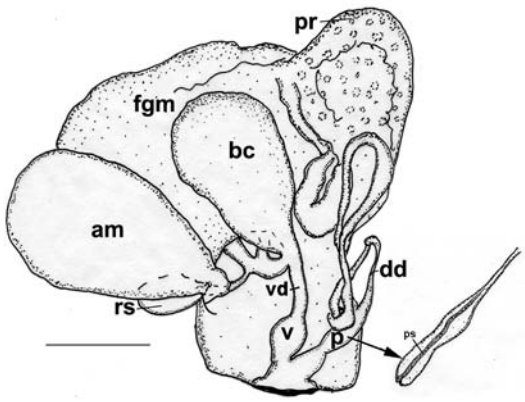



FIGURE 5. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 1 mm.

At the distal end, the vagina is wide and bulbous. The proximal end terminates into the large ovoid bursa copulatrix. From the bursa the oviduct connects to the smaller pyriform receptaculum seminis. A very short uterine duct leads from the receptaculum seminis into the female gland mass.

**Central nervous system.**— As with other species of *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 6). The two pedal ganglia are located below the cerebro-pleural complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

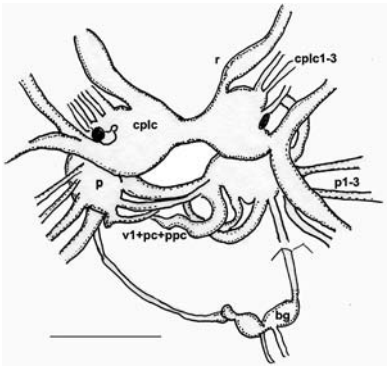



Figure 6. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

**Remarks.—** MacFarland (1905, 1906, 1966) presented thorough external and radular descriptions of this northeastern Pacific species. Anatomical information for the present study has been taken from his paper and corroborated by examining specimens from the type locality and the southern California coast. Ernst Marcus (1961) also published additional anatomical details of this species. However, some characters that were necessary for the present study such as the circulatory, central nervous or digestive systems were not described. Therefore, additional specimens were examined to complete the data.

Risbec (1928) synonymized *A. albopunctatus* MacFarland, 1905 with *A. leuckartii* Verany, 1853 in his lengthy description of *A. leuckartii*. Marcus (1961) noted some external similarity between *A. albopunctatus* and *A. punctilucens* stating that *A. albopunctatus* "agrees with the type species *A. punctilucens*" based upon the papillae on the mantle border of both species.

No other subsequent publications referring to *A. punctilucens* or *A. leuckartii* recognized the synonymy of either species with *A. albopunctatus* (Pruvot-Fol 1954; Fischer et al. 1968; Nordsieck 1972; Schmekel and Portmann 1982; Thompson and Brown 1984). However, Haefelfinger (1968) did synonymize *A. leuckartii* with *A. punctilucens* based upon characters that he thought lie within natural variation. But subsequently, Schmekel and Portmann (1982) separated *A. punctilucens* and *A. leuckartii* as subspecies, distinguishable by their ecology and reproductive cycles. Further remarks on this synonymy are presented under the sections discussing these two species.

The present study confirms that *Aegires albopunctatus* is a valid species with the following characters distinguishing it from *Aegires punctilucens*:

1. External color. *Aegires punctilucens* has very distinctly colored spots on the dorsum. These spots have been described by various authors (Thompson and Brown 1984) as resembling an ocellus: that is, dark brown oval areas containing an iridescent blue-green spot, with or without additional dark spots on the periphery of the ocellated markings. In contrast, MacFarland's description of *A. albopunctatus* is very clear in that the dorsum only has minute dots of pure white, with or without irregularly scattered small dark brown spots. No ocellus spots are noted on any of his specimens.

2. Dorsal tubercle arrangement. *Aegires albopunctatus* has very densely placed tubercles, closely set in rows and continuing behind the rhinophores as a tuberculate ridge that diminishes in prominence

(MacFarland 1905). *Aegires punctilucens* has more widely scattered, larger tubercles that continue as a tuberculate ridge in a crest along the middle of the back (Schmekel and Portmann 1982).

3. REPRODUCTIVE CHARACTERS. *Aegires albopunctatus* has two ducts emerging from the base of the bursa copulatrix, while *A. punctilucens* has only one. The receptaculum seminis duct emerges from the proximal end of the large, bulbous vagina. Additionally, the vagina of *A. albopunctatus* is much more elongate than that of *A. punctilucens*.

4. RADULAR FORMULA. Schmekel and Portmann (1982) reported a radular formula of 16 × 18.0.18 for a 6 mm specimen of *A. punctilucens* with the size of the teeth increasing outwards. Thompson's (1984) 12 mm specimen of *A. punctilucens* from the Isle of Man had a radular formula of 23 × 22.0.22 with the teeth from the midline having a hooked tip, but the teeth from the margins were reported as more smoothly hooked. These reports on the radular formulae differ from MacFarland's reported formula for a 13 mm specimen of *A. albopunctatus* of 16–22 × 17.0.17 with the innermost and outermost teeth being similar in size but smaller than the middle lateral teeth. (See also Fig. 4).

### *Aegires albus* Thiele, 1912

*Aegires albus* Thiele, 1912:222.
*Anaegires protectus* Odhner, 1934:242.
*Aegires protectus* (Odhner) Wägele, 1987:271.

**TYPE MATERIAL**.— HOLOTYPE: No. 63230 (*A. albus*), McMurdo Sound, Antarctica. Zoologisches Museum zu Berlin; Other material: No. 846 (*A. albus*) Naturhistoriska Riksmuseet, Stockholm; HOLOTYPE: No. 1934.10.5.67 (*A. protectus*), British Museum of Natural History, London.

**MATERIAL EXAMINED**.— *Aegires albus* from the Muséum National d'Histoire Naturelle, Paris: Kerguelen Islands, 1 specimen, collected at 15 m, 16 January 1963, no further collection data provided; MD04 G65 DC 155, 1 specimen, no further collection data provided; SMK, 10 specimens, 15–144 m, collected 1972 and 1974 by Guille et al.

**DISTRIBUTION**.— This species has only been recorded from the Antarctic Peninsula, the Ross Sea and the Weddell Sea (Wägele 1987).

**REMARKS**.— *Aegires protectus* is the type species of *Anaegires* Odhner, 1934. *Anaegires* is a synonym of *Aegires* (see Odhner 1934). Wägele (1987) presented a thorough description of *Aegires albus,* with both external and internal anatomy. She demonstrated that *Aegires protectus* is a synonym of this species. Anatomical information has been taken from this publication and from the specimens noted above for use in the present study. Examination of the reproductive system of specimens listed above confirmed the presence of densely placed penial spines extending the length of the penial bulb as reported by Wägele (1987).

### *Aegires pruvotfolae* Fahey and Gosliner, nom. nov.

(Figs. 1B, 7–11)

*Aegires citrinus* Pruvot-Fol, 1930:229-232, junior homonym of *Aegires citrinus* (Bergh, 1875). (See the discussion of *Aegires citrinus*).

**TYPE MATERIAL**.— Collected in New Caledonia, date and collector not specified. NEOTYPE here designated, CASIZ 157477, one specimen, 6 mm, Layag Layag, Caban Island, Philippines, collected T. Gosliner.

**MATERIAL EXAMINED**.— CASIZ 097449, one specimen, 6 mm, dissected, Napili Point, Maui, Hawaii, no depth available, collected 9 April 1994, T. Gosliner. CASIZ 087056, one specimen, 10 mm, Keahou Beach, Hawaii, no depth available, collected 3 September 1973, T. Gosliner. CASIZ

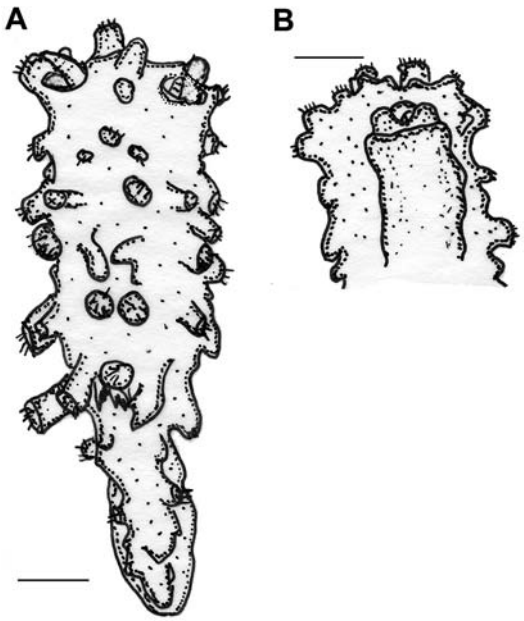



FIGURE 7. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view of head. Scale = 0.4 mm.

087058, three specimens, no depth available, collected 19 February 1986, T. Gosliner. CASIZ 070326, one specimen, 3 mm, dissected, Nosy Tanikely, Madagascar, 1 m depth, collected 14 April 1989, T. Gosliner. CASIZ 088363, one specimen, 8 mm, dissected, Midway Island, Pacific Ocean, 10 m, collected 29 May 1993, T. Gosliner. CASIZ 099286, one specimen, 6 mm, Manahuanja Island, Tanzania, collected 1 Nov 1994, T. Gosliner.

**DISTRIBUTION.**— This species has been recorded from eastern Australia, New Caledonia, the Philippines, Hawaii, Palau, Midway Atoll, Tanzania and Madagascar (Rudman 2004 and present study).

**EXTERNAL MORPHOLOGY.**— The body shape is high and arched (Figs. 1B, 7). The dorsum has tall, anvil-shaped tubercles with flat tops. Spicules protrude from the tops of all tubercles. The rhinophore pocket is elevated and has one tall tubercle on the outside perimeter. There are two prominent tubercles on the head. The posterior end of the foot has low

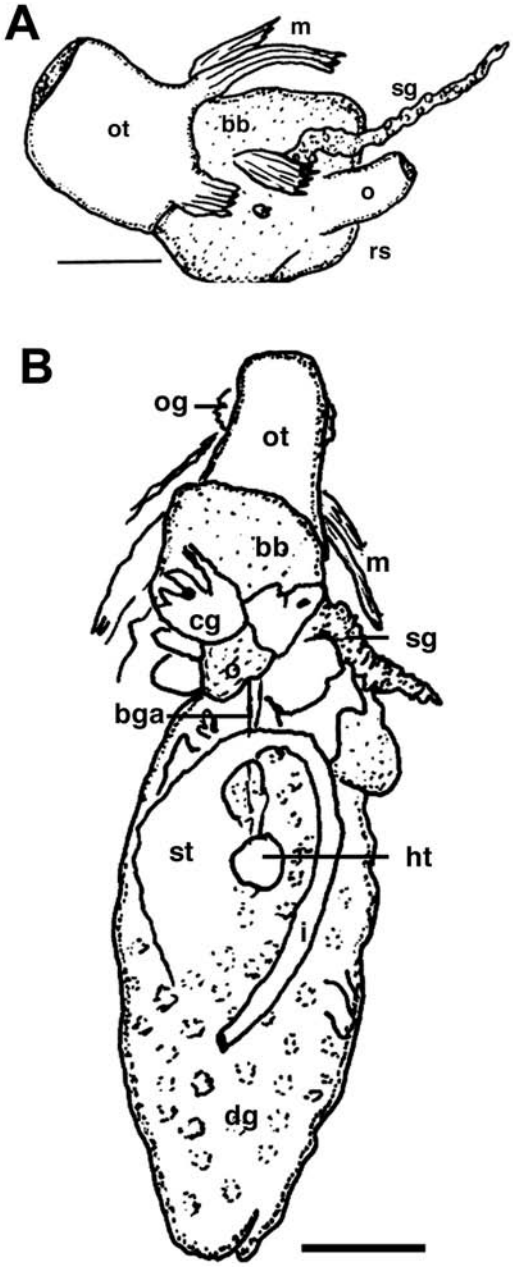



FIGURE 8. *Aegires pruvotfolae* nom. nov. CASIZ 097449. (A) Buccal bulb: bb = buccal bulb, m = muscle, o = esophagus, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.25 mm. (B) Digestive system: bb = buccal bulb, bga = blood gland artery, cg = cerebral ganglia, cns = central nervous system; ht = heart, i = intestine, m = muscle, og = oral gland, ot = oral tube, sg = salivary gland, st = stomach, scale = 0.25 mm.

tubercles that are much smaller than those on the dorsum. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and three large anvil-shaped tubercles protect the anterior side of the gill pocket. The three small gill leaves are tripinnate.

The background color is pale to medium yellow. The tubercles are the same color, as are the rhinophores. There are light brown to tan spots that vary in size along the dorsum median, between the tubercles.

**Digestive system.**— *Aegires pruvotfolae* shares the same general digestive anatomy as other *Aegires* species. That is, there are two glands at the side of the oral tube, near the mouth (Fig. 8). The buccal bulb is nearly round, with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with thick rods at the edge (Fig. 9A). The radular formula is 16 × 11.0.11. The teeth are simply hamate and the three innermost lateral teeth are smaller than the remaining teeth (Figs. 9B–D). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

**Reproductive system.**— The ampulla is relatively small and compact. It branches into a short oviduct and the prostate (Fig. 10). The oviduct enters the female gland mass near its center.

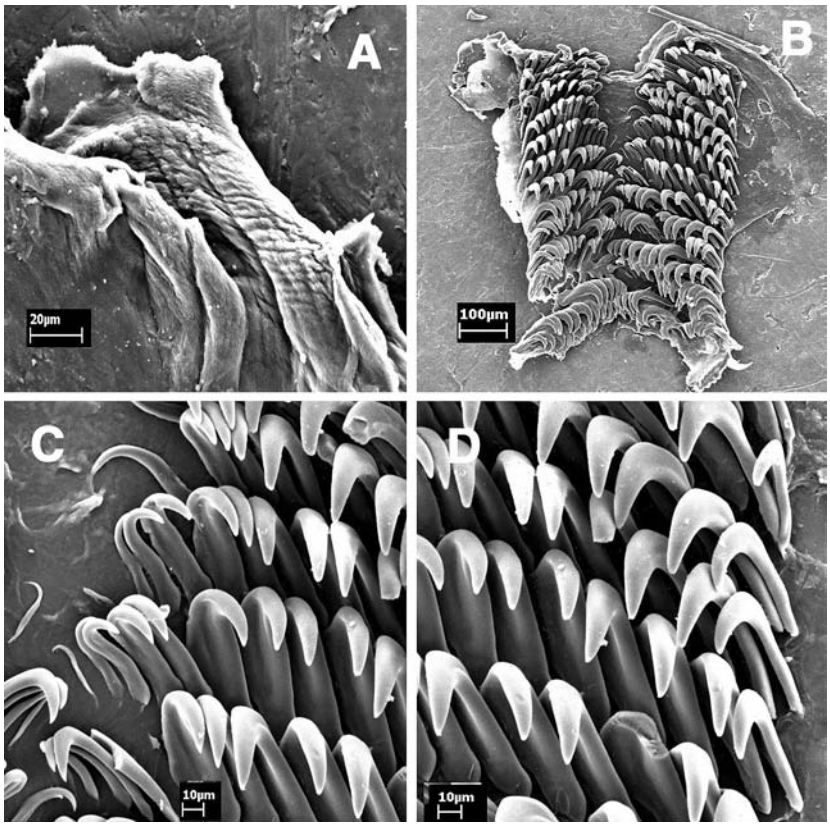



Figure 9. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Buccal morphology: (A) Jaw, scale = 20 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

The prostate is very long, tubular and coiled. It narrows slightly then connects to a wide ejaculatory duct and terminates at the wide penis. There are densely spaced, small hooks inside the penis at the distal tip only. The vagina is short and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end the vaginal duct joins the bursa copulatrix and the seminal receptacle. The uterine duct also leads from this duct. The bursa is spherical and the receptaculum seminis is about the same size though elongated.

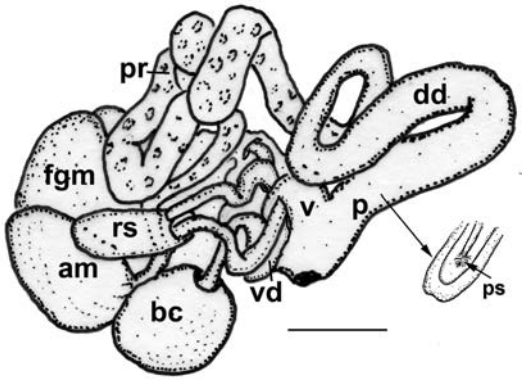



FIGURE 10. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.2 mm.

**CIRCULATORY SYSTEM.—** The heart (Fig. 8) is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**CENTRAL NERVOUS SYSTEM.—** As with other species of *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 11). The two pedal ganglia are located below the cerebro-pleural complex and are joined by pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

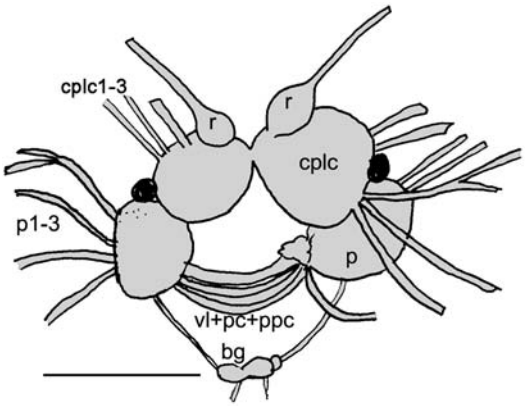



FIGURE 11. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.2 mm.

**REMARKS.—** Pruvot-Fol (1930) presented a very abbreviated description of *Aegires citrinus* collected from New Caledonia. The only information she provided on this new species was that the color was lemon yellow and the specimen had pointed tubercles with light brown color at the tops. Pruvot-Fol wrote that *A. citrinus* resembled *Aegires leuckartii* Verany, 1853 and may be a variant of the latter. We discuss this species in the comparison section below.

Risbec (1953) briefly mentioned Pruvot-Fol's abbreviated description of *A. citrinus*. He thought that since no precise detailed description had been published, *A. citrinus* was probably a variation of *A. leuckartii* (see discussion below).

Rudman (2004) provided additional external morphological information from photographs taken of this species.

For the present study, specimens from the Indian Ocean, Hawaii and Midway Island, Pacific Ocean were examined. This study has revealed that *A. pruvotfolae* is a valid species having sever-

al characteristics that differ from the other *Aegires* species. Those characters are:

1. External coloration. *Aegires pruvotfolae* is similar in coloration to *A. incusus* (present study). That is, both species can have a pale yellow background color and light brown to tan dorsal spots. However, the tubercle color of *A pruvotfolae* is also yellow with tan apices, whereas *A. incusus* has brown to tan tubercles with a darker top. The rhinophores of *A. pruvotfolae* have a tan top whereas those of *A. incusus* do not.
2. Tubercle spicules. The spicules that project from the tops of the tubercles of *A. pruvotfolae* are low and less conspicuous than those of *A. incusus*.
3. Tubercle arrangement. There are two prominent flat-topped tubercles on the head of specimens of *A pruvotfolae*. On *A. incusus*, there are multiple tubercles on the head. The dorsal tubercles of *A pruvotfolae* are less numerous than on specimens of *A. incusus*.
4. Radular characters. *Aegires pruvotfolae* has one small, thin inner lateral tooth that has a very small hook; the next 3–4 inner lateral teeth are smaller than the remainder. All other lateral teeth are the same size. In *A. incusus*, there is also one small inner lateral tooth but it has a distinct hook. The next 2–3 teeth are smaller than the remaining teeth, which are all the same size. In addition, the radular sac does not protrude from the buccal bulb in *A. citrinus* as it does in *A. incusus*.
5. Reproductive characters. *Aegires pruvotfolae* has reproductive characters that distinguish it from the most similar *Aegires* species. Most noticeably, the vagina is very wide as compared to *A. incusus*. In addition, the bursa copulatrix of *A. pruvotfolae* is as large as the ampulla, whereas in *A. incusus* the bursa is comparatively much smaller. The prostate of *A. pruvotfolae* is very long and coiled and does not narrow appreciably before entering the deferent duct. In *A. incusus* the prostate is not nearly as long and it does narrow noticeably before entering the deferent duct.

*Aegires pruvotfolae* also bears some external resemblance to early descriptions of *A. leuckartii*. For example, Schmekel and Portmann (1982) reported both white and brown specimens of *A. leuckartii*. They found that the brown specimens had "somewhat symmetrically arranged, smooth, brown areas, which were not circular". These spots are similar to those found on *A. pruvotfolae*. Risbec (1953) also considered *Aegires pruvotfolae* (formerly *Aegires citrinus*) a probable variation of *A. leuckartii.* However, there are external and internal differences that separate these two species:

1. The foot, veil and oral tentacles of *A. leuckartii* are bluish-white while in *A. pruvotfolae* the entire body, both dorsal and ventral surfaces are pale to muddy yellow. *Aegires pruvotfolae* has yellow rhinophores while the rhinophores of *A. leuckartii* have brown tips and 3 white circles (see Vérany 1853).
2. The dorsal tubercle arrangement differs between these two species. *Aegires leuckartii* has 4 large tubercles on the rhinophore sheath, whereas on *A. pruvotfolae* there are only 3.
3. The dorsal tubercle shape also differs between these two. *Aegires leuckartii* has cylindrical or rounded tubercles while the tubercles of *A. pruvotfolae* are anvil or mushroom-shaped.
4. There is also a difference in the radular morphology between these two species. Schmekel and Portmann reported that the teeth of *A. leuckartii* are all of similar size, whereas in *A. pruvotfolae* the innermost radular tooth is the smallest, then there are 3–4 small teeth and the remainder are all the same size.
5. Vérany did not describe the reproductive morphology of *A. leuckartii* but Schmekel and Portmann (1982) considered that the reproductive anatomy of *A. leukartii* was essentially as found with *A. punctilucens*. As such, there are differences between the reproductive morphology of *A. punctilucens* and *A. pruvotfolae*. We describe the morphology of *A. pruvotfolae* in an earlier section. But to summarize the differences, the prostate in *A. punctilucens* is rounded and in two parts. In *A. pruvotfolae* the prostate is very long, tubular and coiled. The vaginal duct in *A. punctilucens* is very short whereas in *A. pruvotfolae* it is very long. The receptaculum seminis of *A. punctilucens* connects to the uterine duct on a short duct. But in *A. pruvotfolae* this duct is very long and coiled.

The differences in external and internal morphology between *A. leuckartii*, *A. punctilucens, A. pruvotfolae* and *A. incusus* distinguish these four as separate *Aegires* species.

### *Aegires gomezi* Ortea, Luque, and Templado, 1990

(Figs. 1C, 12C–D, 13–15)

*Aegires gomezi* Ortea, Luque, and Templado, 1990:333, Figs 1–2.

**Type material.**— Holotype: 15.05/1034, La Habana, Cuba, Museo Nacional de Ciencias Naturales of Madrid.

**Material examined.**— Holotype: MNCN 15.05/1034, one specimen, 2 mm, La Habana, Cuba, collected July 1988, D. Moreno. CASIZ 077320, one specimen, 5 mm, dissected. Grand Cayman Island, no depth available, collected May 1991, T. Gosliner. CASIZ 077315, one specimen, 3 mm, South Sound, Cayman Islands, no depth available, collected May 1991, T. Gosliner. LACM 2003-41.1, one specimen, 5 mm, dissected. Key Largo, Florida, collected July 2003, A. Valdés.

**Distribution.**— This species was reported from La Habana, Cuba in the original description (Ortea, Luque, and Templado 1990) and from Florida and the Cayman Islands (this study).

**External morphology.**— The external morphology of the specimens collected in the Cayman Islands matches that of the original (1987) description of *A. gomezi*. The color photo of the Cayman specimens (Fig. 1C) matches the descriptions by Templado et al. (1987) and Ortea et al. (1990)

**Digestive system.**— The digestive system of the 5 mm specimen collected in Cayman Islands in 1991 was examined for the present study. The buccal bulb is nearly round, with the radular sac protruding noticeably from the posterior end. There are two long salivary glands extending from under the esophagus. As found in other species of *Aegires*, there are four main muscles attached at the midpoint of the buccal bulb (Fig. 13). The radular formula of this specimen is 18 × 12.0.12 (Fig. 14). The teeth are simply hamate as reported for the holotype. The jaw has numerous rodlets (Fig. 14D).

**Reproductive system.**— One of the specimens from the Cayman Islands was dissected for the present study. The reproductive system is triaulic. The ampulla is elongate. It branches into a short oviduct and the prostate (Fig. 15). The oviduct enters the female gland mass near an edge.

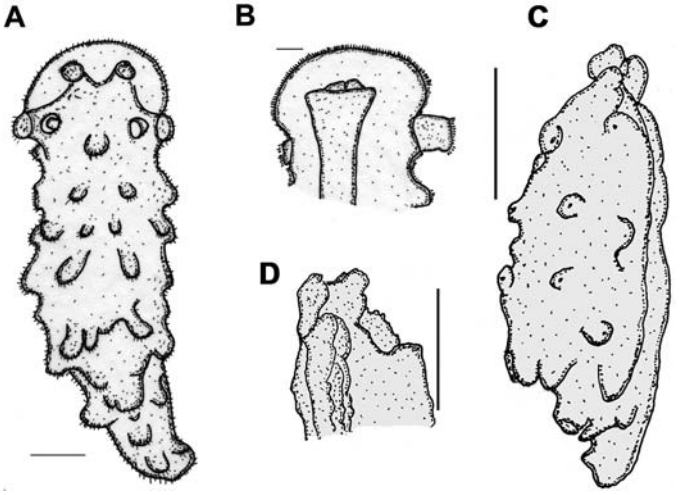



Figure 12. Drawings of preserved animals. *Aegires ortizi* Templado, Luque, and Ortea, 1987. MNCN12-64/1006. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm. (C) *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Dorsal view. (D) Ventral view of head. Scale = 0.7 mm.

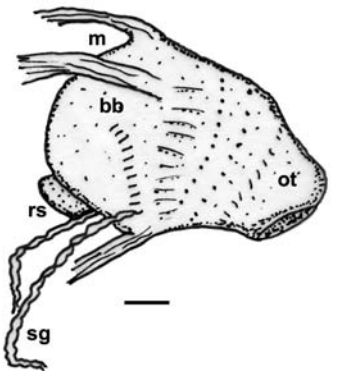



Figure 13. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Buccal bulb: bb = buccal bulb, m = muscle, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.13 mm.

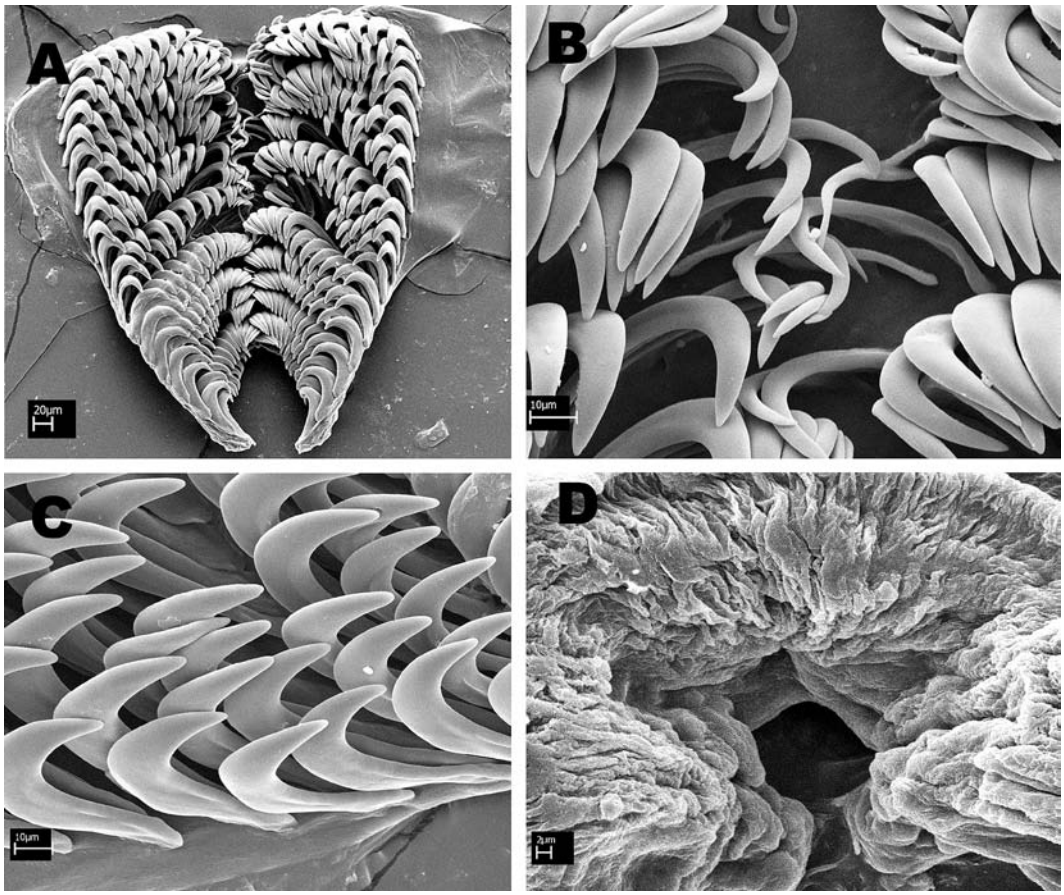
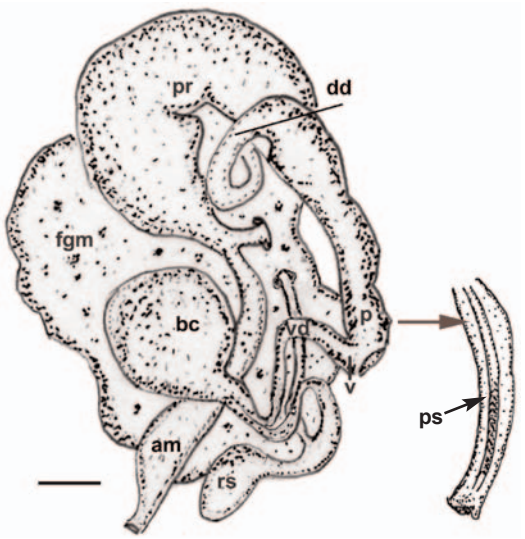



FIGURE 14. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Buccal morphology: (A) Whole radula, scale = 20 µm. (B) Inner lateral teeth, scale = 10 µm. (C) Outer lateral teeth, scale = 10 µm. (D) Jaw, scale = 2 µm.

FIGURE 15. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.08 mm.



The prostate is a thick, coiled tube. It narrows into a small, coiled tube, then connects to a very wide ejaculatory duct and terminates at the glans penis. There are densely packed, small hooks inside the penis extending the entire length of the penial bulb. The vagina is long and narrow. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end it joins the bursa copulatrix. A long separate duct joins the receptaculum seminis to the base of the bursa, and also connects to the female gland mass near the same edge as the oviduct. The bursa is large, spherical and the receptaculum seminis is about one-third the size of the bursa.

**Central nervous system.**— The central nervous system was not available for examination.

**Remarks.**— Ortea et al. (1990) described this species from a single specimen collected in 1988 from a tidepool in La Habana, Cuba. Their description included the external and radular morphology, but the reproductive, central nervous system and digestive systems were not described.

### *Aegires leuckartii* Verany, 1853

*Aegires leuckartii* Verany, 1853:388.
*Aegires leuckartii* (Verany) Bergh, 1883:135.
*Aegires leuckarti* (Verany) Vayssière 1901:55ff.
*Aegires leuckarti* (Verany) Risbec, 1953: 60.
*Aegires leuckarti* (Verany) Pruvot-Fol, 1954:245.
*Aegires leuckarti* (Verany) Haefelfinger, 1960c:355.
*Aegires leuckarti* (Verany) Schmekel, 1968b:116.
*Aegires punctilucens leuckarti,* Schmekel and Portmann, 1982:102.

**Type material.**— Verany described this species from a single specimen collected from Nice, France. Attempts to locate the type specimen were unsuccessful.

**External morphology.**— In the original description, the external morphology and coloration of *Aegires leuckartii* was the only information provided by Verany of the specimen collected. To summarize: The body shape of this species is wedge-shaped, with a straight or flat anterior and terminating in a pointed tail. There is no mantle edge and there is a large frontal veil with rounded lateral lobes. The rhinophore pocket is shaped like a large "horn" that is irregularly trilobed. The three gill leaves are very small, bipinnate and at the anterior and lateral edge of the gill pocket are large tubercles. These are conical and concave, larger along the median and smaller along the edge and scattered fairly regularly on the dorsum. The foot, the frontal veil, the oral tentacles are all bluish-white and the dorsum is yellowish-brown, light along the edges and darker in the center. There are brown spots on the dorsum. The tips of the rhinophores are brown with three white circles.

Verany chose the particular spelling of *leuckartii* for this new species. Subsequent authors, beginning with Vayssière (1901) dropped the last '*i*'. However, the *International Code of Zoological Nomenclature* allows for the Latinate spelling designated by the original author, thus *leuckartii* is correct.

As mentioned previously, Pruvot-Fol (1930) described a specimen of *A. pruvotfolae* from New Caledonia. Risbec thought her specimen was *A. leuckartii*, similar to a specimen he found in New Caledonia. Both these specimens are most likely *A. pruvotfolae*. See the comparison of these species under *A. pruvotfolae*.

**Distribution.**— This species is only found in the Mediterranean.

**Remarks.**— Schmekel and Portmann (1982) described *Aegires punctilucens leuckartii* from Nice, France. They reported external differences from Risbec's New Caledonian specimens that he collected and identified as *A. punctilucens*. (But, see the discussion under *A. pruvotfolae.*) The dor-

sal tubercles on the specimens from France were reported to be cylindrical and/or rounded, as described by MacFarland for *A. albopunctatus*, and not flat tubercles as reported by Risbec. Additionally, Schmekel and Portmann reported three tubercles arranged in a line in the mid-dorsal region, with three large tubercles on the outer edge of the rhinophore sheaths, and several smaller ones on the inner side. Risbec noted four large papillae on the rhinophore sheath.

There are some differences in external coloration between Schmekel and Portmann's specimens and Risbec's. Risbec does not mention the opaque white dots scattered on the dorsum that Schmekel and Portmann observed and also noted by MacFarland for *A. albopunctatus*. Both Risbec and Schmekel and Portmann report dark spots on the foot but MacFarland observed only white on the foot. The color of the rhinophores differs in that the specimens from France had a transverse brown ring, and the tips of the gill leaves were opaque white. Risbec reported only grayish rhinophores and translucent gill leaves and MacFarland reported lemon yellow rhinophores and gill leaves with spots.

The observations of the radular teeth of specimens from the Mediterranean indicate that all teeth were of similar size. The radular formula reported for a 6 mm specimen was 16 × 15.0.15 (Schmekel and Portmann 1982). Bergh (1883) reported a radular formula of 17 × 15–16.0.15–16 for an 8 mm specimen from Trieste.

Schmekel and Portmann's description of *Aegires punctilucens leuckartii* most nearly matches that of *A. albopunctatus* MacFarland, whereas Risbec's description of specimens collected from New Caledonia most nearly match that of *A. leuckartii* Verany.

Nordsieck (1972) listed *A. leuckartii* as a synonym of *A. punctilucens*, but without any justification. The specimens he described externally match *A. punctilucens*.

Regarding the status of *Aegires leuckartii*: without having the description of the reproductive morphology from original material, it would be confusing to synonymize this species with *A. punctilucens* (see Haefelfinger 1968). Descriptions of the background color of *A. leuckartii* are most similar to *A. albopunctatus*, not *A. punctilucens*. The body shape and tubercle arrangement of *A. punctilucens* as illustrated by d'Orbigny (1837) does not match the original description of *A. leuckartii* Verany. The radular formula of *A. leuckartii* noted by Risbec (1928) was 16 × 12.0.12 for a 6 mm specimen and Schmekel and Portmann (1982) reported the formula for an 8 mm specimen of *A. punctilucens leuckartii* as 16 × 15.0.15. Schmekel and Portmann also reported that the teeth increase in size outwards, as they found in *A. punctilucens*.

Schmekel and Portmann also noted the difference in the gill structure between *A. leuckartii* and *A. punctilucens*. The former has bipinnate gill leaves while the latter has a tripinnate structure. MacFarland described *A. albopunctatus* as having three small tripinnate gill leaves.

Schmekel and Portmann did not agree with Haefelfinger's synonymy and stated that the morphological and ecological differences they observed clearly distinguish *A. punctilucens* from *A. leuckartii*. On the same basis, examination of *A. albopunctatus* indicates that it too, should be considered distinct from these two as noted in the previous discussion of *A. albopunctatus* (present study).

Photo images of specimens collected from the Mediterranean and identified as *A. leuckartii* and *A.* cf. *leuckartii* are most likely *A. leuckartii* (Koehler 2004; Tocino 2004).

*Aegires palensis* Ortea, Luque and Templado, 1990 is a probable synonym of *A. leuckartii*. Ortea, Luque, and Templado did not compare their specimen to *A. leuckartii* because they considered *A. leuckartii* as a synonym of *A. punctilucens*.

Risbec (1928, 1953) synonymized *A. leuckartii* with *A. albopunctatus*, in lengthy descriptions of specimens he collected from New Caledonia as discussed above. His specimens are most likely *A. pruvotfolae* as discussed below and in the Remarks section of *A. pruvotfolae*.

Externally, Risbec described his specimens as thin, wedge-shaped and elongate with a pointed posterior end of the foot. *Aegires albopunctatus* in contrast has a high, rounded dorsum with a rounded tail (MacFarland 1966). The dorsal tubercles described and illustrated by Risbec are all flattened and less numerous than those illustrated by MacFarland who reported both rounded and flattened tubercles. Risbec illustrates a specimen with three distinct rows of dorsal tubercles, whereas MacFarland describes tubercles that are more numerous and larger toward the end of the dorsum behind the gill. MacFarland describes the tubercles as forming three rows, only behind the gill. Also, the large gill-protective tubercles on Risbec's specimens are shown as much smaller and more simple than those illustrated by MacFarland.

The external coloration also differs between Risbec's specimens and *Aegires albopunctatus*. Risbec's have grayish rhinophores and the rhinophores on *A. albopunctatus* are lemon yellow with tiny dots of white (MacFarland 1966). The gill plumes of Risbec's specimens are pale yellow with tiny opaque white dots, while those of MacFarland have no dark pigment except for occasional spots (color unspecified by MacFarland). Risbec reports a faint greenish border on the foot, whereas MacFarland mentions white as the only color on the foot of *A. albopunctatus*.

There are radular differences as well. The teeth of Risbec's specimens (1928) have a straighter hook than does *A. albopunctatus*. Risbec reported that all radular teeth of his specimens were of similar size. But MacFarland noted that the teeth of *A. albopunctatus* gradually increased in size from the center, with the outermost tooth being smaller than the rest. The radular formula reported for Risbec's specimen is 16 × 12.0.12 for a 6 mm specimen, whereas MacFarland reports a formula of 16-22 × 17.0.17 for *A. albopunctatus* specimens averaging 13 mm.

Although both authors provided a very limited description of the reproductive system, they both noted that the penis is armed with many small hooks.

It seems likely that the specimens described by Risbec were not *Aegires albopunctatus* MacFarland or *Aegires punctilucens* (d'Orbigny, 1837) but were *A. pruvotfolae.* The most distinguishing feature of *A. punctilucens* is the "ocular" markings on the dorsum. These markings are not present in Risbec's illustrations or discussion.

### *Aegires ortizi* Templado, Luque, and Ortea 1987

(Figs. 12A–B)

*Aegires ortizi* Templado, Luque, and Ortea 1987:306, Figs 1–3.

**Type material**.— Holotype: 15-05/1006, Cayo Bocas de Alonso, Archipelago de los Conerneos, Cuba, Museo Nacional de Ciencias Naturales of Madrid.

**Material examined**.— Holotype MNCN 15-05/1006, one specimen, 5 mm, Cayo Bocas de Alonso, Archipelago de los Canarreos, Cuba, 4 m, collected April 1984, J. Templado.

**Distribution**.— *Aegires ortizi* has only been reported from Cuba by the original authors.

**Remarks**.— Templado et al. (1987) described this species from four specimens collected in 1984 (holotype) and in 1988 (three additional specimens from Cuba). Their description included the external and radular morphology but the reproductive, central nervous system and digestive systems were not described. We were unable to examine the complete reproductive system or nervous system of the holotype, as the specimen appears to have been damaged during the removal of the buccal mass during the original study.

The slide prep of the holotype radula was also examined. Additional material is needed to determine the extent of the pointed denticles on the lateral teeth of *A. ortizi* as described by the original authors.

### *Aegires palensis* Ortea, Luque, and Templado, 1990
(Figs. 16–17)

*Aegires palensis* Ortea, Luque, and Templado, 1990:336, Figs 1-2.

**Type material**.— Holotype: 15.05/1035, Cabo de Palos, SE Spain, Museo Nacional de Ciencias Naturales of Madrid.

**Material examined**.— Holotype MNCN 15.05/1035, one specimen, 6 mm, Cabo de Palos, Bajo de Dentro, Spain, collected July, 1987, J. Templado. MNCN 15.05/27821, one specimen, 2 mm, Aqua Amarga, Spain, 15 m, June 1995, J. Templado.

**Distribution**.— This species has only been reported from Spain (original description).

**External morphology**.— Ortea et al (1990) provided a thorough description and drawings of this species. No additional material was available for examination during the present study. However, drawings were made of the preserved paratype (Fig. 16).

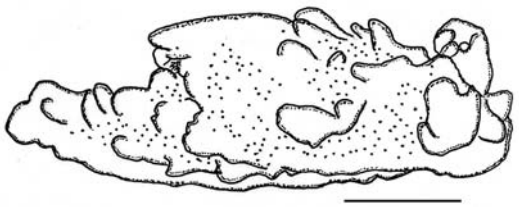


Figure 16. *Aegires palensis* Ortea, Luque, and Templado, 1990. MNCN15.05/1035. Drawing of preserved specimen. Dorsal view. Scale = 0.06 mm.

**Reproductive system**.— The reproductive system examined here is triaulic (Fig. 17). The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils once, then narrows only slightly before entering the long, tubular deferent duct. The deferent duct enters the very wide, long penis. The penis of the specimen was broken off and thus the presence of penial hooks cannot be confirmed. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The short, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects directly to the vaginal duct via a short duct that bifurcates into the oviduct, which leads into the female gland mass. The bursa is nearly round and about two-thirds the size of the ampulla. The receptaculum seminis is ovoid and is approximately one-half the size of the bursa.

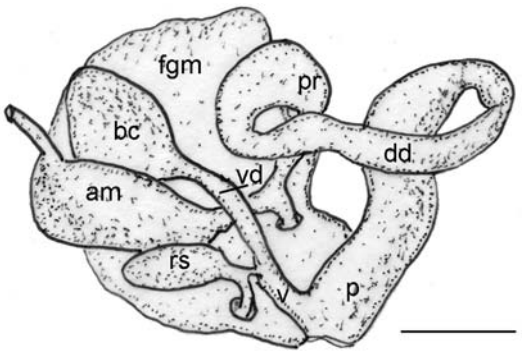



Figure 17. *Aegires palensis* Ortea, Luque, and Templado, 1990. MNCN15.05/1035. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

**Central nervous system**.— The central nervous system was not available for examination.

**Remarks**.— Ortea et al. described this species from a single specimen collected in 1987 at 34 m depth from SE Spain. Their description included the external and radular morphologies, but the reproductive, central nervous and digestive systems were not described. A second specimen was deposited into the Museo Nacional de Ciencias Naturales of Madrid in 1995 and examined for the present study. Photo images of specimens collected from the Mediterranean and identified as *A. leuckartii* and *A.* cf. *leuckartii* are most likely *A. leuckartii* and *A. palensis* may be a synonym of *A. leuckartii* (Koehler 2004; Tocino 2004). Additional material of both *A. leuckartii* and *A. palensis* is needed to determine whether this is the case. However, there have been no further reports on

collections or sightings of *A. palensis* except for the two specimens noted herein. No specimens of *A. leuckartii* were available for examination during this study.

### *Aegires punctilucens* (d'Orbigny, 1837)

*Polycera punctilucens* d'Orbigny, 1837:7, pl 106.
*Aegirus punctilucens* (d'Orbigny) Alder and Hancock 1845/55, pl. 21.
*Aegires hispidus* Hesse, 1872:346.
*Aegires punctilucens* (d'Orbigny) Vayssière 1901:58f.
*Aegires punctilucens* (d'Orbigny) Pruvot-Fol, 1954:243.

**Type material**.— Collected (1826) at the Port of Brest, France. No further data are available. Attempts to locate the type material for examination were not successful.

**Distribution**.— Specimens of *Aegires punctilucens* have been reported from the Atlantic coast of France (d'Orbigny), Scandinavia and the Mediterranean Ocean (Pruvot-Fol 1954).

**External morphology**.— D'Orbigny provided a thorough accounting of the external morphology of *Aegires punctilucens*. To summarize his description: the body is short but strongly convex, bulged in the middle, slightly tough and covered with flattened tubercles. The tubercles are arranged as follows: two between the rhinophores, four lateral and posterior to these, then one large median and many laterally placed tubercles. There is one large tubercle posterior to the gill, along with four round tubercles placed on each side of the tail median. Around the rhinophores are five elevated tubercles, three larger ones and two very small ones. The foot is elongate, ends in a point and is much narrower than the body, though slightly wider at the median. The gill is tri-lobed and multi-pinnate.

The body color is a mixture of yellow and violet, except in between the tubercles where there are spots of bright green surrounded by a border of black. In front of the gill and between the rhinophores are definite points of matte white, with four smaller points lateral to these. On the foot there are many spots of color, more intense than the rest of the body color, placed obliquely or vertically. The bottom of the foot has a slight border.

**Remarks**.— Many authors have published descriptions of *Aegires punctilucens*, the species first described by d'Orbigny (1837) as *Polycera punctilucens*. The original description was confined to the external morphology. Subsequent authors (Schmekel and Portmann 1982; Thompson and Brown 1984; Templado et al. 1987) provided more thorough descriptions, including the radular and reproductive anatomy, however none of the previous authors described the central nervous system or circulatory system.

Baba (1974) provided a detailed description of a specimen from Japan, however this specimen is most likely *Aegires exeches* sp. nov. (See the description further on in the present study).

Haefelfinger (1968) synonymized *Aegires leuckartii* with *A. punctilucens*. Schmekel and Portmann (1982) also noted the consistency between these two species, and designated them as subspecies. Thompson's publication (1984) maintained the synonymy of the two (see discussion under *A. albopunctatus*).

As stated previously, there is no description of the reproductive morphology from the original material. Due to this lack, and the differences in the external morphology between *A. punctilucens*, *A. leuckartii* and *A. albopunctatus* and considering Schmekel and Portmann's argument for separate subspecies, we propose to maintain *A. punctilucens* from the Mediterranean Sea as a separate species from *A. leuckartii* and *A. albopunctatus.*

***Aegires sublaevis* Odhner, 1932**
(Figs. 18–25)

*Aegires sublaevis* Odhner, 1932:39.
*Serigea sublaevis* (Odhner) Nordsieck, 1972:55.

**Type material**.— Puerto de Orotavo, Tenerife, Canary Islands.

**Material examined**.— CASIZ 168921, four specimens, one specimen, 10 mm, dissected, Ponta de Piramede, Azores, no depth available, collected July 1988, T. Gosliner. CASIZ 078393, one specimen, 8 mm, dissected, Punta Cormorant, Isla Floreana, Galápagos Islands, no depth available, collected September 1991, T. Gosliner. CASIZ 072608, three specimens, one specimen, 5 mm, dissected, Ila São Miguel, 1 km E of Caloura, Azores, 20 m, collected July 1988, T. Gosliner. CASIZ 072603, one specimen, 9 mm, Ila São Miguel, Mosteiros, Azores, 3 m, collected July 1988, T. Gosliner. CASIZ 168923, three specimens; one specimen, 12 mm, dissected. Ponta de Galora, Azores, collected July 1988, T. Gosliner.

**distribution**.— This species has been reported from the Mediterranean Sea (Schmekel and Portmann 1982); the Canary Islands (Odhner 1932; Altimira and Ros 1979; Pérez Sánchez, Bacallado and Ortega 1991; Ortea et al. 1996; Ortea et al. 2000)); Panama (Meyer 1977), Bermuda (Thompson 1981) and the Galápagos Islands, which represents the first record from the Pacific (present study).

**External morphology**.— The external morphology of this species has been described extensively in the literature (Odhner 1932; Meyer 1977; Altimira and Ros 1979; Thompson 1981; Schmekel and Portmann 1982; Templado et al. 1987) and will not be repeated here. However, drawings were made of preserved specimens from the Azores to compare to specimens from the type locality (Fig. 18). These specimens match Odhner's original description. We noted one differ-

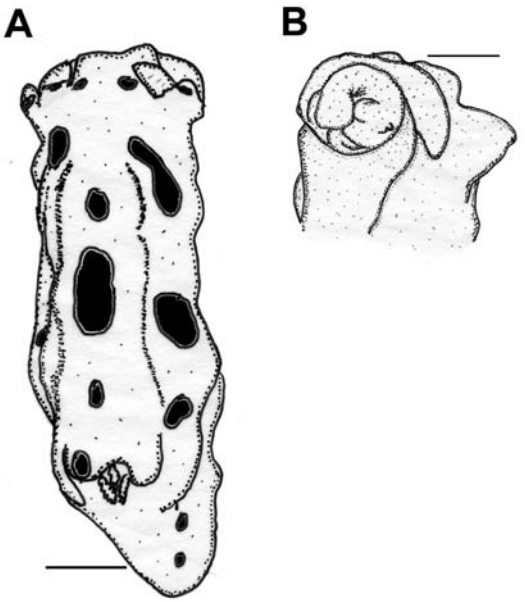



Figure 18. *Aegires sublaevis* Odhner, 1932. CASIZ 168921. Drawing of preserved specimen: (A) Dorsal view. (B) Ventral view of head. Scale = 1.43 mm.

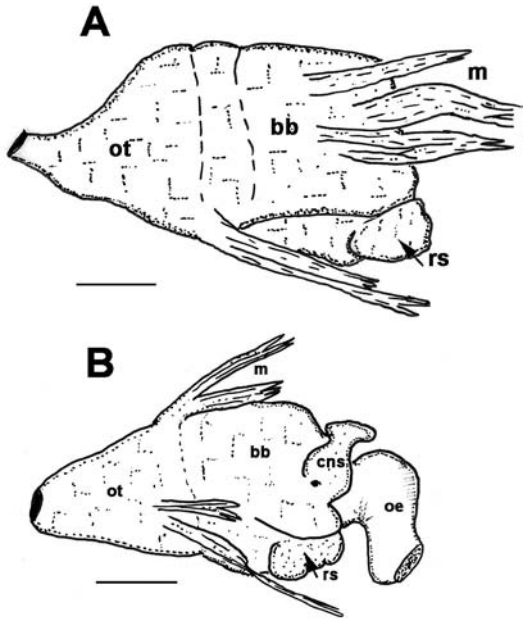



Figure 19. *Aegires sublaevis* Odhner, 1932. Buccal bulbs: (A) CASIZ 072608. (B) CASIZ 078393, bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.33 mm.

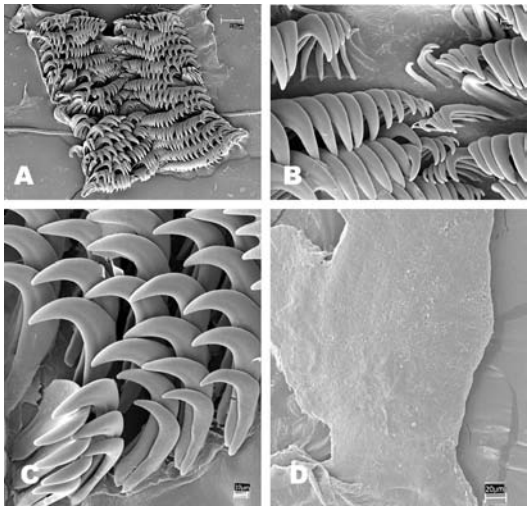



FIGURE 20. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Buccal morphology: (A)Whole radula, scale = 100 µm. (B) Inner lateral teeth, scale = 10 µm. (C) Outer lateral teeth, scale = 10 µm. (D) Jaw, scale = 20 µm.

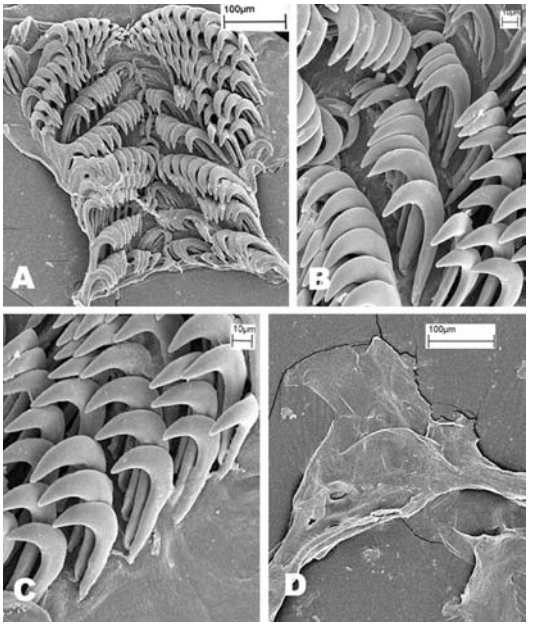



FIGURE 21. *Aegires sublaevis* Odhner, 1932. CASIZ 078393. Buccal morphology: (A) Whole radula, scale = 100 µm. (B) Inner lateral teeth, scale = 10 µm. (C) Outer lateral teeth, scale = 10 µm. (D) Jaw, scale = 100 µm.

ence between specimens examined from the Azores and those from the Galápagos Islands. Specimens from the Azores have one ring of dark pigment on the rhinophores whereas those from the Galápagos have two dark rings.

**DIGESTIVE SYSTEM**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the radular sac protrudes noticeably from the posterior side (Fig. 19). There were no oral glands noted. The radular formula is 17 × 17.0.17 for a 12 mm specimen from the Azores (CASIZ 168921)(Fig. 20) and 12 × 13.0.13 for an 8 mm specimen from the Galápagos (CASIZ 078393) (Fig. 21). The jaw is well developed and has a thickened edge. No labial rods were noted (Figs. 20D, 21D). All teeth are simply hamate, with a pointed hook. Rachidian teeth are absent. The first inner lateral tooth is much smaller than the remaining lateral teeth. The next two lateral teeth are slightly larger than the first lateral tooth. The outermost lateral tooth is shorter than the middle teeth.

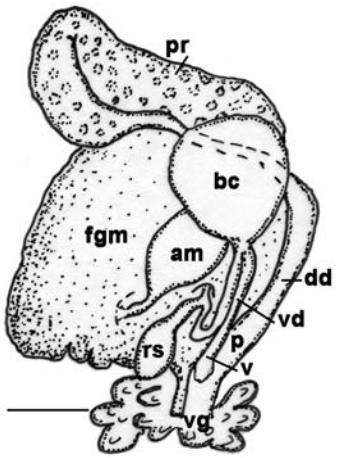



FIGURE 22. *Aegires sublaevis* Odhner, 1932. CASIZ 168921. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, vg = vestibular gland, scale = 0.33 mm.

**REPRODUCTIVE MORPHOLOGY**.— The reproductive morphology of the specimens examined for the present study (Figs. 22–24) closely resembles the drawings and descriptions previously reported by Schmekel and Portmann (1982).

The reproductive system is triaulic. The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils twice, then narrows for a short distance before entering the wider deferent duct. The deferent duct enters the long penis, which is wider than the deferent duct. The penis has small densely packed penial hooks that extend

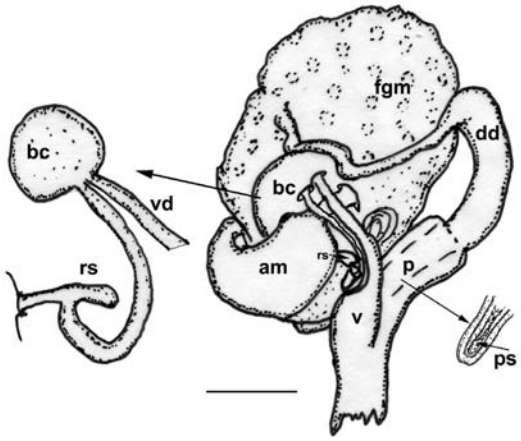



FIGURE 23. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.5 mm. [NB. Vestibular gland not evident.]

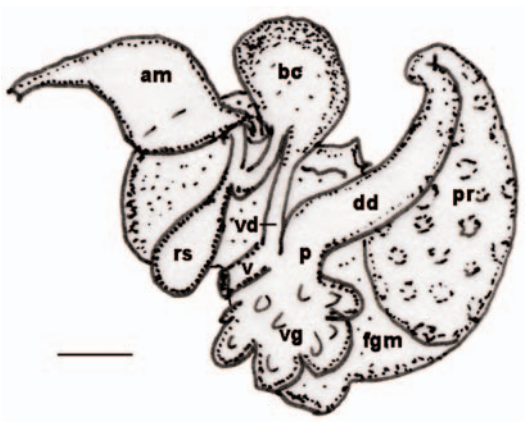



FIGURE 24. *Aegires sublaevis* Odhner, 1932. CASIZ 078393. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, vg = vestibular gland, scale = 0.5 mm.

throughout the length of the penis. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The long, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects to the bursa with a longer duct than the oviduct, which leads from the bursa into the female gland mass. The bursa is round and as large as the ampulla. The receptaculum seminis is ovoid and less than one-half the size of the bursa. Specimens examined have a vestibular gland at the genital atrium (Figs. 22 and 24) as described by Schmekel and Portmann. However, in the specimen examined from the Azores, the vestibular gland was not evident. It may have broken off. No other *Aegires* species has this gland.

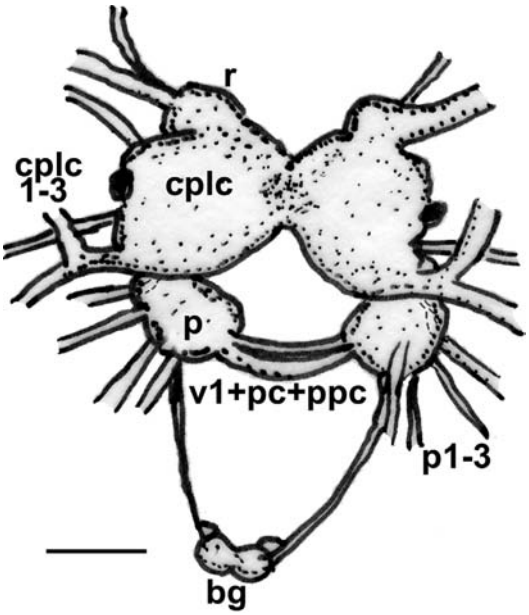



FIGURE 25. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.2 mm.

**CENTRAL NERVOUS SYSTEM**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 25). The eyes are small and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Remarks**.— The specimen from the Galápagos represents the first record of this species from the Pacific. With the exception of having two pigment rings on each rhinophore, Galápagos specimens are identical to Atlantic specimens of *A. sublaevis*.

Odhner's (1932) description of *Aegires sublaevis* is quite detailed but did not include a description of the reproductive system. However, Schmekel and Portmann (1982) provided a complete description of the reproductive anatomy in their thorough study. Templado et al. (1987) described the external and radular morphology of this species. In both these studies, drawings of the examined features accompany the description.

Nordsieck (1972) established a new genus *Serigea* and designated *S. sublaevis* (Odhner, 1931) (with an incorrect date cited) as the type species. He placed *Serigea* in the Family Aegiretidae based on similar characters to *Aegires*. He described the following *Serigea* characters: dorsal papillae, smooth rhinophores, gill with protective valves, among others. However, Nordsieck did not indicate why a new genus was needed for these characters. Altimira and Ros (1978) published a study on the molluscs of the Canary Islands, declaring that *Serigea* equals *Aegires sublaevis* Odhner. Subsequent publications on *Aegires sublaevis* also recognized this name exclusively (Meyer 1977; Thompson 1981; Schmekel and Portmann 1982; Templado et al. 1987).

### *Aegires villosus* Farran, 1905
(Figs. 26–27)

*Aegires villosus* Farran, 1905:329-364, pls 1–6.
*Aegires* spp. Debelius, 1996:192, bottom large photo. Misidentification.

**Type material**.— Collected from the northwest of Cheval Paar, Ceylon.

**Material examined**.— CASIZ 158799, one specimen, 5 mm, dissected. Luzon, Batangas, Philippine Islands, collected 6 May 2001, T. Gosliner. CASIZ 088089, one specimen, 12 mm, dissected. Layag Layag, Batangas, Philippine Islands, collected 27 March 1993, T. Gosliner. CASIZ 105658, one specimen, 8 mm, dissected. Kirby's Rock, Batangas, Philippine Islands, collected 23 February 1995, T. Gosliner. CASIZ 65306, one specimen, 6 mm, Madang, Papua New Guinea, collected 22 January 1988, R. Willan. CASIZ 116888, one specimen, 12 mm, dissected. Coral Ledge, Garden Island, Western Australia, collected 6 January 1999, S. Fahey.

**Distribution**.— *Aegires villosus* has been reported from Ceylon (Farran 1905), Japan (Baba 1955), New Caledonia (Risbec 1928), Dar es Salaam, Tanzania (Edmunds 1971), Papua New Guinea (present study), Bali, Malaysia, Samoa and Australia (Rudman 2004).

**External morphology**.— Several authors have described and/or drawn this species (Farran 1905; Risbec 1928; Baba 1955; Edmunds 1971; Rudman 2004). The specimens examined for the present study from various localities match the existing drawings and descriptions of the external morphology of *Aegires villosus* and no additional detail is necessary.

**Digestive system**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is ovoid and the large radular sac does not protrude noticeably from the posterior-ventral side (Fig. 26). There are numerous ovoid oral glands that cover the sides of the oral tube near the mouth and line the posterior edge of the oral tube. Two tubular salivary glands extend from the underside of the esophagus and lie along the top of the buccal bulb. The radular morphology was described by previous authors and the present study (Fig. 26) confirms the morphology as described by Farran (1905) and Risbec (1928). Edmunds (1971) described the outer lateral tooth as being elongate, but we did not find this to be the case. The radular formula for the 12 mm specimen dissected is 16 × 17.0.17. All teeth are simply hamate, with the innermost tooth being substantially smaller than the remaining teeth in each row. The second

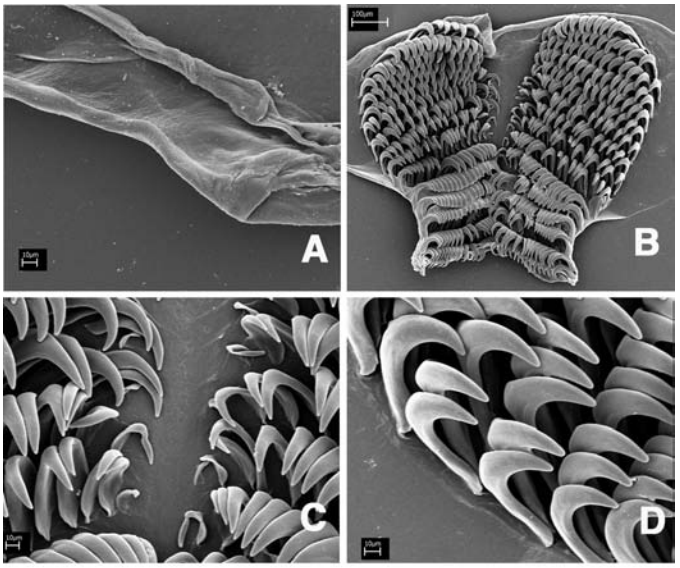
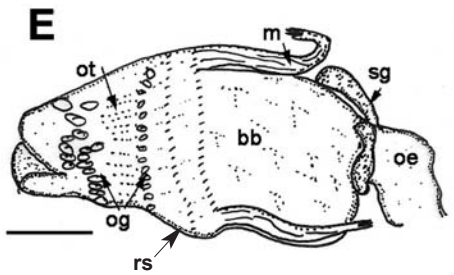
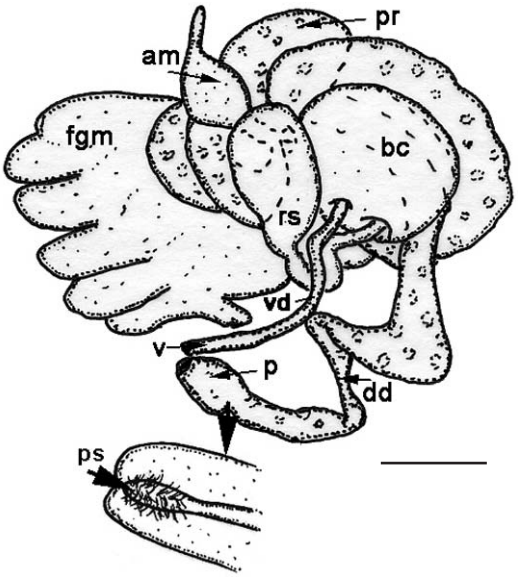



FIGURE 26. *Aegires villosus* Farran, 1905. CASIZ 088089. Buccal morphology: (A) Jaw, scale = 10 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm. (E) Buccal bulb, bb = buccal bulb, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.25 mm.

lateral tooth is also reduced in size.

**REPRODUCTIVE SYSTEM.**— The reproductive morphology has not been thoroughly described previously. The reproductive system is triaulic. The ampulla is small and ovoid. It branches into a short oviduct and the prostate (Fig. 27). The oviduct enters the female gland mass near an edge. The prostate is a very long, thick, coiled tube. It narrows slightly before widening slightly into the ejaculatory duct and terminates at a slightly bulging penis. There are small hooks inside the penis located at the distal end only. The vagina is long and narrow. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end it joins the bursa copulatrix. A long separate duct joins the large ovoid receptaculum seminis to the base of the bursa, and also connects to the female gland mass. The bursa is large, spherical and the receptaculum seminis is over half the size of the bursa.




**CENTRAL NERVOUS SYSTEM.** The central nervous system is as found in other *Aegires* species. That is, it has fused cerebral and pleural ganglia (not shown). The eyes are large and sessile on the cerebral-pleural complex and do not protrude. The pedal ganglia are slightly

FIGURE 27. *Aegires villosus* Farran, 1905. CASIZ 088089. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Remarks**.— Farran (1905) described *Aegires villosus* from one specimen collected from Cheval Paar, Ceylon (Sri Lanka). The description included the external morphology and radular morphology, along with adequate drawings of each. Other authors provided further details of the external anatomy, radular morphology, the central nervous system and/or the reproductive system (Edmunds 1971; Risbec 1928). Except for one difference, the specimens examined for the present study matched the previous descriptions in both external and internal morphology. Edmunds illustrated and described elongate outer radular teeth in the 4 mm specimen he examined. He also stated that the outermost tooth was very small and not illustrated in this immature specimen. The larger 8 mm specimen that he collected was not illustrated. The 8 and 12 mm specimens that we examined had simply hamate outer lateral teeth.

## New Species Descriptions

### Family Aegiridae Fischer, 1883

#### Genus *Aegires* Lovén, 1844

***Aegires ninguis* Fahey and Gosliner, sp. nov.**
(Figs. 1D, 28–32)

=*Aegires* sp. Gosliner, 1987:99, top photograph

**Type material**.— Holotype: CASIZ 073982, one specimen, 6 mm, Phillip's Reef, Algoa Bay, Cape Province, Indian Ocean, South Africa, 10 m, collected January 1991, T. Gosliner. Paratypes: CASIZ 073230, six specimens, 4–6 mm, Phillip's Reef, Cape Province, Indian Ocean, South Africa, 10 m, collected May 1984, T. Gosliner. CASIZ 073929, one specimen, 8 mm, dissected, Llandudno, Cape Province, Atlantic Ocean, South Africa, 23 m, collected October 1982, T. Gosliner. A35568, one specimen, 6 mm, Miller's Point, Indian Ocean, South Africa, 8 m, collected June 1980, T. Gosliner. A35569, one specimen, 8 mm, Bakoven, Atlantic Ocean, South Africa, 15 m, collected September 1982, T. Gosliner.

**Distribution**.— This species has only been reported from the temperate Atlantic and Indian Oceans of South Africa (present study).

**Etymology**.— The specific name *ninguis* is Latin, meaning snowy, which describes the appearance of the dorsum with the white background and tiny opaque white speckles.

**External morphology**.— The body shape is ovoid, slightly raised and has a rounded posterior end of the foot that extends only slightly (Fig. 1D). There is a slightly pronounced oral veil that has a scalloped edge (Fig. 28). The dorsum is covered with short, rounded tubercles, all with rounded tops. There are no tubercles on the posterior end of the foot. There are two prominent tubercles on the anterior of the head region, with smaller tubercles between them, and two prominent tubercles on the poste-

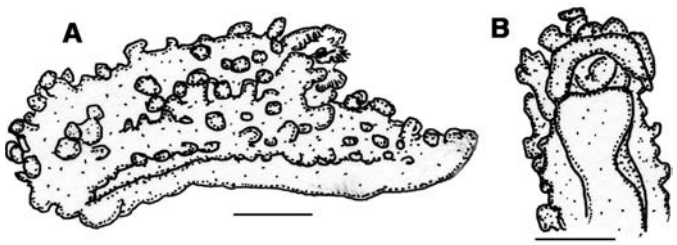



Figure 28. *Aegires ninguis* sp. nov. CASIZ 073982. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 1.5 mm.

rior of the dorsum that appear joined together. There are also two prominent tubercles between the rhinophores with smaller tubercles between them. Numerous spicules protrude from the tops of the tubercles giving a fuzzy appearance. The rhinophore sheath is only slightly elevated but has five papillae, 3 large and 2 small, on all sides except the innermost. The rhinophores are smooth. The gill pocket lies at the posterior third of the dorsum and is protected on the anterior side by extra-branchial papillae that are tri-lobed. The three small gill branches are bipinnate.

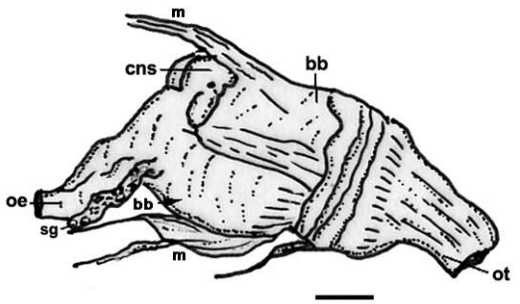



FIGURE 29. *Aegires ninguis* sp. nov. CASIZ 073929. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 0.25 mm.

The background color is white to pale yellow. There are minute white speckles on the dorsum, between the tubercles. There are no additional colors found on the specimens examined. The rhinophores are pale yellow on white specimens and deeper yellow on the yellow specimens. The gill matches the background color of the living animal.

**DIGESTIVE SYSTEM**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the radular sac barely protrudes from the posterior side (Fig. 29). There are two short salivary glands situated beneath the esophagus. There were no oral glands noted. The radular formula is 17 × 16.0.16 for a 8 mm specimen (Fig. 30). The jaw (Fig. 30A) is well developed and has a thickened edge with narrow rod-like elements. All teeth are simply hamate, with pointed hooks. Rachidian teeth are absent. The four inner lateral teeth are smaller than the remaining lateral teeth. The outermost lateral teeth are shorter than the middle teeth.

**REPRODUCTIVE SYSTEM**.— The reproductive system is triaulic (Fig. 31). The ampulla is short but very wide and branches into the oviduct and the prostate. The prostate is a long, thick tube and narrows only very slightly before entering the long, wide penis. The penis, which expands at the genital atrium, has small densely packed hooks only at the distal end. The vagina is long and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the short, wide vaginal duct enters the bursa copulatrix. The receptaculum seminis connects directly to the vagina via a short duct. The oviduct, connected to the

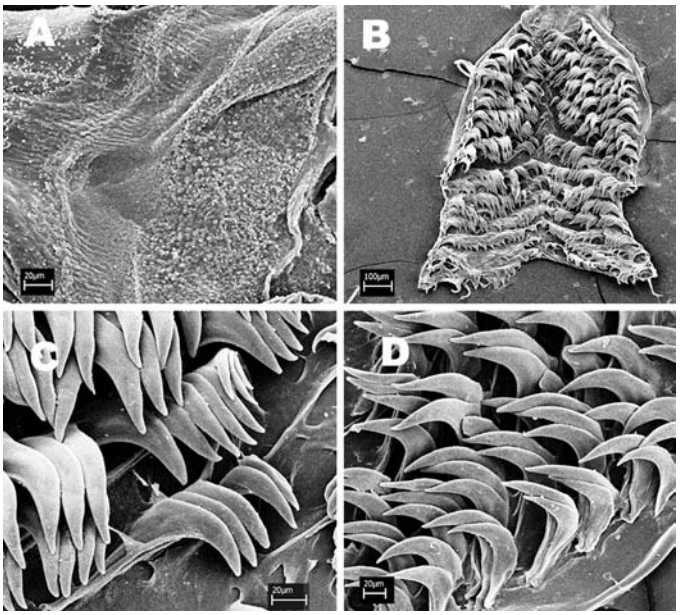



FIGURE 30. *Aegires ninguis* sp. nov. CASIZ 073929. Buccal morphology: (A) Jaw, scale = 20 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

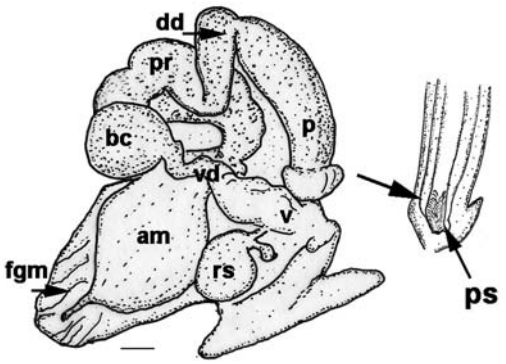



FIGURE 31. *Aegires ninguis* sp. nov. CASIZ 073929. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.33 mm.

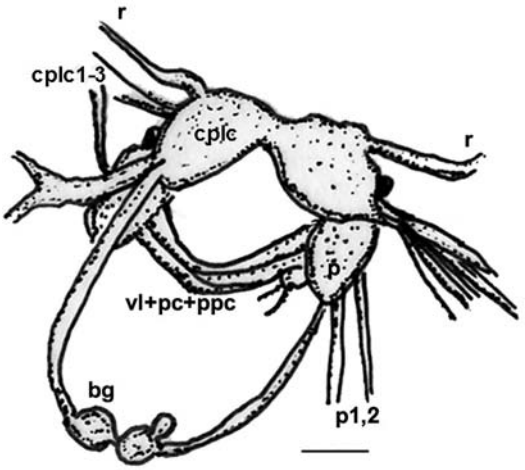



FIGURE 32. *Aegires ninguis* sp. nov. CASIZ 073929. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.14 mm.

receptaculum, enters the female gland mass. The bursa is round and slightly larger than the round receptaculum seminis.

**CENTRAL NERVOUS SYSTEM**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 32). The eyes are small and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**CIRCULATORY SYSTEM**.— (not pictured) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**REMARKS**.— Externally, the white form of *Aegires ninguis* most closely resembles the white form of *A. albopunctatus*. Although neither color form (white or pale yellow) of *A. ninguis* has been found with dark spots on the dorsum, both forms do have minute white dots covering the dorsum as is found on *A. albopunctatus*. Both *A. ninguis* and *A. albopunctatus* have yellow rhinophores. The tubercle arrangement is different between these two species. *Aegires ninguis* has randomly scattered tubercles that vary in size on the notum. There are two prominent tubercles on both the anterior and posterior ends of the notum. There are no tubercles on the posterior end of the foot. In *A. albopunctatus* the tubercles are arranged in two distinct rows like ridges, joined from between the rhinophores and extending to the gill. Behind the gill, the tubercles are arranged in three distinct rows (MacFarland 1966). The tubercles on the rhinophore pocket of each species are different as well. In *A. ninguis*, there are four tubercles on the outside rhinophore pocket and in *A. albopunctatus* there are five.

The gill morphology differs between the two species. *Aegires ninguis* has very small gill leaves that are almost completely covered by the large, flat-topped protective tubercles. *Aegires*

*albopunctatus* has larger gill leaves that protrude vertically with a branching lobe protecting each plume (MacFarland 1966: plate 18).

Internally, the two species also differ. The most noticeable difference in the reproductive morphology is that in *A. ninguis* the receptaculum seminis connects directly to the vagina via a short oviduct. In *A. albopunctatus* the receptaculum connects to the bifurcating oviduct at the base of the bursa copulatrix and to the female gland mass. Also, *A. albopunctatus* has spines throughout the penis while in *A. ninguis* the spines are just at the apex.

The deferent duct of these two species differs markedly. In *A. ninguis* the deferent duct is short and tubular. In *A. albopunctatus* the duct is very long, thin and coiled. The penis of *A. ninguis* is very tubular and long, while that of *A. albopunctatus* is much smaller relative to the other reproductive organs such as the vagina and the bursa.

No other species of *Aegires* has the particular combination of characters displayed by *A. ninguis*. The most externally similar species, *Aegires albopunctatus* is found along the Eastern Pacific while *A. ninguis* has been found only in South Africa.

### *Aegires lemoncello* Fahey and Gosliner, sp. nov.

(Figs. 1E, 33–37)

= *Aegires* sp. 2, Valda Fraser, 2000 and Rudman in SeaSlug Forum.

**Type material**.— Holotype: CASIZ 086465, one specimen, 4 mm, dissected, Barracuda Point, Pig Island, Madang, Papua New Guinea, 9 m, collected June 1992, T. Gosliner.

**Distribution**.— This species has only been reported from Papua New Guinea (present study), South Africa (photo, V. Fraser) and Eastern Australia (no photo, B. Rudman).

**Etymology**.— The specific name *lemoncello* is from the Italian liqueur of the same color as some specimens of this new species.

**External morphology**.— The body shape is elongate, slightly raised and has a very narrow posterior (Fig. 1E). The dorsum has elongate papillae with flattened tops. Spicules protrude from the tops of the tubercles. The extended oral veil has 10–11 rounded tubercles on the dorsal surface (Fig. 33). The rhinophore sheath is slightly elevated, smooth and protected by a single elongated papilla on the outer edge. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and is protected on the anterior side by five elongate papillae that project posteriorly. Posterior to the gill are two small papillae near the center-line. The three small gill branches are bipinnate.

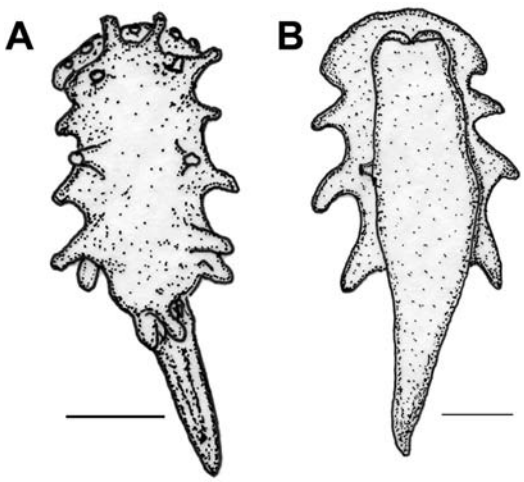



Figure 33. *Aegires lemoncello* sp. nov. CASIZ 086465. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view. Scale = 2.25 mm.

The background color is pale yellowish white to creamy yellow. The papillae are deeper yellow, with a single ring of orange approximately half way along the length. The rhinophores are the same deeper yellow as the papillae. The gill branches are pale yellow.

**Digestive system**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is round and the radular sac barely protrudes from the

posterior side (Fig. 34). There are two elongate salivary glands situated beneath the esophagus. There were no oral glands noted. The radular formula is 13 × 15.0.15 for a 4 mm specimen. The jaw is well developed and has a thickened edge (Figs. 34B, 35). All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are much thinner and less hooked than the remaining lateral teeth. The outer lateral teeth have a short hook.

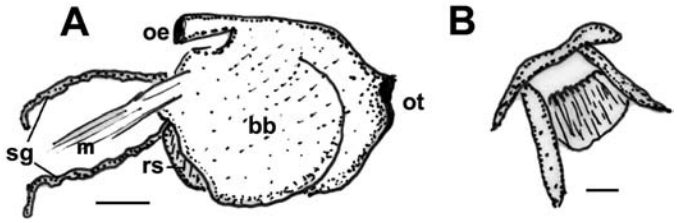



FIGURE 34. *Aegires lemoncello* sp. nov. CASIZ 086465. (A) Buccal bulb: bb = buccal bulb, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.5 mm. (B) Labial cuticle, scale = 0.05 mm.

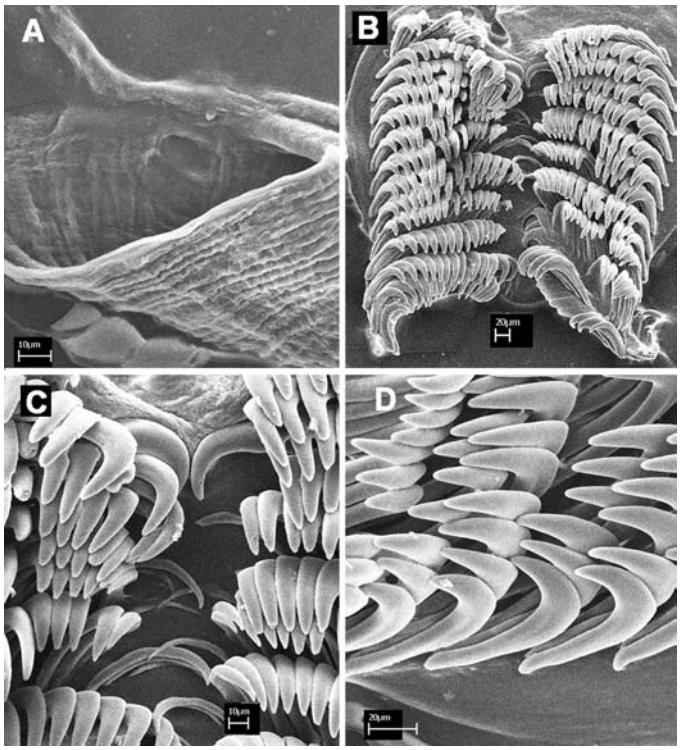



FIGURE 35. *Aegires lemoncello* sp. nov. CASIZ 086465. Buccal morphology: (A) Jaw, scale = 10 μm. (B) Whole radula, scale = 20 μm. (C) Inner lateral teeth, scale = 10 μm. (D) Outer lateral teeth, scale = 20 μm.

**REPRODUCTIVE SYSTEM**.— The reproductive system is triaulic (Fig. 36). The ampulla is elongate and branches into the oviduct and the prostate. The prostate is long and tubular and narrows slightly before entering the elongate deferent duct. The deferent duct widens only slightly, then enters the short, wide penis. The penis has small densely packed penial hooks at the distal tip only. The vagina is much narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa with a separate long duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is ovoid and approximately the same size as the ovoid receptaculum seminis.

**CENTRAL NERVOUS SYSTEM**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 37). The eyes are large and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**CIRCULATORY SYSTEM**.— (not shown) The heart is relatively small as compared to most cryp-

tobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Externally, *Aegires lemoncello* does not resemble any other *Aegires* species. Although *A. lemoncello* has elongate tubercles like *Aegires villosus*, the tubercles in that species are more numerous and more complex especially around the rhinophores where there are 4–5 tubercles on a raised pocket. The tubercles of *A. lemoncello* look more like soft papillae, and there is only one tubercle that lies at the outer side of the rhinophores. The color of these two species is not similar at all. *Aegires lemoncello* has a yellow or whitish background color with orange rings around the rhinophores and tubercles. *Aegires villosus* has a white body color with purple and yellow irregular markings covering the notum.

Internally, the morphological characters also set this species apart from other *Aegires*. *Aegires lemoncello* has three elongate curved inner lateral teeth, a feature found in other *Aegires* (*A. ortizi* and *A. petalis*). *Aegires pruvotfolae* has one elongate inner lateral tooth while both *A. ortizi* and *A. petalis* have two. Neither of these species even closely resembles *A. lemoncello* externally, either in color or tubercle morphology.

The reproductive morphology also sets *A. lemoncello* apart from other *Aegires*. The combination of a long, thin deferent duct leading from a narrow prostate and into a slightly wider penis is not found in other *Aegires*. The species that most closely matches this anatomy, *A. hapsis*, does not share any other internal or external characters. The large ovoid receptaculum that enters the common oviduct at the base of the bursa copulatrix is different from other *Aegires* species also. The receptaculum of other *Aegires* species either enters a common oviduct with the bursa, or enters the vaginal duct or into the vagina directly (*A. ninguis*).

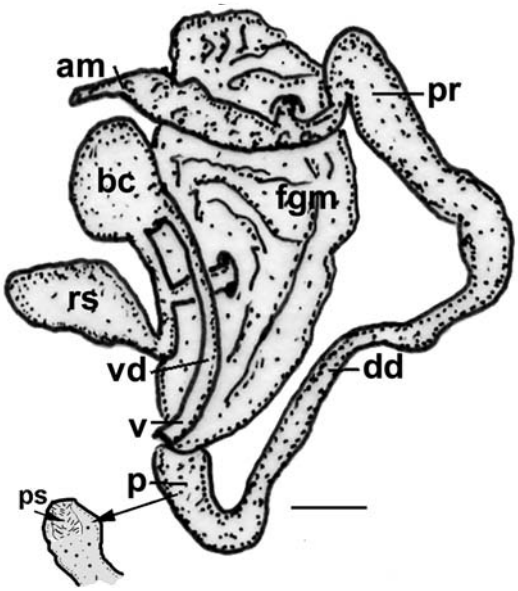



Figure 36. *Aegires lemoncello* sp. nov. CASIZ 086465. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

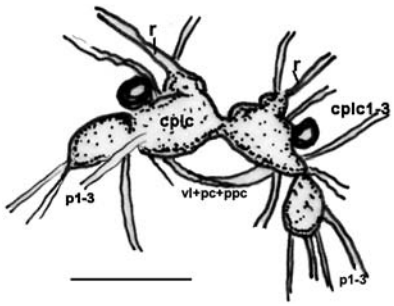



Figure 37. *Aegires lemoncello* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, cl+pc+ppc = visceral loop, scale = 0.25 mm.

The combination of characters exhibited by *Aegires lemoncello* sets it apart as a previously undescribed species of *Aegires*.

***Aegires malinus* Fahey and Gosliner, sp. nov.**
(Figs. 1F, 38–42)

**Type material**.— Holotype: CASIZ 085889, one specimen, 8 mm, Bebbit, Batangas Region, Philippines, collected March 1993, T. Gosliner. Paratypes: CASIZ 168919, one specimen,

15 mm, dissected, Bebbit, Philippines, collected March 1993, T. Gosliner. CASIZ 096248, one specimen, 14 mm, Layag-Layag, Batangas Region, Philippines, collected March 1994, M. Miller.

**Distribution**.— This species has only been reported from the Philippine Islands (present study).

**Etymology**.— The specific name *malinus* is Latin for apple green, the color of the rhinophore and gill appendages of this species.

**External morphology**.— The body shape is elongate and convex. There are tiny pointed, randomly scattered tubercles on the dorsum (Figs. 1F, 38). The rhinophore pockets are raised and the outer edge is taller with 3 flat-topped tubercles of varying size and a lobed frill that resembles tufts of seaweed. The rhinophores are smooth. The gill pocket is protected by 3 tall, flat tubercles. The gill leaves are feathery, resembling tufts of seaweed and are multi-pinnate. They extend beyond the protective tubercles.

The background color of the dorsum is deep reddish-brown. The raised rhinophore pocket is the same as the background color and the lobed frill and tubercles are apple green. The rhinophores are white with concentric bands of brown speckles around the club. The gill leaves are pale yellowish-green and the protective tubercles are bright apple green.

**Digestive system**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is elongate and the large radular sac protrudes noticeably from the posterior-ventral side (Fig. 39). There are numerous ovoid oral glands that extend from the ventral side of the oral tube. Two short salivary glands extend from the underside of the esophagus. The jaw is well developed and has a thickened edge with long rods along the edge (Fig. 40A). The radular formula for a 15 mm specimen is 22 × 8.0.8 (Fig. 40). The teeth are simply hamate, and the 3–5 innermost teeth much smaller and thinner than the remaining teeth. Rachidian teeth are absent. The outermost teeth are larger than the middle lateral teeth.

**Reproductive system**.— The reproductive system is triaulic (Fig. 41). The ampulla is very long and tubular. It branches into the oviduct and the prostate. The tubular prostate is approximately the same length as the ampulla and it coils once before narrowing into the thin, elongate deferent duct. The deferent duct is very long and widens slightly, then enters the long penis. The penis is wider than the deferent duct and it has small densely packed hooks at

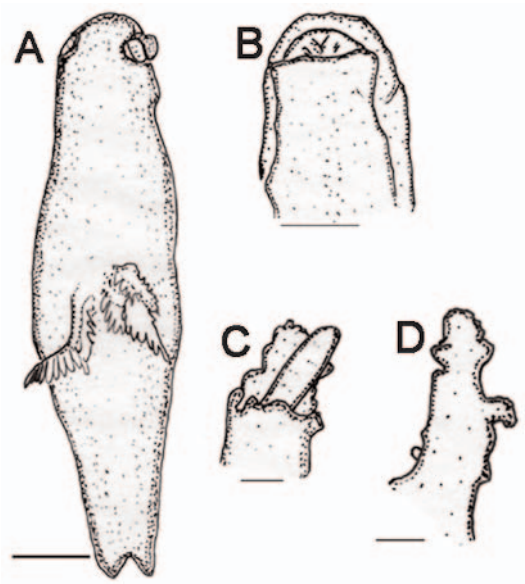



Figure 38. *Aegires malinus* sp. nov. CASIZ 085889. Drawing of preserved animal. (A) Dorsal view, scale = 1.88 mm. (B) Ventral view of head, scale = 1.88 mm. (C) View of rhinophore pocket from inner edge, scale = 0.5 mm. (D) View of rhinophore pocket from outer edge, scale = 0.5 mm.

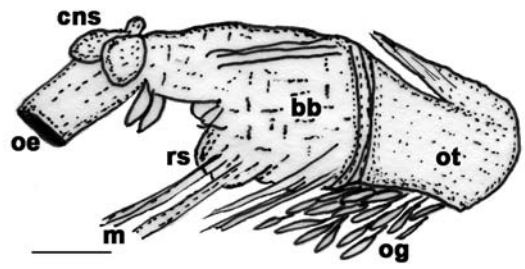



Figure 39. *Aegires malinus* sp. nov. CASIZ 168919. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac, scale = 0.4 mm.

the distal tip only. The vagina is narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa via a separate longer duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is ovoid and slightly smaller than the ovoid receptaculum seminis.

**Central nervous system**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 42). The eyes are large and sessile on the cerebral-pleural complex and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

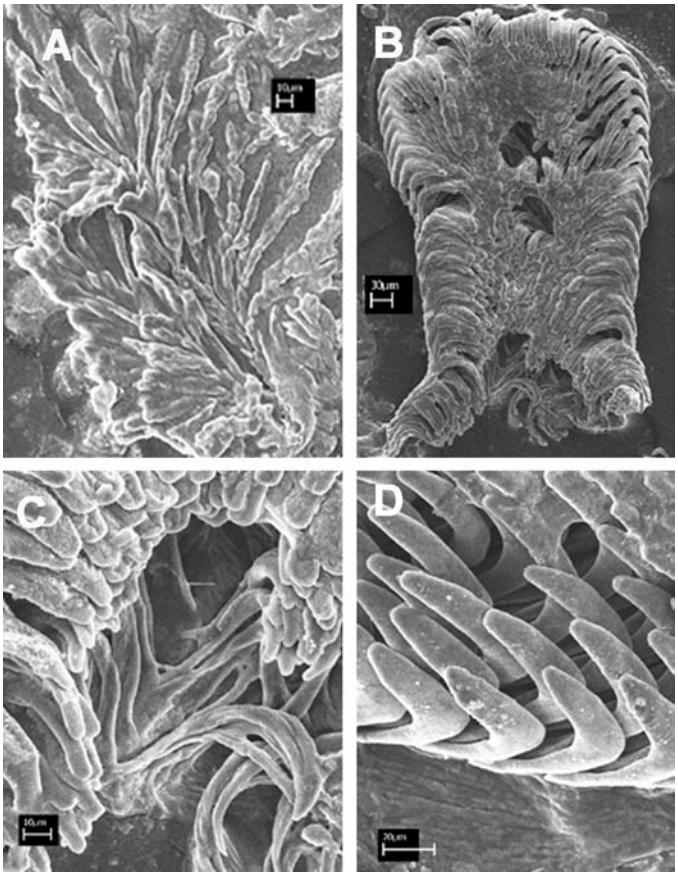



Figure 40. *Aegires malinus* sp. nov. CASIZ 168919. Buccal morphology: (A) Jaw rodlets, scale = 10 µm. (B) Whole radula, scale = 30 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 20 µm.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Externally, *Aegires malinus* does not resemble any other *Aegires* species in either color or body texture. Along with *A. hapsis,* it is one of the two *Aegires* species that does not have prominent dorsal tubercles. However, like other *Aegires*, the rhinophore pockets are lobed, particularly on the outer edge. But the lobes are distinctly different from the texture of the notum. The gill is also protected by appendages, as with other *Aegires*,

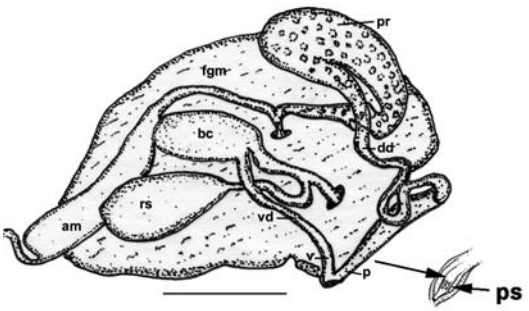



Figure 41. *Aegires malinus* sp. nov. CASIZ 168919. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.86 mm.

but in *A. malinus* the appendages are tall, narrow, yet shorter than the gill leaves. This is unusual for *Aegires*, in which the gill is normally small and almost hidden by the appendages.

Internally, *A. malinus* shares some reproductive characters with other *Aegires* species, such as a bursa and receptaculum that are nearly equal in size, a tubular coiled prostate and an elongate penis with spines. The ampulla in *A. malinus* is extremely elongate, as is found in *A. petalis*. But in *A. petalis*, the penial morphology is different, in that the penis is very short and wide as compared to *A. malinus*, in which it is elongate. Externally, these two species share no common features or color.

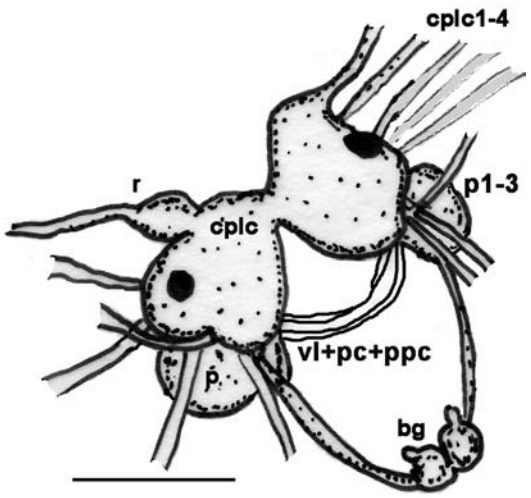



FIGURE 42. *Aegires malinus* sp. nov. CASIZ 168919. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

*Aegires malinus* has numerous oral glands clustered at the base of the oral tube. *Aegires villosus* also has clustered oral glands, but in that species the glands are more numerous and there is a second row of glands along the oral tube (see Fig. 26). The other species in which oral glands were observed are *A. incusus* and *A. hapsis*. But the glands in those two species have a different morphology (see Figs. 44 and 63).

The particular combination of characters sets *Aegires malinus* apart as a new, previously undescribed species.

### *Aegires incusus* Fahey and Gosliner, sp. nov.

(Figs. 1G, 43–47)

*Aegires citrinus* Nakano, 2004:117, no. 242, bottom left photograph. Misidentification.
= *Aegires* sp. 1 Rudman, 2004, leading photo for *Aegires* in SeaSlug Forum.

**TYPE MATERIAL**.— HOLOTYPE: CASIZ 070357, one specimen, 4 mm. Patch Reef, Mora Mora, Tulear, Madagascar, collected April 1989, T. Gosliner. PARATYPES: CASIZ 156668, one specimen, 5 mm, dissected, Cemetary Beach, Maricaban Island, Luzon, Philippines, 0.5 m, collected May 2001, Y. Camacho.

**DISTRIBUTION**.— This species has only been reported from Madagascar, Philippine Islands (Rudman 2004 and present study) and from Japan (Nakano 2004).

**ETYMOLOGY**.— The specific name *incusus* is taken from the Latin word meaning anvil, the shape of many of the tubercles of this new species.

**EXTERNAL MORPHOLOGY**.— The body shape is elongate and slightly rounded (Fig. 1G). There is no obvious oral veil as is found in other *Aegires* species. The posterior third of the body is much narrower than the rest of the body. The dorsum has tall, anvil or mushroom-shaped tubercles with flat tops. There are smaller tubercles along the edge of the posterior end of the foot and one prominent tubercle on the tip. Spicules protrude from the tops of all tubercles. The rhinophore pocket is slightly elevated and is usually surrounded by three tubercles that vary in size. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and three tubercles protect the anterior side of the gill pocket. The small gill leaves are bipinnate.

The background color is creamy white and there are a few rounded blotches of tan or light

brown spots between some of the tubercles. The tubercle stalks are white and the flattened tops are either all white or all tan. The rhinophores are creamy white on the specimens with white tubercle tops, or are yellowish on specimens with tan tubercle tops. The gill leaves are white.

**Digestive system**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the large radular sac protrudes noticeably from the posterior-ventral side (Fig. 44). There are two large pear-shaped oral glands that extend from the ventral side of the buccal bulb. The radular formula for a 5 mm specimen is 16 × 13.0.13 (Fig. 45). The jaw (Fig. 45A) is not well developed but has a thickened edge. The teeth are simply hamate, and the innermost tooth is much smaller and thinner than the remaining teeth. Rachidian teeth are absent. The outermost teeth are slightly larger than the middle lateral teeth.

**Reproductive system**.— The reproductive system is triaulic (Fig. 46). The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils twice, then narrows for a short distance before entering the wider deferent duct. The deferent duct enters the long penis, which is as wide as the deferent duct. The penis has small densely packed penial hooks at the distal tip only. The vagina is narrow and was not examined internally. Thus, the presence of spines or hooks cannot be confirmed. The short, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects to the bursa with a longer duct than the oviduct, which leads from the bursa into the female gland mass. The bursa is round and half the size of the ampulla. The receptaculum seminis is ovoid and is approximately one-half the size of the bursa.

**Central nervous system**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 47). The eyes are mid-sized in comparison to other Aegiridae and are sessile on the cerebral-pleural complex. The pedal

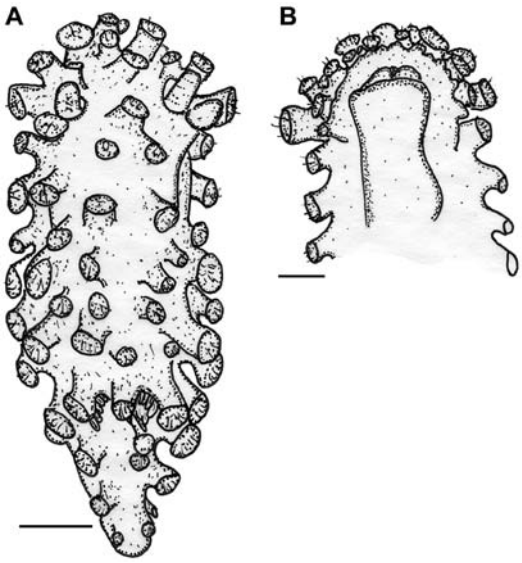



Figure 43. *Aegires incusus* sp. nov. CASIZ 070357. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.57 mm.

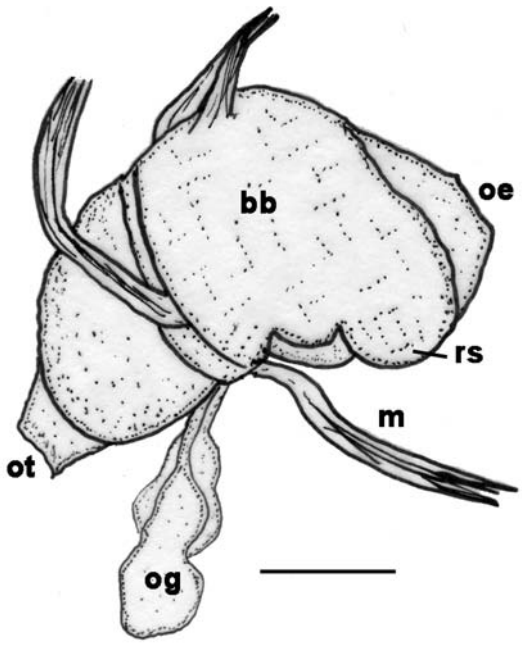



Figure 44. *Aegires incusus* sp. nov. CASIZ 156668. Buccal bulb: bb = buccal bulb, m = muscle, oe = esophagus, og = oral gland, ot = oral tube, rs = radular sac, scale = 0.25 mm.

ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Circulatory system.**— (not pictured) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks.**— *Aegires incusus* is externally most similar to *Aegires pruvotfolae*. For a comparison between these two species, see the section under *Aegires pruvotfolae* in the present study. The particular combi-

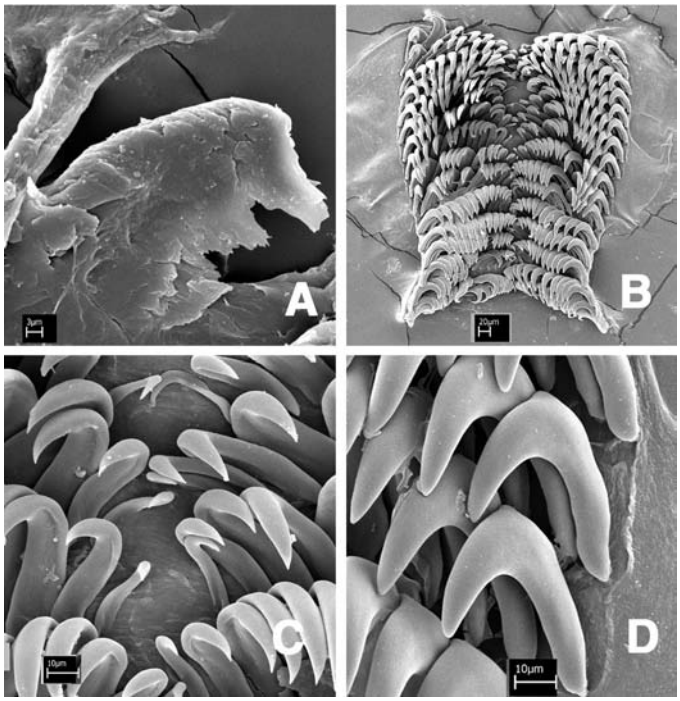



Figure 45. *Aegires incusus* sp. nov. CASIZ 156668. Buccal morphology: (A) Jaw, scale = 3 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

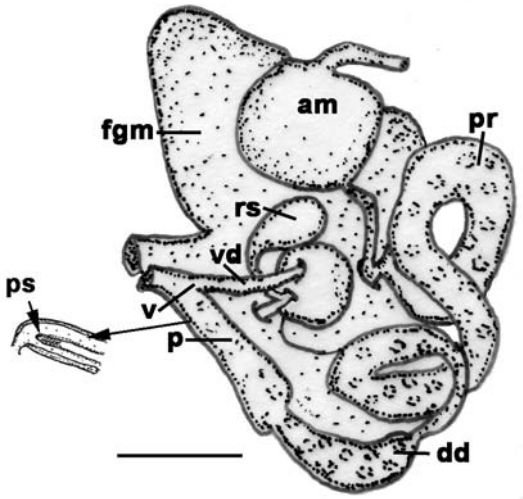



Figure 46. *Aegires incusus* sp. nov. CASIZ 156668. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, ps = penial spines, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

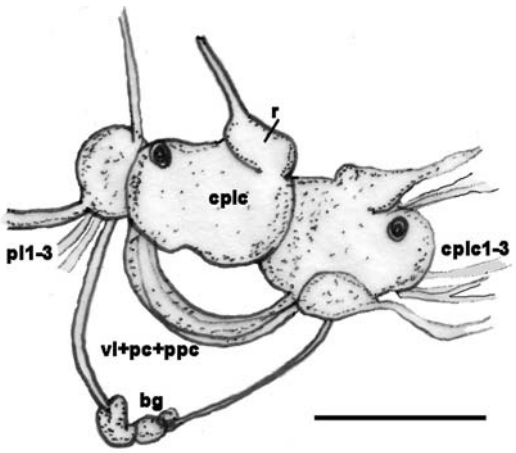



Figure 47. *Aegires incusus* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.25 mm.

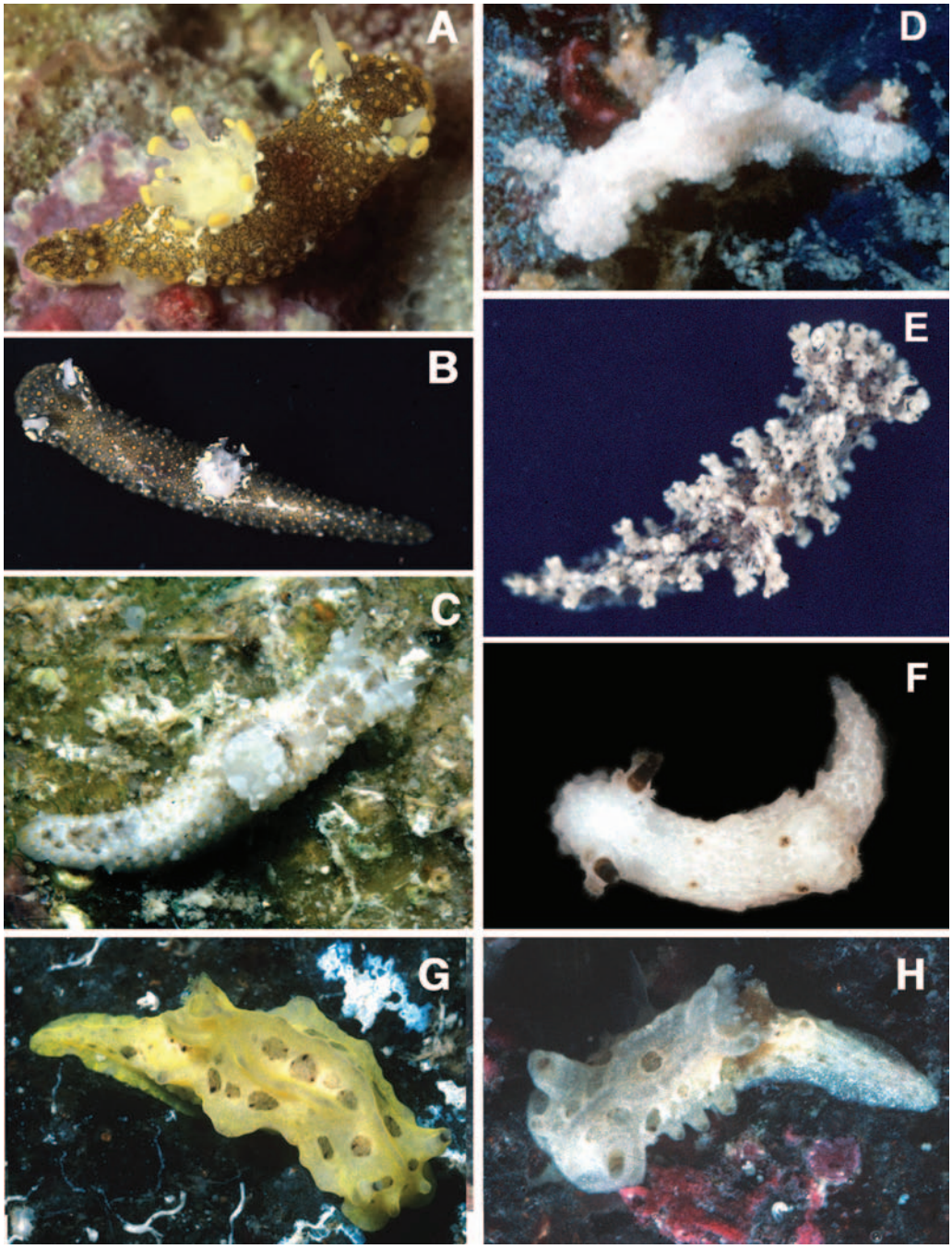



FIGURE 48. Photos of living specimens. (A) *Aegires flores* sp. nov. CASIZ 084277, photo by T. Gosliner, 5 mm. (B) *Aegires flores* sp. nov. CASIZ 078568, photo by P. Fiene, 9 mm. (C) *Aegires flores* sp. nov. CASIZ 120931, photo by S. Johnson, 12 mm. (D) *Aegires petalis* sp. nov. CASIZ 168920, photo by T. Gosliner, 5 mm. (E) *Aegires exeches*. CASIZ 078629, photo by P. Fiene, 4 mm. (F) *Aegires hapsis* sp. nov. CASIZ 115721, photo by R. Bolland, 6 mm. (G) *Aegires sublaevis*. CASIZ168923, photo by T. Gosliner, 12 mm. (H) *Aegires sublaevis* CASIZ, 078393, photo by T. Gosliner, 8 mm.

nation of external, reproductive and radular characters distinguish *A. incusus* as a distinct *Aegires* species.

***Aegires flores* Fahey and Gosliner, sp. nov.**
(Figs. 48A–C, 49–53)

*Aegires citrinus* Nakano, 2004:117, no. 242, top and right photograph. Misidentification.
= *Aegires* sp. 3, Tanaka, 2001 in SeaSlug Forum.

**Type material**.— Holotype: CASIZ 120931, one specimen, 11 mm, Choptop Reef, Enewetak Atoll, Marshall Islands, 8 m, collected August 1988, S. Johnson. Paratypes: CASIZ 120930, one specimen, 13 mm, dissected, Bubble Butt Pinnacle, Enewetak Atoll, Marshall Islands, collected September 1983, S. Johnson. CASIZ 073059, one specimen, 9 mm, Pinnacle, Madang, Papua New Guinea, 5 m, collected, Oct, 1986, T. Gosliner. CASIZ 168922, Outer Reef, Bagabag Island, Papua New Guinea, collected July 1989, T. Gosliner. CASIZ 075909, one specimen, 4 mm, Barracuda Point, Pig Island, Papua New Guinea, 32 m, collected November 1990, T. Gosliner. CASIZ 075877, two specimens, 4 and 7 mm, dissected, Barracuda Point, Pig Island, Madang, Papua New Guinea, 34 m, collected November 1990, T. Gosliner. CASIZ 078568, one specimen, 9 mm, Bunaken Island, Manado, Sulawesi, 3 m, collected May 1991, P. Fiene. CASIZ 084277, one specimen, 5 mm, Devil's Point, Maricaban Island, Luzon, Philippines, 10 m, collected February 1992, T. Gosliner. CASIZ 157153, one specimen, 10 mm, Bethlehem, Maricaban Island, Luzon, Philippines, 7 m, collected May 2001, T. Gosliner.

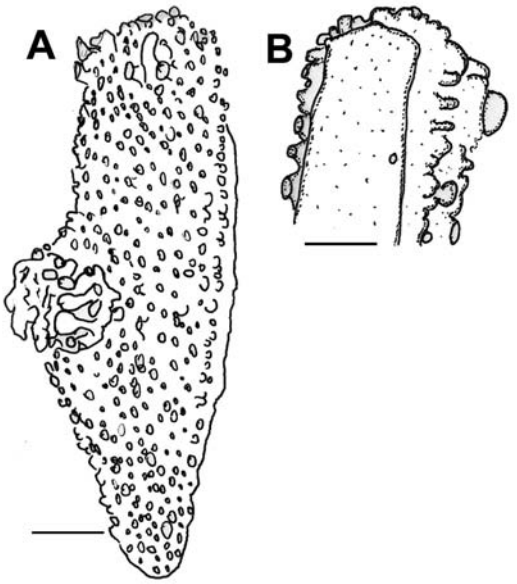



Figure 49. *Aegires flores* sp. nov. CASIZ 120930. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 1.3 mm.

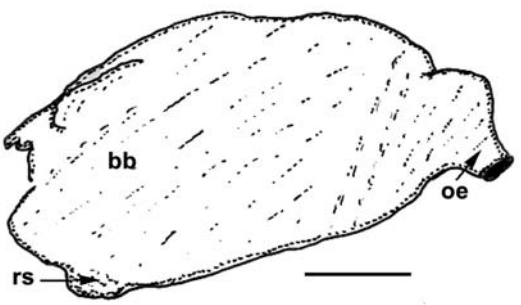



Figure 50. *Aegires flores* sp. nov. CASIZ 120930. Buccal bulb: bb = buccal bulb, rs = radular sac, oe = esophagus, scale = 0.25 mm.

**Distribution**.— This species has been reported from the Marshall Islands, Papua New Guinea, Sulawesi, the Philippine Islands (present study), and from Japan (Nakano and Tanaka 2004).

**Etymology**.— The specific name *flores* is from the Latin word meaning blossom, referring to the shape of the rhinophore and gill protective appendages of this species.

**External morphology**.— The body shape is elongate and slightly rounded (Figs. 48A–C, 49). The dorsum is completely covered by small raised tubercles, some with flat tops and some

with rounded tops. Spicules protrude from the tops of all tubercles. The rhinophore pocket is slightly elevated and is surrounded by approximately five flat-topped tubercles that vary in size. The tubercles on the exterior edge of the rhinophore pocket are large and rounded and look like flower petals. The rhinophores are smooth. The gill pocket lies mid dorsally and is surrounded by approximately twelve flattened, paddle-shaped tubercles in varying sizes, arranged like a crown or an opening flower. The small gill leaves are tripinnate.

The background color of the living animals is cream. The overlying colors range from gray-white with yellow-topped tubercles to brown with orange-topped tubercles. The paddle-shaped tubercles around the gill can be translucent white with white tips or translucent yellow with darker yellow tips. The rhinophores in all color forms are translucent white as are the gill leaves.

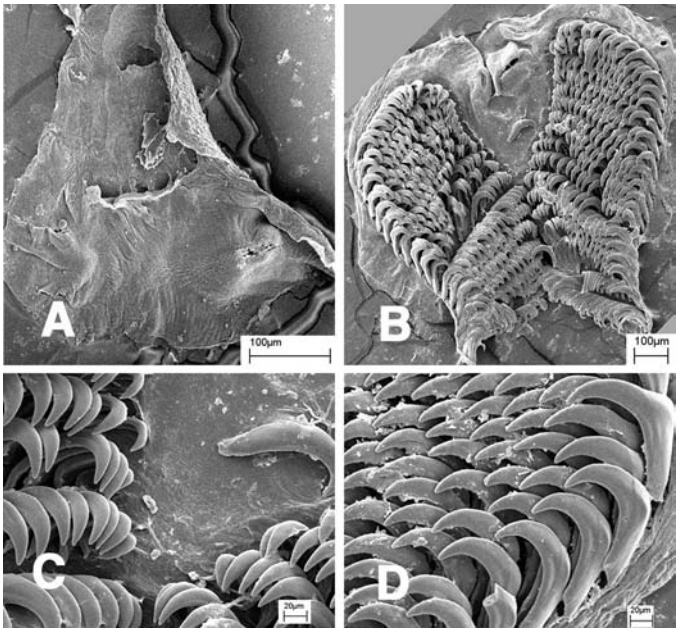



FIGURE 51. *Aegires flores*. sp. nov. CASIZ 120930. Buccal morphology: (A) Jaw, scale =100 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

**DIGESTIVE SYSTEM**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 50). The radular formula is 18 × 17.0.17 for a 7 mm

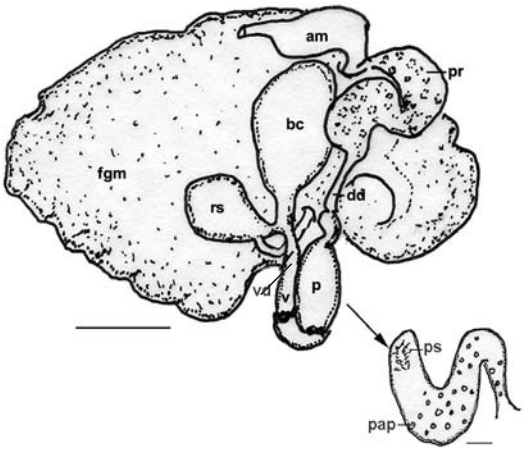



FIGURE 52. *Aegires flores* sp. nov. CASIZ 120930. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pap = papillae, ps = penial spines, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.4 mm.

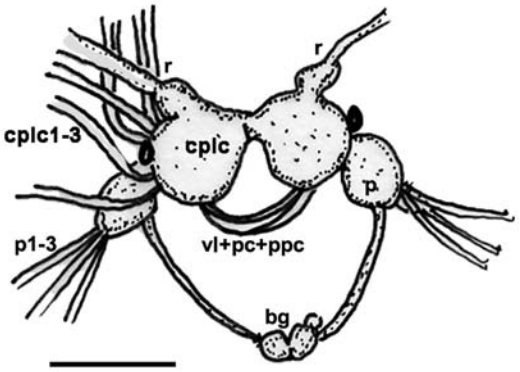



FIGURE 53. *Aegires flores* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

specimen (Fig. 51). The jaw (Fig. 51A) is not well developed but has a thickened edge. All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The oldest teeth have a longitudinal groove on the outer side, a slight bulge at the posterior midpoint and a longer hook than the remaining teeth.

**Reproductive system**.— The reproductive system is triaulic (Fig. 52). The ampulla is short and wide. It branches into the oviduct and the prostate. The prostate is relatively short, tubular and curves once before narrowing into the short deferent duct. The deferent duct then widens into the penis, which has small densely packed penial hooks at the distal tip. There are also several rows of papillae inside the penis, at the proximal end. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters a common duct that connects the bursa copulatrix and the receptaculum seminis. The receptaculum is connected to the oviduct, which enters the female gland mass. The bursa is ovoid and much larger than the ampulla. The receptaculum is ovoid and is approximately one-third the size of the bursa.

**Central nervous system**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 53). The eyes are small, sessile on the cerebral-pleural complex, but protrude slightly. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— *Aegires flores* has a unique external morphology. Although it has an elongate body, a rounded posterior end of the foot, a tuberculate notum, protective tubercles around the rhinophores and gill, and smooth rhinophores, there are several unique characters that set this species apart. Most noticeably, the gill appendages have a unique paddle shape. The tubercles on the outside of the rhinophore pockets also resemble those around the gill, both in shape and in color. The dorsal tubercles are all much lower than the protective tubercles, a feature not shared by other *Aegires* species.

The reproductive morphology is also different from other *Aegires* species. The short, wide ampulla with a short deferent duct is a combination of characters not seen in other *Aegires* species. These features combined with the very short duct leading from the receptaculum to the bursa are not found in other *Aegires*.

The unusual combination of external and internal characters distinguishes *Aegires flores* as a new species.

### *Aegires petalis* Fahey and Gosliner, sp. nov.

(Figs. 48D, 54–57)

**Type material**.— Holotype: CASIZ 168920, one specimen, 5 mm, dissected, Anemone Reef, Madang, Papua New Guinea, collected February 1988, T. Gosliner.

**Distribution**.— This species has only been reported from Papua New Guinea (present study).

**Etymology**.— The specific name *petalis* is taken from the Greek word *petalon* meaning a leaf or petal. This is in reference to the rhinophore sheaths of this new species.

**External morphology**.— The body shape is elongate and the dorsum is high (Fig. 48D).

Flat-topped raised tubercles are arranged in two lines along the anterior half of the dorsum. On the posterior half of the dorsum, the largest tubercles are arranged in a diamond pattern. Additional large, flat-topped tubercles line the edge of the dorsum. Long spicules protrude from the tops of all tubercles (Fig. 54). The rhinophore pocket is tall and cylindrical and has a petal-like outer edge. The rhinophores are smooth. The gill pocket lies mid dorsally and is protected by three appendages that have flattened tops. The small gill leaves are tripinnate.

The background color of the living animal is white, as are the tubercles, the rhinophores and the gill leaves. There are no additional colors on the specimen examined in this study.

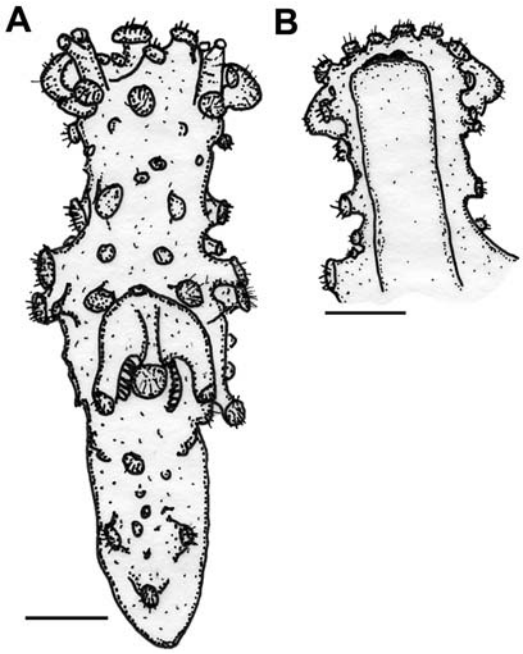



FIGURE 54. *Aegires petalis* sp. nov. CASIZ 168920. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm.

**DIGESTIVE SYSTEM**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 55). The radular formula is 13 × 13.0.13 for the 5 mm holotype (Fig. 56). The jaw (Fig. 56A) is not well developed but has a thickened edge. All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are thinner and smaller than the remaining teeth. The oldest teeth have a shallow longitudinal groove on the outer side.

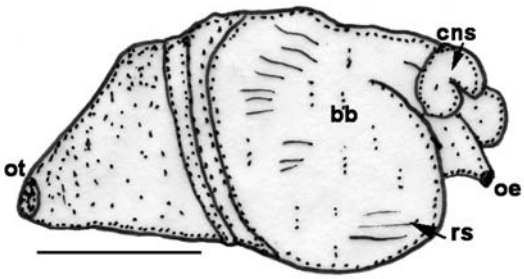



FIGURE 55. *Aegires petalis* sp. nov. CASIZ 168920. Buccal bulb: bb = buccal bulb, cns = central nervous system, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.3 mm.

**REPRODUCTIVE SYSTEM**.— The reproductive system is triaulic (Fig. 57). The ampulla is elongate and narrow. It branches into the oviduct and the prostate. The prostate is long, tubular and coils once before narrowing into the long, thin deferent duct. The deferent duct then widens into the short but wide penis, which has small, densely packed hooks at the distal tip only. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is short and narrow and at the proximal end, enters the bursa copulatrix. A duct from the bursa enters the bifurcating oviduct that originates from the receptaculum. The oviduct enters the female gland mass. The bursa is ovoid and smaller than the round receptaculum.

**CENTRAL NERVOUS SYSTEM**.— The central nervous system has fused cerebral and pleural ganglia (not pictured). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two

buccal ganglia are positioned ventral to the esophagus.

**Circulatory system.**— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks.**— Externally, *Aegires petalis* most closely resembles *A. ortizi*. Both species are either white or creamy yellow (*A. ortizi*) and have dorsal tubercles. However, the tubercles of *A. ortizi* are arranged in four longitudinal rows (Templado et al. 1987) whereas in *A. petalis* the tubercles are randomly scattered. *Aegires ortizi* also has brown coloration and minute white spots between the tubercles, which *A. petalis* does not have. There are three large tubercles on the outside of the rhinophore sheaths of *A. ortizi* but the rhinophore margins of *A. petalis* are elevated and multi-lobed. The three gill appendages of *A. petalis* have flattened tops, but in *A. ortizi* the appendages are pointed.

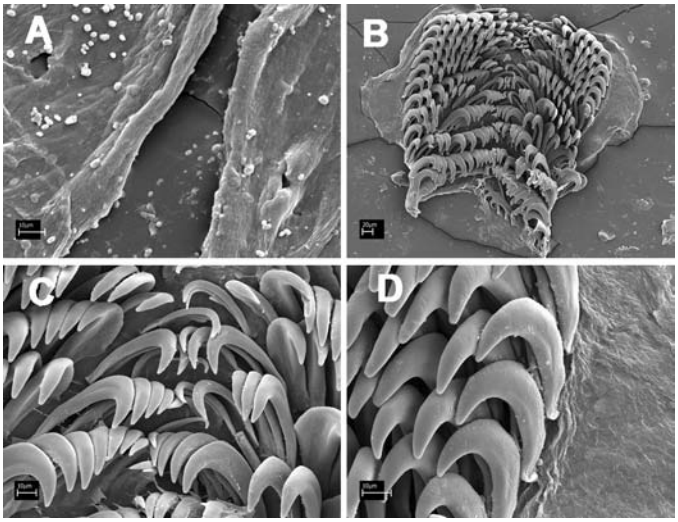



Figure 56. *Aegires petalis* sp. nov. CASIZ 168920. Buccal morphology: (A) Jaw, scale =10 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

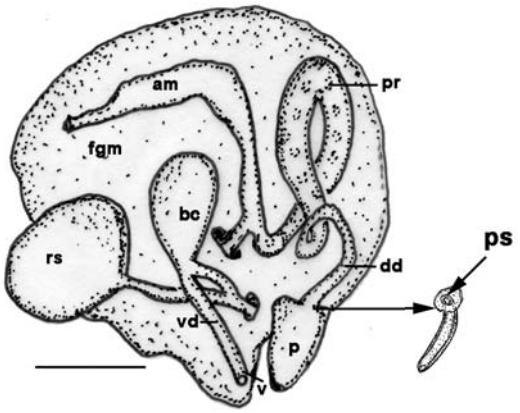



Figure 57. *Aegires petalis* sp. nov. CASIZ 168920. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis; pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina; vd = vaginal duct, scale = 0.5 mm.

The reproductive morphology differs between *Aegires petalis* and *A. ortizi*. Although both have an elongate ampulla, the ampulla of *A. petalis* is relatively longer. The penial morphology is noticeably different. The penis of *A. petalis* is short and thick, and that of *A. ortizi* is very long and wide. In addition, *A. petalis* only has penial spines at the distal tip while they are found throughout the penis of *A. ortizi*. The prostate of *A. ortizi* is also very thick and tubular, whereas in *A. petalis* it is much thinner and coiled. The receptaculum of *A. petalis* is larger than the bursa and connects to the common oviduct. But in *A. ortizi* the receptaculum is much smaller than the bursa and connects on a very long separate duct to the base of the bursa.

This combination of morphological characters sets *A. petalis* apart from other species of *Aegires*.

### *Aegires execheS* Fahey and Gosliner, sp. nov.

(Figs. 48E, 58–61)

*Aegires punctilucens* Nakano, 2004:117, no. 243. Misidentification.

*Aegires punctilucens* Imamoto 2002: photos, SeaSlug Forum. Misidentification.
*Aegires punctilucens* Ono, 1999:71, no. 103. Misidentification.
*Aegires* cf. *punctilucens* Marshall and Willan, 1999:59, pl. 93. Misidentification.
*Aegires punctilucens* Baba, 1974:11-12, Fig. 1. Misidentification.

**Type material**.— Holotype: CASIZ 078629, 4 mm, Hekili Point, Maui, Hawaii, 1 m, collected May 1991, C. Pittman. Paratype: CASIZ 168918, 4 mm, dissected, Hekili Point, Maui, Hawaii, 1 m, collected May 1991, C. Pittman. Paratypes: CASIZ 109790, 3 mm, Pig Island, Madang, Papua New Guinea, no depth available, collected October 1996, T. Gosliner. CASIZ 068750, 2 mm, Jais Aben, Madang, Papua New Guinea, 15 m, collected July 1989, T. Gosliner. CASIZ 075804, 2 mm, between Wongat and Tabat Islands, Madang, Papua New Guinea, 23 m, collected November 1990, T. Gosliner, G. Williams, M. Jebb. CASIZ 079183, 2 mm, Horseshoe Cliffs, Onna Village, Okinawa, 5 m, collected June 1991, T. Gosliner. CASIZ 115394, 4 mm, Maeki-zaki, Seragaki, Okinawa, 46 m, collected, April 1997, R. Bolland.

**Distribution**.— This species has been reported from Hawaii, Japan, Papua New Guinea (present study), the Marshall Islands (S. Johnson photo) and the Great Barrier Reef, Australia (Marshall and Willan 1999).

**Etymology**.— The specific name *exeches* is from the Greek *exechos* meaning jutting out, projecting, prominent, which refers to the shape of the tubercles on this species.

**External morphology**.— The body shape is elongate and the posterior end of the foot ends in a point (Fig. 48E). There are numerous compound tubercles projecting from the dorsum, such that the body appears to be composed completely of tubercles (Fig. 58). The tubercles are elongate and narrow slightly before mushrooming into a flattened plate-like top. From the flattened tops, multiple spicules protrude. The rhinophore pockets are very long and are composed of two main tubercles on the anterior side, two shorter tubercles on the posterior side and much smaller tubercles in between. The rhinophores are smooth and have bifid apices. The gill protective appendages are also composed of elaborate tubercles. The gill leaves themselves are small, inconspicuous and tripinnate.


Figure 58. *Aegires exeches* sp. nov. CASIZ 168918. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm.

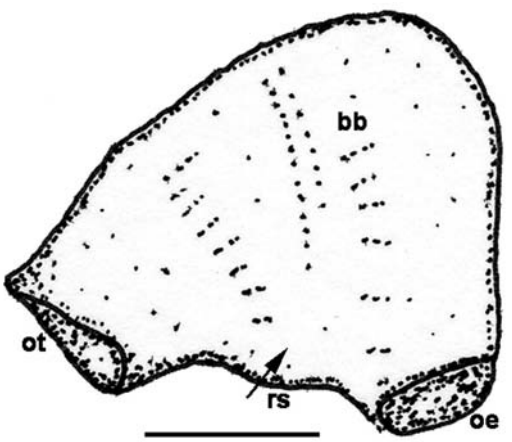



Figure 59. *Aegires exeches* sp. nov. CASIZ 168918. Buccal bulb: bb = buccal bulb, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.17 mm.

The background color ranges from white to tannish-white. The tops of the tubercles on the tan specimens have dark spots. The specimen from Enewetak, Marshall Islands is completely white. It has three evenly spaced, pale tan rings around the rhinophores. The tan specimens have three to four blue spots on the dorsum. These spots are arranged symmetrically, with two just posterior to the rhinophores, one at the centerline in front of the gill and the fourth at centerline just posterior to the gill.

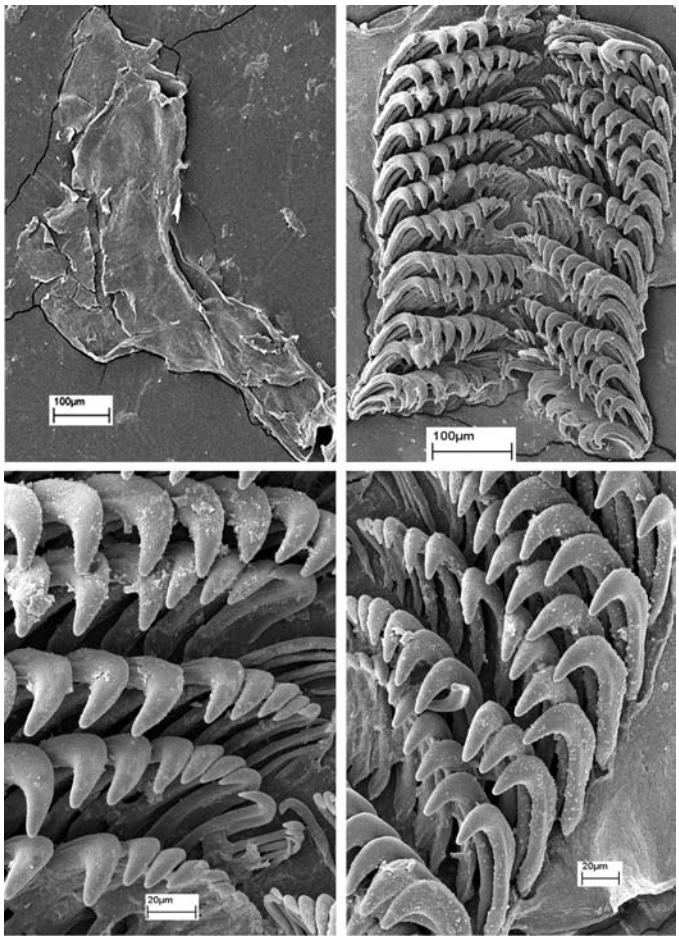



FIGURE 60. *Aegires exeches* sp. nov. CASIZ 168918. Buccal morphology: (A) Jaw. Scale =100 µm. (B) Whole radula. Scale = 100 µm. (C) Inner lateral teeth. Scale = 20 µm. (D) Outer lateral teeth. Scale = 20 µm.

**DIGESTIVE SYSTEM**— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 59). The radular formula is $13 \times 11.0.11$ for the 4 mm specimen (Fig. 60). The jaw is not well developed but has a thickened edge (Fig. 60A). All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are thinner and smaller than the remaining teeth. The oldest teeth have a shallow longitudinal groove on the outer side.

**REPRODUCTIVE SYSTEM**.— The reproductive system is triaulic (Fig. 61). The ampulla is a very long, thick tube. It branches into the oviduct and the prostate. The prostate is shorter, but also tubular and does not coil before narrowing into the very long, thin deferent duct. The deferent duct coils once near the entry to the wide penis, which has small irregularly spaced hooks along the entire length of the penis. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct, which originates from the small ovoid receptaculum seminis, enters the vaginal duct. The oviduct enters the female gland mass. The bursa is small and nearly round.

**CENTRAL NERVOUS SYSTEM**.— The central nervous system has fused cerebral and pleural ganglia (not pictured). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the

visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebropleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Externally, *Aegires exeches* most closely resembles *A. punctilucens* from the Mediterranean. However, there are both external and internal differences that separate these two species. The most obvious external differences are the body shape, rhinophoral apices, gill protective structure morphology and tubercle arrangement. *Aegires exeches* has a very elongate body with extremely elevated, unique tubercles. That is, they are nearly mushroom-shaped, with a flat crown and completely cover the dorsum. D'Orbigny also described the body shape of *A. punctilucens* as being elongate, with a broadening at the midpoint. He described the tubercles of *A. punctilucens* as conical, with a flattened top, and a definite symmetry to their arrangement. Schmekel and Portmann (1982) also illustrated and described the tubercles on the specimens from the Mediterranean as being much shorter and wider at the base and symmetrically arranged, such that there are smooth parts of the dorsum visible between them. In *A. exeches*, no smooth spaces exist between the tubercles, which are taller, narrower at the base and more densely arranged than on *A. punctilucens*.

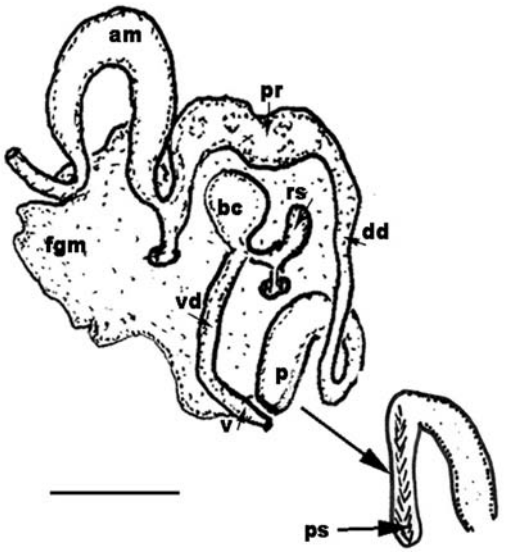



Figure 61. *Aegires exeches* sp. nov. CASIZ 168918. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

The rhinophores of *A. exeches* have bifid apices whereas the rhinophores of *A. punctilucens* do not (see Schmekel and Portmann 1982 for an illustration).

The gill protective structure of *Aegires exeches* is also different from that of *A. punctilucens*. *Aegires exeches* has a very elaborate, lobed gill structure, while *A. punctilucens* has three simple tubercles (see Schmekel and Portmann 1982 for a drawing of the Mediterranean specimens).

When comparing the external coloration, both species can be white or light brown. But Schmekel and Portmann describe minute opaque white dots spotted over the brown color, and the iridescent "eye" spots have a brownish-red circular area around them, bordered with black-brown dots. Specimens of *Aegires exeches* from Okinawa, Hawaii and the Marshall Islands do not have any opaque white dots over the dorsal color, but do have iridescent spots, although in much fewer numbers than is found on *A. punctilucens*. The "eye" spots on *A. exeches* can also be surrounded by a border of black-brown dots and a smooth orange circle surrounding the center as seen in photos on the SeaSlug Forum (Rudman 2004).

There are significant differences in the reproductive morphology between these two species. Although d'Orbigny didn't describe or illustrate the reproductive organs of *A. punctilucens*, Schmekel and Portmann drew the anatomy of specimens from the Mediterranean. Most noticeably, *A. exeches* has a receptaculum seminis that attaches to the base of the bursa copulatrix. In *A. punc-*

*tilucens* the receptaculum connects directly to the bulbous vagina. The prostate of *A. exeches* is short, tubular and nearly as thick as the ampulla, whereas in *A. punctilucens* the prostate is very thick and sausage-shaped and very coiled. *Aegires exeches* has a very long, tubular ampulla, a narrow vagina and a long, thin vaginal duct. *Aegires punctilucens* has a very bulbous ampulla and a very wide vagina, with a thick vaginal duct.

There are two differences in the radular teeth between these two species. Schmekel and Portmann illustrate an inner lateral tooth that is substantially smaller than the rest of the teeth in the row. They also state that the size increases outwards. In *A. exeches*, the first three lateral teeth are smaller than the remaining teeth, which are all the same size. In *A. exeches,* the radular formula is 14 × 11.0.11 for a 4 mm specimen. Schmekel and Portmann give a radular formula for a 6 mm specimen of 16 × 18.0.18.

Baba (1974) described a specimen found in the Sado district of the Japan Sea as *Aegires punctilucens*. Comparison of Baba's drawings and description of that specimen to our specimens of *Aegires exeches* leads us to believe that Baba's specimen is also *A. exeches.*

Whereas *A. exeches* bears some external similarities to the Mediterranean *A. punctilucens*, the Indo-Pacific specimens clearly represent a distinct species.

### *Aegires hapsis* Fahey and Gosliner, sp. nov.

(Figs. 48F, 62–66)

**Type material**.— Holotype: CASIZ 115721, one specimen, 6 mm, dissected, Horseshoe Cliffs, Okinawa, Ryukyu Islands, 3 m, collected March 1998, R. Bolland.

**Distribution**.— This species has only been reported from Okinawa (present study).

**Etymology**.— The specific name *hapsis* is a Greek word meaning mesh or network, a word that describes the fine white webbing that covers the dorsum of this species.

**External morphology**.— The body shape is elongate (Fig. 48F, 62). The dorsum has small raised tubercles, arranged in a somewhat regular fashion on the sides of the dorsum and along the midline behind the gill. Spicules protrude from the tops of all tubercles. The rhinophore pocket is raised and the outer edge is formed by three large tubercles. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and is protected by a tri-lobed appendage. Each appendage is further divided into 4–5 smaller lobes. The small gill leaves are tri-pinnate.

The background color is pale tan and white. There is a fine network of white webbing covering the dorsum, especially noticeable on the posterior third, behind the gill pocket. There are small brown dots on either side of the dorsum midline. The tubercles that lie on the edge of the rhinophore pocket have a dark brown top. The rhinophores are dark brown. The gill branches are white.

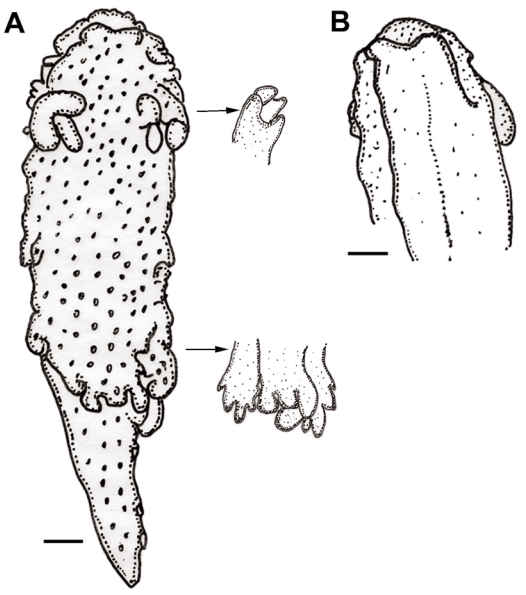
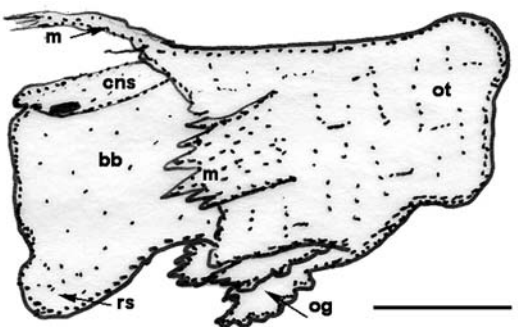



Figure 62. *Aegires hapsis* sp. nov. CASIZ 115721. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.4 mm.

FIGURE 63 (right). *Aegires hapsis* sp. nov. CASIZ 115721. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac, scale = 0.3 mm.



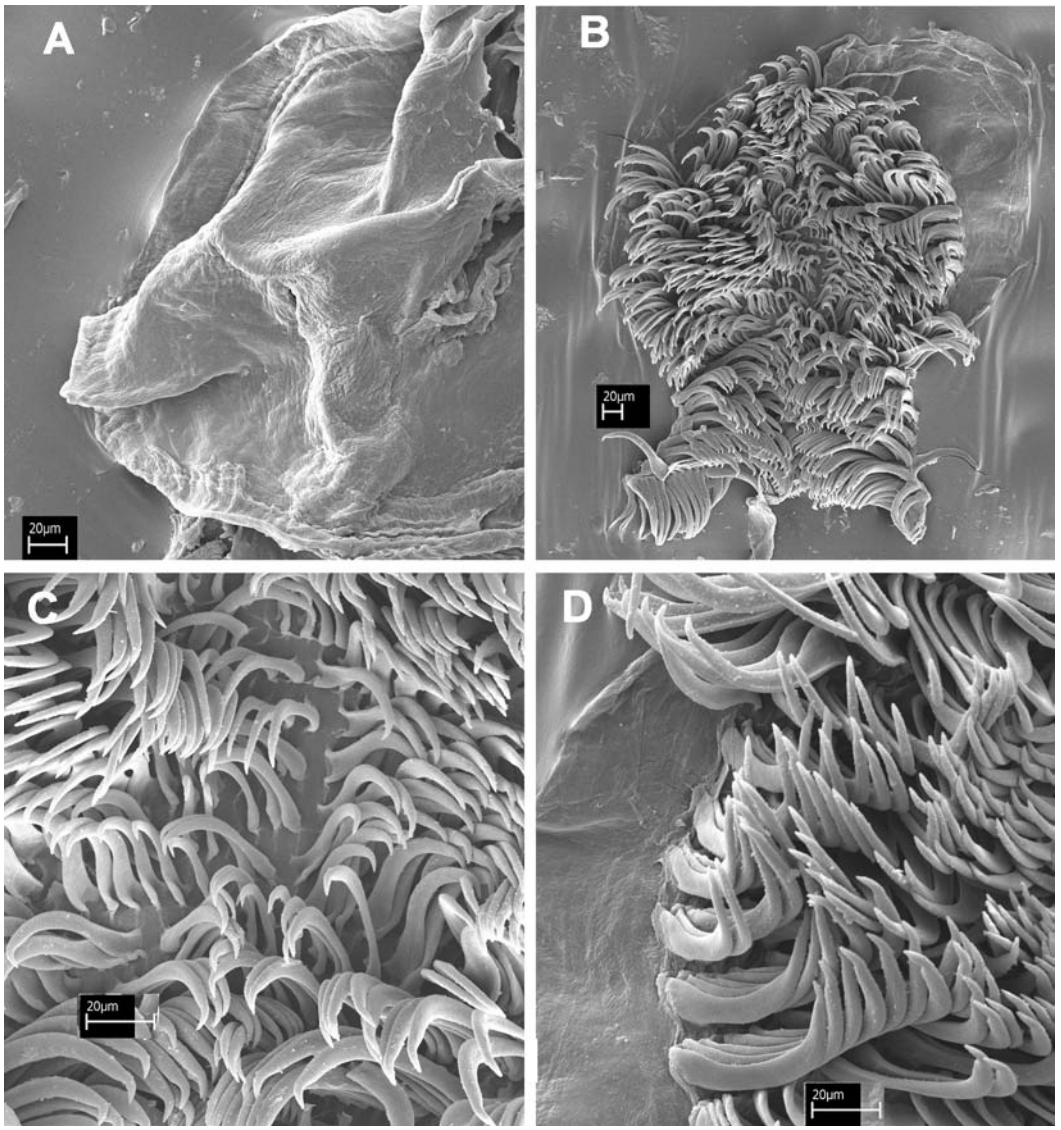




FIGURE 64. *Aegires hapsis* sp. nov. CASIZ 115721. Buccal morphology: (A) Jaw, scale =20 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

**Digestive system**.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes noticeably from the posterior side (Fig. 63). Large oral glands on either side of the oral tube extend markedly from the base of the oral tube. The radular formula is difficult to confirm owing to the very compressed, flattened tooth arrangement, but is approximately 18-20 × 20-21.0.20-21 for the 4 mm specimen (Fig. 64). The jaw (Fig. 64A) has a thickened edge and rounded thickenings at each side. All teeth are hamate, with a long hook on the inner lateral teeth and a shorter hook on the outer teeth. The tips of the teeth are recurved. Rachidian teeth are absent. Some inner lateral teeth have a sharper hook than the remaining teeth. There is no longitudinal groove on the oldest lateral teeth as found in other *Aegires* species.

**Reproductive system**.— The reproductive system is triaulic (Fig. 65). The ampulla is very large and bulbous. It branches into the oviduct and the prostate. The prostate is tubular and coils once before narrowing into the very long, thin deferent duct. The deferent duct then widens into the penis. The penis was subsequently lost during preparation, and thus the presence of hooks could not be confirmed. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct, which originates from the small peanut-shaped receptaculum seminis, enters the vaginal duct. The oviduct enters the female gland mass. The bursa is ovoid and small.

**Central nervous system**.— The central nervous system has fused cerebral and pleural ganglia (Fig. 66). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

**Circulatory system**.— (not shown) As with other species of *Aegires*, the heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Externally, *Aegires hapsis* does not closely resemble any other *Aegires* species. Only *A. malinus* has a similarly smooth dorsum with a fine network pattern overall and tiny dorsal

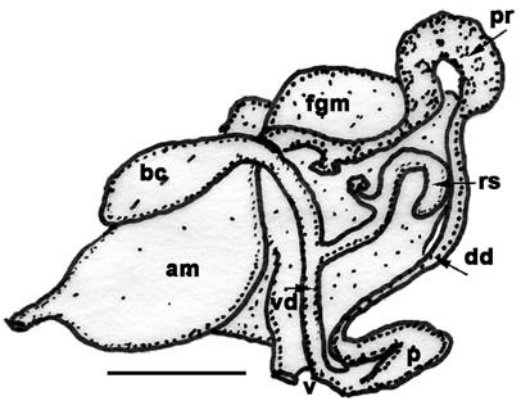



Figure 65. *Aegires hapsis* sp. nov. CASIZ 115721. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, r = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

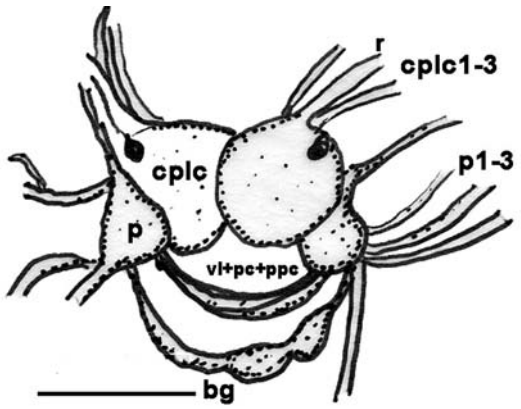



Figure 66. *Aegires hapsis* sp. nov. CASIZ 115721. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.25 mm.

tubercles. But that species has a very different background color (red-brown) and apple green rhinophoral and gill appendages.

The radular teeth of *A. hapsis* are different from other species as well. In *A. hapsis* the teeth are much more elongate and numerous than found in other species. For example, the inner lateral teeth have a longer hook than the outer lateral teeth and most teeth have a downward bend at the tip. This feature is not found in any other *Aegires* species.

The reproductive morphology has some similarities to other *Aegires*. The long thin deferent duct and the wider, tubular prostate are features shared with *A. exeches, A. incusus* and *A. malinus*. *Aegires ninguis* and *A. incusus* also have a large, balloon-shaped ampulla like *A. hapsis*. However, the combination of a large ampulla, a long thin deferent duct with a wider prostate combined with a receptaculum that leads from a separate duct into the vaginal duct is not shared by any of the other *Aegires* species.

The particular combination of morphological characters separates *Aegires hapsis* as a distinct species.

### Taxa formerly included in the Genus *Notodoris* Bergh, 1875

TYPE SPECIES: *Notodoris citrina* Bergh, 1875:64, by monotypy.

**DIAGNOSIS**.— Both Bergh (1875) and Eliot (1906) provided a complete diagnosis for the genus: the body is limaciform, with no distinction between the back and sides. The body is hard, rough and rugose and the surface is filled with spicules. The frontal veil is large. The rhinophores are smooth, retractable and protected by valves. The gill is protected by a large valve, is sometimes quite ramified and not retractable. The radula has no rachidian tooth, but has numerous hamate uniform lateral teeth, which have a rudimentary secondary denticle below the main hook.

**REMARKS**.— Bergh did not assign the family name Notodorididae to his new genus. The first author to use this name was Eliot (1910). See the earlier discussion on the history of the classification.

### *Aegires citrinus* (Bergh, 1875)

(Figs. 67–71)

*Notodoris citrina* Bergh, 1875:53–100
*Aegires citrinus* (Bergh) comb. nov.

**TYPE MATERIAL**.— Rarotonga, Pacific Ocean. The type material has been lost and therefore, specimens from other Indo-Pacific localities have been examined for this study.

**MATERIAL EXAMINED**.— CASIZ 116864, one specimen, 52 mm, dissected. Rottnest Island, Western Australia, collected December 1998, S. Fahey. CASIZ 113597, one specimen, 23 mm, dissected. Laiwan Island, Louisiade Archipelago, Papua New Guinea, collected June 1998, T. Gosliner.

**DISTRIBUTION**.— Australia, Cook Islands, Fiji, Marshall Islands, Papua New Guinea, Solomon Islands, and New Caledonia (Bergh 1875; SeaSlug Forum, accessed 1 March 2004 and present study).

**EXTERNAL MORPHOLOGY**.— Bergh (1878) described the external morphology of this species. No differences were found between Bergh's description and the specimens examined for the present study.

**DIGESTIVE SYSTEM**.— *Aegires citrinus* shares the same general digestive anatomy (Fig. 67) as other *Aegires* (formerly *Notodoris*) species (Figs. 3B, 8B). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the diges-

tive gland. The buccal bulb is nearly round, with four large muscles attached, two per side (Fig. 67). The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with no indication of rods at the edge (Figs. 68A, 69A). The radular teeth of the specimens examined from Western Australia and the Marshall Islands are as described by O'Donoghue (1924). That is, the teeth are so closely packed together that they are difficult to count (Figs. 68–69). The teeth are tall and hamate, with a small denticle under the tip of each tooth. All lateral teeth are similar in size and there is no sign of a rachidian tooth.

**Reproductive system**.— The reproductive system is triaulic (Fig. 70). The ampulla is very long, thick and tubular. It branches into the oviduct and the prostate. The tubular prostate is thinner, though much longer and coiled than the ampulla and it narrows appreciably into the short deferent duct. The deferent duct enters the very wide penis. The penis has small, sparsely spaced penial hooks near the opening at the genital atrium. The vagina is much narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa via a long separate duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is round and the same size as the large, ovoid receptaculum seminis.

**Central nervous system**.— As with species of both *Notodoris* and *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 71). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

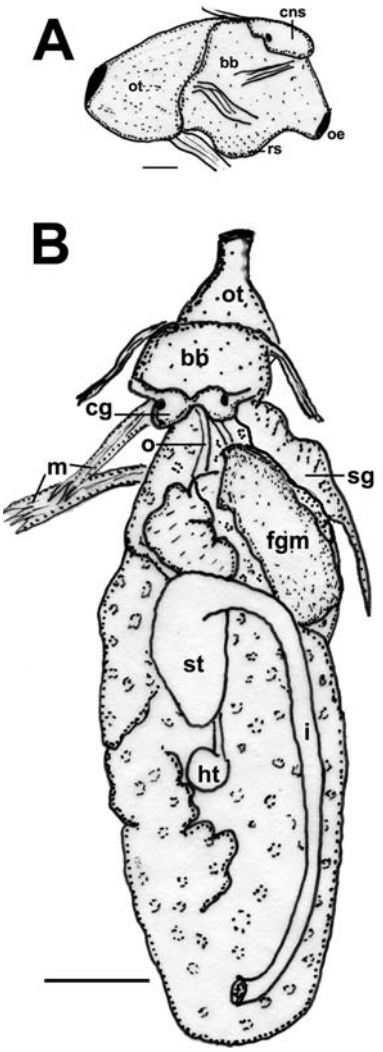



Figure 67. *Aegires citrinus* (Bergh, 1875). (A) Buccal bulb: CASIZ 113597. Scale = 0.46 mm. bb = buccal bulb, cns = central nervous system, oe = esophagus, ot = oral tube, rs = radular sac. (B) Digestive system: CASIZ 116864. Scale = 6.4 mm. bb = buccal bulb, cg = cerebral ganglia, fgm = female gland mass, ht = heart, i = intestine, m = muscles, o = esophagus, ot = oral tube, st = stomach, sg = salivary glands.

**Circulatory system**.— The heart (Fig. 67B) is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Bergh's (1875) description of this species was thorough and his drawings

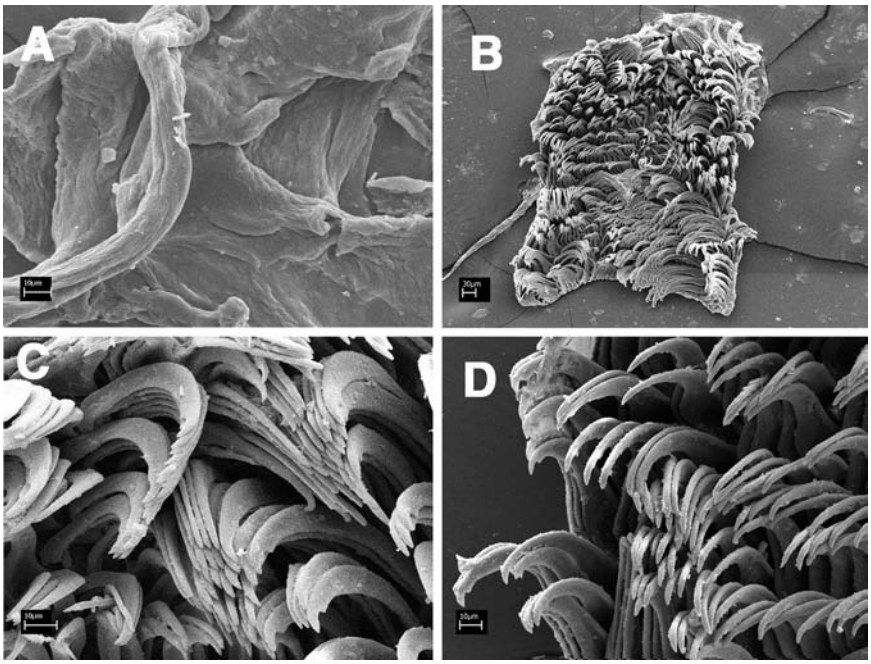



FIGURE 68. *Aegires citrinus* (Bergh, 1875). CASIZ 113597. Buccal morphology: (A) Jaw, scale =10 µm. (B) Whole radula, scale = 30 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

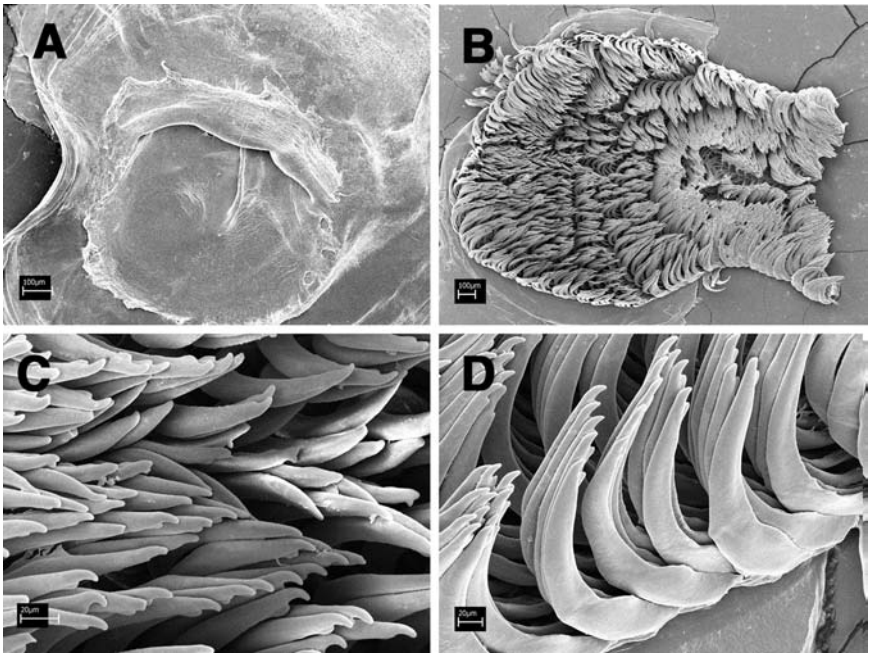



FIGURE 69. *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Buccal morphology: (A) Jaw, scale =100 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

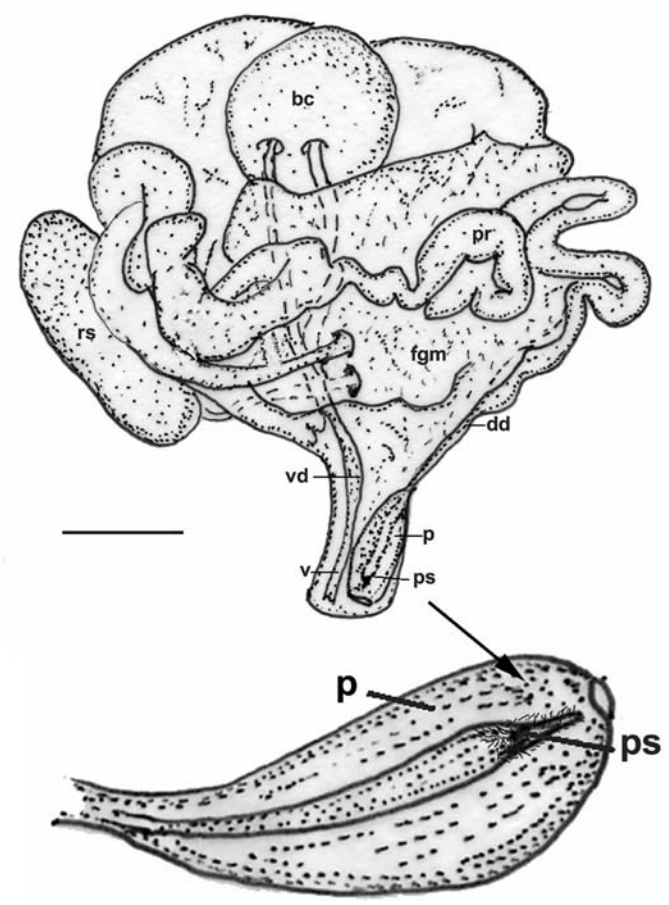



FIGURE 70 (right). *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 1.4 mm.

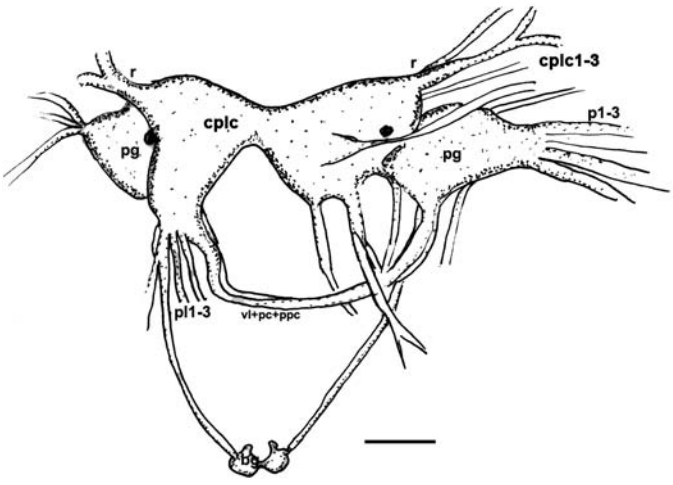



FIGURE 71. *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, pg = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.5 mm.

include the external, radular, reproductive and central nervous system morphology. O'Donoghue (1924) provided additional details of the anatomy and radular morphology and Gosliner and Behrens (1997) examined all *Notodoris* species except *N. citrinus* during their study of the new species, *N. serenae*. However, none of these recent authors confirmed Bergh's descriptions of the central nervous system, reproductive or digestive systems of *Notodoris citrinus*. For the present study, specimens were examined from localities other than the type locality to determine the extent of variation.

### *Aegires gardineri* (Eliot, 1906)

(Fig. 72)

*Notodoris gardineri* Eliot, 1906: 540–573, pl. 32.
*Notodoris megastigmata* Allan, 1932:103.
*Aegires gardineri* (Eliot) comb. nov.

**Type material**.— Hulule, Maldive Islands. Holotype: 1919.10.7.47, one specimen, 3.35 cm, collected by Professor J.S. Gardiner, British Museum of Natural History.

**Material examined**.— CASIZ 106060, one specimen, 50 mm, dissected. Okinawa, Ryukyu Islands, collected 14 May 1995, R. Bolland.

**Distribution**.— Maldive Islands, Indonesia, Papua New Guinea, Okinawa, Western Caroline Islands, Solomon Islands and Australia (Eliot 1906; Marshall and Willan 1999; Coleman 2001; Rudman 2004; present study).

**External morphology**.— The external morphology of *Notodoris gardineri* was described in detail by several authors (O'Donoghue 1924; Yonow 1993; Rudman 2004).

**Reproductive system**.— Gosliner and Behrens (1997) illustrated and described the reproductive anatomy of *Notodoris gardineri*.

**Digestive system**.— *Aegires* (formerly *Notodoris*) *gardineri* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round, with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thin cuticle (see also O'Donoghue 1924 and Yonow 1993). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

**Central nervous system**.— As with other species of previously included *Notodoris*, the cerebral and pleural ganglia are fused together (Fig. 72). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-

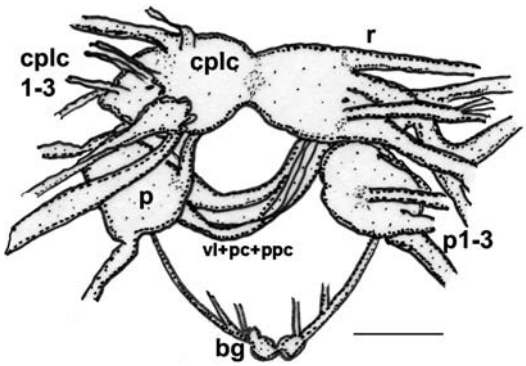



Figure 72. *Aegires gardineri* (Eliot, 1906). CASIZ 106060. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.5 mm.

esophageal, rhinophoral and optical ganglia are present.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Eliot (1906) described both the external and radular morphology of *Notodoris gardineri.* However, he did not describe nor illustrate the radular teeth except to note that they fit Bergh's (1875) plate IX exactly. O'Donoghue (1924) and Yonow (1993) provided further descriptions of the radular morphology.

Eliot also did not examine the reproductive anatomy, stating that the specimen he obtained was "too hardened" to examine. Although Gosliner and Behrens (1997) examined all *Notodoris* species except *N. citrinus*, they did not describe the central nervous systems or the digestive systems of the previously included *Notodoris* species. Therefore, additional specimens were examined to complete the data for the present study.

### *Aegires minor* (Eliot, 1904)

(Figs. 73–74)

*Notodoris minor* Eliot, 1904: 83–105, pls 3–4.
*Aegires minor* (Eliot) comb. nov.

**Type material**.— Chuaka, East coast of Zanzibar. Type: 1919.9.16.4, one specimen, 13 mm. British Museum of Natural History.

**Material examined**.— CASIZ 068668, fourteen specimens; one specimen, 65 mm dissected. Madang, Papua New Guinea, collected August 1989, T. Gosliner.

**Distribution.** Zanzibar, Mauritius, Oman, Philippines, Eastern Caroline Islands, Solomon Islands, Papua New Guinea, Manado, Sulawesi, Indonesia, and Australia (Eliot 1904; Gosliner, Behrens, and Williams 1996; Rudman 2004).

**External morphology**.— The external morphology of the specimens examined for this study is as described by Eliot (1904) and corroborated by O'Donoghue (1924), Yonow (1993) and Gosliner and Behrens (1997).

**Digestive system**.— *Aegires minor* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round (Fig. 73) with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a cuticle. The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

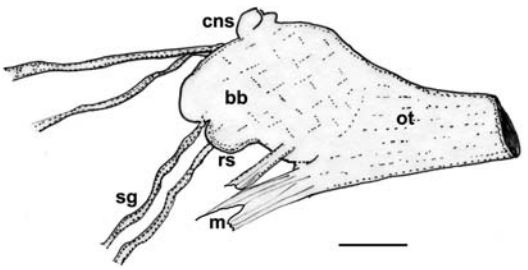



Figure 73. *Aegires minor* (Eliot, 1904). CASIZ 068668. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscles, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 1.75 mm.

**Central nervous system**.— As with other species of *Aegires* (formerly *Notodoris*), the cerebral and pleural ganglia are fused together (Fig. 74). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to

most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— Eliot (1904) described the external and the radular morphology of this species, but only described and drew one feature of the reproductive anatomy: the armed penis. Gosliner and Behrens (1997) examined all *Notodoris* species during their study of the new species *N. serenae*. But they did not describe the central nervous systems or the digestive systems of *Aegires* (*Notodoris*) at that time. Therefore, additional specimens of *Aegires minor* were examined to complete the data for the present study.

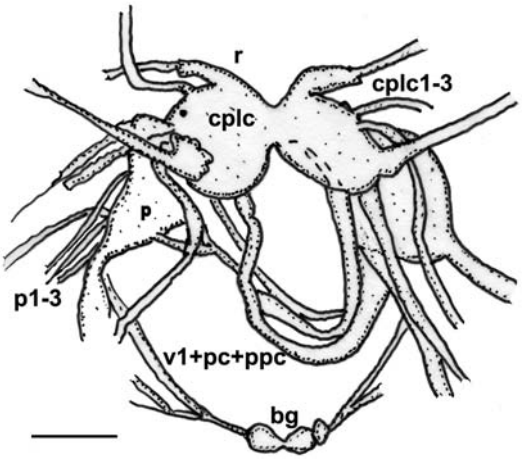



Figure 74. *Aegires minor* (Eliot, 1904). CASIZ 068668. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.75 mm.

### *Aegires serenae* (Gosliner and Behrens, 1997)

(Figs. 75–76)

*Notodoris serenae* Gosliner and Behrens, 1997: 303–307, Figs 7C, 12A–C, 13.
*Aegires serenae* (Gosliner and Behrens) comb. nov.

**Type material**.— For a complete list of the type material see Gosliner and Behrens (1997).

**Material examined**.— Paratype: CASIZ 107229, two specimens; one specimen 57 mm, dissected. Madang, Papua New Guinea, collected August 1989, T. Gosliner and D. Behrens.

**Distribution**.— Belau, Papua New Guinea, Philippines, Indonesia, Malaysia, Pohnpei, Guam, and Okinawa (Gosliner and Behrens 1997; C. Carlson and P.J. Hoff, pers. commun.).

**Digestive system**.— *Aegires serenae* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round (Fig. 75) with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thin cuticle. The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

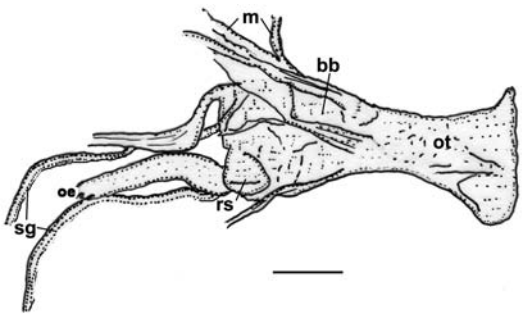



Figure 75. *Aegires serenae* (Gosliner and Behrens, 1997). CASIZ 107229. Buccal bulb: bb = buccal bulb, m = muscles, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 2 mm.

**Central nervous system**.— As with other species of *Aegires* (formerly *Notodoris*),

the cerebral and pleural ganglia are fused together (Fig. 76). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

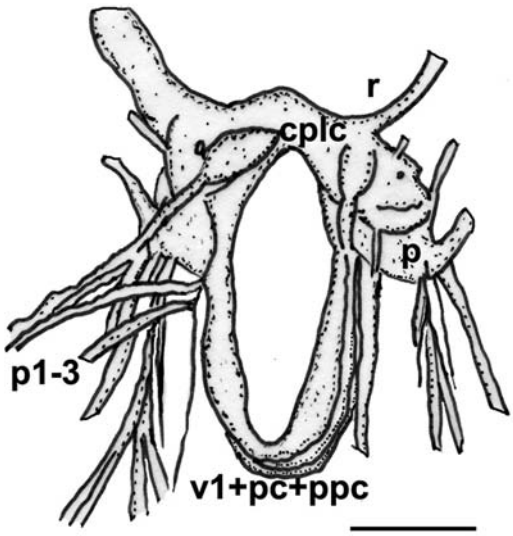



FIGURE 76. *Aegires serenae* (Gosliner and Behrens, 1997). CASIZ 107229. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 1 mm.

**REMARKS**.— Gosliner and Behrens (1997) have recently described this Indo-Pacific species. Anatomical information for the present study has been taken from their paper. However, they did not describe some characters that were necessary for the present study such as the central nervous system and the digestive systems. Therefore, the additional specimens noted above were examined to complete the data.

## Taxon formerly included in the Genus *Triopella* Sars, 1878

TYPE SPECIES: *Triopella incisa* Sars, 1878:310, by monotypy.
(Figs. 77–81)

### *Aegires incisus* (Sars, 1878)

*Triopella incisa* Sars, 1878:310, pl. 27, Fig. 3.
*Aegires incisus* (Sars, 1878) comb. nov.

**DIAGNOSIS**.— Sars' (1878) partial description is as follows: "Small body, oblong and angled, elongate spicules throughout the dorsum. At the posterior end of the mantle are two lobes. The dorsum is highly arched, having superficial dorsal appendages, and longitudinal medial ridges that converge between the tentacles (rhinophores). At the base of the rhinophores there is a single, large tubercle, with 5–7 smaller tubercles arranged longitudinally along the two medial ridges. There are two small tubercles on the anterior of the dorsum. The oral tentacles are inconspicuous. Dorsal rhinophores are short, perfoliate and retractable. The gill has 3 small and sparse branchae, which are arranged in a semi-circle around the anus. The anus is not completely round. The radula has no rachidian tooth, nor denticulate lateral teeth."

**TYPE MATERIAL**.— This species was collected from the Norwegian Arctic Sea. No additional collection data are available. Type material not found in the collections at the Natural History Museum, Oslo.

**MATERIAL EXAMINED**.— D 15983, two specimens, 8–9 mm, Bodø, Norway; D 15988, two specimens, 6–8 mm, Sande Fjord, Norway. No additional collection data are available.

**DISTRIBUTION**.— Norway and Greenland (Sars 1878; Norman 1893; Odhner 1922; Marcus

and Marcus 1969). This species has been mentioned several times in the literature (Fischer 1880–1887; Bergh 1883, 1892; Norman 1893; Odhner 1907; Eliot 1910a; Thiele 1929–31; Odhner 1939).

**External morphology**.— The specimens examined for the present study match the previously published description and drawings mentioned above. A drawing of one of the preserved specimens from the type locality is presented in Figure 77.

**Digestive system**.— *Aegires incisus* shares the same general digestive anatomy as other Aegiridae species (Figs. 3B, 8B). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is nearly round, with four large muscles attached, two per side (Fig. 78). The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick jaw plate at the top of the opening, with thick rods at the edge (Fig. 79A). The radular formula is 13 × 16.0.16. The teeth are simply hamate and the two innermost lateral teeth are smaller than the remaining teeth (Figs. 79B–D).

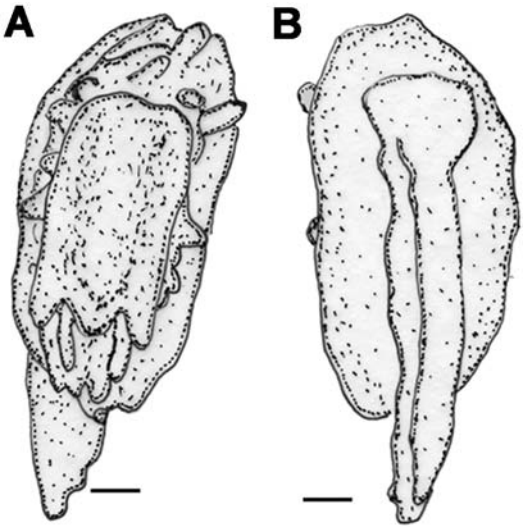



Figure 77. *Aegires incisus* (Sars, 1878). NMNH D15988. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view. Scale = 0.8 mm.

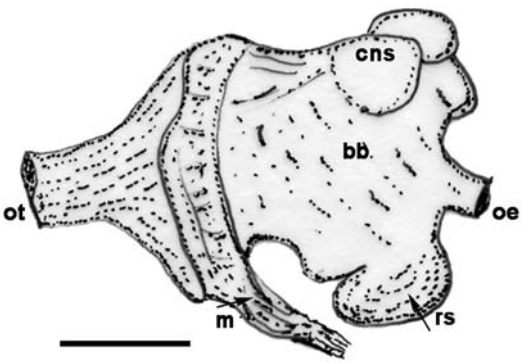



Figure 78. *Aegires incisus* (Sars, 1878). NMNH D15988. Buccal bulb: bb = buccal bulb, m = muscles, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 0.6 mm.

**Reproductive system**.— The reproductive system is triaulic (Fig. 80). The ampulla is large and bulbous at the distal end and tubular at the proximal end. It branches into the oviduct and the prostate. The prostate is wide and narrows before broadening again in the central portion. It narrows before entering into the long sausage-shaped deferent duct. The deferent duct leads to the penis, which is only slightly bulbous at the distal end. There are densely packed hooks along the length of the penis. The vagina is very wide and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is extremely wide and short and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct that originates from the very elongate receptaculum seminis enters the vagina. The oviduct enters the female gland mass. The bursa is round and small.

**Central nervous system**.— The cerebral and pleural ganglia of *Aegires incisus* are fused together (Fig. 81). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cere-

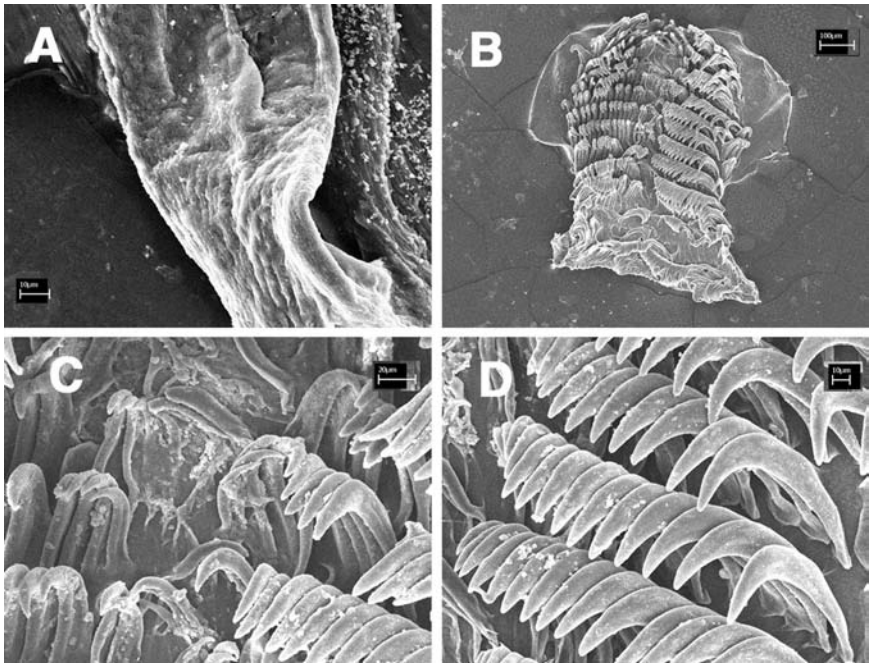



FIGURE 79. *Aegires incisus* (Sars, 1878). NMNH D15988. Buccal morphology: (A) Jaw, scale =10 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 10 µm.

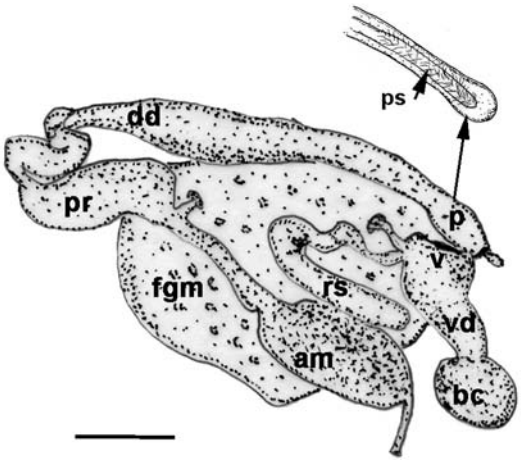



FIGURE 80. *Aegires incisus* (Sars, 1878). NMNH D15988. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

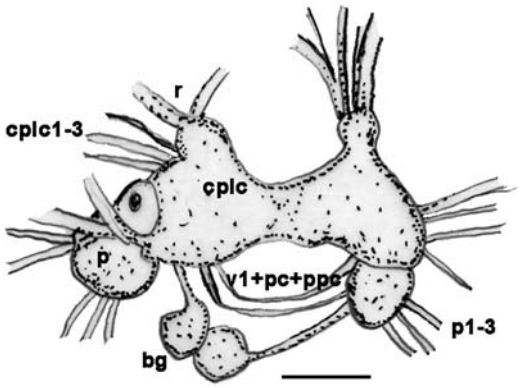



FIGURE 81. *Aegires incisus* (Sars, 1878). NMNH D15988. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.67 mm.

bral ganglia by two relatively short nerves. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

**Circulatory system**.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

**Remarks**.— *Aegires incisus* (formerly *Triopella incisa*) has been often overlooked as a species of Aegiridae as discussed in the earlier section on the history of the classification. However, the species examined from the type locality can be confirmed as *Triopella incisa* Sars, 1878 from the drawings and descriptions provided by Sars and subsequent collectors. Phylogenetic analyses performed for the present study using 58 of the 64 considered morphological characters indicate that *T. incisa* is the sister species of *Aegires sublaevis*. Therefore, *Triopella* cannot be maintained as a separate taxon without rendering *Aegires* paraphyletic. We propose to unite *Triopella incisa* with the *Aegires* with the name *Aegires incisus* (Sars, 1878). Further details are provided in the phylogenetic analysis below.

## Phylogenetic Analysis

The outgroup taxa chosen for the present analysis are discussed in a prior section, Material and Methods. Character states for *Bathydoris abyssorum* were taken from the literature (Bergh 1884; Gosliner and Bertsch 1988; Wägele 1989; Cervera et al. 2000; Valdés 2002). Character states for the additional outgroups were taken both from the literature and from museum material when available. Table 3 (see Appendix) summarizes the information for the outgroup taxa. Morphological data were organized using MacClade, ver 3 (Maddison and Maddison 1998).

**Characters**.— The following characters were considered for use in the analyses of Aegiridae. The character states are indicated as follows: 0: the presumed plesiomorphic condition; 1,2,3: apomorphic condition. For character states that are not applicable, "-" is used and for missing data, "?" is used. The distribution of plesiomorphic and apomorphic character states is presented in Table 2 (see Appendix). Character states for the taxa examined for the present study can be found in Table 4 (see Appendix). "Outgroup taxa" refers to the combination of *Bathydoris,* the six phanerobranchs, the three cryptobranchs and *Hexabranchus*. Only the generic name is used for the outgroup taxa. "Ingroup taxa" refers to all *Aegires,* including those taxa formerly known as *Notodoris* and *Triopella*.

1. *Body shape*: Wide with a distinct mantle (0): all outgroup taxa except for *Holoplocamus*, *Okenia* and *Polycera*. Elongate with a reduced/absent margin (1): all ingroup taxa.
2. *Dorsal ridges*: Absent (0): all outgroup taxa and most ingroup taxa. Present (1): *Aegires albopunctatus, A. palensis, A. punctilucens, A. sublaevis* and *Triopella incisa*.
3. *Dorsal features*: Autotomizable (0): *Bathydoris*. Permanent (1): all other outgroup and ingroup taxa. This character is not applicable to *Hexabranchus*, which does not have dorsal features.
4. *Permanent features*: Low (0): all outgroup taxa except *Holoplocamus* and *Okenia* and over half the ingroup taxa. Elevated (1).
5. *Dorsal feature shape*: Rounded (0): All outgroup taxa and two-thirds of the ingroup species. Flattened (1): one-third of the ingroup taxa.
6. *Tubercles*: Scattered (0): All outgroup taxa except *Okenia* and *Polycera* and over half the ingroup taxa. In rows (1): nearly half the ingroup taxa.
7. *Rhinophores*: Not retractable (0): *Bathydoris* and *Okenia*. Retractable (1): all other taxa.
8. *Rhinophore lamellae*: Transverse or longitudinal (0): all outgroup taxa except *Conualevia*. Smooth (1): all ingroup taxa and *Conualevia*.
9. *Rhinophore pocket*: Simple hole, slit (0): all outgroup taxa except *Hexabranchus*. Raised (1): all ingroup taxa.
10. *Rhinophore tubercles*: None (0): all outgroup taxa. Outer marginal only (1): all ingroup taxa except for *A. palensis, A. punctilucens* and *A. exeches* which all have character state 2. All around (2).

11. *Rhinophore tubercle number*: None (0): all outgroup taxa. Three to five (1): half the ingroup taxa. One tubercle (2): half the ingroup taxa. This character was not included in the final analyses because the character states are included in other characters (#10).
12. *Oral tentacles/hood*: Tentacles (0): *Bathydoris, Calycidoris, Conualevia, Hexabranchus*, and *Holoplocamus*. Oral hood/veil (1): no ingroup taxa have an oral hood or veil. Neither (2): all remaining outgroup taxa and all ingroup taxa.
13. *Oral tentacle size*: Large (0): *Bathydoris* and *Hexabranchus*. Short/small (1): *Conualevia* and *Holoplocamus*. This character is not applicable for the ingroup taxa.
14. *Integumentary spicules*. Present (0): *Actinocyclus, Bathydoris, Hexabranchus, Holoplocamus* and *Polycera*. Absent (1): all other outgroup taxa and all ingroup taxa.
15. *Gill retraction*: Contractile (0): all ingroup taxa and *Bathydoris*, *Holoplocamus*, *Okenia*, and *Polycera*. Retractile (1): all other outgroup taxa.
16. *Gill branches*: Few (0): Most ingroup taxa and *Bathydoris*, *Diaphorodoris*, and *Holoplocamus*. Numerous (1): all remaining outgroup and ingroup taxa.
17. *Gill leaf ramification*: Multi-pinnate (0): *Bathydoris*, *Hexabranchus*, *Holoplocamus*, and *Mandelia*. Not multi-pinnate (1): all other outgroup and ingroup taxa.
18. *Gill arrangement*: Isolated points (0): *Bathydoris*, *Diaphorodoris*, *Hexabranchus*, and *Onchidoris*. One opening (1): all other outgroup and ingroup taxa.
19. *Gill protective structures*: Large, firm (0): all *Notodoris* and *A. hapsis*. Tubercles (1): *Holoplocamus* and half the ingroup taxa. Elongate appendages (2): all remaining *Aegires* species. This character was not included in the final analyses because the character states are included in other characters (#20, #61).
20. *Gill protective structures*: Simple (0): *Holoplocamus* and over half the ingroup taxa. Compound, ramified (1): the remaining ingroup taxa.
21. *Buccal pump*: Absent (0): all ingroup taxa and most outgroup taxa. Present (1): remaining taxa.
22. *Oral glands*: Absent (0): most taxa included in the study. Present (1): *A. villosus, A. malinus, A. incusus*, and *A. hapsis*.
23. *Jaw rodlets*: Absent (0): half the taxa included in the study. Present (1): half the taxa included in the study.
24. *Jaws*: Thick, chitinous (0): *Bathydoris*, *Okenia*, *Polycera* and most ingroup taxa. Thin (1): remaining outgroup taxa except *Mandelia* and all *Notodoris*. Absent (2): *Mandelia*.
25. *Rachidian*: Present (0): *Bathydoris* and *Onchidoris*. Absent (1): all remaining taxa included in the study.
26. *Lateral teeth size*: Outer smallest (0): *Bathydoris* and *Calycidoris*. Inner smallest (1): most ingroup taxa and remaining outgroup taxa. Both small (2): *Conualevia*, *A. albus*, *A. punctilucens*, *Triopella incisa*, and *N. citrina*.
27. *Inner lateral teeth shape*: Elongate (0): *Actinocyclus* and *Bathydoris*. Hamate (1): *Conualevia, Hexabranchus, Holoplocamus, Polycera* and most ingroup taxa . Hooked (2): *Calycidoris*, *Diaphorodoris*, *Okenia*, *Onchidoris*, *A. incusus*, and *A. hapsis*.
28. *Second lateral tooth*: Same size as inner (0): all taxa examined except *Actinocyclus*, *Diaphorodoris*, *Okenia*, and *Onchidoris*. Markedly reduced (1).
29. *Outer lateral tooth*: Present (0): all taxa examined except *Calycidoris*, *Diaphorodoris*, *Okenia*, *Onchidoris*, and *Polycera*. Absent (1).
30. *Outer lateral teeth shape*: Hooked (0): all taxa included in the study except for *Actinocyclus* and *Holoplocamus*. Not hooked (1).
31. *Radular teeth denticulation*: No denticles (0): *Bathydoris*, *Conualevia*, *Holoplocamus*, *Polycera*, and all *Aegires* species. One spur below main cusp (1): all *Notodoris*. Denticulate (2):all remaining outgroup taxa.
32. *Reproductive system*: Diaulic (0) *Bathydoris*. Triaulic (1): all remaining species in the study.
33. *Vagina shape*: Elongate/thin (0): all outgroup taxa except *Diaphorodoris* and *Okenia* and two-thirds of the ingroup species. Wide, bulbous (1): one-third of the ingroup taxa. This character was not included in the final analyses because the state could not be confirmed in several taxa.
34. *Ampulla shape*: Elongate, sausage-shaped (0). Rounded, bulbous (1).
35. *Penis*: Same width as deferent duct (0): all outgroup taxa except *Hexabranchus*, *Mandelia, Okenia*, and *Onchidoris* and over half the ingroup taxa. Wider than deferent duct (1): the remaining ingroup species.
36. *Penial hooks*: Absent (0): *Actinocyclus*, *Bathydoris*, *Conualevia*, *Hexabranchus*, and *Mandelia*. Present

(1): remaining outgroup taxa and all ingroup taxa.

37. *Penial hooks*: Few (0): all outgroup taxa. Many (1): all ingroup taxa. This character was not included in the final analyses because it is the same character as #39.
38. *Penial spines*: Throughout (0): all outgroup taxa and six ingroup taxa. Distal tip only (1): most ingroup taxa.
39. *Penial spines*: Sparse (0): all outgroup taxa. Dense (1): all ingroup taxa.
40. *Vestibular gland*: Absent (0): all taxa included in the present study except *Aegires sublaevis*. Present (1).
41. *Bursa copulatrix ducts*: One duct (0): *Actinocyclus*, *Bathydoris*, *Holoplocamus* and one-third of the ingroup taxa. Two ducts (1): the remaining outgroup taxa and two-thirds of the ingroup species.
42. *Pleural ganglia*: Differentiated (0): *Bathydoris*. Fused with cerebral ganglia (1): all remaining outgroup taxa and all ingroup taxa.
43. *Cerebral ganglia*: Two ganglia on each side (0): *Bathydoris*. Fused (1): all remaining outgroup taxa and all ingroup taxa.
44. *Cerebral nerve number*: Three (0): *Bathydoris*. Four or more (1): all remaining outgroup taxa and all ingroup taxa..
45. *Eyes: Absent* (0): *Bathydoris*. Present (1): all remaining outgroup taxa and all ingroup taxa..
46. *Eye position*: Stalks (0): *Actinocyclus*, *Hexabranchus*, and *Holoplocamus*. Prominent (1): all remaining outgroup taxa and all ingroup taxa except *Notodoris*. Not prominent (2): *Notodoris*.
47. *Ganglionic tubercles*: Absent (0): all taxa included in the study except *Hexabranchus*. Present (1): *Hexabranchus*.
48. *Inner lateral tooth*: Without secondary cusp (0): all taxa included in the study except *Holoplocamus* and *Polycera*. With secondary cusp (1): *Holoplocamus* and *Polycera*.
49. *Gill pocket*: Absent (0): all taxa included in the study except *Actinocyclus*, *Conualevia*, and *Mandelia*. Present (1): *Actinocyclus*, *Conualevia*, and *Mandelia*.
50. *Inner two lateral teeth*: Not elongate (0): all taxa included in the study except *Holoplocamus* and *Polycera*. Elongate (1): *Holoplocamus* and *Polycera*.
51. *Foot corners*: Rounded (0): all taxa included in the study except *Holoplocamus* and *Polycera*. Prolonged (1): *Holoplocamus* and *Polycera*.
52. *Foot dimension*: Same as mouth (0): all taxa included in the study except *Actinocyclus, Conualevia*, and *Mandelia*. Narrower than mouth (1): *Actinocyclus*, *Conualevia*, and *Mandelia*.
53. *Rhinophore stalk*: Long (0): all taxa included in the study except *Actinocyclus*, *Conualevia*, *Diaphorodoris*, *Hexabranchus*, and *Mandelia*. Short (1): *Actinocyclus*, *Conualevia*, *Diaphorodoris*, *Hexabranchus*, and *Mandelia*.
54. *Dorsal pigment*: No dark pigment (0): most outgroup taxa except *Actinocyclus, Calycidoris*, *Mandelia*, and *Onchidoris*. This character is applicable for over half the ingroup taxa. Dark pigment (1): remaining outgroup and ingroup taxa.
55. *Dorsal pigment*: Spots (0): all taxa in the study for which this character is applicable except for *Notodoris minor*. Lines (1): *Notodoris minor*.
56. *Dorsal tubercle pigment*: None (0): all outgroup taxa except *Actinocyclus* and *Polycera*. Most ingroup taxa. Dark apex (1): *Actinocyclus*, *Polycera* and seven ingroup species.
57. *Dorsal ocellae*: Absent (0): all outgroup taxa and most ingroup taxa. Present (1): *Aegires pruvotfolae*, *A. punctilucens*, *A. sublaevis*, *A. incusus*, and *A. exeches*.
58. *Dorsal rings*: Absent (0): all outgroup tax except Mandelia and most ingroup taxa. Present (1): *A. pruvotfolae*, *A. sublaevis*, and *A. incusus*. This character was not included in the final analyses because the states are included in character #57.
59. *Rhinophore color*: No dark pigment (0): all ingroup taxa except *A. ortizi*, *A. palensis*, *A. punctilucens*, *A. sublaevis*, and *A. malinus*. Dark rings (1): *Aegires ortizi*, *A. punctilucens*, and *A. sublaevis.* Dark specks (2): *A. palensis* and *A. malinus*.
60. *Rhinophore color*: same as body (0): all outgroup taxa except Calycidoris and most ingroup taxa. Different color from body (1): *Calycidoris*, *A. albopunctatus*, *Notodoris serenae*, *A. ninguis*, *A. malinus*, *A. incusus*, and *A. hapsis*.
61. *Gill protective structures*: Simple, digitform (0): one-third of the ingroup taxa. Same as dorsal tubercles

(1): one-third of the ingroup taxa. Compound structures (2): the remaining third of the ingroup taxa. Fan-shaped (3): only *A. flores*.

62. *Dorsal webbing*: Absent (0): all taxa included in the study except *A. malinus* and *A. hapsis*. Present (1): *Aegires malinus* and *A. hapsis*.
63. *Finger-like structures*: Simple (0): only four ingroup taxa for which this character is applicable. Lobed (1): only *A. albopunctatus* and *A. lemoncello*.
64. *Dorsal spicules*: Smooth (0): most taxa for which this character is applicable. Furry appearance (1): only *A. malinus* and *A. hapsis*. This character was left out of the final analyses because there were not enough data for the taxa included in the study.

**Results**.— Three most parsimonious trees were obtained with 175 steps and had a consistency index (CI) of 0.38, a retention index (RI) of 0.60 and a homoplasy index (HI) of 0.62. All trees were found in one tree island. The strict consensus tree is shown in Fig. 82A. A majority rule tree from the 3 trees was produced and is shown in Fig. 82B with the character numbers and character reversals. The underlined numbers indicate reversals. The trees indicate that the Aegiridae: *Aegires*, *Notodoris* and *Triopella* form a monophyletic clade and that *Triopella* is nested in a derived clade of *Aegires*. *Notodoris* is nested within *Aegires*. *Bathydoris* is the most basal taxon to the study group. The phanerobranchs included in the analysis are basally situated to Aegiridae and the cryptobranchs included in the study form a sister clade to some suctorian phanerobranchs. A Bremer support analysis shows that most of the clades are poorly supported (Fig. 82A), with the exception of the clade of species formerly known as *Notodoris* and the outgroups.

Analyses performed using *Bathydoris* and the phanerobranchs as outgroups resulted in 6 most parsimonious trees with the same tree scores (trees not shown). The only differences between these trees and those found when using only *Bathydoris* as the outgroup were at the terminal branches. That is, all the deeper nodes remained the same but two polytomies were unresolved: one for all the phanerobranchs other than *Aegires* and one polytomy at the node containing *A. pruvotfolae* and *A. incusus*.

## Discussion

The results from our phylogenetic analysis of Aegiridae support the monophyly of Aegiridae. Additionally, the phanerobranch and the cryptobranch dorids examined for the present study form monophyletic sister clades (Fig. 82). In our strict consensus tree (Fig. 82A) the cryptobranch clade containing *Mandelia, Conualevia* and *Actinocyclus* is closely related to the phanerobranchs examined for the present study: *Onchidoris, Diaphorodoris* and *Calycidoris*. Valdés (2002) showed the cryptobranchs as more derived than the phanerobranchs, including *Aegires*. Specifically, Valdés' phylogeny shows *Aegires* as the most basally situated taxon in his study group, with the cryptobranchs and *Hexabranchus* more derived than *Aegires*. This differs from our results that show *Hexabranchus* as the most basally situated taxon to the clade containing all other taxa examined and *Aegires* as the most derived clade.

Valdés' phylogeny also suggests that phanerobranchs are not monophyletic and our results support this view. However, the sequence of branching is distinct.

The results of the present study also show that *Holoplocamus* and *Polycera* are more closely related to each other and more basally situated to the remaining phanerobranchs and cryptobranchs. Characters that unite this clade are body shape (#1), inner lateral teeth with a secondary cusp (#48), elongate inner two lateral teeth (#50), and prolonged foot corners (#51).

Character mapping also revealed interesting relationships between the suctorians and the cryptobranchs. For example, retractile gills (#15) is the apomorphic state shared by the cryptobranchs and suctorians except for *Okenia*. This indicates that the suctorians are the sister group to the cryp-

tobranchs. In the non-suctorians, the gill is truly non-retractile indicating that this character state has been secondarily derived.

The synapomorphies that unite all *Aegires* (including *Notodoris* and *Triopella*) are the absence of rhinophore lamellae (#8), the presence of rhinophore tubercles only on the outer margin (#10) and the presence of many penial spines (#39).

Our analysis shows that within the study group Aegiridae, there are two major *Aegires* clades. One contains the taxa not found in tropical Indo-Pacific seas. The species in this clade (*Aegires albopunctatus, A. palensis, A. punctilucens, A. sublaevis, A. gomezi, A. ortizi* and *Triopella incisa*) are found only from the Mediterranean, northern Europe, the Caribbean and the west coast of North America. The synapomorphy that supports this clade is dorsal tubercles arranged in rows (#6). The second clade containing *Aegires albus,* found in the Antarctic, is also basally situated but more closely related to the tropical Indo-Pacific clade that contains all other *Aegires* species and all former *Notodoris* species. This Indo-Pacific clade is united by a reproductive synapomorphy, penis wider than the deferent duct (#35). *Notodoris* clusters together in a monophyletic clade that is basally situated to the Indo-Pacific *Aegires*. Synapomorphies that unite the *Notodoris* clade are the presence of large, firm gill protective structures (#19), radular teeth that have one spur below the main cusp (#31) and reduced eyes (#46). In all analyses performed for the present study, the *Notodoris* clade is nested within the *Aegires* sharing multiple synapomorphies with *Aegires* (see Fig. 82B).

The name *Aegires* Lovén, 1844 is the older name having precedence over *Notodoris* Bergh, 1875 as discussed in a previous section. Thus, if only considering precedence, the names of the four *Notodoris* species should be assigned to the genus *Aegires*. The name *Notodoris* has been in general use by both amateurs and scientific researchers to distinguish these four firm bodied nudibranchs from other externally similar nudibranchs (Coleman 1989; Wells and Bryce 1993; Gosliner et al. 1996; Marshall and Willan 1999; Coleman 2001; Rudman 2004). In order to maintain the monophyly of *Aegires* we propose to reassign the four *Notodoris* species to *Aegires*. Thus, *Notodoris citrina* Bergh, 1875 becomes *Aegires citrinus* (Bergh, 1875). *Aegires citrinus* Pruvot-Fol, 1930 must be named *Aegires pruvotfolae* Fahey and Gosliner, 2004, named for Alice Pruvot-Fol who first described *Aegires citrinus* from New Caledonia (1930). The use of a junior homonym is required since the species name *citrinus* is already in use within the Aegiridae (*Aegires citrinus*).

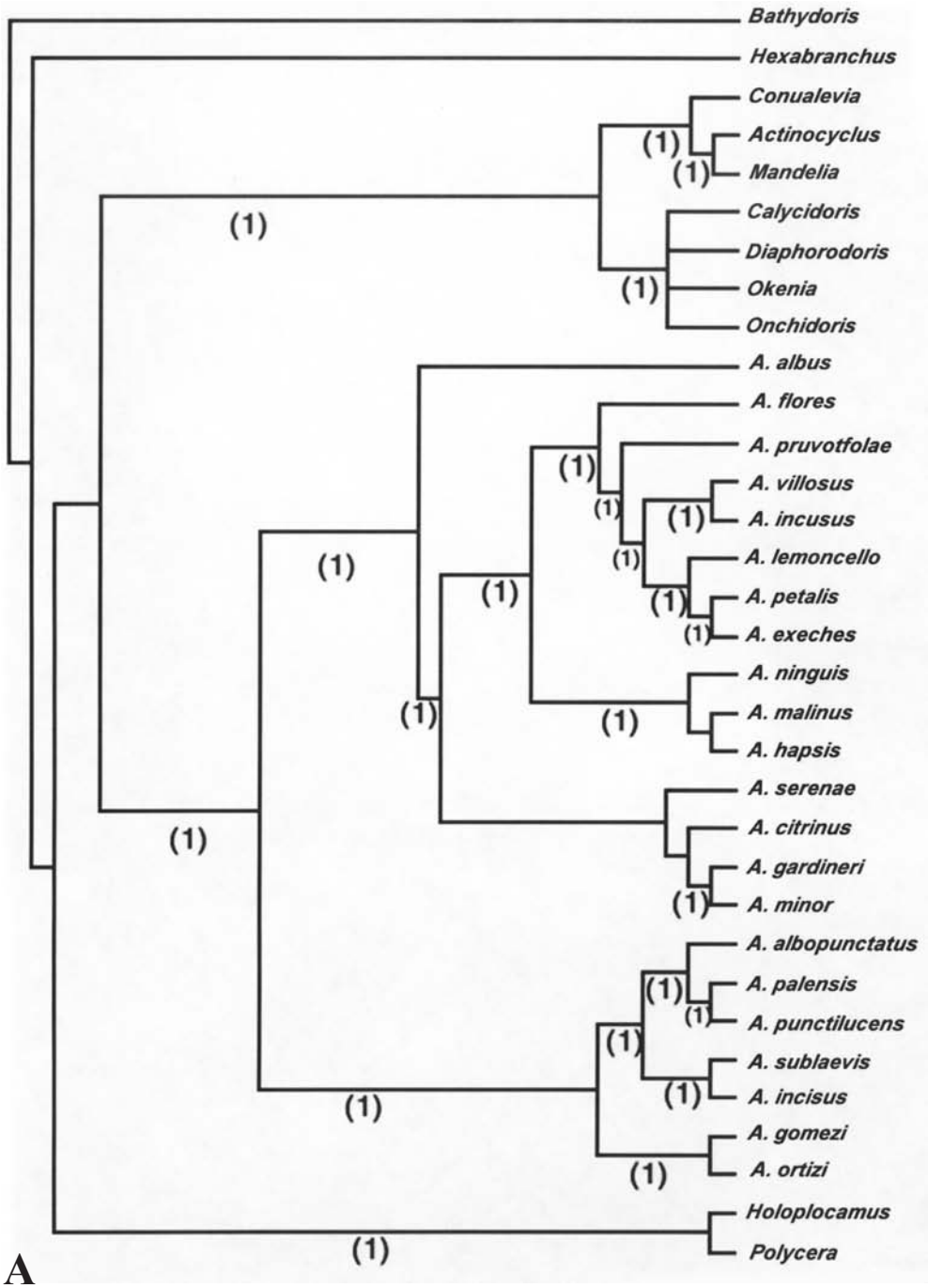
*Notodoris gardineri* becomes *Aegires gardineri* (Eliot, 1906). *Notodoris minor* is *Aegires minor* (Eliot, 1904) and *N. serenae* is *Aegires serenae* (Gosliner and Behrens, 1997).

With regard to *Triopella incisa*, at this time we propose to name this species *Aegires incisus* (Sars, 1878). Our proposal takes into consideration the following points: this species is firmly nested within the *Aegires* clade in all our analyses, the generic name *Aegires* takes precedence over the name *Triopella* and the lack of general use and recognition of the name *Triopella*.

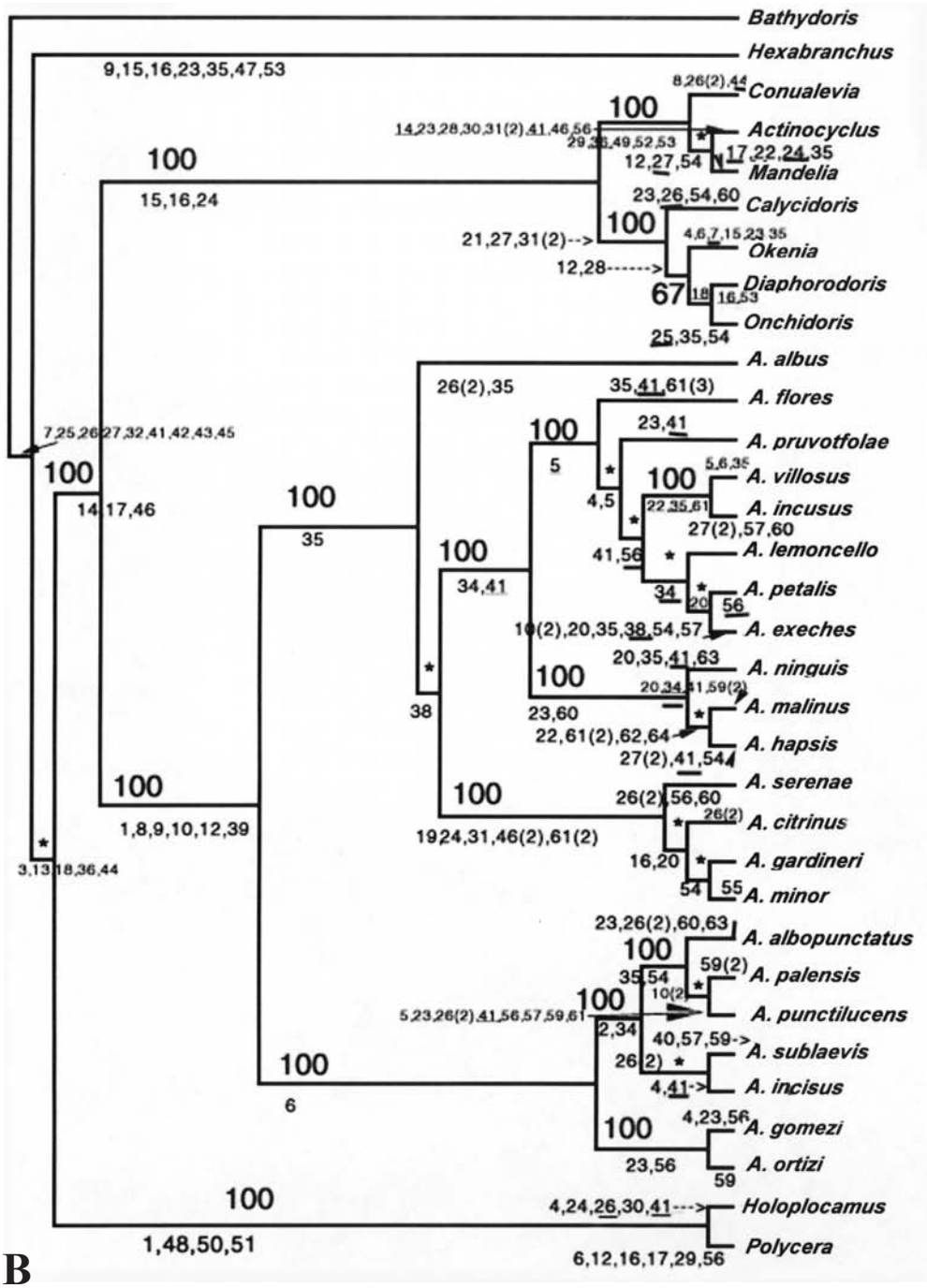
In the present analysis, the traditionally recognized clade Phanerobranchia appears to be paraphyletic and no synapomorphies were found to support the group. Wägele and Willan (2000) and Valdés (2002) also found this to be true. In our analysis, the cryptobranch dorids that we included were nested within the phanerobranchs. Analyses that included only the cryptobranchs and phanerobranchs along with *Aegires albus* also failed to separate the phanerobranchs as a monophyletic clade (tree not shown).

An additional similarity between our analyses and previous studies (Valdés 2002) is the exclusion of *Hexabranchus* from the other cryptobranch or phanerobranch dorids and its placement in a basal position relative to the phanerobranch/cryptobranch clade. Several characters support the position of *Hexabranchus* in the present analysis (Fig. 82B).

In accordance with current perspectives of phylogenetic classification (De Queiroz and




FIGURES 82A–B. Phylogeny of the Aegiridae. (A) (above). Strict consensus tree, 175 steps. Numbers below the branches are Bremer decay values. (B) (right). Majority rule tree of 3 most parsimonious trees. Numbers (100 and 67) above the




**B**

branches are the percentage of the 3 consensus trees that agree on this node. The asterisk also denotes 100% agreement on the node. Numbers shown at the branches are character numbers from Table 2. The underlined numbers indicate reversals.

Gauthier 1994) and based on morphological character analysis we propose that the "family group"Aegiridae contains twenty-three species of *Aegires* descendent from a common ancestor.

## Biogeographical relationships

The phylogeny of the Aegiridae (Fig. 82) shows a clear-cut case of vicariance and offers some insight into species cladogenesis similar to patterns found in other opisthobranch lineages. There are two conspicuous major clades of *Aegires*. One clade contains 15 species found in the Southern Hemisphere and in the Indo-Pacific tropics while the second clade contains 7 species found in the temperate and tropical Atlantic, the Mediterranean and the temperate eastern Pacific (a Northern Hemisphere clade). In the clade from the Southern Hemisphere and the Indo-Pacific, the most basally situated species, *Aegires albus*, is an Antarctic species and sister taxon to the Indo-Pacific clade. The more numerous taxa are found in the tropical Indo-Pacific with the exception of *A. ninguis* found also from the temperate Indian and Atlantic coasts of South Africa. Given that *A. ninguis* is a derived member of this clade, it is most likely that these species were derived from Indo-Pacific ancestors rather than from other cold water or temperate taxa. One possible explanation for this topology is that there has been a little adaptive radiation of the polar or temperate *Aegires* species similar to *Flabellina* and to a lesser extent *Hallaxa* (Gosliner 1995). The phylogeny of *Aegires* demonstrates a considerable degree of speciation within the Indo-Pacific tropics.

Another possible scenario for the distribution pattern seen for this clade of *Aegires* is that *A. albus* is the last surviving species of a group of cold water *Aegires*. Other cold water or temperate *Aegires* that may have previously existed could have radiated from the colder oceans into the warmer waters of the Indo-Pacific. It is notable that within the clade of the Indo-Pacific species is a small clade of all of the *Aegires* previously known as *Notodoris*. This clade is basally situated to the remaining species and has representative species found along both coasts of Australia, from as far south as the temperate ocean of Perth, Western Australia and extending to latitudes north of the equator. This would provide some evidence for the dispersal of the clade from the Antarctic, north along both coasts of Australia, then into the tropical Indo-Pacific regions.

The second major clade is known primarily from the Mediterranean and along the margin of the eastern Atlantic. Only one species of this clade, *A. albopunctatus*, is found along the temperate eastern Pacific, possibly demonstrating vicariance with the closest sister clade of *A. palensis* and *A. punctilucens* from the Mediterranean. It is also possible that the ranges of these temperate species are incomplete and additional records may show that there is a higher degree of overlap than is currently recognizable.

Finally, species of Aegiridae are extremely small, inconspicuous and infrequently encountered, with the exception of those species previously included in *Notodoris*. It is likely that not all species have yet been described, and further collections may add to our knowledge of the pattern of species cladogenesis and vicariance.

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# Appendix

## Tables 1–4

TABLE 1. Summary of the historical classification of AEGIRIDAE

| *Author and Higher level names used* | *Genus names included* |
|---|---|
| **1. Alder & Hancock, 1845–1855** | |
| SUBORDERS: p. 36–37 | |
| ANTHOBRANCHES | |
| Doridídae | |
| Sub-Family Polycerinae | *Aegires* Lovén, 1844:49 |
| | *Thecacera* |
| | *Polycera* |
| | *Idalia* |
| **2. Fischer, 1883** | |
| SUBORDERS: p. 519 | |
| Anthobranchiata | |
| Aglossa: Doridopsidae | |
| Glossophora: | |
| Cryptobranchiata, | |
| Phanerobranchiata | |
| POLYCERIDAE: p. 525 | |
| Acanthodoridinae | |
| Polycerinae | |
| Aegirinae | *Aegires* |
| | *Triopella* Sars, 1878:310 |
| **3. Bergh, 1890,1892** | |
| Phanerobranchiata | |
| Tribe Suctoria | |
| Tribe Non Suctoria | |
| POLYCERIDAE | *Aegires* |
| | *Notodoris* Bergh, 1875d:64 |
| | *Triopella* |
| **4. Eliot, 1910** | |
| NOTODORIDIDAE | *Aegires* |
| | *Notodoris* |
| | *Triopella* |
| **5. Iredale & O'Donoghue 1923** | |
| AEGIRETIDAE | *Aegires* |
| | *Notodoris* |
| | *Triopella* |
| **6. Thiele, 1929–1935** | |
| POLYCERIDAE | |
| NOTODORIDINAE p. 696 | *Aegires* |
| | *Notodoris* |
| | *Triopella* |
| **7. Pruvot-Fol, 1954** | |
| PHANEROBRANCHIATA Bergh | |
| AEGIRETIDAE | *Aegires* |
| (=Notodoridinae Thiele, 1929-35) | *Notodoris* |
| **8. Fischer et al. 1968** | |
| PHANEROBRANCHIA Fischer, 1883 | |
| Anadoridacea Fischer, 1968 | |
| Tribe Non Suctoria Bergh, 1892:141(1133) | |
| AEGIRETIDAE Iredale & O'Donoghue 1923 | *Aegires* |
| (= Notodorididae Eliot, 1910) | *Anaegires* |
| | *Notodoris* |
| | *Triopella* |
| **9. Nordsieck, 1972** | |
| AEGIRETIDAE | *Aegires* |
| | *Anaegires* |
| | *Serigea* Nordsieck, 1972:55 |
| | *Triopella* |
| **10. Thompson, 1976** | |
| NOTODORIDIDAE Odhner, 1926 | *Aegires* |
| | *Notodoris* |
| **11. Rudman, 1998** | |
| AEGIRETIDAE | *Aegires* |
| | *Notodoris* |

TABLE 2. Characters and states examined for the phylogenetic analysis of Aegiridae. 0 = plesiomorphic; 1,2,3 = apomorphic conditions.

| *Characters* | *States* |
|---|---|
| 1. Body shape | 0: wide, distinct mantle; 1: elongate, reduced margin |
| 2. Dorsal ridges | 0: absent; 1: present |
| 3. Dorsal features | 0: autotomizable 1: permanent |
| 4. Permanent features | 0: low; 1: elevated |
| 5. Dorsal feature shape | 0: rounded; 1: flattened; 2: pointed, cones |
| 6. Tubercles | 0: scattered, 1: in rows |
| 7. Rhinophores | 0: not retractable; 1: retractable |
| 8. Rhinophore lamellae | 0: transverse or longitudinal lamellae; 1: smooth |
| 9. Rhinophore pocket | 0: simple hole/slit; 1: raised |
| 10. Rhinophore tubercles | 0: none; 1: outer marginal only; 2: all around |
| 11. Rhinophore tubercle no. | 0: many; 1: three to five; 2: one |
| 12. Oral tentacles/hood | 0: tentacles; 1: oral hood/veil; 2: neither |
| 13. Oral tentacle size | 0: large; 1: short/small |
| 14. Integumentary spicules | 0: present; 1:absent |
| 15. Gill retraction | 0: contractile; 1: retractile |
| 16. Gill branches | 0: few; 1: numerous |
| 17. Gill leaf ramification | 0: multi-pinnate; 1: not multi-pinnate |
| 18. Gill arrangement | 0: isolated points; 1: one opening |
| 19. Gill protective structures | 0: large, firm; 1: tubercles; 2: elongate appendages |
| 20. Gill protective structures | 0: simple; 1: compound/ramified |
| 21. Buccal pump | 0: absent; 1: present |
| 22. Oral glands | 0: absent; 1: present |
| 23. Jaw rodlets | 0: absent; 1: present |
| 24. Jaws | 0: thick, chitinous; 1: thin; 2: absent |
| 25. Rachidian | 0: present; 1: absent |
| 26. Lateral teeth size | 0: outer smallest; 1: inner smallest; 2: both small |
| 27. Inner lateral teeth shape | 0: elongate; 1: hamate; 2: hooked |
| 28. Second lateral tooth | 0: same size as inner; 1: markedly reduced |
| 29. Outer lateral tooth | 0: present; 1: absent |
| 30. Outer lateral teeth shape | 0: hooked; 1: not hooked |
| 31. Radular teeth denticulation | 0: no denticles; 1: one spur below main cusp; 2: denticulate |
| 32. Reproduction system | 0: diaulic; 1: triaulic |
| 33. Vagina shape | 0: elongate/thin; 1: wide/bulbous |
| 34. Ampulla shape | 0: elongate/sausage-shaped; 1: rounded/bulbous |
| 35. Penis | 0: same width as deferent duct; 1: wider than deferent duct |
| 36. Penial hooks | 0: absent; 1: present |
| 37. Penial hooks | 0: few; 1: many |
| 38. Penial spines | 0: throughout; 1: tip only |
| 39. Penial spines | 0: sparse; 1: dense |
| 40. Vestibular gland | 0: absent; 1: present |
| 41. Bursa copulatrix ducts | 0: one duct; 1: two ducts |
| 42. Pleural ganglia | 0: differentiated; 1: fused with cerebral ganglia |
| 43. Cerebral ganglia | 0: two ganglia on each side; 2: fused |
| 44. Cerebral nerve no. | 0: three; 1: four or more |
| 45. Eyes | 0: absent; 1: present |
| 46. Eye position | 0: stalks; 1: prominent; 2: not prominent |
| 47. Ganglionic tubercles | 0: absent; 1: present |
| 48. Inner lateral teeth | 0: no secondary cusp; 1: with secondary cusp |
| 49. Gill pocket | 0: absent; 1: present |
| 50. Inner two lateral teeth | 0: not elongate; 1: elongate |
| 51. Foot corners | 0: rounded; 1: prolonged |
| 52. Foot dimension | 0: same as mouth; 1: narrower than mouth |
| 53. Rhinophore stalk | 0: long; 1: short |
| 54. Dorsal pigment | 0: no dark pigment; 1: dark pigment |
| 55. Dorsal dark pigment | 0: spots; 1: lines |
| 56. Dorsal tubercle pigment | 0: none; 1: dark apex |
| 57. Dorsal ocellae | 0: absent; 1: present |
| 58. Dorsal rings | 0: absent; 1: present |
| 59. Rhinophore color | 0: none; 1: dark rings; 2: dark specks |
| 60. Rhinophore color | 0: same as body; 1: different from body |
| 61. Gill protective structures | 0: simple/digitform; 1: same as dorsal tubercles; 2: compound; 3: fan-shaped |
| 62. Dorsal webbing | 0: absent; 1: present |
| 63. Finger-like structures | 0: simple; 1: lobed |
| 64. Dorsal spicules | 0: smooth; 1: furry |

TABLE 3. Outgroup species and cryptobranch dorids included in the analysis and source of information

| *Species* | *Literature source* | *Additional material examined* |
|---|---|---|
| *Actinocyclus verrucosus* Ehrenberg, 1831 | Ehrenberg, 1831; Valdés and Gosliner, 1999; Valdés, 2002 | |
| *Bathydoris abyssorum* Bergh, 1884 | Wägele, 1989; Valdés, 1999, 2002 | |
| *Calycidoris güntheri* Abraham, 1876 | Abraham, 1876, 1877; Roginskaya, 1972; Valdés, 2002 | |
| *Conualevia marcusi* Collier and Farmer, 1964 | Valdés, 2002; Collier & Farmer, 1964; Valdés, 2002 | CASIZ 018370 (1) |
| *Diaphorodoris luteocinta* (Sars,1870) | Schmekel & Portmann, 1982; Pruvot-Fol, 1954; Valdés, 2002 | CASIZ 072580 (6) |
| *Hexabranchus sanguineus* (Rüppell & Leuckart, 1828) | Cuvier, 1804; Valdés, 2002; Ehrenberg, 1831 | CASIZ 071704 (1)<br>CASIZ 087263 (1) |
| *Holoplocamus papposus* Odhner, 1926 | Odhner, 1926; Marcus & Marcus, 1969 | Two specimens collected Sept. 1981 by T. Gosliner, Gough Island, Tristan de Cunha Group, So. Atlantic |
| *Mandelia mirocornata* Valdés and Gosliner, 1999 | Valdés & Gosliner, 1999, 2001 | |
| *Okenia elegans* (Leuckart 1828) | Pruvot-Fol, 1954; Schmekel & Portmann, 1982; Valdés & Gosliner, 1999 | |
| *Onchidoris bilamellata* (Linnaeus 1767) | Thompson & Brown, 1984; Valdés, 2002 | CASIZ 056306 (6) |
| *Polycera quadrilineata* (Müller 1776) | Alder & Hancock, 1851; Schmekel & Portmann, 1982; Thompson and Brown, 1984; Valdés & Gosliner, 1999 | CASIZ 074446 (1) |

| MatrixTest1 | | 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 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | Body | Dorsi | Tube | Rhin | Rhin | Rhin | Rhin | Rhin | Oral | Oral | Dorsi | Dors | Jaw | Oute | Integ | GillR | GillB | GillL | GillA | GillP | GillP | Jaws | Rach | Inner | Seco | Oute | Radu | Vagir | Bucc | Amp | Penis | Penis | Penis | Vesti | Burs | Pleu | Cere | Cere | Eyes | Eye | Gang | Late | Oral | Repr | Gill |
| 1 | Actinocyclus | 0 | 0 | 0 | 1 | 0 | 0 | 0 | - | 2 | - | 0 | - | 1 | 0 | 1 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | - | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| 2 | Bathydoris | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 1 | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | - | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 |
| 3 | Calycidoris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 2 | 1 | - | 0 | 0 | 1 | 0 | 1 | 1 | ? | 0 | 0 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 1 |
| 4 | Conualevia | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | - | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 |
| 5 | Diaphorodoris | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | - | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | - | - | 1 | 1 | 2 | 1 | - | 2 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 1 |
| 6 | Hexabranchus | 0 | 0 | - | 1 | 0 | 1 | 0 | - | 0 | - | 2 | - | 1 | 0 | 1 | 1 | 1 | 1 | 0 | - | - | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| 7 | Mandelia | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | - | 1 | 1 | - | - | 0 | 1 | 1 | 1 | 1 | - | - | 2 | - | - | - | - | - | 0 | 0 | 0 | 1 | 0 | - | 0 | 0 | 1 | 1 | ? | 1 | ? | 0 | - | 1 | 1 | 1 |
| 8 | Okenia | 1 | 0 | 1 | 0 | 0 | - | - | - | 2 | - | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | - | - | 1 | 1 | 2 | 1 | - | 2 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 0 |
| 9 | Onchidoris | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 2 | - | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | - | - | 1 | 0 | 2 | 1 | - | 2 | 0 | 1 | 0 | ? | 1 | ? | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 1 |
| 10 | Polycera | 1 | 0 | 1 | 0 | 0 | - | - | - | 2 | - | 0 | - | 0 | 1 | 1 | 0 | 1 | 0 | 1 | - | - | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 0 |
| 11 | A. albus | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | - | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 12 | A. albopunctatus | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | - | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 13 | A. citrinus | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | - | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 14 | A. gomezi | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | ? | 0 | ? | ? | ? | - | ? | ? | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 15 | A. ortizi | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | - | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 16 | A. palensis | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | - | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 17 | A. punctilucens | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | - | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | ? | - | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 18 | A. sublaevis | 1 | 1 | - | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | ? | - | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 19 | A. villosus | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| 20 | T. incisa | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | ? | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 21 | N. citrina | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 |
| 22 | N. gardineri | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 |
| 23 | N. minor | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 |
| 24 | N. serenae | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 |
| 25 | A. ninguis | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 26 | A. lemoncello | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 27 | A. malinus | 1 | 0 | - | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| 28 | A. incusus | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| 29 | A. flores | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 30 | A. petalis | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 31 | A. exeches | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| 32 | A. hipsus | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | - | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 |

TABLE 4. Data matrix of character states in the taxa examined for the phylogenetic analysis of Aegiridae. Data codes: 0 = presumed plesiomorphic condition, 1-3 = apomorphic conditions, - = character not applicable, ? = missing data.

| Table4F&G 2 | | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Ampl | Penil | Penil | Penil | Penil | penil | Vestl | Bursi | Pleur | Cerel | Cere | Eyes | EyeF | Gang | innel | Gillpi | innel | footd | footd | rhind | Dorsi | Dorsi | Dors | Dors | Dorsi | Rhini | rhind | GillP | Dorsi | finge | spicu |
| 1 | Actinocyclus | 0 | 0 | 0 | - | - | - | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 2 | Bathydoris | 0 | 0 | 0 | - | - | - | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 3 | Calycidoris | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | - | 0 | - | - |
| 4 | Conualevia | 0 | 0 | 0 | - | - | - | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 5 | Diaphorodoris | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 6 | Hexabranchus | 0 | 1 | 0 | - | - | - | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | - | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 7 | Holoplocamus | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 8 | Mandelia | 0 | 1 | 0 | - | - | - | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | - | 0 | - | - |
| 9 | Okenia | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 10 | Onchidoris | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 11 | Polycera | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | - | 0 | - | - |
| 12 | A. albus | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | A. albopunctatus | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 14 | A. citrinus | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 1 | 0 | - | 0 |
| 15 | A. gomezi | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 |
| 16 | A. ortizi | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 0 | 1 | 0 | 0 | 0 | - | 0 |
| 17 | A. palensis | 1 | 1 | 1 | 1 | ? | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| 18 | A. punctilucens | 1 | 1 | 1 | ? | ? | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | - | 0 |
| 19 | A. sublaevis | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 20 | A. villosus | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 |
| 21 | T. incisa | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | N. citrina | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 2 | 0 | - | 0 |
| 23 | N. gardineri | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | - | 0 |
| 24 | N. minor | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | - | 0 |
| 25 | N. serenae | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 0 | 0 | 1 | 2 | 0 | - | 0 |
| 26 | A. ninguis | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 27 | A. lemoncello | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 |
| 28 | A. malinus | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 2 | 1 | 2 | 1 | - | 1 |
| 29 | A. incusus | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 1 | 1 | 0 | 1 | 1 | 0 | - | 0 |
| 30 | A. flores | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 3 | 0 | - | 0 |
| 31 | A. petalis | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | 0 |
| 32 | A. exeches | 0 | 1 | 1 | 0 | 0 | - | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | - | 0 |
| 33 | A. hapsis | 1 | 0 | 1 | ? | ? | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | - | 1 |

TABLE 4 (continued). Data matrix of character states in the taxa examined for the phylogenetic analysis of Aegiridae. Data codes: 0 = presumed plesiomorphic condition, 1-3 = apomorphic conditions, - = character not applicable, ? = missing data.