Phylogenetic Systematics of *Reticulidia* Bruncknorst, 1990 (Mollusca, Nudibranchia), with the Description of a New Species from the Tropical Indo-Pacific

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ABSTRACT. The genus *Reticulidia* includes three previously described species, *R. halgerda* and *R. fungia* from the tropical Indo-Pacific, and *R. gofasi* from the Atlantic. A new species, *R. suzanneae*, is described on the basis of specimens collected from the Indian Ocean coast of Thailand. This species is distinguishable from the other species by having an orange external coloration with circular black spots and the bursa copulatrix smaller than the seminal receptacle.

A phylogenetic analysis of *Reticulidia* shows that *R. gofasi* is the sister taxon to the Indo-Pacific species, and a vicariant event probably produced this pattern. *Reticulidia suzanneae* is a derived species within *Reticulidia* and is the sister taxon to *R. fungia*. *Reticulidia* is a monophyletic group supported by three synapomorphies related to the shape of the buccal bulb, the oral glands, and the esophageal connection. The dorsal ridges, which were used by other authors to define this genus, are absent in *R. gofasi* and therefore their presence is a synapomorphy of the Indo-Pacific clade.

INTRODUCTION

The genus *Reticulidia* was described by Bruncknorst (1990) to include a single described species of Indo-Pacific Phyllidiidae, *R. halgerda* Bruncknorst and Burn, 1990. This species is characterized by having smooth reticulate ridges on the dorsum and radially arranged glandular discs within the pharyngeal or bucal bulb on the buccal mass. A second species of the genus, *R. fungia,* was subsequently introduced by Bruncknorst and Gosliner (in Bruncknorst, 1993), also from the tropical Indo-Pacific. Separation of these two species was justified on the basis of differences in the external coloration (Bruncknorst, 1993). Later, Valdés and Ortea (1996) described a third species of this genus, collected from western Atlantic seamounts, between 76 and 340 m depth. This new species, *R. gofasi* Valdés and Ortea, 1996, is remarkably different from the two Indo-Pacific members of the genus in having dorsal conical tubercles, rather than dorsal ridges. The two Indo-Pacific species are sympatric, whereas *R. gofasi* is isolated by continental land masses.

Valdés and Gosliner (1999), based on a phylogenetic analysis of the radula-less dorids, found *Reticulidia* to be a monophyletic group, supported by a single synapomorphy, the presence of radially arranged glandular discs on the buccal mass. However, these authors did not propose a hypothesis of the phylogenetic relationships within *Reticulidia.*

The present paper examines the phylogenetic relationships of members of *Reticulidia* and describes a new species collected from the Andaman Sea, Thailand. Previously described species are studied here again in order to describe characters used in the phylogenetic analysis. Additionally, the phylogenetic hypothesis is used to further understand the biogeography of the genus *Reticulidia* and the most likely speciation patterns within this group.

MATERIALS AND METHODS

The material examined is deposited in the Natural History Museum of Los Angeles County (LACM), the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ), and the Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a dissecting microscope by using a camera lucida. Special attention was paid to the morphology of the reproductive and digestive systems. Features of living animals were recorded from photographs or from notes of collectors.

To calculate the most parsimonious phylogenetic tree, data were analyzed with *Phylogenetic analysis using parsimony (PAUP),* Version 4.0b8 (Swofford, 2001) by using the exhaustive algorithm. Characters were polarized by using the outgroup selection of the genera *Phyllidia* Cuvier, 1797 (*Phyllidia varicosa* Lamarck, 1801) and *Phyl-*

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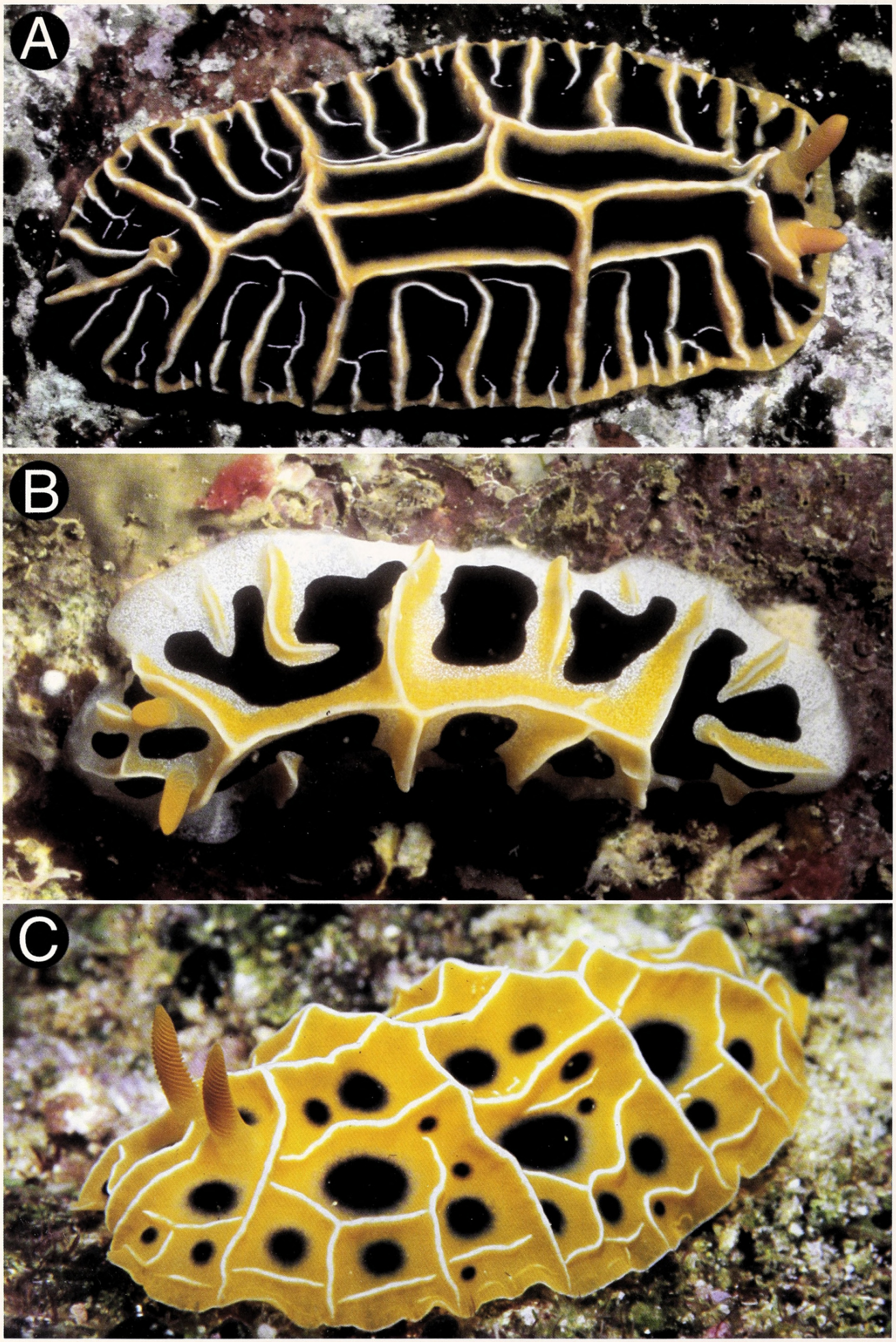
A
B
C

lidiella Bergh, 1869 (*Phyllidiella pustulosa* [Cuvier, 1804]), and subsequent analysis with PAUP. This outgroup selection was made on the basis of the study by Valdés and Gosliner (1999), where the clade containing *Phyllidia* and *Phyllidiella* was hypothesized to be the sister taxon to *Reticulidia*, which is a monophyletic group. Information on *Phyllidia* and *Phyllidiella* was obtained from the literature (Brunckhorst, 1993; Valdés and Gosliner, 1999) and newly examined specimens (Table 1). A Bremer support analysis (Bremer, 1994) was carried out to estimate branch support. See Kitching *et al.* (1998) for a thorough explanation of the advantages of Bremer's method in morphological data analyses. Synapomorphies were identified by the character trace option in *MacClade*, Version 4.0 (Maddison and Maddison, 2000).

SYSTEMATICS

Genus *Reticulidia* Brunckhorst

Reticulidia Brunckhorst, 1990:567–568. Type species: *Reticulidia halgerda* Brunckhorst and Burn, 1990, by original designation.

DIAGNOSIS. Medium-sized phyllidiid nudibranchs with the dorsum normally covered with irregular ridges or exceptionally conical tubercles. Buccal mass with several radially arranged glandular discs (synapomorphy). Esophagus connecting into the dorsal surface of the rounded buccal bulb (synapomorphies). Reproductive system similar to that of other phyllidiid nudibranchs.

Reticulidia halgerda Brunckhorst and Burn, 1990

Figures 1A, 2A–C

Reticulidia halgerda Brunckhorst and Burn in Brunckhorst, 1990:570–575, figs. 2A-C, 3–7.

MATERIAL EXAMINED. North side of Rasch Passage, near Madang, Papua New Guinea, depth 38 m, 17 June 1992, 1 specimen 34 mm preserved length, collected by T.M. Gosliner (CASIZ 086401).

EXTERNAL MORPHOLOGY. The external dorsal morphology of this species was described in detail by Brunckhorst (1993), and a description is not repeated here. A specimen from Madang, Papua New Guinea, is illustrated (Fig. 1A) to confirm the identity of the material examined. Ventrally, the mantle margin is narrow (about one-fourth the foot width). Spots of different sizes are irregularly distributed in one or two rows. Some of them are lobate and some are circular. The oral tentacles are separated from each other and have a lateral longitudinal groove. The respiratory leaves show alternation in size (Fig. 2B).

INTERNAL MORPHOLOGY. The reproductive system is triaulic (Fig. 2A). The ampulla is oval, almost rounded. From its distal portion emerges the postampulary duct, which divides into the prostate and a long oviduct. The prostate is wide, long, and convoluted, distally narrowing and expanding again into the long muscular ejaculatory portion. The distal portion of the deferent duct opens into a short, common atrium with the vaginal duct. The penial hooks have a long and robust pointed cusp and a narrow base (Fig. 2C). They are about 70 μm long. The vaginal duct opens into the bursa copulatrix. The bursa copulatrix is oval and connects to the seminal receptacle by a short duct. Near the seminal receptacle this duct is joined by the uterine duct, which enters the female gland mass. The bursa copulatrix is about five times as large as the oval seminal receptacle.

GEOGRAPHIC RANGE. This species is known from the central and western Pacific Ocean (including Fiji and the Marshall Islands), from eastern Australia to Taiwan (Brunckhorst, 1993).

REMARKS. The anatomy of this species has been studied by Brunckhorst (1993) and Valdés and Gosliner (1999). The reproductive system of the specimen examined here is very similar to those descriptions and no substantial differences have been found.

According to Brunckhorst (1993), this species differs from *R. fungia* in lacking a bluish background coloration and having narrower ridges. Anatomical differences found in this study include a shorter atrium and the presence of two ducts, instead of one, connecting to the bursa copulatrix of *R. halgerda*. In addition, the penial hooks of *R. halgerda* are very large, about 70 μm long, with a robust cusp and a short base, whereas those of *R. fungia* are smaller and have a more delicate, curved cusp and a more elongate base.

Reticulidia fungia Brunckhorst and Gosliner, 1993

Figures 1B, 2D–F

Reticulidia fungia Brunckhorst and Gosliner in Brunckhorst, 1993:78–79, fig. 31D, pl. 9H.

MATERIAL EXAMINED. Ima Anchorage, north coast of Tagula Island, Calvados Chain, Louisiade Archipelago, Solomon Sea, Papua New Guinea, depth 10 m, 3 June 1998, 1 specimen 36 mm preserved length, collected by G. Williams (CASIZ 113687).

EXTERNAL MORPHOLOGY. The external dorsal morphology of this species was described in detail by Brunckhorst (1993), and a description is not repeated here. A specimen from Anilao, Philippines, is illustrated (Fig. 1B). Ventrally, the mantle margin is wide (about one-half the foot width),

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Figure 1 Living animals. **A**, *Reticulidia halgerda*, specimen from Madang, Papua New Guinea, photograph by T. Gosliner. **B**, *Reticulidia fungia*, specimen from Anilao, Batangas, Philippines, photograph by A. Valdés. **C**, *Reticulia suzanneae* sp. nov., holotype (LACM 2897), photograph by M. Strickland.

Table 1. Additional specimens of phyllidiids examined for the phylogenetic analysis, including locality, depth, collection date, collector, and museum registration number.

Species	Locality and depth	Date	Collector	Registration number
Phyllidia varicosa	Dawapia Rocks, Simpson Harbor, Bismarck Arch., 0–12m	24 August 1981	A.J. Ferreira	LACM 1981–27.1
	Pelangi and Putri Islets, Pulau-Pulau Seribu Is., Java, 10–30 m	16–18 May 1986	J.H. McLean	LACM 1986–163.7
Phyllidiella pustulosa	South of Suva Pt., Viti Levu, Fiji, 0–1 m	16–17 May 1979	J.H. McLean	LACM 1979–40.7
	Low Isles, off Port Douglas, Queensland, Australia, 0–1 m	13 August 1981	A.J. Ferreira	LACM 1981–20.1

with a few elongate spots arranged in a single row around the mantle margin. Spots are shorter, almost circular, near the anterior and posterior ends of the foot. The oral tentacles are separated from each other and have a lateral longitudinal groove. The respiratory leaves do not alternate in size (Fig. 2E).

INTERNAL MORPHOLOGY. The reproductive system is triaulic (Fig. 2D). The ampulla is oval, almost rounded. From its distal portion emerge the

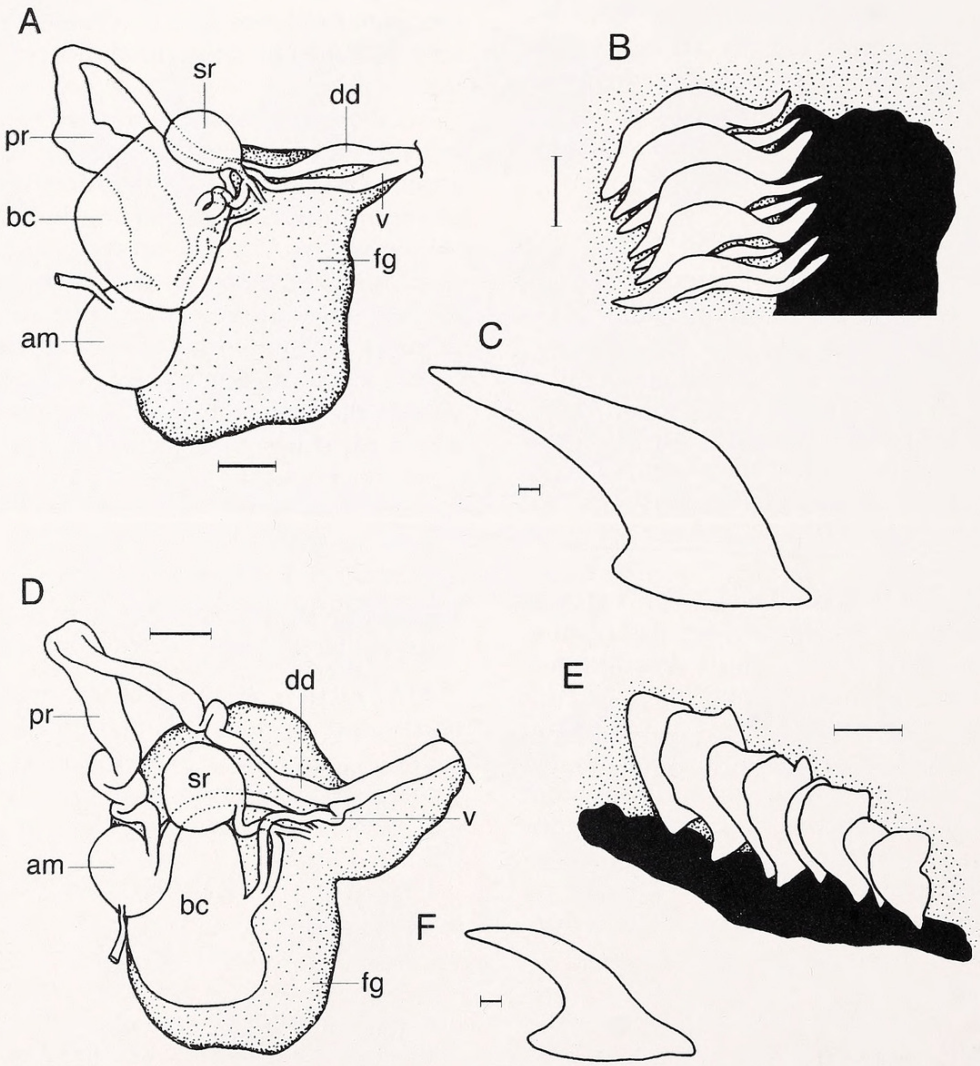

Figure 2 Anatomy of *Reticulidia*. **A**, *Reticulidia halgerda* (CASIZ 086401), reproductive system; scale bar = 1 mm. **B**, Same specimen, ventral respiratory leaves; scale bar = 1 mm. **C**, Same specimen, penial hook; scale bar = 2 μm. **D**, *Reticulidia fungia* (CASIZ 113687), reproductive system; scale bar = 1 mm. **E**, Same specimen, ventral respiratory leaves; scale bar = 1 mm. **F**, Same specimen, penial hooks; scale bar = 2 μm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; v, vagina

prostate and a long oviduct. The prostate is wide, long, and convoluted, distally narrowing and expanding again into the long muscular ejaculatory portion. The distal portion of the deferent duct opens into a very long, common atrium with the vaginal duct. The penial hooks have a curved and delicate cusp and an elongate base. They are about 40 μm long (Fig. 2F). The vaginal duct opens into the bursa copulatrix. The bursa copulatrix is oval. From the vaginal duct, near the bursa copulatrix, leads a duct. This duct connects to the seminal receptacle and to the short uterine duct, which opens into the female glands. The bursa copulatrix is about three times as large as the rounded seminal receptacle.

GEOGRAPHIC RANGE. This species occurs sympatrically with *R. halgerda,* but it is also known from Christmas Island, in the eastern Indian Ocean (Brunckhorst, 1993).

Reticulidia gofasi Valdés and Ortea, 1996

Reticulidia gofasi Valdés and Ortea, 1996:7–8, figs. 1F, 4C, 8.

MATERIAL EXAMINED. Lusitanian seamounts, Josephine Bank (36°40.02′N, 14°16.00′W: Seamount I Expedition station DW61), depth 200–205 m, 7 October 1987, 1 specimen 11 mm preserved length, Holotype (MNHN). Meteor Group seamounts, Atlantis Bank (34°06.20′N, 30°16.00′W: Seamount II Expedition station DW256), 340 m depth, 2 February 1993, 1 specimen 9 mm preserved length, Paratype (MNHN).

EXTERNAL MORPHOLOGY. The external dorsal and ventral morphology of this species was described in detail and figured by Valdés and Ortea (1996: fig. 1F), and another description is not included here.

INTERNAL MORPHOLOGY. Anatomical descriptions are based on the illustrations by Valdés and Ortea (1996:fig. 8B). The reproductive system is triaulic. The ampulla is oval. From its distal portion emerge the prostate and a long oviduct. The prostate is narrow, long, and convoluted, distally narrowing and expanding again into the long muscular ejaculatory portion. The distal portion of the deferent duct opens into a very short, common atrium with the vaginal duct. The vaginal duct opens into the bursa copulatrix. The bursa copulatrix is oval. From the vaginal duct, near the bursa copulatrix, leads another duct that connects to the seminal receptacle and the short uterine duct, which opens into the female glands. The bursa copulatrix is approximately 10 times as large as the pyriform seminal receptacle.

GEOGRAPHIC RANGE. *Reticulidia gofasi* is only known from the Atlantic Ocean (Valdés and Ortea, 1996), in the Meteor Group seamounts (Atlantis Bank), Lusitanian seamounts (Josephine Bank), and the Azores (slope of Terceira).

REMARKS. This is the only species of the genus that lacks dorsal ridges. It was placed in the genus *Reticulidia* by Valdés and Ortea (1996) on the basis of the morphology of the buccal bulb, with several glandular discs, which is characteristic of this genus.

Reticulidia suzanneae, new species

Figures 1C, 3

Reticulidia halgerda (Brunckhorst and Burn): Debelius, 1999:277.

Reticulidia sp. 1 Rudman, 2000: http://www.seaslugforum.net/retisp1.htm.

MATERIAL EXAMINED. Similan Island, Andaman Sea, Thailand, depth 21 m, February 2001, 1 specimen 37 mm preserved length, collected by M. Strickland on coral rubble, Holotype (LACM 2897).

ETYMOLOGY. *Reticulidia suzanneae* is named in recognition of Suzanne Forman, Phuket, Thailand, who was the first to bring this species to our attention and was instrumental in collecting the holotype.

EXTERNAL MORPHOLOGY. The living animals are 40–70 mm in length. The body is oval and high, and the notal surface is covered with a series of sharp ridges that form a reticulate pattern (Fig. 1C). The ridges, which are irregular and serrated, delimit pits of various shapes from square to pentagonal and triangular. The anus is positioned dorsoventrally. The perfoliate rhinophores have 18 lamellae. The background color of the body is bright yellow and the crests of the ridges are white. One or more large black spots are found at the bottom of each pit. The rhinophores are uniformly orange. Ventrally, the mantle margin is approximately as wide as the foot, with several oval spots arranged in two rows around the mantle margin. The spots of the inner row are larger and fewer than those of the outer row. The oral tentacles are separated from each other (Fig. 3D). The respiratory leaves show alternation in size (Fig. 3E).

INTERNAL MORPHOLOGY. The reproductive system is triaulic (Fig. 3A). The ampulla is oval, almost rounded. From its distal portion emerge the prostate and a long oviduct. The prostate is narrow, long, and convoluted, distally narrowing and expanding again into the short muscular ejaculatory portion. The distal portion of the deferent duct opens into a long, common atrium with the vaginal duct. The penial hooks have a wide base and a long, strong, and pointed cusp. They are about 50 μm in length (Fig. 3B). The vaginal duct opens into the bursa copulatrix. The bursa copulatrix is rounded and connects with the seminal receptacle by a long and wide duct. Near the seminal receptacle, this duct is joined by the uterine duct, which enters the female gland mass. The pyriform seminal receptacle is about twice as large as the bursa copulatrix.

The buccal mass is composed of an oval to rounded buccal bulb and the oral tube (Fig. 3C). The buccal bulb is covered with several radially ar-

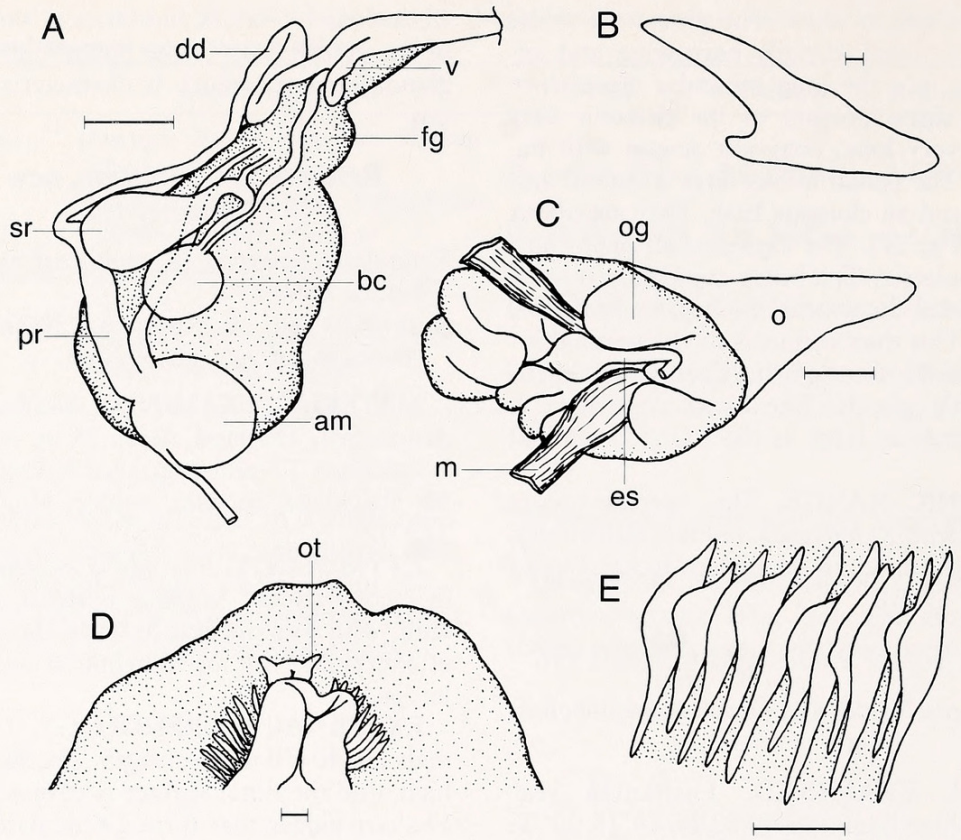

Figure 3 Anatomy of *Reticulidia suzanneae* sp. nov., holotype (LACM 2897). **A,** Reproductive system; scale bar = 1 mm. **B,** Penial hook; scale bar = 2 μm. **C,** Buccal mass; scale bar = 1 mm. **D,** Mouth area; scale bar = 1 mm. **E,** Ventral respiratory leaves; scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; es, esophagus; fg, female gland; m, retractor muscle; o, oral tube; og, oral gland; ot, oral tentacle; pr, prostate; sr, seminal receptacle; v, vagina

ranged glandular discs. The esophagus opens on the dorsal side of the buccal mass, where two large retractor muscles attach.

GEOGRAPHIC RANGE. This species is known only from several localities in the Phuket Province, Andaman Sea, Thailand.

REMARKS. *Reticulidia suzanneae* is clearly distinguishable from other members of the genus. The external coloration resembles that of *R. fungia* by having orange pigment with black spots, but *R. suzanneae* lacks the bluish background pigment present in the latter. Also, the black spots of *R. suzanneae* are always rounded, whereas in *R. fungia* they are irregular in shape. In addition, the ventral side of *R. suzanneae* has two rows of black spots, whereas *R. fungia* has only one. The description of *R. suzanneae* is not based only on the examination of a single specimen, but also on several unpublished (by M. Strickland) and published photos (Debelius, 1999; Rudman, 2000). The four specimens photographed show a very similar and distinct color pattern, and no significant variation has been observed.

The reproductive system of *R. suzanneae* is distinctive in having the bursa copulatrix clearly smaller than the seminal receptacle. Also, the seminal receptacle is pear-shaped, whereas it is oval or rounded in the other species of the genus. The atrium of this species is very elongate, similar to that of *R. fungia*.

PHYLOGENETIC ANALYSIS

TAXA

For a phylogenetic analysis, six taxa have been included. They are all four species of *Reticulidia* and two outgroups, *Phyllidia varicosa* Lamarck, 1801, and *Phyllidiella pustulosa* (Cuvier, 1804).

CHARACTERS

The eight characters of external and internal morphology used to resolve the phylogeny of *Reticulidia* are listed below. All characters are coded as binary. The character states are indicated with numbers, 0: plesiomorphic condition, 1: apomorphic condition. The polarities discussed below have not been obtained *a priori*, but rather as the result of outgroup comparison in the phylogenetic analysis. The distribution of plesiomorphic and apomorphic character states is found in Table 2.

1. **Dorsal morphology.** Species of *Phyllidia* and *Phyllidiella* have the dorsum covered with tubercles, which can be simple or compound, and

Table 2. Data matrix of character states in the taxa involved in the phylogenetic analysis. Data code: 0 = plesiomorphic condition, 1 = apomorphic condition.

	1	2	3	4	5	6	7	8
Phyllidia varicosa	0	0	0	0	0	0	0	0
Phyllidiella pustulosa	0	0	0	0	0	0	0	0
Reticulidia halgerda	1	1	1	1	1	1	0	0
Reticulidia fungia	1	1	0	1	1	1	1	1
Reticulidia gofasi	0	0	1	1	1	1	1	0
Reticulidia suzanneae	1	1	1	1	1	1	0	1

are supported by integumentary spicules [0]. In most species of *Reticulidia*, there are no dorsal tubercles, but rather ridges that are not supported by spicules [1], except for *R. gofasi*, which has simple, conical tubercles [0].

2. **Body texture.** Most phyllidiid nudibranchs, including *Phyllidia varicosa*, *Phyllidiella pustulosa*, and *Reticulidia gofasi* have a very dense network of calcareous spicules in the body [0], which gives the body a rigid texture. In other members of *Reticulidia*, the network of spicules is not so dense and the body texture is softer and more flexible [1].
3. **Ventral respiratory leaves.** The respiratory leaves of *Phyllidia varicosa*, *Phyllidiella pustulosa*, and *Reticulidia fungia* are all similar in size or change size gradually [0], whereas in the other species of *Reticulidia* they show an alternation of larger and smaller ones [1].

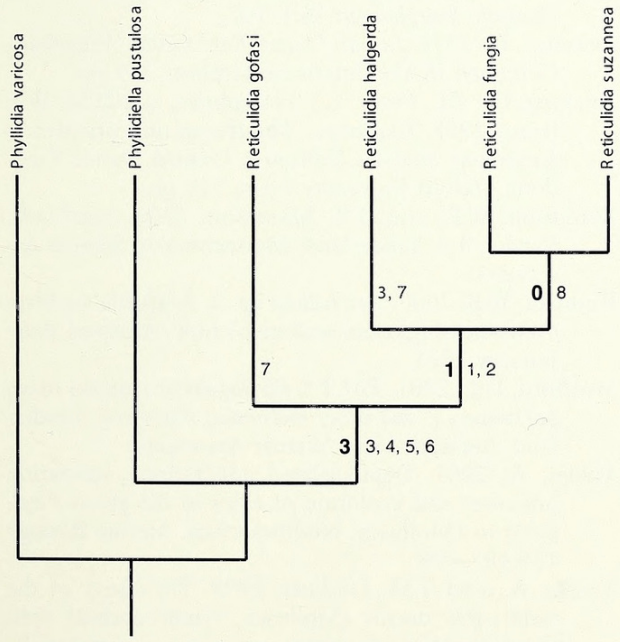

Figure 4 Most parsimonious tree of the phylogenetic relationships of *Reticulidia*, with the Bremer support values in terms of steps on the left side of the each branch (in bold), and character evolution on the right side of each branch. Numbers on the right refer to characters listed in the text. Characters printed in bold and italic face presented one instance of reversal

4. **Buccal bulb shape.** In the genera *Phyllidia* and *Phyllidiella* the buccal bulb is oval to elongate [0], whereas in *Reticulidia* it is more circular [1].
5. **Oral gland shape.** In species of *Phyllidia* and *Phyllidiella* the oral glands are stalked protuberances [0], more densely arranged on the posterior and dorsal sides of the buccal mass. However, in the genus *Reticulidia* the oral glands are radially arranged glandular discs [1].
6. **Esophageal connection.** In all species of *Reticulidia* the esophagus connects to the buccal bulb through its dorsal surface [1], whereas in *Phyllidia* and *Phyllidiella* it connects to the posterior end of the buccal mass [0].
7. **Bursa copulatrix.** The bursa copulatrix of *Phyllidia varicosa*, *Phyllidiella pustulosa*, *Reticulidia halgerda*, and *R. suzanneae* has two ducts leading from it [0]. One of them connects to the seminal receptacle and the uterine duct and the other one becomes the vaginal duct. In *Reticulidia fungia* and *R. gofasi*, there is a single duct leading from the bursa copulatrix that splits into two distally [1].
8. **Genital atrium.** This is the duct formed by the fusion of the deferent duct and the vagina near the reproductive opening. In all species examined here, the atrium is a short structure [0]. However, in two species, *Reticulidia fungia* and *R. suzanneae*, the atrium is very elongate [1].

RESULTS

From the analysis of the data matrix a single most parsimonious tree, 10 steps long, was obtained (Fig. 4). This tree has a consistency index of 0.800 and a retention index of 0.818. The tree is fully resolved and shows that *R. fungia* and *R. suzanneae* are sister taxa, and the sister group to *R. halgerda*. *Reticulidia gofasi* is the most basal member of *Reticulidia*, which is a monophyletic group. The Bremer support analysis shows that the *Reticulidia* clade is well supported (with a value of 3). The genus *Reticulidia* is sustained by three synapomorphies: buccal bulb oval to elongate [4], disc-shaped oral glands [5], and esophagus connected dorsally to the buccal mass [6]. Only one character [3] showed one instance of reversal in *R. fungia*.

DISCUSSION

The evidence from this phylogenetic hypothesis supports *Reticulidia* as a monophyletic group, sustained by three synapomorphies and supported by a high value in the Bremer analysis. This confirms Brunckhorst's (1993) perceptions, which were later sustained in a phylogenetic hypothesis by Valdés and Gosliner (1999).

Reticulidia suzanneae is the sister taxon to *R. fungia*. Resemblances between these two species include the presence of black spots and the small size and similar shape of the penial hooks. These two characters were not included in the phylogenetic analysis, but corroborate the hypothesis proposed. However, as mentioned above, both species are clearly distinguishable in other regards.

BIOGEOGRAPHY

The development of a phylogenetic hypothesis for the genus *Reticulidia* allows further investigation of the biogeography of the group. *Reticulidia gofasi*, which is the only Atlantic member of this clade, is the sister taxon to the other species of the genus. A vicariant event, most likely the closure of the east–west communication in the Suez area during the Oligocene–Miocene transaction (23 Ma), produced the split of the original range of the ancestor of the *Reticulidia* clade and subsequent speciation. Dispersal of Indo-Pacific *Reticulidia* into the Atlantic or vice versa seems to be very unlikely, because of the presence of large land barriers separating both basins. Valdés (2001) hypothesized that the vicariant event derived from the separation of the Indo-Pacific and Atlantic basins explains the presence of a distinct clade of Atlantic and eastern Pacific species in the genus *Phyllidiopsis* Bergh, 1875, which is the sister taxon to some other Indo-Pacific species. Acceptance of this hypothesis implies that the genus *Reticulidia* appeared before the closure of the east–west communication (during the Oligocene or earlier). The absence of species of *Reticulidia* from most of the Indian Ocean and the Mediterranean could be due to subsequent extinction in these areas. The higher stability of the deep sea could account for the survival of a species of *Reticulidia* in the Atlantic Ocean, despite documented environmental changes in shallow areas. Again, Valdés (2001) proposed a similar line of thinking to explain the presence of several deep-water Atlantic species of *Phyllidiopsis*.

Within the tropical Indo-Pacific clade, *R. halgerda* is the sister taxon to the clade containing the other two species, *R. fungia* and *R. suzanneae*. *Reticulidia halgerda* and *R. fungia* are sympatric for the most part, and widespread throughout the central to western Pacific (including Fiji and Micronesia), from eastern Australia to Taiwan. The range of *R. fungia* is the larger of the two species, including populations reaching the eastern Indian Ocean (Christmas Islands). *Reticulidia suzanneae* appears to be endemic to the Indian Ocean coast of Thailand (Andaman Sea); it has never been recorded from other localities in the Indo-Pacific. The ranges of the sister pair *R. fungia–R. suzanneae* do not overlap, and a vicariant event could also be involved in the speciation of these taxa. In this case, their populations are separated by Sumatra and the Malaysian Peninsula. However, given the small number of specimens of *R. suzanneae* collected to date, not much can be said about the geographic range of this taxon.

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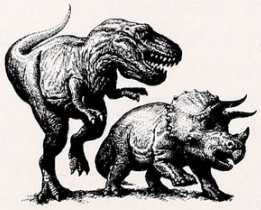

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