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

Ángel Valdés and David W. Behrens
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PHYLOGENETIC SYSTEMATICS OF Reticulidia
Brunckhorst, 1990 (Mollusca, Nudibranchia), with the Description of a New Species from the Tropical Indo-Pacific

Ángel Valdés1 and David W. Behrens2

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.

INTRODUCTION

The genus Reticulidia was described by Brunckhorst (1990) to include a single described species of Indo-Pacific Phyllidiidae, R. halgerda Brunckhorst 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 Brunckhorst and Gosliner (in Brunckhorst, 1993), also from the tropical Indo-Pacific. Separation of these two species was justified on the basis of differences in the external coloration (Brunckhorst, 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-
**SYSTEMATICS**

Genus Reticulidia Brunckhorst


**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 (synapomorphies). Esophagus connecting into the dorsal surface of the rounded buccal bulb (synapomorphies). Reproductive system similar to that of other phyllidiid nudibranchs.

*Reticulidia balgerda* Brunckhorst and Burn, 1990

Figures 1A, 2A–C


**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 postampullary 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. balgerda*. In addition, the penial hooks of *R. balgerda* 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),...
Table 1. Additional specimens of phyllidiids examined for the phylogenetic analysis, including locality, depth, collection date, collector, and museum registration number.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality and depth</th>
<th>Date</th>
<th>Collector</th>
<th>Registration number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phyllidiella pustulosa</td>
<td>South of Suva Pt., Viti Levu, Fiji, 0–1 m</td>
<td>16–17 May 1979</td>
<td>J.H. McLean</td>
<td>LACM 1979–40.7</td>
</tr>
<tr>
<td></td>
<td>Low Isles, off Port Douglas, Queensland, Australia, 0–1 m</td>
<td>13 August 1981</td>
<td>A.J. Ferreira</td>
<td>LACM 1981–20.1</td>
</tr>
</tbody>
</table>

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

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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.
prostata 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

The reproductive system is triaulic. The ampulla is oval. From its distal portion emerges 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.

**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 emerges 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 long, 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


**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-
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.

<table>
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<th>3</th>
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<td>Phyllidiella pustulosa</td>
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<tr>
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<tr>
<td>Reticulidia fungia</td>
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<tr>
<td>Reticulidia gofasi</td>
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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 halgerda, 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].

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.

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.
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 Brunkhorst’s (1993) perceptions, which were later sustained in a phylogenetic hypothesis by Valdès 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. Valdès (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, Valdès (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. balgerda* is the sister taxon to the clade containing the other two species, *R. fungia* and *R. suzanneae*. *Reticulidia balgerda* 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.

ACKNOWLEDGMENTS

We thank Mark Strickland and Suzanne Foreman for collection of type material. We also thank Narongpon Sittihaweepat and Erwin Kohler for additional information on the geographic range of the new species. Additional specimens examined were collected by Terrence Gosliner, James McLean, Gary Williams, and Antonio Ferreira. This paper has been supported by the National Science Foundation through the PEET grant DEB-9978155 Phylogenetic systematics of dorid nudibranchs to Terrence M. Gosliner and the senior author.

LITERATURE CITED


Received 18 January 2001; accepted 5 October 2001.