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Phyllidiidae (Opisthobranchia: Nudibranchia) from Papua New Guinea with the description of a new species of *Phyllidiella*

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Abstract: Species of phyllidiid nudibranchs from Papua New Guinea (and other Indo-Pacific regions) are redescribed in this paper. A new species, *Phyllidiella backeljaui* n. sp., is described and compared with other species of the genus. External characters and internal morphology of the species studied have been examined in detail and illustrated, some of them for the first time such as *Phyllidiopsis pipeki*. In addition, new locations for *Phyllidiella hageni* and *Phyllidiella zeylanica* are reported from Papua New Guinea.

Key words: phyllidiid, morphology, anatomy, new species, new locations

The family Phyllidiidae Rafinesque, 1814 includes gastropods belonging to the order Nudibranchia (Gastropoda: Opisthobranchia). It is widely distributed throughout the tropical Indo-West Pacific Ocean (Risbec 1928, 1956, Baba 1930, Edmunds 1971, 1972, Baba and Hamatani 1975, Lin 1983, Willan and Coleman 1984, Willan *et al.* 1998, Fahrner and Beck 2000). They are predators specializing in suctorial feeding on sponges and have developed a highly toxic chemical defense. This family is characterized by the absence of a dorsal gill, the possession of secondary gill leaflets that are located ventrally around the foot, and by the absence of radula and jaws (Bergh 1869, 1875, Pruvot-Fol 1956, 1957, Brunckhorst 1990a, 1993, Willan *et al.* 1998, Fahrner and Beck 2000).

Several authors have paid special attention to this complicated group, but there is still a great deal of confusion about the correct identification of these specimens, which have been the subject of numerous disagreements (Wägele 1985, Yonow 1986, Brunckhorst and Willan 1989, Gosliner and Behrens 1988, Brunckhorst 1989, 1993, Fahrner and Beck 2000). The main reasons for the misidentifications are the large number of descriptions based on single preserved specimens, the restriction on features of external morphology, and intraspecific variability. Only a few authors have recognized the necessity of accurate anatomical examination for the description of new species (Pruvot-Fol 1956, 1957, Gosliner and Behrens 1988, Brunckhorst 1989, 1990a, 1990b, 1993, Yonow 1996, Fahrner and Beck 2000).

The phyllidiid fauna of the Indo-Pacific was comprehensively reviewed by Brunckhorst (1993), although anatomical data could not be provided for all of the species. Only the type species of each genus was studied anatomically.

Ghiselin (1992) compiled a faunal list from Madang Province, Papua New Guinea. The list represents collections made in Madang by T. Gosliner and M. Ghiselin in 1986 and 1989, T. Gosliner and R. Willan in 1988, T. Gosliner and G. Williams in 1990, and T. Gosliner, G. Williams, and M. Ghiselin in 1992. He concluded that the opisthobranch fauna of the Madang Province is very rich in species and still poorly known. The family Phyllidiidae is particularly conspicuous and abundant.

The present paper is a contribution to the knowledge of phyllidiid fauna based on studies of specimens collected from Papua New Guinea. A few animals from other regions of the Indo-Pacific Ocean are also included. All the species studied are described and illustrated, some of them for the first time. New records for some species are reported from Papua New Guinea, including the very uncommon species *Phyllidiella hageni* Fahner and Beck, 2000, only known to date from Lombok, Indonesia, and *Phyllidiella zeylanica* (Kelaart, 1858), which is moderately common in the Indian Ocean but rare in the western Pacific (Fahrner and Beck 2000). A description of a new phyllidiid species, *Phyllidiella backeljaui* n. sp., is also included in this paper.

MATERIAL AND METHODS

A total of 150 specimens belonging to 13 species of phyllidiid nudibranchs were studied. Seventy specimens were collected during July and August 1996 by J. S. Troncoso and deposited at the Department of Ecology and Animal Biology of the University of Vigo (Spain). The holotype and paratype of the new species, *Phyllidiella backeljaui*, was deposited at the Museo Nacional de Ciencias Naturales of Madrid. The remaining specimens were borrowed from the Royal Belgian Institute of Natural Sciences for identification and are denoted by the abbreviation RBINS.

Most of the studied specimens were collected on the northern coast of Papua New Guinea (PNG) in 1996, mainly in the low coral formation of Laing Island, which is located in Hansa Bay (Domínguez *et al.* 2004). Some specimens were collected at other sites in the bay, including Durangit Reef and Boisa Island. A few animals of the Royal Belgian Institute of Natural Sciences collection were collected from Nossi-Bé (Madagascar), and Îlot Tabou (New Caledonia).

We do not have information about how the specimens deposited at the RBINS were collected and preserved. The specimens captured in 1996 were collected subtidally using SCUBA and intertidally in shallow water. In the laboratory, photographs of live specimens were taken of most of the species before they were anesthetized. The animals were frozen at 0°C prior to fixation in 5% formalin in seawater for 24-48 hours, then transferred to 70% ethanol.

Preserved specimens were measured and examined in detail. All specimen dimensions are given as body length x maximum body width. The drawings of external morphology are based on preserved specimens. All animals were dissected by a dorsal longitudinal incision while viewed with a binocular dissecting microscope. For the illustrations of internal anatomy, the blood gland, aorta, and reproductive system were removed from their natural positions.

SPECIES DESCRIPTIONS

Phyllidia varicosa Lamarck, 1801
(Figs. 1A, 2)

Phyllidia varicosa Lamarck 1801: 66, Edmunds 1971: 388-389, fig. 23, Baba and Hamatani 1975: 174-175, fig. I, Brunckhorst 1993: 26-29, figs. 2, 3A, 23, 24A-D, pl. 1A-D, Debelius 1996: 123, 241, 265, Fahrner and Beck 2000: 202, pl. 2, fig. 6, Fahrner and Schrödl 2000: 164-171, Yonow *et al.* 2002: 863.
Phyllidia trilineata Cuvier 1804: 268, pl. A, figs. 1-6.
Phyllidia arabica Ehrenberg 1831: pages unnumbered.

Material examined

RBINS: Nossi-Bé (55.7 mm × 30.1 mm); PNG (38.6 mm × 14.5 mm, 48.3 mm × 13.5 mm, 54.3 mm × 22.0 mm, 37.5 mm × 11.2 mm, 36.6 mm × 16.8 mm, 41.9 mm × 18.5 mm, 25.2 mm × 9.1 mm, 31.5 mm × 11.4 mm, 43.3 mm × 17.0 mm, 42.1 mm × 19.1 mm, 46.9 mm × 17.5 mm, 60.2 mm × 25.1 mm, 36.6 mm × 14.8 mm, 53.1 mm × 29.3 mm, 43.5 mm × 18.6 mm, 56.0 mm × 19.8 mm); Laing Island (28.8 mm × 17.2 mm, 65.0 mm × 35.7 mm, 30.8 mm × 15.0 mm, 35.4 mm × 18.8 mm).

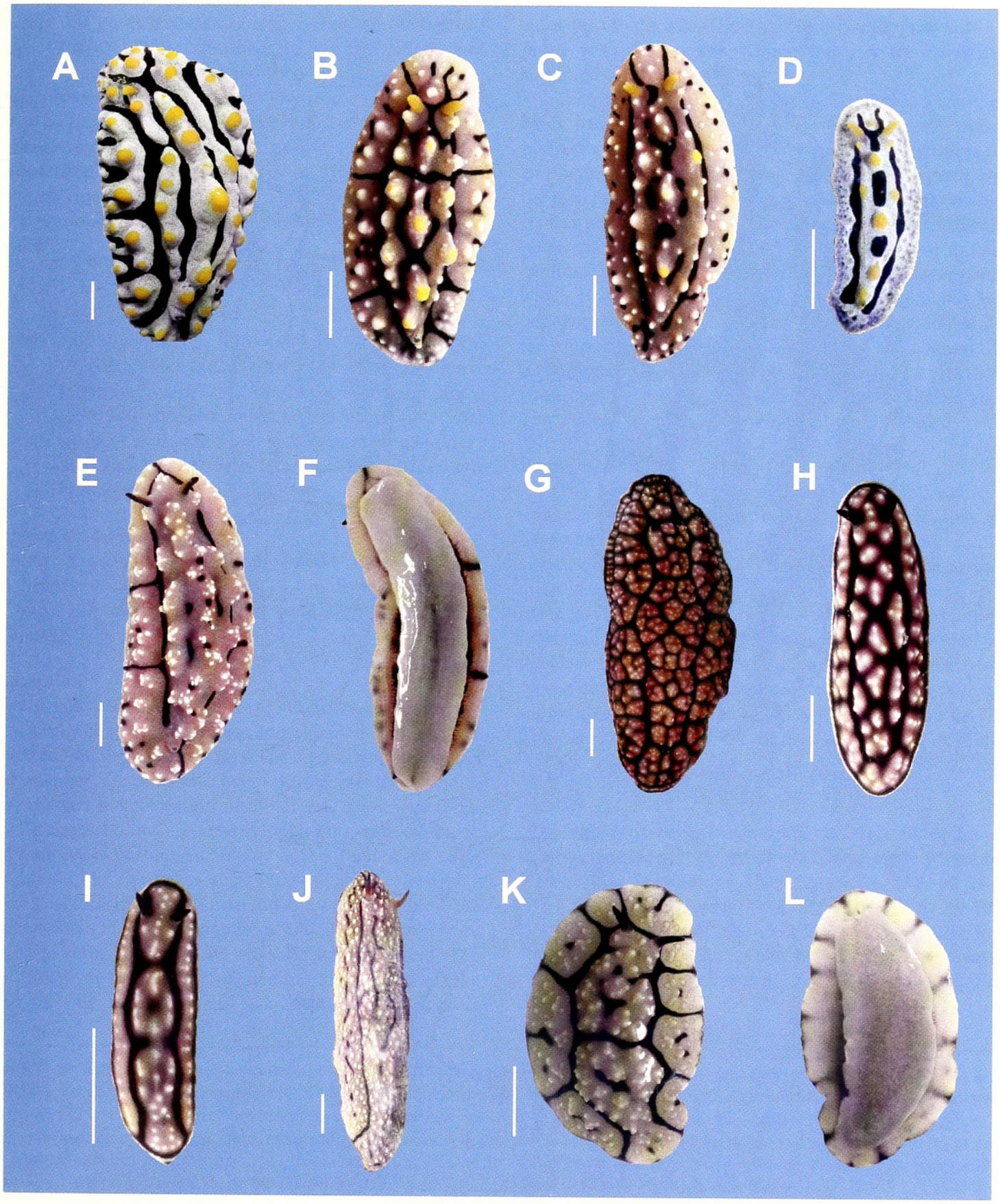
Expedition 1996: Laing Island, 0.5 m depth (49.6 mm × 30.4 mm, 50.9 mm × 26.5 mm, 46.7 mm × 26.55 mm, 28.7 mm × 16.3 mm, 17.6 mm × 9.0 mm, 14.2 mm × 7.6 mm, 40.0 mm × 16.3 mm, 48.7 mm × 26.1 mm); Laing Island, 15 m depth (30.5 mm × 15.2 mm); Laing Island, 16.5 m depth (32.1 mm × 16.0 mm, 50.9 mm × 26.3 mm); Laing Island, 18.5 m depth (33.2 mm × 17.4 mm, 43.0 mm × 24.3 mm, 40.9 mm × 21.3 mm, 43.2 mm × 18.0 mm); Hansa Bay, 28.8 m depth (25.0 mm × 12.9 mm).

Description

All of the specimens share the presence of three longitudinal ridges of tubercles on the median region of the dorsum, separated from each other and from the lateral pustules by bands of dark pigmentation. Many animals have broken ridges and the dorsal bands are interconnected; some specimens have continuous ridges and isolated bands (Fig. 2A). On the sides of the dorsum there are rounded or conical tubercles that form transverse ridges. The live animals (Fig. 1A) have yellow rhinophores and the tubercles are blue-grey at their bases and have yellow-orange apices. Some preserved specimens lack the dorsal black pigmentation. Ventrally the pedal sole has a median black longitudinal stripe that is well preserved in some specimens and partially absent in others.

Internally (Fig. 2B), the short oral tube sometimes has black marks on its sides; the pharyngeal bulb is wide and there are rounded oral glands on either side of it. The pharyngeal retractor muscles are well developed and short and are inserted dorsally onto the pharyngeal bulb. The tubular pharynx leaves the bulb dorsally. The esophagus inserts into the digestive gland mass; the intestine originates to the left of the pericardium, turns to the right and extends to the anal papilla. The reproductive system (Fig. 2C) has a spherical ampulla whose color is pale orange or brown in the preserved state. It connects with a thick and convoluted prostate, which narrows into a short vas deferens. The nidamental gland mass is large and spherical. The bursa copulatrix is spherical and lies next to the receptaculum seminis, which is kidney-shaped. The vaginal duct is long and slightly folded.

Figure 1. Photographs of live specimens used in this study. The orientation is anterior at top in all. A, *Phyllidia varicosa*, dorsal view (Laing Island, depth 18.5 m). B-C, *Phyllidia elegans*, dorsal view (Laing Island, depth 17.4 m). D, *Phyllidia coelestis*, juvenile in dorsal view (Laing Island, depth 17.4 m). E, *Phyllidiopsis krempfi*, dorsal view (Boisa Island, depth 56.4 m). F, *Phyllidiopsis krempfi*, ventral view. G, *Phyllidiella pustulosa*, dorsal view of a large specimen (Laing Island, depth 0.5 m). H, *Phyllidiella pustulosa*, dorsal view of a smaller specimen. I, *Phyllidiella pustulosa*, juvenile in dorsal view. J, *Phyllidiella hageni*, dorsal view (Laing Island, depth 16.5 m). K, *Phyllidiella backeljaui* n. sp., dorsal view (Laing Island, depth 9 m). L, *Phyllidiella backeljaui* n. sp., ventral view. Scale bars = 5 mm.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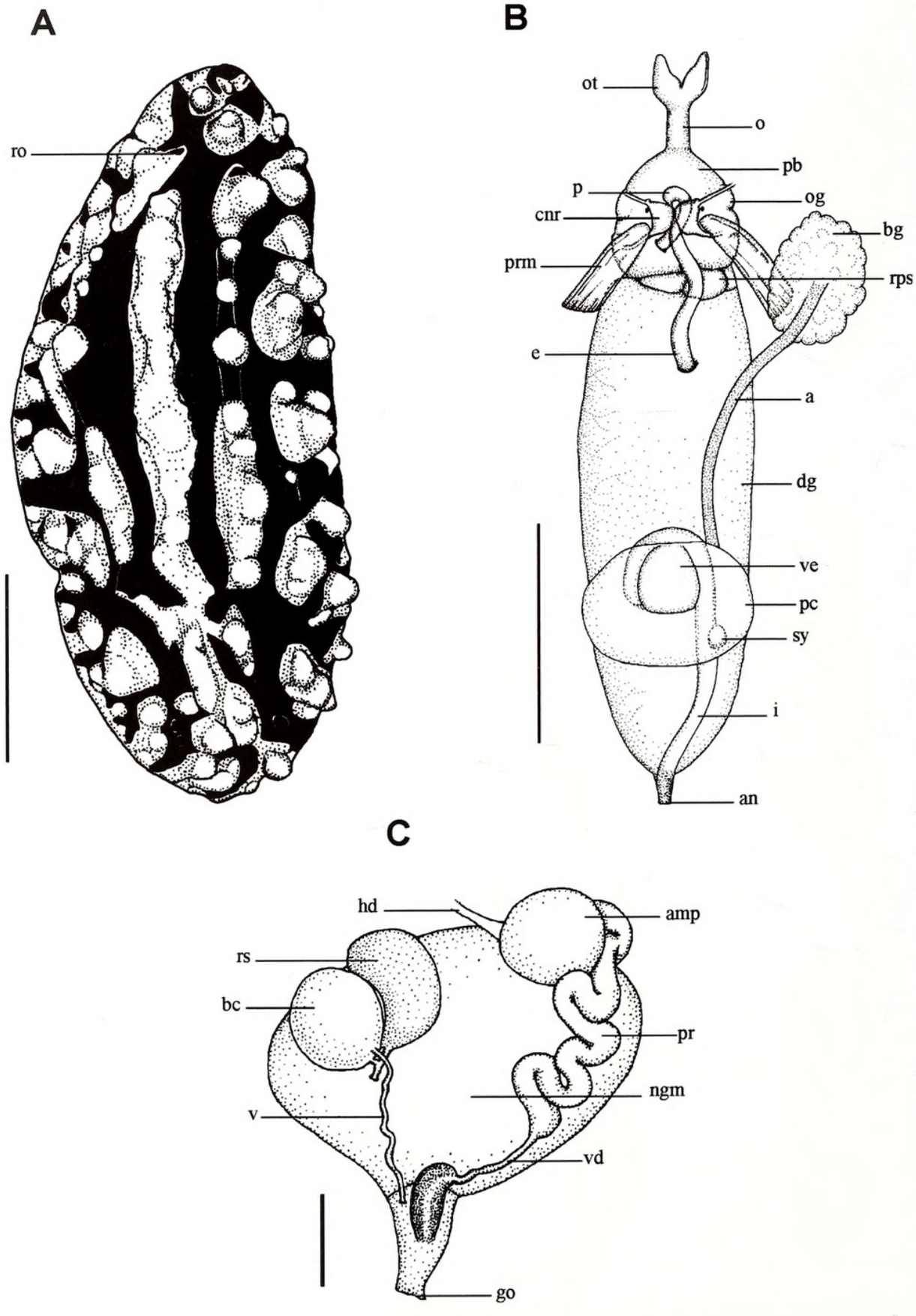
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Remarks

The taxonomic status of *Phyllidia varicosa* Lamarck, 1801 has been the subject of considerable debate for several years (Fahrner and Schrödl 2000). The reason for this controversy was the description of a specimen, on the basis of which Cuvier (1797) established the genus *Phyllidia* and which was considered lost since 1866 (Willan *et al.* 1998). These authors rediscovered the holotype in Paris, which was in a good state of preservation. The holotype has weak, dark marks forming a longitudinal line on the sole; however, this characteristic is not always present in the preserved state. Some specimens appear to have completely lost the black pigmentation dorsally and ventrally, including the stripe on the foot.

Phyllidia elegans Bergh, 1869
(Figs. 1B-C, 3)

Phyllidia elegans Bergh 1869: 439-454, 506-507, pl. 18B, 19, Allan 1957: 5, Coleman 1989: 48, Brunckhorst 1993: 33-34, fig. 25C, pl. 2A-B, Wells and Bryce 1993: 146, species number 190, Debelius 1996: 264, Gosliner *et al.* 1996: 168, species number 594, Marshall and Willan 1999: 122, fig. 220, Fahrner and Beck 2000: 202, pl. 2, figs. 7-8.

Material examined

RBINS: Laing Island (45.2 mm × 18.7 mm).

Expedition 1996: Laing Island, 14.1 m depth (14.1 mm × 6.0 mm), 17.4 m depth (23.8 mm × 12.8 mm, 26.7 mm × 13.0 mm).

Description

Dorsally and medially, there are three longitudinal rows of tubercles that can be simple and rounded, irregular, or coalesced, but never form ridges. The central row ends at the anal opening; the other two begin behind each rhinophore. We observed the coloration in life of two specimens (Figs. 1B, C): the tubercles are creamy-pink with whitish apices. Some tubercles of the median part of the dorsum have yellow apices. The rhinophores are yellow. There are two longitudinal black lines that surround the central area of the dorsum including the rhinophores and the anus; they are joined in some specimens by a black transverse band. The central row of tubercles are sometimes separated from the other ones by a longitudinal black line to each side, or its tubercles may be separated from each other by short, irregular lines. On the mantle margin there are transverse black lines that extend to the mantle edge. Ventrally the sole has a longitudinal black line and there are also black lines on the sides, next to the gills (Fig. 3A). These lines appear to be a bit faded, as in the largest specimen, but they are visible in all specimens.

Internally (Fig. 3B), the short oral tube has a transverse black band at its base. The pharyngeal retractor muscles insert dorsally onto the thick pharyngeal bulb, which is covered with oral glands. The pharynx arises posteriorly from the pharyngeal bulb, extends in front and passes through the central nerve ring. The esophagus inserts into the digestive gland mass. The intestine originates to the left of the pericardium, turns to the right and extends to the anal papilla, which is swollen. The reproductive system (Fig. 3C) has a large, spherical, yellow ampulla. The prostate is folded near the ampulla and it narrows into a short vas deferens. The bursa copulatrix and the receptaculum seminis are small and connected by a short duct that inserts in the female gland. The vaginal duct is very narrow and slightly folded.

Remarks

The pattern of black lines varies intraspecifically; the tubercles do not form continuous ridges, although they may have their bases fused together. *Phyllidia elegans* displays some ontogenetic and individual variations in the arrangement of notal tubercles (Brunckhorst 1993) and some specimens may have only one or just a few yellow capped pustules (Marshall and Willan 1999). However, the coloration and the black markings serve to distinguish it from other related species (Brunckhorst 1993). These features are the pink dorsum with tubercles capped in yellow, black marks on dorsum, and the black line on the foot sole and on its sides.

Phyllidia coelestis Bergh, 1905
(Figs. 1D, 4)

Phyllidia coelestis Bergh 1905: 182-183, pl. 3, fig. 16, Coleman 1989: 49, Brunckhorst 1989: 35-45, figs. 1-4, Brunckhorst 1993: 30-33, fig. 25B, pl. 1F-H, Allen and Steene 1994: 200, Gosliner *et al.* 1996: 168, species number 593, Debelius 1996: 264, Marshall and Willan 1999: 121-122, fig. 219, Fahrner and Beck 2000: 202, pl. 3, fig. 1, Yonow *et al.* 2002: 862, fig. 16B.

Figure 2. *Phyllidia varicosa.* A, Drawing of the dorsal surface of a preserved specimen 40.0 mm long collected in Laing Island, depth 0.5 m. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 10 mm (A, B), 1 mm (C).

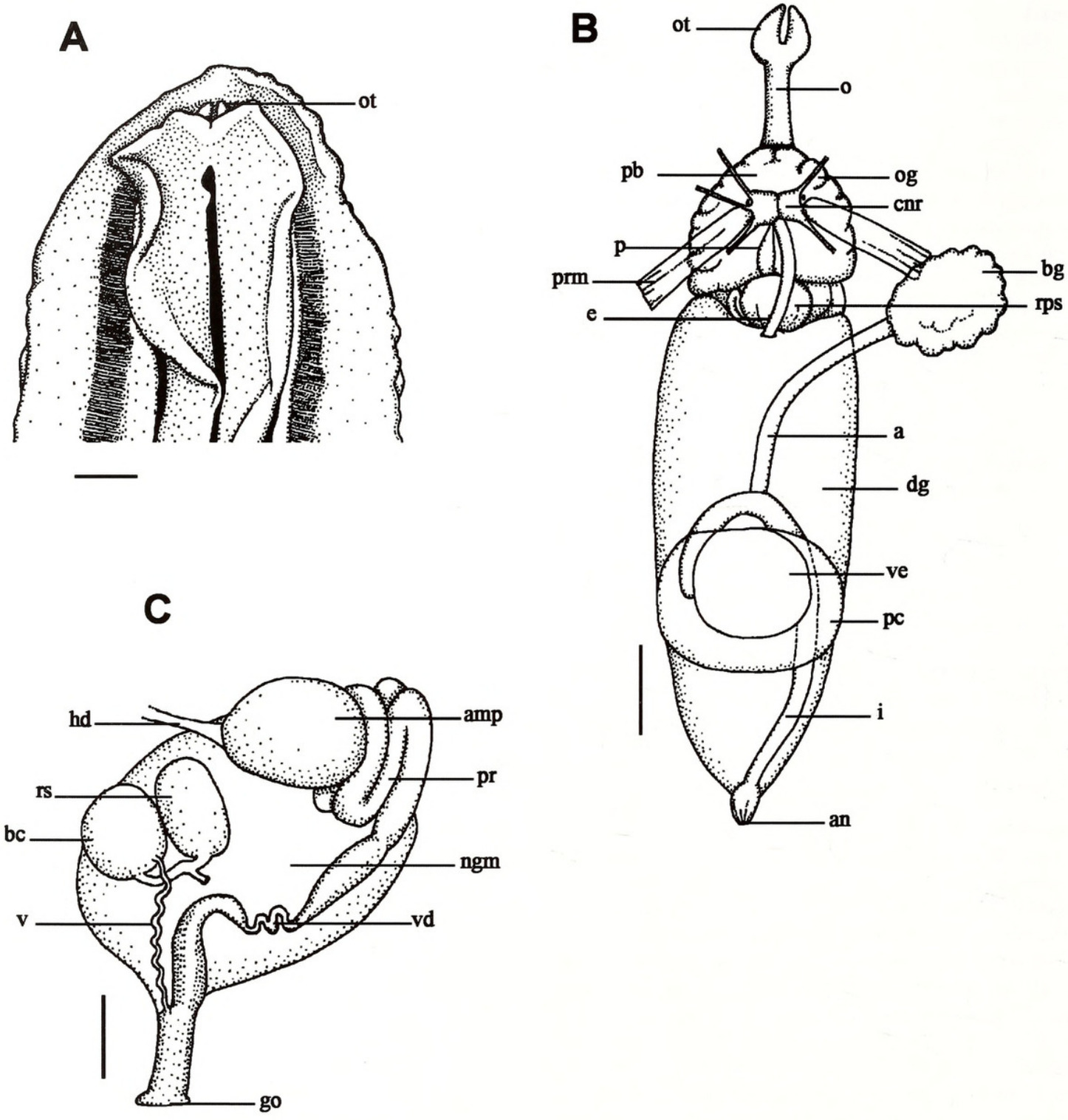

Figure 3. *Phyllidia elegans*. A, Drawing of the anterior end of the ventral surface of a preserved specimen 23.8 mm long, collected in Laing Island, depth 17.4 m. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 3A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B), 1mm (C).

Phyllidia alia Yonow 1984: 224, figs. 6C-D, 7A, 8F-G.
Phyllidia varicosa Gosliner 1987: 90, pl. 152 (non *Phyllidia varicosa* Lamarck, 1801).

Material examined

RBINS: PNG (28.7 mm × 12.4 mm, 20.3 mm × 12.0 mm, 23.3 mm × 11.5 mm, 30.9 mm × 12.7 mm, 24.4 mm × 10.6 mm, 27.9 mm × 14.1 mm); Laing Island (14.1 mm × 8.8 mm, 27.9 mm × 12.2 mm, 18.8 mm × 11.0 mm, 18.3 mm × 9.5 mm, 18.8 mm × 9.7 mm, 22.2 mm × 9.7 mm, 19.2 mm × 9.0 mm, 20.1 mm × 9.8 mm).

Expedition 1996: Laing Island, 0.5 m depth (19.2 mm × 9.8 mm, 10.2 mm × 4.8 mm), 14.1 m depth (30.0 mm × 14.4 mm, 12.4 mm × 6.1 mm), 14.7 m depth (11.5 mm × 4.9 mm), 15 m depth (23.6 mm × 9.4 mm), 15.7 m depth (15.0 mm × 8.2 mm), 16.5 m depth (17.7 mm × 10.1 mm), 17.4 m depth (20.0 mm × 8.3 mm, 14.6 mm × 8.5 mm), 17.8 m depth (14.5 mm × 6.3 mm), 45 m depth (17.9 mm × 8.0 mm).

Description

Living specimens of *Phyllidia coelestis* have blue dorsal surfaces with black bands and rounded tubercles capped in yellow that form three longitudinal rows. The median row is formed by single isolated tubercles, separated from each other by black patches. This row begins anterior to the yellow rhinophores and its posterior tubercles are smaller and may be coalesced. The anal opening is located at the posterior end of this row. The other two rows begin directly behind each rhinophore with a high, rounded, and isolated tubercle. They continue with a series of tubercles forming a ridge. These are followed by two wide black bands with wavy external borders. The mantle margin is broad with rounded tubercles and small black spots, which may be lacking in smaller specimens. In juvenile specimens (Fig. 1D), there is a black "Y" on the anterior part of the dorsum between the rhinophores. Ventrally (Fig. 4A), the foot sole has no black marks and the oral tentacles are separate.

Internally (Fig. 4B), the oral tube has black marks next to the oral tentacles and a transverse black band at its base. On the pharyngeal bulb there are spherical oral glands and the pharyngeal retractor muscles insert dorsally onto the bulb. The pharynx passes through the central nerve ring and connects with a narrow esophagus that inserts into the digestive gland mass. The reproductive system (Fig. 4C) has a large ampulla and the prostate connects to a narrow vas deferens. The largest specimens (41 mm long) possess seminal receptacle longer than the bursa copulatrix. In smaller specimens both organs are the same shape and size. The vaginal duct arises from the bursa copulatrix and is very narrow.

Remarks

Specimens of *Phylidia coelestis* can be distinguished from those of other species by the presence of three rows of tubercles on the median part of the dorsum that are isolated in the midline and two other rows forming ridges (the ridges can be interrupted). The living animals have a blue notum with black bands, tubercles capped in yellow, yellow rhinophores, and the foot sole lacking a black stripe. This species can be also distinguished from other phyllidiids by the "Y" shape of the dorsum (Bergh 1905, Brunckhorst 1989, 1993).

Phyllidia ocellata Cuvier, 1804
(Fig. 5)

Phyllidia ocellata Cuvier 1804: 269, pl. 18A, fig. 7, Gray 1857: 216, Gosliner *et al.* 1996: 169, species number 595, Yonow 1996: 485-487, figs. 1A-G, 4A, table 1.

Material examined

RBINS: PNG (41.2 mm × 20.9 mm); Laing Island (31.8 mm × 21.4 mm, 28.2 mm × 18.5 mm).

Description

The dorsal surfaces of preserved specimens are pale in color with black rings. There is a longitudinal median row of five rounded tubercles that are joined by a small crest (Fig. 5A); the anal opening is located behind this crest. These tubercles are narrowed at their bases and have a rough surface. Anterior to the rhinophores on the midline there is a tubercle surrounded by a black ring. On either side of the midline row there are two black rings, which may be complete or semicircular. On the mantle margins there are small rounded tubercles and in one specimen there are also some small black spots on the posterior region of the dorsum. The rhinophores are pale; next to each one is a rhinotubercle. Ventrally, the sole has no black line and the oral tentacles are separate (Fig. 5B).

The pharyngeal bulb (Fig. 5C) has oral glands (some of them are long). The pharyngeal retractor muscles insert posteriorly and dorsally onto the bulb. The pharynx is not very long, arises posteriorly from the pharyngeal bulb (Fig. 5D), and passes through the central nerve ring. The esophagus is narrow and inserts on the anterior end of the digestive gland. The intestine originates to the left of the pericardium, turns to the right, and extends to the anal papilla. The reproductive system (Fig. 5E) has a rounded ampulla. The prostate narrows into a narrow and coiled vas deferens. The bursa copulatrix is spherical and is connected by a narrow duct to the receptaculum seminis, which is slightly oval.

Remarks

The specimens studied in this paper exhibit the typical dorsal pattern for *Phyllidia ocellata* (Brunckhorst 1993,

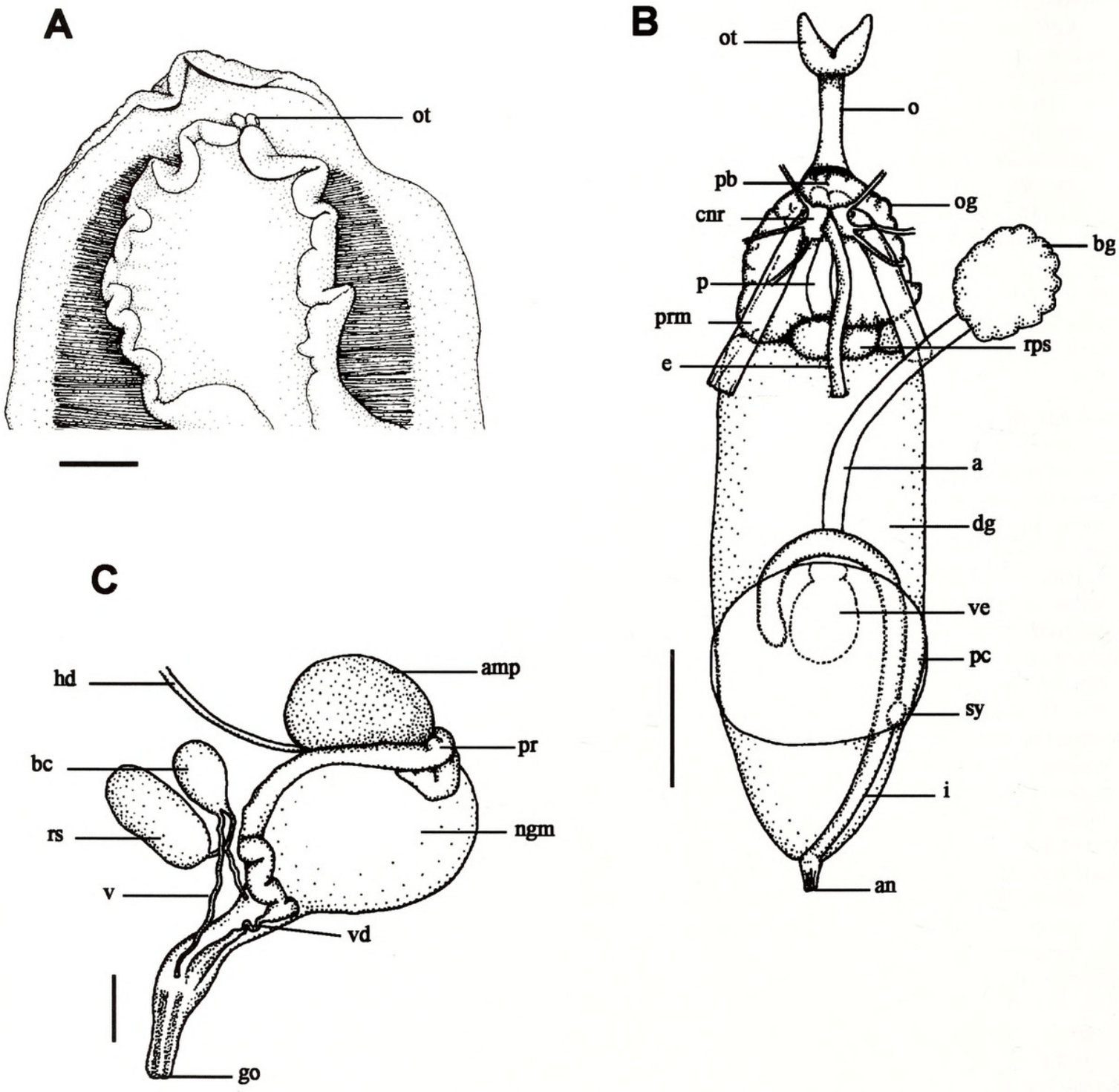

Figure 4. *Phyllidia coelestis.* A, Drawing of the ventral view of the anterior end of a preserved specimen 30.9 mm long, collected in PNG. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 4A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B), 1 mm (C).

Yonow 1996), having five black rings encircling a tubercle; the tubercles have a rough surface and they are aligned along the median dorsal surface, forming a crest.

One animal studied in the preserved state has incomplete rings on the posterior area of the dorsum; it may have lost its black pigment.

Phyllidia picta Pruvot-Fol, 1957
(Fig. 6)

Phyllidia picta Pruvot-Fol 1957: 110, figs. 5-12.
Fryeria rueppelli Baba and Hamatani 1975: 178-179, fig. 5.
Fryeria menindie Bruncknorst 1993: 47-49, fig. 26B, pls. 4G, 5A.
Fryeria picta Yonow 1996: 511-513, figs. 14A-K, table 3.

Material examined

Expedition 1996: Laing Island, 0.5 m depth (25.6 mm × 12.1 mm, 24.8 mm × 11.4 mm).

Description

The body is elongate-ovate in shape and the notum is black with large rounded tubercles near the midline. These tubercles are aligned into three longitudinal rows (Fig. 6A). The midline row is formed by four isolated tubercles (anterior to the rhinophores there is a smaller one). The other two rows are located on either side of the central ridge: Each is formed by 3-4 tubercles that begin posterior to the rhinophore. The rhinophores are pale in color. Between these tubercles there is a short, narrow, longitudinal crest or a series of smaller black tubercles. Pale semicircles with tubercles occur around the mantle margins. These areas have small black spots in some specimens. The oral tentacles are triangular in the preserved state (Fig. 6B). The anus is located ventrally posterior to the edge of the foot (Fig. 6C).

The oral tube is short and has a pale transverse black band on its base (Fig. 6D). The pharyngeal bulb (Fig. 6E) has oral glands on its surface. The pharyngeal retractor muscles insert posteriorly and dorsally onto the bulb near the area where the long pharynx arises. The pharynx narrows and passes through the central nerve ring. It connects to a thick esophagus that inserts into the digestive gland. The intestine originates to the left of the pericardium, turns to the right, and extends to the anal papilla, which opens ventrally. The reproductive system (Fig. 6F) has a large ampulla; the slightly folded prostate connects with the vas deferens. The bursa copulatrix is spherical and connects with the larger receptaculum seminis. Near the bursa copulatrix the vaginal duct is wide; distally it is narrower.

Remarks

Pruvot-Fol (1957) was the first author to describe this species, which she assigned to the genus *Phyllidia*. This species, however, differs from the type of this genus in several ways, including the location of the ventral anus. Later it was assigned to the genus *Fryeria* (Yonow 1996). Bruncknorst (1993) redescribed the genus *Fryeria*, which in his opinion is distinct from *Phyllidia*. However, with the exception of the position of the anus, Valdés and Gosliner (1999) did not find other consistent differences between *Fryeria* and *Phyllidia*, and consequently synonymized these two names.

Externally, *Phyllidia picta* resembles *Phyllidia coelestis* in its pattern and coloration of tubercles. Individuals of *P. picta* can also be confused with other species such as *Phyllidia rueppelli* (Bergh, 1869) because both have rows of isolated tubercles on the dorsum and semicircles of pale notum on the margin, but the mantle of *P. rueppelli* is edged in yellow-orange and is only known from the Red Sea (Yonow 1986, Bruncknorst 1993, Fahrner and Beck 2000). Individuals of *P. picta* also resemble those of *Phyllidia marindica* (Yonow and Hayward, 1991), but this species has a dorsal midline ridge and numerous short black lines on the mantle margin that extend toward the edge.

Phyllidiopsis shireenae Bruncknorst, 1990
(Fig. 7)

Phyllidia sp. Bruncknorst 1989: 7 (color illustration).
Phyllidiopsis shireenae Bruncknorst 1990b: 577-583, figs. 1-4; Bruncknorst 1993: 66-67, figs. 29F-G, pl. 8B, Fahrner and Beck 2000: 200, pl. 1, fig. 5.

Material examined

RBINS: PNG (64.4 mm × 28.5 mm, 59.2 mm × 32.5 mm, 75.5 mm × 32.2 mm, 61.0 mm × 30.2 mm, 69.5 mm × 25.5 mm, 57.0 mm × 24.1 mm, 24.1 mm × 7.4 mm); Laing Island (61.0 mm × 24.9 mm, 64.1 mm × 21.7 mm, 46.0 mm × 17.9 mm, 65.3 mm × 36.3 mm).

Description

The dorsal surface is pale in color with a longitudinal median crest that is continuous, high, and triangular in cross-section (Fig. 7A). The crest can be seen in living and preserved specimens. Posterior to each pale-colored rhinophore is a longitudinal row of simple angular tubercles. A black band surrounds the median part of the dorsum that encloses the rhinophores and the anus; the latter is located at the posterior end of the median ridge. On the mantle margin there are transverse black lines radiating from the black ring that extend toward the edges of the mantle, one anterior, one posterior, and one or two laterals. Some preserved specimens appear faded and seem to have lost the black pigmentation. In some specimens the median crest has a dark spot or a row of spots. One specimen also has a small transverse black line on the dorsum. Ventrally (Fig. 7B), there is a black

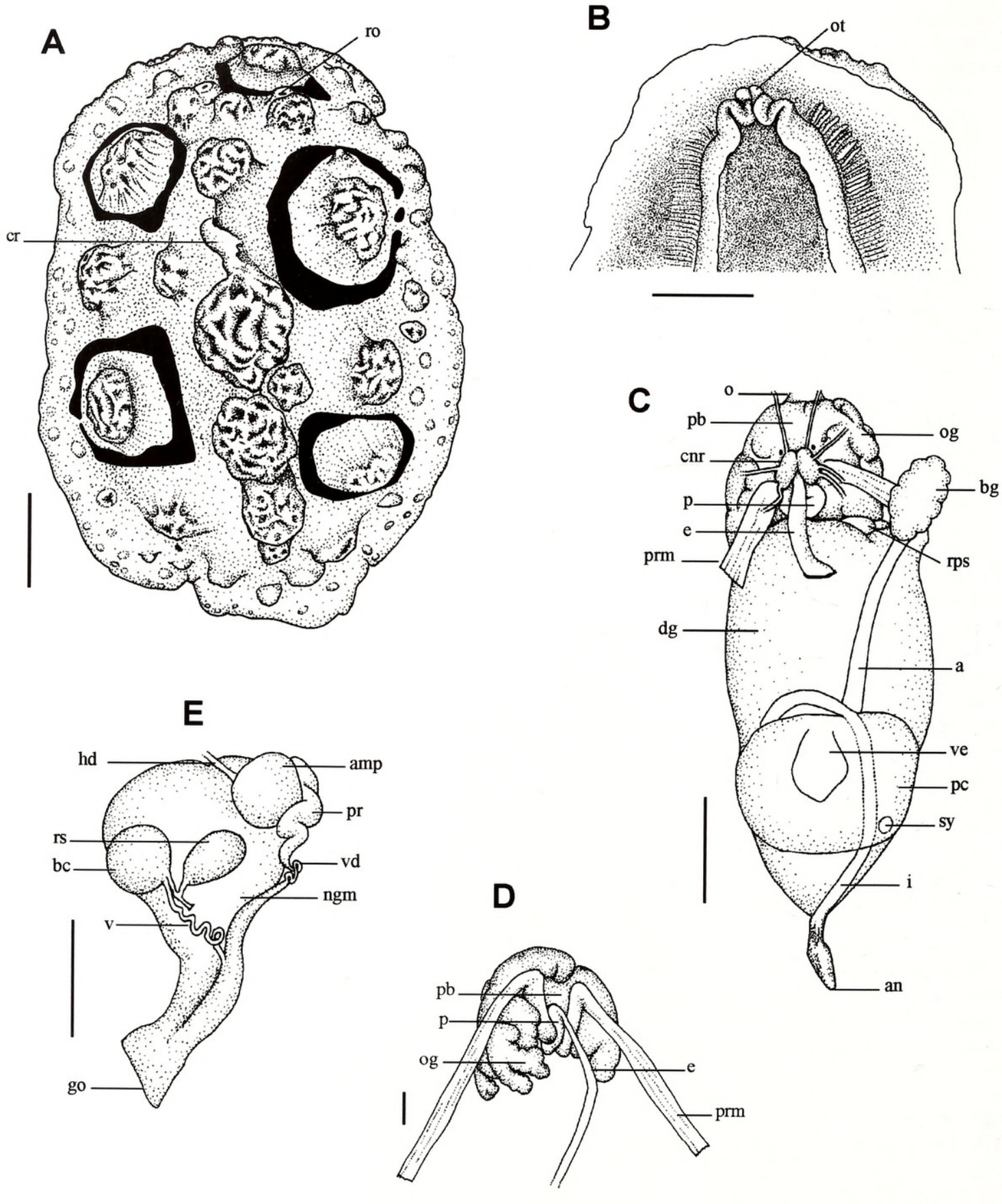
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Figure 5. *Phyllidia ocellata*. A, Drawing of the dorsal view of a preserved specimen 31.8 mm long, collected in Laing Island. B, Drawing of the ventral view of the anterior end (the same specimen illustrated in Fig. 5A). C, Diagram of the internal anatomy of a specimen 28.2 mm long collected in Laing Island. D, Diagram of the dorsal view of the pharyngeal bulb of a specimen 41.2 mm long collected in PNG. E, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; cr, crest; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C), 2 mm (D, E).

stripe on either side of the foot where it meets the gills. The broad oral tentacles are fused and have rounded tips.

The oral tube can be broad or long and narrow. The pharynx is very long, thick, and passes through the central nerve ring (Fig. 7F). The esophagus has a long segment where the buccal ganglia insert, and posteriorly a shorter segment which has circular musculature. In this area insert the esophageal retractor muscles. In three specimens, the posterior end of the esophagus was broad and rounded (Fig. 7C). In the rest of the specimens, the esophagus is "U" shaped and there is a long region with circular musculature and another segment lacking musculature that inserts into the digestive gland (Fig. 7D). The intestine arises from the digestive gland to the left of the pericardium. It turns to the right and extends to the long anal papilla. The reproductive system (Fig. 7E) has a large ampulla partially covered by the prostate. The prostate is long, very coiled, and bound by connective tissue. The bursa copulatrix is large, spherical, and communicates with the smaller oval receptaculum seminis.

Remarks

Phyllidiopsis shireenae has characters in common with two other species belonging to the genus *Phyllidiopsis*: *Phyllidiopsis krempfi* Pruvot-Fol, 1957 and *Phyllidiopsis pipeki* Brunckhorst, 1993. These species have pink dorsal surfaces with black lines and large tubercles, but *P. shireenae* differs from the other two species by having a median crest that is triangular in cross-section, angular tubercles, pink rhinophores, and ventral black bands. *Phyllidiopsis krempfi* and *P. pipeki* have compound or multi-compound tubercles and their rhinophores are black and pink.

We have observed that the external morphological features of *Phyllidiopsis shireenae* are constant but the internal morphology can vary. Most of the specimens studied have rounded esophagi (Fig. 7C) but in three individuals this structure is longer (Fig. 7D).

Phyllidiopsis cardinalis Bergh, 1875
(Fig. 8)

Phyllidiopsis cardinalis Bergh 1875: 670-673, pl. 16, figs. 11-15, Eliot 1904: 284, Dawydoff 1952: 111, Pruvot-Fol 1957: 118-120, fig. 35, Burn 1975: 516, Gosliner and Behrens 1988: 308-309, 312-313, figs. 1B, 3, Brunckhorst 1993: 63-64, figs. 10A-C, 14, 15, pl. 7E-F, Valdés and Gosliner 1999: 319, figs. 1D, 2F, 3F, 4E, 5D, 6D, 10B, 14C, 15C, 20D, 22B, Yonow *et al.* 2002: 869-870, fig. 19B.

Phyllidia tuberculata Risbec 1928: 59-60, fig. 3, pl. 1, fig. 2.

Material examined

RBINS: PNG (20.3 mm × 10.1 mm).

Description

The median region of the dorsal surface has three longitudinal rows of isolated, compound tubercles, most of which are large and globose (Fig. 8A). The midline row is formed by five tubercles: it begins posterior to the rhinophores and extends to the anal opening. On either side of the midline there is another row, each one formed by three tubercles. On the mantle margin there are compound rounded tubercles, and around the edge there are black spots. In the preserved state, the entire body is reddish, as are the rhinophores. The rim of the rhinophoral pocket has a black stain. On the sides of the foot, near the edge, there are small isolated black spots (Fig. 8B). The oral tentacles are fused together.

Phyllidiopsis cardinalis has a long, thick pharyngeal bulb that is displaced towards the left side of the body (Fig. 8C). The pharynx passes through the central nerve ring. At the anterior end of the pharynx are a pair of ganglia that are connected with the central nerve ring. The esophagus is reinforced by circular muscles in the region of the esophageal retractor muscles, and inserts into the digestive gland mass. The intestine exits the gland, turns to the right, and extends to the anal papilla. The reproductive system (Fig. 8D) has a large, oval ampulla that is located next to a folded prostate. The penial sheath is wide and long. The receptaculum seminis is small and rounded; it is connected to the larger bursa copulatrix.

Remarks

Phyllidiopsis cardinalis has a complex, multicolored dorsum, completely different from any other known phyllidiid

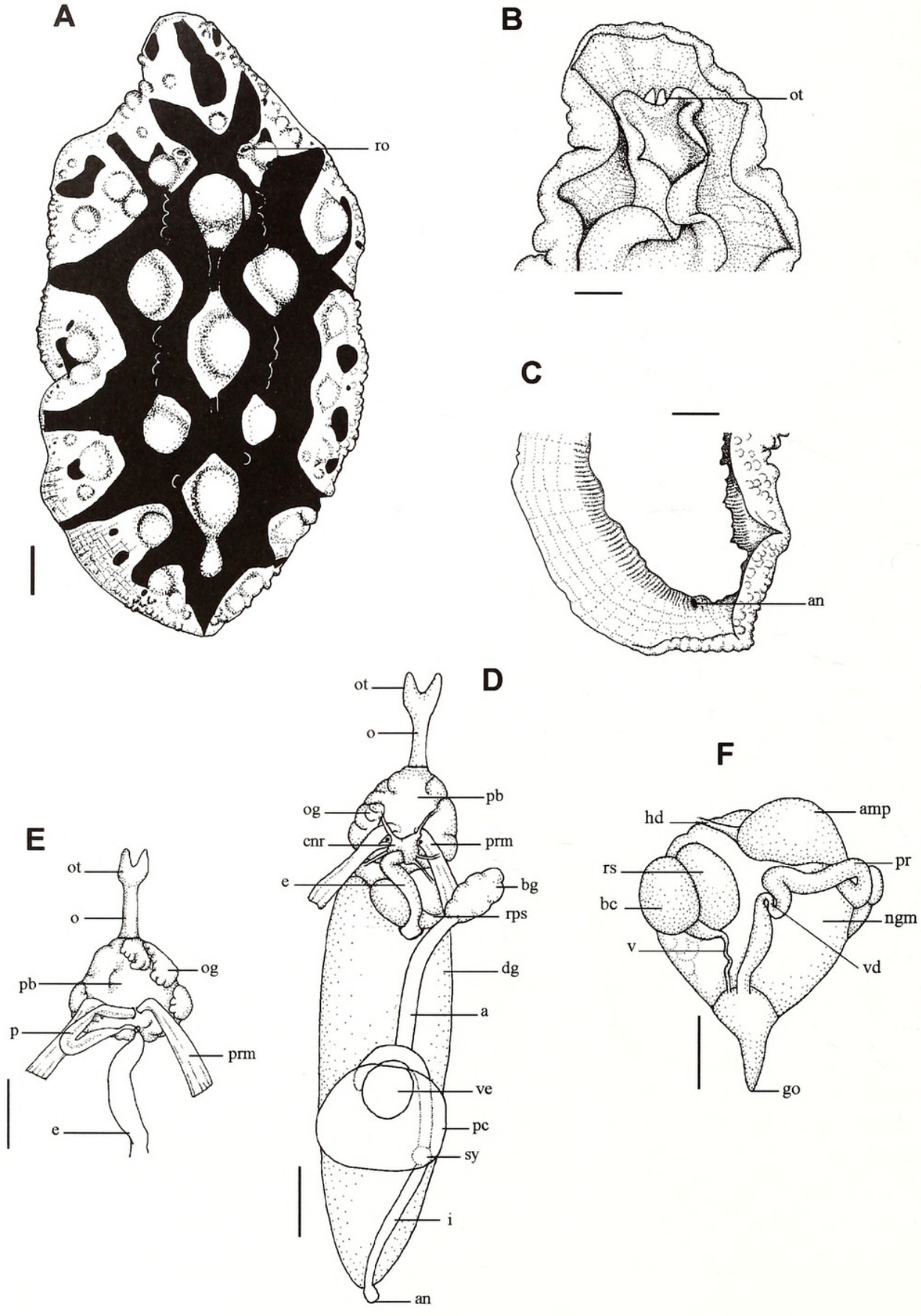
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Figure 6. *Phyllidia picta*. A, Drawing of the dorsal view of a preserved specimen 25.6 mm long, collected in Laing Island, depth 0.5 m. B, Drawing of the ventral view of the anterior end of a preserved specimen 24.8 mm long, collected in Laing Island, depth 0.5 m, showing the oral tentacles. C, Drawing of the ventral view of the posterior end (the same specimen illustrated in the figure 6B), showing the anal opening. D, Diagram of the internal anatomy. E, Diagram of the dorsal view of the pharyngeal bulb (the same specimen illustrated in Fig. 6A). F, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 6A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B, C, D, E), 1 mm (F).

species (Brunckhorst 1993). The specimen studied appears faded, but its identification is possible because of other characters, such as the presence of large, globose, compound tubercles on the median dorsum, which in this specimen are arranged in three longitudinal rows, instead of the two rows mentioned by Brunckhorst (1993). There are also small rounded tubercles and dark spots around the margin. On the sides of the foot there are dark spots and the oral tentacles are fused. *Phyllidiopsis krempfi* Pruvot-Fol, 1957 also has large compound tubercles on the central dorsum, but its general coloration is pale pink and it has black lines.

Phyllidiopsis krempfi Pruvot-Fol, 1957
(Figs. 1E-F, 9)

Phyllidiopsis krempfi Pruvot-Fol 1957: 120-121, figs. 41-49, pl. 1, figs. 7-8, Brunckhorst 1993: 66, fig. 29E, pl. 8A, Fahrner and Beck 2000: 200.

Material examined

Expedition 1996: Boisa Island, 56.4 m depth (36.6 mm × 16.9 mm).

Description

The ground color of the dorsum is pink, with compound tubercles with pink bases and white apices (Fig. 1E). In the median region of the dorsum there are three longitudinal rows of tubercles that can be isolated or joined at their bases. The tubercles on the edge of the mantle are single, rounded, and very small. On either side of the median region there is a longitudinal black line (in this specimen the right line is longer than the left), and both meet anterior to the rhinophores and extend posteriorly in a line to the margin. At the margin there are two transverse black rays on either side. Short black rays and blotches occur between some tubercles and on the mantle margins. The rhinophores are pink at their bases and their anterior surfaces. They have black apices and black posterior surface. Ventrally, the hyponotum is pink. The gills are dark in color and the pedal sole is pinkish-grey (Fig. 1F). The broad oral tentacles are fused and pink.

The oral tube has a thin wall. On either side of the pharyngeal bulb arise narrow pharyngeal retractor muscles (Fig. 9A). The pharynx extends from the posterior part of the bulb and passes through the central nerve ring. The buccal ganglia are situated on the surface of the pharynx. The muscular esophagus is longer than the pharynx. The esophagus has a longer segment that extends near the pericardium and turns forming a "U." In this area insert the esophageal retractor muscles. The esophagus has another segment that is shorter and stouter, and inserts into the digestive gland. The intestine arises to the left of the pericardium, turns to the right, and extends to the narrow anal papilla. The reproductive system (Fig. 9B) has a large and oval ampulla that is connected with the folded prostate. The prostate is bound together by connective tissue. The bursa copulatrix is very large and spherical and the receptaculum seminis is rounded and smaller.

Remarks

It is very difficult to distinguish between *Phyllidiopsis krempfi* and *Phyllidiopsis pipeki* Brunckhorst, 1993, because both species possess very similar characteristics. According to Brunckhorst (1993), individuals in both species have pink dorsal surfaces (according to Fahrner and Beck [2000] the dorsal surface of *P. pipeki* is cream in color), with tubercles that have wide pink bases and the dorsum has two primary longitudinal black lines. Both species have shorter lines extending to the mantle edges and sometimes have black marks and spots, the rhinophores are pink and black, and the coloration is pink and pale grey ventrally, with pink fused oral tentacles. The main difference between these species is that *P. pipeki* can have single or compound tubercles with white rounded apices, but *P. krempfi* has more numerous, compound tubercles with pale pink apices (Brunckhorst 1993). Internally, *P. pipeki* has a longer and wider muscular segment of the esophagus. The region that inserts into the digestive gland is wider and has less musculature than that of *P. krempfi*. The reproductive systems of both species are similar.

Phyllidiopsis pipeki Brunckhorst, 1993
(Fig. 10)

Phyllidiopsis pipeki Brunckhorst 1993: 73, fig. 30B, pl. 9A, Debelius 1996: 269, Marshall and Willan 1999: 128, fig. 231, Fahrner and Beck 2000: 200, pl. 1, fig. 3.
Phyllidia nobilis Lim and Chou 1970: 134, pl. 16, fig. A.

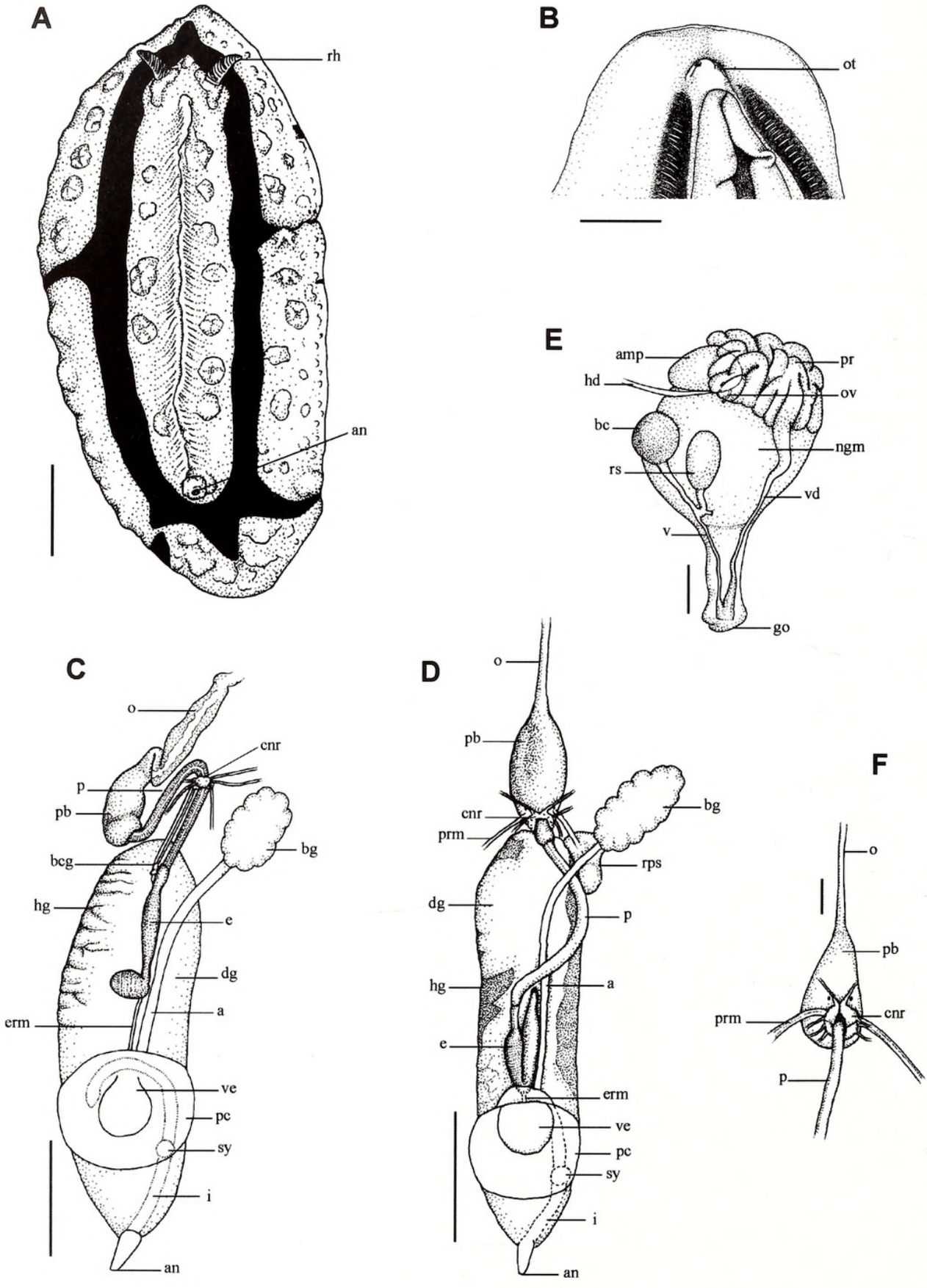
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Figure 7. *Phyllidiopsis shireenae.* A, Drawing of the dorsal view of a preserved specimen 65.3 mm long, collected in Laing Island. B, Drawing of the ventral view of the anterior end (the same specimen illustrated in Fig. 7A), in ventral view. C, Diagram of the internal anatomy (the same specimen illustrated in Fig. 7A), showing how the esophagus ends with a broad rounded region. D, Diagram of the anatomy of a specimen 64.4 mm long, collected in PNG, with the esophagus forming a "U." E, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 7A). F, Diagram of the dorsal view of the pharyngeal bulb of a specimen 59.2 mm long, collected in PNG. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; bcg, buccal ganglia; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; hg, hermaphrodite gland; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; ov, oviduct; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 10 mm (A, B, C, D), 2 mm (E, F).

Material examined

RBINS: PNG (32.3 mm × 12.5 mm).

Description

The dorsum is pale in color. This specimen has two longitudinal black lines that merge anterior to the rhinophores (Fig. 10A) and black lines extending to the mantle edge (one anterior, two on one side and three on the other). The tubercles in the median area are large and compound but are not tall, nor do they form ridges. The apices of the tubercles are paler than the bases. On the mantle margin the tubercles are complex and near the edge they are single, very small, and rounded. The rhinophores are black at the apices and on their posterior surfaces. Their anterior faces are pale in color. In preserved specimens the ventral surface is pale except for the gills, which are dark grey. The oral tentacles are fused and their tips are rounded (Fig. 10B).

The large pharyngeal bulb is folded. The pharynx extends toward the right side, turns to the anterior region of the digestive gland, and passes through the central nerve ring (Fig. 10D). Two sack-shaped structures arise from the bulb and extend to the nerve ring. The anterior portion of the esophagus is short. The mid-esophagus is very long, thick, and reinforced with circular muscles. This segment extends near the pericardium and turns, forming a "U." In this area insert the esophageal retractor muscles. The next region of the esophagus is shorter, stouter, and inserts into the digestive gland (Fig. 10C). The intestine arises to the left of the pericardium, turns to the right and extends to the anal papilla. The reproductive system (Fig. 10E) has a large and compact prostate that is bound together by connective tissue. The bursa copulatrix is spherical and very large. It is connected to a smaller receptaculum seminis and to the vaginal duct.

Remarks

Phyllidiopsis pipeki is very similar to *Phyllidiopsis krempfi*. The differences between these species are mentioned in the discussion of *P. krempfi* above.

Phyllidiella pustulosa (Cuvier, 1804)
(Figs. 1G-I, 11)

Phyllidia pustulosa Cuvier 1804: 268, pl. A, fig. 8.
Phyllidia nobilis Risbec 1928: 58.
Phyllidia melanocera Yonow 1986: 1406-1407, figs. 2, 10F-I.
Phyllidiella pustulosa Brunckhorst 1993: 49-54, figs. 3B, 9B-D, 11-13, 27, 28A-C, pl. 5E-F, Gosliner *et al.* 1996: 169, species number 597, Marshall and Willan 1999: 125-126, fig. 227, Fahrner and Beck 2000: 201, pl. 2, fig. 3, Valdés 2001: 339-341, figs. 1B, 5B-C, 6.

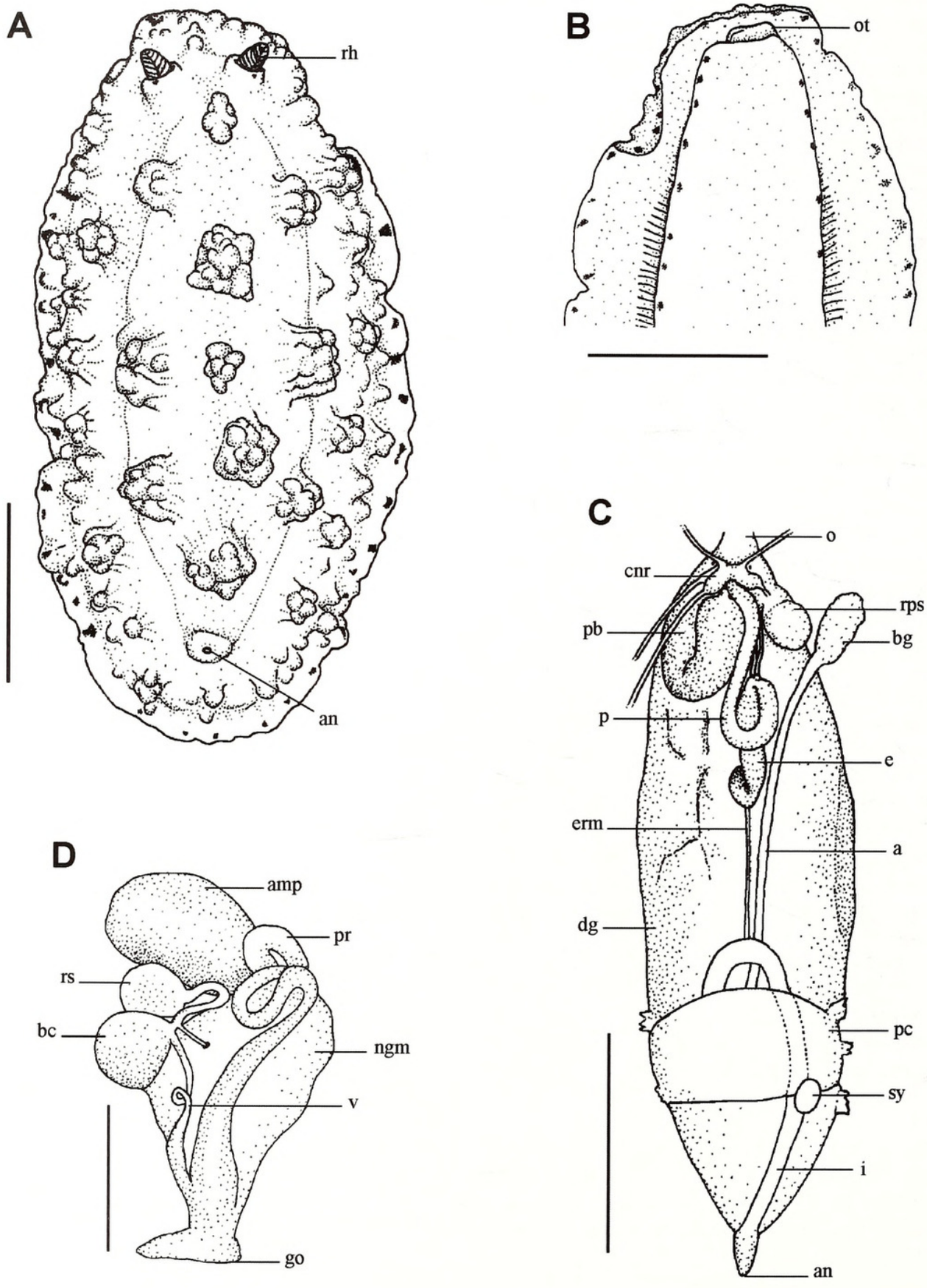
Material examined

RBINS: PNG (32.3 mm × 15.0 mm, 32.8 mm × 11.5 mm, 47.8 mm × 20.7 mm, 36.5 mm × 12.9 mm, 40.0 mm × 15.1 mm, 37.9 mm × 15.2 mm, 13.4 mm × 6.2 mm, 28.5 mm × 9.1 mm, 28.0 mm × 11.2 mm, 30.3 mm × 10.9 mm, 16.8 mm × 5.4 mm, 12.3 mm × 5.0 mm, 28.5 mm × 10.4 mm, 20.3 mm × 7.7 mm, 20.2 mm × 8.1 mm, 24.6 mm × 7.5 mm, 18.9 mm × 9.0 mm); Laing Island (23.0 mm × 10.0 mm, 24.6 mm × 12.8 mm, 19.4 mm × 13.0 mm, 26.3 mm × 10.1 mm, 23.2 mm × 14.5 mm, 13.8 mm × 6.8 mm, 24.0 mm × 14.8 mm); Durangit Reef, 40 m depth (27.4 mm × 13.2 mm), Ilot Tabou (41.0 mm × 18.8 mm).

Expedition 1996: Laing Island, 0.5 m depth (44.1 mm × 19.0 mm, 30.5 mm × 10.8 mm, 27.1 mm × 10.9 mm, 43.1 mm × 19.4 mm, 25.8 mm × 14.2 mm, 26.6 mm × 11.2 mm, 18.2 mm × 11.6 mm, 24.3 mm × 14.4 mm, 23.9 mm × 14.07 mm), Laing Island, 14.1 m depth (25.4 mm × 7.6 mm, 21.9 mm × 7.6 mm, 14.6 mm × 6.4 mm); Laing Island, 15 m depth (31.2 mm × 10.5 mm, 15.6 mm × 5.8 mm, 15.1 mm × 5.0 mm); Laing Island, 15.7 m depth (14.0 mm × 5.5 mm, 8.7 mm × 3.4 mm); Laing Island, 16.5 m depth (30.5 mm × 12.6 mm, 25.6 mm × 8.6 mm); Laing Island, 16.7 m depth (28.8 mm × 11.2 mm, 25.8 mm × 10.8 mm); Laing Island, 18.5 m depth (23.6 mm × 7.9 mm, 12.4 mm × 4.5 mm); Laing Island, 45 m depth (25.6 mm × 12.9 mm, 10.8 mm × 3.5 mm); Hansa Bay, 20-28.9 m depth (22.8 mm × 12.9 mm, 14.1 mm × 5.1 mm).

Description

The dorsal surface is black and the tubercles are pink with paler pink apices, although some specimens were green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when they were collected. The tubercles may be single or compound and are fused to form small groups. The largest specimens (Fig. 1G) have three regions (median, lateral, and marginal) separated by black notum. These regions have tubercles organized in clusters: The median region has three groups—anterior, median, and posterior—and the anus is located posterior to the third group. In the lateral region the clusters are separated by black notum and the marginal region is occupied by small single tubercles. The edges of the mantle of most specimens are narrow and pink, although in some specimens there are areas occupied by black notum. Each of the specimens of medium size (Fig. 1H) has a median region and a lateral region with clusters of tubercles separated by a black notum. In the median region there are three groups (anterior, median, and posterior) between the rhinophores and the anus, although in some animals the groups are not very well defined. The mantle edge is pink. Eleven specimens are juveniles (Fig. 1I), ranging in length from 8.7-16.8 mm; they have three groups of tubercles in the median region that are separated by black lines. Some of the groups have black irregular marks on their centers. The lateral tubercles are separated from the mantle edge by a black line. The mantle edge is pink. The rhinophores are black, however, in the preserved state some rhinophores are paler at their bases. The hyponotum and the pedal sole are grey (Fig. 11A). Dorsally the foot is dark grey. In many specimens the oral tentacles have dark tips.

The oral tube is wide (Fig. 11B) and the thick pharyngeal bulb is slightly folded. On the posterior part of bulb are numerous oral glands that are relatively large. Each gland is joined to the bulb by a short stalk. The pharynx is large and broad at its origin at the pharyngeal bulb, but it narrows as it passes across the central nerve ring. The esophagus is very thin and inserts into the anterior region of the digestive gland. The reproductive system (Fig. 11C) has a large oval ampulla that is brownish-yellow. The prostate is long and folded. The bursa copulatrix is large and oval. It is connected to the small, dark receptaculum seminis by a duct.

Remarks

Underwater the tubercles appear grey or green. This fact has been commented by other authors, such as Brunckhorst (1993). Some preserved specimens have black rhinophores with paler bases. Four specimens are very faded and appear to have lost the black pigmentation of the notum, but they could be identified by the arrangement of tubercles, the black rhinophores, and their anatomical details.

One example of ontogenetic variability which has given room to misidentification is that of *Phyllidiella pustulosa* (see Brunckhorst 1993). There are external differences between the adults and the young specimens because juveniles have tubercles grouped in amalgamated clusters and large animals have separated tubercles (Fig. 1G-I, Brunckhorst 1993, Fahrner and Beck 2000). However, all specimens have black dorsal surfaces with pink single or compound tubercles that may be fused to form small groups. On the median region of the dorsum there are three groups of tubercles (anterior, median, and posterior), and the mantle edge is pink. The rhinophores are black. Internally there are numerous large oral glands; each gland is joined to the pharyngeal bulb by a short stalk.

Phyllidiella zeylanica (Kelaart, 1858)
(Fig. 12)

Phyllidia zeylanica Kelaart 1858: 120.
Phyllidiella zeylanica Brunckhorst 1993: 57-58, pl. 6E-G, Yonow 1996: 502-504, figs. 10A-G, Debelius 1996: 267, Fahrner and Beck 2000: 201, pl. 1, fig. 6, Yonow *et al.* 2002: 868, fig. 19A.

Material examined

RBINS: PNG (15.2 mm × 6.8 mm); Nossi-Bé (27.0 mm × 9.4 mm, 15.2 mm × 6.8 mm).

Expedition 1996: Hansa Bay, 20 m depth (17.9 mm × 8.1 mm).

Description

When the specimens were collected their coloration was pale pink and black. The tubercles are small and rounded and can be isolated or joined. On the median region of the dorsum there is a central black ring (Fig. 12A) that surrounds a group of low tubercles that are fused. Outside this ring there are rows of coalesced tubercles and another ring that encloses the rhinophores and anus. There is a black line near the pink edge of the mantle. The rhinophores are black. The preserved specimen has triangular oral tentacles (Fig. 12B).

The oral tube is broad (Fig. 12C). The pharyngeal bulb

Figure 8. *Phyllidiopsis cardinalis*. A, Drawing of the dorsal view of a preserved specimen. B, Drawing of the ventral view of a preserved specimen. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct. Scale bars = 5 mm (A, B, C), 1 mm (D).

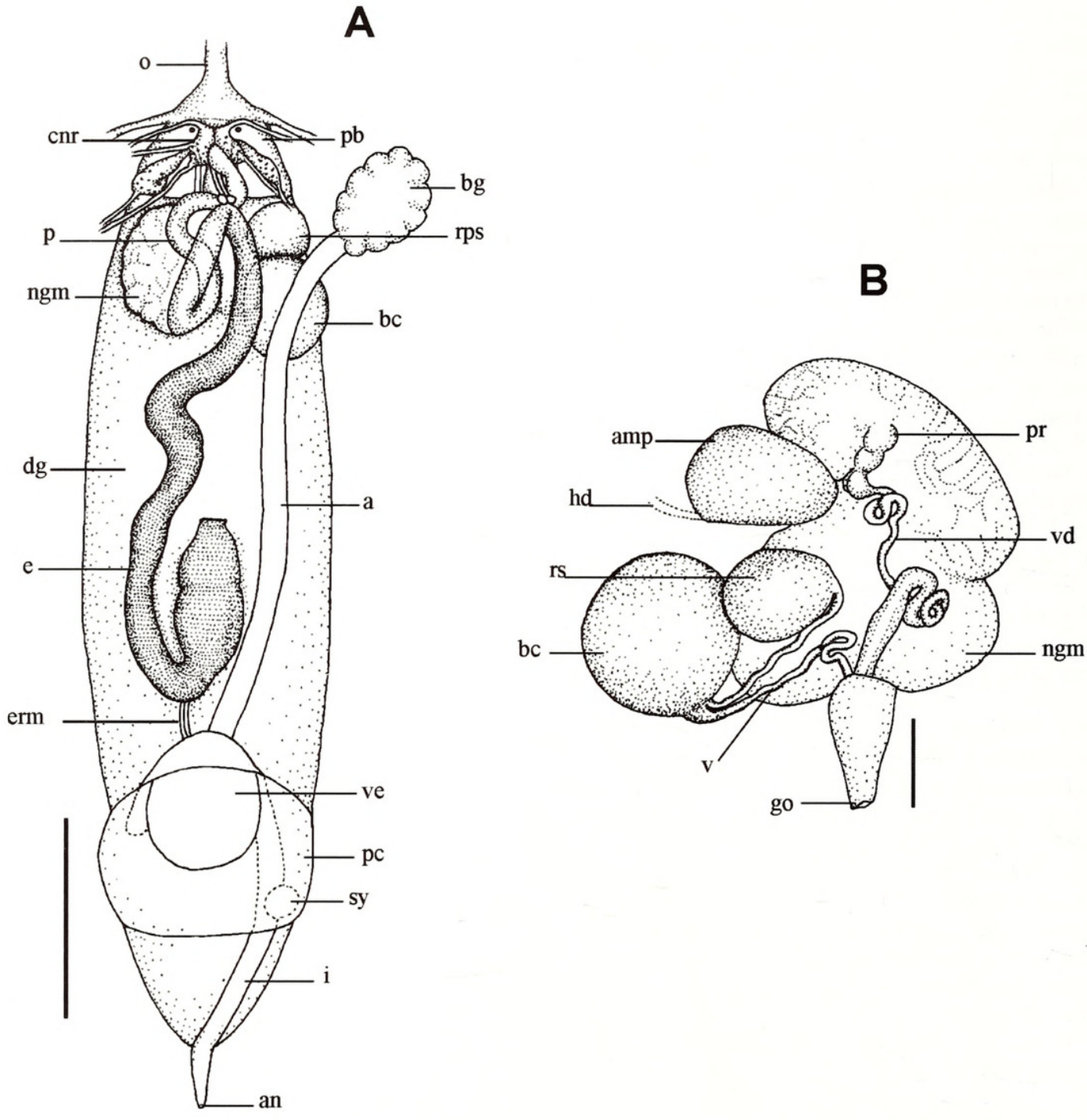
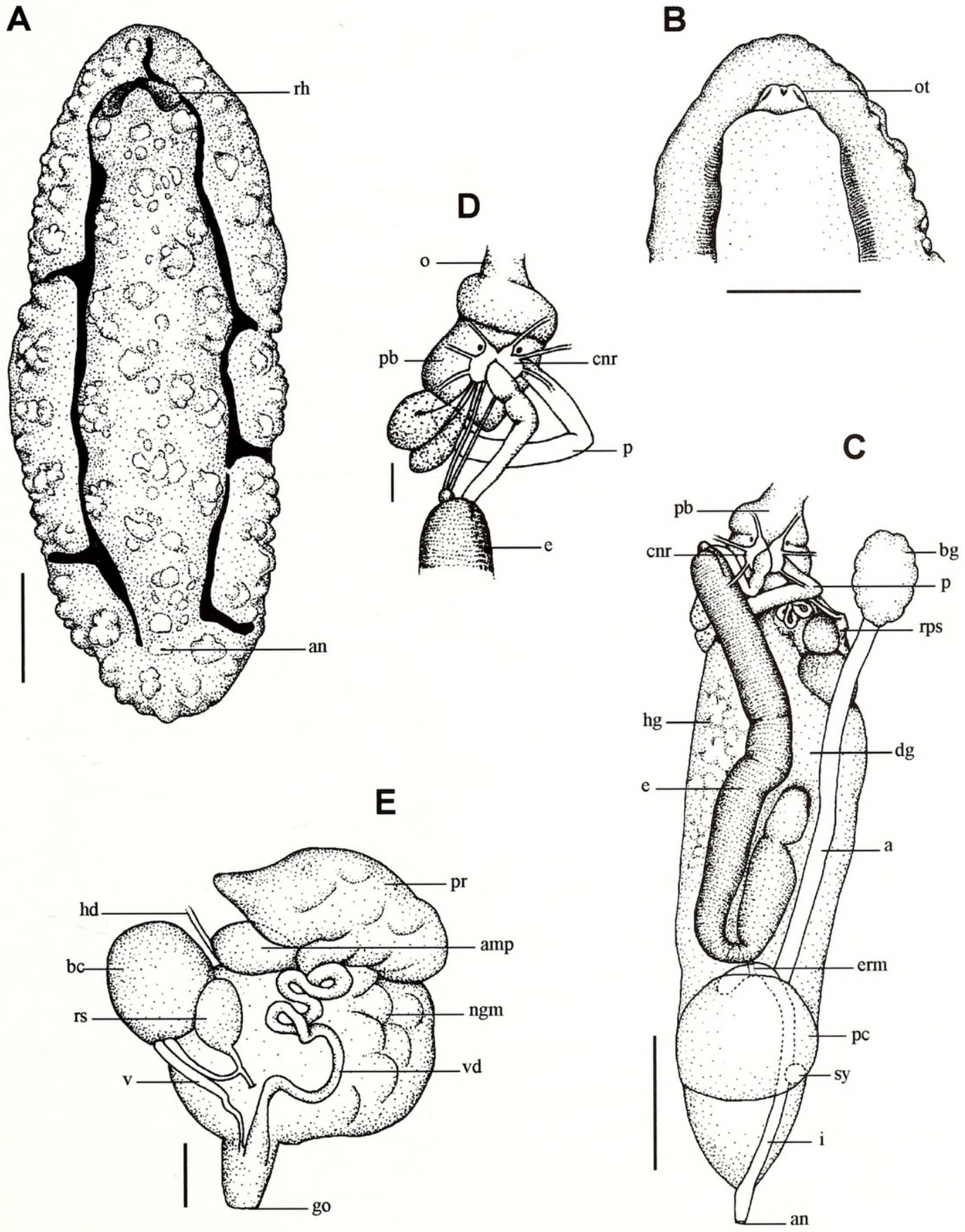


Figure 9. *Phyllidiopsis krempfi*. A, Diagram of the internal anatomy. B, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A), 1 mm (B).

Figure 10. *Phyllidiopsis pipeki*. A, Drawing of the dorsal view of a preserved specimen. B, Ventral view of the anterior end of a preserved specimen. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the pharyngeal bulb. E, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; hg, hermaphrodite gland; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens. Scale bars = 5 mm (A, B, C), 1 mm (D, E).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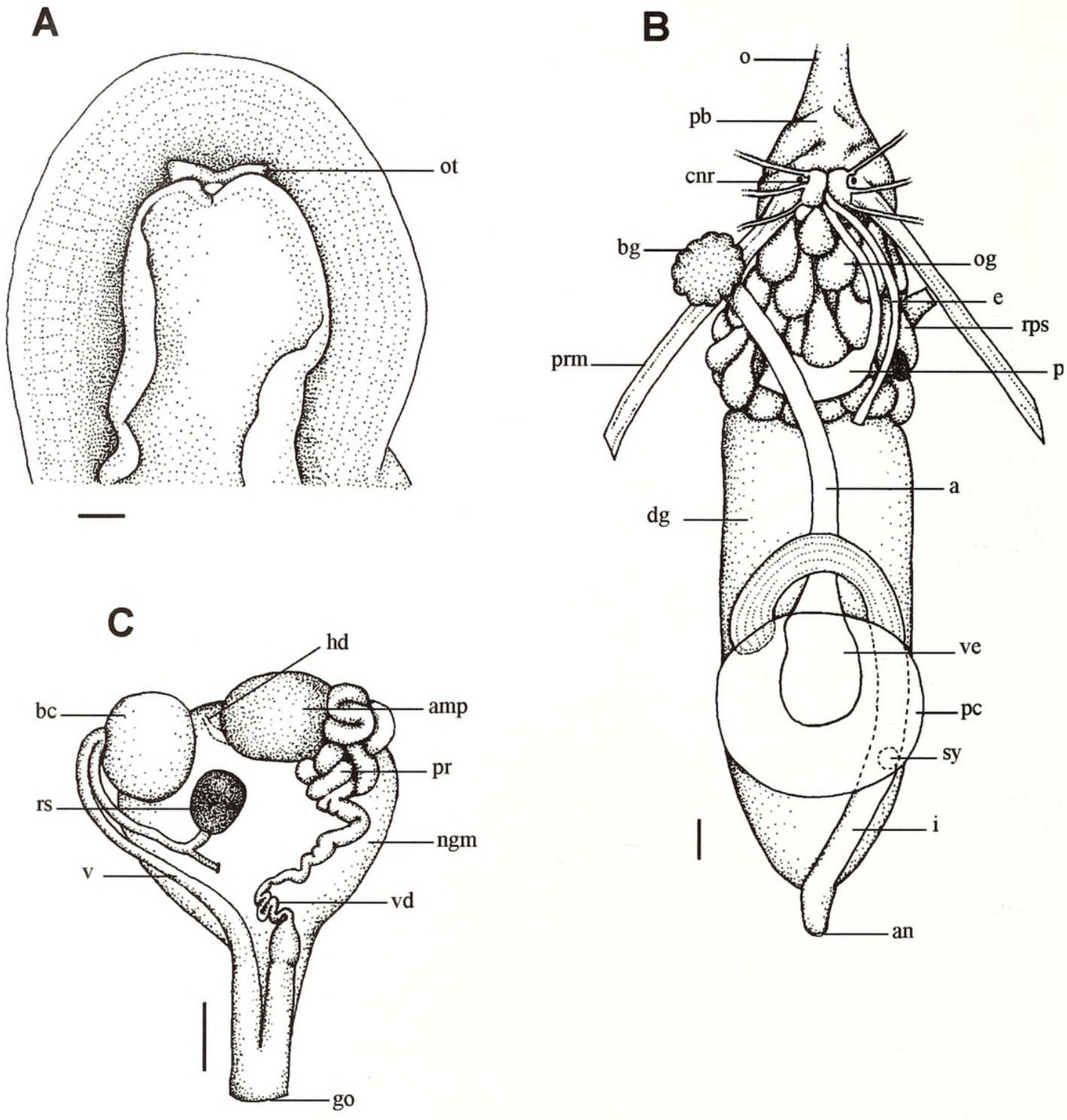

Figure 11. *Phyllidiella pustulosa*. A, Drawing of the ventral view of the anterior end of a preserved specimen 25.4 mm long, collected in Laing Island, depth 14.1 mm. B, Diagram of the internal anatomy of a specimen 30.5 mm long, collected in Laing Island, depth 16.5 m. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 11B). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 1 mm.

has numerous oral glands that form a large white mass. The pharyngeal retractor muscles are long and insert dorsally into the pharyngeal bulb. The pharynx is broad where it arises from the pharyngeal bulb. It narrows abruptly posteriorly and passes through the central nerve ring. The esophagus is thin and inserts into the digestive gland. The reproductive system (Fig. 12D) has a large, spherical ampulla that is connected to a thick and folded prostate. The bursa copulatrix is large and rounded, and is connected to the small and dark receptaculum seminis by a duct.

Remarks

The most important characteristic of *Phyllidiella zeylanica* is the presence of a pale pink notum with black lines forming concentric rings. This species has black rhinophores and triangular oral tentacles with dark apices. *Phyllidiella zeylanica* shows ontogenetic variation; the juvenile stage has a median mass of fused tubercles. During growth, this mass separates into numerous longitudinal ridges (Brunckhorst 1993). *Phyllidiella pustulosa* also has a pink and black dorsum and black rhinophores, but its tubercles are arranged in groups and the black lines do not form rings. *Phyllidiella rudmani* Brunckhorst, 1993 has a pale pink mantle with only two longitudinal black lines and tubercles organized in longitudinal rows that never form ridges. It has black and pink rhinophores but *P. zeylanica* has completely black rhinophores.

Phyllidiella hageni Fahrner and Beck, 2000
(Figs. 1J, 13)

Phyllidiella hageni Fahrner and Beck 2000: 194-196, figs. 5-7, pl. 1, fig. 8, pl. 2, fig. 1.

Material examined

RBINS: PNG (33.3 mm × 15.6 mm); Laing Island (24.9 mm × 13.4 mm).

Expedition 1996: Laing Island, 16.5 m depth (38.1 mm × 20.1 mm).

Description

Dorsally, the notum is pink in the live animals (Fig. 1J) and white in preserved specimens. Small, white, rounded tubercles, which can be isolated or grouped, are evenly distributed on the dorsum. There are two longitudinal black lines that fuse anterior to the rhinophores and extend separately to the posterior mantle edge (Fig. 13A). In the region of the anus they bend towards the center. In two specimen, the lines turn to the lateral margin again and extend to the mantle edge. In the third specimen one line ends near the anus (Fig. 13B). The animals have several irregular longitudinal short black lines between the two longitudinal lines and on the mantle margins. The mantle edge is black and narrow. The rhinophores have black apices and pink bases. The hyponotum and foot are pale in color. One animal has many rectangular and some triangular gill leaflets. The gills of another specimen are triangular in the posterior region of the body and rectangular in the rest. The third animal has triangular gill leaflets only. In the preserved state the oral tentacles are pale, broad (Fig. 13C), and have a triangular shape.

The oral tube is narrow and long (Fig. 13D). The posterior surface of the pharyngeal bulb is covered by oral glands. The pharyngeal retractor muscles insert dorsally onto the pharyngeal bulb. The short pharynx bends, narrows, and passes through the central nerve ring. The esophagus is longer and inserts into the digestive gland. The reproductive system (Fig. 13E) has an oval ampulla. The prostate is broad and straight. The bursa copulatrix (which is spherical and smaller than the ampulla) is connected by a duct to the receptaculum seminis, which is dark in color in one specimen. From this duct emerges another narrower duct that inserts into the large female gland. The long vagina is connected to the bursa copulatrix.

Remarks

The most distinctive external features of *Phyllidiella hageni* are the pale notum, the numerous single or fused tubercles that are evenly distributed, two longitudinal black lines that converge anterior to the rhinophores, short irregular black lines on the median region and on the margin, a black mantle edge, and black and white rhinophores (Fahrner and Beck 2000).

There are few variations between the dorsal pattern of the studied specimens. The dorsal longitudinal lines bend towards the center, and can turn to the margin again or end near the anus. On the mantle margin there are lines describing a zigzag. Two specimens studied have short variable lines on the median part forming incomplete hexagons, but the other specimens have a few short lines and spots scattered on the dorsum. Ventrally, the gill leaflets can be rectangular, triangular, or individuals can have both forms.

In agreement with Fahrner and Beck (2000) we saw that the receptaculum seminis and the bursa copulatrix have long stalks. Although they observed that the receptaculum seminis of *Phyllidiella hageni* is white and the bursa copulatrix is black, the specimens we examined have black receptaculum seminis and pale bursa copulatrix.

This species is similar in external morphology to *Phyllidiella rudmani*, whose dorsum also has a pink background color with two black longitudinal lines and bicolored rhinophores, but *P. rudmani* has tubercles which can be compound, and they are arranged in rows, the black lines of the dorsum are not connected, and the mantle edge is not black. There are no irregular short lines between the two longitu-

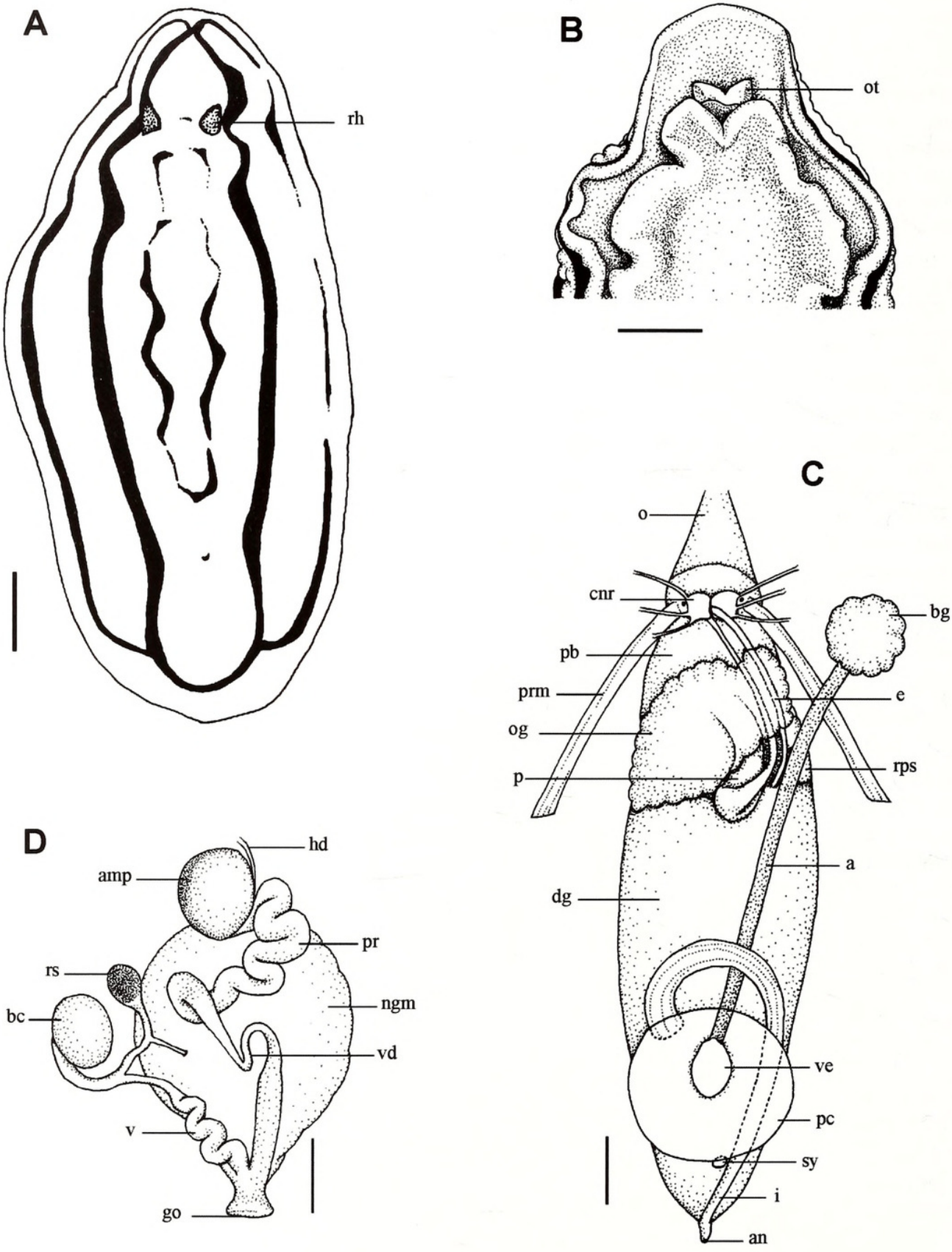
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Figure 12. *Phyllidiella zeylanica.* A, Drawing of the dorsal view of a preserved specimen 17.9 mm long, collected in Hansa Bay (depth 20 m), showing the black rings. B, Drawing of the ventral view of the anterior end of a preserved specimen 27 mm long, collected in Nossi-Bé. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 12B). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B, C), 1 mm (D).

dinal lines and the mantle edge is pink (black in *Phyllidiella hageni*). *Phyllidiella lizae* Brunckhorst, 1993 has a pale pink background with black narrow and irregular lines on the median part of its dorsum, but the rhinophores are black and the mantle edge is pinkish-white.

Phyllidiella backeljaui n. sp.
(Figs. 1K-L, 14)

Material examined

Holotype: Expedition 1996, Laing Island, 9 m depth (20.0 mm × 11.6 mm preserved length), Museo Nacional de Ciencias Naturales of Madrid (MNCN 15.05/46656).

Paratypes: Expedition 1996, Laing Island, 14.1 m depth (24.3 mm × 10.9 mm preserved length), Museo Nacional de Ciencias Naturales of Madrid (MNCN 15.05/46657). RBINS, Laing Island, (23.4 mm × 11.7 mm preserved length), Royal Belgian Institute of Natural Sciences.

Additional material

Expedition 1996: Laing Island, 0.5 m depth (23.0 mm × 12.1 mm). Laing Island, 14.1 m depth (22.2 mm × 11.2 mm).

Etymology

The name *Phyllidiella backeljaui* is in honor of Thierry Backeljau, great malacologist and friend whose endeavors made possible the project in Papua New Guinea in 1996.

Type locality

Laing Island (4°10′30″S, 144°52′47″E), Madang Province, Papua New Guinea. The specimens collected in 1996 were found on the western side of Laing Island.

Description

External anatomy: Body shape elongated and ovate, with a broad mantle (Fig. 1K). Pink dorsal surface, although one specimen was green when collected. Complex tubercles on the median part of dorsum and simple on the mantle margins; their bases have the same color as the notum and the apices are paler. Two longitudinal black bands converge anterior to the rhinophores and extend separately to the posterior region of the dorsum. In the region of the anus they bend towards the center and turn to the margin again. These two lines are connected by a transverse black line that delimits an anterior and a posterior area. These areas have one or two irregular blotches in their centers, black lines crossing over each other forming an "X," or a reticule separating groups of tubercles (Figs. 14A, B). Transverse black lines on margins that delimit semicircles occupied by tubercles and one spot or line. Black and narrow mantle edge. Black rhinophores, although in preserved state the anterior surfaces of their bases are paler. Foot notched anteriorly and grey ventrally (Fig. 1L). The gills are dark and some specimens have rectangular gill leaflets. The oral tentacles have rounded tips (Fig. 14C).

Internal anatomy: Oral tube short and thick (Fig. 14D). Pharyngeal bulb covered by oral glands that form a large mass. The pharyngeal retractor muscles insert dorsally onto the bulb. The thick pharynx is variable in this species. It can arise dorsally or posteriorly to the bulb before it turns, narrows, and passes through the central nerve ring (Fig. 14E). The thin esophagus inserts into the digestive gland.

Reproductive system: The reproductive system (Fig. 14F) has an oval ampulla. Prostate tubular and folded. The spherical bursa copulatrix is smaller than the ampulla. From the bursa copulatrix emerges a thick duct connecting to the ovate receptaculum seminis.

Remarks

According to Brunckhorst (1993), the genus *Phyllidiella* Bergh, 1869 is characterized by having black and pink dorsums, with single, compound, or coalesced tubercles. Tubercles never have yellow apices (Fahrner and Beck 2000). The rhinophores are predominantly black or bicolored (black and pink). Rhinotubercles absent. The foot sole is white to grey, without distinctive markings, and the oral tentacles are separate. Internally, *Phyllidiella* has a huge mass of oral glands that overlies the pharyngeal bulb. The long pharynx is broad and thick and it leaves the pharyngeal bulb posteriorly. The esophagus is narrow and leads into the digestive gland; there is no distinct stomach region. All these characteristics are present in our specimens justifying inclusion in the genus *Phyllidiella.*

Phyllidiella has characteristic differences in its morphology and anatomy when compared to other genera (Brunck-

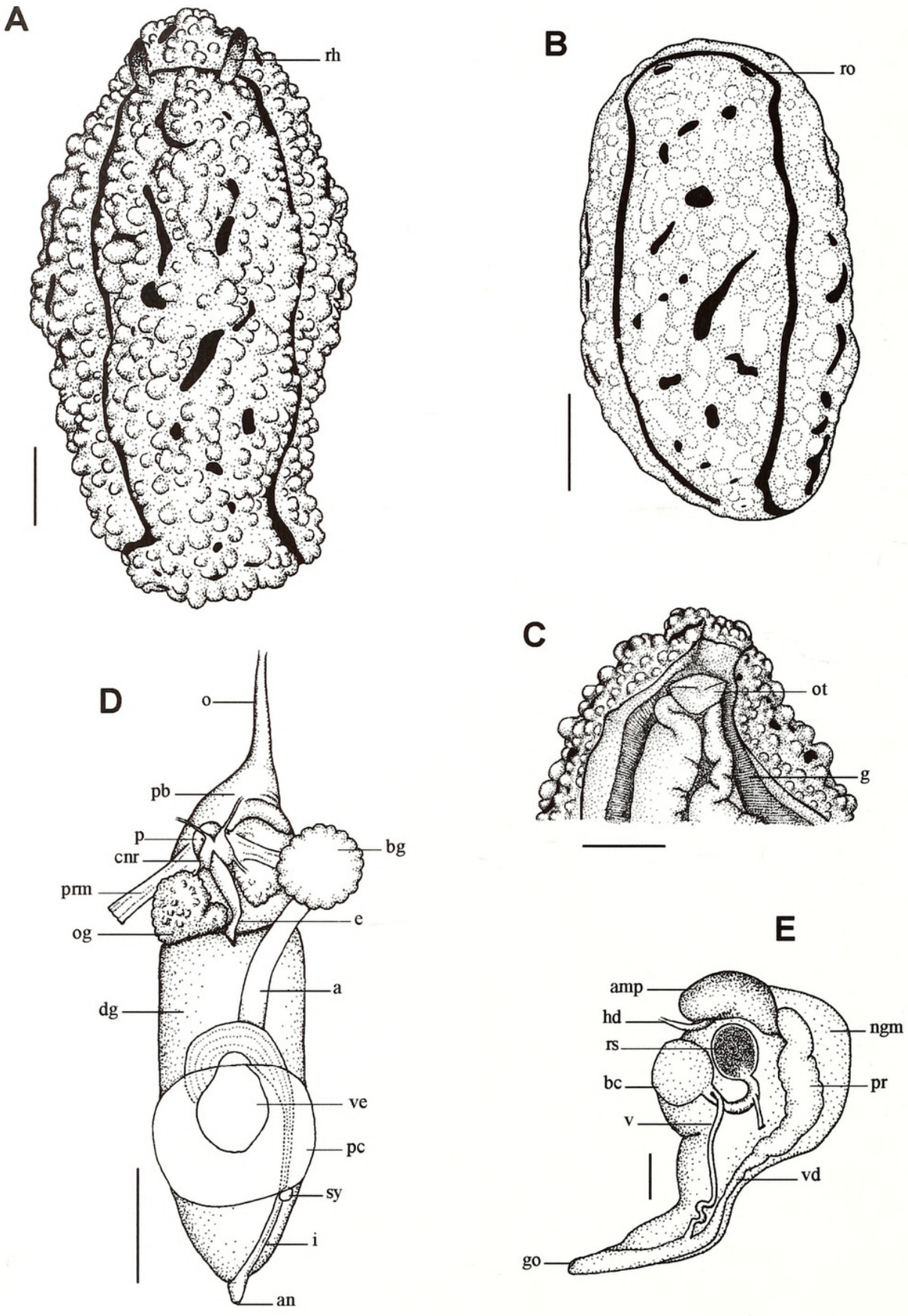
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Figure 13, *Phyllidiella hageni*. A, Drawing of the dorsal view of a preserved specimen 38.1 mm long. B, Drawing of the dorsal view of a preserved specimen 24.9 mm long. C, Drawing of the ventral view of the anterior end (the same preserved specimen illustrated in Fig. 13A). D, Diagram of the internal anatomy (the same preserved specimen illustrated in Fig. 13A). E, Diagram of the dorsal view of the reproductive system (the same preserved specimen illustrated in Fig. 13A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; g, gills; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; ro, rhinophoral opening; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C, D), 1 mm (E).

horst 1993). The genus *Phyllidia* Cuvier, 1797 possesses large notal tubercles, mostly with yellow apices (Fahrner and Beck 2000), cream to golden-yellow rhinophores, and rhinotubercles. Internally, there are firm oral glands which often protrude posteriorly and ventrally from the pharyngeal bulb. The tubular pharynx is short and narrow. *Phyllidiopsis* Bergh, 1875 may have bicolored rhinophores, and the oral tentacles are broad and fused together. The exterior of the pharyngeal bulb appears to be quite smooth and devoid of oral glands (Gosliner and Behrens 1988, Brunckhorst 1993), but it is in fact completely enveloped by minute oral glands (Brunckhorst 1990b, 1993). The pharynx is very long and the esophagus broadens into a swollen muscular segment. The esophagus turns in a "U" before inserting into the digestive gland mass. At the base of the "U" a retractor muscle arises (Bergh 1875, 1889, Gosliner and Behrens 1988, Brunckhorst 1990a, 1990b, 1993). Members of the genus *Ceratophyllidia* Eliot, 1903 possess stalked papillae on the dorsum and partially fused oral tentacles (Brunckhorst 1993, Fahrner and Beck 2000). Individuals have two large oral glands, a long pharynx, and a long esophagus with a glandular segment (Brunckhorst 1993). The genus *Reticulidia* Brunckhorst, 1990 has smooth reticulate ridges on the dorsum (tubercles are absent), and glandular discs within the pharyngeal bulb.

The distinctive features of *Phyllidiella backeljaui* n. sp. include a pink dorsal surface with two longitudinal black bands connected by a transverse black line. The margins possess transverse black lines and the mantle edge is black. There are complex and simple tubercles on the dorsum. The rhinophores are black. The gills are dark and some specimens have rectangular gill leaflets. The oral glands form a large mass. The pharynx is swollen where it leaves the pharyngeal bulb, either dorsally or posteriorly, and the esophagus is very thin.

The main morphological differences between this and other species of *Phyllidiella* are summarized in Table 1. This species shares superficial similarities with other species of the genus such as *Phyllidiella pustulosa*, however, *P. pustulosa* has a black background, the tubercles are arranged in clusters, and the mantle edge is pink, instead of a pink background, single, compound, or coalesced tubercles, and black mantle edge. Members of *P. backeljaui* n. sp. have smaller oral glands than those of *P. pustulosa* and they are more densely grouped. The ground color of *Phyllidiella granulata* Brunckhorst, 1993 is grey, the tubercles are single and conical, and it has three encircling irregular black bands on the dorsum (Brunckhorst 1993). But Fahrner and Beck (2000) also state that *P. granulata* can have a pinkish-grey granular dorsum with three black bands and tall, compound, white tubercles. *Phyllidiella backeljaui* n. sp. externally resembles the specimens studied by Fahrner and Beck (2000), but differs from them by having a narrow black edge and numerous transverse black lines on the margin delimiting areas occupied by irregular lines or spots. *Phyllidiella lizae* also has lines crossing over each other forming an "X" in the median area, but the mantle is pale whitish-pink instead of pink, the tubercles are simple and isolated (*P. backeljaui* has complex and simple tubercles), the edge is pale pinkish-white instead of black, and the rhinophores have three colors (black, pink and white), instead of the rhinophores being entirely black. *Phyllidiella hageni* has narrow lines between the two longitudinal lines on the median part of the dorsum, and spots or black lines on the margins, but its rhinophores are black and pink instead of being entirely black. *Phyllidiella hageni* has a very short pharynx and narrower esophagus than does *P. backeljaui*. The esophagus is clearly longer than the pharynx (*P. backeljaui* has an esophagus and pharynx of similar lengths). *Phyllidiella meandrina* Pruvot-Fol, 1957 is different from *P. backeljaui* because it has tubercles forming ridges, blacks rings, and does not possess transverse black lines on the dorsum. *Phyllidiella annulata* (Gray, 1853) also has black rhinophores and black edge, but is distinct from *P. backeljaui* because the tubercles form rings and the background color of dorsum is black. *Phyllidiella cooraburrana* Brunckhorst, 1993 has black rhinophores and black edges, but the tubercles are multicompound (*P. backeljaui* possesses simple tubercles on the mantle margin) and extremely large (Brunckhorst 1993). *Phyllidiella nigra* (Hasselt, 1824) has a black dorsum with tall, rounded, dark pink to red tubercles with black bases, instead of a pink background and pink tubercles with paler apices. *Phyllidiella rosans* (Bergh, 1873) is distinct from *P. backeljaui* because it has numerous longitudinal pink ridges, a pink mantle edge, and black rhinophores with pink stalks instead of complex and simple tubercles on the dorsum, black margins, and entirely black

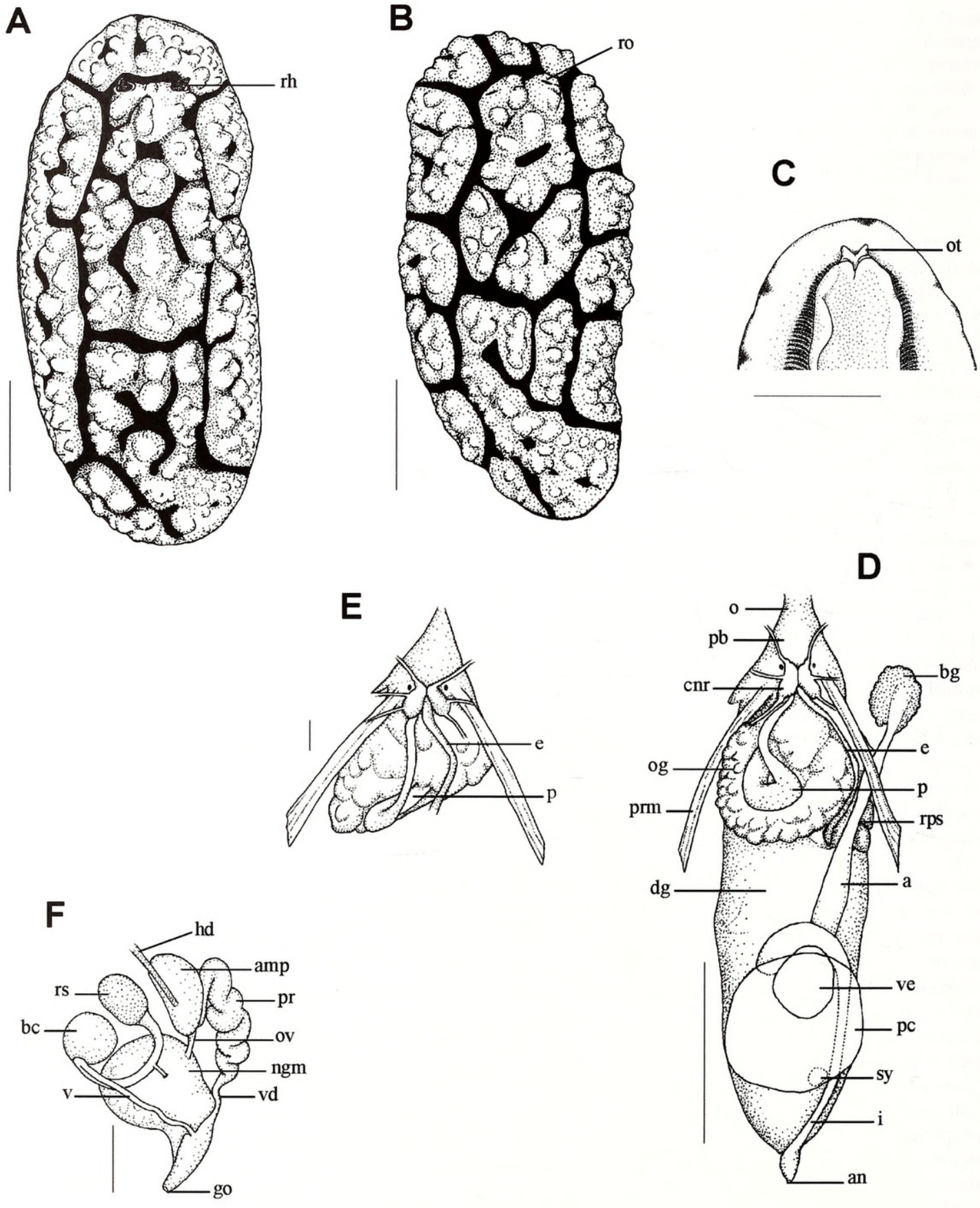
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Figure 14, *Phyllidiella backeljaui* n. sp. A, Drawing of the dorsal view of a preserved specimen 24.3 mm long, collected in Laing Island, depth 14.1 m. B, Drawing of the dorsal view of preserved specimen 22.2 mm long, collected in Laing Island, depth 14.1 m. C, Drawing of the ventral view of the anterior end (the same preserved specimen illustrated in Fig. 14A). D, Diagram of the internal anatomy (the same preserved specimen illustrated in Fig. 14A). E, Diagram of the dorsal view of the pharyngeal bulb of a specimen 23.0 mm long, collected in Laing Island, depth 0.5 m. F, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ov, oviduct; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C, D), 1 mm (E, F).

rhinophores. *Phyllidiella rudmani* has a pink dorsum and two black lines, but the lines are never connected (Fahrner and Beck 2000), the rhinophores are bicolored (black and pink), and the margin is pink. *Phyllidiella zeylanica* has a pink background, black rhinophores, and black lines on the dorsum, but it is different from *P. backeljaui* because the lines form rings, the tubercles are isolated or coalesced in rows, and the mantle edge is pink. The individuals of *P. zeylanica* we examined have a spherical ampulla, the receptaculum seminis is smaller than the bursa copulatrix, and the

Table 1. Comparison between *Phyllidiella backeljaui* n. sp. and other species of *Phyllidiella*.

	Dorsal pattern	Background color	Tubercles	Rhinophores	Mantle edge
Phyllidiella annulata	4 to 14 pink rings	Black	Small and low	Black	Black
Phyllidiella backeljaui	2 longitudinal black bands and short black lines forming "X" or a reticule and spots	Pink	Pink compound on the median	Black	Black
Phyllidiella cooraburrana	Black lines, no tubercles, forming clusters, ridges or groups	Black	Pale pink multi-compound and very large	Black	Black
Phyllidiella granulata	3 encircling irregular black bands	Grey	White compound	Black	Grey
Phyllidiella hageni	2 black longitudinal lines and short black irregular lines and spots	Pink	Coalesced, never isolated, and at the mantle margin they are single and rounded	Pink basally and black apically	Black
Phyllidiella lizae	Short lines forming an "X" medially	Pale whitish-pink	Single and isolated rarely coalesced	Black apically, pink centrally, and white basally	Pale pink to white
Phyllidiella meandrina	Black lines forming rings	Pink	Joined pink tubercles forming ridges	Black	Pink
Phyllidiella nigra	Tubercles evenly distributed (not clustered)	Black	Dark pink to red, always separated and round, very high	Black	No continuous pale edge to the mantle
Phyllidiella pustulosa	Tubercles medially arranged in clusters	Black	Pink, grouped in amalgamated clusters	Black	Pale pink
Phyllidiella rosans	Numerous longitudinal pink ridges	Black	Forming ridges	Black with pink stalks	Pink
Phyllidiella rudmani	2 black longitudinal stripes which are never connected	Pinkish white	Pinkish white, compound, arranged in longitudinal rows	Black apically with pink pale stalks	Same pale pink color as the dorsum
Phyllidiella zeylanica	Black lines forming central rings	Pale pink	Small and rounded, isolated or coalesced in rows	Entirely black	Pale pink

swollen vaginal duct is folded. *Phyllidiella backeljaui* has an ovate ampulla, the receptaculum seminis and the bursa copulatrix are of similar sizes, and the thin vaginal duct is not folded.

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