Review of the family Phyllidiidae in the Atlantic Ocean (Nudibranchia, Doridoidea)

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Abstract: The species of Phyllidiidae from the Atlantic Ocean (Mediterranean Sea excluded) are redescribed in this paper. In light of the study of type material and newly collected specimens, we concluded that *Phyllidiopsis gynenopla* Bouchet, 1977, is a junior synonym of *P. berghi* Vayssière, 1902. Also, anatomical studies supported the placement of *P. papilligera* Bergh, 1890, in the genus *Ceratophyllidia* Eliot, 1903, and *Phyllidiopsis molaensis* Meyer, 1977, in the genus *Phyllidiella* Bergh, 1869. Two new bathyal species, *Reticulidia gofasi* n. sp. and *Phyllidiopsis boucheti* n. sp., are described. The former is the first record of this genus in the Atlantic Ocean.

Key words: Nudibranchia, Phyllidiidae, taxonomy, new species, Atlantic Ocean

A review of the literature shows that few nominal species of the family Phyllidiidae, all lacking bright colors, have been described in the Atlantic Ocean (Mediterranean Sea excluded). This contrasts with the richly and brightly colored phyllidiid fauna of the Indo-Pacific recently reviewed by Brunckhorst (1993).

The first report of this family in Atlantic waters was the description of *Phyllidiopsis papilligera* by Bergh (1890), based on a single specimen collected at 182 m depth from the Gulf of Mexico, during the *Blake* Expedition. *P. papilligera* was later redescribed by Marcus and Marcus (1962, 1967) and Thompson (1980). Several years later, Vayssière (1902b) described *Phyllidiopsis berghi*, a species of uniform white color collected at 1480 m depth from the Bay of Biscay, by the *Talisman* Expedition. In 1977, two new species of *Phyllidiopsis* were reported from the Atlantic Ocean. One of them, *P. gynenopla* Bouchet, 1977, was described on the basis of a single specimen collected at 525-600 m, near the Azores by the *Biaçores* Expedition. In the same paper, Bouchet (1977) redescribed *P. berghi.* The other species, *P. molaensis*, was described by Meyer (1977) from shallow waters of the Caribbean coast of Panama.

In the present paper, we review all the species reported in the Atlantic Ocean, and describe two new species. The Mediterranean species, *Phyllidia flava* Aradas, 1847, and *Fryeria bayi* Bouchet, 1983, have not been included because they were recently reviewed by Brunckhorst (1993).

MATERIAL AND METHODS

Most of the specimens studied were collected during several scientific expeditions (*Z-Thalassa, Biaçores, Seamount I,* and *Seamount II*) organized by the Muséum National d'Histoire Naturelle, Paris, France (MNHN) with the vessels of the French agency for oceanographic research (IFREMER, Institut Français de Recherche pour l'Exploitation de la Mer). Also, type material was examined from the collections of MNHN and the National Museum of Natural History, Washington D. C. (USNM).

Features of living specimens were recorded from original notes and drawings of collectors. Several specimens have been dissected and particularly interesting soft parts have been critical point dried for scanning electron micrography (SEM).

SPECIES DESCRIPTIONS

Genus *Phyllidiella* Bergh, 1869
Type species *Phyllidia pustulosa* Cuvier, 1804, by subsequent designation (Brunckhorst, 1993).

Phyllidiella molaensis (Meyer, 1977)

(Figs. 1A, 2)

Phyllidiopsis molaensis Meyer, 1977: 305-306, fig. 4.

Material Examined
USNM 760616, HOLOTYPE (by original designation),

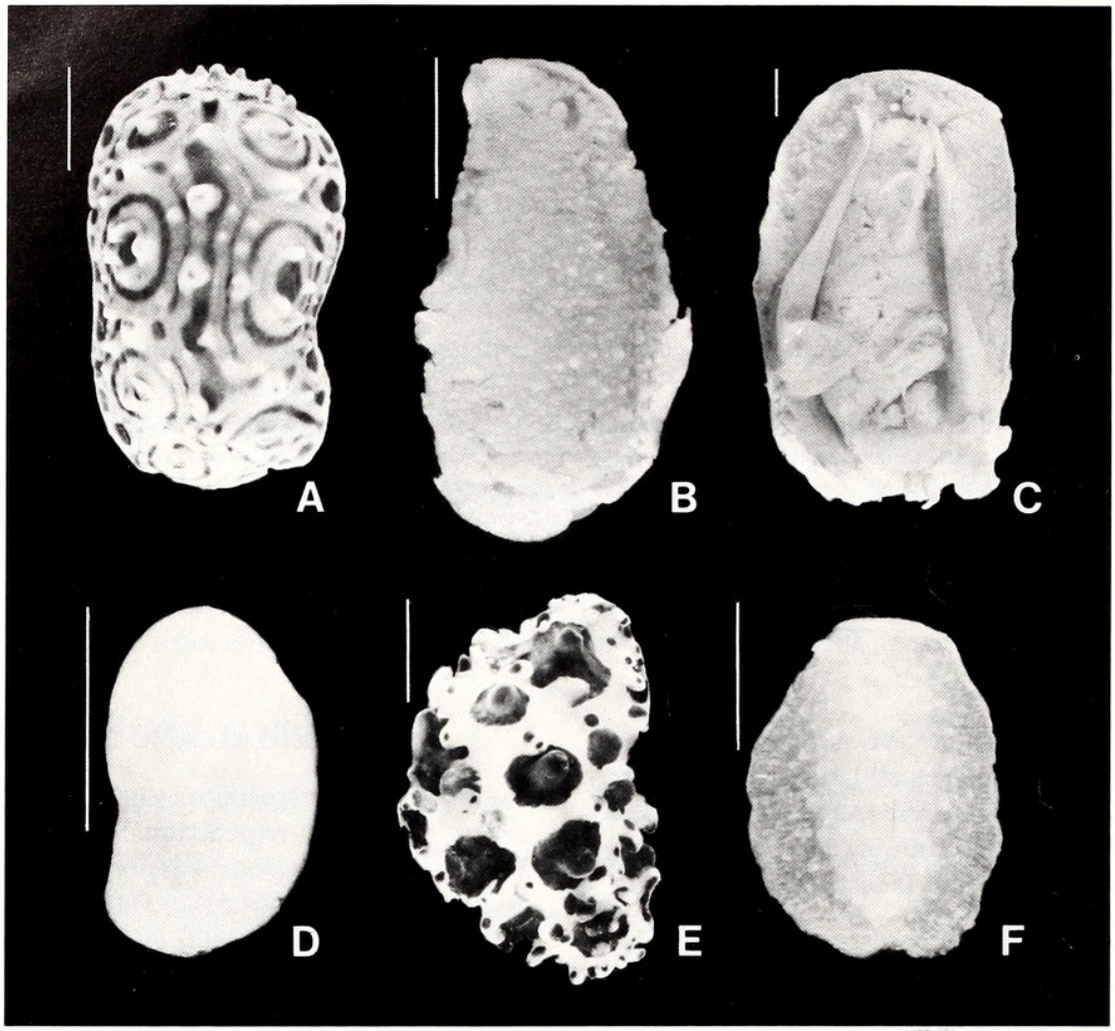

Fig. 1. Dorsal views of preserved type specimens (scale bars = 5 mm). **A.** *Phyllidiella molaensis,* holotype (USNM 760616). **B.** *Phyllidiopsis berghi,* holotype (MNHN). **C.** *P. berghi,* holotype of *Phyllidiopsis gynenopla* (MNHN). **D.** *Phyllidiopsis boucheti,* holotype (MNHN). **E.** *Ceratophyllidia papilligera,* neotype (USNM 856418). **F.** *Reticulidia gofasi,* holotype (MNHN).

Galeta Point, Panama, 15 m depth, 25 May 1971, 20 mm preserved length, coll. Meyer.

USNM 760617, PARATYPE, Portobelo, Panama, 9 m depth, 10 September 1971, 1 spm, 19 mm preserved length, coll. Meyer.

External Morphology

The color in life of this species was described by Meyer (1977) as '...color black and white consisting of three sets of concentric circles along the sides, two more anteriorly and one set posteriorly, each set composed of two concentric white rings each of which has a grey ring running through its middle and separated from one another by a black ring; white lines randomly traversing areas not covered by the rings; rhinophores black with white tips...' In preserved specimens only brown shadows remain of the original black color (Fig. 1A). The dorsum bears simple, conical tubercles, decreasing in size toward the notal margin. The mantle margin is as wide as the notum. The anus opens dorsally. Rhinotubercles (see Brunckhorst, 1993) are absent.

Ventrally, the oral tentacles are separated. The anterior and posterior ends of the foot are notched (Figs. 2B-C). The branchial leaves are very thin and elongated, with alternating large and small ones (Fig. 2D).

Anatomy

The moderately long oral tube dilates into a very folded pharyngeal bulb (Fig. 2A). Two anterior retractor muscles insert at the point where the pharyngeal bulb and oral tube connect; another pair of muscles inserts in both sides of the pharyngeal bulb. The esophagus is long, with no muscular or glandular portions.

Geographical Range

This species has only been recorded from the Caribbean coast of Panama.

Discussion

Anatomical features of this species resemble those

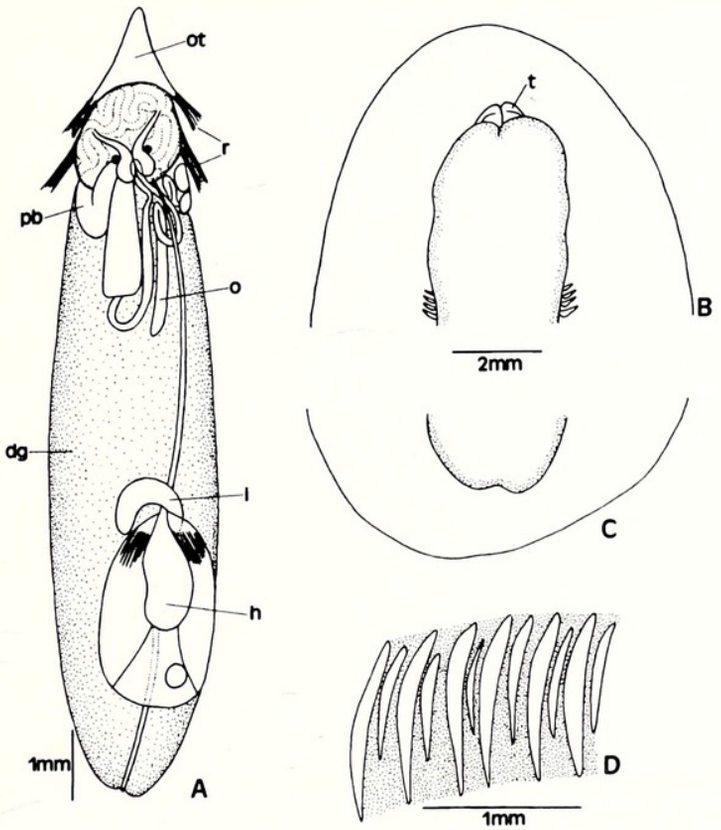

Fig. 2. *Phyllidiella molaensis*, paratype (USNM 760617). **A.** Dorsal view of the anatomy. **B.** Ventral view of the anterior edge of the foot showing the oral tentacles. **C.** Ventral view of the posterior edge of the foot. **D.** Detail of the branchial leaves. dg, digestive gland; h, heart; i, intestine; o, esophagus; ot, oral tube; pb, pharyngeal bulb; r, retractor muscles; t, oral tentacles.

described by Brunckhorst (1993) for the genus *Phyllidiella*, such as the structure of the digestive system with a moderately long oral tube which connects with a folded pharyngeal bulb. Externally, this species has separate oral tentacles, simple tubercles on the dorsum, black rhinophores, and no rhinotubercles, a combination of characters only present in the species of this genus (Brunckhorst, 1993).

Genus *Phyllidiopsis* Bergh, 1875
Type species *Phyllidiopsis cardinalis* Bergh, 1875, by monotypy.

Phyllidiopsis berghi Vayssière, 1902
(Figs. 1B-C, 3, 4A-B, 4D)

Phyllidiopsis berghi Vayssière, 1902a: 1-2 (*nomen nudum*); 1902b: 237-242, pls. 9-10; Bouchet, 1977: 48-49, figs. 16-17.
Phyllidiopsis gynenopla Bouchet, 1977: 50-53, figs. 18-19, syn. nov.

Material Examined
MNHN, HOLOTYPE of *P. berghi* (by monotypy), *Talisman* sta. 141 (45°59.00' N, 04°09.46' W), 1480 m depth, 30 August 1883, 16 mm preserved length, dissected.
MNHN, HOLOTYPE of *P. gynenopla* (by original designation), *Jean Charcot-Biaçores* sta. 159 (37°26.00' N, 25°51.00' W), 525-600 m depth, 31 October 1971, 48 mm preserved length, dissected.
MNHN, *Jean Charcot-Biaçores* sta. 59 (38°22.05' N, 28°48.05' W), 560-580 m depth, 14 October 1971, 2 spms, 7 and 9 mm preserved length.
MNHN, *Z-Thalassa* sta. 435 (48°39.07' N, 09°53.02' W), 1050 m depth, 26 October 1973, 1 spm, 14 mm preserved length, dissected.
MNHN, *Seamount II* sta. DW128, Gran Canaria (28°08.30'

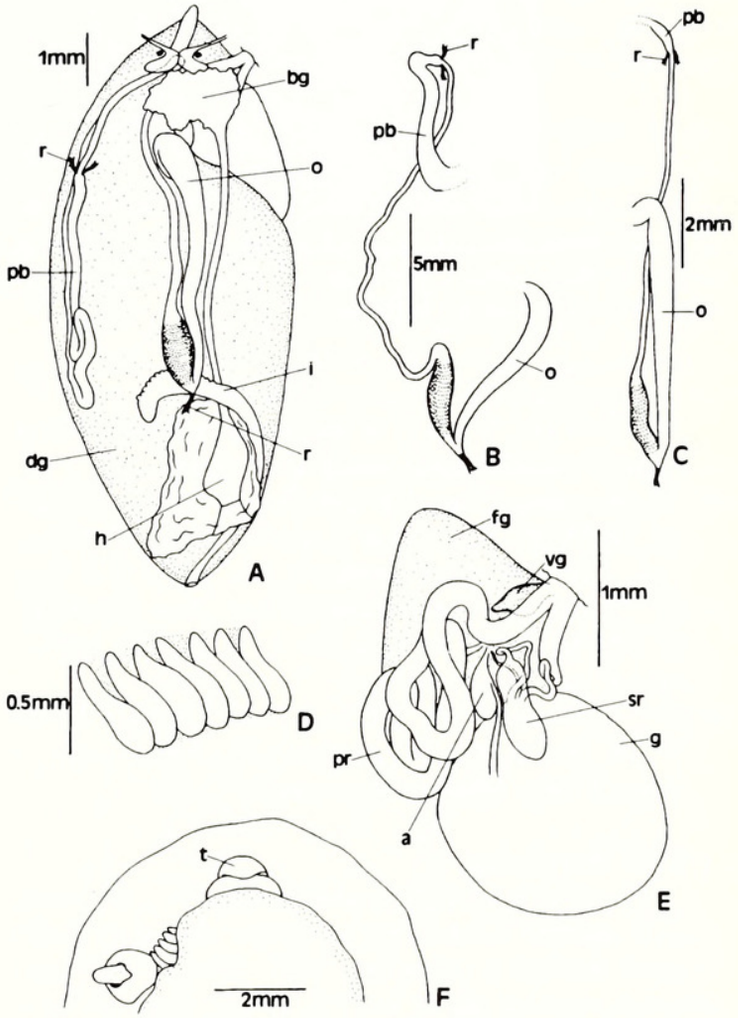

Fig. 3. *Phyllidiopsis berghi.* **A.** Dorsal view of the anatomy of the specimen from Gran Canaria (MNHN). **B.** Detail of the anterior digestive tract dissected from the holotype of *Phyllidiopsis gynenopla* (MNHN). **C.** Detail of the anterior digestive tract dissected from the holotype of *P. berghi* (MNHN). **D.** Detail of the branchial leaves. **E.** Genital system. **F.** Ventral view of preserved holotype of *P. gynenopla* showing the oral tentacles. a, ampulla; bg, blood gland; dg, digestive gland; fg, female gland; g, gametolytic gland; h, heart; i, intestine; o, esophagus; pb, pharyngeal bulb; pr, prostate; r, retractor muscles; sr, seminal receptacle; t, oral tentacles; vg, vestibular gland.

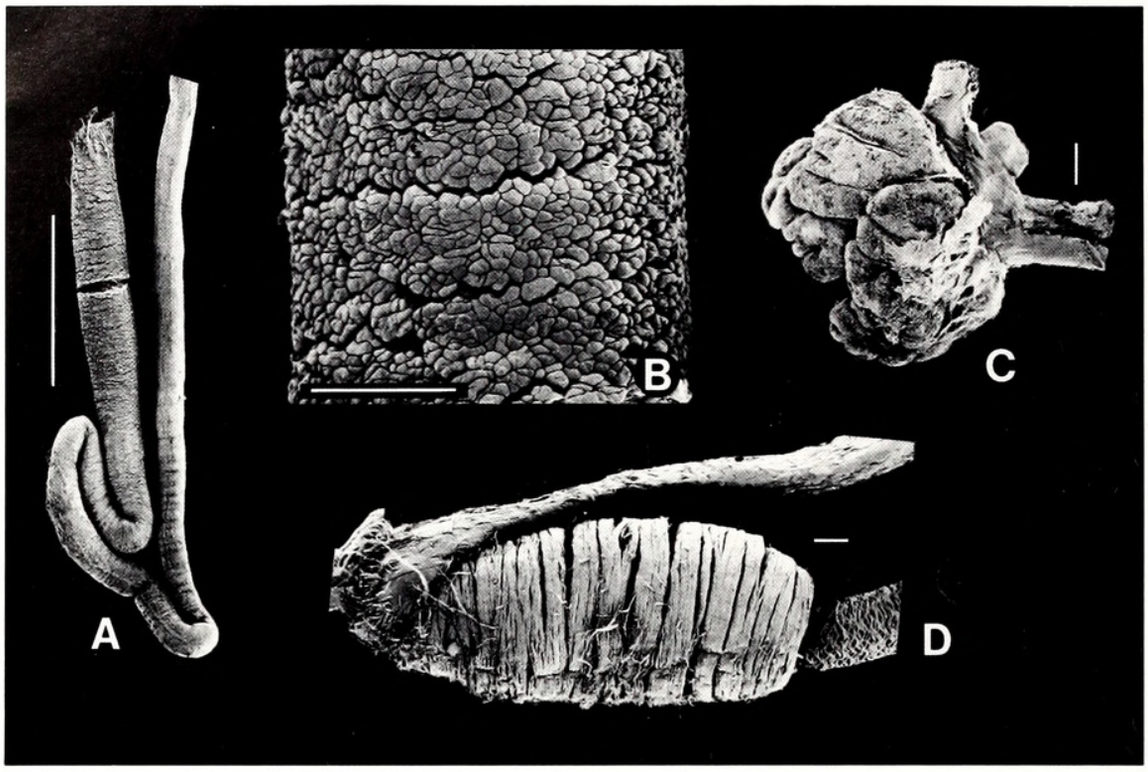

Fig. 4. Scanning electron micrographs (SEM) using critical point drying technique. **A.** Pharyngeal bulb of *Phyllidiopsis berghi.* **B.** Detail of the external glands of the pharyngeal bulb of *P. berghi.* **C.** Pharyngeal bulb of *Reticulidia gofasi.* **D.** Muscular esophageal portion of digestive tract of *P. berghi.* Scale bars = 1 mm (A), 100 μm (B, D), 200 μm (C).

N, 15°52.00' W), 470 m depth, 06 January 1993, 1 spm, 13 mm preserved length, dissected.

MNHN, *Seamount II* sta. DW188, Hyères Bank (31°30.00' N, 28°59.50' W), 310 m depth, 17 January 1993, 1 spm, 7 mm preserved length.

MNHN, *Seamount II* sta. DW200, Hyères Bank (31°19.10' N, 28°36.00' W), 1060 m depth, 17 January 1993, 1 spm, 8 mm preserved length.

MNHN, *Seamount II* sta. DW241, Plato Bank (33°11.90' N, 28°50.30' W), 695 m depth, 31 January 1993, 2 spms, 6 and 9 mm preserved length.

External Morphology

The general body color of live animals is pale cream; in larger specimens black pigment over several tubercles has been described (Bouchet, 1977). The dorsum bears numerous rounded tubercles (Figs. 1B-C). Several larger tubercles are distributed among the others in adult specimens. The border of the mantle is narrow, nearly 1/10 of the notum width. The rhinophores are white. The anus opens dorsally in all specimens observed. Rhinotubercles are absent.

Ventrally, the edge of the mantle shows spicules in reticular disposition. The anterior edge of the foot is not notched and the oral tentacles are spherical and fused (Fig. 3F). The branchial leaves are wide, triangular, and equal in size (Fig. 3D). They are clustered very closely together.

Anatomy

The pharyngeal bulb is very long (Figs. 3A, 4A) and covered by numerous minute glands (Fig. 4B). Two anterior retractor muscles insert at the point where the pharyngeal bulb and the esophagus connect. The esophagus is also very long, with a muscular portion near the end (Fig. 4D) where the posterior retractor muscles are attached. The intestine presents several small tubercles on its anterior portion.

The genital system (Fig. 3E) has a vestibular gland. The ampulla is smaller than the seminal receptacle in all specimens examined. From the gametolytic gland emerge three ducts, one of them connecting with the seminal receptacle, another with the vagina, and the thinnest of them with the female gland. The prostatic portion of the deferent duct is long and folded.

Geographical Range

This species, occurring in deep water, is only known in the North Atlantic (Fig. 5). It has been collected on the continental slope of France, in the Azores (slope of São Jorge), on the seamounts of the Meteor Group (Hyères Bank, Plato Bank), and in the Canary Islands (slope of Gran Canaria).

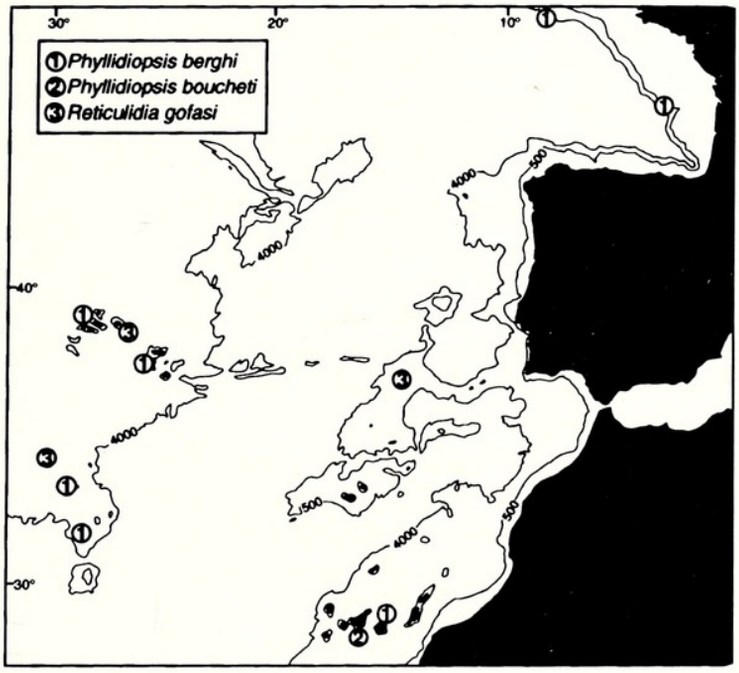

Fig. 5. Distribution map of the eastern Atlantic phyllidiid species.

Discussion

Vayssière (1902a) introduced the name *Phyllidiopsis berghi* but did not give a description (*nomen nudum*). Several months later, Vayssière (1902b) gave a exhaustive description of this species with anatomical details.

Phyllidiopsis gynenopla was described as different from *P. berghi* by Bouchet (1977), on the basis of the distinctive external color pattern and few anatomical details. Observation of the digestive tract of the holotypes of both nominal species showed no significant differences (Figs. 3B-C). Also, the external morphology is identical among the specimens observed. The difference in the external color can be explained by the difference in size (more than 30 mm) between the holotype of *P. gynenopla* and other material examined here assigned to *P. berghi*.

Another species with color pattern similar to *Phyllidiopsis berghi* is *P. blanca* Gosliner and Behrens, 1988, from the Pacific coast of North America. However, that species is distinguished by the disposition of the branchial leaves, all equal in size in *P. berghi*, and with alternation of large and small in *P. blanca* (see Gosliner and Behrens, 1988). Also, the disposition of the dorsal tubercles is different in the two species. In *P. berghi*, they are very close together, and there are two different sizes of tubercles; in *P. blanca* they are scattered and all of them are the same size. Anatomical differences between these species are found in the different disposition of the ducts arranged from the gametolytic gland (three in *P. berghi* and one in *P. blanca*).

Phyllidiopsis boucheti new species

(Figs. 1D, 6)

Material Examined

MNHN, HOLOTYPE, Punta de la Rasca, Tenerife, Canary Islands, 400 m depth, 12 May 1988, 8 mm preserved length, leg. J. J. Bacallado; MNHN, PARATYPE, same locality, 1 spm, 38 mm preserved length, dissected, leg. J. J. Bacallado.

External Morphology

Both specimens were fixed, so that no external features of the living animals were available. The general body color is white in the preserved specimens (Fig. 1D). The dorsum is entirely covered by numerous, minute, simply rounded tubercles. No gradation in size occurs in the tubercles near the notal margin. The rhinophores are white. Rhinotubercles are absent. The mantle margin is as wide as 1/3 of the notum. The anus opens dorsally in all specimens observed.

Ventrally, the branchial leaves are triangular (Fig. 6C). The oral tentacles are long and fused together (Fig. 6B). The mantle margin has spicules in reticular disposition. The anterior edge of the foot is not notched.

Anatomy

The esophagus is very thin and long (Fig. 6A). It has a muscular area in the middle of its length, just behind the intestine. The pharynx is elongate, but approximately half the length of the esophagus.

The reproductive system (Fig. 6A) is bordered by the digestive gland. The smooth prostatic portion of the deferent duct is twice as long as the ampulla, and leads into the short and narrow deferent duct.

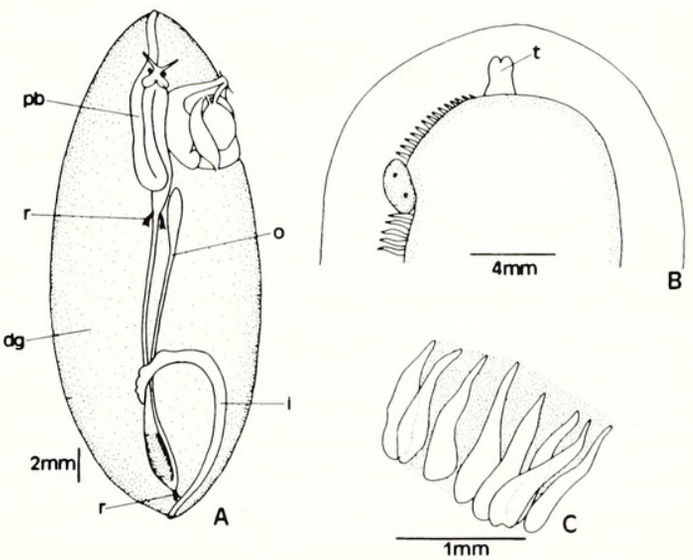

Fig. 6. *Phyllidiopsis boucheti*, paratype (MNHN). **A.** Dorsal view of the anatomy. **B.** Ventral view of preserved specimen showing the oral tentacles. **C.** Detail of the branchial leaves. dg, digestive gland; i, intestine; o, esophagus; pb, pharyngeal bulb; r, retractor muscles; t, oral tentacles.

Geographical Range

This species, occurring in deep water, is only known from the southern slope of Tenerife, Canary Islands (Fig. 5).

Discussion

Phyllidiopsis boucheti is clearly different from *P. berghi*. The species differ in the size, shape, and distribution of the dorsal tubercles; they are very minute and even in size in *P. boucheti,* and larger, and of two different sizes in *P. berghi*. Also, ventrally, the shape and disposition of the branchial leaves are different in the two species.

The differences between *Phyllidiopsis boucheti* and *P. blanca* are the shape and disposition of the dorsal tubercles, very minute and close together in the former and large and scattered in the latter. Also, differences in the shape and disposition of the branchial leaves support separation of the two species.

Brunckhorst (1990b, 1993) has suggested that the nominal species *Phyllidiopsis berghi* and *P. gynenopla*, from the Atlantic Ocean, and *P. blanca*, from the Pacific coast of Northern America, should be included in a new genus, because the published descriptions make no mention of anterior retractor muscles and muscular segments in the esophagus of these species. Detailed anatomical studies of our material shows that Atlantic *Phyllidiopsis* do have anterior retractor muscles and also that there is a muscular portion in the esophagus as in the Indo-Pacific species. New anatomical studies of *P. blanca* will probably also show the presence of these features. Although Atlantic and Indo-Pacific *Phyllidiopsis* show differences, such as the longer pharyngeal bulb in the Atlantic species, we feel that this is not enough to consider the separation of the Atlantic and Indo-Pacific *Phyllidiopsis* as two different genera.

Etymology

The name *Phyllidiopsis boucheti* is in honor of our friend and colleague, Dr. Philippe Bouchet (MNHN), who has made important contributions to the knowledge of mollusks.

Genus *Ceratophyllidia* Eliot, 1903
Type species *Ceratophyllidia africana* Eliot, 1903, by monotypy.

***Ceratophyllidia papilligera* (Bergh, 1890)**
(Figs. 1E, 7)

Phyllidiopsis papilligera Bergh, 1890: 176-178, pls. 2, 7-14; Marcus and Marcus, 1962: 475-479, figs. 20-24; 1967: 99, fig. 123; Thompson, 1980: 93, fig. 12.

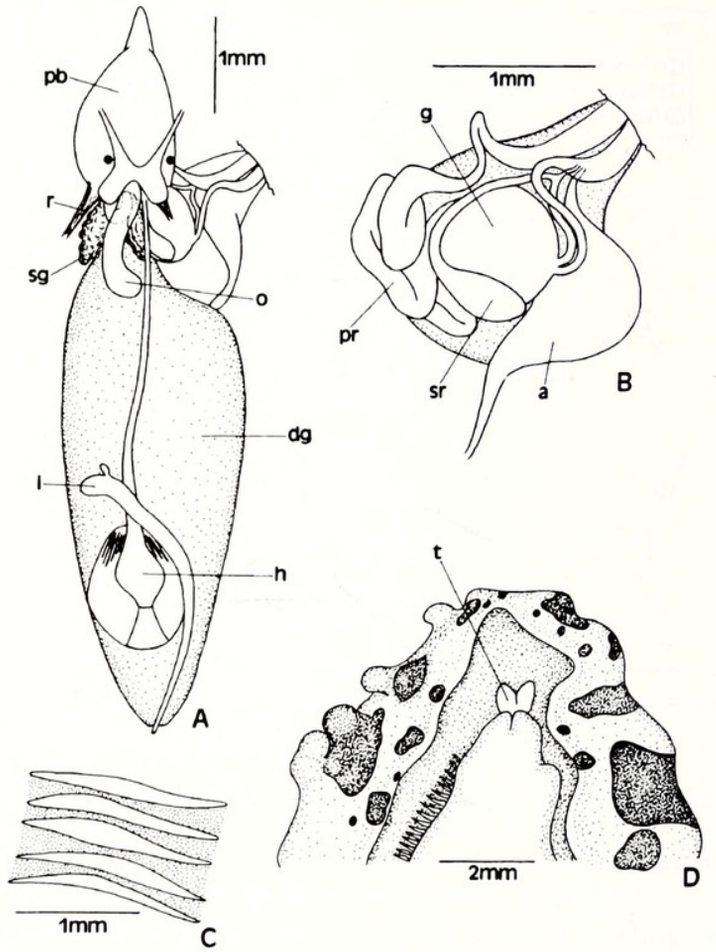

Fig. 7. *Ceratophyllidia papilligera*. **A.** Dorsal view of the anatomy. **B.** Genital system. **C.** Detail of the branchial leaves. **D.** Ventral view of preserved neotype (USNM 856418) showing the oral tentacles. a, ampulla; dg, digestive gland; g, gametolytic gland; h, heart; i, intestine; o, esophagus; pb, pharyngeal bulb; pr, prostate; r, retractor muscles; sg, salivary glands; sr, seminal receptacle; t, oral tentacles.

Material Examined

USNM 856418, NEOTYPE, *Sofla* Expedition sta. 11, (26°16.43' N, 83°46.49' W), 77 m depth, 30 April 1981, 19 mm preserved length.

USNM 856417, *Sofla* Expedition sta. 11, (26°16.43' N, 83°46.49' W), 77 m depth, 30 April 1981, 2 spms, 10 and 12 mm preserved length.

Indian Keys, Cuba, 30 October 1993, 30 m depth, 1 spm, 26 mm long, leg. J. Espinosa.

External Morphology

The general color of the body is white, with rounded black spots of various sizes (Fig. 1E). The body is oval-shaped, with numerous stalked papillae on the dorsum. The placement of the black spots is independent of the papillae; their size is variable but usually very large. The notum is spiculose. The rhinophores are white with black lamellae; each clavus has ten lamellae. Rhinotubercles are absent.

Ventrally, the anterior border of the foot is notched (Fig. 7D). The dark tubercles of the notal margin show through the ventral side. The oral tentacles are separated. The branchial leaves are equal in size (Fig. 7C).

Anatomy

At the point where the esophagus inserts into the musculoglandular pharyngeal bulb, it connects with two conspicuous and brown-colored salivary glands (Fig. 7A). The esophagus is short, and no glandular portion has been observed.

The genital system (Fig. 7B) shows an ampulla larger than the gametolytic gland. No vestibular gland has been observed. The gametolytic gland connects with two ducts, one of them connecting with the vagina, and the other one with the seminal receptacle and the female gland.

Geographical Range

This species appears to be restricted to the Caribbean Sea and Gulf of Mexico. After its original description from the Gulf of Mexico (Bergh, 1890), *Ceratophyllidia papilligera* has been reported from Jamaica (Marcus and Marcus, 1967; Thompson, 1980) and from the Virgin Islands and Bahamas (Marcus and Marcus, 1962).

Discussion

Eliot (1903b) described the new genus *Ceratophyllidia* and included *Phyllidiopsis papilligera* as the type species. In a later paper (Eliot, 1903a), he described the new species *Ceratophyllidia africana*, including a description of the genus *Ceratophyllidia*. According to Brunckhorst (1990b, 1993), the former paper was received in June 1902 but was not published until sometime between July and November 1903. Eliot's description of *C. africana* appeared earlier (March 1903) and therefore constitutes the original description of the genus *Ceratophyllidia* with *C. africana* as the type species by monotypy. The anatomical characters observed in *C. papilligera* present all the features characteristic of the genus *Ceratophyllidia* described by Eliot (1903a, b) and Brunckhorst (1993) based on *C. africana*. The structure of the digestive system, with two conspicuous salivary glands, and the external stalked papillae of *C. papilligera* confirm its placement in the genus *Ceratophyllidia*.

Phyllidiella molaensis shows an external combination of colors similar to *Ceratophyllidia papilligera*. Nevertheless, anatomical features such as the structure of the digestive system (typical of the genus *Phyllidiella* in *P. molaensis*) and external differences such as the shape of the dorsal tubercles (conical tubercles in *P. molaensis* and stalked papillae in *C. papilligera*), the disposition of the branchial leaves (showing alternation in *P. molaensis* and equal in size in *C. papilligera*), and the pattern of color (black rings in *P. molaensis* and black spots in *C. papilligera*) easily separate the two species.

According to Thompson (1980), the type material of *Ceratophyllidia papilligera* is untraceable; however, for nomenclatural stability of this species we considered it desirable to designate a neotype. For this reason, we designated as neotype one specimen, USNM 856418, collected in the Gulf of Mexico, off Florida, close to the original record of this species.

Genus *Reticulidia* Brunckhorst, 1990
Type species *Reticulidia halgerda* Brunckhorst and Burn, 1990, by original designation.

***Reticulidia gofasi* new species**
(Figs. 1F, 4C, 8)

Material Examined

MNHN, HOLOTYPE, *Seamount I* sta. DW61, Josephine Bank (36°40.02' N, 14°16.00' W), 200-205 m depth, 07 October 1987, 11 mm preserved length.

MNHN, PARATYPE, *Seamount II* sta. DW256, Atlantis Bank (34°06.20' N, 30°16.00' W), 340 m depth, 02 February 1993, 1 spm, 9 mm preserved length, dissected.

MNHN, PARATYPE, *Jean Charcot-Biaçores* sta. 11 (38°30.00' N, 27°14.05' W), 76-105 m depth, 08 October 1971, 1 spm, 10 mm preserved length, dissected.

MNHN, *Seamount II* sta. DW274, Atlantis Bank (34°05.10' N, 30°13.60' W), 280 m depth, 05 February 1993, 1 spm, 3 mm preserved length.

External Morphology

The general body color is pale yellow in live specimens. The dorsum is heavily spiculose, covered by conical tubercles, grading to smaller toward the notal margin (Fig. 1F). The mantle margin is as wide as the notum, and translucent. The rhinophores are pale yellow. Rhinotubercles are absent. The anus opens dorsally in all specimens observed.

Ventrally, the anterior edge of the foot is notched (Fig. 8D). The large and conical oral tentacles are separated. The branchial leaves are very thin, and triangular, showing alternation of large and small ones (Fig. 8C). The mantle margin shows radial spicules.

Anatomy

The pharyngeal bulb is embedded on its anterior portion in the transparent oral tube; its edge is surrounded by

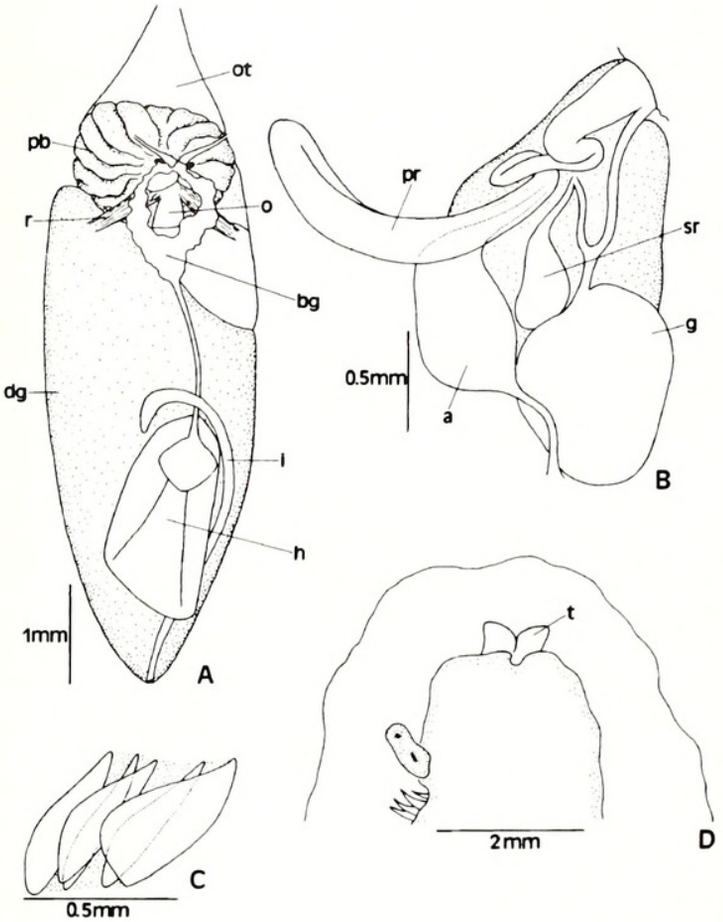

Fig. 8. *Reticulidia gofasi,* paratype from Atlantis Bank (MNHN). **A.** Dorsal view of the anatomy. **B.** Genital system. **C.** Detail of the branchial leaves. **D.** Ventral view of preserved specimen showing the oral tentacles. a, ampulla; bg, blood gland; dg, digestive gland; g, gametolytic gland; h, heart; i, intestine; o, esophagus; ot, oral tube; pb, pharyngeal bulb; pr, prostate; r, retractor muscles; sr, seminal receptacle; t, oral tentacles.

several discs, around a hole through which the short esophagus emerges (Figs. 4C, 8A). Also, two large retractor muscles insert on the pharyngeal bulb at both sides of the esophagus.

The genital system (Fig. 8B) presents an ampulla larger than the seminal receptacle. The prostatic portion of the deferent duct is quite short, with only one fold, and connects with the deferent portion by a short and thin duct.

Geographical Range

Reticulidia gofasi is only known in the Meteor Group seamounts (Atlantis Bank), Lusitanian seamounts (Josephine Bank), and the Azores (slope of Terceira) (Fig. 5).

Discussion

The structure of the pharyngeal bulb of *Reticulidia gofasi*, with several discs and two large retractor muscles, is identical to that described by Bruncknorst (1990a, 1993) for the genus *Reticulidia*. However, the dorsal external morphology of the Indo-Pacific species of this genus, *Reticulidia halgerda* Bruncknorst and Burn, 1990, and *Reticulidia fungia* Bruncknorst and Gosliner, 1993, with bright colors and dorsal ridges, is very different from our species, pale yellow with conical tubercles. The color differences of *R. gofasi* with the other species of the genus could be connected with the bathyal habitat of the former; the same occurs for other deep water phyllidiids such as *Fryeria bayi, Phyllidiopsis berghi*, and *P. boucheti.*

In the external morphology and anatomy, *Reticulidia gofasi* is clearly different from the other Atlantic phyllidiid species. The morphology of the oral tentacles, the shape and distribution of the dorsal tubercles, and the structure of the digestive system are very distinctive characters of this species.

Etymology

The name *Reticulidia gofasi* is in honor of our friend and colleague, Dr. Serge Gofas (MNHN), who collected and made available to us most of the material of this species.

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