



# Systematics and phylogeny of the caryophyllidia-bearing dorids (Mollusca, Nudibranchia), with descriptions of a new genus and four new species from Indo-Pacific deep waters

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The phylogenetic relationships of the caryophyllidia-bearing dorids are studied, based on the examination of the type species of all the genera previously described. The phylogenetic hypothesis supports that the caryophyllidia-bearing dorids are a monophyletic group and the sister group of the clade formed by *Asteronotus* Ehrenberg, 1831 and *Halgerda* Bergh, 1880. Several genera previously considered as valid or regarded as uncertain are here synonymized: *Peronodoris* Bergh, 1904, *Trippa* Bergh, 1877, *Phlegmodoris* Bergh, 1878, *Petelodoris* Bergh, 1881, *Kentrodoris* Bergh, 1876, *Audura* Bergh, 1878, *Centrodoris* P. Fischer, 1883, *Anisodoris* Bergh, 1898, *Awuka* Er. Marcus, 1955, *Rhabdochila* P. Fischer, 1883, *Boreodoris* Odhner, 1939, *Dictyodoris* Bergh, 1880, *Graviera* Vayssière, 1912, *Aporodoris* Ihering, 1886. The following genera are regarded as valid: *Asteronotus*, *Atagama* J.E. Gray, 1850, *Jorunna* Bergh, 1876, *Platydoris* Bergh, 1877, *Diaulula* Bergh, 1878, *Rostanga* Bergh, 1879, *Halgerda* Bergh, 1880, *Baptodoris* Bergh, 1884, *Gargamella* Bergh, 1894, *Alloiodoris* Bergh, 1904, *Sclerodoris* Eliot, 1904, *Taringa* Er. Marcus, 1955, *Thorybopus* Bouchet, 1977. The new genus *Nophodoris* is described based on two new species from New Caledonia deep waters. Two additional new species from New Caledonia belonging to the genera *Atagama* and *Gargamella* are also described. Nomenclatural and taxonomic problems are discussed, and several type species, neotypes and lectotypes are selected.

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## INTRODUCTION

Caryophyllidia are highly specialized structures present in the dorsum of several nudibranch dorids. They are tubercles bearing apical sensory organs, surrounded by a ring of protruding calcareous spicules. The function of caryophyllidia is still unknown and remains open to speculation.

Caryophyllidia were first identified, described and named by Labbé (1929, 1930, 1933) from Atlantic cryptobranch dorids of the genera *Jorunna* Bergh, 1876 and *Rostanga* Bergh, 1879. Kress (1981) studied these organs for the first time using scanning electron microscopy (SEM), and Foale & Willan (1987) investigated the structure of caryophyllidia combining

SEM and transmission electron microscopy (TEM) techniques. Kress (1981) identified caryophyllidia in two species of the phanerobranch genus *Onchidoris* de Blainville, 1816, but Foale & Willan (1978) discounted the homology of these structures with those found in cryptobranch dorids based on the phyletic distance between these taxa. Ev. Marcus (1976) reported caryophyllidia for the first time in the genus *Kentrodoris* Bergh, 1876, Rudman (1978) in *Sclerodoris* Eliot, 1903, Gosliner (1987) in *Baptodoris* Bergh, 1884 and *Gargamella* Bergh, 1894, and Ortea, Pérez-Sánchez & Llera (1982) in *Taringa* Er. Marcus, 1955. A preliminary review of the literature shows that many other genera may also have caryophyllidia. Traditional descriptions of the mantle texture of dorids such as 'fleecy' or 'silky' are normally indicative of the presence of caryophyllidia.

According to Foale & Willan (1987) the caryophyllidia appear to represent the most advanced form

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of spiculose mantle differentiation within the Doridina. These authors suggested that some cryptobranch dorids previously classified in different families (i.e. *Rostanga* and *Jorunna*) should be grouped together because of the joint possession of caryophyllidia.

The present paper reviews the systematics of the caryophyllidia-bearing dorids including several genera newly recognized as having these organs. It also examines the phylogenetic relationships of the caryophyllidia-bearing dorids to determine whether or not they constitute a monophyletic group.

### CARYOPHYLLIDIA

Foale & Willan (1987) and Gosliner (1994) described in detail the fine structure of the caryophyllidia. The caryophyllidia are structures formed by the stretching of the epidermis over a framework of spicules. At the apex, there is a spherical knob (or ciliated tubercle), which bears several tufts of cilia. The concentration of these tufts of cilia varies between different species. The size and shape of the knob is also highly variable. Each caryophyllidium is supported by a variable number of spicules that emerge near the apex and radiate in circular crown. Even after they emerge at the apex, the spicules remain covered with a thin layer of epidermis. In several species, the spicules are longer than the ciliated tubercle, whereas in other species they are shorter. Also, the spicules may be free apically or remain attached to the ciliated tubercle for all of their length. In some cases, the spicules are almost surrounded by the cilia of the ciliated tubercle. The epidermis of the caryophyllidia is entirely covered with a dense mat of microvilli. In addition, the caryophyllidia have muscles and nerves associated with them. These muscles could confer some mobility and retractibility to the caryophyllidia (Labbé, 1929; Foale & Willan, 1987).

There are other species of cryptobranch dorids that have tubercles with protruding spicules. However, in these species the spicules are not organized in a circular pattern and there is no a central ciliated tubercle. On the other hand, Kress (1981) showed caryophyllidia-looking spiculose tubercles in two species of *Onchidoris* Blainville, 1816 (phanerobranch dorids). However, according to Foale & Willan (1987), because of the phylogenetic distance between the genus *Onchidoris* and the caryophyllidia-bearing dorids, any similarities in mantle structures should be attributed to evolutionary convergence. The fine structure of these caryophyllidia-looking tubercles of some phanerobranch dorids has not been investigated in order to determine possible homologies with the caryophyllidia.

Very often, the caryophyllidia are difficult to recognize in preserved specimens. The spicules can be easily dissolved by a number of fixation methods, and

they are often damaged as the consequence of harmful collecting methods. Many of the deep-water specimens examined in this paper have the caryophyllidia partially destroyed. The presence of a ciliated tubercle is normally the best indication of the presence of caryophyllidia in old or poorly preserved material.

### HISTORY OF THE CLASSIFICATION

The classification of the caryophyllidia-bearing dorids, as well as the rest of the cryptobranch dorids, is in need of major revision using contemporary systematics techniques. Several classifications of these animals have been proposed, but none of them are based on a phylogenetic analysis using parsimony.

The caryophyllidia-bearing dorids have never been united in a single group. In all cases they have been divided into different families and arbitrarily grouped with other dorids lacking caryophyllidia, on the basis of other internal or external features.

Bergh (1891) published the first classification of the cryptobranch dorids. At that time, the caryophyllidia were still undescribed, and he did not consider this structure in the diagnosis of the families and genera. Bergh distributed the caryophyllidia-bearing dorids among Discodorididae, Diaululidae and Kentrodorididae, which he ranked as subfamilies of Dorididae, along with other genera lacking these organs.

Pelseneer (1906) and Iredale & O'Donoghue (1923) simplified considerably the classification presented by Bergh and placed in a single family (Dorididae or Dorigitatidae) all the cryptobranch dorids, including those with caryophyllidia.

Thiele (1929–35) and Odhner (1939) reintroduced the scheme presented by Bergh and divided the cryptobranch dorids in several subfamilies. Years later, Odhner (see Franc, 1968) elevated Bergh's subfamilies to the rank of families. Several new families and genera were added, and some genera changed families. The caryophyllidia-bearing dorids were included in the families Rostangidae, Baptdorididae, Discodorididae, Kentrodorididae, Asteronotidae and Platydorididae, in most cases grouped with other genera lacking caryophyllidia. Vaught (1989) proposed a more complex classification and included the caryophyllidia bearing dorids in the families Miamiridae, Aldisidae, Rostangidae, Dorididae, Archidorididae, Discodorididae, Kentrodorididae, Halgerdidae and Platydorididae, again grouped with other genera lacking caryophyllidia.

The most radical reassessment of Odhner's classification in the latest years was first introduced by Willan & Coleman (1984) and later substantiated by Rudman (1998), who divided the cryptobranch dorids into only two families, Chromodorididae and Dorididae. Thus, the caryophyllidia-bearing dorids are

included in Dorididae along with the rest of the cryptobranch non-chromodorids. Several authors have followed this conservative approach in recent years (Wells & Bryce, 1993).

At present, there is no general agreement regarding the classification of the cryptobranch dorids. Specialists agree only that cryptobranch dorids are one of the most systematically difficult groups of opisthobranchs.

## MATERIAL AND METHODS

The type material, additional non-type material or information regarding the types of species studied in the present paper, were obtained through several institutions: Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco (CASIZ), Muséum National d'Histoire Naturelle, Paris (MNHN), Zoologisk Museum, Københavns Universitet, Copenhagen (ZMUC), Naturhistoriska Riksmuseet, Stockholm (SMNHI), The Natural History Museum, London (BMNH), Museum für Naturkunde der Humboldt-Universität, Berlin (MMHB), Museu de Zoologia da Universidade de São Paulo (MZSP) and Museo Nacional de Ciencias Naturales, Madrid (MNCN).

Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a dissecting microscope with a camera lucida. Particularly interesting soft parts were critical point dried for SEM. Special attention was paid to the morphology of the reproductive system, digestive system and central nervous system. The penial and vaginal hooks and the accessory spines of several species were prepared for examination on SEM. Features of living animals were recorded from photographs or notes of collectors. (For index of genera, see Appendix.)

## SYSTEMATIC DESCRIPTIONS

### GENUS *ASTERONOTUS* EHRENBERG, 1831

*Asteronotus* Ehrenberg, 1831: 29. Type species *Asteronotus hemprichii* Ehrenberg, 1831 [= *Asteronotus cespitosus* (van Hasselt, 1824)], by monotypy.

? *Peronodoris* Bergh, 1904: 44–45. Type species *Peronodoris cancellata* Bergh, 1904, by monotypy.

### *Diagnosis*

Body rigid, gelatinous. Dorsum with large tubercles and ridges, lacking caryophyllidia. Rhinophoral and branchial sheaths elevated. Branchial sheath lobate. Prostate massive, with two different portions. Penis and vagina unarmed. Accessory gland with a short spine. Labial cuticle smooth. All radular teeth hamate and smooth.

### *Remarks*

After its introduction by Ehrenberg (1831) the genus *Asteronotus* Ehrenberg, 1831 has been unanimously considered as valid. The original description is clear enough to recognize the features of this genus. In the present paper, by re-examining of the type material, we have confirmed that the usage of the name agrees with the identity of the animals studied by Ehrenberg (1831).

Bergh (1904) introduced the genus *Peronodoris* Bergh, 1904 based on *Peronodoris cancellata* Bergh, 1904. Edmunds (1971) considered *Peronodoris* to be synonymous with *Halgerda*, but Ev. Marcus & Er. Marcus (1970) regarded both genera as distinct. *Peronodoris* is characterized by a rounded, depressed and rigid body with dorsal ornamentation, a wide mantle margin, narrow foot, absence of jaws and rachidian tooth, penis armed with a spine, vagina unarmed and absence of prostate. The drawings of the radular teeth of *Peronodoris cancellata* (Bergh, 1904, pl. 3, figs 20–22) resemble the teeth of *Asteronotus*. In addition, the presence of a spine in the reproductive system, probably in the accessory gland (Bergh consistently misinterpreted the position of the genital spine – see also the discussion of *Jorunna* and *Kentrodoris*) suggests that these genera could be synonyms. Unfortunately, the type material of *P. cancellata* is lost, and, because of the incomplete description of *Peronodoris*, we were not able to confirm its synonymy with *Asteronotus*.

Burn (1962) introduced the name *Tumbia* Burn, 1962, based on *Asteronotus (Tumbia) trenberthi* Burn, 1962, as a subgenus of *Asteronotus*. However, according to the original description of *Asteronotus trenberthi* (Burn, 1962), and, in contrast to *Asteronotus cespitosus*, the reproductive system does not have an accessory gland and the radula has the innermost and outermost lateral teeth denticulate. Therefore we do not consider *Tumbia* to be synonym of *Asteronotus*, and its systematic position is still undetermined.

### *ASTERONOTUS CESPITOSUS* (VAN HASSELT, 1824)

(Figs 1A, 2A, 3, 4, 5B,E)

*Doris cespitosa* van Hasselt, 1824: 238.

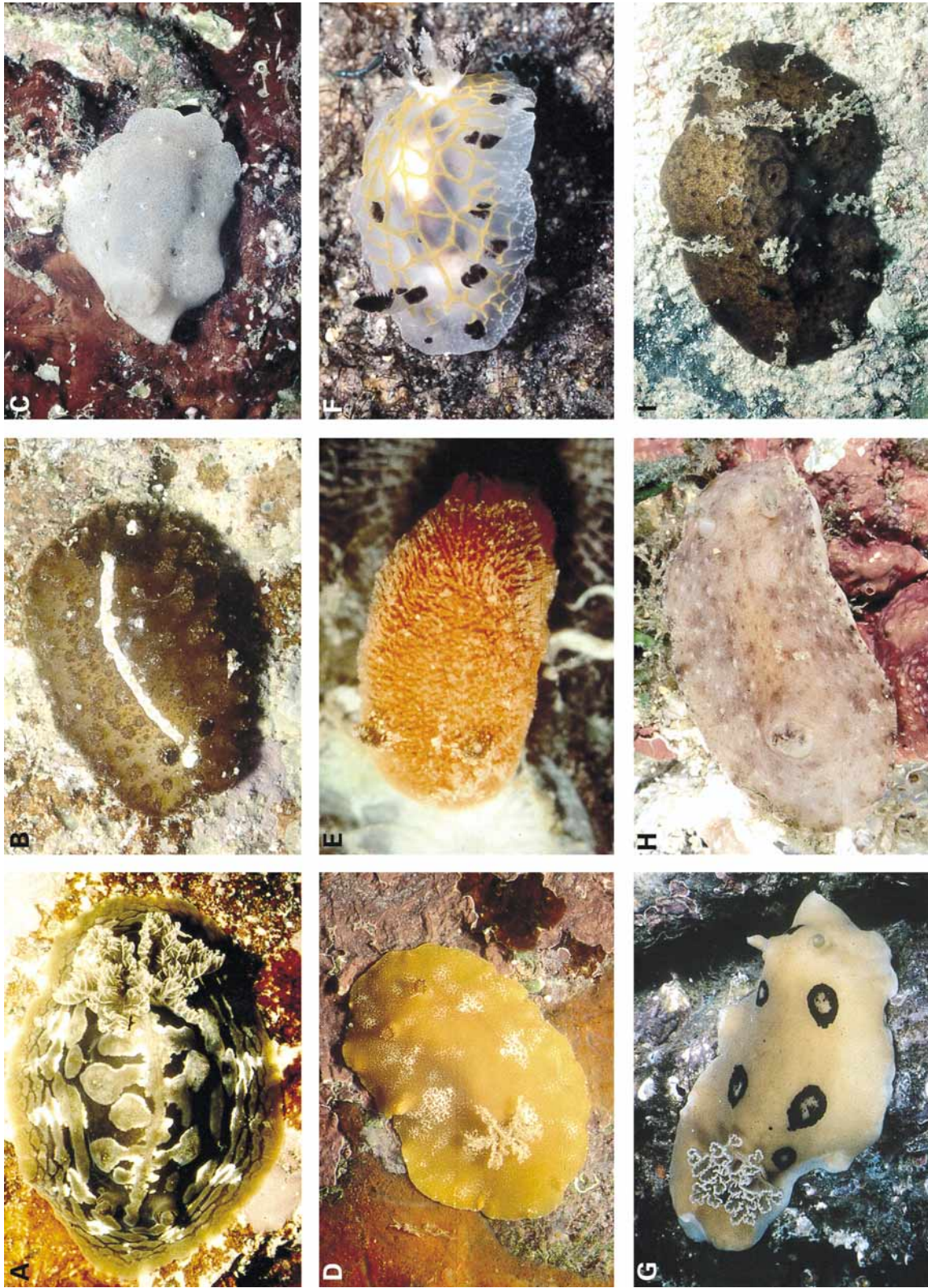
*Asteronotus hemprichii* Ehrenberg, 1831: 29–30.

See Thompson (1975) for a complete list of synonyms.

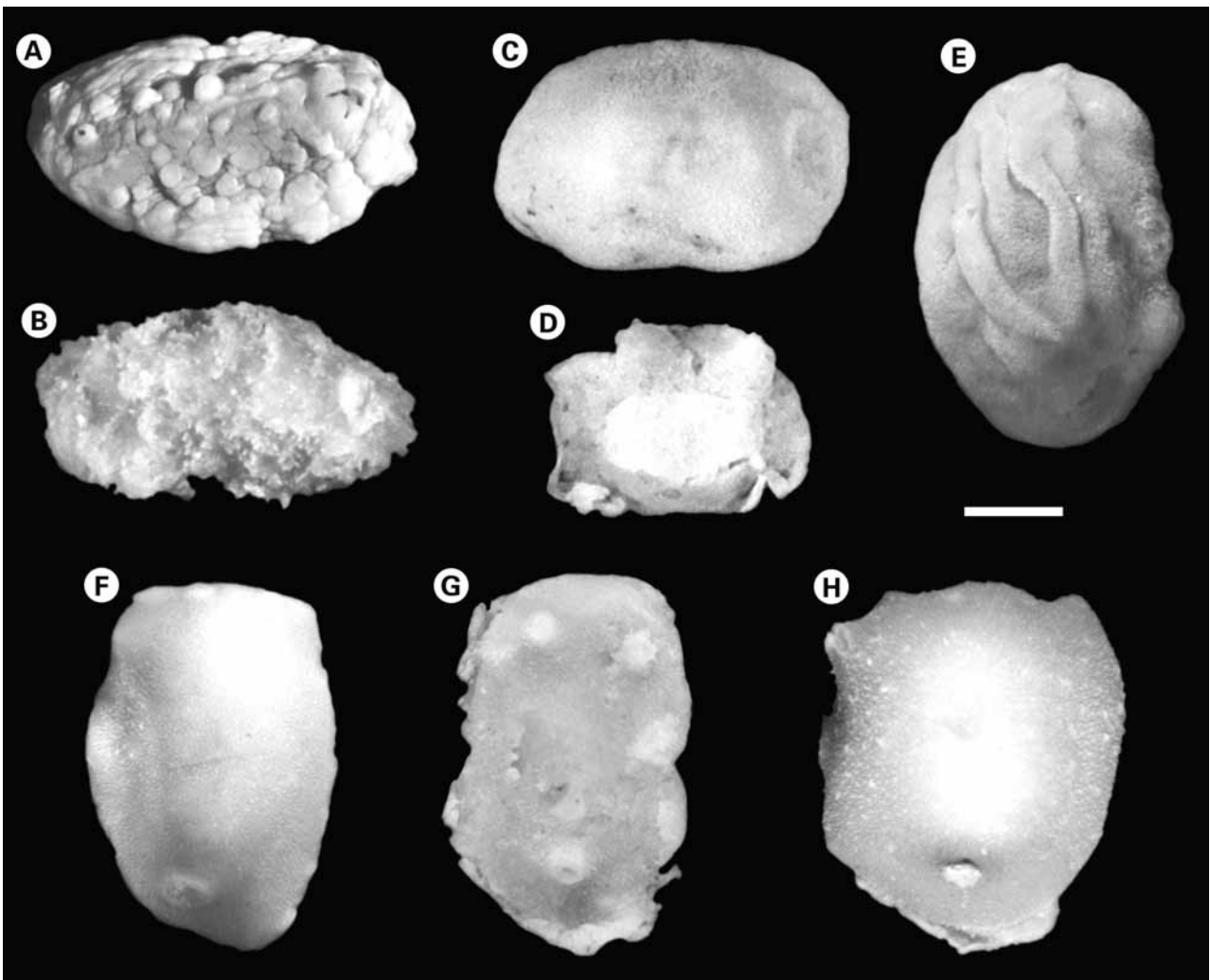
### *Type material*

*Doris cespitosa* van Hasselt, no type material is known to exist. *Asteronotus hemprichii* Ehrenberg, syntypes – 'Massaua' (= Mits'iwa), Egypt, Red Sea, 1830, 2 specimens 68–86 mm preserved length, leg. C.G. Ehrenberg (MMHB 572).





**Figure 1.** Living animals. A, *Asteronotus cespitosus* (CASIZ 074245). B, *Atagema ornata*, Culebra Island, Batangas, Luzon, Philippines. C, *Jorunna tomentosa*, Banyuls, France. D, *Platydoris argo* (CASIZ 114868). E, *Rostanga rubra*, Alborán, Spain. F, *Halgerda formosa*, Adlam's Reef, Sodwana Bay National Park, South Africa. G, *Diacaula sandiegensis*, California. H, *Baptydoris cinnabarina* (MINCN 15.05/32381). I, *Sclerodoris tuberculata* (CASIZ 073247).



**Figure 2.** Preserved specimens. A, syntype of *Asteronotus cespitosus* (MMHB 572), scale bar=18.4 mm. B, holotype of *Atagemma boucheti* (MNHN), scale bar=3.7 mm. C, *Gargamella immaculata* (SMNHI 12520), scale bar=6.8 mm. D, holotype of *Gargamella wareni* (MNHN), scale bar=8.7 mm. E, lectotype of *Alloiodoris marmorata* (ZMUC GAS-2057), scale bar=9.3 mm. F, lectotype of *Taringa millegrana* (BMNH 1980101), scale bar=7.4 mm. G, holotype of *Nophodoris infernalis* (MNHN), scale bar=3.6 mm. H, holotype of *Nophodoris armata* (MNHN), scale bar=9.6 mm.

#### *Additional material*

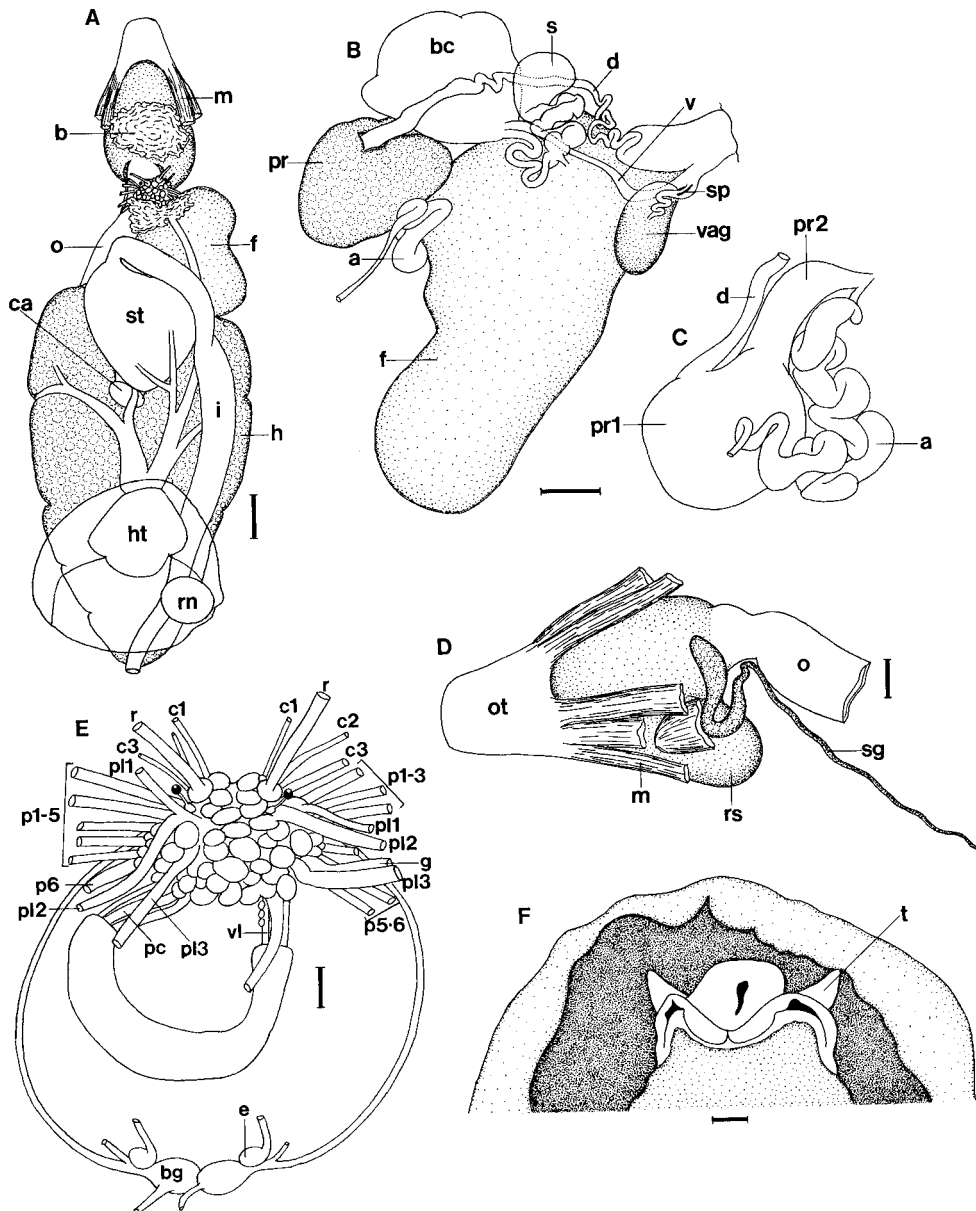
Fiji Islands, 1978–1979, 3 specimens 70–109 mm preserved length, leg. M. P. Morse (CASIZ 072765).

#### *External morphology*

The maximum length is over 220 mm. The body is flat, wide, with a rigid, gelatinous texture. The dorsum has large, irregular tubercles, being larger in the central part of the body (Figs 1A, 2A). The tubercles in the centre of the dorsum are lined up and fused together forming a longitudinal ridge. Other tubercles may be fused in groups of two or three. In the mantle margin, the tubercles may be fused together forming concentric ridges. There are no spicules projecting from the

tubercles. The rhinophoral and branchial sheaths are elevated and irregular. The opening of the branchial sheath has six large lobes pointing towards the centre of the gill. There are six tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. Each branchial leaf protrudes through the space between two lobes. The rhinophores are elongated, having 27 lamellae in a 109 mm preserved length specimen.

The general colour of the living animals varies from yellow to grey-brown, olive-brown or dark brown. In some specimens there are white rings encircling the tubercles. In others the border of the mantle margin has a distinct paler line around it. In the darkest specimens the tubercles may be paler than the rest of



**Figure 3.** *Asteronotus cespitosus* (CASIZ 072765). A, general view of the anatomy; scale bar=5 mm. B, reproductive system; scale bar=3 mm. C, detail of several reproductive organs; scale bar=3 mm. D, lateral view of the buccal bulb; scale bar=3 mm. E, central nervous system; scale bar=1 mm. F, ventral view of the mouth area; scale bar=5 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; ca, caecum; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

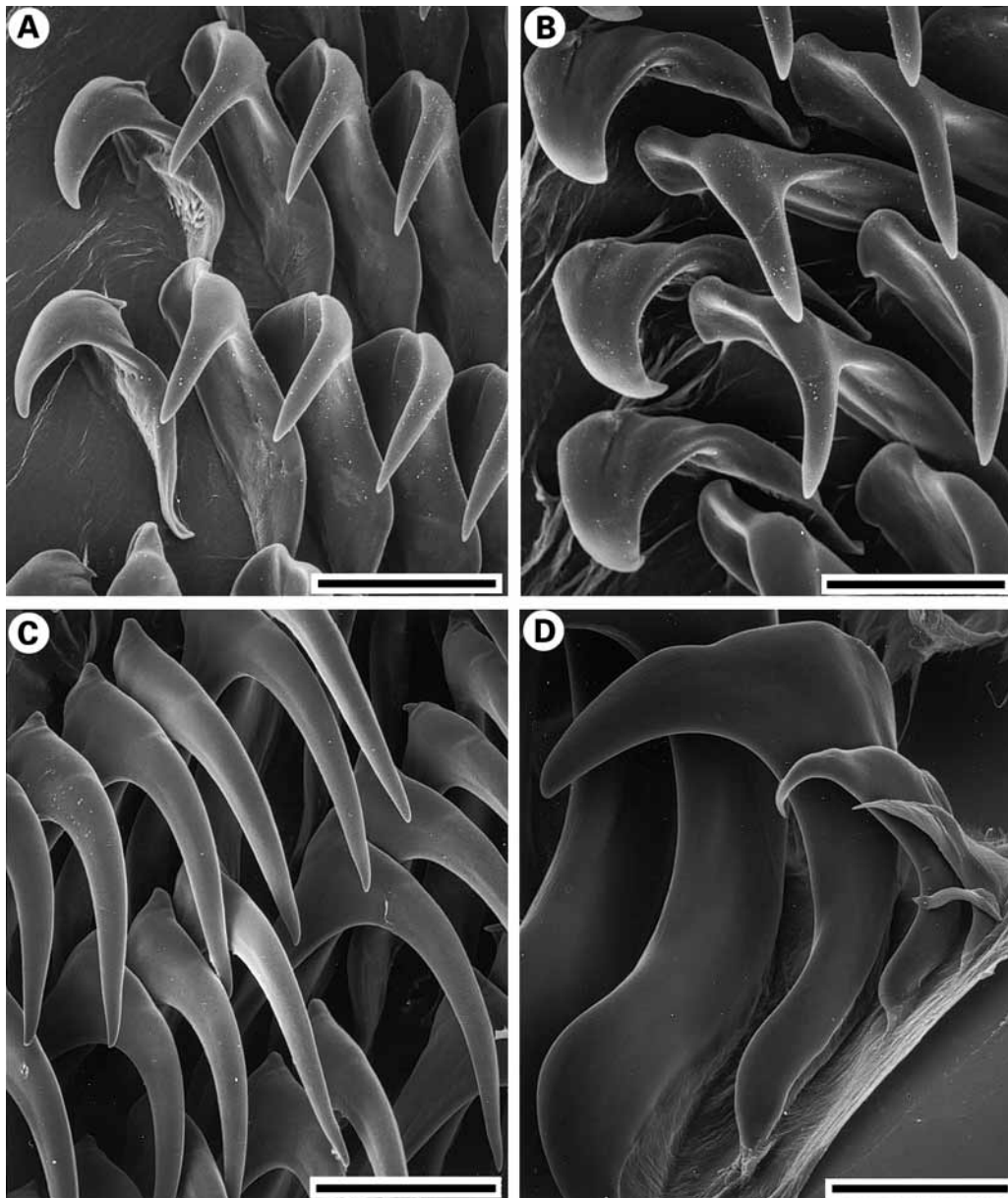
the dorsum. The gill is reddish or brownish with paler tips. The rhinophores have normally the same colour as the dorsum.

Ventrally the anterior border of the foot is notched and grooved (Fig. 3F). The oral tentacles are conical. The ventral colour is the same as the dorsum.

#### Anatomy

The posterior end of the oral tube has eight strong retractor muscles (Fig. 3D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction.



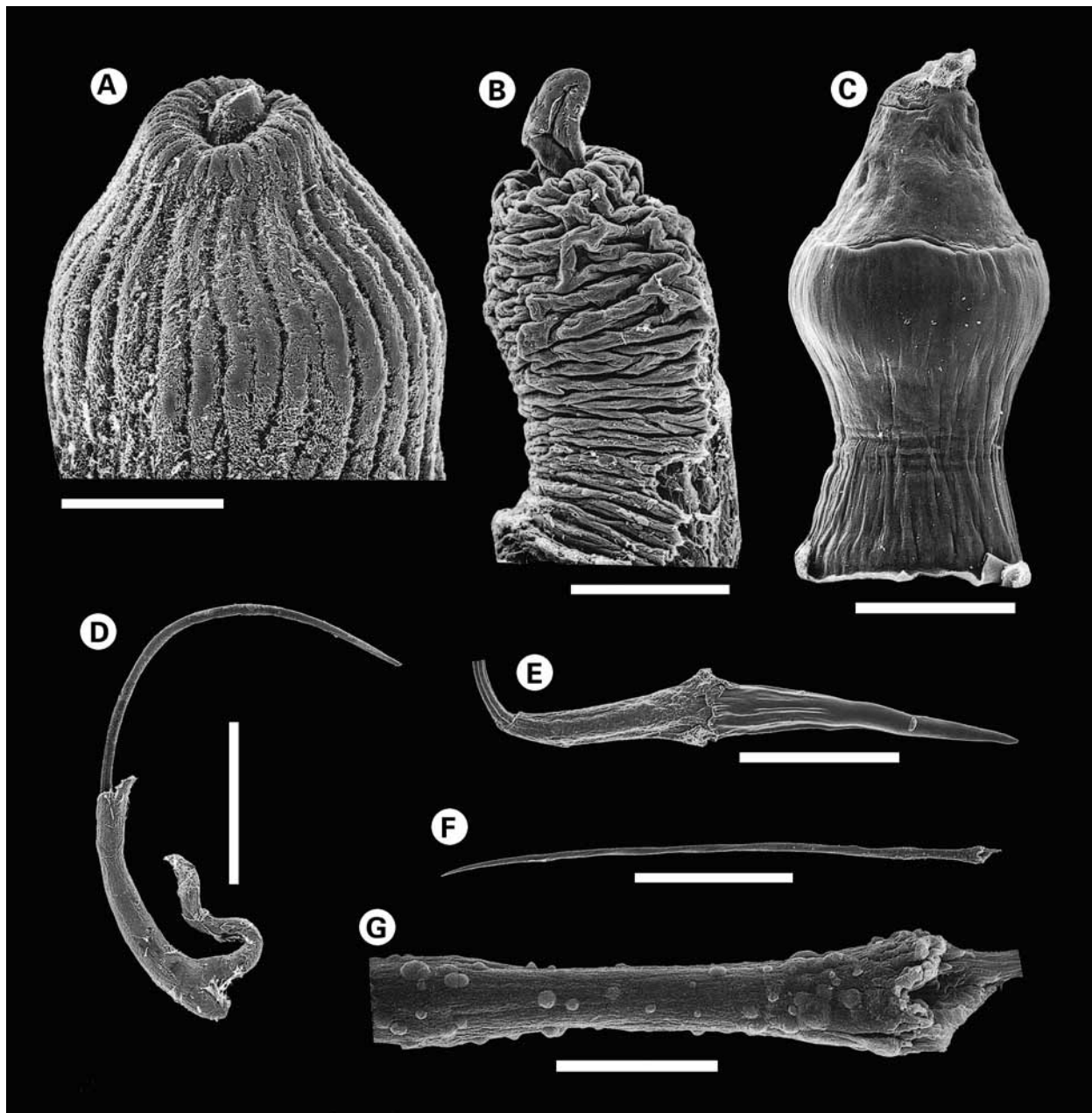


**Figure 4.** *Asteronotus cespitosus* (CASIZ 072765), SEM photographs of the radula. A, inner lateral teeth; scale bar = 100 µm. B, inner lateral teeth; scale bar = 75 µm. C, teeth from the central portion of the half-row; scale bar = 150 µm. D, outer lateral teeth; scale bar = 60 µm.

The buccal bulb is longer than the oral tube. The labial cuticle is smooth. The radular formula is  $35 \times (41.0.41)$  in a 70 mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 4). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 4A–C). The outermost teeth are very small and also lack denticles (Fig. 4D). The oesophagus is long and expands directly into the stomach (Fig. 3A).

The ampulla is very long and convoluted. It branches into a long oviduct and the prostate (Fig. 3C). The oviduct

enters the female glands near their opening. The prostate is massive and granular (Fig. 3B,C). It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the ampulla (Fig. 3C). The deferent duct is very long and narrow. It narrows and expands again into the short ejaculatory portion. The deferent duct opens into a common atrium with the vagina. The penis is unarmed (Fig. 5B). There is an accessory gland connected to the atrium which has a



**Figure 5.** SEM photographs of several reproductive organs. A, *Diaulula sandiegensis* (CASIZ 068277), penis; scale bar = 300  $\mu\text{m}$ . B, *Asteronotus cespitosus* (CASIZ 072765), penis; scale bar = 200  $\mu\text{m}$ . C, *Taringa telopia* (MZSP 25281), penial cuticle; scale bar = 100  $\mu\text{m}$ . D, *Jorunna rubescens* (CASIZ 072838), accessory spine; scale bar = 1 mm. E, *Asteronotus cespitosus* (CASIZ 072765), accessory spine; scale bar = 430  $\mu\text{m}$ . F, *Jorunna tomentosa* (CASIZ 115215), accessory spine; scale bar = 200  $\mu\text{m}$ . G, *Jorunna tomentosa* (CASIZ 115215), base of the accessory spine; scale bar = 30  $\mu\text{m}$ .

spine, about 1 mm long (Fig. 5E). The vagina is long and wide. At its proximal end, the vagina connects to the large and irregular bursa copulatrix. From the bursa copulatrix leads another long and convoluted duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about four times larger than the seminal receptacle.

In the central nervous system (Fig. 3E) the cerebral and pleural ganglia appear to be fused together and distinct from the pedal ganglia. The cerebral and pleural ganglia are entirely covered with large ganglionic tubercles. There are three cerebral nerves leading from the cerebral ganglia, and three pleural nerves lead from each pleural ganglion. There is a series of



three small abdominal ganglia on the right side of the visceral loop. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having six nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop along most of their length.

The circulatory system (Fig. 3A) includes a large heart and two blood glands placed in front and behind the central nervous system.

#### Remarks

Ehrenberg (1831) introduced *Asteronotus hemprichii* Ehrenberg, 1831 unaware of van Hasselt's (1824) description of *Doris cespitosa* van Hasselt, 1824. The synonymy between these names was first recognized by Kay & Young (1969). More recently, Thompson (1975) added to the list of synonyms of *Asteronotus cespitosus* the names *Doris mauritiana* Quoy & Gaimard, 1832, *Doris exanthemata* Kelaart, 1858, *Doris foetida* Pease, 1860, *Doris mabilla* Abraham, 1877, *Asteronotus bertrana* Bergh, 1878, *Doris crescentica* Collingwood, 1881, *Asteronotus fuscus* O'Donoghue, 1924, *Asteronotus brassica* Allan, 1932 and *Asteronotus madrasensis* O'Donoghue, 1932. The large variability in colour and widespread distribution of this species probably account for the abundance of synonyms.

#### GENUS ATAGEMA J.E. GRAY, 1850

*Atagema* J.E. Gray in M.E. Gray, 1842–50 [1850]: 104.

Type species *Doris carinata* Quoy & Gaimard, 1832 [= *Atagema carinata* (Quoy & Gaimard, 1832)], by monotypy.

*Trippa* Bergh, 1877a: 63. Type species *Trippa ornata* Bergh, 1877 [= *Atagema ornata* (Ehrenberg, 1831)], by monotypy. **Syn. nov.**

*Phlegmodoris* Bergh, 1878: 593. Type species *Phlegmodoris mephitica* Bergh, 1878 [= *Atagema spongiosa* (Kelaart, 1858)], here designated.

*Petelodoris* Bergh, 1881a: 227–228. Type species *Petelodoris triphylla* Bergh, 1881 [?= *Atagema ornata* (Ehrenberg, 1831)], by monotypy. **Syn. nov.**

*Glossodoridiformia* O'Donoghue, 1927: 87–89. Type species *Glossodoridiformia alba* O'Donoghue, 1927 [= *Atagema alba* O'Donoghue, 1927], by original designation.

#### Diagnosis

Body flexible. Dorsum with large tubercles and ridges, covered with caryophyllidia. Caryophyllidia with large lateral ciliated areas. Rhinophoral sheaths well elevated. Anterior border of the branchial sheath composed of three lobes. Gill arranged horizontally.

Prostate tubular, with a single portion. Penis and vagina unarmed. Ampulla with a long oviduct. Retractor muscles of the oral tube with glands attached to them. Labial cuticle smooth. All radular teeth hamate and smooth. Blood gland single.

#### Remarks

The original description of the genus *Atagema* J.E. Gray, 1850 (see M.E. Gray, 1842–50) includes a very short text: "Gills very small, at the end of a dorsal sac", and a reference to Quoy & Gaimard's (1832–33) description of *Doris carinata* Quoy & Gaimard, 1832, which is the type species by monotypy. We have re-examined the remaining syntype of *Atagema carinata*, which has a dorsal ridge, caryophyllidia with lateral ciliated areas, and three lobes protecting the gill. The labial cuticle is smooth, the radula has very few hamate, smooth teeth in the half-row and there are no rachidian teeth. Unfortunately the specimen is poorly preserved and partially dissected, so we could not obtain further anatomical information.

The genus *Trippa* was introduced by Bergh (1877a) based on *Trippa ornata* Bergh, 1877. According to the original description, the main diagnostic features of this genus are a body flattened, dorsum covered with hairy tubercles, labial cuticle smooth, absence of rachidian radular teeth, hamate lateral teeth and penis unarmed. We have examined specimens of *Trippa ornata* Bergh (see below), which share with *Atagema carinata* the presence of caryophyllidia with lateral ciliated areas, a dorsal ridge and three lobes protecting the gill.

One year later, Bergh (1878) introduced the genus *Phlegmodoris* based on *Phlegmodoris mephitica* Bergh, 1878, *Doris areolata* Alder & Hancock, 1864 and *Doris spongiosa* Kelaart, 1858. The distinctive features of this genus are the presence of minute dorsal tubercles situated over other larger tubercles, absence of jaws, radula lacking rachidian teeth, presence of simple, hook-shaped radular teeth, and penis unarmed. Bergh (1891) compared the original descriptions of *Phlegmodoris* and *Trippa* and recognized that these names are synonyms. Miller (1989) regarded *Phlegmodoris* as a synonym of *Trippa*. In the present study, we examined specimens of *Phlegmodoris mephitica* (selected here as the type species of *Phlegmodoris*). The external morphology and anatomy of this species are very similar to those of *Atagema*, and there are no differences to support the maintenance of *Phlegmodoris* as a separate genus.

Bergh (1881a) introduced the genus *Petelodoris* based on *Petelodoris triphylla* Bergh, 1881. According to Bergh (1881a), this genus is characterized by the presence of three valves protecting the gill. Other anatomical features included in the original description are the absence of jaws and rachidian teeth,

radula with simple, hamate teeth and penis unarmed. According to Bergh (1881a), *Petelodoris triphylla* is externally covered with minute tubercles, including the rhinophoral sheaths, and the latter are very elevated. Pruvot-Fol (1954) and Thompson & Brown (1974) regarded *Petelodoris* as a synonym of *Atagema*. As mentioned previously, *A. carinata*, *A. ornata* and *A. spongiosa* also have three valves protecting the gill opening, and the rhinophoral sheaths are highly elevated and covered with minute tubercles. Actually, the description of *Petelodoris triphylla* strongly resembles *A. ornata*, which has also been reported from Japan (Baba, 1949). All evidence indicates that *Petelodoris* is a synonym of *Atagema*. Unfortunately, the type material of *P. triphylla* is lost, so it is impossible to confirm whether this species is a synonym of *A. ornata*. In contrast, the genus *Sclerodoris* is clearly distinguishable from *Petelodoris*. The gill sheath is rounded, lacking valves, and the internal anatomy shows remarkable differences (see below).

O'Donoghue (1927) introduced the genus *Glossodoridiformia* based on *Glossodoridiformia alba* O'Donoghue, 1927, from California. McDonald (1983) re-examined the original description of this species and regarded *Glossodoridiformia* as a synonym of *Atagema*. Years later, Bertsch & Gosliner (1986) redescribed *Atagema alba* and confirmed its placement in the genus *Atagema*. The reproductive system and radular morphology of this species, described by Bertsch & Gosliner (1986), are characteristic of *Atagema*.

Eliot (1906a) described the presence of ptyaline glands, besides the salivary glands, in the genus *Trippa*. We have observed, in all the species examined, that the retractor muscles attached to the oral tube have glands on their proximal portion (Fig. 7A–C). It is very probable that these glands attached to the muscles were interpreted by Eliot (1906a) as ptyaline glands.

*ATAGEMA ORNATA* (EHRENBERG, 1831)

(Figs 1B, 6, 7A,D, 8)

*Doris ornata* Ehrenberg, 1831: 27–28.

*Doris intecta* Kelaart, 1858: 107.

*Trippa ornata* Bergh, 1877: 543–546, pl. 58, figs 3–8.

? *Petelodoris triphylla* Bergh, 1881a: 228–230, pl. 7, figs 4–15, **syn. nov.**

*Type material*

*Doris ornata* Ehrenberg: the type material of this species is lost (M. Glaubrecht, pers. comm.), it was collected from 'Tor' (=El Tûr), Egypt. *Doris intecta* Kelaart: the type material of this species appears to be lost; it is not clear whether Eliot (1906a) examined the syntypes of this species collected from Trincomalee,

Sri Lanka. *Trippa ornata* Bergh: *holotype* (by monotypy) – Masinloc, Philippines (the locality and the collection date are not indicated in the original label), 33 mm preserved length (ZMCU GAS-2114). *Petelodoris triphylla* Bergh: the type material is lost, it is not deposited at ZMUC (Jensen, pers. comm.); the type locality is Eno-Shima, Sagami Bay, Japan.

*Additional material*

Sepok Point Reef, south-west side of Maricaban Island, Luzon Island, Philippines, 26 February 1992, 1 specimen 37 mm preserved length, leg. T.M. Gosliner (CASIZ 086027). Twin Rocks, south-west side of Calumpuan Peninsula, Luzon Island, Philippines, 27 March 1993, 1 specimen 15 mm preserved length, leg. T.M. Gosliner (CASIZ 083791).

*External morphology*

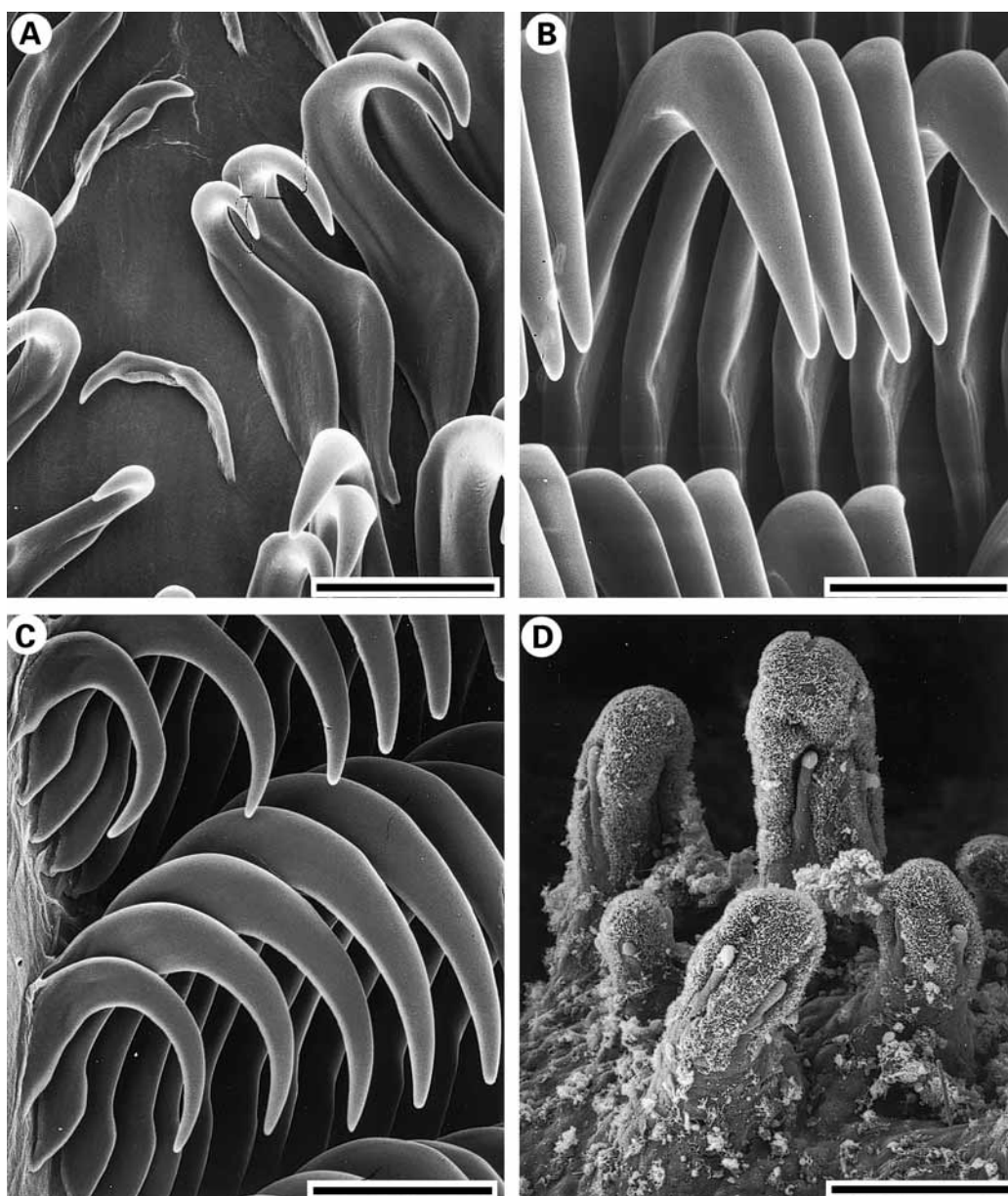
The maximum length is over 60 mm. The body is flattened, wide with a spongy yet flexible texture. The dorsum has large, irregular tubercles (Fig. 1B). The tubercles in the centre of the dorsum are lined up and fused together forming a longitudinal ridge. Each tubercle is covered with a number of small caryophyllidia, about 50 µm long (Fig. 6D). They have a long, cylindrical base, long spicules and a large, rounded ciliated tubercle. There is a large, lateral ciliated area between every two spicules. The rhinophoral sheaths are elongate, covered with caryophyllidia. The branchial sheath is composed of three large lobes (Fig. 7D). There are five tripinnate branchial leaves, arranged horizontally. The elongated anal papilla is closing the circle of branchial leaves posteriorly. The rhinophores are long, having 19 lamellae in a 37 mm preserved length specimen.

The colour of the living animals is variable from red to dark brown or black. The central ridge and the edges of the rhinophoral sheaths are white. There is also white pigment irregularly scattered over the rest of the dorsum, rhinophores and gill. The rhinophores and branchial leaves are the same colour as the rest of the body.

Ventrally the anterior border of the mantle is notched and grooved (Fig. 8G). The oral tentacles are conical. The mantle margin is wider than the foot. The ventral colour is the same as the dorsum.

*Anatomy*

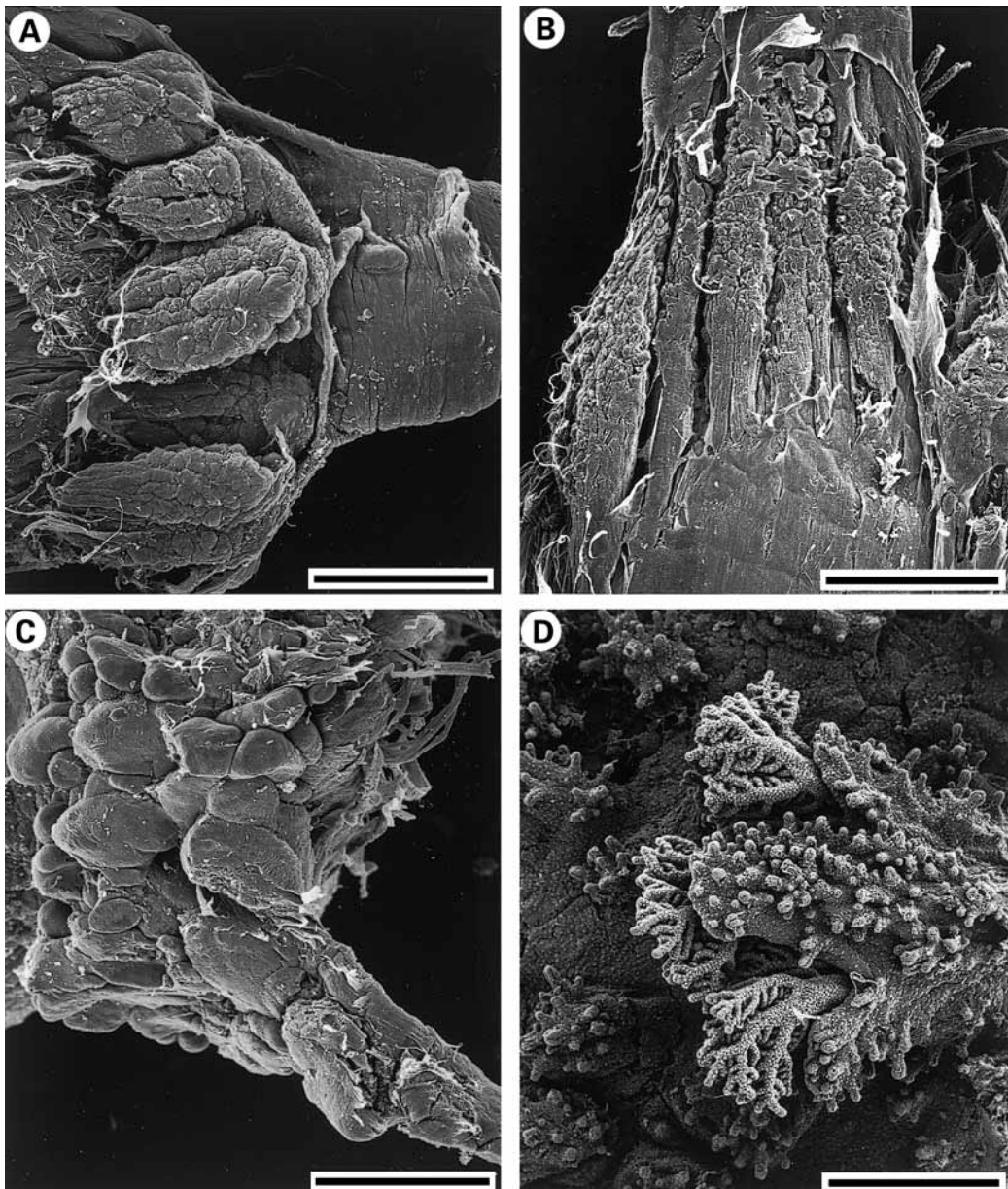
The posterior end of the oral tube has six strong retractor muscles (Fig. 8E) which attach to the body wall. They have glands attached to their distal end (Fig. 7A). The oval, muscular buccal bulb has two additional muscles attached. Two long and thin salivary glands connect to the buccal bulb at the sides



**Figure 6.** *Atagema ornata* (CASIZ 083791), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar=60  $\mu\text{m}$ . B, teeth from the central portion of the half-row; scale bar=60  $\mu\text{m}$ . C, outer lateral teeth; scale bar=60  $\mu\text{m}$ . D, caryophyllidia; scale bar=100  $\mu\text{m}$ .

of the oesophageal junction. The buccal bulb is approximately as long as the oral tube. The labial cuticle is smooth. The radular formula is  $23 \times (34.0.34)$  in a 37 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 6A–C). The teeth increase their size gradually towards the medial portion of the half-row. The outermost teeth are elongate and also lack denticles (Fig. 6C). The oesophagus is long and expands directly into the stomach (Fig. 8A).

The ampulla is very large and convoluted. It branches into a long oviduct and the prostate (Fig. 8D). The oviduct enters the female glands near their opening. The prostate is tubular, long and granular (Fig. 8B). It connects to a long and wide deferent duct. The muscular deferent duct opens into a common, long atrium with the vagina. The penis is unarmed. The vagina is short and wide. It connects to the large and almost rounded bursa copulatrix at its proximal end. From the bursa copulatrix lead the seminal receptacle and another duct connecting to the uterine duct. The



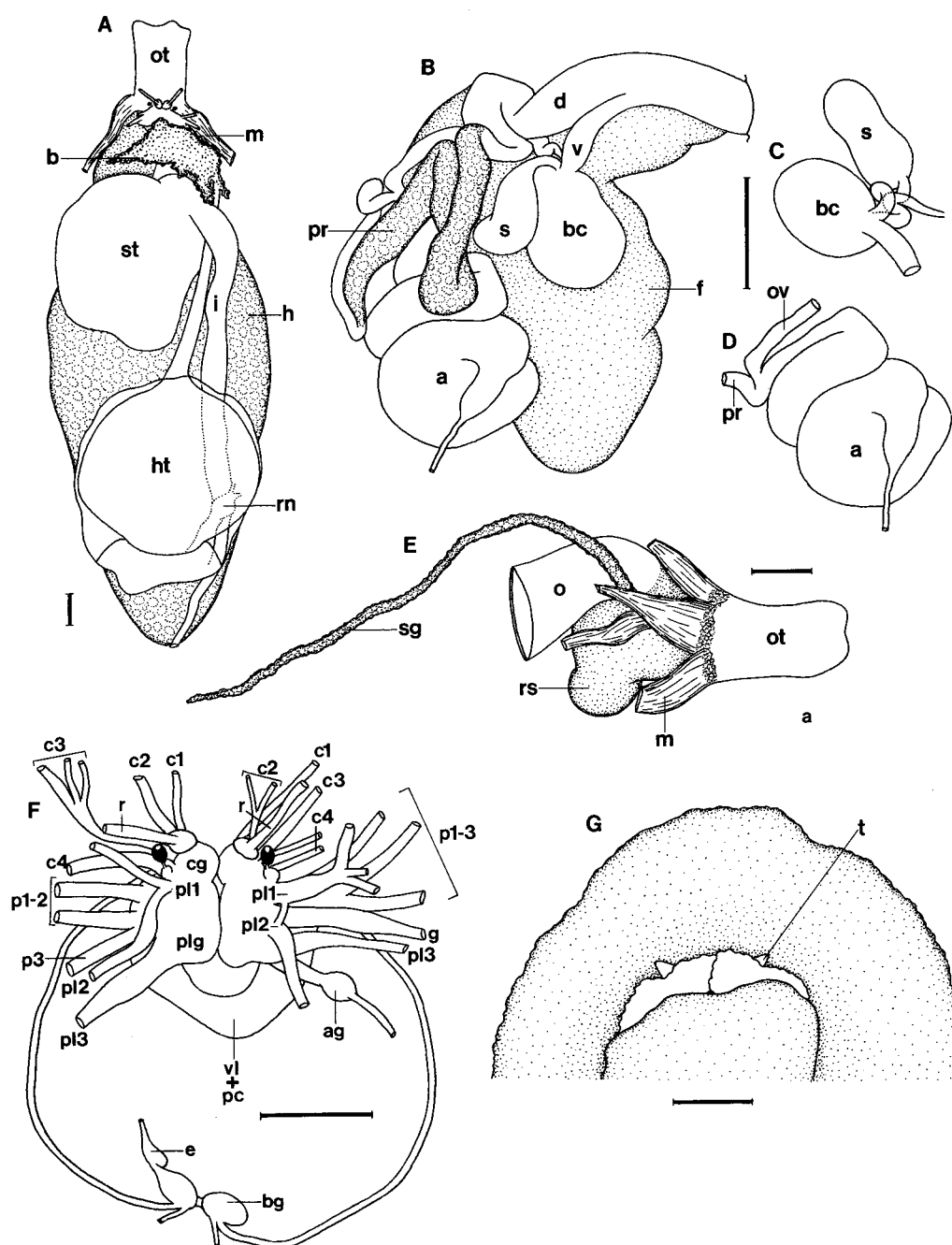
**Figure 7.** SEM photographs of retractor muscles and gill sheath. A, retractor muscles of *Atagema ornata* (CASIZ 083791), scale bar = 430  $\mu\text{m}$ . B, retractor muscles of *Atagema spongiosa* (CASIZ 073386), scale bar = 600  $\mu\text{m}$ . C, retractor muscles of *Atagema boucheti* sp. nov. (MNHN), scale bar = 200  $\mu\text{m}$ . D, gill sheath of *Atagema ornata* (CASIZ 083791), scale bar = 1 mm.

bursa copulatrix is about twice as large as the seminal receptacle (Fig. 8C).

In the central nervous system (Fig. 8F) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from the cerebral ganglia and three pleural nerves leading from each pleural ganglion. There is a distinct, stalked abdominal ganglion on the right side of the visceral loop. The buccal ganglia lie near the rest

of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 8A) includes a large heart and a single blood gland situated in behind the central nervous system.



**Figure 8.** *Atagemma ornata* (CASIZ 083791). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, bursa copulatrix and seminal receptacle connection; scale bar = 1 mm. D, ampulla connections; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, central nervous system; scale bar = 1 mm. G, ventral view of the mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; ov, oviduct; p, pedal nerves; pc, pedal commissure; pcc, parapodal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; r, rhinophoral nerves; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.



*Remarks*

Ehrenberg (1831) described *Doris ornata* Ehrenberg, 1831 as a large, black species with large dorsal tubercles covered with white granules. The rhinophores are brown, and there are 6–7 branchial leaves. Kelaart's (1856) description of *Doris intecta* Kelaart, 1856 mentions that this species is dark brown, nearly black, with a medial white pasty line, brown rhinophores and six golden-brown branchial leaves.

Bergh (1877) described *Trippa ornata* Bergh, 1877 based on a single reddish-brown specimen with a yellowish median longitudinal band. In a subsequent paper, Bergh (1877b) included the species *Doris ornata* Ehrenberg, 1831 in the genus *Trippa* and consequently *Trippa ornata* Bergh, 1877 became a junior secondary homonym of *Doris ornata* Ehrenberg, 1831.

Eliot (1906a) described the original figure of *D. intecta* by Kelaart as representing a reddish-brown specimen with a white line extending from the rhinophores to the gill. He considered *T. ornata* Bergh a probable synonym of *D. intecta* and noted that the only difference between them is the longer oral tentacles of *T. intecta* Bergh. Ev. Marcus & Er. Marcus (1970) also regarded *T. intecta* as a synonym of *T. ornata* Bergh. In our opinion, *D. ornata* Ehrenberg, *D. intecta* and *T. ornata* Bergh are synonyms, with *D. ornata* Ehrenberg being the valid name for this species. In addition, the external and internal features of this species agree with those of *Atagema* (see diagnosis and remarks on the genus) and therefore it is here transferred to that genus.

*Petelodoris triphylla* Bergh, 1881 was described, based on a preserved specimen, as being whitish with brownish dorsal tubercles. This species is also characterized as having large dorsal tubercles with small caryophyllidia over them (Bergh, 1881a: pl. 7, figs 6, 7). The drawings of the radula (Bergh, 1881a: pl. 7, figs 8–14) illustrate the radular teeth that are very similar to those of *A. ornata*, and it is very probable that *P. triphylla* is a synonym of *A. ornata*. Unfortunately, the type material of *P. triphylla* is lost, so this synonymy cannot be confirmed.

*ATAGEMA CARINATA* (QUOY & GAIMARD, 1832)

(Fig. 9)

*Doris carinata* Quoy & Gaimard, 1832: 254, pl. 16, figs 10–14.

*Type material*

*Syntype*: 'Rivière Tamise' (=Thames), New Zealand, date unknown, 1 specimen 9 mm preserved length (MNHN).

*External morphology*

The maximum length is over 40 mm (Willan & Coleman, 1984). The body is flattened, wide with a spongy yet flexible texture. The dorsum has a medial ridge and it is covered with a number of small caryophyllidia, about 50 µm long (Fig. 9C). They have a short, cylindrical base and a large, rounded ciliated tubercle. The spicules of the syntype were dissolved during preservation. Between each spicule there is a large ciliated area. The rhinophoral sheaths are elongate, covered with caryophyllidia. The branchial sheath is composed of three lobes. There are six tripinnate branchial leaves (Willan & Coleman, 1984), arranged horizontally. The elongated anal papilla is closing the circle of branchial leaves.

The colour of the living animals is uniformly white. The rhinophores are pale orange and the branchial leaves are yellowish orange (see Willan & Coleman, 1984).

Ventrally the anterior border of the mantle is notched and grooved. The oral tentacles are triangular. The mantle margin is wider than the foot. The ventral colour is the same as the dorsum.

*Anatomy*

Pruvot-Fol (1934b) dissected the single syntype deposited at MNHN. This specimen is badly preserved and only a part of the radula was suitable for study. The radular formula is  $n \times (17.0.17)$  in the 9 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 9A–C). The teeth increase their size suddenly towards the medial portion of the half-row. The outermost teeth are elongate and also lack denticles (Fig. 9C).

The anatomy of the reproductive, circulatory and nervous systems has not yet been studied.

*Remarks*

Pruvot-Fol (1934b) re-examined the type material of this species and concluded that it should be placed in the genus *Austrodoris* Odhner, 1926. Since then, Ev. Marcus & Er. Marcus (1970) recognized the validity of the genus *Atagema* and regarded *A. carinata* as a valid species.

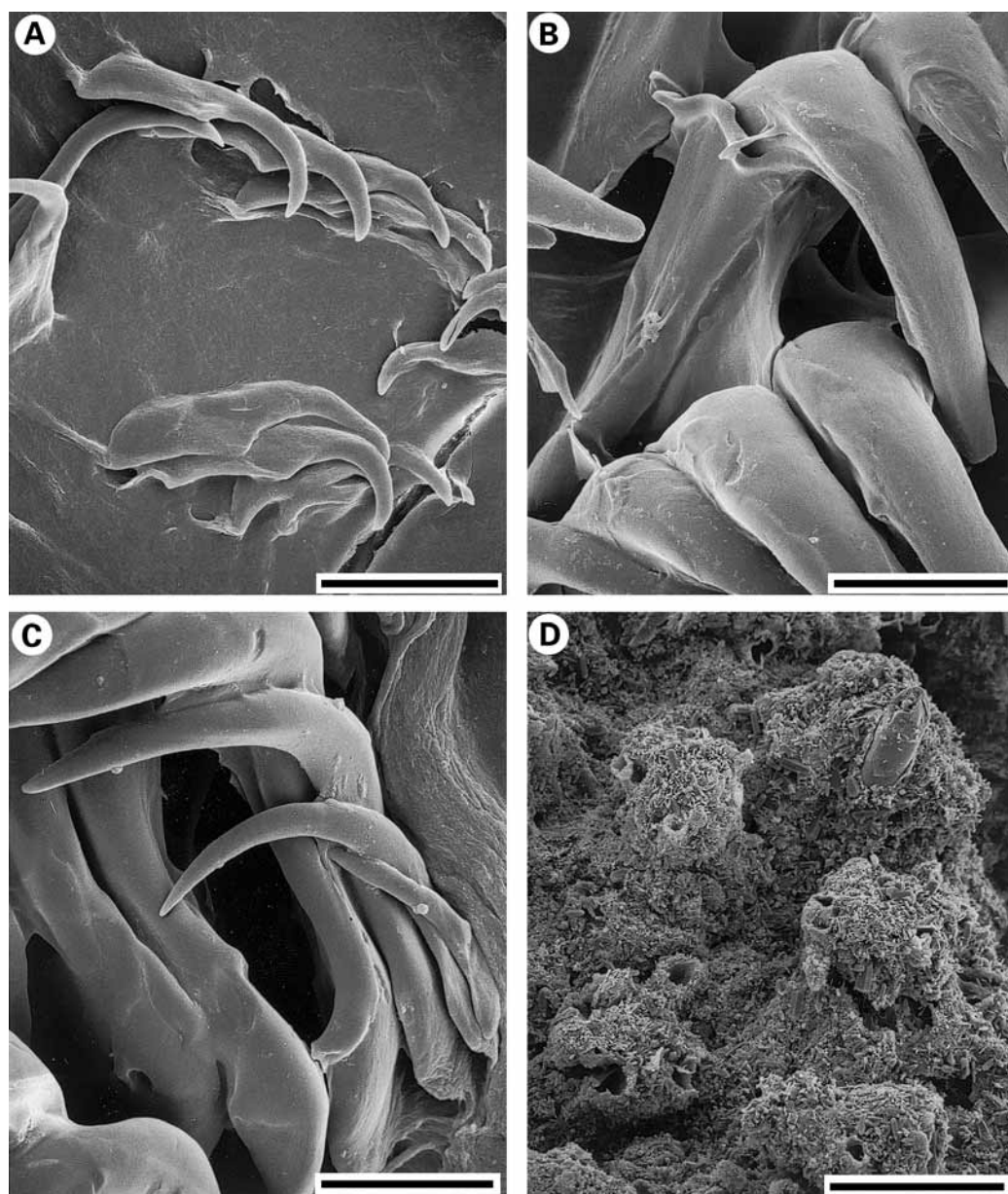
Willan & Coleman (1984) illustrated for the first time a living specimen of *A. carinata*, whose features are identical to the syntype, and undoubtedly the specimens belong to the same species.

*ATAGEMA SPONGIOSA* (KELAART, 1858)

(Figs 7B, 10, 11)

*Doris spongiosa* Kelaart, 1858: 97–98.

*Doris areolata* Alder & Hancock, 1864: 119, pl. 30, figs 1–3 (non *Doris areolata* Stuwitz, 1835).



**Figure 9.** *Atagema carinata* (MNHN), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 43 µm. B, teeth from the central portion of the half-row; scale bar = 60 µm. C, outer lateral teeth; scale bar = 43 µm. D, caryophyllidia; scale bar = 100 µm.

*Phlegmodoris mephitica* Bergh, 1878: 594–597, pl. 66, figs 8–20.

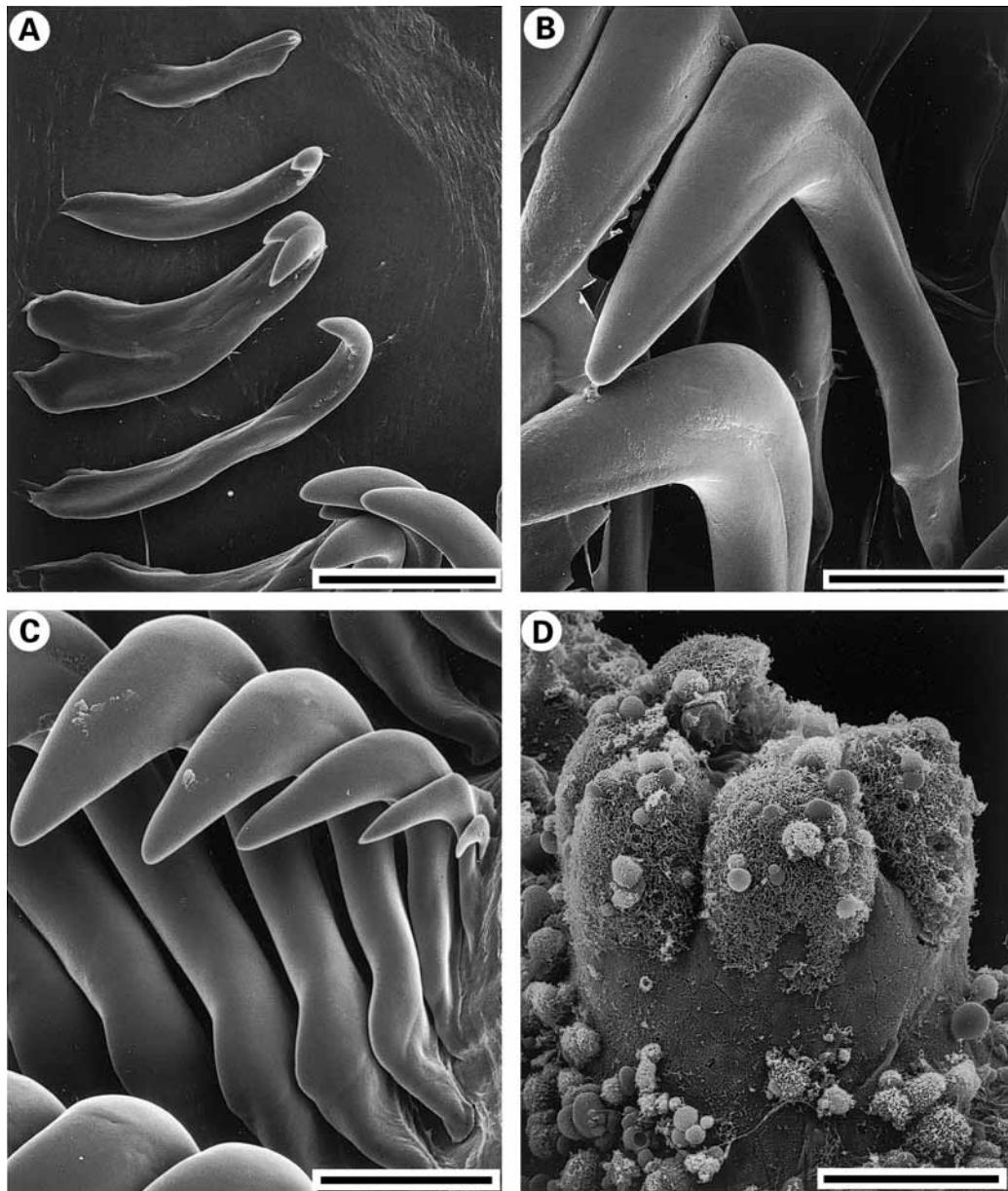
*Type material*

*Doris spongiosa* Kelaart: no type material is known to exist, the type locality is Trincomalee, Sri Lanka. *Doris areolata* Alder & Hancock: Eliot (1906a) supposedly re-examined the syntypes of this species, collected from Waltair (India), and deposited at the Hancock Museum (Newcastle-on-Tyne), but this point was not clearly

confirmed in that paper. *Phlegmodoris mephitica* Bergh: *syntypes* – Laping Channel and Ubay, Philippines, March 1865, 2 specimens 63–82 mm preserved length, leg. Semper (ZMUC GAS-2113).

*Additional material*

Nosy Komba, Madagascar, November 1992, 1 specimen 79 mm preserved length, leg. T.M. Gosliner (CASIZ 086983). Christiansen Research Institute, Madang, Papua New Guinea, 10 October 1986, 2 specimens



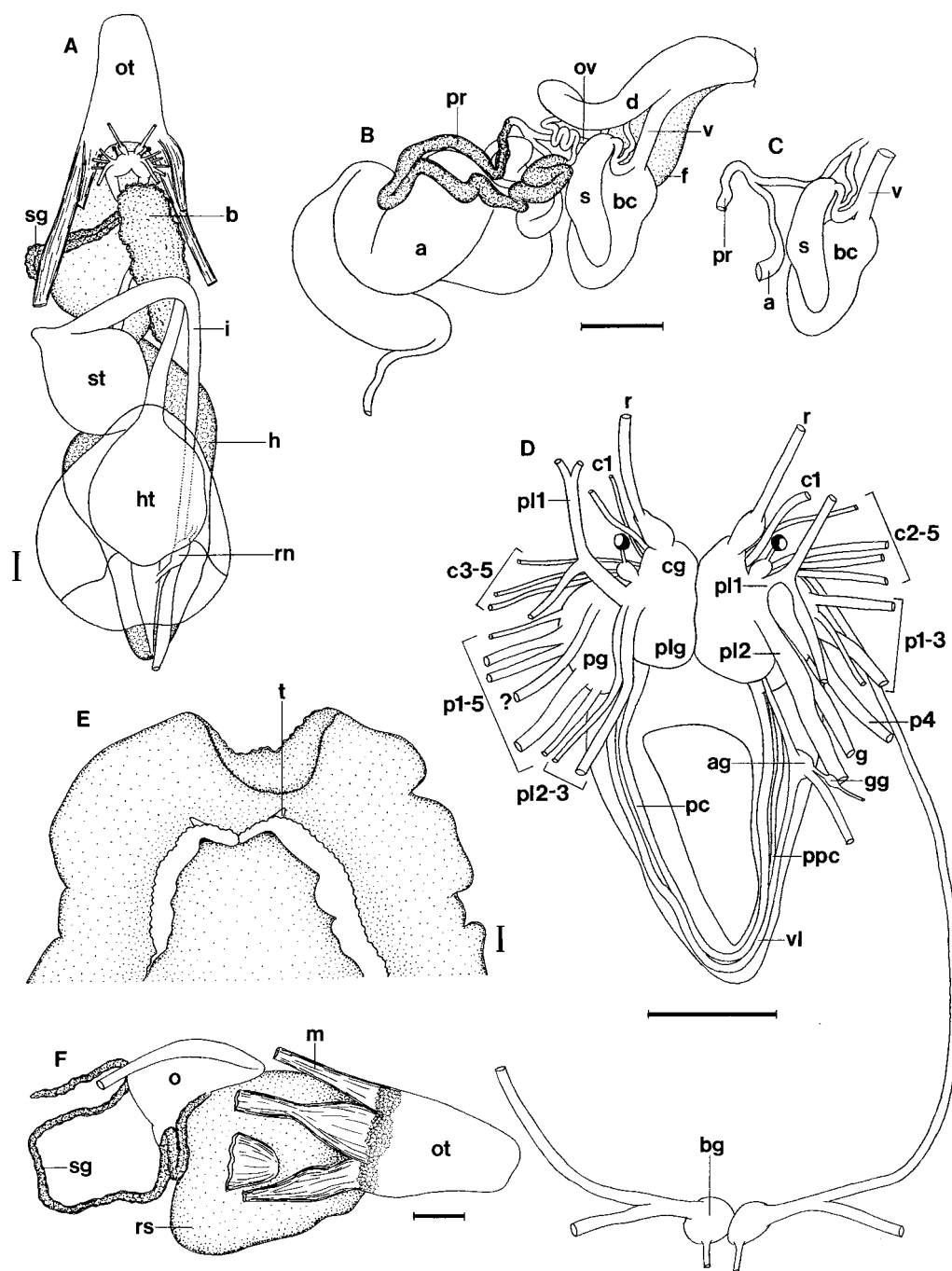
**Figure 10.** *Atagema spongiosa* (CASIZ 073386), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 75  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 100  $\mu$ m. C, outer lateral teeth; scale bar = 75  $\mu$ m. D, caryophyllidium; scale bar = 43  $\mu$ m.

20–32 mm preserved length, leg. T.M. Gosliner (CASIZ 073386).

*External morphology*

The maximum length is over 130 mm. The body is flattened, wide with a spongy yet flexible texture. The dorsum has a number of irregular tubercles of different sizes. The tubercles in the centre of the dorsum are large and appear to be aligned. The tubercles are fused together forming irregular clusters or short ridges. There are several dorsal depressions, or areas that are

not covered with tubercles. The depressions are more numerous near the mantle margin, but larger in the centre of the dorsum. Each tubercle is covered with a number of small caryophyllidia, about 50  $\mu$ m long (Fig. 10D). They have a short, cylindrical base, long spicules and a large, rounded ciliated tubercle. Between each spicule there is a large ciliated area. The rhizophoral sheaths are elongate, covered with caryophyllidia. The branchial sheath is composed of three large lobes. There are five tripinnate branchial leaves, arranged horizontally. The elongated anal papilla is closing the



**Figure 11.** *Atagema spongiosa* (CASIZ 073386). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, detail of several reproductive organs; scale bar=1 mm. D, central nervous system; scale bar=1 mm. E, ventral view of the mouth area; scale bar=0.5 mm. F, lateral view of the buccal bulb; scale bar=1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; gg, genital ganglion; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; ov, oviduct; p, pedal nerves; pc, pedal commissure; pcc, parapedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; r, rhinophoral nerves; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

circle or branchial leaves. The rhinophores are long, having 28 lamellae in a 79 mm preserved length specimen.

The colour of the living animals varies from cream to brown. The depressions are dark brown with some sky-blue pigment in the centre. The rhinophores and branchial leaves are pale brown.

Ventrally the anterior border of the mantle is notched and grooved (Fig. 11E). The oral tentacles are triangular. The mantle margin is wider than the foot.

#### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 11E) which attach to the body wall. They have glands attached to their distal end (Fig. 7B). The oval, muscular buccal bulb has two additional muscles attached. Two long and thin salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is twice as long as the oral tube. The labial cuticle is smooth. The radular formula is  $21 \times (32.0.32)$  in a 32 mm preserved length specimen. Rachidian teeth are absent. All lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 10A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 10A,B). The outermost teeth are smaller and also lack denticles (Fig. 10C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 11A).

The ampulla is very large and convoluted. It branches into a long oviduct and the prostate (Fig. 11C). The oviduct connects to the uterine duct and enters the female glands near the nidamental opening. The prostate is tubular, long and granular (Fig. 11B). It connects to a long and wide deferent duct, which opens into a common, long atrium with the vagina. The penis is unarmed. The vagina is short and wide. At its proximal end, it connects to the large and almost spherical bursa copulatrix. From the vagina leads another duct connecting to the seminal receptacle and the uterine duct. The bursa copulatrix is about twice as large as the seminal receptacle (Fig. 11C).

In the central nervous system (Fig. 11D) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are five cerebral nerves leading from the cerebral ganglia, and two (right side) and three (left side) pleural nerves lead from each pleural ganglion. There is a distinct abdominal ganglion on the right side of the visceral loop, which connects to a small genital ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves

leading from each one. The pedal and parapedal commissures and the visceral loop are not enveloped together.

The circulatory system (Fig. 11A) includes a large heart and a single blood gland placed behind the central nervous system.

#### Remarks

Kelaart (1858) described *Doris spongiosa* Kelaart, 1858 from India as being dull yellow-brown and deeply pitted. He described the dorsum of this species as being like the surface of some species of sponge. Eliot (1906a: pl. 44, fig. 2) reproduced the original drawing by Kelaart and regarded *Phlegmodoris mephitica* as a synonym of *D. spongiosa*, which, in his opinion, belonged to the genus *Trippa*.

Alder & Hancock (1864) described and illustrated *Doris areolata* Alder & Hancock, 1864 (non *Doris areolata* Stuwitz, 1835), but at the same time recognized that in several respects this species resembles *D. spongiosa*. André (1896) suggested for the first time that *D. areolata* could be a synonym of *D. spongiosa*. Eliot (1906a) considered that synonymy probable, but in the absence of additional specimens he was unable to confirm it. From Eliot's (1906a) paper it is not clear whether the type material of both *D. spongiosa* and *D. areolata* is lost or only the types of one of them. However, the original description of both species and the redescription of *D. spongiosa* by Eliot (1906a) are adequate to recognize the external features of *D. areolata* and *D. spongiosa*, which in our opinion are synonyms. Both were described as large, gelatinous species, yellowish to brownish in colour, with deep depressions in the dorsum and five branchial leaves.

Bergh (1878) described *Phlegmodoris mephitica* Bergh, 1878 based on preserved specimens collected from the Philippines. We have examined the two syntypes of this species. The external morphology and the radula are identical to those of our material of *Atagama spongiosa*. The radula of one of the syntypes (63–82 mm preserved length) has a formula  $21 \times (44.0.44)$ , being  $21 \times (32.0.32)$  in a 32 mm preserved length specimen of *A. spongiosa*. In both cases the innermost lateral teeth are slender with very short cusps and the outermost lateral teeth are hamate. It is clear that *D. spongiosa* and *P. mephitica* are synonyms.

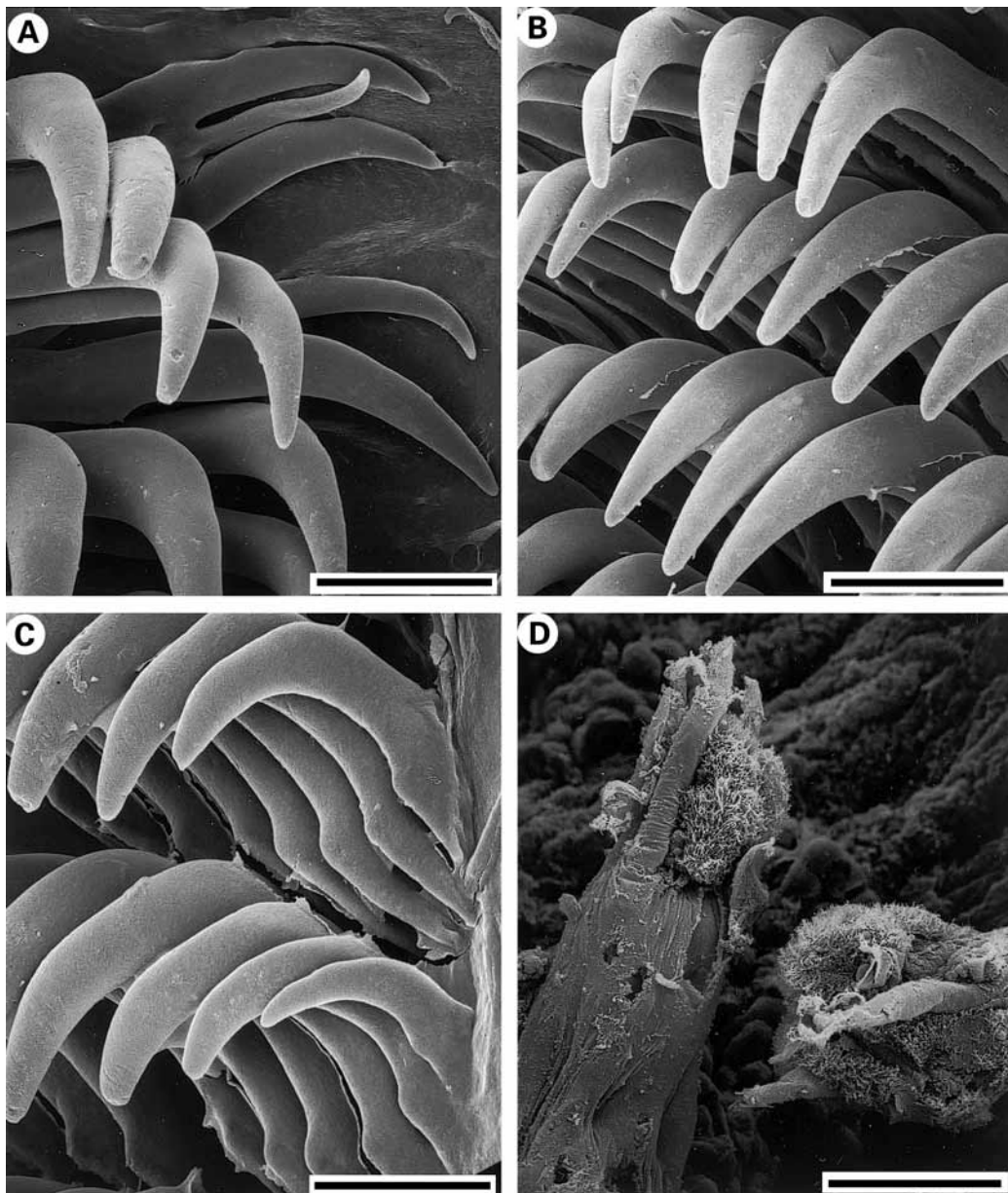
#### ATAGEMA BOUCHETI SP. NOV.

(Figs 2B, 7C, 12, 13)

#### Type material

Bathus 3 Expedition, stn CP 847 (23°03'S, 166°58'E), Ride de Norfolk, New Caledonia, 405–411 m depth, 1 December 1993, 1 specimen 14 mm preserved length, dissected, leg. P. Bouchet (MNHN).





**Figure 12.** *Atagema boucheti* sp. nov. (MNHN), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 43  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 60  $\mu$ m. C, outer lateral teeth; scale bar = 43  $\mu$ m. D, caryophyllidia; scale bar = 60  $\mu$ m.

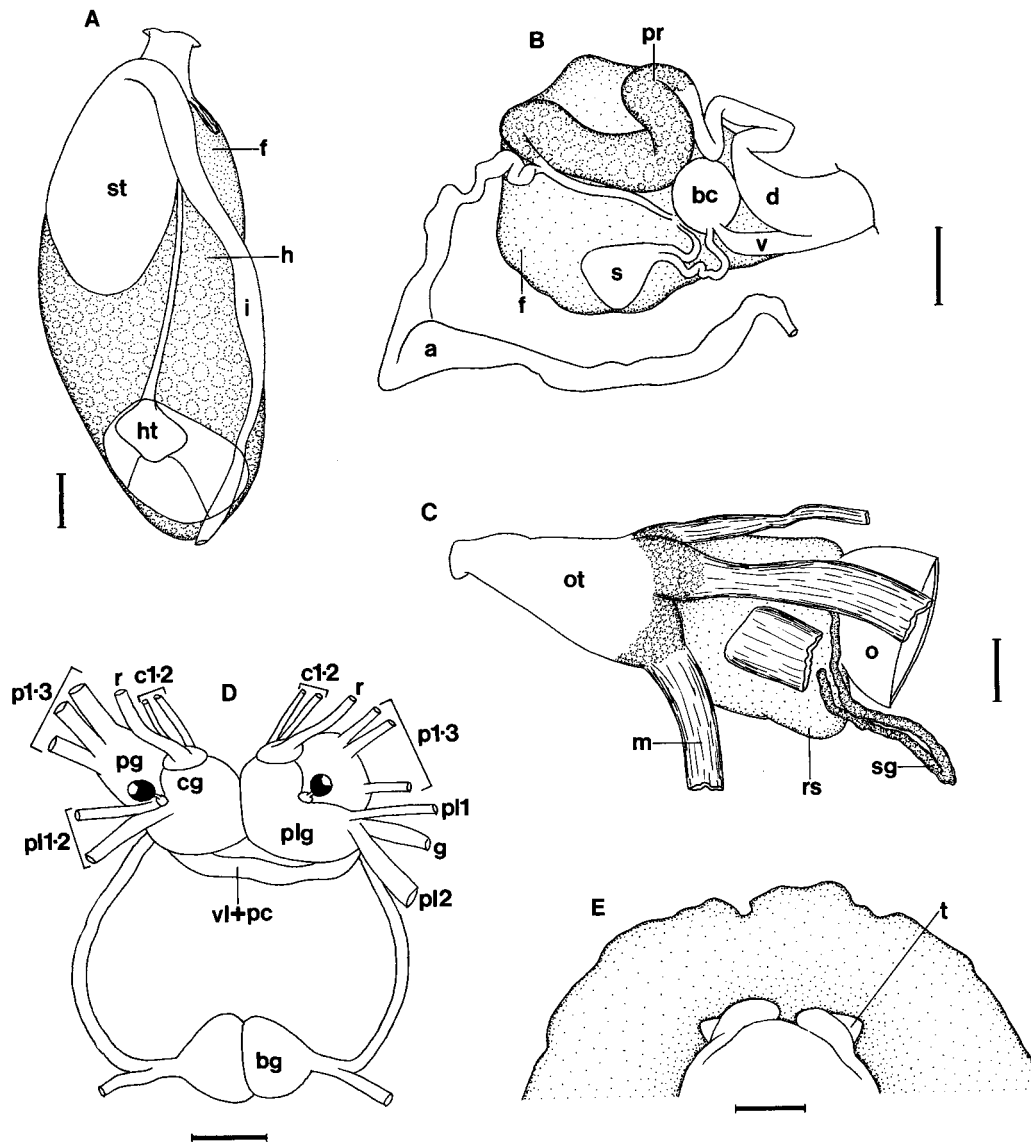
#### *External morphology*

The maximum length is 14 mm. The body is convex, somewhat flattened, wide with a flexible texture. The dorsum has a number of large, irregularly scattered tubercles (Fig. 2B). Each tubercle is covered with a number of long caryophyllidia, about 150  $\mu$ m long (Fig. 12D). They have a very long, cylindrical base, long spicules and a large, rounded ciliated tubercle. Between each two spicules there is a large ciliated area. The rhinophoral sheaths are very elongated, covered with caryophyllidia. The branchial sheath is composed

of three large lobes. There are four bipinnate branchial leaves, arranged horizontally. The elongated anal papilla is closing the circle of branchial leaves posteriorly. The rhinophores are long, with 15 lamellae in a 14 mm preserved length specimen.

The single specimen was preserved and information on the coloration of the living animal is not available. The preserved animal is uniformly pale cream. The rhinophores and branchial leaves are opaque white.

Ventrally the anterior border of the mantle is notched and grooved (Fig. 13E). The oral tentacles are conical.



**Figure 13.** *Atagema boucheti* sp. nov. (MNHN). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 0.5 mm. C, lateral view of the buccal bulb; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, ventral view of the mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; gg, genital ganglion; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; ov, oviduct; p, pedal nerves; pc, pedal commissure; pcc, parapedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; r, rhinophoral nerves; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

The mantle margin is wider than the foot. The ventral colour is the same as the dorsal.

#### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 13C) that attach to the body wall. They have glands attached to their distal end (Fig. 7C). The oval, muscular buccal bulb has two

additional muscles attached. Two long and thin salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is as long as the oral tube. The labial cuticle is smooth. The radular formula is  $16 \times (20.0.20)$  in a 14 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 12A–C). The teeth increase their size

gradually towards the medial portion of the half-row (Fig. 12A,B). The outermost teeth are smaller and also lack denticles (Fig. 12C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 13A).

The ampulla is very large and convoluted. It branches into a long oviduct and the prostate (Fig. 13B). The oviduct enters the female glands near the nidamental opening. The prostate is tubular, short and granular (Fig. 13B). It connects to a short and wide deferent duct, which opens into a common, long atrium with the vagina. The penis is unarmed. The vagina is short and wide. At its proximal end, it connects to the small and almost rounded bursa copulatrix. From the vagina leads another duct connecting to the seminal receptacle and the uterine duct. The bursa copulatrix is about as large as the seminal receptacle (Fig. 13B).

In the central nervous system (Fig. 13D) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are two cerebral nerves leading from the cerebral ganglia and two pleural nerves leading from each pleural ganglion. There is no distinct abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are present. The pedal ganglia have three nerves leading from each one. The pedal and parapedal commissures and the visceral loop are fused together.

The circulatory system (Fig. 13A) includes a large heart and a single blood gland placed behind the central nervous system.

#### *Etymology*

This species is dedicated to Philippe Bouchet who has provided a wealth of new deep-water dorids from New Caledonia deposited at MNHN.

#### *Remarks*

*Atagama boucheti* differs from other species of the genus in that the dorsum is covered with irregular tubercles and that they are not aligned to form ridges. No other species of the genus is known from deep water.

#### GENUS *JORUNNA* BERGH, 1876

*Kentrodoris* Bergh, 1876: 413. Type species *Kentrodoris rubescens* Bergh, 1876 [= *Jorunna rubescens* Bergh, 1876], by subsequent designation by Ev. Marcus (1976). **Syn. nov.**

*Jorunna* Bergh, 1876: 414. Type species *Doris johnstoni* Alder & Hancock, 1845 [= *Jorunna tomentosa* (Cuvier, 1804)], by monotypy.

*Audura* Bergh, 1878 : 567–568. Type species *Audura*

*maima* Bergh, 1878 [= *Jorunna maima* (Bergh, 1878)], by monotypy. **Syn. nov.**

*Centrodoris* P. Fischer, 1880–1887 [1883]: 522 (unjustified emendation for *Kentrodoris* Bergh, 1876).

*Awuka* Er. Marcus, 1955: 155–156. Type species *Awuka spazzola* Er. Marcus, 1955 [= *Jorunna spazzola* (Er. Marcus, 1955)], by original designation.

#### *Diagnosis*

Body flexible. Dorsum covered with elongate caryophyllidia. Rhinophoral and branchial sheaths low. Prostate massive, with two portions. Vagina unarmed. Penis occasionally with hooks. Large accessory gland with two different portions and a long spine. Labial cuticle smooth or armed with jaw rodlets. Inner and mid lateral radular teeth hamate. Outer lateral teeth smooth or multifid.

#### *Remarks*

Bergh (1876) introduced the genus *Kentrodoris* Bergh, 1876 based on three species, *Kentrodoris rubescens* Bergh, 1876, *Kentrodoris gigas* Bergh, 1876 and *Kentrodoris annuligera* Bergh, 1876, all of them characterized by the lack of jaws and rachidian teeth, a penis armed with a long spine and a large vestibular gland, which opens near the vagina.

In the same paper and in a footnote, Bergh (1876) introduced the genus *Jorunna* Bergh, 1876, based on *Doris johnstoni* Alder & Hancock, 1845, as being closely related to *Kentrodoris*. According to Bergh (1876), the main difference between both genera is that the spine of *Kentrodoris* is situated in the penis, whereas in *Jorunna* it is situated in the accessory gland. Bergh obtained the data on *Kentrodoris* from his own dissections, whereas he followed Alder & Hancock's (1845–55) descriptions of *Doris johnstoni* for *Jorunna*.

Two years later, Bergh (1878) described the genus *Audura* Bergh, 1878, based on *Audura maima* Bergh, 1878, which in his opinion is different from *Kentrodoris* because of the presence of jaws. In this case, Bergh understood that the spine of *Audura* was situated in the penis.

After the examination of one specimen of *Doris johnstoni*, Bergh (1880a) recognized that *Kentrodoris* is very similar to *Jorunna* and that both names are probably synonyms. However, in a later paper Bergh (1891) persisted in considering them as different taxa.

*Centrodoris* Fischer, 1883 is an unjustified emendation for *Kentrodoris*. Therefore it is available with its own author and date, and it is a junior objective synonym of *Kentrodoris* (see ICZN, 1999: Article 33b).

Er. Marcus (1955) described the genus *Awuka* Er. Marcus, 1955 based on *Awuka spazzola* Er. Marcus, 1955, with the same features than *Jorunna* and *Kentrodoris*. According to Er. Marcus (1955), the presence

of jaws and one denticle in the innermost radular teeth are the distinctive features of *Awuka*. Er. Marcus also found a genital spine which he considered to be situated in the penis.

Ev. Marcus (1976) reviewed the systematics of *Jorunna* and *Kentrodoris*. She found that the spine described by Bergh (1876) and Er. Marcus (1955) in the penis of *Kentrodoris* was actually situated in the large accessory gland of both *Kentrodoris* and *Jorunna*. However, Ev. Marcus (1976) concluded that *Kentrodoris* is different from *Jorunna* because of “the soft notum, the high gills, the acinous prostate, the loculated spermatocyst and the sheathed male organ” of *Kentrodoris*. She selected *K. rubescens* as the type species of the genus *Kentrodoris* and regarded the other two species originally included by Bergh (1876) in *Kentrodoris* (*K. gigas* and *K. annuligera*) as members of *Jorunna*. According to Ev. Marcus (1976), *K. annuligera* is a junior synonym of *Jorunna funebris* (Kelaart, 1859). She also regarded the genus *Awuka* as a synonym of *Jorunna*.

For the present paper, we have examined the type species of *Kentrodoris* and *Jorunna*. The phylogenetic relationships of these two genera (see below) support the idea that their remarkable morphological differences are just autapomorphies of *Kentrodoris rubescens* and therefore non-informative characters. Thus, the genera *Kentrodoris* and *Jorunna* are here regarded as synonyms. Both names were introduced at the same time in the same paper but in accordance with the principle of the first reviser, Article 24 (ICZN, 1999), we select the name *Jorunna* as having precedence over *Kentrodoris*. In general, the name *Kentrodoris* was used for Indo-Pacific species and *Jorunna* for the Atlantic ones. However, since the paper of Ev. Marcus (1976) a larger number of species were assigned to *Jorunna* than to *Kentrodoris*, which nowadays is only used for *J. rubescens*. In our opinion the selection of *Jorunna* as the valid name of the genus is less nomenclaturally disruptive.

We have also examined the holotype of *Audura maima* which unfortunately has all the internal organs removed. Only some portions of the digestive gland and intestine remain in the preserved specimen. The original description of *A. maima* (Bergh, 1878) is based on this preserved specimen, with no information about the colour of the animal and it is not possible to establish the identity of this species. However, the anatomical characteristics of *A. maima* described in the original description, such as the presence of a spine in the male opening (accessory gland), and some external features obtained from the holotype, such as the presence of elongated caryophyllidia, confirm the synonymy of *Audura* with *Jorunna*. The only other genera of cryptobranch dorid with spines associated

with the reproductive system are *Asteronotus*, *Homoiodoris* Bergh, 1880, *Hoplodoris* Bergh, 1880 and *Paradoris* Bergh, 1884, which lack caryophyllidia.

The genus *Awuka* has the same features as several other species of *Jorunna*. The presence of jaws was reported by Ev. Marcus (1976) in six other species of the genus, and a single denticle in the innermost lateral radular teeth is not considered as a genus-level distinctive feature. Following Ev. Marcus (1976) we consider *Awuka* as a synonym of *Jorunna*.

*JORUNNA TOMENTOSA* (CUVIER, 1804)  
(Figs 1C, 5F,G, 14, 15)

*Doris tomentosa* Cuvier, 1804: 470–472.

*Doris johnstoni* Alder & Hancock, 1845–55 [1845]: 42, xvi, fam. 1, pl. 2, figs 8–11, pl. 5, pl. 46, fig. 4.

*Type material*

*Doris tomentosa* Cuvier: the type material is lost, it is not deposited at MNHN (Valdés & Héros, 1998), the type locality is La Rochelle, France. *Doris johnstoni* Alder & Hancock: the type material is lost, it is not deposited at BMNH, the type locality is Berwick Bay, England.

*Additional material*

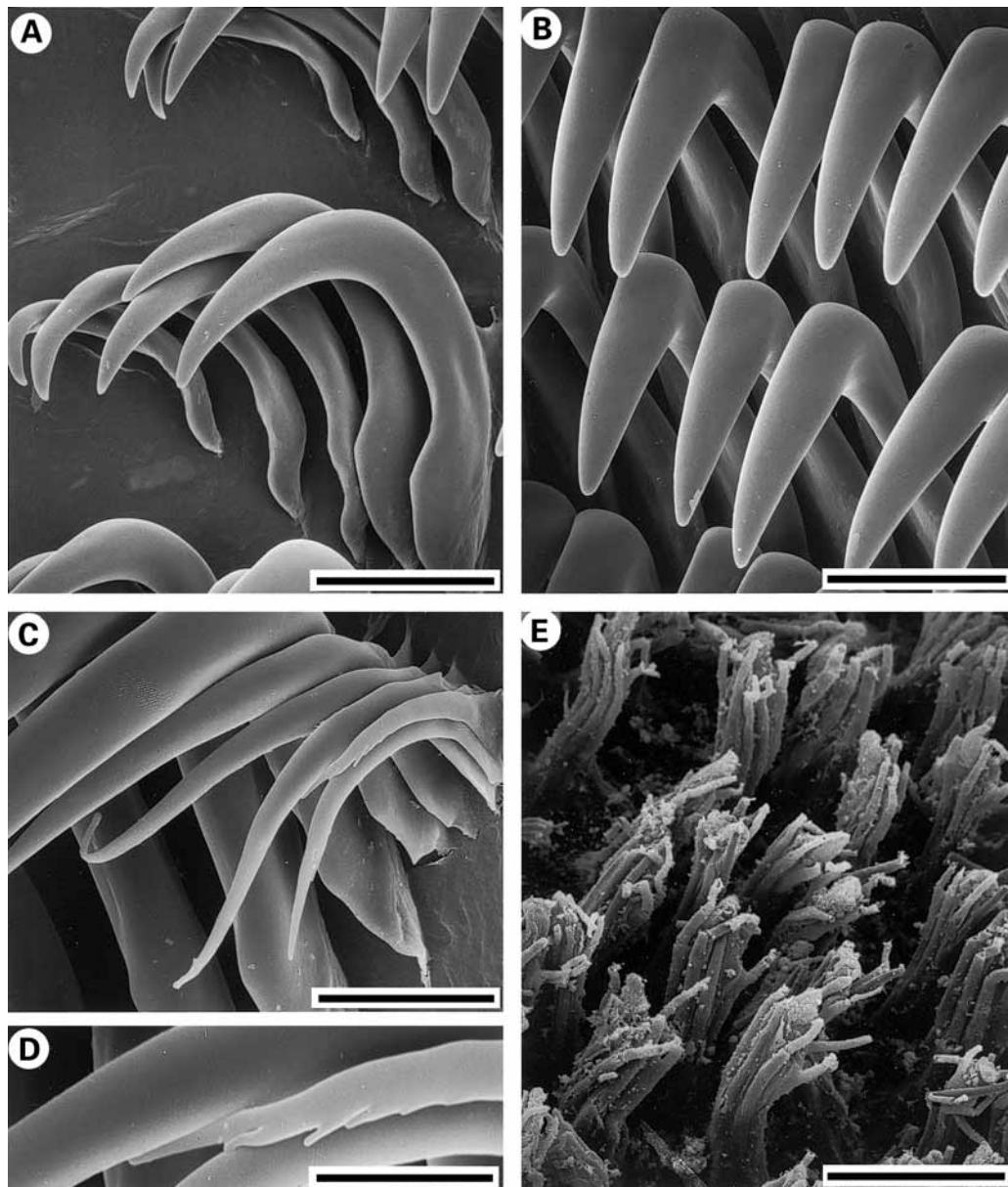
Oviñana, Asturias, Spain, August 1979, 2 specimens 30 mm long, dissected, leg. J. Ortea (CASIZ 115215).

*External morphology*

The maximum length of this species reaches 55 mm (Thompson & Brown, 1984). The body is oval and convex (Fig. 1C), soft, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 150 µm in length (Fig. 14E). They have a long, conical base, long spicules and a small, rounded ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. There are 12 short, bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongate, with 12 lamellae in a 30 mm long specimen.

The general colour of the living animals varies from pale grey to yellow or pale orange. In some specimens there are brown spots irregularly scattered over the dorsum. Some of these spots are darker than others. They are often larger in the centre of the dorsum. The gill and rhinophores normally have the same colour as the dorsum. The rhinophores may have dark brown spots near the apex.

Ventrally, the anterior border of the foot is notched and grooved (Fig. 15F). The oral tentacles are conical. The mantle margin is as wide as the foot. The ventral colour is the same as the dorsal.



**Figure 14.** *Jorunna tomentosa* (CASIZ 115215), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 60  $\mu\text{m}$ . B, teeth from the central portion of the half-row; scale bar = 60  $\mu\text{m}$ . C, outer lateral teeth; scale bar = 30  $\mu\text{m}$ . D, detail of the outermost teeth denticulation; scale bar = 10  $\mu\text{m}$ . E, caryophyllidia; scale bar = 150  $\mu\text{m}$ .

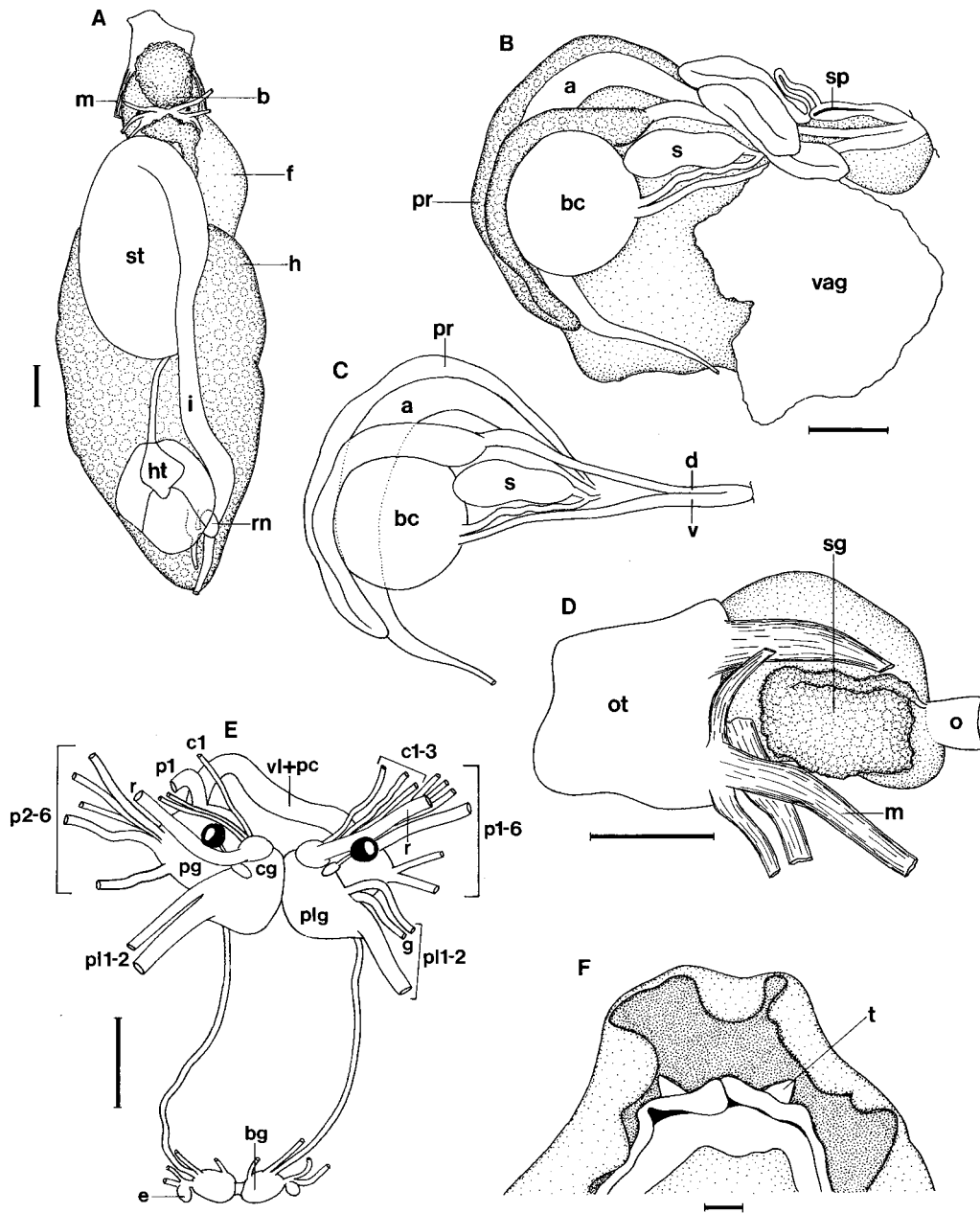
#### Anatomy

The posterior end of the oral tube has eight strong retractor muscles (Fig. 15D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two short, wide salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is as long as the oral tube. The labial cuticle is smooth. The radular formula is  $20 \times (25.0.25)$  in a 30 mm long specimen. Rachidian teeth are absent. The inner lateral teeth are hamate, having a single cusp and lacking denticles

(Fig. 14A). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 14A, B). The outer lateral teeth are smaller but very elongate (Fig. 14C). The two outermost teeth have 1–4 denticles under the cusp (Fig. 14C,D). The oesophagus is short and expands directly into the stomach (Fig. 15A).

The ampulla is very long and branches into a short oviduct and the prostate (Fig. 15C). The oviduct enters the female glands in the centre of the mass. The prostate is tubular, folded and granular (Fig. 15B). It





**Figure 15.** *Jorunna tomentosa* (CASIZ 115215). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, detail of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, central nervous system; scale bar=0.5 mm. F, ventral view of the mouth area; scale bar=1 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; plg, pleural ganglion; pg, pedal ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

connects to a long duct that narrows into the ejaculatory portion of the deferent duct. The prostate is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects

to the deferent duct, whereas the smallest portion is whitish and connects to the ampulla. The thin muscular deferent duct opens into a common atrium with the vagina. There are no penial hooks. There is a large accessory gland connected to the atrium which has a

spine, about 700 µm long (Fig. 5F,G). The accessory gland consists of a muscular portion near the atrium, with a short duct and a large glandular proximal region connected to it (Fig. 15B). The vagina is long, wider than the deferent duct. It connects to the bursa copulatrix at its proximal end. Another duct, connecting to the uterine duct and the seminal receptacle, leads from the bursa copulatrix. The bursa copulatrix is rounded in shape, about four times larger than the seminal receptacle.

In the central nervous system (Fig. 15E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion, and two pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two relatively long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have six nerves leading from each one. The visceral loop, the pedal and the parapedal commissures are enveloped together.

The circulatory system (Fig. 15A) includes a small heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Cuvier (1804) described *Doris tomentosa* Cuvier, 1804 as being a species of dorid with the mantle larger than the foot and a fleecy dorsal texture. Alder & Hancock's (1845–55) description of *Doris johnstoni* Alder & Hancock, 1845 is much more complete, including an anatomical description. *Doris johnstoni* was regarded as a synonym of *Doris tomentosa* by P. Fischer (1869) for the first time, and since then this synonymy has been generally accepted.

Ev. Marcus (1976) split *Jorunna tomentosa* into four different species, two of them, *Jorunna lemchei* Ev. Marcus, 1976 and *Jorunna luisae* Ev. Marcus, 1976, distributed throughout the European coasts.

Thompson & Brown (1984) included *Jorunna lemchei* and, with a question mark, *Jorunna luisae*, in the synonymy of *J. tomentosa*. Thompson & Brown (1984) pointed out that *J. lemchei* is externally and anatomically indistinguishable from *J. tomentosa*. However, according to Ev. Marcus (1976) *J. lemchei* is clearly different from *J. tomentosa* because of the presence of large hooks in the penis and the absence of denticulation in the outermost lateral teeth. *Jorunna luisae* is also different from *J. tomentosa* because of the presence of jaws and the innermost lateral teeth denticulate (Ev. Marcus, 1976). These characteristics are, in our opinion, enough to separate these three species.

#### *JORUNNA RUBESCENS* (BERGH, 1876)

(Figs 5D, 16–18)

? *Doris venosa* Quoy & Gaimard, 1832: 274–275, pl. 20, figs 15, 16.

*Kentrodorid rubescens* Bergh, 1876: 413–419, pl. 33, fig. 8, pl. 49, figs 14–19, pl. 50, figs 1–8.

#### Type material

*Doris venosa* Quoy & Gaimard: the type material is lost, it is not deposited at MNHN (Valdés & Héros, 1998). *Kentrodorid rubescens* Bergh: syntype – Aibukit, Palau (the locality and the collection date are not indicated in the original label), 1 specimen 69 mm preserved length (ZMUC GAS-2108).

#### Additional material

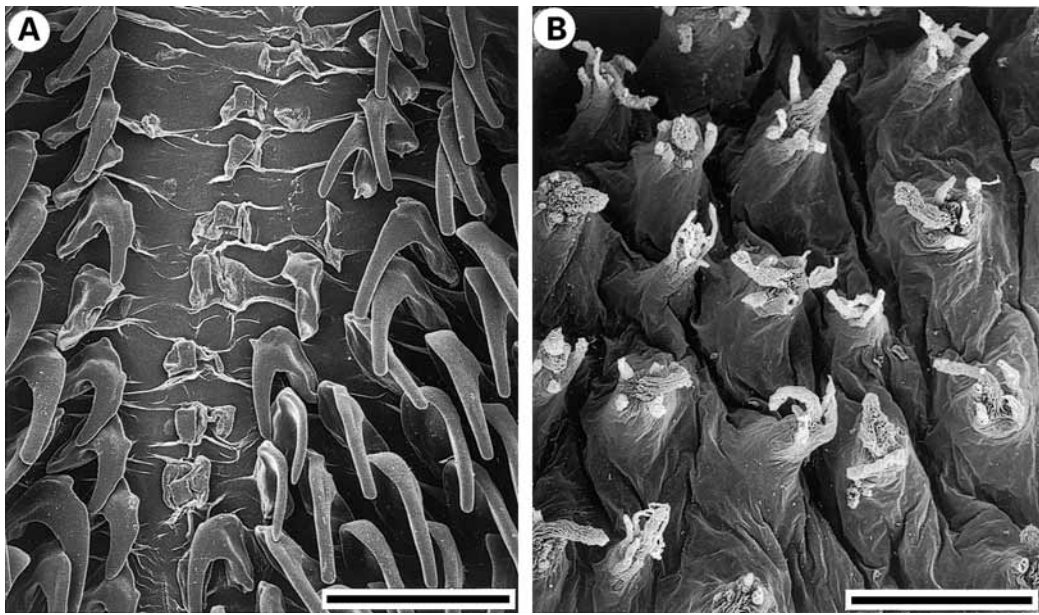
West of Maeki-zaki, Okinawa, Ryukyu Islands, Japan, 15 July 1989, 2 specimens 105–125 mm long, leg. R.F. Bolland (CASIZ 070191). Kranket Island, Near Madang, Papua New Guinea, 7 October 1986, 1 specimen 38 mm preserved length, leg. T. Frohm (CASIZ 072838).

#### External morphology

The maximum length of this species reaches 170 mm (Willan & Coleman, 1984). The body is elongate, narrow and very elevated. The texture is soft and velvety. The dorsum is entirely covered with long caryophyllidia, about 130 µm in length (Fig. 16B). They have a long, conical base, long spicules and a small, elongate ciliated tubercle. The rhinophoral and branchial sheaths are very elevated and regular. There are seven short, bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongate, with 25 lamellae in a 38 mm preserved length specimen.

The general colour of the living animals varies from cream to pale orange. Normally, the anterior and posterior edges of the notum, as well as the edges of the rhinophoral and branchial sheaths, are darker, sometimes almost black. The entire dorsum is covered with numerous longitudinal dark brown streaks. Among them, there are several orange low protuberances, which are also present in the rhinophoral and branchial sheaths. Near the edge of the mantle there are several broken, longitudinal white lines. The rhinophores are dark brown with the apex white. The branchial leaves have the same colour as the dorsum, except for the rachis, which is white proximally and dark brown distally. The rachis of the secondary and tertiary branches is also dark brown. The rhinophores may have dark brown spots near the apex.

Ventrally the anterior border of the foot is notched and grooved (Fig. 17F). The oral tentacles are conical.



**Figure 16.** *Jorunna rubescens*, SEM photographs of the radula and dorsum. A, inner lateral teeth (CASIZ 070191); scale bar = 200  $\mu\text{m}$ . B, caryophyllidia (CASIZ 072838); scale bar = 150  $\mu\text{m}$ .

The mantle margin is wide, but stays close to the laterals of the foot. The foot has the same colour as the dorsum, with an irregular pattern of broken brown streaks. The laterals of the foot have a pattern of white lines and some short brown streaks.

#### Anatomy

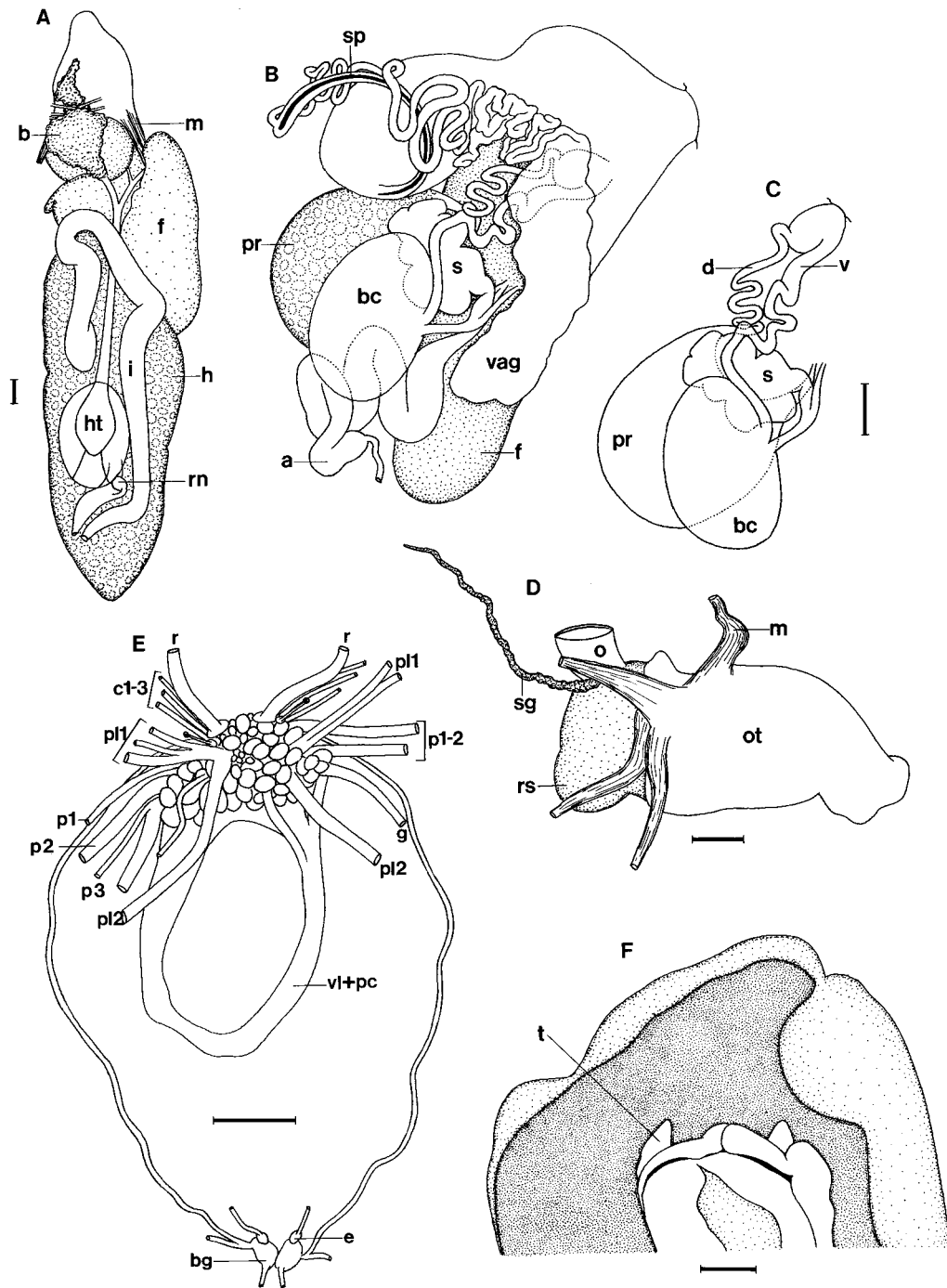
The posterior end of the oral tube has six strong retractor muscles (Fig. 17D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long, tubular salivary glands connect to the buccal bulb at both sides of the oesophageal junction. The buccal bulb is shorter than the oral tube. The labial cuticle is smooth but has numerous regular folds (Fig. 18D). The radular formula is  $32 \times (20.0.20)$  in a 38 mm long specimen. Rachidian teeth are absent. Occasionally, the first lateral teeth in any of the two half-rows are deformed, resembling rachidian teeth (Fig. 16A). The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 18A–C). The point of the cusp is truncate, except in the outermost lateral teeth. The teeth increase their size gradually towards the medial portion of the half-row (Fig. 18A, B). The outermost teeth are smaller but very elongate (Fig. 18C). The oesophagus is short and penetrates into the digestive gland (Fig. 17A).

The ampulla is very long and convoluted. It branches into a short oviduct and the prostate (Fig. 17B). The oviduct enters the female glands in the centre of the mass. The prostate is massive, folded and granular (Fig. 17B). It connects to a long duct that expands into

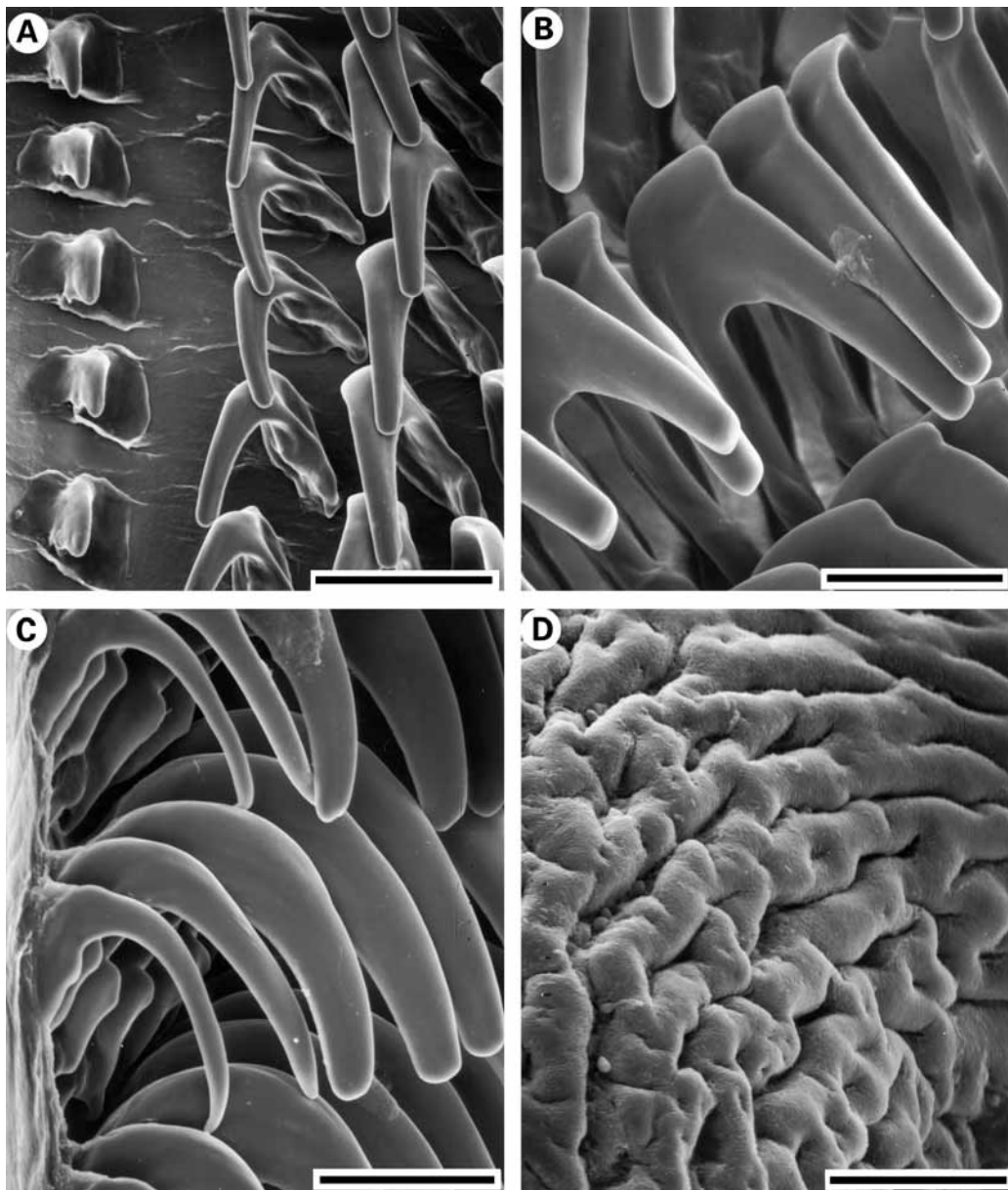
the short ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. There are no penial hooks. There is a large accessory gland connected to the atrium. It consists of a muscular portion, which has a spine, about 3 mm long, a long duct and a glandular proximal region connected to it. The vagina is long, wider than the deferent duct. It connects to the bursa copulatrix at its proximal end. Another duct leads from the bursa copulatrix, connecting to the uterine duct and the seminal receptacle. The bursa copulatrix is rounded in shape about two times larger than the lobate seminal receptacle (Fig. 17C).

In the central nervous system (Fig. 17E) the cerebral and pleural ganglia are fused together and are distinct from the pedal ganglia. The cerebral and pleural ganglia are entirely covered with large ganglionic tubercles. There are three cerebral nerves leading from each cerebral ganglion and two pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two relatively long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have two nerves leading from the right one and three from the left one. The visceral loop, pedal and parapodal commissures are fused together.

The circulatory system (Fig. 17A) includes a small heart and two blood glands placed in front of and behind the central nervous system.



**Figure 17.** *Jorunna rubescens* (CASIZ 072838). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, detail of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, central nervous system; scale bar=1 mm. F, ventral view of the mouth area; scale bar=2 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.



**Figure 18.** *Jorunna rubescens* (CASIZ 072838), SEM photographs of the radula and labial cuticle. A, inner lateral teeth; scale bar = 100 µm. B, teeth from the central portion of the half-row; scale bar = 60 µm. C, outer lateral teeth; scale bar = 60 µm. D, surface of the labial cuticle; scale bar = 43 µm.

*Remarks*

*Doris venosa* Quoy & Gaimard, 1832 is probably a senior synonym of *Jorunna rubescens* (Bergh, 1876). The original description of the former species includes a picture (Quoy & Gaimard, 1832–33: pl. 20, figs 15, 16) in which it is possible to recognize a colour pattern very similar to that of *J. rubescens*. However, the type material of *D. venosa* is lost, so it is impossible to confirm the identity of this species.

*JORUNNA MAIMA* (BERGH, 1878)

*Audura maima* Bergh, 1878: 568–571, pl. 57, figs 13–24.

*Type material*

*Jorunna maima* Bergh: *holotype* (by monotypy) – Camiguin, Luzon Island, Philippines, September 1860, 17 mm preserved length, dissected, leg. Semper (ZMUC GAS-2115).



*Remarks*

The holotype of this species was dissected by Bergh, and only some portions of the digestive gland and intestine remain in the preserved specimen. The original description (Bergh, 1878) does not provide information about the colour of this species and therefore its identification is very difficult.

Other Indo-Pacific species of *Jorunna* with jaws are *Jorunna pantherina* Angas, 1864 and *Jorunna alisonae* Ev. Marcus, 1976 (see Ev. Marcus, 1976). However, there are many other poorly described Indo-Pacific species that could belong to the genus *Jorunna*. A revision of the genus is necessary before *J. maima* can be identified.

*JORUNNA SPAZZOLA* (ER. MARCUS, 1955)

*Awuka spazzola* Er. Marcus, 1955: 156–158, figs 180–192.

*Type material*

*Awuka spazzola* Er. Marcus: the type material is probably lost, it could not be located at MZSP or USNM; the type locality is São Sebastião Island, Brazil.

*Remarks*

According to the redescription of Ev. Marcus (1976) *Jorunna spazzola* is a grey species with dark spots. The internal anatomy is typical of the genus *Jorunna*, with a long spine in the accessory gland. Ev. Marcus (1976) recognized that in the original description of this species (Er. Marcus, 1955) the spine was mistakenly interpreted as situated in the penis instead of the accessory gland.

*Jorunna spazzola* is distinguishable from other species of the genus by the presence of jaws, outermost radular teeth denticulate and innermost lateral teeth with a single denticle (Ev. Marcus, 1976). Unfortunately we were unable to obtain material from this species for the present study.

GENUS *PLATYDORIS* BERGH, 1877

*Argus* Bohadsch, 1761: 65–74 (non *Argus* Scopoli, 1763 – Lepidoptera) suppressed by Opinion 185 (ICZN, 1944) for the purposes of the Principle of Priority, but not for those of the Principle of Homonymy (see Opinion 429, ICZN, 1956). Type species *Argus argo* Linnaeus, 1767 [= *Platydorid argo* (Linnaeus, 1767)], by Linnaean tautonymy.

*Platydorid* Bergh, 1877a: 73–75. Type species *Doris argo* Linnaeus, 1767 [= *Platydorid argo* (Linnaeus,

1767)], by subsequent designation by O'Donoghue (1929a).

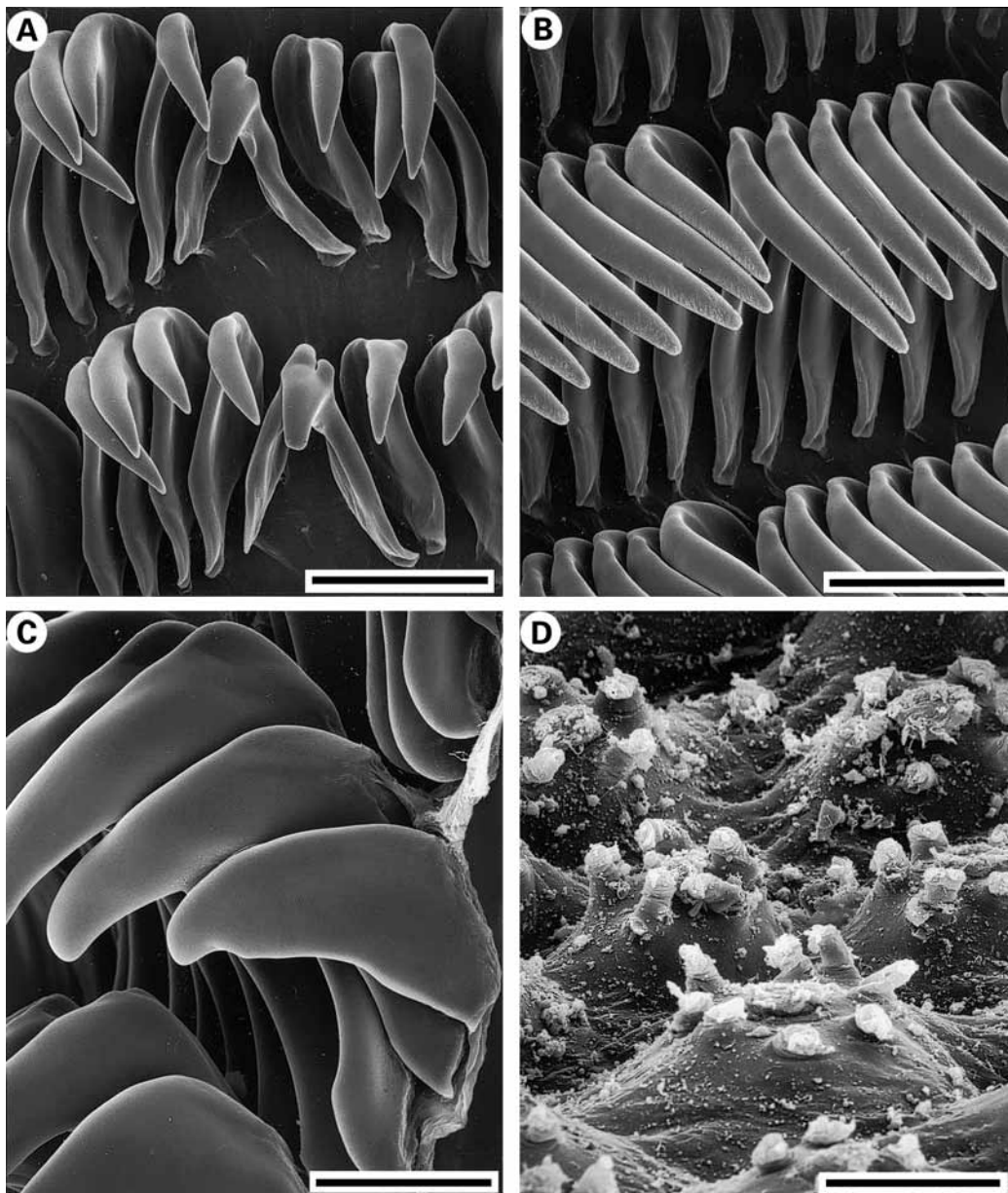
*Diagnosis*

Body wide and flattened, normally rigid. Dorsum covered with very small caryophyllidia. Rhinophoral and branchial sheaths elevated. Branchial sheath lobate. Prostate massive, with two different portions. Oviduct long. Penis armed with hooks. Vagina often armed with large hooks. Accessory gland lobate, without spine. Labial cuticle and radular teeth smooth. Inner and mid lateral radular teeth hamate.

*Remarks*

Bohadsch (1761) introduced the generic name *Argus* Bohadsch, 1761 referring to a single Mediterranean species, but with no mention of any specific name. Bohadsch's Latin description is very complete, including illustrations that are clear enough to recognize this taxon. Linnaeus (1767) regarded *Argus* as a synonym of *Doris* Linnaeus, 1758 and introduced the specific binomial name *Doris argo* Linnaeus, 1767 for the species described by Bohadsch (1761).

Years later, probably unaware of Bohadsch's paper, Bergh (1877a) introduced the generic name *Platydorid* Bergh, 1877 for *Doris argo* Linnaeus, 1767 and other related species of dorids. O'Donoghue (1929a) selected *Doris argo* as the type species of *Platydorid*. At the same time, he indicated that the older name *Argus* should be maintained (having precedence over *Platydorid*), even though Bohadsch's paper was not consistently binomial. A similar point of view was expressed by Engel (1934), who stated that "in many of the cases considered Bohadsch's names may be regarded as valid". In contradiction with the former assessment, he proposed that Bohadsch's names should probably be suppressed, because the change involved with their reintroduction "would result in great confusion". However, in reference to the case of *Argus* he stated "there seems to be no serious objection to this change [the replacement of *Platydorid* for *Argus*], as the name *Platydorid* seldom occurs in general zoological literature". In fact, at that time both names *Argus* and *Platydorid* were used in malacological literature. Despite those opinions, the Commission decided to suppress Bohadsch's book under plenary powers by Opinion 185 (ICZN, 1944), because it was not consistently binomial. No exceptions were made with *Argus* or other names that were in use at that time. The name *Argus* Bohadsch, 1761 was later restored under the provision of the principle of homonymy to prevent the confusion that would arise with the Lepidoptera genus *Argus* Scopoli, 1763 (Opinion 429, ICZN, 1956), but not under the provision of the principle of priority.



**Figure 19.** *Platydoris argo* (CASIZ 115217), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 75  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 75  $\mu$ m. C, outer lateral teeth; scale bar = 43  $\mu$ m. D, caryophyllidia; scale bar = 60  $\mu$ m.

*PLATYDORIS ARGO* (LINNAEUS, 1767)

(Figs 1D, 19–21)

*Doris argo* Linnaeus, 1767: 1083.

*Doris canariensis* d'Orbigny, 1836–42 [1839]: 39.

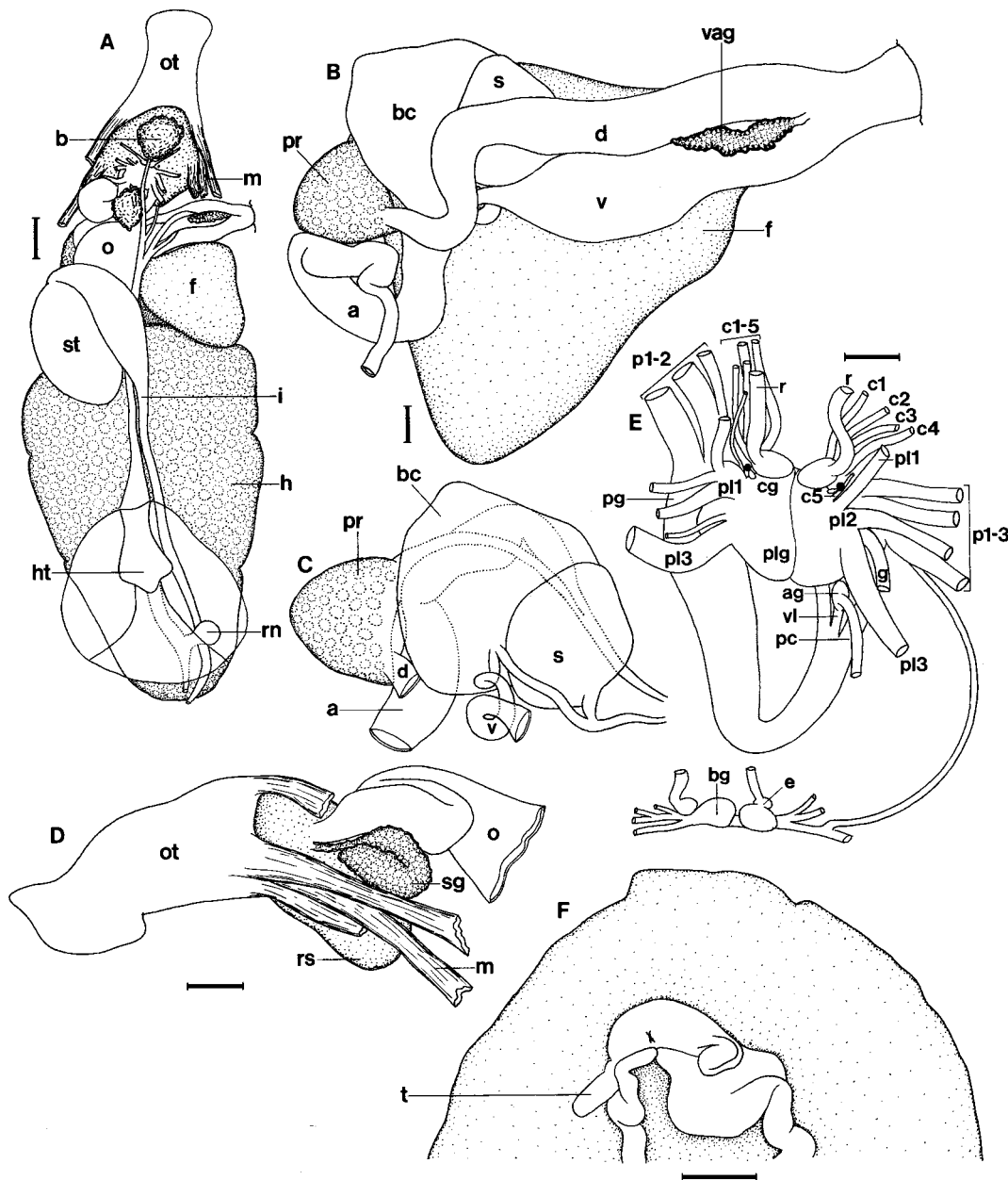
? *Platydoris philippi* Bergh, 1877a: 73.

*Doris subtumida* Abraham, 1877: 250, pl. 27, figs 10, 11.

*Platydoris dura* Pruvot-Fol, 1951: 18–19, fig. 7. **Syn. nov.**

*Type material*

*Doris argo* Linnaeus: no type material is known to exist; the type locality is the Mediterranean Sea. *Doris canariensis* d'Orbigny: the type material is lost, it is not deposited at MNHN (Valdés & Héros, 1998); it was originally collected from Tenerife, Canary Islands. *Platydoris philippi* Bergh: the type material is lost, it is not deposited at ZMCU (Jensen, pers. comm.); it was collected from the Mediterranean Sea. *Doris*

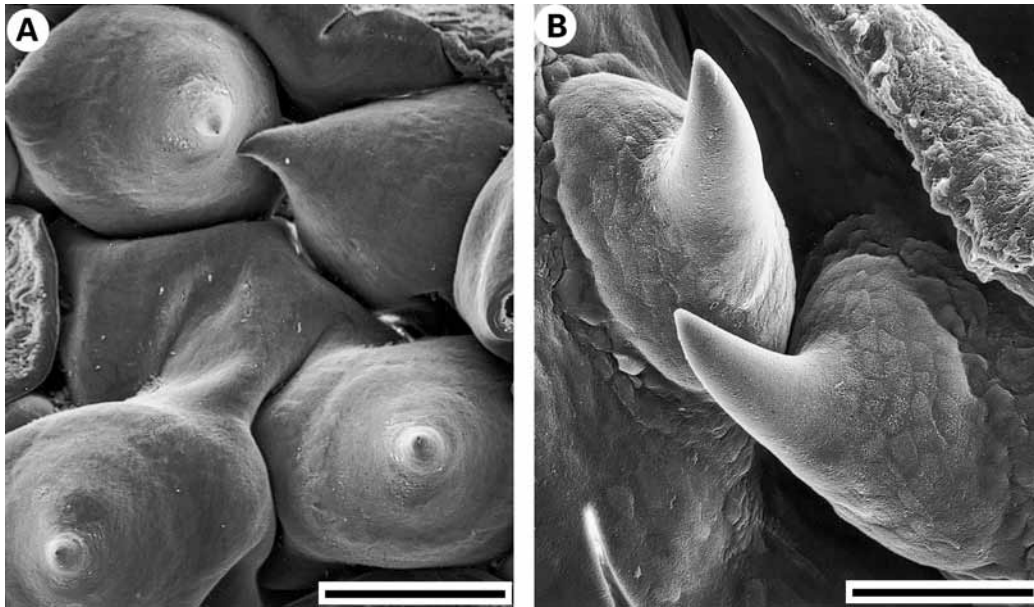


**Figure 20.** *Platydoris argo* (CASIZ 115217). A, general view of the anatomy; scale bar=5 mm. B, reproductive system; scale bar=1 mm. C, detail of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=3 mm. E, central nervous system; scale bar=1 mm. F, ventral view of the mouth area; scale bar=5 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

*subtumida* Abraham (BMNH 1867.5.1.6): not examined. *Platydoris dura* Pruvot-Fol: the type material is lost, it is not deposited at MNHN (Valdés & Héros, 1998); it was collected from Banyuls, France.

#### *Additional material*

Cabo de Palos, Murcia, Spain, August 1980, 2 specimens 62–70 mm preserved length, leg. J. Templado (CASIZ 115217). Lanzarote, Canary Islands, Spain,



**Figure 21.** *Platydoris argo* (CASIZ 115217), SEM photographs of the reproductive system. A, vaginal hooks; scale bar = 300  $\mu\text{m}$ . B, penial hooks; scale bar = 43  $\mu\text{m}$ .

December 1981, 4 specimens 30–63 mm preserved length, leg. J. Ortea (CASIZ 115218). Lazareto, Funchal, Madeira, 10 September 1998, 6 specimens 15–40 mm preserved length, leg. T.M. Gosliner (CASIZ 114868).

#### *External morphology*

The maximum length of this species reaches over 70 mm. The body is very flat, wide (Fig. 1D), with a rigid and hard texture. The dorsum is all covered with minute caryophyllidia, about 50  $\mu\text{m}$  long (Fig. 19D). They have a very short, conical base, short spicules and a small central ciliated tubercle. The rhinophoral and branchial sheaths are elevated and irregular. The opening of the branchial sheath is lobate. There are 5–6 tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The anal papilla is elongate. The rhinophores are elongated, having 22 lamellae in a 70 mm preserved length specimen.

The general colour of the living animals varies from reddish brown to bright red or pale brown. In some individuals the dorsum has a number of small white spots. The rhinophores and gill are normally darker than the dorsum, sometimes black.

Ventrally the anterior border of the foot is notched and grooved (Fig. 20F). The oral tentacles are elongate and grooved. The ventral colour is pale brown with a number of dark brown spots of different sizes in the mantle margin, more densely distributed around the foot.

#### *Anatomy*

Probably because of its large size, *Platydoris argo* is one of the European species of nudibranchs whose anatomy has been more thoroughly studied. A series of papers describing the buccal apparatus (García, García-Gómez & Medel-Soteras, 1988), the penial complex (García & García-Gómez, 1988), the central nervous system (García, García-Gómez & Cervera, 1988) and the circulatory system (García & García-Gómez, 1990) have been published in recent years.

In this species, the posterior end of the oral tube has six strong retractor muscles (Fig. 20D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two short salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is shorter than the oral tube. The labial cuticle is smooth. The radular formula is  $47 \times (96.0.96)$  in a 70 mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 19A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 19A, B). The outermost teeth are smaller and also lack denticles (Fig. 19C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 20A).

The ampulla is very large and convoluted. It branches into a long oviduct and the prostate (Fig. 20C). The oviduct enters the female glands near the opening. The prostate is wide, very small and granular (Fig. 20B,C). It connects to a very long and wide

deferent duct, which opens into a common atrium with the vagina. The penis has three rows of large hooks. They have a large base, about 50 µm wide and a single cusp about 25 µm long (Fig. 21B). There is a granular accessory gland connected to the atrium, which lacks armature. The vagina is long and wide. It is also internally covered with large hooks. The vaginal hooks have a large base, over 300 µm wide, and a single cusp about 25 µm long (Fig. 21A). At its proximal end, the vagina connects to the large and almost rounded bursa copulatrix. From the bursa copulatrix leads another duct connecting to the seminal receptacle and the uterine duct. The bursa copulatrix is about as large as the seminal receptacle (Fig. 20C).

In the central nervous system (Fig. 20E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are five cerebral nerves leading from each cerebral ganglion and three pleural nerves leading from each pleural ganglion. There is a distinct abdominal ganglion on the right side of the visceral loop. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from each ganglion. The pedal and parapedal commissures are fused together with the visceral loop along most of their length.

The circulatory system (Fig. 20A) includes a large heart and two blood glands placed over the central nervous system.

#### Remarks

Several nominal species have been assigned to the genus *Platydoris* in the Mediterranean Sea and adjacent Atlantic waters. *Doris canariensis* d'Orbigny, 1839, described from the Canary Islands, has been regarded by Ortea & Bacallado (1981) as a synonym of *Platydoris argo*.

Abraham (1877) introduced *Doris subtumida* Abraham, 1877, based on museum material. The coloration of the preserved animal is brownish with dark brown spots in the dorsum and also ventrally, scattered in the mantle margin, near the foot (Abraham, 1877). This, and the shape of the specimens illustrated by Abraham (1877, pl. 27, figs 10, 11), is identical to our preserved specimens of *P. argo*. We considered that *D. subtumida* is a synonym of *P. argo*, and examination of the type material is probably not necessary to confirm this point.

*Platydoris philippi* Bergh, 1877 was introduced by Bergh (1877a) for Philippi's (1836) misidentification of *Doris stellata* Gmelin, 1791. According to the description of Philippi (1836), this species is a grey, large, flattened dorid, with minute tubercles on the dorsum.

This description matches the characteristics of *Platydoris argo*, and it could constitute a synonym. Since the type material is lost, it is not possible to confirm this point.

Pruvot-Fol's (1951) *Platydoris dura* is identical to *Platydoris argo*. The reproductive system described by Pruvot-Fol (1951, fig. 7) is not different from that found in our specimens. Also, the external morphology and coloration of *P. dura* fit the normal variability of *P. argo*. The type material of *P. dura* is lost, but there is enough information in the original description to support its placement in synonymy with *P. argo*.

In our opinion, it is very likely that there is only one species of *Platydoris* in the Mediterranean Sea. However, a review of the systematics of the genus is necessary for definitive conclusions.

#### GENUS *DIAULULA* BERGH, 1878

*Diaulula* Bergh, 1878: 567. Type species *Doris sandiegensis* Cooper, 1863, by monotypy.

*Anisodoris* Bergh, 1898: 508. Type species: *Doris punctuolata* d'Orbigny, 1837, by subsequent designation by O'Donoghue (1926). **Syn. nov.**

#### Diagnosis

Body flexible. Dorsum covered with elongate caryophyllidia. Caryophyllidia with small lateral cilia. Rhinophoral and branchial sheaths low. Prostate massive, with two portions. Penis and vagina unarmed. Labial cuticle smooth. Radular teeth hamate and smooth.

#### Remarks

Bergh (1878) introduced the genus *Diaulula* Bergh, 1880 based on *Doris sandiegensis* Cooper, 1863. The main characteristics of this genus are the presence of a villous, silky dorsum, anterior border of the foot notched and grooved, tripinnate branchial leaves, absence of jaws, presence of a large prostate and penis unarmed.

The genus *Anisodoris* Bergh, 1898 was described as a member of the family Archidorididae, which differs from the 'typical' archidoridids by the presence of a larger prostate (Bergh, 1898). In the short diagnosis of this genus, Bergh (1898) also indicated that the penis is unarmed, and that this feature separates *Anisodoris* from *Homoiodoris*. The genus *Anisodoris* was based on several species, including *Anisodoris punctuolata* (d'Orbigny, 1837), *Anisodoris variolata* (d'Orbigny, 1837), *Anisodoris marmorata* Bergh, 1898 and *Anisodoris tessellata* Bergh, 1898. Subsequently O'Donoghue (1926) selected *A. punctuolata* to be the type species. An anatomical examination of newly collected specimens of *A. punctuolata* shows that it has the same features as members of *Diaulula* (see below),

and these two genus names are synonyms. The genus name *Anisodoris* has been used to include species with large, simple dorsal tubercles (Millen, 1982; Schrödl, 1997, 2000) that do not fit the characteristics of the type species. Most of the species previously assigned to *Anisodoris* probably belong to the genera *Peltodoris* Bergh, 1880 or *Archidoris* Bergh, 1878.

Thompson (1975) and McDonald (1983) regarded *Diaulula* as a synonym of *Discodoris*, based on the similar size, shape, mode of life, radula and reproductive organs of both genera. On the other hand, Behrens (1991) did not agree with that synonymization. However, the investigation of the phylogenetic relationships of these taxa, discussed below, shows that there is a large phylogenetic distance between them. The presence of caryophyllidia and the two portions in the prostate of *Diaulula* are the major characteristics that separate these genera.

*DIAULULA PUNCTUOLATA* (D'ORBIGNY, 1837)

(Figs 22, 23)

*Doris punctuolata* d'Orbigny, 1837: 187, pl. 16, figs 4–6.

*Doris punctuolata* var. *cymina* Er. Marcus, 1959: 43–45, figs 91–97.

*Type material*

The type material is lost; it could not be located at BMNH or MNHN. The type locality is near Valparaiso, Chile.

*Additional material*

Chiloé Island, Lacuay Peninsula, Chile, 24 December 1994, 10 m depth, 1 specimen 53 mm preserved length, leg. S. Millen, M. Schrödl and S. Gigglinger (CASIZ 118012).

*External morphology*

The external morphology of this species has been described by d'Orbigny (1837), Er. Marcus (1959) and Schrödl (1996). We have examined a single preserved specimen, with no data on the external coloration. The dorsum is covered with small caryophyllidia about 200 µm long (Fig. 22D).

Ventrally the anterior border of the foot is notched and grooved (Fig. 23F). The oral tentacles are conical. The mantle margin is wider than the foot.

*Anatomy*

The posterior end of the oral tube has six strong retractor muscles (Fig. 23E) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The

buccal bulb is shorter than the oral tube. The labial cuticle is smooth. The radular formula is  $18 \times (25.0.25)$  in a 53 mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 22A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 22A,B). The outermost teeth are very small and elongate, also lacking denticles (Fig. 22C). The oesophagus is long and expands directly into the stomach (Fig. 23A).

The ampulla is long and convoluted (Fig. 23B). It enters the female glands near the centre of their mass. The prostate is massive and granular. It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the female glands, next to the opening of the ampulla. The deferent duct is long. It narrows and expands again into the short, wide ejaculatory portion. The deferent duct opens into a common atrium with the vagina. There are no penial hooks. The vagina is long and wide. At its proximal end, the vagina connects to the large and irregular bursa copulatrix (Fig. 23C). Another duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about three times larger than the seminal receptacle (Fig. 23C).

In the central nervous system (Fig. 23E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three (right side) and two (left side) pleural nerves leading from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are also present. The pedal ganglia have two nerves leading from each one. The pedal and parapetal commissures are enveloped together with the visceral loop. The circulatory system (Fig. 23A) includes a large heart and two blood glands placed in front and behind the central nervous system.

*Remarks*

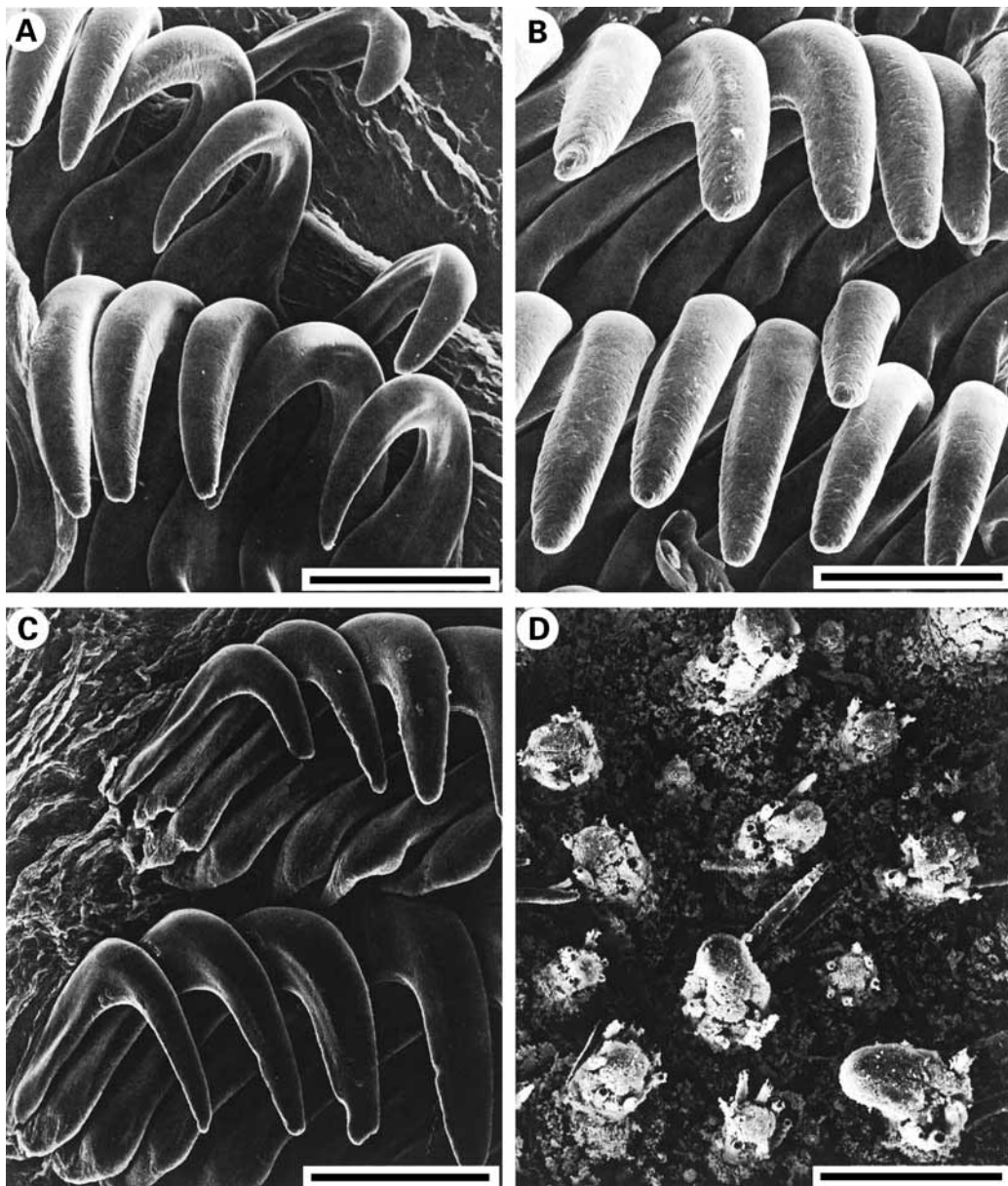
D'Orbigny (1837) described *Doris punctuolata* as a white-yellowish species, 50–60 mm long, oval, with the dorsum covered with very small tubercles, all of them of similar size, with six highly ramified branchial leaves. This description fits with the modern usage of the name by Millen (1982), Schrödl (1996) and with the specimen here examined.

*DIAULULA SANDIEGENSIS* (COOPER, 1863)

(Figs 1G, 5A, 24, 25)

*Doris sandiegensis* Cooper, 1863: 204–205.





**Figure 22.** *Diaulula punctuolata* (CASIZ 118012), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 60  $\mu\text{m}$ . B, teeth from the central portion of the half-row; scale bar = 75  $\mu\text{m}$ . C, outer lateral teeth; scale bar = 75  $\mu\text{m}$ . D, caryophyllidia; scale bar = 200  $\mu\text{m}$ .

#### *Type material*

The type material is lost; it could not be located at CASIZ; the type locality is San Diego, California.

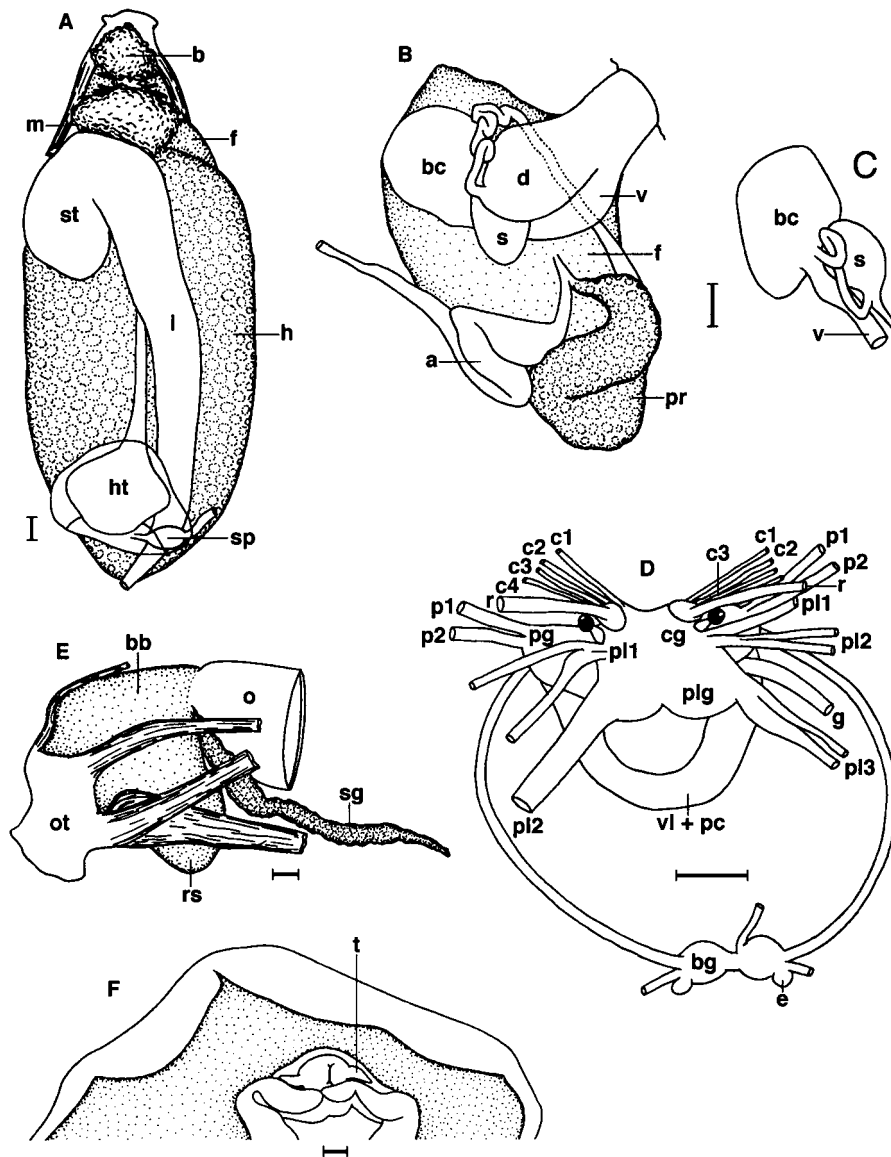
#### *Additional material*

Pigeon Point, San Mateo County, California, 12 December 1970, 1 specimen 38 mm preserved length, leg. G. McDonald (CASIZ 070842). West side of Tomales Bay, Marin County, California, 12 March 1961, 3 specimens 21–46 mm preserved length, leg. A.G. Smith

(CASIZ 068277). Roca Ben, Pacific coast of Baja California, 20 August 1987, 7 specimens 16–36 mm preserved length, leg. T.M. Gosliner (CASIZ 071641).

#### *External morphology*

The maximum length of this species reaches 150 mm (McDonald, 1983). The body is oval and convex (Fig. 1G), soft, with a velvety texture. The dorsum is entirely covered with caryophyllidia, about 120  $\mu\text{m}$  in length (Fig. 24D). There are some smaller tubercles, about



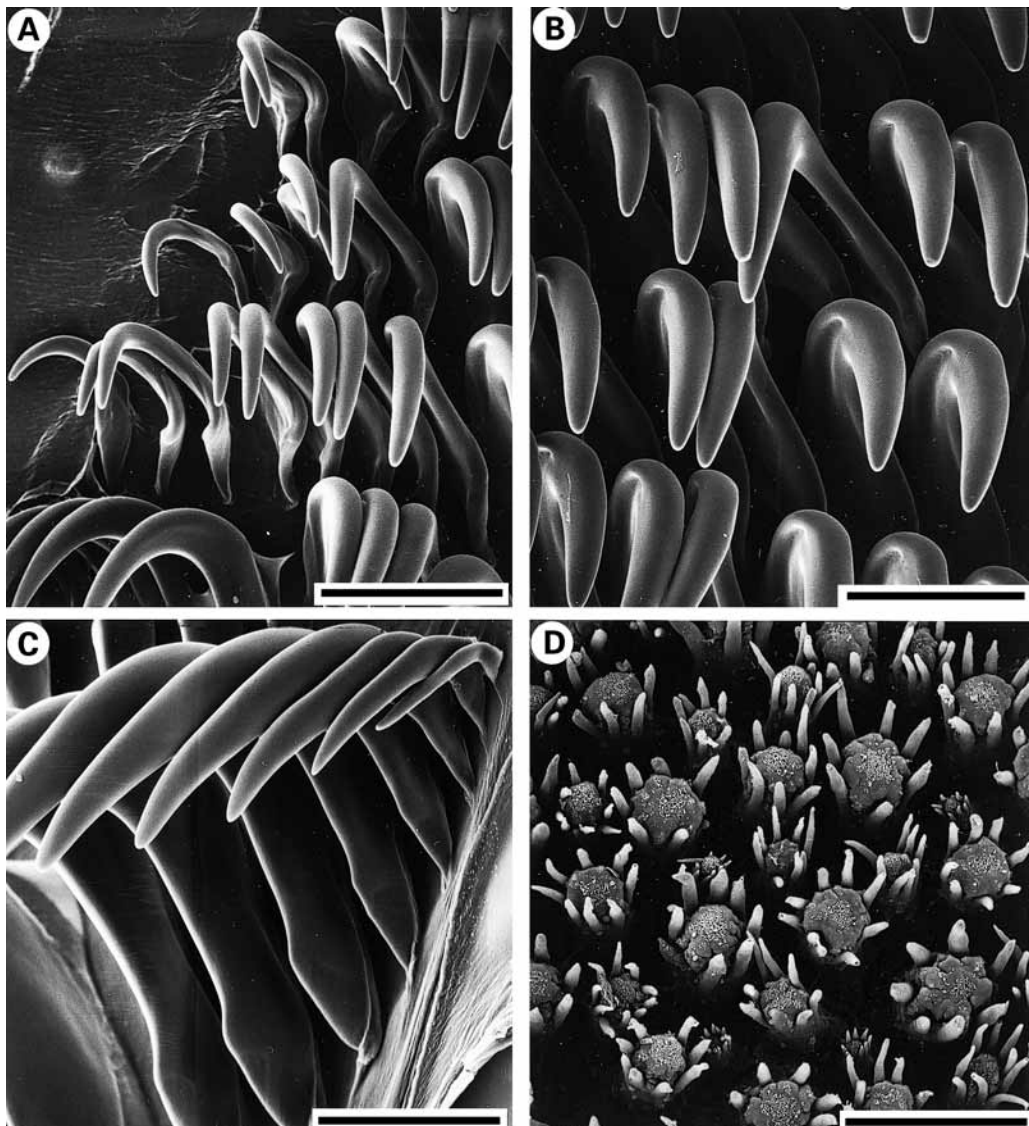
**Figure 23.** *Diaulula punctuolata* (CASIZ 118012). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, disposition of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 2 mm.

80 µm long, scarcely distributed between the larger ones. The caryophyllidia have a short, cylindrical base, long spicules and a very large, rounded ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. There are six long, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 10 lamellae in a 38 mm long specimen.

The general colour of the living animals varies from white to pale brown. The dorsum has several dark brown or black rings, or occasional irregular patches, of various sizes. They are irregularly scattered, but

often they are aligned in two longitudinal rows, one on either side of the body. According to McDonald (1983) specimens from bays are normally darker than specimens from open coastal areas. More northern specimens generally have irregular patches rather than rings. The gill and rhinophores have normally the same colour as the dorsum but somewhat darker. The tips of the branchial leaves are white.

Ventrally the anterior border of the foot is notched and grooved (Fig. 25F). The oral tentacles are conical. The mantle margin is as wide as the foot. The ventral colour is the same as the dorsal.



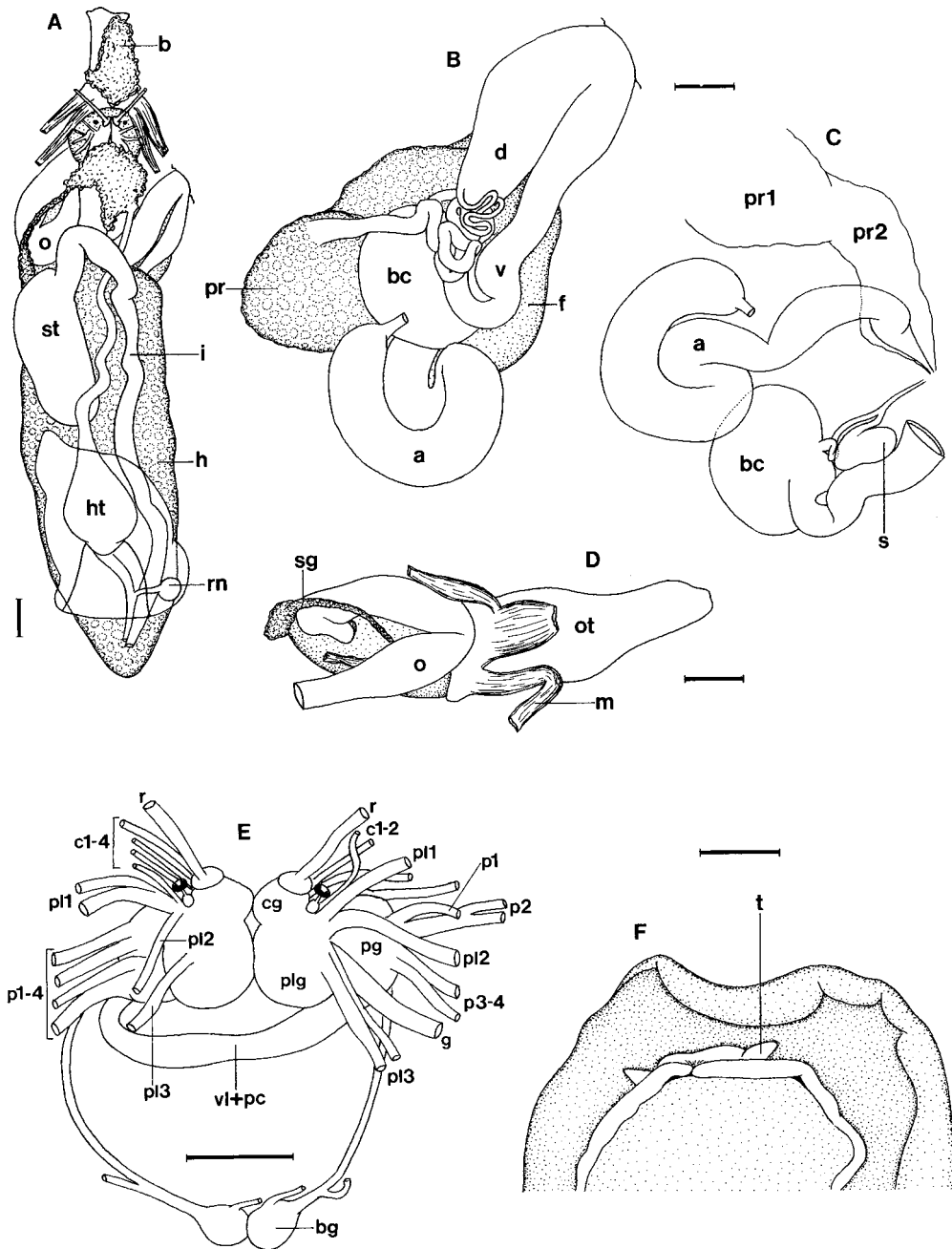
**Figure 24.** *Diaulula sandiegensis* (CASIZ 070842), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 150  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 150  $\mu$ m. C, outer lateral teeth; scale bar = 75  $\mu$ m. D, caryophyllidia; scale bar = 250  $\mu$ m.

### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 25D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is shorter than the oral tube. The labial cuticle is smooth. The radular formula is  $22 \times (27.0.27)$  in a 46 mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 24A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 24A,B). The outermost teeth are very small and elongate, also lacking denticles (Fig. 24C). The

oesophagus is long and expands directly into the stomach (Fig. 25A).

The ampulla is very long and convoluted (Fig. 25C). It enters the female glands near their nidamental opening. The prostate is massive and granular (Fig. 25B). It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the female glands, next to the opening of the ampulla (Fig. 25C). The deferent duct is very long. It narrows and expands again into the short, wide ejaculatory portion. The deferent duct opens into a common atrium with the vagina. There



**Figure 25.** *Diaulula sandiegensis* (CASIZ 068277). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, disposition of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, central nervous system; scale bar=0.5 mm. F, ventral view of the mouth area; scale bar=1 mm.

are no penial hooks (Fig. 5A). The vagina is long and wide. At its proximal end, the vagina connects to the large and irregular bursa copulatrix. Another duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about ten times larger than the seminal receptacle (Fig. 25C).

In the central nervous system (Fig. 25E) the cerebral

and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves leading from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are also present. The pedal ganglia have four nerves leading from each one.

The pedal and parapedal commissures are enveloped together with the visceral loop. The circulatory system (Fig. 25A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

This is one of the most common species of dorid along the California coast. For further geographical information and a list of references see McDonald (1983).

#### GENUS *ROSTANGA* BERGH, 1879

*Rostanga* Bergh, 1879: 353–354. Type species *Doris coccinea* Forbes in Alder & Hancock, 1848 [= *Rostanga rubra* (Risso, 1818)], by original designation. *Rhabdochila* P. Fischer, 1880–1887 [1883]: 521. Type species *Doris coccinea* Forbes in Alder & Hancock, 1848, by subsequent designation by Iredale & O'Donoghue (1923). *Boreodoris* Odhner, 1939: 31–33. Type species *Boreodoris setidens* Odhner, 1939 [= *Rostanga setidens* (Odhner, 1939)], by monotypy. **Syn. nov.**

#### Diagnosis

Body flexible. Dorsum covered with elongate caryophyllidia. Caryophyllidia with small lateral cilia. Rhinophoral and branchial sheaths low. Prostate massive, with two portions. Penis and vagina unarmed. Labial cuticle armed with jaw rodlets. Innermost radular teeth broad, often denticulated. Outermost lateral teeth very elongate and variable denticulate.

#### Remarks

Bergh (1879) introduced the genus *Rostanga* for *Doris coccinea* Forbes in Alder & Hancock, 1848. According to Bergh (1879) the main diagnostic features of *Rostanga* include dorsum covered with small tubercles, bipinnate branchial leaves, digitiform tentacles, anterior border of the foot notched and grooved, absence of jaws, radular teeth with a bifid cusp, short innermost teeth and very elongated outermost teeth.

P. Fischer (1883) introduced the subgenus *Rhabdochila* to unite *Rostanga* and other genera described by Bergh, characterized by the presence of jaws and a rounded branchial opening. Iredale & O'Donoghue (1923) subsequently designated *D. coccinea* as the type species of *Rhabdochila*. With this act, *Rhabdochila* became a junior objective synonym of *Rostanga*.

Odhner (1939) introduced the genus *Boreodoris* Odhner, 1939, based on *Boreodoris setidens* Odhner, 1939. Odhner (1939) recognized the similarities between *Rostanga* and his new genus, but at the same time he considered that the absence of jaws and radular teeth without clear differentiation in *Boreodoris* were enough distinct features to separate it from *Rostanga*.

He defined *Rostanga* as having jaws and the innermost lateral teeth as being very different from the outermost.

A re-examination of *Rostanga rubra* shows that this species has very small jaws whereas, according to Odhner (1939), they are absent in *Boreodoris*. However, this feature is variable in other related genera, such as *Jorunna*, and it was probably lost independently several times in the evolution of dorids. The radula of *B. setidens*, even though different from that of *R. rubra*, shares many features such as the outermost elongated teeth with a single long denticle and the triangular innermost radular teeth. The reproductive system of both species is also very similar, with a large, granular prostate (Odhner misidentified the prostate as the ampulla in *B. setidens*). Therefore we consider that there are not enough differences to maintain *Boreodoris* as distinct from *Rostanga*. In the phylogenetic hypothesis discussed below, *Boreodoris* appears to be the sister group of *Rostanga*, but it is a member of the same clade.

#### *ROSTANGA RUBRA* (RISSO, 1818)

(Figs 1E, 26–28)

*Doris rubra* Risso, 1818: 369.

*Doris coccinea* Forbes, 1844: 133 (*nomen nudum*). Forbes in Alder & Hancock, 1845–55 [1848]: 42, fam. 1, pl. 7, pl. 46, fig. 6.

*Rostanga perspicillata* Bergh, 1881b: 104–107, pl. J, figs 1–15.

*Rostanga rufescens* Iredale & O'Donoghue, 1923: 197, 227 (unnecessary replacement name for *Doris coccinea* Forbes in Alder & Hancock, 1848).

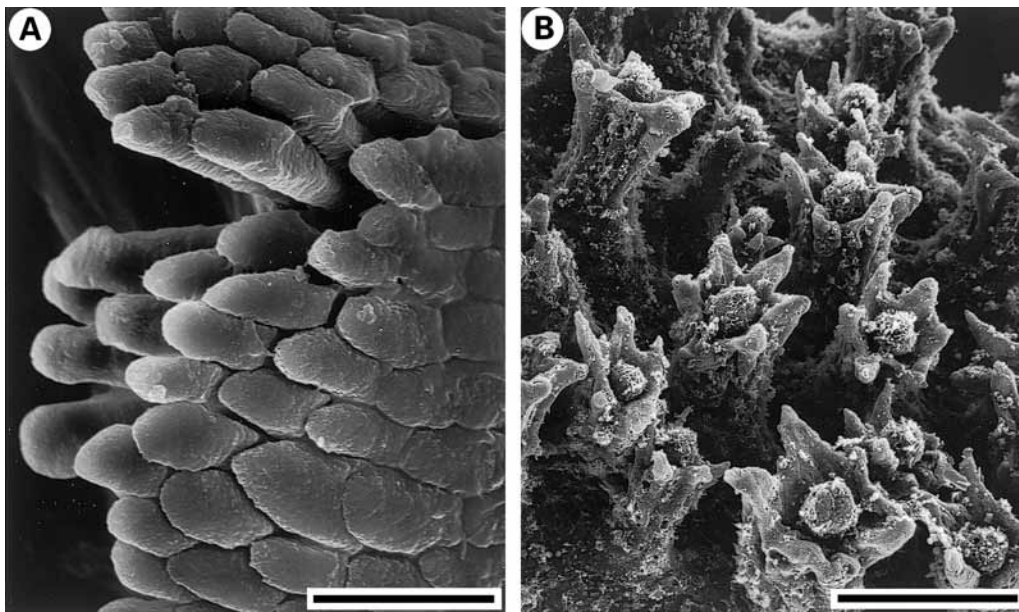
*Rostanga temarana* Pruvot-Fol, 1953: 78–80, figs 26, 26bis.

#### Type material

*Doris rubra* Risso: the type material is lost (see Arnaud, 1977); it was collected from Nice, France. *Doris coccinea* Forbes in Alder & Hancock: *lectotype* (here selected) – Falmouth, England, 10 mm preserved length (BMNH 1858.5.28.146/1); *paralectotypes* – 2 specimens 8–9 mm preserved length (BMNH 1858.5.28.146/2). *Rostanga perspicillata* Bergh: the type material is lost, it is not deposited at ZMUC (Jensen, pers. comm.); it was collected from Trieste, Italy. *Rostanga temarana* Pruvot-Fol: the type material is lost, it is not deposited at MNHN (Valdés & Héros, 1998), the type locality is Temara, Morocco.

#### Additional material

Oviñana, Asturias, Spain, 14 June 1976, 2 specimens 10 mm long, dissected, leg. J. Ortea (CASIZ 115216). Bahia de Murbeira, Ilha de Sal, Cape Verde, 8 March



**Figure 26.** *Rostanga rubra* (CASIZ 115216), SEM photographs of the jaw and dorsum. A, jaw elements; scale bar = 15  $\mu\text{m}$ . B, caryophyllidia; scale bar = 150  $\mu\text{m}$ .

1997, 1 specimen 10 mm preserved length, dissected, leg. F. Talavera (CASIZ 115227).

#### *External morphology*

The maximum length of this species reaches 20 mm (Schmekel & Portmann, 1982). The body is oval and convex (Fig. 1E), soft, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 160  $\mu\text{m}$  in length (Fig. 26B). There are some smaller caryophyllidia, about 100  $\mu\text{m}$  long, scarcely distributed between the larger ones. The caryophyllidia have a long, conical base, long spicules and a small, rounded ciliated tubercle. The spicules are enveloped by a tegument that gives the caryophyllidia the appearance of a star in dorsal view. There are small ciliated areas between each spicule. The rhinophoral and branchial sheaths are low and regular. The tubercles around the rhinophoral sheath are larger. There are eight short, bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are club shaped, with eight lamellae in a 10 mm specimen. The lamellae are arranged almost vertically.

The general colour of the living animals is uniformly bright red. Occasionally specimens may vary from pink to pale-orange yellow (Thompson & Brown, 1984). There may be small spots irregularly scattered over the dorsum. The tubercles around the rhinophores are white-yellow. The gill is also uniformly bright red, but the rhinophores are brown, with the apex white.

Ventrally the anterior border of the foot is notched and grooved (Fig. 27G). The oral tentacles are conical.

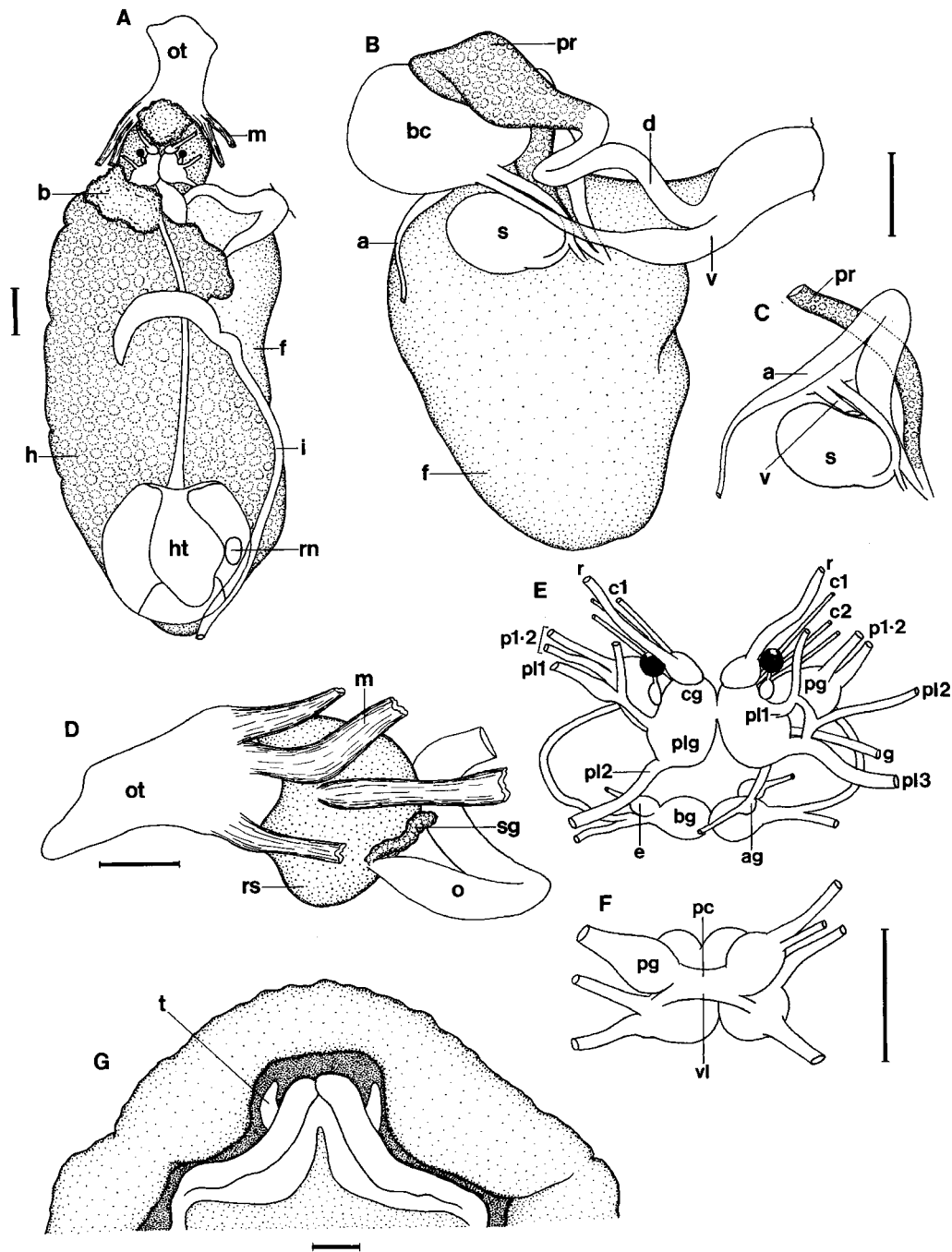
The mantle margin is narrower than the foot. The ventral colour is the same as the dorsum.

#### *Anatomy*

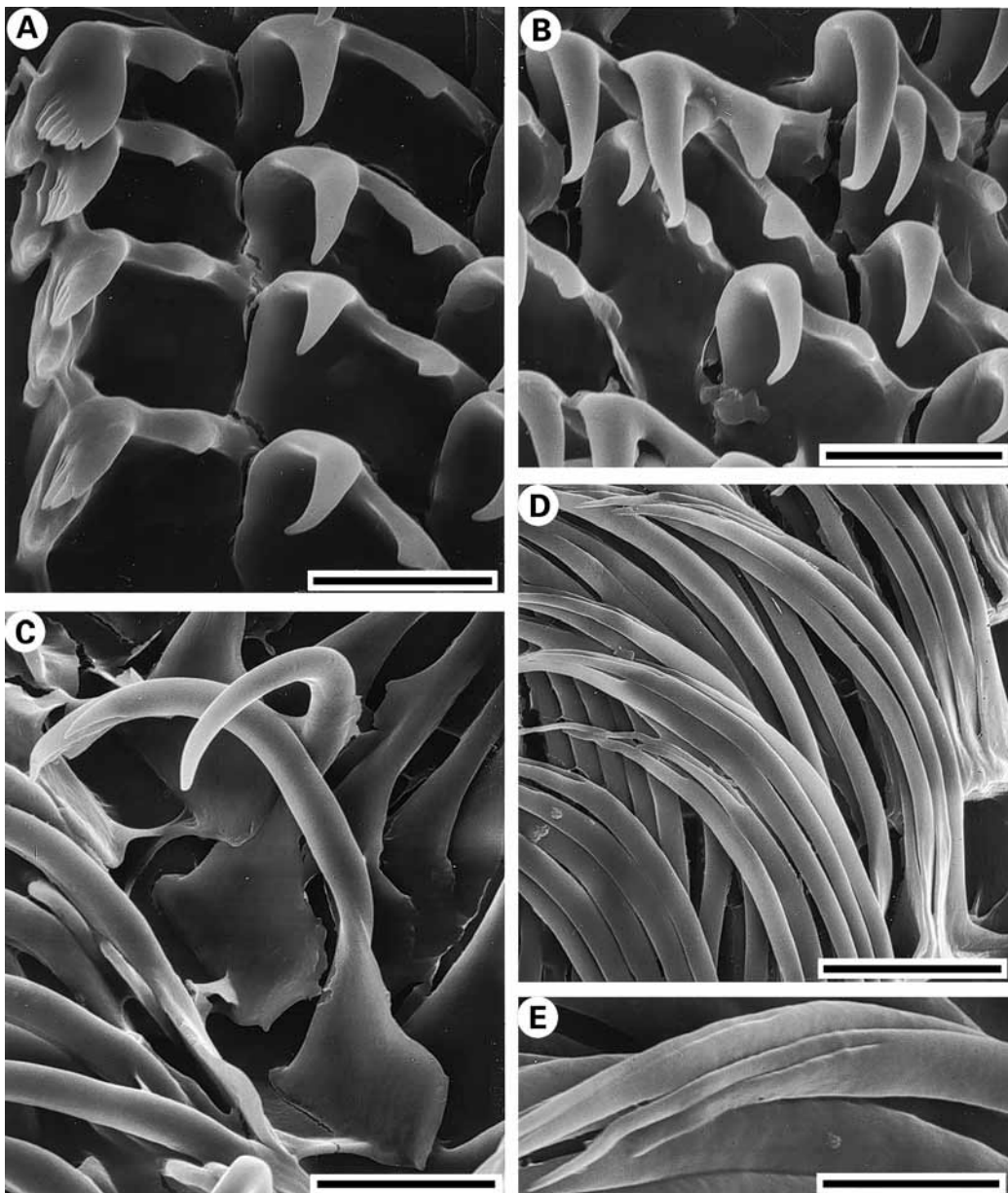
The posterior end of the oral tube has six strong retractor muscles (Fig. 27D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two short salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is as long as the oral tube. The labial cuticle is armed with jaw rodlets (Fig. 26A). The radular formula is  $59 \times (41.0.41)$  in a 10 mm long specimen. Rachidian teeth are absent. The innermost lateral teeth are wide, triangular shaped, having a single central cusp and a lateral small cusp in their outer side (Fig. 28A,B). The first tooth of each row has 4–7 denticles in the inner side of the central cusp (Fig. 28A). The teeth from the middle portion of the half-row are elongate, with a large base and a single denticle very close to the apex of the cusp (Fig. 28C). The outermost teeth are very elongate but with a small base and a single, long denticle (Fig. 28D,E). The oesophagus is short and penetrates into the digestive gland (Fig. 27A).

The ampulla is elongate and branches into a short oviduct and the prostate (Fig. 27C). The oviduct enters the female glands near the centre of the mass. The prostate is massive, folded and granular (Fig. 27B). It connects to a long duct that expands into the ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. There are no penial hooks. The vagina is long, in some





**Figure 27.** *Rostanga rubra* (CASIZ 115216). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, disposition of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the central nervous system; scale bar = 0.5 mm. G, ventral view of the mouth area; scale bar = 0.5 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerve; pc, pedal commissure; pl, pleural nerves; pg, pedal ganglion; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; sg, salivary gland; t, oral tentacle; v, vagina; vl, visceral loop.



**Figure 28.** *Rostanga rubra* (CASIZ 115216), SEM photographs of the radula. A, inner lateral teeth; scale bar = 15 µm. B, teeth from the central portion of the half-row; scale bar = 20 µm. C, first outer lateral teeth; scale bar = 20 µm. D, outermost lateral teeth; scale bar = 25 µm. E, detail of the denticulation of the outermost lateral teeth; scale bar = 10 µm.

portions wider than the deferent duct. It connects to the bursa copulatrix at its proximal end. Another duct, connecting to the uterine duct and the seminal receptacle, leads from the bursa copulatrix. The bursa copulatrix is oval in shape about three times larger than the seminal receptacle (Fig. 27B).

In the central nervous system (Fig. 27E,F) the cerebral and pleural ganglia are fused together and are distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion,

three pleural nerves leading from the right pleural ganglion and two pleural nerves leading from left pleural ganglion. There is no distinctive abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two short connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have two nerves leading from each one. The visceral loop, pedal and parapedal commissures are fused together in a very short commissure.

The circulatory system (Fig. 27A) includes a small heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Rudman & Avern (1989) revised the systematics of the genus *Rostanga* in the Indo-West Pacific and discussed the taxonomic status of other nominal species from different geographic areas. They agreed with Schmekel & Portmann (1982) and Thompson & Brown (1984) in regarding *Doris coccinea* Forbes in Alder & Hancock, 1848, *Rostanga perspicillata* Bergh, 1881 and *Rostanga rufescens* Iredale & O'Donoghue, 1923 as synonyms of *Doris rubra* Risso, 1818. Rudman & Avern (1989) also regarded *Rostanga temarana* Pruvot-Fol, 1953 as a synonym of *D. coccinea*. We agree that all these nominal species are actually synonyms.

The material from Cape Verde Islands here studied is identical to the specimens from Europe.

#### *ROSTANGA SETIDENS* (ODHNER, 1939)

*Boreodoris setidens* Odhner, 1939: 31–33, figs 15–17.

#### Type material

*Boreodoris setidens* Odhner: the type material is probably lost. Odhner (1939) indicated that the single specimen he studied (holotype by monotypy) was deposited at the Zoological Museum in Trondheim, Norway. However, the specimen could not be found in the collections of that institution (T. Bakken, pers. comm.). Sandberg & Warén (1993) mentioned that this specimen was supposed to be at ZMUC, but according to Jensen (pers. comm.) it is not deposited there either. The type locality is Nordfilla, North of Bodö, Norway, at 160 m depth.

#### Remarks

*Rostanga setidens* (Odhner, 1939) is a very rare species that probably has not been collected again since its original description (see Høisæter, 1986). The holotype is the only known specimen and unfortunately it is lost. However, Odhner's (1939) description is very complete, including the external morphology and features of the reproductive system and radula.

This species clearly differs from *Rostanga rubra*, the other North-East Atlantic species of the genus in the morphology of the radular teeth (see discussion of the genus *Rostanga*) and in the external coloration. The radular formula of *R. setidens* is  $125-130 \times (120.0.120)$  in a 20 mm long specimen (Odhner, 1939), whereas we found a formula  $59 \times (41.0.41)$  in a 10 mm preserved length specimen of *R. rubra*. Odhner (1939) described the colour of this species as being entirely greyish except for the rhinophores and gill which are whitish.

This clearly contrasts with the bright red colour of *R. rubra*.

#### GENUS *HALGERDA* BERGH, 1880

*Halgerda* Bergh, 1880b: 190. Type species *Halgerda formosa* Bergh, 1880, by monotypy.

*Dictyodoris* Bergh, 1880c: 75. Type species *Dictyodoris tessellata* Bergh, 1880 [= *Halgerda tessellata* (Bergh, 1880)], by monotypy.

#### Diagnosis

Body rigid, gelatinous. Dorsum covered with ridges and small tubercles, lacking caryophyllidia. Rhinophoral and branchial sheaths low. Prostate massive, with two different portions. Penis and vagina unarmed. Accessory gland absent. Labial cuticle smooth. Inner and mid lateral radular teeth hamate. Outer lateral teeth multidenticulate or rarely simple and smooth.

#### Remarks

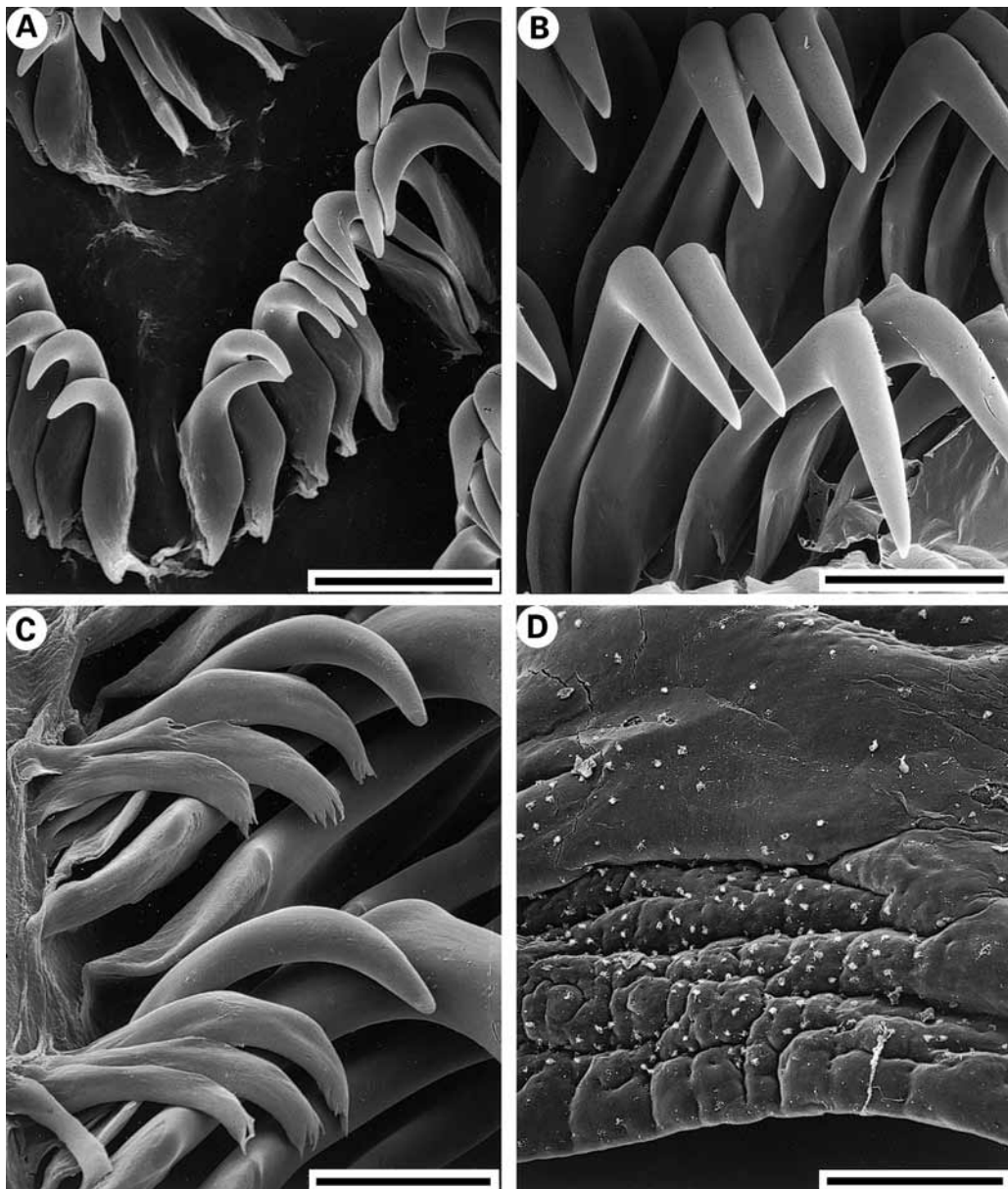
In April 1880, Bergh (1880b) introduced the genus *Halgerda* Bergh, 1880 based on *Halgerda formosa* Bergh, 1880. The main features of this genus include body depressed and rigid, branchial leaves short and tripinnate, absence of oral tentacles, foot narrow, absence of jaws and rachidian teeth, lateral teeth hamate and multidenticulate, outermost lateral teeth serrated, prostate large and penis unarmed.

In the same year, but at an undetermined date (see Winckworth, 1946), Bergh (1880c) introduced *Dictyodoris* Bergh, 1880 based on *Dictyodoris tessellata* Bergh, 1880, and with a question mark *Doris incii* J.E. Gray, 1850. The features of *Dictyodoris* are identical to those of *Halgerda* except for the presence of oral tentacles in *Dictyodoris*. Bergh (1880c) did not compare the features of *Dictyodoris* with those of *Halgerda*. He only commented that *Dictyodoris* differs from other forms in its overall shape, the opening of the gill, the constitution of the gill and the anterior border of the foot.

Despite their similarity, Bergh (1891) maintained *Halgerda* and *Dictyodoris* as different genera and classified them in the families Platydorididae and Di-aululidae respectively.

Rudman (1978) revised the systematics of the genera *Halgerda* and *Sclerodoris*. He considered *Sclerodoris* a different genus, but regarded *Dictyodoris* as a synonym of *Halgerda*.

We have studied the type species of *Halgerda* (*H. formosa*) and *Dictyodoris* (*D. tessellata*) which show no remarkable anatomical differences. The reproductive system and radula are very similar for both species.



**Figure 29.** *Halgerda formosa* (CASIZ 099340), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 20 µm. B, teeth from the central portion of the half-row; scale bar = 43 µm. C, outer lateral teeth; scale bar = 30 µm. D, mantle margin; scale bar = 200 µm.

As does Rudman (1978), we regard these names as synonyms.

*HALGERDA FORMOSA* BERGH, 1880  
(Figs 1F, 29, 30)

*Halgerda formosa* Bergh, 1880b: 191–195, pl. 4, figs 15–20, pl. 5, figs 10–12.

*Type material*

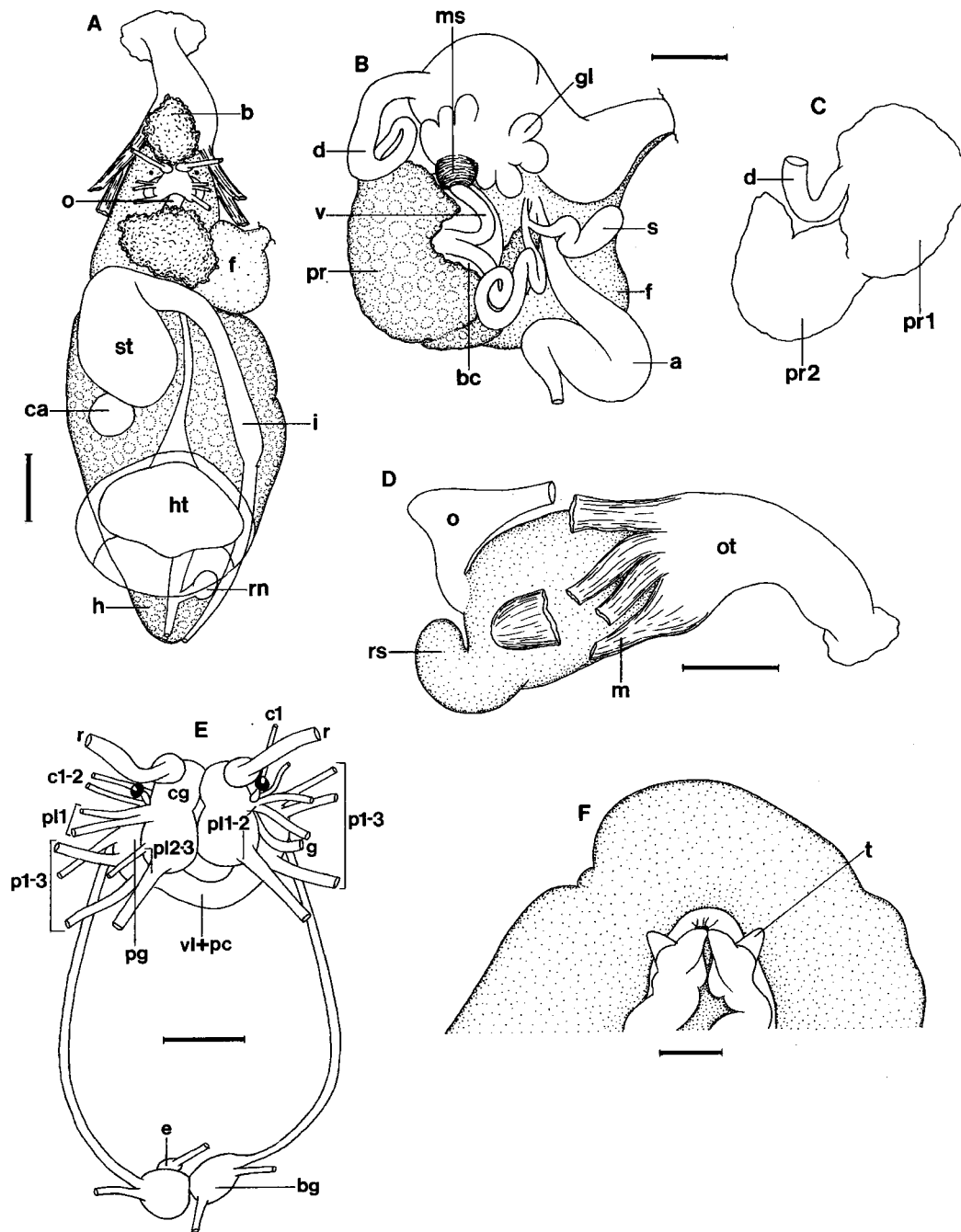
*Halgerda formosa* Bergh: the type material is lost, it is not deposited at ZMUC (Jensen, pers. comm.); the type locality is Réunion Island.

*Additional material*

Grand Baie, Mauritius, 5 March 1990, 1 specimen 12 mm preserved length, leg. H. Debelius (BMNH 1998027). North-East side of Manahuanja Island, Msimbati, Mtwara Region, Tanzania, 4 November 1994, 1 specimen 12 mm preserved length, leg. T.M. Gosliner (CASIZ 099340).

*External morphology*

The maximum length of this species reaches 30 mm. The body is oval and convex, firm, with a rigid, gelatinous texture. The dorsum is entirely covered with



**Figure 30.** *Halgerda formosa* (CASIZ 099340). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=0.5 mm. C, detail of the prostate; scale bar=0.5 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, central nervous system; scale bar=0.5 mm. F, ventral view of the mouth area; scale bar=1 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; ca, caecum; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; gl, vaginal gland; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; ms, vaginal muscular sphincter; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pg, pedal ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vl, visceral loop.

small irregular ridges. In the junctions of two or more ridges, they are raised into a short, conical tubercle. In the mantle margin there is a number of small conical tubercles, but there are no caryophyllidia (Fig. 29D). The rhinophoral and branchial sheaths are low and regular. There are four long, tripinnate branchial leaves, forming a circle, closed posteriorly by the anal papilla. The rhinophores are elongated, having 19 lamellae in a 12 mm long specimen.

The general colour of the living animals is whitish with a grey tinge (see Gosliner, 1987, as *H. punctata*). The ridges are lined with yellow-orange. Black lines or spots, and sometimes shorter, thinner yellow-orange lines are situated in the depressions between the ridges. The ridges closest to the mantle margin may have no yellow-orange coloration. The small tubercles in the mantle margin are opaque white or yellow. There is a thin opaque white or yellow-orange line around the mantle edge. The rhinophores have the laminar area black and the rachis translucent white, with a black longitudinal patch on the posterior edge. The branchial leaves are dark brown or black with the tips white.

Ventrally, the anterior border of the foot is notched and grooved (Fig. 30F). The oral tentacles are digitiform. The mantle margin is as wide as the foot. The ventral colour is the same as the dorsum but there are brown or black spots along the edge of the mantle and foot.

#### Anatomy

The posterior end of the oral tube has eight strong retractor muscles (Fig. 30D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles. The radular sac is very elongate, extending well behind the remainder of the buccal mass. The salivary glands have not been observed. The buccal bulb is shorter than the oral tube. The labial cuticle is smooth. The radular formula is  $36 \times (40.0.40)$  in a 12 mm preserved length specimen. Rachidian teeth are absent. The inner lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 29A). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 29A,B). The outermost teeth are elongate and have a number of small, short denticles (Fig. 29C). The oesophagus is long and expands directly into the stomach (Fig. 30A).

The ampulla is short and convoluted. It branches into a short oviduct and the prostate (Fig. 30B). The oviduct enters the female glands near the nidamental opening. The prostate is massive and granular. It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the ampulla (Fig. 30C). The

deferent duct is long and narrow. It expands into a wide ejaculatory portion, which opens into a common atrium with the vagina. The atrium is glandular near the opening of the vagina. The vagina is thin and short, and it is connected to the atrium by a muscular sphincter. At its proximal end, the vagina connects to the large and rounded bursa copulatrix. Another long and convoluted duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about ten times larger than the seminal receptacle (Fig. 30B).

In the central nervous system (Fig. 30E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are two cerebral nerves leading from each cerebral ganglia, and three pleural nerves leading from the left and two from the right pleural ganglia. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 30A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Fahey & Gosliner (1999) redescribed *Halgerda formosa* Bergh, 1880 based on specimens from the western Indian Ocean. This nominal species was regarded as uncertain by Rudman (1978). Rudman (1978), Gosliner (1987) and Wells & Bryce (1993) misidentified specimens of *H. formosa* as *Halgerda punctata* Farran, 1902.

#### *HALGERDA TESSELLATA* (BERGH, 1880) (Figs 31, 32)

*Dictyodoris tessellata* Bergh, 1880c: 76–78, pl. C, figs 11, 12, pl. F, figs 22, 23.

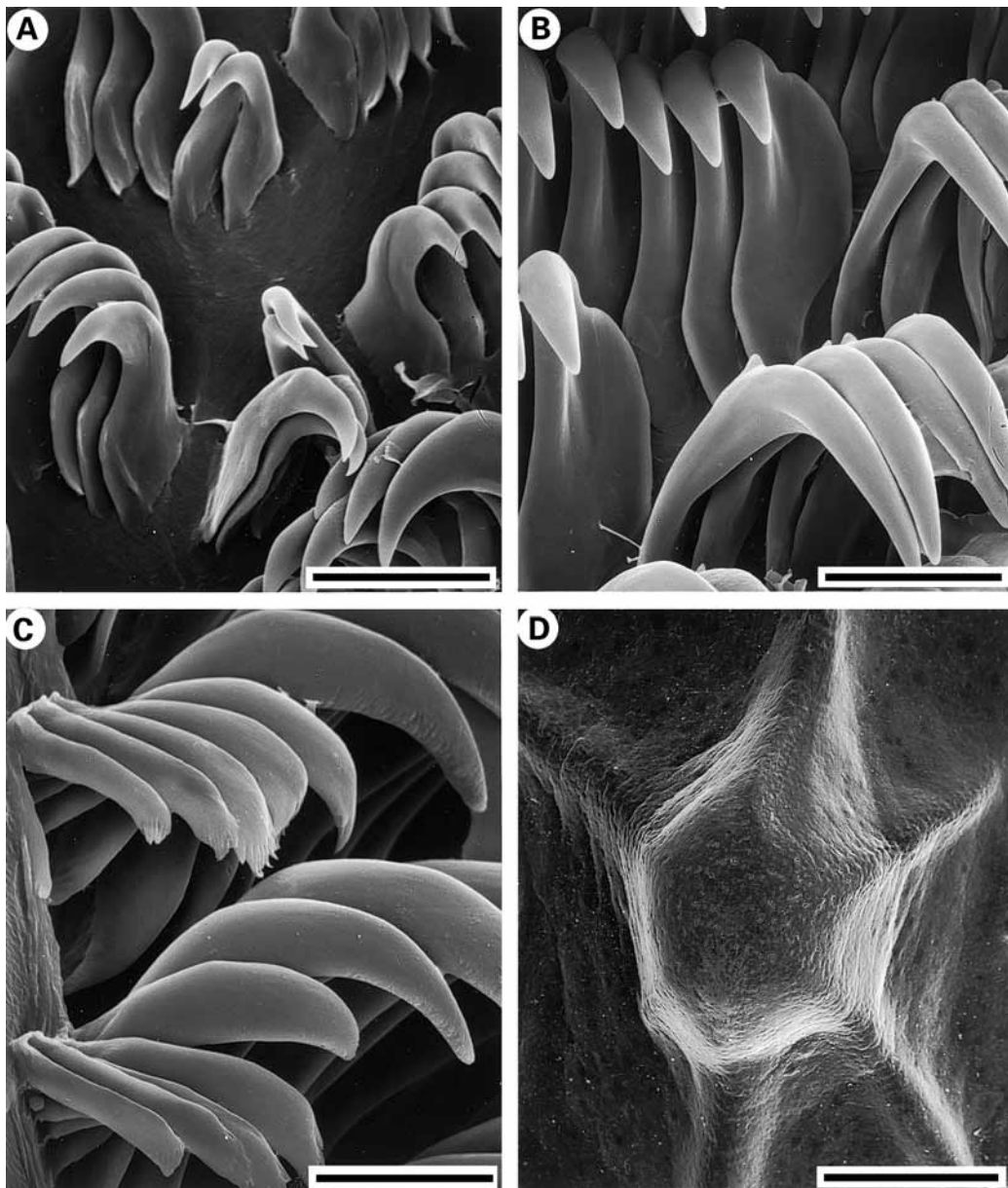
#### Type material

*Dictyodoris tessellata* Bergh: the type material is lost, it is not deposited at ZMUC (Jensen, pers. comm.); the type locality is Palau.

#### Additional material

North-east side of Mana, Huanja Island, Mtwara, Tanzania, 4 November 1994, 1 specimen 24 mm preserved length, leg. T.M. Gosliner (CASIZ 099308). Manado, Sulawesi, Indonesia, 24 May 1989, 3 specimens 13 mm preserved length, leg. P. Fiene-Severns (CASIZ 070309).





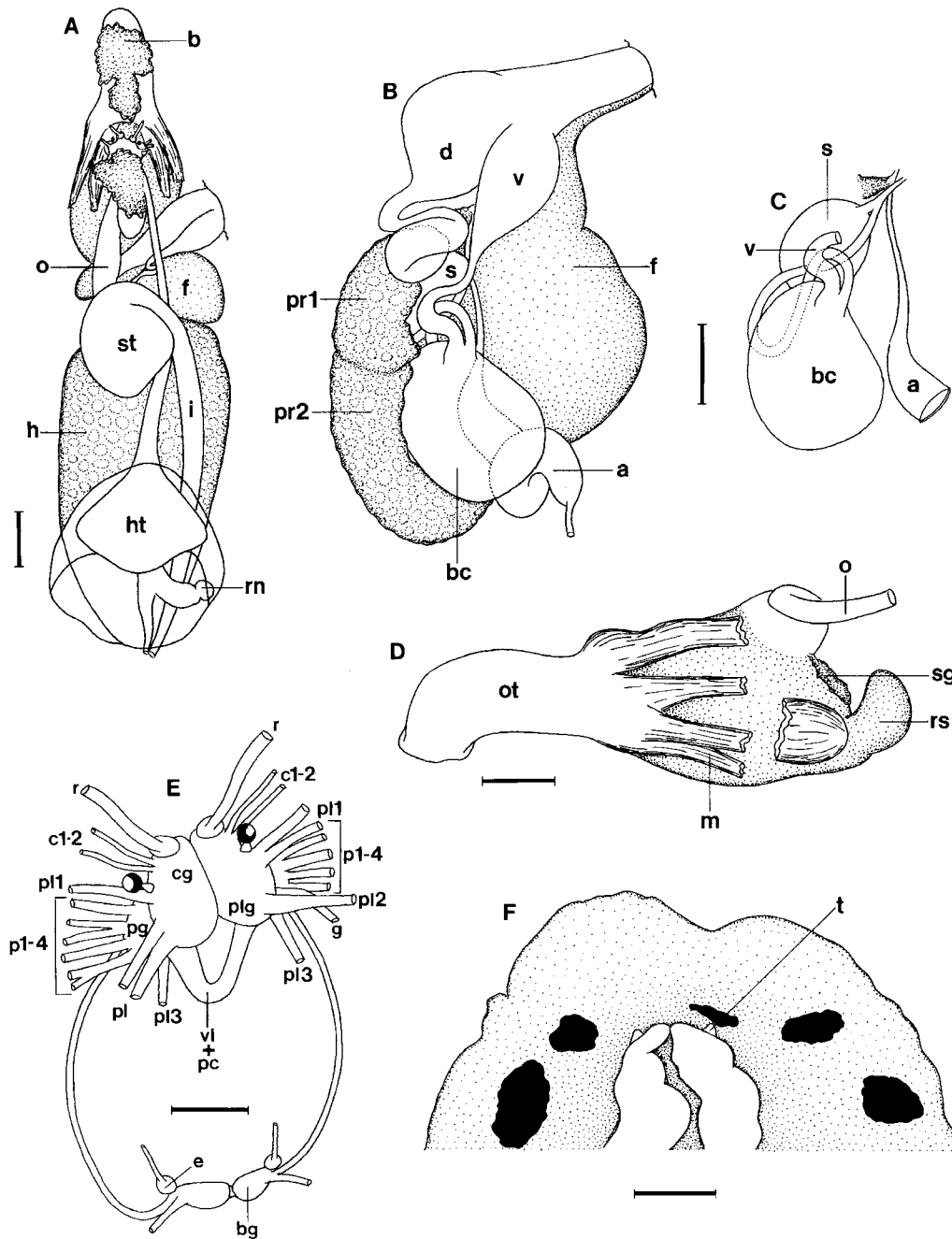
**Figure 31.** *Halgerda tessellata* (CASIZ 099308), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 25 µm. B, teeth from the central portion of the half-row; scale bar = 43 µm. C, outer lateral teeth; scale bar = 30 µm. D, dorsal ridges; scale bar = 750 µm.

#### *External morphology*

The maximum length of this species reaches 30 mm (Willan & Coleman, 1984). The body is oval and convex, firm, with a rigid, gelatinous texture. The dorsum is entirely covered with irregular ridges (Fig. 31D). At the junctions of two or more ridges, they are raised into a short, conical tubercle. In the mantle margin there is a number of small conical tubercles. The rhinophoral and branchial sheaths are low and regular. There are six long, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The

rhinophores are elongate, with 19 lamellae in a 24 mm preserved length specimen.

The general colour of the living animals is brown with a number of small, rounded yellow spots. The ridges are lined with yellow to orange. The ridges closest to the mantle margin are pale orange. The small tubercles in the mantle margin are opaque white or yellow. There is a thin opaque white or yellow-orange line around the mantle edge. The rhinophores have the laminar area and the rachis black to brown, the rest being translucent white. The branchial leaves



**Figure 32.** *Halgerda tessellata* (CASIZ 099308). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=0.5 mm. C, detail of several reproductive organs; scale bar=0.5 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, central nervous system; scale bar=0.5 mm. F, ventral view of the mouth area; scale bar=1 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pg, pedal ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vl, visceral loop.

are white with the rachis and few tips dark brown or black.

Ventrally the anterior border of the foot is notched and grooved (Fig. 32F). The oral tentacles are conical. The mantle margin is wider than the foot. The ventral colour is pale yellow with several large purple-brown spots in the mantle margin. There are numerous, longitudinal brown streaks or spots in the upper half of the sides of the foot.

#### Anatomy

The posterior end of the oral tube has eight strong retractor muscles (Fig. 32D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. The radular sac is very elongate. Two short salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is longer than the oral tube. The labial cuticle is smooth. The radular formula is  $47 \times (26.0.26)$  in a 24 mm preserved length specimen. Rachidian teeth are absent. The inner lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 31A). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 31A,B). The outermost teeth are elongate, multidenticulate plates (Fig. 31C). The denticles are very short and thin. The oesophagus is long and expands directly into the stomach (Fig. 32A).

The ampulla is long and convoluted. It branches into a short oviduct and the prostate (Fig. 32C). The oviduct enters the female glands near the nidamental opening. The prostate is massive and granular (Fig. 32B). It is divided into two different portions that are clearly distinguishable by their texture and coloration. The smallest portion is pale yellow and connects to the deferent duct, whereas the largest portion is whitish and connects to the ampulla (Fig. 32B). The deferent duct narrows and expands again into the long ejaculatory portion. It opens into a common atrium with the vagina. The vagina is long and distally wider. At its proximal end, the vagina connects to the large and oval bursa copulatrix. Another long and convoluted duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about three times larger than the seminal receptacle (Fig. 32B).

In the central nervous system (Fig. 32E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are two cerebral nerves leading from the cerebral ganglia, and three pleural nerves leading from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having four nerves leading from each one. The pedal

and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 32A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Rudman (1978) redescribed *Halgerda tessellata* based on specimens from Kenya and regarded it as a valid species. Our material is identical to that studied by Bergh (1880c) and Rudman (1978).

#### GENUS *BAPTODORIS* BERGH, 1884

*Baptodoris* Bergh, 1884: 671. Type species *Baptodoris cinnabarina* Bergh, 1884, by monotypy.

#### Diagnosis

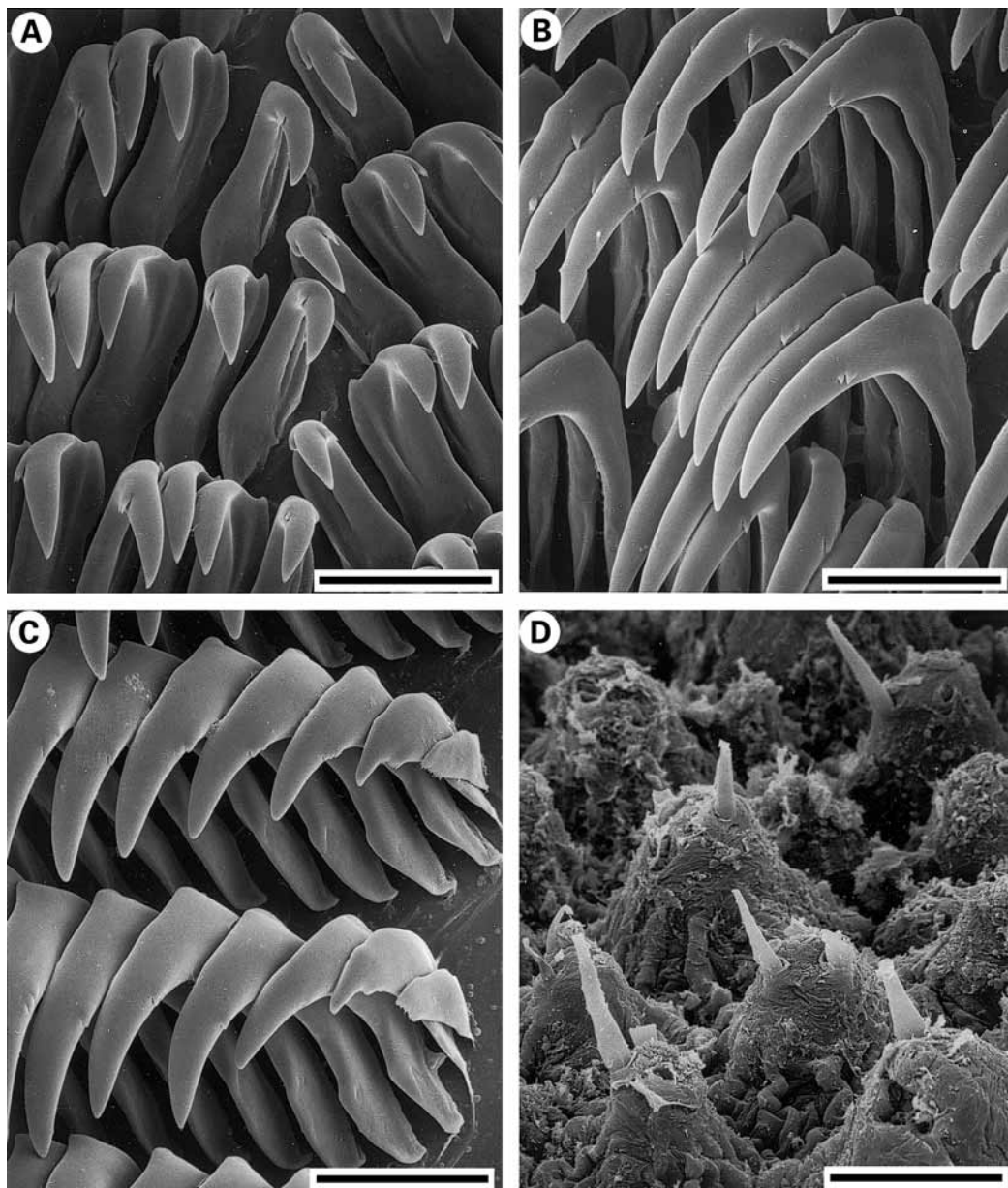
Body flexible. Dorsum covered with very small caryophyllidia. Rhinophoral and branchial sheaths low. Prostate massive, with two different portions. Penis armed with hooks. Atrium armed with very large hooks. Accessory gland lobate, without a spine. Labial cuticle smooth. Inner and mid lateral radular teeth hamate. Outermost teeth multidenticulate.

#### Remarks

Bergh (1884) introduced the genus *Baptodoris* Bergh, 1884 based on *Baptodoris cinnabarina* Bergh, 1884. According to Bergh (1884) this genus is characterized by the presence of minute dorsal tubercles, conical oral tentacles, bipinnate branchial leaves, smooth labial cuticle, pectinate outermost lateral teeth, large prostate and penis armed with hooks. However, in the description of *B. cinnabarina*, Bergh (1884) illustrated the outermost lateral teeth as smooth.

Schmekel & Portmann (1982) and Perrone (1985) redescribed *Baptodoris cinnabarina* based on newly collected specimens. These authors found small denticles in the outermost lateral teeth and improved the diagnosis of *Baptodoris* by including new characteristics such as the presence of caryophyllidia and an accessory gland. The atrial hooks in a species of *Baptodoris* were mentioned for the first time in Gosliner's (1991) description of *Baptodoris mimetica* Gosliner, 1991. More recently, Ballesteros & Valdés (1999) redescribed *B. cinnabarina* as having atrial hooks, differentiated from the penial hooks, and a prostate with two different portions.

Bouchet (1977) considered *Baptodoris* a synonym of *Platydoris* but he provided no further explanation. Garovoy, Valdés & Gosliner (1999) hypothesized that *Baptodoris* is monophyletic and different from *Platydoris* and *Gargamella* Bergh, 1894. The phylogenetic relationships of *Platydoris*, *Baptodoris* and



**Figure 33.** *Baptodoris cinnabarina* (MNCN 15.05/32381), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 60  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 75  $\mu$ m. C, outer lateral teeth; scale bar = 60  $\mu$ m. D, caryophyllidia; scale bar = 75  $\mu$ m.

*Gargamella*, discussed below, support the contention that *Baptodoris* is a monophyletic group, and it is here regarded as a valid genus.

*BAPTODORIS CINNABARINA* BERGH (1884)  
(Figs 1H, 33–35)

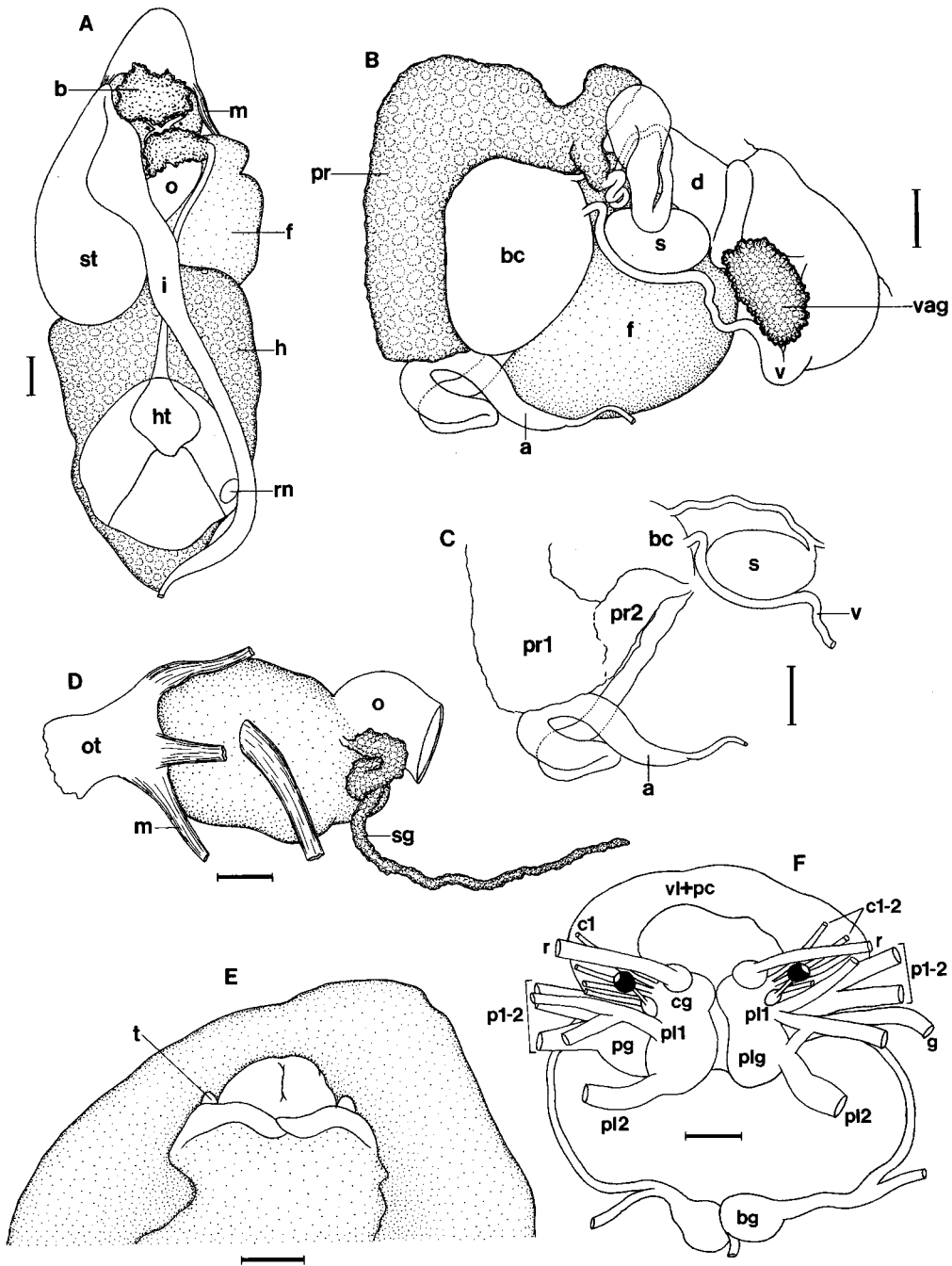
*Baptodoris cinnabarina* Bergh, 1884: 671–677, pl. 69, figs 35, 36, pl. 70, figs 1–19.

*Type material*

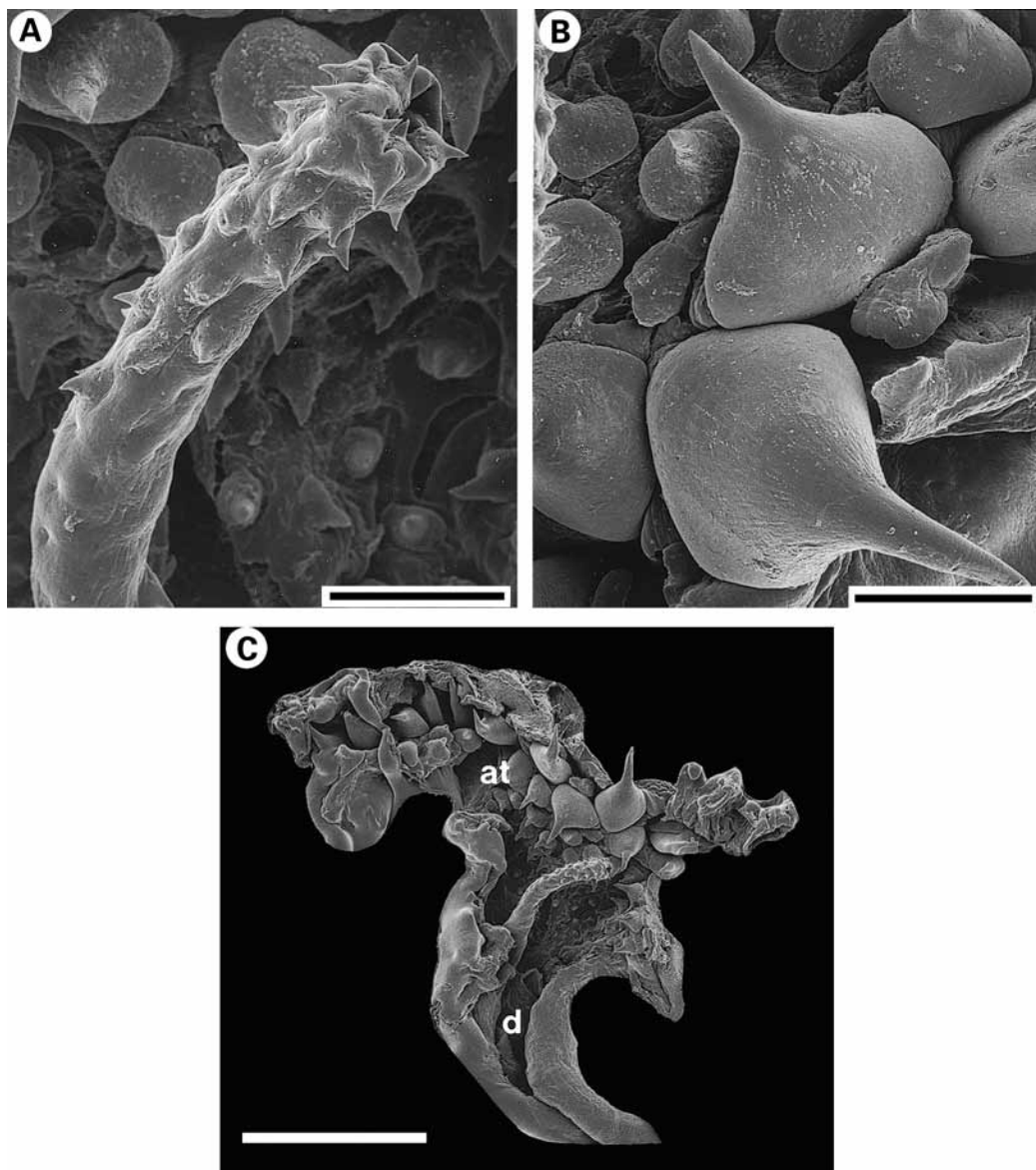
*Baptodoris cinnabarina* Bergh: the type material is lost, it is not deposited at ZMUC (Jensen, pers. comm.), the type locality is Trieste, Italy.

*Additional material*

Fauna Ibérica III Expedition, stn 266A (39°40.50'N, 0°29.25'E), near Islas Columbretes, Spain, 110–113 m



**Figure 34.** *Baptodoris cinnabarina* (MNCN 15.05/32381). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, detail of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=1 mm. E, ventral view of the mouth area; scale bar=1 mm. F, central nervous system; scale bar=0.5 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.



**Figure 35.** *Baptodoris cinnabarina* (MNCN 15.05/32381), SEM photographs of the reproductive system. A, penial hooks; scale bar = 150  $\mu$ m. B, atrial hooks; scale bar = 200  $\mu$ m. C, dissected reproductive system opening; scale bar = 1 mm. Abbreviations: at, atrium; d, deferent duct; v, vagina.

depth, 11 July 1994, 3 specimens 24–36 mm preserved length (MNCN 15.05/32381).

#### *External morphology*

The maximum length of this species reaches 36 mm. The body is oval and convex (Fig. 1H), firm, with a velvety texture. The dorsum is entirely covered with small caryophyllidia, about 40  $\mu$ m in length (Fig. 33D). Characteristics of the caryophyllidia include a short, conical base, long spicules and a very large, rounded ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. There are six short,

bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 19 lamellae in a 36 mm long specimen.

The general colour of the living animals varies from yellow to reddish grey or dark red. There are numerous small white and brown spots irregularly scattered on the dorsum. The gill and rhinophores are whitish, with some dark brown spots and a white apex.

Ventrally the anterior border of the foot is notched and grooved (Fig. 34E). The oral tentacles are conical. The mantle margin is wider than the foot. The ventral colour is whitish.



### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 34D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is three times longer than the oral tube. The labial cuticle is smooth. The radular formula is  $41 \times (53.0.53)$  in a 36 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having one cusp and a single denticle on the outer side (Fig. 33A). The inner teeth increase their size gradually towards the medial portion of the half-row (Fig. 33A,B). The two outermost teeth are smaller and have a number of small denticles (Fig. 33C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 34A).

The ampulla is long and convoluted. The oviduct enters the female glands near the centre of the mass. The prostate is massive, very large and granular (Fig. 34B). It envelops the bursa copulatrix and connects to a long and wide deferent duct that expands into the large ejaculatory portion of the deferent duct. The prostate is divided into two different portions that are clearly distinguishable by their different texture and coloration. The largest portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the female glands (Fig. 34C). The penis has eight rows of large penial hooks, about 30  $\mu\text{m}$  long (Fig. 35A). The atrium is internally covered with large hooks (Fig. 35B). The largest ones have a base about 250  $\mu\text{m}$  wide and a single cusp about 200  $\mu\text{m}$  long. The deferent duct opens into a common atrium with the vagina (Fig. 35C). There is a granular accessory gland connected to the atrium. The vagina is long and narrow, and lacks hooks. At its proximal end, the vagina connects to the large and almost rounded bursa copulatrix. Another duct, connecting to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about ten times larger than the seminal receptacle (Fig. 34B).

In the central nervous system (Fig. 34F) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two pleural nerves leading from each pleural ganglion. There is no distinct abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two short connectives. Rhinophoral and optical ganglia are present. The pedal ganglia have two nerves leading from each one. The pedal and parapodal commissures are enveloped together.

The circulatory system (Fig. 34A) includes a large heart and two blood glands placed over the central nervous system.

### Remarks

After the original description of *Baptodoris cinnabarina* by Bergh (1884), this species was redescribed by Schmekel & Portmann (1982), Perrone (1985) and Ballesteros & Valdés (1999). Our specimens have the same features as those described in the former papers, and all of them are clearly conspecific.

### GENUS *GARGAMELLA* BERGH, 1894

*Gargamella* Bergh, 1894: 175. Type species *Gargamella immaculata* Bergh, 1894, by monotypy.

### Diagnosis

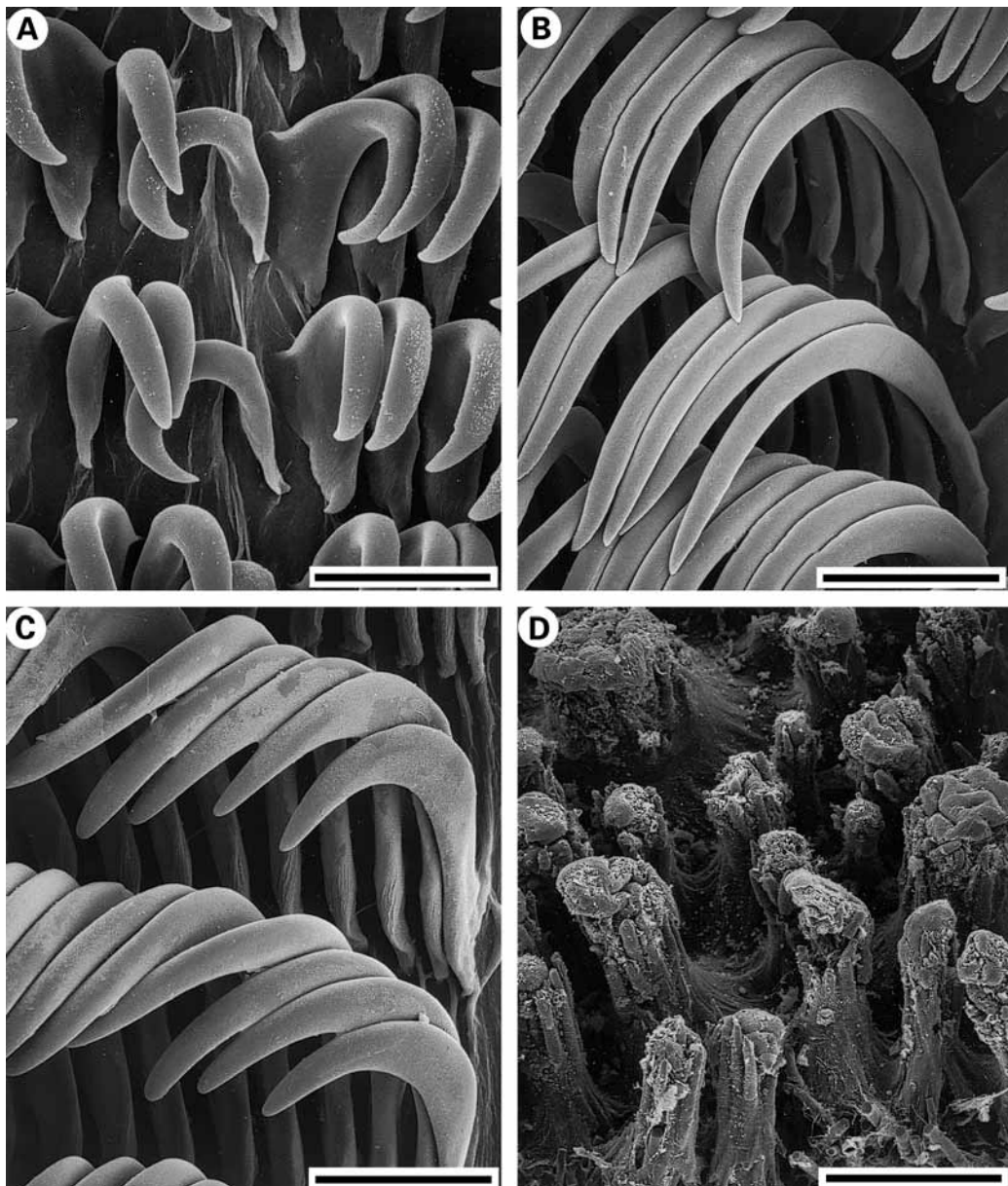
Body flexible. Dorsum covered with caryophyllidia. Rhinophoral and branchial sheaths low. Prostate massive, with two different portions. Penis armed with hooks. Vagina sometimes armed with very large hooks. Accessory gland lobate, without a spine. Labial cuticle smooth. Hamate radular lateral teeth, including the outermost.

### Remarks

Bergh (1894) introduced the genus *Gargamella* Bergh, 1894, based on *Gargamella immaculata* Bergh, 1894. According to Bergh (1894) this genus is characterized by a somewhat depressed body, silky dorsum, oral tentacles digitiform, branchial leaves tripinnate, anterior border of the foot notched and grooved, jaws and rachidian radular teeth absent, lateral teeth hook shaped, prostate large, penis armed with hard spherical hooks, and vestibular gland present.

Er. Marcus (1959) amplified the description of *Gargamella* with anatomical information based on newly collected material. The most outstanding new feature described by Er. Marcus is the presence of large copulatory spines in the atrium of *G. immaculata*. Schrödl (1997a,b) examined more specimens from Chile and described the presence of caryophyllidia. Furthermore, he agreed with Er. Marcus' (1959) description of the reproductive system. Garovoy *et al.* (1999) considered the vestibular hooks described by Er. Marcus (1959) and Schrödl (1997a,b) as actually situated in the opening of the vagina.

Bouchet (1977) regarded *Gargamella* as a synonym of *Platydoris*. In contrast, Garovoy *et al.* (1999), based on a phylogenetic analysis, regarded *Gargamella* as a valid genus, very closely related to *Platydoris* and *Baptodoris*. In the present paper, we studied the same specimens described by Garovoy *et al.* A new phylogenetic analysis has been conducted, including both larger outgroup and ingroup. The phylogeny obtained (see below) supports the hypothesis of Garovoy *et al.* that *Gargamella* is a monophyletic genus.



**Figure 36.** *Gargamella immaculata* (SMNHI 12520), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar=43  $\mu$ m. B, teeth from the central portion of the half-row; scale bar=60  $\mu$ m. C, outer lateral teeth; scale bar=43  $\mu$ m. D, caryophyllidia; scale bar=200  $\mu$ m.

*GARGAMELLA IMMACULATA* BERGH, 1894  
(Figs 2C, 36–38)

*Gargamella immaculata* Bergh, 1894: 175–178, pl. 4,  
figs 10–16, pl. 7, figs 1–3.

*Gargamella latior* Odhner, 1926: 93, pl. 3, figs 52–54.

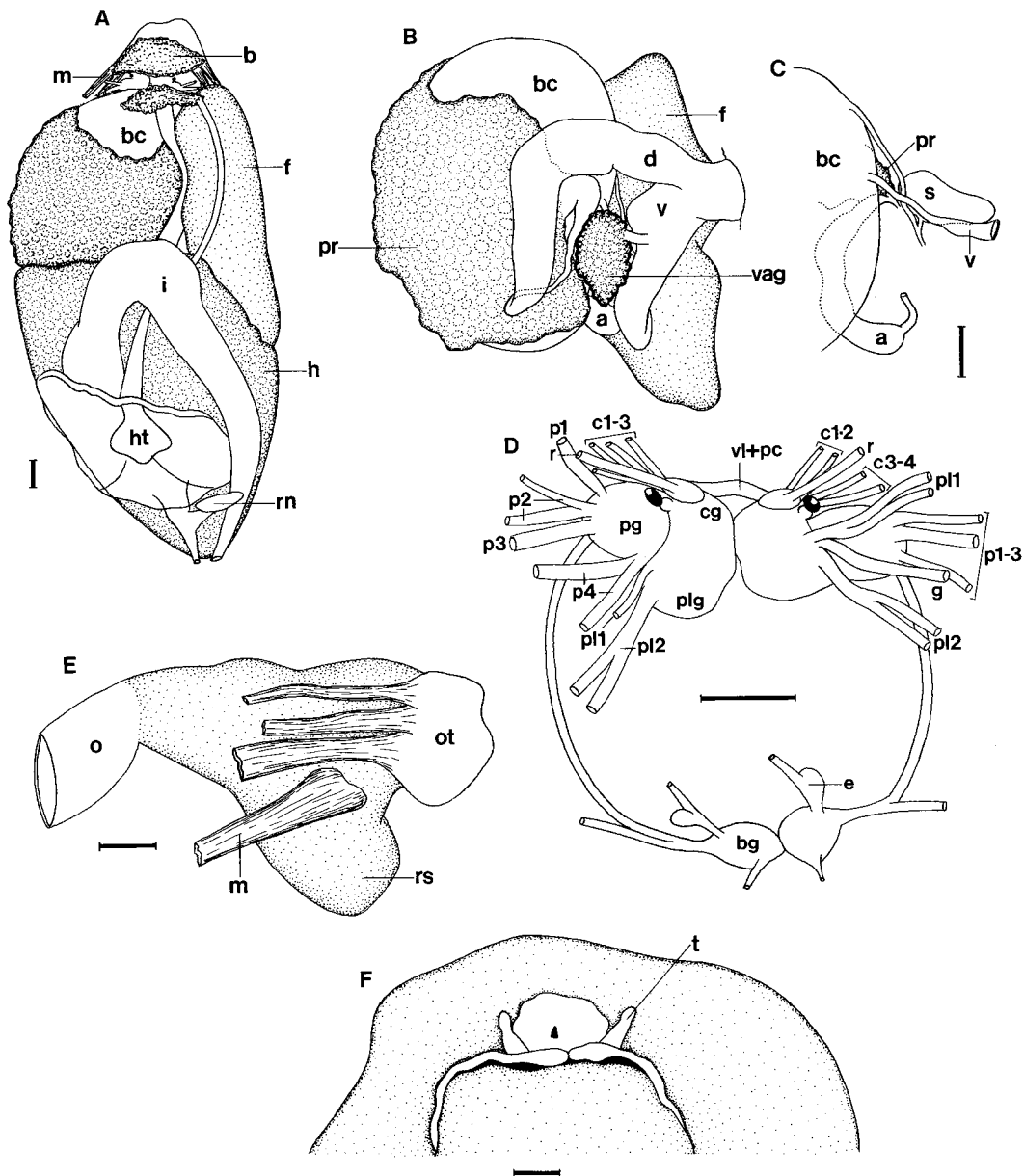
*Type material*

*Gargamella immaculata* Bergh. The type material is lost; it is not deposited at ZMUC (Jensen, pers. comm.).

The type locality is Cape Delgado, Patagonia, Argentina. *Gargamella latior* Odhner, *holotype* (by monotypy) – Última Esperanza, Tierra de Fuego, Argentina (SMNHI 1015), not examined.

*Additional material*

Seno Otway, near Punta Prat, Chile, 5 m depth, 3 January 1995, 2 specimens 24 mm preserved length, one of them dissected, leg. M. Schrödl (SMNHI 12520).

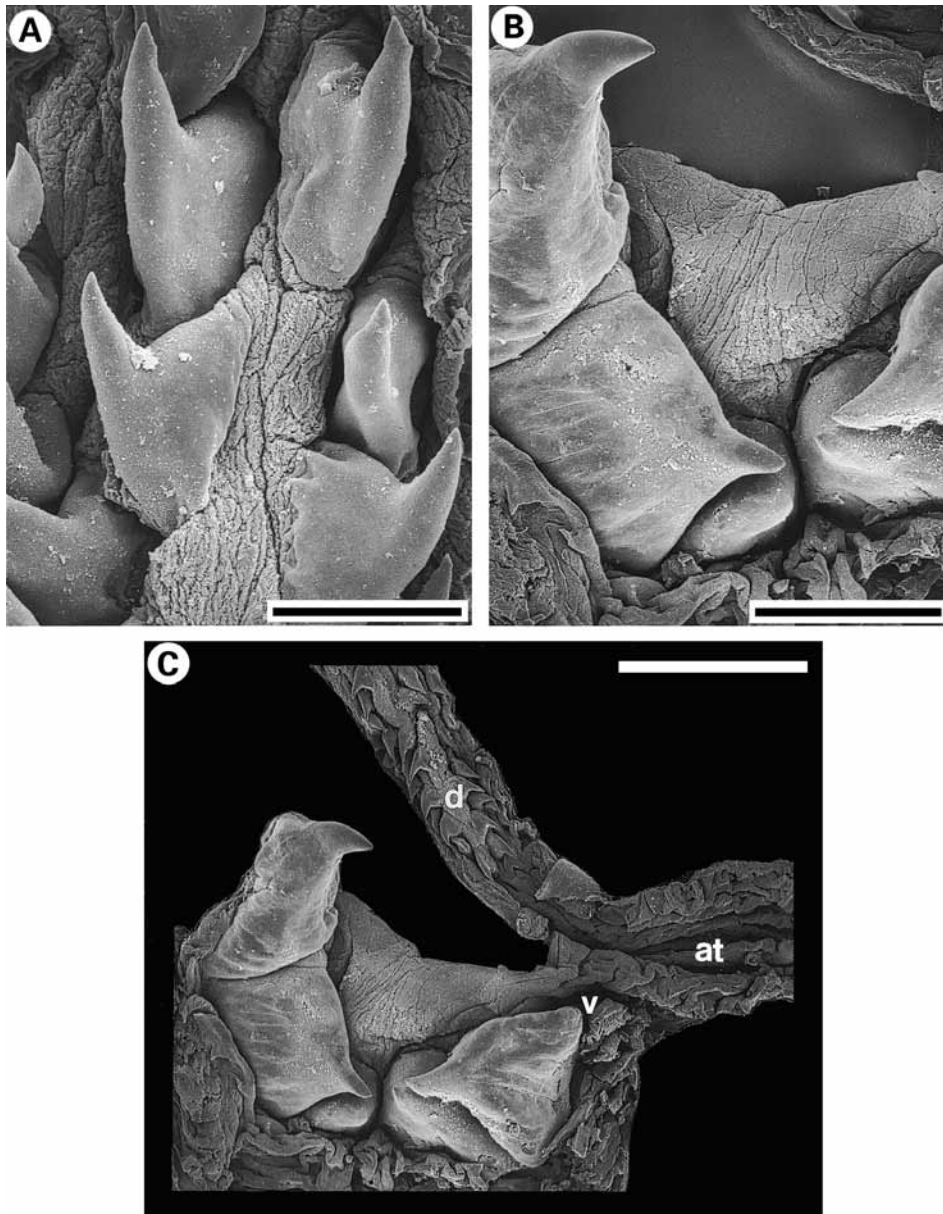


**Figure 37.** *Gargamella immaculata* (SMNHI 12520). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1.5 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

#### *External morphology*

The maximum length of this species reaches 50 mm (Schrödl, 1997a,b). The body is oval and convex (Fig. 2C), firm, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 200  $\mu$ m in

length (Fig. 36D). There are some smaller tubercles, about 80  $\mu$ m long, scarcely distributed between the larger ones. The caryophyllidia have a long, conical base, long spicules and a very large, rounded ciliated tubercle. The rhinophoral and branchial sheaths are



**Figure 38.** *Gargamella immaculata* (SMNHI 12520), SEM photographs of the reproductive system. A, penial hooks; scale bar = 100 µm. B, vaginal hooks; scale bar = 430 µm. C, dissected reproductive system opening; scale bar = 750 µm. Abbreviations: at, atrium; d, deferent duct; v, vagina.

low and regular. There are 11 short, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongate, with 18 lamellae in a 30 mm long specimen.

The general colour of the living animals varies from white to yellow or orange. The gill and rhinophores normally have the same colour as the dorsum but somewhat darker.

Ventrally the anterior border of the foot is notched and grooved (Fig. 37F). The oral tentacles are conical.

The mantle margin is narrower than the foot. The ventral colour is the same as the dorsum.

#### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 37E) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. The salivary glands have not been observed. The buccal bulb is three times as long as the oral tube. The labial cuticle is smooth. The radular formula is

49 × (76.0.76) in a 24 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 36A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 36A,B). The outermost teeth are also hamate and lack denticles (Fig. 36C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 37A).

The ampulla is small and elongate. It branches into a short oviduct and the prostate (Fig. 37C). The oviduct enters the female glands near the centre of the mass. The prostate is massive, very large and granular (Fig. 37B). It envelops the bursa copulatrix and connects to a thin duct that expands into a wide deferent duct. The penis has six rows of large penial hooks. They have a large base, about 100 µm wide and a single cusp about 30 µm long (Fig. 38A). The muscular deferent duct opens into a common atrium with the vagina. There is a granular accessory gland connected to the vagina. The vagina is long and wide, and has five large hooks (Fig. 38C). The largest vaginal hooks have a large base, over 400 µm wide, and a single cusp about 100 µm long (Fig. 38B). At its proximal end, the vagina connects to the large and almost rounded bursa copulatrix. From the bursa copulatrix leads another duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about 20 times larger than the seminal receptacle.

In the central nervous system (Fig. 37D) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and two pleural nerves leading from each pleural ganglion. There is no distinct abdominal ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have three nerves leading from the right one and four from the left one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 37A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Schrödl (1997a,b) revised the South American species of *Gargamella* and concluded that *Gargamella latior* Odhner, 1926 is a synonym of *Gargamella immaculata* Bergh, 1894. Garovoy *et al.* (1999) described two new species from South Africa and found that the large vestibular hooks described by Er. Marcus (1959) and Schrödl (1997a,b) in *G. immaculata* are actually situated in the opening of the vagina.

#### *GARGAMELLA WARENI* SP. NOV.

(Figs 2D, 39, 40)

#### Type material

*Holotype*: Bathus 3 Expedition, stn CP 833 (23°03'S, 166°58'E), Ride de Norfolk, New Caledonia, 441–444 m depth, 30 November 1993, 23 mm preserved length, dissected, leg. P. Bouchet (MNHN).

#### External morphology

The maximum length of this species reaches 23 mm. The body is oval and convex (Fig. 2D), firm, with a velvety texture. The dorsum is entirely covered with short caryophyllidia, about 100 µm in length (Fig. 39D). The caryophyllidia have a long, conical base, long spicules and a large, rounded ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. There are 6 short, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 22 lamellae in a 23 mm preserved length specimen.

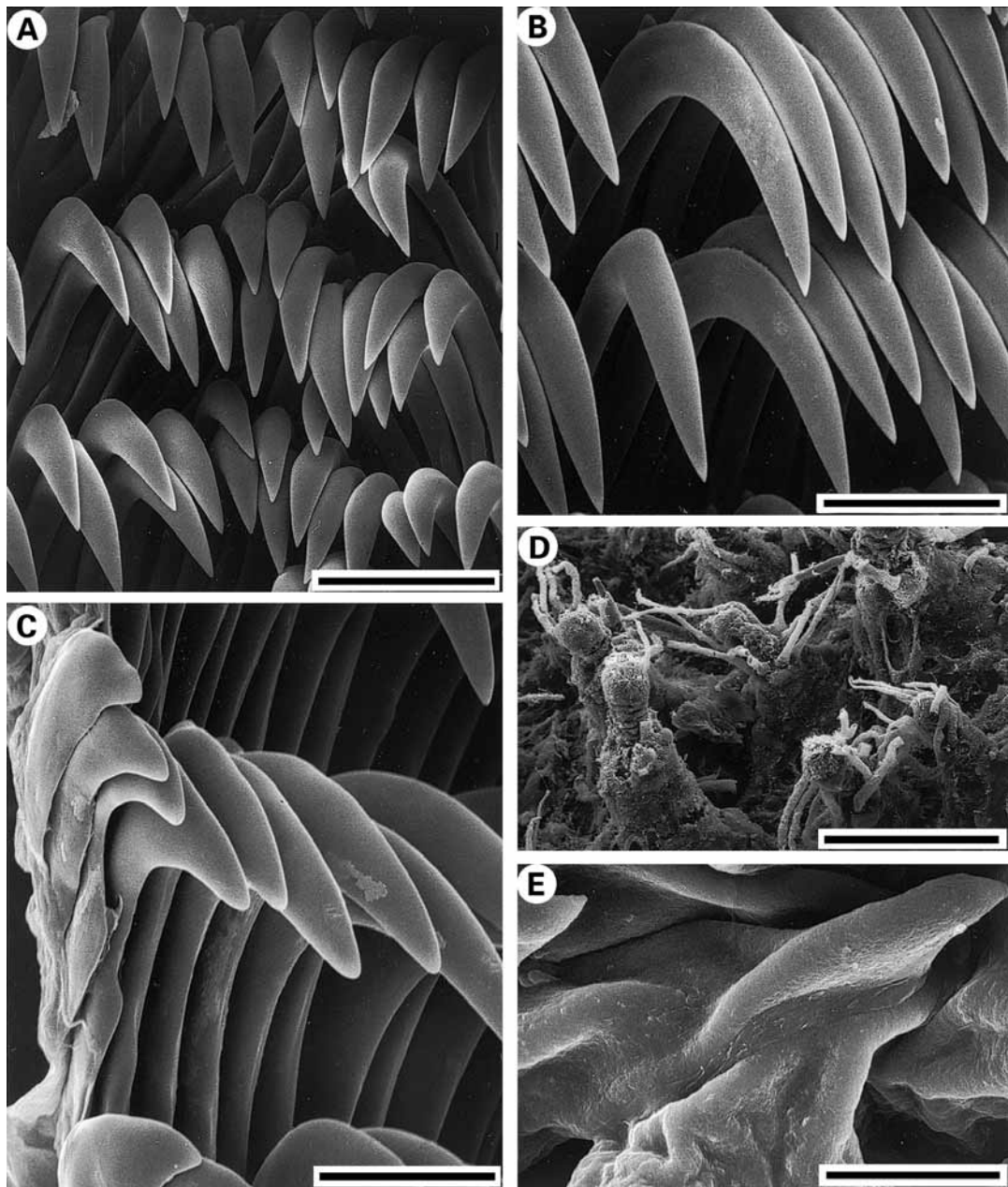
According to the collector's notes, the general colour of the living animals is white, with several large brown patches scattered on the dorsum. The gill and rhinophores are also white.

Ventrally the anterior border of the foot is notched and grooved (Fig. 40F). The oral tentacles are conical. The mantle margin is narrower than the foot. The ventral colour is the same as the dorsum.

#### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 40D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two short salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is as long as the oral tube. The labial cuticle is smooth. The radular formula is 48 × (69.0.69) in a 23 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 39A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 39A,B). The outermost teeth are smaller and also lack denticles (Fig. 39C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 40A).

The ampulla is small and elongate. It branches into a long oviduct and the prostate (Fig. 40B). The oviduct enters the female glands near the centre of the mass. The prostate is elongate and granular (Fig. 40B). It envelops the bursa copulatrix and connects to a very long duct that expands into the ejaculatory portion of the deferent duct. The penis has several rows of small hooks. They have a small base, about 30 µm long and a single cusp about 15 µm long (Fig. 39E). The muscular deferent duct opens into a common atrium with the

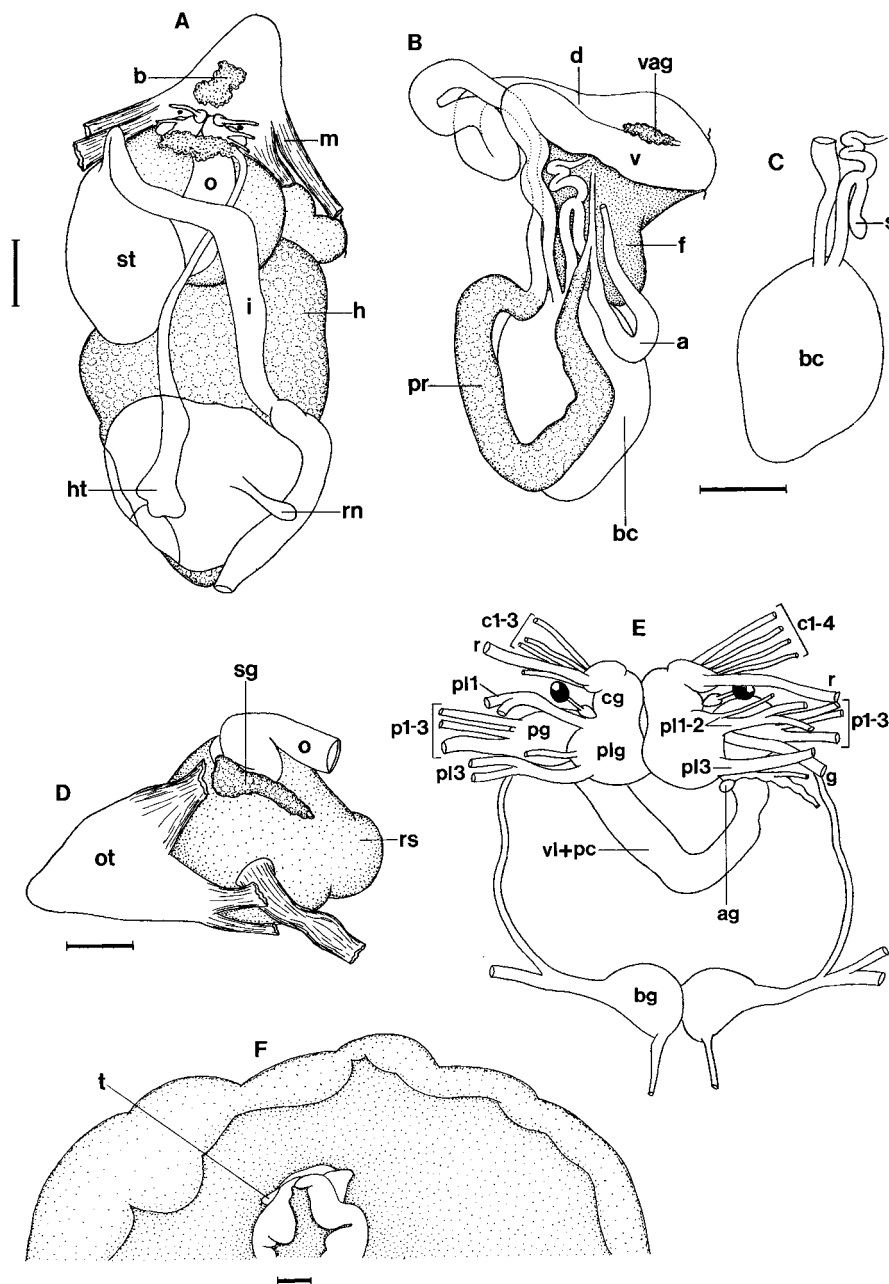


**Figure 39.** *Gargamella wareni* sp. nov. (MNHN), SEM photographs of the radula, dorsum and reproductive system. A, inner lateral teeth; scale bar = 43  $\mu$ m. B, teeth from the central portion of the half-row; scale bar = 43  $\mu$ m. C, outer lateral teeth; scale bar = 25  $\mu$ m. D, caryophyllidia; scale bar = 100  $\mu$ m. E, penial hooks; scale bar = 15  $\mu$ m.

vagina. There is a granular accessory gland connected to the atrium. The vagina is long and wide, and has no hooks. At its proximal end, the vagina connects to the large and almost rounded bursa copulatrix. From the bursa copulatrix leads another duct that connects to the minute seminal receptacle and the uterine duct. The bursa copulatrix is about 20 times larger than the seminal receptacle (Fig. 40C).

In the central nervous system (Fig. 40E) the cerebral

and pleural ganglia are fused together and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves leading from each pleural ganglion. There is a distinct abdominal ganglion in the right side of the visceral loop. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are present. The pedal ganglia have three



**Figure 40.** *Gargamella wareni* sp. nov. (MNHN). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 0.5 mm. C, detail of the bursa copulatrix and seminal receptacle; scale bar = 0.5 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; gg, genital ganglion; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pcc, parapetal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrxinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

nerves leading from each one. The pedal and parapetal commissures are enveloped together with the visceral

The circulatory system (Fig. 40A) includes a large heart and two blood glands situated in front of and behind the central nervous system.



*Etymology*

This species is dedicated to Anders Warén who participated in the collection of the holotype of this species and kindly lent us comparative material of *Gargamella immaculata* deposited at SMNHI.

*Remarks*

*Gargamella wareni* is clearly distinguishable from other species of the genus by both external coloration and internal anatomy. One of the new species from South Africa, illustrated by Gosliner (1987) as *Gargamella* sp. 2 and described by Garovoy *et al.* (1999), is the only species of the genus that is white with dark patches (see Garovoy *et al.*, 1999). However, the patches of the species from South Africa are black; in *G. wareni* they are brown. In addition, *G. wareni* has a very elongate, almost tubular prostate, whereas in the rest of the species the prostate is massive (Garovoy *et al.*, 1999) and the seminal receptacle is very small, being larger in all other species (Garovoy *et al.*, 1999).

According to Miller (1996), *Gargamella novozelandica* Eliot, 1907, described from New Zealand, is a species of *Jorunna* and a synonym of *Jorunna pantherina* (Angas, 1864).

GENUS *ALLOIODORIS* BERGH, 1904

*Alloiodoris* Bergh, 1904: 41–42. Type species *Alloiodoris marmorata* Bergh, 1904, by monotypy.

*Diagnosis*

Body flexible. Dorsum covered with elongate caryophyllidia. Rhinophoral and branchial sheath low. Prostate tubular, with a single portion. Penis armed with small hooks. Vagina unarmed. Ampulla with a short oviduct. Labial cuticle armed with small rodlets. Radular teeth hamate and sometimes denticulate.

*Remarks*

Bergh (1904) introduced the genus *Alloiodoris* Bergh, 1904 based on *Alloiodoris marmorata* Bergh, 1904, characterized by a dorsum covered with minute tubercles, digitiform tentacles, radular teeth denticulate and penis armed with hooks. Bergh noted that the hermaphrodite gland of this genus was separated from the digestive gland in a different mass. Eliot (1907) included *Doris lanuginata* Abraham, 1877, from New Zealand, in *Alloiodoris*, based on a re-examination of the type material and newly collected material. The features of *A. lanuginata* appear to be very similar to those of *A. marmorata*. Three other species assigned to *Alloiodoris* are *A. hedleyi* O'Donoghue, 1924, *A. inhacae* O'Donoghue, 1929 and *A. nivosus* Burn, 1958, all lacking denticles in the lateral teeth, and only one

(*A. inhacae*) has jaws (see O'Donoghue, 1924, 1929b, Burn, 1962).

The presence of caryophyllidia and an elongate, tubular prostate in *Alloiodoris* suggest close phylogenetic proximity of this genus to *Atagema*. In fact, the phylogenetic relationships of *Alloiodoris* and *Atagema*, discussed below, support the idea that both genera are closely related. The main differences between *Alloiodoris* and *Atagema*, that in our opinion qualify it as a different genus, are caryophyllidia lacking lateral tubercles, lack of elevated rhinophoral sheath and lobated branchial pocket, presence of two blood glands, presence of jaws and penial hooks, and absence of glands on the retractor muscles of the oral tube.

*ALLOIODORIS MARMORATA* BERGH, 1904

(Figs 2E, 41–43)

*Type material*

*Lectotype* (here designated): north-west coast of Tasmania, date unknown, 35 mm preserved length, leg. Lodder (ZMUC GAS-2057). *Paralectotypes*: north-west coast of Tasmania, date unknown, 2 specimens 30–35 mm preserved length, leg. Lodder (ZMUC GAS-346).

*External morphology*

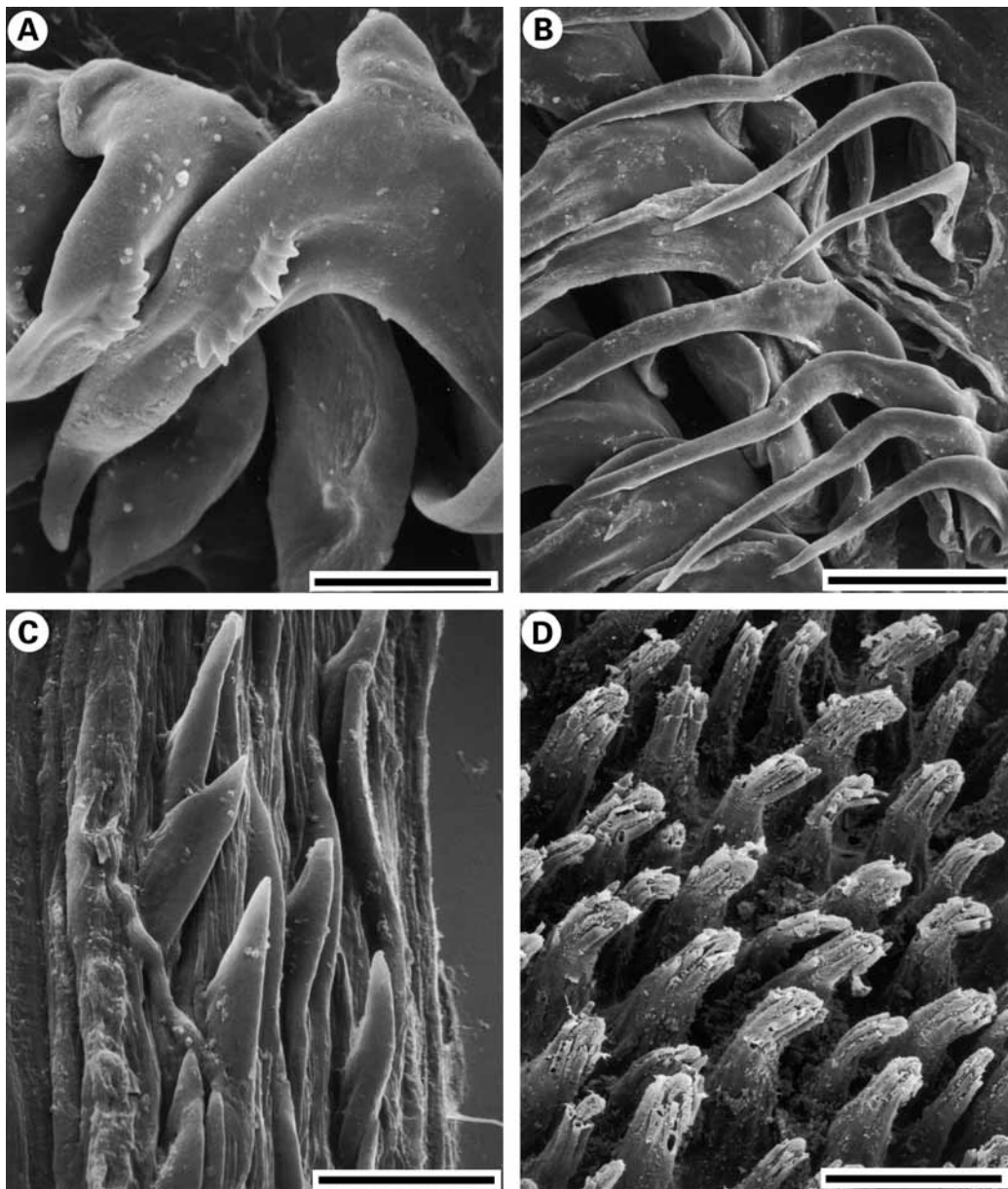
The maximum length of this species reaches 35 mm. The body is oval and convex (Fig. 2E), soft, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 160 µm in length (Fig. 41D). There are some smaller tubercles, about 100 µm long, sparsely distributed between the others. The caryophyllidia have a long, conical base, long spicules and a small, rounded ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. They are situated very anteriorly and posteriorly respectively. There are six short, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are club shaped, with 24 lamellae in a 35 mm long specimen.

The colour of the living animals is unknown. Preserved specimens are uniformly grey, with no traces of other coloration.

Ventrally the anterior border of the foot is notched and grooved (Fig. 42F). The oral tentacles are conical. The mantle margin is narrower than the foot. The ventral colour is the same as the dorsal.

*Anatomy*

The posterior end of the oral tube has six strong retractor muscles (Fig. 42E) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is longer than the oral tube. The jaws

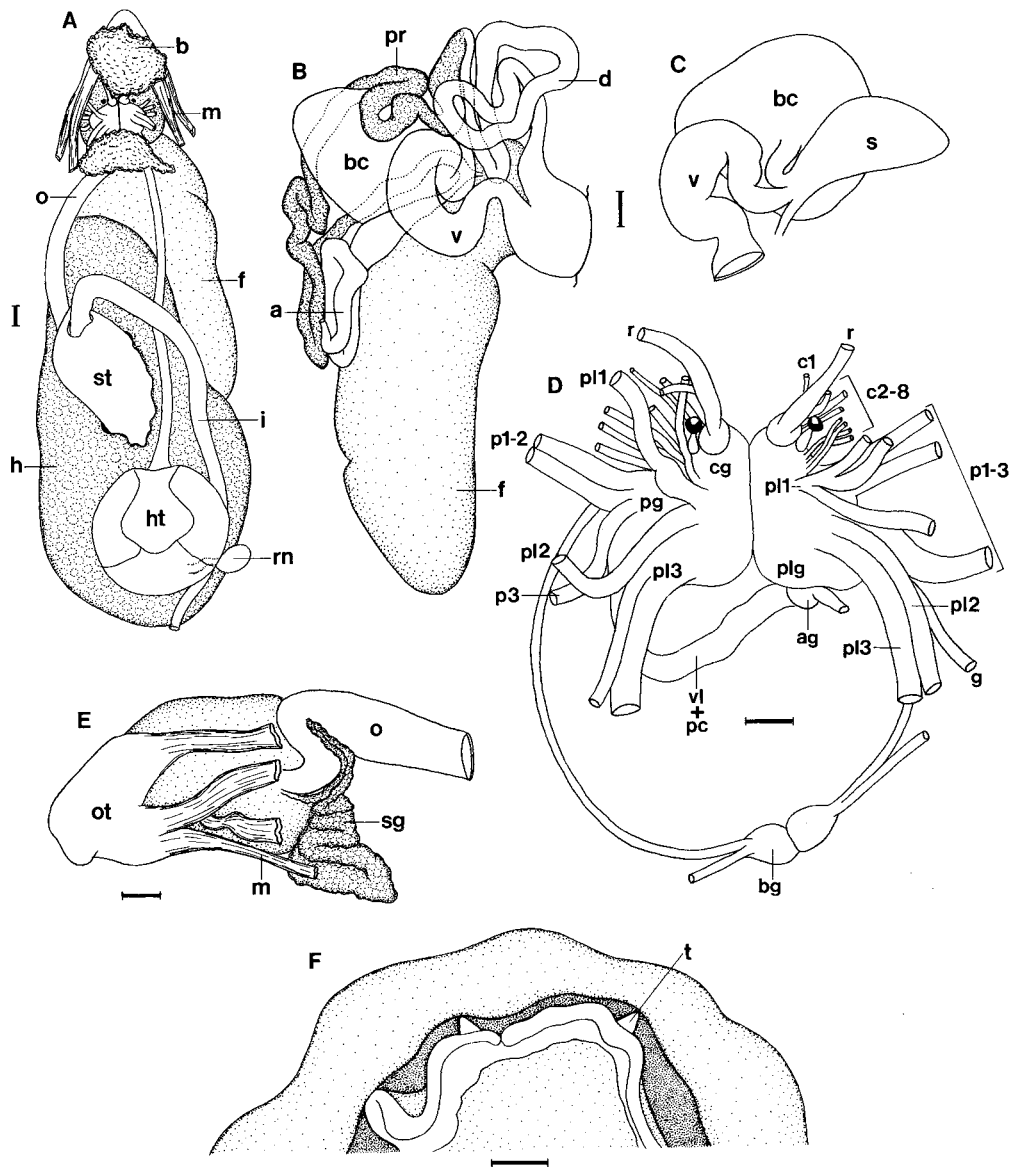


**Figure 41.** *Alloiodoris marmorata* (ZMUC GAS-2057), SEM photographs of the radula, penis and dorsum. A, teeth from the central portion of the half-row; scale bar = 25  $\mu\text{m}$ . B, outer lateral teeth; scale bar = 60  $\mu\text{m}$ . C, penial hooks; scale bar = 20  $\mu\text{m}$ . D, caryophyllidia; scale bar = 300  $\mu\text{m}$ .

consist of numerous thin, irregular elements, about 20–30  $\mu\text{m}$  long (Fig. 43D). The radular formula is  $35 \times (36.0.36)$  in a 35 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp (Figs 41A, 43A,B). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 43A,B). In one of the paralectotypes examined (ZMUC GAS-346) the inner and mid lateral teeth have a single strong denticle (Fig. 43B), whereas in the lectotype (ZMUC GAS-2057) they have 1–9 strong denticles (Fig. 41A). The

outermost teeth are elongated and lack denticles (Figs 41B, 43C). The oesophagus is very long and expands directly into the stomach (Fig. 42A).

The ampulla is very long and convoluted. It branches into a short oviduct and the prostate (Fig. 42B). The oviduct enters the female glands near the nidamental opening. The prostate is tubular, folded and granular (Fig. 42B). The deferent duct is very long and wide, and opens into a common atrium with the vagina. The penis has ten rows of small hooks about 40  $\mu\text{m}$  long (Fig. 41C). They have a triangular cusp about 20  $\mu\text{m}$

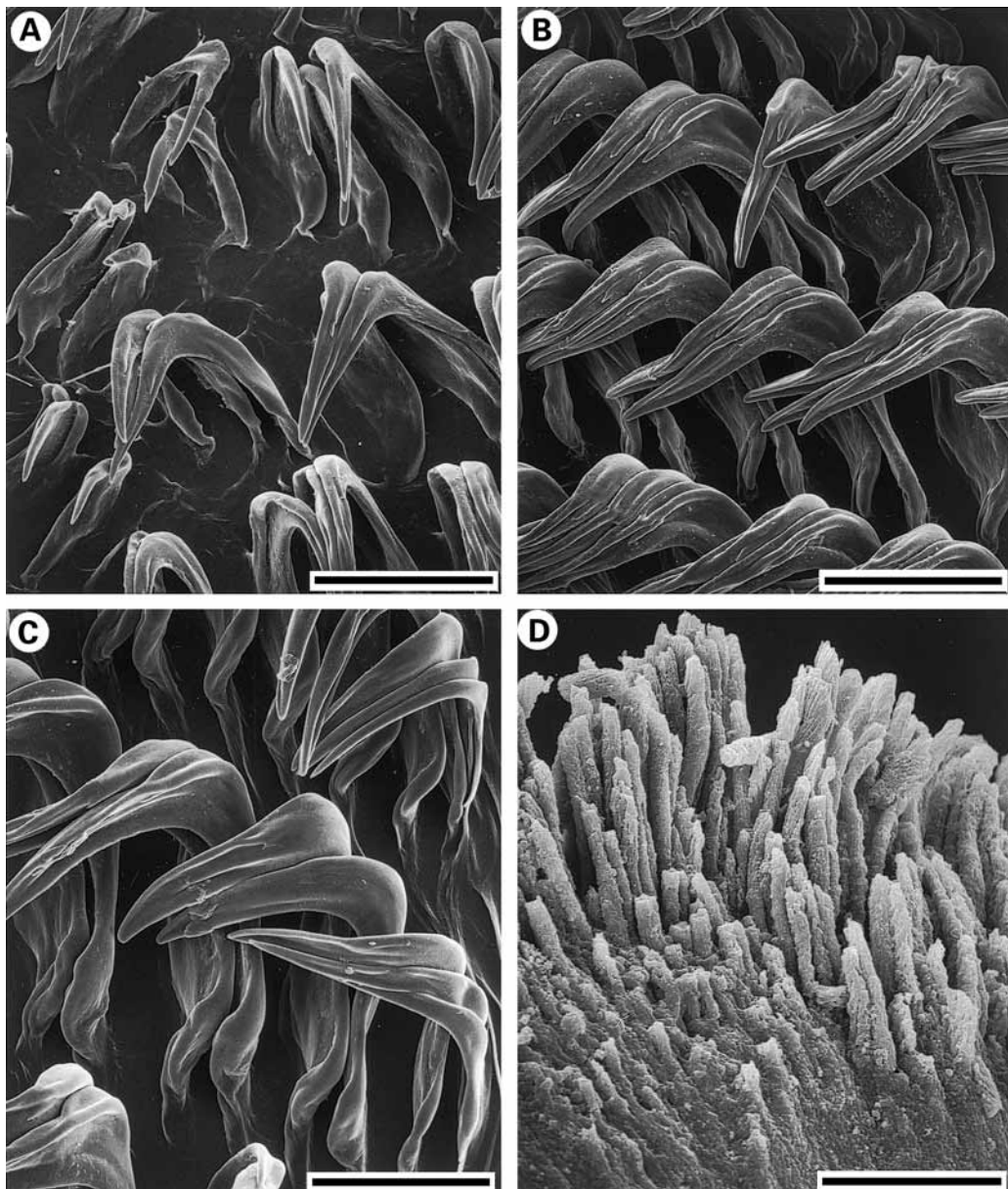


**Figure 42.** *Alloiodoris marmorata* (ZMUC GAS-2057). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1.5 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vl, visceral loop.

long. The vagina is long and wide. At its proximal end, the vagina is joined by a short duct, which connects to the large and irregular bursa copulatrix, the seminal receptacle and the short uterine duct. The bursa copulatrix is about three times the size of the seminal receptacle (Fig. 42C).

In the central nervous system (Fig. 42D) the cerebral and pleural ganglia are fused together and distinct

from the pedal ganglia. There are eight cerebral nerves leading from the cerebral ganglia, and three pleural nerves leading from each pleural ganglion. There is a distinctive abdominal ganglion on the right side of the visceral loop. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are present. The pedal ganglia have three nerves leading



**Figure 43.** *Alloiodoris marmorata*, SEM photographs of the radula and jaws. A, inner lateral teeth (ZMUC GAS-346); scale bar = 100 µm. B, teeth from the central portion of the half-row (ZMUC GAS-346); scale bar = 150 µm. C, outer lateral teeth (ZMUC GAS-346); scale bar = 100 µm. D, jaw elements (ZMUC GAS-2057); scale bar = 25 µm.

from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 42A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

Basedow & Hedley (1905) redescribed *A. marmorata* based on specimens collected from Southern Australia. However, these authors did not find the denticles on the lateral teeth that are clearly visible in the type

specimens. Eliot (1907) considered the specimens seen by Basedow & Hedley (1905) to belong to a different species. O'Donoghue (1924) introduced the new name *Alloiodoris hedleyi* O'Donoghue, 1924 for this species, also based on newly collected material from Western Australia. Years later, and probably unaware of O'Donoghue's (1924) paper, Burn (1962) introduced another new name, *Alloiodoris nivosus* Burn, 1962, for Basedow & Hedley's (1905) misidentification of *A. marmorata*.

Willan & Coleman (1984) depicted living animals that in their opinion belonged to *A. marmorata*.

Because of the lack of anatomical studies, this identification is tentative.

#### GENUS *SCLERODORIS* ELIOT, 1904

*Sclerodoris* Eliot, 1904a: 361. Type species *Sclerodoris tuberculata* Eliot, 1904, here designated.

? *Gravieria* Vayssière, 1912: 29–30. Type species *Gravieria rugosa* Vayssière, 1912, by monotypy.

#### Diagnosis

Body wide and flattened, coriaceous. Dorsum covered with ridges and caryophyllidia. Rhinophoral sheaths somewhat elevated. Branchial sheath rounded. Prostate massive, with two different portions. Oviduct short. Penis armed with hooks. Vagina unarmed. Accessory gland lobate, without spine. Labial cuticle and radular teeth smooth. Inner and mid lateral radular teeth hamate. Outermost lateral teeth multi-denticulate.

#### Remarks

Eliot (1904a) introduced the genus *Sclerodoris* Eliot, 1904 for *Doris osseosa* Kelaart, 1859, *Doris carinata* Alder & Hancock, 1864 (non *Doris carinata* Quoy & Gaimard, 1832), *Doris apiculata* Alder & Hancock, 1864, *Doris tristis* Alder & Hancock, 1864, and four new species, *Sclerodoris tuberculata* Eliot, 1904, *Sclerodoris minor* Eliot, 1904, *Sclerodoris rubra* Eliot, 1904 and *Sclerodoris coriacea* Eliot, 1904.

Thompson & Brown (1974) subsequently designated *Doris osseosa* Kelaart, 1859 as the type species of *Sclerodoris*. However, *Doris osseosa* is, without question, a species of *Atagema*. According to Kelaart (1859), *D. osseosa* has elevated, granular rhinophoral sheaths and five branchial leaves emerging horizontally from under the posterior termination of the dorsal ridge. Eliot (1906b) studied two radulae belonging to the original type specimens of *D. osseosa*, which have 5–6 innermost slender teeth and the rest hamate, the two outermost being degenerate. All these features are typical of the genus *Atagema* (see diagnosis and remarks about that genus). According to this concept of *Sclerodoris*, Ev. Marcus & Er. Marcus (1970) and Thompson & Brown (1974) considered *Sclerodoris* to be a synonym of *Atagema*.

Four years later, unaware of Thompson & Brown's type species selection, Rudman (1978) designated *S. tuberculata* as the type species of *Sclerodoris*. He also redescribed *S. tuberculata*, including complete external and anatomical descriptions. There is an evident contradiction between Thompson & Brown's and Rudman's concepts of *Sclerodoris*, owing to the differences between *D. osseosa* and *S. tuberculata*. It is also clear

that *Sclerodoris sensu* Rudman, based on *S. tuberculata* and related species, is very different from *Atagema*. The prostate of *Sclerodoris* is massive whereas it is tubular in *Atagema*. *Sclerodoris* lacks glands attached to the retractor muscles of the oral tube and lateral ciliated tubercles in the caryophyllidia that are both present in *Atagema*. The branchial sheath of *Sclerodoris* is irregular and somewhat inclined backwards, but it lacks the lobes present in *Atagema*, and the gill is arranged almost vertically, not horizontally. The radula of *Sclerodoris* has denticulate plate-like outermost lateral teeth, whereas in *Atagema* they are smooth and hamate.

The description of *D. osseosa* by Eliot (1904a) also agrees with Rudman's concept of *Sclerodoris*. In fact, Eliot (1906b), after examining the radula of the type material of *D. osseosa*, recognized that the specimens he identified as *D. osseosa* when describing the genus *Sclerodoris* could belong to a different species. This appears to be a case of misidentification of the type species of *Sclerodoris*. It is doubtful that Eliot's concept of *D. osseosa* corresponds to the original description of this species by Kelaart (1859); thus the identity of the type species of *Sclerodoris* is uncertain. Since Rudman's (1978) concept of *Sclerodoris* has been generally accepted, in our opinion *D. tuberculata* should be chosen as the type species, in conformity with the usage of the name *Sclerodoris*. According to the new version of the code (ICZN, 1999), if a type species has been misidentified, an author may select, and thereby fix as type species, the species that will best serve stability and universality (Article 70.3.2). Therefore, *D. tuberculata* is here selected as the type species of *Sclerodoris*.

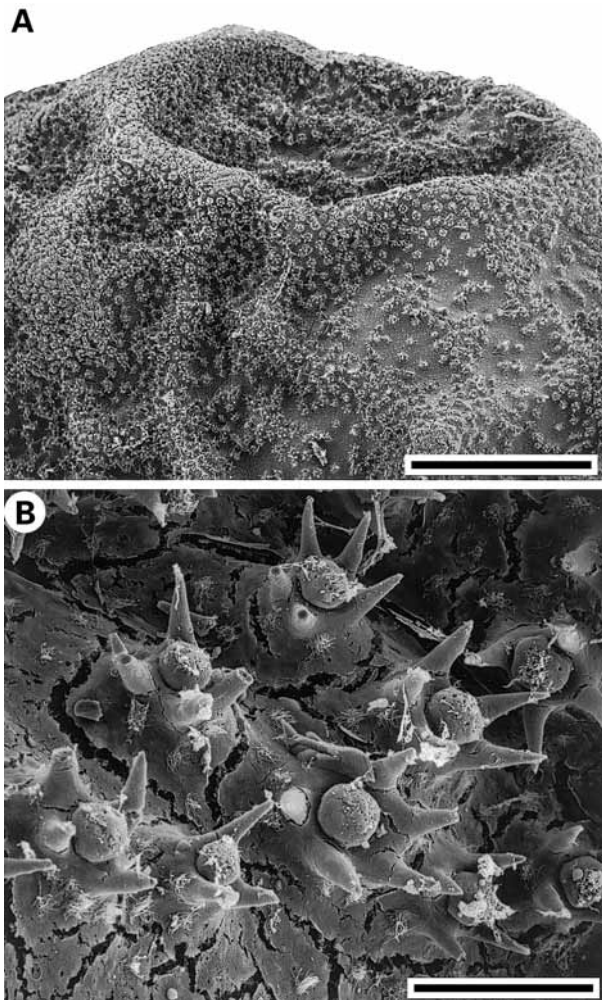
Eliot (1904b) recognized that *Sclerodoris* is a synonym of *Peronodoris* Bergh, 1904. In his opinion, both genera are identical with the exception of the presence of a penial armature (stylet) in *Peronodoris*, which is absent in *Sclerodoris*. Likewise Ev. Marcus & Er. Marcus (1970) considered that the presence of a penial stylet in *Peronodoris* clearly separates this genus from *Sclerodoris*. Rudman (1978) commented that *Peronodoris* is different from *Sclerodoris* because of the absence of a prostate. As a result of this major difference, he chose not to synonymize *Peronodoris* with *Sclerodoris*. Rudman (1978) also considered *Sclerodoris* as a valid genus different from the related *Halgerda*.

#### *SCLERODORIS TUBERCULATA* ELIOT, 1904 (Figs 11, 44–46)

*Sclerodoris tuberculata* Eliot, 1904: 381–382.

#### Type material

The original type material is lost; it is not deposited at BMNH; the type locality is Prison Island, Zanzibar



**Figure 44.** *Sclerodoris tuberculata* (CASIZ 073247), SEM photographs of the dorsum. A, dorsal ridges; scale bar = 1.5 mm. B, caryophyllidia; scale bar = 100  $\mu$ m.

Harbour. *Neotype* (here designated) – Seychelles, 26 October 1946, 38 mm preserved length, leg. Winckworth (BMNH 1960900).

#### *Additional material*

Ambatorao, north end of Île Saint Marie, Madagascar, 7 April 1990, 1 specimen 35 mm preserved length, leg. T.M. Gosliner (CASIZ 073247). Seychelles, 10 January 1941, 2 specimens 22–26 mm preserved length, leg. Winckworth (BMNH 1960897).

#### *External morphology*

The maximum length of this species reaches over 40 mm. The body is flattened, wide with a coriaceous texture. The dorsum has an irregular network of short ridges. In the junctions of two or more ridges, they are raised into a conical tubercle (Fig. 11). These tubercles

are more numerous near the border or the mantle, but larger in the centre of the dorsum. There is a large depression in front of the gill (Figs 11, 44A). The entire dorsum is covered with a number of small caryophyllidia, about 50  $\mu$ m long (Fig. 44B). They have a short, conical base, long spicules and a small, rounded ciliated tubercle. The rhinophoral sheaths are low, covered with caryophyllidia. The branchial sheath is rounded. There are eight bipinnate branchial leaves. The short anal papilla is closing the circle of branchial leaves. The rhinophores are long, with 26 lamellae in a 35 mm preserved length specimen.

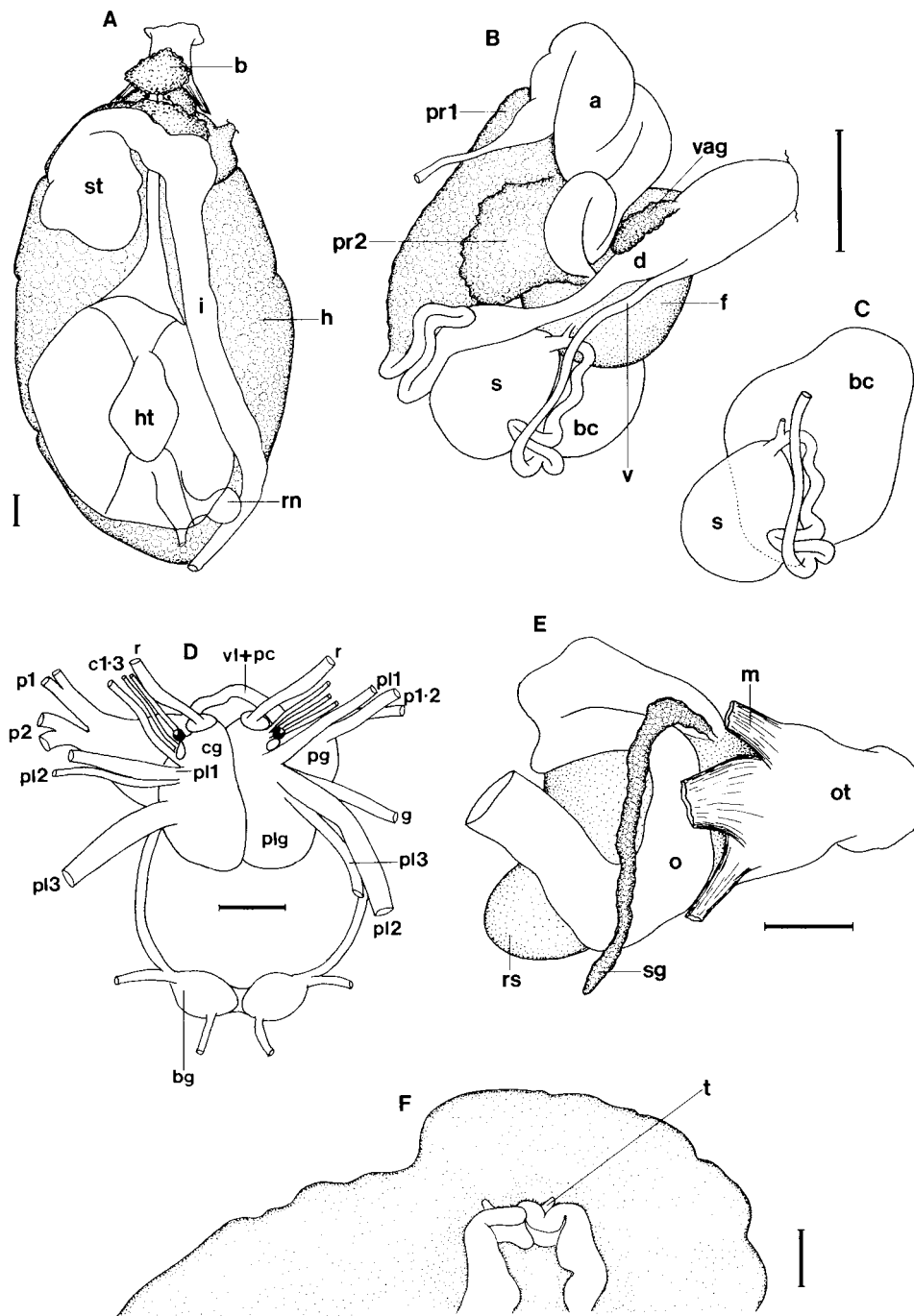
The colour of the living animals is variable from cream to yellow, reddish or brown. The depressions are dark brown with some blue sky pigment in the centre. The rhinophores and branchial leaves are pale brown.

Ventrally the anterior border of the mantle is notched and grooved (Fig. 45F). The oral tentacles are conical. The mantle margin is several times wider than the foot. The ventral colour is pale orange. The underside of the mantle and the edges of the foot have a scattered pattern of diffuse purple-brown spots.

#### *Anatomy*

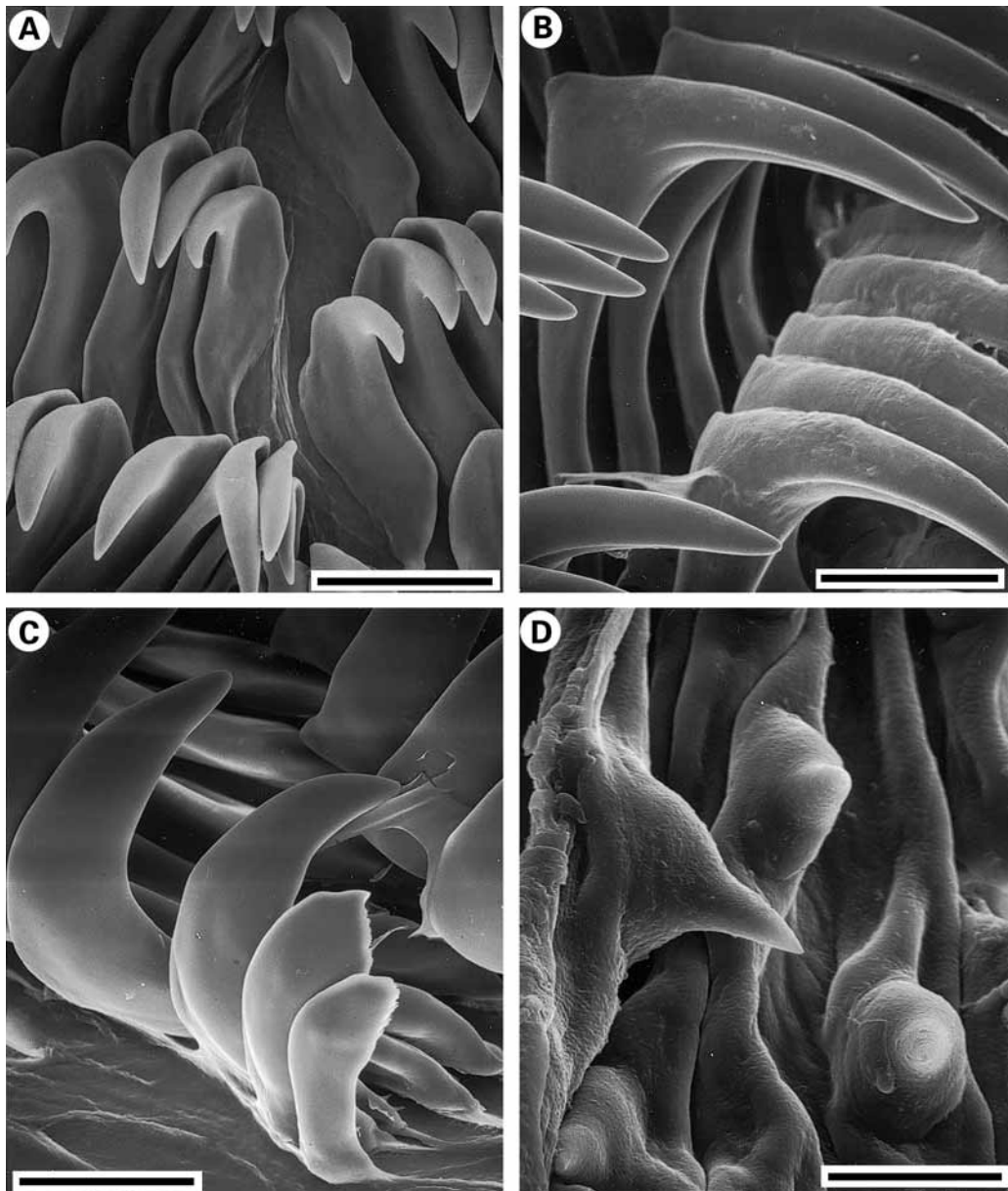
The posterior end of the oral tube has six strong retractor muscles (Fig. 45E) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two long salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is longer than the oral tube. The labial cuticle is smooth. The radular formula is  $28 \times (57.0.57)$  in a 35 mm preserved length specimen. Rachidian teeth are absent. The inner and mid lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 46A, B). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 46A,B). The outermost teeth have a number of small denticles (Fig. 46C). The oesophagus is long and expands directly into the stomach (Fig. 45A).

The ampulla is very long and convoluted. It branches into a short oviduct and the prostate (Fig. 45B). The oviduct enters the female glands near the nidamental opening. The prostate is massive and granular (Fig. 45B). It is divided into two different portions that are clearly distinguishable by their different texture and colour. The larger portion is pale yellow and connects to the deferent duct, whereas the smallest portion is whitish and connects to the ampulla (Fig. 45B). The deferent duct is long and narrow. It narrows and expands again into the long ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis has eight rows of small hooks, about 40  $\mu$ m long (Fig. 46D). They have a triangular cusp about 20  $\mu$ m long. There is an accessory gland connected to the atrium which lacks a spine.



**Figure 45.** *Sclerodoris tuberculata* (BMNH 1960897). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of the bursa copulatrix and seminal receptacle connection; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pg, pedal ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; t, oral tentacle; v, vagina; vl, visceral loop.





**Figure 46.** *Sclerodoris tuberculata* (CASIZ 073247), SEM photographs of the radula and penis. A, inner lateral teeth; scale bar = 60  $\mu\text{m}$ . B, teeth from the central portion of the half-row; scale bar = 60  $\mu\text{m}$ . C, outer lateral teeth; scale bar = 43  $\mu\text{m}$ . D, penial hooks; scale bar = 20  $\mu\text{m}$ .

The vagina is long and wide. At its proximal end, the vagina connects to the large and rounded bursa copulatrix. From the bursa copulatrix leads another long and convoluted duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about the same size as the seminal receptacle (Fig. 45C).

In the central nervous system (Fig. 45D) the cerebral and pleural ganglia appear to be fused together and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion,

and three pleural nerves leading from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapetal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 45A) consists of a large heart and two blood glands placed in front of and behind the central nervous system.

*Remarks*

Rudman (1978) redescribed *Sclerodoris tuberculata* Eliot, 1904 based on specimens from East Africa. The external morphology of Rudman's specimens corresponds with the original description by Eliot (1904a). Our material confirms Rudman's description.

GENUS *TARINGA* ER. MARCUS, 1955

*Aporodoris* Ihering, 1886: 238–239. Type species *Doris millegrana* Alder & Hancock, 1854 [= *Taringa millegrana* (Alder & Hancock, 1854)], by original designation. **Syn. nov.**

*Taringa* Er. Marcus, 1955: 151–152. Type species *Taringa telopia* Er. Marcus, 1955, by original designation.

*Diagnosis*

Body flexible. Dorsum covered with elongate caryophyllidia. Rhinophoral and branchial sheaths low. Prostate massive, with two portions. Vagina unarmed. Penis armed with a cuticular structure. Accessory gland absent. Labial cuticle smooth. Radular teeth denticulate. Inner and mid lateral radular teeth hamate. Outermost teeth multidenticate.

*Remarks*

Von Ihering (1886) introduced the genus *Aporodoris* Ihering, 1886 based on *Doris millegrana* Alder & Hancock, 1854. He explicitly designated *Doris millegrana*, in accordance with the description of Alder & Hancock (1854), as the type species of his new genus. At the same time, he described several specimens collected from the Mediterranean Sea which, in his opinion, belong to the same species. Von Ihering (1886) found several differences in the number of branchial leaves between his material and the description by Alder & Hancock (1854), and included the Mediterranean specimens in the variety *mediterranea*. Ortea *et al.* (1982) claimed that von Ihering (1886) misidentified the type species of the genus *Aporodoris*. In their opinion, the material from the Mediterranean Sea, included by von Ihering in the variety *mediterranea* of *Doris millegrana*, represents a different species that should be named *Aporodoris mediterranea* Ihering, 1886, and that should be considered the type species of the genus. They also found contradictions in the features of the genus *Aporodoris* and the redescription of *D. millegrana* by Eliot (1910), such as the grooved anterior border of the foot, the presence of jaws and the radula with denticles solely in the outermost teeth. However, a review of von Ihering's (1886) and Eliot's (1910) papers shows that neither mention the presence of jaws and both describe the anterior border of the foot as notched and grooved. Apparently, von Ihering

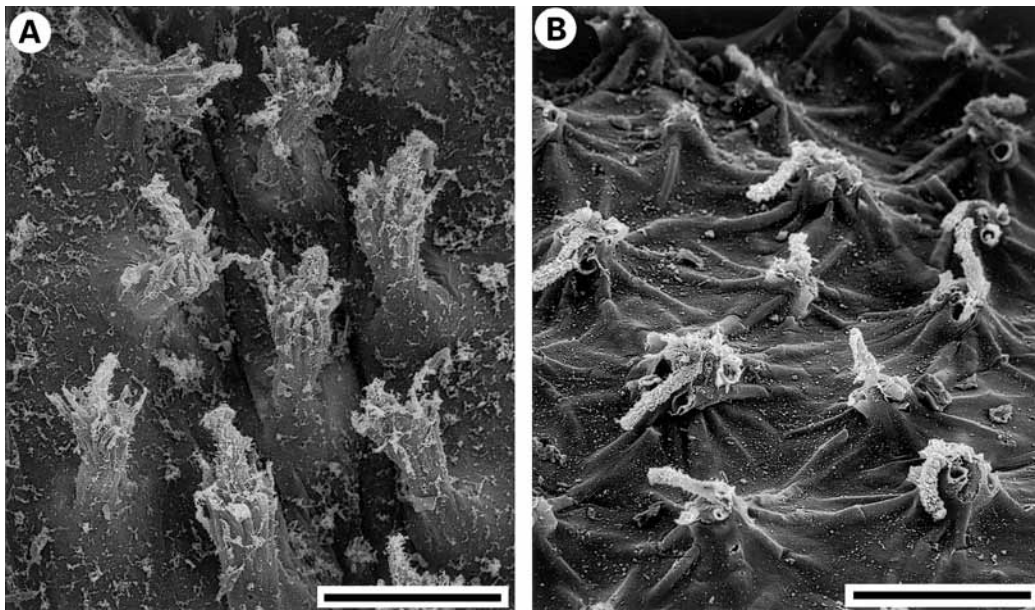
did not mention that the mid lateral teeth of *Aporodoris* are denticulate, as did Eliot, because Alder & Hancock did not describe those denticles. From the original description of *Aporodoris*, it is clear that von Ihering based this genus upon specimens seen by Alder & Hancock (1854), and in our opinion, the type species was not misidentified.

Eliot (1910) considered that *Aporodoris* could be superfluous, but he kept it provisionally valid until it could be synonymized with another older name. Thompson & Brown (1981) re-examined the type material of *Doris millegrana* and concluded that it should be placed in the genus *Discodoris* Bergh, 1877. These authors illustrated the radula of one of the syntypes (selected here as the lectotype), with the outermost teeth pectinate. According to Thompson & Brown (1981), the main diagnostic features of *Aporodoris* are the dorsum covered with minute tubercles, digitiform oral tentacles, margin of the rhinophoral sheaths lobed, anterior border of the foot notched and grooved, absence of jaw elements, radula without rachidian teeth, outermost radular teeth pectinate and penis unarmed.

Er. Marcus (1955) described the genus *Taringa* Er. Marcus, 1955 for *Taringa telopia* Er. Marcus, 1955. This genus is characterized by the presence of flattened, triangular oral tentacles, anterior border of the foot notched, margins of the rhinophoral and branchial sheaths lobed, absence of jaw elements, radula lacking rachidian teeth, outermost radular teeth pectinate, salivary glands lobate, stomach free, prostate well developed, penis with a smooth cuticle and presence of vestibular hooks. At the same time, Er. Marcus (1955) considered *Doris millegrana* a probable synonym of *Thordisa dubia* Bergh, 1894, and *Aporodoris* a possible synonym of *Thordisa* Bergh, 1877. This conclusion was based on the presumed absence of a cuticular penis in *D. millegrana*. However, he indicated that if further investigations revealed the presence of such a cuticle in the penis of *D. millegrana*, then *T. telopia* could be considered a synonym of *D. millegrana*.

The features of *Doris millegrana* described by Alder & Hancock (1854), Thompson & Brown (1981) and the present paper agree with those described by Er. Marcus (1955) for the genus *Taringa*, leading us to conclude that both names are synonyms. The presence of a cuticle in the penis of the type material of *D. millegrana* has been verified here. Moreover, this structure was reported in the original description of other nominal species that are conspecific with *D. millegrana* (see remarks on this species).

The genus *Aporodoris* has not been used as valid since its original description. It has been considered a likely synonym of *Thordisa* (Bergh, 1891; Er. Marcus, 1955; Ortea *et al.*, 1982) or regarded as a synonym of *Discodoris* (Thompson & Brown, 1981). In contrast the



**Figure 47.** SEM photographs of the dorsum. A, *Taringa millegrana* (BMNH 1980102); scale bar = 150 µm. B, *Thorybopus lophatus* (MNHN), scale bar = 150 µm.

genus *Taringa* is widely used in modern literature. According to the new version of the Code (ICZN, 1999), authors will be required not to displace a name which has been used as valid for at least ten authors in 25 publications during the past 50 years by an earlier synonym which has not been used as valid since 1899 (Article 23.9.2). As far as we know, the name *Aporodoris* has not been used as valid since 1886. Eliot (1910) used the name *Aporodoris* for *A. millegrana* but at the same time doubted that this genus should be maintained as valid. On the contrary, the genus *Taringa* is widely used and new species have been described very recently (see Ortea & Martínez, 1992; García-Gómez, Cervera & García-Martín, 1993; Gosliner & Behrens, 1998). We found at least 30 publications during the past 50 years by 15 authors in which the name *Taringa* was used as valid. Therefore, we prefer to displace the name *Aporodoris* (*nomen oblitum*) for its junior synonym *Taringa* (*nomen protectum*) according to the provisions of the Code.

*TARINGA MILLEGRANA* (ALDER & HANCOCK, 1854)  
(Figs 2F, 47A, 48)

*Doris millegrana* Alder & Hancock, 1854: 102–103.  
*Taringa fanabensis* Ortea & Martínez, 1992: 95–101,  
figs 1–3. **Syn. nov.**  
*Taringa tarifaensis* García-Gómez, Cervera & García-  
Martín, 1993. **Syn. nov.**

#### Type material

*Doris millegrana* Alder & Hancock. *Lectotype* (here selected) – Torbay, England, 28 mm preserved length,

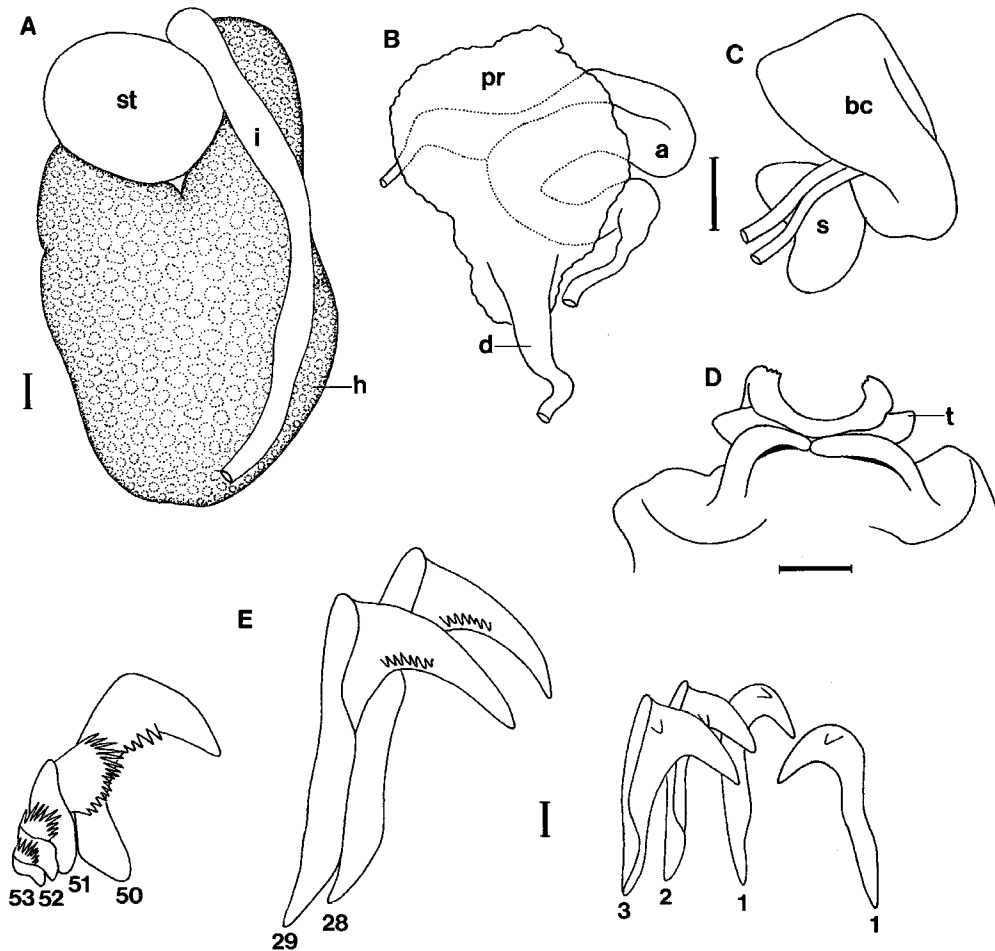
partially dissected (BMNH 1980101). *Paralectotype* – Torbay, England, 25 mm preserved length, dissected (BMNH 1980102). *Taringa fanabensis* Ortea & Martínez: *holotype* (by original designation) – El Médano, Tenerife, Canary Islands, 20 mm long (Museo Insular de Ciencias Naturales, Tenerife BMMO/000169), not examined. *Taringa tarifaensis* García-Gómez, *et al.*: *holotype* (by original designation) – Tarifa, Cádiz, Spain, 23 mm long (Canadian Museum of Nature 92950), not examined.

#### Comments on the type material

In the material borrowed from BMNH, a third specimen was contained in the same vial with the type material of *Doris millegrana*. It has a note by G.H. Brown indicating that this specimen was found unlabelled in the collection of Alder's material and that it is probably one of the three animals representing the type material of this species. This specimen, 15 mm preserved length, differs from the other two in the shape and size of the caryophyllidia and may not belong to the same species. In addition, Alder & Hancock (1854) indicated that they studied only two specimens. Therefore, this third specimen should not be retained within the type specimens of *Doris millegrana*.

#### External morphology

The maximum length of this species reaches 28 mm. The body is oval and convex (Fig. 2F), soft, with a velvety texture. The dorsum is entirely covered with caryophyllidia, about 120 µm in length (Fig. 47A).



**Figure 48.** *Taringa millegrana*. A, general view of the anatomy (BMNH 1980102); scale bar=1 mm. B, disposition of the prostate and ampulla (BMNH 1980102); scale bar=1 mm. C, disposition of the bursa copulatrix and seminal receptacle (BMNH 1980102); scale bar=1 mm. D, ventral view of the mouth area (BMNH 1980102); scale bar=1 mm. E, radular teeth from a half-row (BMNH 1980101); scale bar=20  $\mu$ m. Abbreviations: a, ampulla; bc, bursa copulatrix; d, deferent duct; h, digestive gland; i, intestine; pr, prostate; s, seminal receptacle; st, stomach; t, oral tentacle.

There are some smaller tubercles, about 80  $\mu$ m long, sparsely distributed between the larger ones. The caryophyllidia have a long, conical base, long spicules and a very large, elongate ciliated tubercle. The rhinophoral and branchial sheaths are low and regular. There are six long, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 20 lamellae in a 46 mm long specimen.

The colour of the freshly preserved specimens is dull yellow with one or two small purplish blotches near the margins of the mantle (Alder & Hancock, 1845–55). According to Ortea & Martínez (1992) and García-Gómez *et al.* (1993), the living specimens are brown-orange or dark violet brown with numerous small opaque white areas. The rhinophores are light violet brown with the apex yellowish white. The branchial leaves are yellowish with small dark brown spots.

Ventrally, the anterior border of the foot is notched and grooved (Fig. 47D). The oral tentacles are conical. The mantle margin is as wide as the foot. The ventral colour is lighter than the dorsum with numerous small darker spots irregularly scattered. These spots were noted by Eliot (1910) in the preserved specimens.

#### Anatomy

Very little is known about the anatomy of the type specimens. Thompson & Brown (1981) studied the radula of the paralectotype, but they did not provide information on the reproductive system. We examined fragments of the reproductive and digestive system of the paralectotype (BMNH 1980102) that were dissected by Thompson & Brown (1981) and the radulae of the lectotype (BMNH 1980101). The prostate is large and massive and connects to a wide deferent duct (Fig. 48B). We could identify the remainder of the penial

armature in one of the microscope slides prepared by Thompson & Brown (1981). The ampulla is folded and elongate. The bursa copulatrix is oval and has two ducts leading from it (Fig. 48C). The seminal receptacle is oval, about one-third the size of the bursa copulatrix. The radula has a formula  $29 \times (53.0.53)$ . Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and denticles (Fig. 48E). The number of denticles varies from 1 on the innermost teeth to 4–6 in the middle teeth and 8–13 in the outermost teeth. The denticles are strong in the inner and middle teeth, but very thin and elongated in the outermost teeth, which have a comb-like appearance. The teeth increase their size gradually towards the medial portion of the half-row. The outermost teeth are small plates.

For more information regarding the anatomy of this species see Ortea & Martínez (1992) and García-Gómez *et al.* (1993).

#### Remarks

The identity of *Doris millegrana* has been uncertain since its original description by Alder & Hancock (1845–55). Eliot (1910) re-examined the type material and concluded that *D. millegrana* is a synonym of *Thordisa dubia* Bergh, 1894, described from Brazil. Thompson & Brown (1981) redescribed this species based on the type material and regarded it as a valid species belonging to the genus *Discodoris* Bergh, 1877. However, an examination of the radular morphology of this species shows that it is very similar to that of *T. telopia* and therefore that it belongs to the genus *Taringa*. The teeth are short with a large, triangular cusp. There is one denticle on the innermost lateral teeth, and 4–6 in the mid lateral. The 4 outermost lateral teeth are pectinate small plates with numerous (8–13), thin denticles.

*Taringa fanabensis* was introduced by Ortea & Martínez (1992) under the incorrect spelling “*Taringa fañabensis*”, based on two specimens collected from the Canary Islands.

One year later and unaware of Ortea & Martínez’s paper, García-Gómez *et al.* (1993) described *Taringa tarifaensis* García-Gómez, Cervera & García-Martín, 1993, from the Gibraltar Strait, with the same features as *T. fanabensis*. Juan Lucas Cervera (pers. comm.) recognizes that *T. tarifaensis* is a junior synonym of *T. fanabensis*.

The radular formula and morphology of *T. fanabensis* is very similar to that of *T. millegrana*. The radula of *T. millegrana* has a formula  $29 \times (53.0.53)$ , the five outermost lateral teeth being small pectinate plates, with many denticles in both sides of the cusp. This is identical to the description of Ortea & Martínez (1992) of *T. fanabensis* who found a formula  $36 \times (53.0.53)$  with the five outermost teeth similar in shape to those of *T. millegrana*. García-Gómez *et al.* (1993) described

a formula  $34 \times (51-48.0.51-48)$  for *T. tarifaensis* and a similar radular morphology. Eliot (1910) indicated that all the teeth of *T. millegrana* have denticles, whereas Thompson & Brown (1981) described the innermost lateral teeth of this species as smooth. We have observed a single denticle in the innermost lateral teeth of *T. millegrana* and several denticles in the mid lateral teeth, identical to the description of *T. fanabensis* by Ortea & Martínez (1992). In our opinion *T. fanabensis* and *T. tarifaensis* are synonyms of *T. millegrana*.

Other Atlantic and Mediterranean species of *Taringa* have a different radular morphology (see Ortea *et al.*, 1982; Perrone, 1992).

#### TARINGA TELOPIA ER. MARCUS, 1955

(Figs 49, 50)

*Thordisa dubia* Bergh, 1894: 178–180, pl. 6, figs 6–9.  
*Taringa telopia* Er. Marcus, 1955: 152–155, figs 166–179.

#### Type material

*Thordisa dubia* Bergh: holotype (by monotypy) – Rio de Janeiro, Brazil (ZMUC). *Taringa telopia* Er. Marcus, the type material is probably lost, it is not deposited at the American Museum of Natural History (see Boyko & Sage, 1996); the type locality is São Sebastião Island, Brazil.

#### Additional material

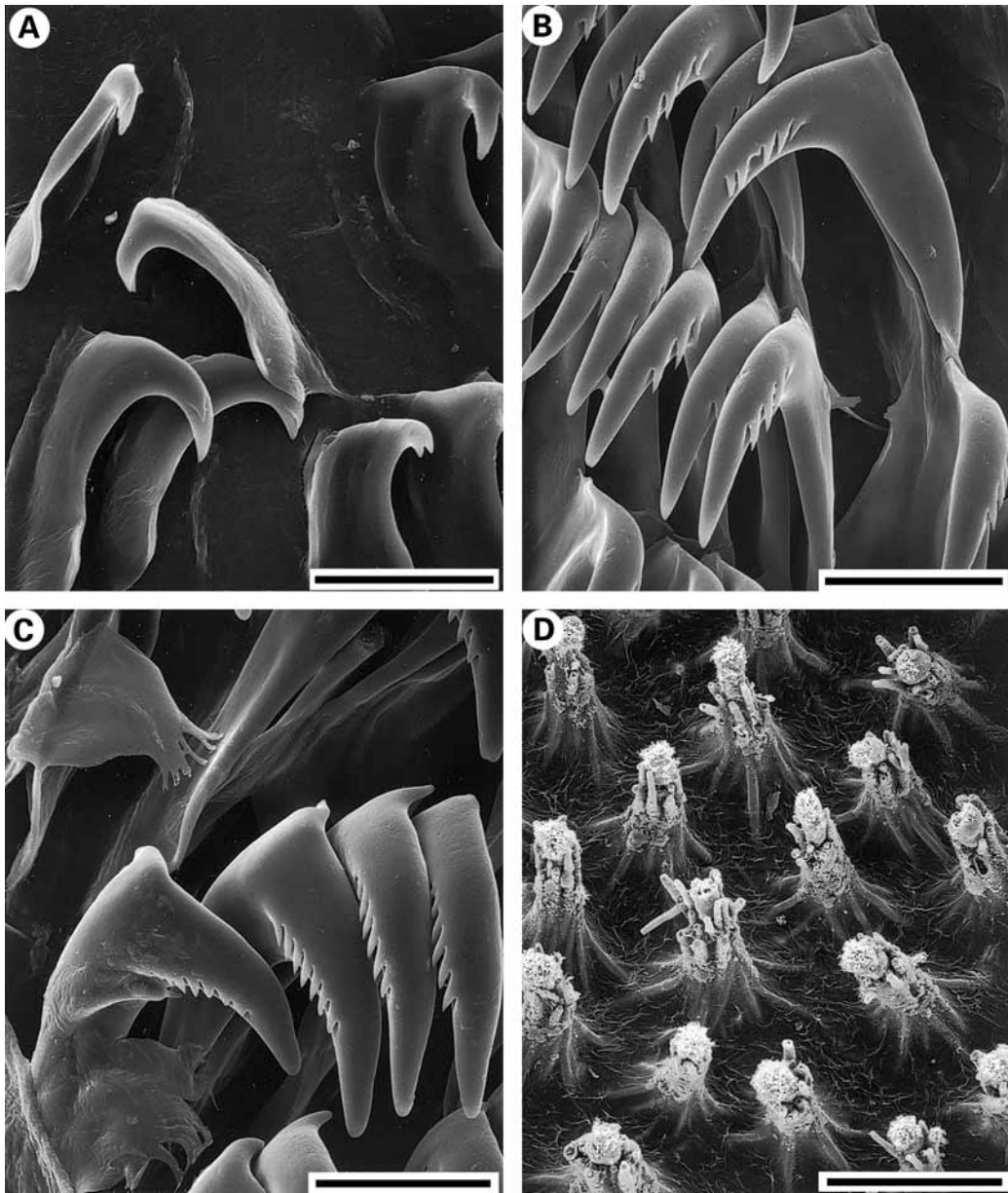
Armação dos Buzios, Cabo Frio, Brazil, July 1957, 3 specimens 9–11 mm preserved length, leg. Tommasi (MZSP 25281).

#### External morphology

The maximum length of this species reaches 30 mm (Er. Marcus, 1955). The body is oval and convex, soft, with a velvety texture. The entire dorsum is covered with a number of large caryophyllidia, about 100  $\mu$ m long (Fig. 49D). They have a long, conical base, long spicules and a large, elongate ciliated tubercle. The rhinophoral and branchial sheaths are low and irregular. There are 6 bipinnate branchial leaves. The long anal papilla is closing the circle of branchial leaves. The rhinophores are long, with 11 lamellae in a 9 mm preserved length specimen.

The colour of the living animals is variable from light yellow to yellowish brown or grey (Er. Marcus, 1955). Some specimens may have dark spots irregularly scattered on the dorsum. White spots may occur around the branchial and rhinophoral sheaths. The colour of the rhinophores and branchial leaves was not described (Er. Marcus, 1955).

Ventrally the anterior border of the mantle is notched



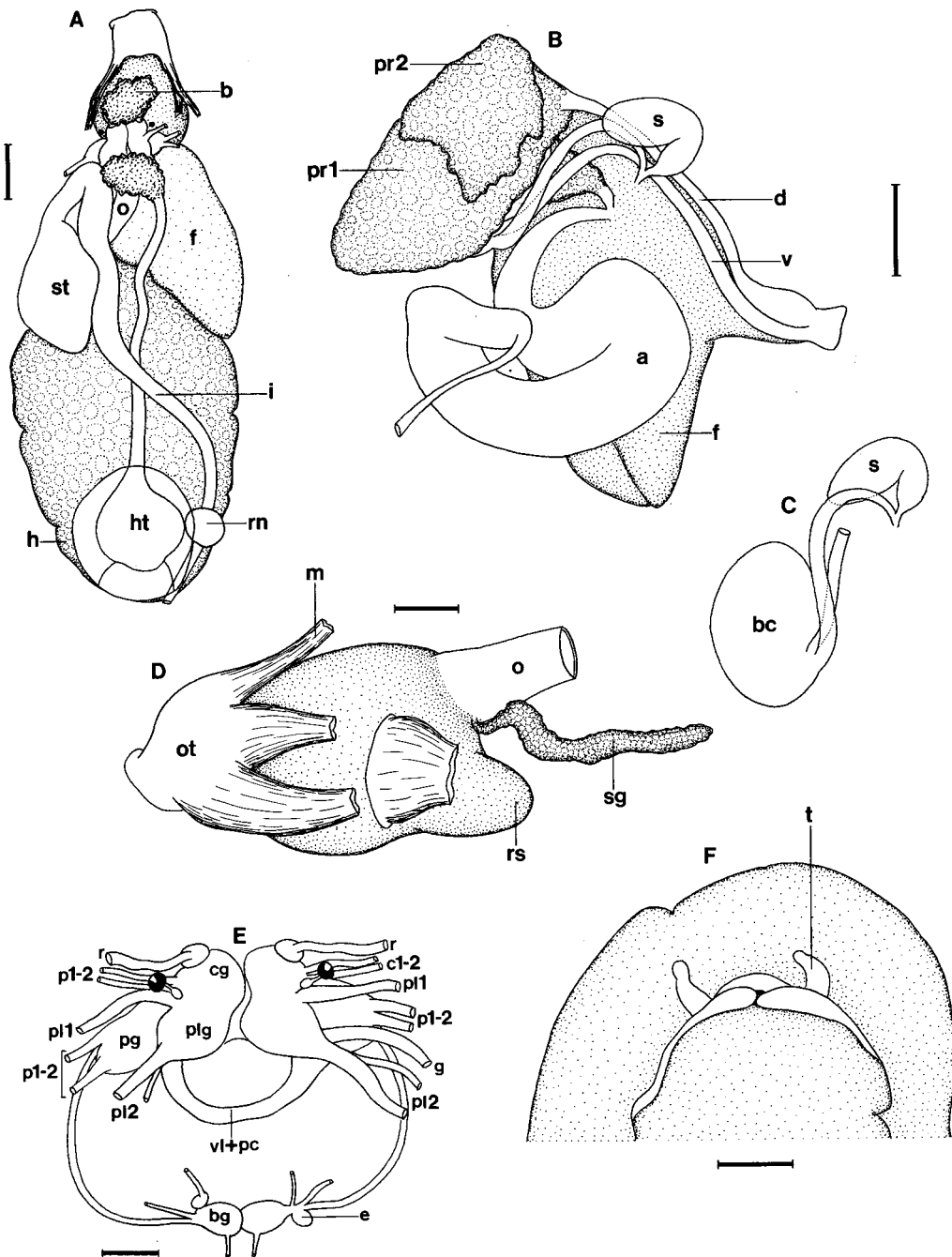
**Figure 49.** *Taringa telopia* (MZSP 25281), SEM photographs of the radula and dorsum. A, inner lateral teeth; scale bar = 25 µm. B, teeth from the central portion of the half-row; scale bar = 30 µm. C, outer lateral teeth; scale bar = 30 µm. D, caryophyllidia; scale bar = 150 µm.

and grooved (Fig. 50F). The oral tentacles are triangular. The mantle margin is as wide as the foot. The ventral colour is light yellow.

#### Anatomy

The posterior end of the oral tube has six delicate retractor muscles (Fig. 50D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles. Two short salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is longer than the oral tube. The labial

cuticle is smooth. The radular formula is  $21 \times (33.0.33)$  in a 9 mm preserved specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and denticles (Fig. 49A–C). The number of denticles varies from one on the innermost teeth to 4–6 in the middle teeth and 8–13 in the outermost teeth. The denticles are strong in the inner and middle teeth, but very thin and elongated in the outermost teeth, which have a comb-like appearance. The teeth increase their size gradually towards the medial portion of the half-row (Fig. 49A,B). The outermost teeth are small plates



**Figure 50.** *Taringa telopia* (MZSP 25281). A, general view of the anatomy; scale bar=1 mm. B, reproductive system; scale bar=1 mm. C, disposition of several reproductive organs; scale bar=1 mm. D, lateral view of the buccal bulb; scale bar=0.5 mm. E, central nervous system; scale bar=0.5 mm. F, ventral view of the mouth area; scale bar=1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pl, pleural nerves; pg, pedal ganglion; plg, pleural ganglion; pr, prostate; rn, syrinx; rs, radular sac; s, seminal receptacle; sg, salivary gland; t, oral tentacle; v, vagina; vl, visceral loop.



(Fig. 49C). The oesophagus is long and expands directly into the stomach (Fig. 50A).

The ampulla is very long and convoluted. It opens directly into the female glands (Fig. 50B). The prostate is massive and granular (Fig. 50B). It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The larger portion is pale yellow and connects to the deferent duct, whereas the smaller portion is whitish and connects to the ampulla (Fig. 50B). The deferent duct is very long and narrow and opens into a common atrium with the vagina. The deferent duct has a cuticular structure near its opening (Fig. 5C). The vagina is long and thin. At its proximal end, the vagina connects to the large and rounded bursa copulatrix which is enveloped by the prostate. From the bursa copulatrix leads another long duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is about four times larger than the seminal receptacle (Fig. 50C).

In the central nervous system (Fig. 50E) the cerebral and pleural ganglia are fused together and also distinct from the pedal ganglia. There are two cerebral nerves leading from the cerebral ganglia and two pleural nerves leading from each pleural ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapodal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 50A) includes a large heart and two blood glands placed in front of and behind the central nervous system.

#### Remarks

*Thordisa dubia* Bergh, 1894 was described from Rio de Janeiro, Brazil, based on a single preserved specimen. Eliot (1910) regarded *T. dubia* as a synonym of *Doris millegrana* Alder & Hancock, 1854, described from England, because of their similar radular morphology.

Er. Marcus (1955), when describing *Taringa telopia* Er. Marcus, 1955, from São Sebastião, Brazil, recognized that it could be a synonym of *T. dubia* and *D. millegrana*. He followed the unpublished opinion of N.H. Odhner (probably following Eliot, 1910), who considered *T. dubia* and *D. millegrana* as synonyms. However, at the same time Er. Marcus pointed out that the outermost lateral teeth of *D. millegrana* were smooth.

The radula of *T. dubia* described and illustrated by Bergh (1894, pl. 6, figs 6–9) is identical to that of *T. telopia*, and we regard these names as synonyms. The name *T. telopia* has often been used in recent literature, whereas the name *T. dubia* was only used as valid in the original description, more than a century ago.

#### GENUS *THORYBOPUS* BOUCHET, 1977

*Thorybopus* Bouchet, 1977: 43–46. Type species *Thorybopus lophatus* Bouchet, 1977, by monotypy.

#### Diagnosis

Body flexible. Dorsum covered with short caryophyllidia. Rhinophoral and branchial sheath low. Prostate tubular, with a single portion. Penis armed with hooks. Vagina unarmed. Atrium with a cuticular structure. Ampulla with a short oviduct. Labial cuticle armed with small rodlets. Radular teeth hamate, without denticles.

#### Remarks

Bouchet (1977) introduced the genus *Thorybopus* Bouchet, 1977, type species by original designation *Thorybopus lophatus* Bouchet, 1977, based on a single specimen collected from Atlantic deep waters. Since its original description no more species have been assigned to this genus.

The phylogenetic relationships of *Thorybopus*, discussed below, indicate that it is closely related to *Alloiodoris* and that they are sister taxa. The main differences are the presence of a cuticle in the atrium and the lack of denticles in the radular teeth of *Thorybopus*. Unfortunately, both *Thorybopus* and *Alloiodoris* are poorly known, and it is not possible to determine whether these differences are consistent. *Thorybopus* is provisionally regarded here as valid until more information becomes available.

#### *THORYBOPUS LOPHATUS* BOUCHET, 1977

(Figs 47B, 51)

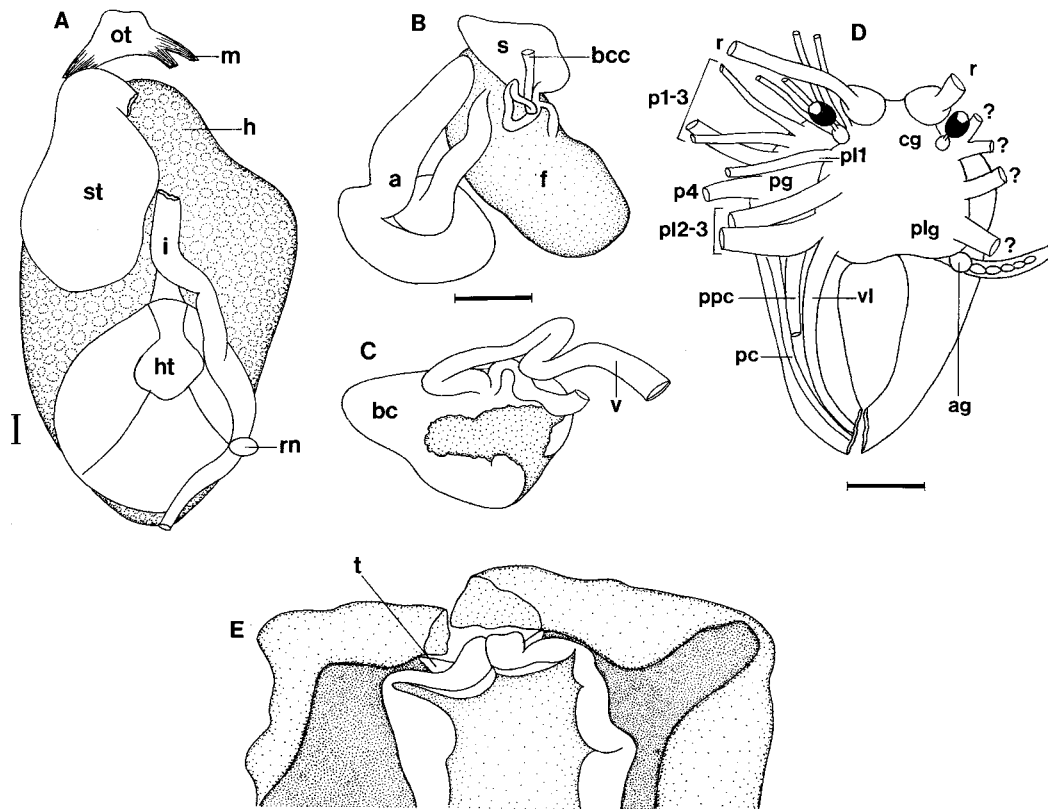
*Thorybopus lophatus* Bouchet, 1977: 43–46, figs 11–13, pl. 1, fig. D.

#### Type material

*Thorybopus lophatus* Bouchet: holotype (by original designation) – Jean Charcot-Biaçores Expedition, stn 241 (37°37'N, 25°32'W), 395–465 m depth, 12 November 1971, 26 mm long, leg. P. Bouchet (MNHN).

#### External morphology

The maximum length of this species reaches 26 mm (Bouchet, 1977). The body is oval and convex, soft, with a velvety texture. The dorsum is entirely covered with short caryophyllidia, about 60 µm in length (Fig. 47B). The caryophyllidia have a short, conical base and a very elongate ciliated tubercle. The spicules are dissolved in the holotype. According to Bouchet (1977), there is a longitudinal ridge situated in the centre of the dorsum. In the specimen, the central part of the dorsum was removed, so we could not observe the ridge. The rhinophoral and branchial sheaths are low



**Figure 51.** *Thorybopus lophatus* (MNHN). A, general view of the anatomy; scale bar=1 mm. B, disposition of the seminal receptacle, female glands and ampulla; scale bar=1 mm. C, bursa copulatrix; scale bar=1 mm. D, central nervous system; scale bar=1 mm. E, ventral view of the mouth area; scale bar=1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; bc, bursa copulatrix; cg, cerebral ganglion; f, female glands; h, digestive gland; ht, heart; i, intestine; m, retractor muscle; ot, oral tube; p, pedal nerves; pc, pedal commissure; pcc, parapedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; s, seminal receptacle; st, stomach; t, oral tentacle; v, vagina; vl, visceral loop.

and regular. There are six short, bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, with 19 lamellae in the 26 mm long specimen.

According to Bouchet (1977) the colour of the preserved specimen is uniformly pale yellow.

Ventrally, the anterior border of the foot is notched and grooved (Fig. 51E). The oral tentacles are conical. The mantle margin is narrower than the foot. The ventral colour is the same as the dorsal.

#### Anatomy

Information regarding the anatomy of this species was mainly obtained from Bouchet (1977). A re-examination of the holotype showed no remarkable differences from the original description.

According to Bouchet (1977) the jaws have a number of thin elements. The radular formula is  $35 \times (62.0.62)$  in the 26 mm long specimen. Rachidian teeth are

absent. The lateral teeth are hamate, having a single cusp and lacking denticles. The inner and outer lateral teeth were not described.

The ampulla is very long and convoluted (Fig. 51B). It connects directly to the female glands. The prostate is tubular, folded and granular (Bouchet, 1977). It connects to a long duct that narrows and then expands into the long ejaculatory portion of the deferent duct. The wide muscular deferent duct opens into a common atrium with the vagina. There are few penial hooks and a cuticular structure in the atrium. The vagina is long and folded. Near its proximal end, it connects to the bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle. The bursa copulatrix is oval in shape, about five times larger than the seminal receptacle (Fig. 51C).

In the central nervous system (Fig. 51D) the cerebral and pleural ganglia are fused together and distinct

from the pedal ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having several nerves leading from each one. The visceral loop, pedal and parapedal commissures are not enveloped together.

The circulatory system (Fig. 51A) includes a large heart. Bouchet (1977) observed only one blood gland, but it was removed from the specimen.

#### Remarks

*Thorybopus lophatus* Bouchet, 1977 is a deep-water species that has not been collected since its original description. No other species have been assigned to this genus.

### GENUS *NOPHODORIS* GEN. NOV.

*Type species: Nophodoris infernalis* sp. nov.

#### Diagnosis

Body flexible. Dorsum covered with large caryophyllidia. Rhinophoral and branchial sheath low. Prostate massive, with a single portion. Deferent duct long or very long. Penis sometimes armed with flattened hooks and a hard structure in the apex. Vagina unarmed. Atrium with three or four simple accessory glands. Labial cuticle armed with small rodlets. Radular teeth hamate and without denticles.

#### Etymology

The name *Nophodoris* (feminine) is derived from the Greek *dnophos*, which means darkness, in reference to the abyssal habitat of this genus. The first 'd' was removed to make this name more euphonious.

#### Remarks

The phylogenetic relationships of the caryophyllidia-bearing dorids, discussed below, show that *Nophodoris* is the sister group of the clade formed by *Atagama*, *Alloiodoris* and *Thorybopus* and therefore is regarded as a new genus. *Nophodoris* differs from those former genera in having a flattened prostate, a long deferent duct, and in lacking dorsal ridges. So far this genus is only known from deep waters in New Caledonia, and two new species are described here.

### *NOPHODORIS INFERNALIS* SP. NOV.

(Figs 2G, 52, 53)

#### Type material

*Holotype* – Bathus 1 Expedition, stn CP 707 (21°43'S, 166°36'E), east coast of New Caledonia, 347–375 m depth, 19 March 1993, 14 mm preserved length, leg.

P. Bouchet (MNHN). *Paratypes* – Musorstom 8 Expedition, stn CP 1074 (15°48'S, 167°24'E), Vanuatu, 775–798 m depth, 4 October 1994, 1 specimen 25 mm preserved length, dissected, leg. P. Bouchet (MNHN). Bathus 1 Expedition, stn CP 656 (21°13'S, 165°54'E), east coast of New Caledonia, 452–460 m depth, 3 specimens 8–15 mm preserved length, leg. P. Bouchet (MNHN). Bathus 3 Expedition, stn CP 845 (23°03'S, 166°56'E), Ride de Norfolk, New Caledonia, 592–622 m depth, 1 December 1993, 1 specimen 22 mm preserved length, dissected, leg. P. Bouchet (MNHN).

#### External morphology

The maximum length of this species reaches 25 mm. The body is oval and convex (Fig. 2G), soft, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 150 µm in length (Fig. 52E). The caryophyllidia have a very long, conical base and a rounded ciliated tubercle. The spicules are long. The rhinophoral and branchial sheaths are low and regular. There are six short, bipinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 27 lamellae in a 25 mm long specimen.

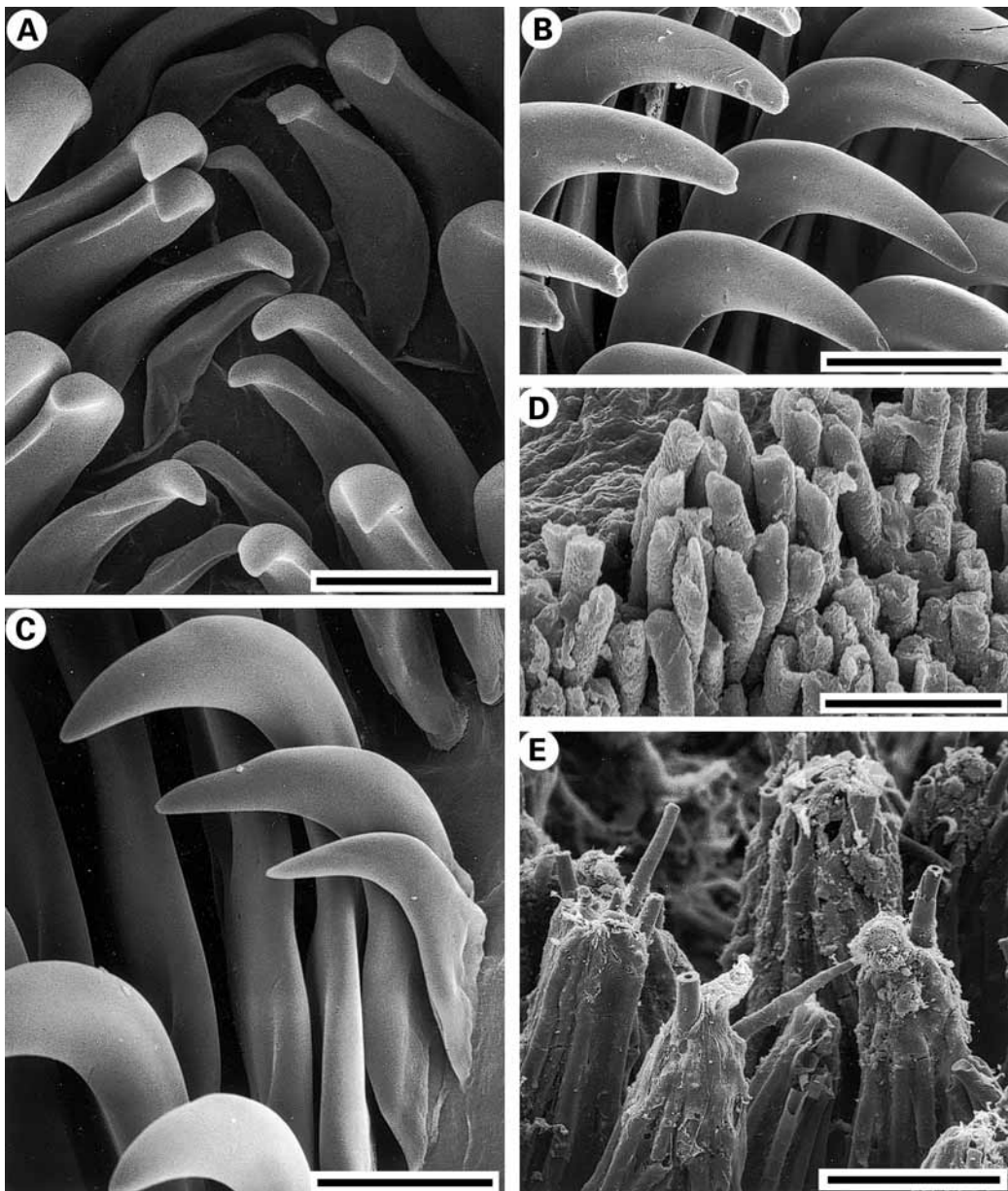
According to the collector notes, the colour of the living animals is pinkish cream with numerous opaque white spots. The colour of the rhinophores and gill is unknown; however, in the preserved specimens they are lighter than the dorsum.

Ventrally the anterior border of the foot is notched and grooved (Fig. 53F). The oral tentacles are conical. The mantle margin is wider than the foot. In the preserved specimens the ventral colour is the same as the dorsal.

#### Anatomy

The posterior end of the oral tube has six strong retractor muscles (Fig. 53D) that attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two long and thin salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is shorter than the oral tube. The jaws have a number of irregular elements 10–30 µm long. The radular formula is 15 × (24.0.24) in a 25 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 52A–C). The teeth increase their size gradually towards the medial portion of the half-row (Fig. 52A,B). The outermost teeth are smaller and also lack denticles (Fig. 52C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 53A).

The ampulla is very large and convoluted. It branches into a short oviduct and the prostate (Fig. 53B). The prostate is flattened, long and granular (Fig. 53B). It connects to a very long deferent duct that opens into a common, large atrium with the vagina.



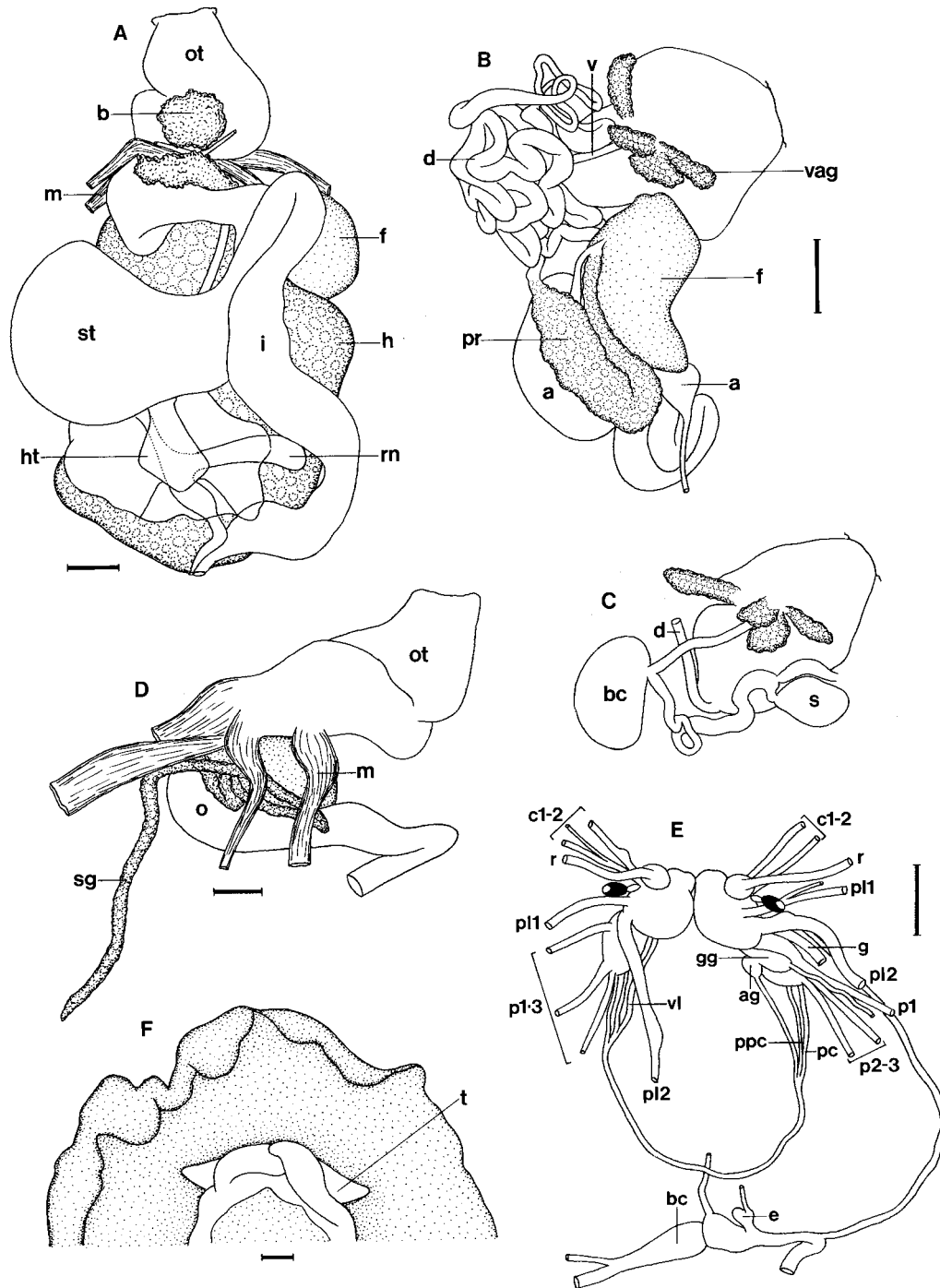
**Figure 52.** *Nophodoris infernalis* sp. nov. (MNHN), SEM photographs of the radula, jaws and dorsum. A, inner lateral teeth; scale bar = 60  $\mu\text{m}$ . B, teeth from the central portion of the half-row; scale bar = 75  $\mu\text{m}$ . C, outer lateral teeth; scale bar = 43  $\mu\text{m}$ . D, jaw elements; scale bar = 20  $\mu\text{m}$ . E, caryophyllidia; scale bar = 100  $\mu\text{m}$ .

The penis is unarmed. There are four vestibular glands that open into the atrium. The vagina is short and narrow. At its proximal end, it connects to the large, oval rounded bursa copulatrix. From the vagina leads another duct connecting to the seminal receptacle and the uterine duct. The bursa copulatrix is about three times larger than the seminal receptacle (Fig. 53C).

In the central nervous system (Fig. 53E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are two cerebral nerves leading from the cerebral ganglia, and two (right side)

or three (left side) pleural nerves leading from each pleural ganglion. There is a distinct abdominal ganglion on the right side of the visceral loop which connects to a large genital ganglion. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two long connectives. Gastroesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have three nerves leading from each one. The pedal and parapetal commissures are partially fused together.

The circulatory system (Fig. 53A) includes a large



**Figure 53.** *Nophodoris infernalis* sp. nov. (MNHN). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the mouth area; scale bar = 1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; gg, genital ganglion; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pcc, parapedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrxinx; s, seminal receptacle; sg, salivary gland; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.

heart and two blood glands placed in front of and behind the central nervous system.

#### *Etymology*

The name *infernalis* is derived from the Latin for 'belonging to the lower regions' in reference to the habitat of this species.

#### *Remarks*

So far, there are only two known species in the genus *Nophodoris*, both of them described here. For a comparison between them see the remarks on *Nophodoris armata*.

### ***NOPHODORIS ARMATA* SP. NOV.**

(Figs 2H, 54–57)

#### *Type material*

*Holotype* – SMIB 8 Expedition, stn DW 179 (23°46'S, 168°17'E), East Banc Jumeau, 400–405 m depth, 30 January 1993, 36 mm preserved length, leg. P. Bouchet (MNHN). *Paratype* – Bathus 3 Expedition, stn DW 818 (23°44'S, 168°16'E), Ride de Norfolk, 394–401 m depth, 28 November 1993, 1 specimen 55 mm preserved length, leg. P. Bouchet (MNHN).

#### *External morphology*

The maximum length of this species reaches 55 mm. The body is rounded and convex (Fig. 2H), soft, with a velvety texture. The dorsum is entirely covered with long caryophyllidia, about 250 µm in length (Fig. 54E). The caryophyllidia have a very wide, conical base and a elongate ciliated tubercle. Some of them are much larger and are irregularly scattered in the dorsum. The spicules are long. The rhinophoral and branchial sheaths are low and regular. There are eight short, tripinnate branchial leaves, forming a circle, posteriorly closed by the anal papilla. The rhinophores are elongated, having 33 lamellae in a 55 mm long specimen.

The colour of the living animals is dirty white, with numerous opaque white spots. The gill is brown, but the colour of the rhinophores is unknown.

Ventrally the anterior border of the foot is notched and grooved (Fig. 55G). The oral tentacles are conical. The mantle margin is wider than the foot. In the preserved specimens the ventral colour is the same as the dorsal.

#### *Anatomy*

The posterior end of the oral tube has six strong retractor muscles (Fig. 55F) that attach to the body wall. The oval, muscular buccal bulb has no additional muscles attached. Two long and thin salivary glands connect to the buccal bulb at the sides of the oesophageal junction. The buccal bulb is as long as

the oral tube. The jaws have a number of irregular elements 10 µm long (Fig. 54D). The radular formula is  $19 \times (33.0.33)$  in a 55 mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 54A–C). The teeth increase their size suddenly towards the medial portion of the half-row (Fig. 54A, B). The outermost teeth are smaller and also lack denticles (Fig. 54C). The oesophagus is long, convoluted and expands directly into the stomach (Fig. 55A).

The ampulla is very large and convoluted. It branches into a long oviduct and the prostate (Fig. 53C). The prostate is flattened, long and granular (Fig. 55B). It connects to a long deferent duct that expands into the ejaculatory portion. The muscular deferent duct opens into a common, large atrium with the vagina. The penis is large and has several flattened hooks (Fig. 56B). The apex of the penis has a hard rounded structure surrounded by cilia (Fig. 56A). There are three accessory glands that open into the point where the vagina opens into the atrium (Fig. 55D). These glands have a hard structure composed of a number of layers (Fig. 57). The vagina is short and narrow. At its proximal end, it connects to the large, oval rounded bursa copulatrix. From the vagina leads another duct connecting to the seminal receptacle and the uterine duct. The bursa copulatrix is about five times larger than the seminal receptacle (Fig. 55B).

In the central nervous system (Fig. 55E) the cerebral and pleural ganglia are fused together and distinct from the pedal ganglia. There are four (right side) or two (left side) cerebral nerves leading from the cerebral ganglia, and three (right side) or two (left side) pleural nerves leading from each pleural ganglion. There is an irregular network of small nerves connecting the rhinophoral and cerebral ganglia on each side. There is a distinct abdominal ganglion on the right side of the visceral loop. The buccal ganglia lie near the rest of the central nervous system, joined to the cerebral ganglia by two short connectives. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia have three nerves (right side) or one nerve (left side) leading from each one. The pedal and parapedal commissures are partially fused together.

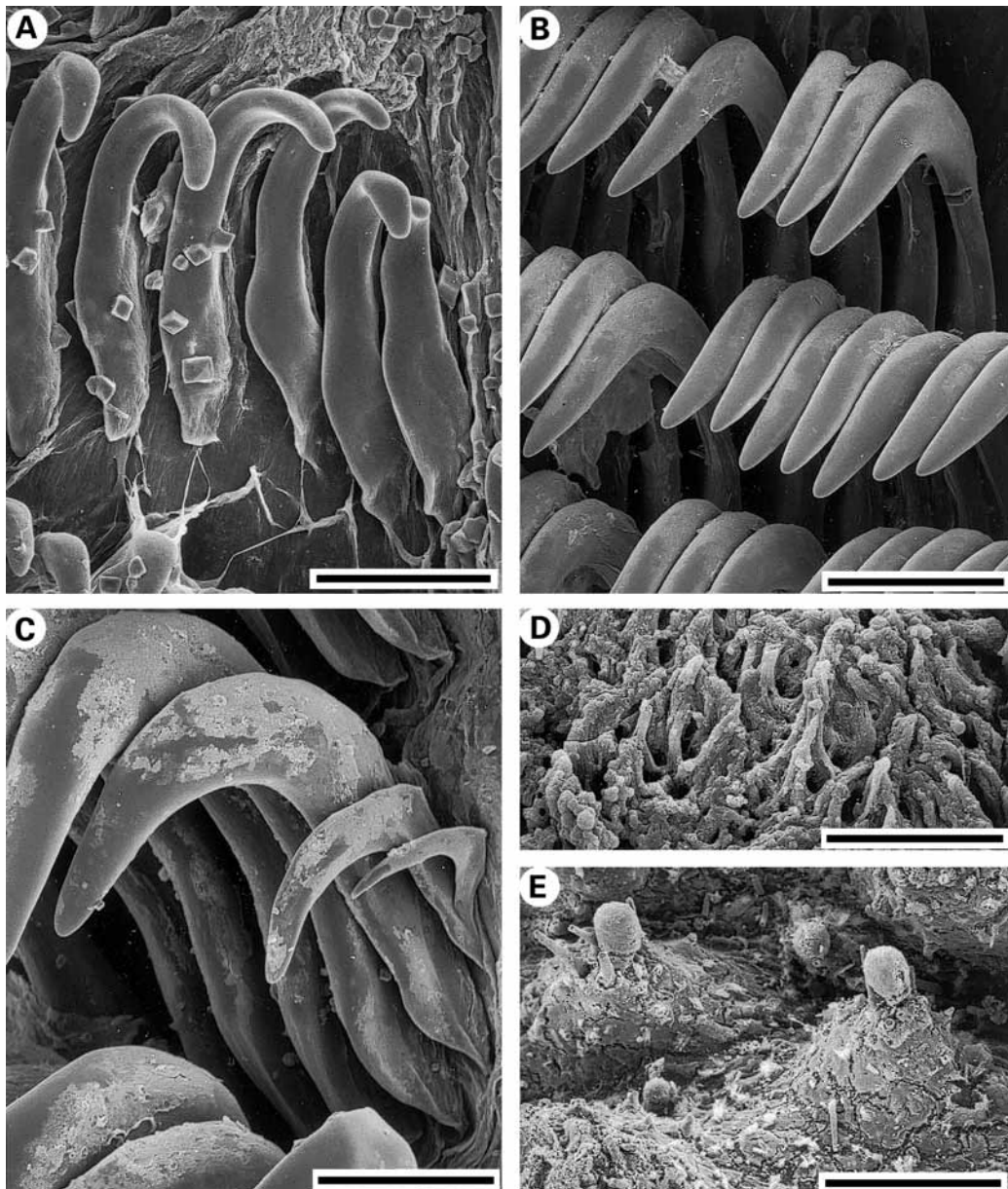
The circulatory system (Fig. 55A) includes a large heart and a single blood gland placed behind the central nervous system.

#### *Etymology*

The name *armata* is derived from the Latin for 'armed' in reference to large penial hooks present in this species.

#### *Remarks*

*Nophodoris armata* differs internally from *D. infernalis*, the other species of the genus *Nophodoris*, in



**Figure 54.** *Nophodoris armata* sp. nov. (MNHN), SEM photographs of the radula, jaws and dorsum. A, inner lateral teeth; scale bar = 60 µm. B, teeth from the central portion of the half-row; scale bar = 200 µm. C, outer lateral teeth; scale bar = 100 µm. D, jaw elements; scale bar = 30 µm. E, caryophyllidia; scale bar = 250 µm.

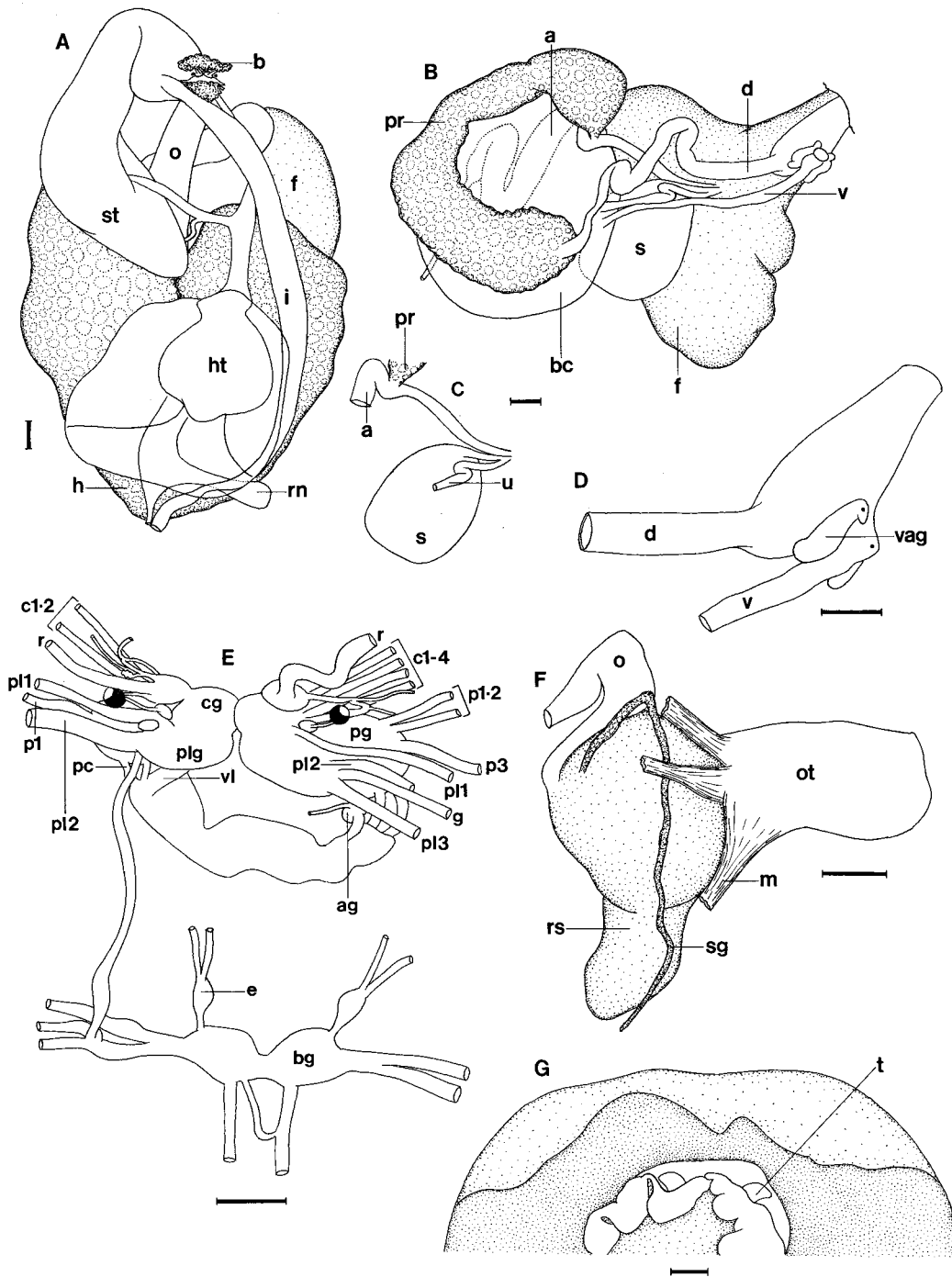
having the penis armed with large and flattened hooks, and in the shape and size of the radular teeth that in *D. armata* increase their size gradually towards the medial portion of the half-row whereas in *D. infernalis* they increase suddenly. Other differences are that *D. armata* has a much shorter deferent duct and hard structures in each accessory gland. Externally, *D. armata* is dirty white with opaque white spots and has very large caryophyllidia (about 250 µm long), whereas *D. infernalis* is pinkish cream and the caryophyllidia are clearly smaller (about 150 µm long).

## PHYLOGENETIC ANALYSIS

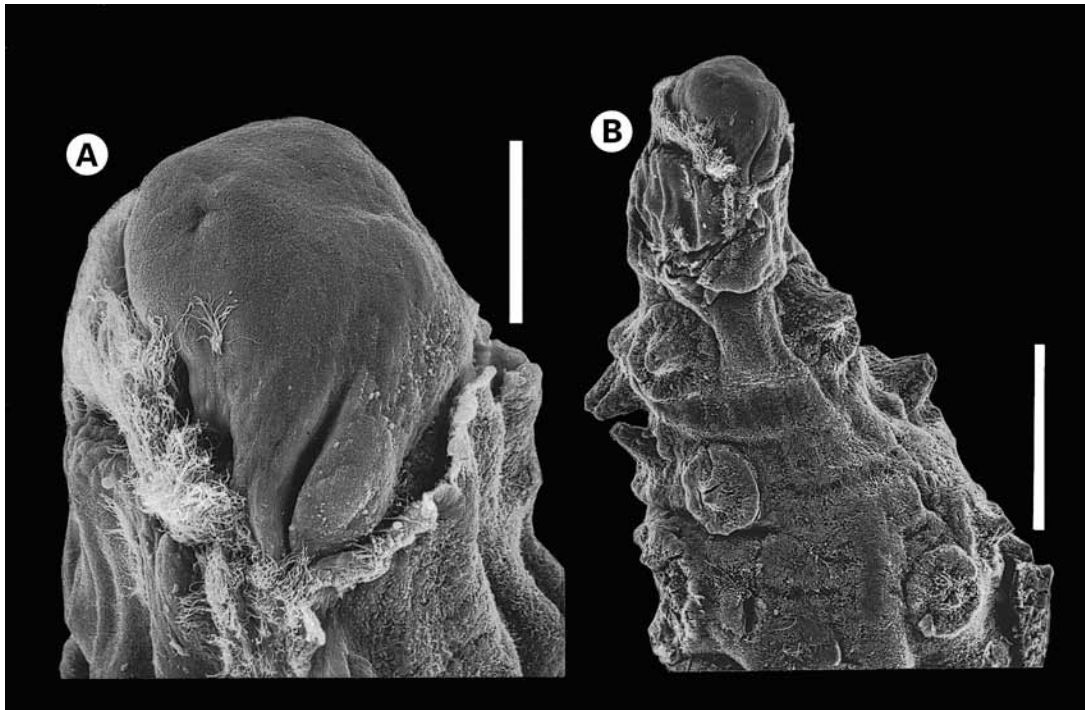
### PHYLOGENETIC METHODS

In order to calculate the most parsimonious phylogenetic tree, data were analysed by means of Phylogenetic Analysis Using Parsimony (PAUP) version 4.0 (Swofford, 1998) using the heuristic algorithm (TBR branch swapping option). Both the accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) optimizations were used for character transformation. In both cases the multistate characters

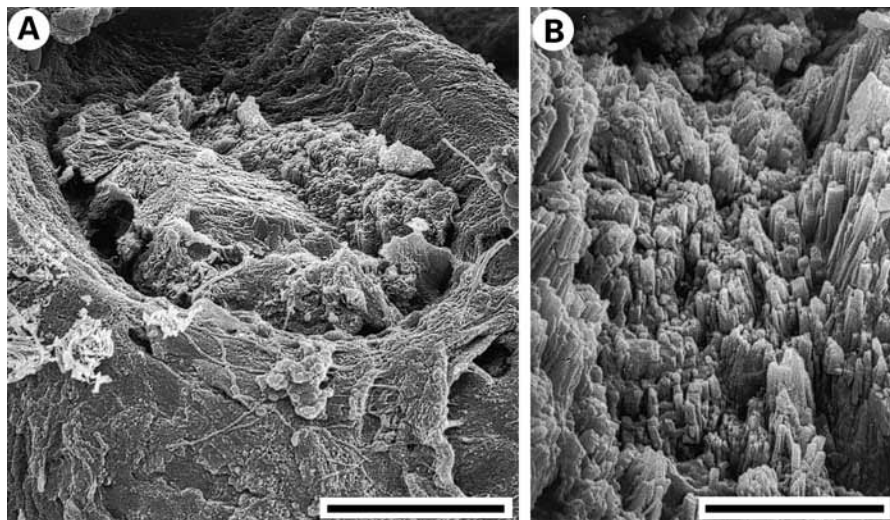




**Figure 55.** *Nophodoris armata* sp. nov. (MNHN). A, general view of the anatomy; scale bar = 2 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, detail of the deferent duct and vagina openings; scale bar = 1 mm. E, central nervous system; scale bar = 1.5 mm. F, lateral view of the buccal bulb; scale bar = 1 mm. G, ventral view of the mouth area; scale bar = 2 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; b, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; d, deferent duct; e, gastro-oesophageal ganglion; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; pr, prostate; rn, syrinx; s, seminal receptacle; sg, salivary gland; t, oral tentacle; v, vagina; vag, accessory gland; vl, visceral loop.



**Figure 56.** *Nophodoris armata* sp. nov. (MNHN), SEM photographs of the penis. A, detail of the hard structure in the apex, scale bar = 43  $\mu$ m. B, general view, scale bar = 150  $\mu$ m.



**Figure 57.** *Nophodoris armata* sp. nov. (MNHN), SEM photographs of the accessory gland hard structures. A, general view of the dissected structure, scale bar = 30  $\mu$ m. B, detail of the surface composition, scale bar = 7.5  $\mu$ m.

were treated as unordered. See Kitching *et al.* (1998) for a thorough explanation of these methods.

One hundred random starting trees were obtained via stepwise addition. Characters were polarized using the outgroup selection of the genera *Actinocyclus* and *Cadlina* and subsequent analysis using PAUP. This outgroup selection is made on the basis of Gosliner &

Johnson's (1994) paper, who showed that the Actinocyclusidae and the Chromodorididae are the sisters to the rest of the cryptobranch dorids. The genera *Actinocyclus* and *Cadlina* are basal within these two clades (Rudman, 1984; Gosliner & Johnson, 1994) and very likely the best choices for outgroup comparison with more derived cryptobranch dorids. A Bremer

**Table 1.** Other species of cryptobranch dorids included in the analysis, with the sources of information

Taxa	Source of information	Locality
<i>Cadlina laevis</i> (Linnaeus, 1767)	Rudman (1984)	–
<i>Actinocyclus verrucosus</i> Ehrenberg, 1831	CASIZ 099250	Okinawa, Japan
<i>Archidoris pseudoargus</i> (Rapp, 1827)	CASIZ 106509	Asturias, Spain
<i>Discodoris boholensis</i> Bergh, 1877	CASIZ 083654	Luzon, Philippines
<i>Peltodoris atromaculata</i> Bergh, 1880	CASIZ 099147	Gerona, Spain
<i>Paradoris indecora</i> (Bergh, 1881)	Ortea (1995)	–

**Table 2.** Data matrix of character states in the taxa involved in the phylogenetic analysis of the caryophyllidia-bearing dorids. Data code: 0 = plesiomorphic condition, 1–3 = apomorphic condition, ? = missing data

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Cadlina laevis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
<i>Actinocyclus verrucosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	?	0	0	0
<i>Archidoris pseudoargus</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	?	0	0	0
<i>Discodoris boholensis</i>	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	?	0	0	0
<i>Peltodoris atromaculata</i>	0	1	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	?	0	0	0
<i>Paradoris indecora</i>	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	2	0	2	0	0	0
<i>Asteronotus cespitosus</i>	1	1	0	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0
<i>Atagema omata</i>	0	1	2	1	2	1	1	1	1	0	1	0	0	0	0	0	0	0	?	0	0	0
<i>Atagema boucheti</i>	0	1	2	1	2	1	1	1	1	0	1	0	0	0	0	0	0	0	?	0	0	0
<i>Jorunna rubescens</i>	0	1	2	1	0	0	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0
<i>Jorunna tomentosa</i>	0	1	2	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0
<i>Platydoris argo</i>	0	1	2	1	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1
<i>Diaulula sandiegensis</i>	0	1	2	1	1	0	1	0	1	0	1	0	0	1	1	0	0	0	?	0	0	0
<i>Rostanga rubra</i>	0	1	2	1	1	0	1	0	0	1	1	1	0	1	1	0	0	0	?	0	0	0
<i>Rostanga setidens</i>	0	1	2	1	?	0	1	0	1	1	1	1	0	1	?	0	0	0	?	0	0	0
<i>Halgerda formosa</i>	1	1	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	?	0	0	0
<i>Baptodoris cinnabarina</i>	0	1	2	1	0	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1	0	1
<i>Gargamella immaculata</i>	0	1	2	1	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1
<i>Alloiodoris marmorata</i>	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0
<i>Sclerodoris tuberculata</i>	1	1	2	1	0	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1	0	0
<i>Taringa millegrana</i>	0	1	2	1	0	0	1	0	1	0	0	0	0	1	1	?	0	0	?	0	1	0
<i>Taringa telopia</i>	0	1	2	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	?	0	1	0
<i>Thorybopus lophatus</i>	0	1	2	1	0	0	1	0	0	0	1	0	0	0	?	0	0	0	?	1	0	0
<i>Dnophodoris infernalis</i>	0	1	2	1	0	0	1	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0
<i>Dnophodoris avernalis</i>	0	1	2	1	0	0	1	0	0	0	1	0	0	1	0	2	0	0	3	1	0	0

analysis (Bremer, 1994) was carried out to estimate branch support. In cases where the number of possible trees exceeded computer memory, the strict consensus was calculated using the first 10 000 trees obtained. See Kitching *et al.* (1998) for a thorough explanation of the advantages of Bremer's method in morphological data analyses.

Synapomorphies were obtained using the character trace option in MacClade 3.04 (Maddison & Maddison, 1992) using the strict consensus tree from the PAUP analysis.

## TAXA

For a preliminary phylogenetic analysis, 27 taxa have been considered. They include the type species of most the caryophyllidia-bearing dorids genera, even if they have been regarded as synonyms in former studies. Those where detailed information was not available, such as *Audura* Bergh, 1878, *Petelodoris* Bergh, 1881, *Peronodoris* Bergh, 1904, *Graviera* Vayssière, 1912, *Awuka* Er. Marcus, 1955 were excluded. *Atagema spongiosa* and *Halgerda tessellata*, type species of the genera *Phlegmodoris* and *Dictyodoris* respectively, were

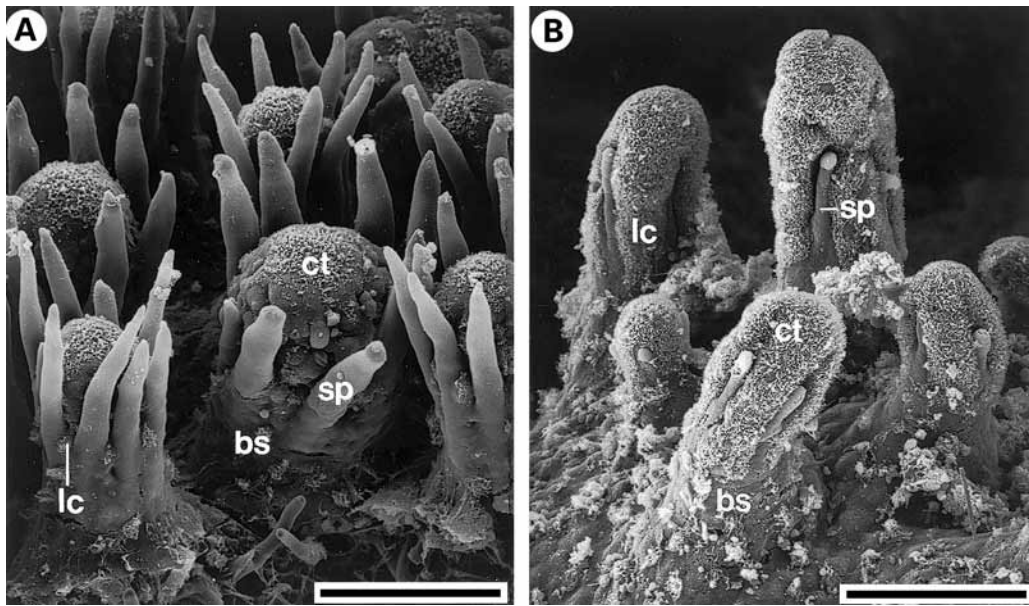
coded in the data matrix identically to *Atagema ornata* and *Halgerda formosa*, and therefore they do not need to be included in the analysis. Objective synonyms have not been included. Other taxa lacking caryophyllidia, but supposedly related to them, such as *Asteronotus* and *Halgerda* have also been considered.

Other cryptobranch dorids genera included in the analysis for comparative purposes, but not described in this paper, are summarized in Table 1.

#### CHARACTERS

The informative characters used to resolve the phylogeny of the caryophyllidia-bearing dorids are listed and below. They reflect a wide range of morphological and anatomical features of the taxa involved. Seventeen characters are binary and five characters are coded as multistate. The character states are indicated with numbers: 0, plesiomorphic condition; 1–3, apomorphic conditions. The polarities discussed below have not been obtained a priori but as the result of outgroup comparison in the phylogenetic analysis. The distribution of plesiomorphic and apomorphic character states is found in Table 2.

- (1) Body firmness. Most cryptobranch dorids have a soft, flexible body (0). Species of the genera *Asteronotus*, *Halgerda* and *Sclerodoris* have a rigid body, with a rubbery texture (1).
- (2) Oral tentacles. The oral tentacles of *Actinocyclus* and *Archidoris* are blunt prolongations of the mouth area (0), whereas, in the rest of the taxa included in the analysis, the tentacles are well formed (1).
- (3) Dorsal tubercle shape. The dorsal tubercles of dorids may be smooth (0) (as in *Actinocyclus*, *Cadlina*, *Archidoris*, *Discodoris* and *Paradoris*), may have spicules irregularly projecting out the surface (1) (as in *Peltodoris*) or may have a ring of spicules protruding in a regular pattern (2) (as in the caryophyllidia-bearing dorids).
- (4) Ciliated tubercle. The tubercles of most dorids have small groups of cilia irregularly scattered on their surface (0), but in the caryophyllidia-bearing dorids they group together in the apex of the tubercle forming a large ciliated area (1), here named a ciliated tubercle.
- (5) Lateral cilia. In *Rostanga* and *Diaulula* (Fig. 61A) there are small lateral ciliated areas between spicules (1) (Fig. 58A). Those areas are very large in *Atagema* (2) (Fig. 58B), but they are absent in the rest of the caryophyllidia-bearing dorids (0).
- (6) Gill arrangement. In most dorids the gill emerges vertically from the branchial sheath (0), but, in the genus *Atagema*, the gill is dorsally protected by a large lobe and it emerges horizontally (1).
- (7) Anterior border of the foot. The anterior border of the foot of *Actinocyclus*, *Cadlina* and *Archidoris* is simple (0). In the rest of the dorids included in the analysis, there is a notched labium bordering the anterior edge of the foot (1).
- (8) Oral tube muscles. In most species of dorids the muscles that attach the oral tube to the body wall are simple (0), whereas in the genus *Atagema* they have glands on attached to them (1).
- (9) Jaw elements. In *Actinocyclus*, *Cadlina*, *Discodoris*, *Paradoris*, *Alloiodoris*, *Thorybopus*, and some species of *Rostanga* and *Nophodoris*, the labial cuticle is armed with a pair of jaws made of hard rodlets (0). In *Jorunna* those jaws may be present, but they are absent in the type species. The rest of the taxa included in the analysis have a smooth labial cuticle (1).
- (10) Inner lateral teeth. The inner lateral teeth of *Rostanga* and *Boreodoris* are triangular and clearly different from the mid lateral teeth (1). In the rest of the taxa they are hamate and similar to the mid lateral teeth (0).
- (11) Mid-outer lateral teeth. In *Actinocyclus*, *Cadlina*, *Taringa* and *Alloiodoris* the mid and outer lateral teeth are denticulate (0). The other dorids included in the analysis have the mid lateral teeth smooth (1).
- (12) Outer lateral teeth simple denticles. In the genera *Rostanga* and in *Jorunna tomentosa*, the outer lateral teeth have simple, elongate denticles (1) that have not been found in the other taxa (0).
- (13) Outer lateral teeth comb shaped. The outermost lateral teeth of *Taringa*, *Sclerodoris*, *Baptodoris* and *Halgerda* are comb shaped as a consequence of having a number of small denticles (1). This type of denticles has not been found in the other taxa (0).
- (14) Prostate shape. In *Cadlina*, *Archidoris*, *Atagema*, *Alloiodoris* and *Thorybopus* the prostate is tubular (0), whereas in other taxa it is flattened (1). In *Actinocyclus* the prostate is rounded and very small (2).
- (15) Prostate portions. In most cryptobranch dorids the prostate has a single part (0). In *Halgerda*, *Asteronotus* and other dorids with caryophyllidia, except *Thorybopus*, *Alloiodoris*, *Atagema* and *Nophodoris*, the prostate has two parts well differentiated in colour and texture (1). Information on *Rostanga setidens* and *Taringa millegrana* was not available.
- (16) Simple accessory glands. In the genus *Asteronotus* there is a single, simple accessory gland connected to the atrium (1). In the genus *Nophodoris* there are several of these simple glands (2). Other taxa included in the analysis lack simple accessory glands (0). This gland is probably not homologous with the vestibular gland of



**Figure 58.** SEM photographs of caryophyllidia. A, *Diaulula sandiegensis* (CASIZ 068277); scale bar = 100 µm. B, *Atagema ornata* (CASIZ 083791); scale bar = 100 µm. Abbreviations: bs, base; ct, ciliated tubercle; lc, lateral cilia; sp, spicule.

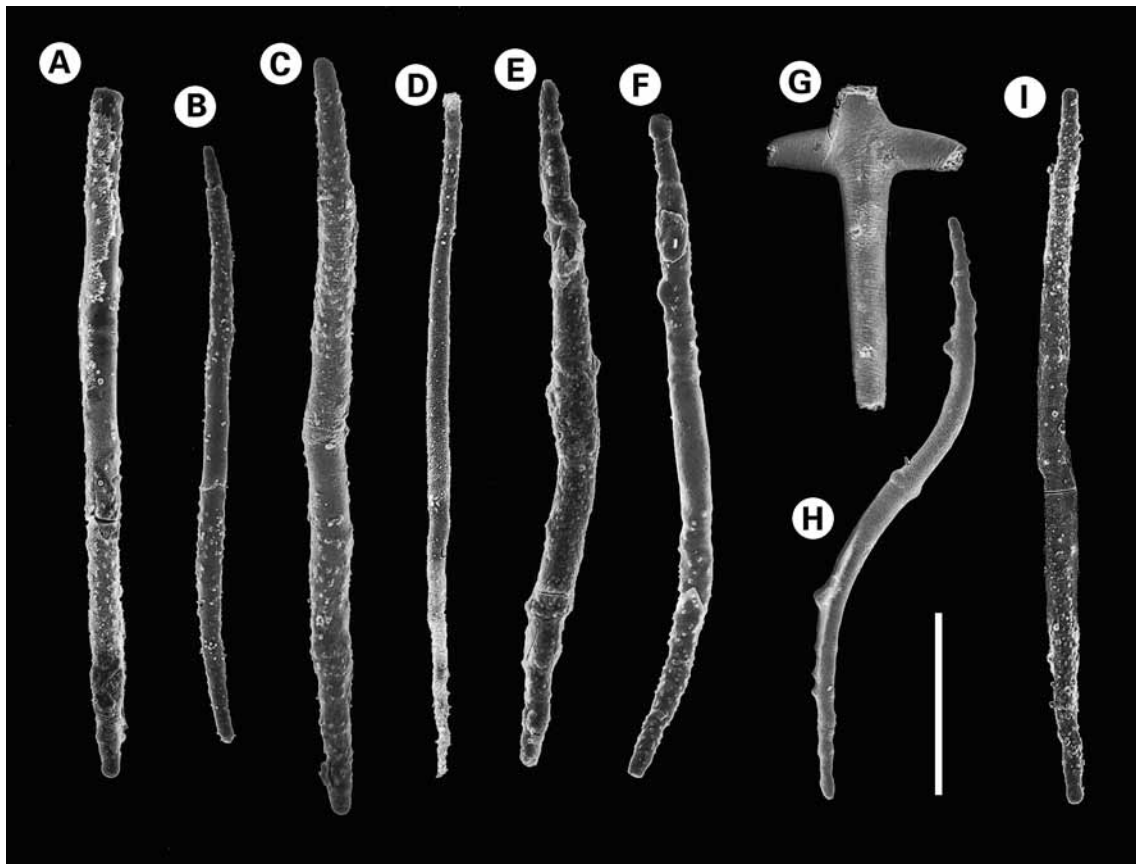
other dorids, which opens into the sexual opening (see Rudman, 1984).

- (17) Lobate accessory gland. Species of *Sclerodoris*, *Platydorid*, *Baptodorid* and *Gargamella* have a large, lobate accessory gland (1) that is not present in any other taxa (0). In *Paradoris* there are several (2). Even though this gland is probably homologous with the simple accessory glands of *Nophodoris* and *Asteronotus* it is regarded as a different character owing to their distinct external appearance.
- (18) Complex accessory gland. In the genus *Jorunna* there are large, complex accessory glands that consist of two different portions connected by a duct (1). This complex glands are absent in other genera (0).
- (19) Sexual hard structures. In several genera there are hard structures associated with the accessory glands. In *Jorunna* and *Asteronotus* there is a spine, more or less long (1). In *Paradoris* there are several spines (2). In *Nophodoris armata* there are several small, hard structures, one inside of each accessory gland (3). The rest of the taxa involved lack any hard structure (0). In the species without accessory glands this character was treated as unknown.
- (20) Penial hooks. The penis of *Baptodoris*, *Gargamella*, *Platydorid*, *Sclerodoris*, *Nophodoris armata*, *Alloiodoris* and *Thorybopus* is armed with several rows of penial hooks (1) that are absent the other taxa studied (0).

- (21) Penial cuticle. In *Taringa* the penis has a hard, cuticular structure (1) that does not exist in other taxa (0).
- (22) Atrial and vaginal hooks. In the genera *Platydorid*, *Baptodoris* and *Gargamella* there are very large hooks situated in the vagina or in the portion of the atrium where the vagina opens (1). These hooks are absent in other genera (0).

Characters that are not present or are variable within the caryophyllidia-bearing dorids (i.e. vestibular gland, mantle glands), have not been considered for the present analysis. In addition, several characters originally included have been removed because they are uninformative. Some other characters that have not been considered here are discussed below.

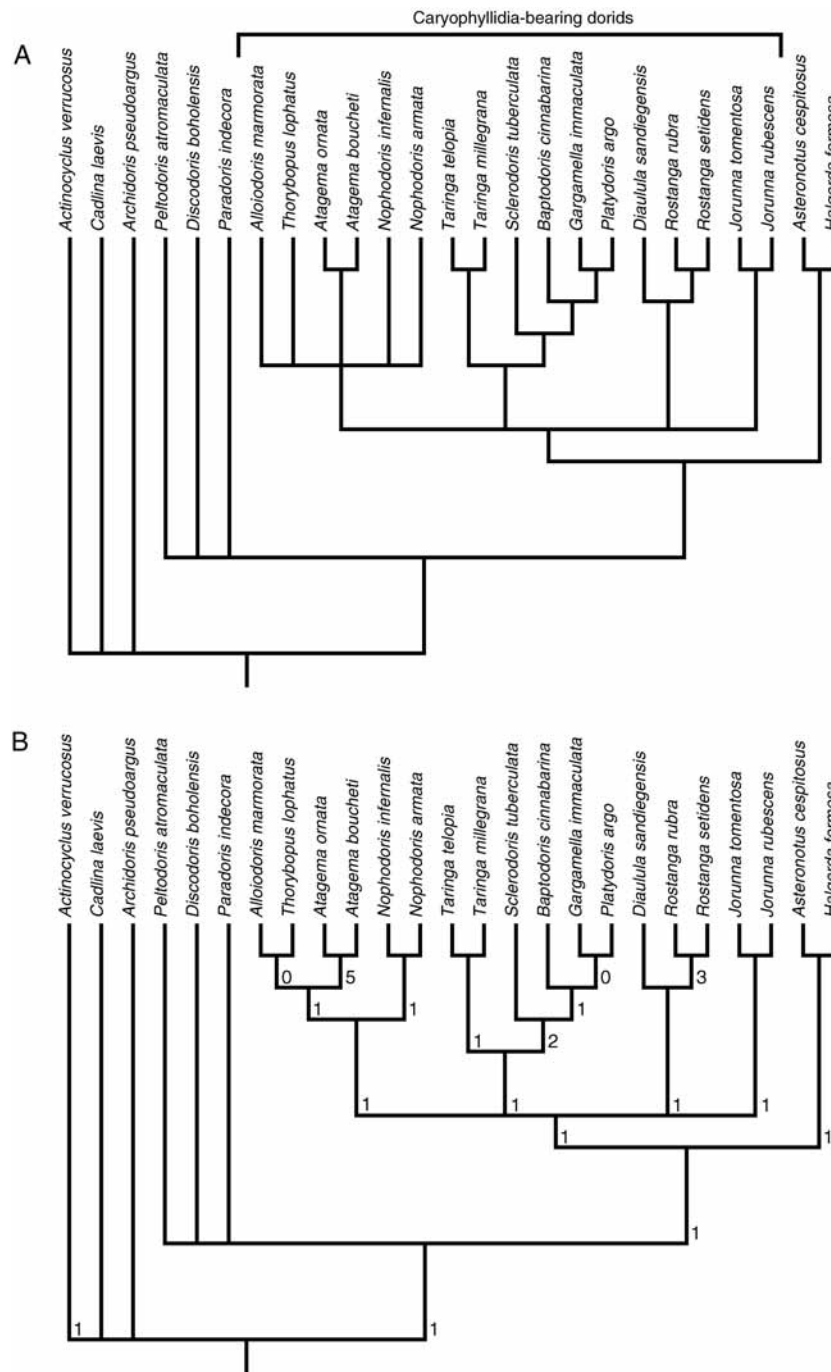
- (1) Spicules. After the examination of the size and shape of the spicules of all the taxa included in the analysis we found no important differences between them (Fig. 59). Only in *Halgerda*: some of the spicules are cross shaped (Fig. 59G), but this is an autoapomorphy of this genus (only one species was included in the analysis) and therefore this character is uninformative.
- (2) Openings of reproductive system. In all crypto-branch dorids the gonoduct has bifurcated twice. However, in several species the vaginal duct and deferent duct have been secondarily fused distally to form a common atrium. The presence of an



**Figure 59.** SEM photographs of integumentary spicules. A, *Atagama ornata* (CASIZ 083791), scale bar=100 µm. B, *Alloiodoris marmorata* (ZMUC GAS-346); scale bar=100 µm. C, *Diaulula sandiegensis* (CASIZ 070842); scale bar=100 µm. D, *Jorunna rubescens* (CASIZ 072838); scale bar=75 µm. E, *Jorunna tomentosa* (CASIZ 115215); scale bar=75 µm. F, *Taringa telopia* (MZSP 25281); scale bar=75 µm. G, *Halgerda formosa* (CASIZ 099340); scale bar=300 µm. H, *Halgerda formosa* (CASIZ 099340); scale bar=150 µm. I, *Asteronotus cespitosus* (CASIZ 072765); scale bar=150 µm.

**Table 3.** Data matrix of character states in the taxa involved in the phylogenetic analysis of the *Platydoris*-*Baptodoris*-*Gargamella* clade. Data code: 0=plesiomorphic condition, 1-2=apomorphic condition, ?=missing data

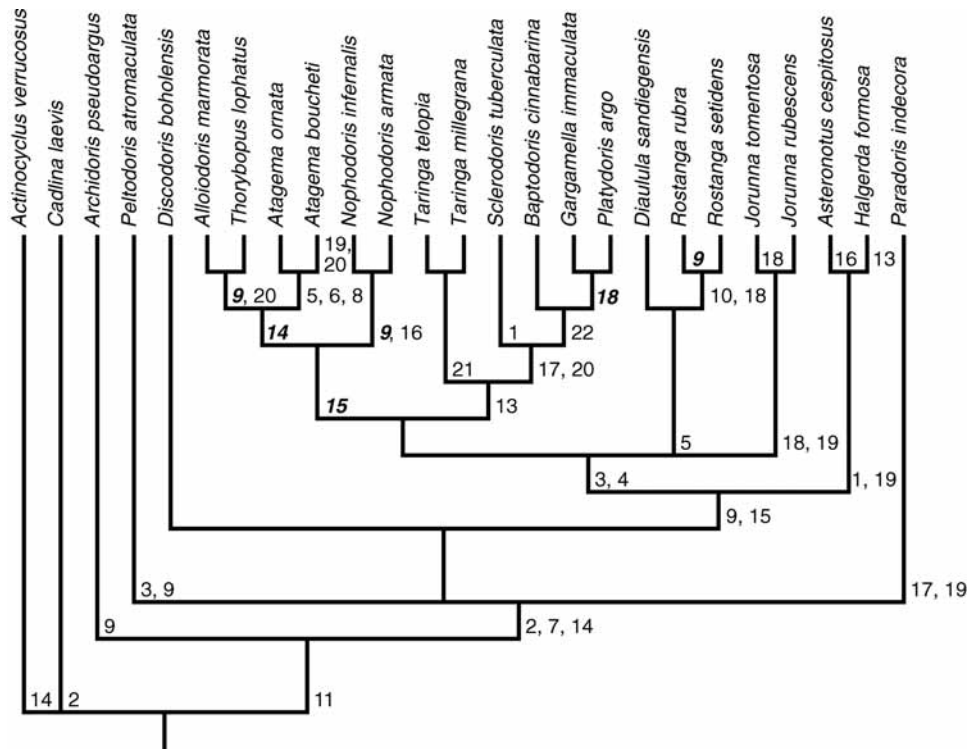
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Diaulula sandiegensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	?	0
<i>Platydoris argo</i>	1	1	1	1	0	0	1	0	1	1	0	1	1	1
<i>Platydoris angustipes</i>	1	1	1	1	0	0	1	0	1	1	0	1	1	1
<i>Platydoris maculata</i>	1	1	0	1	0	0	?	0	0	1	0	1	0	1
<i>Platydoris stomascuta</i>	1	1	0	1	0	0	?	0	0	1	0	1	0	1
<i>Platydoris annulata</i>	1	1	0	1	0	0	1	0	0	1	0	1	0	1
<i>Gargamella immaculata</i>	0	0	0	0	1	0	0	0	0	2	1	1	0	1
<i>Gargamella bovina</i>	0	0	0	0	1	0	0	0	0	2	1	0	?	1
<i>Gargamella gravastella</i>	0	0	0	0	1	0	0	0	0	2	0	0	?	1
<i>Gargamella wareni</i>	0	1	0	0	1	0	0	0	0	1	0	0	?	1
<i>Baptodoris cinnabarina</i>	0	1	0	1	0	1	1	1	0	1	1	1	0	1
<i>Baptodoris mimetica</i>	0	1	0	1	0	1	1	1	0	1	0	1	0	1



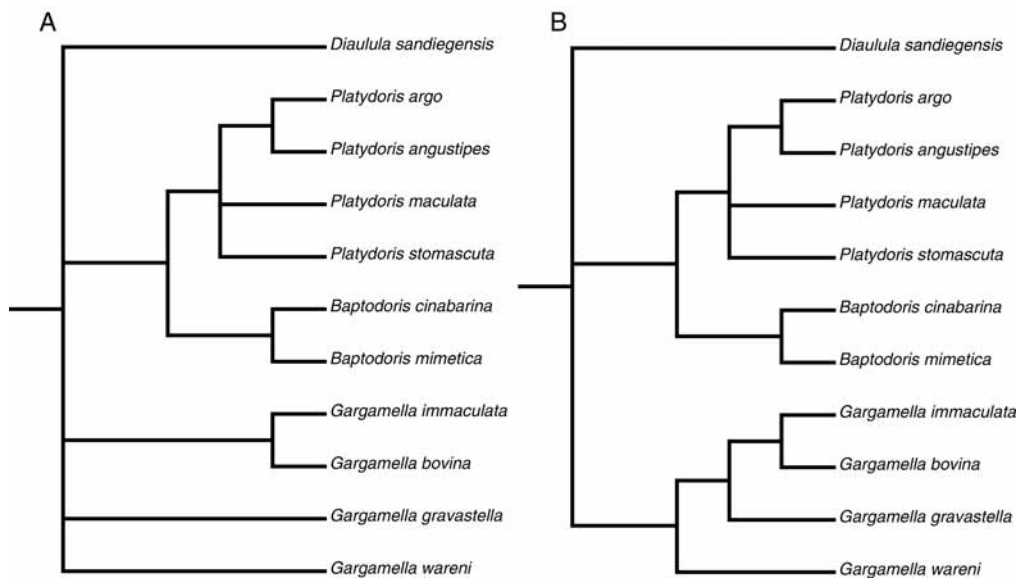
**Figure 60.** Phylogeny of the caryophyllidia-bearing dorids. A, consensus tree with all the characters included in the analysis. B, consensus tree with the character 'presence of jaws' removed from the analysis with the Bremer support values in terms of steps.

- atrium is not very clear in several species, where the point of fusion of vaginal duct and deferent duct is very close to the reproductive opening.
- (3) Shape of egg mass. There is no information on the egg mass morphology of most of the species studied, and therefore this character has not been considered in the present analysis.
  - (4) Sperm morphology. As in the case of the egg mass this character has not been included owing to lack of information about most of the species involved. Healy & Willan (1991) described the ultrastructure of the spermatozoa of several species of nudibranchs, but they do not include many of the taxa included in this analysis.





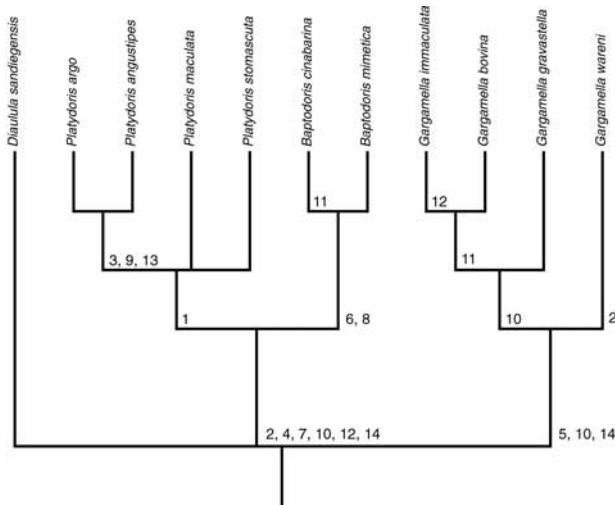
**Figure 61.** Arbitrarily selected tree to trace the character evolution within the caryophyllidia-bearing dorids. Numbers refer to characters listed in the text. Characters printed in bold and italic face presented at least one instance of reversal.



**Figure 62.** Phylogeny of the *Platydorid*–*Baptodorid*–*Gargamella* clade. A, consensus tree with all the characters included in the analysis. B, most parsimonious tree with the character ‘foot width’ removed from the analysis.

(5) Central nervous system. Examination of the nervous system of all caryophyllidia-bearing dorids revealed a similar morphology. The presence of

abdominal, genital and gastro-oesophageal ganglia may vary between different species, but it is also variable within the same species, and



**Figure 63.** Character evolution within the *Platydoris*–*Baptodoris*–*Gargamella* clade. Numbers refer to characters listed in the text.

therefore is not informative for phylogenetic purposes.

In order to obtain more resolution in the clade formed by *Platydoris*, *Gargamella* and *Baptodoris* when the new species from Indo-Pacific deep waters is included, we have used the database by Garovoy *et al.* (1999) and added the new taxon. Based on the polarities discussed by Garovoy *et al.* (1999), the distribution of plesiomorphic and apomorphic character states is found in Table 3. In this case, the genus *Diaulula* (which appears to be a basal caryophyllidia-bearing dorid) was selected as the outgroup. Data were analysed using the exhaustive algorithm.

## RESULTS

For the analysis of the first data matrix, 96 most parsimonious trees 42 steps long were obtained, all of them with a consistency index of 0.659 and a retention index of 0.792. All the trees were found in a single island. The strict consensus tree (Fig. 60A) shows very little resolution within the clade formed by *Alloiodoris*, *Thorybopus*, *Atagema* and *Nophodoris*. In order to obtain more resolution we performed a second analysis removing the character ‘presence of jaws’ [9], which exhibits several cases of homoplasy. From this second analysis, 78 most parsimonious trees 37 steps long were obtained, all of them with a consistency index of 0.718 and a retention index of 0.828. All these trees were also found in a single island. From them, a single consensus tree was produced (Fig. 60B). In this tree, the genus *Nophodoris* is monophyletic and the sister group of the clade containing *Atagema*, *Alloiodoris* and

*Thorybopus*. From this tree it is also evident that the caryophyllidia-bearing dorids are a monophyletic group, being the sister group of the clade containing *Halgerda* and *Asteronotus*. There is little resolution at the base of the clade containing the caryophyllidia-bearing dorids. The Bremer support analysis shows that most of the clades are poorly supported (Fig. 60B).

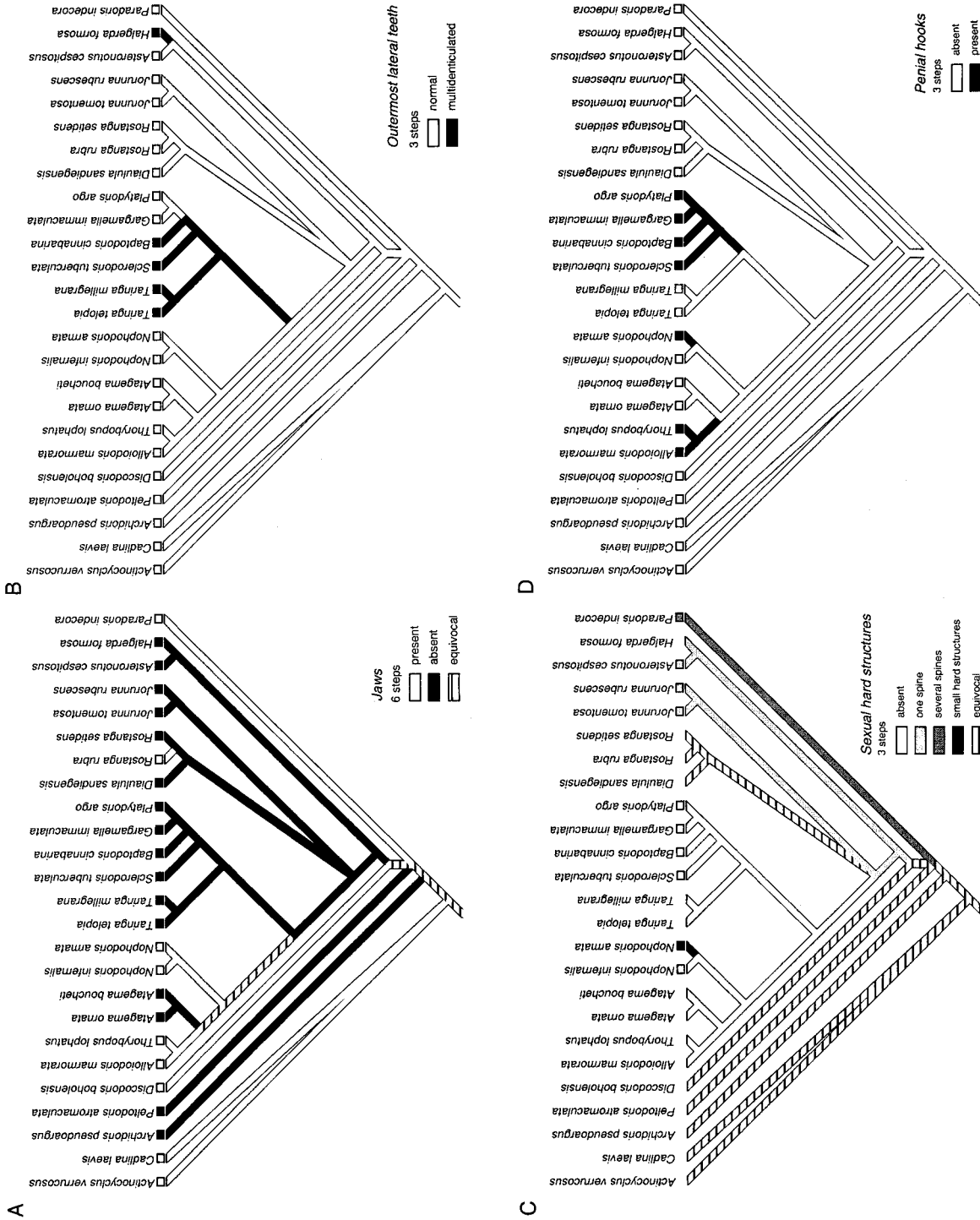
One of the most parsimonious trees was arbitrarily selected to trace the character evolution (Fig. 61). In this tree, four characters exhibit at least one instance of reversal. The jaws [9] have been lost several times in the evolution of the caryophyllidia-bearing dorids, the denticles of the outermost lateral teeth [13] have been lost in *Baptodoris* and *Platydoris*, the prostate becomes secondarily flattened [14] in *Atagema*, *Alloiodoris* and *Thorybopus* and it lost the two portions in *Atagema*, *Alloiodoris*, *Nophodoris* and *Thorybopus*. In addition, eight characters exhibit parallelism [1, 2, 9, 12, 13, 16, 19, 20].

From the second data matrix, three most parsimonious trees 18 steps long were obtained, all of them with a consistency index of 0.833 and a retention index of 0.893. From them a single consensus tree was produced (Fig. 62A), which shows very little resolution. However, when the character ‘foot width’ [2] was excluded, a single most parsimonious tree was obtained (Fig. 62B). This tree is 16 steps long and has a consistency index of 0.875 and a retention index of 0.92. In this tree, which has better resolution, it is clear that *Gargamella*, *Baptodoris* and *Platydoris* are monophyletic groups, *Gargamella wareni* being the sister group to other species of *Gargamella*. The synapomorphies supporting the clades are traced in Figure 63.

## DISCUSSION

According to the phylogenetic hypothesis depicted above, the caryophyllidia-bearing dorids are a monophyletic group. Obviously, the acquisition of this complex dorsal structures has happened only once in the evolution of the Doridina. *Halgerda* and *Asteronotus* are closely related to the caryophyllidia-bearing dorids and share with most of them the presence of a prostate with two differentiated portions. However, this phylogeny does not provide enough resolution within the major clades of the caryophyllidia-bearing dorids, probably because of the absence of a sufficient number of informative characters.

The lack of informative characters is due to the high degree of homoplasy that occurs within the cryptobranch dorids. It appears that, in the dorids with caryophyllidia, the shape of the radula has evolved several times to similar morphology. For example, the outermost lateral teeth pectinate have been acquired



**Figure 64.** Evolution of problematic characters. A, presence of the outermost lateral teeth. B, shape of the outermost lateral teeth. C, sexual hard structures. D, presence of penial hooks.

independently by *Halgerda* and *Baptodoris*, *Sclerodoris* and *Taringa* (Fig. 64B). The jaws have been lost several independent times (Fig. 64A). The copulatory hard structures associated with the accessory gland and the penial hooks have been evolved at least different three times (Fig. 64C,D). With this panorama it is very difficult to resolve the groupings among the caryophyllidia-bearing dorids.

#### CLASSIFICATION

Traditionally, as mentioned above, the caryophyllidia-bearing dorids have been divided within several families, and the presence of caryophyllidia has never been used as a character in the classification of dorids. According to the phylogeny obtained in the present paper, none of those prior classifications is correct, and all the caryophyllidia-bearing dorids should be united in a single taxon.

Several family group names have been introduced based on caryophyllidia-bearing genera in different attempts of classification that should probably be regarded as synonyms.

- Kentrodorididae Bergh, 1891: 135. Type genus *Kentrodoris* Bergh, 1876.  
 Platydorididae Bergh, 1891: 135. Type genus *Platydoris* Bergh, 1877.  
 Diaululidae Bergh, 1892: 1097. Type genus *Diaulula* Bergh, 1878.  
 Baptodorididae Odhner, 1926: 54. Type genus *Baptodoris* Bergh, 1884.  
 Halgerdidae Odhner, 1926: 54. Type genus *Halgerda* Bergh, 1880.  
 Asteronotidae Thiele, 1929–35 [1931]: 438. Type genus *Asteronotus* Ehrenberg, 1831.  
 Argidae Thiele, 1929–35 [1931]: 439. Type genus *Argus* Bohadsch, 1761, suppressed by Opinion 185 (ICZN, 1944).  
 Rostangidae Pruvot-Fol, 1951: 277. Type genus *Rostanga* Bergh, 1879.  
 Trippidae Kay & Young, 1969: 189. Type genus *Trippa* Bergh, 1877.

Also, several genera with caryophyllidia have been included in the families Dorididae Rafinesque, 1815, Archidorididae Bergh, 1892, Discodorididae Bergh, 1891, Miamiidae Bergh, 1891 and Aldisidae Odhner, 1939.

Prior to determining the relative rank of the taxa including the caryophyllidia-bearing dorids, the phylogenetic relationships of all the cryptobranchid dorids must be studied. This phylogeny is now in preparation and until all the information has been put together a new classification will not be proposed. The results of this analysis are still provisional, and the extraction of conclusions from it could be premature.

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## APPENDIX

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