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A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia)

ÁNGEL VALDÉS

Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA and Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA

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The phylogenetic relationships of the cryptobranch dorids are studied based on morphological characters of species belonging to all previously described genera. The phylogenetic hypothesis supports the cryptobranch dorids as a monophyletic group. There are two major clades within the Cryptobranchia: the radula-less dorids (Porostomata), and the radula-bearing dorids (**Labiostomata new taxon**). Labiostomata consists of those taxa sharing a more recent common ancestor with *Actinocyclus* than with *Mandelia*, and includes several monophyletic groups: Actinocyclidae, Chromodorididae, Dorididae and Discodorididae. The traditional group Phanerobranchia is probably paraphyletic. The new classification proposed for the Cryptobranchia addresses concepts of phylogenetic nomenclature, but is in accordance with the rules of the International Code of Zoological Nomenclature. The following genera of cryptobranch dorids are regarded as valid: *Doris* Linnaeus, 1758, *Asteronotus* Ehrenberg, 1831, *Atagema* J. E. Gray, 1850, *Jorunna* Bergh, 1876, *Discodoris* Bergh, 1877, *Platydoris* Bergh, 1877, *Thordisa* Bergh, 1877, *Diaulula* Bergh, 1878, *Aldisa* Bergh, 1878, *Rostanga* Bergh, 1879, *Aphelodoris* Bergh, 1879, *Halgerda* Bergh, 1880, *Peltodoris* Bergh, 1880, *Hoplodoris* Bergh, 1880, *Paradoris* Bergh, 1884, *Baptodoris* Bergh, 1884, *Geitodoris* Bergh, 1891, *Gargamella* Bergh, 1894, *Alloiodoris* Bergh, 1904, *Sclerodoris* Eliot, 1904, *Otinodoris* White, 1948, *Taringa* Er. Marcus, 1955 , *Sebadoris* Er. Marcus & Ev. Marcus, 1960, *Conualevia* Collier & Farmer, 1964, *Thorybopus* Bouchet, 1977, *Goslineria* Valdés, 2001, *Pharodoris* Valdés, 2001, *Nophodoris* Valdés & Gosliner, 2001. Several genera previously considered as valid are here regarded as synonyms of other names: *Doridigitata* d'Orbigny, 1839, *Doriopsis* Pease, 1860, *Staurodoris* Bergh, 1878, *Fracassa* Bergh, 1878, *Archidoris* Bergh, 1878, *Anoplodoris* Fischer, 1883, *Etidoris* Ihering, 1886, *Phialodoris* Bergh, 1889, *Montereina* MacFarland, 1905, *Ctenodoris* Eliot, 1907, *Carryodoris* Vayssière, 1919, *Austrodoris* Odhner, 1926, *Guyonia* Risbec, 1928, *Erythrodoris* Pruvot-Fol, 1933, *Neodoris* Baba, 1938, *Siraius* Er. Marcus, 1955, *Tayuva* Ev. Marcus & Er. Marcus, 1967, *Nuvuca* Ev. Marcus & Er. Marcus, 1967, *Doriorbis* Kay & Young, 1969, *Pupsikus* Er. Marcus & Ev. Marcus, 1970, *Percunas* Ev. Marcus, 1970, *Verrillia* Ortea & Ballesteros, 1981 . The genera *Artachaea* Bergh, 1882, *Carminodoris* Bergh, 1889 and *Homoiodoris* Bergh, 1882 have been poorly described and no type material is known to exist. They are regarded as *incertae sedis* until more material becomes available. The genus names *Xenodoris* Odhner *in* Franc, 1968 and *Cryptodoris* Ostergaard, 1950 are unavailable within the meaning of the Code. *Hexabranchus* Ehrenberg, 1831 is not a cryptobranch dorid, as suggested by other authors, because of the lack of a retractile gill. Other nomenclatural and taxonomic problems are discussed, and several type species, neotypes and lectotypes are selected. *Zoological Journal of the Linnean Society,* 2002, **136**, 535–636.

ADDITIONAL KEYWORDS: Mollusca – Nudibranchia – Doridoidea – Cryptobranchia – phylogenetic systematics – nomenclature – new classification – new taxa.

INTRODUCTION

Recent phylogenetic studies on several clades of the Doridoidea (Wägele, 1989b; Gosliner & Johnson, 1994, 1999; Valdés & Gosliner, 1999, 2001) have provided a preliminary outline of the evolution of the crypto-

E-mail: avaldes@nhm.org

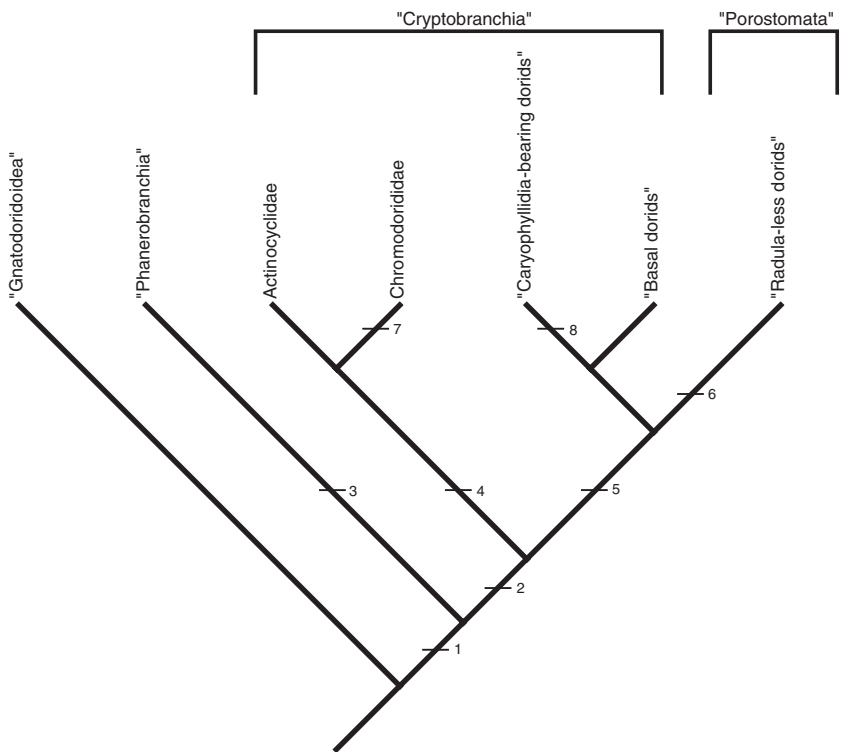

Figure 1. Preliminary hypothesis of the phylogenetic relationships of the Doridina, based on a compilation of several published phylogenetic analyses.

branch dorids. Figure 1 shows a nonparsimonious compilation of these phylogenies. According to this hypothetical tree, including the radula-less dorids within the Porostomata as traditionally defined, renders the Cryptobranchia paraphyletic only if Porostomata is excluded. The Porostomata are therefore regarded as cryptobranch dorids for the purposes of this paper (see Valdés & Gosliner, 1999). The tree additionally shows the cryptobranch dorids as divided into two major clades, one containing the families Actinocyclidae and Chromodorididae (Gosliner & Johnson, 1994; Gosliner & Johnson, 1999), the other containing the caryophyllidia-bearing dorids (Valdés & Gosliner, 2001), the radula-less dorids (Valdés & Gosliner, 1999) and a group of dorids characterized by the absence of apomorphic features. This group, which is probably paraphyletic, includes the genera *Doris* Linnaeus, 1758, *Discodoris* Bergh, 1877, *Archidoris* Bergh, 1878, and *Peltodoris* Bergh, 1880. There are also a number of other taxa lacking caryophyllidia and having a radula that have not been studied phylogenetically. For instance, nothing is known about the phylogenetic position of several genera such as *Hexabranchus* Ehrenberg, 1831, *Thordisa* Bergh, 1877, *Aldisa* Bergh, 1878, *Aphelodoris* Bergh, 1879 or *Hoplodoris* Bergh, 1880.

Recent studies on dorid molecular phylogenetics (Thollesson, 1999; Wollscheid & Wägele, 1999) have failed to provide information on the relationships and possible monophyly of the traditional groups of dorid nudibranchs, due to the lack of significant support.

The objective of the present paper is to review the systematic status of, and provide a phylogenetic hypothesis for, the cryptobranch dorids, based on complete and updated morphological studies of several genera previously described, as well as data obtained from the literature.

HISTORY OF THE CLASSIFICATION

There have been several historical attempts to classify the cryptobranch dorids. The name Cryptobranchia (as Cryptobranchiata) was introduced in 1883 by Fischer (1880–1887) to include dorids able to retract the gill into a cavity. He divided this group into two families: Doridopsidae P. Fischer, 1883, which included the radula-less dorids with a dorsal gill, and Dorididae P. Fischer, 1883, which comprised the cryptobranch dorids with a radula and included the genera *Doris* Linnaeus, 1758; *Hexabranchus* Ehrenberg, 1831 and *Chromodoris* Alder & Hancock, 1855.

Table 1. Summary of the classification of the cryptobranch dorids proposed by Bergh (1891). Junior homonyms and suppressed names are accompanied by available synonyms

Family group names	Genus-group names
BATHYDORIDIDAE Bergh, 1891	*Bathydoris* Bergh, 1884
HEXABRANCHIDAE Bergh, 1891	*Hexabranchus* Ehrenberg, 1831
ARCHIDORIDIDAE Bergh, 1891	*Archidoris* Bergh, 1878
	Homoiodoris Bergh, 1880
	Staurodoris Bergh, 1878 (= *Doris* Linnaeus, 1758)
	Echinodoris Bergh, 1874
	Artachaea Bergh, 1880
	Petelodoris Bergh, 1881
DISCODORIDIDAE Bergh, 1891	*Discodoris* Bergh, 1877
	Geitodoris Bergh, 1891
	Carminodoris Bergh, 1889
	Fracassa Bergh, 1878
	Paradoris Bergh, 1884
	Hoplodoris Bergh, 1880
	Audura Bergh, 1878
	Halla Bergh, 1876 (= *Hallaxa* Eliot, 1909)
	Rostanga Bergh, 1879
DIAULULIDAE Bergh, 1891	*Diaulula* Bergh, 1878
	Thordisa Bergh, 1877
	Aldisa Bergh, 1878
	Trippa Bergh, 1877
	Halgerda Bergh, 1880
	Baptodoris Bergh, 1884
	Peltodoris Bergh, 1880
	Phialodoris Bergh, 1890
CADLINIDAE Bergh, 1891	*Cadlina* Bergh, 1879
KENTRODORIDIDAE Bergh, 1891	*Kentrodoris* Bergh, 1876
	Jorunna Bergh, 1876
PLATYDORIDIDAE Bergh, 1891	*Platydoris* Bergh, 1877
	Asteronotus Ehrenberg, 1831
	Dictyodoris Bergh, 1880
CHROMODORIDIDAE Bergh, 1891	*Chromodoris* Alder & Hancock, 1855
	Ceratosoma J. E. Gray *in* M. E. Gray, 1850
	Thorunna Bergh, 1877
	Aphelodoris Bergh, 1879
MIAMIRIDAE Bergh, 1891	*Miamira* Bergh, 1875
	Orodoris Bergh, 1875
	Sphaerodoris Bergh, 1877

The earliest comprehensive classification of the cryptobranch dorids was published by Bergh (1891), who divided this group into 10 subfamilies. He included *Bathydoris* Bergh, 1884 and *Hexabranchus* Ehrenberg, 1831 within the Cryptobranchia, despite the fact that their gills are not retractable. As radulaless dorids, the Porostomata were excluded from this classification, even though some of them are able to retract the gill into a dorsal cavity (family Dendrodoridae). Table 1 summarizes Bergh's (1891) classification, which was mainly based on the shape and texture of the body, the morphology of the anterior border of the foot, the presence or absence of jaw elements, the shape of the radular teeth, the presence or absence of penial or other copulatory spines or hooks and the shape of the prostate.

Pelseneer (1906) and Iredale & O'Donoghue (1923) simplified the classification presented by

Bergh, and placed in a single family (Doridiidae or Dorigitatidae) all the cryptobranch dorids, except for the Porostomata.

Odhner (1934) considered that the genera *Bathydoris* and *Doridoxa* had several 'primitive' characters that related them to the Arminacea and Dendronotacea, and that they deserved to be separated from the remaining dorids, so he introduced the new name Gnathodoridacea for *Bathydoris* and *Doridoxa*, and Eudoridacea for the rest of the dorids, which 'lack mandibles'. He maintained the names Cryptobranchia and Phanerobrancha within Eudoridacea.

Thiele (1929–35) and Odhner (1939) reintroduced the scheme presented by Bergh, and divided the cryptobranch dorids (Porostomata excluded) into several subfamilies. Years later, Odhner (see Franc, 1968), using basically the same characters as Bergh (1891), elevated most of Bergh's subfamilies to the rank of families. Several new families and genera were added, and the placement of some genera in different families changed. The basic scheme of Odhner's classification (Table 2) is still in use, with modifications, by most authors. Odhner in Franc (1968) also introduced the new name Anadoridacea to replace Phanerobranchia, and regarded Eudoridacea as a synonym of Cryptobranchia. He did not provide clarification for these changes.

Thompson (1976) for the first time used the names Anadoridacea and Eudoridacea as family group level names, changing the ending to Anadoridoidea and Eudoridoidea. Subsequently, other authors maintained the usage of this names as superfamilies, sometimes as junior synonyms of Phanerobranchia and Cryptobranchia (Schmekel & Portmann, 1982) and sometimes as valid names (Rudman, 1998). According to Article 29 of the International Code of Zoological Nomenclature (ICZN, 1999) family group names must be formed by adding a suffix to the stem of the name of the type genus, or to the entire name of the type genus. As the genus names 'Anadoris' or 'Eudoris' do not exist, the names Anadoridacea and Eudoridacea cannot be used at the family group level.

Rudman (1984) changed the classification of the Chromodorididae altogether. For the first time, the Cadlinidae and Chromodorididae were united within a single family, many genera were synomyzed and new genera were described. Rudman's classification gained universal acceptance and is presently widely used; later, Gosliner & Johnson (1999) provided the phylogenetic bases for it.

Schmekel (1985) proposed a intuitive phylogenetic hypothesis of the nudibranch dorids. She considered the radula-less dorids to be the probable sister group to both the cryptobranch and phanerobranch dorids. In this scenario, the gill became retractile twice independently.

The most radical reassessment of Odhner's classification in recent years was provided by Rudman (1998), who divided the cryptobranch dorids into only two families, Chromodorididae and Doridiidae, moved the radula-less dorids to the Cryptobranchia (as Eudoridoidea), and also included *Hexabranchus* in this group. Rudman (1998) introduced the name Doridina for all dorid nudibranchs including *Bathydoris*. Wägele & Willan (2000) used the same scheme but recognized Conualeviidae as a distinct family.

Based on his morphological phylogenetic analysis Brunckhorst (1993) proposed that Dendrodorididae should be transferred from the Porostomata to the Cryptobranchia, keeping the other porostomid family, Phyllidiidae, with a superfamilial rank. Baranetz & Minichev (1993) proposed a new classification supporting a similar point of view. Based on their interpretation of the evolution of the gill in nudibranchs, they included Dendrodorididae with the other dorids with a dorsal gill, and elevated Phyllidiidae to the rank of order. In contrast, Valdés & Gosliner (1999) found the Porostomata to be a monophyletic group. This hypothesis was further supported by Thollesson (2000), based on molecular data.

Wägele & Willan (2000) demonstrated that the dorid nudibranchs form a monophyletic group, and used the name Anthobranchia, instead of Doridina, for this clade. They also showed that *Bathydoris* is the sister group to both phanerobrach and cryptobranch dorids. Their phylogeny shows the phanerobranch dorids to be paraphyletic, as *Hexabranchus* is the sister group to the cryptobranch dorids. The phylogeny is not detailed enough to reach further conclusions on the relationships within the Cryptobranchia.

Valdés & Gosliner (2001), based upon phylogenetic analysis, found that the caryophyllidia-bearing dorids, previously divided into several families, constitute a monophyletic group. However, these authors did not propose any change in the classification.

Currently, there is no general agreement regarding the classification of the cryptobranch dorids. Specialists agree only that the classification of this group is in need of major revision using contemporary systematics techniques.

MATERIAL AND METHODS

Type material, additional non-type material and information regarding the types of species studied in the present paper were obtained from 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), The Natural History Museum, London (BMNH), Naturhistoriska

Table 2. Summary of the classification of the cryptobranch dorids proposed by Odhner *in* Franc (1968). Junior homonyms and suppressed names are accompanied by available synonyms

Family group names	Genus-group names
HEXABRANCHIDAE Bergh, 1891	*Hexabranchus* Ehrenberg, 1831
ECHINOCHILIDAE Odhner *in* Franc, 1968	
ECHINOCHILINAE Odhner *in* Franc, 1968	*Cadlinella* Thiele, 1929
	Jeanrisbecia Odhner *in* Franc, 1968
	Echinochila Mörch 1868, = *Cadlina* Bergh, 1879
	Chromocadlina Odhner *in* Franc, 1968
LISSODORIDINAE Odhner *in* Franc, 1968	*Lissodoris* Odhner, 1934
CHROMODORIDIDAE Bergh, 1891	*Ceratodoris* J. E. Gray *in* M. E. Gray, 1850
	Gruvelia Risbec, 1928
	Otinodoris White, 1948
	Chromodoris Alder & Hancock, 1855
	Hypselodoris Stimpson, 1855
	Babaina Odhner *in* Franc, 1968
	Thorunna Bergh, 1877
ACTINOCYCLIDAE Pruvot-Fol, 1934	*Actinocyclus* Ehrenberg, 1831
	Hallaxa Eliot, 1909
MIAMIRIDAE Bergh, 1891	*Casella* H. & A. Adams 1854
	(= *Glossodoris* Ehrenberg, 1831
	Ceratosoma J. E. Gray *in* M. E. Gray, 1850
	Miamira Bergh, 1875
	Orodoris Bergh, 1875
	Gravieria Vayssière, 1912
ALDISIDAE Odhner, 1939	*Aldisa* Bergh, 1878
ROSTANGIDAE Pruvot-Fol, 1951	*Awuka* Er. Marcus, 1955
	Boreodoris Odhner, 1939
	Rostanga Bergh, 1879
DORIDIDAE Rafinesque, 1815	
DORIDINAE Rafinesque, 1815	*Doris* Linnaeus, 1758
	Austrodoris Odhner, 1926
	Siraius Er. Marcus, 1955
ARTACHAEINAE Odhner *in* Franc, 1968	*Artachaea* Bergh, 1880
	Alloiodoris Bergh, 1904
ARCHIDORIDIDAE Bergh, 1891	*Archidoris* Bergh, 1878
	Etidoris Ihering, 1886
	Ctenodoris Eliot, 1907
	Atagema J. E. Gray *in* M. E. Gray, 1850
	Trippa Bergh, 1877
	Petelodoris Bergh, 1881
	Peronodoris Bergh, 1904
GEITODORIDIDAE Odhner *in* Franc, 1968	*Geitodoris* Bergh, 1891
HOMOEODORIDIDAE Odhner, 1926	*Homoeodoris* Bergh, 1882, error for *Homoiodoris*
BAPTODORIDIDAE Odhner, 1926	*Baptodoris* Bergh, 1884
	Carminodoris Bergh, 1889
	Paradoris Bergh, 1884
	Dystylodoris Odhner, 1959
DISCODORIDIDAE Bergh, 1891	
TARINGINAE Odhner *in* Franc, 1968	*Taringa* Er. Marcus, 1955
NEODORIDINAE Odhner *in* Franc, 1968	*Neodoris* Baba, 1938
DISCODORIDINAE Bergh, 1891	*Thordisa* Bergh, 1877
	Aporodoris Ihering, 1886
	Nirva Bergh, 1905
	Discodoris Bergh, 1877
	Anisodoris Bergh, 1898

Table 2. *Continued*

Family group names	Genus-group names
	Peltodoris Bergh, 1880
	Diaulula Bergh, 1878
	Phialodoris Bergh, 1890
CENTRODORIDIDAE Bergh, 1891	*Audura* Bergh, 1878
	Centrodoris Odhner *in* Franc, 1968
	(= *Kentrodoris* Bergh, 1876)
	Jorunna Bergh, 1876
ASTERONOTIDAE Thiele, 1931	*Aphelodoris* Bergh, 1879
	Halgerda Bergh, 1880
	Sclerodoris Eliot, 1904
	Asteronotus Ehrenberg, 1831
PLATYDORIDIDAE Bergh, 1891	
PLATYDORIDINAE Bergh, 1891	*Platydoris* Bergh, 1877
	Gargamella Bergh, 1894
HOPLODORIDINAE Odhner *in* Franc, 1968	*Hoplodoris* Bergh, 1880
	Xenodoris Odhner in Franc, 1968, *nomen nudum*

Riksmuseet, Stockholm (SMNHI), The National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), The Yale Peabody Museum (YPM), Museum für Naturkunde der Humboldt-Universität, Berlin (MNHB), Museo Nacional de Ciencias Naturales, Madrid (MNCN), and the Hancock Museum, Newcastle-upon-Tyne (HMNC).

Specimens were dissected by dorsal incision. Their internal features were examined and drawn under a dissecting microscope using a camera lucida. Particularly interesting soft parts, including the dorsal surface of the mantle, were critical-point dried for SEM. Special attention was paid to the morphology of the reproductive, digestive and central nervous systems. The penial and vaginal hooks and accessory spines of several species were similarly prepared. Features of living animals were recorded from photographs or notes of collectors.

ABBREVIATIONS USED IN THE FIGURES

a, ampulla; b, blood gland; bb, buccal bulb; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; ca, caecum; cg, cerebral ganglion; d, deferent duct; f, female gland mass; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; o, oesophagus; og, gastro-oesophageal ganglion; ot, oral tube; p, pedal nerves; pc, pedal commissure; pg, pedal ganglion; pl, pleural nerves; plg, pleural ganglion; ppc, parapedal commissure; pr, prostate; r, rhinophoral nerves; rs, radular sac; s, seminal receptacle; sg, salivary gland; sp, syrinx; st, stomach; t, oral tentacle, v, vagina; vl, visceral loop.

SYSTEMATIC DESCRIPTIONS

GENUS *DORIS* LINNAEUS, 1758

Doris Linnaeus, 1758: 653. Type species: *Doris verrucosa* Linnaeus, 1758, by monotypy.

Doridigitata d'Orbigny, 1836–42 [1839]: 39–40, suppressed by Opinion 1980 (ICZN, 2001). Type species: *Doris verrucosa* Linnaeus, 1758, by subsequent designation by J. E. Gray (1847).

Doriopsis Pease, 1860: 32–33. Type species: *Doriopsis granulosa* Pease, 1860, by monotypy, **syn. nov.**

Staurodoris Bergh, 1878a: 578–579, suppressed by Opinion 1980 (ICZN, 2001). Type species: *Doris verrucosa* Linnaeus, 1758, by original designation.

Archidoris Bergh, 1878b: 616–617. Type species: *Doris pseudoargus* Rapp, 1827, by subsequent designation by Iredale & O'Donoghue (1923) **syn. nov.**

Anoplodoris Fischer, 1880–87 [1883]: 521. Type species: *Doris pseudoargus* Rapp, 1827, by subsequent designation by Iredale & O'Donoghue (1923) **syn. nov.**

Ctenodoris Eliot, 1907: 338. Type species: *Staurodoris pecten* Eliot, 1906, by subsequent designation by Baba (1937), **syn. nov.**

Austrodoris Odhner, 1926: 67–68. Type species: *Archidoris rubescens* Bergh, 1898, by original designation, **syn. nov.**

Guyonia Risbec, 1928: 102. Type species: *Guyonia flava* Risbec, 1928, here designated **syn. nov.**

Neodoris Baba, 1938: 13–14. Type species: *Neodoris tricolor* Baba, 1938, by original designation, **syn. nov.**

Siraius Marcus, 1955: 134. Type species: *Siraius ilo* Er. Marcus, 1955, by original designation, **syn. nov.**

Doriorbis Kay & Young, 1969: 177–178. Type species: *Doris immonda* Risbec, 1928, here designated **syn. nov.**

Diagnosis

Dorsum covered with simple rounded tubercles, stiffened by integumentary spicules, which do not protrude from the dorsal surface. Head with two lateral prolongations. Anterior border of the foot grooved but not notched. Labial cuticle lacking rodlets. Radula composed of simple, hamate teeth. Outermost teeth may be simple or denticulate. Reproductive system with a tubular, granular and simple prostate. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

Linnaeus (1758) introduced the genus *Doris* for *Doris verrucosa*, with a short and confusing Latin description. It is not clear whether Linnaeus studied specimens himself or whether his description was based on the two pre-Linnaean and nonbinomial bibliographical references cited (Rumphius, 1705; Seba, 1735). These two papers describe different animals. 'Limax marina verrucosa', described by Rumphius (1705: 38), could be any shell-less gastropod, but probably a species of Phyllidiidae collected from Ambon, Indonesia. Seba's (1735: pl. 61, fig. 5) 'Mitella verrucosa' is a nudibranch mollusc very likely identifiable as the Indo-Pacific species *Phyllidiella pustulosa* (Cuvier, 1804). However, *Doris verrucosa* has been identified by most authors as the European species described below, characterized by having hemispherical tubercles on the dorsum and numerous unipinnate branchial leaves. The name *Doris* has also been applied to the relatives of this species, first to all dorid nudibranchs having a circlet of dorsal respiratory leaves, and more recently to just a few species closely related to the mentioned European species. Bouchet & Valdés (2000) submitted a proposal to the ICZN in order to maintain the current usage of the generic and specific names *Doris verrucosa* by the designation of a neotype. This proposal was endorsed by the ruling of the Commission in Opinion 1980 (ICZN, 2001).

D'Orbigny (1836–1842) [1839] segregated *Doris* into several discrete species groups, which he treated as subgenera. For the new species *Doris bertheloti*, from the Canary Islands, he established *Doridigitata*, where he also allocated *Doris verrucosa* (applying this name to the species mentioned above). Gray (1847) validly fixed *Doris verrucosa* as the type species of *Doridigitata*. The genus *Doridigitata* d'Orbigny, 1839 is an objective junior synonym of *Doris* because they are based on the same type species. Bergh (1878a) recognized that the original description of *Doris* did not fit with the usage of the name by most of the authors, and considered that *Doridigitata* was the valid name for this genus. At the same time, Bergh (1878a) introduced the new name *Staurodoris* to replace *Doridigitata*, which according to him was improperly formed. Therefore, *Staurodoris* and *Doridigitata* have the same type species and are objective synonyms.

Bergh (1878b) introduced the genus *Archidoris* based on Cuvier's (1804) misapplication of the name *Doris tuberculata* Müller, 1778 (see also remarks on *Doris pseudoargus*), *Doris flammea* Alder & Hancock, 1844 and *Doris montereyensis* Cooper, 1862. At the same time he mentioned: 'The spawn and a fragment of the ontogeny of the type of this form [*Archidoris*] is known (see Alder & Hancock)'. Iredale & O'Donoghue (1923) interpreted this comment to mean that Bergh (1878b) had selected a misapplication of the name *Doris tuberculata* by Alder & Hancock to be the type species of *Archidoris*. Actually, Bergh's (1878b) comment cannot be interpreted as the designation of a type species (see ICZN, 1999: Article 68.2). Therefore, Iredale & O'Donoghue (1923) were the first authors to designate a type species for the genus *Archidoris*, by subsequent designation. It is clear from the list of species and synonyms included in *Archidoris* that these authors meant to select the misapplication of the name *Doris tuberculata* by most authors (= *Doris pseudoargus* Rapp, 1827; see below) as the type species. Thus, according to Article 69.2.4 (ICZN, 1999), Iredale & O'Donoghue (1923) are deemed to have selected *Doris pseudoargus* Rapp, 1827 as the type species of *Archidoris*.

Examination of the external morphology and anatomy of *Doris pseudoargus* shows that this species is very similar to *Doris verrucosa*, with the exception of the presence of large and rounded dorsal tubercles, unipinnate branchial leaves and pectinate outermost teeth in the latter. The phylogenetic analysis carried out (see below) showed that they are members of the same clade. There are no consistent differences that justify the maintenance of two different genera for these closely related taxa.

Fischer (1880–1887) [1883] introduced the new genus *Anoplodoris* Fischer, 1883 to accommodate several nominal genera (and species) previously described. One of these species was cited as '*Doris tuberculata* Linné', which constitutes an incorrect citation rather than a misapplication. The name *Doris tuberculata* was never mentioned by Linnaeus in any of his works. Iredale & O'Donoghue (1923) subsequently designated '*Doris tuberculata* Linné' as the type species of *Anoplodoris*. Again, it is clear that these authors were referring to the misapplication of the name *Doris tuberculata* by most authors (= *Doris pseudoargus* Rapp, 1827; see below), and by the provi-

sions of Article 69.2.4 (ICZN, 1999), Iredale & O'Donoghue (1923) are deemed to have selected *Doris pseudoargus* Rapp, 1827 as the type species of *Anoplodoris*. Because *Anoplodoris* and *Archidoris* are based on the same type species they are objective synonyms.

Odhner (1926) described the genus *Austrodoris* based on *Archidoris rubescens* Bergh, 1898. According to this author, *Austrodoris* differs from *Doris* and *Archidoris* by having short, wide nonattached salivary glands. In the following years, there was a great deal of confusion between the name *Archidoris* and *Austrodoris*, but in general (with a few exceptions) the former was used for species from the northern hemisphere and the latter for species from the southern hemisphere, regardless of the anatomical features of the animals described. Wägele (1990) redescribed the genus *Austrodoris* and concluded that all species previously described are synonyms of *Austrodoris kerguelenensis* (Bergh, 1884). She also maintained the usage of the genus *Austrodoris*, which differs from *Archidoris* by having most of the deferent duct covered with a muscular sheath, lacking a glans penis and having the seminal receptacle and the bursa copulatrix inserting opposite and not serially on the vaginal duct. The examination of the type species of the genera *Doris* and *Archidoris* has revealed that they also have these features. Thus, there are no consistent differences between these taxa that justify the maintenance of different genus names.

Baba (1938) described the genus *Neodoris* based on *Neodoris tricolor* Baba, 1938, the type species by original designation, as different from *Doris*, *Archidoris* and *Anisodoris*. According to Baba (1938) the main distinctive feature of this genus is the absence of a glans penis. He considered *Neodoris* to be closely related to *Austrodoris* and *Archidoris*, but distinguishable by having a prostate gland and band-like salivary glands. Later, Baba (1998) recognized that *Neodoris* is a synonym of *Archidoris*, and suggested that *Austrodoris* could be a synonym as well.

Marcus (1955) described the genus *Siraius* for *Siraius ilo* Er. Marcus, 1955 from Brazil. He characterized this new genus by the presence of hook-shaped lateral and pectinate marginal teeth, short and grooved oral tentacles, short and wide salivary glands, tubular prostate and penis unarmed.

Kay & Young (1969) introduced the genus *Doriorbis* for a misidentification of *Doris nucleola* Pease, 1860 (see remarks on *Doris immonda* Risbec, 1928). They characterized this new genus as having simply pinnate branchial leaves arranged as a circlet about a posterior anus, hamate radular teeth with the outermost laterals denticulate, and a Y- or T-shaped medial streak extending from the rhinophores to the middorsum. According to Article 70.3 (ICZN, 1999) if the type species of a nominal genus is found to be misidentified an author may select and fix as the type species the species that will, in his or her judgement, best serve stability. In this case the selection of *Doris immonda* as the type species clearly serves stability better, as *Doris nucleola* in the sense of its original description (Pease, 1860) is an unidentifiable species, which has well-developed oral tentacles and probably belongs to a different genus.

Brodie & Willan (1993) redescribed *Doris immonda* (as *Doris nucleola*) and considered that it belongs to the genus *Siraius* Er. Marcus, 1955. Therefore *Doriorbis* became a synonym of *Siraius*. At the same time, they distinguished *Siraius* from other cryptobranch dorids on the basis of two synapomorphies, the presence of papillae of unequal size around the rhinophoral sheaths, and pectinate outermost lateral teeth. The first character does not have, in my opinion, much phylogenetic significance, and the second is also present in other species of *Doris*, such as *D. pseudoargus*. Brodie & Willan (1993) considered *Siraius* to be closely related to *Etidoris* Ihering, 1886; which is a synonym of *Thordisa* Bergh, 1877 (see below). Baba (1998) regarded *Siraius* as a different genus on the basis of the presence of pectinate outermost teeth.

The genus *Doriopsis* was introduced by Pease (1860) based on *Doriopsis granulosa*. Pease (1860) justified the creation of a new genus on the basis of the arrangement of the gill, which has the leaves 'disposed in the form of a semicircle, on the posterior portion of the back, and retractile into a similarly formed slit, the convex portion posteriorly'. Four years later, Alder & Hancock (1864) introduced the new genus *Doridopsis*, which has the same features as *Dendrodoris* Ehrenberg, 1831 (see Valdés *et al*., 1996), and only one letter difference from the name *Doriopsis* Pease, 1860. Later, Pease (1871a) reaffirmed his genus name *Doriopsis* as valid and different from *Doridopsis*. He also argued that *Doridopsis* should be considered invalid, to avoid confusion with *Doriopsis*, and erected the replacement name *Hanstellodoris* Pease, 1871 for it. However, Bergh (1876) regarded *Doriopsis* and *Doridopsis* as synonyms, not in the meaning of Pease (1860) but in the meaning of Alder & Hancock (1864), and accepted *Doriopsis* as the valid name of the genus. This opinion was accepted by most authors in the following years, and *Doriopsis* was regarded as a junior synonym and a member of the Porostomata (radulaless dorids). O'Donoghue (1924) considered that Ehrenberg's name *Dendrodoris* was valid, and treated *Doriopsis* and *Doridopsis* as junior synonyms of the former. Pruvot-Fol (1931) suggested for the first time since Pease (1860, 1871a) that *Doriopsis* is not a synonym of *Dendrodoris*, but a distinct genus that should be place in the family Archidorididae. On the other

hand, *Doridopsis* is currently regarded as a synonym of *Dendrodoris* (Valdés *et al*., 1996).

Probably unaware of Pease's (1860) work, Eliot (1907) described the new subgenus *Ctenodoris* Eliot, 1907 to include *Staurodoris pecten* Eliot 1906 and *Doris flabellifera* Cheesman, 1881. Baba (1937) subsequently selected *Staurodoris pecten* Eliot, 1906 to be the type species. According to Eliot (1907) the main distinctive feature of *Ctenodoris* is the structure of the gill, which has the leaves 'arranged in a line of crescent, and the upper lip of the pocket shuts down over them like a single valve'. This description is very similar to that of *Doriopsis*, and these two names are clearly synonyms. The genus *Guyonia* was described by Risbec (1928) on the basis of *Guyonia flava* Risbec, 1928, *Doris pecten* Collingwood, 1881 and *Doriopsis viridis* Pease, 1861. *Guyonia flava* is here designated as the type species. Risbec (1928) described *Guyonia* as having the general shape of a *Platydoris*, with small papillae on the dorsum. Radula with unicuspid teeth and penis unarmed. Gill formed of pinnate leaves inserted anteriorly to the anus and forming an convex arch that is retractile under a semicircular lamellae. This description fits with the characteristics of *Doriopsis*. Baba & Hamatani (1961) regarded *Ctenodoris* and *Guyonia* as synonyms of *Doriopsis* for the first time.

The phylogenetic analysis carried out in this paper clearly shows that *Doriopsis* is a derived member of the clade containing the members of the genus *Doris*. If *Doriopsis* is maintained as a separate genus, *Doris* becomes paraphyletic. The same would probably occur for the rest of the synonyms of *Doris* if more species were included in the analysis.

DORIS VERRUCOSA LINNAEUS, 1758 (FIGS 2, 3)

Doris verrucosa Linnaeus, 1758: 653.
Doris derelicta Fischer, 1867: 7–8.
Doris biscayensis Fischer, 1872: 6–8.
Staurodoris januari Bergh, 1878a: 583–585, pl. 63, fig. 24, pl. 64, figs 8–12.
Staurodoris verrucosa var. *mollis* Eliot, 1906a: 338–339.
Staurodoris bobretzkii Gadzikiewicz, 1907: 509–510.

Type material

Doris verrucosa Linnaeus, NEOTYPE (designated by Bouchet & Valdés, 2000 and validated by Opinion 1980 – ICZN, 2001): Castropol, Asturias, Spain, leg. J. Cigarría (MNHN). *Doris derelicta* Fischer, NEOTYPE (designated by Bouchet & Valdés, 2000): Castropol, Asturias, Spain, leg. J. Cigarría (MNHN). The type material of *Staurodoris januari* Bergh could not be located at ZMUC and is presumed lost; the original type locality is near Rio de Janeiro, Brazil.

Additional material

Naples, Italy 1898, three specimens, 28–33 mm preserved length, leg. F. M. MacFarland (CASIZ 082119).

External morphology

The external morphology of this species has been described and illustrated by many authors. Three recent examples can be found in the papers by Schmekel (1968), Ortea, Pérez & Llera (1982) and Thompson & Brown (1984).

The general colour of the living animals is uniformly yellow to yellowish-grey. The whole dorsum is covered with hemispherical tubercles varying in size (Fig. 2D). The largest tubercles are situated in the central region of the body. The rhinophoral sheath has one prominent, stalked tubercle on each side. The branchial sheath has 8–12 stalked tubercles all around. There are 13–18 unipinnate branchial leaves, forming a circle. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 11 lamellae in a 28-mm preserved length specimen.

Ventrally there are no oral tentacles, but two blunt prolongations on each side of the mouth opening (Fig. 3F). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six 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 with it at each side of the oesophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $38 \times (50.0.50)$ in a 33-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 2A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 2B). The outermost teeth are smaller and also lack denticles (Fig. 2C). The oesophagus is short, convoluted and connects directly to the stomach (Fig. 3A).

The ampulla is very large and branches into a short oviduct and the prostate (Fig. 3C). The oviduct enters the female gland mass near to its centre. The prostate is tubular, folded and granular (Fig. 3B). It connects with a long duct that narrows and expands again into the long ejaculatory portion of the deferent duct. The

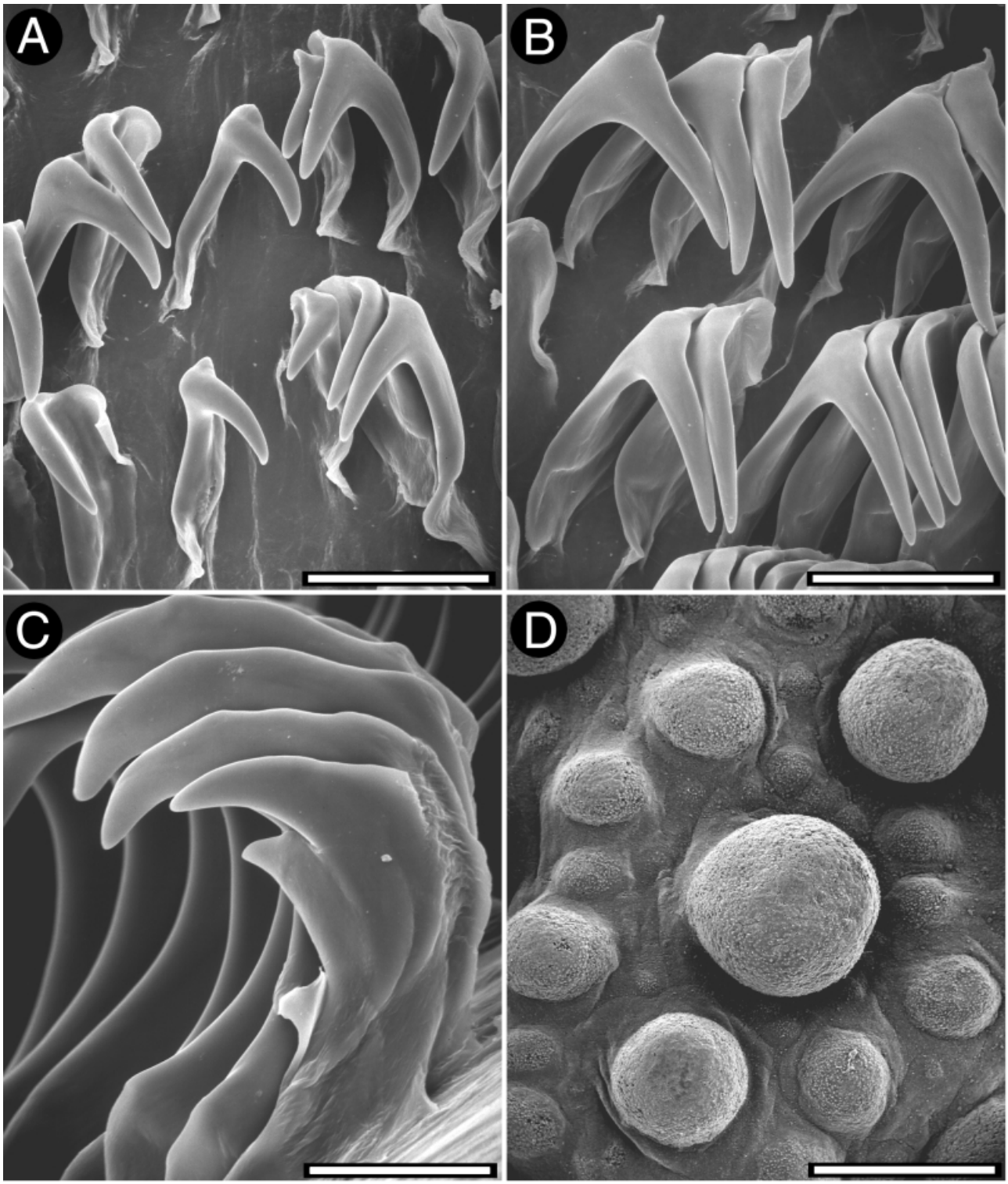

Figure 2. *Doris verrucosa* (CASIZ 082119), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 60 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 30 μm. D, dorsal tubercles; scale bar = 1.5 mm.

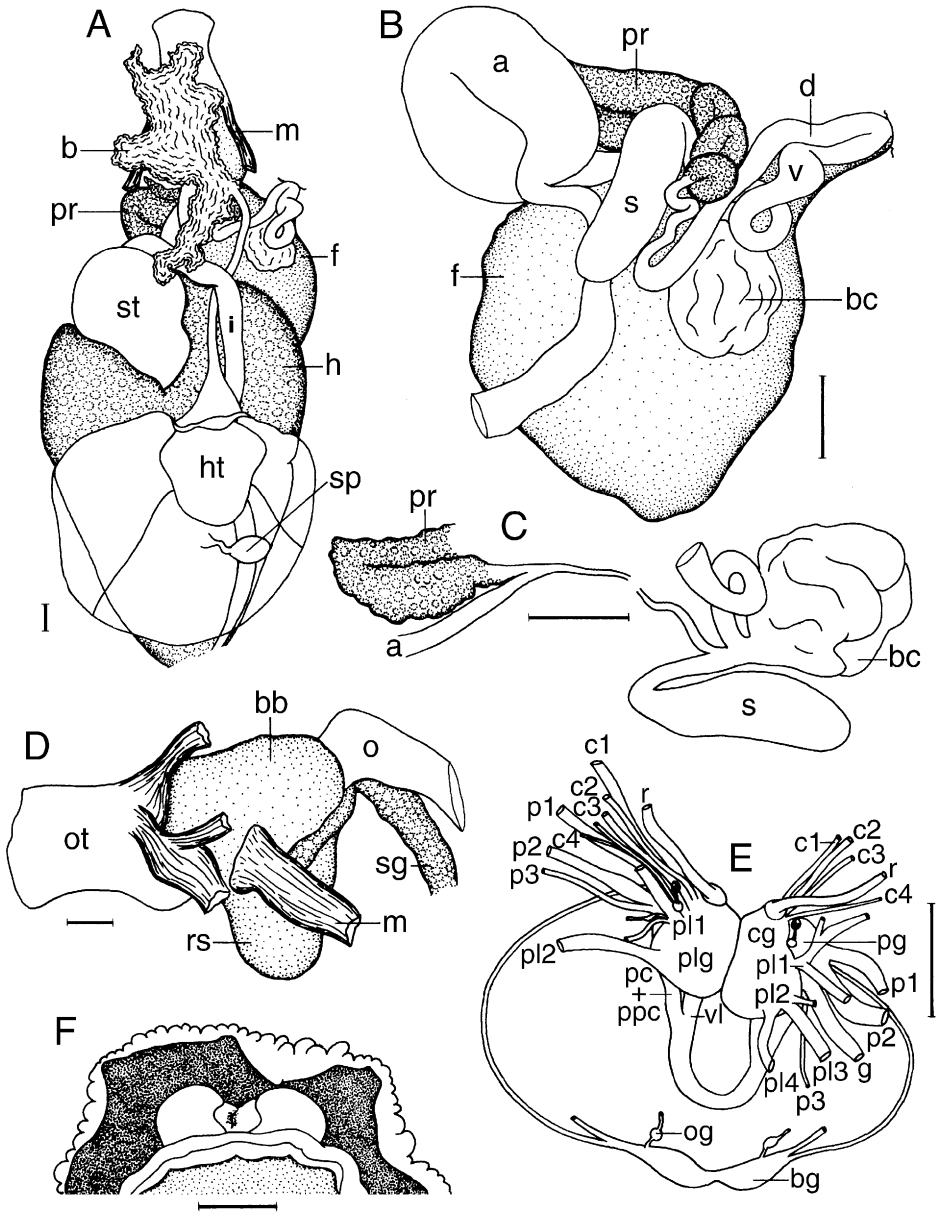

Figure 3. *Doris verrucosa* (CASIZ 082119). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 1 mm. F, Ventral view of the mouth area; scale bar = 5 mm. See 'Abbreviations used in figures'.

muscular deferent duct opens into a common atrium with the vagina. The vagina is long and undulate. Near to its proximal end it joins the duct connecting the bursa copulatrix and the seminal receptacle. The uterine duct also leads from this duct. The bursa copulatrix is irregular in shape, about twice as large as the seminal receptacle (Fig. 3C).

In the central nervous system (Fig. 3E) the cerebral and pleural ganglia are more or less fused and distinct from the pedal ganglia. There are four cerebral nerves leading from the right cerebral ganglion and five from the left one, and four pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. 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, and also partially enveloped with the visceral loop.

The circulatory system (Fig. 3A) consists of a large heart and a single large blood gland situated over the central nervous system.

Remarks

Doris verrucosa, in the sense of the neotype proposed by Bouchet & Valdés (2000) and other many authors (e.g. Schmekel, 1968; Ortea *et al*., 1982; Thompson & Brown, 1984), is a well-known species distributed through the Atlantic and Mediterranean coasts of Europe down to the Canary Islands. Records from the Atlantic coast of the Americas probably belong to this species (Marcus, 1955; Franz, 1970). Indeed, *Doris januari* Bergh, 1878, originally described from Brazil, is very likely a synonym (Thompson & Brown, 1984). Gosliner's (1987) reference to South Africa probably represents a distinct species.

Fischer (1867), recognized that the specific name *Doris verrucosa* Linnaeus originally refers to a species from the Indian Ocean and cannot be used for a European species. For the latter he introduced the name *Doris derelicta*. Bouchet & Valdés (2000) proposed designating the same specimen as the neotype of *Doris verrucosa* Linnaeus and *Doris derelicta* P. Fischer, so these two names would become objective synonyms. They also proposed that *Doris derelicta* P. Fischer should be placed in the Official List of Rejected and Invalid Specific Names in Zoology. These proposals were endorsed by the ruling of the ICZN in Opinion 1980 (ICZN, 2001).

Doris biscayensis was described by Fischer (1872) with the same characteristics of *Doris verrucosa*. The uniform pale yellow colour, the presence of two tubercles in the rhinophoral sheath (one on each side), the presence of 13 unipinnate branchial leaves arranged in a circle, and the absence of oral tentacles, are the main diagnostic features of this species. *Doris verrucosa* is the only species from the Atlantic coast of Europe that has this combination of external characteristics. The variety *mollis* of *Staurodoris verrucosa* described by Eliot (1906a), is also identical to *Doris verrucosa* and is here regarded as a synonym. Gadzikiewicz (1907) described *Staurodoris bobretzkii* on the basis of several specimens collected from the Black Sea, characterized by having a bright orange body covered by large tubercles spotted in black. The eight branchial leaves have the same colour as the body and vary in size, the anterior ones being much longer than the posterior ones. The gill and rhinophoral sheaths are surrounded by tubercles similar to the dorsal tubercles. The tubercles around the gill sheath are much larger than the ones around the rhinophoral sheaths. This description fits with the characteristics of *D. verrucosa* described above, and both names are regarded as synonyms. The three names discussed in this paragraph have been already considered by Thompson & Brown (1984) as synonyms of *Doris verrucosa*.

Thompson & Brown (1984) also included *Doris seposita* P. Fischer, 1872 and *Doris eubalia* P. Fischer, 1872 in the synonymy of *Doris verrucosa*. However, these two species are easily differentiated from *D. verrucosa* on the basis of their external morphology. *Doris eubalia* is characterized by the presence of large, dark tubercles surrounded by a purple area (Fischer, 1872). This and other features of this species are very similar to those of *Doris sticta* Iredale & O'Donoghue, 1923, and both names are probably synonyms. *Doris seposita* is an uncertain species. According to Fischer (1872) it is different from *Doris biscayensis* (= *Doris verrucosa*) in having a different rhinophoral morphology, a small number of branchial leaves, the dorsal tubercles more compacted and a darker colour. It is difficult, however, a definitive identification of this species based on the original description, and anatomical studies would be necessary. Unfortunately, the type material of *Doris seposita* could not be located in MNHN, and is presumed lost.

DORIS PSEUDOARGUS RAPP, 1827 (FIGS 4A, 5, 6)

Doris pseudoargus Rapp, 1827: 519.
Doris flavipes Leuckart, 1828: 14.
Doris leuckartii Delle Chiaje, 1841: 19, pl. 40, fig. 3.
Doris schembrii Verany, 1846: 21–22.

Type material

Doris pseudoargus Rapp, the type material, collected from Le Havre, France, is untraceable. NEOTYPE (here designated): Locmariaquer, France, 13 April 1972, one specimen, 22 mm preserved length, leg. P. Bouchet (MNHN). *Doris flavipes* Leuckart, the type material collected from the Mediterranean Sea is untraceable. *Doris leuckartii* Delle Chiaje, the type material collected from Nice, France, is untraceable. *Doris schembrii* Verany, SYNTYPES: Gulf of Geneva, Italy, two specimens (MNHN). The type material of *Doris britannica* Leach could not be located at BMNH and is probably lost.

Additional material

Las Llanas Beach, Muros de Nalón, Asturias, Spain, 16 August 1987, one specimen, 17 mm preserved length, leg. A. Valdés (CASIZ 121105). Naples, Italy

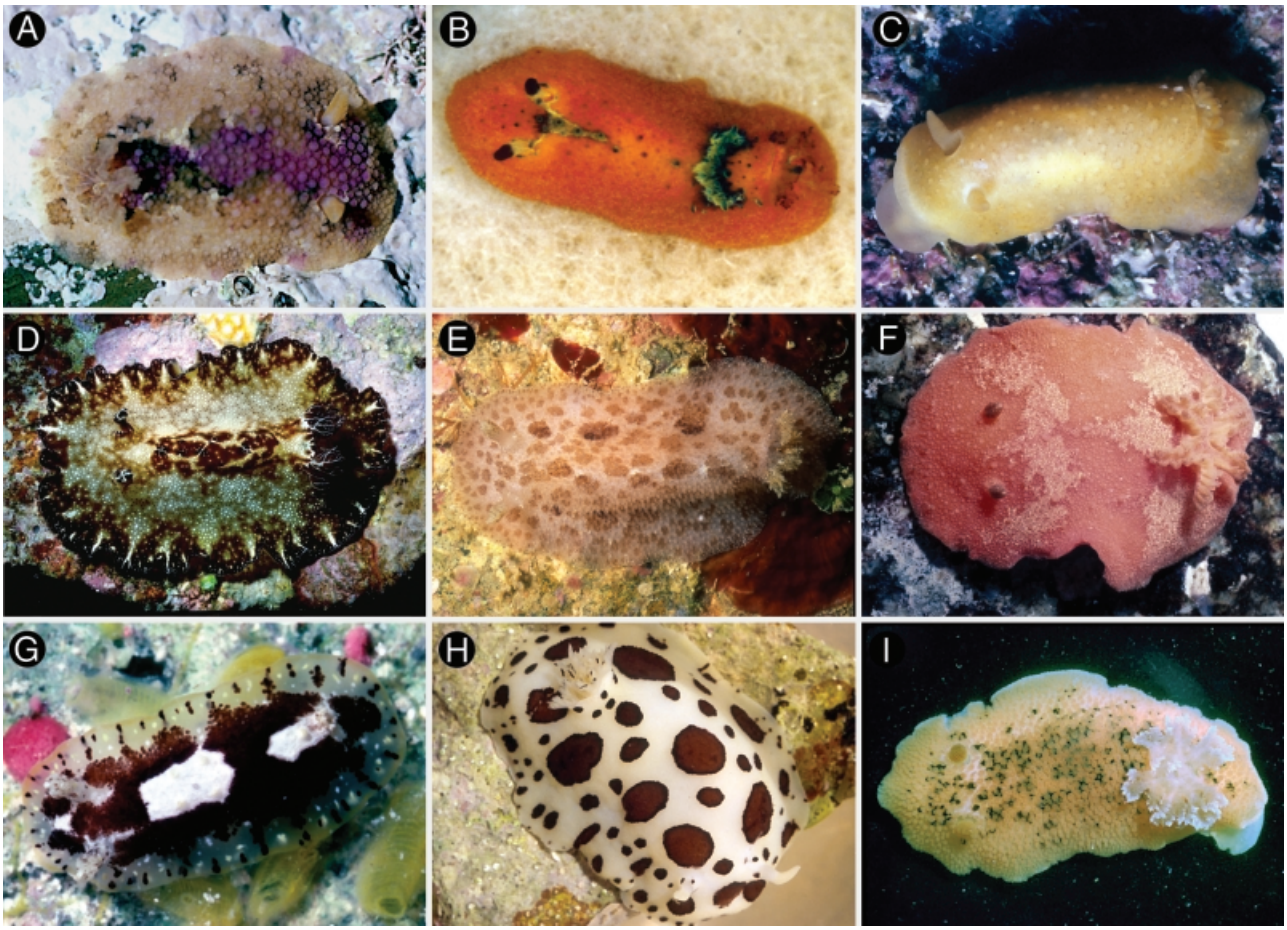

Figure 4. Living animals. A, *Doris pseudoargus* (CASIZ 121105). B, *Doris immonda* (CASIZ 089023), photo by T. M. Gosliner. C, *Doris granulosa* (CASIZ 073536), photo by T. M. Gosliner. D, *Discodoris boholiensis* (CASIZ 083654), photo by T. M. Gosliner. E, *Discodoris ketos*, San Pedrillo, Puntarenas, Costa Rica, photo by T. M. Gosliner. F, *Thordisa rubescens* (CASIZ 015860), photo by T. M. Gosliner. G, *Aphelodoris antillensis* (CASIZ 077289), photo by T. M. Gosliner. H, *Peltodoris atromaculata* (CASIZ 119474). I, *Peltodoris nobilis*, Monterey Bay, California, photo by A. Smith.

1902–03, one specimen, 33 mm preserved length, leg. F. M. MacFarland (CASIZ 081871).

External morphology

The general colour of the living animals varies from yellowish to pale brown, with pale purple, whitish, green, dark brown or reddish irregular patches on the dorsum (Fig. 4A). In some specimens there are only dark brown patches. The rhinophores and the gill are yellowish to pale brown. The whole dorsum is covered with rounded and simple tubercles, all of them similar in size (Fig. 5D). The largest tubercles are those situated in the central region of the body. The rhinophoral and branchial sheaths have several tubercles which are slightly stalked but otherwise similar to the rest of the dorsal tubercles. There are 8–9 tripinnate branchial leaves, forming a circle. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 14 lamellae in a 17-mm preserved length specimen.

Ventrally, there are no oral tentacles, but two blunt prolongations on each side of the mouth opening (Fig. 6E). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 6D) which attach to the body wall. Two long salivary glands connect with the buccal bulb at each side of the oesophageal junction. The buccal bulb is several times longer than the glandular portion of the oral tube. The labial

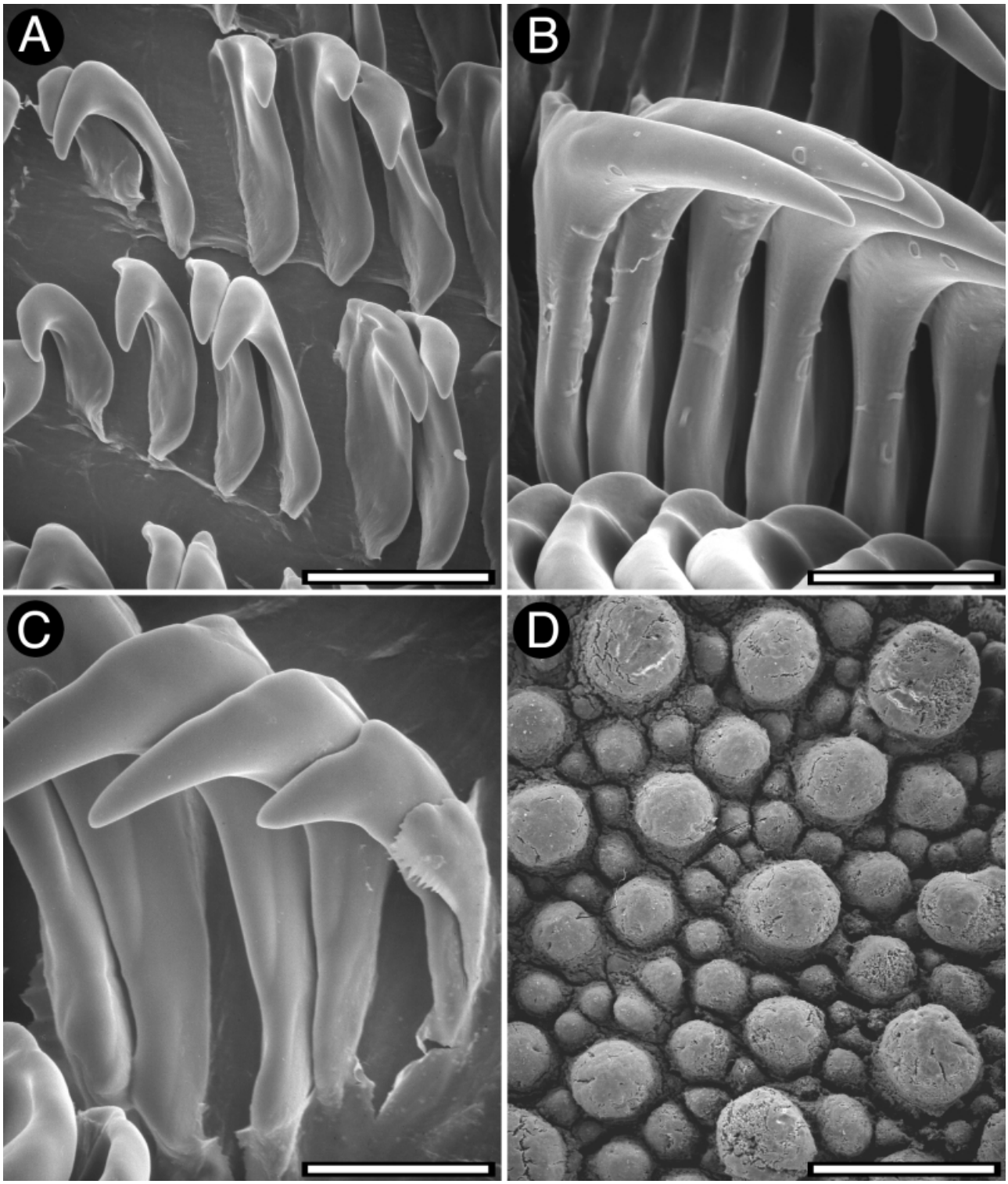

Figure 5. *Doris pseudoargus* (CASIZ 081871), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 75 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 43 μm. D, dorsal tubercles; scale bar = 750 μm.

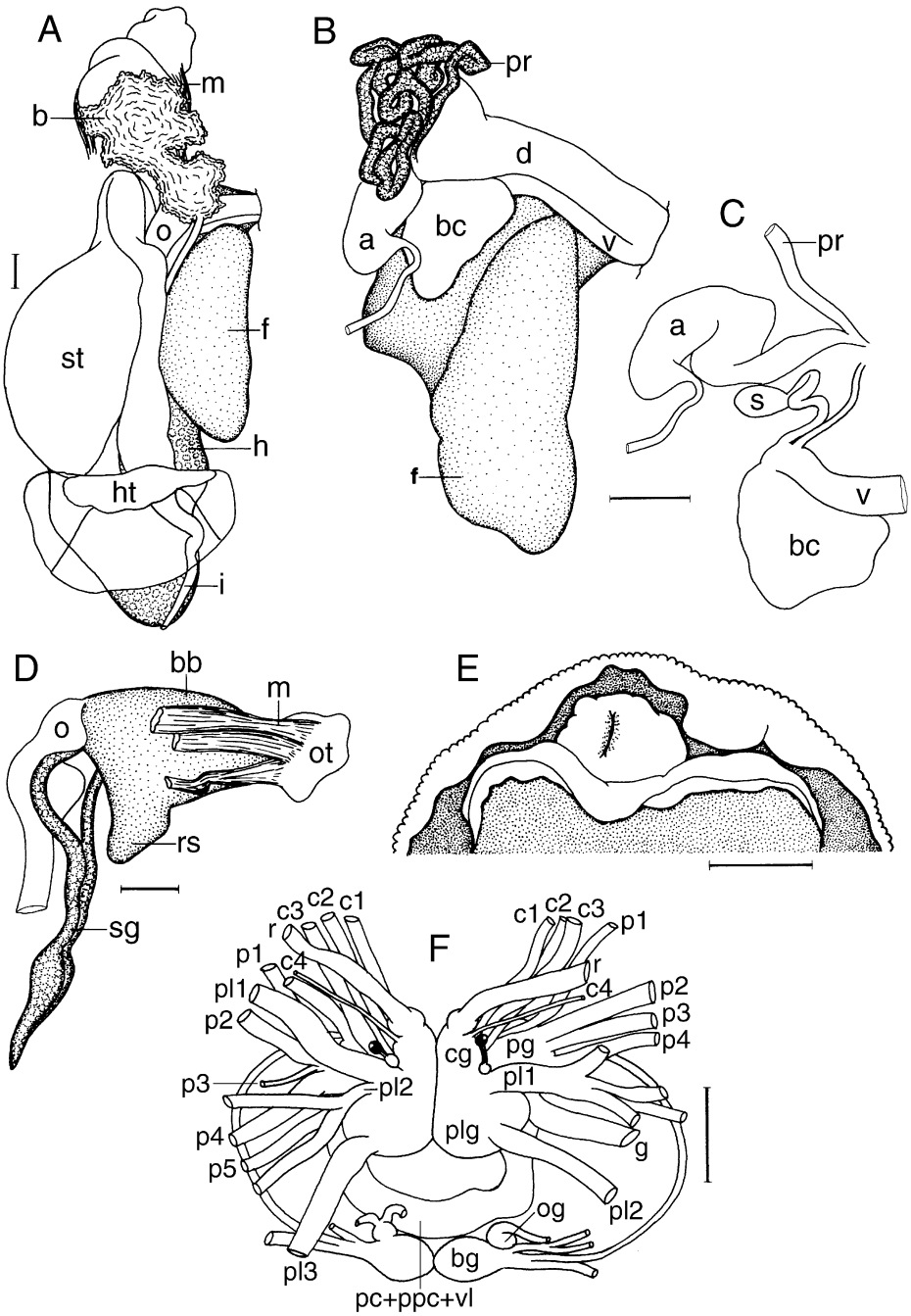

Figure 6. *Doris pseudoargus* (CASIZ 081871). A, general view of the anatomy; scale bar = 2 mm. B, reproductive system; scale bar = 2 mm. C, detail of several reproductive organs; scale bar = 2 mm. D, lateral view of the buccal bulb; scale bar = 2 mm. E, ventral view of the mouth area; scale bar = 5 mm. E, central nervous system; scale bar = 1 mm.

cuticle is smooth. The radular formula is 41 × 73.0.73 in a 33-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 5A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 5B). The outermost teeth are smaller and have a number of thin denticles (Fig. 5C). The oesophagus is short and connects directly to the stomach (Fig. 5A).

The ampulla is convoluted and branches into a short oviduct and the prostate (Fig. 6C). The oviduct enters

the female gland mass near to its centre. The prostate is tubular, very long, folded and granular (Fig. 6B). It connects with a long duct that narrows and expands again into the huge ejaculatory portion of the deferent duct. The muscular deferent duct opens into a short common atrium with the vagina. The vagina is long and wide. Near to its proximal end it joins the duct connecting the bursa copulatrix and the seminal receptacle. The uterine duct also leads from this duct. The bursa copulatrix is irregular in shape, about 10 times larger than the seminal receptacle (Fig. 6C).

In the central nervous system (Fig. 6F) the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves leading from the left pleural ganglion and two from the right one. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having five nerves leading from the left ganglion and four from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 6A) consists of a large heart and a single large blood gland situated over the central nervous system.

Remarks

Doris tuberculata Müller, 1778 was described on the basis of an undetermined number of specimens collected from Norway. Müller (1778) described the animals as golden, patelliform, with the dorsum covered with numerous hair-like yellowish tubercles. The description of the animals clearly represents a species of phanerobranch dorid, probably a member of the genera *Acanthodoris* J.E. Gray, 1850, *Adalaria* Bergh, 1878 or *Onchidoris* Blainville, 1816.

Years later, Cuvier (1804) reported *Doris tuberculata* Müller, 1778 from the Atlantic coast of France based on two newly collected specimens, but indicating that his material was clearly different from Müller's (1778). The animals described by Cuvier are large cryptobranch dorids with the dorsum covered with rounded tubercles. Rapp (1827) described *Doris pseudoargus* from Le Havre, France, with the same characteristics of the specimens studied by Cuvier (1804): 'ash colour with dull reddish spots', and therefore this is the first valid introduction of a name for this species.

Johnston (1838) introduced the names *D. britannica* and *D. montagui*, without a description and in the synonymy of *D. Tuberculata*. Therefore they are *nomina nuda* and if they have not been used as valid before 1961 they are also not available (ICZN, 1999).

In the following years most authors referred to this species as *Doris tuberculata*, but with authorship of Cuvier. Examples include Delle Chiaje (1841), Bergh (1878b), Eliot (1910), Vayssière (1913) O'Donoghue (1929), Pruvot-Fol (1935), Odhner (1939). The scientific influence of Cuvier's papers probably explains why subsequently many authors applied the name *Doris tuberculata* to this cryptobranch dorid species.

The usage of the name *Doris tuberculata* for this species was challenged by the British School. Early on, Iredale & O'Donoghue (1923) for some unexplained reason decided that the animals named *Doris tuberculata* by Cuvier are a different species from specimens identified as such by Alder & Hancock and Eliot; they used the unavailable name *Doris britannica*, combined with the genus name *Archidoris*, for the latter. On the other hand, Pruvot-Fol (1931) argued that all these animals belonged to the same species – *Doris tuberculata* with authorship of Cuvier the valid name. The name *Doris britannica* very rarely appears in the literature. Thompson (1966) reintroduced the usage of the name *Doris pseudoargus*, also combined with *Archidoris*, but without a justification.

Both *Doris pseudoargus* and *Doris tuberculata* have been equally used in modern literature, usually combined with the genus name *Archidoris*. Examples of the former in taxonomic papers include Schmekel & Portmann (1982), Thompson & Brown (1984), Cattaneo-Vietti *et al*. (1990), Picton & Morrow (1994); examples of the latter include Ros (1975), Barletta (1981), Swennen & Dekker (1987), Sabelli, Giannuzzi-Savelli & Bedulli (1990). In addition, most papers on physiology, ecology or histology of this species have used the former (Thompson, 1966; Rose, 1971; Potts, 1983; Jonas, 1986), whereas biochemistry papers have used the latter (Cimino *et al*. 1993). In no cases did authors specify their reasons for using one or the other name, which increased the general confusion. Because both names are currently in use, the maintenance of the usage of the valid name for this species, *Doris pseudoargus*, would certainly not cause a larger disruption than the validation of the name *Doris tuberculata*.

Doris pseudoargus is a well-known species that ranges from Nordkapp (Norway), Iceland and the Faroes to the Mediterranean Sea (Thompson & Brown, 1984). The name *D. tuberculata* has been used for specimens that occur beyond the geographical range of this species. Savigny (1817) reported this species from the Red Sea, Bergh (1894) from the North Pacific and Lemche (1929) from the Gulf of Mexico. These three records are probably misidentifications (see Pruvot-Fol, 1935 and Thompson & Brown, 1984,

who have also listed several other synonyms for this species discussed here).

Doris schembrii Verany, 1846 was originally described with the same external features of *A. pseudoargus* (see Verany, 1846), and the re-examination of its type material confirmed that these names are synonyms. Also, the original descriptions of *Doris flavipes* (see Leuckart, 1828) and *Doris leuckartii* (see Delle Chiaje, 1841) clearly show that they should be regarded as junior synonyms of *A. pseudoargus*.

Doris flammea Alder & Hancock, 1844 and *Doris mera* Alder & Hancock, 1844 have been regarded as synonyms of *D. pseudoargus* (see Thompson & Brown, 1984). However, the original description of these species (Alder & Hancock, 1845–55) shows that they are externally very different from *D. pseudoargus*. *Doris flammea* is a bright orange-scarlet species, occasionally blotched with purple. The dorsum is covered with short, obtuse, spiculose tubercles. The rhinophores are large, tapering, orange with 10 or 11 scarlet lamellae. There are nine scarlet branchial leaves. This description resembles *Rostanga rubra* Risso, 1818, but whether these two names are synonyms requires further investigation. *Doris mera* was described as a white species, 'rather broad and elevated on the back'. This is very different from *D. pseudoargus*, which is a brownish species. Also, the dorsal tubercles of *D. mera* were described as being moderately sized, unequal and round. This is very similar to *Aldisa zetlandica* (Alder & Hancock, 1854), for which *D. mera* could be a synonym.

DORIS IMMONDA RISBEC, 1928 (FIGS 4B, 7, 8)

Platydoris immonda Risbec, 1928: 84, pl. 1, fig. 4, text fig. 12.

Type material

SYNTYPE: New Caledonia, date unknown, one specimen, leg. J. Risbec (MNHN).

Additional material

Tengan Pier, 14 km west of Ikei-Shima, Okinawa, Ryukyu Islands, Japan, 12 m depth, 20 March 1993, one specimen, 21 mm long, leg. T. M. Gosliner (CASIZ 089023).

External morphology

The background colour of the living animals is yellow-orange to pale brown. There is an opaque white or brown inverted 'Y' or hourglass pattern extending mid-dorsally from between the rhinophores to just in front of the gill (Fig. 4B). In some specimens this pattern can be interrupted or almost absent. Some of the dorsal tubercles, and those situated on the dorsal hourglass pattern, are dark purple-brown. The rhinophores have a purple club and a white base. The branchial leaves are yellow-orange with some of the apices dark brown. The whole dorsum is covered with rounded, slightly conical tubercles, all of them similar in size (Fig. 7D). The largest tubercles are those situated in the central region of the body. The rhinophoral sheaths have several slightly stalked tubercles, larger than those surrounding the sheath, but not larger than the largest tubercles on the dorsum. The tubercles surrounding the branchial sheath are similar to the rest of the dorsal tubercles. There are five tripinnate branchial leaves, forming a circle. The anal papilla is small, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having eight lamellae in a 21-mm preserved length specimen.

Ventrally there are no oral tentacles, but two blunt prolongations on each side of the mouth opening (Fig. 8E). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 8C) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two short salivary glands connect with the buccal bulb at each side of the oesophageal junction. The buccal bulb is several times longer than the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $34 \times 43.0.43$ in a 21-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 7A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 7B). The mid-lateral teeth near to the outer edge bear 2–3 large and blunt denticles on the main cusp. The 2–4 outermost teeth are smaller and have a number of thin denticles (Fig. 7C). The oesophagus is short and connects directly to the stomach.

The ampulla is long and convoluted, and branches into a short oviduct and the prostate (Fig. 8B). The oviduct enters the female gland mass near to its centre. The prostate is tubular, long, folded and granular. It connects with a short duct that narrows and expands again into the ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. Near to its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct that connects to the uterine duct and the seminal receptacle. The bursa

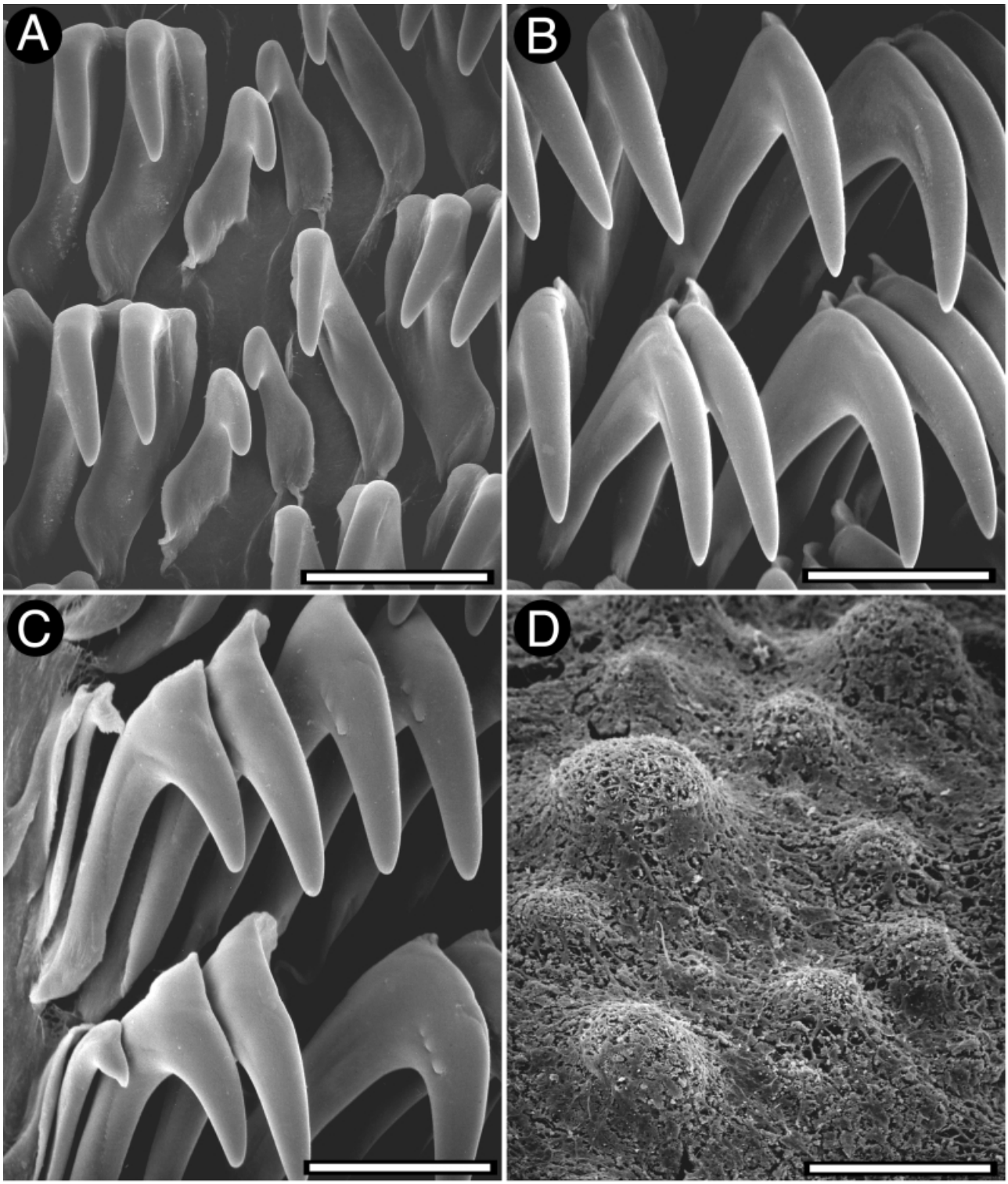

Figure 7. *Doris immonda* (CASIZ 089023), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 43 μm. B, mid-lateral teeth; scale bar = 43 μm. C, outer lateral teeth; scale bar = 43 μm. D, dorsal tubercles; scale bar = 300 μm.

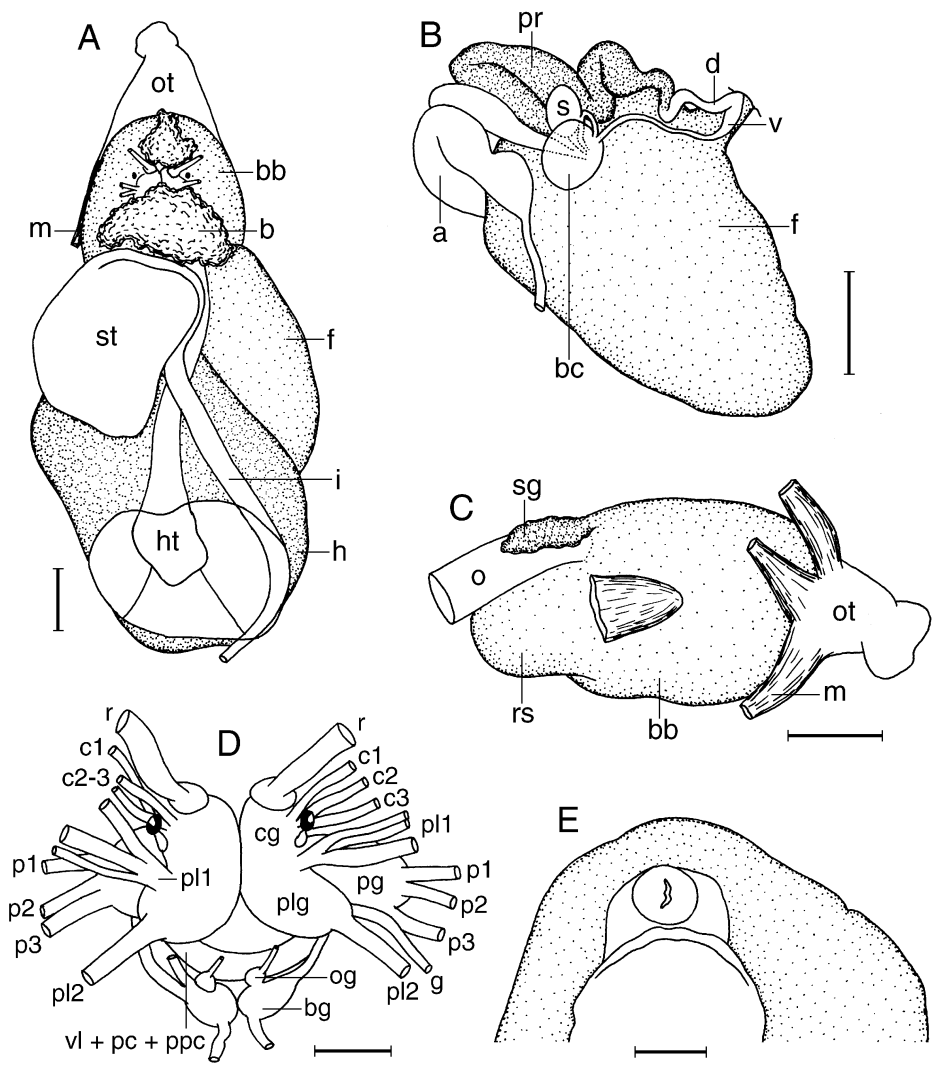

Figure 8. *Doris immonda* (CASIZ 089023). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, lateral view of the buccal bulb; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, ventral view of the mouth area; scale bar = 5 mm.

copulatrix is oval in shape, about three times larger than the seminal receptacle.

In the central nervous system (Fig. 8D) the cerebral and pleural ganglia are fused 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 on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. 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) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Pease (1860) described *Doris nucleola* based on specimens collected from Hawaii as an orange species, dusky along the dorsal region and shaded with purple on each side of the branchiae. Pruvot-Fol (1947) revised the original description of this species and regarded it as nonidentifiable.

Kay & Young (1969) redescribed *Doris nucleola* also from Hawaiian material and introduced the new genus *Doriorbis* to include this species. Their animals were described as having a brown or grey-blue background colour with a T or Y shaped yellow pattern extending mid-dorsally from the rhinophores. They synonymized *Doris papillosa* Pease, 1860 and *Doris tincta* Pease, 1864 with *Doris nucleola*.

Brodie & Willan (1993) studied some specimens from Australia and Norfolk Island, which they assigned to *Doris nucleola*. At the same time they regarded *Doriorbis* Kay & Young, 1969 as a synonym of *Siraius* Er. Marcus, 1955 and added *Doris carinata* Alder & Hancock, 1864, *Doris carina* Abraham, 1877, *Platydoris immonda* Risbec, 1928 to the synonymy of this species. The Australian specimens are dull orange-yellow with a pale hourglass-shaped patch extending mid-dorsally from between the rhinophores to just in front of of the gill.

More recently Rudman (2000) argued that Pease (1860) did not mention any dorsal markings between the rhinophores and the gill. He also posted a copy of Garret's illustration of Pease's (1860) original specimen published by Bergh (1881) in which there are no traces of the hourglass pattern between the gills and the rhinophores. Therefore he considered that Pease's *Doris nucleola* is a different species, and that the first name available and recognizable for the species studied by Kay & Young (1969) and Brodie & Willan (1993) is *Platydoris immonda* Risbec, 1928. A close examination of the drawing by Garret reveals that *Doris nucleola* has well-developed oral tentacles that are absent in *Doris immonda* and the material examined by Kay & Young (1969) and Brodie & Willan (1993), and it is very likely that *Doris nucleola* belongs to a different genus. Rudman (2000) also commented that *Doris carinata* Alder & Hancock, 1864 is a different species because of the higher body profile and larger number of branchial leaves compared to those of *Doris immonda*. A re-examination of Alder & Hancock's (1864) paper shows not only that, but the rhinophores are described as brownish, whereas they are whitish or cream with the club black or violet in *Doris immonda*. The identity of *Doris nucleola* and *Doris carina* remains unknown.

DORIS GRANULOSA PEASE, 1860 (FIGS 4C, 9, 10)

Doriopsis granulosa Pease, 1860: 32–33.
Doriopsis scabra Pease, 1871a: 300, pl. 19, fig. 2A–C.
Doris? flabellifera Cheeseman, 1881: 222–223.
Doris (Ctenodoris) aurantiaca Eliot, 1913: 5–7, pl. 1, fig. 1.
Guyonia flava Risbec, 1928: 103–104, pl. 3, fig. 6, text fig. 21.

Type material

The type specimens of *Doriopsis granulosa* and *Doriopsis scabra* are untraceable; the type material of *Doris flabellifera*, as well as that of other nudibranchs described by Cheeseman, is lost (Bruce Marshall, pers. comm.). SYNTYPE of *Guyonia flava* Pease: New Caledonia, date unknown, one specimen, leg. J. Risbec (MNHN).

Additional material

Small island south of the strait between Île Saint Marie and Île aux Nattes, Madagascar, 5 April 1990, one specimen, 12 mm preserved length, leg. T. M. Gosliner (CASIZ 073536).

External morphology

The background colour of the living animals is yellow-orange. There is a number of small brown dots scattered on the surface, more densely arranged around the dorsal tubercles (Fig. 4C). The rhinophores and gill are also yellow-orange. The whole dorsum is covered with rounded, simple tubercles, all of them similar in size (Fig. 9D). The largest tubercles are those situated in the central region of the body. The rhinophoral and branchial sheaths have a few tubercles, similar to the rest of the dorsal tubercles. There are six tripinnate branchial leaves, arranged horizontally. The anal papilla is small, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 12 lamellae in a 12-mm preserved length specimen.

Ventrally there are no oral tentacles, but two blunt prolongations on each side of the mouth opening (Fig. 10F). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 10D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two short salivary glands connect with the buccal bulb at each side of the oesophageal junction. The buccal bulb is shorter than the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $47 \times 47.0.47$ in a 12-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 9A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 9B). The outermost teeth are smaller and also smooth (Fig. 9C). The oesophagus is short and connects directly to the stomach (Fig. 10A).

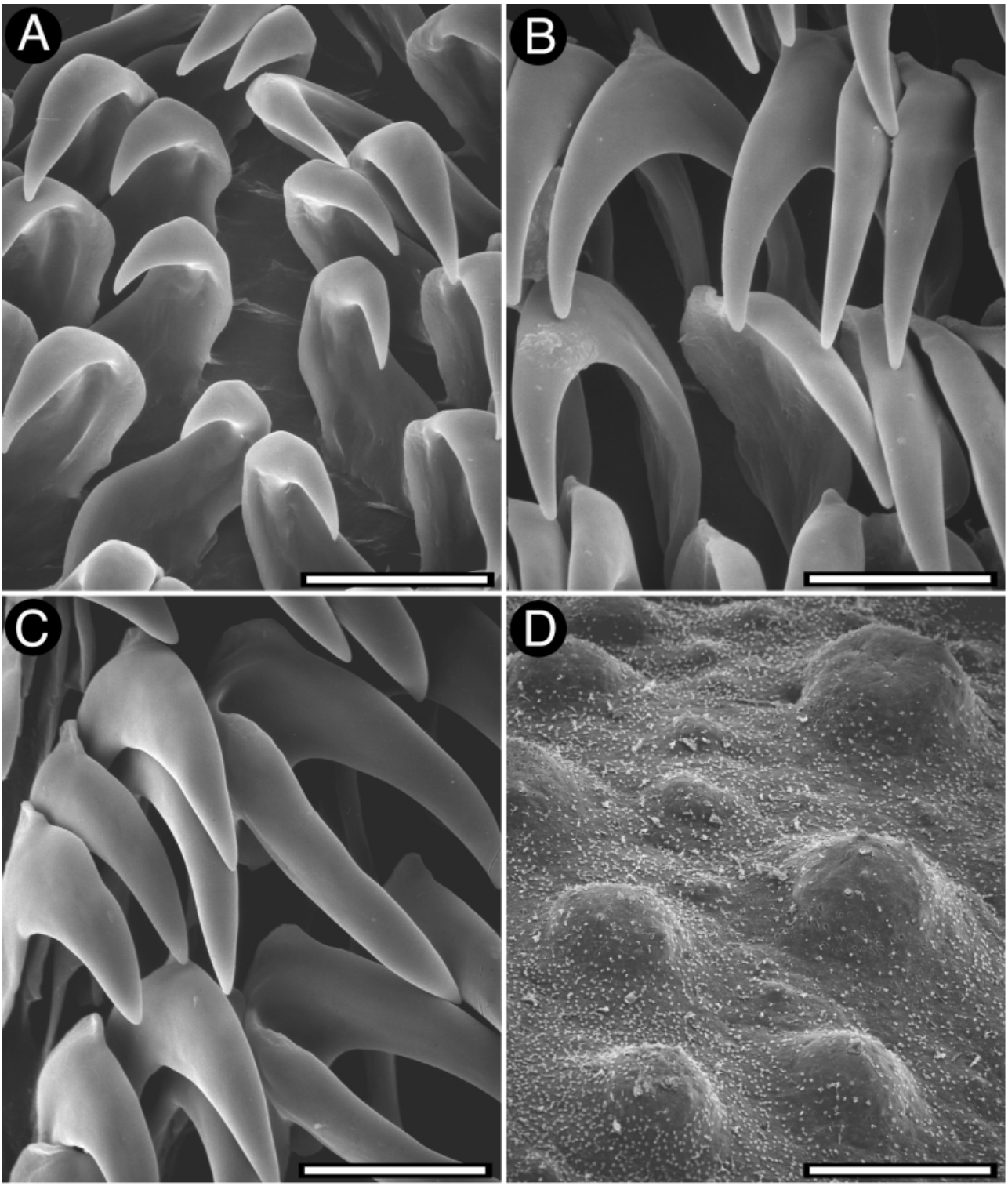

Figure 9. *Doris granulosa* (CASIZ 073536), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 30 μm. B, mid-lateral teeth; scale bar = 30 μm. C, outer lateral teeth; scale bar = 25 μm. D, dorsal tubercles; scale bar = 420 μm.

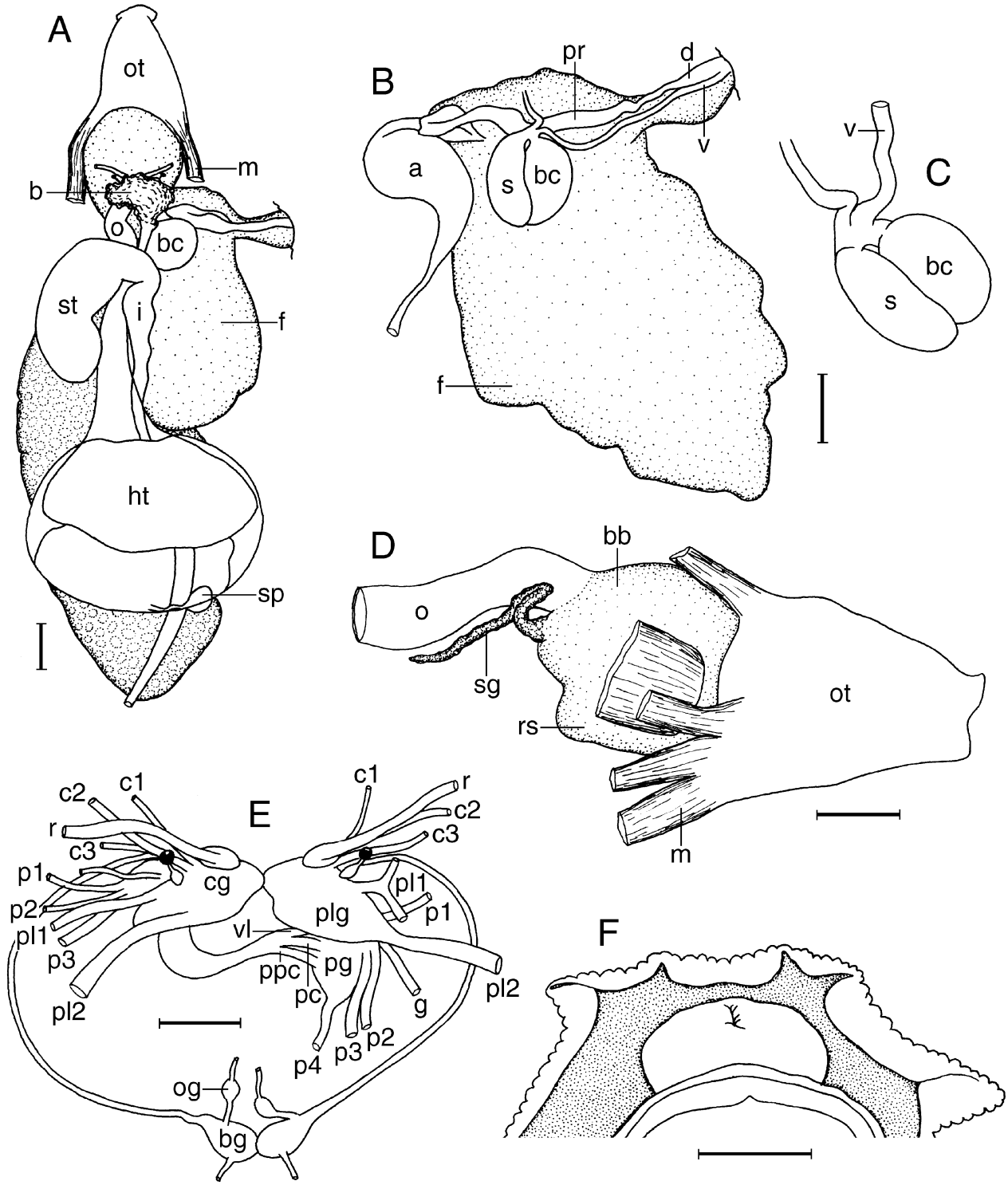

Figure 10. *Doris granulosa* (CASIZ 073536). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of the bursa copulatrix and seminal receptacle; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the mouth area; scale bar = 2 mm.

The ampulla is long and convoluted, and branches into a short oviduct and the prostate (Fig. 10B). The oviduct enters the female gland mass near to its centre. The prostate is tubular, short, folded and granular. It connects with a short duct that narrows and expands again into the ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. Near to its proximal end it joins the bursa copulatrix and the seminal receptacle. The uterine duct also leads from the vagina. The bursa copulatrix is oval in shape, about as large as the seminal receptacle.

In the central nervous system (Fig. 10D) the cerebral and pleural ganglia are fused 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 on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from the left ganglion and four from the right. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 10A) consists of a large heart and a small blood gland situated in front of the central nervous system.

Remarks

Baba & Hamatani (1961) redescribed this species, under the name *Doriopsis aurantiaca* (Eliot, 1913), based on specimens collected from Japan. Kay & Young (1969) reported this species from Hawaii, this time under the name *Doriopsis granulosa* Pease, 1860, and figured its reproductive system and the radula for the first time. They also suggested that *Doris aurantiaca*, *Doriopsis scabra* Pease, 1871, *Guyonia flava* Risbec, 1928 and *Doris flabellifera* Cheeseman, 1881 could be synonyms.

Edmunds (1971) studied specimens from Tanzania which are similar to those from Hawaii, and confirmed the list of synonyms suggested by Kay & Young (1969). In contrast, Willan & Coleman (1984) considered that *Doriopsis flabellifera* is a distinct species, although they provided no anatomical evidence.

DORIS KERGUELENENSIS (BERGH, 1884) (FIGS 11, 12)

Archidoris kerguelenensis Bergh, 1884b: 85–89, pl. 1, figs 1–12.
Archidoris australis Bergh, 1884b: 89–91, pl. 1, figs 13–18, pl. 2, fig. 13.
Archidoris rubescens Bergh 1898: 501–503, pl. 29, figs 17–20.
Austrodoris michaelseni Odhner, 1926: 68–71, pl. 2, figs 30–32, text figs 47–50.
Austrodoris crenulata Odhner, 1926: 75–76, pl. 2, figs 38, 39, text fig. 54.
Austrodoris macmurdensis Odhner, 1934: 260–263, pl. 2, figs 21–23, text figs 25–27.
Austrodoris tomentosa Odhner, 1934: 265–267, pl. 2, figs 19, 20, text fig. 32.
Austrodoris nivium Odhner, 1934: 267–269, pl. 2 figs 21–23, text figs 33–35.
Austrodoris mishu Marcus, 1985: 219–222, figs 1–12.
Austrodoris vicentei Marcus, 1985: 214, 217.
Austrodoris georgiensis García *et al*. 1993: 417–421, figs 1–8.

Type material

For a list of the extant type material of the nominal species included in the genus *Austrodoris* see Wägele (1990).

Additional material

North-west of Explorer's Cove, New Harbor, west side of McMurdo Sound, Antarctica, 17 December 1985, two specimens, 54–66 mm preserved length, leg. K. A. Miller (CASIZ 087312).

External morphology

The external morphology of this species has been described in detail by Wägele (1990). My specimens were preserved, so no data on the living animals are available.

The general colour of the living animals is uniformly white (Wägele, 1990). The rhinophores and gill are also white. The whole dorsum is covered with rounded and simple tubercles varying in size and shape (Fig. 11D). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheath are surrounded by tubercles similar to the rest of the dorsal tubercles. There are 7–9 tripinnate branchial leaves, forming a circle. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 32 lamellae in a 66-mm preserved length specimen.

Ventrally there are no oral tentacles, but two blunt prolongations on each side of the mouth opening (Fig. 12F). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 12D) which

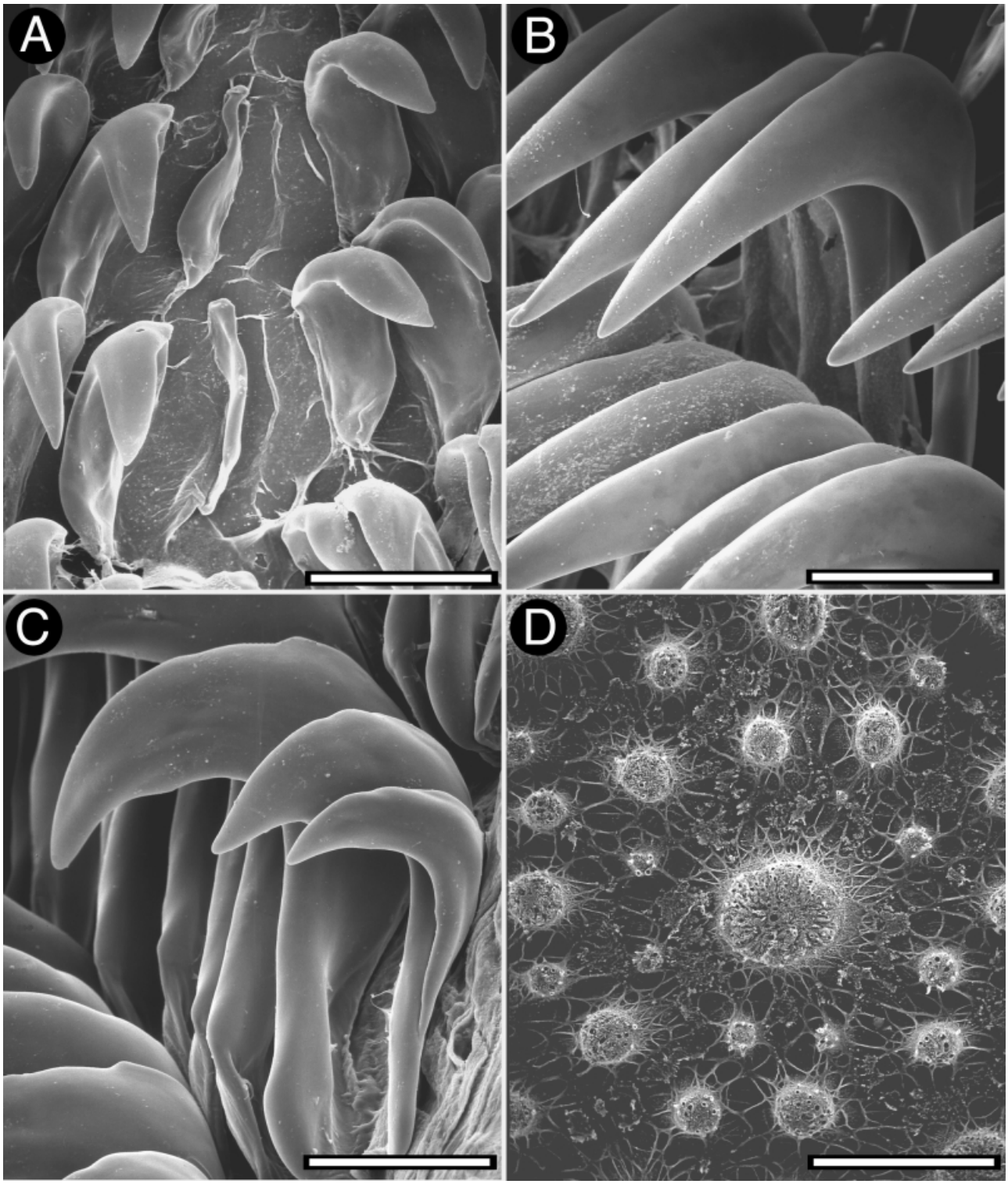

Figure 11. *Doris kerguelenensis* (CASIZ 087312), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 200 μm. B, mid-lateral teeth; scale bar = 150 μm. C, outer lateral teeth; scale bar = 100 μm. D, dorsal tubercles; scale bar = 1 mm.

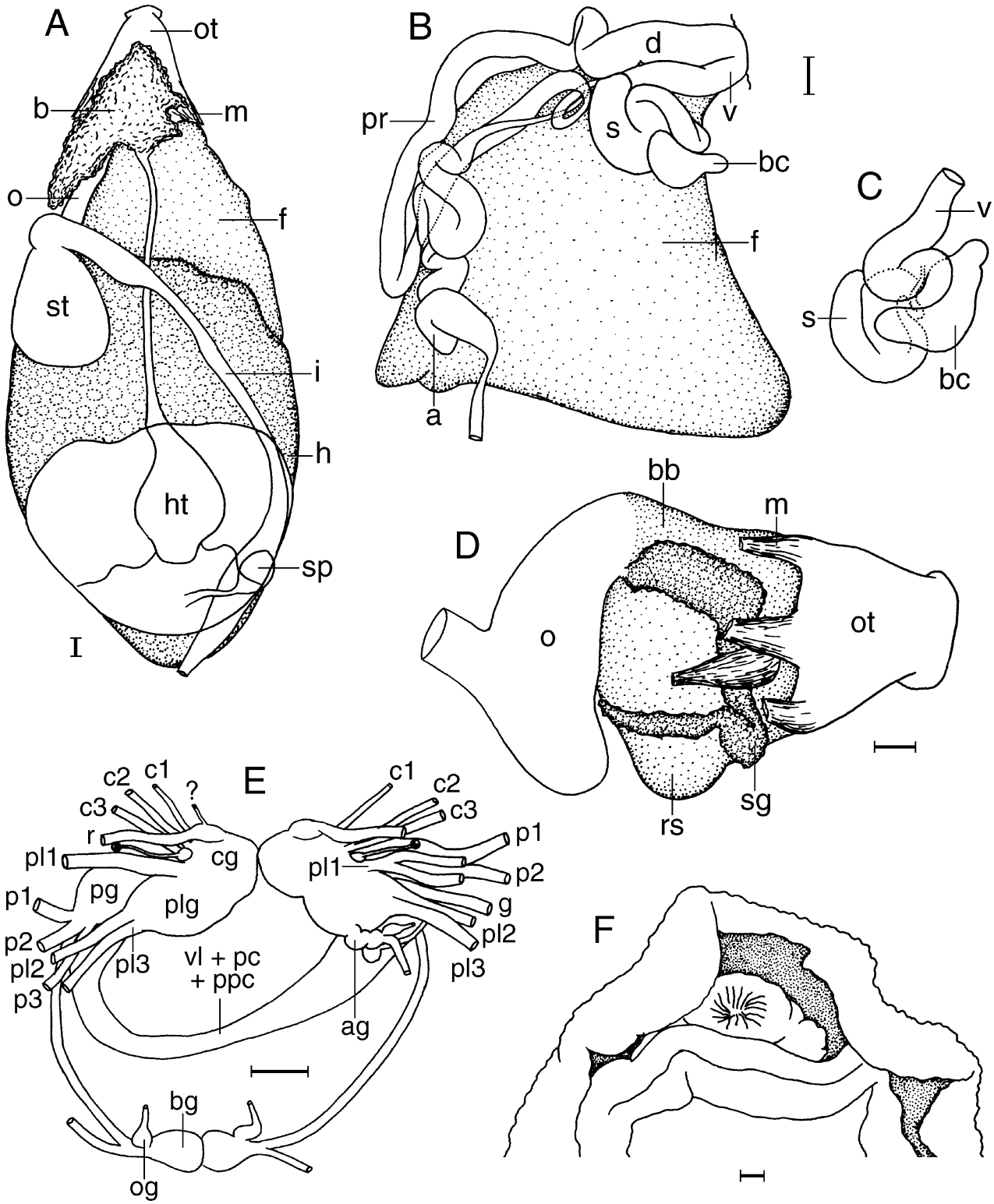

Figure 12. *Doris kerguelenensis* (CASIZ 087312). A, general view of the anatomy; scale bar = 2 mm. B, reproductive system; scale bar = 2 mm. C, detail of the bursa copulatrix and seminal receptacle; scale bar = 2 mm. D, lateral view of the buccal bulb; scale bar = 2 mm. E, central nervous system; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 2 mm.

attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached; two long and wide salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is twice as long as the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $24 \times 37.0.37$ in a 54-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 11A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 11B). The outermost teeth are smaller and also lack denticles (Fig. 11C). The oesophagus is short and connects directly to the stomach (Fig. 12A).

The ampulla is very long and convoluted. It branches into a short oviduct and the prostate (Fig. 12B). The oviduct enters the female gland mass near to its centre. The prostate is tubular, very long and folded (Fig. 12B). It connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The muscular deferent duct opens into a short common atrium with the vagina. The vagina is short and wide. Near to its proximal end it joins the bursa copulatrix and the seminal receptacle. The uterine duct also leads from this duct. The bursa copulatrix is irregular in shape, about as large as the seminal receptacle (Fig. 12C).

In the central nervous system (Fig. 12E) the cerebral and pleural ganglia are fused 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. There is a separate abdominal ganglion on the right side of the visceral loop. This ganglion appears to have several distinctive portions and one of them seems to be the genital ganglion. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from the left ganglion and two from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 12A) consists of a large heart and a single large blood gland situated in front of the central nervous system.

Remarks

Wägele (1990) revised the genus *Austrodoris* and concluded that all the Antarctic species previously assigned to it are synonyms of *Austrodoris kerguelensis* (Bergh, 1884). She also described in detail the anatomy and external morphology of this species.

More recently García *et al*. (1993) described the new species *Austrodoris georgiensis*, which is also a synonym of *Austrodoris kerguelensis*. García *et al*. (1993) based *Austrodoris georgiensis* on a single specimen collected from South Georgia, in the Atlantic Antarctic sector. The only difference between *A. georgiensis* and *A. kerguelenensis* is the presence of an elongate bursa copulatrix in the former. As other features of both nominal species (e.g. external morphology, radula, other reproductive organs), are identical, it is likely that the single specimen assigned to *A. georgiensis* is just an aberrant specimen of *A. kerguelenensis*. Another possibility is that the bursa copulatrix is more variable than assumed until now.

Doris ilo (Er. Marcus, 1955)

Remarks

This is the type species of the genus *Siraius* Er. Marcus, 1955. It was originally described from near São Paulo (Southern Brazil), based on a single specimen characterized by having a greyish yellow colour with the dorsal tubercles darker. The most remarkable feature of this species is the presence of 22 branchial leaves.

Marcus (1958) extended the range of this species to Cabo Frio and Marcus & Marcus (1970b) to Curaçao Island in the Caribbean Sea. Unfortunately, I was unable to obtain specimens of this species for the present study.

Genus *Hexabranchus* Ehrenberg, 1831

Hexabranchus Ehrenberg, 1828–31 [1831]: 30. Type species: *Hexabranchus praetextus* Ehrenberg, 1828, by subsequent designation of J. E. Gray (1847).

Heptabranchus A. Adams, 1848: 494–495. Type species: *Heptabranchus burnettii* A. Adams, 1848, by original designation.

Rhacodoris Mörch, 1863: 34. Type species: *Doris lacera* Cuvier, 1804, by original designation.

Aethedoris Abraham, 1877: 237. Type species: *Aethedoris indica* Abraham, 1877, by monotypy.

Albania Collingwood, 1881: 132–133. Type species: *Albania formosa* Collingwood, 1881, by monotypy.

Diagnosis

Dorsum smooth, lacking tubercles. Head with two large, flattened and lobate oral tentacles. Anterior border of the foot simple. Gill contractile, not retractile. Radula composed of simple, hamate teeth. Labial cuticle completely covered with rodlets and having several transverse grooves. Buccal mass with numerous and strong muscles attached. Reproductive sys-

tem with a tubular, non differentiated prostate. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

The genus *Hexabranchus* was originally introduced by Ehrenberg (1828–31) based on three species: *Hexabranchus praetextus* Ehrenberg, 1831, *Doris sanguinea* Rüppell & Leuckart, 1830 and '*Doris laciniata* Cuvier' (error for *Doris lacera* Cuvier, 1804). *Hexabranchus praetextus* was subsequently selected by Gray (1847) as the type species. This species was detailed described and illustrated by Ehrenberg, (1828–31), and its features agree with the current usage of the name.

Adams (1848) described the genus *Heptabranchus*, type species by original designation *Heptabranchus burnettii* A. Adams, 1848, as being very close to *Hexabranchus*, but showing several differences in the number of gills and mantle widtH. In his opinion, these differences supported the separation of two different genera. Nowadays it is known that species of *Hexabranchus* can contract and spread out the mantle margin (Thompson, 1972), so the same animal is able to show a narrow mantle margin with the foot extending beyond it (as described by Adams, 1848) or a wide mantle completely covering the foot. In addition, the number of branchial leaves is variable among the same species. Therefore, there is no doubt that *Heptabranchus* is a junior synonym of *Hexabranchus*.

Mörch (1863) introduced the name *Rhacodoris* for *Hexabranchus sensu* Gray non Ehrenberg, with '*Doris laciniata* Cuvier' (error for *Doris lacera* Cuvier, 1804) as the type species by original designation. He also stated that *Doris lacera* was mistakenly reported as belonging to the genus *Hexabranchus*, from which it differs in having a special cavity for each branchial leaf and one common cavity for all the gill. The examination of the type material and original description of *Doris lacera* (Cuvier, 1804), show that this species clearly belongs to the genus *Hexabranchus*, and therefore *Rhacodoris* is a junior subjective synonym.

The genus *Aethedoris* and the species *Aethedoris indica* were erected by Abraham (1877) based on a picture of Alder & Hancock (1864; pl. 33, fig. 20) which represents a contracted, probably dead specimen. The two large and lobate oral tentacles shown in the picture clearly identified the specimen as belonging to the genus *Hexabranchus*, but they were considered by Abraham as the most striking feature of his new taxa. He interpreted them as a 'bilobed head, each lobe being semicrescentic, with the apex curving backwards and the margin bearing 12–14 conical dentations'. The type material of *Aethedoris indica* could not be located in BMNH and is probably lost. However, it is very likely that the animal figured by Alder & Hancock was a dead specimen of *Hexabranchus*.

Collingwood (1881) introduced the new genus *Albania* with *Albania formosa* Collingwood, 1881 as the single included species (type by monotypy). The features of *Albania* are identical to those of the genus *Hexabranchus*. In this case the type material of *Albania formosa* is also lost but there are not doubts that this nominal species belong to the genus *Hexabranchus*.

HEXABRANCHUS SANGUINEUS (CUVIER, 1804) (FIGS 13, 14)

Doris lacera Cuvier, 1804: 452, 453–465, 473, pl. 73, figs 1–3 (*nomen oblitum*).
Doris sanguinea Rüppell & Leuckart, 1830: 30–31, pl. 1, fig. 1 (*nomen protectum*).
Hexabranchus praetextus Ehrenberg, 1828–31 [1831]: 30–31, pl. 1, fig. 1A–C.
Heptabranchus burnettii A. Adams, 1848: 494.
Aethedoris indica Abraham, 1877: 237.
Albania formosa Collingwood, 1881: 133, pl. 10, figs 1–5.

Only the type species of synonyms of *Hexabranchus* are listed here; for a complete list of synonyms see Thompson (1972).

Type material

Doris lacera Cuvier, SYNTYPES: Indian Ocean (= Mer des Indes), date and exact locality unknown, two specimens, 30 and 76 mm preserved length, dissected (MNHN). *Hexabranchus praetextus* Ehrenberg, SYNTYPE: El Tûr (= Tor), Egypt, date unknown, one specimen, 125 mm preserved length (MNHB 566). SYNTYPE: El Tûr (= Tor), Egypt, date unknown, one specimen, 110 mm preserved length, partially dissected (MNHB 567). The holotypes of *Heptabranchus burnettii* (originally collected from Borneo), *Aethedoris indica* (originally collected from Madras, India) and *Albania formosa* (originally collected from Ke-lung, Formosa) could not be located at BMNH and are probably lost. The type material of other synonyms of *Hexabranchus* has not been traced.

Additional material

Reef near Hotel Coelacanth, North end of Moroni, Grand Comore Island, Mozambique Channel, 6 March 1975, one specimen, 104 mm preserved length, leg. S. Earle and A. Giddings (CASIZ 068296). Tire Reef, 2 km north of Mora Mora Village, Madagascar, 9 April 1989, two specimens, 94–100 mm preserved length, leg. T. M. Gosliner (CASIZ 071897).

External morphology

The external morphology and behaviour of this species have been widely described. Thompson (1972) and Gohar & Soliman (1963) found wide chromatic variation.

The general colour of the living animals is very variable. It normally varies from pale orange to bright red. In some specimens there is a number of small white or yellowish dots on some areas or on the entire dorsum. Other specimens have large bright red or pinkish spots, or a pale concentric band. Sometimes the mantle margin is surrounded by a yellow line. The rhinophores are red to yellowish, with white spots in some specimens. The gill has normally the same colour as the dorsum, with the rachises of the branchial leaves white or yellowish. The dorsum is smooth. There are 7–9 tripinnate, non-retractile branchial leaves. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 45 lamellae in a 100-mm preserved length specimen.

Ventrally there are two large, flattened and lobate oral tentacles (Fig. 13F). The anterior border of the foot is simple.

Anatomy

The posterior end of the glandular portion of the oral tube has 18 strong retractor muscles (Fig. 13E) which attach to the body wall. The oval, muscular buccal bulb has several additional muscles attached together; two long and wide salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is three times longer than the glandular portion of the oral tube. The labial cuticle is completely covered with simple rodlets (Fig. 14D). The radular formula is $36 \times 77.0.77$ in a 100-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 14A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 14B). The outermost teeth are smaller and also lack denticles (Fig. 14C).

The ampulla is very long and convoluted. It branches into a short oviduct and the prostatic portion of the deferent duct (Fig. 13C). The oviduct enters the female gland mass near to its centre. There is no differentiated prostate, but a long, folded and tubular deferent duct (Fig. 13B). The prostatic region of the deferent duct expands into the huge ejaculatory portion, which opens into a short common atrium with the vagina. The vagina is long and wide. Near to its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct that connects to the uterine duct and the seminal receptacle. The bursa copulatrix is rounded in shape and several times larger than the elongate seminal receptacle (Fig. 13B).

In the central nervous system (Fig. 13D) the cerebral and pleural ganglia are fused 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 each cerebral ganglion and two pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. 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. 13A) consists of a large heart and a single large blood gland situated beneath the central nervous system.

Remarks

First Eliot (1910) and then Thompson (1972) considered that most of the nominal species assigned to the genus *Hexabranchus* are synonyms. Only the Atlantic *Hexabranchus mormosus* Marcus & Marcus, 1962 was dubiously regarded as a different species for biogeographical reasons. The arguments of Eliot and Thompson are convincing, but despite the latter's suggestion that *Doris sanguinea* Rüppell & Leuckart, 1830 has priority over other synonyms, the name *Doris lacera* Cuvier, 1804 is much older and must be the valid name for the Indo-Pacific species of *Hexabranchus*. A re-examination of the syntypes of *Doris lacera* confirmed they are conspecific with *Hexabranchus sanguineus*. *Doris lacera* has been ignored by all authors dealing with *Hexabranchus*. According to Article 23.9.1 (ICZN, 1999), if a senior synonym has not been used as a valid name since 1899, and its junior synonym has been used for the same species in at least 25 papers, published by at least 10 authors in the immediately preceding 50 years and encompassing a span not less than 10 years, the usage of the junior synonym must be maintained. The name *D. lacera* has only been used as valid in its original description in 1804, whereas the name *H. sanguineus* is in constant usage in the literature. More than 30 papers, books and field guides using the name *H. sanguineus* as valid have been published during the last 20 years by more than 15 authors. Therefore, the name *H. sanguineus* is here conserved (*nomen protectum*) and *H. lacer* is regarded as invalid (*nomen oblitum*).

The type species of other synonymous generic names: *Hexabranchus praetextus* Ehrenberg, 1828, *Heptabranchus burnettii* A. Adams, 1848 and

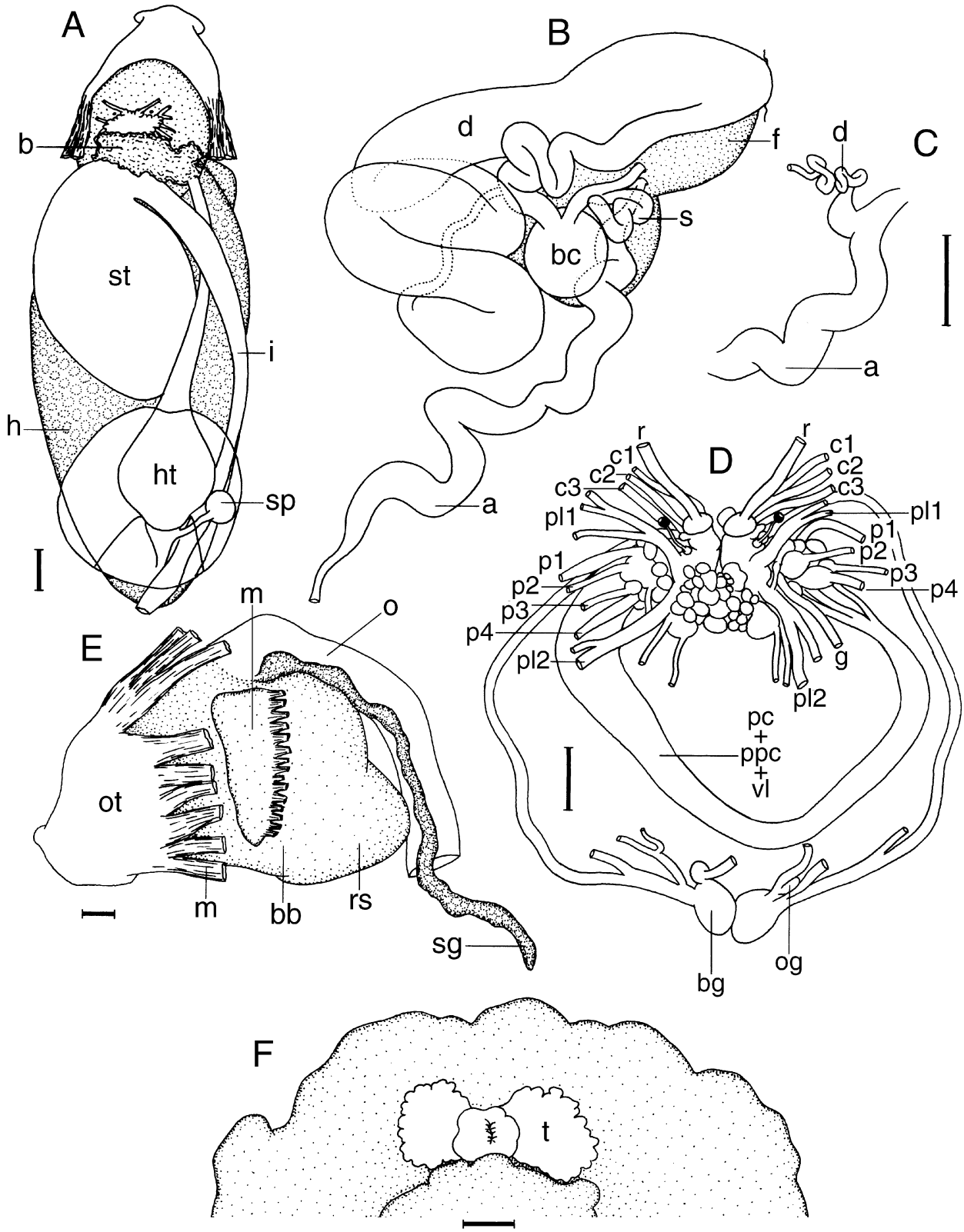

Figure 13. *Hexabranchus sanguineus* (CASIZ 071897). A, general view of the anatomy; scale bar = 2 mm. B, reproductive system; scale bar = 2 mm. C, detail of the ampula; scale bar = 2 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 2 mm.

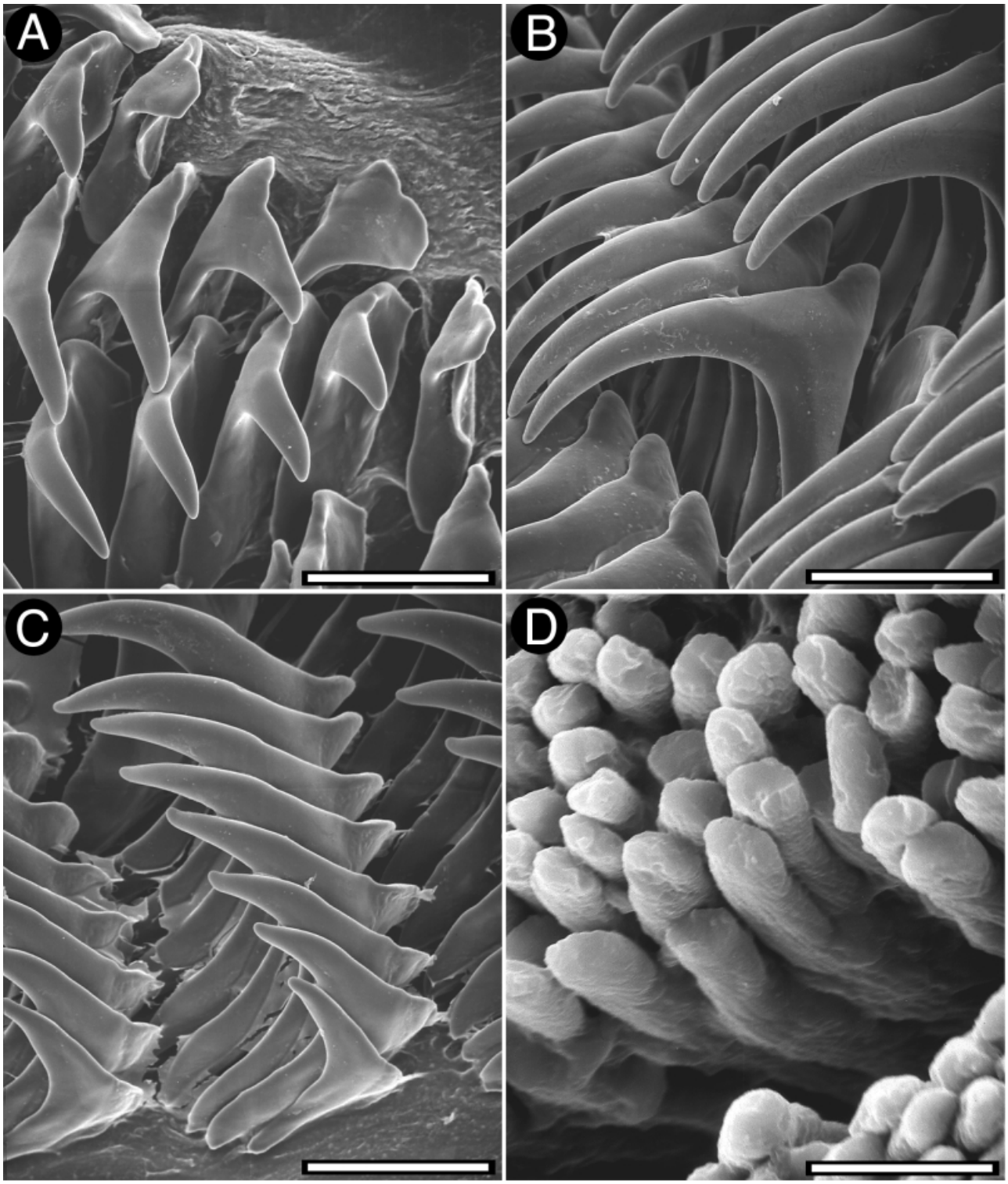

Figure 14. *Hexabranchus sanguineus* (CASIZ 071897), SEM images of the radula and jaws. A, inner lateral teeth; scale bar = 100 μm. B, mid-lateral teeth; scale bar = 100 μm. C, outer lateral teeth; scale bar = 150 μm. D, jaw elements; scale bar = 10 μm.

Aethedoris indica Abraham, 1877, are also regarded as synonyms of *Hexabranchus sanguineus*.

GENUS *DISCODORIS* BERGH, 1877

Discodoris Bergh, 1877a: 518. Type species: *Discodoris boholiensis* Bergh, 1877, by subsequent designation by O'Donoghue (1926).

Fracassa Bergh, 1878a: 598. Type species: *Fracassa zibethina* Bergh, 1878, by monotypy, **syn. nov.**

Erythrodoris Pruvot-Fol , 1933: 133. Type species: *Erythrodoris dollfusi* Pruvot-Fol, 1933, by monotypy, **syn. nov.**

Tayuva Marcus & Marcus, 1967b: 191–192. Type species: *Tayuva ketos* Ev. Marcus & Er. Marcus, 1967, by original designation, **syn. nov.**

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules, which occasionally protrude from the dorsal surface in an irregular fashion. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial cuticle armature with rodlets. Radula composed of simple, hamate teeth. The outermost teeth may be simple or denticulate. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

Bergh (1877b) introduced the genus *Discodoris* based on *Doris granulata* Ehrenberg, 1831, *Doris crucis* Mörch, 1863, *Doris pardalis* Alder & Hancock, 1864, *Doris concinna* Alder & Hancock, 1864, *Doris fragilis* Alder & Hancock, 1864, and eight hitherto undescribed species: *Discodoris boholiensis*, *D. meta*, *D. cebuensis*, *D. notha*, *D. muta*, *D. modesta* and *D. schmeltziana*. Bergh (1877a) described these species, and at the same time reproduced the original description of the genus *Discodoris*. O'Donoghue (1926) subsequently designated *Discodoris boholiensis* Bergh, 1877 as the type species. Bergh's (1877a) paper was published in December 1877 (see Winckworth, 1946), whereas the date of publication of Bergh (1877b) is unspecified. According to Article 21.3 (ICZN, 1999), as the exact day of publication is not specified for any of these papers, and one of them was published in December, the date of publication of both papers is determined to be the last day of 1877. If Bergh's (1877b) paper is selected to be the original description of the genus, *D. boholiensis* is not eligible to be the type species (it was undescribed). Therefore, acting as First Reviser (ICZN, 1999: Article 24), I select Bergh's (1877a) paper as the original description of the genus; thus *D. boholiensis* becomes eligible to be the type species.

Bergh (1878a) described the genus *Fracassa* for *Fracassa zibethina* Bergh, 1878, collected from the Philippines. According to Bergh (1878a) this genus is characterized by having a quite smooth dorsum, conical oral tentacles, tripinnate branchial leaves, wide foot with the anterior border grooved and notched, presence of jaws, radular teeth simple and hamate, large differentiated prostate and penis unarmed. Re-examination of the holotype of *Fracassa zibethina* revealed that the dorsum of this species is covered with small, rounded simple tubercles. All these characteristics are also present in the genus *Discodoris*, for which *Fracassa* is a synonym.

Pruvot-Fol (1933) described the genus *Erythrodoris* based on *Erythrodoris dollfusi* Pruvot-Fol, 1933, characterized by having a labial cuticle with articulated plates, elongated body and unarmed penis. These features of *Erythrodoris* are also present in *Discodoris*, and these names are regarded as synonyms. It is impossible to determine the identity of *Erythrodoris dollfusi* Pruvot-Fol, 1933 based on the original description and the type material is probably lost.

Marcus & Marcus (1967b) introduced the new genus *Tayuva* for *Tayuva ketos* Ev. Marcus & Er. Marcus, 1967. The diagnosis of *Tayuva* included the following characteristics: pointed tentacles, labial plates with rodlets, hook-shaped radular teeth, stout penial papilla, large vestibule (atrium) stiffened by spicules and lodging the penial papilla and the vaginal aperture, nidamental opening independent from that of the atrium. This structure of the genital opening was considered 'aberrant' by Marcus & Marcus (1967b) and they could not find another genus that could 'receive' that species. In fact, this anatomical arrangement is present in all species of cryptobranch dorids. The combination of the characters described above and simple dorsal tubercles indicates that *Tayuva ketos* clearly belongs to the genus *Discodoris*; thus *Tayuva* is a junior synonym of *Discodoris*.

DISCODORIS BOHOLIENSIS BERGH, 1877 (FIGS 4D, 15, 16)

Discodoris boholiensis Bergh, 1877a: 519–522, pl. 60, fig. 23, pl. 61, figs 6–12.

Discodoris meta Bergh, 1877a: 522–526, pl. 60, figs 24, 25, pl. 61, figs 25–28.

Type material

SYNTYPES of *Discodoris boholiensis*: Bohol, Aibukit, Philippines, date unknown, three specimens, 45 mm (decapitated) 70 mm preserved length, leg. C. Semper

(ZMUC GAS-2122). HOLOTYPE (by monotypy) of *Discodoris meta*: Cebu, Ubay, Philippines, leg. C. Semper (ZMUC).

Additional material

North side of Sombrero Island, Batangas, Luzon, Philippines, 19 February 1992, three specimens, 20–49 mm preserved length, leg. T. M. Gosliner (CASIZ 083654).

External morphology

The background colour of the living animals varies from pale cream in the centre of the dorsum to pale ochre near to the mantle edge (Fig. 4D). The dorsum is covered with a number of rounded white spots situated on each dorsal tubercle. These white spots are more densely concentrated on the mantle margin, forming several radial white lines. There is an irregular pattern of dark brown patches and lines on the centre of the dorsum, from behind the rhinophores to the gill. A similar pattern also occurs near to the mantle edge. Both areas are connected by irregular, faded pale brown lines forming a broken network. The rhinophoral and branchial sheaths are elevated and surrounded by a dark brown line, which in the case of the branchial sheath is interrupted by several white spots. The rhinophores are dark brown to black, with several irregular white lines. The branchial leaves are also dark brown, almost black, with dark grey rachises. The whole dorsum is covered with small, conical tubercles, which have spicules protruding on their dorsal surface (Fig. 15E). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths have tubercles similar to those on the rest of the dorsum. There are six tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 26 lamellae in a 49-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 16F). The oral tentacles are elongate, with a blunt apex.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 16E) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is shorter than the glandular portion of the oral tube. The labial cuticle is armed with a number of small, simple rodlets (Fig. 15D). The radular formula is 29 × 35.0.35 in a 49-mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 15A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 15B). The outermost teeth are smaller and also lack denticles (Fig. 15C). The oesophagus is short and connects directly to the stomach (Fig. 16A).

The ampulla is long and simple (Fig. 16C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is large and flattened. It has two different portions that are clearly distinguishable in colour and texture (Fig. 16B). The prostate connects with a very long and convoluted duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The penis is unarmed. The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. At its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle. The bursa copulatrix is rounded in shape, about three times as large as the seminal receptacle.

In the central nervous system (Fig. 16D) the cerebral and pleural ganglia are fused 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 a separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two long nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from the left ganglion and three from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 16A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Discodoris boholiensis is a well-known Indo-Pacific species characterized by having a background brown colour with black and white spots and lines on the body, and a relatively flat dorsum with undulating margins and a prominent central hump. Examination of the type material of *Discodoris meta* Bergh, 1877 confirmed that it is a synonym of *D. boholiensis*.

DISCODORIS ZIBETHINA (BERGH 1878) (FIGS 17, 18)

Fracassa zibethina Bergh, 1878a: 598–601, pl. 66, figs 21–26, pl. 67, figs 1, 2.

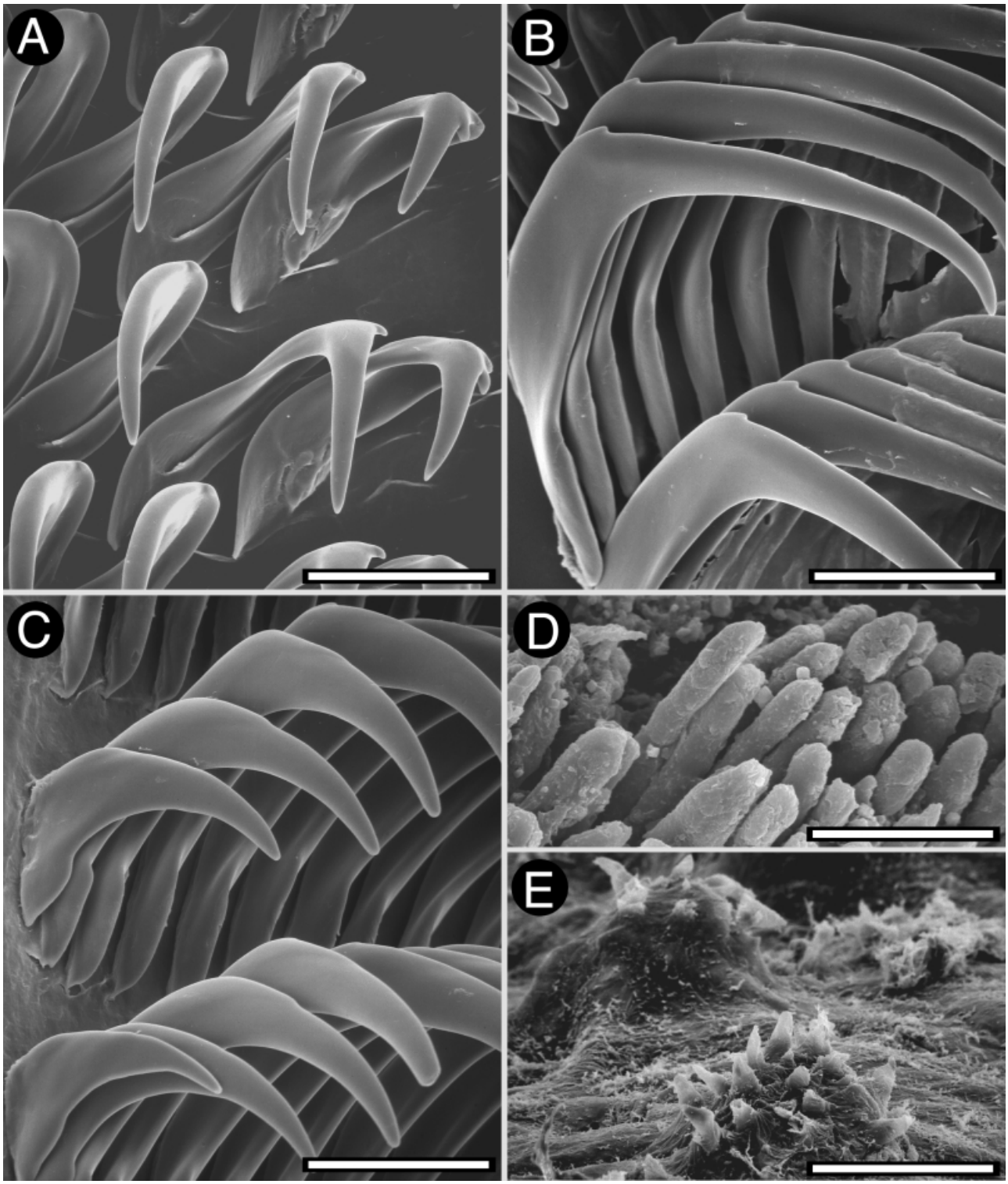

Figure 15. *Discodoris boholiensis* (CASIZ 083654), SEM images of the radula, jaws and dorsal tubercles. A, inner lateral teeth; scale bar = 75 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 75 μm. D, jaw elements; scale bar = 20 μm. E, dorsal tubercles; scale bar = 150 μm.

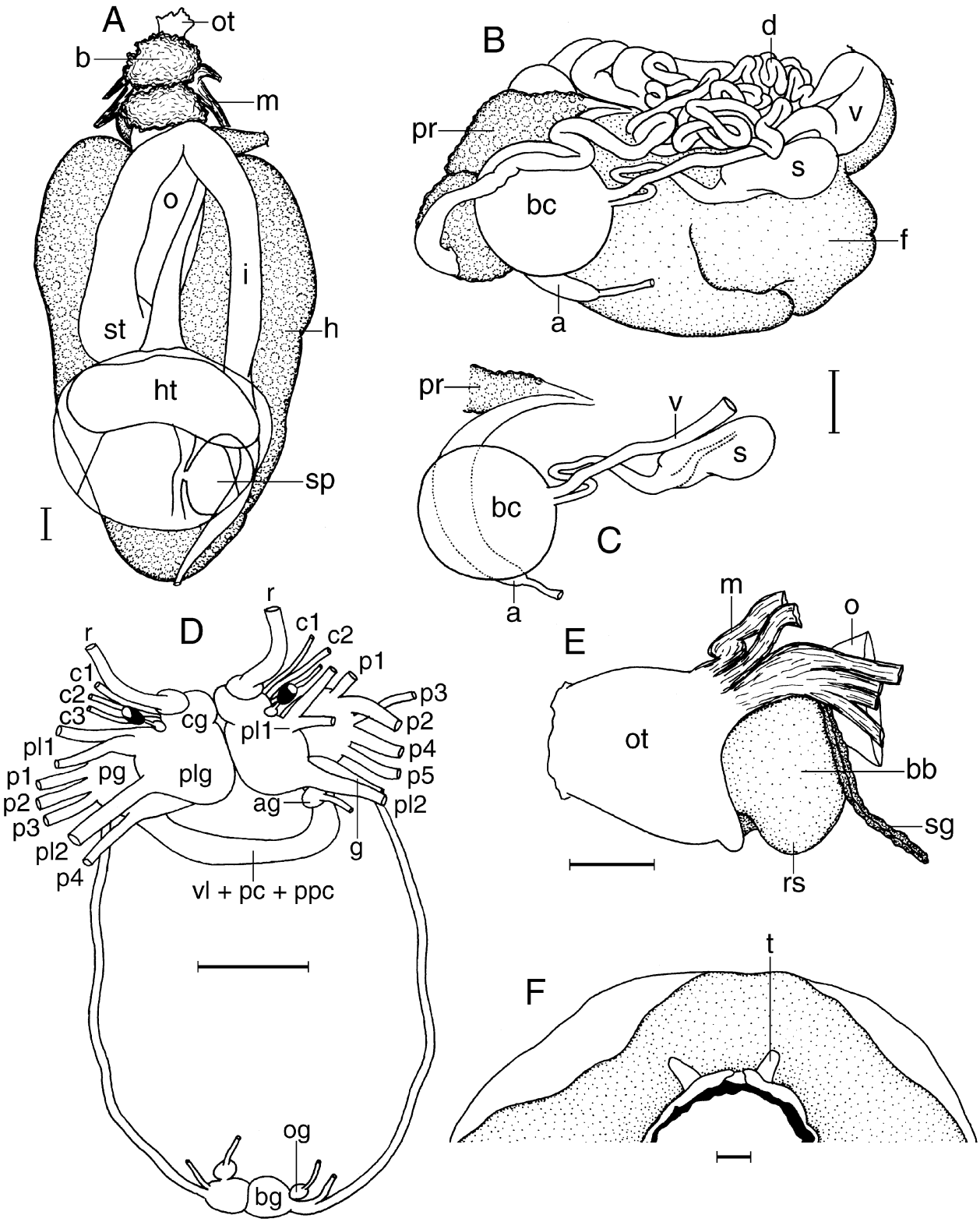

Figure 16. *Discodoris boholiensis* (CASIZ 083654). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 2 mm.

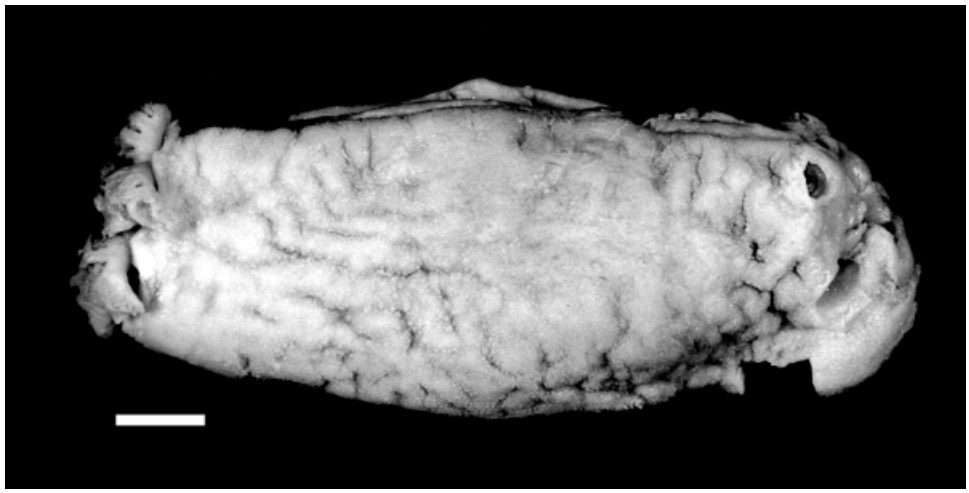

Figure 17. *Discodoris zibethina* (ZMUC GAS-2112). dorsal view of the preserved holotype.

Type material

HOLOTYPE (by monotypy): Canal at Lapinig, Philippines, March 1865, 54 mm preserved length, leg. C. Semper (ZMUC GAS-2112).

Description

The colour of the living animal is unknown (Fig. 17). The body is very elongate and narrow, with a very reduced mantle margin, which is completely absent in some areas. The gill is situated on the posterior border of the body. The dorsum is covered with a number of small, rounded tubercles (Fig. 18E). The rhinophoral and branchial sheaths have tubercles similar to those on the rest of the dorsum. There are six tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. Ventrally the anterior border of the foot is grooved and notched.

The labial cuticle is armed with a number of small, simple rodlets (Fig. 18D). The observed radular formula is $n \times 83.0.83$. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 18A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 18B). The outermost teeth are smaller and also lack denticles (Fig. 18C).

Remarks

The holotype of *Discodoris zibethina* is the only known specimen of this species. The specimen was studied and dissected by Bergh (1878a), and only the skin and some internal organs, including the radula, remain. The description of the species was based on preserved material and there is no information on the features of the living animal. With the preserved holotype it is not possible a positive identification of this species. Therefore this name is here regarded as *nomen dubium*.

The shape of the animal strongly resembles the remains of some species of *Discodoris* or *Sebadoris* after the autotomization of the notum (Gohar & Soliman, 1967; Soliman, 1980; pers. obs.).

DISCODORIS KETOS (EV. MARCUS & ER. MARCUS, 1967) (FIGS 4E, 19, 20)

Tayuva ketos Marcus & Marcus, 1967b: 192–194, figs 52–56.

Type material

LECTOTYPE (here designated): Playa Norse, Puerto Peñasco, Sonora, Mexico, 2 November 1963, 28 mm preserved length, leg. P. Pickens (USNM 678409).

Additional material

North of Gauiola, Mazatlán, Sinaloa, Mexico, 1 December 1953, one specimen, 42 mm preserved length, leg. L. O. Miles (CASIZ 081808). Las Cruces, Baja California Sur, Mexico, 25 January 1984, one specimen, 30 mm preserved length, leg. T. M. Gosliner (CASIZ 072843).

External morphology

The background colour of the living animals is pale grey (Fig. 4E). The dorsum is covered with numerous rounded or oval dark brown patches, which are larger in the centre of the dorsum. There are a few darker patches, almost black, situated in two rows on both sides of the visceral hump and several opaque white

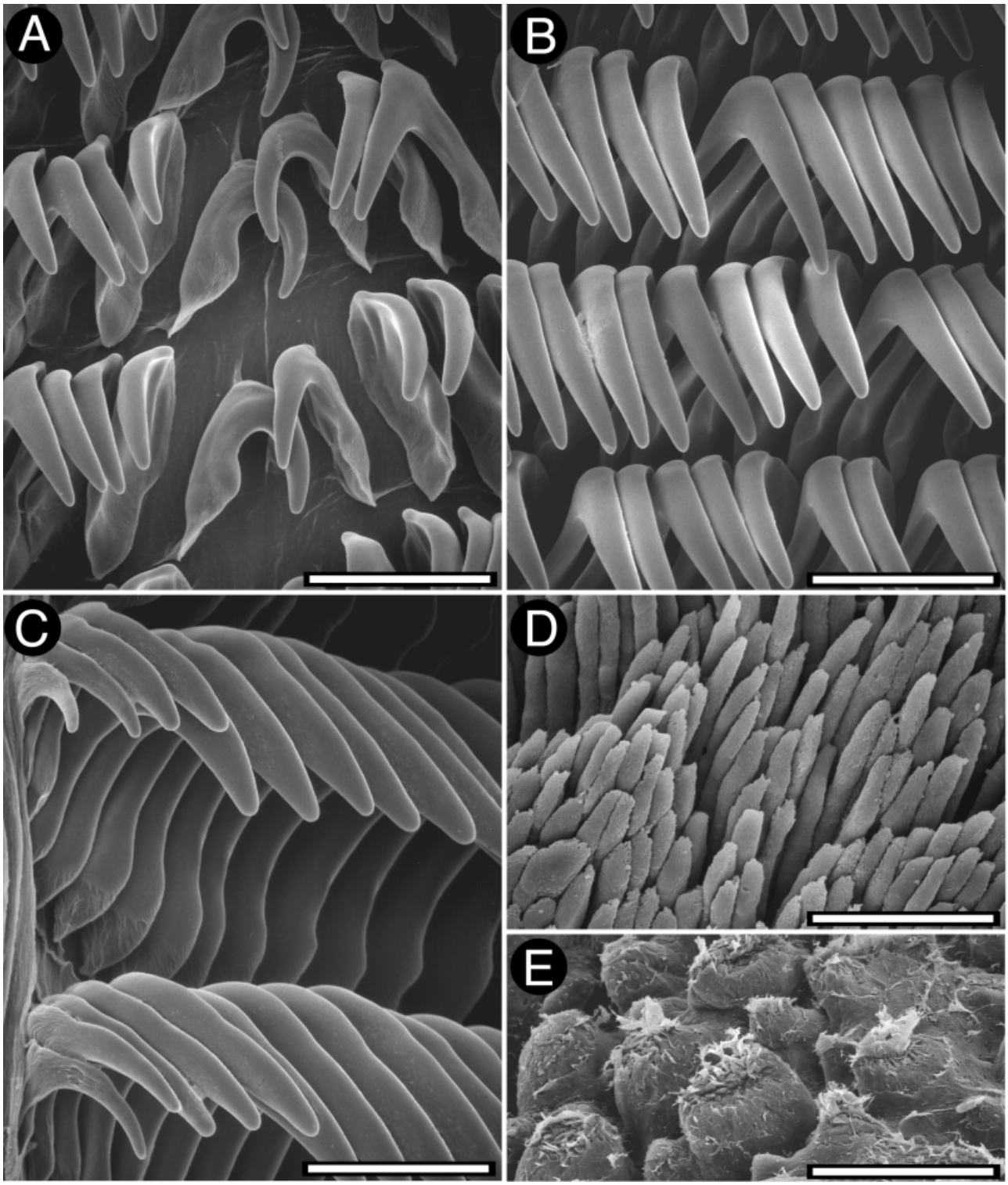

Figure 18. *Discodoris zibethina* (ZMUC GAS-2112), SEM images of the radula, jaws and dorsal tubercles. A, inner lateral teeth; scale bar = 100 μm. B, mid-lateral teeth; scale bar = 150 μm. C, outer lateral teeth; scale bar = 100 μm. D, jaw elements; scale bar = 30 μm. E, dorsal tubercles; scale bar = 430 μm.

spots irregularly distributed. The rhinophoral and branchial sheaths are low and surrounded by several white spots. The rhinophores are grey, with a number of small dark brown spots. The branchial leaves are also grey, having dark grey spots and white patches. The whole dorsum is covered with small, conical tubercles (Fig. 19D). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths have tubercles similar to those on the rest of the dorsum. There are six tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 21 lamellae in a 30-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 20E). The oral tentacles are short and conical.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 20C) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is longer than the glandular portion of the oral tube. The labial cuticle is armed with a number of small rodlets (Fig. 19E). The radular formula is $23 \times 32.0.32$ in a 42-mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 19A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 19B). The outermost teeth are smaller and also lack denticles (Fig. 19C). The oesophagus is short and connects directly to the stomach.

The ampulla is very long and convoluted (Fig. 20B). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is large and flattened. It has two different portions that are clearly distinguishable in colour and texture. The prostate connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The penis is unarmed. The muscular deferent duct opens into a large, common atrium with the vagina. The vagina is short. At its proximal end it joins 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 three times as large as the elongate seminal receptacle.

In the central nervous system (Fig. 20D) the cerebral and pleural ganglia are fused 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 no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively long nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from the left ganglion and three from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 20A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Marcus & Marcus (1970a) described the new subspecies *Tayuva ketos juva* from the tropical Indo-Pacific. The description, based on a single preserved specimen, is not complete and does not include detailed anatomical information. It is very likely that this description corresponds to a tropical species of *Discodoris*, rather than a subspecies of *Discodoris ketos*, which is probably restricted to the Panamic biogeographical region of the eastern Pacific

Another subspecies of *Discodoris ketos*, *Tayuva ketos gila*, was described by Marcus & Marcus (1970b) based on material from Curaçao, Caribbean Sea. Again, it is difficult to determine the identity of the preserved animals they saw, but it is unlikely that they belong to the same species. Marcus & Marcus (1970b) mentioned the presence of denticles on the innermost teeth of the two specimens of *Tayuva ketos gila*; these are absent in the Panamic specimens examined here.

GENUS *THORDISA* BERGH, 1877

Thordisa Bergh, 1877a: 540. Type species: *Thordisa maculigera* Bergh, 1877, by subsequent designation by Bergh (1905).

Etidoris Ihering, 1886: 234. Type species: *Etidoris ladislavii* Ihering, 1886, by monotypy.

Nuvuca Marcus & Marcus, 1967a: 621. Type species: *Nuvuca lurca* Ev. Marcus & Er. Marcus, 1967, by original designation, **syn. nov.**

Pupsikus Marcus & Marcus, 1970a: 167–168. Type species: *Pupsikus pinguis* Er. Marcus & Ev. Marcus 1970, by original designation, **syn. nov.**

Diagnosis

Dorsum covered with soft, elongate tubercles. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial cuticle smooth, lacking rodlets. Radula composed of simple, hamate teeth. Outermost lateral teeth multidenticulate. Reproductive system with a flattened, granular prostate,

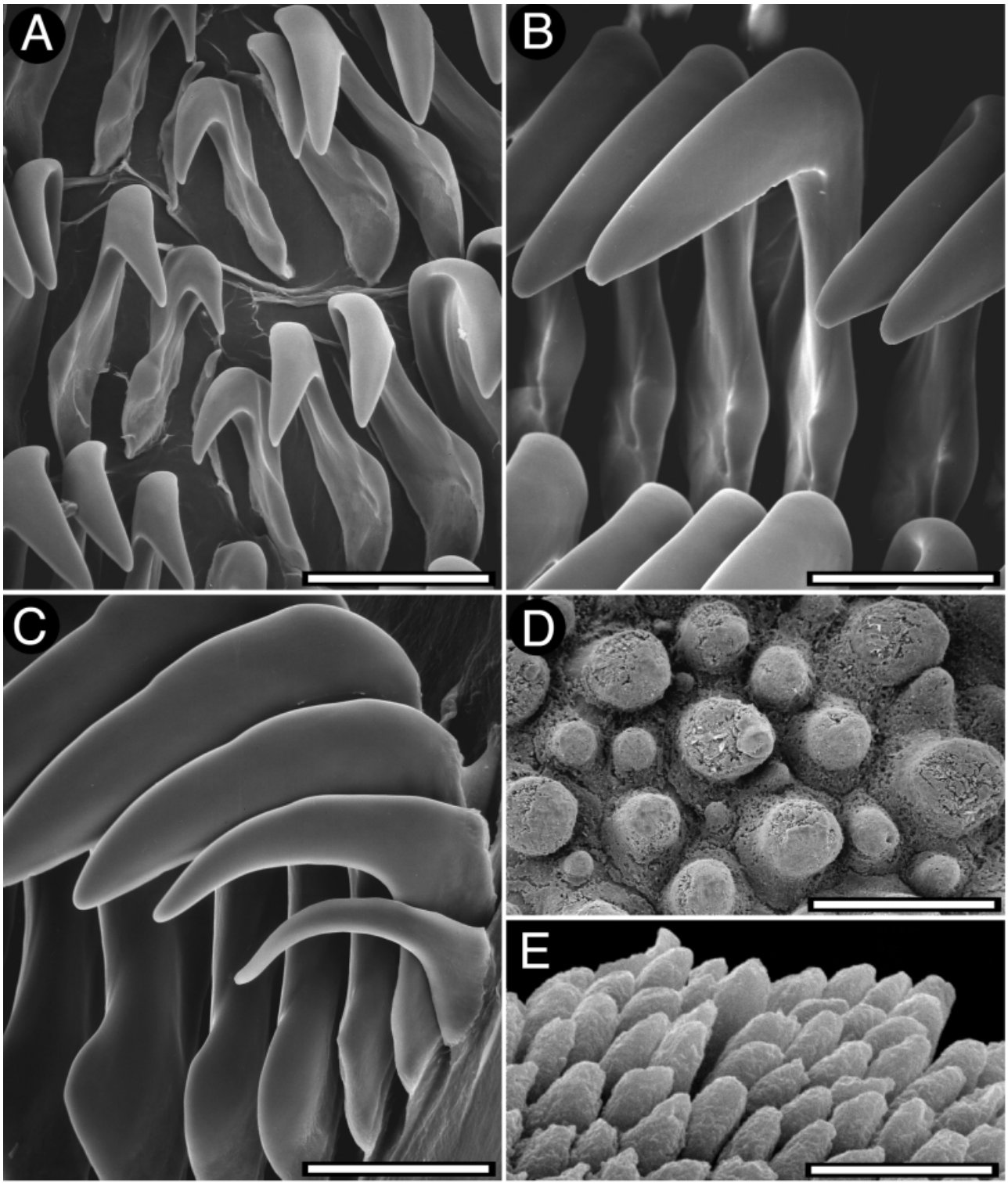

Figure 19. *Discodoris ketos* (CASIZ 081808), SEM images of the radula, jaws and dorsal tubercles. A, inner lateral teeth; scale bar = 75 μm. B, mid-lateral teeth; scale bar = 71 μm. C, outer lateral teeth; scale bar = 42 μm. D, dorsal tubercles; scale bar = 750 μm. E, jaw elements; scale bar = 30 μm.

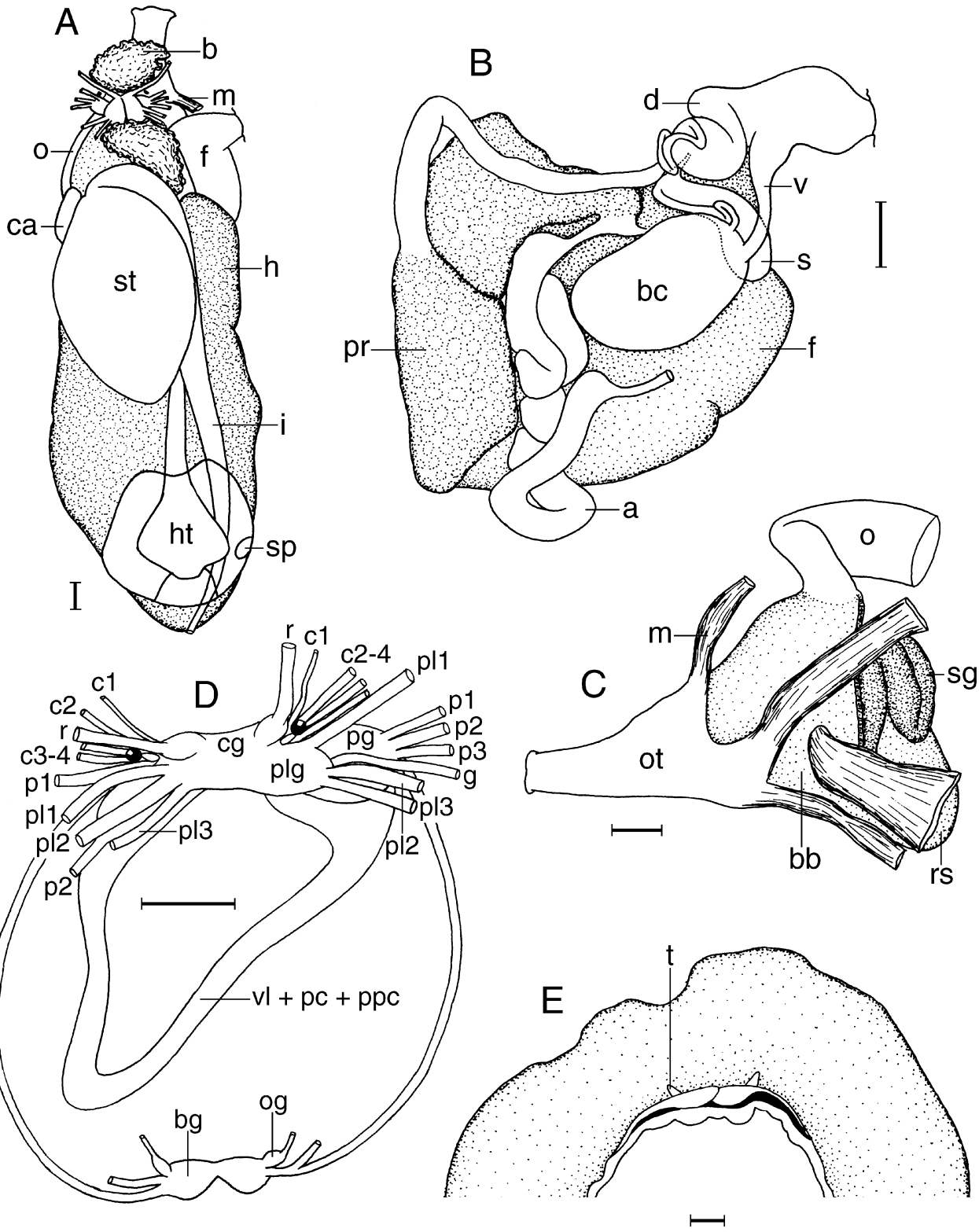

Figure 20. *Discodoris ketos* (CASIZ 081808). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, lateral view of the buccal bulb; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, ventral view of the mouth area; scale bar = 2 mm.

having two well differentiated regions. Penis armed or not with hooks. One or more accessory glands present, having one or more associated copulatory spines.

Remarks

Bergh (1877a) described the genus *Thordisa* based on *Thordisa maculigera* Bergh, 1877, but at the same time mentioned that *Doris villosa* Alder & Hancock, 1864, also belongs to this genus. According to Bergh (1877a) the main distinctive feature of this genus is the presence of elongate tubercles on the dorsum and pectinate outermost lateral teeth. Bergh (1891) regarded *Etidoris* Ihering, 1886 as a synonym of *Thordisa*. Bergh (1905) added the new species *T. carinata* Bergh, 1905, *T. tristis*, *T. hilaris* and with a question mark *T. maculosa* to the list of species of *Thordisa*, and designated *T. maculigera* as the type species.

The genus *Nuvuca* was described by Marcus & Marcus (1967a) on the basis of a single specimen of the new species *Nuvuca lurca* Ev. Marcus & Er. Marcus, 1967. According to these authors, the diagnostic features of this genus are: strongly spiculate body, unequal papillae on the dorsum, smooth labial cuticle, inner radular teeth with a short base and long cusp and pectinate outer teeth; a dart or copulatory spine joined to the male atrium; penis unarmed. Examination of the holotype of the type species revealed the presence of large dorsal papillae similar to those present in other species of *Thordisa*. The only remarkable difference between *Nuvuca* and *Thoridisa* is the absence of jaws in the former. This could be due to either interspecific variation or to Marcus & Marcus's (1967a) neglecting to find this structure. Unfortunately, the parts of the foregut of the holotype dissected by Marcus & Marcus are not preserved with the rest of the specimen, and re-examination is not possible. Because the rest of the external and anatomical features of *Nuvuca* are identical to those of *Thordisa*, they are here regarded as synonyms.

Marcus & Marcus (1970a) described the genus *Pupsikus* based on the new species *Pupsikus pinguis* Ev. Marcus & Er. Marcus, 1970. According to these authors, *Pupsikus* is characterized by having a ridge connecting the tentacles with the foot, labial armature with rodlets and 'a radula containing denticulate lateral and feathered marginal teeth'. The prostate is voluminous, the penis is armed with hooks and there is an accessory gland with a copulatory spine. The ridges that connect the oral tentacles and the foot in the single preserved specimen examined by Marcus & Marcus (1970a), are probably an artifact of observation. A re-examination of the holotype has revealed an oral morphology similar to that of other cryptobranch dorids. No trace of the ridge mentioned by Marcus & Marcus (1970a) has been found. The specimen was dissected and no anatomical information could be extracted from it, but the drawings and descriptions of Marcus & Marcus (1970a) are sufficient to identify it as a member of the genus *Thordisa*.

THORDISA VILLOSA (ALDER & HANCOCK, 1864)

Doris villosa Alder & Hancock, 1864: 119–120, pl. 33, fig. 1.
Thordisa maculigera Bergh, 1877a: 540–542, pl. 61, figs 19–24, pl. 62, figs 1, 2.
Thordisa stellata Eliot, 1904: 368.

Type material

Doris villosa Alder & Hancock, SYNTYPES: Madras, India, two specimens, 7–13 mm preserved length, dried, leg. W. Elliot (HMNC 20, 42). *Thordisa maculigera* Bergh, HOLOTYPE (by monotypy): Cebu, Philippines 1864, 15 mm preserved length, leg. C. Semper (ZMUC GAS-2102). The type material of *Thordisa stellata* Eliot is untraceable; it could not be located in BMNH.

Remarks

Alder & Hancock (1864) described *Doris villosa* from India, based on two specimens having the dorsum covered with processes with filaments. The living animals were ochre yellow to orange with large brown botches surrounding the mantle margin. Bergh (1877a) described *Thordisa maculigera* from the Philippines, but provided no information of the colour in the living animal. Years later, Bergh (1902) reported this species from the Gulf of Thailand and recognized that it is probably a synonym of *Doris villosa*.

Eliot (1904) redescribed *Doris villosa* based on one specimen from East Africa, which clearly fits with the original description by Alder & Hancock (1864). At the same time, he synonymized it with *Thordisa maculigera*, with some reservations due to differences in the radular morphology. Later, Eliot (1906c) reaffirmed his opinion on the synonymy of *D. villosa* and *T. maculigera*, based on the examination of more specimens. He also examined the type material of *Doris villosa*, but the two syntypes had the buccal mass removed, and comparison of the radular morphology was not possible. Eliot (1906c) also regarded *Thordisa stellata* Eliot, 1904 as a synonym of *D. villosa*.

Unfortunately I was unable to find complete specimens for this study. The syntypes of *Doris villosa* are poorly preserved, but I found the radula, mounted on a slide, in the HMNC collections. This radula is very similar to the drawings of the radula of *Thordisa maculigera* by Bergh (1877a) and there is no doubt these two names are synonyms.

THORDISA LURCA (EV. MARCUS & ER. MARCUS, 1967)

Nuvuca lurca Marcus & Marcus, 1967a: 621–623, figs 48–50.

Type material

HOLOTYPE (by monotypy): Off the Caribbean coast of Colombia and Panama, 67–69 m depth, 14 mm long, leg. F. M. Bayer (USNM 679055).

Remarks

This species was described on the basis of a single specimen collected from a depth of 67–69 m , characterized by a dull orange background colour, with cream papillae and the gill and rhinophores dull brown. No more specimens have been assigned to this species since then. The holotype was dissected and no information on the internal anatomy was obtained.

THORDISA PINGUIS (EV. MARCUS & ER. MARCUS, 1970)

Pupsikus pinguis Marcus & Marcus, 1970a: 168–169, figs 33–39.

Type material

HOLOTYPE (by monotypy): Mitirapa, Tahiti, French Polynesia 1964, 9 mm preserved length, leg. R. L. Sixberry (USNM 576010).

Remarks

Described on the basis of a single, preserved specimen, this species has not been collected since. Based on the original description (Marcus & Marcus, 1970a), a positive identification of this species is not possible. The dissected holotype did not reveal additional information.

THORDISA RUBESCENS BEHRENS & HENDERSON, 1981 (FIGS 4F, 21–23)

Thordisa rubescens Behrens & Henderson, 1981: 120–124, figs 1–7, 13, 14.

Type material

Big Kelp Reef, Paradise Cove, Los Angeles County, California, USA, 17 October 1979, 67 mm preserved length, leg. R. Henderson (CASIZ 015860).

Additional material

Off Los Angeles, Los Angeles County, California, USA., June 1989, one specimen, 47 mm preserved length, leg. R. Fay (CASIZ 068976).

External morphology

The background colour of the living animals is bright red-orange (Fig. 4F). The dorsum is covered with gold flecks forming a halo around the branchial pit, a mid-dorsal stripe and half crescents posterior to the rhinophores. The intensity of this pattern varies between individuals. In some specimens there are small black and opaque white spots. There is a black spot on top of the largest dorsal papillae. The rhinophores are orange to brown, with several irregular white spots and a white apex. The branchial leaves are the same colour as the dorsum. The whole dorsum is covered with soft and inflated papillae of various shapes and sizes (Fig. 21D). The papillae are contracted when the animal is under stress (Behrens & Henderson, 1981), and are surrounded by irregularly protruding spicules. Some larger papillae are randomly distributed among the others. The rhinophoral and branchial sheaths have papillae similar to those on the rest of the dorsum. There are six tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 20 lamellae in a 47-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 22F). The oral tentacles are conical.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 22D) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached. Two short salivary glands connect with the buccal bulb at each side of the oesophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $39 \times 40.0.40$ in a 47-mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 21A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 21B). The outermost teeth are smaller and have a number of small denticles (Fig. 21C). The oesophagus is long and connects directly to the stomach.

The ampulla is long and folded (Fig. 22C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is large and flattened. It has two different portions that are clearly distinguishable in colour and texture. The prostate connects with a long duct that expands into the ejaculatory portion of the deferent duct (Fig. 22B). The penis is armed with a series of large hooks, which have a wide and flat base and a curved cusp (Fig. 23A). The muscular deferent duct opens into a common atrium with the vagina. At the vaginal connection with the atrium there are two

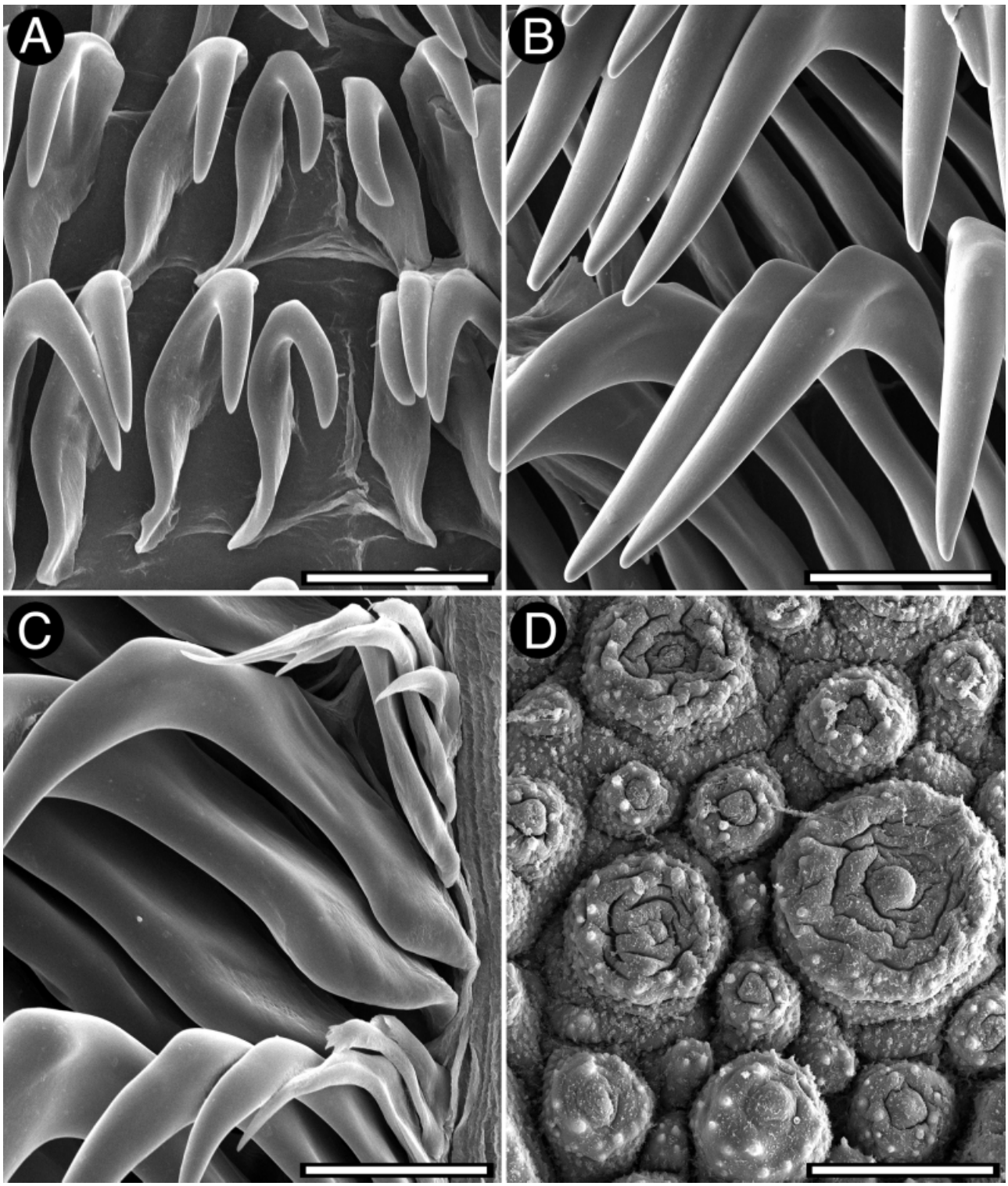

Figure 21. *Thordisa rubescens* (CASIZ 068976), SEM images of the radula and dorsal papillae. A, inner lateral teeth; scale bar = 43 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 75 μm. D, dorsal papillae; scale bar = 250 μm.

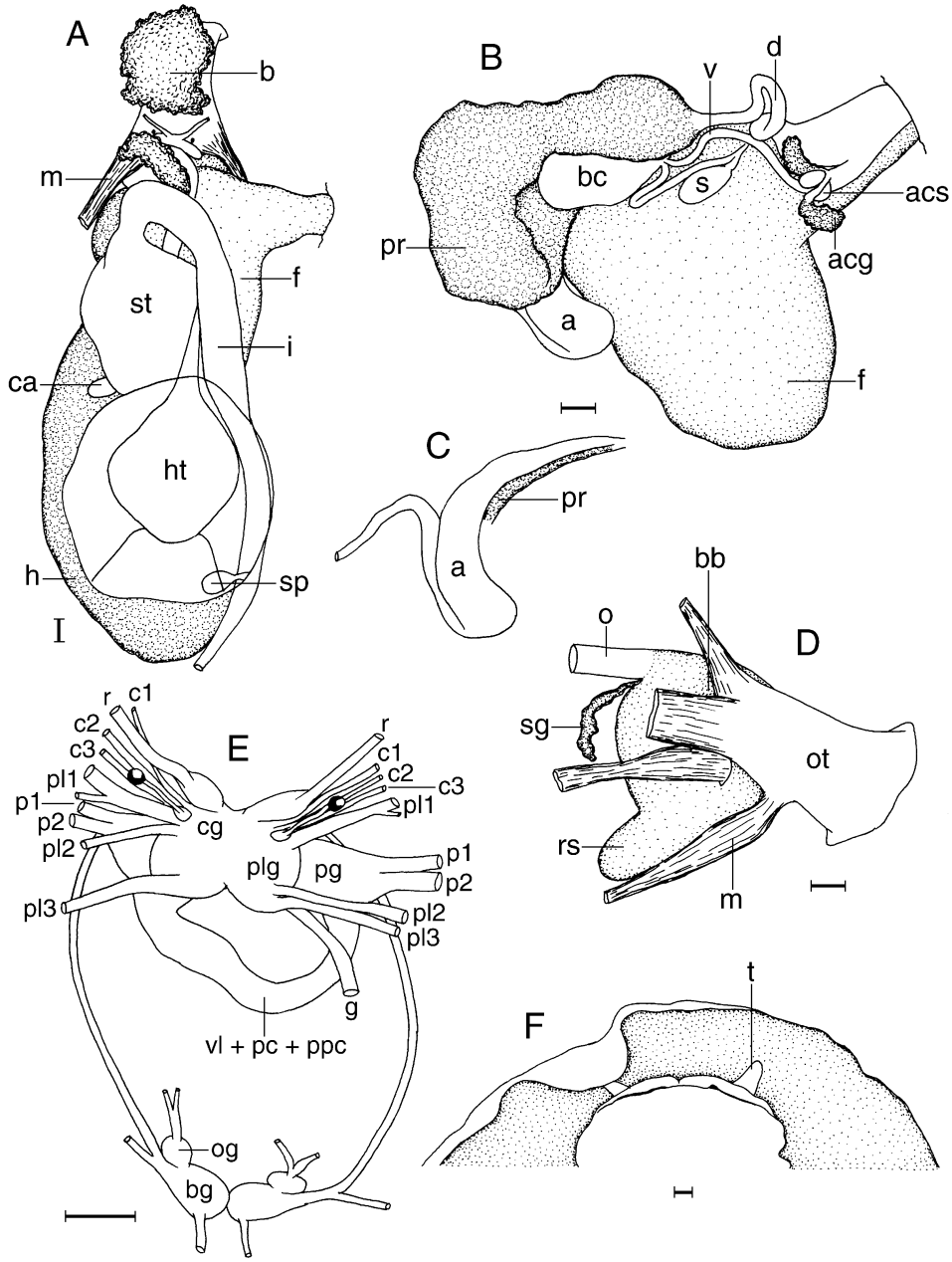

Figure 22. *Thordisa rubescens* (CASIZ 068976). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of the ampulla; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1 mm.

small accessory glands attached, and two small sacs each containing a short and irregular hard structure (Fig. 23B). At its proximal end the vagina joins 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 15 times as large as the elongate seminal receptacle.

In the central nervous system (Fig. 22E) the cerebral and pleural ganglia are fused 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. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral gan-

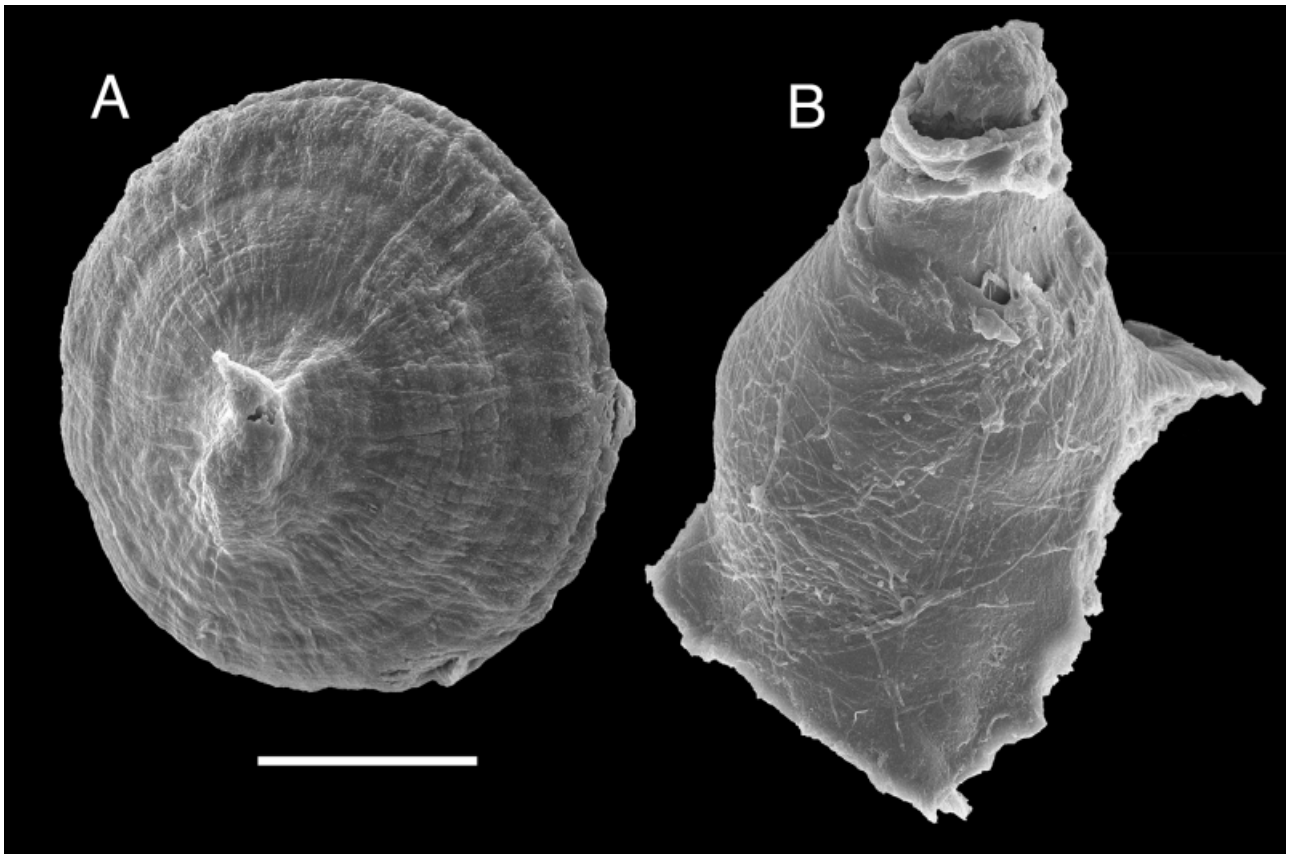

Figure 23. *Thordisa rubescens* (CASIZ 068976), SEM images of several reproductive structures. A, penial hook; scale bar = 75 μm. B, copulatory spine; scale bar = 100 μm.

glia by two relatively long nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 22A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

This is a well-known species of *Thordisa* described from California by Behrens & Henderson (1981). It was included in the analysis because it is the only species described so far that has penial hooks. Other features of this species agree with the original description of the genus (see Behrens & Henderson, 1981).

GENUS *ALDISA* BERGH, 1878

Aldisa Bergh, 1878b: XXXVIII. Type species: *Doris zetlandica* Alder & Hancock, 1854, by monotypy.

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules, which do not protrude from the dorsal surface. Anterior border of the foot grooved, but not notched. Head with two lateral prolongations. Labial armature lacking rodlets. Radula composed of very thin and elongate teeth, which have a triangular base and denticles on the apex and outer edge. Reproductive system with a tubular, granular and simple prostate. Penis armed with hooks. Vestibular or accessory glands absent.

Remarks

Bergh (1878b) described the genus *Aldisa* based on *Doris zetlandica* Alder & Hancock, 1854, and defined using radular characters. The radula of *Aldisa* was described as having erect teeth, staff-shaped, with a serrated external edge.

Since the original description several species have been assigned to this genus, later reviewed by Millen & Gosliner (1985). All of them share the presence of very elongate radular teeth, with a wide, triangular base, and denticles on the outer edge and the cusp.

ALDISA ZETLANDICA (ALDER & HANCOCK, 1854) (FIGS 24, 25)

Doris zetlandica Alder & Hancock, 1854: 102.

Type material

SYNTYPE: Shetland Islands, Scotland, one specimen, 11 mm preserved length, leg. J. Alder (BMNH 1858.5.28.210).

Additional material

Sixten Bocks, Skagerakexpedition 1937, stn. 24.7B (58°56′N, 9°55′W), Norway, 50–100 m depth, one specimen, 12 mm preserved length (SMNHI 1759). North of Hassen, Trondheimsfjord, Norway, 250 m depth, 19 June 1936, two specimens, 3–10 mm preserved length (SMNHI 1691). Trondheimsfjord, Norway, date unknown, one specimen, 15 mm preserved length (SMNHI 1540). Trondheimsfjord, Norway, 4 July 1924, one specimen, 14 mm preserved length, leg. B. Hamstrom (SMNHI 1503).

External morphology

The external morphology of this species has been described in detail by Thompson & Brown (1984). My specimens were preserved, so no data on the living animals were available.

The general colour of the living animals is white to grey-green. The rhinophores and gill are pale yellow. The whole dorsum is covered with conical and elongate tubercles varying in size and shape (Fig. 24C). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths are surrounded by tubercles similar to the rest of the dorsal tubercles. There are six bipinnate branchial leaves, forming a circle. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 11 lamellae in a 15-mm preserved length specimen.

Ventrally there are two short, blunt and grooved oral tentacles on each side of the mouth opening (Fig. 25F). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 25E) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached. Two short salivary glands connect with the buccal bulb at each side of the oesophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is undeterminable owing to the thin, elongate and overlapping teeth. The radular teeth are very thin and long, having a wide triangular base and a rounded upper edge (Fig. 24A). The teeth have a series of 19–22 elongated denticles on their outer and upper edges (Fig. 24B).

The ampulla is very short and convoluted, and branches into a short oviduct and the prostate (Fig. 25C). The oviduct enters the female gland mass near to its centre. The prostate is tubular, short, folded and granular. It connects with a long duct that narrows and expands again into the ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina (Fig. 25B). The vagina is long. Near to its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is oval in shape, about three times as large as the seminal receptacle.

In the central nervous system (Fig. 25D) the cerebral and pleural ganglia are fused 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 no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. 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. 25A) consists of a large heart and a small blood gland situated in front of the central nervous system.

Remarks

Aldisa zetlandica (Alder & Hancock, 1854) was redescribed by Millen & Gosliner (1985) in the framework of a revision of the genus *Aldisa*. They compared its anatomy and external morphology with that of other members of this genus and concluded that it constitutes a valid species.

GENUS *APHELODORIS* BERGH, 1879

Aphelodoris Bergh, 1879: 107–108. Type species: *Aphelodoris antillensis* Bergh, 1879, by monotypy.

Diagnosis

Body soft, lacking integumentary spicules. Dorsum smooth, with no tubercles. Anterior border of the foot grooved but not notched. Head with two large and

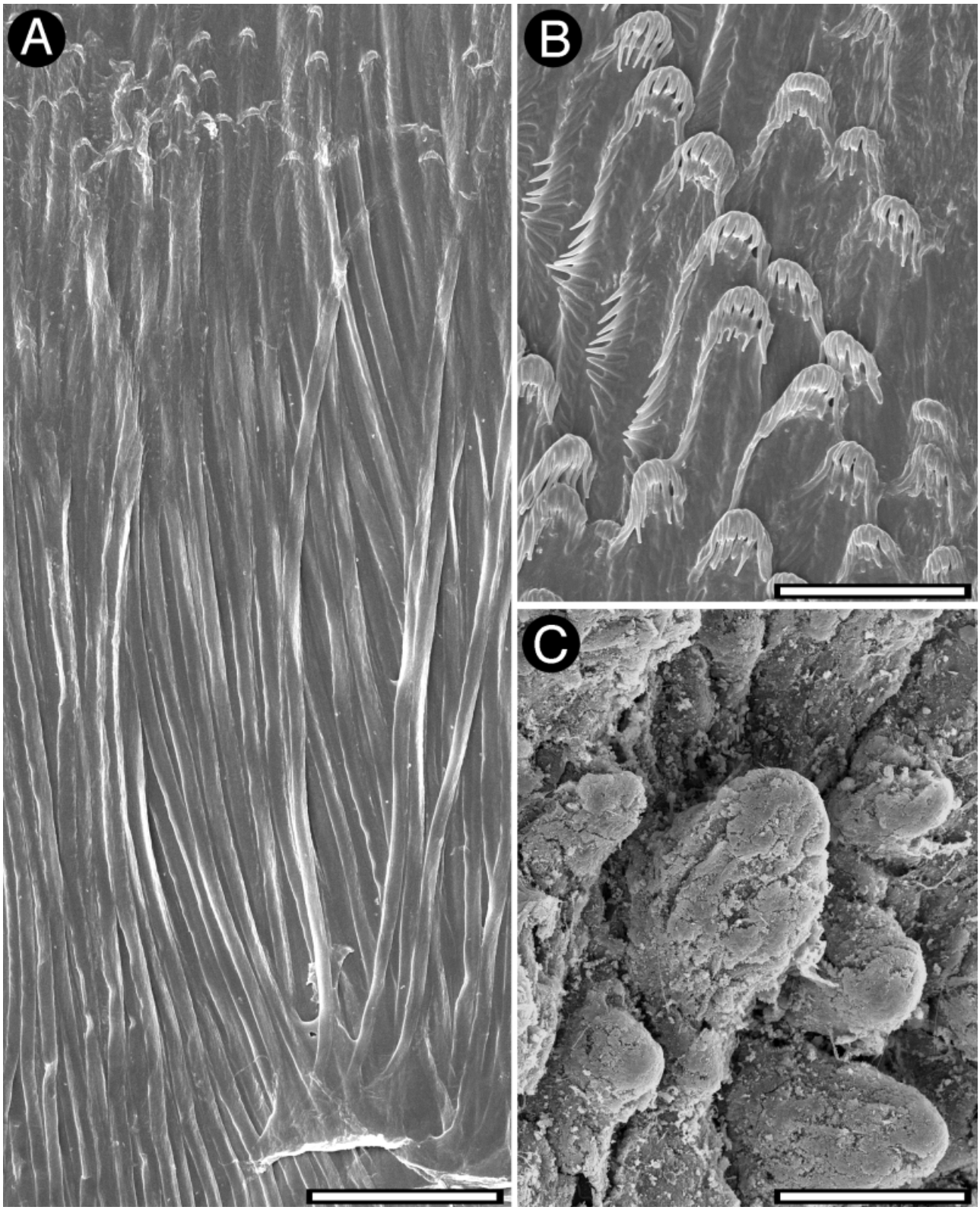

Figure 24. *Aldisa zetlandica* (SMNHI 1540), SEM images of the radula and dorsal tubercles. A, general view of the lateral teeth; scale bar = 43 μm. B, detail of the lateral tooth cusps; scale bar = 15 μm. C, dorsal tubercles; scale bar = 250 μm.

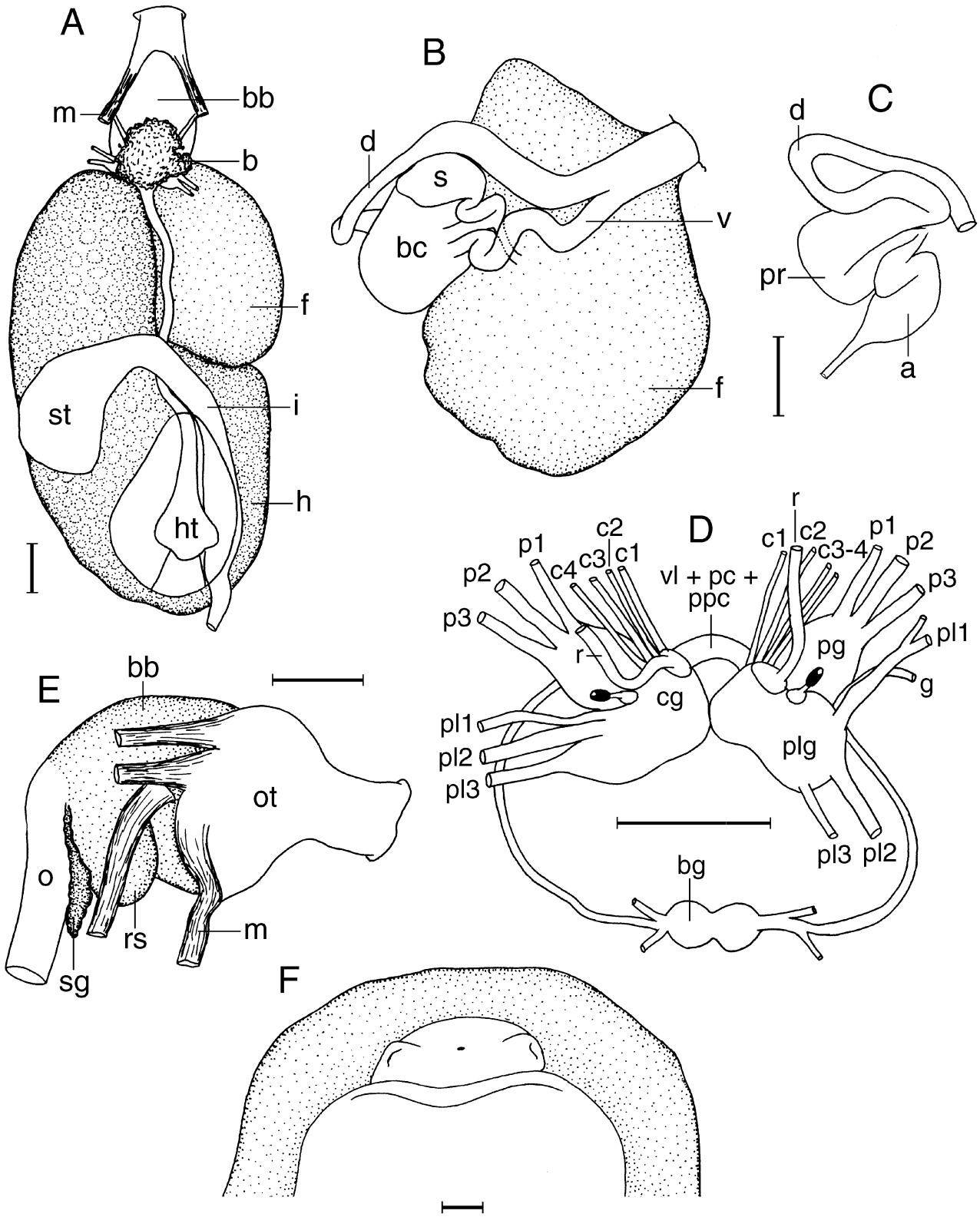

Figure 25. *Aldisa zetlandica* (SMNHI 1540). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of the ampulla and prostate; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 0.5 mm.

grooved lateral prolongations. Labial cuticle lacking rodlets. Radula composed of simple, hamate teeth. The innermost teeth may be simple or denticulate. Reproductive system with a tubular, granular and simple prostate. Penis and vagina unarmed. Vestibular or accessory glands absent.

Remarks

The genus *Aphelodoris* was introduced by Bergh (1879) for *Aphelodoris antillensis* Bergh, 1879, the type species by monotypy. According to Bergh (1879) *Aphelodoris* is very similar in body shape to the chromodorids, but it differs from this latter group in having a narrow mantle margin and a short posterior end of the foot. Other differences include the shape of the oral tentacles, which are grooved, and the presence of multipinnate branchial leaves. Internally the differences are even more obvious, with the absence of jaws and the presence of a single blood gland. Bergh (1879) regarded *Aphelodoris* as a member of the family Chromodorididae, but Odhner (see Franc, 1968) later transferred it to the family Asteronotidae.

APHELODORIS ANTILLENSIS BERGH, 1879 (FIGS 4G, 26, 27)

Aphelodoris antillensis Bergh, 1879: 108–113.
Doris bistellata Verrill, 1900: 548, pl. 66, fig. 2.

Type material

The type material of *Aphelodoris antillensis* could not be located at ZMUC (K. Jensen, pers. comm.) and is presumed lost.

Additional material

Off ferry dock, Puerto Morelos, South of Cancún, Quintana Roo, Mexico, 28 March 1985, one specimen, 10 mm preserved length, leg. T. M. Gosliner (CASIZ 071876). Burger King Reef, near Soto's Reef, South of West Bay, Grand Cayman Island, Cayman Islands, 8 May 1991, one specimen, 18 mm long, leg. J. Hamann (CASIZ 077289).

External morphology

The background colour is translucent pale cream, with numerous opaque white, yellow and brown spots (Fig. 4G). The arrangement, size and abundance of these spots is extremely variable. This variability has been described and illustrated in detail by Hamann (1992). The rhinophores and gill are also translucent pale cream, having brown, yellow or opaque white spots, which vary in size and arrangement. The dorsum is smooth, bearing a few low and soft tubercles. The rhinophoral and branchial sheaths have no tubercles. There are six bipinnate branchial leaves, forming a circle. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having nine lamellae in a 10-mm preserved length specimen.

Ventrally there are two large, blunt and grooved oral tentacles (Fig. 26F). The anterior border of the foot is grooved but not notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 26D), which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $31 \times 43.0.43$ in a 10-mm preserved length specimen. Rachidian teeth are absent. The innermost lateral teeth are triangular, having a long cusp with 5–6 denticles (Fig. 27A). The following teeth are smooth. The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 27B). The outermost teeth are smaller and also lack denticles (Fig. 27C). The oesophagus is short and connects directly to the stomach.

The ampulla is very long and convoluted (Fig. 26B). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is short and flattened. It connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. At its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle (Fig. 26C). The bursa copulatrix is oval in shape, about four times as large as the seminal receptacle.

In the central nervous system (Fig. 26E) the cerebral and pleural ganglia are fused 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 separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

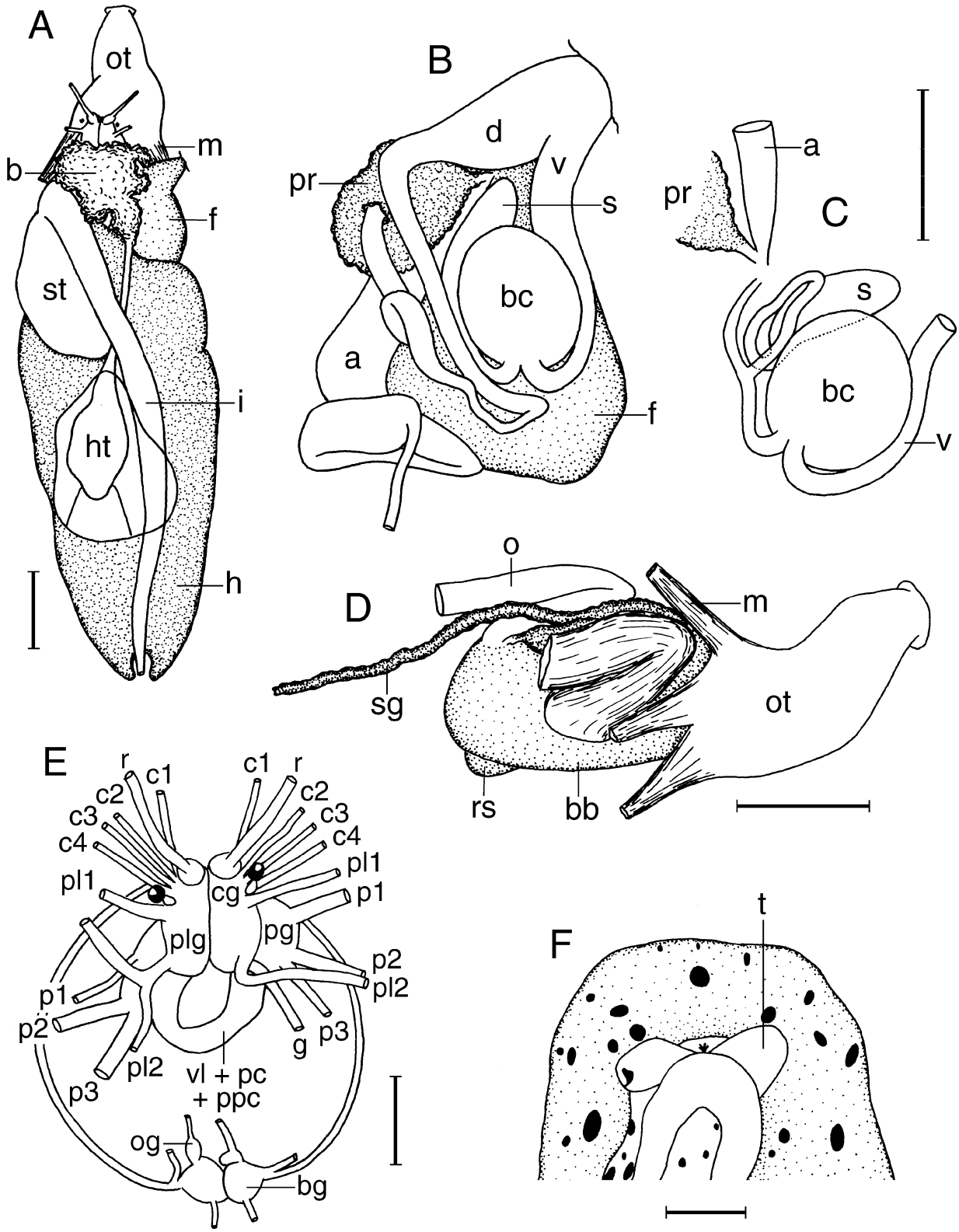

Figure 26. *Aphelodoris antillensis* (CASIZ 071876). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the mouth area; scale bar = 2 mm.

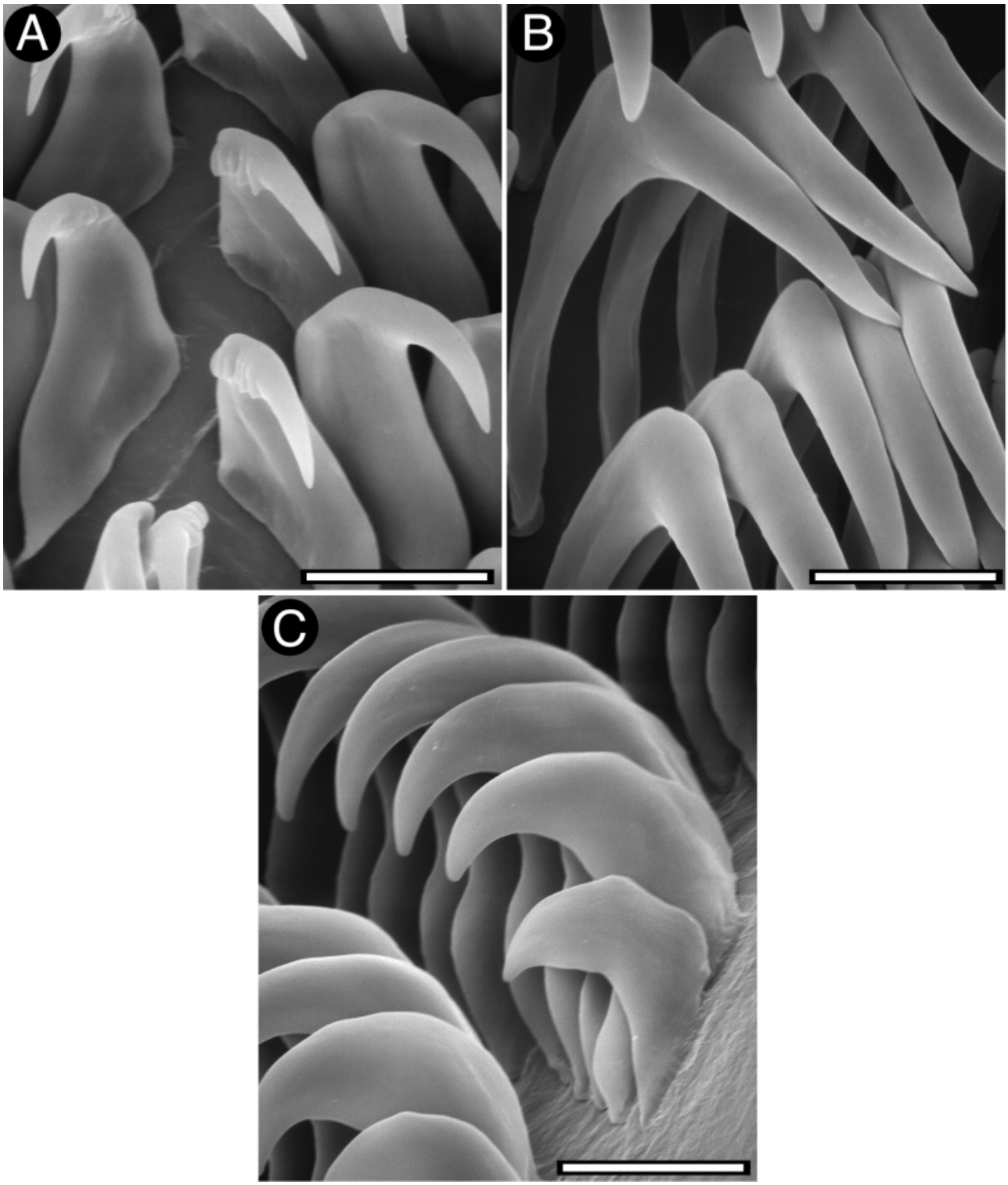

Figure 27. *Aphelodoris antillensis* (CASIZ 071876), SEM images of the radula. A, inner lateral teeth; scale bar = 15 μm. B, mid-lateral teeth; scale bar = 15 μm. C, outer lateral teeth; scale bar = 15 μm.

The circulatory system (Fig. 26A) consists of a large heart and a blood gland situated behind the central nervous system.

Remarks

This common Caribbean species was described by Bergh (1879) based on several preserved specimens from St. Thomas, Virgin Islands. Ev. Marcus & Er. Marcus (1963) illustrated and described living animals for the first time. Hamann (1992) redescribed *A. antillensis* and synonymized it with *Doris bistellata* Verrill, 1900.

GENUS *PELTODORIS* BERGH, 1880

Peltodoris Bergh, 1880: 41. Type species: *Peltodoris atromaculata* Bergh, 1880, by subsequent designation by O'Donoghue (1929).

Phialodoris Bergh, 1889: 908. Type species: *Phialodoris podotria* Bergh, 1889, by monotypy, **syn. nov.**

Montereina MacFarland, 1905: 38. Type species: *Montereina nobilis* MacFarland, 1905, by original designation, **syn. nov.**

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules, which occasionally protrude from the dorsal surface in an irregular fashion. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial armature smooth. Radula composed of simple, hamate teeth. The outermost teeth may be simple or denticulate. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

Bergh (1880) described the genus *Peltodoris* based on *Peltodoris atromaculata* Bergh, 1880. *Peltodoris* is characterized by having the dorsum covered with tubercles, finger-like oral tentacles, tripinnate gill, labial armature without jaws, radula with simple, hamate teeth, large prostate and penis and vagina unarmed. Bergh (1880) distinguished *Peltodoris* from *Discodoris* on the basis of the harder body consistency and especially because of the lack of jaws.

Bergh (1889) introduced the new genus *Phialodoris* based on *Phialodoris potrida* Bergh, 1889 from Amboine. He regarded *Phialodoris* as very close to *Discodoris* and *Peltodoris*, and only distinguishable from the latter by the peculiar shape of the penis. The penis of *Phialodoris potrida* is cylindrical with a cup-shaped apex armed with very small cones. Other characteristics of this species are similar to those of other members of *Peltodoris*, including the absence of jaws. There is no doubt that *Phialodoris* is a synonym of *Peltodoris*, and the peculiar penis shape is probably due to a preservation artifact or interspecific variation.

MacFarland (1905) described the genus *Montereina* based on *Montereina nobilis* MacFarland, 1905. The diagnostic features of this genus are firm body, tuberculate dorsum, long and conical tentacles, large gill, differentiated prostate and vagina and penis unarmed. No further species have been assigned to this genus, which was later synonymized with *Anisodoris* Bergh, 1898 by MacFarland (1906). According to Valdés & Gosliner (2001), the genus *Anisodoris*, which is a synonym of *Diaulula* Bergh, 1878, is characterized by having the dorsum covered with caryophyllidia. The anatomy of *M. nobilis* is similar to that of species of *Peltodoris*, and both names are here regarded as synonyms. Other species from the Pacific coast of South America, such as *Doris variolata* d'Orbigny, 1837, previously assigned to the genus *Anisodoris*, should also probably be transferred to *Peltodoris*.

Eliot (1906b) pointed out that *Peltodoris* only differs from *Discodoris* in lacking a labial armature (jaws) and it should be regarded as a subgenus of *Discodoris*. Later, Thompson (1975) synonymized *Peltodoris* with *Discodoris* with no justification. In the following years a few authors followed Thompson's authority and cited the type species of *Peltodoris* in the binomen *Discodoris atromaculata* (Cattaneo-Vietti *et al*., 1990). However, most authors maintained the usage of *Peltodoris* as a valid genus (Castiello *et al*., 1980; Barletta, 1981; Schmekel & Portmann, 1982; Jonas, 1986; Perrone, 1992; Ávila, 1996).

The phylogenetic analysis carried out in the present paper indicates that *Discodoris* and *Peltodoris* belong in two different clades (see below); therefore, the genus *Peltodoris* is retained as valid.

PELTODORIS ATROMACULATA BERGH, 1880 (FIGS 4H, 28, 29)

Peltodoris atromaculata Bergh, 1880: 45–46.

Type material

SYNTYPE: Naples, Italy, spring of 1880, one specimen, 34 mm preserved length (ZMUC GAS-2054)

Additional material

Islas Medas, La Escala, west coast of Gerona, Spain, three specimens, 25–34 mm preserved length, leg. T. M. Gosliner (CASIZ 099147). Cala Salada, Ibiza, Spain, one specimen, 49 mm preserved length, leg. A. Valdés (CASIZ 119474). 1 km east of Caloura, Ilha São

Miguel, Azores, Portugal, eight specimens, 44–67 mm preserved length, leg. T. M. Gosliner (CASIZ 072584).

External morphology

The general colour of the living animals is whitish to pale cream (Fig. 4H). There is a number of dark brown or black large patches distributed on the dorsum, varying in shape and size. The rhinophores and gill are white or pale cream. The branchial leaves have some small dark brown or black spots. The whole dorsum is covered with small, conical tubercles, which have spicules protruding on their dorsal surface (Fig. 28D). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths have tubercles similar to those of the rest of the dorsum. There are six tripinnate branchial leaves, forming a circle. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 22 lamellae in a 52-mm preserved length specimen.

Ventrally there are two short and conical oral tentacles (Fig. 29F). The anterior border of the foot is grooved and notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 29D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is longer than the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $22 \times 48.0.48$ in a 54-mm preserved length specimen. Rachidian teeth are absent. The inner lateral teeth are short, having a long, curved cusp and lacking denticles (Fig. 28A). They also have a secondary, short and blunt cusp situated behind the main cusp. The teeth from the middle portion of the half-row are hamate, long and larger than those closer to the medial portion of the radula (Fig. 28B). The outermost teeth are smaller and also smooth (Fig. 28C). The oesophagus is short and connects directly to the stomach (Fig. 29A).

The ampulla is long and thin, and branches into a short oviduct and the prostate (Fig. 29C). The oviduct enters the female gland mass near to its centre. The prostate is flattened, long, folded and granular (Fig. 29B), with two differentiated portions distinguishable by their colour and texture. It connects with a long duct that narrows and expands again into the small ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. Near to its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct that connects to the seminal receptacle and the uterine duct. The bursa copulatrix is oval in shape, about 10 times as large as the seminal receptacle.

In the central nervous system (Fig. 29E) the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are four cerebral nerves leading from the left cerebral ganglion and three from the right one, and three pleural nerves leading from each pleural ganglion. There is a separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively long nerves. 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. 29A) consists of a large heart and a two blood glands situated in front of and behind the central nervous system.

PELTODORIS NOBILIS (MACFARLAND, 1905) (FIGS 4I, 30, 31)

Montereina nobilis MacFarland, 1905: 38–39.

Type material

HOLOTYPE (by original designation): Monterey Bay, California, leg. F. M. MacFarland (USNM 181284), not examined.

Additional material

Pacific Grove, Monterey Bay, California, USA, July–August 1923 and May 1926, 10 specimens, 24–67 mm preserved length, leg. F. M. MacFarland (CASIZ 068237).

External morphology

The general colour of the living animals varies from whitish to orange-yellow (Fig. 4I). There is a number of dark brown or black small spots distributed on the entire dorsum below the level of the tubercles. The rhinophores have a light yellow base and a orange club. The gill is pale yellow with the apices of the leaves opaque white. The whole dorsum is covered with small, rounded tubercles (Fig. 30D). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths have tubercles no different from those on the rest of the dorsum. There are five tripinnate branchial leaves, forming a circle. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 17 lamellae in a 54-mm preserved length specimen.

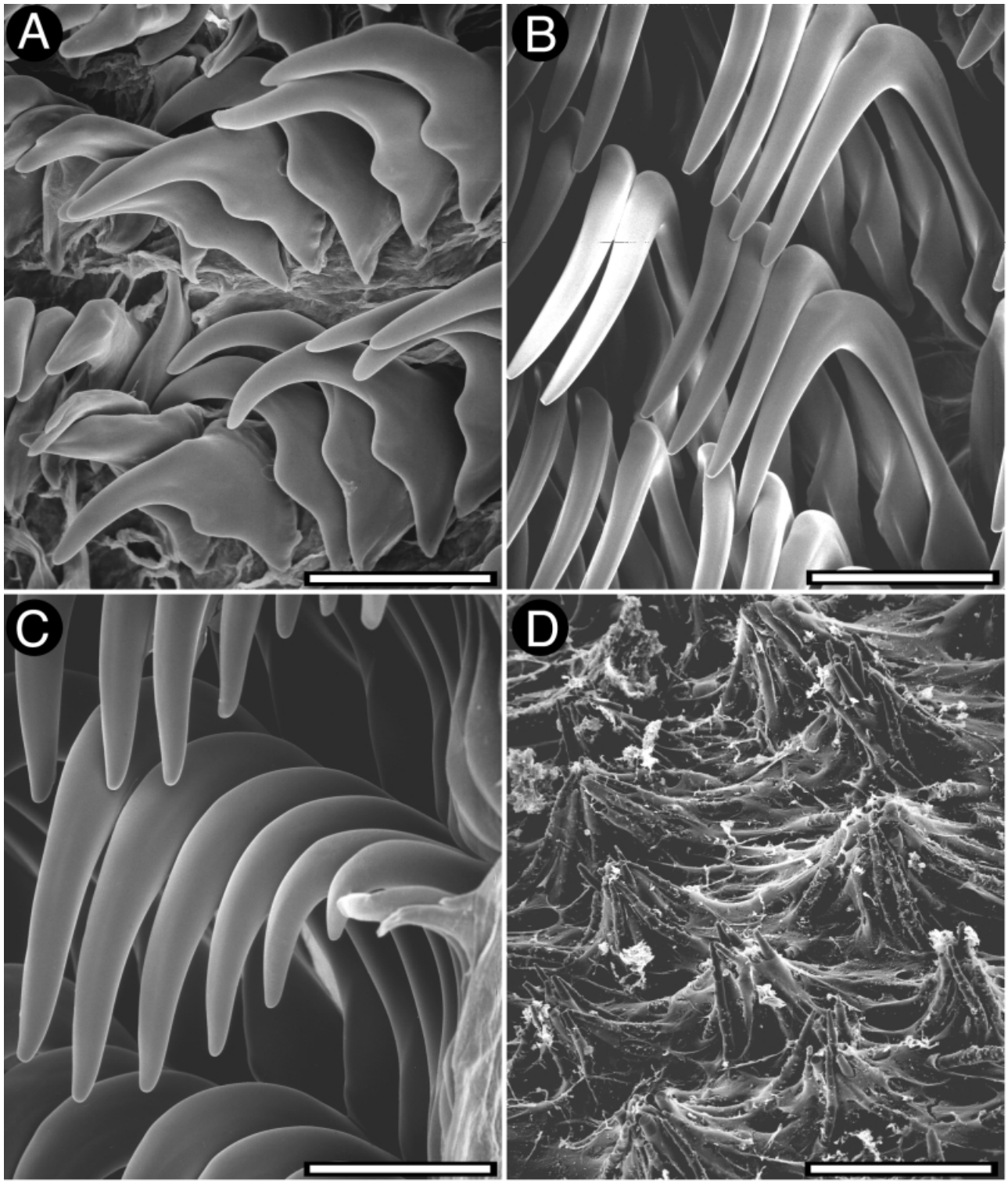

Figure 28. *Peltodoris atromaculata* (CASIZ 072584), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 75 μm. B, mid-lateral teeth; scale bar = 250 μm. C, outer lateral teeth; scale bar = 150 μm. D, dorsal tubercles; scale bar = 250 μm.

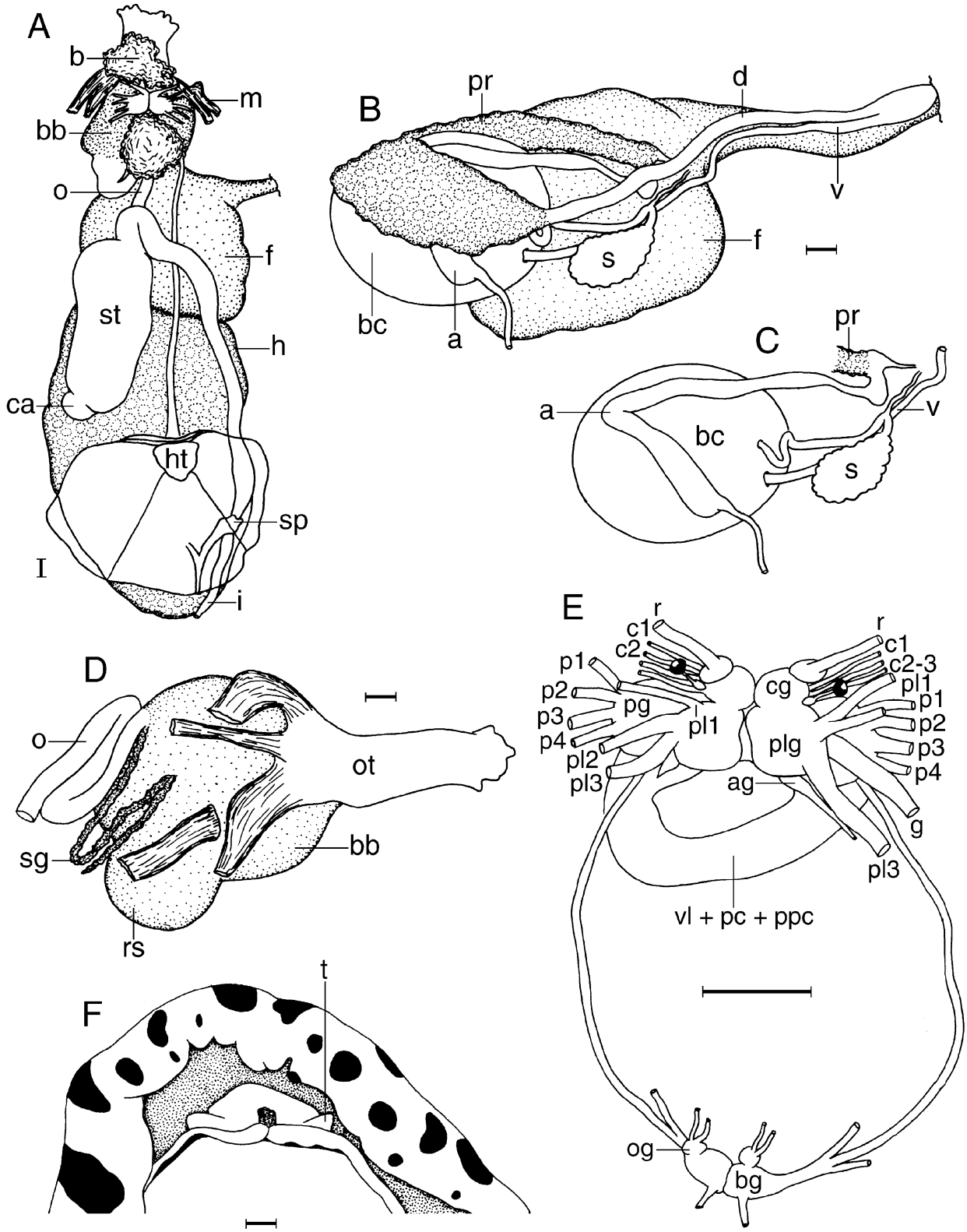

Figure 29. *Peltodoris atromaculata* (CASIZ 072584). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 0.5 mm. F, ventral view of the mouth area; scale bar = 1 mm.

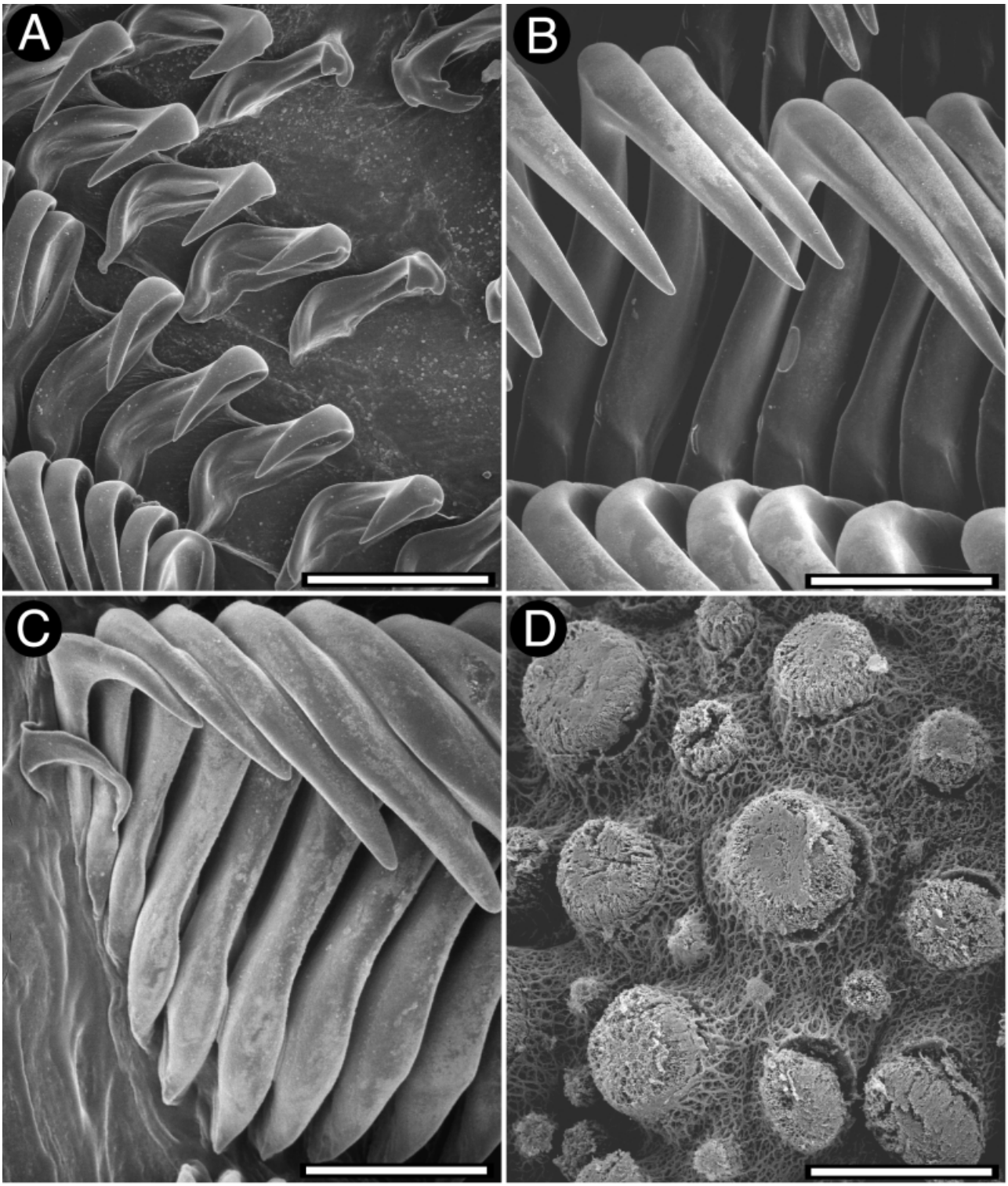

Figure 30. *Peltodoris nobilis* (CASIZ 068237), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 200 μm. B, mid-lateral teeth; scale bar = 200 μm. C, outer lateral teeth; scale bar = 150 μm. D, dorsal tubercles; scale bar = 1 mm.

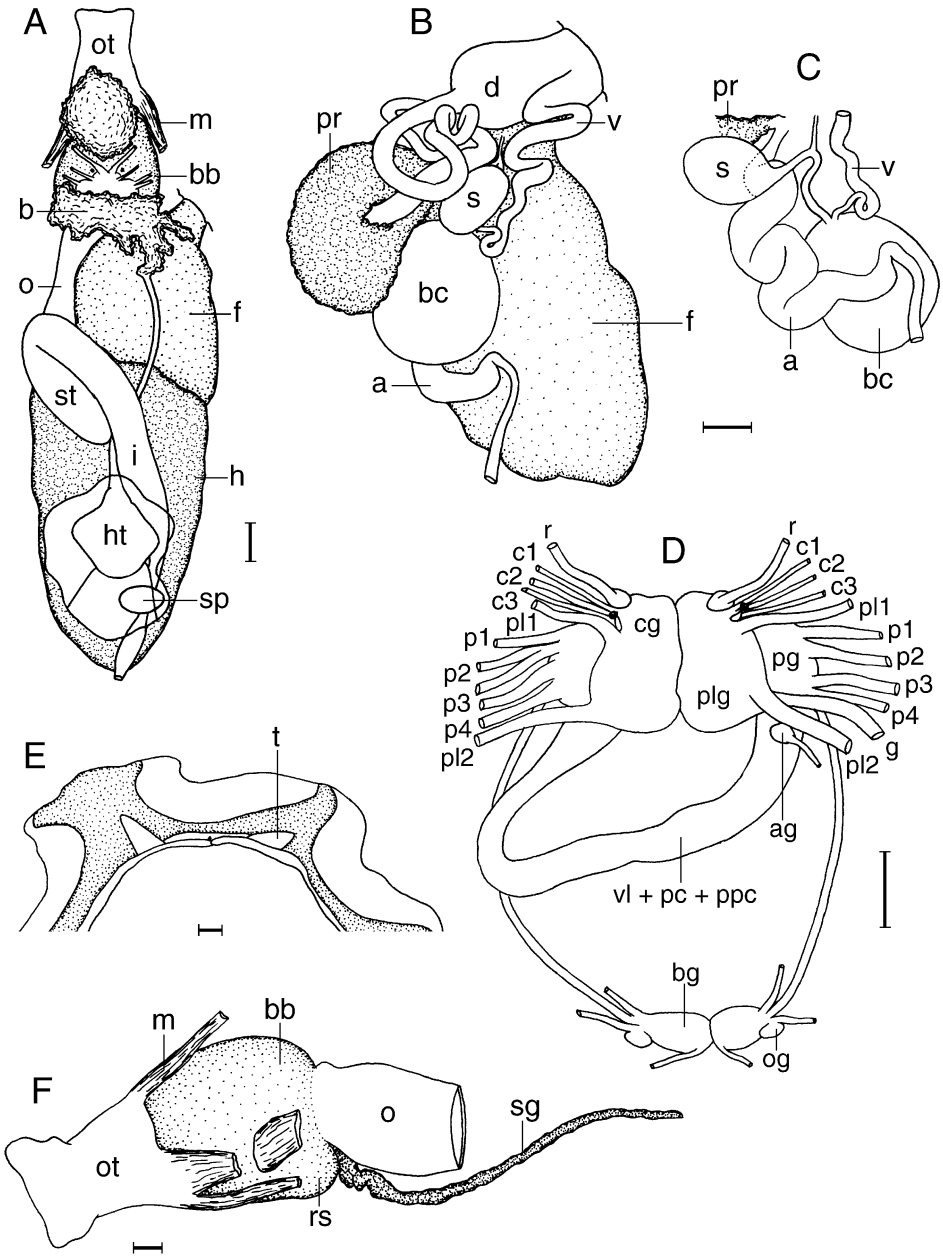

Figure 31. *Peltodoris nobilis* (CASIZ 068237). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 0.5 mm. E, ventral view of the mouth area; scale bar = 1 mm. F, lateral view of the buccal bulb; scale bar = 1 mm.

Ventrally there are two long and conical oral tentacles (Fig. 31E). The anterior border of the foot is grooved and notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 31D) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached; two long and wide salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is twice the length of the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $27 \times 57.0.57$ in a 54-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 30A). The teeth from the middle portion of the

half-row are larger than those closer to the medial portion of the radula (Fig. 30B). The outermost teeth are smaller and also lack denticles (Fig. 30C). The oesophagus is short and connects directly to the stomach (Fig. 31A).

The ampulla is very long and convoluted (Fig. 31C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is flattened and has two portions distinguishable by their colour and texture (Fig. 31B). It connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The muscular deferent duct opens into a short common atrium with the vagina. The vagina is long and convoluted. At its proximal end it joins 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 eight times as large as the seminal receptacle (Fig. 31B).

In the central nervous system (Fig. 31D) the cerebral and pleural ganglia are fused 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 a separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having four nerves each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 31A) consists of a large heart and a two blood glands situated in front of and behind the central nervous system.

Remarks

Peltodoris nobilis is a well-known species from the Pacific Coast of North America (see McDonald, 1983). It was originally described in the genus *Montereina* (MacFarland, 1905) and later transferred to the genus *Anisodoris*.

GENUS *HOPLODORIS* BERGH, 1880

Hoplodoris Bergh, 1880: 51. Type species: *Hoplodoris desmoparypha* Bergh, 1880, by monotypy.

Diagnosis

Dorsum covered with simple, large and rounded tubercles, stiffened by integumentary spicules. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial armature armed with jaw elements. Radula composed of simple, hamate teeth, occasionally denticulate. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis armed with hooks. Vagina devoid of armature. One or two large and pedunculated accessory glands armed with copulatory spines.

Remarks

Bergh (1880) described the genus *Hoplodoris* based on *Hoplodoris desmoparypha* Bergh, 1880, the type species by monotypy. The genus *Hoplodoris* is characterized by having the dorsum covered with long tubercles, the anterior border of the foot grooved and notched, presence of jaws, hamate radular teeth, large prostate, penis armed with hooks and presence of an accessory gland with a spine. The type species of *Hoplodoris* has not been collected since, and there is no information on its external morphology. Unfortunately, the type material of this species collected from Palau could not be located at ZMUC and is presumed lost. The information for this genus used in the phylogenetic analysis has been obtained from *Hoplodoris novaezelandiae* (Bergh, 1904).

Thompson (1975) regarded *Carminodoris* as a junior synonym of *Hoplodoris* based on his description of *Hoplodoris nodulosa* Angas, 1864 from Australia. However, the original description of *Carminodoris* (Bergh, 1889), based on *Carminodoris mauritiana*, states that this genus is characterized by having the anterior border of the foot grooved and notched, the dorsum covered with small tubercles, presence of jaws, hamate lateral teeth, denticulate outermost lateral teeth, large prostate and penis armed with hooks. As mentioned below, it is probable that *Carminodoris*, which lacks accessory glands and has small dorsal tubercles, is a synonym of *Discodoris*, but this point needs confirmation.

Other genera having accessory glands with spines are *Asteronotus* Ehrenberg, 1831; *Jorunna* Bergh, 1876 and *Paradoris* Bergh, 1884. According to the results of the phylogenetic analysis (see below), all these taxa belong to different clades, and it is very likely that they acquired the copulatory spines independently.

Several species have been added to the genus *Hoplodoris* since its original description. Burn (1969) transferred *Doris nodulosa* Angas, 1864, Miller (1991) transferred *Homoiodoris novaezelandiae* Bergh, 1904 and Gosliner & Behrens (1998) described the new species *Hoplodoris estrelyado* Gosliner & Behrens, 1998. Some Indo-Pacific species previously assigned to the genus *Carminodoris* Bergh, 1889, should also probably be transferred to *Hoplodoris* (see Gosliner & Behrens, 1998). Gosliner & Behrens (1998) described some variation within *Hoplodoris* to accommodate species with one or two accessory glands armed or unarmed with

spines. All the species included in *Hoplodoris* are characterized by having rounded dorsal tubercles, except for *Hoplodoris desmoparypha*, which has elongate tubercles.

HOPLODORIS NOVAEZELANDIAE (BERGH, 1904) (FIGS 32, 33)

Homoiodoris novaezelandiae Bergh, 1904: 35–37, pl. 3, figs 3–7.

Type material

SYNTYPES: Port Chalmers, New Zealand, date unknown, four specimens, 10–12 mm preserved length, leg. H. Suter (ZMUC GAS-2105).

External morphology

The animals here examined were preserved, so no information on the external coloration was available. The external morphology of this species has been described and illustrated by Miller (1991). In the examined specimens the entire dorsum is covered with large, rounded tubercles (Fig. 32F). Some larger tubercles are randomly distributed among the others. The rhinophoral and branchial sheaths have papillae similar to those on the rest of the dorsum. There are 10 tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 14 lamellae in a 12-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 33F). The oral tentacles are conical.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 33D) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is shorter than the glandular portion of the oral tube. The labial cuticle is armed with thin elements (Fig. 32D). The radular formula is $40 \times 25.0.25$ in a 12-mm preserved length specimen. Rachidian teeth are absent. The innermost lateral teeth are hamate and have up to seven irregular denticles on the inner side of the cups (Fig. 32A). The next lateral teeth are hamate and lack denticles (Fig. 32B). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula. The outermost teeth are smaller and have irregular denticles (Fig. 32C). The oesophagus is long and connects directly to the stomach.

The ampulla is short (Fig. 33C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is short and flattened (Fig. 33B) and has two different portions that are clearly distinguishable in colour and texture. It connects with a long duct that expands into the large ejaculatory portion of the deferent duct. The penis is armed with a series of small hooks (Fig. 32E). The muscular deferent duct opens into a common atrium with the vagina. There are two large and pedunculated accessory glands connected to the atrium, each one bearing a copulatory spine. At its proximal end the vagina joins 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 as large as the elongate seminal receptacle.

In the central nervous system (Fig. 33E) the cerebral and pleural ganglia are fused 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 separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively long nerves. Rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 33A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Miller (1991) redescribed this species based on newly collected specimens from New Zealand. He examined all the New Zealand species of dorids known to exist and no other species come at all close to the specimens he re-described as *Hoplodoris novaezelandiae*. Even though he was sure that his specimens were correctly examined he found some differences with Bergh's (1904) description. Re-examination of the type material of this species confirms that Miller (1991) identified his specimens correctly, and that the anatomy of the syntypes of *Hoplodoris novaezelandiae* examined here is identical to that of his specimens.

GENUS *PARADORIS* BERGH, 1884

Paradoris Bergh, 1884a: 686. Type species: *Paradoris granulata* Bergh, 1884, by monotypy.

Percunas Marcus, 1970: 945. Type species: *Percunas mulciber* Ev. Marcus, 1970; by original designation.

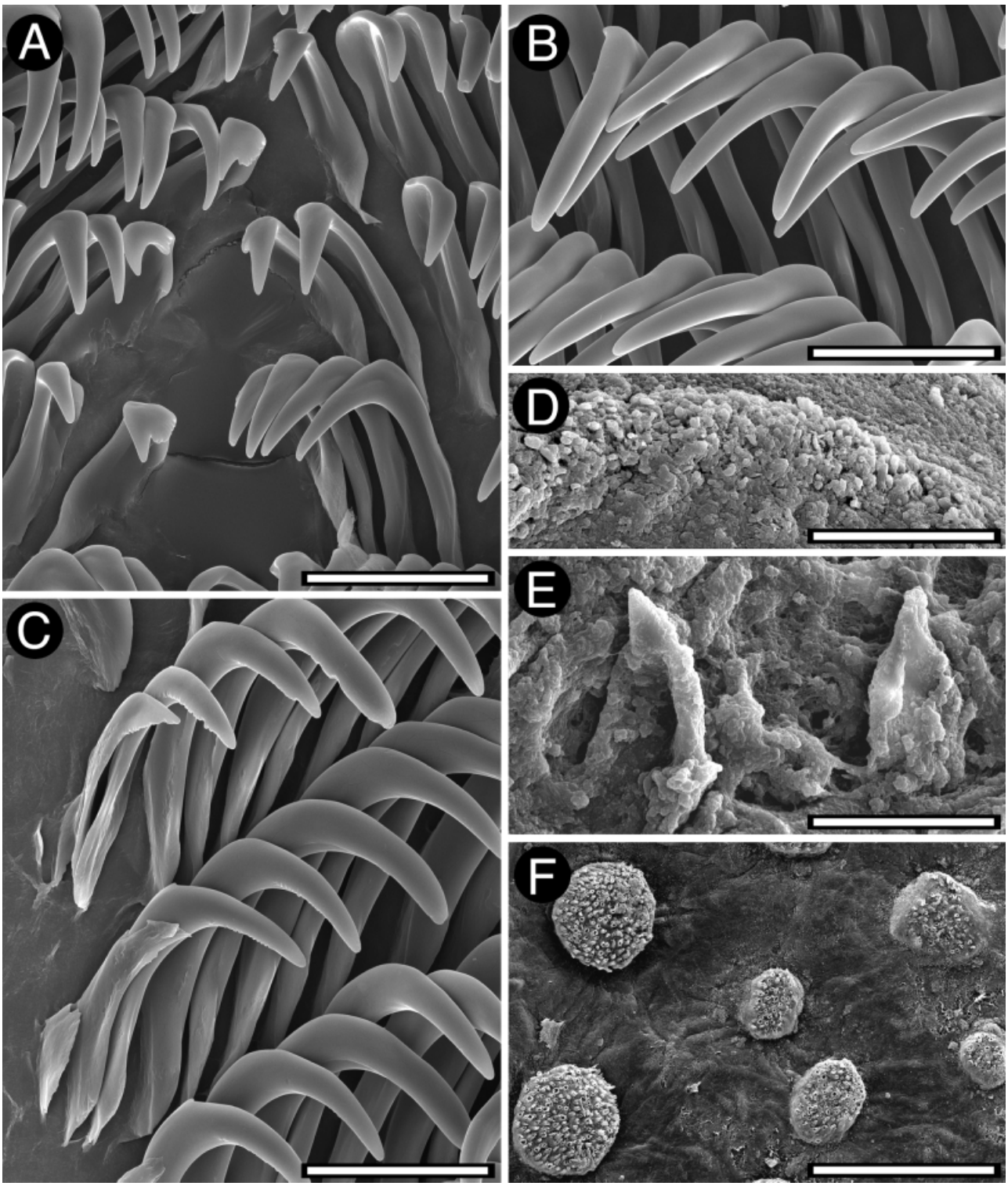

Figure 32. *Hoplodoris novaezelandiae* (ZMUC GAS-2105), SEM images of the radula, jaws, penial hooks and dorsal tubercles. A, inner lateral teeth; scale bar = 43 μm. B, mid-lateral teeth; scale bar = 43 μm. C, outer lateral teeth; scale bar = 43 μm. D, jaw elements; scale bar = 20 μm. E, Penial hooks; scale bar = 30 μm. F, dorsal tubercles; scale bar = 350 μm.

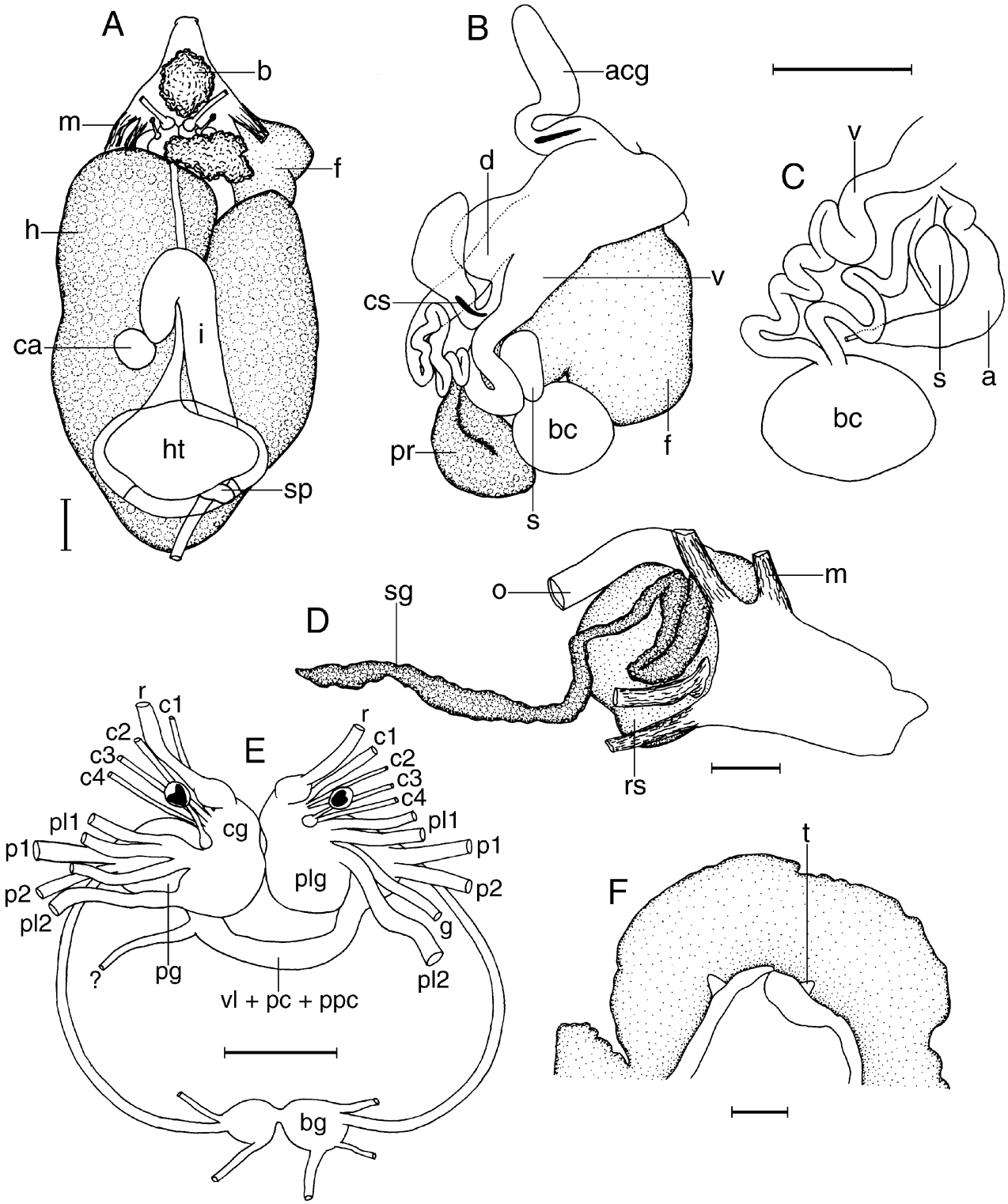

Figure 33. *Hoplodoris novaezelandiae* (ZMUC GAS-2105). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, central nervous system; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1 mm.

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial armature with rodlets. Radula composed of simple, hamate teeth, with a short, strong cusp. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis and vagina devoid of hooks. Accessory glands and sacs armed with copulatory spines are normally present.

Remarks

Bergh (1884a) described the genus *Paradoris* based on *Paradoris granulata* Bergh, 1884, as being a 'typical dorid' characterized by having the jaws divided into three portions, several accessory glands and several sacs with copulatory spines. According to Bergh (1884a) the relationships of *Paradoris* are uncertain, and this genus is probably close to the archidorids, from which it differs by having jaws.

Marcus (1970) described *Percunas* based on *Percunas mulciber* Marcus, 1970 as having the labial cuticle divided into four areas with rodlets, all radular teeth hook-shaped, massive prostate, several darts in the muscular diverticula and multiple glands annexed to the penial papilla. Baba (1989), Miller (1995), and Ortea (1995) recognized that *Percunas* is a synonym of *Paradoris*.

Perrone (1990) transferred *Discodoris indecora* Bergh, 1881 to the genus *Paradoris*, without any justification, and Ortea (1995) regarded *P. indecora* as a synonym of *P. granulata*. The type material of *P. indecora* is lost, but in the original description there is enough information to recognize it as a synonym of *P. granulata*.

Miller (1995) and Ortea (1995) found some variability in *Paradoris* when describing new species, and modified the diagnosis of the genus to accommodate these new species. According to these authors some species, such as *Paradoris leuca* Miller, 1995 and *Paradoris ceneris* Ortea, 1995, lack both accessory glands and copulatory spines, whereas *Paradoris mollis* Ortea, 1995 has copulatory spines but lacks accessory glands.

PARADORIS INDECORA (BERGH, 1881) (FIGS 34A, 35, 36)

Discodoris indecora Bergh, 1881: 108–112, pl. J, figs 26–33, pl. K, figs 11–19.

Paradoris granulata Bergh, 1884a: 686–691, pl. 76, figs 10–24.

Paradoris granulata var. Bergh, 1884a: 691–693, pl. 77, figs 25–32.

Type material

Discodoris indecora Bergh. The original type material, collected from Trieste, Italy, is lost. *Paradoris granulata* Bergh, 1884. LECTOTYPE (here selected): Trieste, Italy, April–May 1979–80, 24 mm preserved length, leg. Graeffe (ZMUC GAS-2120); PARALEC TOTYPES: Trieste, Italy, April–May 1979–80, six specimens, 8–24 mm preserved length, leg. Graeffe (ZMUC).

Two other specimens labelled as *Paradoris granulata* var. belong to the same species. They were probably collected from Trieste, Italy, April–May 1979–80, 11–19 mm preserved length, leg. Graeffe (ZMUC GAS-2121).

Additional material

Cabo de Palos, Murcia, Spain, 4 August 1984, one specimen, 14 mm preserved length, leg. J. Templado (MNCN 15.05/18231).

External morphology

The general colour of the living animals is uniformly pale grey with a pale brown tinge in the centre of the dorsum (Fig. 34A). There are several dark brown spots on the tips of the larger tubercles, also associated with groups of small opaque white dots. The rhinophores are dark brown with the apex and some spots opaque white. The gill is pale grey with the apices of the leaves bright yellow and dark brown. The whole dorsum is covered with small, rounded tubercles (Fig. 35E). The largest tubercles occur in two lines running from the rhinophores to the gill. The rhinophoral and branchial sheaths have tubercles no different from those on the rest of the dorsum. There are eight tripinnate branchial leaves, forming a circle. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 14 lamellae in a 24-mm preserved length specimen.

Ventrally there are two long and conical oral tentacles (Fig. 36E). The tentacles are grooved longitudinally. The anterior border of the foot is grooved and notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 36C) which attach to the body wall. The oval, muscular buccal bulb has two additional muscles attached; two long and thin salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is half the length of the glandular portion of the oral tube. The labial cuticle has two areas covered with a number of simple rodlets (Fig. 35D). The radular formula is

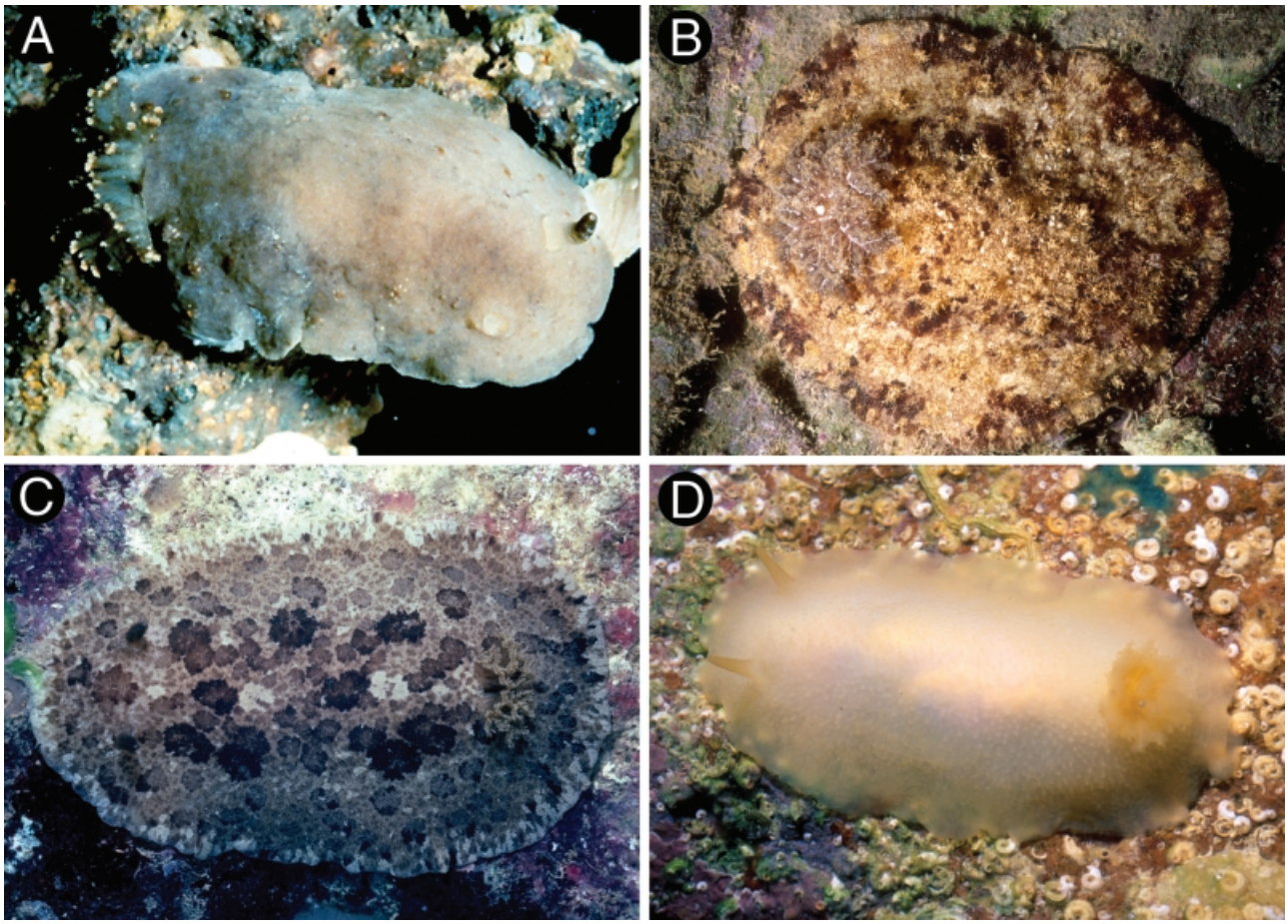

Figure 34. Living animals. A, *Paradoris indecora*, Southern Spain, photo by D. Moreno. B, *Otinodoris* sp. (CASIZ 073238), photo by T. M. Gosliner. C, *Sebadoris nubilosa*, Seychelles, photo by T. M. Gosliner. D, *Conualevia marcusi*, La Paz Bay, Baja California Sur.

$20 \times 22.0.22$ in a 24-mm long specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 35A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula, and they have a short and strong cusp compared to the base (Fig. 35B). The outermost teeth are smaller and also lack denticles (Fig. 35C). Some of them completely lack a cusp. The oesophagus is long and connects directly to the stomach (Fig. 36A).

The ampulla is very long and convoluted (Fig. 36C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is tubular and has two portions distinguishable by their colour and texture (Fig. 36B). It connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The muscular deferent duct opens into a short common atrium with the vagina. Connected to the atrium there us a large, ramified accessory gland and two muscular sacs each containing a rigid spine. The vagina is long and thin. At its proximal end it joins 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 four times as large as the seminal receptacle (Fig. 36B).

In the central nervous system (Fig. 36D) the cerebral and pleural ganglia are fused 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. There is a separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

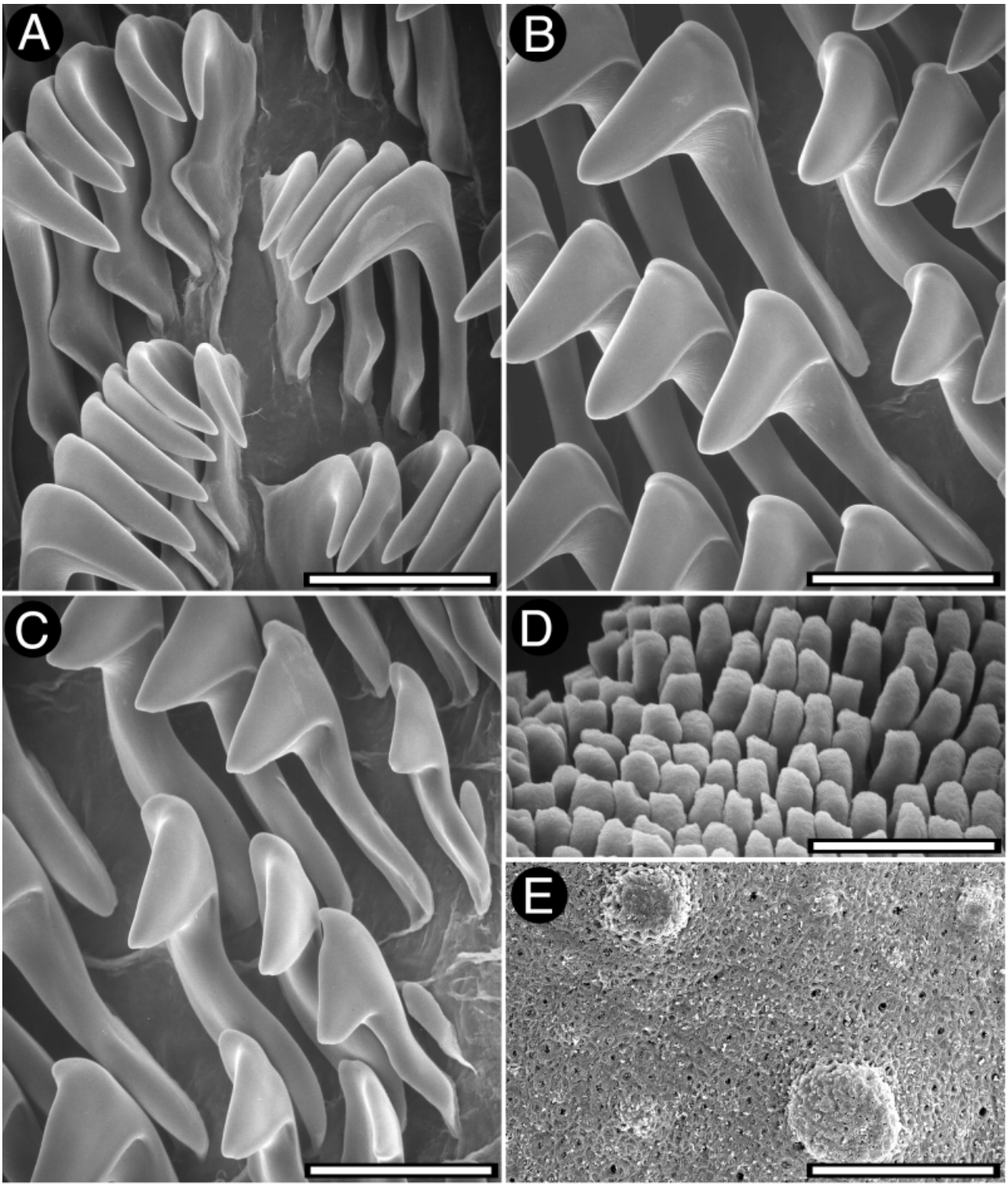

Figure 35. *Paradoris indecora* (ZMUC), SEM images of the radula, jaws and dorsal tubercles. A, inner lateral teeth; scale bar = 60 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 60 μm. D, jaw elements; scale bar = 30 μm. E, dorsal tubercles; scale bar = 250 μm.

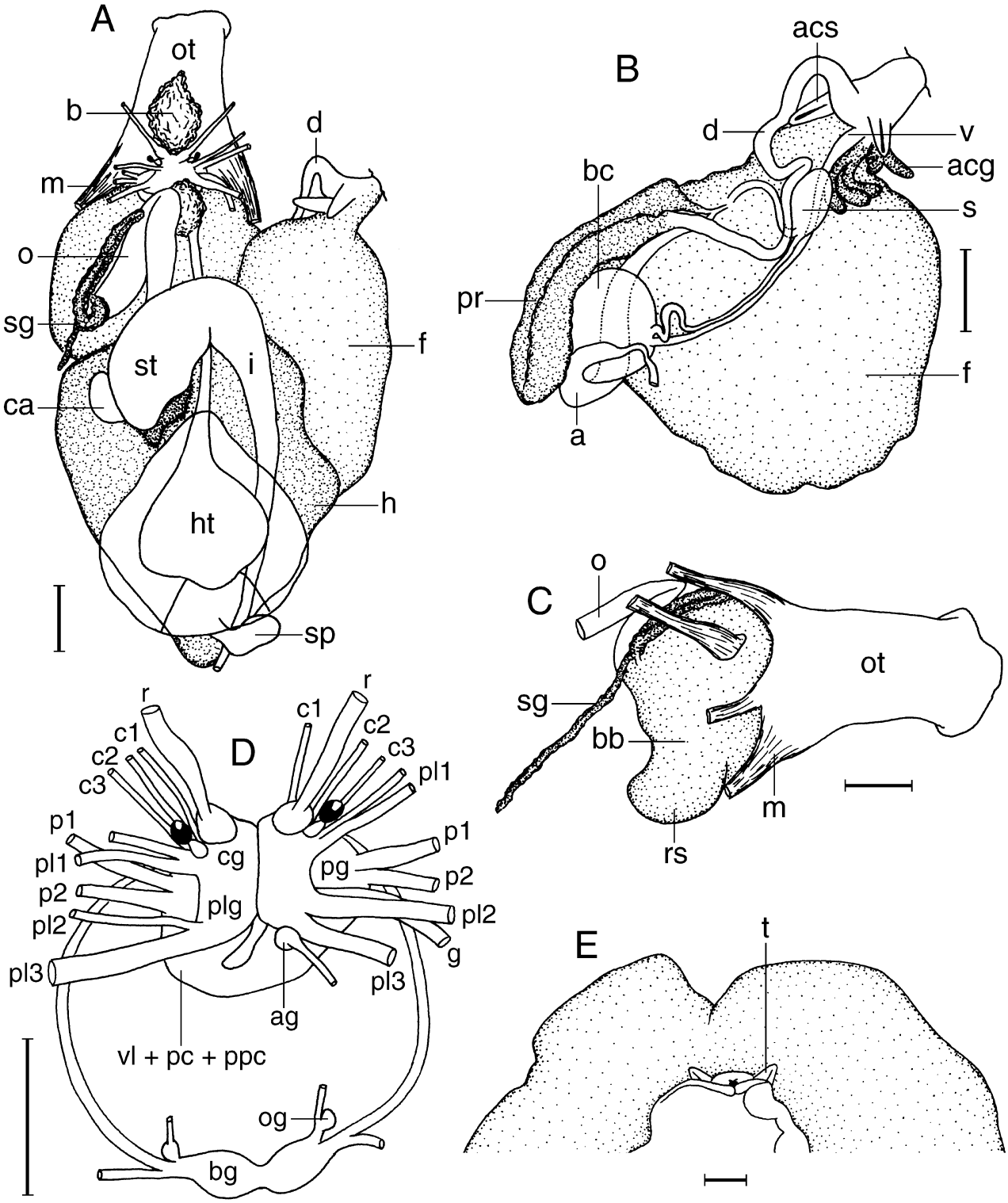

Figure 36. *Paradoris indecora* (MNCN 15.05/18231). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, lateral view of the buccal bulb; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, ventral view of the mouth area; scale bar = 2 mm.

The circulatory system (Fig. 36A) consists of a large heart and a two blood glands situated in front of and behind the central nervous system.

Remarks

Ortea (1995) revised the Atlantic species of *Paradoris* and concluded that *Paradoris granulata* Bergh, 1884, the type species of the genus, is a junior synonym of *Discodoris indecora* Bergh, 1881. The material from the Mediterranean examined here is identical to Ortea's (1995) redescription of this species. He also described more new species from the area that appear to be distinct in several anatomical details.

GENUS *GEITODORIS* BERGH, 1891

Geitodoris Bergh, 1891: 130. Type species: *Doris complanata* Verrill, 1880, by monotypy.

Carryodoris Vayssière, 1919: 67. Type species: *Carryodoris joubini* Vayssière, 1919, by original designation.

Verrillia Ortea & Ballesteros, 1981: 341. Type species *Geitodoris bonosi* Ortea & Ballesteros, 1981, by monotypy.

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules, which occasionally protrude from the dorsal surface in an irregular fashion. Head with two conical oral tentacles. Anterior border of the foot grooved and notched. Labial armature armed with jaw elements. Radula composed of hamate teeth, occasionally denticulate. Outermost lateral teeth multidenticulate. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis and vagina devoid of hooks. There is a peduculate accessory gland, in some species armed with several copulatory hard structures.

Remarks

Bergh (1891) introduced the genus *Geitodoris* based on *Doris complanata* Verrill, 1880, type species by monotypy, with a very short Latin description. According to Bergh (1891) *Geitodoris* is characterized by having the labium of the anterior border of the foot notched in the middle, the inner lateral teeth strong, hamate and outermost slender, multidenticulate, and by lacking a differentiated prostate. This diagnosis was based on Verrill's (1880) original description of *Doris complanata*, rather than on newly examined specimens. Bergh (1894) completed the description of *Geitodoris* with anatomical studies based on one of Verrill's original specimens.

Eliot (1906b) considered *Geitodoris* to be similar to *Rostanga and* also closely related to some archidorids, such as *Archidoris stellifera* Vayssière, 1904. In contrast, Odhner (1926) speculated that *Geitodoris* is closely related to *Discodoris*, and is distinguished from it by the peculiar form of the outer radular teeth. He also noted other diagnostic characteristics of *Geitodoris*: the unarmed penis, absence of prostate and stomach, presence of jaws, anterior border of the foot notched and finger-like oral tentacles.

Vayssière (1919) described the genus *Carryodoris* for the new species *Carryodoris joubini* Vayssière, 1919. In his description he did not mention *Geitodoris* or refer to the papers by Bergh (1891), Eliot (1906b) or Odhner (1926). *Carryodoris* was characterized by the presence of jaws with small rodlets and a radula with spatula-shaped outermost lateral teeth. Other features of this genus are the anterior border of the foot notched, perfoliate rhinophores and tripinnate branchial leaves.

Schmekel (1973) described a new species of *Carryodoris* from the Mediterranean, and considered this genus to be distinct from *Geitodoris*. She based her conclusion on two major differences between these two taxa, the absence of a differentiated prostate in *Geitodoris*, which is present in *Carryodoris*, and the absence of denticles on the outermost lateral teeth of *Geitodoris*, also present in *Carryodoris*. She also transferred *Geitodoris ohshimai* Baba, 1926 to this genus.

Ortea & Ballesteros (1981) regarded *Carryodoris* as a subgenus of *Geitodoris*. According to these authors, the name *Geitodoris* should be used for *G. complanata* and other species with smooth lateral teeth and lacking a differentiated prostate and *Carryodoris* for species with denticulate lateral teeth an a differentiated prostate. In addition, Ortea & Ballesteros (1981) described the new subgenus *Verrillia* for *Geitodoris bonosi*, which has smooth lateral teeth and a differentiated prostate. Other authors (Perrone, 1984; Cervera, García-Gómez & García, 1985; Miller, 1996) followed this classification including three different subgenera, in subsequent papers. Martínez, Ortea & Ballesteros *et al*. (1996) considered that the presence of denticles on the lateral teeth of *Geitodoris* 'should be considered as a specific character rather than a generic one', but at the same time continued using the same classification.

An anatomical study of *G. complanata*, the type species of *Geitodoris*, shows that this species has a well developed prostate and therefore there are virtually no differences between *Geitodoris* and *Verrillia*. I agree with most of the authors mentioned above in that the presence of denticles in some mid-lateral teeth should not on its own be used to separate the two genera, and thus I regard *Carryodoris* as a synonym of *Geitodoris*.

GEITODORIS PLANATA (ALDER & HANCOCK 1846) (FIGS 37, 38)

?*Doris testudinaria* Risso, 1818: 370–371.
Doris planata Alder & Hancock, 1846: 292–293.
Doris complanata Verrill, 1880: 399.

Type material

The type material of *Doris testudinaria* Risso is untraceable (Valdés & Héros, 1999). SYNTYPE of *Doris planata*: Cumbray Island, Scotland, one specimen, 11 mm preserved length, dried (HMNC, no registration number). SYNTYPES of *Doris complanata*: R/V Fish Hawk, United States Fish Commercial Steamer, Sta. 872 (40°02′36′-N, 70°22′58′-W), 157 m depth, South of Martha's Vineyard, Massachusetts, USA, 4 September 1880, five specimens, 15–37 mm preserved length (YPM 10405).

Additional material

Off Martha's Vineyard, Massachusetts, USA, 267 m depth, 1881, two specimens, 38–41 mm preserved length (USNM 804925). R/V Iselin, Central Atlantic Benchmark Program, Sta. A1 (39°14′42′-N, 72°47′18′-W), 91 m depth, Off New Jersey, USA, one specimen, 6 mm preserved length (USNM 832719).

External morphology

The colour of living animals from the North-Western Atlantic is unknown; preserved specimens are uniformly pale brown. The general colour of living animals from the North-Eastern Atlantic is reddish-brown (Cervera *et al*., 1985; Ortea, 1990). There is a number of dark brown patches irregularly scattered on the dorsal surface. The patches situated near to the mantle margin are smaller than those on the centre of the dorsum. The rhinophores are pale cream with some brown and opaque white spots and the apices white. The gill is dark brown with the apices of the leaves opaque white. The whole dorsum is covered with small, rounded tubercles (Fig. 37E). There are a few larger tubercles surrounded by areas with smaller tubercles. The rhinophoral and branchial sheaths have tubercles no different from those on the rest of the dorsum. There are nine tripinnate branchial leaves arranged in an oval pattern. The rhinophores are elongate, having 27 lamellae in a 36-mm preserved length specimen.

Ventrally there are two short oral tentacles (Fig. 38E). The anterior border of the foot is grooved and notched.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 38D) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is shorter than the glandular portion of the oral tube. The labial cuticle has two areas with a number of simple rodlets (Fig. 37D). The radular formula is $13 \times 20.0.20$ in a 27-mm preserved length specimen. Rachidian teeth are absent. The lateral teeth are narrow and elongate, having a single cusp and lacking denticles (Fig. 37A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 37B). The cusp of the inner and mid-lateral teeth is very short compared to the base of the teeth. The 5–7 outermost teeth are elongated, lack a cusp and have a number of thin denticles on each side (Fig. 37C). The oesophagus is long and connects directly to the stomach.

The ampulla is long and curved (Fig. 38C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is long and flattened and has two portions distinguishable by their colour and texture (Fig. 38B). It connects with a very long and convoluted duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The muscular deferent duct opens into a common atrium with the vagina. From the atrium, near to the vaginal opening leads a muscular and elongate accessory gland. The vagina is long. At its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle (Fig. 38C). The bursa copulatrix is oval in shape, about 10 times as large as the seminal receptacle.

In the central nervous system (Fig. 38F) the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. There are three cerebral nerves leading from each cerebral ganglion and four pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having three nerves leading from the left ganglion and four from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 38A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Risso (1818) described *Doris testudinaria* from the Mediterranean coast of France. Later Risso (1826)

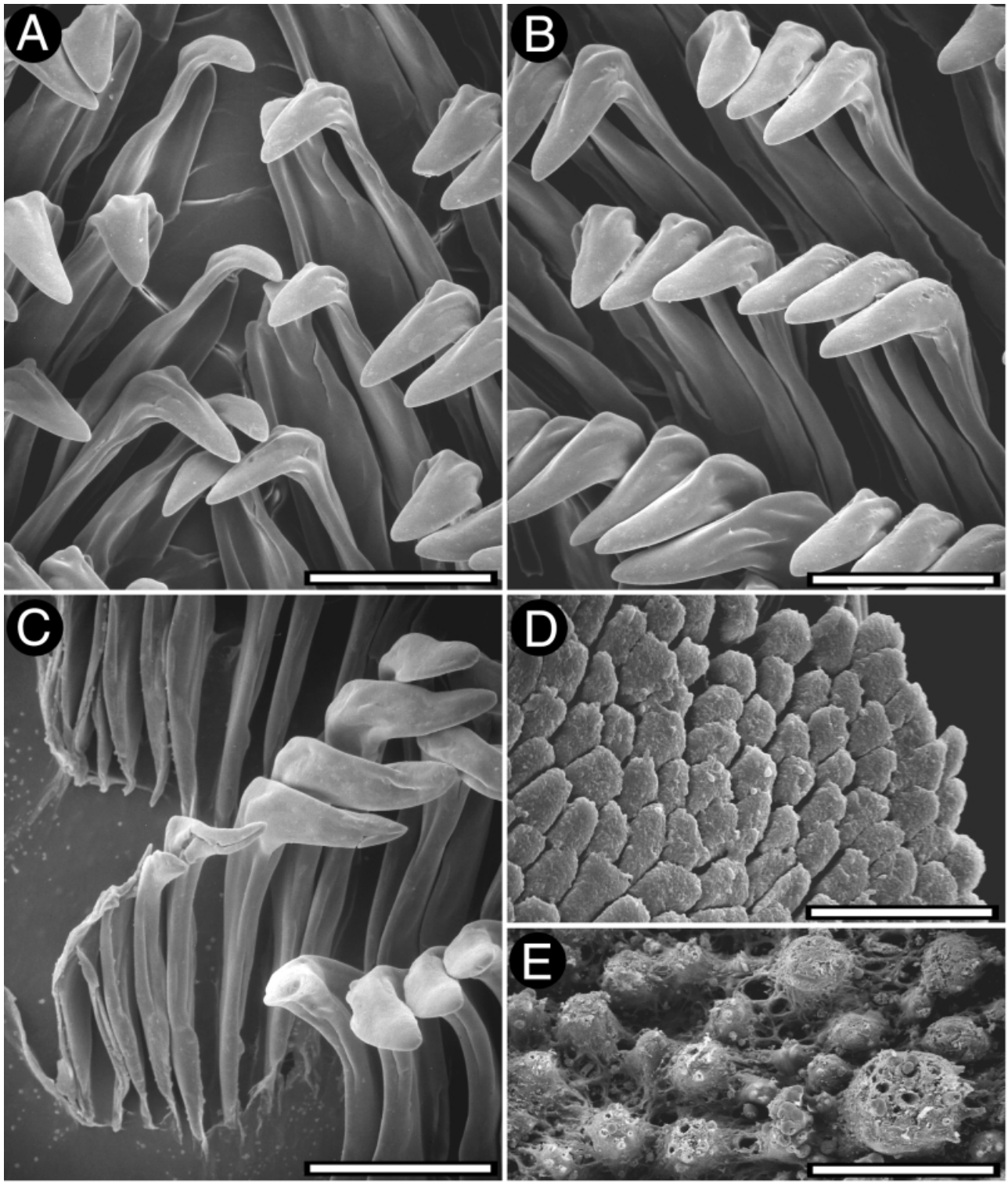

Figure 37. *Geitodoris planata* (YPM 10405), SEM images of the radula, jaws and dorsal tubercles. A, inner lateral teeth; scale bar = 100 μm. B, mid-lateral teeth; scale bar = 100 μm. C, outer lateral teeth; scale bar = 75 μm. D, jaw elements; scale bar = 30 μm. E, dorsal tubercles; scale bar = 300 μm.

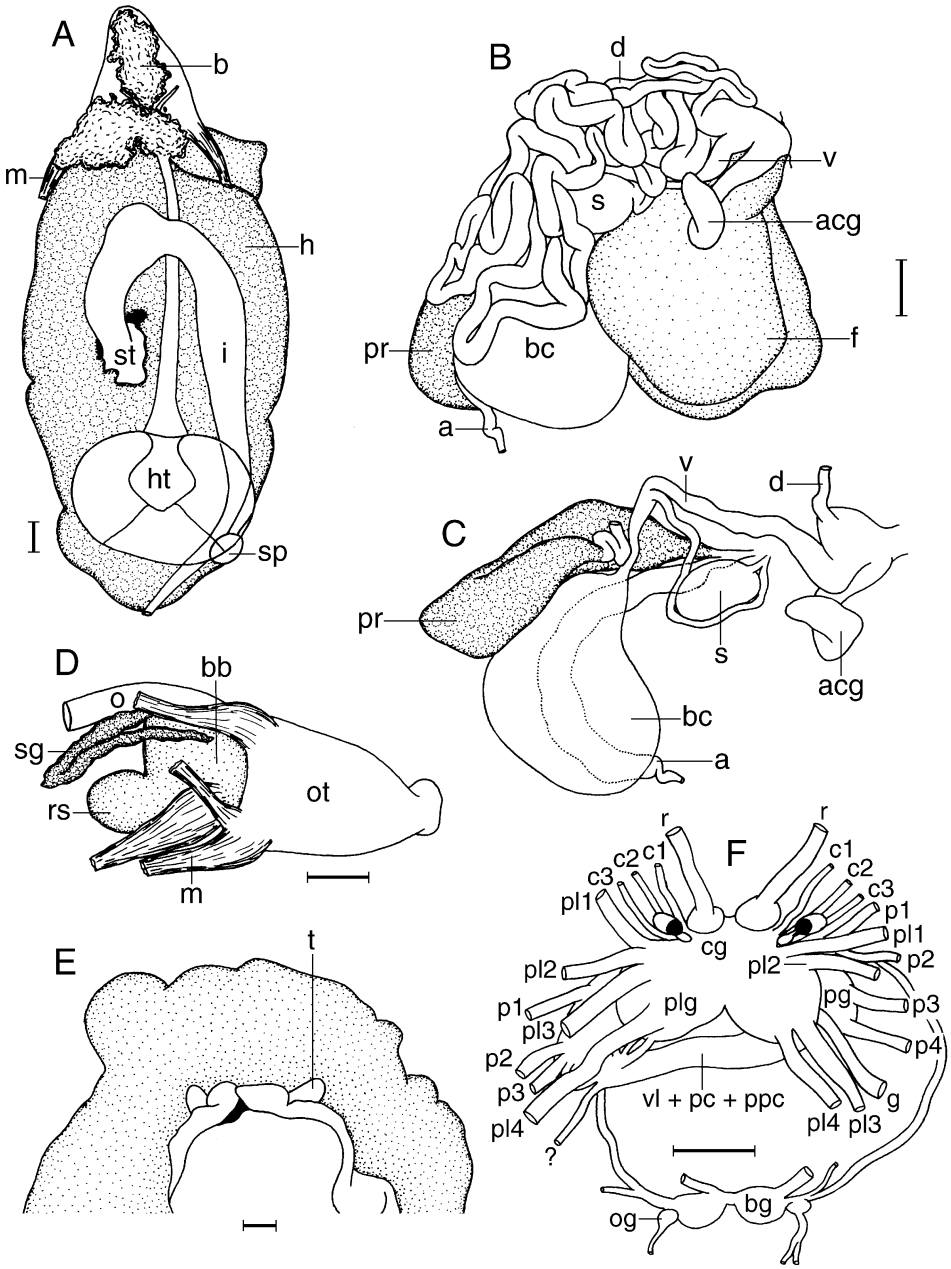

Figure 38. *Geitodoris planata* (YPM 10405). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 0.5 mm. C, detail of several reproductive organs; scale bar = 0.5 mm. D, lateral view of the buccal bulb; scale bar = 1 mm. E, ventral view of the mouth area; scale bar = 1 mm. F, central nervous system; scale bar = 1 mm.

illustrated this species, which has a dark body, brownish towards the mantle margin with yellowish lines that form small regular polyhedrons on the dorsum, and a reddish-orange underside.

Alder & Hancock (1846) described *Doris planata* from Scotland, as reddish brown, interspersed with dull lemon-yellow and purple-brown patches, the whole sprinkled with minute dark brown spots. A few irregular patches of dull yellow run down each side. Other distinctive features of this species are the dorsum covered with obtuse warty tubercles, mostly minute but of very unequal sizes, the anterior border of the foot grooved and notched and the seven branchial leaves small in size and strongly blotched with opaque yellowish white and dark brown. The colour of the foot was described as deep lemon.

Alder & Hancock (1862) redescribed *Doris testudinaria* as a different species from *Doris planata*, based on material from the British Isles. At the same time they recognized that *Doris planata* could be a juvenile form of *Doris testudinaria*. The only differences they found between these two species are the smaller branchial leaves, the more conspicuous dark brown markings and the presence of a central branchial leave in *D. planata*.

Years later Verrill (1880) described *Doris complanata* from Massachusetts, based on preserved specimens, pale brown to dusky brown, more or less mottled, back nearly smooth with few minute verrucae. Bergh (1894) studied one of Verrill's original specimens and described the anatomy in full detail. No information on the colour of the living animals of this species is available.

Vayssière (1904) described *Archidoris stellifera* based on von Ihering's manuscript notes and specimens he collected himself in the Mediterranean Sea. This species is characterized by having a reddish-brown or greyish-brown dorsum with darker spots and also several large, star-shaped, yellow patches arranged in three lines in the centre of the body. The underside is yellowish-orange. There are no jaws and the radular teeth are simple and hamate.

Eliot (1905a) suggested that *Doris planata* and *Doris complanata* are probably synonyms. The only differences he found between specimens from both sides of the Atlantic are the smaller size, smaller radula and smaller number of branchial leaves of the European specimens. Eliot (1905b) also suggested that the Mediterranean *Doris testudinaria* Risso, 1818 could be a synonym of *Geitodoris planata*. Only one year later Eliot (1906b) described a new species of *Geitodoris* from Cape Verde Islands, named *Geitodoris reticulata* Eliot, 1906.

Thompson & Brown (1984) regarded *Doris testudinaria* and *Archidoris stellifera* as synonyms of *Geitodoris planata* (as *Discodoris planata*). They did not provide detailed explanation for these synonymies but based their conclusions on Alder's authority.

Cervera *et al*. (1985) and Ortea (1990) redescribed *G. planata* based on animals collected from southern Spain and the Canary Islands. According to these authors this species is reddish-brown with some dark spots in a dorsal-lateral position fading toward the cream edges. The dorsum also has several yellowish, star-shaped patches situated in two rows along the centre of the body. This coloration is also very similar to that described by Vayssière (1904) for *Archidoris stellifera*. Cervera *et al*. (1985) and Ortea (1990) considered that *Archidoris stellifera* is a different species from *Geitodoris planata* because of differences in the radular morphology. Perrone (1987) redescribed *Archidoris stellifera* from Italy (in the binomen *Discodoris stellifera*) and confirmed the absence of jaws, the presence of hamate radular teeth and also described the existence of caryophyllidia. This evidence indicates that *Archidoris stellifera* should be placed in a genus of caryophyllidia-bearing dorids and is different from *Geitodoris planata*.

Examination of the type material of *Geitodoris complanata* and its comparison with anatomical studies on the European *Geitodoris planata* and the radula of the syntype of this species deposited at HMNC, confirms that these two names are synonyms. More problematic is the case of *Doris testudinaria* Risso, 1818. The external characteristics of this species, described by Risso (1826) are similar to those of *Geitodoris planata* and *Archidoris stellifera*, and it is not possible to determine its identity at this point. Also, the type material of *Doris testudinaria* is untraceable.

Geitodoris reticulata, redescribed by Martínez *et al*. (1996) is clearly a distinct species. The reproductive system and the radula differ considerably from those of *G. planata*. There are several more species of *Geitodoris* described from the Mediterranean Sea and the Canary Islands.

GENUS *OTINODORIS* WHITE, 1948

Otinodoris White, 1948: 203–204. Type species *Otinodoris winckworthi* White, 1948, by monotypy.

Diagnosis

Dorsum covered with ramified and elongate tubercles. Head with two flattened oral tentacles. Anterior border of the foot grooved and notched. Labial armature smooth. Radula composed of simple, hamate teeth. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis armed with hooks. Vagina devoid of hooks and covered with a cuticular lining. Vestibular or accessory glands absent.

Remarks

White (1948) introduced the genus *Otinodoris* based on a single preserved specimen collected from Sri Lanka. The specimen was dissected but the reproductive system and the radula were only partially described. No more specimens of this species have been collected since the original description. Externally, *Otinodoris winckworthi* is characterized by 'having branched processes on the mantle, ear-like oral tentacles and six branchiae' (White, 1948).

Internally, this species has an armed penis and lacks a prostate. Re-examination of the drawings by White (1948) shows that she probably misinterpreted the reproductive system and regarded the prostate as

the hermaphrodite gland. The prostate of this animal seems to be large and flattened. The radula has denticulate teeth similar to those of *Taringa* Er. Marcus, 1955 or *Alloiodoris* Bergh, 1904 (see Valdés & Gosliner, 2001), but other anatomical features appear to distinguish it from these two genera (presence of penial hooks in *Taringa* and absence of jaws in *Alloiodoris*).

Unfortunately, specimens of *Otinodoris winckworthi* were not available for the present study.

The examination of material belonging a new species of *Otinodoris* revealed that this genus shares numerous features with *Peltodoris*. The main differences between *Peltodoris* and *Otinodoris* are the presence or ramified tubercles and flattened oral tentacles in the later. Due to these two synapomorphies of *Otinodoris*, it is here maintained as a different taxon. According to the phylogenetic analysis carried out in this paper, there is insufficient resolution to determine the relationships between the genera. A more complete analysis, including all the species of both genera, is necessary to determine whether *Otinodoris* is a synonym of *Peltodoris*.

Otinodoris sp.
(Figs 34B, 39–41)

Type material

Off Hotel Soanambo, Île Saint Marie, Madagascar, 5 April 1990, 155 mm preserved length, leg. H. Chaney (CASIZ 073238).

External morphology

The background colour of the living animals is sandy yellow (Fig. 34B). The dorsum is covered with large, irregular brown and opaque white patches of different sizes and shapes. There is a black spot on top of the longest dorsal tubercles. The rhinophores are pale violet, with a number of irregular white spots. The branchial leaves are also pale violet with white rachises. The anal papilla is white. The whole dorsum is covered with a number of soft, elongate and ramified tubercles of various shapes and sizes (Fig. 39D). Some larger tubercles are randomly distributed among the others. The rhinophoral and branchial sheaths have papillae similar to those on the rest of the dorsum. There are six tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 26 lamellae in a 155-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 40F). The oral tentacles are very large and flattened, with an irregular shape.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 40E) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is longer than the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $41 \times 76.0.76$ in a 155-mm preserved length specimen. Rachidian teeth are absent. The inner lateral teeth are hamate and lack denticles (Fig. 39A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 39B). The outermost teeth are smaller and also lack denticles (Fig. 39C). The oesophagus is long and connects directly to the stomach.

The ampulla is very long and folded (Fig. 40C). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is large and flattened (Fig. 40B). It has two different portions that are clearly distinguishable in colour and texture. The prostate connects with a long duct that expands into the ejaculatory portion of the deferent duct. The penis is armed with large hooks (Fig. 41A) and covered by a hard cuticle. The muscular deferent duct opens into a common atrium with the vagina. The vagina is very long and convoluted, internally covered with a cuticular lining (Fig. 41B). At its proximal end it joins the large and irregular bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle. The bursa copulatrix is about 10 times as large as the elongate seminal receptacle. The seminal receptacle is elongate and granular.

In the central nervous system (Fig. 40D) the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. The cerebral and pleural ganglia are entirely covered with large ganglionic tubercles. There is one cerebral nerve leading from the left cerebral ganglion and two from the right one, and three pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively long nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from each one. The pedal and parapedal commissures are enveloped together with the visceral loop.

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

Remarks

White's (1948) original description of *Otinodoris winckworthi* includes very little information, but two

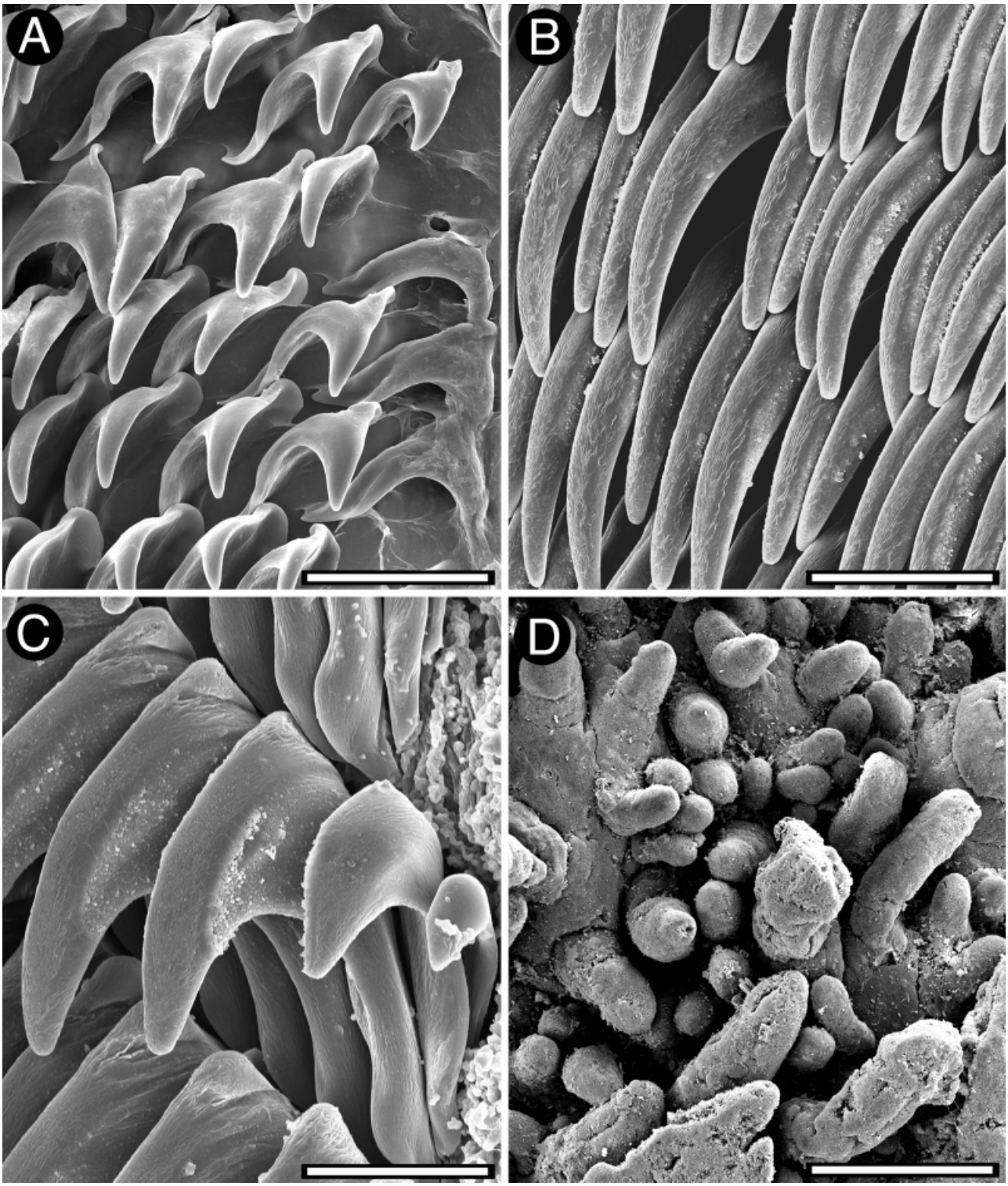

Figure 39. *Otinodoris* sp. (CASIZ 073238), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 75 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 43 μm. D, dorsal tubercles; scale bar = 350 μm.

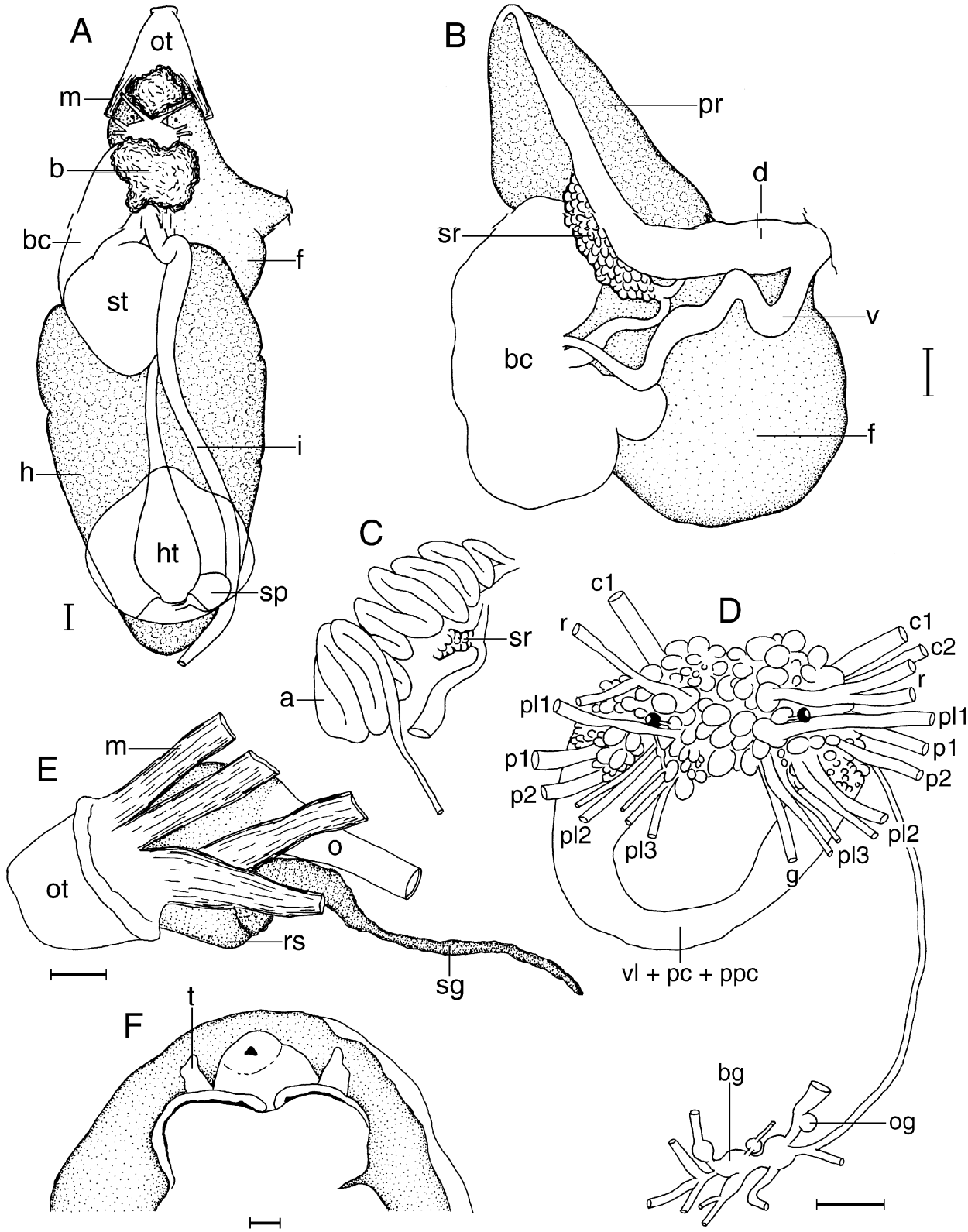

Figure 40. *Otinodoris* sp. (CASIZ 073238). A, general view of the anatomy; scale bar = 4 mm. B, reproductive system; scale bar = 5 mm. C, detail of several reproductive organs; scale bar = 5 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 4 mm. F, ventral view of the mouth area; scale bar = 5 mm.

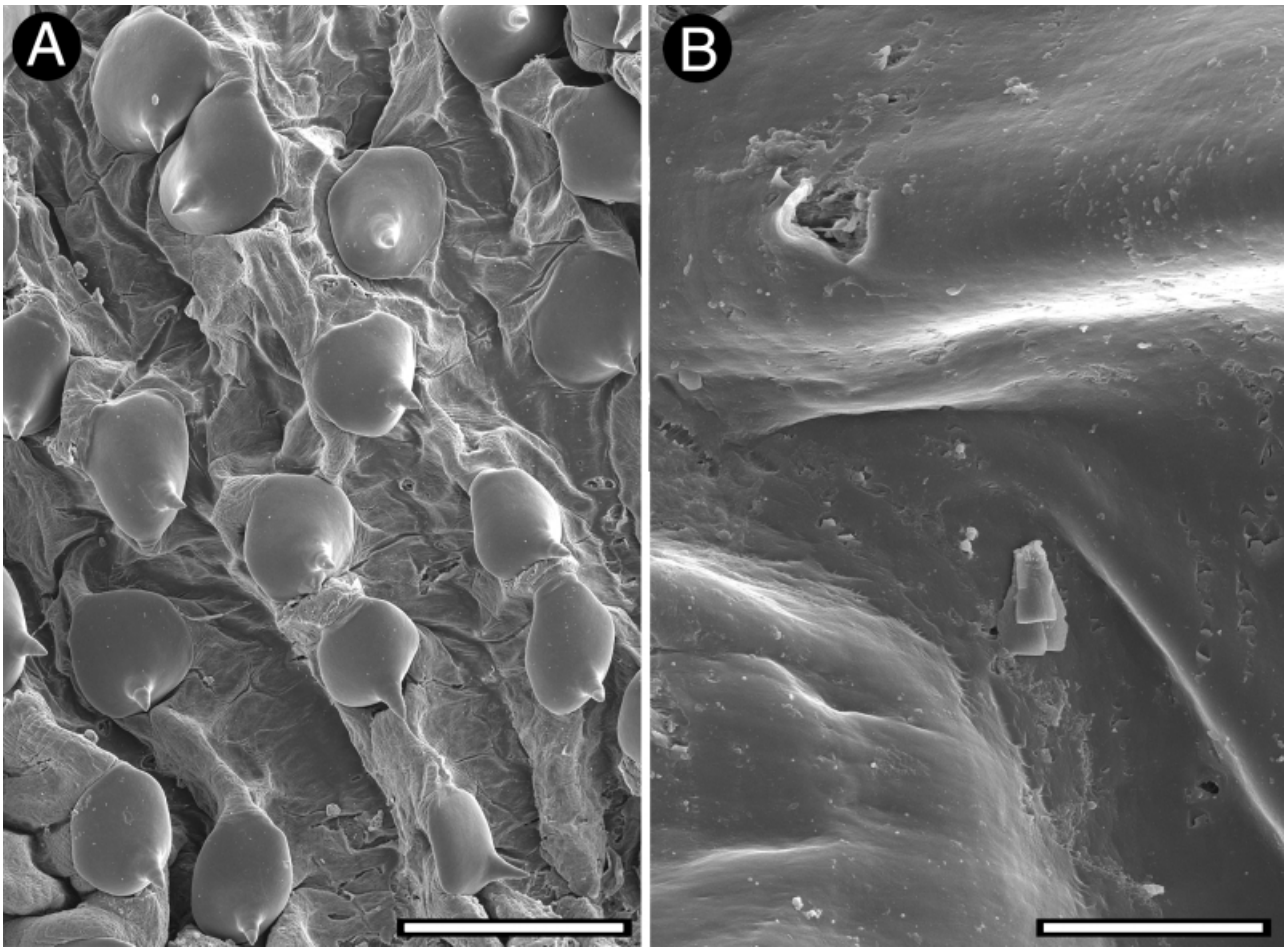

Figure 41. *Otinodoris* sp. (CASIZ 073238), SEM images of the penial hooks and vagina. A, penial hooks; scale bar = 500 μm. B, vaginal cuticular lining; scale bar = 100 μm.

features she described for this species (the presence of denticulate lateral teeth and auriculated oral tentacles), clearly distinguishes it from the species studied here, which has smooth teeth and lacks auriculated oral tentacles.

Otinodoris sp. clearly belongs to the genus *Otinodoris* by having flattened oral tentacles and the dorsum covered with long and ramified tubercles.

SEBADORIS ER. MARCUS & EV. MARCUS, 1960

Sebadoris Marcus & Marcus, 1960: 904–905. Type species: *Thordisa crosslandi* Eliot, 1904, by original designation.

Diagnosis

Dorsum covered with thick and soft papillae. Anterior border of the foot grooved and notched. Labial armature with jaws. Radula composed of simple, hamate teeth. Reproductive system with a flattened, granular prostate, having two well differentiated regions. Penis and vagina devoid of hooks. Penis internally covered with irregular, soft lamellae. Vestibular or accessory glands absent.

Remarks

Marcus & Marcus (1960) introduced the genus *Sebadoris* based on *Thordisa crosslandi* Eliot, 1904. According to these authors, *Sebadoris* is a 'discodorididae in the sense of Odhner', whose notum has papillae of different sizes, some of them rounded and some pointed. Other diagnostic features are: oral tentacles with finger shape, anterior border of the foot grooved and notched, branchial leaves tripinnate, jaws armed with two areas of elements, radula without rachidian teeth and with hamate lateral teeth; prostate clearly differ-

entiated from the deferent duct; penis spiral, with two longitudinal series of spines; bursa copulatrix and seminal receptacle arranged serially. All these characteristics are also present in other species of *Discodoris*, with the exception of the complex dorsal morphology with soft papillae and the spiral penis with two longitudinal series of spines. A re-examination of specimens of the type species of *Sebadoris*, shows that the spines seen by Marcus & Marcus (1960) are internal folds in the penis and not hard structures. It is not clear whether *Sebadoris* is a synonym of *Discodoris*. A more detailed phylogenetic analysis of the *Discodoris* clade, with all the species included would solve this problem. In the meanwhile the genus *Sebadoris* is maintained as valid.

SEBADORIS NUBILOSA (PEASE, 1871) (FIGS 34C, 42, 43)

Doris nubilosa Pease, 1871b: 13–14, pl. 6.
Thordisa crosslandi Eliot, 1904: 368–369, pl. 32, fig. 3, pl. 33, figs 4–8.
Diaulula gigantea Bergh, 1905: 119–120, pl. 15, figs 11–16.

Type material
The type material of *Doris nubilosa*, collected from Huaheine Island, Society Islands, French Polynesia, is untraceable. The holotype of *Thordisa crosslandi*, collected from Chuaka, Zanzibar, could not be located at BMNH and is probably lost. The holotype of *Diaulula gigantea* could not be located at ZMUC and is also presumed lost.

Additional material
Reef flat South of Avera, Rututu Island, Austral Islands, French Polynesia, 28 January 1983, one specimen, 64 mm preserved length, leg. G. Paulay (CASIZ 071727)

External morphology
The background colour of the living animals is brownish grey (Fig. 34C). The dorsum is covered with large, dark grey, oval patches, which are larger in the centre of the dorsum. There are also numerous small opaque white spots. The rhinophores and gill are brownish grey with white apices. The dorsum is covered with soft, think and pointed papillae. Some of the papillae are larger than the rest, and have a elongate prolongation on the tip. Larger papillae are surrounded by several small ones (Fig. 42E). The rhinophoral and branchial sheaths have small papillae, similar to those on the rest of the dorsum. There are five tripinnate branchial leaves. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 25 lamellae in a 64-mm preserved length specimen.

Ventrally the anterior border of the foot is grooved and notched (Fig. 43F). The oral tentacles are conical. The colour of the underside of the mantle is yellowish cream, with a submarginal, dark brown band, surrounding the entire mantle margin and several dark brown, rounded spots irregularly arranged. There are also numerous opaque white spots. The foot sole is yellow with dark brown spots.

Anatomy
The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 43C), which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two long salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The labial cuticle is armed with a number of small rodlets. The radular formula is $54 \times 124.0.124$ in a 64-mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 42A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 42B). The outermost teeth are smaller and also lack denticles (Fig. 42C). The oesophagus is short and connects directly to the stomach.

The ampulla is long and convoluted (Fig. 43B). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is elongate. It has two different portions that are clearly distinguishable in colour and texture. The prostate connects with a long duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The penis is unarmed but internally covered with soft lamellae (Fig. 42D). The muscular deferent duct opens into a common atrium with the vagina. The vagina is wide and short. At its proximal end it joins the bursa copulatrix. From the bursa copulatrix leads another duct connecting to the uterine duct and the seminal receptacle (Fig. 43C). The bursa copulatrix is oval in shape, about three times as large as the elongate seminal receptacle.

In the central nervous system (Fig. 43D) the cerebral and pleural ganglia are fused and distinct from the pedal ganglia. The cerebral and pleural ganglia are entirely covered with large ganglionic tubercles. There are five cerebral nerves leading from the left cerebral ganglion and four from the right one, and three pleural nerves leading from each pleural ganglion. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are

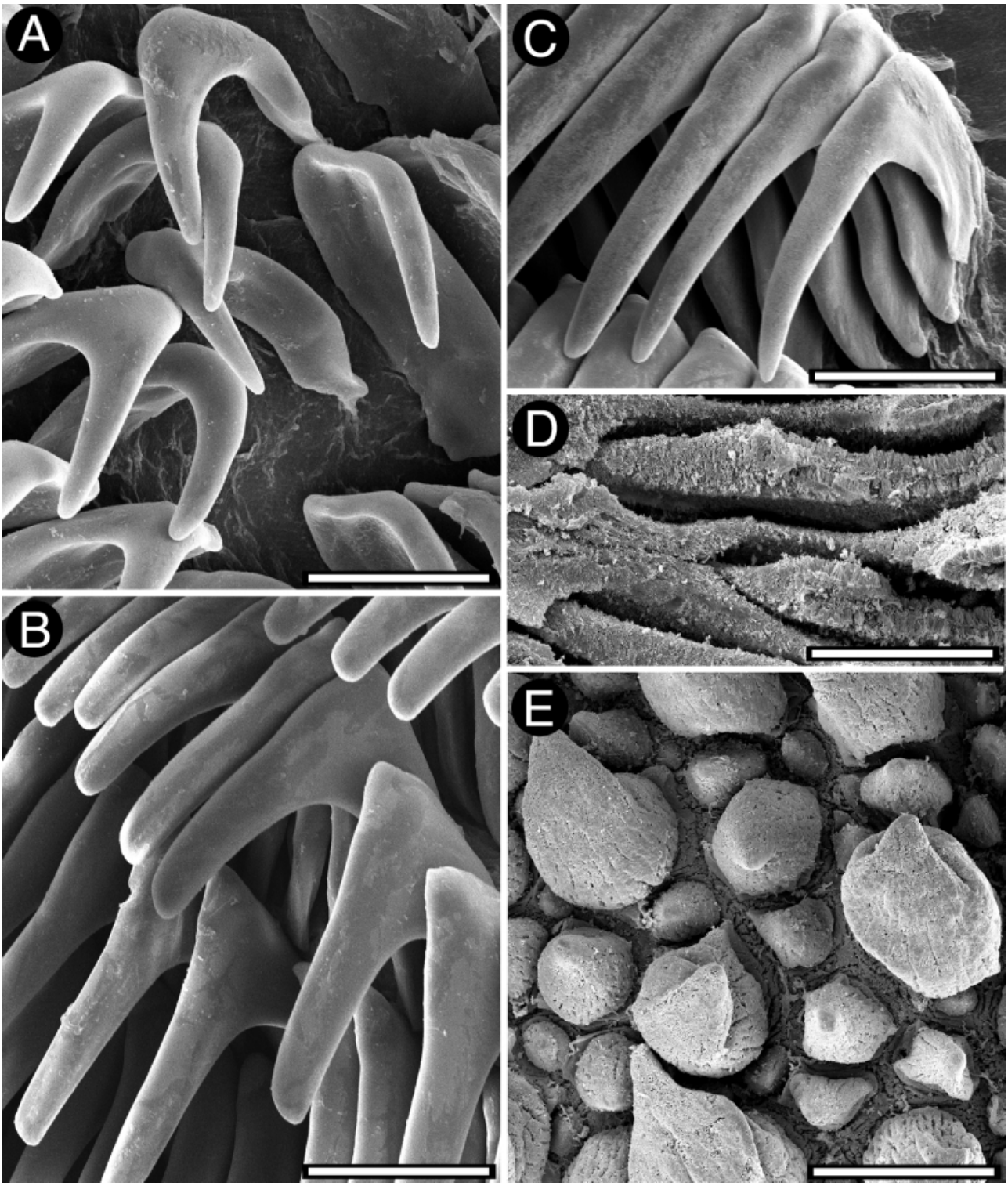

Figure 42. *Sebadoris nubilosa* (CASIZ 071727), SEM images of the radula, penis and dorsal papillae. A, inner lateral teeth; scale bar = 50 μm. B, mid-lateral teeth; scale bar = 75 μm. C, outer lateral teeth; scale bar = 43 μm. D, penial lamellae; scale bar = 100 μm. E, dorsal papillae; scale bar = 500 μm.

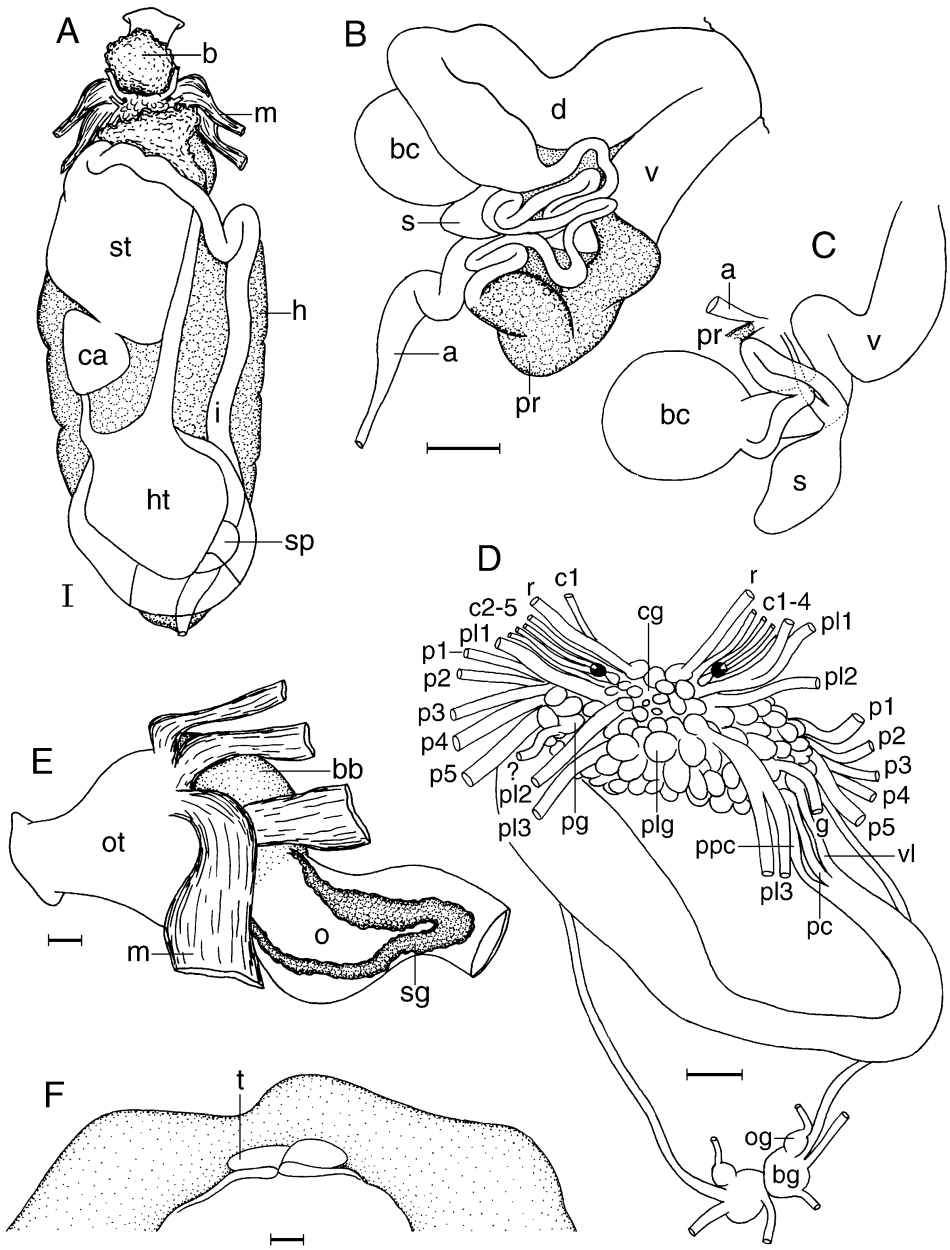

Figure 43. *Sebadoris nubilosa* (CASIZ 071727). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, detail of several reproductive organs; scale bar = 1 mm. D, central nervous system; scale bar = 1 mm. E, lateral view of the buccal bulb; scale bar = 1 mm. F, ventral view of the mouth area; scale bar = 1 mm.

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

The circulatory system (Fig. 43A) consists of a large heart and two blood glands situated in front of and behind the central nervous system.

Remarks

Pease (1871b) described *Doris nubilosa* from Huaheine Island, Society Islands, as large, flaccid, the dorsum covered with soft papillae, mottled with different shades of brown and grey, and with two dorsal longitudinal rows of cloud-like brown patches. The excellent colour illustration published by Pease (1871b: pl. 6) makes this species easy to recognize.

Eliot (1904) described *Thordisa crosslandi* based on several specimens collected from the East coast of

Africa. The living animals were described as follows: sandy with blotches of brown irregularly bordered with black; the underside whitish with numerous brownish spots and a brownish border; the dorsal tubercles thick-set pointed papillae, some of which are developed into distinct filaments at their extremities. Eliot (1904) studied the anatomy of several specimens and found the penis to be twisted spirally and provided with two rows of tubercles. He later (Eliot, 1910) suggested that *Thordisa crosslandi* could be a synonym of *Doris nubilosa* Pease, 1871.

Bergh (1905) described *Diaulula gigantea* as a brownish grey species with numerous lighter specks and large black patches; the dorsum covered with conical and rounded tubercles about 2 mm long; the underside yellowish with a dark brown band near to the border of the mantle and dark spots. All these features agree with the descriptions of *Doris nubilosa* and *Thordisa crosslandi*.

Marcus & Marcus (1960) redescribed *Thordisa crosslandi* from the Red Sea, and introduced the genus *Sebadoris* based on it, due to the particular shape of the penis. They considered the tubercles described by Eliot (1904), and also seen by themselves, to be penial spines.

Kay & Young (1969) and Edmunds (1971) regarded *Thordisa crosslandi* and *Diaulula gigantea* as synonyms of *Doris nubilosa* Pease, 1871. Kay & Young (1969) transferred this species to the genus *Archidoris*, whereas Edmunds (1971) maintained the usage of the genus name *Sebadoris*.

Soliman (1980) studied specimens of *Sebadoris crosslandi* from the Red Sea, and at the same time considered that this species differs from *Thordisa crosslandi* in texture and colour of the dorsum, radular teeth and reproductive system. According to Soliman (1980) these two nominal species could be different.

The anatomy and external morphology of the specimens studied by Eliot (1904), Bergh (1905), Kay & Young (1969), Edmunds (1971) and Soliman (1980) are identical to those of the material examined here, and there is no question that all of them belong to the same species.

GENUS *CONUALEVIA* COLLIER & FARMER, 1964

Conualevia Collier & Farmer, 1964: 381. Type species: *Conualevia marcusi* Collier & Farmer, 1964, by original designation.

Diagnosis

Dorsum covered with simple tubercles, stiffened by integumentary spicules, which do not protrude from the dorsal surface. Mantle glands present. Head with two lateral prolongations. Rhinophores almost smooth, with several irregular and inconspicuous lamellae. Anterior border of the foot grooved but not notched. Radula composed of simple, hamate teeth. Reproductive system with a tubular, granular and simple prostate. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

Collier & Farmer (1964) described the genus *Conualevia* as being different from other dorids due to the presence of smooth rhinophores. Other distinctive characteristics are the minutely papillose notum, the short oral tentacles (lateral prolongations), the radula without rachidian teeth, the absence of jaws and the penis unarmed. Internally, *Conualevia* is characterized by having a semiserial seminal receptacle, described by Collier & Farmer (1964) as an X pattern at the end of a long vaginal duct. Two species were originally introduced, *Conualevia marcusi* Collier & Farmer, 1964, the type species by original designation, and *C. alba* Collier & Farmer, 1964, both of them from the Pacific coast of North America.

Since then, no more species have been assigned to the genus *Conualevia*, which remained in use for these two species. The single synapomorphy of this genus is the presence of smooth rhinophores. According to the phylogenetic analysis carried out here, this appears to be a monophyletic group.

CONUALEVIA MARCUSI COLLIER & FARMER, 1964 (FIGS 34D, 44–46)

Conualevia marcusi Collier & Farmer, 1964: 381–383, fig. 1C–H, pl. 2.

Type material

HOLOTYPE (by original designation): 6 km south of Puertecitos, Baja California, Mexico 1963, 15 mm preserved length, leg. C. L. Collier (CASIZ 018370). PARATYPES: 6 km south of Puertecitos, Baja California, Mexico 1963, one specimen, 10 mm preserved length, leg. C. L. Collier (CASIZ 018371).

Additional material

Puerto Refugio, Isla Ángel de la Guarda, Baja California, Mexico 1963, one specimen, 18 mm preserved length, leg. C. L. Collier (CASIZ 018372). Centro de Aquicultura, Bahía Tortugas, Baja California Sur, 1 July 1984, one specimen, 10 mm preserved length, leg. T. M. Gosliner (CASIZ 071531). 80 km south of Puertecitos, Baja California, Mexico, 10 April 1973, two specimens, 8–9 mm preserved length, leg. G. McDonald (CASIZ 069116).

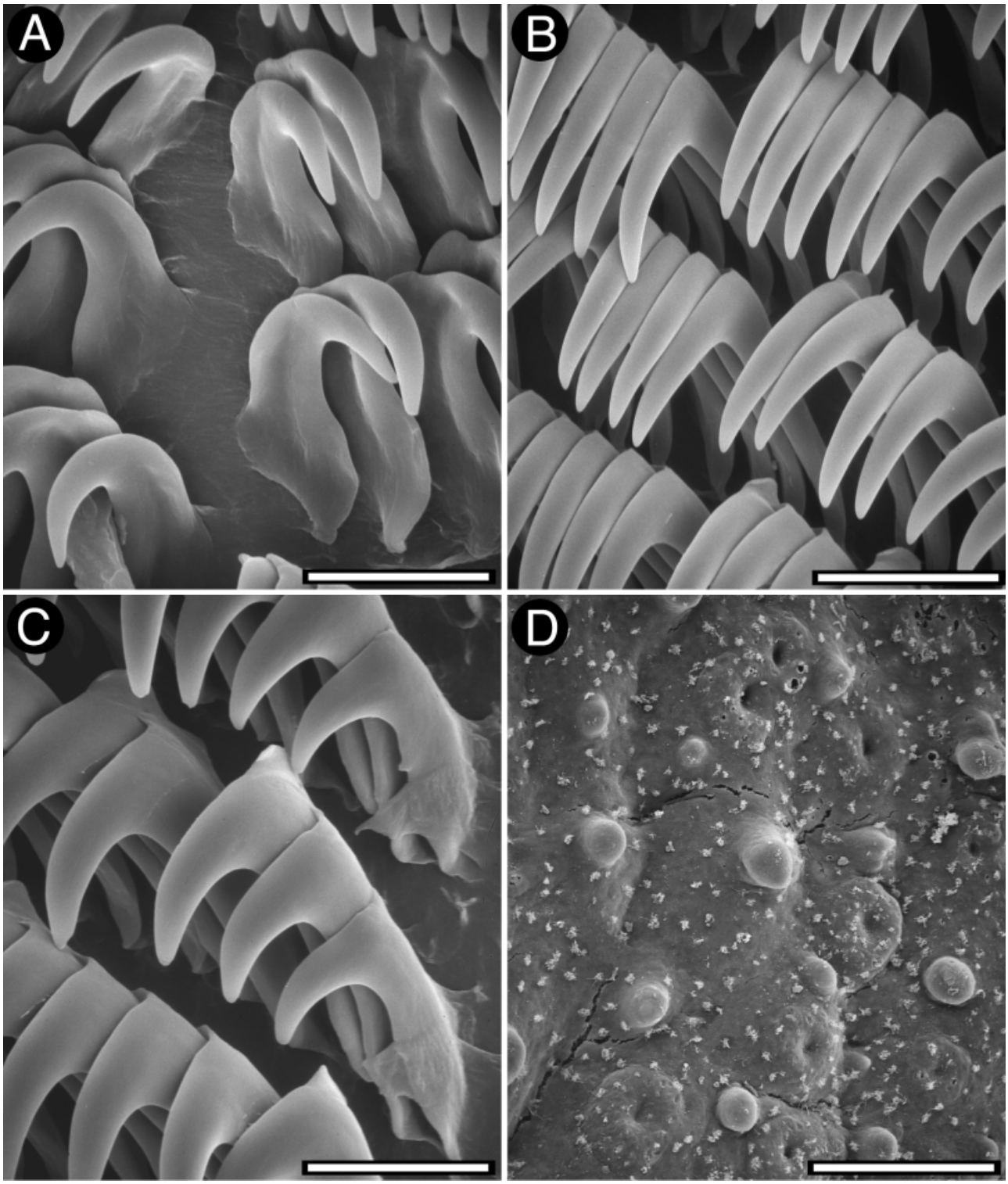

Figure 44. *Conualevia marcusi* (CASIZ 071531), SEM images of the radula and dorsal tubercles. A, inner lateral teeth; scale bar = 15 μm. B, mid-lateral teeth; scale bar = 25 μm. C, outer lateral teeth; scale bar = 20 μm. D, dorsal tubercles; scale bar = 150 μm.

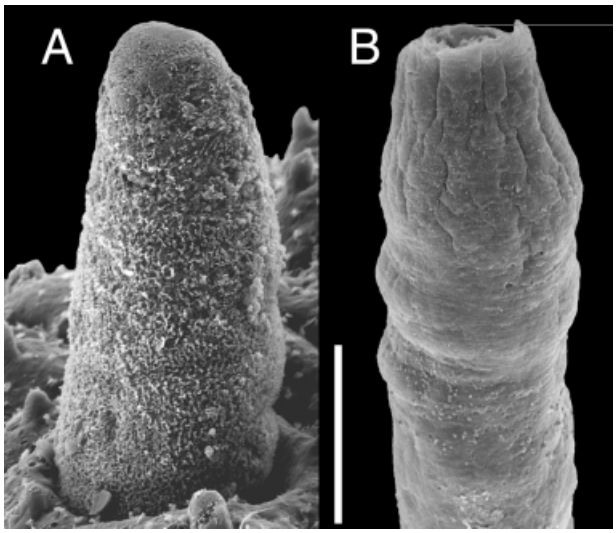

Figure 45. *Conualevia marcusi* (CASIZ 071531), SEM images of a rhinophore and the penis. A, rhinophore; scale bar = 150 μm. B, penis; scale bar = 150 μm.

External morphology

The general colour of the living animals is uniformly cream or pale yellow (Fig. 34D). The rhinophores and gill are yellow or cream, somewhat darker than the dorsum. The viscera are visible through the dorsal skin. The whole dorsum is covered with small, rounded tubercles (Fig. 44D). The largest tubercles are situated in the central region of the body. The rhinophoral and branchial sheaths have tubercles similar to those on the rest of the dorsum. There are seven unipinnate branchial leaves, forming a circle. The anal papilla is situated in the centre of the branchial circle of leaves. The rhinophores are elongate and almost smooth, with several irregular and inconspicuous lamellae (Fig. 45A).

Ventrally the anterior border of the foot is grooved but not notched (Fig. 45E). There are no oral tentacles, but two blunt prolongations on both sides of the mouth area.

Anatomy

The posterior end of the glandular portion of the oral tube has six strong retractor muscles (Fig. 46C) which attach to the body wall. The oval, muscular buccal bulb has two large additional muscles attached; two short salivary glands connect with it at each side of the oesophageal junction. The buccal bulb is longer than the glandular portion of the oral tube. The labial cuticle is smooth. The radular formula is $33 \times 51.0.51$ in a 10-mm long specimen. Rachidian teeth are absent. The lateral teeth are hamate and lack denticles (Fig. 44A). The teeth from the middle portion of the half-row are larger than those closer to the medial portion of the radula (Fig. 44B). The outermost teeth are smaller and also lack denticles (Fig. 44C). The oesophagus is short and connects directly to the stomach (Fig. 46A).

The ampulla is very long and folded (Fig. 46B). It branches into a short oviduct and the prostate. The oviduct enters the female gland mass near to its centre. The prostate is tubular and connects with a short duct that narrows and expands again into the large ejaculatory portion of the deferent duct. The penis is unarmed (Fig. 45B). The muscular deferent duct opens into a common atrium with the vagina. The vagina is long. At its proximal end it joins 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 twice as large as the seminal receptacle.

In the central nervous system (Fig. 46D) the cerebral and pleural ganglia are fused 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. There is no separate abdominal ganglion on the right side of the visceral loop. The buccal ganglia are near to the rest of the central nervous system, joined to the cerebral ganglia by two relatively short nerves. Gastro-oesophageal, rhinophoral and optical ganglia are present. The pedal ganglia are clearly separated, having two nerves leading from the left ganglion and three from the right one. The pedal and parapedal commissures are enveloped together with the visceral loop.

The circulatory system (Fig. 46A) consists of a large heart and a blood gland situated in front of the central nervous system.

Remarks

Conualevia marcusi appears to be different from *Conualevia alba*, the other member of the genus, by its external morphology and anatomy. According to Collier & Farmer (1964), *C. alba* is a much thinner animal than *C. marcusi*, and more delicate in appearance and the mantle glands of *C. alba* are more evident. In addition, the rhinophores of *C. alba* are longer relative to their width than those of *C. marcusi*, and *C. alba* has half as many branchial leaves as *C. marcusi*. Anatomically, the main difference between these two species is the arrangement of the bursa copulatrix and the seminal receptacle, which are on opposing sides in *C. marcusi* and on the same side in *C. alba*.

INCERTAE SEDIS

GENUS *ARTACHAEA* BERGH, 1882

Artachaea Bergh, 1882: 231. Type species: *Artachaea rubida* Bergh, 1882, by monotypy.

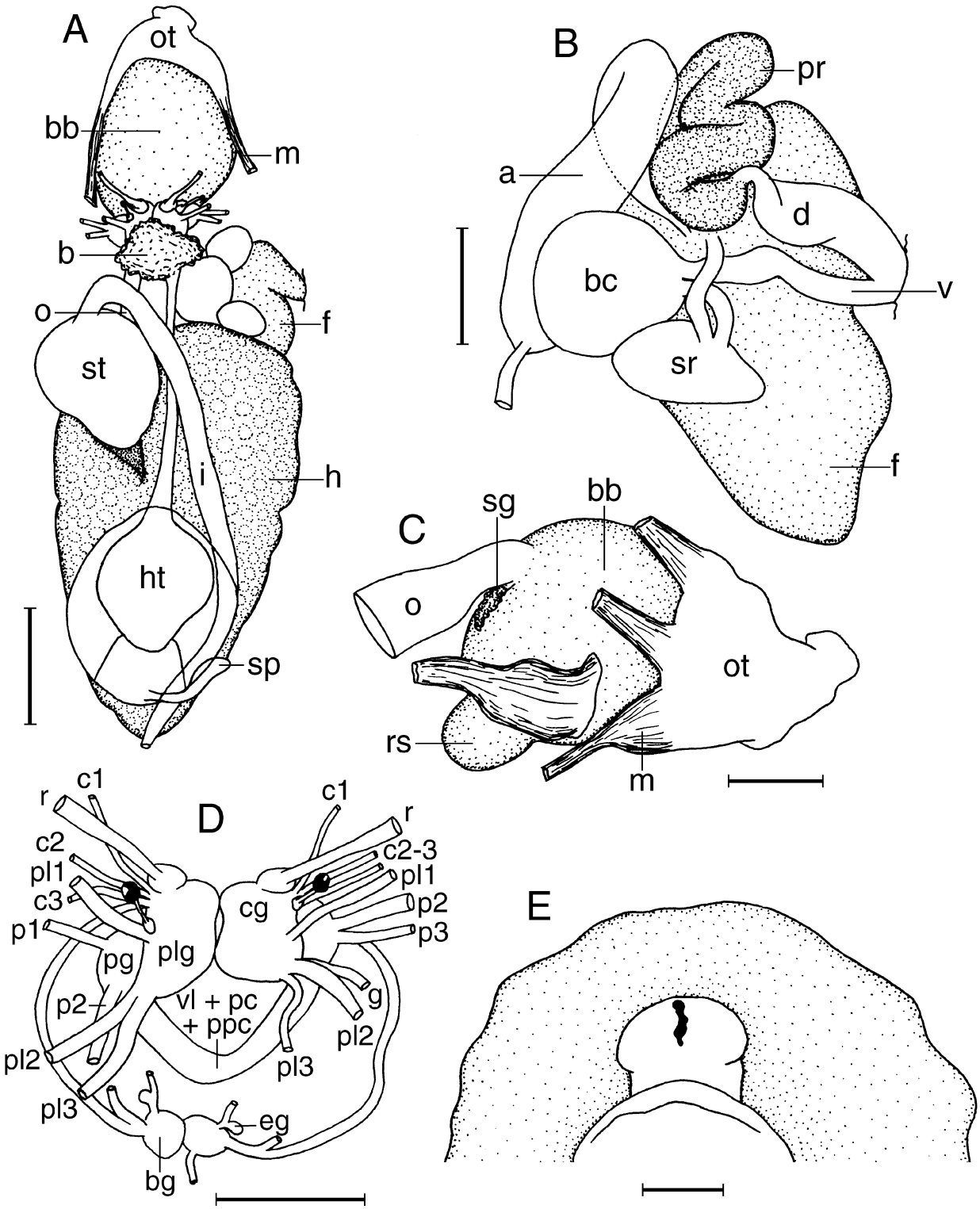

Figure 46. *Conualevia marcusi* (CASIZ 071531). A, general view of the anatomy; scale bar = 1 mm. B, reproductive system; scale bar = 1 mm. C, lateral view of the buccal bulb; scale bar = 0.5 mm. D, central nervous system; scale bar = 0.5 mm. E, ventral view of the mouth area; scale bar = 1 mm.

Remarks

The genus *Artachaea* was described by Bergh (1882) based on the new species *Artachaea rubida* Bergh, 1882. He defined this new genus as having a not too hard consistency and a coarsely granulated dorsum. The anterior border of the foot is rounded, and apparently simple, but there are oral tentacles. There are no jaws and the radular teeth are finely denticulate. The penis is armed with spines.

Bergh (1882) recognized the similarity of *Artachaea* with members of the genus *Cadlina* Bergh, 1878, but they are clearly differentiated by the presence of jaws. Unfortunately, the type material of *Artachaea rubida* is lost (K. Jensen, pers. comm.), and clarification of its systematic relationships is not possible. Eliot (1908) Eales (1938) and White (1950) assigned more species to this genus, some of them armed with copulatory spines.

GENUS *CARMINODORIS* BERGH, 1889

Carminodoris Bergh, 1889: 818. Type species: *Carminodoris mauritiana* Bergh, 1889, by monotypy

Remarks

Bergh (1889) introduced the genus *Carminodoris*, based on *Carminodoris mauritiana* Bergh, 1889. The diagnostic features of this genus are as follows: anterior border of the foot grooved and notched; dorsum covered with small tubercles; presence of jaws; hamate lateral teeth, denticulate outermost lateral teeth; large prostate and penis armed with hooks. All, with the exception of the penial hooks and denticulate outermost teeth, are present in the type species of *Discodoris*. These differences could be due to specific variation, but further detailed study, including anatomical investigation of *Carminodoris mauritiana*, is necessary before a definitive synonymization can be made. Meanwhile, *Carminodoris* is provisionally regarded as uncertain. Several authors (Thompson, 1975; Gosliner & Behrens, 1998) proposed that it could be a synonym of *Hoplodoris*; however, it lacks the latter's characteristic accessory glands with spines. Most of the Indo-Pacific species assigned to *Carminodoris* should probably be transferred to *Hoplodoris*, whereas the Atlantic species *Carminodoris boucheti* Ortea, 1979 and *Carminodoris spinobranchialis* Ortea & Martínez, 1992 fit the original description of the genus *Carminodoris* (see Ortea, 1979 and Ortea & Martínez, 1992).

The identity of the type species of *Carminodoris*, *C. mauritiana*, is the main obstacle to determining the phylogenetic relationships of this genus. Since its original description, *C. mauritiana* has not been collected again.

Eliot (1910) and Edmunds (1971) assigned specimens collected from the Solomon Islands and Tanzania to the species *C. mauritana*, which they included in the genus *Peltodoris*. However, the anatomy of their animals, which lack penial hooks and jaws and have simple hamate radular teeth, is very different from the original description of *C. mauritana*, described as having penial hooks, jaws and denticulate radular teeth. Marshall & Willan (1999) transferred *C. mauritiana* to the genus *Discodoris*, while retaining the name *Carminodoris* as valid for other species; however, they overlooked the fact that *C. mauritiana* is the type species of *Carminodoris*. The lack of anatomical description in their paper prevents a precise generic placement for their animals.

GENUS *HOMOIODORIS* BERGH, 1882

Homoiodoris Bergh, 1882: 222–223. Type species: *Homoiodoris japonica* Bergh, 1882.

Remarks

Bergh (1882) described *Homoiodoris*, based on *Homoiodoris japonica* Bergh, 1904, as very similar to *Archidoris*. *Homoiodoris* is characterized by having a depressed body with the dorsum covered with large tubercles. The tubercles around the rhinophoral and branchial sheaths are very large and apparently distinct from the rest. The oral tentacles are short and thick with a lateral groove. Internally, the labial cuticle is smooth and the radula is composed of simple hamate teeth, the prostate is large and the vagina is armed with hooks.

Homoiodoris appears to be very similar to *Doris*, but in the original description (Bergh, 1882), there is not enough information about other features of this genus, such as the shape of the anterior border of the foot, to permit a definitive conclusion. Unfortunately the type material of *Homoiodoris japonica* could not be located at ZMUC and is presumed lost. Major differences between *Homiodoris* and *Doris* are the presence of a large prostate and vaginal hooks in *Homoiodoris*.

Homoiodoris novaezelandiae (Bergh, 1904) is clearly a species of *Hoplodoris* (see above). There are no more species assigned to this genus.

UNAVAILABLE NAMES

XENODORIS ODHNER *IN* FRANC (1968)

Remarks

Odhner *in* Franc (1968) introduced the name *Xenodoris* with no description (*nomen nudum*). The genus was based on *Doris sordida* Rüppell & Leuckart, 1830 The original description of *D. sordida* (Rüppell &

Leuckart, 1828–30) includes a short description in Latin and German, but no drawings. The dorsum of this species is dark brown in colour, vaulted, covered with large tubercles that are brighter than the rest of the body, some of them red-brown. The six ramified branchial leaves are black-brown, with brighter borders. The skin is leathery and the mantle margin projects considerably over the foot. This description fits with the characteristics of *Asteronotus cespitosus* (van Hasselt, 1824), which is also found in the Red Sea, and it is very likely that *Xenodoris* is a synonym of *Asteronotus*.

Cryptodoris Ostergaard, 1950

Remarks

The name *Cryptodoris* was introduced by Ostergaard (1950) based on the description of the egg-mass of an unknown animal. No species name was included in the description and no type species was designated, therefore *Cryptodoris* is not available (ICZN, 1999: Article 13.3). A few years later Ostergaard (1955) described the new species *Doridopsis macfarlandi*; at the same time he mentioned that 'the structures of egg filament and veliger larva are figured and described in Ostergaard (1950: 108–109) under *Cryptodoris* sp'. According to Brodie, Willan & Collins (1997) *Doridopsis macfarlandi* is a synonym of *Dendrodoris nigra* (Stimpson, 1855); thus *Cryptodoris* is a synonym of *Dendrodoris* Ehrenberg, 1831.

PHYLOGENETIC ANALYSIS

Phylogenetic methods

In order to calculate the most parsimonious phylogenetic tree, data were analysed using the heuristic algorithm (TBR branch swapping option) in PAUP, version 4.0b4a (Swofford, 2000). In cases where a taxon had two states for a given character they were treated as uncertain. Both ACCTRAN and DELTRAN optimizations were used for character transformation. In both cases multistate characters were treated as unordered. One hundred random starting trees were obtained via stepwise addition.

Characters were polarized using the outgroup selection of the genera *Berthella* de Blainville, 1824 and *Bathydoris* Bergh, 1884, and subsequent analysis using PAUP. This selection was made on the basis of the papers by Wägele (1989b) and Wägele & Willan (2000), which showed that the Pleurobranchoidea (in which *Berthella* is included) are the sister group to the Nudibranchia and *Bathydoris* the sister group to the rest of the dorids. Information on *Berthella* and *Bathydoris* was obtained from the literature (Wägele, 1989a; Cervera *et al*., 2000).

A Bremer 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. Synapomorphies were obtained using the character trace option in MacClade 3.08a (Maddison & Maddison, 1999). See Kitching *et al*. (1998) for a thorough explanation of these methods and their advantages.

Taxa

Fifty-one taxa were considered for the phylogenetic analysis. They included the majority of the described cryptobranch dorid genera, even where these have been regarded as synonyms in the present study. However, most chromodorid genera were excluded. The systematics of the Chromodorididae was thoroughly revised by Rudman (1984) and its phylogenetic relationships reconstructed by Gosliner & Johnson (1999). The genus *Cadlina*, which belongs to the most basal clade of the Chromodorididae (Gosliner & Johnson, 1999), and *Chromodoris*, which is a more derived chromodorid and the type genus of the family, have been selected here to represent the rest of the group. Information on chromodorids was obtained from Rudman (1984) and Gosliner & Johnson (1999). Other dorid taxa not treated extensively in the present paper but included in the phylogenetic analysis were the radula-less and caryophyllidia-bearing dorids (revised by Valdés & Gosliner, 1999, 2001). Finally, data on the recently described deep-sea taxa *Goslineria* and *Pharodoris* were extracted from Valdés (2001).

Objective synonyms or long established synonyms have been excluded from the analysis. Those uncertain taxa where detailed information was not available, such as *Fracassa* Bergh, 1878, *Artachaea* Bergh, 1882, *Homoiodoris* Bergh, 1882, *Phialodoris* Bergh, 1889, *Carminodoris* Bergh, 1889, *Erythrodoris* Pruvot-Fol, 1933, *Nuvuca* Ev. Marcus & Er. Marcus, 1967 and *Pupsikus* Er. Marcus & Ev. Marcus, 1970, were not included in the analysis, but in most cases their synonymy with other valid senior taxa was established on the basis of anatomical data.

At this stage in the study of the phylogenetic relationships of the cryptobranch dorids, there are few detailed phylogenies available for most taxa down to the level of species. These would allow us to identify the most basal members of each genus and their subsequent inclusion in the phylogenetic analysis. Due to the lack of data, this study is based on information extracted from the type species of each nominal genus and in some cases additional species reflecting the anatomical variability of each genus. For genera in which material of the type species was not available,

Table 3. Other species of phanerobranch dorids included in the analysis with their sources of information

Species	Locality	Museum number
Onchidoris bilamellata (Linnaeus, 1767)	Elkhorn Slough, California	CASIZ 070511
Diaphorodoris luteocinta (Sars, 1870)	Ilha São Miguel, Azores	CASIZ 072580
Aegires albopunctatus MacFarland, 1905	Point Reyes, California	CASIZ 072857
Calycidoris guntheri Abraham, 1876	Wainwright, Alaska	CASIZ 086915

another species which appeared to be basal within that genus was used in the phylogenetic analysis.

Some phanerobranch dorid genera have been included in the analysis for comparative proposes. They include *Onchidoris* J. E. Gray, 1840, *Diaphorodoris* Iredale & O'Donoghue, 1923, *Calycidoris* Abraham, 1876, *Aegires* Lovén, 1844 and *Hexabranchus* Ehrenberg, 1831. Information on these genera was obtained from the study of museum material. Table 3 summarizes the sources of information for these taxa except for *Hexabranchus*, which is described in the text.

CHARACTERS

The characters used to resolve the phylogeny of the cryptobranch dorids are detailed below. They reflect a wide range of morphological and anatomical features of the taxa involved. Fifty-nine characters are coded as binary and 20 characters 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 4.

1. *Body shape*: in *Berthella* and *Bathydoris* the body is elevated with a large dorsal hump (0). Phanerobranch and cryptobranch dorids have a more flattened body (1).
2. *Mantle margin*: in *Berthella*, *Bathydoris* and the majority of the phanerobranch dorids including *Aegires* this is a narrow rib (0), whereas it is wide in *Onchidoris*, *Calycidoris*, *Hexabranchus*, and most cryptobranch dorids (1).
3. *Rhinophore position*: in *Berthella* the rhinophores are placed anteriorly, beneath the mantle margin (0). In contrast, in both cryptobranch and phanerobranch dorids they are in a dorsal position (1).
4. *Rhinophore shape*: in *Berthella* the rhinophores are rolled (0), whereas in dorids they are solid (1).
5. *Rhinophore lamellae*: in *Berthella* and *Aegires* the rhinophores are smooth (0), whereas in *Bathydoris* and most of the dorids they have transversal or longitudinal lamellae (1). In *Conualevia*, the rhinophores appear to be smooth, but examination with SEM (Fig. 45A) reveals several irregular and inconspicuous lamellae (2).
6. *Shell*: *Berthella* has an internal shell (0), which is absent in dorids (1).
7. *Integumentary spicules*: the bodies of *Berthella*, *Bathydoris* and most of the dorids are stiffened with a network of integumentary spicules, more or less densely arranged (0). In several groups, such as *Hexabranchus*, *Actinocyclus*, *Chromodoris*, *Aphelodoris* and *Dendrodoris*, these spicules are absent (1).
8. *Spicule size*: *Berthella*, *Bathydoris*, phanerobranch and most cryptobranch dorids including *Mandelia* have small spicules, never longer than 400 μm (0). In *Doriopsilla* and phyllidiids some spicules are very large, over 600 μm long (1) (see Valdés & Gosliner, 1999). In species without spicules this character is treated as not applicable.
9. *Mouth morphology*: externally, the buccal area in *Berthella*, *Bathydoris* and phanerobranch dorids has a wide protuberance called the velum, usually bearing large velar or oral tentacles (0). In cryptobranch dorids the buccal area is narrow and the oral tentacles, if present, are small (1). In radulaless dorids the mouth is reduced to a pore (2), and the oral tentacles, if present are very small (see Valdés & Gosliner, 1999).
10. *Labium*: in cryptobranch dorids, the anterior edge of the foot has a labium (1), which in some cases can be notched. This labium is absent in *Berthella*, *Bathydoris* and phanerobranch dorids (0).
11. *Labium notch*: a group of cryptobranch dorids including the caryophyllidia-bearing dorids and *Discodoris*, *Peltodoris*, *Geitodoris*, *Thordisa*, *Hoplodoris*, *Paradoris* and others have a notched labium (1); in the remainder it is not notched (0). In species lacking a labium this character has been treated as not applicable.
12. *Foot corners*: in *Berthella* the anterior border of the foot has two lateral prolongations (0) that are absent in all dorids, including *Bathydoris* (1).
13. *Mouth position*: the mouth opens anteriorly in *Berthella*, *Armina*, *Bathydoris*, phanerobranch

Table 4. Data matrix of character states in the taxa involved in the phylogenetic analysis. 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	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79
Berthella	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	?	0	?	?	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	1	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Bathydoris	0	0	1	1	1	1	0	0	0	0	?	1	0	0	0	0	0	1	0	1	0	0	0	0	?	0	1	0	0	0	1	0	0	0	0	0	0	2	1	0	0	1	0	0	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	?	?	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Onchidoris	1	1	1	1	1	1	0	0	0	0	?	1	0	1	?	?	0	1	0	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	2	2	2	0	0	?	?	?	?	0	0	0	1	0	0	0	0	1	1	0	?	?	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Diaphorodoris	1	1	1	1	1	1	0	0	0	0	?	1	0	1	?	?	0	1	0	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	2	2	2	0	0	?	?	?	?	0	0	0	1	0	0	0	0	1	1	0	?	?	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Calycidoris	1	1	1	1	1	1	0	0	0	0	?	1	0	1	?	?	0	1	0	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	1	2	2	2	0	0	?	?	?	?	0	0	0	1	0	0	0	0	1	1	0	?	?	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Aegires	1	0	1	0	2	1	0	0	0	0	?	1	0	0	0	0	0	1	0	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	0	?	?	0	?	0	0	0	0	0	0	0	0	1	1	0	0
Hexabranchus	1	1	1	1	1	1	1	?	0	0	?	1	0	0	0	0	0	0	?	0	0	?	?	?	?	0	1	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	0	?	?	0	?	0	0	0	0	0	0	0	0	1	1	0	1
Actinocyclus	1	1	1	1	1	1	1	?	1	1	0	1	0	1	?	?	0	1	0	0	0	0	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	0	?	?	?	?	0	0	0	1	0	0	0	2	2	1	1	0	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Cadlina	1	1	1	1	1	1	0	0	1	1	0	1	0	0	1	2	0	1	0	0	0	1	0	0	?	1	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	?	?	?	?	0	0	0	1	0	0	0	0	2	1	1	1	0	0/1	0	0	1	0	0	0	0	1	0	1	1	0	0
Chromodoris	1	1	1	1	1	1	1	?	1	1	0	1	0	0	0	1	0	0/1	0	0	0	0	0	0	?	1	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	?	?	?	?	0	0	0	1	0	0	0	0	2	1	1	1	0	0/1	0	0	1	0	0	0	0	1	0	1	1	0	0
Aphelodoris	1	1	1	1	1	1	1	?	1	1	0	1	0	2	1	2	0	0	?	0	0	?	?	?	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Doris	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	2	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Siraius/Doriorbis	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1/3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	2	1	1	0	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Archidoris	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1/3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	2	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Austrodoris	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	2	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Doriopsis	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	1	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	2	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Thordisa	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0/1	?	0	0	2	1	0	1	1	0	1	1	0	0
Peltodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Montereina	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Otinodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	2	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	0	1	1	0	1
Geitodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	2	0/2	0	1	1	0	1	1	0	0
Discodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Sebadoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Tayuva	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Hoplodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	2	1	0	1	1	0	1	1	0	0
Conualevia	1	1	1	1	2	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	1	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	0	0	?	0	0	0	0	0	0	1	0	1	1	0	0
Aldisa	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	3	3	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	0	0/1	0	0	0	0	0	0	0	1	0	1	1	0	0
Paradoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	2	0/1	0	1	1	0	1	1	0	0
Pharodoris	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	0	0	?	0	0	1	1	0	0	1	0	1	1	0	0
Goslineria	1	1	1	1	1	1	0	0	1	1	0	1	0	2	1	2	0	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	0	0	?	0	0	1	1	0	0	1	0	1	1	0	0
Asteronotus	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	1	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	2	1	0	1	1	0	1	1	0	1
Halgerda	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	1	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0/2	0	0	1	1	0	1	1	0	0
Diaulula	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Atagema	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	1	0	0	1	2	1	2	0	1	1	1	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Jorunna	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	1	1	1	0	0	1	1	0	0	0	1	0	0	2/3	0	0	0	0	1	1	1/3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	3	1	0	1	1	0	1	1	0	0
Platydoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1/3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	3	0	0/1	1	1	0	1	1	0	0
Rostanga	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	2/3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Gargamella	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	3	0	1	1	1	0	1	1	0	0
Baptodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	3	0	1	1	1	0	1	1	0	0
Alloiodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	1	0	1	1	0	0
Sclerodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	1	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	3	0	0	1	1	0	1	1	0	0
Taringa	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	3	0	0	0	0	1	1	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0	?	1	0	0	0	0	1	1	0	1	1	0	0
Thorybopus	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	0	0	0	0	0	1	1	0	1	1	0	0
Nophodoris	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	2/3	0	0	0	0	1	1	3	0	0	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	1	0/1	0	0	0	3	0/3	0	1	1	0	1	1	0	0
Mandelia	1	1	1	1	1	1	0	0	2	1	0	1	1	1	?	?	3	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	0	0	0	1	0	1	?	1	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0	0	?	0	0	0	0	0	0	0	1	1	1	2	0
Doriopsilla	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	3	1	0	0	0	1	0	0	?	0	1	1	0	0	1	1	1	0	1	1	0	1	?	1	?	?	?	?	?	?	1	1	0	0	0	0	1	1	0/1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	2	0
Dendrodoris	1	1	1	1	1	1	1	?	2	1	0	1	1	1	?	?	3	0/1	0/1	0	0	0	0	0	?	0	1	1	0	0	1	1	0	0	1	1	0	1	?	1	?	?	?	?	?	?	1	1	0	0	1	1	2	0	1	1	1	1	0	0	1	1	1	1	0	0/1	1	0	0/1	0	0	0	0	0	1	1	1	2	1
Phyllidiopsis	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	3	1	1	0	1	1	0	0	?	0	2	?	?	1	1/2	1	1	0	1	1	0	1	?	1	?	?	?	?	?	?	1	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0
Phyllidia	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	1	1	1	0	1	1	0	0	?	0	2	?	?	1	1	1	0	1	2	2	0	1	?	1	?	?	?	?	?	?	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0
Phyllidiella	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	1	1	1	0	1	1	0	0	?	0	2	?	?	1	1	1	0	1	2	2	0	1	?	1	?	?	?	?	?	?	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0
Ceratophyllidia	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	2	1	1	0/1	1	0/1	0	0	?	0	2	?	?	1	1	1	1	0	1	1	0	1	?	1	?	?	?	?	?	?	1	1	0	0	1	1	1/2	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0
Reticulidia	1	1	1	1	1	1	0	1	2	1	0	1	1	1	?	?	1	1	1	0	1	1	0	0	?	0	2	?	?	1	1	1	0	1	2	2	0	1	?	1	?	?	?	?	?	?	1	1	1	2	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0

dorids and most cryptobranch dorids (0). However, in the radula-less dorids the mouth opens more posteriorly (1), in a notch of the anterior border of the foot (see Valdés & Gosliner, 1999).

14. *Oral tentacles*: *Berthella*, *Bathydoris* and most phanerobranch and cryptobranch dorids have a pair of oral tentacles, situated at the base of the mouth area, which may vary in shape and size (0). In phanerobranch dorids they are usually called velar tentacles, and are probably homologous with the oral tentacles of cryptobranch dorids (0). Some species of phanerobranch and cryptobranch dorids (including the radula-less dorids) lack them (1). In some cryptobranch dorids they are situated more anteriorly, at both sides of the mouth area (2).
15. *Oral tentacles shape*: elongate in most cryptobranch dorids as well as *Berthella* and *Bathydoris* (0), blunt prolongations in others (1).
16. *Oral tentacles size*: large in *Berthella*, *Bathydoris* and the phanerobranch dorids included in the analysis (0), small conical appendages (1) or very reduced prolongations (2) in most cryptobranch dorids. In species with no oral tentacles this character has been treated as non-applicable.
17. *Mouth anterior prolongations*: radula-less dorids have anterior prolongations in the mouth area that are absent in other dorids and *Berthella* (0). They have been assumed to be homologous with the oral tentacles of other dorids (Brunckhorst, 1993; Valdés & Gosliner, 1999) but they are here regarded as a different structure to test their homology. They are separate in *Phyllidia*, *Phyllidiella* and *Reticulidia* (1), partially fused in *Ceratophyllidia* (2) and completely fused in *Phyllidiopsis*, *Doriopsilla*, *Dendrodoris* and *Mandelia* (3) (see Valdés & Gosliner, 1999).
18. *Dorsal tubercles*: absent in most of the species of *Berthella*, *Chromodoris* and *Dendrodoris*, as well as all the species of *Hexabranchus* and *Aphelodoris* (0); present in most phanerobranch and cryptobranch dorids (1).
19. *Dorsal tubercle general shape*: may be simple (0) as in phanerobranch and cryptobranch dorids, compound (1) as in *Atagema* and some species of *Dendrodoris*, or ramified (2) as in *Otinodoris winckworthi* White, 1948.
20. *Dorsal tubercle texture*: in *Bathydoris*, *Thordisa* and *Sebadoris* the dorsal tubercles are soft, probably filled with fluids (1), whereas in the rest of the dorids they are solid and contain supporting spicules (0).
21. *Dorsal ridges*: absent in *Berthella*, *Bathydoris*, phanerobranch dorids and most species of cryptobranch dorids (0); present in *Asteronotus*, *Halgerda* and the Phyllidiidae (1).
22. *Tubercular spicules*: in most dorids the dorsal tubercles are stiffened by spicules (0), but *Bathydoris*, *Actinocyclus*, the tuberculated species of *Dendrodoris* and one species of *Ceratophyllidia* (*C. africana*) lack them (1). The absence of spicules in the tubercles appears not to be related to the absence of integumentary spicules in the rest of the body, as *C. africana* has a strong network of spicules in the dorsum.
23. *Tubercular spicules arrangement*: in the majority of tuberculated species the surface of the tubercles is smooth or the spicules protrude in an irregular pattern (0) (Fig. 47A–C). However, the caryophyllidia-bearing dorids, such as *Diaulula*, *Atagema*, *Jorunna*, *Platydoris*, *Rostanga*, *Gargamella*, *Baptodoris*, *Alloiodoris*, *Sclerodoris*, *Taringa*, *Thorybopus* and *Nophodoris*, exhibit a regular ring of spicules protruding near to the apex of each tubercle (1) (Fig. 47D).
24. *Ciliated tubercle*: the tubercles of most dorids have small groups of cilia irregularly scattered on their surface (0), but in the caryophyllidia-bearing dorids these groups are joined together on the apex of the tubercle, forming a large ciliated area (1), hence ciliated tubercle.
25. *Lateral cilia*: in *Rostanga*, *Diaulula* there are small lateral ciliated areas between spicules (1). Lateral cilia are also present in *Atagema*, but forming large protuberances (2). These ciliated areas are absent in the rest of the caryophyllidia-bearing dorids (0). This character is treated as not applicable for species lacking caryophyllidia.
26. *Mantle glands*: these are defensive organs situated in the mantle margin of species of chromodorididae (*Cadlina*, *Chromodoris*) (1). They also called Mantle Dermal Formations (García-Gómez *et al.,* 1990, 1991; Wägele, 1998) and are absent in most other cryptobranch dorids (Ávila & Durfort, 1996). The genera *Conualevia* and *Jorunna* also have small glandular structures situated around the mantle margin (1). Most phanerobranch dorids, *Berthella* and *Bathydoris* lack mantle glands (0). Wägele (1998) included under the same name the defensive structures present in *Limacia clavigera*, but due to the large phyletic distance between *Limacia* and the Chromodorididae, it is very unlikely that these structures are homologous with the mantle glands.
27. *Gill morphology*: the gill of *Berthella* is situated laterally (0). *Bathydoris*, the phanerobranch dorids and the majority of the cryptobranch dorids have a posterodorsal gill formed by several branched leaves (1). In Phyllidiidae the gill is absent (2).
28. *Gill protection*: in *Berthella*, *Bathydoris* and phanerobranch dorids the gill is contractile (0),

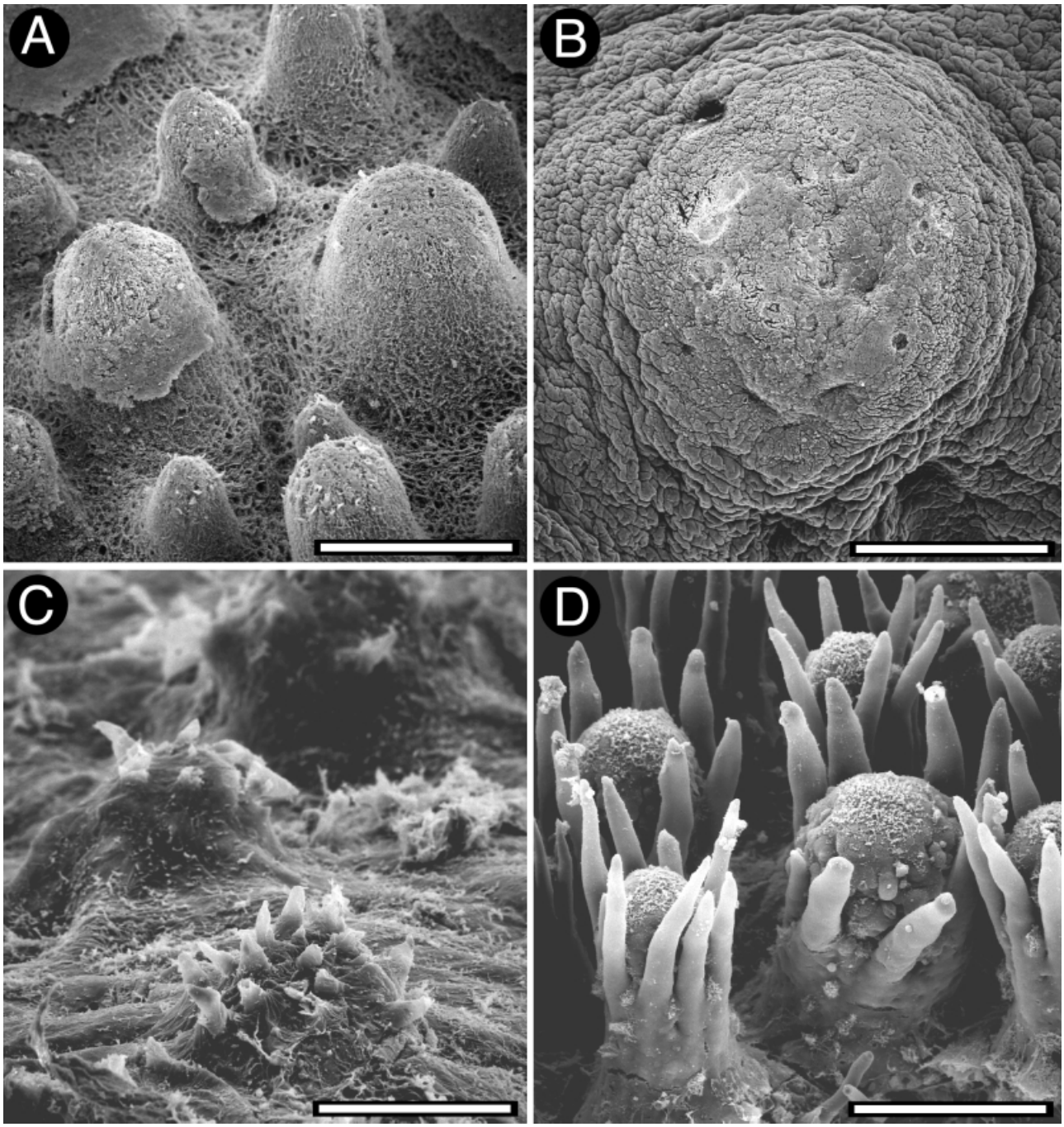

Figure 47. SEM images of dorsal tubercles. A, *Onchidoris bilamellata* (CASIZ 070511); scale bar = 430 μm. B, *Actinocyclus verrucosus* (CASIZ 099250), scale bar = 600 μm. C, *Discodoris boholiensis* (CASIZ 083654); scale bar = 150 μm. D, *Diaulula sandiegensis* (CASIZ 068277); scale bar = 250 μm.

whereas in cryptobranch dorids it is retractile into a cavity (1).

29. *Dorsal gill arrangement:* in *Bathydoris*, phanerobranch dorids and most cryptobranch dorids the gill emerges vertically from the branchial sheath (0), but in *Atagema* and some species of *Doris*, formerly united as *Doriopsis*, it is dorsally protected by a large lobe and it emerges horizontally (1).
30. *Ventral respiratory leaves*: the respiratory function in phyllidiids is carried out by numerous

triangular-shaped respiratory plates arranged in ventral position, between the foot and the mantle margin (1). In *Berthella*, *Bathydoris*, phanerobranch and other cryptobranch dorids respiratory leaves are absent (0).

31. *Anus opening*: in *Berthella* the anus opens on the lateral surface of the body (0), whereas in *Bathydoris*, phanerobranch and cryptobranch dorids the anus is always posterior, and either dorsal (1) or ventral (2) to the mantle rim (1).
32. *Cavity around the anus*: around the anus of the cryptobranch dorids there is a cavity into which the branchial leaves can be retracted (1). This cavity also exists in phyllidiids, even though the gill has been lost. Because both cavities occupy the same position and have a similar shape, I consider them homologous. This cavity is absent in *Bathydoris* and phanerobranch dorids (0).
33. *Buccal bulb shape*: for the present analysis, I consider that the buccal bulb of dendrodorids and phyllidiids is homologous with that of *Berthella* and other dorids despite the fact that there is no radula inside. Two states have been included for this character. An oval buccal bulb, more or less elongate, is present in most of the species included in the analysis (0), whereas species of *Phyllidiopsis* and *Ceratophyllidia* have a very elongate buccal bulb (1).
34. *Buccal bulb opening*: in phanerobranch and most cryptobranch dorids, as well as in *Berthella* and *Bathydoris*, the buccal bulb connects to the oesophagus posteriorly (0), whereas in *Phyllidia*, *Reticulidia* and *Phyllidiella* the oesophageal connection has migrated to the dorsal region of the buccal bulb (1).
35. *Position of the buccal bulb muscles*: the retractor muscles associated with the buccal bulb are very variable in size and arrangement within dorids. In *Berthella*, *Bathydoris*, *Mandelia*, phanerobranch and cryptobranch dorids the muscles are inserted laterally on the buccal bulb (0), whereas in *Dendrodoris*, *Doriopsilla*, *Phyllidiopsis* and *Ceratophyllidia*, they insert posteriorly (1). In *Phyllidia*, *Phyllidiella* and *Reticulidia*, they are attached anteriorly (2).
36. *Number of oral tube and buccal bulb muscles*: in *Berthella*, *Bathydoris* and phanerobranch dorids, the buccal bulb and oral tube have numerous small muscles (0). In most cryptobranch dorids the number of muscles has been reduced to three or four pairs of large muscles on the oral tube and one pair attached to the posterior side of the buccal bulb (1). In dendrodorids and phyllidiids the transformation of the foregut for suctorial feeding has involved large transformations in the associated muscles of the buccal bulb, and two different forms can be recognized. *Phyllidia*, *Phyllidiella* and *Reticulidia* have two very large muscles attached to the anterior region of the buccal bulb (2). In *Phyllidiopsis*, *Doriopsilla*, *Ceratophyllidia*, *Mandelia* and *Dendrodoris* two or more small muscles are present in the posterior end of the buccal bulb (1), which is similar to that of other cryptobranch dorids.
37. *Buccal pump*: this muscular structure uniquely characterizes a group of several phanerobranch dorids called Suctoria, including *Calycidoris* and *Onchidoris*, which use it for suctorial feeding of Bryozoa and Tunicata (1). It is absent in *Berthella*, *Bathydoris*, cryptobranch and most other phanerobranch dorids (0).
38. *Labial cuticle*: this hard structure is present in all cryptobranch and phanerobranch dorids as well in *Bathydoris* and *Berthella* (0), but it is absent in both dendrodorids and phyllidiids (1).
39. *Jaws*: areas of the labial cuticle covered with numerous elements having different shapes and sizes. The jaws of *Berthella* have numerous complex elements with lateral denticulation (0). In *Bathydoris* there are no jaws but the labial armature is composed of a pair of thick, chitinous structures (1). In other dorids the jaws are composed of elements with different shapes and sizes (2) or are absent, the labial cuticle being smooth (3).
40. *Radula*: *Berthella*, *Bathydoris* and most dorids and gastropods generally have a radula (0), which is an essential instrument in feeding. However this structure is lost in Dendrodorididae and Phyllidiidae (1).
41. *Radular teeth number*: two states are recognized for this character. The radulae of *Berthella*, *Bathydoris*, *Aegires* and *Hexabranchus* and cryptobranch dorids have many small teeth (0), whereas in most phanerobranch dorids there are normally only a few large teeth (1). All radular characters are treated as not applicable in radula-less dorids.
42. *Rachidian teeth*: a row of these in *Bathydoris* and some chromodoridids such as *Cadlina* and *Chromodoris* (1); absent in *Berthella* and other dorids (0).
43. *Lateral teeth*: in *Berthella*, *Bathydoris*, *Hexabranchus*, *Aegires* and cryptobranch dorids all the lateral teeth are similar in shape (0). However, in many phanerobranch dorids including *Calycidoris* and *Onchidoris* the inner lateral teeth are very different in shape and size from the outer ones, which are normally rectangular plates (1).
44. *Inner lateral teeth shape*: very variable in nudibranchs. Several categories are recognized here: elongate (0) present in *Bathydoris* and *Actinocyclus*; hamate (1) present in most cryptobranch

dorids, *Berthella*, *Aegires* and *Hexabranchus*; hook-shaped (2) present in *Calycidoris*, *Onchidoris* and most phanerobranch dorids; long (3) present in *Aldisa*.

45. *Outer lateral teeth shape*: as in the previous character, several states are recognized: elongate (0) present in *Berthella*, *Bathydoris* and *Actinocyclus*; hamate (1) present in most cryptobranch dorids, *Aegires* and *Hexabranchus*; plate-shaped (2) present in *Calycidoris*, *Onchidoris* and most phanerobranch dorids; long (3) present in *Aldisa*.
46. *Radular teeth denticulation: Berthella, Actinocyclus, Cadlina, Chromodoris, Aldisa, Alloiodoris* and *Taringa* have denticulate radular teeth (0). In *Sclerodoris, Baptodoris, Rostanga, Halgerda, Pharodoris, Goslineria, Hoplodoris, Thordisa, Geitodoris* and some species of *Siraius* and *Archidoris* only the few, generally outermost radular teeth bear denticles (1). *Onchidoris* and *Calycidoris* have denticles only on the innermost teeth (2). In other dorid genera all the radular teeth are smooth, with no denticles (3).
47. *Salivary glands*: a pair of elongated glands that lead from the buccal bulb of *Berthella*, *Bathydoris* and the majority of dorids (0). In dorids lacking a radula there are no glands with a similar morphology (1).
48. *Oral glands*: the buccal bulbs of all species of dendrodorids and phyllidiids have oral glands, which are variable in shape, size and position (1). These oral glands are not homologous with the salivary glands of other dorids (Valdés & Gosliner, 1999), *Berthella* or *Bathydoris* (0), and their function is probably different. The ptyaline glands of *Dendrodoris* and *Ceratophyllidia* are considered here as oral glands joined to the buccal opening by a duct (1).
49. *Oral gland size*: very small in *Doriopsilla*, *Dendrodoris*, *Mandelia*, *Ceratophyllidia* and *Phyllidiopsis*, very small oral glands are present (0), large in *Phyllidia*, *Phyllidiella* and *Reticulidia* (1). They are treated as not applicable in the remaining taxa.
50. *Oral gland shape*: the oral glands in most of dendrodorids and phyllidiids are simple (0). However, *Phyllidiella* has stalked or leaf-shaped oral glands (1), and in *Reticulidia* they have the appearance of discs arranged around a cavity leading to the oesophagus (2).
51. *Oral gland arrangement*: in *Mandelia*, *Doriopsilla*, *Phyllidiopsis*, *Phyllidia*, *Phyllidiella* and *Reticulidia*, the oral glands are placed over the whole surface of the buccal bulb (0). In *Dendrodoris* and *Ceratophyllidia* they are separated and joined by a duct within the buccal opening (1). There are no oral glands in *Bathydoris*, so this character has been polarized based on the phylogeny proposed by Valdés & Gosliner (1999), who found *Mandelia* to be the sister group to the rest of the radula-less dorids.
52. *Oesophageal glands*: *Dendrodoris* and *Ceratophyllidia* are characterized by the presence of two small, oval glands arranged on the oesophagus (1). According to Valdés & Gosliner (1999), these are not homologous with the salivary glands of other dorids, which lead from the buccal bulb and are long glandular structures, very different from these two rounded glands. Absent in *Berthella*, *Bathydoris* and other phanerobranch and cryptobranch dorids (0).
53. *Oesophageal region differentiated:* in *Dendrodoris, Doriopsilla, Phyllidiopsis* and *Ceratophyllidia* there is a differentiated region in the oesophagus. In *Phyllidiopsis, Doriopsilla* and *Ceratophyllidia papilligera* it is muscular (1), whereas in *Ceratophyllidia africana* and *Dendrodoris* it is glandular (2). This region is absent in *Berthella, Bathydoris* and other phanerobranch and cryptobranch dorids (0).
54. *Retractor muscles on the oesophagus*: the oesophageal muscular region of *Phyllidiopsis*, *Ceratophyllidia* and *Doriopsilla* may have one or two retractor muscles (1) which are absent in *Berthella*, *Bathydoris* and other phanerobranch and cryptobranch dorids (0).
55. *Pyloric sac or sacs*: a pouch or a group of pouches; present in the proximal region of the intestine of *Dendrodoris*, *Phyllidiopsis*, *Ceratophyllidia* and most of the species of *Doriopsilla*, absent in *Berthella*, *Bathydoris* and other dorids (0).
56. *Stomach*: in *Berthella*, *Bathydoris* and some phanerobranch and cryptobranch dorids there is a clearly differentiated stomach (0), which is a dilatation of the proximal region of the intestine. In contrast, *Onchidoris*, *Calycidoris*, *Actinocyclus*, the Chromodorididae and the radula-less dorids lack a differentiated stomach.
57. *Caecum*: a pouch situated on the intestine, near to the opening of the intestine from the digestive gland (Fig. 48). In some species it is clearly visible, whereas in others it is embedded inside the digestive gland and further dissection is necessary to detect its presence. *Berthella*, *Bathydoris* and all phanerobranch and most cryptobranch dorids have a caecum (0); it is absent in radula-less dorids (1). This is not considered homologous with the pyloric sacs because the position of the latter varies considerably. Whereas the caecum is situated near to the opening of the intestine, the pyloric sac is on the upper part of the intestine.
58. *Intestine*: *Berthella* and most species of dorids have a large intestine, which runs over a large

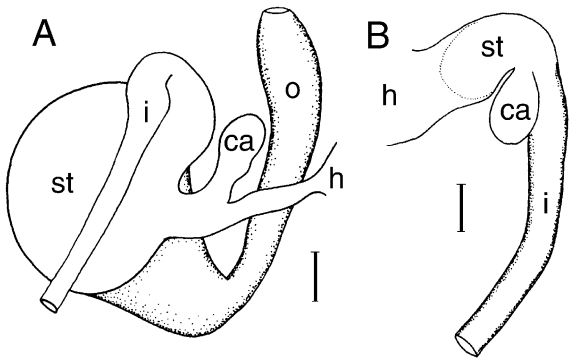

Figure 48. Morphology of the caecum. A, *Doris verrucosa* (CASIZ 082119); scale bar = 1 mm. B, *Calycidoris guntheri* (CASIZ 086915); scale bar = 1 mm.

portion of the digestive gland (0). It opens near to the anterior end of the digestive gland and runs forward before curving to the right side and running backwards to open in the anal papilla, at the posterior end of the digestive gland. In radula-less dorids the intestine is greatly reduced, and occupies a small portion of the digestive gland (1).

59. *Ampulla shape*: oval in species of phyllidiids (1); in some cases it is almost rounded. Elongate in *Berthella*, *Bathydoris*, phanerobranch dorids and the majority of cryptobranch dorids, including dendrodorids (0).
60. *Ampullar openings*: in some species of phyllidiids the division of the distal gonoduct into the prostate and the oviduct occurs directly after the end of the ampulla, with the effect of having practically no distal gonoduct (1). In the rest of the dorids, there is a distinct, more or less long, distal gonoduct, which divides into the prostate and the oviduct (0). In *Actinocyclus* the hermaphroditic duct connects into the gonoduct (2), instead of into the prostate.
61. *Seminal receptacle connection*: the seminal receptacle of dorid nudibranchs is connected either serially or semiserially. *Bathydoris* lacks a seminal receptacle and for this taxon the character is treated as nonapplicable. In *Berthella* there is no uterine duct and this is treated as plesiomorphic (0) according to Cervera *et al*. (2000). In most phanerobranch and cryptobranch dorids the seminal receptacle connection is serial (1), whereas it is semiserial in *Actinocyclus*, *Cadlina* and *Chromodoris* (2).
62. *Seminal receptacle position*: in *Berthella* and most phanerobranch and cryptobranch dorids the seminal receptacle is connected to a more or less long duct (0), whereas in species of *Doris*, *Archidoris*, *Austrodoris*, *Doriopsis* and *Siraius* it is connected directly to the bursa copulatrix (1). *Bathydoris* lacks a seminal receptacle and for this taxon this character is treated as nonapplicable.
63. *Prostate*: an undifferentiated tube in *Berthella*, *Bathydoris* and phanerobranch dorids (0). may be tubular or flattened in cryptobranch dorids. It is a clearly differentiated glandular organ, and easily distinguishable from the ejaculatory portion of the deferent duct (1).
64. *Prostate shape*: two states have been considered – tubular and flattened. *Berthella*, *Bathydoris* and phanerobranch dorids have nondifferentiated prostates, and this character is treated as missing. Tubular in the Chromodorididae and species of *Aphelodoris*, *Doris*, *Siraius*, *Archidoris*, *Austrodoris*, *Doriopsis*, *Conualevia*, *Aldisa*, *Pharodoris*, *Goslineria*, *Atagema*, *Alloiodoris* and *Thorybopus* (0) flattened in the rest of the cryptobranch dorids (1).
65. *Prostate portions:* in most cryptobranch dorids the prostate has a single part (0). In species of *Asteronotus, Halgerda, Paradoris, Peltodoris, Montereina, Geitodoris, Discodoris, Sebadoris, Otinodoris, Tayuva, Thordisa, Hoplodoris* and in caryophyllidia-bearing dorids, except *Thorybopus, Alloiodoris, Atagema* and *Nophodoris*, the prostate has two parts clearly differentiated in colour and texture (1). For *Berthella, Bathydoris* and phanerobranch dorids this character is treated as missing.
66. *Penial hooks:* absent in *Berthella* and *Bathydoris* (0). Present in species of *Onchidoris, Calycidoris, Otinodoris, Hoplodoris, Platydoris, Gargamella, Baptodoris, Alloiodoris, Aldisa, Sclerodoris* and *Doriopsilla* as well as phyllidiids (1). Can also be present in some species of *Cadlina, Chromodoris*, *Nophodoris* and *Dendrodoris* (1).
67. *Penial hook shape*: the penial hooks of most dorids have a short base (0), whereas in *Dendrodoris* they have two long prolongations on each side of the base (1). In species with no penial hooks this character is treated as unordered.
68. *Penial cuticle*: the penises of species of *Otinodoris*, *Platydoris*, *Baptodoris*, *Gargamella* and *Taringa* have a hard cuticle (1), which is absent in *Berthella* and other dorids (0).
69. *Vestibular gland*: this is located next to the distal end of the female gland mass that opens into the albumen gland. It is not homologous with the accessory glands of other dorids that open into the genital atrium. There are vestibular glands in some species of *Cadlina*, *Chromodoris* and *Dendrodoris* (1). *Berthella* and other dorids do not have them (0).
70. *Accessory glands*: in *Pharodoris* and *Goslineria* there are several simple accessory glands (1). In

Sclerodoris, *Platydoris*, *Baptodoris*, *Paradoris*, *Gargamella* and some species of *Halgerda* there is a lobate accessory gland (2). Species of *Asteronotus*, *Nophodoris*, *Geitodoris*, *Thordisa*, *Hoplodoris* and *Jorunna* have pedunculate accessory glands (3). Other taxa included in the analysis lack accessory glands (0).

71. *Sexual hard structures*: in several genera there are hard structures associated with the accessory glands. In *Jorunna*, *Asteronotus*, *Thordisa*, *Paradoris*, *Goslineria*, *Pharodoris*, *Hoplodoris* there are one to several spines, more or less long (1). In some species of *Geitodoris* there are several long hard structures inside the single accessory gland (2). In one species of *Nophodoris* there are several small, hard structures, one inside each accessory gland (3). The rest of the taxa involved lack hard structures (0).
72. *Atrial and vaginal hooks*: in *Baptodoris* and *Gargamella* and in some species of *Platydoris* 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).
73. *Blood gland*: a flattened structure connected to the heart through the aorta. In *Berthella*, *Bathydoris*, phanerobranch dorids and some cryptobranch dorids such as *Actinocyclus*, *Archidoris*, *Austrodoris*, *Doris*, *Aphelodoris*, *Conualevia*, *Aldisa*, *Pharodoris*, *Goslineria*, the Chromodorididae and the radula-less dorids, the blood gland is simple (0), whereas in other cryptobranch dorids it consists of two portions separated by a gap or two completely divided glands (1).
74. *Blood gland position*: in *Berthella*, *Bathydoris*, phanerobranch dorids and radula-less dorids, situated behind the central nervous system (0); in the rest of the cryptobranch dorids it is situated in front of the central nervous system (1). See also Wägele (1998).
75. *Pedal commissure*: this connects the pedal ganglia together, completing the nervous ring around the oesophagus. In *Berthella*, *Bathydoris* and most dorids it is long because the pedal ganglia are lateral to the cerebral ganglia (0). In dendrodorids and phyllidiids, the pedal ganglia are placed beneath the cerebral ganglia and are very close together, rendering the pedal commissure very short (1).
76. *Pleural ganglia*: in *Berthella* and *Bathydoris* they are clearly differentiated from the cerebral ganglia (0); in phanerobranch and cryptobranch dorids they are fused partially or completely with the cerebral ganglia (1).
77. *Cerebral ganglia*: in *Berthella* and *Bathydoris* these are divided into two ganglia on each side (0). In phanerobranch and cryptobranch dorids the cerebral ganglia on each side are completely fused together (1).
78. *Cerebro-buccal connective:* in *Berthella*, *Bathydoris* and most dorids this is long (0). In *Phyllidiopsis* and *Ceratophyllidia papilligera*, the buccal ganglia are actually placed over the muscular region of the oesophagus, and the cerebro-buccal connective is very long (1). In *Dendrodoris*, *Doriopsilla*, *Phyllidia*, *Phyllidiella* and *Reticulidia* the buccal ganglia lie immediately behind the central nervous system, and therefore the cerebro-buccal connective is short (2).
79. *Ganglionic tubercles:* the central nervous system of *Hexabranchus*, *Asteronotus*, *Dendrodoris* and *Otinodoris* is covered by a number of protuberances (1), named ganglionic tubercles. These are absent in *Berthella*, *Bathydoris* and other dorids (0).

Results

For the analysis of the first data matrix, 408 most parsimonious trees 167 steps long were obtained, with a consistency index of 0.635 and a retention index of 0.865. All the trees were found in a single island. From them, a strict and a majority rule consensus tree were produced. The strict consensus tree (Fig. 49) shows very little resolution within several clades, but provides a general outline of the phylogeny of the Cryptobranchia. The majority rule tree (Fig. 50) has a better resolution in the terminal branches of several clades. The Bremer support analysis shows that most of the clades are poorly supported (Fig. 49), with the exception of the radula-less dorids (with a value of 12), the Cryptobranchia (with a value of 6), and the Doridacea (with a value of 6). Other smaller clades containing the Onchidorididae and some members of the Phyllidiidae are also very well supported (with values of 8). One of the most parsimonious trees was arbitrarily selected to trace character evolution (Fig. 51).

DISCUSSION

Monophyletic groups

The selected tree (Fig. 51) shows the presence of several monophyletic groups, some of them already recognized by several authors. Cryptobranchia is a monophyletic group, supported by several synapomorphies: labium present [# 10], dorsal gill retractable (when present) [# 28], cavity around the anus [# 32], reduced number of oral tube and buccal bulb muscles [# 36], prostate differentiated [# 63].

The radula-less dorids, or Porostomata, also constitute a monophyletic group supported by numerous

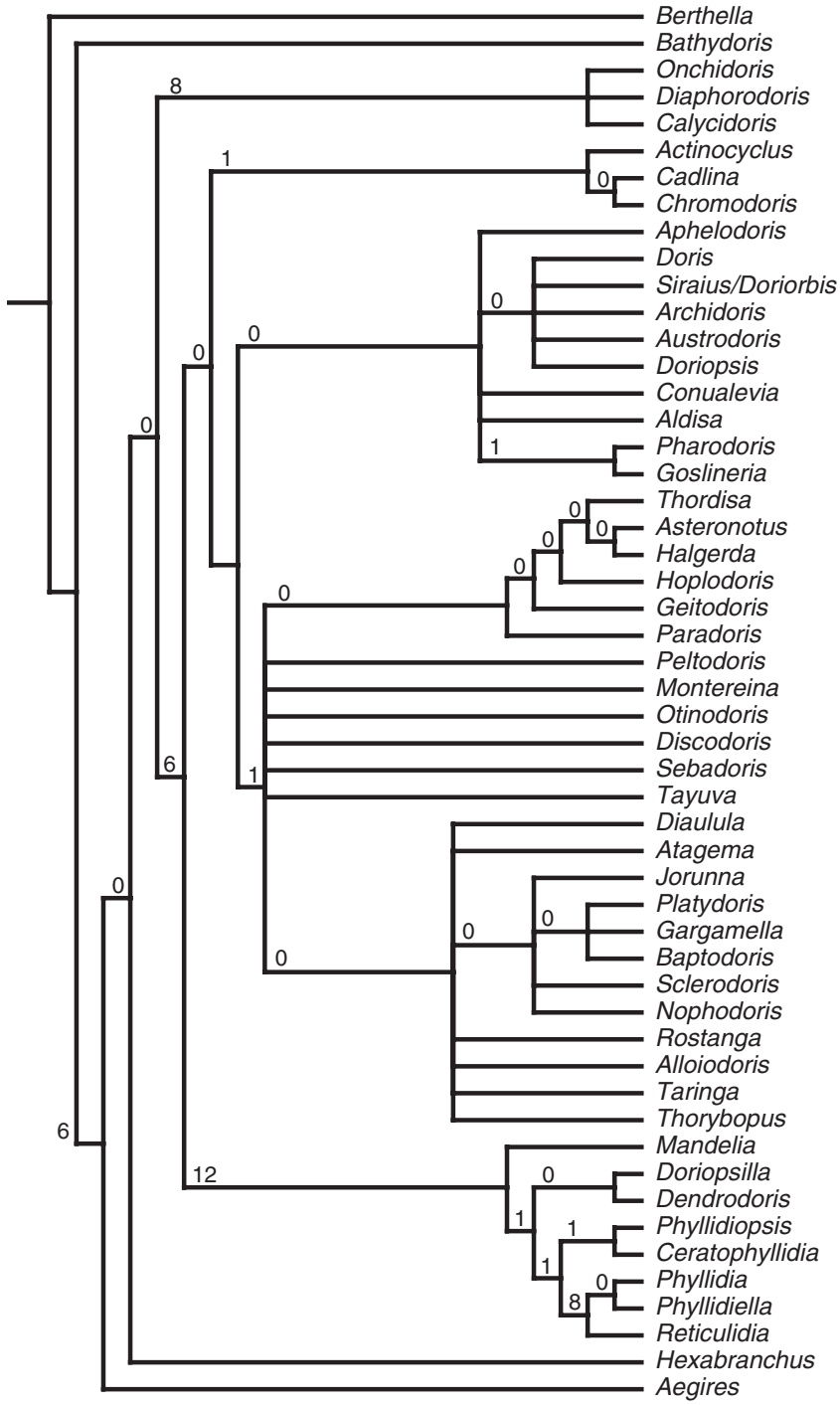

Figure 49. Strict consensus tree of the phylogenetic relationships of the cryptobranch dorids with the Bremer support values in terms of steps.

synapomorphies: mouth area reduced to a pore [# 9], mouth opening moved posteriorly [# 13], labial cuticle absent [# 38], radula absent [# 40], salivary glands absent [# 47], oral glands present [# 48], caecum absent [# 57], intestine reduced [# 58], pedal commissure short [# 75]. All these features are probably functionally linked to the specialized mode of feeding of these organisms, but they strongly support the monophyly of this clade. The monophyly of this group was already shown by Valdés & Gosliner (1999) based on

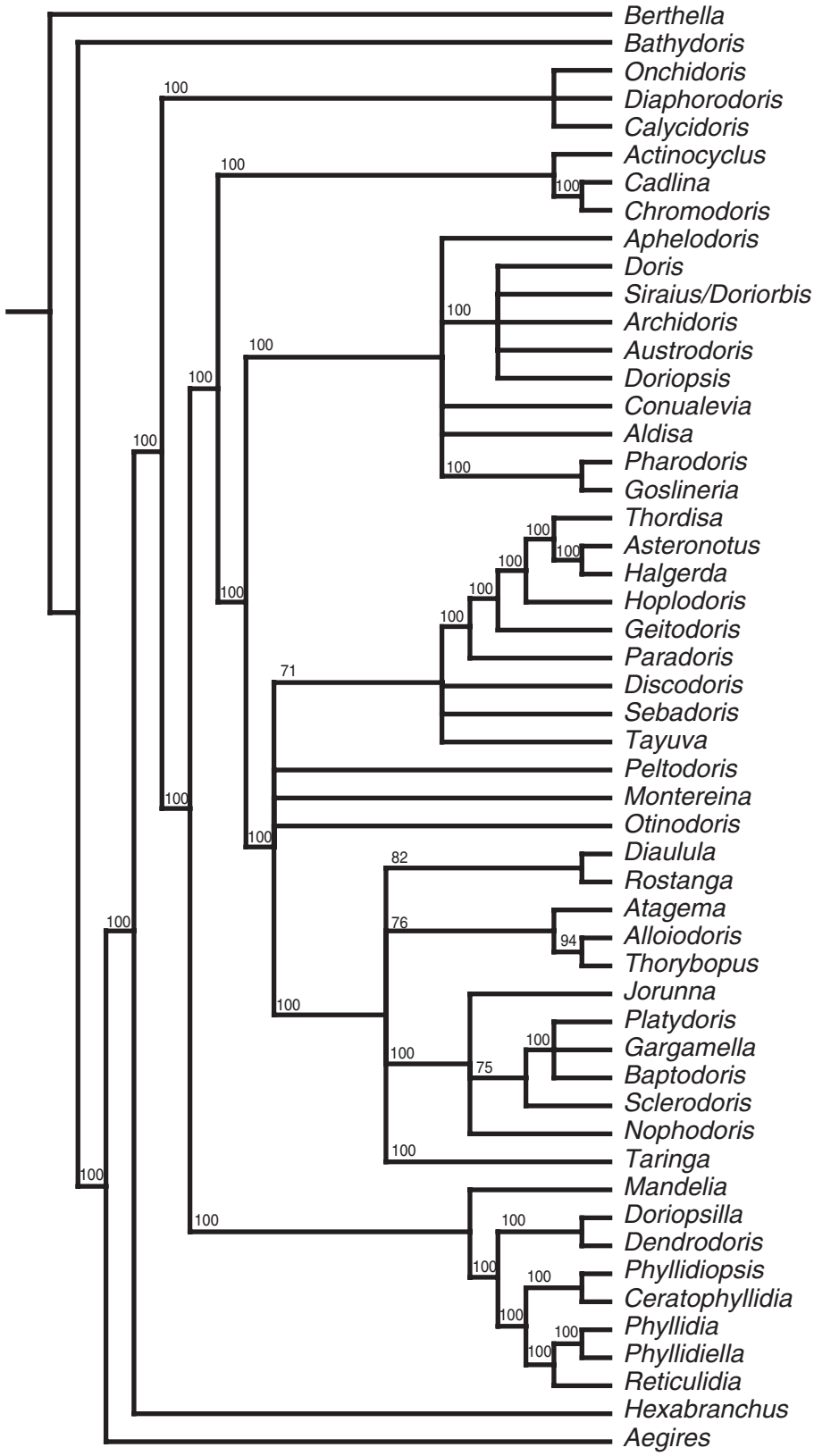

Figure 50. Majority rule (50%) consensus tree of the phylogenetic relationships of the cryptobranch dorids with the percentage level of consensus.

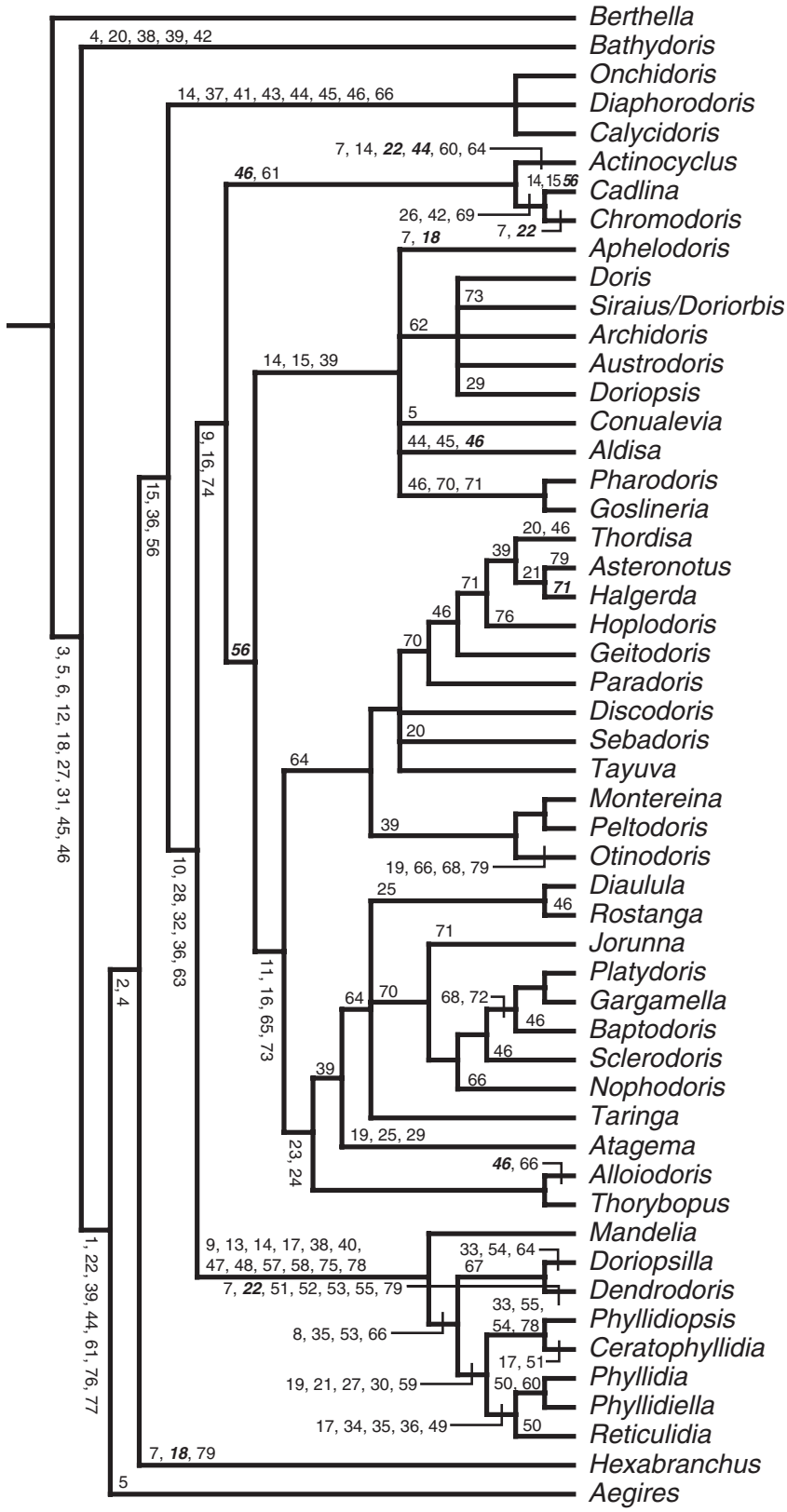

Figure 51. Arbitrarily selected tree to trace the character evolution within the cryptobran dorids. Numbers refer to characters listed in the text. Characters printed in bold and italic face presented at least one instance of reversal.

morphological characters and by Thollesson (2000), based on molecular data. However, the position of this group with respect to the rest of the Cryptobranchia was unknown. According to this phylogeny the Porostomata is sister group to the rest of the Cryptobranchia, which also constitutes a monophyletic group. Thus, the name Labiostomata **new taxon** is introduced for the radula-bearing cryptobranch dorids. This taxon is defined as follows: Labiostomata consists of those taxa sharing a more recent common ancestor with *Actinocyclus* than with *Mandelia*. It contains all the cryptobranch dorids having a radula and labial armature. Synapomorphies for this clade are narrow, but well-developed mouth area [# 9], small oral tentacles [# 16] and blood gland situated in front of the central nervous system [# 74].

Another monophyletic group is the clade containing Actinocyclidae + Chromodorididae, recognized by Gosliner & Johnson (1994) as the sister group to the rest of the cryptobranch dorids. The only synapomorphy of this clade is the presence of a semiserial seminal receptacle [# 61]. Within this clade the monophyly of the Actinocyclidae and the Chromodorididae was demonstrated by Gosliner & Johnson (1994; 1999), respectively, based on morphological phylogenetic analyses. However, more recently Thollesson (2000) found molecular evidence for a possible exclusion of *Cadlina* from the chromodorid clade.

Foale & Willan (1987) first suggested that the caryophyllidia-bearing dorids could be a monophyletic group. This was later confirmed by Valdés & Gosliner (2001) based on a phylogenetic analysis. The synapomorphies of this clade are characters referring exclusively to the dorsal morphology of the animals. They include tubercles surrounded by a ring of protruding spicules [# 23] and presence of ciliated tubercles [# 24]. According to this phylogeny there is insufficient resolution to determine the sister group to the caryophyllidia-bearing dorids. There are a number of genera that share several apomorphies with them, but the phylogenetic relationships cannot be determined at this point. The maintenance of the caryophyllidia-bearing dorids as a separate taxon would probably render these other taxa as a paraphyletic group. The caryophyllidia-bearing dorids plus these other taxa therefore form a monophyletic group, which is here called Discodorididae. The synapomorphies for this clade are: labium notched [# 11], small conical oral tentacles [# 16], prostate with two differentiated portions [# 65], blood gland with two portions [# 73].

The other major clade within the Labiostomata includes several taxa sharing the presence of small and blunt oral tentacles at both sides of the mouth area [# 14, 15], labial cuticle smooth [# 39]. This clade is here called Doridinae.

Paraphyletic groups

In this phylogenetic analysis no synapomorphies have been found to support the traditional group Phanerobranchia. This group includes all the dorids that are not able to retract the gill inside of a cavity, which is a plesiomorphic feature. Wägele & Willan (2000) also found the Phanerobranchia to be paraphyletic when *Hexabranchus* is regarded as a phanerobranch dorid. However, these authors found that the phanerobranch dorids with penial hooks are a monophyletic group, supported by this single synapomorphy. This is probably an artifact due to the absence of cryptobranch dorids with penial hooks in their analysis. The great variability in external morphology, digestive system and radula morphology and reproductive system anatomy within the Phanerobranchia makes it impossible to find synapomorphies for this group and suggests that it is paraphyletic. In the present phylogenetic analysis, the Onchidorididae, which has a external morphology similar to cryptobranch dorids, is the sister group to the Cryptobranchia. However, further detailed phylogenetic analysis including more taxa is required to determine the relationships between the different clades of phanerobranch dorids.

Classification

The tree obtained from the phylogenetic analysis indicates that the traditional classifications of the cryptobranch dorids have to be revised.

The difference between the present classification and recent classifications proposed by Rudman (1998) and other authors is the inclusion of the Porostomata in the Cryptobranchia and the maintenance of Discodorididae as a different family from the Doridinae. Synonymization of *Doriopsis*, *Archidoris*, *Austrodoris*, *Neodoris*, *Siraius* and *Doriorbis* with *Doris* constitutes a considerable change from previous classifications. It would appear that it is no longer necessary to involve a large number of traditional taxa in an explanation of the limited diversification that took place in this clade. The monophyly of the traditional taxa synonymized with *Doris* is unlikely; this provides further justification for the proposed synonymization, although this can only be determined in a future species-level phylogenetic analysis.

Another significant change is the exclusion of *Hexabranchus* from the Cryptobranchia, due to the absence of all the synapomorphies present in the cryptobranch dorids. In the phylogeny by Wägele & Willan (2000), *Hexabranchus* is the sister group of the cryptobranch dorids, whereas in the present phylogeny it is more basal, being the sister group to some 'phanerobranch dorids' and the Cryptobranchia. One feature that Wägele & Willan's (2000) and the present phylog-

Table 5. Summary of the classification of the cryptobranch dorids proposed in the present paper

High-rank names	Family-group names	Genus-group names
POROSTOMATA Bergh, 1891	PHYLLIDIIDAE Rafinesque, 1814	*Phyllidia* Cuvier, 1797
		Phyllidiella Bergh, 1869
		Phyllidiopsis Bergh, 1875
		Ceratophyllidia Eliot, 1903
		Reticulidia Brunckhorst, 1990
	DENDRODORIDIDAE O'Donoghue, 1924	*Dendrodoris* Ehrenberg, 1831
		Doriopsilla Bergh, 1880
	MANDELIIDAE Valdés and Gosliner, 1999	*Mandelia* Valdés and Gosliner, 1999
LABIOSTOMATA **new taxon**	ACTINOCYCLIDAE Kay and Young, 1969	*Actinocyclus* Ehrenberg, 1831
		Hallaxa Eliot, 1909
	CHROMODORIDIDAE Bergh, 1891	*Glossodoris* Ehrenberg, 1831
		Thorunna Bergh, 1877
		Ceratosoma J. E. Gray, 1850
		Hypselodoris Stimpson, 1855
		Chromodoris Alder and Hancock, 1855
		Cadlina Bergh, 1879
		Tyrinna Bergh, 1898
		Noumea Risbec, 1928
		Verconia Pruvot-Fol, 1931
		Cadlinella Thiele, 1931
		Risbecia Odhner, 1934
		Mexichromis Bertsch, 1977
		Pectenodoris Rudman, 1984
		Ardeadoris Rudman, 1984
		Digidentis Rudman, 1984
		Durvilledoris Rudman, 1984
	DORIDIDAE Rafinesque, 1815	*Doris* Linnaeus, 1758
		Aldisa Bergh, 1878
		Aphelodoris Bergh, 1879
		Conualevia Collier and Farmer, 1964
		Pharodoris Valdés, 2001
		Goslineria Valdés, 2001
	DISCODORIDIDAE Bergh, 1891	*Asteronotus* Ehrenberg, 1831
		Atagema J.E. Gray, 1850
		Jorunna Bergh, 1876
		Discodoris Bergh, 1877
		Thordisa Bergh, 1877
		Platydoris Bergh, 1877
		Diaulula Bergh, 1878
		Rostanga Bergh, 1879
	DISCODORIDIDAE Bergh, 1891	*Halgerda* Bergh, 1880
		Peltodoris Bergh, 1880
		Hoplodoris Bergh, 1880
		Baptodoris Bergh, 1884
		Paradoris Bergh, 1884
		Geitodoris Bergh, 1891
		Gargamella Bergh, 1894
		Alloiodoris Bergh, 1904
		Sclerodoris Eliot, 1904
		Otinodoris White, 1948
		Taringa Marcus, 1955
		Sebadoris Marcus and Marcus, 1960
		Thorybopus Bouchet, 1977
		Nophodoris Valdés and Gosliner, 2001
	INCERTAE SEDIS	*Artachaea* Bergh, 1882
		Carminodoris Bergh, 1889
		Homoiodoris Bergh, 1882

Table 6. Family level synonymy proposed in this paper

Family	Synonyms
DORIDIDAE Rafinesque, 1815	DORIOPSIDAE Bergh, 1876
	ARCHIDORIDIDAE Bergh, 1891
	DORIDIGITATIDAE Iredale & O'Donoghue, 1923
	ALDISIDAE Odhner, 1939
	CONUALEVIIDAE Collier & Farmer, 1964
	NEODORIDIDAE Odhner, 1968
DISCODORIDIDAE Bergh, 1891	KENTRODORIDIDAE Bergh, 1891
	PLATYDORIDIDAE Bergh, 1891
	DIAULULIDAE Bergh, 1891
	HALGERDIDAE Odhner, 1926
	BAPTODORIDIDAE Odhner, 1926
	ASTERONOTIDAE Thiele, 1931
	ARGIDAE Thiele, 1931
	ROSTANGIDAE Pruvot-Fol, 1951
	HOPLODORIDIDAE Odhner, 1968
	GEITODORIDIDAE Odhner, 1968
	TARINGIDAE Odhner, 1968
	TRIPPIDAE Kay & Young, 1969
	SEBADORIDIDAE Soliman, 1980

eny have in common is that 'Phanerobranchia' appears to be paraphyletic.

The classification proposed here will need further refinement and improvement. For instance, the monotypic genus *Sebadoris* is very similar to *Discodoris*, as is *Otinodoris* to *Peltodoris*, and they might be synonyms. Further phylogenetic analysis at the species level, including all the species described for each clade, is necessary to clarify the relationships between these taxa.

For this classification the rules of the ICZN (ICZN, 1999) have been observed. However, for taxa above 'family group' level the rules do not apply. Therefore the resultant classification (Table 5) is hierarchical but unranked at the higher levels, in accordance with modern perspectives of phylogenetic classification (de Queiroz & Gauthier, 1994).

SYNONYMY

A number of family group names have been synonymized. As family group names are based on genus-group types (ICZN, 1999: Article 63), determination of synonymy is straightforward. However, the name Discodorididae has several synonyms described at the same time by Bergh (1891). These include Diaululidae, Kentrodorididae and Platydorididae. In this case, the name Discodorididae has been selected to be the valid name for the family under the principle of first reviser (ICZN, 1999: Article 24).

A full synonymy to explain the changes proposed here is included in Table 6. Determination of name precedence has been done according to strict application of the Principle of Priority (ICZN, 1999: Article 23).

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