

SYSTEMATIC REVISION OF *JORUNNA* BERGH, 1876 (NUDIBRANCHIA: DISCODORIDIDAE) WITH A MORPHOLOGICAL PHYLOGENETIC ANALYSIS

YOLANDA E. CAMACHO-GARCÍA¹ AND TERRENCE M. GOSLINER²

¹Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, Apdo 2060, San Pedro de Montes de Oca, San José, Costa Rica;

²Department of Invertebrate Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA

(Received 31 December 2004; accepted 10 January 2008)

ABSTRACT

The genus *Jorunna* is characterized by a dorsum covered with caryophyllidia, a prostate with two sections, a penis usually unarmed but occasionally armed with hooks, a copulatory spine, the presence of an accessory gland and a labial cuticle smooth or armed with jaw elements. The examination of 216 non-type specimens, 30 types, and a review of the literature show that there are 16 valid species of the genus *Jorunna*: *J. tomentosa* (Cuvier, 1804); *J. funebris* (Kelaart, 1859); *J. pantherina* Angas, 1864; *J. rubescens* (Bergh, 1876); *J. labialis* (Eliot, 1908); *J. parva* (Baba, 1938); *J. spazzola* (Marcus, 1955); *J. hartleyi* (Burn, 1958); *J. alisonae* Marcus, 1976; *J. lemchei* (Marcus, 1976); *J. evansi* (Eliot, 1906); *J. pardus* Behrens & Henderson, 1981; *J. ramicola* Miller, 1996 and *J. onubensis* Cervera, García-Gómez & García, 1986. In addition, two new species from the Eastern Pacific are described: *J. osae* n. sp. and *J. tempisqueensis* n. sp. We propose two new combinations: *Jorunna parva* and *J. evansi*. New records for the genus *Jorunna* are provided from Italy, Algeria, Seychelles, Madagascar, Thailand, Marshall Islands, New Caledonia, Île de la Réunion, Sudan, Papua New Guinea, Indonesia, Panama, Costa Rica, Bahamas, and Southern Mexico. We present the first preliminary phylogenetic analysis of this cryptobranch dorid genus, based on morphological anatomical data, and discuss the biogeography and evolution of several characters in this group. The phylogeny supports the hypothesis that the genus *Jorunna* is a monophyletic group and shows that *Kentrodoris* is nested within it.

INTRODUCTION

The genus *Jorunna* Bergh, 1876 was previously composed of 19 species described from the Atlantic, Eastern Pacific, and the Indo-Pacific. Valdés (2002) proposed that this genus belongs to the family Discodorididae Bergh, 1891. The first reference to species of this genus was the description of *Doris tomentosa* Cuvier, 1804 from La Rochelle, France. Since then, additional species have been described by Kelaart (1859), Angas (1864), Bergh (1876, 1878, 1881), Eliot (1906, 1908), Baba (1938), Er. Marcus (1955), Ev. Marcus (1976), Risbec (1956), Burn (1958), Behrens & Henderson (1981), Cervera, García-Gómez & García (1986) and Miller (1996). Kay & Young (1969) considered all specimens worldwide to represent a single species, *Jorunna tomentosa*, and this idea was supported by Edmunds (1971).

Bergh (1876) established the genera *Jorunna* and *Kentrodoris*. He based *Kentrodoris* on three species, with *Kentrodoris rubescens* Bergh, 1876 from the tropical Indo-Pacific as its type. The other two species were *Kentrodoris gigas* Bergh, 1876 and *Kentrodoris annuligera* Bergh, 1876. All were characterized by a penis armed with a long spine (which we show is associated with the accessory gland rather than the penis), a large accessory gland which opens near the vagina, and a lack of jaws and rachidian teeth. Bergh (1876) based *Jorunna* on *Doris johnstoni* Alder & Hancock, 1845, which is considered a synonym of *Jorunna tomentosa* (Cuvier, 1804) (Fischer, 1869). The main features of the genus include a dorsum covered with caryophyllidia, low rhinophoral and branchial sheaths, a massive prostate with two sections, an unarmed vagina, a penis

occasionally with hooks, an accessory gland with a spine, a labial cuticle (either smooth or with jaw elements), inner and lateral hamate radular teeth, and outermost teeth either smooth or denticulate (Valdés & Gosliner, 2001). According to Bergh (1876), the main difference between *Jorunna* and *Kentrodoris* is that the spine of *Kentrodoris* is situated on the penis, whereas it is in the accessory gland in *Jorunna*.

Er. Marcus (1955) described the genus *Awuka*, based on *Awuka spazzola* Marcus, 1955, with the same features as *Jorunna* and *Kentrodoris*. According to this description, the presence of jaws and one single denticle on the innermost radular teeth are the distinctive features of *Awuka*. Marcus also described a genital spine situated on the penis. Later, Ev. Marcus (1976) regarded the genus *Awuka* as a synonym of *Jorunna*. Marcus (1976) also found that the spine described by Bergh (1876) and Er. Marcus (1955) on the penis of *Kentrodoris*, was actually situated in the large accessory gland of both *Kentrodoris* and *Jorunna*. However, she concluded that *Kentrodoris* was different from *Jorunna* because of the 'soft notum, the high gills, the acinous prostate, the loculated spermatocyst and the sheathed male organ' of *Kentrodoris*. She designated *K. rubescens*, the type species of the genus, as the only member of *Kentrodoris* and regarded the other two species, originally included by Bergh (1876) in *Kentrodoris* (*K. gigas* and *K. annuligera*), as members of *Jorunna*.

The genus *Jorunna* was reviewed by Ev. Marcus (1976) who demonstrated significant differences in the anatomy of species from different regions, described five new species and reinstated several others. She characterized *Jorunna* as having stiffened notal tubercles or caryophyllidia, simple lateral radular teeth, marginal radular teeth (sometimes with irregular denticles), a smooth prostatic epithelium, an unsheathed male duct ending with a spineless papilla, or even without a papilla, and an accessory gland with a spine.

Correspondence: Y. E. Camacho-García; e-mail: ycamacho_99@yahoo.com

The phylogenetic relationships of the genera *Kentrodorid* and *Jorunna* were studied by Valdés & Gosliner (2001), supporting the idea that the morphological differences between the genera are just autapomorphies of *Kentrodorid rubescens*. They therefore regarded *Kentrodorid* and *Jorunna* as synonyms, and the name *Jorunna* was selected as having precedence over *Kentrodorid* (ICZN, 1999: Art. 24).

The aims of the present study are: (1) to provide a comprehensive systematic revision of the genus *Jorunna*; (2) to test whether *Jorunna* is a monophyletic group and to present the first phylogenetic analysis of the genus; (3) to discuss the biogeography and evolution of several characters in the context of the phylogeny. No phylogenetic studies based on cladistic criteria have previously been published for *Jorunna*.

MATERIAL AND METHODS

Living animals, non-type material and type material were studied from the collections of several museums and institutions: Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco (CASIZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Zoologisk Museum, Copenhagen (ZMC); National Museum of Natural History, Washington DC (USNM); Natural History Museum, London (BMNH); and University of Costa Rica (UCR) (which now houses the collections of the Instituto Nacional de Biodiversidad, INBio).

In total, 246 specimens were examined, including 30 types. Eighty-eight of these specimens were dissected. For most of the specimens that were dissected we observed the external coloration and morphology (such as dorsum-caryophyllidia, gills, lamellae, oral tentacles, foot, rhinophores, mantle glands etc.), and the internal anatomy (labial cuticle, radula and reproductive system). For the rest of the specimens that were not dissected, we observed the external coloration and morphology. Specimens were dissected by dorsal incision. Their reproductive systems were examined and drawn under a dissecting microscope with camera lucida. At least two specimens of each species were examined anatomically. The buccal bulb was extracted from the specimen by making two dorsal longitudinal incisions from behind the rhinophores to the gill. The jaw and radula were dissected and isolated from each other. Radulae were placed in a 10% solution of NaOH to remove tissue. Jaws and radulae were examined by scanning electron microscope. Mantle samples were taken from each specimen, placed in 100% alcohol and critical-point dried. The accessory gland was dissected from the reproductive system, stained using acid fuchsin, dehydrated in a series of ethanol, cleared in xylol and mounted on a slide. The copulatory spine was drawn using a microscope with camera lucida.

Jorunna has one of the most difficult reproductive systems to draw among dorids. We tried to represent the different structures in our drawings exactly as we saw them. In most of the cases, however, we had to produce up to three drawings (with the exception of *J. parva* and *J. ramicola*) to represent these structures. For example, in most of the cases the first thing we see is the accessory gland (covering at least 25–70% of the reproductive system in mature individuals), part of the bursa copulatrix, seminal receptacle and sometimes part of the prostate and ampulla. Second, we had to move or remove the accessory gland to see the details of the seminal receptacle, bursa copulatrix and ducts. Third, in most cases after moving or removing the bursa copulatrix and seminal receptacle we were able to see the connections between the ampulla and prostate.

Photographs of living animals for most of the species were taken by the collectors and used to record features of living animals. External morphological data were obtained from the

original descriptions, and from redescrptions when specimens or type material were not available. The names of the species have been treated in chronological order as they were originally described.

SYSTEMATIC DESCRIPTIONS

Part A: The genus *Jorunna* (including *Kentrodorid* and new taxa)

Family DISCODORIDIDAE Bergh, 1891

Genus *JORUNNA* Bergh, 1876

Kentrodorid Bergh, 1876: 413. Type species *Kentrodorid rubescens* Bergh, 1876 (= *Jorunna rubescens* Bergh, 1876), by subsequent designation by Ev. Marcus (1976).

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

Audura Bergh, 1878: 567–568. Type species *Audura maima* Bergh, 1878 [= *Jorunna maima* (Bergh, 1878)], by monotypy.

Centrodorid P. Fischer, 1880–1887 [1883]: 522 (unjustified emendation of *Kentrodorid* Bergh, 1876).

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

Diagnosis: Body oval-elongate. Dorsum covered with high caryophyllidia with a long conical base, long spicules and a small, rounded ciliated tubercle. Rhinophoral and branchial sheaths low. Branchial leaves unipinnate to tripinnate. Prostate divided into two sections. Vagina unarmed. Penis usually unarmed but occasionally armed with hooks. Large accessory gland with a copulatory spine. Labial cuticle smooth or armed with jaw elements. Inner and mid lateral radular teeth usually hook-like. Outer lateral teeth smooth or pectinate.

Remarks: Valdés & Gosliner (2001), as first revisers of the synonymous genera *Kentrodorid* and *Jorunna*, selected the name *Jorunna* as having precedence over *Kentrodorid* (ICZN, 1999: Art. 24).

Jorunna tomentosa (Cuvier, 1804)

(Figs 1A, B, 2, 3, Table 4)

Doris tomentosa Cuvier, 1804: 470–472 [La Rochelle, France; type lost, not at MNHN (Valdés & Héros, 1998; Valdés & Gosliner, 2001); neotype here designated MNHN].

Jorunna tomentosa—Bergh, 1876: 414.

Doris obvelata Johnston, 1838: 52, pl. 2, figs 4–7.

Doris johnstoni Alder & Hancock, 1845: 42, xvi, fam. 1, pl. 2, figs 8–11, pl. 5, pl. 46, fig. 4 [Berwick Bay, England; 2 syntypes, 7–9 mm preserved length, not dissected, Hancock Museum, Newcastle (02/04/11)].

Jorunna johnstoni var. *alba* Bergh, 1881: 199, pl. J, figs 17–21, pl. K, figs 29–36; 1884, pl. 70, fig. 20.

Types: Neotype: La Rochelle, France, 20 mm preserved length (MNHN).

Additional material examined: Robin Hoods Bay, North Yorkshire, England, April 1976, 1 specimen (dissected), poor preservation, leg. L. Harris & C. Todd (CASIZ 079486); Quiberon, Morbihan, France, September 1975, 3 specimens, 15–16 mm preserved length (MNHN); Atlantic coast, France,

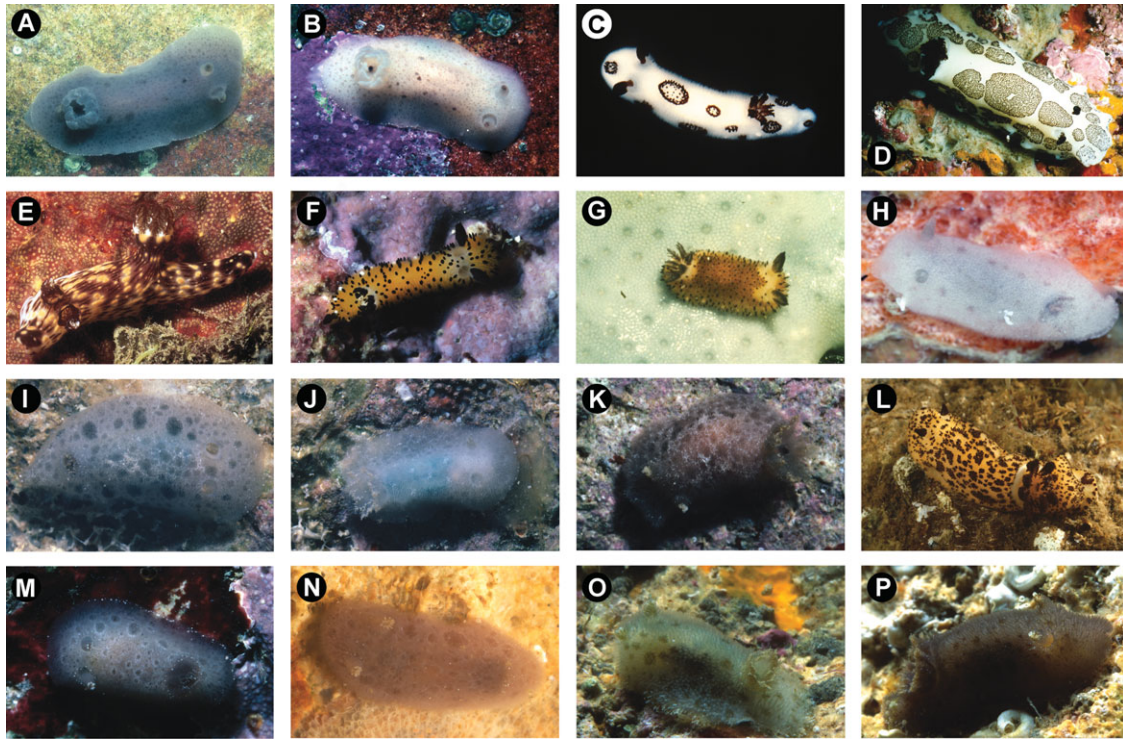


Figure 1. Living animals. **A.** *Jorunna tomentosa* (South Africa, CASIZ 075991), photo by T. Gosliner. **B.** *Jorunna tomentosa* (South Africa), photo by T. Gosliner. **C.** *Jorunna funebris* (Japan, CASIZ 079367), photo by T. Gosliner. **D.** *Jorunna funebris* (Marshall Islands, CASIZ 120962), photo by T. Gosliner. **E.** *Jorunna rubescens* (Papua New Guinea, animal not collected), photo by T. Gosliner. **F.** *Jorunna parva* (Papua New Guinea, CASIZ 075929), photo by T. Gosliner. **G.** *Jorunna parva* (Seychelles, CASIZ 074251), photo by T. Gosliner. **H.** *Jorunna spazzola* (Costa Rica, CASIZ 175768), photo by A. Valdés. **I, J.** *Jorunna alisonae* (Hawaii, CASIZ 087101), photo by T. Gosliner. **K.** *Jorunna alisonae* (Hawaii, CASIZ 061457), photo by T. Gosliner. **L.** *Jorunna pardus* (California, CASIZ 072862), photo by T. Gosliner. **M.** *Jorunna ramicola* (Papua New Guinea, CASIZ 068724), photo by T. Gosliner. **N.** *Jorunna ramicola* (Philippines, CASIZ 157016), photo by T. Gosliner. **O.** *Jorunna osae* n. sp. (Costa Rica), photo by L. Moro. **P.** *Jorunna tempisqueensis* n. sp. (Costa Rica), photo by L. Moro.

December 1990, 12 specimens, 0.7–19 mm preserved length (MNHN); Banyuls, France, 2 specimens, 16–20 mm preserved length (MNHN); La Rochelle, France, 2 specimens, 19–20 mm preserved length (MNHN); St Vaast, France, 3 specimens, 23–28 mm preserved length (MNHN); Roscoff, France, 3 specimens, 16–21 mm preserved length (MNHN); Roscoff, Finistère, France, 1 September 1975, 1 specimen, 13 mm preserved length (MNHN); St Vaast, France, 1 specimen, 18 mm preserved length (MNHN); La Rochelle, France, 22 specimens, 11–20 mm preserved length (MNHN); St Vaast, France, 3 specimens, 24–30 mm preserved length (MNHN); Marseille, France, 2 specimens, 1.8–3 mm preserved length (MNHN); Locmiquel, 12 December 1972, 1 specimen, 10 mm preserved length (MNHN); Palermo, Sicily, Italy, 8 specimens, 18–26 mm preserved length (MNHN); Palermo, Sicily, Italy, 2 specimens, 20–25 mm preserved length (MNHN); Porsangen Fjord, Norway, 2 specimens (1 dissected), 18–23 mm preserved length (MNHN); Annaba, Algeria, 2 specimens, 18–19 mm preserved length (MNHN); Oviñada, Asturias, Spain, August 1979, 2 specimens, 30 mm preserved length, leg. J. Ortea (CASIZ 115215), Ilha São Miguel, Mosteiros, Azores, intertidal, 17–18 July 1988, 3 specimens (1 dissected), 8–13 mm preserved length, leg. A. F. Martins (CASIZ 72598); Ilha São Miguel, Ponta de Pirimide, Azores, intertidal, 13 July 1988, 8 specimens (1 dissected), 5–22 mm preserved length, leg. T. Gosliner (CASIZ 77444); Eland's Bay, Cape Province, South Africa, 17 February 1980, 2 specimens (both dissected), 11–16 mm preserved length (CASIZ 073939); Kommetjie, Cape Province, South Africa, 24 September 1980, 3 specimens, 20–28 mm preserved length (A

35388 South African Museum Cape Town); South Africa, February 1981, 1 specimen (dissected), 15 mm preserved length (CASIZ 086912); Hottentot's Huissie, Cape Province, South Africa, 8 January 1981, 1 specimen (dissected), 11 mm preserved length (CASIZ 086942); Kommetjie, Cape Province, South Africa, no date, 2 specimens (1 dissected), both 20 mm, leg. T. Gosliner (CASIZ 75991).

External morphology: Body oval, convex (Fig. 1A, B). Caryophyllidia elongate, *c.* 150 μm in length, homogeneously distributed around the branchial, rhinophoral sheaths and notum, with short spicules and ciliated tubercles (Fig. 2E). Eleven bipinnate gills and rhinophores with 14 lamellae in 16 mm preserved length specimen (CASIZ 073939). Ten bipinnate gills and 13 lamellae in 15 mm preserved length specimen (CASIZ 086912). Eleven bipinnate gills and 14 lamellae in 13 mm preserved length specimen (CASIZ 072598). Gills imbricate, perpendicular relative to body.

Background colour of living animal yellow-cream to grey (Fig. 1A, B). Three to six small, light brown spots distributed randomly over dorsum forming two vertical lines relative to rhinophores. Light spots composed of aggregation of minute spots. In specimens with yellow-cream background, rhinophores and gill also yellow-cream. Apices of rhinophores same colour, but with some dark brown pigmentation on lamellae. Branchial leaves also with some dark brown pigmentation on some branches at their apices. Specimens with a greyish background with rhinophores and gills of same colour, although apices of rhinophores yellow to cream. Small, white, spherical glandular structures surrounding mantle edge.

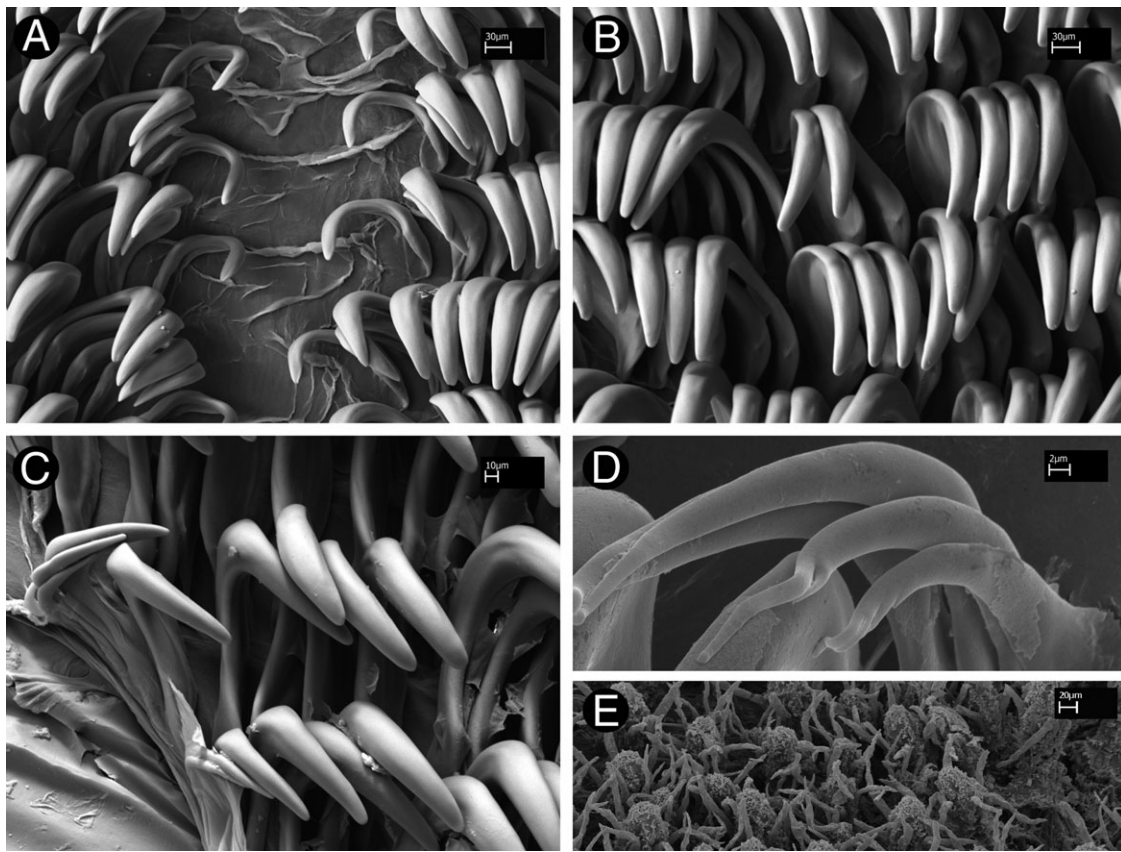


Figure 2. *Jorunna tomentosa* (South Africa, CASIZ 073939), SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Detail of the outermost teeth (CASIZ 115215). **E.** Caryophyllidia (CASIZ 073939).

Anal papilla with seven divisions, speckled with dark pigment. Foot and hyponotum same colour as notum without spots. Cream oral tentacles, conical in shape. Posterior end of foot visible dorsally when animal moves.

Anatomy: Labial cuticle smooth. Radular formula of 16 mm preserved length specimen $22 \times (23.0.23)$ (CASIZ 073939), and $17 \times (15.0.15)$ of 16 mm preserved length specimen from Quiberon (MNHN). Rachidian teeth absent. Innermost teeth thick, short (Fig. 2A). Midlateral teeth hamate, thick, lacking cusp (Fig. 2B). Lateral teeth increase in size from inner to midlateral. Outermost teeth small, elongate, normally smooth (Fig. 2C), sometimes having up to 4 denticles (Fig. 2D). Presence or absence of denticles varying even within a single radula. In the type collection of the Hancock Museum in Newcastle there is a slide (3/16/17) mounted with the radula of a specimen of *D. johnstoni*, radular formula $23 \times (23.0.23)$. On this slide teeth number 21, 22 and 23 are clearly pectinate.

Ampulla very long, divided into the short oviduct and prostate (Fig. 3A, C). Ampulla entering female glands near upper part of mass. Prostate very large, granular, narrowing into short, coiled deferent duct, expanding again into muscular, wide ejaculatory portion. Deferent duct opening into common atrium with vagina (Fig. 3B). Penial hooks absent. Long, convoluted accessory gland connecting to atrium (Fig. 3A). Accessory gland with spine about $920 \mu\text{m}$ long. Spine straight, pointed (Fig. 3D). Vagina long, tubular, wider than deferent duct. Uterine duct short, thin, opening in distal part of female gland mass. Seminal receptacle oval, at least one-fifth as large as rounded bursa copulatrix (Fig. 3B).

Distribution: From 65°N on the Norwegian coast to Faeroes, all coasts of Britain, France, Portugal, Morocco (Marcus, 1976), and South Africa (Gosliner, 1987), Italy and Algeria (present study).

Remarks: Cuvier (1804) incompletely described *Doris tomentosa* as a species with a white to grey semi-translucent background colour, a curved body, a mantle larger than the foot, and a woolly dorsal texture. Johnston (1838) described *Doris obvelata* as having a uniform yellowish-white background colour, usually dashed with a few dark spots, a broad margin, caryophyllidia on the dorsum, and bipinnate gills.

A more complete description of *Doris johnstoni* Alder & Hancock, 1845, was later published by Alder & Hancock (1845–1855), including an anatomical description. Fischer (1869) synonymized *Doris johnstoni* with *Doris tomentosa* for the first time.

In her revision of the genera *Kentrodorid* and *Jorunna*, Marcus (1976) divided *Jorunna tomentosa*, into four different species: *J. malcomi*, *J. alisonae*, *J. lemchei* and *J. luisae*, based on differences in the radular and jaw morphology and the reproductive system.

Thompson & Brown (1984) synonymized *J. lemchei* with *J. tomentosa*, noting that these two are indistinguishable in habits, external morphology and internal anatomy. These authors also included *J. luisae* as a possible synonym of *J. tomentosa*. Later, Valdés & Gosliner (2001) indicated that these three species (*J. luisae*, *J. lemchei* and *J. tomentosa*) have sufficient differences to justify their separation as different species. According to these authors, *J. lemchei* is clearly different from *J. tomentosa* because of the presence of large hooks on

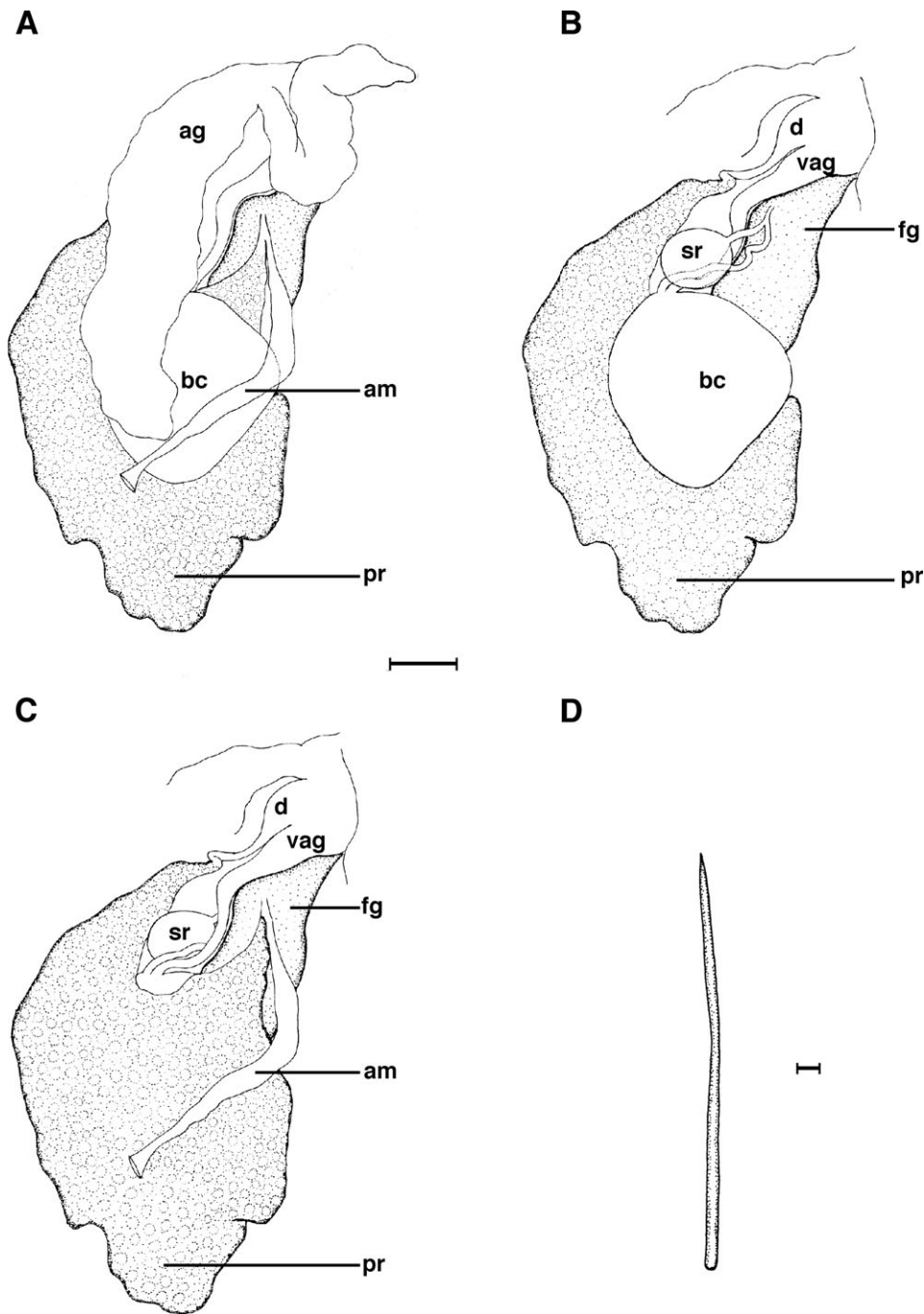


Figure 3. *Jorunna tomentosa* (South Africa, CASIZ 073939). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

the penis and the absence of denticulation on the outermost lateral teeth. *Jorunna luisae* differs from this last species in the presence of jaws and denticulated innermost lateral teeth. However, in our study we have synonymized *J. luisae* with *J. spazzola* (Marcus, 1955).

In a specimen from Plymouth, England, Marcus (1976) described the outer lateral teeth from the right side of the radula as having denticles, whereas some of the teeth on the left side do not have denticles. The specimen studied by

Cervera, García & García (1986) from Spain lacks denticles on the outermost teeth. In the present study, we examined several specimens of *J. tomentosa* from different localities and we found that the specimens from Spain (CASIZ 115215) and England (CASIZ 079486) show intra-specific variation, whereas specimens from South Africa (CASIZ 073939), Norway (MNHN, no catalogue number), and Quiberon, France (MNHN, no catalogue number) do not have any denticles on the outermost lateral teeth.

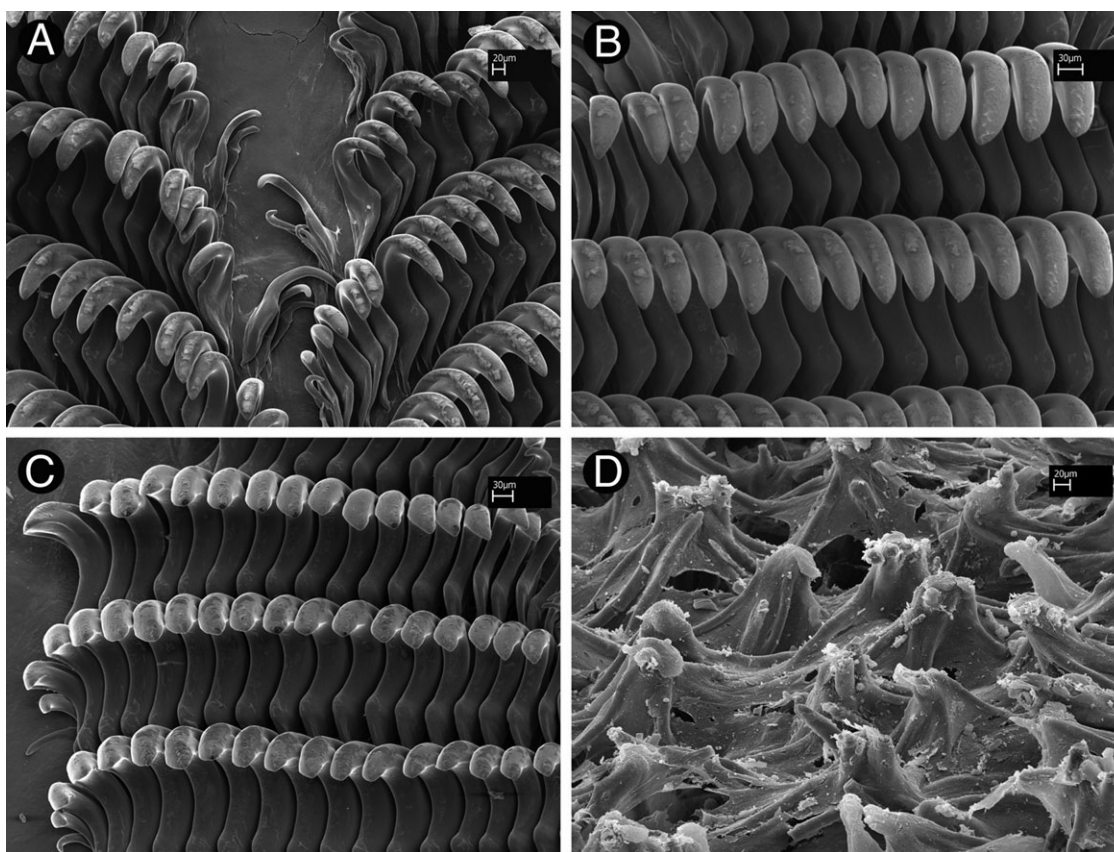


Figure 4. *Jorunna funebris* (Marshall Islands, CASIZ 120962). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Caryophyllidia.

Jorunna onubensis Cervera, García-Gómez & García, 1986 from Huelva, Spain, *J. labialis* Marcus, 1976 from the Indian Ocean (Tanzania), and *J. alisonae* Marcus, 1976 from Hawaii can be distinguished from *J. tomentosa* by the presence of a labial cuticle with jaw elements, their radular morphology and differences in the reproductive system. *Jorunna onubensis* has a non-prostatic deferent duct with two regions, which is absent in *J. tomentosa*. *Jorunna alisonae* has only one small denticle on the outermost teeth, whereas *J. tomentosa* has more than one denticle on two or more of the outermost teeth, in some cases. Additionally, while the background colour of *J. tomentosa* is yellow-cream to grey with small light spots randomly distributed, *J. labialis* has a white to very dark grey background colour with light brown spots and *J. alisonae* has a pale grey background colour with two vertical lines of black spots and opaque white spots around the mantle margin.

***Jorunna funebris* (Kelaart, 1859)**

(Figs 1C, D, 4, 5, Table 2)

Doris funebris Kelaart, 1859: 293 [Sri Lanka, holotype, slide of radula (03/21/06), Hancock Museum, Newcastle].

Jorunna funebris—Marcus, 1976: 22–30, figs 20–21.

Kentrodoris annuligera Bergh, 1876: 423, pl. 41, fig. 1 (1875) [Philippines, syntype, 1 specimen 45 mm preserved length (ZMUCGAS-2109). Specimen with two labels, one records: “The Philippines, leg. C. Semper, 1876,” the second one records: “Aibukit, Philippines (one specimen) and Samor (one specimen), leg. C. Semper, 1862”].

Kentrodoris gigas Bergh, 1876: 419–422: pl. 50, figs 1–5, syn. nov. [Aibukit, Philippines, 1 specimen, 92 mm preserved length, leg. C. Semper, 1862 (ZMUCGAS-2162)].

Kentrodoris maculosa Eliot, 1906: 649, 1001; 1907: 85.

Discodoris wetleyi Allan, 1932: pl. 4, figs 1–2.

Jorunna zania Marcus, 1976: 44–45, figs 31–32, syn. nov.

Additional material: Île de France, Île Maurice, 1 specimen, 45 mm preserved length, leg. Mathieu (MNHN); Nouvelle Calédonie, 1 specimen, 45 mm preserved length, Musée des Colonies entrée 1863 (MNHN); Nosy Bé, Madagascar, 19 May 1993, 1 specimen, 15 mm preserved length, 5 m depth (MNHN); Passe Femme, Aldabra Atoll, Indian Ocean (9°S, 46°E), 24 March 1986, 1 specimen, 15 mm preserved length, leg. T. Gosliner (CASIZ 074203); Horseshoe Cliffs, Okinawa, Ryukyu Islands (26° 30'N, 127° 50.9'E), 16 July 1989, 1 specimen, 0.8 mm preserved length, 3 m depth (CASIZ 070192); Horseshoe Cliffs, Okinawa, Ryukyu Islands 26 July 1991, 1 specimen, 6 mm preserved length, leg. R. F. Rolland, 3 m depth (CASIZ 079367); Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April 1996, 1 specimen (dissected), 20 m depth, 6 mm preserved length, leg. T. Gosliner (CASIZ 106445); Gulf of Thailand, Thailand (10° 26' 04"N, 99° 17' 33"E), 17 May 1960, 1 specimen (dissected), 3 mm preserved length (CASIZ 082106); Ulebsechel Island, Palau, 1 specimen, 35 mm preserved length, leg. F. di Crisi (CASIZ 107466); Koror, Palau (07°20'N, 134° 30'E), 23–26 February 1978, 2 m depth, 2 specimens (both dissected), 38–40 mm preserved length, length A. J. Ferreira (CASIZ 76340); 200 yds West of Orahal (Orakuru) Island, North of Aimeliik Municipality,

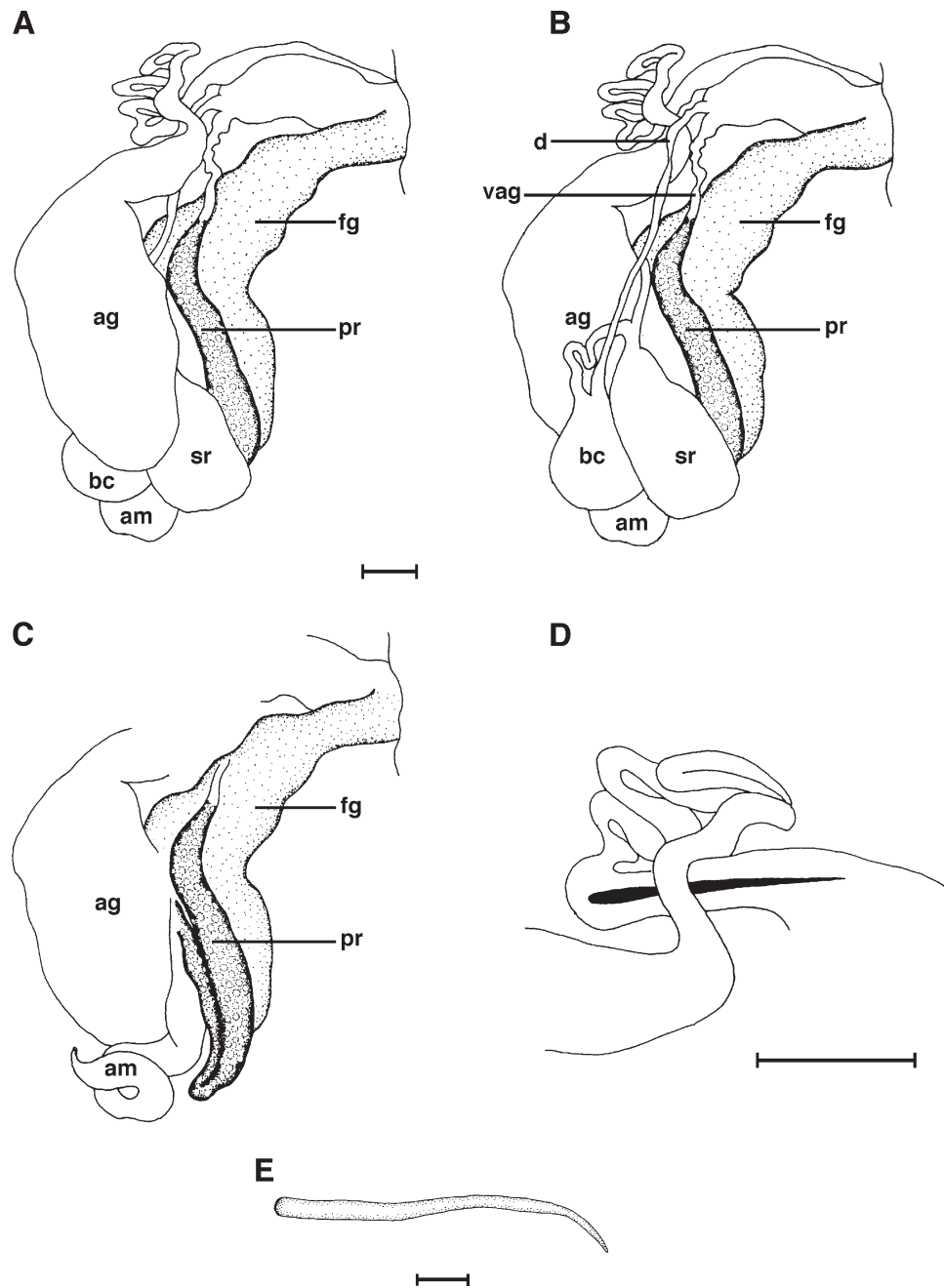


Figure 5. *Jorunna funebris* (Marshall Islands, CASIZ 120962). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Detail of the accessory gland that carries the copulatory spine; scale bar = 1.0 mm. **E.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

Babelthuap, Palau, (07°29'05"N, 134° 28' 58"E), 26 September 1956, 1 specimen (dissected), 22 mm preserved length, leg. S.Warbou (CASIZ 81840); Kwajalein Atoll, Little Bustard Reef, Marshall Islands, 1983, 1 specimen (dissected), 20 mm preserved length, leg. J. Wedge (CASIZ 120962); Madang, Papua New Guinea, September–October 1986, 5 specimens, 24–65 mm preserved length (CASIZ 073055); New Caledonia (20° 46.5'S, 165° 14'E), September 1993, 1 specimen, 5 mm preserved length, 1–4 m depth (MNHN); Shark Bay, Australia, no collection date, 1 specimen, 34 mm preserved length, leg. Peron (MNHN).

External morphology: Body rigid, finely tomentose. Body profile high, dorsum densely covered with caryophyllidia, about 220 µm in length (Fig. 4D). Rhinophoral and branchial leaves low. Six tripinnate branchial leaves and 14 lamellae on rhinophores in a 20 mm preserved length specimen (CASIZ 120962), 6 tripinnate gills, 15 lamellae in 11 mm preserved length specimen (CASIZ 106445), 6 tripinnate gills, 20 lamellae in 15 mm preserved length specimen (CASIZ 074203). Branchial leaves large in size when compared to size of animals, varying in length within a single gill circle. Posterior prolongation of foot visible dorsally when animal moves.

Background colour of dorsum and foot white to yellow-cream. Notum with several dark brown to black rings of different sizes, larger in middle portion of middle body (Fig. 1C). Dark rings not completely covered with pigment, instead each ring composed of several minute dark brown to black spots homogeneously distributed inside. Border of notum and hyp-notum scattered with similar dark spots all around margins. No rings present on sole of foot; however a couple of dark brown dots at each side of notched upper lip in some specimens. Rhinophores white with black clubs. Branchial leaves white, rachises of first and second pinnae of each leaf with black line. White mantle glands present around margin of notum.

Anatomy: Labial cuticle smooth, devoid of rodlets. Radular formula of 20 mm preserved length specimen $21 \times (21.0.21)$ (CASIZ 120962) and $17 \times (19.0.19)$ in an 11 mm preserved length specimen (CASIZ 106445). Inner lateral teeth hamate, shorter, thinner than midlateral teeth and gradually increasing in size towards middle of half-row, lacking denticles (Fig. 4A). Midlateral teeth thick, hamate (Fig. 4B). Outermost teeth hamate, smaller than midlateral teeth, lacking denticles (Fig. 4C).

Wide, tubular ampulla convoluted in middle region, branching into the short oviduct and prostate (Fig. 5C). Oviduct enters closely adjacent to female gland mass. Female gland about the same size as accessory gland. Short vas deferens separates from ampulla and opens into the longer, widened portion of glandular prostate. Prostate consists of two distinct glandular sections, well differentiated. Deferent duct short, undulate. Long uterine duct emerges from female gland mass, joining pyriform seminal receptacle at its base (Fig. 5B). Duct connecting seminal receptacle and oval bursa copulatrix, long, coiled. Bursa copulatrix smaller than seminal receptacle in some specimens, whereas in others, twice as large as seminal receptacle (Fig. 5B). Vaginal duct emerging from base of bursa copulatrix long, thin, smooth. Muscular deferent duct opens into common atrium with vagina. No penial hooks. Large accessory gland connected to atrium (Fig. 5A). Accessory gland consisting of a muscular portion, with a curved, pointed spine about $717 \mu\text{m}$ long (Fig. 5D, E).

Distribution: South Africa (Gosliner, 1987), Tanzania (Marcus, 1976), Seychelles (present study), Ceylon (Kelaart, 1859), India (Alder & Hancock, 1864), Thailand (present study), Vietnam (Risbec, 1956), Singapore (Eliot, 1906), Central China Sea (Marcus, 1976), Philippines (Bergh, 1876), Marshall Islands (present study), Indonesia (Bergh, 1890), Palau and Caroline Islands (Marcus, 1965), and New Caledonia (present study).

Remarks: Kelaart (1859) described *Doris funebris* as a dorid with an ivory-white mantle ornamented with jet-black spotted circles and half-rings or imperfect annular spotted figures. Alder & Hancock's (1864) redescription is more complete, including an illustration of the animal.

Bergh (1876) introduced two species from the Philippines. *Kentrodoris annuligera*, described as having a bright yellowish mantle, with black rings and rhinophores and a black gill, for which he included anatomical descriptions and illustrations of the species and its radular teeth, and *Jorunna gigas*, which was characterized by caryophyllidia, black rhinophores, oral tentacles with black tips, a black-brown foot, curved body, an accessory gland with a spine, a labial cuticle smooth, six tripinnate branchial leaves, a dorsum with blackish marks, and hamate teeth without denticles. According to Marcus (1976), the description of these two species is very similar. Their radular

morphology is very similar, and they both have dark blotches or rings on the dorsum, and oral tentacles with black tips.

Considering the similarity between these two descriptions, and the fact that both species come from the same locality (Aibukit, Philippines), we synonymize them.

Eliot (1906) described *Kentrodoris maculosa* as having a yellow background with black ring-like spots, black rhinophores with white bases and apices, a yellow gill with black rachises, and oral tentacles with black apices. This species was synonymized by Marcus (1976) with *J. funebris*.

The original description of *Discodoris wetleyi* Allan, 1932 includes two figures (Allan, 1932: pl. 4, figs 1, 2) in which it is possible to recognize a colour pattern very similar to that of *J. funebris*. *Discodoris wetleyi* was described as having a notum with minute granulations, a prolongation of the foot that is visible when the animal is in motion, a yellowish cream background colour with irregular sized patches of dark brown composed of minute dots. The rhinophoral club is black with a white base. Branchial leaves are yellow-cream with dark brown tips and have numerous small dark spots along the marginal end of the foot. Kenny (1970) synonymized this species with *J. funebris* and, after studying the original descriptions, we agree with this conclusion.

According to Marcus (1976) the differences between *J. zania* and *J. funebris* are the size and shape of the penial papilla, which is large and bulbiform in *J. funebris* and smaller in *J. zania*. In addition, Marcus (1976) found that in *J. funebris* the atrium and the copulatory spine are longer, whereas in *J. zania* the atrium is partly everted and the copulatory spine smaller. Marcus (1976) also mentioned that both species have black spots on their notched upper lip and that *J. zania* sometimes has a few needle-like serrations in one or two of the outermost teeth, a feature that was not reported by Edmunds (1971) nor was found in the material studied here. The examination of several specimens of *J. funebris*, and the review of the original description and subsequent redescriptions, confirms that the external and internal features of *J. zania* fits with those of *J. funebris*. The presence of a smooth labial cuticle, a pointed accessory spine, the simple hamate shape of the teeth lacking denticulations, the external coloration of the body, including the presence of black spots on the notum and the presence of black spots on their notched upper lip, are characteristics of *J. funebris*. The presence of an everted atrium and the size and shape of the penial papilla could be due to preservation or intra-specific variation. For these reasons, we do not consider the features mentioned by Marcus (1976) enough to justify the existence of two different species, and therefore synonymize *J. zania* with *J. funebris*.

Jorunna pantherina (Angas, 1864)

(Table 2)

Doris pantherina Angas, 1864: 47–48 (Port Jackson, Australia; type lost, not at Australian Museum, nor BMNH).

Jorunna pantherina—Thompson, 1975: 492–493, pl. I(h), (i); fig. 4.

Gargamella novozealandica Eliot, 1907: 341.

? *Jorunna hartleyi* Burn, 1958: 28–29.

Distribution: Australia (Thompson, 1975; Marcus, 1976; Willan & Coleman, 1984), New Zealand (Miller, 1996).

Remarks: The redescriptions of *J. pantherina* from Australia by Thompson (1975) and Marcus (1976) closely resemble the

redescription of the same species by Miller (1996) in the radular and external morphology and details of the reproductive system. According to these authors, *J. pantherina* is characterized by having a purplish brown or dark grey to pale brown or greenish background colour with small dark blotches, bipinnate branchial leaves, an accessory gland with a spine and hamate outermost and midlateral teeth, lacking denticles. However, Thompson (1975) and Marcus (1976) reported the presence of jaw elements in their specimens, a feature that is not present in the description by Miller (1996). Marcus (1976) illustrated the jaw elements in her description. Miller (1996) mentioned that there are some differences between specimens from New Zealand and Australia; the former can be very dark in colour, with a smooth labial cuticle and without autotomization of the mantle rim.

Unfortunately, due to the absence of material, we are unable to clarify the presence of jaw elements to confirm the identity of this species. The presence of acutely pointed lateral teeth and jaws in *J. hartleyi* Burn, 1958, and *J. pantherina* (Angas, 1864), the verification that *J. hartleyi* possesses an accessory gland spine and that both species are found in Australia, strongly suggest that they are possible synonyms.

Jorunna rubescens (Bergh, 1876)

(Figs 1E, 6, 7, Table 2)

Kentrodoris rubescens Bergh, 1876: 413–419, pl. 33, fig. 8, pl. 49, figs 14–19, pl. 50, figs 1–8 [Aibukit, Philippines, syntype, 1 specimen, 75 mm (ZMUGAS-2108) leg. C. Semper in 1876 or 1862 (two labels with different years)].

Jorunna rubescens—Valdés & Gosliner, 2001: 127–130, figs 16–18.
? *Doris venosa* Quoy & Gaimard, 1832: 272–275, pl. 20, figs 15, 16 [Île de la Réunion, type lost, not at MNHN (Valdés & Héros, 1998; Valdés & Gosliner, 2001)].

Additional material: St Gilles, Île de la Réunion, 15 November 1993, 2 specimens, 38–65 mm preserved length, 30 m depth, leg. M. Jay (MNHN); Okinawa, Ryukyu Islands (26° 30.2'N, 127° 51.7'), 15 July 1989, 2 specimens (1 dissected), 45–66 mm preserved length, 1.5 m depth, leg. R. Bolland (CASIZ 070191); Okinawa, Ryukyu Islands (26° 30.2'N, 127° 51.7'), 24 June 1989, 1 specimen (dissected), 80 mm preserved length, 2 m depth, leg. R. Bolland (CASIZ 070070); Kwajalein Atoll, Marshall Islands, August 1988, 2 specimens, 60–80 mm preserved length, 1 m depth, leg. S. Johnson and S. Jazwinski (CASIZ 120645); Ennubuj-Ennylabegan Reef, Ennubuj Island, Kwajalein Atoll, Marshall Islands, 22 May 1995, 1 specimen (dissected), 18 mm preserved length, leg. A. Vaccaro (CASIZ 120646); near Madang, Papua New Guinea, 7 October 1986, 1 specimen (dissected), 38 mm preserved length, leg. T. Frohm (CASIZ 72838); North of Madang, Papua New Guinea, 21 July 1989, 1 specimen, 42 mm preserved length, leg. J. Markham (CASIZ 068673); Pig Island, Madang Lagoon, Papua New Guinea, 31 October 1996, 1 specimen (dissected), 35 mm preserved length, leg. T. Gosliner (CASIZ 109797); Near Madang, Papua New Guinea, 5 October 1986, 1 specimen 41 mm preserved length, leg. J. Darr (CASIZ 073074); Run Islands, Banda Islands, Moluccas, Indonesia, 15 November 1993, 2 specimens, 38–50 mm preserved length, leg. P. Fiene (CASIZ 098708); Banda Islands, Moluccas, Indonesia; 15 November 1993, 2 specimens, 35–47 mm preserved length, leg. P. Fiene (CASIZ 098708); Arthur's Rock, Calumpun Peninsula, Batangas Province, Luzon, Philippines, 11 May 2001, 1 specimen, 55 mm preserved length, leg. T. Gosliner (CASIZ 173705).

External morphology: Body elongate, elevated (Fig. 1E). Caryophyllidia about 176 µm in length, densely distributed covering entire dorsum, with long, ciliated base, spicules projecting over tip and elongate tubercle (Fig. 6E). Rhinophoral and branchial sheaths highly elevated. Seven tripinnate branchial leaves and 23 lamellae on rhinophores in 35 mm preserved length specimen (CASIZ 109797), 6 tripinnate gills, 23 lamellae in 42 mm preserved length specimen (CASIZ 068673), 7 tripinnate gills, 25 lamellae in 41 mm preserved length specimen (CASIZ 073074).

Background colour cream greyish to yellow, with a distinctive pattern on dorsum in living animals that can also be seen in preserved specimens. Pattern consisting of several oval yellow spots surrounded by a cream ring, distributed all over dorsum. Several horizontal black stripes along body (Fig. 1E). Anterior part of head black with some yellow dots. Rhinophoral sheaths black. Base of rhinophores black or cream yellowish, club black-spotted with some cream white spots. Branchial sheaths black-spotted with some oval yellow spots at base becoming bigger at tip. Base of branchial leaves white, rachises dark brown. Upper lip of anterior border of foot speckled with black. Sole of foot white-creamish with some black stripes also present on laterals of foot. Posterior end of foot dorsally visible when the animal moves. Foot cream greyish to yellow with some dark black spots on edges. Ventrally, anterior border of foot grooved, notched. Oral tentacles conical, white to yellow.

Anatomy: Labial cuticle smooth. Radular formula of 35 mm preserved length specimen 22 × (29.0.29) (CASIZ 109797) and 26 × (18.0.18) in 18 mm preserved length specimen (CASIZ 120646). Rachidian teeth absent (Fig. 6A). Midlateral teeth long, elongated and blunt having a single cusp, lacking denticles (Fig. 6B). Teeth increase in size gradually towards the medial portion of half-row. Outer lateral teeth shorter, curved and pointed (Fig. 6C).

Ampulla long and convoluted (Fig. 7B), branching into short oviduct and prostate. Flattened prostate short, wide with a loop in middle portion (Fig. 7C). Prostate narrowing into long, convoluted deferent duct, expanding into ejaculatory portion. Penis unarmed. Highly differentiated, pear-shaped accessory gland (Fig. 7A) with spine about 3.7 mm in length (Fig. 6D). Vagina long, almost straight. At proximal end, branching into duct that connects to a lobate seminal receptacle and uterine duct (Fig. 7B). Uterine duct short, wide opening near the upper part of female gland mass. Seminal receptacle one-third as large as oval bursa copulatrix.

Distribution: Western Pacific – Japan, China Sea, Marshall Islands, Malaysia, Thailand, Philippines, Indonesia, Papua New Guinea and Australia (Marcus, 1976); Western Indian Ocean – Aldabra Atoll, Mauritius, Sri Lanka, Île de la Réunion (present study).

Remarks: According to Valdés & Gosliner (2001), *Doris venosa* Quoy & Gaimard, 1832 is a likely senior synonym of *J. rubescens* (Bergh, 1876). *Doris venosa* was described as being a dorid with a white background and broken irregular reddish lines resembling 'veins' on the dorsum, and which also has yellow along the edges with some orange spots; the mantle has blue dark spots and the animal has an elevated body. Although the description resembles that of *J. rubescens*, we regard *Doris venosa* as a possible synonym, following Valdés & Gosliner (2001), due to the uncertainty in establishing the generic position of the species and lack of type material.

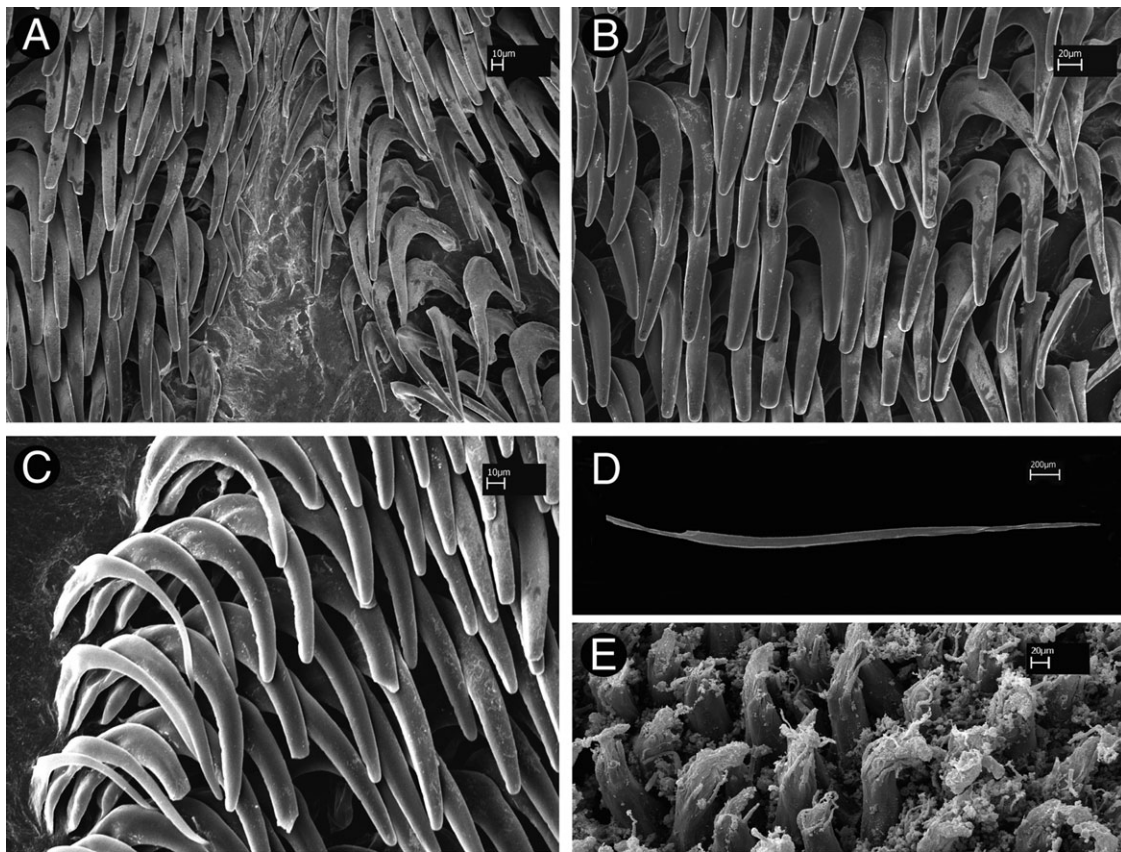


Figure 6. *Jorunna rubescens* (Papua New Guinea, CASIZ 109797). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Copulatory spine. **E.** Caryophyllidia.

***Jorunna evansi* (Eliot, 1906) new comb.**

(Fig. 25B, C)

Rostanga evansi Eliot, 1906: 144, pl. 14, fig. 6a–c [Porto Praia, Cape Verde Islands, lectotype, not dissected, 4 mm preserved length, leg. T. G. Evans (BMNH 1919.10.7.43–45); paralectotypes: 2 dissected specimens, 6–9 mm preserved length, leg. T. G. Evans (BMNH 1919.10.7.44–45). Slide with atrium of 9 mm preserved specimen mounted, with same number].

Distribution: Cape Verde Islands only (Eliot, 1906).

Remarks: This species was originally placed in the genus *Rostanga* by Eliot (1906), presumably because of the presence of a prostate, unipinnate branchial leaves and caryophyllidia. According to Rudman & Avern (1989), the narrow radula (with twenty or less teeth in a half row) is a characteristic of the genus *Jorunna* rather than *Rostanga*.

Rudman & Avern (1989) also mentioned that *J. spazzola* (Marcus, 1955), described from Brazil, is similar to this species in external coloration and radular morphology. However, Marcus (1955) described an accessory gland with a spine in *J. spazzola*, a characteristic that was not found by Eliot (1906) in *J. evansi*.

The present study of one of the paralectotypes (9 mm) of *Rostanga evansi* showed that an accessory gland with a curved copulatory spine is present (Fig. 25B). In addition, although Eliot (1906) mentioned the lack of oral tentacles in the specimens studied from Cape Verde, the 4 mm lectotype specimen showed oral tentacles (Fig. 25C).

From the descriptions of *J. evansi* and *J. spazzola*, as well as the examination of a new specimen from Costa Rica, we concluded that these two species share a similar external morphology and anatomy. The only difference we can see is the absence of a denticle on the innermost teeth in *J. evansi* that is sometimes present in *J. spazzola*. Whether these two species are synonyms or not remains uncertain in the absence of new material for comparison from Cape Verde.

***Jorunna labialis* (Eliot, 1908) new comb.**

(Figs 8, 9, Table 4)

Kentrodonis labialis Eliot, 1908: 112–113 [Red Sea, type lost, not at BMNH; neotype here designated (CASIZ 174617)].

Jorunna tomentosa—Edmunds, 1971: 364, fig. 11A–G (not Cuvier, 1804).

Jorunna malcomi Marcus, 1976: 41–43, figs 28–30 [Tanzania, holotype (BMNH 19752W)], syn. nov.

Type material: Neotype: Port Sudan, Sudan, 11 January 1958, 1 specimen (dissected), 7 mm preserved length, leg. F. Steiner, with three SEM stubs with mounted radula, jaw and mantle (CASIZ 174617).

Additional material: Port Sudan, Sudan, 11 January 1958, 3 specimens (all dissected), 7–10 mm preserved length, leg. F. Steiner (CASIZ 081804).

External morphology: Body oval, convex, with velvety texture. Dorsum covered with caryophyllidia, about 190 µm in

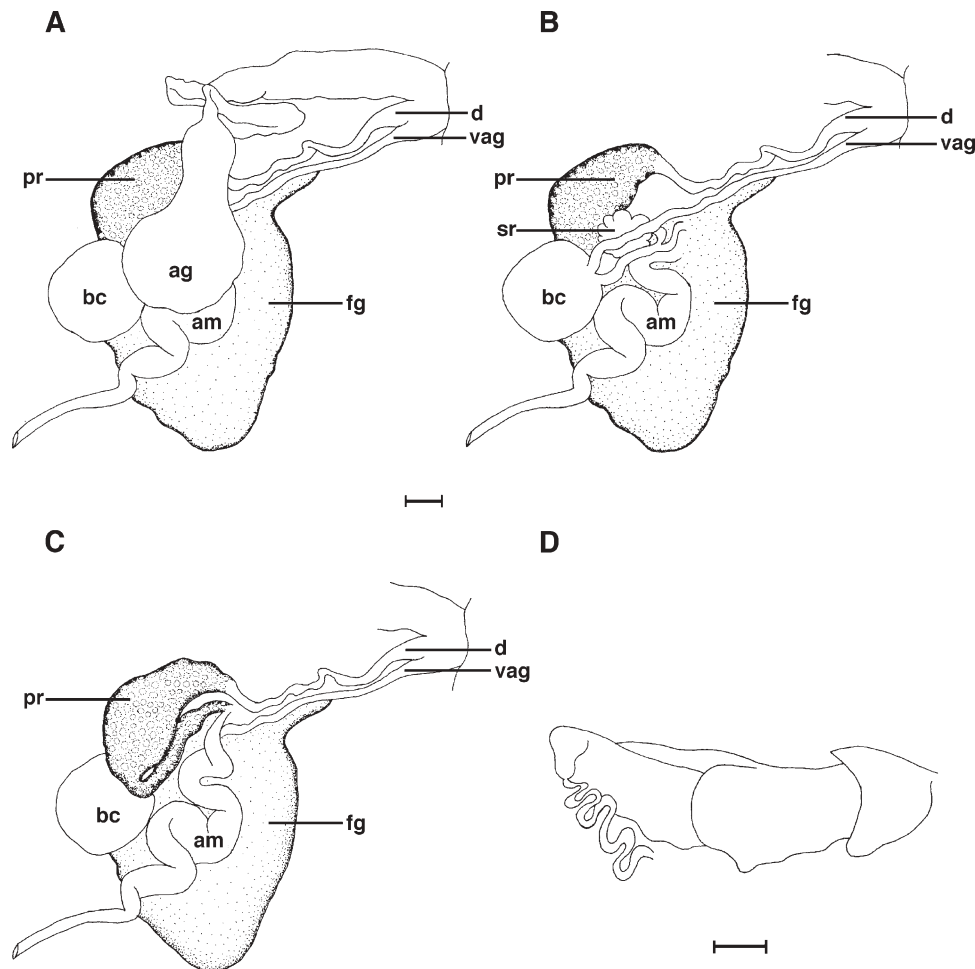


Figure 7. *Jorunna rubescens* (Papua New Guinea, CASIZ 109797). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Detail of the accessory gland that carries the copulatory spine; scale bar = 1.0 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

length (Fig. 8E) with long conical base, long spicules, short and rounded, ciliated tubercle. Spicules higher than tubercles. Rhinophoral and branchial sheaths low, regular. Eleven bipinnate branchial leaves forming a circle. Rhinophores wide, with eight lamellae in 10 mm preserved length specimen (CASIZ 081804). Eleven gills and 11 lamellae in 10 mm preserved length specimen (CASIZ 081804). Lamellae arranged almost vertically.

According to Eliot (1908), the colour of living specimens of *J. labialis* may vary from white to very dark dull grey with light brown spots. The general colour of preserved animals studied here is uniformly cream yellowish without spots. Rhinophores and gills same colour as mantle. Anterior border of foot notched and grooved. Oral tentacles conical. Mantle margin slightly wider than foot. Ventral colour same as dorsum in preserved animals.

Anatomy: Labial cuticle armed with jaw elements (Fig. 8D). Radular formula of 10 mm preserved length specimen $19 \times (17.0.17)$ (CASIZ 081804) and $19 \times (19.0.19)$ in 7 mm preserved length specimen (CASIZ 174617). Rachidian teeth absent. Innermost lateral teeth hamate, elongate, having a single cusp close to base of teeth (Fig. 8A). Midlateral teeth long, hamate, lacking denticles (Fig. 8B). Teeth increase in size gradually towards the medial portion of half-row. Outer lateral teeth shorter, hamate, pointed (Fig. 8C).

Ampulla elongate, tubular, with a loop in middle portion, branching into a short oviduct and prostate (Fig. 9C). Oviduct enters female gland near distal part of mass. Prostate flattened, folded, granular (Fig. 9C), connecting to a long duct leading into ejaculatory portion of deferent duct. Deferent duct thinner in its proximal part and opening into a common atrium with vagina. No penial hooks. Accessory gland, amorphous, convoluted, connecting to the atrium (Fig. 9A), with a muscular portion, a curved spine about $600 \mu\text{m}$ long (Fig. 9D), a wide duct, and glandular region connected to it. Vagina long, with some loops, thinner than deferent duct, connecting to bursa copulatrix at its distal end. Another duct, connecting to both the uterine duct and seminal receptacle leading from bursa copulatrix. Bursa copulatrix oval, about three times larger than oval seminal receptacle (Fig. 9B).

Distribution: Suez and Suakin, Red Sea (Eliot, 1908); Tanzania and Madagascar (Marcus, 1976); Sudan (present study).

Remarks: Eliot (1908) described *Kentrodoris labialis* from the Red Sea as a dorid with caryophyllidia, jaw elements, bipinnate gills, hamate outermost teeth without denticles, a curved spine and a white to dark dull grey mantle with some light brown spots.

Edmunds (1971) redescribed *J. tomentosa* (Cuvier, 1804) from Tanzania as having caryophyllidia, a labial cuticle with jaw elements, a convoluted prostate, outermost teeth with no

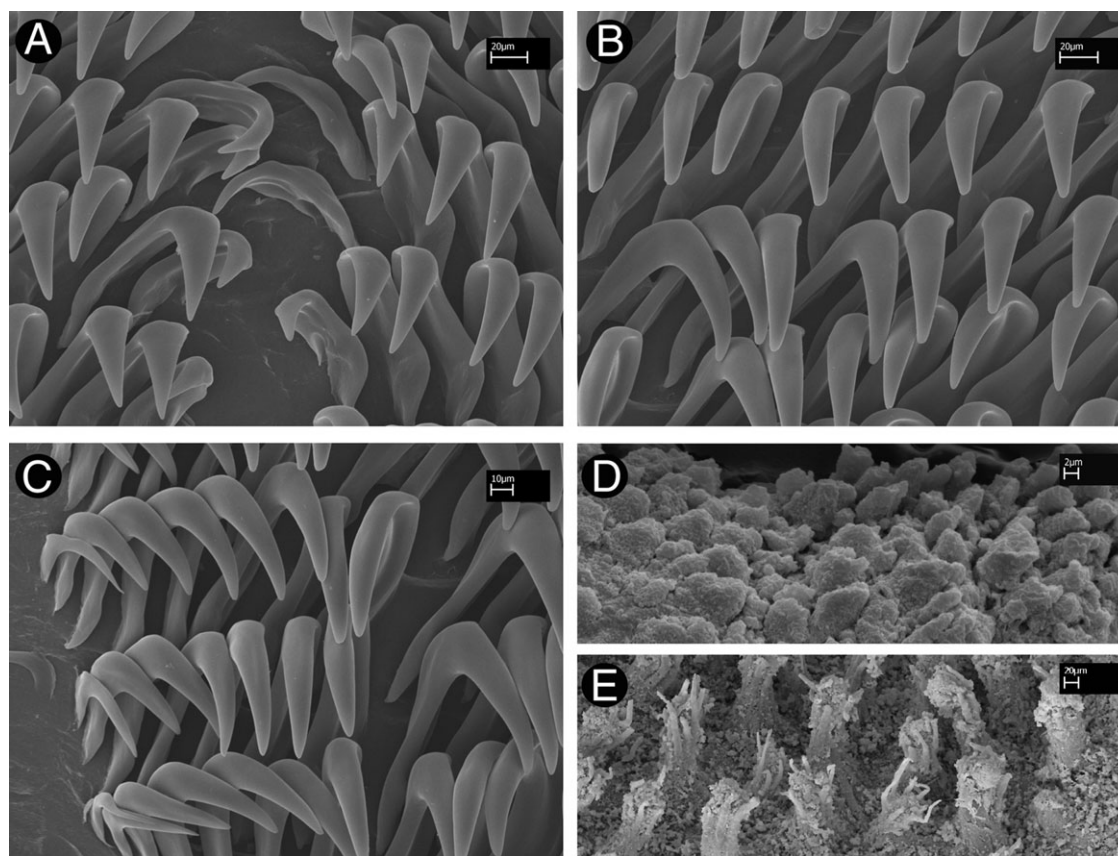


Figure 8. *Jorunna labialis* (Sudan, CASIZ 081804). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Jaw elements. **E.** Caryophyllidia.

basal plate, a lanceolate cusp, and a pale grey-green to grey background colour speckled with dark or purple-brown spots and white dots along the edges. Edmunds considered that *J. tomentosa* was a cosmopolitan species extending from Europe to the Marshall and Hawaiian Islands, following Kay & Young (1969).

Later, Marcus (1976) described *J. malcomi*, based on the specimens identified by Edmunds (1971) as *J. tomentosa* from Tanzania. According to Marcus (1976) *J. malcomi* is present in both the Atlantic Ocean (Ghana) and the Indian Ocean (Tanzania and Madagascar). Although the drawings of the reproductive systems provided by Marcus (1976) show no significant differences, the presence of this species in both areas seems very unlikely from a biogeographical perspective. The identification of Atlantic specimens remains doubtful until more specimens from both localities are studied.

Comparing the original descriptions of *J. malcomi* Marcus, 1976 from Tanzania and Ghana and of *J. labialis* (Eliot, 1908) from Suakin and Suez, we found that both species share the presence of caryophyllidia, a yellowish brown to pale grey-green background colour with rows of dark brown spots along the sides speckled with white marks, a labial cuticle with jaw elements, an accessory gland with a spine, midlateral and outermost teeth hamate and lacking denticles, and bipinnate gills. In addition, the reproductive system of these two species is very similar (Eliot, 1908; Edmunds, 1971; Marcus, 1976).

Our material from Port Sudan fits these descriptions and, therefore, *J. malcomi* and *J. labialis* are synonyms, the latter being the older name. *Jorunna labialis* differs from *J. tomentosa* by the presence of a labial cuticle with jaw elements, the shape of the outermost teeth and the absence of denticles. There are

also some differences in the reproductive system such as the absence of a large penial papilla in *J. labialis*. Finally *J. labialis* is white to very dark grey with light spots, while *J. tomentosa* is cream yellowish to grey with light spots that form two vertical lines. *Jorunna labialis* is distinguished from other species found in the Red Sea (*J. funebris*) and Indian Ocean (*J. rubescens*) by the external and radular morphology. *Jorunna funebris* and *J. rubescens* both have the mantle covered with dark rings or stripes, whereas these are not present in *J. labialis*. In addition, *J. rubescens* and *J. funebris* lack jaw elements.

***Jorunna parva* (Baba, 1938) new comb.**

(Figs 1F, G, 10, 11, Table 2)

Thordisa parva Baba, 1938: 15, fig. 11 (Seto, Kii, Japan).

Additional material: Mana Huanja Island, Mtwara Region, Tanzania, 4 November 1994, 1 specimen, 2 mm preserved length, leg. T. Gosliner (CASIZ 099315); Passe Femme, Aldabra Atoll, Seychelles (9°S, 46°E), 19 March 1986, 1 specimen, 6 mm preserved length, leg. T. Gosliner (CASIZ 074251); Okinawa, Ryukyu Islands, Japan, 27 June 1987, 1 specimen, 11 mm preserved length, leg. R.F. Bolland (CASIZ 69943); Seragaki, Okinawa, Ryukyu Islands, Japan (26° 30' 40"N, 127° 52' 60"), 6 July 1998, 2 specimens (both dissected), 11–13 mm alive length, 61 m depth, leg. R. Bolland (CASIZ 115730); Club Ocellaris, Balayan Bay, Batangas Province, Philippines, 24 April 1997, 1 specimen, 8 mm preserved length, leg. C. Carlson (CASIZ 110391); Christiansen Research Institute, Madang, Papua New Guinea, 9 November

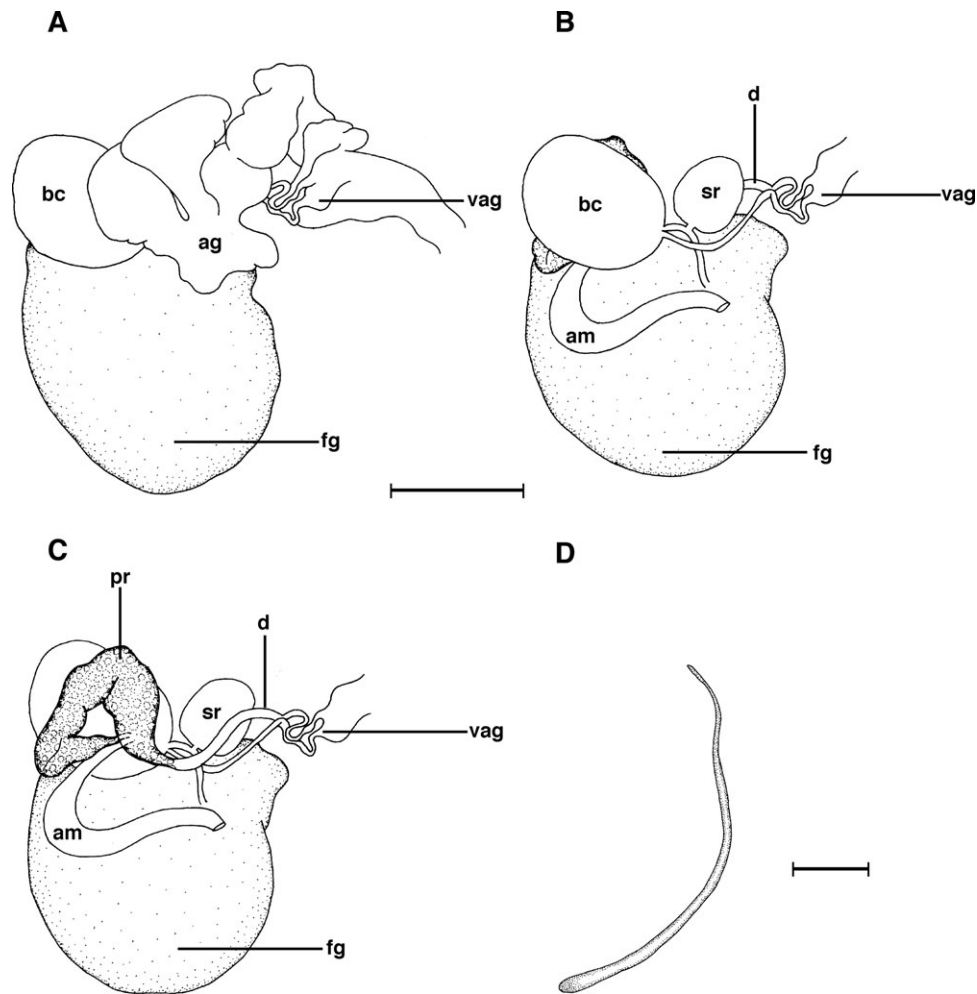


Figure 9. *Jorunna labialis* (Sudan, CASIZ 081804). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

1990, 1 specimen (dissected), 4 mm preserved length, leg. T. Gosliner (CASIZ 075929).

External morphology: Body elongate. Dorsum with long caryophyllidia, about 250 μm in length (Fig. 10D). Caryophyllidia with long cylindrical base, long spicules, and long ciliated tubercle. Caryophyllidia of different shapes and sizes, the larger ones sparsely distributed between the smaller ones. Larger caryophyllidia leaf-like in shape, homogeneously distributed, the rest generally smaller, elongated. Rhinophoral and branchial sheaths low. Seven short bipinnate branchial leaves and rhinophores with 15 lamellae in 8 mm preserved length specimen (CASIZ 115730). Six bipinnate gills and 14 lamellae in 6 mm preserved length specimen (CASIZ 74251).

Background colour of living animal dark yellow-orange to dark brown (Fig. 1F, G). Most specimens with a dark yellow background colour becoming lighter in areas close to rhinophores and gill. Other specimens with a dark brown colour in central part of dorsum, becoming dark yellow towards edges of mantle (forming a V-shape in area behind rhinophores). Light yellow colour following, becoming darker again towards front part of rhinophores (Fig. 1G). Higher caryophyllidia dark brown in colour, resembling dark spots in mantle. In some specimens, base of rhinophore rachis light yellow with dark brown clubs, base of gill light yellow with dark brown tips. Other specimens with

rhinophores with dark brown rachises containing light yellow clubs and light yellow gills with dark brown rachises. Foot with a dark brown line on middle part of visible portion, with dark brown spots along edges clearly visibly when the animal moves. Large white mantle glands around mantle.

Anterior border of foot notched, grooved. Oral tentacles elongate. Margin of hyponotum with dark brown spots. Upper lip yellowish with two brown spots on each side of lip in some specimens.

Anatomy: Labial cuticle smooth. Radular formula of 6 mm preserved length specimen $20 \times (15.0.15)$ (CASIZ 115730) and $17 \times (18.0.18)$ in a 4 mm preserved length specimen (CASIZ 075929). Rachidian teeth absent. Lateral teeth increasing in size gradually towards medial portion of half-row. Innermost teeth hamate, elongate, lacking denticles (Fig. 10A). Midlateral teeth hamate without a prominent cusp (Fig. 10B). Outermost teeth smaller, less hamate than midlateral teeth (Fig. 10C). Five outermost teeth pectinate.

Ampulla long, curved, branching into a short oviduct and prostate (Fig. 11B). Oviduct entering female glands close to distal part of mass. Prostate flattened, glandular, folded in middle region, connecting to a short folded duct expanding into short ejaculatory portion of deferent duct. Muscular deferent duct opening into a common atrium with vagina.

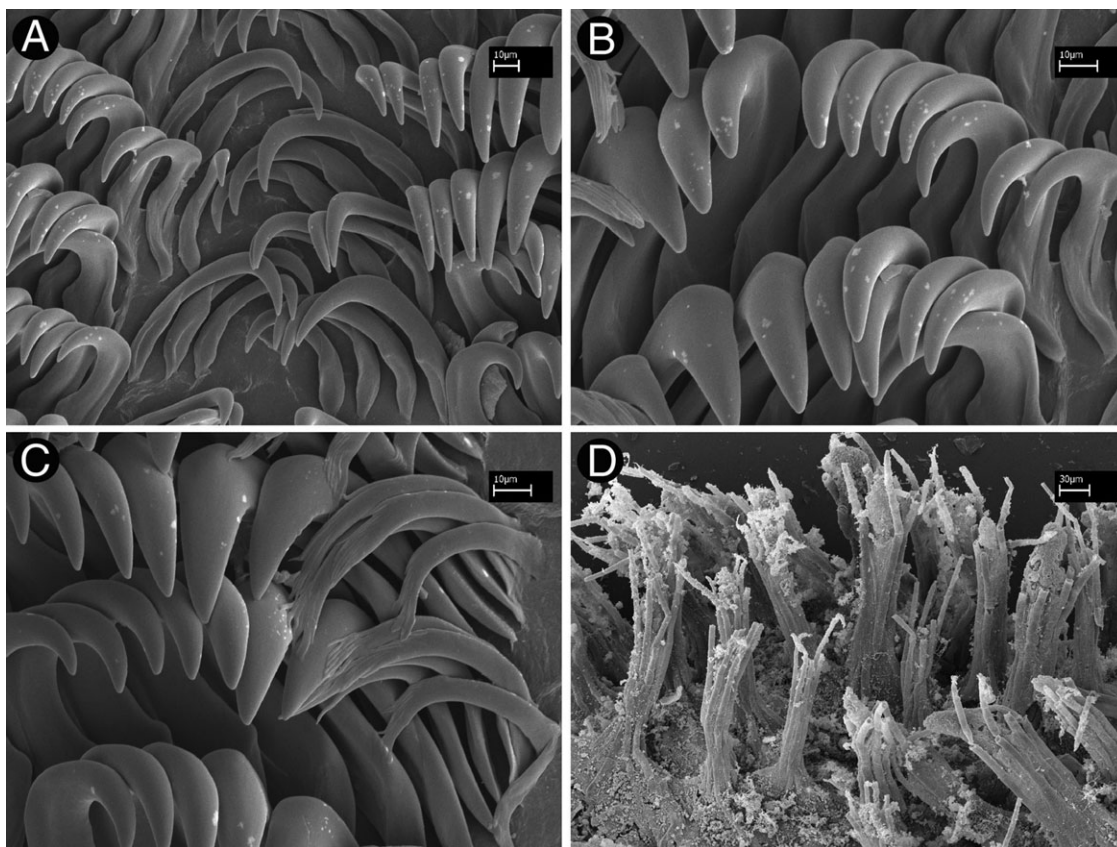


Figure 10. *Jorunna parva* (Japan, CASIZ 115730). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Caryophyllidia.

No penial hooks. Large, convoluted accessory gland connecting to atrium, with a muscular portion, a pointed spine about 477 μm long (Fig. 11C), a long, thin folded duct and a glandular, convoluted proximal area. Vagina short, wider in its proximal region connecting to oval bursa copulatrix. Another thin duct leading from bursa copulatrix, connecting to long uterine duct and pear-shaped seminal receptacle. Bursa copulatrix larger than seminal receptacle (Fig. 11A).

Distribution: Tanzania, Seychelles (present study) to Kii Peninsula (Baba, 1938) and Okinawa in Japan, Philippines and Papua New Guinea (present study).

Remarks: According to Baba (1938), *Thordisa parva* is characterized by having digitiform oral tentacles, a smooth labial cuticle, some black spots on the dorsal tubercles and on the edges of the hyponotum, black rhinophoral tips and branchial leaves, most lateral teeth hamate without denticles and pectinate outermost teeth. From this and our own material of *Thordisa parva*, we conclude that this species should be transferred to the genus *Jorunna*, because of the presence of caryophyllidia and a large accessory gland with a long spine. In *Thordisa*, there are simple elongate tubercles and the accessory gland is much smaller with short spines (Chan & Gosliner, 2007).

Jorunna parva differs from other species of *Jorunna* from the Indo-Pacific in its external coloration and radular morphology. *Jorunna parva* is the only species of the genus that has dark tubercles resembling dark spots on the mantle; a visible foot with a dark brown line on the middle part of the dorsal side with dark brown spots on the edges is also a characteristic of

the species. Although the radular morphology of *J. parva* is similar to that of *J. ramicola*, there are some differences. The labial cuticle of *J. parva* is smooth, whereas there are jaw elements in the other species. Also, there are no denticles on the innermost teeth of *J. parva*, whereas they are present in *J. ramicola*.

Jorunna spazzola (Marcus, 1955)

(Figs 1H, 12, 13, Table 4)

Aiwuka spazzola Marcus, 1955: 156, figs 180–192 [São Sebastião Island, Brazil, type probably lost, not at MZSP or USNM according to Valdés & Gosliner (2001)]. Marcus, 1958: 57. Marcus & Marcus, 1964: 199. Marcus, 1970c: 210.

Jorunna spazzola—Marcus, 1976: 35–38, figs 23–26.

Jorunna tomentosa—Schmekel, 1968: 115, 148 (not Cuvier, 1804).

Jorunna luisae Marcus, 1976: 45–50, figs 33–46, syn. nov. [Naples, Italy, holotype, 1 specimen, 9 mm preserved length, leg. L. Schmekel (USNM 710702)]. Schmekel & Portmann, 1982: 92–93, Taf. 20, fig. 10, Taf 31, fig. 12.

Additional material: Cozumel, Quintana Roo, Mexico 31 December 1977, 1 specimen, 3 mm preserved length (CASIZ 076244); Long Island, Cape Santa Maria, Bahamas (23° 41'N, 75° 30'W), 24 August 1975, 1 specimen (dissected), 9 mm preserved length, 25–40 m depth, leg. A. Ferreira and E. Daily (CASIZ 003521); Punta Mona, Manzanillo, Costa Rica, 30 December, 2005, 1

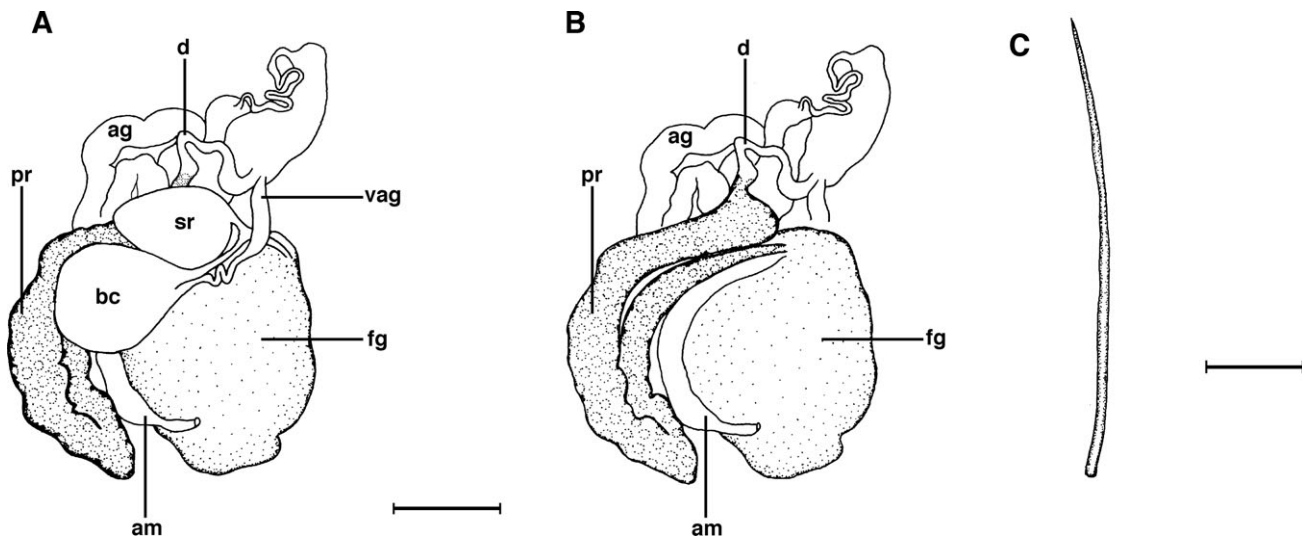


Figure 11. *Jorunna parva* (Japan, CASIZ 115730). **A–B.** Detail of the reproductive system; scale bar = 1.0 mm. **C.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

specimen (dissected), 7 mm preserved length, 7.5 mm depth, leg. A. Valdés (CASIZ 175680).

External morphology: Body elongated. Dorsum covered with long caryophyllidia about 133 μm in length (Fig. 12E) with long cylindrical base, short spicules and a long ciliated tubercle. Six bipinnate gills and 13 lamellae in rhinophores in a 7 mm preserved length specimen (CASIZ 175680).

Background colour of living animal varies from light grey (Fig. 1H) or white-yellow to orange with several minute dark spots around dorsum but concentrated in middle part. Viscera pinkish, clearly visible through body in some specimens. White mantle glands around mantle edge. Rhinophores light grey speckled with brown minute spots, opaque white on tips. Gills light grey, speckled with minute brown spots, opaque glandular structures on tips. Foot and hyponotum same colour as notum, without spots. Cream oral tentacles conical in shape.

Anatomy: Labial cuticle with elongated jaw elements (Fig. 12D). Radular formula $15 \times (20.0.20)$ in 7 mm preserved length specimen (CASIZ 175680). Rachidian teeth absent. Innermost teeth lacking a denticle (Fig. 12A). Midlateral teeth hamate lacking a cusp (Fig. 12B). Lateral teeth increase in size from inner to midlateral. Outermost teeth small, pectinated (Fig. 12C).

The reproductive system of the holotype of *J. luisae* was studied. Ampulla thick and convoluted, divided into short oviduct and prostate (Fig. 13A). Ampulla entering small female gland near upper part of mass. Prostate large, granular and folded into itself, expanding into short ejaculatory portion. Deferent duct opening into common atrium with vagina. Penial hooks absent. Convoluted accessory gland connecting to atrium, with a spine visible through the tissue (Fig. 13B). Vagina wider than deferent duct, tubular and coiled. Duct that connects bursa copulatrix with seminal receptacle long and coiled. Seminal receptacle absent.

The reproductive systems of the specimens from Costa Rica and the Bahamas were not fully mature. Ampulla particularly wide in both specimens examined (Fig. 13D), entering small female gland near distal part of mass. Prostate granular, flattened, connecting to deferent duct, other portion

connecting to female gland. Deferent duct long and coiled, expanding again into tubular ejaculatory portion. Deferent duct opening into a common atrium with vagina. No penial hooks.

Small accessory gland connecting to atrium (Fig. 13D). No spine was found in the immature specimens. Vagina long, tubular, connecting to oval bursa copulatrix at its distal end. Another convoluted duct, connecting to oval seminal receptacle and uterine duct, leading from bursa copulatrix. Bursa copulatrix bigger than seminal receptacle (Fig. 13D).

Distribution: Mediterranean, and in Western Atlantic from Brazil, Mexico, Costa Rica and the Bahamas (present study).

Remarks: The holotype of *J. luisae* has been dissected. The coloration of the preserved animal is unknown, the specimen being stained with purple ink. There are caryophyllidia all over the dorsum. The radula and jaws (buccal bulb) of the holotype are missing. The reproductive system remains in the body, all the organs are present but the receptaculum seminis (Fig. 13A). The penis is everted and the spine is visible through the tissue (Fig. 13B). Other internal organs such as stomach, digestive gland and intestine are missing. Twelve lamellae in rhinophores. No branchial leaves present. Oral tentacles present.

Er. Marcus (1955) described *Awuka spazzola* from Brazil. Later, Ev. Marcus (1976) redescribed the same species and placed it in the genus *Jorunna*. Ev. Marcus was aware of the error in the original description, where the accessory spine was interpreted as situated in the penis instead of in the accessory gland, as noted by Valdés & Gosliner (2001).

Jorunna spazzola differs from most other members of the genus by the presence of jaws. The innermost lateral teeth are with or without a denticle and the outermost radular teeth are denticulate. However, *J. luisae* Marcus, 1976 from the Mediterranean is another species that shares these features. According to the original descriptions (Er. Marcus, 1955; Ev. Marcus, 1976), they both have caryophyllidia, a labial cuticle with jaw elements, unarmed penis, an accessory gland with a spine, the innermost radular teeth with a small denticle, outermost teeth with irregular denticles and uni to tripinnate leaves. According to the redescription of *J. luisae* by Schmekel &

Portmann (1992) based on several specimens from Naples, this species has innermost teeth lacking a denticle and outermost teeth pectinate (2–4 denticles). In the specimen we examined from Costa Rica, we also found the innermost teeth lacking denticles but the outermost tooth pectinate. The presence or absence of denticles in the innermost teeth seems to be variable within the species.

The drawings of the reproductive systems in the original descriptions of these two species are very similar. No major differences can be identified other than the absence of loops in some of the ducts in *J. spazzola*, which could be due to the manipulation of the organs during dissection. Marcus (1976) stated that “... the differences between *J. spazzola* and *J. luisae* are insignificant...”, however she preferred to keep the species from the Mediterranean separate from the Brazilian one. These differences are a larger number of lamellae on the rhinophores and teeth, shorter jaw elements, and a smaller female gland mass in *J. luisae*.

The similarity between these two species does not allow us to justify their separation of the species, so we regard them as synonyms. See also remarks on *J. evansi* from Cape Verde Islands.

Jorunna hartleyi (Burn, 1958)

(Fig. 25A, Table 2)

Rostanga hartleyi Burn, 1958: 28–29, text fig. 5, pl. 2, figs 12–13 [Breamlea, Victoria, Australia, holotype, 12 mm preserved length, leg. R. Burn, 6 January 1958 (National Museum Victoria F19471), accessory gland mounted on slide (National Museum Victoria F19471a)].

Jorunna hartleyi—Burn, 1962: 163–165, figs 15–16.

Distribution: Only from northwestern Kawau Island, Victoria, Australia (Burn, 1958).

Remarks: The generic position of this species from southern Australia has recently been clarified by Rudman & Avern (1989). According to these authors, *Rostanga hartleyi* is most appropriately placed in the genus *Jorunna*, because of the radular morphology and the anatomy of the reproductive system. *Jorunna hartleyi* is characterized by having a pale pink mantle with large brown patches encircled with white or dark purple spots, caryophyllidia, an accessory gland without a spine, a smooth labial cuticle, an unarmed penis, elongate outermost teeth lacking denticles, and hamate midlateral and innermost teeth lacking denticles. In contradiction to what these authors found in the accessory gland, we examined the holotype of *R. hartleyi* and found that the accessory gland is partially extruded, so that we could confirm the presence of a long spine of about 198 μm (Fig. 25A).

Comparing the original descriptions of *J. hartleyi* (Burn, 1958) and of *J. pantherina* (Angas, 1864), we found that these species share the presence of pointed lateral teeth and the presence of jaws, and both have been found in Australia. This suggests that they are possible synonyms, remains uncertain in the absence of new material for comparison.

Jorunna alisonae Marcus, 1976

(Figs 11–K, 14, 15, Table 2)

Jorunna alisonae Marcus, 1976: 39–41, fig. 27A–G [Honolulu, Hawaii, holotype, 6 mm preserved length, leg. E. A. Kay, 17 April 1965 (USNM 710701)].

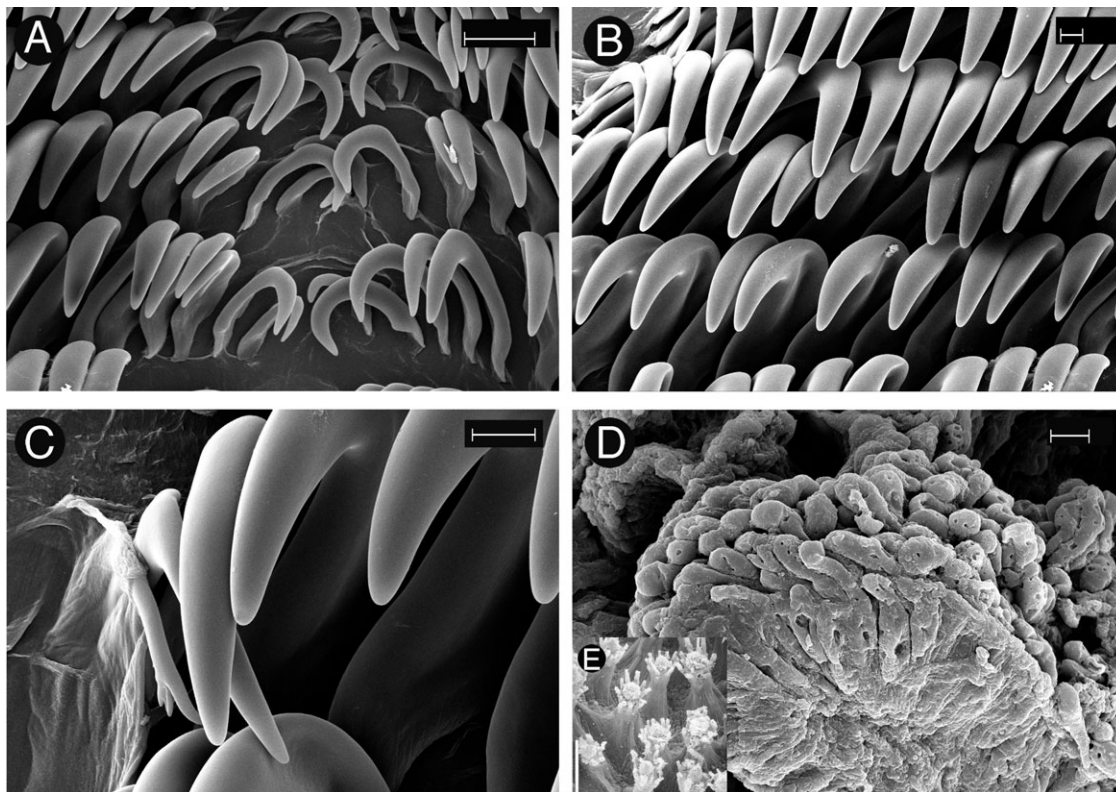


Figure 12. *Jorunna spazzola* (Costa Rica, CASIZ 175768). SEM photographs of the radula. **A.** Inner lateral teeth, scale bar = 30 μm . **B.** Lateral teeth, scale bar = 10 μm . **C.** Outermost teeth, scale bar = 10 μm . **D.** Jaw elements, scale bar = 10 μm . **E.** Caryophyllidia (Mexico, CASIZ 076244), scale bar = 100 μm .

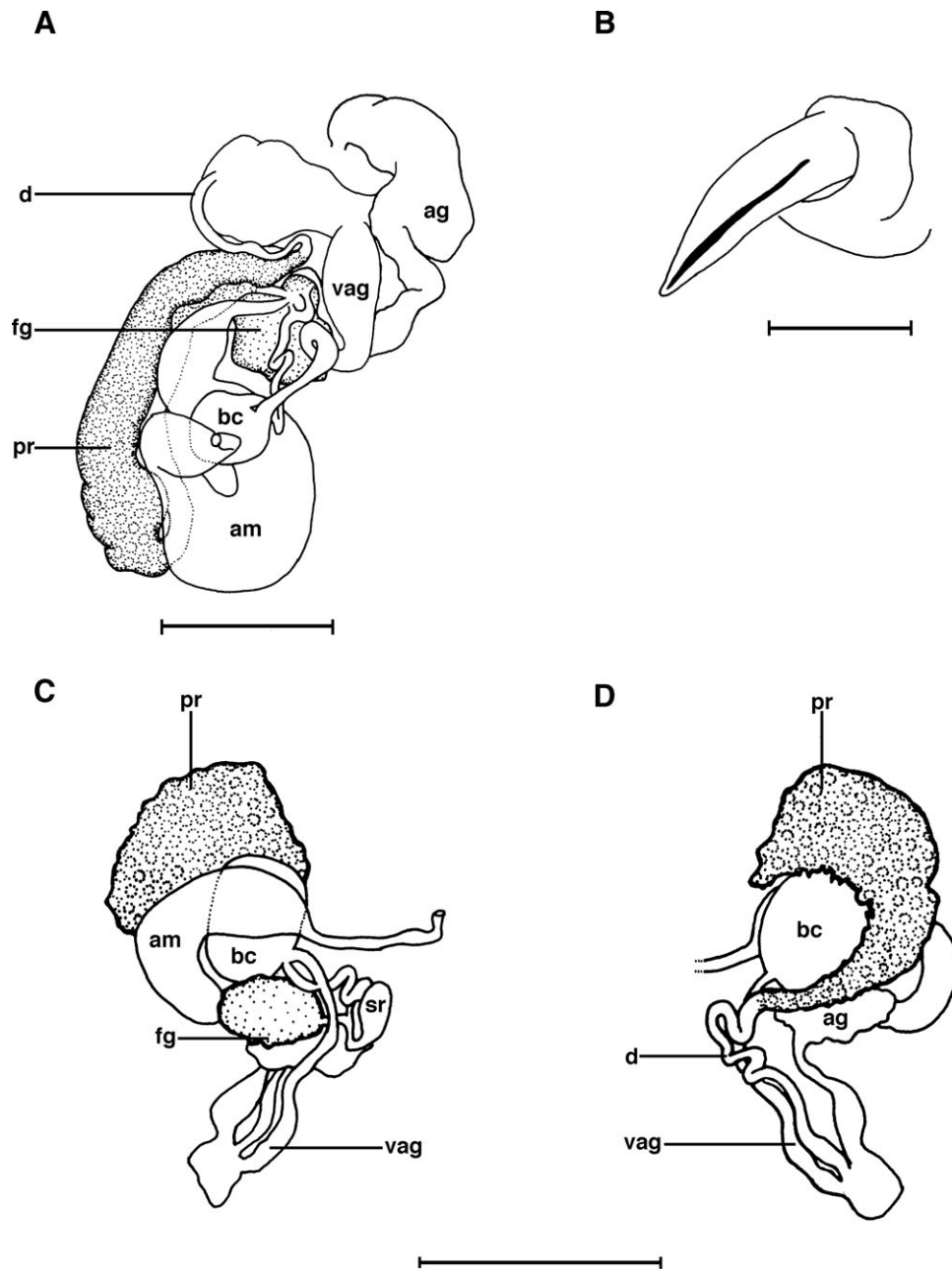


Figure 13. **A.** Detail of the reproductive system of the holotype of *Jorunna luisae* (USNM 710702); scale bar = 1.0 mm. **B.** Penis of the holotype of *Jorunna luisae* (USNM 710702); scale bar = 1.0 mm. **C.** Detail of the reproductive system of *Jorunna spazzola* (Costa Rica, CASIZ 175768); scale bar = 1.0 mm. **D.** Detail of the reproductive system of *Jorunna spazzola* (Costa Rica, CASIZ 175768); scale bar = 1.0 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

Jorunna tomentosa—Young, 1967: 168 (not Cuvier, 1804).
 Kay & Young, 1969: 184, figs 11, 17 (not Cuvier, 1804).

Additional material: Hawaii, 1924, 1 specimen, 14 mm preserved length (CASIZ 067416); Maui, Hawaii, June 1997, 1 specimen, 12 mm preserved length, leg. C. Pittman (CASIZ 118774); Waikiki Beach, Honolulu, Oahu, Hawaii, 17 May 1924, 13 specimens (2 dissected), 8–14 mm preserved length, 5 m depth, leg. C. Edmondson (CASIZ 031866); Waianae, Oahu Island, Hawaii, 9 February 1986, 1 specimen, 0.9 mm preserved length, intertidal, leg. T. Gosliner (CASIZ 061457); Kewalo Sea Wall, Oahu Island, Hawaii, 13 September 1987, 2 specimens, 11–19 mm preserved length, intertidal, leg. T. Gosliner (CASIZ 087101); Hekili Point, Maui, Hawaii,

15 November 2000, 1 specimen, 10 mm alive length, intertidal, leg. C. Pittman (CASIZ 142961); Hekili Point, Maui, Hawaii, 23 October 2000, 1 specimen, 13 mm alive length, intertidal, leg. C. Pittman (CASIZ 142960); Kanaio, Maui, Hawaii, 9 January 1990, 1 specimen (dissected), 12 mm alive length, intertidal, leg. P. Fiene (CASIZ 087122); Enewetak, Marshall Islands, 3 September 1983, 1 specimen, 0.7 mm preserved length, leg. S. Johnson (CASIZ 121126); Enewetak, lagoon side of island, Marshall Islands, 16 May 1983, 1 specimen (dissected), 20 mm alive length, 5 m depth, leg. S. Johnson (CASIZ 121127); Bunaken Island, Manado, Sulawesi, Indonesia, August 1991, 2 specimens (both dissected), 5–6 mm preserved length, 0.5 m depth, leg. P. Fiene (CASIZ 078561).

External morphology: Body oval. Dorsum covered with caryophyllidia about 133 µm long (Fig. 14F). Caryophyllidia elongate, with long spicules. Twelve tripinnate branchial leaves and 10 lamellae in rhinophores in both specimens of 9 and 10 mm preserved length (CASIZ 031866). Oral tentacles conical. Anterior portion of foot notched, grooved.

Background colour pale grey, with numerous grey dots of different sizes on mantle margin (Fig. 11–K). Two lines of spots nearly forming two vertical lines arranged from rhinophores to gills. Viscera visible in the centre of dorsum. Rhinophores cream-brownish with a pale grey-brownish club. Gill grey to dirty brown with some cream glandular spots. Ventral part of animal, the same colour as dorsum. Posterior end of foot visible dorsally when animal moves.

Anatomy: Labial cuticle with jaw elements (Fig. 14E). Radular formula 16 × (17.0.17) in a 20 mm preserved length specimen (CASIZ 031866) and 19 × (21.0.21) in a 12 mm preserved length specimen (CASIZ 087122). No rachidian teeth. Innermost teeth shorter than midlateral ones, hamate, pointed, lacking denticles (Fig. 14A). Midlateral teeth, hamate, pointed, smooth (Fig. 14B). Outermost teeth small, elongate, smooth (Fig. 14C). Outermost teeth occasionally with a single denticle near middle of cusp (Fig. 14D).

Ampulla long, thin with a loop in distal portion, dividing into short oviduct and prostate (Fig. 15B). Ampulla entering female gland mass near upper middle part of mass. Prostate large, flattened, glandular, convoluted in middle section, narrowing into short, coiled deferent duct, and expanding again into muscular, narrow ejaculatory portion. Penis unarmed. Amorphous accessory gland with a distinct stylet sac containing a spine about 1.15 mm in length (Fig. 15A). Copulatory spine straight, pointed (Fig. 15D). Deferent duct opening into a common atrium with vagina. Vagina long, tubular (Fig. 15C). Uterine duct short, thin, opening in upper middle part of female gland mass. Convoluted duct from oval bursa copulatrix leading to seminal receptacle. Seminal receptacle slightly oval, almost as large as bursa copulatrix (Fig. 15C).

Distribution: Only from Hawaii (Marcus, 1976), Marshall Islands and Indonesia (present study).

Remarks: The holotype has not been dissected; it is well preserved and of creamish colour. There are 15 bipinnate branchial leaves. There are 15 bipinnate branchial leaves. We could only count about six lamellae in the rhinophores, which are strongly retracted into their rhinophoral sheaths. The penial papilla is partially everted. *Jorunna alisonae* (Marcus, 1976) can be differentiated from *J. tomentosa*, a similar species from the northeastern Atlantic, Mediterranean and South Africa, by the presence of jaw elements, a single denticle on the outermost teeth that is present in some specimens, and tripinnate branchial leaves.

According to Marcus (1976), the presence of a single denticle close to the tip on the outermost lateral teeth in *J. alisonae* may be a malformation. Among the several specimens examined in this study from Hawaii and the Marshall Islands, we found a single denticle present in only one. We conclude that its presence is not a malformation, but a variable feature of this species.

Jorunna lemchei Marcus, 1976

(Table 4)

Jorunna lemchei Marcus, 1976: 50–53, figs 47–52 [Ballyvaughan Bay, W. Ireland (53° 08.2'N, 09° 07.0'W),

holotype, 12 mm preserved length, intertidal, leg. H. Lemche, 8 November 1971 (USNM 710703)].

Distribution: Only from western Ireland (Marcus, 1976).

Remarks: The holotype has been dissected and largely destroyed. The coloration of the preserved animal is creamish. The radula and jaws (buccal bulb) of the holotype are missing. The oral tube is present. Most of the internal organs of the holotype are also missing (reproductive system, stomach, intestine); however, part of the digestive gland is present. There are 11–12 bipinnate branchial leaves and about 15 lamellae in the rhinophores. Oral tentacles present.

Although the external coloration of this species is very similar to that of *J. tomentosa*, *J. lemchei* is clearly different from this and all other congeners owing to the presence of cuticular spines on the penial papilla and male atrium (Marcus, 1976). Confirmation of this feature in other specimens from the type locality would be highly desirable.

Jorunna pardus Behrens & Henderson, 1981

(Figs 1L, 16, 17, Table 3)

Jorunna pardus Behrens & Henderson, 1981:124–128, figs 8–12, 15, 16 [Cat Rock, Anacapa Island, California (34° 00' 15"N; 119° 25' 20"W), holotype, 45 mm preserved length, 5 m depth, leg. D. Behrens, 21 October 1979, (CASIZ 015862); paratypes: Cat Rock, Anacapa Island, California (34° 00' 15"N; 119° 25' 20"W), 3 specimens, 33–35 mm preserved length, 5 m depth, leg. D. Behrens, 21 October 1979 (CASIZ 015863); Cat Rock, Anacapa Island, California (34° 00' 15"N; 119° 25' 20"W), 3 specimens, 25–38 mm preserved length, 5 m depth, leg. D. Behrens, 18 October 1971 (LACM 1949)].

Additional material: Anacapa Island, Channel Islands, California, October 1979, 3 specimens (2 dissected), 28–32 mm preserved length, 6 m depth (CASIZ 072359); Anacapa Island, Channel Islands, California, May 1990, 2 specimens, 24–28 mm preserved length, 8 m depth, leg. D. Behrens (CASIZ 072420); Anacapa Island, Channel Islands, California, 9 September 1998, 4 specimens, 21–29 mm preserved length, 18 m depth, leg. D. Behrens (CASIZ 115285); Santa Cruz Island, Channel Islands, September 1979, 1 specimen (dissected), 24 mm preserved length, leg. S. Anderson (CASIZ 072423); Frenchy's Cove, Palos Verdes, Los Angeles County, 4 January 1979, 1 specimen (dissected), 32 mm preserved length, leg. B. Henderson (CASIZ 072347); San Clemente Island, Channel Islands, May, 1990, 1 specimen, 32 mm preserved length, leg. C. Lorraine (CASIZ 072456); Eel Point, San Clemente Island, Channel Islands, California, 20 October 1985, 1 specimen (dissected), 21 mm preserved length, 15–18 m depth, leg. T. Gosliner (CASIZ 072862); Cedros Islands, Baja California, Mexico (28° 20' 25"N, 115° 11' 20"W), 18 October 1971, 1 specimen, 22 mm preserved length, 5–12 m depth, leg. J. McLean and P. Lafollete (LACM 71-151); Cedros Island, Baja California, Mexico, 23 August 1980, 1 specimen, 12 mm preserved length, 18 m depth, leg. J. Hamann (CASIZ 072422); Cedros Islands, Baja California, Mexico, 1 specimen, 11 mm preserved length, leg. D. Behrens (CASIZ 081951).

External morphology: Body shape oval, elongate (Fig. 1L). Centre of dorsum elevated. Dorsum densely covered with caryophyllidia, about 170 µm, homogeneously distributed on mantle. Border of mantle undulate. Rhinophoral sheath moderately elevated. Eight tripinnate gills and 14 lamellae in a

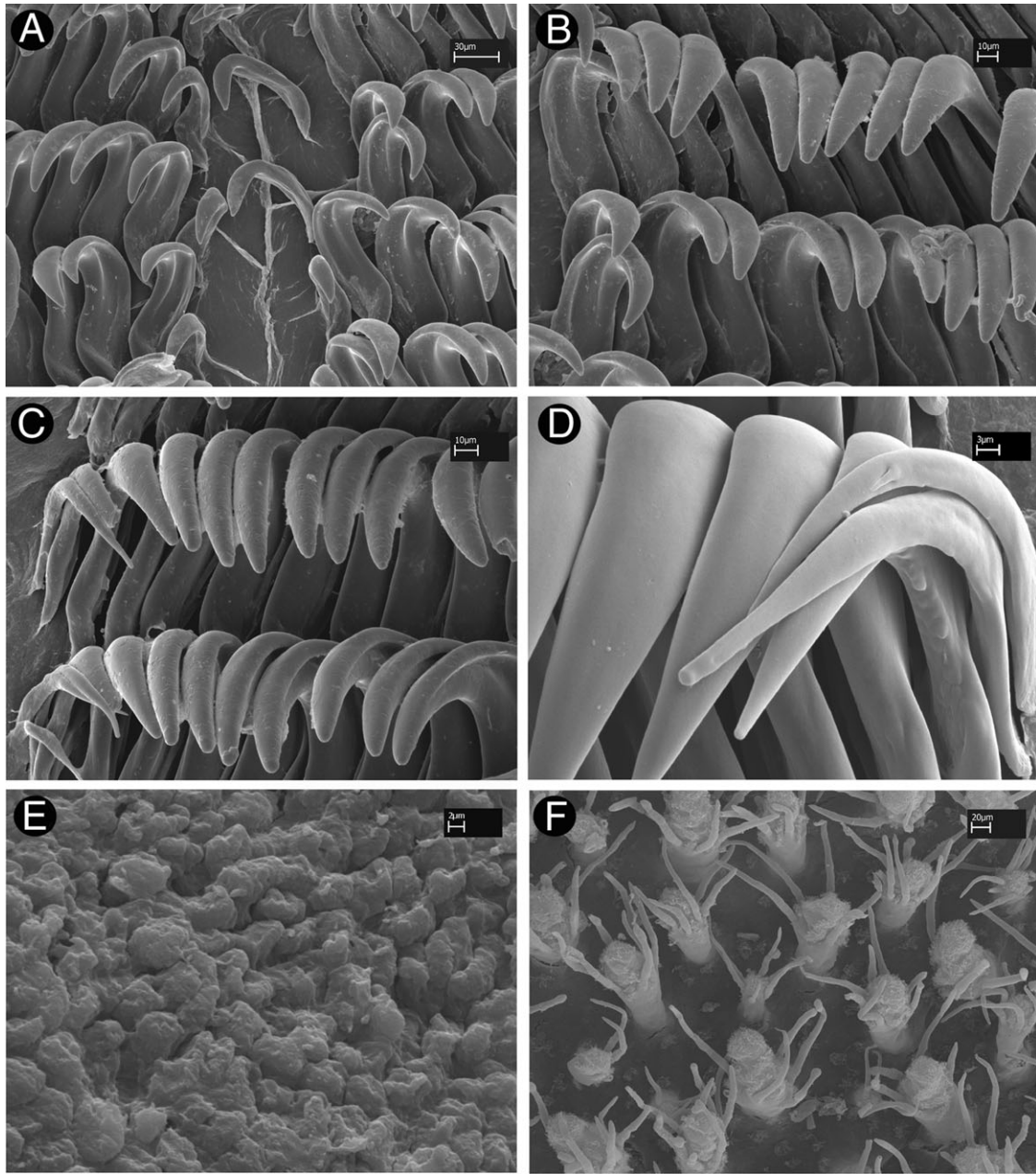


Figure 14. *Jorunna alisonae* (Hawaii, CASIZ 031866). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Detail of the outermost teeth (Indonesia, CASIZ 078561) **E.** Jaw elements. **F.** Caryophyllidia.

35 mm preserved length specimen (CASIZ 072359), 9 gills, 16 lamellae in 29 mm preserved length specimen (CASIZ 072420). Anal papilla located in centre of branchial leaves. Anterior border of foot grooved, notched. Oral tentacles long, digitiform with a bifid tip present in some specimens.

Background colour of body yellow-cream. Entire dorsum speckled with numerous dark brown spots of different sizes composing of minute dark brown dots. Caryophyllidia present within these brown spots (Fig. 16E) also spotted dark brown, the rest yellow-cream. Base of branchial sheaths and rachis yellow-cream with dark brown tips. Rhinophores dark brown with base and rachis yellow-cream. In some specimens, the yellow-cream sole of foot and notum are lightly speckled with small dark brown spots. Anterior border of foot with large dark brown dots on upper lip. Foot dorsally visible when the animal moves. Big dark brown spots around margin of foot.

Anatomy: Labial cuticle smooth. Radular formula $41 \times (80.0.80)$ (CASIZ 115285) in 20 mm long specimen. Rachidian teeth absent. Innermost teeth short, hamate, thicker at their base (Fig. 16A). Midlateral teeth hamate, having a single cusp, lacking denticles (Fig. 16B). Teeth increase in size gradually towards medial portion of half-row. Outermost teeth short, sometimes with as many as six denticles or entirely smooth (Figs. 16C).

Ampulla long, wider in middle part (Fig. 17B), entering female gland near distal part of mass. Prostate flattened, granular, divided into two different portions, as in other members of genus. Thicker portion of prostate connecting to deferent duct, other portion connecting to female gland, next to opening of ampulla. Deferent duct short, expanding again into short, narrow ejaculatory portion. Deferent duct opening into a common atrium with vagina. No penial hooks (Fig. 16F).

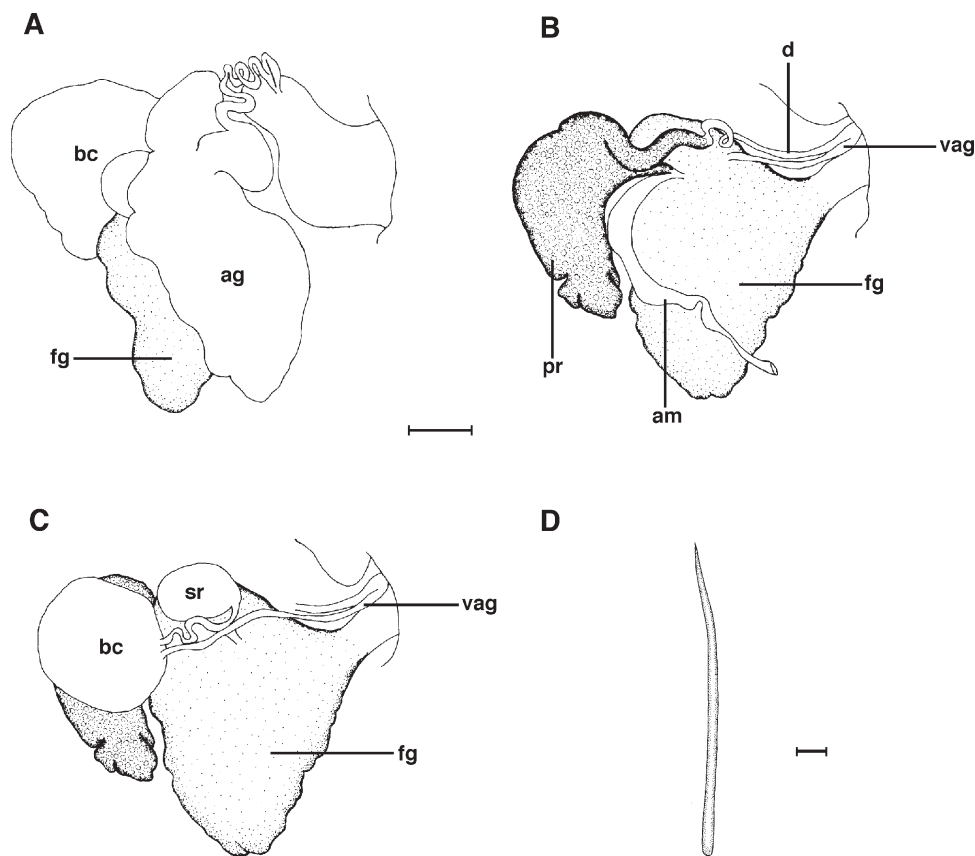


Figure 15. *Jorunna alisonae* (Hawaii, CASIZ 031866). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

Large, convoluted accessory gland connecting to atrium (Fig. 17A), consisting of a muscular portion with a pointed spine 950 μm long (Fig. 17D), a long and thin folded duct and a granular convoluted area connected to it. Vagina long, wide, connecting to oval bursa copulatrix at its distal end (Fig. 17C). Another convoluted duct, connecting to oval seminal receptacle and uterine duct, leading from bursa copulatrix about the same size as seminal receptacle (Fig. 17C).

Distribution: Southern California (Behrens & Henderson, 1981) to Sacramento Reef, Baja California (Behrens & Gatewood, 1986). It is found on rocks in the intertidal and subtidal, from 5 to 18 m depth.

Remarks: The holotype and the paratypes are in good condition and not dissected. All of the specimens have caryophyllidia on the notum. The background colour of the specimens is cream yellowish with dark black spots all over the dorsum and dark gills and rhinophores. There are dark spots around the margin of the foot in most of the specimens.

The holotype has an extruded buccal bulb covered with dark spots. The penis in the holotype and in the 32-mm paratype specimen (CASIZ 15863) is extruded and a pointed spine is visible outside. An extruded buccal bulb with dark spots is also found in the 28-mm paratype specimen (CASIZ 15863). The 30-mm paratype specimen (CASIZ 15863) has a partially extruded penis, the mantle is damaged on the right side. The margin of the foot has a few spots around the mantle margin. Both tips of the oral tentacles are bifurcate. One of the oral tentacles of the paratype specimen of 28 mm preserved length is bifurcate as well.

Behrens & Henderson (1981) described *J. pardus* as a species that has caryophyllidia, leopard-like spots on the notum, a smooth labial cuticle, an accessory gland with a spine, a marginal foot with dark spots, and outermost teeth with denticles. This description is consistent with the characteristics of the specimens we studied.

Based on two of the paratypes, we observed that the oral tentacles are bifurcate or with four prolongations. We also found considerable variability in the presence or absence of denticles in the outermost teeth. This was also found in specimens of *J. tomentosa* and *J. alisonae*. Intra-specific and/or ontogenetic radular variation may explain these findings.

Jorunna pardus can be distinguished from *J. funebris* by its external features such as the absence of rings on the notum, the presence of dark spots on the edges of the foot and by differences in the reproductive system. *Jorunna parva*, an Indo-Pacific species, differs from *J. pardus* by the presence of higher brown caryophyllidia, dark rhinophoral clubs, mantle glands, bipinnate brachial leaves and the presence of five outermost teeth with up to five pectinate denticles.

***Jorunna onubensis* Cervera, García-Gómez & García, 1986**
(Fig. 18, Table 4)

Jorunna onubensis Cervera, García-Gómez & García, 1986: 119–129, figs 9–16 [El Portil, Huelva, Spain (37° 12'

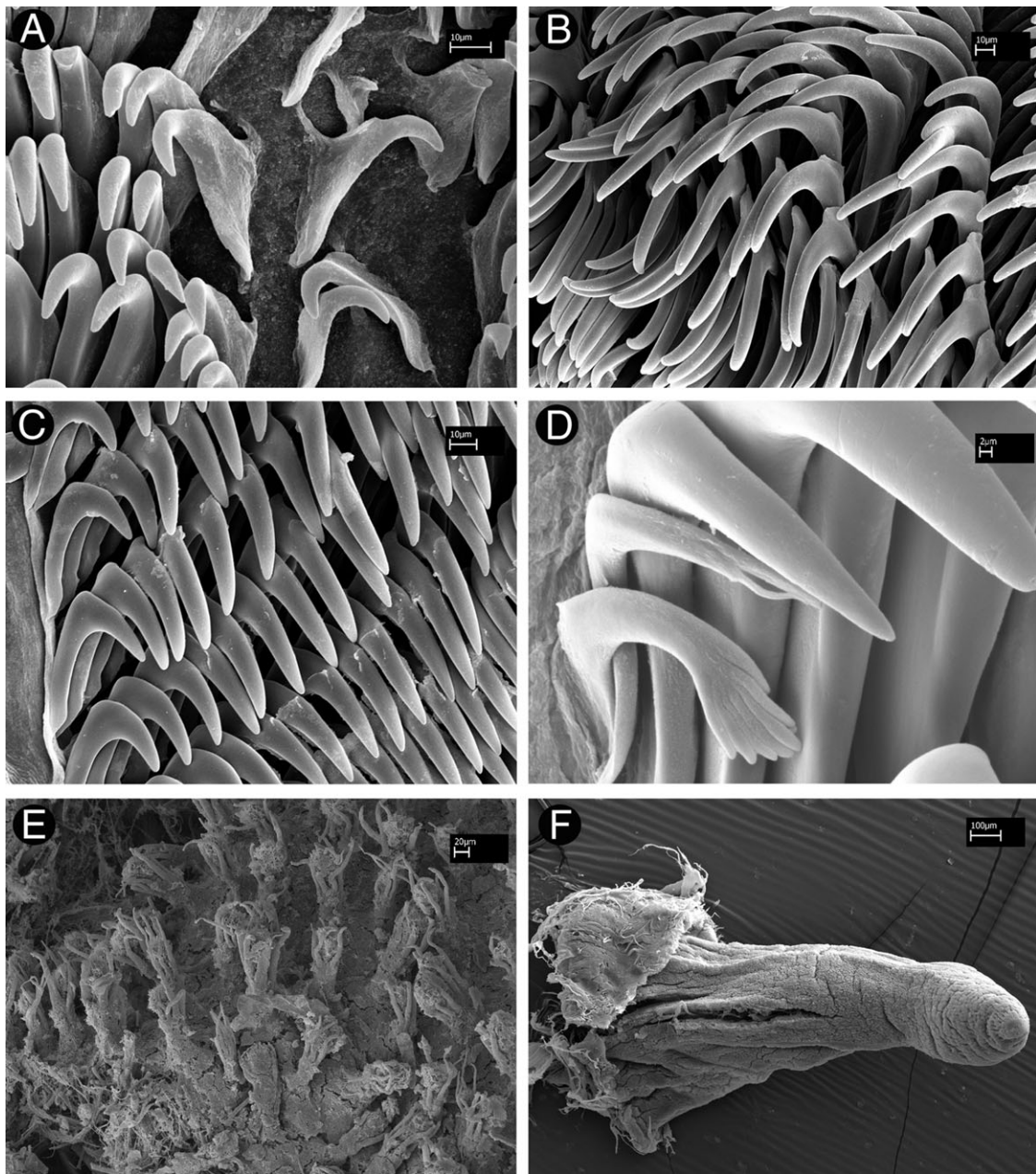


Figure 16. *Jorunna pardus* (California, CASIZ 115285). SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Detail of the outermost teeth (California, CASIZ 072420). **E.** Caryophyllidia. **F.** Penis.

40°N; 7° 7' 50"W), holotype, 0.9 mm preserved length, 1984 (MNHN) and mounted radula on slide 209].

External morphology: For a complete description of the species see Cervera *et al.* (1986).

Anatomy: Outermost teeth of radula of holotype, hamate with a short base, a large cusp. None of teeth with denticulations (Fig. 18A, B). Labial cuticle with jaw elements (J. Cervera, pers. comm.).

Distribution: Only from Portil, Huelva, Spain (Cervera *et al.*, 1986).

Remarks: Examination of the type material confirms the original description (Cervera *et al.*, 1986). This species is the only

member of the genus known to have a non-prostatic deferent duct composed of two regions: a long convoluted proximal part, and a distal part that is short, thin, and slightly sinuous. The study of the reproductive system of the holotype verified the presence of this unique feature.

According to Cervera, García & García (1986) *J. tomentosa* differs from *J. onubensis* by the presence of 5–6 dark spots on both sides of the body, the absence of the non-prostatic deferent duct and labial cuticle with jaw elements. *Jorunna onubensis* differs from *J. lemchei* by the presence of a labial cuticle with jaw elements and the absence of spines on the penial papilla.

Jorunna onubensis can also be distinguished from *J. tomentosa* by the presence of jaw elements and the absence of outermost teeth with denticles. Although the external coloration of *J. onubensis* is similar to that of *J. labialis*, it differs by the length of the deferent duct. In *J. labialis*, the deferent duct is

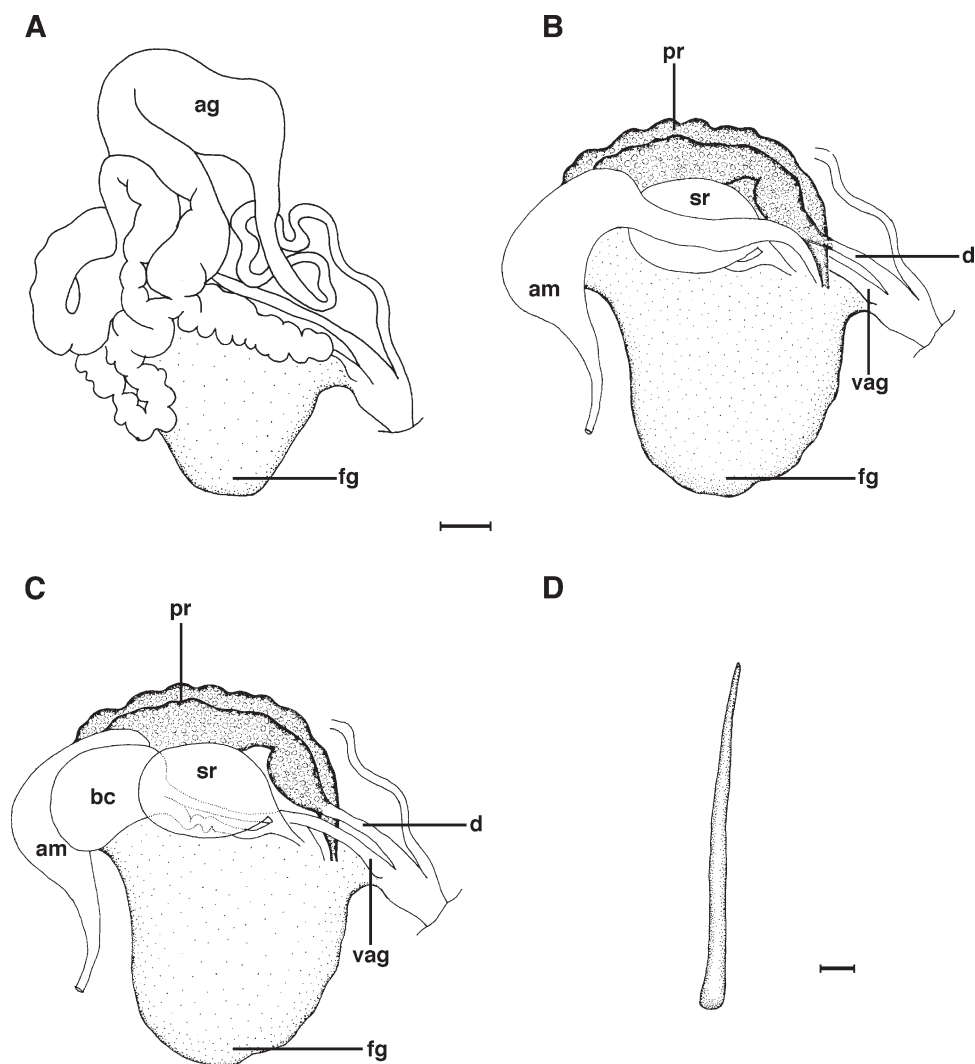


Figure 17. *Jorunna pardus* (California, CASIZ 115285). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

short with some small loops, whereas in *J. onubensis* the deferent duct is extremely long and convoluted. Also, the radula formula differs and *J. labialis* does not have a long non-prostatic deferent duct (see Table 4).

Jorunna spazzola and *J. lemchei* are also distinguished from *J. onubensis*. The former has innermost with or without denticles and outermost teeth pectinated and a different external coloration, whereas *J. lemchei* has plate-like, elongate outermost teeth, a smooth labial cuticle and an armed penis.

***Jorunna ramicola* Miller, 1996**

(Figs 1M, N, 19, 20, Table 2)

Jorunna ramicola Miller, 1996: 1103–1107, figs 6–8 [Northwestern Kawaii Islands, holotype (MNZ M. 118395) and two paratypes (MNZ M. 118396) Museum of New Zealand, Wellington].

Additional material: Andilana, Madagascar, 20 April 1992, 1 specimen (dissected), 7 mm preserved length, leg. T. Gosliner (CASIZ 086996) Lembah Island, Sulawesi, Indonesia, 29 October 1993, 3 specimens (1 dissected), 5 mm preserved

length, leg. P. Fiene (CASIZ 097588); Barracuda Point, Madang, Papua New Guinea, 19 August 1989, 2 specimens (both dissected), 5–9 mm preserved length, 23 m depth, leg. T. Gosliner (CASIZ 068724); Arthur's Rock, Calumpan Peninsula, Batangas Province, Luzon, Philippines, 11 May 2001, 1 specimen (dissected), 8 mm preserved length, 15 m depth, leg. A. Valdés (CASIZ 158336); Dead Point, Batangas, Luzon Island, Philippines, 10 May 2001, 1 specimen (dissected), 7 mm preserved length, 15 m depth, leg. A. Valdés (CASIZ 157016); Monoc Island, Mindanao, Philippines, 14 June 1973, 1 specimen (dissected), 6 mm preserved length, intertidal, leg. F. Steiner (CASIZ 082061); Luzon Island, Batangas, NW side of Calumpan Peninsula, Koala, Philippines, 25 March 1993, 2 specimens (1 dissected), 4–6 mm preserved length, 15 m depth, leg. T. Gosliner (CASIZ 085911); Cement Mixer Reef, Madang, Papua New Guinea, 16 July 1989, 1 specimen (dissected), 6 mm preserved length, 6 m depth, leg. T. Gosliner (CASIZ 068809).

External morphology: Body oval to elongate. Dorsum with long caryophyllidia about 400 μ m long. Caryophyllidia with elongate base, long spicules, long ciliated tubercle (Fig. 19F).

Ten bipinnate branchial leaves and nine lamellae in rhinophores in a 5 mm preserved length specimen (CASIZ 068724), 10 bipinnate gills, 7 lamellae in 4.5 mm preserved length specimen (CASIZ 097588), 10 bipinnate gills, 10 lamellae in 3 mm preserved length specimen (CASIZ 097588). Oral tentacles digitiform. Foot notched and grooved. Posterior portion of foot visible dorsally when the animal moves.

Background of living animals pale grey to light brown (Fig. 1M, N). Dorsum with a number of light grey to light brown patches of different sizes. Patches composed of an aggregate of minute dark brown spots more densely arranged near centre of notum. Minute dark spots homogeneously distributed over dorsum. Rhinophores pale grey speckled with dark brown and white on club. Branchial leaves dark grey. White spots around margin. Branchial and rhinophoral sheaths with small white glandular structures. Anterior border of foot notched and grooved. Oral tentacles conical. Hyponotum and notum same colour as dorsum.

Anatomy: Labial cuticle with thick, almost rectangular, jaw elements (Fig. 19E). Radular formula $14 \times (18.0.18)$ (CASIZ 068724) of 5 mm preserved length specimen, $15 \times (17.0.17)$ (CASIZ 157016) of 7 mm preserved length specimen, $12 \times (16.0.16)$ (CASIZ 085911) of 6 mm preserved length specimen and $18 \times (19.0.19)$ (CASIZ 086996) of 7 mm preserved length specimen. Rachidian teeth absent. Innermost teeth elongated, hamate with up to three denticles near cusp (Fig. 19A, B). Lateral teeth hamate, pointed, lacking denticles (Fig. 19C). Teeth increase in size gradually towards medial portion of half-row. In most specimens, first three outermost teeth with up to three denticles (Fig. 19C, D). In some other specimens, only first outermost tooth with denticles.

Ampulla long, thick, tubular, convoluted in its distal part (character consistent in all specimens examined; Fig. 20B). Ampulla enters female gland in middle portion. Prostate flattened, granular, convoluted, divided into two different portions clearly distinguishable by their different texture and coloration. Deferent duct short, expanding into wide ejaculatory portion, opening into a common atrium with vagina. No penial hooks. Small accessory gland connected to atrium, consisting of a muscular portion with a pointed spine 2.2 mm long (Fig. 20C).

Penis entirely covered by cilia (Fig. 19G). Vagina short, with a loop in middle portion, connecting to large oval bursa copulatrix at its distal end. Another duct, connecting to rounded seminal receptacle and uterine duct, leading from bursa copulatrix. Seminal receptacle slightly smaller than bursa copulatrix (Fig. 20A).

Distribution: Northwestern Kawaii Islands, New Zealand (Miller, 1996), Madagascar, Philippines, Papua New Guinea and Indonesia (present study).

Remarks: *Jorunna ramicola* is clearly distinguishable from other members of the genus by having a brown mantle with irregular brown to pale grey patches, light grey to light brown spots, denticulate innermost radular teeth, long and denticulate outermost teeth, and a labial cuticle with jaw elements. According to Miller (1996), *J. ramicola* also differs from other Indo-Pacific species by the presence of jaw elements that are rounded at the base and flat on top with up to 12 denticles. In the specimens studied here, the SEM photographs show that the jaw elements do not have as many regular denticles as those described by Miller (1996); however, other features studied match those that he described.

Jorunna ramicola can be distinguished from other Indo-Pacific species by the external morphology, radular morphology and anatomy. *Jorunna rubescens*, *J. funebris* and *J. parva* do not have jaw elements, whereas in *J. ramicola* they are well developed.

The dorsum of these three species has stripes (*J. rubescens*), rings (*J. funebris*) or elevated dark tubercles resembling dark spots in the mantle (*J. parva*). In contrast, *J. ramicola* has a brown to light grey dorsal colour with some irregular brown patches.

Jorunna hartleyi from Australia differs from *J. ramicola* by the absence of denticulate outermost teeth, as well as by the external coloration. *Jorunna hartleyi* has a pale pink background with large brown patches encircled with white papillae.

Two other Indo-Pacific species, *J. pantherina* from Australia and New Zealand and *J. alisonae* from Hawaii and Marshall Islands, differ from *J. ramicola* by the radular morphology and external coloration. In these species, the outermost teeth can be hamate and smooth (*J. pantherina*), smooth, or a single denticle may be present near the tip (*J. alisonae*); also, the innermost teeth in both species lack denticles. In addition, the dorsal colour of *J. pantherina* is purplish brown to dark grey or black with patches and opaque white spots, whereas *J. alisonae* is pale grey with two vertical lines of spots.

Jorunna osae new species

(Figs 10, 21, 22, Table 3)

Type material: Holotype: Playa Gallardo, Golfito, Osa Conservation Area, Costa Rica ($8^{\circ}38'33''N$, $83^{\circ}13'40''W$), 2 December 1997, 8 mm preserved length, dissected, intertidal, leg. S. Avila (UCR-INB0003701453), SEM stub with radula and jaw (UCR-INB0003799440); paratype: Playa Avellanas, Tempisque Conservation Area, Costa Rica ($10^{\circ}13'35''N$, $85^{\circ}51'55''W$), 15 January 2001, 1 specimen (dissected) 6 mm preserved length, intertidal, leg. J. Magaña (CASIZ 162254), SEM stub with radula and jaw.

Additional material: Playa Avellanas, Guanacaste, Costa Rica ($10^{\circ}13'35''N$, $85^{\circ}50'26''W$), 15 January 2001, 1 specimen, 5 mm preserved length, intertidal, leg. J. Magaña (UCR-INB0003118105); Parque Nacional Marino Ballena, Puntarenas, Costa Rica ($9^{\circ}06'26''N$, $83^{\circ}43'39''W$) 17 January 2000, 1 specimen (dissected), 3.5 mm preserved length, 7 m depth, leg. M. Calderón (UCR-INB0003792183); Punta Uvita, Puntarenas, Osa Conservation Area, Costa Rica ($9^{\circ}56'03''N$, $83^{\circ}40'50''W$), 17 January 2000, 3 specimens (all dissected), 2–6 mm preserved length, intertidal, leg. M. Calderón (UCR-INB0001496535); Punta Uvita, Puntarenas, Osa Conservation Area, Costa Rica ($9^{\circ}08'55''N$,

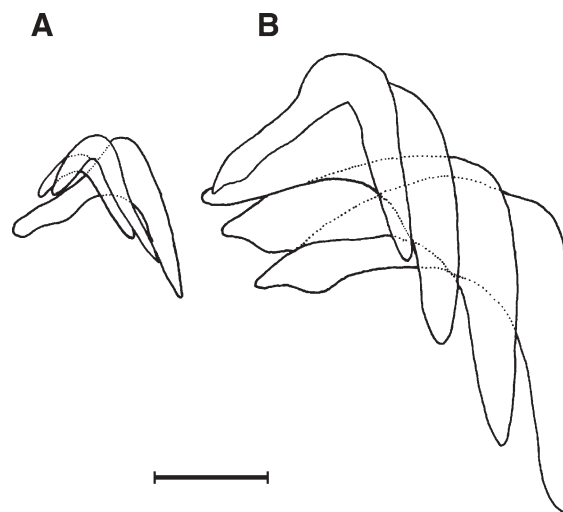


Figure 18. Drawing of the radular morphology of the holotype of *Jorunna onubensis*. **A.** Outermost teeth. **B.** Lateral teeth.

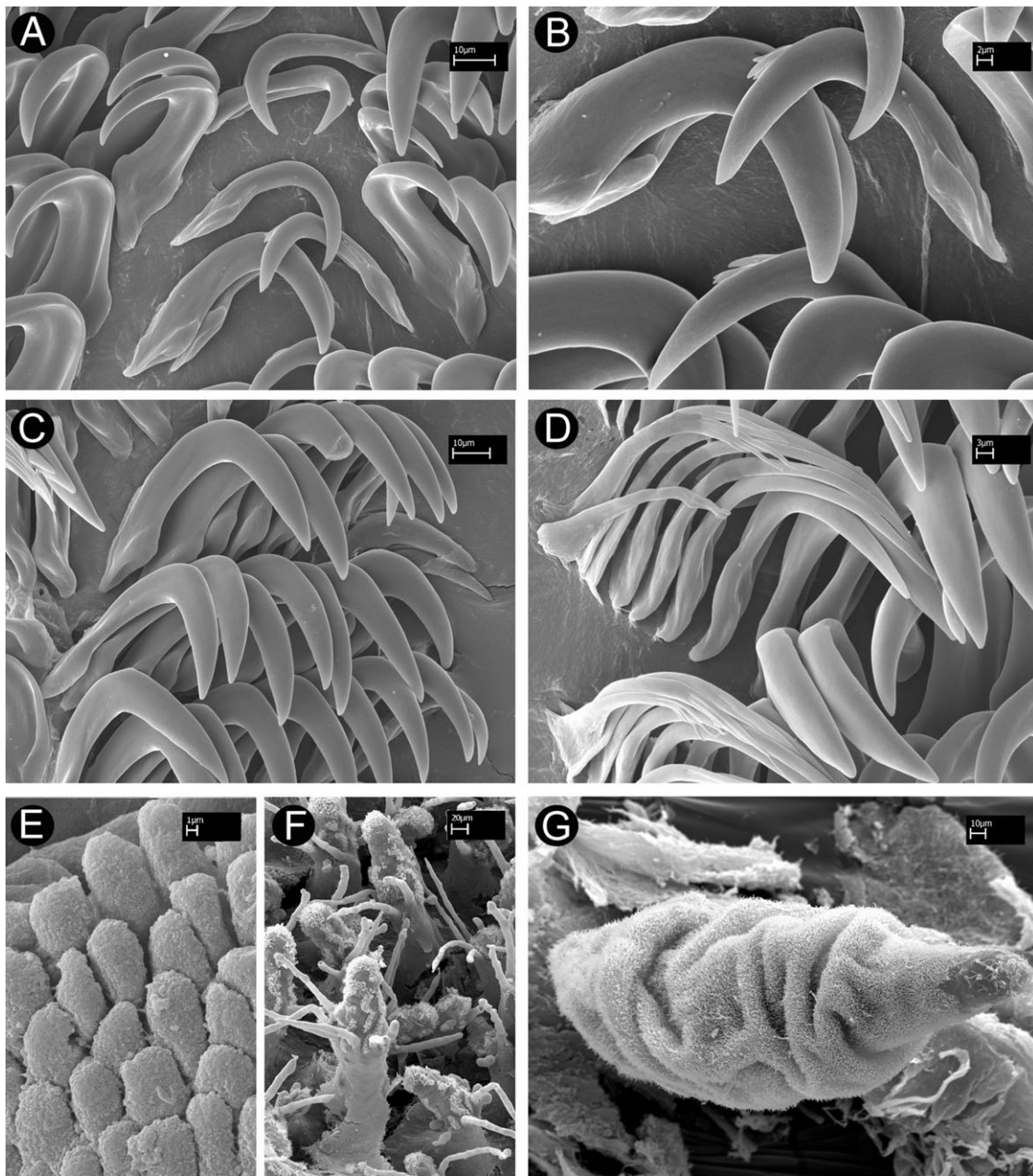


Figure 19. *Jorunna ramicola*, SEM photographs. **A–C.** (Papua New Guinea, CASIZ 068724), radula. **A.** Inner lateral teeth. **B.** Detail of the inner lateral teeth. **C.** Lateral teeth. **D, E.** (Indonesia, CASIZ 097588) **D.** Outermost teeth. **E.** Jaw clements. **F, G.** (Papua New Guinea, CASIZ 068724). **F.** Caryophyllidia. **G.** Penis.

83°46'00"W), 29 March 1999, 1 specimen (dissected) 5 mm preserved length, intertidal, leg. A Berrocal (UCR-INB0003701273); Roca la Viuda, Osa Conservation Area, Costa Rica (8°37'02"N, 83°14'12"W), 11 February 1997, 1 specimen (dissected) 4 mm preserved length, between 9 and 13 m depth, leg. M. Lobo (UCR-INB0003701270).

Etymology: *Jorunna osae* is named after the Osa Conservation Area in Costa Rica.

External morphology: Body oval, elongate (Fig. 10). Dorsum with elongate caryophyllidia, about 410 µm long. Caryophyllidia with a conical base, long spicules, a small elongate ciliated tubercle (Fig. 21D). Rounded, ciliated areas covering base of caryophyllidia. Body pale cream to yellow. Dorsum with light

yellow-brown patches or spots, darker in some specimens. Patches homogeneously arranged on mantle, composing of minute dark spots. Some white glandular structures along mantle edge, larger posteriorly, visible only in living animals.

Rhinophoral sheaths low, pale cream or yellow, speckled brown. Gill sheath pale cream or yellow speckled with brown spots. Rhinophores conical, pale cream or yellow with white apex, club lightly speckled brown. Gill pale, cream to yellow. Twelve erect bi-tripinnate branchial leaves and 10 lamellae in rhinophores in a 5 mm preserved length specimen (UCR-INBI01496535), imbricated in living animals, 12 bipinnate gills, 10 lamellae in a 6 mm preserved length specimen (CASIZ 162254), six tripinnate gills, 10 lamellae in a 3.5 mm preserved length specimen (UCR-INB03792183). Oral tentacles conical. No spots present on sole of foot or ventral part of notum.

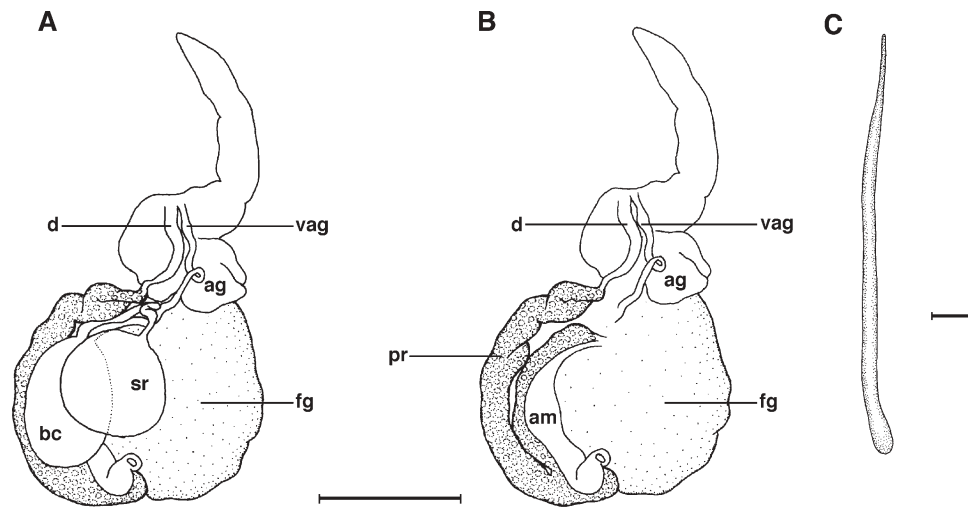


Figure 20. *Jorunna varicicola* (Papua New Guinea, CASIZ 068724). **A, B.** Detail of the reproductive system; scale bar = 1.0 mm. **C.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

Anatomy: Labial cuticle smooth. Radular formula of 6 mm preserved length specimen $16 \times (18.0.18)$ (UCR-INB0001496535) and $12 \times (16.0.16)$ in a 5 mm preserved length specimen (UCR-INB0003118105). Rachidian teeth absent. Innermost teeth hamate small, lacking denticles (Fig. 21A). Lateral teeth hamate, with a single cusp, lacking denticles (Fig. 21B). Teeth increase in size gradually towards medial portion of half-row. Outermost teeth small, elongate, lacking denticles (Fig. 21C).

Ampulla thick, long, convoluted in middle portion (Fig. 22C), dividing into a short oviduct entering female glands near their nidamental opening. Prostate flattened, granular, convoluted, dividing into two different portions clearly distinguishable by different texture and coloration. Deferent duct short, expanding into narrow ejaculatory portion.

Convoluted accessory gland (Fig. 22A) containing copulatory spine $600 \mu\text{m}$ in length. Spine curved, pointed (Fig. 22D). Vagina short, wide, with a curve in middle portion, connecting to small, oval bursa copulatrix at its proximal end. Another convoluted duct, connecting to oval seminal receptacle and uterine duct, leading from bursa copulatrix. Bursa copulatrix about same size as seminal receptacle (Fig. 22B).

Distribution: Pacific Coast of Costa Rica from Playa Gallardo to Playa Avellanas. It occurs in intertidal areas, under rocks to 13 m depth.

Remarks: This species differs from *J. tempisquensis*, another species found in the tropical American Pacific, by the presence of mantle glands on the margin, and the erect gill with imbricate branchial branches, and the external and radular morphology. *Jorunna osae* has a pale cream to brown background colour with light brown spots, whereas *J. tempisquensis* varies from white creamish to dark black purplish with dark brown spots on the dorsum and has a spreading gill. There are jaw elements present in *J. tempisquensis*, but these are absent in *J. osae*. Although *J. osae* has small and elongate outermost teeth, very similar to those in *J. tempisquensis*, the innermost teeth have a shorter base than those of *J. tempisquensis*.

Jorunna osae can also be distinguished from *J. pardus* from California and *J. spazzola* from Brazil and the Mediterranean by external and radular morphology. *Jorunna pardus* has a cream yellowish background colour with large dark brown

spots, dark brown rhinophores with cream yellowish bases, and cream yellowish branchial leaves with dark brown tips. *Jorunna spazzola* has a light grey or white yellow to orange background with brown spots on each side of the notum lined up to form a row, and grey rhinophores, whereas in *J. osae* the background colour is pale cream to yellow with light brown-yellowish patches and the rhinophores are pale cream to yellow with white apices. In addition, *J. spazzola* has outermost teeth with up to four irregular denticles and innermost teeth sometimes with a small denticle, whereas in *J. osae* the outermost and innermost teeth lack denticles. *Jorunna pardus* also differs from *J. osae* by the presence of denticles in the outermost teeth.

Jorunna osae also differs from other similar species in the Mediterranean and Western Atlantic by its internal anatomy. For example, *J. tomentosa* has outermost teeth with denticles, whereas in *J. osae* the outermost are smooth. *Jorunna lemchei* and *J. onubensis* are distinct from *J. osae*; the former has an armed penis and the latter a very long non-prostatic duct. *Jorunna osae* lacks these features.

Jorunna tempisquensis new species

(Figs 1P, 23, 24, Table 3)

Type material: Holotype: Cabo Blanco, Costa Rica ($9^{\circ}34'50''\text{N}$, $85^{\circ}08'26''\text{W}$), 26 January 1999, 9 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0003542376); paratypes: Cabo Blanco, Costa Rica ($9^{\circ}34'50''\text{N}$, $85^{\circ}08'26''\text{W}$), 26 January 1999, 2 specimens, 7 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0003542377); Cabo Blanco, Costa Rica, 26 January 1999, 1 specimen, 6 mm preserved length, intertidal, leg. F. Alvarado (LACM 152760); Lindomar, Bahía de Banderas, Jalisco, México (20.00° $35.00''\text{N}$ 105.00° $17.00''\text{W}$), 19 February 2003, 3 specimens (two dissected), 9–16 mm preserved length, leg. A. Hermosillo (CASIZ 166890) including two slides with radula and jaw of the 9 mm preserved length specimen.

Additional material: Punta Mita, Nayarit, Mexico, 10 June 2003, 1 specimen, 15 mm preserved length, leg. A. Hermosillo (CASIZ 167976); Punta Conchal, Playa Conchal, Guanacaste, Costa Rica ($10^{\circ}24'25''\text{N}$, $85^{\circ}48'23''\text{W}$), 16 April 2004, 1

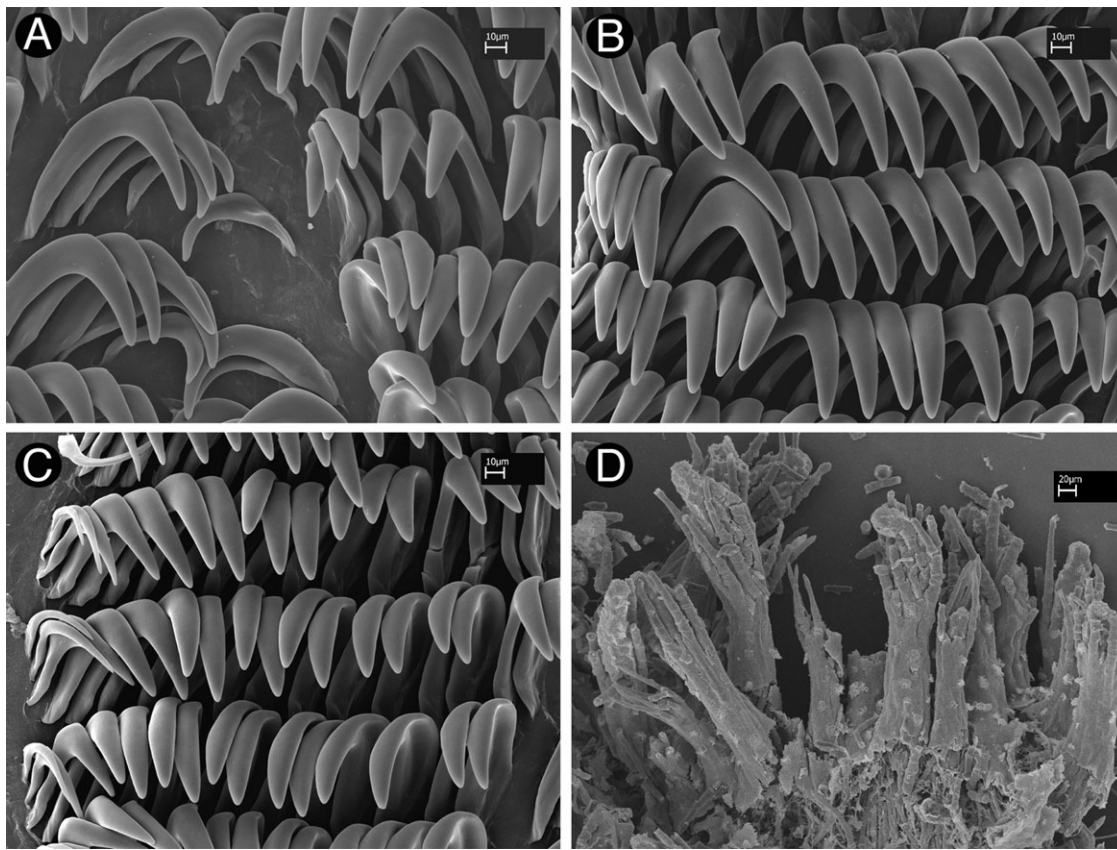


Figure 21. *Jorunna osae* n. sp. (Costa Rica, UCR-INBI01496535), SEM photographs of the radula. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Caryophyllidia.

specimen (dissected), 4 mm preserved length, 4 m depth, leg. T. Gosliner (UCR-INB03836150); Cabo Blanco, Costa Rica, 26 January 1999, 1 specimen, 6 mm preserved length, intertidal, leg. F. Alvarado (CASIZ 162255); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica, (9°34'49"N, 85°08'28"W), 26 January 1999, 1 specimen (dissected), 3 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0003701272); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica (9°34'49"N, 85°08'28"W), 16 May 1998, 1 specimen (dissected), 6 mm preserved length, 2 m depth, leg. A. Berrocal (UCR-INB0001496449); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica (9°34'49"N, 85°08'28"W), 17 May 1998, 1 specimen, 6 mm preserved length, 2 m depth, leg. S. Avila (UCR-INB0001496483); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica (9°34'53"N, 85°08'28"W), 28 January 1999, 10 specimens (1 dissected), 4–9 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0001496481); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica (9°34'49"N, 85°08'28"W), 16 May 1998, 2 specimens (both dissected), 5–6 mm preserved length, 2 m depth, leg. A. Berrocal (UCR-INB0001496448); San Miguel Station, Cabo Blanco, Tempisque Conservation Area, Costa Rica (9°34'50"N, 85°08'26"W), 26 January 1999, 8 specimens (6 dissected), 3–9 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0001496480); Punta Mala, 400 m SW from the Station, Reserva Vida Silvestre Playa Hermosa, Puntarenas, Costa Rica (9°31'01"N, 84°33'26"W), 20 May 2004, 1 specimen (dissected), 5 mm preserved length, intertidal, leg. M. Zúñiga (UCR-INB003867351); Manuel Antonio National Park, Puntarenas, Costa Rica (9°22'51"N, 84°08'50"W), 16 February

2003, 1 specimen (dissected), 5 mm preserved length, intertidal, leg. M. Zúñiga (UCR-INB0003572314); Playa Coralito, Peñón del Coral, Costa Rica (9°39'52"N, 85°11'32"W), 29 January 1999, 1 specimen, 6 mm preserved length, intertidal, leg. F. Alvarado (UCR-INB0001496279); Punta Uvita, Puntarenas, Osa Conservation Area, Costa Rica (9°08'55"N, 83°46'00"W), 29 March 1999, 1 specimen, 3 mm preserved length, intertidal, leg. A. Berrocal (UCR-INB0001496528); Punta Uvita, Puntarenas, Osa Conservation Area, Costa Rica (9°08'55"N, 83°46'00"W), 29 March 1999, 2 specimens (both dissected), 7 mm preserved length, intertidal, leg. A. Berrocal (UCR-INB0001496450); San Pedrillo, Osa Conservation Area, Costa Rica (8°36'53"N, 83°44'18"W), 20 January 2000, 2 specimens (both dissected), 4 mm each one preserved length, intertidal, leg. M. Calderón (UCR-INB0001496526); Punta Larga, Golfo Dulce, Costa Rica (8°37'38"N, 83°11'45"W), 29 November 1997, 2 specimens (both dissected), 6 mm preserved length, intertidal, leg. M. Madrigal (UCR-INB0001496537); Punta Larga, Golfo Dulce, Costa Rica (8°37'28"N, 83°11'26"W), 12 December 1997, 1 specimen (dissected), 2 mm preserved length, intertidal, leg. M. Madrigal (UCR-INB0001496534).

Etymology: *Jorunna tempisqueensis* is named after the Tempisque Conservation Area in Costa Rica.

External morphology: Body oval, wide. Dorsum with caryophyllidia, about 200 µm in length (Fig. 23E). Caryophyllidia with a long, conical base, long spicules and a small, elongate, ciliated tubercle. Rhinophoral and branchial sheaths low. Eleven long, widely spreading, tripinnate branchial leaves and nine lamellae in rhinophores in 8 mm preserved length

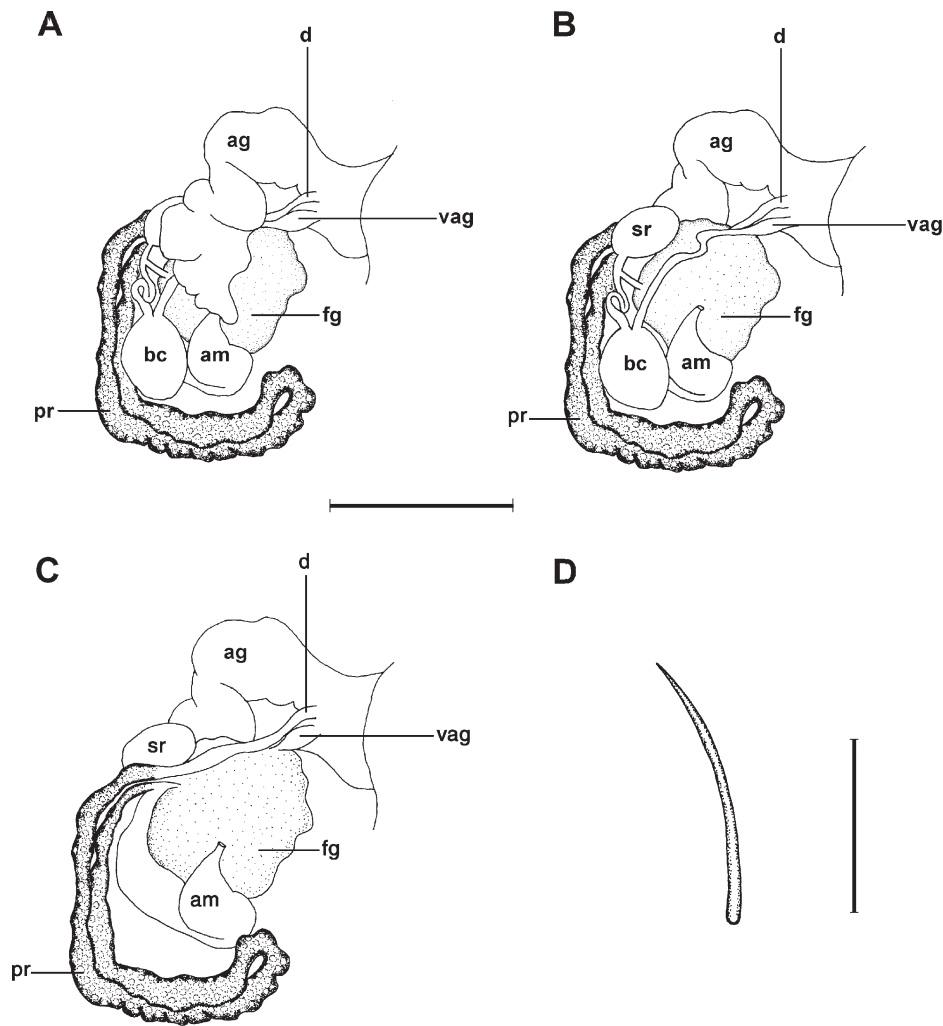


Figure 22. *Jorunna osae* n. sp. (Costa Rica, UCR-INBI01496535). **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

specimen (UCR-INBI01496480), 12 tripinnate gills, 11 lamellae in 14 mm preserved length specimen (CASIZ 167976), 10 tripinnate gills, 10 lamellae in 16 mm preserved length specimen (CASIZ 166890). Gills not imbricate, forming circle around anal papilla.

Background colour of living animal light cream, light brown to dark purplish black. In darker specimens, centre of dorsum covering with large, light brown or black spots of different sizes. Dorsum with minute dark brown spots homogeneously arranged, covering tubercles and caryophyllidia. Rhinophores light cream to light brown, speckled with minute dark brown spots. Tips of rhinophores yellowish white. Base of branchial leaves dark brown to almost purple with light yellow tips and some minute brown spots.

Anterior border of foot notched, grooved with minute brown spots more densely arranged on edges of mantle. Oral tentacles conical. Small brown spots present on ventral side of head including tentacles. Foot same colour as dorsum, with some minute dark spots irregularly distributed. Posterior end of foot visible dorsally when the animal moves.

Anatomy: Labial cuticle with numerous jaw elements (Fig. 23D). Radular formula of 7 mm preserved length specimen (UCR-INB0001496450), $17 \times (18.0.18)$, and

$17 \times (15.0.15)$ of 9 mm preserved length specimen (UCR-INB000166890). Rachidian teeth absent. Innermost and lateral teeth hamate, having a single cusp, lacking denticles (Fig. 23A). Apices of cusps pointed. Midlateral teeth hamate, pointed (Fig. 23B). Teeth increase in size gradually towards medial portion of half-row. Outermost teeth hamate, small, thin, elongate (Fig. 23C). In some rows, outermost teeth almost plate-like in shape, lacking denticles.

Ampulla short, convoluted, branching into a short oviduct and prostate (Fig. 24C). Oviduct enters female gland in centre of mass. Prostate flattened, folded, granular (Fig. 24C), connecting to a long, convoluted duct expanding into short ejaculatory portion of deferent duct. Deferent duct opening into common atrium with vagina. Vagina long, wide as deferent duct. Convoluted accessory gland (Fig. 24A), connecting to atrium with a distinct stylet sac containing a $550 \mu\text{m}$ long copulatory spine, almost entirely straight, pointed (Fig. 24D). Vagina connecting to oval bursa copulatrix at its proximal end. Another duct leading from bursa copulatrix to uterine duct and seminal receptacle. Bursa copulatrix slightly larger than oval seminal receptacle (Fig. 24B).

Distribution: Southern Mexico and Costa Rica. It occurs in intertidal areas, under rocks from 0 to 2 m depth.

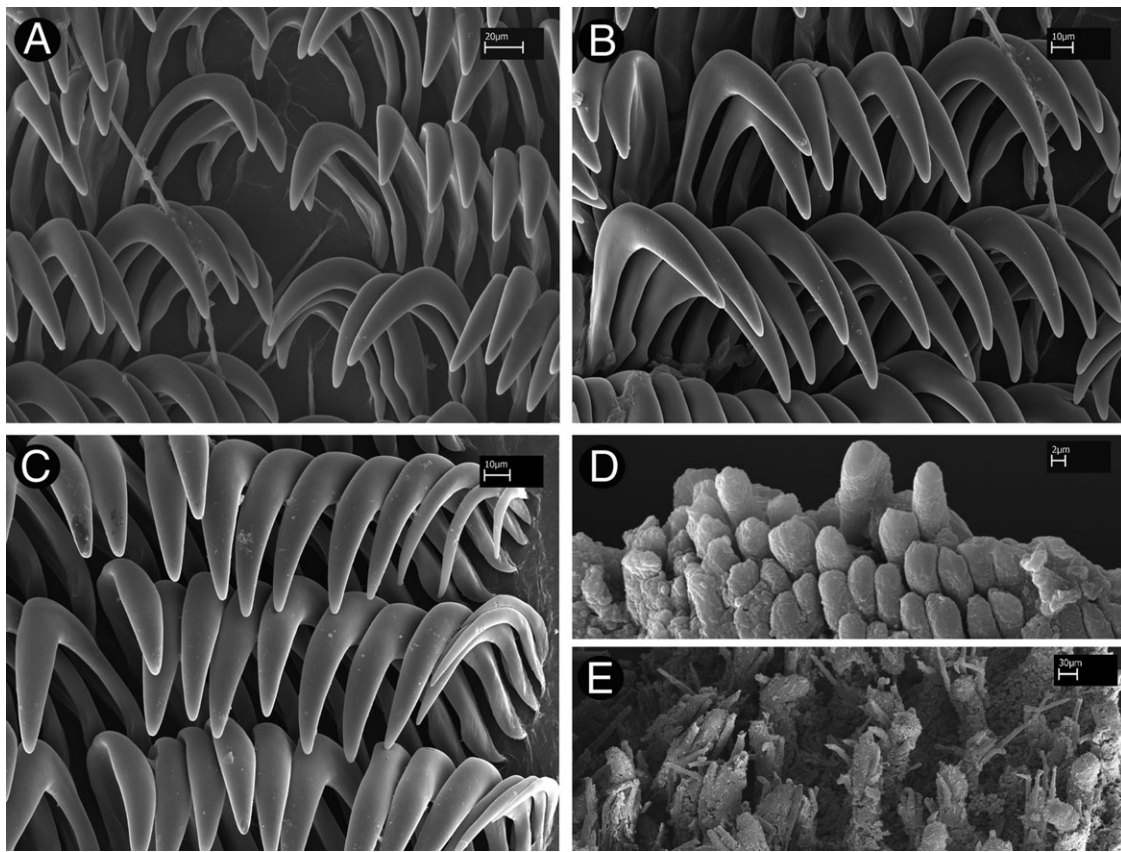


Figure 23. *Jorunna tempisquensis* n. sp. (Costa Rica, UCR-INBI01496480). SEM photographs. **A.** Inner lateral teeth. **B.** Lateral teeth. **C.** Outermost teeth. **D.** Jaw elements. **E.** Caryophyllidia.

Remarks: *Jorunna tempisquensis* can be distinguished from *J. osae*, also from Costa Rica, by the external coloration, the presence of jaw elements, the absence of mantle glands, by having a spreading rather than erect gill and by differences in radular morphology such as the shape of the innermost teeth.

Jorunna tempisquensis also differs from *J. pardus* from California and *J. spazzola* from Brazil and the Mediterranean by the external and radular morphology. *Jorunna pardus* has cream yellowish background colour with large dark brown spots, dark brown rhinophores with cream yellowish bases and cream yellowish brachial leaves with dark brown tips. *Jorunna spazzola* has a light grey or white yellow to orange background with brown spots on each side of the notum forming a row, whereas *J. tempisquensis* has a cream white to dark purplish brown background with light brown spots on the dorsum. *Jorunna pardus* also differs from *J. tempisquensis* by the absence of jaw elements and by the presence of denticles on the outermost teeth. Additionally, *Jorunna spazzola* has outermost teeth with up to four irregular denticles and innermost teeth sometimes with a small denticle. *Jorunna tempisquensis* lacks denticles on the outermost and innermost teeth.

Part B. Misidentified and doubtful species of *Jorunna* and *Kentrodoris*

There are several species of dorids which have been erroneously classified as members of the genus *Jorunna* (*K. pseudo-fusca*, *J. marchadi*), some whose status within *Jorunna* remains uncertain (*J. atypha*, *K. nigra*, *Jorunna* sp., *Kentrodoris* (?) sp.) and others which were included by Marcus (1976) as

‘potential’ members of the genus *Jorunna* (*Platydoris inframaculata*, *Doris infraevata*), and which recently have been considered as members of *Platydoris* by Dorgan, *et al.* (2002) and Dayrat (2006). These are discussed in detail in this section.

Jorunna atypha Bergh, 1881

Jorunna atypha Bergh, 1881: 145, pl. J, figs 22–25 (Trieste, Italy, type probably lost, not at ZMC).

Remarks: According to Bergh (1881), *J. atypha* has a greyish white to light yellowish-white background colour, white rhinophores with brown upper lamellae, white brachial sheaths, a yellowish foot, rhinophores with 20 lamellae, 11 bi- to tripinnate brachial leaves, short and flat caryophyllidia, broad oral tentacles, an accessory gland with a spine, hamate midlateral teeth and outermost teeth with 3–4 denticles. The presence of jaw elements in this species could not be confirmed by Bergh (1881) due to the bad preservation of the single specimen. Bergh (1881) also mentioned that the shape of the oral tentacles is quite different from other members of the genus *Jorunna*. Due to the incomplete description provided by this author (also emphasized by Marcus 1976), and his own hesitation about whether this species really belongs to the genus *Jorunna*, the generic position of this species remains unclear.

Kentrodoris nigra Risbec, 1928

Kentrodoris nigra Risbec, 1928: 91, pl. 2, fig. 6 (New Caledonia, type probably lost, not at MNHN).

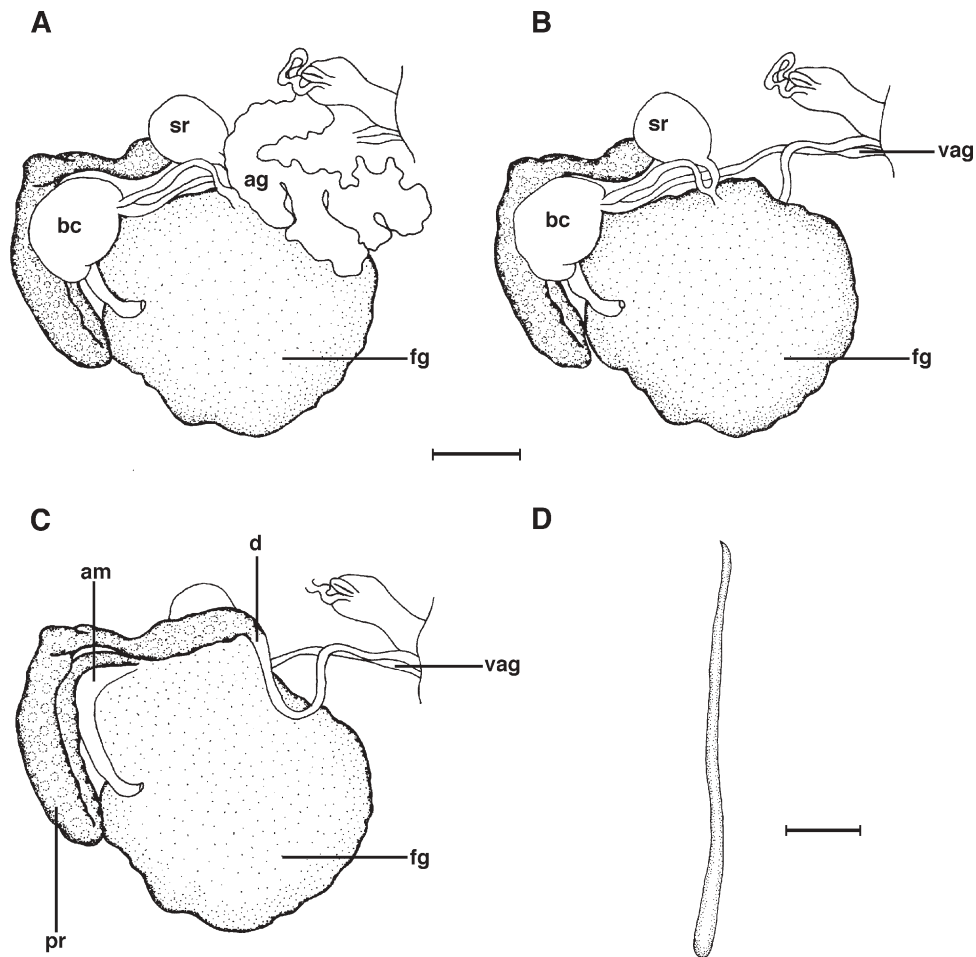


Figure 24. *Jorunna tempisquensis* n. sp. (Costa Rica, UCR-INBI01496480) **A–C.** Detail of the reproductive system; scale bar = 1.0 mm. **D.** Copulatory spine; scale bar = 0.1 mm. Abbreviations: ag, accessory gland; am, ampulla; bc, bursa copulatrix; d, deferent duct; fg, female gland; pr, prostate; sr, seminal receptacle; vag, vagina.

Remarks: The original descriptions of *Kentrodoris nigra* from New Caledonia is very incomplete and although it included illustrations it is impossible to recognize it as a member of *Jorunna*. As Marcus (1976) stated, there are no features clearly present that warrant the placement of this species in the family Kentrodorididae. The generic position of this species remains uncertain.

***Jorunna* sp. Pruvot-Fol, 1953**

Jorunna sp. Pruvot-Fol, 1953:78.

Remarks: Pruvot-Fol (1953) described *Jorunna* sp. from Dakar, Senegal. According to Marcus (1976), the little information provided in the original description is insufficient to allow placement in this genus. There is no mention of the presence of an accessory gland with a spine, one of the principal features of *Jorunna*.

***Kentrodoris* (?) sp. Burn, 1966**

Kentrodoris (?) sp. Burn, 1966: 275 (Point Lonsdale, Victoria, Australia).

Remarks: Burn (1966) collected two specimens from Port Phillip Bay, southeastern Australia. According to Burn, the background colour of the animals is creamy-white with dark brown spots scattered over the back. Unfortunately, he did not provide any further description that would allow us to determine the generic position of the specimens.

***Platydoris inframaculata* (Abraham, 1877)**

Doris inframaculata Abraham, 1877: 248, pl. 27, figs 5–7 [Ambon, Moluccas, Indonesia, holotype, 47 mm preserved length, leg. Mr Frank (BMNH 1868.6.25.48. a); paratype: 1 specimen, 45 mm preserved length, leg. Mr Frank (BMNH 1868.6.25.48.b)].

Platydoris inframaculata—Dorgan, Valdés & Gosliner, 2002: 288–290, figs 2A, 6G, H, 18–19.

Distribution: Amboina, Sri Lanka, Philippines (Dorgan *et al.*, 2002).

Remarks: Marcus (1976) included this species as a potential member of *Jorunna*. She was not certain whether this species belonged to *Jorunna* or *Platydoris*, although she agreed that “Farran’s (1905) figures of teeth and elements of penial spines

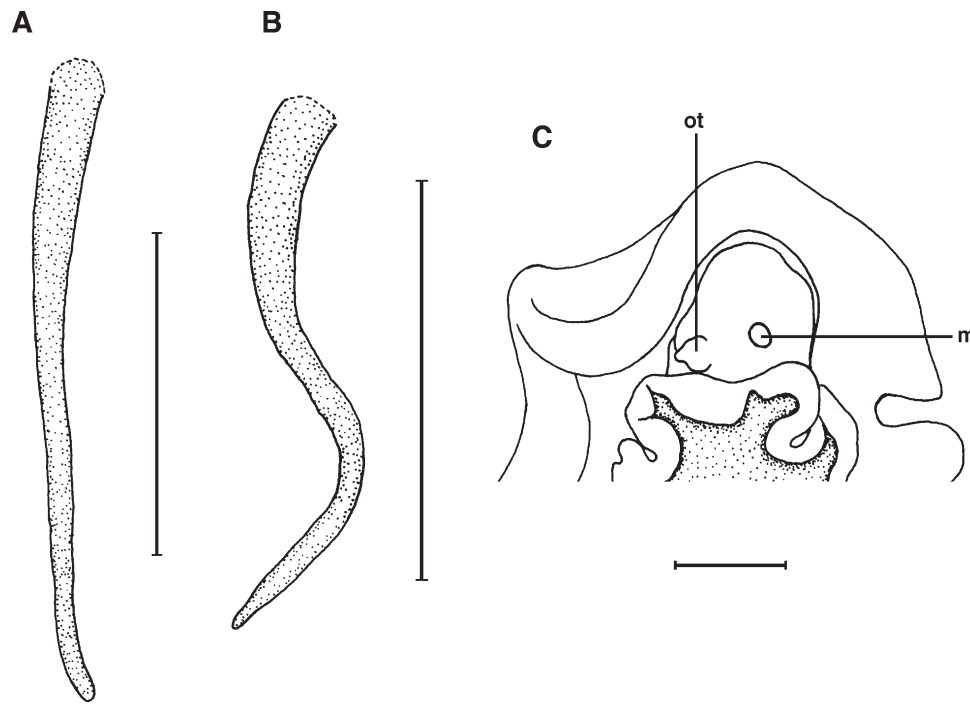


Figure 25. Copulatory spines. **A.** *Jorunna hartleyi* (NMV F 19471), scale bar = 0.2 mm. **B.** *Jorunna evansi* (BMNH 1919-10.7.44-45), scale bar = 0.2 mm. **C.** *Jorunna evansi* (BMNH 1919-10.7.44-45), ventral view, scale bar = 1.0 mm. Abbreviations: m, mouth, ot, oral tentacles.

and vaginal plates certainly belong to a *Platydoris*". Dorgan *et al.* (2002) placed this species in the genus *Platydoris* based on the similarity of the external morphology of the original specimens, specifically the presence of large and small brown spots on the ventral side, with the preserved specimens they examined from the Philippines.

***Doris infranaevata* Abraham, 1877**

Doris infranaevata Abraham, 1877: 248, pl. 27, fig. 8 [in Mediterranean Sea, holotype, 42 mm preserved length, leg. Capt. Spratt, (BMNH 1873.4.19)].

Remarks: Marcus (1976) included this species as a potential member of *Jorunna*, stating that it was possibly synonymous with *J. tomentosa*.

Based on the examination of the external morphology of the holotype we confirm, with Dayrat (2006), that this species belongs to the genus *Platydoris*. The body is depressed, the mantle is wide with a crenulate border, and the oral tentacles are flattened and grooved.

***Platydoris ellioti* (Alder & Hancock, 1864)**

Doris ellioti Alder & Hancock, 1864: 116–117, pl. 28, figs 1, 2. *Platydoris ellioti*—Dorgan, Valdés & Gosliner, 2002: 284–286, figs 2D, 6C, D, 14, 15.

Doris speciosa Abraham, 1877: 250–251, pl. 28, figs 10, 11.

Kentrodoris pseudofusca Risbec, 1928: 92–94, pl. 3, fig. 2 (New Caledonia, type probably lost, not at MNHN).

Distribution: India, New Caledonia, Papua New Guinea (Dorgan *et al.*, 2002).

Remarks: Dorgan *et al.* (2002) synonymized *Kentrodoris pseudofusca* with *Platydoris ellioti* (Alder & Hancock, 1864) based on

the external morphology, specifically the dorsal coloration and mottling and the distinct ventral pigmentation.

***Asteronotus cespitosus* van Hasselt, 1824**

Asteronotus cespitosus van Hasselt, 1824: 237–245.

Jorunna marchadi Risbec, 1956: 16–17, pl. 11, figs 54–57 [Île Pattle, Vietnam, holotype, 78 mm preserved length (MNHN), syn. nov].

Remarks: The study of the holotype and additional material indicates that *Jorunna marchadi* Risbec, 1956 from Vietnam is synonymous with *Asteronotus cespitosus* (van Hasselt, 1824). There are no caryophyllidia present on the dorsum of the holotype of *J. marchadi*. The body is flat, rigid and gelatinous, with irregular tubercles that are fused together forming longitudinal ridges.

***Jorunna maima* (Bergh, 1878)**

Audura maima Bergh, 1878: 568–571, pl. figs 13–2 [Camiguin, Luzon Island, Philippines, holotype, 17 mm preserved length, dissected, leg. Semper, September 1860, (ZMUC-GAS-2115)].

Jorunna maima—Valdés & Gosliner, 2001: 123, 130–131.

Remarks: Bergh (1878) described *Audura maima* from the Philippines as having a yellowish white background colour, grey viscera that could be seen through the notum, oval body, finger-like oral tentacles, rhinophores with 15 lamellae, caryophyllidia on the dorsum, 6 bipinnate branchial gills, innermost teeth with at least two denticles, midlateral teeth with denticles, outermost teeth with 4–9 denticles, jaw elements and an accessory gland with a spine. Valdés & Gosliner (2001) examined the holotype of *A. maima* and could not determine the identity of the species, however they concluded that 'the

anatomical characteristics of *A. maima* described in the original description, such as the presence of a spine in the accessory gland and the presence of elongated caryophyllidia confirm the synonymy of *Audura* with *Jorunna*.

The drawings of the radular morphology and copulatory spine made by Bergh (1878) show a very wide base and short copulatory spine instead of a slender and long spine that is characteristic of the genus *Jorunna*. Also, the wide base in most of the outermost teeth is different from the thin base and elongated shape of the outermost teeth of *Jorunna*. Since some of the features of *J. maima* resemble those present in the genus *Sclerodoris*, the identity of this species remains unclear.

PHYLOGENETIC ANALYSIS

Phylogenetic methods

The characters described below were placed in a data matrix (Table 1) using MacClade 4.0 (Maddison & Maddison, 2000).

Data were analysed by Phylogenetic Analysis Using Parsimony (PAUP) version 4.0 (Swofford, 2000) to find the most parsimonious phylogenetic tree, using an heuristic search. The stepwise addition option of Random Trees was used, with 100 replicates. The multistate characters were treated as unordered and unweighted. The percentage of missing data in the matrix was 4%. The strict consensus tree was used to trace character evolution using the character trace option in MacClade 4.0 (Maddison & Maddison, 2000). A Bremer support (or decay) analysis was performed using a heuristic search by PAUP to estimate branch support (Bremer, 1994).

Characters were polarized using the outgroup taxa *Discodoris boholiensis* Bergh, 1877 and *Doris verrucosa* (Linnaeus, 1758), which were used for rooting the tree. *Diaulula sandiegensis* (Cooper, 1863) was also included for comparison since, like *Jorunna*, it has caryophyllidia. This outgroup selection was made following Valdés & Gosliner (2001) and Valdés (2002), who showed that these taxa are basal to the rest of the caryophyllidia-bearing dorids, and that *Diaulula sandiegensis* forms a polytomy with *Jorunna*.

Taxa

Sixteen members of *Jorunna* were selected to sample the morphology of the group and 35 characters were included in the data matrix (Table 1). Data were obtained from the examination of preserved and living specimens, from some types and, in a few cases, from the literature (see Systematic Descriptions). Poor original descriptions and lack of living animals for studies of *J. lemchei*, *J. hartleyi* and *J. evansi* added noise to the analysis. These species were excluded *a posteriori* from the analysis due to the lack of complete anatomical information.

Characters

The characters used are listed below. Thirty-five characters were coded as either binary or multistate. The character states are indicated with numbers: 0, presumed plesiomorphic condition that was tested by the phylogenetic analysis; 1–3, apomorphic states. All multi-state characters were treated as unordered. Characters 1–22 are from external morphology, 23–28 from radular morphology, and 29–35 from the reproductive system.

(1) *Oral tentacles*: Some species of cryptobranch dorids, including *Doris verrucosa*, lack oral tentacles (0). In some other cryptobranch dorids such as *Jorunna* there is a pair

of oral tentacles around the buccal area that are digitiform in shape (1).

- (2) *Prolongation of the posterior foot*: In most *Jorunna* and some other dorids, the foot is relatively long and extends a short distance from the posterior end of the mantle (1), whereas in the outgroup taxa and some *Jorunna* there is no extension of the foot (0).
- (3) *Angle of the gill*: The angle of the gill is variable between taxa. There are species in which the gill is held vertically erect (0); in others, the gill is relatively spreading, and the individual leaves are held almost horizontally above the notum (1).
- (4) *Imbricated branchial leaves*: In some species of *Jorunna* the gill branches emerge vertically and overlap each other (1); while in others and most dorids the branchial leaves do not overlap (0).
- (5) *Anterior border of the foot*: In *Doris* the anterior border of the foot is grooved but not notched (0). In *Jorunna* and in *Diaulula* the anterior border of the foot is grooved and notched (1).
- (6) *Ciliated tubercle*: In *Jorunna*, as well as other caryophyllidia-bearing dorids such as *Diaulula*, there are groups of cilia joined together at the apex of the tubercle (1), whereas in the outgroup taxa ciliated areas are not present (0).
- (7) *Shape of the tubercles*: The tubercles are elongate (1) in *Jorunna* and *Diaulula*, but rounded in *Doris* and *Discodoris* (0).
- (8) *Body colour*: Some species of *Jorunna* have a brown (0) body colour. The outgroup taxa have brown body colour and so this state is plesiomorphic. Most species of *Jorunna* have a body colour that is grey, purple or black (1), or white (2), while a few have a yellow-orange body (3).
- (9) *Dark rings on the dorsum*: Some species of *Jorunna* have dark rings on the dorsum, in which the centre of the ring lacks pigment (1), whereas in other species and in the outgroup these rings are not present (0).
- (10) *Spots on the notum*: In some species of *Jorunna* there are light spots (0), whereas in others there are black spots scattered on the notum composed of an aggregation of dark pigment (1).
- (11) *Distribution of spots*: Several character states can be identified here. In some species, the spots are arranged in two lines (0); in others, spots are arranged randomly (1) or around the margin (2).
- (12) *Mantle glands*: A few species of *Jorunna* have a few mantle glands distributed around the mantle edge (1). These are absent in other caryophyllidia-bearing dorids and in the outgroup taxa (0).
- (13) *Rhinophoral pigment*: Most *Jorunna* species have pigmentation on the rhinophores that is the same colour as the body (0), whereas a few species have black pigmentation on the rhinophoral club (1).
- (14) *Rhinophoral tip pigment*: There is some white pigment present on the apices of the rhinophores of some species (1) that is absent in others (0).
- (15) *Dark pigment on gill*: A few species of *Jorunna* have dark pigment distributed on their gill (1), whereas the dark pigment is absent in most of the species (0).
- (16) *Gill tip pigment*: In some species, the pigment present on the apices of the branchial leaves is the same colour as the body (0), whereas this pigment is white in other species (1).
- (17) *Black spots on the notched upper lip*: In some *Jorunna* there are black spots on the notched upper lip (1), whereas in others these spots are not present (0).
- (18) *Colour of the tips of the tentacles*: The tips of the tentacles are speckled with black (0) or not speckled (1).
- (19) *Spots on the sole of the foot*: In some species of *Jorunna* and some of *Discodoris*, there are spots scattered on the sole of

Table 1. Data matrix of character states in the taxa used in the phylogenetic analysis of the genus *Jorunna*. See text for description of characters and states.

Species	Character number																																				
	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		
<i>D. verrucosa</i>	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	?		
<i>D. boholiensis</i>	1	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	?	0	0	?	0	0	
<i>D. sandiegensis</i>	1	0	1	0	1	1	1	2	1	1	0/1	0	0	0	0	0	0	1	0	0	0	1	0	0	?	0	0	0	0	0	?	?	?	0	?	1	0
<i>J. rubescens</i>	1	1	1	0	1	1	1	2	0	0	1	0	1	0	1	0	1	1	0	1	?	0	0	0	?	0	0	0	1	0	1	1	0	1	0	0	
<i>J. tomentosa</i>	1	1	0	1	1	1	1	1	0	0	0/1	0/1	0	0	0	0	0	1	0	0	0	0	0	0	?	0/1	0	0	1	0	1	1	1	1	1	1	
<i>J. funebris</i>	1	1	1	0	1	?	1	2	1	1	1	1	1	0	1	0	1	0	1	0/1	1	1	0	0	?	0	0	0	1	1	1	1	1	0	1	0	
<i>J. pantherina</i>	1	1	0	0	1	?	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	
<i>J. labialis</i>	1	0	0	?	1	1	1	1	0	0	?	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	
<i>J. spazzola</i>	1	1	0	0	1	1	1	1	0	0	0/2	0	0	1	0	1	0	?	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	
<i>J. alisonae</i>	1	1	0	0	1	1	1	1	0	0	0/1	0	0	1	0	1	0	1	0	0	0	0	0	1	0/1	1	0	0	0	1	0	1	1	0	1	1	
<i>J. lemchei</i>	1	0	?	?	1	1	1	1	0	1	?	0	0	0	0	0	0	1	0	0	0	0	1	?	0	0	0	0	0	1	1	1	1	1	1	?	
<i>J. pardus</i>	1	1	1	0	1	1	1	3	1	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	?	0/1	0	0	1	0	1	1	1	1	1	0	
<i>J. onubensis</i>	1	1	0	?	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	
<i>J. hartleyi</i>	1	?	?	?	1	?	1	1	0	1	0	?	0	?	0	?	0	1	0	0	?	0	1	0	?	0	0	?	1	1	1	1	1	1	1	?	
<i>J. ramicola</i>	1	0	0	?	1	1	1	1	0	0	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	1	0	1	1	1	1	0	
<i>J. parva</i>	1	1	0	0	1	1	1	3	0	1	?	1	1	0	1	0	0	?	?	1	1	2	0	0	?	1	0	1	1	0	1	1	0	1	0	0	
<i>J. osae</i>	1	0	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	
<i>J. tempisquensis</i>	1	1	1	0	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	?	0	0	0	1	0	1	1	1	1	1	0	
<i>J. evansi</i>	1	?	?	?	1	?	?	1	0	1	?	1	0	?	?	?	0	?	?	0	?	?	1	1	0	1	0	0	1	1	1	1	?	?	?		

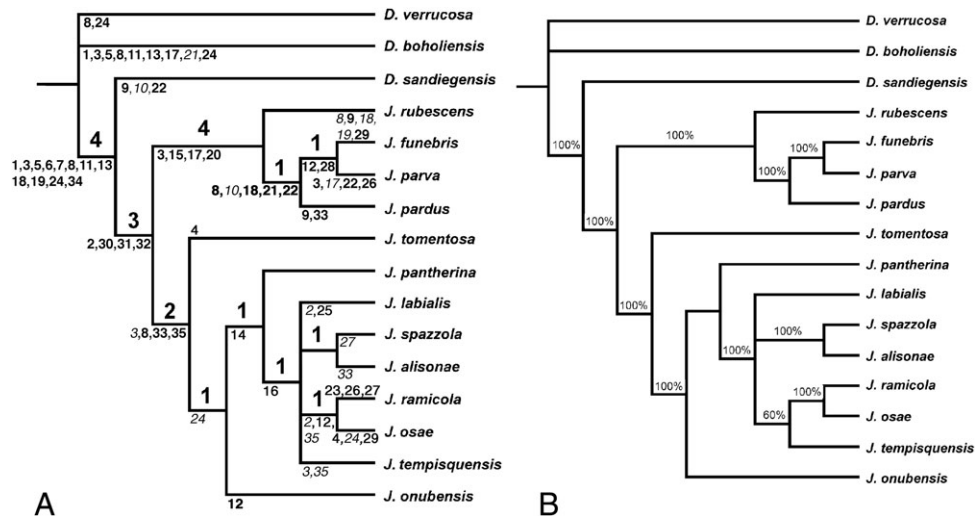


Figure 26. **A.** Preliminary phylogeny of the genus *Jorunna*. Strict consensus tree with Bremer support analysis. Large numbers on the branches show the Bremer support values, small numbers show the character evolution (see text). Italic numbers indicate reversals. **B.** 50% Majority rule tree of five most parsimonious trees.

the foot (1), whereas in the outgroup, *Doris boholiensis*, *Diaulula* and some other species of *Jorunna* these spots are absent (0).

- (20) *Spots on the dorsal visible part of the foot:* Some species have black spots scattered on the dorsal part of the foot that is visible when the animal is in motion (1). On the contrary, other species as well as the outgroup taxa lack these spots (0).
- (21) *Spots on the ventral side of the foot:* In three species of *Jorunna* there are some spots present on the ventral side of the animal (1), whereas these spots are absent in all other species of *Jorunna* as well as *Diaulula* and one of the outgroup taxa (0).
- (22) *Coloured tubercles:* In most species of *Jorunna* as well as in the outgroup taxa the mantle has no coloured tubercles (0), whereas in a few *Jorunna* and *Diaulula sandiegensis* the coloured tubercles are arranged either in a cluster (1) or singly (2).
- (23) *Outer-lateral teeth shape:* The shape of the outermost radular teeth is very different among species. In some *Jorunna* and the outgroup, the teeth are hamate (0), whereas in other species of *Jorunna* they have a plate-like shape (1).
- (24) *Labial cuticle:* Jaw elements are present in most of the cryptobranch dorids including some species of *Jorunna* (0), whereas in others the labial cuticle is smooth (1).
- (25) *Shape of the jaw elements:* In some species the jaw elements are well developed, with a rectangular shape (1), whereas in others the jaw elements are amorphous (0).
- (26) *Outermost lateral teeth:* Two character states can be recognized in the outer lateral teeth: they can be smooth (0) as in most species of *Jorunna*, or in a few species denticulate (1).
- (27) *Innermost radular teeth with denticles:* Two members of *Jorunna* have one to three denticles on the inner lateral tooth (1), whereas in other species and in the outgroup taxa the innermost tooth is smooth (0).
- (28) *Basal extension of lateral teeth:* The radula of most species of *Jorunna* has a swelling on the lateral teeth that can be situated basally (0), or in the middle of the teeth (1).
- (29) *Shape of the copulatory spine tip:* The shape of the copulatory spine can be curved with a little hook (1), or straight and lacking a hook (0).

- (30) *Stomach free:* In *Jorunna* the stomach is not covered by the digestive gland (1), whereas in the outgroup the stomach is covered by the digestive gland (0).
- (31) *Accessory gland:* The accessory gland consists of a structure located next to the distal part of the female gland mass, which opens into the albumen gland. There is an accessory gland present in all species of *Jorunna* (1). *Doris*, *Discodoris* and *Diaulula* lack an accessory gland (0).
- (32) *Copulatory spine:* All species of *Jorunna* have a copulatory spine present in the accessory gland, which is used in the copulatory process (1). The outgroup taxa lack a copulatory spine (0).
- (33) *Shape of accessory gland:* The accessory gland can be globular in shape (0), or not globular (1).
- (34) *Prostate portions:* In *Jorunna* and *Diaulula* (as well as other genera such as *Halgerda* and *Asteronotus*), the prostate has two parts that are well differentiated in colour and texture (1), whereas in most dorids the prostate has a single part (0).
- (35) *Relative size of bursa:* The bursa copulatrix can be the same size as the seminal receptacle (0), or much larger (1).

RESULTS AND DISCUSSION

The heuristic analysis of the data set produced five equally parsimonious trees with a length of 65 steps. The Consistency Index (CI = 0.585) and the Retention Index (0.675) show that 42% of all characters exhibit homoplasy (reversal and/or parallelism). The strict consensus tree is shown in Figure 26A. The italic numbers indicate reversals or parallelism. All the branches but one were present in each of the equally parsimonious trees, i.e. 100% in the majority rule tree (Fig. 26B).

The strict consensus tree shows that the genus *Jorunna* is a monophyletic group supported by four synapomorphies, with *Diaulula sandiegensis* being the sister group to *Jorunna* (Fig. 26A). The synapomorphies of the genus *Jorunna* are: prolongation of the posterior foot (2), stomach free (30), accessory gland (31) and copulatory spine (32). The synapomorphies that support the sister relationship of *Diaulula sandiegensis* and *Jorunna* are: oral tentacles (1), angle of the gills (3), anterior border of the foot (5), ciliated tubercle (6), shape of the

Table 2. Comparative morphology of the valid species of the genus *Jorunna* from the Indo-Pacific.

	<i>J. funebris</i> (Kelaart, 1859)	<i>J. pantherina</i> (Angas, 1864)	<i>J. rubescens</i> (Bergh, 1876)	<i>J. parva</i> (Baba, 1938)	<i>J. hartleyi</i> (Burn, 1958)	<i>J. alisonae</i> Marcus, 1976	<i>J. ramicola</i> Miller, 1996
Geographic Range	Indo-Pacific and Indo-West Pacific	Australia and New Zealand	Indo-Pacific and Western Indian Ocean	Japan, Philippines, Tanzania, Papua New Guinea, Seychelles	Southern Australia	Hawaii, Marshall Islands, Indonesia	Indonesia, Papua New Guinea, New Zealand, Philippines
Dorsal colour	White to yellow-cream with dark brown rings of different sizes homogeneously distributed	Purplish brown to pale brown with dark patches, largest in the central part, with opaque white spots	Cream-grey to yellow with oval yellow spots surrounded by cream-coloured rings and horizontal black stripes along the body	Dark orange to dark brown. Taller caryophyllidia are dark brown	Pale pink with large brown patches encircled with white or dark purple spots	Pale grey with dark grey spots on mantle margin. Two lines of spots arranged longitudinally from the rhinophores to the gill	Pale grey to light brown with patches of the same colour.
Rhinophore colour	White with black apices	Base colourless, uppermost lamellae speckled in white	Base black or cream-yellow, club black-spotted with white or cream-coloured spots	Bases of rachises light yellow with dark clubs, or dark brown rachises with light yellow clubs	White	Cream-brown with a pale grey-brown club	Pale-grey, speckled with dark brown and white on the club
Gill colour	White with delineations in dark black	–	Base of the branchial sheaths spotted in black and yellow, base of gill white, rachises dark brown	Light yellow base with dark brown tips or light yellow leaves with dark brown rachises	White	Gray to brown with cream glandular spots	Dark grey
Foot dorsal colour	–	–	–	Dark brown central line with dark brown spots on edges	–	–	–
Ventral colour	Yellow-cream with dark spots around the margin of the foot	Sole of the foot light, margins of the foot sparsely speckled translucent white	Sole of the foot white or cream-coloured with black stripes that are also visible on the laterals of the foot	Several dark spots around the margin of the foot	Pink	Pale grey	–
Upper lip colour	Yellow-cream	–	Cream yellow speckled with black	Yellowish, sometimes with two brown spots on each side of the lip	–	Cream in preserved animals	–
Oral tentacles colour	Yellow-cream with dark brown spots in some specimens	Speckled	Light white to yellow	Yellowish	White	Pale grey	–
Gills	6, tripinnate	11, bi-tripinnate	7, tripinnate	7, bipinnate	10, bipinnate	12, tripinnate	10, bipinnate
Mantle glands	White in colour, distributed around the mantle edge	–	–	White in colour, distributed around the mantle edge	–	Absent	White in colour, distributed around the mantle edge

Continued

Table 2. Continued

	<i>J. funebris</i> (Kelaart, 1859)	<i>J. pantherina</i> (Angas, 1864)	<i>J. rubescens</i> (Bergh, 1876)	<i>J. parva</i> (Baba, 1938)	<i>J. hartleyi</i> (Burn, 1958)	<i>J. alisonae</i> Marcus, 1976	<i>J. ramicola</i> Miller, 1996
Foot	Dorsally visible when the animal is in motion	–	Dorsally visible when the animal is in motion	Dorsally visible when the animal is in motion	–	Dorsally visible when the animal is in motion	No prolongation present
Radula	21 × (21.0.21) in 20-mm-long preserved specimen	20 × (28.0.28) no more information	22 × (29.0.29) in 35-mm-long preserved specimen	20 × (15.0.15) in 6-mm-long preserved specimen	21 × (23.0.23) in 18-mm-long preserved specimen	16 × (17.0.17) in 20-mm-long preserved specimen	14 × (18.0.18) in 5-mm-long preserved specimen
Innermost teeth	Hamate, shorter and thinner than midlateral teeth, lacking denticles	Hamate, small, lacking denticles	Hamate, blunt, lacking denticles	Hamate, elongated, lacking denticles	Hamate, lacking denticles	Hamate, pointed, shorter than the midlateral teeth, lacking denticles	Hamate, elongated, with up to 3 denticles near the cusp
Midlateral teeth	Hamate, thicker than innermost teeth, lacking denticles	Hamate, lacking denticles	Elongated, blunt, and lacking denticles	Hamate, without a prominent cusp, lacking denticles	Hamate, lacking denticles	Hamate, pointed, lacking denticles	Hamate, pointed, lacking denticles
Outermost teeth	Hamate, lacking denticles	Hamate, lacking denticles	Shorter than midlateral teeth, curved and pointed, lacking denticles	Smaller than midlateral teeth. The 5 outermost have up to 5 denticles	Elongated, lacking denticles	Small, elongated, smooth or sometimes with a single denticle near the cusp	Elongated, first three outermost teeth with up to 3 denticles
Labial cuticle	Smooth	With jaw elements	Smooth	Smooth	With jaw elements	With jaw elements	With jaw elements
Accessory gland and spine	Present, with a curved spine <i>c.</i> 717 μm long	Present, with a long pointed spine	Present, with a curved spine <i>c.</i> 3.7 mm long	Present, with a spine <i>c.</i> 477 μm long	Present, with a spine <i>c.</i> 198 μm long	Present, with a curved spine <i>c.</i> 1.03 mm long	Present, with a curved spine <i>c.</i> 2.25 mm long

– No information available.

Note: penial hooks, non-prostatic deferent duct divided into two regions absent in all species listed.

tubercles (7), body colour (8), distribution of spots (11), rhinophoral pigment (13), colour of the tips of the tentacles (18), spots on the sole of the foot (19), labial cuticle (24) and prostatic portions (34) (Fig. 26A).

Two main clades within *Jorunna* can be identified. The clade including *J. rubescens*, *J. funebris*, *J. parva* and *J. pardus* is supported by four synapomorphies: angle of the gills (3), dark pigment on gill (15), rhinophoral pigment (16), black spots on the notched upper lip (17), and spots on the visible part of the foot (20). Within the second clade, composed of the rest of the species, *J. tomentosa* followed by *J. onubensis* and then *J. pantherina* are the most basal. There is a polytomy composed of *J. labialis* and *J. tempisquensis*, *J. spazzola*, *J. alisonae*, *J. ramicola* and *J. osae*. The topology of the 50% majority rule tree is the same, except for the clade in which *J. tempisquensis* is basal to *J. ramicola* and *J. osae* (Fig. 26B). Bremer support values range from one to four on the nodes of the tree (Fig. 26A).

There is a high degree of homoplasy (HI = 42%) within *Jorunna*, and insufficient informative characters to allow full

resolution of the tree. For example, *Jorunna* in the jaws have been lost twice independently. However, other characters that have been used to classify other cryptobranch dorids such as the dorsal morphology, the penial hooks and the prostatic shape have been informative in resolving the phylogeny of the genus.

In order to test how colour characters affect the topology of the tree, a heuristic analysis was conducted after removal of all the colour characters. The strict consensus tree (not shown) remained almost the same, with only a slight difference in the topology. In the clade of *J. pardus*, this species is located basally, followed by *J. rubescens*.

Character evolution

The strict consensus tree is used to illustrate character evolution. Character analysis indicates that some of the characters were subject to at least one instance of homoplasy (Fig. 26A). Some of these characters are: prolongation of the posterior foot (2), angle of the gill (3), mantle glands (12) and black spots on the notched upper lip (17).

Table 3. Comparative morphology of the valid species of the genus *Jorunna* from the Eastern Pacific.

	<i>J. pardus</i> Behrens & Henderson, 1981	<i>Jorunna osae</i> new species	<i>Jorunna tempisqueusis</i> new species
Geographic range	California to Sacramento Reef, Baja California	Costa Rica	Southern Mexico and Costa Rica
Dorsal colour	Yellow-cream with dark brown spots; spots actually an aggregate of minute dark brown specks	Pale cream to yellow with light yellow-brown patches	Light cream, light brown to dark purple with light brown to black spots on the dorsum
Rhinophore colour	Dark brown with yellow-cream bases and rachises; there is no pigment on the rhinophoral apices	Pale cream to yellow with white apices, club speckled in brown	Light cream to light brown finely speckled in dark brown spots, yellowish apices
Gill colour	Yellow-cream base with dark brown tips	Pale cream to yellow	Dark brown, almost purple bases with light yellow apices finely speckled in brown
Foot dorsal colour	Yellow-cream with some large dark brown spots around the margin	–	Light cream with some minute dark spots
Ventral colour	Yellow-cream, speckled with some small dark brown spots	Pale cream to yellow	Light cream with some minute brown spots more densely arranged on mantle edges
Upper lip colour	Yellow-cream with large dark brown spots on the upper lip	Pale cream to yellow	Light cream
Oral tentacles colour	Yellow-cream	Pale cream to yellow	Greyish finely speckled in brown
Gills	8, tripinnate	12, tripinnate	11, tripinnate
Mantle glands	Absent	White, distributed around the mantle	Absent
Foot	Dorsally visible when the animal is in motion	Not dorsally visible	Dorsally visible when the animal is in motion
Radula	41 × (80.0.80) in 20-mm-long preserved specimen	16 × (18.0.18) in 6-mm-long preserved specimen	17 × (18.0.18) in 7-mm-long preserved specimen
Innermost teeth	Hamate, short, thicker at the base, lacking denticles	Hamate, small, lacking denticles	Hamate, with a single cusp, lacking denticles
Midlateral teeth	Hamate, with a single cusp, lacking denticles	Hamate, with a single cusp, lacking denticles	Hamate, with a single cusp, lacking denticles
Outermost teeth	Small, short, smooth or sometimes with 6 denticles	Small, elongate, lacking denticles	Hamate, small, thin, elongate, lacking denticles
Labial cuticle	Smooth	Smooth	With jaw elements
Accessory gland and spine	Present, with a spine c. 950 µm long	Present, with a spine c. 600 µm long	Present, with a spine c. 550 µm long
Penial hooks	Absent	Absent	Absent
Non-prostatic deferent duct divided into two regions	Absent	Absent	Absent

–No information available.

Biogeography

The two major clades of *Jorunna* suggest a different biogeographical history for each. The clade containing *J. rubescens*, *J. funebris*, *J. parva* and *J. pardus* includes species restricted to the tropical Indo-Pacific and temperate California. *Jorunna pardus*, from California, is sister to two Indo-Pacific species, *J. parva* and *J. funebris*. The sister to these three is *J. rubescens*, also from the Indo-Pacific, suggesting that *J. pardus* is likely derived from an Indo-Pacific ancestor.

In the other major clade two Atlantic species are situated basally. In the subclade of *J. tempisqueusis*, *J. osae* and *J. ramicola*, the eastern Pacific *J. tempisqueusis* is basal to another eastern Pacific species, *J. osae*, plus an Indo-Pacific species, *J. ramicola*. Other patterns mix Atlantic and Indo-Pacific members of the clade. No overall, clearly defined, pattern of distribution is represented in the phylogenetic relationships. Future studies should be conducted (including additional taxa and molecular data) to test these relationships,

in order to determine whether the lack of a clear biogeographical pattern is a result of complex biogeographical history or a weak phylogenetic signal.

ACKNOWLEDGEMENTS

This paper has been supported in part by the National Science Foundation through the PEET grants DEB-9978155 and 0329054 to Terrence M. Gosliner and Ángel Valdés, and the Lakeside Foundation through a scholarship to the senior author at the California Academy of Sciences. The fieldwork in Costa Rica was also possible thanks to the Cooperative Agreement between the Ministry of Environment and Energy (MINAE) and the Instituto Nacional de Biodiversidad (INBio).

The types and museum material were provided by E. Kools (CAS), A. Valdés (LACM), V. Héros (MNHN), A. Cambell and K. Way (BMNH), T. Schiøtte (ZMUC), C. Bright (SMNHI), C. Rowley (Museum Victoria) and R. Vargas

Table 4. Comparative morphology of the valid species of the genus *Jorunna* from the Mediterranean and Western Atlantic.

	<i>J. tomentosa</i> (Cuvier, 1804)	<i>J. labialis</i> (Eliot, 1908)	<i>J. spazzola</i> (Marcus, 1955)	<i>J. lemchei</i> Marcus, 1976	<i>J. onubensis</i> Cervera, García-Gómez, & García, 1986
Geographic range	Norwegian coast to the Faeroes, Britain, France, Portugal, Italy, Morocco, Adriatic Sea, South Africa, Algeria	Red Sea: Suez and Suakin; Indian Ocean: Tanzania and Madagascar	Mediterranean and Western Atlantic	West Ireland	Portil, Huelva, Spain
Dorsal colour	Yellow-cream to grey with small light spots randomly distributed or forming two vertical lines along the dorsum	White to very dark grey with light brown spots	Light to grey with spots near the margin or light yellow to orange with brown spots on each side of notum, forming a row	Cream without any spots	Light brown to pink with some dark spots. Some tubercles have white apices
Rhinophore colour	Yellow-cream to grey with dark brown pigmentation on the lamellae	–	Light grey	Cream	White with a dark brown stripe in some lamellae, base of rhinophores transparent
Gill colour	Yellow-cream with dark brown pigmentation on some branches	–	Light grey	–	White with some minute brown spots
Foot dorsal colour	Yellow-cream	–	–	–	–
Ventral colour	Same colour as the dorsum	–	White	–	Light brown to pink
Upper lip colour	Yellow-cream	–	–	–	–
Oral tentacles colour	Cream	–	–	–	Light brown
Gills	11, bipinnate	11, bipinnate	7–12, uni to tripinnate	11–12, bipinnate	9–10, bipinnate
Mantle glands	Present	–	Present	–	Present
Foot	Dorsally visible when the animal is in motion	–	–	–	Dorsally visible when the animal is in motion
Radula	22 × (23.0.23) in a 16-mm-long preserved specimen	19 × (17.0.17) in a 10-mm-long preserved specimen	19 × (16-17.0.16-17) no more information; 15 × (20.0.20) in a 7 mm-long preserved specimen	18-19 × 2-5.18-19.0.18-19.2-5 no more information	19-7 × (26-21.0.21-26) no more information
Innermost teeth	Hamate, thick, short, lacking denticles	Hamate, elongated with a cusp close to the base of the teeth, lacking denticles	Sometimes with a single small denticle	Hamate, lacking denticles	Hamate, lacking denticles
Midlateral teeth	Hamate, thick, lacking denticles	Hamate, elongated, lacking denticles	Hamate, lacking denticles	Hamate, lacking denticles	Hamate, lacking denticles
Outermost teeth	Small, elongate, smooth or sometimes with up to 4 denticles	Hamate, short, pointed, lacking denticles	With up to 4 irregular denticles	Almost plate-like, elongate, lacking denticles	Hamate, short, lacking denticles
Labial cuticle	Smooth	With jaw elements	With jaw elements	Smooth	With jaw elements
Accessory gland and spine	Present, with a spine app. 920 µm long	Present, with a spine app. 600 µm long	Present, with a spine app. 300–640 µm long	Present, with a spine app. 500 µm long	Present, with a spine app. 1.3 mm long
Penial hooks	Absent	Absent	Absent	Present	Absent
Non-prostatic deferent duct divided into two regions	Absent	Absent	Absent	Absent	Present

–No information available.

(UCR). Parataxonomists at INBio collected the material from Costa Rica. Lucas Cervera, A. Sánchez, A. Hermosillo, G. Calado, S. Anderson, D. Behrens, C. Carlson, J. Wedge, R. Bolland, S. Johnson, S. Jazwinski, E. Daily, A. Ferreira, P. Fiene, F. Steiner, C. Pittman, C. Edmondson, B. Henderson, C. Lorraine, J. McLean, P. Lafollete and J. Hamann collected some of the material deposited at CAS. Leopoldo Moro took the photographs of the living animals from Costa Rica. We would like to thank Ángel Valdés for his help and guidance during the preparation of the manuscript. Shireen Fahey and D. Butvill also made constructive comments on the manuscript. We are very thankful to M. Schrödl and Lucas Cervera for their constructive and very helpful thorough review of the manuscript. Scott Serata provided technical training for the scanning electron microscope and staff of the Academy library provided invaluable help with literature. The 'Nudibranch Central' Team and the IZ & G staff provided incredible support to the senior author at CAS.

REFERENCES

- ABRAHAM, P. 1877. Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. *Proceedings of the Zoological Society of London*, **1877**: 196–269.
- ALDER, J. & HANCOCK, A. 1845–1855. *A monograph of the British nudibranchiate Mollusca*. Ray Society, London.
- ALDER, J. & HANCOCK, A. 1864. Notice of a collection of nudibranchiate Mollusca made in India by Walter Elliot Esq., with descriptions of several new genera and species. *Transactions of the Zoological Society of London*, **5**: 113–147.
- ALLAN, J. 1932. Australian nudibranchs. *Australian Zoologist*, **7**: 87–105.
- ANGAS, G. 1864. Description d'espèces nouvelles appartenant à plusieurs genres de mollusques nudibranches des environs de Port-Jackson (Nouvelle-Galles du Sud), accompagnée de dessins faits d'après nature. *Journal de Conchyliologie, série 3*, **12**: 43–70.
- BABA, K. 1938. Opisthobranchia of Kii, middle Japan. *Journal of the Department of Agriculture, Kyushu Imperial University*, **6**: 1–19.
- BEHRENS, D. & HENDERSON, R. 1981. Two new cryptobranch dorid nudibranchs from California. *Veliger*, **24**: 120–128.
- BEHRENS, D. & GATEWOOD, J. 1986. New opisthobranch records for the west coast of Baja California. *Shells and Sea Life*, **18**: 139–142.
- BERGH, L.S.R. 1876. Malacologische Untersuchungen. *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate, Band 2, Theil 2*, Heft 10: 377–427, pls 49–53. C.W. Kreidel, Wiesbaden.
- BERGH, L. S. R. 1878. Malacologische Untersuchungen. *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate, Band 2, Theil 2*, Heft 13: 547–601, pls 62–65. C.W. Kreidel, Wiesbaden.
- BERGH, L. S. R. 1881. Malacologische Untersuchungen. *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate, Band 2, Theil 4*, Heft Supplement 2: 79–128, pls G, H, J-L. C.W. Kreidel, Wiesbaden.
- BERGH, L. S. R. 1884. Malacologische Untersuchungen. *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate, Band 2, Theil 3*, Heft 15: 647–754, pls 69–76. C.W. Kreidel, Wiesbaden.
- BERGH, L. S. R. 1890. Die Nudibranchien der Sunda-Meeress. Malacologische Untersuchungen. *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate, Band 2, Theil 3*, Heft 17: 873–991, pls 85–89. C.W. Kreidel, Wiesbaden.
- BREMER, K. 1994. Branch support and tree stability. *Cladistics*, **10**: 295–304.
- BURN, R. 1958. Further Victorian Opisthobranchia. *Journal of the Malacological Society of Australia*, **2**: 20–36.
- BURN, R. 1966. Port Philip Survey 1957–1963. Opisthobranchia. *Memoirs of the National Museum of Victoria*, **27**: 265–288.
- CERVERA, J., GARCÍA GOMEZ, J. & GARCÍA, F. 1986. Il genere *Jorunna* Bergh, 1876 (Mollusca: Gastropoda: Nudibranchia) nel litorale iberico. *Lavori Società Italiana di Malacologia*, **22**: 111–132.
- CUVIER, G. 1804. Memoire sur le genre *Doris*. *Annales de Museum National d'Histoire Naturelle, Paris*, **4**: 447–473.
- CHAN, J. & GOSLINER, T. 2007. Preliminary phylogeny of *Thordisa* (Nudibranchia: Discodorididae) with descriptions of five new species. *Veliger*, **48**: 284–308.
- DAYRAT, B. 2006. A taxonomic revision of *Paradoris* sea slugs (Mollusca, Gastropoda, Nudibranchia, Doridina). *Zoological Journal of the Linnean Society*, **147**: 125–238.
- DORGAN, K., VALDÉS, A. & GOSLINER, T. 2002. Phylogenetic systematics of the genus *Platydoris* (Mollusca, Nudibranchia, Doridoidea) with descriptions of six new species. *Zoologica Scripta*, **31**: 271–319.
- EDMUNDS, M. 1971. Opisthobranchiate Mollusca from Tanzania (suborder Doridacea). *Zoological Journal of the Linnean Society*, **59**: 339–396.
- ELIOT, C. 1906. Report upon a collection of Nudibranchiata from the Cape Verd Islands, with notes by C. Crossland. *Proceedings of the Malacological Society of London*, **7**: 131–159.
- ELIOT, C. 1907. Nudibranchs from New Zealand and the Falkland Islands. *Proceedings of the Malacological Society of London*, **7**: 327–361.
- ELIOT, C. 1908. Reports on the marine biology of the Sudanese Red Sea. XI. Notes on a collection of nudibranchs from the Red Sea. *Journal of the Linnean Society, London, Zoology*, **31**: 86–122.
- FARRAN, G. 1905. Report on the opisthobranchiate Mollusca collected by Professor Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar (Supplement)*, **21**: 329–364.
- FISCHER, P. 1869. Catalogue de nudibranches et cephalopodes des côtes océaniques de la France (I Supplément). *Journal de Conchyliologie*, **3**: 17–5–10.
- FISCHER, P. 1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles*. F. Savy, Paris.
- GOSLINER, T. 1987. Biogeography of the opisthobranch gastropod fauna of southern Africa. *American Malacological Bulletin*, **5**: 243–258.
- INTERNATIONAL COMMISSION FOR ZOOLOGICAL NOMENCLATURE. 1999. *International Code of Zoological Nomenclature*. Edn 4. International Trust for Zoological Nomenclature, London.
- HASSELLT J. VAN 1824. In: André Férussac. Extrait d'une lettre de F. C. van Hasselt sur les mollusques de l'île de Java, adressée au Prof. van Swinderen à Groningue. (Algem. konst en Letterbode, Octobre 1823) Ceram, Province de Bantam; febr. 1823. *Bulletin des Sciences Naturelles et de Géologie*, **3**: 81–87.
- JOHNSTON, G. 1838. Miscellanea Zoologica. IV. The Scottish Mollusca Nudibranchia. *Annales and Magazine of Natural History*, **1**: 44–56.
- KAY, E. & YOUNG, D. 1969. The Doridacea (Opisthobranchia: Mollusca) of the Hawaiian Islands. *Pacific Science*, **23**: 172–231.
- KELAART, E. 1859. Descriptions of new and little-known species of Ceylonese nudibranchiate mollusks. *Annales and Magazine of Natural History*, **3**: 291–304.
- KENNY, R. 1970. Queensland faunistic records — IX. A second collection of opisthobranch molluscs from Queensland. *Papers of the Department of Zoology, University of Queensland*, **3**: 83–96.
- MADDISON, W. & MADDISON, D. 2000. *MacClade*. Version 4.06. Sinauer Associates, Sunderland, MA.
- MARCUS, Er. 1955. Opisthobranchia from Brazil. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia*, **20**: 89–261.
- MARCUS, Er. 1965. Some Opisthobranchia from Micronesia. *Malacologia*, **3**: 263–286.
- MARCUS, Ev. 1970. On some opisthobranchs from Cananéia, Brazil. *Boletim de Zoologia e Biologia Marinha*, **27**: 207–228.

REVISION OF *JORUNNA*

- MARCUS, Ev. 1976. On *Kentrodoris* and *Jorunna* (Gastropoda: Opisthobranchia). *Boletim de Zoologia, Universidad de São Paulo*, **1**: 11–68.
- MARCUS, Ev. & MARCUS, Er. 1964. Verzeichnis der euthyneuren Meeresschnecken Brasiliens. *Beitrag zur Neotropischen Fauna*, **3**: 195–206.
- MILLER, M. 1996. The dorid nudibranch genus *Jorunna* Bergh, 1876 (Gastropoda, Opisthobranchia) in New Zealand. *Journal of Natural History*, **30**: 1095–1109.
- PRUVOT-FOL, A. 1953. Étude de quelques opisthobranches de la côte Atlantique du Maroc et du Sénégal. *Travaux de l'Institut Scientifique Cherifien Zoologie*, **5**: 1–105.
- QUOY, J.R.C. & GAIMARD, J.P. 1832–1833. Zoologie, Mollusca 2. In *Voyage de découvertes de l'Astrolabe execute par ordre du Roi, pendant les années 1826-1829 sous le commandement de M. J. Dumont D'Urville*. Tastu, Paris.
- RISBEC, J. 1928. Contribution à l'étude des nudibranches Néo-Calédoniens. Thèse présentée à la faculté des sciences de l'Université de Paris pour obtenir le grade de docteur es-sciences naturelles. *Faune des Colonies Françaises*, **2**: 1–328.
- RISBEC, J. 1956. Nudibranches du Viet-Nam. *Archives du Museum National d'Histoire Naturelle, Paris*, **7**: 1–34.
- RUDMAN, W. & AVERN, G. 1989. The genus *Rostanga* Bergh, 1879 (Nudibranchia: Dorididae) in the Indo-West Pacific. *Zoological Journal of the Linnean Society*, **96**: 281–338.
- SCHMEKEL, L. 1968. Ascoglossa, Notaspidea und Nudibranchia im Litoral des Golfes von Neapel. *Revue Suisse de Zoologie*, **75**: 103–155.
- SCHMEKEL, L. & PORTMANN, A. 1982. *Opisthobranchia des Mittelmeeres. Nudibranchia und Sacoglossa. Fauna e Flora del Golfo di Napoli*. **40**. Springer Verlag, Heidelberg.
- SWOFFORD, D. 2000. *PAUP**. *Phylogenetic Analysis Using Parsimony (and Other Methods)*. Version 4. Sinauer Associates, Sunderland, MA.
- THOMPSON, T. 1975. Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). *Journal of Zoology*, **176**: 477–517.
- THOMPSON, T. & BROWN, G. 1984. *Biology of Opisthobranch Molluscs*, 2. Ray Society, London.
- VALDÉS, A. & HÉROS, V. 1998. The types of Recent and certain fossil opisthobranch molluscs in the Museum national d'Histoire naturelle, Paris. *Zoosystema*, **20**: 695–742.
- VALDÉS, A. & GOSLINER, T. 2001. Systematics and phylogeny of the caryophyllidia-bearing dorids (Mollusca, Nudibranchia), with descriptions of a new genus and four new species from Indo-Pacific deep waters. *Zoological Journal of the Linnean Society*, **133**: 103–198.
- VALDÉS, A. 2002. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Journal of the Linnean Society*, **136**: 535–636.
- WILLAN, R. & COLEMAN, N. 1984. *Nudibranchs of Australasia*. Australasian Marine Photographic Index, Sydney.
- YOUNG, D. 1967. New records of Nudibranchia (Gastropoda Opisthobranchia) from the Central and West-Central Pacific with a description of a new species. *Veliger*, **10**: 159–173.