

Review of the systematics of the genus *Roboastra* Bergh, 1877 (Nudibranchia, Polyceridae, Nembrothinae) with the description of a new species from the Galápagos Islands

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The nudibranch genus *Roboastra* was first described by Bergh in 1877, with *R. gracilis* as the type species. Since then a further six species have been described, but two are currently regarded as synonyms. A review of the literature shows that their original descriptions, as well as a few published additional studies, offer limited information. This has caused a great deal of confusion, with field guides and websites often containing misidentified photographs. The genus *Roboastra* is characterized by the possession of large oral tentacles developed as dorsolaterally grooved cylindrical projections equal in length to the rhinophores, reduced radular rachidian teeth with three well-defined denticles, and a small prostatic gland confined to a coiled glandular section of the vas deferens. It is distributed throughout tropical and temperate areas in the Atlantic, Eastern Pacific and Indo-Pacific. The phylogenetic relationships within the genus are unknown, as well as its position within the phylogeny of the phanerobranch dorids. In the present paper we conduct a preliminary review of the species included in *Roboastra* and a study of their phylogenetic relationships based on morphological characters. We also describe a new species, *Roboastra leonis*, from the Galápagos Islands. © 2005 The Linnean Society of London, Zoological Journal of the Linnean Society, 2005, 144, 167–189.

ADDITIONAL KEYWORDS: Doridoidea – Mollusca – new taxa – Phanerobranchia – phylogenetic systematics.

INTRODUCTION

Nembrothinae are nonsuctorian phanerobranch dorids. There is no consensus concerning their taxonomic rank: most authors treat them as a subfamily (Burn, 1967; Rudman, 1998a) within Polyceridae, while some consider them to be a separate family. The subfamily includes three genera (*Nembrotha* Bergh, 1877, *Tambja* Burn, 1962 and *Roboastra* Bergh, 1877) and is considered to be overdue for taxonomic revision.

Nembrotha was introduced with six new species, the first of which, *N. nigerrima* Bergh, 1877 was later designated as type by Burn (1967). Bergh's original six species were similar in many ways, and were separated according to the shape of the radular teeth into

three groups. However, Bergh never gave them different generic names. In his description of one of the new species, *N. gracilis*, Bergh (1877) introduced a footnote indicating that it should probably be placed in a new genus ('*Roboastra*, Bgh').

Burn (1967) separated the species formerly attributed to *Nembrotha* into three distinct genera (*Nembrotha* Bergh, 1877, *Tambja* Burn, 1962 and *Roboastra*, Bergh, 1877) based on radular and genital differences. He defined the undiagnosed genus *Roboastra* as 'seaslugs with oral tentacles strongly developed as dorsolaterally grooved cylindrical projections equal in length to the rhinophores; rachidian reduced with three prongs or well-defined denticles, lateral tooth deeply bifid, marginal plate reduced, linear, 1–3 in number; buccal collar very weak and labial armature absent; prostate gland small and confined to a coiled glandular section of the vas deferens' and

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included *R. arika* in addition to *R. gracilis*, the type species of the genus. Seven species have been described since then (Pola, Cervera & Gosliner, 2003).

The genus is distributed throughout tropical and temperate areas in the Atlantic, Eastern Pacific and Indo-Pacific (Pola *et al.*, 2003). Species of *Roboastra* are easily recognized by their limaciform and corrugated body surface. However, a review of the literature reveals that most species are poorly described and are either unidentifiable or synonyms of other species of this or other genera. Recent phylogenetic studies on several clades of the Doridoidea (Wägele, 1989a, b; Gosliner & Johnson, 1994, 1999; Fahey & Gosliner, 1999; Valdés & Gosliner, 1999, 2001; Garovoy, Valdés & Gosliner, 2001; Johnson & Valdés, 2001; Valdés, 2002) have provided a preliminary outline of the evolution of the cryptobranch dorids but no similar studies have been undertaken on the phanerobranch dorids. Wägele & Willan (2000) and Valdés (2002) stated that phanerobranchs are probably paraphyletic.

The objectives of this paper are to: (1) review the systematic status of *Roboastra*, (2) provide a phylogenetic hypothesis for the genus, based on a morphological analysis of all the species described, and (3) describe its distribution. A new species from the Galápagos Islands is described.

MATERIAL AND METHODS

The material examined for this study is deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), the Natural History Museum of Los Angeles County, Los Angeles (LACM), the Museo Nacional de Ciencias Naturales, Madrid (MNCN), the Museu Municipal de Funchal (Historia Natural) (MMF), the Museo de la Estación Científica Charles Darwin (MECCD) and the Western Australian Museum, Perth (WAM).

The specimens were dissected and a morphological examination facilitated by first making a dorsal incision. The internal features were examined using a dissecting microscope with a camera lucida. The buccal mass was dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, and dried and mounted for examination by scanning electron microscopy. Special attention was paid to the morphology of the reproductive system, including the penial hooks. The penis was critical point dried.

In order to calculate the most parsimonious phylogenetic tree, data were analysed with PAUP v. 4.0b10 (Swofford, 2001) using the heuristic algorithm (branch swapping option: TBR). In cases where a taxon had two states for a given character they were treated as

uncertain. Both ACCTRAN and the DELTRAN optimizations were used for character transformation. In both cases multistate characters were treated as unordered. One hundred random starting trees were obtained via stepwise addition. Characters were polarized in the PAUP analysis using genera *Bathydoris* Thiele, 1912, *Polycera* Müller, 1776 and *Polycerella* Verrill, 1880 as outgroup.

We used *Bathydoris* in this analysis based on the papers by Wägele & Willan (2000), Schrödl, Wägele & Willan (2001) and Valdés (2002), where the Bathydorididae was concluded to be the sister taxon to the Doridoidea. Information of the outgroup taxa was obtained from Thompson & Brown (1984), Behrens & Gosliner (1988), Wägele (1989a, b), Wägele & Willan (2000), Valdés (2002) and García Gómez (2002).

A bootstrap analysis with a hundred replicates of random trees was carried out to estimate branch support. Synapomorphies were obtained using the character trace option in MacClade 4.03 (Maddison & Maddison, 2000) based on the 50% majority-rule consensus tree from the PAUP analysis.

DESCRIPTION OF TAXA

FAMILY POLYCERIDAE ALDER & HANCOCK, 1845

SUBFAMILY NEMBROTHINAE BURN, 1967

GENUS *ROBOASTRA* BERGH, 1877

ROBOASTRA GRACILIS (BERGH, 1877)

(FIGS 1, 2, 3A, 4A)

Nembrotha gracilis Bergh, 1877: 458, pl. 56, figs 11–17.

Nembrotha rubropapulosa Bergh, 1905: 198, pl. 5, fig. 14, pl. 18, figs 19–22.

Material examined: Cebu Island: White Beach (Moalboal area), Philippines, April 1996, 1 specimen, 0–21 m depth, collected by T.M. Gosliner (CASIZ: 106591). Marshall Islands: Enewetak North, Pacific Ocean, February 1982, 1 specimen, 1 m depth, collected by S. Johnson under dead coral (CASIZ: 120670). Koror Municipality: Ngederrak Lagoon, Palau, September 1996, 2 specimens, collected by Clay Carlson (CASIZ: 109707). North coast, near Madang, Barracuda Point, Papua New Guinea, November 1990, 2 specimens, 6 m depth, collected by T.M. Gosliner (CASIZ: 075839). North coast, near Madang, Christiansen Research Institute's Clam Tanks, Papua New Guinea, November 1991, 1 specimen, collected by T.M. Gosliner (CASIZ: 086900). North coast, near Madang, outer barrier reef between Pig Island and Rasch Pass, Papua New Guinea, June 1992, 1 specimen, collected by T.M. Gosliner (CASIZ: 086496). Luzon, Batangas Province, Maricaban Island, Philippines, 1 specimen, collected by M. Miller (CASIZ: 103732). Molokini Island, Hawaii, April 1990, 1 specimen, 6 m depth, col-

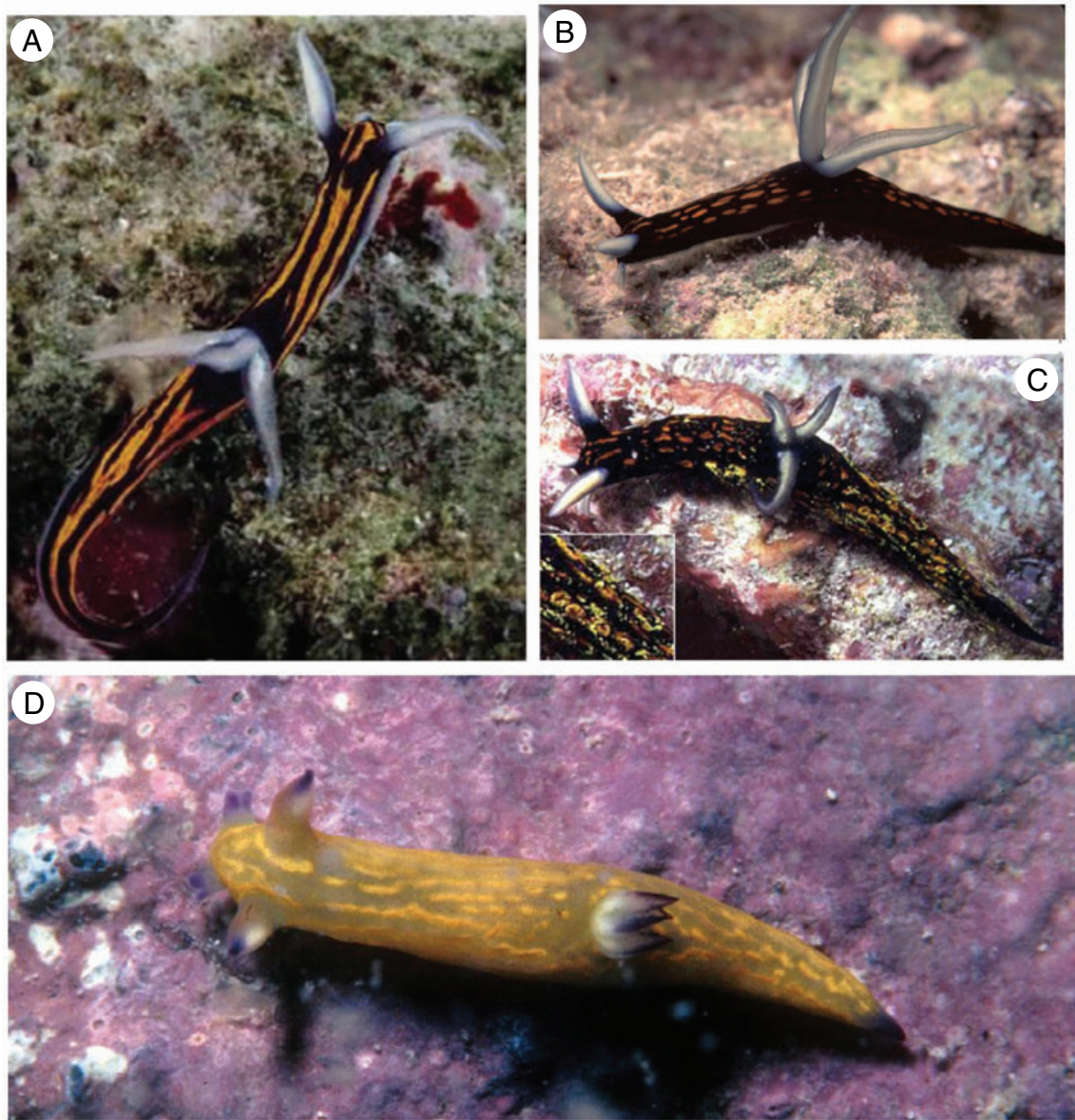


Figure 1. *Roboastrea gracilis*: living specimens from: A, Fiji (photo K. Tucker); B, Cebu, Philippines (photo M. Miller); C, Sulawesi, Indonesia (photo L. Warren); and D, Hawaii (photo P. Fiene).

lected by P. Fiene under rubble. Identified as '*Roboastrea* n. sp., aff. *gracilis*' (CASIZ: 087131). Maui, Hawaii, April 1990, 1 specimen, 10 m depth, collected by P. Fiene. Identified as '*Roboastrea* sp. like the one in Scott Johnson's book' (CASIZ: 088547). Oahu Island R. cf. *gracilis* and Makua, Hawaii, June 1980, 1 specimen, 5 m depth, collected by S. Johnson and identified as 'light background' (CASIZ: 116819). Kimberley, Ashmore Reef, Western Australia, July 1994, 1 specimen, 5–15 m depth, collected by C.W. Bryce (WAM: S23267). North of Cartier Island, Western Australia, September 1988, 1 specimen, collected

by C.W. Bryce & F.E. Wells (WAM: S23236). Off Fremantle, Hall Bank, Western Australia, December 1981, 1 specimen, collected by S.M. Slack-Smith & C.M. Bryce (WAM: S23233).

Distribution: Tropical Indo-Pacific: South Africa, Red Sea (Saudi Arabia), Malaysia, Indonesia (SE Sulawesi, Bali), Palau, Philippines (the type locality), Papua New Guinea, Solomon Is., Japan, Australia, Western Australia, New South Wales, N. Queensland, Pacific Ocean (Marshall Is.), Fiji and many other records (Baba, 1936; Burn, 1967; Hamatani & Baba,

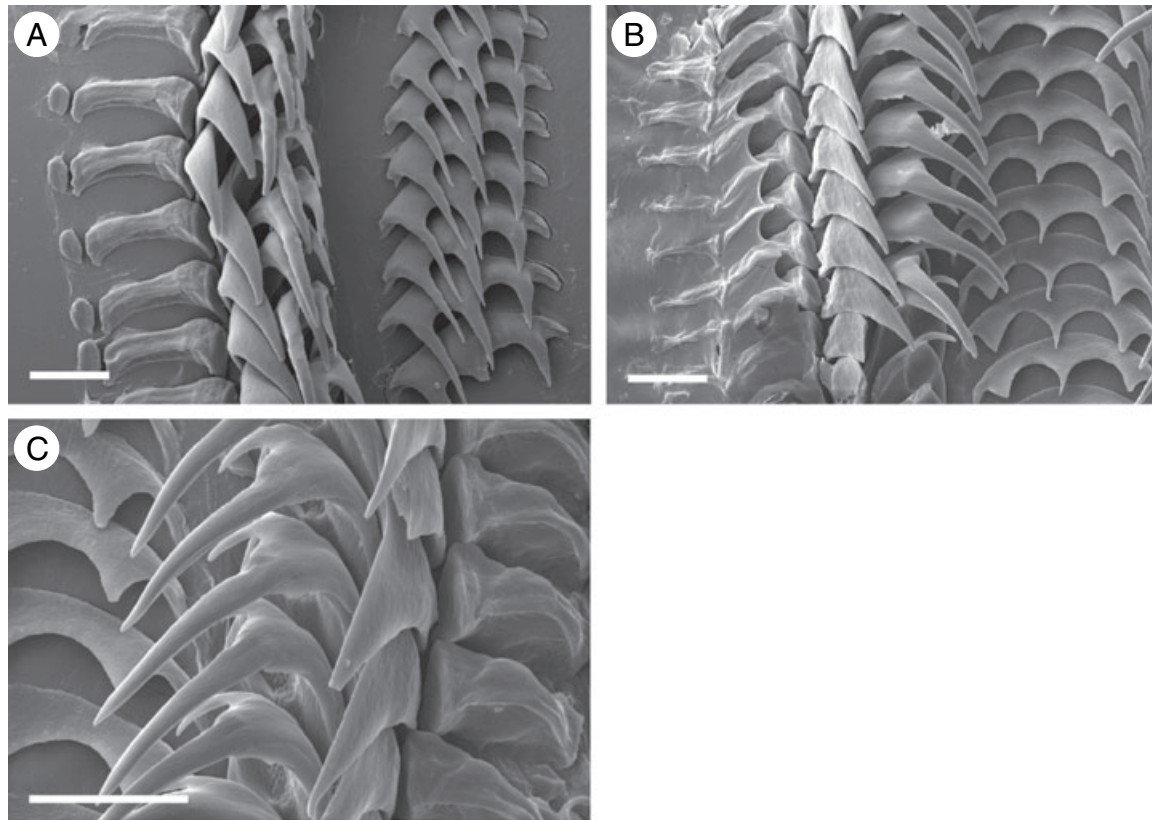


Figure 2. Radular morphology of *Roboastra gracilis*. Scanning electron micrographs. A, left half of the radula (WAMS23233). B, left half of the radula (CASIZ 083858). C, inner lateral teeth (CASIZ 083858). Scale bars = 30 μ m.

1976; Baba, 1977; Coleman, 1989, 2001; Ono, 1999, 2004; Suzuki, 2000; Takamasa, 2003; Nakano, 2004).

External morphology: Small, measuring 10–30 mm in length. Body elongate and limaciform with a long and pointed posterior end of the foot. The foot is linear and blue-grey. The ground colour of the body is blue-black with yellow-orange longitudinal lines, which can be continuous or discontinuous (Fig. 1A, B). If the lines are discontinuous they give the appearance of yellow-orange spots. The longitudinal lines or spots are arranged in the following pattern: 2 stripes in the median part of the back between the head and the front of the gills, 2 in the lateral parts of the back between the rhinophores and the rear of the gills, 1 around the margin of the mantle and 3–4 on the sides of the body. Usually the yellow lines are narrower than the blue-black background. All these lines consist of a series of glandular pits, which give them a corrugated aspect (Fig. 1C). The oral tentacles are smooth, very well developed and dorsolaterally grooved. The perfoliate rhinophores are very large, with 15–25 packed lamellae. There are from three to six very large and nonretractile unipinnate gills. The gills form a semicircle surrounding the anal papilla,

which is not elevated. These proportionally large rhinophores and gills are a very characteristic feature of this species. The genital pore opens on the right side, slightly closer to the rhinophores than to the gills. The oral tentacles, the rhinophores and the gills can be deep blue, blue-grey or purple depending on the specimens.

Internal morphology: The anterior digestive tract begins with a long and muscular oral tube that continues into the buccal mass. At the junction of the oral tube and the buccal mass a pair of thick elongated pouches opens into the digestive system. These pouches are arranged similarly in all *Roboastra* spp. (Fig. 10A). There are two small, short salivary glands on the buccal bulb, flanking the oesophagus. The buccal mass is shorter in length than the oral tube. The labial cuticle is smooth and very weak. The radular formula of the two 15-mm-long specimens (preserved) is $30 \times 3-2.1.1.1.2-3$; that of the 4-mm and 6-mm-long specimens (preserved) is $25 \times 2.1.1.1.2$. The rachidian tooth is rectangular, with a slightly arched upper edge and three denticles. These denticles, while are usually the same size, can be highly asymmetrical (Fig. 2A, B). The inner lateral tooth has typically a strongly curved

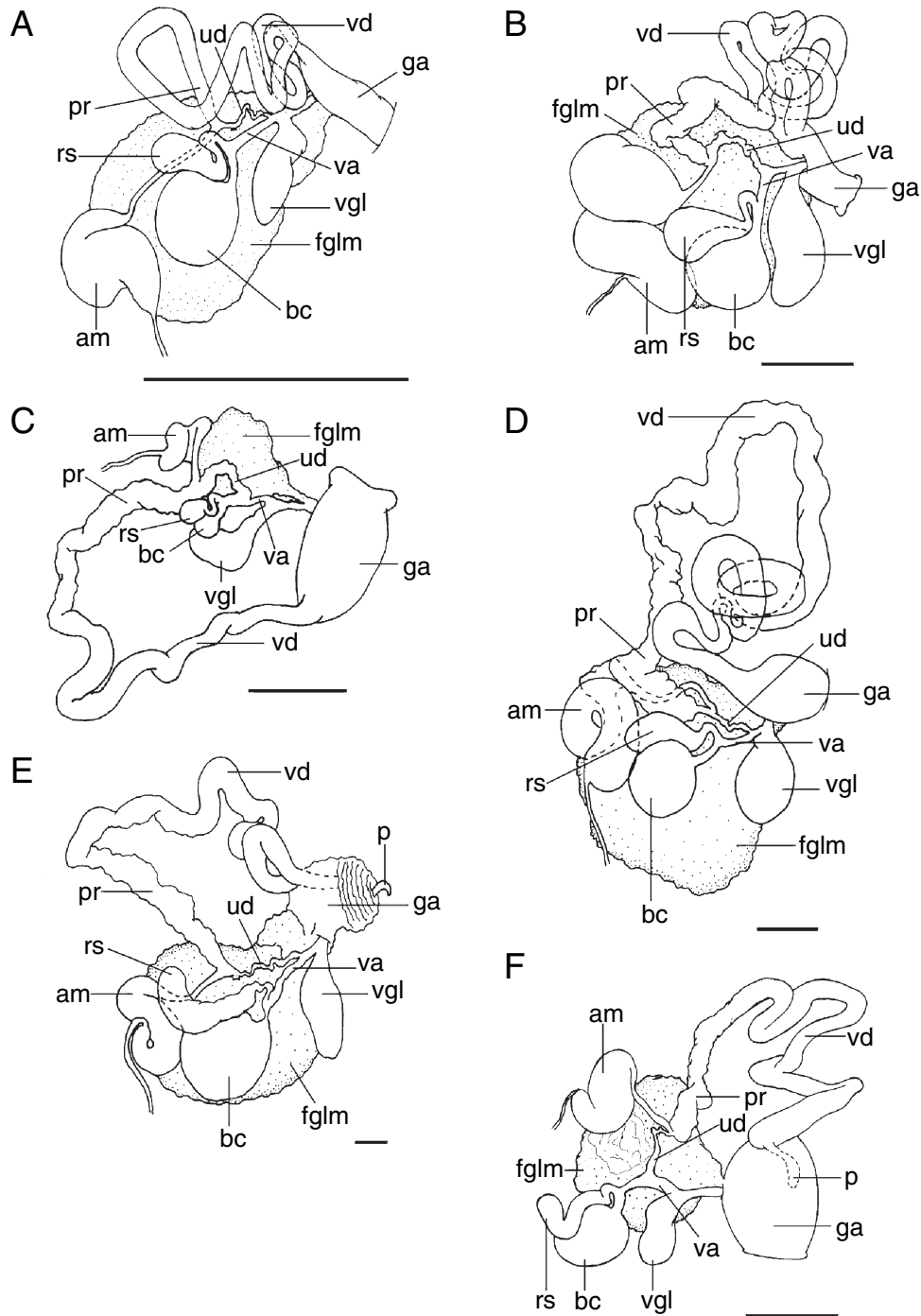


Figure 3. Drawings of reproductive systems of *Roboastra* spp. A, *R. gracilis*. B, *R. luteolineata*. C, *R. tigris*. D, *R. europaea* (adapted from Pola *et al.*, 2003). E, *R. caboverdensis*. F, *R. leonis* sp. nov. Scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; p, penis; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

bifid inner cusp. The upper denticle of this inner cusp is strong and little developed; the outer cusp is slender and well developed (Fig. 2C). The proximal outer lateral teeth become smaller near the margin. The inner

outer lateral teeth are longer and larger than the remaining outer lateral teeth (Fig. 2A, B).

The reproductive system is triaulic (Fig. 3A). The genital mass fills the whole of the second quarter of

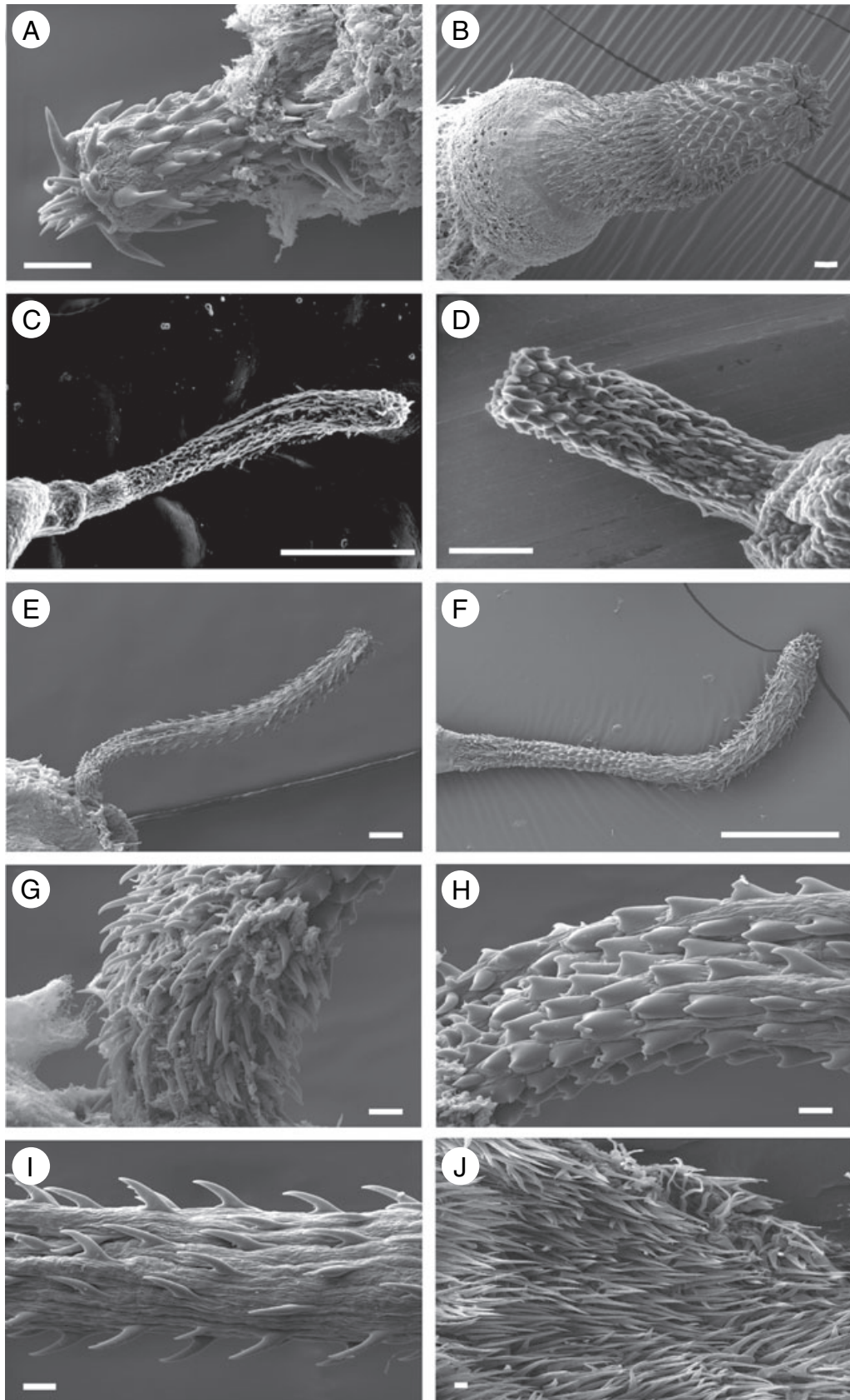


Figure 4. Penial morphology of *Roboastrea* spp. A, *R. gracilis* (CASIZ 087131), scale bar = 30 µm; B, *R. luteolineata* (CASIZ 115739), scale bar = 30 µm. C, *R. tigris* (NHMLAC 140747), scale bar = 300 µm. D, *R. europaea* (MNCN 15.05/46613), scale bar = 50 µm. E, *R. caboverdensis* (MNCN 15.05/46614), scale bar = 90 µm. F, *R. leonis* sp. nov. (CASIZ 097577), scale bar = 300 µm. G–I, detail of the three different kinds of spines in *R. caboverdensis* (MNCN 15.05/46614), scale bar = 10 µm. J, *T. morosa* (CASIZ 142786; 35 mm preserved), scale bar = 20 µm.

the body cavity. The hermaphroditic duct widens into a large S-shaped ampulla. The ampulla narrows into a long thin postampullary duct that connects with the oviduct and the prostate. The short oviduct enters the massive female gland mass. The deferent duct lacks a morphologically well-differentiated prostate but it has soft glandular walls that skirt around the seminal receptacle. The distal muscular vas deferens is much narrower and shorter than the prostatic part. It terminates in a dilated penial section. The penis is armed with at least three different kinds of hooked, chitinous spines arranged in helicoidal rows (Fig. 4A). The vaginal duct is long, normally straight and connects to the large, round bursa copulatrix. The seminal receptacle, smaller and more elongate than the bursa copulatrix, has a short duct that connects to the vagina near the bursa after making two loops. A slender uterine duct leaves the vagina and joins the oviduct. The vagina shares a common aperture within the genital atrium with the vaginal gland, which is very well developed, elongate, flattened, with muscular walls.

Remarks: Bergh (1877) described *Roboastrea gracilis* (as *Nembrotha gracilis*) based on specimens collected from the Philippines. His types were two specimens preserved in alcohol; there are neither notes on, nor sketches of, the living animals. Baba (1949) depicted another specimen from Japan and said that *N. gracilis* may have either two or three marginal plates. Burn (1967) discovered two new specimens from northern New South Wales (Australia) and redescribed the species under the name *Roboastrea gracilis* justified by radular and genital differences. He included a drawing of the living animal made from a colour transparency and drawings of the half row of radula and the reproductive system.

Hamatani & Baba (1976) made a taxonomic comparison between *R. gracilis* and *R. luteolineata* using 16 specimens of the former, collected from Japan. In these notes they included a drawing of one specimen and two drawings of the left half row of the radula. No comment was made about the reproductive system. Later Baba (1977) described *R. gracilis* as being collected from Seto, Japan. He described in further detail both the colour and radula of this small animal; however, again there was no description of the reproductive system.

Although Burn's and Baba's descriptions of *R. gracilis* are not very detailed, they are consistent with our specimens. This species has very character-

istic features: extremely long rhinophores and gills (the latter simply pinnate), which are unique within the genus, while the body surface is covered with glandular pits. In recent years, many pictures have appeared in different field books and web pages devoted to sea slugs and marine invertebrates. It has been reported that when the animals are disturbed, the yellow-orange spots along the body open, releasing an acidic yellow fluid (Fig. 1C). Once the chemical has been released, they close the spots again. Presumably, this is a defence mechanism but it appears to be quite noxious to other sea slugs (Warren, 2000). At the moment there are no feeding records for this species. However, as a typical *Roboastrea*, it most likely feeds on other polycerids.

In our studies we found specimens in CASIZ that have different colours (but the same pattern of coloration) and other differences in their external anatomy (Fig. 1D). They were collected from Hawaii and are 6 mm in length (preserved). Their ground colour is transparent white with lines or spots of brilliant yellow. The end of the oral tentacles, the tips of the rhinophores and gills and the end of the foot are purple. They have 3–4 simply pinnate gills, although these are shorter than in larger specimens from other areas within the Indo-Pacific. Initially, we thought that they might be a different species, but study of their internal anatomy revealed that they are *R. gracilis*. They are similar in colour to the specimens illustrated by Bertsch & Johnson (1982) and Suzuki (2000).

Roboastrea rubropapulosa was the second species of the genus described by Bergh (1905). It too has an Indo-Pacific distribution. In his report on the Siboga material, Bergh (1905: 198) described a brightly coloured papillate species (Fig. 5A) as *N. rubropapulosa*. This differed from his *R. gracilis* only in that there was one elongate marginal plate on each side of the radular rows. Burn (1967) stated that the number of plates is not a characteristic which can be used to separate the species from its congeners because the division between the marginal plates can be very difficult to see. Thus *N. rubropapulosa* cannot be effectively separated from *R. gracilis* and is presently considered to be a synonym of the latter.

Nevertheless, photographs have appeared in a number of publications (e.g. Gosliner, Behrens & Willians, 1996) and in web pages (www.medslug.de; www.diveoz.au.com), where the animal is misidentified as *R. rubropapulosa* (Fig. 5B). Moreover, we have

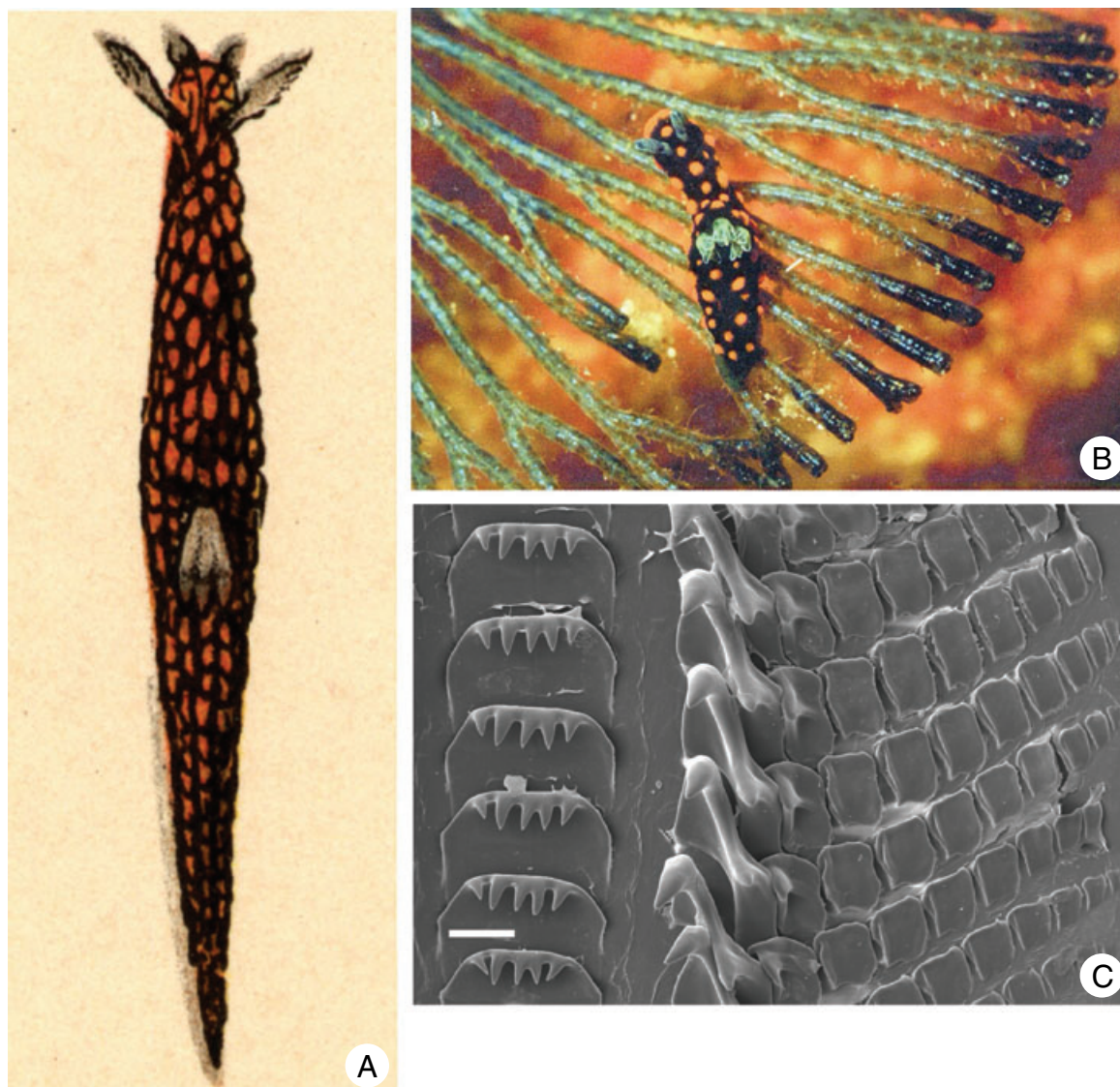


Figure 5. *Roboastra rubropapulosa*. A, original painting of *Nembrotha rubropapulosa* (Bergh, 1905). B, photograph of the living animal identified as *R. rubropapulosa* by T.M. Gosliner (Gosliner *et al.*, 1996). C, right half of the radula of *Nembrotha* sp. (CASIZ 106531), previously identified as *R. rubropapulosa*. Scale bar = 90 µm.

studied some of the specimens deposited at CASIZ (075236, 082920, 082922, 106531) and we have been able to confirm that they represent juvenile specimens of *Nembrotha* sp., perhaps *N. kubaryana*, because they have a radula typical of this genus (Fig. 5C).

ROBOASTRA LUTEOLINEATA (BABA, 1936)
(FIGS 3B, 4B, 6A, 7A, B, 8B)

Nembrotha luteolineata Baba, 1936: 26–27, pl. 3, fig. 7; text-fig. 14.

Material examined: North coast, near Madang, Papua New Guinea, June 1992, 1 specimen, 24 m depth,

40 mm preserved, collected by T.M. Gosliner (CASIZ: 086319). Ryukyu Island, Okinawa, Japan, March 1997, 1 specimen previously identified as *Tambja affinis*, 115 mm in life (70 mm preserved), 55 m depth, collected by R.F. Bolland from a bottom of mixed rock and coral rubble (CASIZ: 115739). South Mulron Island, Western Australia, August 1995, 1 specimen previously identified as *Tambja affinis*, 45 mm preserved, collected by C.W. Bryce (WAM: S23322).

Distribution: Originally described from Japan (Baba, 1936), this species has been also reported from New Zealand, Australia (Lord Howe Is., Heron Is.), Solomon Is., Kerama Is. (Okinawa, Japan), Thailand,

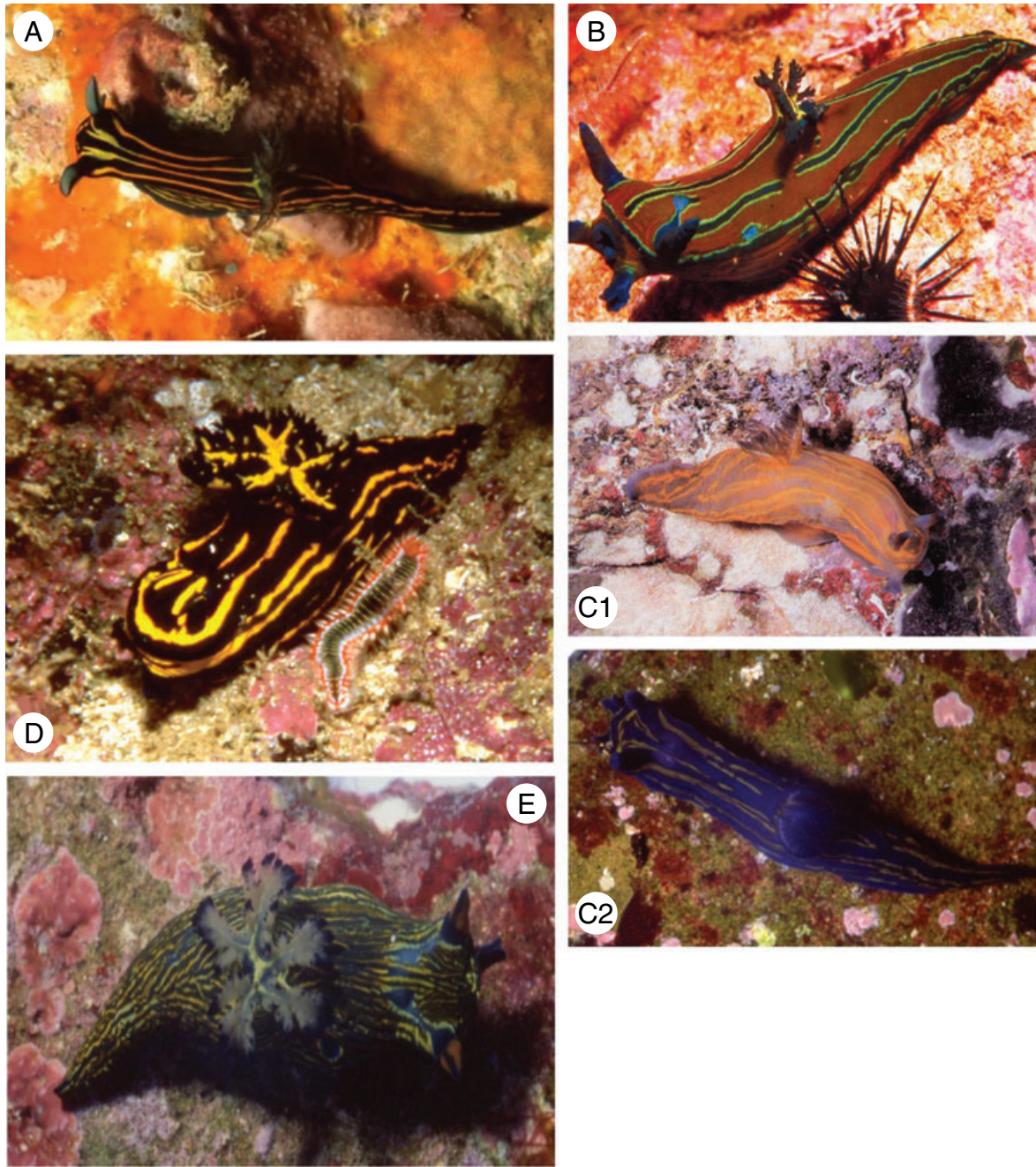


Figure 6. Photographs of living animals: A, *Roboastrea luteolineata*, Papua New Guinea (photo T.M. Gosliner). B, *R. tigris*, Mar de Cortés (photo H. Debelius). C1, *R. europaea*, Carroñera, Spain (light form) (photo L. Tocino). C2, *R. europaea*, Tarifa, Spain (black form) (photo T.M. Gosliner). D, *R. caboverdensis*, Cape Verde (photo P. Wirtz). E, *R. leonis* sp. nov., the Galápagos Islands (photo T.M. Gosliner).

Indonesia (Bali) and South Africa (Durban) (Hamatani & Baba, 1976; Gosliner, 1987; Coleman, 1989; Debelius 1998; Ono, 1999, 2004; Suzuki, 2000; Armstrong & Armstrong, 2001; Coleman, 2001; Johnson, 2001; Takamasa, 2003; Nakano, 2004).

External morphology (Fig. 6A): Body elongate and limaciform with a long and pointed posterior end of the foot. The preserved animals are 35–70 mm in length. The body surface is smooth or lightly wrinkled with numerous (6–8) yellow longitudinal stripes on

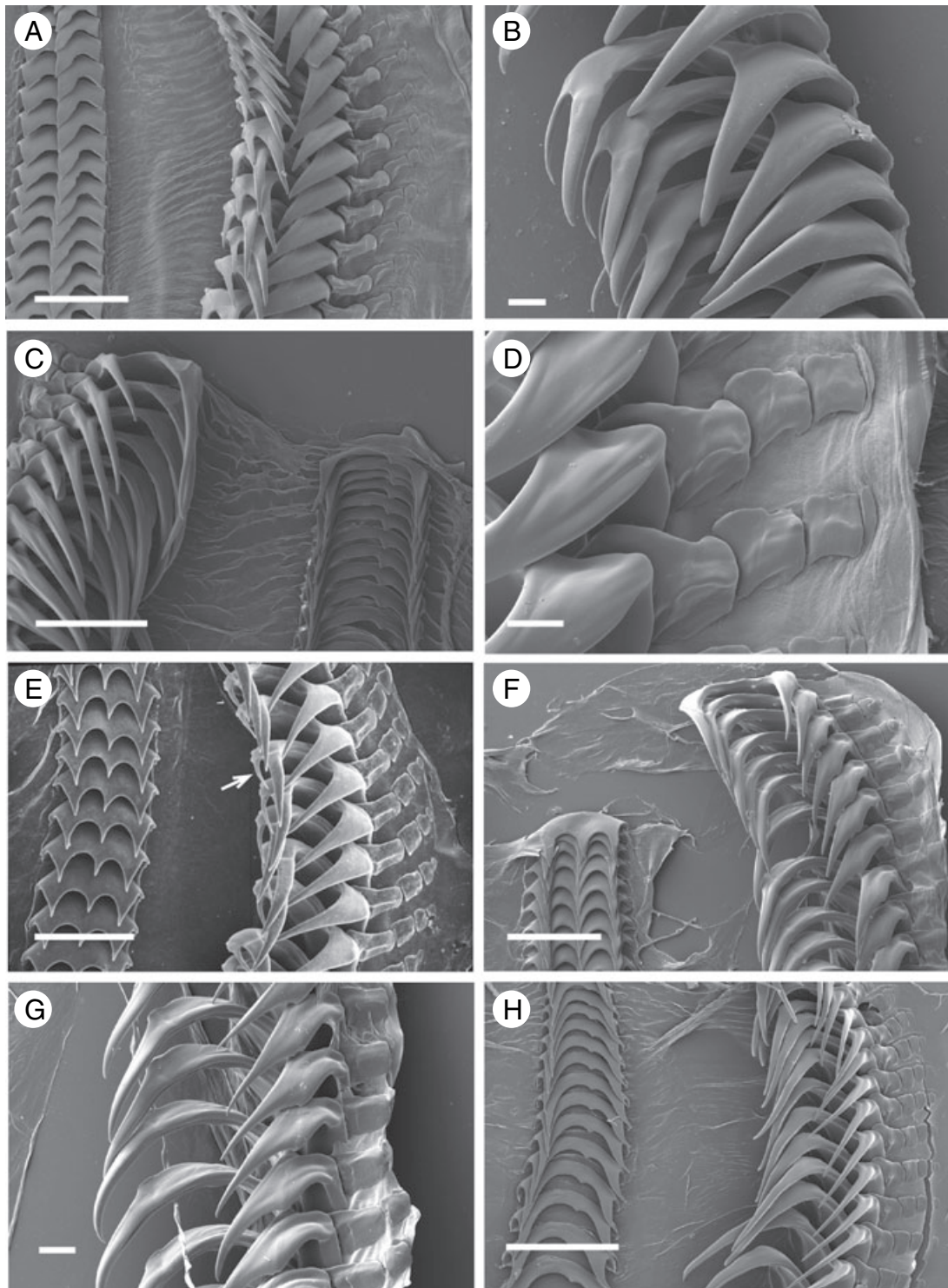


Figure 7. Scanning electron micrographs of the radula. A, right half of the radula, *Roboastra luteolineata* (CASIZ 115739), scale bar = 300 µm. B, innermost lateral teeth, *R. luteolineata* (CASIZ 086319), scale bar = 30 µm. C, left half of the radula, *R. tigris* (CASIZ 057321), scale bar = 300 µm. D, outermost lateral teeth, *R. tigris* (CASIZ 068357), scale bar = 90 µm. E, innermost lateral teeth, *R. europaea* (CASIZ 166053); white lines indicate the bifid upper cusp of some inner teeth, scale bar = 200 µm. F, right half of the radula, *R. caboverdensis* (MNCN 15.05/46614), scale bar = 300 µm. G, innermost lateral teeth, *R. caboverdensis* (MNCN 15.05/46614), scale bar = 90 µm. H, right half of the radula, *R. leonis* sp. nov. (CASIZ 097577), scale bar = 300 µm.

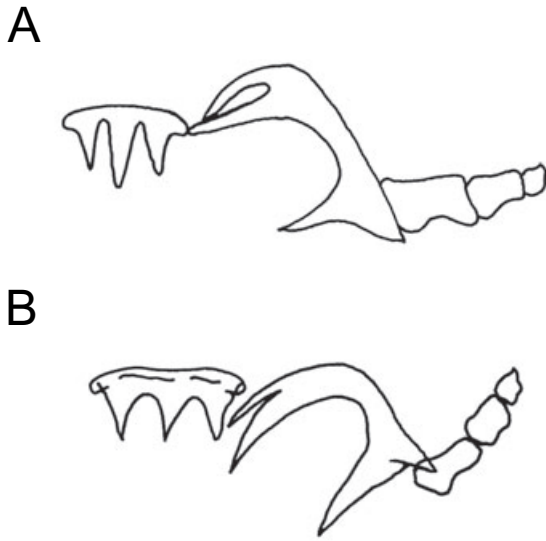


Figure 8. Half row of radula of two specimens of: A, *Roboastra arika* Burn, 1967 and B, *R. luteolineata* (Baba, 1936). Redrawn from their original descriptions.

either side of the body. A wide yellow submarginal band follows the inner notal edge. There are two stripes on the back, which pass posterior to the base of the gills. The stripes in the lateral parts of the back each arise from the outer corner of the rhinophores. In some specimens all these lines can also be green or orange or, more typically, a mix of bright yellow and green. There are two milky green markings between the rhinophores.

The ground colour is dark green or deep blue-black. The foot is linear and the edge of the foot is dark green or blue-black. The head is slightly expanded with a pair of conical, completely retractile perfoliate rhinophores with approximately 45 tightly packed lamellae. The oral tentacles are strongly developed and dorso-laterally grooved along a part of their length and they are also blue-black. There are five nonretractile tripinnate gills, with the three anteriormost being more highly developed. The gills form a semicircle surrounding the anal papilla, which is elevated and is also blue-black. The gills are dark, the same colour as the body, but the outer and inner sides of the rachis are green. The sheaths of the rhinophores, rhinophores, oral tentacles and pinnae of the gills are black. The genital pore opens on the right side, midway between the gills and the rhinophores.

Internal morphology: The anterior digestive tract begins with a long and muscular oral tube, that continues into the buccal mass. At the junction of the oral tube and the buccal mass a pair of large, thick, elongated pouches open into the digestive system. There

are two small and elongated salivary glands on the buccal bulb, flanking the oesophagus. Green and small-developed blood gland, granular in texture, located above the intestinal loop. The buccal mass is shorter than the length of the oral tube. The labial cuticle is smooth. The radular formula of the 40-mm-long specimen (preserved) is $35 \times 3.1.1.1.3$; that of the 115-mm-long specimen (in life) is $40 \times 4.1.1.1.4$. The rachidian tooth is rectangular, with a slightly curved upper edge and three denticles; the central one is longer (Fig. 7A). The inner lateral tooth typically has a strongly curved bifid inner cusp. The upper denticle of this inner cusp is slender and well developed, while the outer cusp is strong and well developed (Fig. 7B). The outer lateral teeth are plate-like and become smaller near the margin (Fig. 7A).

The hermaphroditic reproductive system is triaulic (Fig. 3B). The genital mass fills the second quarter of the body cavity. The ampulla is large, folded thrice upon itself, with soft and thin walls. From its distal portion emerges the postampullary duct, which divides into the prostate and the oviduct. The prostate is wide, long and convoluted, distally narrowing and expanding again into the long muscular ejaculatory portion. The vas deferens is highly coiled. The distal portion of the deferent duct opens into a long, wide common atrium with the vaginal duct. The penis is located within the distal end of this muscular portion and it is armed with at least three different kinds of hooked and chitinous spines arranged in helicoidal rows (Fig. 4B). The vaginal duct is thin, elongate and enters the large, spherical bursa copulatrix. Another duct connects the vagina to the smaller and pyriform seminal receptacle after making two loops. Distally to the bursa copulatrix, a short and coiled uterine duct leaves the vagina and enters the female gland mass. The vaginal gland is well developed, elongate and joins with the vagina before opening into the genital atrium.

Remarks: *Roboastra luteolineata* was described by Baba (1936) as *Nembrotha luteolineata*, based on a 30-mm-long specimen collected in Ishigakishima, Japan, and another specimen, 70 mm long, collected in the same locality. Baba (1936) gave two radular formulae ($35 \times 3.1.1.1.3$ and $40 \times 3.1.1.1.3$) while Hamatani & Baba (1976) gave one: $36 \times 4.1.1.1.4$. These results, together with the description of the external morphology, are almost entirely consistent with our description. The specimens studied here have five tripinnate gills instead of three (Baba, 1936). Hamatani & Baba (1976) described five bipinnate gills, but we can see that they are tripinnate. The reproductive system of this species has not been previously described.

Roboastra luteolineata has been identified in a number of popular books on Australian nudibranchs (Wil-

lan & Coleman, 1984; Coleman, 1989; Debelius, 1998) as *Tambja affinis* (Eliot, 1904). However, that species, originally described from East Africa, was described as having a single median yellow stripe. Moreover, apart from other features, such as the milky green marking between the rhinophores, the radular teeth of *R. luteolineata* and *T. affinis* are very distinct. *R. luteolineata* feeds on other polycerids, such as *Tambja verconis* (Basedow & Hedley, 1905) (Armstrong & Armstrong, 2001), rather than the arborescent bryozoan *Bugula dentata*, on which *Tambja verconis* feeds (Rudman, 1998b). Ono (1999, 2004) included photographs of *R. luteolineata* feeding on another species of *Tambja* / *Nembrotha* in Japan.

ROBOASTRA ARIKA BURN, 1967
(FIG. 8A)

Remarks: Burn (1967) described a new species, *R. arika*, from Lowe Howe Island, more than 600 km from the east coast of Australia. The description was based on a single preserved specimen, 12 mm long, deposited in the Australian Museum. However, it appears that the holotype has been lost (Rudman, pers. comm.). The only available information about this species stems from the original description. Comparison of the drawing of the half row of radula (Fig. 8A) from Burn (1967) with that of the radula (Fig. 8B) of *R. luteolineata* from Baba (1936) reveals that they appear to be very similar. Since we do not have any more information, and as we are not sure that both are the same species, we nominate *R. arika* as a *taxon dubium*. It is important to emphasize that, in the last few years, pictures of a nudibranch incorrectly identified as *R. arika* have appeared in a number of popular books (Gosliner *et al.*, 1996; Debelius, 1998; Coleman, 2001) and web pages (www.seaslugforum.net, www.medslug.de, www.aqualife.com, etc.). These pictures are from an unknown species of *Tambja*, which is currently being described.

ROBOASTRA TIGRIS FARMER, 1978
(FIGS 3C, 4C, 6B, 7C, D)

Material examined: Bahía de Los Angeles, Baja California, Gulf of California, Mexico, October 1975, 3 specimens, 12–21 m depth, 20–35 mm preserved length, collected by M. Michel & D. Mulliner. (LACM: 140747). Bahía de Los Angeles, Baja California, Gulf of California, Mexico, October 1984, 1 specimen, 7–10 m depth, 30 mm preserved, collected by R. Van Syoc & A.J. Ferreira (CASIZ: 057321). Bahía de Los Angeles, Baja California, Gulf of California, Mexico, January 1985, 1 specimen, 1–7 m depth, 40 mm preserved, collected by R. Van Syoc *et al.* (CASIZ: 057613).

Isla San Esteban, Sonora, Gulf of California, Mexico, April 1985, 1 specimen, 12 m depth, 40 mm preserved, collected by L. Dunne (CASIZ 072629). Baja California Sur, Gulf of California, Mexico, September 1965, 1 specimen, 30 m depth, collected by D. Wobber (CASIZ: 68357).

Distribution: *Roboastra tigris* has been reported from offshore islands in the central and southern Gulf of California (Islas San Pedro, Monserrate and San Diego, Guaymas, and islands in the region of Bahía de Los Angeles and La Paz) (Farmer, 1978).

External morphology (Fig. 6B): Body elongate and limaciform with a long and pointed posterior end of the foot. The preserved animals are 20–40 mm in length. The body surface is lightly wrinkled with most of the wrinkles following the longitudinal stripes on the notum and both sides of the body. The predominant body colour is a greenish, yellow-ochre, or brown, with five longitudinal dark navy blue stripes outlined by light green. There is a band surrounding the notal edge. Another midline extends from the anterior part, near the edge of the notum, to the middle gills and continues behind these gills. Two other lines start from the rhinophore sheaths and run parallel until they join in the postbranchial region. The line that results from the two joined lines continues to the posterior end of the foot.

The eyespots are bluish in colour and well defined. They join with the rhinophores to form two shorter lines that continue for a little way behind the eyespots. The sides may have an interrupted stripe. The sole of the foot is blue-black and the foot margin is blue. The head is rounded with a pair of conical, completely retractile perfoliate rhinophores with approximately 35 tightly packed lamellae. The oral tentacles are strongly developed and dorsolaterally grooved along a part of their length and they also are blue-black. There are five nonretractile tripinnate gills; the three anteriormost gills are more highly developed. The gills form a semicircle surrounding the anal papilla, which is elevated and is blue-black. The pinna of the gills is dark blue, while the inner side of the rachis is yellow. The rhinophores and their sheaths are blue-black with light green central axes. The oral area is cobalt blue. The genital pore opens on the right side, midway between the gills and the rhinophores.

Internal morphology: All specimens were dissected. The anterior digestive tract begins with a long, thick-walled, muscular oral tube, which continues into the buccal mass. The buccal mass is elongate and tubular, with a pair of slender elongate pouches opening into the digestive system at the junction of the oral tube and the buccal mass. The salivary glands are small and short, entering on the buccal mass and flanking

the oesophagus. The labial cuticle and the labial armature are absent. There is a well-developed blood gland that is granular in texture. The radular formula of one 40-mm-long specimen (preserved) is $28 \times 4.1.1.1.4$; that of the 30-mm-long specimen (preserved) is $30 \times 4-3.1.1.1.3-4$. The rachidian tooth (Fig. 7C) is broad, thin and very arched at its base with two well-differentiated lateral cusps and a small one in the middle. The inner lateral tooth (Fig. 7C) is very curved, with two very well developed cusps. The inner cusp is simple and larger than the outer one, which is very slender. The remaining lateral radular teeth (3–4) are quadrangular, lack cusps or denticulation and become smaller near the margin (Fig. 7D).

The reproductive system is triaulic. Figure 3C shows that of the 40-mm-long specimen (preserved) (CASIZ: 072629). The whole genital mass is very small, filling a third of the second body cavity. The hermaphroditic duct widens into a small S-shaped ampulla. The ampulla narrows into a large and wide postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The deferent duct, which lacks a morphologically well-differentiated prostate, is long and coiled, ending in a dilated and darkly pigmented penial sac. The deferent duct has a uniform width, but it is slightly wider and thicker in the prostatic part.

The distal part of the vas deferens enters the wide penial bulb. The penis is located within the distal end of this muscular portion, and it is armed with at least three different kinds of hooked and chitinous spines arranged in helicoidal rows (Fig. 4C). The bursa copulatrix and seminal receptacle are very small. The former is rounded and the latter is elongate; both are similar in size. The seminal receptacle has a short duct that connects to the vagina after making two loops near the bursa. The vagina is long and straight. Nearly halfway along its length, it branches into the uterine duct, which is long and convoluted and joins with the oviduct. There is a large, thick-walled, inverted L-shaped vaginal gland, which joins the distal part of the vagina; both open into the genital atrium. The reproductive system in this species is very small in the context of the total size of the specimens, and when compared with that of the other species.

Remarks: *Roboastrea tigris* was described by Farmer (1978). It is easily distinguishable by its colour pattern and large size. Farmer suggested that its size might be linked to its feeding mechanism and explained the role of the coelomic cavity. *Roboastrea tigris* feeds on other polycerids, such as *Tambja abdere* Farmer (1978) and *T. eliora* (Marcus & Marcus, 1967). It was named *R. tigris* for its stripes and carnivorous appetite.

Carté & Faulkner (1983, 1986) and Faulkner & Ghiselin (1983) studied the defensive metabolites of *R. tigris*. This species, and its prey *T. abdere* and *T. eliora*, contain tambjamines A–D. These have been traced to a food source, the bryozoan *Sessibugula translucens* and are implicated in the chemical defence mechanism of the *Tambja* species. The radula of *R. tigris* is very similar to that of *R. leonis* sp. nov., but in fully mature specimens the reproductive system is smaller than in *R. leonis*. The bursa copulatrix and the seminal receptacle are both similar in size while in *R. leonis* they are unequal in size. These differences were consistent in all specimens of each species examined here.

ROBOASTRA EUROPAEA GARCÍA GÓMEZ, 1985
(FIGS 3D, 4D, 6C, 7E)

Material examined: Torre, Marbella, Spain, July 1995, 1 specimen, 10 m depth, 30 mm, collected by J.L. González (MNCN 15.05/46612). Torre, Marbella, Spain, September 1995, 1 specimen, 10 m depth, 18 mm, collected by M.T. Barrea (CASIZ 166049). Torre, Marbella, Spain, August 1996, 2 specimens, 10.7 m depth, 15 & 19 mm, collected by K.L. Schick (CASIZ 166053). La Herradura, Granada, Spain, February 1993, 1 specimen, 12 m depth, 14 mm, collected by A. Barrajón and M. Zarauz (MNCN 15.05/29203). Arrecife La Cañonera, Strait of Gibraltar, Spain, June 2002, 1 specimen, 17 m depth, 50 mm, collected by Alma Sánchez (MNCN 15.05/46650). Funchal, Madeira, June 1999, 1 specimen, 100 m depth, 35 mm (MMF 31021). Ponta do Baleeira, Sagres, Portugal, July 2002, 1 specimen, 20 m depth, 14 mm, collected by M. Pola (MNCN 15.05/46613). Ponta do Baleeira, Sagres, Portugal, July 2002, 1 specimen, 20 m depth, 10 mm, collected by M.A. Malaquias (MNCN 15.05/46613). Specimens were collected on rocks and were measured following preservation.

Distribution: This species is known mainly from the Strait of Gibraltar and southern Iberian Peninsula (García Gómez, 1985, 2002; Cervera *et al.*, 1988; García Gómez *et al.*, 1989, 1991; Moreno & Templado, 1998; Schick, 1998; Megina, 2000; Ocaña *et al.*, 2000; Sánchez-Tocino, Ocaña & García 2000; Grande *et al.*, 2002; Megina & Cervera, 2003). One misidentified specimen of *Plocamopherus* from Madeira deposited at the Natural History Museum (London) (1863.9.19.3), supposedly collected by Rev. R. Lowe, was correctly identified as belonging to *Roboastrea*, very probably *R. europaea*. This hypothesis has been strongly supported by the recent collection of one specimen (also photographed) of this species at Funchal harbour.

This species has been also recorded in southwestern Portugal (Calado *et al.*, in press) and Catalo-

nian coasts (north-eastern Iberian Peninsula, Mediterranean Sea) (Schick, pers. comm.). Poddubetskaia & Petit de Voice (2003) provide an illustration of *R. europaea* from Dakar (Senegal). This is the southernmost record of this species in the Atlantic.

External and internal morphology: Described in detail and figured by Pola *et al.* (2003). Regarding the colour pattern, this species can exhibit two colour varieties (Fig. 6C1, C2). The radular formula of two 15-mm-long specimens (preserved) is $23 \times 4.1.1.1.4$; that of the 30-mm-long specimen (preserved) is $25 \times 4.1.1.1.4$ (Fig. 7E). The reproductive system is triaualic (Figs 3D, 4D). The hermaphroditic duct widens into a S-shaped ampulla that has thick walls. The bursa copulatrix is rounded and the seminal receptacle is elongate; both are similar in size. The seminal receptacle has a short duct that connects to the vagina, near the bursa. The deferent duct, which lacks a morphologically well-differentiated prostate, is long and coiled, ending in a dilated penial atrium. The vaginal gland is large with muscular walls, convex on one side and concave on the other. The penis is located within the distal end of this muscular portion and is armed with at least three different kinds of hooked and chitinous spines arranged in helicoidal rows. Anatomical descriptions are based on the illustrations by Pola *et al.* (2003).

Remarks: *Roboastra europaea* was described by García Gómez (1985) as the first species of the genus in the Atlantic Ocean, from the Strait of Gibraltar. Pola *et al.* (2003) redescribed the species and updated its geographical range to south-western Portugal (Calado *et al.*, in press) and the Catalan coast (north-eastern Spain).

The anatomy of this species and the reproductive system of the specimen examined (MNCN 15.05/46650) are very similar to those descriptions and no substantive differences have been found, except with regard to identification of the uterine duct, which was not reported before. The uterine duct is long and convoluted, going from the middle of the vagina to the oviduct. García Gómez (1985) mentioned the presence of a fertilization duct, but did not draw it. More recently, *R. europaea* was included in studies relating to molecular phylogeny (Grande *et al.*, 2002) and feeding ecology (Megina & Cervera, 2003).

ROBOASTRA CABOVERDENSIS POLA *ET AL.*, 2003
(FIGS 3E, 4E, G–I, 6D, 7F, G)

Material examined: *Holotype*: 15 miles NW Santo Antao Island, Cape Verde Archipelago, July 2002, 1 specimen, 38 m depth (CASIZ 166047). *Other material*: Tarrafal, Cape Verde Archipelago, December 1998, 1 specimen, 25 mm, P.Wirtz (MMF35083).

Banco Joao Valente, Boavista Island, Cape Verde Archipelago, August 2002, 2 specimens, 20 m depth, 26/30 mm (70 mm in life), M.A. Malaquias (MNCN. 15.05/46614). Banco Joao Valente, Boavista Island, Cape Verde, August 2002, 2 specimens, 30 m depth, 31/37 mm (70 mm in life), M.A. Malaquias (CASIZ 166052). Boavista Island, August 2002, 3 specimens, 13/15/18 mm, C. Grande (MNCN. 15.05/46617). Sao Vicente, Cape Verde, October 2002, 1 specimen, 20 mm, G. Calado (CASIZ 166050). Specimens were collected on rocks and were measured preserved.

Distribution: This species is known only from the Cape Verde Archipelago.

External and internal morphology: Described in detail and figured by Pola *et al.* (2003) and not repeated here. A specimen from Tarrafal, Cape Verde Archipelago, is illustrated (Fig. 6D) to confirm the identity of the material examined. The radular formula of two specimens of 70 mm (in life) is $33 \times 3-4.1.1.1.3-4$ (Fig. 7F). The rachidian tooth is broad, clearly curved at the base, having three well-differentiated cusps. The inner lateral tooth is hooked with two well-developed elongate cusps. The inner one is very long, with sharp and curved edges on the inner side and a prominent projection on the outer one. The outer lateral teeth (3–4) are smaller and quadrangular without prongs, and decrease in size from the inner to the outer side of the radula.

The reproductive system is shown in Figure 3E. The hermaphroditic duct has an S-shaped ampulla that continues into the spermoviduct. The vas deferens is long and coiled, with a uniform width. It is slightly narrower in the prostatic part. It ends in a dilated penial section. The penis is armed with at least three different kinds of spines arranged in helicoidal rows. Types of spines and their arrangement on the penis are shown in Figure 4G–I and E, respectively. The bursa copulatrix is rounded and the seminal receptacle is elongate; both are similar in size. The seminal receptacle joins the vagina near the bursa via a short duct. The vagina is short and straight, opening into the genital atrium, near the vaginal gland. This gland is very well developed, flattened, with muscular walls.

Remarks: This species is the second to be described from the Atlantic Ocean. *Roboastra caboverdensis* is very similar to *R. europaea* (García Gómez, 1985), but some external and internal features permit us to distinguish it from its congeneric Atlantic species. The two species differ in their colour pattern. The arrangement of the yellow lines differs in both species; it is denser in *R. europaea*. The base of the rachidian radular tooth is more curved in *R. caboverdensis* than in *R. europaea*. The upper cusp of the inner lateral tooth is simple in *R. caboverdensis* and bifid in *R. europaea*.

(see Fig. 7E). *R. caboverdensis* has been reported feeding on other polycerids, such as *Tambja fantasmalis* (Malaquias, pers. comm.). This species has been misidentified as *T. ambja simplex* in <http://www.medslug.de> and a picture of it is also shown in Wirtz & Debelius (2003) identified as *Roboastra* sp. nov.

***ROBOASTRA LEONIS* SP. NOV.**

(FIGS 3F, 4F, 6E, 7H, 9, 10)

Roboastra sp., Farmer, 1978: 384, fig. 20.

Roboastra sp., Debelius, 1998: 181.

Type material: *Holotype*: Isla San Cristóbal, León Dormido, Kicker Rock, Galápagos Islands, Ecuador, May 1994, 1 specimen, 80 mm, collected by T.M. Gosliner aboard *Mistral II*, max. depth 26 m (MECCD 4023). *Paratypes*: same data as for holotype, 60 and 70 mm (CASIZ 097548). *Other material*: Isla Isabela, Punta Vicente Roca, Galápagos Islands, Ecuador, May 1994, 5 specimens, 25, 35, 45, 53 and 80 mm, collected by T.M. Gosliner aboard *Mistral II*, max. depth 23 and 31 m (CASIZ 097577). Isla Darwin, NE side, Galápagos Islands, Ecuador, May 1994, 1 specimen, 25 mm, collected by T.M. Gosliner aboard *Mistral II*, max. depth 18 m (CASIZ 097554). The specimens were measured while preserved.

Etymology: Holotype found in the locality of León Dormido. It is also named *leonis* for its aggressive predatory habits.

Distribution: Currently reported from the Galápagos Islands, but Farmer (1978) included an illustration of a similar animal from La Paz (Gulf of California). Debelius (1998) reported it as endemic to the Galápagos Islands.

External morphology (Fig. 6E): Body elongate and limaciform with a long and pointed posterior end of the foot. The preserved animals are 25–80 mm in length. The body surface is strongly wrinkled with numerous stripes of yellow ochre, green and bluish-black on the notum and both sides of the body. Some of the stripes are lighter in shade and can be continuous or discontinuous. The foot is linear and the edge of the foot is blue-black. The head is rounded with a pair of conical, completely retractile, perfoliate rhinophores with approximately 40 tightly packed lamellae. The base of the rhinophores is blue-black with a similar core; the leaves are bright orange and tipped in blue-black. The eyespots are brilliant blue. The oral tentacles are strongly developed and dorsolaterally grooved along part of their length and they are also blue-black. There are five nonretractile tripinnate gills; the three anteriormost gills are more highly developed. The gills form a semicircle surrounding the anal papilla, which is elevated and is blue-black in colour. The gills are

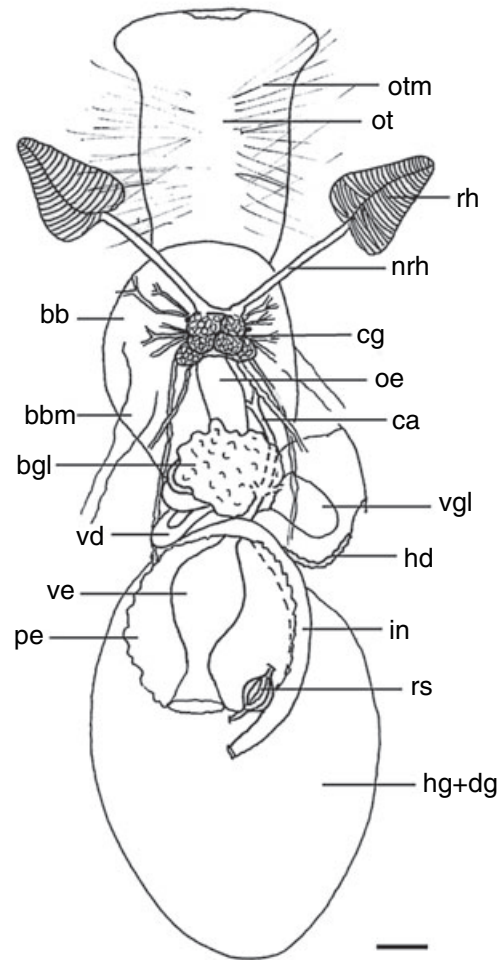


Figure 9. *Roboastra leonis* sp. nov. General arrangement of the internal organs. Scale bar = 1 mm. **Abbreviations:** bb, buccal bulb; bbm, buccal bulb muscle; bgl, blood gland; ca, cephalic artery; cg, cerebral ganglion; hd, hermaphroditic duct; hg+dg, hermaphrodite gland + digestive gland; in, intestine; nrh, rhinophoral nerve; oe, oesophagus; ot, oral tube; otm, oral tube muscle; pe, pericardium; rh, rhinophore; rs, renal syrinx; vd, vas deferens; ve, ventricle; vgl, vaginal gland.

blue-black distally and white proximally and the inner side of the rachis of each has a yellow line. The dark blue genital pore opens on the right side, midway between the gills and the rhinophores.

Internal morphology: Four specimens were dissected. The general arrangement of the internal organs is shown in Figure 9. The anterior digestive tract begins with a long, thick-walled muscular oral tube, which continues into the buccal mass. At their junction, a pair of slender elongate pouches opens into the digestive system (Fig. 10A, B). The salivary glands are short and thick, opening on to the buccal mass and

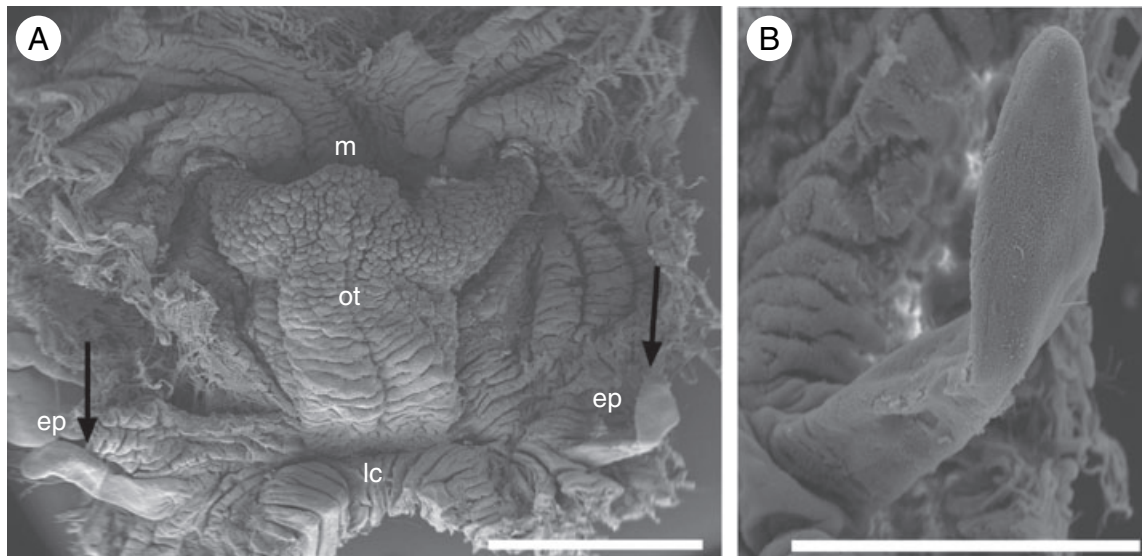


Figure 10. *Roboastra leonis* sp. nov. (CASIZ 097577). A, scanning electron micrograph of the oral tube, scale bar = 2 mm. The drawing shows the oral tube opened and the presence of a pair of elongate pouches opening into the digestive system. B, detail of the right elongate pouch, scale bar = 1 mm. *Abbreviations:* ep, elongate pouches; lc, labial cuticle; m, mouth; ot, oral tube.

flanking the oesophagus. The labial cuticle is weak and lacks any armature. There is a well-developed blood gland, which is granular in texture. The radular formula of two 35-mm-long specimens (preserved) is $26 \times 4.1.1.1.4$; that of the 60-mm-long specimen (preserved) is $32 \times 4.1.1.1.4$ (Fig. 7G). The rachidian tooth is broad, thin and very arched at its base, with two well-differentiated lateral cusps and a small one in the middle. The inner lateral tooth is very curved, having two very well developed cusps. The inner cusp is simple and larger than the outer one, which is very slender. The remaining lateral radular teeth are quadrangular, lack cusps or denticulation and become smaller near the margin.

The reproductive system is triaulytic. That of one 45-mm-long specimen (preserved) (CASIZ 097577) is shown in Figure 3F. The genital mass is small compared with the total size of the specimens, but larger than in *R. tigris*. The hermaphroditic duct widens into a large S-shaped ampulla, which has thick walls. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass.

The deferent duct, which lacks a morphologically well-differentiated prostate, is long and coiled, ending in a dilated and darkly pigmented penial atrium. The duct has a uniform width, but is slightly narrower and thinner in the prostatic part. The penis is located within the distal end of this muscular portion and is armed with at least three different kinds of hooked and chitinous spines arranged in helicoidal rows. The

types of spines and their arrangement on the penis are shown in Figure 4F.

The bursa copulatrix and the seminal receptacle are well developed. The former is rounded and large, while the latter is elongate and smaller in size. The seminal receptacle has a short duct that connects to the vagina, near the bursa. The vagina is long and straight, opening into the genital atrium. The vaginal gland is very well developed, elongate, flattened, with muscular walls and joins the vagina at the distal part.

Remarks: *Roboastra leonis* is clearly distinguishable from other members of the genus. The external coloration is consistently different, while the number of lines on the notum and both sides of the body is higher than in the other species.

Roboastra luteolineata (Baba, 1936) also has many lines on its body, but the pigmentation of the gills, the rhinophores and most of the lines is different. There are also differences in the radular morphology of the two species. In *R. leonis* the rachidian tooth is highly arched at its base, with two well-developed lateral cusps and a small one in the middle. In *R. luteolineata* it is rectangular, with a slightly curved upper edge and three denticles (the central one is longer). Furthermore, the inner lateral tooth of *R. leonis* has a simple inner cusp while in *R. luteolineata* it is bifid.

R. tigris Farmer, 1978, which is biogeographically the closest species to *R. leonis*, has a similar radular morphology, but its predominant body colour is greenish, yellow-ochre, or brown, with a few longitudinal

dark navy blue stripes outlined in light green. These differences do not just involve coloration. In *R. leonis* there are consistently more lines covering the body than in *R. tigris*. Reproductive differences noted in the discussion of *R. tigris* were consistent in the numerous mature specimens examined here.

Roboastra leonis is the first species of the genus to have been found in the Galápagos Islands. It has been reported feeding on *Tambja mullineri* Farmer, 1978 (Gosliner, unpublished data). Farmer (1978) provided a drawing of an animal similar to *R. leonis* from La Paz, but the specimen was devoured by one of its *R. tigris* companions in transit from the field to the laboratory. The external description of that species suggests that *R. leonis* is also present in the Gulf of California; a photograph appears in Hickman & Finet (1999) and Debelius (1998).

PHYLOGENETIC ANALYSIS

TAXA

For the phylogenetic analysis, 15 taxa were included (Table 1). The ingroup comprised six valid species of *Roboastra*, including the new species described in this paper. It also included three species of *Tambja* and three species of *Nembrotha*. The morphological and anatomical features of these 12 species were studied and the information was obtained directly from the available material.

CHARACTERS

Thirty-seven characters were used. All the characters of external and internal morphology used to resolve

the phylogeny of *Roboastra* are listed below. Thirty-one characters are coded as binary and six as multi-state. The character states are indicated as follows: 0 = plesiomorphic; 1 or 2 = apomorphic. The polarities discussed below have not been obtained a priori, but as the result of outgroup comparison. The distribution of plesiomorphic and apomorphic character states is found in Table 2.

[Note: Characters preceded by an asterisk were deleted from the first analysis, because they are phylogenetically uninformative].

1. **Body shape*: (0) elevated, with a large dorsal hump (*Bathydoris*); (1) flattened (phanerobranch dorids).
2. *Integumentary spicules*: (0) present (*Bathydoris* and *Polycera*; more or less densely arranged); (1) absent (*Polycerella* and *Roboastra*).
3. *Cephalic processes*: (0) absent (*Bathydoris*, cryptobranchs and pleurobranchs); (1) present (some polycerids, e.g. *Polycera quadrilineata*).
4. *Extrabranchial processes*: (0) absent (*Bathydoris*, cryptobranchs and pleurobranchs); (1) present (some polycerids, e.g. *P. quadrilineata*).
5. *Oral tentacle size*: (0) slightly developed (*Bathydoris*, cryptobranchs and other phanerobranchs); (1) strongly developed (*Nembrotha* and *Roboastra*).
6. *Oral tentacle shape*: (0) oral tentacles not developed as dorsolaterally grooved cylindrical projections; (1) oral tentacles developed as dorso-laterally grooved cylindrical projections (unique to *Roboastra*).
7. *Gill type*: (0) highly pinnate; (1) simple.
8. *Rhinophoral sheaths*: (0) absent; (1) present.

Table 1. Species included in the analysis, with sources of information

Taxa	Source of information
<i>Bathydoris clavigera</i> Thiele, 1912	Wägele (1989a), Wägele & Willan (2000), Valdés (2002)
<i>Polycera quadrilineata</i> (Müller 1776)	Thompson & Brown (1984)
<i>Polycerella emertoni</i> Verrill, 1880	Behrens & Gosliner (1988), García Gómez (1985)
<i>Nembrotha lineolata</i> (Bergh, 1905)	Directly from the available material
<i>Nembrotha chamberlaini</i> Gosliner & Behrens, 1997	Directly from the available material
<i>Nembrotha kubayana</i> (Bergh, 1877)	Directly from the available material
<i>Tambja morosa</i> (Bergh, 1877)	Directly from the available material
<i>Tambja eliora</i> (Marcus & Marcus, 1967)	Directly from the available material
<i>Tambja ceutae</i> García Gómez & Ortea, 1988	Directly from the available material
<i>Roboastra gracilis</i> (Bergh, 1877)	Directly from the available material
<i>Roboastra luteolineata</i> (Baba, 1936)	Directly from the available material
<i>Roboastra tigris</i> Farmer, 1978	Directly from the available material
<i>Roboastra europaea</i> García Gómez, 1985	Directly from the available material
<i>Roboastra caboverdensis</i> Pola, Cervera & Gosliner, 2003	Directly from the available material
<i>Roboastra leonis</i> sp. nov.	Directly from the available material

Table 2. Data matrix. Character states present in species of *Roboastra* and in species of the outgroup

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>B. clavigera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. quadrilineata</i>	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1
<i>P. emertoni</i>	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	2	1	1
<i>N. lineolata</i>	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1	0
<i>N. chamberlaini</i>	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1	0
<i>N. kubaryana</i>	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1	0
<i>T. morosa</i>	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0
<i>T. eliora</i>	1	1	0	0	0	0	0	1	0	0	0	0	0	0/1	0	1	1	0
<i>T. ceutae</i>	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
<i>R. gracilis</i>	1	1	0	0	1	1	1	1	0	1	1	1	1	2	1	2	1	0
<i>R. luteolineata</i>	1	1	0	0	1	1	0	1	0	0	0	1	0	2	1	2	1	0
<i>R. tigris</i>	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	1	0
<i>R. europaea</i>	1	1	0	0	1	1	0	1	0	0	0	1	1	1	1	2	1	0
<i>R. caboverdensis</i>	1	1	0	0	1	1	0	1	0	0	0	1	1	1	1	2	1	0
<i>R. leonis</i> sp. nov.	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	1	0

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
<i>B. clavigera</i>	0	–	0	0	0	0	0	–	–	–	–	–	–	–	0	0	0	0	0
<i>P. quadrilineata</i>	–	–	–	–	1	–	0	–	–	0	0	0	0	0	1	0	1	0	1
<i>P. emertoni</i>	–	–	–	–	0	1	1	0	0	0	0	1	1	–	0	0	1	0	1
<i>N. lineolata</i>	1	2	0	1	0	1	0	–	–	1	0	0	1	0	2	1	2	2	1
<i>N. chamberlaini</i>	1	2	0	1	0	1	0	–	–	1	0	0	1	0	2	1	2	2	1
<i>N. kubaryana</i>	1	2	0	0	0	1	0	–	–	1	0	0	1	0	2	1	2	2	1
<i>T. morosa</i>	1	0	1	–	0	1	1	1	0	1	0	0	1	0	1	1	1	0	1
<i>T. eliora</i>	1	2	1	–	0/1	1	0	–	–	1	0	0	1	0	1	1	1	?	1
<i>T. ceutae</i>	1	2	1	–	0	1	1	0	0	1	0	0	1	0	1	1	1	?	1
<i>R. gracilis</i>	1	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	2	1	1
<i>R. luteolineata</i>	1	2	0	1	0	1	1	1	1	1	0	0	1	0	1	1	2	1	1
<i>R. tigris</i>	1	1	0	1	0	1	0	–	–	1	1	0	1	0	1	1	2	1	1
<i>R. europaea</i>	1	0	0	0	0	1	1	1	1	1	1	0	1	0	1	1	2	1	1
<i>R. caboverdensis</i>	1	1	0	0	0	1	0	–	–	1	1	0	1	0	1	1	2	1	1
<i>R. leonis</i> sp. nov.	1	1	0	1	0	1	0	–	–	1	1	0	1	0	1	1	2	1	1

9. **Rhinophores*: (0) lamellate; (1) smooth.

10. **Anal papilla*: (0) elevated (*Bathydoris* and the majority of the phanerobranch dorids); (1) not elevated (*R. gracilis*).

11. **Body surface covered with low pustules*: (0) absent; (1) present (unique to *R. gracilis*).

12. *Salivary gland size*: (0) large; (1) small.

13. *Salivary gland shape*: (0) very elongated; (1) slightly elongated.

14. *Elongated pouches in the oral tube*: (0) absent (outgroup taxa, *Tambja* and *Nembrotha*); (1) thick and elongated (*R. gracilis* and *R. luteolineata*; this character is unique to the genus); (2) slender and elongated, at the junction of the oral tube and the buccal mass (the rest of the species of *Roboastra*; also found in some specimens of *T. eliora*). The apomorphic character states are treated as unordered.

15. *Oral tube*: (0) short (*B. clavigera* and the rest of the outgroup taxa); (1) very long (*Roboastra* spp.).

16. *Jaws*: (0) well-developed jaws present; (1) reduced to a strong labial cuticle (*Tambja* spp.); (2) reduced to a thin labial cuticle (*Roboastra*, *Nembrotha* and *Polyserella emertoni*).

17. **Radula*: (0) multidenticulate. (1) paucidenticulate.

18. *Rachidian teeth*: (0) present; (1) absent.

19. **Rachidian teeth shape*: (0) nearly triangular (*B. clavigera*); (1) rectangular (all other taxa). In species with no rachidian teeth this character has been treated as nonapplicable.

20. *Shape of the upper edge of the rachidian teeth*: (0) slightly arched (*T. morosa*, *R. europaea* and *R. gracilis*); (1) very arched (*R. caboverdensis*, *R. tigris* and *R. leonis*); (2) slightly curved (*R. luteolineata*, *Nembrotha* spp. and most of *Tam-*

bja spp.). This character and 21 are treated as nonapplicable in species lacking a rectangular rachidian tooth shape. In both cases the characters are considered to be unpolarized.

21. *Denticles of the rachidian teeth*: (0) present; (1) absent. In *Polycera quadrilineata* and *Polycerella emertoni* this character is treated as nonapplicable, as is 22.
22. *Size of the denticles of the rachidian teeth*: (0) similar in size (*B. clavigera*); (1) different sizes (*R. tigris*, *R. leonis*, *R. luteolineata*, *N. lineolata* and *N. chamberlaini*).
23. **Number of inner lateral teeth*: (0) one (*B. clavigera* and all the species of the ingroup); (1) two (*P. quadrilineata*). In some specimens of *T. eliora* it is possible to see a small vestigial second inner tooth.
24. **Number of cusps of the inner lateral teeth*: (0) one (*B. clavigera*); (1) two (all other taxa).
25. *Inner cusp of the inner lateral teeth*: (0) simple (*B. clavigera* and *P. quadrilineata*); (1) bifid (all other taxa).
26. *Inner cusp, upper denticle*: (0) denticle short (*P. emertoni*, *T. ceutae* and *R. gracilis*; Fig. 2C); (1) superior cusp of the inner lateral teeth longer (*T. morosa*, *R. europaea* and *R. luteolineata*).
27. *Inner denticle of the upper cusp*: (1) strong (*P. emertoni*, *T. morosa* and *R. gracilis*); (1) slender (the other species of *Roboastra*).
28. *Outer cusp of the lateral teeth*: (0) hardly developed (outgroup taxa, except *B. clavigera*, in which this character is coded as missing); (1) well developed (*Roboastra* spp.; Fig. 7).
29. *Robustness of the outer cusp of the lateral teeth*: (0) robust (outgroup taxa, and some species of *Roboastra*; in *B. clavigera* this character is coded as missing); (1) slender (Fig. 7).
30. *Outer lateral teeth, number*: (0) multidenticulate; (1) reduced in number.
31. **Outer lateral teeth shape*: (0) hook-shaped; (1) plate-like.
32. **Length of the outer lateral teeth ($r : L/l$, where L = width, l = height)*: (0) $r > 1$ (*P. quadrilineata* and most of the species of the ingroup); (1) $r < 1$ (*R. gracilis*).
33. *Ampulla, shape*: (0) elongate (*B. clavigera* and *P. emertoni*); (1) S-shaped (*P. quadrilineata* and the species of the ingroup); (2) highly convoluted (*Nembrotha* spp.).
34. *Bursa copulatrix, shape*: (0) elongate (outgroup); (1) spherical (ingroup).
35. *Penial spines*: (0) absent; (1) one or two different kinds; (2) three different kinds.
36. *Arrangement of the spines on the penis*: (0) randomly distributed; (1) helicoidal lines or rows.
37. **Reproductive system*: (0) diaulic; (1) triaulic.

RESULTS

Analysis of the data matrix produced five most parsimonious trees, 48 steps long (CI = 0.67, RI = 0.78), found in a single island. From these a 50% majority rule consensus tree was produced (Fig. 11). The majority rule tree has a good resolution in most of the branches. Bootstrap support analysis shows that most of the basal clades are well supported and that *Roboastra* is monophyletic (with a bootstrap value of 93). The tree is fully resolved and shows that *R. gracilis* and *R. luteolineata*, the Indo-Pacific species, are the basal species in the clade. *R. tigris*, *R. leonis*, *R. caboverdensis* and *R. europaea* constitute the Atlantic and Eastern Pacific clade. The relationships between them are depicted in Figure 11.

The 50% majority rule consensus tree reveals the presence of several monophyletic groups. *Roboastra* is a monophyletic group, supported by several synapomorphies (Fig. 12): oral tentacles developed as dorso-laterally grooved cylindrical projections (6: 1); small salivary glands (12: 1); presence of elongated pouches at the junction of the oral tube and the buccal mass (14: 1/2); oral tube long (15: 1), and penis with spines arranged in helicoidal rows (36: 1).

DISCUSSION

Bergh (1877) described the genus *Nembrotha*, including six new species. In that paper, he described *N. gracilis* and in a footnote he stated that it would probably become a new genus (*Roboastra*). Burn (1967) defined *Roboastra* properly for the first time, using the available generic name proposed by Bergh. Thus, *N. gracilis* became the type species of this genus. Six species have been described since then, although some are currently regarded as synonyms (*R. rubropapulosa* a synonym of *R. gracilis*), while in this paper one (*R. arika*) has been proposed as a *nomen dubium* due to lack of information and the loss of the holotype. A review of the literature shows that there are five nominal species of *Roboastra*, but the original descriptions as well as a few published additional studies offer limited information. This lack of information has produced a great deal of confusion in the literature, with wrongly identified specimens appearing in field guides and on web pages.

The phylogenetic hypothesis has produced relevant biogeographical information. The two most basal species of *Roboastra* in the clade are found in the Indo-Pacific (as are all *Nembrotha*) whereas the Atlantic and eastern Pacific species form a derived, monophyletic clade. This general pattern, in which in which some or all of the eastern Pacific species are sister to the Atlantic species, has been found in other species of nudibranchs (Gosliner, 1995; Gosliner & Johnson,

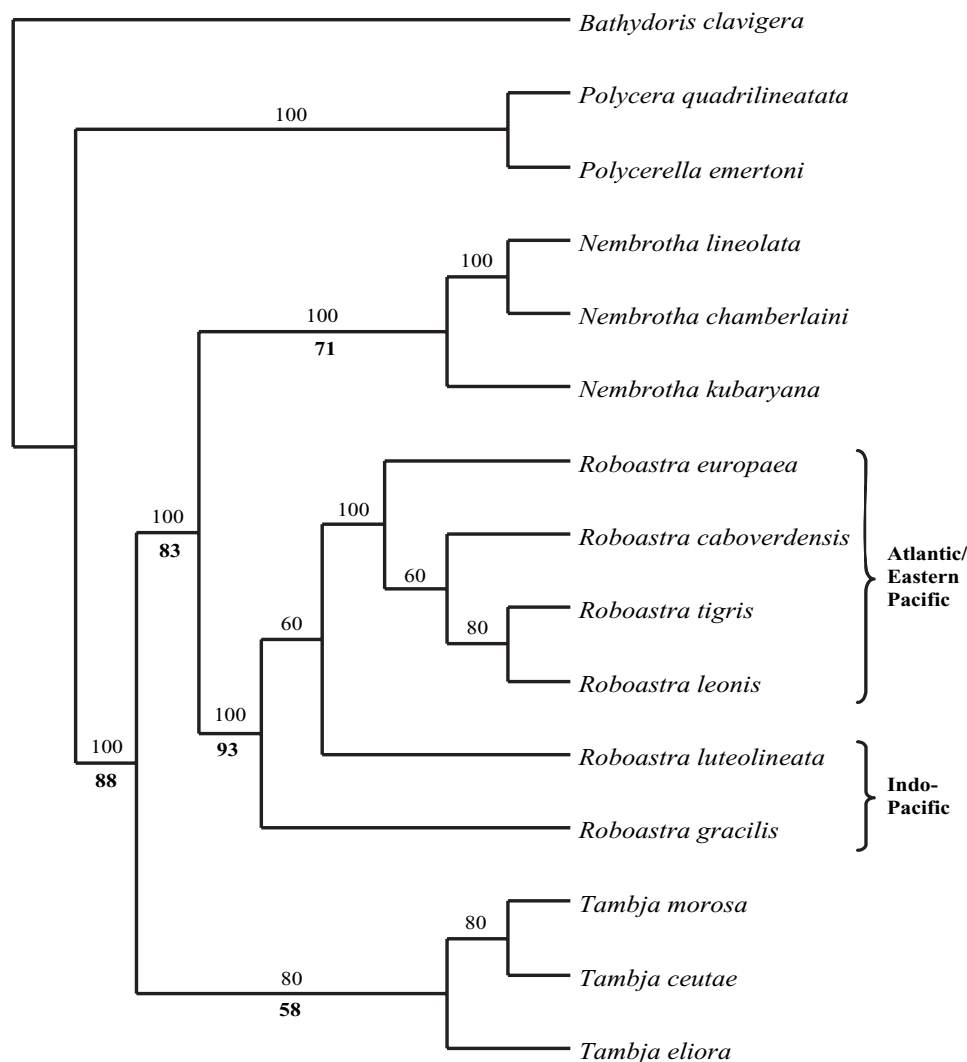


Figure 11. Majority rule (50%) consensus tree of the phylogenetic relationships of the genus *Roboastra*. Numbers above the branches refer to percentage of trees supporting the branch, numbers below to the bootstrap support values.

1999; Garovoy *et al.*, 2001; Dorgan, Valdés & Gosliner, 2002; Valdés & Behrens, 2002). It is unequivocally related to major geological events. A vicariant event, most likely the closure of east–west communication in the Suez area during the Oligocene–Miocene transition, 23 Mya, produced the split of the original range of the ancestor of the *Roboastra* clade and subsequent speciation. The subsequent closure of the Panamanian Isthmus, 3.5 Mya, would have isolated the eastern Pacific from the Atlantic lineages.

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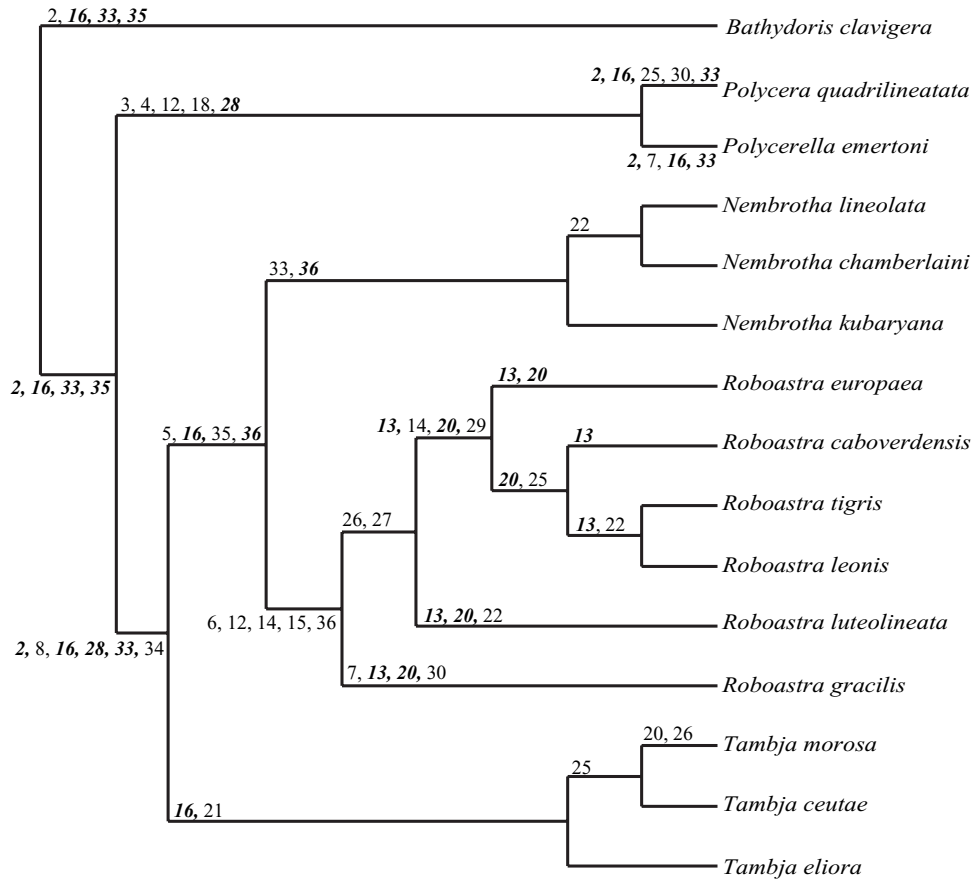


Figure 12. Majority rule (50%) consensus tree of five most parsimonious trees showing character tracing. Numbers refer to characters listed in the text. Characters printed in bold and italic face presented at least one instance of reversal.

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