Taxonomic revision and phylogenetic analysis of the genus *Tambja* Burn, 1962 (Mollusca, Nudibranchia, Polyceridae)

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This paper discusses the systematics and phylogeny of the genus *Tambja* Burn, 1962 throughout tropical and temperate areas in the Atlantic, eastern Pacific and Indo-Pacific. The phylogenetic relationships within *Tambja* are unknown and a comprehensive taxonomic revision is necessary in order to construct a phylogeny of the genus. To date, *Tambja* comprises 28 nominal species, 22 of which have been examined morphologically based on newly collected and type material. The reproductive systems of four species (*T. limaciformis* (Eliot, 1908), *T. sagamiana* (Baba, 1955), *T. amakusana*, Baba, 1987 and *T. olivaria*, Yonow, 1993) were studied for the first time and two species previously considered as valid, *Tambja morosa* (Bergh, 1877) and *Tambja kushimotoensis* Baba, 1987, are here synonymized. Of the remaining six nominal species, no additional material has been found since their original description. The holotypes of three (*T. diaphana* (Bergh, 1877), *T. gratiosa* (Bergh, 1890) and *T. marbellensis* Schick & Cervera, 1998) have been re-examined and the original descriptions improved. *Tambja diaphana* is regarded as *nomen dubium*. *Tambja amitina* (Eliot, 1905), *T. divae* (Marcus, 1958) and *T. anayana* Ortea, 1989 remain as valid species until further comparison with new specimens can be made. New structures are also described for several taxa. Morphological and anatomical data from 22 nominal *Tambja* species have been used to construct a phylogeny. The phylogenetic analysis rejects the monophyly of *Tambja* and shows its preliminary relationships within the subfamily Nembrothinae.

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Introduction

Burn (1967) provided justification for placement of *Tambja* Burn, 1962, *Nembrotha* Bergh, 1877, and *Roboastra* Bergh, 1877 in the subfamily Nembrothinae. Since the genus *Tambja* was erected, 28 nominal species have been described or transferred to it from around the world. The review of the literature shows that many of 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, including field guides and websites, which often contain misidentified photographs. A complete and comprehensive taxonomic revision is necessary in order to run cladistic analyses.

The genus *Tambja* is characterized by having a vestigial frontal veil, laminate rhinophores which are contractile into sheaths, a gill with 3–5 branches, a strong labial collar, rachidian teeth rectangular or quadrangular with notched or smooth upper margin, inner lateral teeth with two cusps and the inner cusp either simple or bifid, outer lateral plates numbering between 3 and 7 and a small prostate gland confined to a glandular section of the vas deferens.

The first comprehensive studies on Nembrothinae were done for the genus *Roboastra* (Pola *et al*. 2005a), which appears to be a monophyletic group, as well as a preliminary phylogeny of the subfamily based on molecular data (Pola *et al*. 2006). Pola *et al*. (2005b,c) describe four new species of the genus *Tambja* from the Indo-Pacific and one species from the Atlantic and give an historical account of the genus. The present study provides an in-depth look at the systematics of the genus and also examines its phylogenetic relationships to determine whether or not it constitutes a monophyletic group.

Materials 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), Funchal (MMF), the Western Australian Museum, Perth (WAM), the Muséum National d'Histoire Naturelle, Paris (MNHN), the Zoologische Staatssammlung München (ZSM), the Instituto Nacional de Biodiversidad, Costa Rica (INBIO), the Zoologisk Museum, University of Copenhagen, Denmark (ZMUC) and the Smithsonian National Museum of Natural History, Washington, DC (USNM).

All *Tambja* species are described and discussed according to the year of publication. The specimens were dissected and a morphological examination was 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 for scanning electron microscopy. Features of living animals were recorded from photographs and notes by collectors. The external and internal anatomy of previously well-described species is not repeated here for reasons of space. References are made to the original descriptions where possible. Only undescribed features are pointed out. *Tambja verconis* (Basedow & Hedley, 1905) is fully described because it is the type species of the genus. In species in which 'a vestigial tooth' is present, it is considered to be the 'inner lateral tooth' while the next well-developed tooth is considered to be the 'second lateral tooth'. In the remaining species, the first lateral tooth is considered to be the 'inner lateral tooth'. The elongated pouches at the junction of the buccal mass and the oral tube present in some other species of *Roboastra* and *Tambja* (Pola *et al*. 2003, 2005a; present study) are mentioned only in those species in which they have been seen. Their absence is not commented on. Similar considerations govern the description of 'lateral slots' (Yonow 1994; Pola *et al*. 2005b,c; present study).

In order to calculate the most parsimonious phylogenetic trees, data were analysed with PAUP ver. 4.0b10 (Swofford 2001), using the heuristic algorithm tree-bisection-reconnection (TBR) option. In cases where a taxon had two states for a given character they were treated as uncertain. Both accelerated (ACCTRAN) and delayed (DELTRAN) optimizations were used for character transformation. In both cases the analyses were performed treating the characters as unordered. One thousand random starting trees were obtained via stepwise addition. The trees were rooted using the outgroup selection of the genus *Bathydoris* and subsequent analysis using PAUP.

Characters were polarized in the PAUP analysis using the outgroup selection of *Bathydoris clavigera* Thiele, 1912, *Polycera quadrilineata* (Müller, 1776), *Polycerella emertoni* Verrill, 1881, four species of *Nembrotha* Bergh, 1877 and six species of *Roboastra* Bergh, 1877. We used *Bathydoris* following Wägele & Willan (2000), Schrödl *et al*. (2001), and Valdés (2002), where the Bathydorididae was concluded to be the sister taxon to the Doridoidea. *Polycera quadrilineata* and *Polycerella emertoni* were chosen as representatives of the closely related subfamily Polycerinae due to availability of material. Finally, *Nembrotha* and *Roboastra* species were chosen in order to provide a preliminary test of the monophyly of the subfamily Nembrothinae. The sources of information for outgroup and ingroup taxa are shown in Table 1. A Bremer support or decay analysis was performed using a heuristic search by PAUP to estimate branch support. Synapomorphies were obtained using the character trace option in MacClade ver. 4.03 (Maddison & Maddison 2000) based on the strict consensus tree from the PAUP analysis.

Description of taxa

Family POLYCERIDAE Alder & Hancock, 1845

Genus *Tambja* Burn, 1962. Type species: *Nembrotha verconis* Basedow & Hedley, 1905, by original designation.

Diagnosis. Polycerids, without frontal or velar processes and a vestigial frontal veil. Rhinophores laminate, contractile into sheaths. Gill branches 3–5 in number. Jaws not present, replaced by a strong labial collar. Rachidian teeth rectangular or quadrangular with notched or smooth upper margin, inner lateral tooth with two cusps, and the inner cusp either simple or bifid, outer lateral plates numbering from 3 to 7. Prostate gland small, confined to a glandular section of the vas deferens. Penis armed.

Tambja diaphana (Bergh, 1877)

Nembrotha diaphana Bergh, 1877: 92–93, pl. 4, figs 3–5.

Material examined. Holotype, Palau Islands, Philippines, July 1862, collected by Semper. (ZMUC GAS-2080).

Distribution. Aibukit (Palau Islands).

Anatomy. Body elongate, limaciform, with pointed posterior end. Foot narrow, grooved in front. 40 mm in length. Body smooth. Large, conical, perfoliate rhinophores (approx. 40 lamellae) retractile in sheaths. Oral tentacles short, dorso-ventrally flattened and horizontally grooved. Five tripinnate gill branches surround anus. Genital pore on right side, midway between gill and rhinophores. Lamellated structures located between rhinophores and oral tentacles. Labial cuticle smooth. Radular formula unknown, but slide with the eight first rows of radular teeth from holotype was available for study. Rachidian teeth rectangular, without denticles, smooth at upper margin.

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

Taxa	Source of information
Bathydoris clavigera Thiele, 1912	Wägele (1989a,b), Wägele & Willan (2000), Valdés (2002), Fahey & Gosliner (2004)
Polycera quadrilineata (Müller, 1776)	Directly from the available material, Thompson & Brown (1984), García-Gómez (2002)
Polycerella emertoni Verrill, 1880	Directly from the available material, Behrens & Gosliner (1988), García-Gómez & Bobo (1986)
Nembrotha lineolata (Bergh, 1905)	Directly from the available material
Nembrotha chamberlaini Gosliner & Behrens, 1997	Directly from the available material
Nembrotha kubayana Bergh, 1877	Directly from the available material
Roboastra gracilis (Bergh, 1877)	Pola *et al*. (2005a)
Roboastra luteolineata (Baba, 1936)	Pola *et al*. (2005a)
Roboastra tigris Farmer, 1978	Pola *et al*. (2005a)
Roboastra europaea García-Gómez, 1985	Pola *et al*. (2005a)
Roboastra caboverdensis Pola, Cervera & Gosliner, 2003	Pola *et al*. (2005a)
Roboastra leonis Pola, Cervera & Gosliner, 2005	Pola *et al*. (2005a)
Tambja morosa (Bergh, 1877)	Directly from the available material
Tambja affinis (Eliot, 1904)	Directly from the available material
Tambja verconis (Basedow & Hedley, 1905)	Directly from the available material
Tambja capensis (Bergh, 1907)	Directly from the available material
Tambja limaciformis (Eliot, 1908)	Directly from the available material
Tambja sagamiana (Baba, 1955)	Directly from the available material
Tambja eliora (Marcus & Marcus, 1967)	Directly from the available material
Tambja oliva Meyer, 1977	Directly from the available material, Meyer (1977)
Tambja abdere Farmer, 1978	Directly from the available material
Tambja mullineri Farmer, 1978	Directly from the available material
Tambja fantasmalis Ortea & García-Gómez, 1986	Directly from the available material
Tambja amakusana Baba, 1987	Directly from the available material
Tambja ceutae García-Gómez & Ortea, 1988	Directly from the available material
Tambja marbellensis Schick & Cervera, 1998	Schick & Cervera (1998); review of the holotype
Tambja simplex Ortea & Moro, 1999	Directly from the available material
Tambja olivaria Yonow, 1994	Directly from the available material
Tambja victoriae Pola, Cervera & Gosliner, 2005	Pola *et al*. (2005b)
Tambja tentaculata Pola, Cervera & Gosliner, 2005	Directly from the available material; Pola *et al*. (2005b)
Tambja zulu Pola, Cervera & Gosliner, 2005	Pola *et al*. (2005b)
Tambja gabrielae Pola, Cervera & Gosliner, 2005	Pola *et al*. (2005b)
Tambja tenuilineta Miller & Haagh, 2005	Miller & Haagh (2005); Directly from the available material
Tambja stegosauriformis Pola, Cervera & Gosliner, 2005	Pola *et al*. (2005c)

Inner lateral tooth elongate, with two cusps; inner cusp simple. Outer laterals teeth roughly rectangular, smaller towards the outer margin.

Remarks. Bergh (1877) described *T. diaphana* from a single preserved specimen collected during the Siboga expedition. The review of the holotype has permitted us to improve the description of the species, although the reproductive system, together with some other internal features, remains unknown because the internal organs had been previously removed. *Tambja diaphana* reminds one of *T. morosa* in its coloration (preserved) and distribution, but *T. morosa* has notched rachidian teeth, while the inner cusp of the inner lateral teeth is bifid. Rudman (1999) stated that the original description is worthless and that as there are few important differences in the radular morphology of most species of the genus, the name should be treated as unidentifiable. Thus in this paper we treat *T. diaphana* as *nomen dubium*.

Pruvot-Fol (1927) attributed the name of *Tambja diaphana* (quoted as *Nembrotha*) to a specimen collected from the Moroccan coast. Some authors (García-Gómez 1985; Ortea & García 1986; García-Gómez & Ortea 1988; Schick & Cervera 1998; Sánchez-Tocino *et al*. 2000a) considered that the Pruvot-Fol species could be a different taxon since it was found in the Atlantic whereas Bergh's animal was from the western Pacific. Moreover, Schick & Cervera (1998) pointed out that since every species of the genus *Tambja* has a restricted geographical range, it is practically impossible that the Pruvot-Fol species is conspecific with Bergh's *T. diaphana* from Palau.

***Tambja morosa* (Bergh, 1877) (Figs 1A,B, I, 2A–F, 3A)**
Nembrotha morosa Bergh, 1877: 457.
Tambja kushimotoensis Baba, 1987: 13. **syn nov**.

Material examined. Neotype, here designated, Malapascua Island, Philippines, 29 April 2003, 1 spec. 69 mm alive, 7 m

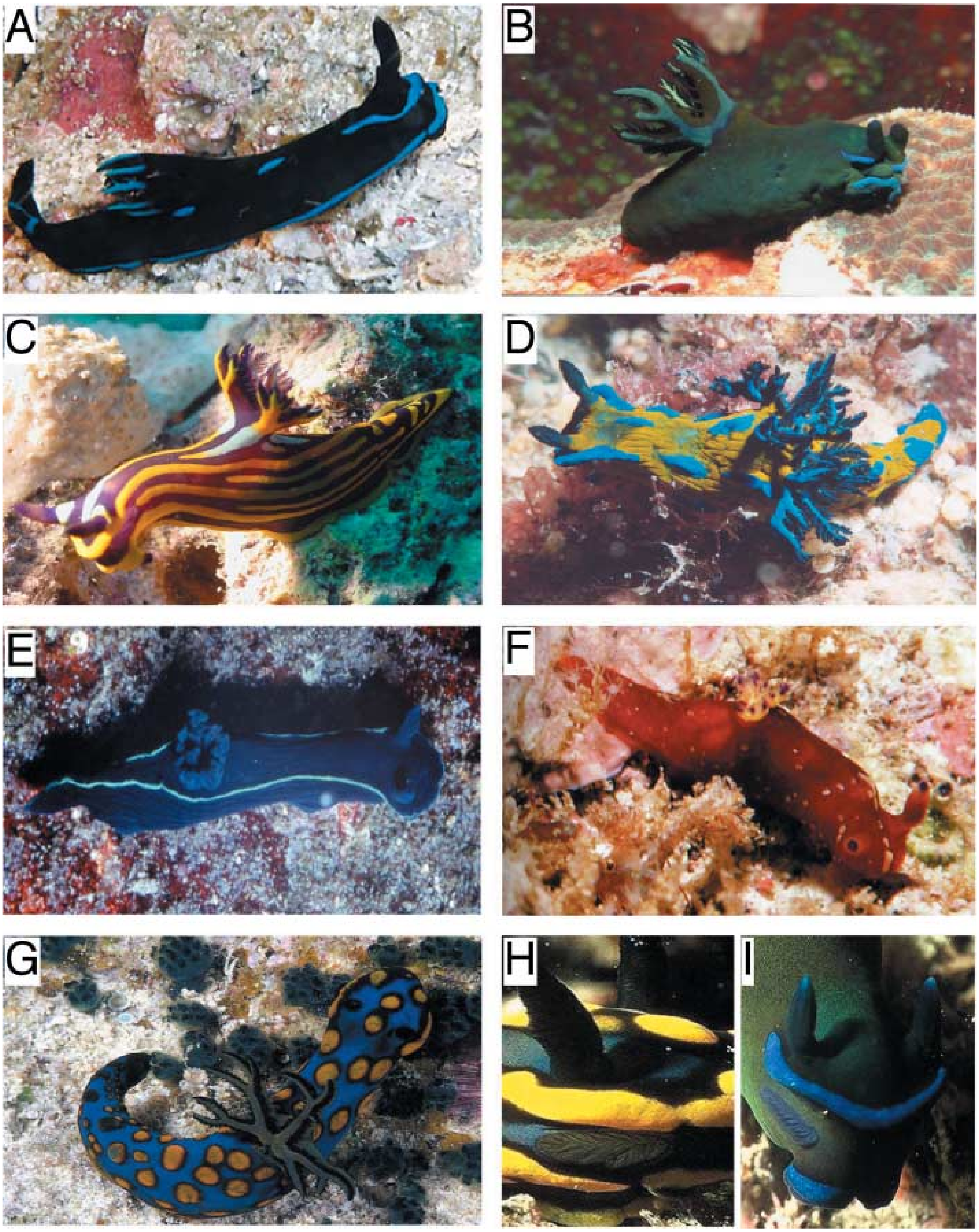

Fig. 1 A–I. Photographs of the living animals: —A. *Tambja morosa*, specimen from Horseshoe Bay, Indonesia (photo: Sabine Noack). —B. *Tambja morosa*, specimen from Cebu Island, Philippines (photo: Erwin Köhler). —C. *Tambja affinis*, specimen from Comores Island, Indian Ocean (photo: Marina Poddubetskaia). —D. *Tambja verconis*, specimen from Port Stephens, New South Wales (photo: David and Leanne Atkinson). —E. *Tambja capensis*, specimen from Port Elizabeth, Cape Province, South Africa (photo: Terrence M. Gosliner). —F. *Tambja limaciformis*, specimen from Amami-Ooshima Island, Japan (photo: Jun Imamoto). —G. *Tambja sagamiana*, specimen from Japan (photo: A. Ono). —H. Detail of 'lateral slots' in *Tambja sagamiana*, specimen from Taiwan (photo: Todd Garthwaite). —I. Detail of 'lateral slots' in *Tambja morosa*, specimen from Taiwan (photo: Todd Garthwaite).

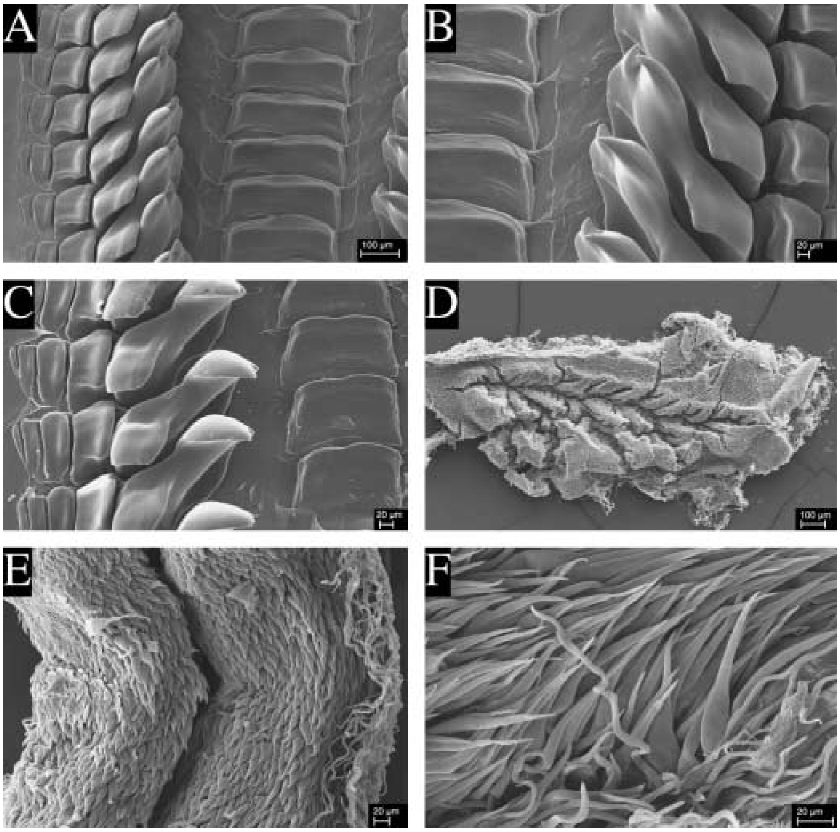

Fig. 2 A–F. Scanning electron micrographs of *Tambja morosa*. —A. Left half of the radula (CASIZ 065279). —B. Innermost lateral teeth (CASIZ 065279). —C. Left half of the radula (CASIZ 157151). —D. Lateral slot (CASIZ 157151). —E,F. Penial spines (CASIZ 065279).

depth, collected by E. Köhler (MNCN 15.05/46674). Near lighthouse, north coast, Madang, Papua New Guinea, 15 January 1988, 1 spec. 12 mm preserved, dissected, 34 m depth, collected by R. C. Willan (CASIZ 065279). Bethlehem, Maricaban Island, Batangas Province, Luzon, Philippines, 12 May 2001, 1 spec. 15 mm preserved, dissected, 23 m depth, collected by S. Fahey. Note: 1 colour slide (CASIZ 157151). Msimbati, Mtwara Region, Tanzania, 01 November 1994, 1 spec. 42 mm preserved, dissected, 27 m max depth, collected by T. M. Gosliner. Note: 1 colour slide (CASIZ 099392). Mooloolaba, south-eastern coast Queensland, Australia, 23 September 2000, 1 spec. 35 mm preserved, dissected, collected by S. Fahey. Note: continuous blue line along mantle edge (CASIZ 142786). Zamami Island, Kerama Island, Okinawa, Japan, 17 March 2003, 2 specs. 15 & 20 mm preserved, collected by A. Ono (MNCN 15.05/46673). Boia-Boia-Waba Island (off of East Cape), Milne Bay Province, Papua New Guinea, 27 May 1988, 1 spec. 30 mm preserved, dissected, 18 m depth, collected by T. M. Gosliner. Note: 1 colour slide (CASIZ 113641). Moalboal, Cebu Island, Philippines, 11 May 2003, 1 spec. 45 mm alive, 22 m depth, collected by E. Köhler (MNCN 15.05/46675). Tongo Point, Cebu Island, Philippines, 11 May 2003, 1 spec. 54 mm alive, dissected, 18 m depth, collected by E. Köhler (MNCN 15.05/46676). Moalboal, Cebu Island, Philippines, 12 May 2003, 1 spec. 72 mm alive, dissected, 24 m depth, collected by E. Köhler (MNCN 15.05/46677).

Distribution. Throughout the tropical Western Pacific: Philippines (Debelius 1996; present study); Hawaii (Debelius 1996; Fiene, pers. comm.; http://slugsite.us/bow/nudwk140htm), Guam (Carlson & Jo Hoff 2003); Indonesia (Debelius 1996; Takamasa 2003), Thailand (http://www.seaslugforum.net/display.cfm?id=2236); Japan (Baba 1987; Nakano 2004; Ono 1999, 2004); Taiwan (http://www.seaslugforum.net/display.cfm?id=10503), Papua New Guinea (present study; http://www.seaslugforum.net/display.cfm?id=5367), western Australia to Queensland, Lord Howe Islands, Heron Island, New South Wales (Wells & Bryce 1993; Willan & Coleman 1984; Coleman 1989, 2001; Marshall & Willan 1999; http://www.seaslugforum.net/display.cfm?id=10550), North and South Islands of New Zealand (Willan & Coleman 1984; Willan & Morton 1984; Haagh 2002) and southern Africa (Gosliner 1987; Yonow & Hayward 1991; Debelius 1996; present study).

External morphology. Body large, robust and limaciform (Fig. 1A,B). Foot linear, posterior end pointed. Body surface usually smooth, wrinkled in some specimens. Preserved

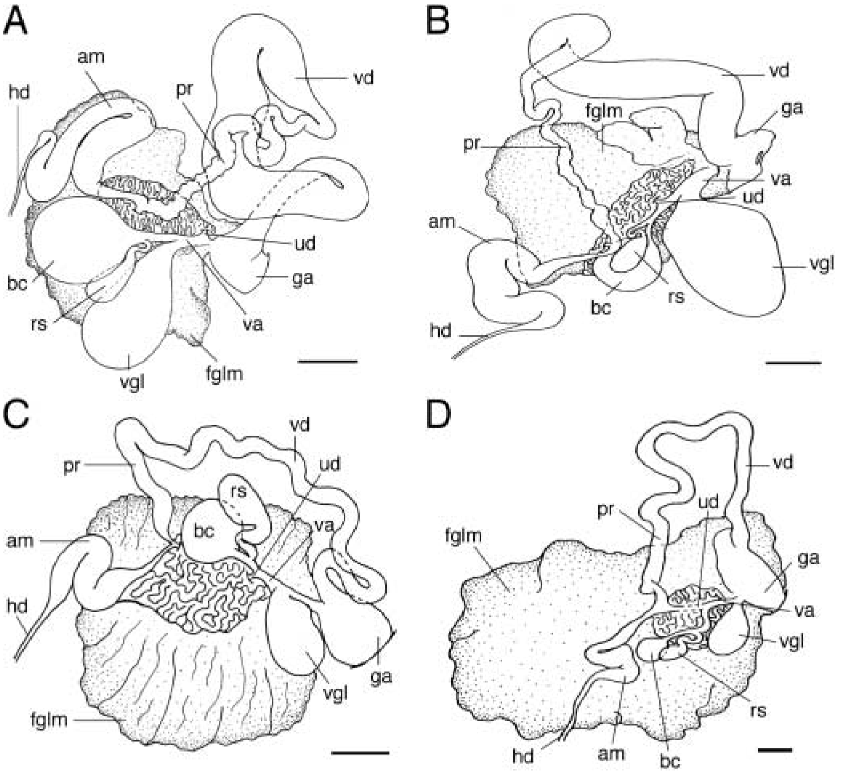

Fig. 3 A–D. Reproductive system of four *Tambja* species: —A. *T. morosa* (MNCN 15.05/46676). —B. *T. affinis* (MNHN). —C. *T. verconis* (MNCN 15.05/46654). —D. *T. capensis* (CASIZ 075154). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

animals 15–45 mm long, living animals may exceed 70 mm. Head rounded, with a pair of perfoliate rhinophores (approx. 40 lamellae), retractile in elevated sheaths. Oral tentacles short, blunt folds. 3–5 tripinnate gill branches. Anus between gill branches above an elongate papilla. Genital pore on right side of body, midway between rhinophores and anterior end of gill. Most of the examined specimens have a long black-ridged structure or 'lateral slots' (Yonow 1994; Pola *et al.* 2005b,c; present study) below the rhinophores, appearing as a dark groove along side of head (Figs 1I and 2D); in some specimens this is heavily innervated, indicative of a sensory function. Ground colour, black to green, with usually a few blue spots or lines scattered over the notum and tail.

Anatomy. Anterior digestive tract begins with a relatively short and slightly muscular oral tube, buccal mass longer than oral tube. A pair of large, wide, elongated salivary glands on buccal mass, flanking oesophagus. Chitinous labial cuticle well developed, lacking denticles. Radular formulae: 20 x 3.1.1.1.3 (CASIZ 065279), 14 x 4.1.1.1.4 (CASIZ 157151), 16 x 4.1.1.1.4 (CASIZ 099392), 18 x 3-4.1.1.1.3-4 (CASIZ 142786), 17 x 4.1.1.1.4 (MNCN 15.05/46676) and 20 x 3-4.1.1.1.4-3 (MNCN 15.05/46677). Rachidian teeth rectangular or subquadrate, without denticles, notched at upper margin (Fig. 2A,B). Innermost lateral tooth elongate and large with two cusps; inner cusp bifid, with two sharp denticles (Fig. 2B), outer cusp well developed and rectangular in shape. Outer lateral teeth roughly rectangular, decreasing in size towards the outer margin, outermost being small or lacking. Large well-developed granular blood gland inserts into dorsal surface of oesophagus above gut. Oval renal syrinx is visible under the pericardium. Reproductive system triaulic (Fig. 3A). Hermaphroditic duct continues as an 'S'-shaped ampulla. Ampulla narrows into postampullary duct that connects with oviduct and prostate. Short oviduct enters massive female gland mass. Large prostate gland confined to a coiled soft section of vas deferens. At end of prostate, vas deferens widens into large and convoluted duct, distally containing numerous unordered and elongate penial spines (Fig. 2E,F). Vaginal duct short, usually straight, connecting to large, round, bursa copulatrix. Seminal receptacle pyriform, smaller or similar in size to bursa copulatrix. A short duct connects seminal receptacle to vagina after completing two loops, near bursa. Slender uterine duct leaves vagina from distal position and joins with female gland. Vagina and vaginal gland share common aperture within genital atrium. Vaginal gland large, elongate, flattened, with muscular walls. Mucous gland well developed. Genital mass fills whole of second quarter of body cavity.

Remarks. Bergh (1877) described *Nembrotha morosa* from the Philippines. Bergh (1905) stated that *T. morosa* was only known

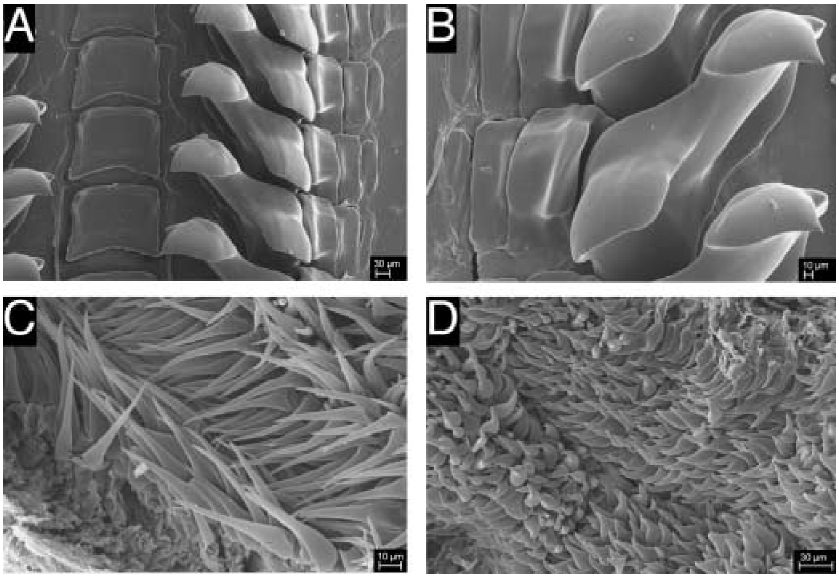

Fig. 4 A–D. Scanning electron micrographs of *Tambja affinis* (CASIZ 099226). —A. Right half of the radula. —B. Innermost lateral teeth. —C,D. Detail of the penial spines.

from Semper's illustration and that the type animal seemed to be lost. He described a new specimen depicted alive from the Siboga expedition and said that the illustration corresponded with that presented by Semper. The original external description together with the radular formula (23 x 3.1.1.1.3) perfectly matches those specimens described by Baba (1987) as *T. kushimotoensis*. Baba (1987) never compared both species. *Tambja morosa* appears to be variable in colour and colour pattern. Thus, most field books (Debelius 1996; Marshall & Willan 1999; Coleman 1989, 2001; Takamasa 2003; Nakano 2004; Ono 1999, 2004) and web pages (www.seaslugforum.net, www.robertosozzani.it/Manado/Nudy/nudy21-2.html, www.waterworxbali.com/tambja-morosa.shtml) show pictures of this species with black background and bright blue lines or spots or even completely blue without any spots. In this study we have examined specimens with both coloration patterns (black ground and bright blue lines or spots vs. green background with blue spots) from different regions and were unable to find any consistent differences between them. Thus, *T. morosa* and *T. kushimotoensis* should be considered as synonyms. Barnard (1927) and Macnae (1958) considered *T. capensis* (Bergh 1907) to be a synonym of *T. morosa*, but *T. capensis* can be distinguished by the interrupted, blue-green notal margin and pigment of the same colour which extends onto the gill and by several anatomical differences discussed under *T. capensis*.

***Tambja gratiosa* (Bergh, 1890)**
Nembrotha gratiosa Bergh, 1890: 172, pl. 3, figs 1–4.

Material examined. Holotype, Mexican Gulf, 24°26′N; 83°16′W, 1890, collected by the 'Blake' expedition. (ZMUC GAS-2086).

Distribution. Gulf of Mexico.

Remarks. Bergh (1890) described *Tambja gratiosa* from the Gulf of Mexico. To date, the only available information about this species stems from the original description. *Tambja gratiosa* was described from a preserved specimen 22 mm long. Bergh (1890) figured the radular teeth and the reproductive system. The most distinctive feature of this species is the presence of a caudal crest, similar to that of *T. divae* (Marcus, 1958). Nevertheless, the latter species has a straight upper margin of the rachidian tooth, the upper cusp of the inner lateral tooth is simple and there are 6–7 outer lateral teeth (Marcus 1958). Bergh (1890) also stated that *T. gratiosa* resembles *T. diaphana* (Bergh, 1877), but that *T. diaphana* lacks a caudal crest.

***Tambja affinis* (Eliot, 1904) (Figs 1C, 3B and 4A–D)**
Nembrotha affinis Eliot, 1904: 92, pl. 4, figs 3–5.

Material examined. Mana Huanja Island, Mtwara Region, Tanzania, 2 November 1994, 1 spec., dissected, collected by T. Gosliner (CASIZ 099226). Reef de Peitro, Kongou, Mayotte, Comoros Islands, 1 spec. 15 November 2003, 70 mm alive, dissected, 11 m depth, collected by Marina Poddubetskaia (MNHN).

Distribution. Zanzibar, Red Sea (Yonow 1990; Reyniers 2003) and the Comoros Islands (present study).

External morphology. Body elongate, limaciform with long, pointed posterior end of foot (Fig. 1C). Foot narrow, grooved in front. Living animals up to 70 mm in length. Body smooth, with four lateral stripes and one mediodorsal. Stripes interrupted in places, particularly on posterior end of foot where there are some elongated spots between them. A ridge extends anteriorly around head and converges behind gill but does not form a single line. A wide longitudinal line circumscribes both sides of body, surrounding the basal part of oral tentacles and mouth, ending in posterior end of foot. Another stripe borders the foot. A pair of large, conical, perfoliate rhinophores (approx. 30–35 lamellae), completely retractile into elevated rhinophoral sheaths. Oral tentacles short, dorsoventrally flattened and horizontally grooved. Three well-developed, nonretractile, tripinnate gill branches form semicircle surrounding tubular elevated anal papilla. Genital pore on right side, midway between gill and rhinophores. Dull violet lateral slots of unknown function located on both sides of body between rhinophores and oral tentacles.

Anatomy. Buccal mass longer than oral tube. A pair of elongate, narrow and granular salivary glands on buccal mass, flanking the oesophagus. Chitinous labial cuticle, lacking denticles. Radular formulae: 16 x 3.1.1.1.3 (CASIZ 099226) and 15 x 4-3.1.1.1.3-4 (MNHN). Rachidian teeth quadrangular, without denticles, smooth and straight at anterior edge (Fig. 4A). Innermost laterals much larger than outer ones with two well-developed, wide cusps: inner cusp bifid, with an upper denticle short but sharp and a smaller denticle on its inner edge (Fig. 4B); outer cusp well developed, rectangular in shape. Outer laterals teeth rectangular plates, lacking cusps, smaller towards outer margin. Reproductive system triaulic (Fig. 3B). Preampullatory duct elongate and narrow expanding into a thick-walled, 'S'-shaped ampulla, which divides into spermoviduct and vas deferens. Prostate gland confined to a narrow coiled section of vas deferens. At end of prostate gland vas deferens widens into swollen and coiled duct. Penis armed with numerous, unordered penial spines, arranged in longitudinal lines. Penial spines thick, rounded at base and with strong triangular cusp becoming shorter in distal part (Fig. 4C,D). Vagina short, straight, connects to oval bursa copulatrix. Seminal receptacle pyriform, smaller than bursa copulatrix. Short duct connects seminal receptacle to vagina, after completing two loops. Near distal third of its length, vagina branches into uterine duct, which enters the albumen gland after a short distance. Vagina shares common aperture within genital atrium with vaginal gland. Vaginal gland large, thick walled, well developed. Female gland well developed.

Remarks. The original description of *T. affinis* (Eliot, 1904) includes drawings of the external anatomy and the radular teeth. The coloration and pattern of lines of the living animal are described in detail, as well as the radular formula. All these features, as originally described, are consistent with the present material. The reproductive system is described in this paper for the first time. Yonow (1990) recorded this species from Saudi Arabia. However, *T. affinis* has frequently been misidentified in different books or web pages with *Roboastra luteolineata* (see Coleman 1989; Marshall & Willan 1999; www.waterworxbali.com; www.esc.aukland.ac.nz), *R. arika* (www.medslugs.de; www.slugsite.us) and *R. gracilis* (see Wells & Bryce 1993; Suzuki 2000), but this species can be easily distinguished from *Roboastra* species, apart from its colour pattern, because it has a radula whose morphology is similar to that of most of the *Tambja* species and lacks dorsolaterally grooved oral tentacles. *Tambja affinis* has also been confused (Willan & Coleman 1984; Willan & Morton 1984; Coleman 1989) with a new recently described species of *Tambja* from the Indo-Pacific, *T. victoriae* (Pola *et al.* 2005a). This species differs from *T. affinis* in its coloration. Within the reproductive system, *T. victoriae* has the penis armed with hooked spines arranged in longitudinal rows, while *T. affinis* has a higher density of large and unordered spines. All of the records of *T. affinis* in Australia and New Zealand refer to the presence of *Roboastra luteolineata*.

There are also some specimens of *Tambja* that have the same pattern of longitudinal lines as *T. affinis* and *T. victoriae*, but they have a green ground colour with yellow-orange longitudinal bands bordered by black lines. These specimens have been reported from Thailand and the Maldives. Pictures can be found in Debelius (1996) and http://slugsite.us/bow/nudiwk86.html. We lack specimens in order to study their anatomy. We have examined also a specimen from Western Australia (WAM S23266) that we thought could be *T. affinis* since its internal features are very similar to the latter (17 x 3.1.1.1.3 (WAM S23266)). Nevertheless, since we only have one specimen, the picture of the living animal is not very good, the distribution is far away from the original description and there are other species similar in external appearance, we have decided not to include this specimen in the distribution of *T. affinis* and thus to wait for the study of potential additional material that can solve its status. To date, *T. affinis* is restricted to the Indian Ocean.

***Tambja verconis* (Basedow & Hedley, 1905) (Figs 1D, 3C and 5A–D)**

Nembrotha (?) *verconis* Basedow & Hedley, 1905: 29, p. 158, pl. 2, figs 1–3.

Material examined. Spring Beach, Tasmania, 02 June 2000, 1 spec. 45 mm preserved, dissected, 7.5 m depth, collected by Nerida Wilson (MNCN 15.05/46653). Nelson Bay beach, Port Stephens, New South Wales, Australia, 31 January 2004, 1 spec. 30 mm preserved, dissected, 14 m depth, collected by David and Leanne Atkinson (MNCN 15.05/4665).

Distribution. New South Wales (Australia) (Basedow & Hedley 1905; Burn 1962; Willan & Morton 1984; Willan & Coleman

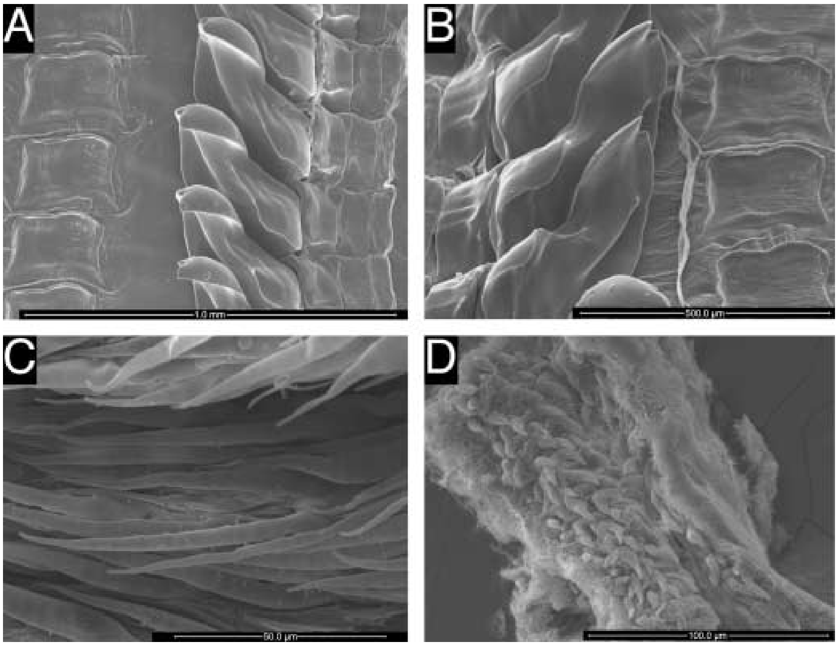

Fig. 5 A–D. Scanning electron micrographs of *Tambja verconis* (MNCN 15.05/46654). —A. Right half of the radula. —B. Innermost lateral teeth. —C,D. Detail of the penial spines.

1984; Coleman 1989, 2001; Debelius 1996; present study), New Zealand (Willan & Coleman 1984; Willan & Morton 1984; Coleman 2001; Haagh 2002) and Tasmania (Willan & Morton 1984; present study). Reports of this species can also be found in www.seaslugforum.net/factsheet.cfm?base=tambverc.

External morphology. Body elongate, limaciform, widest and highest at level of gill. Pointed posterior end of foot (Fig. 1D). Length of living animals between 30 and 130 mm. Body surface noticeably wrinkled with large disconnected blunt tubercles arranged indistinctly on notum and sides of body, usually forming a dorsal line from head to gill and also along posterior end of foot. Vestigial frontal veil composed of three ridges; two laterals skirting around rhinophore sheaths and gradually fading out along the pallial line of tubercles. Perfoliate rhinophores (bearing 35 lamellae), retractile in high, conical rhinophoral sheaths. Five large nonretractile, tripinnate gill branches form semicircle around conical anal papilla. Oral tentacles short, dorsoventrally flattened, with horizontal groove. Genital pore on right side, midway between rhinophores and gill. Lateral slots of unknown function located between rhinophores and oral tentacles. Ground colour bright yellow to olive brown with light blue tubercles. Vestigial frontal veil, oral tentacles, lateral slots, foot, inner and outer branchial rachis, genital aperture and anus, light blue; rhinophores, pinnae and border of foot, deep blue. Rhinophoral sheaths and base of anal papillae, yellow.

Anatomy. Anterior digestive tract begins with a relatively large, muscular oral tube, shorter in length than buccal mass. Elongated pouches at junction of buccal mass and oral tube present in other species of *Roboastra* and *Tambja* (Pola *et al*. 2003, 2005a; present study), absent. A pair of large, elongate salivary glands on buccal mass, flanking oesophagus. Chitinous labial cuticle well developed, lacking denticles. Radular formula of two specimens: 20 x 4-3.1.1.1.3-4. Rachidian tooth subquadrate, without denticles, and notched upper margin. Innermost lateral tooth elongate and large with two cusps; inner cusp bifid, with an outer denticle short but sharp, smaller denticle on its inner edge (Fig. 5A,B), outer cusp well developed and rectangular. Outer lateral teeth roughly rectangular, decreasing in size towards the outer margin, most remote, being small or lacking. A large granular well-developed blood gland inserts into dorsal surface of oesophagus above gut. Oval renal syrinx visible under pericardium. Reproductive system triaulic (Fig. 3C). Genital mass fills whole second quarter of body cavity. Female gland well developed, above where reproductive organs are located. Hermaphroditic duct continues as a wide thick walled 'S'-shaped ampulla, located in ventral surface of genital mass, just at junction of mucous and albumen glands. Ampulla narrows into short postampullary duct, which divides into oviduct and vas deferens. Short oviduct enters the albumen portion of female gland mass. Vas deferens elongated, without morphologically differentiated prostate. In original position, vas deferens runs along middle of genital mass surrounding distal part of seminal receptacle. Penis located within distal end of muscular portion of vas deferens. Proximal penial spines, large, uniform; distal spines smaller and hooked (Fig. 5C,D). Vaginal duct straight, elongate and connecting to large, round bursa copulatrix. Seminal receptacle pyriform, similar in length

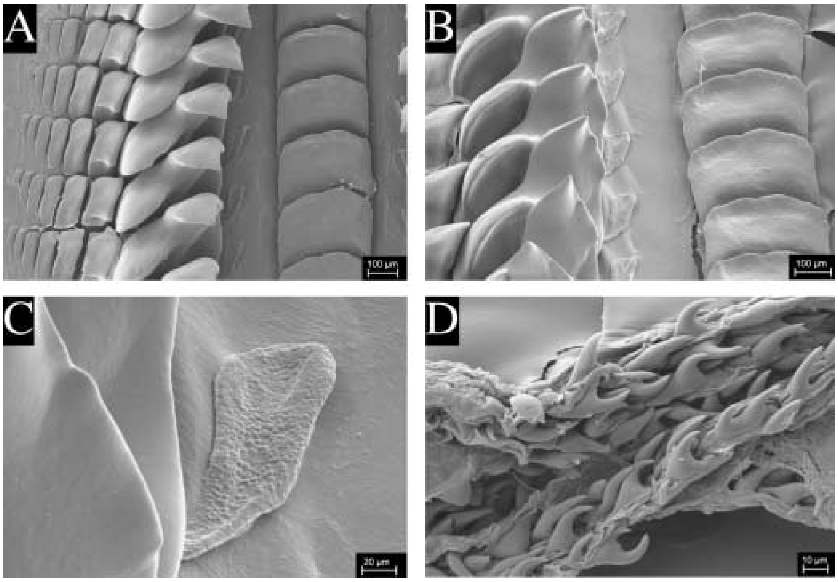

Fig. 6 A–D. Scanning electron micrographs of *Tambja capensis* (CASIZ 086873). —A. Left half of the radula. —B. Second lateral teeth. —C. Detail of the vestigial tooth. —D. Detail of the penial spines.

to bursa copulatrix. Short duct connects seminal receptacle to vagina, after completing two loops, near bursa. Near middle of its length, it branches into uterine duct, entering albumen gland after short distance. Vagina shares common aperture within genital atrium with vaginal gland. Vaginal gland large, elongate, flattened, with muscular walls.

Remarks. Tambja verconis has been described three times before, the first time being the description of the holotype (Basedow & Hedley 1905), the second a limited account of a small specimen from the Victorian coast (Burn 1962) and finally a revision of the species based on specimens from New Zealand (Haagh 2002). This species is clearly distinguished from the other species of *Tambja* and usually it is well identified in the literature based in its coloration. Some other species of the genus also have dorsal spots, but all of them differ in the colour pattern. *Tambja morosa* (Bergh, 1877) has a few blue spots on the dark blue or black notum while *T. sagamiana* (Baba, 1955) has a higher number of yellow or orange spots surrounded by a ring of dark brown pigment on a blue notum. *Tambja gabrielae* (Pola, Cervera & Gosliner, 2005b) and *T. olivaria* (Yonow, 1994) also have yellow spots, but scattered on a dark green notum, while the 'painted' *Tambja* sp. and the 'lemon' *Tambja* sp. (see Coleman 1989, 2001; Marshall & Willan 1999) have yellow ground colour with and without black spots, respectively. *Tambja verconis* has also been reported from Japan (Nakano 2004), Korea and New Zealand (identified as *Tambja* cf. *verconis*) (http://www.seaslugforum.net/factsheet.cfm?base=tambcfve). Although these specimens resemble *T. verconis*, their colour is orange instead of yellow. Moreover, since *T. verconis* is usually found in Australia and New Zeland, the records from Japan are very far from its original distribution and we lack specimens in order to study their anatomy, they cannot be assigned to *T. verconis* with certainty at the moment. *Tambja verconis* has been reported feeding on the green, arborescent ectoproct *Bugula dentata* (see Debelius 1996; Coleman 2001; Miller & Haagh 2005).

Tambja amitina (Bergh, 1905)

Nembrotha amitina Bergh, 1905: pl. 17, figs 23–28.

Remarks. To date, the only available information about this species stems from the original description (Bergh 1905). *Tambja amitina* was described from a badly preserved specimen 15 mm in length. The radular formula is similar to that of other species of the genus and the kind of penial spines are characteristic of other species such as *T. morosa*, *T. sagamiana*, *T. verconis*, *T. olivaria* and *T. gabrielae*. However, the colour pattern of *T. amitina* differs from all of them. We have not found the holotype (at the Zoological Museum, University of Copenhagen).

Tambja capensis (Bergh, 1907) (Figs 1E, 3D and 6A–D)

Nembrotha capensis Bergh, 1907: p. 68, pl. xii, figs 8–17.

Material examined. Syntypes. Kalk Bay, South Africa 1907, 3 specs. 38, 42 & 67 mm, dissected, collected by R. Bergh (ZMUC-2087). Cape Province, False Bay, Buffles Bay, South Africa, December 1990, 2 specs. 30 mm preserved, dissected, collected by T. M. Gosliner (CASIZ 086873). Cape Province, South Africa, February 1991, 1 spec. 30 mm preserved, dissected, collected by T. M. Gosliner (CASIZ 075154). Strawberry Bay, Bakoven, Cape Town, South Africa, 24 February 2005, 3 specs. 22, 26 and 40 mm alive, 5 m depth, collected by G. Calado (MNCN 15.05/46686).

Distribution. Temperate waters around South Africa (Bergh 1907; Barnard 1927; Macnae 1958; Gosliner 1987; present study).

External morphology. Body firm, limaciform with long, pointed posterior end (Fig. 1E). Mantle margin reduced, indistinct. Preserved specimens up to 40 mm. Entire body surface textured with pattern of longitudinal wrinkles. Short, circular shaped oral tentacles with a depression at centre of each. Perfoliate rhinophores, bearing about 20 lamellae, retractile in sheaths. Five to seven tripinnate gill branches surrounding anal papilla, not elevated. Genital aperture on right side, midway between gill and rhinophores.

Anatomy. Anterior digestive tract begins with relative long, thin-walled muscular oral tube that continues into large buccal mass. A pair of large, wide, elongated salivary glands on buccal mass, flanking oesophagus. Labial cuticle forming strong, chitinous disk, without distinct armature but with folds in its internal edge. Radular formulae: 24 x 6.1.(1).1.(1).1.6 (CASIZ 075154) and 20 x 7-6.1. (1).1.(1).1.6-7 (CASIZ 086873, 2 specimens) (Fig. 6A). Rachidian teeth rectangular, without denticles and a slightly curved upper margin notched anterior. Second lateral teeth broad, elongate and large with two cusps; upper cusp bifid, with a small and blunt inner denticle and a larger and sharp outer edge (Fig. 6B). Outer lateral teeth roughly rectangular, decreasing in size towards outer margin. A small projection, between rachidian and second lateral teeth, is present (Fig. 6B). This structure is elongate and similar to a small tooth and we have therefore termed it a 'vestigial tooth' (Fig. 6C). Reproductive system triaulic (Fig. 3D). Female gland mass well developed. Remaining sexual organs lie over middle of female gland. Preampulatory duct long and narrow, expands into a wide 'S'-shaped ampulla, which divides into oviduct and vas deferens. From this point oviduct enters massive female gland via short duct. Deferent duct lacks a morphologically well-differentiated prostate, same diameter along its entire length. It has soft glandular walls that, *in situ*, skirt around the seminal receptacle. Deferent duct relatively elongate, coiled over it. Outer muscular vas deferens terminates in dilated penial section, where penis is located. Penis armed with small, hooked, chitinous spines (Fig. 6D). Seminal receptacle, smaller and more elongate than globular bursa copulatrix, with short duct that connects to vagina after making two loops, midway to bursa. A slender uterine duct leaves vagina and joins with oviduct. A small vaginal gland is present.

Remarks. *Tambja capensis* is apparently endemic to temperate waters of the Cape Province (Gosliner 1987). This species was described in the genus *Nembrotha* but placed in *Tambja* based on its radular characteristic (Burn 1967). Barnard (1927) and Macnae (1958) stated that *T. capensis* should be regarded as synonymous with *Tambja morosa* (Bergh, 1877). However, there are several external and internal differences, as well as their coloration (Gosliner 1987). *Tambja capensis* is characterized by having the dorsum covered with a pattern of longitudinal wrinkles and the colour is uniformly black or dark-blue with a blue-green marginal line. *Tambja capensis* shares a radular feature with another species of the genus, *T. amakusana*. Both species have a series of 'vestigial teeth' between the rachidian and the innermost lateral teeth, while the distribution, the coloration and the internal and external features of the two species are quite different. The presence of those small teeth might have important relevance to the phylogeny of the subfamily since most of the members of the family Polyceridae (*Polycera*, *Triopha*, *Kaloplocamus*, *Plocamopherus*, *Limacia*) have two inner lateral teeth while all other members of the Nembrothinae have only one. Thus, these 'vestigial teeth' could be the result of the reduction of the inner lateral teeth well developed in other members of the family. *Tambja capensis* has been reported feeding on arborescent bryozoans and has been found both in intertidal locales and at depths of at least 30 m (Gosliner 1987).

***Tambja limaciformis* (Eliot, 1908) (Figs 1F, 7A–H and 8A)**
Nembrotha limaciformis Eliot, 1908: 98.
Polycera tabescens Risbec, 1928: 202, pl. 5, fig. 9, text fig. 62.
Nembrotha tabescens (Risbec, 1928): 103, text fig. 62.

Material examined. Horseshoe Cliffs, Ryukyu Islands, Okinawa, Japan, 21 June 1992, 1 spec. 6 mm preserved, dissected, 3 m depth, collected by R. F. Bolland in mixed live/dead stony coral reef (CASIZ 087919). Moluccas, Banda Island, Karang Hatta, Indonesia, 15 November 1993, 5 specs. 10–14 mm alive, 3 dissected, 7–12 m depth, collected by Pauline Fiene (CASIZ 093964). Bunaken Island, North Sulawesi, Indonesia, 25 October 1993, 1 spec. 12 mm alive, dissected, collected by P. Fiene (CASIZ 097605). North coast: north of Madang, Papua New Guinea, 12 February 1988, 1 spec. 12 mm alive, 9 m depth, collected by G. Williamson (CASIZ 071199). North coast, North of Madang, Papua New Guinea, 11 February 1988, 2 specs. 6 mm alive, 30 m depth, collected by T. M. Gosliner (CASIZ 070434). Houtmans Abrolhos Islands, eastern group 'Gas Bottle', east side of Suomi Island, Western Australia, 22 July 2004, 2 specs. 23 mm alive, dissected, 10 m depth, collected by Fred Wells (WAM S13472). Houtmans Abrolhos Islands, north of Suomi Island, Western Australia, 23 July 2004, 1 spec. 20 mm alive, 3 m depth, collected by Marta Pola (WAM S13494). Kerama Islands, Okinawa, Japan, 7 May 2004, 1 spec. 5 mm preserved, collected by A. Ono (MNCN 15.05/46689).

Distribution. Red Sea (Eliot 1908; Debelius 1996), Japan (Coleman 2001; Ono 1999, 2004; Nakano 2004; present study),

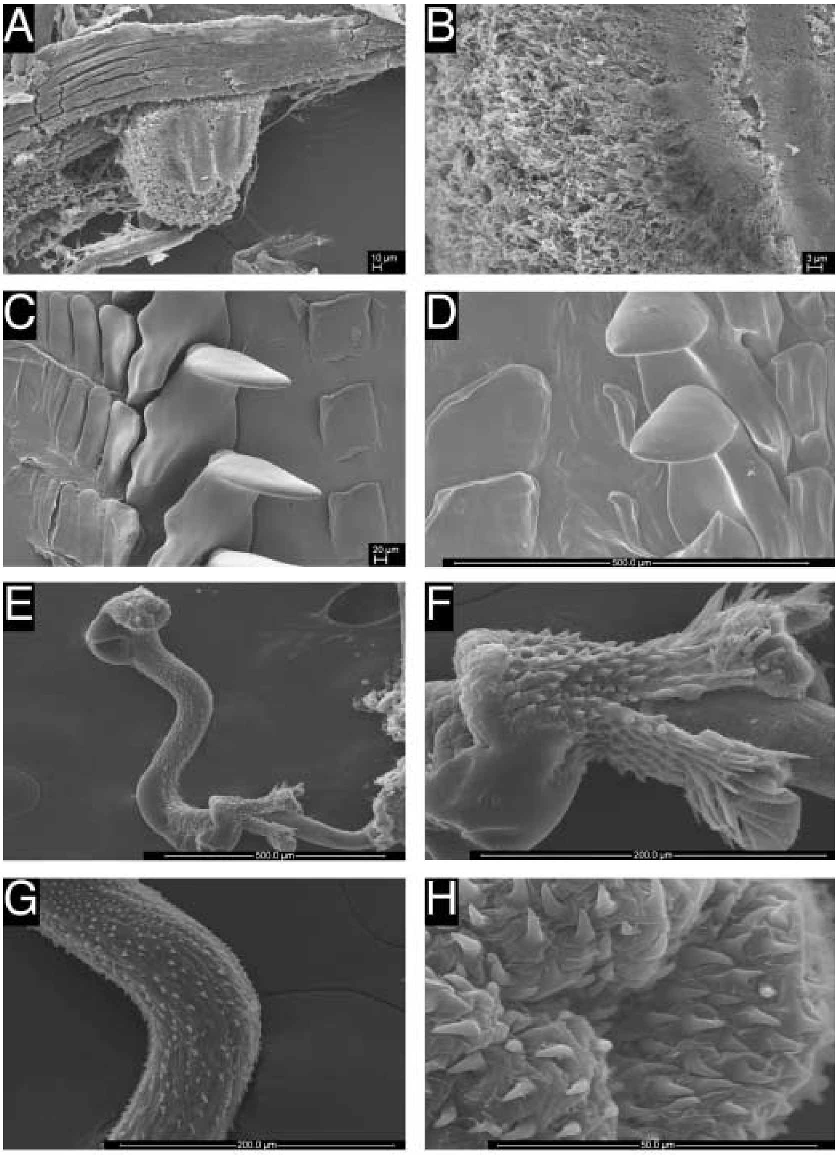

Fig. 7 A–H. Scanning electron micrographs of *Tambja limaciformis*. —A. Lateral pouch (CASIZ 097605). —B. Detail of the surface of the lateral pouch. —C. Left half of the radula (CASIZ 093919). —D. Detail of the vestigial tooth and the second lateral tooth. —E. Penis (WAM S13472). —F,G,H. Detail of the penial spines (WAM S13472).

Indonesia (present study), Papua New Guinea (present study), Philippines (http://www.vibrantsea.net/nudibranchs_taxonomy2.html), Mariana Islands (Carlson & Jo Hoff 2003), Hawaii (Fiene, pers. comm.), Western Australia (Wells & Bryce 1993; present study) and Heron Island (Marshall & Willan 1999).

External morphology (Fig. 1F). Eliot (1908) and Baba (1960) gave thorough external descriptions of this species. The specimens examined for the present study matched their descriptions and thus there is no additional information to present.

Anatomy. Anterior digestive tract begins with short, thick-walled muscular oral tube that continues into a large buccal mass. A pair of small, elongated pouches, at the junction of the oral tube and the buccal mass, is present in some specimens (Fig. 7A). These structures seem to open into the digestive system; they are innervated and with many muscles. At higher magnification, the surface of the pouches is covered with cilia (Fig. 7B). The function of these lateral pouches is still unknown. A pair of small, elongate and narrow salivary glands on buccal mass, flanking the oesophagus. Labial cuticle very weak and seems to be wrinkled along its internal edge. Radular formulae of six specimens are: 11 x 6.1.1.1.6 (CASIZ 087919); 11 x 5-6.1.1.1.6-5 (CASIZ 093964; 2 specimens), 12 x 6.1.1.1.6 (CASIZ 097605) and 12 x 6-7.1. (1).1.(1).1.6-7 (WAM S13472, WAM S13494) (Fig. 7C,D). Rachidian teeth subquadrate, without denticles and smooth upper margin. Innermost lateral

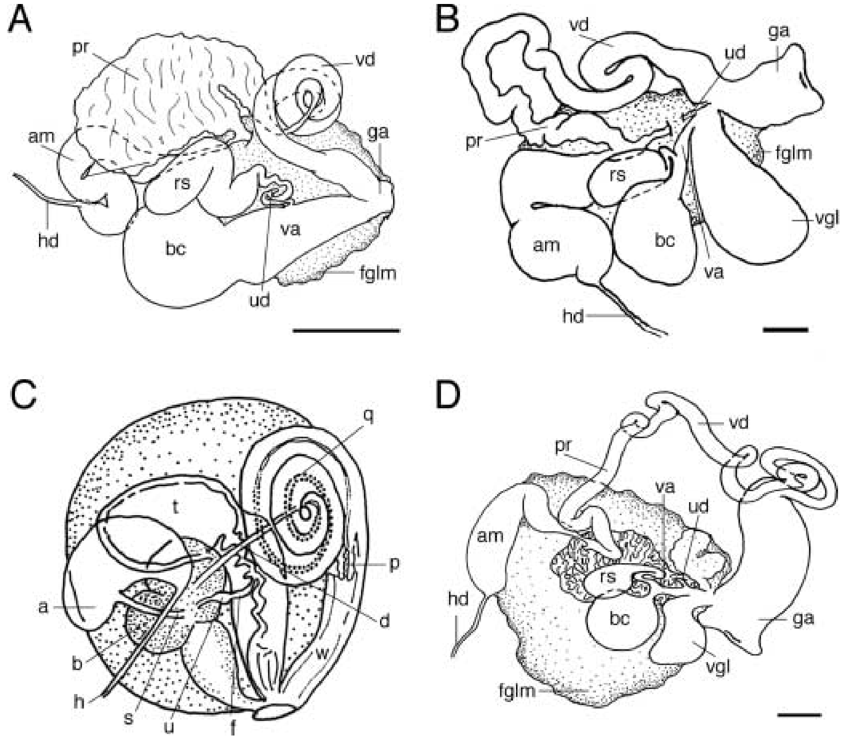

Fig. 8 A–D. Reproductive system of four *Tambja* species: —A. *T. limaciformis* (WAM S13472). —B. *T. sagamiana* (CASIZ 070198). —C. *T. divae* (modified from Marcus 1958; a, ampulla; b, albumen gland; d, male duct; f, fertilizing duct; h, hermaphrodite duct; p, penial papilla; q, prostatic part of male duct; s, spermoviduct; t, spermatheca; u, spermatocyst; v, vagina; w, male vestibule). —D. *T. eliora* (CASIZ 082117). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

teeth elongate and large with two cusps; upper cusp simply hamate, well developed, wide and sharp; outer cusp very small. A wide body joins both cusps. Outer lateral teeth roughly rectangular, decreasing in size towards the outer margin. In specimens from Abrolhos Islands, between the rachidian and second lateral tooth, and very difficult to find in some cases, a small vestigial tooth is present (Fig. 7D). A small blood gland is positioned above the intestinal loop. Reproductive system triaulic (Fig. 8A). Preampullary duct elongate and narrow expanding into a wide 'S'-shaped ampulla, which divides into short oviduct and vas deferens. From this point oviduct enters massive female gland via short duct; we were unable to see the uterine duct. Branch of vas deferens widens into a large, curved prostatic portion, having a dense network of interconnecting tubules over its surface. The vas deferens again narrows into a thin duct, which descends through the centre of the large and highly convoluted final portion of the vas deferens. *In situ*, the bursa is partially surrounded by the prostate. Towards the distal end of this muscular portion is the penis, which has three different kinds of spines (Fig. 7E): (1) basal spines elongated and sharp, covering just less than a quarter of the penis; (2) spines that are shorter, wider and higher in number than the basals, also covering a small part of the length of the penis (Fig. 7F); (3) distal spines that are very numerous, smaller, hooked and sharp (Fig. 7G,H). Bursa copulatrix large, rounded. Seminal receptacle elongated, wide and longer than the bursa copulatrix but in a specimen from Japan (CASIZ 087919) it is smaller. Seminal receptacle joins the proximal part of vagina via a thin, long, highly convoluted duct, with two well-differentiated loops. The elongate, wide vagina emerges from base of bursa and joins vas deferens near genital aperture. No vaginal gland.

Remarks. *Tambja limaciformis* is known from two small specimens from the Red Sea (Eliot 1908), three from Japan (Baba 1960) and two from Heron Island (Great Barrier Reef) (Marshall & Willan 1999). The external anatomy, coloration and radula described by the previous authors agree with those of our specimens, except for the presence of very inconspicuous rhinophoral sheaths, which have not been previously noticed. The reproductive system is described here for the first time. The presence of purple spots on the tips of the rhinophores and on the tips of the gill is distinctive in this species, although two other species from the Indo-Pacific and from the Caribbean, *T. amakusana* Baba, 1987 and *T. oliva* Meyer, 1977, also have the rhinophores and gill tipped in purple or dark blue. Baba (1960) used this feature to distinguish *T. limaciformis* from *T. divae* (Marcus, 1958), a similar species described from Brazil. *Tambja limaciformis* also resembles *T. amakusana* in its small size and in several internal features. Both species appear to have lateral pouches at the junction of the oral tube and the buccal mass and 'vestigial teeth' in the radula, two quite peculiar features found only in a few species of the genus (present study). The inner lateral teeth have a simple inner cusp. *Tambja*

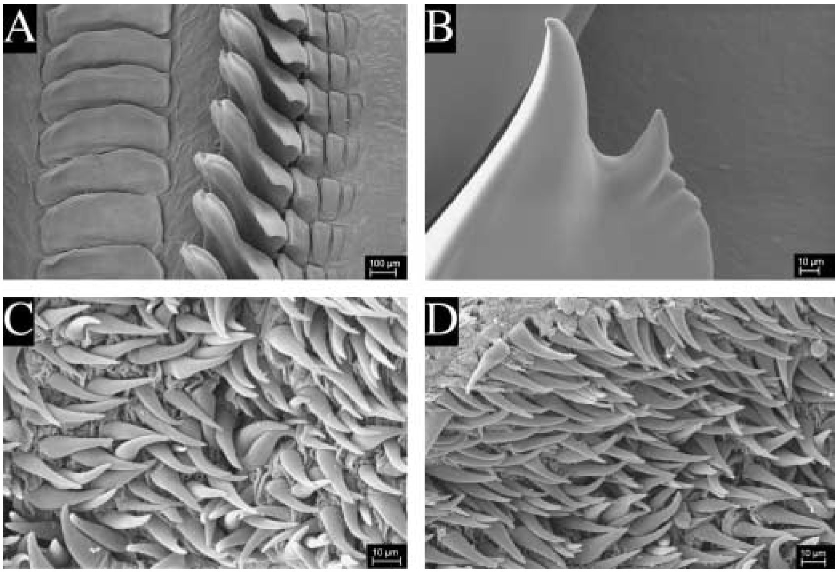

Fig. 9 A–D. Scanning electron micrographs of *Tambja sagamiana*. —A. Right half of the radula (CASIZ 070198). —B. Detail of the inner cusp of the innermost lateral teeth (CASIZ 115757). —C,D. Detail of the penial spines (CASIZ 070198).

abdere and *T. amakusana* also share several features of the reproductive system. Both species lack a vaginal gland and have a well-differentiated morphological prostate. An elongate, straight, wide vagina is present in *T. amakusana*, while a very long and coiled vagina is typical of *T. abdere*. Nevertheless, there are also several important differences between the species compared here. *T. limaciformis* is saffron red with small yellowish to white dots scattered on the notum while *T. oliva* and *T. amakusana* are yellowish green. Both *T. limaciformis* and *T. amakusana* have the second innermost lateral teeth with simple upper cusps; they are elongate and sharp in *T. limaciformis* and wide and blunt in *T. amakusana*. With regard to the reproductive system, *T. limaciformis* has three different kinds of penial spines while *T. amakusana* and *T. oliva* have only one.

***Tambja sagamiana* (Baba, 1955) (Figs 1G–H, 8B and 9A–D)**
Nembrotha sagamiana Baba, 1955: 16, pl. 5, fig. 15.

Material examined. Seragaki, Ryukyu Islands, Okinawa, Japan, 15 February 1997, 1 spec. 88 mm alive, dissected, 56 m depth, collected by R. Bolland (CASIZ 115757). Ryukyu Islands, Okinawa, Japan, 21 March 1987, 1 spec. 48 mm preserved, dissected, 56 m depth, collected by R. Bolland (CASIZ 070198). Amuro Island, Kerama Islands, Japan, 6 March 2003, 1 spec. 15 mm preserved, collected by A. Ono (MNCN 15.05/46657).

Distribution. Japan (Baba 1955; Ono 1999, 2004; Suzuki 2000; Coleman 2001) and Taiwan (Garthwaite 2003).

External morphology. Body elongate, limaciform, with long, pointed posterior end (Fig. 1G). Living animals reach up to 130 mm. Body smooth with large disconnected tubercles arranged indistinctly on notum and sides of body. Tubercles are smaller and more numerous at end of foot. Frontal veil reduced to a wide ridge. Perfoliate rhinophores (approx. 55 lamellae), retractile in high, conical sheaths. Three large, non-retractile, tripinnate gill branches arranged in semicircle around conical anal papilla. Lateral gill branches deeply bifurcated. Oral tentacles small, dorsoventrally flattened with horizontal groove. Genital pore on right side, midway between rhinophores and gill. Raised oval lamellated structures (Fig. 1H), on sides of body, between rhinophores and oral tentacles, which in preserved specimens are visible as longitudinal slots with a thickened edge.

Anatomy. Buccal mass shorter than oral tube. A pair of elongate, wide, granular salivary glands on buccal mass, flanking the oesophagus. Chitinous labial cuticle, lacking denticles. Radular formulae of two specimens: 20 x 3.1.1.1.3 (CASIZ 115757) and 26 x 3.1.1.1.3 (CASIZ 070198) (Fig. 9A,B). Rachidian teeth rectangular, much wider than tall, without denticles, notched anterior edge. Inner lateral teeth much larger than outer ones, with two well-developed cusps; inner cusp bifid, with two sharp denticles, usually the outer one a little bit longer with inner edge of upper cusp serrated (Fig. 9B), outer cusp well developed and rectangular in shape. Outer lateral teeth plate-like, lacking cusps and decreasing in size towards the outer margin. Reproductive system triaulic (Fig. 8B). Preampullatory duct elongate and narrow expanding into a large and thick-walled 'S'-shaped ampulla, which divides into spermoviduct and vas deferens. Prostate gland small, slightly morphologically differentiated, with soft glandular walls, confined to a coiled section of elongate vas deferens. Penis located within distal end of muscular portion of vas deferens, armed with numerous, unordered and elongate penial spines (Fig. 9C,D). Vaginal duct short, usually straight, connecting to large, round bursa copulatrix. Seminal receptacle pyriform, smaller than bursa copulatrix. A short duct connects seminal receptacle to vagina after completing two loops, half way to bursa. A slender uterine duct leaves vagina from distal position and joins with female gland. A large, thick-walled, well-developed vaginal gland opens to same aperture of vagina. Female gland also well developed.

Remarks. *Nembrotha sagamiana* was described from Japan by Baba (1955). Burn (1967) placed it within *Tambja* based on characteristics of the radular morphology. Previously, the only available information about this species stemmed from the original description. The reproductive system is described for the first time in this paper. *Tambja sagamiana* differs from three other species of the genus — *T. morosa* (Bergh, 1877), *T. verconis* (Burn, 1862) and *T. gabrielae* Pola, Cervera & Gosliner, 2005 — in having spots irregularly scattered, but the colour pattern is different in all cases. The latter three species, plus *T. olivaria* Yonow, 1994, share some other external and internal features: presence of 'lateral slots' of unknown function, penis armed with very numerous, unordered and elongate spines and inner cusp of the innermost lateral teeth bifid. The inner edge of the upper cusp is serrated in *T. sagamiana* but smooth in *T. morosa*, *T. verconis*, *T. gabrielae* and *T. olivaria*. Moreover, to date *T. sagamiana* has only been found in the waters of Japan and Taiwan.

Tambja divae **(Marcus, 1958)**

Nembrotha divae Marcus, 1958

Distribution. Cabo Frio, Brazil.

Remarks. *Tambja divae* has not been recorded since Marcus (1958), who described it from a single colourless preserved specimen about 12 mm long. Thus, the only available information about this species stems from the original description. Reproductive system is shown in Fig. 8C.

Tambja divae was the only nembrothid known from Brazil until two years ago when an undescribed species of *Roboastra* was reported from the same place (Krause 2003). Moreover, a new species of *Tambja*, *T. stegosauriformis*, also from Brazil, has been recently described (Pola *et al*. 2005c). The reproductive system of *T. divae* resembles that of *T. amakusana* and *T. limaciformis* (present study) in having an elongate, straight, wide vagina and lacking a vaginal gland. Nevertheless, the prostate of *T. divae* is slightly morphologically differentiated from the rest of the vas deferens, while in *T. amakusana* and *T. limaciformis* there is a prostatic portion constituted by a dense network of interconnecting tubules over its surface. *Tambja limaciformis* has a similar, not identical, colour pattern to *T. divae*. Marcus (1958) differentiated both species by the rachidian tooth of the radula, which 'is reflexed and bifid or indistinctly jagged'.

Tambja eliora **(Marcus & Marcus, 1967) (Figs 8D, 10A and 11A,B)**

Nembrotha eliora Marcus & Marcus, 1967: 194, figs 57, 58.
Nembrotha hubbsi Lance, 1968: pp. 6–8, pl. 1, fig. 6.

Material examined. Isla San Diego, Baja California, Mexico, April 1974, 6 specs. 20–30 mm preserved, 5 dissected, 5–13 m depth, collected by E. Janss (LACM 34797). Bahía Tortugas, Los Morros, Baja California Sur, Mexico, 01 July 1984, 1 spec. 37 mm preserved, dissected, 3–5 m depth, collected by Bertsch, Catania, Syoc, Ghiselin & Klontz (CASIZ 071536). Isla San Esteban, Sonora, Gulf of California, Mexico, 16 April 1985, 1 spec. 25 mm preserved, dissected, 12 m depth, collected by L. Dunne (CASIZ 074506). South end of Los Fragiles Bay, Gulf of California, Mexico, 01 April 1976, 2 specs. 25 mm preserved, dissected, 9 m depth, collected by B. Markham (CASIZ 082117). South end of Bahia de Los Angeles, Baja California Norte, Gulf of California, Mexico, 05 October 1984, 2 specs. 15 mm preserved, dissected, 2–8 m depth, collected by R. V. Syoc (CASIZ 057324). Playa Tamarindo, Guanacaste, Costa Rica, 12 January 2001, 3 specs., subtidal collected by J. Magana (INBIO 0003118103). Isla Catalina, Guanacaste, Costa Rica, 23 January 2001, 2 specs., subtidal, dissected, collected by S. Avila (INBIO 0003118036). La Abnegada, Cabo San Lucas, Baja California Sur, 10 March 1996, 1 spec. 20 mm preserved, 15 m depth, collected by M. Costez (MNCN 15.05/46663). Los Islotes, Baja California Sur, 20 March 1997, 1 spec. 15 mm preserved, subtidal, collected by O. Angulo (MNCN 15.05/46664). Los Islotes, Baja California Sur, 28 June 2003, 1 spec. 35 mm preserved, dissected, 9 m depth, collected by O. Angulo (MNCN 15.05/46665). Roca Suani, Baja California Sur, 29 July 2003, 3 specs. 25–30 mm preserved, dissected, 5 m depth, collected by O. Angulo (MNCN 15.05/46666).

Distribution. Gulf of California (Marcus & Marcus 1967; Farmer 1978; Kerstich 1989; Behrens 1991), Costa Rica (present study; Ajtai 2002; www.inbio.ac.cr, www.medslugs.de) and Ecuador (Luna 2003).

External and internal anatomy. Thorough descriptions provided by Marcus & Marcus (1967) and Farmer (1978). The specimens examined for the present study match their descriptions, although we are able to provide a few more details: ridged structures or 'lateral slots' (Yonow 1994; Pola *et al*. 2005b,c; present study) below rhinophores in some specimens, appearing as a dark groove along the side of the head (function unknown but heavily innervated); a pair of small elongated pouches at junction of buccal mass and oral tube in some specimens. (function

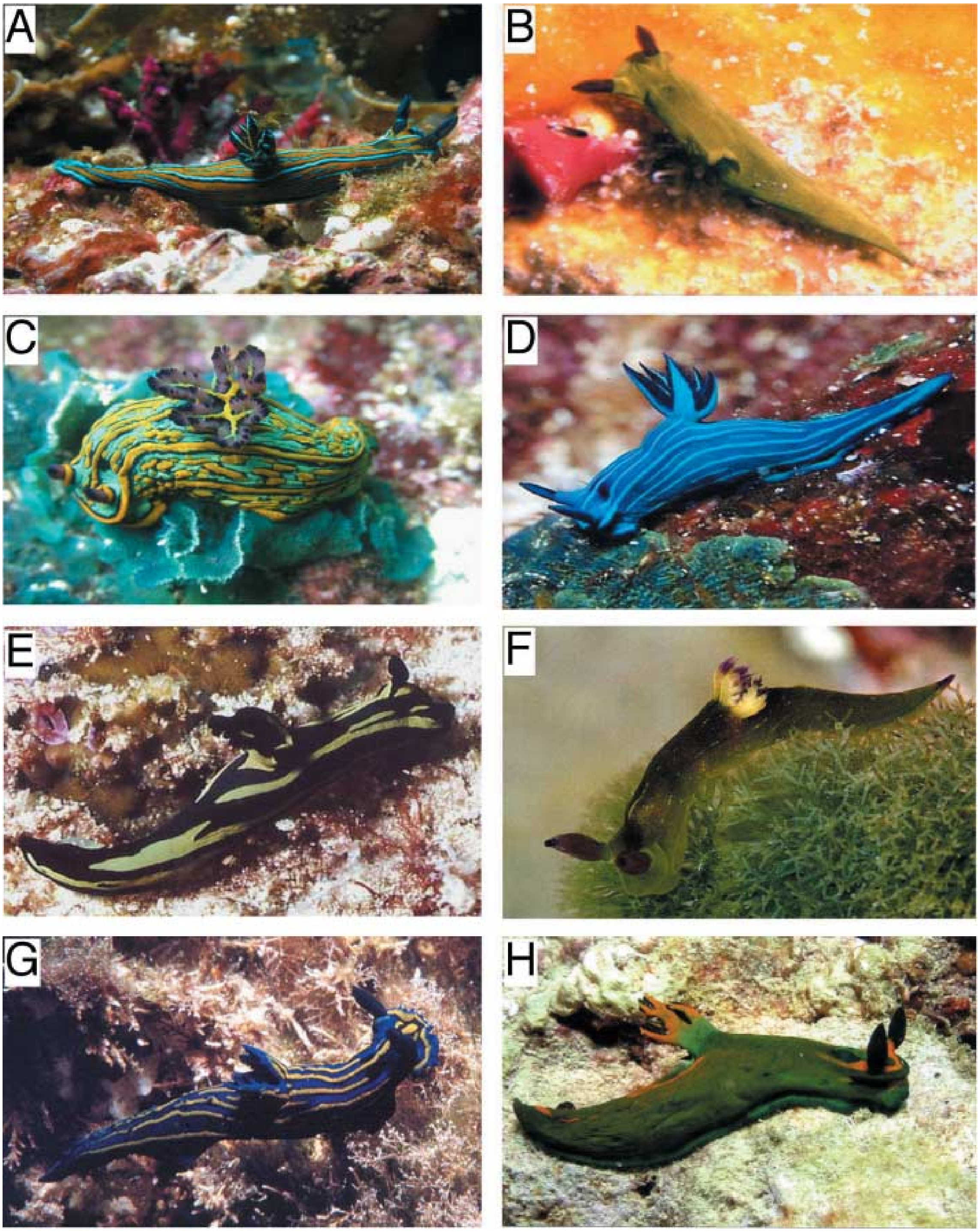

Fig. 10 A–H. Photographs of the living animals: —A. *Tambja eliora*, specimen from Jalisco, Baja California (photo: Alicia Hermosillo). —B. *Tambja oliva*, specimen from the Bahamas (photo: Jack Worsfold). —C. *Tambja abdere*, specimen from Jalisco, Baja California. (photo: Alicia Hermosillo). —D. *Tambja mullineri*, specimen from North Seymour Island, Galápagos Island (photo: Patricia Dilworth). —E. *Tambja fantasmalis*, specimen from Sal Island, Cape Verde (photo: Gerard Breton). —F. *Tambja amakusana*, specimen from Kerama Islands (photo: A. Ono). —G. *Tambja ceutae*, specimen from Azores, Portugal (photo: Peter Wirtz). —H. *Tambja olivaria*, specimen from Malapascua Island, Philippines (photo: Erwin Köhler).

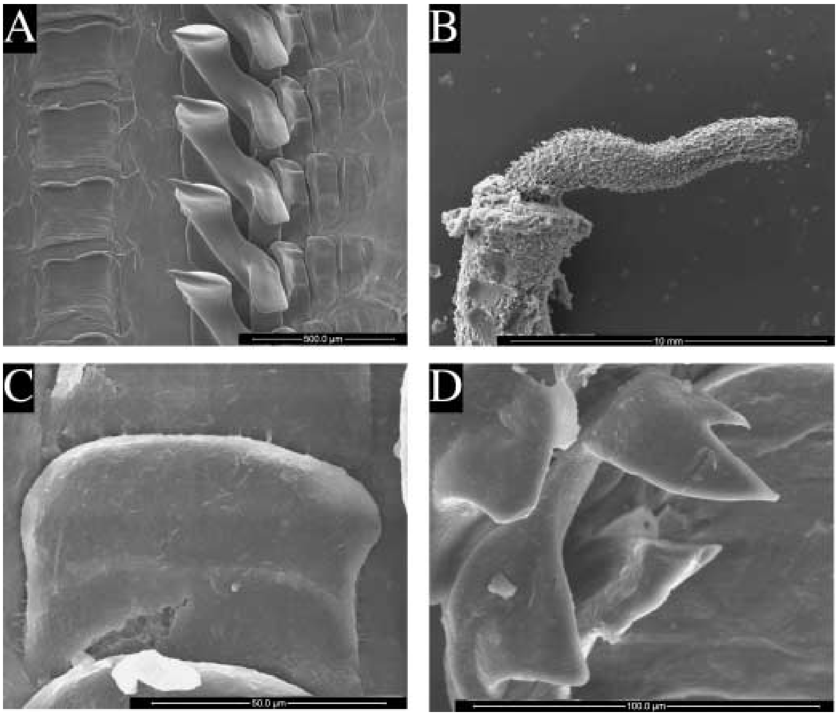

Fig. 11 A–D. Scanning electron micrographs of *Tambja eliora* and *Tambja oliva*. —A,B. *T. eliora* (MNCN 15.05/46665). —A. Right half of the radula. —B. Penis. —C,D. *T. oliva* (INBIO00003348523). —C. Rachidian tooth. —D. Innermost lateral teeth.

remains unknown); radular formulae of preserved specimens are: 16 x 4.1.1.1.4 (three specimens 28–30 mm and one specimen 22 mm), 15 x 4.1.1.1.4 (25 mm) and 13 x 5-4.1.1.1.4-5 (15 mm). See Figs 10A, 11A,B and 8D for pictures of living animal, radula, penis and reproductive system, respectively.

Remarks. Tambja eliora was described by Marcus & Marcus (1967) from Pacific Mexico. The authors included figures showing the living slug from a colour photograph and a half-row of the radula. Two weeks after the original Marcus & Marcus *eliora* paper, Lance published an article in which he named the species *Nembrotha hubbsi*. Although the picture and the external morphology described by Lance (1968) were in agreement with Marcus & Marcus (1967) the radula illustrated was of a *Roboastra*. Since the type of *N. hubbsi* is an intact specimen (CASIZ type series no. 315) the confusion was probably that the illustrated radula corresponded to another specimen of the similar species, *Roboastra tigris*.

Two other valid species of the genus are present in the eastern Pacific: *T. abdere* Farmer, 1978 and *T. mullineri* Farmer, 1978. *Tambja abdere* differs from *T. eliora* in the colour pattern and also in features of the reproductive system. The basic body coloration of *T. abdere* is turquoise, with mottled patches of yellowish and bluish ochre splattered throughout and separated by black lines, while in *T. eliora* the colour of the body varies from yellow-ochre to brown-grey, with a series of longitudinal distinctive turquoise-blue bands margined with a thin black line. With respect to the reproductive system, *T. abdere* has a very long and coiled vas deferens with a morphological differentiated prostate and a bilobed bursa copulatrix; the vaginal gland is absent. *Tambja eliora* has a shorter vas deferens without a morphological differentiated prostate and a rounded bursa copulatrix; the vaginal gland is well developed. *Tambja mullineri* is very similar to *T. eliora* in the external pattern and internal features, but in *T. mullineri* the colour of the body is patterned with alternating turquoise-blue and dark blue stripes bordered with black lines. *Tambja eliora* has also been reported from Costa Rica and Ecuador, but in those specimens the turquoise bands are broken into a series of spots which are joined by a black line. *Tambja eliora* grazes on Ectoprocta and this species has been the object of several chemical studies (Carté & Faulkner 1983, 1986).

Tambja oliva Meyer, 1977 (Figs 10B and 11C,D)

Tambja oliva Meyer, 1977: 302, figs 1, 2.

Material examined. Paratype. Galeta Point, Canal Zone, Panama, 9 September 1973, 1 spec. 7 mm preserved, examined, 11 m depth, collected by K. B. Meyer (USNM 76021). Manzanillo, Limón, Costa Rica, 12 October 2000, 1 spec. 3 mm preserved, dissected, 25 m depth, collected by A. Berrocal (INB0003348523).

Distribution. Caribbean coast of the Panama Canal Zone, Costa Rica (Espinosa & Ortea 2001) and Bahamas (Schick & Cervera 1998).

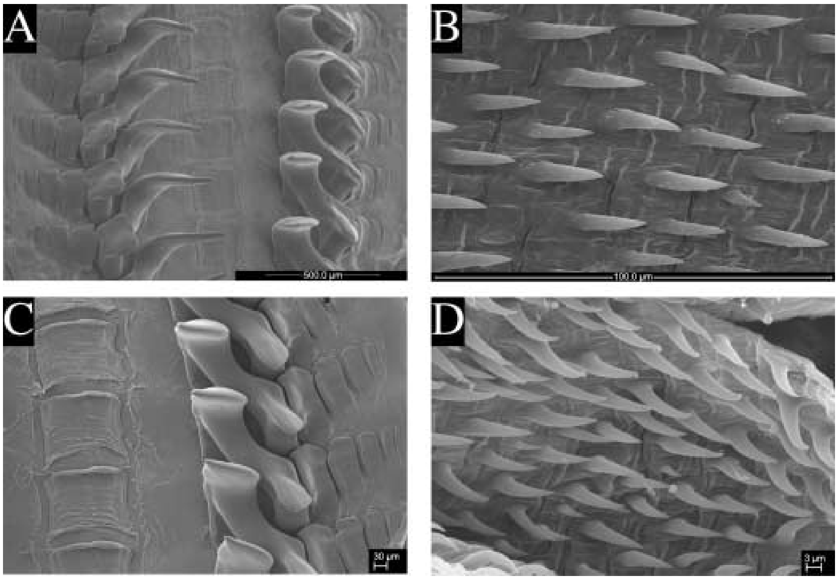

Fig. 12 A–D. Scanning electron micrographs of *Tambja abdere* and *Tambja mullineri*. —A. *T. abdere*. Left half of the radula (MNCN 15.05/46659). —B. *T. abdere*. Detail of the penial spines (LACM 34799). —C,D. *T. mullineri* (CASIZ 067100). —C. Right half of the radula. —D. Detail of the penial spines.

External and internal anatomy. Thorough descriptions provided by Meyer (1977). The specimens examined for the present study matched the descriptions and thus there is no additional information to present. Our specimen was not useful for describing the reproductive system owing to its immaturity. See Figs 10B and 11C,D for pictures of the living animal and radula.

Remarks. The holotype and the remaining specimens of the type series appear to be lost, but we were able to examine the external morphology and the radula slide of one paratype. *Tambja oliva* resembles the Indo-Pacific *T. amakusana* in several features, including the small and general greenish colour of the body. Although Baba (1987) stated that both species are similar in their radular morphology, they differ from each other in details of the radula. The rachidian teeth of *T. amakusana* are notched at the upper margin while in *T. oliva* this upper margin is smooth and rounded. The inner lateral tooth of *T. amakusa* has a simple, wide inner cusp while in *T. oliva* it is bifid. Moreover, in *T. amakusana*, between the rachidian tooth and the innermost lateral tooth, a small but elongate projection very similar to a small tooth is present (present study). The reproductive system of both species is also different since the prostate of *T. amakusana* is morphologically well differentiated from the vas deferens, the vagina is very wide and the vaginal gland is absent.

***Tambja abdere* Farmer, 1978 (Figs 10C, 12A,B and 13A)**
Tambja abdere Farmer, 1978: 377, figs 4–6.
Tambja fusca Farmer, 1978: 378, figs 7–9.

Distribution. Pacific coast of Mexico (Farmer 1978; Kerstich 1989; Behrens 1991; Debelius 1996) and Costa Rica (Ajtai 2002; Pola *et al*. 2006).

External and internal anatomy. Recently described in detail and figured by Pola *et al.* (2006). No additional specimens have been examined for the present study. The radular formula is 14–16 x 4.1.1.1.4. See Figs 10C, 12A,B and 13A for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. Farmer (1978) described *Tambja abdere* and *T. fusca* as distinct species based on the latter's relatively darker coloration and more robust first lateral tooth. Pola *et al.* (2006) synonymized both species based on morphological and molecular studies. The reproductive system of *T. abdere* is very characteristic, with a very large and convoluted vas deferens, a well-differentiated prostate, bursa copulatrix with two different portions and a very long and convoluted duct that joins the seminal receptacle and the bursa copulatrix (Fig. 13A).

***Tambja mullineri* Farmer, 1978 (Figs 10D, 12C,D and 13B)**
Tambja mullineri Farmer, 1978: 379, figs 10–12.

Material examined. North Seymour Island, Galápagos Islands, Ecuador, 13 August 1998, 2 specs. 8 mm preserved, one dissected, 15 m depth, collected by K. Kaiser (CASIZ 067100). Isla Darwin, Galápagos Islands, Ecuador, May 1994, 2 specs. 18 mm preserved, one dissected, 18 m depth, collected by T. M. Gosliner (CASIZ 097551). Isla Isabela, Galápagos Islands, Ecuador, May 1994, 2 specs. 8 mm preserved, dissected, 23 m depth, collected by T. M. Gosliner (CASIZ 097573).

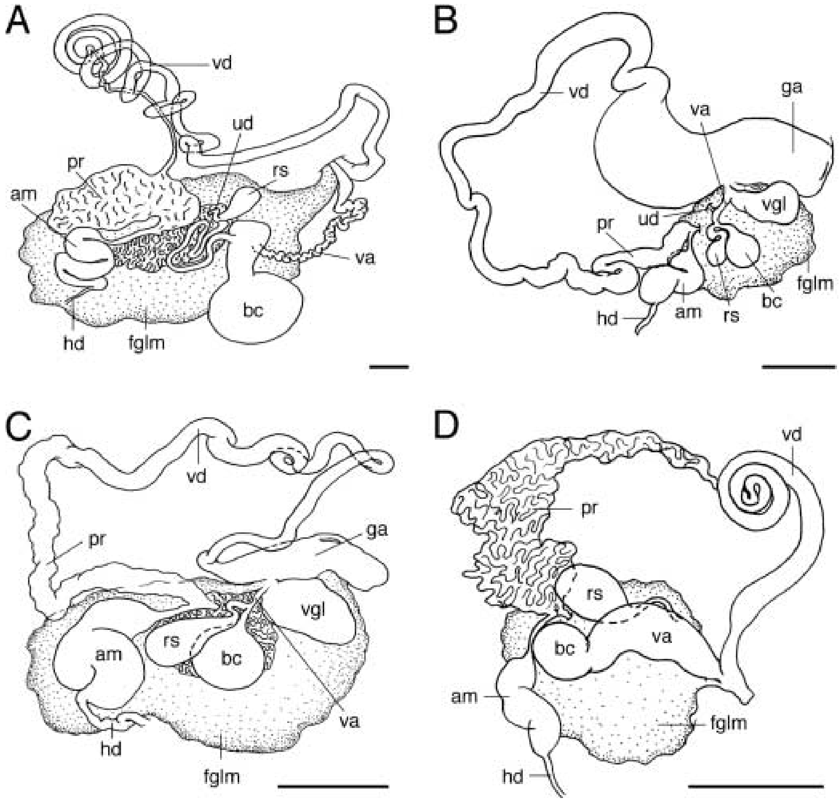

Fig. 13 A–D. Reproductive system of four *Tambja* species: —A. *T. abdere* (CASIZ MNCN15.05/46659, reproduced from Pola *et al*. 2006. Annales Zoologici Fennici, vol. 43, pp. 52–64). —B. *T. mullineri* (CASIZ 097573). —C. *T. fantasmalis* (MNCN 15.05/ 46671). —D. *T. amakusana* (CASIZ 071147). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

Distribution. Galápagos Islands (Farmer 1978; Gosliner 1991; Debelius 1996; Hickman & Finet 1999).

External and internal anatomy. Thorough descriptions provided by Farmer (1978) and Gosliner (1991). Additional information provided by our dissected specimens includes a pair of very large, wide salivary glands on buccal mass, flanking the oesophagus. In CASIZ 097551 there was a pair of elongated pouches at the junction of the buccal mass and oral tube; these structures of unknown function seem to be lamellate and open into the digestive system. Radular formula of three specimens: 15 x 5-4.1.1.1.4-5. See Figs 10D, 12C,D and 13B for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. Tambja mullineri appears to be endemic to the Galápagos Islands (Farmer 1978; Gosliner 1991; Debelius 1996; Hickman & Finet 1999). There are two other species of the genus described from the eastern Pacific: *T. eliora* (Marcus & Marcus 1967) and *T. abdere* (Farmer 1978). *Tambja mullineri* is very different from *T. abdere* in several external and internal features (Pola *et al*. 2006) while it is quite similar in appearance to *T. eliora*. However, in *T. eliora*, the morphology of the head is very characteristic, with the frontal edge dipping into a 'V' or 'U' shape and the colour pattern is orange-brown with several turquoise bands, which are bordered by a black line.

Tambja fantasmalis Ortea & García-Gómez, 1986 (Figs 10E, 13C and 14A–D)

Tambja fantasmalis Ortea & García-Gómez, 1986: 1, fig. 1.

Material examined. Boavista Island, Cape Verde Archipelago, May 1986, 1 spec. 25 mm preserved, 5 m depth, collected by P. Wirtz (MNCN 15.05/46667). Santo Antao Island, Cape Verde Archipelago, 28 July 2002, 3 specs. 30 mm preserved, dissected, 38 m depth, collected on rocks by M. Malaquias (CASIZ 166062). Baía das Gatas, Boavista Island, Cape Verde Archipelago, 01 August 2002, 3 specs. 10–20 mm preserved, dissected, 9 m depth, collected on rocks by M. Malaquias (CASIZ 166064). Baía do Porto Ferreira, Boavista Island, Cape Verde Archipelago, 04 August 2002, 3 specs. 35 mm preserved, dissected, 2 m depth, collected on rocks by M. Malaquias (CASIZ 166065). Santo Antao Island, Cape Verde Archipelago, 27 July 2002, 3 specs. 25–30 mm preserved, 36 m depth, collected on rocks by M. Malaquias (MNCN 15.05/46668). Santo Antao Island, Cape Verde Archipelago, 28 July 2002, 4 specs. 20, 30, 30 & 35 mm preserved, 36 m depth, collected on rocks by M. Malaquias (MNCN 15.05/ 46669). Baía das Gatas, Boavista Island, Cape Verde Archipelago, 01 August 2002, 3 specs. 10–15 mm preserved, 9 m depth, collected on rocks by M. Malaquias (MNCN 15.05/ 46670). Santo Antao Island, Cape Verde Archipelago, 28 July

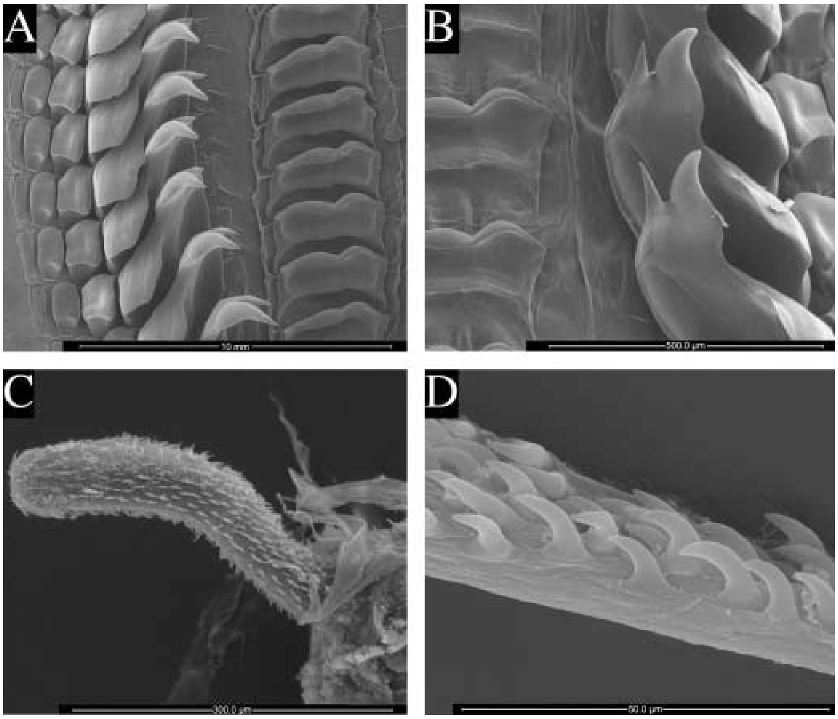

Fig. 14 A–D. Scanning electron micrographs of *Tambja fantasmalis* (MNCN 15.05/46671). —A. Left half of the radula. —B. Innermost lateral teeth. —C,D. Penis and detail of the penial spines.

2002, 3 specs. 30, 30 & 35 mm preserved, 38 m depth, collected on rocks by M. Malaquias (MNCN 15.05/46671). Sal Island, Cape Verde Archipelago, September 2003, 1 spec. 15 mm preserved, 15 m depth, collected from a step wall by P. Wirtz (MNCN 15.05/46672).

Distribution. Cape Verde Archipelago (Ortea & García-Gómez 1986; Wirtz & Debelius 2003).

External and internal anatomy. Described and figured by Ortea & García-Gómez (1986). The specimens examined for the present study matched their description and thus there is no additional information to present. Radular formulae of five specimens: 20-21 x 3-4.1.1.1.4-3. See Figs 10E, 13C and 14A–D for pictures of the living animal, reproductive system, radula and penis, respectively.

Remarks. *Tambja fantasmalis* Ortea & García-Gómez, 1986 was the first species of the genus recorded from the eastern Atlantic. Since its discovery, four new species have also been reported from the eastern Atlantic: *T. ceutae* García-Gómez & Ortea, 1988, *T. anayana* Ortea, 1989, *T. marbellensis* Schick & Cervera, 1998 and *T. simplex* Ortea & Moro 1998). Schick & Cervera (1998) presented a comparative table of these species (except *T. simplex*) and included the rest of the western Atlantic species of the genus. To date, *T. anayana* and *T. simplex* have also been recorded only from Cape Verde Archipelago. Ocaña *et al*. (2004) used the specimens of *T. simplex* from the original description to study the ontogenetic radular variation in species of *Tambja* from the eastern Atlantic Ocean and the Mediterranean Sea. *Tambja fantasmalis* is easily distinguishable from the rest of the species of the genus by its coloration and pattern of lines. This species lives on the rocky coasts of the Cape Verde Islands, down to at least 15 m depth (Wirtz & Debelius 2003). Colour photographs of this species are shown in Wirtz & Debelius (2003), www.medslugs.de and www.seaslugforum.net.

***Tambja amakusana* Baba, 1987 (Figs 10F, 13D and 15A–F).**
Tambja amakusana Baba, 1987: 13.

Material examined. North coast, near Madang, Barracuda Point, Papua New Guinea, 07 February 1988, 3 specs. 5–7 mm preserved, 2 dissected, 8 m depth, collected by T. M. Gosliner and M. Jebb. Note: colour in life is green (CASIZ 070427). North coast, near Madang, Barracuda Point, Papua New Guinea, 29 January 1988, 1 spec. 12 mm preserved, dissected, 14 m depth, collected by T. M. Gosliner (CASIZ 071147). Seragaky Tombs, Ryukyu Islands, Okinawa, Japan, 13 June 1993, 1 spec. 18 mm alive, dissected, 6 m depth, collected by R. F. Bolland (CASIZ 088490). North coast, near Madang, Rash Passage, Papua New Guinea, 09 June 1992, 2 specs. 7 mm preserved, one dissected, 43 m depth, collected by T. M. Gosliner (CASIZ 086389). Dave's cave, Long Reef, Louisiade Archipelago, Solomon Sea, Papua New Guinea, 05 June 1998, 1 spec. 6 mm preserved, dissected, subtidal to

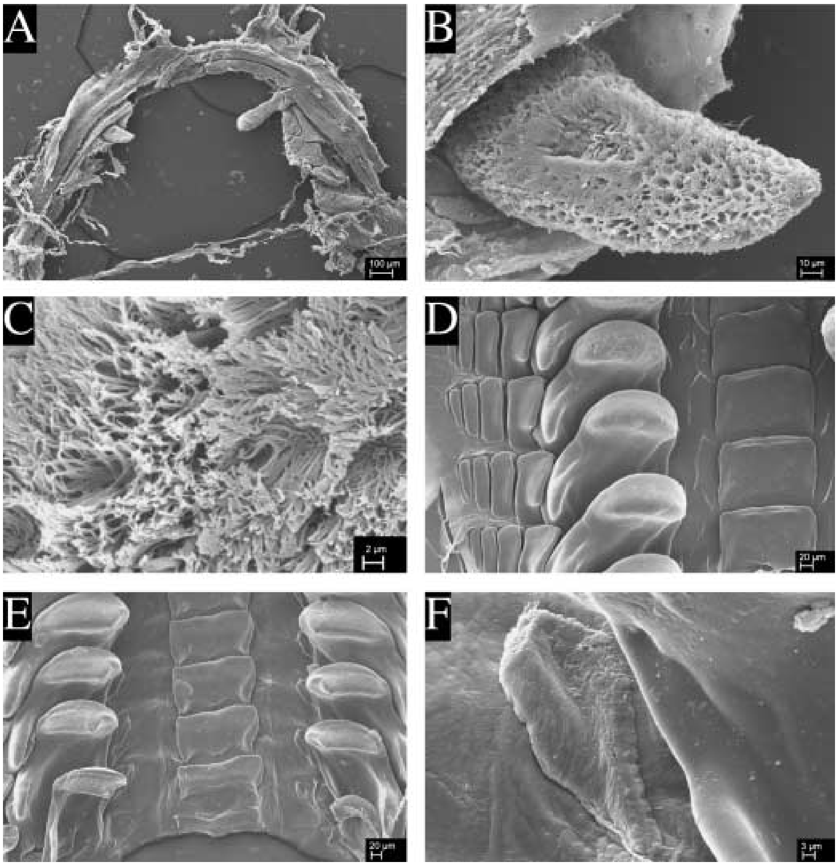

Fig. 15 A–F. Scanning electron micrographs of *Tambja amakusana*. —A–C. Lateral pouches (CASIZ 071147). —A. Lateral pouches on the oral tube. —B. Detail of the lateral pouch of the right side. —C. Detail of the surface of a lateral pouch. —D. Left half of the radula (CASIZ 070427). —E. Vestigial teeth and second lateral teeth (CASIZ 088490). —F. Detail of the vestigial tooth (CASIZ 088490).

33 m depth, collected by T. M. Gosliner (CASIZ 113663). Kerama Island, Okinawa, Japan, 10 April 2004, 3 specs. 4, 4 & 6 mm preserved, one dissected, collected by A. Ono (MNCN 15.05/46660).

Distribution. Japan (Baba 1987; Suzuki 2000; Ono 1999, 2004), Great Barrier Reef (Marshall & Willan 1999) and Papua New Guinea (present study).

External morphology. Body very small, elongate, limaciform with long and pointed posterior end of foot. Mantle smooth, reduced, with few indistinct tubercles on mantle edge on each side. Preserved specimens up to 12 mm long. Living animals (Fig. 10F) measure over 18 mm. Ground colour uniformly yellowish green with or without any trace of whitish spots. A pair of short, perfoliate rhinophores (with approx. 15–20 lamellae), retractile in elevated sheaths. Oral tentacles are thin flat lobes. 3–5 short, tripinnate nonretractile gill branches form a semicircle around the anal papilla, not elevated. Rhinophores, rhinophoral sheaths, oral tentacles and outer and inner branchial rachises, yellowish green; tips of rhinophores, branchial plumes and tail deep blue or purple. In some specimens, the whole rhinophore, rather than just the tip, is dark blue. Genital pore opens on right side, midway between gill and rhinophores.

Anatomy. Anterior digestive tract begins with a short thick-walled muscular oral tube that continues into a large buccal mass. Pair of small and elongated pouches at the junction of the oral tube and buccal mass (Fig. 15A). These structures seem to open into the digestive system; they are innervated and have many muscles. Under higher magnification, the surface of the pouches appears covered with cilia (Fig. 15B,C). Their function is still unknown. A pair of elongate but small and narrow, granulated salivary glands, on buccal mass, flank the oesophagus. Chitinous labial cuticle well developed, lacking denticles, appearing wrinkled in its internal edge. Radular formulae of five specimens: 13 x 5.1.(1).1.(1).1.5 (Fig. 15D). Rachidian teeth broad, nearly quadrangular in shape, without denticles and smooth or slightly notched at anterior edge. Second lateral teeth much larger than outer ones, having bifid upper cusp, with an elongate, wide and blunt terminal denticle and a very small inner one. Basal cusp shorter. A very wide body joins both cusps (Fig. 15D,E). Outer lateral teeth roughly rectangular, decreasing in size towards outer margin.

In all the specimens examined, a small projection, between the rachidian tooth and the second lateral tooth, is present (Fig. 15E,F). In some cases its presence is obscured. This structure is elongate and very similar to a small tooth, so we have called it 'a vestigial tooth'. Reproductive system triaulic (Fig. 13D). Preampullary duct short and narrow, expandsinginto a large, wide, thick-walled 'S'-shaped ampulla. Postampullary duct connects to short oviduct and vas deferens. Oviduct enters massive female gland mass via a short duct but we have not been able to see the uterine duct. Short branch of vas deferens widens into a very well differentiated and irregular prostatic portion, which has a dense network of interconnecting tubules over its surface. Distally, vas deferens narrows into a short, thin section, which descends through the centre of the following highly coiled final portion of the vas deferens. Distal end of this muscular portion armed with large, thin penial spines. Bursa copulatrix spherical and smaller than pyriform seminal receptacle. Seminal receptacle joins proximal part of vagina via a thin and slightly coiled duct. Elongate, wide and straight vagina emerges from base of bursa and joins vas deferens near genital aperture. We have not established the presence of a vaginal gland. Female gland mass well developed. *In situ*, the bursa is entirely surrounded by the prostate. In Fig. 13D prostate is shown positioned to the side.

Remarks. Tambja amakusana was described from Japan by Baba (1987) from a single living specimen 8 mm in length. After the original description this small species was recorded from Australia (Marshall & Willan 1999). In both cases, the descriptions of the specimens are in agreement with our specimens, but a more detailed description is given in this paper. Marshall & Willan (1999) emphasized that the body colour is variable; green, olive green, dull orange, or yellow, and specked and/or streaked with superficial white pigmentation. However, all the specimens described to date were olive green. The purple apices to the rhinophores, the gill, and the tip of the tail are good indicators for this species. The internal anatomy of this species has several remarkable features, which have not been recorded previously: the presence of two 'lateral pouches' at the junction of the oral tube and the buccal mass, the presence of 'vestigial teeth' between the rachidian and second lateral teeth, and a wide, blunt upper denticle of the upper cusp of the innermost lateral tooth. The reproductive system is described for the first time and is also very characteristic and easily distinguished from other species of the genus. The vaginal gland is absent, the vagina is wide, straight and large and the prostate is spread over the bursa copulatrix. All these features, together with the small size of the specimens, make this species very remarkable for the genus. The lateral pouches can also be found in some specimens of *T. eliora* and *T. mullineri* but the geographical range (eastern Pacific vs. Indo-Pacific) and the external and internal features are very different. Another species from South Africa, *T. capensis*, has a vestigial tooth similar to the one described for *T. amakusana*, but *T. capensis* has dark green to black ground colour and the radular formula and the reproductive system are distinct. *Tambja abdere* and *T. limaciformis* also share several features of the reproductive system. Both species lack a vaginal gland and have a well-differentiated prostate. An elongate, straight and wide vagina is present in *T. limaciformis*, while a very long and coiled vagina is characteristic for *T. abdere*.

Baba (1987) and Marshall & Willan (1999) compare *T. amakusana* with the Caribbean species *T. oliva*. Both species seem to be similar in the small size of the body, general coloration and radular formula, but as only one juvenile specimen of *T. oliva* has been found since its original description a further comparison is difficult to make. However, in the dissected specimen of *T. oliva* (INB0003348523) as well as in the holotype (USNM 76021), the vestigial teeth of *T. amakusana* are not present; the inner lateral teeth are also different since *T. amakusana* has a simple inner cusp while in *T. oliva* it is bifid.

***Tambja ceutae* García-Gómez & Ortea, 1988 (Figs 10G, 16A–D and 17A)**

Tambja ceutae García-Gómez & Ortea, 1988: 302, figs 1–7.

Material examined. Praia dos Reis Magos, Madeira, Portugal, 26 May 1994, 4 specs. 15, 23, 27, 28 mm preserved, dissected (MMF 29890). Porto Santo, Marina, Madeira, Portugal, 22 November 2000, 3 specs. 14–15 mm preserved, 2 dissected (MMF 31627). Isla de Faial, Azores, Portugal, 13 June 2002, 3 specs., dissected, 3–8 m depth, collected by G. Calado (MNCN 15.05/46661). Arrecife Punta San García, Straits of Gibraltar, Cádiz, Spain, June 2000, 1 spec. 20 mm alive, 16 m depth, collected by A. Sánchez (MNCN 15.05/46662).

Distribution. Strait of Gibraltar (Ceuta) (García-Gómez & Ortea 1988; García-Gómez 2002), Granada, Tarifa, Almería (Schick 1998; Sánchez-Tocino *et al*. 2000b; Sánchez-Tocino 2003; Ocaña *et al*. 2004), Madeira (Wirtz 1995, 1999; Caballer *et al*. 2001), Azores (Wirtz & Martins 1993; Wirtz & Debelius 2003) and Canary Islands (Ortea *et al*. 1997; Caballer *et al*. 2001).

External and internal anatomy. Described in detail and figured by García-Gómez & Ortea (1988). The specimens examined for the present study matched their description and thus there is no additional information to present. The radular formulae of our preserved specimens are: 17 x 4.1.1.1.4 (specimens 15, 23 and 28 mm long), 15 x 4.1.1.1.4 (specimen 27 mm long) and 13 x 4.1.1.1.4 (specimen 16 mm long). See Figs 10G, 16 and 17A for pictures of the living animal, radula, penis and reproductive system, respectively. In most of the examined specimens there are long ridged structures or 'lateral slots' (Yonow 1994; Pola *et al*. 2005b,c; present study) below the rhinophores.

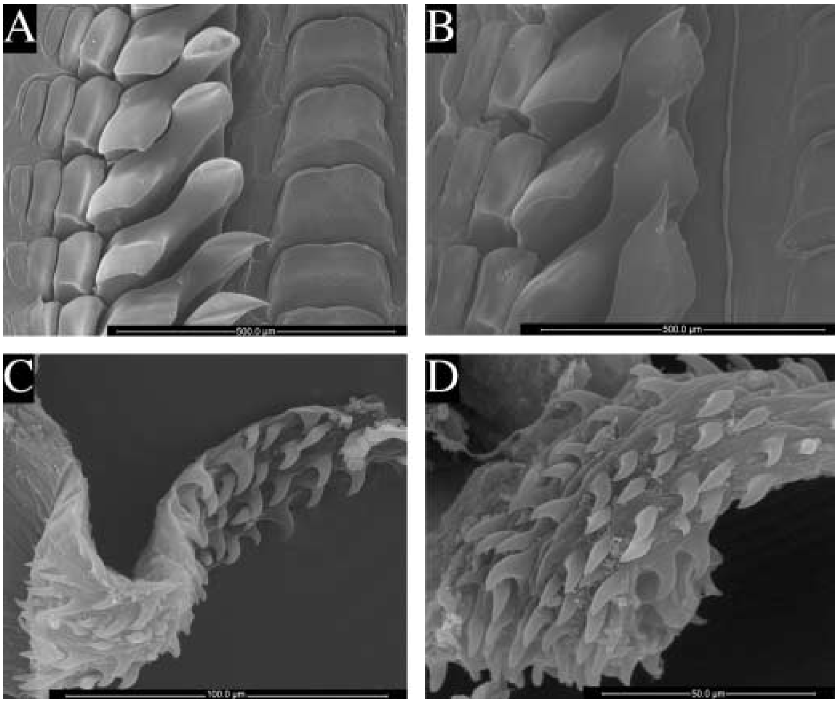

Fig. 16 A–D. Scanning electron micrographs of *Tambja ceutae* (LACM 34797). —A. Left half of the radula. —B. Innermost lateral teeth. —C,D. Detail of the penial spines.

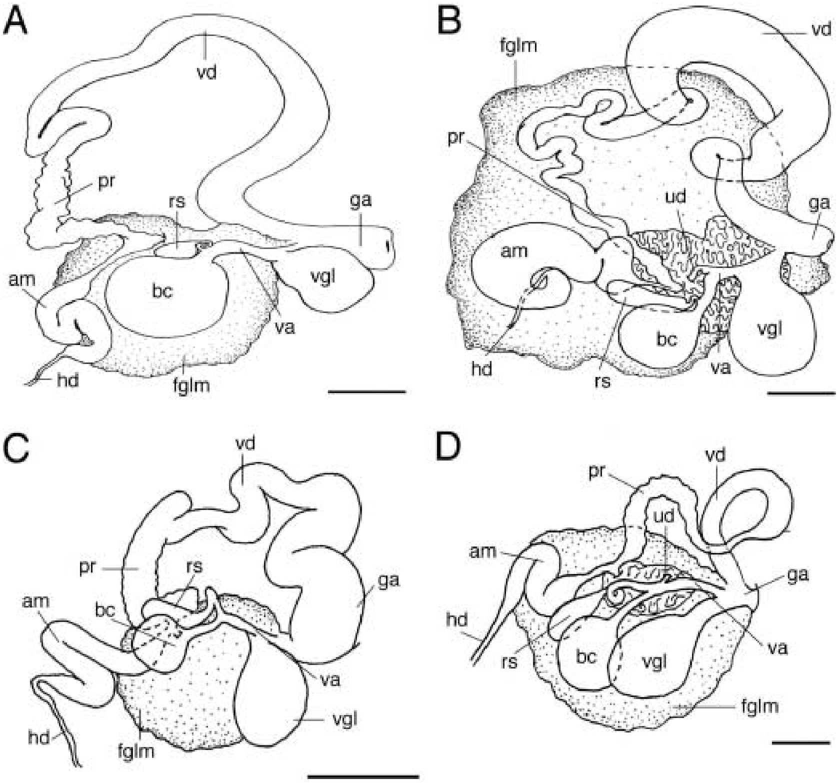

Fig. 17 A–D. Reproductive system of four *Tambja* species: —A. *T. ceutae* (MMF 29890). —B. *T. olivaria* (MNCN 15.05/46679). —C. *T. marbellensis* (MNCN 15.05/26031). —D. *T. simplex* (MNHN 15.05/3320). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

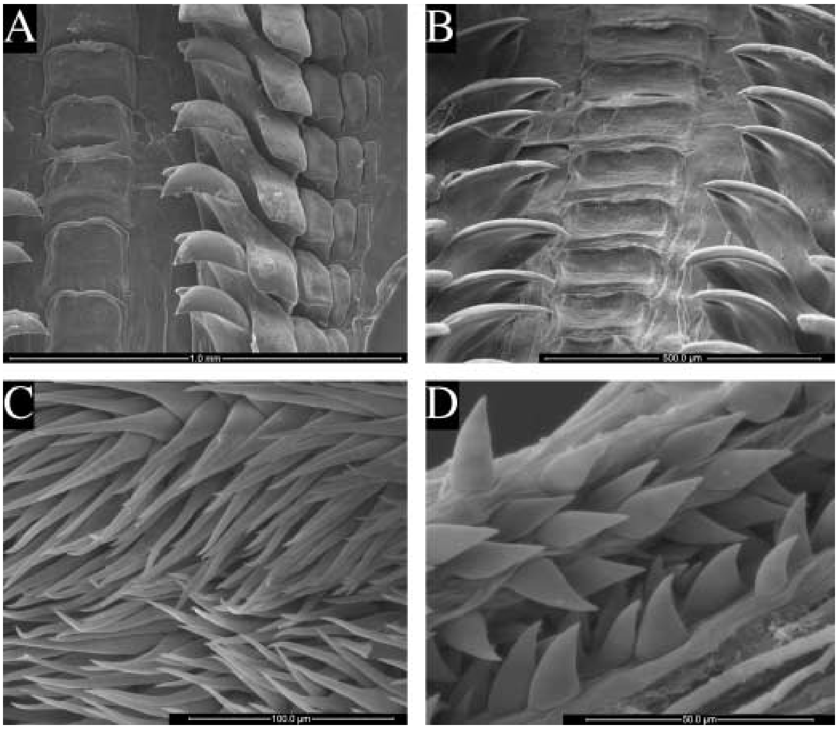

Fig. 18 A–D. Scanning electron micrographs of *Tambja olivaria* (MNCN 15.05/46688). —A. Right half of the radula. —B. Detail of the inner cusps of the inner lateral teeth. —C,D. Detail of the penial spines.

Remarks. García-Gómez & Ortea (1988) described *T. ceutae* as the second species of the genus from the eastern Atlantic and the first in European waters. Since then, this species has been the focus of several studies (Schick & Cervera 1998; Sánchez-Tocino *et al*. 2000a; Caballer *et al*. 2001; Ocaña *et al*. 2004). *Tambja ceutae* differs from congeners in several external and internal features. The most distinguishing external feature is the presence of pointed tubercles (variable in size) along the edge of the notum and the tail, which are even more conspicuous in young specimens (Schick & Cervera 1998). A new species from Brazil recently described, *T. stegosauriformis* Pola, Cervera & Gosliner, 2005, also has very well developed tubercles; however, they are not distributed along the edge of the mantle but form an elongate crest behind the gill to the end of the foot. The morphology of the head of *T. stegosauriformis* is also similar to that of *T. ceutae* where the anterior margin of the notum dips into a 'U' shape. However, both species clearly differ in the colour pattern and also in the characteristic of the inner edge of the inner lateral tooth. *Tambja marbellensis* is the most similar species from the eastern Atlantic, but lacks the conical papillae of the notal ridge and tail, the yellow lines on the inner branchial rachis and also the two large dark blue spots behind the rhinophores of *T. ceutae*.

***Tambja anayana* Ortea, 1989**
Tambja anayana Ortea, 1989: 14, p. 29, figs 1, 2.

Distribution. Boavista Island, Cape Verde (Ortea 1989).

Remarks. Ortea (1989) described this species from a single 6 mm specimen from Cape Verde. To date, this species has not been found again so the only available information stems from the original description. No picture of the living animal is published.

***Tambja olivaria* Yonow, 1994 (Figs 10H, 17B and 18A–D)**
Tambja olivaria Yonow, 1994: 109, figs 6–8.

Material examined. Holotype, Vihafushi Tila (Baa Atoll), Maldive Islands, 6 March 1991, 50–55 mm alive, examined, 37 m depth, collected by H. Voigtmann. Radula slide. (C169463) (Australian Museum). 'Lapus-Lapus', Malapascua Island, Philippines, 23 February 2003, 1 spec. 61 mm alive, dissected, 8 m depth, collected by E. Köhler (MNCN 15.05/46688). Lipayo, Negros Oriental Island, Philippines, 7 May 2003, 1 spec. 46 mm alive, 17 m depth, collected by E. Köhler (MNCN 15.05/46678). 'Kasay wall', Moalboal, Cebu Island, Philippines, 15 May 2003, 1 spec. 46 mm alive, dissected, 30 m depth, collected by E. Köhler (MNCN 15.05/46679). Msimbati Beach, Mnazi Bay, Mtwara Region, Tanzania, 31 October 1994, 2 specs., 35 & 45 mm preserved, dissected, collected by T. M. Gosliner (CASIZ 099367).

Distribution. Maldives (Yonow 1994; Debelius 1996; Coleman 2001), Philippines and Tanzania (present study; Osmond 2004). Takamasa (2003) shows a picture of a species called *Tambja* sp. D from Bali which we believe is also *T. olivaria*.

External morphology. Yonow (1994) gave a thorough description. Additional information from our dissected specimens includes: living animals reaching up to 60 mm (Fig. 10H); rhinophores deeply retractile within smooth, elevated sheaths bearing about 40–45 leaves; three large deeply branched non-retractile tripinnate gill leaves form a semicircle around the elevated tubular anal papilla; base of gill elevated, giving the aspect of being raised in relation to the surface of the body; oral tentacles short, dorsoventrally flattened and horizontally grooved.

Anatomy. Buccal mass larger than oral tube. A pair of elongate, wide, granular salivary glands on buccal mass, flanking the oesophagus. Labial cuticle thick and chitinous, lacking denticles. Radular formulae: 17 x 4.1.1.1.3-4 (MNCN 15.05/46678, MNCN 15.05/46679) and 18 x 3.1.1.1.3 (MNCN 15.05/46688). Morphology of rachidian teeth variable within the same radula, rectangular in some rows and quadrangular in others, without denticles and with notched anterior edge (Fig. 18A). Inner lateral teeth much larger than outer ones, with two well-developed cusps: inner cusp bifid, with outer denticle longer (Fig. 18B); outer cusp smaller and rectangular in shape. Outer lateral teeth plate-like, simple and decreasing in size towards outer margin. Reproductive system triaulic (Fig. 17B). Preampullary duct elongate and narrow, expanding into a large and thick-walled 'S'-shaped ampulla. Ampula connects to spermoviduct and vas deferens. Vas deferens highly coiled, starting with a slightly differentiated soft-walled prostate gland and widening into a swollen coiled duct. Within the third part of this swollen duct is the penis. Penis armed with very numerous, unordered penial spines, more elongate in basal part and shorter distally (Fig. 18C,D). Vaginal duct connects to large, round bursa copulatrix. Seminal receptacle pyriform, similar in length to bursa copulatrix. Short duct connects seminal receptacle to vagina after completing two loops, half way to bursa. A slender uterine duct leaves vagina from distal position and joins with female gland. Vagina gland large, thick-walled and well developed. Female gland mass well developed.

Remarks. Tambja olivaria is easily distinguishable from the other species of the genus by its colour pattern. The animals from the Philippines that we studied lack much of the yellow pattern mentioned in the original description. The reproductive system is described for the first time is this paper. With respect to the radula, the original description stated that the inner lateral tooth is large and spatulate and in the SEM picture it appears to have a simple upper cusp. However, our SEM photographs show a bifid inner cusp. *Tambja morosa* (Bergh, 1877), *T. sagamiana* (Baba, 1955), *T. verconis* (Burn, 1962) and *T. gabrielae* Pola, Cervera & Gosliner, 2005 also have a bifid inner cusp of the inner lateral teeth, 'lateral slots' and a penis armed with numerous, unordered and elongate spines. Yonow (1994) notes that this animal was found on the bryozoan *Bugula dentata* and the collector (S. Harwood) reported that it exuded masses of green pigment when touched and produced an acid-like burn on the collector's hands.

Tambja marbellensis Schick & Cervera, 1998 (Figs 17C, 19A and 20A–D)

Tambja marbellensis Schick & Cervera, 1998: 344, figs 1–3.

Material examined. Holotype, Torre del Cable, Marbella, Spain, July 1995, 45 mm, collected by K-L. Schick (MNCN 15.05/26031).

Distribution. Southern Spain (Schick & Cervera 1998; Schick 1998; Ocaña *et al*. 2000, 2004; Sánchez-Tocino *et al*. 2000a,b; García-Gómez 2002) and Portugal (Malaquias & Morenito 2000).

Remarks. Tambja marbellensis has been cited several times from southern Spain since its original description (Schick & Cervera 1998; Schick 1998; Ocaña *et al*. 2000, 2004; Sánchez-Tocino *et al*. 2000a,b; García-Gómez 2002) and also from Portugal (Malaquias & Morenito 2000). However, except for Schick & Cervera (1998) and Sánchez-Tocino *et al*. (2000a) none of these papers provide a morphological description but only a list of species. We have re-examined the holotype of this species and added some details in order to improve the original description. From the review of the holotype we have seen that lamellated structures on both sides of the body between the rhinophores and the oral tentacles present in other species of the genus (Yonow 1994; Pola *et al*. 2005b,c; present study) are also visible in this species.

Tambja simplex Ortea & Moro, 1998 (Figs 17D, 19B and 20E,F)

Tambja simplex Ortea & Moro, 1998: 149, lam.1, fig. 1A.

Material examined. Tarrafal, Ilha do Santiago, Cape Verde Archipelago, December 1998, 6 specs. 11–30 mm preserved, 4 dissected, 10–35 m depth, collected by P. Wirtz (MNCN 15.05/3320). Isla de San Vicente, Cape Verde Archipelago, 8 October 2002, 3 specs. 10 mm preserved, 20 m depth, collected by G. Calado (MNCN 15.05/46680).

Distribution. Cape Verde Archipelago (Ortea & Moro 1998; Cervera *et al*. 2000; Wirtz & Debelius 2003).

External and internal anatomy. Described by Ortea & Moro (1998) and Cervera *et al*. (2000). The specimens examined for the present study matched their description and thus there is no additional information to present. The radular formula of three preserved specimens 27–37 mm long is 17 x

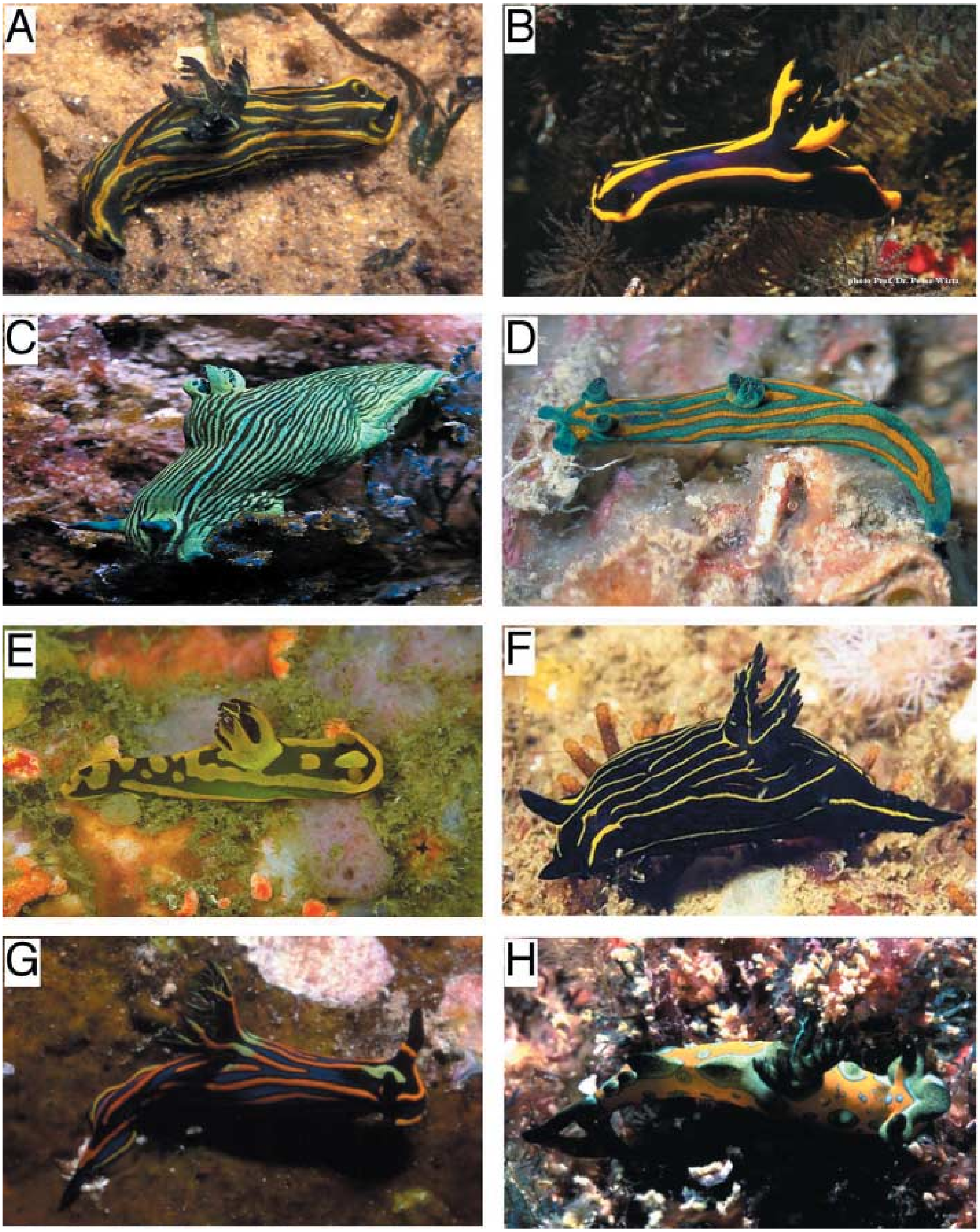

Fig. 19 A–H. Photographs of the living animals: —A. *Tambja marbellensis*, specimen from Algarve (photo: Paulo Morenito). —B. *Tambja simplex*, specimen from Santiago Island, Cape Verde Archipelago (photo: Peter Wirtz). —C. *Tambja tenuilineata*, specimen from Port Stephens, New South Wales (photo: David Harasti). —D. *Tambja tentaculata*, specimen from Guam, Marianas Islands (photo: Marta Pola). —E. *Tambja gabrielae*, specimen from Sulawesi, Indonesia (photo: Dave Behrens). —F. *Tambja zulu*, specimen from South coast KwaZulu-Natal, South Africa (photo: Valda Fraser). —G. *Tambja victoriae*, specimen from Papua New Guinea (photo: Terrence M. Gosliner). —H. *Tambja stegosauriformis*, specimen from Rio de Janeiro, Brazil (photo: Marcelo Krause).

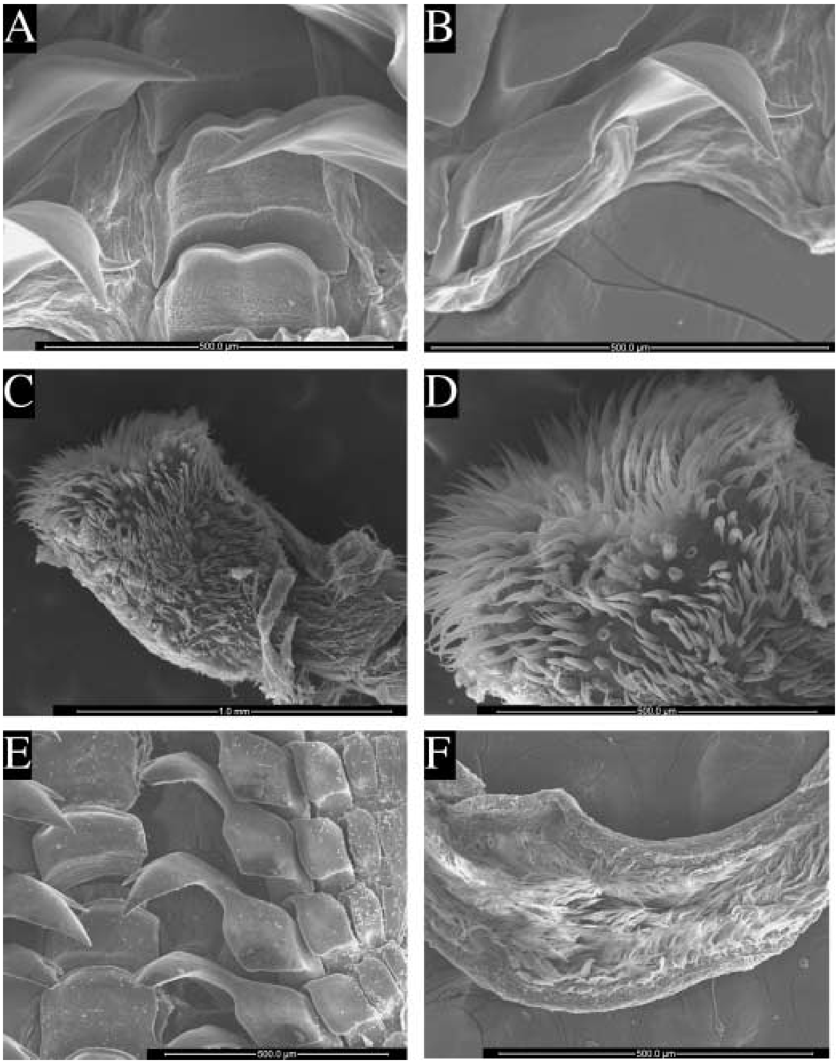

Fig. 20 A–F. Scanning electron micrographs of *Tambja marbellensis* and *T. simplex*. —A–D. *T. marbellensis* (Holotype: MNCN 15.05/26031). —A. Rachidian teeth. —B. Innermost lateral teeth. —C,D. Penis. —E,F. *T. simplex* (MNCN 15.05/3320). —E. Right half of the radula. —F. Penis.

4.1.1.1.4 while that of a specimen 12 mm long is 15 x 4.1.1.1.4. See Figs 17D, 19B and 20E,F for pictures of the living animal, reproductive system, radula and penis and, respectively.

Remarks. Ortea & Moro (1998) described *T. simplex* from the Cape Verde Archipelago on the basis of a single specimen. Two years later, Cervera *et al*. (2000) provided useful additional information on this species, including eight more specimens collected from the same archipelago; they described the reproductive system of this species for the first time and separated *T. simplex* from *T. gratiosa* (Bergh, 1890), *T. capensis* (Bergh, 1907), *T. divae* (Marcus, 1958), *T. oliva* Meyer, 1977, *T. fantasmalis* Ortea & García-Gómez, 1986, *T. ceutae* García-Gómez & Ortea, 1988 and *T. marbellensis* Schick & Cervera, 1998, based on the ground colour and the yellow striped pattern on the notum and both flanks of the body. Ocaña *et al*. (2004) used the data for *T. simplex* from previous papers to study the ontogenetic radular variation in species of *Tambja* from the eastern Atlantic Ocean and the Mediterranean Sea. In the present study we used the six undissected specimens deposited by Cervera *et al*. (2000) at the Museo Nacional de Ciencias Naturales (Madrid, Spain) with the catalogue number 15.05/3320, plus a newly collected specimen, to review the species. The external anatomy, coloration, radula and reproductive system described by Ortea & Moro (1998) and by Cervera *et al*. (2000) are in agreement with those of our specimens. Colour photographs of this species are shown in Wirtz & Debelius (2003) and www.medslugs.de and www.seaslugforum.net.

Tambja tenuilineata Miller & Haagh, 2005 (Figs 19C, 21A,B and 22A)

Tambja tenuilineata Miller & Haagh, 2005: 56, figs 1–3.

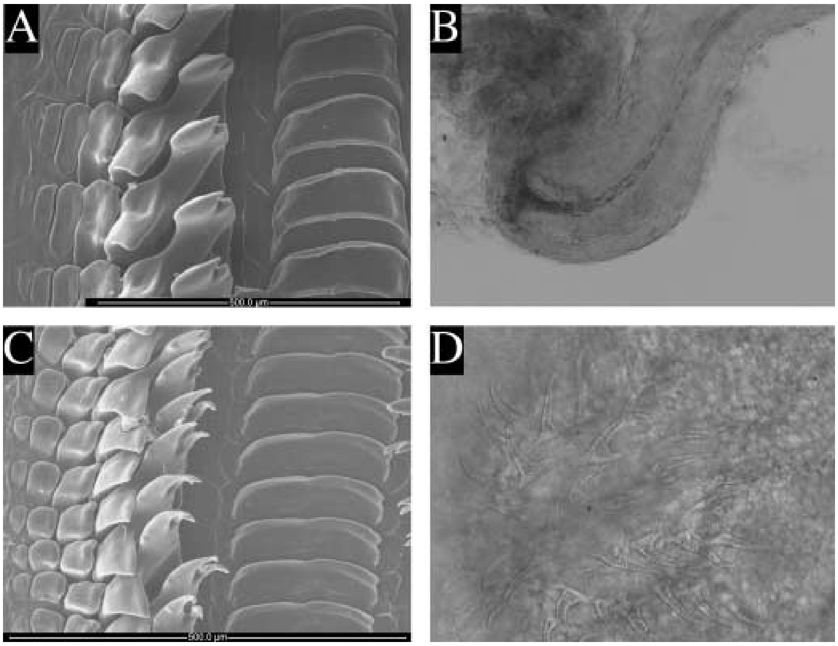

Fig. 21 A–D. Scanning electron micrographs and digital photographs of *Tambja tenuilineata* and *T. tentaculata*. —A,B. *T. tenuilineata* (MNCN 15.05/46687). —A. Left half of the radula. —B. Penis. —C,D. *T. tentaculata* (CASIZ 162639). —C. Left half of the radula. —D. Detail of the penial spines.

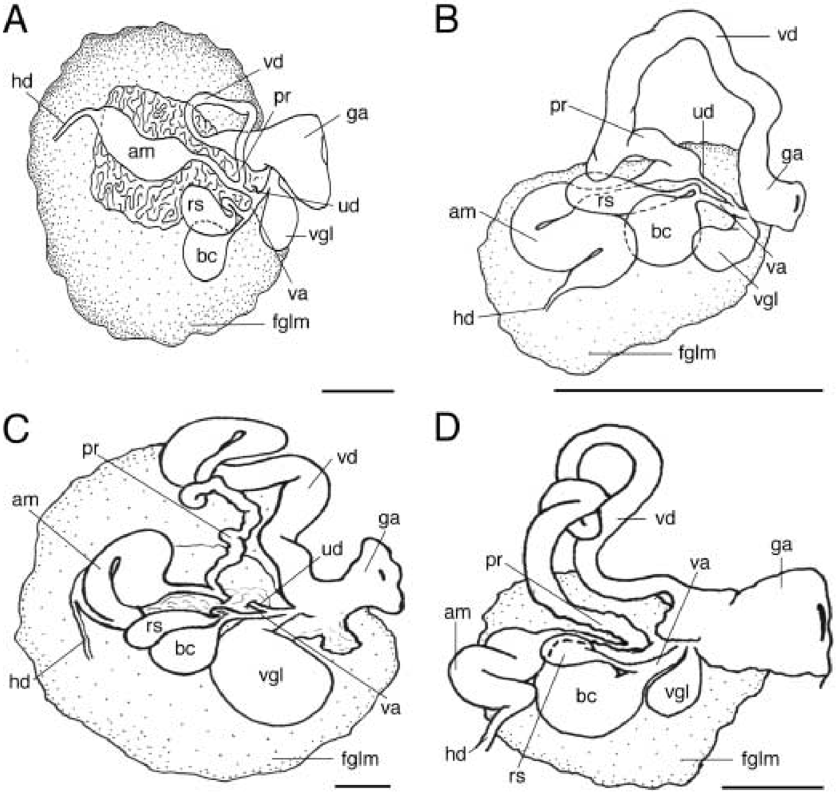

Fig. 22 A–D. Reproductive system of four *Tambja* species: —A. *T. tenuilineata* (MNCN 15.05/46687). —B. *T. tentaculata* (CASIZ 162639), from Pola *et al*. (2005b). —C. *T. gabrielae* (CASIZ 162701), from Pola *et al*. (2005b). —D. *T. zulu* (NSMA E6323 T2006), from Pola *et al*. (2005b). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland. Parts B,C and D reproduced by permission of the Malacological Society of London.

Material examined. New South Wales, Australia, 22 August 2004, 2 specs. 20 mm alive, dissected, 14 m depth, collected by David and Leanne Atkinson (MNCN 15.05/46687).

Distribution. Northern New Zealand (Miller & Haagh 2005; Coleman 2001) and east Australia (Coleman 2001; www.seaslugforum.net/factsheet.cfm?base=tambnsw; present study).

External and internal anatomy. Recently described by Miller & Haagh (2005). The specimens examined in the present study matched their description and thus there is no additional information to present. Radular formula 15 x 4.1.1.1.4. See Figs 19C, 21A,B and 22A for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. Tambja tenuilineata has recently been described by Miller & Haagh (2005). This species appears in some field guides (Coleman 2001) and web pages (www.diveoz.com.au, www.ianskipworth.com) identified as *Tambja* sp. ('Fine-lined *Tambja*') but Miller & Haagh (2005) also report that *T. tenuilineata* was previously identified as *Nembrotha kubaryana* Bergh, 1877, *Tambja affinis* (Eliot, 1904) and *Roboastra luteolineata* (Baba, 1936). *Tambja tenuilineata* differs from the rest of the species of the genus by its regular longitudinal pattern of integumentary ridges and lines of green and brown colour. This species is similar to *Nembrotha milleri* (Gosliner & Behrens, 1997), although the rachidian tooth of the latter is clearly different and the animals are much smaller.

***Tambja tentaculata* Pola, Cervera & Gosliner, 2005 (Figs 19D, 21C,D and 22B)**

Tambja tentaculata Pola, Cervera, Gosliner, 2005: 258, figs 1A, 2A,B, 3A and 4A.

Material examined. South side of Western Shoals, Apra Harbour, Guam, Mariana Islands, 15 September 2004, 2 specs. 17 & 20 mm alive, dissected, 14 m depth, collected by M. Pola (MNCN 15.05/46681). Apra Harbour, south side of Western Shoals, Guam, 15 September 2004, 1 spec. 15 mm alive, 8 m depth, collected by M. Pola (MNCN 15.05/46682). Apra Harbour, south side of Western Shoals, Guam, 24 September 2004, 1 spec. 25 mm alive, 8 m depth, collected by M. Pola (MNCN 15.05/46683).

Distribution. Guam (Pola, Cervera & Gosliner 2005b).

External and internal morphology. Described in detail and figured by Pola *et al*. (2005b). The specimens described for the present study matched the description and thus there is no additional information to present. Radular formula of two specimens dissected is: 14 x 4.1.1.1.4 (MNCN 15.05/46681). See Figs 19D, 21C,D and 22B for pictures of the living animal, radula, penis and reproductive system, respectively.

***Tambja gabrielae* Pola, Cervera & Gosliner, 2005 (Figs 19E, 21E,F and 22C)**

Tambja gabrielae Pola, Cervera & Gosliner, 2005: 258, figs 1B, 2C,D, 3B, 4B.

Distribution. Indonesia (Coleman 2001; Takamasa 2003; Pola *et al*. 2005b), Papua New Guinea (Pola *et al*. 2005b) and Philippines (Biddittu 2005).

External and internal morphology. Described in detail and figured by Pola *et al*. (2005b). No additional specimens have been examined for the present study. Radular formula 18 x 3.1.1.1.3. See Figs 19E, 21E,F and 22C for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. Tambja gabrielae has recently been described by Pola *et al*. (2005b) from Indonesia and Papua New Guinea. Since then, this species has been recorded from the Philippines (Biddittu 2005) but the specimen was not collected. Pola *et al*. (2005b) compare *T. gabrielae* with *T. morosa*, *T. sagamiana*, *T. olivaria*, and others, but it is easily distinguished by its colour pattern and internal features.

***Tambja zulu* Pola, Cervera & Gosliner, 2005 (Figs 19F, 22D and 23A,B)**

Tambja zulu Pola, Cervera & Gosliner, 2005: 262, figs 1D, 2E,F, 3C and 4C.

Distribution. Durban, South Africa [Gosliner (1987; referred to as *Tambja* sp).; Fraser (2000; referred to as *Tambja* sp.3); Pola *et al*. (2005b)].

External and internal morphology. Described in detail and figured by Pola *et al*. (2005b). No additional specimens have been examined for the present study. Radular formula 17-19 x 3-4.1.1.1.3-4. See Figs 19F, 22D and 23A,B for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. Tambja zulu appears to be endemic to South African waters. The photographs and drawings refer to the specimens studied by Pola *et al*. (2005b) as no other specimens have been collected since then. *Tambja zulu* differs from the rest of the Indian Ocean species by its external coloration and details of its internal anatomy.

***Tambja victoriae* Pola, Cervera & Gosliner, 2005 (Figs 19G, 23C–E and 24A)**

Tambja victoriae Pola, Cervera & Gosliner, 2005: 266, figs 1E, 2G, H, 3D and 4D.

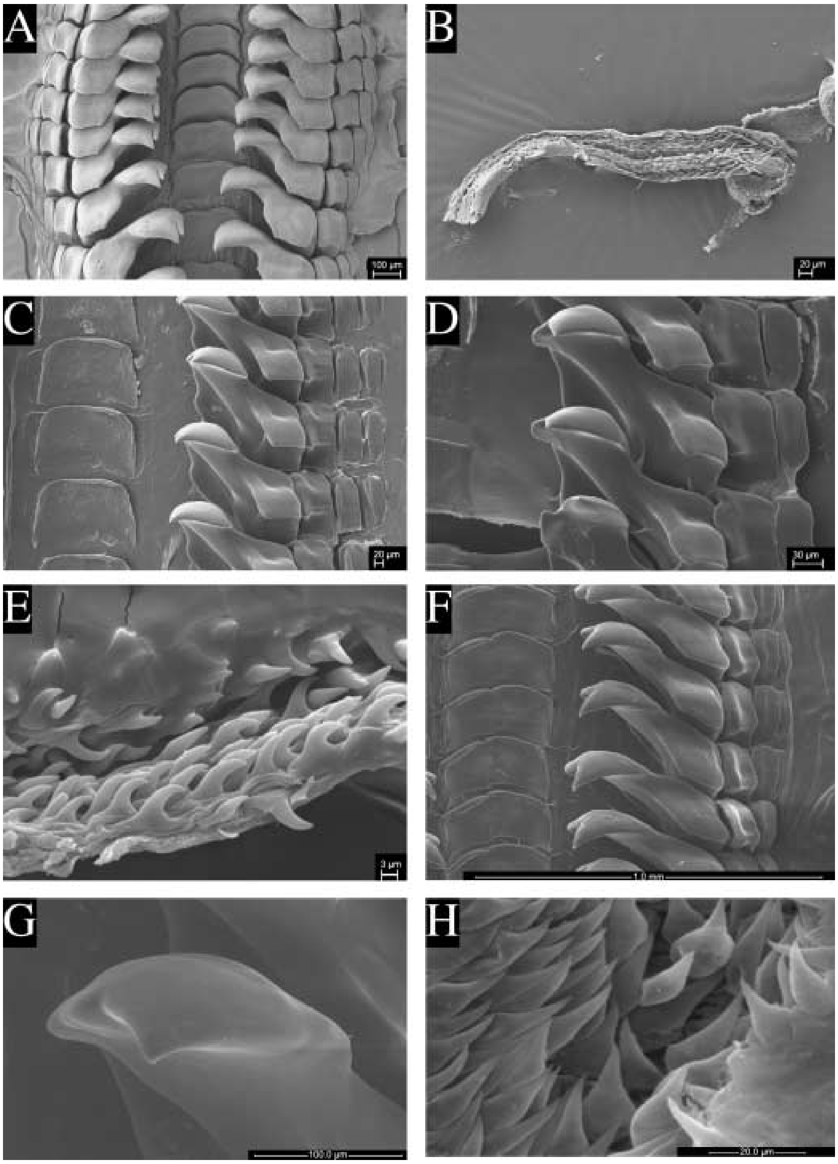

Fig. 23 A–H. Scanning electron micrographs of *Tambja zulu*, *T. victoriae* and *T. stegosauriformis*. —A,B. *T. zulu* (NMSA E6323/T2006) from Pola *et al*. (2005b). —A. Radula. —B. Penis. —C,D. *T. victoriae* from Pola *et al*. (2005b). —C. Right half of the radula (CASIZ 075810). —D. Innermost lateral teeth (CASIZ 076335). —E. Penial spines (CASIZ 075810). —F–H. *T. stegosauriformis* (MZSP 44650). —F. Right half of the radula. —G. Detail of the inner cusp of the inner lateral tooth. —H. Detail of the penial spines (from Pola *et al*. 2005c). Parts A,B,C and D reproduced by permission of the Malacological Society of London. Part H reproduced with permission from the Journal of the Marine Biological Association of the United Kingdom (vol. 85, pp. 979–984).

Distribution. Papua New Guinea and Australia (Coleman 1989, 2001; Marshall & Willan 1999 (referred to as *Roboastra arika*; Pola *et al*. 2005b).

External and internal morphology. Described in detail and figured by Pola *et al*. (2005b). No additional specimens have been examined for the present study. Radular formula 14–18 x 4.1.1.1.4. See Figs 19G, 23C–E and 24A for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. *Tambja victoriae* has recently been described by Pola *et al*. (2005b) from Papua New Guinea and Australia. The description given in this paper refers to the specimens studied in the original description. Pola *et al*. (2005b) discuss the confusion surrounding this species because it has been misidentified several times as *Roboastra arika* and *Tambja affinis* (Coleman 1989, 2001; Marshall & Willan 1999).

Tambja stegosauriformis Pola, Cervera & Gosliner, 2005 (Figs 19H, 23F–H and 24B)
Tambja stegosauriformis Pola, Cervera & Gosliner, 2005: 979, figs 1–3.

Distribution. Brazil (Pola *et al*. 2005c).

External and internal morphology. Described in detail and figured by Pola *et al*. (2005c). No additional specimens have

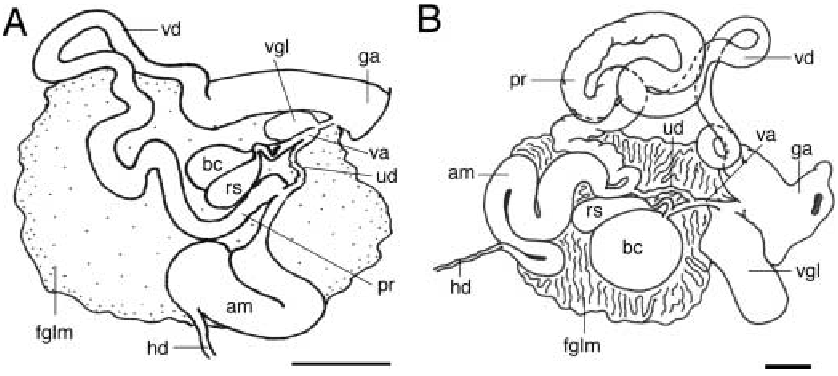

Fig. 24 A, B. Reproductive system of two *Tambja* species: —A. *T. victoriae* (CASIZ 075810), from Pola *et al.* (2005b). —B. *T. stegosauriformis* (MZSP 39126), from Pola *et al.* (2005c). Scale bars, 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland. Part A reproduced by permission of the Malacological Society of London. Part B reproduced with permission from the Journal of the Marine Biological Association of the United Kingdom (vol. 85, pp. 979–984).

been examined for the present study. Radular formula 15 x 4.1.1.1.4. See Figs 19H, 23F–H and 24B for pictures of the living animal, radula, penis and reproductive system, respectively.

Remarks. This species is easily distinguished from the rest of the species of the genus by external and internal features since its colour is very characteristic and it has prominent tubercles forming a crest behind the gill ending on the tip of the tail. Pola *et al*. (2005c) compare it with *T. divae* and the rest of the species of *Tambja* present in the western Atlantic area. We have also examined a specimen from the Caribbean Bahamas (see picture in Humann & Deloach 2002) that we thought could be *T. stegosauriformis* since its internal features are very similar to those of the latter. Nevertheless, since we only have one specimen and the colour pattern is not identical we have decided not to include this specimen in the distribution of *T. stegosauriformis* and wait for the study of potential additional material that can solve its status.

Phylogenetic analysis

Taxa. Thirty-five taxa have been included in the phylogenetic analysis (Table 1). The ingroup includes most of the valid species of the genus *Tambja*. *T. gratiosa* (Bergh, 1890), *T. amitina* (Eliot, 1905), *T. divae* (Marcus, 1958) and *T. anayana* Ortea, 1989 were excluded due to the lack of complete descriptions or additional material to study, while *T. diaphana* (Bergh, 1877) was excluded for being considered *nomen dubium*. *Bathydoris clavigera* Thiele, 1912 and representatives of Nembrothinae and Polycerinae genera *Nembrotha* Bergh, 1877, *Roboastra* Bergh, 1877, *Polycera* Cuvier, 1817 and *Polycerella* Verrill, 1881 have been included in the analysis for outgroup comparative purposes. The outgroup taxa chosen for the present analysis are discussed in the Materials and Methods.

Characters. Forty-nine characters have been used to resolve the phylogeny of *Tambja* (see Appendix 1). They reflect a wide range of morphological and anatomical features of the taxa involved. The character states are indicated as follows: 0 is the presumed plesiomorphic condition; 1, 2 and 3 the apomorphic conditions. '—' indicates character states that are not applicable, '?' indicates missing data. The distribution of plesiomorphic and apomorphic states is presented in Table 2. Character states for the data examined for the present study can be found in Appendix 1. [Note: Characters preceeded by an asterisk were deleted from the first analysis, because they are phylogenetically uninformative].

Results

The heuristic search of the data matrix set produced between 12 and 107 most parsimonious trees with a tree length of 84 steps when 20 replicates of a thousand random start trees were performed. The consistency index (CI = 0.48) and the retention index (RI = 0.79) show that more than 50% of all characters exhibit homoplasy (reversal and/or parallelism). The strict consensus tree is shown in Fig. 25. The numbers in bold in the strict consensus tree indicate reversals or parallelism (Fig. 26).

The strict consensus tree shows that *Tambja* is paraphyletic since species of *Roboastra* are included within the same clade. Thus, within the latter group, two clades can be identified in the tree: the clade including *T. amakusana* and *T. limaciformis* and the clade including the remaining species of *Tambja* and *Roboastra*. The clade including *T. amakusana* and *T. limaciformis* is supported by three synapomorphies: presence of poorly developed elongated pouches in the oral tube (19), poorly developed outer cusp of the second lateral teeth (32) and prostate partially surrounds the bursa copulatrix (39). The clade including *T. capensis* and the remaining species of *Tambja* and *Roboastra* shares three synapomorphies: bifid inner cusp of the second lateral tooth (29), narrow vagina (41) and the presence of a vaginal gland (43). In *T. capensis*, as well as in *T. amakusana* and *T. limaciformis*, the first lateral tooth is present while in the clade containing the remaining species of *Tambja* and *Roboastra*, the first lateral tooth has disappeared (this state is also shared by the genus *Nembrotha*). Within this

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

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
B. clavigera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. quadrilineata	1	0	1	1	0	0	0	0	0/1	0/1	0	0	0	0	0	1	0	1	0	0	1	1	—	—
P. emertoni	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	—	—
N. lineolata	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	3	1	0	0	0
N. chamberlaini	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	3	1	0	0	0
N. kubaryana	1	1	0	0	1	0	0	1	0/1	1	0	0	1	0	0	0	1	0	0	3	1	0	0	0
N. cristata	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	3	1	0	0	0
R. gracilis	1	1	0	0	1	0	0	0	0/1	0/1	0	1	1	1	1	1	1	1	2	2	1	0	0	1
R. luteolineata	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	2	2	1	0	0	1
R. tigris	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	2	2	1	0	0	1
R. europaea	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	2	2	1	0	0	1
R. caboverdensis	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	2	2	1	0	0	1
R. leonis	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	1	2	2	1	0	0	1
T. abdere	1	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. eliora	1	1	0	0	1	0	1	1	1	0/1	0	0	0	0	0	0	0	0	0/1	1	1	0	1	—
T. oliva	1	1	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. mullineri	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0/1	1	1	0	1	—
T. ceutae	1	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	—
T. marbellensis	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. fantasmalis	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. simplex	1	1	0	0	1	0	?	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. capensis	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	—
T. sagamiana	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. amakusana	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	—
T. limaciformis	1	1	0	0	1	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0/1	1	1	0	1	—
T. affinis	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. morosa	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. olivaria	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. verconis	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. victoriae	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. tentaculata	1	1	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	—
T. zulu	1	1	0	0	1	0	?	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. gabrielae	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. stegosauriformis	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	—
T. tenuilineata	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	—

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
B. clavigera	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	—	0	0
P. quadrilineata	—	0	0	1	0	—	0	2	1	1	0	2	0	1	0	1	0	0	0	0	0	1	0	1	1
P. emertoni	—	1	—	1	1	0	0	1	1	0	0	2	0	1	0	0	1	0	0	1	0	1	0	1	1
N. lineolata	1	1	—	1	0	—	0	2	0	1	0	0	0	1	1	1	0	1	0	1	0	1	0	1	2
N. chamberlaini	1	1	—	1	0	—	0	2	0	1	0	0	0	1	1	1	0	1	0	1	0	1	0	1	2
N. kubaryana	1	1	—	1	0	—	0	2	0	1	0	0	0	1	1	1	0	0	0	1	0	1	1	1	2
N. cristata	1	1	—	1	0	—	0	2	0	1	0	0	0	1	1	1	0	0	0	1	0	1	1	1	2
R. gracilis	1	1	—	1	1	0	0	2	1	1	1	1	0	0	0	0	1	0	1	1	0	1	1	1	3
R. luteolineata	1	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	3
R. tigris	1	1	—	1	0	—	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	3
R. europaea	1	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	3
R. caboverdensis	1	1	—	1	0	—	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	3
R. leonis	1	1	—	1	0	—	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	3
T. abdere	0	1	—	1	0	—	0	2	1	1	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1
T. eliora	0	1	—	1	0	—	1	2	0/1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. oliva	1	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. mullineri	0	1	—	1	0	—	1	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. ceutae	0	1	—	1	1	1	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. marbellensis	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. fantasmalis	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. simplex	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1

Table 2 *Continued.*

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
T. capensis	0	0	1	1	1	1	0	2	0	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. sagamiana	0	1	—	1	1	0	1	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. amakusana	0	0	1	1	0	—	0	1	0	1	0	1	0	1	1	0	0	0	0	1	0	1	0	1	1
T. limaciformis	1	0/1	1	1	0	—	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1
T. affinis	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. morosa	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. olivaria	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. verconis	0	1	—	1	1	0	0/1	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. victoriae	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. tentaculata	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. zulu	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1
T. gabrielae	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1
T. stegosauriformis	0	1	—	1	1	0	1	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1
T. tenuilineata	0	1	—	1	1	0	0	2	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1

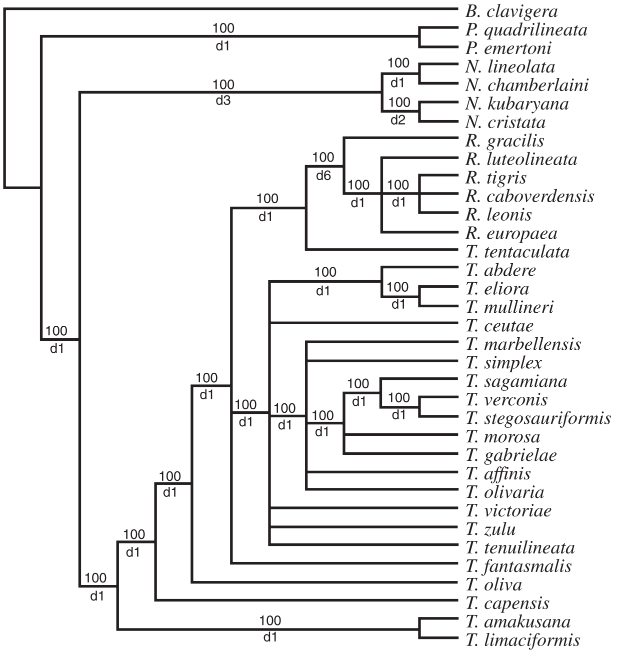

Fig. 25 Strict consensus tree with Bremer support analysis. Numbers above the branches refer to percentage of trees supporting the branch. Numbers above the branches refer to the decay index.

last clade, *T. oliva* is the sister species of the group including three main clades: the clade including *T. tentaculata* and *Roboastra* species, which is supported by having strongly developed oral tentacles (13) and tentacles developed as dorsolaterally grooved projections (14), the clade including *T. fantasmalis* and the clade including the remaining species of the genus *Tambja*. This latter clade is divided into six polytomies: *T. ceutae*, *T. victoriae*, *T. zulu* and *T. tenuilineata* are basal polytomies and their relationships remain unknown; *T. eliora* and *T. mullineri* are sister species being the sister group of *T. abdere*. These three species constitute an eastern Pacific clade. The last polytomy includes the remaining species of *Tambja*.

The strict consensus tree also indicates that the Nembrothinae species included in the analysis are monophyletic. Nevertheless, further ingroup and outgroup taxa as well as molecular data must be added to confirm it. The Bremer support analysis (Fig. 25) shows that *Roboastra* is a well-supported monophyletic group (Bremer support value of 6), *Nembrotha* is also a monophyletic group (Bremer support value of 3). The Bremer support values for the rest of the clades are 1 except for the clade including *Nembrotha kubaryana* and *N. cristata* (Bremer support value of 2).

Biogeography

All *Nembrotha* species are restricted to the Indo-Pacific and this clade is basal to Nembrothinae suggesting that the subfamily initially evolved in Indo-Pacific waters. Within the clade including *Tambja* + *Roboastra* the most basal species of *Tambja* (*T. amakusana* and *T. limaciformis*) are also found in the Indo-Pacific as well as most of the species of *Tambja*, but the genus is also present in Atlantic (*T. oliva*, *T. capensis*, *T. fantasmalis*, *T. ceutae*, *T. marbellensis*, *T. simplex* and *T. stegosauriformis*) and eastern-Pacific waters (*T. abdere*, *T. eliora* and *T. mullineri*). A plausible explanation of the biogeographical distribution of dorid nudibranchs is given by Valdés (2004).

Discussion

To date, no phylogenetic analysis has been undertaken for members of the genus *Tambja*. In the absence of phylogenetic studies, the genus was assumed to be monophyletic following the traditional genus concept. Thus, Burn (1967) proposed a generic diagnosis for *Tambja* based on a few characters of the

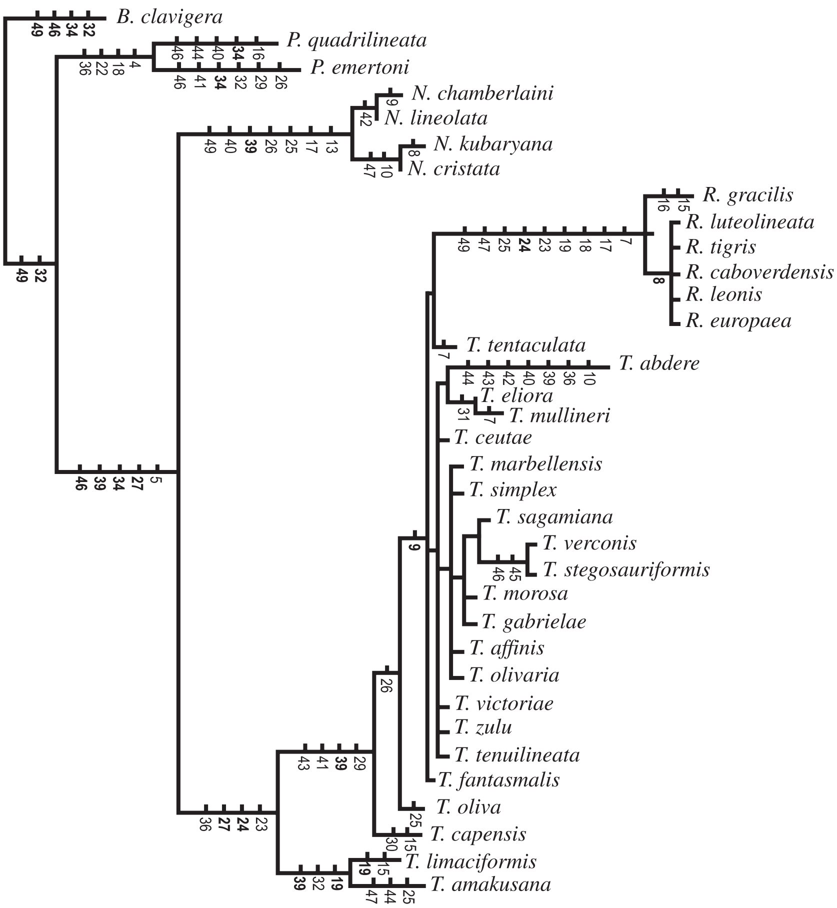

Fig. 26 Strict consensus tree showing character tracing. Numbers refer to characters listed in the text. Characters printed in bold face presented at least one instance of reversal.

radula and the reproductive system. Nevertheless, those traditional characters appear not to be sufficient and need major revision when further *Tambja* species are added. It is therefore important to conduct a phylogenetic analysis of members of this taxon. To facilitate such an analysis, a complete review of the genus, based on morphological and anatomical studies, was undertaken. Most data used to construct the matrix for phylogenetic analysis are derived from the morphological studies presented here. The phylogenetic analysis included most of the valid species of *Tambja* except *T. gratiosa*, *T. amitina*, *T. divae* and *T. anayana*. These four species were described from a single preserved specimen and no additional material has since been collected. In addition, the original descriptions of *T. amitina* and *T. anayana* (Eliot 1905; Ortea 1989) lack information about the reproductive system. Thus, we preferred to exclude these species from the phylogenetic analysis and we consider that there is no problem with the taxon sampling since only four species of the 26 valid species are missing.

The phylogenetic hypothesis carried out in this paper shows that *Tambja* is paraphyletic. Some hypotheses are proposed to explain the paraphyly of the genus. It could be that the character set chosen for this analysis is inadequate or insufficient to adequately resolve the phylogeny (Valdés & Gosliner 2001; Wägele 2005; Dayrat & Gosliner 2005). The choice of characters is often a drawback for morphological phylogenetic inference. However, in this case we believe that this is not relevant here since there is significant phylogenetic signal in the data set and the characters properly resolve the monophyly of the genus *Roboastra*. Therefore, we are inclined to consider that lack of resolution is the consequence of a process of a rapid radiation, in which almost simultaneous speciation events led to the current lineages. During such a rapid radiation the time that has elapsed between successive splitting events is so short that the probability of character fixation during each single speciation event may be minimal. Consequently, the internodes are very short and it is unlikely that they would be recovered during the phylogenetic analysis, thus resulting in a polytomy. Support for this hypothesis is suggested by the large number of synapomorphies supporting the genera *Nembrotha* and *Roboastra*; lineages were able to change morphologically before and after the evolutionary radiation, so there is no evident reason to justify lack of morphological change, other than lack of time resulting from a rapid radiation, associated with speciation events in *Tambja*.

The second pattern also requires further evolutionary explanation. *Roboastra* is well supported as a clade, but it originates within *Tambja*. Two hypotheses can be proposed to account for this pattern: either the ancestor of current *Roboastra* experienced an early process of accelerated morphological differentiation, or *Roboastra* has been subjected to a recent burst of speciation. Differences between these two processes lie in the time-frame associated with morphological differentiation. In the first hypothesis (early acceleration of morphological change, likely a consequence of developmental alteration in the ancestor to *Roboastra*) most of the morphological changes should have occurred early (e.g. synapomorphies for *Roboastra*), but a significant number of changes should also be distributed along other internodes within *Roboastra*, since time was likely not a limitation for possible changes to occur and become fixed. On the other hand, if the second hypothesis is correct, there is little space for morphological change after the burst of speciation, and therefore the internodes should be short. *Tambja*'s fundamental shift from feeding on bryozoans to being a predatory specialist on other polycerids could account for a rapid morphological shift in the ancestor of *Roboastra*.

Testing all these hypotheses cannot be achieved by only using our current data set. A detailed morphological analysis including all *Nembrotha* species and a larger set of outgroups is necessary to test for the rapid radiation hypothesis, while a comprehensive molecular data set, of a completely independent marker, not associated with morphological changes (e.g. mtDNA) should be used to discriminate between the completing hypotheses for *Tambja* and *Roboastra* evolution.

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Appendix 1 Characters used to resolve the phylogeny of *Tambja*

Characters preceded by an asterisk were deleted from the first analysis because they are phylogenetically uninformative.

1 *Body shape: in *Bathydoris* the body is elevated with a large dorsal hump (0). In the remaining outgroup and ingroup taxa the body is elongate and limaciform (1).

2 Integumentary spicules: the body of *Bathydoris* and *Polycera quadrilineata* is stiffened with a network of integumentary spicules, more or less densely arranged (0). In other genera such as *Polycerella*, *Nembrotha*, *Roboastra* and *Tambja* these spicules are absent (1).

3 *Cephalic processes: *Bathydoris*, cryptobranchs and pleurobranchs do not have these processes (0). They are present in some polycerids, such as *Polycera quadrilineata* (1).

4 Extrabranchial processes: *Bathydoris*, cryptobranchs and pleurobranchs do not have these processes (0). They are present in some polycerids, such as *Polycera quadrilineata* and *Polycerella emertoni* (1).

5 Rhinophoral sheaths: *Bathydoris clavigera*, *Polycera quadrilineata* and *Polycerella emertoni* lack rhinophoral sheaths (0). Rhinophoral sheaths are present in all *Roboastra*, *Nembrotha* and *Tambja* species (1).

6 *Rhinophoral lamellae: in the vast majority of outgroup and ingroup taxa the rhinophores are characterized by having crowed lamellae along most of their length (0). In *Polycerella emertoni* the rhinophores are smooth (1).

7 Lateral slots ('pre-rhinophoral pits'): in the outgroup taxa, *T. abdere*, *T. mullineri*, *T. fantasmalis*, *T. capensis*, *T. amakusana* and *T. limaciformis* the lateral slots are absent (0). In most species of *Tambja*, on the sides between the rhinophores and oral tentacles, there is a raised oval lamellated structure (1). In *T. oliva*, *T. simplex* and *T. zulu* this character is treated as unknown.

8 Lines on inner branchial rachis: Most of the outgroup taxa, *T. oliva*, *T. capensis*, *T. amakusana*, *T. limaciformis* and *T. tentaculata*, lack lines on the inner branchial rachis (0). The rest of the studied species have well-defined lines on the inner branchial rachis (1).

9 Longitudinal lines: *Bathydoris clavigera* lacks longitudinal lines on the notum and both sides of the body; thus this state is coded as plesiomorphic (0). In most of *Roboastra* and *Tambja* species this character is present (1).

10 Irregular spots or patches: the vast majority of outgroup and ingroup taxa lack irregular spots or patches on the body surface (0). *Nembrotha kubaryana*, *N. cristata*, *Tambja abdere*, *T. sagamiana*, *T. morosa*, *T. verconis*, *T. gabrielae* and *T. stegosauriformis* have irregular spots (1).

11 *Mantle edge tubercles: the outgroup taxa and the vast majority of the ingroup taxa lack tubercles or have tubercles scattered on the dorsal surface of the body (0). The presence of small tubercles just along the edge of the mantle is characteristic of *Tambja ceutae* (1).

12 *Body surface covered with low pustules: this kind of skin is unique to *R. gracilis* (1). The absence of low pustules in the body surface is considered plesiomorphic (0).

13 Oral tentacle size: slightly developed in *Bathydoris*, cryptobranchs and other phanerobranchs (0). Strongly developed in *Nembrotha*, *Roboastra* and *T. tentaculata* (1).

14 Oral tentacle shape: *Bathydoris*, *Polycera*, *Polycerella*, *Nembrotha* and the vast majority of *Tambja* species have oral tentacles developed as dorsoventrally flattened and horizontal grooved (0). Oral tentacles developed as elongate and dorsolaterally grooved projections are unique to *Roboastra* and *T. tentaculata* (1).

15 Anal papilla: in *Bathydoris* and in the majority of the phanerobranch dorids the anal papilla is elevated (0). In *Roboastra gracilis*, *T. capensis* and *T. amakusana* the anal papilla is not elevated (1).

16 Gill: in *Bathydoris*, *Polycerella* and most of the remaining studied taxa the gill is highly pinnate (0). Unipinnate gill branches present in *Polycera quadrilineata* and *Roboastra gracilis* are considered the apomorphic state (1).

17 Oral tube: in *Bathydoris*, *Polycera*, *Polycerella* and all *Tambja* species the oral tube is short (0). *Nembrotha* and *Roboastra* species have a long oral tube (1).

18 Salivary glands: *Bathydoris clavigera* and all the species of *Nembrotha* and *Tambja* have large salivary glands (0). Small salivary glands are present in *Polycera quadrilineata*, *Polycerella emertoni* and *Roboastra*. Reduction in the size of the salivary glands is considered the apomorphic state (1).

19 Elongated pouches in the oral tube: these elongated pouches are present neither in the outgroup taxa, nor in *Nembrotha* or the vast majority of *Tambja* species. Lack of elongated pouches in the oral tube is considered the plesiomorphic state (0). The presence of not well developed pouches is characteristic of *T. amakusana* (1) and some specimens of *T. eliora*, *T. mullineri* and *T. limaciformis* (0/1). Well developed elongated pouches are present in all *Roboastra* species (2).

20 Jaws: *Bathydoris clavigera* and *Polycera quadrilineata* have a pair of well-developed jaws (0). In *Polycerella emertoni* and *Tambja* spp., the jaws are reduced to a strong labial cuticle (1) while the reduction to a thin labial cuticle with a strong inner border is present in species of *Nembrotha* (2). *Roboastra* species have a thin and all weak labial cuticle (3), but in all genera there is considerable variability. As this is the case, the character was excluded from the final analysis.

21 *Radula: the multidenticulate radula is considered to represent the plesiomorphic state (0). The paucidenticulate radula is the apomorphic state (1).

22 Rachidian teeth: in *Bathydoris clavigera*, *Nembrotha* and *Roboastra* species and the ingroup taxa a rachidian tooth is present (0), whereas *Polycera quadrilineata* and *Polycerella emertoni* lack any rachidian tooth (1).

23 Denticles of the rachidian teeth: *Bathydoris clavigera* and all *Nembrotha* and *Roboastra* species have denticles in the rachidian teeth and this is considered the plesiomorphic state (0). All *Tambja* species lack denticles on the rachidian teeth (1). In *Polycera quadrilineata* and *Polycerella emertoni* this character is treated as non-applicable.

24 Outer denticles of the rachidian teeth: *Bathydoris clavigera*, *Nembrotha* species, *R. gracilis*, *R. europaea* and *R. caboverdensis* have not enlarged outer denticles of the rachidian teeth; this state is considered to be the plesiomorphic state (0), while enlarged outer denticles present in *R. luteolineata*, *R. tigris and R. leonis*, is the apomorphic state (1). In *Polycera quadrilineata*, *Polycerella emertoni* and *Tambja* spp. this character is treated as non-applicable.

25 Shape of the upper edge of the rachidian teeth: *Bathydoris clavigera* and the vast majority of *Tambja* especies have a notched upper margin (0), whereas *Nembrotha*, *Roboastra*, *T. oliva* and *T. limaciformis* have an un-notched upper edge of the rachidian teeth (1). This character is treated as non-applicable in species lacking rachidian teeth.

26 First lateral teeth: in *Bathydoris clavigera*, *Polycera quadrilineata*, *T. capensis*, *T. amakusana* and some specimens of *T. limaciformis* the first lateral tooth is present (0). In the rest of the species of this study the first lateral tooth has disappeared (1).

27 First lateral teeth, size: a large first lateral tooth is present in *Bathydoris clavigera* and *Polycera quadrilineata* (0). The reduction of the first lateral tooth into a vestigial tooth is considered the apomorphic state (1). This character is treated as non-applicable in species lacking first lateral teeth.

28 *Number of cusps of the second lateral teeth: *Bathydoris clavigera* has the second lateral teeth with only one cusp (0). The rest of the species in study have the inner lateral teeth with two cusps (1).

29 Inner cusp of the second lateral teeth: *Bathydoris clavigera*, *Polycera quadrilineata*, *Nembrotha* spp., *Roboastra tigris*, *R. caboverdensis*, *R. leonis*, *T. abdere*, *T. eliora*, *T. mullineri*, *T. amakusana* and *T. limaciformis* have a simple inner cusp of the second lateral teeth (0). The remaining species of this study have a bifid inner cusp (1).

30 Inner denticle of the inner cusp: in *Polycerella emertoni*, *Roboastra gracilis*, *R. luteolineata*, *R. europaea* and the vast majority of *Tambja* species the inner denticle of the inner cusp is well developed (0). In *T. ceutae* and *T. capensis* the inner denticle of the inner cusp is not well developed (1). This character is treated as non-applicable in species lacking second lateral teeth with bifid upper cusp.

31 Inner edge denticulation of the second lateral tooth: in the outgroup and most ingroup taxa, secondary denticles of the inner cusp are absent (0), whereas in *T. eliora*, *T. mullineri*, *T. sagamiana*, *T. stegosauriformis* and some specimens of *T. verconis* they are present (1). This character is treated as non-applicable in species lacking second lateral teeth with bifid upper cusp.

32 Outer cusp of the lateral teeth: in *Bathydoris clavigera* the outer cusp of the lateral teeth is absent (0). In *Polycerella emertoni*, *T. amakusana* and *T. limaciformis* the outer cusp of the second inner lateral teeth is hardly developed (1). In the rest of the species studied in this paper the innermost lateral teeth have a well developed outer cusp (2).

33 Outer lateral teeth, number: the multidenticulate radula is considered to represent the plesiomorphic state (0). The reduction in the number of outer lateral teeth is considered as the apomorphic state (1). *T. eliora* might have both states (0/1). Since the number of remaining outer lateral teeth appears to vary considerably, this character was excluded from the final analysis.

34 *Outer lateral teeth, shape: outer laterals not differentiated from the inner laterals are considered to be the plesiomorphic, whereas the simplification of the outer laterals into plates ('marginals') is the apomorphic state. Outer hook-shaped laterals are present in *Bathydoris clavigera* and *Polycerella emertoni* (0); in the ingroup taxa the outer laterals are plate-like (1).

35 *Length of the outer lateral teeth (r:L/l): (L = width; l = height). In the outgroup taxa and the vast majority of ingroup taxa $r > 1$ and this is considered the plesiomorphic state (0). In *Roboastra gracilis* $r < 1$ (1).

36 Ampulla, shape: the ampulla is convoluted in *Bathydoris clavigera*, *Nembrotha* species and *Tambja abdere* (0). *Roboastra* and the vast majority of ingroup taxa have an 'S'-shaped ampulla (1). *Polycera quadrilineata* and *Polycerella emertoni* have an elongated ampulla (2).

37 *Bursa copulatrix, shape: in the outgroup and most of the ingroup taxa the bursa copulatrix has a spherical shape (0). *Tambja abdere* has a bursa copulatrix with two differentiated portions (1).

38 Prostate: *Bathydoris clavigera*, *Roboastra* spp. and the vast majority of *Tambja* species have a slightly morphologically differentiated prostate (0). *Polycera quadrilineata*, *Polycerella emertoni*, all *Nembrotha* species and three species of *Tambja* (*T. abdere*, *T. amakusana* and *T. limaciformis*) have a well-differentiated prostatic section (1). However, the state of development is different in *Nembrotha* from species of *Tambja* and intermediate conditions are found in some species. Because of these intermediate states this character was excluded from the final analysis.

39 Prostate arrangement: in most of the outgroup taxa, and the vast majority of *Tambja* species the prostate is confined to a coiled section of the vas deferens (0). In all *Nembrotha* species and *T. abdere*, *T. amakusana* and *T. limaciformis* the prostate, *in situ*, surrounds entirely or partially the bursa copulatrix (1).

40 Vagina, length: in most of the outgroup and ingroup taxa the vagina is short (0), whereas in *Nembrotha* spp. and *T. abdere* the vagina is long (0).

41 Vagina, width: in *Bathydoris clavigera*, *Polycera quadrilineata*, *Nembrotha* species, *T. amakusana* and *T. limaciformis* the vagina is wide (0), whereas in the rest of the taxa studied it is narrow (1).

42 Vagina, shape: in the outgroup and the vast majority of the ingroup taxa the vagina is straight (0), whereas in *Nembrotha lineolata*, *N. chamberlaini* and *T. abdere* it is highly convoluted (1).

43 Vaginal gland: a vaginal gland is absent in *Bathydoris clavigera*, *Polycera quadrilineata*, *Polycerella emertoni*, *Nembrotha* species and in *T. abdere*, *T. amakusana* and *T. limaciformis* (0). The remaining species of the ingroup taxa and *Roboastra* have a well-developed vaginal gland (1).

44 Duct of the seminal receptacle: in *T. abdere* and *T. limaciformis* the duct joining the seminal receptacle to the bursa copulatrix is long (0), whereas in the rest of the studied taxa it is short (1). In *Bathydoris clavigera* this character is treated as missing.

45 Deferent duct: the outgroup taxa and the vast majority of the ingroup taxa have a narrow deferent duct (0), while *T. marbellensis*, *T. simplex*, *T. sagamiana*, *T. affinis*, *T. morosa*, *T. olivaria* and *T. gabrielae* have a wide deferent duct (1).

46 Penial spines, number: *Bathydoris clavigera* lacks penial spines within the vas deferens and thus the absence of spines is considered the plesiomorphic state (0). A low density of spines is found in most of the ingroup taxa (1) whereas *T. marbellensis*, *T. simplex*, *T. sagamiana*, *T. affinis*, *T. morosa*, *T. olivaria* and *T. gabrielae* have a high density of penial hooks (2).

47 Penial spines, types: the presence of one or two different kinds of spine is found in *Polycera quadrilineata*, *Polycerella emertoni*, *N. lineolata*, *N. chamberlaini* and the vast majority of *Tambja* species (0), while *Nembrotha kubaryana*, *N. cristata*, *Roboastra* spp., *T. limaciformis* and *T. zulu* have three different kinds of spines (1). In *Bathydoris clavigera* this character is treated as missing.

48 *Reproductive system arrangement: having a diaulic reproductive system is considered the plesiomorphic state (0). The rest of the species of this study have a triaulic condition (1).

49 Food: *Bathydoris clavigera* is a generalist predator (0), while *Polycera quadrilineata*, *Polycerella emertoni* and *Tambja* species feed on bryozoans (1). *Nembrotha* species feed on ascidians (2), while species of *Roboastra* feed on other nudibranchs, mainly polycerids (3).