FOUR NEW SPECIES OF *TAMBJA* BURN, 1962 (NUDIBRANCHIA: POLYCERIDAE) FROM THE INDO-PACIFIC

MARTA POLA[1], J. LUCAS CERVERA[1] AND TERRENCE M. GOSLINER[2]

[1]*Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Apdo. 40, 11510 Puerto Real, Cádiz, Spain;*
[2]*Department of Invertebrate Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA*

(Received 21 June 2004; accepted 20 January 2005)

ABSTRACT

The genus *Tambja* previously included 24 described species. Four new species, *T. tentaculata* n. sp., *T. gabrielae* n. sp., *T. zulu* n. sp. and *Tambja victoriae* n. sp., from the Indo-Pacific are described. *Tambja tentaculata* n. sp., from Guam, is the only known species in the genus with well developed, dorsolaterally grooved, oral tentacles. Its inner lateral teeth have a bifid inner cusp with two long, sharp denticles. The oral tentacles of *T. tentaculata* are more typical of *Roboastra* species, while the shape of the inner lateral teeth is more typical of *Tambja*. Nevertheless, the arrangement of the two cusps of the inner lateral teeth and the presence of a rachidian tooth without denticles and with a central notch at the anterior edge, typical of the species of the genus *Tambja*, suggest the placement within this genus. *Tambja gabrielae* n. sp., from Indonesia and Papua New Guinea, has dark green to dark brown ground colour with bright yellow patches scattered on the body. *Tambja zulu* n. sp. from Durban, South Africa, is characterized by a black ground colour with slender yellow longitudinal lines. *Tambja victoriae* n. sp. is a new species from Papua New Guinea and Australia that has frequently been misidentified as *Roboastra arika*, characterized by its blue body colour and yellow lines. The four species are distinguishable based on differences in body coloration, of characters of the radula and of the reproductive system. An overview on distinguishing features of all known Indo-Pacific *Tambja* species is presented.

INTRODUCTION

The genus *Tambja* was introduced by Burn (1962) for two species of *Nembrotha* from the Indo-Pacific, *Nembrotha verconis* Basedow & Hedley, 1905, designated as the type species, and *N. sagamiana* Baba, 1955, from Japan. Until the description of this new genus, *Nembrotha* was erroneously placed in the subfamily Gymnodorididae. Burn (1962) demonstrated that *Nembrotha* is a relative of *Tambja* and placed it, together with *Roboastra* (Bergh, 1877), within the family Polyceridae and in a new subfamily, Nembrothinae, based upon several external and internal differences. The genus *Roboastra* is unique in having oral tentacles strongly developed as dorsolaterally-grooved cylindrical projections; the labial cuticle can be weak (*Roboastra, Nembrotha*) or thick (*Tambja*); the rachidian radular tooth can be rectangular with four to five denticles along upper margin (*Nembrotha*), rectangular with notched or smooth upper margin (*Tambja*), or reduced with three prongs or well-defined denticles (*Roboastra*); and the prostate gland can be large, racemose and spread over the bursa copulatrix (*Nembrotha*) or small, confined to a glandular section of the deferent duct (*Tambja, Roboastra*).

Burn (1967) considered *Tambja* to be composed of 11 nominal species: *T. diaphana* (Bergh, 1877), *T. morosa* (Bergh, 1877), *T. gratiosa* (Bergh, 1877), *T. affinis* (Eliot, 1904), *T. verconis* (Basedow & Hedley, 1905), *T. amitina* (Bergh, 1905), *T. capensis* (Bergh, 1907), *T. limaciformis* (Eliot, 1908), *T. tabescens* (Risbec, 1928), *T. sagamiana* (Baba, 1955) and *T. divae* (Marcus, 1958), most of them with an Indo-Pacific distribution.

Correspondence: Marta Pola; e-mail: marta.pola@uca.es

To date, knowledge of the genus *Tambja* has been increased with the description of six additional species in the Atlantic Ocean (*T. oliva* Meyer, 1972; *T. fantasmalis* Ortea & García-Gómez, 1986; *T. ceutae* García-Gómez & Ortea, 1988; *T. anayana* Ortea, 1989; *T. marbellensis* Schick & Cervera, 1998, *T. simplex* Ortea & Moro, 1999); three new species from the Eastern Pacific (*T. eliora* Farmer, 1978; *T. abdere* Farmer, 1978) and Galápagos Islands (*T. mullineri* Farmer, 1978) and three new species from the Indo-Pacific (*T. amakusana* Baba, 1987; *T. kushimotoensis* Baba, 1987; *T. olivaria* Yonow, 1994). The present paper describes four new species of the genus *Tambja* from the Indo-Pacific and compares them with the rest of the Indo-Pacific species of the genus based upon radular and genital differences.

MATERIAL AND METHODS

The material examined for this study is deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), the Natal Museum, South Africa (NMSA), and the Zoologische Staatssammlung München, Munich (ZSM).

The specimens were dissected and morphological examination was facilitated by first making a dorsal incision. The internal features were examined and drawn using a dissecting microscope with a camera lucida. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, 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.

 doi:10.1093/mollus/eyi034

SYSTEMATIC DESCRIPTIONS

Suborder DORIDOIDEA

Family POLYCERIDAE Alder & Hancock, 1845

Genus *Tambja* Burn, 1962

Type species: *Tambja verconis* (Basedow & Hedley, 1905)

Diagnosis: Polycerids, without frontal or velar processes and a vestigial frontal veil. Rachidian rectangular with notched or smooth upper margin, lateral tooth bifid or with a simple cusp and from three to seven marginal plates. Strong buccal collar and labial armature absent. Prostate gland small and confined to a glandular section of the vas deferens.

***Tambja tentaculata* new species**

(Figures 1A, 2A, B, 3A, 4A)

Type material: Holotype: CASIZ 162638, Apra Harbour, Western Shoals, Guam, July 2003, collected by C. Carlson, 20 mm alive, 8 m depth. Paratypes: CASIZ 162639, 1 spec., Apra Harbour, Western Shoals, Guam, July 2003, collected by C. Carlson, 20 mm alive, 8 m depth; CASIZ 162640, 1 spec., Apra Harbour, Sponge Mound, Guam, January 1997, collected by C. Carlson, 20 mm alive, 21 m depth.

Other material: CASIZ 072561, 1 spec., Apra Harbour, Guam, June 1975, collected by E. W. Iverson, 25 mm preserved, 0–1.5 m depth. Four additional specs of 15–23 mm alive were collected by M. Pola in Apra Harbour, Western Shoals, Guam, September 2004, 9–14 m depth, but not studied in this paper.

Etymology: The name *tentaculata* refers to the large and well developed oral tentacles, more similar to the oral tentacles of species of *Roboastra* than to those of *Tambja*.

External morphology: Body elongate, limaciform, with long, pointed posterior end of foot. Preserved animals 10 mm long, living animals (Fig. 1A) 20 mm. Body surface smooth, foot linear. Morphology of head characteristic where anterior margin of notum dips into 'V' or 'U' shape. A pair of conical, completely retractile, perfoliate rhinophores with *ca* 20 lamellae. Rhinophoral sheaths well developed. Oral tentacles well developed, grooved dorsolaterally along outer part of their length. Five non-retractile, bipinnate gills surround tubular anal papilla, forming a half circle; three central gills larger than two lateral. Genital pore opens on right side, midway between gills and rhinophores. Ground colour green with several longitudinal yellow bands. Oral tentacles, rhinophoral sheaths, rhinophores, genital pore and gills also green, as well as anterior and lateral margins of notum. Base of oral tentacles bears yellow pigment. Three dorsal bands; two submarginal and one mid-dorsal; two submarginal yellow bands run along inner sides of notal lateral margins and rhinophoral sheaths, joining at posterior end of notum and again at anterior part of head; from this junction another yellow band extends posteriorly to anterior end of rachis of central branch continuing again for short distance behind tubular anal papilla. Two further bands along each side of body; upper bands join between anterior notal margin and oral tentacles; lower yellow bands arise from base of oral tentacles, almost reaching posterior end of foot and uniting or remaining separate (in different specs). Minute brown pigmentation surrounds outer edges of all yellow bands. Small lateral slots of unknown function, difficult to see in some specs, located between rhinophores and oral tentacles.

Internal morphology: Anterior digestive tract begins with short thick-walled muscular oral tube that continues into buccal mass. A pair of large, wide salivary glands on buccal mass, flanking oesophagus. Buccal bulb large. Chitinous labial cuticle orange, thick, smooth. Radular formula $19 \times 4.1.1.1.4$ (2 specs, 20 mm long alive). Rachidian tooth (Fig. 2A) broad, rectangular, without denticles; central notch at anterior edge. Inner lateral tooth elongate with two well developed, wide cusps; inner cusp bifid, with two long, sharp denticles; outer denticle of inner cusp usually longer and sharper than inner one (Fig. 2B); outer cusp well developed, triangular. Outer lateral teeth roughly rectangular, decreasing in size towards outer margin. A small, rounded yellow blood gland located near reproductive system. Renal syrinx visible under pericardium, close to anal papilla.

Reproductive system triaulic (Fig. 3A). Hermaphroditic duct has a large, thick-walled, S-shaped ampulla that continues into spermoviduct. Vas deferens short, with uniformly wide, undifferentiated prostatic part, ending in small penial section. Penis armed with hooked spines (Fig. 4A). Vaginal duct wide, short, connecting to rounded bursa copulatrix. Seminal receptacle prolonged and longer than bursa copulatrix. Uterine duct leaves vagina in distal position, before duct of seminal receptacle, joins with oviduct. A small pyriform vaginal gland opens with vagina in common aperture within genital atrium. Mucous gland well developed. Genital mass fills whole second quarter of body cavity.

Distribution: So far only known from Guam.

Remarks: *Tambja tentaculata* could be misidentified as a member of the genus *Roboastra* in having well developed, grooved, dorsolateral oral tentacles. Nevertheless, the presence of a thick labial cuticle, its radula with a notched, rectangular rachidian tooth without denticles, and the ground shape of the inner lateral tooth, lead us to include this species within the genus *Tambja*. A lateral tooth having a deeply bifid inner cusp was considered typical of *Roboastra* (Burn, 1967). However, *R. tigris* Farmer, 1978 (Farmer, 1978) and *R. caboverdensis* Pola, Cervera & Gosliner, 2003 (Pola, Cervera & Gosliner, 2003) have a lateral tooth with a simple inner cusp. *Tambja tentaculata* is also clearly distinguishable from other species of this genus by its coloration (see Table 1). No other known Indo-Pacific species of this genus has a green ground colour with wide longitudinal yellow bands. *Tambja tentaculata* also differs from the other Indo-Pacific species by the morphology of the head, where the anterior margin of the notum dips into a V or U shape. This feature is shared by an eastern Pacific species, *Tambja eliora* (Farmer, 1978). Other differences include the morphology of the reproductive system, with a larger seminal receptacle than that found in other species of *Tambja*.

***Tambja gabrielae* new species**

(Figures 1B, 2C, D, 3B, 4B)

Type material: Holotype: CASIZ 162702, N Sulawesi, Lembeh Strait, Indonesia, April 2002, collected by C. Petrinos, 50 mm alive. Paratypes: CASIZ 073172, 1 spec., Cowo Island, Banda Sea, Indonesia, September 1986, collected by J. McCosker, 30 mm preserved; CASIZ 162701, 1 spec., N. Sulawesi, Lembeh Strait, Indonesia, April 2002, collected by C. Petrinos, 40 mm alive; ZSM-Moll 20033884, 4 specs, NE Sulawesi, Lembeh Strait: 'Nudi Falls', Indonesia, July 2003, collected by M. Schrödl, 15, 20, 25 and 28 mm preserved; ZSM-Moll 20034036, 2 specs, NE Sulawesi, Lembeh Strait: 'Nudi Falls', Indonesia, July 2003, collected by M. Schrödl, 18 and 30 mm preserved.

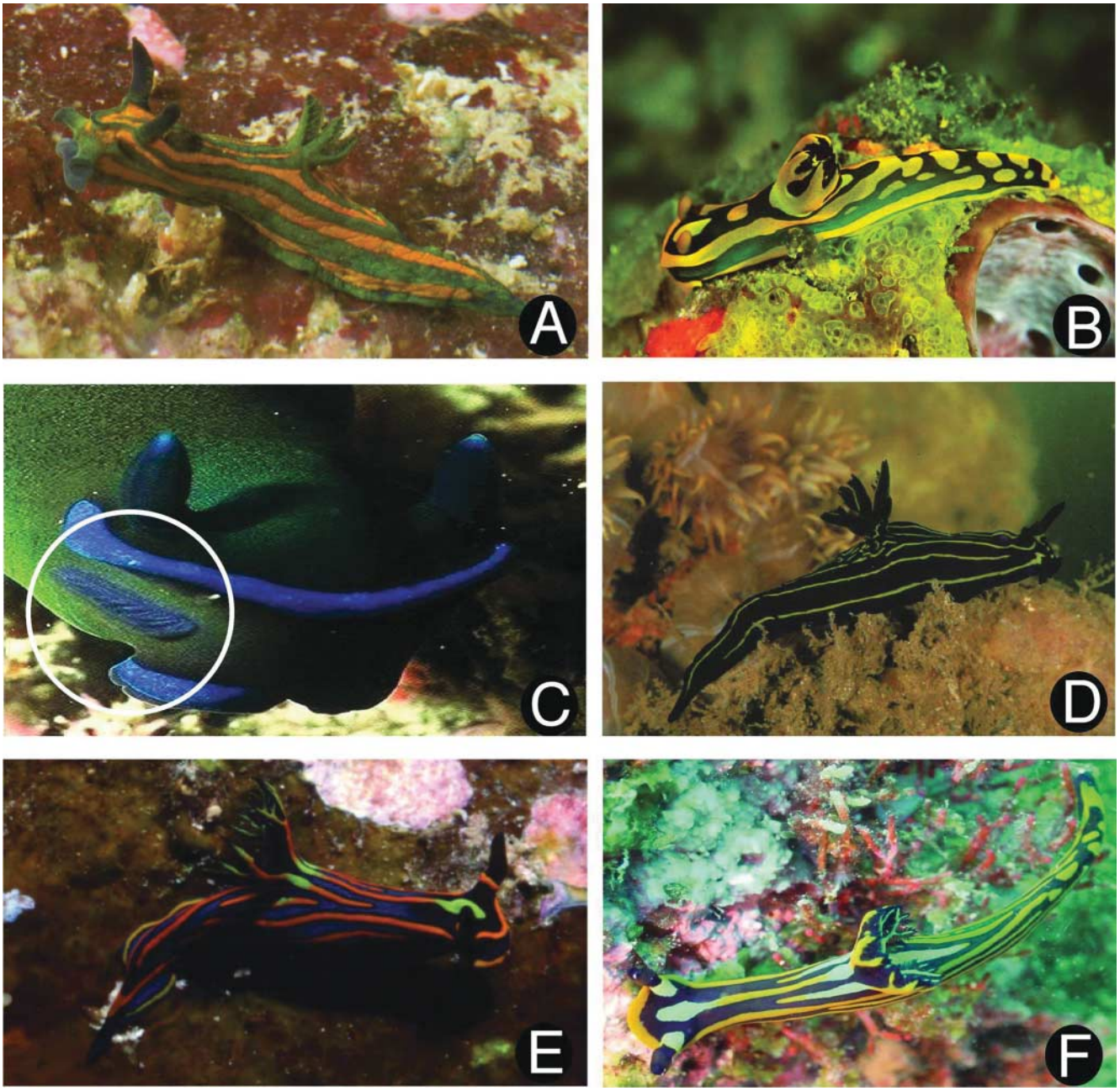

Figure 1. Photographs of the living animals. **A.** *Tambja tentaculata* n. sp. (CASIZ 162638), Apra Harbour, Guam. Photo by Clay Carlson. **B.** *Tambja gabrielae* n. sp. (CASIZ 162702), Sulawesi, Indonesia. Photo by Constantinos Petrinos. **C.** *Tambja morosa*, Taiwan. Photo by Todd Garthwaite. Circle indicates the lateral slots. **D.** *Tambja zulu* n. sp. (NMSA E6323/T2006), Durban, South Africa. Photo by D. Herbert. **E.** *Tambja victoriae* n. sp. (CASIZ 075810), Papua New Guinea. Photo by T. M. Gosliner. **F.** *Tambja affinis*, The Comores, Indian Ocean. Photo by Marina Poddubetskaia.

Etymology: This species is dedicated to Gabriela Pola, the first niece of the first author of this paper.

External morphology: Body elongate, limaciform, with long pointed posterior end of foot. Preserved animals 15–40 mm long. Living animals (Fig. 1B) may reach 45 mm. Body surface smooth. Foot linear. Head wide with pair of conical, completely retractile, perfoliate rhinophores with *ca* 40 tightly packed lamellae. Rhinophoral sheaths well developed. Oral tentacles short, dorso-ventrally flattened, with horizontal groove. Three well developed, non-retractile, tripinnate gills form semicircle surrounding tubular anal papilla. Genital pore opens on right side, midway between gills and rhinophores. Ground colour dark green, with bright yellow patches scattered on dark green ground; wide bright yellow band around edge of notum extends to posterior part of gills. Another band of same colour runs on both flanks of body interrupted posteriorly, but continues along back of tail to its end; this bright yellow band also covers oral tentacles. Another wide bright yellow band also runs along edge of foot. There are two large yellow patches on anterior part of body, one between rhinophores and other located just behind former and gills. Yellow patches on posterior part of body have an irregular arrangement. Gills dark green, but a yellow line runs along inner and outer side of rachis of each. Base of gill circle bright yellow. Rhinophoral sheaths dark green, rhinophores and oral tentacles bright

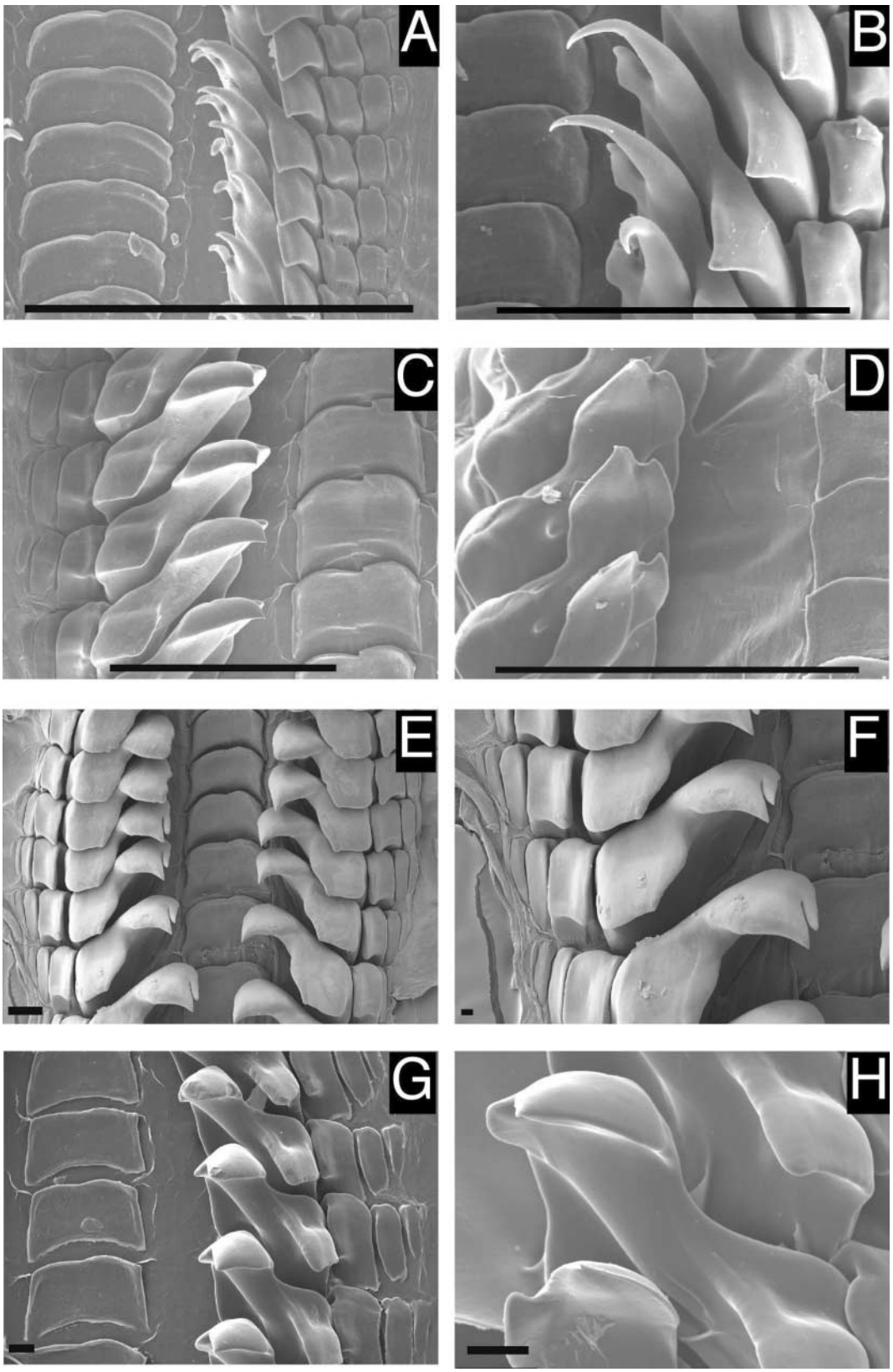

Figure 2. Scanning electron micrographs of the radula of four *Tambja* species. **A.** Left half of radula, *T. tentaculata* n. sp. (CASIZ 162639). Scale bar = 500 μm. **B.** Innermost lateral teeth, *T. tentaculata* n. sp. (CASIZ 162639). Scale bar = 300 μm. **C.** Left half of radula, *T. gabrielae* n. sp. (CASIZ 162702). Scale bar = 500 μm. **D.** Innermost lateral teeth, *T. gabrielae* n. sp. (CASIZ 162702). Scale bar = 300 μm. **E.** Radula, *T. zulu* n. sp. (NMSA E6323/T2006). Scale bar = 100 μm. **F.** Innermost lateral teeth, *T. zulu* n. sp. (NMSA E6323/T2006). Scale bar = 20 μm **G.** Right half of radula, *T. victoriae* n. sp. (CASIZ 075810). Scale bar = 30 μm. **H.** Innermost lateral teeth, *T. victoriae* n. sp. (CASIZ 076335). Scale bar = 30 μm.

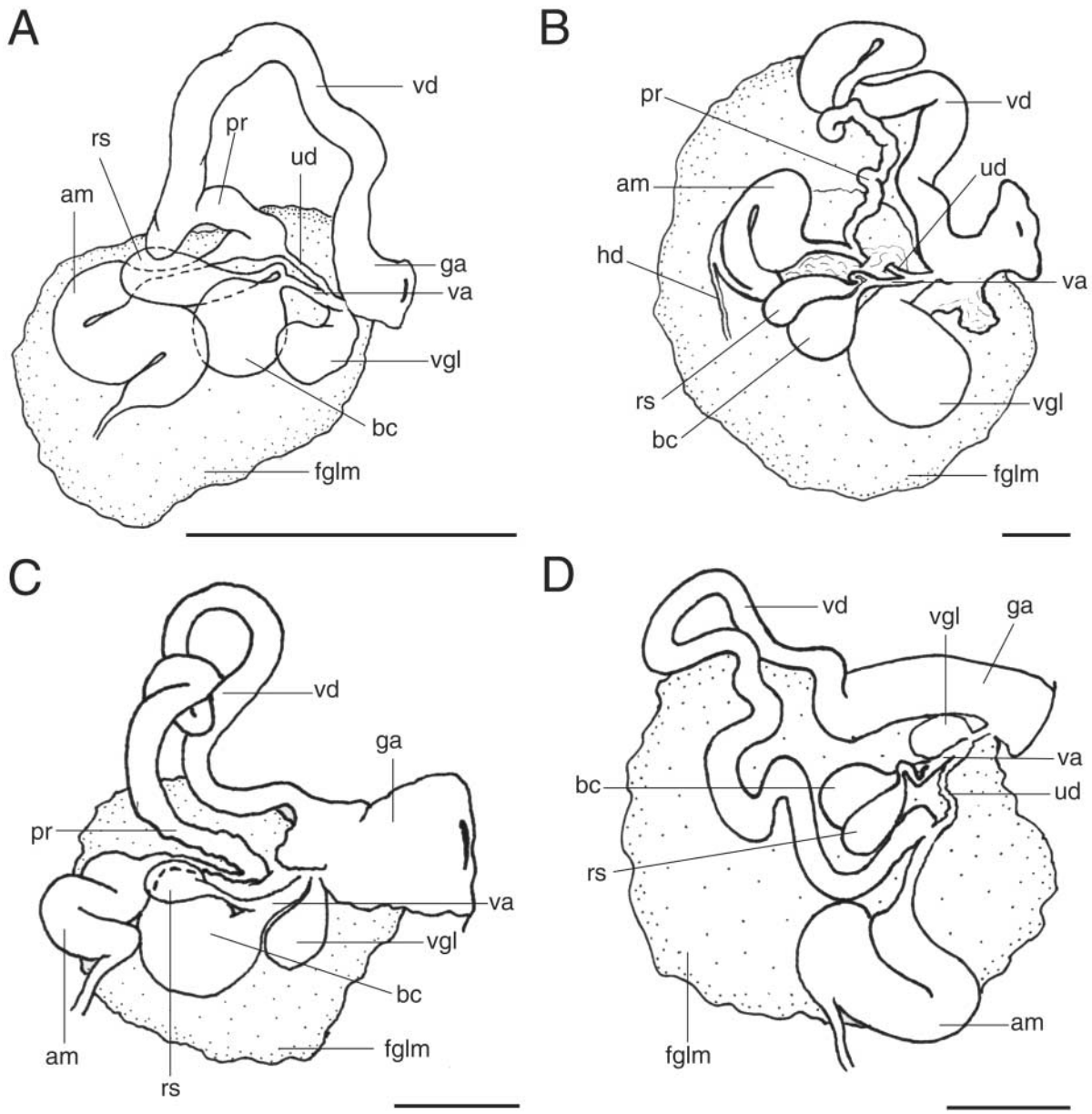

Figure 3. Reproductive systems of four *Tambja* species. **A.** *T. tentaculata* n. sp. **B.** *T. gabrielae* n. sp. **C.** *T. zulu* n. sp. **D.** *T. victoriae* n. sp. Scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; p, penis; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens; vgl, vaginal gland.

yellow. Lateral slots of unknown function located between rhinophores and oral tentacles.

Internal morphology: Anterior digestive tract begins with short, thick-walled, muscular oral tube, continuing into buccal mass. A pair of large, wide salivary glands on buccal mass, flanking oesophagus. Buccal bulb small in comparison with reproductive system. Chitinous labial cuticle thick, devoid of rodlets. Radular formula 18 × 3.1.1.1.3 (2 specs, 40 and 50 mm long alive). Rachidian tooth (Fig. 2C) blunt, quadrangular, without denticles, notched at anterior edge. Inner lateral tooth elongate, two well developed wide cusps; inner cusp bifid, with small denticle on inner edge (Fig. 2C, D). Outer lateral teeth roughly rectangular, decreasing in size towards outer margin. In some rows there can be four teeth with last one very small. A large blood gland on intestinal loop. Renal syrinx visible under pericardium, close to anal papilla.

Triaulic reproductive system (Fig. 3B). A long and slender hermaphroditic duct continues as S-shaped ampulla with thick walls. Ampulla narrows into postampullary duct that connects to oviduct and prostate. Short oviduct enters massive female gland mass. Prostate gland small, slightly morphologically differentiated, confined to coiled section of vas deferens with soft glandular walls. At end of prostate vas deferens widens into large duct with numerous unordered, elongate penial spines (Fig. 4B). Vaginal duct short, usually straight, connects to large, round bursa copulatrix. Seminal receptacle pyriform, similar in size to bursa copulatrix. Short duct connects seminal receptacle to vagina, after completing two loops, near bursa. Slender uterine duct leaves vagina in distal position before duct of seminal receptacle and joins with female gland. Vagina shares common aperture within genital atrium with vaginal gland. Vaginal gland very large, elongate, flattened, with

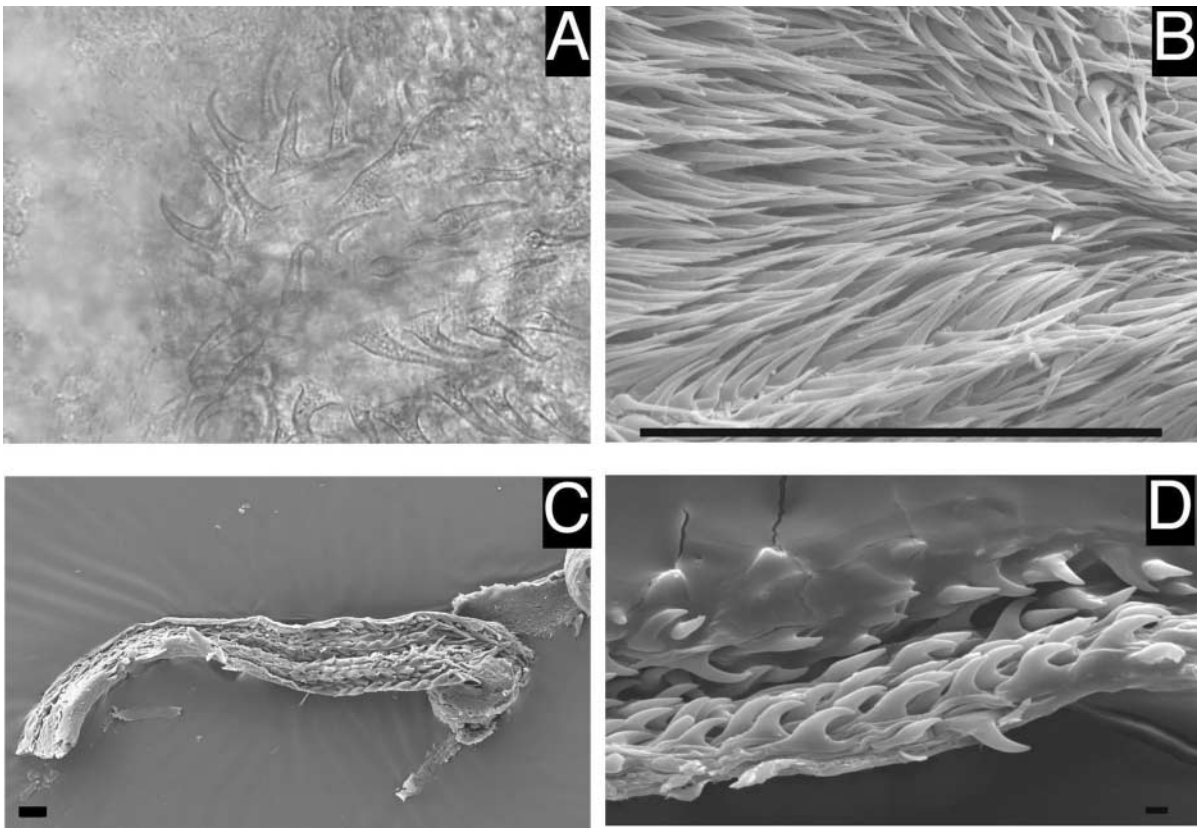

Figure 4. Penial morphology of four *Tambja* species. **A.** *T. tentaculata* n. sp. (CASIZ 162639). **B.** *T. gabrielae* n. sp. (CASIZ 162701). Scale bar = 300 μm. **C.** *T. zulu* n. sp. (NMSA E6323/T2006). Scale bar = 20 μm. **D.** *T. victoriae* n. sp. (CASIZ 075810). Scale bar = 3 μm.

muscular walls. Mucous gland well developed. Genital mass fills whole of second quarter of body cavity.

Distribution: So far known from Sulawesi (Indonesia) and Papua New Guinea.

Remarks: This species is clearly distinguishable from the other species of *Tambja* by having large bright yellow spots on the dark green notum. *Tambja morosa* and *T. sagamiana* also have dorsal spots, but both of them differ from *T. gabrielae* in the colour pattern. *Tambja morosa* has a few blue spots on the dark blue or black notum while *T. sagamiana* has a higher number of yellow or orange spots surrounded by a ring of dark brown pigment on a blue notum. These three species also differ anatomically (Table 1). The rachidian teeth are rectangular in *T. morosa* and *T. sagamiana*, whereas they are quadrangular in *T. gabrielae*. The upper cusp of the innermost lateral tooth is bifid in the three species, but in *T. morosa* and *T. sagamiana* it has two well developed denticles, while in *T. gabrielae* the inner denticle is small, more similar to a wide brim than a real denticle. The reproductive system shares important features in these species. All of them have an armed penis with many unordered spines and a large vaginal gland. *Tambja gabrielae*, *T. morosa*, *T. sagamiana*, *T. olivaria*, *T. affinis* and *T. victoriae* share another interesting feature. All of them, on both sides of the body between the rhinophores and the oral tentacles, have lateral slots (Fig. 1C) whose function is unknown. These structures are heavily innervated, so they may be chemosensory and used to locate food (presumably colonies of Ectoprocta). Pictures of this species from Sulawesi have been reported in the *Seaslug Forum* as *Tambja* sp. 5 (http://www.seaslugforum.net/tambsp5.htm).

***Tambja zulu* new species**

(Figures 1D, 2E, F, 3C, 4C)

Type material: Holotype: NMSA E6323/T2006, Durban, South Africa, April 1989, collected by D. Herbert, 20 mm preserved, 25–28 m depth. Paratype: CASIZ 074085, 1 spec., Durban, Natal, South Africa, August 1980, collected by W. R. Liltved, 20 mm preserved, 3 m depth under stones.

Etymology: The specific name refers to KwaZulu-Natal and the Zulu Kingdom, the traditional home of the Zulu people. This South African province includes Durban, which is the type locality of the species.

External morphology: Body elongate, limaciform, with long pointed posterior end of foot (Fig. 1D). Preserved animals 20 mm long. Body surface smooth with longitudinal stripes on notum and both sides. Ground colour dark blue or black. A greenish yellow band follows notal edge, surrounding anterior part of head, and joins in middle part of posterior end of foot. Another two longitudinal bands, arising from this anterior notal edge, border rhinophoral sheaths and continue to outer rachis of two anteriormost gills. Between longitudinal and notal band another greenish yellow band continues to base of gills. A greenish yellow line laterally, above mouth, bifurcates in two; these two lines continue until they almost contact posterior end of foot. Foot linear, edge of foot dark blue or black. Head slightly expanded with pair of conical, completely retractile perfoliate rhinophores. Oral tentacles short, dorsoventrally flattened, with horizontal groove. Five non-retractile tripinnate gills form semicircle surrounding elevated, black, anal papilla. Gills black, but outer and inner sides of rachis

Table 1. Comparison of the Indo-Pacific species of the genus *Tambja* Burn, 1962.

	T. diaphana (Bergh, 1877)	*T. morosa* (Bergh, 1877)	*T. affinis* (Eliot, 1904)	*T. verconis* (Basedow & Hedley, 1905)	*T. amitina* (Bergh, 1905)	*T. capensis* (Bergh, 1907)
Ground colour	Greenish-grey, darker at sides of head, on sides, at brim of foot, at rhinophores and at gill (preserved material).	Body shining in a metallic dark green, front of head bordered in dark blue.	Dull violet-black with dull yellow stripes on sides and brighter ones of same colour on back; light green between rhinophores and rhinophoral sheaths.	Bright yellow sparsely covered by dark blue spots.	Dark notum, grey-blue.	Colour uniformly deep blackish blue or black; sole of foot yellowish white; edge of notum green.
Rhinophores	Not described.	Light green; perfoliate.	Fine purple, 35 perfoliations.	Deep blue with yellow stalk, about 30 lamellae.	Red-yellowish.	Blue black, 30 lamellae.
Gills	Not described.	5, large, branched; light green.	3, thick rachis, bipinnate; pinnae fine purple; stems and bases light green.	5, tripinnate; dark yellow at base, rich blue along stems and small purple tufts.	2, black.	7, tripinnate; gills with axes black, finer branches blue.
Oral tentacles	Not described.	Not described.	Two hard, black ridges, curved downwards and sideways.	Not described.	Not described.	Short, refolded on top.
Foot	Darker line on keel of the tail.	Back of tail and brim of foot blue.	Very narrow and grooved in front.	Square in front, dilated outwardly at anterior edge.	Red-yellowish.	'As usual in Nembrothinae'.
Radula	Not described.	23 × 3.1.1.1.3. Upper cusp of innermost lateral tooth bifid.	13 × 3.1.1.1.3. Upper cusp of innermost lateral tooth bifid.	18 × 4.1.1.1.4. Upper cusp of innermost lateral tooth bifid.	18 × 3–4.1.1.1.3–4. Upper cusp of innermost lateral tooth simple.	14–19 × 5–6.1.1.1.5–6. Upper cusp of innermost lateral tooth simple.
Reproductive system	Not described.	Genital mass oval. Penis armed with closely packed thorns. Vagina with very strong longitudinal folds.	Not described.	Not described.	Penis with characteristic spines, tightly packed.	Deferent duct lacking morphologically differentiated prostate. Bursa copulatrix bigger than seminal receptacle. Vaginal gland present. Penis with spines.
Geographical range	Philippines	Tropical Indo-Pacific Ocean.	East Coast of Zanzíbar (Tanzania); Comores Islands; Red Sea.	Australia.	Indonesia.	Cape Province (South Africa).
References	Bergh (1877)	Bergh (1877, 1905); Marshall & Willan (1999).	Eliot (1904); Yonow (1990); Reyniers (2003); present study.	Basedow & Hedley, 1905); Burn (1962).	Bergh (1905).	Bergh (1907); Barnard (1927); Macnae (1958); Gosliner (1987).

Continued

Table 1. (*continued*)

	T. limaciformis (Eliot, 1908)	*T. tabescens* (Risbec, 1928)	*T. sagamiana* (Baba, 1955)	*T. amakusana* (Baba, 1987)	*T. kushimotoensis* (Baba, 1987)	*T. olivaria* (Yonow, 1994)
Ground colour	Deep saffron-red, back and sides flecked with yellowish or entirely plain; sole uniformly saffron-red.	Deep red with yellow patches as 'V' behind gills.	Yellow spots irregularly scattered on indigo-black ground of body.	Yellowish green without any trace of spots, but with a few indistinct tubercles on mantle edge on either side.	Deep green; bold roundish blue spots on each side of back posterior to gills and near tip of the tail; velar margin blue.	Olive green with black and yellow-orange markings, latter becoming yellow-green in places.
Rhinophores	Saffron-red, with subapical purple spot.	Red with yellow on tips.	Indigo black.	Yellow with deep blue on tips.	Green, tips blue.	Black.
Gills	3–5, bipinnate; yellowish white, tipped with purple.	3, bipinnate; yellowish.	3, the lateral ones deeply bifurcated; rachis green.	5, bipinnate; branchial rachices yellowish green; deep blue on tips.	3, tripinnate; green pinnae black; inner rachis yellow; outer rachis blue.	3, deeply bifurcate; yellow orange to yellow green, bordered along edges and base by deep green band.
Oral tentacles	Lobiform.	Not described.	'As usual grooved'.	Thin flat lobes, their margin may be folded ventrally.	Grooved, blue.	Deep green.
Foot	Not described.	Not described.	Foot margins green.	Not described.	Foot margin and sole blue.	Margin brighter green, edged in blue.
Radula	8–12 × 5–6.1.1.1.5–6. Upper cusp of innermost lateral tooth simple.	11–12 × 7–8.1.1.1.7–8. Upper cusp of innermost lateral tooth simple.	18 × 3.1.1.1.3. Upper cusp of the innermost lateral tooth bifid.	10 × 4–5.1.1.1.4–5. Upper cusp of innermost lateral tooth bifid (one of two denticles very small).	18–22 × 3–4.1.1.1.3–4. Upper cusp of innermost lateral tooth bifid.	16 × 3.1.1.1.3. Innermost lateral tooth large and spathulate.
Reproductive system	Not described.	Not described.	Not described.	Not described.	Not described.	Not described.
Geographical range	Japan.	New Caledonia.	Japan.	Japan.	Japan; Mauritius.	Maldive Islands.
References	Baba (1960).	Risbec (1928).	Baba (1955).	Baba (1987).	Baba (1987); Yonow & Hayward (1991).	Yonow (1994).

Continued

Table 1. (*continued*)

	T. tentaculata n.sp.	*T. gabrielae* n.sp.	*T. zulu* n.sp.	*T. victoriae* n.sp.
Ground colour	Green ground (including rhinophoral sheaths), with several longitudinal yellow bands; outer edges of yellow bands surrounded by minute brown pigmentation.	Black with scattered bright yellow patches; wide bright yellow band around edge of notum extending to posterior part of gills.	Dark blue or black with greenish-yellow longitudinal lines.	Blue with orange or yellowish stripes bordered with a wide black line; same colour on rhinophoral sheaths; green patches between the rhinophores and stems of gills.
Rhinophores	20 lamellae; green.	40 lamellae; bright yellow.	Dark blue or black.	40 lamellae; dark blue or back.
Gills	5, bipinnate; green.	3, tripinnate; black with inner and outer rachis yellow; base of gill circle also bright yellow.	5, tripinnate; dark blue or black; inner and outer rachis with narrow greenish-yellow line.	3, multipinnate, very bifurcated; inner rachis and tips green; outer rachis orange or yellowish.
Oral tentacles	Green; well developed and grooved dorso-laterally.	Yellow; shorts, dorso-ventrally flattened, with horizontal groove.	Dark blue or black; short, dorso-ventrally flattened, with horizontal groove.	Dark blue; short, dorso-ventrally flattened, with a horizontal groove.
Foot	Linear; green.	Linear; yellow.	Linear; black.	Orange or yellowish.
Radula	19 × 4.1.1.1.4. Upper cusp of innermost lateral tooth bifid (both denticles well developed).	18 × 3.1.1.1.3. Upper cusp of innermost lateral tooth bifid (inner denticle smaller).	17–19 × 3–4.1.1.1.3–4. Upper cusp of innermost lateral tooth bifid.	14–18 × 4.1.1.1.4. Upper cusp of innermost lateral tooth bifid.
Reproductive system	Deferent duct lacking morphologically differentiated prostate. Seminal receptacle larger than bursa copulatrix. Small vaginal gland present. Penis with a few hooked spines.	Deferent duct with prostate slightly morphologically differentiated. Bursa copulatrix and seminal receptacle of equal size. Large vaginal gland present. Penis with many and unordered spines.	Deferent duct with prostate slightly morphologically differentiated. Bursa copulatrix bigger than seminal receptacle Small vaginal gland present. Penis with three kinds of spines in longitudinal lines.	Deferent duct without a differentiated prostate. Bursa copulatrix similar in size to seminal receptacle. Small vaginal gland present. Penis with hooked spines in longitudinal lines.
Geographical range	Guam.	Indonesia; Papua New Guinea.	Durban (South Africa).	Papua New Guinea; Eastern Australia.
References	Present study.	Present study.	Present study.	Present study.

have narrow green-yellow line. Oral tentacles, rhinophores and rhinophoral sheaths dark blue or black. Genital pore opens on right side, midway between gills and rhinophores.

Internal morphology: Anterior digestive tract begins with short, thick-walled muscular oral tube that continues into buccal mass. One pair of large, wide salivary glands on buccal mass, flanking oesophagus. Chitinous labial cuticle strong and smooth. Radular formula of paratype (CASIZ 074085) $19 \times 3–4.1.1.1.4–3$, of holotype (E6323) $17 \times 4.1.1.1.4$ (Fig. 2E, F). Rachidian tooth rectangular, without denticles, slightly notched at anterior edge. Inner lateral tooth elongate with two well developed wide cusps; inner cusp bifid with sharp denticle on inner edge. Outer lateral teeth roughly rectangular, decreasing in size towards outer margin. A small blood gland on intestinal loop. Renal syrinx visible under pericardium, close to anal papilla.

Reproductive system (Fig. 3C) with short and narrow preampullary duct that expands into S-shaped ampulla with thick walls, continuing into postampullary duct that divides into oviduct and prostate. Short oviduct enters massive female gland mass. Prostate gland small, slightly morphologically differentiated, confined to coiled section of vas deferens with soft glandular walls. Vas deferens long and convoluted, ending in dilated penial atrium. Penis armed with at least three different kinds of spines arranged in longitudinal rows; basal spines elongate, straight; spines of middle and distal region smaller and hooked (Fig. 4C). Vaginal duct short, wide, connected to large, round, bursa copulatrix. We have not been able to identify the uterine duct in this specimen. Pyriform seminal receptacle much smaller than bursa copulatrix, with short, wide, straight duct that connects to vagina near bursa. Vagina shares common aperture within genital atrium with vaginal gland, which is small and elongate. Mucous gland well developed.

Distribution: Known only from Durban, South Africa.

Remarks: Three other species of *Tambja* have also been recorded from the Indian Ocean coast of South Africa: *Tambja morosa* (Bergh, 1877), *Tambja affinis* (Eliot, 1904) and (from the Cape Province) *Tambja capensis* (Bergh, 1907). *Tambja zulu* is clearly distinguishable from these by its external coloration. *Tambja capensis* has dark blue to black ground colour without any longitudinal lines or spots, but has a dark green notal margin. *Tambja morosa* has blue spots on the dark blue or black notum. These are both very different from *T. zulu*, which has dark ground colour with several yellow longitudinal lines on the notum and both sides of the body, more similar to *T. affinis*. However, the ground colour of *T. affinis* is violet-black and the rhinophoral sheaths have the same colour as the stems and bases of the gills and the pigment found between the rhinophores (Fig. 1F). Internally, important differences include the radula and the penial morphology. *Tambja zulu* has at least three different kinds of penial spines arranged in longitudinal lines, whereas *T. morosa* and *T. affinis* have only one kind of penial hook, which are more numerous and unordered. In the dissected specimens of *T. capensis*, we were unable to see all the penial spines, but it appears to have only one kind of hooked spines, as reported in the original description of Bergh (1907). The most important features of these species are compared in Table 1. The holotype of *T. zulu* has a teratological feature within its radula (Fig. 2D). The paratype has the innermost lateral teeth with a bifid inner cusp, but the holotype has the innermost lateral teeth of all the right rows with a simple inner cusp, while all the innermost lateral teeth of the left side have innermost lateral teeth with a bifid inner cusp similar to that of the paratype (CASIZ 074085). The reproductive system of the paratype specimen was completely dry, so we were unable to obtain any information from it. The paratype is reported in Gosliner (1987) as *Tambja* sp. A picture of this species from Natal (South Africa) is given by Fraser (2000).

***Tambja victoriae* new species**

(Figures 1E, 2G, H, 3D, 4D)

Roboastra arika—Coleman, 1989: 12; Coleman, 2001: 45; Marshall & Willan, 1999: 54, fig. 84 (not Burn, 1967)

Type material: Holotype: CASIZ 076335, Swain Reef, Great Barrier Reef, Australia, December 1977, collected by A. J. Ferreira, 1–10 m depth. Paratype: CASIZ: 075810, 1 spec., outer barrier reef, near Madang, Papua New Guinea, November 1990, collected by T. M. Gosliner & M. Jebb, 18 m depth.

Etymology: This species is dedicated to Victoria Hurtado de Mendoza, wife of the second author of this paper.

External morphology: body elongate, limaciform, with long, pointed posterior end of foot. Preserved animals 10–30 mm long. Body surface smooth, longitudinally striped with orange, orange yellowish or yellow streaks outlined in black (Fig. 1E). Ground colour sky blue to indigo. A ridge that extends anteriorly around head suggests a mantle margin; this same ridge converges behind gills but does not form a single line. A wide longitudinal line circumscribes both sides of body, surrounding basal part of oral tentacles and mouth, ending at posterior end of foot. On second part of posterior portion of foot, there are several irregular patches of same colour as longitudinal lines. Longitudinal lines yellow, orange or orange yellowish. Patches between rhinophores, base of gills and part of line continuing posterior to gills are green or light blue. Tips of gills green or light blue. Head slightly expanded with pair of conical, completely retractile, perfoliate rhinophores with *ca* 40 lamellae. Oral tentacles short, dorso-ventrally flattened, with horizontal groove. Three non-retractile, multipinnate gills, sparsely branched, form semicircle surrounding elevated anal papilla. Rhinophoral sheaths, base of oral tentacles and line surrounding foot yellow, orange or orange yellowish. Genital pore opens on right side, midway between gills and rhinophores. Lateral slots of unknown function between rhinophores and oral tentacles.

Internal morphology: Anterior digestive tract begins with short, slightly thick-walled, muscular, oral tube, that continues into buccal mass. Pair of long, wide salivary glands on buccal mass, flanking oesophagus. Chitinous labial cuticle strong, smooth. Radular formula of paratype (CASIZ 075810) $18 \times 4.1.1.1.4$, of holotype (CASIZ 076335) $14 \times 4.1.1.1.4$. Rachidian tooth rectangular, without denticles, slightly notched at anterior edge. Inner lateral tooth elongate, with two well developed cusps; inner cusp bifid, but smaller denticle has wide brim that continues on inner edge of tooth in one of specs (CASIZ 076335) (Fig. 2G, H). Outer lateral teeth roughly rectangular, decrease in size towards outer margin. Outermost lateral tooth small. Large, granular blood gland located on intestinal loop. Renal syrinx visible under pericardium, close to anal papilla. Reproductive system triaulic (Fig. 3D). Genital mass fills whole second quarter of body cavity. Hermaphroditic duct widens into large S-shaped ampulla. Ampulla narrows into long, thin, postampullary duct that connects with oviduct and prostate. Short oviduct enters massive female gland mass. Deferent duct lacks morphologically well-differentiated prostate, but has soft glandular walls that envelop seminal receptacle. Outer muscular vas deferens terminates in dilated penial portion. Penis armed with hooked, chitinous spines arranged in

longitudinal rows (Fig. 4D). Vaginal duct short, straight, connects to round bursa copulatrix. Seminal receptacle similar in size to bursa copulatrix, with short duct that connects to vagina, after completing two loops, near bursa. A slender uterine duct leaves vagina before duct of seminal receptacle and joins with oviduct. Vagina shares common aperture within genital atrium and has small vaginal gland. Mucous gland well developed.

Distribution: So far this species is known from Papua New Guinea and Australia.

Remarks: This species has been misidentified as *Roboastra arika* in several field guides (Coleman, 1989, 2001; Marshall & Willan, 1999). It has a radula similar to most of the *Tambja* species (Fig. 2E, F), it lacks dorso-laterally grooved oral tentacles, and has a strong labial cuticle. *Tambja victoriae* has been found feeding on the ectoproct *Bugula dentata*, whereas most species of *Roboastra* feed on other nudibranchs (Farmer, 1978; Carté & Faulkner, 1983, 1986; Debelius, 1996; Megina & Cervera, 2003). There is another species of *Tambja*, *T. affinis* (Eliot, 1904) that has been misidentified as *Roboastra arika* Burn, 1967 (www.seaslugforum.net/roboarik.htm; Debelius, 1996) and which can be also confused with *Tambja victoriae*. The main differences between them are the distribution and colour pattern. *Tambja affinis* (Fig. 1F) was described from Zanzibar, Tanzania (Eliot, 1904) and has been also reported from the Red Sea (Yonow, 1990; Reyniers, 2003) and the Comores, Indian Ocean (M. Poddubetskaia, unpublished), whereas *T. victoriae* is known only from Papua New Guinea and the Great Barrier Reef. *Tambja victoriae* has a blue ground colour and the rhinophoral sheaths are the same colour as the orange stripes of the body, while *T. affinis* is violet-black in colour and the rhinophoral sheaths are the same colour as the stems and bases of the gills and the pigment found between the rhinophores. 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. The studied specimens of *T. affinis* from Indian Ocean also have lateral slots located between the rhinophores and the oral tentacles.

ACKNOWLEDGEMENTS

Our sincere gratitude to Clay Carlson and Patty Jo Hoff, Dave Behrens, Constantinos Petrinos, Michael Schrödl, W. R. Liltved, E. W. Iverson, D. Herbert, the late Antonio J. Ferreira, M. Jebb, Todd Garthwaite and Marina Poddubetskaia, who collected and photographed many of the dissected specimens of *Tambja*. We also thank Mr Agustín Santos for his help in some aspects of the elaboration of the manuscript, and Mr Jose María Geraldia of the Electron Microscopy Service of the University of Cádiz for the facilities to take the scanning electron microscope photographs. Finally, we thank two anonymous referees for comments that improved the manuscript. This paper was supported by the following projects REN2001–1956-C17-02/GLO (Spanish Ministry of Science and Technology), REN2000–0890/GLO (Spanish Ministry of Science and Technology) and PEET Grant DEB-9978155 (National Science Foundation, USA). One of the authors (M.P.) has benefited from a predoctoral fellowship and a grant for stays at the California Academy of Sciences and the University of Guam, both funded by the Spanish Ministry of Education, Culture and Sports.

REFERENCES

BABA, K. 1955. *Opisthobranchia of Sagami Bay*, *Supplement*. Iwanami Shoten, Tokyo.

BABA, K. 1960. The genera *Gymnodoris* and *Nembrotha* from Japan (Nudibranchia-Polyceridae). *Publications from the Seto Marine Biological Laboratory*, **8**: 71–75.

BABA, K. 1987. Two new green-coloured species of *Tambja* from Japan (Nudibranchia: Polyceridae). *Venus*, **4**: 13–18.

BARNARD, K.H. 1927. South African nudibranch Mollusca, with descriptions of new species, and a note on some specimens from Tristan da Cunha. *Annals of the South African Museum*, **25**: 171–215.

BASEDOW, H. & HEDLEY, C. 1905. South Australian nudibranchs, and an enumeration of the known Australian species. *Transactions of the Royal Society of South Australia*, **29**: 134–160.

BERGH, L.S.R. 1877. Malacologische Untersuchungen. In: *Reisen im Archipel der Philippinen. Wissenschaftliche Resultate* (C. Semper, ed.), **2**(11): 429–494.

BERGH, L.S.R. 1905. Die Opistobranchiata der Siboga-Expedition. *Siboga Expedition Monographs*, **50**: 1–248.

BERGH, L.S.R. 1907. The Opisthobranchiata of South Africa. *Transactions of the South African Philosophical Society*, **17**: 1–144.

BURN, R. 1962. Descriptions of Victorian nudibranchiate Mollusca, with a comprehensive review of the Eolidacea. *Memoirs of the National Museum of Victoria*, **25**: 95–128.

BURN, R. 1967. Notes on an overlooked nudibranch genus, *Roboastra* Bergh, 1877, and two allied genera (Mollusca: Gastropoda). *Australian Zoology*, **14**: 212–222.

CARTÉ, B. & FAULKNER, J. 1983. Defensive metabolites from three nembrothid nudibranchs. *Journal of Organic Chemistry*, **48**: 2314–2318.

CARTÉ, B. & FAULKNER, J. 1986. Role of secondary metabolites in feeding associations between a predatory nudibranch, two grazing nudibranchs, and a bryozoan. *Journal of Chemical Ecology*, **12**: 795–804.

COLEMAN, N. 1989. *Nudibranchs of the South Pacific*, **1**. Sea Australia Resource Centre, Springwood, Queensland.

COLEMAN, N. 2001. *1001 Nudibranchs. Catalogue of Indo-Pacific sea slugs*. Neville Coleman's Underwater Geographic Pty Ltd., Springwood, Queensland.

DEBELIUS, H. 1996. *Nudibranchs and sea snails: Indo Pacific field guide*. IKAN—Unterwasserarchiv, Frankfurt.

ELIOT, C. 1904. On some Nudibranchs from East Africa and Zanzibar. Part 5. *Proceedings of the Zoological Society of London*, **2**: 83–105.

FRASER, V. 2000 (July 28). *Tambja sp*. from South Africa. [Message in] *Sea Slug Forum*, http://www.seaslugforum.net/find.cfm?id = 2271.

GOSLINER, T.M. 1987. *Nudibranchs of southern Africa. A guide to opisthobranch molluscs of southern Africa*. Sea Challengers, Monterey, California.

MACNAE, W. 1958. The families Polyceridae and Goniodorididae (Mollusca, Nudibranchiata) in southern Africa. *Transactions of the Royal Society of Southern Africa*, **35**: 341–372.

MARSHALL, J.G. & WILLAN, R.C. 1999. *Nudibranchs of Heron Island, Great Barrier Reef. A survey of the Opisthobranchia (sea slugs) of Heron and Wistari Reefs*. Backhuys, Leiden.

MEGINA, C. & CERVERA, J.L. 2003. Diet, prey selection and cannibalism in the hunter opisthobranch *Roboastra europaea*. *Journal of the Marine Biological Association of the United Kingdom*, **83**: 489–495.

POLA, M., CERVERA, J.L. & GOSLINER, T.M. 2003. The genus *Roboastra* Bergh, 1877 (Nudibranchia: Polyceridae: Nembrothinae) in the Atlantic Ocean. *Proceedings of the California Academy of Sciences*, **54**: 381–392.

REYNIERS, J. 2003 (May 3). *Tambja affinis* from Sudan. [Message in] *Sea Slug Forum*, http://www.seaslugforum.net/find.cfm?id = 9616.

RISBEC, J. 1928. Contribution à l'étude des nudibranches Néo-Calédoniens. *Fauna des Colonies Françaises*, **2**: 1–328.

YONOW, N. 1990. Red Sea Opisthobranchia 3: The orders Sacoglossa, Cephalaspidea, and Nudibranchia: Doridacea (Mollusca, Opisthobranchia). *Fauna de Saudi Arabia*, **11**: 286–299.

YONOW, N. 1994. Opisthobranchs from the Maldive Islands, including descriptions of seven new species (Mollusca: Gastropoda). *Revue Française d'Aquariologie*, **20**: 97–129.

YONOW, N. & HAYWARD, P.J. 1991. Opistobranches de I'Ile Maurice, avec la description de deux espèces nouvelles (Mollusca: Opisthobrancia). *Revue Française d'Aquariologie*, **18**: 1–30.