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Neubert & Hirschfelder
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Naturalis Biodiversity Center
Darwinweg 2, P.O. Box 9517, NL-2300RA Leiden
Tel. +31(0)71-5687614, Fax. +31(0)71-5687666,
e-mail: info@basteria.nl

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Description of three new species of *Tambja* (Gastropoda, Nudibranchia, Polyceridae) from the western Pacific Ocean reveals morphological characters with taxonomic and phylogenetic significance for traditional Polyceridae and related 'phaneorobranth' nudibranchs

RICHARD C. WILLAN

Museum and Art Gallery of the Northern Territory, G.P.O. Box 4646, Darwin,
Northern Territory 0801, Australia; richard.willan@nt.gov.au [corresponding author]

YEN-WEI CHANG

Department of Marine Recreation, National Penghu University of Science and Technology, Magong City 880, Taiwan;
bard8088@msn.com.

Former addresses: Institute of Marine Biology and Asia-Pacific Ocean Research Center, National Sun Yat-sen University, Kaohsiung 804, Taiwan; Museum and Art Gallery of the Northern Territory, G.P.O. Box 4646, Darwin, Northern Territory 0801, Australia

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Three new species of *Tambja* Burn, 1962 (Nudibranchia, Polyceridae, Nembrothinae) are described and illustrated, and two new genera are introduced. *Tambja draconus* spec. nov. occurs in (cool temperate) southeastern Australian and northern New Zealand waters; *T. caeruleocirrus* spec. nov. occurs more widely in (warm temperate) southwestern Pacific waters with its distribution centered in eastern Australia; *T. pulcherrima* spec. nov. occurs very widely throughout the (tropical, subtropical and warm temperate) western Pacific Ocean from southern Japan to northern New Zealand. The fact that there is no remaining type series of *Nembrotha* (?) *verconis* Basedow & Hedley, 1905 (presently *Tambja verconis*) is taxonomically significant, not only because it is the type species of the genus *Tambja*, but also because that species must be distinguished unequivocally from one of the species newly named here, *T. pulcherrima*, which it resembles externally. To remedy this nomenclatural gap, a neotype is herein designated for *Nembrotha* (?) *verconis* Basedow & Hedley, 1905. These three new species and the investigated morphological characters they possess have important phylogenetic implications for the genus

Tambja within the traditional family Polyceridae. This genus is presently an assemblage of at least two distinct clades. In particular, we suggest that all, not just some, species of *Tambja* sensu stricto possess a pre-rhinophoral sensory organ that is probably homologous with those possessed by (at least some) species of *Thecacera* and *Gymnodorididae*. Five small species lacking this organ and constituting a clade genetically are here shifted out of *Tambja* into *Martadoris* gen. nov., thus rendering *Tambja* monophyletic. Neither is another traditional nembrothine genus, *Roboastra* Bergh, 1877, monophyletic. On account of rows of sensory pits all along the body (none being homologous with the pre-rhinophoral sensory organ) we suggest *Roboastra* sensu stricto should accommodate only the type species, the relatively small *R. gracilis* (Bergh, 1877). The large species that lack these pits and are predatory on other nembrothines previously classified in *Roboastra* are herein shifted into *Tyrannodoris* gen. nov.

Key words: Gastropoda, Nudibranchia, morphology, taxonomy, phylogeny, dietary specialisation, biogeography, Indo-Pacific Ocean.

Burn (1962a) introduced the genus *Tambja* in the family Gymnodorididae with two included species on the basis that the radula and reproductive system differed from those of the similar-looking genus *Nembrotha* Bergh, 1877. Over the subsequent 50 years, the genus *Tambja* has been shifted to the family Polyceridae (subfamily Nembrothinae) (herein termed the 'traditional Polyceridae' and 'traditional Nembrothinae') and some 30 additional species have either been newly described as members of *Tambja* or transferred there (Gofas & Bouchet, 2015).

A review of the taxonomic history of the genus is given here to explain the present concept of *Tambja* (i.e. that held by Gofas & Bouchet, 2015, and Dominguez et al., 2015). Independently in 2005, two groups of malacologists presented reappraisals of *Tambja* in conjunction with the description of new species (Miller & Haagh, 2005; Pola et al., 2005a). Miller & Haagh (2005) stated that the only characters separating this genus from *Nembrotha* were the central tooth of the radula that lacked denticles and the strongly cuticularised labial disc (= buccal collar). In presenting a more comprehensive taxonomic revision and phylogenetic analysis which incorporated the findings of Miller & Haagh (2005), Pola et al. (2006b) used a morphology-based phylogenetic analysis and argued *Tambja* was definitely distinct from *Nembrotha*, but they rejected the monophyly of *Tambja*, with three outlier species (*Tambja tentaculata* Pola et al., 2005, *T. limaciformis* (Eliot, 1908) and *T. amakusana* Baba, 1987) plus the genus *Roboastra* Bergh, 1877, occurring in the same clade as the 'core' species of *Tambja*. Moreover, Pola et al. (2006a) used a molecular analysis (COI and COI+16S) to conclude the non-monophyly of *Tambja*. These authors did not propose a new system of classification in either the 2005 or 2006 papers. The following year, the same authors presented a more extensive phylogenetic analysis based on both morphology and mitochondrial DNA (Pola et al., 2007). *Roboastra* was proposed as monophyletic by inclusion of *T. tentaculata* (i.e. that species was transferred into *Roboastra*). However, *Tambja* remained either para- or polyphyletic, depending on the analysis performed. Again *T. limaciformis* and *T. amakusana* fell outside the 'core' group of *Tambja*. These authors summarised the position of *Tambja* with the following prudent statement: "... traditional characters appear not to be sufficient and need major revision when further *Tambja* species are added." (Pola et al., 2006b: 524). The present paper, whilst describing three new species that clearly fall within the 'core' group of *Tambja* morphologically (i.e. *Tambja sensu stricto*), goes some distance to fulfilling this request in that it helps explain and refine

these "traditional characters". Importantly, we argue that one hitherto unresolved character, the pre-rhinophoral sensory organ, is actually possessed by all *Tambja* species (i.e. under our definition of *Tambja*) instead of just some species or some individuals within particular species. Therefore, it is highly important phylogenetically (see below). A summary of the taxonomic characters of the genus *Tambja* as we define it is given at the end of this paper.

It has to be acknowledged that species of *Tambja* vary both intraspecifically and ontogenetically, with some species apparently varying more than others. *Tambja morosa* is a good example of a species that varies greatly in colour between individuals (Marshall & Willan, 1999; Pola et al., 2006b), and *T. ceutae* Garcia-Gomez & Ortea, 1988, and *T. marbellensis* Schick & Cervera, 1988 are good examples of species that vary ontogenetically (Sánchez-Tocino et al., 2000). Indeed, identification of juvenile individuals of these two *Tambja* species to the level of species is particularly problematic on morphological and anatomical grounds (Sánchez-Tocino et al., 2000; Pola et al., 2006a), and it is clear that the colour pattern and also the radular formula change significantly as an individual matures (Sánchez-Tocino et al., 2000).

For the sake of completeness of our coverage of *Tambja*, we sought the etymology of the genus from its author, Robert Burn. He has advised us that *Tambja* takes its name directly from a rural property north of Geelong in central Victoria, Australia. The exact meaning of the name 'Tambja' is unknown (R. Burn, personal communication December 2012).

MATERIAL AND METHODS

Specimens were observed alive where possible. They were narcotised with magnesium sulphate and fixed in either 70% ethanol (for morphological examination) or absolute ethanol (for genetic analysis). They were dissected and sketched using an Olympus SZH stereodissecting microscope with a camera lucida attached. The buccal bulb was dissected out and the soft tissue was dissolved in 10% potassium hydroxide. The radula and labial cuticle were rinsed thoroughly in water and mounted for scanning electron microscopy. They were gold-coated using a SPI module, and examined/scanned with a JEOL 5610 LV SEM using an accelerating voltage of 15 KV and working distances of 10–15 mm at Charles Darwin University.

Since Penney (2008) had mentioned that sparse, integumentary spicules were present in (some species of) the 'traditional Polyceridae', we took the opportunity to search for them in freshly collected material of one of the new species described herein. Tissue from four regions of the body (i.e. dorsal mantle, foot,

rhizophore, gills) of a paratype of *Tambja dracomus* (NTM P.48730) that had been fixed in absolute ethanol for only three days following its collection was dissolved in 10% potassium hydroxide according to the method employed by Chang et al. (2013). We used a light microscope (Leica DMLS) to scrutinise each sample for spicules for 20-30 minutes.

Abbreviations used: AMS – Australian Museum (Sydney, Australia); BMNH – The Natural History Museum (London, England), CDU – Charles Darwin University (Darwin, Australia); IMBNSYSU – Institute of Marine Biology, National Sun Yat-sen University (Kaohsiung, Taiwan); MV – Museum Victoria (Melbourne, Australia); NTM – Museum and Art Gallery of the Northern Territory (Darwin, Australia); SAM – South Australian Museum (Adelaide, Australia).

SYSTEMATIC PART

Order Nudibranchia Cuvier, 1817

 Infraorder Doridacea Rafinesque, 1815

 Superfamily Polyceroidea Alder & Hancock, 1845

 Family Polyceridae Alder & Hancock, 1845

 Subfamily Nembrothinae Burn, 1967

Tambja Burn, 1962

Type species (by original designation): *Nembrotha* (?) *verconis* Basedow & Hedley, 1905. Recent, South Australia. Gender feminine.

Type series of *Nembrotha* (?) *verconis* Basedow & Hedley, 1905. – In their description of *Nembrotha* (?) *verconis*, Basedow & Hedley (1905: 158) gave the type locality as “Dredged in 20 fathoms, off Newland Head, Backstairs Passage, January 1903 (Verco).” The original description was certainly based on more than one specimen because of the statement on pages 158-159: “A large specimen is in the Australian Museum collection; it measures 40 mm in length, whereas the contracted body of our type barely measures 30 mm.” Therefore, the authors had at least two specimens before them, and both these specimens constitute the name-bearing type series and must be considered as syntypes (ICZN 1999: Article 73.2); neither was expressly designated as a holotype. Therefore, the reference by Pola et al. (2006b: 500) to a “holotype” for this species cannot be correct according to the International Code of Zoological Nomenclature. However, we acknowledge that Basedow and Hedley did probably consider their January 1903 specimen as their “type” since it was collected and painted by Herbert Basedow while on Sir Joseph Verco’s dredging expedition in the Backstairs Passage that year. Charles Hedley was one of the party on Verco’s subsequent expedition (January

1904), and the recorded larger syntype was probably collected/dredged then, and retained by Hedley for the Australian Museum collection (Robert Burn personal communication, November 2012). Presumably, the smaller syntype (which was in the SAM) was dissected by Herbert Basedow, its radula was figured in the original publication (pl. 2 fig. 3), and the specimen discarded, because it is now lost (Thierry Laperousaz personal communication, April 2012). We expected the larger syntype from 1904 still to be in the AM, but received advice from Amanda Reid, Collection Manager in Malacology, that there is definitely no type series there. She checked the present day electronic database (EMu), the older malacology card catalogue and the general mollusc wet collection for us, but located nothing that could possibly be the 1904 specimen. Therefore, it seems there is actually no existing type series for *Nembrotha* (?) *verconis*. Burn (1962b: 149) had already reached this conclusion as regards all the (six) species described as new by Basedow & Hedley (1905). He stated: “Fortunately the figures and descriptions are very good and clear, for the specimens upon which they are based are either lost, destroyed, or in an unknown repository” and nothing has come to light in the intervening 50 years to change this conclusion (Robert Burn personal communication, April 2012). It seems we will never know for sure what happened to them.

It is essential to have a type series of *Nembrotha* (?) *verconis* Basedow & Hedley, 1905, not only because that is the type species of the genus *Tambja*, but also because that species resembles externally one of the new species described here, i.e. *T. pulcherrima* spec. nov., and could potentially occur sympatrically with it. To remedy this nomenclatural gap, a neotype is herein designated for *Nembrotha* (?) *verconis* Basedow & Hedley, 1905. This neotype (SAM D.19411, Photo Index number PD0958) (Fig. 1) measures 30 mm in preserved length. It was found on the arborescent bryozoan *Virididentula dentata* (Lamouroux, 1816) [formerly *Bugula dentata*], in 4-6 m depth, at Peneshaw Jetty, northeastern coast of Kangaroo Island, Backstairs Passage, South Australia (35°43’S, 137°56’E), and was collected by K.L. Gowlett-Holmes on 5 May 1999. This specimen then matches Basedow & Hedley’s 1903 specimen from Backstairs Passage in size and location.

Since its original description, *Tambja verconis* has been redescribed by Burn (1962a, 1967), Willan & Coleman (1984), Rudman 1998 (radula figured) and Pola et al. (2006b). This species is now very well known by divers and is frequently photographed because of its vivid and strongly contrasting colours. We have included some photographs of living animals herein (Figs 1, 2) and provide details of some

anatomical features (Figs 15, 22, 23, 27) of *T. verconis* (MV F21625) where they are necessary for comparison with the three new species. The one point we would make that is not clear from the published literature relates to the intraspecific variability of the background colour of this species, which ranges from primrose yellow (most frequently), through green, to blue, even to black. Blue spots are consistently present on top of this background.

***Tambja dracomus* spec. nov.**
(Figs 7-11, 12, 16-18, 24, 28-29)

Tambja sp. nov. – Burn 1990: 11.

Tambja sp. 2 – Rudman, 2000.

Tambja sp. – Coleman 2001: 46 (Southern *Tambja*); Coleman, 2008: 366 and 367 (Southern *Tambja*); Kodiac et al., 2012.

Tambja sp. 1 – Burn, 2006: 19; Burn 2015: 178.

Material examined. – Type series. Holotype (NTM P.48729), 45 mm preserved length, 6 m depth, Blairgowrie Pier, Port Phillip Bay, Victoria (38°21.35'S, 144°46.43'E), coll. A.J. Missen, 14.iv.2012. Paratypes (NTM P.48730), 3 specimens (dissected), 50, 45, 40 mm preserved length, same data as holotype.

Additional (non-type) material (all from Australia). Victoria – 1 specimen (MV F.30664), 4 m depth, Portsea, Victoria, coll. N. Coleman, 27.vi.1979; 2 specimens (MV F.30797), 4 m depth, Flinders, Victoria, coll. N. Coleman, 17.vi.1977; 1 specimen (MV not registered), subtidal, Cape Woolamai, Phillip Island, coll. I. Kirwen, ix.1977; 2 specimens (MV not registered) (dissected), subtidal, amongst rubble, Portsea jetty, Port Phillip Bay, coll. I. Kirwen, 26.vii.1980; 1 specimen (MV not registered), at low tide, under a stone, on top of reef, Point Danger, Torquay, coll. Marine Research Group of Victoria, 10.iv.1996.

Images examined. – Besides the photographs of the neotype and those publicly available in printed works (Coleman, 2001, 2008) and electronically on the Internet (Rudman, 2000; Kodiac et al., 2012), we have also examined the following images of this species. Tasmania – 1 specimen (SAM D.19410), 6-10 m depth, on jetty pile, woodchip wharf, Spring Bay, Triabunna, coll. K. Gowlett-Holmes, 30.vii.1988 [One of several specimens observed, feeding on *Virididentula dentata*. Also mating and laying eggs.]. New Zealand – 1 specimen, photographed subtidally, Poor Knights Islands, J. Iken, 4.i.2008.

Etymology. – The specific name is formed by the combination of two Latin nouns, i.e. *draco*, a dragon, and *mus*, a mouse. It represents the Latinisation of Dragon Mouse Diving, the name of Ashley Missen's company. Ashley kindly collected several specimens of this new species for us to study, posted them to us immediately after collection, and provided information on the habits and behaviour of this new species. Furthermore, Dragon Mouse Diving was a sponsor for the international nudibranch workshop held at Lissening Island,

Papua New Guinea, in March 2012. The name is intended as a noun in apposition.

Description. – Medium-sized polycerid; maximum extended crawling length 80 mm, average extended crawling length 40 mm. Body elongate, limaciform, narrow throughout, approximately 4 times as long as broad, tail capable of compression dorsally into low fin that produces lateral flexion for propulsion during (weak) swimming. Maximum body height at level of pericardium immediately in front of gills. Dorsal integument smooth, completely devoid of pustules everywhere; lateral integument with irregular, longitudinal ridges most obvious when individual is crawling actively. Skin very thick and glandular. Integumentary spicules completely absent. Body without notal (mantle) brim. Gills located at middle of body. Foot narrowing slightly anteriorly, front edge curved and grooved, fronto-lateral corners not expanded, narrowing posteriorly gradually to rounded tip. Head with expanded and sharp-edged anterior brim. Mantle raised into low sheath surrounding base of rhinophore, simple margin to rhinophoral sheath. Mantle not raised into branchial pocket. Oral tentacles frontal-lateral, directed downward, ear-like, relatively large, but not extending beyond level of notal brim, grooved shallowly, lower lip of oral tentacle groove projecting beyond upper lip. Opening of pre-rhinophoral sensory organ a horizontal slit immediately above and behind oral tentacle (arrowed in Fig. 10); aperture of dilated slit measuring 2 mm in 40 mm preserved paratype. Rhinophores retractile, peduncle swollen, less than half height of clavus; clavus swollen, tapering, held erect when fully extended, clavus with up to 35 even, sloping lamellae; apical knob short, small and slight rounded. Gills partly tripinnate, relatively bushy, generally 5 in number, clearly separated from each other, lying nearly horizontal when fully expended; with narrow, somewhat sinuous rachis that lacks lines on inner and outer faces; forming almost complete circle around anus. Anal papilla not elevated. Genital aperture on right side of body, at approximately one-third of body length, slightly in front of anterior end of pericardium.

Colour. – Head and body uniformly dull, dark drab khaki green (most often), or brownish orange (rarely). Foot and penis (Fig. 8) dull, pale, translucent orange, contrasting noticeably with much darker body. Rhinophores dark reddish brown; apex darker, purple with very fine white streak posteriorly. Gills dull red, outer faces of rachides dark, similar in colour to gill pinnae; inner faces of rachides white, contrasting obviously with gill pinnae. Spawn golden orange. Individuals emit a vivid yellow-green fluid when preserved in ethanol.

Internal anatomy. – Foregut (Fig. 12) commencing with relatively long oral tube continuous with muscular buccal mass. Oral tube longer than buccal mass. Pair of large salivary gland adhering dorsally to buccal mass, flanking oesophagus. No pouches visible at junction of oral tube and buccal mass. Radula (Figs 16-18) (3 examined – NTM P.48730) multidentulate, with formula: $23 \times 5-6.1.1.1.5-6$ (45 mm preserved length, NTM P.48730); $16 \times 5-6.1.1.1.5-6$ (30 mm preserved length, MV not registered); $25 \times 4-5.1.1.1.4-5$ (28 mm preserved length, MV not registered). Central (rachidian) tooth thin, subrectangular-rhomboid, width approximately 3 times height (both measurements made at middle of tooth), anterior margin straight to slightly undulating (definitely not notched), recurved, cutting edge not denticulate at all, antero-lateral corners rounded, postero-lateral corners extended. Lateral tooth large and thick, approximately 3 times height of central tooth, wide at base with triangular flange, shaft hardly narrowing and curving to apex towards axis of radula, cusp well developed, inner denticle also well developed, but not reaching level of main cusp (approximately 66% height of main cusp). Marginal teeth much smaller than lateral tooth, decreasing progressively in size outwards, all higher than wide, thin and plate-like; first (inner) marginal widest anteriorly because of large inward-facing flange, basal plate subquadrate, angular; second and third marginals slightly narrower, with markedly smaller flange; fourth and subsequent marginals much narrower, without any flange. Labial disc (Fig. 24) well-developed, cuticularised – most heavily thickened dorsally, but not thickened into recognisable jaws, dome-shaped in profile, lacking denticles at opening.

Reproductive system (Figs 28-29) hermaphroditic, triaulic. Following account relates to fully sexually mature individual that has mated. Ototestis overlying and covering entire digestive gland except for stomach ventrally. Main hermaphrodite duct relatively long, doubling its width to form long, tubular (S-shaped in situ), opaque white ampulla. Ampulla narrowing gradually distally where it bifurcates into proximal vas deferens and proximal oviduct, both very narrow. Vas deferens enlarging almost immediately into long, coiled, tubular prostatic section then narrowing to long, tubular, coiled muscular section. Prostatic section of vas deferens not surrounding bursa copulatrix. Muscular section of vas deferens approximately twice length of prostatic section, but slightly narrower than prostatic section. Terminal section of distal vas deferens enlarging into penial sheath which opens into common genital atrium and which contains acrembolic penis armed with numerous, simple, curved spines. Penis swollen or humped

near rear base, surface granular. Proximal oviduct short, widening into fertilisation chamber, then constricting before bifurcating into proximal vagina and uterine duct. Vagina short, straight, widening as common stalk to bursa copulatrix and receptaculum seminis (Fig. 29). Bursa copulatrix spherical, thin-walled with straight duct. Receptaculum seminis similar in size to bursa copulatrix but club-shaped, with coiled duct longer and narrower than duct to bursa copulatrix. Vaginal gland large (approximately twice size of bursa copulatrix), on short stalk, sac-like, thin-walled. Female gland mass spherical, flattened, large – approximately equal in length to penial sheath, extensively convoluted.

Distribution. – Australia (New South Wales, Victoria, Tasmania, South Australia), New Zealand (only Poor Knights Islands, Northland).

Remarks. – According to Robert Burn's file notes, the first specimen of this species was collected from 3-5 m depth at Portsea Pier, Port Phillip Bay, Victoria, by Jeanette Watson on 16 November 1970. It was juvenile (20 mm extended length). The species first entered the literature in a list with the annotation (footnote 22): "Large (to 60 mm) dull dark green animal with reddish-brown rhinophores and gills. Easily distinguished from the larger blue-spotted yellow *T. verconis*." (Burn, 1990).

Tambja dracomus spec. nov. is characterised by the thick skin, dark khaki green body, and darker reddish brown rhinophores and gills, smooth mantle without any pustules, wide central tooth, very strong and tall lateral tooth with a strong denticle, and relatively more marginal teeth (5-6) as compared with other species of *Tambja*. When the gills are contracted, the rachides form a net- or ribbon-like screen over the delicate pinnae. The diagnostic characters of the reproductive system are the long, S-shaped ampulla and the long stalk to the receptaculum seminis. The egg ribbon is relatively solid (compared to that of *T. verconis*). Individuals are predominantly but not exclusively subtidal. Like *T. verconis*, it feeds on the green arborescent bryozoan *Virididentula dentata* (Ashley Missen personal communication, August 2011; Karen Gowlett-Holmes personal communication, October 2011) and its occurrence is seasonal (Karen Gowlett-Holmes personal communication, October 2011). At a particular locality, for example at Blairgowrie, Port Phillip Bay, it is much commoner at night than during the day, and so it apparently has a nocturnal habit there, retreating amongst the encrusting fauna to hide during the day (Ashley Missen personal communication, April 2012).

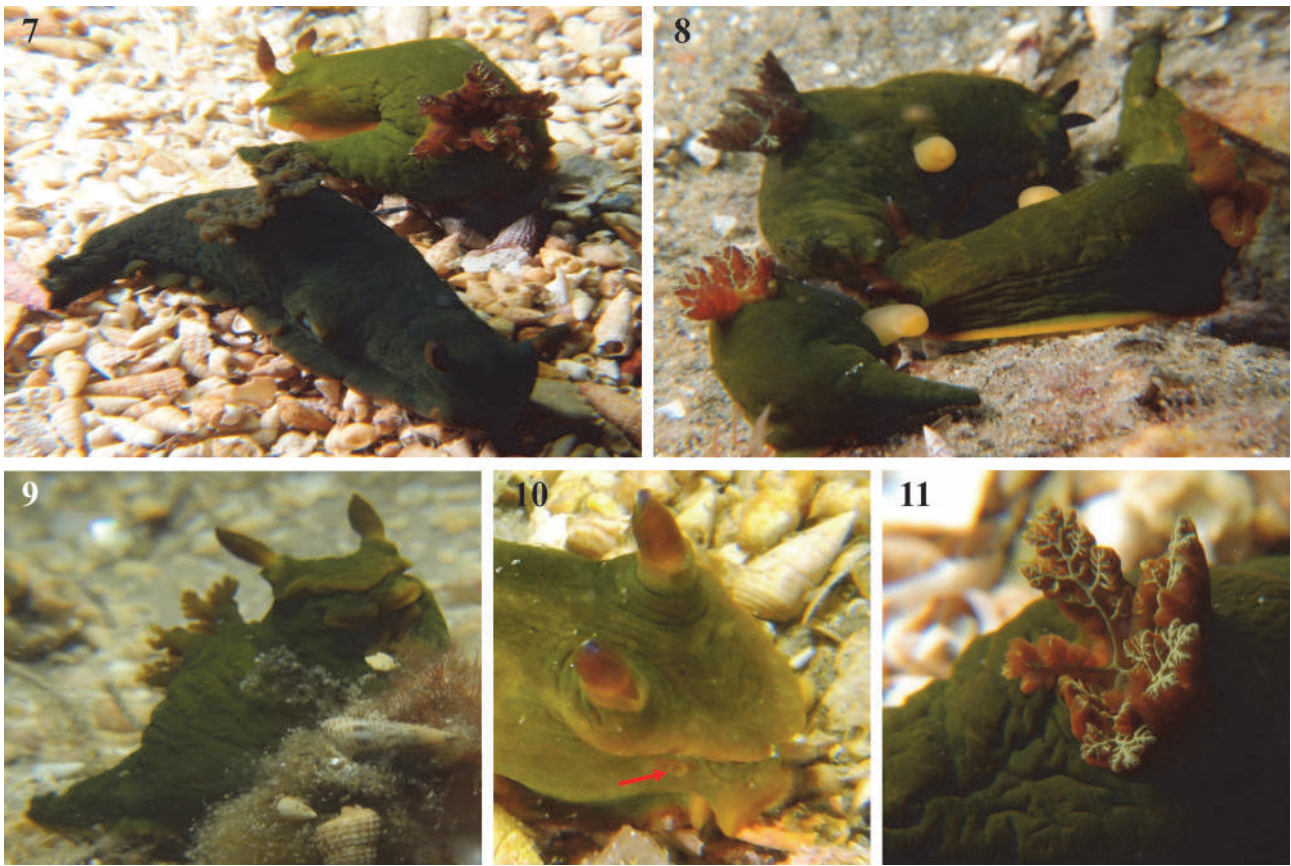
As stated above, most individuals of *Tambja dracomus* spec. nov. have a dark khaki green body with reddish brown rhinophores and dull red gills. A few



Figs 1–6. Living *Tambja* nudibranchs (family Polyceridae). **1**, Neotype of *T. verconis* (SAM D19411), 30 mm extended length, 4–6 m depth, Penneshaw Jetty, northeastern coast of Kangaroo Island, Backstairs Passage, South Australia (35°43'S, 137°56'E); photo K.L. Gowlett-Holmes, 5.v.1999. **2**, *T. verconis*, 45 mm extended length (with arrow indicating pre-rhinophoral sensory organ), 4 m depth, Blairgowrie Pier, Port Phillip Bay, Victoria; photo A. Missen, 2.iv.2011. **3**, *T. caeruleocirrus* spec. nov., holotype (NTM P.28179), 26 mm extended length, 13 m depth, 'Wait-a-While' dive site, Inner Gneering Shoals, east of Point Cartwright, Mooloolaba, Sunshine Coast, Southern Queensland; photo G. Cobb, 28.viii.2011. **4**, *T. caeruleocirrus* spec. nov., 25 mm extended length, 18 m depth, 'C Spot' dive site, Currimundi Reef, Sunshine Coast, Southern Queensland (26°45.574'S 153°10.984'E); photo T. Farr & J. Schubert, 12.xi. 2011. **5**, *T. pulcherrima* spec. nov., holotype (NTM P.48717), 25 mm extended length, 10 m depth, Wai-an, Pesacadores Islands (Penghu), Taiwan (23°33.575'N, 119°29.286'E); photo Y. Su, 4.vi.2007. **6**, *T. pulcherrima* spec. nov., Perhentian, Malaysia; photo R. Ng, 30.iii.2008.

individuals have either a dark chocolate body or a relatively pale brownish orange body with dull orange rhinophores and gills. The dark khaki green colour form of this species is similar in colour to *Tambja olivaria* Yonow, 1994 from the tropical Indo-west Pacific Ocean and to *Tambja tenuilineata* Miller & Haagh, 2005 from eastern Australia and northern New Zealand. The former species, which can attain a similar body length to *T. dracomus* spec. nov., has a pale olive green body with yellow-green pigment on the head, anterior face of the gills and tail (Gosliner et al., 2008). The lat-

ter species is bluish green with (usually) narrow, dark brown, longitudinal lines on the dorsal and lateral sides of the mantle and much smaller and more sparsely branched gills (Miller & Haagh, 2005). Occasional individuals of *T. tenuilineata* lack the black lines (Cobb & Mullins, 2012), but the pigmentation on the rhinophores and gills as well as the shape of the gills is completely different to *T. dracomus* spec. nov. *Tambja dracomus* spec. nov. shares the broad central radular tooth with *T. tenuilineata*. *Tambja dracomus* spec. nov. also shares the long stalk to the receptaculum seminis



Figs 7–11. Live *Tambja dracomus* spec. nov., 35–50 mm extended length, 4 m depth, Blairgowrie Pier, Port Phillip Bay, Victoria (38°21.35'S, 144°46.43'E), 4.ii.2012 & 14.iv.2012. 7, Colour variation. 8, Three individuals of *T. dracomus* spec. nov., each with its penis everted (the translucent orange organ on the right side). 9, Detail of head showing deeply grooved oral tentacles. 10, Detail of head showing pre-rhinophoral sensory organ (arrowed). 11, Detail of gills and anus. All photos by A. Missen.

with *T. tenuilineata* (whereas Pola et al., 2006b: 530 indicate that the stalk is short in the species of *Tambja* they studied), but the ampulla of *T. dracomus* spec. nov. is tubular, whereas it is enlarged and sausage-shaped in *T. tenuilineata*.

***Tambja caeruleocirrus* spec. nov.**
(Figs 3–4, 13, 19, 25, 30)

Tambja sp. 1 – Cobb & Willan, 2006: 76, Debelius & Kuitert, 2007: 71.

Tambja sp. 11 – Rudman, 2007.

Tambja sp. – Coleman, 2001: 46 (Black-streak *Tambja*), Coleman, 2008: 366 (Black-striped *Tambja*), Kodiat et al., 2012.

Material examined. – Type series. Holotype (NTM P.28179) (dissected), preserved length 26 mm, 13 m depth, 'Wait-a-While' dive site, Inner Gneering Shoals, east of Point Cartwright, Mooloolaba, Sunshine Coast, Southern Queensland, Australia (26°41.00'S, 153°08.00'E), coll. G. Cobb, 28.viii.2004.

Images examined. – Besides the photographs of the holotype and those publicly available in printed works (Cobb &

Willan, 2006; Debelius & Kuitert, 2007; Coleman, 2008) and electronically on the Internet (Rudman, 2007; Kodiat et al., 2012), we have also examined the following images of this species. Queensland – 1 specimen, 25 m depth, 'Pinnacles' dive site, Sunshine Coast, photo D. Mullins, 9.viii.2003; 1 specimen, 16 m depth, 'The Trench' dive site, Sunshine Coast, photo G. Cobb, 27.viii.2004; 1 specimen, 18 m depth, 'C Spot' dive site, Currimundi Reef, north of Caloundra, Sunshine Coast, photo J. Schubert, 12.xi.2011. New Zealand – 1 specimen, 12 m depth, 'Middle Channel' dive site, between Aorangi and Tawhiti Rahi Islands, Poor Knights Islands, Northland, photo I. Scott, iv.2001.

Etymology. – The specific name is formed by the combination of two Latin nouns, *caeruleus*, meaning sky blue, and *cirrus*, a lock of hair. The word *cirrus* has given its name to a type of atmospheric cloud characterised by thin, wispy strands and the longitudinal markings of this species recall these streaks of clouds. The name is intended as a noun in apposition.

Description. – Medium-sized polycerid; maximum extended crawling length 50 mm, average extended crawling length 30 mm. Body elongate, limaciform,

narrow throughout, pointed at tail; widest and highest at head and at level of gills, approximately 7 times as long as broad. Dorsal integument smooth, without any pustules; lateral integument with very sparse grooves near foot. Body without notal (mantle) brim. Gills located anterior of middle, approximately two-fifths of distance along body. Front edge of foot grooved and expanded. Head expanded, with prominent, 'U'-shaped anterior brim. Mantle raised into strong sheath surrounding base of rhinophores, with smooth rim, with a single raised lobe on inner margin of rim. Rim of branchial pocket not raised. Oral tentacles fronto-lateral, relatively small, triangular, flap-like. Rhinophores retractile, peduncle swollen, less than half height of clavus; clavus tall and elongate, tapering, with up to 35 lamellae. Pre-rhinophoral sensory organ opening via a horizontal slit immediately above oral tentacle, slit small, shorter than width of rhinophore. Gills relatively simple, relatively narrow, uni-pinnate or bipinnate distally, always 5 in number, clearly separate from each other, held erect when full extended. Genital aperture on right side of body, at approximately one-quarter of body length.

Colour. – Head and body intense sky blue. Anterior brim and oral tentacles with broad, intense, sky blue band. Pre-rhinophoral sensory organ same blue colour as surrounding lateral mantle. Dorsal mantle with 3, longitudinal, black stripes originating from black semicircle on head and extending continuously to gills, median stripe being most prominent and running from between rhinophores to just in front of gills, median stripe somewhat expanded on top of head and pericardium. Two outer stripes run continuously past gills to join dorsally some distance behind gills. Additional continuous or discontinuous, narrow, black stripes present on sides of body. Few black spots on top and sides of tail. Continuous, narrow, submarginal black stripe on upper surface of foot. Foot sole pale blue (paler than dorsum). Rhinophore sheath and peduncle uniform intense sky blue – same colour as dorsum; clavus darker blue than dorsum – almost royal blue (appearing black in photographs). Gill pinnae themselves jet black, outer and inner faces of rachides intense sky blue – same colour as dorsum.

Internal anatomy. – Radula (Fig. 19) (1 examined; holotype) multidenticulate, with formula: $15 \times 3.1.1.1.3$ (26 mm preserved length). Central (rachidian) tooth thin, subrectangular - nearly square, width approximately 1.5 times height (both measurements made at middle of tooth), anterior margin strongly notched - slightly higher on right side than left side, cutting edge not denticulate at all, antero-lateral corners square on one side and rounded on the other (this difference is probably merely intraindividual variation, not specifically diagnostic), postero-lateral corners extended a

short distance, pointed. Lateral tooth large and thick, approximately 3.8 times height of central tooth, wide at base with triangular flange, shaft narrowing considerably and curving to apex towards axis of radula, cusp well developed, inner denticle not well developed, and not reaching level of main cusp (approximately 75% height of main cusp). Marginal teeth much smaller than lateral tooth, decreasing progressively in size outwards, all higher than wide, thin and plate-like; first (inner) marginal widest anteriorly, with stepped boss at inner edge of base, basal plate subquadrate, angular, without basal flange. Second marginal only slightly smaller than first marginal, higher and slightly narrower than first marginal. Third marginal much smaller and shorter than second marginal, without basal flange. Labial disc (Fig. 25) well-developed, cuticularised, not thickened into recognisable jaws, dome-shaped in profile, lacking denticles.

Reproductive system (Fig. 30) hermaphroditic, tri-aulic. Following account relates to holotype, which is a fully sexually mature individual that has mated. Otestis overlying and covering entire digestive gland except for stomach ventrally. Main hermaphroditic duct long (approximately 2.5 mm when unraveled, not enlarging its width along its course), rapidly tripling its width distally to form long, tubular (S-shaped in situ), opaque white ampulla. Ampulla narrowing gradually distally where it bifurcates into proximal vas deferens and proximal oviduct, both very narrow. Vas deferens tubular, enlarging almost immediately into coiled, glandular prostatic section, then becoming coiled muscular section. Prostatic section and muscular section almost equal in length and width. Prostatic section not surrounding bursa copulatrix. Distal vas deferens enlarged into enormous (three times width of muscular section), very long, recurved, thin-walled penial sheath which opens into common genital atrium and which contains acembolic penis armed with numerous, simple, identical, curved spines. Proximal oviduct short, widening into fertilisation chamber, then constricting before bifurcating into proximal vagina and uterine duct. Vagina short, straight, widening as common stalk to bursa copulatrix and receptaculum seminis. Bursa copulatrix spherical, thin-walled, with straight duct, contents brownish in preservative. Receptaculum seminis much smaller in size than bursa copulatrix, finger-shaped. Vaginal gland thin-walled, approximately twice size of bursa copulatrix. Female gland mass spherical, extensively convoluted, not flattened, less than half length of penial sheath, consisting of two morphologically distinct glandular sections – a smaller, solid proximal section that is dark orange in preservative and a larger, extensively convoluted distal section that is white in preservative.

Distribution – Australia (Southern Queensland), Lord Howe Island, New Zealand (only Poor Knights Islands, Northland).

Remarks. – This species was first photographed at Lord Howe Island by Neville Coleman in November 1979 (Coleman 2001: 46; 2008: 366). Julie Marshall also photographed it there in February 2003 (Marshall 2003). Ian Scott photographed it at the Poor Knights Islands, New Zealand, in April 2001. David Mullins photographed it at Mooloolaba, Queensland, Australia, in 2003 (personal communication). A specimen (the holotype) was collected by Gary Cobb at Mooloolaba, in 2004. The first descriptive account was published by Cobb & Willan (2006: 76).

This species is characterised by intense sky blue body with three longitudinal black stripes, and darker blue rhinophores, intense sky blue gills, and mantle without any pustules. The mantle is raised into a strong sheath surrounding the base of the rhinophores with a smooth rim with a single raised lobe on the inner face. The radula is characterised by the notched central tooth and the ridge on the outer edge of the base of the inner marginal tooth. The reproductive system is characterised by the prostatic and muscular sections of the vas deferens being almost the same length and width as each other, the very large and long penial sheath, the very large penis, and the finger-like shape of the receptaculum seminis that is much smaller than the bursa copulatrix.

Most individuals have an intense sky blue body and gills with darker blue rhinophores. When an individual is photographed with a strong flash light, its body appears blue-green in colour. The only elements of intraspecific variation we noted were the form of the gills and the colour of the oral tentacles. Some individuals, such as the holotype, have solely unipinnate gills, whereas (seemingly most) others have gills that are entirely bipinnate or only bipinnate distally. The oral tentacles have a black tip in some individuals. *Tambja caeruleocirrus* spec. nov. does not emit a coloured substance when irritated or handled or preserved. It feeds on arborescent bryozans of the family Bugulidae.

The intense sky blue colour of this new species recalls that of three other species of *Tambja*, i.e. *T. mullineri* Farmer, 1998 from the Galapagos Islands, eastern Pacific Ocean, *Tambja morosa* (Bergh, 1877) from the Indo-Pacific Ocean including, Australia and New Zealand, and *T. zulu* Pola et al., 2005 from the Indian Ocean coast of South Africa. *Tambja mullineri*, which can attain a similar body length to that of *T. caeruleocirrus* spec. nov., actually has a reversed colour pattern to it. In other words, the background of *T. mullineri* is dark blue, almost black, and the longitudinal stripes are paler blue outlined with a thin

dark blue black edge. Furthermore, *T. mullineri* usually has more numerous longitudinal lines (more than 4 lines) than *T. caeruleocirrus* spec. nov. *Tambja morosa* usually has a velvet-black body with dark blue trimmings (few individuals have a deep blue body) and there are usually no longitudinal lines on the mantle. The colour form *kushimotoensis* of *Tambja morosa* has some longitudinal blue lines, but they are much broader and darker. *Tambja zulu*, which only attains 35 mm in extended length, has a dark blue or black background with a pattern of thin yellow longitudinal lines. Amongst all these somewhat similar longitudinally-lined species of *Tambja*, only *T. caeruleocirrus* spec. nov. has an intense sky blue body with black lines.

Tambja pulcherrima spec. nov.
(Figs 5-6, 14, 20-21, 26, 31)

Tambja sp. – Tan et al., 1987: 73, 78, 86; Kodiat et al., 2012.

Tambja ? cf. *verconis* – Rudman, 1999; Koh, 2006: 82, Wu, 2008: 41
(caption for image second to top on right hand column).

Tambja verconis – Nakano, 2004: 110; Wu, 2008: 41 (caption for image at top of right hand column).

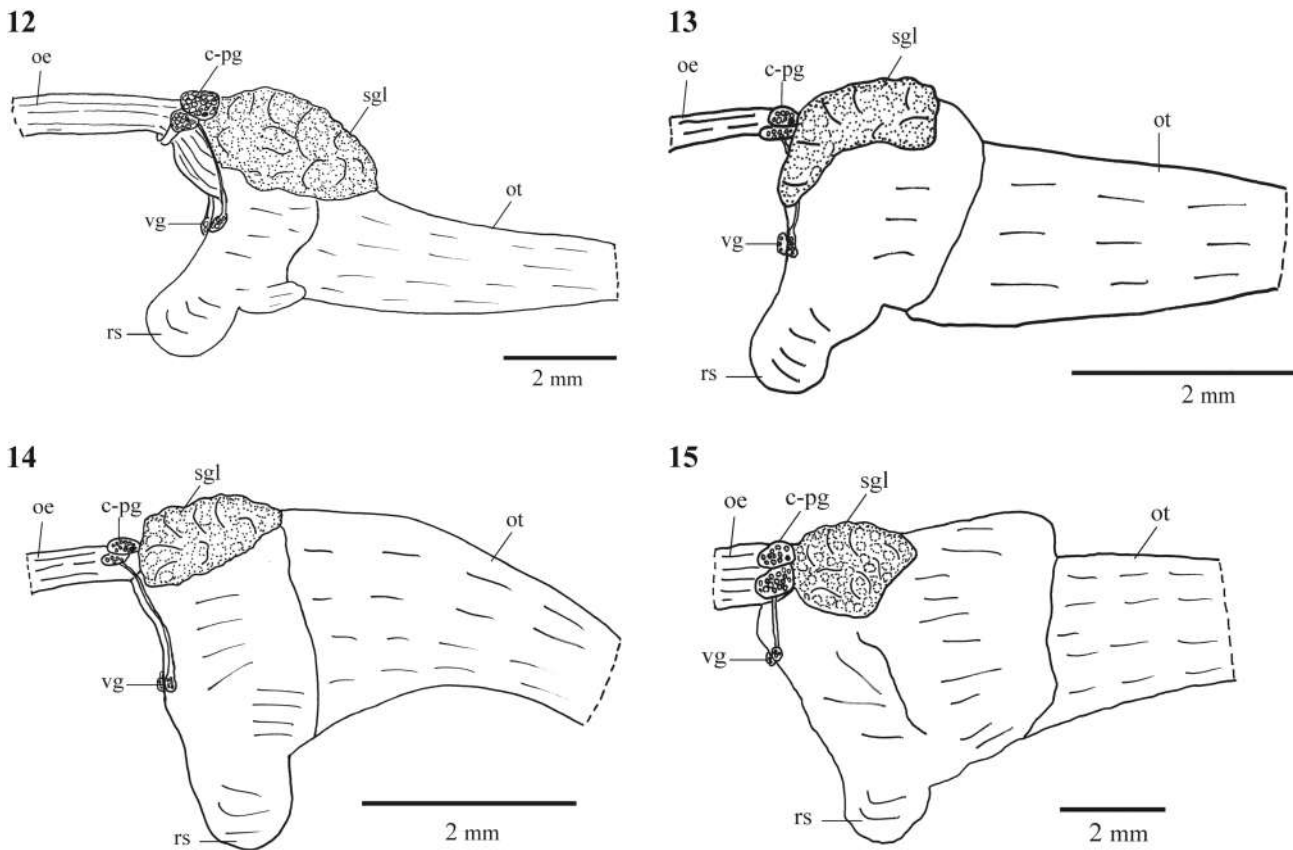
Tambja aff. *verconis* – Chan & Su, 2012.

Tambja sp. 2 – Chan & Su, 2012.

Tambja sp. 1 – Gosliner et al., 2015: 126.

Type series. Holotype (NTM P.48717; formerly IMBNSYSU 538) (dissected), 25 mm extended crawling length, 10 m depth, Wai-an, Pescadores Islands (Penghu), Taiwan (23°33.575'N, 119°29.286'E), coll. Y. Su, 4.vi.2007.

Images examined. – Besides the photographs of the holotype and those publicly available in published works (Tan et al., 1987; Nakano, 2004; Koh, 2006; Wu, 2008) and electronically on the Internet (Rudman, 1999; Kodiat et al., 2012), we have also examined the following images of this species. Queensland – 1 specimen, 48 mm extended crawling length, 6 m depth, off Shute Harbour jetty, photo J. Cruise, 13.vi.1994; 1 specimen, 19 m depth, east of Port Mackay, photo C. Astbury, 29.x.2012; 3 specimens, approximately 20 mm extended crawling length, 15 m depth, Cochrane Artificial Reef, near Bundaberg, photo D. Aston, 17.viii.2012; 1 specimen, approximately 25 mm extended crawling length, approximately 25 m depth, wreck of S.S. Yongala, approximately 22 km east of Cape Bowling Green, central section of Great Barrier Reef Marine Park, photo S. Foale, 18.i.2015; New South Wales – 1 specimen, 25 mm extended crawling length, crawling over turfing algae, on rock ledges, 6.5 m depth, 'Fly Point' dive site, Nelson Bay, Port Stephens, photo D. Aston, 7.xii.2015; 1 specimen, approximately 20 mm extended crawling length, feeding on green arborescent bryozoan, on rocky reef, 8 m depth, 'Little Beach' dive site, Nelson Bay, Port Stephens, photo T. Davis, 27.xi.2015. New Zealand – 1 specimen, photographed subtidally, Poor Knights Islands, Northland, photo G. Climie, vii.2002; 1 specimen, length not



Figs 12–15. Detail of foregut of *Tambja* species. 12, *T. draconus* spec. nov. (NTM P.48730). 13, *T. caeruleocirrus* spec. nov. (NTM P.28179). 14, *T. pulcherrima* spec. nov. (NTM P.48717). 15, *T. verconis* (MV F21625). Abbreviations: bb – buccal (= pharyngeal) bulb; c-pg – cerebral ganglion; oe – oesophagus; ot – oral tube; rs – radular sac; sgl – salivary gland; vg – visceral ganglion.

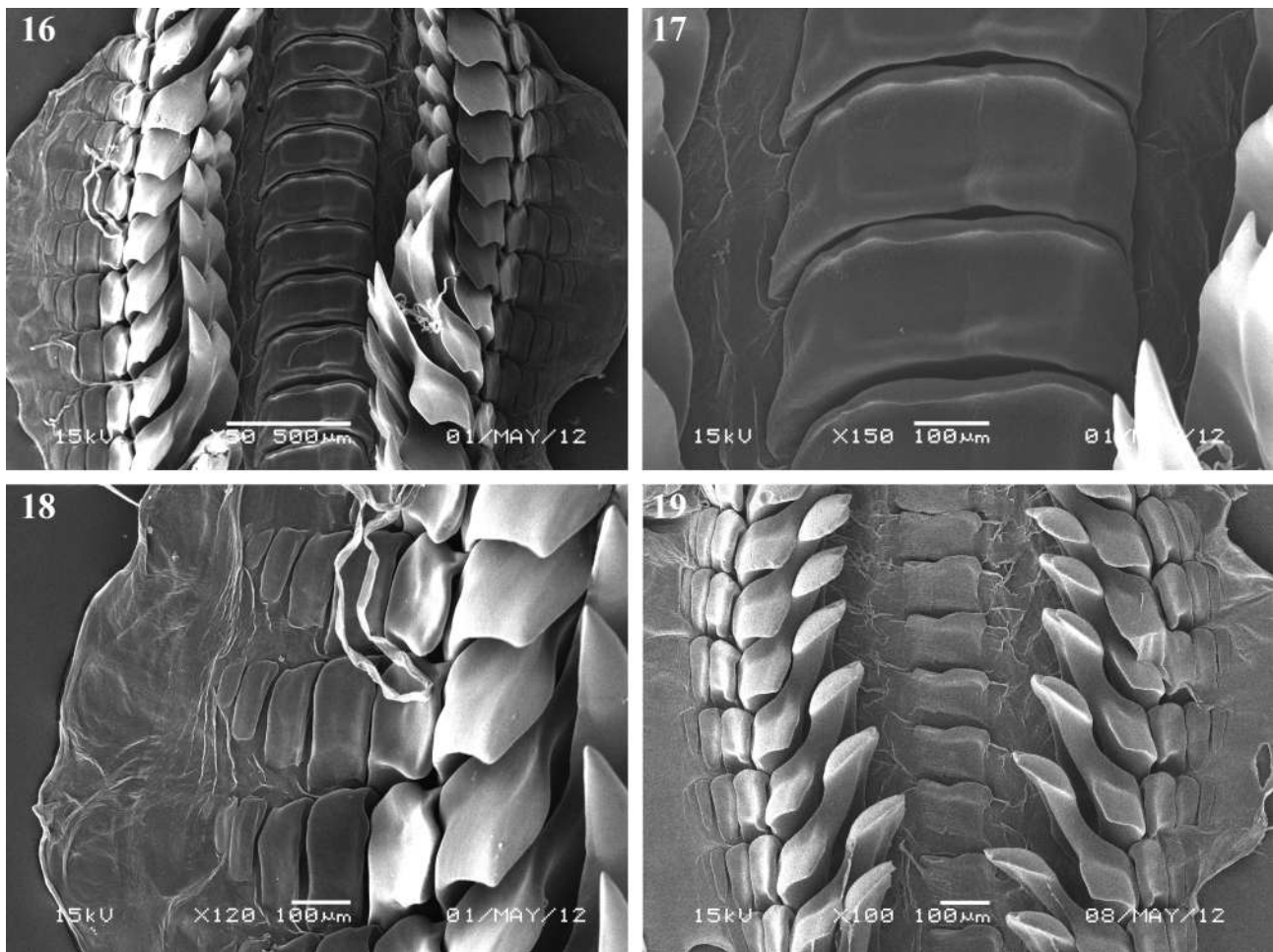
recorded, 10 m depth, 'Bernie's Air Bubble' dive site, near Middle Arch, western side of Tawhiti Rahi Island, Poor Knights Islands, Northland, photo S. Roselt, 26.i.2014.

Etymology. – The specific name chosen for this new species presents the Latin adjective *pulcher* (meaning beautiful) in its superlative form. The name is intended to be adjectival.

Description. – Medium-sized polycerid; maximum extended crawling length 80 mm, average extended crawling length 46 mm. Body elongate, limaciform, widest and highest at head and at level of gills, approximately 5 times as long as broad. Dorsal integument smooth, but raised into some evenly rounded, low pustules. Pustules located dorsally, continuing behind gills to tail, largest on dorsal midline behind gills. Body without notal (mantle) brim, except for anterior of head where there is a prominent, wide, 'U'-shaped, anteriorly flanged brim that is very close to base of rhinophores. Foot narrowing posteriorly to pointed tip. Mantle raised into sheath surrounding base of rhinophores, sheath with smooth rim. Rim of branchial pocket smooth, not raised. Oral tentacles

fronto-lateral, relatively short and thick, semicircular, lip-like, with groove anteriorly. Rhinophores retractile, peduncle slightly swollen, less than half height of clavus; clavus tall and elongate, tapering, with up to 35 lamellae. Opening of pre-rhinophoral sensory organ a horizontal slit immediately above oral tentacle. Gills located immediately anterior to middle of body, bipinnate, relatively narrow and sparsely branched, 3-5 in number (most often 4), not forming semicircle around anal papilla; pinnae relatively long. Genital aperture on right side of body, located approximately one-quarter body length from anterior end.

Colour. – Ground colour of body rich, vivid golden brown. Foot, mantle spots (pustules) and head brim intense dark sky blue (with a paler summit to pustule in some individuals), each surrounded by a narrow black circle with an indistinct darker halo. Anterior brim and oral tentacles with paler blue band, exceptionally cream-green. Foot sole sky blue (paler than dorsum). Rhinophore sheath same golden colour as mantle, but darkening to brown at rim, peduncle uniform intense dark sky blue (appearing black in photographs). Gill pinnae themselves jet black, outer and inner faces of rachides with narrow black line at base,



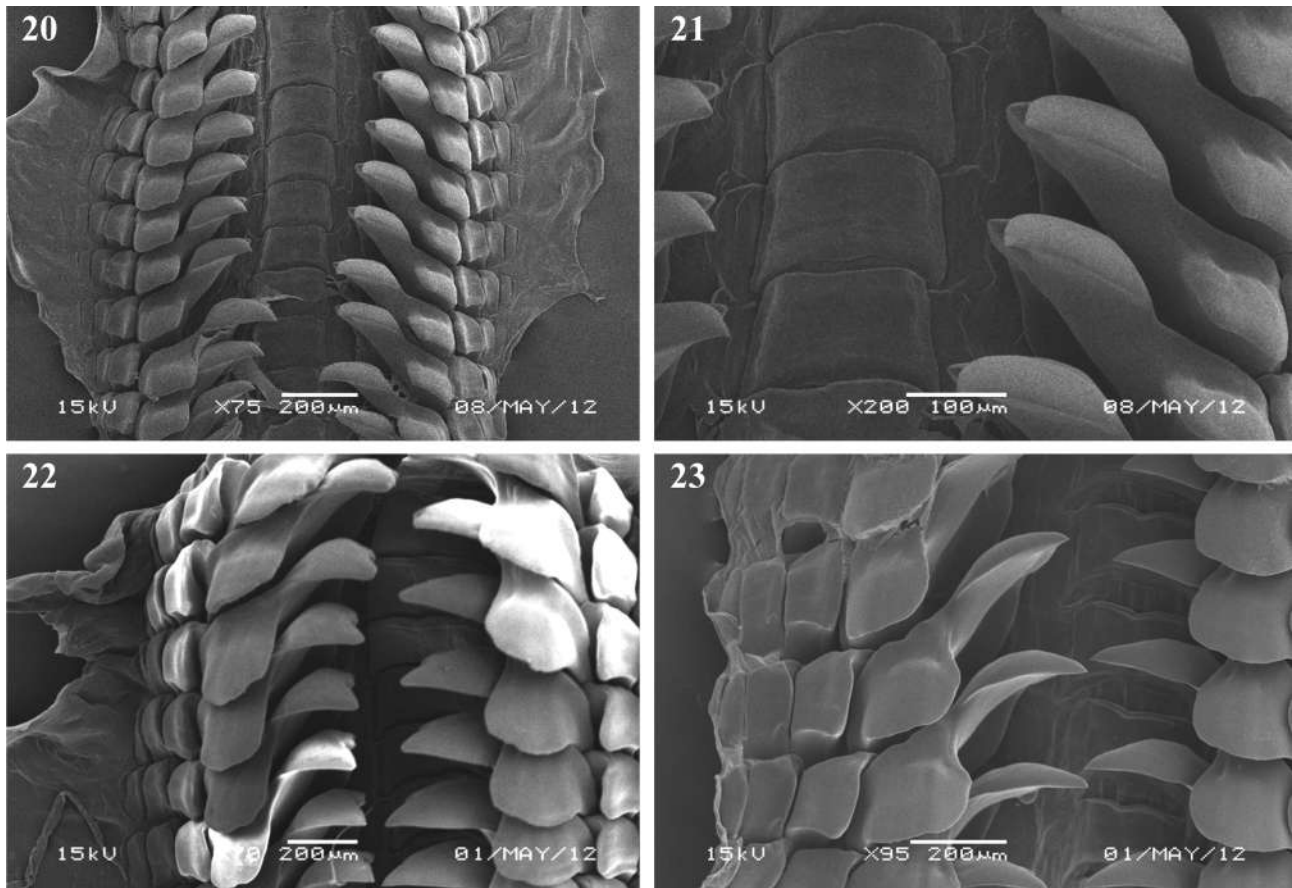
Figs. 16–19. Scanning electron microscope photographs of radular teeth of *Tambja* species. 16, Dorsal view of whole radula of *T. dracomus* spec. nov. (NTM P.48730). 17, Detail of central teeth of *T. dracomus* spec. nov. (NTM P.48730). 18, Detail of lateral teeth of *T. dracomus* spec. nov. (NTM P.48730). 19, Dorsal view of whole radula of *T. caeruleocirrus* spec. nov. (NTM P.28179).

then dark sky blue for a short distance, then pale green to tip. Anal papilla pale green.

Internal anatomy. – Radula (Fig. 20–21) (1 examined; holotype) multidentulate, with formula: 16 x 3.1.1.1.3 (25 mm extended crawling length). Central (rachidian) tooth thin, nearly square, width approximately 1.25 times height (both measurements made at middle of tooth), anterior margin not – or at most weakly – notched, cutting edge not denticulate at all, antero-lateral corners rounded, postero-lateral corners extended, pointed. Lateral tooth large and thick, approximately twice height of central tooth, wide at base with triangular flange, shaft narrowing considerably and curving to apex towards axis of radula, cusp well developed, inner denticle poorly developed, shorter than level of main cusp. Marginal teeth much smaller than lateral tooth, but all 3 almost same height as each other, all higher than wide, thin and plate-like; first (inner) marginal widest posteriorly, with strong ridge on outer posterior corner. Second marginal only slightly smaller than first marginal, but

slightly narrower. Third marginal almost same height as second marginal, but half its width. Labial disc (Fig. 26) well-developed, cuticularised, not thickened into recognisable jaws, dome-shaped in profile, lacking denticles.

Reproductive system (Fig. 31) hermaphroditic, tri-aulic. The following account relates to the holotype, which is a fully sexually mature individual that has mated. Ototestis overlying and covering entire digestive gland except for stomach ventrally. Main hermaphrodite duct long (approximately 2 mm when unravelled, not enlarging in width along its course), rapidly quadrupling its width distally to form long, tubular (S-shaped in situ), opaque white ampulla. Ampulla narrowing gradually distally where it bifurcates into proximal vas deferens and proximal oviduct, both very narrow ducts. Vas deferens tubular, enlarging almost immediately into short, coiled, glandular, prostatic section, thence coiled muscular section. Prostatic section equal to two-thirds of muscular section, both equal in width. Prostatic section



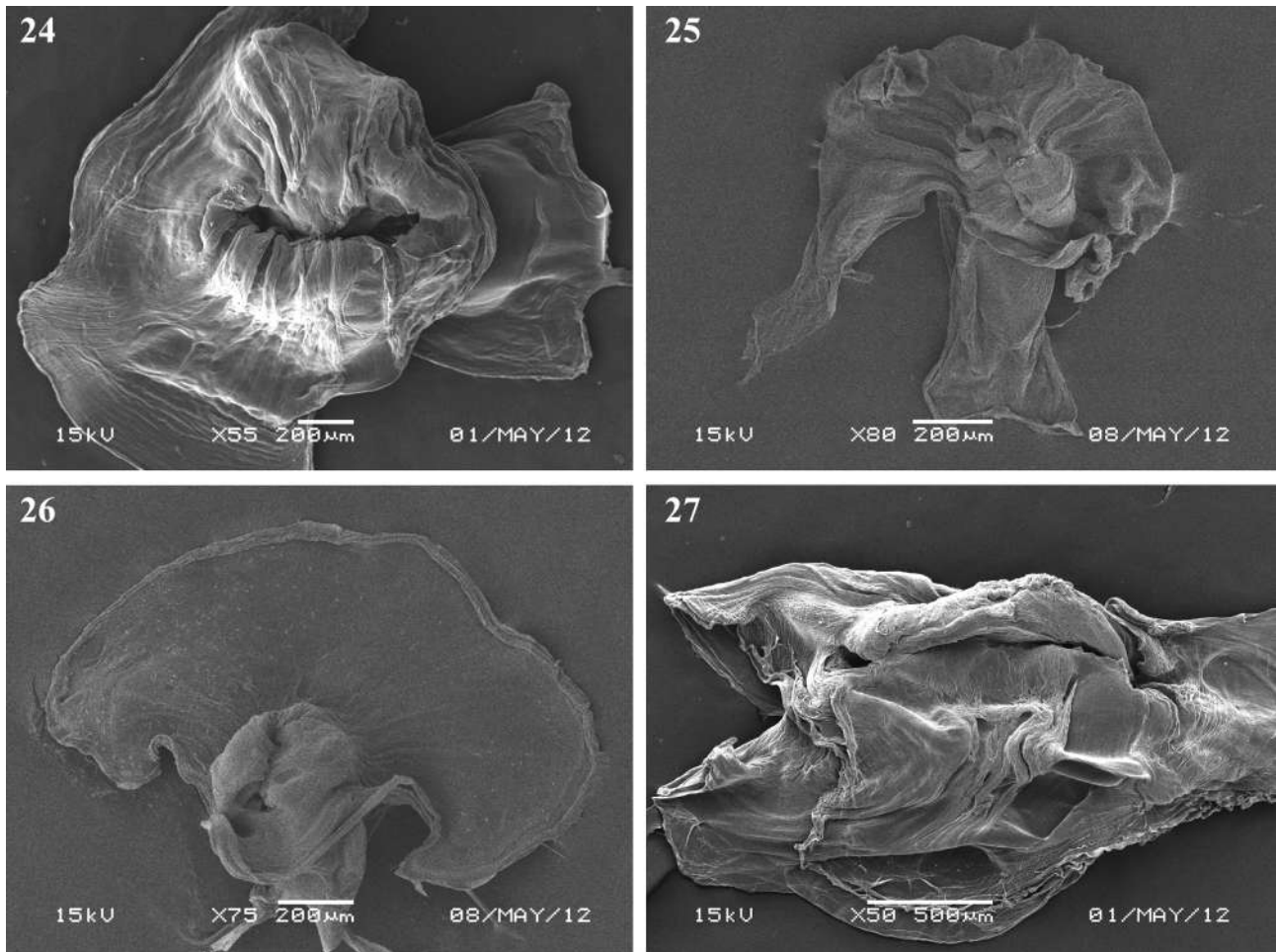
Figs. 20–23. Scanning electron microscope photographs of radular teeth of *Tambja* species. 20, Dorsal view of whole radula of *T. pulcherrima* spec. nov. (NTM P.48717). 21, Detail of central and inner lateral teeth of teeth of *T. pulcherrima* spec. nov. (NTM P.48717). 22, Dorsal view of radula of *T. verconis* (MV F21625). 23, Detail of central plus half row of teeth of *T. verconis* (MV F21625).

not surrounding bursa copulatrix. Distal vas deferens enlarged into very thin-walled and transparent penial sheath. Penial sheath approximately double width of muscular vas deferens, opening into common genital atrium, and containing long, acrembolic penis armed with numerous, simple, curved spines. Penial gland embedded in body wall at base of penial sheath, finger-like, flattened, thin-walled. Proximal oviduct short, widening into fertilisation chamber, then constricting before bifurcating into proximal vagina and uterine duct. Vagina short, straight, widening as common stalk to bursa copulatrix and receptaculum seminis. Bursa copulatrix spherical, thin-walled, with straight duct, contents creamish in preservative. Receptaculum seminis slightly smaller in size than bursa copulatrix, spherical, thick-walled. Vaginal gland thick-walled, approximately triple height of bursa copulatrix. Female gland mass spherical, extensively convoluted, not flattened, consisting of 2 distinct morphological glandular sections – solid (dark orange in preservative) proximal section and larger extensively convoluted (white in preservative) distal section.

Distribution. – South Korea, Japan, Taiwan, Malaysia, Papua New Guinea, Australia (Queensland and New South Wales), New Zealand (only Poor Knights Islands, Northland).

Remarks. – As far as we can ascertain, the first photograph of this species was published by Tan et al. (1987) based on material from Taiwan, which we now know is towards the northern end of the geographical range for this species (see above). Later, Rudman (1999) recognised it on the basis of a specimen photographed by Graham Climie at the Poor Knights Islands, northern New Zealand. Ironically, this locality is at the very southern end of the species' geographical range. This biogeographical point will be elaborated further in the Discussion in this paper.

Tambja pulcherrima spec. nov. is characterised by the rich, vivid golden brown body, and intense dark sky blue rhinophores and gills, and smooth mantle with a few dark sky blue pustules surrounded by a narrow black circle with an indistinct darker halo. The radula is characterised by the nearly square central tooth that is not notched, relatively smaller lateral tooth compared to central tooth, poorly developed



Figs. 24–27. Scanning electron microscope photographs of oral cuticle of *Tambja* species (exterior views from the front). 24, *T. dracomus* spec. nov. (NTM P.48730). 25, *T. caeruleocirrus* spec. nov. (NTM P.28179). 26, *T. pulcherrima* spec. nov. (NTM P.48717). 27, *T. verconis* (MV F21625).

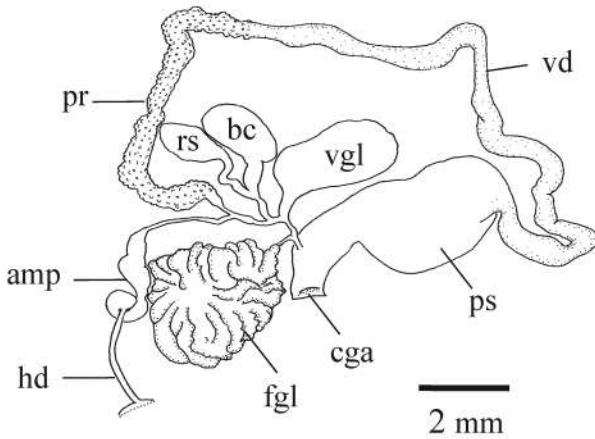
denticle on the inner lateral tooth, and the marginal teeth being almost the same height as each other. The reproductive system is characterised by the very large ampulla, relatively short vas deferens (though both prostatic proximal and muscular distal are present), thin-walled penial sheath, long penis and, particularly, a penial gland.

Most individuals have a golden body and head brim with intense dark sky blue pigment. However, a few individuals have a pale golden brown body or pale dark sky blue head brim. Most individuals have similar-sized pustules on the mantle, whereas a few have a variety of different sized pustules.

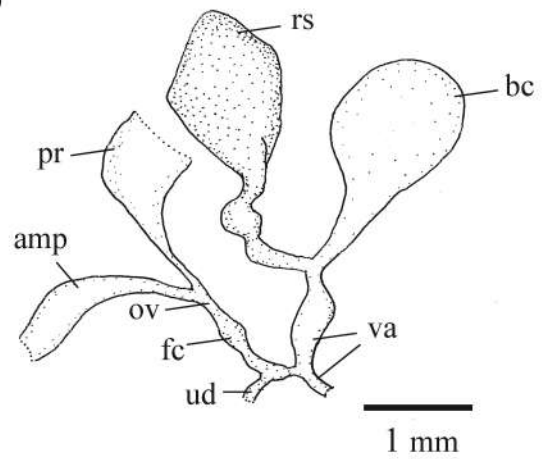
In colouration, *Tambja pulcherrima* spec. nov. is most similar to *T. verconis* from southern Australia and *T. stegosauriformis* Pola et al., 2005, from southern Brazil [the range of this species has been expanded into Santa Catarina state by Padula et al. (2011)], both these species attaining a similar length to *T. pulcherrima* spec. nov. In comparison, the background colour of *T. verconis* (Figs 1, 2) is usually pale yellow and the

spots are blue and irregular in outline in *T. verconis*, whereas *T. pulcherrima* spec. nov. has blue-green circular patches, each surrounded by a black ring with a dark halo. Such rings and haloes are always absent in *T. verconis*. In *T. verconis* there is one blue spot on the head between the rhinophores and a second one on top of the pericardium, whereas in *T. pulcherrima* spec. nov. there is one, or a few, spots in the middle of the dorsum. Furthermore, *T. verconis* has regular, longitudinal ridges on its mantle whereas *T. pulcherrima* spec. nov. has a completely smooth mantle. *Tambja stegosauriformis* is characterised by the well-developed pustules on the mantle, especially those in a row extending from the gills to the tail. Additionally, in *T. stegosauriformis* the head brim is considerably wider and more lobed than that of *T. pulcherrima* and the band on the head brim is also different; it is dark green and the hind margin is notched into a “V” shape in *T. stegosauriformis*, whereas it is royal blue and not notched in *T. pulcherrima* spec. nov. In comparison to *T. pulcherrima* spec. nov., *T. verconis* (Fig.

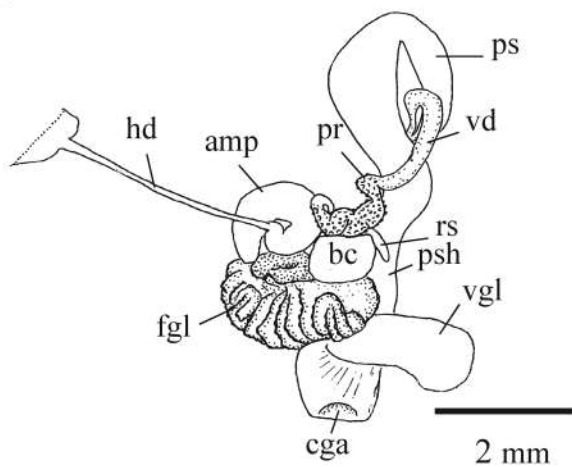
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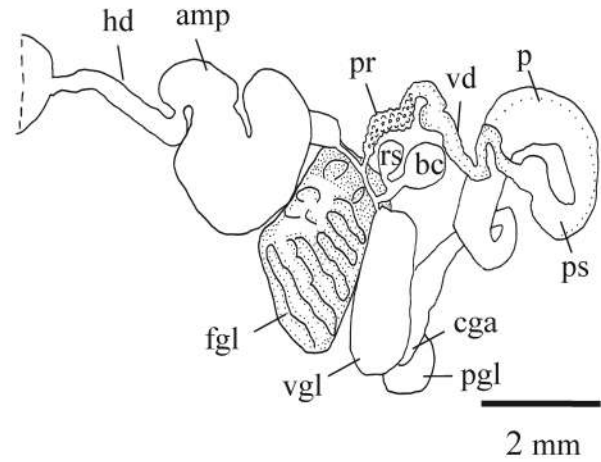
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30



31



Figs. 28–31. Reproductive system (unravelling, semi-schematic drawings) of *Tambja* species. 28, *T. dracomus* spec. nov. (NTM P.48730). 29, Detail of vagina and allosperm vesicles of *T. dracomus* spec. nov. (NTM P.48730) to show connections and relative sizes. 30, *T. caeruleocirrus* spec. nov. (NTM P.28179). 31, *T. pulcherrima* spec. nov. (NTM P.48717). Abbreviations: amp – ampulla; bc – bursa copulatrix; cga – common genital aperture; hd – hermaphrodite duct; fc – fertilisation chamber; fgl – female (= nidamental) gland mass; ov – oviduct; pr – prostatic section of (proximal) vas deferens; p – penis (inside penial sheath); pgl – penial gland; ps – penial sheath; psh – distal penial sheath; rs – receptaculum seminis; ud – uterine duct; va – vagina; vd – distal section of vas deferens; vgl – vaginal gland.

22-23) has a more deeply notched anterior edge to the central radular tooth, relatively narrower shaft on the lateral tooth, and triangular flange at the base of the lateral tooth (square in *T. pulcherrima* spec. nov.). In comparison to *T. pulcherrima* spec. nov., *T. verconis* lacks a penial gland, has a smaller ampulla (this organ is relatively much larger in *T. pulcherrima* spec. nov.), a relatively longer vas deferens, and a relatively much larger female gland mass. *Tambja sagamiana* (Baba, 1955) from the northwestern Pacific Ocean is superficially similar to *T. pulcherrima* spec. nov. in external appearance, but *T. sagamiana* actually has the colours reversed – the background is blue and the spots are orange ocellated with a black ring. An interesting (presumably natural) photograph published in Debelius & Kuiter (2007: 68, bottom left) taken by Yasuko

Matsuno at Kashiwajima, Japan, shows an individual of *T. sagamiana* alongside two individuals of *T. pulcherrima* spec. nov. This photograph demonstrates that these species can both occur together in the same microhabitat.

PHYLOGENETIC SIGNIFICANCE OF SOME CHARACTERS IN THE GENUS *TAMBJA*

Biology and biogeography. – Members of the genus *Tambja* raise some contradictions in terms of their biology and biogeography. Whenever their food has been determined, it is an arborescent bryozoan of the family Bugulidae (phylum Bryozoa, class Gymnolaemata, order Cheilostomata, suborder Neocheilostomina), either a species of *Virididentula* or *Sessibulula*, but sig-

nificantly never *Bugula* itself. The species most often reported as the food is the blue-green *Virididentula dentata* [previously universally called *Bugula dentata*], a species well known for its secondary metabolites that are toxic alkaloids called tambjamines (Blackman & Li, 1994). For instance, the six sympatric species of *Tambja* that occur at the Poor Knights Islands off the northern North Island of New Zealand (see below) have all been reported to eat only *V. dentata*. An excellent close up photograph of a juvenile *Tambja tenuilineata* with its oral tube everted feeding on *Virididentula dentata* is given by Armstrong (2004). Pola et al. (2015: 631) have speculated that *Roboastra gracilis* could eat bryozoans, and bryozoans are eaten by (as far as we know, all) other members of the 'traditional polycerid' genera (*Polycera*, *Polycerella*, and *Thecacera*), triophids (*Plocamopherus*, *Kaloplocamus*) and some gymnodorids [e.g. *Gymnodoris arnoldi* (Burn, 1957) and *Paliolla cooki* (Angas, 1864), both of which eat the encrusting bryozoan *Baenia magellanica* (Beaniiidae, superfamily Buguloidea)] (Robert Burn personal communication, September 2014). Unlike the reddish brown *Bugula neritina* (Linnaeus, 1758), that is frequently part of the fouling community on ships' hulls and so has been transported around the world (Stafford & Willan, 2007), the almost cosmopolitan distribution of *Virididentula dentata* is assumed to be natural.

Given that the genus *Tambja* sensu stricto has such a restricted diet, it is highly unusual among antho-branch nudibranchs that it should be so speciose (we estimate it contains about 40 species). So, as many of the species of *Tambja* are wide-ranging, there must be intense interspecific competition for food when species co-occur.

The majority of species of *Tambja* occur in the tropical Indo-Pacific Ocean (Pola et al., 2005a, 2005b), and the majority of those range widely within that enormous biogeographic realm. Such a pattern indicates to us that many species must achieve long-distance dispersal by long-lived planktotrophic larvae. This hypothesis can be tested at a unique location in the southwestern Pacific that is world-renowned for the presence of 'tropical' marine species in an otherwise temperate coastal environment – that is the Poor Knights Islands (35°28'S, 174°44'E) off the coast of Northland in New Zealand (Doak, 1971; Morton & Miller, 1973; Brook et al., 2001; Ayling & Schiel, 2003). The waters around those islands, bathed by the East Australian Current, are consistently 2°C warmer than those of the adjacent mainland of New Zealand (Willan & Perkins, 2011). They support many marine species recruited as larvae or juveniles in the plankton from the north of the North Island (Willan & Perkins, 2011). Many of these species have never been recorded on the mainland North Island coast beyond

the Poor Knights Islands. Incorporating the new species described in this paper, there are now records of six species of *Tambja* from the Poor Knights Islands, i.e. *T. verconis*, *T. morosa*, *T. tenuilineata*, *T. dracomus*, *T. caeruleocirrus*, *T. pulcherrima*. These islands are regularly visited by scientifically-knowledgeable divers and observations by them over the last 40 years have shown there is a resident population of the first three species, but that sightings of the latter three species (i.e. those described in this paper) are much more sporadic. In fact, there are no records of any of the three new species described in this paper from anywhere else in New Zealand other than the Poor Knights Islands. We conclude that the occurrence of the other three species at the Poor Knights Islands are the result of single sporadic recruitment events, or pseudopopulations (i.e. populations consistently replenished from the southwest Pacific), or temporary populations that only self-recruit during warm spells.

Beyond the Poor Knights Islands, the records of *Tambja verconis*, *T. tenuilineata* and *T. morosa* are very sparse from the New Zealand mainland probably indicating only temporary populations there. *Tambja morosa* is known from just one individual that was observed by the senior author of this paper at Matai Bay (34°49'S, 173°12'E) at the outermost tip of Karikari Peninsula in March 1975. *Tambja verconis* is known from two individuals that were observed at Matai Bay by the senior author of this paper and Jim Dollimore in February 1988 and by one individual from the Mokohinau Islands (35°55'S, 175°08'E) situated at the outermost Hauraki Gulf immediately southeast of the Poor Knights Islands in April 2003 (Burnett 2003). *Tambja tenuilineata* is known from three individuals from the Mokohinau Islands (Miller & Haagh, 2005).

Colour and pattern. – The majority of *Tambja* species, both those presently described species, and the 10 (at least) undescribed species (Kodiat et al., 2012), are vividly marked with bright colours and boldly striped or spotted, and they do not hide during the daytime. As we mentioned above for *T. verconis*, these species are immediately noticed by divers and, presumably, also by fishes which might prey upon them. This is certainly the case for two of the new species described here, *T. caeruleocirrus* and *T. pulcherrima*. In contrast, the other new species described here, *T. dracomus*, is dull in colour without any contrasting stripes or spots and it hides during the daytime and is active at night. In the cases where the secondary metabolites of *Tambja* species have been studied they have been found to be a subset of the tambjamine alkaloids and an aldehyde that are derived from the bryozoan food *Virididentula dentata*

(Pereira et al., 2012). We hypothesise that the vividly coloured species of the genus *Tambja* sequester a large range of secondary metabolites (or the most toxic metabolites) that are toxic to fishes, so their colours represent aposomatism and they are diurnally active. In contrast, we suggest that the dull coloured species, such as *T. dracomus*, sequester few secondary metabolites (or the least toxic ones), so they are cryptically coloured and mostly active only at night.

Pre-rhinophoral sensory organ. – We believe that the pre-rhinophoral sensory organ of some ‘phanerobranch’ nudibranchs is, what Wägele (1998) would term, a specialised organ with the potential to yield characters of great phylogenetic significance.

The organ, variously termed a “sensory pit” (Rudman, 2003), “lappets (or ledges)” (Rudman, 2009), “pre-rhinophoral pit” (Pola et al., 2006b: 528) or “lateral slot” (Pola et al., 2005a: 262) in *Tambja*, is revealed most dramatically in a set of three images taken by Todd Garthwaite of an individual *Tambja morosa* (colour form *kushimotensis*) from Taiwan (Rudman, 2003). Those images show the dilated organ consists of a deep vertical slit with both the walls ornamented with raised, pinnately branched, vertical lamellae. Similarly, Fig. 2 in this present paper shows the organ dilated in *T. verconis*. Although it is hardest to discern when it is closed in species of *Tambja* with black or dark blue bodies, incongruously it would seem to be most often dilated to some extent in the field in the dark species *T. morosa*.

Up until now the pre-rhinophoral sensory organ has been largely overlooked in ‘phanerobranch’ nudibranchs and where its presence has been noted, the interpretations of its significance have differed widely. It has been thought to be specific to (just some) *Tambja* species (e.g. Yonow, 1995), or to just some individuals (Pola et al., 2006c: 496). For example, Pola et al. (2006b) recorded its presence in 13 species (including *T. morosa* and *T. verconis*), its absence in 19 species, and its status was not known in a further three species. Indeed, even most recently, Pola et al. (2014: 631) stated that it was only present in “some” species of *Tambja*. Rudman (1998: 994) took quite the opposite view, claiming that this organ was “usually present” in all members of the ‘traditional Nembrothinae’. We could not detect it in any species of *Nembrotha* we studied, no matter how close we looked [we did not investigate histologically]. However, we found that this organ was present in every animal of *Tambja sensu stricto* we studied when we looked closely (see Table 1), but it is impossible to detect in specimens that have been inadequately fixed and its confirmation requires careful dissection after relaxation and adequate fixation, so our conclusion is that it is actually present in *all* species of *Tambja*, at least

in all species of *Tambja sensu stricto*.

In *Tambja*, this organ is situated horizontally on either side of the head half way between the base of the rhinophore and the oral tentacle. Our dissections of fresh *T. dracomus* showed that this organ is well supplied by fibres originating from the rhinophoral nerve, thus confirming its sensory function suggested by Pola et al. (2005a: 262). A comparative histological study of this organ is urgently needed to describe its structure in detail.

We conclude that the pre-rhinophoral sensory organ is under the control of an individual. Most of the time it is closed shut with its aperture merely a slit. This explains why it is often not visible in photographs of living animals, and often tightly closed and nearly impossible to locate in most preserved specimens. However, occasionally in life an animal dilates one of these organs (or both of them simultaneously), presumably to obtain some sensory input, and then they can be seen very easily.

The conclusion that all species of species of *Tambja sensu stricto* possess pre-rhinophoral sensory organs has considerable phylogenetic significance in that it renews questions about the relationships within the (subfamilies of) ‘traditional Polyceridae’, and more widely between the (families of) ‘traditional Polyceridae’ and ‘traditional Gymnodorididae’. The deep, crescentic, often very large and elaborate pits on the head of all *Thecacera* species – i.e. in *Thecacera picta* (Baba, 1972), *T. pennigera* (Willan, 1976), *T. boyla* (Willan, 1989), and an unnamed species (Kodiat et al., 2012) are probably homologous with the organs present in *Tambja*. Similarly, the elaborate pits on the head of traditional gymnodorids – e.g. *Gymnodoris alba* (Bergh, 1877) (Cobb & Willan, 2006: 87 bottom photograph) are presumably also homologous with the pre-rhinophoral sensory organs of *Tambja*. When this newly recognised organ is incorporated with the fact that *Tambja* also shares the diet of arboreal bryozoans with *Thecacera* and (some) traditional gymnodorids, it suggests the possibility of a closer phylogenetic relationship between them than any possess with *Nembrotha* (a genus in which all species definitely lack pre-rhinophoral sensory organs and whose diet is exclusively solitary ascidians (Pola et al., 2008a)). Perhaps it this organ is apomorphic for all ‘traditional Polyceridae’?

Radular teeth. – Our observations of the radular teeth of *Tambja verconis* and the new species described herein highlight the need for a reconsideration of some of the polarities argued by Pola et al. (2006c) for their phylogeny of *Tambja*. In particular, we are uncomfortable with the distinction between a “notched” rachidian and an “un-notched” rachidian.

Pola et al. (2006c) polarised the character as plesiomorphically notched in the outgroup and “the vast majority of *Tambja* species” (sic), and apomorphically “un-notched” in *Nembrotha*, *Roboastra*, *Tambja oliva* and *T. limaciformis*. A distinct notch is certainly present in *T. verconis*, the type species of the genus (personal observation), but it is impossible to make a clear distinction in the other species we studied because the determination depends greatly on the way the radula is orientated for examination. We think this character is merely species-specific, and not sufficiently precise to polarise for a future broad phylogenetic study.

TAXONOMIC RAMIFICATIONS OF THIS STUDY

Given that multiple phylogenetic studies, both morphological and molecular, conducted over nearly the last 20 years (Tholleson, 1999, 2000; Wägele & Willan, 2000), have indicated the ‘traditional’ family Polyceridae is not monophyletic, it is clearly time for some radical thinking. This conclusion, combined with the fact that Marta Pola and her colleagues have thrice failed to resolve the limits of genera within the ‘traditional Nembrothinae’ (Pola et al., 2007, 2008a, 2014), suggests malacologists must go back to square one with the phylogeny of the ‘phanerobranch’ nudibranchs themselves, a demonstrably non-monophyletic group (Pola et al., 2007). Indeed, retention of the ‘traditional phanerobranch’ families Polyceridae, Gymnodorididae and Triophidae may well mask the true phylogeny of this group. In a parallel example, retention of the traditional genera had handicapped the understanding of another traditional family of dorid nudibranchs, the Chromodorididae, until they were dismembered by Johnson & Gosliner (2012). The morphological synapomorphies holding the three genera that presently constitute the ‘traditional Nembrothinae’ – *Nembrotha*, *Tambja* and *Roboastra* – are certainly not strong. Pola et al. (2014) mention colourfulness, large size and striking appearance, but these are subjective characters and there are exceptions to every one of them. Rudman (1998: 995) mentioned that the relationship between the ‘traditional’ families Polyceridae and Gymnodorididae was not clear with a suggestion that *Gymnodoris* has a “close relationship” with the ‘traditional Nembrothinae’.

Part of this re-evaluation has to be morphologically based within the context of novel characters such as the pre-rhinophoral sensory organ, lateral pits, integumentary spicules, radular teeth, defensive chemicals and diet, and must incorporate numerous representatives from other undisputedly related ‘phanerobranch’ dorids such as those of the genera *Thecacera*, *Gymnodoris*, *Paliolla*, *Triopha*, *Lecithophorus*,

Kalinga, *Crimora* and *Kaloplocamus*.

To start this renaissance, the genera that constitute the ‘traditional Nembrothinae’ must be clearly understood and defined (and delineated) more precisely as monophyletic units. We do this here.

Tambja Burn, 1962. – We herein restrict *Tambja* to those species that are closest to the type species, *T. verconis*; that is the group we have termed *Tambja* sensu stricto throughout this paper (see Table 1). In order to render *Tambja* more nearly monophyletic, we remove five species into a monophyletic genus, *Martadoris* gen. nov., with the diagnosis and composition below. *Tambja* as we now understand it, is also defined below. We stress that all species of *Tambja* sensu stricto possess pre-rhinophoral sensory organs and all species feed on bugulid bryozoans. Though their placement is uncertain, we leave *T. abdere*, *T. capensis* and *T. zulu* within *Tambja* for the meantime, and we note that each requires further evaluation from fresh material in light of our redefinition of *Tambja*.

In summary, we define the genus *Tambja* to include nudibranchs of the ‘traditional Polyceridae’ with the following characters (synapomorphies in bold): body elongate, fusiform; possessing a distinct oral brim that, like the mantle brim, lacks tentaculate processes; body surface smooth or – in a minority of species – with low pustules; body lacking integumentary spicules (microscleres); rhinophoral sheath distinct, with raised rim; **pre-rhinophoral sensory organ present, slit-like, deep, able to be dilated or closed at will; oral tentacles lobe-like (lappets), dorso-ventrally flattened, with outer edge grooved horizontally**; anal papilla not elevated; large salivary glands sessile on buccal bulb; nerve ring with separate cerebral and plural ganglia, situated at rear end of buccal bulb; **strongly cuticularised labial disc**; central tooth of radula large and rectangular, thin but strong, notched or un-notched, **non-denticulate**; lateral tooth simple or bifid, usually smooth but rarely denticulate; marginal teeth 3-7, all simple; penis armed with spines; vagina sometimes with distal gland or pouch; bursa copulatrix and receptaculum seminis together on short junction of vagina and allosperm duct; proximal section of vas deferens prostatic, small in length, tubular, slightly wider than rest of duct; **diet consisting of arborescent bryozoans of the family Bugulidae**. This summary is an amalgamation of the characters presented by Burn (1962a, 1967), Carté & Faulkner (1983, 1986), Miller & Haagh (2005), Pola et al. (2005a, 2006b, 2007, 2014), Cimino & Ghiselin (2009) and the authors’ own observations.

Another character that has the potential to be phylogenetically significant in *Tambja* is the presence of pigmented patches immediately above the position of

the central nervous system (including the eyes) behind the rhinophores (see Ajtai 2002). These patches are present in at least *T. abdere* and *T. eliora* and *T. ceutae*.

***Martadoris* Willan & Chang, gen. nov.** – Type species: *Palio amakusana* Baba, 1960. Recent, Indo-Pacific, gender feminine. Included species: *M. amakusana*, *M. limaciformis* (Eliot, 1908), *M. divae* (Er. Marcus, 1958), *M. oliva* K. Meyer, 1977, *M. mediterranea* (Dominguez *et al.* 2015). *Martadoris* is diagnosed with the following characters (synapomorphies in bold): small nudibranchs belonging to the ‘traditional Polyceridae’ (less than 30 mm extended length); oral tentacles not enlarged, with a ventral longitudinal slit; greatly reduced rhinophoral sheath, lacking pre-rhinophoral sensory organs; lacking oblique pits on body; **possessing elongate pouches at junction of oral tube and buccal bulb**; rachidian tooth of radula nearly quadrangular, inner laterals with bifid cusp; **possessing well-differentiated prostate gland composed of dense network of interconnecting tubules over its surface**; lacking vaginal gland; diet consisting of arborescent bryozoans. What appears to be a pre-rhinophoral sensory organ in one photograph of a living *M. limaciformis* (http://www.medslugs.de/E/Ind-NW/Tambja_limaciformis/Tambja_limaciformis_06.htm) is, on very close inspection of the image, merely a streak of opaque white pigment on the forehead. Pola *et al.* (2006a, 2006b, 2008a, 2014) and Dominguez *et al.* (2015) have shown this group has very high molecular support as a monophyletic clade (i.e. a genus as we interpret it). The name of the new genus is derived by combining the name Marta (from Marta Pola, in recognition of her pioneering molecular studies on this group of nudibranchs) and *doris*.

Roboastra Bergh, 1877 – The small (less than 27 mm extended length, though 15–25 mm is usual for adults) *Roboastra gracilis* Bergh, 1877, is sufficiently distinct morphologically and genetically to form a clade (i.e. a genus as we interpret it) of its own (Pola *et al.*, 2006a, 2006b, 2007: 739; personal observation) apart from all the remaining species presently in *Roboastra*. A perfect precedent exists elsewhere in nudibranchs, where the monotypic genus *Cuthona* Alder & Hancock, 1855 is distinct morphologically and genetically from its much larger sister genus *Tenellia* Costa, 1866 (Miller, 2004; Cella *et al.*, 2016). *Roboastra* is diagnosed with the following characters (synapomorphies in bold): small species of nudibranch belonging to the traditional Polyceridae; **uniquely elongate rhinophores**; **presence of longitudinal rows of pits all over the body**; relatively short oral tentacles with dorso-lateral slit; **sparse and unipinnate gills**. The pits on the body are shown extremely well in the lateral view of a 25

mm specimen from Mactan Island, the Philippines (Willan & P. Poppe, 2010: 372, Fig. 3). The diet is probably bryozoans. We completely agree with Pola *et al.* (2014: 631) that the nudibranch supposedly attacking a living *Nembrotha kubaryana* Bergh, 1877 (Gudgeon 2006) is a juvenile *Tyrannodoris luteolineata* (see immediately following paragraph to explain the generic allocation) because it has no lateral pits on its body (in contrast to *Roboastra* that possesses them) and bipinnate compound gills (instead of the unipinnate gills of *Roboastra*), so this can be dismissed as a possible example of carnivory in *R. gracilis*.

Tyrannodoris* Willan & Chang, gen. nov.** – Type species: *Nembrotha luteolineata* Baba, 1936. Recent, Indo-Pacific, gender feminine. *Tyrannodoris* accommodates all the species previously in *Roboastra* (see Table 2), except for *R. gracilis*. *Tyrannodoris* is diagnosed with the following characters (synapomorphies in bold): large nudibranchs belonging to the ‘traditional Polyceridae’ (some up to 150 mm extended length); **oral tentacles enlarged**, with dorso-lateral longitudinal slit; lacking pre-rhinophoral sensory pits; lacking oblique pits on body; possessing multiple large compound gills; **possessing large rachidian and lateral teeth in the radula**; possessing vaginal gland; **food consisting of other ‘phanerobranch’ nudibranchs - apparently most often species of *Tambja. Members of this genus are rapaciously carnivorous, attacking and devouring soft-bodied polycerids (particularly *Tambja* spp.) and other ‘phanerobranchs’. The name of the new genus is derived by a combination of the Latin word *tyrannus* meaning terrible and *doris*.

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Table 1. Annotated list of species of *Tambja* Burn, 1962, as defined herein.

Tambja abdere Farmer, 1978. Feeds on arborescent bryozoans (Camacho-García et al. 2005, <http://www.seaslugforum.net/find/tambabde>), specifically those of the genus *Sessibugula* (Bugulidae) (Hermosillo et al. 2006: 72). Pola et al. (2006a: 60) reported that the pre-rhinophoral sensory organs “appear to be absent in this species”. Pola et al. (2014) concluded this species does not cluster genetically with other *Tambja* species. Requires further investigation.

Tambja affinis (Eliot, 1904). Pre-rhinophoral sensory organ observed in living individuals by us, recorded by Pola et al. (2005a: 267, 2006c: 498), also shown in photographs (<http://www.seaslugforum.net/message/14480>, <http://www.seaslugforum.net/message/14810>, and <http://www.seaslugforum.net/find/22305>). Feeds on bryozoan *Virididentula dentata* (Bugulidae).

Tambja amitina (Bergh, 1905). Still only known from the original description of a single evidently badly preserved individual. All the existing type series of the species described by Bergh (1905) from the Siboga Expedition are deposited in the Zoological Museum, University of Copenhagen (Willan & Cattaneo-Vietti, 1995: 10), and the specimen is not there (Pola et al., 2006c: 500). Indeed, that specimen probably no longer exists because Bergh apparently completely disposed of the specimens from the Siboga Expedition after he had dissected them (Willan & Cattaneo-Vietti, 1995: 10). We could find no mention of either the pre-rhinophoral sensory organ or the food of this species in the literature.

Tambja anayana Ortea, 1989. Still only known from a single specimen. Sánchez-Tocino et al. (2000) speculated that it was juvenile. We could find no mention of either the pre-rhinophoral sensory organ or the food of this species in the

literature.

Tamba blacki Pola et al., 2006. Pre-rhinophoral sensory organ observed in living individuals by us. Reported by Pola et al. (2006b: 407). Feeds on bryozoan *Amastigia rudis* (Candidae). The correct specific name for this bryozoan is *rudis*. The spelling “*rudii*” appearing in Willan & Coleman (1984), Coleman (1989) and Marshall & Willan (1999) is an inadvertent error.

Tamba brasiliensis Pola et al., 2014. Pre-rhinophoral sensory organ present (Pola et al., 2014: 616). Feeds on bryozoan *Virididentula dentata* (Bugulidae) (Pola et al., 2014: 618).

Tambja caeruleocirrus Willan & Chang, 2017. Described herein. Pre-rhinophoral sensory organ present - recorded in present paper.

Tambja capensis (Bergh, 1907). Apparently feeds on arborescent bryozoans (Gosliner, 1987: 100, <http://www.seaslugforum.net/find/tambcape>), also more specifically on *Virididentula dentata* (Bugulidae) and “a variety of species of bryozoans” (Zsilavec, 2007: 64). Pola et al. (2014) concluded it does not cluster genetically with other *Tambja* species. Requires further investigation.

Tamba ceutae (García-Gómez & Ortea, 1988). Pre-rhinophoral sensory organ reported by Pola et al. (2006b: 513), also visible in photo <http://www.nudipixel.net/photo/00035165/>.

Tamba crioula Pola et al., 2014. Pre-rhinophoral sensory organ present (Pola et al., 2014: 619).

Tambja dracomus Willan & Chang, 2017. Pre-rhinophoral sensory organ observed by us in living animals, and also shown present paper in Fig. 10.

Tamba eliora (Er. & Ev. Marcus, 1967). Pre-rhinophoral sensory organ reported by Pola et al. (2006b: 505) “in some specimens”, also shown at http://www.umiushizukan.com/eng/dispatch_pic.php?pic_id=10494, also <http://www.nudipixel.net/photo/00035177/>. Feeds on bryozoans (Hemosillo et al., 2006: 72), or more specifically arborescent bryozoans (Camacho-García et al., 2005).

Tamba fantasmalis Ortea & García-Gómez, 1986. We could find no mention of either the pre-rhinophoral sensory organ or the food of this species in the literature.

Tamba gabriellae Pola et al., 2005. Pre-rhinophoral sensory organ shown in Debelius & Kuitert, 2007: 73, and by Humann & Deloach, 2010: 304), also <http://slugsite.us/bow2007/nudwk622.htm>, and <http://www.seaslugforum.net/find/16041>, also <http://www.seaslugforum.net/find/20673>, and http://www.daveharasti.com/Lombok/Nudibranchs/slides/Tambja_gabriellae.html.

Tamba gratiosa (Bergh, 1890). Still only known from the original description of a single preserved individual. We could find no mention of either the pre-rhinophoral sensory organ or the food of this species in the literature.

Tamba haidari Pola et al., 2006. Pre-rhinophoral sensory organ reported by Pola et al. (2006b: 406), also visible in photo <http://www.seaslugforum.net/find/10473>.

Tamba kava Pola et al., 2014. Pre-rhinophoral sensory organ pres-

- ent (Pola et al., 2014: 622).
- Tamba marbellensis* Schick & Cervera, 2014. Pre-rhinophoral sensory organ present (Pola et al., 2006b: 515, Pola et al., 2014: 627), also visible in photo at <http://opisthobranquis.info/en/guia/nudibranchia/euctenidiacea/doridacea/tambja-marbellensis/#gsc.tab=0>. Feeds on bryozoan *Sessibugula barrosoi* (Bugulidae) (Pontes et al., 2017).
- Tamba morosa* (Bergh, 1877). Pre-rhinophoral sensory organ observed by us in living animals. Reported by Pola et al. (2006b: 496), also photographs in Doak, 1971: 77, Pola et al., 2005a: Figure 1C, Willan, 2010: 440, Willan & P. Poppe (2010: 368 centre left photo), and also at <http://www.seaslugforum.net/find/10513>, <http://www.seaslugforum.net/find/10503>, and http://www.medslugs.de/E/Pac-W/Tambja_morosa/Tambja_morosa_62.htm.
- Tamba mullineri* Farmer, 1987. Pre-rhinophoral sensory organ visible in photo at <http://www.seaslugforum.net/find/16351>.
- Tamba olivaria* Yonow, 1995. Pre-rhinophoral sensory organ reported by Yonow (1994: 109) and by Pola et al. (2005a: 262), also visible in photographs in Willan & P. Poppe (2010: 371) and <http://slugsite.us/bow/nudwk277.htm> and <http://www.seaslugforum.net/find/12539> and <http://www.seaslugforum.net/find/20339>. Feeds on bryozoan *Virididentula viridis* (Bugulidae) (Yonow, 1995).
- Tambja pulcherrima* Willan & Chang, 2017. Pre-rhinophoral sensory organ present. Observed by us in living animals, also shown present paper in Fig. 6, and also <http://slugsite.us/bow2007/nudwk808.htm>.
- Tambja sagamiana* (Baba, 1955). Pre-rhinophoral sensory organ recorded by Pola et al. (2005a: 262, 2006c: 504), also visible in photos in Masuda (1999: 91), Debelius & Kuitert (2007: 68, bottom right photo), Jie et al. (2009: 110), and <http://www.seaslugforum.net/find/10504>.
- Tamba simplex* Otrera & Moro, 1988. We could find no mention of either the pre-rhinophoral sensory organ or the food of this species in the literature.
- Tamba stegosauriformis* Pola et al., 2005. Possesses pre-rhinophoral sensory organ (Pola et al., 2005c: 981). The photograph of a living animal in situ from Cabo Frio, Rio de Janeiro, Brazil, clearly reveals it feeding on an erect bryozoan (Bugulidae) (Pola et al., 2005b: Figure 1 top photo).
- Tamba tenuilineata* M.C. Miller & Haagh, 2005. Pre-rhinophoral sensory organ visible in photo at <http://www.nudibranch.com.au/pages/0112.htm>. Feeds on bryozoan *Virididentula viridis* (Bugulidae) (<http://www.seaslugforum.net/find/12261>, also <http://www.seaslugforum.net/message/19907>).
- Tamba verconis* (Basedow & Hedley, 1905). Type species of genus. Pre-rhinophoral sensory organ observed by us in living animals, also shown in present paper in Fig. 2, also visible in photos by Gaskell et al. (2009: 171, 172), also http://www.ianskipworth.com/photo/d90uw/d901345/DSC_1564.jpg, and <http://slugsite.us/bow2007/nudwk870.htm> and <http://www.seaslugforum.net/find/20424>. Feeds on bryozoan *Virididentula viridis* (Bugulidae).
- Tamba victoriae* Pola et al., 2005. Pre-rhinophoral sensory organ recorded by Pola et al. (2006b: 262), also visible in photo at <http://www.nudipixel.net/photo/00002027/>, also <http://www.seaslugforum.net/find/19614>. Reported to feed on bryozoan *Virididentula dentata* (Bugulidae) (Pola et al., 2006b: 267).
- Tambja zulu* Pola et al., 2005. Possesses pre-rhinophoral sensory organs (Pola et al., 2014: 631). Generic placement requires further investigation (Pola et al., 2014: 631).

Table 2. Annotated list of species of *Tyrannodoris* Willan & Chang gen. nov. as defined herein.

- Tyrannodoris caboverdensis* (Pola et al., 2003). Diet not recorded.
- Tyrannodoris ernesti* (Pola et al., 2014). Observed feeding on nudibranch *Tambja stegosauriformis* and speculated also to feed on *T. brasiliensis* (Polyceridae) (Pola et al., 2014: 612).
- Tyrannodoris europaena* Garcia-Gomez, 1985. Observed feeding on nudibranchs of genera *Polycera* (Polyceridae), *Polycerella* (Polyceridae), *Limacia* (Triophidae) as well as conspecifics in the field (Megina & Cervera 2003), also *Tambja* (Polyceridae) in the laboratory (<http://www.seaslugforum.net/find/823>). The complete mitochondrial genome was analysed by Grande et al. (2002), and the authors advocated it supported the monophyly of the Opisthobranchia.
- Tyrannodoris leonis* (Pola et al., 2005). Feeds on nudibranch *Tambja mullineri* (Polyceridae) (<http://slugsite.us/bow/nudwk517.htm>).
- Tyrannodoris luteolineata* (Baba, 1936). Type species of genus. Feeds on nudibranchs of genera *Tambja* (Polyceridae) (Willan 2003: 104; <http://www.seaslugforum.net/find/12673>; <http://www.seaslugforum.net/find/5558>; Pola et al., 2014: 631) and *Nembrotha* (<http://www.seaslugforum.net/find/15757>).
- Tyrannodoris nikolasi* (Pola et al., 2014). Diet not recorded.
- Tyrannodoris ricei* (Pola et al., 2008). Feeds on nudibranchs of genus *Tambja* (Polyceridae) (Pola et al., 2014: 631).
- Tyrannodoris tigris* Farmer, 1978. Feeds on nudibranch *Tambja eliora* (Polyceridae) (Behrens, 2005: 108) <http://www.seaslugforum.net/find/robotigr>; <http://slugsite.us/bow/nudiwk89.html>, and also cannibalises its own species (Behrens, 2005: 109). Species of *Tambja* seem to be preferred prey, but other dorids and aeolids are also accepted (<http://slugsite.us/bow/nudiwk70.html>).
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