

Revision of the Indo-Pacific genus *Nembrotha* (Nudibranchia: Dorididae: Polyceridae), with a description of two new species

MARTA POLA^{1,2}, J. LUCAS CERVERA¹ and TERRENCE M. GOSLINER²

¹Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Apdo. 40,
11510 Puerto Real, Cádiz, Spain.

²Department of Invertebrates Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco,
CA 94103, USA. E-mail: mpolaperez@calacademy.org

SUMMARY: Anatomical examination of new material collected from the Indo-Pacific and the review of several collections from around the world allows for the revision of the genus *Nembrotha* Bergh, 1877. Two new species, *Nembrotha rosannulata* n. sp. and *Nembrotha aurea* n. sp., are described. The oldest available name for the genus is *Nembrotha nigerrima* Bergh, 1877, which was subsequently designated as the type species by O'Donoghue, 1924. The study of the original type material of *N. nigerrima* confirmed that it is a senior synonym of another name introduced subsequently, *Nembrotha kubaryana* Bergh, 1877, the name most commonly used for this species. However, according to the provisions of the International Code of Zoological Nomenclature (Article 23.9.1), there is no reason to invalidate the senior name *Nembrotha nigerrima*, since it has been used as valid after 1899. *Nembrotha cristata* Bergh, 1877, *N. lineolata* Bergh, 1905, *N. purpureolineata* O'Donoghue, 1924, *N. livingstonei* Allan, 1933, *N. megalocera* Yonow, 1990 and *N. guttata* Yonow, 1993, which are poorly known, are redescribed. *Nembrotha rutilans* (Pruvot-Fol, 1931) is synonymised with *N. purpureolineata*. *Nembrotha yonowae* Goethel and Debelius, 1992 is synonymised with *N. guttata*. The radulae of *Nembrotha milleri* Gosliner and Behrens, 1997 and *N. mullineri* Gosliner and Behrens, 1997 are redescribed.

Keywords: Nudibranchia, Nembrothinae, *Nembrotha*, Indo-Pacific, synonym.

RESUMEN: REVISIÓN DEL GÉNERO INDOPACÍFICO *NEMBROTHA* BERGH, 1877 (MOLLUSCA: NUDIBRANCHIA: POLYCERIDAE), CON LA DESCRIPCIÓN DE DOS NUEVAS ESPECIES. – El estudio anatómico de nuevo material procedente del Indo-Pacífico así como el examen de diferentes colecciones de todo el mundo ha permitido la revisión del género *Nembrotha* Bergh, 1877. Se describen dos nuevas especies, *Nembrotha rosannulata* n. sp. y *Nembrotha aurea* n. sp. El nombre disponible más antiguo relativo a este género es *Nembrotha nigerrima* Bergh, 1877, que fue designado subsiguientemente como especie tipo por O'Donoghue, 1924. El estudio del material tipo original de *N. nigerrima* confirmó que se trata de un sinónimo más antiguo de otro nombre introducido con posterioridad, *Nembrotha kubaryana* Bergh, 1877, el nombre usado más comúnmente para esta especie. Sin embargo, según lo previsto en el Código Internacional de Nomenclatura Zoológica (Artículo 23.9.1), no hay razón alguna para invalidar el sinónimo más antiguo, *Nembrotha nigerrima*, ya que este nombre ha sido utilizado como válido después de 1899. *Nembrotha cristata* Bergh, 1877, *N. lineolata* Bergh, 1905, *N. purpureolineata* O'Donoghue, 1924, *N. livingstonei* Allan, 1933, *N. megalocera* Yonow, 1990 and *N. guttata* Yonow, 1993, especies pobremente conocidas, son redescritas. *Nembrotha rutilans* (Pruvot-Fol, 1931) es sinonimizada con *N. purpureolineata*. *N. Nembrotha yonowae* Goethel and Debelius, 1992 es sinonimizada con *N. guttata*. Se redesciben las rádulas de *Nembrotha milleri* Gosliner and Behrens, 1997 and *N. mullineri* Gosliner and Behrens, 1997.

Palabras clave: Nudibranchia, Nembrothinae, *Nembrotha*, Indopacífico, sinónimo.

INTRODUCTION

A number of species belonging to the genus *Nembrotha* have been described from the tropical Indo-Pacific (Table 1). Most of the nominal species were distinguished when originally introduced by differences in the colour pattern. Eliot (1904) described *N. caerulea* from East Africa and suggested that it was highly probable that all the common species of *Nembrotha* (*N. nigerrima*, *N. kubaryana* and *N. cristata*) were varieties of the same species. Since then, ten new species of *Nembrotha* have been introduced. Bergh (1905) described *Nembrotha lineolata* from Indonesia. O'Donoghue (1924) designated *N. nigerrima* as the type species of the genus, but at the same time he described a new species, namely *N. purpureolineata* from western Australia. *Nembrotha rutilans*, unfortunately named as *Kentiella rutilans* by Pruvot-Fol (1931) on the basis of a painting in a book by William Saville-Kent (1893), can only be identified from a colour painting. Allan (1933) justified the introduction of *N. livingstonei* from western Australia, based on the presence of a conspicuous star-shaped patch of pale yellow extending down to the anterior frontal margin. Characteristic features of the genus *Nembrotha* (after Burn, 1967) are the limaciform form, the rectangular rachidian teeth with 4 to 5 denticles along the upper margin, the lateral teeth with a simple cusp and 6 to 14 marginal plates. The buccal collar is weak, and the labial armature is very weak or absent. The prostate gland is large, racemose and spread over the bursa copulatrix.

Since Burn's publication, *N. megalocera* Yonow, 1990 from the Red Sea, *N. yonowae* Goethel and Debelius, 1992 and *N. guttata* Yonow, 1993 from

the Maldive Islands and *N. chamberlaini*, *N. milleri* and *N. mullineri* (Gosliner and Behrens, 1997) from the Indo-Pacific have been described. Moreover, a recent study on the Phylogenetic relationships of Nembrothinae based on molecular and morphological data (Pola *et al.*, 2007) includes all the available nominal species of *Nembrotha* to date. In the present study, we review the systematics of the genus and propose a revised taxonomy based on the study of specimens collected from different localities around the Indo-Pacific, the geographical range of the genus. We also describe two additional species of *Nembrotha*, which are included in the above-mentioned phylogenetic analysis as *Nembrotha* sp. 3 (*N. aurea* n. sp.) and *Nembrotha* sp. 4 (*N. rosannulata* n. sp.).

MATERIAL AND METHODS

The material examined is deposited at the following institutions: California Academy of Sciences, San Francisco, USA (CASIZ), Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), Western Australian Museum, Perth, Western Australia (WAM), Australian Museum, Sydney, Australia (AM), South Australian Museum, Adelaide, Australia (SAM), Muséum National d'Historie Naturelle, Paris (MNHN), Zoologische Staatssammlung München, Munich (ZSM) and Zoologisk Museum, University of Copenhagen, Denmark (ZMUC).

All *Nembrotha* species are described and discussed according to the year of publication. Features of living animals were recorded from photographs and notes by collectors. The specimens were dissected by dorsal incision to facilitate a morphological

TABLE 1. – Available nominal species names introduced for Indo-Pacific species of *Nembrotha*, including authorship, publication date and type locality.

Species name	Type locality
<i>Nembrotha nigerrima</i> Bergh, 1877	Aibukit, Palau Island
<i>Nembrotha kubaryana</i> Bergh, 1877	Ngadarrak ref., Palau Island
<i>Nembrotha cristata</i> Bergh, 1877	Philippines
<i>Nembrotha caerulea</i> Eliot, 1904	Sii Island (East Africa)
<i>Nembrotha lineolata</i> Bergh, 1905	Saleyer Island (Indonesia)
<i>Nembrotha purpureolineata</i> O'Donoghue, 1924	Abrolhos Island (Western Australia)
<i>Nembrotha rutilans</i> (Pruvot-Fol, 1931)	Great Barrier Ref. (Australia)
<i>Nembrotha livingstonei</i> Allan, 1933	Broome (West Australia)
<i>Nembrotha megalocera</i> Yonow, 1990	Shaab Rumi, Sudan (Red Sea)
<i>Nembrotha yonowae</i> Goethel and Debelius, 1992	Maaya Tila, Maldive Island
<i>Nembrotha guttata</i> Yonow, 1993	Maaya Tila, Maldive Island
<i>Nembrotha chamberlaini</i> Gosliner and Behrens, 1997	Kirby's Rock, Luzon (Philippines)
<i>Nembrotha milleri</i> Gosliner and Behrens, 1997	Dakak, Mindanao (Philippines)
<i>Nembrotha mullineri</i> Gosliner and Behrens, 1997	Layaglayag, Luzon (Philippines)

examination. The internal features were examined using a dissecting microscope with a camera lucida. 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. The buccal mass was dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried and mounted for examination by scanning electron microscopy. The external and internal anatomy of previously well-described species are not repeated in this paper in order to reduce the length of the manuscript. Also, since the reproductive system of the different species is very similar and they are well illustrated, only the reproductive system of the first species described and those of the new species are described in detail in order to reduce the descriptions and avoid being repetitive. Differences among reproductive systems are noted. In Figures 4 and 16, the prostate is shown positioned to the side. References to the original descriptions are made when possible.

SYSTEMATICS

Family POLYKERIDAE Alder and Hancock, 1845
 Subfamily NEMBROTHINAE Burn, 1967
 Genus *Nembrotha* Bergh, 1877

Nembrotha Bergh, 1877: 450, pl. XXXIII, Fig. 5. Type species (subsequent designation by C. H. O'Donoghue, 1924): *Nembrotha nigerrima* Bergh, 1877: 451, pl. 33, Fig. 5.

Diagnosis. The body is limaciform, with dorsum smooth or covered with pustules. Head rounded, without frontal or velar processes and with two large oral tentacles with a depression at the centre of each. Gill bi- or tripinnate and not retractile. Rachidian teeth with 4-5 denticles along the upper margin, lateral teeth elongate, with two cusps, the inner cusp simple. Marginal plates 6-14. A labial cuticle is present, lacking armature. The prostate gland is large, racemose and spread over the bursa copulatrix. The penis is armed. A vaginal gland is absent.

Remarks. The genus *Nembrotha* was introduced by Bergh, 1877 with six new species. These species were easily divided into different groups according to the shape of the radula but Bergh never gave them different generic names. In 1924, O'Donoghue stated that there was a possibility that the generic name

Nembrotha Bergh, 1877 would have to be replaced by *Angasiella* Angas and Cross, 1864, since the form described by the latter was very similar to those in Bergh's genus. However, O'Donoghue (1924) could not confirm this possibility until he obtained further specimens for closer examination. Some years later, Marcus (1958) in his discussion of *Tambja divae* [*Nembrotha*], thought that the genus *Angasiella* must not be substituted for *Nembrotha* because the species *Angasiella edwardsi* Angas, 1864 was described as spinous while the species of *Nembrotha* were smooth. Burn (1967) separated the species formerly attributed to *Nembrotha* into three different genera (*Nembrotha* Bergh, 1877, *Roboastra* Bergh, 1877 and *Tambja* Burn, 1962) based on radular and genital differences and assigned them to a new subfamily, Nembrothinae, family Polyceridae. Prior to this, the three genera were included in the family Gymnodorididae (Odhner, 1941; Marcus, 1958; Marcus and Marcus, 1964), or the subfamily Gymnodoridinae (Macnae, 1958). The phylogenetic analysis performed by Pola *et al.* (2007) supports the separation made by Burn (1967) of *Nembrotha* from *Roboastra* and *Tambja*, based on morphological characters. This analysis supports the existence of two clades in *Nembrotha*, one formed by the so-called "spotted" *Nembrotha* and other by the so-called "lined" *Nembrotha*.

Nembrotha nigerrima Bergh, 1877
 (Figs. 1A-F, 2-3, 4A, 5)

Nembrotha nigerrima Bergh, 1877: 451, pl. 32, Fig. 5.
Nembrotha kubaryana Bergh, 1877: 454.

Material examined. GAS-2079, Syntypes, Kreiangel Island, Palau, Philippines, July 1862, one specimen 33 mm alive, collected by Semper. Cebu Island, Philippines, 1865, one specimen 22 mm preserved, collected by Semper. CASIZ 078598, Bunaken Island, Manado, Celebes Sea, Sulawesi, Indonesia, 05/2001, one specimen 35 mm preserved, dissected, 13 m depth, collected by P. Fiene. CASIZ 065765, near Madang, north coast, Papua New Guinea, 11/01/88, three specimens 34, 36 and 44 mm preserved, dissected, 3-7 m depth, collected by R.C. Willan. WAM S11553, "Talisay Tree", Cabilao Island, Philippines, 28/02/03, one specimen 95 mm alive, dissected, 25 m depth, collected by E. Köhler. MNCN 15.05/46711, Lighthouse, Cabilao Island, Philippines, 27/02/03, two specimens 58 and 66 mm alive, 35 m depth, collected by E. Köhler. MNCN 15.05/46712, "El Dorado house-reef", Lipayo, Negros Oriental Island, Philippines, 08/03/03, one specimen 11 mm alive, 12 m depth, collected by E. Köhler. WAM S11554, "El Dorado house-reef", Lipayo, Negros Oriental Islands, Philippines, 06/05/03, one specimen 34 mm alive, dissected, 14 m depth, collected by E. Köhler. MNCN 15.05/46713, Aka Island, Kerama Islands, Okinawa, Japan, 25/05/03, two specimens 25 and 30 mm preserved, dissected, collected by A. Ono. CASIZ 083848, Devil's Point, Maricaban Island, Batangas Province, Luzon Island, Philippines, 19/02/92, two specimens 30 mm preserved, dissected, collected by T.M. Gosliner. CASIZ 087268, Manado, Celebes Sea, Sulawesi, Indonesia, April 1988, one specimen, collected by P. Fiene-Severns. CASIZ 107481, Seven Beaches, Palau, 10/02/94, one specimen, collected by C. Carlson. CASIZ 107482, Malkal Island, Palau, 12/02/94, one

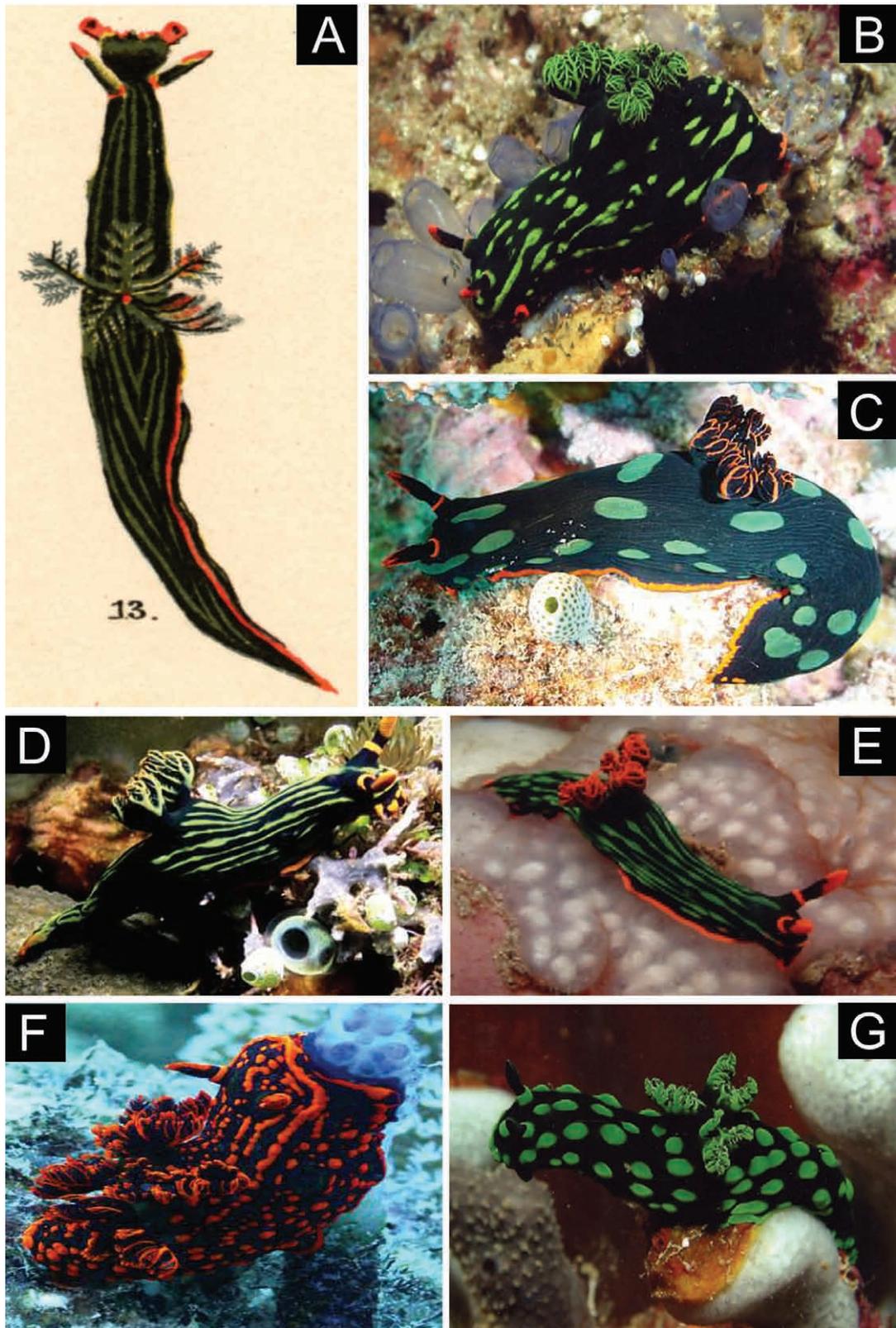


FIG. 1. – A-F: *Nembrotha nigerrima* Bergh, 1877; A, original drawing, *Nembrotha kubaryana* (Bergh, 1905). B-F: living animals; B, E, specimens from Philippines, photo by Erwin Köhler (B. WAM S11553, E. WAM S11554); C, specimen from Mauritius, photos by Marina Poddubetskaia; D, specimen from Japan, photo by Atsushi Ono (MNCN 15.05/46713); F, specimen from Exmouth, Western Australia, photo by Mick Tait. G: *Nembrotha cristata*, Bergh, 1877, living animal, specimen from Philippines, photo by Erwin Köhler (MNCN 15.05/46714).

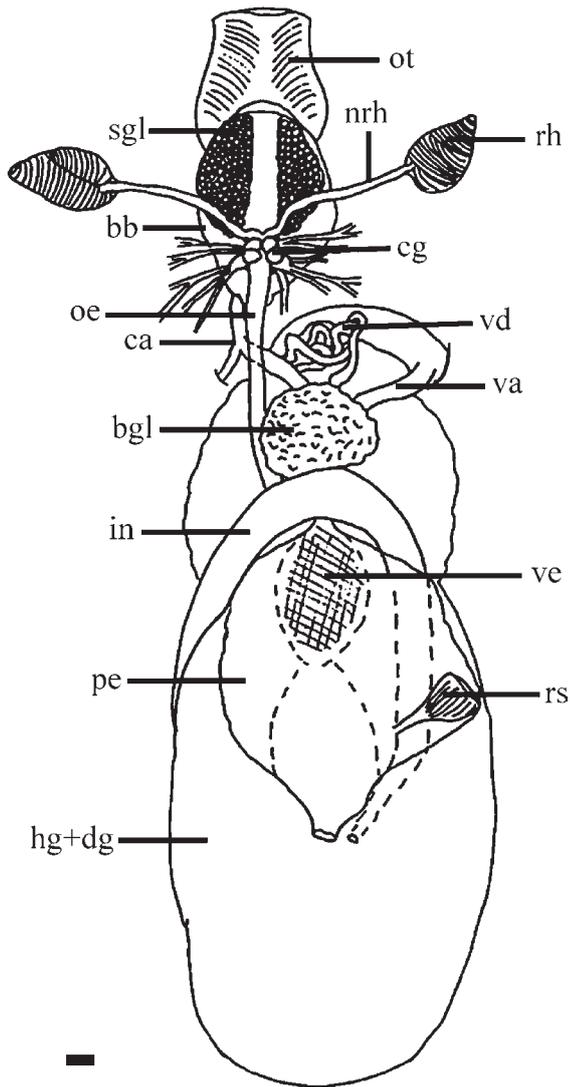


FIG. 2. – *Nembrotha nigerrima* Bergh, 1877. General arrangement of the internal organs. Scale bar = 1 mm. Abbreviations: bb, buccal bulb; bgl, blood gland; ca, cephalic artery; cg, cerebral ganglion; hg+dg, hermaphrodite gland + digestive gland; in, intestine; nrh, rhinophoral nerve; oe, oesophagus; ot, oral tube; pe, pericardium; rh, rhinophore; rs, renal syrinx; sgl, salivary gland; va, vagina; vd, vas deferens; ve, ventricle.

specimen, collected by M.T. Ghiselin. CASIZ 120928, Kwajalein Atoll, Marshal Island, Pacific Ocean, one specimen, collected by D. Johnson. CASIZ 158256, Devil's Point, Maricaban Island, Batangas Province, Luzon Island, Philippines, 06/05/01, one specimen 30 mm preserved, 3 m depth, collected by Y. Camacho.

External morphology. The body is elongate and limaciform but robust and widest at the gill. The posterior end of the foot is long and pointed (Figs. 1A-F). The head is rounded. The adult living animals may grow up to 100 mm in total length. The body wall is highly muscularised. The notum is covered with a series of longitudinally oriented creases or wrinkles and pustules (or spots) scattered on the notum and both sides of the body (Figs. 1A-F). A notal margin

is absent. There is a pair of large and conical, perfoliate rhinophores, which are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are well-developed, circular in shape with a depression at the centre of each. There are five tripinnate, non-retractile well-developed branchial leaves. The two posterior leaves of each side share a common base. The anus is situated in the centre of the branchial circle on elevated elongate papillae. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The general colour of the living animals is highly variable (Figs. 1A-F). The ground colour is black with green pustules scattered randomly on the notum and both sides of the body. There are also some small orange pustules usually located at the end of the foot and on the frontal edge. In some specimens, the green pustules are joined forming green longitudinal ridges over the entire body (Figs. 1A,D,E). Those pustules around the frontal edge also tend to form a ridge. The edge of the foot has a bright orange stripe, as well as the rhinophoral sheaths and the oral tentacles. The rhinophores are black with orange pigmentation on the upper lamellae. The gill branches are orange, green or may have both colours at the same time (Figs. 1A-F). In some specimens, all the green markings are orange (Fig. 1F).

Anatomy. *Nembrotha nigerrima* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a muscular oral tube that continues into the buccal mass. There is a pair of large, wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown chitinous disk, corrugated but without any armature or rodlets (Fig. 3A). The radular formulae are: 35 mm specimen (preserved), 30 x 11.1.1.1.11 (CASIZ 078598), 95 mm specimen (alive) and 30 mm specimen (preserved), 28 x 9.1.1.1.9 (WAM S11553; MNCN 15.05/46713, respectively), 34 mm specimen (preserved), 26 x 9.1.1.1.9 (CASIZ 065765), and 34 mm specimen (alive), 24 x 10-9.1.1.1.9-10 (WAM S11554) (Fig. 3B). The shape of the rachidian teeth is highly variable, usually with five asymmetrically arranged triangular denticles along the upper margin (Figs. 3A-F). The innermost laterals are well developed; they are larger and longer than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a shorter more basal one. The outer lateral teeth are rectangular plates, from 9 to 11, becoming smaller near

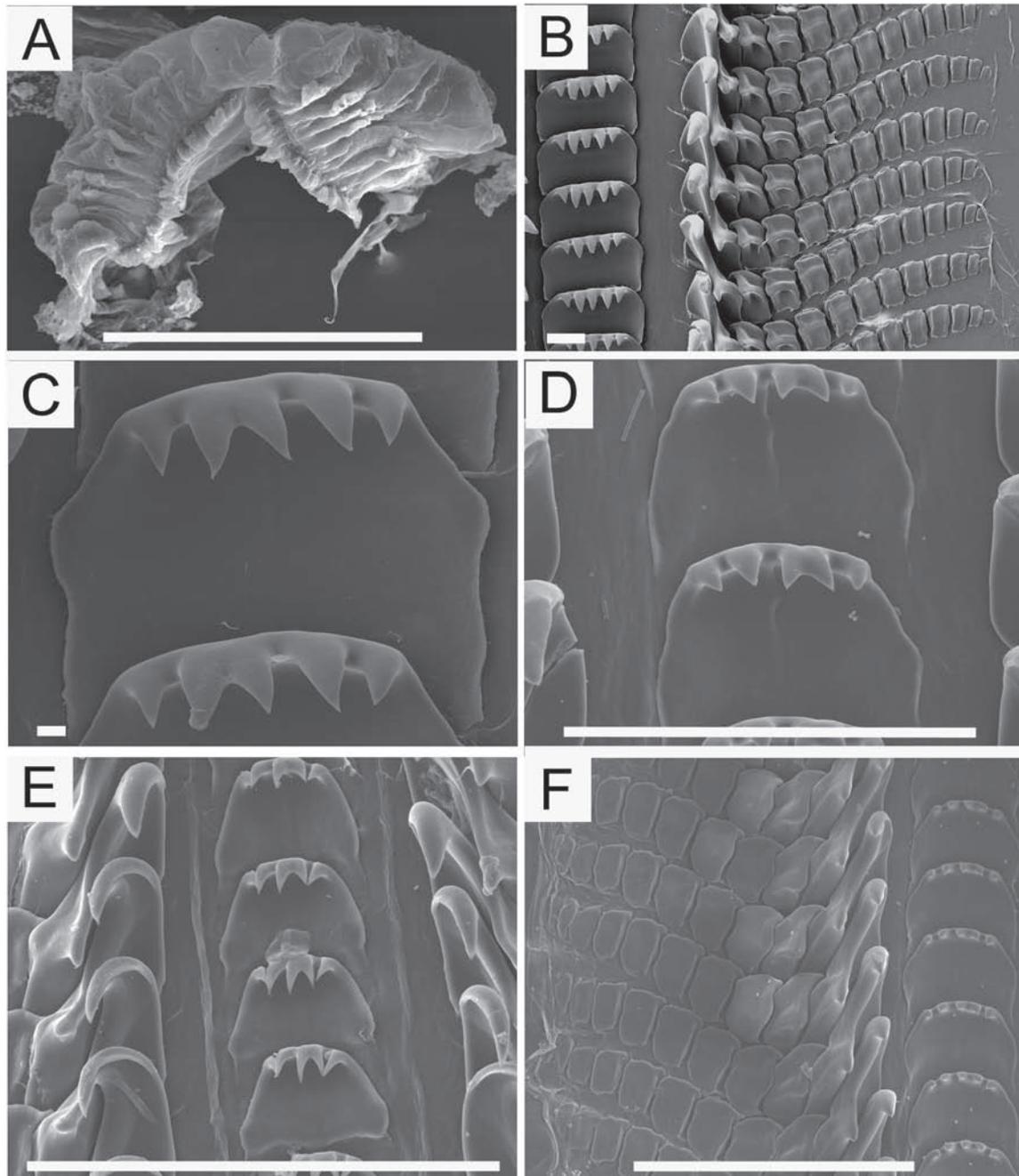


FIG. 3. – Scanning electron micrographs of *Nembrotha nigerrima* Bergh, 1877. A, labial cuticle (WAM S11554, scale bar: 500 µm); B, right half-row of radular teeth (WAM CASIZ 078598, scale bar: 100 µm); C-F, rachidian teeth: C, CASIZ 065765, scale bar: 10 µm; D, WAM S11553, scale bar: 300 µm; E, WAM S11554, scale bar: 300 µm; F, MNCN 15.05/46713, scale bar: 500 µm.

the margin. The inner one bears a large upper cusp while the remaining teeth lack cusps or dentition (Figs. 3B,E,F). There is a blood gland located above the intestine. A cup-shaped renal syrinx is present under the thin pericardium, close to the elevated anal papilla. An elongate and muscularised ventriculum is visible under the pericardium.

The reproductive system is triaulic (Fig. 4A). The hermaphroditic duct is long. It expands into an

elongate and convoluted ampulla. The postampullary duct branches into the prostatic portion of the vas deferens and the short oviduct that connects to the female glands. The prostatic portion of the vas deferens is very large and consists of a spherical mass, which appears to be formed by a dense network of interconnecting tubules entirely surrounding the bursa copulatrix. The distal end of the prostatic mass connects to an elongate and convoluted

vas deferens. The vas deferens opens into a common atrium with the vagina but without a strongly differentiated muscular ejaculatory portion. The penis is armed with chitinous penial spines. Two different kinds of spines can be differentiated based on their size and shape (Fig. 5A). The basal spines are short and curved, all of them supported by the same rachis, and they constitute the eighteen first rows of spines (Fig. 5B). The remaining spines are longer and hooked, but it is not clear whether they are supported by the same rachis (Figs. 5C,D). The vagina is wide, long and straight. At its proximal end, it

connects to the rounded bursa copulatrix, which, *in situ*, is entirely surrounded by the prostate. From the bursa copulatrix leads another duct that connects to the pyriform seminal receptacle and the female glands via a long, narrow uterine duct. The vagina is separated from the vas deferens along its entire length. There is no vaginal gland. In Figure 4A, the prostate is shown positioned to the side.

Remarks. Bergh described *Nembrotha nigerrima* in 1877 from two different specimens collected at Palau and Cebu Island. The external and internal

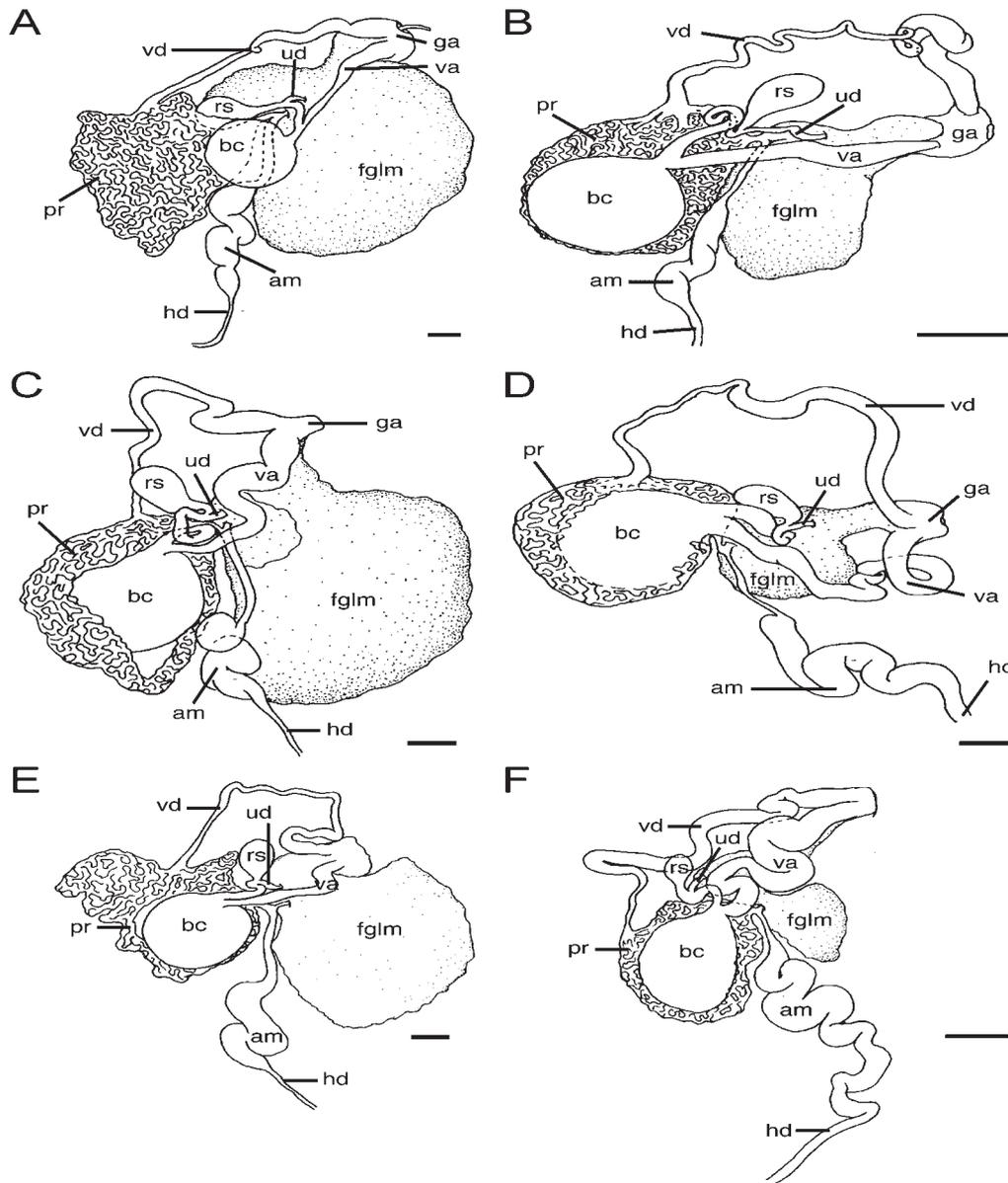


FIG. 4. – Drawings of reproductive systems of *Nembrotha* spp. A, *N. nigerrima* (MNCN 15.05/46713); B, *N. cristata* (CASIZ 157483); C, *N. lineolata* (WAM S11562); D, *N. purpureolineata* (WAM S11564); E, *N. livingstonei* (MNCN 15.05/46716); F, *N. megalocera* (ZSM-Moll 19991127). Scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens.

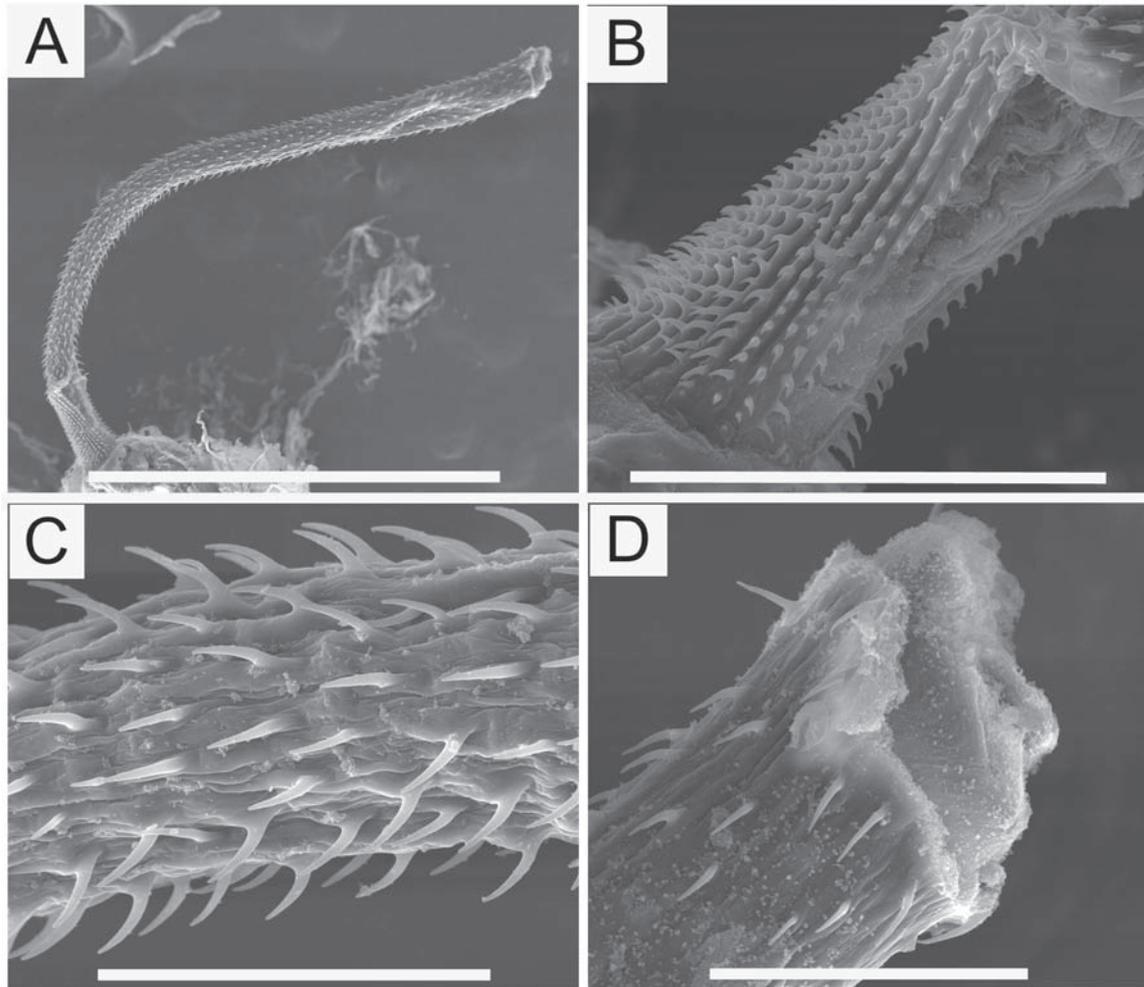


FIG. 5. – Scanning electron micrographs of *Nembrotha nigerrima* Bergh, 1877, penis (MNCN 15.05/46713). A, general view, scale bar: 1 mm; B, detail of the basal penial spines, scale bar: 200 μ m; C-D, details of the distal spines, scale bar: 100 μ m.

description of this species is very complete and the external colouration was depicted according to the living animal (Fig. 1A). In the same paper, Bergh described *N. kubaryana* also from Palau but never gave a description of the specimen. In the short comment about this new species he suggested that *N. kubaryana* could be only a variety of *N. nigerrima* but distinguished both species according to differences in colour, the number of marginal plates, small differences in the shape of the penial spines and the receptaculum seminis. However, all these features are very variable between specimens of *Nembrotha*, so *N. kubaryana* is a junior synonym of *N. nigerrima*. Similar conclusions have already been presented by Yonow and Hayward (1991), who formally synonymised both names, by Baba (unpublished data) and by Debelius (1996), but they never supported their conclusion with anatomical studies.

All modern authors have been using the name *Nembrotha kubaryana* for specimens of *N. nigerrima* since Yonow synonymised both names in 1990. Thus, Yonow (1990) considered *N. nigerrima* as a synonym of *N. kubaryana*. According to the international Code of Zoological Nomenclature (ICZN 2000), if a senior synonym has not been used as a valid name after 1899 and its junior synonym has been used for the same species in at least 25 papers, published by at least 10 authors in the immediately preceding 50 years and encompassing a span not less than 10 years, the usage of the junior synonym must be maintained (Article 23.9.1). Nevertheless, in this case, the name *N. nigerrima* has been used as a valid name after 1899 and there is therefore no reason to invalidate the senior name *N. nigerrima*. Thus, all names introduced subsequently must be synonymised with *N. nigerrima*, which is in addition the type species of the genus.

Rudman's seaslugforum (1998-2005) and an increasing number of web pages and field guides, provide a large number of photographs showing specimens of *Nembrotha nigerrima* with remarkable differences in colouration and pattern of lines and pustules. (Debelius, 1996; Coleman, 2001; Wells and Bryce, 1993; Tonzuka, 2003; www.philippine-sea-slugs.com; www.seaslugforum.net; http://www.philippine-sea-slugs.com/DORIDINA/Nembrotha_livingstonei_04.htm).

Geographic range. This species, originally described from Palau and Cebu Islands, is also known from Indonesia (Debelius, 1996; Coleman, 2001; Tonzuka, 2003; Debelius and Kuitert, 2007), Mauritius Islands (Yonow and Hayward, 1991; Debelius and Kuitert, 2007), Great Barrier Reef, Western Australia (Willan and Coleman, 1984; Wells and Bryce, 1993; Coleman, 1989; 2001; Debelius and Kuitert, 2007), Kerama Islands (Ono, 1999), Ryukyu Islands (Ono, 2004), Papua New Guinea, Marshal Island (present study), Malaysia and Solomon Island (<http://www.seaslugforum.net/factsheet.cfm?base=nembkuba>).

***Nembrotha cristata* Bergh, 1877**
(Figs. 1G, 4B, 6)

Nembrotha cristata Bergh, 1877: 458, pl. 33, Fig. 6

Material examined. CASIZ 073068, north coast, near Madang, Papua New Guinea, 03/10/1986, 18 m depth, one specimen, collected by T. M. Gosliner. CASIZ 076014, Banda Island, Banda Sea, Indonesia, 27/09/1986, two specimens 25 mm preserved, dissected, 29 m depth, collected by P. Fiene. CASIZ 157483, one specimen, Balayan Bay, Batangas Province, Luzon, Philippines, 09/05/2001, one specimen, 10 m depth, collected by T. M. Gosliner. MNCN 15.05/46714, 'Chapel', Apo Island, Philippines, 06/03/2003, one specimen 65 mm alive, dissected, 18 m depth, collected by E. Köhler. MNCN 15.05/46715, 'Black Forest', Balicasag Island, Panglao Island, Philippines, 01/03/2003, one specimen 88 mm alive, dissected, 24 m depth, collected by E. Köhler.

External morphology. The body is firm and limaciform with a linear and pointed posterior end of the foot. The head is rounded. The mantle is reduced and indistinct (Fig. 1G). The preserved specimens are up to 40 mm. The living animals' measure up to 120 mm with the body surface covered with roundish, elongate and irregularly-shaped, hardly-elevated pustules or spots (Fig. 1G). On the front edge, the tubercles extend around the head suggesting a wide mantle margin. There is a pair of perfoliate rhinophores that are completely retractile into their rhinophoral sheaths, with 25 lamellae. The oral tentacles are short and circular in shape with a depres-

sion at the centre of each. There are five non-retractile, strongly developed multipinnate gill branches. The two posterior gill branches of each side share a common base. The anus is situated between the gill branches on elevated papillae just behind the kidney opening. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The ground body colour is black with green tubercles (Fig. 1G). The rhinophores are black with a green tip. The outer branchial surface, the inner rachis of each gill branch (except the base), the pinnae, the rhinophoral sheaths and the edge of the oral tentacles are also green. The edge of the foot is bordered with a green band.

Anatomy. *Nembrotha cristata* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long but thin oral tube that continues into the buccal mass. Two long wide salivary glands connect to the buccal bulb at both sides of the oesophageal junction. The thin chitinous labial cuticle is corrugated without distinct armature or rodlets. The radular formulae are: 65 mm specimen, 27 x 9.1.1.1.9 (MNCN 15.05/46714), 88 mm specimen, 24 x 9.1.1.1.9 (MNCN 15.05/46715), 25 mm specimens, and 23 x 10-9.1.1.1.9-10 (CASIZ 076014) (Figs. 6A,B). The rachidian teeth are broad and rectangular with five asymmetrically arranged triangular denticles almost similar in size. The two inner denticles of the right half of the rachidian are joined at the base (Fig. 6B). The inner laterals are well developed; they are larger and longer than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a shorter more basal one. The outer lateral teeth are rectangular plates, becoming smaller near the margin. The innermost one bears an upper cusp while the remaining teeth lack cusps or dentition (Fig. 6A).

The reproductive system is triaulytic (Fig. 4B). The hermaphroditic duct is short and narrow. It expands into the ampulla. The long straight postampullary duct divides into a short oviduct and a wide prostatic portion of the vas deferens. The prostatic segment is very large and consists of a spherical mass. The distal end of the prostatic mass branches into a narrow, elongate and highly convoluted vas deferens. The distal end of the vas deferens widens into a muscular ejaculatory portion, which opens into the genital atrium. The chitinous penial spines are numerous and they are arranged in longitudinal lines.

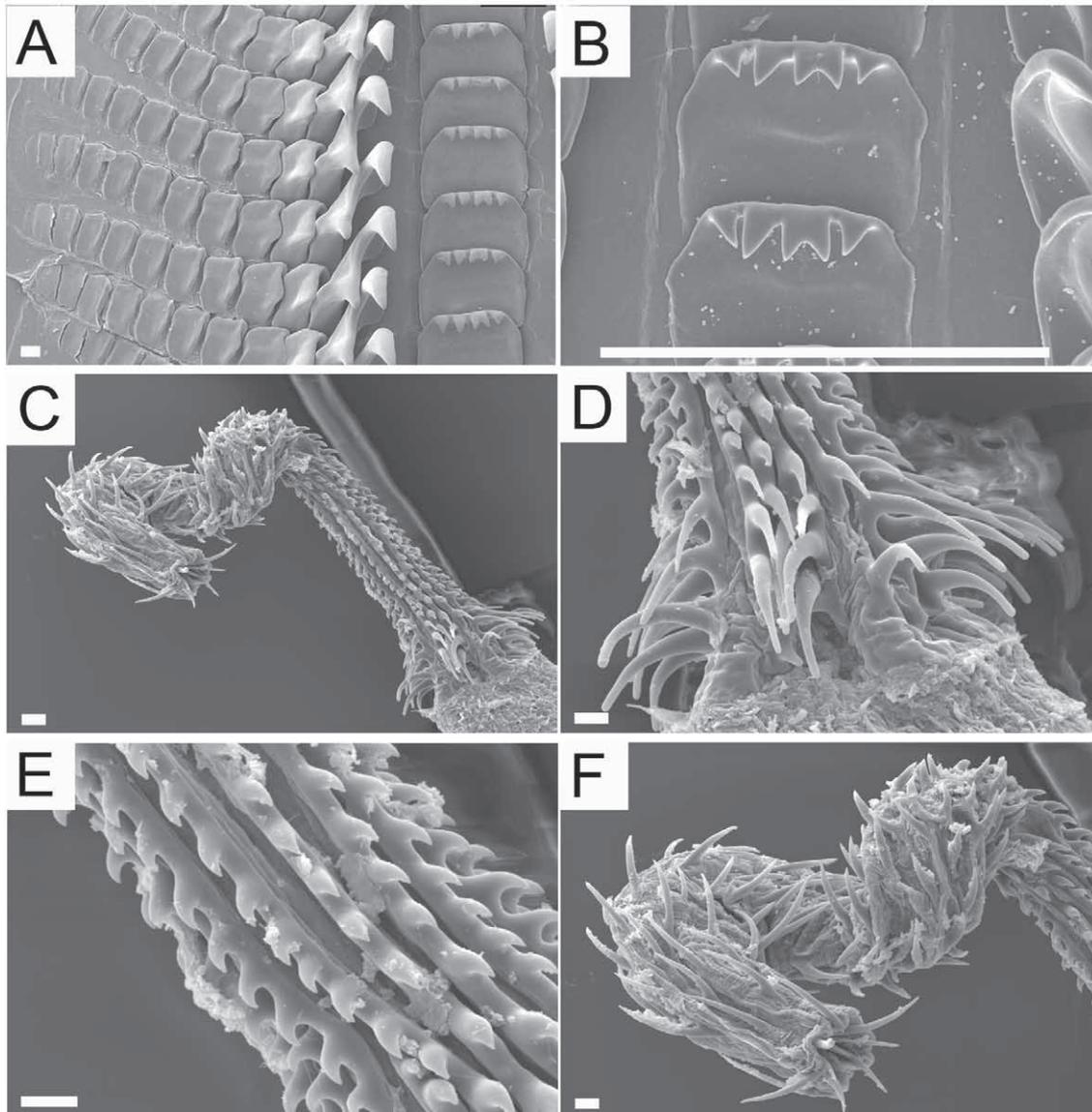


FIG. 6. – Scanning electron micrographs of *Nembrotha cristata* Bergh, 1877. A, left half-row of radular teeth (CASIZ 076014, scale bar: 30 μ m); B, rachidian teeth (MNCN 15.05/46714, scale bar: 400 μ m); C, penis (CASIZ 076014, scale bar: 20 μ m); D-F, penial spines (CASIZ 076014, scale bar: 10 μ m); D, detail of basal penial spines; E, detail of second type of penial spines; F, detail of distal penial spines.

They can be differentiated into three different kinds of spines based on their size and shape (Figs. 6C-F). The basal spines are large, elongate and curved. They constitute the first three or four rows of spines (Fig. 6D). The spines immediately after these are much smaller and hooked (Figs. 6E). The remaining spines are also hooked and slightly more elongate than the second group but shorter than the basal spines (Fig. 6F). The vagina is wide, long and slightly convoluted. At its proximal end, the vagina connects to the rounded, thin-walled bursa copulatrix, which, in situ, is entirely surrounded by the prostate. From the bursa copulatrix leads another duct that connects

to the pyriform seminal receptacle and the female glands via a long, distally convoluted uterine duct. The vagina is separate from the vas deferens along its entire length.

Remarks. *Nembrotha cristata* was described by Bergh (1877) from Semper's individual collected from the Philippine Sea. Semper illustrated this animal in living condition, but the animal was lost. Thus, the species is known only from the illustration. In 1905, Bergh collected 3 additional specimens from the reef at Tual, Niedrig-Kei Island. The smaller one was strongly contracted, and the other 2

specimens were similarly large (50 and 58 mm) and resembled each other. All the specimens dissected in this study identified as *N. cristata* perfectly match Bergh's description, though he described three gills instead of five. We assume that he counted the two lateral branches of each side as only one. Eliot (1904) described three specimens of *N. cristata* from the east coast of Zanzibar as very dark but brilliant green with black spots, and also narrow stripes of brighter and lighter green. At the end of his description he stated that these specimens might be a variety of *N. nigerrima*. Yonow and Hayward (1991) rejected this idea and stated that Eliot's description was not applicable to either *N. cristata* or *N. nigerrima*.

N. cristata differs mainly from *N. nigerrima* by the absence of any red or orange colouration. The features of the radula and the reproductive system are very similar in both species, but *N. cristata* has three well-differentiated types of penial spines while in *N. nigerrima* there appear to be only two types. *Nembrotha cristata* has been found feeding on the compound green ascidian *Eudistoma olivaceum* (http://www.philippine-sea-slugs.com/DORIDINA/Nembrotha_cristata.htm; Willan and Coleman, 1984).

Geographic range. This species, originally described from the Philippines, is also known from Indonesia (Coleman, 2001; Houghton, 2002; Tono-zuka, 2003; Debelius and Kuitert, 2007), Malaysia, Solomon Island (www.seaslugforum.net/factsheet.cfm?base=nembcris), Papua New Guinea (present study; McNeil, 1999), Kerama Island (Ono, 1999), Ryukyu Islands (Ono, 2004), Maldivas (Debelius, 1996) and North Queensland and Western Australia (Willan and Coleman, 1984; Coleman, 2001; Debelius and Kuitert, 2007).

Nembrotha caerulea Eliot, 1904

Nembrotha caerulea Eliot, 1904: 91

Remarks. Eliot (1904) described *Nembrotha caerulea* from East Africa but it has not been reported since then. No notes on the living animal exist, except that it was blue and had apparently no red or green mottled colouration. Thus, Eliot described the species from freshly preserved specimens as being a fine bright indigo with the whole body marked with deep indigo spots. Although he stated that this species was closely allied to *N. nigerrima*, he distin-

guished it by its colouration, the slightly projecting edges of the rhinophoral sheaths, the absence of labial armature and a different form of tentacles. Nevertheless, Baba (unpublished data) in his notes about *Roboastra*, *Tambja* and *Nembrotha* in Japan, described the general colouration of *N. nigerrima* and *N. kubaryana* as deep black ground colour with blue stripes and blue spots. These descriptions confirm that the descriptions of the colouration of preserved specimens could be wrong. Thus, in this paper, we consider *N. caerulea* as *nomen dubium*.

Nembrotha lineolata Bergh, 1905 (Figs. 7, 4C, 8)

Nembrotha lineolata Bergh, 1905: 199, pl. 2, Fig. 10. pl. 18, Fig. 15-18.

Nembrotha lineolata var. Bergh, 1905: 200, pl. 2, Fig. 11.

Material examined: CASIZ 70276, Manado, Sulawesi, Indonesia, 25/05/89, one specimen 25 mm alive, dissected, 44 m depth, collected by M. Severns. CASIZ 084291, Layag-Layag, Batangas, Luzon Island, Philippines, 18/02/92, two specimens 33 and 25 mm preserved, dissected, 22 m depth, collected by M. Miller. CASIZ 158257, "Devil's Point", Maricaban Island, Batangas Province, Luzon, Philippines, 06/04/01, one specimen 30 mm preserved, 3 m depth, collected by Y. Camacho. CASIZ 69751, north coast, near Madang, Papua New Guinea, 26/07/89, one specimen 25 mm preserved, dissected, 14 m depth, collected by M. Ghiselin. CASIZ 158797, Sepok Island, Maricaban Island, Batangas Province, Luzon, Philippines, 06/05/01, one specimen 40 mm preserved, 8 m depth, collected by B. Castillo. CASIZ 65223, SE side of Bairakaseru Island, Palau, 22/09/87, one specimen 25 mm preserved, 36.5 m depth, collected by R. Van Syoc and M. Campbell. CASIZ 65355, north coast, near Madang, Papua New Guinea, 17/01/88, two specimens 15 and 25 mm preserved, dissected, 6 m depth, collected by G. Williamson. CASIZ 99289, Msimbati, Mtwara Region, Tanzania, 2/11/94, two specimens 25 mm preserved, dissected, 22 m depth, collected by T. M. Gosliner. MNCN 15.05/46724, "Sarah's Place", Lipayo, Negros Oriental Island, Philippines, 07/03/03, 66 mm alive, dissected, 18 m depth, collected by E. Köhler. MNCN 15.05/46725, "Pier", Lipayo, Negros Oriental Island, Philippines, 05/05/03, 64 mm alive, dissected, 16 m depth, collected by E. Köhler. WAM S11561, "Pier", Lipayo, Negros Oriental Island, Philippines, 05/05/03, 34 mm alive, dissected, 14 m depth, collected by E. Köhler. MNHN-Paris, "N'gouja", Passe Bateau, Mayotte, Comoros Island, 02/11/03, one specimen 25 mm alive, dissected, 14.5 m depth, collected by M. Poddubetskaia. MNHN-Paris, Passe en S. bouée 7 bis, Mayotte, Comoros Island, 04/11/03, one specimen 15 mm alive, 12 m depth, collected by M. Poddubetskaia. AM C205323, "Chocolate Island", Cebu, Philippines, 29/10/04, two specimens 10 and 25 mm preserved, 10 m depth, collected by M. Guido.

External morphology. The body is elongate and limaciform reaching, up to 70 mm in living adults. The posterior end of the foot is long and pointed. The head is rounded. The entire body surface has a pattern of longitudinal wrinkles (Fig. 7). The dorsum continues to the side of the body without a demarcating line or pallial edge. Externally the animals are characterised by the presence of longitudinal stripes that are sometimes broken. The number and distribu-

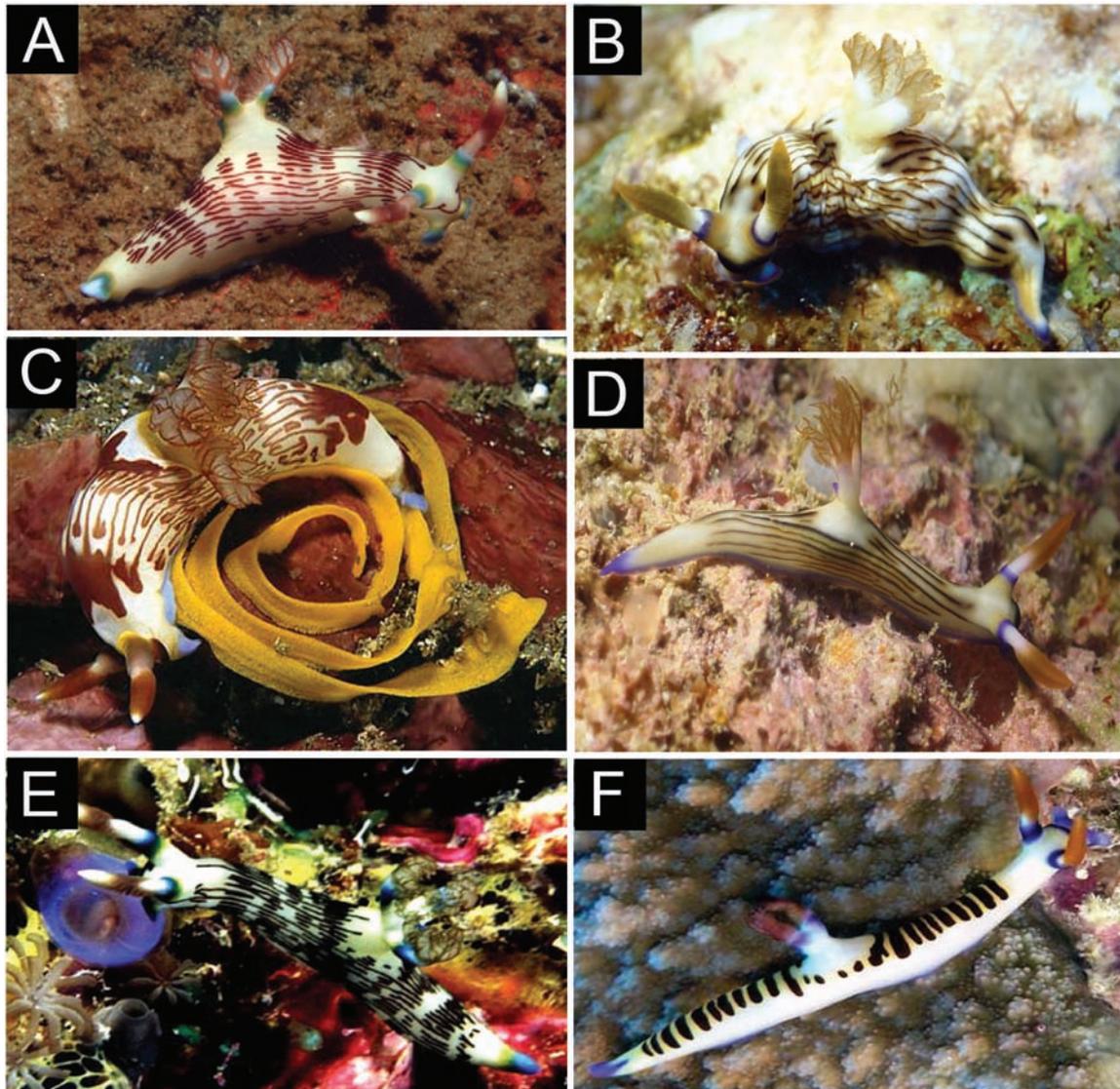


FIG. 7. – *Nembrotha lineolata* Bergh, 1905. Living animals: A, specimen from Philippines, photo by Erwin Köhler (MNCN 15.05/46724); B, D, specimens from Comoros, photos by Marina Poddubetskaia (MNHN-Paris); C, specimen from Philippines, photo by Erwin Köhler; E, specimen from Philippines, photo by Erwin Köhler; F, specimen from Australia, photo by David R. Bush.

tion of these stripes is variable (Fig. 7) and in many cases they merge to form the transverse bands found in some colour forms of this species (Fig. 7C). There is a pair of large conical, perfoliate rhinophores that bear 30-35 lamellae and are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are thick and elongate with a depression at the centre of each one. There are three large multipinnate, non-retractile branchial leaves. The anus is mid-dorsal, located in the centre of the branchial circle on elevated elongate papillae. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The ground colour of the body is yellowish white or cream white with numerous brown lines on the

notum and both sides of the body (Fig. 7). In all cases, a thin dark line continues forward, anterior to the rhinophores. The margin of the foot is delineated by a blue to purple band, within which a yellow band is usually present. The oral tentacles are also blue or purple followed by a yellow band. The rhinophores are red. The rhinophoral sheaths are blue or purple above, sometimes with a green band below, and yellow at the base of the rachis. In some specimens from the Comoros Islands the rhinophores are yellow rather than red (Fig. 7B). There are two variable-sized translucent spots posterior to the rhinophores, through which the dermal eyes are visible. The branchial leaves are red or vermilion above, blue or purple below and yellow at the base. It is also pos-

sible to find specimens without a trace of blue or purple colour in the gill (Figs. 7B,D).

Anatomy. *Nembrotha lineolata* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long and thin muscular oral tube that continues into the buccal mass. The buccal mass is smaller than the oral tube. There is a pair of large, wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown corrugated chitinous disk, usually devoid of rodlets but with a central and two lateral areas, in which in some specimens a weak armature is present. The radular formulae of some dissected specimens are: 33 and 25 mm specimens, 32 x 7.1.1.1.7, 34 x 9.1.1.1.9 (CASIZ 084291), 66 mm specimen, 32 x 8.1.1.1.8 (MNCN 15.05/46724), 64 mm specimen, 28 x 6.1.1.1.6 (MNCN 15.05/46725), 25 mm specimen, 23 x 5-6.1.1.1.6-5 (MNHN-Paris). The rachidian teeth are broad and rectangular with five triangular denticles (Figs. 8A,B). The two outer denticles are smaller than the inner ones. The two inner denticles on the right side are joined at the base. Thus, both denticles might be described as a single bifid denticle. The inner laterals are well developed; they are large and strongly hooked with two cusps (Fig. 8A). The outer lateral teeth are rectangular plates, from 5 to 8, which lack cusps or dentition and become smaller near the margin. There is a blood gland located above the genitalia, usually closer to the buccal mass than to the digestive gland.

The reproductive system is triaulic (Fig. 4C). The hermaphroditic duct is elongate and wide. It expands into a very long and highly convoluted ampulla. The prostatic portion of the vas deferens is very large. The distal end of the prostatic mass connects to an elongate, highly convoluted vas deferens that opens into a common atrium with the vagina but without a strongly differentiated muscular ejaculatory portion. The penis is armed with rows of curved, chitinous hooks except at the base (Figs. 8C,D). The chitinous penial spines are numerous and similar in size and shape (Figs. 8C,D). The vagina is very wide, long and convoluted. At its proximal end, the vagina connects to the rounded, thin-walled bursa copulatrix. In situ, the bursa copulatrix is entirely surrounded by the prostate.

Remarks. *Nembrotha lineolata* was described by Bergh (1905) from Indonesia based on three living

specimens with a drawing of the largest specimen (60 mm in total length). The specimens described in that paper were yellowish white with many short brown longitudinal lines. The arrangement of the lines of those specimens appears to be nearly in agreement with the specimens described by Baba (1976) from Japan, with one exception. The lines in Baba's specimens are not as numerous on the upper surface of the body and they are longer and not as frequently interrupted in their length as in the type specimens. The colour of the rhinophores, gill and the edge of the foot were also similar. The radular formula of the specimen described by Bergh (1905) is 32-36 x 7.1.1.1.7, with 4-5 denticles on the upper edge of the rachidian teeth. The radular formula of Baba's specimens (30 to 50 mm in length) is 27 x 5-6.1.1.1.5-6 with four denticles; the second denticle on the right side was bifid at the tip, which is also in agreement with the Indian Ocean specimen described by Eales (1938) and also with our specimens. The reproductive system of *N. lineolata* was not described by either Bergh (1905) or Baba (1976) but the anatomy was drawn by Eales (1938).

The number, arrangement and width of the lines in *N. lineolata* appear to be highly variable throughout its geographic range. A large number of pictures of different colour forms and pattern of lines in this species are shown in Figure 7 as well as in Rudman's seaslugforum (1998-2005) and many field guides (Willan and Coleman, 1984; Coleman, 2001; Wells and Bryce, 1993; Debelius, 1996; Ono, 1999, 2004; Suzuki, 2000; King and Fraser, 2002; Tonozuka, 2003; Nakano, 2004; Debelius and Kuitert, 2007) and web pages (www.medslugs.de; www.bunaken.pwp.blueyonder.co.uk/sss-nem-lin-02.htm; www.philippine-sea-slugs.com/DORIDINA/Nembrotha_lineolata.htm; www.umiushi.info/HTML_eng/Nembrothalineolata.html). Rudman (2000 (Aug 17), 2005 (Jun 15) (Fig. 7F), (Aug 2)) shows pictures of animals with transversal lines which strongly resemble *N. lineolata*, and he identified the specimens as "strange colour varieties of *Nembrotha lineolata*". Debelius and Kuitert (2007) also include pictures of these animals with transversal lines and identify them as *N. lineolata* (unusual pattern). Ono (2004) and Rudman (2002 (April 22)) show pictures of animals that have some similarities in shape and colour to *Nembrotha lineolata*. Debelius and Kuitert (2007) show a picture from Raja Ampat (Indonesia) identified as *N. lineolata* that is clearly another species, probably *N. purpureolineata*. However, since

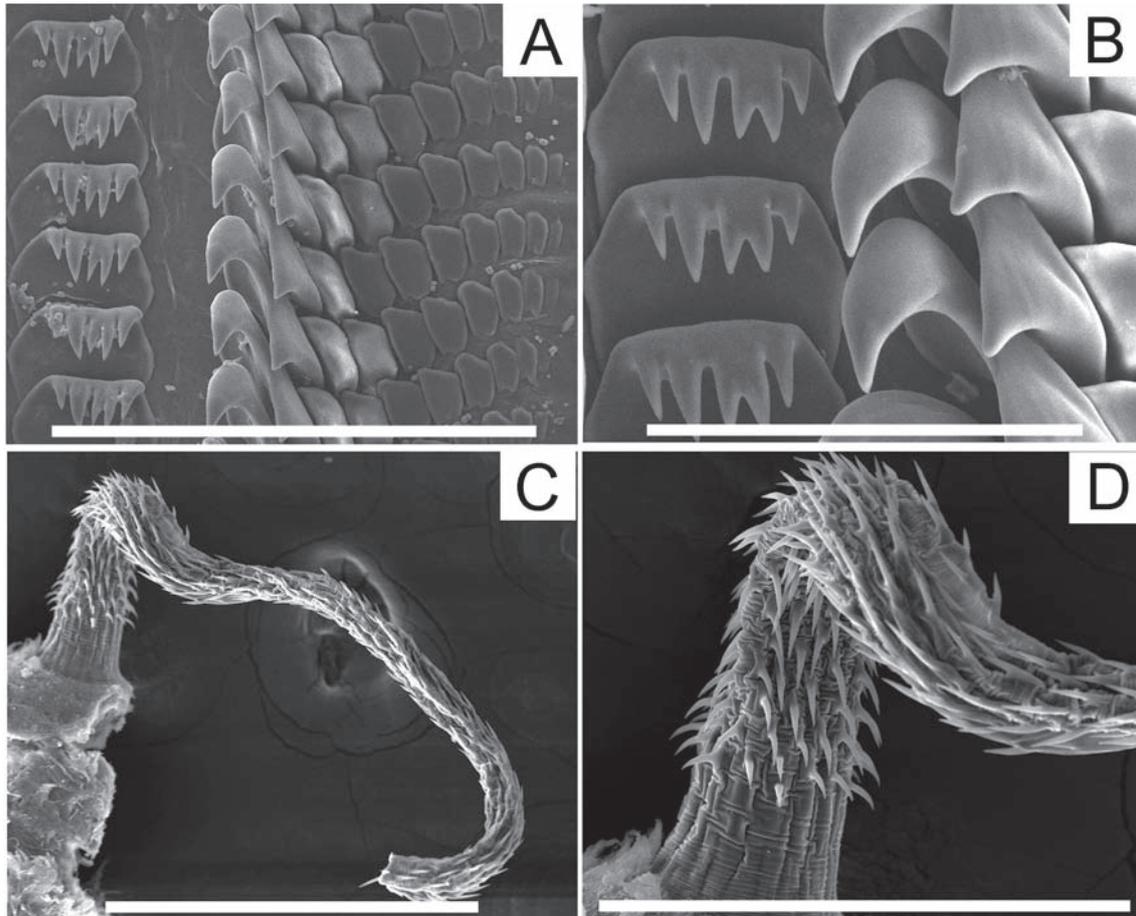


FIG. 8. – Scanning electron micrographs of *Nembrotha lineolata* Bergh, 1905: A, right half-row of radular teeth (MNCN 15.05/46724, scale bar: 400 μ m); B, rachidian and innermost lateral teeth (MNCN 15.05/46725, scale bar: 200 μ m); C, penis (MNCN 15.05/46725, scale bar: 500 μ m); D, base of the penis (MNCN 15.05/46725, scale bar: 300 μ m).

we lack specimens in order to study their anatomy, they cannot be assigned to *N. lineolata* with certainty at the moment. Gosliner, Behrens and Williams (1996) reported *N. lineolata* feeding on the ascidians *Clavelina* spp., *Rhopalaea* sp., and *Oxycorynia fascicularis*.

Geographic range. This species, originally described from Indonesia, is also known from Bali (Tonozuka, 2003), Fiji (Gosliner *et al.* 1996; Atkinson, 2003), Palau (present study), Papua New Guinea (Gosliner *et al.* 1996; Coleman, 2001; present study), Malaysia (Ho, 2005), Japan (Baba, 1976; Suzuki, 2000; Nakano, 2004), Kerama Islands (Ono, 1999), Ryukyu Islands (Ono, 2004), the Philippines (Debelius, 1996; present study), Australia (Willan and Coleman, 1984; Coleman, 1989, 2001; Wells and Bryce, 1993; Debelius, 1996; Marshall and Willan, 1999), the Indian Ocean (Eales, 1938), the Seychelles (Debelius, 1996; Debelius and Kuitert, 2007), Tanzania and Comoros Island (present study).

***Nembrotha purpureolineata* O'Donoghue, 1924**
(Figs. 9, 4D, 10)

Nembrotha purpureolineata O'Donoghue, 1924: 568, pl. 28, Figs. 16,17, pl. 30, Figs. 60,61.
Kentiella rutilans Pruvot-Fol, 1931: 754, pl. 13, Fig. 9, syn. nov.

Material examined. WAM S11563, north of Suomi Island, Houtman Abrolhos Islands, Western Australia, 23/07/04, one specimen 55 mm alive, dissected, 13 m depth, collected by M. Pola. WAM S11564, Houtmans Abrolhos Islands, Western Australia, 24/07/04, three specimens 70, 75 and 80 mm alive, two dissected, 20 m depth, collected by M. Pola. WAM S11565, Houtmans Abrolhos Islands, Western Australia, 24/07/04, two specimens 85 and 95 mm alive, one dissected, 22 m depth, collected by C. Todt. CASIZ 156076, Rottnes Island, Western Australia, Australia, 12/08/00, one specimen 40 mm preserved, collected by S. Fahey. MNCN 15.05/46726, Nelson Bay Beach, Port Stephens, New South Wales, Australia, 31/01/04, one specimen 15 mm preserved, collected by N. Wilson. AM C205326, Nelson Bay Beach, Port Stephens, New South Wales, Australia, 05/12/04, one specimen 90 mm alive, dissected, 12 m depth, collected by N. Wilson. AM C205327, Nelson Bay Beach, Port Stephens, New South Wales, Australia, 13/03/04, one specimen 30 mm preserved, dissected, 12 m depth, collected by N. Wilson.

External morphology. The body is elongate and limaciform, reaching up to 100 mm in length in living adults. The posterior end of the foot is long and

pointed (Fig. 9). The head is rounded. The entire body surface has a pattern of longitudinal wrinkles. The dorsum continues to the side of the body without a line of demarcation or pallial edge. Externally the animals are characterised by the presence of a broad longitudinal band on the notum (Fig. 9). A thinner line passes round the front, anterior to the rhinophores, and back on each side of the notum. Behind the gill, these two lines converge and meet, about halfway between the gill and the posterior end, to form one line in the middle, which runs back to the end of the tail. Another line runs parallel to the edge of foot on each side. There is a pair of large conical, perfoliate rhinophores. The rhinophores, bearing 35-45 lamellae, are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are thick, and elongate with a depression at the centre of each. There are from three to five large multipinnate, non-retractile branchial leaves. The anus is mid-dorsal, located in the centre of the branchial circle on an elevated elongate papilla. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The ground colour of the body is yellowish white or cream white with a broad brown or black band on the notum and lines of the same colour on each side of the body (Fig. 9). The margin of the foot is delineated by a blue to purple band, usually with an internal submarginal yellow band. The oral tentacles are also blue or purple followed by a yellow band. The rhinophoral lamellae are red or vermillion with blue or purple tips. The base is pink. The rhinophoral sheaths are blue or purple above and yellow below. There are two, variable sized, translucent spots posterior to the rhinophores, through which the dermal eyes are visible. The branchial leaves are red or vermillion above, blue or purple below and yellow at the base.

Anatomy. *Nembrotha purpureolineolata* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long and thin muscular oral tube that continues into the buccal mass. The buccal mass is smaller than the oral tube. There is a pair of large, wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown

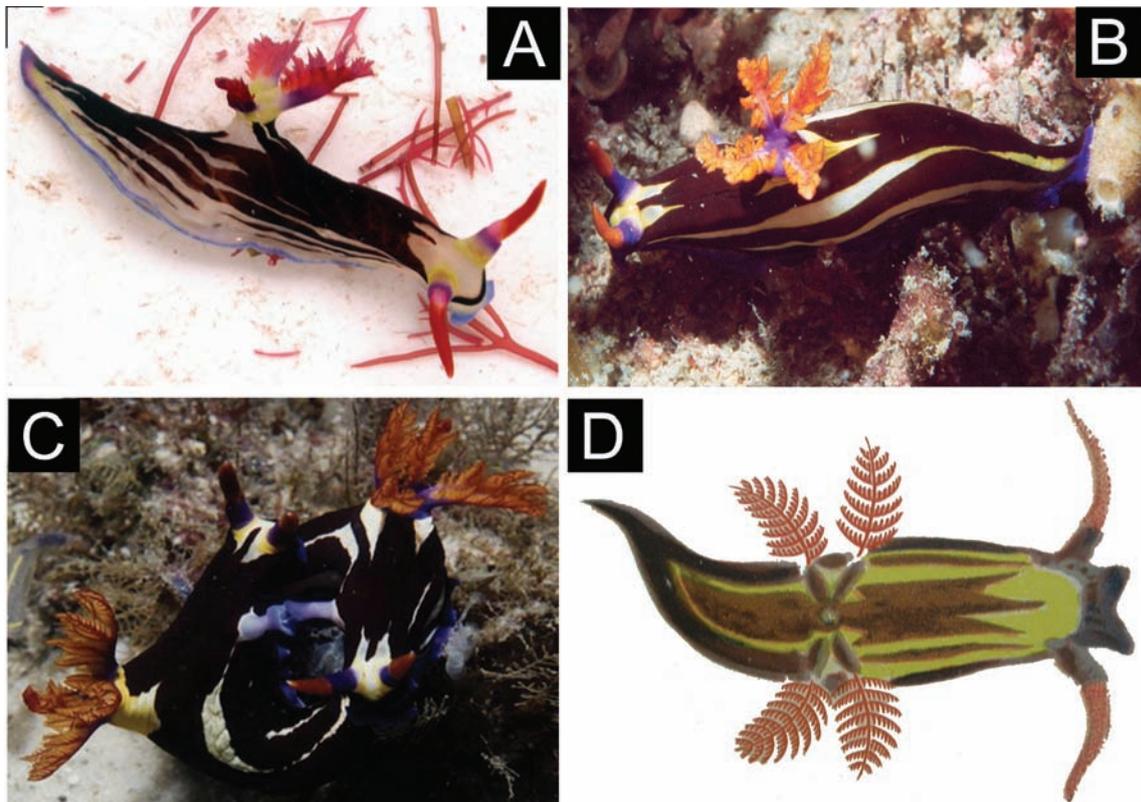


FIG. 9. – *Nembrotha purpureolineolata* O'Donoghue, 1924: A, specimen from Abrolhos Islands, Western Australia, photo by Marta Pola (AM C205326); B, specimen from Port Stephens, New South Wales, photo by David and Leanne Atkinson (AM C205326); C, specimen from Port Stephens, New South Wales, photographs by David and Leanne Atkinson; D, *Nembrotha rutilans* (Pruvot-Fol, 1931), original drawing by Saville Kent.

corrugated chitinous disk, usually devoid of rodlets but with a central and two lateral areas, which, in some specimens have a weak armature (Figs. 10A,B). The radular formulae of the dissected specimens are: 15 mm specimen (preserved), 32 x 7-8.1.1.1.7-8 (AM C205326), 30 mm specimen (preserved), 30 x 10.1.1.1.10 (AM C205327), 75-80 mm specimens, 30-33 x 8-9.1.1.1.8-9 (WAM S11564), 85 mm specimen, 30 x 9-10.1.1.1.9-10 (WAM S11564), 40 mm specimen (preserved), 32 x 10.1.1.1.10 (CASIZ 156076) (Figs. 10C,E). The rachidian teeth are broad and rectangular with five asymmetrically arranged triangular denticles along the upper margin (Figs. 10C-F). The two outer denticles are smaller than the inner ones. The two inner denticles on one side are joined at the base, so both denticles might be described as having a single bifid denticle. The arrangement and length of these joined denticles is variable even between specimens with exactly the same external pattern (Figs. 10C-F). The inner laterals are well developed; they are large and strongly hooked with two cusps. The outer lateral teeth are rectangular plates, from 7 to 10, which lack cusps or dentition and become smaller near the margin (Figs. 10C,E). There is a blood gland located above the genitalia, usually closer to the buccal mass than to the digestive gland.

The reproductive system is triaulic (Fig. 4D). The hermaphroditic duct is elongate and wide. It expands into a very long and highly convoluted ampulla. The prostatic portion of the vas deferens is very large. The distal end of the prostatic mass connects to an elongate, thin and highly convoluted vas deferens. The vas deferens opens into a common atrium with the vagina but without a strongly differentiated muscular ejaculatory portion. The penis is armed with rows of curved, chitinous hooks except at the base (Figs. 10G,H). The chitinous penial spines are numerous and they are similar in size and shape (Figs. 10G-H). The vagina is wider than the vas deferens, long and convoluted. At its proximal end, the vagina connects to the rounded, thin-walled bursa copulatrix.

Remarks. O'Donoghue (1924) described *N. purpureolineata* from a single preserved specimen 35 mm long collected from the Abrolhos Islands (Western Australia). He described the general colour as a dirty yellowish grey marked with pale brown lines and showed a drawing of the radula. Both the external pattern of lines and colours and the description of the radula from the type specimen perfectly match our recently collected material from the Abrolhos Islands (see also Wells

and Bryce, 1993), which might have three or five gill leaves. The reproductive system of *N. purpureolineata* is described for the first time in this study.

In 1976, Baba described two additional specimens from Japan. The material examined in that paper had fewer lines than the type specimen of *N. lineolata* and they were rather thick, more similar to those of *N. purpureolineata* O'Donoghue (1924). The number of gill leaves (3) and the colouration were also very similar to the above descriptions but a large patch of orange was present in the middle of the back. This feature was used by Cervera *et al.* (1996) and Gosliner (pers. comm.) to conclude that the specimens depicted by Baba (1976) and Gosliner (1987) probably represent one or more undescribed species. However, Baba (1976) suggested that *N. lineolata* and *N. purpureolineata* could be synonyms. We are in agreement with Cervera *et al.* (1996) and consider that those specimens with a large orange patch in the middle of the back from Japan (Baba, 1976; Suzuki, 2000; Nakano, 2004), Indonesia (Debelius, 1996; Tonozuka, 2003), Western Australia (Coleman, 2001; Debelius and Kuitert, 2007), the Philippines and East Timor (Debelius and Kuitert, 2007) and South Africa (Gosliner, 1987; Fraser, 1999; King and Fraser, 2002) represent one or more undescribed species.

Nembrotha rutilans [*Kentiella*] was described from the Great Barrier Reef in 1931 by Pruvot-Fol from a painting done in 1892 (Fig. 9D) by an artist named William Saville-Kent. Pruvot-Fol did not describe the internal anatomy, and there are no type specimens to examine. The colouration as described by Pruvot-Fol is chocolate brown and pale yellow alternating with longitudinal stripes, and the pattern colour is identical to O'Donoghue's description (1924). In the present study we examined several specimens from Eastern and Western Australia with the same colour pattern as described above. Cervera *et al.* (1996) showed a comparative table of the features of the three colour forms discussed above. The synonymisation of *N. rutilans* with *N. purpureolineata* based on the lack of description of the internal anatomy is therefore justified.

Geographic range. This species, originally described from Western Australia (O'Donoghue, 1924; Willan and Coleman, 1984 as *Nembrotha* sp.; Coleman, 1989 as *Nembrotha rutilans*; Wells and Bryce, 1993; Coleman, 2001; present study), is also known from Eastern Australia (Pruvot-Fol, 1931; Rudman, 1999 (July 2)).

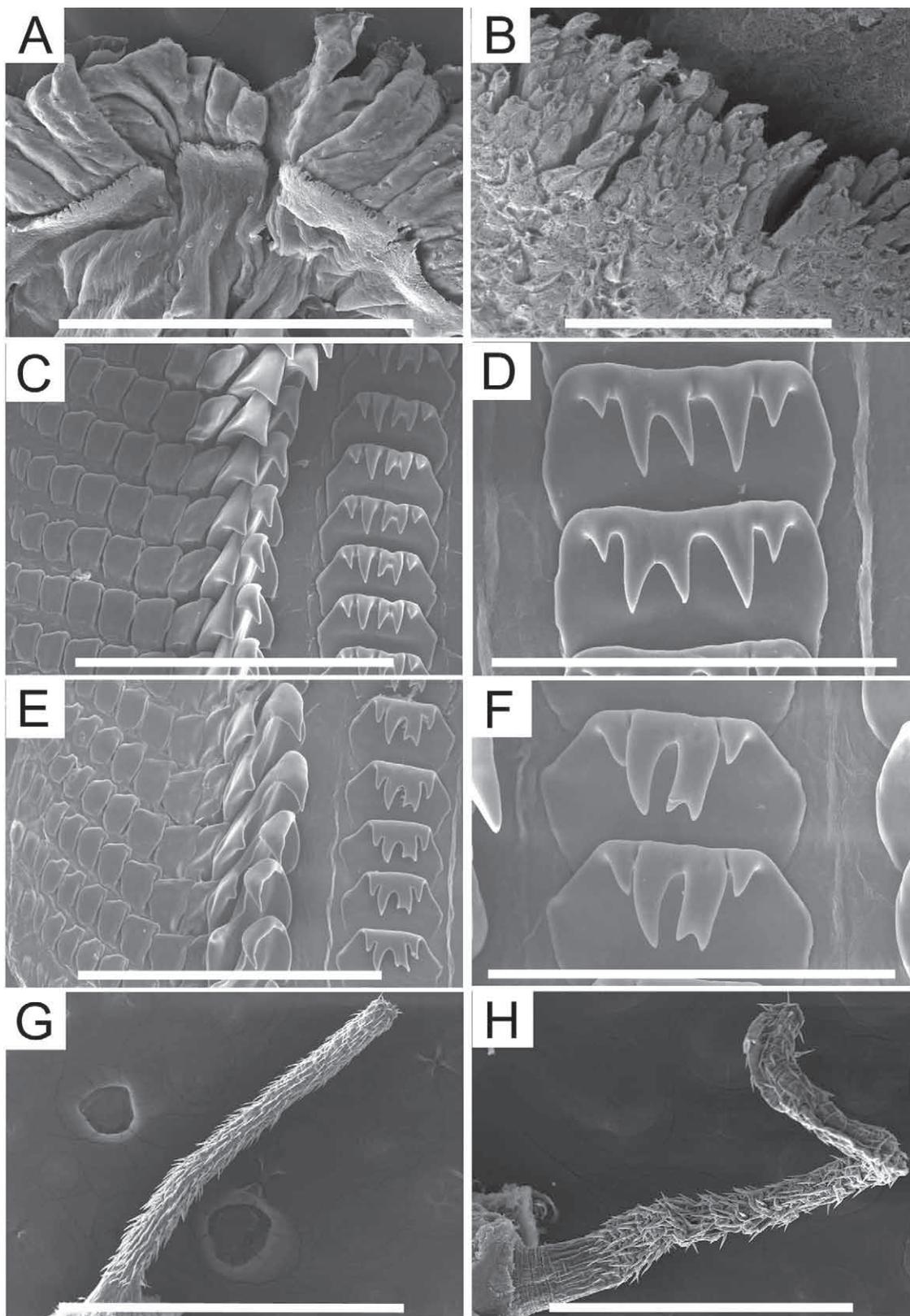


FIG. 10. – Scanning electron micrographs of *Nembrotha purpureolineata* O'Donoghue, 1924: A, labial cuticle (AM C205327, scale bar: 1 mm); B, detail of the rodlets (AM C205327, scale bar: 50 μm); C, left half-row of radular teeth (WAM S11564, scale bar: 500 μm); D, rachidian teeth (WAM S11565, scale bar: 300 μm); E, left half-row of radular teeth (AM C205327, scale bar: 500 μm); F, rachidian teeth (AM C205326, scale bar: 300 μm); G, penis (WAM S11564, scale bar: 1 mm); H, penis (AM C205327, scale bar: 500 μm).

Nembrotha livingstonei Allan, 1933
(Fig. 11A-D, 4E, 12)

Nembrotha livingstonei Allan, 1933: 450, pl. 56, Fig. 15.

Material examined. MNCN 15.05/46716, "Maria's Point", Malapascua Island, Philippines, 29/04/03, one specimen 52 mm alive, dissected, 8 m depth, collected by E. Köhler. WAM S11555, Lilo An, Cebu Island, Philippines, 27/1/03, one specimen 42 mm alive, dissected, 13 m depth, collected by E. Köhler. MNCN 15.05/46717, Kerama Islands, Okinawa, Japan, 02/01/03, two specimens 20 mm preserved, dissected, 7 m depth, collected by A. Ono.

External morphology. The body is elongate and limaciform, reaching up to 55 mm in length in living adults. The posterior end of the foot is long and pointed. The head is rounded. The entire body surface has a pattern of longitudinal wrinkles with small irregular spots scattered over the notum and both sides of the body (Figs. 11A-D). In some specimens the spots are strongly marked, becoming pustules, while in other specimens the spots appear as irregular patches between the wrinkles. Externally, the animals are characterised by the presence of a cross-like mark between the rhinophores (Figs. 11A-D). There is a pair of large conical, perfoliate rhinophores. The rhinophores, bearing 20-25 lamellae, are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are thick and elongate with a depression at the centre of each. There are five strong multipinnate, non-retractile branchial leaves. The two posterior leaves of each side share a common base. The anus is mid-dorsal, located in the centre of the branchial circle. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The general colour of the living animals is dark reddish brown with orange, reddish brown, green or white spots (Figs. 11A-D). The rhinophores are orange-reddish with bluish-white pigmentation at their base. The rhinophoral sheaths are tipped in orange and their base is also white and blue. The conspicuous characteristic cross-like mark between the rhinophores is white to pale yellow in colour. The edge of the foot has a bright orange stripe, as do as the oral tentacles. The gill branches are reddish brown with orange-reddish tips. The base is white or pale yellow with electric blue above. The spots located at the end of the tail and those on the front edge are bright orange.

Anatomy. *Nembrotha livingstonei* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with

a muscular oral tube that continues into the buccal mass. The buccal mass is smaller than the oral tube. There is a pair of large, wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown corrugated chitinous disk, usually devoid of rodlets but with a central and two lateral areas (Fig. 12A). The radular formulae are: 52 mm specimen, 27 x 8-9.1.1.1.8-9 (MNCN 15.05/46716), 42 mm specimen, 25 x 8.1.1.1.8 (WAM S11555), and 20 mm specimen (preserved), 23 x 9.1.1.1.9 ((MNCN 15.05/46717) (Figs. 12B-D). The shape of the rachidian teeth is shown in Figures 12B-D. There are five asymmetrically arranged triangular denticles along the upper margin. Two of the inner denticles might share a common base but their arrangement is variable. The innermost laterals are well developed; they are larger and longer than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a shorter more basal one (Figs. 12B-D). The outer lateral teeth are rectangular plates, 8 to 9 in number, becoming smaller near the margin. The inner one bears an upper cusp while the remaining teeth lack cusps or dentition. There is a large blood gland located above the intestine.

The reproductive system is triaulic (Fig. 4E). The hermaphroditic duct is long. It expands into an elongate and convoluted ampulla. The prostatic portion of the vas deferens is very large. The distal end of the prostatic mass connects to an elongate, convoluted vas deferens. The vas deferens opens into a common atrium with the vagina but without a strongly differentiated muscular ejaculatory portion. The penis is armed with chitinous penial spines that can be distinguished into two different kinds of spines based on their size and shape (Figs. 12E,F). The basal spines are short and curved, all of them supported by the same rachis, and they constitute approximately the first twenty rows of spines (Fig. 12G). The remaining spines are longer and hooked, but it is not clear whether they are supported by the same rachis (Figs. 12E,F). In one of the dissected specimen from the Philippines (MNCN 15.05/46716) there appear to be three different types of penial spines, since at the base of the penis there are a few rows of large, curved spines followed by the two other types described above (Fig. 12H). The vagina is wide, long and straight in the specimens from the Philippines but it is convoluted in the specimen examined from Japan. At its proximal end, the vagina connects to the rounded bursa copulatrix, which, in situ, is entirely surrounded by the prostate.

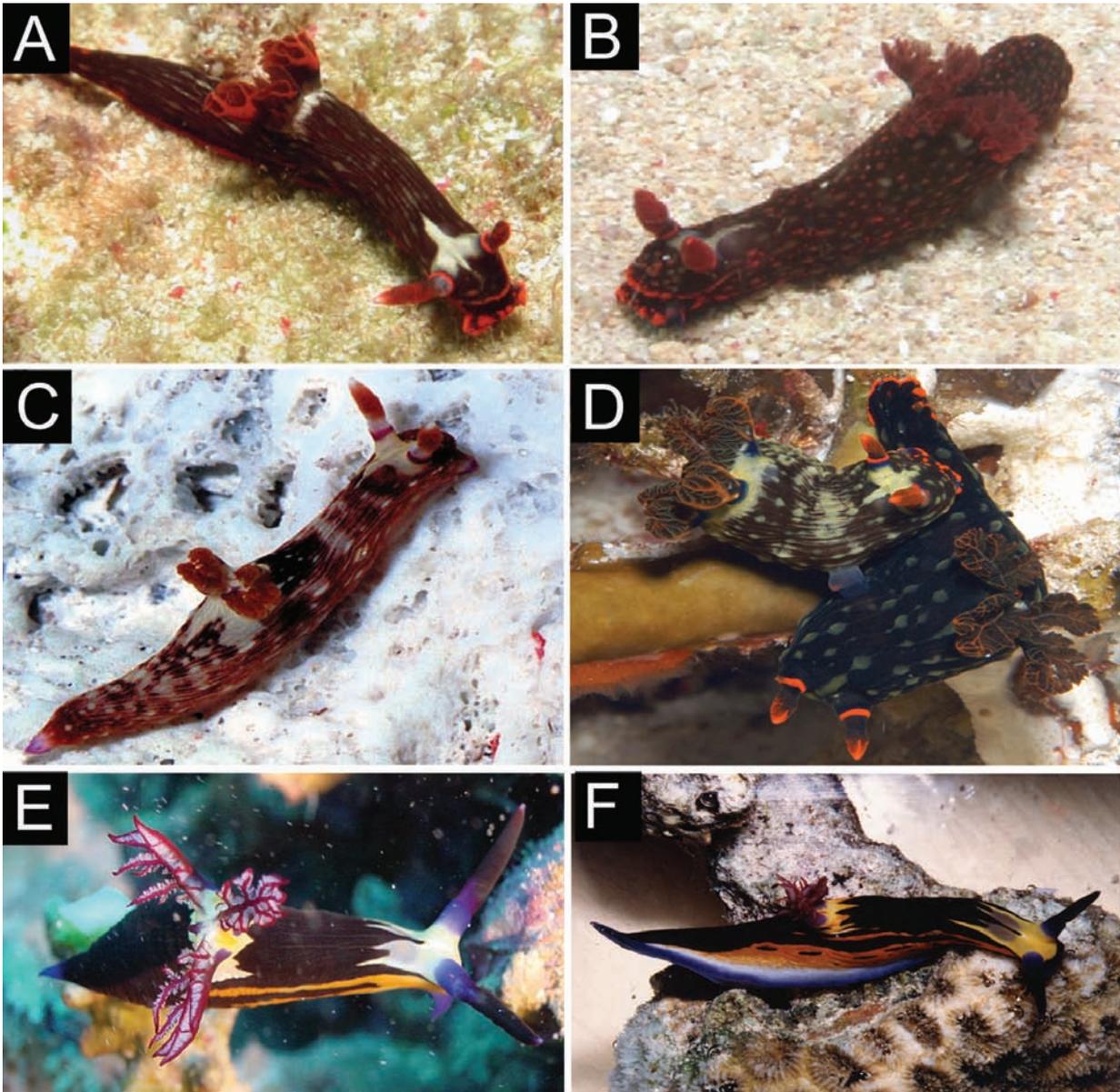


FIG. 11. – A-D, *Nembrotha livingstonei* Allan, 1933, living animals: A, B, D, specimens from Philippines, photos by Erwin Köhler (A. WAM S11555, B. MNCN 15.05/46716); C, specimen from Japan, photo by Atsushi Ono (MNCN 15.05/46717). E-F, *Nembrotha megalocera* Yonow, 1990, living animals: E, specimen from Red Sea, photo by Marina Poddubetskaia (MNCN 15.05/46729); F, specimen from Red Sea, photo by José Carlos García Gómez.

Remarks. *Nembrotha livingstonei* was introduced by Allan (1933) based on the external colouration without any internal description. These features, as originally described, are consistent with the present material. The reproductive system is described in this paper for the first time. *Nembrotha livingstonei* is easily distinguishable from the remaining species of *Nembrotha* by the possession of the white cross-like mark between the rhinophores. However, some of the colour forms of *N. livingstonei* strongly resemble those of *N. nigerrima* (Fig. 11D). Externally, *N. livingstonei* shares the orange colouration of the rhinophoral

sheaths, the oral tentacles, the spots of the frontal edge and the posterior end of the tail and the line bordering the foot with *N. nigerrima*. In some cases, the colouration of the gill circle is also similar. The pattern of wrinkles, lines and spots is also very similar in many specimens since the variability of both species is very high. With respect to the internal anatomy, *N. livingstonei* and *N. nigerrima* are the only two described species of the genus with two different types of penial spines. Moreover, in both species, the muscular ejaculatory portion of the vas deferens is not strongly developed and the vagina is not as wide as in the re-

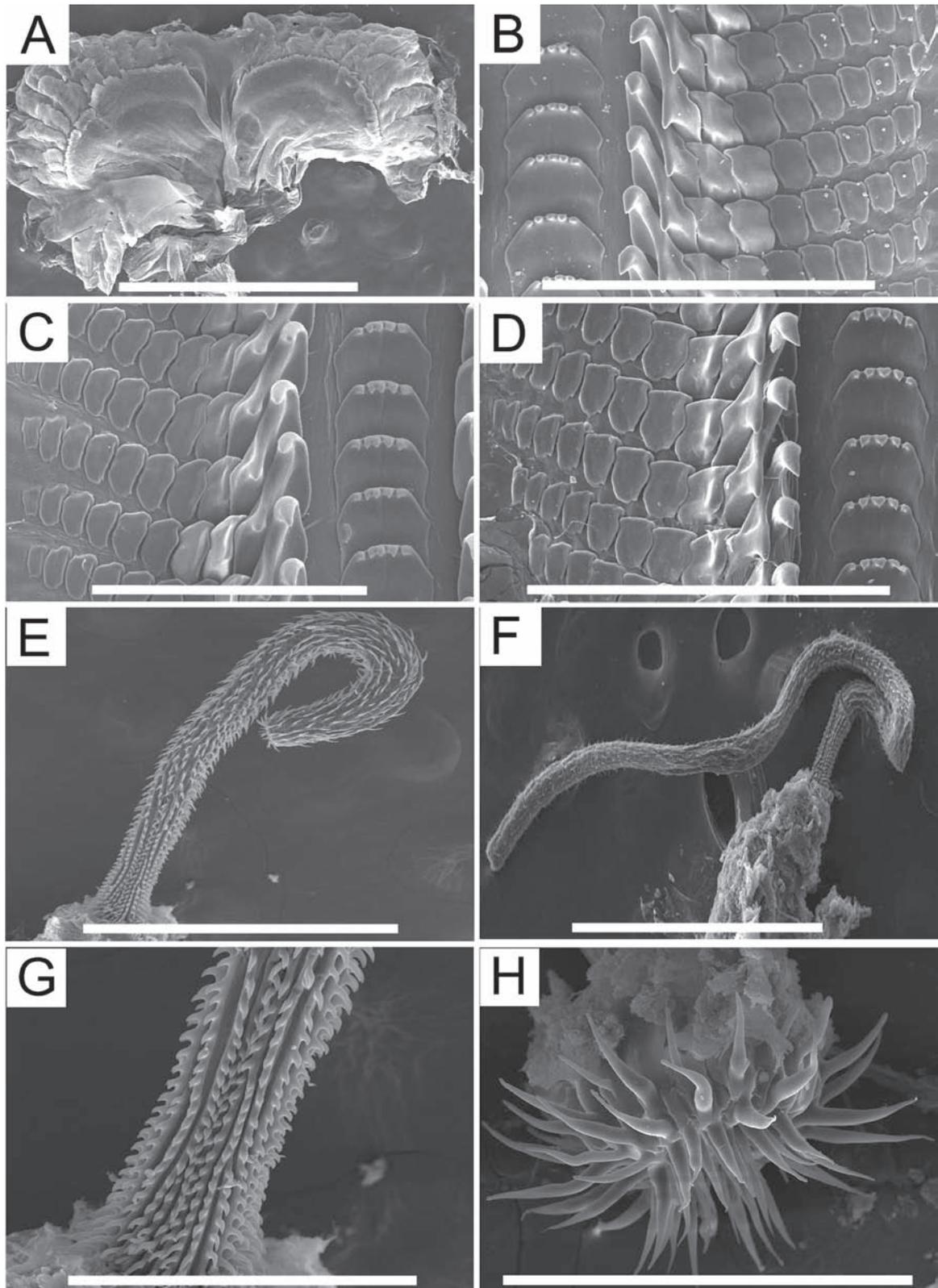


FIG. 12. – Scanning electron micrographs of *Nembrotha livingstonei* Allan, 1933: A, labial cuticle (MNCN 15.05/46716, scale bar: 1 mm); B, right half-row of radular teeth (WAM S11555, scale bar: 500 μm); C, left half-row of radular teeth (MNCN 15.05/46716, scale bar: 500 μm); D, right half-row of radular teeth (MNCN 15.05/46717, scale bar: 500 μm); E, penis (WAM S11555, scale bar: 500 μm); F, penis (MNCN 15.05/46717, scale bar: 1 mm); G, base of the penis (WAM S11555, scale bar: 500 μm); H, base of the penis (MNCN 15.05/46716, scale bar: 200 μm).

maintaining species of the “spotted group” of *Nembrotha*. The radular formulae and the teeth of *N. livingstonei* and *N. nigerrima* are also very similar. Figure 11D shows a specimen identified as *N. livingstonei* mating with a specimen of *N. nigerrima*.

Rudman’s seaslugforum (1998-2005) and several field guides (Coleman, 2001; Ono, 2004; and web pages (<http://slugsite.us/bow/nudwk274.htm>; http://www.philippine-sea-slugs.com/DORIDINA/Nembrotha_livingstonei.htm; <http://rfbolland.com/okislugs/nemblivi.html>) show different specimens that are variable in colour, but all of them are characterised by the presence of the conspicuous star-shaped patch between the rhinophores. *N. livingstonei* from Australia appears to have spots rather than lines. Slight differences in the reproductive system between different specimens do not show any consistent pattern and do not allow us to distinguish between specimens from the Philippines and Japan. All the specimens have an identical radular morphology. Debelius (1996) and Köhler (2001) show photographs of specimens from Tanzania and the Philippines, respectively, that they identified as *N. livingstonei*. However, we believe that they do not represent *N. livingstonei*. Debelius and Kuitert (2007)

show a picture from South Africa identified as *Nembrotha* sp.4, which we believe is *N. livingstonei*.

Geographic range. This species, originally described from Broome (Western Australia), is also known from Eastern Australia (Willan and Coleman, 1984 as *Nembrotha* sp.; Coleman, 1989 as *Nembrotha tabescens*; 2001; Marshall and Willan, 1999; Debelius and Kuitert, 2007), Indonesia (Bartlett, 2002; Debelius and Kuitert, 2007), the Ryukyu Islands (Ono, 2004), Japan and the Philippines (present study).

***Nembrotha megalocera* Yonow, 1990**
(Figs. 11E-F, 4F, 13)

Nembrotha megalocera Yonow, 1990: 292, pl. 10.

Material examined. ZSM-Moll 20006510, Dahab, Sinai, Egypt, 10/2000, one specimen 23 mm preserved, dissected, collected by M. Schrödl. ZSM-Moll 19991127, “Three Pools”, Dahab, Golf von Aqaba, Rotes Meer, Egypt, one specimen 22 mm preserved, dissected, collected by G. Försterra. MNCN 15.05/46729, “Coral Garden”, Dahab, Egypt, 27/02/05, one specimen 45 mm alive, partially dissected, collected by M. Poddubetskaia.

External and internal morphology. The external and internal anatomy of this species is described in detail and figured by Cervera *et al.* (1996). The spec-

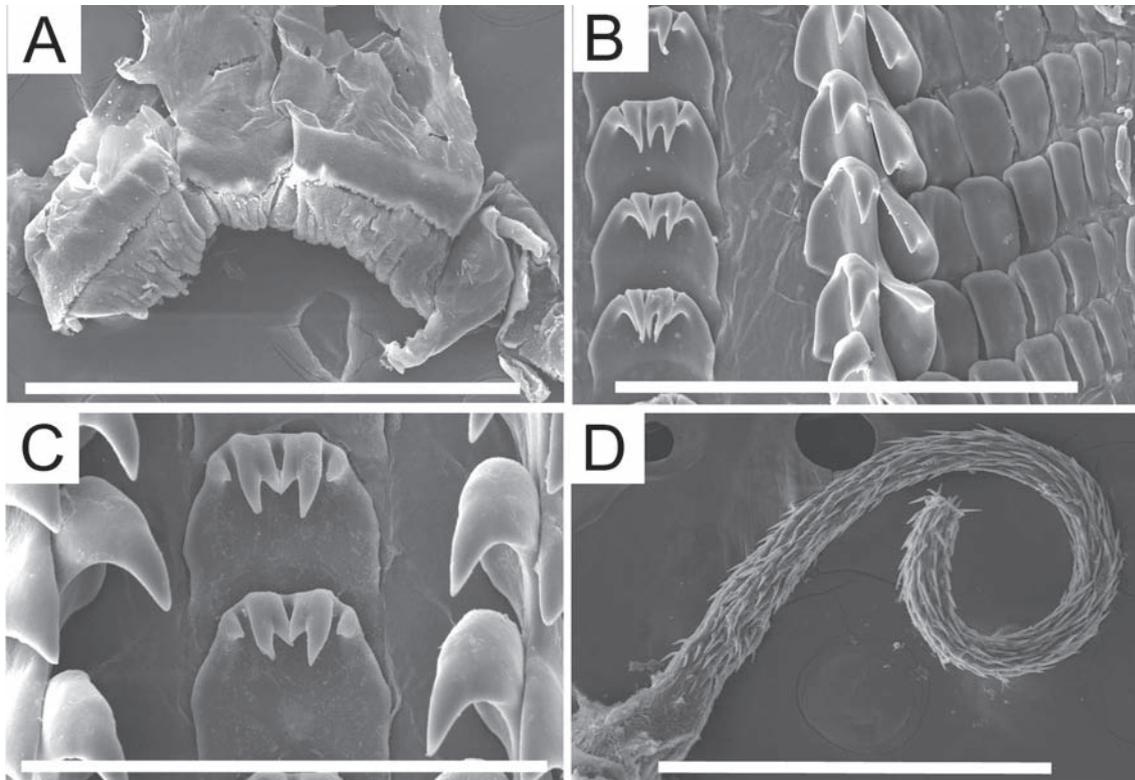


FIG. 13. – Scanning electron micrographs of *Nembrotha megalocera* Yonow, 1990: A, labial cuticle (ZSM-Moll 19991127, scale bar: 1 mm). B, right half-row of radular teeth (ZSM-Moll 20006510, scale bar: 200 μ m); C, rachidian teeth (ZSM-Moll 19991127, scale bar: 200 μ m); D, penis (MNCN 15.05/46729, scale bar: 500 μ m).

imens described for the present study matched their description and thus there is no additional information to present. The radular formula of our 22 and 23 mm preserved specimens is 23 x 6-7.1.1.1.7-6 (ZSM-Moll 19991127, ZSM-Moll 20006510). The penis is armed with rows of curved, chitinous hooks except at its base. See Figs. 11E-F, 4F, 13 for pictures of the living animals, the reproductive system and the labial cuticle, the radula and the penis, respectively.

Remarks. *Nembrotha megalocera* was originally described by Yonow (1990) from four specimens collected from the Red Sea. In that paper the author presented a description of the external morphology and colouration and provided a radular formula and a photo of one specimen. More recently, Cervera *et al.* (1996) provided a more detailed description of both the external and internal anatomy of this species based on one specimen (Fig. 11F) from Egypt (Red Sea) and compared *N. megalocera* with the closely related species *N. lineolata*, *N. purpureolineata* and *N. rutilans*. The specimens examined for the present study are in agreement with the description of both Yonow (1990) and Cervera *et al.* (1996).

Nembrotha megalocera looks very similar to *N. purpureolineata* and *N. chamberlaini* but differences in the external morphology such as the extremely long rhinophores and the constant number of gill leaves (3), as well as differences in colouration (black ground colour and orange sides with black markings) and subtle differences in the internal morphology such as a constantly square rachidian tooth, also allow us to distinguish it from the remaining species of the genera. Moreover, to date, *N. megalocera* has only been reported from the Red Sea, while the remainder of the several similarly coloured forms of *N. lineolata* are co-distributed throughout the tropical Indo-Pacific. Beautiful photographs of *N. megalocera* are shown in Debelius, 1996; Coleman, 2001; www.seaslugforum.net/factsheet.cfm?base=nembmega; www.medslugs.de/E/Ind-NW/Nembrotha_megalocera.htm; [www.scuba-equipment-usa.com/marine/NOV04/Great_Nembrotha\(Nembrotha_megalocera\).html](http://www.scuba-equipment-usa.com/marine/NOV04/Great_Nembrotha(Nembrotha_megalocera).html); www.meerwasser-lexikon.de/de/71/1288/Nembrotha/megalocera.htm).

Geographic range. Thus far this beautiful species is only known from warm tropical waters of the Red Sea off northern Africa (Yonow, 1990; Debelius, 1996; Coleman, 2001; Debelius and Kuitert, 2007).

Nembrotha yonowae Goethel and Debelius, 1992 (Figs. 14A-D, 15, 16A)

Nembrotha yonowae Goethel and Debelius, 1992: 517, Fig. 20.
Nembrotha guttata Yonow, 1993: 108, figs. 2F, 6E, 8C.

Material examined. AM C169462, Holotype, Maaya Tila (Ari Atoll), 31/05/1991, 30 x 10 mm (preserved, S.H), 31 m depth. WAM S11556, Siguijor Wall, Siguijor Island, Philippines, 01/03/03, one specimen 31 mm alive, dissected, 16 m depth, collected by E. Köhler. MNCN 15.05/46179, "Lapus-Lapus", Malapascua Island, Philippines, 23/04/05, one specimen 66 mm alive, dissected, 9 m depth, collected by E. Köhler. CASIZ 082920, north coast, near Madang, outer barrier ref., north of the Pinnacle, Papua New Guinea, 07/11/90, one specimen 5 mm alive, dissected, 18 m depth, collected by T. M. Gosliner and M. Jebb. CASIZ 082922, north coast, near Madang, outer barrier reef, north of the Pinnacle, Papua New Guinea, 12/11/90, one specimen 5 mm alive, dissected, 18 m depth, collected by T. M. Gosliner and G. Williams. CASIZ 106531, Wall of death, Philippines, 22/08/94, one specimen 13 mm preserved, dissected, collected by M. Miller.

External morphology. The body is elongate and limaciform but robust and widest at the gill. The posterior end of the foot is long and pointed (Figs. 14A-C). The head is rounded. The mantle is small and indistinct. The adult living animals may grow up to 55 mm in total length with the body surface covered with randomly scattered pustules. The pustules around the frontal edge rise to form a ridge. There is a pair of perfoliate rhinophores that bear 25 lamellae and are completely retractile into their rhinophoral sheaths. The oral tentacles are short and circular in shape with a depression at the centre of each one. There are five non-retractile multipinnate gill branches. The two posterior gill branches of each side share a common base. The anus is situated between the gill branches on elevated papillae just behind the kidney opening. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The ground body colour is black or dark brown with scattered orange-red pustules all over. The pustules have greenish borders (Figs. 14A-C). The rhinophores are black, sometimes tipped with orange. The edge of the foot, the rhinophoral sheaths and the oral tentacles may vary from orange to greenish. The gill leaves are green.

Anatomy. *Nembrotha yonowae* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long but thin oral tube that continues into the buccal mass. Two long, wide salivary glands connect to the buccal bulb at both sides of the oesophageal junction. The thin chitinous labial cuticle is corrugated with a central and two lateral areas devoid of denticles (Fig. 15A). The radular formulae are: 31

mm specimen, 21 x 9.1.1.1.9 (WAM S11556), 13 mm specimen (preserved), 20 x 9.1.1.1.9 (CASIZ 106531) and 5 mm specimens, 18 x 6.1.1.1.6 (CASIZ 082920) (Figs. 15B,C). The rachidian teeth are broad and rec-

tangular with five asymmetrically arranged triangular denticles almost similar in size (Figs. 15B,C). The two inner denticles of the right half of the rachidian teeth are joined at the base. The inner laterals are

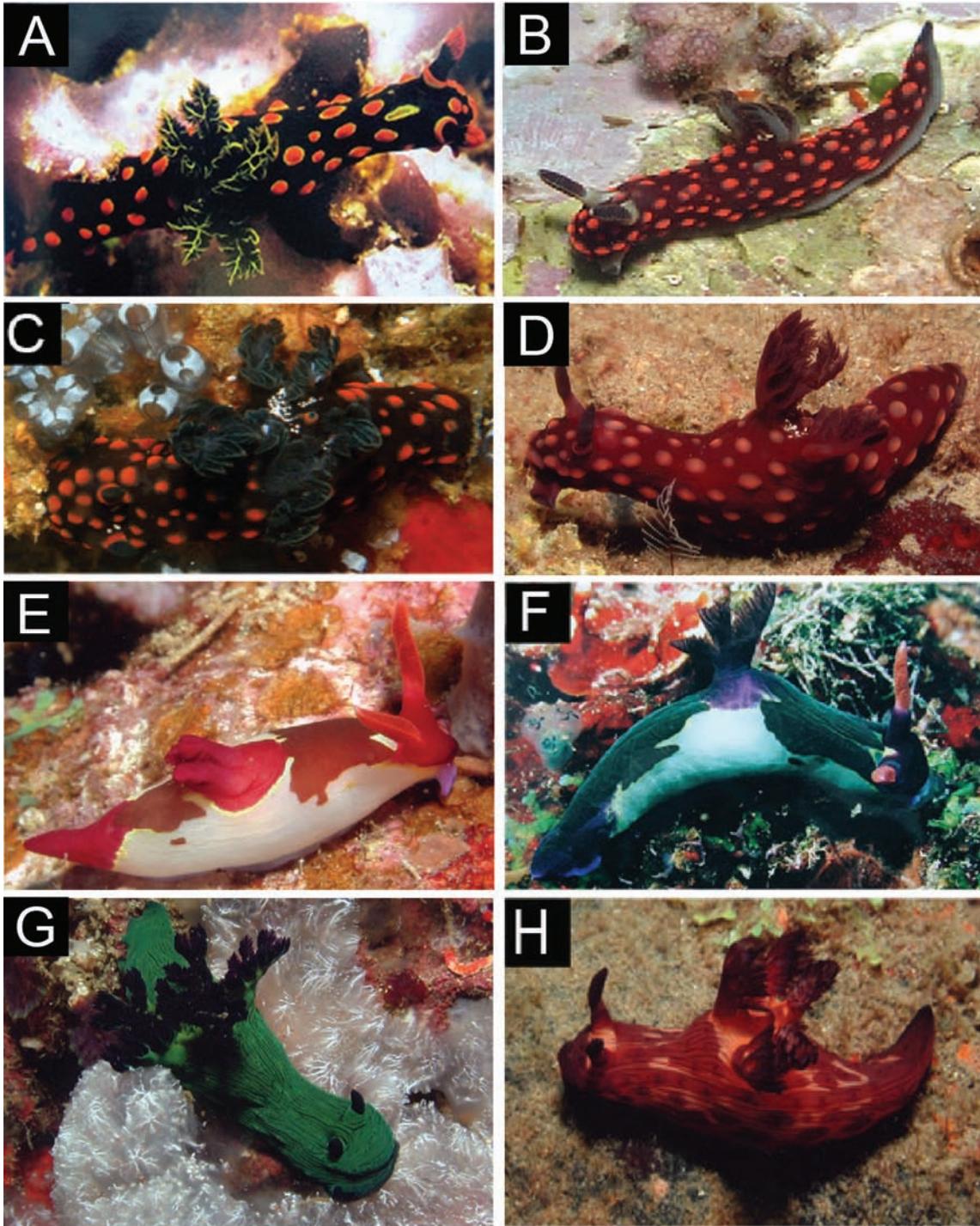


FIG. 14. – A-C, *Nembrotha yonowae* Goethel and Debelius, 1992, living animals: A, specimen from Mauritius, photo by H. Frei; B-C, specimens from Philippines (B. WAM S11556, C. MNCN 15.05/46719). D, *Nembrotha* sp. specimen from Philippines (WAM S11557). E, *Nembrotha chamberlaini* Gosliner and Behrens, 1997, living animal from Philippines (MNCN 15.05/46728). F, *Nembrotha* sp., living animal from Philippines. G, *Nembrotha milleri* Gosliner and Behrens, 1997, specimen from Philippines (MNCN 15.05/46721). H, *Nembrotha mullineri* Gosliner and Behrens, 1997, specimen from (MNCN 15.05/46722). Photos by Erwin Köhler.

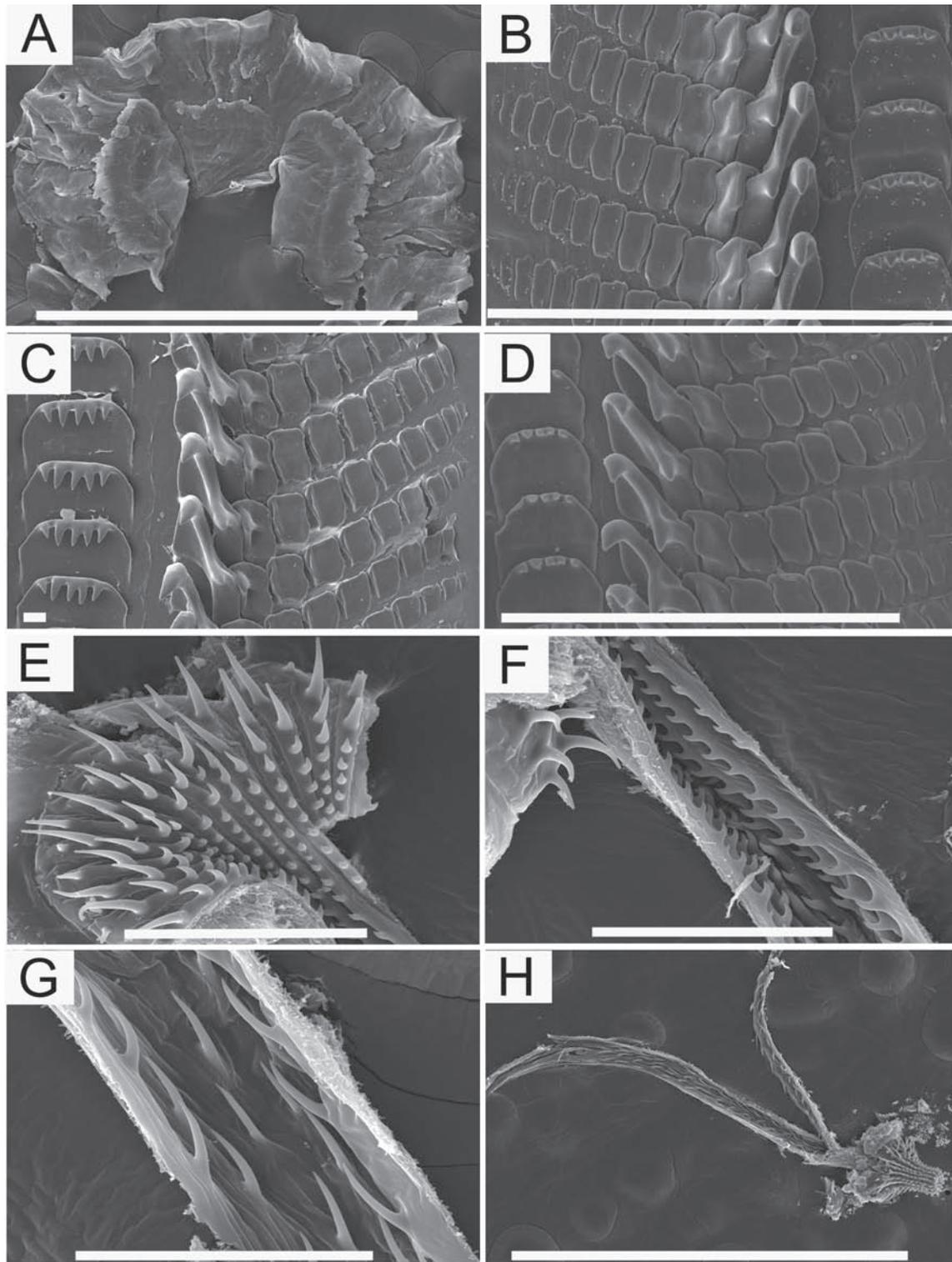


FIG. 15. – Scanning electron micrographs of *Nembrotha yonowae* Goethel and Debelius, 1992: A, labial cuticle (WAM S11556, scale bar: 1 mm); B, left half-row of radular teeth (WAM S11556, scale bar: 1 mm); C, right half-row of radular teeth (CASIZ 106531, scale bar: 30 µm); D, right half-row of radular teeth (WAM S11557, scale bar: 400 µm); E, basal penial spines (WAM S11556, scale bar: 100 µm); F, second types of penial spines (WAM S11556, scale bar: 100 µm); G, distal penial spines (WAM S11556, scale bar: 100 µm); H, penis (MNCN 15.05/46744, scale bar: 1 mm).

well developed; they are larger and longer than the outer ones with a rectangular base and two cusps, an

elongate terminal cusp and a shorter more basal one. The outer lateral teeth are rectangular plates, be-

coming smaller near the margin. The innermost one bears an upper cusp while the remaining ones lack cusps or dentition (Figs. 15B,C). There is a blood gland located above the intestine.

The reproductive system is triaualic (Fig. 16A). The hermaphroditic duct is short and narrow, expanding into an elongate, wide and convoluted ampulla. The postampullary duct divides into a short oviduct and a wide prostatic portion of the vas deferens. The oviduct enters the massive female gland mass. The prostatic segment of the vas deferens is very large. The distal end of the prostatic mass branches into a narrow elongate and highly convoluted vas deferens. The distal end of the vas deferens widens into a muscular ejaculatory portion. The chitinous penial spines are numerous and they seem to be arranged in longitudinal lines. They can be distinguished into three different kinds of spines based on their size and shape (Figs. 15E-H). The basal spines are large, elongate and curved. They constitute the first three or four rows of spines (Figs. 15E,H). The spines immediately after these are much smaller and hooked (Figs. 15F,H). The remaining spines are also hooked and slightly more elongate than the second group but shorter than the basal spines (Figs. 15G,H). The vagina is wide, long and slightly convoluted.

Remarks. Almost sixty years after Allan's study, Goethel and Debelius (1992) described a new species of *Nembrotha* from the Maldives, *N. yonowae*. This species strongly resembles *N. nigerrima*, *N. cristata* and *N. livingstonei* but the authors introduced it based on the presence of orange pustules bordered with green and on its distribution. No anatomical description was given and no available type specimen exists. One year later, Yonow (1993) introduced *N. guttata*, also from the Maldives. The specimen described by Yonow is identical to *N. yonowae* but this author stated that as the type specimen of *N. yonowae* was not available, the illustrations depicted additional material not collected (Fig. 14A), and there are many difficulties in distinguishing the different species within the genus *Nembrotha*, the specimen described by Goethel and Debelius (1992) could not represent the same species as the one she was describing. We considered that since there are no specimens of *N. yonowae* to examine, the type locality of both species is the same and the external description is identical, so *N. guttata* and *N. yonowae* are synonyms.

Moreover, according to the International Code of Zoological Nomenclature (ICZN 2000), since before 1999 depositing of type material was not required when a new species was described, *N. yonowae* was described in a publication sensu Article 8.1, and the external description permits the recognition of the species, we consider that *N. guttata* Yonow (1993) is a junior synonym of *N. yonowae* Goethel and Debelius (1992).

There are problems of colour variation surrounding the taxonomy of this species. Additional specimens (with a different colour pattern) from the Philippines (Figs. 14D,15D) have also been examined. But since the internal anatomy of the species complex *nigerrima-cristata-yonowae* is very similar, we are not going to refer those specimens as any of them. Further morphological and molecular studies need to be done to fully resolve these issues.

Geographic range. This species originally described from the Maldives (Goethel and Debelius, 1992; Yonow, 1993; Debelius, 1996; Debelius and Kuitert, 2007) is also known from Indonesia (Debelius, 1996; Debelius and Kuitert, 2007 identified as *N. nigerrima*), the Philippines and Papua New Guinea (present study).

Nembrotha chamberlaini Gosliner and Behrens, 1997 (Figs. 14E, 16B, 17)

Nembrotha chamberlaini Gosliner and Behrens, 1997: 292, figs. 1B,C; 4A,B; 5; 6A-D.

Material examined. CASIZ 107227, holotype, Kirby's Rock, Maricaban Island, off Batangas, Luzon, Philippines, 18/02/92, 10-25 m depth, collected by T. M. Gosliner. CASIZ 110377, Caban Island, Batangas Province, Luzon, Philippines, 19/04/97, two specimens 50 mm preserved, dissected, collected by G.C. Williams. CASIZ 96300, Bohol, Balcasag Island, Philippines, 21/03/94, one specimen 40 mm preserved, dissected, collected by M. Miller. CASIZ 156940, "Sepok Wall", Maricaban Island, Batangas Province, Luzon, Philippines, 12/05/01, three specimens 45-50 mm preserved, one dissected, collected by T.M. Gosliner. CASIZ 157148, Balayan Bay, Batangas Province, Luzon, Philippines, 09/05/01, one specimen 50 mm preserved, 15 m depth, collected by T.M. Gosliner. CASIZ 158812, Eagle Point, Batangas Province, Luzon, Philippines, 05/05/01, two specimens, 20 m depth, collected by Y. Vallés and S. Fahey. MNCN 15.05/46727, "Paliton Wall", Siguijor Island, Philippines, 02/03/03, one specimen 71 mm alive, dissected, 12 m depth, collected by E. Köhler. MNCN 15.05/46728, "Paliton Wall", Siguijor Island, Philippines, 02/03/03, one specimen 72 mm alive, dissected, 11 m depth, collected by E. Köhler. WAM S11566, "Paliton Wall", Siguijor Island, Philippines, 02/03/03, one specimen 52 mm alive, 14 m depth, collected by E. Köhler.

External and internal morphology. The external and internal anatomy of this species is described in detail and figured by Gosliner and Behrens (1997). The specimens described for the present study matched their description and thus there is no ad-

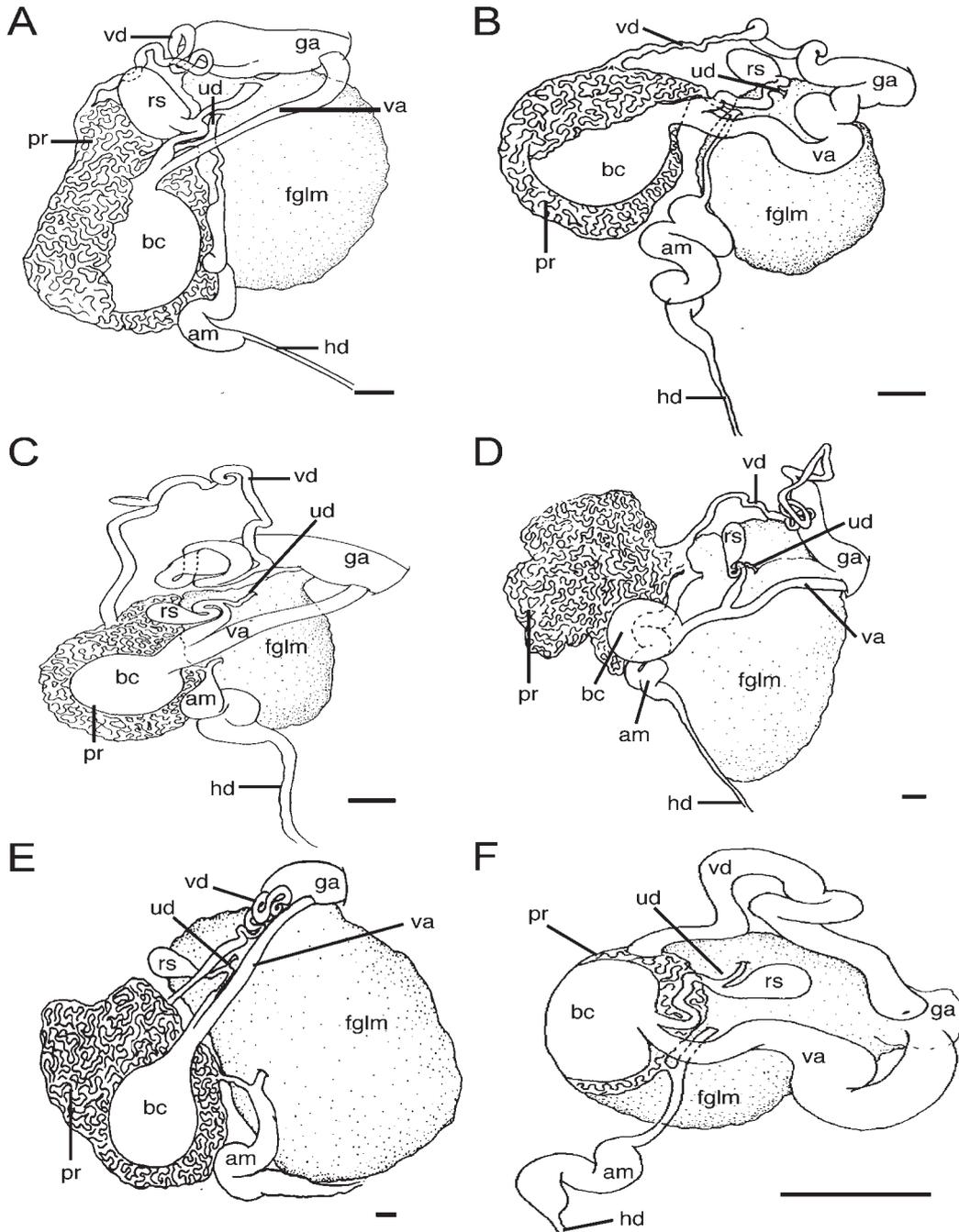


FIG. 16. – Drawings of reproductive systems of *Nembrotha* spp.: A, *N. yonowae* (C. MNCN 15.05/46719); B, *N. chamberlaini* (MNCN 15.05/46727); C, *N. milleri* (MNCN 15.05/46721); D, *N. mullineri* (MNCN 15.05/46723); E, *N. rosannulata* n. sp. (SAM D19354); F, *N. aurea* n. sp. (MHN-PARIS). Scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fglm, female gland mass; ga, genital atrium; hd, hermaphrodite duct; pr, prostate; rs, receptaculum seminis, ud, uterine duct; va, vagina; vd, vas deferens.

ditional information to present. The radular formulae of our specimens are: 50 mm specimens, 33-37 x 9.1.1.1.9 (CASIZ 110377), 71-72 mm specimens, 30-31 x 8-9.1.1.1.8-9 (MNCN 15.05/46727, MNCN 15.05/46728), 47 mm specimen, 32 x 8.1.1.1.8 (CASIZ 156940) and 40 mm specimen (preserved), 27 x 9.1.1.1.9 (CASIZ 96300). Usually, the two inner denticles of the right half of the rachidian may re-

present a single bifurcate denticle that is united only at the base (Fig. 17A) but in the 71 mm specimen the right two denticles are united while those on the left remain separated (Fig. 17B). The innermost lateral is large and hooked with two cusps. The upper cusp is elongate, sharp and larger than the basal triangular cusp. No other denticles are present, with the exception of one specimen (MNCN 15.05/46727), in

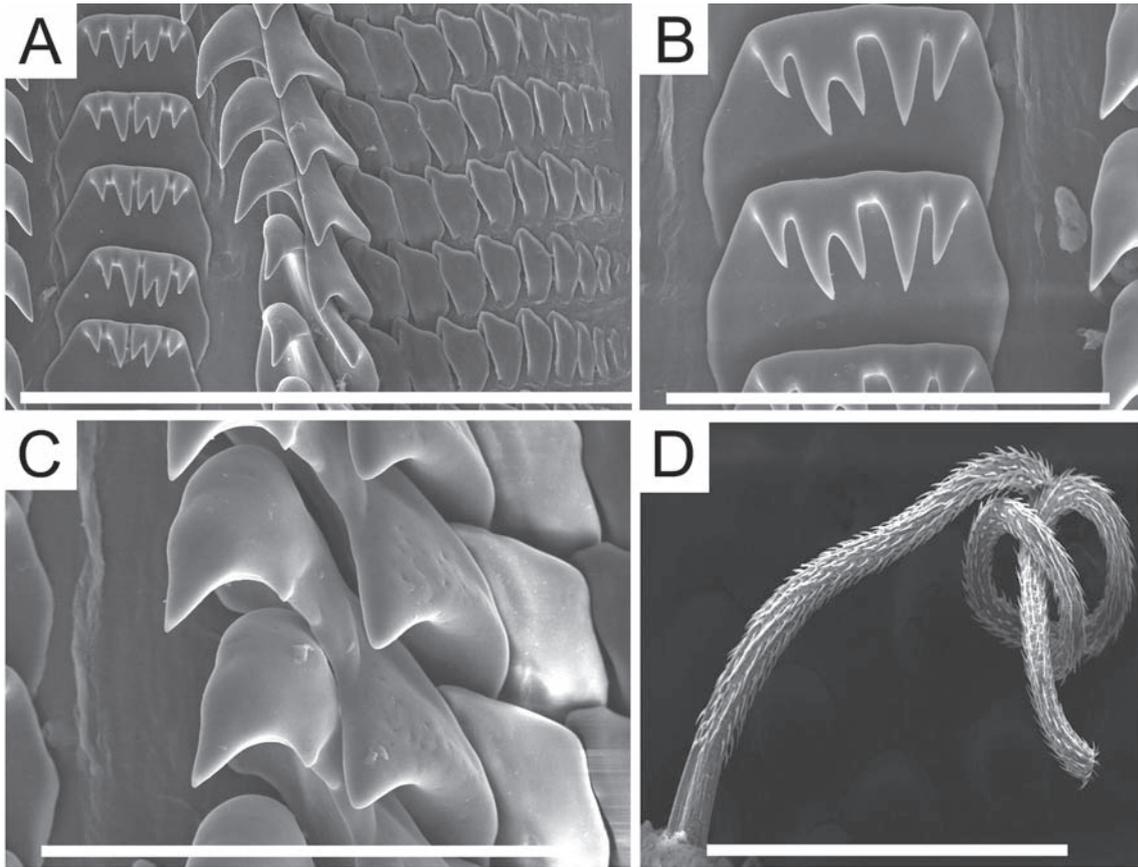


FIG. 17. – Scanning electron micrographs of *Nembrotha chamberlaini* Gosliner and Behrens, 1997: A, right half-row of radular teeth (CASIZ 096300, scale bar: 500 µm); B, rachidian teeth (MNCN 15.05/46727, scale bar: 200 µm); C, innermost lateral teeth (MNCN 15.05/46728, scale bar: 200 µm); D, penis (MNCN 15.05/46727, scale bar: 500 µm).

which a small secondary upper denticle is present (Fig. 17C). The penis is armed with numerous similar curved-chitinous hooks arranged in helicoidal lines. The base of the penis lacks penial spines (Fig. 17D). See Figs. 14E, 16B for pictures of the living animal and reproductive system, respectively.

Remarks. *N. chamberlaini* Gosliner and Behrens, 1997 is another very similar colour form of *N. purpureolineata*, *N. lineolata* and *N. megalocera*, originally described from the Philippines and Okinawa but also present in Indonesia. The authors provided a complete description of this species based on three specimens but with a single specimen examined and also figured the variation in distribution of colour pattern. In the remarks section for *N. chamberlaini* a comparison is made with *N. lineolata*, *N. purpureolineata*, *N. rutilans* and *N. megalocera* and the only consistent difference noted by the authors is the rhizophores and gill leaves having uniform red pigment throughout. The authors also stated that the rachidian teeth of *N. chamberlaini* and *N. purpureolineata*

are broader near the middle, while in *N. lineolata* and *N. megalocera* the rachidian teeth are broadest basally. However, since the number of specimens examined in the present study is higher than in all original descriptions, we can confirm that most of the specimens of *N. lineolata* and *N. megalocera* examined also have rachidian teeth broader near the middle and thus it is not an informative character. Regarding the reproductive system, there are no significant differences between *N. megalocera*, *N. lineolata*, *N. purpureolineata* and *N. chamberlaini*. All these species have a penis without penial spines at the base followed by numerous rows of hooked penial spines. The number of rows is very difficult to determine since it is necessary for the penis to be completely extruded. Our specimens perfectly match those described by Gosliner and Behrens (1997). *N. chamberlaini* is common at shallow depths, and Gosliner and Behrens (1997) reported it feeding on the tunicates *Rhopalaea* sp., *Clavelina moluccensis* and *Oxycorynia fascicularis*. Nice pictures of this beautiful species are shown in (<http://www.seaslugforum>).

net/factsheet.cfm?base=nembcham; http://www.medslugs.de/Opi/Nembrotha_chamberlaini.htm.

Figure 14F shows a photograph of one specimen (not collected) from the Philippines, which is very similar to *N. chamberlaini* and *N. purpureolineata* but with a different colour pattern. *Nembrotha chamberlaini*, *N. purpureolineata*, *N. lineolata* and *N. megalocera* are members of the so-called “lined” species of *Nembrotha* according to the phylogenetic analysis conducted by Pola *et al.* (2007). Thus, the relationships in this clade based on morphological characters are not resolved. However, molecular data clearly distinguished between these different species. For this reason, we cannot assign the uncollected specimen of Figure 14F to any of the species of the “lined” *Nembrotha* clade since it was not examined for molecular study.

Geographic range. Thus far this species is known from the Philippines (Gosliner and Behrens, 1997; Debelius, 1996; Debelius and Kuitert, 2007; present study), Okinawa (Okutani, 1994; Gosliner and Behrens, 1997) and Indonesia (Tonozuka, 2003; Debelius and Kuitert, 2007). Other pictures of this species are available from <http://www.seaslugforum.net/factsheet.cfm?base=nembcham>.

***Nembrotha milleri* Gosliner and Behrens, 1997**
(Figs. 14G, 16C, 18)

Nembrotha milleri Gosliner and Behrens, 1997: 296, figs. 7A, 8A,B, 9A-D.

Material examined. CASIZ 096302, Paratype, Black Forest, Balcasag Island, off Bohol, Philippines, 22/03/1994, one specimen 55 mm preserved, dissected, 29 m depth, collected by G.C. Williams. MNCN 15.05/46720, Malapascua Island, “Gato Cave”, Philippines, 24/02/2003, one specimen 78 mm alive, dissected, 23 m depth, collected by E. Köhler. MNCN 15.05/46721, Lipayo, “El Dorado Housereef”, Negros Oriental, Philippines, 04/03/2003, one specimen 85 mm alive, 12 m depth, collected by E. Köhler. AM C205319, Lipayo, “El Dorado Housereef”, Negros Oriental, Philippines, 06/05/2003, one specimen 112 mm alive, dissected, 9 m depth, collected by E. Köhler. AM C205320, Aka Island, Kerama Island, Okinawa, Japan, 10/07/2003, one specimen 30 mm preserved, collected by A. Ono. WAM S11558, Southwest of Wooded Island, Houtmans Abrolhos Islands, Western Australia, 21/07/2004, one specimen 90 mm alive, 6 m depth, collected by M. Pola. WAM S11559, north of Suomi Island, Houtmans Abrolhos Islands, Western Australia, 24/07/2004, two specimens 100 and 120 mm alive, one dissected, 28 m depth, collected by M. Pola.

External morphology. Gosliner and Behrens (1997) provided a complete description of the external anatomy of this species. The specimens examined for the present study matched their descriptions and there is no additional information presented. See Figure 14G for a photo of a living animal from the Philippines.

Anatomy. *Nembrotha milleri* shares the same general digestive anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a large and long oral tube that continues into the buccal mass. Both are almost similar in size. There is a pair of large and wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown corrugated chitinous disk, but without any armature or rodlets. The radular formulae are: 55 mm specimen, 30 x 10.1.1.1.10 (CASIZ 096302), 78 mm specimen, 26 x 10.1.1.1.10 (MNCN 15.05/46720), 85 mm specimen, 30 x 10.1.1.1.10 (MNCN 15.05/46721), 112 mm specimen, 30 x 10.1.1.1.10 (AM C205319), 30 mm specimen (preserved), 27 x 11.1.1.1.11 (AM C205320), and 120 mm specimen, 35 x 14.1.1.1.11 (WAM S11559) (Figs. 18A-D). The rachidian teeth are broad, variable in shape, usually with five asymmetrically arranged triangular denticles. The two outermost denticles are a bit smaller than the inner ones. Usually, two of the inner denticles are joined at the base but the arrangement of these denticles may vary from the right to the left side (Figs. 18A-D). In one of the dissected specimens (MNCN 15.05/46720), there are only four symmetrical denticles (Fig. 18B). The inner laterals are larger than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a shorter more basal one. The three inner outer laterals bear large cusps of decreasing size, while the remaining laterals are rectangular without cusps (Fig. 18A). There is a large blood gland located in between the intestinal loop. A cup-shaped renal syrinx is present under the pericardium, close to the anal papilla. An elongate and muscularised ventriculum is present but not visible under the thick pericardium.

The reproductive system is triaulic (Fig. 16C). The hermaphroditic duct is relatively long and narrow. It expands into an elongate and slightly convoluted ampulla. The prostatic portion of the vas deferens is very large. The distal end of the prostatic mass connects to an elongate and highly convoluted vas deferens. The distal end of the vas deferens widens into a muscular ejaculatory portion. The penis is armed with numerous penial spines. They can be distinguished into three different kinds of spines arranged in longitudinal lines (Figs. 18E,F). The short uterine duct emerges from the female gland and joins the pyriform seminal receptacle via a short and curved duct and continues proximally until it widens, joining with the vagina. Together they enter the rounded, thin-walled bursa copulatrix, which, in

situ, is entirely surrounded by the prostate. The elongate, wide and straight vagina also emerges from the base of the bursa and shares a common base with the uterine duct.

Remarks. The specimens we examined of *N. milleri* closely match the description of Gosliner and Behrens (1997). However, the rachidian teeth and the penial spines of the animals we examined differed

slightly from Gosliner and Behrens's description. Gosliner and Behrens (1997) described four denticles on the rachidian teeth but this is probably an aberration rather than a diagnostic feature, since within the specimens examined in this study only one specimen had four denticles instead of the typical five (Fig. 18B). In their study, the penial spines also differ from those of our specimens. It appears that in the single specimen dissected by the authors the pe-

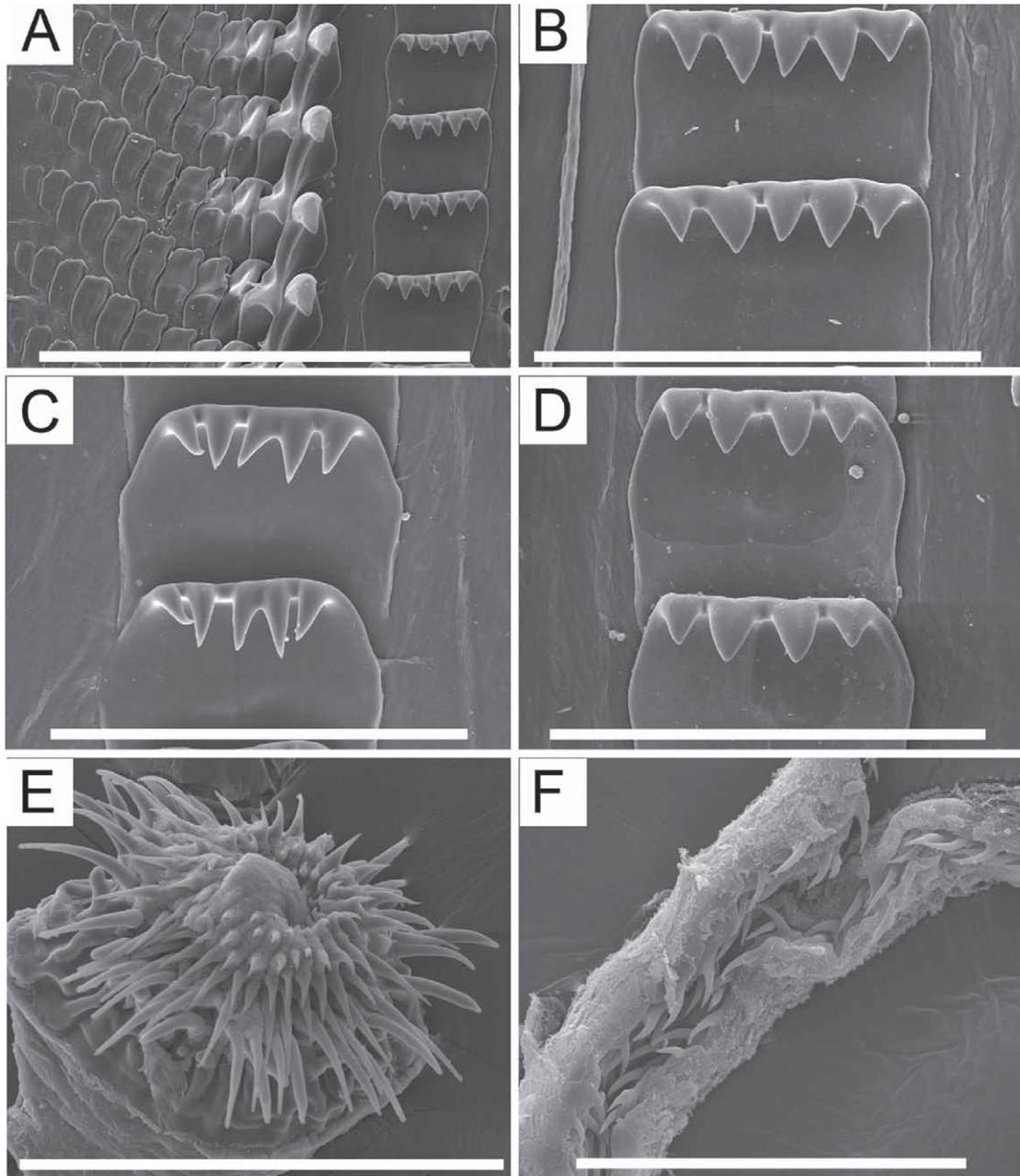


FIG. 18. – Scanning electron micrographs of *Nembrotha milleri* Gosliner and Behrens, 1997: A, left half-row of radular teeth (MNCN 15.05/46721, scale bar: 1 mm); B, rachidian teeth (CASIZ 096302, scale bar: 500 μ m); C, rachidian teeth (AM C205320, scale bar: 300 μ m); D, rachidian teeth (MNCN 15.05/46720, scale bar: 400 μ m); E, first and second types of penial spines (WAM S11559, scale bar: 300 μ m); F, distal penial spines (MNCN 15.05/46720, scale bar: 200 μ m).

nis was not completely extended, so they described only two types of penial spines. However, the penis of our specimens is armed with three different types of spine: the basal ones elongated and curved; the ones immediately distal to them short and curved; and the distal ones medium-sized and about twice the length of the shortest ones. *Nembrotha milleri* is clearly distinguishable from the other species of the genus by its robust, wrinkled green body. *N. kubaryana* and *N. cristata* also have green pigmentation on the body but it is found on large rounded tubercles, which are absent in *N. milleri*.

Geographic range. Originally described from the Philippines and Indonesia (Gosliner and Behrens, 1997), this species is also known from Norfolk Island (Coleman, 2001), Western Australia (Coleman, 2001; present study), Kerama and the Ryukyu Islands (Ono, 1999; 2004; present study) and Tanzania (Debelius and Kuitert, 2007).

***Nembrotha mullineri* Gosliner and Behrens, 1997**
(Figs. 14H, 16D, 19)

Nembrotha mullineri Gosliner and Behrens, 1997: 300, figs. 7B, 10A,B, 11A-D.

Material examined. CASIZ 103724, paratype, Hamilo, Batangas Province, Luzon, Philippines, 04/03/1995, one specimen 38 mm preserved, dissected, 10 m depth, collected by T. M. Gosliner. CASIZ 106508, paratypes, Sepok Point, Maricaban Island, Batangas Province Luzon, Philippines, 16/04/1996, two specimens 60 mm preserved, one dissected, 12 m depth, collected by M. Miller and J. Allen. CASIZ 158269, Layaglayag Point, Maricaban Island, Batangas Province, Luzon, Philippines, 08/05/2001, one specimen 85 mm preserved, dissected, collected by T. M. Gosliner. MNCN 15.05/46722, Sarah's Place, Lipayo, Negros Oriental, Philippines, 07/03/2003, one specimen 71 mm alive, 18 m depth, collected by E. Köhler. MNCN 15.05/46723, Lapus-Lapus, Malapascua Island, Philippines, 21/03/2003, one specimen 98 mm alive, dissected, 17 m depth, collected by E. Köhler. AM C205321, 'Gato-Cave', Malapascua Island, Philippines, 22/03/2003, one specimen 113 mm alive, dissected, 16 m depth, collected by E. Köhler. WAM S11560, north of Suomi Island, Houtmans Abrolhos Islands, Western Australia, 24/07/2004, one specimen 130 mm alive, 28 m depth, collected by M. Knapp and M. Pola.

External morphology. Gosliner and Behrens (1997) provided a complete description of the external anatomy of this species. The specimens examined for the present study matched their descriptions and thus there is no additional information to present. See Fig. 14H for photo of living animal from the Philippines.

Anatomy. *Nembrotha mullineri* shares the same general digestive anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with

a large and muscular oral tube that continues into the buccal mass. The buccal mass is larger than the oral tube. There is a pair of large and wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown corrugated chitinous disk, but without any armature or rodlets. The radular formulae are: 38 and 60 mm specimen (preserved), 27-29 x 11-10.1.1.1.10-11 (CASIZ 103724; CASIZ 106508), 85 mm specimen (preserved), 32 x 11.1.1.1.11 (CASIZ 158269), 98 mm specimen, 25 x 11-10.1.1.1.10-11 (MNCN 15.05/46723) and 113 mm specimen, 29 x 11-10.1.1.1.10-11 (AM C205321) (Fig. 19A). The rachidian teeth are broad and variable in shape, with five asymmetrically arranged triangular denticles. The two outermost denticles might be a bit smaller than the inner ones. Usually, the two inner denticles of the right side are joined at the base (Figs. 19A-D). The inner lateral teeth are elongate and larger than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a shorter more basal one. The three inner outer laterals bear large cusps of decreasing size, while the remaining laterals are rectangular without cusps (Fig. 19A). There is a large blood gland located in between the intestinal loop. A cup-shaped renal syrinx is present under the pericardium, close to the anal papilla. An elongate and muscularised ventriculum is present but not visible under the thick pericardium.

The reproductive system is triaulic (Fig. 16D). The hermaphroditic duct is relatively long and narrow. It expands into an elongate and highly convoluted ampulla. The prostatic portion of the vas deferens is very large. The distal end of the prostatic mass connects to an elongate and highly convoluted vas deferens. The distal end of the vas deferens widens into a muscular ejaculatory portion. The penis is armed with numerous penial spines, which can be distinguished into three different kinds of spines arranged in longitudinal lines (Figs. 19E,F). The uterine duct emerges from the female gland and joins the pyriform seminal receptacle via a short, curved duct and continues proximally until it widens, joining with the vagina. Together they enter the rounded, thin-walled bursa copulatrix, which, in situ, is entirely surrounded by the prostate. The elongate, wide and straight vagina also emerges from the base of the bursa and shares a common base with the uterine duct.

Remarks. *Nembrotha mullineri* is distinctive as it is the only member of the genus with a cream-coloured body with brown spots and blotches. The

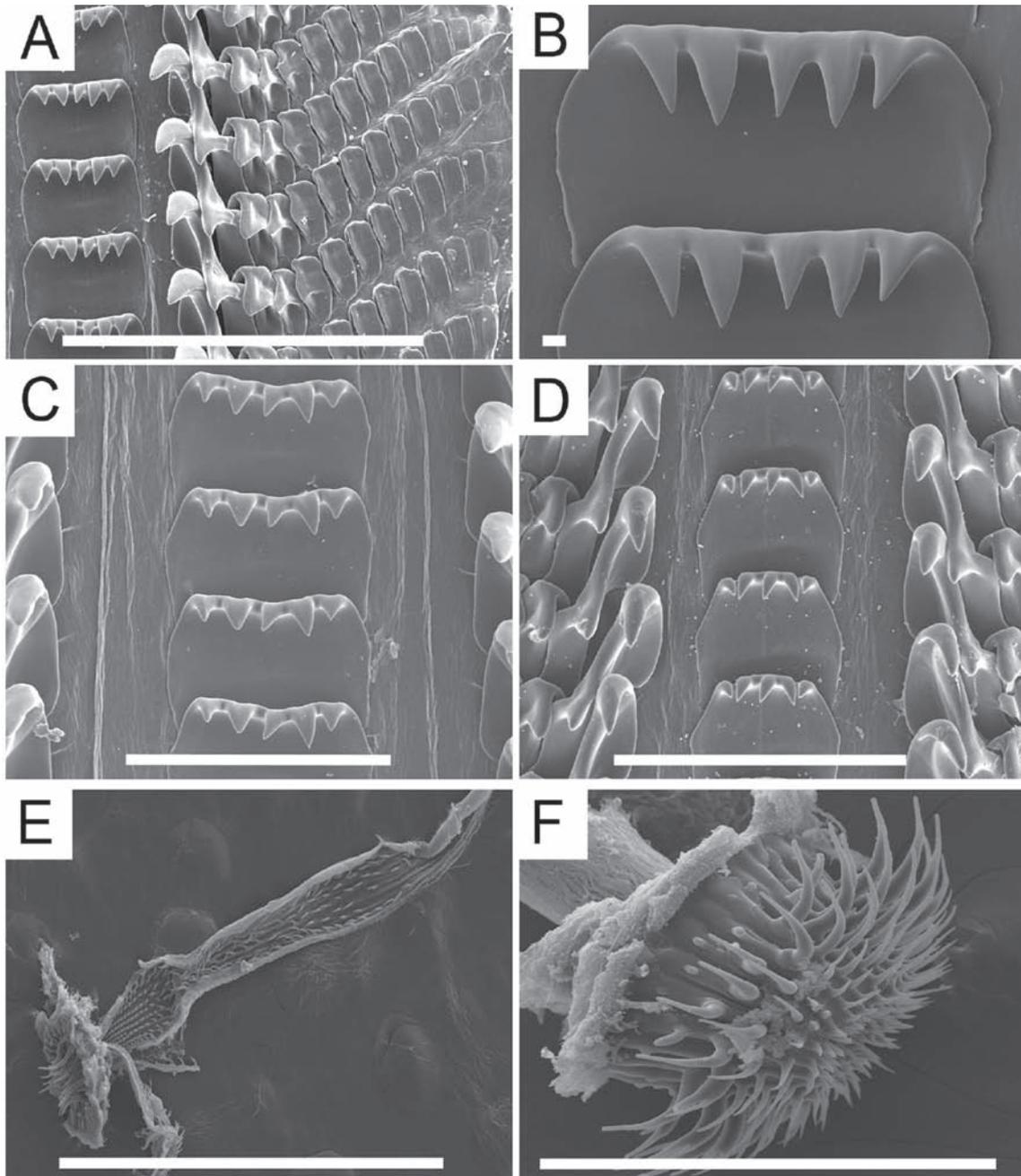


FIG. 19. – Scanning electron micrographs of *Nembrotha mullineri* Gosliner and Behrens, 1997: A, left half-row of radular teeth (CASIZ 103724, scale bar: 500 µm); B, rachidian teeth (CASIZ 106508, scale bar: 20 µm); C, rachidian teeth (CASIZ 103724, scale bar: 500 µm); D, rachidian teeth (MNCN 15.05/46723, scale bar: 500 µm); E, penis (AM C205321, scale bar: 1 mm); F, basal penial spines (CASIZ 103724, scale bar: 300 µm).

extent of brown colouration is quite variable from specimen to specimen: from a simple series of spots and lines to dense patches of brown. The specimens of *N. mullineri* we examined closely match the description of Gosliner and Behrens (1997). However, Gosliner and Behrens (1997) described *N. mullineri* as “unique among described members of the genus in having an arched masticatory margin without distinctly separated denticles”, while our specimens

have the rachidian teeth very similar to the remaining species of the genus, with five asymmetrically denticles on the masticatory margin. Since Gosliner and Behrens only dissected one specimen from their type material, and we have dissected more specimens including two paratypes, we conclude that the rachidian teeth described by these authors were just an aberration of that specimen. Regarding the penial spines, they are very similar to that of *N. cristata*, *N.*

guttata and *N. milleri* but the number and distribution of the penial spines is difficult to determine with precision because they are dependent on the degree of extension of the penis when they were preserved.

Geographic range. Originally described from the Philippines (Gosliner and Behrens, 1997), this species is also known from Indonesia (Tonozuka, 2003), Vietnam (Debelius and Kuitert, 2007), Eastern Australia (Ellis, 1999) and Western Australia (present study).

***Nembrotha rosannulata* n. sp.**
(Figs. 20A-D, 16E, 21)

Material examined. Holotype: SAM D19353, adult specimen, 60 mm preserved, Cabbage Tree Island, Port Stephens, New South Wales, 8 m depth, collected by N. Wilson, 08 May 2004. Paratype: SAM D19354, one adult specimen, 55 mm preserved, Cabbage Tree Island, Port Stephens, New South Wales, 8 m depth, collected by N. Wilson, 08 May 2004.

Etymology. The specific name refers to the large pink rings.

External morphology. The body is elongate and limaciform but robust and widest at the level of the gill circle (Figs. 20A-D). The posterior end of the foot is long and pointed. The head is rounded. The preserved animals are 55-60 mm long. The living animals are large, reaching up to 120 mm. The body wall is highly muscularised. The entire body surface is textured with a pattern of longitudinal wrinkles and with large disconnected blunt tubercles arranged on the notum and on both sides of the body. The tubercles extending around the head suggest a wide mantle margin. The margin may continue as a broken series of tubercles along the edge of the mantle until the end of the foot. Dorsally, from the anterior margin to the base of the gill branches, there are usually three large tubercles. On both sides of the body there are a variable number of similar scattered tubercles. The number and the arrangement of these protruding structures vary in different individuals (Figs. 20A-D). There is a pair of large and conical, perfoliate rhinophores, bearing around 35 lamellae. The rhinophores are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are circular in shape with a depression at the centre of each. The two posterior gill branches on each side have a common base. The genital aperture is located on the right side, midway between the gill and the rhinophores.

The ground colour is olive green (Figs. 20A-D). The tubercles are black bordered with wide circular rings of pink colour. The anterior edge of the notum is pink with some black spots. The outer rachis of each gill branch (except the base), the subapical area of the rhinophoral sheaths and the base of the oral tentacles are also pink. The rhinophores and the pinnae are black, the same colour as the centre of the tubercles, the tip of the rhinophoral sheaths and the tip of the oral tentacles. The foot is blue or purple. The rings on the larger adults are generally fluorescent bright pink, while the rings on the juveniles tend to be bright orange in colour (Harasti, pers. comm., Fig. 20D).

Anatomy. *Nembrotha rosannulata* shares the same general digestive anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long muscular oral tube that continues into the buccal mass. The buccal mass is nearly the same size as the oral tube. A pair of elongate, wide granular salivary glands connects to the buccal bulb at both sides of the oesophageal junction. The chitinous labial cuticle is corrugated but without any armature or rodlets. The radular formula of the 55 mm specimen (preserved) is 30 x 9.1.1.1.9 (Fig. 21A). The rachidian teeth are broad and quadrangular with five triangular denticles of the same size (Fig. 21B). The inner laterals are larger and longer than the outer ones with a rectangular base and two cusps, an elongate terminal cusp and a slightly shorter more basal one. The second and third laterals bear large cusps of decreasing size, while the remaining laterals are rectangular without cusps (Fig. 21A). There is a very large blood gland located above the dorsal surface on the oesophagus. A cup-shaped renal syrinx is present under the pericardium, close to the anal papilla. An elongate and muscularised ventriculum is present but not visible under the pericardium.

The reproductive system is triaulic (Fig. 16E). The hermaphroditic duct is short and wide. The ampulla is large and convoluted. It branches into a short oviduct and the prostate. The oviduct enters the massive female glands, which in the specimen dissected is very well developed. The prostatic segment of the vas deferens consists of a large, wide portion, which has a dense network of interconnecting tubules over its surface. It connects to an elongate straight section followed by a long, narrow and highly convoluted ejaculatory segment, which opens into a common atrium with the vagina and the female gland. The penis is located in the latter portion. The chitinous

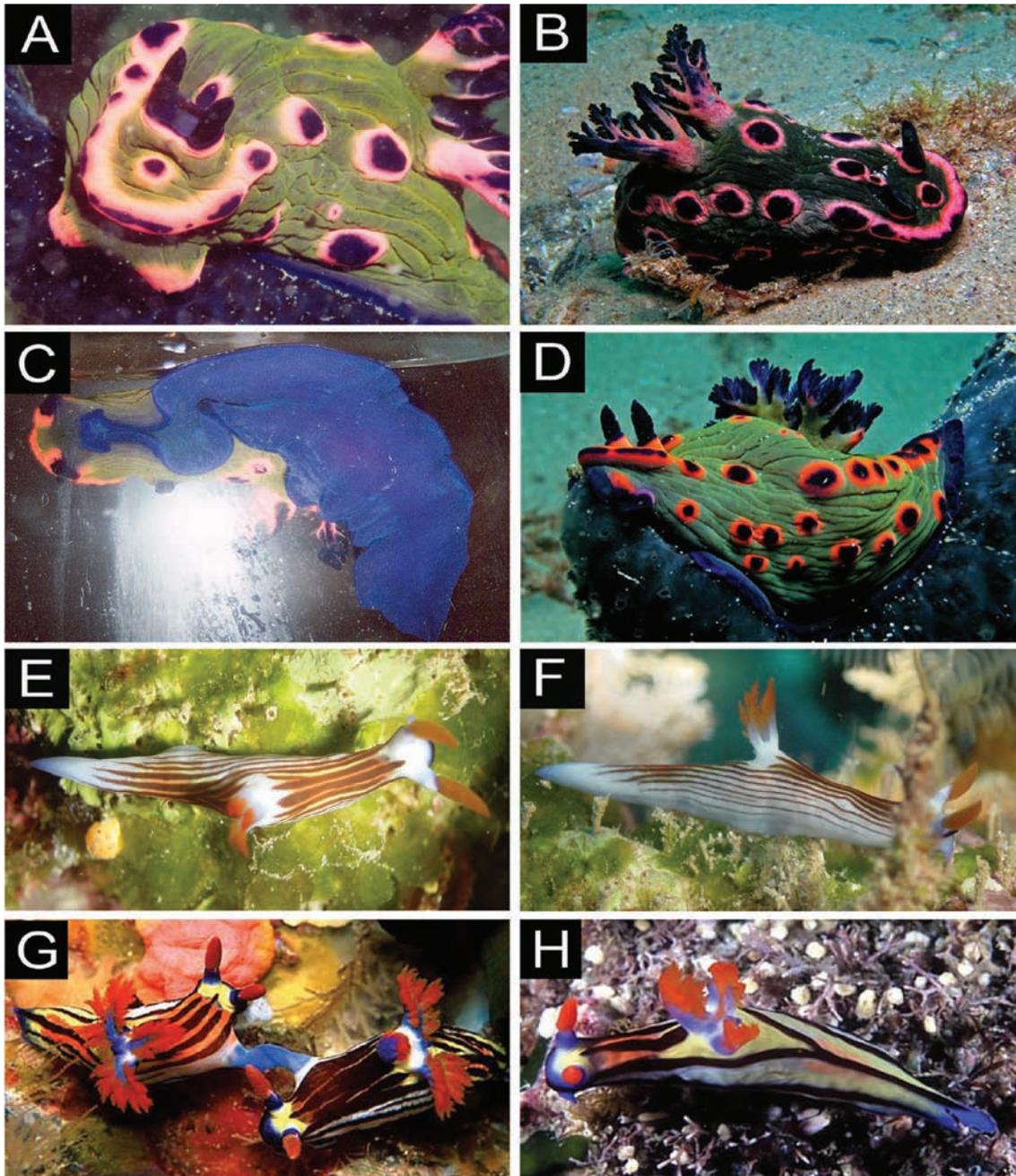


FIG. 20. – A-D, *Nembrotha rosannulata* n. sp. living animals, specimens from Port Stephens, New South Wales: A, C, photos by David and Leanne Atkinson (SAM D19354); B, D, photos by David Harasti. E-H, *Nembrotha aurea* n. sp. living animals: E-F, specimens from Comoros, photos by Marina Poddubetskaia (MNHN-Paris); G, specimen from Indonesia, photo by Ken Knezick - Island Dreams; H, specimen from Japan, photo by Yasuhiro Shirai.

penial spines are numerous and arranged in longitudinal lines (Figs. 16C-F). It appears that there are at least two kinds of penial spines. The spines at the base of the penis are smaller and more hooked than the distal ones (Fig. 16C-F), increasing their size gradually along the penis. The vagina is long, wide and straight. At its proximal end, the vagina connects to the large and rounded bursa copulatrix. From the bursa copulatrix leads another duct connecting to the

seminal receptacle and the uterine duct. This duct is initially of the same diameter as the vagina but narrows about half way to the uterine duct. The seminal receptacle is pyriform and smaller in size than the bursa copulatrix. There is no accessory gland. In situ, the bursa is totally surrounded by the prostate.

Remarks. In a recent publication (Delbelius and Kuitert, 2007, p. 59) a species is identified by the name

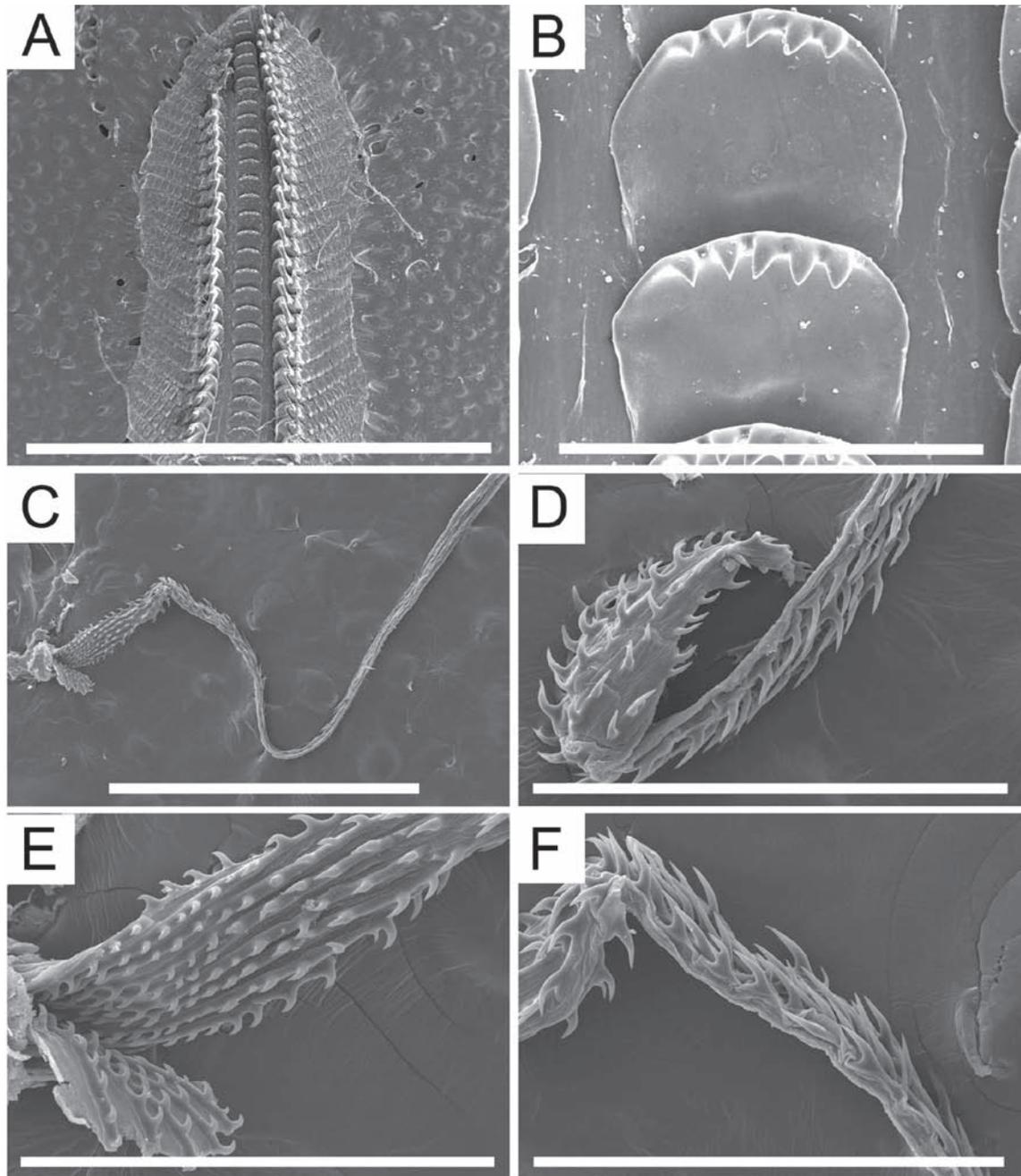


FIG. 21. – Scanning electron micrographs of *Nembrotha rosannulata* n. sp. paratype (SAM D19354): A, radula, scale bar: 5 mm; B, rachidian teeth, scale bar: 500 µm; C, general view of the penis, scale bar: 1 mm; D, base of the penis, scale bar: 400 µm; E, detail of the first type of penial spines, scale bar: 300 µm; F, second type of penial spines, scale bar: 400 µm.

Nembrotha rosannulata Pola, 2006. That name was inadvertently used because the authors did not follow the advice of reviewers that this was a species manuscript name that was still unpublished. Thus, Debelius and Kuitert introduced a *nomen nudum* and the name is not available in accordance with the International Code of Zoological Nomenclature (ICZN art. 16.1 and 16.4). The formal name should be *Nembrotha rosannulata* Pola, Cervera and Gosliner, 2008.

Prior to the publication of Debelius and Kuitert's book (2007), this species has been commonly referred to as "Donut *Nembrotha*" because of the large pink rings that look like donuts on their body. This feature makes it distinctly different from any other species of the genus and it is actually considered "naturally rare" in New South Wales (Harasti, pers. comm.). *Nembrotha rosannulata* and *N. milleri* are both robust species, which have green ground colour.

However, *N. milleri* lacks the large pink rings and its penis has three different types of penial spines, while in *N. rosannulata* there appear to be only two kinds. *Nembrotha kubaryana* and *N. livingstonei* also have only two different kinds of penial spines but they are easily distinguishable from *N. rosannulata* by the external colouration.

Geographic range. Thus far this species is known only from New South Wales, Australia (present study, Coleman, 2001) and from the Great Barrier Reef (www.daveharasti.com/articles/speciesspotlight/donutnembrotha.htm, [www.scuba-equipment-usa.com/marine/JAN05/Donut_Nembrotha\(Nembrotha_sp\).html](http://www.scuba-equipment-usa.com/marine/JAN05/Donut_Nembrotha(Nembrotha_sp).html)).

***Nembrotha aurea* n. sp.**
(Figs. 20E-H 16F, 22)

Material examined. Holotype: CASIZ 099294, Msimbati, Mtwara Region, Tanzania, 01/11/1994, one specimen, 30 m depth max. collected by T.M. Gosliner. Paratypes: MNHN-Paris, Passe en S. bouée 8 bis, Mayotte, Comoros, 04/11/03, one specimen 20 mm alive, dissected, 20.5 m depth, collected by M. Poddubetskaia. MNHN-Paris, Passe en S. bouée 7 bis, Mayotte, Comoros, 04/11/03, one specimen 20 mm alive, dissected, 19 m depth, collected by M. Poddubetskaia. MNHN-Paris, Passe Brandélé, Mayotte, Comoros, 11/11/03, one specimen 25 mm alive, dissected, 19 m depth, collected by M. Poddubetskaia. CAS176987, North Point, Two mile reef, between Benguera and Bazaruto Islands, Bazaruto archipelago, Vilanculos, Mozambique, 27/01/07, one specimen 20 mm alive, 20 m depth max. collected by M. Pola and J. Reis. CAS177008, Batfish Pinnacle, Jangamo Reef, Inhambane, Mozambique, 06/01/07, one specimen 40 mm alive, 19.1 m depth max. collected by M. Pola and J. Reis. CAS177009, Batfish Pinnacle, Jangamo Reef, Inhambane, Mozambique, 06/01/07, one specimen 20 mm alive, 19.1 m depth max. collected by M. Pola and J. Reis.

Etymology. The specific name refers to the beautiful golden colour ornamenting the dorsal surface of the animal. From latin: “aureus” = golden (having the colour of gold; highly ornamented).

External morphology. The body is elongate and limaciform, reaching up to 55 mm in length in living adults (Figs. 20E-F). The posterior end of the foot is long and pointed. The head is rounded. The body surface is corrugated. The dorsum continues to the side of the body without a line of demarcation or pallial edge. Externally the animals are characterised by the presence of longitudinal stripes and large patches of bright colouration. Usually, the stripes are arranged as follows: one strong stripe on the mid-dorsal line between the rhinophores and the gill and two shorter ones of the same width on each side of the middle stripe; a thinner stripe round at the margin of the mantle, and back on each side of the notum.

Behind the gill, these two lines converge and meet to form a single line, about halfway between the gill and the posterior end, which runs back to the end of the foot. Thus, there are three to seven longitudinal lines on each side of the body (Figs. 20E-F). There is a pair of large conical, perfoliate rhinophores that bear around 30 lamellae and are completely retractile into their elongate rhinophoral sheaths. The oral tentacles are thick and elongate with a depression at the centre of each one. There are three large multipinnate, non-retractile branchial leaves. The anus is mid-dorsal, located in the centre of the branchial circle on an elevated, elongate papilla. The genital pore opens on the right side, midway between the rhinophores and the anterior portion of the gill.

The ground colour of the body is white. The stripes are brown in colour. A large orange yellow patch is present in the middle on the back and in the midlength of the posterior end of the foot (Figs. 20E-F). The oral tentacles and the margin of the foot are delineated by a blue to purple band. The rhinophores are red. The rhinophoral sheaths are white bordered with light blue to purple according to specimens. The branchial leaves are red. The rachis of each gill and the base of the gill are also light blue or purple. It is also possible to find specimens without a trace of blue or purple colour on the rhinophoral sheaths or the gill. The sole is colourless.

Anatomy. *Nembrotha aurea* shares the same general internal anatomy as other *Nembrotha* species (Fig. 2). The anterior digestive tract begins with a long, thin muscular oral tube that continues into the buccal mass. The buccal mass is smaller than the oral tube. There is a pair of large, wide salivary glands on the buccal mass, flanking the oesophagus. The labial cuticle forms a brown corrugated chitinous disk, devoid of rodlets but with a central and two lateral areas. The radular formulae of the paratypes are: 20 mm specimens, 21 x 6.1.1.1.6 and 23 x 7-6.1.1.1.6-7 (MNHN-Paris), 25 mm specimen, 21 x 6.1.1.1.6 ((MNHN-Paris). The rachidian teeth are variable in shape (Figs. 22A-C). Usually, they are broad and hexagonal with the upper side narrower than the basal one. The masticatory margin has five triangular denticles, the two outer ones much smaller than the inner ones. The two inner denticles of the right side are distally joined. In one specimen, the two joined denticles were those of the left side and they were joined at the base. The inner laterals are well developed; they are large and strongly hooked

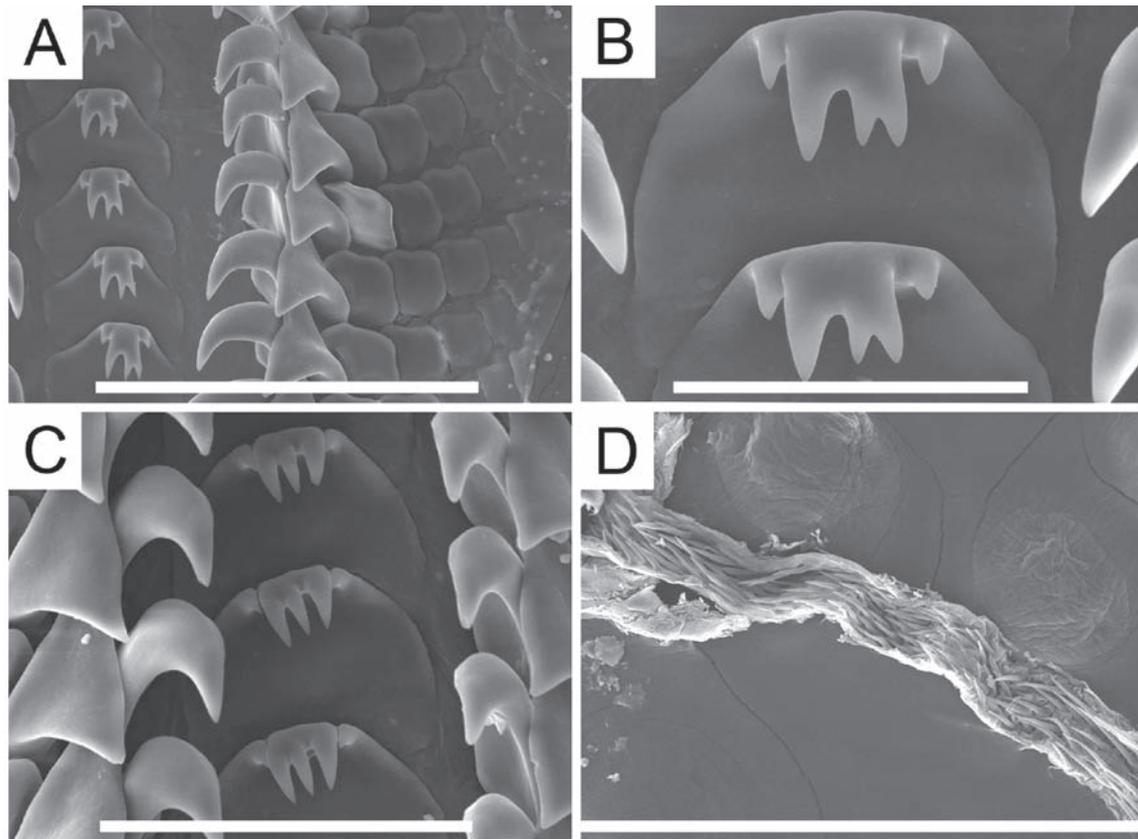


FIG. 22. – Scanning electron micrographs of *Nembrotha aurea* n. sp. (MNHN-Paris): A, right half-row of radular teeth, scale bar: 200 µm; B, rachidian teeth, scale bar: 50 µm; C, rachidian teeth, scale bar: 100 µm; D, penial spines, scale bar: 500 µm.

with two cusps. The outer lateral teeth are rectangular plates, from 6 to 7, which lack cusps or dentition and become smaller near the margin (Fig. 22A-C).

The reproductive system is triaulic (Fig. 16F). The hermaphroditic duct is elongate and wide. It expands into a very long and highly convoluted ampulla. The long straight postampullary duct branches into the prostatic portion of the vas deferens and the short oviduct that connects to the female glands. The prostatic portion of the vas deferens is very large and consists of a spherical mass, which appears as a dense network of interconnecting tubules entirely surrounding the bursa copulatrix. The distal end of the prostatic mass connects to an elongate, highly convoluted vas deferens. The vas deferens opens into a common atrium with the vagina but without a strongly differentiated muscular ejaculatory portion. The penis is armed with rows of curved, chitinous hooks except at the base. The chitinous penial spines are numerous and they are similar in size and shape (Fig. 22D). The vagina is very wide, long and convoluted. At its proximal end, the vagina connects to the rounded, thin-walled bursa copulatrix. In situ, the bursa copulatrix is entirely surrounded by the pros-

tate. In Figure 16F, the prostate is shown positioned to the side. From the bursa copulatrix leads another convoluted duct that connects to the pyriform seminal receptacle and the female glands via the uterine duct. The vagina is separated from the vas deferens along its entire length. There is no vaginal gland.

Remarks. *Nembrotha aurea* is described from South Africa, Tanzania, Mozambique and the Comoros Islands. This species is easily distinguishable from *N. lineolata* and *N. purpureolineata* by the large orange yellow patch over the middle of the back and the tail. The pattern of lines is also different from the latter species. The longitudinal stripes in *N. lineolata* are rather narrow and more numerous than in *N. aurea* while in *N. purpureolineata* there is only one broad stripe on the notum. The rachidian teeth of *N. purpureolineata* are broader than those of *N. aurea*, while the shape of the rachidian teeth of *N. lineolata* appears to vary from both extremes. There are no significant differences in the reproductive anatomy of these three species. The external and internal anatomy of our specimens is very similar to those of the specimens described by Baba (1976) from Japan

as *Nembrotha purpureolineata* O'Donoghue, 1924 (for a picture of a similar living animal see Nakano, 2004). The major difference between Baba's specimens and our examined material is the presence of only one strong stripe on the mid-dorsal line. Nevertheless, photographs of additional specimens from Japan (Suzuki, 2000), Indonesia (Debelius, 1996; Tonozuka, 2003) and Western Australia (Coleman, 2001) (Figs. 20G-H) show the same three strong stripes on the notum as *N. aurea*, but those specimens have fewer longitudinal lines on both sides of the body. Since we have not been able to examine any of those specimens and the geographical range is far away from the type of *N. aurea*, we cannot confirm that both Baba's (1976) specimens and the specimens in the above field guides are variant colour forms of *N. aurea*.

Geographic range. This species is described from South Africa, Tanzania, Mozambique and the Comoros Islands (present study; Gosliner, 1987; Fraser, 1999; King and Fraser, 2002; Debelius and Kuitert, 2007).

DISCUSSION

The genus *Nembrotha* is distributed throughout the tropical Indo-Pacific, from South Africa to Eastern Australia, but it is absent from other tropical areas in the Atlantic and the Eastern Pacific. Recently, Pola *et al.* (2005, 2006a,b) proposed several phylogenies of the genera *Roboastra* and *Tambja* based on both morphological and molecular data. These studies demonstrate that the genus *Roboastra* is monophyletic, based on morphological characters, while the genus *Tambja* appears to be paraphyletic no matter which traditional classification is chosen. In these studies only a few species of *Nembrotha* were included in the analysis, so a hypothesis about the relationships of *Nembrotha* and its origin was not proposed. Nevertheless, Pola *et al.* (2007) analysed the Phylogenetic relationships of Nembrothinae based on both morphological and molecular markers. In this case, the monophyly of the genus *Nembrotha* was recognised in all the analyses. Moreover, within *Nembrotha* two well-supported major clades were recovered.

There are several synapomorphies of *Nembrotha*, including the fact that they feed on tunicates, that the labial cuticle forms a brown corrugated weak chiti-

nous disk usually devoid of rodlets but with a central and two lateral areas, and that they have a very well differentiated prostate that completely surrounds the bursa copulatrix. Within *Nembrotha*, there appear to be two different groups of species that are easily distinguishable based on their external pattern. One group includes *N. nigerrima*, *N. cristata*, *N. yonowae*, *N. livingstonei*, *N. milleri*, *N. mullineri* and *N. rosannulata*, characterised by having large pustules or spots scattered on the body; and the other group includes *N. lineolata*, *N. purpureolineata*, *N. chamberlaini*, *N. megalocera* and *N. aurea*, characterised by having longitudinal lines or bands on the notum. Regarding the internal anatomy, the radular teeth and the reproductive system are very similar in all *Nembrotha* species. However, the "lined" group have a penis with only one type of penial spines, none of them at the base, while within the "spotted" group *N. cristata*, *N. yonowae*, *N. milleri* and *N. mullineri* appear to have two or three different types of penial spines. *Nembrotha nigerrima*, *N. livingstonei* and *N. rosannulata* only have two different types of penial spines, in all cases starting at the base of the penis. Other differences in the reproductive system between both groups of species are a convoluted ampulla and a straight vagina present in *N. nigerrima*, *N. cristata*, *N. yonowae*, *N. livingstonei*, *N. milleri*, *N. mullineri* and *N. rosannulata*, whereas *N. lineolata*, *N. purpureolineata*, *N. chamberlaini*, *N. megalocera* and *N. aurea* have a highly convoluted ampulla and a convoluted vagina.

Steps towards the synonymisation of some species of *Nembrotha* have been suggested by different authors (Eliot, 1904, 1906; Baba, 1976; Yonow, 1990; Yonow and Hayward, 1991). Rudman (1998-2005) shows that the colour pattern of *Nembrotha* species is extremely variable and also suggests that most of the species may be varieties of the same species, but insufficient anatomical evidence has been provided to demonstrate this proposal. The other interesting aspect is that some members of these complexes are sympatric, thus reducing the possibility that they are just geographical variants of a single species. Since the external variability within *Nembrotha* is very high and we have not been able to examine all different colour forms and intermediate states of each species, in this paper we have preferred to adopt a conservative point of view and thus to maintain most of the nominal species of the genus. Further anatomical and molecular studies, as well as studies of populations, need to be done in order to determine

whether most *Nembrotha* species are just varieties of two or more species.

ACKNOWLEDGEMENTS

The authors are very grateful to several individuals who provided the material for the study: E. Koehler, M. Poddubetskaia, A. Ono, N. Wilson, Y. Camacho, A. Valdés, S. Fahey, M. Schrödl, R. Willan, P. Fiene, C. Carlson, M. Ghiselin, D. Johnson, G. Williams, M. Miller, J. Allen, M. Knapp, B. Castillo, R. Van Syoc and M. Campbell, G. Williamson, M. Guido, C. Todt and G. Försterra. We are also very grateful to several photographers who allowed us to use their photos: David and Leanne Atkinson, Bernard Picton, Julie Marshall, John Chuk, Anthony Holley, Jeff Rosenfeld, Georg Heinze, Ken Knezick, Paul Osmond, Mary James Adams, Neil Miller, Jim Anderson and Jose Carlos García Gómez. We also thank Agustín Santos, Miriam Hampel and Michael Schrödl for their help in some aspects of the drafting of the manuscript, and Mr. Jose María Geraldía and Juan González of the Electron Microscopy Service of the University of Cádiz for supplying the facilities to take the scanning electron microscope photographs. This paper was supported by the projects REN2001-1956-C17-02/GLO (Spanish Ministry of Science and Technology), and PEET Grant DEB-9978155 (National Science Foundation, USA). One of the authors (M.P.) has been the beneficiary of a predoctoral fellowship funded by the Spanish Ministry of Education, Culture and Sports.

REFERENCES

- Allan, J.K. – 1933. Opisthobranchs from Australia. *Rec. Aust. Mus.*, 18(9): 443-450.
- Atkinson, L. and D. Atkinson. – 2003 (Jun 14). *Nembrotha lineolata* from Fiji. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=10194>.
- Baba, K. – 1976. Two species of *Nembrotha* (s.s.) new to Japan (Nudibranchia: Doridoidea: Polyceridae). *Veliger*, 19: 131-134.
- Bartlett, J. – 2002 (Dec 17). *Nembrotha livingstonei* from Indonesia. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=8507>.
- Bergh, L.S.R. – 1877. Malacologische Untersuchungen, In: C. Semper (ed.), *Reisen im Archipel der Philippinen*. Zweiter Theil, Wissenschaftliche Resultate, 2(11): 429-494.
- Bergh, L.S.R. – 1905. Die Opisthobranchiata der Siboga-Expedition. *Siboga-Expeditie*, 50: 1-248.
- Burn, R. – 1967. Notes on an overlooked nudibranch genus, *Roboastra* Bergh, 1877, and two allied genera (Mollusca: Gastropoda). *Aust. Zool.*, 14: 212-222.
- Cervera, J.L., J.C. García-Gómez and C. Megina. – 1996. Redescription of *Nembrotha megalocera* Yonow, 1990 (Gastropoda: Nudibranchia: Polyceratidae) from the Red Sea. *Veliger*, 39(1): 55-59.
- Coleman, N. – 1989. *Nudibranchs of the South Pacific*, Vol.1, Springwood, Queensland: Sea Australia Resource Centre.
- Coleman, N. – 2001. *1001 Nudibranchs. Catalogue of Indo-Pacific Sea Slugs*. Neville Coleman's Underwater Geographic Pty Ltd. Springwood, Queensland, Australia.
- Debelius, H. – 1996. *Nudibranchs and Sea Snails: Indo Pacific Field Guide*. Ed. MandG Difusión, S.L. Germany.
- Debelius, H. and R. Kuitert. – 2007. *Nudibranchs of the world*. IKAN-Unterwasserarchiv. Frankfurt, Germany.
- Eales, N. – 1938. A systematic and anatomical account of the Opisthobranchia. John Murray Expedition 1933-34. *Sci. Rep. British Mus. (Nat. Hist.)*, 5(4): 77- 122.
- Eliot, C. – 1904. On some Nudibranchs from East Africa and Zanzibar. Part 5. *Proc. Zool. Soc. Lond.*, 2: 83-105.
- Eliot, C. – 1906. On the Nudibranchs of Southern India and Ceylon, with special reference to the Drawings by Kelaart and the Collections belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. No.2. *Proc. Zool. Soc. Lond.*, 2: 999-1008.
- Ellis, W. – 1999 (Jul 22). *Nembrotha mullineri* from Cairns? [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=1095>.
- Fraser, V. – 1999 (Dec 20). *Nembrotha purpureolineata* from South Africa. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=1658>.
- Goethel, H. and H. Debelius. – 1992. Nacktschnecken der Maldiven, mit der Beschreibung einer neuen Art. *DATZ (Die Aquarien- und Terrarienzeitschrift)*, 1992(8): 512-519.
- Gosliner, T.M. – 1987. *Nudibranchs of Southern Africa. A guide to Opisthobranch Molluscs of Southern Africa*. Sea Challengers, Monterey, California.
- Gosliner, T.M., D.W. Behrens and G.C. Williams. – 1996. *Coral reef animals of the Indo-Pacific*. Sea Challengers, Monterey, California.
- Gosliner, T.M. and D.W. Behrens. – 1997. Description of four new species of phanerobranch dorids (mollusca: Nudibranchia) from the Indo-Pacific, with a redescription of *Gymnodoris aurita* (Gould, 1852). *Proc. Cal. Acad. Sci.*, 49(9): 287-308.
- Ho, W.K.A. – 2005 (Sep 12). *Nembrotha lineolata* from west Malaysia. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=14679>.
- Houghton, R. – 2002 (Jul 15). *Nembrotha cristata* from Indonesia. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=7484>.
- ICZN. – 2000. *International Code of Zoological Nomenclature*. International Trust for Zoological Nomenclature 2000, London.
- King, D. and V. Fraser. – 2002. *More Reef Fishes and Nudibranchs. East and South coast of Southern Africa*. Struik, Cape Town.
- Köhler, E. – 2001 (Jul 4). *Nembrotha livingstonei* from the Philippines. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=4591>.
- Macnae, W. – 1958. The families Polyceridae and Goniodorididae (Mollusca, Nudibranchiata) in southern Africa. *Trans. R. Soc. S. Afr.*, 35: 341-372.
- Marcus, E. – 1958. Notes on Opisthobranchs. *Bol. Inst. Oceanogr. Sao Paulo*, 7: 31-78.
- Marcus, E. and E. Marcus. – 1964. Verzeichnis der euthyneuren Meeresschnecken Brasiliens. *Beitr. Neotr. Fauna*, 3(3): 195-206.
- Marshall, J.G. and R.C. Willan. – 1999. *Nudibranchs of Heron Island, Great Barrier Reef. A Survey of the Opisthobranchia (Sea Slug) of Heron and Wistari Reefs*. Backhuys Publishers Leiden, Netherlands.
- McNeil, G. – 1999 (Jul 8). *Nembrotha cristata* from Papua New Guinea. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=995>.
- Nakano, R. – 2004. *Opisthobranchs of Japan Islands*. Rutles Inc., Tokyo.

- Odhner, N. – 1941. New Polycerid Nudibranchiate Mollusca and remarks on this Family. *Göteborg. Vet. Vitterh.-Samh. Handl.*, F. 6, (B), 1(11): 1-20.
- O'Donoghue, C.H. – 1924. Report on Opisthobranchiata from the Abrolhos Islands, Western Australia, with Description of a new parasitic Copepod. *J. Linn. Soc.*, 35(237): 521-579.
- Okutani, T. – 1994. *Marine Invertebrates*. Yama to Keikoku sha, Tokyo.
- Ono, A. – 1999. *Opisthobranchs of Kerama Islands*. TBS-Britannica, Tokyo.
- Ono, A. – 2004. *Opisthobranchs of Ryukyu Islands*. Rutles Inc., Tokyo.
- Pola, M., J.L. Cervera and T.M. Gosliner. – 2005. Review of the systematics of the genus *Roboastra* Bergh, 1877 (Nudibranchia, Polyceridae, Nembrothinae) with the description of a new species from Galápagos Islands. *Zool. J. Linn. Soc.*, 144: 167-189.
- Pola, M., Y. Vallès, J.L. Cervera, M. Medina and T.M. Gosliner. – 2006a. Taxonomic status of *Tambja abdere* and *Tambja fusca* based on morphological and molecular evidence, with comments on the phylogeny of the subfamily Nembrothinae (Nudibranchia, Polyceridae). *Ann. Zool. Fen.*, 43: 52-64.
- Pola, M., J.L. Cervera and T.M. Gosliner. – 2006b. Taxonomic review and phylogenetic analysis of the genus *Tambja* Burn, 1962 (Mollusca, Nudibranchia, Polyceridae). *Zool. Scr.*, 35(5): 491-530.
- Pola, M., J.L. Cervera and T.M. Gosliner. – 2007. Phylogenetic relationships of Nembrothinae (Mollusca: Doridacea: Polyceridae) inferred from morphology and mitochondrial DNA. *Mol. Phyl. Evol.* 43: 726-742.
- Pruvot-Fol, A. – 1931. Nudibranches australiens figurés par Saville-Kent dans son grand ouvrage "The great Australian barrier-reef", et qui ne sont ni décrits ni nimmés. *Bull. Mus. Nat. His. Nat.*, Paris, 2ème Serie, 3(8): 754-755.
- Rudman, W.B. – 1999-2005. *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net>.
- Rudman, W.B. – 1999 (July 2). *Nembrotha rutilans* (Pruvot-Fol, 1931). [In] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/factsheet.cfm?base=nembruti>.
- Rudman, W.B. – 2000 (Aug 17). Comment on Transverse lines on *Nembrotha lineolata* by Dirk Hasberg. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=2894>.
- Rudman, W.B. – 2002 (April 22). *Nembrotha sp. 13* [In] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/factsheet.cfm?base=nembrsp13>
- Rudman, W.B. – 2005 (Aug 2). Comment on Re: *Nembrotha lineolata* with transverse lines by David Bush. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=14449>.
- Rudman, W.B. – 2005 (Jun 15). Comment on *Nembrotha lineolata* with transverse lines by David R. Bush. [Message in] *Sea Slug Forum*. Australian Museum, Sydney. Available from <http://www.seaslugforum.net/find.cfm?id=14060>
- Suzuki, K. – 2000. *Opisthobranchs of Izu Peninsula*. TSB-Britannica, Tokyo, 1-178 pp.
- Thiele, J. – 1931. Handbuch der Systematischen Weichtierkunde. Band 1, vi + 778 pp. A. Asher and Co., Amsterdam, reprint 1963.
- Tonozuka, T. – 2003. *Opisthobranchs of Bali and Indonesia*. Hankyu Communications Co., Ltd., Tokyo.
- Wells, F.E. and C.W. Bryce. – 1993. *Sea Slugs of Western Australia*. Western Australian Museum, Perth, Western Australia.
- Willan, R.C. and N. Coleman. – 1984. *Nudibranchs of Australasia*. Sydney, Australasian Marine Photographic Index.
- Yonow, N. – 1990. Red Sea Opisthobranchia 3: The orders Sacoglossa, Cephalapidea, and Nudibranchia: Doridacea (Mollusca, Opisthobranchia). *Fauna Saudi Arabia*, 11: 286-299.
- Yonow, N. – 1993. Opisthobranchs from the Maldives Islands, including descriptions of seven new species (Mollusca: Gastropoda). *Revue fr. Aquariol.*, 20: 97-129.
- Yonow, N. and P.J. Hayward. – 1991. Opisthobranchs de l'île Maurice, avec la description de deux espèces nouvelles (Mollusca: Opisthobranchia). *Revue fr. Aquariol.*, 18: 1-30.

Scient. ed.: J.D. Ros.

Received March 1, 2007. Accepted December 13, 2007.

Published online February 25, 2008

