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# Complementary anatomy of *Actinocyclus verrucosus* (Nudibranchia, Doridoidea, Actinocyclidae) from Indo-Pacific

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## Abstract

The last review of the genus *Actinocyclus* consider only two valid species for the genus: *Actinocyclus verrucosus* Ehrenberg, 1831 (type species of the genus) and *Actinocyclus papillatus* (Bergh, 1878), both with a geographical distribution in the Indo-Pacific. The anatomy of these species is still unknown, except for some scanty anatomical information. A detailed anatomical study of *Actinocyclus verrucosus* is performed, including inedited structures such as digestive system, odontophore muscles and circulatory system, beyond complementary information on the commonly studied structures, in order to clarify the taxonomy and distribution.

## Key Words

Actinocyclidae
*Actinocyclus verrucosus*
comparative morphology
systematics
Indo-Pacific

## Introduction

The family Actinocyclidae comprises two genera, *Actinocyclus* Ehrenberg, 1831 [type species: *Actinocyclus verrucosus* Ehrenberg, 1831, by subsequent designation of Gray (1847)], with two valid species: the type species and *A. papillatus* (Bergh, 1878) (Rosenberg 2010); and *Hallaxa* Eliot, 1909 with 15 valid species (Bouchet 2011).

The current systematics of this family is mainly based on Gosliner and Johnson (1994) who studied the phylogenetic relationship of the *Hallaxa*, and hypothesized *Actinocyclus* as its sister taxa, considered only these two genera as members of Actinocyclidae, and this family as sister taxon of Chromodorididae (Valdés 2002). The last review of *Actinocyclus* was based on some traditional characters, such as the external morphology, the reproductive system and radular data (Valdés 2002). As have been seen in recent papers (e.g., DaCosta et al. 2007, Simone 2011, Lima and Simone 2015), the scenario of the morphological characters is an effective tool to better understanding the relationship among species and has been useful to clarify and refine their taxonomy.

In this paper the morphological data of *Actinocyclus verrucosus* are described in more details, including previously unexplored structures, such as digestive tubes, odontophore muscles and circulatory system, and builds a conceptual scenario for comparative characters in future analysis.

## Material and methods

The studied material belongs to museum collections, consisting of specimens preserved in 70% ethanol; a complete information follows description. Dissections were performed under a stereomicroscope by standard techniques (Simone 2004, 2011). The initial steps of the anatomical investigation were done through a longitudinal cut on the integument covering the dorsal visceral mass. Digestive, circulatory, excretory, reproductive and central nervous systems were investigated in detail. The terminology used

for odontophore muscles was based on Ponder et al. (2008), Simone (2011) and Lima and Simone (2015). Drawings were done with the aid of a camera lucida. Scanning electron microscopy (SEM) was used to examine details of the radula at the Laboratório de Microscopia Eletrônica of Museu de Zoologia da Universidade de São Paulo (MZSP).

The following abbreviations are used herein: **aa**: anterior aorta; **ab**: afferent branchial vein; **am**: ampulla; **an**: anus; **ap**: posterior aorta; **au**: auricle; **at**: aortic trunk; **bc**: bursa copulatrix; **bg**: blood gland; **bl**: branchial leaves; **bs**: buccal sphincter; **cb**: buccal commissure; **ce**: cerebral ganglia; **cl**: pleural commissure; **cp**: pedal commissure; **cu**: caecum; **dd**: duct of digestive gland; **dg**: digestive gland; **dt**: digitiform tentacle; **eb**: efferent branchial vein; **es**: oesophagus; **ey**: eye; **fg**: female gland; **ft**: foot; **gb**: buccal ganglia; **gc**: gill circle; **ge**: gonopore; **gg**: gastro-oesophageal ganglia; **gp**: pedal ganglia; **hg**: hermaphrodite gland; **il**: inner lip; **in**: intestine; **mo**: mouth; **ms**: medial sinus; **m2 – m10**: odontophore muscles; **mt**: oral tube muscle; **ne**: nephrostome; **oc**: odontophore cartilage; **ol**: outer lip; **ot**: oral tube; **ov**: oviduct; **pc**: pericardium; **pe**: penis; **pl**: pleural ganglia; **pr**: prostate; **ra**: radula; **ri**: rhinophore; **rg**: rhinophoral ganglia; **rm**: gill retractor muscle; **rn**: rinophoral nerve; **rp**: reproductive system; **rs**: radular sac; **rv**: renal vesicle; **sg**: salivar gland; **sm**: subradular membrane; **sn**: nervous system; **sr**: seminal receptacle; **st**: stomach; **sy**: statocysts; **tu**: dorsal tubercles; **ud**: uterine duct; **va**: vagina; **vd**: vas deferent; **ve**: ventricle.

**Institutional abbreviation**

| | |
|---|---|
| AUS | Australian Museum Research Institute, Sydney |
| CASIZ | Invertebrate Zoology and Geology of the California Academy of Science, San Francisco |
| MHUB | Museum für Naturkunde der Humboldt-Universität zu Berlim |
| ZMUC | Zoologisk Museum, Kobenhavns Universitet, Copenhagen |
| MNHN | Muséum National d'Histoire Naturalle, Paris |

# Results

### Family Actinocyclidae O'Donoghue, 1929

### Genus *Actinocyclus* Ehrenberg, 1831

**Type species.** *Actinocyclus verrucosus* Ehrenberg, 1831, by subsequent designation of J. E. Gray (1847)

### *Actinocyclus verrucosus* Ehrenberg, 1831

Figs 1–31

*Actinocyclus verrucosus* Ehrenberg, 1831: 28.
*Sphaerodoris punctata* Bergh, 1877: 66 (*nomen nudum*); Bergh 1878: 587, pl. 65, figs 1–5.
*Sphaerodoris laevis* Bergh, 1890: 925, pl. 88, figs 3–12; Odhner 1919: 40.
*Sphaerodoris japonica* Eliot, 1913: 23.
*Aldisa nhatrangensis* Risbec, 1956: 14, pl. 20, fig. 109, pl. 22.

**Type material.** See Valdés (2002).

**Type locality.** Massawa, Eritrea.

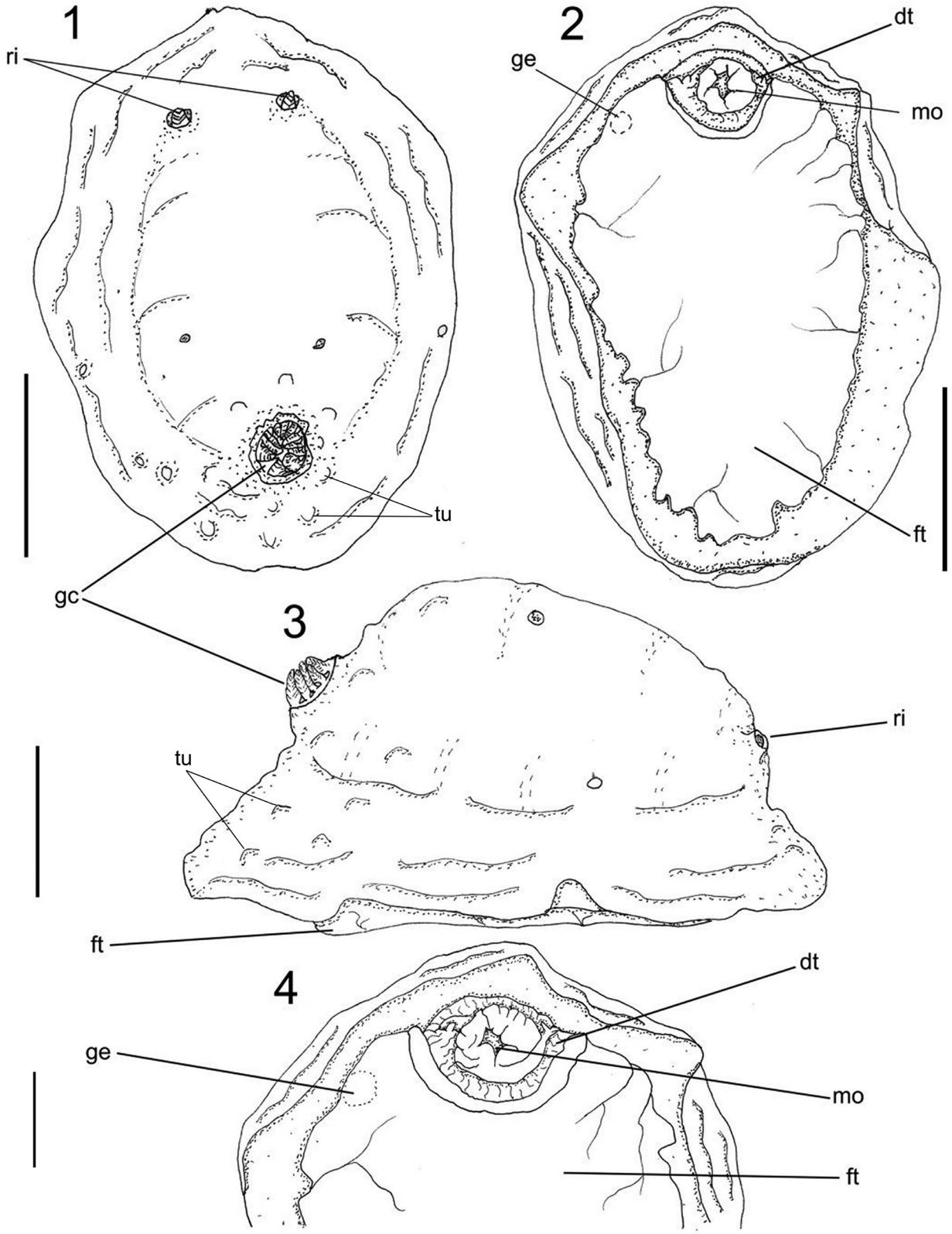
**Material examined.** AUSTRALIA, Coral Sea, North East Herald Cay, AUS 333868.001, 2 specimens (M. Preker, coll., 24/vi/1997, beach rock, SE side of cay, LT at dusk). VANUATU, Espiritu Santo Island, Palikulo Peninsula (15°28.90'S 167°15.50'E (DDM)), CAS 179791, 1 specimen (M. Pola-Perez, Y. Camacho-Garcia et al. Coll., 15/ix/2006, intertidal, soft bottom).

**Diagnosis.** Body of grayish color, with some black dots and some tubercles. Anterior border of foot concave and not bilabiate nor longitudinally notched. Presence of m7a odontophore muscles and pleural commissure.

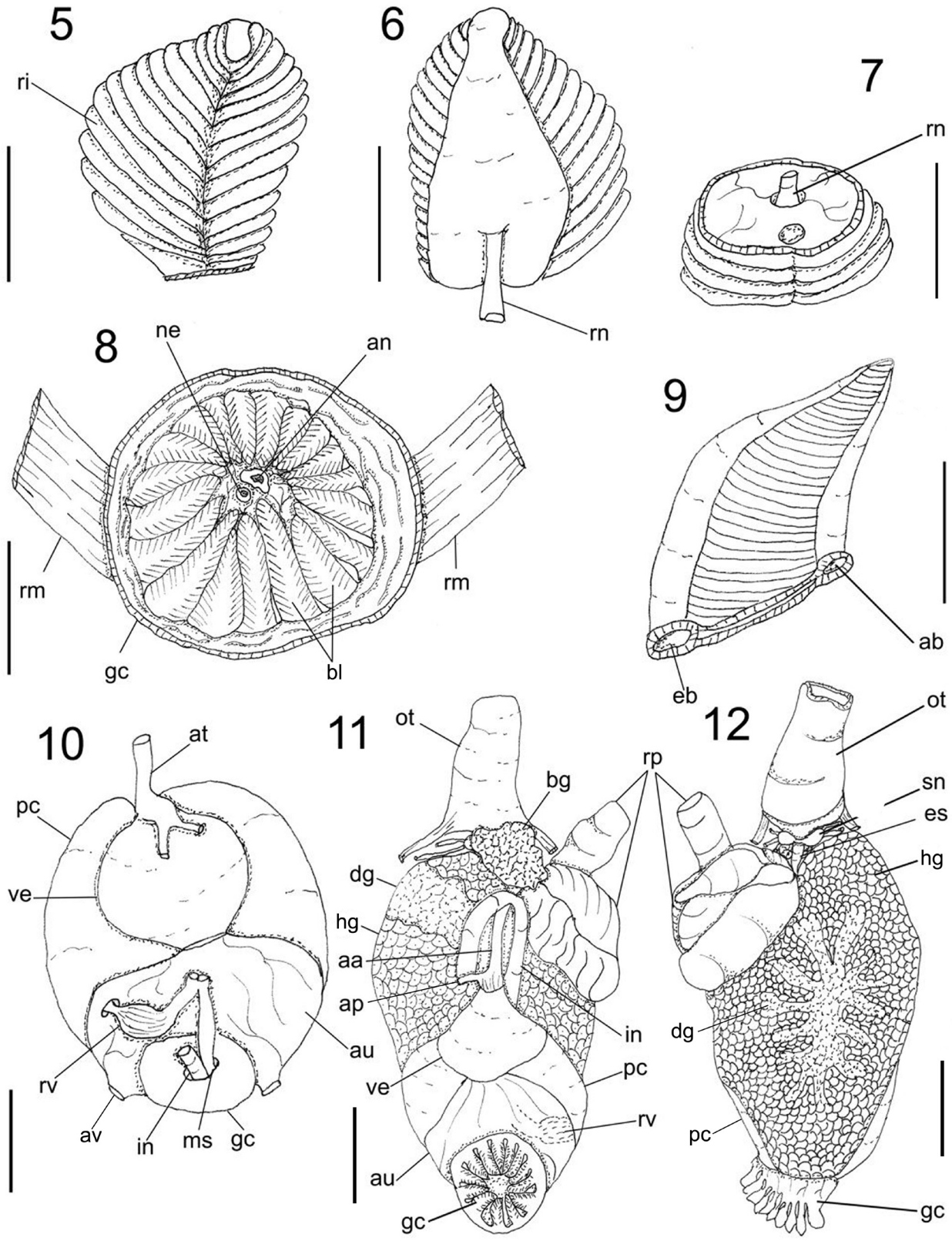
**Redescription.** *External morphology* (Figs 1–9): Size, ~12mm length, ~10mm width. Color grayish with some black dots in preserved specimen. Body rounded, oval, almost as long as wide; elevated dorsum with some several simple dorsal tubercles scattered irregularly (Figs 1–3). Mantle smooth without spicules. Rhinophores with ~17 transverse lamellae (preserved specimen with ~12mm-long CASIZ 179791) (Figs 5–7); rhinophoral sheaths smooth. Gill circle composed of 16–19 unipinnate branchial leaves surrounding anus (preserved specimen with ~12mm-long) (Figs 8–9); branchial sheaths smooth. Mouth opening in anterior ventral region, between anterior region of notum and foot (Fig. 2). Digitiform tentacles very small, one on each side of mouth (Fig. 4). Anterior border of foot concave, not bilabiate, nor longitudinally notched (Fig. 4). Foot not exceeding notum in a preserved specimen (Fig. 2).

*Haemocoel organs* (Figs 11–12): pericardium and posterior half of visceral mass occupying ~40 % of haemocoel volume. Buccal mass located anteriorly, occupying ~20 % of haemocoel volume. Nervous system dorsal to buccal mass, covered by blood gland, occupying ~10 % of haemocoel volume. Genital system on right side; occupying ~20 % of haemocoel volume. Stomach internal to digestive gland, intestine with small curve at anterior portion, both occupying ~10 % of haemocoel volume.

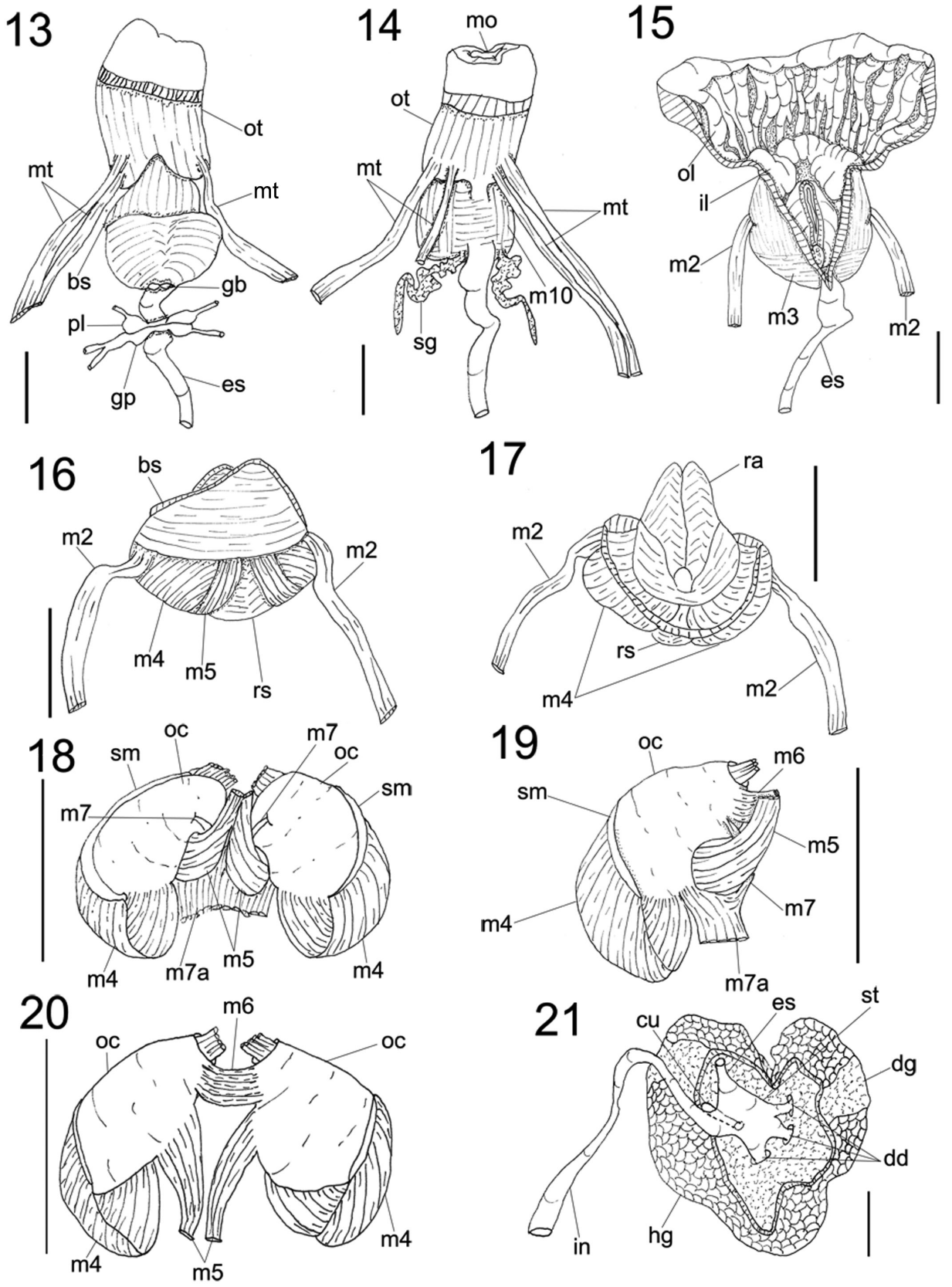
*Circulatory and excretory systems* (Figs 8–11): pericardial cavity dorsal and posterior to digestive gland, anterior to gill circle. Afferent and efferent veins located at edge of each branchial leaves (Fig. 9). Gill retractor muscle divided in two fibers originating from base of gill circle, running lateral to haemocoel longitudinally up to half of foot level, inserting into dorsal surface of foot (Fig. 8). Auricle funnel-like (wider anteriorly) with thin walls (Fig. 10). Ventricle slightly taller than wide, with thick muscular walls (Fig. 10). Aortic trunk anterior to pericardium, connected to anterior ventricular region (Figs 10–11); posterior artery branched into anterior artery irrigating reproductive system, buccal mass, odontophore and nervous system inserting on blood gland; anterior artery irrigating stomach, caecum and digestive gland



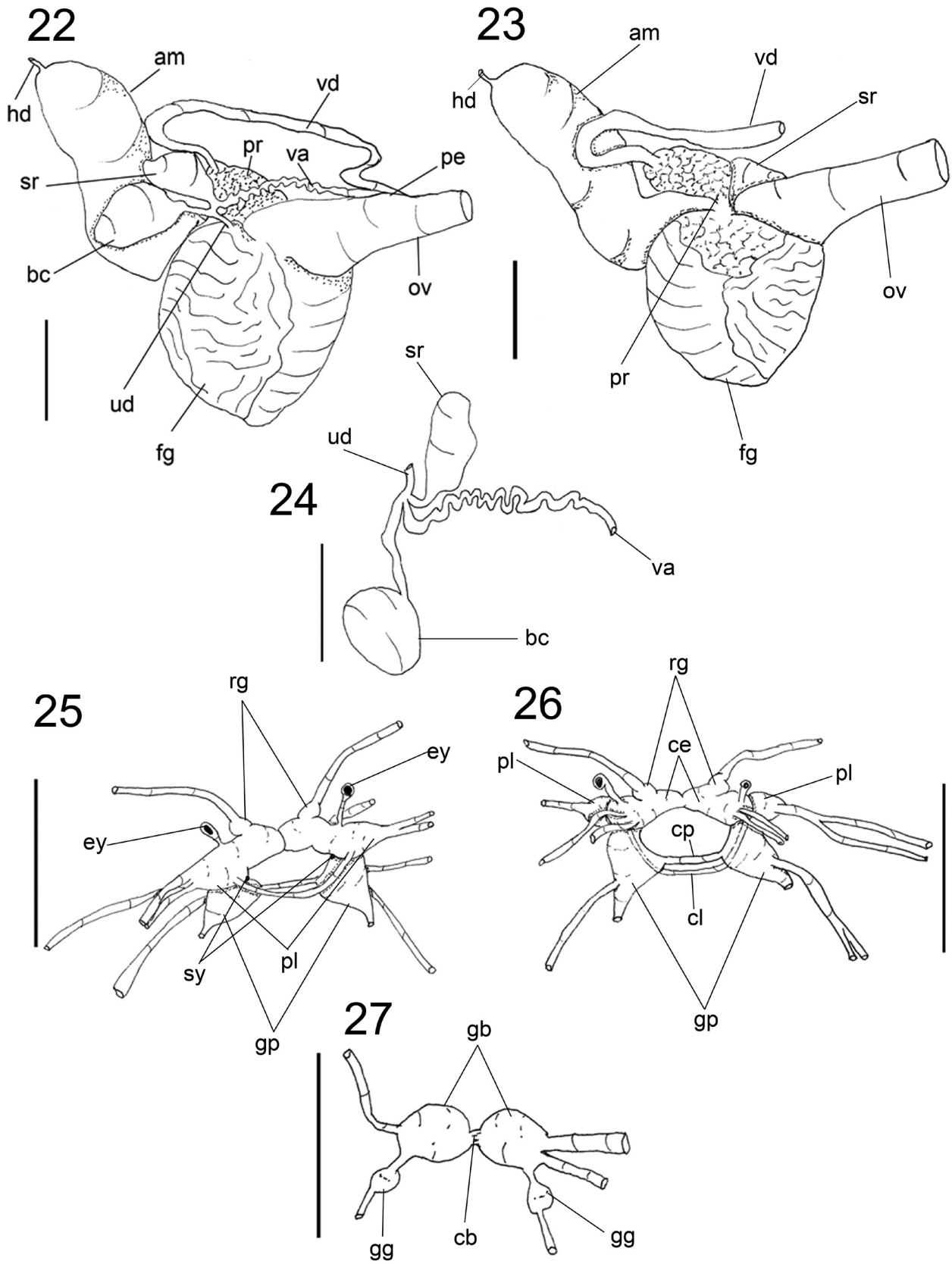

**Figures 1–4.** External morphology of *Actinocyclus verrucosus.* **1.** Whole dorsal view, scale: 5 mm. **2.** Whole ventral view, scale: 5 mm. **3.** Whole right lateral view, scale: 5 mm. **4.** Detail of anterior border of foot, ventral view, scale: 2 mm.




**Figures 5–12.** Anatomical details of *Actinocyclus verrucosus*. **5.** Rhinophore extracted, ventral view, scale: 0.5 mm. **6.** Same dorsal view, scale: 0.5 mm. **7.** Same, transverse section, scale: 0.5 mm. **8.** Gill circle with retractor muscle, dorsal view, scale: 1 mm. **9.** Detail of gill filament, scale: 1 mm. **10.** Detail of circulatory system (structures of pericardium), ventral view, scale: 2 mm. **11.** Extracted visceral mass, dorsal view, scale: 2 mm. **12.** Same, ventral view, scale: 2 mm.




**Figures 13–21.** *Actinocyclus verrucosus* details of digestive system. **13.** Foregut and nerve ring, ventral view, some adjacent structures also shown as in situ, scale: 1 mm. **14.** Same dorsal view, scale: 1 mm. **15.** Same, longitudinally sectioned, showing internal oral tube, dorsal view, scale: 1 mm. **16–20.** Odontophore anatomy, scales: 1 mm. **16.** Whole ventral view, sphincter removed. **17.** Whole dorsal view, esophagus removed. **18.** Dorsal view, radula removed, each cartilage slightly deflected. **19.** Whole right view. **20**. Ventral view, m4 and m5 folded down to expose odontophore cartilage; m7 and m7a removed. **21.** Midgut as in situ, dorsal view, scale: 2 mm.




**Figures 22–27.** *Actinocyclus verrucosus* reproductive system. **22.** Dorsal whole view, most structures uncoiled, scale: 1 mm. **23**. Same, ventral view, scale: 1 mm. **24**. Detail of uncoiled female structures, dorsal view, scale: 1 mm. **25–27.** Central nervous system. **25.** Dorsal view, scale: 1 mm. **26.** Ventral view, scale: 1 mm. **27.** Detail of buccal and gastroesophageal ganglia, ventral view, scale: 0.5 mm.

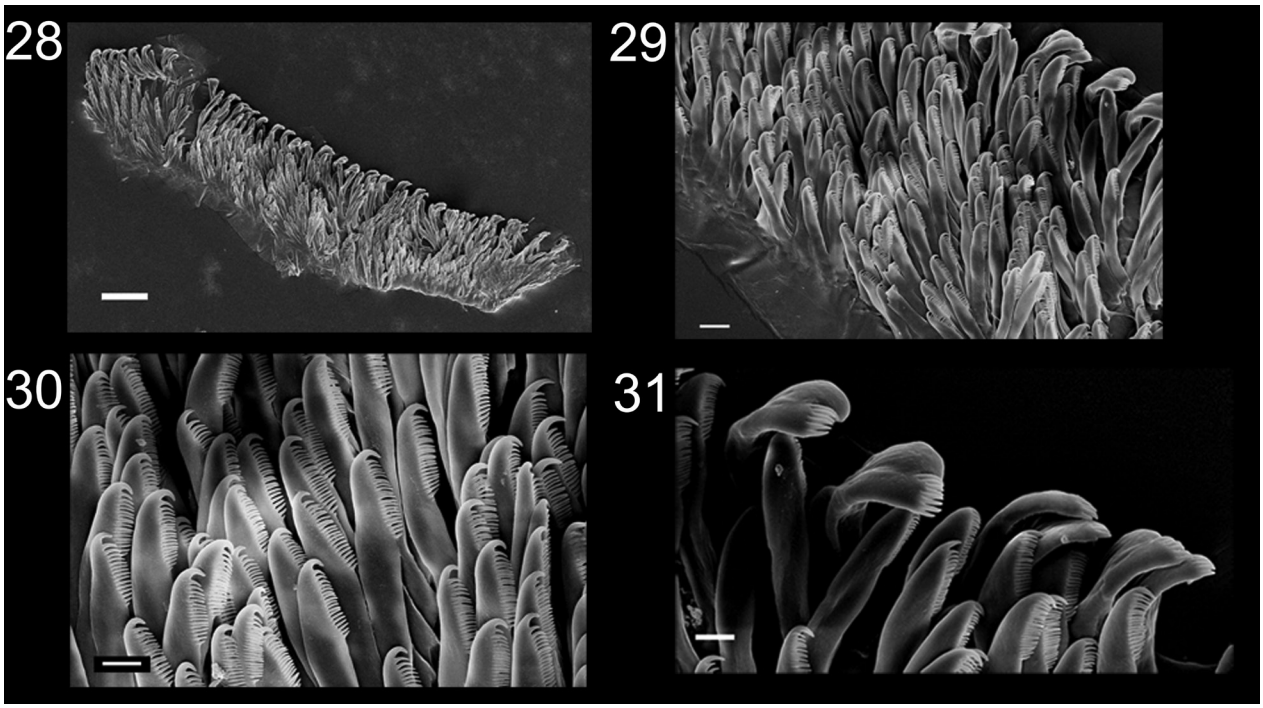
**Table 1.** Comparative table of some features between *Actinocyclus verrucosus*, *Hallaxa apefae* and *Chromodoris magnifica* (all these features of the three species was analyzed in Lima 2016).

| | Anterior border of foot | Foot | Nephrostome | Jaws | M7a | Ducts of digestive gland | Cecum | Pedal commissure |
|---|---|---|---|---|---|---|---|---|
| *Actinocyclus verrucosus* Ehrenberg, 1831 | Concave, not bilabiate nor notched | Not projected beyond the notum | Readily visible | Present | Present | 3 | Present | Present |
| *Hallaxa apefae* Er. Marcus, 1957 | Convex, bilabiated not notched | Pointed, poserior projected beyond the notum | Not readily apparent | Absent | Absent | 1 | Absent | Absent |
| *Chromodoris magnifica* (Quoy & Gaimard, 1832) | Convex, bilabiated not notched | Pointed, poserior projected beyond the notum | Readily visible | Absent | Absent | 2 | Absent | Absent |

(Fig. 11). Auricular vessels connecting lateral cavities of integument to auricle (Fig. 10). Medial sinus connected to afferent branchial ring, irrigating entire digestive gland. Renal vesicle located on right dorsal side of pericardium, near base of auricle, connected to inner surface of pericardium; renal chamber elliptical, with longitudinal folds, ~1/4 of size of ventricle (Fig. 10). Renal chamber extending from dorsal to medial sinus, previously connected to renal vesicle, extending posteriorly to center of gill circle and opening in nephrostome, next to anus pore (Fig. 8). Blood gland undivided (Fig. 11).

*Digestive system* (Figs 8, 13–21, 28–31): Oral tube composed of outer lip, with pleats lengthwise; inner lip with transverse fold; **mt**, two pairs of retractor muscles of buccal mass, originating on oral tube, running dorsally and ventrally to oral tube, inserting on body side, about three times as wide and twice as long as **m10** (Fig. 15). Odontophore oval, connected to oral tube by several fine longitudinal dorsal and ventrolateral protractors muscles of buccal sphincter, originating in anterior region of odontophore, inserting in posterior region of integument, close to oral tube (**m10**) (Fig. 14); Buccal sphincter surrounding chitinous part of oral tube. Odontophore muscles: **m2**, pair of strong retractor muscles of buccal mass, six times longer than wide, originating on anterior dorsal odontophore, running laterally to m4 and inserting ventrally on dorsal portion of foot; **m3**, two times wider than long, transverse fibers between esophagus and odontophore (Figs 15–16); **m4**, pair of dorsal tensor muscles of radula, strong and broad, 1/2 winder than long, covering externally 2/3 of cartilage, inserting on ventral portion of subradular membrane; **m5**, pair of dorsal auxiliary tensor muscles of radula, twice as long as wide, originating on most posterior region of odontophore cartilages, covering ~1/3 of posterior cavity of odontophore, as long as, but with ~1/3 of m4 width, inserting on ventral side of subradular membrane, around radular sac; **m6**, unpaired horizontal muscle, with transverse fibers connecting anterior surfaces of left and right odontophore cartilages, as long as wide, about same length and half as wide as m4 (Fig. 20); **m7**, pair of thin muscles originating each into an odontophore cartilages and inserting on **m7a** passing ventrally by **m5**, and on radular sac (Fig. 19); **m7a**, originating on posterior region of odontophore cartilage and inserting on radular sac, m7' auxiliary (Fig. 19). Pair of odontophore cartilages slender, elliptical. Subradular membrane thin, strong, translucent (Fig. 18). Radular sac ~1/6 of odontophore (Fig. 16). Jaw elements not analyzed. Radular teeth (Figs 28–31): rachidian teeth absent; formula 50 x 17.0.17 (preserved specimen, ~15 mm-long, AUS C333868001). Innermost lateral teeth broad and thick, with large and rounded cusp and about six to eight cusps along inner edge (Fig. 31). Mid-lateral teeth narrow basally and elongated, with apical cusp larger than other, twenty-one lateral cusps (Fig. 30). Outermost teeth shorter than middles laterals, about sixteen to eighteen cusps (Fig. 29). Pair of salivary glands long, tubular, about same length as esophagus; duct inserting in anterior region of esophagus, extending posteriorly to anterior region of digestive gland (Fig. 14). Esophagus simple, originating dorsally to odontophore, inserting directly in anterior region of stomach, internal longitudinal folds with same diameter along entire length (Figs 14–15). Stomach internal to digestive gland, oval, close to anterior region of intestine, with distinct digestive ducts (Fig. 21). Intestine with longitudinal folds along its entire length, diameter same as esophagus diameter. Caecum as an elongated sac, located ventrally to stomach, opening on anterior portion of stomach (Fig. 21), close to esophageal insertion, ~½ length and ~1/2 of width of stomach. Digestive gland dark brown, internal to hermaphrodite gland, cone-shaped; inner face of gland sponge-like, bearing three ducts (Fig. 21). Anus opening into pore at center of gill circle (Fig. 8); anal papilla absent.

*Genital system* (Figs 2, 11–12, 22–24): located between buccal mass and digestive gland, mainly on right and dorsal sides. Hermaphrodite gland around digestive gland, dark beige in color (Figs 11–12). Hermaphrodite duct thin, long located posterior end of ampulla (Figs 22–23). Ampulla located on female gland, elongated and tubular, about same length as oviduct, inserting distally at junction of oviduct and prostate (Fig. 23). Prostate glandular, connected to female gland, ~1/2 of ampulla's length. Vas deferens and penis muscular, cylindrical, elongated, ~1/2 of prostate's width (Fig. 22). Female gland well-developed, rounded, occupying ~40% of reproductive system volume, about same length and twice width as oviduct (Figs 22–23). Oviduct occupying ~1/3 of female gland volume (Figs 22–23). Uterine duct located at base of bursa cop-




**Figures 28–31.** *Actinocyclus verrucosus*, radula in SEM. **28.** Panoramic view, scale: 100 µm. **29.** higher magnification in central region, scale: 40 µm. **30.** Outer lateral teeth, scale: 10 µm. **31.** Detail of marginal teeth tip, scale: 10 µm.

ulatrix and seminal receptacle, inserted in female gland near oviduct, relatively short, ~1/10 of vagina's length and same diameter as vagina (Figs 22, 24). Seminal receptacle pyriform, as large as bursa copulatrix, connected to vagina near uterine duct through short stalk (Figs 22, 24). Bursa copulatrix rounded, connected to vagina after seminal receptacle, length ~1/6 of vagina's length, also through stalk three times longer than uterine duct (Figs 22, 24). Vagina cylindrical, elongated, same width and four times longer than penis, followed ventrally by prostate and located parallel to penis on gonopore (Fig. 24). Gonopore on right side, located in anterior fifth of length of animal from head, between foot and notum (Fig. 2).

*Central nervous system* (Figs 25–27): located dorsally to odontophore, mostly covered by blood gland. Pair of cerebral and pleural ganglia fused with each other dorsally and ventrally. Pedal ganglia fused with cerebral and pleural ganglia ventrally, not fused among themselves, connected by long and thin pleural commissure. Pedal commissure simple, ½ of length of pleural commissure, both surrounding esophagus and salivary glands (Fig. 26). Buccal ganglia short, located ventrally to odontophore, between radular sac and anterior portion of esophagus, connected to cerebral ganglia through long and slender connective tissue, united to gastro-esophageal ganglia by short connective tissue. Gastro-esophageal ganglia with length ~1/4 of buccal ganglia length, spherical (Fig. 27). Rhinophoral ganglia bulb-shaped, connected to anterior portion of cerebral ganglia (Fig. 25). Dorsal eyes located on cerebral ganglia with short stalk, pedunculated. Statocysts small and iridescent, located ventrally between pedal and pleural ganglia (Fig. 25).

**Distribution.** West and Central Indo Pacific [Red Sea (Ehrenberg 1831), Philippines, and Indonesia (Bergh 1878, 1890), East Africa, Malaysia and Japan (Eliot 1904, 1913), Vietnam (Ribesc 1956), Hawaii (Kay and Young 1969), Queensland (Willan and Coleman 1984), Western Australia (Wells and Bryce 1993), Madagascar and Marshall Island (Valdés 2002)].

## Discussion

The presence of a short pair of digitiform tentacles around the mouth (Fig. 4) is noteworthy, they were also reported by Gosliner and Johnson (1994). However, these digitiform tentacles have been reported as absent by Kay and Young (1969) and Valdés (2002). The most external differences of *A. verrucosus*, when compared to other Doridoidea, for example *Hallaxa apefae*, *Chromodoris magnifica* and *Doris verrucosa* (Tab. 1), is the presence of an anterior border of foot concave, not convex and not grooved, nor notched (Figs 2, 4).

The rhinophores have 17 lamellae instead of 20 described by Valdés (2002), and the number of branchial leaves ranges from 16 to 19, instead of only 16. Regarding the color of the body, no alive specimens have been analyzed.

In the circulatory system, interesting features were found in the position in relation to gill circle, the afferent and efferent vessels, the gill retractor muscle, medial sinus, renal chamber and nephrostome. Despite some of these features have already used in phylogenetics analyzes (Lima 2016), because of lack of further information, a deeper analysis is still difficult.

The oral tube is composed of a pair of retractor muscles, which attaches to the body wall (mt), in *A. verrucosus* there are two pairs of mt, while in *Hallaxa apefae*, and the most species of Doridoidea, present three pairs (Lima 2016). A buccal sphincter and the m3 (transverse muscle) involve the odontophore (Figs 15–16) that have a pair of long retractor muscles (m2) (Figs 15–17). A group of muscles are described for the first time (m4, m5, m6, m7) (Figs 16–20), with similar functions of their counterparts in other heterobranchs (Simone 2011). The odontophore cartilage is well-developed (Fig. 18) like in other nudibranchs as, e.g., *Doris verrucosa* Linnaeus, 1758 (Lima and Simone 2015). However, some differences are visible between *A. verrucosus* and *D. verrucosa* as following: m5 pair originates on the middle region of the odontophore cartilages in *A. verrucosus* (Figs 19–20) instead on the posterior region in *D. verrucosa* (Lima and Simone 2015, fig. 8B); m6 located more anteriorly in *A. verrucosus* (Fig. 20), whereas in *D. verrucosa* the m6 connects the both odontophore cartilages anteriorly and posteriorly (Lima and Simone 2015, Figs 8A-B). However, the most significant difference of odontophore muscles of *A. verrucosus* and others Doridoidea species appears to be the presence of the pair m7a.

The reproductive system seems to be similar to those described by Valdés (2002), but it has some different features from the interpretation by Kay and Young (1969) that described the prostate without the glandular portion, which was not observed in the present studied samples (Figs 23–24).

In the central nervous system, the abdominal ganglion described by Valdés (2002) was not observed, but a pleural commissure (Figs 25–26), that is not mentioned by him, was found. This last feature was uncovered as autapomorphy in a recent phylogenetic study (Lima 2016) as well as the presence of m7a – originating on posterior region of odontophore cartilage and inserting on radular sac, probably m7's auxiliary.

In the same recent phylogenetic study (Lima 2016) *Hallaxa apefae* appears more related to Chromodorididae (Tab. 1) clade and could be considered as sister group based on the posterior projection of the foot beyond the notum and the absence of integumentary spicules. In the same analysis, *A. verrucosus* resulted as sister group of a clade that united Doridiidae and Discodorididae with two characters: radula with many lateral teeth and buccal commissure readily visible.

The present complementary anatomical investigation improved the species delimitation of *A. verrucosus*. In addition, allowed to evaluate the characters usually used in taxonomy and phylogenetic studies, as well as the discovery of new characters with phylogenetic signal and provided more bases for the synonymies. The evaluation of new morphological characters will improve the knowledge of the *Actinocyclus* evolutionary history, or even Doridoidea. This paper also shows the importance in investigating systems and organs beyond the traditional external features, radula and genital structures, which sometimes bear clearer data for comparative analysis as, e.g., the odontophore muscles.

## Acknowledgements

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